

Octoblepharum peristomiruptum (Octoblepharaceae) a new species from the Neotropics

Noris Salazar Allen¹, José A. Gudiño¹

¹ Smithsonian Tropical Research Institute Apartado 0843-03092, Balboa, Ancón Panama, Panama

Corresponding author: Noris Salazar Allen (salazarn@si.edu)

Academic editor: M. von Konrat | Received 5 March 2020 | Accepted 31 August 2020 | Published 21 October 2020

Citation: Salazar Allen N, Gudiño JA (2020) *Octoblepharum peristomiruptum* (Octoblepharaceae) a new species from the Neotropics. PhytoKeys 164: 1–9. <https://doi.org/10.3897/phytokeys.164.51783>

Abstract

Octoblepharum peristomiruptum, a new species of moss in the family Octoblepharaceae from Panama and Brazil, is described and illustrated. The new species is characterised by plants with a reddish-purple colour particularly at the leaf bases, peristomes of eight teeth, each tooth composed of two rows of cells, fenestrate and usually completely separated at the base, strongly vertically striate-reticulate, some striations forked-like in shape. At the base of the teeth, some striations are horizontally orientated, poorly developed or absent, particularly on the cell wall that is rupturing in the separation of the vertical rows of the cells that form each tooth.

Keywords

Brazil, Bryophyta, fenestrate, Panama, peristome, reticulate

Introduction

Octoblepharum Hedw. is a widely-distributed moss genus that is found in tropical and subtropical regions. The genus was erected by J. Hedwig in his *Species Muscorum Frondosorum* in 1801. It was described to include plants with single peristomes of eight teeth, capsules with an apophysis and autoicous gametangia (*flos masculus femineo*) (Hedwig 1801). The name derives from the Greek words *okto* (ὀκτο: eight) and *blepharis* (βλεπηαρις: an eyelash), based on the eight peristome teeth of the type species, *O. albidum* Hedw., which was described from material collected by Swartz in Jamaica (Hedwig 1801). Of the 20 species recognised worldwide (see Salazar Allen and Chantanaorrapint 2018, for details on species distribution), eleven are reported for the

Neotropics (Salazar Allen 1991, 1992, 1994). These are *O. albidum*, *O. ampullaceum* Mitt., *O. costatum* H.A. Crum, *O. cocuiense* Mitt., *O. cylindricum* Schimp. ex Mont., *O. erectifolium* Mitt., *O. leucobryoides* O. Yano, *O. pulvinatum* (Dozy & Molk.) Mitt., *O. raphidostegium* Müll. Hal., *O. stramineum* Mitt. and *O. tatei* (Williams) E.B. Bartram. The report of *O. africanum* from Brazil (Yano 1992) is doubtful as illustrations of the peristome do not correspond to the peristome described in the protologue (Cardot 1899), nor those observed by the senior author at (H). The status of *O. costatum* is also doubtful: based on the description by Crum (1983), Frahm (1994) suggested that this species could be a synonym of *O. cocuiense*.

Our taxonomic revision of numerous (over 300) neotropical specimens, thought to represent the pantropical *O. albidum*, showed very similar gametophytic morphology, but significantly distinct peristome structure and ornamentation. After reviewing specimens of *O. albidum* from the Province of Coclé in Panama, Brazil and other countries and relevant literature (Cardot 1899; Yano 1992; Salazar Allen 1992, 1994; Salazar Allen and Tan 2010; Salazar Allen and Chantanaorrapint 2018), we concluded that the examined material from the said specimens from Coclé in Panama and Brazil represent an undescribed species, which we formally describe below as *Octoblepharum peristomiruptum*.

Materials and methods

From 2017–2019, we conducted morphological studies of fresh specimens from Panama and herbarium specimens from South America. Photographs of specimens in the field were taken with a LG K10, 2017 cell phone. Measurements of the morphological characters were made using a Leica-MZ6 stereomicroscope and an Olympus DPX50 light microscope. Microphotographs were obtained with an Olympus DP25 digital camera mounted on the latter microscope. Scanning electron micrographs (SEM) were made of samples from Panama and Brazil, following a modification of the methodology used by Salazar Allen (1993). Samples were viewed at different magnifications using a Zeiss Model Evo 40 vp SEM, with a backscattered electron detector and an acceleration voltage of 25 Kv, setting at the Smithsonian Tropical Research Institute (STRI), Panama. Digitised SEM images were post-processed and assembled in multipart figures using Adobe Photoshop.

Taxonomic treatment

Octoblepharum peristomiruptum Salazar Allen & Gudiño, sp. nov.

Figs 1–4

Diagnosis. *Octoblepharum peristomiruptum* is distinguished by its reddish to dark-purple coloured leaf bases, containing purple-coloured chlorocysts, with hyaline lamina 8–14 cells wide, unequally wide on each side of the costa, with purple cell walls, the exerted

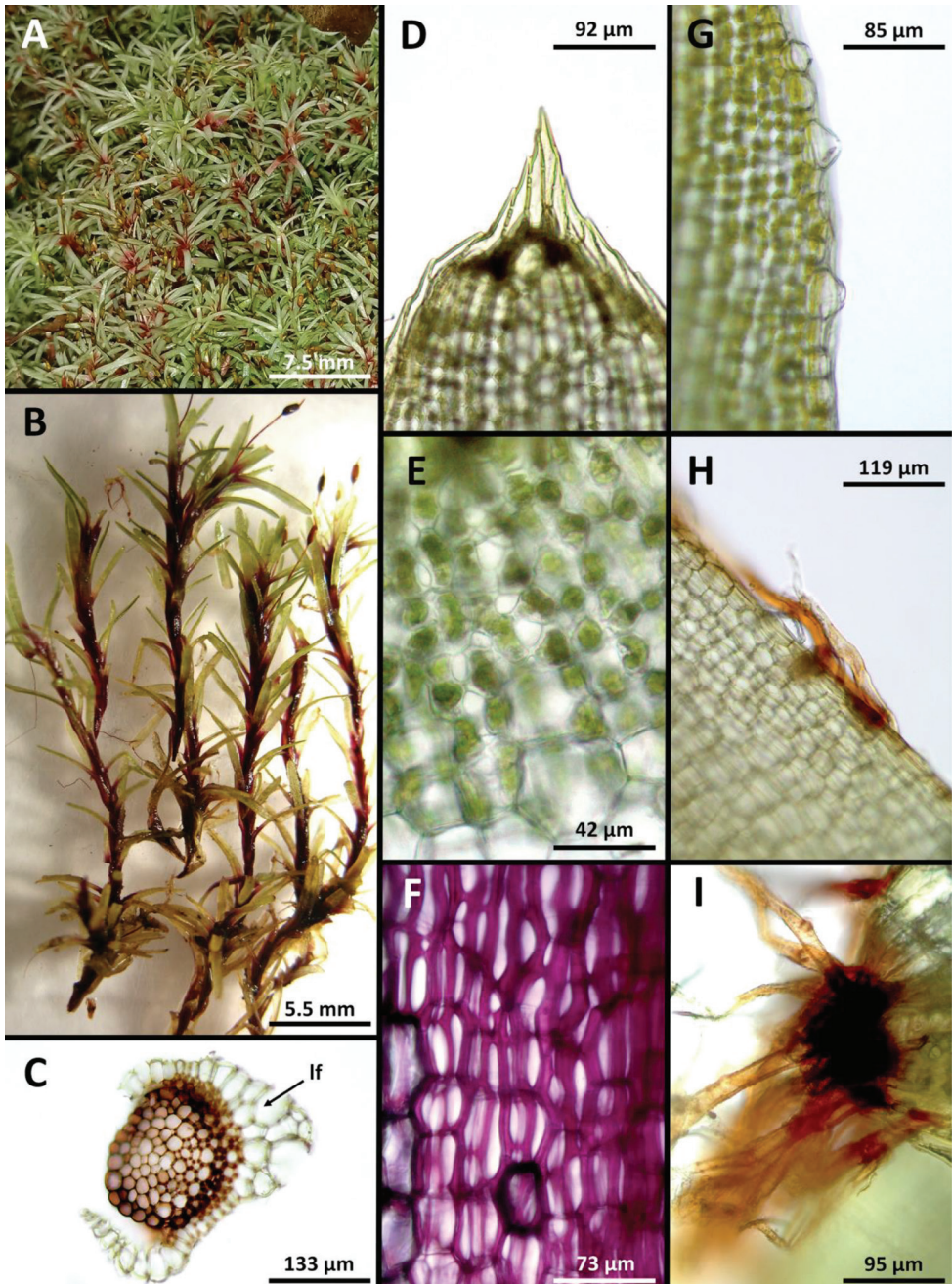


Figure 1. *Octoblepharum peristomiruptum* Salazar Allen & Gudiño. Photographs **A** habit in its natural environment **B** enlarged group of plants. Microphotographs **C** cross section of stem with young leaf (lf) **D** apex of leaf **E** chlorocysts near apex of leaf **F** chlorocysts at base of leaf (note the strong reddish-purple colouration) **G** enlarged hyalocysts on leaf border **H** rhizoids originating from border of leaf chlorocysts **I** rhizoids at apex of leaf. All from *Gudiño 3519* (PMA).

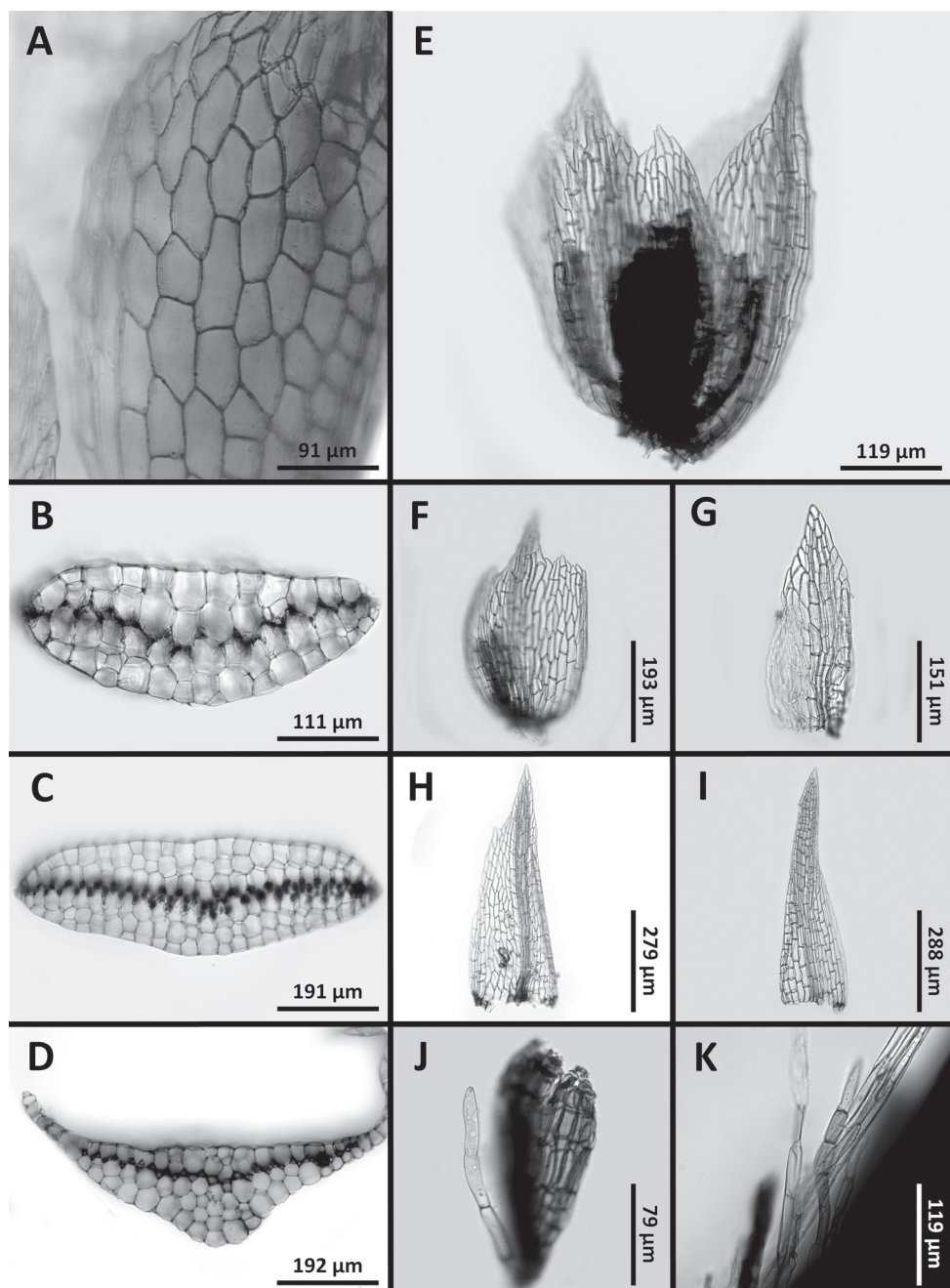


Figure 2. *Octoblepharum peristomiruptum* Salazar Allen & Gudiño. Microphotographs **A** leaf, hyaline lamina **B–D** cross sections of leaf **B** near apex **C** at mid-leaf **D** at base **E** androecium **F–I** male bracts **J** antheridium and paraphysis **K** paraphyses of gynoecium **A** taken from *Kuhlmann* 1621 (NY), **B–K** taken from *Gudiño* 3519 (PMA).

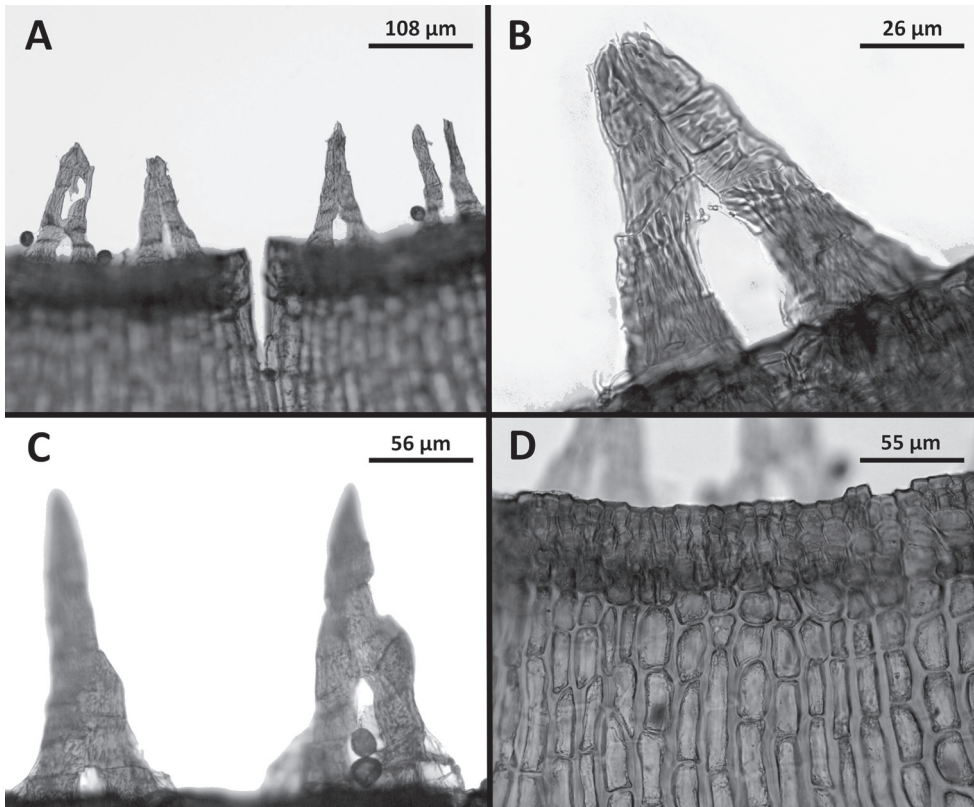


Figure 3. *Octoblepharum peristomiruptum* Salazar Allen & Gudiño. Microphotographs **A** four peristome teeth **B** dorsal view of peristome teeth with the two vertical rows of cells composing the teeth separating at base **C** two teeth with early and late separation of the two rows of cells **D** border and upper exothecial cells of capsule. **A, B, D** taken from *Occhioni* 668 (H), **C** taken from *Gudiño* 3519 (PMA).

cylindrical capsule with long rostrate operculum and eight strongly vertically striate-reticulate teeth with the two rows of cells forming each tooth frequently separated at base.

Type. PANAMA. Coclé: Distrito de Penonomé, above Chiguirí Arriba, Mariposario Cerro La Vieja, 8°39.88'N, 80°12.07'W, 360 m alt., 1 Jan 2019, *J.A. Gudiño* L. 3519 (holotype: PMA!; isotypes H!, NY!).

Description. *Plants* (2.3–)3.5–5.0 cm tall. *Stems* erect, lacking a central strand of differentiated cells and thick-walled border cells, slightly tomentose at base, branching monopodial (pseudodichotomous), innovations arising early, during development of sporophyte. *Rhizoids* dark orange-red, arising from stem and leaves. Leaves ligulate, dentate in distal half, smooth at base, erect to slightly reflexed in upper third, (4.0–)5.5–6.7(–8.0) mm long, (0.4–)0.5–1.2 mm wide at base, including hyaline lamina; apex apiculate, ending in an elongate cell flanked by 2 hexagonal cells; margins of leaf slightly undulate due to swollen hyalocysts, these single or in groups of 2–3 cells. *Limbidium* extending from leaf apex to mid-leaf, 2(–3) cells

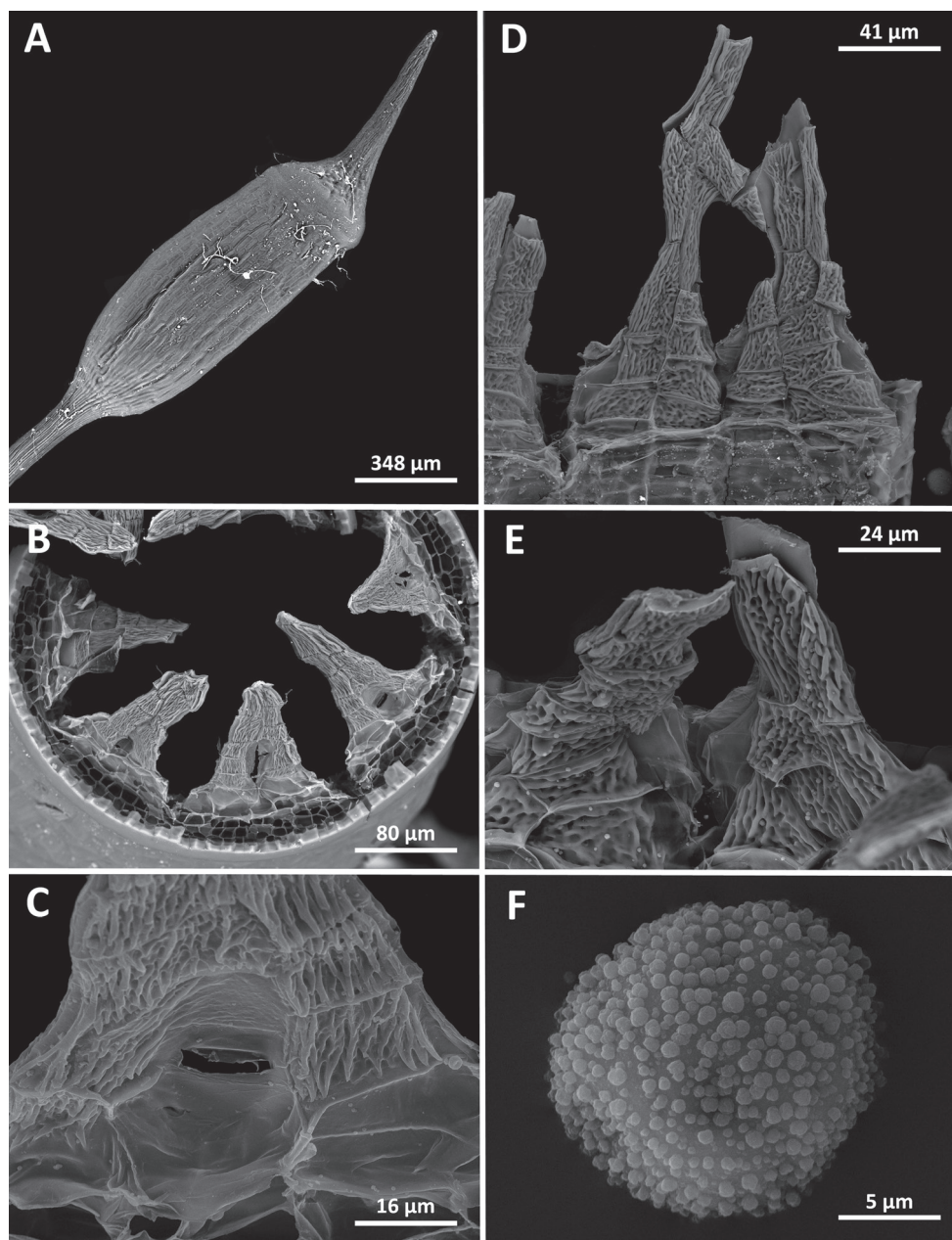


Figure 4. *Octoblepharum peristomirruptum* Salazar Allen & Gudiño. Scanning electron microscopy micrographs **A** sporophyte **B** peristome teeth dorsal view **C** close-up of rupturing wall **D** ventral view of two teeth **E** ventral view at base of two teeth **F** spore **A–C, E, F** taken from *Gudiño 3519* (PMA), **D** taken from *Strudwick & Sobel 3443* (NY).

wide, thinner at base. *Hyaline lamina* adpressed to stem, unistratose, composed of thin-walled pitted hyalocysts, the hyalocysts long and hexagonal at apex, hexagonal to pentagonal at mid-lamina next to costa and rectangular, quadrate and short

pentagonal basally. **Costa** in cross-section composed of ventral and dorsal porose hyalocysts supporting a unistratose, median network of small, thick-walled chlorocysts, in cross-section chlorocysts forming an irregularly zig-zag row, quadrate to triangular at base and triangular to tear-shaped above; the chlorocysts at leaf base, below hyaline lamina, surrounded by one layer of porose hyalocysts ventrally and three layers dorsally, at hyaline lamina hyalocysts in 1–2 rows ventrally and 4 rows dorsally, at mid-leaf in 3 layers ventrally and 3–4 layers dorsally, near apex 2 layers ventrally and two dorsally. **Autoicous**, perigonia axillary in short branches below the archegonia, antheridia surrounded by 5–7 small, mostly hyaline leaves (in some, only the central area of the leaf with chlorocysts), paraphyses 4–5 cells long with 1–2 brown basal cells, perichaetia terminal, archegonia with paraphyses to 10 cells long and with 1–2 short brown basal cells. **Setae** dark orange-red, smooth, sinistrorse, 4–5 mm long. **Capsules** dark red when mature, cylindrical (1.3–)1.6–2.0 mm long, the exothecial cells at mouth of capsule quadrate, dark red with slightly thickened transversal walls, at mid-capsule rectangular and quadrate with dark orange, thick longitudinal walls and thin transversal walls, (56–)80–92(–115) μm , becoming shorter towards mouth of capsule (26–)32–44 μm , phaneroporous stomata present at base of capsule. **Prostome** present. **Peristome** of eight elongate triangular teeth, inserted in mouth of capsule, each tooth composed of 2 rows of cells, basally fenestrate, strongly striate vertically, sometimes striations horizontally orientated at base and fading or absent in areas where separation of the rows of cells composing the tooth occurs. **Operculum** conic, long – rostrate, slightly curved. **Calyptra** cucullate, apex dark red, beige below. **Spores** brown, spheroid, densely gemmate, 14–16 μm .

Additional specimens examined (paratypes). Brazil. Pará: Belem, Museu Goeldi, 29 Aug 1927, *P. Occhioni* 668 (H), Belem, 13 Aug 1923, *J.G. Kulmann s.n.* (HBR-H), 1½ hr. upstream from Lageira airstrip, on Rio Maicuru, 0°55'S, 54°26'W, 243.84 m alt., 23 Jul 1981, *J.J. Strudwick & G.L. Sobel* 3443 (NY); Matto Grosso: Pacca Nova, affl. do Mamoré, 23 Sept 1923, *J.G. Kulmann* 516 (HBR-H).

Habitat, distribution and phenology. *Octoblepharum peristomiruptum* was found on the cortex of a shrub, at 2 m above soil level in a private butterfly garden in the Coclé Province, Panama. The site is on the edge of the road. The climate in this area is characterised by average temperatures ranging from 23–30 °C (<http://www.accuweather.com>, accessed Jan 2020). In Brazil, the plant was found in three sites, on a living tree trunk in the “Museu Goeldi” reserve in Belem (Pará), on the trunk of a palm tree in a forested area in Matto Grosso and on a living tree trunk in a seasonally-flooded (varzea) forest. It is distributed in southern and northern Brazil and Central America (Panama). Plants with sporophytes were collected in Panama in January and, in Brazil in July, August and September.

Eponymy. The species name refers to the character of the peristome teeth that rupture at base separating the two rows of cells that compose each tooth.

Conservation status. The new species has been found in Coclé Province, Panama in a private conservation site and in the State of Pará, Brazil, on trees in the garden of the “Museu Goeldi” that is considered a reserve site. The conservation status of the other collection sites in Brazil is unknown. It is most probable that the species also occurs in

other Central and South American countries. Given the limited knowledge of the current state of the sites where collections were made, the conservation status cannot be properly assessed. Thus, this new species is temporarily considered Data Deficient (DD).

Discussion

Octoblepharum peristomiruptum is characterised by its tall habit, reddish stems, leaves with a strong dark reddish-purple colour at the base, exserted setae, cylindrical capsules and eight vertically striate-reticulate peristome teeth, each with two rows of cells separating at the base. Amongst other *Octoblepharum* species with eight peristome teeth, some populations of *O. albidum* have slightly pink-coloured leaves, 4–6(–8) mm long, but with the peristome mostly smooth or faintly striate, unlike *O. peristomiruptum*. Furthermore, Salazar Allen (1992) reported another *O. albidum* specimen (Salazar # 6588) with red-purple leaves and strongly striate teeth with pronounced trabeculae, but this latter character is not present in *O. peristomiruptum*. Peristome teeth in most populations of *O. albidum* studied are solid, although sometimes they may have perforations at the base, as reported by Yano (1992). These perforations, however, are not as pronounced as those of *O. peristomiruptum*. Finally, the recent segregation of a new *Octoblepharum* species, previously included in *O. albidum* by Salazar Allen and Chantanaorrapint (2018), indicates that the specimen recorded in Salazar Allen (1992) needs further examination to ascertain its proper taxonomic status. *Octoblepharum albidum*, as currently construed, might comprise a complex of cryptic species sharing similar gametophytic morphology, but with distinctive peristome structures and ornamentation (Salazar Allen and Chantanaorrapint 2018).

Other species of *Octoblepharum* with eight peristome teeth are *O. ampullaceum*, *O. benitotanii* Salazar Allen & Chantanaorr., *O. cylindricum*, *O. erectifolium*, *O. pocsii* Magill & B.H. Allen and *O. raphidostegium*. Compared to *O. peristomiruptum*, the leaves of *O. ampullaceum* are longer (7–10 mm), tumid and the peristome is composed of eight pairs of slender, smooth teeth (Yano 1992). *Octoblepharum benitotanii*, an Asiatic species, has shorter leaves (4.5–5.5 mm) with a prominent apiculus and the peristome has teeth with strongly foveolate-reticulate ornamentation on both surfaces and faint trabeculae (Salazar Allen and Chantanaorrapint 2018). *Octoblepharum cylindricum* has longer leaves (6–12 mm) with a light pink colouration at the base, the sporophyte has a long seta (10–18 mm) and the peristome teeth have a thickened mid-line and prominent trabeculae (Salazar Allen 1994). *Octoblepharum erectifolium* gametophytes have longer (15–25 mm), fragile leaves (Yano 1992) and the sporophyte has a long seta (to 16 mm) and eight elongate peristome teeth with pronounced trabeculae and reticulate ornamentation (Salazar Allen 1994). *Octoblepharum pocsii* is an African species with longer leaves (10–13 mm) and a peristome of short, fragile and smooth teeth (Magill and Allen 2013). *Octoblepharum raphidostegium* is dioicous, rather than monoicous as in *O. peristomiruptum* and the other species discussed above and it has a peristome with faint vertical striations, prominent trabeculae and a thickened mid-line (Müller 1895).

Acknowledgements

The authors are grateful to STRI for research funds to Salazar Allen and to the following herbaria for loans of *Octoblepharum*: F, G, H, JE and NY. One of us (José Gudiño) took photos of the habit and prepared samples for SEM. Our deepest gratitude goes to J. Ceballos (STRI – SEM technician) for SEM micrographs and to I. A. Valdespino, A. Aiello and L.L. Forrest for revision of the manuscript and the English. Finally, we acknowledge support by the STRI Scientific Permit Office with revision and submission of the permit forms and to the Ministry of the Environment of Panama for collecting permits.

References

- Cardot J (1899) Nouvelle classification des Leucobryacées. *Revue Bryologique* 26: 1–6. https://data.bnf.fr/en/12342667/jules_cardot/
- Crum HA (1983) *Octoblepharum costatum*. In: Magdefrau K (Ed.) The bryophyte vegetation of the forests and paramos of Venezuela and Colombia. *Nova Hedwigia* 38: 1–54.
- Frahm J-P (1994) A contribution to the bryoflora of the Chocó region, Colombia. I. Mosses. *Tropical Bryology* 9: 89–110. <https://doi.org/10.11646/bde.9.1.13>
- Hedwig J (1801) Species muscorum frondosorum descriptae et tabulis aeneis XXXVII coloratis illustratae. Opus posthumum editum a Frederico Schwaegrichen Lipsiae [Leipzig], 50 pp. <https://doi.org/10.5962/bhl.title.26>
- Magill R, Allen BH (2013) *Octoblepharum pocsii*, sp. nov. a fragile- and long-leaved species in the *O. albidum* – complex from Africa. *Polish Botanical Journal* 58(1): 45–47. <https://doi.org/10.2478/pbj-2013-0004>
- Müller K (1895) *Octoblepharum raphidostegium* n.sp. In: Brotherus VF (Ed.) Beiträge zur Kenntniss der brasilianischen Mossflora. *Hedwigia* 34: 1–119.
- Salazar Allen N (1991) A preliminary treatment of the Central American species of *Octoblepharum* (Musci, Calymperaceae). *Tropical Bryology* 4: 85–97. <https://doi.org/10.11646/bde.4.1.10>
- Salazar Allen N (1992) Notas para la revisión de las especies de *Octoblepharum* del neotrópico. *Tropical Bryology* 6: 171–179. <https://doi.org/10.11646/bde.6.1.20>
- Salazar Allen N (1993) A Revision of the Pantropical Moss Genus *Leucophanes*. Brid. J. Cramer, Berlin, Germany, 281 pp.
- Salazar Allen N (1994) *Octoblepharum*. In: Allen BH (Ed.) Moss flora of Central America. Part 1. Sphagnaceae–Calymperaceae. Monographs in Systematic Botany, Missouri Botanical Garden 49: 182–189.
- Salazar Allen N, Chantanaorrapint S (2018) *Octoblepharum benitotanii* (Octoblepharaceae) a new species from the Old World tropics. *Philippine Journal of Systematic Biology* 12: 58–66. <https://doi.org/10.26757/pjsb.2018a12005>
- Salazar Allen N, Tan B (2010) *Octoblepharum arthrocormoides* (Calymperaceae) N. Salazar Allen & B.C. Tan, sp. nov., a new species from tropical Asia. *Botany* 88: 439–442. <https://doi.org/10.1139/B10-022>
- Yano O (1992) *Octoblepharum* Hedw. Leucobryaceae (Bryopsida) do Brasil. PhD Thesis, Universidade de São Paulo, Brazil, 158–160, 209–213.

Tongoloo arguta (Apiaceae), a new species from southwest China

Ling-Jian Gui¹, Jun Wen¹, Yan-Ping Xiao¹,
Ting Ren¹, Hong-Yi Zheng¹, Xing-Jin He¹

¹ Key laboratory of Bio-Resources and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, 610065, Chengdu, Sichuan, China

Corresponding author: Xing-Jin He (xjhe@scu.edu.cn)

Academic editor: Y. Mutaftchiev | Received 31 May 2020 | Accepted 9 September 2020 | Published 21 October 2020

Citation: Gui L-J, Wen J, Xiao Y-P, Ren T, Zheng H-Y, He X-J (2020) *Tongoloo arguta* (Apiaceae), a new species from southwest China. PhytoKeys 164: 11–19. <https://doi.org/10.3897/phytokeys.164.54927>

Abstract

A new species *Tongoloo arguta* (Apiaceae) is described and illustrated in this article. The new species grows in alpine bushes and meadows in south-western China. It resembles *T. silaifolia*, but differs from the latter by the length of the stem, ultimate segments of leaf and rays of the umbel. Phylogenetic analysis, based on nuclear ribosomal DNA internal transcribed spacer (ITS) sequences, is provided, as well as comparative morphology between related species.

Keywords

Apiaceae, China, new species, phylogeny, *Tongoloo*

Introduction

Tongoloo H. Wolff (Apiaceae) is a genus comprising about 15–20 species distributed mainly in southwest China, with a few species extending westwards to central Nepal (Watson 1999; Pan and Watson 2005; Zhou et al. 2009). *Tongoloo* species are characterised by having conic taproots, inflated and membranous leaf sheaths, cordate fruit base and filiform fruit ribs (Wolff 1925; Mukherjee and Constance 1991; Pimenov and Kljuykov 2000; Pan and Watson 2005). Some species have been described in *Pimpinella* L. due to the morphological similarity (Boissieu 1902, 1906). The genus *Tongoloo* was formally established by Wolff (1925) and accepted as an inde-

pendent genus (Pimenov and Kljuykov 1995; Pimenov 2017). Molecular phylogenetic analyses, based on limited materials of nuclear ribosomal DNA internal transcribed spacer (ITS) and chloroplast markers, indicated that *Tongoloa* is part of the East Asia clade of Apioideae (Apiaceae) (Zhou et al. 2009; Downie et al. 2010).

So far, 15 species of *Tongoloa* have been identified from different regions of China (Pimenov 2017), most of which being known from the Hengduan Mountains. While studying specimens in herbariums (CDBI, PE), we noticed several interesting specimens of *Tongoloa* collected from Sichuan and Yunnan, which have short stems and fewer rays of the umbel (3–8). Through field investigation and anatomical study, we confirmed that this species does not match any previously-published description of *Tongoloa* found from southwest China to central Himalaya. Further molecular analysis revealed significant differences between this species and its relatives. The results allow us to infer that these newly-collected specimens from Sichuan and Yunnan belong to a new species.

Materials and methods

We collected an unknown *Tongoloa* species from several populations in Yunnan and Sichuan Provinces. In addition to the samples collected in the field, the type specimens of *Tongoloa* and high-resolution type specimen photos were examined, including the specimens deposited in K, P, E, B, A, GB, LD, MW, NY, GH, W, US, PE, KUN, CDBI, WUK and HNWP. Considering the similarity between the new species and *T. silaifolia*, as well as other related species, we compared their morphological characteristics. The fresh fruits were preserved with formaldehyde-acetic acid-alcohol (FAA) for anatomical study. The mericarp transverse sections were examined using a stereomicroscope (Nikon SMZ25, Japan) after safranin O-fast green staining.

A plant genomic DNA kit (CWBIO, China) was used to extract total DNA from silica-dried leaves. Referring to the previous studies (White et al. 1990; Zhou et al. 2009), we used nuclear ribosomal DNA internal transcribed spacer (ITS) sequences for phylogenetic inference. Amplification was undertaken using a volume of 30 µl with 15 µl 2 × Taq MasterMix (CWBIO, China), 10 µl ddH₂O, 1.5 µl forward primer, 1.5 µl reverse primer and 2 µl total DNA. The PCR reaction was performed in Geneamp PCR System 9700 (USA) with initial denaturation at 95 °C for 2 min, 35 cycles of 94 °C for 60 s, 52.5 °C for 45 s and 72 °C for 60 s and a final extension of 72 °C for 7 min. PCR products were sent to BGI (China) for sequencing. The GenBank accession numbers and sample information of the ITS sequences used in this study are shown in Table 1.

To determine the systematic position of the new species, 37 ITS sequences with accession numbers were obtained from GenBank, including 9 species of *Tongoloa* (Table 1). Taxa of *Chamaesium* clade were selected as the outgroup (Downie et al. 2010). Maximum Likelihood (ML) analyses with GTR + G + I model and 1000 bootstrap (BS) replicates was performed using MEGA7 (Kumar et al. 2016). Bayesian Inference (BI) analysis was conducted with MrBayes version 3.2 (Ronquist et al. 2012) and the Markov Chain Monte Carlo (MCMC) search was performed for 1 × 10⁸ generations.

Table 1. Taxa and voucher information of the used ITS sequences.

Taxon	Locality	Voucher information	GenBank number
<i>Bupleurum chinense</i>	China, Anhui, Dabieshan	CB Wang 09017 (SZ)	GU570615
<i>Bupleurum gibraltaricum</i>	Spain, Sevilla	S.S. Neves 35 (E)	AF479851.1
<i>Bupleurum tenuissimum</i>	Portugal, Beira Litoral	S.S. Neves 22 (E)	AF481932.1
<i>Chamaesium paradoxum</i>	China, Sichuan, Daocheng-Litang	ZJ0560 (KUN)	EU236161.1
<i>Chamaesium thalictrifolium</i>	China, Sichuan, Zhangla-Caowan	ZJ0607 (KUN)	EU236162.1
<i>Chamaesium wolffianum</i>	China, Yunnan, Shudu Lake	ZJ0525 (KUN)	EU236163.1
<i>Changium smyrnioides</i>	China, Jiangxi, Jiujiang, Pengze	PZ2 (NAS)	HQ185254.1
<i>Chuanminshen violaceum</i>	China, Sichuan, Cangxi, Xinlong nursery	J105 (KUN)	FJ385040.1
<i>Cyclorhiza peucedanifolia</i>	China, Yunnan, YuLong, Daju, Xiahutiao	J034 (KUN)	FJ385042.1
<i>Cyclorhiza waltonii</i>	China, Sichuan, Derong	ZJ0536 (KUN)	EU236165.1
<i>Hansenia forbesii</i>	China	QH6	KJ999463.1
<i>Hansenia oviformis</i>	China, Qinghai, Maqin	H43 (WNU)	MF787544.1
<i>Hansenia weberbaueriana</i>	China, Yunnan, KIB nursery	ZJ0697 (KUN)	EU236180.1
<i>Haplophaera phaea</i>	China, Yunnan, Shudu Lake	ZJ0521 (KUN)	EU236167.1
<i>Hepaptera anisoptera</i>	Iran, Lorestan	Pimenov et al. 438 (MW)	AY941273.1, AY941301.1
<i>Hymenidium nanum</i>	Kirghizstan, Sarydzhas basin	Kozhevnikova s.n. (LE)	GQ379333.1
<i>Hymenolaena candollei</i>	India, Jammu and Kashmir	Pimenov and Kljuykov 59 (MW)	FJ469958.1, FJ483497.1
<i>Hymenolaena badachschanica</i>	Tadjikistan, Badakhshan, Andarob	Sultanov 1121 (LE)	GQ379332.1
<i>Hymenolaena pimpinellifolia</i>	Kirghizia, Kyrgyz Alatau	Pimenov 398 (MW)	FJ469959.1, FJ483498.1
<i>Komarovia anisosperma</i>	Uzbekistan, Zeravscshtan	178(MW)	AF077897.1
<i>Phyospermopsis delavayi</i>	China, Yunnan, YuLong Snow Mt.	J033 (KUN)	FJ385056.1
<i>Pleurospermum amabile</i>	China, Yunnan, Deqin, Baimaxueshan	GLJ19100605 (SZ)	MT124614
<i>Pleurospermum franchetianum</i>	China, Sichuan	YY (WNU)	KY848849.1
<i>Pleurospermum violense</i>	China, Liaoning	LQX031 (NAS)	JF977839.1
<i>Pterocyclus angelicoides</i>	China, Xizang	G19082501(SZ)	MN689078
<i>Pterocyclus rotundatus</i>	China	G18092501-1 (SZ)	MK078059.1
<i>Sinolimprichtia alpina</i> YN	China, Yunnan, Deqin, Baimaxueshan	GLJ19100702 (SZ)	MT124613
<i>S. alpina</i> XZ	China, Xizang	0465919 (KUN)	FJ385064.1
<i>S. alpina</i> SC	China, Sichuan, Yajiang, Jianziwanshan	LH2018081402 (SZ)	MT124609
<i>Tongoloo arguta</i> YN1	China, Yunnan, Shangri-la, Daxueshan	A11 (SZ)	MT124619
<i>T. arguta</i> YN2	China, Yunnan, Deqin, Baimaxueshan	GLJ18082102 (SZ)	MT124599
<i>T. arguta</i> SC1	China, Sichuan, Yajiang, Kazilashan	GLJ18092002 (SZ)	MT124615
<i>T. arguta</i> SC2	China, Sichuan, Yajiang, Jianziwanshan	GLJ19092802 (SZ)	MT124612
<i>Tongoloo dunni</i>	China, Hubei, Shennongjia	GLJ18091102 (SZ)	MT124601
<i>Tongoloo elata</i>	China, Sichuan, Songpan, Huangshengguan	GLJ19080404 (SZ)	MT124607
<i>Tongoloo loloensis</i>	China, Yunnan, Eryuan, Baicaluo	GLJ18103002_1 (SZ)	MN630615
<i>Tongoloo stewardii</i>	China, Fujian, Taining, Huangyanfeng	GLJ18090802_2 (SZ)	MN630614
<i>Tongoloo silaifolia</i>	China, Chongqing, Chengkou	JQP19081607_2 (SZ)	MT124617
<i>Tongoloo</i> sp.	China, Qinghai, Yushu, Jiangxigou	GLJ19092201 (SZ)	MT124610
<i>Tongoloo taeniophylla</i>	China, Sichuan, Kangding, Paomashan	GLJ18082902 (SZ)	MT124598
<i>Tongoloo tenuifolia</i>	China, Yunnan, YuLong Snow Mt.	J075 (KUN)	FJ385066.1
<i>Trachydium roylei</i>	Pakistan, Hazara	B. Dickore, 13244	FJ469972.1, FJ483510.1
<i>Trachydium simplicifolium</i>	China, Yunnan, Lijiang, Yulongxueshan	GLJ19111401 (SZ)	MT124618
<i>Trachydium souliei</i> YN1	China, Yunnan, Deqin, Baimaxueshan	GLJ18082103 (SZ)	MT124603
<i>T. souliei</i> YN2	China, Yunnan, NW part, Degen Co.	Pimenov et al. 472 (MW)	FJ469973.1, FJ483511.1

Note: Province's names were indicated near the manes of the species if two or several different samples were used for the molecular analysis. YN = Yunnan, SC = Sichuan, XZ = Xizang (Tibet).

Results and discussion

Phylogenetic analysis

The total length of ITS sequence alignment with gaps was 467 bp (without 5.8S rDNA genes). *Tongoloo arguta* yielded high sequence divergence values with related species, such as *T. silaifolia* (3.2%–4.0%), *T. elata* (3.7%–4.6%) and *T. taeniophylla* (5.0%–5.5%). Analysis of the data using ML and BI methods obtained similar trees with high ML BS and BI posterior probability (PP). Phylogeny reconstruction showed that *T. arguta* positioned in the *Tongoloo* clade and different populations of this species formed a strongly-supported monophyletic group (ML BS $\geq$ 90% and BI PP $\geq$ 0.90) (Fig. 1).

These results supported *T. arguta* as an undescribed and distinct species of *Tongoloo*.

Taxonomy treatment

Tongoloo arguta L.J.Gui & X.J.He, sp. nov.

urn:lsid:ipni.org:names:77212299-1

Figs 2, 3, Table 2

Type. CHINA. Sichuan: Kangding, Zheduoshan Pass, 4300 m alt., 30°4'N, 101°48'E, 26 Sep 2019, *Lingjian Gui* GLJ19092601 (**holotype**: SZ).

Diagnosis. *Tongoloo arguta* sp. nov. is morphologically similar to *T. silaifolia*. However, the new species can be distinguished from the latter by its short stems (10–50 cm), while *T. silaifolia* has longer ones (28–60 cm); The ultimate segments of the lower leaf of *T. arguta* are acute and short (1–4 mm), while those of *T. silaifolia* are linear and longer (5–18 mm). The umbels of *T. arguta* have 3–8 rays, which are significantly less than those of *T. silaifolia* (8–22).

Description. Plants 10–50 cm. Root usually long-conic. Stem thinly ribbed, glabrous, purplish to green, branched. Leaf sheaths inflated, membranous; blade triangular in outline, 3–5 × 2–3.5 cm, 2–3-ternate/pinnate; ultimate segments lanceolate, 1–4 × 1–2 mm, apex acute. Umbels terminal or lateral; bracts often absent or sometimes 1, leaf-like, ca. 2–4 × 1 cm, bracteoles absent; rays 3–8; umbellules 13–25-flowered. Calyx teeth minute; petals obovate, white to purple, apex obtuse; stylopodium depressed, dark purple; styles short, reflexed. Fruit broadly ovoid, ca. 2 × 1.7 mm, base cordate; ribs 5, filiform; vittae 3 in each furrow, ca. 4 on commissure. Ventral surface of endosperm slightly concave to plane.

Etymology. The species epithet “arguta” was given to describe the acute tips of the ultimate segments of leaves.

Phenology. The species was observed flowering from August to September and fruiting from September to October.

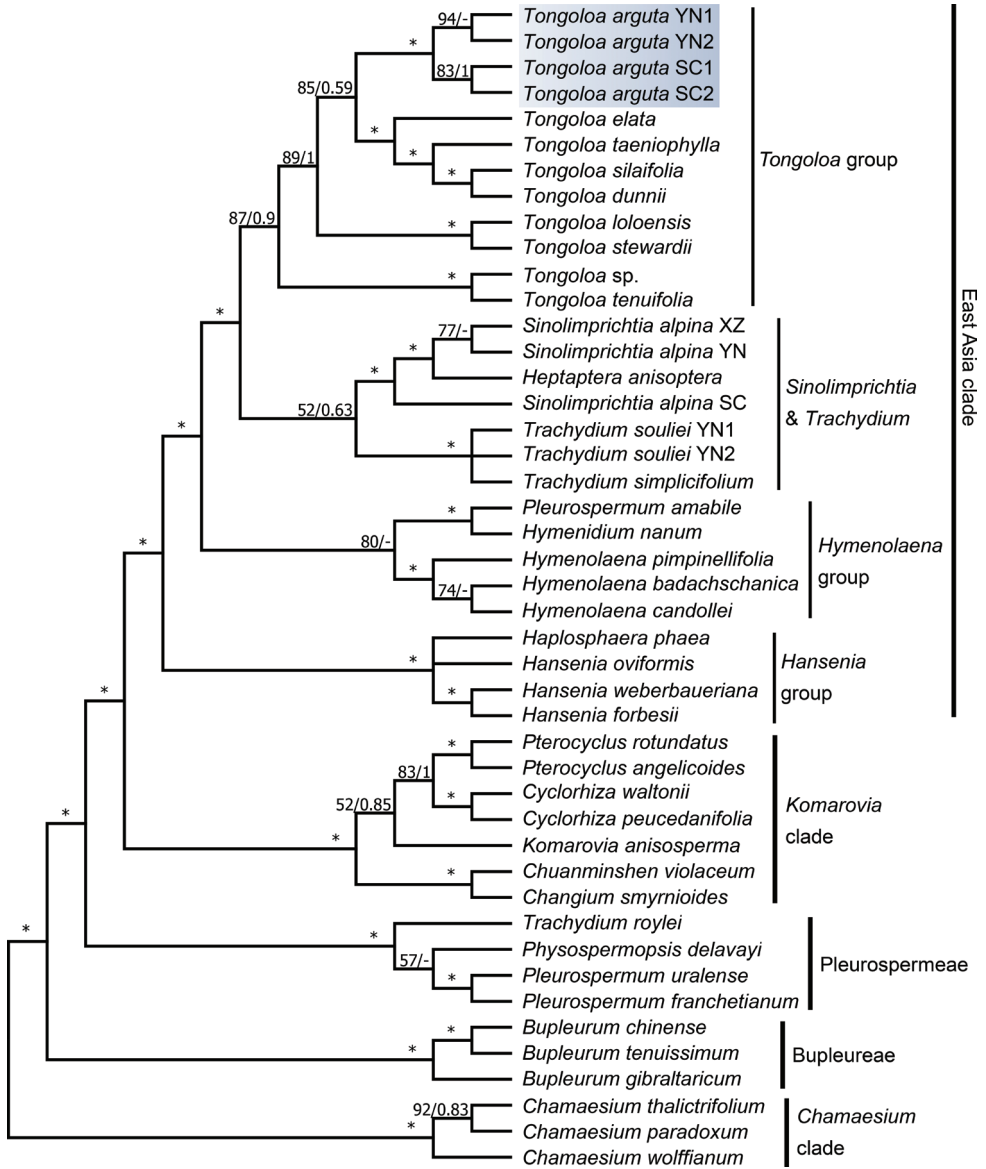


Figure 1. Phylogenetic tree of *Tongoloa* and related groups inferred from ITS based on ML and BI methods. ML BS / BI PP values were shown above the branches. Asterisks (*) denoted strong support (ML BS $\geq$ 90% and BI PP $\geq$ 0.90).

