PhytoKeys 177: 1–9 (2021)
doi: 10.3897/phytokeys.177.62741
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Lycoris wulingensis, a dwarf new species of Amaryllidaceae from Hunan, China

Si-Yu Zhang[1], Ying Huang[1], Pei Zhang[2], Ke-Run Zhu[1],
Yong-Bing Chen[3], Jian-Wen Shao[1,4]

1 *College of Life Sciences, Anhui Normal University, Wuhu, Anhui 241000, China* **2** *Linli Jidong Cement Limited Company, Changde, Hunan 415200, China* **3** *Sanjie Nationalized Forest Farm, Chuzhou, Anhui 239400, China* **4** *The Key Laboratory of Conservation and Employment of Biological Resources of Anhui, Anhui Normal University, Wuhu, Anhui 241000, China*

Corresponding author: Jian-Wen Shao (shaojw@ahnu.edu.cn)

Academic editor: Lorenzo Peruzzi | Received 4 January 2021 | Accepted 1 April 2021 | Published 21 April 2021

Citation: Zhang S-Y, Huang Y, Zhang P, Zhu K-R, Chen Y-B, Shao J-W (2021) *Lycoris wulingensis*, a dwarf new species of Amaryllidaceae from Hunan, China. PhytoKeys 177: 1–9. https://doi.org/10.3897/phytokeys.177.62741

Abstract

Lycoris wulingensis S.Y. Zhang, a new species from Hunan Province (central South China), is described and illustrated. This new species is a fertile diploid plant and its karyotype is 2n = 22. It is most similar to *L.* × *haywardii* in morphology, but the latter is a hybrid species and distributed in East China and the plant is much larger. Amongst the original species, *L. wulingensis* is similar to *L. radiata*, but differs from it in its flowers being rose-red (vs. red) and stamens and tepals are nearly the same length (vs. stamens significantly longer than tepals).

Keywords

Amaryllidaceae, China, *Lycoris wulingensis*, morphology, taxonomy

Introduction

Lycoris Herb. (Amaryllidaceae) is a genus distributed only in Asia, including about 24 species, 19 of which are distributed in China, which is the distribution centre of this genus (Hsu et al. 1994; Ji and Meerow 2000; Kim 2004; Hori et al. 2006; Quan et al. 2013; Meng et al. 2018; Lu et al. 2020). Due to the high compatibility amongst most interspecific crosses, hybrids are very common in *Lycoris*. Amongst the 21 karyotype reported species, only seven species are original diploid and the remaining 14 are hybrid species, including allotriploid (such as *L. incarnata*, 2n = 4M+3T+1m+22A = 30), euploid (such as *L.* × *haywardii*, 2n = 22A = 22) and aneuploid hybrids (such as *L.* × *albiflora*, 2n = 5M+1T+11A = 17) (Kurita 1986; Hsu et al. 1994). The karyotype is an important auxiliary method for identifying *Lycoris* species.

Although there were 43 taxa names of *Lycoris* in the International Plant Name Index (IPNI, https://www.ipni.org/), Hsu et al. (1994) researched and revised the species taxonomy in this genus, based on hybridisation experiments, cytology and morphology and only recognised 20 species and seven varieties. In Korea, Kim revised native *Lycoris* and published two new species, i.e. *L. flavescens* and *L. uydoensis* (Kim 2004). Recently, three new species of *Lycoris* have been discovered and reported in China, namely *L. hunanensis* (Quan et al. 2013), *L.* × *hubeiensis* (Meng et al. 2018) and *L. tsinlingensis* (Lu et al. 2020).

During the long-term investigation and collection of Chinese *Lycoris* plant resources over many years, we accidentally discovered this dwarf unique *Lycoris* in the Wuling Mountains area (Hunan Province) in 2016. After four years of observation and cultivation, we confirm that it is a new species and it is described here.

Materials and methods

To observe and compare morphology characters, about 270 bulbs from nine populations (Table 1) of the putative new species and its relatives (*L. radiata* and *L.* × *haywardii*) were collected and brought back for cultivation in August 2015 or 2016. In 2019, the morphological data for bulb diameter, leaf length and width and flower size (tepal length) were measured and recorded from cultivated populations. In 2020, bulb roots were induced by burying in wet sand and the chromosome number was observed using the methods described by Chen and Li (1985). Pollen vitality was tested using the TTC staining method (Oberle and Watson 1953). All statistical analyses were performed in SPSS ver. 19.0.

Table 1. The information of sampled populations.

Code	Locations	Altitude
L. wulingensis		
A1	Matouxi Village, Yongding District, Zhangjiajie City, Hunan Province	276 m
A2	Xiejiapu Village, Shimen County, Changde City, Hunan Province	75 m
A3	Fawang Village, Taoyuan County, Changde City, Hunan Province	52 m
L. × *haywardii*		
B1	Heyi Village, Beilun District, Ningbo City, Zhejiang Province	30 m
B2	Shanjuan Village, Yixing City, Wuxi City, Jiangsu Province	59 m
B3	Shanhu Village, Linhai City, Zhejiang Province	18 m
L. radiata		
C1	Luogongpo Village, Wulingyuan District, Zhangjiajie City, Hunan Province	286 m
C2	Luojiarong Village, Taoyuan County, Changde City, Hunan Province	52 m
C3	Shanbanqiao Village, Linli County, Changde City, Hunan Province	92 m

Taxonomic treatment

***Lycoris wulingensis* S.Y. Zhang, sp. nov.**
urn:lsid:ipni.org:names:77216601-1
Figs 1, 2

Type. China. Hunan, Zhangjiajie County, Wangjiaping Town, Matouxi Village, 29°0'54.7"N, 110°48'3.7"E, under broad-leaved forest, beside the water ditch, 276 m a.s.l., 22 August 2020, *S.Y. Zhang*, *ZSY202008001* (holotype: ANUB; isotypes: PE, KUN).

Diagnosis. Most similar to *L.* × *haywardii*, but differs from it by smaller plant and flower sizes (Figs 3, 4, Table 2) and it is restricted to north-western Hunan Province (Fig. 5).

Description. Perennial herb. Bulbs nearly spherical, 2–3 cm in diameter, covered brown epidermis, with fine lines on the epidermis. Leaves ligulate, often 4–7, blunt apex, appearing in mid-September, 15–27 cm long, 3–5 mm wide; upper surface dark green, mid-vein distinctly pale; bottom surface light green with a raised mid-rib. Inflorescence scapose, 25–30 cm high, green or reddish-brown; 2 spathe bracts, lanceolate, 2–2.5 cm long, 5–7 mm wide, semi-closed to wrap the bud; 3–7 flowers per umbels, pedicels 1.5–2 cm long, diameter 1.5–2 mm; flowers rose-red; perianth lobes oblanceolate, 2.5–2.8 cm long, about 5 mm wide, apex slightly reversed and undulate; floral tubes light red, about 3 mm long. Filaments 3–3.5 cm long, rose-red, slightly longer than tepals, anther yellow, 2–3 mm long; pistil length 4–4.5 cm, middle and lower part diameter 0.8 mm, rose-red, apex diameter about 0.4 mm, dark-red. Ovary 4 mm in diameter, spherical and green. Capsules three-lobed, green or pale when mature; seeds black, spherical, 5–7 mm in diameter.

Phenology. Flowering from mid-July to late-August; fruiting in September; and leaves growing in mid-September.

Distribution. *Lycoris wulingensis* is distributed in the east of Wuling Mountains and its surrounding areas, such as Cili, Linli, Li, Taoyuan and Yongding Counties (Fig. 5).

Habitat. *Lycoris wulingensis* is partial to grow on the edge of forest roads, farmland or riverside beaches, usually under deciduous trees (such as *Alangium chinense* and *Pterocarya stenoptera*) and accompanied by *Pinellia ternata*, *Commelina communis*,

Table 2. Comparison the morphology and distribution of *Lycoris wulingensis* and its related species.

