

Revisiting the taxonomy of the Neotropical Haemodoraceae (Commelinales)

Marco O. O. Pellegrini¹, Ellen J. Hickman², Jorge E. Gutiérrez³,
Rhian J. Smith⁴, Stephen D. Hopper²

1 Universidade de São Paulo, Departamento de Botânica, Rua do Matão 277, CEP 05508-900, São Paulo, SP, Brazil **2** University of Western Australia, Centre of Excellence in Natural Resource Management and School of Biological Sciences, Albany, Western Australia 6330, Australia **3** Jardín Botánico Nacional, Universidad de La Habana, La Habana, Cuba **4** Royal Botanic Gardens, Kew, Kew Green, Richmond, Surrey TW9 3AB, UK

Corresponding author: Marco O. O. Pellegrini (marcooctavio.pellegrini@gmail.com)

Academic editor: P. Boyce | Received 26 August 2020 | Accepted 7 November 2020 | Published 4 December 2020

Citation: Pellegrini MOO, Hickman EJ, Gutiérrez JE, Smith RJ, Hopper SD (2020) Revisiting the taxonomy of the Neotropical Haemodoraceae (Commelinales). *PhytoKeys* 169: 1–59. <https://doi.org/10.3897/phytokeys.169.57996>

Abstract

Based on extensive herbarium, field, botanical illustration, and molecular phylogenetic research, five genera and eight species are recognised for the Neotropical Haemodoraceae. New taxa include *Cubanicula* Hopper et al., *Xiphidium pontederiiflorum* M.Pell. et al. and *Schiekia timida* M.Pell. et al. Two new combinations are made, *Cubanicula xanthorrhizos* (C.Wright ex Griseb.) Hopper et al. and *Schiekia silvestris* (Maas & Stoel) Hopper et al. We also correct the author citation for *Xiphidium*, provide the necessary typifications for several names and present an updated identification key, comments, and photo plates for all species. Finally, we provide high-quality illustrations for most of the recognised species and their diagnostic characters.

Keywords

Cubanicula, *Lachnanthes*, Philydraceae, Pontederiaceae, *Pyrrochiza*, *Schiekia*, *Xiphidium*

Introduction

Haemodoraceae is a small monocot family of 14 genera and ca. 120 species currently recognised (Simpson 1998b; Hopper et al. 2009; Smith et al. 2011; The Plant List 2013; Pellegrini 2019; POWO 2020). The family is placed in the order Commelinales

as the sister to Pontederiaceae, with both families having Philydraceae as their sister-group (Saarela et al. 2008; APG IV 2016; Pellegrini et al. 2018; Pellegrini 2019). All three families possess distichously-alternate and unifacial or cylindrical leaf-blades, with xylem and phloem alternate or, rarely, phloem circular with central xylem (with a reversion to bifacial leaves in Pontederiaceae and xylem and phloem alternate near the centre of the blades, plus xylem abaxial and phloem adaxial near the margins; Pellegrini et al. 2018); the presence of styloid crystals; perianth petaloid with the presence of tannin cells, flowers always bisexual, mainly zygomorphic and enantiostylous; pollen released with adhering raphides, the presence of placental sclereids; seeds longer than wide with longitudinal wings or striations (with a reversion in subfamily Haemodoroideae; Simpson 1990); and abundant helobial endosperm of a unique type (Simpson 1985, 1987, 1990, 1993; Rudall 1997; Prychid et al. 2003; Simpson and Burton 2006; Pellegrini 2019). Furthermore, the relationship between Haemodoraceae and Pontederiaceae is morphologically supported by the presence of a hypanthium, endothecium with a basal thickening, baculate exine, septal nectaries, and phenylphenanones (Simpson 1987, 1990, 1993; Pellegrini et al. 2018).

Haemodoraceae is clearly a monophyletic family, characterised by vascular bundles enveloped by a fibrous layer and a peculiar inferior ovary. They are classified into twosubfamilies: Haemodoroideae and Conostylidoideae (Simpson 1990, 1998a; Hopper et al. 1999, 2009; Aerne-Hains and Simpson 2017; Pellegrini 2019). Members of the family are generally associated with semi-arid to temperate environments due to the diversity of taxa in Australia (Macfarlane et al. 1987; Hopper et al. 2006, 2009; Smith et al. 2011). Nonetheless, most genera of Haemodoraceae possess representatives that inhabit wetlands or swamps, with some genera being utterly dependent on these aquatic environments (Simpson 1998b; Hickman and Hopper 2019; Pellegrini 2019). The family possesses an unusually disjunct distribution, with Australia-New Guinea as its centre of diversity (Simpson 1998b; Hopper et al. 2009). Subfamily Conostylidoideae, with six genera and ca. 70 species, is endemic to southwest Australia. The subfamily occurs together with the species-rich genus *Haemodorum* Sm. (from subfamily Haemodoroideae), which occurs in Australia and New Guinea. (Simpson 1998b; Hopper et al. 2009). The Americas and South Africa are secondary centres of diversity for Haemodoraceae, with nine small genera and ca. 20 species (Helme and Linder 1992; Simpson 1998b; Hopper et al. 2009; Manning and Goldblatt 2017; Pellegrini 2019; Hopper et al. in prep.).

The Neotropical Region was the focus of a comprehensive floristic study on Haemodoraceae 27 years ago (Maas and Maas-van de Kamer 1993). However, recent field, herbarium, and phylogenetic studies have shed some light on this still poorly-understood group and provided evidence of the need for several taxonomic changes (Hickman and Hopper 2019; Pellegrini 2019; Hopper et al. in prep.). As an attempt to clarify the taxonomy and systematics of Neotropical Haemodoraceae, the present study revisits the *Flora Neotropica* monograph for Haemodoraceae, with the description of a new genus, two new species, and two new combinations. In addition, we provide an updated identification key, distribution maps, photo plates for all species, added to comments, illustrations, and the necessary typifications.

Methods

The species' descriptions and phenology were based on data from herbaria, spirit collections, fresh material, and literature. Specimens from the following herbaria were also analysed: AD, ALCB, B, BA, BHC, BHZB, BM, BOTU, BRIT, C, CAL, CANB, CBG, CEN, CEPEC, CESJ, CGE, CGMS, CNMT, COL, COR, CORD, CVRD, DR, EAC, ESA, F, FCAB, FCQ, FLOR, FURB, GUA, HAMAB, HAS, HB, HBR, HDCE, HRB, HRCB, HSTM, HUCC, HUEFS, HUFJSJ, HURB, IAC, IAN, ICN, INPA, JOI, K, L, MBM, MBML, MEL, MG, MO, MY, NBG, NSW, NY, P, PACA, PERTH, PMS, R, RB, RFA, RFFP, SCP, SP, SPF, SPSE, U, UEC, UFRN, UP, US, USF, W, WAG, and WU (herbaria acronyms according to Thiers, continually updated). All species of Neotropical Haemodoraceae, except for *Pyrrorhiza neblinae* Maguire & Wurdack, were observed in the field by the authors through the course of several field trips across Central and South America, Cuba and the eastern USA, from 1990–2016. Indumentum and shape terminology follow Radford et al. (1974); the inflorescence and general morphology terminology follow Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994); the seed terminology follows Faden (1991); and general morphology follows Simpson (1990, 1998b). The conservation assessments follow the recommendations of the IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The distribution of the species is based on herbarium materials, field data, and literature.

Results

The present study recognises five genera and eight species of Neotropical Haemodoraceae. This number differs from the previous study by Maas and Maas-van de Kamer (1993; four genera and five species), due to the description of a new genus (i.e., *Cubanricula* Hopper et al., gen. nov.), the description of a new species of *Xiphidium* and one of *Schiekia* and the recognition of *S. orinocensis* subsp. *silvestris* Maas & Stoel at species rank. Thus, we present an updated identification key for the Neotropical Haemodoraceae, complete descriptions for the new genus and the two new species, as well as comments, illustrations, and some nomenclatural updates for all taxa.

Updated key to the Neotropical Haemodoraceae

- 1 Inflorescences and flowers lanate; flowers resupinate (medial stamen superior axis), outer tepals $\frac{1}{2}$ times shorter than the inner, anthers coiling at post-anthesis, ovary inferior, septal nectaries 3, interocular; fruits lacking thickened septal ridges; seeds minutely scabrid, winged, cleft towards the embryo-tega *Lachmanthes caroliniana* (Lam.) Dandy (Figs 6–8)
- Inflorescences and flowers sparsely tomentose, glandular-pubescent or glabrous; flowers non-resupinate (medial stamen inferior), outer and inner tepals more or

- less equal to each other in length, anthers straight at post-anthesis, ovary superior, when present septal nectaries 2, infralocular; fruits with thickened septal ridges; seeds obviously ornate, not winged, not cleft towards the embryotege.....**2**
- 2 Roots lacking a rhizosheath, not sand-binding; perianth with a long tube, basally aperturate, tepals lacking an apical black mucron, 2 staminode-like filiform projections adnate to the lateral outer perianth lobes, lateral anthers with an apical connective appendage, anthers 3 to 4 times shorter than the filaments, stigma capitate; seeds deltoid.....**3**
- Roots with a rhizosheath, sand-binding; perianth with a short or lacking a tube, without basal apertures, tepals with an apical black mucron, staminode-like projections absent, lateral anthers lacking connective appendages, anthers as long as to ca. ½ times shorter than the filaments, stigma crateriform; seeds lenticellate or cuboid.....**5**
- 3 Rhizome long and trailing; stems elongate; leaves membranous, evenly distributed along the stem; thyrses corymb-like; flowers pendulous, stamens with apex recurved, medial filament terete; capsules green when immature, becoming chocolate brown when mature; seed testa reticulate and with sparse and short coarse trichomes.....***Schiekia silvestris* (Maas & Stoel) Hopper et al. (Figs 15–17)**
- Rhizome short; stems inconspicuous to short; leaves fibrous, congested forming a rosette; thyrses spike-like; flowers upright to patent, stamens with apex incurved, medial filament inflated; capsules orange when immature, becoming medium to dark red when mature; seed testa evenly reticulate.....**4**
- 4 Leaves with inconspicuous veins; flowers chasmogamous, clearly bilabiate, 0.7–1.3 cm diam., pedicels apically gibbous, tepals apices reflexed, apricot to cream, upper tepals with three dark orange to orange-brown nectar guides, lateral filaments clavate, staminode-like projections almost as long as their subtending tepal, thick (0.4–0.6 mm wide) and fusiform; capsules broader than long.....***Schiekia orinocensis* (Kunth) Meisn. (Fig. 13)**
- Leaves with deeply impressed to impressed veins; flowers cleistogamous, not obviously bilabiate and narrowly tubular, 0.2–0.4 cm diam., pedicels not apically gibbous, tepals apices straight, light to medium green, upper tepals lacking nectar guides, lateral filaments filiform, staminode-like projections 1/3 to 2/3 the length of their subtending tepals, thin (0.1 mm wide) and filiform; capsules slightly longer than broad or as broad as long.....***Schiekia timida* M. Pell. et al. (Figs 19, 20)**
- 5 Stems elongate; anthers introrsely rimose, but functionally poricidal; capsules subglobose to globose, indehiscent, somewhat fleshy at maturity; seeds cuboid, testa tuberculate**6**
- Stems contracted; anthers extrorsely rimose; capsules trigonous, 3-valved, dry at maturity; seeds lenticellate, testa covered with coarse trichomes**7**
- 6 Flower buds white to cream-coloured, flowers 0.7–1.2 cm diam., perianth actinomorphic, inner lobes elliptic with acute apex, upper tepals only basally connate, basally green and without nectar guides; capsules 4.8–6.4 × 5.2–6.6 mm, orange to red when mature; seeds black.....***Xiphidium caeruleum* Aubl. (Figs 22–24)**
- Flower buds apricot to light orange, flowers 1.9–2.7 cm diam., perianth zygomorphic, inner lobes obovate with obtuse to round apex, upper tepals connate

- in the basal third or halfway through, with three orange-yellow to orange nectar guides; capsules 6.8–8.9 × 7.2–10.1 mm, dark red to vinaceous when mature; seeds dark reddish-brown to reddish-black.....
*Xiphidium pontederiiflorum* M. Pell. et al. (Fig. 26)
- 7 Cormose herbs; thyrsi composed of 2–4, unbranched cincinni; flower non-enantiostylous, upper tepals lacking nectar guides, stamen 1, filament straight, anther sacs symmetric, staminodes 2, filiform; ovary glabrous, septal nectaries vestigial..
*Pyrrorhiza neblinae* Maguire & Wurdack (Figs 10, 11)
- Rhizomatous herbs; thyrsi composed of 9–27, 1–2-branched cincinni; flower enantiostylous, upper tepals with three orange-yellow to orange nectar guides, stamens 3, lateral filaments twisted, medial filament bent upwards, anther sacs asymmetric, staminodes absent; ovary with long hairs along the septal ridges, septal nectaries absent ...*Cubanicula xanthorrhizos* (C.Wright ex Griseb.) Hopper et al. (Figs 1–4)

1. *Cubanicula* Hopper, J.E. Gut., E.J. Hickman, M. Pell. & Rhian J. Sm., gen. nov.
 urn:lsid:ipni.org:names:77213181-1
 Figs 1–4

Type species. *Cubanicula xanthorrhizos* (C. Wright ex Griseb.) Hopper et al. (≡ *Xiphidium xanthorrhizon* C. Wright ex Griseb.).

Diagnosis. Similar to *Xiphidium* Loefl. in inflorescence and floral morphology, differing due to its contracted stems, leaves congested into an apical rosette, 1–2-branched cincinni, extrorsely rimose anthers, capsules trigonous, 3-valved, with thickened and tomentose septal ridges, dry at maturity, dehiscence loculicidal, lenticellate, with coarse trichomes on margins and outer testa.

Etymology. Named for Cuba, in which the genus is narrowly endemic. The diminutive ‘*icula*’ is an allusion to the fact that this genus is second only to *Pyrrorhiza* in Haemodoraceae in its restricted geographical range.

Taxonomic history. The types of *Xiphidium xanthorrhizon* were collected by the American botanist Charles H. Wright (1811–1885), who, between 1856–1867, ‘travelled all over Cuba with the exception of the highest mountains and tripled the number of the phanerogamous plant species known from this territory’ (Borhidi 1991: 16). New taxa collected by Wright were described by Göttingen’s Professor August H.R. Grisebach (1814–1879), primarily in his *Plantae Wrightianae e Cuba Orientali*, published in two parts from 1860–1862. However, *X. xanthorrhizon* was not published until 1866, in Grisebach’s *Catalogus Plantarum Cebensium*, in which he attributed the new species’ name to Wright.

Ascertaining Wright’s itinerary during his three periods on Cuban expeditions has been problematic: ‘[...] his travels were confined chiefly to the two ends of the island, leaving the great central portion largely unexplored. It is unfortunate that the labels on his plants, at least in most of the collections where they are to be found, bear only the inscription “Cuba” or “in Cuba orientali”.’ (Underwood 1905: 291). Moreover, many of Wright’s collections made in western Cuba were irrevocably damaged in transport

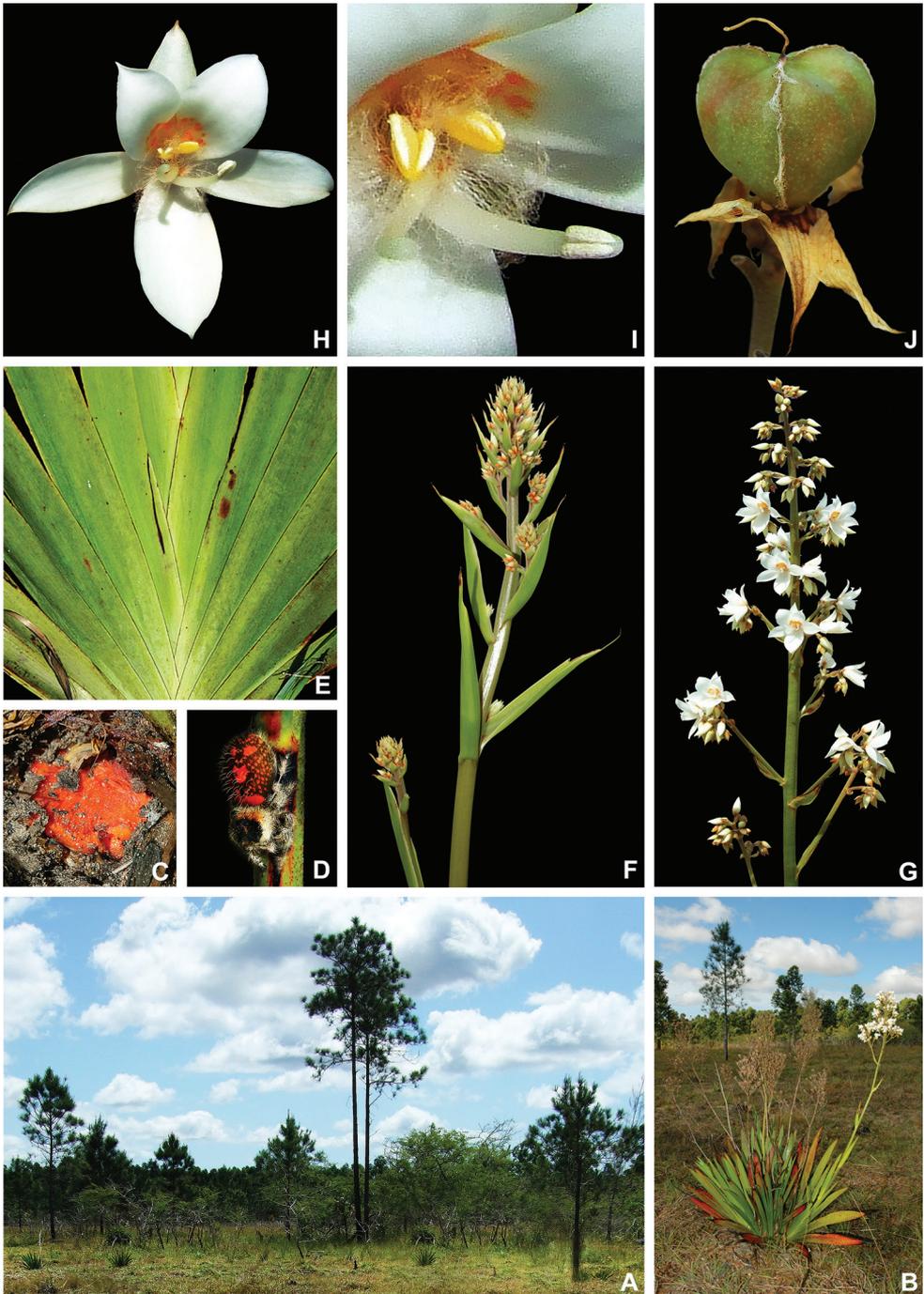


Figure 1. *Cubanicula xanthorrhizos* (C.Wright ex Griseb.) Hopper et al. **A** habitat **B** habit **C** cross-section of the stem showing the bright orange colouration **D** female regal jumping spider (*Phidippus regius*, Salticidae) well camouflaged on *C. xanthorrhizos* **E** detail of the equitant leaves **F, G** inflorescence: **F** immature inflorescence **G** mature inflorescence **H** flower **I** detail of the androecium and gynoecium **J** immature capsule showing the persistent hairs along the septal ridges. All photos by R.J. Smith.

to the USA: 'It appears from Wright's correspondence that a considerable portion of his collection was lost, mainly that collected in the rich tobacco region of the western end of the island (Pinar del Rio). How extensive this loss may have been, probably cannot now be estimated, but it was certainly considerable.' (Underwood 1905: 291). The author also quotes some sentences found in Dr Gray's Letters (2: 555) that explain the cause of the loss of these specimens: 'April 8th [1867] It grieves my heart and will grieve yours badly when I tell you that your boxes were put under a cargo of wet sugar, which drained into them and have [*sic*] ruined the collection. [...] As to specimens to dispose of, say only one-half or one-third of the whole mass is left fit for it... [Ever your disconsolate A. GRAY.]' (Gray 1867 *apud* Underwood 1905: 291, 292).

These problems aside, Underwood (1905) managed to assemble a sketch of Wright's many Cuban itineraries through 200 letters written to Asa Gray and other sources that mentioned dates and place names. Perhaps because of a shipment earlier than the calamity referred to above by Asa Gray, Wright's collections of *Xiphidium xanthorhizon* persist. Wright probably collected *X. xanthorhizon* when he was stationed at Retiro – 'a finca near Taco Taco where Don Jose Blain lived' (Underwood 1905: 297), either in June–September 1863 or, more likely, in January–May 1864. This can be deduced from labels on the types that provide the dates 1860–1864 and a statement in a letter written in Havana on 28 July 1864: 'plants boxed ready to embark' (Underwood 1905: 298).

The type location and Wright's collection number of *X. xanthorhizon* is cited by Maas and Maas-van de Kamer (1993: 31) as 'Cuba. Pinar del Rio: San Cristobal, Wright 3259'. The only reference to San Cristobal cited by Underwood (1905: 298) is for a letter written at Retiro on the 15 June 1866 – 'went again to San Cristobal on the 10th'. Since San Cristobal is only 10 km ENE of Retiro on the main road to Havana, it is clearly a place that Wright would have gone through whenever visiting Retiro in the years 1863, 1864, and 1866. For example, on 19 May 1864, Wright wrote: "Made an excursion of ten days eastward and southward to La Concordia, San Leon, etc." (Underwood 1905: 298).

Subsequent collections filled in knowledge of the geographical distribution of *X. xanthorhizon*, including an early collection from the 1860s by Jose Blain first recording the species from the northern portion of Isla de Juventud (= Isla de Pinos). The specimen (in the Field Museum) was annotated as *Xiphidium floribundum* Sw (= *X. caeruleum*), yet associated notes said (Millsbaugh 1900: 426): '[...] In Cuba this species grows only in shady situations in glens, never on the open savannas; here, however, it seeks the open plains far from shade – Blain.' Moreover, an old handwritten slip attached to the Field Museum specimen, presumably written by Charles Wright, gave the species as *X. xanthorhizon*, and this is undoubtedly the identity of Blain's specimen. It is *X. xanthorhizon*, not *X. caeruleum*, that is common on open savannahs on Isla de Juventud, a view affirmed in subsequent maps and accounts of Cuban Haemodoraceae (Maas and Maas-van de Kamer 1993; Urquiola Cruz et al. 2000). The species' range has not been extended from the open pine woodlands on the white sands of Pinos del Rio Province and the Isla de Juventud, despite extensive modern collections across Cuba, such as the 20,000 sheets made by Borhidi (1991) and colleagues in 1969–1970 and 1974–1976, for phytogeographic and vegetation mapping purposes.



Figure 2. *Cubanicula xanthorrhizos* (C. Wright ex Griseb.) Hopper et al. Full colour whole plant illustration. Illustration by E.J. Hickman. Scale bar: 1 cm.

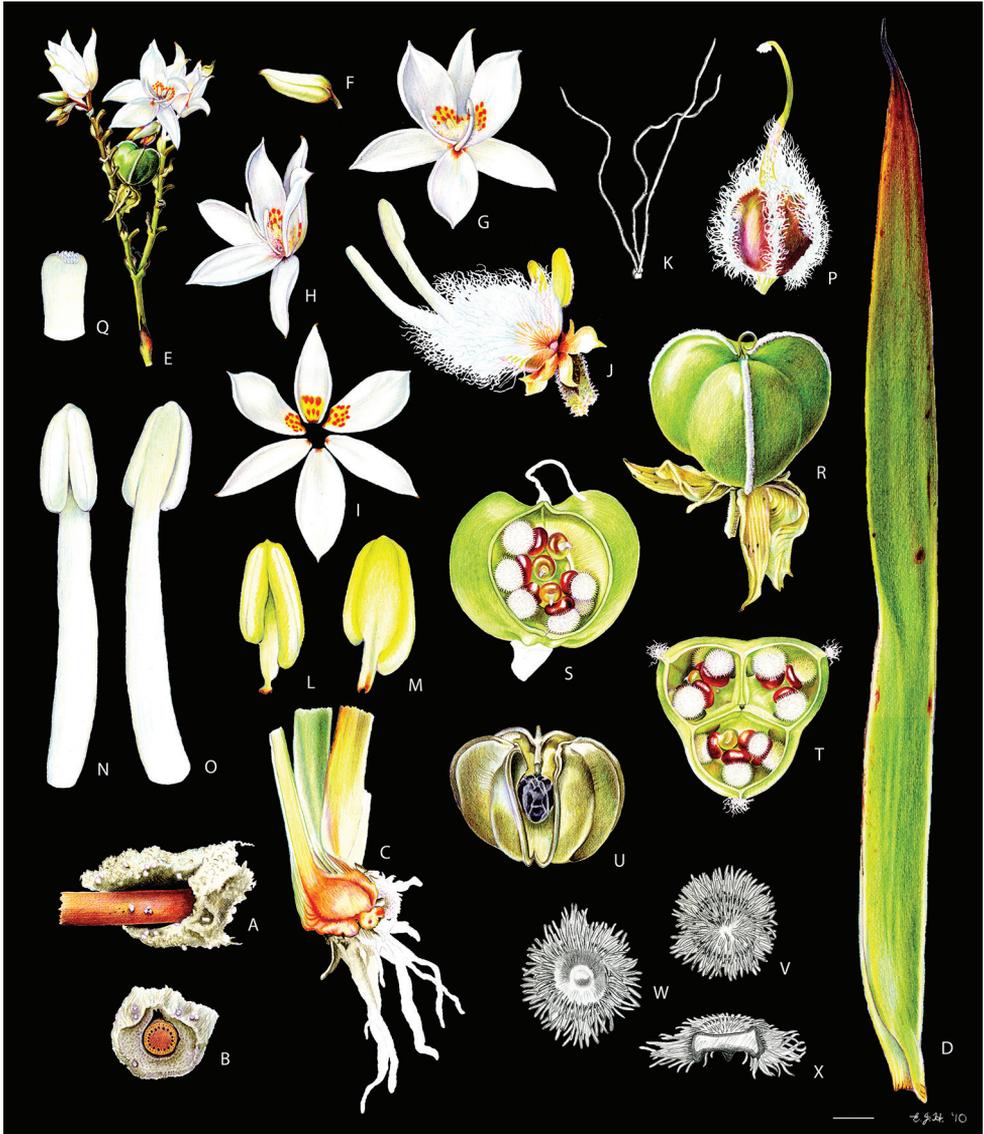


Figure 3. *Cubanricula xanthorrhizos* (C.Wright ex Griseb.) Hopper et al. **A, B** root: **A** root **B** cross-section **C** rhizome **D** leaf **E** branched cincinnus **F** flower bud **G, H** flower: **G** frontal view **H** side view **I** dissected perianth, showing nectar guides **J** flower with removed perianth, showing the androecium and gynoecium **K** hairs **L-O** stamens: **L** frontal view of a lateral stamen **M** dorsal view of a lateral stamen **N** frontal view of the medial stamen **O** dorsal view of the medial stamen **P, Q** gynoecium: **P**, gynoecium **Q** stigma **R-U** fruit: **R** immature capsule **S** capsule in longitudinal section **T** capsule in cross-section **U** dehiscent capsule **V-X** seed: **V** dorsal view **W** ventral view **X** longitudinal section. Illustration by E.J. Hickman. Scale bars: 1.5 mm (**A, B, J, P**); 1 cm (**C, E**); 10.5 mm (**D**); 5 mm (**F-I**); 0.5 mm (**K**); 0.75 mm (**L-O**); 0.37 mm (**Q**); 3 mm (**R-U**); 0.9 mm (**V-X**).

Until now, treatments of *X. xanthorrhizon* after the original description have not challenged the generic placement of the species (León 1946; Simpson 1990, 1998b; Maas and Maas-van de Kamer 1993; Urquiola Cruz et al. 2000). Indeed, Simpson (1990: 729) remarked, ‘*Xiphidium* consists of *X. caeruleum* [sic] and *X. xanthorrhizos* [sic], which differ only in minor morphological features and are likely more closely related to one another than to any other genus. However, because no definitive synapomorphy is evident for *Xiphidium*, its monophyly cannot be affirmed.’ Although he undertook a comprehensive examination of the morphology and anatomy of the genera of Haemodoraceae, Simpson (1990) did not include both species of *Xiphidium* in his study in order to test the genus’ monophyly. Instead, he chose only to represent the genus by sampling *X. caeruleum*. An examination of seeds alone would have raised questions about the generic placement of *X. xanthorrhizon*.

Simpson (1993) discovered the unusual absence of septal nectaries in both *Xiphidium* species and interpreted this trait as an autapomorphy for the genus associated with buzz pollination by bees, which was known for *X. caeruleum* (Buchmann 1980), but the pollination ecology of *X. xanthorrhizon* was not documented. Maas and Maas-van de Kamer (1993: 11) speculated that ‘The differently coloured nectar guide on the three adaxial tepals of *X. xanthorrhizon* suggest that an insect pollinator alights in a consistent orientation, forwardly directed to collect pollen from the shorter stamens, in the meantime being dusted by the largest stamen.’ Simpson (1993) affirmed an observation of Maas and Maas-van de Kamer (1993) that *X. xanthorrhizon* has longitudinal anther dehiscence, whereas *X. caeruleum* anthers commence with nearly poricidal dehiscence, becoming longitudinal as flowers age or dry out (Buchmann 1980). Such a difference echoed a number of other traits overlooked by many authors that call into question the hypothesis that *X. xanthorrhizon* and *X. caeruleum* are sister taxa.

Regarding generic relationships of *Xiphidium*, Simpson (1998a: 217) elaborated: ‘Within this superior-ovaryed group [of subfamily Haemodoroideae], *Wachendorfia* and *Barberetta* are united in having a similar pollen ultrastructure (Simpson 1983, 1990) and *Schiekia* and *Pyrrothiza* are united in having staminodes and similarities in ovule anatomy (M.G. Simpson, 1990, unpubl.). The exact relationships of *Xiphidium* to these genera is unclear.’ Molecular phylogenetic analyses have yet to clarify the systematic position of *Xiphidium* in this clade (Hopper et al. 1999, 2009).

Maas and Maas-van de Kamer (1993: fig. 5) were the first to illustrate and compare SEM micrographs of the seeds of *X. xanthorrhizon* and *X. caeruleum*, which differ significantly. Indeed, seeds of *X. xanthorrhizon* resemble those of *Pyrrothiza* in being large (i.e., 2.5–3.5 mm long) and covered with 1–1.5 mm long coarse hairs (Fig. 4D, H), whereas *X. caeruleum* has cuboid, black seeds 0.5–1.0 mm in diameter and they are minutely tuberculate, lacking hairs (Fig. 4L), similar to seeds of *Schiekia* (i.e., *S. orinocensis* and *S. timida*). Maas and Maas-van de Kamer (1993: 10) suggested that ‘the hairy seeds of *Xiphidium xanthorrhizon* and *Pyrrothiza neblinae*, both savanna plants, might very well be dispersed by animals having seeds adhering to their body (i.e., exozoochoric dispersal).’

Simpson (1990: 754) scored *X. caeruleum* as enantiostylous, but with ‘actinomorphic and erect (not zygomorphic and horizontal) flowers without any bilaterally sym-

metric nectar guides.’ Maas and Maas-van de Kamer (1993: 11) affirmed that *X. xanthorhizon* ‘clearly displays’ enantiostyly of the latter kind, differing significantly from the flowers of *X. caeruleum*. Despite these floral differences and significantly divergent seed morphologies between *X. xanthorhizon* and *X. caeruleum*, these authors retained the traditional circumscription of *Xiphidium* s.lat. With the recognition of a second species of *Xiphidium* s.str. in the present study, it became clear that the inclusion of *X. xanthorhizon* in *Xiphidium* s.lat. was untenable from the morphological perspective (Pellegrini 2019), added to strong molecular support (Hopper et al. in prep).

Comments. *Cubanicula* is recovered with strong bootstrap support in a clade with *Xiphidium* s.str. and *Pyrrothiza* Maguire & Wurdack, sister to the latter genus, not *Xiphidium*, in which the species of *Cubanicula* was initially placed (Hopper et al., in prep). This clade can be morphologically supported by the presence of sand-binding roots, campanulate and pollen rewarding flowers, tepals with an apical black mucron, anthers as long as to ca. ½ times shorter than the filaments, vestigial or completely lacking septal nectaries, crateriform stigmas, and enlarged placental attachments subtending the ovules (Hickman 2019; Pellegrini 2019). *Cubanicula* can be differentiated from *Pyrrothiza* by its rhizomatous underground system (vs. cormose in *Pyrrothiza*), thyrsi 1–2-branched cincinni (vs. always unbranched), flower enantiostylous (vs. non-enantiostylous), upper tepals with three orange-yellow to orange nectar guides (vs. lacking nectar guides), stamens 3 (vs. one), lateral filaments twisted and medial filament bent upwards (vs. lateral stamens staminodial and medial filament straight) and staminodes absent (vs. staminodes 2, filiform). The difference between *Cubanicula* and *Xiphidium* s.str. is especially evident in capsule and seed characters, as well as floral size. These genera can be differentiated by the characters summarised in Table 1 and the fruit and seeds characters illustrated in Fig. 4.

1.1. *Cubanicula xanthorrhizos* (C. Wright ex Griseb.) Hopper, J.E. Gut., E.J.Hickman, M.Pell. & Rhian J.Sm., comb. nov.

urn:lsid:ipni.org:names:77213182-1

Figs 1–4

Xiphidium xanthorrhizon C.Wright ex Griseb., Cat. Pl. Cub. 1: 252. 1866. Lectotype (designated by Maas and Maas-van de Kamer 1993). CUBA. Artemisia: Pinar del Río, San Cristóbal, La Palma, fl., fr., 1860–1864, C. Wright 3259 (GOET barcode GOET004074!; isolectotypes: G barcode G00098226!, GH barcode GH00030236!, K barcode K000574288!, NY barcodes 00073224!, 00073225!, P barcodes P04457878!, P00643765!, S accession no. S-R-6536!, US barcodes US00092055!, US00092056!).

Description. *Herbs* ca. 50–180 cm tall, perennial, rhizomatous with a definite base, terrestrial in white sand. *Roots* slightly tuberous, densely tomentose with long light brown to grey hairs forming a rhizosheath, sand-binding. *Rhizomes* underground, short, ex-

ternal surface light to medium brown, internal surface yellow to orange. **Stems** inconspicuous, fibrous, unbranched. **Leaves** distichously-alternate, equitant, congested at the apex of the stems forming a rosette, sessile, the apical ones gradually smaller than the basal ones; sheaths 8.6–15.2 cm long, glabrous; blades (5–)15.7–60.3–(85) × 0.3–3.4 cm, coriaceous, unifacial, medium green, drying yellowish-green to olive-green, linear-elliptic to narrowly elliptic, slightly ensiform, glabrous, base sheathing, margins green, glabrous to sparsely ciliate, apex acuminate; midvein inconspicuous, secondary veins inconspicuous to slightly impressed, becoming prominent when dry. **Inflorescences** terminal or apparently so, consisting of a pedunculate many-branched thyrse, sometimes with one to several co-florescences; peduncles 43.7–75.2 cm, densely tomentose, hairs pilate, light brown; basal bract 5.1–7.8 × 0.5–1.5 cm, leaf-like, linear-elliptic, slightly ensiform to ensiform, glabrous or sparsely tomentose at base, hairs pilate, white, base truncate to slightly sheathing, margin ciliate at apex, apex acuminate, secondary veins inconspicuous; cincinnus bract 0.8–6 × 0.1–0.4 cm, linear-lanceolate to lanceolate, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin ciliate, apex acuminate; cincinni 9–27 per thyrse, 1–2-branched, alternate, 3–19-flowered, peduncle 0.2–3.4 cm long, green, sparsely tomentose to densely tomentose, hairs pilate, white; bracteoles 2.8–6.3 × 1.3–2 mm, elliptic to ovate, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin glabrous, apex acute. **Flowers** 1.3–2.6 cm diam., bisexual, chasmogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds 3.2–8.2 × 1.5–3.5 mm, narrowly ovoid, white to apricot; pedicels 1.4–5.6 mm long, green, tomentose to densely tomentose, hairs pilate, white, upright and slightly elongate in fruit; perianth zygomorphic, lobes free, except for the upper 3 lobes which are connate on the basal third to mid-length, nectar guide yellow with reddish-orange spots, on the basal third of the connate lobes, with an apical black mucron, outer lobes 7.3–13.2 × 2.5–5.6 mm, subequal, the upper slightly shorter, elliptic to narrowly obovate, external surface white to apricot, glabrous to sparsely tomentose, hairs pilate, white, internal surface white, glabrous, base cuneate, margins glabrous, apex acute- to obtuse-mucronate, mucron dark brown to black, inner lobes 9.5–14.5 × 4.8–8.6 mm, subequal, the upper two slightly shorter and deflexed, obovate to broadly oblong, external surface white to apricot, rarely light orange, glabrous, internal surface white, glabrous, base cuneate, margins glabrous, apex obtuse- to round-mucronate, greenish-yellow to apricot, mucron dark brown to black; stamens 3, lateral stamens with filaments 1.5–3.5 mm long, slightly twisted, basally cream to apricot, apically white, glabrous, anthers 1.8–2.8 × 0.6–1 mm, dorsifixed, rimose, oblongoid, thecae unequal, light yellow, medial stamen with filament 4.2–5.6 mm long, bent upwards, basally cream to apricot, apically white, glabrous, anthers 0.9–2.2 × 0.3–0.7 mm, dorsifixed, rimose, broadly oblongoid, white; ovary 0.8–1 × 0.6–0.7 mm, broadly ellipsoid, 3-loculate, reddish-orange green, smooth, densely tomentose along the septal ridges, style 5.8–7.3 mm, bent upwards, basally cream to apricot, apically white, glabrous, stigma crateriform, white, papillose. **Capsules** 6–8.1 × 6.4–9.8 mm, subglobose to depressed ovoid, trigonous, medium green when immature, dark brown when mature, glabrous, 3-valved. **Seeds** 1.9–3 × 1.7–3.2 mm, lenticellate, testa dark

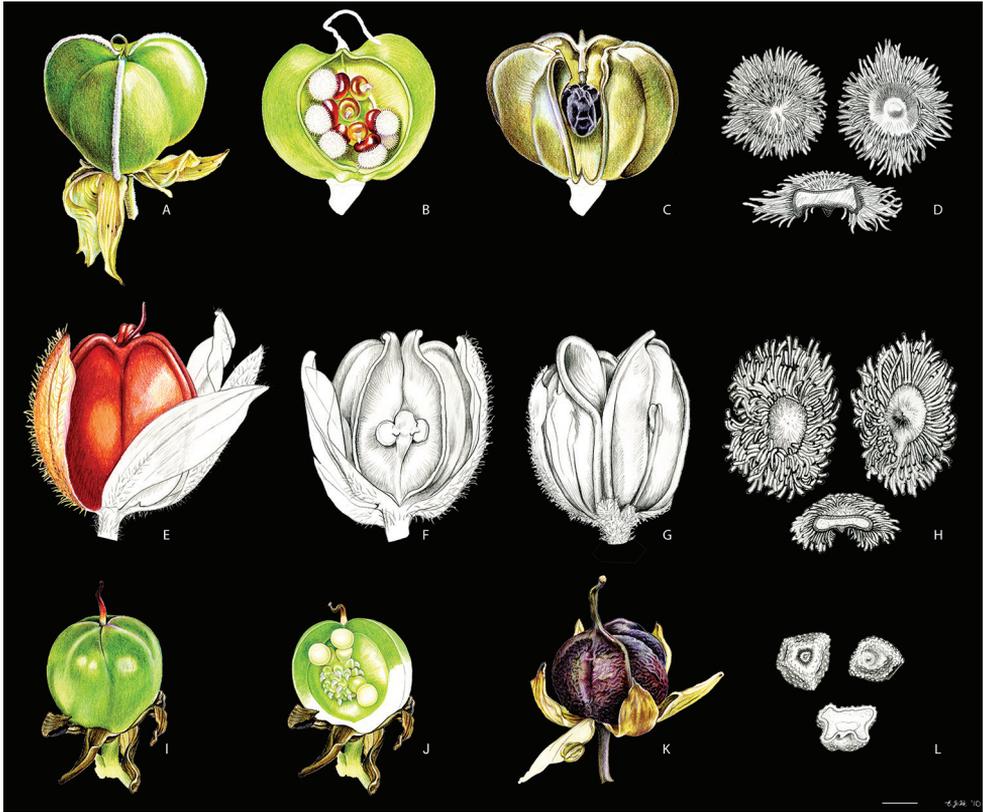


Figure 4. Comparison of fruit and seed morphology of *Cubanacula* Hopper et al., *Pyrrothiza* Maguire & Wurdack, and *Xiphidium* Loeffl **A–D** *C. xanthorrhizon* (C. Wright ex Griseb.) Hopper et al.: **A** immature fruit **B** fruit in longitudinal section **C** dehiscent mature fruit **D** seed (dorsal view, ventral view, and longitudinal section) **E–H** *P. neblinae* Maguire & Wurdack: **E** immature fruit **F** fruit in longitudinal section **G** dehiscent mature fruit **H** seed (dorsal view, ventral view, and longitudinal section) **I–L** *X. caeruleum* Aubl.: **I** immature fruit **J** fruit in longitudinal section **K** non-dehiscent mature fruit **L** seed (ventral view, dorsal view, and longitudinal section). Illustration by E.J. Hickman. Scale bars: 2 mm (**A–C**, **E–G**, **I–K**); 1 mm (**D**, **H**, **L**).

Table 1. Morphological differences between *Cubanacula* Hopper et al. and *Xiphidium* Loeffl.

Character	<i>Cubanacula</i>	<i>Xiphidium</i> s.str.
Stems	Contracted	Elongated
Leaves	Congested at the apex of the stems forming a rosette	Evenly distributed along the stems
Cincinni	1–2-branched	Unbranched
Flowers	Large, bicoloured	Small, uniformly coloured, rarely bicoloured
Stamens	Dimorphic, anthers extorsely rimose, anther sacs asymmetric	Monomorphic, anthers introrsely rimose, but functionally poricidal, anther sacs symmetric
Enlarged placental attachment	Capitate, vertically compressed, red	Cylindrical, truncate, green
Capsules	Trigonus, loculicidal 3-valved, dry at maturity, septal ridges tomentose at maturity	Subglobose to globose, indehiscent, somewhat fleshy at maturity, septal ridges glabrous at maturity
Seeds	Lenticellate	Cuboid
Testa	Coarse trichomes on margins and outer surface, glabrous on hilar surface	Tuberculate

brown to black, covered with finger-like hairs on the dorsal surface, hairs concentrated to the margins on the ventral side, sparser in the centre, orange to red; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen. CUBA. **Isla de la Juventud:** near Managua, fl., 11 Jul 1900, W. Palmer & J.H. Riley 1101 (US); near km 7 of the road between Nueva Genova and Santa Fé, fl., fr., 27 Oct 1920, E.L. Ekman 11940 (NY, US); east of Los Indios, fl., 17 May 1910, O.E. Jennings 315 (BM, GB, NY, US, USF); fl., 17 May 1910, O.E. Jennings 668 (NY, US); vicinity of San Pedro, fl., 15–17 Feb 1916, N.L. Britton et al. 14341 (F, GH, MO, NY, US); Santa Bárbara, fl., fr., 9 Feb 1953, E.P. Killip 42656 (US); along road from Nueva Gerona to Santa Bárbara, fl., fr., 19 Nov 1955, E.P. Killip 45173 (US); Reserva Natural Los Indios Norte, arenas blancas com pinar, fl., fr., 27 Feb 2002, W. Greuter et al. 25923 (NY); Siguanea region, fl., 19 Apr 1954, E.P. Killip 44041 (P, US); fl., 20 Nov 1955, E.P. Killip & H.S. Cunniff 45185 (US); in white sands near San Pedro, fl., fr., 8 Feb 1956, C.V. Morton 10028 (US). **Pinar del Río:** Arroyo del Sumidero, fr., 7–9 Aug 1912, J.A. Shafer & B. León 13576 (BM, F, NY, US); Guane, Los Ocujes, 1.6 km along track leading north from the road to Mantua at the W extent of Guane, fr., 17 Apr 2010, R.J. Smith et al. RJS290 (HAJB, K); Laguna Santa Maria, fl., fr., 8 Sep 1910, N.L. Britton et al. 7119 (NY); mountains near El Guama, fr., 25 Mar 1900, W. Palmer & J.H. Riley 423 (US); Ovas, El Punto, fl., fr., 29 Apr 1989 A. Urquiola 5392 (NY); Pinar del Río, pinelands 12 km off the highway to Coloma, fl., 28 Oct 1923, E.L. Ekman 17802 (K, S); Sandino, 4 km NE of Sandino adjacent to old Air Base of San Julian, 100 m S of main road, fl., fr., 19 Apr 2010, R.J. Smith et al. RJS292 (HAJB, K).

Distribution and ecology. *Cubanicula xanthorrhizos* is endemic to western Cuba and restricted to the Province of Pinar del Río and the Special Municipality of Isla de la Juventud (known until 1978 as Isla de Pinos) (Fig. 5). It is found in pinelands or open, anthropogenic tropical savannah, on deep, acidic, quartzitic sand, with some organic matter and quartzite/laterite gravel at the surface. Such habitats qualify as old, climatically-buffered infertile habitats (OCBIL *sensu* Hopper 2009).

Cubanicula habitats surveyed as part of the collection of specimens by some of the authors in 2010 included pine woodland edge, open anthropogenic savannah with scattered trees, open lakeside vegetation, and a seasonally-dry lake basin with open vegetation. In the pineland habitat, *Cubanicula* was found at the woodland edge, bordering a road cutting, occurring under a canopy of *Xylopia aromatica* (Lam.) Mart. (Annonaceae), *Tabebuia lepidophylla* (A.Rich.) Greenm. (Bignoniaceae) and *Acoelorrhapha wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc. (Arecaceae), at the edge of *Pinus caribaea* Morelet (Pinaceae) woodland. Other components of the vegetation included *Alibertia edulis* (Rich.) A.Rich. and *Roigella correifolia* (Griseb.) Borhidi (Rubiaceae), *Brya microphylla* Bisse (Fabaceae), *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), *Casearia spinescens* (Sw.) Griseb. (Salicaceae), *Cassytha filiformis* L. (Lauraceae), *Cecropia peltata* L. (Urticaceae), *Cochlospermum vitifolium* (Willd.) Spreng. (Bixaceae), *Croton cerinus* Müll.Arg. (Euphorbiaceae), *Davilla rugosa* Poir. and *Doliocarpus dentatus* (Aubl.) Standl. (Dilleniaceae), *Didymopanax morototoni* (Aubl.) Decne. & Planch. (Araliaceae), *Lantana involucrata* L. (Verbenaceae), *Ouratea nitida* (Sw.) Engl. (Ochnaceae) and *Pachyanthus mantuensis* Britton & P.Wilson (Melastomataceae).

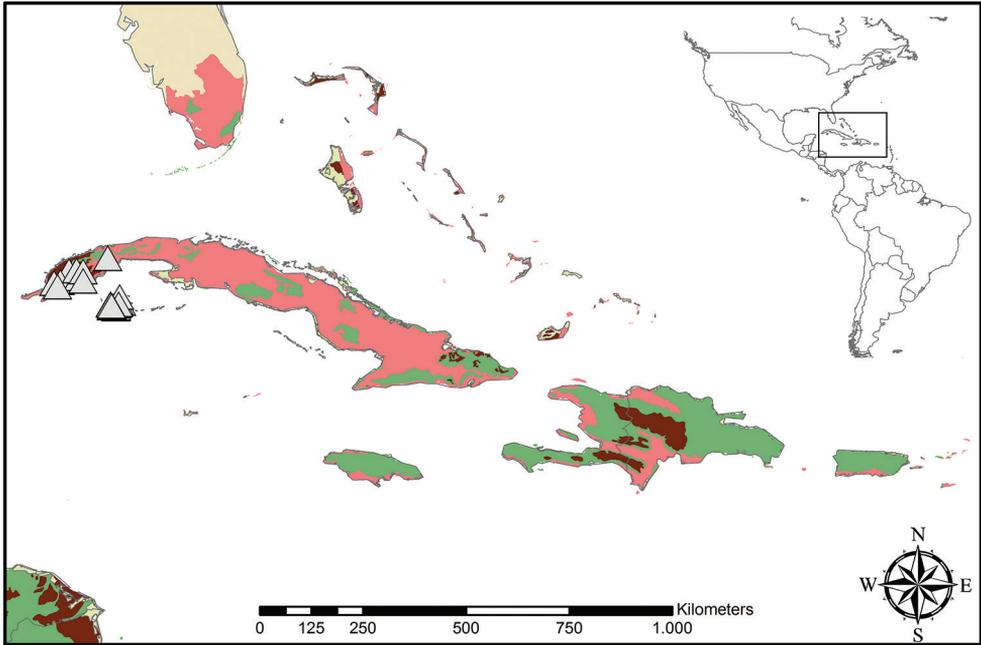


Figure 5. Distribution of *Cubanicula xanthorrhizos* (C.Wright ex Griseb.) Hopper et al. Beige – Temperate Coniferous Forests and Boreal Forests; Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests.

In the open anthropogenic savannah habitat (a degraded pineland with adjacent *Eucalyptus* spp. plantation and scattered *Pinus caribaea* and *Eucalyptus* trees), *Cubanicula* was found in full sun in a grassy sward with *Angelonia pilosella* J.Kickx f. and *Bacopa longipes* (Pennell) Standl. (Plantaginaceae), *Cassytha filiformis*, *Chamaecrista diphylla* (L.) Greene and *Mimosa pudica* L. (Fabaceae), *Diodia* sp. (Rubiaceae), Eriocaulaceae, *Hypericum styphelioides* A.Rich. (Hypericaceae), *Melochia savannarum* Britton and *Waltheria indica* L. (Malvaceae), *Paspalum notatum* Flügge (Poaceae), *Phyllanthus* sp. (Phyllanthaceae), *Scirpus* sp. (Cyperaceae), *Stachytarpheta* sp. (Verbenaceae), *Tetramicra eulophiae* Rchb.f. ex Griseb. (Orchidaceae), *Tetrazygia discolor* (L.) DC. (Melastomataceae) and *Xyris* spp. (Xyridaceae).

In the lakeside vegetation, *Cubanicula* was found in a range of microhabitats from sparse grass/sedgeland to the shallow slopes of wet seeps, with abundant *Drosera* spp. (Droseraceae). The main associated grassland species were *Blechnum serrulatum* Rich. (Blechnaceae), *Cassytha filiformis*, *Chamaecrista* sp. and *Desmodium* sp. (Fabaceae), *Drosera intermedia* Hayne, *Hypericum styphelioides*, *Lycopodiella* sp. and *Lycopodium* sp. (Lycopodiaceae), *Polygala squamifolia* C.Wright ex Griseb. (Polygalaceae), *Rhexia* sp. (Melastomataceae), *Scirpus* sp., *Spiranthes* sp. (Orchidaceae), and *Xyris* sp., with occasional shrubs, including *Byrsonima crassifolia*, *Pachyanthus* sp., and *Tetrazygia discolor*.

Finally, in the lake basin habitat, *Cubanicula* was found on sandy soils with a higher organic matter content at the surface than in the other habitats. The population

was scattered through dense tussock sedges and growing through dense leaf litter in association with *Telmatoblechnum serrulatum* (Rich.) Perrie et al. (Blechnaceae), *Centella asiatica* (L.) Urb. (Apiaceae), *Chamaecrista diphylla* and *Rhynchospora* sp. (Cyperaceae), with occasional *Chrysobalanus icaco* L. (Chrysobalanaceae).

The altitudinal range of these sites ranged from 3 m a.s.l. in the lake basin to 54 m a.s.l. in the pinelands.

Phenology. Flowering and fruiting between October and April.

Conservation status. *Cubanicula xanthorrhizos* possesses a narrow EOO (10,132 km²) and AOO (ca. 96 km²), being endemic to western Cuba. Thus, following IUCN's (2001) recommendations, *C. xanthorrhizos* should be considered as Endangered [EN, A2ac+B2b(ii, iii)+C1].

2. *Lachnanthes* Elliott, Sketch Bot. S. Carolina 1: 47. 1816.

Figs 6–8

Camderia Dumort., Anal. Fam. Pl.: 80. 1829, nom. illeg. Type species. *Heritiera tinctorum* Walter ex J.F.Gmel. [= *Lachnanthes caroliniana* (Lam.) Dandy].

Heritiera J.F.Gmel., Syst. Nat. (ed. 13) 2(1): 113. 1791, nom. illeg., non *Heritiera* Aiton, nec *Heritiera* Retz. Type species. *Heritiera tinctorum* Walter ex J.F.Gmel. [= *Lachnanthes caroliniana* (Lam.) Dandy].

Gyrotheca Salisb., Trans. Hort. Soc. London 1: 327. 1812, nom. nud.

Type species. *Lachnanthes tinctoria* (Walter ex J.F.Gmel.) Elliott [= *Lachnanthes caroliniana* (Lam.) Dandy].

Comments. *Lachnanthes* is morphologically and phylogenetically related to *Dilatris* P.J.Bergius s.str., a yet undescribed African genus and *Haemodorum*, due to their red to orange roots, branched cincinni, upright tepals, three fertile stamens, inferior ovary and lenticellate and winged seeds (Simpson 1990, 1998b; Hopper et al. 1999, 2009; Pellegrini 2019; Hopper et al., in prep.). *Lachnanthes* can be differentiated from *Haemodorum*, based on their roots being sand-binding or not (roots lacking a rhizosheath and not sand-binding in *Lachnanthes* vs. with a rhizosheath and sand-binding in almost all species of *Haemodorum*), pubescence (present vs. absent), the consistency of the tepals (succulent vs. coriaceous) and the number of ovules per carpel (5–7 vs. 2) (Hickman 2019; Pellegrini 2019). On the other hand, *Lachnanthes* can be differentiated from *Dilatris* s.str. by its roots lacking a rhizosheath and not sand-binding (vs. with a rhizosheath and sand-binding in *Dilatris* s.str.), outer tepals ½ times shorter than the inner tepals (vs. outer and inner tepals equal), tepals erect and lacking apical glands (vs. tepals patent, with apical glands), monomorphic stamens (vs. dimorphic), septal nectaries interocular (vs. supralocular), 5–7 ovules per locule (vs. one), the absence of an anthocarp (vs. anthocarp present) and loculicidal capsules (vs. septifragal) (Hickman 2019; Pellegrini 2019). The differences between *Lachnanthes* and the undescribed genus will be posteriorly discussed (Hopper et al. in prep.; Pellegrini et al., in prep.).

2.1. *Lachnanthes caroliniana* (Lam.) Dandy, J. Bot. 70: 329. 1932.

Figs 6–8

Dilatrix caroliniana Lam., Tabl. encycl. 1: 127. 1791, as “*Caroliana*”. Holotype.

UNITED STATES. North Carolina: s.loc., fl., fr., s.dat., Fraser s.n. (P-LA barcode P00382893!).

Heritiera tinctorium Walter ex J.F.Gmel., Syst. Nat. 2: 113. 1791, nom. superfl.*Heritiera gmelinii* Michx., Fl. Bor.-Amer. 1: 21, pl. 4. 1803, as “*Gmelini*”, nom. superfl.*Dilatrix heritiera* Pers., Syn. Pl. 1: 54. 1805, nom. superfl.*Gyrotheca tinctoria* Salisb., Trans. Hort. Soc. London 1: 327. 1812; *Gyrotheca tinctoria*

W.Stone, Pl. S. New Jersey 1: 354. 1911[1912], isonym.

Dilatrix tinctoria Pursh, Fl. Amer. Sept. 1: 30–31. 1813[1814].*Lachnanthes tinctoria* Elliott, Sketch Bot. S. Carolina 1(1): 47. 1816.*Lachnanthes tinctoria* var. *major* C.Wright ex Griseb., Cat. Pl. Cub.: 252. 1866. Lec-

totype (designated by Maas and Maas-van de Kamer 1993). CUBA. s.loc., fl.,

fr., 1860–1864, C. Wright 3270 (GOET barcode GOET004073!; isolectotypes:

BM barcode BM000923988!; G barcode G00098220!, K barcode K000574289!,

MO accession no. MO-202080!, NY barcodes 00073226!, 00073227!, P barcodes

P00753470!, P00753471!, S accession no. S-R-3123!).

Anonymos tinctoria Walter, Fl. Carol.: 68. 1788, nom. rej.

Distribution and habitat. *Lachnanthes caroliniana* is known to occur from Nova Scotia (Canada) to Florida (USA), reaching Cuba (Fig. 9). It grows in marshy and acidic environments, swampy grasslands, and moist pine forests throughout its range, generally producing extensive clonal populations.

Phenology. Flowers and fruits from April to November.

Conservation status. *Lachnanthes caroliniana* possesses a wide EOO (1,886,962 km²) but a narrow AOO (ca. 616 km²). Nonetheless, although generally abundant within its native range, *L. caroliniana* is listed as Endangered in four USA States (i.e., Connecticut, Maryland, New York, and Tennessee), as Threatened in Rhode Island and of Special Concern in Massachusetts (USDA-NRCS 2013) and as Threatened in Canada (COSEWIC 2009). Thus, following IUCN’s (2001) recommendations, *L. caroliniana* should be considered as Vulnerable (VU).

Comments. *Lachnanthes caroliniana* is morphologically variable regarding stature and colouration, with much of this variation being related to environmental conditions. The roots and underground organs can range from yellowish-orange to dark red, the leaves, peduncles, bracts, and the outside of the tepals can range from light to dark green to bluish-green, and the tepals can be internal surface light green to yellowish-green to bright yellow. Aside from that, plants can range from 10 cm to over 100 cm tall.

Lachnanthes caroliniana is commonly considered a widespread weed in blueberry and cranberry crops (Meggett and Aldrich 1959; Robertson 1976; Meyers et al. 2013), pastures (Ferrell et al. 2009) and to form extensive clonal populations followed by feral swine rooting disturbance (Boughton et al. 2016). Nonetheless, *L. caroliniana*

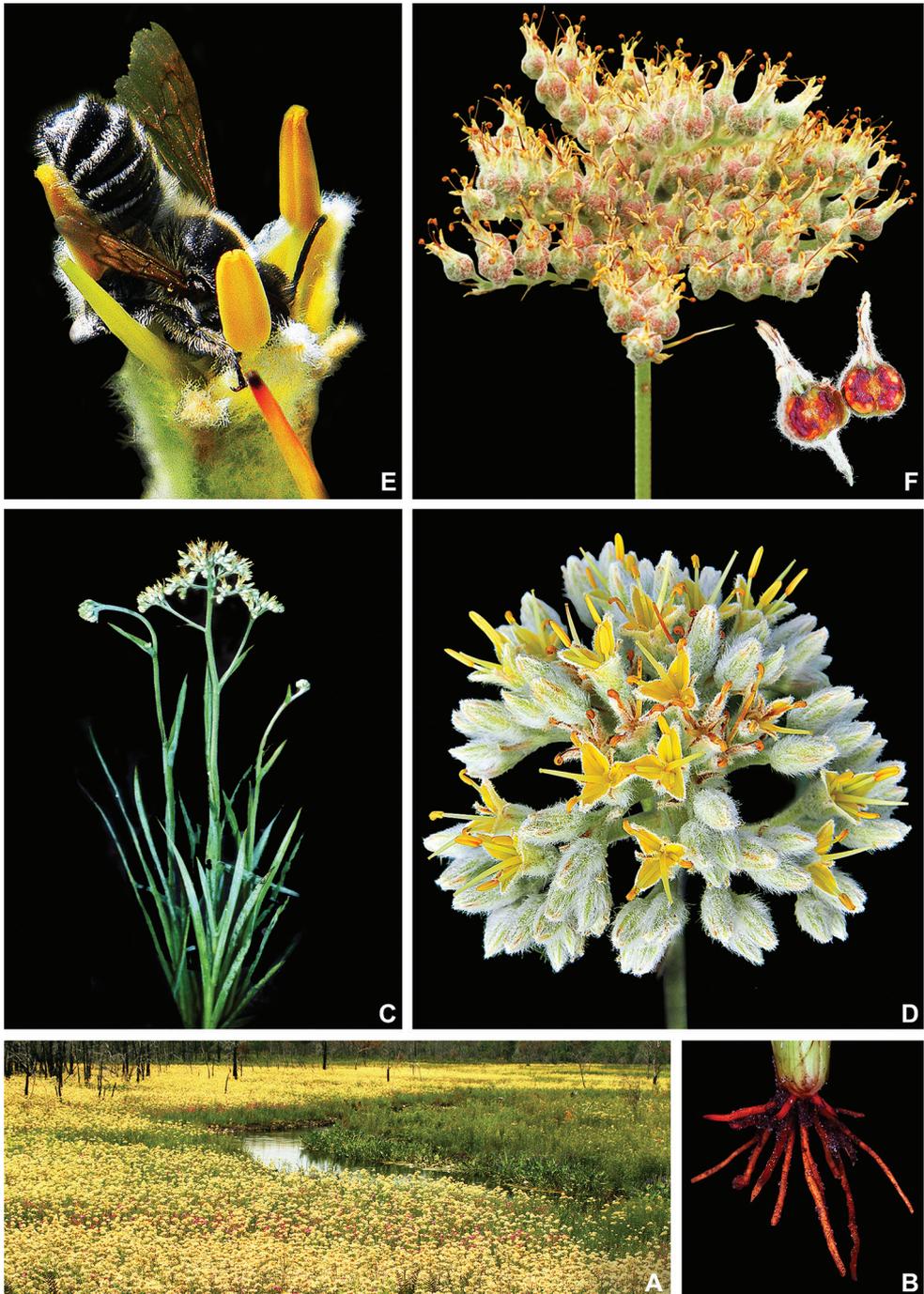


Figure 6. *Lachnanthes caroliniana* (Lam.) Dandy **A** swampy environment **B** detail of the red roots **C** habit of an adult flowering specimen **D** inflorescence showing external surface lanate and internal surface glabrous and yellow perianth **E** detail of a flower being visited by a bee **F** fruiting inflorescence, with the detail of a fruit in longitudinal section. **A** by U. Lorimer, **B** by J. Fowler, **C, F** by S. Zona and **D, E** by B. Peterson, fruit detail by J. Bradford.



Figure 7. *Lachnanthes caroliniana* (Lam.) Dandy. Full colour whole plant illustration. Illustration by E.J. Hickman. Scale bar: 1 cm.

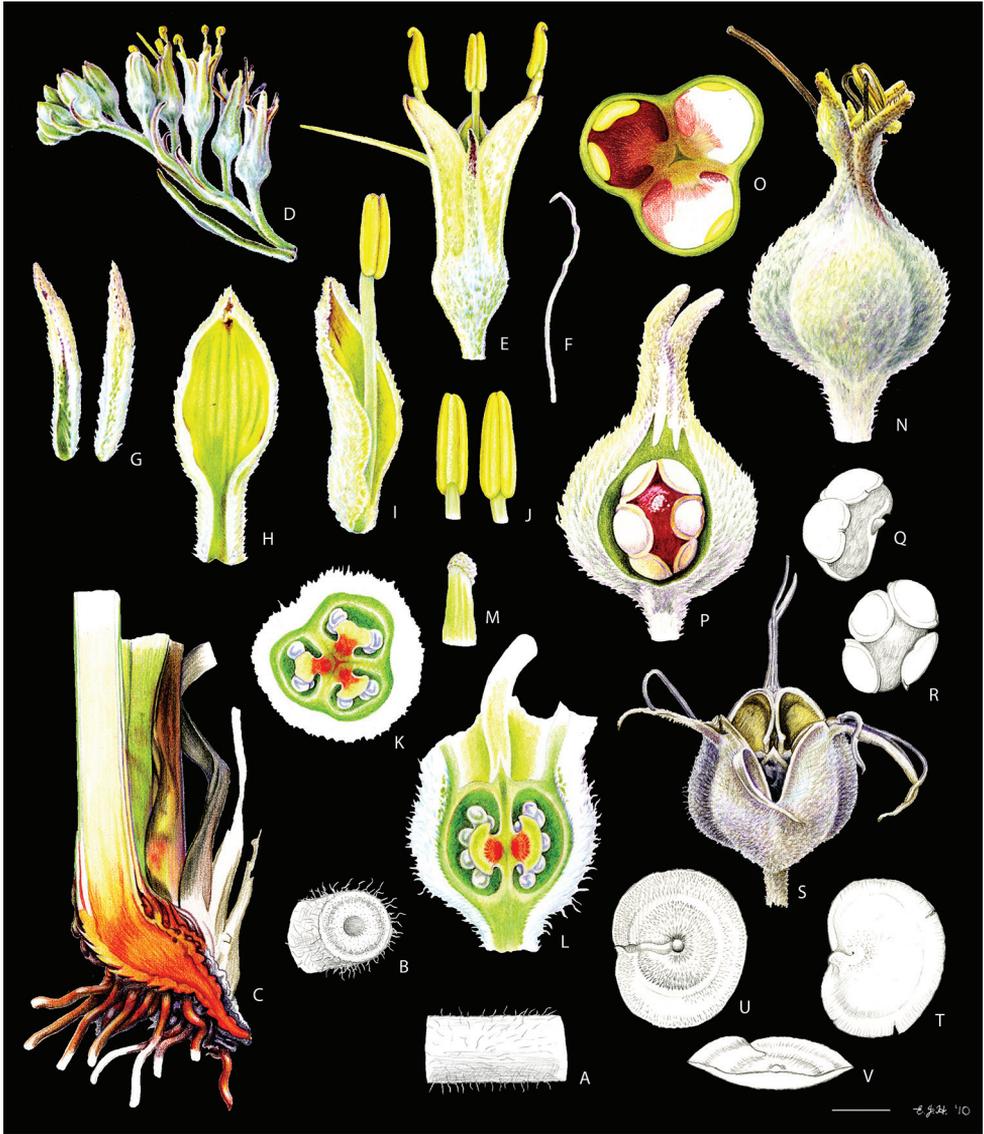


Figure 8. *Lachnanthes caroliniana* (Lam.) Dandy **A, B** root: **A** portion of the root **B** cross-section **C** rhizome in longitudinal section **D** cincinnus **E** flower **F** hair **G–I** perianth: **G** outer tepal (frontal and dorsal view) **H** dorsal view of a inner tepal **I** side view of the inner tepal with epipetalous stamen **J** anther (frontal and dorsal view) **K–M** gynoeceum: **K** cross-section **L** longitudinal section **M** stigma **N–S** fruit: **N** immature capsule **O** cross-section **P** longitudinal section **Q** placenta with ovules in side view **R** placenta with ovules in dorsal view **S** dehiscent capsule **T–V** seed: **T** dorsal view **U** ventral view **V** longitudinal section. Illustration by E.J. Hickman. Scale bars: 0.8 mm (**A, B**); 1 cm (**C, D, T–V**); 2 mm (**E, G–J, N–S**); 0.4 mm (**F**); 1.25 mm (**K, L**); 0.62 mm (**M**).

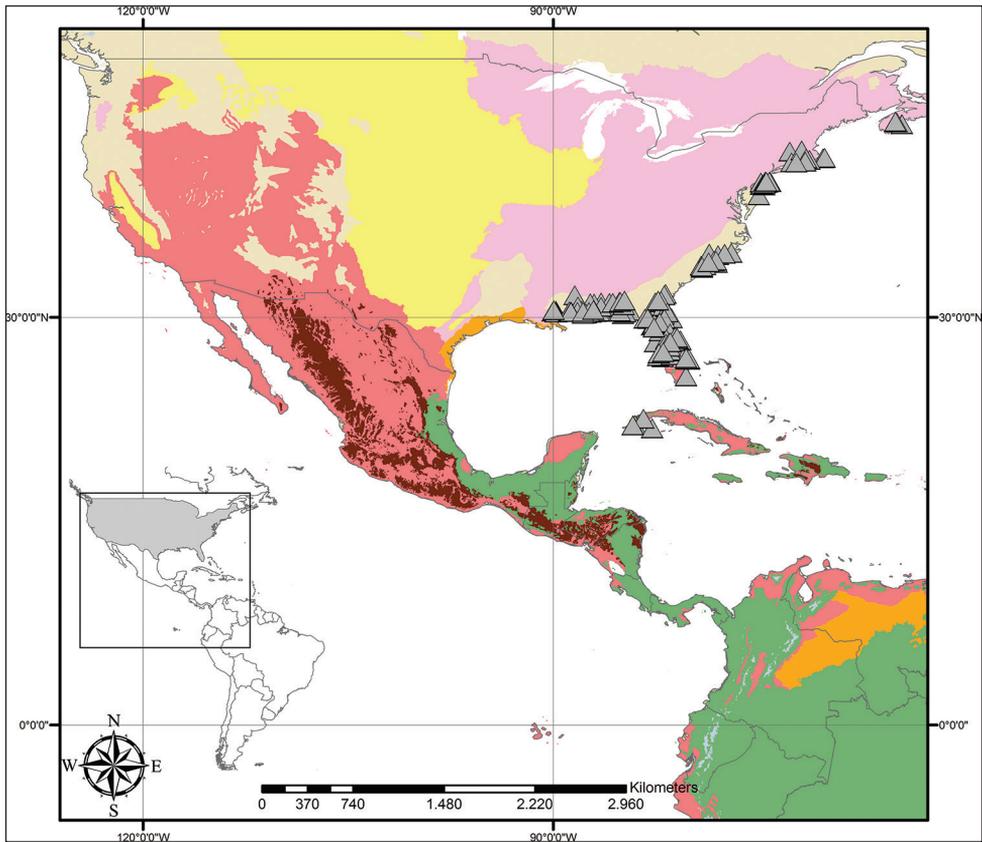


Figure 9. Distribution of *Lachnanthes caroliniana* (Lam.) Dandy. Beige – Temperate Coniferous Forests and Boreal Forests; Yellow – Temperate Grasslands, Savannahs and Shrublands; Pink – Temperate Broadleaf and Mixed Forests; Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

is an important nectar source for many insects (Hopper, pers. observ.) and a pollen source for bees and certain flies. It is viewed as an important “bridge species” supporting flower visitors in summer until fall (autumn) daisies begin to bloom (Boughton et al. 2016). Its seeds also constitute an important food source for sandhill cranes (Valentine and Noble 1970).

3. *Pyrrorhiza* Maguire & Wurdack, Mem. New York Bot. Gard. 9(3): 318. 1957.
Figs 10, 11

Type species. *Pyrrorhiza neblinae* Maguire & Wurdack.