Distribution and habitat. *Tongoloa arguta* is distributed from Sichuan (Kangding, Yajing) to Yunnan (Deqin, Shangri-la) in south-western China. It grows in alpine bushes and meadows from 4000 m up to 4500 m alt.

Additional specimens examined. CHINA. Sichuan: Kangding, Xinduqiao, Zheduoshan, 4000 m alt., 3 Sep 1982, *Taichang Wei* 29664 (CDBI0095011);

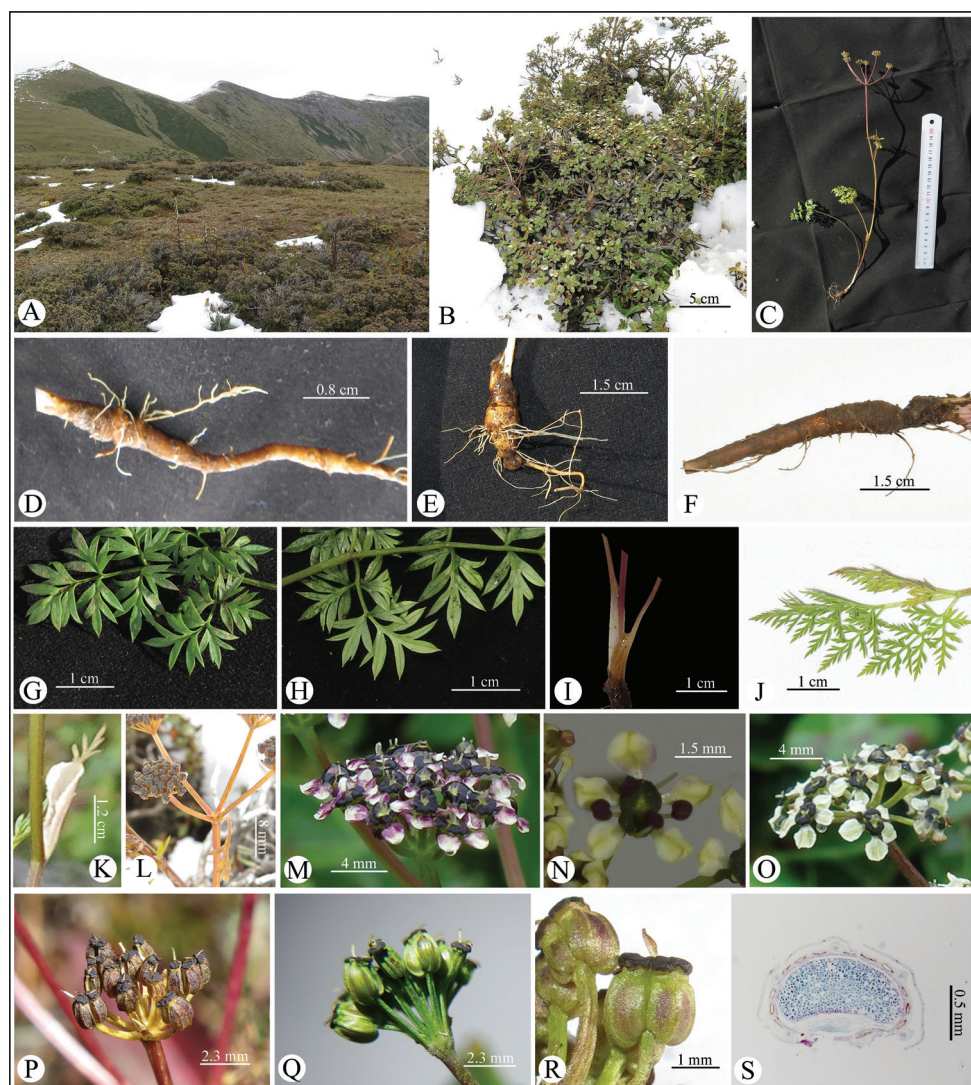


Figure 2. *Tongoloa arguta* sp. nov. **A** species habitat (Mt. Jianziwanshan, Sichuan, China) **B** plant in the bush surrounded by snow **C** plant **D–F** roots **G, H** basal leaf, ventral and dorsal view **I** membranous sheath of basal leaves **J** middle leaf **K** upper leaf with membranous petiole **L** umbel and bract **M–O** flowers; **P–R** fruits **S** mericarp transverse section.

Kangding, north slope of Zheduoshan, 4000 m alt., 22 Sep 1984, *Yongjiang Li* 454 (CDBI0172327); Yajiang County, Jianziwanshan, 4400 m alt., 28 Sep 2019, *Lingjian Gui & Chang Peng* GLJ19092802 (SZ); Yajiang County, Kazilashan, 4400 m alt., 20 Sep 2018, *Lingjian Gui* GLJ18092002 (SZ). Yunnan: Deqin County, Baimaxueshan pass, 4350 m alt., 21 Aug 2018, *Lingjian Gui* GLJ18082102 (SZ); Shangri-la, Daxueshan pass, 4340 m alt., *Yanping Xiao* A11 (SZ); Zhongdian, Deqin, Beima Shan, on the south side of road, 4675 m alt., 25 Sep 1994, *ACE* 1287 (PE00755697).

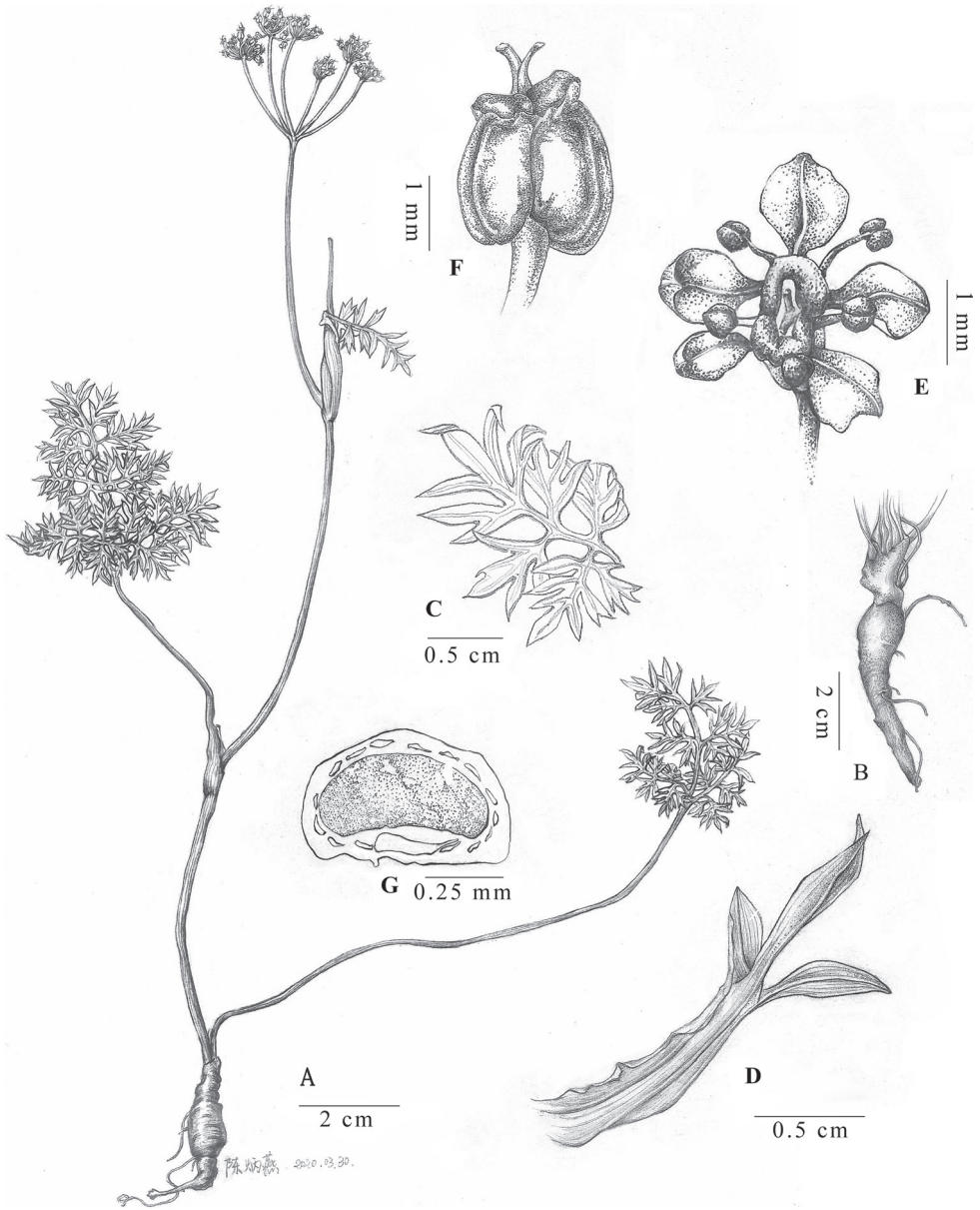


Figure 3. *Tongoloa arguta* sp. nov. **A** habit **B** root **C** basal leaf blade **D** leaf-like bract, only appears in some individuals **E** flower **F** fruit **G** mericarp transverse section. Drawn by Bing-yan Chen.

Conservation status. *Tongoloa arguta* is common in some alpine bushes and meadows at an altitude of about 4300 m in Yunnan and Sichuan, where human activities and especially yak grazing pose a potential threat to its survival. We categorise *T. arguta* as Near Threatened (NT), according to IUCN (2019).

Table 2. Morphological comparison between *Tongoloa arguta* and similar species.

Characters	<i>T. arguta</i>	<i>T. silaifolia</i>	<i>T. elata</i>	<i>T. gracilis</i>
Height	10–50 cm	28–60 cm	20–75 cm	25–75 cm
Root	long-conic	conic	conic	slender
Stem	purplish	purplish	purplish	purplish
Lower leaves	2–3-ternate/pinnate, ultimate segments lanceolate, 1–4 mm, apex acute	2–3-ternate/pinnate, ultimate segments linear, 5–18 mm, apex acute	3–4-ternate/pinnate, ultimate segments linear, 5–15 mm	3-ternate/pinnate, ultimate segments linear-lanceolate, 3–15 mm
Bracts	often absent, sometimes 1, leaf-like	absent	absent	absent
Bracteoles	absent	usually absent or 1–5, linear	absent	absent
Rays	3–8	8–22	6–16	5–11
Petal	apex obtuse	apex obtuse	apex obtuse-rounded	apex with incurved tips
Fruit	broadly ovoid	broadly ovoid	broadly ovoid	oblong-ellipsoid
Ribs	filiform	filiform	slender	filiform

Acknowledgements

The authors thank Alexander P. Sukhorukov for his assistance in revising this paper. Thanks to Bing-yan Chen for her drawing and Wei Gou for his assistance in collecting literature. This research was supported by the National Natural Science Foundation of China (Grant No. 31872647), the Chinese Ministry of Science and Technology through the “National Science and Technology Infrastructure Platform” project (Grant No. 2005DKA21403-JK), Sichuan Science and Technology Program (Grant No. 2018TJPT0027) and the fourth national survey of traditional Chinese medicine resources (Grant No. 2019PC002).

References

Boissieu HD (1902) Note sur quelques Ombellifères de Chine d’après les collections du Muséum d’Histoire naturelle de Paris. Bulletin de l’Herbier Boissier 2(2): 801–810.

Boissieu HD (1906) Note sur quelques Ombellifères de la Chine, d’après les collections du Muséum d’Histoire naturelle de Paris. Bulletin de la Société Botanique de France 53(6): 418–437. <https://doi.org/10.1080/00378941.1906.10831189>

Downie SR, Spalik K, Katz-Downie DS, Reduron JP (2010) Major clades within Apiaceae subfamily Apioideae as inferred by phylogenetic analysis of nrDNA ITS sequences. Plant Diversity and Evolution 128(1–2): 111–136. <https://doi.org/10.1127/1869-6155/2010/0128-0005>

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee, Cambridge. <https://www.iucn-redlist.org/resources/redlistguidelines>

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. Molecular Biology and Evolution 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>

- Mukherjee PK, Constance L (1991) New taxa and transfers in Indian Umbelliferae. *Edinburgh Journal of Botany* 48(1): 41–44. <https://doi.org/10.1017/S0960428600003589>
- Pan ZH, Watson MF (2005) *Tongoloa*. In: Wu ZY, Peter HR, Hong DY (Eds) *Flora of China*, Vol. 14. Science Press & Missouri Botanical Garden Press, 34–37.
- Pimenov MG (2017) Updated checklist of Chinese Umbelliferae: Nomenclature, synonymy, typification, distribution, distribution. *Turczaninowia* 20(2): 106–239. <https://doi.org/10.14258/turczaninowia.20.2.9>
- Pimenov MG, Kljuykov EV (1995) Notes on Himalayan *Schulzia* (Umbelliferae). *Kew Bulletin* 50(3): 637–644. <https://doi.org/10.2307/4110340>
- Pimenov MG, Kljuykov EV (2000) Taxonomic revision of *Pleurospermum* Hoffm. and related genera of Umbelliferae II. The genera *Pleurospermum*, *Pterocyclus*, *Trachydium*, *Keraymonia*, *Pseudotrachydium*, *Aulacospermum*, and *Hymenolaena*. *Feddes Repertorium* 111(7–8): 517–534. <https://doi.org/10.1002/fedr.4911110718>
- Ronquist F, Teslenko M, Mark PVD, 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>
- Watson MF (1999) *Tongoloa*. In: Grierson AJC, Long DG (Eds) *Flora of Bhutan*, Vol. 2, Part 2. Royal Botanic Garden Edinburgh and Royal Government of Bhutan, 478–479.
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR Protocols: A Guide to Methods and Applications*. Academic Press Inc, San Diego, 315–322. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>
- Wolff H (1925) Neue Umbelliferen-Gattung aus Ostasien. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9(84): 275–280. <https://doi.org/10.2307/3994550>
- Zhou J, Gong X, Downie SR, Peng H (2009) Towards a more robust molecular phylogeny of Chinese Apiaceae subfamily Apioideae: Additional evidence from nrDNA ITS and cp-DNA intron (*rpl16* and *rps16*) sequences. *Molecular Phylogenetics and Evolution* 53(1): 56–68. <https://doi.org/10.1016/j.ympev.2009.05.029>

A new synonym from Hawaii and lectotypification of *Plagiothecium longisetum* (Plagiotheciaceae)

Grzegorz J. Wolski¹, Jarosław Proćków²

1 Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Lodz, ul. Banacha 12/16, 90-237 Lodz, Poland **2** Department of Plant Biology, Institute of Biology, Faculty of Biology and Animal Science, Wrocław University of Environmental and Life Sciences, ul. Kozuchowska 7a, 51-631 Wrocław, Poland

Corresponding author: Grzegorz J. Wolski (grzegorz.wolski@biol.uni.lodz.pl)

Academic editor: Matt Renner | Received 16 July 2020 | Accepted 8 September 2020 | Published 21 October 2020

Citation: Wolski GJ, Proćków J (2020) A new synonym from Hawaii and lectotypification of *Plagiothecium longisetum* (Plagiotheciaceae). *PhytoKeys* 164: 21–31. <https://doi.org/10.3897/phytokeys.164.56612>

Abstract

Plagiothecium mauiense was first described in 1927 by V.F. Brotherus, based on materials from Hawaii. It has, so far been, treated as a separate species. A detailed analysis of the original material housed in the New York Botanical Garden Herbarium (NY01256708) found the specimen to be characterised by a lack of metallic lustre; concave, asymmetrical, lanceolate to lanceolate-ovate leaves, shrunken in their dry condition; a straight, not denticulate, acute to apiculate apex; elongate-hexagonal cells in irregular transverse rows, 101–131 × 15–21 µm at mid-leaf; very lax areolation, with decurrencies composed of three rows of cells. These characteristics indicate that this species is identical to the original material of *P. longisetum* (e.g. H-SOL 1563 011; PC0132572). Hence, we propose that *P. mauiense* should be recognised as a new synonym of *P. longisetum*. In addition, a review of *P. longisetum* syntypes found one (H-SOL 1563 011) to have the same date of collection as the protologue, and to possess a quite abundant gametophyte turf with well-preserved sporophytes, indicating it to be fertile. Considering the above, we propose that specimen H-SOL 1563 011 be designated the lectotype of *P. longisetum*.

Keywords

Codes of Botanical Nomenclature, *Orthophyllum* section, *Plagiothecium*, *Plagiothecium mauiense*, *Plagiothecium nemorale*, typification

Introduction

In this paper we demonstrate that all the characteristics of the original material of *P. mauiense* Broth. are identical to those of the *P. longisetum* Lindb. type. Hence, we propose *P. mauiense* as a new synonym of *P. longisetum*. In addition, among the three syntypes of *P. longisetum*, we propose the specimen (H-SOL 1563 011) deposited at the Herbarium of the University of Helsinki (Finland) as the lectotype of this name. The aim of the work is to demonstrate that *P. mauiense* and *P. longisetum* are synonyms, and to propose a lectotype for the name of the latter.

The study was based on herbarium specimens analysed during research conducted at the NY Herbarium (The New York Botanical Garden, New York, U.S.A.) from November to December 2018 and November to December 2019, as well as at the PC Herbarium (Muséum National d'Histoire Naturelle, Paris, France) in January 2019; and on specimens loaned from the H Herbarium (The University of Helsinki, Helsinki, Finland). However, due to renovation ongoing at the S Herbarium (The Swedish Museum of Natural History, Stockholm, Sweden) and the temporary closure of some herbaria, some less important specimens could not be examined; despite this, they are cited in the manuscript to present the most complete dataset possible. Specimens that were analysed directly were marked with an exclamation mark.

Plagiothecium mauiense account

In *Hawaiian Mosses*, V.F. Brotherus described a new species, *Plagiothecium mauiense*, based on materials collected by D.D. Baldwin from Hawaii (Brotherus 1927). In the diagnosis, the author indicated that, among others, the plant was relatively large, soft with a thick, light green to yellow green turf (“*robustiusculum, caespitosum, caespitibus, densiusculis, mollibus, lutescenti-viridibus*”); with loosely-arranged and complanate-foliate (“*laxiscule et complanate foliosus*”), decurrent (“*folia haud decurrentia*”), concave (“*concaviuscula*”), asymmetrical (“*asymmetrica*”), long-ovate leaves (“*ovate-oblong [sic.]*”); the leaf apex was short, acute to acuminate (“*breviter acumianta, acuta vel subula brevissima terminata*”); the leaves were 2.25 mm long and 1.1 mm wide (“*ad 2.25 mm longa et ad 1.1 mm lata, integra*”), costae were short and thin (“*nervis binis, brevibus, tenuibus*”); cells at mid-leaf are 12–15 × 75–100 µm (“*cellulis medianis folii 12–15 µm longis et 75–100 µm latis*”) (Brotherus 1927). Additionally, Brotherus (1927) added that the species *P. mauiense* was similar to *P. sylvaticum* (Brid.) Schimp., however, its cell areolation was narrower.

During the revision of *Plagiothecium nemorale sensu lato*, the original materials collected by D.D. Baldwin from Hawaii were found in four herbaria: Harvard University Herbarium (FH00220142), New York Botanical Garden Herbarium (NY01256708), Miami University Herbarium (MU 000000546), and Yale University Herbarium (YU 233890). On the envelopes of two specimens, from the MU and NY Herbaria, notes indicating them to be isotypes of *P. mauiense* were also found. In 1967, a similar note was added to the specimen from the NY Herbarium (NY01256708) by H.A. Miller, who studied this material (Fig. 1). Since that time, this specimen has served as the “iso-

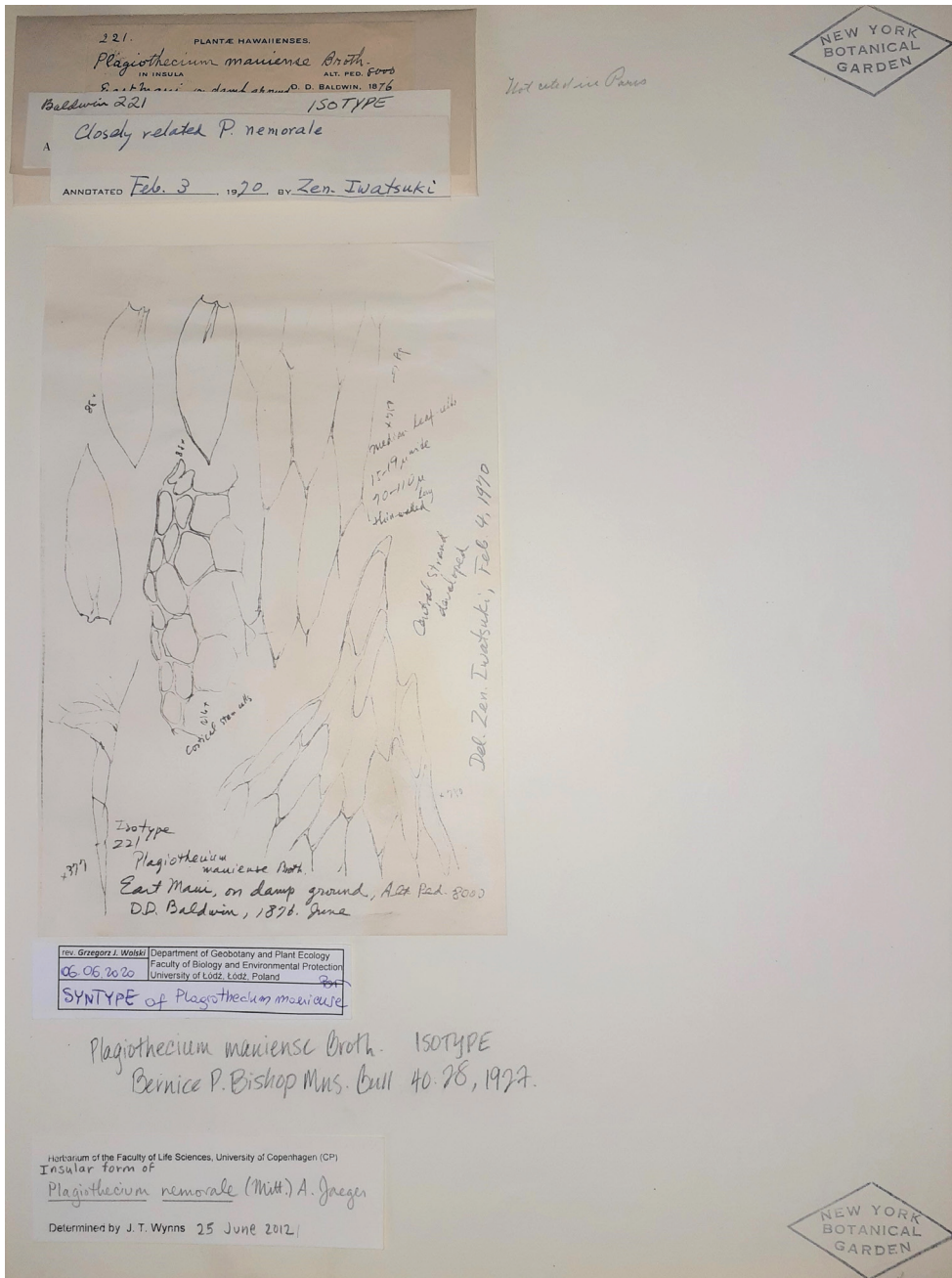


Figure 1. The syntype of *P. mauiense* (NY01256708) housed at the NY Herbarium.

type” (e.g. in the database of the Consortium of North American Bryophyte Herbaria, <https://bryophyteportal.org/portal/> – access: May 2020).

However, given the above, and according to Article 9.6 of the *Shenzhen Code* (Turland et al. 2018) stating that “A syntype is any specimen cited in the proto-

logue when there is no holotype, or any one of two or more specimens simultaneously designated in the protologue as types” as well as Article 40.2 (Note 1) stating that “When the type is indicated by reference to an entire gathering, or a part thereof, that consists of more than one specimen, those specimens are syntypes (see Art. 9.6.)”, all the above-mentioned original specimens of *P. mauiense* should be regarded as syntypes.

Three years later, on April 3, 1970, following a study by H.A. Miller, Z. Iwatsuki analysed the same material (NY01256708) and attached a note (dated April 4, 1970) to the examined specimen, together with hand-drawn pictures of its gametophyte (Fig. 1). Based on the remaining notes, it appears that Iwatsuki characterised the material as follows: stems with a developed central strand; leaves rather asymmetrical; decurrencies composed of one row; the apex very slightly denticulate; thin-wall cells in irregular transverse rows, at mid-leaf $15\text{--}19 \times 90\text{--}110\text{ }\mu\text{m}$. Additionally, Iwatsuki left a note that *P. mauiense* is closely related to *P. nemorale* (Mitt.) A. Jaeger (Iwatsuki 1970 unpubl.). However, in an analysis of *P. nemorale* in a taxonomic revision of the genus *Plagiothecium* published the same year, Iwatsuki (1970) does not mention *P. mauiense* or its similarity to this species.

Over 40 years later (June 25, 2012), the specimen deposited at the New York Herbarium (NY01256708) was reviewed by J.T. Wynn, who added the note: “Insular form of *Plagiothecium nemorale* (Mitt.) A. Jaeger”. In addition, in his revision of the genus *Plagiothecium*, he also added next to *P. mauiense* that the material did not differ from the type of *Stereodon nemoralis* Mitt. (being a basionym of *P. nemorale*) (Wynn 2015).

Despite the above-presented assumptions indicating that *P. mauiense*, recorded from Hawaii, is closely related or even identical to *S. nemoralis*, the two are still treated as separate species (see: Hoe 1974; Staples et al. 2004).

The features given in the diagnosis by Brotherus (1927), and indicated by Iwatsuki (1970 unpubl.) based on the analysis of the original material (Fig. 1), clearly qualify the described collections as a taxon representing the genus *Plagiothecium* and belonging to the section *Orthophyllum* Jedl. They even classified it as belonging to *P. nemorale sensu lato*. However, as some of the features given by Brotherus and Iwatsuki contradict each other, particularly the most taxonomically significant one, i.e. the length of the cells of the central part of the leaves, it is impossible to clearly assess this material.

Its light green to yellow green turf colour, leaf asymmetry and narrow cell areolation and irregular arrangement of cells reported by Brotherus (1927) and Iwatsuki (1970 unpubl.) are all characteristic of *P. longisetum*; in addition, Iwatsuki (1970 unpubl.) described the presence of a denticulate apex, corresponding to that of *P. nemorale*. Most importantly, the two authors differ in their opinion of the cell length at mid-leaf, one of the most taxonomically important features of this genus: Brotherus (1927) reported the length to be $75\text{--}100\text{ }\mu\text{m}$, which clearly matches *P. nemorale*, while Iwatsuki (1970 unpubl.) reported it as $90\text{--}110\text{ }\mu\text{m}$, corresponding to *P. longisetum*. In addition to the leaf cells, another very important feature of the whole genus, which is characteristic of individual sections, is the nature of leaf decurrencies (e.g. Nyholm 1965; Smith 2001; Wynn et al. 2017). Iwatsuki (1970 unpubl.) reported the presence of a single row of decurrent cells, which is a feature shared with representatives of section *Leptophyllum* Jedl. rather than section *Orthophyllum*, which is characterised

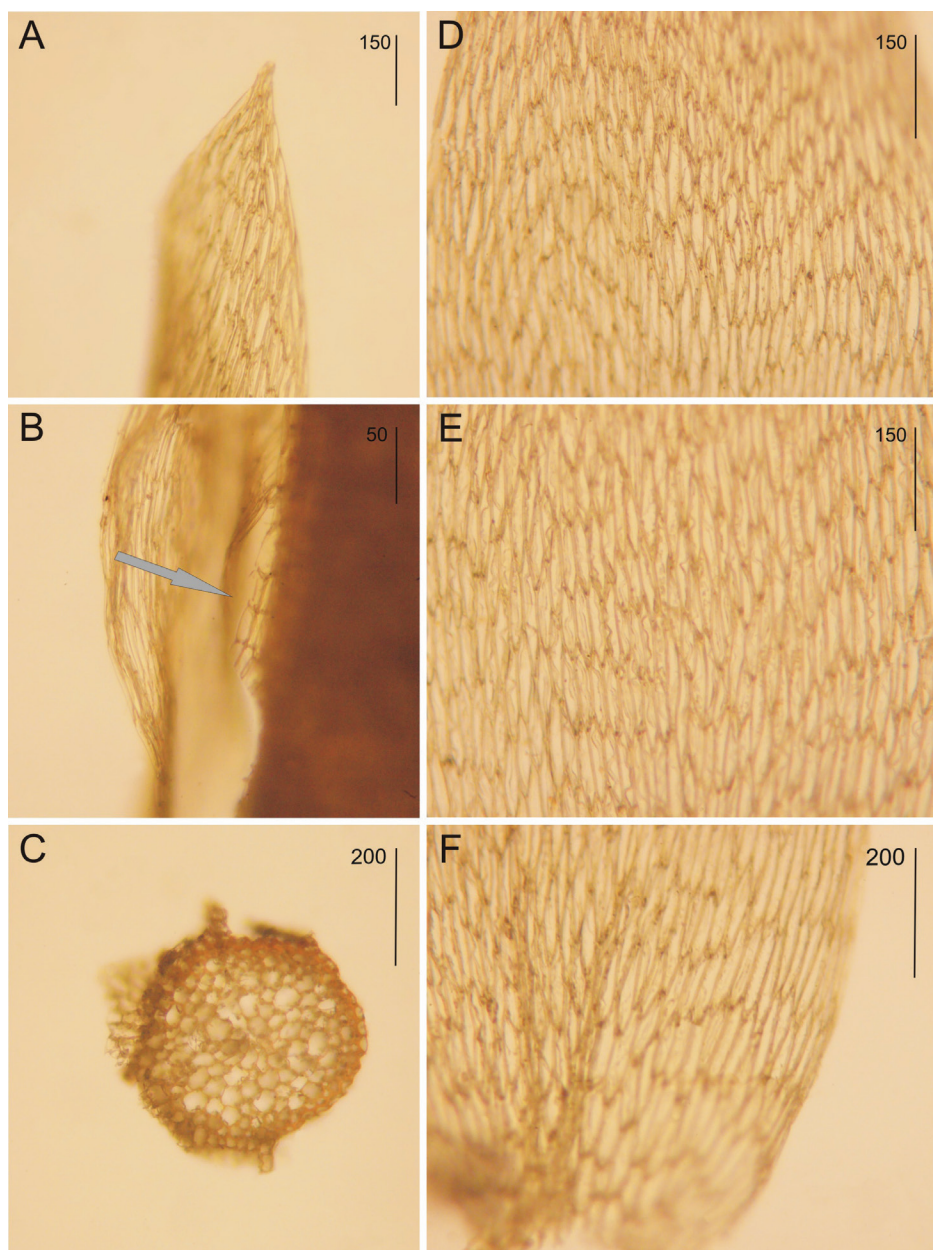


Figure 2. *Plagiothecium mauianse* from the NY Herbarium (D.D. Baldwin 221, NY01256708) **A** the plain leaf apex **B** the grey arrow indicates the three rows of decurrencies **C** the stem cross section **D–F** the shape and dimensions of cells from individual leaf zones: **D** from the upper part **E** from the middle part **F** from the lower part of the leaf. Scale bars: 50 µm (**B**); 150 µm (**A, D, E**); 200 µm (**C, F**).

by 2–3 rows of decurrent cells (Figs 1, 2). The remaining set of features provided by both authors are characteristic of both species: a large plant with a thick turf; loosely arranged and complanate-foliate; large (2.25 mm long and 1.1 mm wide), concave,

long-ovate leaves; two costae; an acute to acuminate apex; a developed central strand; thin-wall cells (Brotherus 1927; Iwatsuki 1970 unpubl.; Wolski 2017, 2018, 2020; Wolski and Nowicka-Krawczyk 2020).

The above-presented features and a detailed analysis of the specimen deposited at the New York Herbarium (NY01256708) indicated that this material represents *P. longisetum*. The specimen is large, light green to yellowish green, without metallic lustre; stems up to 2–2.5 cm long, complanate-foliate, rounded in cross-section, 330–380 µm in diameter, a developed central strand, epidermal cells 7–16 × 14–24 µm, parenchyma thin-walled, 22–47 × 19–43 µm; leaves gently concave, asymmetrical, lanceolate to lanceolate-ovate, spreading, shrunken in dry conditions, those from the middle of the stem 2.5–2.7 mm long, and 1.1–1.5 mm in width, measured at the widest point; the apex straight, not denticulate, acute to apiculate; two costae, extending almost to ½ leaf length, reaching 0.50–0.70 mm; elongate-hexagonal cells in irregular transverse rows, areolation very lax; cells reach 85–134 × 15–20 µm at the apex, 101–131 × 15–21 µm at mid-leaf, and 113–170 × 18–25 µm at the lower part of the leaf; decurrencies of three rows of rectangular cells, 32–44 × 15–31 µm (Fig. 2).

As only one syntype was examined (NY01256708), and due to the current inability to examine specimens from the other three herbaria (from FH, MU, YU), lectotypification of *P. mauiense* will be carried out later, once all original materials collected by D.D. Baldwin from Hawaii have been examined.

***Plagiothecium longisetum* account**

Lindberg described *Plagiothecium longisetum* in *Contributio ad Floram Cryptogamam Asiae Boreali-Orientalis* based on materials collected by C. Maximovicz from Japan (Lindberg 1872) (Fig. 3). After this fact, in the 19th and 20th centuries, the species was noted in the most important bryological studies of that time (Jaeger 1875–1876; Paris 1894–1898), however, it was not given from Europe, and its range was limited only to East Asia (China and Japan) (Schimper 1876; Lindberg 1879; Gravet 1883; Mitten 1891; Kindberg 1897; Brotherus 1929; Grout 1932; Podpéra 1954; Sakurai 1954).

At the beginning of the 20th century, Cardot (1912) indicated a relationship between *P. longisetum* and *P. sylvaticum*, writing that the former, similarly to *P. nemorale*, was just a form of *P. sylvaticum*. Wijk et al. (1967) indicated that *P. longisetum* was a synonym of *P. sylvaticum*, whereas Iwatsuki (1970) wrote that *P. longisetum* was a synonym of *P. nemorale*, adding that the former was only a habitat modification of the latter. After Iwatsuki (1970), for the next 50 years, this view spread throughout Europe and Asia (Lewinsky 1974; Iwatsuki 2004; Wynns 2015; Suzuki 2016). However, at the beginning of the 21st Century, as a result of a taxonomic revision of *P. nemorale sensu lato*, Wolski and Nowicka-Krawczyk (2020) proposed the resurrection of *P. longisetum*, and for it to be treated as separate from *P. nemorale*, which also was distributed in Eurasia. Subsequent studies have revealed a number of differences between the two species in the micromorphology of their sporophyte; they also documented their presence in North America, thus extending their global range (Wolski 2020; Wolski et al. 2020).

30. *Plagiothecium longisetum* n. sp. LINDB.

Dioicum, robustum; ramis arcuato-deflexis; foliis breviter acuminatis, nervo longiore et crassiore, cellulis duplo latioribus, perfecte rhombeis: seta longissima, flexuosa; thecae ore purpureo; peristomio minore et brevior, multo intensius colorato, endostomio laevissimo, processibus latioribus ciliisque brevioribus, tenuioribus et vix nodulosis; operculo longiore et acutior.

Hab. ad Nikosan ins. Kiusiu, fertile, 16 Junii 1863.

Cespites laxos, sed ob flagella copiosa intricatos, lurido- vel fulvo-viridulos pauloque nitentes formans. *Caulis* primarius 5–6 cm. longus, humifusus, tenuis, parvifolius, fusco-radiculosus, ramos emittens 2–3 cm. longos et 4–5 mm. latos, arcuatos, apice acutiusculo saepe flagellari-attenuatos et radiculiferos, vulgo supra basin ramulum simillimum, sed saepe

Contributio ad floram cryptogamam Asiae boreali-orientalis.

233

magis erectum proferentes, sat densifolios et complanatos. *Folia* vulgo leniter secunda, sicca leniter torta et undulata, longissime decurrentia, parte decurrente inferne sensim desinente, paulo asymmetrica, ovata, sat distincte acuminata, acumine brevi et latissimo, margine supra medium usque recurvo et ubique integerrimo, valde concava, nervo vulgo gemello, longiore et crassiore; *cellulae* laxissimae, magnae, subrhombae. *Perichetia* paucissima, 1 vel 2, supra basin rami axillaria, maxime fusco-radicantia. *Bractae* perichetii minutae, vaginantes, apice ovato-triungulares, acutae, margine ubique plano et integerrimo, nervo tenuiore, supra medium dissoluto, cellulis angustis, prosenchymatico-rectangularibus, laxissimis. *Vaginula* breviter conica, paraphyses et pistillidia paucissima gerens. *Seta* longissima, 4–5 cm. alta, vulgo hic illic valde flexuosa, rubra, superne flava, laevissima, sinistrorsum, supra medium dextrorsum torta. *Theca* sat parva, rubro-pallida, opaca, paulo nutans et asymmetrica, sicca quoque laevissima, oblongo-obconica, ore magno, purpureo, cellulis sat magnis et incrassatis, irregulariter rectangulo-quadratis, in collo sat longo stomatibus paucis, minutissimis, superficialibus. *Annulus* latus, triplex. *Exostomium* dentes 16, dolabriliformes, acutissimi, transverse densissime striolati, superne papilloso et supra medium dense trabeculati, lutei; *endostomium* luteolo-pallidum, laevissimum, membrana ad dimidiam altitudinem exostomii elevata, processus altitudine dentium, profunde carinati, acutissimi, medio haud vel vix perforati, cilia bina — quaterna, breviora, tenuissima, vix nodulosa. *Spori* minutissimi, laevissimi, ferrugineo-pallidi. *Operculum* luteolum, alte conicum, fere sensim angustatum in rostellum dimidia longitudine capsulae, suberectum et acutum. *Calyptra* straminea, apice brunneola, nitida, laevissima, ad medium thecae dependens.

Planta mascula nobis ignota.

Affinissimum *Plagiothecium silvaticum* (Huds.) B. S., quod in Japonia quoque crescit, secundum specimina a clar. TEXTOR lecta, facile distinguitur, diagnosi, supra data, collata, ut et parte decurrente folii inferne magis abrupte desinente, apice folii acuto, margine ejus magis et altius recurvo, foliis minus concavis, cellulis duplo angustioribus et minus incrassatis.

Figure 3. The diagnosis of *Plagiothecium longisetum* (Lindberg 1872).

During this revision, the specimens on which Lindberg (1872) described *P. longisetum* were found in three herbaria: the University of Helsinki Herbarium (H-SOL1563011), the Herbarium of Swedish Museum of Natural History (S-B160017) and Muséum National d'Histoire Naturelle (PC0132572). The latter specimen is marked as the “isotype” (Fig. 4). Based on this information, and according to Article 9.6 and 40.2 Note 1 of the *Shenzhen Code* (Turland et al. 2018) cited above, all specimens listed above should be considered syntypes.

In addition to the description of gametophyte morphology given in the diagnosis of *P. longisetum*, Lindberg (1872) indicated that this material has sporophytes (i.e. is “fertile”) and was collected on 16 June, 1863 (“16 Junii 1863”) near Nikosan on Kyushu island (“ad Nikosan ins. Kiusiu”) in Japan (Fig. 3). Addition-

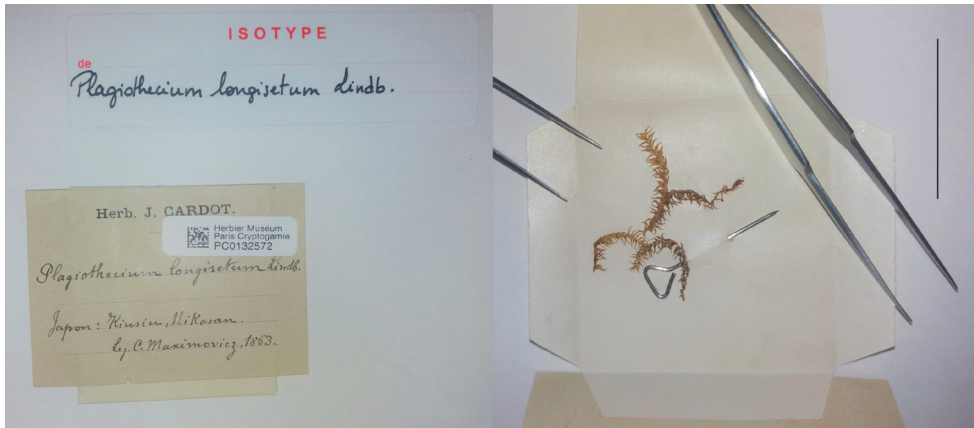


Figure 4. Sheet of *Plagiothecium longisetum* marked as the “isotype” and three stems of gametophyte deposited in the herbarium of the Muséum National d’Histoire Naturelle (PC0132572). Scale bar: 3 cm.

ally, Lindberg (1872) indicates, among others, that *P. longisetum* is characterised by a very long seta (“*seta longissima*”) and a long operculum (“*operculo longiore et acutiore*”). The presence of such a long seta, i.e. up to 5 cm in length, and a long operculum, distinguish the sample from other species of *Plagiothecium*; these characteristics, combined with the gametophyte features, are unique to *P. longisetum* (Wolski and Nowicka-Krawczyk 2020).

The specimen deposited at the herbarium in Helsinki (H-SOL 1563 011) was awarded the same date of collection as in the prologue, and is characterised by a fairly large, well-preserved gametophyte turf with three sporophytes (Fig. 5). The material deposited in Stockholm (S-B160017) also has a full collection date; however, due to the ongoing renovation of this herbarium, the loan and subsequent analysis of this material is impossible. Unfortunately, the specimen housed in the herbarium in Paris (PC0132572) has an incomplete collection date (“1863”), and only three gametophyte stems, without sporophytes (Fig. 4).

The material deposited in Helsinki (H-SOL 1563 011) is distinguished from other analysed syntypes by the presence of a fairly large gametophyte turf and more importantly, well-preserved sporophytes (Fig. 5), which (as Lindberg described in the diagnosis) confirm that the specimen is prolific (“*fertile*”). Based on these facts, and according to Article 9.3 of the *Shenzhen Code* (Turland et al. 2018) cited above, we propose that specimen H-SOL1563011 should be designated as the lectotype of *P. longisetum* (Fig. 5). In addition, due to the fact that the specimen from Muséum National d’Histoire Naturelle (PC0132572) was examined at the beginning of 2019, and we did not have access to the specimen deposited at the Herbarium of the Swedish Museum of Natural History (S-B160017), a request was sent to both institutions to change the status of these specimens to the isolectotype.

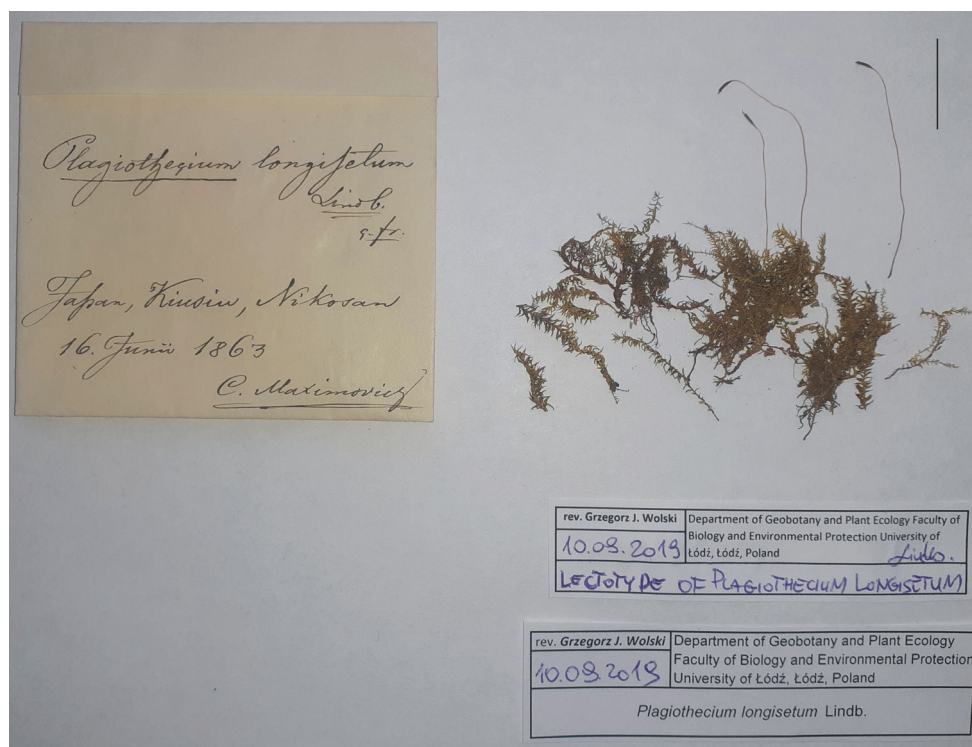


Figure 5. Envelope and turf with sporophytes of *Plagiothecium longisetum* from the University of Helsinki Herbarium (H-SOL 1563 011). Scale bar: 2 cm.

Taxonomic treatment

Plagiothecium longisetum Lindb., Acta Soc. Sci. Fenn. 10: 232 (1875). – Lectotype (designated here): [Japan], ad Nikosan ins. Kiusiu, [fertile], 16 Junii 1863, *S.O. Lindberg s.n.* (lecto-: H-SOL 1563 011!, isolecto-: PC0132572!, S-B160017) = *P. mauiense* Broth., Bernice P. Bishop Museum Bulletin 40: 28 (1927), syn. nov. Type: [United States], Hawaii, E Maui, Haleakala, 8000 ft., in damp ravines, fertile, June 1876, *D.D. Baldwin* 221 (syn-: NY01256708!, FH00220142, MU000000546, YU233890).

Acknowledgements

We are grateful to Sannamaija Laaka-Lindberg, PhD, the Curator of Collections of the Briological Herbarium at the University of Helsinki (Finland) and Laura Briscoe, MSc, Collections Manager of the Cryptogamic Herbarium NY (New York Botanical Garden, USA) for the loan of type specimens.