Characters	*L. wulingensis*	*L.* × *haywardii*	*L. radiata*
Leaf	15–27 cm long, 3–5 (mean = 4.0) mm broad	40–55 cm long, 8–12 mm broad	25–45 cm long, 5–10 mm broad
Bulb	2–3 cm in diameter	3.5–5.5 cm in diameter	3–4.5 cm in diameter
Scape	25–30 cm tall, 4–6 mm in diameter	40–50 cm tall, 8–12 mm in diameter	35–40 cm tall, 6–9 mm in diameter
Flower	Flower rose-red, tepals 2.5–2.8 cm long, apex slightly reversed and slightly undulate, stamen 3–3.5 cm long.	Flower rose-red, tepals 4.5–6 cm long, apex slightly reversed and slightly undulate, stamen 6–8 cm long.	Flower red, tepals 3–3.5 cm long, strongly reversed and undulate, stamen 6–8 cm long.
Distribution	North-western Hunan (China)	Southeast Anhui, Southern Jiangsu, Eastern Zhejiang (China)	Southeast Asia; Southwest, South and East China; Japan; South Korea

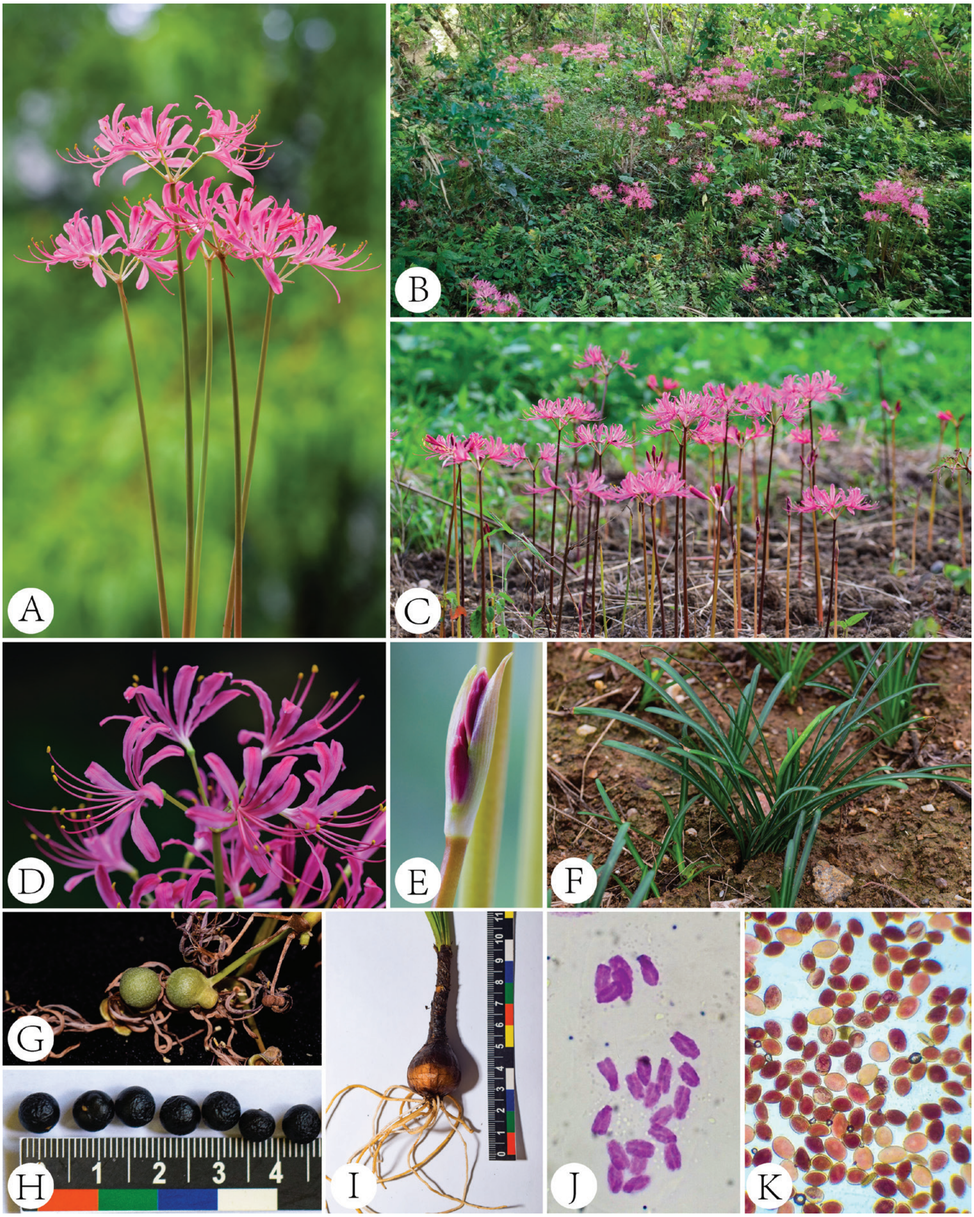


Figure 1. Morphology of *Lycoris wulingensis* S. Y. Zhang, sp. nov. **A** inflorescence **B, C** habitat **D** flower **E** flower bud **F** leaf **G** fruit **H** seeds **I** bulb **J** karyotype (2n = 22) **K** pollen (stained by TTC).

Arthraxon hispidus and *Ophiopogon bodinieri* etc. The surrounding residents sometimes cultivate it as an ornamental plant.

Vernacular name. 武陵石蒜 [wǔ líng shí suàn].

Etymology. The specific epithet comes from its distribution area of the Wuling Mountains, which is an important biodiversity hotspot in South Central China.

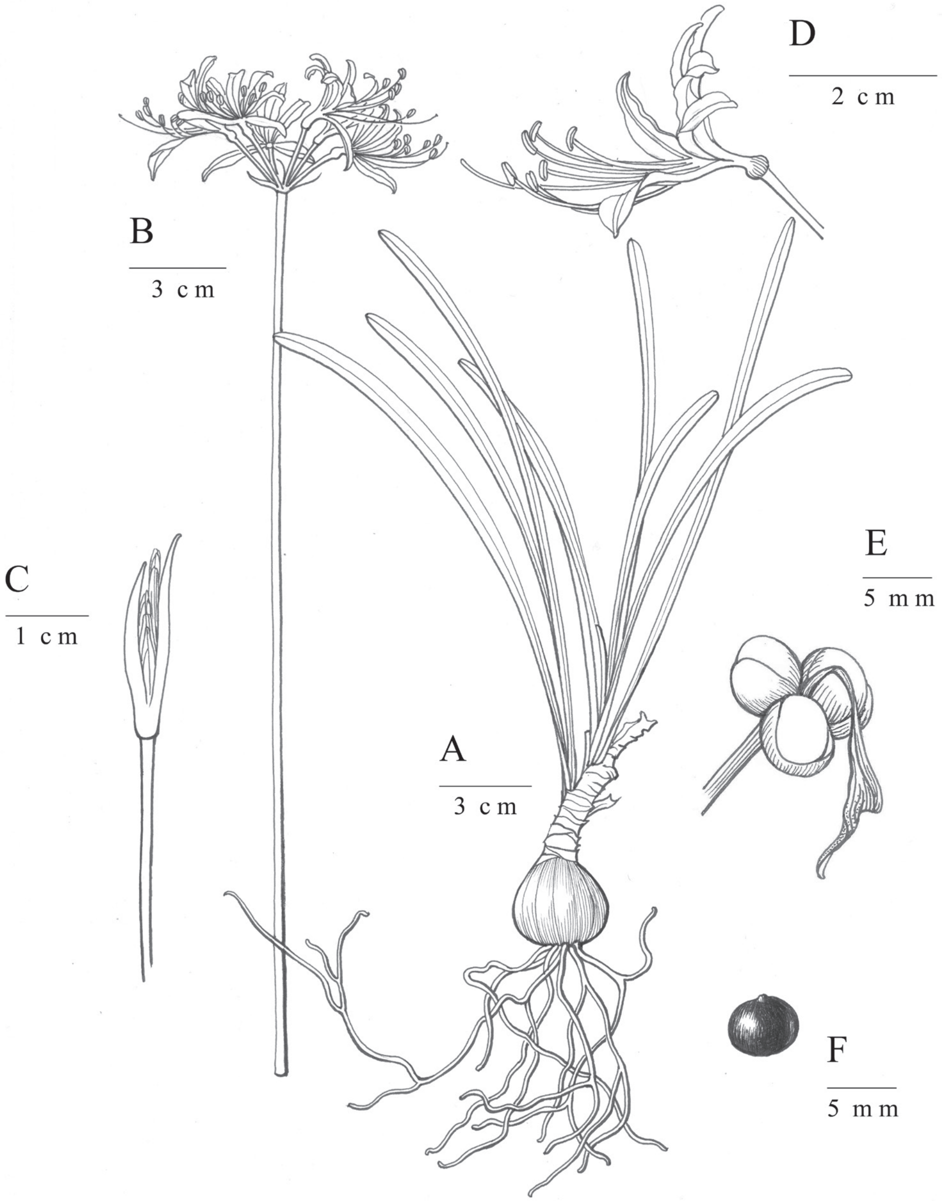


Figure 2. Morphology of *Lycoris wulingensis* S. Y. Zhang, sp. nov. **A** plant **B** inflorescence **C** flower bud **D** flower **E** fruit **F** seed. The picture was drawn by Ling Wang.

Karyotype. 2n = 22 (Fig. 1J).

Reproduction. This species can reproduce asexually by duplication of bulbs (1.5–2 times per year) and can also sexually reproduce through seeds.