Comments. *Pyrrorrhiza* was initially considered as being closely related to *Schiekia* Meisn. (Maguire and Wurdack 1957), a view supported by the morphological phylogeny of Simpson (1990), but not supported by the anatomical studies of Aerne-Hains and Simpson (2017), the molecular phylogeny of Hopper et al. (in prep.) and the new morphological phylogeny for the family (Pellegrini 2019). As currently understood, *Pyrrorrhiza* is sister to *Cubanicula*, with both being sister to *Xiphidium* s.str. (Hopper et al. in prep.). The supposed relation between *Pyrrorrhiza* and *Schiekia* was thought to be supported by the zygomorphic perianth, dimorphic stamens, and the discontinuous subexterior exine wall (Simpson 1983, 1990). However, the first two characters are clearly homoplastic in Haemodoroideae, while the third seems to be a convergence between *Pyrrorrhiza* and *Schiekia* (Pellegrini 2019). *Pyrrorrhiza* shares with *Cubanicula* and *Xiphidium* s.str. the sand-binding roots, campanulate and pollen rewarding flowers, mainly white perianth, tepals with an apical black mucron, anthers as long as to ca. ½ times shorter than the filaments and enlarged placental attachments subtending the ovules and fruits with thickened septal ridges (Pellegrini 2019). It shares exclusively with *Cubanicula* the peculiar lenticellate seeds with the testa's margin covered with coarse trichomes (Hickman 2019; Pellegrini 2019).

3.1. *Pyrrorrhiza neblinae* Maguire & Wurdack, Mem. New York Bot. Gard. 9(3): 318, fig. 63a–g. 1957.

Figs 10, 11

Type material. Holotype. VENEZUELA. Amazonas: Río Yatua, Cerro de la Neblina, locally frequent in open savannah, 5 km SW of cumbre camp, alt. 1900 m, fl., fr., 6 January 1954, B. Maguire et al. 37108 (NY barcode 00247967!; **isolectotypes:** COL barcode COL000000167!, F barcode V0045883F!, GH barcode GH00030234!, IAN barcode IAN091102!, K barcode K000574291!, MICH barcode MICH1192344!, MO barcode MO-202079!, NY barcode 00247968, P barcode P00753469, S accession no. S-R-5402!, U barcode U0002447!, UC barcode UC1035482!, US barcode US00092054!, VEN barcode VEN39086!, W n.v.).

Distribution and habitat. *Pyrrorrhiza neblinae* is at present only known to occur at the Venezuelan side of the Cerro de la Neblina (Fig. 12), but most likely also reaches the Brazilian side. It grows in open, acidic, and swampy *Heliamphora* Benth. (Sarraceniaceae) and *Bonnetia maguireorum* Steyerl. (Bonnetiaceae) savannahs, with *Euterpe* Mart. (Arecaceae), along streams, between 1800–2100 m alt. Due to its cormose underground system producing cormlets, *P. neblinae* forms dense clonal clusters. Its pollination syndrome is unknown, but based on the vestigial pair of septal infralocular nectaries, it is most likely a pollen-rewarding, self-compatible species.

Phenology. It was found in bloom and fruit from November to February.

Conservation status. As aforementioned, *Pyrrorrhiza neblinae* is only known from a single Amazonian mountain. It possesses very narrow EOO (20 km²) and AOO (ca.

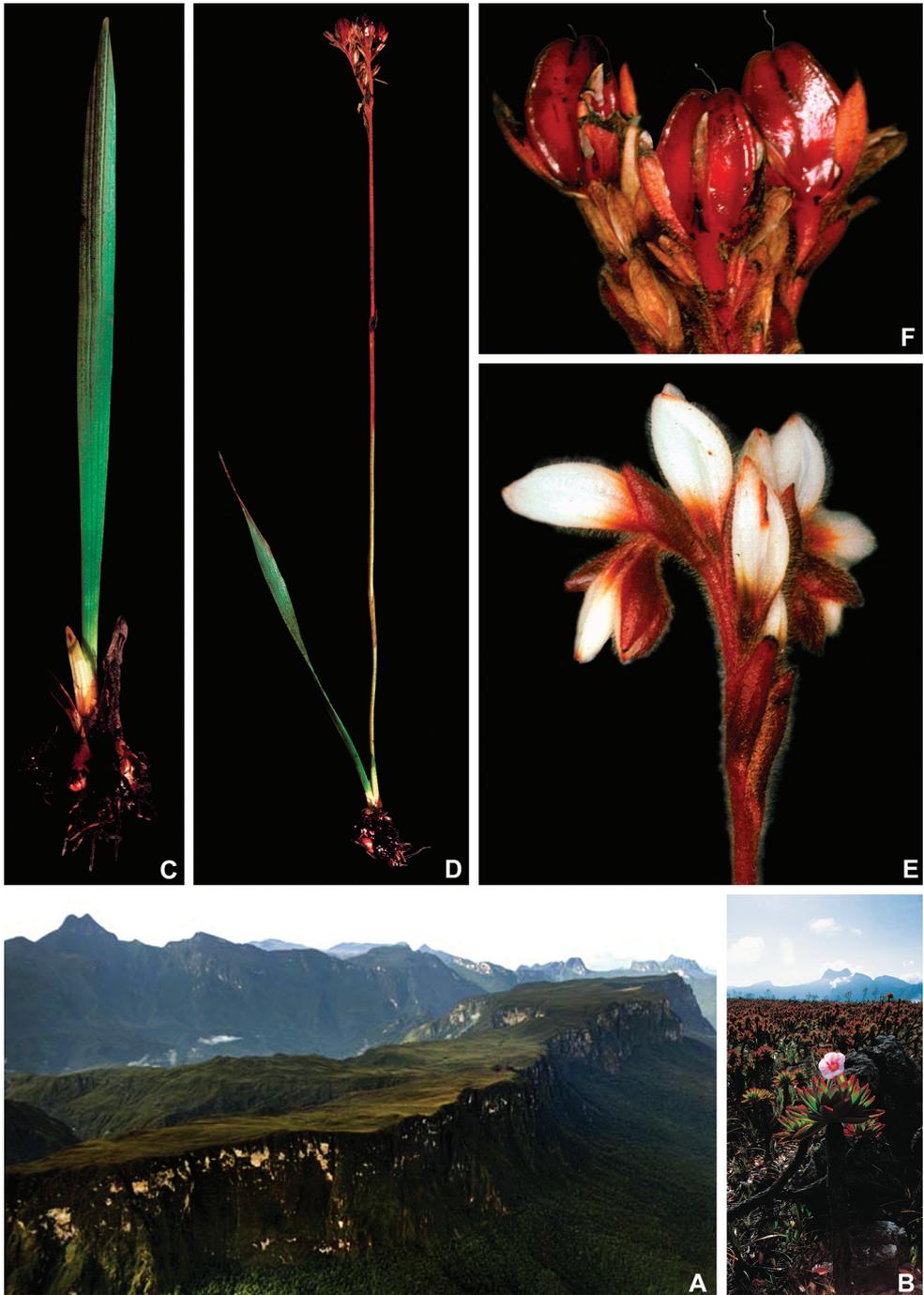


Figure 10. *Pyrrorhiza neblinae* Maguire & Wurdack **A** Cerro de la Neblina **B** detail of the vegetation at the top of the Cerro de la Neblina with *Bonnetia maguireorum* in flower **C** habit **D** flowering habit **E** inflorescence showing the spatheaceous bracteoles and floral buds **F** inflorescence bearing immature capsules. **A** by B. Means, **B** by C. Brewer-Carias, **C–F** by A. Weitzman.



Figure 11. *Pyrrorrhiza neblinae* Maguire & Wurdack **A** whole plant **B, C** cincinnus: **B** young cincinnus with flower buds **C** older cincinnus with fruits, pre-anthesis flowers and flower buds **D** hairs **E** flower bud with bracteole **F** flower at pre-anthesis **G** dissected perianth, showing the lack of nectar guides **H** filiform staminode **I–J** stamen: **I** frontal view **J** dorsal view **K** flower with the perianth removed, showing the androecium and gynoecium **L** stigma **M–O** fruit: **M** immature capsule **N** capsule in longitudinal section **O** dehiscent capsule **P–R** seed: **P** dorsal view **Q** ventral view **R** longitudinal section. Illustration by E.J. Hickman. Scale bars: 2 cm (**A, G, M–O**); 0.5 cm (**B, C, H**); 0.25 mm (**D**); 1.5 mm (**E, F**); 1 mm (**I, J, P–R**); 0.75 mm (**K**); 0.1 mm (**L**).

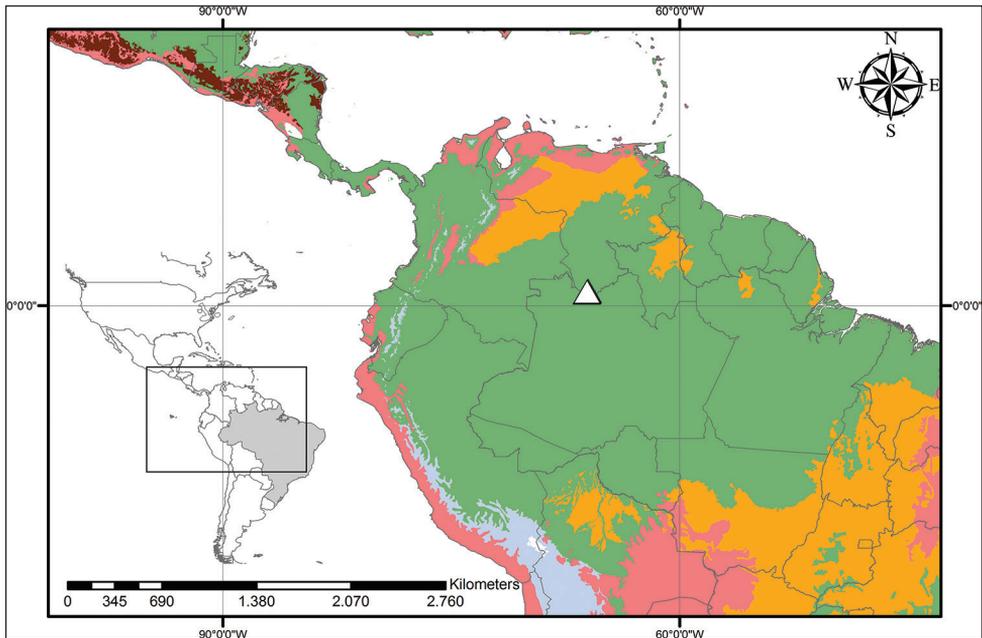


Figure 12. Distribution of *Pyrrorrhiza neblinae* Maguire & Wurdack. Light Green– Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands, and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

13 km²) and, thus, following IUCN's (2001) recommendations, *P. neblinae* should be considered as Critically Endangered [CR, B1a+C2a(ii)+D2].

Comments. *Pyrrorrhiza neblinae* is still poorly known, with only a handful of collections. Nonetheless, it is known that *P. neblinae* is restricted to swampy and rocky montane savannah (i.e., tepuis). The peculiar cormose underground system of *P. neblinae* is only comparable to those of *Barberetta* Harv., *Wachendorfia* Burm. (both Haemodoroideae) and *Tribonanthes* Endl. (Conostylidoideae) (Simpson 1998b). Nonetheless, the corms in *Barberetta* and *Wachendorfia* are further connected by long, stolon-like flagelliform-shoots, which are unique in the family (Pellegrini 2019). The seeds covered with coarse trichomes might function in adherence to animal fur or feathers as an aid to dispersal (Maas and Maas-van de Kamer 1993). Alternatively, the seeds covered with coarse trichomes might also be an adaptation to hydric stress. These projections might help the seed to quickly absorb and store water, which could come in handy in such an inconstant environment such as the Amazonian tepuis (i.e., *Pyrrorrhiza*), white sand savannahs (i.e., *Cubanicula*), and the seasonally-dry fynbos from South Africa (i.e., *Wachendorfia*) (Pellegrini, pers. observ.). Seeds with coarse trichomes are recovered as a synapomorphy for the clade composed by *Barberetta*, *Cubanicula*, *Pyrrorrhiza*,

Schiekia, *Wachendorfia*, and *Xiphidium*. Nonetheless, coarse trichomes in the seed testa are independently lost several times, such as in *Barberetta* (smooth), *Schiekia* (reticulate in *S. orinocensis* and *S. timida*), *Wachendorfia* (smooth in *W. thyrsoiflora* Burm.), and *Xiphidium* (tuberculate) (Pellegrini 2019).

4. *Schiekia* Meisn., Pl. Vasc. Gen. 2(12): 300. 1842.

Figs 13, 15–17, 19, 20

Troschelia Klotzsch & M.R.Schomb. in Reisen, Br.-Guiana: 1066. 1849, nom. nud.

Type species. *Wachendorfia orinocensis* Kunth. [≡ *Schiekia orinocensis* (Kunth) Meisn.].

Comments. *Schiekia* is indisputably closely related to *Wachendorfia* (Hopper et al. 1999, 2009; Hickman 2019; Pellegrini 2019; Hopper et al., in prep.), which is shown by its taxonomic history and due to several morphological characters. *Schiekia* and *Wachendorfia* share some unique floral traits, such as the perianth apertures (produced by the connation of five tepals, giving the flowers a peculiar bilabiate appearance and producing two basal pouches; Simpson 1990) and the infralocular septal nectaries with commissure slits which channel the nectar to the perianth apertures (Simpson 1993; Pellegrini 2019). These features serve as strong morphological synapomorphies that support the clade composed by *Schiekia* + (*Wachendorfia* + *Barberetta*), with a posterior loss of the perianth apertures in *Barberetta* (Pellegrini 2019). The nectary apparatus in *Barberetta* is also remarkably similar to that of *Wachendorfia* and *Schiekia* and only lacks the ducts that would carry the secreted nectar to the perianth apertures (Simpson 1993). Furthermore, *Schiekia* and *Wachendorfia* share the presence of tapering trichomes, while *Barberetta* and *Wachendorfia* share the unifacially-plicate leaves, which are unique in the family and the order as a whole (Simpson 1990; Pellegrini 2019). The staminode-like structures are synapomorphic to *Schiekia* (Pellegrini 2019) and cannot be considered actual staminodes, in fact, representing a *de novo* structure (Simpson 1990; Pellegrini 2019). These staminode-like structures seem to represent some kind of corona (i.e., a perianth projection), comparable to the ones observed in many Amaryllidaceae and Passifloraceae. Their function is most likely associated with the genus' floral biology and could represent enlarged osmophores, which would aid in the attraction of pollinators, together with the nectar. Nonetheless, reproductive biology studies in *Schiekia* are entirely lacking and are necessary to understand the function of these staminode-like structures. Furthermore, ontogenetic studies are also necessary to understand the origin and to propose a more suitable and definite name to these structures.

4.1. *Schiekia orinocensis* (Kunth) Meisn., Pl. Vasc. Gen. 2(12): 300. 1842.

Fig. 13

Wachendorfia orinocensis Kunth, Nov. Gen. Sp. (quarto ed.) 1(3): 319. 1816. Lectotype (designated here). VENEZUELA. Isla de Pararuma, in humidis, in ripa Orinoco propter

confluentem Sinaruci et in insula Pararuma, fl., fr., May, F.W.H.A. Humboldt & A.J.A. Bonpland 843 (P barcode P00669614!; isolectotype: P barcode P00669615!). *Xiphidium angustifolium* Willd. ex Link, Jahrb. Gewächsk. 1(3): 73. 1820, nom. superfl., Syn nov.

Troschelia orinocensis (Kunth) Klotzsch & M.R.Schomb., Reis. Br.-Guiana 1066, 1120. 1849.

Schiekia flavescens Maury, J. Bot. (Morot) 3: 269. 1889. Lectotype (designated here). VENEZUELA. Upper Río Orinoco, Atures, Salvajito, fl., 3 Apr 1887, M. Gaillard 52 (P barcode P06891121!, pro parte, the two specimens on the sides).

Schiekia congesta Maury, J. Bot. (Morot) 3: 269, f. 12. 1889, nom. nud.

Schiekia orinocensis subsp. *savannarum* Maguire & Wurdack, Mem. New York Bot. Gard. 9(3): 320. 1957. Holotype. VENEZUELA. Amazonas: Cerro Yapacana, Río Orinoco, in savannah no. 1, northwest base of the mountain, fl., fr., 31 Dec 1950, B. Maguire et al. 30496 (NY barcode 00214486!; isotypes: F barcode V0045884F!, K barcode K000574294!).

Nomenclatural notes. When describing *Wachendorfia orinocensis*, Kunth (1816) mentions a collection made on Isla de Pararuma, Río Orinoco, but makes no reference to the collector, collection number, or herbarium. During a visit to P herbarium, we came across two specimens in which the labels matched the locality in the protologue and also had a label indicating it had been part of the Bonpland & Humboldt herbarium. The specimen P00669614 is clearly what the majority of the original illustration was based upon, while P00669615 was only used to illustrate the fruits. Thus, since the specimen P00669614 possesses well-preserved leaves and stems, floral buds, and mature flowers, it is here designated as the lectotype.

When describing *Schiekia flavescens*, Maury (1889) mentions two collections, *Gaillard 52* and *Chaffanjon 185*. During a visit to P, we were unable to locate the collection *Chaffanjon 185* but managed to find *Gaillard 52*. The latter was cited by Maury as a mixed gathering, with two specimens of his *S. flavescens* and a central specimen of *S. orinocensis*. Thus, we designate the two lateral specimens (right and left) as comprising the lectotype for *S. flavescens*.

Distribution and habitat. *Schiekia orinocensis*, in its current circumscription, is a far more geographically-restricted taxon than traditionally accepted. It is known to occur in Colombia, Guyana, Venezuela, and Brazil (States of Amazonas, Pará, and Roraima) (Fig. 14), in tepuis and other montane formations in the Guyana Shield, in seasonally-flooded environments.

Phenology. It was found in flower and fruit from June to October, during the dry season.

Conservation status. *Schiekia orinocensis* possesses a wide EOO (1,193,173 km²) but a relatively narrow AOO (ca. 224 km²). This narrow AOO might be related to the relatively reduced number of collections, especially when compared to *S. timida*. The relatively small number of specimens might be due to the difficulty of reaching and collecting in tepuis and other mountainous formations in the Amazon Region. Nonetheless, field observations by one of us (EJH) indicate that *S. orinocensis* forms consid-

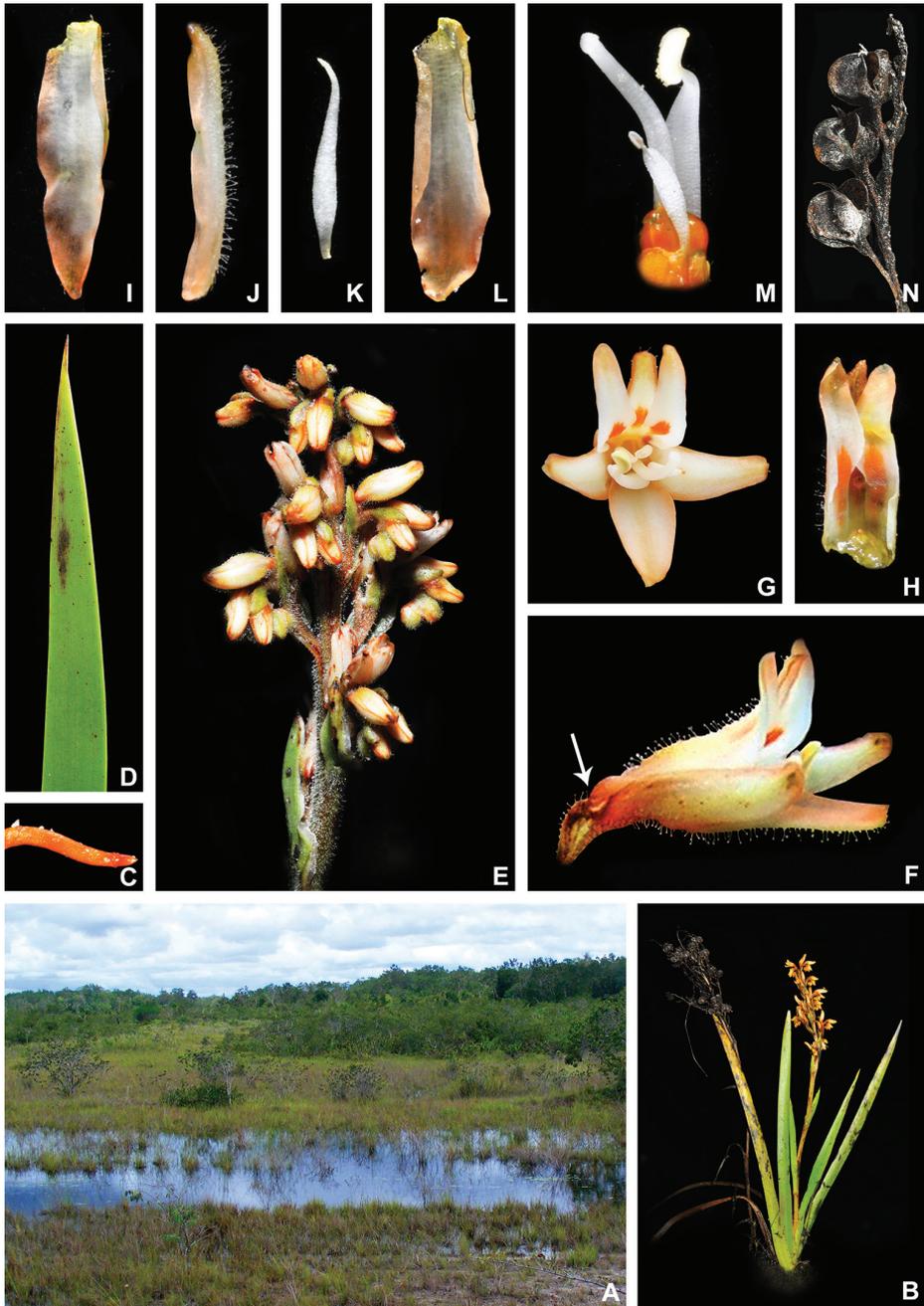


Figure 13. *Schiekia orinocensis* (Kunth) Meisn **A** habitat **B** habit, showing an inflorescence from this flowering season and an old one from the previous year bearing dehiscent capsules **C** root **D** leaf blade **E** inflorescence **F, G** flower: **F** side view of a flower showing the nectar drop (arrow) in the perianth aperture **G** frontal view of a flower **H–L** perianth segments: **H** upper perianth tepals showing their connate bases and the nectar guides **I** lower lateral tepal **J** side view of the lower lateral tepal showing the glandular pubescence **K** staminode-like projection **L** lower medial tepal **M** flower with perianth removed, showing the androecium and gynoecium. **N**, dehiscent capsules. All photos by E.J. Hickman.

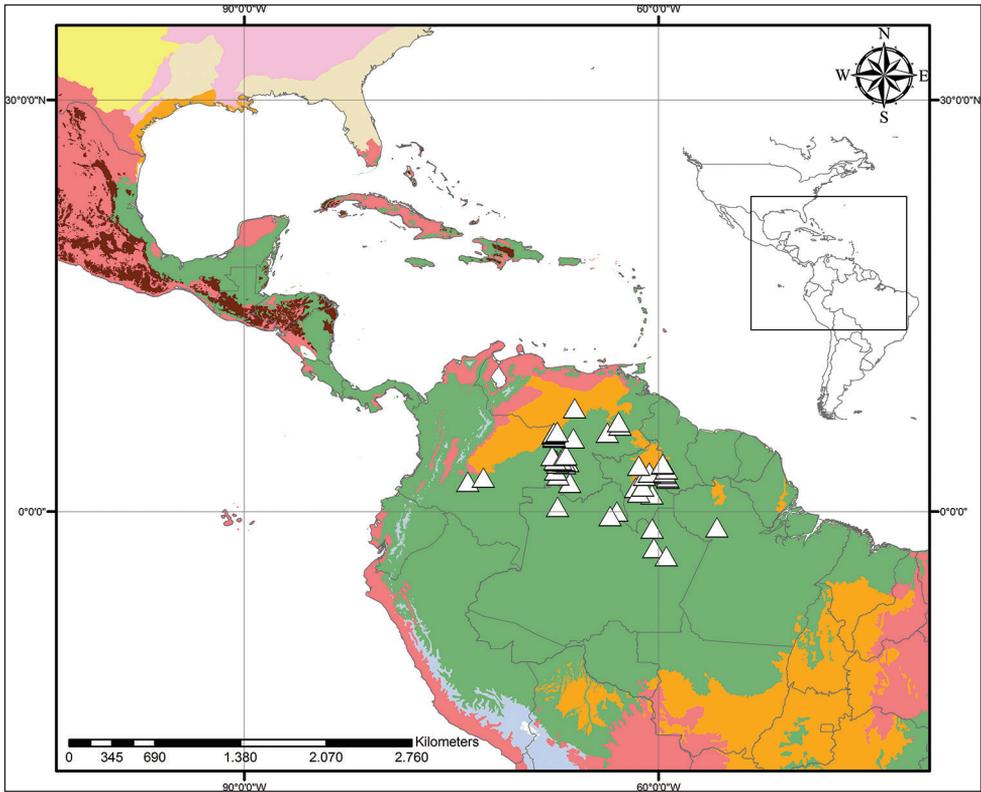


Figure 14. Distribution of *Schiekia orinocensis* (Kunth) Meisn. Beige – Temperate Coniferous Forests and Boreal Forests; Yellow – Temperate Grasslands, Savannahs and Shrublands; Pink – Temperate Broadleaf and Mixed Forests; Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

erably smaller and more restricted subpopulations than *S. timida*, which might indicate it is ecologically more specific in its requirements. Thus, following IUCN's (2001) recommendations, *S. orinocensis* should be considered as Vulnerable [VU, A2ab+C2a(i)].

Comments. *Schiekia* has consistently been treated as a monospecific genus until the present study, given that *S. flavescens* has been considered a synonym of *S. orinocensis* since very early days. Nonetheless, previous studies, such as Maguire and Wurdack (1957) and Maas and Maas-van de Kamer (1993), have treated the polymorphism observed in herbarium specimens by recognising different subspecies. Both previous attempts to divide *S. orinocensis* were almost entirely based on vegetative morphology (Maguire and Wurdack 1957; Maas and Maas-van de Kamer 1993), with the second one also relying on the proportion between the leaves and the inflorescences (Maas and Maas-van de Kamer 1993). The observed variation in plant stature and leaf length and width, which was used by previous authors to recognise subspecies (Maguire and Wurdack 1957; Maas and Maas-van de Kamer 1993), seems to be environmental and, thus, is here disregarded as

taxonomically relevant. Our present treatment is based on extensive field and herbarium studies. It suggests that three species can be recognised based on ecological preferences, rhizome morphology, leaf morphology, tepal arrangement and colouration, the width of the filiform staminode-like projections, capsules morphology and colouration, and seed ornamentation. *Schiekia orinocensis* s.str. is morphologically similar to *S. timida* due to its rhizome morphology, leaf arrangement and consistency, inflorescence architecture, upright to patent flowers, inflated medial filament, and tuberculate seeds. *Schiekia orinocensis* s.str. can be differentiated by its leaves with inconspicuous veins (vs. conspicuously veined in *S. timida*), chasmogamous and bilabiate flowers (vs. cleistogamous and narrowly tubular), pedicels gibbose at the apex (vs. not gibbous), tepals with apex reflexed and apricot to cream (vs. straight and light to medium green), upper tepals with three dark orange to orange-brown nectar guides (vs. lacking nectar guides), staminode-like projections fusiform and almost as long as its subtending tepal (vs. filiform and 1/3 the length of its subtending tepals) and capsules broader than long (vs. slightly longer than broad or as broad as long). *Schiekia orinocensis* s.str. and *S. silvestris* share the chasmogamous flowers and upper tepals with nectar guides, thick and fusiform staminode-like projections and capsules slightly longer than broad or as broad as long. Nonetheless, they can be easily differentiated based on vegetative morphology, flower orientation, inflation of the medial filament, capsule colouration, and seed ornamentation (see below).

4.2. *Schiekia silvestris* (Maas & Stoel) Hopper, E.J.Hickman, Rhian J.Sm. & M.Pell., stat. nov.

urn:lsid:ipni.org:names:77213183-1

Figs 15–17

Schiekia orinocensis subsp. *silvestris* Maas & Stoel in Maas PJM and Maas-van de Kamer H, Fl. Neotrop. Monogr. 61: 21. 1993. Holotype. BRAZIL. Amazonas: Rio Negro, road from Camanaus to Vaupés airport, fl., 30 Oct 1971, G.T. Prance et al. 15864 (INPA barcode INPA34082!; isotypes: F, K barcode K000574292!, MG n.v., MO n.v., NY barcode NY00247969!, S barcode S06-6076!, U barcode U0002448!, US barcode US00592174!).

Distribution and habitat. Brazil (States of Amazonas, Pará, and Roraima), Colombia, French Guiana, Surinam, and Venezuela (Fig. 18). Found growing in the seasonally-flooded forest understorey, near rivers.

Phenology. It was found in flower and fruit from January to November, but peaking during the dry season.

Conservation status. *Schiekia silvestris* possesses a wide EOO (1,634,289 km²) but a relatively narrow AOO (ca. 392 km²). This narrow AOO might, once again, be related to the difficulty for collection in the Amazon Region. Nonetheless, the number of known collections is relatively large, which leads us to believe this species might be

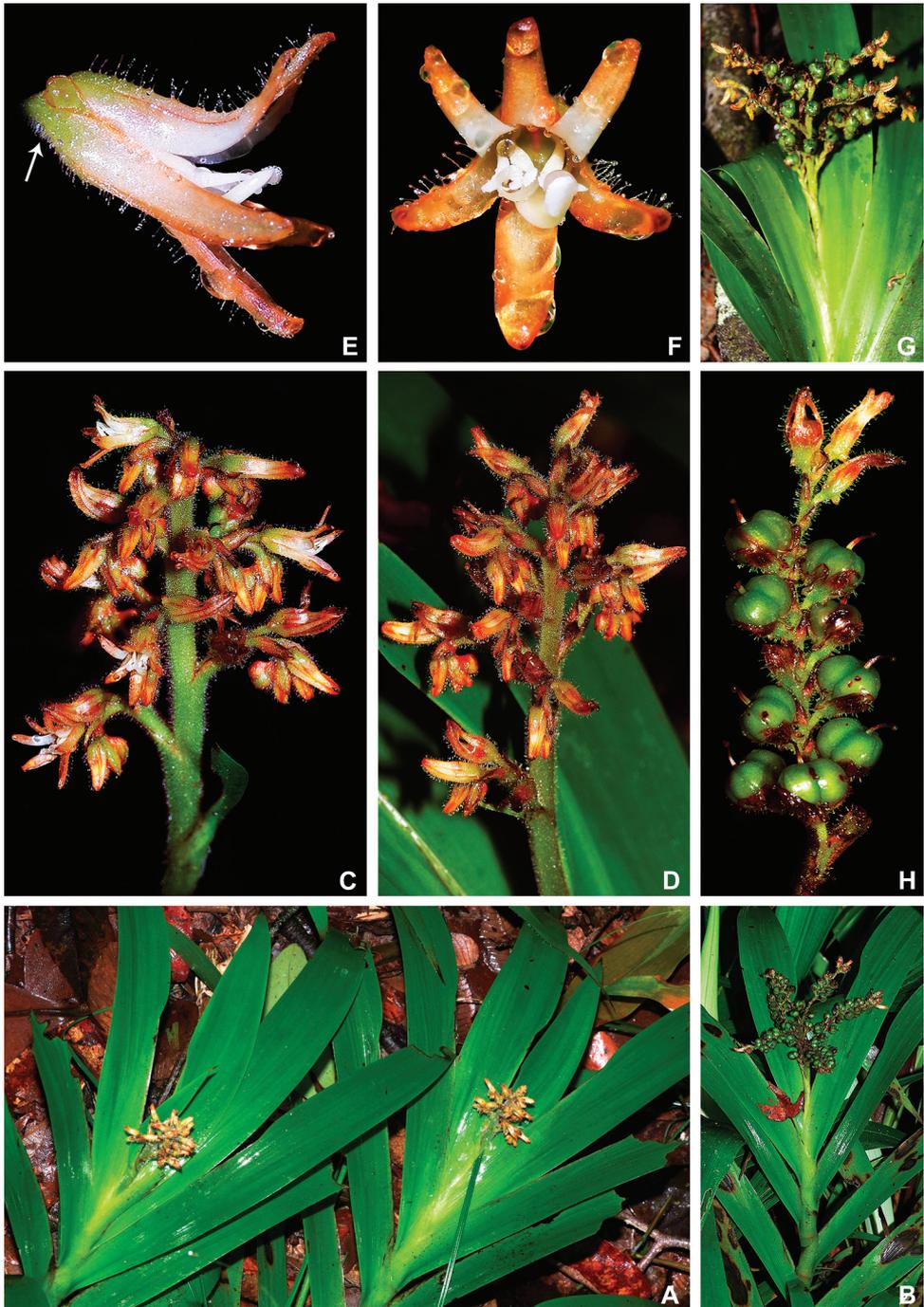


Figure 15. *Schiekia silvestris* (Maas & Stoel) Hopper et al. **A** habit of two flowering specimens **B** habit of a fruiting specimen **C, D** inflorescence: **C** inflorescence with flowers at anthesis **D** inflorescence with flowers at post-anthesis **E, F** flower: **E** side view of a flower showing the nectar drop (arrow) in the perianth aperture **F** frontal view of a flower **G** inflorescence bearing last few flowers and several capsules **H** detail of the cincinnus showing immature capsules. All photos by H. Galliffet, except for G by S. Sant.



Figure 16. *Schiekia silvestris* (Maas & Stoel) Hopper et al. Full colour whole plant illustration. Illustration by E.J. Hickman. Scale bar: 1 cm.

much more common than Maas and Maas-van de Kamer (1993) were led to believe. Thus, following IUCN's (2001) recommendations, *S. silvestris* should be considered as Least Concern (LC).

Comments. *Schiekia silvestris* is by far the easiest species to differentiate from the three accepted by us in the present study. It is the only species to exclusively inhabit understorey and other mesic habitats and has a growth form similar to that of *Xiphidium caeruleum*, with its long and trailing rhizomes and leaves evenly distributed along the stem. Aside from that, the leaves are considerably more delicate and broader, and herbarium specimens of *S. silvestris* are commonly misidentified as *X. caeruleum* in Brazilian herbaria. Furthermore, the inflorescences of *S. silvestris* generally possess a corymb-like appearance, added to the diminutive and strongly bilabiate, pendulous, apricot to orange-yellow flowers, with tepals recurved in the upper half and non-inflated medial filament. The capsules of *S. silvestris* also tend to be much broader than those of *S. orinocensis* and *S. timida*, ranging from green when immature to chocolate brown when mature. Finally, it is the only species of *Schiekia* to present seeds with short and coarse trichomes scattered across the reticulate testa (Fig. 17U–W). On the other hand, *S. orinocensis* and *S. timida* (Fig. 20T–V) present evenly reticulate testa.



Figure 17. *Schiekia silvestris* (Maas & Stoel) Hopper et al. **A, B** rhizome: **A** rhizome, showing persistent leaf bases **B** longitudinal section **C** cincinnus **D** flower bud **E** flower in frontal view **F** hairs **G-I** perianth: **G** upper perianth lobes, showing the nectar guides **H** lateral outer perianth lobe with adnate staminode-like structure **I** medial inner perianth lobe **J** staminode-like structure **K** flower with the perianth removed, showing the androecium and gynoecium **L, M** stamens: **L** lateral stamen (frontal and dorsal view) **M** medial stamen (frontal and dorsal view) **N, O** gynoecium: **N** style **O** stigma **P-T** fruit: **P** immature capsule **Q** capsule in longitudinal section **R** capsule in cross-section **S** placenta with ovules **T** dehiscent capsule **U-W** seed: **U** dorsal view **V** ventral view **W** longitudinal section. Illustration by E.J. Hickman. Scale bars: 1 cm (**A, B, G-I, K**); 1.5 mm (**C-E, P-R, T**); 0.3 mm (**F**); 0.75 mm (**J, L-N, S, U-W**); 0.15 mm (**O**);

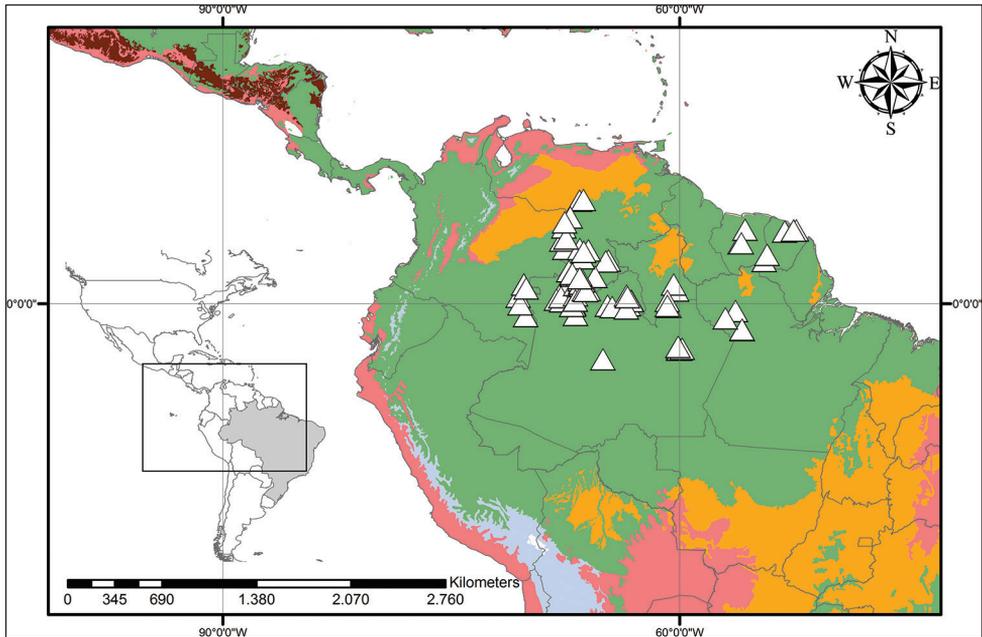


Figure 18. Distribution of *Schiekia silvestris* (Maas & Stoel) Hopper et al. Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

4.3. *Schiekia timida* M.Pell., E.J.Hickman, Rhian J.Sm. & Hopper, sp. nov.

urn:lsid:ipni.org:names:77213184-1

Figs 19, 20

Diagnosis. Similar to *Schiekia orinocensis* (Kunth) Meisn. in rhizome morphology, leaf arrangement and consistency, inflorescence architecture, floral orientation, and filiform staminode-like projections, but differs due to its leaves with impressed veins, narrowly tubular and cleistogamous flowers, tepals with apex straight and light to medium green, upper tepals lacking nectar guides, medial filament inflated, staminode-like projection 1/3 the length of its subtending tepal and capsules slightly longer than broad or as broad as long.

Type. BRAZIL. Tocantins: Natividade, Serra da Natividade, fl., fr., 6 Mar 2015, R.C. Forzza et al. 8562 (RB!; isotypes: CEPEC!, HTO!, UPCB!).

Description. *Herbs* ca. 40–100 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal in boggy areas. *Roots* thick, fibrous, orange to red, sand-binding, emerging from the rhizome. *Rhizomes* underground, short, new shoots external surface reddish-orange to red, older shoots external surface brown to reddish-brown, internal surface orange to reddish-orange to red. *Stems* inconspicuous to short, ascending to erect, fibrous, unbranched; internodes inconspicuous when sterile, 2.5–7.9 cm long when fertile, green to orange to reddish-orange, glabrous to tomentose,

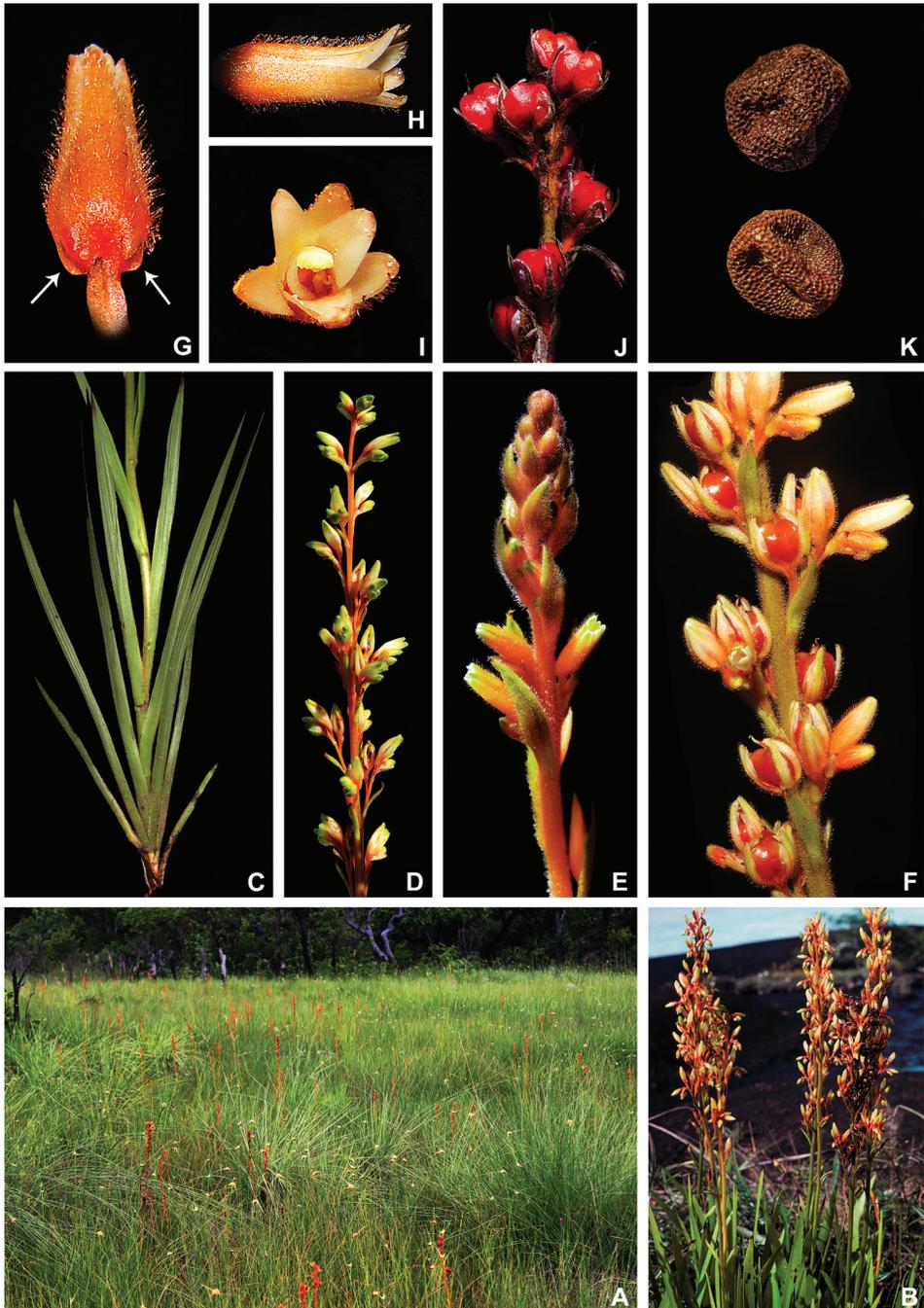


Figure 19. *Schiekia timida* M. Pell. et al. **A** habitat **B** flowering habit **C** detail of the leaves **D, E** inflorescence: **D** inflorescence with many-flowered cincinni **E** inflorescence with 1-flowered cincinni **F** inflorescence bearing young capsules **G-I** flower: **G** upper view of a flower showing both perianth apertures and their respective nectar drops (arrows) **H** side view of a flower **I** frontal view of a flower **J** mature capsules before opening **K** seeds. **A** by G. Antar, **B** by G. Davidse, **C, F** by M.E. Engels, **D** by C. Castro, **E** by V.A.O. Dittrich, **G-I** by P.L. Viana and **J, K** by S.E. Martins.

hairs pilate, light to medium brown. **Leaves** distichously-alternate, equitant, congested at the apex of the stem when sterile, some evenly distributed along the elongated stem when fertile, sessile, the apical ones gradually smaller than the basal ones; sheaths 2.2–14.8 cm long, light green, glabrous to sparsely tomentose, margin glabrous to ciliate, hairs pilate, light to medium brown; blades 1.7–29.2 × 0.4–1 cm, fibrous to coriaceous, unifacial, yellowish-green to medium green to bluish-green, drying olive-green to brown, linear to linear-elliptic, slightly ensiform to ensiform, glabrous to tomentose, hairs pilate, light to medium brown, base sheathing, margins green, glabrous to ciliate, apex acuminate; midvein inconspicuous, secondary veins 4–6, impressed to deeply impressed, becoming more prominent when dry. **Inflorescences** terminal, solitary, consisting of a pedunculate many-branched thyrse; peduncles 7.7–38.8 cm, tomentose to densely tomentose, with a mixture of pilate glandular hairs, light to medium brown; basal bract 1.8–7.3 × 0.1–0.4 cm, leaf-like, linear to linear-elliptic, straight to slightly ensiform, glabrous to tomentose, with a mixture of pilate glandular hairs, light brown, base truncate to slightly sheathing, margin ciliate, apex acuminate, secondary veins inconspicuous; cincinnus bract absent; cincinni 6–28 per thyrse, alternate, 1–6-flowered, sessile, bright orange to reddish-orange, glandular-tomentose to densely glandular-tomentose, hairs light brown; bracteoles 4.6–8.8 × 1.4–3.1 mm, lanceolate to elliptic to broadly elliptic, bright orange to reddish-orange, apex sometimes green to yellowish-green, glandular-tomentose, hairs light brown, base cuneate, margin glabrous, hyaline, apex acute. **Flowers** 0.2–0.4 cm diam., bisexual, cleistogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds 4.2–8.2 × 2–2.9 mm, ovoid, orange to reddish-orange, base generally white to cream, apex light green; pedicels 2.3–7.2 mm long, not gibbous at apex, orange to reddish-orange, densely tomentose with a mixture of pilate and glandular hairs, white to light brown, upright to patent and elongate in fruit; perianth zygomorphic, upper lobes connate to 2/3 of their length, upper and lower lateral lobes basally connate forming two lateral perianth pouches, nectar guide absent, outer lobes 8.3–10.1 × 1.8–2.3 mm, subequal, the upper slightly broader and longer, the lateral ones asymmetric, elliptic to spatulate or lanceolate, external surface white to cream, base apricot to bright orange to reddish-orange, apex medium to light green, rarely completely apricot to bright orange to reddish-orange, glandular-tomentose to densely glandular-tomentose, hairs white to light brown, internal surface white to cream, base light orange to apricot, apex medium to light green, rarely completely light orange to apricot, glabrous, base truncate or cuneate, symmetric in the upper, asymmetric in the lateral ones, margins glabrous, apex obtuse, inner lobes 7.2–10.2 × 4.8–7.3 mm, subequal, the lower slightly broader, the upper ones asymmetric, elliptic to spatulate, external surface white to cream, base apricot to bright orange to reddish-orange, apex medium to light green, rarely completely apricot to bright orange to reddish-orange, glabrous, tomentose along the midvein, white to light brown, internal surface white to cream, base light orange to apricot, apex medium to light green, rarely completely light orange to apricot, glabrous, base cuneate, the upper ones asymmetric, the lower one symmetric, margins glabrous, apex obtuse to slightly emarginate; staminode-like projections 2, 3.5–3.7 × 0.1–0.2 mm, adnate to the base of the lateral outer perianth lobes, thin, filiform,



Figure 20. *Schiekia timida* M. Pell. et al. **A** whole plant **B** cincinnus **C** flower bud **D** hairs **E, F** flower: **E** side view **F** frontal view **G-I** perianth: **G** upper perianth lobes, showing the lack of nectar guides **H** medial inner perianth lobe **I** lateral outer perianth lobe with adnate staminode-like structure **J** flower with the perianth removed, showing the androecium and gynoecium **K, L** stamens: **K** lateral stamen **L** medial stamen **M-N** gynoecium: **M** ovary **N** stigma **O-S** fruit: **O** immature capsule covered by the persistent perianth **P** immature capsule with perianth removed **Q** capsule in longitudinal section **R** capsule in cross-section **S** dehiscent capsule **T-V** seed: **T** dorsal view **U** ventral view **V** longitudinal section. Illustration by E.J. Hickman. Scale bars: 1.5 cm (**A**,); 0.35 mm (**B**); 2 mm (**C, E, F**); 0.25 mm (**D**); 1.75 mm (**G-I**); 1.25 mm (**J, O-Q, S**); 1 mm (**K-M, R**); 0.5 mm (**N**); 0.75 mm (**T-V**)

white; stamens 3, lateral stamens with filaments 4.4–5.1 mm long, slender, slightly sigmoid, apex filiform, incurved, cream, basally apricot, apically white, glabrous, anthers 0.5–0.6 × 0.4–0.6 mm, basifixed, deciduous, extrorsely rimose, broadly oblongoid to broadly ellipsoid, with an apical connective appendage, cream, medial stamen with filament 5.1–5.8 mm long, sigmoid, slightly spirally coiled either to the left or to the right, apex incurved, cream, basally apricot, apically white, glabrous, anthers 1.1–1.4 × 0.6–0.8 mm, dorsifixed, extrorsely rimose, broadly oblongoid to broadly ovoid, cream; ovary 1.4–1.7 × 1.5–1.8 mm, broadly ovoid to subglobose, slightly trigonous, 3-loculate, apricot to bright orange, smooth, glabrous, style 3.4–3.8 mm, slightly sigmoid, apex incurved, white, basally cream to apricot to light orange, glabrous, stigma capitate, white, papillose. **Capsules** 6.4–7.1 × 4.6–5.7 mm, broadly ellipsoid in outline, trigonous, dry, thick-walled, orange when immature, becoming medium to dark red when mature, loculicidal, 3-valved. **Seeds** 1.6–2.2 × 1.3–1.7 mm, deltoid, each face sunken, testa medium to dark brown, evenly reticulate; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen (paratypes). **BRAZIL. Amazonas:** Rio Negro, across Comunidade Aparecida, 1 km up from Rio Taurí, fl., fr., 7 Nov 1987, D.W. Stevenson et al. 890 (K, NY). **Goiás:** Salinas, fl., Mar–Jul 1844, M.A. Weddell 2087 (P); Caiapônia, 46 km N de Caiapônia, fl., fr., 23 Feb 1982, P.I. Oliveira & W.R. Anderson 425 (MBM, MICH, MO, NY). **Maranhão:** Carolina, Cachoeira do Garrote, margem esquerda do Rio Garrote, ca. 4.3 km W da estrada, fl., 24 Feb 2005, G. Pereira-Silva et al. 9624 (CEN); Parque Nacional da Chapada das Mesas, Gleba II, fl., fr., 9 Apr 2016, A.C. Sevilha et al. 5742 (CEN); perto de Carolina, fl., 26 May 1950, J.M. Pires & G.A. Black 2262 (IAN); BR-010, Transamazônica, Pedra Caída, fr., 13 Apr 1983, M.F.F. Silva et al. 1084 (IAN, INPA, MG, MO, NY); Vereda do Seu Zico, ca. 3.5 km do asfalto, fl., fr., 27 Feb 2005, G. Pereira-Silva et al. 9702 (CEN); estrada Carolina/Babaçulândia, km 8.2, margem direita do Rio Tocantins, kms marcados da Igreja São Francisco, Bairro Brejinho, fr., 22 May 2010, G. Pereira-Silva et al. 15292 (CEN); Riachão, estrada Riachão/Vila Nova de Carli, Proceder III, ca. 30 km S de Riachão, fl., 21 Mar 2000, B.M. Walter et al. 4426 (CEN); rodovia Vila Gerais das Balsas/Riachão, km 153, fl., 24 Mar 1999, G. Pereira-Silva et al. 4140 (CEN). **Mato Grosso:** Canabrava do Norte, Serra do Roncador, ca. 60 km N of Xavantina, fr., 25 May 1966, H.S. Irwin et al. 16002 (K, MO, NY, RB, U, UB, US); Cataqui-imaúí, Campos dos Urupós, Cab. do Cantário, fl., Dec 1918, J.G. Kuhlmann 1647 (RB); Rio Turvo, ca. 210 km N of Nova Xavantina, fr., 29 May 1966, H.S. Irwin et al. 16283 (K, NY, RB, UB, US); Nova Canaã do Norte, resgate de flora da UHE Colider, estrada de acesso à UHE, fl., fr., 26 Feb 2015, M.E. Engels & M. Lautert 2839 (CNMT, HERBAM, MBM, RB, TANG); fr., 27 Apr 2016, H.R.W. Zanin 373 (CNMT, HERBAM, RB); Nova Xavantina, km 85 from Nova Xavantina-Cachimbo road, fr., 31 May 1966, D.R. Hunt & J.F. Ramos 5695 (K, NY, UB); Serra do Roncador, ca. 84 km N of Nova Xavantina, fr., 6 Jun 1966, H.S. Irwin et al. 16454 (MO, NY, RB, UB, UMO, US); 60 km from Nova Xavantina, fl., fr., 6 Jun 1966, D.R. Hunt & J.F. Ramos 5835 (K, NY, UB); 20 km NE of Base Camp of the Expedition, fl., fr., 4 Mar 1968, D.R. Gifford 2657 (K, NY, UB); Km 57 N from Nova

Xavantina-Cachimbo road, fl., 16 Jan 1968, D. Philcox & A. Ferreira 4080 (K, UB); km 241 from Nova Xavantina-Cachimbo road, fl., fr., 16 Mar 1968, D. Philcox & A. Ferreira 4563 (K); ca. 1 km E from km 242 from Nova Xavantina-Cachimbo road, fl., fr., 18 Mar 1968, D. Philcox & A. Ferreira 4567 (K, MO, NY, P, RB, S, UB); ca. 15 km S of Base Camp of the Expedition, Lagoa do Sucuri, close to the Nova Xavantina-São Felix road, fr., 13 Jun 1968, R.R. Santos et al. 1767 (IAN, K, NY, P, UB); 270 km N of Nova Xavantina, Lagoa do Leo, 8 km SW of Base Camp of the Expedition, fl., fr., 8 May 1968, J.A. Ritter et al. 1362 (K, NY, UB); Santa Cruz do Xingu, Parque Estadual do Xingu, limite norte do parque, fl., fr., 4 Mar 2011, D.C. Zappi et al. 3091 (K, RB, UNEMAT); Vila Bela da Santíssima Trindade, topo da Cachoeira do Jatobá, fl., fr., 17 May 2013, J.E.Q. Faria et al. 3508 (CEN, RB, SP, UB). **Pará:** Belém do Pará, Ariramba, igarapé Quebra-Dente, fl., 30 May 1957, G.A. Black et al. 57-19801 (IAN); Itaituba, arredores da base Aérea do Cachimbo, próximo ao destacamento km 6 da estrada para o Aeroporto, km 794, fr., 25 Apr 1983, M.N. Silva et al. 73 (INPA, K, RB). **Roraima:** Boa Vista, estrada do Cantá, fl., 31 Jul 1986, J.A. Silva et al. 539 (MO, NY, UB); estrada para Serra Grande, fl., 4 Aug 1986, E.L. Sette-Silva et al. 665 (K, MIRR, MO, NY); Ilha de Maracá, sandy savannah at Santa Rosa, at the E side of the island, fl., fr., 8 Oct 1987, J. Pruski et al. 3417 (INPA, K, MG, MO, NY); Caracará, estrada Perimetral Norte [BR-210], 9 km do entroncamento com as estrada Manaus/Caracará [BR-174], próximo a Novo Paraíso, fl., fr., 28 Aug 1987, C.A. Cid Ferreira et al. 9210 (INPA, NY, U). **Tocantins:** [Goyaz] between Natividade and Conceição, fl., Feb 1866, G. Gardner 4014 (BM, G, K, NY, P); Almas, RPPN Fazenda Minnehaha, campo úmido limpo bordado pelo Cerrado que desce a barra do Rio Lapa com o Rio Laurentino, fr., 21 Apr 2004, J.M. Felfili et al. 522 (RB); Barra do Ouro, margem direita do Rio Tauá, ca. 12 km de Barra do Ouro, ponte suspensa, fl., 15 Jan 2010, G. Pereira-Silva et al. 14926 (CEN); Centenário, Bacia do Tocantins, Sub-bacia do Rio Manuel Alves Pequeno, fl., fr., 27 Mar 2010, M.L. Fonseca et al. 6494 (IBGE, RB); Goiatins, Área Indígena Krahô, Aldeia Nova, fr., 8 Mar 2000, E. Rodrigues 695 (PMSP); estrada Aldeia Indígena Krahô Santa Cruz/Itacajá, km 10, margem direita do Riozinho, próximo a Kapey, fr., 27 Apr 2009, G. Pereira-Silva et al. 14314 (CEN); estrada Goiatins/Itacajá, margem esquerda do Ribeirão Cartucho, fr., 4 May 2009, G. Pereira-Silva et al. 14391 (CEN); Reserva Indígena Krahô, Aldeia Pedra Branca, fl., fr., 6 May 2000, A.A. Santos et al. 659 (CEN); Guaraí, margem esquerda da Ferrovia Norte Sul, estrada vicinal Guaraí/Itupiratins, fl., fr., 24 Apr 2009, G. Pereira-Silva et al. 14217 (CEN); Gurupi, rodovia Belém/Brasília, 5 km S de Gurupi, fl., fr., 24 Mar 1976, G. Hatschbach & R. Kummrow 38313 (MBM, MO, NY); Itupiratins, Bacia do Tocantins, Sub-bacia do Rio Tocantins, fl., fr., 24 Mar 2010, F.C.A. Oliveira et al. 1834 (IBGE, RB); Kraolandia, próximo a cidade de Peritoró, fl., 20 Mar 1974, J.S. Assis 26 (RB); Lagoa da Confusão, Bacia do Araguaia, Sub-bacia Rio Formoso, fr., 22 Mar 2010, F.C.A. Oliveira et al. 1666 (IBGE, RB); Mateiros, fr., 3 May 2001, R. Farias et al. 363 (CEN, UB); entorno do Parque Estadual do Jalapão, estrada Mateiros/Ponte Alta, ca. 2 km do Rio Novo, fr., 15 Jun 2002, T.B. Cavalcanti et al. 2831 (CEN); margem esquerda do Rio Novo, fl., fr., 8 May 2001, C.E.B. Proença et al. 2523 (UB); estrada

Mumbuca/Boa Esperança, Vereda do Bebedouro, fl., fr., 8 Mar 2006, G.H. Rua et al. 787 (CEN); Parque Estadual do Jalapão, Vereda do Porco Podre, fl., fr., 15 Feb 2005, J.M. Rezende et al. 1019 (CEN); Pindorama do Tocantins [Pindorama de Goiás], fl., fr., 21 Apr 1978, R.P. Orlandi 78 (RB). **BOLIVIA. Santa Cruz:** Velasco, Parque Nacional Noel Kempff Mercado, Campamento Huanchaca II, fl., 8 Mar 1997, S. Jiménez et al. 1254 (MO, U); Campamento Las Torres, margen del Río Iténez [Guaporé], frontera con Mato Grosso, lado noreste del Serranía Huanchaca, 24 km S Flor de Oro, fr., 24 May 1991, M. Peña & R. Foster 222 (U); Lago Caimán, fl., 15 Jan 1997, T. Killeen et al. 8151 (U, USZ). **COLOMBIA. Guainía:** Casuarito, immediately S of Casuarito, lasjas along the Río Orinoco, fl., 22 Jun 1984, G. Davidse & J.S. Miller 26411 (MO, U). **Guajira:** Barrancas, Río Quatiquia, fl., 16 Jul 1897, Lehmann 8841a (K); llanos on Río Meta and Río Quatiquia, fl., fr., 16 Jul 1897, Lehmann 8841b (K). **GUYANA. Rupununi:** Manari, fl., 24 Jul 1995, M.J. Jansen-Jacobs et al. 4621 (K, P, U). **VENEZUELA. Amazonas:** Atures, alrededores de Puerto Ayacucho, ca. 4 km SE, sabana de los alrededores del vivero de MARNR, alto Caño Carinagua, fl., 17 Jun 1977, O. Huber 841 (MO, U, VEN); Carretera Coromoto, along Río Coromoto, Tobogán de la Selva, 35 km SE of Puerto Ayacucho, fl., 14 May 1980, J.A. Steyermark et al. 122561 (F, U, VEN); Oripopos, 7 km N of Puerto Ayacucho on the road to El Burro, fl., 22 Jun 1984, J.S. Miller 1608 (MO, U); San Juan de Manapiare, sobanas sobre los cerros de arenisca al Norte del Cerro Movocoy, arriba del sitio llanado “Pazo de la Carlina” a unos 12 km al Oeste de San Juan de Manapiare, fl., fr., 16 Oct 1977, O. Huber 1205 (MO, U).

Etymology. The epithet means “shy” and makes reference to the cleistogamous flowers, which open only a few millimetres. This is the first record of cleistogamy in Neotropical Haemodoraceae, which was previously recorded only for the Paletropical genus *Haemodorum*.

Distribution and habitat. *Schiekia timida* is currently known for Bolivia, Brazil (States of Amazonas, Pará, Roraima, Tocantins, Maranhão, Goiás, and Mato Grosso), Colombia, Guyana, and Venezuela (Fig. 21). Found growing in seasonally-flooded grasslands.

Phenology. It was found in flower and fruit from November to June, rarely during July and August, but peaking during the rainy season.

Conservation status. *Schiekia timida* possesses wide EOO (5,598,459 km²) and AOO (ca. 580 km²). Thus, following IUCN’s (2001) recommendations, *S. timida* should be considered as Least Concern (LC).

Vernacular name and use. According to specimen labels, *S. timida* is called “ahtu” in the language spoken by the native Brazilian Krahô tribe. It seems to be used in some religious ceremonies, mixed in a drink with some confirmed psychoactive plants.

Comments. *Schiekia timida* is morphologically similar to *S. orinocensis* due to its rhizome morphology, leaf arrangement and consistency, inflorescence architecture, floral orientation, and inflated medial filament. Nonetheless, it differs due to its conspicuously veined leaves, narrowly tubular and cleistogamous flowers, pedicels not apically gibbous, tepals with apex straight and light to medium green, upper tepals lacking nectar guides, staminode-like projections filiform and 1/3 the length of its subtending

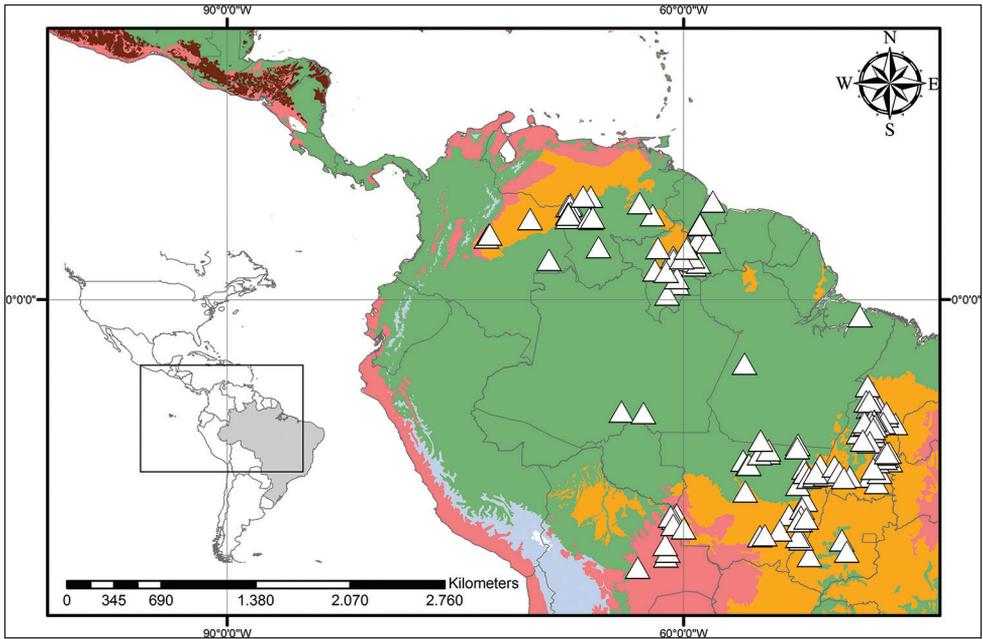


Figure 21. Distribution of *Schiekia timida* M.Pell. et al. Light Green— Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

tepals and capsules slightly longer than broad or as broad as long. Until the present work, both species were treated under a broad concept of *S. orinocensis* subsp. *orinocensis*, as proposed by Maas and Maas-van de Kamer (1993). However, as noticed during fieldwork, *S. timida* seems to be a cleistogamous species, with flowers never opening more than a few millimetres.

5. *Xiphidium* Loeffl., *Iter Hispan.*: 179. 1758.

Figs 22–24, 26

Tonduzia Boeckeler ex Tonduz, Bull. Herb. Boissier 3: 464. 1895, nom. nud.

Durandia Boeckeler, Allg. Bot. Z. Syst. 2: 160, 173. 1896, Syn. nov. Type species.

Durandia macrophylla Boeckeler (= *Xiphidium caeruleum* Aubl.).

Type species. *Xiphidium caeruleum* Aubl.

Nomenclatural history. It has been widely accepted that the original place of publication of the generic name *Xiphidium* is “Histoire des Plantes de la Guiane Française” by Aublet (1775). Nonetheless, Aublet never clearly states to be proposing a new genus. This seems to follow his publication’s formatting, where none of the new taxa present

any explicit statement indicating that they are newly proposed. At the end of the Latin diagnosis and French comments, Aublet (1775: 35) mentions that his new species differs from the one described by Loeffling (1758) due to its “fine stems and leaves furnished with hairs, blue flowers, and oval and acute petals”. This statement makes it clear that Aublet had access to Loeffling’s publication (1758) and knew of the description of his new genus *Xiphidium*. Finally, Dorr and Wiersema (2010) give the final support to our interpretation when they explain that in several instances, Loeffling (1758) cited a genus published earlier by Linnaeus or P. Browne, followed by a full stop, (an) alternative generic name(s) and a description. The authors also point out that, on some occasions, this formatting has been misinterpreted as the proposal of species’ names (i.e., binary combinations), which they are not. That was the case of *Xiphidium* Loefl., which was misinterpreted as representing a new species, *Ixia xiphidium* Loefl. (e.g., Maas and Maas-van de Kamer 1993), instead of the publication of a new genus. Thus, the genus *Xiphidium* was originally described by Loeffling (1758), without the inclusion of any species. The proposal of *Xiphidium* by Loeffling (1758) is based on the author not agreeing on the inclusion of all elements/species by Linnaeus in his *Ixia* L.

The first species name to be validly published in *Xiphidium* was only proposed almost 20 years later, by Aublet (1775), as *X. caeruleum* Aubl. The publication of the generic name *Xiphidium* by Loeffling (1758) makes it clear that the author recognised a sole species for that genus. The practice of not providing a specific epithet when describing monospecific new genera was common practice at the time. A similar situation, with the description of the type genus of Haemodoraceae – *Haemodorum* (Smith 1798) –, supports this interpretation. When first described, *Haemodorum* was considered monospecific and, therefore, was not given a specific epithet, according to the standard practice of J.E. Smith (1798). Only seven years later, another author (Vahl 1805) provided an epithet for Smith’s plant, as *H. corymbosum* Vahl. Thus, as the first species formally published and associated with *Xiphidium*, *X. caeruleum* automatically typifies this generic name.

Comments. *Xiphidium* has traditionally been considered an ill-circumscribed genus, lacking any obvious synapomorphy (Simpson 1990, 1993, 1998b). However, with the transfer of *X. xanthorrhizon* to *Cubanicula*, *Xiphidium* s.str. can be easily defined by its introrsely rimose, but functionally poricidal anthers (an adaptation to buzz-pollination; Buchmann 1980), the complete loss of septal nectaries (also an adaptation to buzz-pollination), capsules bright-coloured, indehiscent, lacking thickened septal ridges and somewhat fleshy at maturity (a possible adaptation to endozoochory) and cuboid seeds (Hickman 2019; Pellegrini 2019). All these characters are unique in the family and observed on the two species of *Xiphidium* accepted by us in the present study. The anther morphology of *Xiphidium* and its floral biology are reminiscent of some species of *Dichorisandra* J.C. Mikan (Commelinaceae, Commelinales) that also possess introrsely rimose but functionally poricidal anthers (Pellegrini and Faden 2017). However, studies on the reproductive biology of *Xiphidium* are non-existent, save that by Buchmann (1980). Further studies focusing on effective pollination and seed dispersal are necessary. The genus is well-documented as medicine for snakebite (Odonne et al. 2013) and has antimalarial and leishmanicidal properties (Valadeau et

al. 2009). *Xiphidium caeruleum* also shows the most significant genetic divergence levels for any species of Haemodoraceae amongst populations across its wide Neotropical range (Hopper et al., in prep.). A further detailed taxonomic study is recommended, combining extensive fieldwork, molecular data, and traditional taxonomy.

5.1. *Xiphidium caeruleum* Aubl., Hist. Pl. Guiane 1: 33, pl. 11. 1775.

Figs 22–24

Xiphidium floribundum var. *caeruleum* (Aubl.) Hook., Bot. Mag. 84: t. 5055. 1858.

Lectotype (designated by Maas and Maas-van de Kamer 1993). [Illustration]

Original parchment plate of Histoire des Plantes de la Guiane Française and later published in Aublet, Hist. Pl. Guiane 1: 33, pl. 11. 1775.

Xiphidium floribundum Sw., Prodr.: 17. 1788.

Xiphidium albidum Lam., in Lamarck & Poirer Tabl. Encycl. 1: 131. 1791, nom. superfl.

Xiphidium album Willd., Sp. Pl. Editio quarta 1(1): 248. 1798.

Xiphidium floribundum var. *albiflorum* Hook., Bot. Mag. 84: t. 5055. 1858, nom. superfl. (≡ *X. floribundum* Sw. var. *floribundum*).

Xiphidium caeruleum var. *albidum* (Lam.) Backer, Handb. Fl. Java 3: 80. 1924.

Xiphidium loeflingii Mutis, Diario 2: 51. 1958, nom. nud.

Ecchremis scabra Kuntze, Revis. Gen. Pl. 3(3): 316. 1898. Holotype. destroyed (B†).

Lectotype (designated here). BOLIVIA. Cochabamba: Chapare, Río Juntas, fr., 13–21 Apr 1892, C.E.O. Kuntze 461 (NY barcode 00841967!), Syn. nov.

Xiphidium giganteum Lindl., Edwards's Bot. Reg. 32: page prior to t. 67. 1846. Type. (K?, not found).

Xiphidium fockeanum Miq., Linnaea 17: 63. 1843. Lectotype (designated by Maas and Maas-van de Kamer 1993). SURINAM. prope Paramaribo, fl., April 1654, H.C. Focke 293 (U barcode U0002449!; isolectotype: P barcodes P00753474!, P02188828!).

Xiphidium rubrum D. Don, Edinburgh New Philos. J. 13: 235. 1832. Lectotype (designated here). PERU. s.loc., fl., s.dat., J.A. Pavón 358 (BM barcode BM000923989!; isolectotype: MA barcode MA810534!).

Ornithogalum rubrum Ruiz & Pavón ex D. Don, Edinburgh New Philos. J. 13: 235. 1832, nom. not validly published, pro. syn.