References

- Brotherus VF (1927) Hawaiian Mosses. Bernice P. Bishop Museum. Bulletin 40: 1–28.
- Brotherus VF (1929) *Symbolae Sinicae*. Teil IV: Musci. Verlag von Julius Springer, Wien.
- Cardot J (1912) Mousses nouvelles du Japon et de Corée. Bulletin de la Société Botanique de Genève, sér. 2. 4: 378–387.
- Gravet F (1883) Enumeratio Muscorum Europaeorum – Bibliographie – Nouvelles. Revue Bryologique Paraissant Tous Les Deux Mois 2: 1–34.
- Grout AJ (1932) Moss Flora of North America North of Mexico (Vol. 3). Published by the author, Newfane.
- Hoe WJ (1974) Annotated Checklist of Hawaiian Mosses. *Lyonia* 1: 1–45.
- Iwatsuki Z (1970) A revision of *Plagiothecium* and its related genera from Japan and her adjacent areas. The Journal of the Hattori Botanical Laboratory 33: 331–380.
- Iwatsuki Z (2004) New catalog of the mosses of Japan. The Journal of the Hattori Botanical Laboratory 96: 1–182.
- Jaeger A (1875–1876) [1877] Genera et Species Muscorum Systematicae Disposita; Seu, Adumbratio Florae Muscorum Totius Orbis Terrarum (Continuatio). Sancti Galli (St. Gallen), W. Haussknecht, 444–454.
- Kindberg NC (1897) European and N. American Bryineae (Mosses). Linköping, Sweden. <https://doi.org/10.5962/bhl.title.56766>
- Lewinsky J (1974) The family Plagiotheciaceae in Denmark. *Lindbergia* 2: 185–217.
- Lindberg SO (1872) Contributio ad floram cryptogamiam Asiae Boreali-Orientalis. Helsingforsiae.
- Lindberg SO (1879) Musci Scandinavici in systemate novo naturali dispositi. Upsaliae.
- Mitten W (1891) On the species of Musci and Hepaticae recorded from Japan. Transactions of the Linnean Society of London 3(3): 178–179. <https://doi.org/10.1111/j.1095-8339.1891.tb00626.x>
- Nyholm E (1965) Family Plagiotheciaceae. Illustrated Moss Flora of Fennoscandia. II. Musci. Fascicle 5, The Botanical Society of Lund.
- Paris EG (1894–1898) Index bryologicus sive, Enumeratio muscorum hucusque cognitorum adjunctis synonymia distributioneque geographica locupletissimus. Parisiis. <https://doi.org/10.5962/bhl.title.643>
- Podpéra J (1954) Conspectus Muscorum Europaeorum. Nakladatelství Československé Akademie Věd, Prague.
- Sakurai K (1954) *Muscologia japonica*. Iwanami Shoten, Tokyo.
- Schimper WPh (1876) Synopsis muscorum Europaeorum: praemissa introductione de elementis bryologicis tractante (Vol. 1), Stuttgartiae.
- Smith AJE (2001) The moss flora of Britain and Ireland. Cambridge University Press.
- Staples GW, Imada CT, Hoe WJ, Smith CW (2004) A revised checklist of Hawaiian mosses. *Tropical Bryology* 25: 35–69. <https://doi.org/10.11646/bde.25.1.7>
- Suzuki TA (2016) Revised new catalog of the mosses of Japan. *Hattoria* 7: 9–223.
- 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>
- van der Wijk R, Margadant WD, Florschütz PA (1967) Index Muscorum, vol. 4. International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy. Utrecht.
- Wolski GJ (2017) Morphological and anatomical variability of *Plagiothecium nemorale* in Central Poland. *Herzogia* 30(1): 36–50. <https://doi.org/10.13158/heia.30.1.2017.36>
- Wolski GJ (2018) Are *Plagiothecium cavifolium*, *P. nemorale* and *P. succulentum* indeed variable species? *Pakistan Journal of Botany* 50(4): 1579–1589.
- Wolski GJ (2020) Reassessing the taxonomic diversity of *Plagiothecium* section *Orthophyllum* in the North American bryoflora. *Brittonia* 72(3): 1–14. <https://doi.org/10.1007/s12228-020-09631-y>
- Wolski GJ, Bihun M, Białecka B, Rewicz A (2020) SEM differences in sporophyte micromorphology of *Plagiothecium nemorale* and *P. longisetum* (Plagiotheciaceae, Bryophyta). *Folia Cryptogamica Estonica*. [in press]
- Wolski GJ, Nowicka-Krawczyk P (2020) Resurrection of the *Plagiothecium longisetum* Lindb. and proposal of the new species – *P. angusticellum*. *PLOS One* 15(3): e0230237. <https://doi.org/10.1371/journal.pone.0230237>
- Wynns JT (2015) Molecular phylogeny and systematic revision of the pleurocarpous moss genus *Plagiothecium*. PhD Thesis, University of Copenhagen, Denmark.
- Wynns JT, Munk KR, Lange CBA (2017) Molecular phylogeny of *Plagiothecium* and similar hypnalean mosses, with a revised sectional classification of *Plagiothecium*. *Cladistics* 34(5): 469–501. <https://doi.org/10.1111/cla.12210>

The Morelloid clade of *Solanum* L. (Solanaceae) in Argentina: nomenclatural changes, three new species and an updated key to all taxa

Sandra Knapp¹, Franco Chiarini², Juan J. Cantero^{2,3}, Gloria E. Barboza²

1 Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK **2** Museo Botánico, IMBIV (Instituto Multidisciplinario de Biología Vegetal), Universidad Nacional de Córdoba, Casilla de Correo 495, 5000, Córdoba, Argentina **3** Departamento de Biología Agrícola, Facultad de Agronomía y Veterinaria, Universidad Nacional de Río Cuarto, Ruta Nac. 36, km 601, 5804, Río Cuarto, Córdoba, Argentina

Corresponding author: Sandra Knapp (s.knapp@nhm.ac.uk)

Academic editor: L. Giacomini | Received 20 May 2020 | Accepted 28 August 2020 | Published 21 October 2020

Citation: Knapp S, Chiarini F, Cantero JJ, Barboza GE (2020) The Morelloid clade of *Solanum* L. (Solanaceae) in Argentina: nomenclatural changes, three new species and an updated key to all taxa. *PhytoKeys* 164: 33–66. <https://doi.org/10.3897/phytokeys.164.54504>

Abstract

Since the publication of the Solanaceae treatment in “Flora Argentina” in 2013 exploration in the country and resolution of outstanding nomenclatural and circumscription issues has resulted in a number of changes to the species of the Morelloid clade of *Solanum* L. (Solanaceae) for Argentina. Here we describe three new species: *Solanum hunzikeri* Chiarini & Cantero, **sp. nov.**, from wet high elevation areas in Argentina (Catamarca, Salta and Tucumán) and Bolivia (Chuquisaca and Tarija), *S. marmoratum* Barboza & S.Knapp, **sp. nov.**, from central Argentina in Catamarca, La Pampa, La Rioja, San Juan and San Luis, and *S. tiinae* Barboza & S.Knapp, **sp. nov.**, from the mountains of Jujuy, La Rioja, Salta and Tucumán. We provide descriptions, illustrations and distribution maps for all new taxa. A table of nomenclatural changes and additional taxa now known to occur in Argentina summarizes additions and changes since the “Flora Argentina”. We also provide an updated key, including all new taxa for the country, to facilitate identification and further exploration.

Keywords

Andes, black nightshades, dry forests, endemic, glandular pubescence, identification, new species, rarity

Introduction

Solanum L., with 1,400 species, is one of the largest genera of flowering plants (Frodin 2004). Its species occur worldwide, with highest diversity in South America, and in a wide variety of habitats, from deserts to tropical rainforests to high elevation grasslands. The genus comprises 13 major clades, one of which, the *Leptostemonum* clade or spiny solanums, contains approximately half the species. The non-spiny solanums are a paraphyletic grade (Särkinen et al. 2013) within which several monophyletic groups are resolved (Särkinen et al. 2013); one of these is the Morelloid clade (see Särkinen et al. 2015). Members of the clade are usually herbs or small short-lived subshrubs and the group is sister to the *Dulcamaroid* clade, a group of woody vines (See Knapp 2013). Species of the Morelloid clade are found worldwide and are being treated in a series of monographs (e.g., Old World taxa in Särkinen et al. 2018; Caribbean, North and Central American taxa in Knapp et al. 2019; South American taxa in G.E. Barboza et al., in prep); by far the highest diversity occurs in western South America (Särkinen et al. 2015). Of the 62 species of South American morelloids, 38 species are found in Argentina with 8 species occurring as country endemics (Table 1; 37 with 7 endemics excluding *S. concarense* Hunz., see below), making the country a hotspot for morelloid diversity. It is equalled only by Bolivia also with 38 species, 21 of which are in common with Argentina.

Solanaceae were treated in the multi-volume “*Flora Argentina*” in 2013 (Anton and Zuloaga 2013), and the treatment of the Morelloid clade recognised 30 species (Grupo VII. Moreloide; Barboza et al. 2013). Further exploration of the country and herbaria, coupled with taxonomic and nomenclatural work as part of the monograph, has resulted in an additional seven species for the country, and name changes for three species treated in the *Flora* (see Table 1). Here we document changes, describe new taxa and provide a revised key and provincial distribution (Table 2) for all morelloid species in the country.

Materials and methods

Our species circumscriptions are based on revision of herbarium material accompanied by detailed examination of living plants in the field and, where possible, in cultivation at the Instituto Multidisciplinario de Biología Vegetal (IMBIV) in Córdoba, Argentina. We have also used published and unpublished results from molecular phylogenetic study of the entire Morelloid clade (Särkinen et al. 2015; R. Hilgenhof, pers. comm.) to include or exclude taxa from the group. Descriptions for the new species are based on specimens from 14 herbaria (acronyms follow Index Herbariorum, <http://sweetgum.nybg.org/science/ih/>): BAA, BAB, BM, BR, CORD, CTES, E, G, K, LIL, MO, SI, US, W. Many more herbaria have been consulted during the course of monographic work on the Morelloid clade; these will be listed in full in the upcoming monograph, and details of all specimens seen to date from Argentina can be found in the Suppl. materials 1, 2: (SM 1, all morelloid species; SM 2, the three new species described here) and on the NHM Data Portal (<https://doi.org/10.5519/0062836>).

Table 1. Members of the Moreloid clade occurring in Argentina with their treatment in *Flora Argentina* (Barboza et al. 2013) and the reasons for changes here. Circumscription changes and nomenclatural details will be treated in full in the upcoming monograph (G.E. Barboza et al. in prep.). Country endemics are in **bold face** type. NB: *Solanum concarense* (*) is included for consistency with *Flora Argentina* (Barboza et al. 2013), although it has been shown to belong to the Dulcamaroid (see text) rather than the Moreloid clade.

Species recognised here	Treatment in <i>Flora Argentina</i> (Barboza et al. 2013)	Reason for change
<i>Solanum aloysiifolium</i> Dunal	same	
<i>Solanum americanum</i> Mill.	same	
<i>Solanum annuum</i> C.V.Morton	same	
<i>Solanum caesium</i> Griseb.	same	
<i>Solanum chenopodioides</i> Lam.	same	
<i>Solanum cochabambense</i> Bitter	as synonym of <i>S. aloysiifolium</i> Dunal	new circumscription based on examination of material from northern South America
<i>Solanum concarense</i> Hunz. *	same (included here for continuity)	now placed as a member of the Dulcamaroid clade (see text)
<i>Solanum echegarayi</i> Hieron.	same	new circumscription, now includes <i>S. hastatilobum</i> Bitter
<i>Solanum fiebrigii</i> Bitter	same	
<i>Solanum furcatum</i> Dunal	same	
<i>Solanum gilioides</i> Rusby	same	
<i>Solanum glandulosopilosum</i> Bitter	same	
<i>Solanum grandidentatum</i> Phil.	as <i>S. excisiorhombeum</i> Bitter	Older name (nomenclatural change)
<i>Solanum buayavillense</i> Del Vitto & Peten.	same	
<i>Solanum bunzikeri</i> Chiarini & Cantero	not included	described here
<i>Solanum marmoratum</i> Barboza & S.Knapp	not included	described here
<i>Solanum michaelis</i> Särkinen & S.Knapp	not included	new distribution record based on <i>Kiesling 8354</i> (CORD, SI)
<i>Solanum nitidibaccatum</i> Bitter	same	
<i>Solanum palitans</i> C.V.Morton	same	
<i>Solanum paucidens</i> Bitter	not included	new distribution record based on <i>Johnson 843</i> (CORD)
<i>Solanum physalidicalyx</i> Bitter	as <i>S. tweedeanum</i> Hook.	see text
<i>Solanum physalifolium</i> Rusby	same	
<i>Solanum pilcomayense</i> Morong	same	
<i>Solanum profusum</i> C.V.Morton	same	
<i>Solanum pygmaeum</i> Cav.	same	
<i>Solanum riojense</i> Bitter	as synonym of <i>S. echegarayi</i> Hieron.	new circumscription based on examination of more material
<i>Solanum salamancae</i> Hunz. & Barboza	same	
<i>Solanum salicifolium</i> Phil.	treated as member of the Dulcamaroid clade	new phylogenetic position as member of the Moreloid clade clarified (Särkinen et al. 2015)
<i>Solanum sarrachoides</i> Sendtn.	same	
<i>Solanum sinuatiexcisum</i> Bitter	same	
<i>Solanum sinuatirecurvum</i> Bitter	same	
<i>Solanum tiinae</i> Barboza & S.Knapp	not included	described here
<i>Solanum triflorum</i> Nutt.	same	
<i>Solanum tripartitum</i> Dunal	same	
<i>Solanum tweedeanum</i> Hook.	as <i>S. atriplicifolium</i> Gillies ex Nees	see text
<i>Solanum weddellii</i> Phil.	as <i>S. chamaesarachidium</i> Bitter	older name (nomenclatural change)
<i>Solanum woodii</i> Särkinen & S.Knapp	not included	new distribution record based on <i>Nee & Bohs 50823</i> (NY)
<i>Solanum zuloagae</i> Cabrera	same	

Measurements were made from dried herbarium material supplemented by measurements and observations from living and cultivated material. Colours (e.g., corollas, fruits, etc.) are described from living material or from herbarium label data. Specimens with latitude and longitude data on the labels were mapped directly. Some species had few or no georeferenced collections; in these cases we retrospectively georeferenced the collections using available locality data. Maps were constructed with the points in the

Table 2. Morelloid species occurring in each province of Argentina (specimens seen by the authors, see Suppl. materials 1, 2 and NHM Data Portal, <https://doi.org/10.5519/0062836>). No morelloid species have been collected from Tierra del Fuego or Antarctica. *Solanum concarense* is included for consistency with *Flora Argentina* (Barboza et al. 2013), although it has been shown to belong to another clade (see text). NB: *Solanum concarense* (*) is included for consistency with *Flora Argentina* (Barboza et al. 2013), although it has been shown to belong to the Dulcamaroid (see text) rather than the Morelloid clade.

Province	<i>Solanum</i> species with records
Buenos Aires (incl. DF)	<i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. nitidibaccatum</i> , <i>S. palitans</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. sarrachoides</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
Catamarca	<i>S. aloysifolium</i> , <i>S. annuum</i> , <i>S. cochabambense</i> , <i>S. echegarayi</i> , <i>S. huayavillense</i> , <i>S. hunzikeri</i> , <i>S. marmoratum</i> , <i>S. nitidibaccatum</i> , <i>S. palitans</i> , <i>S. physalidicalyx</i> , <i>S. physalisifolium</i> , <i>S. salamancae</i> , <i>S. salicifolium</i> , <i>S. sarrachoides</i> , <i>S. sinuatirecurvum</i> , <i>S. tweedeanum</i> , <i>S. weddellii</i>
Chaco	<i>S. aloysifolium</i> , <i>S. americanum</i> , <i>S. caesium</i> , <i>S. chenopodioides</i> , <i>S. nitidibaccatum</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. sarrachoides</i> , <i>S. tweedeanum</i>
Chubut	<i>S. furcatum</i> , <i>S. nitidibaccatum</i> , <i>S. triflorum</i>
Córdoba	<i>S. aloysifolium</i> , <i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. echegarayi</i> , <i>S. nitidibaccatum</i> , <i>S. palitans</i> , <i>S. physalidicalyx</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. salicifolium</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
Corrientes	<i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. paucidens</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i>
Entre Ríos	<i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. nitidibaccatum</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. salicifolium</i> , <i>S. sarrachoides</i> , <i>S. tweedeanum</i>
Formosa	<i>S. americanum</i> , <i>S. pilcomayense</i> , <i>S. tweedeanum</i>
Jujuy	<i>S. aloysifolium</i> , <i>S. annuum</i> , <i>S. caesium</i> , <i>S. chenopodioides</i> , <i>S. cochabambense</i> , <i>S. fiebrigii</i> , <i>S. gilioides</i> , <i>S. glandulosopilosum</i> , <i>S. grandidentatum</i> , <i>S. huayavillense</i> , <i>S. michaelis</i> , <i>S. palitans</i> , <i>S. physalidicalyx</i> , <i>S. physalisifolium</i> , <i>S. profusum</i> , <i>S. riojense</i> , <i>S. salicifolium</i> , <i>S. sinuatiexcisum</i> , <i>S. sinuatirecurvum</i> , <i>S. tiinae</i> , <i>S. tripartitum</i> , <i>S. tweedeanum</i> , <i>S. weddellii</i> , <i>S. woodii</i>
La Pampa	<i>S. chenopodioides</i> , <i>S. marmoratum</i> , <i>S. pygmaeum</i> , <i>S. salicifolium</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
La Rioja	<i>S. aloysifolium</i> , <i>S. chenopodioides</i> , <i>S. cochabambense</i> , <i>S. echegarayi</i> , <i>S. marmoratum</i> , <i>S. nitidibaccatum</i> , <i>S. physalidicalyx</i> , <i>S. riojense</i> , <i>S. salicifolium</i> , <i>S. tiinae</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i> , <i>S. weddellii</i>
Mendoza	<i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. echegarayi</i> , <i>S. nitidibaccatum</i> , <i>S. salicifolium</i> , <i>S. sarrachoides</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
Misiones	<i>S. americanum</i> , <i>S. paucidens</i> , <i>S. pilcomayense</i>
Neuquén	<i>S. furcatum</i> , <i>S. nitidibaccatum</i> , <i>S. pygmaeum</i> , <i>S. triflorum</i>
Río Negro	<i>S. chenopodioides</i> , <i>S. furcatum</i> , <i>S. nitidibaccatum</i> , <i>S. salicifolium</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
Salta	<i>S. aloysifolium</i> , <i>S. americanum</i> , <i>S. annuum</i> , <i>S. caesium</i> , <i>S. chenopodioides</i> , <i>S. cochabambense</i> , <i>S. echegarayi</i> , <i>S. fiebrigii</i> , <i>S. glandulosopilosum</i> , <i>S. huayavillense</i> , <i>S. hunzikeri</i> , <i>S. michaelis</i> , <i>S. nitidibaccatum</i> , <i>S. palitans</i> , <i>S. physalidicalyx</i> , <i>S. physalisifolium</i> , <i>S. pilcomayense</i> , <i>S. profusum</i> , <i>S. riojense</i> , <i>S. salamancae</i> , <i>S. salicifolium</i> , <i>S. sarrachoides</i> , <i>S. sinuatiexcisum</i> , <i>S. sinuatirecurvum</i> , <i>S. tiinae</i> , <i>S. tweedeanum</i> , <i>S. tripartitum</i> , <i>S. weddellii</i> , <i>S. zuloagae</i>
San Juan	<i>S. echegarayi</i> , <i>S. marmoratum</i> , <i>S. nitidibaccatum</i> , <i>S. physalidicalyx</i> , <i>S. salicifolium</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
San Luis	<i>S. aloysifolium</i> , <i>S. chenopodioides</i> , <i>S. concarense</i> *, <i>S. echegarayi</i> , <i>S. marmoratum</i> , <i>S. nitidibaccatum</i> , <i>S. physalidicalyx</i> , <i>S. pygmaeum</i> , <i>S. salicifolium</i> , <i>S. sarrachoides</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i>
Santa Cruz	<i>S. nitidibaccatum</i> , <i>S. triflorum</i>
Santa Fé	<i>S. americanum</i> , <i>S. chenopodioides</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. triflorum</i>
Santiago del Estero	<i>S. aloysifolium</i> , <i>S. americanum</i> , <i>S. nitidibaccatum</i> , <i>S. physalidicalyx</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. sarrachoides</i> , <i>S. tweedeanum</i>
Tucumán	<i>S. aloysifolium</i> , <i>S. americanum</i> , <i>S. annuum</i> , <i>S. chenopodioides</i> , <i>S. cochabambense</i> , <i>S. fiebrigii</i> , <i>S. gilioides</i> , <i>S. glandulosopilosum</i> , <i>S. huayavillense</i> , <i>S. hunzikeri</i> , <i>S. nitidibaccatum</i> , <i>S. palitans</i> , <i>S. physalidicalyx</i> , <i>S. pilcomayense</i> , <i>S. pygmaeum</i> , <i>S. riojense</i> , <i>S. salamancae</i> , <i>S. salicifolium</i> , <i>S. sinuatiexcisum</i> , <i>S. tiinae</i> , <i>S. triflorum</i> , <i>S. tweedeanum</i> , <i>S. weddellii</i> , <i>S. zuloagae</i>

centres of degree squares in a 1° square grid. Conservation threat status was assessed following the IUCN Red List Categories and Criteria (IUCN 2019) using the GIS-based method (Bachman et al. 2011) as implemented in the online assessment tools in GeoCat (<http://geocat.kew.org>). The Extent of Occurrence (EOO) measures the range of the species, and the Area of Occupancy (AOO) represents the number of occupied points within that range based on the default grid size of 2 km². We have given more weight to the EOO in the threat assessments for relatively widespread species; AOO is very sensitive to georeferencing bias and collecting effort.

Taxonomic treatment

Name changes for Moreloid species in Argentina

Changes for inclusion and nomenclature for morelloids since the publication of “Flora Argentina” (Barboza et al. 2013) are summarised in Table 1, but some comment is necessary here. The widespread and highly variable species *S. salicifolium* Phil. was treated as a member of the Dulcamaroid clade by Knapp (2013) and in the *Flora*, but further work with DNA sequence data places *S. salicifolium* nested amongst the “Black nightshade” group of Särkinen et al. (2015). Further analyses have supported this position (E. Gagnon et al., pers. comm.). *Solanum salicifolium* is included here in the key for clarity, even though it was included in the Dulcamaroid clade earlier (Knapp 2013).

Solanum concarense was included as a member of the clade in Barboza et al. (2013), but subsequent phylogenetic analysis (R. Hilgenhof, pers. comm.) has revealed that it instead is nested within the Dulcamaroid clade. We include it here in the key for clarity, but it will not be treated as a member of the group in the upcoming monograph and a full species description is available on Solanaceae Source (<http://solanaceaesource.org>).

Several names have changed due to the clarification and subsequent resurrection (Särkinen et al. 2015) of older names coined by R.A. Philippi for species from high elevation areas of Chile adjacent to Argentina (Philippi 1891); *S. weddellii* Phil. is the older name for what was previously recognised (Barboza 2004) as *S. chamaesarachidium* Bitter and *S. grandidentatum* Phil. for the taxon previously recognised (Edmonds 1972) as *S. excisirhombeum* Bitter. These names have been in use since Särkinen et al. (2015). *Solanum cochabambense* Bitter was treated as a synonym of *S. aloysiifolium* Dunal in Barboza et al. (2013), but subsequent study through the entire range of *S. cochabambense* (north to Peru) has shown the two taxa to be distinct; we therefore recognise them as separate here.

Re-evaluation of synonymy in two common glandular-pubescent taxa

Re-evaluation of taxon circumscription and types for the upcoming monograph has revealed that two names for species with glandular trichomes and accrescent calyces were previously incorrectly applied in “Flora Argentina” and elsewhere (Barboza et al. 2013; Särkinen and Knapp 2016). In Barboza et al. (2013), two taxa were recognised, *S. “tweedieanum”* Hook. (a mis-spelling of *S. tweedieanum*, see below) and *S. atriplicifolium* Gillies ex Nees, both of which are glandular-pubescent with ovate, shallowly toothed leaves. *Solanum physalidicalyx* Bitter, the name recognised here for a distinct species with highly inflated calyces, was erroneously put into synonymy with *S. tweedieanum*; the type of *S. tweedieanum* does not match these specimens but is a better match for plants called *S. atriplicifolium* in 2013. The type of *S. tweedieanum* comes from a plant cultivated at Kew that was collected in flower only; it lacks the diagnostic calyx characters (see Fig. 1 and the key presented here) that enable easy identification

in this group, but anther length can also be used to distinguish those plants not in fruit. Plants with inflated calyces have shorter anthers than do those with calyces that are merely accrescent and tightly investing the berry; the types of both *S. tweedieanum* and *S. atriplicifolium* have longer (to 6 mm) anthers and belong to the same species, for which the oldest name is *S. tweedieanum*. We present here a revised synonymy for the two species of glandular-pubescent morelloids with anthers more than 3 mm long that occur in Argentina to correct the error in “Flora Argentina” (Barboza et al. 2013).

***Solanum physalidicalyx* Bitter, Repert. Spec. Nov. Regni Veg. 11: 212. 1912**

Fig. 1G–I

Solanum physalidicalyx Bitter var. *integrascens* Bitter, Repert. Spec. Nov. Regni Veg. 11: 213. 1912. Type. Argentina. Salta: [Dtto. La Caldera], Pasaje del Río Juramento, P.G. Lorentz & G. Hieronymus [no number cited] (no explicit type material located; likely homotypic with species).

Solanum physalidicalyx Bitter var. *plurilobulatum* Bitter, Repert. Spec. Nov. Regni Veg. 11: 213. 1912. Type. Argentina. Salta: [Dtto. La Caldera], Pasaje del Río Juramento, P.G. Lorentz & G. Hieronymus [no number cited] (no explicit type material located; likely homotypic with species).

Type. ARGENTINA. Salta: [Dtto. La Caldera], Pasaje del Río Juramento, Feb 1873, P.G. Lorentz & G. Hieronymus 364 (holotype: B [destroyed]; lectotype, designated by Barboza et al. 2013, pg. 262: GOET [GOET003574]; isoelectotypes: CORD [CORD00004269], DR [DR054234], US [00027741, acc. # 282274]).

Distribution. Bolivia and Argentina.

Notes. Type material for the varietal names coined by Georg Bitter in the original publication of *S. physalidicalyx* (Bitter 1912) may correspond to duplicates of the type collection of the species itself, making all three names homotypic. In describing var. *integrascens* Bitter (1912) states “var. integrifolia quod in descriptione specie pro typo habui” [var. integrifolia I had in the description of the type of the species] suggesting this name at least is based on Lorentz & Hieronymus 364. Bitter often used duplicates with minor leaf variations as material for describing infraspecific variation (Knapp 2013). None of the duplicates of these Lorentz and Hieronymus collections from Salta have annotations in Bitter’s hand, and we have found no other collections of *S. physalidicalyx* made by Lorentz and Hieronymus from “Pasaje de Juramento”.

***Solanum tweedieanum* Hook., Bot. Mag. 62: tab. 3385. 1835, as “*Tweedieanum*”**

Fig. 1D–F

Solanum atriplicifolium Gillies ex Nees, Nov. Act. Acad. Caes. Leop. 19, Suppl. 1: 386. 1843. Type. Argentina. Mendoza: El Diamante, [no date], J. Gillies s.n. (lecto-

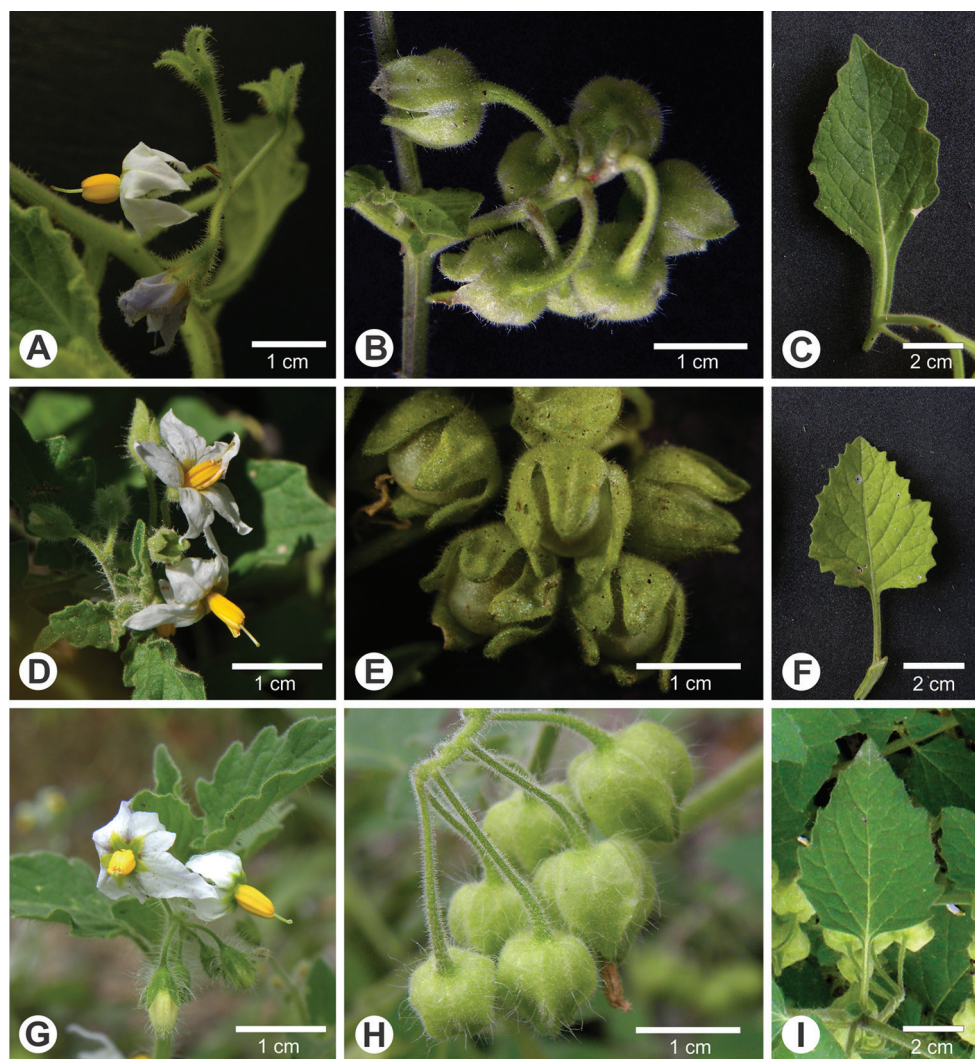


Figure 1. *Solanum hunzikeri* Chiarini & Cantero (**A–C**) compared to *S. tweedieanum* Hook. (**D–F**) and *S. physalidicalyx* Bitter (**G–I**) **A** habit (Barboza et al. 4763) **B** calyx morphology of developing fruits (Barboza et al. 4763) **C** leaf from mature stem (Barboza et al. 4763) **D** habit (Barboza et al. 3496) **E** calyx morphology of developing fruits (Barboza et al. 4798) **F** leaf from mature stem (Barboza et al. 4798) **G** habit (Barboza et al. 3983) **H** calyx morphology of developing fruits (Barboza et al. 3983) **I** leaf from mature stem (Barboza et al. 3983). Photos **A–C, E, F** by M. Gritti, **D** by S. Knapp, **G–I** by G.E. Barboza.

type, designated by Barboza et al. 2013, pg. 239): E [E00112916]; isoelectotypes: E [E00057545], K[K000585737], NY [00139057]).

Solanum haarupii Bitter, Repert. Spec. Nov. Regni Veg. 11: 210. 1912. Type. Argentina. Mendoza: Estancia Santa Rosa, 1904, *A.C. Jensen-Haarup s.n.* (holotype: UPS; isotype: US [00027594, acc. # 1081085]).

Solanum meizonanthum Bitter, Repert. Spec. Nov. Regni Veg. 11: 214. 1912. Type. Argentina. Entre Ríos: Paraná, 16 Aug 1892, G. Niederlein 270 (holotype: B [destroyed, F neg. 2783]; lectotype, designated here: F [V0361924F, acc. # 621142]). *Solanum atriplicoides* Herter, Rev. Sudamer. Bot. 7: 226. 1943, nom. illeg. superfl. Type. Based on *Solanum atriplicifolium* Gillies ex Nees

Type. Cultivated at the Glasgow Botanical Garden [protologue] from seeds sent by J. Tweedie from “near Buenos Ayres”, *Anon. s.n.* (lectotype, designated by Edmonds 1972, pg. 102 [as “holotype”], second step designated here: K [K000585739]; isolecotype: K [K000585738]).

Distribution. Bolivia and Argentina.

Notes. Edmonds (1972) stated that the holotype of *S. tweedieanum* was held at K; Barboza et al. (2013) repeated this citation but added reference to a single sheet (K000585739). This is not effective lectotypification under Art. 9.23 of the Code (Turland et al. 2018). The specimen cited as holotype by Barboza et al. (2013) and selected as lectotype here (K000585739) has open flowers and several buds and is a better match for the illustration in the protologue than the other sheet at Kew (K000585738); both specimens are annotated “S. Tweedianum Hook./B^{os}. Ayres. Cult.” in W.J. Hooker’s handwriting and bear the herbarium stamp “Herbarium Hookerianum/1867” indicating they come from Hooker’s own herbarium. There is no evidence on the specimens themselves that they were taken from the plants cultivated in Glasgow mentioned in the protologue, nor that they were collected prior to 1835; but the top part of the stem mounted on the sheet we have selected as the lectotype at Kew (K000585739, <https://plants.jstor.org/stable/pdf/10.5555/al.ap.specimen.k000585739>) is an excellent (mirror-image) match for Tab. 3385 in the protologue (Hooker 1835; see <https://www.biodiversitylibrary.org/item/14341#page/36/mode/1up>) suggesting it does represent original material. The original, and all subsequent, spelling of the name was “Tweedianum” where John Tweedie’s name was implicitly latinized as “Tweedius” in which the terminal vowel was eliminated. This is not acceptable under Art. 60.9(a)(1) of the Code (Turland et al. 2018) and the name should be formed as “tweedieanum” (e.g., Art. 60.9, Ex. 31, Turland et al. 2018).

New species descriptions

Solanum hunzikeri Chiarini & Cantero, sp. nov.

urn:lsid:ipni.org:names:77212300-1

Figs 1A–C, 2

Diagnosis. Like *Solanum tweedieanum* Hook. but differing in sessile leaves with broadly winged petioles, pedicels in flower longer than 1 cm, larger flowers and anthers more than 1 mm wide.

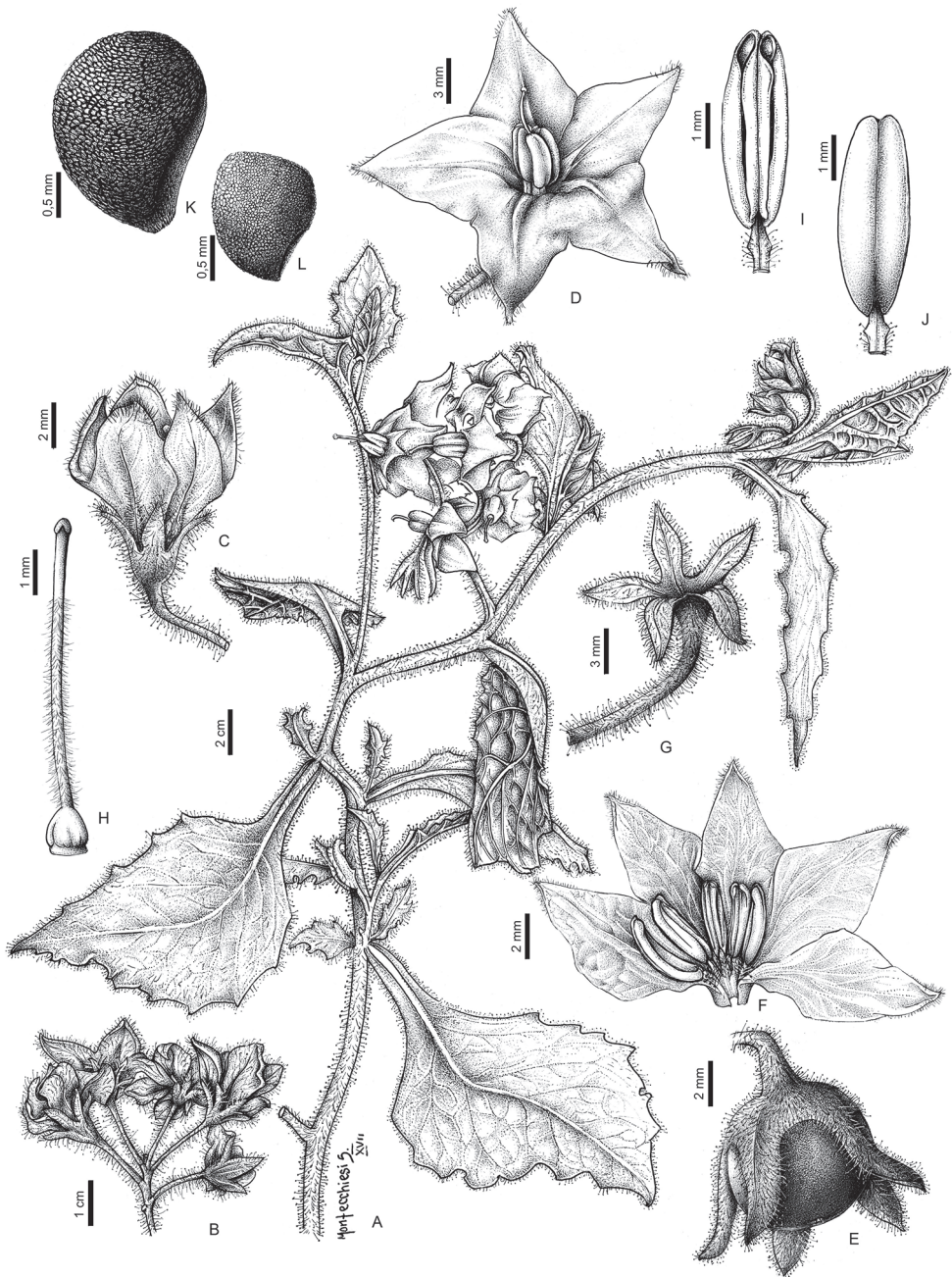


Figure 2. *Solanum bunzikeri* Chiarini & Cantero **A** flowering stem **B** inflorescence **C** flower **D** open flower **E** immature fruit showing the accrescent calyx not completely covering the berry **F** flower showing pubescent adaxial surface of the filaments **G** calyx **H** style with pubescence confined to the portion inside the anther cone **I** adaxial surface of the anther showing the pores elongating with age **J** abaxial surface of the anther **K** seed **L** stone cell (sclereid).

Type. ARGENTINA. Catamarca: Dtto. Ambato, Los Morteritos, Sierra de Ambato, falda E, subiendo desde El Rodeo hacia el Cerro Manchado [Cerro Manchao], 2300–2400 m, 13 Jan 1973, *A.T. Hunziker & R. Subils* 22205 (holotype: CORD [CORD00013086]).

Description. Herb or subshrub from a woody base ca. 50 cm tall; stems terete or only slightly angled, densely glandular pubescent with glandular papillae and transparent spreading simple 3–8-celled uniseriate trichomes 0.5–1 mm long, some to 1.5 mm long; bark of older stems pale brown, glabrescent; new growth densely glandular pubescent with simple uniseriate trichomes to 1 mm long. Sympodial units plurifoliate, the leaves not geminate. Leaves simple to shallowly toothed, (2–)4.5–14 cm long, (1.1–)2–7 cm wide, elliptic in outline, membranous or somewhat thick and fleshy, concolorous; adaxial surface moderately and evenly glandular pubescent with transparent spreading, simple uniseriate trichomes ca. 0.5 mm long on the lamina, ca. 1 mm long on the veins; abaxial surface moderately and evenly glandular pubescent like the adaxial surface, but the trichomes denser and longer, to 1.5 mm long; principal veins 4–7 pairs, densely glandular pubescent; base attenuate and strongly decurrent onto the petiole; margins entire or shallowly toothed, the teeth if present 1–2 mm long, 2–3 mm wide, broadly deltate with somewhat rounded tips; apex acute; petioles absent and the leaves sessile or 0–0.1 mm long, the decurrent leaf bases running onto the stem, glandular pubescent like the stems and leaves. Inflorescences 2.5–4 cm long, opposite the leaves, unbranched but occasionally forked (*Rodríguez 1421*), with 10–20 flowers, densely glandular pubescent with transparent spreading simple uniseriate trichomes to 1.5 mm long; peduncle 1.2–2.5 cm long; pedicels 1.3–1.5 cm long, 0.5–0.7 mm in diameter at the base, ca. 1.5 mm in diameter at the apex, spreading at anthesis, densely glandular pubescent, articulated at the base; pedicel scars irregularly spaced 1–2 mm apart. Buds ellipsoid, the corolla ca. halfway exserted from the calyx before anthesis. Flowers 5-merous, perfect. Calyx tube 2–3 mm long, conical, the lobes 2.5–4 mm long, long-triangular, densely glandular pubescent with simple uniseriate trichomes like the pedicels and rest of the inflorescence, the tips acuminate and somewhat recurved at anthesis. Corolla 1.6–2.5 cm in diameter, pale lilac to violet with a yellow-green central star, stellate, lobed ca. 1/2 way to the base, the lobes 5–5.5 mm long, 4–5.5 mm wide, deltate, reflexed or spreading at anthesis, adaxially glabrous, abaxially sparsely glandular papillate especially on the midvein, tips and margins; stamens equal; filament tube 0.35–0.5 mm; free portion of the filaments 1–1.5 mm, almost glabrous, but with a few tangled transparent eglandular simple uniseriate trichomes adaxially; anthers 4–5.5 mm long, 1.25–1.6 mm wide, ellipsoid, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary conical, glabrous; style 7–8 mm long, densely papillate with a few longer simple trichomes in the lower third; stigma large capitate to slightly bilobed, the surface minutely papillate. Fruit a globose berry, 1–1.2 cm in diameter, green (?) at maturity, opaque, the surface of the pericarp glabrous, thin, matte; fruiting pedicels 1.5–2 cm long, ca. 1.5 mm in diameter at the base, ca. 2 mm in diameter at the apex, somewhat woody, deflexed from the weight of the berry, glandular pubescent to somewhat glabrescent; fruiting calyx accrescent in young

fruit tightly investing the berry, the tube 3–5 mm long, later tearing and the berry exposed, the lobes 3–5 mm long, ca. 3 mm wide, appressed to spreading. Seeds ca. 40 per berry, 1.5–2 mm long, 1–1.7 mm wide, flattened teardrop shaped with an apical hilum, reddish brown, the surfaces minutely pitted, testal morphology not clearly seen. Stone cells 10–11 per berry, 1–1.3 mm in diameter, globose, scattered throughout the berry. Chromosome number not known (but see comments on DNA content below).

Distribution (Figure 3). *Solanum hunzikeri* occurs in Argentina in the provinces of Catamarca and adjacent Salta and Tucumán and extends north to Bolivia in the departments of Tarija and Chuquisaca. The distribution is somewhat disjunct possibly due to loss of the wet high elevation foggy grassland habitat in the intervening areas.

Ecology and habitat. *Solanum hunzikeri* is confined to wet cloud forests and foggy grasslands above 1800 m elevation; it also grows in the ecotones between these vegetation types. These foggy grasslands are dominated by tall grasses (e.g., *Festuca hieronymi* Hack., *Cinnagrostis polygama* Griseb., *Elionurus muticus* (Spreng.) Kuntze [Poaceae]) and shrubs (e.g., *Baccharis* spp., *Stevia* spp. [Asteraceae]). *Solanum hunzikeri* can also be locally frequent on open grassy terraces with scattered palms, in narrow valleys with the lower slopes covered in seasonally moist forest dominated by *Parajubaea torallyi* (C.Mart.) Burret (Arecaceae) and with abundant *Podocarpus* spp. (Podocarpaceae) and can be found on steep, stony slopes in undisturbed grassland areas.

Etymology. This species is named in honour of the late Ing. Armando T. Hunziker of IMBIV in Córdoba, whose life work on the Solanaceae inspired a generation of solanologists, in both Argentina and globally.

Preliminary conservation status (IUCN 2019). AOO (80 km² – EN); EOO (97,627 km² – LC). Although the large extent of occurrence would suggest *S. hunzikeri* is not of conservation concern, the limited number of localities, the specialised habitat and the disjunct distribution suggest the species should be considered at risk. *Solanum hunzikeri* occurs in a very restricted habitat in which there are few officially protected areas. In these landscapes the main threat to the ecosystem is over-grazing; the introduction of alien forage species such as *Pennisetum clandestinum* Hochst. ex Chiov. (Poaceae) has severely altered the nature of the high elevation foggy grasslands and forest edges in which *S. hunzikeri* occurs. Although some populations are found in currently protected areas such as the Parque Nacional Aconquija, these areas are considered too small and isolated to provide long term conservation (Brown 1995). Based on the area of occupancy, the number of localities (ca. 8) in a disjunct distribution and threats to the habitat, we assign a preliminary threat status of Vulnerable (VU B2a,biii) for *S. hunzikeri*. The exploration of these relatively inaccessible habitats in the area between the currently known populations of *S. hunzikeri* is a priority.

Notes. *Solanum hunzikeri* had been recognized as distinct from other glandular-pubescent species in Argentina in the early 20th century by the German botanist Georg Bitter as “*Solanum catamarcae*”, a name already occupied in *Solanum* (*S. catamarcae* Bitter ex Brücher, a synonym of *S. boliviense* Dunal, see Spooner et al. 2019). Morton (1976) in his treatment of *Solanum* for Argentina, cited *Sleumer 2259* as part of his concept of *S. atriplicifolium* and stated “This last appears to be a local form that has the

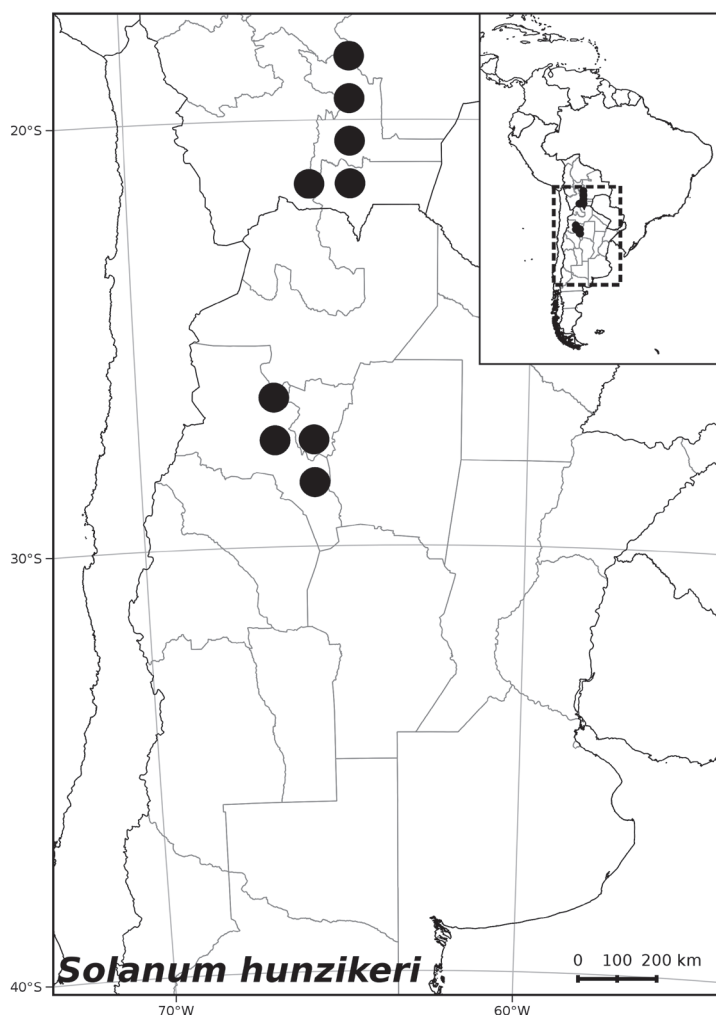


Figure 3. Distribution of *Solanum hunzikeri* Chiarini & Cantero.

petioles broadly winged nearly throughout instead of at the apex only. According to determinations by Dr. Sleumer this plant was given the unpublished name of “*Solanum catamarcae*” by Bitter.” Morton annotated the sheet of *Sleumer* 2259 in US as “*Solanum atriplicifolium* var. *sleumeri* Morton HOLOTYPE” in 1971 but did not publish the infraspecific epithet; he also annotated *Sleumer* 2311 (US) as a paratype of the same.

The species is now known from a wider distribution, and additional specimens have clarified its differences from the widespread and highly variable *S. tweedieanum*. *Solanum hunzikeri* can be distinguished from *S. tweedieanum* populations in similar high elevation areas in its strongly attenuate and winged leaf bases, those of *S. tweedieanum* are more truncate. The single collection we have seen of *S. hunzikeri* with ma-

ture fruit (*Rodríguez 1421* from Salta) has the calyx not covering any part of the mature berry; berries of *S. tweedieanum* are tightly covered by the accrescent calyx for at least 50% of their length. More collections of *S. hunzikeri* in fruit are needed to assess these differences. Preliminary data on DNA content for *S. hunzikeri* and *S. tweedieanum* (F. Chiarini unpubl.) show differences but suggest that, like *S. tweedieanum* (Moscone 1992), *S. hunzikeri* is diploid.