Conservation status. Compared with other species in the *Lycoris*, the distribution range of *Lycoris wulingensis* is relatively narrow. Based on preliminary

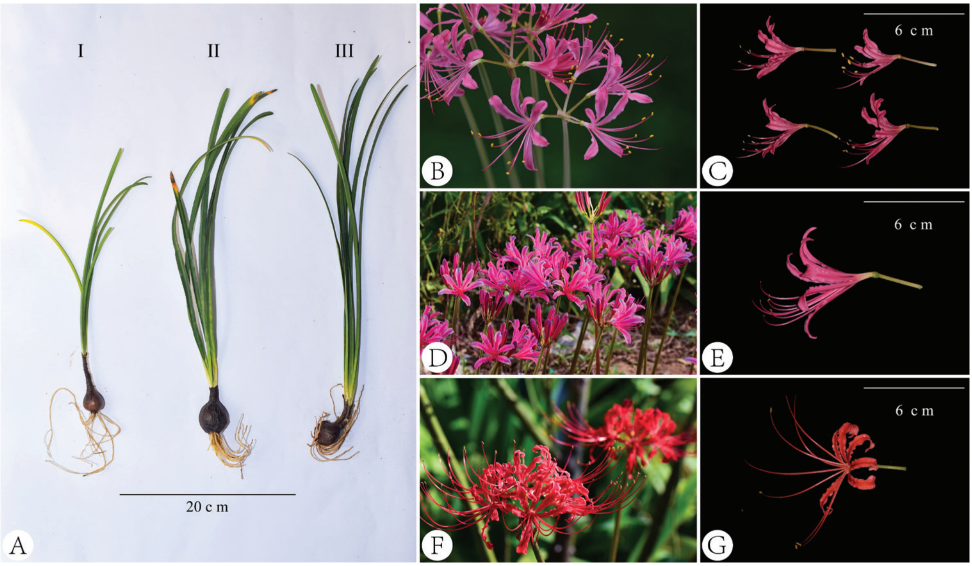


Figure 3. Comparison morphology of *Lycoris wulingensis* and similar species **A** plants (**I**-*L. wulingensis*, **II**-*L.* × *haywardii*, **III**-*L. radiata*) **B–G** flowers (**B, C** *L. wulingensis* **D, E** *L.* × *haywardii* **F, G** *L. radiata*).

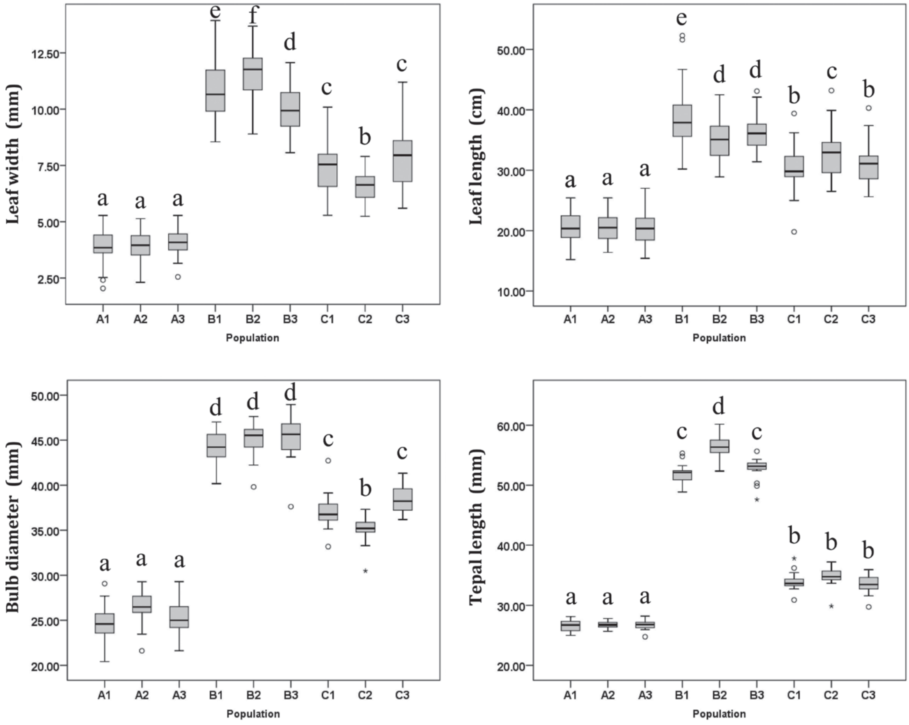


Figure 4. Comparison and variation of leaf width and length, bulb diameter and tepal length (flower size) of *L. wulingensis* (A1–A3), *L.* × *haywardii* (B1–B3) and *L. radiata* (C1–C3). In the boxplot, the horizontal line shows the median, the bottom and top of the box show the first and third quartiles. Boxplot marked with different letters differ significantly (post hoc test, P < 0.05).

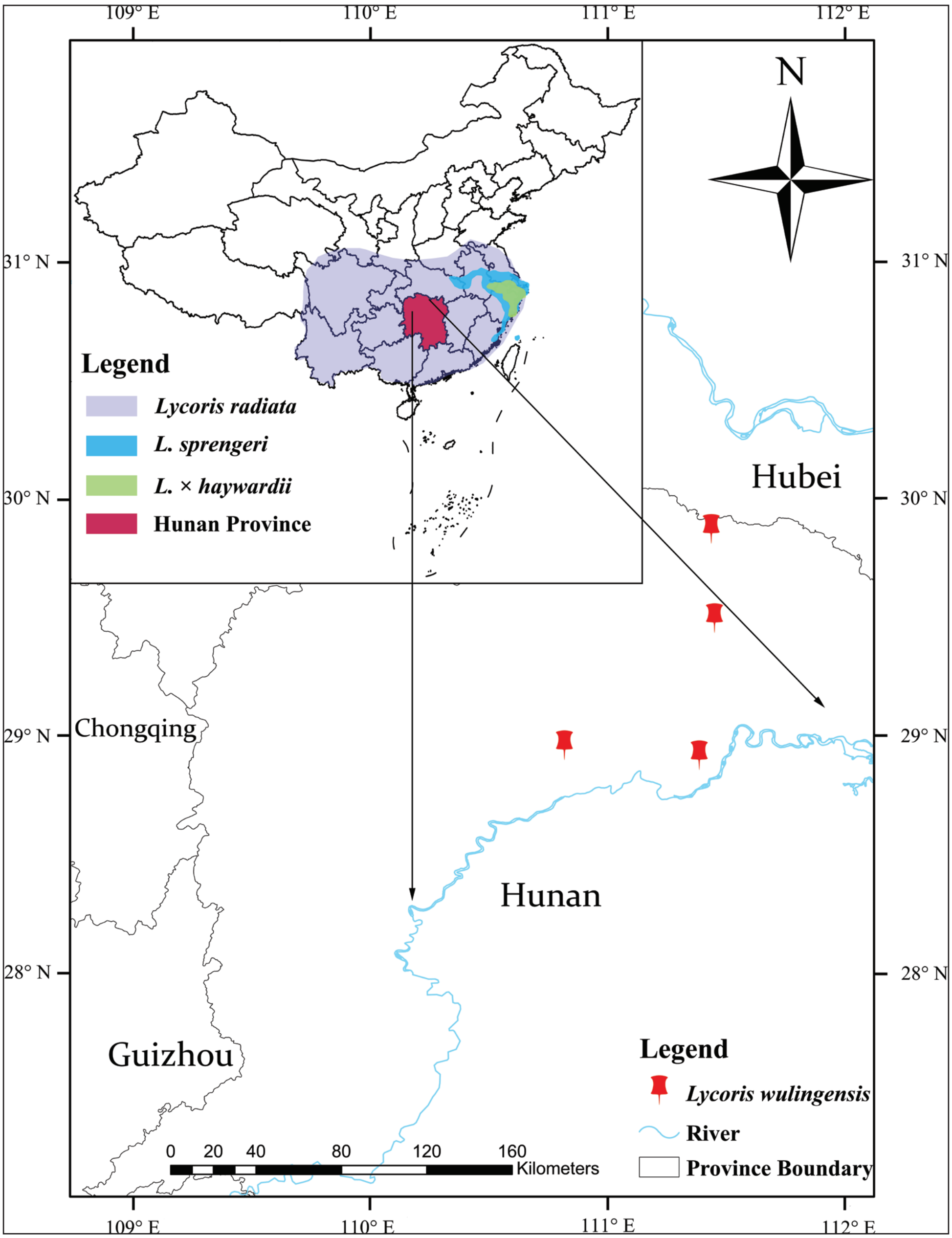


Figure 5. Distribution map of *Lycoris wulingensis* S.Y. Zhang and its related species.

investigation, we found only four large populations and some sporadic distribution points. However, considering the lack of in-depth investigation and also considering that some populations may occur in other similar habitats, we classified its conservation status as Data Deficient (DD), according to the IUCN Red List Criteria (IUCN 2019).

Discussion

After four years of cultivation and observation, we found that the plant size of *Lycoris wulingensis* was consistently small (Figs 3, 4). Amongst different wild populations and even under different cultivation conditions, its leaf length was always less than 27 cm, bulb diameter was about 2–3 cm and flower tepal length was less than 3 cm (Figs 3, 4). To our knowledge, the body size of this new species is the smallest in *Lycoris* (Hsu et al. 1994; Ji and Meerow 2000). The flowers of *L. wulingensis* are rose-red and their filaments are nearly equal to tepals in length, which is most similar to *L.* × *haywardii*. However, previous hybridisation experiments, molecular studies and field investigations have shown that *L.* × *haywardii* is a hybrid species which is only distributed in eastern China (the overlapping area of its two parents, *L. radiata* and *L. sprengeri*) (Hsu et al. 1994; Shi et al. 2006), while *L. wulingensis* is now known to be distributed in the east of Wuling Mountains and its surrounding areas in north-western Hunan Province, central South China. In addition, possibly due to the scape of *L. sprengeri* (one parent) being tall and strong, the scape of *L.* × *haywardii* is stronger and longer than that of *L. radiata* and *L. wulingensis* (Figs 3, 4) and the flower of *L.* × *haywardii* is about twice the size of *L. wulingensis* (Figs 3, 4). In terms of leaf morphology, *L. wulingensis* and *L. radiata* both have narrow dark green leaves with a clear white band in the centre. However, there are many obvious differences between these two species in flower characters, such as the colour of the former being rose-red and the stamen length is about equal to the petal length, while the latter's are red and stamens are about twice as long as the tepals. Thus, it is easy to distinguish *L. wulingensis* from its related species by plant size, floral characters and distribution range (Table 2).