Durandia macrophylla Boeckeler, Allg. Bot. Z. Syst. 2: 173. 1896. Holotype. COSTA RICA. s.loc., fl., Nov 1893, A. Tonduz 8402 (B barcode BR0000006885779!), Syn. nov.

Tonduzia macrophylla Boeckeler ex Tonduz, Bull. Herb. Boissier 3: 464. 1895, nom. nud.

Nomenclatural notes. The taxonomic circumscription of *X. caeruleum* is greatly impaired by the lack of knowledge of the current whereabouts of the type material of several of its associated synonyms. Types for the names *X. caeruleum* and *X. fockeanum* were successfully located and designated by Maas and Maas-van de

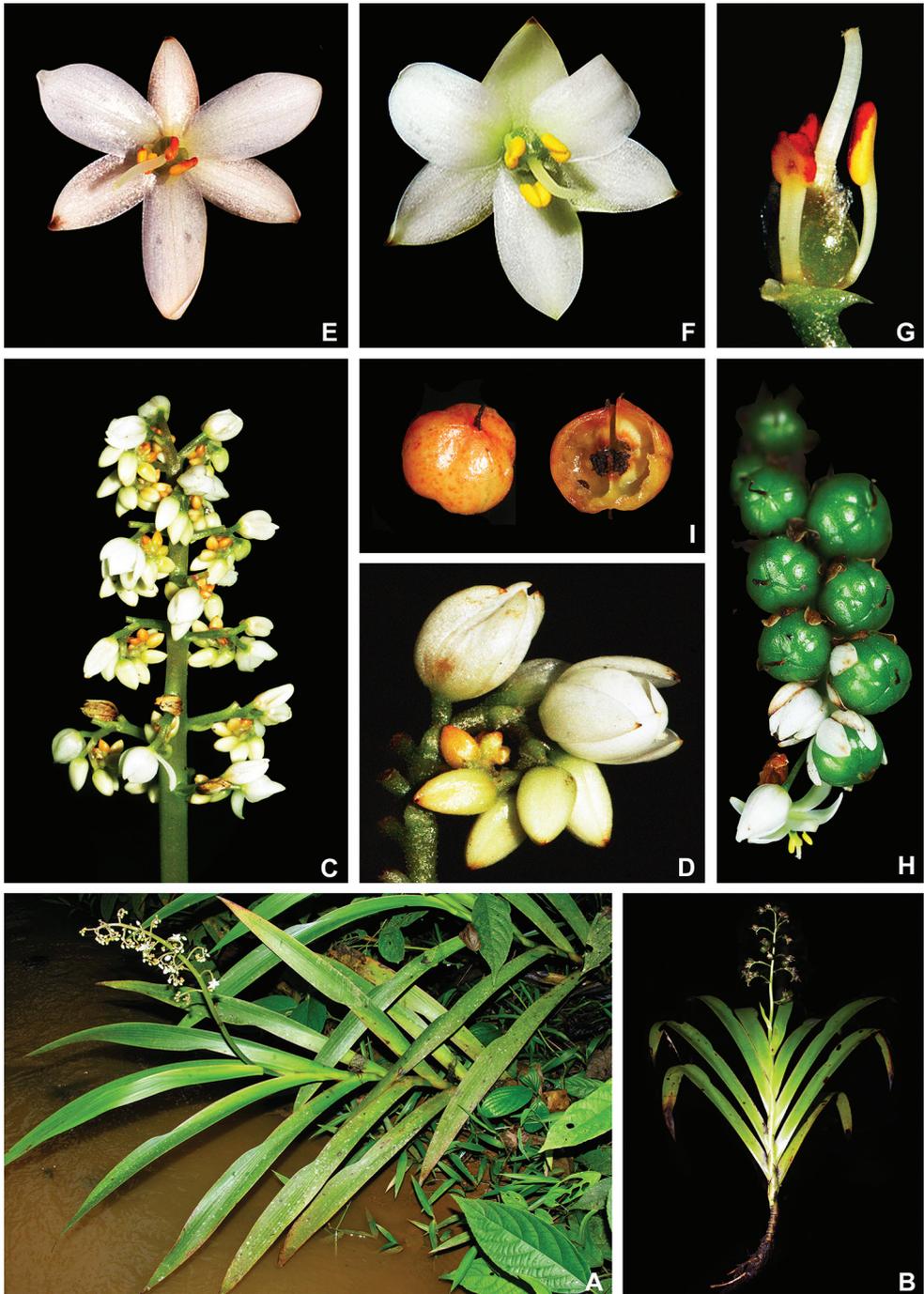


Figure 22. *Xiphidium caeruleum* Aubl. **A** specimen growing in a flooded forest **B** habit **C** inflorescence **D** cincinnus **E, F** flower: **E** flower with subequal, narrow, and pale apricot perianth lobes **F** flower with equal, broad, and white perianth lobes **G** flower with perianth removed showing androecium and gynoecium with ovary pubescent long the septal ridges **H** cincinnus with immature berries **I** mature berries. **A, F** by R. Aguilar, **B** by H. Medeiros, **C–D, G, I** by M.O.O. Pellegrini, **E** by A. Yakovlev, and **H** by R. Cumming.

Kamer (1993), while types for the names *X. rubrum*, *Eccremis scabra*, and *Durandia macrophylla* were located by us and had lectotypes designated when necessary. Nonetheless, we have been unable to locate a type specimen, or illustration for *X. giganteum*, which prevents us from knowing if this name matches any of the *X. caeruleum* morphs recognised by us.

Maas and Maas-van de Kamer (1993) erroneously designated plate 66 from Lindley (1846) as the lectotype of *X. giganteum*. The indicated plate actually depicts *Swainsona greyana* Lindl. (Fabaceae) and obviously cannot be the type for *X. giganteum*. In fact, the original publication (Lindley 1846) provides no illustration for *X. giganteum*. Lindley (1846) mentions that a live specimen was brought from Caraccas and flowered in Syon [Park], London, UK. After searching for specimens that matched these data at K herbarium, we were unable to locate any. We have also searched for a possible unpublished illustration that might serve as the type for *X. giganteum*, but were also unsuccessful. Thus, we are currently unable to designate a lectotype for *X. giganteum*, since this name completely lacks any original material (Art. 9.4., Turland et al. 2018). Since the original description is not enough to undoubtedly apply this name, we also feel it is premature to designate a neotype until natural populations from Caraccas have been studied. Finally, we also choose to tentatively retain it under the synonymy of *X. caeruleum* until further information becomes available.

As explained by Dorr and Wiersema (2010), *Ixia xiphidium* Loeffl. represents a misinterpretation by Maas and Maas-van de Kamer (1993) of Loeffling's (1758) publication. The author never intended to publish a new species but published a new genus, rejecting the application of *Ixia* L. for American plants. Thus, *Ixia xiphidium* Loeffl. was never published and should not be included in databases.

When describing *X. rubrum*, Don (1832) mentions his new species is based on a Ruiz & Pavón collection, but without indicating a collection number or herbarium information. We came across a specimen matching the protologue with a label in Pavón's handwriting during a visit to BM, saying, "*Ornithogalum rubrum* sp. n., Fl. Per.". This specimen is here selected as the lectotype.

Kuntze (1898) described *Eccremis scabra*, based on a collection from Río Juntas, Bolivia. The author mentions a specimen at B, but we were unable to locate it, and it might have been lost during WWII. Luckily, we were able to locate a duplicate at NY, which is designated here as the lectotype.

Distribution and habitat. *Xiphidium caeruleum* is widely distributed in the Neotropics, ranging from Mexico, reaching the Antilles, to northern South America (Fig. 25). It can be found growing in permanently or seasonally-wet environments, more rarely in dry and rocky environments.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. As currently circumscribed, *Xiphidium caeruleum* is widely distributed, with equally wide EOO (14,922,959 km²) and AOO (ca. 3,056 km²). Thus, following IUCN's (2001) recommendations, *X. caeruleum* should be considered as Least Concern (LC).

Comments. *Xiphidium caeruleum* is a widely-distributed species and still a variable taxon even in our present circumscription. Despite our best efforts, we have been

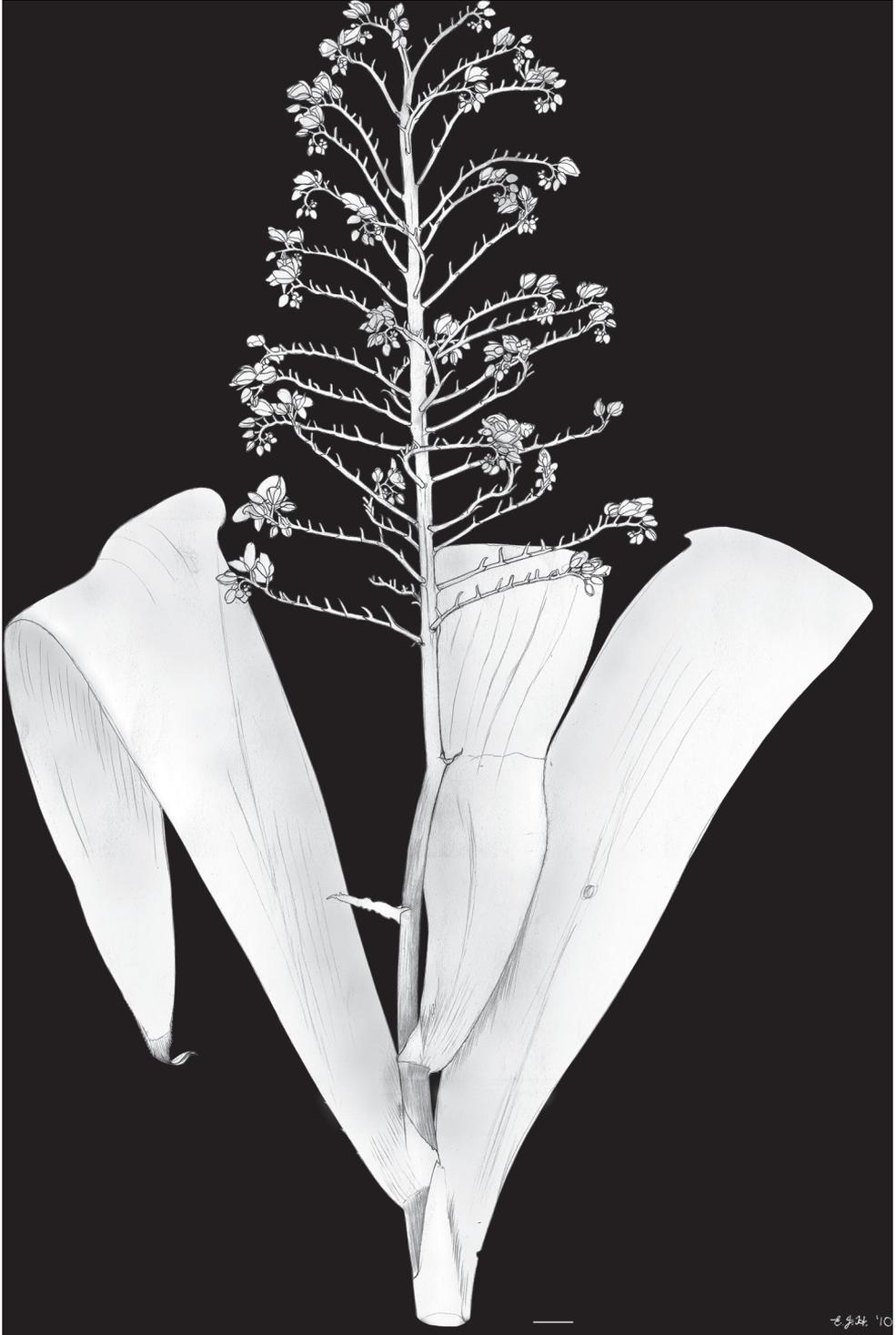


Figure 23. *Xiphidium caeruleum* Aubl. Line drawing of the inflorescence. Illustration by E.J. Hickman. Scale bar: 1 cm.



Figure 24. *Xiphidium caeruleum* Aubl. **A** roots in cross-section **B–D** rhizome: **B** naked rhizome **C** longitudinal section **D** lateral branch **E** cincinnus **F** flower bud **G** hairs **H, I** flower: **H** frontal view **I** side view **J** flower with the perianth removed, showing the androecium and gynoecium **K** lateral stamen (frontal and dorsal view) **L** stigma **M–P** fruit: **M** immature berry **N** berry in cross-section **O** berry in longitudinal section **P** indehiscent and old berry **Q–T** seed: **Q** dorsal view **R** lateral view **S** ventral view **T** longitudinal section. Illustration by E.J. Hickman. Scale bars: 0.8 mm (**A**); 1.5 cm (**B–D**); 0.75 mm (**E**); 2 mm (**F, H, I, M–P**); 0.4 mm (**G**); 1.75 mm (**J**); 1 mm (**K**); 0.5 mm (**L, Q–T**).

unable to correlate any of the observed morphological variability to any of the previously proposed names in *Xiphidium*. After careful study of protologues, we concluded that *X. loeflingii* Mutis, *X. caeruleum* var. *albidum* (Lam.) Backer, *X. floribundum* var.

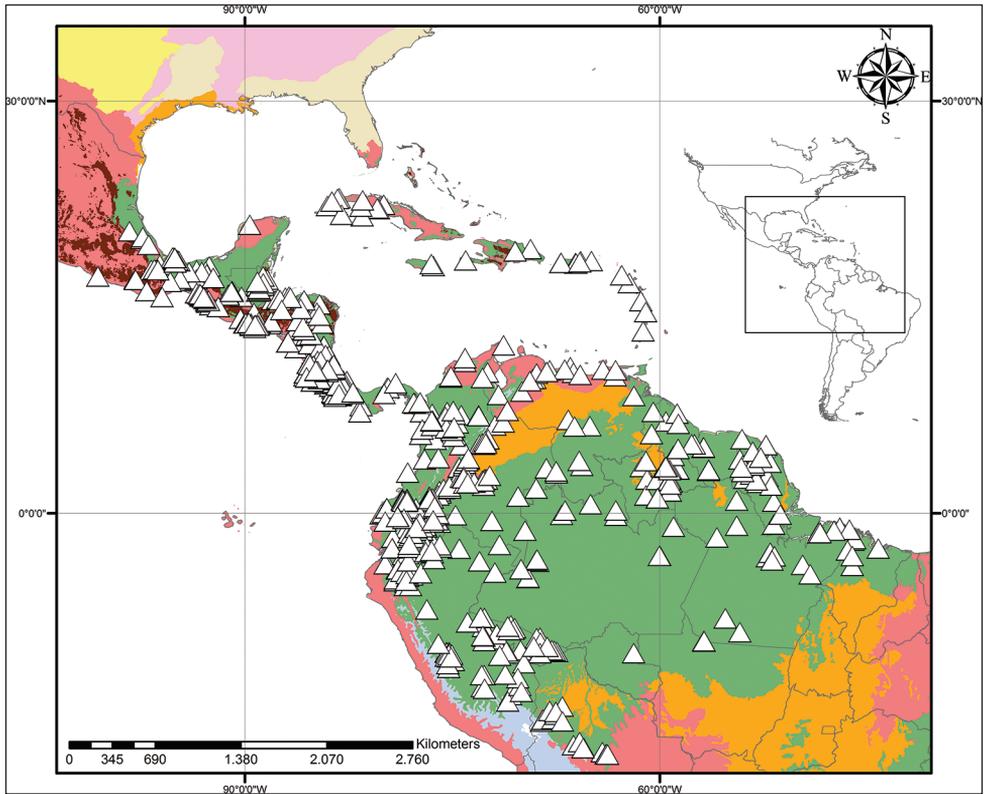


Figure 25. Distribution of *Xiphidium caeruleum* Aubl. Beige – Temperate Coniferous Forests and Boreal Forests; Yellow – Temperate Grasslands, Savannahs and Shrublands; Pink – Temperate Broadleaf and Mixed Forests; Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

albiflorum Hook., *X. album* Willd., *X. albidum* Lam. and *X. floribundum* Sw. actually represent homotypic synonyms and are unambiguously conspecific with the type of *X. caeruleum*. Alternatively, *Durandia macrophylla* Boeckeler, *Eccremis scabra* Kuntze, *X. fockeanum* Miq. and *X. rubrum* D. Don represent heterotypic synonyms. *Xiphidium giganteum* Lindl. is tentatively kept here as a heterotypic synonym of *X. caeruleum* until further information on its type specimen is acquired.

All diagnostic characters provided by the original authors in their respective prologues can be easily observed in the typical morph of *X. caeruleum*. Some peculiar specimens of *X. caeruleum* are recorded for French Guiana (in which the specimens seem to present peculiarly large, red, crustose, and trigonous fruits), Costa Rica (where some specimens possess flowers with three inconspicuous green nectar guides at the base of the upper tepals) and Mexico (where specimens present inner tepals much longer than the outer tepals and perianth generally with apricot to pinkish hue). Furthermore, it is also known for berries of *X. caeruleum* to range from yellowish-orange to

orange with reddish-orange spots, to completely red. We were unable to find any obvious correlation between the different colours of berries, geographical distribution, and the observed genetic diversity. Nonetheless, due to limited access to such morphs and also due to herbarium specimens in *Xiphidium* being generally poorly preserved, we consider it premature to recognise or propose any taxonomic status for these morphs. Thus, we propose that studies focusing on population genetics and reproductive biology, associated with a morphometric study and intense field studies, are necessary to properly deal with the issue.

5.2. *Xiphidium pontederiiflorum* M. Pell., Hopper & Rhian J. Sm., sp. nov.

urn:lsid:ipni.org:names:77213185-1

Fig. 26

Diagnosis. Similar to *Xiphidium caeruleum* Aubl. in habit and inflorescence morphology, differing due to its leaves marginally ciliate at apex, apricot to light orange flower buds, larger and zygomorphic flowers, inner lobes obovate with obtuse to round apex, upper tepals connate in the basal third or halfway through with three orange-yellow to orange nectar guides, dark red to vinaceous mature capsules and dark reddish-brown to reddish-black seeds.

Type. ECUADOR. Esmeraldas: Lita, Río Lita and tributaries, 120 km NW of Ibarra, 14 km of Lita, fl., fr., 7 May 1987, D.C. Daly & P. Acevedo-Rodríguez 5142 (US!; isotype: NY!).

Description. *Herbs* ca. 35–185 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal in boggy areas. *Roots* thin, fibrous, brown, sand-binding, emerging from the rhizome. *Rhizomes* underground, long, trailing, external surface brown to reddish-brown, internal surface reddish-orange to red. *Stems* ascending to erect, fibrous, unbranched; internodes 4.3–7 cm long, green, glabrous to sparsely tomentose, hairs pilate, white. *Leaves* distichously-alternate, equitant, evenly distributed along the stems, sessile, the apical ones gradually smaller than the basal ones; sheaths 0.6–2.2 cm long, light green, glabrous to sparsely tomentose, margin ciliate, hairs pilate, white; blades 18.7–47.3 × (0.9–1.6–)2.4–5 cm, fibrous, succulent, unifacial, medium green, drying olive-green to brown, linear-elliptic to narrowly elliptic, slightly ensiform to ensiform, glabrous, base sheathing, margins green, glabrous to ciliate at the apex, apex acuminate; midvein inconspicuous, secondary veins 5–8, slightly impressed to impressed, becoming more prominent when dry. *Inflorescences* terminal, solitary, consisting of a pedunculate many-branched thyrse; peduncles (1.5–)2.4–7.8 cm, sparsely tomentose to densely tomentose, hairs pilate, white; basal bract 5–5.7 × 0.4–0.5 cm, leaf-like, linear-elliptic, slightly ensiform to ensiform, glabrous or sparsely tomentose at base, hairs pilate, white, base truncate to slightly sheathing, margin ciliate at apex, apex acuminate, secondary veins inconspicuous; cincinnus bract 2.8–4.4 × 1.2–4 mm, broadly triangular to narrowly triangular, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin ciliate, apex acuminate; cincinni (9–)12–41 per

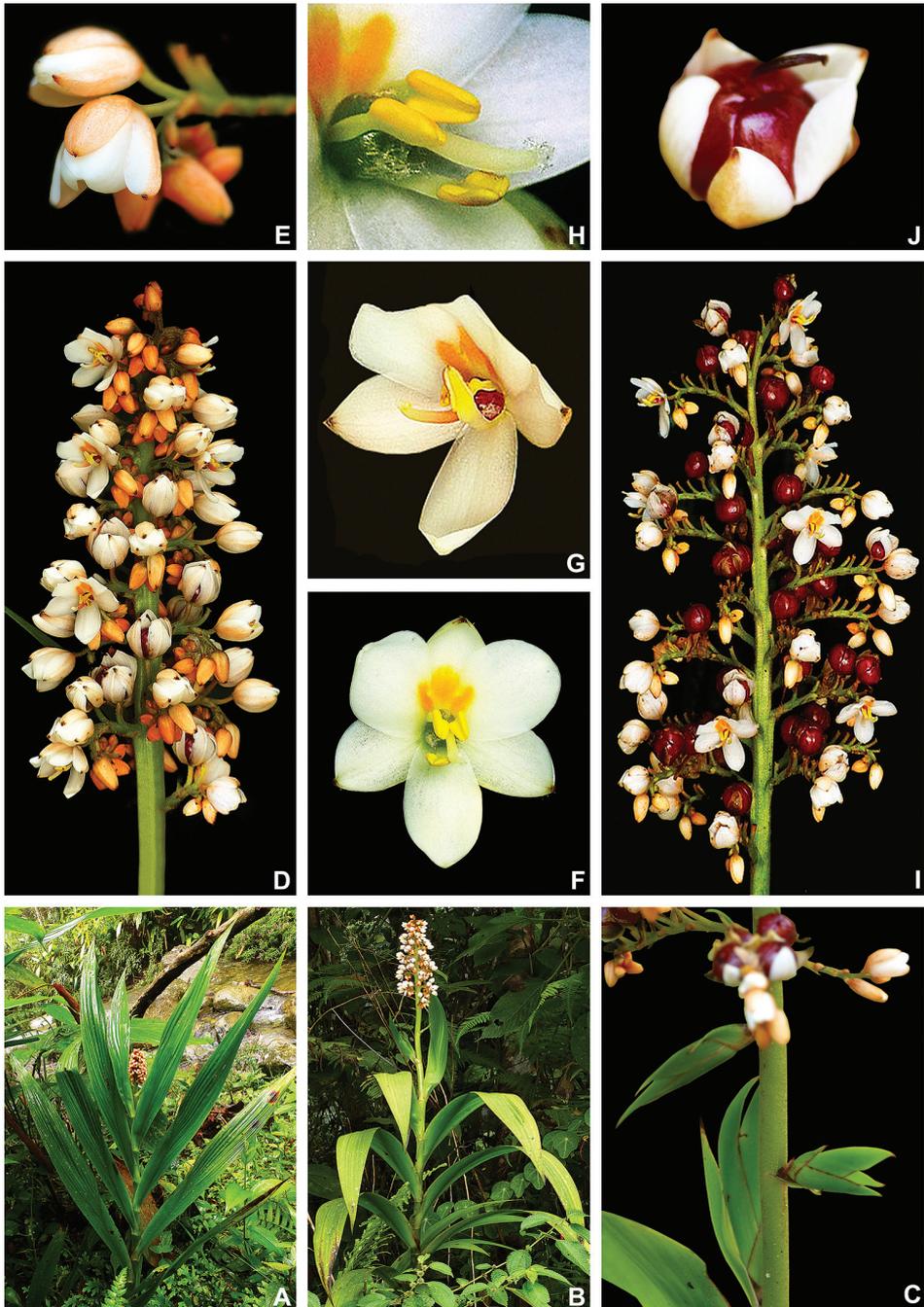


Figure 26. *Xiphidium pontederiiflorum* M. Pell. et al. **A–C** habit: **A** vegetative habit **B** flowering habit with a young inflorescence **C** viviparous inflorescence with three axillary propagules **D** inflorescence with open flowers and apricot floral buds **E** floral buds and flowers at pre-anthesis **F, G** flower: **F** white flower with green ovary **G** pale apricot flower with vinaceous ovary **H** detail of the androecium and gynoecium, showing the ovary pubescence along the septal ridges **I** inflorescence with open flowers and mature berries **J** mature berry. **C, E, J** by A.R. Jonker, remaining photos by A. Kay.

thyrses, alternate, 3–18-flowered, peduncle 0.3–1.7 cm long, green, sparsely tomentose to densely tomentose, hairs pilate, white; bracteoles 0.8–1.3 × 0.6–1 mm, broadly triangular to broadly depressed ovate, green, glabrous to sparsely tomentose, hairs pilate, white, base amplexicaulous, non-perfoliate, margin glabrous, apex acute. **Flowers** 1.9–2.7 cm diam., bisexual, chasmogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds 4.8–6 × 2.2–3 mm, ovoid, apricot to light orange; pedicels (2–)5.1–7.3 mm long, upright and slightly elongate in fruit, green, tomentose to densely tomentose, hairs pilate, white; perianth zygomorphic, lobes free, except for the upper 3 lobes which are connate on the basal third to mid-length, nectar guide orange-yellow to orange on the basal third of the connate lobes, with an apical black mucron, outer lobes 8.5–13.1 × 3.5–4.7 mm, subequal, the upper slightly shorter, narrowly obovate to obovate, external surface apricot to light orange, rarely white, glabrous to sparsely tomentose, hairs pilate, white, internal surface white, glabrous, base cuneate, margins glabrous, apex acute- to obtuse-mucronate, mucron dark brown to black, inner lobes 9.7–13.2 × 4.8–7.3 mm, subequal, the lower slightly narrower and cucullate, obovate to broadly obovate to broadly obtrullate, external surface white to apricot, rarely light orange, glabrous, internal surface white, glabrous, base cuneate, margins glabrous, apex obtuse- to round-mucronate, greenish-yellow to apricot, mucron dark brown to black; stamens 3, lateral stamens with filaments 1.6–1.8 mm long, straight, basally cream to apricot, apically white, glabrous, anthers 1.4–1.7 × 0.6–0.9 mm, dorsifixed, introrsely rimose but functionally poricidal, broadly oblongoid to sagittate, yellow, medial stamen with filament 3.7–4.3 mm long, bent upwards, basally cream to apricot, apically white, glabrous, anthers 2–2.4 × 0.7–1.1 mm, dorsifixed, introrsely rimose but functionally poricidal, broadly oblongoid to sagittate, yellow; ovary 1.8–2.2 × 1.7–2 mm, broadly ellipsoid to globose, 3-loculate, green to red to vinaceous, smooth, densely tomentose between the locules, style 5.6–8.3 mm, bent upwards, basally cream to apricot to light orange, apically white, glabrous, stigma crateriform, white, papillose. **Capsules** 5.2–7.4 × 5.8–8 mm, subglobose to globose, somewhat fleshy, medium green to dark red when immature, dark red to vinaceous when mature, glabrous, indehiscent. **Seeds** 0.78–0.84 × 0.65–0.67 mm, cuboid to polygonal, each face sunken, testa dark reddish-brown to reddish-black, tuberculate; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen (paratypes). **COLOMBIA.** **Antioquia:** Frontino, km 23 of road Nutibara/La Blanquita, region of Murri, fl., fr., 4 Nov 1988, J.L. Zarucchi et al. 7140 (MO, US). **Guarira:** Sierra Nevada de Santa Marta, entre Riohacha y Pueblo Viejo, fr., 7 Feb 1959, H.G. Barclay & P. Juajibioy 6838 (US). **Putamayo:** road from Sibundoy to Mocoa, fl., fr., 15 Mar 1953, R.E. Schultes & I. Cabrera 18823 (GH, U, US); Intendencia of Putamayo, steep roadside slopes along road from Mocoa towards Sibundoy, fl., fr., 27 Jan 1976, J.L. Luteyn et al. 5062 (F, NY, US). **Valle del Cauca:** km 100, on Cali/Buena-Ventura highway, fl., fr., 5 Dec 1946, O. Haught 5324 (US). **Vaupés:** Puerto Hevea, confluence of Macaya and Ajaju rivers, fl., Jul 1943, R.E. Schultes 5654 (GH, US). **ECUADOR.** **El Oro:** 11 km West of Pinas, on the new road to Santa Rosa, fl., fr., 8 Oct 1979, C.H. Dodson et al. 9012 (SEL, US); Pichincha: virgin forest along Río Toachi near Santo Domingo, fr., 3 Aug 1962, C. Jativa & C. Epling 322 (US).

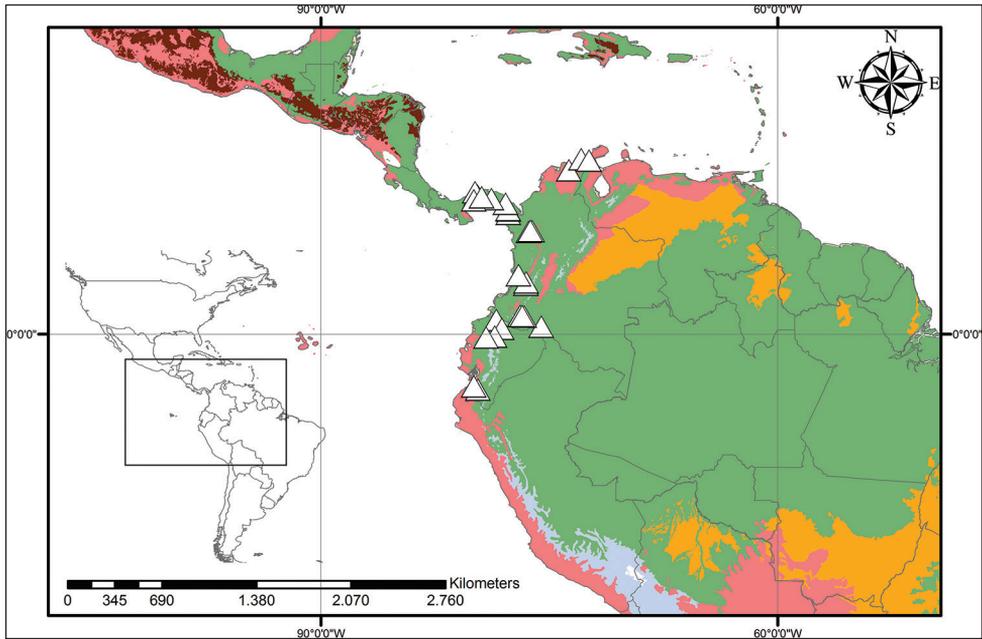


Figure 27. Distribution of *Xiphidium pontederiiflorum* M. Pell. et al. Light Green – Subtropical Coniferous Forests; Red – Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange – Tropical/Subtropical Grasslands, Savannahs and Shrublands; Maroon – Dry Broadleaf Forests; Green – Moist Broadleaf Forests; Lilac – Montane Grasslands and Shrublands.

PANAMA. Colón: Canal Zone, Las Cascadas Plantation, near Summit, fr., 2 Dec 1923, P.C. Standley 25671 (US); hills north of Frijoles Station, fr., 19 Dec 1923, P.C. Standley 27414 (US); Gamboa, fr., 26 Dec 1923, P.C. Standley 28397 (US); near Fort Randolph, fr., 28 Dec 1923, P.C. Standley 28734 (US). **Darien:** Cerro Pirre, fr., 9–10 Aug 1967, J.A. Duke & T.S. Elias 13747 (GH, US); Río Chico, from Yaviza at junction with Río Chucunaque to ca. 1 hour by outboard from junction, fr., 19 Dec 1966, D. Burch et al. 1096 (GH, K, NY, UC, US). **Panamá:** Río La Maestra, fr., 4 Dec 1936, P.H. Allen 67 (MO, US). **Panamá Oeste:** Capira, about 50 km southwest of Panama City, fl., fr., Sep 1932, B. Paul 141 (US).

Etymology. The epithet refers to the similarity between our new species' floral morphology and some species of *Pontederia* s.lat. (Pellegrini et al. 2018).

Distribution and habitat. *Xiphidium pontederiiflorum* is known to occur in Colombia, Ecuador, and Panama (Fig. 27), in the understory in rainforests, generally near rivers, along streams, and other water bodies.

Phenology. Blooms and fruits from March to August.

Conservation status. *Xiphidium pontederiiflorum* possesses a relatively narrow EOO (849,856 km²) and AOO (ca. 132 km²). Thus, following IUCN's (2001) recommendations, *X. pontederiiflorum* should be considered as Endangered [EN, A2ac+C2a(i)].

Comments. *Xiphidium pontederiiflorum* is morphologically similar to *X. caeruleum* in overall habit and inflorescence morphology. However, *X. pontederiiflorum* can be differentiated by its leaves marginally ciliate at apex (vs. glabrous in *X. caeruleum*), apricot to light orange flower buds (vs. white to cream, rarely apricot in Mexican populations), larger and zygomorphic flowers (vs. smaller and actinomorphic flowers), inner lobes obovate with obtuse to round apex (vs. elliptic with acute apex), upper tepals connate in the basal third or halfway through with three orange-yellow to orange nectar guides (vs. only basally connate and lacking nectar guides, rarely with green nectar guides in some Costa Rican populations), capsules dark red to vinaceous when mature (vs. orange to medium red) and dark reddish-brown to reddish-black seeds (vs. black). Added to that, *X. pontederiiflorum* is generally a more robust plant, growing erect up to 2 m tall, while *X. caeruleum* reaches up to 1 m tall, and its stems tend to lean due to the plant's weight, especially when in bloom or fruit.

Xiphidium pontederiiflorum was first collected in 1923 in Panama by the pioneering Neotropical botanist P.C. Standley (1884–1963) from the United States (Williams 1963). Reference to it was included under *X. caeruleum* in Standley's (1928) *Flora of the Panama Canal Zone*.

Conclusion

The Neotropical species of Haemodoraceae represent morphological outliers in the family that have remained poorly studied for far too long, despite previous comprehensive studies dealing with macro- and micromorphology and the systematics of the Haemodoraceae (Simpson 1985, 1987, 1990, 1993, 1998a, 1998b; Hopper et al. 2006, 2009; Smith et al. 2011; Aerne-Hains and Simpson 2017). Furthermore, most of its species dwell deep in the Amazon Forest, and key and enigmatic taxa, like *Pyrrorhiza neblinae*, are restricted to almost impossible to reach tepuis. This paper is the result of the author's combined efforts, as part of a global collaboration, hoping that these new data will update our current knowledge on Haemodoraceae and encourage further studies on the family, as well as in Commelinales.

All Neotropical Haemodoraceae are placed in subfamily Haemodoroideae and, except for *Lachnanthes*, are also placed in a well-supported clade by both molecular (Hopper et al. 1999, 2009, in prep.) and morphological data (Simpson 1990; Pellegrini 2019). Ongoing studies seem to indicate the need to revisit the family's classification and formally recognise this clade, as well as others (Hopper et al., in prep.; Pellegrini 2019). A similar scenario is observed for the other families of Commelinales, where several systematic-based classification updates are still needed for several groups (Pellegrini 2019). Pontederiaceae is currently the most systematically up-to-date family in the order, thanks to recent contributions (Pellegrini 2017; Pellegrini and Horn 2017; Pellegrini et al. 2018). Nonetheless, the remaining four families (i.e., Commelinaceae, Haemodoraceae, Hanguanaceae, and Philydraceae) are still in need of much updating.

Finally, the present study takes the first vital step towards standardising the morphological terminology used in Haemodoraceae. As part of the first authors' systematics studies in Commelinales (Pellegrini 2019), it became clear that much of the difficulty in finding morphological synapomorphies for the order, as well as its backbone and families, is related to the disparate terminology used in each of the five families. Thus, it is crucial for the descriptive terminology used for Commelinales to be standardised to enable the inclusion of morphology in phylogenetic studies. This standardisation also dramatically decreases the degree of homoplasy in the morphological dataset and increases its congruence with the molecular data (Pellegrini 2019). A publication focusing on the standardisation of the morphological terminology for Commelinales is in the works and should be published in the near future.

Acknowledgements

The authors would like to thank Reinaldo Aguilar, Guilherme Antar, John Bradford, Charles Brewer-Carias, Cristian Castro, Russell Cumming, Gerrit Davidse, Vinícius A. O. Dittrich, Jim Fowler, Hervé Galliffet, Anneke R. Jonker, Andreas Kay (*in memoriam*), Ulrich Lorimer, Suzana E. Martins, Bruce Means, Herison Medeiros, Bob Peterson, Sébastien Sant, Anna Weitzman, Pedro L. Viana, Alexey Yakovlev and Scott Zona for the field images of Neotropical Haemodoraceae; Mathias E. Engels for all his support with field collections, spirits samples and photographs of Haemodoraceae from Central-Western Brazil; Angela Leiva Sanchez, Rosa Rankin and Cristina Panflet of Jardín Botánico Nacional de Cuba and Johannes Bisse Herbario and Katiuska Izquierdo Medero, Pedro & Felicita Morejori, Lazaro Hernandez and Armando Pimentel Chirinos for assistance in Cuba; Mike Hopkins at Instituto Nacional de Pesquisas da Amazônia (INPA) for assistance in Brazil; and Sandy, Duane and Justin De Freitas, Danielle Wilson, Trevor Chan, Claudius Perry, Wayne Jones and Leon Baird at Dadanawa Ranch and Ben ter Welle for assistance in Guyana. We would also like to thank the Botanic Garden and Botanical Museum Berlin-Dahlem, Fairchild Tropical Botanic Garden, the Field Museum, Georg-August-Universität Göttingen, Marburg Botanical Garden, Montreal Botanical Garden, National Herbarium of New South Wales, the Royal Botanic Garden Sydney and David Orr, Waimea Valley for samples and information on *Xiphidium*. G.B Edwards kindly identified the jumping spider on *Cubanicula*. We would also like to thank Rafael Felipe de Almeida for suggestions on an early version of the manuscript; Jefferson Prado at Instituto de Botânica for suggestions on the manuscript and nomenclatural assistance; and Michael G. Simpson at San Diego State University for information on *Xiphidium*, for putting MOOP in contact with SDH and making this study possible and for general assistance in our Haemodoraceae and MOOP's Commelinales research. Finally, we are very grateful to Michael G. Simpson and Terry D. Macfarlane for valuable comments and contributions during the review process. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001, through the PhD fellowship granted to MOOP, besides Fundação Flora

de Apoio à Botânica and Smithsonian Institution for his REFLORA grant. This study was carried out as part of the first author's PhD degree in Botany at Programa de Pós-Graduação em Botânica, Instituto de Biociências, Universidade de São Paulo – USP. EJH was supported by a University of Western Australia Research Grant and a Winston Churchill Fellowship to undertake fieldwork in North and South America. Part of the work was undertaken while EJH was studying for a PhD, supported by an Australian Postgraduate Award with a University of Western Australia Top-Up Award. SDH was supported by the Royal Botanic Gardens, Kew, an Australian Research Council Discovery Outstanding Researcher Award under Discovery Project DP140103357, and grants from the Great Southern Development Commission and Jack Family Trust in Albany.

References

- Aerne-Hains L, Simpson MG (2017) Vegetative anatomy of the Haemodoraceae and its phylogenetic significance. *International Journal of Plant Sciences* 178(2): 117–156. <https://doi.org/10.1086/689199>
- APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181(1): 1–20. <https://doi.org/10.1111/boj.12385>
- Aublet JBCF (1775) *Histoire des Plantes de la Guiane Française* (Vol. 1). Pierre-François Didot, London & Paris, 621pp.
- Bachman S, Moat J, Hill AW, Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: Smith V, Penev L (Eds) *e-Infrastructures for data publishing in biodiversity science*. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Borhidi A (1991) *Phytogeography and Vegetation Ecology of Cuba*. AkadCmi Kiado Publishing House, The Hungarian Academy of Sciences.
- Boughton EH, Boughton RK, Griffith C, Bernath-Plaisted J (2016) Reproductive traits of *Lachnanthes caroliniana* (Lam.) Dandy related to patch formation following feral swine rooting disturbance. *The Journal of the Torrey Botanical Society* 143(3): 265–273. <https://doi.org/10.3159/TORREY-D-15-00064.1>
- Buchmann SL (1980) Preliminary anthecological observations on *Xiphidium caeruleum* Aubl. (Monocotyledoneae: Haemodoraceae). *Panama Journal of the Kansas Entomological Society* 53(4): 685–699.
- COSEWIC – Committee on the Status Of Endangered Wildlife in Canada (2009) COSEWIC Assessment and Status Report on the Redroot, *Lachnanthes caroliniana* in Canada. COSEWIC, Ottawa, 34 pp.
- Don D (1832) On the characters and affinities of certain genera in the Flora Peruviana. *Edinburgh New Philosophical Journal* 13: 233–244.
- Dorr LJ, Wiersema JH (2010) Names of American vascular plants published in Loeffling's *Iter Hispanicum* (1758) and its German translation (1766). *Taxon* 59(4): 1245–1262. <https://doi.org/10.1002/tax.594022>

- Faden RB (1991) The morphology and taxonomy of *Aneilema* R. Brown (Commelinaceae). *Smithsonian Contributions to Botany* 76(76): 1–181. <https://doi.org/10.5479/si.0081024X.76>
- Ferrell J, Sellers B, Walter J (2009) Control of redroot (*Lachnanthes caroliniana*) in pastures. University of Florida Cooperative Extension Service, Publication #SS AGR 290, Gainesville, 2 pp.
- Helme NA, Linder HP (1992) Morphology, evolution and taxonomy of *Wachendorfia* (Haemodoraceae). *Bothalia* 22(1): 59–75. <https://doi.org/10.4102/abc.v22i1.826>
- Hickman EJ (2019) Discovery through illustration – botanical art, traits and their phylogeny in the Haemodoraceae. PhD thesis, The University of Western Australia.
- Hickman EJ, Hopper SD (2019) Discovery through illustration – A revision of the tiurdinds (*Tribonanthes*, Haemodoraceae). *Nuytsia* 30: 87–154.
- Hopper SD (2009) OCBIL theory: Towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically-buffered, infertile landscapes. *Plant and Soil* 322(1–2): 49–86. <https://doi.org/10.1007/s11104-009-0068-0>
- Hopper SD, Fay MF, Rossetto M, Chase MW (1999) A molecular phylogenetic analysis of the bloodroot and kangaroo paw family, Haemodoraceae: Taxonomic, biogeographic and conservation implications. *Botanical Journal of the Linnean Society* 131(3): 285–299. <https://doi.org/10.1111/j.1095-8339.1999.tb00770.x>
- Hopper SD, Chase MW, Fay MF (2006) A molecular phylogenetic study of generic and subgeneric relationships in the south-west Australian endemics *Conostylis* and *Blancoa* (Haemodoraceae). In: Columbus JT (Eds) *Monocots: Comparative Biology and Evolution*, *Aliso* 22: 527–538. <https://doi.org/10.5642/aliso.20062201.41>
- Hopper SD, Smith RJ, Fay MF, Manning JC, Chase MW (2009) Molecular phylogenetics of Haemodoraceae in the Greater Cape and Southwest Australian Floristic Regions. *Molecular Phylogenetics and Evolution* 51(1): 19–30. <https://doi.org/10.1016/j.ympev.2008.11.015>
- Hopper SD, Smith RJ, Chase MW, Fay MF, Gutiérrez JE, Hickman EJ, Manning JC, Pellegrini MOO, Rourke JP, Simpson MG (in prep.) Near-complete taxon sampling for Haemodoraceae phylogenetics helps resolve enigmatic relationships in and between the Americas, South Africa, and Australia.
- IUCN (2001) The IUCN Red List Of Threatened Species, version 2010.4. IUCN Red List Unit, Cambridge U.K. <http://www.iucnredlist.org/> [accessed: 2 February 2019]
- Kunth CS (1816) *Nova Genera et Species Plantarum*, ed. 4, Vol. 1, part 3. Librairie Grcque-Latine-Allemande, Paris, France, 377 pp. [96 tab.]
- Kuntze CEO (1898) *Revisio Generum Plantarum*, Vol. 3, part 3. Arthur Felix & al., Leipzig, London, Milano & New York, 576 pp.
- León H (1946) *Flora de Cuba* (Vol. 1). Gymnosperms Monocotyledons. *Contribuciones Ocasionales del Museo de Historia Natural Colegio La Salle* 8, Cultural S.A., La Habana.
- Lindley J (1846) *New Garden Plant*. *Edwards's Botanical Register* 32: page prior to t. 67.
- Loefling P (1758) *Iter Hispanicum*. Tryckt på Direct & Lars Salvii Kostnad, Stockholm, 316 pp.
- Maas PJM, Maas-van de Kamer H (1993) Haemodoraceae. *Fl. Neotropica* 61: 1–44.
- Macfarlane TD, Hopper SD, Purdie RW, George AS, Patrick SJ (1987) Haemodoraceae. *Flora of Australia* 45: 55–57.

- Maguire B, Wurdack JJ (1957) The Botany of the Guayana Highland— Part II. *Memoirs of the New York Botanical Garden* 9(3): 235–392.
- Manning JC, Goldblatt P (2017) A review of *Dilatris* P.J.Bergius (Haemodoraceae: Haemodoroideae). *South African Journal of Botany* 113: 103–110. <https://doi.org/10.1016/j.sajb.2017.08.001>
- Maury PJB (1889) Énumération des plantes du Haut-Orénoque. *Journal de Botanique (Morot)* 3: 266–273.
- Meggitt WF, Aldrich RJ (1959) Amitrol for control of redroot in cranberries. *Weeds* 7(3): 271–276. <https://doi.org/10.2307/4040334>
- Meyers SL, Jennings KM, Monks DW, Jordan DL, Ballington JR (2013) Effect of PRE and POST Herbicides on Carolina Redroot (*Lachnanthes caroliniana*) growth. *Weed Technology* 27(4): 747–751. <https://doi.org/10.1614/WT-D-13-00029.1>
- Millspaugh CF (1900) *Plantæ Utowanæ*. Plants collected in Bermuda, Porto Rico, St. Thomas, Culebras, Santo Domingo, Jamaica, Cuba, The Caymans, Cozumel, Yucatan, and the Alacran Shoals. Dec. 1898 to Mar. 1899. The Antillean cruise of the Yacht Utowana. Mr. Allison V. Armour, Owner and Master, part I – Catalogue of the Species. Publications of the Field Columbian Museum, Botanical Series 2: 3–110. <https://www.biodiversitylibrary.org/page/46063084>
- Odonne G, Valadeau C, Alban-Castillo J, Stien D, Sauvain M, Bourdy G (2013) Medical ethnobotany of the Chayahuita of the Paranaपुरa basin (Peruvian Amazon). *Journal of Ethnopharmacology* 146(1): 127–153. <https://doi.org/10.1016/j.jep.2012.12.014>
- Panigo E, Ramos J, Lucero L, Perreta M, Vegetti A (2011) The inflorescence in Commelinaceae. *Flora* 206(4): 294–299. <https://doi.org/10.1016/j.flora.2010.07.003>
- Pellegrini MOO (2017) Two new synonyms for *Heteranthera* (Pontederiaceae, Commelinales). *Nordic Journal of Botany* 35(1): 124–128. <https://doi.org/10.1111/njb.01152>
- Pellegrini MOO (2019) Systematics of Commelinales focusing on Neotropical lineages. PhD thesis. Universidade de São Paulo, São Paulo, SP, Brazil.
- Pellegrini MOO, Faden RB (2017) Recircumscription and taxonomic revision of *Siderasis*, with comments on the systematics of subtribe Dichorisandrinae (Commelinaceae). *PhytoKeys* 83: 1–41. <https://doi.org/10.3897/phytokeys.83.13490>
- Pellegrini MOO, Horn CN (2017) Two peculiar new species of *Heteranthera* Ruiz & Pav. (Pontederiaceae) from Brazil, with notes on inflorescence architecture in the family. *PhytoKeys* 82: 35–56. <https://doi.org/10.3897/phytokeys.82.13752>
- Pellegrini MOO, Horn CN, Almeida RF (2018) Total evidence phylogeny of Pontederiaceae (Commelinales) sheds light on the necessity of its recircumscription and synopsis of *Pontederia* L. *PhytoKeys* 108: 25–83. <https://doi.org/10.3897/phytokeys.108.27652>
- Pellegrini MOO, Horn CN, Faden RB, Hopper SD, Evans TM (in prep.) Morphological phylogeny of Commelinales (Monocots), based on a giant taxon-character matrix.
- POWO – Plants of the World Online (2020) Facilitated by the Royal Botanic Gardens, Kew. <http://www.plantsoftheworldonline.org> [accessed: 31 October 2020]
- Prychid CJ, Furness CA, Rudall PJ (2003) Systematic significance of cell inclusions in Haemodoraceae and allied families: Silica bodies and tapetal raphides. *Annals of Botany* 92(4): 571–580. <https://doi.org/10.1093/aob/mcg172>

- Radford AE, Dickison WC, Massey JR, Bell CR (1974) *Vascular Plant Systematics*. Harper & Row Publishers, New York, 891 pp.
- Robertson (1976) The genera of Haemodoraceae in the southeastern United States. *Journal of the Arnold Arboretum* 57: 205–216. <https://doi.org/10.5962/bhl.part.28166>
- Rudall PJ (1997) The nucellus and chalaza in Monocotyledons: Structure and systematics. *Botanical Review* 63(2): 140–181. <https://doi.org/10.1007/BF02935930>
- Saarela JM, Prentis PJ, Rai HS, Graham SW (2008) Phylogenetic relationships in the monocot order Commelinales, with a focus on Philydraceae. *Botany (Canada)* 86(7): 719–731. <https://doi.org/10.1139/B08-063>
- Simpson MG (1983) Pollen ultrastructure of the Haemodoraceae and its taxonomic significance. *Grana* 22(2): 79–103. <https://doi.org/10.1080/00173138309431969>
- Simpson MG (1985) Pollen ultrastructure of the Philydraceae. *Grana* 24(1): 23–31. <https://doi.org/10.1080/00173138509427420>
- Simpson MG (1987) Pollen ultrastructure of the Pontederiaceae: Evidence for exine homology with the Haemodoraceae. *Grana* 26(2): 113–126. <https://doi.org/10.1080/00173138709429941>
- Simpson MG (1990) Phylogeny and classification of the Haemodoraceae. *Annals of the Missouri Botanical Garden* 77(4): 722–784. [pl. XXI–XXIII.] <https://doi.org/10.2307/2399670>
- Simpson MG (1993) Septal nectary anatomy and phylogeny in the Haemodoraceae. *Systematic Botany* 18(4): 593–613. <https://doi.org/10.2307/2419536>
- Simpson MG (1998a) Reversal in ovary position from inferior to superior in the Haemodoraceae: Evidence from floral ontogeny. *International Journal of Plant Sciences* 159(3): 466–479. <https://doi.org/10.1086/297564>
- Simpson MG (1998b) Haemodoraceae. In: Kubitzki K (Ed.) *The Families and Genera of Vascular Plants* (Vol. 4). Springer Verlag, Berlin, 212–128.
- Simpson MG, Burton DH (2006) Systematic floral anatomy of Pontederiaceae. *Aliso* 22(1): 499–519. <https://doi.org/10.5642/aliso.20062201.39>
- Smith JE (1798) The characters of twenty new genera of plants. *Transactions of the Linnean Society of London* 4(1): 213–223. <https://doi.org/10.1111/j.1096-3642.1798.tb00530.x>
- Smith RJ, Hopper SD, Shane MW (2011) Sand-binding roots in Haemodoraceae: Global survey and morphology in a phylogenetic context. *Plant and Soil* 348(1–2): 453–470. <https://doi.org/10.1007/s11104-011-0874-z>
- Spjut RW (1994) *A Systematic Treatment of Fruit Types*. The New York Botanical Garden, New York, 181 pp.
- Standley PC (1928) *Flora of the Panama Canal Zone*. US Government Printing Office.
- The Plant List (2013) *The Plant List*. Version 1.1. <http://www.theplantlist.org/> [accessed: 12 August 2018]
- Thiers B (continually updated) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Gardens' Virtual Herbarium. <http://sweetgun.nybg.org/ih/> [accessed: 15 January 2019]
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (Eds) (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)* adopted by the Nineteenth International Botanical Congress Shenzhen,

- China, July 2017. *Regnum Vegetabile* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- Underwood LM (1905) A summary of Charles Wright's explorations in Cuba. *Bulletin of the Torrey Botanical Club* 32(6): 291–300. <https://doi.org/10.2307/2478811>
- Urquiola Cruz A, Aguilar Trujillo JR, Betancurt Betancurt Z, Betancurt Gandul M (2000) Haemodoraceae. In: Greuter W (Ed.) *Flora de la República de Cuba. Series A. Plantas Vasculares. Fascículo 5(2)*, Koeltz Scientific Books, Königst, 2 pp.
- USDA-NRCS – U.S. Department of Agriculture-Natural Resources Conservation Service (2018) PLANTS Profile- *Lachnanthes caroliniana* (Lam.) Dandy. Carolina redroot. <https://plants.usda.gov/core/profile?symbol=LACA5> [accessed: 8 February 2018]
- Vahl M (1805) *Martini VahlII, profess. botan. Haun. membr. societ. lit. plur. Enumeratio Plantarum: vel ab aliis, vel, ab ipso observatum, cum earum differentiis specificis, synonymis selectis et descriptionibus succinctis* (Vol. 2). Typis N. Mölleri et Filli, Aulae Regiae et Universitatis Typographorum. Impensis Viduae, 423 pp. <https://www.biodiversitylibrary.org/page/545915>
- Valadeau C, Pabon A, Deharo E, Albán-Castillo J, Estevez Y, Lores FA, Rojas R, Gamboa D, Sauvain M, Castillo D, Bourdy G (2009) Medicinal plants from the Yanasha (Peru): Evaluation of the leishmanicidal and antimalarial activity of selected extracts. *Journal of Ethnopharmacology* 123(3): 413–422. <https://doi.org/10.1016/j.jep.2009.03.041>
- Valentine Jr JM, Noble RE (1970) A colony of sandhill cranes in Mississippi. *The Journal of Wildlife Management* 34(4): 761–768. <https://doi.org/10.2307/3799141>
- Weberling F (1965) Typology of inflorescences. *Botanical Journal of the Linnean Society* 59: 15–221. <https://doi.org/10.1111/j.1095-8339.1965.tb00058.x>
- Weberling F (1989) *Morphology of Flowers and Inflorescences*. Cambridge University Press, Cambridge, 348 pp.
- Williams LO [Ed.] (1963) *Homage to Standley. Papers in honor of Paul C. Standley* Published by the Chicago Natural History Museum.

Pogostemon guamensis Lorence & W.L.Wagner (Lamiaceae), a new species from Guam, Mariana Islands

David H. Lorence¹, Warren L. Wagner², Kenneth R. Wood¹, Gabriel Johnson²

1 National Tropical Botanical Garden, 3530 Papalina Road, Kalāheo, HI 96741, USA **2** Department of Botany, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

Corresponding author: David H. Lorence (lorence@ntbg.org)

Academic editor: A. Paton | Received 29 August 2020 | Accepted 31 October 2020 | Published 4 December 2020

Citation: Lorence DH, Wagner WL, Wood KR, Johnson G (2020) *Pogostemon guamensis* Lorence & W.L.Wagner (Lamiaceae), a new species from Guam, Mariana Islands. *PhytoKeys* 169: 61–73. <https://doi.org/10.3897/phytokeys.169.58107>

Abstract

While undertaking a botanical survey of the Andersen Air Force Base on Guam (Mariana Islands) in 1994, botanists from the National Tropical Botanical Garden collected an unusual suffrutescent, non-aromatic member of the Lamiaceae family growing on limestone cliffs in the northeastern part of the island. Based on morphology and molecular data (*trnLF*, *matK*), it was determined to belong to the genus *Pogostemon* Desf., a genus previously unknown from the Micronesian, Melanesian, and Polynesian region. Moreover, the analysis also showed that it was not conspecific with *P. cablin* (patchouli), and of the species available to include in the phylogenetic analyses it is sister to *P. hirsutus*, a species from India and Sri Lanka. Differing from its congeners by its large, loose inflorescence 2.5–5 cm wide and up to 7 cm wide in fruit, it is here illustrated and described as a new species, *Pogostemon guamensis* Lorence & W.L. Wagner and its habitat and conservation status are discussed.

Keywords

conservation, Guam, Lamiaceae, Mariana Islands, Micronesia, *Pogostemon*

Introduction

Micronesia comprises the Caroline, Mariana, Gilbert, and Marshall Islands in the western Pacific Ocean and forms part of the Polynesia-Micronesia global biodiversity hotspot (Conservation International 2007). The Micronesian bioregion spans an area

of the Pacific Ocean comparable in size to the continental United States or Australia, but the total land area of all the islands within this area is approximately 2,628 km², smaller than the US state of Rhode Island. Recent studies suggest that Micronesia has the world's highest percentage of plant endemism per square kilometer out of all globally recognized insular biodiversity hotspots, with a total of 364 vascular plant species endemic to Micronesia (Costion and Lorence 2012). A new endemic species of *Syzygium* (Myrtaceae) was recently described from Palau, Caroline Islands (Byng et al. 2019), underscoring the need for further botanical exploration and study of the Micronesian flora.

The Mariana Islands are the northernmost of the island groups in Micronesia, and Guam is the southernmost island in the Mariana group with a land area of ca. 541 km². The Marianas have 54 vascular plant endemics, with 11 single island endemics restricted to Guam, including two pteridophytes and nine angiosperms. The Lamiaceae are poorly represented in Micronesia, however, with only a single endemic species, *Callicarpa lamii* Hosok. restricted to the Marianas (Costion and Lorence 2012). A new species belonging to the genus *Pogostemon* was collected in Guam and is described herein. Along with the new *Syzygium* species from Palau, this brings the total number of known Micronesian endemic vascular plant species to 366.

Pogostemon Desf. (Lamiaceae: Lamioideae) is a genus of about 80 species of herbs or subshrubs with a center of diversity in tropical and subtropical Asia, with another five species endemic to Africa (Bhatti and Ingrouille 1997; Yao et al. 2015; Bongcheewin et al. 2017). Species diversity is highest in the Indian subcontinent. Diagnostic characters of the genus are exerted stamens bearded with moniliform hairs medially along the filaments, uni-thecal anthers, and a 2-lipped corolla with a 3-lobed upper lip and 1-lobed lower lip or subequally 4-lobed (Harley et al. 2004; Yao et al. 2015). The genus is named for its bearded staminal filaments (Latin/Greek *pogos*, beard, and *stemon*, stamen). *Pogostemon cablin* (Blanco) Benth. is well known and widely cultivated as the source of patchouli oil, an essential oil obtained from the leaves and used in soaps and perfumes. *Dysophylla* Blume, previously recognized as a distinct genus based on its small flowers and aquatic or marshland habitat, was reduced to a section of *Pogostemon* by Bhatti and Ingrouille (1997). Recent molecular phylogenetic studies suggest that *Pogostemon* s.l., including *Dysophylla*, is strongly supported to be monophyletic (Bendiksby et al. 2011).

An unusual species of Lamiaceae growing on the limestone cliffs of northeastern Guam (Mariana Islands) was first collected in 1982 by Derral Herbst and again in 1994 by Kenneth Wood and Steven Perlman of the National Tropical Botanical Garden during a botanical survey of the Andersen Air Force Base sponsored by the U.S. Fish and Wildlife Service (Perlman and Wood 1994). This is an area harboring rich native flora but with highly restricted access, and consequently its flora had not been well documented prior to this survey. Morphological and molecular studies have revealed it to be an undescribed species of *Pogostemon* apparently endemic to Guam which we describe and illustrate below.

Methods and materials

This study is based on field observations in Guam and on herbarium collections from the Bernice P. Bishop Museum (**BISH**), the National Tropical Botanical Garden (**PTBG**), and the US National Herbarium (**US**). Besides the specimens cited below, no additional collections of this taxon were located in any other herbaria including the University of Guam Herbarium (**GU**) (Wei Xiao, pers. comm. 5 October 2020). Available gene sequences were downloaded from GenBank to ascertain whether it indeed belonged to the genus *Pogostemon* which it clearly does based on both morphological and molecular evidence. For the conservation assessment, we used the IUCN Red List categories and criteria (IUCN 2019).

Molecular methods

Total DNA was extracted from silica dried leaf material taken from 4 individuals collected in 1994, two collected by both S. Perlman and K. R. Wood. Fragments of leaf tissue approximating 1.0 cm² were transferred to 2.0 mL screw-capped, wide-base microcentrifuge tubes containing ~0.1 mL 1.0 mm diameter glass beads and ten 2.3 mm diameter silica-zirconium beads (Biospec Products Inc., Bartlesville, OK, USA). Sample tubes were immersed in liquid nitrogen for 2 minutes and then tissues were homogenized into a fine powder using a MP FastPrep96 (MP BioMedicals LLC., Solon, OH, USA) at 1800 rpm for 1 minute. To increase total yield from each sample, 6 separate tubes were prepared for each collection. To each tube, 500 µL pre-warmed lysis buffer AP1 was added. After mixing, 10 µL (50 mg/mL) proteinase K (Bioline Inc., Taunton, MA, USA) and 10 µL β-mercaptoethanol (Sigma-Aldrich, St. Louis, MO, USA) were added and the solutions incubated at 65 °C for 1 hour and then reduced to 54 °C overnight while agitating at 500 rpm on a VorTemp rotary incubator (Labnet International, Inc., Edison, NJ, USA).

Each lysate was mixed with 150 µL precipitation buffer P3 and incubated on ice for 5 minutes before centrifuging at 13,500 rpm for 15 minutes at 4 °C to pelletize debris. The cleared supernatant was centrifuged at 13,500 rpm for 2 minutes through QiaShredder columns; all 6 lysates prepared for one sample were processed through the same column. Resulting eluates were pooled into a 15 mL conical vial and mixed with a 1.5× volume of binding buffer AW1 and centrifuged in 600 µL increments through a DNeasy column at 8,000 rpm for 1 minute. The remainder of the extraction was conducted according to the manufacturer's protocol.

A portion of the *maturase K* (*matK*) gene was amplified in two sections with the 1Fa and 3R primers for the 5' part and the 3F and 5Rb for the 3' end as described by Bendiksby et al. (2011). The 5' end of the *trnL*^(UUA) intron was amplified using the c and d primers from Taberlet et al. (1991). The PCR amplifications and subsequent Sanger sequencing was conducted using the methods of Acevedo-Rodríguez et al. (2017).

The resulting chromatograms were edited and assembled into consensus sequences using Sequencher ver. 5.2.4 (Gene Codes, Ann Arbor, MI, USA). These sequences

were compared with published *matK* and *trnL* intron sequences on GenBank (Scheen et al. 2010; Bendiksbjy et al. 2011; Chen et al. 2016; Yao et al. 2016; Yi and Kim 2016; Zhang et al. 2019). Alignments were created using MAFFT ver. 7 (Kato and Standley 2013) and were analyzed with MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) to generate phylogenetic reconstructions with Bayesian Inference and the GTR + I + Γ evolutionary model. Four Markov Chain Monte Carlo chains were run, each starting from a different random tree. One tree was sampled in every 1,000 of 2,000,000 generations when the standard deviation between split frequencies was less than 0.01. After discarding the first 25% of trees as burn-in, the remaining trees were used to calculate posterior probabilities and a 50% majority-rule consensus tree (Fig. 1).

Molecular results

DNAs obtained from *Pogostemon guamensis* collections by Wood and Perlman in 1994 were highly degraded. The use of the modified DNeasy extraction method described here with combining DNAs from six lysates for one DNeasy column increased the total yield. This enabled regions of *trnL* intron and *matK* to be PCR amplified and sequenced for half the extracts. Other common phylogenetic markers failed to amplify presumably due to the poor DNA quality. Collection information and GenBank accession numbers for the two samples that yielded sequenceable DNA are shown in Table 1.

The *matK* region obtained for *P. guamensis* was diverged 0.6% from the closest related *matK* accession on GenBank, *P. hirsutus* Benth. (HQ911397). In this pairwise comparison, 7 SNPs were identified over 1146 bp while *trnL* intron sequences were identical between *P. guamensis* and *P. hirsutus* (FJ854298). In contrast, at least 36 SNPs were identified between *matK* for *P. guamensis* and various accessions of the common horticultural herb patchouli, *P. cablin* (EF529553, EF529543, EF529554, and EF529546). Pairwise comparisons between 1,212 bp *matK* from patchouli and *P. guamensis* differed 3.1–3.6% depending on the accession. With the more conserved *trnL* intron, they were 0.8% divergent.

The phylogenetic analyses were included for two specific purposes: 1) to determine if the species from Guam was indeed a member of *Pogostemon*; and 2) to determine whether it was a native part of the Guam flora or an introduction of *P. cablin*. In phylogenetic reconstructions of *Pogostemon* using *matK* sequences from GenBank, *P. guamensis* formed a strongly supported clade with *P. hirsutus*, *P. mollis* Benth., and *P. wightii* Benth. (Fig. 1). This group was nested within a larger well-supported clade containing other taxa from subgenera *Allopogostemon* (sensu Bhatti and Ingrouille 1997) and *Dysophyllus* section *Verticillatus*, Yao et al. (2016) placing subgen. *Allopogostemon* in synonymy of subgen. *Dysophyllus*. The clade containing *P. guamensis* was in a polytomy with a well-supported clade containing *P. cablin* with various species in subgen. *Pogostemon* and a clade of *P. barbatus* Bhatti & Ingr. and *P. auricularius* (L.) Hassk. (Fig. 1). Although the resolving power was much lower, the topology of a Bayesian tree estimated with *trnL* intron data did not conflict with that generated from *matK* (data not shown).

Molecular-Phylogenetic data (*trnL*, *matK*)

Table 1. Collection information and GenBank accession numbers for the two specimens used in the molecular analyses in this study.

Name	Collector	Coll. No.	Coll. Date	Locality	<i>matK</i>	<i>trnL</i> ^(UUA) intron
<i>Pogostemon guamensis</i>	Wood and Perlman	3300	07/02/94	Guam, Pati Point	MT446026	MT446028
	Perlman and Wood	14266	07/02/94	Guam, Pati Point	MT446025	MT446027

Systematics

Pogostemon guamensis Lorence & W.L.Wagner, sp. nov.

urn:lsid:ipni.org:names:77213186-1

Figures 2, 3

Type. MARIANA ISLANDS. Guam: Yigo Municipality. Andersen Air Force Base, Pati Point, just west of point, 10 degrees north aspect, 2 July 1994, *S. P. Perlman* & *K. R. Wood* 14266 (Holotype PTBG 061045!; Isotypes BISH!, GU!, K!, NY!, UC!, US!).

Diagnosis. Shrub or subshrub growing on limestone cliffs, distinguishable from its congeners by its non-aromatic parts; inflorescence a loose thyrse, 2.5–5 cm wide and up to 7 cm wide in fruit; calyx equally 5(6)-toothed, externally densely hirtellous and internally glabrous; corolla white, weakly bilabiate, tube 8–10 mm long, externally sparsely white pilosulous in distal half, glabrous in basal half, internally pilosulous up to base of lobes; stamens long-exserted with filaments 13–14 mm long, bearded with septate, non-moniliform trichomes in basal half and glabrous in distal half or occasionally with trichomes along entire length, with anthers reniform, 0.4 mm long; style plus stigma ca. 15–16 mm long, stigma lobes 2, equal, linear, 1.6–2.2 mm long.

Description. Diffusely branching, non-aromatic perennial shrub or subshrub 75–130 cm tall, main stem to 2 cm diameter at base, bark pale brown, a pair of branches usually developing below each inflorescence, mature stems solid, weakly 4-angled, 3–3.2 mm wide, 4-sulcate, yellowish green when fresh, drying brown, stems, petioles, and inflorescences densely hirtellous with brown, patent, multicellular, non-glandular, 4–6-celled trichomes 0.1–0.2 mm long mixed with shorter capitate glandular trichomes < 0.1 mm long. Leaves opposite, when fresh somewhat fleshy, yellowish green adaxially, paler abaxially, drying brown, chartaceous, blade broadly ovate to ovate-cordate, (4.5–)6–13.5 cm long, (3.5–)5–8.5 cm wide, adaxially uniformly hirtellous with antrorsely curved pale brown or whitish hairs 0.2–0.3 mm long, abaxially similarly hirtellous but with hairs denser on midrib, veins, and margin, surface densely yellowish-brown glandular punctate, margin serrate-crenate or biserrate-crenate, teeth obtuse, 0.4–1 cm apart, apex acute to short acuminate, the acumen to 1 cm long, base cordate to subcordate or sometimes truncate and rounded, secondary veins (4)5–6 on each side, basal pair arising near petiole insertion, tertiary venation reticulate, prominulous on both surfaces; petiole (2–)4–7 cm long, 1.2–1.5 mm wide, densely brown hirtellous. Inflorescence terminal, a single loose, densely flowered, cylindrical thyrse (3–)4.5–19 cm long, 2.5–5 cm wide, elongating to 20 cm long and 7 cm wide in fruit, when fresh

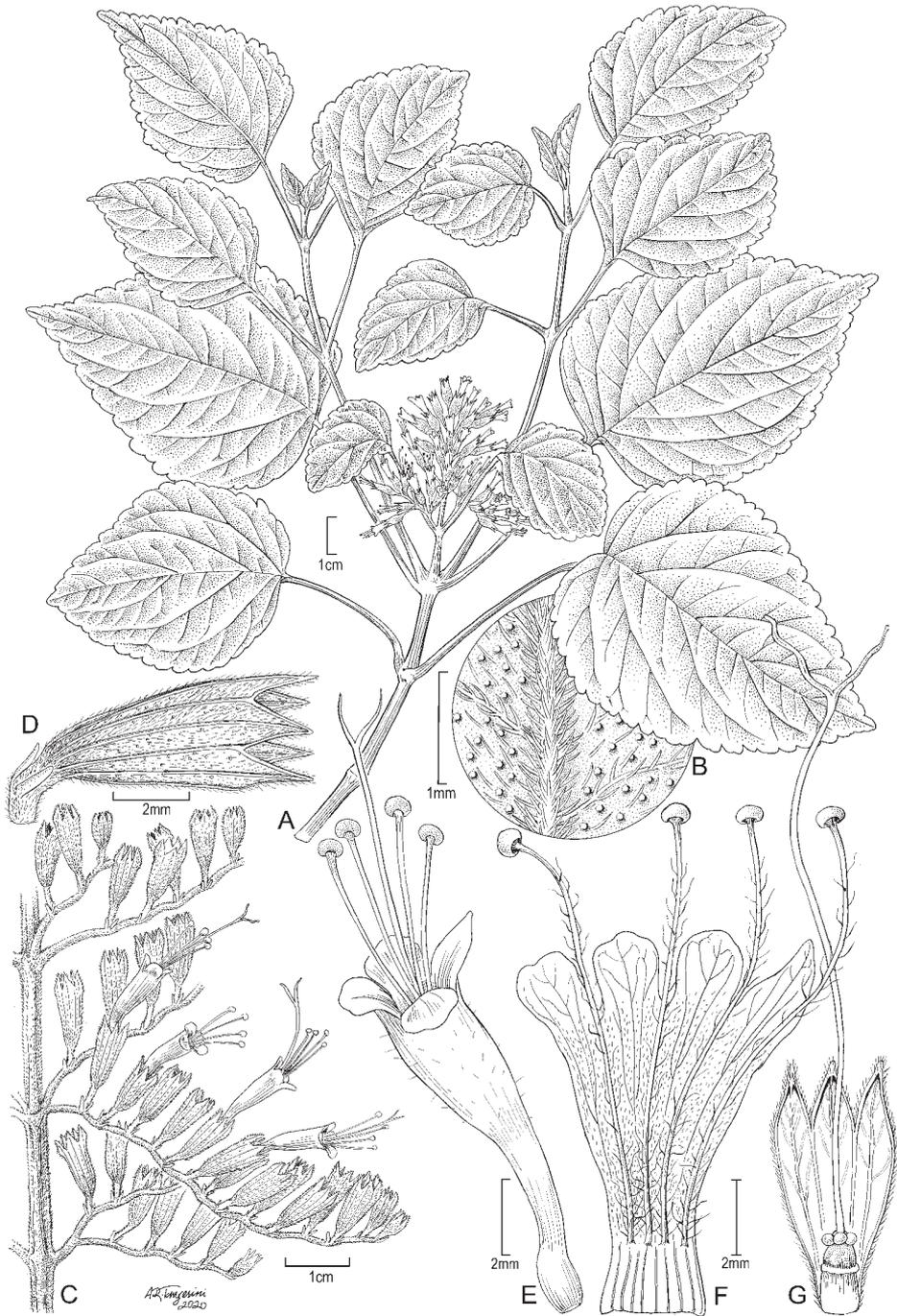


Figure 2. *Pogostemon guamensis* Lorence and W.L.Wagner **A** habit, stem with leaves and inflorescence **B** detail of abaxial leaf surface showing pubescence and sessile glands **C** portion of inflorescence showing cymes with calyces and four corollas **D** calyx **E** corolla at anthesis **F** corolla, opened along one side **G** gynoecium with portion of calyx removed showing ovary and style. Drawn from *Perlman and Wood 14295 (A, B)*, *Wood and Perlman 3359 (C-E)*, and *Wood and Perlman 3300 (F, G)*. Illustration by Alice Tangerini.