Additional specimens examined (paratypes). ARGENTINA. **Catamarca:** Dtto. Ambato, camino desde El Rodeo rumbo al Cerro el Manchado [Manchao], Falda El Morro, 2593 m, 24 Feb 2016, *Barboza et al. 4703* (CORD); Dtto. Ambato, Sierra de Ambato (falda E), subiendo desde El Rodeo hacia el Cerro Manchado [Manchao], 2300 m, 23 Feb 1967, *Hunziker 19073* (CORD, US); Dtto. Pomán, Rumbo al Cerro Manchado [Manchao], Sierra de Ambato, falda E, subiendo El Rincon hacia Las Casitas, rumbo al Cerro Manchado [=Cerro del Manchao], 2300–2500 m, 18 Feb 1970, *Hunziker & Ariza 20319* (CORD); Dtto. Pomán, Rumbo al Cerro Manchado, Sierra de Ambato, falda E, subiendo El Rincon hacia Las Casitas, rumbo al Cerro Manchado [= Cerro del Manchao], 2300–2500 m, 18 Feb 1970, *Hunziker & Ariza 20329* (CORD); Dtto. Ambato, Los Morteritos, Sierra de Ambato, falda E, subiendo desde El Rodeo hacia el Cerro Manchado [Manchao], Los Morteritos, 2300–2400 m, 13 Jan 1973, *Hunziker & Subils 22205* (CORD); Dtto. Ambato, Los Morteritos, Sierra del Ambato, falda E, subiendo desde El Rodeo hacia el Cerro Manchado [Manchao], 2300–2400 m, 13 Jan 1973, *Hunziker & Subils 22206* (CORD); Dtto. Andalgalá, Río Potrero, 2600 m, 13 Feb 1942, *Rohmeder s.n.* (LIL); Dtto. Andalgalá, Río Lampacillo-Río Potrero, Entre Río Lampacillo y Río Potrero, 2700–2900 m, 26 Feb 1951, *Sleumer 1834* (LIL, US); Dtto. Andalgalá, Mesada La Primera, Mesada La Primera, Las Estancias, 1900 m, 11 Feb 1952, *Sleumer 2132* (LIL); Dtto. Andalgalá, Los Queñoales, arriba de la Mesada de Las Rosas, 2300–2400 m, 15 Jan 1952, *Sleumer 2259* (G, LIL, US); Dtto. Andalgalá, Cuesta de la Negrilla, cerca de la Mina de Capillas, 3000–3100 m, 2 Mar 1952, *Sleumer 2690* (CORD, G, US); Dtto. Andalgalá, Cuesta de la Negrilla cerca de la Mina de Capillitas, 3100 m, 2 Mar 1952, *Sleumer 2691* (CORD, G, US, W); Dtto. Andalgalá, Mina de las Capillitas, cerca de los edificios, 2350 m, 2 Jan 1952, *Sleumer 2692* (US, W). **Salta:** Dtto. Cafayate, Peñas Blancas, Cerros de Cajón [Sierras de Quilmes], 4040 m, 30 Mar 1914, *Rodríguez 1421* (BR, CORD, SI). **Tucumán:** Dtto. Alberdi, Escaba, 2300 m, 27 Dec 1913, *Monetti 1838* (LIL); Dtto. Alberdi, Estancia Yunka Suma, Valle del Río Las Chacras [as Catamarca, Dtto. Andalgalá on labels], 1800 m, 23 Feb 1951, *Sleumer 1610* (LIL); Dtto. Alberdi, Cumbres de Suncho, Quebraditas del Portezuelo Sta. Anna [as Catamarca, Dtto. Andalgalá on labels], 2150 m, 8 Feb 1952, *Sleumer 2311* (LIL, US).

BOLIVIA. **Chuquisaca:** prov. Zudañez, a 82 km de Sucre, entre Tarabuco y Sudanéz, paraje Lambayo, 2756 m, 25 Feb 2004, *Cocucci et al. 3357* (CORD); prov. Azurduy, Tarvita, ca. 3 km S of summit on road from Tarvita to Azurduy, 2800 m, 4 Dec 1999, *Wood et al. 15303* (K); prov. Tomina, ca. 1 km W of summit of pass between Villa Tomina and Villa Serrano, 2700 m, 17 Mar 2002, *Wood 17868* (K); prov. Azurduy. Bajando de la cumbre hacia Duraznal en el camino de Azurduy, 2459 m, 11 Dec 2004,

Wood & Huaylla 21130 (K); prov. Tomina, entre Villa Serrano y Tomina, en la cumbre, 2580 m, 4 Mar 2006, *Wood et al. 22394* (K); prov. Zudañez, AMNI El Palmar, AMNI El Palmar, along trail from Torotoro to El Palmar crossing Río Mission Waypu., 2800 m, 2 Feb 2007, *Wood et al. 22612* (K). **Tarija:** Sama, between Tarija and Villazón, 3546 m, 27 Feb 1939, *Balls 6111* (E, K, US); de Tarija a Narváez, 2000–2500 m, 19 Mar 1982, *Kiesling et al. 3734* (SI); de Tarija a Iscayachi, 2000–3000 m, 20 Mar 1982, *Kiesling et al. 3845* (SI); Mun. O'Connor, at the top of the first pass W of Entre Ríos on road to Narváez and Tarija, 1800 m, 21 Jan 2001, *Wood & Goyder 16901* (K).

Cultivated. ARGENTINA. **Córdoba:** IMBIV, Universidad Nacional de Córdoba [plant grown from *Barboza et al. 4703*], 450 m, 15 Feb 2017, *Barboza 4763* (CORD).

***Solanum marmoratum* Barboza & S. Knapp, sp. nov.**

urn:lsid:ipni.org:names:77212301-1

Figs 4, 5

Diagnosis. Like *Solanum nitidibaccatum* Bitter but differing in eglandular, white pubescence, strongly winged stems, fleshy calyx lobes that are spreading in fruit and larger berries; also similar to *S. americanum* Mill. but differing in strongly winged stems and dark green mature berries marbled with white markings.

Type. ARGENTINA. La Pampa: Dtto. Loventué, 10 km al W de Luan Toro, rumbo a Loventué, 297 m, 9 Feb 2020, *G.E. Barboza, S. Knapp, F. Chiarini & R. Fortunato 5099* (holotype: CORD [CORD00007007]; isotypes: BAB, BM).

Description. Watery annual herb, 10–100 cm tall, sprawling and somewhat prostrate when very large. Stems strongly winged, the wing to 1 mm side, sometimes with spinose processes (old trichome bases), sparsely to moderately pubescent with spreading to appressed eglandular simple 5–8-celled uniseriate trichomes 0.5–1 mm long, these drying white; new growth densely pubescent with eglandular, white simple uniseriate trichomes 0.5–1 mm long; older stems greenish white, not woody. Sympodial units difoliate, the leaves not geminate, axillary shoots common. Leaves simple and shallowly toothed, 2–10 cm long, 1.5–6 cm wide, much larger in older plants, ovate, widest in the lower third, membranous, watery and somewhat succulent, concolorous, very bright green on live plants; adaxial and abaxial surfaces evenly white-pubescent with eglandular simple 5–8-celled uniseriate trichomes 0.5–1 mm long, these longer and denser on the veins; principal veins 5–6 pairs; base attenuate onto the petiole; margins shallowly and irregularly toothed, the teeth 2–4 mm long, 2.4– mm wide, broadly deltate, with blunt tips; apex acute; petioles 0.5–2.5 cm long, somewhat winged from the attenuate leaf base, pubescent with simple uniseriate trichomes like the stems and leaves. Inflorescences (1)2–3 cm long, internodal and extraaxillary, unbranched, with 5–7 flowers clustered at the tip, usually only 1–2 open at a time, sparsely and evenly pubescent with antrorse simple uniseriate trichomes 0.5–1 mm long like the stems and leaves; peduncle 1.4–2.5 cm long; pedicels 0.4 cm long, ca. 0.5 mm in diameter at the base, ca. 0.6 mm in diameter at the apex, slightly tapering, spreading, eglandular pubescent like the rest of the inflorescence, articulated at the base; pedicel scars tightly packed at the tip of the in-

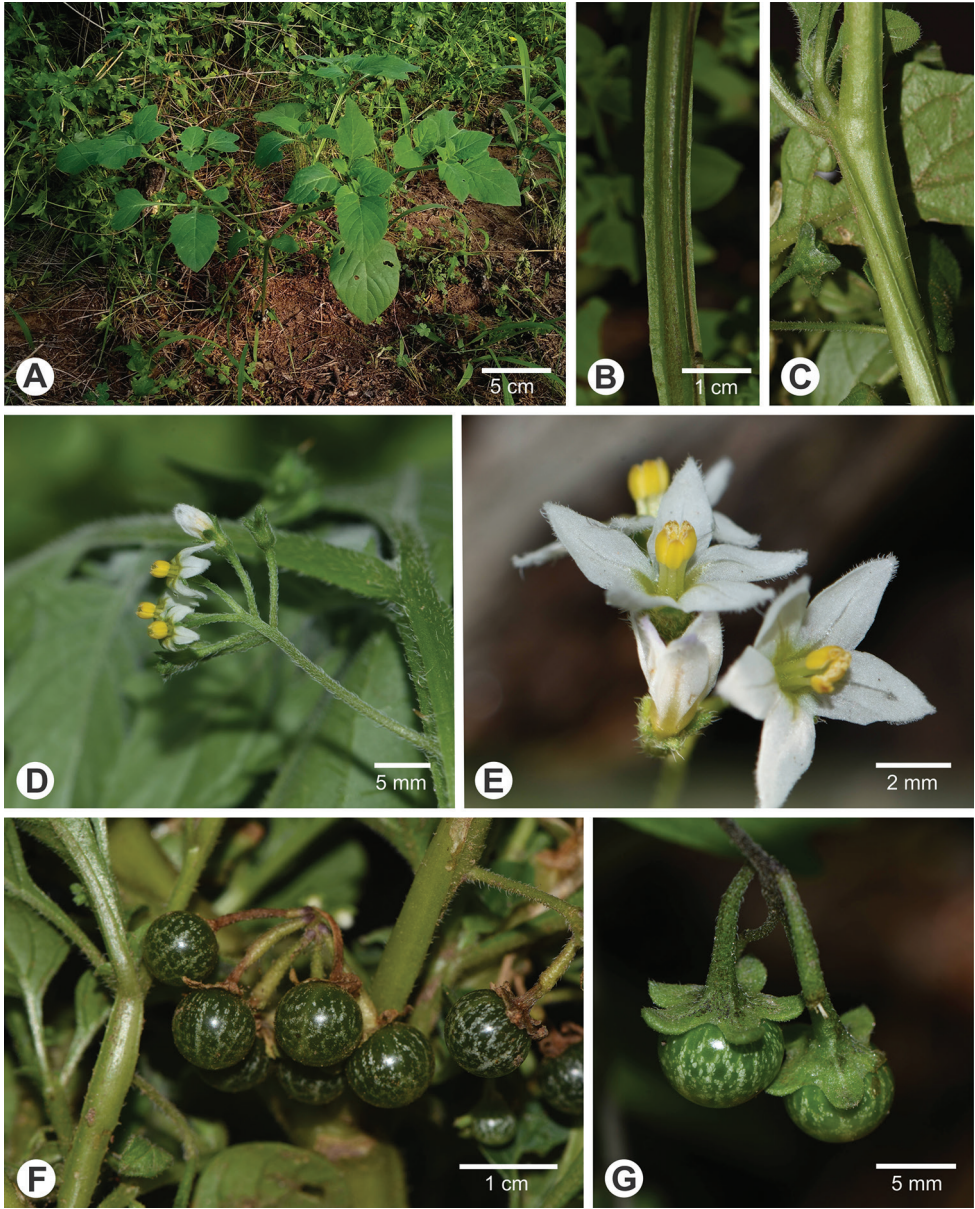


Figure 4. *Solanum marmoratum* Barboza & S.Knapp **A** habit (Barboza *et al.* 5099) **B, C** details of the winged stems (both at the same scale, B from Barboza *et al.* 5136, C from Barboza *et al.* 5073) **D** inflorescence (Barboza *et al.* 5136) **E** flowers, showing the included style and the filaments that elongate with flower age (Barboza *et al.* 5136) **F** mature fruits (Barboza *et al.* 5073) **G** Detail of berries showing the spreading fleshy calyx in fruit (Barboza *et al.* 5130). All photographs by S. Knapp.

florescence, 0.5–1.5 mm apart. Buds broadly ellipsoid, the corolla included in the calyx tube until just before anthesis. Flowers 5-merous, perfect. Calyx tube 1.2–1.5 mm long, cup-shaped, the lobes 1–1.5 mm, narrowly deltate-triangular, fleshy and recurved in live



Figure 5. *Solanum marmoratum* Barboza & S.Knapp (Barboza et al. 3668, BM [BM001134643]).

plants, sparsely pubescent with eglandular white trichomes on both surfaces like the rest of the plant. Corolla 0.5–0.8 cm in diameter, white with a green central star, stellate, lobed ca. halfway to the base, the lobes ca. 2.5 mm long, ca. 2 mm wide, spreading to slightly reflexed at anthesis (flowers closing daily and lasting for several days), adaxially glabrous, abaxially densely pubescent with tiny simple uniseriate trichomes especially at the tips. Stamens equal or slightly unequal with one anther marginally longer than the rest; filament tube ca. 0.1 mm long; free portion of the filaments 0.5–1 mm long, elongating through anthesis, with a few tangled transparent simple uniseriate trichomes adaxially; anthers 1–1.5 mm long 0.6–1 mm wide, ellipsoid, yellow, poricidal at the tips, the pores elongating with age. Ovary conical, glabrous; style 2–2.5 mm, included within the anther cone or the stigma just beyond, densely papillate in the lower 3/4; stigma large capitate, held at the level of the anthers when flowers first open, later included within the anther cone, bright green in life plants, the surfaces minutely papillate. Fruit a globose berry, 0.8–1.5 cm in diameter, dark green marbled with white at maturity, glabrous, translucent, the pericarp surface thin, shiny; fruiting pedicels 1.2–1.5 cm long, ca. 1 mm in diameter at the base, ca. 1.5 mm in diameter at the apex, fleshy and watery, tapering to the spreading calyx, strongly deflexed at maturity, with a distinct bend at the pedicel base; fruiting calyx somewhat expanded, the tube 3–4 mm long, the lobes 4–5 mm long, ca. 3 mm wide, spreading and fleshy, the tips rounded. Seeds 50–70 per berry, ca. 2 mm long, ca. 1.7 mm wide, flattened teardrop shape with an apical hilum, pale tan to reddish brown, the surfaces minutely pitted, the testal cells mostly rectangular to pentagonal in outline, more sinuate towards the seed centre. Stone cells 1–2, 1–1.1 mm in diameter, found randomly positioned in the berry. Chromosome number: not known.

Distribution (Figure 6). *Solanum marmoratum* is endemic to Argentina and occurs in the provinces of Catamarca, La Pampa, La Rioja, San Juan and San Luis; we expect it also to be found in Mendoza, because several collections are known from Desaguadero (San Luis) a locality very close to the provincial border that crosses through uniform habitat.

Ecology and habitat. *Solanum marmoratum* is found in shady areas in *Prosopis* woodlands (Fig. 4A) and at the edges of arable fields; it usually grows under trees and shrubs with a number of other herbaceous plants such as *S. tweedieanum*, various species of Asteraceae and grasses. Specimens have been collected from 200 to 1400 m elevation.

Etymology. The species is named for its distinctive marbled berries (Fig. 4F, G) that easily distinguish it from the similar tiny-flowered eglandular species *S. americanum*.

Preliminary conservation status (IUCN 2019). AOO (84 km² – EN); EOO (239,336 km² – LC). *Solanum marmoratum* is a relatively widespread species, the extent of occurrence suggests it should be given a status of least concern. The small area of occupancy perhaps reflects a lack of collecting in the dry forest and partially degraded habitats where *S. marmoratum* occurs. The number of localities (ca. 9) is probably an underestimate due to the widespread perception that these habitats are not interesting; most collections are quite old and the species has not been collected recently (except by us). The large-scale conversion of land in the range of *S. marmoratum* to intensive monoculture of commercial crops such as maize, peanuts and sunflowers poses a risk for this and other species in these habitats; use of herbicides and elimination of patches

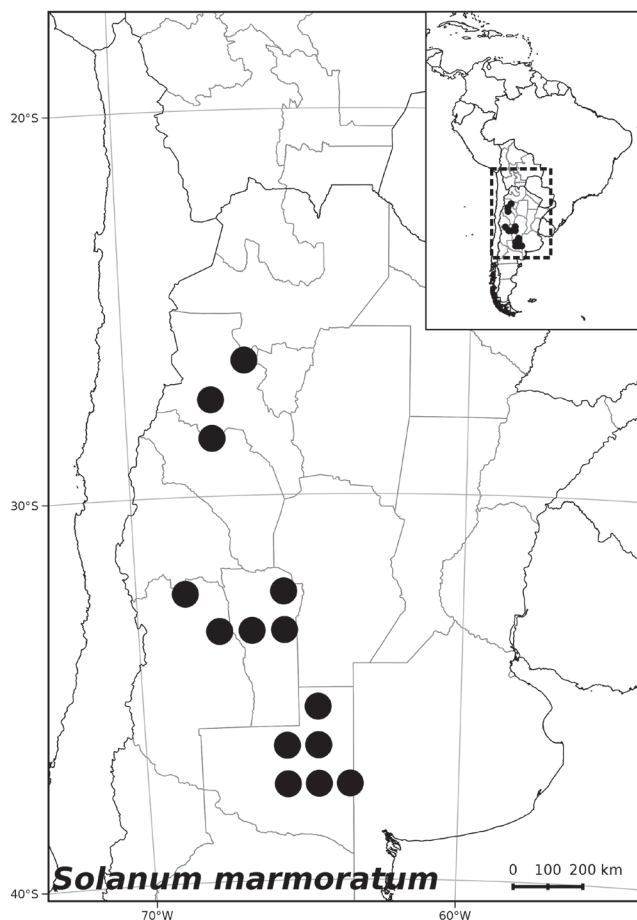


Figure 6. Distribution of *Solanum marmoratum* Barboza & S.Knapp.

of forest leave little room for even weedy species to persist. We suggest a preliminary threat status of Least Concern (LC) to *S. marmoratum*, but the widespread habitat conversion in central Argentina warrants further studies as to population status across the species' historical range.

Notes. *Solanum marmoratum* has long confused botanists working with Argentinian solanums. In the herbarium at CORD specimens of *S. marmoratum* collected by P. Steibel in the province of San Luis were the subject of correspondence with A.T. Hunziker over their identification; they were tentatively identified as *S. adventitium* Polg., a synonym of *S. americanum* described from adventive material in Hungary (Särkinen et al. 2018). None of the pre-1970s specimens we have seen were cited in Morton (1976), but *Semper s.n.* at US (barcode 02837698) was annotated “*Solanum dolichopteryx* Morton, paratype” by C.V. Morton in 1971. We have not found specimens annotated as other types at US or elsewhere. A.T. Hunziker had kept specimens

of this species aside with the herbarium name “*Solanum alatocaule*”, a reference to the strongly winged stems (Fig. 4B, C) on the folder, but never described it. We collected *S. marmoratum* in 2013 (Barboza *et al.* 3668) along with *S. tweedieanum*, and mistakenly noted the leaves of *S. marmoratum* as sticky (see Fig. 5); it was only examination of the dried specimens that alerted us to our error. Careful examination of all morelloid collections at CORD in early 2020 showed the distinctness of *S. marmoratum*, and its relatively widespread distribution.

The flowers of *S. marmoratum* are among the tiniest in the morelloid solanums (Fig. 4D, E) rivalled only by the globally distributed *S. americanum* and *S. nitidibaccatum* Bitter and the North American *S. emulans* Raf. (see Knapp *et al.* 2019). *Solanum nitidibaccatum* also has somewhat marbled berries but is always extremely sticky and covered with glandular trichomes, in contrast to the eglandular pubescence of *S. marmoratum*. *Solanum americanum* and *S. emulans* both have eglandular pubescence but have purplish black rather than green marbled berries. The fleshy spreading calyx lobes of *S. marmoratum* (Fig. 4G) are distinct from those of all of these taxa with tiny flowers.

Solanum marmoratum appears to be highly autogamous and is perhaps entirely self-fertilising. The style is completely included within the anther cone (Fig. 4D, E) and the filaments appear to elongate through anthesis (see Fig. 4E) bringing the style further into the cone as the flower ages. Flowers stay open for several days (closing at night) and in cultivation the plant goes from bud to flower to fruit in 15–18 days with all flowers setting fruit. Over the course of anthesis the style becomes enclosed in the anther cone (Fig. 4E), with the anthers as they dehisce leaving pollen directly on the stigma. Ripe berries last more than two weeks after being gathered from desiccated plants, remaining unchanged as to colour or odour.

Additional specimens examined (paratypes). ARGENTINA. **Catamarca:** Dtto. Santa María, Chiñucán, Sierra de la Aconquija, falda O, Chiñucán, 12 Apr 1948, *Reales 1264* (CORD); Dtto. Belén, Yacutula, Mar 1879, *Schickendantz 113* (CORD). **La Pampa:** Dtto. Toay, Reserva Provincial Parque Luro, pasando la laguna Luro, 233 m, 18 Jan 2013, *Barboza et al. 3668* (BM, CORD, SI); Dtto. Utracán, Valle de Daza, rumbo a la Laguna El Loro, 10–12 km de la RP 18, 290 m, 8 Feb 2020, *Barboza et al. 5073* (BM, CORD); Dtto. Toay, Reserva Parque Luro, ingreso S por ruta 35 desde General Acha, 116 m, 9 Feb 2020, *Barboza et al. 5079* (BM, CORD); Bajo Lucero, cruce entre RP 11 y RP 10, 255 m, 9 Feb 2020, *Barboza et al. 5094* (BM, CORD); Dtto. Atreucó, sin. loc., Mar 1960, *Cano 960* (US); Dtto. Rancul, Chamaicó, 2 Mar 1984, *Steibel & Troiani 7960* (CORD); Chamaicó, 2 Mar 1984, *Steibel & Troiani 7963* (CORD); Dtto. Atreucó, Laguna Chillhué, 5 Apr 1984, *Steibel et al. 8035* (CORD); Dtto. Capital, Barrancas Coloradas, 28 Feb 1991, *Steibel 10111* (CORD); Dtto. Toay, Parque Luro, 8 Mar 1991, *Steibel 10118* (CORD); Dtto. Capital, El Guanaco, 30 km al N de Santa Rosa, 13 Feb 1977, *Troiani 4688* (CORD); Dtto. Atreucó, Laguna Chillhué, 13 Mar 1982, *Troiani et al. 6820* (CORD); Dtto. Loventué, Luan Toro, 10 km al W, 10 Feb 1985, *Troiani 8564* (CORD). **La Rioja:** Dtto. Famatina, Ruta 40 [now Ruta Prov. 11] (km 640/641), yendo de Famatina a Tinogasta, 20 Mar 1960, *Hunziker et al. 15172* (CORD); Ruta 40 [now Ruta Prov. 11] (km 692), yendo de Famatina a

Tinogasta, entre Santa Cruz y el límite con Catamarca, 20 Mar 1960, *Hunziker et al. 15206* (CORD,US). **San Juan:** Dtto. Sarmiento, a 2 km de la estancia El Acequión, desde El Pedernal hacia el enpalme con Ruta provincial 412, por Ruta Prov. 312, 1400 m, 9 Apr 2004, *Matesevach 10 C*, (CORD). **San Luis:** Dtto. General Pedernera, Villa Mercedes, Estancia Agropecuaria INTA San Luis, lote 16, bajo, 510 m, 9 Jan 1969, *Anderson & Galvani 1511* (CORD); Sierra El Morro, cuenca interior, querencia pisoteada, 1200 m, 27 Dec 1977, *Anderson et al. 3427* (CORD); Dtto. Capital, Estancia Las Tres Marías, 30 km al sur de San Luis-Quemado, 700 m, 21 Mar 1979, *Anderson et al. 3643* (CORD); Dtto. Chacabuco, Concarán, cerca de 2 km desde Concarán rumbo a Santa Rosa de Conlara, por el camino de tierra (RP 23), 660 m, 24 Feb 2020, *Barboza et al. 5130* (BM, CORD); Concarán, cerca de 5.5 km desde Concarán rumbo a Santa Rosa de Conlara, por el camino de tierra (RP 23), 652 m, 24 Feb 2020, *Barboza et al. 5136* (BM, CORD); Dtto. Capital, Potrero de los Funes, 2 Apr 1989, *Del Vitto & Petenatti 3455* (CORD); Los Puquios, a 200 m del badén sobre el río Los Puquios en la ruta El Volcán-Cruz de Piedra, rumbo a Cruz de Piedra, 21 May 1972, *Giordano & Guerreiro 23* (CORD); Dtto. Chacabuco, a ca. 3 km al N de Concarán, rumbo a Santa Rosa, por el viejo camino de tierra, 17 Feb 1989, *Hunziker et al. 25335* (CORD); Dtto. Belgrano, Sierra del Gigante (falda O), Desaguadero, inmediaciones de Paso de Tropas, 7 Apr 1944, *Ruiz Leal 9191* (CORD); Dtto. Capital, entre Estación Jarilla y Desaguadero., 500 m, 7 Apr 1944, *Semper s.n.* (BM, US).

***Solanum tiinae* Barboza & S.Knapp, sp. nov.**

urn:lsid:ipni.org:names:77212302-1

Figs 7, 8

Diagnosis. Like *Solanum aloysiifolium* Dunal but differing in narrower leaves decurrent onto the stems, antrorse pubescence, ellipsoid buds and strongly deflexed fruiting pedicels.

Type. ARGENTINA. Tucumán: Dtto. Taí del Valle, El Infiernillo, en el parador, 3042 m, 13 Feb 2012, *G.E. Barboza, S. Knapp & T. Särkinen 3496* (holotype: CORD [CORD00013848]; isotypes: BM [BM001115408, BM001115409], others to be distributed).

Description. Perennial herbs or subshrubs sprawling from a woody base, to 50 cm tall. Stems narrowly winged, the wing to 0.5 mm wide, often invested with spinose processes (enlarged trichome bases), sparsely pubescent with antrorse eglandular, simple uniseriate trichomes, 6–10-celled, ca. 0.5 mm long, these white when dry; new growth densely to moderately pubescent with antrorse eglandular, simple 2–8-celled uniseriate trichomes, ca. 0.5 mm long; bark of older stems pale greenish brown, glabrescent. Sympodial units plurifoliate, the leaves not geminate. Leaves simple, 2–5 cm long, 0.6–2 cm wide, narrowly elliptic to almost lanceolate in some individuals, membranous, concolorous; adaxial surfaces sparsely and evenly pubescent with antrorse eglandular simple 2–4-celled uniseriate trichomes to 0.5 mm long, the trichomes slightly longer on the veins, white when dry; abaxial surfaces with similar, but denser eglandular antrorse pubescence; principal veins 4–6 pairs, drying yellow, especially abaxially;

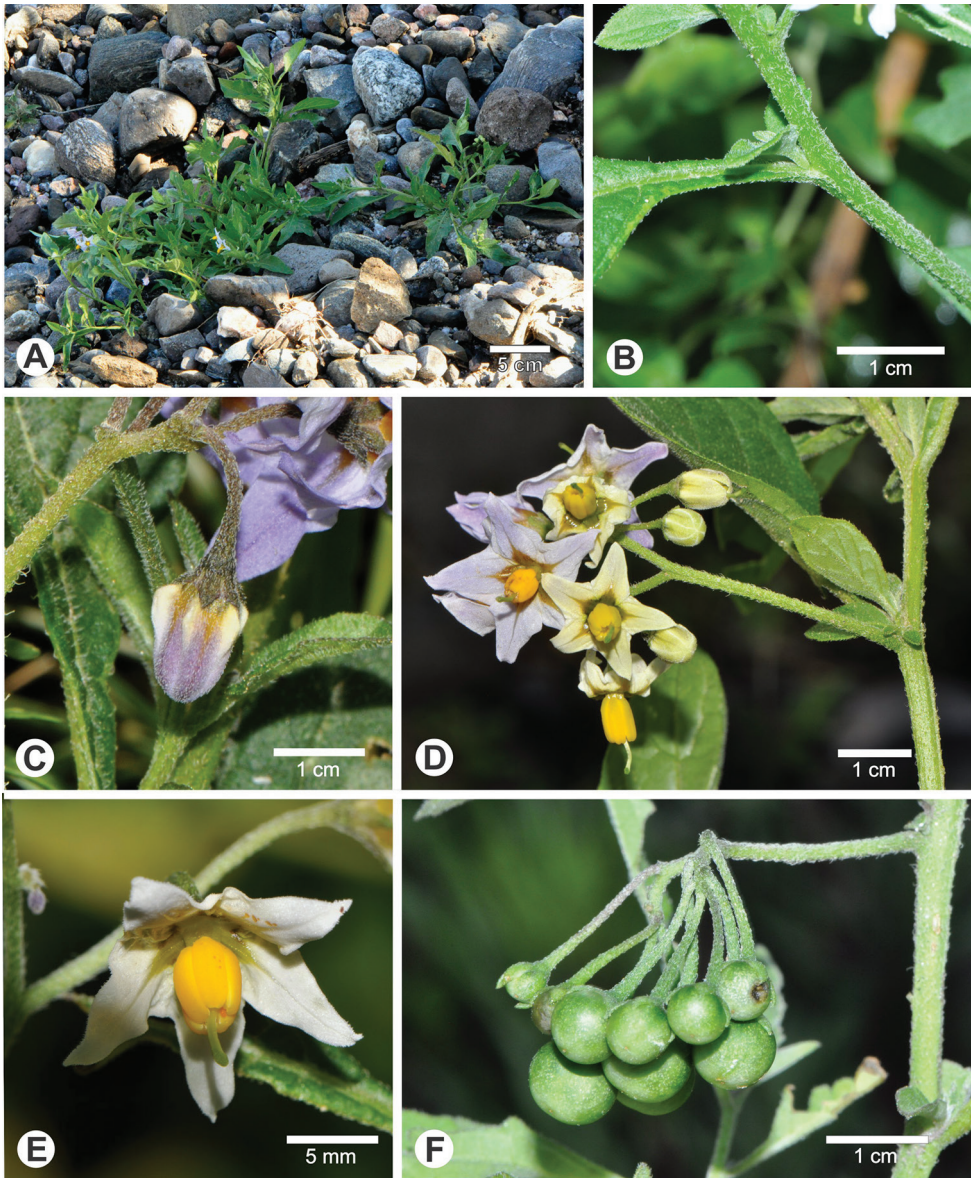


Figure 7. *Solanum tiinae* Barboza & S.Knapp **A** habit (Barboza *et al.* 3491) **B** details of the attenuate leaf base and winged stems with antrorse trichomes (Barboza *et al.* 3491) **C** flower bud (Barboza *et al.* 3496) **D** inflorescence (Barboza *et al.* 3491) **E** flowers at anthesis, note the changing colour and size (Barboza *et al.* 3491) **F** mature fruits (Barboza *et al.* 3491). All photographs by S. Knapp.

base attenuate and decurrent onto the winged stem and the leaves sessile or nearly so; margins entire or with a few teeth ca. 2 mm long, ca. 2 mm wide with blunt tips in the lower third to half; apex acute to slightly blunt-tipped; petiole absent to 0.2 mm long, eglandular pubescent like the stems and leaves. Inflorescences 2.5–5 cm long, opposite the leaves or internodal, forked with 2 short branches, with 10–20 flowers clustered

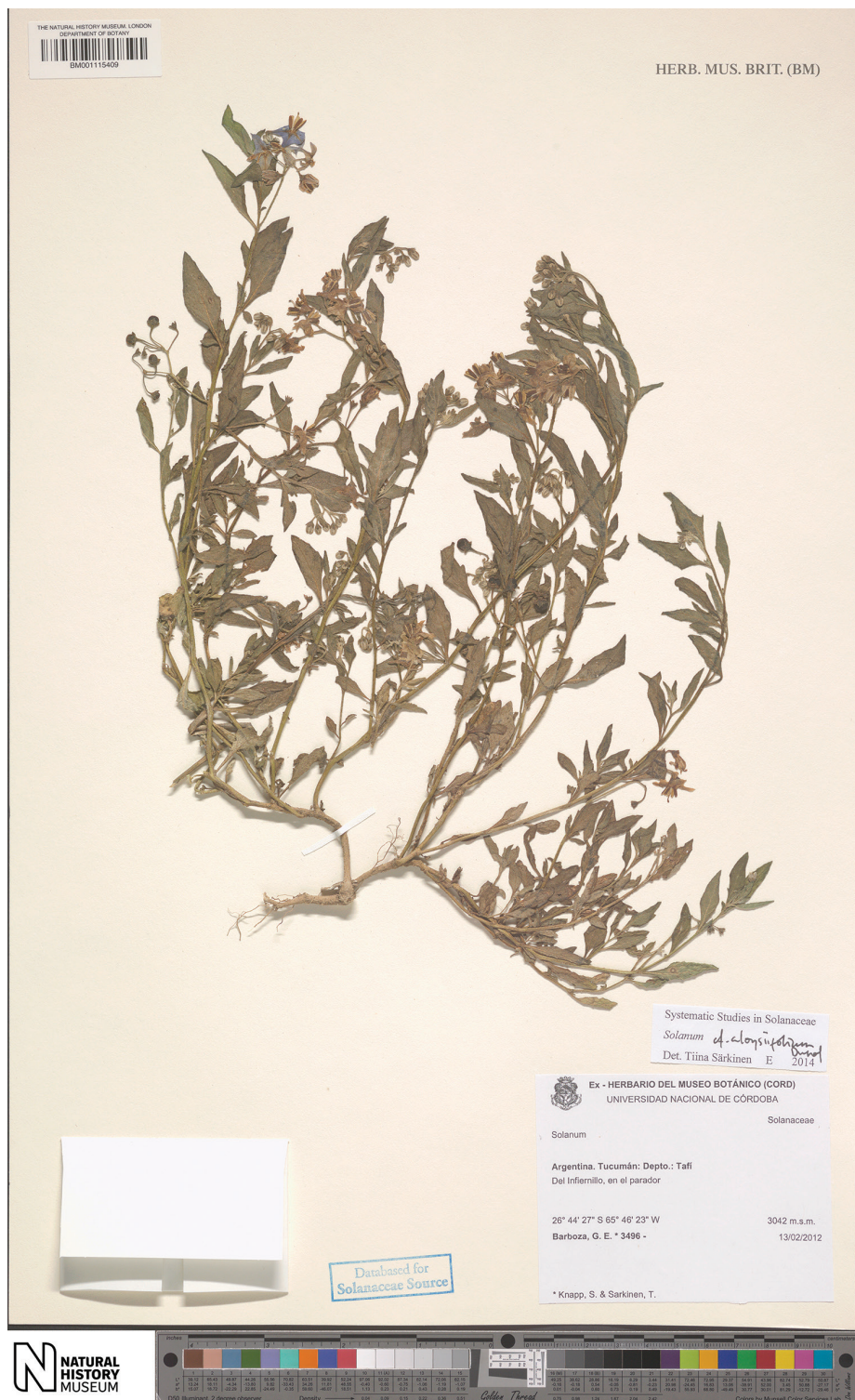


Figure 8. *Solanum tiinae* Barboza & S.Knapp (isotype: Barboza et al. 3496, BM [BM001115409]).

at the tips of the inflorescence branches, sparsely pubescent with antrorse eglandular simple uniseriate trichomes like those of the stems; peduncle 1.2–2.5 cm long; pedicels 0.8–1 cm long, ca. 0.5 mm in diameter at the base, ca. 1 mm in diameter at the apex, strongly tapering, spreading to somewhat deflexed at anthesis, sparsely to moderately sparsely pubescent with antrorse eglandular simple uniseriate trichomes like the rest of the inflorescence, articulated at the base; pedicel scars clustered at the tips of the inflorescence branches, ca. 0.5 mm apart. Buds ellipsoid to somewhat turbinate (widest in lower third), the corolla strongly exerted from the calyx tube before anthesis, the style sometimes exerted from the bud before anthesis. Flowers 5-merous, perfect. Calyx tube 1.5–2 mm long, conical, the lobes (0.5)1–2 mm long, deltate with lanceolate tips, the sinuses rounded, sparsely pubescent with antrorse eglandular trichomes like the pedicels. Corolla 1.2–2.2 cm in diameter, white, pale violet or white tinged with violet, sometimes changing colour through anthesis, with a brownish yellow to yellow-green central star edged with brownish purple, stellate, lobed halfway to the base, the lobes 5–8 mm long, 4–5 mm wide, deltate to triangular, spreading or slightly reflexed at anthesis, adaxially glabrous, abaxially densely pubescent with eglandular papillae and simple uniseriate trichomes to 0.2 mm long. Stamens equal; filament tube minute; free portion of the filaments 0.5–1 mm long, adaxially densely pubescent with tangled transparent simple uniseriate trichomes; anthers 4–5 mm long, 1–1.25 mm wide, ellipsoid, yellow, the abaxial surfaces occasionally papillate, poricidal at the tips, the pores lengthening to slits with age. Ovary conical, glabrous; style 7–10 mm long, pubescent along almost the entire length, more densely in the lower half with tangled transparent simple trichomes to 0.5 mm long; stigma capitate to clavate, bright green in live plants, the surface minutely papillose. Fruit a globose berry, 0.8–0.9 cm in diameter, green with tiny white spots (immature?), opaque, the pericarp surface thin, matte, glabrous; fruiting pedicels 0.8–1 cm long, ca. 0.75 mm in diameter at the base, ca. 1.5 mm in diameter at the apex, thickened but not woody, strongly deflexed with a distinct bend at the pedicel base; fruiting calyx not enlarged or accrescent, the lobes appressed to the surface of the berry. Seeds 10–30 per berry, 1.7–2 mm long, 1–1.5 mm wide, not markedly flattened, teardrop shaped with an apical hilum, pale tan, the surfaces minutely pitted, the testal cells sinuate in outline. Stone cells 4–9 per berry, 0.7–1.5 mm in diameter, 2 usually larger than the rest. Chromosome number: $n=12$ (Moscone 1992, as *S. lorentzii* Bitter var. *montigenum* C.V.Morton).

Distribution (Figure 9). *Solanum tiinae* is endemic to Argentina; it has been collected from the provinces of Jujuy, La Rioja, Salta and Tucumán, with most collections from the area around the type locality at El Infiernillo.

Ecology and habitat. *Solanum tiinae* grows among rocks and in open areas in pre-puna habitats in the Andes (Fig. 7A), from 2400 to 4000 m elevation.

Etymology. *Solanum tiinae* is named in honour of our long-term collaborator and colleague Dr. Tiina Särkinen of the Royal Botanic Garden Edinburgh; she was the first to notice the uniqueness of these plants, giving them the field name “*Solanum misterioso*” while in the field in 2012.

Preliminary conservation status (IUCN 2019). AOO (76 km² – EN); EOO (41,143 km² – NT). Most collections of *S. tiinae* are from a very few commonly vis-

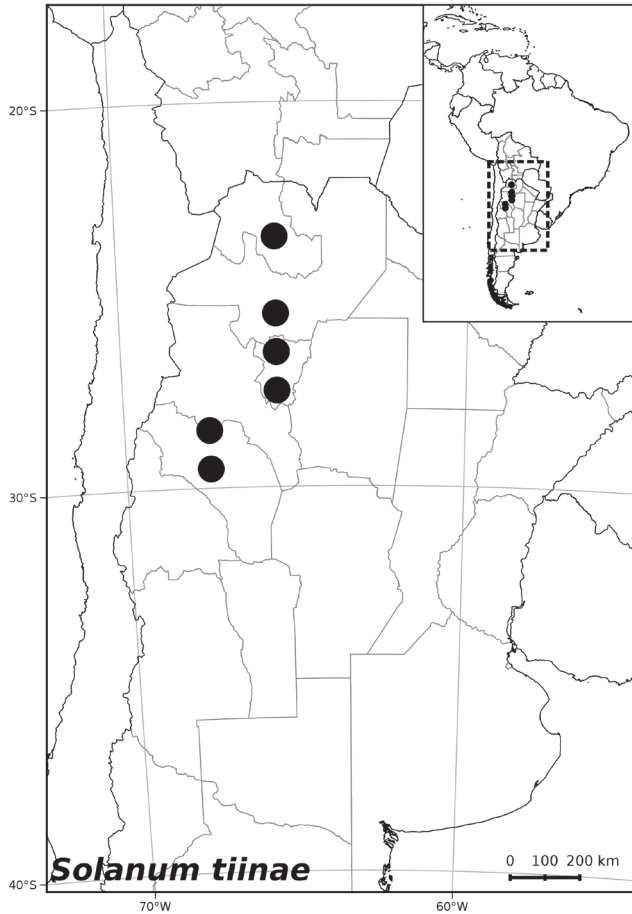


Figure 9. Distribution of *Solanum tiinae* Barboza & S.Knapp.

ited localities and the main road between Tafí del Valle and Amaicha del Valle in the province of Tucumán. *Solanum tiinae* is not found in protected areas, and based on the number of localities (ca. 5), the area of occupancy and the extent of occurrence, we assign a preliminary threat status of Vulnerable (VU B2a,biii). Where it occurs *S. tiinae* is not common or weedy, although it does grow in open areas.

Notes. It is surprising that *S. tiinae* has not been described previously, as the area from which the type and many other collections come is one of the most intensively collected Andean areas in Argentina. None of the collections we cite here were cited in Morton (1976). We have encountered specimens of *S. tiinae* identified as *S. aloysiifolium* (and its synonyms, see Barboza et al. 2013) and *S. cochabambense*. It is similar to those taxa in its forked inflorescence with a long peduncle, but differs from *S. aloysiifolium* in its larger, less deeply stellate purple or purplish cream (rather than white) corollas, and from *S. cochabambense* in its smaller habit and winged stems. The strongly antrorse pubescence of *S. tiinae* is distinctive and not found in either *S. aloysiifolium* or *S. cochabambense*.

Solanum tiinae also resembles the highly variable species *S. salicifolium*, from which it can be distinguished by its shorter (1–2 mm versus 2.5–3 mm long) calyx lobes, the strongly antrorse pubescence (Fig. 7B), the strictly furcate (versus only occasionally once branched) inflorescences with more flowers (10–20 versus 4–10) (Fig. 7B, C) and the calyx lobes (Fig. 7F) that are tightly appressed to the berry (versus spreading and slightly recurved). These two taxa have been collected in the same habitat (e.g., Barboza *et al.* 3491, *S. tiinae* and Barboza *et al.* 3494, *S. salicifolium* from km 92 on the Amaicha del Valle to Tafi del Valle road) and can be easily distinguished in the field using corolla shape – those of *S. salicifolium* are deeply stellate with relatively narrow lobes, while those of *S. tiinae* are less deeply and more broadly lobed (Fig. 7E).

Additional specimens examined (paratypes). ARGENTINA. **Jujuy:** Dtto. Tilcara, Sierra de Zenta, 4000 m, Feb 1931, *Budin* 7471 (CORD). **La Rioja:** Dtto. Famatina, Rodeo de las Vacas, 3000–4000 m, Feb 1913, *Flossdorf* 55 (SI); Quebrada Encrucijada, 3500–5000 m, Mar 1913, *Flossdorf* 56 (SI). **Salta:** Dtto. San Carlos, Amblayo, 2371 m, 16 Mar 1943, *Hunziker* 2623 (CORD); Dtto. Cachi, Ruta Prov. 33, de Piedra del Molino a El Carril, La Herradura, 3110 m, 26 Feb 2009, *Zuloaga et al.* 11256 (CORD, SI). **Tucumán:** Dtto. Tafi del Valle, Pinar de los Ciervos, Km 70, 2400 m, 6 Mar 1998, *Barboza et al.* 139 (CORD); Dtto. Tafi del Valle, Pinar de Los Ciervos, km 70, 2400 m, 6 Mar 1998, *Barboza et al.* 140 (CORD); Dtto. Tafi del Valle, entre Tafi del Valle y Amaichá: Km 76, 6 Mar 1998, *Barboza et al.* 150 (CORD); Dtto. Tafi del Valle, entre Tafi del Valle y Amaichá: Km 76, 6 Mar 1998, *Barboza et al.* 151 (CORD); Dtto. Tafi del Valle, entre Tafi del Valle y Amaicha, 6 Mar 1998, *Barboza et al.* 152 (CORD); Dtto. Tafi del Valle, El Infiernillo, 2920 m, 19 Mar 2006, *Barboza et al.* 1705 (CORD); Dtto. Tafi del Valle, Carapunco, rumbo a Amaicha del Valle por RP307, 2864 m, 24 Feb 2009, *Barboza et al.* 2167 (CORD); El Infiernillo, 2960 m, 24 Feb 2009, *Barboza et al.* 2172 (CORD); Dtto. Tafi del Valle, La Quebradita, a unos pocos km de Tafi del valle rumbo a Amaicha del Valle, 2053 m, 21 Feb 2011, *Barboza et al.* 3014 (CORD); Dtto. Tafi del Valle, a 28 km de Tafi rumbo a Amaicha del Valle, 2857 m, 21 Feb 2011, *Barboza et al.* 3019 (CORD); Dtto. Tafi del Valle, desde Amaicha del Valle rumbo a Tafi del Valle, entre km 92–91, 3000 m, 13 Feb 2012, *Barboza et al.* 3491 (BM, CORD); Dtto. Tafi del Valle, entre Tafi del Valle y Amaichá, El Infiernillo, 19 Feb 1988, *Cocucci et al.* 293 (CORD); Tafi del Valle, 2500 m, 24 Feb 1998, *Cocucci* 989 (CORD); Dtto. Tafi del Valle, Km. 82, al N de Tafi del Valle, hacia la quebrada del Barón, 3100 m, 26 Feb 1959, *Diers* 285 (SI); Dtto. Tafi del Valle, El Molle, en el camino entre Tafi del Valle y Amaicha, km 91–92, 2800–2900 m, 12 Feb 1986, *Hunziker et al.* 24878 (BM, CORD [x2], E, MO); Dtto. Tafi del Valle, El Molle, en el camino entre Tafi del Valle y Amaicha, km 91–92, 2800–2900 m, 12 Feb 1986, *Hunziker et al.* 24879 (CORD); Dtto. Tafi del Valle, viniendo desde Tafi del Valle, rumbo a Amaicha del Valle, entre kms 75 y 76, 2600–2700 m, 14 Dec 1995, *Hunziker et al.* 25546 (CORD); Dtto. Tafi del Valle, El Infiernillo, 22 km de Tafi del Valle, 2950 m, 18 Mar 1972, *Krapovickas et al.* 21885 (CTES); Tafi, 2000 m, 4 Dec 1908, *Lillo* 8691 (CORD, LIL, SI, US); Dtto. Tafi del Valle, La Ciénaga; Sierra de Tucuman, 10 Jan 1874, *Lorentz & Niederlein* 565 (CORD); Dtto. Tafi del Valle, 16 km N de Tafi del Valle, Mojon, K [km] 78, 16 Mar

1972, *Maruñak et al.* 209 (CTES); Infiernillo, Tafi del Valle, 1850 m, 2 Mar 1972, *Meyer s.n.* (LIL); Dtto. Tafi del Valle, Ruta 40, ca. 10 km NW de Tafi del Valle, Cumbres Calchaquíes, 2985 m, 26 Jan 2007, *Paula-Souza et al.* 7912 (CTES); Dtto. Tafi del Valle, Infiernillo, 3040 m, 8 Mar 1955, *de la Sota* 236 (CORD); Dtto. Tafi del Valle, Cumbres Calchaquí, Quebrada Honda, 3100 m, 23 Jan 1952, *Sparre* 9232 (CORD); Dtto. Tafi del Valle, Cumbres Calchaquí, Quebrada Honda, 3100 m, 23 Jan 1952, *Sparre* 9233 (CORD); Dtto. Tafi del Valle, Tafi del Valle, 4 Dec 1960, *Subils & Artico* 285 (BM, CORD); Dtto. Tafi del Valle, Colalao del Valle, alrededores, 17 Feb 1979, *Subils & Bernardello* 2670 (CORD); Dtto. Tafi del Valle, pasando Tafi del Valle rumbo a Amaicha, Carapunco, 2942 m, 1 Apr 2012, *Urdampilleta et al.* 760 (CORD); Dtto. Tafi del Valle, Tafi del Valle, 2900 m, 29 Jul 1971, *Without Collector s.n.* (BAA); Dtto. Tafi del Valle, El Infiernillo, RP 307, 2995 m, 18 Mar 2018, *Zuloaga et al.* 16415 (SI).