Initially, we speculated that *L. wulingensis* was a haploid type of *L. radiata* and its dwarfism characters were possibly induced by the loss of half of its chromosomes. However, its chromosome number is 2n = 22 (Fig. 1J), which is similar to the original species of *L. radiata*, *L. sprengeri* and *L. sanguinea* (Hsu et al. 1994; Hori et al. 2006). TTC staining showed that the vitality of its pollen was normal (Fig. 1K). Furthermore, *L. wulingensis* can sexually produce offspring by seeds in wild habitats and under cultivated conditions and the seeds can also germinate and develop into seedlings. Therefore, we suppose that *L. wulingensis* is likely to be an original diploid species, which possibly has high value in terms of horticultural breeding.

Acknowledgements

We are grateful to Yang Hu and Meng-han Wei for their assistance in sampling. This work was supported by China's National Basic Science and Technology Program (2019FY101810).

References

Chen YH, Li MX (1985) Karytype analyses of four species (varieties) of *Lycoris* Herb. Yuan Yi Xue Bao 12(1): 57–60.

Hori TA, Hayashi A, Sasanuma T, Kurita S (2006) Genetic variations in the chloroplast genome and phylogenetic clustering of *Lycoris* species. Genes & Genetic Systems 81(4): 243–253. https://doi.org/10.1266/ggs.81.243

Hsu PS, Kurita S, Yu ZZ, Lin JZ (1994) Synopsis of the genus *Lycoris*. SIDA, Contributions to Botany 16: 301–331.

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf [accessed 22 December 2020]

Ji Z, Meerow AW (2000) *Lycoris*. In: Wu ZY, Raven PH (Eds) Flora of China. Science Press & Missouri Botanical Garden Press, Beijing & St. Louis.

Kim MY (2004) A taxonomic review of Korean *Lycoris* (Amaryllidaceae). Korean Journal of Plant Taxonomy 34(1): 9–26. https://doi.org/10.11110/kjpt.2004.34.1.009

Kurita S (1986) Variation and evolution in the karyotype of *Lycoris*, Amaryllidaceae I. General karyomorphological characteristics of the genus. Cytologia 51(4): 803–815. https://doi.org/10.1508/cytologia.51.803

Lu JY, Wang T, Wang YC, Zhang PC (2020) *Lycoris tsinlingensis* (Amaryllidaceae), a new species from Shaanxi, China. Annales Botanici Fennici 57(4–6): 193–196. https://doi.org/10.5735/085.057.0424

Meng WQ, Zheng L, Shao JW, Zhou SB, Liu K (2018) A new natural allotriploid, *Lycoris × hubeiensis* hybr. nov. (Amaryllidaceae), identified by morphological, karyological and molecular data. Nordic Journal of Botany 2018(6): e01780. https://doi.org/10.1111/njb.01780

Oberle GD, Watson R (1953) The use of 2,3,5-triphenyl tetrazolium chloride in viability test of fruit pollen. Proceedings of the American Society for Horticultural Science 61: 299–303.

Quan MH, Ou LJ, She CW (2013) A new species of *Lycoris* (Amaryllidaceae) from Hunan, China. Novon: A Journal for Botanical Nomenclature 22(3): 307–310. https://doi.org/10.3417/2011013

Shi SD, Qiu YX, Wu L, Fu CX (2006) Interspecific relationships of *Lycoris* (Amaryllidaceae) inferred from inter-simple sequence repeat data. Scientia Horticulturae 110(3): 285–291. https://doi.org/10.1016/j.scienta.2006.07.011

PhytoKeys 177: 11–15 (2021)
doi: 10.3897/phytokeys.177.64042
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Lectotypification of *Plagiothecium mauiense*, a Hawaiian synonym of *Plagiothecium longisetum* (Plagiotheciaceae)

Grzegorz J. Wolski[1], Jarosław Proćków[2]

[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 Environmental Biology, Faculty of Biology and Animal Science, Wrocław University of Environmental and Life Sciences, ul. Kożuchowska 7a, 51-631 Wrocław, Poland*

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

Academic editor: Matt Renner | Received 5 February 2021 | Accepted 29 March 2021 | Published 21 April 2021

Citation: Wolski GJ, Proćków J (2021) Lectotypification of *Plagiothecium mauiense*, a Hawaiian synonym of *Plagiothecium longisetum* (Plagiotheciaceae). PhytoKeys 177: 11–15. https://doi.org/10.3897/phytokeys.177.64042

Abstract

In 2020, *Plagiothecium mauiense* Broth. was recognised as a synonym of *P. longisetum* Lindb.; however, due to the inability to compare all known original material, the conducted taxonomic analysis was not completed with lectotypification of the name. Syntypes of *P. mauiense* were found in four American herbaria: Harvard University Herbarium (FH00220142), Miami University Herbarium (MU 000000546), New York Botanical Garden Herbarium (NY01256708) and Yale University Herbarium (YU 233890). Considering the condition of the found material and Articles 9.3, 9.11 and 9.12 of the International Code of Nomenclature for algae, fungi and plants (*Shenzhen Code*) that is currently in force, a specimen NY01256708 was proposed to be the lectotype of *P. mauiense*.

Keywords

Baldwin collection, Codes of Botanical Nomenclature, *Orthophyllum* section, typification

Introduction

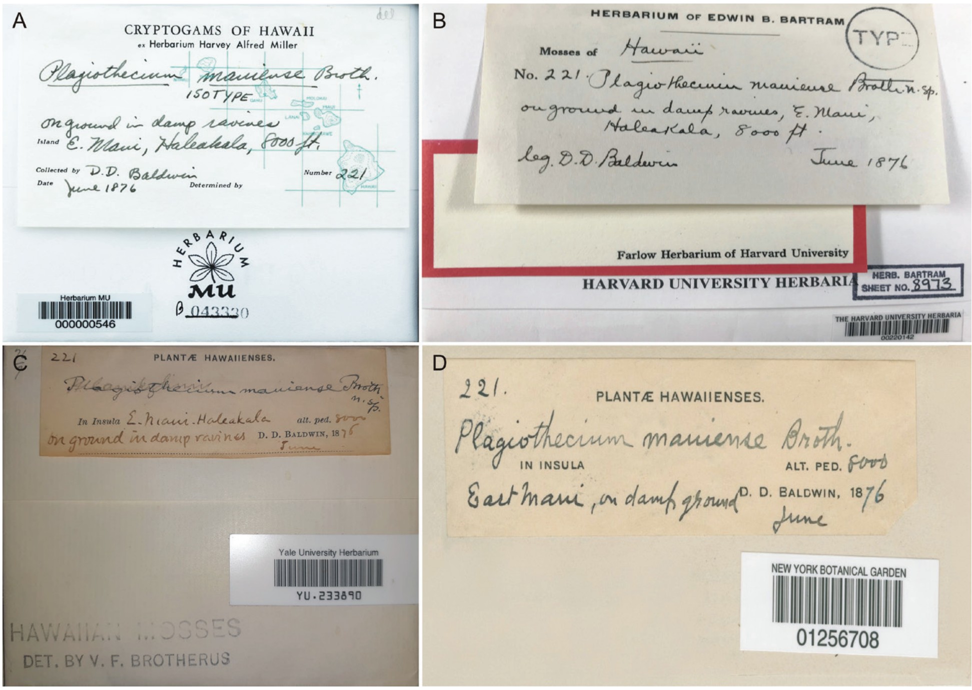
V.F. Brotherus described a new species, *Plagiothecium mauiense* (Brotherus 1927), based on specimens collected by D.D. Baldwin. A detailed comparative taxonomic analysis of the qualitative and quantitative features of the original material confirmed that the name is synonymous with *P. longisetum* Lindb. Additionally, the conducted research found all original specimens of *P. mauiense* to be syntypes (Wolski and Proćków 2020).

Unfortunately, to date, it was not possible to compare all known original material, so the lectotypification of *P. mauiense* was not completed (Wolski and Proćków 2020). However, this now appears possible and is the purpose of the present paper.

Wolski and Proćków (2020) confirmed that syntypes of *P. mauiense* are deposited in four American herbaria: Harvard University Herbarium (FH00220142), Miami University Herbarium (MU 000000546), New York Botanical Garden Herbarium (NY01256708) and Yale University Herbarium (YU 233890). Although it was possible to take on loan the described material from only two of them (Herbaria NY and YU), all four herbaria were able to provide the necessary assistance, as well as a wealth of data, including microscopic photographs of the described original material.