Figure 3. *Pogostemon guamensis* Lorence and W.L. Wagner (Perlman & Wood 14266, holotype PTBG-061045).

yellowish green, densely hirtellous, peduncle (4–)10–15 mm long; flowers (25–) 50 to several hundred (rarely to ca. 700) per inflorescence; opposite cymes sessile or on peduncle 2–3 mm long, occasionally subtended by a narrowly triangular-subulate bract 3.5–6 mm long, cymes usually branched once, each branch (3–)6–20-flowered, rachis slightly undulating or zig-zag, elongating to 35 mm in fruit; flowers secund, on pedicel 0.5–2 mm long, subtended by (1–)2 narrowly subulate bracteoles 1–1.2 mm long; calyx radially symmetrical, equally 5(6)-toothed, externally densely hirtellous with patent or slightly ascending non-glandular trichomes, tube 4.5–6 mm long, obconic-cylindrical, 10(12)-veined, internally glabrous, teeth equal to slightly subequal, narrowly triangular-acute, 1.5–2.5 mm long, 0.8–1 mm wide at base, with distinct mid and marginal vein, densely hirtellous on both surfaces with scattered sessile glands; corolla white, venose when dry, exerted from calyx, funnellform, tube 8–10 mm long, slightly gibbous at base, 0.7–0.8 mm wide medially, 2–3 mm wide at apex of tube, 2-lipped, upper lip 3-lobed, lobes obtuse, ca. 1.3 mm long and wide, lower lip entire, 1.8–2 mm long, corolla tube externally sparsely white pilosulous in distal half, glabrous in basal half, internally pilosulous up to base of lobes; stamens 4, exerted 5–7 mm beyond corolla lobes, attached ca. 2–3 mm from base of tube, filaments 13–14 mm long, sparsely villous bearded in basal half with white septate (non-moniliform) trichomes and glabrous in distal half or occasionally with trichomes along entire length; anther reniform, 0.4 mm long; style terminal, glabrous, exerted, slightly longer than stamens, style plus stigma ca. 15–16 mm long, stigma lobes 2, equal, linear, 1.6–2.2 mm long. Nutlets 4, ellipsoid, smooth, c. 0.3 mm long, 0.2 mm wide (immature), mature nutlets not seen, said to be brown-black (*Wood 3370*, PTBG).

Distribution. Known only from the karstic limestone cliffs of northeastern Guam, Mariana Islands.

Phenology. Flowers were collected in April and July and immature fruit in July. In the many of the specimens examined flowers and nutlets had been eaten by herbivorous insects in the field, and consequently mature nutlets were not available for study.

Habitat and ecology. The northern end of Guam is characterized by a reef-associated limestone plateau that has been uplifted above sea level and flanked by cliffs that can exceed 190 m (c. 600 ft) high (Fig. 4). The forests growing on the elevated limestone plateau surrounding Andersen Air Force Base (AAFB) contain some of the richest native plant communities on Guam, although the forests and cliff habitat are often impacted by severe typhoons. The sharp, treacherously jagged karstic limestone makes it extremely dangerous for exploration and rappelling with ropes.

Pogostemon guamensis is known only from the dry to mesic karstic limestone cliffs of northeastern Guam at 370–550 ft (113–168 m) elevation, with small groupings occurring between Lafac Point to the south and the Tarague cliffs to the north. The coastal cliff community is dominated by halophytic scrub vegetation with woody species such as *Aglaiia mariannensis* Merr., *Bikkia tetrandra* (L.f.) A. Rich., *Eugenia bryanii* Kaneh., *E. palumbis* Merr., *E. reinwardtiana* (Blume) DC., *Excoecaria agollocha* L., *Ficus prolixa* G. Forst., *Guamia mariannae* (Safford) Merr., *Leptopetalum foetidum* (G. Forst.) Neupane & N. Wikstr., *Macaranga thompsonii*



Figure 4. Coastal limestone cliffs of NE Guam, photo courtesy of Toni Mizerek.

Merr., *Meiogyne cylindrocarpa* (Burck) Heusden, *Ochrosia mariannensis* A. DC., *Pemphis acidula* J.R. Forst. & G. Forst., *Phyllanthus mariannensis* W. L. Wagner & Lorence, *P. marianus* Muell.-Arg, *Pipturus argenteus* (G. Forst.) Wedd., *Polyscias grandifolia* Volkens, *Premna serratifolia* L., *Psychotria mariana* Bartl. ex DC., *Scaevola taccada* (Gaertn.) Roxb., *Syzygium thompsonii* (Merr.) N. Snow, *Triphasia trifolia* (Burm.f.) P. Wilson, and *Wikstroemia elliptica* Merr., with associated herbaceous species including *Cassytha filiformis* L., and *Peperomia mariannensis* A. DC. Invasive alien plant species competing with the new species include *Chromolaena odorata* (L.) R.M. King & H. Rob., *Passiflora suberosa* L., *Sporobolus farinosus* Hosok., and *Triphasia trifolia* (Burm.f.) P. Wils. Feral pigs (*Sus scrofa*) and the introduced Philippine or sambar deer (*Rusa marianna*) are also serious threats to the surrounding habitat, in addition to wind damage from severe typhoons.

Conservation status. During separate cliff rappels five subpopulations ranging in size from 1 to 30–50 plants were observed on vertical cliff faces, for a total of 113 individuals observed (Perlman and Wood 1994) (Fig. 5). Based on the IUCN categories and criteria this species is assigned a preliminary Red List status of Critically Endangered (CR) based on its AOO of <10 km² (i.e., 4 km²) and its EOO of <100 km² (i.e.,

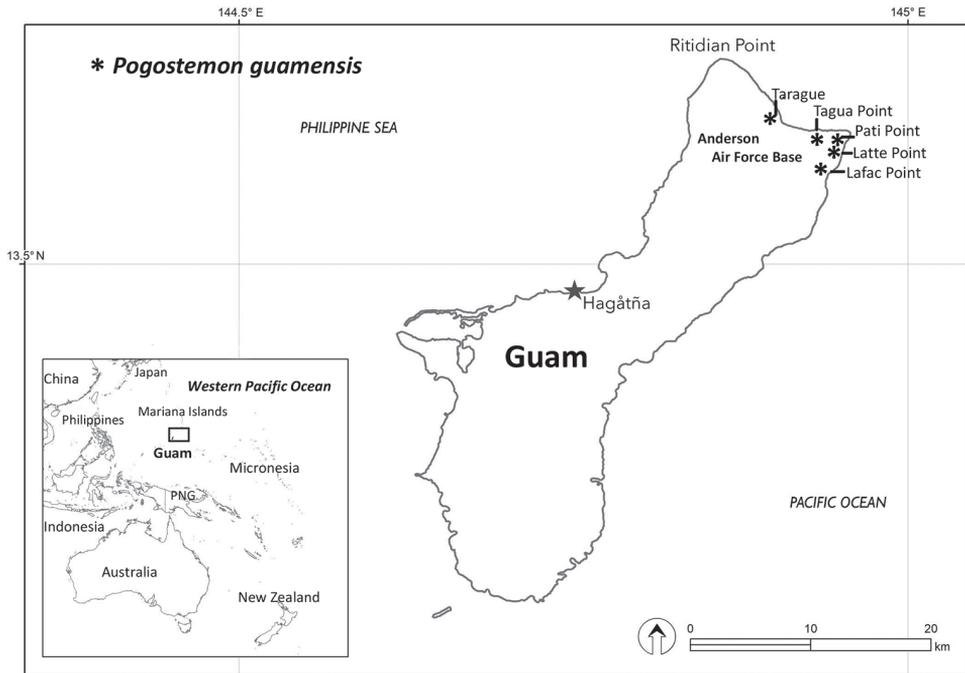


Figure 5. Distribution map showing five known localities for *Pogostemon guamensis* on NE part of Guam.

4 km²), and it has only one known location, with continuing decline in both AOO and EOO inferred.

Specimens examined (Paratypes). **MARIANA ISLANDS:** Guam: YIGO MUNICIPALITY. Pati Point, ca. 500 ft., edge of limestone cliff, 14 April 1982, *D. Herbst* 6656 (BISH); Andersen Air Force Base, Pati Point area; 400–600 ft., N aspect. 2 July 1994, *K. R. Wood* 3300 (BISH, CAS, GU, MBK, NY, P, PTBG [2], US, WU); Andersen Air Force Base, near Tarague, steep cliffs around beach access road, 137 m, 18 Jul 1994, *K. R. Wood* 3370 (GU, PTBG, P, US); Andersen Air Force Base, Pati Pt., 350 degrees north aspect, rappel between 400–600 ft., 9 July 1994, *K. R. Wood & S. P. Perlman* 3359 (GU, PTBG, US); Andersen Air Force Base, just north of Latte Point, between Latte and Pati Point, 5 July 1994, *S. P. Perlman* 14289 (GU, PTBG, MO, US); Andersen Air Force Base, west of Tagua, 400–550 ft., 330 deg. asp., 7 July 1994, *K. R. Wood & S. P. Perlman* 3337 (GU, PTBG); Andersen Air Force Base, west of Tagua, between Tagua and Tarague, off Crow Transect 9, on cliff, 7 July 1994, *S. P. Perlman & K. R. Wood* 14295 (GU, PTBG).

Acknowledgments

Field research in Guam was supported by the U.S. Fish and Wildlife Service (USFWS). The illustration was skillfully drawn by Alice Tangerini (Smithsonian Institution). For

the molecular results all or portions of the laboratory and/or computer work were conducted in, and with the support of, the Laboratories of Analytical Biology facilities of the National Museum of Natural History or its partner labs. We thank Steven Perlman for useful discussions, information on habitat and ecology, and constructive comments on the manuscript, and also the anonymous reviewers whose comments improved the quality of the paper. Ben Nyberg assisted with preparation of the map, and Toni Mizerek contributed the photo of cliffs of NE Guam used in Fig. 3. We are grateful to Lauren Weisenberger for assistance with USFWS data. We thank the curators of the following herbaria for loans or permission to study their specimens: BISH, GU, PTBG, US. The contribution by WLW to this study was partially supported by the Smithsonian Research Opportunities Fund and while appointed as McBryde Chair at the National Tropical Botanical Garden.

References

- Acevedo-Rodríguez P, Wurdack KJ, Ferrucci MS, Johnson G, Dias P, Coelho RG, Somner GV, Steinmann VW, Zimmer EA, Strong MT (2017) Generic relationships and classification of tribe Paullinieae (Sapindaceae) with a new concept of supertribe Paullinioidae. *Systematic Botany* 42: 96–114. <https://doi.org/10.1600/036364417X694926>
- Bendiksby M, Thorbek L, Scheen AC, Lindquist C, Ryding O (2011) An updated phylogeny and classification of Lamiaceae subfamily Lamioideae. *Taxon* 60(2): 471–484. <https://doi.org/10.1002/tax.602015>
- Bhatti GR, Ingrouille M (1997) Systematics of *Pogostemon* (Labiatae). *Bulletin of the Natural History Museum. Botany Series* 27(2): 77–147.
- Bongcheewin B, Pramali K, Traipermp P, Chantaranonthai P, Paton A (2017) *Pogostemon nudus* sp. nov. (Lamiaceae) from Thailand. *Nordic Journal of Botany* 35: 289–299. <https://doi.org/10.1111/njb.01439>
- Byng J, Lorence DH, Xio W (2019) An annotated and illustrated checklist to *Syzygium* (Myrtaceae) 1: Micronesia. *Phytotaxa* 427(2): 115–130. <https://doi.org/10.11646/phytotaxa.427.2.2>
- Chen ZD, Yang T, Lin L, Lu LM, Li HL, Sun M, Liu B, Chen M, Niu YT, Ye JF, Cao ZY (2016) Tree of life for the genera of Chinese vascular plants. *Journal of Systematics and Evolution* 54(4): 277–306. <https://doi.org/10.1111/jse.12219>
- Conservation International (2007) Biodiversity Hotspots. Center for Applied Biodiversity Science. Published on the Internet. <http://www.biodiversityhotspots.org/> [Accessed 23 July 2008]
- Costion CM, Lorence DH (2012) The Endemic Plants of Micronesia: a Geographical Checklist and Commentary. *Micronesica* 43: 51–100. <https://doi.org/10.3417/2011048>
- Harley RM, Atkins S, Budantsev AL, Cantino PD, Conn BJ, Grayer R, Harley MM, de Kok RPJ, Krestovskaja T, Morales R, Paton AJ, Ryding O, Upton T (2004) Labiatae. In: Kubitzki K (Ed.) *The Families and Genera of Vascular Plants* (Vol. VI). Springer-Verlag, Berlin, Heidelberg, New York, 167–275. https://doi.org/10.1007/978-3-642-18617-2_11

- Hutchinson DW, Strasburg JL, Shaffer C (2005) Cleaning microsatellite PCR products with Sephadex in 96-well filtration plates enhances genotyping quality. *Biotechniques* 38(1): 56–58. <https://doi.org/10.2144/05381BM07>
- IUCN (2019) The IUCN Red List of Threatened Species. Categories & Criteria. Version 2020-2). <http://www.iucnredlist.org> [Downloaded on 15 October 2020]
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Perlman S, Wood KR (1994) Anderson (*sic*) Air Force Base rare plant survey of their limestone Forests and cliffs, Northern Marianas Islands, Guam. Prepared for the U.S. Fish and Wildlife Service. National Tropical Botanical Garden, Botanical Survey Report (unpublished), 39 pp.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Scheen AC, Bendiksy M, Ryding O, Mathiesen C, Albert VA, Lindqvist C (2010) Molecular phylogenetics, character evolution, and suprageneric classification of Lamiioideae (Lamiaceae) 1. *Annals of the Missouri Botanical Garden* 97(2): 191–217. <https://doi.org/10.3417/2007174>
- Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of the three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109. <https://doi.org/10.1007/BF00037152>
- Yao G, Deng Y-F, Ge X-J (2015) A taxonomic revision of *Pogostemon* (Lamiaceae) from China. *Phytotaxa* 200: 1–67. <https://doi.org/10.11646/phytotaxa.200.1.1>
- Yao G, Drew BT, Yi TS, Yan HF, Yuan YM, Ge XJ (2016) Phylogenetic relationships, character evolution and biogeographic diversification of *Pogostemon* s.l. (Lamiaceae). *Molecular Phylogenetics and Evolution* 98: 184–200. <https://doi.org/10.1016/j.ympev.2016.01.020>
- Yi DK, Kim K (2016) The complete chloroplast genome sequences of *Pogostemon stellatus* and *Pogostemon yatabeanus* (Lamiaceae). *Mitochondrial DNA Part B* 1(1): 571–573. <https://doi.org/10.1080/23802359.2016.1192509>
- Zhang C, Liu T, Yuan X, Huang H, Yao G, Mo X, Xue X, Yan H (2019) The plastid genome and its implications in barcoding specific-chemotypes of the medicinal herb *Pogostemon cablin* in China. *PloS ONE* 14(4): e0215512. <https://doi.org/10.1371/journal.pone.0215512>

Hidden biodiversity of Amazonian white-sand ecosystems: two distinctive new species of *Utricularia* (Lentibulariaceae) from Pará, Brazil

Paulo Minatel Gonella^{1,2}, Rafael Gomes Barbosa-Silva^{3,4}, Andreas S. Fleischmann⁵, Daniela C. Zappi^{3,6}, Paulo Cesar Baleeiro⁷, Caroline Oliveira Andrino^{3,4}

1 Universidade Federal de São João del-Rei, Departamento de Ciências Exatas e Biológicas, Campus Sete Lagoas, Rodovia MG-424, km 47, Sete Lagoas, MG, 35701-970, Brazil **2** Instituto Nacional da Mata Atlântica, Av. José Ruschi, 4, Santa Teresa, ES, 29500-000, Brazil **3** Instituto Tecnológico Vale, Rua Boaventura da Silva 955, Nazaré, 66055-090, Belém, PA, Brazil **4** Museu Paraense Emílio Goeldi, Coord. Botânica, Av. Perimetral 1901, 66077-830, Belém, PA, Brazil **5** Botanische Staatssammlung München, Menzinger Strasse 67, D-80638, Munich, Germany **6** Programa de Pós-Graduação em Botânica, Instituto de Ciências Biológicas, Universidade de Brasília, DF, 70910-900, Brazil **7** University of Queensland, Brisbane, QLD, 4072, Australia

Corresponding author: Paulo Minatel Gonella (pmgonella@gmail.com)

Academic editor: E. Fischer | Received 14 August 2020 | Accepted 6 October 2020 | Published 4 December 2020

Citation: Gonella PM, Barbosa-Silva RG, Fleischmann AS, Zappi DC, Baleeiro PC, Andrino CO (2020) Hidden biodiversity of Amazonian white-sand ecosystems: two distinctive new species of *Utricularia* (Lentibulariaceae) from Pará, Brazil. *PhytoKeys* 169: 75–98. <https://doi.org/10.3897/phytokeys.169.57626>

Abstract

As deforestation and fire move forward over pristine vegetation in the Amazon, many species remain undiscovered and may be threatened with extinction before being described. Here, we describe two new species of *Utricularia* (Lentibulariaceae) collected during recent fieldwork in an area of white-sand vegetation in the eastern Amazon Basin named Campos do Ariramba. Further herbarium revision revealed that both species were first collected over 60 years ago in the same area, remaining unnamed until now. The new species, named *U. ariramba* **sp. nov.** and *U. jaramacaru* **sp. nov.**, are placed in *U.* sect. *Aranella* and *U.* sect. *Setiscapella*, respectively. We provide full descriptions, illustrations, photographs, a distribution map, and taxonomic discussion for both species. Additionally, we provide a preliminary list of Lentibulariaceae from the Campos do Ariramba. Both new species are assessed as Vulnerable, however, yet known only from a few collections each, highlighting the urgency and importance of fieldwork and taxonomic revisions in the Amazon biogeographic region in order to provide essential data for the conservation of both known and still unknown biodiversity.

Keywords

Amazon savannas, *campinaranas*, carnivorous plants, deforestation, taxonomy, *Utricularia ariramba*, *Utricularia jaramacaru*, wetlands

Introduction

Brazil is an extremely diverse country, home to the greatest floristic diversity in the world, in addition to being one of the best documented tropical countries in terms of its flora (Forzza et al. 2012; Flora do Brasil 2020 under construction). However, Brazil leads the number of new plant species described yearly (RBG Kew 2016; Cheek et al. 2020), showing that its vast territory still needs to be explored and studied if we are to attain a better understanding of the true dimension of its biodiversity.

Large remote areas of Brazil, especially those difficult to access, still lack taxonomic surveys and are in their majority concentrated in the Amazon Rainforest biome (Oliveira et al. 2016; BFG 2018). Regarded as the most biodiverse rainforest in the world, this region has fewer scientific collections in relation to other Brazilian biomes, with a strong bias of collection effort around large urban centers (Nelson et al. 1990) and along navigable rivers, while over 40% of its total area remains under-sampled and poorly studied (Schulman et al. 2007). Knowledge is even scarcer if one considers the herbaceous plants that grow in open Amazonian vegetation, as the majority of inventories still focus on woody plants (Miranda 1993; Miranda et al. 2002, 2006; Devecchi et al. 2020). Much faster than we are able to provide suitable studies regarding the Amazonian biodiversity, the rapid increase of the deforestation reaching these unexplored areas is potentially causing the extinction of a considerable proportion of undescribed plant species (Stroop et al. 2020).

Although the Amazon is predominantly known for its exuberant evergreen lowland rainforest, there are patches of open areas of outstanding biological diversity, such as the Pantepui (highland vegetation), the Amazonian *canga* (ferruginous *campo rupestre*), inselbergs, *campinaranas* (white sand vegetation) and Amazonian *savannas* (Pires and Prance 1985; Gröger 1994; Prance 1996; BFG 2015; Adeney et al. 2016; Barbosa-Silva et al. 2016, 2020; Mota et al. 2018; Costa et al. 2019; Zappi et al. 2019; Andriano et al. 2020; Devecchi et al. 2020; Fonseca-da-Silva et al. 2020), altogether representing approximately 5% of the Amazon biome in Brazil (IBGE 2020).

All of the above-mentioned open vegetation areas in the Amazon have oligotrophic, acidic soils (consisting of bare sandstone, ferruginous or granite escarpments, or alluvial plains of white sands) with the presence of seasonally or perennially wet to flooded areas (García-Villacorta et al. 2016). In contrast to the surrounding Amazon lowland forests, these habitats have a scattered vegetation cover, often herbaceous or at the most shrubby, and comprise very exposed sites with lower vegetation cover and competition, representing “islands” within the Amazon forest (Prance 1996). These conditions, especially low availability of nitrogen and phosphorus, favor the occurrence

of carnivorous plants (Givnish et al. 2018), and indeed several species of *Drosera* L. (Droseraceae), *Genlisea* A.St.-Hil. and *Utricularia* L. (Lentibulariaceae) can be found in those areas (Rivadavia et al. 2009; Fleischmann 2012a; Fleischmann et al. 2017).

The genus *Utricularia* is the most diverse of three genera of the carnivorous plant family Lentibulariaceae (Lamiales, Eudicots), with over 240 species currently accepted, presenting centers of diversity in the Neotropics and northern Australia, where most of its species are associated with seasonally wet areas of savanna vegetation (Taylor 1989; Fleischmann 2012b, 2015; Jobson et al. 2018). In Brazil, *Utricularia* is represented to date by 67 species (18 endemics), being most diverse in the Cerrado (Central Brazilian Savanna) and the Amazon Rainforest, both with 45 species each (Flora do Brasil 2020 under construction).

Utricularia is composed of small to medium-sized herbs, usually associated with wetlands, that can be recognized by the atypical morphology, lacking true roots, presence of leaf-like shoots (phylloclades), and bladder-like structures of foliar origin, the utricles, that inspired its generic epithet. The inflorescences are bracteose racemes, the flowers have a bilobate calyx (except in the early-branching *U.* sect. *Polypompholyx* (Lehm.) P.Taylor, and a few members of other lineages, such as *U. flaccida* A.DC. from *U.* sect. *Setiscapella* (Barnhart) P.Taylor, which can have a tetramerous calyx), a bilabiate personate corolla (snapdragon flower-type), with a spur, two stamens and ovary with central-free placentation (Taylor 1989; Jobson et al. 2003). *Utricularia* shows a great diversity of habitat types and life forms, occurring as aquatics (affixed or free-floating), terrestrials, lithophytes, rheophytes, and epiphytes (Taylor 1989).

Taylor (1989) presented the most comprehensive revision of the genus to date, classifying the accepted species into subgenera and sections. About 30–40 species (depending on species concepts) have been described after Taylor's monograph (for compiling works, see Fleischmann 2012b, 2015; Jobson et al. 2018), and the infrageneric classification has undergone a few changes based on molecular phylogenetic data (Jobson et al. 2003; Müller and Borsch 2004). In recent years, several new species have been described or reestablished for the genus in Brazil (Bove 2008; Fleischmann and Rivadavia 2009; Souza and Bove 2011; Baleeiro et al. 2015, 2019; Gonella and Baleeiro 2018; Guedes et al. 2019; Baleeiro et al. in prep.), revealing the potential for the discovery of new species even in a genus that had been thoroughly revised taxonomically in the late 20th century (Taylor 1989). The late botanist Peter Taylor meticulously studied *Utricularia* for over 40 years, culminating in his elaborate monograph that considered ca. 600 published names for 214 accepted species (see Fleischmann 2012b).

During a field trip to perform a floristic inventory of the Campos do Ariramba, an area of *campinarana* and savanna at the westernmost point of the state of Pará, several new records of Lentibulariaceae were made, including two collections of *Utricularia* that did not fit any of the currently recognized species. Here we describe these two new taxa and provide comments on their taxonomy, habitat, distribution, and their conservation status. We also provide a list of the species of the family registered in the area to contribute to the knowledge of the Amazonian grassland biodiversity, still so underestimated.

Material and methods

An expedition to Campos do Ariramba region (Municipality of Óbidos) was carried out in the period between 5–10 June 2019. Specimens were collected and deposited in the herbarium MG with duplicates sent to SPF. Specimens of the herbaria ALCB, B, BHCB, BM, DIAM, ESA, ESAL, F, HUEFS, HUFJSJ, HUFU, HURB, IAN, INPA, IPA, K, M, MG, MBM, MBML, MO, NY, OUPR, P, R, RB, SP, SPF, UB, UEC, UFRN, US, and VIES were also studied as part of the ongoing taxonomic study of the family for the Flora of Brazil 2020 project. The online databases Refflora Virtual Herbarium (REFLORA 2020), SpeciesLink (INCT 2018), and Global Biodiversity Information Facility (GBIF.org 2020) were also searched for further specimens of these taxa and for other specimens from Campos do Ariramba, Jaramacaru (including orthographic variants), Óbidos and Oriximiná. The descriptions were based on live material and dry specimens, which were analyzed using a stereomicroscope. Herbarium acronyms follow Thiers (2020 continuously updated).

For SEM photography, seeds from herbarium specimens were mounted on a carbon sticker-covered SEM stub, coated with platinum for 240 sec. under vacuum in a SCD 050 sputter coater (Bal-Tec, Germany), and imaged under SEM (Leo, Germany) at 25 mm working distance and 15.00 kV.

The distribution map was generated with the software QGIS (QGIS Development Team 2020) using layers available from IBGE (2020). The TerraBrasilis platform (Assis et al. 2019), which uses the Sistema de Detecção do Desmatamento em Tempo Real (DETER) of the Instituto Nacional de Pesquisas Espaciais (INPE), was used to acquire recent data on deforestation and fire records in the area. Coordinates were obtained in the field using GPS tracking. Given that the two species are known from a few locations each and lack population data, their conservation status were inferred based on criteria for the Area of Occupancy (AOO) of IUCN (2012), which was calculated by employing the IUCN standard 4 km² cell in the GeoCAT Tool (Bachman et al. 2011).

Morphological terminology and description structure are adapted with modifications from Taylor (1989).

Results

Taxonomic treatment

Utricularia ariramba Gonella, Baleeiro & Andrino, sp. nov.

urn:lsid:ipni.org:names:77213187-1

Figs 1–3

Type. BRAZIL. Pará: Floresta Estadual de Trombetas, comunidade Jaramacaru, cachoeira do Rio Jaramacaru; 9 Jun. 2019; D.C. Zappi, C.O. Andrino, R.G. Barbosa-Silva & C. Maurity 4853 (holotype MG; isotype SPF).

Diagnosis. *Utricularia ariramba* belongs to *U.* sect *Aranella* (Barnhart) P.Taylor, being most similar to *U. costata* P.Taylor, but distinguished by its taller inflorescences 5.3–12.0 cm long (vs. 2–7 cm long), the less conspicuous nerves on the calyx lobes, the upper calyx lobe with acute apex (vs. obtuse and obscurely denticulate), spur swollen and dorsiventrally flattened in the apical 2/3 (vs. cylindrical with apex narrowing towards the tip), lower corolla lip trapezoid with margin entire or finely denticulate (vs. transversely oblong with margin entire or shallowly 3-lobed), and upper corolla lip narrowly ovate with acute apex (vs. ovate, with apex rounded or subacute).

Description. Small-sized, probably annual, terrestrial. *Rhizoids* few, capillary, from the peduncle base, sometimes also from the basalmost scales, with short papillose branches, up to 0.8 mm long, 0.1–0.2 mm in diameter. *Stolons* few, capillary, terete, sparsely branched, a few cms long, c. 0.1 mm in diameter. *Leaves* few, on the stolons, petiolate, lamina narrowly linear, 1-nerved, up to 5 mm long, 0.1–0.2 mm wide. *Traps* numerous on the leaves and stolons, ovoid, stalked, 0.15–0.20 mm long, the mouth lateral with a single, conical, dorsal appendage and a longer, deeply bifid, ventral appendage. *Inflorescence* a bracteose raceme, erect, simple, solitary, 53–120 mm long; peduncle capillary, terete, glabrous, 0.2–0.3 mm in diameter, reddish-green. Scales, bracts, and bracteoles basifixed and single-nerved. *Scales* few to numerous, ovate-deltoid to ovate, with apex acute, 0.5–1.0 mm long. *Bracts* ovate-deltoid to lanceolate, with apex acute, 0.7–1.1 mm long. *Bracteoles* subulate, slightly shorter than the bract, with apex acute, 0.7–1.0 mm long. *Flowers* 1–6; pedicel ascending, filiform, terete, 0.5–2 mm long, c. 0.1 mm in diameter. *Calyx* lobes unequal, glabrous, with 9–13 very conspicuous, simple, parallel, raised nerves, green to greenish-red in color; upper lobe ovate with apex acute, convex, 2.0–2.5 × 1.2–1.5 mm; lower lobe ovate, convex, with apex bifid, 2.6–3.3 × 1.5–2.0 mm. *Corolla* white or lavender, with the lower lip with a yellow-orange mark on the top and violet nerves on the limb, 8–11 mm long, finely papillose; *upper lip* narrowly ovate 4.0–5.5 × 2–3 mm, apex acute, lateral margins retroflexed, basal sac with ciliated rim; *lower lip* limb trapezoid, margin entire or finely denticulate, straight or retroflexed, shallowly 3 lobed, 3–5 × 3–7 mm, palate with papillose rim; *spur* conical, swollen and dorsoventrally flattened in the apical 2/3, the apex truncate to sub-acute, projected to the front, longer than and +/- parallel to the lower lip, 5.0–6.1 × 2.2–3.1 mm, papillose and finely ciliated. *Filaments* curved, c. 0.8 mm long, the anther thecae sub-distinct, anther c. 0.70 × 0.25 mm. *Ovary* globose, 0.5 mm long; style short, c. 0.2 mm long; stigma bilabiate, lower lip semicircular, 0.3 mm wide, upper lip broadly deltoid. *Capsule* and *seeds* not seen.

Etymology. The epithet “*ariramba*” is a name in apposition, referring to the Campos de Ariramba, where this new species was discovered. The word “*ariramba*” comes from the Tupi language “*uarirãmba*” and refers to the birds of the Galbulidae family, which are commonly found in the area.

Phenology. The species was collected in full bloom at the end of the rainy season, in May and June.

Distribution and habitat. So far, only known from two subpopulations at the margins of the Jaramacaru River, in the Campos do Ariramba region. The area lies

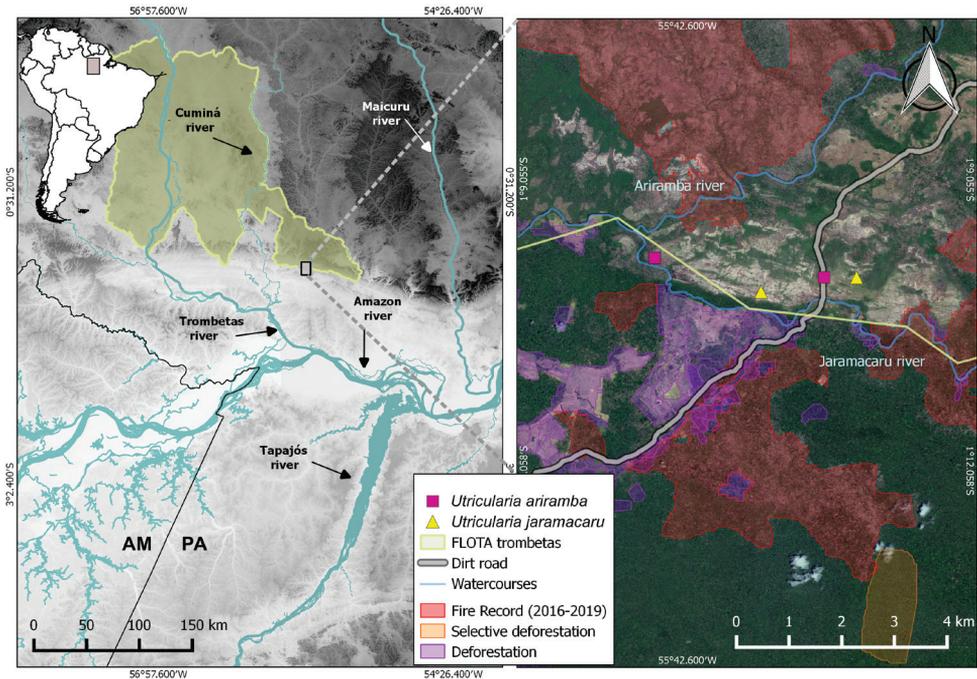


Figure 1. Distribution map of the new species of *Utricularia* in the Amazon. On the left map, the main rivers of the hydrographic basin of the region and which cross the FLOTA Trombetas (highlighted in green). The map to the right shows the records of *Utricularia ariramba* (squares) and *Utricularia jaramacaru* (triangle), which are near the FLOTA limits, as well the as threats to the area, including recent fires, full deforestation, and selective deforestation of timber species.

within the conservation unit of the Floresta Estadual de Trombetas (FLOTA Trombetas), in western Pará state, N Brazil. The species occurs on white sandy soils on a flat sandstone outcrop in *campinarana* (white sand vegetation).

Conservation status. Vulnerable: VU D2. *Utricularia ariramba* is known from only three collections, one of which was made over 60 years ago and lacked georeferenced data. The recently collected specimens were found ca. 3 km distant from each other, near the border of the FLOTA Trombetas (Fig. 1). Areas under active deforestation were observed just outside the conservation unit (Fig. 1), and during the fieldwork activities in 2019, fire was observed in a waterfall 6 km upriver from the Jaramacaru community, suggesting environmental disturbance generated by cattle farming and other human activities. In fact, large areas were recently impacted by fires less than 1 km away from the subpopulations (Fig. 1; data from Assis et al. 2019). In addition, the site is sought by tourists from nearby municipalities because of the Jaramacaru waterfall, therefore leading to negative anthropogenic impact on the populations. Although the Campos do Ariramba are a botanically unexplored region with vast areas of habitats similar to those where the species was collected and the population size has not been ascertained, the available data suggests that the species is restricted to a

few locations. An AOO of just 8 km² was calculated for this species, and we observed threats that might impact its habitat quality and AOO in the short term and lead to a reduction in population size and area of occupancy. Therefore, we assign the species to the Vulnerable category based on criterion D2 of IUCN (2012).

Taxonomic notes. *Utricularia ariramba* is placed in *U.* sect. *Aranella* based on its characteristic trap morphology (a single subulate dorsal appendage and a deeply bifid ventral appendage), and the presence of a clearly defined basal sac in the upper corolla lip.

Utricularia ariramba is the eleventh species of *Utricularia* sect. *Aranella* (Taylor 1989; Fleischmann and Rivadavia 2009), a section almost completely endemic to tropical South America, with a single species (*U. simulans* Pilger) extending to Central America, the Caribbean and tropical Africa (Taylor 1989).

Utricularia ariramba is most similar to *U. costata*, sharing similar bract and bracteole morphology, and the lavender (to white) corolla with darker violet venation in the lower lobe. It is distinguished by the relatively larger inflorescences 5.3–12.0 cm tall (vs. 2–7 cm tall), the less prominent nerves on the calyx lobes, the upper calyx lobe with acute apex (vs. obtuse and obscurely denticulate), the swollen spur in the apical 2/3 (vs. apex tapering towards the tip), the lower corolla lip trapezoid with margin entire or finely denticulate (vs. transversely oblong with margin entire or shallowly 3-lobed), and the upper corolla lip narrowly ovate with acute apex (vs. ovate, with apex rounded or subacute). For photos of *U. costata*, see Costa et al. (2016: 11, Fig. 3D, E) and Mota and Zappi (2018: 126, Fig. 3a–c).

Utricularia costata occurs in Venezuela and Brazil, where it is recorded from the states of Roraima, Pará, Mato Grosso, Goiás, Bahia, Sergipe and Alagoas (Taylor 1989, 1999; Fleischmann and Rivadavia 2009; Carregosa and Costa 2014; Costa et al. 2016; Guedes et al. 2018; Flora do Brasil 2020 under construction). In Pará, the species is recorded from the southeast region of the state, in the Serra dos Carajás (Mota and Zappi 2018).

Variation in corolla color and spur morphology was observed in the studied specimens of *U. ariramba*, where it varies from white to lavender, and the different corolla colors are associated with different spur shapes: both variants show a dorsoventrally flattened spur in the apical 2/3, but the white variant (represented by the type specimen) shows a higher degree of flattening, a ventral concavity (Fig. 2c), and a truncate apex (Fig. 3a), while the lavender variant (represented by the paratypes) has a spur only slightly flattened, without the concavity, and with an acute apex (Figs 2i, 3b, d). Furthermore, in the white morphotype, the apex of the lower corolla lip is reflexed (Figs 2h, 3a). Despite these differences in corolla color and shape, both morphotypes are considered conspecific as the specimens share similar morphology in all other characters. Variation in corolla color and shape is common in other species of *U.* sect. *Aranella*, as exemplified by intra-populational variation observed in *U. laciniata* A.St.-Hil. & Girard and *U. purpureocaerulea* A.St.-Hil. & Girard in several areas across their range (PMG pers. obs.), as well as in lavender- and white-flowered color morphs of *U. blanchetii* A.DC. in the Chapada Diamantina (Taylor 1989; Rivadavia 2000).

Seeds were not available for study, however, Taylor (1989: 237) notes that seed morphology is rather uniform in *U.* sect. *Aranella*, hence not having great taxonomic

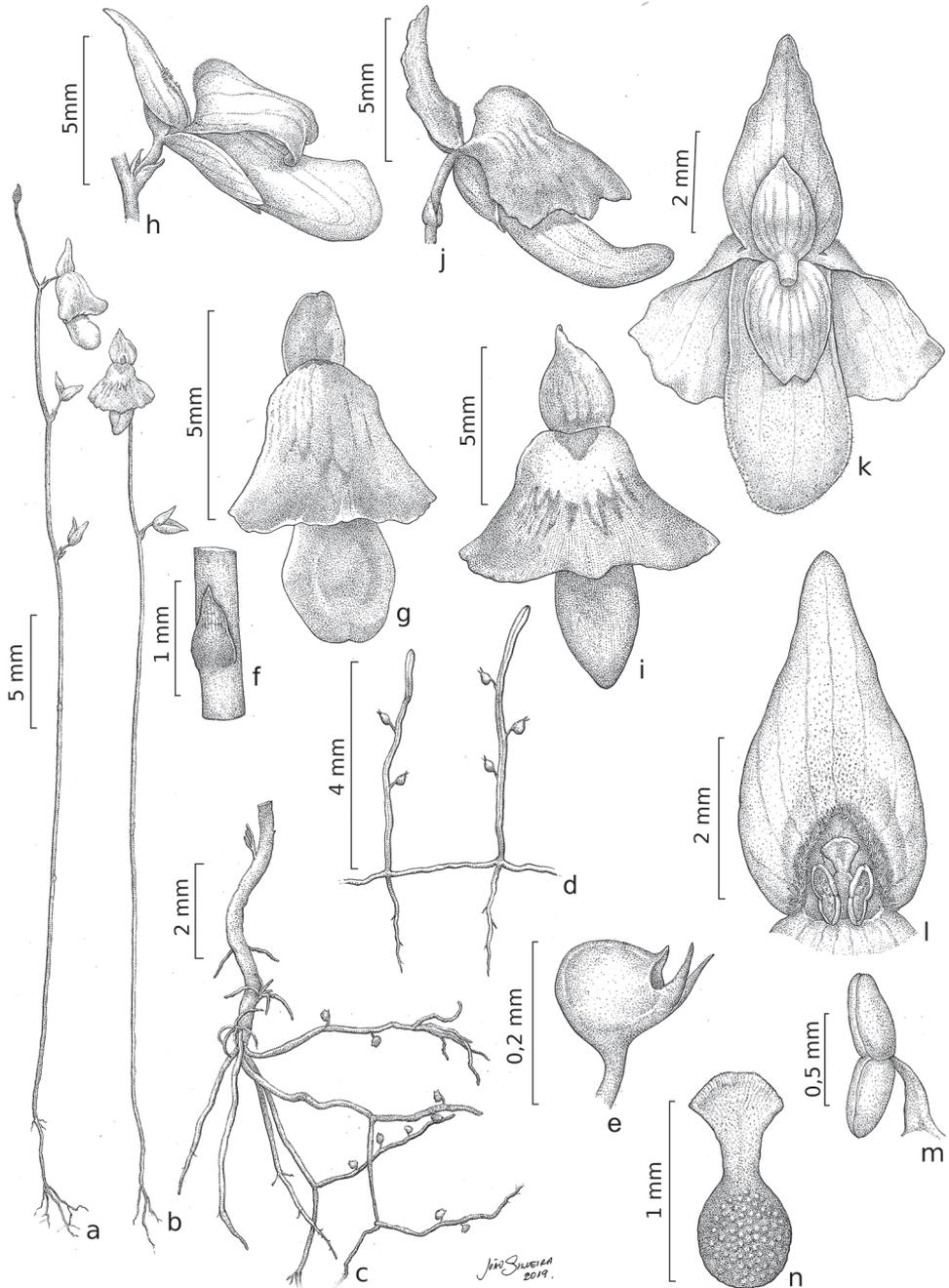


Figure 2. *Utricularia ariramba* **a, b** habit, in flower **c** base of plant with stolon, rhizoids, and peduncle base **d** part of stolon, with rhizoids, and leaves with traps **e** utricle, side view **f** scale **g, h** flower of the white morphotype in anterior (**g**) and side (**h**) view **i, j** flower of the lavender morphotype in anterior (**i**) and side (**j**) view **k** flower of the white morphotype in posterior view **l** upper lip of the corolla, androecium, and gynoecium **m** stamen **n** pistil **a, c–h, k–n** based on the holotype; **b, i, j** based on *C.O. Andrino 560*. Illustrations by João Silveira.

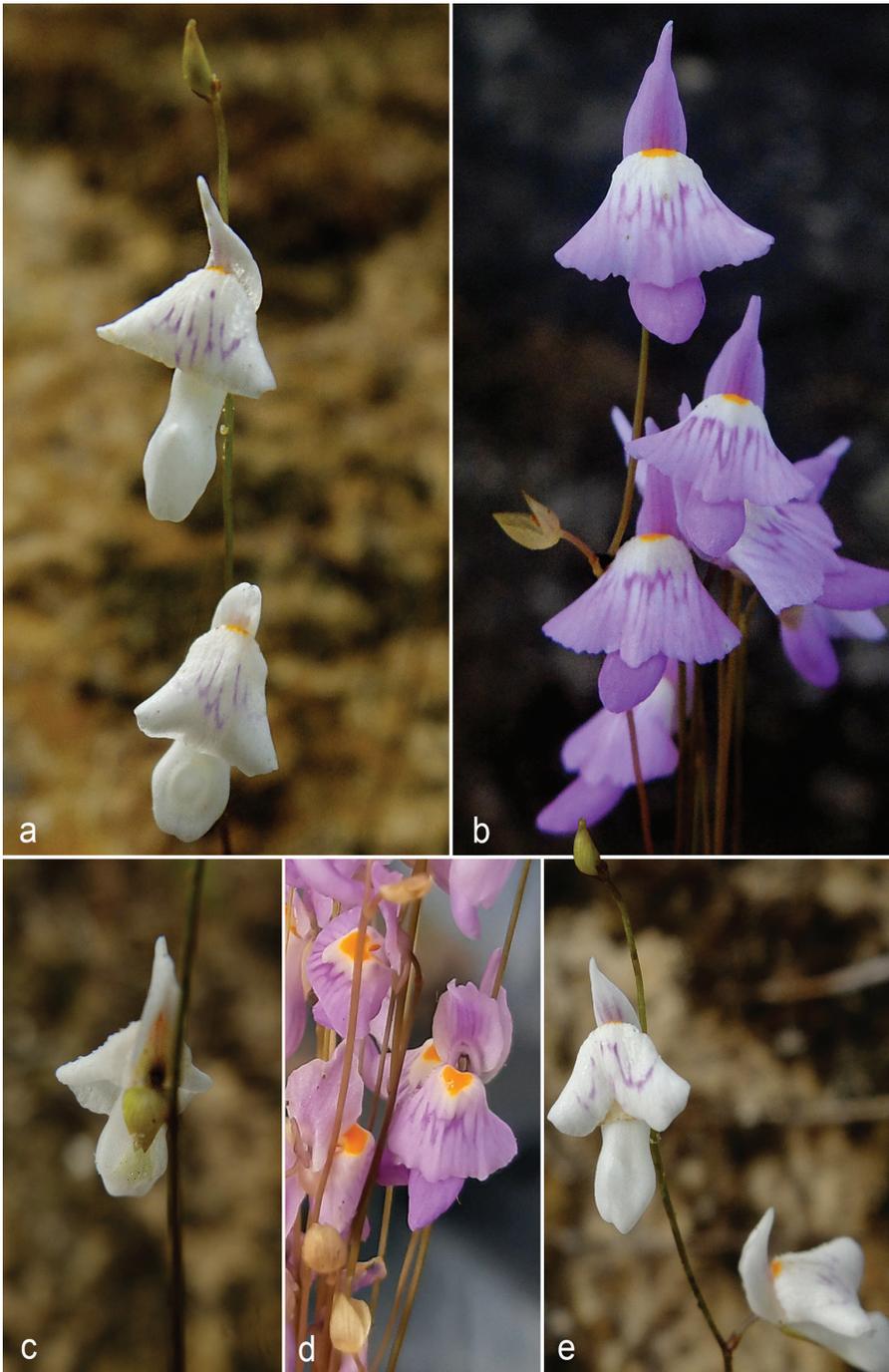


Figure 3. *Utricularia ariramba* **a** inflorescence apex with flowers and bud of the white corolla morphotype, showing the reflexed apex of lower corolla lip **b** flowers of the lavender corolla morphotype, with a calyx of a developing fruit to the left **c** flower of the white corolla morphotype in posterior view, showing the calyx lobes and the concavity in the ventral portion of the spur **d** flowers of the lavender corolla morphotype **e** inflorescence apex of the white corolla morphotype showing variation in spur morphology.

significance (compared to other sections of the genus, where some species might be identified by a single seed grain alone; Taylor 1964, 1989).

Additional specimens examined (paratypes). BRAZIL • Pará; [Óbidos]; Campo do Jamaracará [*sic*], perto do barracão, região do Ariramba; 26 May 1957; G.A. Black, W. Egler, P. Cavalcante & A. Silva 57-19633 (IAN 95750) • Óbidos; FLOTA Trombetas, comunidade Jaramacaru; 10 Jun. 2019; C.O. Andrino 560 (MG, SPF).

Key to *Utricularia* sect. *Aranella*

Adapted from Taylor (1989: 238) and Fleischmann and Rivadavia (2009: 158) with the addition of *U. ariramba* as follows:

- 7 Lowermost scales deeply fimbriate *U. laciniata*
 7' Lowermost scales entire..... **8**
 8 Upper corolla lip narrowly ovate with acute apex; spur of the corolla swollen and dorsoventrally flattened in the apical 2/3..... *U. ariramba*
 8' Upper corolla lip transversally elliptic, quadrate or ovate, with apex rounded to crenate; spur of the corolla tapering towards the tip and never dorsoventrally flattened..... **9**
 9 Spur of corolla with apex obtuse, 2–3 times as long as the lower lip; upper lip scarcely longer than wide; calyx very strongly nerved, the lower lobe longer....
 *U. costata*
 9' Spur of corolla with apex acute or shortly bifid, shorter or scarcely longer than the lower lip; calyx not very strongly nerved, the lobes \pm equal or the upper lobe longer at anthesis..... **10**
 10 Upper lip of corolla not wider than calyx, quadrate to elliptic, scarcely longer than wide, constricted below the middle; spur curved upwards; calyx upper lobe with apex acute, enclosing the capsule in fruit; seed truncate-obovoid....
 *U. rostrata*
 10' Upper lip of corolla much wider than calyx, transversely elliptic, much wider than long, not constricted; spur straight; calyx upper lobe with apex 3-dentate, not enclosing the capsule in fruit; seed ovoid.....
 *U. purpureocaerulea*

Utricularia jaramacaru Gonella, Baleeiro & Andrino, sp. nov.

urn:lsid:ipni.org:names:77213188-1

Figs 1, 4–6

Type. BRAZIL. Pará: Óbidos; Floresta Estadual de Trombetas, Ariramba, Rio Jaramacaru; 10 Jun. 2019; C.O. Andrino, R.G. Barbosa-Silva, D.C. Zappi & C. Maurity 559 (holotype MG; isotypes M, SPF).

Diagnosis. *Utricularia jaramacaru* belongs to *U.* sect. *Setiscapella* (Barnhart) P.Taylor but is distinct from all other members of this section by the traps with reduced, denticulate appendages (vs. subulate, branched), white corolla (vs. yellow or lilac), the upper corolla lip with bilobate apex (vs. obtuse, rounded, truncate or retuse), and the lower corolla lip narrowly rhombic (vs. cuneate, trullate, rhombic to very broadly rhombic in outline).

Description. Small-sized, probably annual, terrestrial. *Rhizoids* 2–4, from the base of peduncle, terete, with short papillose branches, up to 1 cm long, c. 0.25 mm in diameter. *Stolons* numerous, capillary, sparsely branched, up to 1 cm long (in the available material), up to 0.1 mm in diameter. *Leaves* numerous, at the base of the peduncle and on the stolons, lamina narrowly linear, simple, the base narrowing gradually into a short petiole, apex obtuse to acute, green to reddish, 1-nerved, 2–6 × 0.2–0.5 mm. *Traps* numerous on the stolons and leaves, ovate, stalked, 0.1–0.2 mm long, the mouth lateral with two dorsal and very short denticulate, simple appendages. *Inflorescence* a bracteose raceme, erect, solitary, 60–130 mm tall. *Peduncle* capillary, terete, simple or eventually laterally simple-branched, glabrous, 0.2–0.3 mm in diameter, wine red. *Scales* numerous, peltate, ovate to narrowly ovate, inferior apex rounded to obtuse, superior apex acute, 0.5–0.9 mm long, similar to the bracts. *Bracts* ovate, basisolute, peltate, 0.5–0.7 × 0.4–0.5 mm, amplexicaul, the inferior apex rounded, the superior apex rounded to obtuse. *Bracteoles* absent. *Flowers* 4–13, the rhachis elongate, flexuous, without sterile bracts; pedicels ascending, capillary, terete, 3–9 mm long (longer towards the base of the inflorescence), pedicels with a mucilage droplet at their base in living specimens. *Calyx* lobes unequal, glabrous, nerves inconspicuous, simple, not extending to the margin; upper lobe ovate, with apex obtuse, convex, 0.9–1.1 mm long in flower, up to 1.3 mm in fruit; lower lobe obovate, with apex emarginate to rounded, convex, equal in length with the upper lobe in flower, slightly longer in fruit, up to 1.7 mm in fruit. *Corolla* 5 mm long, lower lip white with a pale yellow mark on the gibbose palate, spur pale yellow, upper lip pale yellow with reddish marks; upper lip oblong with apex bilobed, the basal sac with an eglandular pubescent marginal rim, the pubescence spreading towards the apex, c. 1.5 mm long; lower lip limb narrowly rhombic in outline, the base with a very prominent bilobed swelling, the apex 3-lobed, 0.3–4.5 mm; palate pubescent; spur cylindrical, apex rounded, equal to or slightly longer or shorter than the lower lip, 0.35–0.40 mm long. *Filaments* curved, 0.8–1.0 mm long, the anther thecae sub-distinct, anther 0.4–0.5 mm long. *Ovary* globose, 0.8–0.9 mm long; style very short; stigma lower lip nearly circular, upper lip obsolete. *Capsule* globose, c. 1.2 mm in diam., shorter than the calyx lobes, dehiscent by an elliptic ventral pore. *Seeds* obovoid to angulate-ellipsoid, 0.20–0.25 mm long, 0.13–0.20 mm wide, testa cells c. 0.01 mm wide, elongate, anticlinal boundaries deeply sunken and more or less straight, periclinal walls convex, smooth.

Etymology. The epithet “*jaramacaru*” is a noun in apposition (hence it is invariant), referring to the Jaramacaru river, where the new species was discovered. “Jaramacaru” comes from the Tupi language “*iamandakaru*”, referring to species of the genus

Cereus Mill. (Cactaceae). However, no cactus of this genus was located during the field trip undertaken by COA, RGBS, and DCZ in 2019.

Phenology. *Utricularia jaramacaru* was collected with flowers in April, May, and June.

Distribution and habitat. So far, only known from two very close localities near the Jaramacaru waterfall, in the Campos do Ariramba, part of the FLOTA Trombetas, western Pará, N Brazil. The species occurs on white sandy soils with outcrops of sandstone, in *campinarana* vegetation.

Conservation status. Vulnerable: VU D2. Similarly to that described for *U. ariramba*, *U. jaramacaru* is known from only two localities (AOO=8 km²) near the limits of FLOTA Trombetas and the threats the populations are subject to are fully explained in the above species. Therefore, based on available data, *U. jaramacaru* is to be assigned to the category of Vulnerable based on criterion D2 of IUCN (2012).

Taxonomic notes. The basisolute, peltate scales and bracts, and the calyx and seed morphology (Figs 4–6) undoubtedly place this species in *U.* sect. *Setiscapella*, representing the tenth species of the section (following the species circumscriptions of Taylor 1989). However, based on morphology alone, it is not possible to assign the closest affinity of *U. jaramacaru*, as it bears several apomorphic characteristics, most remarkably regarding its trap and corolla morphology.

Up to now, *U.* sect. *Setiscapella* was composed of nine species (Taylor 1989), of which eight have yellow corollas (regarding the phylogenetic switch from lilac to yellow corolla color in *Utricularia* and *Genlisea*, see Fleischmann et al. 2010). One exception in terms of color is *U. physoceras* P.Taylor, also endemic to the state of Pará, but with larger (7–10 mm long vs. 5 mm) pink to lilac corolla. The whitish corolla of *U. jaramacaru* is, therefore, a second exception among the species of the section. *Utricularia physoceras* also shares the short spur with rounded apex with *U. jaramacaru* and similar seed morphology. *Utricularia physoceras* occurs in the *cangas* (ferruginous *campo rupestre*) of the Serra dos Carajás (Taylor 1989; Mota and Zappi 2018; Giuliatti et al. 2019), distant ca. 815 km to the southeast from the area where *U. jaramacaru* was collected. For photos of *U. physoceras*, see Mota and Zappi (2018: 129, Fig. 4a–e) and Giuliatti et al. (2019: 369, fig. 7 bottom three images).

Traps of *U. jaramacaru* are unlike any other species of *U.* sect. *Setiscapella* in that the appendages are reduced to two denticulate structures (Fig. 4d). All other species of the section bear subulate or filiform appendages near the trap door that are sparsely to copiously branched. Reduced appendages are found in different sections of *Utricularia*, which suggests it is a homoplastic character in the genus. Taylor (1989) enumerates a few species with reduced trap appendages, such as *U. cornuta* Michx. and *U. juncea* Vahl (both of *U.* sect. *Stomoisia* (Raf.) Komiya), *U. nana* A.St.-Hil. & Girard (*U.* sect. *Benjaminia* P.Taylor), *U. guyanensis* A.DC. (*U.* sect. *Stylothea* A.DC.) and *U. viscosa* Spruce ex Oliv. (*U.* sect. *Sprucea* P.Taylor), all presenting only a small prolongation of the body of the trap on the dorsal side of the door.

The presence of a droplet of mucilage at the insertion of the pedicel in the peduncle (Fig. 5b) is shared with *U. flaccida*, *U. nigrescens* Sylvén and *U. pusilla* Vahl (P.M. Gonella and A. Fleischmann, pers. obs.), and its function remains unclear.

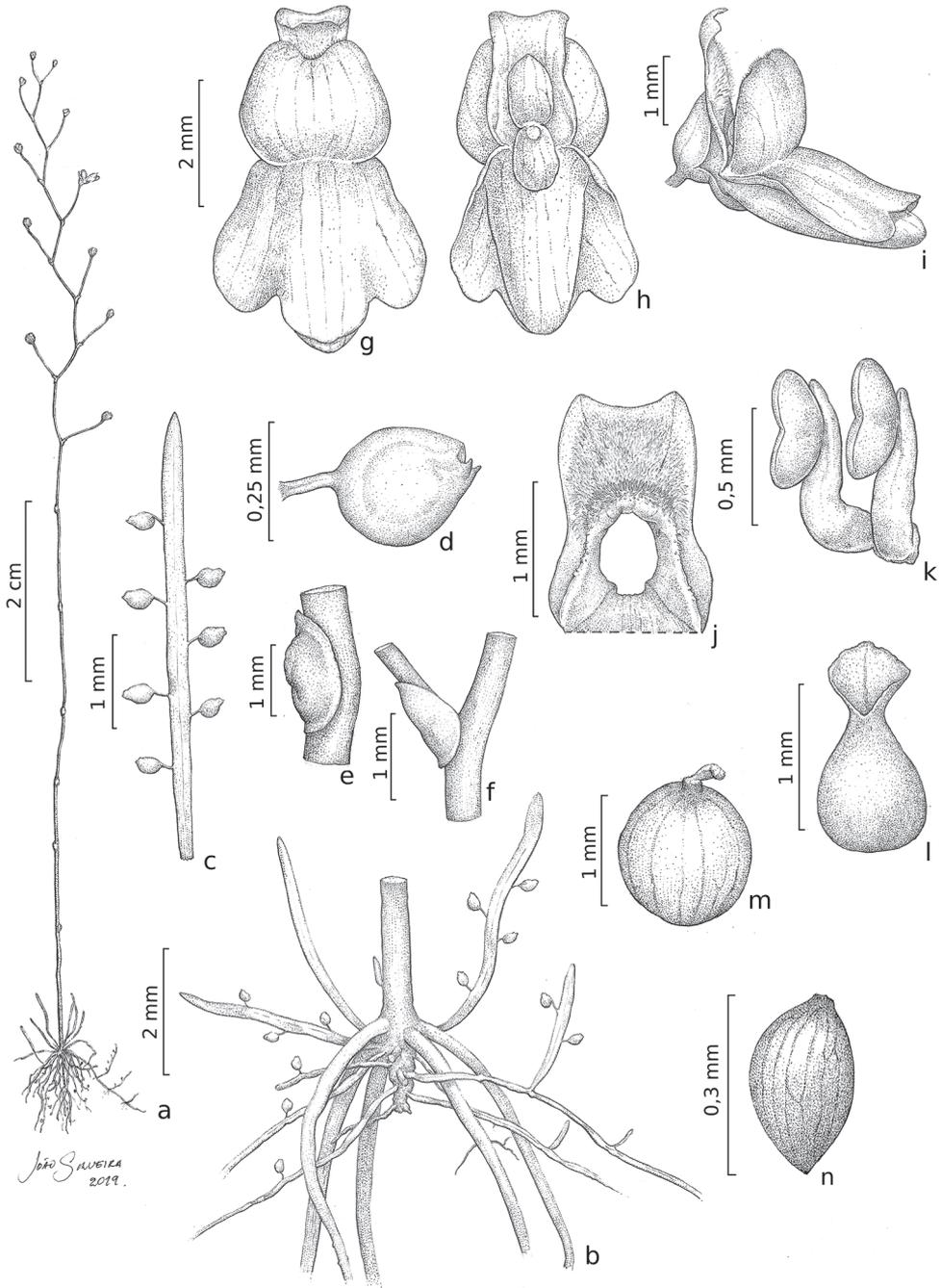


Figure 4. *Utricularia jamamacaru* **a** habit, in flower **b** base of plant with stolons with traps, rhizoids, leaves with traps, and peduncle base **c** leaf with traps **d** utricle, side view **e** scale **f** base of the pedicel, and bract **g** flower, in anterior **h** flower, in posterior view **i** flower, in lateral view **j** upper lip of the corolla **k** stamens **l** pistil **m** fruit **n** seed. All based on the holotype. Illustrations by João Silveira.



Figure 5. *Utricularia jaramacaru* **a** inflorescence apex with open flowers and bud **b** detail of inflorescence apex showing mucilage droplet in the axil of a pedicel **c** inflorescence apex with a flower in posterior view, highlighting the calyx (**cl**) **d** flower in anterior view; **e**, peduncle bases with stolons and leaves.



Figure 6. SEM microphotographs of seeds of *Utricularia jaramacaru* at 420× magnification, in dorsal, lateral and oblique view (from the holotype).

Additional specimens examined (paratypes). BRAZIL • Pará; [Óbidos]; Rio Jaramacaru, entre o acampamento e a cachoeira; 26 May 1957; G.A. Black, W. Egler, P. Cavalcante & A. Silva 57-19500 (IAN 95620) • *ibid.*; trilha após a ponte do rio Jamaracaru [*sic*], em direção à cachoeira; 01°10'12.99"S, 055°41'50.69"W; 80 m; 27 Apr. 2018; J.A. Siqueira Filho 4112 (HVASF 23703).

Key to *Utricularia* sect. *Setiscapella*

Adapted from Taylor (1989: 523) with the addition of *U. jaramacaru* as follows:

- | | | |
|----|---|----------------------|
| 1 | Corolla pink, lilac or white | 2 |
| 1' | Corolla yellow..... | 3 |
| 2 | Trap with filiform and sparsely branched appendages; corolla pink or lilac, 7–10 mm long, upper lip apex rounded or truncate..... | <i>U. physoceras</i> |
| 2' | Trap with denticulate and simple appendages; corolla white, c. 5 mm long, upper lip apex bilobed | <i>U. jaramacaru</i> |

List of other Lentibulariaceae species recorded in the Campos do Ariramba

Below, we present the preliminary list of the Lentibulariaceae from the Campos do Ariramba region followed by the specimen(s) examined, comprising 12 species (including the new species here described). This number is certainly an underestimation of the family's diversity in the area, as we still believe the site remains under-sampled. Further fieldwork covering a broader area and different months are deemed necessary to present a more comprehensive list in the future.

Genlisea oxycentron P.Taylor

BRAZIL. Pará: Óbidos; FLOTA Trombetas, Comunidade Jaramacaru, Rio Jaramacaru; 10 Jun. 2019; C.O. Andrino 558 (MG).

Utricularia adpressa Salzm. ex A.St.-Hil. & Girard

BRAZIL. Pará: Óbidos; FLOTA Trombetas, Estrada para Tabuleta, Campos do Ariramba; 11 Jun. 2019, R.G. Barbosa-Silva 1167 (MG) • *ibid*; comunidade Jaramacaru, Estrada para a Cachoeira do Rio Jaramacaru; 12 Jun. 2019; C.O. Andrino 572 (MG) • *ibid*; Campos Gerais (Ariramba), a cerca de 5 km da ponte do Jaramacaru em linha reta; 9 Jun. 2019; J.F. Maciel-Silva 400 (MG).

Utricularia amethystina Salzm. ex A.St.-Hil. & Girard

BRAZIL. Pará: Óbidos; trilha após a ponte do rio Jaramacaru [*sic*] em direção à cachoeira; 01°10'05.49"S, 055°42'35.39"W; 76 m; 27 Apr. 2018; J.A. Siqueira Filho 4115 (HVASF 23706); • *ibid*; FLOTA Trombetas, comunidade Jaramacaru, Cachoeira do Rio Jaramacaru; 9 Jun. 2019; D.C. Zappi 4846 (MG) • *ibid*; comunidade Jaramacaru, Rio Jaramacaru; 10 Jun. 2019; C.O. Andrino 557 (MG) • *ibid*; Estrada para Tabuleta, Campos do Ariramba; 11 Jun. 2019; R.G. Barbosa-Silva 1149 (MG) • *ibid*; Campos Gerais (Ariramba), à cerca de 5 km da ponte do Jaramacaru em linha reta; 9 Jun. 2019; J.F. Maciel-Silva 402 (MG) • *ibid*; Campos Gerais (Ariramba), campina a 300 m a nordeste da cachoeira do Jaramacaru; 7 Jun. 2019; C.S. Nunes 486 (MG).

Utricularia hispida Lam.

BRAZIL. Pará: Região do Ariramba, Igarapé Quebra-dente; 30 May 1957; G.A. Black et al. 19802 (IAN 96255).

Utricularia hydrocarpa Vahl

BRAZIL. Pará: Óbidos; FLOTA Trombetas, comunidade Jaramacaru, Cachoeira do Rio Jaramacaru; 9 Jun. 2019; D.C. Zappi 4836 (MG) • *ibid*; Campo do Jaramacaru [*sic*], perto do barracão, região do Ariramba; 26 Jun. 1957; G.A. Black et al. 19620 (IAN 95738).

Utricularia longeciliata A.DC.

BRAZIL. Pará: Oriximiná; Campos do Ariramba, campinas inundáveis da margem do Rio Jaramacaru, afloramentos areníticos; 70 m a.s.l.; 08 Jun. 1980; G. Martinelli et al. 6880 (RB 203406) • *ibid*, G. Martinelli et al. 6897 (RB).

Utricularia neottioides A.St.-Hil. & Girard

BRAZIL. Pará: Óbidos; FLOTA Trombetas, comunidade Jaramacaru, Estrada para Tabuleta, Campos do Ariramba, Igarapé do Mutum; 11 Jun. 2019; R.G. Barbosa-Silva 1134 (MG).

Utricularia pusilla Vahl

BRAZIL. Pará: Óbidos; FLOTA Trombetas, comunidade Jaramacaru, Beira da Cachoeira do Rio Jaramacaru; 12 Jun. 2019; C.O. Andrino 584 (MG);

Utricularia simulans Pilg.

BRAZIL. Pará: Óbidos; FLOTA Trombetas, Estrada para Tabuleta, Campos do Ariramba; 7 Jun. 2019; D.C. Zappi 4799 (MG).

Utricularia subulata L.

BRAZIL. Pará: Óbidos; perimetral norte, Rio Jaramacaru, área alagada entre os afloramentos rochosos próximo à casa de Juarez; 01°10'16.89"S, 055°41'16.39"W; 80 m a.s.l.; 27 Apr. 2018; J.A. Siqueira Filho 4107 (HVASF 23698) • *ibid*; FLOTA Trombetas, comunidade Jaramacaru, Cachoeira do Rio Jaramacaru; 9 Jun. 2019; D.C. Zappi 4851 (MG) • *ibid*; Rio Jaramacaru; 10 Jun. 2019; C.O. Andrino 561 (MG) • *ibid*; Floresta Estadual do Trombetas, Campos Gerais (Ariramba), cerca de 1 km a sul da Vila do Jaramacaru; 11 Jun. 2019; M. Pastore 947 (MG) • Oriximiná; Campos de Ariramba, Campinas inundáveis da margem do afloramento arenítico; 8 Jun. 1980; G.M. Martinelli 6878 (INPA, MG).

Discussion and concluding remarks

Both species described here were first collected over 60 years ago, and the specimens remained undetermined until the preparation of this work. This is not an isolated event since more than half of the new species described in recent years were published decades after being first collected and deposited in herbarium collections (Bebber et al. 2010). In the case of these new *Utricularia* species, a few factors can be listed to explain the lag between first collection and description, which are common in other plant groups. First, Amazonian herbaria are quite distant from most botanical research centers, receiving fewer resources, both human and financial, therefore being less visited by specialists (Hopkins 2019; de Gasper et al. 2020). This is also reflected by the still low number of imaged specimens in the collections housed in these herbaria, hindering the remote access by specialists and leaving a considerable number of these specimens 'undetermined'. This means that the average number of species not yet de-

scribed deposited in these herbaria tends to be higher, accentuating the urgent debate on taxonomy in describing diversity in the current biodiversity crisis (Dubois 2003; Giam et al. 2011; Tedesco et al. 2014). Also, it is worth highlighting that, in this case, the identification of the historical herbarium specimens as new species could only be confirmed after new collections were made, therefore reinforcing both the importance of funding for fieldwork in remote areas and the relevance of such herbaria collections as sources for identification of the still undescribed diversity (for further examples of similar cases, see: Ferreira et al. 2016; Barbosa-Silva et al. 2018; Farroñay et al. 2018).

Similarly to several areas of open vegetation in the Amazon and the Amazon rainforest itself, the vegetation of the Campos do Ariramba is poorly understood, and, until recently, few botanical expeditions were carried out to the area. The most significant botanical contributions to the area were conducted by Adolpho Ducke in 1905 and 1906, resulting in the description of several new species for the region, such as *Dyckia duckei* L.B.Sm. (Smith 1958), *Ouratea duckei* Huber (Huber 1913), and *Caraiipa myrcioides* Ducke (Ducke 1922). Later, another expedition conducted by Walter A. Egler and George Alexander Black resulted in the first and only preliminary floristic list published for the area (Egler 1960). Egler (1960) makes it clear that the list is unfinished because Black died tragically after the expedition, and his material was not found, disappearing together with his valuable observations and field records that possibly resulted in the aforementioned gaps in Egler's study, which was dedicated posthumously to Black. An example of these gaps are the Lentibulariaceae, which are cited in the text as important elements of the wetlands but not listed in the work (Egler 1960). This further justifies the presentation of a full list for the family herewith.