Artificial key to morelloid species occurring in Argentina*

- 1 Plants glandular pubescent, sticky to the touch; glandular trichomes usually several-celled.....2
- Plants not glandular pubescent or sticky to the touch; glandular trichomes, if present, very small and usually papillate.....14
- 2 Corolla campanulate, purplish blue; anthers with the connective enlarged abaxially3
- Corolla variously stellate, white or purple; anthers without obvious connective enlargement4
- 3 Inflorescence forked or several times branched, with 11–50+ flowers; calyx lobes triangular, shorter than the tube; fruiting calyx scarcely accrescent..... *Solanum fiebrigii* Bitter
- Inflorescence unbranched, subumbellate, with 4–7 flowers; calyx lobes narrowly triangular, longer than the tube; fruiting calyx accrescent, but leaving the berry exposed *Solanum sinuatiexcisum* Bitter
- 4 Anthers 0.8–2.5 mm long5
- Anthers 2.5–5(6) mm long8
- 5 Calyx lobes broadly deltate with rounded tips *Solanum grandidentatum* Phil.
- Calyx lobes variously triangular with pointed tips6
- 6 Calyx completely enclosing the bud; fruiting calyx covering more than half the berry; mature berry green; inflorescence leaf-opposed; plants delicate annuals *Solanum sarrachoides* Sendtn.
- Calyx not completely enclosing the bud; fruiting calyx covering less than half the berry; mature berry green with white marbling; inflorescence usually internodal, occasionally some inflorescences on a plant almost leaf-opposed; plants woody at the base, or more robust annual weeds7

* *Solanum concarense* is included here although molecular data have shown it to belong to the Dulcamaroid clade (see above).

- 7 Anthers ca. 2 mm long; fruiting calyx lobes spreading, with very marked venation; plants woody at the base *Solanum physalifolium* Rusby
- Anthers less than 1 mm long; fruiting calyx lobes not markedly spreading, the venation not marked; plants usually not woody at the base..... *Solanum nitidibaccatum* Bitter
- 8 Erect herbs or small shrubs, usually woody at the base; buds elongate ellipsoid, the corolla strongly exerted from the calyx in bud; inflorescence furcate (rarely unbranched); berry purple or green, less than 0.6 cm in diameter.....*Solanum glandulosipilosum* Bitter
- Decumbent or spreading herbs, sometimes woody at the base; buds broadly ellipsoid, variously covered by the calyx in bud; inflorescence unbranched (rarely furcate); berry green or green marbled with white, usually more than 0.6 cm in diameter.....9
- 9 Fruiting calyx accrescent and inflated, completely enclosing the berry *Solanum physalidicalyx* Bitter
- Fruiting calyx variously accrescent, but never inflated, only partially enclosing the berry if at all.....10
- 10 Fruiting calyx lobes spreading to reflexed, not appressed to the basal portion of the berry; stone cells absent in berry.....11
- Fruiting calyx lobes accrescent, appressed to the berry at least in early fruit, not spreading; stone cells present or absent in berry12
- 11 Anthers 3–3.8 mm long, wider at the base; corolla strongly exerted from the bud before anthesis, exceeding the tips of the lobes
..... *Solanum woodii* Särkinen & S.Knapp
- Anthers 2.5–3.2 mm long, ellipsoid, of equal width along entire length; corolla barely exceeding the calyx lobe tips before anthesis..... *Solanum michaelis* Särkinen & S.Knapp
- 12 Anthers 3–3.5 mm long; calyx lobes triangular; leaves narrowly elliptic to lanceolate; stone cells absent *Solanum profusum* C.V.Morton
- Anthers longer than 3.5 mm (occasionally in poorly developed flowers as short as 2.6 mm long), usually 4–5 mm long; calyx lobes narrowly triangular; leaves rhombic to elliptic in outline; stone cells present.....13
- 13 Leaf bases truncate, distinctly narrowing to a petiole; anthers ca. 1 mm wide; stone cells 6–8 per berry..... *Solanum tweedieanum* Hook.
- Leaf bases attenuate onto the petiole and stem, the petiole winged; anthers 1.2–1.5 mm wide; stone cells more than 10 per berry....*Solanum hunzikeri* Chiarini & Cantero
- 14 Anthers less than 3 mm long.....15
- Anthers more than 3 mm long.....28
- 15 Inflorescences forked or several times branched (occasionally with unbranched inflorescences on the same plant, but always some branched).....16
- Inflorescences unbranched20
- 16 Leaves entire, at most the margins shallowly toothed17
- Leaves deeply divided or entire and pinnatisect on the same plant19

- 17 Robust procumbent perennial herbs; berries red; leaves elliptic, the base attenuate; filaments glabrous; anthers ca. 1.7 mm long; currently only known from a local population in Salta..... ***Solanum tripartitum* Dunal**
- Various erect or spreading plants; berries green or purple; leaves ovate to broadly elliptic, with a distinct petiole, the base acute or truncate; filaments with tangled white pubescence adaxially (inside the anther cone); anthers greater than 2 mm long **18**
- 18 Stem slightly winged and with spinulose processes; leaf margins toothed, not finely ciliate; pedicels 4–7.5 mm long; style long-exserted from the anther cone, approximately equal to or longer than the anthers; stone cells more than 10 per berry ***Solanum furcatum* Dunal**
- Stem not winged or with spinulose processes; leaf margins usually entire and finely ciliate, if toothed then still finely ciliate; pedicels more than 8 mm long; style not long exserted from the anther cone, usually shorter than the anthers; stone cells 6–8 per berry..... ***Solanum zuloagae* Cabrera**
- 19 Tiny annual herbs; leaves pinnatisect, occasionally with both divided and entire leaves on the same plant, pubescent; corolla pentagonal; calyx accrescent in fruit; mature berry green ***Solanum annuum* C.V.Morton**
- Robust procumbent perennial herbs; leaves deeply three-parted, glabrous; corolla stellate; calyx not accrescent in fruit; mature berry red ... ***Solanum tripartitum* Dunal**
- 20 Tiny annual herbs; corolla pentagonal to rotate; fruiting calyx variously accrescent; seeds tuberculate..... **21**
- Annual or perennial herbs or subshrubs; corolla stellate; fruiting calyx not markedly accrescent; seeds minutely pitted, not tuberculate **23**
- 21 Fruiting calyx not enclosing the berry, accrescent but the entire fruit visible; inflorescence with 8–12 flowers; berry with only 2 seeds.... ***Solanum annuum* C.V.Morton**
- Fruiting calyx partly to completely enclosing the berry; inflorescence with 2–5 (6) flowers; berry with more than 2 seeds (to 20) **22**
- 22 Calyx lobes broadly elliptic to ovate, rounded at the tips, only partially enclosing the berry at maturity; anthers ca. 1 mm long; style only just exceeding the anther cone ***Solanum weddellii* Phil.**
- Calyx lobes long-triangular, pointed at the tips, inflated and completely enclosing the berry at maturity; anthers usually more than 1 mm long; style exserted from the anther cone ***Solanum gilioides* Rusby**
- 23 Inflorescences elongate with widely spaced flowers; berries yellow or greenish purple when mature **24**
- Inflorescences subumbelliform (with flowers clustered at the tips); berries green or purple when mature..... **25**
- 24 Prostrate herbs with stems often rooting at the nodes; leaves deeply three-parted; corolla rotate; filaments glabrous; berries translucent yellow ***Solanum palitans* C.V.Morton**
- Erect herbs or subshrubs; leaves entire or shallowly toothed; corolla stellate; filaments pubescent; berries purple or greenish purple when mature ***Solanum furcatum* Dunal**

- 25 Buds elongate oblong; corolla more than 1 cm in diameter; anthers 2–2.8 mm long, narrowly ellipsoid.....**26**
- Buds ellipsoid to more or less globose; corolla less than 1 cm in diameter; anthers ca. 1 mm long or less, broadly ellipsoid.....**27**
- 26 Mature berry surface matte; stone cells absent; pubescence usually appressed and drying white; peduncle and pedicels strongly deflexed in fruit***Solanum chenopodioides* Lam.**
- Mature berry surface shiny; stone cells 2; pubescence spreading; peduncle not deflexed in fruit, the pedicels deflexed and somewhat secund....***Solanum paucidens* Bitter**
- 27 Stem strongly winged and fleshy; calyx lobes narrowly deltate or triangular; mature berry bright green marbled with white; calyx lobes in fruit spreading, somewhat elongating (to ca. 5 mm long)***Solanum marmoratum* Barboza & S.Knapp**
- Stem unwinged, if winged not strongly so, not fleshy; calyx lobes deltate; mature berry black or purplish black; calyx lobes in fruit strongly reflexed, not elongating.....***Solanum americanum* Mill.**
- 28 Leaves deeply divided to pinnatifid, the segments linear or triangular**29**
- Leaves entire or shallowly toothed, not deeply divided into distinct lobes**31**
- 29 Annual herbs with rooting stems; buds narrowly ellipsoid; anthers ca. 0.5 mm wide, very narrowly ellipsoid***Solanum triflorum* Nutt.**
- Perennial plants, the base woody or the stems arising from rhizomes; buds broadly ellipsoid; anthers more than 0.5 mm wide, usually 1 mm wide or wider**30**
- 30 Perennial herbs from rhizomes, the base of the plant not markedly woody; leaves completely glabrous; calyx lobes deltate, equal in length to the tube; mature berry pale translucent yellow, with 8 large (more than 1 mm in diameter) stone cells.....***Solanum concarense* Hunz.**
- Subshrubs to shrubs, the base of the plant markedly woody; leaves variously pubescent with appressed simple trichomes; calyx lobes long-triangular to lanceolate, longer than the tube; mature berry green or whitish green, with ca. 10 small (less than 1 mm in diameter) stone cells.....***Solanum salicifolium* Phil.**
- 31 Anthers 3–3.5 mm long, 2–2.5 times longer than wide; buds globose to plump-ellipsoid**32**
- Anthers 3.5–6 mm long, 3–6 times longer than wide; buds ellipsoid**33**
- 32 Corolla yellow or cream-colored throughout; calyx lobes deltate to broadly triangular; leaf margins not ciliate***Solanum huayavillense* Del Vitto & Peten.**
- Corolla white with a green eye; calyx lobes narrowly triangular; leaf margins ciliate***Solanum zuloagae* Cabrera**
- 33 Inflorescence branched (forked to many times branched).....**34**
- Inflorescence unbranched.....**38**
- 34 Fleshy herbs, larger plants sometimes woody at the base; stems decumbent or somewhat erect; leaves glabrous and fleshy; flowers widely spaced on the inflorescence axis; corolla uniformly white; mature berries yellow or pale orange***Solanum caesium* Griseb.**
- Shrubs, subshrubs or herbs with woody bases; stems erect; leaves variously pubescent, membranous; flowers closely spaced on inflorescence axis; corolla white

- or lilac, with a central greenish or yellow-green eye; mature berries green or purple35
- 35 Pubescence of stems and leaves appressed; stem winged from decurrent leaf bases; fruiting pedicels strongly deflexed36
- Pubescence of stems and leaves spreading; stem not winged; fruiting pedicels spreading37
- 36 Pubescence strongly antrorse; inflorescence with 10–20 flowers; calyx lobes 1–2 mm long, deltate with lanceolate tips ***Solanum tiinae* Barboza & S. Knapp**
- Pubescence appressed but not strongly antrorse; inflorescence with 4–10 flowers; calyx lobes 2.5–3 mm long, long-triangular to lanceolate... ***Solanum salicifolium* Phil.**
- 37 Buds narrowly ellipsoid; corolla deeply stellate, lobed ca. 3/4 of the way to the base; inflorescences generally forked, only rarely more than once branched; berries ca. 0.5 cm in diameter ***Solanum aloysiifolium* Dunal**
- Buds ellipsoid; corolla stellate, lobed ca. halfway to the base; inflorescences usually many times branched; berries more than 0.5 cm in diameter ***Solanum cochabambense* Bitter**
- 38 Leaves thick and somewhat fleshy, the margins sharply toothed and often revolute in the sinuses39
- Leaves thin and membranous, the margins entire or shallowly toothed, never revolute42
- 39 Buds narrowly ellipsoid; anthers less than 1 mm wide; pubescence of stiff antrorse trichomes; annual herbs ***Solanum triflorum* Nutt.**
- Buds ellipsoid to broadly ellipsoid; anthers 1 mm wide or wider; pubescence of unicellular papillae or tangled white trichomes, not stiff and antrorse; perennials from a woody base (resprouting from the rhizome every season)40
- 40 Stems glabrous or with an even covering of minute papillate unicellular trichomes; inflorescence with more than 4 flowers; corolla white or pale violet ***Solanum echeagarayi* Hieron.**
- Stems with pubescence of tangled white multicellular trichomes; inflorescences with fewer than 4 flowers; corolla violet or deep purple41
- 41 Flowering pedicels 1–2 cm long; calyx lobes acute at the tips; corolla 1–1.2 cm in diameter, deep purple; anthers 4–5.5 mm long; fruiting pedicels 1.5–2 cm long; berry 1–1.5 cm in diameter, bright yellow at maturity... ***Solanum sinuatirecurvum* Bitter**
- Flowering pedicels 0.8–1.1 cm long; calyx lobes rounded at the tips; corolla 1.8–2 cm in diameter, pale lilac or white and lilac; anthers 3.5–4.5 mm long; fruiting pedicels 1.3–1.5 cm long; berry to 1.1 cm in diameter, green or purple ***Solanum riojense* Bitter**
- 42 Stem with prominent spinulose processes; sympodial units difoliate, the leaves usually geminate; fruiting calyx accrescent and inflated, completely enclosing the berry ***Solanum salamancae* Hunz. & Barboza**
- Stem terete or angled, without spinulose processes; sympodial units difoliate or plurifoliate, the leaves not geminate; fruiting calyx not accrescent nor completely enclosing the berry43

- 43 Subshrubs from a markedly woody base; stem angled or very narrowly winged from the decurrent leaf bases; pedicels inserted in enlarged swellings of the inflorescence rhachis, clustered; plants sometimes with entire, toothed and deeply pinnatifid leaves on the same plant.....*Solanum salicifolium* Phil.
- Herbs, the base of the plant not distinctly woody; stem terete; pedicels not inserted in enlarged swellings from the inflorescence rhachis, spaced or loosely clustered; leaves not markedly variable on the same plant, if variable some leaves with a few basal teeth44
- 44 Delicate rhizomatous herbs, the stems lax and weak; leaf bases acute to attenuate; leaves elliptic to narrowly elliptic; inflorescence with 2–6 flowers; calyx lobes 1.5–1.8 mm long, narrowly triangular, with acute sinuses; mature berry greyish green..... *Solanum pygmaeum* Cav.
- Large herbs with sprawling stems, not rhizomatous; leaf bases truncate to somewhat hastate (occasionally slightly cordate); leaves ovate-triangular; inflorescence with 5–15 flowers; calyx lobes 1–1.5 mm long, triangular, with rounded sinuses; mature berry purplish black *Solanum pilcomayense* Morong

Acknowledgements

We thank the curators of herbaria who lent specimens in their care and provided images of specimens generously when we needed them; Sarah Ficinski prepared the maps; Dr Tiina Särkinen and the late Ing. Armando Hunziker have both supplied inspiration and joy in the study of Solanaceae. Funding for this work came from various sources: National Science Foundation (USA) Planetary Biodiversity Initiative (PBI Solanum, DEB-1354791 to SK), Natural History Museum's Departmental Investment Fund (to SK for travel to Argentina), Secretaría de Ciencia y Tecnología-UNC (Res. 411/18; 99/19), CONICET (PIP Res. 0112/17), and Agencia Nacional de Promoción Científica y Tecnológica (PICT 2016/1525) to GB and FC.

References

- Anton AM, Zuloaga FO [Eds] (2013) Solanaceae. In: Barboza GE (coord.) Flora Argentina (Vol. 13), Solanaceae. IOBDA-IMBIV, CONICET, Buenos Aires & Córdoba, 349 pp.
- Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Barboza GE, Knapp S, Särkinen T (2013) Grupo VII. Moreloide. In: Anton AM, Zuloaga FO (Eds) Barboza GE (coord.) Flora Argentina (Vol. 13), Solanaceae. IOBDA-IMBIV, CONICET: Buenos Aires & Córdoba, Argentina, 231–264.
- Bitter G (1912) Solana nova vel minus cognita. III. Repertorium Specierum Novarum Regni Vegetabilis 11(9–15): 202–237. <https://doi.org/10.1002/fedr.19120110917>

- Brown AD (1995) Ecology and conservation of the Argentine montane forest. In: Hamilton LS, Juvik JO, Scatena FN (Eds) *Tropical Montane Cloud Forests. Ecological Studies (Analysis and Synthesis)*, vol 110. Springer, New York, 107–115. https://doi.org/10.1007/978-1-4612-2500-3_5
- Edmonds JM (1972) A synopsis of the taxonomy of *Solanum* Sect. *Solanum* (*Maurella*) in South America. *Kew Bulletin* 27(1): 95–113. <https://doi.org/10.2307/4117874>
- Frodin DG (2004) History and concepts of big plant genera. *Taxon* 53(3): 753–776. <https://doi.org/10.2307/4135449>
- Hooker WJ (1835) *Solanum Tweedianum*. *Curtis's Botanical Magazine* 62: Tab. 3385.
- IUCN (2019) Guidelines for using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> [accessed: 1 May 2020]
- Knapp S (2013) A revision of the Dulcamaroid clade of *Solanum* L. (Solanaceae). *PhytoKeys* 22(0): 1–432. <https://doi.org/10.3897/phytokeys.22.4041>
- Knapp S, Barboza GE, Bohs L, Särkinen T (2019) A revision of the Morelloid Clade of *Solanum* L. (Solanaceae) in the Caribbean and North and Central America. *PhytoKeys* 123: 1–144. <https://doi.org/10.3897/phytokeys.123.31738>
- Morton CV (1976) A Revision of the Argentine Species of *Solanum*. Academia Nacional de Ciencias. Córdoba, 260 pp.
- Moscone EA (1992) Estudios en cromosomas meióticos en Solanaceae de Argentina. *Darwiniana* 31: 261–297. <http://www.jstor.org/stable/23222568>
- Philippi RA (1891) *Catalogus praevious plantarum in itinere ad Tarapaca a Friderico Philippi lectarum* (*Catalogus plantarum in itinere Tarapacano lectarum*). *Anales del Museo Nacional de Chile, Segunda Sección, Botánica* 1891 [8]: 1–94. [2 tab.]
- Särkinen T, Knapp S (2016) Two new non-spiny *Solanum* (Solanaceae) from the Gran Chaco Americano and a key for the herbaceous glandular-pubescent solanums from the region. *PhytoKeys* 74: 19–33. <https://doi.org/10.3897/phytokeys.74.10159>
- Särkinen T, Olmstead RG, Bohs L, Knapp S (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology* 13: 214. <https://doi.org/10.1186/1471-2148-13-214>
- Särkinen T, Barboza GE, Knapp S (2015) True Black nightshades: Phylogeny and delimitation of the Morelloid clade of *Solanum*. *Taxon* 64(5): 945–958. <https://doi.org/10.12705/645.5>
- Särkinen T, Poczai P, Barboza GE, van der Weerden GM, Baden M, Knapp S (2018) A revision of the Old World black nightshades (Morelloid clade of *Solanum* L., Solanaceae). *PhytoKeys* 106: 1–223. <https://doi.org/10.3897/phytokeys.106.21991>
- Spooner DM, Jansky S, Rodríguez F, Simon R, Ames M, Fajardo D, Castillo RO (2019) Taxonomy of wild potatoes in northern South America (*Solanum* section *Petota*). *Systematic Botany Monographs* 108: 1–305.
- 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. Koelz Botanical Books, Gläshutten. <https://doi.org/10.12705/Code.2018>

Supplementary material 1

SM 1 – all morelloid species

Authors: Sandra Knapp, Franco Chiarini, Juan J. Cantero, Gloria E. Barboza

Data type: occurrences

Explanation note: SM 1 – Specimens of all morelloid species occurring in Argentina.

A csv format file of all specimens examined to date with each duplicate as a separate line. Column headings are: Herbarium = herbarium acronym acc. to Index Herbariorum; Category = specimen or photograph of specimen; SpecID = brahms specimen ID; Brahms = Brahms collection event ID; Accession = accession number of specimen; Barcode = barcode of specimen; Collector = principal collector; Prefix = collection number prefix (if applicable); Number = collection number; Suffix = collection number suffix (if applicable); AddColl = additional collectors; Type = type of type; Type of = type of what species; Day = day of collection; Month = month of collection; Year = year of collection; DateRes = date resolution (if applicable); Family = plant family; Genus = genus name; Species = species epithet; Author = species author name(s); Country = country of collection; Majorarea = first political division; Minorarea = second political division; Gazetteer = nearby town or place; Locnotes = locality; Habitattxt = vegetation characteristics; Lat = latitude; NS = north or south; Longitude = longitude; EW = east or west; LLunit = coordinate units (DD = decimal degrees; DM = decimal minutes; DMS = degrees, minutes, seconds); LLres = coordinate resolution (4 = nearest minute; 7 = area centroid); LLorigin = origin of coordinates; LatLong = coordinates in DMS; LatDec = decimal latitude; LongDec = decimal longitude; Alt = elevation minimum; AltMax = elevation maximum; AltRes = elevation resolution; AltUnit = elevation units (all metres); AltRange = elevational range.

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.164.54504.suppl1>

Supplementary material 2

SM 2– the three new species described here

Authors: Sandra Knapp, Franco Chiarini, Juan J. Cantero, Gloria E. Barboza

Data type: occurrences

Explanation note: SM 2 – Specimens of the new morelloid species described here (*Solanum hunzikeri*, *S. marmoratum* and *S. tiinae*). A csv format file of all specimens examined to date with each duplicate as a separate line. Column headings are as in SM 1.

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.164.54504.suppl2>

Revisiting the taxonomy of *Dioclea* and related genera (Leguminosae, Papilionoideae), with new generic circumscriptions

Luciano Paganucci de Queiroz¹, Cristiane Snak^{1,2}

1 Programa de Pós-Graduação em Botânica, Universidade Estadual de Feira de Santana, Av. Transnordestina s/n, Novo Horizonte, 44036-900, Feira de Santana, BA, Brazil **2** Departamento de Engenharia de Pesca e Ciências Biológicas, Universidade do Estado de Santa Catarina, Rua Cel. Fernandes Martins 270, Progresso, 88790-000, Laguna, Santa Catarina, Brazil

Corresponding author: Luciano P. de Queiroz (luciano.paganucci@gmail.com)

Academic editor: P. Herendeen | Received 17 June 2020 | Accepted 19 August 2020 | Published 21 October 2020

Citation: Queiroz LP, Snak C (2020) Revisiting the taxonomy of *Dioclea* and related genera (Leguminosae, Papilionoideae), with new generic circumscriptions. *PhytoKeys* 164: 67–114. <https://doi.org/10.3897/phytokeys.164.55441>

Abstract

The *Dioclea* clade comprises four genera and approximately 60 species of the tribe Diocleae: *Cleobulia* (4 species), *Cymbosema* (1), *Dioclea* (ca. 50), *Luzonia* (1) and *Macropsychnanthus* (3–4). *Dioclea* has been demonstrated to be a non-monophyletic genus, but low sampling in previous phylogenetic studies hampered the adoption of new taxonomic arrangements. We carried out densely sampled phylogenetic analyses of the *Dioclea* clade using molecular markers that had performed well in previous studies: the ITS and ETS nuclear ribosomal regions and the plastid *trnK/matK*. Our results support the maintenance of the genera *Cleobulia* and *Cymbosema* with their current circumscriptions, but confirmed the polyphyly of *Dioclea*, with its species falling into three different positions: (1) the puzzling species, *Dioclea paniculata*, was highly supported as a member of the Galactia clade; (2) *Dioclea* subg. *Dioclea* appeared as sister to a clade composed of *Cleobulia* and *Cymbosema*; and (3) the species of *Dioclea* subgenera *Pachylobium* and *Platylobium* composed a paraphyletic grade nesting the genera *Luzonia* and *Macropsychnanthus*. We thus propose that the circumscription of *Dioclea* should be restricted to *Dioclea* subg. *Dioclea*, with 13 species and that the limits of *Macropsychnanthus* should be widened to include the genus *Luzonia*, as well as the *Dioclea* subgenera *Pachylobium* and *Platylobium*, with 46 species. Taxonomic summaries, new combinations and synonyms are presented for all genera of the *Dioclea* clade. *Cleobulia* and *Cymbosema* were retained in their original circumscriptions. We presented an illustrated taxonomic conspectus of all genera of the *Dioclea* clade including 44 new combinations, one new name, ten new synonyms, two re-established holotypes, 38 lectotypes, two epitypes and one neotype.

Keywords

Cleobulia, *Cymbosema*, Diocleae, Fabaceae, *Luzonia*, *Macropsychnanthus*, phylogeny, recircumscription

Introduction

The genus *Dioclea* Kunth is one of the most important groups of tropical rainforest lianas. It includes some of the largest plants in primary forests, which are capable of spreading over wide areas on the canopies of the highest trees, often at heights above 30 m. With approximately 50 species in its current circumscription, the genus is distributed throughout the humid tropics of the Americas, Africa, Asia and the Pacific Islands. *Dioclea* is included in Diocleae, a tribe of Papilionoid legumes with 14 genera and approximately 200 species (Queiroz et al. 2015). Together with four other small genera, it composes the Dioclea clade, a monophyletic lineage that includes the geographically restricted genera *Cleobulia* Mart. ex Benth. (four species from the Neotropics), *Cymbosema* Benth. (one Amazonian and Mesoamerican species), *Luzonia* Elmer (one species from the Philippines) and *Macropsyчанthus* Harms (2–3 species from New Guinea and neighbouring islands) (Queiroz et al. 2015).

In addition to a woody, coarse lianescent habit, the genera of the Dioclea clade also share trifoliolate leaves with stipellate leaflets, a pseudoracemose inflorescence with woody multiflorous nodes, rather large and robust firm flowers, a pseudomonadelphous androecium (i.e. with the 10 stamens joined in a tube, but with the vexillary stamen free at the base, forming fenestration via two holes at the base of the staminal tube) and a fleshy and robust intrastaminal nectary disc. Their large flowers are mostly pollinated by large carpenter bees, but some species are adapted for bird pollination (Arroyo 1981; Franco 1995; Peçanha 2014). Most species have large fruits and large seeds with long and linear (or short and oblong) hilum (Lackey 1981; Maxwell and Taylor 2003; Queiroz et al. 2003) and disperse their seeds through autochory, but some species have buoyant sea-drifted seeds (Muir 1933; Armstrong 2001).

The Dioclea clade is one of three highly-supported major lineages of the tribe Diocleae, as revealed by a multilocus molecular phylogeny using the nuclear ITS/5.8S and ETS regions and the plastid *matK* gene and the *trnT-Y* region (Queiroz et al. 2015). Previous studies, based on either morphological (Maxwell and Taylor 2003; Queiroz et al. 2003) or molecular (nrITS) data with sparser sampling (Varela et al. 2004), suggested its existence, but with low support. None of the previous studies supported the monophyly of the genus *Dioclea* and, instead, it was recovered as a biphyletic group roughly corresponding to long-recognised infrageneric taxa: the species of *Dioclea* sect. *Dioclea* grouping with the New World genera *Cleobulia* and *Cymbosema* (Maxwell & Taylor 2003; Queiroz et al. 2003, 2015; Varela et al. 2004; Sede et al. 2009) and the species belonging to sections *Pachylobium* Benth., *Platylobium* Benth. and *Macrocarpon* Amshoff nesting the representatives of the Old World genus *Macropsyчанthus* (Maxwell and Taylor 2003; Queiroz et al. 2015). More recently, we included a sequence of the plastid *matK* gene of *Luzonia purpurea* Elmer in a broader phylogenetic analysis of the Leguminosae and it appeared as a sister to *Macropsyчанthus*, nested within the second lineage of *Dioclea*, but with low support (LPWG 2017).

The morphological recognition of the two major lineages that include the species of *Dioclea* can be traced back to Bentham (1837), who divided the genus into the

sections *Dioclea* (as *Eudioclea*) and *Pachylobium*. He later added a third section, *Platylobium* (Bentham 1859). Those three sections were diagnosed by a combination of just a few morphological traits: sect. *Dioclea* with stipules not prolonged beyond their base, keel petals straight and erostrate, all anthers fertile and uniform, fruits elastically dehiscent and seeds with a linear hilum; sect. *Platylobium* sharing with sect. *Dioclea* non-prolonged stipules, but with the keel strongly incurved, anthers alternately fertile and sterile, fruits flat compressed and obovate with 2–3 seeds near the apex and seeds with a short and oblong hilum; and sect. *Pachylobium* sharing with sect. *Platylobium* flowers with an incurved and rostrate keel and the anthers alternately fertile and sterile, but with stipules prolonged beyond their base, fruits indehiscent or partially dehiscent and seeds with a linear hilum encircling more than half of the seed's circumference.

The circumscriptions of Bentham's sections became less clear with the discovery of some Amazonian species that combined the diagnostic features of different sections, as was the case with *Dioclea macrocarpa* Huber and *D. erecta* Hoehne, which have androecia typical of sect. *Dioclea* and seeds typical of sect. *Platylobium*. Amshoff (1939) then created sect. *Macrocarpon* to include the species of *Dioclea* with stipules not prolonged beyond their base, androecium with uniform anthers, fruits mostly oblong with 4–5 seeds evenly distributed along their length and seeds with a short, oblong hilum. Maxwell (2011) elevated those three sections created by Bentham to subgenera and included Amshoff's sect. *Macrocarpon* into subg. *Platylobium*.

Despite the existence of phylogenetic studies focusing on the tribe Diocleae, there has been no re-appraisal of the taxonomy of the Dioclea clade incorporating those findings. We can speculate that the situation probably reflects the rather sparse sampling of taxa across the morphological and geographical ranges of the included genera. Here, we thus provide a re-assessment of the taxonomy of the Dioclea clade in light of robust and densely-sampled phylogenetic analyses. These analyses sought to: (1) test the previous findings of paraphyly of the genus *Dioclea* and its relationships with the remaining genera of the Dioclea clade; (2) re-examine the monophyly of the infrageneric groups of *Dioclea*; and, (3) provide a new generic classification that reflects the phylogenetic structure of the Dioclea clade.

Materials and methods

Taxon sampling was designed to test the monophyly of the Dioclea clade of the tribe Diocleae as identified by Queiroz et al. (2015), to test the monophyly of its genera and to explore relationships between the genera. The sampling included 62 accessions corresponding to: one species of the monospecific *Cymbosema*, four species of *Cleobulia* (100% of all species in the genus), one species of the monospecific *Luzonia*, one species and two varieties of *Macropsyчанthus* (50% of the species and 33% of all taxa) and 36 described species (+ six inedit) of *Dioclea* (60%). *Canavalia bonariensis* Lindl. (*Canavalia* clade), *Cratylia mollis* Mart. ex Benth. and *Collaea stenophylla* (Hook. & Arn.) Benth. (*Galactia* clade) were selected as outgroups for phylogenetic analyses in

the tribe Diocleae and *Deguelia nitidula* (Benth.) A.M.G. Azevedo & R.A. Camargo and *Muelleria obtusa* (Benth.) M.J. Silva & A.M.G. Azevedo (Millettieae) were selected as more remote outgroups to root the trees. A complete list of the vouchers associated with GenBank accessions are presented in Table 1.

The DNA regions used in this study are the same as those used by Queiroz et al. (2015): the plastid *trnK/matK* (the *matK* gene and partial flanking *trnK* introns) and ribosomal nuclear ETS (partial 3' end of the External Transcribed Spacer) and ITS (5.8S and flanking Internal Transcribed Spacers 1 and 2) (Table 2).

Total genomic DNA was extracted from silica gel-dried leaves using the 2× CTAB protocol of Doyle and Doyle (1987). For herbarium samples, DNA was extracted using the DNeasy Plant Mini Kit (QIAGEN GmbH, Hilden, Germany). PCR reactions were performed using the TopTaq Master Mix Kit (QIAGEN GmbH, Hilden, Germany) according to the manufacturer's protocols, with a final volume of 10 µl. For herbarium samples, the PCR reactions also included 2 µl of TBT-PAR [trehalose, bovine serum albumin (BSA), polysorbate-20 (Tween-20)] (Samarakoon et al. 2013) and, for ITS, they also included 0.2 µl of 99.5% DMSO (dimethyl sulphoxide) to avoid secondary conformations. Primers and PCR conditions are summarised in Table 2.

The PCR products were cleaned using 11% PEG (Paithankar and Prasad 1991) and then sequenced in both directions using the Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Austin, Texas, USA) according to the following protocol: a hot start followed by 3 min of initial denaturation at 96 °C, 30 cycles of 96 °C denaturation for 20 s, 50 °C annealing for 15 s and a 60 °C extension for 4 min. Sequencing products were cleaned using 80% isopropanol and 70% ethanol and analysed on a 3130xl Genetic Analyser (Applied Biosystems/HITACHI, Tokyo, Japan) at the Laboratório de Sistemática Molecular de Plantas of the Universidade Estadual de Feira de Santana (LAMOL/UEFS).

The original electropherograms were assembled into final sequences using the Geneious platform (Drummond et al. 2012). The sequences were automatically aligned in MUSCLE with default settings (Edgar 2004) and then checked using Geneious for manual adjustments. We carried out maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses for both individual and combined (nrITS, nrETS and *trnK/matK*) DNA datasets. Conflicts amongst datasets were evaluated by the incongruence length difference test (ILD; Farris et al. 1995), performed in PAUP v.4.0b10 (Swofford 2002) between nuclear regions and between the nuclear and plastid regions, using a heuristic search with 1000 replicates, random taxa-addition and tree bisection and reconnection (TBR) branch-swapping, saving 15 trees per replicate.

The search for the most parsimonious trees was carried out in PAUP v. 4.0b10 (Swofford 2002). Heuristic searches were made with 1000 random taxon-addition and tree bisection-reconnection (TBR) branch swapping, saving 15 trees per replicate. The trees saved in this first round were used as starting trees for a subsequent round of TBR swapping. All character state transformations were weighted equally and unordered (Fitch 1971). Non-parametric bootstrap resampling was used to estimate

Table 1. Voucher information and GenBank accession numbers for the DNA sequences used in this study. Original sequences are presented with an asterisk.

Taxon	Voucher	Locality	GenBank accession numbers		
			ITS	ETS	trnK/matK
OUTGROUPS (Tribe Millettieae)					
<i>Deguelia nitidula</i> (Benth.) A.M.G. Azevedo & R.A. Camargo	L.P. Queiroz 14503 (HUEFS)	Brazil, Bahia	*MT565565	KC779809	KC779548
<i>Muelleria obtusa</i> (Benth.) M.J. Silva & A.M.G. Azevedo	L.P. Queiroz 13959 (HUEFS)	Brazil, Bahia	*MT565566	KC779808	KC779550
TRIBE DIOCLEAE					
CANAVALIA CLADE					
<i>Canavalia bonariensis</i> Lindl.	C. Snak 518 (HUEFS)	Brazil, Paraná	KT751426	KT751375	KT751472
GALACTIA CLADE					
<i>Collaea stenophylla</i> (Hook. & Arn.) Benth.	L.P. Queiroz 12460 (HUEFS)	Brazil, Rio Grande do Sul	KC779802	KC779908	KC779566
<i>Cratylia mollis</i> Mart. ex Benth.	L.P. Queiroz 8024 (HUEFS)	Brazil, Bahia	KC779675	KC779879	KC779568
DIOCLEA CLADE					
<i>Cleobulia</i> Mart. ex Benth.					
<i>Cleobulia crassistyla</i> R.H. Maxwell	S. Ronán 12224 (E)	Mexico, Guerrero	KC779672	KC779817	*MT565534
<i>Cleobulia leiantha</i> Benth.	I.P. Miranda 37 (INPA)	Brazil, Pará		KC779818	
<i>Cleobulia multiflora</i> Mart. ex Benth.	P.C.N. Jesus 13 (HUEFS)	Brazil, Bahia	KC779673	KC779819	KC779564
<i>Cleobulia diocleoides</i> Benth.	L.P. Queiroz 16306 (HUEFS)	Brazil, Bahia	*MT565567	*MT565546	*MT565535
<i>Cymbosema</i> Benth.					
<i>Cymbosema roseum</i> Benth.	D. Cardoso 2868 (HUEFS)	Brazil, Amazonas	KC779676	KC779816	KC779569
<i>Cymbosema roseum</i> Benth.	C. Snak 1211 (HUEFS)	Brazil, Pará	*MT565568	*MT565547	*MT565536
<i>Dioclea</i> Kunth					
<i>Dioclea</i> subgen. <i>Dioclea</i>					
<i>Dioclea</i> aff. <i>virgata</i>	C. Snak 1233 (HUEFS)	Brazil, Pará	*MT565569	*MT565548	*MT565537
<i>Dioclea apurensis</i> Kunth	L.P. Queiroz 13044 (HUEFS)	Brazil, Pará	KC779677		
<i>Dioclea apurensis</i> Kunth	N. Costa 2312 (HUEFS)	Brazil, Pará		KC779828	
<i>Dioclea burkartii</i> R.H. Maxwell	R.C. Salas s.n. (CTES)	Argentina, Corrientes	KC779680	KC779830	KC779571
<i>Dioclea fimbriata</i> Huber	C. Snak 1223 (HUEFS)	Brazil, Pará	*MT565571	*MT565551	*MT565539
<i>Dioclea guianensis</i> var. <i>guianensis</i> Benth.	M. Sanchez s.n. (CIAT 9311)	Colombia, Vichada	KC779689		KC779575
<i>Dioclea guianensis</i> var. <i>holtiana</i> Pittier ex R.H. Maxwell	E. Ventura 2837 (MEXU)	Mexico, Chiapas	*MT565572	*MT565552	*MT565540
<i>Dioclea lasiophylla</i> Mart.ex Benth.	D. Cardoso 2324 (HUEFS)	Brazil, Bahia	KC779692	KC779832	KC779578
<i>Dioclea sericea</i> Kunth	R. Schultze-Kraft s.n. (CIAT 9578)	Colombia, Cauca	KC779715	KC779823	KC779588
<i>Dioclea ulei</i> ined.	E.H.G. Ule 7169 (L)	Brazil, Piauí	*MT565582		
<i>Dioclea vallisensis</i> R.H. Maxwell	D.J. Belalcázar s.n. (CIAT 17892)	Colombia, Antioquia	KC779718	KC779824	KC779591
<i>Dioclea virgata</i> var. <i>crenata</i> R.H. Maxwell	R. Schultze-Kraft s.n. (CIAT 18631)	Brazil, Pará	KC779682	KC779831	KC779572
<i>Dioclea virgata</i> var. <i>virgata</i> (Rich.) Amshoff	D. Cardoso 2917 (HUEFS)	Brazil, Rondônia	KC779723	KC779827	KC779593
<i>Dioclea</i> subgen. <i>Pachylobium</i> (Benth.) R.H. Maxwell					
<i>Dioclea aurea</i> R.H. Maxwell	A. Gentry 17811 (MEXU)	Colombia, Chocó		*MT565549	
<i>Dioclea densiflora</i> Huber	L.P. Queiroz 15904 (HUEFS)	Brazil, Pará	*MT565570	*MT565550	*MT565538
<i>Dioclea edulis</i> Kuhlman.	L.P. Queiroz 15226 (HUEFS)	Brazil, Bahia	KC779683	KC779835	KC779573

Taxon	Voucher	Locality	GenBank accession numbers		
			ITS	ETS	trnK/matK
<i>Dioclea glabra</i> Benth.	L.P. Queiroz 10381 (HUEFS)	Brazil, Mato Grosso	KC779684	KC779837	
<i>Dioclea grandiflora</i> Mart. ex Benth.	L.P. Queiroz 7325 (HUEFS)	Brazil, Bahia	KC779686	KC779839	KC779574
<i>Dioclea grandistipula</i> L.P. Queiroz	H.C. Lima 6634 (HUEFS)	Brazil, Rio de Janeiro	KC779688	KC779840	
<i>Dioclea latifolia</i> Benth.	C. van den Berg 1163 (HUEFS)	Brazil, Bahia	KC779696	KC779843	KC779579
<i>Dioclea malacocarpa</i> Ducke	L.P. Queiroz 13076 (HUEFS)	Brazil, Pará	KC779698	KC779845	
<i>Dioclea marginata</i> Benth.	L.P. Queiroz 9136 (HUEFS)	Brazil, Bahia	KC779700	KC779847	KC779581
<i>Dioclea megacarpa</i> Rolfe	L.P. Queiroz 10135 (HUEFS)	Brazil, Piauí	KC779701		
<i>Dioclea paraguayensis</i> Hassl.	Cabid s.n. (CTES)	Argentina, Corrientes	KC779702	KC779848	
<i>Dioclea pulchra</i> Moldenke	M. Sousa 11095 (MEXU)	Panama, Darién	*MT565575	*MT565557	*MT565542
<i>Dioclea reflexa</i> Hook. f.	C. van den Berg 1796 (HUEFS)	Venezuela, Bolívar	KC779706	KC779856	KC779583
<i>Dioclea rugosa</i> ined.	B.A. Krukoff 8433 (P)	Brazil, Amazonas	*MT565576		
<i>Dioclea ruschii</i> ined.	L.P. Queiroz 15254 (HUEFS)	Brazil, Espírito Santo	KC779717	KC779854	KC779590
<i>Dioclea schottii</i> Benth.	S. Buzato 28114 (UEC)	Brazil, São Paulo	KC779710	KC779852	
<i>Dioclea sclerocarpa</i> Ducke	L.P. Queiroz 15911 (HUEFS)	Brazil, Pará	*MT565577	*MT565558	*MT565543
<i>Dioclea ucayalina</i> Harms	A. Grijalva 310 (MEXU)	Ecuador, Napo	*MT565581	*MT565562	
<i>Dioclea violacea</i> Mart. ex Benth.	D. Cardoso 637 (HUEFS)	Brazil, Bahia	KC779721		
<i>Dioclea violacea</i> Mart. ex Benth.	L.P. Queiroz 10135 (HUEFS)	Brazil, Piauí		KC779855	KC779855
<i>Dioclea wilsonii</i> Standl.	L.P. Queiroz 4899 (HUEFS)	Brazil, São Paulo	KC779725	KC779857	KC779594
<i>Dioclea</i> sp. nov.	L.T. Colín 1209 (MEXU)	Honduras, El Paraíso	*MT565579	*MT565560	*MT565545
<i>Dioclea</i> sp. nov.	J. Stehman 4721 (BHCB)	Brazil, Espírito Santo	*MT565579	*MT565561	
<i>Dioclea</i> subgen. <i>Platylobium</i> (Benth.) R.H. Maxwell					
<i>Dioclea bicolor</i> Benth.	L.P. Queiroz 10523 (HUEFS)	Brazil, Mato Grosso	KC779679	KC779833	
<i>Dioclea coriacea</i> Benth.	L.P. Queiroz 14315 (HUEFS)	Brazil, Goiás	KC779681	KC779834	
<i>Dioclea huberi</i> Ducke	J. Revilla 728 (MEXU)	Peru, Loreto		*MT565553	
<i>Dioclea huberi</i> Ducke	R. Vasquez 21022 (NY)	Peru, Amazonas		*MT565554	
<i>Dioclea macrocarpa</i> Huber	L.P. Queiroz 13910 (HUEFS)	Brazil, Amazonas	KC779697	KC779844	KC779580
<i>Dioclea paniculata</i> Killip ex R.H. Maxwell	M. Nee 8911 (MEXU)	Panama, Canal Zone	*MT565573	*MT565555	*MT565541
<i>Dioclea paniculata</i> Killip ex R.H. Maxwell	F.W. Pennel 2829 (NY)	Colombia, Cundinamarca	*MT565574	*MT565556	
<i>Dioclea pygmaea</i> ined.	L.P. Queiroz 10246 (HUEFS)	Brazil, Bahia	KC779704	KC779849	KC779582
<i>Dioclea rostrata</i> var. <i>lanata</i>	R. Schultze-Kraft s.n. (CIAT 8541)	Brazil, Tocantins	KC779691	KC779841	KC779577
<i>Dioclea rostrata</i> var. <i>rostrata</i> Benth.	L.P. Queiroz 14788 (HUEFS)	Brazil, Piauí	KC779708	KC779850	
<i>Dioclea scabra</i> (Rich.) R.H. Maxwell	L.P. Queiroz 13897 (HUEFS)	Brazil, Amazonas	KC779709	KC779851	KC779584
<i>Dioclea</i> sp. nov.	R. Farias 399 (CEN)	Brazil, Tocantins	*MT565578	*MT565559	*MT565544

Taxon	Voucher	Locality	GenBank accession numbers		
			ITS	ETS	<i>trnK/matK</i>
<i>Luzonia</i> Elmer					
<i>Luzonia purpurea</i> Elmer	Soejarto 7967 (F)	Philippines, Luzon	*MT565583	*MT565563	KX652152
<i>Macropsychanthus</i> Harms ex K. Schumann & Lauterbach					
<i>Macropsychanthus lauterbachii</i> Harms var. <i>lauterbachii</i>	M. Hopkins 1360 (K)	Papua New Guinea	KP262490		KP658375
<i>Macropsychanthus lauterbachii</i> var. <i>hirsutus</i> Verd.	A.N. Millar NGF13855 (L)	Papua New Guinea, Morobe	*MT565584	*MT565564	

clade support (Felsenstein 1985), which was assessed through 2000 replicates (Hedges 1992; Müller 2005), simple taxon-addition and TBR algorithm, saving 15 trees per replicate. Only bootstrap percentages > 85% were considered as strong support (Kress et al. 2002).

Bayesian analyses were performed using MrBayes v.3.2.7a (Ronquist et al. 2012) in CIPRES Science Gateway v.3.3 (Miller et al. 2010). Nucleotide substitution models were selected using the Akaike Information Criterion (AIC) in MrModeltest v.2.3 (Nylander 2004) for each DNA region (Table 3). Two runs using the Metropolis-coupled MCMC (Markov Chain Monte Carlo) algorithm, each with four random-initiated chains (one ‘cold’ and three ‘heated’), involved 10 million generations and those were sampled every 1000 generations. The convergence of the runs was assessed by checking if the standard deviation of split frequencies reached a value below 0.01. The first 2500 trees of each run were excluded as burn-ins and the effective sample size (ESS) of all parameters was checked to verify if the values were > 200. The remaining trees were summarised into a majority-rule consensus tree including the posterior probabilities (PP) as branch support estimates. Only PP values ≥ 95 were considered as strong support (Erixon et al. 2003). *Deguelia nitidula* was chosen as the outgroup in the Bayesian analyses.

Maximum likelihood analyses were carried out using RAxML v.8.2.12 (Stamatakis 2014) in CIPRES Science Gateway v.3.3 (Miller et al. 2010) under a GTRGAMMA model, with the ‘-f a’ option (search for the best-scoring ML tree and a rapid bootstrap analysis) and 1000 bootstrap replicates. The MP strict consensus trees, ML trees and Bayesian 50% majority-rule consensus trees were visualised and partially edited in FigTree v.1.4.4 (Rambaut 2018).

Results

We generated 51 new sequences for the Dioclea clade (19 of the nuclear ETS, 20 of the nuclear ITS and 12 of the plastid *trnK/matK*). The most variable dataset was ETS, followed by ITS and *trnK/matK*, respectively (Table 3). In terms of informativeness as measured by the retention index (RI) of each dataset, the ETS and the ITS performed similarly and slightly worse than *trnK/matK*, suggesting that part of the variation in the nuclear datasets are homoplasious (Table 3).

Table 3. Features of the DNA datasets used in this study, based on one of the most parsimonious trees from the combined parsimony analysis and nucleotide substitution models selected for Bayesian analyses. (bp = base pairs; CI = consistency index; RI = retention index; Best-fit model for the Bayesian analysis was selected by AIC in MrModeltest 2.3).