The analysis of the obtained data showed that all syntypes on the envelopes are described identically, of course, apart from the details related to individual herbaria or additional annotations from persons who previously reviewed the material. The envelopes of the analysed syntypes give a name of the species with the abbreviation of the author's name "*Plagiothecium mauiense* Broth."; collection number "221"; collector's name "D.D. Baldwin"; date "June 1876"; habitat "on ground in damp ravines"; location "E. Maui, Haleakala" and the relative height at which these plants grew "8000 ft." (Fig. 1).

However, the analysis of the protologue indicates that the above data differ from what was published in 1927. Regarding the locality and habitat, after the description of the features of *P. mauiense* and before remarking that it is similar to "*P. silvatico* (Hud-



A

del

CRYPTOGAMS OF HAWAII
ex Herbarium Harvey Alfred Miller
Plagiothecium mauiense Broth.
ISOTYPE
on ground in damp ravines
Island E. Maui, Haleakala, 8000 ft.
Collected by D.D. Baldwin
Date June 1876
Determined by
Number 221

HERBARIUM MU
β 043330

Herbarium MU
000000546

B

HERBARIUM OF EDWIN B. BARTRAM
TYP
Mosses of Hawaii
No. 221. Plagiothecium mauiense Broth. n. sp.
on ground in damp ravines, E. Maui,
Haleakala, 8000 ft.
leg. D.D. Baldwin June 1876

Farlow Herbarium of Harvard University
HARVARD UNIVERSITY HERBARIA
HERB. BARTRAM SHEET NO. 8973
THE HARVARD UNIVERSITY HERBARIA
00220142

C

221
PLANTÆ HAWAIIENSES.
Plagiothecium mauiense Broth. n. sp.
In Insula E. Maui. Haleakala alt. ped. 8000
on ground in damp ravines D. D. Baldwin, 1876
June

Yale University Herbarium
YU.233890

HAWAIIAN MOSSES
DET. BY V. F. BROTHERUS

D

221.
PLANTÆ HAWAIIENSES.
Plagiothecium mauiense Broth.
IN INSULA ALT. PED. 8000
East Maui, on damp ground D. D. BALDWIN, 1876
June

NEW YORK BOTANICAL GARDEN
01256708

Figure 1. Envelope fronts of four syntypes of *Plagiothecium mauiense* **A** MU 000000546 (photo from the Consortium of North American Bryophyte Herbaria, accessed 15 Nov 2020) **B** FH00220142 (photo by Genevieve E. Tocci) **C** YU 233890 **D** NY01256708. (**C, D** photo by Grzegorz J. Wolski).

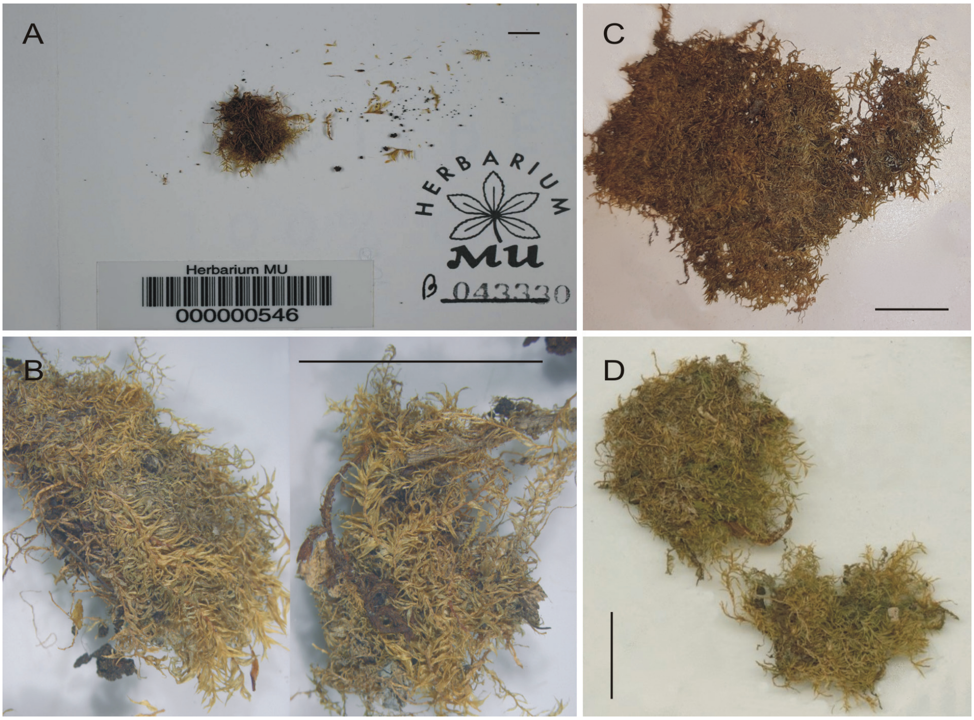


Figure 2. Syntypes of *Plagiothecium mauiense* **A** MU 000000546 (photo by Mike Vincent) **B** FH00220142 (photo by Genevieve E. Tocci) **C** YU 233890 **D** NY01256708. (**C, D** photo by Grzegorz J. Wolski). Scale bar: 2 cm.

son)", Brotherus (1927) provides: "Maui: on ground, elevation 2,400 meters (B. 221)". This is obviously a much poorer description than that contained on the envelopes of all original specimens (Fig. 1). Nevertheless, all of them are syntypes of *P. mauiense* collected from Hawaii (i.e. specimens No. 221 from the D.D. Baldwin collection), on the basis of which V.F. Brotherus (1927) in *Hawaiian Mosses* described *P. mauiense*.

The analysis of the contents of the envelopes indicates that not all specimens are preserved in good condition. The specimen stored at the Miami University Herbarium (MU 000000546) is the smallest one within the analysed original material, with few loose stems (Fig. 2A). The specimen deposited in the Yale University Herbarium (YU 233890) is represented by a fairly large turf, but it is stuck to a small piece of paper. The use of glue could explain the change in colour of its turf: it is extremely dark compared to other specimens (Fig. 2C). The specimens stored at the Harvard University Herbarium (FH00220142) and New York Botanical Garden Herbarium (NY01256708) are represented by two quite large pieces of well-preserved turfs (Fig. 2B, D).

Taking into account the above data and the fact that the specimen stored at NY is well preserved and has recently been described in detail (Wolski and Proćków 2020), as well as the fact that this material (NY01256708) consists of an additional permanent preparation of a large fragment of the stem, that was probably made by Iwatsuki in 1970 and, according to Article 9.3 of the *Shenzhen Code* (Turland et al. 2018), stating that "A lectotype is one specimen or illustration designated from the original material (…) as the nomenclatural type, in conformity with Art. 9.11 and 9.12, if the name was published without a holotype (…)" and that "in lectotype designation, an isotype must be chosen if such exists, or otherwise a syntype or isosyntype if such exists" (Art. 9.12), we propose that specimen NY01256708 should be designated as the lectotype of *P. mauiense* Broth. (Fig. 2D).

Additionally, due to the fact that two specimens were not physically available to us, we will send a request to the Harvard University Herbarium (FH00220142) and Miami University Herbarium (MU 000000546) to change the status of these specimens to isolectotypes, labelling them appropriately, after the article is published.

Taxonomic treatment

Plagiothecium longisetum Lindb., Contributio ad Floram Cryptogamam Asiae Boreali-Orientalis, Acta Soc. Sci. Fenn. 10: 232 (1872)

Type. [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). – ***Lectotype*** (designated here): [United States], Hawaii, E Maui, Haleakala, 8000 ft., in damp ravines, fertile, June 1876, *D.D. Baldwin 221* (NY01256708!); isolecto-: FH00220142 (available online)!, MU000000546 (available online)!, YU233890!).

Thus, the selection of the lectotype formally completed the taxonomic revision of the original material of *Plagiothecium mauiense*, collected by D.D. Baldwin from Hawaii, U.S.A.

Acknowledgements

We would like to thank the curators and employees of the New York Botanical Garden Herbarium and Yale University Herbarium for the loan of the original material of *P. mauiense*; we would also like to thank the curators and employees of the Harvard University Herbarium and Miami University Herbarium for all their help in making the creation of this manuscript possible.

References

Brotherus VF (1927) Hawaiian Mosses. Bernice P. Bishop Museum. Bulletin 40: 1–28.

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

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

PhytoKeys 177: 17–24 (2021)
doi: 10.3897/phytokeys.177.63346
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Utricularia lihengiae (Lentibulariaceae), a new species from Northwest Yunnan, China

Zhuo Cheng[1,2], Qiong Fang[1,2], Fei Wang[1], Chun-Lin Long[1,2,3]

1 *College of Life and Environmental Sciences, Minzu University of China, Beijing 100081, China* **2** *Key Laboratory of Ethnomedicine (Minzu University of China), Ministry of Education, Beijing 100081, China* **3** *Key Laboratory of Ecology and Environment in Minority Areas (Minzu University of China), National Ethnic Affairs Commission, Beijing 10 0081, China*

Corresponding author: Chun-Lin Long (long@mail.kib.ac.cn; long.chunlin@muc.edu.cn)

Academic editor: Alan Paton | Received 19 January 2021 | Accepted 13 April 2021 | Published 26 April 2021

Citation: Cheng Z, Fang Q, Wang F, Long C-L (2021) *Utricularia lihengiae* (Lentibulariaceae), a new species from Northwest Yunnan, China. PhytoKeys 177: 17–24. https://doi.org/10.3897/phytokeys.177.63346

Abstract

Utricularia lihengiae, a new species from the Dulongjiang region of northwest Yunnan, China, is here described and illustrated. The new species belongs to the section *Oligocista* and is similar to *U. bifida* L. and *U. scandens* Benj., from which it can be easily distinguished by the dark purple stripe on the corolla. The new species also differs in its shorter inflorescence and the shape of the calyx lobes.