The access to the Campos do Ariramba, currently only possible by dirt road, is the result of a failed attempt to connect the site to the savannas in the northern limit of Pará state (called by Ducke and Egler as Campos Gerais; currently the Tumucumaque Indigenous Park), intending to create areas for livestock (Ducke 1910; Egler 1960). The construction of this road has impacted the area through deforestation and modification into cattle pastures adjacent to the road to the FLONA (Fig. 1). This is not an isolated occurrence in the municipalities of Óbidos and Oriximiná, as roads intensify deforestation in the Amazon, while protected areas mitigate this impact (Pfaff et al. 2007; Barber et al. 2014). This scenario, coupled with the current environmental policy that is incapable or unwilling to preserve the Amazon Rainforest biome is increasing deforestation and accelerating climate change (Rajão et al. 2020), representing a poor prospect especially for range-restricted, inconspicuous species that might be extinct even before being collected and identified.

Acknowledgments

We are grateful to João Silveira for the illustrations; to Helena Joseane Raiol Souza for the images of the Lentibulariaceae specimens deposited at IAN; to curators of the herbaria cited and staff members of the Museu Paraense Emilio Goeldi. We also thank field companions Clóvis Maurity, André S. Gil, Clebiana Nunes, Juliene Maciel, Ma-

yara Pastore, and Dona Dalva and family for their help and support. IDEFLOR issued collecting permits (SISBIO 60465) and provided field support. Instituto Nacional da Mata Atlântica (INMA) for providing the facilities for the study. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided financial support for PMG (grant 302306/2019-6), RGS (380010/2020-8) and COA (380001/2020-9), and DCZ currently holds a research grant from CNPq.

References

- Adeney JM, Christensen NL, Vicentini A, Cohn-Haft M (2016) White-sand Ecosystems in Amazonia. *Biotropica* 48(1): 7–23. <https://doi.org/10.1111/btp.12293>
- Andrino CO, Barbosa-Silva RG, Lovo J, Viana PL, Moro M, Zappi DC (2020) Iron islands in the Amazon: Investigating the floristic network of *canga* outcrops. *PhytoKeys* 165: 1–25. <https://doi.org/10.3897/phytokeys.165.54819>
- Assis LFFG, Ferreira KR, Vinhas L, Maurano L, Almeida C, Carvalho A, Rodrigues J, Maciel A, Camargo C (2019) TerraBrasilis: A Spatial Data Analytics Infrastructure for Large-Scale Thematic Mapping. *ISPRS International Journal of Geo-Information* 8: e513. <https://doi.org/10.3390/ijgi8110513>
- Bachman S, Moat J, Hill A, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Baleeiro PC, Jobson RW, Sano PT (2015) Morphometric approach to address taxonomic problems: The case of *Utricularia* sect. *Foliosa* (Lentibulariaceae). *Journal of Systematics and Evolution* 54(2): 175–186. <https://doi.org/10.1111/jse.12186>
- Baleeiro PC, Sano PT, Jobson RW (2019) Molecular Phylogeny of the *Utricularia amethystina* Complex (*Utricularia* sect. *Foliosa*) Assessed Using Plastid and Nuclear Sequence Data. *Systematic Botany* 44(2): 398–404. <https://doi.org/10.1600/036364419X15562052252045>
- Barber CP, Cochrane MA, Souza Jr CM, Laurance WF (2014) Roads, deforestation, and the mitigating effect of protected areas in the Amazon. *Biological Conservation* 177: 203–209. <https://doi.org/10.1016/j.biocon.2014.07.004>
- Barbosa-Silva RG, Labiak PH, Gil ADSB, Goldenberg R, Michelangeli FA, Martinelli G, Coelho MAN, Zappi DC, Forzza RC (2016) Over the hills and far away: New plant records for the Guayana Shield in Brazil. *Brittonia* 68(4): 397–408. <https://doi.org/10.1007/s12228-016-9435-3>
- Barbosa-Silva RG, Trovó M, Martinelli G, Campostrini Forzza R (2018) Up on the table mountains in Brazil: New Bromeliaceae and Eriocaulaceae (Poales) from the Pantepui in the Guayana Shield. *Plant Ecology and Evolution* 151(1): 130–141. <https://doi.org/10.5091/plevevo.2018.1392>
- Barbosa-Silva RG, Bueno ML, Labiak PH, Coelho MAN, Martinelli G, Forzza RC (2020) The Pantepui in the Brazilian Amazon: vascular flora of Serra do Aracá, a cradle of diversity, richness and endemism. *The Botanical Review*. <https://doi.org/10.1007/s12229-020-09235-x>
- Bebber DP, Carine MA, Wood JRI, Wortley AH, Harris DJ, Prance GT, Davidse G, Paige J, Pennington TD, Robson NKB, Scotland RW (2010) Herbaria are a major frontier for

- species discovery. Proceedings of the National Academy of Sciences of the United States of America 107(51): 22169–22171. <https://doi.org/10.1073/pnas.1011841108>
- Bove CP (2008) A new species of *Utricularia* (Lentibulariaceae) from central Brazil. Revista Brasileira de Botânica. Brazilian Journal of Botany 31(4): 555–558. <https://doi.org/10.1590/S0100-84042008000400002>
- Brazil Flora Group [BFG] (2015) Growing knowledge: an overview of Seed Plant diversity in Brazil. Rodriguésia 66: 1085–1113. <https://doi.org/10.1590/2175-7860201566411>
- Brazil Flora Group [BFG] (2018) Brazilian Flora 2020: Innovation and collaboration to meet Target 1 of the Global Strategy for Plant Conservation (GSPC). Rodriguésia 69(4): 1513–1527. <https://doi.org/10.1590/2175-7860201869402>
- Carregosa T, Costa SM (2014) Ampliação da distribuição geográfica de três espécies de *Utricularia* (Lentibulariaceae) para o bioma Mata Atlântica. Rodriguésia 65(2): 563–565. <https://doi.org/10.1590/S2175-78602014000200017>
- Cheek M, Lughadha EN, Kirk P, Lindon H, Carretero J, Looney B, Douglas B, Haelewaters D, Gaya E, Llewellyn T, Aisnworth AM, Gafforov Y, Hyde K, Crous P, Hughes M, Walker BE, Forzza RC, Wong KM, Niskanen T (2020) New scientific discoveries: Plants and fungi. Plants People Planet 2(5): 371–388. <https://doi.org/10.1002/ppp3.10148>
- Costa SM, Bittrich V, Do Amaral MCE (2016) Lentibulariaceae from the Viruá National Park in the northern Amazon, Roraima, Brazil. Phytotaxa 258(1): 1–25. <https://doi.org/10.11646/phytotaxa.258.1.1>
- Costa FM, Terra-Araujo MH, Zartman CE, Cornelius C, Carvalho FA, Hopkins MJG, Viana PL, Prata EMB, Vicentini A (2019) Islands in a green ocean: Spatially structured endemism in Amazonian white-sand vegetation. Biotropica 52(1): 34–45. <https://doi.org/10.1111/btp.12732>
- de Gasper AL, Stehmann JR, Roque N, Bigio NC, Sartori ALB, Grittz GS (2020) Brazilian herbaria: An overview. Acta Botanica Brasílica 34(2): 352–359. <https://doi.org/10.1590/0102-33062019abb0390>
- Devecchi MF, Lovo J, Moro MF, Andrino CO, Barbosa-Silva RG, Viana PL, Giulietti AM, Antar G, Watanabe MTC, Zappi DC (2020) Beyond forests in the Amazon: Biogeography and floristic relationships of the Amazonian savannas. Botanical Journal of the Linnean Society 193(4): 478–503. <https://doi.org/10.1093/botlinnean/boaa025>
- Flora do Brasil (2020) (under construction) Flora do Brasil online 2020, Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/> [accessed 16.10.2020]
- Dubois A (2003) The relationships between taxonomy and conservation biology in the century of extinctions. Comptes Rendus Biologies 326: 9–21. [https://doi.org/10.1016/S1631-0691\(03\)00022-2](https://doi.org/10.1016/S1631-0691(03)00022-2)
- Ducke A (1910) Explorações científicas no Estado do Pará. Boletim do Museu Goeldi (Museu Paraense) de Historia Natural e Ethnographia: 100–197.
- Ducke A (1922) Plantes nouvelles ou peu connues de la région amazonienne. Archivos do Jardim Botânico do Rio de Janeiro 3: e217.
- Egler WA (1960) Contribuições ao conhecimento dos campos da Amazônia. I – Os campos do Ariramba. Boletim do Museu Paraense Emílio Goeldi Série Botânica 4: 1–40.
- Farroñay F, Adrianzén MU, Perdiz RDO, Vicentini A (2018) A new species of *Macrolobium* (Fabaceae, Detarioideae) endemic on a Tepui of the Guyana Shield in Brazil. Phytotaxa 361(1): 97–105. <https://doi.org/10.11646/phytotaxa.361.1.8>

- Ferreira GE, Chautems A, Hopkins MJG, Perret M (2016) Independent evolution of pouched flowers in the Amazon is supported by the discovery of a new species of *Lesia* (Gesneriaceae) from Serra do Aracá tepui in Brazil. *Plant Systematics and Evolution* 302(8): 1109–1119. <https://doi.org/10.1007/s00606-016-1320-8>
- Fleischmann A (2012a) Monograph of the Genus *Genlisea*. Redfern Natural History, Poole, 727 pp.
- Fleischmann A (2012b) The new *Utricularia* species described since Peter Taylor's monograph. *Carnivorous Plant Newsletter* 41: 67–76.
- Fleischmann A (2015) Taxonomic *Utricularia* news. *Carnivorous Plant Newsletter* 44: 13–16.
- Fleischmann A, Rivadavia F (2009) *Utricularia rostrata* (Lentibulariaceae), a new species from the Chapada Diamantina, Brazil. *Kew Bulletin* 64(1): 155–159. <https://doi.org/10.1007/s12225-008-9086-y>
- Fleischmann A, Schäferhoff B, Heubl G, Rivadavia F, Barthlott W, Müller KF (2010) Phylogenetics and character evolution in the carnivorous plant genus *Genlisea* A. St.-Hil. (Lentibulariaceae). *Molecular Phylogenetics and Evolution* 56(2): 768–783. <https://doi.org/10.1016/j.ympev.2010.03.009>
- Fleischmann A, Costa SM, Bittrich V, do Amaral MCE, Hopkins M (2017) A new species of corkscrew plant (*Genlisea*, Lentibulariaceae) from the Amazon lowlands of Brazil, including a key to all species occurring north of the Amazon River. *Phytotaxa* 319(3): 289–297. <https://doi.org/10.11646/phytotaxa.319.3.9>
- Fonseca-da-Silva TL, Lovo J, Zappi DC, Moro MF, Leal ES, Maurity C, Viana PL (2020) Plant species on Amazonian *canga* habitats of Serra Arqueada: the contribution of an isolated outcrop to the floristic knowledge of the Carajás region, Pará, Brazil. *Brazilian Journal of Botany* 43: 315–330. <https://doi.org/10.1007/s40415-020-00608-5>
- Forzza RC, Baumgratz JFA, Bicudo CEM, Canhos DAL, Carvalho Jr AA, Coelho MAN, Costa AF, Costa DP, Hopkins MG, Leitman PM, Lohmann LG, Lughadha EN, Maia LC, Martinelli G, Menezes M, Morim MP, Peixoto AL, Pirani JR, Prado J, Queiroz LP, Souza S, Souza VC, Stehmann JR, Sylvestre LS, Walter BMT, Zappi DC (2012) New Brazilian Floristic List Highlights Conservation Challenges. *Bioscience* 62(1): 39–45. <https://doi.org/10.1525/bio.2012.62.1.8>
- García-Villacorta R, Dexter KG, Pennington T (2016) Amazonian White-Sand Forests Show Strong Floristic Links with Surrounding Oligotrophic Habitats and the Guiana Shield. *Biotropica* 48(1): 47–57. <https://doi.org/10.1111/btp.12302>
- GBIF.org (2020) GBIF Home Page. <https://www.gbif.org> [accessed 20.05.2020]
- Giam X, Scheffers BR, Sodhi NS, Wilcove DS, Ceballos G, Ehrlich PR (2011) Reservoirs of richness: least disturbed tropical forests are centres of undescribed species diversity. *Proceedings of the Royal Society B: Biological Sciences* 279(1726): 67–76. <https://doi.org/10.1098/rspb.2011.0433>
- Giulietti AM, Giannini TC, Mota NFO, Watanabe MTC, Viana PL, Pastore M, Silva UCS, Siqueira MF, Pirani JR, Lima HC, Pereira JBS, Brito RM, Harley RM, Siqueira JO, Zappi DC (2019) Edaphic Endemism in the Amazon: Vascular Plants of the *canga* of Carajás, Brazil. *Botanical Review* 85(4): 357–383. <https://doi.org/10.1007/s12229-019-09214-x>
- Givnish TJ, Sparks KW, Hunter SJ, Pavlovic A (2018) Why are plants carnivorous? Cost/benefit analysis, whole-plant growth, and the context-specific advantages of botanical carnivory. In: Ellison AM, Adamec L (Eds) *Carnivorous Plants: Physiology, ecol-*

- ogy and evolution. Oxford University Press, Oxford, 233–255. <https://doi.org/10.1093/oso/9780198779841.003.0018>
- Gonella PM, Baleeiro PC (2018) *Utricularia biceps* (Lentibulariaceae), a new carnivorous species endemic to the campos rupestres of Brazil. *Phytotaxa* 376(5): 214–222. <https://doi.org/10.11646/phytotaxa.376.5.4>
- Gröger A (1994) Análisis preliminar de la florula y vegetación del Monumento Natural Piedra La Tortuga, Estado Amazonas, Venezuela. *Acta Botanica Venezuelica* 17: 128–153.
- Guedes FM, Garcia GS, Versieux LM, Matias LQ, Alves M (2018) Insights on underestimated Lentibulariaceae diversity in northeastern Brazil: New records and notes on distribution, diversity and endemism in the family. *Brazilian Journal of Botany* 41(4): 867–887. <https://doi.org/10.1007/s40415-018-0497-1>
- Guedes FM, Garcia GS, Araújo GB, Coan AI, Alves M (2019) Rediscovery of *Utricularia cutleri* Steyerl. (Lentibulariaceae) in Rio Grande do Norte, Brazil: Taxonomic Reestablishment, Geographic Distribution, and Notes on Pollen and Bladder-Trap Micromorphology. *Systematic Botany* 44(3): 708–718. <https://doi.org/10.1600/036364419X15620114943864>
- Hopkins MJG (2019) Are we close to knowing the plant diversity of the Amazon? *Anais da Academia Brasileira de Ciências* 91(Supl. 3): e20190396. <https://doi.org/10.1590/0001-3765201920190396>
- Huber J (1913) *Plantae Duckeanae Austro-Guyanenses*. *Bulletin de la Société Botanique de Genève* 5(2): 179–212.
- IBGE (2020) BDIA, Banco de Dados de Informações Ambientais. <https://bdiaweb.ibge.gov.br/#/home> [accessed 21.04.2020]
- INCT (2018) *Herbário Virtual da Flora e dos Fungos*. <http://inct.splink.org.br/> [accessed 12.06.2020]
- IUCN (2012) *IUCN Red List Categories and Criteria: Version 3.1*. Second edition. Gland, Switzerland and Cambridge, UK, 32 pp. <https://portals.iucn.org/library/sites/library/files/documents/RL-2001-001-2nd.pdf>
- Jobson RW, Playford J, Cameron KM, Albert VA (2003) Molecular phylogenetics of Lentibulariaceae inferred from plastid *rps16* intron and *trnL-F* DNA sequences: Implications for character evolution and biogeography. *Systematic Botany* 28: 157–171.
- Jobson RW, Baleeiro PC, Guisande C (2018) Systematics and evolution of Lentibulariaceae: III. *Utricularia*. In: Ellison AM, Adamec L (Eds) *Carnivorous Plants: Physiology, ecology and evolution*. Oxford University Press, Oxford, 89–104. <https://doi.org/10.1093/oso/9780198779841.003.0008>
- Kew RBG (2016) *The State of the World's Plants Report – 2016*. Royal Botanic Gardens, Kew, 80 pp. https://stateoftheworldsplants.org/2016/report/sotwp_2016.pdf
- Miranda IS (1993) Estrutura do estrato arbóreo do cerrado amazônico em Alter-do-Chão, Pará, Brasil. *Brazilian Journal of Botany* 16: 143–150.
- Miranda IS, Absy ML, Rebêlo GH (2002) Community Structure of Woody Plants of Roraima Savannas, Brazil. *Plant Ecology* 164(1): 109–123. <https://doi.org/10.1023/A:1021298328048>
- Miranda IS, Almeida SS, Dantas PJ (2006) Florística e estrutura de comunidades arbóreas em cerrados de Rondônia, Brasil. *Acta Amazonica* 36(4): 419–430. <https://doi.org/10.1590/S0044-59672006000400004>

- Mota NFO, Watanabe MTC, Zappi DC, Hiura AL, Pallos J, Viveros RS, Giulietti AM, Viana PL (2018) Amazon canga: the unique vegetation of Carajás revealed by the list of seed plants. *Rodriguésia* 69(3): 1435–1487. <https://doi.org/10.1590/2175-7860201869336>
- Mota NF de O, Zappi DC (2018) Flora of the canga of Serra dos Carajás, Pará, Brazil: Lentibulariaceae. *Rodriguésia* 69(1): 119–132. <https://doi.org/10.1590/2175-7860201869110>
- Müller K, Borsch T (2004) Phylogenetics of *Utricularia* (Lentibulariaceae) and molecular evolution of the *trnK* intron in a lineage with high substitutional rates. *Plant Systematics and Evolution* 250(1–2): 39–67. <https://doi.org/10.1007/s00606-004-0224-1>
- Nelson BW, Ferreira CAC, da Silva MF, Kawasaki ML (1990) Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature* 345(6277): 714–716. <https://doi.org/10.1038/345714a0>
- Oliveira U, Paglia AP, Brescovit AD, de Carvalho CJB, Silva DP, Rezende DT, Leite FSF, Batista JAN, Barbosa JPPP, Stehmann JR, Ascher JS, de Vasconcelos MF, De Marco Jr P, Löwenberg-Neto P, Dias PG, Ferro VG, Santos AJ (2016) The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. *Diversity & Distributions* 22(12): 1232–1244. <https://doi.org/10.1111/ddi.12489>
- Pfaff A, Robalino J, Walker R, Aldrich S, Caldas M, Reis E, Perz S, Bohrer C, Arima E, Laurance W, Kirby K (2007) Road Investments, Spatial Spillovers, And Deforestation In The Brazilian Amazon. *Journal of Regional Science* 47(1): 109–123. <https://doi.org/10.1111/j.1467-9787.2007.00502.x>
- Pires JM, Prance GT (1985) The vegetation types of the Brazilian Amazon. In: Prance GT, Lovejoy TE (Eds) *Amazonia: Key Environments*. Pergamon Press, 109–145.
- Prance GT (1996) Islands in Amazonia. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 351(1341): 823–833. <https://doi.org/10.1098/rstb.1996.0077>
- QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org> [accessed 25.01.2020]
- Rajão R, Soares-Filho B, Nunes F, Börner J, Machado L, Assis D, Oliveira A, Pinto L, Ribeiro V, Rausch L, Gibbs H, Figueira D (2020) The rotten apples of Brazil's agribusiness. *Science* 369: 246–248. <https://doi.org/10.1126/science.aba6646> PubMed
- REFLORA 2020 (2020) Refflora – Virtual Herbarium. <http://reflora.jbrj.gov.br/reflora/herbarioVirtual/> [accessed 31.05.2020]
- Rivadavia F (2000) The giant *Genlisea uncinata* P.Taylor & Fromm-Trinta. *Carnivorous Plant Newsletter* 29: 83–86.
- Rivadavia F, Vicentini A, Fleischmann A (2009) A new species of sundew (*Drosera*, Droseraceae), with water-dispersed seed, from the floodplains of the northern Amazon Basin, Brazil. *Ecotropica* (Bonn) 15: 13–21.
- Schulman L, Toivonen T, Ruokolainen K (2007) Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography* 34(8): 1388–1399. <https://doi.org/10.1111/j.1365-2699.2007.01716.x>
- Smith LB (1958) Três Bromeliáceas novas do Museu Paraense Emilio Goeldi. *Boletim do Museu Paraense Emílio Goeldi. Série Botânica* II 1: 1–5.
- Souza PCB, Bove CP (2011) A New Species of *Utricularia* (Lentibulariaceae) from Chapada dos Veadeiros (Central Brazil). *Systematic Botany* 36(2): 465–469. <https://doi.org/10.1600/036364411X569642>

- Stroop J, Umbelino B, Correia RA, Campos-Silva JV, Ladle RJ, Malhado ACM (2020) The ghosts of forests past and future: Deforestation and botanical sampling in the Brazilian Amazon. *Ecography* 43(7): 979–989. <https://doi.org/10.1111/ecog.05026>
- Taylor P (1964) The genus *Utricularia* L. (Lentibulariaceae) in Africa (south of the Sahara) and Madagascar. *Kew Bulletin* 18(1): 1–245. <https://doi.org/10.2307/4115510>
- Taylor P (1989) The Genus *Utricularia*: a Taxonomic Monograph. *Kew Bulletin Additional Series* 14, 724 pp.
- Taylor P (1999) Lentibulariaceae. In: Berry PE, Yatskievych K, Holst BK (Eds) *Flora of the Venezuelan Guayana* (Vol. 5). Missouri Botanical Garden Press, St. Louis, 782–803.
- Tedesco PA, Bigorne R, Bogan AE, Giam X, Jézéquel C, Hugueny B (2014) Estimating How Many Undescribed Species Have Gone Extinct. *Conservation Biology* 28(5): 1360–1370. <https://doi.org/10.1111/cobi.12285>
- Thiers B (2020 continuously updated). Index Herbariorum. <http://sweetgum.nybg.org/science/ih/> [accessed 01.01.2020]
- Zappi DC, Moro MF, Walker B, Meagher T, Viana PL, Mota NFO, Watanabe MTC, Lughadha EN (2019) Plotting a future for Amazonian canga vegetation in a campo rupestre context. *PLoS ONE* 14(8): e0219753. <https://doi.org/10.1371/journal.pone.0219753>

Leucheria cantillanensis (Nassauvieae, Asteraceae), a new species endemic to Central Chile

Nicolás Lavandero^{1,2}, Benito Rosende¹, María Fernanda Pérez^{1,2}

1 Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Avenida Libertador B. O'Higgins 340, Santiago, Chile **2** Instituto de Ecología y Biodiversidad (IEB), Universidad de Chile, Las Palmeras 3425, Santiago, Chile

Corresponding author: Nicolás Lavandero (nglavand@uc.cl)

Academic editor: P. de Lange | Received 12 August 2020 | Accepted 6 October 2020 | Published 8 December 2020

Citation: Lavandero N, Rosende B, Pérez MF (2020) *Leucheria cantillanensis* (Nassauvieae, Asteraceae), a new species endemic to Central Chile. PhytoKeys 169: 99–117. <https://doi.org/10.3897/phytokeys.169.57532>

Abstract

A new species, *Leucheria cantillanensis* **sp. nov.**, endemic to the coastal mountain range of Central Chile, is described. By using both nDNA and cpDNA, phylogenetic relationships of the new species were investigated. This new species belongs to the acaulescent/subacaulescent clade of *Leucheria*, which is congruent with the morphology of the species. A detailed description, distribution map, insights about its habitat, conservation status, and illustrations are provided. An updated key for acaulescent/subacaulescent species of *Leucheria* from Central Chile is also given.

Keywords

Asteraceae, Cantillana, *Leucheria*, rupicolous flora, taxonomy

Introduction

The ecosystems found in central and southern Chile are one of 35 world biodiversity hotspots, owing to their combination of great diversity and high levels of endemism, and a past and ongoing loss of habitat and biodiversity (Myers et al. 2000; Mittermeier et al. 2005). Central Chile features a Mediterranean-type climate, although important climatic heterogeneity can be found due to latitudinal and altitudinal gradients (Armesto et al. 2007). This heterogeneity, accompanied by the climatic history throughout the Quaternary, must have contributed to the increased species richness and endemism

in the area (Arroyo et al. 1995; Villagrán 1995). Many genera show a high number of species within this area, such as *Adesmia* DC., *Chaetanthera* Ruiz & Pav., *Mutisia* L.f., *Oriastrum* Poepp., *Senecio* L., and *Leucheria* Lag., occurring in all available environments, from the coastal dunes, sclerophyllous forests and matorral to Andean vegetation near 4000 m above sea level (a.s.l.).

The genus *Leucheria* comprises 49 species (Crisci 1976; Katinas et al. 2008; Katinas et al. 2018; Jara-Arancio et al. 2019) distributed in Peru, Bolivia, Chile, and Argentina on the continent, plus the Falkland Islands. Most species are concentrated within the Patagonian-Andean and the Subantarctic phytogeographic domains (Cabrera and Willink 1973). The region of Chile with the greatest diversity of *Leucheria* overlaps with the Central and southern Chile biodiversity hotspot, with most species richness and endemism occurring within this area (Moreira-Muñoz et al. 2012). The available specimen coverage of *Leucheria* in Chile is reasonably good, with more than 1200 collected specimens distributed between the most important herbaria in the country, SGO and CONC. However, their collection localities are clustered mainly on accessible regions and along main highways, such as border crossings between Chile and Argentina and Bolivia, ski centres, or the Pan American Route 5 in the North of Chile. Furthermore, many species are poorly collected (e.g. *Leucheria apiifolia* Phil., *Leucheria glabriuscula* Reiche, *Leucheria graui* Katinas, M.C. Tellería & Crisci), and many other species have important geographic gaps among their collections (e.g. *Leucheria achilleifolia* Hook. & Arn., *Leucheria polyclados* (J. Remy) Reiche). Since the most comprehensive revision of the genus (Crisci, 1976), at least two new species (Katinas et al. 2008; Katinas et al. 2018) and a new variety (Ratto et al. 2014), which was later elevated to species level (Jara-Arancio et al. 2019), have been described.

In the context of the ongoing taxonomic revision of the genus, unusual specimens of *Leucheria* were collected at the Reserva Natural Altos de Cantillana (MMA 2018). The locality is known as one of the 72 priority sites for the conservation of biodiversity in Chile and the top in priority within the Metropolitan Region (CONAMA 2004). Altos de Cantillana is located in the coastal mountain range of the Metropolitan Region of Chile, a paradoxically species-rich area with high levels of endemism, but poorly collected and with only a few updated floristic catalogues (Romero and Teillier 2009; García 2010; Flores-Toro and Amigo 2013; Romero-Gárate and Teillier 2014). This work aims to describe a new species of *Leucheria* and investigate its phylogenetic affinities based on molecular data. We also provide a distribution map as well as information on its habitat and phenology, and a provisional assessment of its conservation status.

Methods

Herbarium and fieldwork

During the austral summer of 2019, a botanical exploration was made to the coastal mountain range of the Metropolitan Region of Chile, specifically to the Reserva Natural Altos de Cantillana (Fig. 1). Specimens of *Leucheria* that could not be assigned to

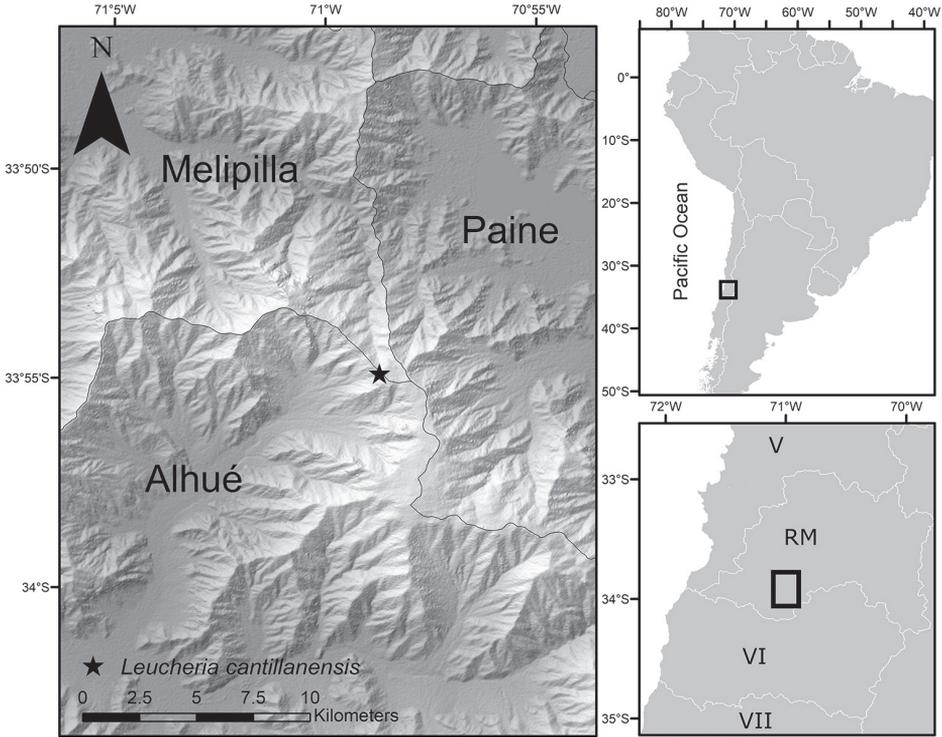


Figure 1. Distribution map of *Leucheria cantillanensis* (star) in Chile, Región Metropolitana, based on the type locality.

any of the accepted species for the genus were found. Herbarium specimens were collected, together with leaf material preserved in silica gel, as well as material preserved in alcohol 70%. Herbarium specimens were deposited to CONC and SGO herbaria. A systematic examination of herbarium specimens of *Leucheria* found at CONC and SGO, as well as online digital images of specimens available on E, K, and P, was carried out. The descriptions and keys were prepared after examining all available specimens. Terminology for describing floral parts follows Simpson (2010) and Beentje (2016).

Conservation status

The assessment of the conservation status of the species was made using the International Union for Conservation of Nature (IUCN 2017) criteria. The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCat (Bachman et al. 2011).

Taxon sampling for phylogenetic analysis

DNA sequences for nDNA (ITS), as well as cpDNA intergenic spacers (*rpl32-trnL* and *trnF-trnL*) were obtained from GenBank (www.ncbi.nlm.nih.gov/Genbank) for all species of *Leucheria* recognized in the phylogenetic reconstruction of the genus

(Jara-Arancio et al. 2017). Sequences for the putative new species were generated in the present study. As outgroups, we used sister taxa of *Leucheria* from Nassauvieae tribe: *Moscharia pinnatifida* Ruiz & Pav., *Moscharia solbrigii* Crisci, *Marticorenia foliosa* (Phil.) Crisci and *Spinoliva ilicifolia* (Hook et. Arn.) G. Sancho.

DNA extraction, amplification, sequencing, and phylogenetic analyses

Total genomic DNA was extracted from silica-dried material collected in the field from the type specimen using the Qiagen DNeasy Plant Mini Kit (QIAGEN, Santiago, Chile) following the manufacturer's instructions. Genomic DNA was used to amplify by PCR the internal transcribed spacer region (ITS) and the chloroplast *trnL-trnF* (Taberlet et al. 1991) and *rpl32-trnL* (Shaw et al. 2007) intergenic spacers. We amplified all regions in 25 µl PCR reactions following thermocycling procedures used in Jara-Arancio et al. (2017). Sanger sequencing was performed in the Plataforma de Secuenciación y Tecnologías Ómicas, Pontificia Universidad Católica de Chile, using the ABI PRISM 3500 xl Genetic Analyzer (Applied Biosystems). GenBank accession numbers for all DNA sequences are given in Suppl. material 1.

The assembled sequences were aligned using the ClustalW algorithm in Geneious Prime 2019.1.1 (<https://www.geneious.com>). Phylogenetic analyses were carried for both Maximum-likelihood (ML, Felsenstein 1981), using RAxML-AVX3 version (Stamatakis 2014) included in RAxMLGUI v.2.0 beta (Silvestro and Michalak 2012, Edler et al. 2019) and Bayesian inference (BI) using MrBayes x64 v3.2.7 (Ronquist et al. 2012) respectively. The best-supported model of nucleotide sequence evolution for each partition was determined based on the Akaike Information Criterion (AIC) using MrModeltest v2 (Nylander 2004). For the combined analysis with BI, three partitions were used corresponding for each region, in which evolutionary models for each one were: SYM+I+G in ITS; GTR+G in *rpl32-trnL* and GTR+I+G in *trnL-trnF*. Maximum likelihood analyses were run using the GTRGAMMA approximation, which approximates to a GTR model. Substitutions parameters were estimated independently for the nuclear and plastid partitions. The analysis included 1000 ML slow bootstrap replicates with 100 runs. Bayesian analyses were conducted under the respective best fit models for each partition, with two independent runs for 15 million generations, sampling every 10000 generations. Time series plots and effective sample size (ESS) were analyzed using TRACER v.1.7 (Rambaut et al. 2018) in order to check convergence for each run. The first 3 million generations were discarded as burn-in.

Results

Molecular phylogenetic analyses

The DNA matrix contained 2962 nucleotide characters (782 ITS, 1224 *rpl32-trnL* and 956 *trnL-trnF*), representing 44 ingroup and 4 outgroup accessions. BI and ML analyses yielded congruent topologies. The topology of the phylogenetic tree constructed in this

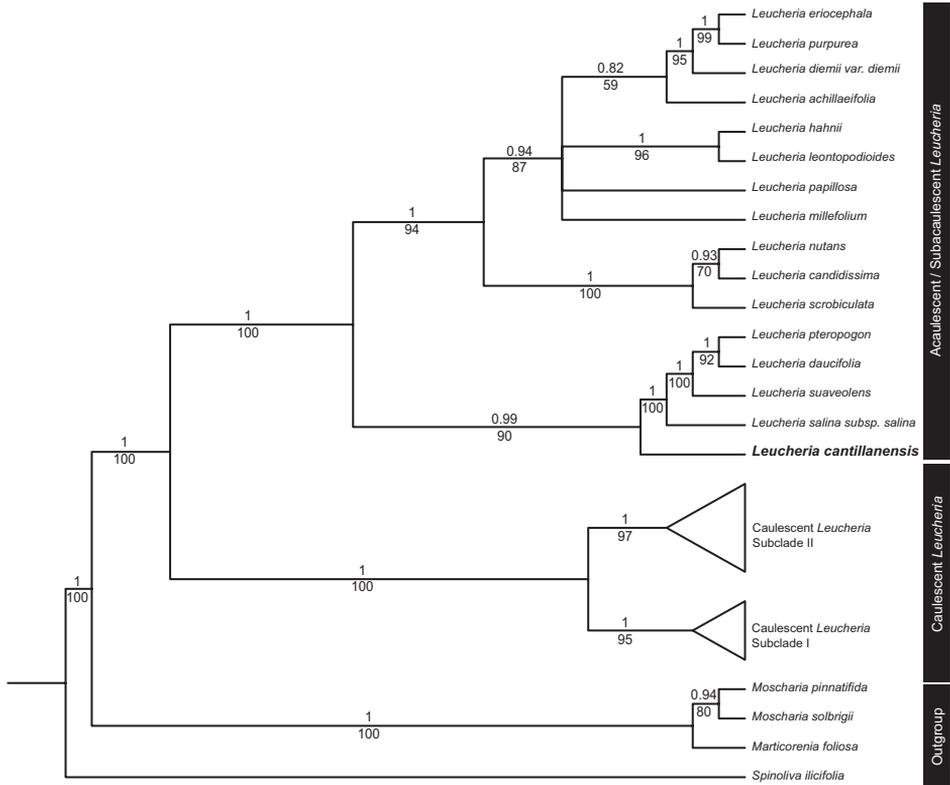


Figure 2. Phylogeny of *Leucheria* resulting from Bayesian analysis of the combined nuclear ITS and plastid *rpl32-trnL* and *trnL-trnF* dataset. Numbers above and below the branches represent the Posterior probabilities from the BI analysis and bootstrap values from the ML analysis, respectively. Nodes with <0.5 PP were collapsed to polytomies. The new species, *Leucheria cantillanensis* is highlighted in bold.

study is congruent with the three major clades within the genus found by Jara-Arancio et al. (2017), with slight differences at lower resolution (Fig. 2). Both caulescent clades I and II formed a well-supported clade (BS=97, PP=1.0; BS=95, PP=1.0, respectively). The acaulescent/subcaulescent clade formed a well-supported clade (BS=90, PP=0.99). *Leucheria cantillanensis* is nested within the latter clade, being sister taxa to *Leucheria salina* (J. Remy) Hieronymus subsp. *salina*, *Leucheria suaveolens* (D'Urv.) Spegazzini, *Leucheria pteropogon* (Griseb.) Cabrera and *Leucheria daucifolia* (Don) Crisci.

Taxonomic treatment

Leucheria cantillanensis Lavadero, sp. nov.

urn:lsid:ipni.org:names:77213224-1

Figures 3, 4

Diagnosis. *Leucheria cantillanensis* is similar to *L. salina* but differs in its flat lamina and chartaceous texture (vs. foliar segments perpendicular or oblique to the lamina axis and

leathery texture) (Figs 5C, D, 6G, I), conspicuously prominent venation, with the secondary and tertiary veins forming a raised pattern above and below the lamina (vs. non-prominent venation, with no raised pattern of veins in either side of the lamina) (Fig. 6G, I), 27–30 flowers per capitula (vs. 40–60), purple anther apical appendages (vs. greenish-yellow) (Fig. 6D, F). *Leucheria cantillanensis* is also similar to coastal forms of *L. runcinata* D. Don with white corollas, but it differs by its underground creeping rhizome with nodes and leaf scars and remnants of dry leaf petioles along the rhizome (vs. a lignified taproot with leaf scars concentrated at the base of the stem at the surface of the ground) (Fig. 6K, L), entirely glandular indumentum in the leaves (vs. glandular on the adaxial side and glandular and lanate on the abaxial side) (Fig. 6H, I), conspicuous prominent venation on both sides of the lamina (vs. inconspicuous and only midvein prominent on the abaxial side) and purple anther apical appendages (vs. greyish-blue) (Fig. 6E, F).

Type. CHILE. Región Metropolitana: Provincia de Melipilla, entre el límite de Alhué y Melipilla, Reserva Natural Altos de Cantillana, 33°54'54.24"S, 70°58'43.57"W, 2007 m., 27 December 2019, fl. And fr., *Lavandero* 700 (holotype: CONC!; Isotype SGO!).

Description. *Perennial* caulescent herb 15–30(–40) cm tall, decumbent, forming clumps of 5–6 aerial stems arising from the apex and nodes of the distal end of the rhizome. **Rhizome** dark brown, round, 10–15 mm wide, oblique to creeping, leafless below, but with remnants of dry leaf petioles, roots arising from the internodes. **Roots** dark brown, ca. 2 mm wide, round in cross-section. **Stems** purplish at the base, green at the top, 1.0–5.5 mm wide, simple or branching, round in cross-section, internodes up to 4 cm long, densely covered by glandular, capitate, (87–)115–180 µm long, multicellular (6–12-celled) trichomes with clear resin, fragrant, with pungent citric scent (same indumentum up to the corolla tube). **Leaves** dark green, alternate; basal leaves petiolate, semi-densely arranged at the base; petiole compressed, winged, vaginate, 2–2.5(–3.5) cm long; upper leaves sessile, amplexicaul, loosely arranged, gradually reduced in size towards the capitulescences. **Lamina** obovate, (10–)50–100(–140) × (5–)20–25(–35) mm; base attenuate, amplexicaul, apex mucronate; margin serrate, texture chartaceous, densely glandulous on both surfaces; pinnatisect to entire towards the tip; segments at the base entire, rarely 1(–2)-dentate, apex mucronate; segments in the middle (3–)4–6(–7)-dentate; apical segments fused, doubly dentate; venation conspicuously prominent, with the secondary and tertiary veins forming a raised pattern on both sides of the lamina, pinnate, semicraspedodromous, with primary vein ending in apical mucro, secondary veins either ending in second-order teeth or joining other distal secondary veins. **Capitulescences** a corymbiform cyme. **Capitula** 1–6 per stem, pedunculate, (0.5–)1.2–2.8(–3.6) cm long, homogamous, discoid. **Involucres** hemispheric 7.0–7.2 × 8.2–8.3 mm, two-seriate, alternate. A third series of involucre bracts with intermediate characters between outer and inner involucre bracts rarely present. **Receptacle** slightly convex, epaleate, glabrous. **Outer involucre bracts** 5–6, green, lanceolate, concave on the inner face, 6.6–7.6 × 1.10–1.21(–1.36) mm, with 3 dark-green longitudinal stripes (including the midrib), apex ciliate, margin entire, texture leaf-like, abaxial lamina and margins densely covered by glandular trichomes, adaxial lamina glabrous. **Middle involucre bracts** rarely present, 1–2, green, lanceolate, concave to flat, with 6.5–7.0 × 1.08–1.19 mm, with 3 dark-green longitudinal

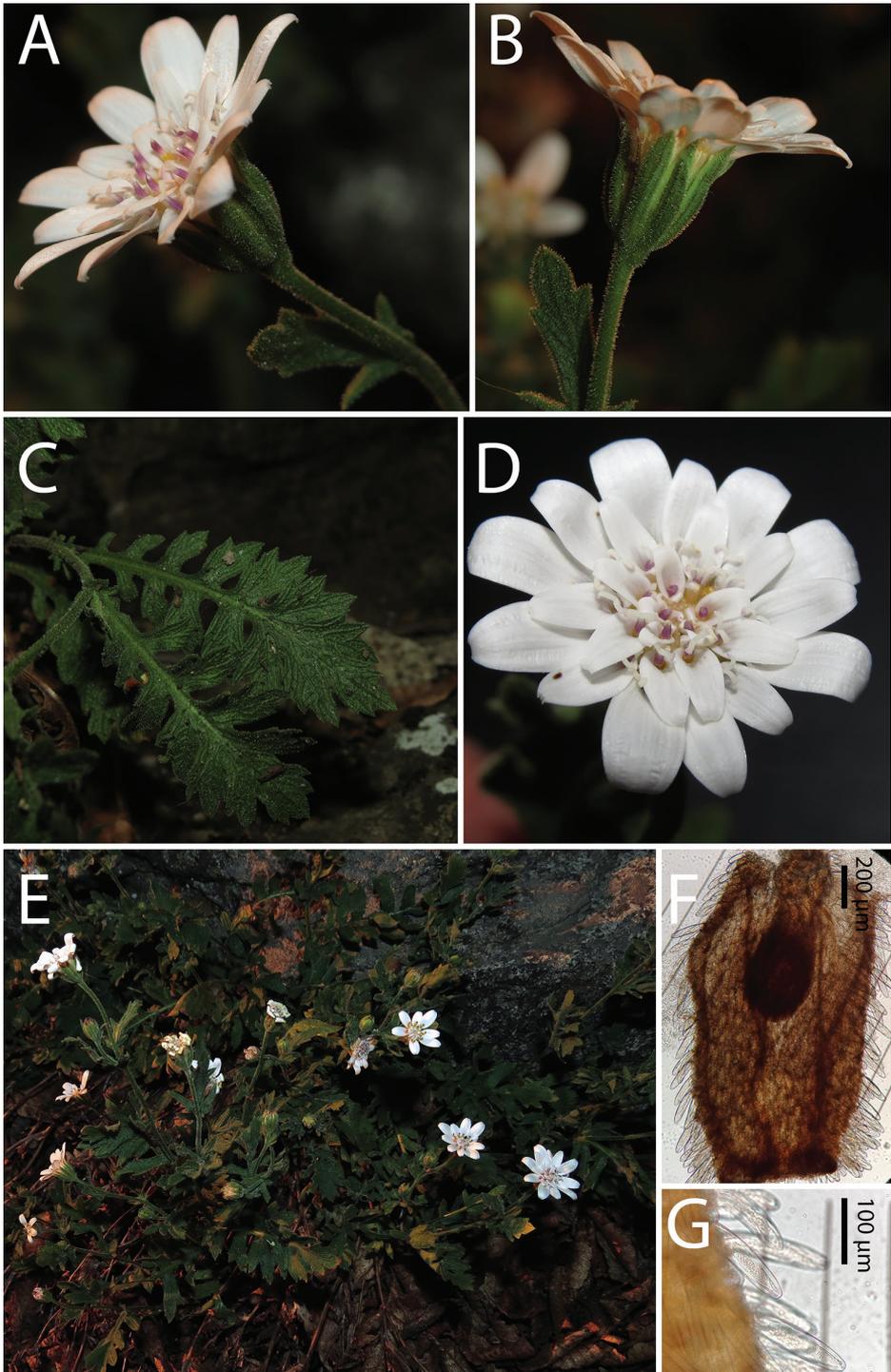


Figure 3. *Leucheria cantillanensis* Lavandero, sp. nov. **A** capitulum, sideways view **B** capitulum, detail of involucre bracts **C** leaves **D** capitulum, upper view **E** plants growing in natural habitat **F** cypsel **G** detail of trichomes in cypsel. All photographs by Nicolás Lavandero.

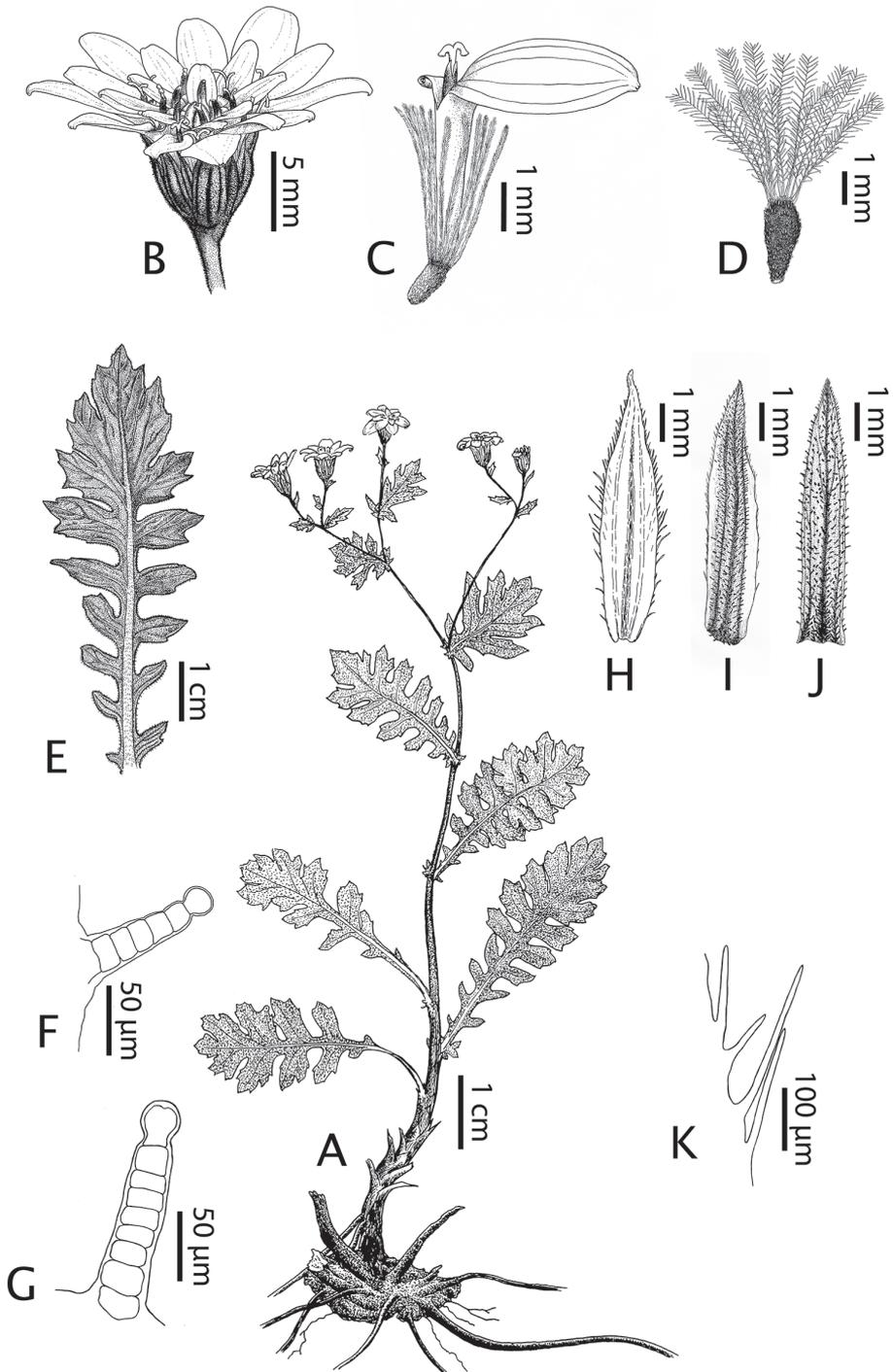


Figure 4. *Leucheria cantillanensis* Lavandero, sp. nov. **A** habit **B** capitulum **C** detail of flower **D** fruit **E** basal leaf **F** leaf trichome **G** stem trichome **H** inner involucral bract **I** middle involucral bract **J** outer involucral bract **K** ciliate margin of inner involucral bract (detail). Illustrations by Benito Rosende.

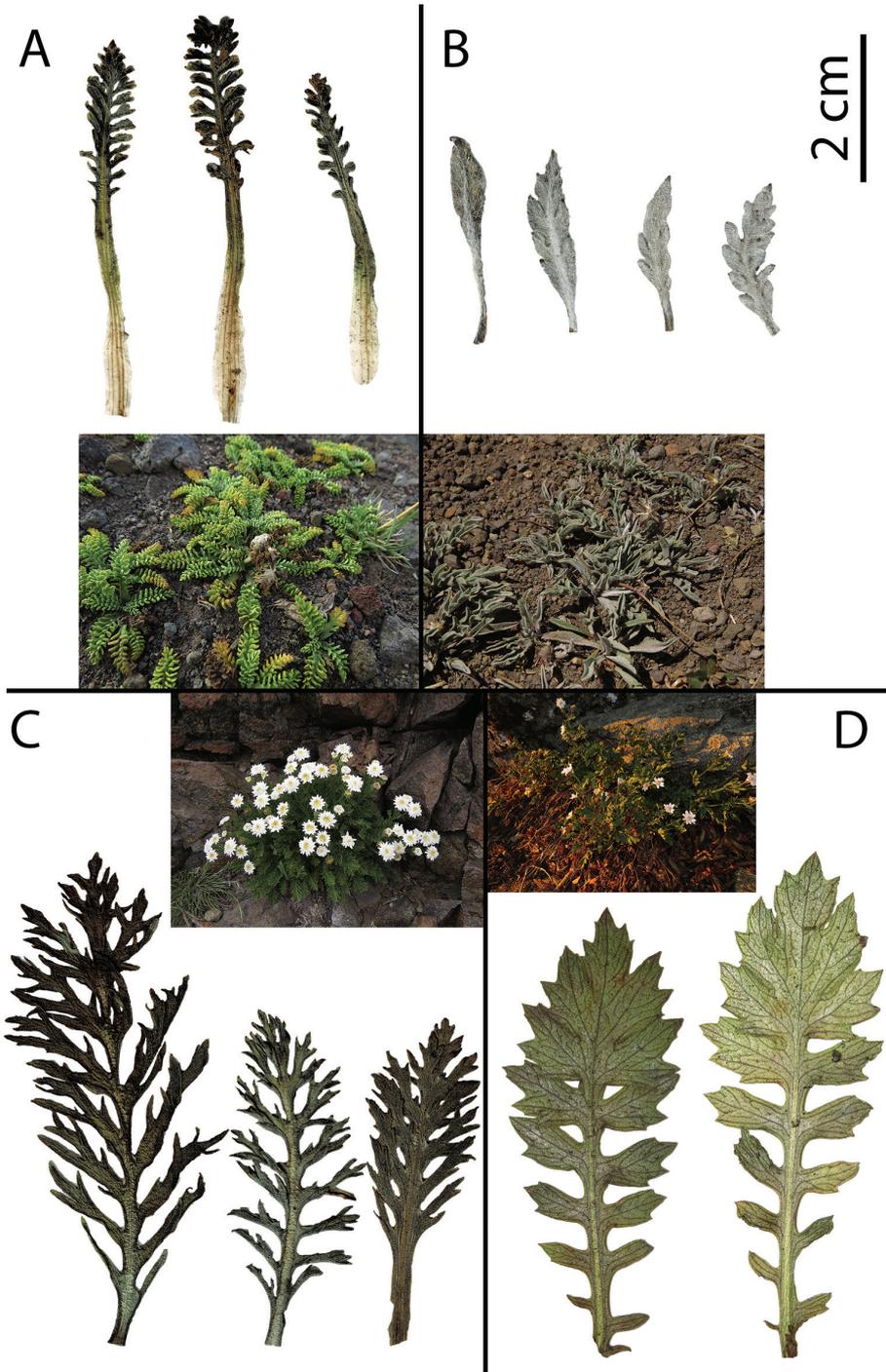


Figure 5. Leaf morphology and habit of acaulescent/subacaulescent *Leucheria* from Central Chile **A** *Leucheria scrobiculata* (NL433, CONC), inset: Habit **B** *Leucheria candidissima* (Lavandero, Santilli & Ossa 36, CONC), inset: Habit **C** *Leucheria salina* (Lavandero & Abello 40, CONC), inset: Habit **D** *Leucheria cantillanensis* (NL700, CONC), inset: Habit. All photographs by Lavandero.

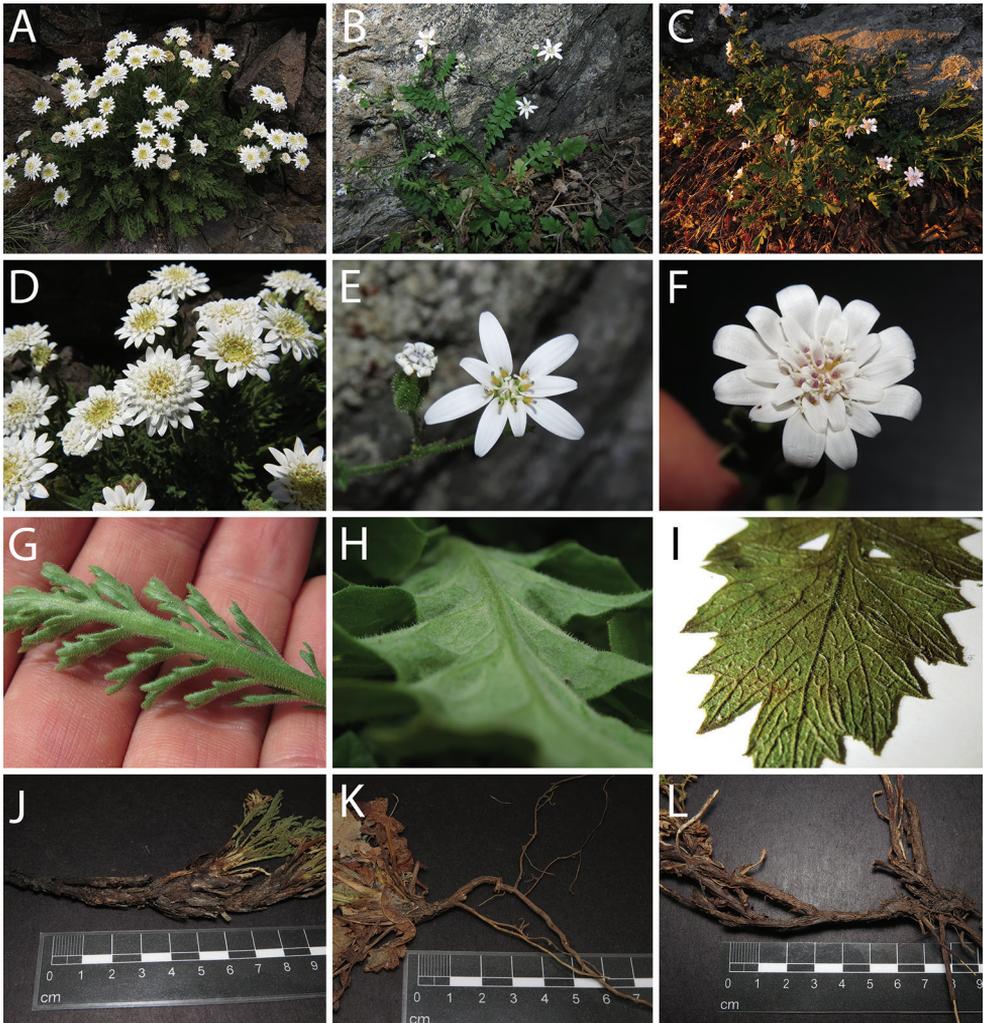


Figure 6. *Lecheria salina* (A, D, G, J) (Valle Nevado, Región Metropolitana, Chile), *Lecheria runcinata* (B, E, H, K) (Reserva Natural Altos de Cantillana, Región Metropolitana, Chile), and *Lecheria cantillanensis* (C, F, I, L) (Reserva Natural Altos de Cantillana, Región Metropolitana, Chile) A–C habit D–F capitula G–I abaxial side of leaves J–L belowground structures. All Photographs by Lavandero.

stripes (including the midrib), apex ciliate, texture leaf-like to hyaline towards the margins, margin ciliate, rarely glandular, central portion of the abaxial lamina covered by glandular trichomes, hyaline lamina glabrous. **Inner involucrel bracts** 5–6(–8), green, lanceolate, concave to flat $6.2\text{--}7.1 \times 1.06\text{--}1.25\text{--}(1.51)$ mm, with 3 dark-green longitudinal stripes (including the midrib), apex acute, texture leaf-like to hyaline-membranaceous towards both lateral margins, margin ciliate, cilia $(0.11\text{--})0.17\text{--}0.21\text{--}(0.24)$ mm long, central portion of the abaxial lamina densely covered by glandular trichomes, hyaline lamina glabrous, adaxial lamina glabrous. **Flowers** isomorphic, bisexual, 27–30 per capitulum. **Corollas** bilabiate, white, before anthesis pinkish-white,

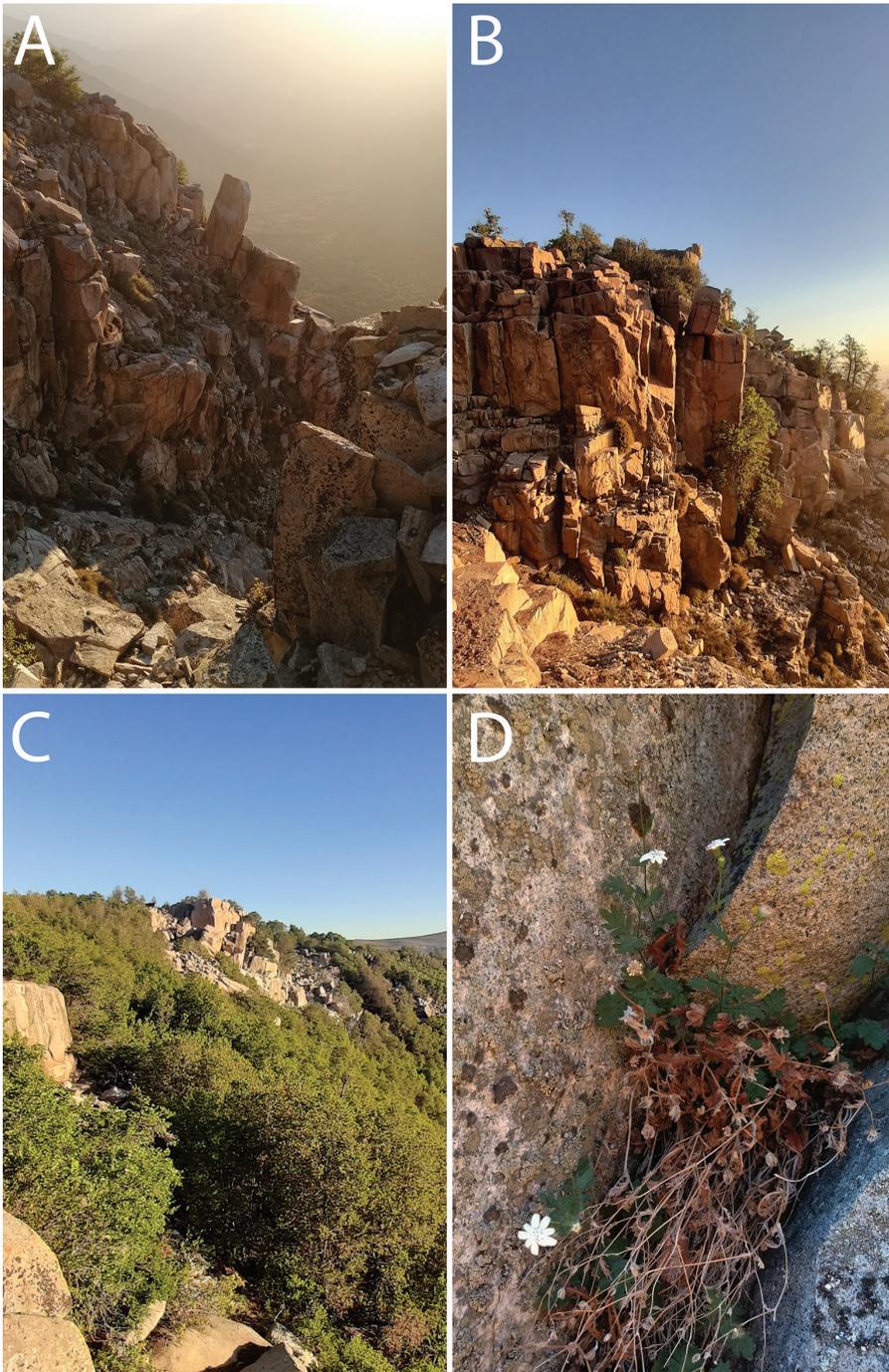


Figure 7. Habitat of *Leucheria cantillanensis* in Central Chile **A** southwest facing rock outcrops, ca. 2000 m elevation **B** rock outcrops in Cantillana, general view **C** general view of rock outcrops among *Nothofagus macrocarpa* (A.DC.) F.M. Vázquez & R.A. Rodr. forests in the Cantillana plateau **D** *Leucheria cantillanensis*, detail of the plant growing between rock crevices. Photographs **A, D** by Lavandero, **B, C** by Fabiola Gamboa.

tube 3.7–4.0 mm long, 0.5–1.1 wide; corolla tube sparsely covered by glandular trichomes. **Outer lip** oblanceolate, 3.6–3.9 × 2.0–2.2 mm at its widest, apex 3-toothed, teeth equal, 4-veined, glabrous. **Inner lip** bifid, lacinae linear, 2.7–2.8 × 0.24–0.37 mm at its widest, connivent, glabrous. **Stamens** 5, 3.8–4.0 mm long, glabrous. **Anthers** sagittate, 3.25–3.29 mm long; apical appendages purple, lanceolate, 1.19–1.23 mm long, apex acute; tails long, lanceolate, ca. 0.6 mm long, apex acute, smooth to ciliate. **Styles** white, 4.2–5.0 mm long, cleft into two truncate branches, branches 0.54–0.73 mm long, with stigmatic papillae on internal surface. **Cypselae** dark-brown, 1.0–1.2 × 2.4–2.5 mm, obovoid, strigose; trichomes transparent, cylindrical, terete, (150–)167–170(–180) μm , ascending, unicellular, subtended by two globose exocarpic cells. **Pappus** uniseriate, fused at their bases into a ring, deciduous; bristles 19–20, white, capillary, sub-plumose, 4.5–5 mm long; pectines long, filiform, 0.21–0.35(–0.46) mm long, laterally inserted.

Distribution and habitat. *Leucheria cantillanensis* seems to be endemic to the Cantillana Mountain Range, which is part of the coastal mountain range of central Chile. It grows in shaded crevices of rocky outcrops near 2000 m a.s.l. with SW orientation (Fig. 7). It is known thus far only from the type locality (Fig. 1). *L. cantillanensis* occurs associated with other rupicolous taxa such as *Calceolaria andina* Benth.

Phenology. Collected flowering and fruiting in December.

Etymology. The specific epithet refers to the coastal mountain range where the species was found, Altos de Cantillana.

Conservation status. *Leucheria cantillanensis* is assessed here as Critically Endangered (CR) under the IUCN categories and criteria B2ab(i,ii,iii). Criterion B2 was selected because its Area of Occupancy is $<10 \text{ km}^2$ (4 km^2). Criterion “a” was selected because it is known to exist at only a single location, with only one subpopulation. Criterion b(i,ii,iii) was selected because we expect a continuing decline of suitable area for the species to exist in since it is only found at the highest elevations within the mountain coastal range with very specific soil types and exposition. The quality of its habitat has also been deteriorating over time. The overall precipitation and snow cover in the Cantillana plateau has decreased dramatically over the past 20 years, affecting not only the Andean relict flora but all the vegetation in the area. Fog events which compensate for the drought over the summer, are not as common as before. *Leucheria cantillanensis* is present in the private reserve “Reserva Natural Altos de Cantillana”.

Key to acaulescent/subacaulescent species of *Leucheria* of Central Chile (31°–34°S)

The caulescent herbs with lignified taproots and annual species are excluded. It is important to observe the belowground structures in fresh and dry specimens in order to correctly assign the species to this group. For the habit, please refer to the insets in Figure 5.

- 1 Plants densely tomentose, greyish; Corolla pink..... *L. candidissima*
- Plants not densely tomentose, glabrous or glandulous; Corolla white to bluish....2

- 2 Plants caespitose, up to 8 cm tall, glabrous to glabrescent..... *L. scrobiculata*
 – Plants erect or decumbent, taller than 8 cm, densely glandulous **3**
 3 Lamina with foliar segments perpendicular or oblique to the axis of the lamina, non-prominent venation; flowers 40–60 per capitula, anther apical appendages greenish-yellow; Andes of Chile and Argentina above 3000 m.a.s.l. *L. salina*
 – Lamina flat with foliar segments on the same axis of the lamina, conspicuously prominent venation; flowers 27–30 per capitula; anther apical appendages purple. Coastal Cordillera of Chile near 2000 m.a.s.l. *Leucheria cantillanensis*

Discussion

The ability to establish infrageneric relationships using classic chloroplast markers and ITS within *Leucheria* is demonstrated in the present study. We were able to corroborate our initial conjectures about the phylogenetic position of *Leucheria cantillanensis* within the genus. Based on belowground structures (rhizome and roots), we assumed this species belonged to the acaulescent/subacaulescent group found by Jara-Arancio et al. (2017). This group is characterized by plants with a basal and compact rosette, with one or few monocephalic (sometimes with more capitula) scapes. In the first phylogenetic study with molecular data, Jara-Arancio et al. (2017) found that the independent acaulescent evolutionary lines (*L. candidissima* and *L. salina* lines) proposed by Crisci (1976) were paraphyletic, as they should include the species *L. achillaeifolia* and *L. nutans* in order to be monophyletic. We believe that this finding is highly supported by morphologic characters, as all the species within this clade have the same belowground structures, such as horizontal rhizomes covered by old leaves, and rounded in cross-section, long, dark roots. These characters are distinctly different from the other clades found by Jara-Arancio et al. (2017), which can be either annual or perennial plants with a lignified taproot. *Leucheria cantillanensis* evidently belongs to the acaulescent/subacaulescent group, as it has a creeping rhizome that grows between rock crevices and long dark roots (Figs 4, 6). Among the genus *Leucheria*, *L. cantillanensis* can be easily distinguished by its unique combination of vegetative (Figs 5, 6) and sexual characters (Figs 3, 4, 6), as described in detail in the diagnosis.

From the biogeographic point of view, it is interesting to note that the closest species of *L. cantillanensis* are mainly found at high elevations in the Andes range (except for *L. suaveolens*, which is endemic to the Falkland Islands). Although we do not have a time-calibrated phylogeny for *Leucheria*, it is possible to hypothesize, based on Villagrán (2001) and Villagrán and Armesto (2005), that the species diverged from this mainly Andean clade during the repeated glacial/interglacial cycles during the Quaternary. Cold-adapted species occupied lower elevation during glacial periods, and a subsequent shift upwards towards high elevations in both Andean and coastal mountain ranges during warmer periods likely provided the opportunity for allopatric speciation.

Leucheria cantillanensis is an exclusively rupicolous species. Plant communities on rocky places are characterized by having high levels of endemism caused by the high

specialization that plants require to thrive in these specific habitats (Porembski et al. 1994; Larson et al. 2005). Currently, only one population of *L. cantillanensis* is known. The area of Cantillana mountain range with elevations >2000 m comprises an area of near 15 km² (EULA-Chile 2004) but the specific rocky outcrops and exposition where the species is found, dramatically reduces the suitable habitat for the species. What is more, during the last decade, Central Chile has experienced a severe deficit in precipitation, the so-called Mega Drought (Garreaud et al. 2020), which has caused major damage and changes to the vegetation in the area (Miranda et al. 2020). Observations by the Park rangers over the past years reveal a decrease in snow cover in the mountain plateau and a reduction of fog and cloud events, an important source of water for rupicolous taxa. In this scenario, it is possible to infer a continuous decline in the quality of its habitat and a projected decline of suitable habitat and population size in the near future. *Ex situ* conservation measures could be a cost-efficient method to preserve the species, but more information about its distribution, ecology and population size is needed.

The discovery of this new species, which is restricted to mountain tops in the Cantillana Mountain Range in Central Chile, highlights the importance of this site in terms of its unique biodiversity. Cantillana harbours several taxa endemic to the Mediterranean region of Chile (Romero and Teiller 2009, Romero-Gárate and Teillier 2014) and several new species of insects, lizards and amphibians have been described over the recent years (Vaz-de-Mello and Halffter 2006; Núñez 2007; Zúñiga-Reinoso and Cid-Arcos 2013; Charrier et al. 2015) in the area. Rock communities have been rarely studied in Chile (García 2010). Further botanical surveys in rocky outcrops may reveal a hidden diversity of plants in this biodiversity hotspot and will provide important information needed for the management and conservation of *L. cantillanensis*.