DNA region	N	Aligned length (bp)	Number variable sites		Number Potentially parsimony informative sites		Number of changes/variable sites	Fitch tree length	CI	RI	Best-fit model
ETS region	55	439	277	(63.10%)	205	(46.70%)	2.40	666	0.62	0.82	GTR+G
ITS region	56	687	320	(46.58%)	239	(34.79%)	2.38	762	0.60	0.81	mixed
ITS1		278	158	(56.83%)	118	(42.45%)	2.44	385	0.60	0.79	SYM+G
5.8S		164	13	(7.93%)	10	(6.10%)	1.15	15	0.87	0.94	K80
ITS2		245	149	(60.82%)	111	(45.31%)	2.43	362	0.59	0.82	SYM+G
<i>trnK</i> introns	40	407	76	(18.67%)	43	(10.57%)	1.29	98	0.85	0.90	GTR+I+G
<i>matK</i> gene		1539	244	(15.85%)	149	(9.68%)	1.25	306	0.83	0.86	mixed
<i>matK</i> (1 st positions)		513	71	(13.84%)	44	(8.58%)	1.23	87	0.85	0.87	GTR+G
<i>matK</i> (2 nd positions)		513	64	(12.48%)	39	(7.60%)	1.16	74	0.88	0.93	GTR
<i>matK</i> (3 rd positions)		513	109	(21.25%)	66	(12.87%)	1.33	145	0.8	0.8	GTR+G
Combined (all data)	60	3072	917	(29.85%)	636	(20.70%)	1.73	1832	0.66	0.82	mixed

The individual phylogenetic analyses demonstrated similar results in recovering the same major clades and presenting no strongly-supported incongruences (Suppl. material: Figs S1–S3). The ETS trees were better resolved than those from ITS and *trnK/matK* (Suppl. material: Figs S1–S3). However, resolution within the main clades of the tree (see below) varied amongst datasets and thus a better overall topology was obtained in the combined analyses. Since the ILD test indicated no incongruence between nuclear datasets ($p = 0.3$) or between nuclear and plastid datasets ($p = 0.5$), we performed combined analyses, which provided a better overall topology and higher support values for the nodes. Thus, we present and discuss the results from the combined analyses (Fig. 1).

The Dioclea clade, comprising the genera *Cleobulia*, *Cymbosema*, *Dioclea*, *Luzonia* and *Macropsyчанthus*, was recovered as monophyletic with high support with the exclusion of *Dioclea paniculata* (Fig. 1). Two major clades were recovered: clade A, including the genera *Cleobulia* and *Cymbosema*, together with *Dioclea* subg. *Dioclea*; and clade B, including the genera *Luzonia* and *Macropsyчанthus*, together with *Dioclea* subgs. *Pachylobium* and *Platylobium*. *Dioclea paniculata* (subg. *Platylobium*) grouped with the genera of the Galactia clade. The genus *Dioclea*, therefore, appears polyphyletic, while the rest of genera in Dioclea clade were resolved as monophyletic with high support.

Within clade A, *Cleobulia* and *Cymbosema* comprise a highly-supported clade, sister to *Dioclea* subg. *Dioclea*. Clade B presents two major clades: C and D. Clade C brings together species of *Dioclea* subg. *Platylobium*; and clade D includes species of *Dioclea* subg. *Pachylobium* together with *D. huberi* (subg. *Platylobium*) and nests the representatives of the genera *Luzonia* and *Macropsyчанthus* within it.

The phylogenetic structure of Clade D shows some geographical and ecological trends in its two major clades, E and F. Clade E includes species mostly from eastern South America, including a subclade of species found in Atlantic rainforests (clade G), which is a sister to a clade of species found in seasonally dry forests (clade H). Clade F is mostly composed of species found in rainforests of the Amazon region, but includes the pantropical sea-drifted *D. reflexa* and *D. wilsonii*, as well as the Australasian genera *Luzonia* and *Macropsyчанthus*.

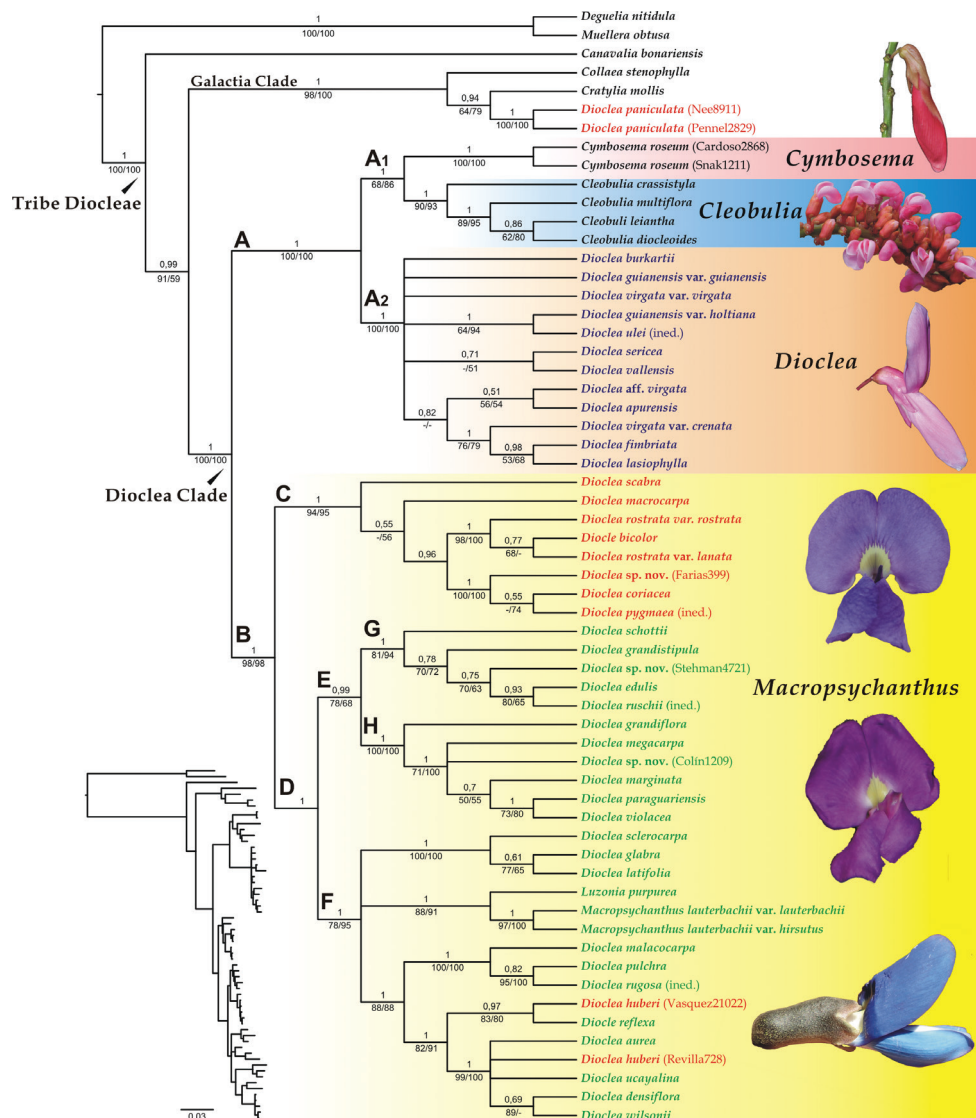


Figure 1. Majority rule Bayesian tree and respective phylogram of the *Dioclea* clade resulting from the combined nuclear (ETS, ITS) and plastid (*trnK/matK*) analysis. Bayesian posterior probabilities are reported above branches and parsimony (left) and maximum likelihood (right) bootstrap support values are reported below branches. Bootstrap values below 50% are represented by hyphens. The coloured boxes represent the four genera as circumscribed here – names in colour represent the subgenera of the genus *Dioclea* (according to Maxwell 2011): blue *Dioclea* subg. *Dioclea*, red *Dioclea* subg. *Platyllobium*, green *Dioclea* subg. *Pachylobium* – pictures: *Cymbosema roseum* (from Snak 1211), *Cleobulia coccinea* (from Queiroz 16029), *Dioclea fimbriata* (from Snak 1223), *Macropsyчанthus marginatus* (from Queiroz 15225), *Macropsyчанthus lauterbachii* (from Poulsen, unvouchered).

Discussion

Criteria for genera circumscriptions

As the genus *Dioclea* has been demonstrated here (and elsewhere) as non-monophyletic (Varela et al. 2004; Maxwell and Taylor 2003; Queiroz et al. 2003, 2015; LPWG 2017), it should be reclassified to preserve the principle of monophyly. In deciding which monophyletic groups should be named, other principles besides monophyly should be taken into consideration to maximise support for monophyly, for phylogenetic information and for ease of identification (diagnosability; Backlund and Bremer 1998).

One possible taxonomic solution for resolving the non-monophyly of *Dioclea* would be to merge all of the genera of the *Dioclea* clade into a widely-circumscribed *Dioclea*, thus subsuming the genera *Cleobulia*, *Cymbosema*, *Luzonia* and *Macropsychanthus* within *Dioclea*. Although having high phylogenetic support, such a broadly-circumscribed genus would lack diagnosability with respect to other genera of the tribe Diocleae because it would result in a highly-heterogeneous genus, presenting variations in almost all of the characters used to diagnose the genera in the tribe Diocleae. At the other extreme, another taxonomic solution would be to split *Dioclea* into several smaller genera to preserve *Luzonia* and *Macropsychanthus* in their current circumscriptions (Queiroz et al. 2015; LPWG 2017). That option presents several drawbacks, however, as some of the smaller clades within clade B lack support and such narrowly-circumscribed genera would be highly redundant, as they would be defined by the same set of morphological traits and would therefore lack diagnosability.

We opted for the intermediate solution of splitting *Dioclea* into two genera corresponding to the two major clades, A2 and B. Clade A2 then corresponds to *Dioclea* subg. *Dioclea* and includes *D. sericea* Kunth, the type species of *Dioclea* and would, therefore, retain the name of the genus. Clade B then corresponds to the subgenera *Pachylobium* and *Platylobium*, plus the genera *Luzonia* and *Macropsychanthus*. The genus name *Macropsychanthus* has priority for this clade. Both of the proposed genera are monophyletic, have high phylogenetic support (Fig. 1) and are diagnosed by clear macromorphological characters – thus presenting low redundancy (as will be discussed below).

The genus *Dioclea* with a narrower circumscription

The circumscription of *Dioclea* is restricted here to the subg. *Dioclea* (sensu Maxwell 2011) or sect. *Dioclea* (sensu Bentham 1837). This group had been recovered as monophyletic in most phylogenetic studies, based on either morphological (Queiroz et al. 2003) or DNA data (Varela et al. 2004; Queiroz et al. 2015). It has also been supported as sister to a clade composed of the genera *Cleobulia* and *Cymbosema* (Queiroz et al. 2015) or to the genus *Cymbosema* (Varela et al. 2004; *Cleobulia* was not sampled in that study).

Table 4. Morphological comparison between the genera of the *Dioclea* clade as circumscribed here.

Characters	<i>Cleobulia</i>	<i>Cymbosema</i>	<i>Dioclea</i>	<i>Macropsychnanthus</i>
Habit	Woody vines.	Woody vines.	Woody vines.	Mostly lianas, less frequently woody vines or shrubs.
Stipules	Basifixed.	Basifixed.	Basifixed.	Medifixed or basifixed.
Inflorescence	Axillary and with an arched axis.	Axillary and erect.	Axillary and erect.	Erect, mostly axillary but frequently cauliflorous.
Inflorescence nodes	Multiflorous and secundiflorous, sessile, globose.	Multiflorous and secundiflorous, sessile.	Multiflorous and secundiflorous, sessile.	Multiflorous and secundiflorous, stalked.
Flower position	Resupinate (i.e. the standard petal backwards and the set wing-keel petals upwards).	Not resupinate.	Not resupinate.	Not resupinate.
Calyx	Cylindrical, 4-lobed, the lobes shorter than the tube and of the same length; upper lobe entire and truncate (wider than longer).	Campanulate, 4-lobed, the lobes having almost the same length and matching the length of the tube; upper lobe triangulate.	Campanulate, 4-lobed, the lobes having almost the same length and matching the length of the tube; upper lobe triangulate.	Campanulate, rarely cylindrical, upper edge humped or convex, 4–5-lobed or deeply bilabiate, the lower lobe much longer than the remaining.
Standard petal	Pink or purple, pubescent towards the apex, ecallose and spreading or reflexed ca. 90°.	Bright red, pubescent towards the apex, ecallose and spreading.	Mostly purple, rarely reddish-purple, pubescent towards the apex, ecallose, reflexed.	Mostly purple, rarely blue, glabrous, 2-callose, reflexed.
Wing petals	Dwarf, much shorter than the other petals and sagittate.	As long as the keel.	As long as the keel.	About twice as long as the keel.
Keel petals	Upcurved ca. 90° with a truncate apex, upper margin smooth.	Straight, oblanceolate, apex rounded, upper margin smooth.	Straight, elliptic to obovate, apex rounded, upper margin upper margin dentate, serrate or fimbriate.	Triangular or semilunar, extending distally into a slender, obtuse or truncate beak.
Androecium	Pseudomonadelphous, the staminal tube pubescent at the base.	Diadelphous, the staminal sheath glabrous.	Pseudomonadelphous, the staminal tube glabrous.	Pseudomonadelphous, the staminal tube glabrous, rarely pubescent at the base.
Anthers	Monomorphic, all fertile.	Monomorphic, all fertile.	Monomorphic, all fertile.	Mostly dimorphic, 5 fertile alternating with 5 sterile or 6 fertile and 4 sterile or anthers monomorphic and all 10 fertile.
Intrastaminal disc	10-lobed.	Entire with a smooth rim.	Entire with a smooth rim.	10-dentate or 10-lobed.
Gynoecium	Ovary sessile, 6–8-ovulate; style not swollen.	Ovary sessile, 5–6-ovulate; style not swollen.	Ovary stipitate, 7–15-ovulate; style not swollen.	Ovary sessile, 2–5 (10)-ovulate; style swollen and frequently flattened distally.
Fruit	Oblong-linear, elastically dehiscent; thin ribs at the margins	Shortly oblong, elastically dehiscent, margins lacking ribs or wings	Oblong-linear, elastically dehiscent; upper margin provided with ribs or wings.	Various, cylindrical to flat compressed, indehiscent, passively dehiscent or elastically dehiscent; upper margin smooth or provided with ribs or wings.
Seeds	Lenticular with a linear hilum encircling ca. 1/2 of the seed circumference	Lenticular with a linear hilum encircling ca. 1/2 of the seed circumference	Lenticular with a linear hilum encircling ca. 1/2 of the seed circumference	Massive, orbicular or without a defined shape; hilum linear encircling 1/2 to 4/5 of the seed's circumference or short and oblong.

Dioclea, as re-circumscribed here (hereafter *Dioclea* s.s.), *Cleobulia* and *Cymbosema* compose a clade of morphologically-similar genera, sharing fruits mostly oblong-linear, smaller than those of clade B (ranging from 9 to 13 cm long and 1.5 to 2 cm wide in clade A vs. 10 to 34 cm long and 3.5 to 6.5 cm wide in clade B), with flat and elastically-dehiscing valves. The seeds of those genera are also quite similar, being relatively small (ranging from 7 to 10 mm long, 4 to 7 mm wide and 2 to 4 mm thick in clade A vs. 20 to 35 mm long, 22 to 30 mm wide and 4 to 15 mm thick in clade B), with narrowly elliptic or oblong outlines, lenticular (i.e. slightly laterally compressed – elliptic in cross section), a linear hilum encircling almost half of the seed's circumference and a hard, bony testa (mostly marbled). All species of those genera also share an androecium with ten fertile stamens (Table 4).

Cymbosema was placed within *Dioclea* by Zamora (2000). It was found to be supported, however, as sister to *Cleobulia* and merging it into *Dioclea* would require that *Cleobulia* should likewise be placed into *Dioclea* s.s. *Cymbosema* can be differentiated from *Dioclea* s.s. by having diadelphous androecium, with the vexillary stamen free (vs. joined into a pseudomonadelphous androecium in *Dioclea* s.s.), petals bright red (vs. purple, white or reddish-purple), standard petal spreading (vs. reflexed $> 90^\circ$), keel petals with margins entire (vs. upper margin serrate to fimbriate) and fruits short and oblong, ca. $2.5\times$ longer than wide, with a long, downcurved persistent style and about 4 seeds (vs. fruits linear, $\geq 5\times$ longer than wide, with 6–10 seeds). Maxwell (1970) reported the standard petal as spreading in *D. fimbriata* Huber and *D. macrantha* Huber, but the examination of more specimens than were available before evidenced that the flowers in anthesis of those species show a reflexed standard.

Cleobulia is quite distinct from *Dioclea* s.s. and *Cymbosema* in terms of flower and fruit traits. The flowers of *Cleobulia* are functionally resupinate due to the downcurved inflorescence rachis and show dwarf wings of less than half of the keel length that barely exceed the calyx (vs. wings and keel petals $\pm$ the same size in *Dioclea* s.s. and *Cymbosema*), a strongly upcurved keel bent ca. 90° (vs. keel straight), short calyx lobes with the upper ones broad and emarginate (vs. all calyx lobes triangulate and acute) and the base of the androecium pubescent (vs. androecium glabrous). The fruits of *Cleobulia* lack the distinct ribs (or wings) close to the upper suture that are characteristic of *Dioclea* s.s. fruits (Maxwell 1977).

With the exclusion of the species of the subgenera *Pachylobium* and *Platylobium*, *Dioclea* s.s. can be diagnosed by having the standard petal ecallose and pubescent towards the apex on the outer surface, wing and keel petals approximately the same length, keel petals straight with rounded apices and serrate to fimbriate upper margins, fruits oblong-linear with flat and elastically dehiscent woody valves, seeds 6–10, lenticular, with a linear hilum encircling almost half of the seed's circumference.

The genus *Macropsychanthus* with a broader circumscription

Macropsychanthus, in its original circumscription (Harms 1900; Verdcourt 1978, 1979), included three species from Malesia. Its circumscription is broadened here to include *Luzonia*, *Dioclea* subg. *Pachylobium* and *Dioclea* subg. *Platylobium*.

Macropsychanthus was usually compared to *Dioclea* subg. *Pachylobium*, with the major distinguishing feature being an androecium with ten fertile stamens in *Macropsychanthus*, vs. five fertile anthers alternating with five reduced and vestigial sterile anthers in *Dioclea* subg. *Pachylobium* (Harms 1900; Maxwell 1969, 2011; Verdcourt 1978, 1979). However, some species of *Dioclea* sect. *Pachylobium* present six fertile and four sterile stamens [e.g. *Dioclea hexandra* (Ralph) Mabb.] or all ten stamens fertile (e.g. *Dioclea umbrina* Elmer), thus making a morphological bridge with the Malesian *Macropsychanthus*.

In their original circumscriptions, both *Luzonia* and *Macropsychanthus* have distinctive calyx morphologies. *Luzonia* (sensu Elmer 1907) has a very distinctive calyx, with the lobes joined into two deeply separate, entire and obtuse lips. *Macropsychanthus* (sensu Harms 1900) has a cylindrical calyx with five subequal and obtuse teeth. *Dioclea* subgenera *Pachylobium* and *Platylobium* typically have a 4-lobed campanulate calyx, with the upper lobe shorter and broader than the others, with the lower lobe longer, upcurved and long acuminate.

The highly-supported clade C corresponds to *Dioclea* subg. *Platylobium*, as defined by Maxwell (2011), including both sections *Platylobium* and *Macrocarpon* (but with the exclusion of *D. huberi*, which appeared nested in clade D). A clade, composed of taxa of subg. *Platylobium*, was recovered only in analyses using molecular data (Queiroz et al. 2015); in analyses using morphological data, the taxa belonging to that subgenus comprised a paraphyletic grade nesting the representatives of *Dioclea* subg. *Pachylobium* (Queiroz et al. 2003), as well as the genera *Luzonia* and *Macropsychanthus* (Maxwell and Taylor 2003). The enigmatic species *Dioclea paniculata* Killip ex R.H. Maxwell, tentatively placed in subg. *Platylobium* by Maxwell (1978), appeared more closely related to the Galactia clade (and its phylogenetic and taxonomic position will be addressed in another article).

Thus, in the new circumscription presented here, *Macropsychanthus* is polymorphic in both androecium and calyx traits, but can be diagnosed by woody and robust pseudoracemes with the peduncle up to 1.5 cm thick, inflorescence nodosities stalked and secundiflorous, calyx with a humped or convex tube on the upper side, standard petal glabrous and bicallose towards the blade base, keel petals strongly upcurved, intrastaminal disc 10-lobed, ovary sessile and large fruits and seeds.

Taxonomic treatment

Key to the genera of the *Dioclea* clade

- 1 Flowers with petals entirely glabrous; seeds 13–50+ mm long and 3–40+ mm wide with circular, squarish, ovate or elliptic outlines (if ovate or elliptic, then flat compressed, not biconvex), either with a short and oblong or long and linear hilum (then encircling 1/2 to 4/5 of the seed's circumference) *Macropsychanthus*
- Flowers with the standard petal pubescent towards the apex on the outer surface; seeds up to 14 mm long and 3 mm wide with elliptic outlines, lenticular

- (biconvex) and with a linear hilum encircling ca. 1/2 of the seed's circumference; **2**
- 2 Flowers resupinate because of the arching inflorescence; wing petals dwarf, much shorter than the standard and keel petals; keel petals upcurved with truncate apices; staminal tube pubescent at the base; upper calyx lobe broad, usually widely emarginate; fruits without ribs or wings near or at the upper margin ***Cleobulia***
- Flowers not resupinate, wing petals not dwarf, approximately the same (or half of the) length of the keel; keel petals straight with rounded apices; androecium glabrous; upper calyx lobe triangulate and acute; fruits with the upper margin ribbed or narrowly winged **3**
- 3 Flowers with the vexillary stamen free, the androecium consequently diadelphous; standard petal bright red, usually spreading; fruit broadly oblong with ca. 4 seeds and a long, downward rostrum ***Cymbosema***
- Flowers with the vexillary stamen fused with the staminal sheath in the middle, the androecium then pseudomonadelphous; standard petal purple, rarely withish-purple or reddish-purple, reflexed; fruit linear with (6)10–12 seeds and a shortly apiculate apex ***Dioclea***

Conspectus of the *Dioclea* clade with new classification including new combinations, synonyms and typifications

1. *Dioclea* Kunth, Nov. Gen. Sp. (quarto ed.) 6: 437. 1823 [Sept. 1824].

Hymenospron Spreng., Syst. Veg. [Sprengel] 4(2): 283. 1827. Type: *Hymenospron apurense* (Kunth) Spreng. [= *Dioclea apurensis* Kunth].

Dioclea Kunth sect. *Dioclea* ['*Eudioclea*'] in Benth., Comm. Legum. Gen. 2: 69. 1837. *Crepidotropis* Walp., Linnaea 14: 296. 1840. Type: *Crepidotropis brasiliensis* Walp. [= *Dioclea virgata* (Rich.) Amshoff].

Dioclea Kunth subg. *Dioclea* in R.H. Maxwell, Novon 21(2): 227. 2011.

Dioclea Kunth ser. *Dioclea* in R.H. Maxwell, Novon 21(2): 227. 2011.

Dioclea ser. *Virgatae* R.H. Maxwell, Novon 21(2): 229. 2011. Type: *Dioclea virgata* (Rich.) Amshoff.

Type. [lectotype, designated by Britton and Wilson (1924)]. *Dioclea sericea* Kunth.

Description. Woody vines along forest edges, trailing or shrubby in open habitats. **Stipules** basifixed, not prolonged beyond their bases. **Leaves** pinnately trifoliate, stipellate, leaf rachis short, mostly < 5 mm long. **Inflorescence** an erect pseudoraceme, nodes multiflorous, woody, sessile, secundiflorous; bracteoles chartaceous or membranous. **Flowers** with calyx chartaceous, campanulate, the four lobes having almost the same length, upper lobe entire, triangulate, obtuse or acute, the other three lobes triangulate, acute, the lower lobe as long as the upper lobe; petals membranous, mostly purple, rarely withish-purple or reddish-purple, standard petal reflexed, ecallose, but slightly thickened near the base, provided with two basal and reflexed

auricles, pubescent towards the apex on the outer surface, wing petals as long as the keel, oblong to obovate, provided with a basal spur on the upper margin, keel petals straight, elliptic to obovate, upper margin dentate, serrate or fimbriate; androecium pseudomonadelphous, the 10 stamens joined into a tube but the filament of the vexillary stamen free at the base, anthers monomorphic, all 10 stamens fertile; intrastaminal nectary disc entire, collar-shape; pistil sigmoid, ovary mostly 7–15-ovulate, stipitate, style not swollen. **Fruits** linear, mostly 5× longer than wide, up to 2.5 cm wide, elastically dehiscent, the thin woody valves explosively twisting to release the seeds, upper margin straight and provided with a longitudinal rib or wing to each side of the suture. **Seeds** small, up to 14 mm long and 8 mm wide, lenticular (slightly biconvex); testa hard (bony), smooth, mostly mottled; hilum linear, encircling almost half of the seed's circumference (Fig. 2G–K).

Discussion. *Dioclea* was described by Kunth (1823 [1824]) with two new species based on specimens collected by Humboldt and Bonpland: *D. apurensis*, from a depauperate fruiting specimen and *D. sericea*, with four flowering specimens and illustrated in plate 576. *Dioclea sericea* was selected as the type for the genus by Britton and Wilson (1924).

A few months after Kunth's publication, Sprengel (1825) used the name *Dioclea* Spreng. for a genus of Boraginaceae. Later, Sprengel (1827) created the genus *Hymenospron* to which he transferred both of Kunth's species, together with a species currently ascribed to *Galactia* [*G. rubra* (Jacq.) Urb.]. *Dioclea* Spreng. is a later homonym in relation to *Dioclea* Kunth and thus illegitimate. *Hymenospron* Spreng. is a superfluous name with respect to *Dioclea* Kunth. The genus *Crepidotropis* was created by Walpers (1840) with just one species (*C. brasiliensis*) that is conspecific with *Dioclea virgata* (Rich.) Amshoff.

The genus *Dioclea* was named after Diocles of Carystus, a Greek philosopher from the 3rd century BC., probably because he associated the word 'beans' with the genus *Dolichos* L., which, in its original circumscription, included species now ascribed to *Dioclea* (Candolle, 1825: 379–380).

Dioclea is diagnosed by the combination of flowers with a pseudomonadelphous androecium, standard petal reflexed and pubescent towards the apex, fruits with an oblong-linear, flat compressed body and explosive dehiscence and seeds elliptic-oblong, lenticular, with a long and linear hilum encircling about half of their circumference.

As circumscribed here, *Dioclea* includes 13 species from the tropical Americas, ranging from coastal central Mexico to northern Argentina and Paraguay. *Dioclea virgata* was introduced into the Old World and became a garden escape plant in Malaysia, Borneo and Ethiopia (Maxwell 1969; Adema 1998).

1.1. *Dioclea albiflora* R.S. Cowan, Mem. New York Bot. Gard. 10(1): 150. 1958.

Type. Venezuela, Bolivar, Piedra Marimare, Wurdack & Monachino 39980 (holotype: NY! [00007720]; isotypes: F! [0059182F], G! [00364887], K! [000502897], RB! [00540228], S! [S-R-9700], US! [00004623], VEN! [43808]).

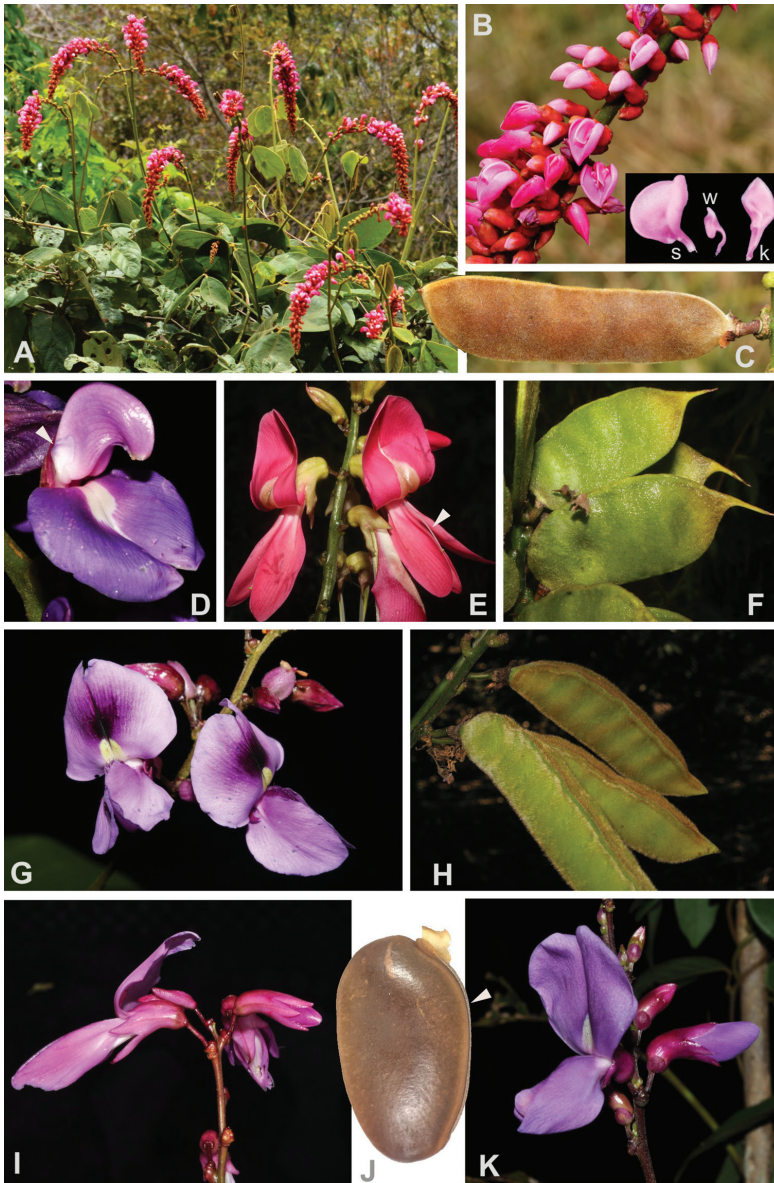


Figure 2. Representatives of the clade A. *Cleobulia coccinea* (Mart. ex Benth.) L.P. Queiroz **A** flowering vine showing the arcuate inflorescences **B** detail of the inflorescence showing resupinate flowers; the inset highlights the wing petals (w) much shorter than the standard (s) and keel petals (k) **C** fruit (from Queiroz 16029). *Cleobulia diocleoides* Benth. **D** a resupinate flower showing the reduced wing (from Queiroz 16036). *Cymbosema roseum* Benth. **E** part of the inflorescence showing the bird pollinated flowers and the free adaxial stamen (arrow) **F** immature fruits showing the characteristic broad oblong fruit body and the long beak (from Cardoso 2868). *Dioclea virgata* (Rich.) Amshoff **G** flowers (from Cardoso 2374) **H** fruits (from Cardoso 2100). *Dioclea fimbriata* Huber **I** flowers (from Snak 1223). *Dioclea burkartii* R.H. Maxwell **J** a seed showing the marbled testa and the elongate hilum encircling about half of its circumference (arrow; from Snak 826). *Dioclea apurensis* **K** flowers (from Queiroz 13035). Photos **A–D**, **J–K**: L.P. Queiroz; **E–H**: D. Cardoso; **I**: C. Snak.

1.2. *Dioclea apurensis* Kunth, Nov. Gen. Sp. 6: 438–439. 1823 [1824].

Hymenospron apurense (Kunth) Spreng., Syst. Veg. [Sprengel] 4(2): Cur. Post. 282. 1827.
Cymbosema apurense (Kunth) Pittier, Bol. Soc. Venez. Ci. Nat. 7: 154. 1941.

Type. Venezuela, Crescit ad ripam fluminis Orinoci, ad confluentem Apurem, *Humboldt & Bonpland s.n.* (holotype: P! [00660130]; isotype: B-W! [13395-01 0]).

1.3. *Dioclea burkartii* R.H. Maxwell, Darwiniana 16(1–2): 413–416, f. 1–2. 1970.

Type. Argentina, Corrientes, Ituzaingo, *Bertoni 5325* (holotype: LIL! [000609]).

1.4. *Dioclea fimbriata* Huber, Bol. Mus. Goeldi Hist. Nat. Ethnogr. 5(2): 409–410. 1909.

Type. Brazil, Pará, Prainha, rio Marapy, *Ducke 3577* (lectotype, designated here amongst the syntypes: MG! [003577], photo and fragments F! [0059185F]).

1.5. *Dioclea guianensis* Benth., Comm. Legum. Gen.: 70. 1837.

Dioclea guianensis var. *villosior* Benth., J. Bot. (Hooker) 2(10): 60. 1840. Type: Guyana, *Schomburgk 629* (lectotype, designated here amongst the isotypes: K! [000502839]; isolectotypes BM! [000931784], BR! [0000005170203], G! [00364900], LE! [00002536], NY! [00007726], P! [02961764], US! [00004616]).

Dioclea panamensis Duchass. ex Walp., Flora 36: 229. 1853. Type: Panama, *Duchassaing s.n.* (holotype: GOET! [004985]).

Dioclea comosa var. *panamensis* (Duchass. ex Walp.) Kuntze, Revis. Gen. Pl. 1: 179. 1891. Type: based on *Dioclea panamensis* Duchass. ex Walp.

Type. Guyana, *Schomburgk 83* (lectotype, designated here amongst the isotypes: K! [000502841]; isolectotypes: BM! [000931784], E! [00531193], F! [0059187F], GH! [00277378], K! [000502840], P! [00708474], TCD! [0004427], U! [0003526], US! [00004617]).

1.6. *Dioclea holtiana* Pittier ex R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 584. 1990.

Type. Venezuela, Amazonas, Boca del Vichada, *Holt & Gehrigier 224* (holotype: US! [00004615]; isotype: VEN).

1.7. *Dioclea lasiophylla* Mart. ex Benth., Comm. Legum. Gen.: 70. 1837.

Dioclea guianensis var. *lasiophylla* (Mart. ex Benth.) R.H. Maxwell ex G.P. Lewis, Legumes Bahia: 254. 1987.

Type. Brazil, Bahia, Cachoeira, *Martius s.n. Obs. 2040* (lectotype, designated here amongst the isotypes: M! [0240656]; isolectotype: M! [0240657]).

1.8. *Dioclea lehmannii* Diels, Biblioth. Bot. 116: 97. 1937.

Type. Ecuador, Guayas, Naranjal (Naravjae), *Lehmann 5754* (holotype: B†; lectotype, designated here amongst the isotypes: K! [000502891]; isolectotypes: F, K! [000502892], US).

1.9. *Dioclea macrantha* Huber, Bol. Mus. Goeldi Hist. Nat. Ethnogr. 5: 408. 1909.

Type. Brazil, Pará, Almeirim, *Ducke 3484* (holotype: MG! [003484]; isotype: G! [00364766]).

1.10. *Dioclea ovalis* R.H. Maxwell, Novon 21(2): 227–229, f. 1. 2011.

Type. Colombia, Cundinamarca, Pacho, *Uribe 1648* (holotype: US! [01050065]; isotype: COL).

1.11. *Dioclea sericea* Kunth, Nov. Gen. Sp. 6: 437–438, pl. 576. 1823 [1824].

Hymenospron sericeum (Kunth) Spreng., Syst. Veg. [Sprengel] 4(2): Cur. Post. 283. 1827.

Type. Colombia, Honda, *Humboldt & Bonpland 1681* (lectotype, designated here amongst the isotypes: P! [00708483]; isolectotype: P! [00708482]).

1.12. *Dioclea vallensis* R.H. Maxwell, Novon 21(2): 229–232, f. 2A–K. 2011.

Type. Colombia, Valle del Cauca, río Cajambre, *Cuatrecasas 17499* (holotype: US! [01050066]; isotype: F).

1.13. *Dioclea virgata* (Rich.) Amshoff, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 52: 69. 1939.

Dolichos virgatus Rich., Actes Soc. Hist. Nat. Paris: 1: 111. 1792.

Mucuna virgata Desv. ex Steudel, Nomencl. Bot. (ed. 2) 2(9): 164. 1841.

Type. French Guiana, *Leblond 182* (lectotype, designated here amongst the isotypes: P! [00708485]; isolectotype: G! [00364885]).

Note. The specimen in P provides no information concerning its collector, but that information is recorded on the duplicate at G and agrees with the information of the protologue (Richard 1792).

1. 13. 1. *Dioclea virgata* (Rich.) Amshoff var. *virgata*

Dioclea lasiocarpa Mart. ex Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Bahia, Salvador ('Soteropolis'), *Martius s.n. Obs. 2016* (lectotype, designated here amongst the syntypes: M! [0240665]; isolectotypes: M! [0240664], M! [0240663]). Note: Bentham (1837) did not cite any specimen for his species *D. lasiocarpa*. He recognised three unnamed varieties (α , β and γ); we selected the specimen cited for var. ' α ' as the lectotype of the species.

Crepidotropis brasiliensis Walpers, Linnaea 14: 296. 1840. Type: Brazil, Bahia, Cruz de Casma [probably Salvador], *Luschnath s.n.* (lectotype, designated here amongst the isotypes: HAL! [0120300]; isolectotype: LE). Note: Maxwell (1969) said that duplicates in LE are annotated with different numbers (#206, #781, #2054), but probably from the same gathering.

Canavalia bracteolata Merrill, J. Straits Br. Royal As. Soc. 86: 313. 1922. Type: Malaysia, Sabah, Sandakan, (Borneo), *Ramos 1511* (holotype: PHN; isotypes: A! [00059980], BM! [000958604], GH! [00059979], K! [000898374], L! [0018940], P! [00708471], US! [00004634]).

Canavalia peruviana Piper, Publ. Field Mus. Bot. 4: 94. 1925. Type: Peru, La Merced, *Macbride 5551* (holotype: F! [0043480F]; isotypes: G! [00364938], US! [00004655]).

1.13.2. *Dioclea virgata* var. *crenata* R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 585. 1990.

Type. Brazil, Amapá, rio Calcoene, *Pires & Cavalcante 52528* (holotype: U! [1249084]; isotypes: F! [1615326], HUEFS! [27288], NY! [1239737], SP! [000990], S! [S-R-9713], US! [00324272]).

2. *Cymbosema* Benth., J. Bot. (Hooker) 2: 61. 1840.

Type. *Cymbosema roseum* Benth.

Description. Woody twining vines. **Stipules** basifixed, not prolonged beyond their base. **Leaves** pinnately trifoliolate, long, stipellate, leaf rachis 5–20 mm. **Inflorescence** an erect pseudoraceme, nodes multiflorous, sessile, secundiflorous; bracteoles chartaceous. **Flowers** with calyx chartaceous, campanulate, the four lobes of almost the same length, upper lobe entire, triangulate, obtuse, lower lobe ovate and acute; petals membranous, bright red, standard petal spreading, rarely reflexed, ecallose, provided with two basal and reflexed auricles, pubescent towards the apex on the outer surface, wing petals as long as the keel, oblong to obovate, provided with a basal spur at the upper margin, keel petals straight, oblanceolate, margins smooth; androecium diadelphous, the vexillary stamen free, the nine remainder fused but free distally, anthers monomorphic, all 10 stamens fertile; intrastaminal nectary disc entire, collar-shaped; pistil almost straight, ovary mostly 5–6-ovulate, sessile, style not swollen. **Fruits** shortly oblong, 2.4–2.5× longer than wide, up to 2 cm wide, elastically dehiscent, the thin woody valves explosively twisting to release the seeds, upper margin straight, lacking ribs or wings, style persistent and extending as a downcurved rostrum. **Seeds** small, up to 10 mm long and 6 mm wide, lenticular (slightly biconvex); testa hard (bony), smooth; hilum linear, encircling almost half of the seed's circumference. (Fig. 2E–F).

Discussion. Our results support the recognition of *Cymbosema* as a monospecific genus, as originally proposed by Bentham (1840, 1859) and maintained by Maxwell (1970). Zamora (2000) synonymised *Cymbosema* in *Dioclea*, a proposal that is not supported by our results, which recovered *Cymbosema* as sister to *Cleobulia* rather than to *Dioclea*.

Cymbosema is diagnosed as having flowers with a diadelphous androecium with the vexillary stamen free, petals bright red, the standard petal spreading (only rarely reflexed), keel petals with smooth margins and fruits oblong and falcate.

Distributed in the Amazon region, extending north to the Pacific coast of Mexico in wet forests.

2.1. *Cymbosema roseum* Benth., J. Bot. (Hooker) 2: 60–61. 1840.

Dioclea purpurea Poepp., Nov. Gen. Sp. Pl. 3: 59. 1845. Type: Brazil, Amazonas, Tefé, Poeppig D-2619 (holotype: W! [0048636]).

Dioclea rosea (Benth.) N. Zamora, Novon 10: 179. 2000. Type: based on *Cymbosema roseum* Benth.

Type. Brazil: Rio Branco (Roraima), *Schomburgk* 850 (lectotype, designated by Maxwell 1970: K! [000502745]; isoelectotypes: BM! [000931430], F! [V0059084F], K! [000502746], US! [00004551], W! [1889-0020599]).

3. *Cleobulia* Mart. ex Benth., *Comm. Legum. Gen.*: 67. 1873.

Type. *Cleobulia multiflora* Mart.ex Benth. [= *Cleobulia coccinea* (Vell.) L.P. Queiroz]

Description. Woody vines. **Stipules** basifixed, not prolonged beyond their base. **Leaves** pinnately trifoliolate, the rachis reduced, sometimes absent, stipellate. **Inflorescence** a pseudoraceme, arcuate, nodes multiflorous, sessile, globose, secundiflorous; bracteoles fleshy. **Flowers** resupinate because of the arching inflorescence; calyx fleshy, cylindrical, the 4 lobes much shorter than the tube, upper lobe truncate to slightly emarginate, lower lobe triangulate and acute; petals firmly chartaceous, pink to purple, standard petal spreading or reflexed, ecallose, provided with two basal and reflexed auricles, pubescent towards the apex on the outer surface, wing petals dwarf, ca. 1/3 of the keel length, sagittate, keel petals upcurved with truncate apices; androecium pseudomonadelphous, staminal tube pubescent at the base, anthers monomorphic, all 10 stamens fertile; intrastaminal nectary disc 10-lobed; pistil straight then upcurved ca. 90° in the middle, ovary 6–8-ovulate, sessile, style not swollen. **Fruits** linear-oblong, 3–5× longer than wide, elastically dehiscent, the thin woody valves explosively twisting to release the seeds, upper margin straight to undulate, with thin ribs. **Seeds** small, under 10 mm long and 6 mm wide, lenticular (slightly biconvex); testa hard (bony), smooth; hilum linear encircling almost half of the seed's circumference (Fig. 2A–D).

Discussion. Since first being described, *Cleobulia* was distinguished from *Dioclea* by having dwarf wings with a semi-sagittate blade (Bentham 1837; see Fig. 2B). *Cleobulia* could likewise be diagnosed by having an inflorescence with a long and arching peduncle, leaving its flowers resupinate (i.e. with the standard petal in a lower position and the keel above), a pseudomonadelphous androecium, the base of the staminal tube pubescent, with uniform anthers, a 10-lobed intrastaminal disc, and a sessile and straight ovary.

Three species are found from eastern Brazil to the eastern Brazilian Amazon and one species from western-central Mexico, all mostly in semi-deciduous forests.

3.1. *Cleobulia coccinea* (Vell.) L.P. Queiroz, *comb. nov.*

urn:lsid:ipni.org:names:77212303-1

Basionym: *Dolichos coccineus* Vell., Fl. Flumin.: 321, 1829 [1825]. Ic. 7 pl. 158. 1831.

Type: Brazil, Rio de Janeiro, “Habitat silvis, fruticetisque maritimis”, Vellozo (lectotype, designated here: plate 158 in *Florae Fluminensis* vol. 7, Vellozo 1831). Epitype: Brazil, Bahia, Lençóis, L.P. Queiroz et al. 16029 (epitype, designated here: HUEFS! [200008453]; isoeotypes: ALCB! [046364!], RB! [1173635!], US! [3698469]).

Cleobulia multiflora Mart. ex Benth., *Comm. Legum. Gen.*: 67. 1837. Type: Brazil, Minas Gerais, *Martius s.n.* (lectotype, designated here: M! [0240673]), syn. nov.

Note. A link between *Dolichos coccineus* Vell. and *Cleobulia multiflora* Mart. ex Benth. was established by Maxwell (1977), who speculated that they could be synonymous.

The description provided by Vellozo (1829: 321) is exceedingly brief, but presents some traits characteristic of this species, such as flowers small and perianth purpureum. The illustration provides more elements to confirm its identity as *C. multiflora* as it shows resupinate flowers with the standard spreading, the wing petals sagittate and much shorter than the others and the pistil with a straight ovary and style upcurved ca. 90°. There are issues regarding the publication dates of several sections of the *Florae Fluminensis* but the main text in volume 1 (pages 1 to 329) is considered as having been distributed between 7 September to 28 November 1829 and the illustration volumes on 29 October 1831 (Carauta 1969, 1972; Stafleu and Cowan 1985; Lima 1995), thus predating and having priority over *Cleobulia multiflora* published by Bentham in 1837. To avoid misinterpretation of the name proposed by Vellozo (1831), we are designating an epitype with leaf, flowers and fruits.

3.2. *Cleobulia crassistyla* R.H. Maxwell, *Phytologia* 51: 361. 1982.

Type. Mexico, Guerrero, Galeano, *Hinton 14996* (holotype: RSA! [LAM] [0003239]; isotypes: K! [000297082], LL! [00371269], NY! [00006420], US! [00067941]).

3.3. *Cleobulia diocleoides* Benth., *Fl. Bras.* 15(1): 168. 1859.

Type. Brazil, Minas Gerais, *Saint Hilaire s.n. Cat. 1311* (holotype: P! [00758522]). Epitype (designated here): Brazil, Bahia, Campo Formoso, *Queiroz et al. 16306* (HUEFS! [000274630]).

Note. The holotype is the only remanant of the material used by Bentham (1859) for describing *C. diocleoides*. The material now consists of a branch with leaves and a dissected flower bud within an envelope. A detached calyx from a mature flower is the only element that allows us to check that this plant presents flowers much larger than the other species of *Cleobulia* as described by Bentham (1859) and Maxwell (1977). We selected an epitype from a more complete material with flowers and immature fruits.

3.4. *Cleobulia leiantha* Benth., *Fl. Bras.* 15(1): 162. 1859.

Cleobulia multiflora var. *leiantha* (Benth.) R.H. Maxwell, *Phytologia* 38: 57. 1977.

Type. Brazil, Pará, Santarém, *Spruce [10 03]* (lectotype, designated here from the syntypes: K! [000502886]; isolectotypes: FI! [009795], G! [00364892], K! [000930235], M! [0240670], NY! [00006421], P! [00708488], TCD! [0004431]).

Note. When describing the new species *C. leiantha*, Bentham (1859) cited the specimen collected by Spruce near Santarém. We selected as the lectotype the specimen with a handwritten label and with the collection number 1003 found in other duplicates.

4. *Macropsychanthus* Harms in K. Schumann & Lauterbach, Fl. Schutzgeb. Südsee 366. 1900.

Type. *Macropsychanthus lauterbachii* Harms.

Description. Stout, high-climbing lianas with twining stems, less frequently shrubs or woody vines in open habitats. **Stipules** medifixed and prolonged below their insertion (peltate) or basifixed and not prolonged below their insertion. **Leaves** pinnately trifoliolate, stipellate or estipellate. **Inflorescence** a stout, woody, erect pseudoraceme, nodes multiflorous, woody, stalked and secundiflorous; bracteoles fleshy. **Flowers** massive; calyx with the tube fleshy coriaceous, upper edge convex or humped, 4-lobed, with the upper lobe either entire and triangulate to obtuse or emarginate and then with the resulting tips rounded or 5-lobed with the two upper lobes rounded and the other three lobes triangulate, the lower lobe much longer than the remaining lobes or deeply bilabiate with two oblong lips; petals firm, the standard petal reflexed, somewhat fleshy, bicallose, provided with two basal and folded auricles, wing petals ca. twice as long as the keel, obliquely oblong, obliquely ovate, obovate, elliptic to almost quadrate, basal spur at the upper margin present or lacking, keel upcurved, the keel petals triangular or semi-lunar, extending distally into a slender, obtuse or truncate beak; androecium pseudomonadelphous, the 10 stamens joined in a tube, but the filament of the vexillary stamen free at the base, anthers mostly dimorphic, 5 fertile alternating with 5 sterile or 6 fertile and 4 sterile or anthers uniform and all 10 fertile; intrastaminal nectary disc 10-dentate or 10-lobed; ovary sessile, style usually swollen distally. **Fruit** indehiscent, passively dehiscent or elastically dehiscent with twisting woody valves, turgid, slightly compressed or flat compressed, valves coriaceous, fleshy or woody, upper margin smooth or provided with ribs or wings. **Seeds** 3–5 to 9, massive, either orbiculate and slightly compressed with a hard testa or soft overgrown and without a definite shape, with flat contact planes or elliptic and flat compressed; hilum linear, encircling 1/2 to 4/5 of the seed's circumference or short and oblong. Fig. 3.