Keywords

Bladderwort, insectivorous plant, taxonomy, Yunnan Province

Introduction

Lentibulariaceae is a monophyletic family composed of three carnivorous genera: *Utricularia* Linnaeus (1753: 18), *Pinguicula* Linnaeus (1753: 17) and *Genlisea* Saint-Hilaire (1833: 428) (Taylor 1989; Fleischmann et al. 2010). *Utricularia* spp., commonly called bladderworts, is the largest genus in this family (Taylor 1974). For a long time, *Utricularia* has attracted a great deal of interest in its peculiar morphology and carnivorous characteristics (Taylor 1974; Li 1988; Fleischmann et al. 2010). *Utricularia* plants are typically small but complex in structure, with vegetative organs that are highly variable. It is difficult to dissect and observe *Utricularia* specimens after they are dried, providing difficulties in the accurate identification and classification of taxa within the genus (Albert et al. 1992).

In his monograph, Taylor (1989) recognized a total of 214 species in *Utricularia* worldwide and classified them into two subgenera and 35 sections. Since then, some sixty species of *Utricularia* have been published from different parts of the world. Currently, about 274 species of *Utricularia* have been described (Fleischmann 2012, 2015; Delprete 2014; Kumar et al. 2018; Hong et al. 2021).

Utricularia is the largest carnivorous plant genus and also one of the most widely distributed. The genus is known to occur on every continent except for Antarctica (Taylor 1989). The vast majority of species are found in tropical and sub-tropical regions, particularly where conditions are seasonally wet, with high or very high annual rainfall.

Currently, 25 species of *Utricularia* have been reported in China. Most of them are mainly distributed in the provinces to the south of the Yangtze River. With 13 species, Yunnan has the highest diversity of *Utricularia* in China (Li 1990, 2007).

In August 2019, the authors visited Dulongjiang in Northwest Yunnan, an isolated area of the Eastern Himalayas, to conduct a survey on traditionally used plants and biodiversity associated traditional knowledge (Figure 1). The Dulongjiang region is located in the core area of Gaoligongshan National Nature Reserve, adjacent to Chayu County (Tibetan Autonomous Region, China) to the north and Kachin State (Myanmar) to the west and south. Dulongjiang region has among the highest levels of flora and faunal biodiversity in China (Li et al. 2011). During the survey work, a species of *Utricularia* was discovered growing in moss at the north entrance of the Dulongjiang tunnel. With dark purple stripes on the corolla, the species is very distinctive. After reviewing Taylor's monograph (1989), it can be determined that this species belongs to the section *Oligocista* Taylor (1989: 305) as explained in Taxonomic Notes below. In November, the authors visited the Dulongjiang area again to collect specimens for further investigations. After detailed examinations, the taxon is here described as a new species, *Utricularia lihengiae*.

Material and methods

This study was based on field observations and detailed examinations of herbarium specimens. Herbarium specimens collected from northwest Yunnan were deposited at the Herbarium, Kunming Institute of Botany, Chinese Academy of Sciences (**KUN**) (Thiers 2020). A comparative study of herbarium collections (PE, KUN, IBK, WUK, and IBSC) revealed an undescribed taxon in the genus *Utricularia*. Dried specimens were examined using a dissecting microscope (XTL-Iab, Beijing Keyi Electro-optical Instrument Factory). Detailed observation and measurement of the collected individuals were conducted covering the rhizoid, stolon, leaf, traps, calyx lobe, bracts, flowers, and spurs. Conservation status was assessed applying the IUCN Red List categories and criteria, version 3.1 (IUCN 2012). For comparison, the unknown species and related specimens in herbaria, the monographs of Taylor (1989) and the contribution of Li (1990, 2007) were also referenced.

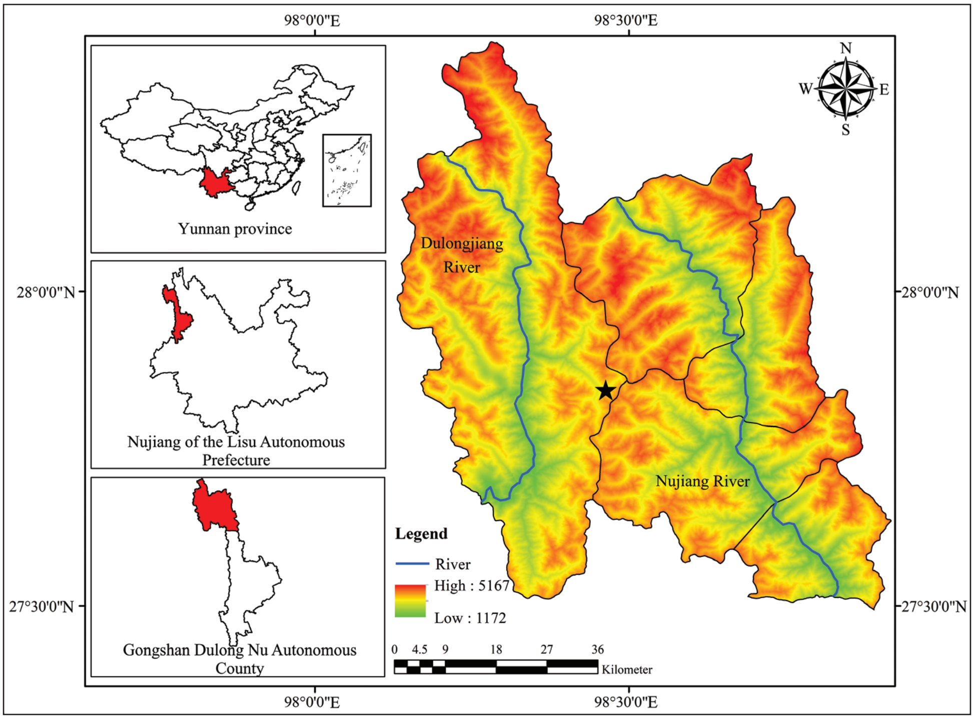


Figure 1. Distribution of *Utricularia lihengiae*.

Taxonomic treatment

Utricularia lihengiae C. L. Long & Z. Cheng, sp. nov.

urn:lsid:ipni.org:names:77216662-1
"李恒挖耳草" (Li Heng Wa Er Cao)
Figure 2, Table 1

Diagnosis. *U. lihengiae* is similar to *U. bifida* L. (1753: 18), but differs by the inflorescences 2–4 cm long (vs. mostly 10–20 cm long in *U. bifida*), calyx upper and lower with apex acuminate (vs. calyx upper lobe, apex obtuse, calyx lower lobe, apex rounded or very shortly bifid in *U. bifida*), 3–5 dark purple stripes on the upper corolla lip, 3 dark purple stripes on lower corolla lip (vs. absent in the upper and lower corolla lip in *U. bifida*); *U. lihengiae* is similar to *U. scandens* Benj. (1847: 309), but differs by the smaller inflorescence 2–4 cm long (vs. mostly 15–35 cm long in *U. scandens*), peduncle of *U. lihengiae* is erect (vs. peduncle usually twining in *U. scandens*), calyx lower lobe with apex acuminate (vs. calyx lower lobe with apex rounded or very shortly bifid in *U. scandens*), upper calyx lobe of *U. lihengiae* is shorter than upper corolla lip (vs. upper calyx lobe longer than upper corolla lip in *U. scandens*), 3–5 dark purple stripes on the upper corolla lip, 3 dark purple stripes on lower corolla lip (vs. absent in the upper and lower corolla lip in *U. scandens*).