Additional specimens examined

Leucheria salina. **CHILE. Atacama:** Huasco, Quebrada Cantarito, 28°39'S, 69°50'W, Feb 1981, Kalin 81614 (CONC); **Coquimbo:** Limarí, Cordillera de Ovalle, Río Mostazal, 30°46'S, 70°30'W, Feb 1956, Jiles 2971 (CONC); Cordillera de Ovalle, San Miguel, 30°51'S, 70°31'W, Jan 1954, Jiles 3638 (CONC); Gordito, 31°04'S, 70°23'W, Jan 1954, Jiles 2546 (CONC); **Valparaíso:** Los Andes, entre estero Caracoles y Cristo Redentor, 34°00'S, 70°06'W, Apr 1933, Looser 67007 (CONC), Caracoles, 32°50'S, 70°07'W, Jan 1964, Marticorena & Matthei (CONC); Portillo 32°50'S, 70°08'W, Feb 1951, Ricardi 1207 (CONC); **Región Metropolitana:** Santiago, Cordillera Santiago ad limit nivis perpet, Feb 1854, Philippi s/n (SGO); SN Yerba Loca, Cuenca Estero La Leonera, 33°16'S, 70°15'W, Feb 2000, Kalin et al. 201451 (CONC); Subida al Portezuelo de El Cepo, 33°18'S, 70°12'W, Mar 1956, Schlegel 1087 (CONC); Farelones, La Parva, 33°19'S, 70°16'W, Jan 1991, Ruthsatz 6995; Farelones, Laguna Piuquenes, 33°19'S, 70°15'W, Feb 2019, Lavandero & Abello 1890 (SGO); Cerca de la Parva, 33°18'S, 70°17'W, Jan 1979, Muñoz & Meza 1372 (SGO); Río Colorado, 33°28'S, 70°00'W, Jan 1930, Behn s/n (CONC); San Ramón, 33°28'S, 70°25'W, Jan 1967, Zoellner 1430 (CONC); El Volcán, 33°48'S, 70°10'W, Feb 1947, Gunckel

20683 (CONC); Maipo, Cajón del Maipo, 33°48'S, 70°44'W, Jan 1980, Niemeyer s/n (CONC); Santiago, Parque Nacional El Morado, 33°49'S, 70°05'W, Jan 1991, Teillier et al. 2402 (CONC, SGO); Cercanías glaciario La Paloma, Feb 2014, Medina 2616 (SGO).

Leucheria runcinata. **CHILE. Valparaíso:** Nogales, Cordillera El Melón, Estero Garretón 32°39'S, 71°02'W, Nov 2010, Flores-Toro s/n (SANT); Quillota, Cerro La Campana, sector La Gotera, 32°58'S, 71°08'W, Jan 1937, Garaventa 3253 (CONC); Cerro La Campana, 32°57'S, 71°08'W, Nov 1962, Weisser 395 (CONC); Cerro La Campana, Trayecto Placa Darwin a Mina, 32°57'S, 71°08'W, Dec 1981, Villagrán & Meza 3174 (SGO); Quillota, Cerro Vizcachas, 33°05'S, 71°02'W, Nov 1973, Stebbins 8912 (SGO); **Región Metropolitana:** Chacabuco, Altos de Chicauma, sector Tranque, 33°10'S, 70°58'W, Jan 2003, García & Faúndez 3637 (CONC); Melipilla, Reserva Natural Altos de Cantillana, sendero camino a cerro Horcón de Piedra, 33°53'S, 71°00'W, 27 Dec 2019, Lavandero 753 (SGO).

Acknowledgements

We are grateful to the curators and staff of CONC and SGO herbaria. We thank Gioconda Peralta and Loreto Carrasco of the Plataforma de Secuenciación y Tecnologías Ómicas, Pontificia Universidad Católica de Chile for laboratory support and expert capillary electrophoresis analysis (CONICYT-FONDEQUIP EQM150077). We would like to thank Prof. Sergei Mosyakin and one anonymous reviewer for the helpful comments on the submitted manuscript. Thanks to Fabiola Gamboa for providing photos of Altos de Cantillana. We are indebted to Martin Gardner (RBGE), who carefully revised the manuscript. We would like to thank Sebastian Teillier for his helpful comments on the manuscript and his keen interest in the flora of the Metropolitan Region. We would like to thank the logistic support from "Proyecto GEF 5135" MMA and ONU Medio Ambiente, that invited us to participate in their floristic survey in their permanent plots of flora in Altos de Cantillana, part of the SIMBIO RMS. Herbarium and lab work were funded by the Comisión Nacional de Investigación Científica y Tecnológica (CONICYT) from the Government of Chile (Fondecyt grant 1171369). Special thanks to Corporación Altos de Cantillana for the logistic support in the field and all the hard work they do to keep this Natural Reserve preserved.

References

- Armesto JJ, Arroyo MTK, Hinojosa LF (2007) The Mediterranean environment of central Chile. In: Veblen TT, Young KR, Orme AR (Eds) *The Physical Geography of South America*. Oxford University Press, New York, 184–199.
- Arroyo MTK, Cavieres L, Marticorena C, Muñoz-Schick M (1995) Convergence in the Mediterranean Floras in Central Chile and California: Insights from Comparative Biogeogra-

- phy. In: Arroyo MTK, Zedler PH, Fox MD (Eds) *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*. Springer, New York, 43–88. https://doi.org/10.1007/978-1-4612-2490-7_3
- Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. In: Smith V, Penev L (Eds) *e-Infrastructures for data publishing in biodiversity science*. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Beentje H (2016) *The Kew Plant Glossary, an illustrated dictionary of plant terms*. Kew Publishing, Royal Botanic Gardens Kew, Richmond.
- Cabrera AL, Willink A (1973) *Biogeografía de América Latina*. Secretaría General de la Organización de los Estados Americanos, 120 pp.
- Charrier A, Correa C, Castro C, Méndez MA (2015) A new species of *Alsodes* (Anura: Alsodidae) from Altos de Cantillana, central Chile. *Zootaxa* 3915(4): 540–550. <https://doi.org/10.11646/zootaxa.3915.4.5>
- CONAMA (2004) *Estrategia para la conservación de la biodiversidad en la Región Metropolitana de Santiago*. Gobierno de Chile, 98 pp. http://metadatos.mma.gob.cl/sinia/articles-48844_EstrategiaRegionalBiodiversidadPDA_13.pdf
- Crisci JV (1976) Revisión del género *Leucheria* (Compositae: Mutisieae). *Darwiniana* 20: 9–126.
- Eidler D, Klein J, Antonelli A, Silvestro D (2019) raxmlGUI 2.0 beta: A graphical interface and toolkit for phylogenetic analyses using RAxML. *bioRxiv* 800912. <https://doi.org/10.1101/800912>
- EULA-Chile (2004) *Establecimiento de un Ordenamiento Territorial orientado a la protección y uso sustentable del área del Cordón de Cantillana*. Informe Final. Centro EULA-Chile, Universidad de Concepción, Chile. http://metadatos.mma.gob.cl/sinia/articles-37027_eula.pdf
- Felsenstein J (1981) Evolutionary trees from DNA sequences: A maximum likelihood approach. *Journal of Molecular Evolution* 17(6): 368–376. <https://doi.org/10.1007/BF01734359>
- Flores-Toro L, Amigo J (2013). Flora autóctona de la cordillera El Melón y del cerro Tabaco, sitios prioritarios para la conservación de la biodiversidad, Región de Valparaíso, Chile. *Chloris Chilensis* 16(1). <http://www.chlorischile.cl/amigo-flores-1-2013/flores-Amigo-EL%20MELON-EL%20TABACO.htm>
- García N (2010) Caracterización de la flora vascular de Altos de Chicauma, Chile (33° S). *Gayana. Botánica* 67(1): 65–112. <https://doi.org/10.4067/S0717-66432010000100007>
- Garreaud RD, Boisier JP, Rondanelli R, Montecinos A, Sepúlveda HH, Veloso-Aguila D (2020) The Central Chile Mega Drought (2010–2018): A climate dynamics perspective. *International Journal of Climatology* 40(1): 421–439. <https://doi.org/10.1002/joc.6219>
- Jara-Arancio P, Vidal PM, Panero JL, Marticorena A, Arancio G, Arroyo MTK (2017) Phylogenetic reconstruction of the South American genus *Leucheria* Lag. (Asteraceae, Nassauvieae) based on nuclear and chloroplast DNA sequences. *Plant Systematics and Evolution* 303(2): 221–232. <https://doi.org/10.1007/s00606-016-1366-7>
- Jara-Arancio P, Ratto F, Bartoli A, Arancio G, Carmona-Ortiz MR (2019) A new species of the genus *Leucheria* (Asteraceae, Nassauvieae) from Argentina. *Phytotaxa* 404(1): 51–57. <https://doi.org/10.11646/phytotaxa.404.1.5>

- Katinas L, Tellería MC, Crisci JV (2008) A new species of *Leucheria* (Asteraceae, Mutisieae) from Chile. *Novon: A Journal for Botanical Nomenclature* 18(3): 366–369. <https://doi.org/10.3417/2006108>
- Katinas L, Crisci JV, Marticorena A (2018) Una Nueva especie de *Leucheria* (Asteraceae), endémica de Chile. *Boletín de la Sociedad Argentina de Botánica* 53(1): 93–98. <https://doi.org/10.31055/1851.2372.v53.n1.19909>
- Larson DW, Matthes U, Kelly PE (2005) *Cliff Ecology: Pattern and Process in Cliff Ecosystems*. Cambridge University Press, 360 pp.
- Ministerio del Medio Ambiente (2018) Informe Estación de Monitoreo, Reserva Natural Altos de Cantillana. Desarrollado y financiado por: Proyecto GEFSEC ID 5135 MMA-ONU Medio Ambiente, Santiago, Chile, 33 pp. http://gefmontana.cl/wp-content/uploads/2019/02/Informe-monitoreo-Cantillana_divulgaci%C3%B3n.pdf
- Miranda A, Lara A, Altamirano A, Di Bella C, González ME, Camarero JJ (2020) Forest browning trends in response to drought in a highly threatened mediterranean landscape of South America. *Ecological Indicators* 115: 106401. <https://doi.org/10.1016/j.ecolind.2020.106401>
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, Da Fonseca GAB (2005) *Hotspots revisited: Earth's biologically richest and most threatened ecoregions*. CEMEX, Mexico City, 391 pp.
- Moreira-Muñoz A, Morales V, Muñoz-Schick M (2012) Actualización sistemática y distribución geográfica de Mutisioideae (Asteraceae) de Chile. *Gayana. Botánica* 69(1): 9–29. <https://doi.org/10.4067/S0717-66432012000100003>
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858. <https://doi.org/10.1038/35002501>
- Núñez H (2007) *Liolaemus frassinettii*, nueva especie de lagartija para los Altos de Cantillana, Región Metropolitana (Reptilia: Sauria). *Boletín del Museo Nacional de Historia Natural* 56: 81–87. http://publicaciones.mnhn.gob.cl/668/articles-64544_archivo_01.pdf
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Porembski S, Barthlott W, Dörrstock S, Biedinger N (1994) Vegetation of rock outcrops in Guinea: Granite inselbergs, sandstone table mountains and ferricretes—remarks on species numbers and endemism. *Flora* 189(4): 315–326. [https://doi.org/10.1016/S0367-2530\(17\)30612-6](https://doi.org/10.1016/S0367-2530(17)30612-6)
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67(5): 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ratto F, Bello M, Bartoli A (2014) Novedades en *Leucheria* (Asteraceae, Mutisieae). *Boletín de la Sociedad Argentina de Botánica* 49(1): 91–92. <https://doi.org/10.31055/1851.2372.v49.n1.7827>
- Romero F, Teillier S (2009) Comunidades vegetales de altura en los altos de Cantillana. Cordillera de la Costa, Región Metropolitana, Chile. *Chloris Chilensis* 12(1). <https://www.chlorischile.cl/Cantillana/cantillana%20vegetacion.htm>
- Romero-Gárate F, Teillier S (2014) Flora vascular de los Altos del Cantillana, Región Metropolitana, Chile: pisos de vegetación subandino y andino. *Chloris Chilensis* 17(1). <http://www.chlorischile.cl/Cantillana/cantillana%20vegetacion.htm>

- chlorischile.cl/cantillana%20flora-romero-Teillier/Romero-Cantillana-flora%20chloris%202014.htm
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Shaw J, Lickey EB, Schilling EE, Small RL (2007) Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The tortoise and the hare III. *American Journal of Botany* 94(3): 275–288. <https://doi.org/10.3732/ajb.94.3.275>
- Silvestro D, Michalak I (2012) raxmlGUI: A graphical front-end for RAxML. *Organisms, Diversity & Evolution* 12(4): 335–337. <https://doi.org/10.1007/s13127-011-0056-0>
- Simpson MG (2010) *Plant Systematics* (Second Edition). Elsevier Academic Press, 740 pp. <https://doi.org/10.1016/B978-0-12-374380-0.50001-4>
- Stamatakis A (2014) Raxml version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* (Oxford, England) 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- IUCN (2017) Guidelines for using the IUCN red list categories and criteria, version 13. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17(5): 1105–1109. <https://doi.org/10.1007/BF00037152>
- Vaz-de-Mello FZ, Halffter G (2006) A new dung beetle genus with two new species from Chile (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 1193(1): 59–68. <https://doi.org/10.11646/zootaxa.1193.1.4>
- Villagrán C (1995) Quaternary history of the Mediterranean vegetation of Chile. In: Arroyo MTK, Zedler PH, Fox MD (Eds) *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia*. Springer, New York, 3–20. https://doi.org/10.1007/978-1-4612-2490-7_1
- Villagrán C (2001) Un modelo de la historia de la vegetación de la Cordillera de La Costa de Chile central-sur: La hipótesis glacial de Darwin. *Revista Chilena de Historia Natural* 74(4): 793–803. <https://doi.org/10.4067/S0716-078X2001000400007>
- Villagrán C, Armesto JJ (2005) Fitogeografía histórica de la Cordillera de la Costa de Chile. In: Smith C, Armesto JJ, Valdovinos C (Eds) *Biodiversidad y Ecología de los Bosques de la Cordillera de la Costa de Chile*, Editorial Universitaria, Santiago, 99–115.
- Zúñiga-Reinoso A, Cid-Arcos M (2013) *Callyntra hibrida* n. sp.: Un nuevo tenebriónido de Chile central (Coleoptera: Tenebrionidae). *Gayana (Concepción)* 77(2): 132–135. <https://doi.org/10.4067/S0717-65382013000200007>

Supplementary material I

Table S1. GenBank accession numbers used in this study

Authors: Nicolás Lavandero

Data type: molecular data

Explanation note: GenBank accession numbers for the ITS, trnL-trnF and rpl32-trnF sequences used in this study. GenBank accessions in bold are new to this study.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.169.57532.suppl1>

Monadelpha (Euphorbiaceae, Plukenetieae), a new genus of Tragiinae from the Amazon rainforest of Venezuela and Brazil

Lynn J. Gillespie¹, Warren M. Cardinal-McTeague^{1,2}, Kenneth J. Wurdack³

1 Research & Collections, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario, K1P 6P4, Canada **2** Agriculture and Agri-Food Canada, Ottawa Research and Development Centre, 960 Carling Ave, Ottawa, Ontario, K1A 0C6, Canada **3** Department of Botany, National Museum of Natural History, Smithsonian Institution, MRC-166, P.O. Box 37012, Washington DC 20013-7012, USA

Corresponding author: Lynn J. Gillespie (lgillespie@nature.ca)

Academic editor: D. Geltman | Received 2 October 2020 | Accepted 20 November 2020 | Published 8 December 2020

Citation: Gillespie LJ, Cardinal-McTeague WM, Wurdack KJ (2020) *Monadelpha* (Euphorbiaceae, Plukenetieae), a new genus of Tragiinae from the Amazon rainforest of Venezuela and Brazil. *PhytoKeys* 169: 119–135. <https://doi.org/10.3897/phytokeys.169.59244>

Abstract

Monadelpha L.J. Gillespie & Card.-McTeag., **gen. nov.**, is described as a new member of Euphorbiaceae tribe Plukenetieae subtribe Tragiinae, to accommodate *Tragia guayanensis*, a species known from western Amazonas, Venezuela and, newly reported here, from Amazonas, Brazil. The genus is unique in the subtribe for having 5-colpate pollen and staminate flowers with filaments entirely connate into an elongate, cylindrical staminal column terminated by a tight cluster of anthers. Phylogenetic analyses based on nuclear rDNA ITS and sampling 156 accessions across the diversity of Tragiinae (all 12 genera and 77 of ~195 species) also support *Monadelpha* as a distinct lineage that is separate from *Tragia*. A revised key to the genera of Tragiinae in South America and Central America is provided.

Keywords

Brazil, ITS, molecular phylogeny, Plukenetieae, pollen, *Tragia*, Venezuela

Introduction

Members of tribe Plukenetieae are morphologically unusual within Euphorbiaceae for frequently possessing stinging hairs, twining vine or liana habit, and colorful pseudanthia (in *Dalechampia*). The tribe is characterized by apetalous flowers, valvate staminate

sepals, and undivided styles that are basally to entirely connate. Plukenetieae contains three subtribes (i.e., Dalechampiinae, Plukenetiinae, Tragiinae), of which Tragiinae is the largest and most diverse, with 12 genera and ~195 species as currently circumscribed (Webster 2014; with updates by Medeiros et al. 2013; Cardinal-McTeague and Gillespie 2016) (Table 1). Subtribe Tragiinae is distinguished from Plukenetiinae by stinging hairs and consistently 3-locular ovaries and eglandular leaves, and from Dalechampiinae by racemose or thyrsoid inflorescences rather than bibracteate pseudanthia (Gillespie 1994a; Webster 2014).

Among Tragiinae, the most species-rich genus is *Tragia*, which includes ~150 species, whereas the other 11 genera are much smaller with only one to 11 species each (Table 1). The complex infrageneric classification of *Tragia* currently comprises two subgenera, six sections (including sect. *Monadelphae* L.J.Gillespie), one species group, and two unplaced species (Table 1). A single species has been segregated as *T.* subg. *Mauroya* (Leandri 1971); however, our preliminary research suggests this species is closely allied with sect. *Agirta* and does not warrant subgeneric status. All other species belong to *T.* subg. *Tragia*. Three other sections, sects. *Leptorhachis* (Klotzsch) Müll. Arg., *Leucandra* (Klotzsch) Müll.Arg. and *Ratiga* Müll.Arg., that are sometimes considered distinct are included here within sect. *Tragia*, a position supported by pollen (Gillespie 1994a) and molecular studies (Cardinal-McTeague and Gillespie 2016). *Tragia* species exhibit very diverse pollen and floral morphology that is correlated in part with its infrageneric classification (Gillespie 1994a, b). The genus was suggested to be highly paraphyletic based on this morphological diversity (Gillespie 1994a), which is confirmed by recent molecular phylogenetic studies focused on Plukenetieae (Cardinal-McTeague and Gillespie 2016). Three sections of *Tragia*, sects. *Bia* (Klotzsch) Müll. Arg., *Ctenomeria* (Harv.) Benth., and *Zuckertia* (Baill.) Müll.Arg., were recently reinstated as genera (Webster 2007, 2014; Medeiros et al. 2013) based on inferences from pollen morphology (Gillespie 1994a), floral morphology, and preliminary molecular results (Wurdack et al. 2005), and are supported by our more in-depth molecular study (Cardinal-McTeague and Gillespie 2016).

One of the most unusual species of *Tragia* is *T. guayanensis* L.J.Gillespie, which was considered so distinct as to merit its own monotypic section, *Monadelphae* L.J.Gillespie (Gillespie 1994b). The species is characterized by two features unique in Tragiinae: 5-colpate pollen and filaments entirely connate into an elongate cylindrical staminal column (Figs 1, 2). All other *Tragia* species have 3-aperturate pollen, which is mostly 3-colpate, sometimes 3-porate or with three poorly defined apertures (Table 1), with the exception of 4-colpate in *T. rubiginosa* Huft (preliminary observations in Gillespie 1994b), a species unplaced in the sectional classification. Filaments in staminate flowers of *Tragia* are usually distinct to sometimes basally connate. The only other species having filaments entirely connate is *T. lassia* Radcl.-Sm. & Govaerts of sect. *Lassia*, which has stamens connate into a very short disc-like structure (Baillon 1858: pl. 4, figs 24, 25; pers. obs.), and very different from that of *T. guayanensis*. When describing *T. guayanensis*, Gillespie (1994b) suggested the species was distinct and not closely related to any other *Tragia* species. Nevertheless, she maintained the species within

Table 1. Tragiinae genera and infrageneric taxa of *Tragia*: species number, geographic distribution, and pollen morphology. Adapted from Cardinal-McTeague and Gillespie (2016) with pollen characters from Gillespie (1994a, 1994b) and taxonomic updates from this paper.

Genus/section	spp. #	Geographic distribution	Pollen apertures	Pollen tectum
<i>Acidoton</i> Sw.	5	Hispaniola, Jamaica	inaperturate	rugulate
<i>Bia</i> Klotzsch	5	Costa Rica to South America	inaperturate	foveolate-fossulate or finely reticulate
<i>Cnesmone</i> Blume	11	SE Asia	weakly 3-colpate	punctate
<i>Ctenomeria</i> Harv.	2	South Africa	weakly 3-aperturate	finely foveolate-reticulate
<i>Gitara</i> Pax & K.Hoffm.	1	Central and South America	3-colpate	finely foveolate-reticulate
<i>Megistostigma</i> Hook.f.	5	SE Asia	weakly 3-colpate to inaperturate	punctate
<i>Monadelpha</i> L.J.Gillespie & Card.-McTeag., gen. nov.	1	Venezuela (Amazonas), Brazil (Amazonas)	5-colpate	foveolate
<i>Pachystylidium</i> Pax & K.Hoffm.	1	SE Asia	weakly 3-porate	punctate
<i>Platygyne</i> P.Mercier	7	Cuba	inaperturate	reticulate or rugulate
<i>Sphaerostylis</i> Baill.	2	Madagascar	unknown	unknown
<i>Tragia</i> L.	~150	Pantropical to warm temperate		
sect. <i>Agirta</i> Baill.	5	Madagascar	unknown	unknown
sect. <i>Lassia</i> (Baill.) Müll.Arg.	2	Madagascar	3-colpate	reticulate
sect. <i>Leptobotrys</i> (Baill.) Müll.Arg.	2	SE USA	weakly 3-porate	punctate
sect. <i>Tagina</i> Müll.Arg.	82	Africa, Madagascar, S Asia	3-colpate	reticulate
sect. <i>Tragia</i>	53	S USA to South America, Caribbean	3-colpate	intectate-baculate
Australian species group	3	Australia	3-porate	punctate
<i>T. biflora</i> Urb. & Ekman (unplaced)	1	Hispaniola	unknown	unknown
<i>T. rubiginosa</i> Huft (unplaced)	1	Venezuela	4-colpate	punctate
subg. <i>Mauroya</i> Leandri	1	Madagascar	weakly 3-aperturate	finely reticulate
<i>Tragiella</i> Pax & K.Hoffm.	4	E and S Africa	3-colpate	reticulate
<i>Zuckertia</i> Baill.	2	Mexico, Central America	3-colpate	finely reticulate

Tragia in its own section pending further study and anticipating that a major reclassification along phylogenetic lines would be necessary.

Here we present molecular phylogenetic results placing *T. guayanensis* within subtribe Tragiinae that supports its recognition as a distinct genus. The new genus *Monadelpha* is described for *T. guayanensis* based on its unique pollen and floral morphology and isolated phylogenetic position within Tragiinae. This is the first of several contributions towards a new phylogenetic classification of subtribe Tragiinae.

Material and methods

Molecular phylogeny

To determine the phylogenetic relationships of *Monadelpha*, we sequenced and analyzed the Internal Transcribed Spacer (ITS) region (including complete ITS1, 5.8S, and ITS2, and flanking portions of 18S and 26S) of nuclear rDNA. ITS has been

shown to provide good resolution of Tragiinae in the prior studies (e.g., Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019) from which our core taxon sampling is drawn and presents few alignment problems across genera. Orthologous plastid data could not be recovered from the degraded *Monadelpha* sample, but the limited phylogenetic resolution of the more slowly evolving plastid loci is established and their addition would be unlikely to change our findings. Our taxon sampling of 156 accessions included 77 of ~195 species of Tragiinae (39% of total diversity) with representatives of all 12 Tragiinae genera and seven of the eight sections/species groups in *Tragia* (excluding the Madagascar subg. *Mauroya*, only known from its type collection of *T. ivohibeensis* Leandri). Due to unusually high GC content in the close relatives of Tragiinae (which results in challenging DNA alignments and recovers some questionable relationships; Cardinal-McTeague, unpublished data), we rooted the tree using three accessions from the sister clade of Plukenetieae, which contains tribes Bernardieae and Caryodendreae (Wurdack et al. 2005; Cervantes et al. 2016).

Extractions of genomic DNA, fluorescent Sanger sequencing, and contig assembly for the ITS sequences followed the protocols of previous molecular studies in Plukenetieae (Cardinal-McTeague and Gillespie 2016; Cardinal-McTeague et al. 2019). The paratype of *T. guayanensis* (*Williams 14990*, US) was sampled and sequenced at the Smithsonian separately from all other new data, under more stringent conditions for degraded museum samples following protocols in Dorr et al. (2018). That specimen is well preserved and the data appear authentic based on appropriate negative controls and unique phylogenetic placement. The sequences were aligned using the auto-select algorithm of MAFFT ver. 7.450 (Katoh and Standley 2013) in Geneious ver. 11.1.5 (BioMatters, Auckland, New Zealand), and the optimal model of nucleotide evolution was ranked by AIC (Akaike Information Criterion) using default search parameters across three substitution schemes in jModeltest2 ver. 2.1.6 on XSEDE (Darriba et al. 2012; Miller et al. 2010). Subsequent analyses were conducted on all data in the alignment and potentially ambiguous regions were few.

We estimated a phylogenetic tree using Bayesian inference with MrBayes ver. 3.2.6 on XSEDE (Ronquist et al. 2012), executing an (MC)³ analysis with two runs of 3 million generations and sampling every 1000 generations, using the optimal model of nucleotide evolution on an unpartitioned alignment (remaining parameters as default). Runs were considered converged if ESS (effective sample size) of each parameter were >500 in Tracer ver. 1.7 (Rambaut et al. 2018), and if PSRF (potential scale reduction factor) and the standard deviation of split frequencies were close to 1.0 and <0.005, respectively, as determined by the MrBayes output. A 50% majority rule consensus tree was calculated following a 25% burn-in, resulting in Bayesian posterior probability (PP) values based on posterior distribution of 4500 trees from the combined runs. For an additional estimate of branch support, we inferred maximum likelihood bootstrap percentages (MLBP) using 1000 rapid bootstrap replicates under default parameters with RAxML-HPC ver. 8 on XSEDE (Stamatakis 2014). In the Results, we interpret strong branch support as PP >0.95 and MLBP >85. Discussion

of the subclades (T1–T10) follows the naming convention of Cardinal-McTeague and Gillespie (2016) with minor adjustments.

Data resources

The data underpinning the analyses reported in this paper (DNA alignment and resulting Bayesian tree) are deposited in the Dryad Data Repository at <https://doi.org/10.5061/dryad.5hqbzkh4d>.

Morphology

Specimens were examined at CAN and US, on loan from MO, NY, and P (herbarium acronyms following Index Herbariorum (<http://sweetgum.nybg.org/science/ih/>), and from other herbaria via online images in the Global Biodiversity Information Facility (GBIF.org 01 Oct 2020 Occurrence Download <https://doi.org/10.15468/dl.upmgky>). The key was adapted from Gillespie (1994b), modified and updated based on examination of specimens and the following references: Mulgura de Romero and Gutierrez de Sanguinetti (1989); Radcliffe-Smith (2001); Medeiros et al. (2013); Steinmann and Ramírez-Amezcuca (2013); Cardinal-McTeague and Gillespie (2016); Webster (2014).

Phylogenetic results

Our 159-terminal (80 taxa) ITS dataset, including 55 new sequences, had an aligned length of 795 characters (410 variable, 353 parsimony informative [44%], 0.7% missing data), and GTR+I+G was identified as its optimal model of nucleotide evolution. Bayesian and ML analyses revealed very similar results. The 50% majority rule Bayesian topology was well resolved with most clades strongly supported by PP and MLBP (Fig. 3).

The phylogeny is divided into two major clades with strong to moderate support, the Old World Tragiinae clade (T1–T3) and the New World Tragiinae clade (T4–T10). The resolution of subclades T1–T3 was strongly supported, with subclade T1 (*Ctenomeria*) sister to T2 (*Cnesmone*, *Megistostigma*) + T3 (*Tragia* sect. *Tagira*, embedded with *T.* sects. *Agirta* and *Lassia*, and *Tragiella*). Subclades T4–T10 were mostly strongly supported, with the exception of the modified subclade T6/9, which includes the new genus *Monadelpha* with moderate support (PP = 0.92, MLBP = 56). The New World Tragiinae clade contains a small successive grade of subclades T4 (*Bia*) and T5 (*Acidonton*, *Platygyne*) that culminates into the strongly supported Core New World Tragiinae clade (T6–T10). This core clade comprises a weakly supported clade (PP = 0.90, MLBP < 50) with three distinctive subclades, T6/9 (*Gitara*, *Monadelpha*, and *Zuckertia*) sister to T7 (*Tragia* sect. *Leptobotrys*) + T8 (Australian *Tragia*, *Pachystylidium*, and *Sphaerostylis*), which together are sister to the large subclade T10 (*Tragia* sect. *Tragia*). *Monadelpha* is on a long branch, moderately supported as sister to *Zuckertia* + *Gitara* (PP = 0.92, MLBP = 56), and well separated from *Tragia* and other Tragiinae genera.

Discussion

The phylogenetic relationships of Tragiinae recovered here largely agree with previous phylogenetic analyses of Plukenetieae based on ITS and plastid *psbA-trnH* data (Cardinal-McTeague and Gillespie 2016). Our increased Tragiinae taxon sampling (77 here compared to 50 previously) improved both resolution and support, despite including only ITS data. A noteworthy difference is the revised placement of *Gitara* (subclade T9, formerly weakly supported as sister to *Tragia* sect. *Tragia*, T10; Cardinal-McTeague and Gillespie 2016), which is here strongly supported as sister to *Zuckertia* (T6), with *Monadelpha* sister to both of them. *Monadelpha* is an isolated lineage, clearly distinct from New World and Old World clades of *Tragia*. Support for its relationship with *Gitara* and *Zuckertia* (subclade T6/9) is not strong, which suggests that its position on the phylogeny may not be stable and could vary with additional sequence data. Inclusion of the *Monadelpha* ITS sequence in a broader analysis of Plukenetieae that sampled six loci (nuclear ribosomal ETS, ITS; low copy *KEA1*, *TEB*; plastid *matK*, *ndbF*; results not shown) recovered similar results with strong support for subclade T6/9, the inclusion of *Monadelpha* in subclade T6/9, and with weak support for generic relationships therein (Cardinal-McTeague et al., unpublished).

The 5-colpate pollen of *Monadelpha* is unique among Plukenetieae. All other Plukenetieae have 3-aperturate or inaperturate pollen, with the exception of *T. rubiginosa* (discussed below). Among New World Tragiinae, *Gitara*, *Zuckertia*, and *Tragia* sect. *Tragia* pollen is 3-colpate, whereas pollen of *Acidoton*, *Bia*, and *Platygyne* is inaperturate, and *T.* sect. *Leptobotrys* is 3-porate (Gillespie 1994a, 1994b) (Table 1). *Monadelpha* shares uneven colpus margins with the 3-colpate taxa. Its tectate-foveolate exine is more similar to the tectate and finely fossulate-reticulate or finely reticulate exines of *Gitara* and *Zuckertia* than to the intectate-baculate exine of *Tragia* sect. *Tragia*.

Monadelpha is also morphologically distinct, especially its staminate flowers with filaments completely connate into a long cylindrical staminal column bearing a tight terminal cluster of ± 5 anthers. *Acidoton*, *Bia*, *Gitara*, *Platygyne*, and *Zuckertia* all have numerous free stamens, the large *Tragia* sects. *Tragia* and *Tagira* have 3 stamens (sometimes more, to 22) that are distinct or connate only at the base, and *T.* sect. *Leptobotrys* has two stamens (rarely 3) connate basally. Only the distantly related *Tragia lassia* (*T.* sect. *Lassia*) of Madagascar has stamens or filaments entirely connate, but this feature has obviously evolved independently. Its androecium, consisting of a small 3-anthered disc-shaped structure on a very short narrow column, is very different from that of *Monadelpha*.

Other characters of *Monadelpha* that are unusual for Tragiinae include unisexual inflorescences and long, mostly distinct styles. Whereas most Tragiinae have bisexual inflorescences with pistillate flowers proximal, *Monadelpha* shares unisexual inflorescences with *Gitara* and the Caribbean genera *Acidoton* and *Platygyne* (plus a few species of Old World Tragiinae). Styles of *Monadelpha* are slender, cylindrical, mostly smooth (papillose only at the apex), up to 10 mm long, and connate basally (up to $\frac{1}{4}$ their length). Most New World Tragiinae and Old World *Tragia* have styles that are much shorter, relatively thicker, and basally to mostly connate into a thick stylar

column. Perhaps most similar is *Zuckertia* with somewhat longer (to 5 mm), slender cylindrical styles that are connate into a slender column, but differ in the degree of connation (1/2–3/4 their length) and the free portion papillose adaxially.

Tragia rubiginosa from Amazonian Peru is another morphologically unusual *Tragia* species (Huft 1989) that is unplaced in the present sectional classification. The species has 4-colpate pollen (preliminary observations in Gillespie 1994b) and is the only species in Tragiinae other than *Monadelpha* with a pollen aperture number greater than three. Its broad, thick, subsessile stigmas are unique in Tragiinae and its staminate flowers with five sessile anthers are unusual. The species is morphologically distinct from *Monadelpha*, and the two taxa are unlikely to be closely related. Molecular data is not yet available to determine its phylogenetic position within Tragiinae.

The isolated phylogenetic position (including a long branch length), and accompanying distinctive stamen and pollen morphology all support the recognition of *Monadelpha* as a new genus separate from *Tragia*. Our results suggest a possible relationship with the northern South American and Central American monotypic genus *Gitara* and the Mexican and Central American ditypic genus *Zuckertia*.

Taxonomic treatment

***Monadelpha* L.J.Gillespie & Card.-McTeag., gen. nov.**

urn:lsid:ipni.org:names:77213225-1

Tragia section *Monadelphae* L.J.Gillespie, Novon 4: 331. 1994.

Diagnosis. Similar to *Tragia* and other Tragiinae genera but differing in having 5-colpate pollen and monadelphous stamens with filaments entirely connate into an elongate, cylindrical staminal column with anthers tightly clustered together at apex.

Type and only known species. *Monadelpha guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag.

Description. *Habit* climbing vines, apparently monoecious; latex absent; stems twining; stems, leaves and inflorescences with stinging and simple hairs. *Stipules* narrowly triangular or lanceolate, small, caducous. *Leaves* simple, alternate, evergreen, petiolate, eglandular; blades elliptic, ovate-elliptic, broadly elliptic, broadly ovate-elliptic, or suborbicular, chartaceous, apex acuminate, base narrowly cordate, margins irregularly serrulate or denticulate with minute glandular setae, venation pinnate; petiolar and laminar glands absent. *Inflorescences* slender racemes, unisexual, flowers single per node in bract axil; bracts small, lanceolate or narrowly lanceolate, eglandular; staminate inflorescence axillary; pistillate inflorescence (known only in fruiting stage) terminal but appearing leaf-opposed. *Staminate flowers* pedicellate; sepals 5, narrowly oblong, valvate; corolla and disc absent; stamens apparently 5, monadelphous; filaments connate into an elongate, ±cylindrical staminal column, bearing a dense cluster of ±5 anthers; pollen 5-colpate, oblate-spheroidal to suboblate, amb pentagonal, exine

tectate-perforate, tectum foveolate and microverrucate, colpi with uneven margins. *Pistillate flowers* (description based on old flowers on infructescence axis) pedicellate; sepals 6, ovate, distinctly imbricate, margins entire; corolla and disc absent; ovary 3-locular with 1 ovule per locule, 3-lobed, densely covered with stinging hairs; styles 3, long-cylindrical, mostly distinct, connate basally for 10–25% length, papillose at apex. *Fruits* 3-lobed capsules, dehiscing into 3 bivalved mericarps; pericarp woody, sparsely covered with stinging hairs; columella persistent, with 3 perpendicular apical arms; seeds 3, subglobose, abaxial surface somewhat obtusely angular, ecarunculate; sepals persistent.

Etymology. The genus name is combined from *monos* (Greek, one) and *adelphos* (Greek, brother), and refers to monadelphous with filaments united and to *Tragia* section *Monadelpheae*.

***Monadelphe guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag., comb. nov.**

urn:lsid:ipni.org:names:77213226-1

Figures 1, 2

Tragia guayanensis L.J.Gillespie, Novon 4: 330–338. 1994.

Type. VENEZUELA. Amazonas: Río Casiquiare entre la boca del [Río] Siapa y el caño Momoni, 18 Feb–4 Mar 1986, *B. Stergios & G. Aymard 9182* (holotype: MO-260419! – staminate; isotype: NY-00076710! – pistillate).

Description. See Gillespie (1994b). Emended here (based on *Ule 5013*): *Leaves*: petiole 2–8 cm long, blade elliptic, ovate-elliptic, broadly elliptic, broadly ovate-elliptic, or suborbicular, 12–25 × 6–17 cm, apex with acumen 1–2 cm long, base cordate with narrow sinus 0.8–2.5 cm deep, margins irregularly serrulate or denticulate. *Staminate inflorescences* ~3–18 cm long.

Etymology. The specific epithet is derived from Guayana, and refers both to the Guayana Shield region of northern South America and to the Guayana Region of Venezuela where the species is native. Guayana is of Amerindian derivation by European colonists, and may come from the tribe Guayanos or the Indigenous word *uayana*, meaning pale (see Berry et al. 1995).

Additional collections examined. BRAZIL. Amazonas: Rio Juruá, Nov 1900, *E.H.G. Ule 5013* (L-0160690, K-001205092). VENEZUELA. Amazonas: En la isla de Trapichote, Delta del Ventuari, [3°57'31.45"N, 67°12'7.45"W], alt. 125 m, 21 Apr 1942, *L. Williams 14990* (paratypes: F-1189188, US-1833601).

Distribution and preliminary conservation status. Known from only three collections. The two from Venezuela are ~220 km apart in lowland rainforests of the upper Orinoco Basin and Río Casiquiare of western Amazonas. The Brazilian collection occurs at least 500 km to the south along the Rio Juruá (locality imprecise) in Amazonas. They occur in remote, pristine rainforest and their IUCN Red List Category presently should be Data Deficient given limited information of distribution and threats.

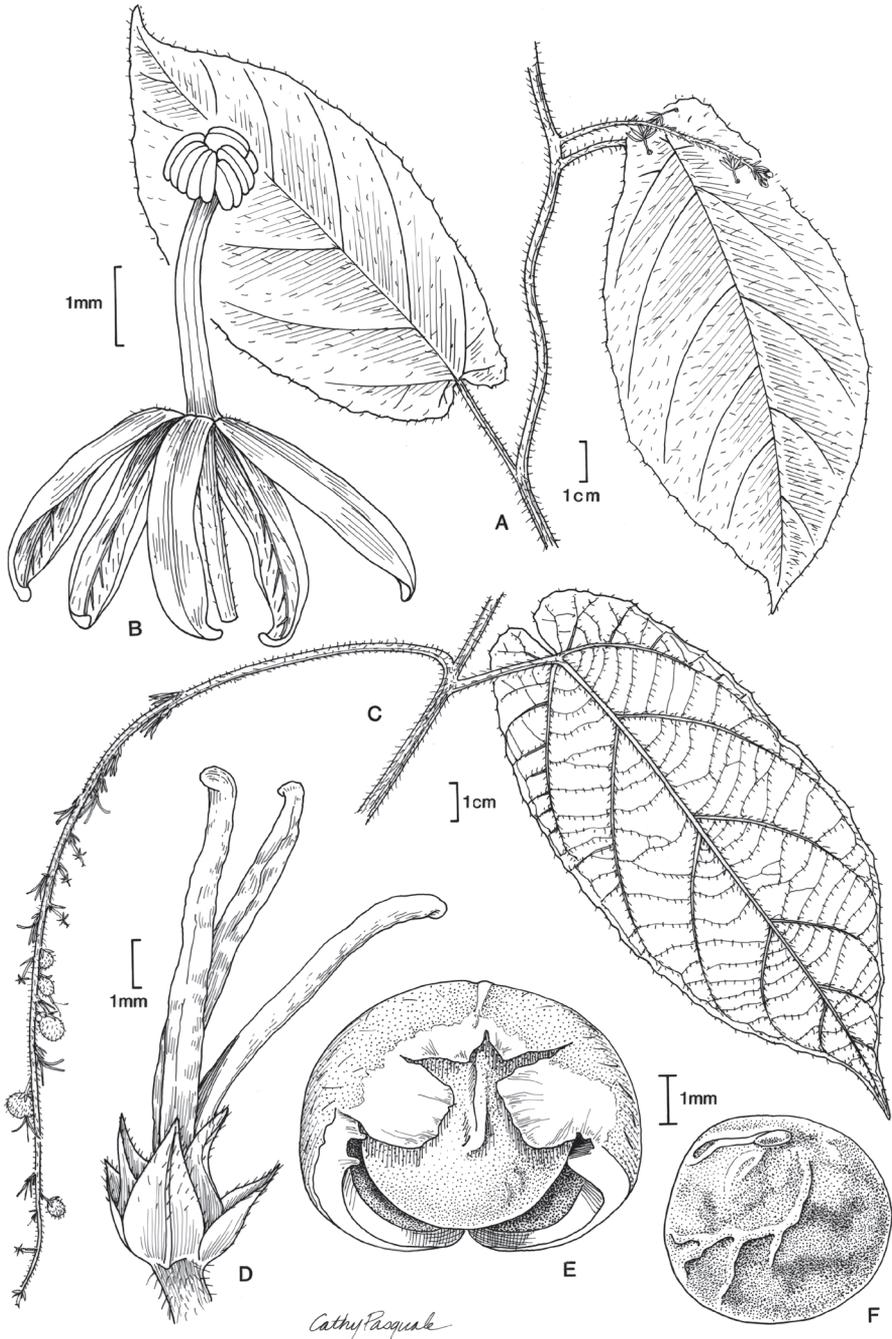


Figure 1. Illustration of *Monadelpha guayanensis*. **A** habit showing staminate inflorescence **B** staminate flower **C** habit showing infructescence **D** pistillate flower **E** mericarp of dehiscent capsule with enclosed seed **F** seed, lateral view with hilum at top. Sources: **A, B** based on *Stergios & Aymard 9182* (MO) **C–F** based on *Stergios & Aymard 9182* (NY). Illustration by Cathy Pasquale reproduced from Gillespie (1994b) with permission from the Missouri Botanical Garden Press.

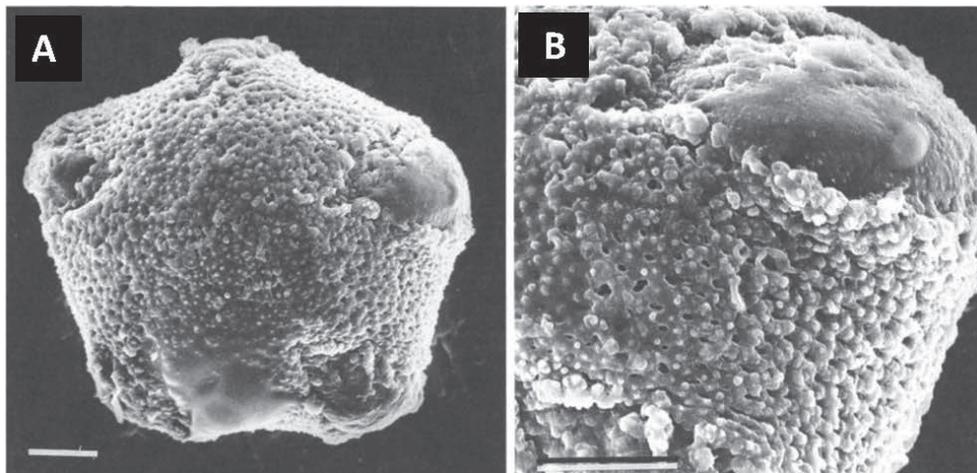


Figure 2. Pollen morphology of *Monadelphpha guayanensis* **A** SEM of pollen grain showing polar view with five colpi **B** closeup of mesocolpium and two colpi. Source: *Stergios & Aymard 9182* (MO). Figure reproduced from Gillespie (1994b) with permission from the Missouri Botanical Garden Press.

Notes. *Monadelphpha guayanensis* is newly reported here from Brazil based on one 1900 collection by E.H.G. Ule. Staminate inflorescences on this collection (L-0160690 sheet) are considerably longer than previously described, and are closer in length to the pistillate inflorescence. It appears that the staminate inflorescence on the holotype may be damaged and partly missing or possibly less mature. Leaf blades are more variable in size and shape than on the two Venezuelan collections, some blades being very similar, others larger and relatively broader.

Monadelphpha guayanensis has unisexual inflorescences and is likely monoecious (rather than dioecious). Although unisexual inflorescences are not found on the same branch, the type collection, *Stergios & Aymard 9182*, has inflorescences of both sexes, and is thus monoecious if one assumes branches originate from a single individual. Further collections are needed to confirm this character.

Key to Tragiinae in South America and Central America

- 1 Filaments absent or entirely connate into an elongate staminal column; pollen 4- or 5-colpate; inflorescences unisexual, racemose; staminate flowers with 5 sepals and 5 stamens **2**
- Filaments distinct or rarely partly connate; pollen 3-colpate, weakly 3-porate, or inaperturate; inflorescences bisexual (unisexual in *Gitara*), racemose or paniculate with a single branch; staminate flowers with 3–5 (6) sepals and (1) 2–40+ stamens **3**
- 2 Anthers in a dense cluster on an elongate \pm cylindrical staminal column; pollen 5-colpate; styles cylindrical, 6–10 mm long..... *Monadelphpha*
- Anthers sessile; pollen 4-colpate; stigmas sessile, broad... *Tragia rubiginosa*

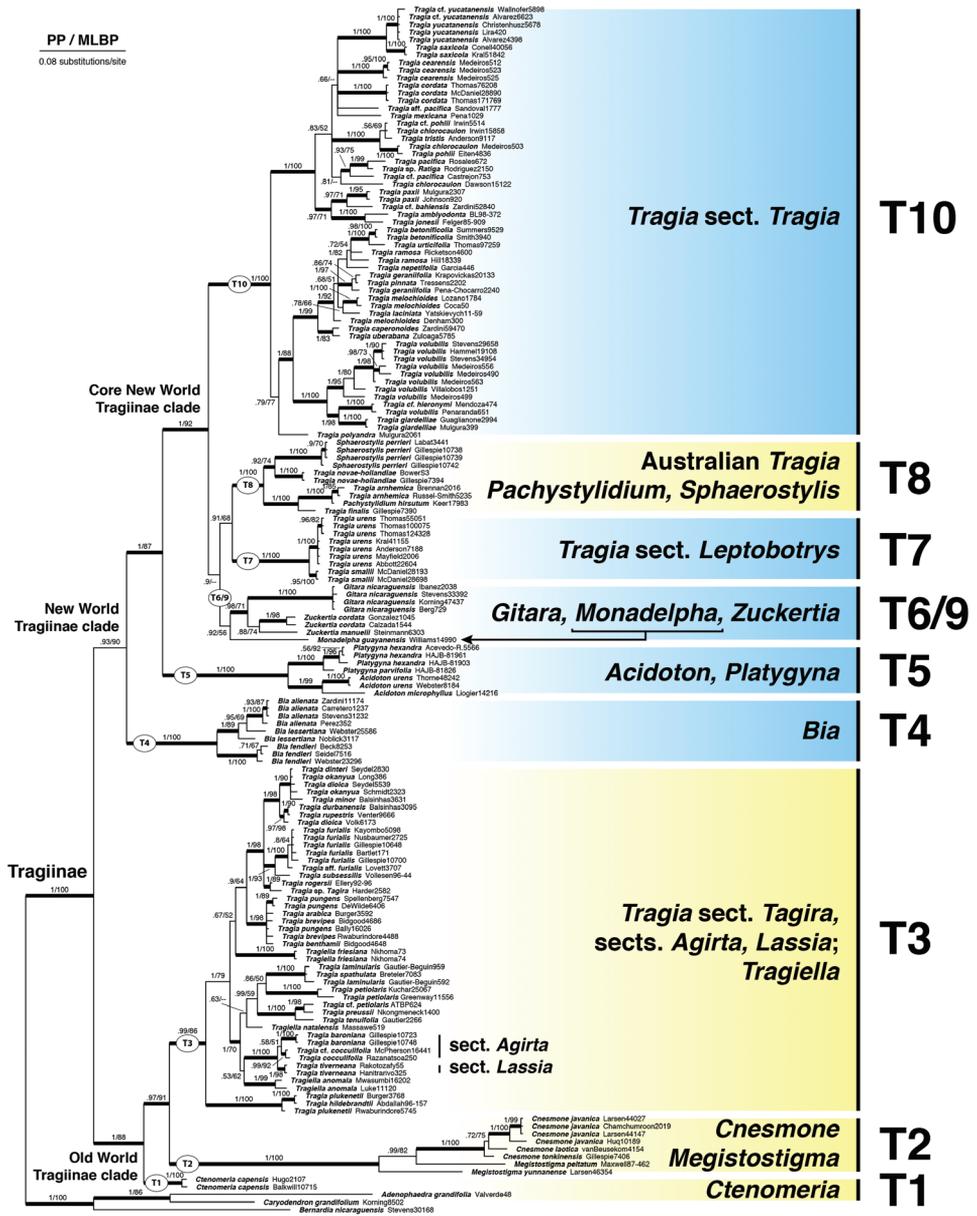


Figure 3. Phylogenetic relationships of *Monadelpha*. Bayesian 50% majority rule consensus tree for the 159-accession (80 taxa) ITS dataset of Tragiinae, demonstrating the distinct phylogenetic placement of *Monadelpha* (subclade T6/9). Subclade naming system follows Cardinal-McTeague and Gillespie (2016) with minor adjustments. Branches are labeled with Bayesian posterior probabilities (PP) and maximum likelihood bootstrap percentages (MLBP). Bold branches indicate strong support (PP > 0.95, MLBP > 85) and coloured boxes indicate general distribution (New World = blue, Old World = yellow).

- 3 Inflorescences unisexual; dioecious, erect shrubs; anther connective with tuft of stinging hairs *Gitara*
- Inflorescences bisexual with pistillate flowers basal; monocious vines, herbs, or subshrubs; anther connective lacking tuft of stinging hairs or present but minute **4**
- 4 Inflorescences racemose, with 1 (2) pistillate flower(s) at the basal 1 (–9) node(s) (*T. polyandra* with (1) 2–4 (5) flowers on a short basal branch); stamens (1) 2–5 (–22); staminate disc usually absent, if present comprising a single central structure; pollen exine intectate, baculate *Tragia* (sect. *Tragia*)
- Inflorescences consisting of a racemose staminate main axis and a single elongate basal branch bearing 5–30 pistillate flowers (branch short with (1) 2–4 flowers in *Zuckertia manuelii*); stamens 6–40+; staminate disc segmented or absent; pollen exine tectate, finely reticulate or foveolate-fossulate **5**
- 5 Staminate flowers with 3 (4) sepals, 5–10 disc segments, and 6–20 stamens; leaf blades 5–16 cm long, usually unlobed; pollen inaperturate; South America to Costa Rica *Bia*
- Staminate flowers with 5 or 6 sepals, no disc, and 17–40+ stamens; leaf blades (7–) 12–25 cm long, unlobed to 3-lobed; pollen tricolpate; Mexico and Central America *Zuckertia*

Acknowledgements

We thank the Missouri Botanical Garden Press, St. Louis, for granting permission to reproduce Figures 1, 2, and 7 from Gillespie (1994b: 332, 334). The laboratory work was conducted with support of the Molecular Biodiversity Laboratory of the Canadian Museum of Nature and the Smithsonian's Laboratories of Analytical Biology of the National Museum of Natural History. We thank Kanchi Gandhi (GH) for advice on orthography, Geoff Levin, Paul Berry, Gordon McPherson and an anonymous reviewer for helpful comments on the manuscript, and the following institutions for the loan of material or for facilitating examination of collections: MO, NY, P and US. This work was supported by the Canadian Museum of Nature.

References

- Baillon H (1858) *Étude Générale du Groupe des Euphorbiacées*. V. Masson, Paris.
- Berry PE, Holst BK, Yatskievych K (1995) Introduction. In: Berry PE, Holst BK, Yatskievych K (Eds) *Flora of the Venezuelan Guayana*. Volume 1: Introduction. Missouri Botanical Garden & Timber Press, Portland, xv–xxii.
- Cardinal-McTeague WM, Gillespie LJ (2016) Molecular phylogeny and pollen evolution of Euphorbiaceae tribe Plukenetieae. *Systematic Botany* 41(2): 329–347. <https://doi.org/10.1600/036364416X691759>

- Cardinal-McTeague WM, Wurdack KJ, Sigel EM, Gillespie LJ (2019) Seed size evolution and biogeography of *Plukenetia* (Euphorbiaceae), a pantropical genus with traditionally cultivated oilseed species. *BMC Evolutionary Biology* 19(1): 29. <https://doi.org/10.1186/s12862-018-1308-9>
- Cervantes A, Fuentes S, Gutiérrez J, Magallón S, Borsch T (2016) Successive arrivals since the Miocene shaped the diversity of the Caribbean Acalyphoideae (Euphorbiaceae). *Journal of Biogeography* 43(9): 1773–1785. <https://doi.org/10.1111/jbi.12790>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. <https://doi.org/10.1038/nmeth.2109>
- Dorr LJ, Romero-Hernández C, Wurdack KJ (2018) A new large-flowered species of *Andeimalva* (Malvaceae, Malvoideae) from Peru. *PhytoKeys* 110: 91–99. <https://doi.org/10.3897/phytokeys.110.29376>
- Gillespie LJ (1994a) Pollen morphology and phylogeny of the tribe Plukenetieae (Euphorbiaceae). *Annals of the Missouri Botanical Garden* 81(2): 317–348. <https://doi.org/10.2307/2992101>
- Gillespie LJ (1994b) A new section and two new species of *Tragia* (Euphorbiaceae) from the Venezuelan Guayana and French Guiana. *Novon* 4(4): 330–338. <https://doi.org/10.2307/3391440>
- Huft MJ (1989) New and critical taxa of Euphorbiaceae from South America. *Annals of the Missouri Botanical Garden* 76(4): 1077–1086. <https://doi.org/10.2307/2399692>
- Katoh K, Standley D (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Leandri JD (1971) Un sous-genre malgache nouveau de *Tragia* (Euphorbiacées). *Adansonia*, sér. 2 11: 435–439.
- Medeiros D, de Senna Valle L, Valka Alves RJ (2013) Revalidation of the genera *Bia* and *Zuckertia* (Euphorbiaceae) with *B. capivarensis* sp. nov. from Serra da Capivara, Brazil. *Nordic Journal of Botany* 31(5): 595–602. <https://doi.org/10.1111/j.1756-1051.2012.01616.x>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the 2010 Gateway Computing Environments Workshop (GCE)*, New Orleans, 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Mulgura de Romero M, Gutierrez de Sanguinetti M (1989) Actualización taxonomica de *Tragia* (Euphorbiaceae) para Argentina y regiones limitrofes. *Darwiniana* 29(1–4): 77–138.
- Radcliffe-Smith A (2001) *Genera Euphorbiacearum*. Royal Botanic Gardens, Kew.
- Rambaut A, Drummond A, Xie D, Baele G, Suchard M (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67(5): 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)* 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>

- Steinmann VW, Ramírez-Amezcuca Y (2013) *Bia manuelii* (Euphorbiaceae: Acalyphoideae), a new species from Sierra de Coalcomán, Michoacán, Mexico. *Revista Mexicana de Biodiversidad* 84(3): 746–750. <https://doi.org/10.7550/rmb.32014>
- Webster GL (2007) Taxonomic and nomenclatural changes in American Euphorbiaceae sensu lato. *Contributions from the University of Michigan Herbarium* 25: 235–239.
- Webster GL (2014) Euphorbiaceae. In: Kubitzki K (Ed.) *The Families and Genera of Vascular Plants*. Volume XI. Flowering Plants. Eudicots. Malpighiales. Springer Verlag, Berlin and Heidelberg, Germany, 51–216. https://doi.org/10.1007/978-3-642-39417-1_10
- Wurdack KJ, Hoffmann P, Chase MW (2005) Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcL* and *trnL-F* DNA sequences. *American Journal of Botany* 92(8): 1397–1420. <https://doi.org/10.3732/ajb.92.8.1397>

Appendix I

Sources for ITS data used in phylogenetic analyses. Voucher data (country, collector, number, herbarium code) are provided, with new GenBank numbers in bold and beginning with MK and MW.

Outgroup: *Adenophaedra grandifolia* (Klotzsch) Müll.Arg. COSTA RICA • Valverde 48 (NY), **MK780909**. *Bernardia nicaraguensis* Standl. & L.O. Williams NICARAGUA • Stevens 30168 (MO), KP794419. *Caryodendron grandifolium* (Müll.Arg.) Pax ECUADOR • Korning 8502 (MO), KP794421. **Ingroup:** *Acidoton microphyllus* Urban DOMINICAN REPUBLIC • Liogier 14216 (NY), **MK780907**. *Acidoton urens* Sw. JAMAICA • Thorne 48242 (MO), KP794316. *Acidoton urens* Sw. JAMAICA • Webster 8184 (DAV), **MK780908**. *Bia alienata* Didr. BOLIVIA • Carretero 1237 (MO), KP794320. *Bia alienata* Didr. Paraguay • Pérez 352 (MO), KP794318. *Bia alienata* Didr. PARAGUAY • Stevens et al. 31232 (MO), **MK780928**. *Bia alienata* Didr. PARAGUAY • Zardini 11174 (MO), KP794319. *Bia fendleri* Müll.Arg. BOLIVIA • Beck 8253 (MO), KP794321. *Bia fendleri* Müll.Arg. PARAGUAY • Seidel and Herzog 7516 (DAV), **MK780930**. *Bia fendleri* Müll.Arg. PERU • Webster 23296 (DAV), **MK780929**. *Bia cf. lessertiana* BRAZIL • Noblick 3117 (DAV), **MK780931**. *Bia lessertiana* Baill. BRAZIL • Webster 25586 (DAV), **MK780932**. *Cnesmone javanica* Blume BANGLADESH • Huq 10189 (US), **MK780937**. *Cnesmone javanica* Blume THAILAND • Chamchumroon 2019 (L), KP794430. *Cnesmone javanica* Blume THAILAND • Larsen 44027 (MO), KP794427. *Cnesmone javanica* Blume THAILAND • Larsen 44147 (MO), KP794428. *Cnesmone laotica* (Gagnep.) Croizat THAILAND • van Beusekom 4154 (L), KP794431. *Cnesmone tonkinensis* (Gagnep.) Croizat VIETNAM • Gillespie 7406 (CAN), **MK780938**. *Ctenomeria capensis* (Thunb.) Harv. ex Sond. SOUTH AFRICA • Balkwill and Balkwill 10715 (MO), **MK780939**. *Ctenomeria capensis* (Thunb.) Harv. ex Sond. SOUTH AFRICA • Hugo 2107 (MO), KP794322. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie BRAZIL • Berg et al. 729 (CAN), **MK780953**. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie ECUADOR • Korning 47437 (MO), KP794398.

Gitara nicaraguensis (Hemsl.) Card.-McTeag. & L.J.Gillespie NICARAGUA • Stevens 33392 (MO), **MK780954**. *Gitara nicaraguensis* (Hemsl.) Card.-McTeag. & L.J.Gillespie PANAMA • Ibañez 2038 (MO), KP794397. *Megistostigma peltatum* (J.J.Sm.) Croizat THAILAND • Maxwell 87-462 (L), **MK780958**. *Megistostigma yunnanense* Croizat THAILAND • Larsen 46354 (L), **MK780959**. *Monadelpha guayanensis* (L.J.Gillespie) L.J.Gillespie & Card.-McTeag. VENEZUELA • Williams 14990 (US-1833601), **MW264490**. *Pachystylidium hirsutum* (Blume) Pax & K.Hoffm. THAILAND • Keer 17893 (L), KP794408. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • Acevedo-Rodríguez 5566 (NY), KP794317. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • HAJB 81903 (MICH), **MK780963**. *Platygyne hexandra* (Jacq.) Müll.Arg. CUBA • HAJB 81961 (MICH), **MK780964**. *Platygyne parvifolia* Alain CUBA • HAJB 81826 (MICH), **MK780965**. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10738 (CAN), KP794413. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10739 (CAN), KP794414. *Sphaerostylis perrieri* Leandri MADAGASCAR • Gillespie 10742 (CAN), KP794415. *Sphaerostylis perrieri* Leandri MADAGASCAR • Labat 3441 (MO), KP794412. *Tragia* aff. *furialis* TANZANIA • Lovett 3707 (MO), KP794344. *Tragia* aff. *pacifica* EL SALVADOR • Sandoval 1777 (MO), KP794388. *Tragia amblyodonta* (Müll. Arg.) Pax & K.Hoffm. USA • B.L. 98-372 (MO), KP794376. *Tragia arabica* (Müll. Arg.) Baill. ex Prain ETHIOPIA • Burger 3592 (US), **MK780910**. *Tragia arnhemica* P.I.Forst. AUSTRALIA • Brennan 2016 (DNA), KP794410. *Tragia arnhemica* P.I.Forst. AUSTRALIA • Russel-Smith 5235 (DNA), KP794409. *Tragia baroniana* Prain MADAGASCAR • Gillespie et al. 10723 (CAN), **MK780911**. *Tragia baroniana* Prain MADAGASCAR • Gillespie et al. 10748 (CAN), **MK780912**. *Tragia benthamii* Baker TANZANIA • Bidgood 4648 (MO), KP794328. *Tragia betonicifolia* Nutt. USA • Smith 3940 (MO), KP794364. *Tragia betonicifolia* Nutt. USA • Summers 9529 (MO), KP794363. *Tragia brevipes* Pax TANZANIA • Bidgood 4686 (MO), KP794325. *Tragia brevipes* Pax UGANDA • Rwaburindore 4488 (MO), KP794329. *Tragia caperonoides* Pax & K. Hoffm. PARAGUAY • Zardini and Gamarra 59470 (MO), **MK780967**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 512 (R), **MK780968**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 523 (R), **MK780969**. *Tragia cearensis* Pax & K.Hoffm. BRAZIL • Medeiros et al. 525 (R), **MK780970**. *Tragia cf. bahiensis* PARAGUAY • Zardini 52840 (MO), KP794378. *Tragia* cf. *cocculifolia* MADAGASCAR • McPherson and van der Werff 16441 (CAN), **MK780913**. *Tragia* cf. *hieronymi* BOLIVIA • Mendoza 474 (NY), **MK780975**. *Tragia* cf. *pacifica* MEXICO • Castrejón 753 (MO), KP794392. *Tragia* cf. *petiolaris* UGANDA • ATBP 624 (MO), KP794351. *Tragia* cf. *pohlii* BRAZIL • Irwin 5514 (NY), **MK780971**. *Tragia* cf. *yucatanensis* MEXICO • Álvarez 6623 (MO), KP794383. *Tragia* cf. *yucatanensis* GUATEMALA • Wallnöfer 5898 (MO), KP794381. *Tragia chlorocaulon* Baill. BRAZIL • Dawson 15122 (MO), KP794390. *Tragia chlorocaulon* Baill. BRAZIL • Irwin 15858 (MO), KP794391. *Tragia chlorocaulon* Baill. BRAZIL • Medeiros et al. 503 (R), **MK780973**. *Tragia cocculifolia* Prain MADAGASCAR • Razanatsoa 250 (MO), KP794331. *Tragia cordata* Michx. USA • McDaniel 28890 (MO), KP794395. *Tragia cordata* Michx. USA • Thomas 171769 (MO), KP794396. *Tragia cordata* Michx. USA • Thomas 76208 (CAN), KP794394.

Tragia dinteri Pax NAMIBIA • Seydel 2830 (L), **MK780914**. *Tragia dioica* Sond. NAMIBIA • Seydel 5539 (MO), KP794335. *Tragia dioica* Sond. NAMIBIA • Volk 6173 (MO), KP794332. *Tragia durbanensis* Kuntze SOUTH AFRICA • Balsinhas 3095 (MO), KP794333. *Tragia finalis* P.I.Forst. AUSTRALIA • Gillespie 7390 (CAN), KP794411. *Tragia furialis* Bojer ex Prain MADAGASCAR • Gillespie 10648 (CAN), KP794342. *Tragia furialis* Bojer ex Prain MADAGASCAR • Gillespie 10700 (CAN), **MK780917**. *Tragia furialis* Bojer ex Prain MADAGASCAR • Nusbaumer 2725 (MO), KP794343. *Tragia furialis* Bojer ex Prain MAYOTTE • Barthlet 171 (MO), KP794341. *Tragia furialis* Bojer ex Prain TANZANIA • Kayombo 5098 (MO), KP794340. *Tragia geraniiifolia* Klotzsch ex Baill. ARGENTINA • Krapovickas 20133 (MO), KP794368. *Tragia geraniiifolia* Klotzsch ex Baill. PARAGUAY • Peña-Chocarro 2240 (MO), KP794370. *Tragia giardelliae* M.M.Gutiérrez & M.E.Múlgura ARGENTINA • Guaglianone 2994 (MO), KP794360. *Tragia giardelliae* M.M.Gutiérrez & M.E.Múlgura ARGENTINA • Múlgura 399 (NY), **MK780974**. *Tragia hildebrandtii* Müll.Arg. TANZANIA • Abdallah 96/157 (MO), KP794355. *Tragia jonesii* Radcl.-Sm. & Govaerts MEXICO • Felger 85-909 (MO), KP794377. *Tragia laciniata* (Torr.) Müll.Arg. MEXICO • Yatskievych 11-59 (MO), **MK780976**. *Tragia laminularis* Müll.Arg. CÔTE D'IVOIRE • Gautier-Béguin 592 (MO), KP794349. *Tragia laminularis* Müll.Arg. CÔTE D'IVOIRE • Gautier-Béguin 959 (MO), KP794348. *Tragia melochioides* Griseb. BOLIVIA • Coca 50 (MO), KP794373. *Tragia melochioides* Griseb. BOLIVIA • Lozano 1784 (MO), KP794372. *Tragia melochioides* Griseb. URUGUAY • Denham et al. 300 (SI), **MK780978**. *Tragia mexicana* Müll.Arg. BELIZE • Peña 1029 (MO), KP794393. *Tragia minor* Sond. SOUTH AFRICA • Balsinhas 3631 (MO), KP794338. *Tragia nepetifolia* Cav. MEXICO • García 446 (MO), KP794366. *Tragia novae-hollandiae* Müll.Arg. AUSTRALIA • Bower S3 (CAN), **MK780960**. *Tragia novae-hollandiae* Müll.Arg. AUSTRALIA • Gillespie 7394 (CAN), KP794417. *Tragia okanyua* Pax BOTSWANA • Long 386 (MO), KP794336. *Tragia okanyua* Pax ZAMBIA • Schmidt 2323 (MO), KP794337. *Tragia pacifica* McVaugh EL SALVADOR • Rosales 672 (MO), KP794389. *Tragia paxii* Lourteig & O'Donnell ARGENTINA • Johnson 920 (MO), KP794380. *Tragia paxii* Lourteig & O'Donnell ARGENTINA • Múlgura 2307 (MO), KP794379. *Tragia petiolaris* Radcl.-Sm. TANZANIA • Greenway and Polhill 11556 (L), **MK780920**. *Tragia petiolaris* Radcl.-Sm. TANZANIA • Kuchar 25067 (MO), KP794354. *Tragia pinnata* (Poir.) A.Juss. ARGENTINA • Tressens 2202 (MO), KP794369. *Tragia plukenetii* Radcl.-Sm. ETHIOPIA • Burger 3768 (US), **MK780919**. *Tragia plukenetii* Radcl.-Sm. UGANDA • Rwaburindore 5745 (MO), KP794356. *Tragia pohlii* Müll.Arg. BRAZIL • Eiten 4836 (UBC), **MK780979**. *Tragia polyandra* Vell. ARGENTINA • Múlgura 2061 (MO), KP794375. *Tragia preussii* Pax CAMEROON • Nkongmeneck 1400 (MO), KP794352. *Tragia pungens* (Forssk.) Müll. Arg. ETHIOPIA • De Wilde 6406 (MO), KP794327. *Tragia pungens* (Forssk.) Müll.Arg. SOMALIA • Bally 16026 (MO), KP794326. *Tragia pungens* (Forssk.) Müll.Arg. YEMEN • Spellenberg 7547 (L), **MK780921**. *Tragia ramosa* Torr. USA • Hill 18339 (MO), KP794371. *Tragia ramosa* Torr. USA • Ricketson 4600 (MO), KP794367. *Tragia rogersii* Prain SOUTH AFRICA • Ellery 92/96 (MO), KP794339. *Tragia rupestris* Sond. SOUTH AFRICA • Venter 9666 (MO), KP794334. *Tragia saxicola* Small USA • Conell

40056 (MO), KP794386. *Tragia saxicola* Small USA • Kral 51842 (MO), KP794387. *Tragia smallii* Shinners USA • McDaniel 28193 (MO), KP794401. *Tragia smallii* Shinners USA • McDaniel 28698 (MO), KP794402. *Tragia* sp. *Ratiga* EL SALVADOR • Rodriguez and Tejada 2150 (MO), **MK780980**. *Tragia* sp. *Tagira* ZAMBIA • Harder and Bingham 2582 (CAN), **MK780923**. *Tragia spathulata* Benth. TOGO • Breteler 7083 (MO), KP794350. *Tragia subsessilis* Pax TANZANIA • Vollesen 96/44 (MO), KP794345. *Tragia tenuifolia* Benth. CÔTE D'IVOIRE • Gautier 2266 (MO), KP794353. *Tragia tiverneana* Leandri MADAGASCAR • Hanitrarivo 325 (CAN), **MK780925**. *Tragia tiverneana* Leandri MADAGASCAR • Rakotozafy et al. 55 (CAN), **MK780924**. *Tragia tristis* Müll.Arg. BRAZIL • Anderson 9117 (NY), **MK780981**. *Tragia uberbana* Müll.Arg. ARGENTINA • Zuloaga 5785 (MO), KP794374. *Tragia urens* L. USA • Abbott 22604 (MO), **MK780957**. *Tragia urens* L. USA • Anderson 7188 (MO), KP794407. *Tragia urens* L. USA • Kral 41155 (MO), KP794406. *Tragia urens* L. USA • Mayfield 2006 (MO), **MK780956**. *Tragia urens* L. USA • Thomas 100075 (MO), KP794404. *Tragia urens* L. USA • Thomas 124328 (MO), KP794405. *Tragia urens* L. USA • Thomas 55051 (CAN), KP794403. *Tragia urticifolia* Michx. USA • Thomas 97259 (CAN), KP794365. *Tragia volubilis* L. BOLIVIA • Peñarando et al. 651 (MO), **MK780987**. *Tragia volubilis* L. BOLIVIA • Villalobos et al. 1251 (MO), **MK780988**. *Tragia volubilis* L. BRAZIL • Medeiros and Cardinal-McTeague 556 (R), **MK780984**. *Tragia volubilis* L. BRAZIL • Medeiros and Cardinal-McTeague 563 (R), **MK780985**. *Tragia volubilis* L. BRAZIL • Medeiros et al. 490 (R), **MK780983**. *Tragia volubilis* L. BRAZIL • Medeiros et al. 499 (R), **MK780982**. *Tragia volubilis* L. COSTA RICA • Hammel 19108 (MO), KP794362. *Tragia volubilis* L. NICARAGUA • Stevens 29658 (MO), KP794361. *Tragia volubilis* L. NICARAGUA • Stevens and Montiel 34954 (MO), **MK780986**. *Tragia yucatanensis* Millsp. GUATEMALA • Christenhusz 5678 (MO), KP794384. *Tragia yucatanensis* Millsp. MEXICO • Alvarez 4398 (MO), KP794382. *Tragia yucatanensis* Millsp. MEXICO • Lira 420 (MO), KP794385. *Tragiella anomala* (Prain) Pax & K.Hoffm. TANZANIA • Luke 11120 (MO), KP794324. *Tragiella anomala* (Prain) Pax & K.Hoffm. TANZANIA • Mwasumbi 16202 (MO), KP794323. *Tragiella friesiana* (Prain) Pax & K.Hoffm. ZAMBIA • Nkhoma 73 (MO), KP794346. *Tragiella friesiana* (Prain) Pax & K.Hoffm. ZAMBIA • Nkhoma 74 (MO), KP794347. *Tragiella natalensis* (Sond.) Pax & K.Hoffm. TANZANIA • Massawe 519 (MO), KP794330. *Zuckertia cordata* Baill. COSTA RICA • González 1045 (MO), KP794399. *Zuckertia cordata* Baill. MEXICO • Calzada 1544 (MO), KP794400. *Zuckertia manuelii* (V.W.Steinm. & Ram.-Amezcu) Card.-McTeag. & L.J.Gillespie MEXICO • Steinmann et al. 6303 (CAN), **MK780989**.