Discussion. *Macropsychanthus* Harms is the earliest validly-published genus name for this group. Two older names, *Lepidamphora* Zolling, and *Taurophtalmum* Duchassaing, were not validly published. *Lepidamphora volubilis* Zolling, was published as a synonym of *Dioclea javanica* Benth. with the citation of two specimens (“*Herb. n. 763 et 867 Z.*”; Miquel 1855: 217). *Lepidamphora volubilis* was probably just a name on herbarium sheets and is invalid because it was published as a synonym (ICN Article 36.1; Turland et al. 2018) and because it was published as a species, but the genus to which it was assigned was not validly published at the same time or was not validly published previously (Art. 35.1; Turland et al. 2018).

The Panamanian *Taurophtalmum pulchrum* Duchassaing was another invalidly-published name that could be related with *Macropsychanthus* as defined here. It was originally published as a synonym of *Canavalia miniata* (Kunth) DC. by Griesebach (1866: 76). However, Urban (1899: 473) placed *T. pulchrum* as a synonym of *Dioclea reflexa* Hook. f. (= *Macropsychanthus comosus*), based on the calyx description provided earlier by Griesebach (1866). The only specimen of *Canavalia* or *Dioclea* collected by Duchassaing that we were able to track is the type of *Dioclea panamensis* Duchassaing ex Walp.

(*Duchassaing s.n.* [GOET 004985]), which is a synonym of *Dioclea guianensis* Benth. and thus does not belong to *Macropsychanthus* as circumscribed here. There is a plate from Duchassaing housed at GOET (and annotated as *Canavalia miniata* by Griesebach) that probably represents the only remnant of the original material of *Tauroptalmum pulchrum*. It is a watercolour painting of a fruit and a seed with a pencil sketch of a flower and a detailed description by Duchassaing (Fig. 4). The fruit represented probably belongs to *Macropsychanthus megacarpus* and not to *M. comosus* as supposed by Urban (1899). The name *Tauroptalmum* literally means “bull’s eye” and was probably derived from the Spanish name “ojo de buey” for several species of *Macropsychanthus* (also common in Portuguese as “olho-de-boi”), but not for species of *Dioclea*. In the absence of a specimen and taking the painting in GOET as evidence, we are considering *Tauroptalmum* as related to *Macropsychanthus*, although it is an invalid name.

Two major clades were recovered corresponding to the circumscription of *Macropsychanthus* proposed here. One (clade D) brings together species formerly ascribed to the genera *Luzonia* and *Macropsychanthus*, as well as to *Dioclea* subg. *Pachylobium* and *Dioclea huberi* (subg. *Platylobium* sect. *Macrocarpon*; Maxwell 2011). Clade C comprises all of the other species formerly ascribed to *Dioclea* subg. *Platylobium*. Clade D includes species with mostly medifixed stipules, fruits indehiscent or passively dehiscent and turgid seeds with a long, linear hilum; clade C includes species with basifixed stipules, fruits flat-compressed and elastically dehiscent and seeds with a short and oblong hilum. Our finding that the puzzling *Dioclea huberi* (formerly classified in subg. *Platylobium* sect. *Macrocarpon*) is part of clade D blurs the distinction between those major clades, because it shares basifixed stipules and flat-compressed fruits and seeds with *D.* subg. *Platylobium*, but seeds with a long linear hilum with *D.* subg. *Pachylobium*. Likewise, *Dioclea macrocarpa*, recovered in clade C, shows the basifixed stipules and the short and oblong hilum of *D.* subg. *Platylobium* together with the turgid fruits and seeds of *D.* subg. *Pachylobium*. Thus, clades B and C are diagnosed by only a few morphological traits (see below) and we chose to recognise them as subgenera of a largely polymorphic genus instead of treating them as two separate genera.

Macropsychanthus is a pantropical genus with 46 species. It is most diverse in the New World (36 species), with eleven species from the Philippines and Indonesia to New Guinea and two Pantropical sea-drifted species extending to continental Africa and Madagascar.

4.1. *Macropsychanthus* Harms subg. *Macropsychanthus*

Dioclea sect. *Pachylobium* Benth., Comm. Legum. Gen.: 69. 1837. Lectotype [designated here]: *Dioclea violacea* Mart. ex Benth.

Lepidamphora Zoll., Fl. Ned. Ind. 1(1): 217. 1855. Type: *Lepidamphora volubilis* Zoll. [= *Macropsychanthus comosus* (G. Mey.) L.P. Queiroz & Snak], nom. inval. pro syn.

Tauroptalmum Duchass. in Griesebach, Cat. Pl. Cub.: 76. 1886. Type: *Tauroptalmum pulchrum* Duchass. [= *Macropsychanthus megacarpus* (Rolfe) L.P. Queiroz & Snak], nom. inval. pro syn.

Luzonia Elmer, Leaflet. Philipp. Bot. 1: 220. 1907. Type: *Luzonia purpurea* Elmer.

Dioclea subg. *Pachylobium* (Benth.) R.H. Maxwell, Novon 21(2): 234. 2011. Type: based on *Dioclea* sect. *Pachylobium* Benth.

Description. Stipules medifixed, prolonged below their insertion. Leaves stipellate, stipels mostly setaceous. Fruit indehiscent or passively dehiscent, turgid, slightly compressed (elastically dehiscent with twisting woody valves only in *M. huberi*). Seeds with a long and linear hilum encircling 1/2 to 4/5 of the seed's circumference (Fig. 3A–F).

The distribution of this section is the same as that of the genus. Species of subg. *Macropsychanthus* are typical rainforest elements, where they occur as high-climbing lianas over the tallest trees. Few species are found in the savannahs of central Brazil or in the seasonally-dry woodlands of South America.

4.1.1. *Macropsychanthus apiculatus* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212304-1

Basionym: *Dioclea apiculata* R.H. Maxwell, Novon 21(2): 235–237. 2011. Type: Bolivia, La Paz, N Yungas, near Coroico, *Buchtien* 664 (holotype: MO; isotypes: F! [588818], G! [00364742]).

4.1.2. *Macropsychanthus aureus* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212305-1

Basionym: *Dioclea aurea* R.H. Maxwell, Ann. Missouri Bot. Gard. 67(3): 664–665. 1981. Type: Colombia, Caldas, Pueblo Rico, *Sneidern* 5555 (holotype: S! [S-R-9703]; isotype: NY! [01365123]).

4.1.3. *Macropsychanthus carolinensis* Kanehira & Hosokawa, Trans. Nat. Hist. Soc. Taiwan 24: 414. 1934.

Type. Caroline Islands, Palau, *Kanehira* 1711 (holotype: TAI!; isotype: P! [02752991]).

4.1.4. *Macropsychanthus circinatus* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212306-1

Basionym: *Dioclea circinata* R.H. Maxwell, Novon 21(2): 237. 2011. Type: Colombia, Meta, *Phillipson et al.* 1405 (holotype: COL! [000001743]; isotypes: BM! [000931783], MEDEL! [000156], S! [S-R-9704], US! [01050064]).



Figure 3. Representatives of the clade B. *Macropsyчанthus* subg. *Macropsyчанthus* (**A–F**). *Macropsyчанthus grandiflorus* (Mart. ex Benth.) L.P. Queiroz & Snak **A** flowering vine (from Queiroz 15227). *Macropsyчанthus marginatus* (Benth.) L.P. Queiroz & Snak **B** mature fruit showing dehiscence through the lower suture only **C** one of the valves removed to show the seeds with a long linear hilum (arrow; from Queiroz 15225). *Macropsyчанthus edule* (Kuhl.) L.P. Queiroz & Snak **D** the indehiscent and fleshy fruit decahing to release the seeds (from Popovkin 1546). *Macropsyчанthus lauterbachii* Harms var. *lauterbachii* **E** giant flowers with bluish petals (unvouchered). *Macropsyчанthus megacarpus* (Rolfe) L.P. Queiroz & Snak **F** flower (from Queiroz 10135). *Macropsyчанthus* subg. *Platyllobium* (**G–J**). *Macropsyчанthus scabrus* (Rich.) L.P. Queiroz & Snak **G** flowers (from Cardoso 2907). *Macropsyчанthus bicolor* (Benth.) L.P. Queiroz & Snak **H** part of the pseudoracemous inflorescence **I** mature (left) and dehiscent (right) fruits **J** seed, showing the short hilum (arrow; from Queiroz 15874). Photos **A–C**, **F**, **H–J**: L.P. Queiroz; **D**: A. Popovkin; **E**: A.D. Poulsen; **G**: D. Cardoso.

4.1.5. *Macropsychanthus comosus* (G. Mey.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212307-1

Basionym: *Dolichos comosus* G. Mey, Prim. Fl. Esseq. 241. 1818. Type: Guyana, Essequibo, *Rodschied* 93 (holotype: GOET! [004986]).

Dioclea reflexa Hook. f., Niger Fl. 306–307. 1849. Type: West Africa: Cape Palmas and region of Fernando Poo, *Vogel* 32 (holotype: K; isotype: GH! [00066325]), syn. nov.

Lepidamphora volubilis Zoll., Fl. Ned. Ind. 1(1): 217. 1855, nom. inval. pro syn. Type: Guyana, Essequibo, *Rodschied* 93 (holotype: GOET! [004986]).

Dioclea comosa (G.Mey.) Kuntze, Revis. Gen. Pl. 1: 179. 1891. Type: based on *Dolichos comosus* G. Mey.

4.1.6. *Macropsychanthus densiflorus* (Huber) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212308-1

Basionym: *Dioclea densiflora* Huber, Bol. Mus. Goeldi Hist. Nat. Ethnogr. 5(2): 406–407. 1909. Type: Brazil, Pará, Oriximiná, *Ducke s.n. MG 7903* (holotype: MG! [007903]; isotype: RB! [00174878]).

Note. Huber (1909: 406–407) did not cite any specimen in the original description of *Dioclea densiflora* and, in the absence of a type, Maxwell (1969: 254–255) indicated the specimen *Ducke s.n. RB 11744* (collected on 20 Dec 1919) as a neotype. However, in the introductory pages of his work, Huber (1909) stated that all species were described, based on specimens collected by A. Ducke from 1902 to 1907 and housed at the Museu Goeldi herbarium (MG). He also transcribed Ducke's field notes showing that he collected in Oriximiná in December of 1906 (Huber 1909: 301), which coincides with the date and locality of the specimen *A. Ducke s.n. MG 7903*. Thus, we are assuming that this specimen is the same one used by Huber (1909) when describing the new species and consider the material housed at MG as the holotype.

4.1.7. *Macropsychanthus dictyoneurus* (Diels) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212309-1

Basionym: *Dioclea dictyoneura* Diels, Biblioth. Bot. 116: 97. 1937. Type: Colombia, Putumayo, La Concepción, *Cuatrecasas 10836* (neotype, here designated: COL! [000054481]).

Note. The holotype of *Dioclea dictyoneura* (Diels 929) came from Puyo, in Napo-Pastaza, in Ecuadorian Amazon. It was housed at B and was destroyed and we could

not trace any duplicate. Maxwell (1969) cited four other specimens, from which we choose as the neotype the material from Concepción as it fits the protologue and was encountered ca. 280 km distant from the area where the original type was collected in the southern Colombian Amazon.

4.1.8. *Macropsychanthus dolichobotrys* Holth., *Blumea* 5: 192. 1942.

Type. Indonesia, Talaud Islands, Pasir Malap, *Lam 3002* (holotype: L! [0019084]; isotypes: BO, L! [0019085], L! [0019086]).

4.1.9. *Macropsychanthus edulis* (Kuhlm.) L.P. Queiroz & Snak, *comb. nov.*

urn:lsid:ipni.org:names:77212310-1

Basionym: *Dioclea edulis* Kuhlm., *Anais Reunião Sul-Amer. Bot.* 3: 79, pl. 6–7. 1940.
Type: Espírito Santo, Linhares, Picada da Lagoa do Braz, *Kuhlmann 218* (holotype: RB! [00540230] + fruit coll. RB! carpo [00770250]; isotypes: RB! [00755077], RB! [00755078]).

4.1.10. *Macropsychanthus ferrugineus* Merr., *Philipp. J. Sc.* 5, *Bot.*: 121. 1910.

Dioclea decandra Amshoff ex Adema, *Blumea* 43: 234. 1998. Type: based on *Macropsychanthus ferrugineus* Merr.

Type. Philippines, Mindanao, Lake Lanao, *Clemens 419* (lectotype, designated by Adema 1998: US! [00004643]; isolectotypes: F! [0059545F], K! [000900292], K! [000900293]).

Note. The transfer of *M. ferrugineus* to *Dioclea* was proposed by Amshoff in an unpublished manuscript and validated by Adema (1998). As the name *Dioclea ferruginea* was already occupied by *D. ferruginea* Ducke, Adema (1998) proposed the new name *Dioclea decandra*. However, the original name *M. ferrugineus* is its correct name in *Macropsychanthus* [see also note under *M. duckei*].

4.1.11. *Macropsychanthus flexuosus* (Ducke) L.P. Queiroz & Snak, *comb. nov.*

urn:lsid:ipni.org:names:77212311-1

Basionym: *Dioclea flexuosa* Ducke, *Arch. Jard. Bot. Rio de Janeiro* 4: 92–93. 1925.
Type: Brazil, Pará, Rio Branco de Óbidos, *Ducke s.n. RB 17271* (holotype: RB! [00616992]; isotypes: RB! [00540232], RB! [00616991]).

4.1.12. *Macropsychanthus funalis* (Poepp.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212312-1

Basionym: *Dioclea funalis* Poepp., Nov. Gen. Sp. Pl. 3: 59. 1845. Type: Peru, Pampagaio, *Poeppig 1452* (holotype: W! [0048638]; isotypes: F! [0043445F], NY! [00007725], W! [0048637]).

4.1.13. *Macropsychanthus glabrus* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212313-1

Basionym: *Dioclea glabra* Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Goiás, San Izidro, *Pohl 1578* (lectotype, designated by Maxwell 1990: W! [2002-0002133]; isoelectotypes: [as *Pohl s.n.*] K! [000502843], W! [2002-0002132]).

Dioclea leiophylla Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 91–92, pl. 5, 1925. Type: Brazil, Pará, rio Tapajós, *Ducke s.n. RB 17269* (lectotype, designated here from the syntypes: [in two sheets] RB! [00540234] & [00547582]).

4.1.14. *Macropsychanthus grandiflorus* (Mart. ex Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212314-1

Basionym: *Dioclea grandiflora* Mart. ex Benth., Comm. Legum. Gen.: 68–69. 1837. Type: Brazil, Bahia, Juazeiro, *Martius 2406* (holotype: M! [0240655]).

4.1.15. *Macropsychanthus grandistipulus* (L.P. Queiroz) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212315-1

Basionym: *Dioclea grandistipula* L.P. Queiroz, Novon 8(4): 433, f. 1. 1998. Type: Brazil, São Paulo, Iguape, *Cordeiro & Anunciação 1360* (holotype: SP! [000989]; isotypes: HUEFS! [000001844], RB! [00516041]).

4.1.16. *Macropsychanthus haughtii* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212316-1

Basionym: *Dioclea haughtii* R.H. Maxwell, Novon 21(2): 239. 2011. Type: Colombia, Meta, Los Llanos, *Haught 2583* (holotype: COL! [000001747]; isotypes: GH, RB, S! [S-R-9705], US, VEN).

4.1.17. *Macropsychanthus hexander* (Ralph) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212317-1

Basionym: *Mucuna hexandra* Ralph, IC. Carp., 30, t. 34, f. 5. 1849. Type: The plate of *Dolichos hexandrus* Roxb. (*nom. nud.*), Ic. 2328 (holotype K [available at Kew 2006, <http://apps.kew.org/floraindica/displayImages.do?index=6>]).

Dolichos coriaceus Graham ex Wall., Numer. List [Wallich] n. 5562. 1831, *nom. inval.* (*nom. nud.*). Type: Singapore, Penang, *Wallich Cat. no. 5562* (holotype: K! [001121297]).

Dioclea coriacea (Graham ex Wall.) Rusby, Mem. Torrey Bot. Club 3(3): 22. 1893. Type: based on *Dolichos coriaceus* Graham ex Wall.

Macropsychanthus novo-guineensis Pulle, Nova Guinea 8: 382. 1910. Type: Indonesia, Irian Jaya, *Versteeg 1028* (lectotype, designated here amongst the syntypes: L! [0018939]; isoelectotypes: BO, U! [1248394]).

Dioclea hexandra (Ralph) Mabb., Taxon 29(5–6): 605–606, 1980. Type: based on *Mucuna hexandra* Ralph.

Note. Adema (1998) considered that plate 5 of *Parrana rubra* Rumph. in Rumphius (1747) should be taken as the type of *Mucuna hexandra* Ralph. In our opinion, the illustration of *Parrana rubra* does not provide sufficient elements to allow associating it with *Macropsychanthus hexander* (or with any species of *Macropsychanthus*). When publishing *Mucuna hexandra*, Ralph (1849) illustrated the fruit and explicitly stated that he took the drawing from the unpublished painting of *Dolichos hexandrus* in Roxburgh icon 2328 that fits quite well with the diagnostic features of *Mucuna hexandra*, including the androecium with six fertile stamens (Fig. 5). We thus consider the original Roxburgh figure as the holotype of the basionym.

4.1.18. *Macropsychanthus huberi* (Ducke) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212318-1

Basionym: *Dioclea huberi* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 172–173. 1922. Type: Brazil, Pará, Gurupá, *Ducke s.n. MG 16533* (lectotype, designated here amongst the syntypes: [in two parts] RB! [00540233] & [00547679]; isoelectotype: S! [S-R-9706]).

4.1.19. *Macropsychanthus javanicus* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212319-1

Basionym: *Dioclea javanica* Benth., Pl. Jungh. 2: 236. 1852. Type: Indonesia, Java, *Junghuhn s.n. [=108?]* (lectotype, designated here: K! [000898373]; isoelectotype: L! [0018938]).

Dioclea fergusonii Thwaites, Enum. Pl. Zeyl. 5: 412. 1864. Type: Sri Lanka, near Colombo, *Ferguson 3817* (holotype: BM! [000958602]; isotypes: G! [00364007], K! [000898372], P! [00708478]).

4.1.20. *Macropsychanthus jamesonii* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212320-1

Basionym: *Dioclea jamesonii* R.H. Maxwell, Novon 21(2): 239, f. 7. 2011. Type: Ecuador. “Collectio Reichenbach fil., Acqu. 1889”, *Jameson s.n.* (holotype: W! [125398]; isotype: W! [125301]).

4.1.21. *Macropsychanthus latifolius* (Benth.) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212321-1

Basionym: *Dioclea latifolia* Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Goiás?, San Izidro, *Pohl 1565* (lectotype, designated here from the syntypes: W! [2002-0002134]; isotypes: K! [000189688], NY! [00007731]).

4.1.22. *Macropsychanthus lauterbachii* Harms, in Schumann & Lauterb. Fl. Schutzgeb. Südsee 367. 1900.

Type. Papua New Guinea, Nurufuss, *Lauterbach s.n.* (lectotype, designated here from the syntypes: WRS!; isolectotype: B †).

4.1.22.1. *Macropsychanthus lauterbachii* Harms var. *lauterbachii* in Verdcourt, Kew Bull. 32(2): 455. 1978.

4.1.22.2. *Macropsychanthus lauterbachii* var. *glabricalyx* (Verd.) Adema, Blumea 43: 236. 1998.

Macropsychanthus lauterbachii subsp. *glabricalyx* Verd., Kew Bull. 32(2): 456. 1978.

Type. Papua New Guinea, Northern District, near Kokoda, *Hoogland 3953* (holotype: K! [000900297]; isotypes: A! [00057463], BM! [000958600] & [000958601], BRI! [AQ0050313], CANB! [74008.1], L! [0019087], LAE, MEL! [81601], US! [00170444]).

4.1.22.3. *Macropsychanthus lauterbachii* var. *hirsutus* Verd., Kew Bull. 32(2): 456. 1978.

Type. Papua New Guinea, Morobe District: near Lae, *Millar in NGF 13819* (holotype: K! [000900298]; isotypes: A! [00057464], E! [00531192], BRI! [AQ0050930], L! [0019088], LAE).

4.1.22.4. *Macropsychanthus lauterbachii* var. *parviflorus* (Verd.) Adema, Blumea 43: 236. 1998.

Macropsychanthus lauterbachii subsp. *parviflorus* Verd., Kew Bull. 32(2): 456-457. 1978. Type: based on *Macropsychanthus lauterbachii* var. *parviflorus* (Verd.) Adema. *Macropsychanthus lauterbachii* subsp. *neobritannicus* Verd., Kew Bull. 32(2): 456-457. 1978. Type: Papua New Guinea, New Britain, Talasea subdistrict, Kapiura river, *Henty in NGF 29391* (holotype: LAE; isotypes: A! [00057465], BOG, BRI! [AQ0052463], CANB, K! [000900299], L! [0019091], SING).

Type. Papua New Guinea, Milne Bay District, Rossel Island, *Brass 28335* (holotype: K! [000900300]; isotypes: A! [00057466], L! [0019089] & [0019090], LAE, S! [S10-10521], US! [00170445]).

4.1.23. *Macropsychanthus malacocarpus* (Ducke) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212322-1

Basionym: *Dioclea malacocarpa* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 170–172. 1922. Type: Brazil, Pará, Belém, *Ducke in MG 15808* (lectotype, designated here from the syntypes: MG! [015700]; isolectotypes: BM! [000931774], G! [00364764], RB!, US! [00004611]).

4.1.24. *Macropsychanthus marginatus* (Benth.) L.P. Queiroz & Snak, comb. nov.
urn:lsid:ipni.org:names:77212323-1

Basionym: *Dioclea marginata* Benth., Fl. Bras. 15(1): 166. 1859. Type: Brazil, Bahia, near villa da Barra, *Blanchet 3085* (lectotype, designated here from the isotypes: K! [000206534]; isolectotypes: BM! [000931779], G! [00364023], K! [000206533], LE! [00002537], MO! [2071255], NY! [00007732], P! [00708476]).

4.1.25. *Macropsychanthus megacarpus* (Rolfe) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212324-1

Basionym: *Dioclea megacarpa* Rolfe, Bull. Misc. Inform. Kew 1901: 139. 1901. Type: Trinidad, St. Ann, *Hart 6406* (lectotype, designated by Amshoff (1939): K! [000502846]).

Dioclea reflexa var. *grandiflora* Benth., Fl. Bras. 15(1): 162. 1859. Type: Brazil, Piauí, inter Boa Esperança et Sant'Anna das Mercês, *Gardner 2117* (lectotype, designated here from the isotypes: K! [000206505]; isotypes: BM! [000931778], K! [000206506]).

Taurophthalmum pulchrum Duchass. in Griesbach, Cat. Pl. Cub.: 76. 1886, nom. inval. pro syn. Lectotype [designated here]: watercolour painting by Duchassaing (GOET!), syn. nov. (Fig. 4).

4.1.26. *Macropsychanthus mindanaensis* Merr., Philipp. J. Sci. 5: 120. 1910.

Type. Philippines, Mindanao, Province of Surigao, *Bolster 330* (holotype: PNH †).

Note. Merrill (1910) did not refer to the herbarium where the type is housed and we were unable to track it. The PNH herbarium curator confirmed that the holotype was housed at PNH (as PNH 4697) but that it was destroyed during World War II (L. Evangelista, Philippine National Herbarium, National Museum, pers. comm.). Adema (1998) speculated that it could be more closely related to (or conspecific with) *M. ferrugineus* as it was described as having ten fertile stamens.

4.1.27. *Macropsychanthus mollicomus* (Ducke) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212325-1

Basionym: *Dioclea mollicoma* Ducke, Trop. Woods 90: 19–20. 1947. Type: Brazil, Amazonas, Esperança, *Ducke 1598* (lectotype, designated here from the syntypes: MG! [018160]; isolectotypes: A! [00277380], F! [0059198F], GH, K! [000978042], NY! [00007734], R! [000054824], RB! [00649170; 00540238], UC! [1204097], US! [00004610]).

4.1.28. *Macropsychanthus pulchrus* (Moldenke) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212326-1

Basionym: *Dioclea pulchra* Moldenke, Phytologia 1(1): 6–7. 1933. Type: Colombia, Boyaca, El Umbo region, *Lawrence 528* (holotype: NY! [00007739]; isotypes: A!



Figure 4. Lectotype of *Taurophthalmon pulchrum* Duchassaing. This watercolour painting housed at GOET is the only remnant of the original material of this species cited in Griesebach (1866).

[00277304], BM! [000931782], F! [0059201F], FI! [005117], G! [00364763], K! [000502890], MG, MO! [277051], NY! [00007738], S! [S-R-9708], U! [0008110], UC, US! [00004604]).

4.1.29. *Macropsyчанthus purpureus* (Elmer) L.P. Queiroz & Snak, comb.nov.

urn:lsid:ipni.org:names:77212327-1

Basionym: *Luzonia purpurea* Elmer, Leaflet. Philipp. Bot. 1: 220. 1907. Type: Philippines, Luzon, Province of Tayabas, Lucban, May 1907, *Elmer 9013* (holotype: PNH; isotypes: A! [00057462], E! [00301634], L! [0019058], MO! [256507], NY! [00016167], US! [00004668]).

4.1.30. *Macropsyчанthus rufescens* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212328-1

Basionym: *Dioclea rufescens* Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Minas Gerais?, “Frigina do Alfonso”, *Pohl s.n.* (lectotype, designated here from the isotypes: K! [000189690] [labelled as number 1102]; isolectotypes: F! [0059204F], K! [000189689], NY! [00007743], W! [2002-0002137; 2002-0002138]).

Dioclea rubiginosa Tul., Arch. Mus. Hist. Nat. 4: 72. 1844. Type: Brazil, Minas Gerais, *Claussen 958*, 1838 (lectotype designated here: P! [00708479]; isolectotype: P! [00708480]).

4.1.31. *Macropsyчанthus schimpffii* (Diels) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212329-1

Basionym: *Dioclea schimpffii* Diels, Biblioth. Bot. 116: 97. 1937. Type: Ecuador, Chimborazo, Naranjapata, rio Chanchan, *Schimpff 565* (holotype: B†; lectotype, designated here: G! [00364005]; isolectotypes: MO! [289358; 289359]).

4.1.32. *Macropsyчанthus schottii* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212330-1

Basionym: *Dioclea schottii* Benth., Comm. Legum. Gen.: 70. 1837. Type: Brazil, Rio de Janeiro, “in campis”, *Schott s.n.* (lectotype, designated here from the isotypes: W! [2002-0002135]; isolectotypes: F! [0059206F], K! [000502844], NY! [00007745], W! [2002-0002136]).

4.1.33. *Macropsyчанthus sclerocarpus* (Ducke) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212331-1

Basionym: *Dioclea sclerocarpa* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 169–170. 1922. Type: Brazil, Pará, Monte Alegre, *Ducke s.n. MG 17152* (lectotype, designated here from the syntypes: RB! [00540242]; isolectotypes: BM! [000931772], MG, P! [02752764]).



Figure 5. Original painting of Roxburgh icon 2328 (K) from *Dolichos hexandrus* that was used by Ralph (1849) to propose *Mucuna hexandra* Ralph. Note the androecium with six fertile stamens typical of *Macropsychanthus hexander* (Ralph) L.P. Queiroz & Snak. Available Roxburgh's Flora Indica (Kew 2006) at <http://apps.kew.org/floraindica/displayImages.do?index=6>.

Dioclea reflexa var. *glabrescens* Benth., Fl. Bras. 15(1): 162–163. 1859. Type: Brazil, Maranhão, *Gardner 5988* (lectotype, designated here from the syntypes: K! [000502898]; isoelectotypes: BM! [000931773]).

4.1.34. *Macropsyчанthus ucayalinus* (Harms) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212332-1

Basionym: *Dioclea ucayalina* Harms, Notizbl. Bot. Gart. Berlin-Dahlem 9: 262. 1925. Type: Peru, middle Ucayali, Yarina Cocha, *Tessmann 3464* (holotype: B† [photo F! [F0BN002411]; lectotype, designated here from the isotypes: S! [S-R-9711]; isoelectotypes: G! [00364004], NY! [00007748], US! [00004646]).

4.1.35. *Macropsyчанthus umbrinus* (Elmer) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212333-1

Basionym: *Dioclea umbrina* Elmer, Leaflet. Philipp. Bot. 1: 224. 1907. Type: Philippines, Leyte, *Elmer 7249* (holotype: PHN; isotype: K! [000898375]).

Note. In the protologue of the basionym, Elmer (1907) cited the type specimen as “9015, A. D. E. Elmer, Palo, Province of Leyte, Leyte, January, 1906”. All of that information is on the label of the Kew specimen, although that label gives the collector number as 7249. As all of the other elements fit the protologue, we are considering the Kew specimen as an isotype.

4.1.36. *Macropsyчанthus violaceus* (Mart. ex Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212334-1

Basionym: *Dioclea violacea* Mart. ex Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Bahia?, Mucuri fluv., *Wied s.n.* (lectotype, designated here from the syntypes: BR! [0000005194667]; isoelectotypes: BR [0000005196715; [0000005194995]).

Dolichos altissimus Vell., Fl. Flumin.: 320. 1825 [1829], non *Dolichos altissimus* Jacq., Enum. Syst. Pl. 27. 1760, nom. illeg. Type: Brazil, Rio de Janeiro, “Habitat silvis maritimis”, *Vellozo* (lectotype, designated here: tab. 154 in *Vellozo, Fl. Flumin. Ic.* vol. 7, 1829).

Dioclea pilifera Tul., Arch. Mus. Hist. Nat. 4: 71. 1844. Type: Brazil, *Claussen s.n.* (holotype: P! [00708484]).

Dioclea paraguariensis Hassl., Repert. Spec. Nov. Regni Veg. 16: 228–229. 1919. Type: Paraguay, Lake Ypacaray, *Hassler 12460* (lectotype, designated here from the syntypes: G! [00381578]; isoelectotypes: C! [10012111], E! [00531190], G! [00381577], K! [000502900], S! [S-R-9701]).

Dioclea altissima (Vell.) Rock, Legum. Pl. Hawaii: 201. 1920. Type: based on *Dolichos altissimus* Vell.

4.1.37. *Macropsyчанthus wilsonii* (Standl.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212335-1

Basionym: *Dioclea wilsonii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 310–311. 1929. Type: Honduras, *Wilson 336* (holotype: F! [0059180F]; isotypes: NY! [00007718], US [00004644]).

Dioclea atropurpurea Pittier, Bol. Tecn. Minist. Agric. 5: 79, f. 34, 1944. Type: Venezuela, Sucre, entre Cumaná y Cumanacoa, *Pittier 14660* (holotype: VEN [4439]; isotypes: K! [000502895], S! [S-R-9702]).

4.2. *Macropsyчанthus* subg. *Platylobium* (Benth.) L.P. Queiroz

Dioclea sect. *Platylobium* Benth., Fl. Bras. 15(1): 164. 1859.

Dioclea sect. *Macrocarpon* Amshoff, Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 52: 68. 1939. Type [designated by Maxwell, 2011]: *Dioclea macrocarpa* Huber.

Dioclea subg. *Platylobium* (Benth.) R.H. Maxwell, Novon 21(2): 232, 2011. Type: based on *Dioclea* sect. *Platylobium* Benth.

Type. [designated by Maxwell, 2011]: *Dioclea bicolor* Benth. Stipules basifixed, not prolonged below their insertion. Leaves estipellate. Fruit flat, compressed and elastically dehiscent, with twisting woody valves, rarely indehiscent or passively dehiscent and turgid (*M. ruddiae*). Seeds with a short and oblong hilum (Fig. 3 G–J).

This subgenus fits the circumscription of *Dioclea* subg. *Platylobium* (sensu Maxwell, 2011) with the transfer of *Macropsyчанthus huberi* to the section *Macropsyчанthus*.

Nine species are known from South America, centred in the Amazon and Guyana region and three species extend southward into the Cerrado biome in central Brazil.

4.2.1. *Macropsyчанthus bicolor* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212336-1

Basionym: *Dioclea bicolor* Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Amazonas [‘Rio Negro’], Coari, *Martius s.n. Obs. 2877* (lectotype, designated here from the syntypes: M! [0240649]; isolectotype: M! [0240648]).

Dioclea rostrata Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, “Villa Nova do Almeida”, *Wied s.n.* (lectotype, designated here from the isotypes: BR! [0000005197378]; isolectotype: BR! [0000005197040]), *syn. nov.*

Dioclea rostrata var. *nitida* Benth., Fl. Bras. 15(1): 168. 1859. Type: Brazil, Mato Grosso?, ‘Salto do Curaú, rio Pardo’, *Riedel 452 (560)* (lectotype, designated here from the isotypes: LE! [00002539]; isolectotypes: A! [00066322], F! [0059202F], K! [000502901], NY! [01583820]), *syn. nov.*

4.2.2. *Macropsychanthus coriaceus* (Benth.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212337-1

Basionym: *Dioclea coriacea* Benth., Comm. Legum. Gen.: 69. 1837. Type: Brazil, Goiás?, Corgo do Padre, *Pohl 1966* (lectotype, designated here from the syntypes: W! [2002-0002131]; isolectotypes: K! [000189687], NY [00007724]).

4.2.3. *Macropsychanthus duckei* L.P. Queiroz & Snak, nom. nov.

Basionym: *Dioclea ferruginea* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 93, pl. 7. 1925. Type: Brazil, Pará, rio Tapajós, lago Quataquara, *Ducke in RB 17266* (holotype: RB! in three parts [00616768; 00616767; 00540231]).

Note. The specific epithet of the basionym *Dioclea ferruginea* cannot be used to make a new combination in *Macropsychanthus* because the name *M. ferrugineus* is already occupied. We propose the new name honouring the botanist A. Ducke who made huge contributions to our knowledge of the Amazon flora and discovered this species.

4.2.4. *Macropsychanthus erectus* (Hoehne) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212338-1

Basionym: *Dioclea erecta* Hoehne, Comm. Lin. Telegr., Bot. 45(8): 92, t. 151, 159. 1919. Type: Brazil, Mato Grosso, Juruena, *Hoehne 1886* (lectotype, designated here from the syntypes: R! [000211395]).

4.2.5. *Macropsychanthus hispidimarginatus* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212339-1

Basionym: *Dioclea hispidimarginata* R.H. Maxwell, Novon 21(2): 232. 2011. Type: Peru, Amazonas, Valle de Rio Santiago, Caterpiza, *Huashikat 1654* (holotype: MO! [713605]; isotype: JEF).

4.2.6. *Macropsychanthus macrocarpus* (Huber) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212340-1

Basionym: *Dioclea macrocarpa* Huber, Bol. Mus. Goeldi Hist. Nat. Ethnogr. 5(2): 410–411. 1909. Type: Brazil, Pará, rio Ariramba, *Ducke s.n. MG 8071* (holotype: MG! [8071]; isotypes: BM! [000931775], G! [00365046]).

4.2.7. *Macropsychanthus rigidus* (R.S. Cowan) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212341-1

Basionym: *Dioclea rigida* R.S. Cowan, Mem. New York Bot. Gard. 10(1): 150–151. 1958. Type: Venezuela: Amazonas, Cerro Paru, *Cowan & Wurdack 31252* (holotype: Y! [00007744]; isotype: US! [00004603]).

Dioclea steyermarkii R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 585–587, f. 1. 1990. Type: Venezuela, Amazonas, Atures, *Huber 4476* (holotype: US! [00324271]; isotypes: K! [00324271], MYF, NY! [00007746]), syn. nov.

4.2.8. *Macropsychanthus ruddiae* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212342-1

Basionym: *Dioclea ruddiae* R.H. Maxwell, Ann. Missouri Bot. Gard. 75(2): 730–732, f. 1. 1988. Type: Venezuela, Amazonas, Cerro Huachamacari, *Maguire et al. 29930* (holotype: US! [00067942]; isotypes: F! [0059203F], GH! [00066323], K, IAN, MO, NY, P, RB! [00540240], S! [S-R-9709], U! [0003527], VEN! [43782]).

4.2.9. *Macropsychanthus scabrus* (Rich.) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212343-1

Basionym: *Dolichos scaber* Rich., Actes Soc. Hist. Nat. Paris 1: 111. 1792. Type: French Guyana, *Leblond 183* (holotype: G! [00364886]).

Dioclea scabra (Rich.) R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 578. 1990.

Note. Maxwell (1990) designated a neotype for *Dolichos scaber* (*de la Cruz 3090*, UC), but that neotype should be substituted after the finding of the *Leblond* specimen, which was part of a set of plants sent by Leblond from French Guyana (Richard 1792).

4.2.9.1. *Macropsychanthus scabrus* (Rich.) L.P. Queiroz & Snak var. *scabrus*

Dioclea elliptica R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 578. 1990, nom. inval. (nom. nud.).

Note. Maxwell (1969) proposed the name *Dioclea elliptica* in his Ph.D. dissertation, using as the type the specimen *de la Cruz 3090* from Essequibo, Guyana. That dissertation is not considered an effective publication, however, under ICN Article 30.9 (Turland et al. 2018). It was later published as a synonym of *D. scabra* by Maxwell (1990), but with no description, thus being a nomen nudum (ICN Art. 38.1, Turland et al. 2018).

4.2.9.2. *Macropsychanthus scabrus* var. *brownii* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212344-1

Basionym: *Dioclea scabra* var. *brownii* R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 579, 581. 1990. Type: Venezuela, Amazonas, Atabapo, *Davidse et al. 17450* (holotype: MO! [277050]; isotypes: MYF, NY).

4.2.9.3. *Macropsychanthus scabrus* var. *schulzii* (R.H. Maxwell) L.P. Queiroz & Snak, comb. nov.

urn:lsid:ipni.org:names:77212345-1

Basionym: *Dioclea scabra* var. *schulzii* R.H. Maxwell, Ann. Missouri Bot. Gard. 77(3): 581. 1990. Type: Guyana, Essequibo, Potaro, *Atkinson 116* (holotype: BM! [000931781]; isotypes: NY! [01365181], US).

Acknowledgements

We thank to the curator of the herbaria that sent material on loan or that allowed us to study their collections (A, AAU, ALCB, B, BA, BHCB, BM, BR, C, CAS, CEN, CEPEC, CTES, CVRD, E, EAC, ESA, F, G, GOET, HPEH, HRB, HST, HSTM, HUEFS, IAN, ICN, INPA, JPB, K, L, LE, LIL, LP, M, MBM, MBML, MEXU, MG, MO, NY, P, PEUFR, R, RBSP, S, SI, SPF, TEPB, U, UEC and W). Marc Appelhans (GOET) and Craig Brough (K) helped in locating old images that were selected as the types of *Taurophtalmum pulchrum* and *Mucuna hexandra*, respectively. We thank Alex Popovkin (*Macropsychanthus edule*); Axel Dalberg Poulsen (*M. lautherbachii*); and Domingos Cardoso (*Cymbosema roseum*, *Dioclea virgata*, and *Macropsychanthus scabrus*) for sharing their beautiful photographs and Pat Herendeen and two anonymous reviewers for their comments on the manuscript. Roy Funch revised the English language. CS thanks the CNPq for the PDJ fellowship (process 152886/2018-4).

LPQ work on legume systematics was supported by CNPq (processes 303585/2016-1 and 440487/2015-3) and FAPESB (PTX0004/2016 and APP0096/2016). The use of DNA from the Brazilian species is authorised by SISGEN n° AEB0728.

References

- Adema F (1998) Notes on Malesian Fabaceae (Leguminosae-Papilionoideae) 3. The genera *Dioclea*, *Luzonia*, and *Macropsychnanthus*. *Blumea* 43: 233–239. <http://www.repository.naturalis.nl/record/525756>
- Amshoff GJH (1939) On South American Papilionaceae. *Mededeelingen van het Botanisch Museum en Herbarium van de Rijks Universiteit te Utrecht* 52: 1–78. <http://www.repository.naturalis.nl/record/535079>
- Armstrong WP (2001) Notes on the Ocean dispersal of Coral Beans. *The Drifting Seed* 7: 5–6. <http://www.seabean.com/newsletters/vol07-1.pdf>
- Arroyo MTK (1981) Breeding systems and pollination biology in Leguminosae. In: Polhill, RM, Raven, PH (Eds) *Advances in Legume Systematics*, part 2. Royal Botanic Gardens, Kew, 723–769.
- Backlund A, Bremer K (1998) To be or not to be. Principles of classification and monotypic Plant Families. *Taxon* 47(2): 391–400. <https://doi.org/10.2307/1223768>
- Baldwin BG, Markos S (1998) Phylogenetic utility of the external transcribed spacers (ETS) of 18S–26S rDNA: Congruence of ETS and ITS trees of *Calycadenia* (Compositae). *Molecular Phylogenetics and Evolution* 10(3): 449–463. <https://doi.org/10.1006/mpev.1998.0545>
- Bentham G (1837) *Commentationes de Leguminosarum Generibus*. Zollinger, Vienna, 1–488.
- Bentham G (1840) Contributions towards a Flora of South America. – Enumeration of Plants collected by Mr. Schomburgk in British Guiana. *Le Journal de Botanique* 2: 38–103.
- Bentham G (1859) Leguminosae 1, Papilionaceae. In: Martius, CFP, Endlicher, S, Urban, I (Eds) *Flora Brasiliensis*, vol. 15, part 1. Frid. Fleisher, Munich.
- Britton NL, Wilson P (1924) *Botany of Porto Rico and the Virgin Islands*, vol. 5, part 3. New York Academy of Sciences.
- Candolle AP (1825) *Prodromus Systematis Naturalis Regni Vegetabilis*, part 2. Sumptibus Sociorum Treuttel et Würtz, Paris.
- Carauta JPP (1969) A data efetiva da publicação da "Flora Fluminensis". *Vellozia* 7: 26–33.
- Carauta JPP (1972) A data efetiva da publicação da Flora Fluminensis. 11. O texto impresso em 1825. In: *Anais do XXII Congresso Nacional de Botânica*, Garanhuns, Brasil, 141–147.
- Doyle JJ, Doyle JL (1987) A rapid DNA isolation method for small quantities of fresh tissues. *Phytochemical Bulletin* 19: 11–15.
- Drummond AJ, Ashton B, Cheung M, Heled J, Kearse M, Moir R, Stones-Havas S, Thierer T, Wilson A (2012) Geneious version 6.1.6. Available at <https://www.geneious.com>
- Edgar R (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Elmer ADE (1907) Some new Leguminosae. *Leaflets of Philippine Botany* 1: 220–232.
- Erixon P, Svennblad B, Britton T, Oxelman B (2003) Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology* 52(5): 665–673. <https://doi.org/10.1080/10635150390235485>

- Farris JF, Källersjö M, Kluge AG (1995) Constructing a Significance Test for Incongruence. *Systematic Biology* 44(4): 570–572. <https://www.jstor.org/stable/2413663>
- Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution; International Journal of Organic Evolution* 39(4): 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Fitch WM (1971) Towards defining the course of evolution: Minimum change for a specific tree topology. *Systematic Zoology* 20(4): 406–416. <https://doi.org/10.2307/2412116>
- Franco ALM (1995) Ecologia da polinização e biologia reprodutiva de sete espécies de Phaseoleae (Fabaceae). PhD Thesis, Universidade Estadual de Campinas, Brazil. http://repositorio.unicamp.br/jspui/bitstream/REPOSIP/315404/1/Franco_AndreaLucieneMonerat_D.pdf
- Grisebach A (1866) *Catalogus plantarum cubensium exhibens collectionem Wrightianam aliasque minores ex insula Cuba missas*. Gulielmum Engelmann, Leipzig, 1–301. <https://doi.org/10.5962/bhl.title.177>
- Harms HAT (1900) Familie Leguminosae. In: Schumann K, Lauterbach K (Eds) *Die Flora der Deutschen Schutzgebiete in der Südsee*. Verlag von Gebrüder Borntraeger, Leipzig, 342–372.
- Hedges SB (1992) The number of replications needed for accurate estimation of the bootstrap p value in phylogenetic studies. *Molecular Biology and Evolution* 9: 366–369. <https://doi.org/10.1093/oxfordjournals.molbev.a040725>
- Hu J, Lavin M, Wojciechowski MF, Sanderson MJ (2000) Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast trnK/matK sequences and its implications for evolutionary patterns in the Papilionoideae. *American Journal of Botany* 87(3): 418–430. <https://doi.org/10.2307/2656638>
- Huber J (1909) *Materiaes para a flora amazonica VII. Plantae Duckeana austro-guyanenses*. Boletim do Museu Goeldi de História Natural e Ethnographia 5: 294–436.
- Kew [Royal Botanic Gardens, Kew] (2006) *Roxburgh's Flora Indica*. Published on the internet; <http://www.kew.org/floraIndica> [accessed 16 June 2020]
- Kollipara KP, Singh RJ, Hymowitz T (1997) Phylogenetic and genomic relationships in the genus *Glycine* Willd. based on sequences from the ITS region of nuclear rDNA. *Genome* 40(1): 57–68. <https://doi.org/10.1139/g97-008>
- Kress WJ, Prince LM, Williams KJ (2002) The phylogeny and a new classification of the gingers (Zingiberaceae): Evidence from molecular data. *American Journal of Botany* 89(10): 1682–1696. <https://doi.org/10.3732/ajb.89.10.1682>
- Kunth KS (1823 [1824]) *Nova genera et species plantarum: quas in peregrinatione ad plagam aequinoctialem orbis novi collegerunt /descripserunt, partim adumbraverunt* Amat. Bonpland et Alex. de Humboldt, vol. 6. Typ. J. Smith, Paris.
- Lackey JA (1981) Tribe Phaseoleae DC (1825). In: Polhill RM, Raven PH (Eds) *Advances in Legume Systematics, Part 1*. Royal Botanic Gardens, Kew, 301–327.
- Lima HC (1995) Leguminosas da Flora Fluminensis - J.M. da C. Vellozo - lista atualizada das espécies arbóreas. *Acta Botanica Brasílica* 9(1): 123–146. <https://doi.org/10.1590/S0102-33061995000100006>
- LPWG [The Legume Phylogeny Working Group] (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66: 44–77. <https://doi.org/10.12705/661.3>

- Maxwell RH (1969) The genus *Dioclea* (Fabaceae) in the New World. PhD Dissertation, Southern Illinois University, Carbondale, U.S.A.
- Maxwell RH (1970) The genus *Cymbosema* (Leguminosae): Notes and distribution. *Annals of the Missouri Botanical Garden* 57(2): 252–257. <https://www.jstor.org/stable/2395112>. <https://doi.org/10.2307/2395112>
- Maxwell RH (1977) A resumé of the genus *Cleobulia* (Leguminosae) and its relation to the genus *Dioclea*. *Phytologia* 38: 51–65. <https://doi.org/10.5962/bhl.part.23376>
- Maxwell RH (1978) Problems in the placement of *Dioclea paniculata* Killip MS. (Leguminosae). *Phytologia* 40: 243–252. <https://doi.org/10.5962/bhl.part.28268>
- Maxwell RH (1990) A new combination in *Dioclea* Kunth (Fabaceae – Diocleinae) from the clarification of *D. glabra* Benthams, Flora Brasiliensis. *Annals of the Missouri Botanical Garden* 77(3): 578–583. <https://doi.org/10.2307/2399522>
- Maxwell RH (2011) New species and notes in the genus *Dioclea* s.l. (Fabaceae, subtribe Diocleinae). *Novon* 21(2): 226–243. <https://doi.org/10.3417/2002014>
- Maxwell RH, Taylor DW (2003) Phylogenetic relationships of the Diocleinae with particular emphasis on the subgroups of *Dioclea*. In: Klitgaard BB, Bruneau A (Eds) *Advances in Legume Systematics, Part 10. Higher Level Systematics*. Royal Botanic Gardens, Kew, 325–353.
- Merrill ED (1910) An enumeration of Philippine Leguminosae with keys to the genera and species. *Philippine Journal of Science* 5: 95–136.
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, U.S.A., 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Miquel FAW (1855) *Flora van Nederlandsch Indië*, vol. 1. C.G. van der Post, Amsterdam. <https://doi.org/10.5962/bhl.title.93>
- Muir J (1933) The beach drift of South Africa. *Veld & Flora* 18: 5–10. <https://journals.co.za/docserver/fulltext/veld/18/1/1481.pdf?expires=1597604471&id=id&accname=guest&checksum=4102131131E5C4F3F2E87B4620445D62>
- Müller KF (2005) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. *BMC Evolutionary Biology* 5(1): 58. <https://doi.org/10.1186/1471-2148-5-58>
- Nylander JAA (2004) MrModeltest v. 2. Program Distributed by the Author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- Paithankar KR, Prasad KSN (1991) Precipitation of DNA by polyethylene glycol and ethanol. *Nucleic Acids Research* 19(6): 1346. <https://doi.org/10.1093/nar/19.6.1346>
- Peçanha AF (2014) Caracterização anatômica do desenvolvimento da calosidade na pétala estandarte em flores de espécies de *Dioclea* Kunth (Fabaceae-Diocleinae). PhD Thesis, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Brazil. http://w2.files.scire.net.br/atrio/jbrj-ppgenbt_upl//THESIS/135/alinyfpecanha_psdefesa.pdf
- Queiroz LP, Fortunato RH, Giulietti AM (2003) Phylogeny of the Diocleinae (Papilionoideae: Phaseoleae) based on morphological characters. In: Klitgaard BB, Bruneau A (Eds) *Advances in Legume Systematics Part 10, Higher Level Systematics*. Royal Botanic Gardens, Kew, 303–324.