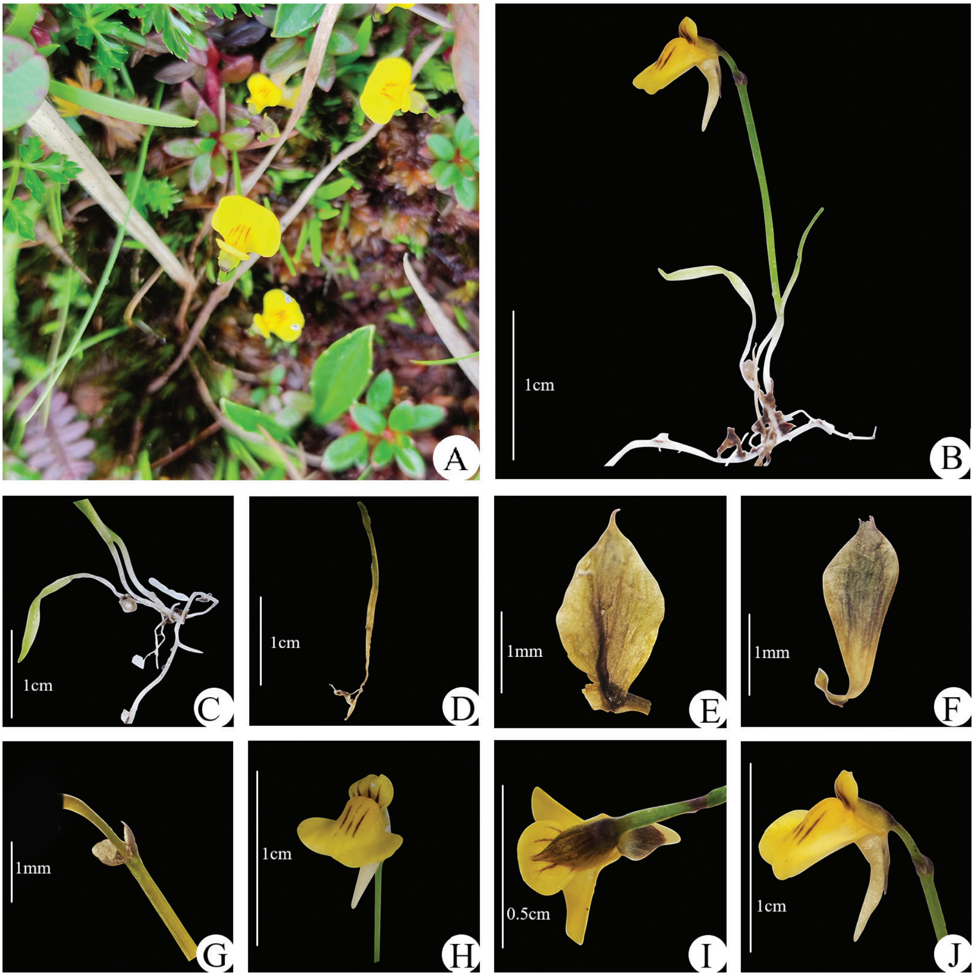


Figure 2. *Utricularia lihengiae* (**A–J**) **A** habitat **B** whole plant **C** traps and laminar leaves **D** leaf **E** calyx upper lobe **F** calyx lower lobe **G** bracts **H–J** frontal, dorsal and lateral view of the flower (**A–J** Photos by Z. Cheng.).

Type. China, Yunnan Province, Nujiang Lisu Autonomous Prefecture, Gongshan Dulong and Nu Autonomous County, Dulongjiang Township, 2844 m a.s.l., 27°50'36"N, 98°27'48"E, 3 September, 2019, *Chun Lin Long & Zhuo Cheng DXH066*, (holotype: KUN!; isotype: KUN!).

Description. Small annual herbs. Rhizoids few, capillary, 0.5 cm to 2 cm long, 0.15–0.3 mm thick, with numerous short papillose branches. Stolons few, capillary, branched, up to 4 cm long, ca. 0.2 mm thick, the internodes mostly 2–4 mm long. Leaves few, from the stolon nodes, petiolate, the lamina narrowly linear, with apex rounded or subacute, 1–nerved, 0.5–1 mm wide, total length up to 1.5 cm. Traps rather few on the stolon internodes and leaves, globose, shortly stalked, 0.5–1 mm long, the mouth basal with 2 simple, subulate, reflexed, dorsal appendages and with a ± distinct rounded swelling on the ventral side of the mouth or on the adjacent distal part of the stalk. Inflorescence erect, solitary, simple or rarely sparsely branched, 2–4 cm long; peduncle terete, glabrous, 0.2–0.4 mm thick. Scales few, similar to the bracts. Bracts basifixed, ovate, with apex obtuse to acute, 1–2 mm long, 1–5 nerved. Bracteoles subulate, with apex acute, much shorter than the bract. Flowers 1–2, the raceme axis elongate; pedicels spreading at anthesis, decurved in fruit, capillary, broadly winged, 2–6 mm long. Calyx lobes slightly unequal, broadly ovate, 1–3 mm long, the upper lobe with apex obtuse to acute, the lower lobe slightly smaller with apex obtuse to acute. Corolla yellow, 3–7 mm long; upper lip slightly constricted below the middle, the superior part oblong or oblong–obovate, with apex rounded, bearing 3–5 dark purple stripes on the upper corolla lip, radial, the inferior part broadly ovate–deltoid; lower lip limb galeate, approximately circular, the base with a prominent rounded swelling, the apical margin rounded; palate margin ciliate; 3 dark purple stripes on the lower corolla lip, parallel; spur subulate, with apex acute, curved, about as long as and widely diverging from the lower lip. Filaments straight, 1 mm long, the anther thecae distinct. Ovary ovoid, dorsiventrally compressed; style distinct; stigma lower lip semicircular, the upper lip very short or ± obsolete. Capsule broadly ellipsoid, dorsiventrally compressed, 2.5–3 mm long, the wall uniformly membranous, dehiscing by dorsal and ventral longitudinal slits. Seeds obliquely obovoid, the major end with apex subtruncate, 0.4–0.5 mm long, the testa cells elongate with anticlinal boundaries much raised and longitudinally striate, somewhat sinuate, the periclinal walls tabular, conspicuously longitudinally striate.

Distribution and habitat. The only known locality of this taxon is in Dulongjiang Township, Gongshan Dulong and Nu Autonomous County, Northwest Yunnan, China. The site is located in an open area in a primeval forest dominated by Fagaceae, Magnoliaceae and Ericaceae. The observed population is very small, with fewer than 80 plants growing in the moss amongst damp grass on the roadside, accompanied by the moss *Polytrichum commune* Hedwig (1801: 88), as well as *Vaccinium chaetothrix* Sleumer (1941: 432), and *Acorus tatarinowii* Schott (1859: 101). The elevation is 2800–2900 metres above sea level. The climate here is rainy and humid, with rain falling for most of the year.

Phenology. Flowering and fruiting occurs from August to November.

Etymology. Named in honor of Prof. Li Heng, a Chinese botanist who has made significant contributions to the knowledge of the flora of Dulongjiang region.

Conservation status. This species has not been recorded or described so far, and there is only one known site in Dulongjiang region, which is relatively unknown to botanists. In addition, *Utricularia lihengiae* is very small and has a short flowering period, making it easily overlooked. This species satisfies the IUCN 3.1 Red List CR (Critically Endangered) Criteria B1ab(ii,iii)+2ab(i,ii,iii) (IUCN 2012), which has an EOO (Extent of occurrence) < 100 km^2 and AOO (Area of occupancy) < 10 km^2, it may be classified as "critically endangered" (CR). The distribution site of *Utricularia lihengiae* is next to the road, which is at great risk of human disturbance and extreme

Table 1. Morphological comparison among *Utricularia lihengiae*, *U. bifida*, and *U. scandens*.

Character	*U. lihengiae*	*U. bifida*	*U. scandens*
Inflorescence	erect, 2–4 cm long	erect, mostly 10–20 cm long	erect or twining, mostly 15–35 cm long
Peduncle	peduncle erect	peduncle usually erect	peduncle usually twining
Calyx upper lobe	apex acuminate	apex obtuse	apex acuminate
Calyx lower lobe	apex acuminate	apex rounded or very shortly bifid	apex shortly and acutely bifid
Calyx upper lobe and upper corolla lip	upper calyx lobe shorter than upper corolla lip	upper calyx lobe shorter than upper corolla lip	upper calyx lobe longer than upper corolla lip
Upper corolla lip	3–5 dark purple stripes	stripes absent, upper lip slightly constricted below the middle	stripes absent, upper lip constricted below the middle
Lower corolla lip	3 dark purple stripes	stripes absent, the base with a prominent rounded swelling	stripes absent, the base distinctly swollen, with 2 or 4 rounded, longitudinal ridges, the apex rounded or obscurely 2–3 crenate

weather, such as tourist activities, road building, grazing and landslides. Additionally, regional management in pursuit of economic development is likely to pose a threat through trampling and pollution of soil and water, causing negative impacts to the small and fragile habitat.

Taxonomic notes. The new species belongs to *Utricularia* section *Oligocista* due to the following characters: traps globose, the mouth basal with 2 simple subulate dorsal appendages and leaves linear to obovate (Taylor 1989). There were five species belonging to *Utricularia* section *Oligocista* in China prior to the discovery of *U. lihengiae*. From the perspective of geographical distribution, *U. bifida* and *U. scandens* are both distributed in Yunnan, *U. scandens*, is mainly distributed in northwestern Yunnan, whereas *U. bifida* is mainly found in south Yunnan. According to the key to the species of *Utricularia* occurring in China (Li 2007), the morphology of *U. lihengiae* is similar to *U. bifida* and *U. scandens* in the yellow corolla. However, it can be clearly distinguished by the dark purple stripes of the corolla, shorter inflorescence and by the shape of the calyx lobes. A comparative summary of the characters that differentiate these three taxa is presented in Table 1.

Additional specimens examined. China, Yunnan Province, Nujiang Lisu Autonomous Prefecture, Gongshan Dulong and Nu Autonomous County, Dulongjiang Township, 2844 m a.s.l., 27°50'36"N, 98°27'48"E, 3 September 2019, *Chun Lin Long & Zhuo Cheng DXH066*, *Chun Lin Long & Zhuo Cheng DXH067*, *Chun Lin Long & Zhuo Cheng DXH068*, *Chun Lin Long & Zhuo Cheng DXH069*, *Chun Lin Long & Zhuo Cheng DXH070* (KUN!).