Nomenclatural and taxonomic updates in *Rourea* subgen. *Rourea* sect. *Multifoliolatae* (Connaraceae)

Cassio A. P. Toledo¹, Vinicius Castro Souza², Eve J. Lucas³

1 Programa de Pós-Graduação em Biologia Vegetal. Instituto de Biologia, Universidade Estadual de Campinas-UNICAMP, Rua Monteiro Lobato, 255, Campinas, SP. CEP: 13083-862, Brazil **2** Departamento de Ciências Biológicas. Escola Superior de Agricultura “Luiz de Queiroz”-ESALQ. Universidade de São Paulo-USP, Av. Pádua Dias, 11, Piracicaba, SP. CEP: 13428-900, Brazil **3** Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

Corresponding author: Cassio A. P. Toledo (cassioxtoledo@gmail.com)

Academic editor: Blanca León | Received 14 May 2020 | Accepted 4 June 2020 | Published 8 December 2020

Citation: Toledo CAP, Souza VC, Lucas EJ (2020) Nomenclatural and taxonomic updates in *Rourea* subgen. *Rourea* sect. *Multifoliolatae* (Connaraceae). *PhytoKeys* 169: 137–175. <https://doi.org/10.3897/phytokeys.169.54297>

Abstract

The pantropical genus *Rourea* Aubl. (Connaraceae) is composed of ca. 70 species, most of which occur in the Neotropics. *Rourea* is currently subdivided into three subgenera, with the American taxa included in *Rourea* subgen. *Rourea*. Forero (1976) recognised six sections for the species of the New World, with *Rourea* subgen. *R. sect. Multifoliolatae* being exclusive to Brazil, characterised by multifoliolate leaves, relatively small leaflets and the staminal tube (0.8–)1–1.5 mm long. Following Forero’s (1976) treatment, additional botanical collections have become available in Brazilian herbaria, allowing re-evaluation of species concepts. This work recognises and revises 12 species in this section, mainly restricted to southeastern Brazil and southern Bahia. A nomenclatural and taxonomic study of these species is here presented, including an identification key, morphological descriptions, illustrations and geographic distribution maps. A new species is also described.

Keywords

Brazil, Cnestideae, new species, Oxalidales, systematics, typification

Introduction

Rourea Aubl. is the second largest genus in Connaraceae and includes about 70 species (Lemmens 1989a), mainly from lowland tropical forests and savannahs of South America, Central Africa and Asia (Leenhouts 1958; Jongkind 1989; Lemmens 1989a). Its centre of species richness lies on the Neotropics, especially in the Amazon and Atlantic domains, comprising ca. 45 American species (Forero 1983). *Rourea* differs morphologically from other Connaraceae genera by the leaves usually 5 or more foliolate, petals epunctate, flowers 5-carpelate, fruits with calyx accrescent and seeds without endosperm (Forero 1983; Lemmens et al. 2004).

The most recent phylogenetic study and currently accepted classification of Connaraceae was an early cladistic study, based exclusively on morphological evidences (Lemmens 1989b). Four tribes were recognised in the family, with *Rourea* included in Cnestideae Planch., sister to a clade formed by the genera *Cnestidium* Planch. and *Cnestis* Juss.

The circumscription of *Rourea* has varied greatly since the publication of the genus by Aublet (1775). De Candolle (1825), for example, treated the genus as a synonym of *Connarus* L. Later, Planchon (1850) included *Rourea* within the tribe Connareae and described new genera and recognised others that are currently treated in synonymy of *Rourea*, such as *Bernardinia* Planch., *Byrsocarpus* Schumach. and *Roureopsis* Planch. Schellenberg (1938) was even more liberal: he followed Planchon's concepts and segregated additional taxa from *Rourea*, which resulted in the description of new generic names (e.g. *Santaloides* G. Schellenb.). On the other hand, Baillon (1869) and Leenhouts (1958) adopted a broader concept for the genus and placed several genera – including some mentioned above – in *Rourea*, resulting in new synonymisations and combinations. Most of their contributions – although with minor changes – have been followed in modern taxonomic treatments (Forero 1983; Jongkind 1989; Lemmens et al. 2004).

Infrageneric classification of *Rourea* has also varied depending on author's concept. Planchon (1850) subdivided the genus into two sections, *Rourea* sect. *Dalbergioideae* and *R.* sect. *Mimosoideae*, with the former represented by the American species and the latter, African and Asian species. Leenhouts (1958) proposed another classification for the genus and recognized three subgenera: *Rourea* subgen. *Rourea*, *R.* subgen. *Jaundea* (Gilg) Leenh. and *R.* subgen. *Palliathus* Leenh. In this subdivision, the American species were included in the former, together with some taxa from western Africa. Forero (1976) adopted Leenhouts's classification and, while preparing a revision of *Rourea* to the New World, divided the American species into six sections (*Rourea* subgen. *Rourea* sect. *Rourea*, *R.* subgen. *R.* sect. *Adenophorae* G. Schellenb., *R.* subgen. *R.* sect. *Cordatae* Forero, *R.* subgen. *R.* sect. *Glabrae* G. Schellenb., *R.* subgen. *R.* sect. *Indutae* G. Schellenb. and *R.* subgen. *R.* sect. *Multifoliolatae* Forero). Morphological distinction of these sections was mainly based on number of leaflets, leaflet and calyx indumentum and length of the staminal tube.

This treatment includes the species belonging to *Rourea* subgen. *Rourea* sect. *Multifoliolatae*, which are restricted to Brazil and morphologically characterised by the leaves (3–)9–41-foliolate, leaflets usually oblong or narrowly elliptic and smaller than those

found in other neotropical *Rourea* and flowers with staminal tubes (0.8–)1–1.5 mm long (Forero 1976, 1983 – with some modifications).

After Forero's (1976) revisional work, new collections of *R.* subgen. *Rourea* sect. *Multifoliolatae* have been available in Brazilian herbaria thanks to modern field expeditions in the country. This has allowed identification of overlooked morphological characters and, thus, re-evaluation of species concepts in this group. It is also of note that many species of this section are very common in the Brazilian territory, although widely misidentified in herbarium collections. This study presents morphological descriptions of the referred taxa, an identification key, illustrations, geographic distribution maps and detailed taxonomic and nomenclatural notes, along with a new species.

Methods

The present study was primarily developed based on consultation of literature specific to the genus (Planchon 1850; Baker 1871; Schellenberg 1938; and Forero 1976, 1983) and analysis of specimens from the following herbaria (acronyms according to Thiers 2020): ALCB, BHCB, BR, C, CEN, CEPEC, COL, CVRD, EAC, ESA, F, G, HUEFS, HUEG, HUFU, HUTO, IAN, K, M, MBM, MBML, MG, MO, MPU, NY, P, R, RB, S, SPF, UB, UEC, US, VIC, VIES and W. Fieldwork was carried out by the first author, which allowed collection of botanical samples, photographs and observation of species in their natural habitat. These expeditions took place in Brazil, comprising the municipalities of Conceição da Barra and Guarapari (Espírito Santo) and the district of Gama (Distrito Federal).

General morphological terms mainly follow Font Quer (1953) and Radford et al. (1974), while the venation pattern is based on Ellis et al. (2009) and inflorescence architecture on Weberling (1992).

Geographic distribution maps were prepared using ArcGIS 10.5 (ESRI 2016), based on the localities indicated on herbarium sheet labels. The lists of specimens examined follow alphabetical order by states, then by collectors.

While referring to Brazilian states, the following abbreviations were adopted: Bahia (BA), Distrito Federal (DF), Espírito Santo (ES), Minas Gerais (MG) and Rio de Janeiro (RJ).

Taxonomic treatment

***Rourea* Aubl. subgen. *Rourea* sect. *Multifoliolatae* Forero, Mem. New York Bot. Gard. 26(1): 37. 1976.**

Type. *Rourea blanchetiana* (Progel) Kuhlmann.

Description. *Lianas*, subshrubs, shrubs or scandent shrubs, rarely treelets, (0.35–)0.5–4(–7) m tall; branchlets usually lenticelate. **Leaves** alternate, (3–)9–41-foliolate,

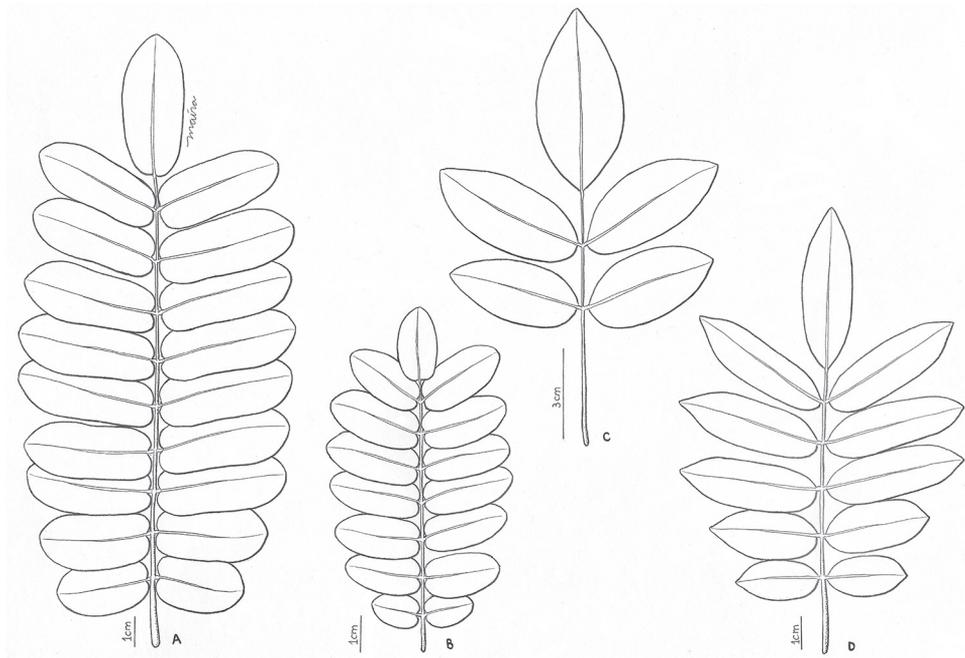


Figure 1. Leaves in *Rourea* subgen. *R. sect. Multifoliolatae*: **A** *R. discolor* **B** *R. martiana* **C** *R. tenuis* **D** *R. cnestidifolia*.

loosely disposed or congested, without stipules; petiole and rachis with glandular trichomes or eglandular; **leaflets** subsessile or pulvinulus 1–2 mm long; blades usually oblong, narrowly elliptic or narrowly ovate, less frequently elliptic, ovate or narrowly obovate, occasionally orbicular on basal leaflets, chartaceous, less frequently coriaceous or membranaceous, abaxially brownish, greenish or glaucous, rarely vinaceous, glabrous, subglabrous, hirsute or villous, base slightly asymmetric to asymmetric, rarely symmetric, apex usually rounded or narrowly rounded, less frequently obtuse, rarely acute (apical leaflets), margin flat, slightly revolute or revolute; secondary venation brochidodromous, tertiary venation reticulate. **Inflorescences** in cymes, occasionally panicles or thyrses, axillary or subterminal, rarely terminal; peduncle, rachis and lateral branches (if present) with glandular trichomes or eglandular. **Flowers** loosely disposed or congested apically; pedicel with glandular trichomes or eglandular; sepals 5, slightly connate at base, outer surface with glandular trichomes or eglandular; petals 5, epunctate; stamens 10, connate at base by (0.8–)1–1.5 mm, shorter series 5, epipetalous, longer series 5, episepalous, anthers rimose; carpels 5, only 1 developing into a fruit, free, sessile, stigma lobate, ovules 2, only 1 developing into a seed. **Fruits** follicular, ellipsoid, straight, calyx accrescent, sepals ascending; **seeds** 1, ellipsoid, black, without endosperm, arillode covering the base.

Diversity and distribution. *Rourea* subgen. *R. sect. Multifoliolatae* is composed of 12 species exclusively found in the Brazilian states of Bahia, Distrito Federal, Espírito Santo, Minas Gerais and Rio de Janeiro.

Recognition. This section is characterised by multifoliolate leaves, leaflets relatively small, normally oblong or narrowly elliptic with rounded apex (Fig. 1), inflorescences mostly with glandular trichomes and stamens connate at base by (0.8–)1–1.5 mm. Species of this section vegetatively resemble several Leguminosae due to the characteristics cited above, but differ because Connaraceae members do not bear stipules.

Key to the species of *Rourea* subgen. *Rourea* sect. *Multifoliolatae*

- 1 Plants eglandular..... **2**
- Plants with glandular trichomes on inflorescence rachis, pedicel and/or outer surface of sepals **5**
- 2 Leaves 3–7(–9)-foliolate; calyx covering two thirds of the fruit
..... *R. macrocalyx*
- Leaves 7–41-foliolate; calyx covering one third of the fruit **3**
- 3 Inflorescence rachis 3.5–11.5 cm long *R. discolor*
- Inflorescence rachis up to 1.8 cm long **4**
- 4 Leaves 11–17(–41)-foliolate; inflorescence rachis sparsely pubescent to pubescent; ovary hirsute..... *R. bahiensis*
- Leaves 7–11-foliolate; inflorescence rachis glabrous or subglabrous; ovary hirsute only on one side *R. barbata*
- 5 Leaves 27–39-foliolate; leaflets abaxially glaucous; petals 9–14 mm long
..... *R. blanchetiana*
- Leaves 3–27-foliolate; leaflets abaxially greenish or brownish; petals (4–)5–8(–9) mm long **6**
- 6 Subshrubs **7**
- Lianas, shrubs or scandent shrubs **8**
- 7 Subshrubs erect; leaflets coriaceous; inflorescence rachis 4–9.5 cm long; fruits 1–1.4 × 0.4–0.6 cm, completely velutinous externally *R. chrysomalla*
- Subshrubs prostrate; leaflets chartaceous; inflorescence rachis 1.3–2.2 cm long; fruits 0.8–1 × 0.3–0.4 cm, sparsely hirsute externally *R. prostrata*
- 8 Leaves 5–7-foliolate **9**
- Leaves 9–27-foliolate **10**
- 9 Petiole 1.3–2.2 cm long; basal pair of leaflets 1.4–2 cm long; inflorescences in cymes..... *R. diamantina*
- Petiole 2.7–7 cm long; basal pair of leaflets 2.3–7.7 cm long; inflorescences in thyrses or panicles *R. tenuis*
- 10 Leaflet apex rounded, rarely obtuse; pedicel ca. 2 mm long..... *R. martiana*
- Leaflet apex obtuse or narrowly rounded, rarely acute or rounded; pedicel 3–14 mm long..... **11**
- 11 Peduncle 2.8–8 cm long; flowers congested apically; central and north-eastern MG *R. cnestidifolia*
- Peduncle 0.2–1.7 cm long; flowers loosely disposed; central and southern BA, eastern ES and eastern and central RJ **12**

- 12 Branchlets subglabrous or sparsely pubescent; leaves 5–9(–13)-foliolate; rachis 3–6(–8.5) cm long; petals 2.5–3 mm wide; central BA... ***R. diamantina***
- Branchlets densely velutinous to glabrescent; leaves (9–)15–27-foliolate; rachis 9–24 cm long; petals 1.5–2 mm wide; southern BA, east coast ES and eastern RJ ***R. glazioui***

***Rourea bahiensis* Forero, Mem. New York Bot. Gard. 26(1): 103. 1976.**

Fig. 2

Type. BRAZIL. Bahia: Belmonte, mata costeira, 31 Jan 1967 (fr.), R. P. Belém & R. S. Pinheiro 3225 (**Holotype:** NY barcode NY 00010955!; **isotypes:** CEPEC!, MG!, NY!, UBI!).

Description. *Lianas* or scandent shrubs, 1–7 m tall; branchlets glabrous or sparsely puberulous, lenticels abundant, conspicuous or inconspicuous. **Leaves** (9–)11–17(–41)-foliolate, congested; petiole 0.6–2.2 cm long, villous to glabrescent, eglandular; rachis 3.5–6.5 cm long, villous to glabrescent, eglandular; **leaflets** subopposite to alternate, subsessile or pulvinulus ca. 1 mm long; blade of the basal pair of leaflets 0.6–1.1 × 0.5–0.8 cm, orbicular, others 1.1–2.2(–2.4) × 0.7–1 cm, narrowly elliptic, oblong or narrowly ovate, chartaceous or coriaceous, concolorous, rarely discolorous, sparsely villous to glabrescent on both surfaces, more densely on midvein, abaxially brownish or greenish, adaxially dull, base slightly asymmetric, cordate, subcordate or rounded, apex rounded, margin flat to revolute, glabrous or ciliate; midvein abaxially slightly prominent, adaxially flat, secondary veins 4–5 pairs, flat on both surfaces, tertiary veins flat on both surfaces. **Inflorescences** in axillary or ramiflorous cymes or determinate thyrses; bracts ca. 2 mm long; peduncle 1–10 mm long, sparsely pubescent to pubescent, eglandular; rachis 0.3–1.7 cm long, sparsely pubescent to pubescent, eglandular; lateral branches 0.8–2.5 cm long, glabrous or pubescent, eglandular. **Flowers** loosely disposed; buds 2–3 × 2 mm, ellipsoid or obovate; pedicel 7–12 mm long, eglandular, 1–2 bracteoles located up to the lower half, persistent; sepals 4–4.5 × 1.5 mm, chartaceous, ovate, outer surface glabrous, subglabrous or sparsely pubescent, eglandular, inner surface glabrous or subglabrous, margin ciliate, more densely at the apex; petals 5–6 × 1.5–2 mm, narrowly elliptic or narrowly obovate, glabrous on both surfaces; stamens connate at base by 0.8–1 mm, shorter series 2–4 mm long, longer series 2.5–6 mm long, glabrous; ovary 1–1.2 mm long, hirsute, style 2–2.5 mm long, sparsely hirsute, glabrous only at the apex, stigma peltate, bilobate. **Fruits** 1.1–1.3 × 0.4–0.6 cm, yellowish or reddish, outer surface sparsely puberulous, inner surface glabrous, apex obtuse, style partially persistent, calyx covering one third of the fruit; **seeds** ca. 0.8–1 × 0.3–0.5 cm, arillode orangish.

Distribution, habitat and phenology. This species has only been found in Bahia and Espírito Santo (Fig. 3). In BA, populations of *R. bahiensis* are distributed in the southern portion of the state, occurring mainly in coastal areas from the municipality of Una to Porto Seguro and Alcobça. In ES, specimens have been collected both in the interior of the state and coastal zones, ranging from northern to southern portions.

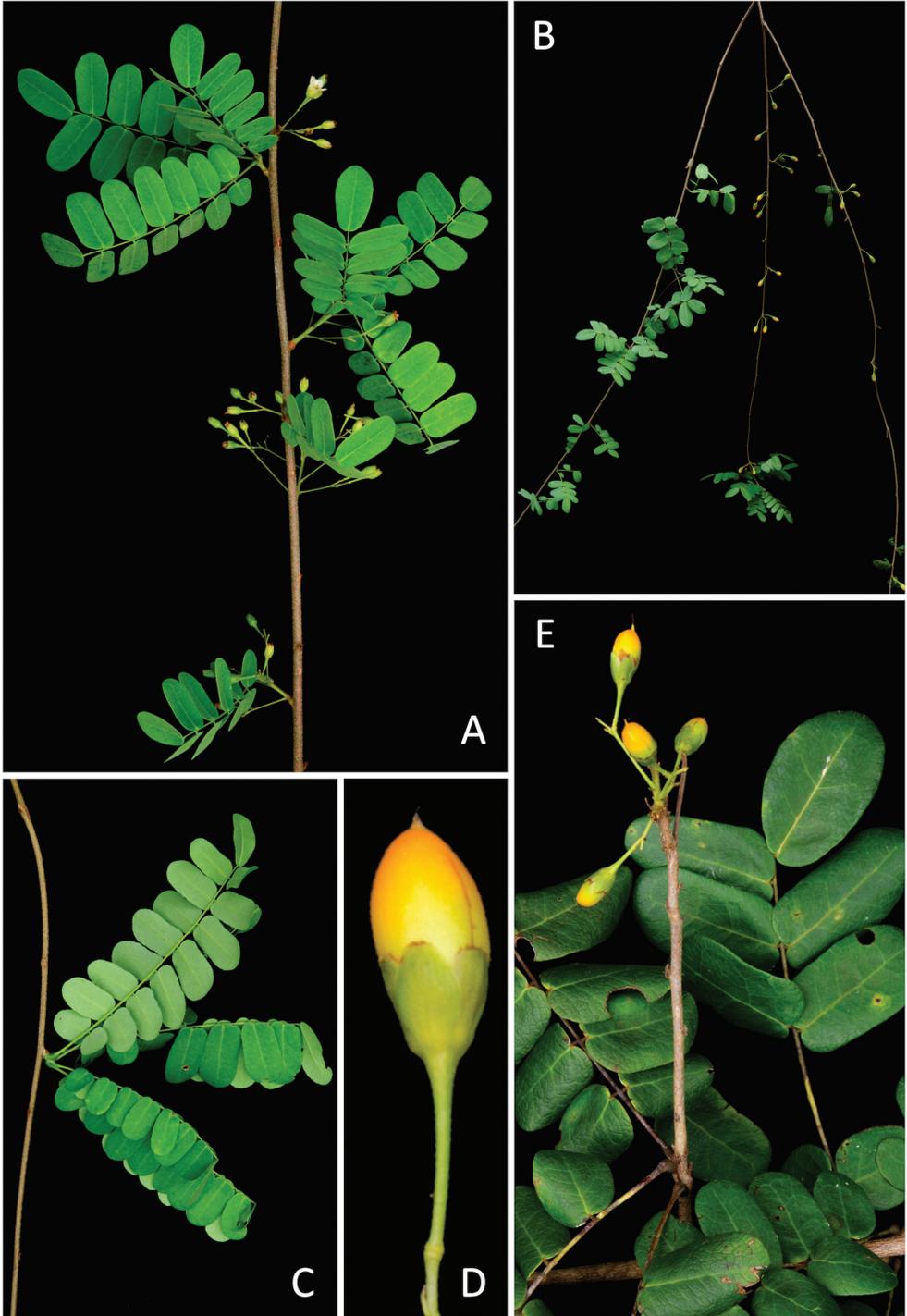


Figure 2. *Rourea bahiensis*: **A** flowering branchlet **B** habit **C** congested leaves **D** fruit **E** fruiting branchlet.

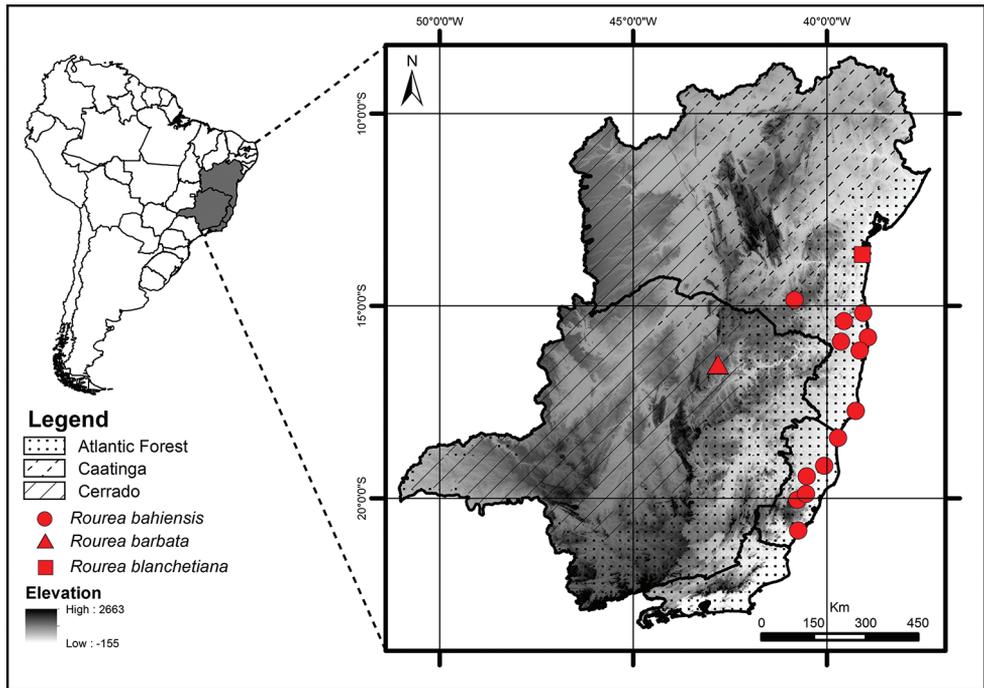


Figure 3. Geographic distribution of *Rourea bahiensis* (circles), *R. barbata* (triangles) and *R. blanchetiana* (squares).

Individuals of *Rourea bahiensis* are lianas or scandent shrubs up to 7 m tall. This species occurs in the Atlantic Rain Forest, growing on “Tabuleiro” or swamp forests, although sometimes it is also found in degraded areas. Specimens have been collected with flowers from October to November and with fruits from September to January.

Specimens examined. BRAZIL. Bahia: Porto Seguro, RPPN Veracruz (Veracel Celulose), rodovia que atravessa a reserva, antiga entrada para Santa Cruz Cabrália, ca. 2 km do centro de visitantes, 16°09'27"S, 39°09'15"W, 02 Nov 2001 (fl.), *J. G. Jardim & R. V. Lopes* 3952 (CEPEC, HUEFS, NY); Itapebi, estrada para o distrito de Caubi, ca. 7 km da BR 101, Fazenda Palmeiras, ca. 10.5 km na entrada, 15°55'36"S, 39°38'09"W, 04 Nov 2001 (fl.), *J. G. Jardim & R. V. Lopes* 3954 (HUEFS, NY); Una, Reserva Biológica de Una (REBIO de Una), entrada ca. 45 km S de Ilhéus, margem da estrada que leva à sede da reserva, 15°10'46"S, 39°03'50"W, 13 Jan 2001 (fr.), *F. Juchum & E. Forero* 116 (CEPEC, NY, RB); Vitória da Conquista, Reserva do Poço Escuro, 26 Nov 2011 (fl.), *L. C. Marinho et al.* 218 (HUEFS); Camacan, trilha da Bapeba, 15°23'30"S, 39°33'35"W, 02 Apr 2009 (fr.), *R. de O. Perdiz et al.* 357 (CEPEC); Caravelas, rodovia BR 418, a 27 km SW de Alcobaça, 16 Sep 1978 (fr.), *T. S. dos Santos et al.* 3361 (CEPEC). **Espírito Santo:** Marilândia, Liberdade (Água Viva, Pedra do Cruzeiro), prop.: Aguilar A. Lovucini, 18 Jan 2006 (fl., fr.), *V. Demuner et al.* 1626 (MBML, UB); Conceição da Barra, próximo à Itaúnas, 18°25'41"S, 39°42'56"W, alt. 10 m, 30 Oct 2014 (fr.), *J. E. Q. Faria & T. N. C. Vasconcelos* 4231 (UB); Linhares,

Reserva Natural da Companhia Vale do Rio Doce, Aceiro Aracruz, primeira elevação após o entroncamento das 3 reservas, CVRD, Sooretama e Aracruz-Fazenda Calliman, 31 Oct 2007 (st.), *F. L. R. Filardi* 776 (RB); Reserva Natural Vale, estrada Farinha Seca, RFL-001/80, Bloco E, Trat 1, 30 Oct 2010 (fl.), *D. A. Folli* 5407 (CVRD, ESA); Estrada Gávea, 30 Oct 2003 (fl.), *D. A. Folli* 4659 (CVRD, ESA); Piuma, Apr 1993 (fr.), *Helder José s. n.* (SPF 77169); Santa Maria de Jetiba, Rio nove, Sítio de L. Kollmann, 26 Jan 2004 (fl.), *L. Kollmann* 6361 (BHCB, MBML, UB); Santa Teresa, Reserva Biológica Augusto Ruschi, 05 Dec 2002 (fl.), *L. Kollmann & E. Bausen* 5823 (MBML); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi. Altitude 800 m, 28 Nov 2001 (fl.), *L. Kollmann et al.* 5072 (MBML); Itaúnas, área da Fíbria com plantação de eucalipto, 18°29'27"S, 39°44'12"W, 21 Oct 2018 (fl., fr.), *C. A. P. Toledo & N. C. Bigio* 399 (ESA); Estrada para Lombardia, 25 Apr 2002 (fr.), *R. R. Vervloet & E. Bausen* 194 (MBML, UB); Trilha antiga, sede lado direito, 26 Mar 2003 (fr.), *R. R. Vervloet & E. Bausen* 2053 (MBML, UB).

Recognition and notes. *Rourea bahiensis* is morphologically similar to *R. prostrata* due to their narrowly elliptic or oblong leaflets usually measuring $0.9\text{--}2.2 \times 0.5\text{--}1$ cm. However, they are differentiated because *R. bahiensis* is a lianescent species without glandular trichomes, while *R. prostrata* is a prostrate subshrub with glandular trichomes. *Rourea bahiensis* can also be mistaken for *R. discolor*, from which it mainly differs by the smaller leaflets ($1.1\text{--}2.2\text{--}(2.4) \times 0.7\text{--}1$ cm) and inflorescence rachis $0.3\text{--}1.7\text{--}(3.7)$ cm long vs. larger leaflets ($(1.3\text{--})2.2\text{--}4.5\text{--}(5.8) \times (0.8\text{--})1.2 \times 1.7\text{--}(2.3)$ cm) and inflorescence rachis $3.5\text{--}11.8$ cm long in *R. discolor*. Additionally, the petiole and leaf rachis are subglabrous to villous and the fruits are smaller ($1.1\text{--}1.3 \times 0.4\text{--}0.5$ cm) in *R. bahiensis*, while, in *R. discolor*, the petiole and leaf rachis are glabrous and the fruits are larger ($1.2\text{--}1.7 \times 0.4\text{--}0.6$ cm).

This species varies considerably in the characteristics of leaflet size, indumentum and texture. Some specimens, for example, have larger and chartaceous leaflets, which are usually sparsely villous abaxially; the opposite of this combination is composed of specimens with smaller, coriaceous and glabrous leaflets. This seems a common variation in the species probably related to branch and leaf development as few materials were found with the two conditions mentioned above (e.g. *J. G. Jardim et al.* 3952). Additionally, deciduousness of trichomes may explain why some leaf blades are glabrous and others, sparsely villous.

***Rourea barbata* C. Toledo, Phytotaxa 408(2): 118. 2019.**

Illustration: Forero (2003, as *R. discolor*) and Toledo and Souza (2019)

Type. BRAZIL. Minas Gerais: Grão Mogol, cerrado na estrada para o rio Ventania, ca. $16^{\circ}32'S\text{--}42^{\circ}49'W$, ca. 900 m alt., 5 Nov 1990 (fl.), *J. R. Pirani* CFCR13358 (**Holotype:** SPF barcode SPF 69503!; **isotypes:** ESA!, NY!).

Description. *Shrubs*, ca. 1.5 m tall; branchlets glabrous or subglabrous, lenticels absent. **Leaves** 7–11-foliolate, congested; petiole 0.8–1.7 cm long, glabrous or

subglabrous, eglandular; rachis 3.5–4.4 cm long, glabrous or subglabrous, eglandular; **leaflets** opposite to subopposite, sessile; blade of the basal pair of leaflets 1–1.6 × 0.6–0.9 cm, ovate, others 1.3–3.2 × 0.8–1.4 cm, narrowly ovate or narrowly elliptic, chartaceous, discolorous, glabrous on both surfaces, abaxially vinaceous, adaxially greyish, slightly shining, base symmetric or slightly asymmetric, subcordate, apex obtuse, rounded or narrowly rounded, margin slightly revolute, glabrous; midvein abaxially prominent, adaxially slightly impressed, secondary veins 5–7 pairs, slightly prominent on both surfaces, tertiary veins slightly prominent on both surfaces. **Inflorescences** in axillary or pseudoterminal cymes; bracts 2–3 mm long; peduncle 0.2–3.5 cm long, glabrous or subglabrous, eglandular; rachis 0.7–1.8 cm long, glabrous or subglabrous, eglandular. **Flowers** loosely disposed or congested apically; buds 4–3 × 3 mm, orbicular; pedicel 6–12 mm long, eglandular, 2 bracteoles located up to the lower half, persistent; sepals 4–4.5 × 2 mm, chartaceous, ovate or narrowly ovate, outer surface subglabrous, eglandular, inner surface glabrous or subglabrous, margin ciliate, more densely at the apex; petals 5.5–6 × 2 mm, oblong or narrowly obovate, glabrous on both surfaces; stamens connate at base by ca. 1 mm, shorter series ca. 3.5 mm long, longer series 5–5.5 mm long, glabrous; ovary 1–1.2 mm long, densely hirsute only on one side, glabrous or almost so elsewhere, style ca. 2 mm long, sparsely hirsute at base, glabrescent towards the apex, stigma peltate, bilobate. **Fruits** unknown.

Distribution, habitat and phenology. This species is only known from the type location (Fig. 3). It has a shrubby habit and grows in areas of cerrado, at ca. 900 m altitude. The only flowering specimen was collected in November.

Recognition and notes. *Rourea barbata* is mainly recognised by the glabrous leaflets and the ovary, which is hairy only on one side of the structure. It is similar to *R. martiana* due to the number, size and shape of leaflets, but these are glabrous in *R. barbata* and hirsute or villous in the latter.

Forero (2003) identified the type of *R. barbata* as *R. discolor*; however, the former differs by the leaves 7–11-foliolate, inflorescence rachis 0.7–1.8 cm long and the ovary with a tuft of trichomes, while the latter has leaves 9–29-foliolate, inflorescence rachis 3.5–11.5 long and ovary completely hirsute.

***Rourea blanchetiana* (Progel) Kuhlm., Arq. Inst. Biol. Veg. 1: 40. 1934.**

Illustration: Progel (1877) and Schellenberg (1938)

Eichleria blanchetiana Progel, in Martius, Fl. Bras. 12(2): 518. 1877.

Type. BRAZIL. Bahia: S. d. (fl., fr.), *J. S. Blanchet 1050* (**Lectotype:** BR barcode BR 00000528168!, designated here; **isolectotypes:** G!, S!, W!).

Description. Lianas: branchlets sparsely hirsute to hirsute, lenticels abundant, inconspicuous. **Leaves** 27–39-foliolate, loosely disposed; petiole 1.4–2.2 cm long, sparsely hirsute to hirsute, with glandular trichomes; rachis (8–)10–14.5 cm long, sparsely hirsute to hirsute, with glandular trichomes; **leaflets** subopposite to alternate, pulvinulus ca. 1

mm long; blade of the basal pair of leaflets 0.9–1.5 × 0.6–0.9 cm, orbicular or oblong, others 1.3–2.9 × 0.6–1 cm, oblong, the apical ones elliptic, membranaceous to subchartaceous, discolorous, abaxially glabrous, subglabrous or sparsely hirsute on the midvein, glaucous, adaxially glabrous, dull, base symmetric or slightly asymmetric, rounded or subcordate, obtuse in the apical leaflet, apex rounded, rarely truncate, obtuse in the apical leaflet, margin flat, glabrous; midvein abaxially slightly prominent, rarely prominent, adaxially slightly impressed, rarely impressed, secondary veins 5–7 pairs, abaxially slightly prominent or flat, adaxially flat, tertiary veins flat on both surfaces. **Inflorescences** in axillary cymes; bracts ca. 1 mm long; peduncle (2–)3.5–6.7 cm long, densely hirsute, with glandular trichomes; rachis 0.5–2.2 cm long, densely hirsute, with glandular trichomes. **Flowers** congested apically; buds 3–6 × 2–3 mm, elliptic; pedicel 8–13 mm long, with glandular trichomes, 1–2 bracteoles located in the middle portion, deciduous; sepals 4–6 × 1–1.5 mm, chartaceous, lanceolate, outer surface hirsute, with glandular trichomes, inner surface subglabrous, margin ciliate; petals 9–14 × 2 mm, oblong or narrowly obovate, glabrous on both surfaces; stamens connate at base by ca. 1 mm, shorter series ca. 1 mm long, longer series ca. 2 mm long, with sparse glandular trichomes; ovary ca. 1.2 mm long, hirsute, style ca. 2.5 mm long, sparsely hirsute, subglabrous or glabrous only at the apex, stigma peltate, bilobate. **Fruits** 1.2 × 0.6–0.7 cm, colour not seen, outer surface sparsely hirsute, inner surface not seen, apex acuminate, style deciduous, calyx covering one third of the fruit; **seeds** ca. 1 × 0.4 cm, arillode colour not seen.

Distribution, habitat and phenology. Most of the known specimens of *R. blanchetiana* are old collections with no precise locations. The most recently analysed specimen was collected in the municipality of Nilo Peçanha, which is located in southern Bahia (Fig. 3). Therefore, it seems that *R. blanchetiana* is a rare species and most likely restricted to the south portion of Bahia. This is a lianescent species growing on ombrophilous forests of the Atlantic domain. The specimen *J. S. Blanchet* s. n. (NY barcode NY00393553) was collected with flowers and fruits in August.

Specimens examined. BRAZIL. Bahia: Locality unknown: Aug 1835 (fl., fr.), *J. S. Blanchet* s. n. (NY barcode NY00393553); s. d. (fl.), *J. S. Blanchet* s. n. (?) (P barcode P05487855). Nilo Peçanha, estrada a ca. 4 km da comunidade Quilombola de Jatimane na estrada para Ituberá, fazenda Outeiro do Chapeú, 13°40'06"S, 39°04'50"W, 14 Apr 2012 (st.), *L. P. de Queiroz & F. H. F. Nascimento 15452* (HUEFS); Locality unknown, s. d. (fl.), *J. S. Blanchet 297* (P barcode P05487854); s. d. (fl.), *P. Salzmann* s. n. (MO 1704495, P barcode P05487856).

Recognition and notes. *Rourea blanchetiana* is easily recognised by the leaves with 27–39 leaflets, which are usually membranaceous, oblong and abaxially glaucous, aside from the flowers congested in the inflorescences, comparatively larger peduncle and petals 9–14 mm long. It is similar to *R. discolor* due to the leaflets abaxially glaucous and pedicel relatively long, but differs by the hirsute inflorescence rachis, elliptic flower buds and petals 9–14 mm long vs. glabrous or subglabrous inflorescence rachis, orbicular or ovate flower buds and petals (4–)6–8 mm long.

In the protologue of the basionym of *Rourea blanchetiana* from *Flora Brasiliensis*, the only specimen cited by Progel (1877) was Blanchet 1050, without indication of

herbarium. Schellenberg (1938) inadvertently selected the lectotype from P. However, of the six specimens of *R. blanchetiana*, collected by Blanchet in P, none is annotated with number 1050. Specimens of Blanchet 1050 were found in BR, G, S and W and only the collection from G is fruiting, the rest, only flowering. Of these, the specimen from BR has an original label of “Herbarium Martii”, identified as “*Eichleria blanchetiana* Prog. in Mart. fl. Br.” and bears an attached pencil drawing containing floral details of the referred species. The characteristics of the branchlet of this specimen (number and shape of leaflets, inflorescence architecture and flower structures) and the detailed drawing match accurately with the illustration in Progel (1877, plate 116). In addition, considering that Progel worked in M and the original *Flora Brasiliensis* collection from M was sold to BR, then the specimen Blanchet 1050, deposited in the latter, seems the best candidate to be lectotype of *R. blanchetiana*, which is here proposed.

Rourea blanchetiana was originally described in Oxalidaceae (Progel 1877). The author published the basionym under his new genus *Eichleria*, based on the similarity between Connaraceae and Oxalidaceae with respect to the imparipinnate leaves and heterostylous flowers with apocarpous gynoecium. Kuhlmann (1934) firstly noticed this confusion and proposed the prompt combination after concluding that the species bear two ovules with marginal placentation, characteristic of Connaraceae. The close relationship between Connaraceae and Oxalidaceae has been confirmed by modern phylogenetic analyses and they form a monophyletic group within Oxalidales (APG IV 2016); Connaraceae differs morphologically from Oxalidaceae by the completely free carpels and follicular fruits.

***Rourea chrysomalla* Glaz. ex G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 196. 1938.**

Fig. 4

Type. BRAZIL. Goiás: Chemin du Rio Paranauá á Chico Lobo, dans les campos, 08 Nov 1894 (fr.), *A. F. M. Glaziou 20871* (**Lectotype:** P barcode P02274085!, designated here; **isolectotypes:** F!-frag., G, K!, MPU!, P!, R!, RB!, S!).

Description. *Subshrubs* erect, 0.35–0.65(–0.8) m tall; branchlets densely velutinous, lenticels absent. **Leaves** 9–17-foliolate, loosely disposed; petiole 0.5–2 cm long, velutinous, with glandular trichomes; rachis 4.5–10 cm long, velutinous, with glandular trichomes; **leaflets** opposite to subopposite, sessile; blade of the basal pair of leaflets (0.9–)1.2–1.8 × (0.4–)0.8–1.6 cm, orbicular or ovate, others 1.6–3.7 × 0.9–1.6 cm, ovate, narrowly elliptic or narrowly ovate, the apical ones usually elliptic, coriaceous, discolourous, abaxially hirsute to densely hirsute, brownish or greenish, adaxially sparsely hirsute to hirsute, dull, base symmetric or slightly asymmetric, cordate, subcordate or rounded, apex obtuse or rounded, margin flat or slightly revolute, ciliate; midvein abaxially prominent, adaxially flat, secondary veins 4–6 pairs, abaxially prominent or slightly prominent, adaxially flat or slightly prominent, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent. **Inflorescences** in axillary or terminal determinate thyrses or panicles; bracts

ca. 3 mm long; peduncle 0.7–3 cm long, densely hirsute, with glandular trichomes; rachis 4–9.5 cm long, densely hirsute, with glandular trichomes; lateral branches 0.7–2(–3) cm long, densely hirsute, with glandular trichomes. **Flowers** loosely disposed; buds 4–7 × 3–4 mm, elliptic or broadly elliptic; pedicel 1–4 mm long, with glandular trichomes, 2 bracteoles located up to the lower half, deciduous or persistent; sepals (5–)6–8 × 1.5–2.5 mm, coriaceous, ovate or narrowly elliptic, outer surface densely velutinous or densely hirsute, with glandular trichomes, inner surface subglabrous, margin ciliate; petals 7–9 × 2–3 mm, narrowly elliptic or narrowly obovate, with sparse glandular trichomes on both surfaces; stamens connate at base by ca. 0.8 mm, shorter series 3–5 mm long, longer series 4–6 mm long, with sparse glandular trichomes; ovary 1–1.3 mm long, densely hirsute, style 2–4 mm long, hirsute, stigma peltate, bilobate. **Fruits** 1–1.4 × 0.4–0.6 cm, reddish or orangish, outer surface completely velutinous, inner surface subglabrous, apex acuminate, style partially persistent, calyx covering one third or rarely half of the fruit; **seeds** 0.7–1 × 0.4 cm, arillode yellowish.

Distribution, habitat and phenology. *Rourea chrysomalla* is apparently restricted to Distrito Federal (DF), in the midwest region of Brazil (Fig. 5). The type specimen label indicates that the material was collected in Goiás state, but it is more likely to have been collected in DF (within the current boundaries of Goiás), which is supported by evidence from several sources. Firstly, the herbarium sheet label of Glaziou's specimen is from "Chemin du Rio Paranauá, a Chico Lobo"; although the name of this river has been taken as "Paraná", the penultimate letter more closely resembles a "U", than an "N". Secondly, Paranauá stands for Paranoá, a river course from DF, subject of study by Glaziou between 1894 and 1895. This can be confirmed by reports and letters from Glaziou to Missão Cruls (Cruls' mission), a large scientific expedition in the Brazilian Central Plateau, promoted to investigate the viability of transferring the capital of Brazil to the Midwest (available at: <http://doc.brazilia.jor.br/HistDocs/Relatorios/1896-missao-Cruls-Glaziou-lago-Paranoa.shtml>). Glaziou sent detailed reports on aspects of vegetation, soil quality and climate around the Paranoá River and clearly demonstrated his advice to dam its riverbed to set up an artificial lake, which was undertaken only in 1959. This lake is called Lago Paranoá and it was probably built following Glaziou's reports, suggesting that the botanist indeed collected in areas that are today part of DF. It is also of note that Glaziou's reports are contemporaneous with his collection of *R. chrysomalla*. Lastly, according to the description of his itinerary (Glaziou 1906), the author collected in Goiás from 1894 to 1895 and visited sites around and within what is now DF, indicating that his collections from Goiás also included specimens from DF. This evidence, in addition to the fact that *R. chrysomalla* is only found in DF, suggests that the type was collected in the present DF. Unfortunately, no information on "Chico Lobo" location was found.

In DF, individuals of *R. chrysomalla* can be found in the districts of Brasília, Gama, Riacho Fundo, Sobradinho and Taguatinga. This species is a subshrub up to 65(–80) cm tall, occurring in the central Brazilian Cerrado, more specifically in areas of cerrado *s. s.* or "campo sujo". *Rourea chrysomalla* is apparently the only species of the genus in which the roots develop a xylopodium. Specimens have been collected with flowers from August to October and in April and with fruits from September to October.

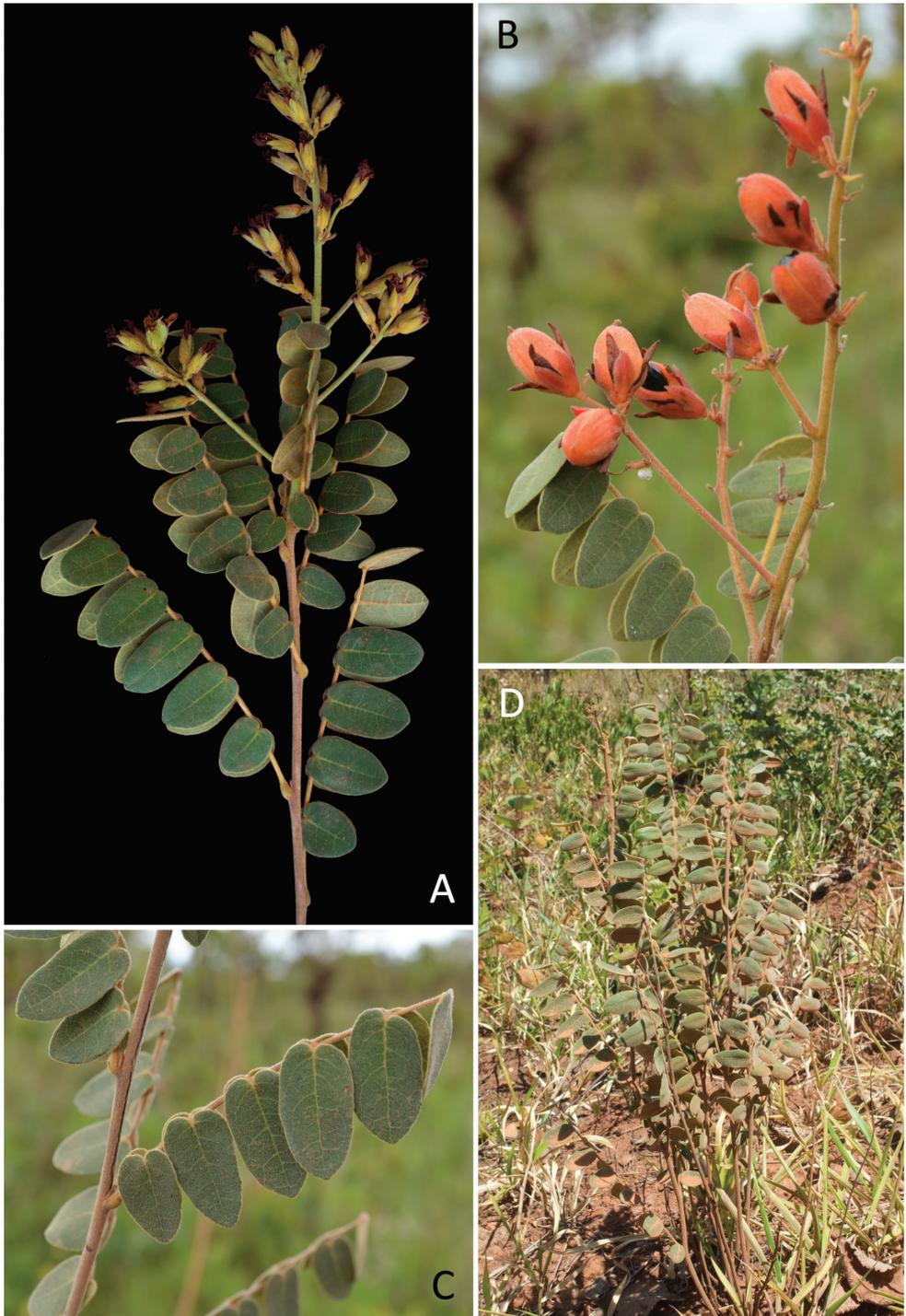


Figure 4. *Rourea chrysomalla*: **A** flowering branchlet **B** fruiting branchlet (photo by Jair Faria) **C** leaves (photo by Jair Faria) **D** habit.

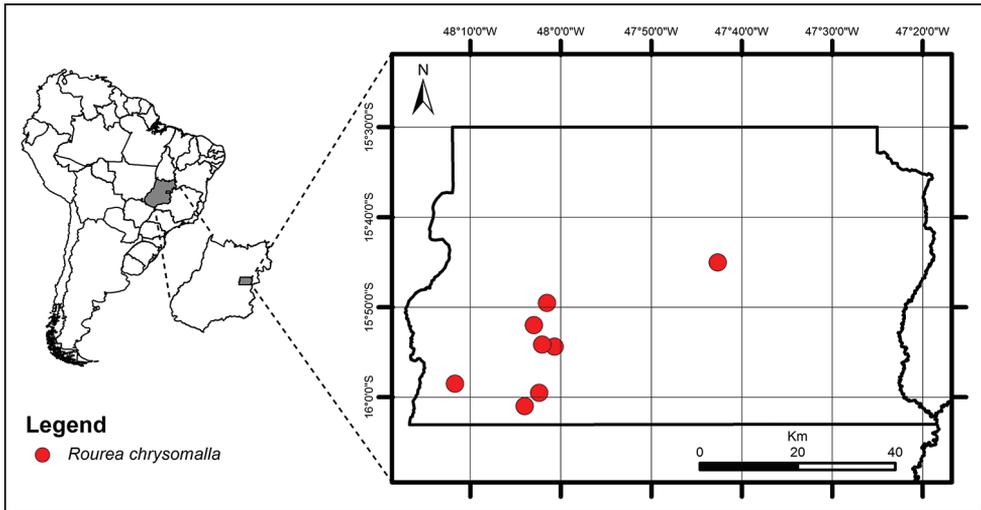


Figure 5. Geographic distribution of *Rourea chrysomalla*.

Specimens examined. BRAZIL. Distrito Federal: Sobradinho, 10 Apr 1974 (fl.), *E. P. Heringer* 13232 (UB); Taguatinga, Brasília, 15 Aug 1964 (fl.), *E. P. Heringer* 9750 (UB, US); Brasília, ca. 15 km E. of Brasília, 30 Oct 1964 (fl.), *H. S. Irwin & T. D. Soderstrom* 5724 (NY); Disturbed areas in cerrado, ca. 32 km S.W. of Brasília on road to Anápolis, 04 Sep 1964 (fl.), *H. S. Irwin & T. D. Soderstrom* 6001 (NY, P, UB, US); Riacho Fundo, 15 Oct 1999 (fl.), *L. C. Milhomens et al.* 03 (UB); Riacho Fundo, (fl.), *L. C. Milhomens et al.* 04 (UB); A ca. de 25 km sudoeste de Brasília, caminho para Anápolis, 15 Oct 1999 (fl.), *L. C. Milhomens & W. R. Anderson* 05 (HUEG, UB); Coletada em campo sujo de Cerrado, c/ intensa ação antrópica, 15 Oct 1999 (fl.), *L. C. Milhomens* 06 (EAC, HUEG, HUFU, HUTO, UB); Riacho Fundo, (st.), *L. C. Milhomens et al.* 07 (UB); Coletada em campo sujo de Cerrado, c/ intensa ação antrópica, 15 Oct 1999 (fl.), *L. C. Milhomens* 08 (HUTO, UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 09 (UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 10 (UB); CINDACTA, -16.01666705, -48.066667, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 11 (UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 12 (UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 13 (UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 14 (UB); CINDACTA, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 15 (UB); Gama, área pertencente ao CINDACTA, pouco depois do balão de entrada do Gama, 16°01'S, 48°04'W, 05 Oct 1999 (fr.), *L. C. Milhomens et al.* 16 (EAC, UB); Fazenda Sucupira, áreas nativas a Oeste da sede do Laboratório-BBGA, 15°52'S, 48°00'W, 08 Nov 1996 (fr.), *R. V. Nunes et al.* 59 (CEN); Riacho Fundo, 25 Sep 1998 (st.), *C. E. B. Proença* 2063 (UB); Riacho Fundo, (st.), *C. E. B. Proença* 2064 (UB); Riacho Fundo, (st.), *C. E. B. Proença* 2065 (UB); Riacho Fundo, (fr.), *C. E. B. Proença* 2066 (UB); Riacho Fundo, (fr.), *C. E. B. Proença* 2067 (UB); Samambaia, Parque Boca da Mata do lado esquerdo da polícia, 15°52'S, 48°03'W, 07 Aug 1995 (fl.), *J. M. de Rezende* 49 (CEN);

Cerrado sensu stricto, estrada de terra na saída da cidade, 15°59'31"S, 48°02'24"W, 10 Oct 2017 (fl.), C. A. P. Toledo & J. R. L. da Paz 347 (ESA).

Recognition and notes. *Rourea chrysomalla* is easily distinguished by the combination of the following characters: branchlets velutinous, leaflets sessile, coriaceous, abaxially densely hirsute, sepals coriaceous, petals with glandular trichomes and fruits with outer surface completely velutinous. This species can be confused with *R. prostrata* due to their sub-shrubby habit; however, *R. chrysomalla* is an erect subshrub (vs. prostrate subshrub), has coriaceous leaflets (vs. chartaceous), inflorescences usually terminal (vs. axillary) and fruits measuring 1–1.4 × 0.4–0.6 cm, completely velutinous externally (vs. fruits 0.8–1 × 0.3–0.4 cm, sparsely hirsute especially at apex). *Rourea chrysomalla* is also similar to *R. glazioui*, but differs by the subshrubby habit, coriaceous leaflets and petals and stamens with glandular trichomes vs. lianescent habit, chartaceous leaflets and petals and stamens eglandular.

Rourea chrysomalla was described by Glaziou (1906, written as “*chrysomala*”), but his work is listed in the Suppressed works (Appendix I) of the *Code* (Turland et al. 2018), so the name is considered not validly published. Schellenberg (1938) validly published *Rourea chrysomalla* and gave credits to Glaziou, so the authorship of the name has been attributed to Glaziou ex Schellenberg. The type (*Glaziou 20871*) indicated by Schellenberg (1938) is from P and, in this herbarium, there are two sheets belonging to this collection. Although each sheet bears the same label from P, only one (barcode P02274085) has an original label with Glaziou’s handwriting indicating location and date, so the two specimens are considered duplicates (Turland et al. 2018, Art. 8.3); then a lectotype is here proposed.

***Rourea cnestidifolia* G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 198. 1938.**

Fig. 1D

Type. BRAZIL. Minas Gerais: S. d., *F. Sellow* s. n. (**Holotype:** B†). BRAZIL. Minas Gerais: Lagoa Santa, s. d. (fl.), *J. E. B. Warming 1849* (**Lectotype:** K barcode K 000633716!, designated by Forero 1976).

Description. *Shrubs* or scandent shrubs, 1–2.5 m tall; branchlets hirsute to glabrescent, lenticels abundant, inconspicuous. *Leaves* 9–13-foliolate, loosely disposed; petiole 1.9–2.8 cm long, sparsely hirsute to hirsute or sparsely villous, with glandular trichomes; rachis 4–11 cm long, sparsely hirsute to hirsute or sparsely villous, with glandular trichomes; *leaflets* opposite to alternate, pulvinulus ca. 1 mm long; blade of the basal pair of leaflets 2.3–4.7 × 1.3–2 cm, ovate, elliptic or oblong, others 4–7.2 × 1.6–3.2 cm, narrowly ovate, oblong or narrowly elliptic, the apical ones always elliptic or narrowly elliptic, chartaceous, slightly discolourous, abaxially hirsute or villous, occasionally subglabrous, more densely in the midvein, brownish or greenish, adaxially glabrous or subglabrous, usually sparsely villous on midvein, slightly shining or dull, base slightly asymmetric to asymmetric, usually symmetric in the apical leaflet, rounded, cordate or subcordate, occasionally acute in the apical leaflet, apex obtuse, acute or narrowly rounded, margin flat, rarely slightly revolute, ciliate or sparsely ciliate; midvein abaxially prominent

or slightly prominent, adaxially impressed or slightly impressed, secondary veins 6–7 pairs, abaxially slightly prominent, adaxially flat, tertiary veins abaxially slightly prominent or flat, adaxially flat or slightly prominent. **Inflorescences** in axillary cymes, rarely pseudoterminal; bracts 2–3 mm long; peduncle 2.8–8 cm long, hirsute, with glandular trichomes; rachis 0.8–1.9 cm long, hirsute, with glandular trichomes. **Flowers** congested apically; buds 2.5–4 × 2–3 mm, orbicular or broadly elliptic; pedicel 3–5 mm long, with glandular trichomes, 2 bracteoles located up to the lower third, deciduous; sepals 4–5 × 2–2.5 mm, chartaceous, ovate, outer surface hirsute, with glandular trichomes, inner surface subglabrous or sparsely sericeous, margin ciliate; petals 7–8 × 2–3 mm, narrowly obovate or narrowly elliptic, glabrous on both surfaces; stamens connate at base by ca. 1.5 mm, shorter series ca. 1.5 mm long, longer series ca. 2.5 mm long, glabrous; ovary 1–1.3 mm long, densely hirsute, style 2–4 mm long, hirsute, stigma peltate, bilobate. **Fruits** 1.3–1.4 × 0.4–0.5 cm, orangish, outer surface subglabrous, sparsely hirsute at the apex, inner surface glabrous or subglabrous, apex acuminate, style partially persistent, calyx covering one third of the fruit; **seeds** 0.9–1 × 0.4 cm, arillode colour not seen.

Distribution, habitat and phenology. There are only few records of this species, which seems to be restricted to central and northeastern Minas Gerais (Fig. 6). This shrubby species occurs in the Atlantic Forest or at the transition with the Cerrado, where it is distributed in areas of “Cerradão” and seasonal forests; it grows in rocky or limestone outcrops, at approximately 600–1,000 m altitude. Specimens have been collected with flowers from August to November and with fruits from October to December.

Specimens examined. BRAZIL. Minas Gerais: Rio Doce, localidade Figueira, 11 Sep 1930 (fl.), *J. G. Kuhlmann 348* (IAN, RB); Matozinhos: fazenda Cauaia, 31 Oct 1996 (fr.), *J. A. Lonbardi 1453* (BHCB); Fazenda Castelo da Jagoara, 19°28'12.0"S, 43°58'59.1"W, 683 m alt., 21 Oct 2006 (fr.), *J. C. F. Melo et al. 514* (BHCB, SPF). Vespasiano, região metropolitana de Belo Horizonte, afloramento calcário, adjacente à Lavra da Cia de Cimento Portland Itáu, Dec 1990 (fr.), *M. A. L. Rollo 37* (SPF); Serra do Cipó, Aug 1895 (fl.), *Senna s. n. (Herb. Schwacke 11747)* (NY, P, RB); Lagoa Santa, s. d. (fl.), *E. Warming s. n.* (P).

Recognition and notes. *Rourea cnestidifolia* is recognised by the presence of glandular trichomes, relatively large middle and apical leaflets (4–7.2 × 1.6–3.2 cm), obtuse, acute or narrowly-rounded leaflet apex, a long peduncle (2.8–8 cm long) and a short pedicel (3–5 mm long).

The morphological limits separating *Rourea cnestidifolia* and *R. glazioui* present slight discontinuities, but these, along with distribution patterns, are sufficient to distinguish them. They are similar in the presence of glandular trichomes on petiole, leaf rachis and inflorescences, leaflet size and shape and in overall characteristics of flowers and fruits. Schellenberg (1938) separated them based on pedicel length, while Forero (1976, 1983) used number of leaflets. These are useful distinctions despite some overlapping characters, so this revision considers that *R. cnestidifolia* differs from *R. glazioui* by the leaves 9–13-foliolate (Fig. 1D), peduncle 2.8–8 cm long, flowers congested in the inflorescence apex and pedicel 3–5 mm long vs. leaves 13–27-foliolate (Fig. 10), peduncle 0.2–1.7 cm long, flowers loosely disposed in the inflorescences and pedicel 5–10(–14) mm long. Additionally, the indumentum of branchlets and leaflets (lower

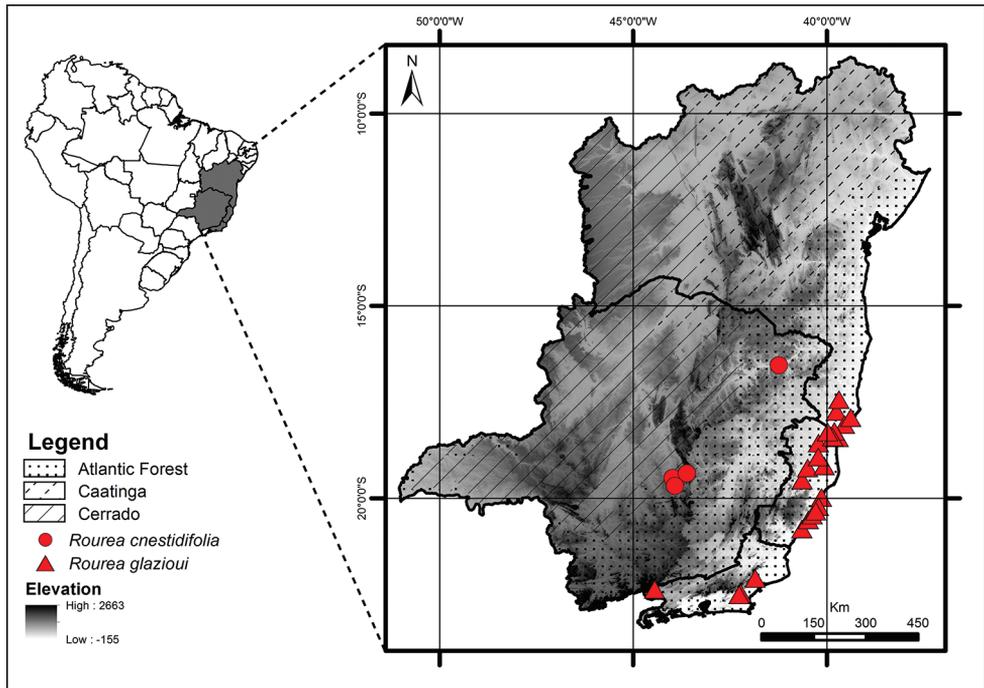


Figure 6. Geographic distribution of *Rourea cnestidifolia* (circles) and *R. glazioui* (triangles).

surface) is denser in *R. glazioui* than it is in *R. cnestidifolia*. Geographic distribution may also be useful for recognition: *R. cnestidifolia* is apparently restricted to central and northeast portions of Minas Gerais, while *R. glazioui* is very common in the coastal zone between southern Bahia and central Rio de Janeiro (Fig. 6).

Forero (1976) selected the lectotype of *R. cnestidifolia*, as the type from B is considered missing. The specimen indicated by Forero (1976) from K has no collection date, although the author cited “18 Nov 1864”, probably because he considered it the same collection of specimen Warming 1849/3 from C (barcode C 10009584) and Warming 1849/1 from GH (barcode GH 00043365). However, there are, in C, many specimens Warming 1849, in which collection number is subdivided from 1 to 5 and present different collection dates. All specimens of Warming 1849 from C, GH and K seem to correspond to the same gathering, but as they do not match in collection dates and subdivision of main collection number, the lectotype from K is here considered a unicate.

***Rourea diamantina* C. Toledo, sp. nov.**

urn:lsid:ipni.org:names:77213227-1

Fig. 7

Type. BRAZIL. Bahia: Itatim, interior da mata da base do Inselberg, 12°45'12"S, 39°46'59"W, 26 Jan 1997 (fl.), *E. Melo et al.* 1985 (**Holotype:** ESA 84255!; **isotypes:** HUEFS!, UEC!, VIC!).

Diagnosis. Akin to *R. martiana* due to the presence of glandular trichomes, relatively small leaves and leaflets and flowers and fruits with similar characteristics, but differs by the leaves 5–9(–13)-foliolate (vs. 9–15-foliolate), leaflet apices narrowly rounded or obtuse (vs. rounded) and pedicels 5–13 mm long (vs. ca. 2 mm long).

Description. *Lianas*, shrubs or scandent shrubs, rarely treelets, 3–4 m tall; branchlets subglabrous or sparsely pubescent, lenticels abundant, conspicuous. *Leaves* 5–9(–13)-foliolate, congested; petiole 1.3–2.2 cm long, sparsely hirsute to glabrescent, eglandular; rachis 3–6(–8.5) cm long, sparsely hirsute to glabrescent, eglandular; *leaflets* opposite to subopposite, pulvinulus ca. 1 mm long; blade of the basal pair of leaflets 1.4–2 × 0.9–1.4 cm, ovate, others 2–4.5(–5.8) × (0.8–)1.2–1.7(–2.2) cm, narrowly ovate, rarely oblong, chartaceous, occasionally membranaceous, slightly discoloured, abaxially hirsute or villous, brownish or greenish, adaxially subglabrous, dull, base slightly asymmetric, rounded or subcordate, rarely obtuse, apex narrowly rounded or obtuse, margin flat or slightly revolute, ciliate; midvein abaxially prominent, adaxially flat or slightly impressed, secondary veins 5–7 pairs, abaxially slightly prominent, adaxially flat, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent. *Inflorescences* in pseudoterminal cymes, rarely ramiflorous; bracts 1.5–2.5 mm long; peduncle 0.8–1.7 cm long, sparsely hirsute, eglandular; rachis 1–2.5 cm long, sparsely hirsute, eglandular. *Flowers* loosely disposed; buds not seen; pedicel 5–13 mm long, with glandular trichomes, 2 bracteoles located up the lower half, persistent; sepals 4.5–5 × 2–3 mm, chartaceous, ovate, outer surface pubescent, with glandular trichomes, inner surface sericeous, margin ciliate; petals 7–8 × 2.5–3 mm, narrowly obovate, glabrous on both surfaces; stamens connate at base by ca. 1 mm, shorter series 2–3 mm long, longer series 3–4 mm long, glabrous; ovary ca. 1 mm long, densely hirsute, style ca. 4 mm long, sparsely hirsute, stigma peltate, bilobate. *Fruits* 1.1–1.4 × 0.6–0.7 cm, yellowish or orangish, outer surface subglabrous, sparsely hirsute at the apex, inner surface subglabrous, apex acuminate, style partially persistent, calyx covering one third of the fruit; *seeds* 0.7–0.9 × 0.4–0.5 cm, arillode colour not seen.

Distribution, habitat and phenology. *Rourea diamantina* is only known from the east side of Chapada Diamantina, a mountain range of about 41,700 km² and approximately 2,000 m altitude, located in the centre of Bahia (Fig. 8). Individuals of the new species are mostly shrubs with scandent branches, occurring in seasonal forests of Inselbergs. Specimens have been collected with flowers from September to December and with fruits from November to February and in July.