- Queiroz LP, Pastore JFB, Cardoso D, Snak C, de Lima AL, Gagnon E, Vatanparast M, Holland AE, Egan AN (2015) A multilocus phylogenetic analysis reveals the monophyly of a recircumscribed papilionoid legume tribe Diocleae with well-supported generic relationships. *Molecular Phylogenetics and Evolution* 90: 1–19. <https://doi.org/10.1016/j.ympev.2015.04.016>
- Ralph TS (1849) *Icones Carpologicae; or, figures and descriptions of fruits and seeds*. William Pamplin, London, 1–48. <https://doi.org/10.5962/bhl.title.140683>
- Rambaut A (2018) FigTree: tree figure drawing tool, version 1.4.4, November 2018. <http://tree.bio.ed.ac.uk/software/figtree/> [accessed 1 May 2019]
- Richard L (1792) *Catalogus Plantarum, ad Societatem, ineunte anno 1792, e Cayenna misarum a domino Le Blond*. *Actes de la Société d'Histoire Naturelle de Paris* 1: 105–114.
- 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>
- Rumphius GE (1747) *Herbarium Amboinense: plurimas complectens arbores, frutices, herbas, plantas terrestres & aquaticas, quae in Amboina et adjacentibus reperiuntur insulis accuratissime descriptas iuxta earum formas, cum diuersis denominationibus cultura, usu, ac virtutibus, quod & insuper exhibet varia insectorum animaliumque genera, plurima cum naturalibus eorum figuris depicta*. Part 5. Fransicum Changuion, Joannem Catuffe, Hermannum Uytwerf, Amsterdam, 1–492.
- Samarakoon T, Wang SY, Alford MH (2013) Enhancing PCR amplification of DNA from recalcitrant plant specimens using a trehalose-based additive. *Applications in Plant Sciences* 1(1): 1200236. <https://doi.org/10.3732/apps.1200236>
- Sede SM, Tosto D, Talia P, Luckow M, Poggio L, Fortunato RH (2009) Phylogenetic relationships among southern South American species of *Camptosema*, *Galactia* and *Collaea* (Diocleinae: Papilionoideae: Leguminosae) on the basis of molecular and morphological data. *Australian Journal of Botany* 57(1): 76–86. <https://doi.org/10.1071/BT08091>
- Sprengel KPJ (1825 [1824]) *Caroli Linnaei Systema Vegetabilium*, ed. 16, vol. 1. Sumtibus Librariae Dieterichianae, Gottingen.
- Sprengel KPJ (1827) *Caroli Linnaei Systema Vegetabilium*, ed. 16, vol. 4, part 2. Sumtibus Librariae Dieterichianae, Gottingen.
- Staffeu FA, Cowan RS (1985) *Taxonomic Literature: A selective guide to botanical publications and collections with dates, commentaries and types*. V - Sal-St. *Regnum Vegetabile*: 112. [Scheltema and Holkema, Bohn.]
- 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>
- Sun Y, Skinner DZ, Liang GH, Hulbert SH (1994) Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theoretical and Applied Genetics* 89(1): 26–32. <https://doi.org/10.1007/BF00226978>
- Swofford DL (2002) *PAUP*: Phylogenetic Analysis using Parsimony (*and other methods)*, Version 4.0b10. Sinauer, Sunderland, U.S.A.
- Turland NJ, Wiersma 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. <https://doi.org/10.12705/Code.2018>
- Urban I (1899) *Symbolae Antillanae, seu, Fundamenta florae Indiae Occidentalis*, vol. 1. Fratres Borntraeger, Berlin, Paris. <https://doi.org/10.5962/bhl.title.144>
- Varela ES, Lima JPMS, Galdino AS, Pinto LS, Bezerra WM, Nunes EP, Alves MAO, Grangeiro TB (2004) Relationships in subtribe Diocleinae (Leguminosae; Papilionoideae) inferred from Internal Transcribed Spacer sequences from nuclear ribosomal DNA. *Phytochemistry* 65(1): 59–69. <https://doi.org/10.1016/j.phytochem.2003.08.005>
- Vellozo JM da C (1829 [1825]) *Florae fluminensis, seu, Descriptionum plantarum praefectura fluminensi sponte nascentium*. Typographia Nacional, Rio de Janeiro, Brazil.
- Vellozo JM da C (1831 [1827]) *Florae fluminensis Icones*, vol. 7. Litogr. Senefelder, Paris.
- Verdcourt B (1978) New Taxa of Leguminosae from Papua New Guinea. *Kew Bulletin* 32(2): 455–473. <https://www.jstor.org/stable/4117269>. <https://doi.org/10.2307/4117116>
- Verdcourt B (1979) *A Manual of New Guinea Legumes*. Botany Bulletin n 11.: Office of Forests, Division of Botany, Lae, Papua New Guinea.
- Walpers WG (1840) Leguminosae. In: de Schlechtendal DFL (Ed.) *Collectio plantarum Bahiensium a Luschnatio decerpitarum, exsiccatarum et veno positarum*. *Linnaea* 14: 285–302.
- Wojciechowski MF, Lavin M, Sanderson M (2004) A phylogeny of legumes (Leguminosae) based on analysis of the plastid *matK* gene resolves many well supported subclades within the family. *American Journal of Botany* 91(11): 1846–1862. <https://doi.org/10.3732/ajb.91.11.1846>
- Zamora N (2000) Nuevas especies y combinaciones en leguminosas de Mesoamerica. *Novon* 10(2): 175–180. <https://doi.org/10.2307/3393023>

Supplementary material I

Figure S1

Authors: Luciano Paganucci de Queiroz, Cristiane Snak

Data type: molecular data

Explanation note: Bayesian 50% consensus cladogram and respective phylogram of the *Dioclea* clade resulting from the ETS analysis. Bayesian posterior probabilities are reported above branches and parsimony (left) and maximum likelihood (right) bootstrap support values are reported below branches. Bootstrap values below 50% are represented by hyphens.

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.164.55441.suppl1>

Supplementary material 2

Figure S2

Authors: Luciano Paganucci de Queiroz, Cristiane Snak

Data type: molecular data

Explanation note: Bayesian 50% consensus cladogram and respective phylogram of the *Dioclea* clade resulting from the ITS analysis. Bayesian posterior probabilities are reported above branches and parsimony (left) and maximum likelihood (right) bootstrap support values are reported below branches. Bootstrap values below 50% are represented by hyphens.

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.164.55441.suppl2>

Supplementary material 3

Figure S3

Authors: Luciano Paganucci de Queiroz, Cristiane Snak

Data type: molecular data

Explanation note: Bayesian 50% consensus cladogram and respective phylogram of the *Dioclea* clade resulting from the trnK/matK analysis. Bayesian posterior probabilities are reported above branches and parsimony (left) and maximum likelihood (right) bootstrap support values are reported below branches. Bootstrap values below 50% are represented by hyphens.

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.164.55441.suppl3>

Two new species of *Microlicia* D. Don (Melastomataceae, Microlicieae) from Chapada dos Veadeiros, Goiás State, Brazil

Jean Correa Fontelas¹, Rosana Romero²

1 Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, Universidade Federal de Uberlândia, Rua Ceará, s.n., 38400-902, Uberlândia, Minas Gerais, Brazil **2** Instituto de Biologia, Universidade Federal de Uberlândia, Rua Ceará, s.n., 38400-902, Uberlândia, Minas Gerais, Brazil

Corresponding author: Jean Correa Fontelas (fontelas@ufu.br)

Academic editor: R. Kriebel | Received 13 August 2020 | Accepted 7 September 2020 | Published 21 October 2020

Citation: Fontelas JC, Romero R (2020) Two new species of *Microlicia* D. Don (Melastomataceae, Microlicieae) from Chapada dos Veadeiros, Goiás State, Brazil. *PhytoKeys* 164: 115–126. <https://doi.org/10.3897/phytokeys.164.57569>

Abstract

Microlicia gracilis and *Microlicia xylopodifera*, endemic to Chapada dos Veadeiros, Goiás State, Brazil, are described, illustrated and the conservation status is also provided. Both species resemble *Microlicia ordinata* and *Microlicia ramosa* that are also endemic to Goiás, by having sessile leaf with serrate and ciliate margin, pedicellate flower, triangular and short sepal and dimorphic stamens with bicolorous and polysporangiate anthers. However, *M. gracilis* differs by the long internode (2–4 mm long), concolorous, semi-amplexicaul and lanceolate leaf, and petal acuminate at the apex. *Microlicia xylopodifera* differs in having a robust xylopodium, horizontal or slightly ascending leaf and a dense crown of glandular trichomes at the apex of flower bud.

Resumo

Microlicia gracilis e *Microlicia xylopodifera*, endêmicas da Chapada dos Veadeiros, são descritas, ilustradas e o estado de conservação fornecido. Ambas espécies se assemelham à *Microlicia ordinata* e *Microlicia ramosa*, também endêmicas de Goiás, por apresentarem folha séssil, com margem serrado-ciliada, flor pedicelada, sépala triangular, curta e estames dimórficos com anteras bicolores e poliesporangiadadas. Contudo, *M. gracilis* diferencia-se pelo entrenó longo (2–4 m compr.), folha concolor, lanceolada e semiamplexicaule, e pétala acuminada no ápice. *Microlicia xylopodifera* difere por apresentar xilopódio robusto, folha horizontal ou levemente ascendente e uma coroa densa de tricomas glandulares no ápice do botão floral.

Keywords

Cerrado rupestre, endemism, Microlicieae, taxonomy

Introduction

Microlicia D.Don is a Brazilian genus with 166 species exclusive to Brazil (Flora do Brasil 2020) and with only 11 species occurring in Bolivia, Peru, Venezuela and Colombia (Renner 1993; Rull 2003; Romero 2003a; Michelangeli and Cotton 2008; Romero and Woodgyer 2015; Mendoza-Cifuentes et al. 2019; Pacifico et al. 2020a; Versiane et al. 2020). The genus reaches high diversity mainly in the campo rupestre of Bahia, Minas Gerais and Goiás (Romero 2003a, b).

The Chapada dos Veadeiros, located in the north-eastern part of the State of Goiás, is considered an important floristic component of the Cerrado biome with different phytophysognomies at elevations that vary from 800 to 1650 metres (Munhoz and Felfili 2006; Felfili et al. 2007; Souza and Bove 2011; Romero et al. 2017). The region stands out as one of the centres of diversity of Microlicieae, being related as a recent radiation area of the tribe, due to the high number of endemic rates and high endemism scores (Pacifico et al. 2020b). The region exhibits a significant number of endemic species of *Chaetostoma* (Silva et al. 2018), *Trembleya* (Pacifico et al. 2019) and *Microlicia* (Pilger 1903; Wurdack 1959; Diniz-Neres and Silva 2017a, 2017b; Romero et al. 2017). Moreover, at least 20 species of *Microlicia* in the State of Goiás occur in the Chapada dos Veadeiros (Naudin 1845; Cogniaux 1883; Pilger 1903; Smith 1955; Wurdack 1959; Almeda and Martins 2001; Romero et al. 2017; Diniz and Silva 2019).

Microlicia has been traditionally characterised in having solitary flowers with five, rarely six petals, free ovary with three or five locules and capsules with longitudinal dehiscence from the apex to the base (Almeda and Martins 2001; Romero 2003a). However, recent molecular studies show that *Microlicia*, as currently delimited, is paraphyletic and most of the morphological characters used for the circumscription of each genus in Microlicieae are homoplastic. Thus, species of *Chaetostoma* DC., *Lavoisiera* DC., *Stenodon* Naudin and *Trembleya* DC. will be included in *Microlicia*, resulting in a monophyletic genus (Versiane 2019).

In the course of preparing a taxonomic treatment of Microlicieae for the State of Goiás, some collections from Chapada dos Veadeiros could not be recognised under any name in the genus and so we concluded that these collections refer to two new undescribed species. The new species are described, compared morphologically with similar species and information about geographic distribution and conservation status is provided, as well as images of morphological structures of the two species.

Material and methods

This study was based on the morphological analysis of specimens of *Microlicia* from the following herbaria: HEPH, HUFU, IBGE, MBM, MO, NY, UB, UEC and US (acronyms according to Thiers 2020). Specimens seen on the online platforms Reflora Virtual Herbarium (2020, <https://reflora.jbrj.gov.br/reflora/herbarioVirtual>), speciesLink (2020, <https://www.splink.org.br/>) and Tropicos (<http://www.tropicos.org>) were referred to

here with barcode numbers. For general morphological terminology, we follow Radford et al. (1974) and the indumentum terminology follows Wurdack (1986). The leaves, colour of the petals, stamens and style were observed only in dry material. According to georeferenced data from the cited collections, the area of occupancy (AOO) and extent of occurrence (EOO) were calculated using GEOCAT (Bachman et al. 2011). The conservation status was based on the IUCN guidelines and criteria (IUCN 2019). Images of vegetative and reproductive structures were obtained using a digital camera coupled to a Zeiss stereoscopic microscope and organised on Adobe Photoshop CS6.

Taxonomic treatment

Microlicia gracilis Fontelas & R.Romero, sp. nov.

urn:lsid:ipni.org:names:77212346-1

Fig. 1

Type. BRAZIL. Goiás: Alto Paraíso de Goiás, Fazenda Água Fria, ca. 10 km em direção a Teresina de Goiás, 1448 m elev., 14°04'21.7"S, 47°30'33.6"W, 27 March 2001 (fl, fr), *C. Munhoz et al.* 2649 (holotype: IBGE! [IBGE00050788]; isotypes: HUFU!, MO! [MO-2024291]).

Diagnosis. The new species can be recognised by the long internode (2–4 mm long), lanceolate leaf blade, attenuate and semi-amplexicaul at the base, conspicuous calyx tube (0.2 mm long) and petal acuminate at the apex.

Description. Subshrub, 0.4–0.6 m tall, erect, much-branched. Stem terete, glabrous, decorticating with age. Branch fastigiate, younger branch green, quadrangular, older branch brownish, becoming terete, glabrescent and leafless with age. Branch, both surfaces of the leaf, hypanthium and sepal covered by spherical glands and setose trichomes 0.2–0.4 mm long. Leaf sessile, horizontal or ascending, lax, internode 2–4 mm long; blade 2–3 × 0.5–1 mm, concolorous, green, chartaceous, lanceolate, acute at the apex, with a terminal setose trichome ca. 0.2 mm long, base attenuate, semi-amplexicaul, margin flat, serrate, ciliate, 3-veined, usually inconspicuous on abaxial surface. Flower 5-merous, solitary, terminal or lateral, perianth actinomorphic; pedicel ca. 0.5 mm long; hypanthium 2.5–3 × 1–1.5 mm, purple or green with purple stains, urceolate, calyx tube ca. 0.2 mm long, sepal 0.5–1 × 3.5–5 mm, shorter than the length of the hypanthium, triangular, acute at the apex, with a terminal setose trichome ca. 0.2 mm long; petal 4–4.5 × 3–3.5 mm, magenta, obovate, acuminate at the apex, margin entire, glabrous; stamen 10, dimorphic, anther polysporangiate; larger (antesepalous) stamen 5, filament 2–2.5 mm long, magenta, pedoconnective 2–2.5 mm long, magenta, ventral appendage ca. 1 mm long, yellow, obtuse at the apex, anther ca. 1.8 mm long including beak, vinaceous, ovate-oblong, beak ca. 0.5 mm long; smaller (antepetalous) stamen 5, filament 2–2.5 mm long, magenta, pedoconnective 0.5–1 mm long, yellow, ventral appendage ca. 0.2 mm long, yellow, rounded at the apex, anther ca. 1.5 mm long

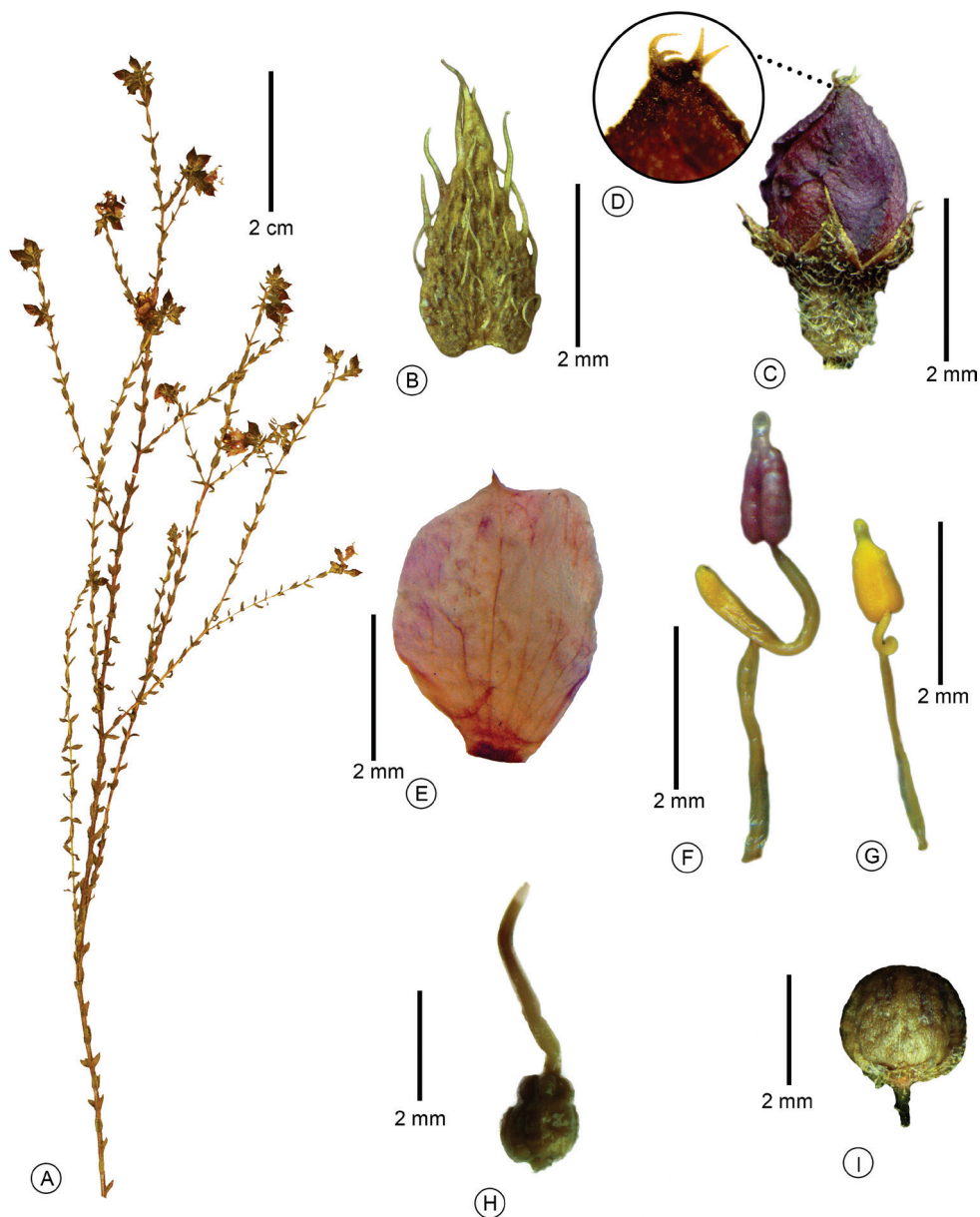


Figure 1. *Microlicia gracilis* Fontelas & R.Romero **A** flowering branch **B** leaf adaxial surface **C** flower bud **D** detail of the flower bud **E** petal **F** larger (antesealous) stamen **G** smaller (antepetalous) stamen **H** gynoecium **I** closed capsule (**A–I**: C. Munhoz *et al.* 1519). Photos: Jean Fontelas.

including beak, yellow, ovate-oblong, beak ca. 0.3 mm long; ovary ca. 1.5×1 mm, 3-locular, pyriform, superior, glabrous; style ca. 3 mm long, magenta, terete, slightly curved; stigma punctiform. Capsule ca. 2×2 mm, brownish, globose, dehiscent into 3 valves from the apex, hypanthium partially covering the capsule; seed ca. 0.5×0.3 mm, brown, oblong, testa foveolate.

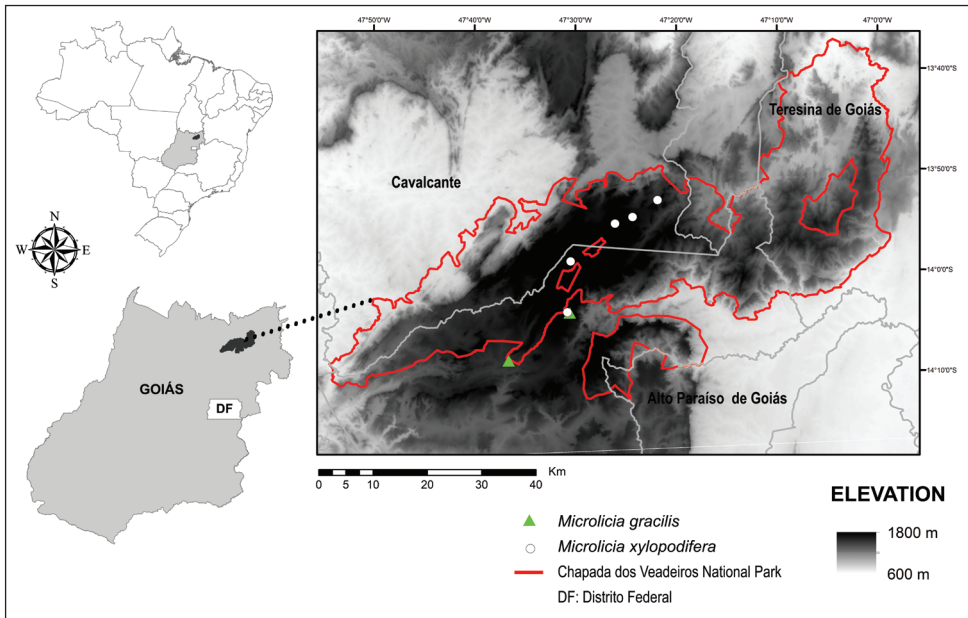


Figure 2. Geographical distribution of *Microlicia gracilis* and *M. xylopodifera* in the state of Goiás, Brazil.

Distribution and habitat. *Microlicia gracilis* is endemic to Chapada dos Veadeiros, Goiás, Brazil, occurring in wet grasslands close to rocky outcrops and in cerrado rup-estree, between 1115 m and 1448 m elevation (Fig. 2).

Conservation status. *Microlicia gracilis* has a restricted extent of occurrence (EOO = 10 km²) and area of occupancy (AOO = 8 km²) and, according to the IUCN Categories and Criteria (IUCN 2019), is preliminarily assessed as Critically Endangered [CR B1ab (iii) + 2ab (iii)]. So far, collections of *M. gracilis* have been made only outside the boundaries of the Chapada dos Veadeiros National Park and, therefore, it is not protected by any conservation units. The restricted distribution of *M. gracilis* also contributes to its degree of threat, since its populations are exposed to frequent burning caused by farmers, in addition to the expansion of agricultural borders in the region (Felfili et al. 2007; Alves et al. 2013).

Phenology. Flowers have been collected in March, May and June and fruits in May and June.

Etymology. The specific epithet “*gracilis*” refers to the very delicate and fragile branches and leaves and the small size of the flowers.

Additional specimens examined (paratypes). BRAZIL. Goiás: Alto Paraíso de Goiás, Fazenda Água Fria, 14°4'21"S, 47°30'33"W, 1 May 1998 (fl, fr), *R.C. Oliveira et al.* 1059 (HEPH! [HEPH00020094], MBM!, UB! [UB-0110744]); Chapada dos Veadeiros, ca. 11 km da cidade, 1115 m elev., 14°09'68.5"S, 47°36'37.0"W, 16 June 1998 (fl, fr), *R. Romero et al.* 5522 (HUFU!, UEC!); Fazenda Água Fria, ca. 10 km em direção à Teresina de Goiás, 1448 m elev., 14°04'21.7"S, 47°30'33.6"W, 3 June 2000 (fl, fr), *C. Munhoz et al.* 1519 (HUFU!, MO! [MO-2024287]).

***Microlicia xylopodifera* Fontelas & R.Romero, sp. nov.**

urn:lsid:ipni.org:names:77212347-1

Fig. 3

Type. BRAZIL. Goiás: Alto Paraíso de Goiás, ca. 40 km N, 1250 m elev., 24 March 1971 (fl, fr), *H.S. Irwin et al.* 33108 (holotype: UEC!, isotypes: CAS! [CAS0519655], NY!, US! [US-01899836]).

Diagnosis. The new species can be recognised by the robust xylopodium, cespitose habit, indumentum of spherical glands, setose and glandular trichomes on branch, leaf, hypanthium and sepal and flower bud with a dense crown of glandular trichomes at the apex.

Description. Subshrub, 0.1–0.2 m tall, cespitose, robust xylopodium present. Stem terete, glabrous. Branch fastigiate, younger branch green, quadrangular, older branch brownish, becoming terete, glabrescent and leafless with age. Branch, both surfaces of the leaf, hypanthium and sepal covered by spherical glands, setose and glandular trichomes 0.2–1.5 mm long. Leaf sessile, horizontal or ascending, lax, internode 2–6 mm long; blade 2.5–9 × 1.5–5.5 mm, discolorous, adaxial surface darker than the abaxial surface (in dry state), chartaceous, ovate or ovate-lanceolate, acute at the apex, with a terminal glandular trichome, 0.5–1 mm, base rounded or slightly cordate, margin flat, serrate, ciliate, 3-veined, usually inconspicuous on both surfaces. Flower 5-merous, solitary, terminal or lateral, perianth actinomorphic; pedicel 0.7–1 mm long; hypanthium 3.5–4.5 × 1.5–2 mm, green, urceolate; calyx tube ca. 0.2 mm long; sepal 1–2 × 1–1.5 mm, triangular, acute at the apex, with a terminal glandular trichome ca. 0.5 mm long; petal 5–10 × 2.5–5 mm, pink, obovate, obovate-oblong or oblong, acute at the apex, flower bud with a crown of glandular trichomes, during anthesis, the trichomes are only at the apex, margin entire; stamen 10, dimorphic, anther polysporangiate; larger (antesepalous) stamen 5, filament 2.5–3.5 mm long, pinkish, sometimes yellow, pedoconnective 2–3 mm long, pinkish, sometimes yellow; ventral appendage 1.5–2 mm long, yellow, truncate or rounded at the apex, rarely obtuse, anther 1.5–2 mm long including beak, vinaceous, ovate-oblong, beak 0.3–0.5 mm long; smaller (antepetalous) stamen 5, filament ca. 3 mm long, pinkish, sometimes yellow, pedoconnective ca. 1 mm long, pinkish, sometimes yellow, ventral appendage ca. 0.3 mm long, yellow, acute at the apex, anther ca. 1.5 mm long including beak, yellow, ovate-oblong, beak 0.3–0.5 mm long; ovary ca. 2.5 × 1.5 mm, 3-locular, pyriform, superior, glabrous; style ca. 6 mm long, pinkish, terete, slightly curved at the apex; stigma punctiform. Capsule ca. 2 × 2 mm, brown, globose, dehiscing into 3 valves from the apex, hypanthium partially covering the capsule; seed ca. 0.6 × 0.3 mm, brown, oblong, testa foveolate.

Distribution and habitat. *Microlicia xylopodifera* is endemic to Chapada dos Veadeiros, Goiás State, Brazil, occurring in cerrado rupestre and campo limpo, on sandy soil, between 1000 m and 1800 m elevation (Fig. 2).

Conservation status. *Microlicia xylopodifera* has a restricted extent of occurrence (EOO = 80 km²) and area of occupancy (AOO = 20 km²) and, therefore, we recommend that it be considered Endangered [EN B1ab (ii, iii, iv)] if all IUCN (2019) guide-

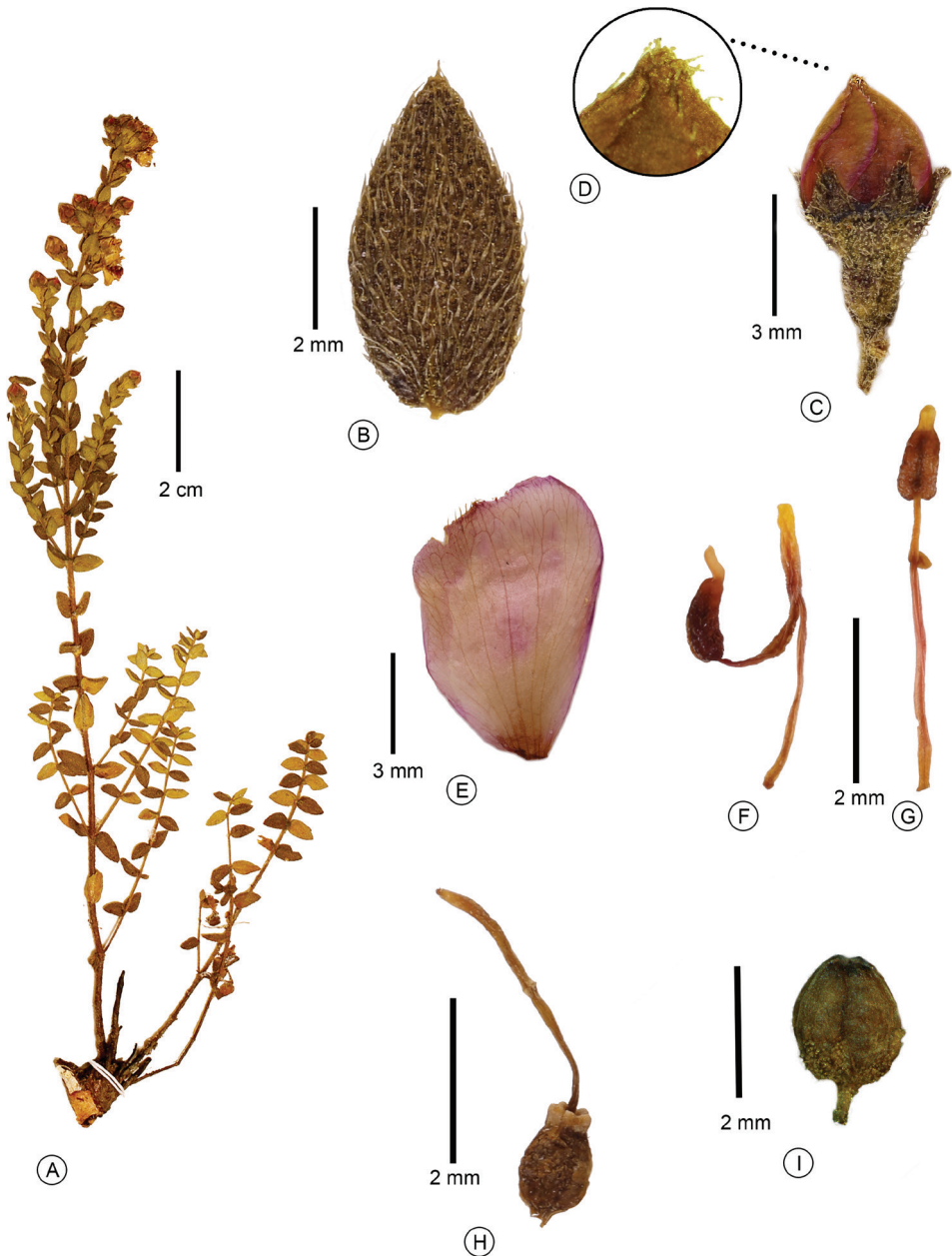


Figure 3. *Microlicia xylopodifera* Fontelas & R.Romero **A** habit, showing a xylopodium **B** leaf adaxial surface **C** flower bud **D** detail of the apex of the flower bud with a crown of glandular trichomes **E** petal **F** larger (antesealous) stamen **G** smaller (antepetalous) stamen **H** gynoecium **I** closed capsule (**A–I**: *H.S. Irwin et al.* 33108). Photos: Jean Fontelas.

lines are followed. So far, all populations of *M. xylopodifera* have been found inside the park boundaries, where we believe the species is protected.

Phenology. Flowers and fruits have been collected in March.

Etymology. The specific epithet “xylopodifera” refers to the robust xylopodium (also described as lignotubers) present in all specimens examined. Xylopodium or lignotuber is an organ that buffers the plant against extremes of water loss, temporal mineral or nutritional deficiency, providing also protection against fire (Gottsberger and Silberbauer-Gottsberger 2006).

Additional specimens examined (paratypes). BRAZIL. Goiás: Alto Paraíso de Goiás, ca. 30 km ao norte da Chapada dos Veadeiros, 1000 m elev., 16 March 1969 (fl), *H.S. Irwin et al.* 24490 (NY!); ca. 19 km N, 1250 m elev., 20 March 1971 (fl), *H.S. Irwin et al.* 32788 (NY!, UEC!, US!); 8 km N, 1500 m elev., 6 March 1973 (fl), *W.R. Anderson* 6433 (NY!, US!); ca. 29 km N, 800 m elev., 9 March 1973 (fl), *W.R. Anderson* 6742 (NY!, US!). Teresina de Goiás, 31 km na estrada ao sul para Alto Paraíso de Goiás, 1500 m elev., 16 March 1973 (fl), *W.R. Anderson* 7162 (NY!, US!).

Discussion

Using the key to the species of *Microlicia* of the Chapada dos Veadeiros National Park proposed by Diniz and Silva (2019), *M. gracilis* and *M. xylopodifera* should be positioned close to *M. latifolia* D.O.Diniz & M.J.Silva since they have branch, leaf, hypanthium and sepal covered by setose trichomes and spherical glands, sessile and concolorous leaf blade, 2(–3)-veined, with serrate and ciliate margin, pedicellate flower, pink petal and stamens with bicolorous and polysporangiate anthers. *Microlicia latifolia* differs in having elliptic or ovate-elliptic leaf blade, apiculate at the apex, campanulate hypanthium, linear sepal, apiculate at the apex, glabrous petal and sub-isomorphic stamens with oblong anthers. Table 1 includes additional features comparing the species most similar to *M. gracilis* and *M. xylopodifera*.

Microlicia gracilis bears some resemblance to *Microlicia xylopodifera* in having sessile leaf with a lax arrangement on the branches, pedicellate flower (pedicel 0.7–1 mm long), urceolate hypanthium, dimorphic stamens with bicolorous and polysporangiate anthers. However, *M. xylopodifera* differs in having a caespitose habit, robust xylopodium and glandular trichomes covering branch, both leaf blade surfaces, hypanthium and sepal. Moreover, the apex of the flower bud is densely hairy-glandular, forming a crown at its apex and, during anthesis, the trichomes are concentrated at the apex of the petal. *Microlicia gracilis* resembles *Microlicia ramosa* Pilger, which is endemic to Goiás (Flora do Brasil 2020), for both species have branch, leaf, hypanthium and sepal covered with setose trichomes and spherical glands, sessile and ascending leaf blade, pedicellate flower, triangular sepal, magenta petal and dimorphic stamens with bicolorous and polysporangiate anthers. However, *M. ramosa* differs in having a typical branching pattern in which the branches have short secondary branches (Versiane et al. 2016), discoloured leaf (darker adaxial surface), ovate or ovate-lanceolate leaf blade with rounded or cordate base, longer pedicel (ca. 1 mm long) and the petal acute or retuse at the apex.

Microlicia xylopodifera is distinguished from other species of *Microlicia* by the presence of a robust xylopodium and a crown of glandular trichomes at the apex of the flower bud, which are concentrated at the apex of the petal. The new species is similar to

Table 1. Comparative features of *Microlicia gracilis*, *M. xylopodifera* and relatives.

Characters	<i>M. gracilis</i>	<i>M. ordinata</i>	<i>M. ramosa</i>	<i>M. vestita</i>	<i>M. xylopodifera</i>
Indumentum of branch, leaf, hypanthium and sepal	Setose trichomes and spherical glands	Glandular trichomes and spherical glands	Setose trichomes and spherical glands	Setose trichomes and spherical glands	Setose, glandular trichomes and spherical glands
Leaf colour	Concolorous	Discolorous	Discolorous	Concolorous	Discolorous
Leaf base	Attenuate	Rounded or cordate	Slightly cordate, rarely rounded	Rounded or slightly cordate	Rounded or cordate
Petal apex	Acuminate	Retuse or truncate	Acute	Acute	Acute
Petal indumentum	Glabrous	Single glandular trichome at the apex	Glabrous	Single setose trichome at the apex	Glandular trichomes at the apex
Anther colours	Vinaceous and yellow	Yellow	Vinaceous and yellow	Yellow	Vinaceous and yellow
Anther, numbers of sporangia	Polysporangiate	Polysporangiate	Polysporangiate	Tetrasporangiate	Polysporangiate
References HUEG, HUFU, K, MBM, NY, UB, UEC	<i>C. Munhoz et al.</i> 2649 (HUFU)	<i>G. & M. Hatschbach et al.</i> 60297 (HUFU, MBM)	<i>J.N. Nakajima et al.</i> 5049 (UEC, HUEG, HUFU, K, MBM, UB)	<i>M.L. Fonseca et al.</i> 105 (HUFU, IBGE)	<i>H.S. Irwin et al.</i> 33108 (UEC, NY)

M. ramosa Pilger in having sessile, discolorous and ovate or ovate-lanceolate leaves that are rounded or slightly cordate at the base, pedicellate flower, triangular sepal and dimorphic stamens with bicolorous, polysporangiate and ovate-oblong anthers. However, *M. ramosa* differs in having shorter secondary branches, 3–5-veined leaf and a vinaceous or greenish hypanthium often with vinaceous stains. *Microlicia xylopodifera* also resembles *M. ordinata* (Wurdack) Almeda & A.B.Martins, which is endemic to Goiás (Versiane et al. 2016; Machado and Romero 2020), in having branch, leaf, hypanthium and sepal covered with glandular trichomes and spherical glands, sessile and discolorous leaf, ovate-lanceolate leaf blades that are rounded or cordate at the base, triangular sepal and dimorphic stamens with bicolorous and polysporangiate anthers. However, *M. ordinata* has leaf with larger dimensions (5–20 × 2.5–13.5 mm), 3–5-veined, shorter pedicel (ca. 0.5 mm long) and petal with a single glandular trichome at the apex. In addition, the anther of the antesealous stamen is yellow with orange stains. The new species bears some resemblance to *M. vestita* DC. which occurs in the Distrito Federal and States of Bahia, Minas Gerais, Goiás, Mato Grosso do Sul and Pará (Flora do Brasil 2020). *Microlicia vestita* also has setose trichomes and spherical glands on the branch, leaf, hypanthium and sepal, sessile leaf, ovate or ovate-lanceolate leaf blade with serrate and ciliate margin, triangular sepal and dimorphic stamens with bicolorous anthers. However, *M. vestita* differs in having imbricate leaf, denser indumentum covering the whole plant, campanulate hypanthium and tetrasporangiate anthers.

Acknowledgements

The authors are grateful to curators and staff of HEPH, HUFU, MO, MBM, NY, UB, UEC and US herbaria for loan of specimens, to Daniela Ramalho (HEPH), Marina Fonseca (IBGE) and Jim Solomon (MO) for sending images of the isotypes, to Pró-Reitoria de Pesquisa e Pós-Graduação, Universidade Federal de Uberlândia (PROPP/

UFU) for financial support and facilities for the field expedition and to Cynthia Sothers for the English revision; to Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, process APQ 01911–16) for supporting research on Melastomataceae. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

References

- Almeda F, Martins AB (2001) New combinations and new names in some Brazilian Microlicieae (Melastomataceae), with notes on the delimitation of *Lavoisiera*, *Microlicia*, and *Trembleya*. *Novon* 11(1): 1–7. <https://doi.org/10.2307/3393198>
- Alves MM, Matricardi EAT, Pereira RS (2013) Dinâmica espaço-temporal do fogo entre 1999 a 2009 no Parque Nacional da Chapada dos Veadeiros. *Enciclopédia Biosfera* 9(1): 752–768.
- Bachman S, Moat J, Hill AW, 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>
- Cogniaux CA (1883) *Microlicia*. In: Martius CFP, Eichler AW, Urban I (Eds) *Flora Brasiliensis*. Leipzig: Fleischer 14(3): 38–121.
- Diniz OD, Silva MJ (2019) *Microlicia* D. Don (Microlicieae, Melastomataceae) in the Chapada dos Veadeiros National Park, Goiás State, Brazil. *Hoehnea* 47: e322019. <https://doi.org/10.1590/2236-8906-32/2019>
- Diniz-Neres OD, Silva MJ (2017a) *Microlicia veadeirana* (Melastomataceae, Microlicieae), a new species from the Chapada dos Veadeiros National Park, Brazil. *Brittonia* 70(1): 84–89. <https://doi.org/10.1007/s12228-017-9492-2>
- Diniz-Neres OD, Silva MJ (2017b) A remarkable new species of *Microlicia* (Melastomataceae) including an identification key to species of the genus from the Chapada dos Veadeiros National Park, Goiás, Brazil. *Systematic Botany* 42(3): 554–561. <https://doi.org/10.1600/036364417X696014>
- Felfili JM, Rezende AV, Silva-Júnior MC (2007) Biogeografia do Bioma Cerrado: Vegetação e Solos da Chapada dos Veadeiros. Brasília: Universidade de Brasília/Finattec, 256 pp.
- Flora do Brasil (2020) Melastomataceae. Jardim Botânico do Rio de Janeiro. <https://florado-brasil.jbrj.gov.br/> [Sep 2020]
- Gottsberger G, Silberbauer-Gottsberger I (2006) Life in the Cerrado: a South American Tropical Seasonal Vegetation (Vol. 1). Origin, Structure, Dynamics and Plant Use. Ulm: Reta Verlag, Germany, 277 pp.
- Machado AIMR, Romero R (2020) Melastomataceae in the Parque Estadual da Serra Dourada, Goiás state, Brazil. *Phytotaxa* 450(1): 17–54. <https://doi.org/10.11646/phytotaxa.450.1.3>
- Mendoza-Cifuentes H, Ariza W, Granados DE, Romero R (2019) A new species of *Microlicia* (Melastomataceae): First record of the genus for Colombia. *PhytoKeys* 122: 87–96. <https://doi.org/10.3897/phytokeys.122.34171>
- Michelangeli FA, Cotton E (2008) Melastomataceae In: Hokche O, Berry PE, Huber O (Eds) *Nuevo Catálogo de la Flora Vascular de Venezuela* (Vol. 859) Caracas: Fundación Instituto Botánico de Venezuela, 466–484.

- Munhoz CBR, Felfili JM (2006) Floristics of the herbaceous and subshrub layer of a moist grassland in the Cerrado biosphere reserve (Alto Paraíso de Goiás), Brazil. *Edinburgh Journal of Botany* 63(2–3): 343–354. <https://doi.org/10.1017/S0960428606000539>
- Naudin C (1845) *Melastomacearum monographicae descriptionis*. *Annales des Sciences Naturelles Botanique* 3(3): 162–192.
- Pacifico R, Almeda F, Carmo AA, Fidanza K (2019) A new species of *Trembleya* (Melastomataceae: Microlicieae) with notes on leaf anatomy and generic circumscription. *Phytotaxa* 391(5): 289–300. <https://doi.org/10.11646/phytotaxa.391.5.2>
- Pacifico R, Almeda F, Frota A, Fidanza K (2020b) Areas of endemism on Brazilian mountaintops revealed by taxonomically verified records of Microlicieae (Melastomataceae). *Phytotaxa* 450(2): 119–148. <https://doi.org/10.11646/phytotaxa.450.2.1>
- Pacifico R, Almeda F, Rodrigues L, Fidanza K (2020a) Novelities in *Microlicia* (Melastomataceae: Microlicieae) from the Bolivian Cerrado. *Phytotaxa* 433(3): 225–234. <https://doi.org/10.11646/phytotaxa.433.3.4>
- Pilger RKF (1903) Melastomataceae In: Engler A (Ed.) *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 33(72): 1–18.
- Radford AE, Dickison WC, Massey JR, Bell CR (1974) *Vascular Plant Systematics*. New York: Harper and Row Publishers, 891 pp.
- Reflora Virtual Herbarium (2020) Jardim Botânico do Rio de Janeiro. <http://reflora.jbrj.gov.br/reflora/herbarioVirtual/> [Sep 2020]
- Renner SS (1993) Phylogeny and classification of the Melastomataceae and Memecylaceae. *Nordic Journal of Botany* 13(5): 519–540. <https://doi.org/10.1111/j.1756-1051.1993.tb00096.x>
- Romero R (2003a) Revisão taxonômica de *Microlicia* sect. *Chaetostomoides* (Melastomataceae). *Brazilian Journal of Botany* 26(4): 429–435. <https://doi.org/10.1590/S0100-84042003000400001>
- Romero R (2003b) A newly described species of *Microlicia* (Melastomataceae) from Minas Gerais, Brazil. *Novon* 13(1): 116–118. <https://doi.org/10.2307/3393575>
- Romero R, Woodgyer E (2015) *Microlicia*: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB9782> [Sep 2020].
- Romero R, Versiane AFA, Fontelas JC, Diniz-Neres DO, De-Paula OC (2017) A new species of *Microlicia* (Melastomataceae) with bright golden cuticle from Chapada dos Veadeiros, Goiás (Central Brazil). *Systematic Botany* 42(3): 562–568. <https://doi.org/10.1600/036364417X696069>
- Rull V (2003) An illustrated key for the identification of pollen from Pantepui and the Gran Sabana (eastern Venezuelan Guayana). *Palynology* 27(1): 99–133. <https://doi.org/10.2113/27.1.99>
- Silva DN, Diniz DO, Koschnitzke C, Guimarães PJF (2018) *Chaetostoma hexapetalum* (Microlicieae, Melastomataceae): A new species from the Chapada dos Veadeiros, Goiás, Brazil. *Systematic Botany* 43(4): 986–992. <https://doi.org/10.1600/036364418X697805>
- Smith LB (1955) Notes on Brazilian phanerogams. *Journal of the Washington Academy of Sciences* 45: 197–200.
- 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>

- SpeciesLink (2020) Centro de Referência em Informação Ambiental, CRIA. <https://splink.org.br/> [accessed September 2020]
- IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. <https://iucnredlist.org/documents/RedListGuideLines.pdf> [Sep 2020]
- 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/> [Sep 2020]
- Versiane AFA (2019) Phylogenetic studies in *Microlicia* D. Don (Melastomataceae, Microlicieae). Doctoral Thesis, Universidade Estadual de Campinas, Instituto de Biologia, Campinas, São Paulo, 1–126.
- Versiane AFA, Santos ML, Romero R (2016) Melastomataceae na Serra dos Pireneus, Goiás, Brasil. *Rodriguésia* 67(3): 721–759. <https://doi.org/10.1590/2175-7860201667314>
- Versiane AFA, Silva DN, Romero R (2020) A new species of *Microlicia* (Melastomataceae) from Bolivia and Brazil, a new synonym, and an identification key for the genus in Mato Grosso, Brazil. *Phytotaxa* 455(1): 9–20. <https://doi.org/10.11646/phytotaxa.455.1.2>
- Wurdack JJ (1959) The Machris Brazilian expeditions. Botany: Phanerogamae, Melastomataceae and Polygalaceae. Los Angeles County Museum Contributions in Science 28: 3–11.
- Wurdack JJ (1986) Atlas of hair for neotropical Melastomataceae. *Smithsonian Contributions to Botany* 63(63): 1–80. <https://doi.org/10.5962/bhl.title.122493>