Paratypes. BRAZIL. Bahia: Estrada para o Riacho do Meio, 12°18'18"S, 40°29'11"W, 07 Feb 2005 (fr.), *D. Cardoso* 242 (CEPEC, HUEFS, NY); Itaberaba, Fazenda Itaberaba, ilhas de vegetação em Inselbergs, 12°30'06"S, 40°05'03"W, 08 Feb 2007 (fr.), *J. L. Ferreira et al.* 301 (HUEFS); Morro do Agenor, 12°42'S, 39°46'W, 26 Nov 1995 (fl.), *F. França et al.* 1482 (HUEFS); Morro das Tocas: 12°43'S, 39°42'W, 28 Sep 1996 (fl.), *F. França et al.* 1844 (ALCB, HUEFS, SPF); 29 Sep 1996 (fl.), *F. França et al.* 1866 (HUEFS, SPF). Mucugê, Chapada Diamantina, caminho para Marimbus, 14 Dec 2013 (fr.), *M. K. Guedes et al.* 21064 (ALCB); Chapada Diamantina, Marimbus, 12°76'30"S, 41°30'91"W, 14 Nov 2014 (fr.), *M. K. Guedes et al.* 23112 (ALCB, MBML); Rodovia BR 116, Feira de Santana, Milagres, 12°43'S, 39°42'W, 24 Nov 2001 (fr.), *J. G. Jardim*

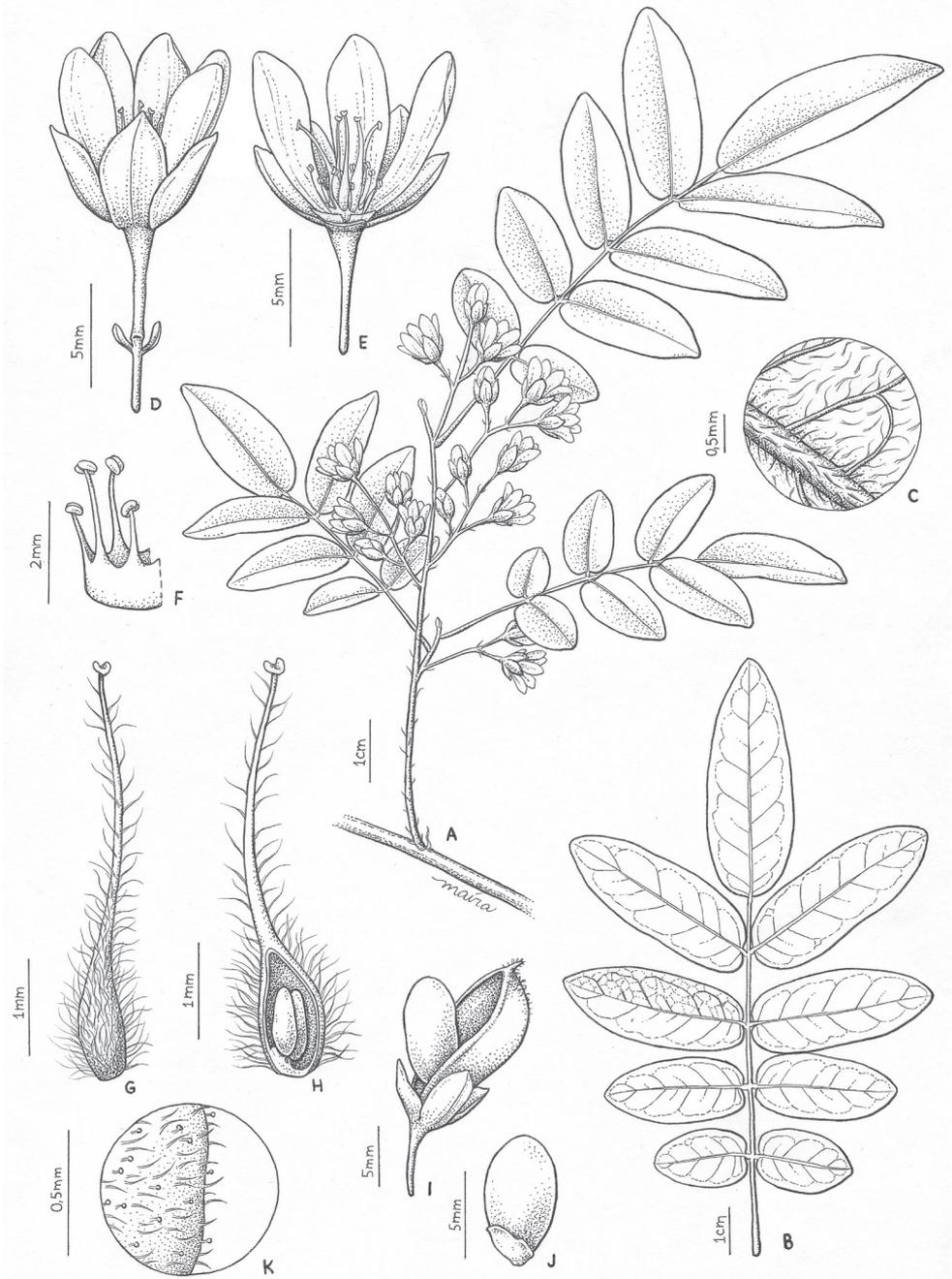


Figure 7. *Rourea diamantina*: **A** flowering branchlet **B** leaf, abaxial surface **C** indumentum, leaflet abaxial surface **D** flower, external view **E** flower, internal view **F** stamens **G** ovary, external view **H** ovary, internal view and ovules **I** fruit and seed, external view **J** seed, external view **K** sepal indumentum, external view.

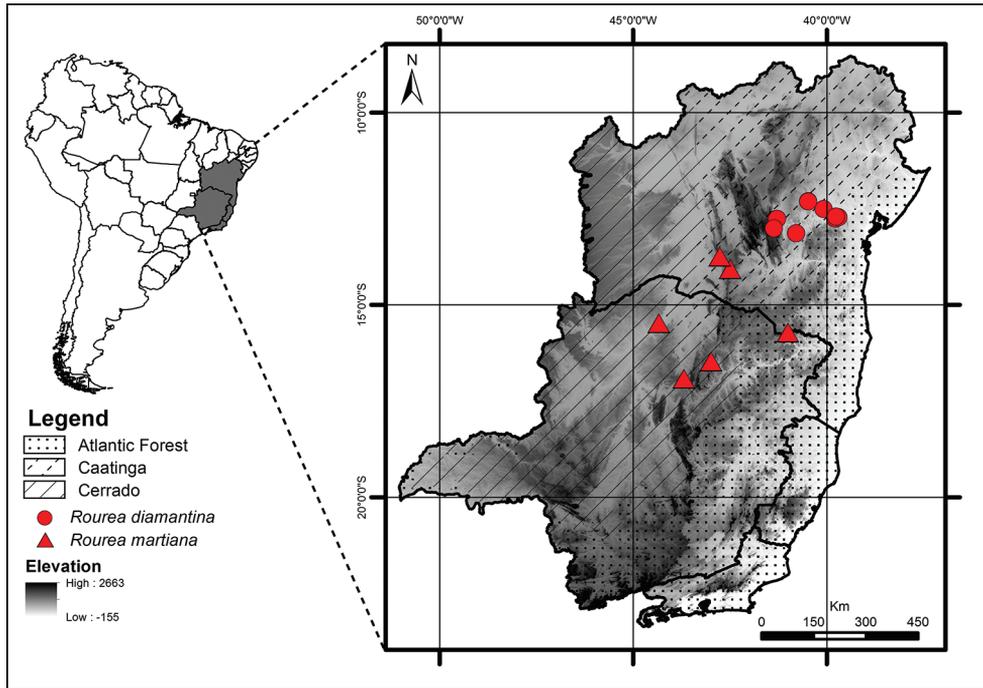


Figure 8. Geographic distribution of *Rourea diamantina* (circles) and *R. martiana* (triangles).

3973 (CEPEC, HUEFS); Morro do Agenor ou da Madeira, 12°43'S, 39°42'W, 17 Dec 1995 (fl.), *E. Melo et al.* 1409 (ALCB, HUEFS); Morro da Torre, 12°43'S, 39°42'W, 09 Nov 1996 (fr.), *E. Melo et al.* 1832 (ESA, HUEFS, RB); Itatim, interior da mata da base do Inselberg, 12°45'12"S, 39°46'59"W. 26 Jan 1997 (fr.), *E. Melo et al.* 1981 (ESA, HUEFS, UEC); Andaraí, Alagados Marimbus, 12°45'55"S, 41°18'52"W, 07 Dec 2012 (fr.), *E. Melo et al.* 11815 (HUEFS); Rui Barbosa, Serra do Orobó, base da encosta da serra, 12°18'S, 40°29'W, 18 Dec 2004 (fl.), *L. P. de Queiroz et al.* 9894 (HUEFS); Machado Portello, 23 Jul 1915 (fr.), *J. N. Rose & P. G. Russel* 19932 (NY, US); Cachoeira, 03 Jan 1977 (fr.), *P. de Souza s. n.* (ALCB, CEPEC).

Etymology. The specific epithet “diamantina” refers to Chapada Diamantina (Bahia, Brazil), where the new species is presumed to be endemic. This epithet is a noun in apposition (Turland et al. 2018, Art. 23.5).

Recognition and notes. *Rourea diamantina* is recognised by the leaves 5–9(–13)-foliolate, leaflets abaxially hirsute or villous, pedicel with glandular trichomes and sepals with indumentum sericeous internally. An interesting characteristic is the leaves whose leaflets become significantly larger towards the apex. The new species is similar to *R. martiana*, but differs by the reduced number of leaflets (usually 5–9), which are normally narrowly ovate with obtuse or narrowly-rounded apex, and longer pedicel (5–13 mm long) vs. leaves 9–15-foliolate, leaflets normally oblong or narrowly elliptic

with rounded apex and a shorter pedicel (ca. 2 mm long). Additionally, both species are geographically isolated by the Chapada Diamantina (Fig. 8).

Some specimens, cited here under *Rourea diamantina*, were previously identified as *R. martiana* by Schellenberg (1938) and Forero (1976, 1983). After analysing modern collections from Bahia and Minas Gerais, this revision considers that the morphological differences indicated above and their disjunct distribution provide evidence to recognise *R. diamantina* apart from *R. martiana*. For a complete discussion on this subject, see “Recognition and notes” section of *R. martiana*.

***Rourea discolor* Baker, in Martius, Fl. Bras. 14(2): 180. 1871.**

Fig. 1A

Santalodes discolor (Baker) Kuntze, Revis. Gen. Pl. 1: 155. 1891.

Eichleria lucida Progel, in Martius Fl. Bras. 12(2): 1877. *Rourea progeliana* Kuhlmann, Arq. Inst. Biol. Veg. 1: 40. 1934. Type. BRAZIL. Bahia: S. d. (fl.), J. S. Blanchet 3145A (Lectotype: P barcode P 02274093!, designated by Forero 1983; isolectotypes: G!, OXF, W!).

Type. BRAZIL. Bahia: Ilheos, 04 Sep 1839 (fl.), B. Luschmuth s. n. (**Holotype:** BR barcode BR 697465!).

Description. *Lianas* or scandent shrubs, 2–3 m tall; branchlets glabrous, lenticels sparse or abundant, conspicuous or inconspicuous. **Leaves** 9–25(–29)-foliolate, loosely disposed; petiole 1.7–4 cm long, glabrous or subglabrous, rarely sparsely villous, eglandular; rachis 6.7–12.5(–18) cm long, glabrous or subglabrous, rarely sparsely villous, eglandular; **leaflets** opposite to subopposite, pulvinulus 1–2 mm long; blade of the basal pair of leaflets 1.3–2.7(–3.3) × 0.8–1.6 cm, elliptic, narrowly elliptic, oblong or narrowly ovate, others 1.8–4.5(–5.8) × 0.8–1.7(–2.3) cm, narrowly elliptic, oblong or narrowly obovate, apical ones usually elliptic, chartaceous or subcoriaceous, discolorous, abaxially glabrous, sparsely puberulous, rarely pubescent, glaucous, occasionally greenish, adaxially glabrous, dull or shining, base symmetric or slightly asymmetric, cordate, subcordate, occasionally truncate, sometimes obtuse in the apical leaflet, apex rounded, occasionally slightly obtuse, margin flat or revolute, glabrous; midvein abaxially prominent, adaxially flat, secondary veins 6–8 pairs, abaxially flat, adaxially slightly prominent, tertiary veins abaxially flat, adaxially slightly prominent. **Inflorescences** in axillary or pseudoterminal cymes or panicles; bracts ca. 1 mm long; peduncle 0.2–2.7 cm long, glabrous or subglabrous, eglandular; rachis 3.5–11.5 cm long, glabrous or subglabrous, eglandular; lateral branches 2.2–9.5 cm long, glabrous or subglabrous, eglandular. **Flowers** loosely disposed; buds 2–3 × 2–3 mm, orbicular or ovate; pedicel 6–16 mm long, eglandular, 1–2 bracteoles located up the lower half, deciduous; sepals (3.5–)4.5–5.5 × 2–2.5 mm, chartaceous, ovate, outer surface glabrous, pubescent only at the apex, eglandular, inner surface glabrous, margin glabrous or ciliate; petals (4–)6–8 × 2–2.5 mm, narrowly obovate, glabrous on both surfaces;

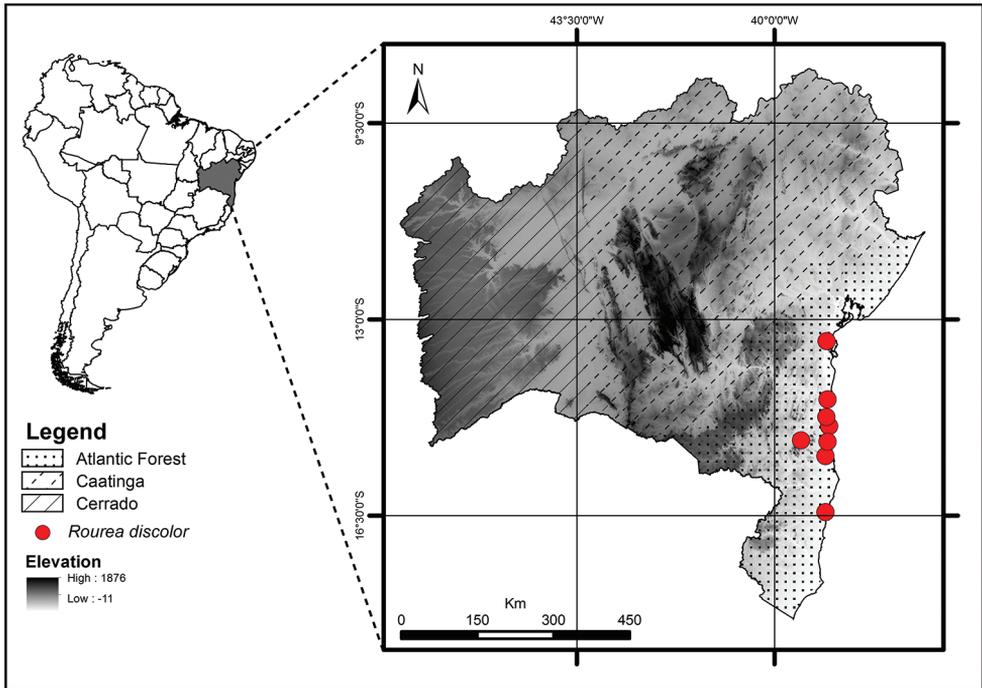


Figure 9. Geographic distribution of *Rourea discolor*.

stamens connate at base by ca. 1 mm, shorter series ca. 2.5 mm long, longer series ca. 3.5 mm long, glabrous; ovary ca. 1 mm long, densely hirsute, style ca. 1 mm long, sparsely hirsute, stigma peltate, bilobate. **Fruits** 1.2–1.7 × 0.4–0.6 cm, orangish or reddish, outer surface glabrous or subglabrous, sparsely hirsute only at the apex, inner surface glabrous, apex acuminate, style partially persistent or deciduous, calyx covering one third of the fruit; **seeds** ca. 1.3 × 0.5 cm, arillode yellowish.

Distribution, habitat and phenology. *Rourea discolor* is exclusive to Bahia, where the individuals are distributed mainly in the southern coastal zone (Fig. 9). Its limits range from the municipality of Valença (near Itacaré) to the municipality of Porto Seguro. This is a lianescent species up to 3 m tall and occurs in dense ombrophilous, “Tabuleiro” or swamp forests, sometimes reaching areas of restinga (coastal vegetation), growing on clay or sandy soils. Specimens have been collected with flowers from August to September and with fruits from October to February.

Specimens examined. BRAZIL. Bahia: Estrada que liga Serra Grande/Itacaré, coletas a 8 km partindo da Serra Grande, 26 Aug 1992 (fl.), *A. M. Amorim* 671 (CEPEC, HUEFS, NY); Reserva Biológica do Mico-Leão (IBAMA), estrada no km 48 da Rod. BA-001 Ilhéus/Una, região da mata higrófila Sul Baiana, 15°09'S, 39°05'W, 18 Aug 1997 (st.), *A. M. Amorim et al.* 2069 (CEPEC); Jussari, RPPN Serra do Teimoso, rodovia Jussari-Palmira, estrada ca. 7.5 km de Jussari, 15°09'16"S, 39°31'52"W, *A. M. Amorim et al.* 4135 (CEPEC); 10 km S de Pontal (Ilhéus), caminho a Olivença, local de extracção de arena, aprox. 14°54'S, 39°02'W, 04 Dec 1992

(fr.), *M. M. Arbo et al.* 5559 (SPF); Reserva Biológica de Una, estrada no km 46 da Rodovia BA-001, Ilhéus/Una, estrada principal para a sede, trilha piedade, 15°09'S, 39°05'W, 10 Sep 2006 (fl.), *A. M. Amorim et al.* 6274 (CEPEC, NY, SPF); Valença, estrada para Orobó, com entrada no km 3 da estrada Valença/BR 101, coletas entre o km 3–10 do ramal para Orobó, 07 Feb 1983 (fr.), *A. M. de Carvalho & T. Plowan* 1506 (CEPEC); Distrito de Serra Grande, 7.3 km na estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S, 30°01'W, 11 Nov 1991 (fl.), *A. M. de Carvalho et al.* 3512 (ALCB, CEPEC, HUEFS, NY, US); Olivença, mata do Balneário Tararomba, 15°26'S, 39°06'W, 17 Sep 2016 (fl.), *M. L. Guedes et al.* 24980 (ALCB); Rod. BA-001 Ilhéus/Una ca. 50,5 km de Ilhéus, área de influência da REBIO de Una, 12 Aug 2000 (fl.), *J. G. Jardim et al.* 3094 (CEPEC, NY, RB); Distrito de Serra Grande, Faz. Lagoa do Conjunto e Conjunto Faz. Santa Cruz, ramal que dá acesso à sede da fazenda, ca. 300 m da rodovia, 07 Jan 2000 (fr.), *F. do S. Juchum et al.* 09 (CEPEC, NY); Porto Seguro, 02 Sep 1961 (fl.), *A. P. Duarte* 6118 (NY, RB, US); Una, Reserva Biológica da Una (REBIO da Una), estrada ca. 45 km S de Ilhéus, margem da estrada que lava à sede da reserva, 15°10'46"S, 39°03'50"W, Jan 2001 (fr.), *F. do S. Juchum et al.* 117 (CEPEC, NY); Rod. Una-Camandatuba, mata litorânea, solo arenoso na Faz. De Antônio Pimenta, 26 Oct 1971 (fr.), *R. S. Pinheiro* 1656 (CEPEC, NY); Ilhéus, Sep 1821 (fl.), *L. Riedel s. n.* (NY barcode NY 00393556); Serra Grande, 25 Aug 1996 (fl.), *A. L. B. Sartori et al.* 293 (CEPEC, UEC); 3 km north of Rodoviária, Mata da Esperança, forest north of dam and reservoir, 14°46'55"S, 39°04'09"W, 20 Sep 1994 (fl.), *W. W. Thomas et al.* 10574 (MBM, NY); Uruçuca, 7.3 km north of Serra Grande on road to Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'24"S, 39°03'38"W, 15 Nov 1995 (fr.), *W. W. Thomas et al.* 11015 (CEPEC).

Recognition and notes. *Rourea discolor* is recognised by the glabrous or subglabrous inflorescence rachis measuring 3.5–11.5 cm long and pedicel 6–16 mm long. It is morphologically similar to *R. glazioui* due to the number and shape of its leaflets; however, individuals of *R. discolor* do not have glandular trichomes and the inflorescence rachis is glabrous or subglabrous, while in *R. glazioui*, they have glandular trichomes and the inflorescence rachis is hirsute or densely so. *Rourea discolor* can be confused with *R. bahiensis* as well, although they are differentiated by the characteristics of the leaflets and inflorescences (see “Recognition and notes” section of *R. bahiensis*).

In the original description, Baker (1871) indicated only the specimen *Luschmuth s. n.*, without mentioning either herbarium, collector number or date. This specimen is deposited in BR and is likely to be the holotype, as no other duplicate has been found.

Rourea discolor was once treated in Oxalidaceae by Progel (1877) under *Eichleria lucida*. Kuhlmann (1934) proposed the combination of *Eichleria* in *Rourea*, but the basionym *Rourea lucida* already existed, so he named it as *R. progeliana*. This name is, however, a heterotypic synonym of *R. discolor*, as the latter had been published previously (Baker 1871).

Rourea glazioui G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 289. 1938.

Fig. 10

Rourea polyphylla G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 197. 1938, *nom. illeg., non R. polyphylla* Blume (1849).

Type. BRAZIL. Rio de Janeiro: Rezende, 22 Nov 1876 (fr.), *A. F. M. Glaziou* 8625 (**Holotype:** B†; **lectotype:** P barcode P 02274098!, selected by Forero 1976; **isolectotypes:** C!, F-frag., K!).

Description. *Lianas* or scandent shrubs, 0.9–1.5 m tall; branchlets densely velutinous to glabrescent, lenticels sparse or abundant, conspicuous or inconspicuous. **Leaves** (9–)15–27-foliolate, loosely disposed; petiole 1.9–3.5(–4.5) cm long, densely velutinous or hirsute, with glandular trichomes; rachis (8–)10–24 cm long, densely velutinous or hirsute, with glandular trichomes; **leaflets** opposite to alternate, subsessile or pulvinulus ca. 1 mm long; blade of the basal pair of leaflets 1.3–3.3 × (0.8–)1.2–2.6 cm, ovate, oblong or orbicular, rarely elliptic, others (1.5–)2.6–6.5(–8.2) × (0.8–)1.3–2.6 cm long, narrowly ovate, narrowly obovate, oblong or narrowly elliptic, rarely elliptic, apical ones usually elliptic, chartaceous, discolorous, abaxially hirsute to densely hirsute, greenish or brownish, adaxially subglabrous to sparsely hirsute, more densely on midvein, dull, base slightly asymmetric to asymmetric, very rarely symmetric, rounded, subcordate, cordate or truncate, rarely obtuse, occasionally acute in the apical leaflet, apex narrowly rounded or obtuse, rarely rounded, occasionally acute in the apical leaflet, margin slightly revolute to revolute, rarely flat, ciliate; midvein abaxially prominent, adaxially slightly impressed, occasionally flat, secondary veins 6–8(–9) pairs, abaxially prominent or slightly prominent, rarely flat, adaxially slightly impressed or flat, tertiary veins abaxially slightly prominent or flat, adaxially slightly impressed or flat. **Inflorescences** in axillary cymes, rarely panicles; bracts 2–3 mm long; peduncle 0.2–1.7 cm long, hirsute to densely hirsute, with glandular trichomes; rachis 0.3–4(–8) cm long, hirsute to densely hirsute, with glandular trichomes; lateral branches 0.3–1.5(–2.8) cm long, hirsute to densely hirsute, with glandular trichomes. **Flowers** loosely disposed; buds 3–4 × 2–3 mm, ovate, orbicular or ellipsoid; pedicel 5–10(–14) mm long, with glandular trichomes, 1–2 bracteoles located up the lower third, deciduous or persistent; sepals (4–)4.5–5.5 × 1.5–2 mm, chartaceous, ovate or elliptic, outer surface hirsute or sparsely hirsute, with glandular trichomes, inner surface sericeous or sparsely sericeous, margin ciliate; petals (5–)6–7.5 × 1.5–2 mm, narrowly obovate or oblong, glabrous on both surfaces; stamens connate at base by 0.8–1 mm, shorter series 2.5–4 mm long, longer series 4–5 mm long, glabrous; ovary 1–1.2 mm long, densely hirsute, style (1.5–)4–5.5 mm long, sparsely hirsute, subglabrous or glabrous only at the apex, stigma peltate, bilobate. **Fruits** 1.1–1.5(–1.6) × 0.5–0.6(–0.8) cm, orangish, reddish or yellowish, outer surface partially or completely hirsute, usually more densely at the apex, inner surface glabrous or subglabrous, apex

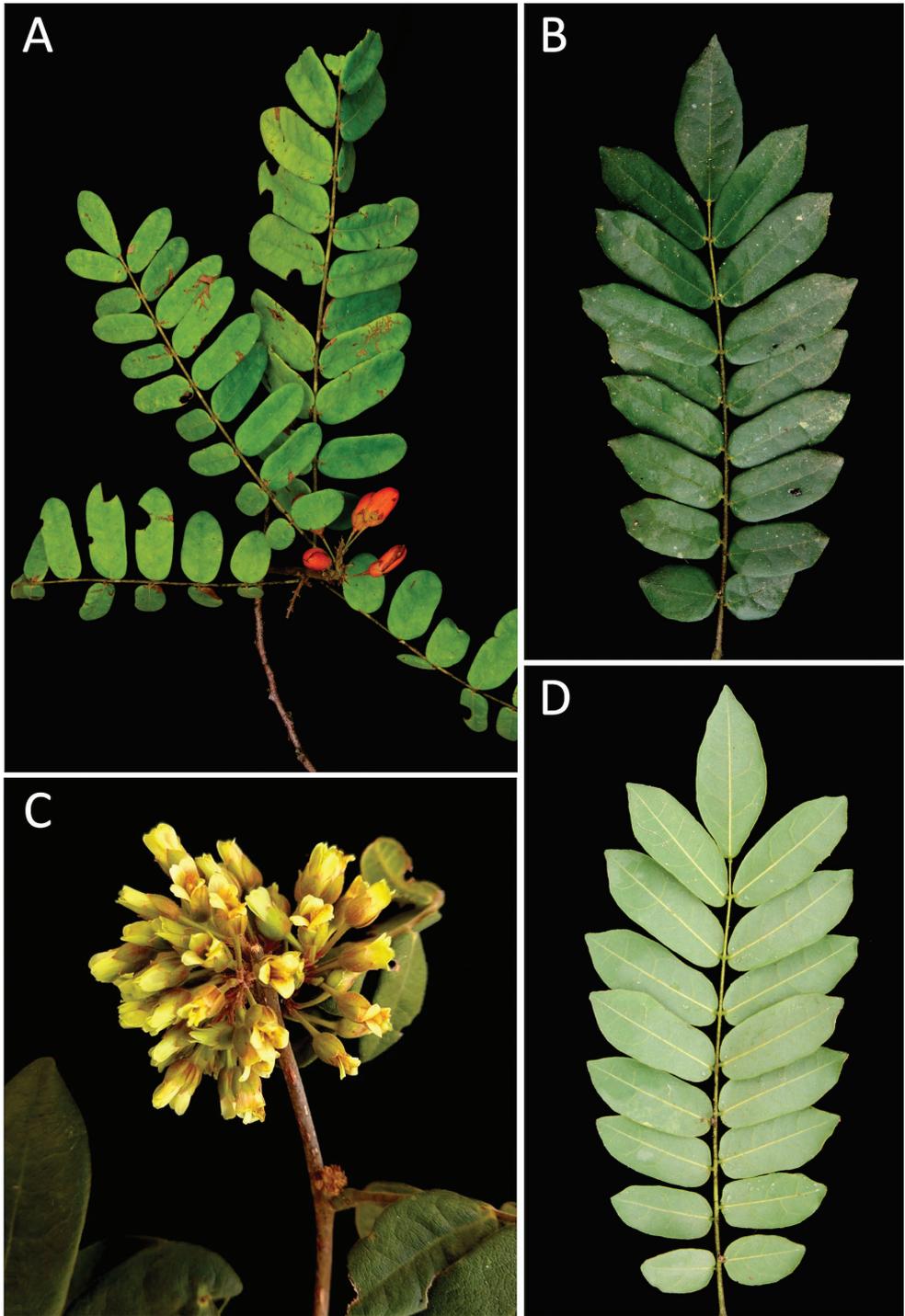


Figure 10. *Rourea glazioui*: **A** fruiting branchlet **B** leaf, adaxial surface **C** inflorescence (photo by Thiago Flores) **D** leaf, abaxial surface.

acuminate or rounded, style partially persistent or deciduous, calyx covering one third of the fruit; **seeds** 0.9–1.1(–1.3) × 0.3–0.5(–0.6) cm, arillode yellowish.

Distribution, habitat and phenology. *Rourea glazioui* is found in Bahia, Espírito Santo and Rio de Janeiro (Fig. 6). In ES, the species has been widely collected along the central and east parts of the state, whereas in BA it is restricted to the southern region, and in RJ, it is sparsely distributed in the eastern side. The type location (Rezende, RJ) might be mistaken as no other record has been found nearby. It is a liana or scandent shrub up to 1.5 m tall, mainly occurring in areas of ombrophilous or “Tabuleiro” forests, although sometimes found in swamp forests or disturbed environments, such as small fragments or in *Eucalyptus* plantations, growing on clay or sandy soils. Specimens have been collected with flowers and fruits almost throughout the year, although more frequently during the spring season.

Specimens examined. **BRAZIL. Bahia:** Nova Viçosa, ca. 61 km na estrada de Caravelas para Nanuque, 06 Sep 1989 (fr.), *A. M. de Carvalho et al.* 2499 (CEPEC, MBM); Picadão, extremo Sul, área da Aracruz Celulose, 23 Aug 1993 (fr.), *M. L. Guedes* 2971 (ALCB, CEPEC); Caravelas, área de influência da CAF, 17°44'07"S, 39°45'16"W, 03 Feb 2002 (fr.), *M. L. Guedes* 9705 (ALCB); Teixeira de Freitas. BR-101 ca. 11 km da cidade, 17°25'49"S, 39°41'14"W, 18 Jun 2005 (fl.), *J. G. Jardim et al.* 4620 (CEPEC, HUEFS); Assentamento “Paulo Freire” (MST), ramal com entrada no km 15 da Rodovia Macuri/Itabatan, 2 km antes da sede do assentamento, 04 Oct 2000 (fr.), *L. A. Matos-Silva et al.* 4140 (ALCB, CEPEC, HUEFS, NY, UESC); Mucuri, 14–17 km a W de Mucuri, 13 Sep 1978 (fl.), *S. A. Mori et al.* 10436 (CEPEC, NY); Macuri, área de restinga com algumas manchas de campos, a 7 km a NW de Macuri, 14 Sep 1978 (fl., fr.), *S. A. Mori et al.* 10532 (CEPEC, NY); Nova Viçosa, 3 km após posto da mata, sentido Posta da Mata divisa BA-MG, 08 Nov 1999 (fr.), *A. A. Santos et al.* 553 (CEN); Vale do Rio Alcobaca, 12 May 1971 (fl.), *T. S. dos Santos* 1613 (CEPEC, US). **Espírito Santo:** Boa Esperança, Bela Vista, 18°33'21"S, 40°13'10"W, 115 m alt., 1 Dec 2010 (fr.), *A. M. Assis & M. D. S. Demuner* 2608 (MBML); Sooretama, REBIO Sooretama, Quirininho, 19°03'14"S, 40°09'35"W, 80 m alt., 2 Nov 2013 (fl.), *A. M. Assis et al.* 4030 (VIES); Guarapari, Barro Branco, próximo da BR 101, 20°33'11"S, 40°28'39"W, 17 Jul 2018 (fr.), *A. M. Assis et al.* 4516 (VIES); Reserva Fazenda São Joaquim, 14 Oct 1985 (fr.), *H. Q. Boudet & W. Boone* 2027 (MBM, RB); Pinheiros, Reserva Biológica do Córrego do Veado, trilha que vai para mata de água limpa, 09 Jul 2010 (fr.), *I. S. Broggio* 26 (VIES); Guarapari, Parque Natural Municipal Morro da Pescaria, 20.6591S, 40.4731W, 09 Feb 2014 (fl.), *A. C. S. Dal Col & J. Rodrigues Filho* 265 (VIES); Governador Lindemberg, Mata da Prefeitura, 14 Nov 2006 (fr.), *V. Demuner et al.* 3069 (MBM, UB); Conceição da Barra. 16 Aug 1965 (fl., fr.), *A. P. Duarte* 8888 (NY, RB); Entre Linhares e São Matheus, 4 Nov 1953 (fr.), *A. P. Duarte & J. C. Gomes* 3960 (RB); Comunidade de Lajinha, Fazenda Rancho Tropical II, restinga arbustiva alta com moitas, 05 Jul 2007 (fl., fr.), *C. Farney et al.* 4764 (RB); Pedro Canário, estradas vicinais, próximas ao eixo da BR 101 entre o Rio Itaúnas e 5 km em direção a Pinheiro, 21 Oct 2008 (fr.), *C. Farney et al.* 4881 (RB); Reserva Biológica do Córrego Grande, estrada no meio da reserva, 28 Dec 2012 (fr.), *T. B. Flores & G. O. Romão* 1257 (ESA, RB); Flo-

resta Nacional do Rio Preto, trilha da Lagoa Seca, 29 Aug 2012 (fr.), *T. B. Flores & G. O. Romão* 1284 (ESA); Presidente Kennedy, 6 Feb 1988 (fl.), *J. M. L. Gomes* 476 (VIES); Próximo à antiga casa do guarda, estrada Aderne, 04 Jul 1995 (fl.), *D. A. Folli* 2342 (CEPEC, CVRD, ESA); Próximo ao Rio Barra Seca, estrada Aderne, 06 Oct 1994 (fr.), *D. A. Folli* 2385 (CEPEC, CVRD, ESA); Jueirana, estrada Aceiro com Eucalipto, 25 Jul 2001 (fl.), *D. A. Folli* 3996 (CVRD, ESA); BR 101, próximo à entrada para Conc. da Barra, 27 Aug 2007 (fl.), *D. A. Folli* 5684 (CVRD, ESA); Mata de restinga sobre feixes de cordões arenosos, vegetação localizada à direita da estrada principal da vila de Itúnas, 06 Oct 2007 (fr.), *A. O. Giaretta et al.* 248 (RB); Vegetação de restinga, mata seca, entrada localizada adjacente à estrada principal da Vila de Itaúnas, área de preservação permanente à PEI, 14 Jun 2008 (fr.), *A. O. Giaretta et al.* 276 (RB); Jaguaré, Rod. BR-101, 23 Aug 1987 (fr.), *G. Hatschbach & A. C. Cervi* 51416 (MBM, US); Rod. ES-421, km 5–8, 09 Oct 1998 (fr.), *G. Hatschbach et al.* 68346 (CEPEC, MBM, US); Itaúnas, 09 Jun 1992 (fl.), *O. J. Pereira* 3419 (VIES); 20 May 1999 (fl.), *G. Hatschbach et al.* 69202 (CEPEC, ESA, MBM, SPF, US); Praia Setibana, ES-060 at 6 km E of BR-101, 18 Jan 1993 (fr.), *J. A. Kallunki & J. R. Pirani* 345 (NY, SPF); Colatina, estrada do Patrimônio, perto de Colatina, 16 May 1934 (fl.), *J. G. Kuhlmann* 351 (IAN, NY, RB); Reserva Biológica do Córrego Grande, coletado próximo na mata próxima a sede da rebio, 10 Jan 2012 (fr.), *L. Marcarini et al.* 38 (VIES); Próximo ao Bairro Litorâneo, seguindo uma estrada de terra atrás do campus da Universidade (UFES), 01 Aug 2007 (fr.), *R. F. A. Martins et al.* 38 (RB); Rodovia do Sol, road linking BR-101 to the São Mateus, Bairro Litorâneo, fragmento de mata ciliar próximo ao campus da universidade, 03 Oct 2009 (fr.), *A. G. Oliveira & M. Ribeiro* 656 (VIES); Anchieta, Estrada para Castellanos, tipo do morro, 2 Feb 2012 (fl.), *N. E. Oliveira Filho* 79 (VIES); Mata seca de restinga, 23 Jun 2002 (fl.), *O. J. Pereira et al.* 3536 (VIES); Área 126 da Aracruz Celulose S. A., 2 Apr 1992 (fr.), *O. J. Pereira* 4283 (VIES); Serra, Bicanga, 22 Apr 1993 (fl.), *O. J. Pereira* 4529 (VIES); Itaúnas, área 135 da Aracruz Celulose S. A., 18°25'10"S, 39°42'32"W, 21 Sep 1993 (fr.), *O. J. Pereira et al.* 4890 (VIES); Interlagos, Rodovia do Sol ES060, 20°19'47"S, 40°17'32"W, 1 Jun 1995 (fr.), *O. J. Pereira* 5468 (VIES); Itaúnas, 13 Jul 1991 (fr.), *P. C. Vinha* 1271 (VIES); Linharinho, 6 Nov 1996 (fr.), *O. J. Pereira et al.* 5726 (VIES); Vila Velha. 20°25'42.7"S, 40°22'46.7"W, 10 Jan 2001 (fl.), *O. J. Pereira & E. Espindula* 6713 (VIES); Parque Estadual de Itaúnas, 24 Aug 2002 (fr.), *O. J. Pereira et al.* 6983 (VIES); Serra, Nova Zelândia, 20°10'52"S, 40°12'54"W, 21 Jul 2015 (fr.), *O. J. Pereira et al.* 8021 (VIES); Linhares, Reserva Natural Vale, aceiro c/ BR 101 jueirana, 21 Aug 2006 (fr.), *G. S. Siqueira* 240 (CVRD, ESA); Parque Estadual de Itaúnas, Trilha Alméscar, 18.4033S, 39.7019W, 08 Aug 2013 (fr.), *W. O. Souza et al.* 146 (VIES); Conceição da Barra, Itaúnas, área da Fíbria com plantação de eucalipto, 18°29'27"S, 39°44'12"W, 21 Oct 2018 (fr.), *C. A. P. Toledo & N. C. Bígio* 400 (ESA); Guarapari, Parque Estadual Paulo César Vinha, 21 Oct 2006 (fr.), *R. T. Valadares* 304 (VIES); Aracruz, Estação Biológica Marinha Augusto Ruschi, Santa Cruz, 19°58'14"S, 40°08'26"W, 1 Apr 2018 (fr.), *Wandekoken et al.* 257 (VIES); Parque Ecológico da CST, área de Tabuleiro, Bosque dos Jacarandás, área dominada por espécies exóticas plantadas, 21 Apr 1995 (fl.), *I. Weiler Junior et al.* 166 (VIES). **Rio de Janeiro:** Casimiro de

Abreu, Morro de S. João, 03 Feb 1970 (fr.), *CPJ* s. n. (RB 261147); Reserva Biológica do Poço das Antas, mata da Osmarina, 26 May 1982 (fr.), *H. C. de Lima & G. Martirelli 1733* (RB); Silva Jardim, Est. Juturnaiba, esquerda – km 5, Reserva Biológica de Poço das Antas, 11 Jan 1994 (fr.), *C. Luchiari et al. 349* (RB); Conceição de Macabu, km 12 da BR 101, a 62 km de Campos, 10 Jan 1985 (fr.), *J. R. Pirani & D. C. Zappi 1046* (NY, SPF); Horto Florestal de Rezende, s. d. (st.), *A. da Silva* s. n. (IAN 67552).

Recognition and notes. *Rourea glazioui* resembles *R. cnestidifolia* as they have glandular trichomes and similar characteristics of leaflet shape and size, flowers and fruits. However, the former has leaves (9–)15–27-foliolate, peduncle 0.2–1.5 cm long, flowers loosely disposed on the inflorescences and pedicel 5–10(–14) mm long, while the latter has leaves 9–13-foliolate, peduncle 2.8–8 cm long, flowers congested in the inflorescence apex and pedicel 3–5 mm long. *Rourea glazioui* is commonly confused with *R. chrysomalla* in herbarium specimens, but differs in the characteristics described in the “Recognition and notes” section of *R. chrysomalla*.

In the protologue, *Rourea glazioui* was named as *R. polyphylla* (Schellenberg 1938). After noticing that he created a homonym of *R. polyphylla* Blume (1849), Schellenberg (1938) added an appendix in the same work and replaced *R. polyphylla* for *R. glazioui*. This does not preclude valid publication of *R. glazioui*, as this replaced name, although indicated in the same work, presented a clear and crossed reference of a corresponding description (Turland et al. 2018, Art. 41.3).

The type collection of *R. glazioui* morphologically resembles the type of *R. fulgens* Planch. (*Wallich 8524*, deposited in K), a species restricted to Singapore. Both type specimens share densely-velutinous branchlets, multifoliolate leaves, and oblong or narrowly-elliptic leaflets with rounded apex, which are also discolorous and abaxially hirsute. Some other species from south-eastern Asia, such as *R. mimosoides* (Vahl) Planch., also have multifoliolate leaves with oblong or narrowly-elliptic leaflets, so this raises the question whether *Rourea* species from the New World are a monophyletic group. Morphological similarities between the multifoliolate species of *Rourea* from America and south-eastern Asia were firstly noticed by Forero (1976), who cited *R.* sect. *Mimosoideae* Planch. *p. p.* under *R.* subgen. *R.* sect. *Multifoliolatae*, thus drawing attention to possible relationships. Nevertheless, this subject should be addressed by future molecular investigations.

***Rourea macrocalyx* Carbonó, Forero & Vidal, Revista Brasil. Bot. 7(1): 68. 1984.**
Illustration: Forero et al. (1984)

Type. BRAZIL. Bahia: Município de Santa Cruz de Cabrália, 2–4 km a W de Sta. Cruz de Cabrália, pela estrada antiga, área de campos e restinga, 21 Oct 1978 (fr.), *S. A. Mori 10938* (**Holotype:** CEPEC barcode CEPEC 15308!; **isotypes:** COL!, K!, NY!, RB!).

Description. *Lianas* or scandent shrubs, ca. 3 m tall; branchlets subglabrous or sparsely pubescent, lenticels abundant, inconspicuous. **Leaves** 3–7(–9)-foliolate, congested; petiole 1.1–3 cm long, subglabrous, eglandular; rachis 1.5–3.4 cm long, subglabrous, eglandular; **leaflets** subopposite to alternate, pulvinulus ca. 1 mm long; blade

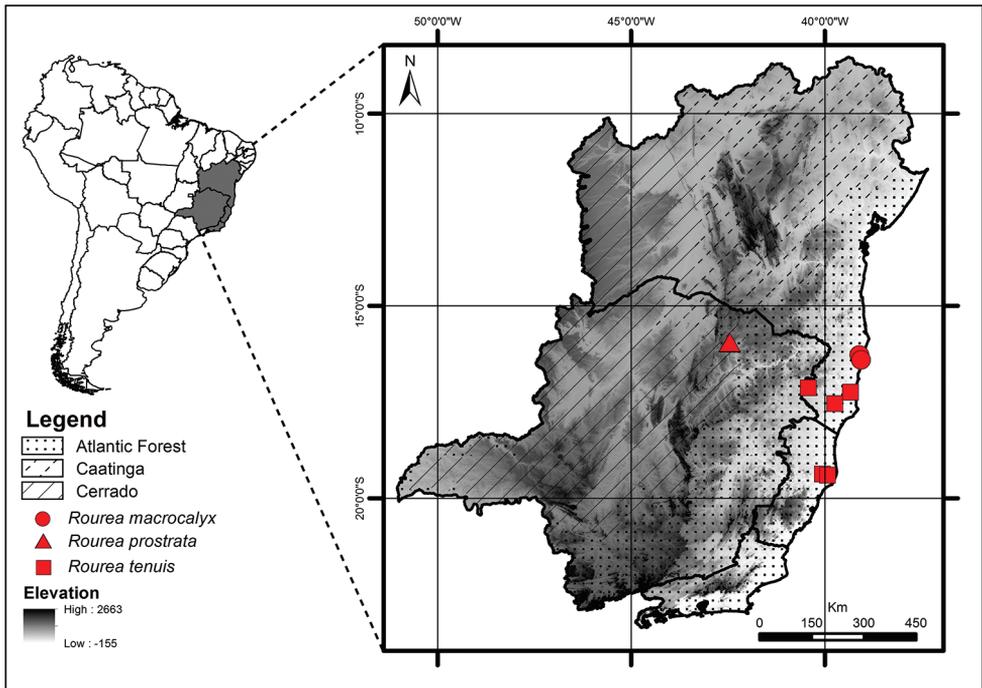


Figure 11. Geographic distribution of *Rourea macrocalyx* (circles), *R. prostrata* (triangles) and *R. tenuis* (squares).

of the basal pair of leaflets $1.1\text{--}2.8 \times 0.5\text{--}1.7$ cm, ovate, oblong or elliptic, others $1.6\text{--}6(-7.2) \times 1.3\text{--}2.5(-3.7)$ cm, elliptic or oblong, rarely ovate, chartaceous, discolorous, glabrous on both surfaces, abaxially brownish or greenish, adaxially dull, base slightly asymmetric or symmetric, cordate, subcordate or rounded, apex rounded, rarely narrowly rounded, margin flat or slightly revolute, glabrous; midvein abaxially prominent, adaxially flat or impressed, secondary veins 6–8 pairs, flat or slightly prominent on both surfaces, tertiary veins abaxially flat, adaxially flat or slightly prominent. **Inflorescences** in axillary cymes or panicles; bracts 1–2 mm long; peduncle 1.3–2.3 cm long, glabrous or subglabrous, eglandular; rachis 2–4 cm long, glabrous or subglabrous, eglandular; lateral branches 2.4–4.9 cm long, glabrous or subglabrous, eglandular. **Flowers** unknown, loosely disposed; buds unknown; pedicel 9–18 mm long, eglandular, 1–2 bracteoles located up to the lower half, deciduous; sepals (persistent on fruits) elliptic, outer surface glabrous or subglabrous, eglandular, inner surface glabrous or subglabrous, margin ciliate, more densely at the apex; petals (Forero et al. 1984) $6\text{--}7 \times 2$ mm, oblong, glabrous on both surfaces; stamens (Forero et al. 1984) connate at base by 1.1–1.2 mm, shorter series 3–4.5 mm long, longer series 5–6 mm long, glabrous; ovary (Forero et al. 1984) 1–1.2 mm long, hirsute, style 2.2–2.5 mm long, sparsely hirsute, stigma bilobate. **Fruits** $1.4\text{--}1.5 \times 0.5\text{--}0.6$ cm, brownish, outer surface subglabrous, hirsute at the apex, inner surface glabrous, apex obtuse, style partially persistent, calyx covering two thirds of the fruit; **seeds** ca. $0.9\text{--}1.1 \times 0.4\text{--}0.6$ cm, arillode orangish.

Distribution, habitat and phenology. *Rourea macrocalyx* is only known from southern Bahia, occurring in the coastal zone ranging from the municipality of Porto Seguro to Santa Cruz de Cabrália (Fig. 11). This is a lianescent species growing on “Tabuleiro” forests with sandy soils. Specimens have been collected with fruits from October to February.

Specimens examined. **BRAZIL. Bahia:** Porto Seguro, RPPN VERACEL, ramal para Sta. Cruz Cabrália, ca. 10 km do Centro de visitantes, 05 Feb 2000 (fr.), *J. G. Jardim & M. Alves 2686* (NY); Santa Cruz Cabrália, 16°18'49"S, 39°1'35"W, 11 Oct 2010 (fr.), *B. M. da Silva et al. 24* (HUEFS).

Recognition and notes. *Rourea macrocalyx* is morphologically recognised by the leaves with 3–7(–9) leaflets, pedicel measuring 9–18 mm long and the strongly accrescent calyx, which covers two thirds of the fruits. It is similar to *R. discolor* due to the glabrous leaflets and length of pedicel, but differs mainly by the number of leaflets (3–9 vs. 9–29).

***Rourea martiana* Baker, in Martius, Fl. Bras. 14(2): 178. 1871.**

Fig. 1B

Santalodes martianum (Baker) Kuntze, Revis. Gen. Pl. 1: 155. 1891.

Type. **BRAZIL. Minas Gerais:** Tabuleiro ad. fl. S. Francisco, prope Salgado, s. d. (fl.), *C. F. P. von Martius 1675* (**Lectotype:** M, first step designated by Schellenberg 1938; **lectotype:** M barcode M-0243940!, second step designated here; **isolectotype:** M!).

Description. *Shrubs* or scandent shrubs, (0.8–)1–3 m tall; branchlets sparsely hirsute to hirsute, lenticels abundant, inconspicuous. **Leaves** 9–13(–15)-foliolate, congested or loosely disposed; petiole 0.8–1.8 cm long, sparsely hirsute, with glandular trichomes; rachis 4–6 cm long, sparsely hirsute, with glandular trichomes; **leaflets** opposite to subopposite, subsessile; blade of the basal pair of leaflets 0.9–1.8 × 0.6–1.2 cm, orbicular, ovate or narrowly elliptic, others 1.2–3(–4) × 0.7–1.6 cm, oblong, narrowly elliptic or narrowly obovate, chartaceous, slightly discolorous, abaxially hirsute or villous, brownish or greenish, adaxially subglabrous, sparsely hirsute or sparsely villous, dull, base slightly asymmetric or symmetric, cordate, subcordate or rounded, apex rounded, rarely obtuse, margin flat, ciliate; midvein abaxially prominent, adaxially flat, secondary veins ca. 6 pairs, abaxially slightly prominent, adaxially flat, tertiary veins slightly prominent on both surfaces. **Inflorescences** in axillary or pseudoterminal cymes; bracts ca. 3 mm long; peduncle 0.9–3.8 cm long, hirsute, with glandular trichomes; rachis 0.5–2.2 cm long, hirsute, with glandular trichomes. **Flowers** congested apically; buds 4 × 2.5–3 mm, elliptic or orbicular; pedicel ca. 2 mm long, with glandular trichomes, 2 bracteoles located up to the lower half, persistent; sepals 5 × 2–2.5 mm, chartaceous, ovate, outer surface hirsute, with glandular trichomes, inner surface glabrous or subglabrous, sparsely sericeous at the apex, margin ciliate, more densely at the apex; petals ca. 7 × 2.5 mm, narrowly obovate, glabrous on both surfaces; stamens connate at base by ca. 1 mm, shorter series ca. 5 mm long, longer series ca. 7 mm long, glabrous; ovary ca. 1 mm long, hirsute, style ca. 2 mm long, hirsute,

glabrous only at the apex, stigma peltate, bilobate. **Fruits** 1–1.2 × 0.4–0.5 cm, orangish or reddish, outer surface subglabrous or sparsely villous, more densely at the apex, inner surface glabrous or subglabrous, apex obtuse, style partially persistent, calyx covering one third of the fruit; **seeds** ca. 0.8–0.9 × 0.4–0.5 cm, arillode yellowish.

Distribution, habitat and phenology. This species occurs in central and north-east Minas Gerais and southwest Bahia (Fig. 8). *Rourea martiana* is a shrub, occasionally with climbing branches and grows in the Cerrado or in transitional areas with Caatinga or Atlantic Forest. Specimens have been collected with flowers in April and August and with fruits in October.

Specimens examined. BRAZIL. Bahia: Caetité, 5–8 km S, 21 Oct 1995 (fl.), *G. Hatschbach & J. T. Motta* 63237 (RB); Riacho de Santana, Estrada para Igaporá, km 89, 13.7487S, 42.7673W, 12 Oct 2007 (fr.), *J. Paula-Souza et al.* 9376 (CTES, SI, SPF). **Minas Gerais:** Grão Mogol, Assentamento Americana. 19 Nov 2014 (fr.), *A. B. Giroldo & J. B. Pereira* 330 (CEN); Divisópolis, próximo da cidade, s. d. (fl.), *G. M. Magalhães* 15790 (BHCB); Januária, Vale do Peruaçu, Carascal, 26 Oct 1997 (fr.), *A. Salino & L. C. N. Neto* 3706 (BHCB, MBM, SPF); Comunidade Boa Vista, 02 Nov 2006 (fr.), *A. C. Sevilha* 4597 (CEN); Juramento, Plantar MG 15, Fazenda Tamanduá, 10 Apr 2005 (fl.). *E. Temeirão Neto* 4225 (BHCB); *E. Temeirão Neto* 4273 (BHCB).

Recognition and notes. *Rourea martiana* is recognised by possessing glandular trichomes, a relatively long-peduncle (0.9–3.8 cm) and a short pedicel (ca 2 mm long).

Baker (1871) described *Rourea martiana* based on the collections of Martius 1675 and Warming 1849, without mentioning the type; the former is only deposited in M, while the latter is deposited in C, GH and K. Schellenberg (1938) inadvertently indicated the lectotype of *R. martiana* (Martius 1675) and described *R. cnestidifolia*, citing Warming 1849 as paratype. Forero (1976) followed Schellenberg's position, although he called the specimen Martius 1675 holotype of *R. martiana*, and selected Warming 1849 from K as lectotype of *R. cnestidifolia* after the holotype from B (Sellow s. n.) was considered missing. Baker (1871) indeed described *R. martiana* based on two specimens that should be treated as different taxa, so Schellenberg (1938) was right in selecting a type for *R. martiana* and describing *R. cnestidifolia*. The former differs by the middle and apical leaflets up to 4 cm long with usually rounded apex, while in the latter, leaflets are longer than 4 cm with obtuse, acute or narrowly rounded apex.

After fixing the application of *R. martiana* to Martius 1675, however, both Schellenberg (1938) and Forero (1976, 1983) seem to have confused the identity of the species and grouped specimens morphologically distinct and geographically isolated. The type of *R. martiana* was collected in Minas Gerais and, although without a precise location, this specimen matches those collected in central and northeast of the state and south-western Bahia, which are characterised by leaves 9–15-foliolate and a short pedicel (ca. 2 mm long). The specimens, here treated under a new species (*R. diamantina*) – but identified as *R. martiana* by Schellenberg (1938) and Forero (1976, 1983) – are restricted to central Bahia and characterised by leaves 5–9(–13)-foliolate and a longer pedicel (5–13 mm long). Additionally, leaflets in *R. martiana* become slightly larger towards the apex and are usually oblong or narrowly elliptic with rounded

apex (Fig. 1B), whereas in *R. diamantina*, they become significantly larger towards the apex and are usually narrowly ovate with obtuse or narrowly-rounded apex (Fig. 7B). Both species are morphologically similar due to the presence of glandular trichomes, leaves and leaflets relatively small and flowers and fruits with similar characteristics. Geographically, these two species are separated by the Chapada Diamantina (Fig. 8), a mountain range located in central Bahia approximately 41,700 km² long and altitudes up to 2,000 m. They also occur in different environments: *R. martiana* grows in areas of Cerrado *s. s.* (occasionally with rocky soils), while *R. diamantina* grows in seasonal forests on Inselbergs.

The position taken by Schellenberg (1938) and Forero (1976, 1983) may be explained because the specimens from Minas Gerais were not available at the time. Nevertheless, the disjunct distribution and the morphological differences are consistent enough to recognise *R. martiana* and *R. diamantina* as distinct species.

The type collection from M is composed of two herbarium sheets mounted separately, but one of them (barcode M-0243940) has an original blue label of Martius, whereas the other (barcode M-0243941) has a different label. According to the *Code* (Turland et al. 2018, Art. 8.3, Ex. 10), these should be regarded as duplicates, so a second step lectotypification is here proposed.

***Rourea prostrata* C. Toledo, Phytotaxa 408(2): 120. 2019.**

Illustration: Toledo and Souza (2019)

Type. BRAZIL. Minas Gerais: Rio Pardo de Minas, Vereda Funda, parcela 4, 15°57'20"S, 42°27'23"W, 981 m alt., 11 Dec 2008 (fr.), *A. C. Sevilha et al. 5011 (Holotype: CEN barcode CEN 00097193!; isotype: ESA!)*.

Description. *Subshrubs* prostrate; branchlets tomentose, lenticels sparse, inconspicuous. *Leaves* 13–17(–21)-foliolate, loosely disposed; petiole 0.2–1 cm long, villous, with glandular trichomes; rachis 3–5.5 cm long, villous, with glandular trichomes; *leaflets* subopposite, subsessile; blade of the basal pair of leaflets 0.5–1 × 0.3–0.7 cm, orbicular, others 0.9–1.7 × 0.5–1 cm, oblong, rarely elliptic or narrowly obovate, chartaceous, discolorous, abaxially villous, greenish, adaxially sparsely villous, dull, base slightly asymmetric, rounded or subcordate, apex rounded, margin flat, ciliate; midvein abaxially prominent, adaxially flat, secondary veins 5–6 pairs, abaxially slightly prominent, adaxially flat or slightly prominent, tertiary veins flat on both surfaces. *Inflorescences* in axillary cymes; bracts ca. 2 mm long; peduncle 0.7–1.8 cm long, hirsute, with glandular trichomes; rachis 1.3–2.2 cm long, hirsute, with glandular trichomes. *Flowers* unknown, loosely disposed; pedicel 3–8 mm long, with glandular trichomes, 1–2 bracteoles located up the lower half; sepals (persistent on fruits) with outer surface sparsely hirsute, with glandular trichomes, inner surface subglabrous, margin ciliate; petals (persistent on fruits) glabrous; stamens (persistent on fruits) with sparse glandular trichomes; ovary (persistent on fruits) densely hirsute, style subglabrous, stigma not seen. *Fruits* 0.8–1 × 0.3–0.4 cm, colour not seen, outer

surface sparsely hirsute, more densely at the apex, inner surface glabrous, apex acuminate, style partially persistent, calyx covering one third of the fruit; **seeds** 0.7–0.8×0.4 cm, arillode colour not seen.

Distribution, habitat and phenology. *Rourea prostrata* is only known from the type location (15°57'20"S, 42°27'23"W), which is near the municipality of Rio Pardo de Minas, MG (Fig. 11). It is the only known species of Connaraceae reported as a prostrate plant. The type was collected with fruits in December.

Recognition and notes. *Rourea prostrata* is morphologically similar to *R. bahiensis* due to the number and size of leaflets. However, *R. prostrata* is a prostrate subshrub with glandular trichomes, while *R. bahiensis* is a liana or scandent shrub eglandular. *Rourea prostrata* can also be mistaken for *R. chrysomalla*, although it mainly differs by its prostrate habit, chartaceous leaflets and sparsely hirsute fruits measuring 0.8–1 × 0.3–0.4 cm vs. erect habit, coriaceous leaflets and completely velutinous fruits measuring 1–1.4 × 0.4–0.6 cm.

***Rourea tenuis* G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 199. 1938.**

Figs 1C, 12; illustration: Forero et al. (1984, as *R. carvalhoi*)

Rourea carvalhoi Forero, Carbonó & L. A. Vidal, Revista Brasil. Bot. 7(1): 72. 1984.

Type. BRAZIL. Bahia: Km. 6 da rod. Teixeira de Freitas a Alcobaça, 9 Oct 1971 (fr.), T. S. Santos 2094 (*Holotype*: CEPEC 7633!; *isotypes*: COL!, NY!).

Type. BRAZIL. Vittoria, s. d. (fr.), *F. Sellow s. n.* (*Holotype*: B†). BRAZIL. S. d. (fl.), *J. Pohl s. n.* (*Neotype*: BR barcode BR 000000697468!, selected by Forero 1976).

Description. *Lianas* or scandent shrubs, (0.5–)1–3 m tall; branchlets sparsely hirsute to glabrescent, lenticels absent or sparse, inconspicuous. **Leaves** 5–7-foliolate, loosely disposed or congested; petiole 2.7–7 cm long, sparsely hirsute, with glandular trichomes; rachis 2.6–6.5 cm long, sparsely hirsute, with glandular trichomes; **leaflets** opposite to subopposite, pulvinulus 1–2 mm long; blade of the basal pair of leaflets 2.3–5.7(–7.7) × 1.4–2.5(–4) cm, elliptic or ovate, others 3.5–8.4(–13) × 2.1–3(–6.7) cm, elliptic or ovate, rarely oblong, chartaceous, slightly discoloured, abaxially sparsely hirsute, more densely on the veins, brownish or greenish, adaxially sparsely hirsute on the veins, dull, base slightly asymmetric, symmetric in the apical leaflet, rounded, obtuse or subcordate, occasionally acute in the apical leaflet, apex obtuse or narrowly rounded, occasionally short-acuminate, margin flat to revolute, ciliate; midvein abaxially prominent, adaxially flat or slightly impressed, secondary veins 5–7 pairs, abaxially slightly prominent, adaxially flat, tertiary veins flat on both surfaces. **Inflorescences** in axillary or pseudoterminal determinate thyrses, rarely panicles; bracts ca. 2 mm long; peduncle 1.9–6.4 cm long, hirsute, with glandular trichomes; rachis (0.7–)2–5.8(–7.7) cm long, hirsute, with glandular trichomes; lateral branches 0.5–3 cm long, hirsute, with glandular trichomes. **Flowers** loosely disposed or congested



Figure 12. *Rourea tenuis*, flowering branchlet (photo by Thiago Flores).

apically; buds 2.5–4 × 1.5–2 mm, orbicular or elliptic; pedicel 5–10 mm long, with glandular trichomes, 2 bracteoles located up the lower third, persistent or deciduous; sepals 4–5 × 1–2 mm, chartaceous, ovate, outer surface sparsely hirsute, with glandular trichomes, inner surface glabrous, margin ciliate, more densely at the apex; petals 5–7 × 1.5–2 mm, oblong or narrowly oblong, glabrous or subglabrous on both surfaces; stamens connate at base by ca. 0.8 mm, shorter series 3–3.5 mm long, longer series ca. 5 mm long, glabrous; ovary ca. 1 mm long, densely hirsute, style ca. 1.5 mm long, sparsely villous, subglabrous at the apex, stigma peltate, trilobate to pentalobate. **Fruits** 1.3–1.5 × 0.6–0.8 cm, reddish or orangish, outer surface sparsely hirsute, more densely at the apex, inner surface glabrous, apex acuminate, style partially persistent, calyx covering one third of the fruit; **seeds** 1.2–1.3 × 0.5–0.7 cm, arillode colour not seen.

Distribution, habitat and phenology. *Rourea tenuis* occurs in Bahia and Espírito Santo, with limits ranging from the municipalities of Itanhém (North) to Linhares (South) (Fig. 11). This species is lianescent and grows in ombrophilous or “Tabuleiro” forests. Specimens have been collected with flowers from April to June and from October to November and with fruits from August to October and in March.

Specimens examined. **BRAZIL. Bahia:** Porto Seguro, Parque Nacional de Monte Pascoal, área limite entre o PARNA e a Reserva Indígena Barra Velha, da tribo Pataxó, 13 Apr 1998 (fl.), *A. M. Amorim et al.* 2530 (CEPEC, NY); Itamarajú, Estrada a Piraji, km 4, 17°15'S, 39°20'W, 1 Jun 1983 (fl.), *R. Callejas et al.* 1612 (NY); Itamarajú, 2 km de estrada a Piraji, km 4, 5 Apr 1971 (fl.), *T. S. dos Santos* 1558 (NY!); Itanhém, Fazenda Pedra Grande, 16.2 km west of Itanhém on road to Batinga, then 0.6 km north to Fazenda (owner Otevaldo Resende da Silva), 17°07'57.8"S, 40°25'17.8"W, 18 Mar 2001 (fr.), *W. W. Thomas et al.* 12351 (CEPEC, NY, RB, SPF). **Espírito Santo:** Reserva Natural Vale, estrada Fruta de arara, 1 Jun 2001 (fl.), *D. A. Folli* 3940 (CVRD, ESA); Reserva Natural Vale, estrada Braúna Preta, 12 Apr 2002 (fr.), *D. A. Folli* 4352 (CVRD, ESA); Linhares. 5 km S, 5 Aug 1983 (fr.), *G. Hatschbach* 46735 (CEPEC, MBM); Floresta Atlântica de Tabuleiro, área com corte seletivo, em regeneração, 19.4000S, 39.9722W, 3 Oct 2000 (fr.), *O. J. Pereira et al.* 6541 (VIES).

Recognition and notes. *Rourea tenuis* is recognised by leaves 5–7-foliolate, leaflets usually elliptic or ovate, abaxially hirsute and inflorescences in thyrses or panicles with glandular trichomes.

Forero (1976) included *Rourea tenuis* in *Rourea* subgen. *R.* sect. *Multifoliolatae* mainly due to the long staminal tube, reduced inflorescences and leaflets hairy. Aside from that, this species does not resemble other members of the section in overall similarity of leaves: in *R. tenuis*, the number of leaflets is reduced and they are usually relatively larger, with elliptic or ovate shape (vs. oblong, narrowly elliptic or narrowly ovate) (Fig. 1C). Forero (1976) firstly noticed that *R. tenuis* could be a borderline species between those of *R.* subgen. *R.* sect. *Multifoliolatae* with those from the Amazon, then suggested that the morphological limits of the section should be re-evaluated (Forero et al. 1984). The present study, therefore, considers that the circumscription of the whole group should be tested using molecular and phylogenetic approaches.

Conclusions and discussion

Rourea subgen. *R.* sect. *Multifoliolatae* is a small group of this pantropical genus, with species restricted to south-eastern Brazil and southern Bahia. Most of the species in this section are presumably rare and present restricted distributions, such as *R. blanchetiana*, *R. chrysomalla* and *R. diamantina* and some are only known by the type collection (e.g. *R. barbata* and *R. prostrata*). An exception is *R. glazioui*, which is more widely distributed, very common from north ES to central RJ and well represented in herbarium collections.

Although *Rourea* species have been grouped within different taxonomic ranks (subgenera and sections) over time, none has been tested using molecular data. By comparing the species of *R.* subgen. *R.* sect. *Multifoliolatae* with some *Rourea* from south-eastern Asia, such as *R. fulgens* and *R. mimosoides*, it has been noted that there is a strong morphological resemblance, both in overall similarity of the referred taxa and when particular species are compared (e.g. *R. glazioui* vs. *R. fulgens*). This suggests uncertainty regarding currently-accepted infrageneric classifications. Molecular-based phylogenies are, therefore, essential to achieve a better understanding on the classification, evolution and distribution of the genus.

Similarly, such molecular approaches could also be used to re-evaluate the morphological circumscription traditionally applied to *R.* subgen. *R.* sect. *Multifoliolatae*.

Acknowledgements

The authors thank FAPESP for supporting a large-scale project on Connaraceae (process number 2019/03173-0), CAPES for providing a scholarship to CAPT (process number 88882.329252/2018-01) and IAPT for the 2019 grant research conceded to the same author. This work was successfully developed thanks to the curators of BHCB, CEN, CVRD, SPF and UB herbaria who sent specimens for consultation. A special acknowledgement to Jefferson Prado and Gustavo Shimizu who helped with nomenclatural issues and Hans-Joachim Esser who kindly shared images of type specimens from M herbarium. The authors finally thank Máira Mezzacappa for the illustrations and Jair Faria and Thiago Flores for sharing photographs.

References

- Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181(1): 1–20. <https://doi.org/10.1111/boj.12385>
- Aublet JBCF (1775) *Histoire des Plantes de la Guiane Française* 1. P. F. Didot jeune, London/Paris, 1–621. <https://doi.org/10.1038/001052a0>
- Baillon HE (1869) *Connaracées. Histoire des Plantes* 2. Librairie Hachette, Paris, 1–20.

- Baker JG (1871) Connaraceae. In: Martius CFP von (Ed.) *Flora Brasiliensis* 14, pt. 2. R. Oldenbourg, Munich & Leipzig, 172–196.
- Blume CL von (1849) *Museum botanicum Lugduno-Batavum, sive, Stirpium exoticarum novarum vel minus cognitarum ex vivis aut siccis brevis expositio et descriptio* 1. E.J. Brill, Lugduni-Batavorum, 1–396. <https://doi.org/10.5962/bhl.title.274>
- de Candolle AP (1825) Connaraceae. *Prodromus systematis naturalis regni vegetabilis* 2. Sumptibus Sociorum Treuttel et Würtz, Paris, 84–87.
- Ellis B, Daly D, Hickey LJ, Kirk RJ, Mitchell J, Wilf P, Wing SL (2009) *Manual of Leaf Architecture*. Cornell University Press, New York, 1–190.
- ESRI (Environmental Systems Research Institute) (2016) ArcGIS Release 10.5. Environmental Systems Research Institute, Redlands, CA. <https://support.esri.com/es/Products/Desktop/arcgis-desktop/arcmap/10-5-1>
- Font Quer P (1953) *Diccionario de Botánica*. Ediora Labor S.A, Barcelona, 1–1244.
- Forero E (1976) A revision of the American species of *Rourea* subgenus *Rourea* (Connaraceae). *Memoirs of the New York Botanical Garden* 26(1): 1–119.
- Forero E (1983) Connaraceae. *Flora Neotropica Monograph* 36. New York Botanical Garden Press, New York, 1–208.
- Forero E (2003) Flora de Grão-Mogol, Minas Gerais: Connaraceae. *Boletim de Botânica da Universidade de São Paulo* 21(1): 235–236. <https://doi.org/10.11606/issn.2316-9052.v21i1p235-236>
- Forero E, Carbonó E, Vidal LA (1984) Nuevas especies de Connaraceae Neotropicales. *Revista Brasileira de Botanica. Brazilian Journal of Botany* 7(1): 65–77.
- Glaziou AFM (1906) *Plantae Brasiliae centralis a Glaziou lectae: liste des plantes du Brésil central recueillies em 1861–1895*. *Bulletin de la Société Botanique de France* 56, Mem. 3(b): 113–200. <https://doi.org/10.5962/bhl.title.4336>
- Jongkind CCH (1989) *Rourea* Aublet. In: Breteler FJ (Ed.) *The Connaraceae: A taxonomic study with emphasis on Africa*. Agricultural University Wageningen Papers, Wageningen, 310–368. <https://edepot.wur.nl/282394>
- Kuhlmann JG (1934) O gênero *Eichleria* sinônimo de *Rourea*. *Archivos do Instituto de Biologia Vegetal* 1: 39–40.
- Kuntze CEO (1891) *Revisio Generum Plantarum* 1. A. Felix, Leipzig; Dulau & Co., London; U. Hoepli, Milan; Gust. E. Stechert, New York, 1–374.
- Leenhouts PW (1958) Connaraceae. *Flora Malesiana* I 5(4): 495–541. <https://www.repository.naturalis.nl/document/570467>
- Lemmens RHMJ (1989a) Geographical distribution. In: Breteler FJ (Ed.) *The Connaraceae: A taxonomic study with emphasis on Africa*. Agricultural University Wageningen Papers, Wageningen, 11–13. <https://edepot.wur.nl/282394>
- Lemmens RHMJ (1989b) Phylogeny. In: Breteler FJ (Ed.) *The Connaraceae: A taxonomic study with emphasis on Africa*. Agricultural University Wageningen Papers, Wageningen, 103–116. <https://edepot.wur.nl/282394>
- Lemmens RHMJ, Breteler EJ, Jongkind CCH (2004) Connaraceae. In: Kubitzki K (Ed.) *The families and genera of vascular plants VI*. Springer, Berlin/Heidelberg/New York, 74–81. https://doi.org/10.1007/978-3-662-07257-8_9

- Planchon JE (1850) Prodrumus monographiae ordinis Connaracearum. *Linnaea* 23: 411–442.
- Progel A (1877) Oxalideae, Geraniaceae, Vivianiaceae. In: Martius CFP von (Ed.) *Flora Brasiliensis* 12(2): 473–528.
- Radford AE, Dickinson WC, Massey JR, Bell CR (1974) *Vascular plant systematic*. Harper & Row, New York, 1–70.
- Schellenberg G (1938) Connaraceae. In: Engler A (Ed.) *Das Pflanzenreich IV* (127) (Heft 103). W. Engelmann, Leipzig, 1–326.
- Thiers B (2020) [continuously updated]. *Index Herbariorum*. A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/> [accessed: 24 March 2020]
- Toledo CAP, Souza VC (2019) Two new species of *Rourea* (Connaraceae) from Minas Gerais, Brazil. *Phytotaxa* 408(2): 117–122. <https://doi.org/10.11646/phytotaxa.408.2.4>
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. *Regnum Vegetabile* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- Weberling F (1992) *Morphology of flowers and inflorescences*. Cambridge University Press, Cambridge, 1–348.