Specimens of *Utricularia bifida* examined. CHINA. Guangdong: Renhua County, 16 November 1973, *C.J. Huang & Y.T. Zhang 077* (PE); Deqing County, 5 August 1958, *Y.G. Liu 01303* (PE), 2 August 1930, *J.L. Zuo 22497* (IBK), 6 July 1958, *X.G. Li 202078* (IBK). Guangxi: Yongning District, 6 July 1984, *Z.Y. Li 10984* (PE); Lingui County, 5 September 1997, *G.Z. Li 16229* (PE), 11 October 1958, *Y.K Li 402165* (IBK), 19 October 1948, *S.G. Li 200104* (IBK). Yunnan, 2 June 1939, *M.K. Li 1698* (WUK). Jiangxi, 19 September 1963, *J.S. Yue et al. 3983* (IBSC), 26 June 1932, *Y. Jiang 9967* (IBSC).

Key to species of *Utricularia* section *Oligocista* occurring in China

1 Corolla yellow **2**

– Corolla violet, mauve, lilac, or white **4**

2 Peduncle erect; pedicel strongly recurved in fruit; upper calyx lobe shorter than upper corolla lip, apex obtuse **3**

– Peduncle twining to erect; pedicel erect in fruit; upper calyx lobe longer than upper corolla lip, apex shortly acuminate .... ***U. scandens***

3 Dark purple stripes in upper corolla lip and lower corolla lip .... ***U. bifida***

– Stripes absent in upper corolla lip and lower corolla lip .... ***U. lihengiae***

4 Peduncle twining; pedicel strongly deflexed in fruit .... ***U. foveolata***

– Peduncle erect; pedicel erect to spreading in fruit **5**

5 Fruiting pedicel as long as or shorter than fruiting calyx; calyx lobes suborbicular in fruit; seeds globose, with isodiametric reticulations; leaf blade 2.5–4.5 cm × 1.5–6 mm .... ***U. uliginosa***

– Fruiting pedicel much longer than fruiting calyx; calyx lobes ovate in fruit; seeds ovoid to ellipsoid, with elongate reticulations; leaf blade 0.4–2 cm × 0.8–3 mm .... ***U. graminifolia***

Acknowledgements

We are very grateful to the Dulong (Drung) people of Dulongjiang Township, Yunnan, who guided us to the habitats of *Utricularia* and continued to send us information in different seasons. Many thanks go to Prof. Zhenyu Li, a respected taxonomist and expert of Lentibulariaceae from the Institute of Botany, Chinese Academy of Sciences, for his confirmation of this new species. We also thank Prof. Guangwan Hu from Wuhan Botanical Garden, Chinese Academy of Sciences, and Jun Yang from the Kunming Institute of Botany, Chinese Academy of Sciences for their helpful suggestions. This work was supported by grants from the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment of China (2019HJ2096001006), National Natural Science Foundation of China (No. 31761143001, 31870316), Key Laboratory of Ethnomedicine (Minzu University of China) of Ministry of Education of China (KLEM-ZZ201904 & KLEM-ZZ201906), and Jiansheng Fresh Herb Medicine R & D Foundation (JSYY-20190101-043).

References

Albert VA, Williams SE, Chase MW (1992) Carnivorous plants: Phylogeny and structural evolution. Science 257(5076): 1491–1495. https://doi.org/10.1126/science.1523408

Benjamin L (1847) Linnaea: Ein Journal für die Botanik in ihrem ganzen Umfange, Berlin, 309 pp.

Delprete PG (2014) *Utricularia julianae* (Lentibulariaceae), a new species from the savannas of the Oyapock River, French Guiana. Phytotaxa 156(2): 74–78. https://doi.org/10.11646/phytotaxa.156.2.2

Fleischmann A (2012) The new *Utricularia* species described since Peter Taylor's monograph. Carnivorous Plant Newsletter 41: 67–76.

Fleischmann A (2015) Taxonomic *Utricularia*. Carnivorous Plant Newsletter 44: 13–16.

Fleischmann A, Schäferhoff B, Heubl G, Rivadavia F, Barthlott W, Müller KF (2010) Phylogenetics and character evolution in the carnivorous plant genus *Genlisea* A.St.–Hil. (Lentibulariaceae). Molecular Phylogenetics and Evolution 56(2): 768–783. https://doi.org/10.1016/j.ympev.2010.03.009

Hedwig J (1801) Species Muscorum Frondosorum, 88 pp.

Hong YM, Huang ZJ, Li MH (2021) The checklist of *Utricularia* in the world. https://scietymol.huijiwiki.com/p/695

IUCN (2012) IUCN red list categories and criteria: Version 3.1. Second edition. IUCN, Gland, Switzerland and Cambridge, UK. https://portals.iucn.org/library/node/10315

Kumar VVN, Prabhukumar KM, Jagadeesan R, Harinarayanan CM, Nair MC, Janarthanam MK, Balachandran I (2018) *Utricularia sunilii* (Lentibulariaceae), a striking new species from southern Western Ghats, Kerala, India. Phytotaxa 371(2): 140–144. https://doi.org/10.11646/phytotaxa.371.2.9

Li ZY (1988) A revision of the genus *Utricularia* in China. Bulletin of Botanical Research 8(2): 25–29.

Li ZY (1990) Lentibulariaceae. In: Wang WC (Ed.) Flora Reipublicae Popularis Sinicae 69 Science Press, Beijing, 582–605.

Li ZY (2007) Lentibulariaceae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China (Vol. 19). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, 480–491.

Li R, Dao ZL, Li H (2011) Seed plant species diversity and conservation in the northern Gaoligong Mountains in western Yunnan, China. Mountain Research and Development 31(2): 160–165. https://doi.org/10.1659/MRD-JOURNAL-D-10-00056.1

Linnaeus C (1753) Species Plantarum 1. Impensis Laurentii Salvii, Stokholm, 17–18.

Saint-Hilaire A (1833) Voyage dans le District des Diamans, volume 2. Librarie-Gide, Paris, 456 pp.

Schott HW (1859) Oesterreichische Botanische Zeitschrift 9: 1–101. https://doi.org/10.1007/BF02310393

Sleumer HO (1941) Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 71(4): 1–432.

Taylor P (1974) Lentibulariaceae. Flora Malesiana–Series 1. Spermatophyta 8(1): 275–300.

Taylor P (1989) The genus *Utricularia* – a taxonomic monograph. Kew Bulletin Addition Series XIV. Royal Botanic Garden, Kew, 724 pp.

Thiers B (2020) [continuously updated] Index Herbariorum. A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih [accessed 06 October 2020]

PhytoKeys 177: 25–42 (2021)
doi: 10.3897/phytokeys.177.62915
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Evaluating the monophyly of *Mammillaria* series *Supertextae* (Cactaceae)

Cristian R. Cervantes[1,2], Silvia Hinojosa-Alvarez[3], Ana Wegier[1], Ulises Rosas[1], Salvador Arias[1]

1 *Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito Exterior, Ciudad Universitaria, Coyoacán, Ciudad de México 04510, Mexico* **2** *Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México, 04510, Mexico* **3** *Tecnologico de Monterrey, School of Engineering and Sciences, Ave. Eugenio Garza Sada 2501, Monterrey, N.L. 64849, Mexico*

Corresponding author: Cristian R. Cervantes (cristoichkov@gmail.com)

Academic editor: Alice Calvente | Received 8 January 2021 | Accepted 13 April 2021 | Published 28 April 2021

Citation: Cervantes CR, Hinojosa-Alvarez S, Wegier A, Rosas U, Arias S (2021) Evaluating the monophyly of *Mammillaria* series *Supertextae* (Cactaceae). PhytoKeys 177: 25–42. https://doi.org/10.3897/phytokeys.177.62915

Abstract

Mammillaria (Cactaceae) taxonomy has been historically problematic due to the morphological variability and sympatry of the species. This has led to several proposals for infrageneric classification, including subgeneric, section and series categories. *Mammillaria* ser. *Supertextae* is one of 15 series and is made up of a variable set of species that are mainly distributed in southern Mexico and Central America. However, the phylogenetic relationships within *M.* ser. *Supertextae* and its relationship to other *Mammillaria* taxa are far from fully understood. Here we attempt to elucidate these relationships using complete terminal sampling and newly obtained chloroplast marker sequences and comparing them to *Mammillaria* species sequences from GenBank. Our phylogenetic analyses showed that *M.* ser. *Supertextae* comprises a well-supported monophyletic group that diverged approximately 2.1 Mya and has *M.* ser. *Polyacanthae* as its sister group; however, relationships within *M.* ser. *Supertextae* remain unresolved. The topology obtained within *M.* ser. *Supertextae* must also be interpreted under the distribution shared by these taxa, but it is difficult to differentiate ancestral polymorphisms from possible introgression, given the short time elapsed and the markers used. Our results show that the infrageneric units of *M. haageana* and *M. albilanata* can be considered independent evolutionary units. We also suggest that the relationship between *M. haageana* and *M. albilanata* is convoluted because their distribution overlaps (mainly towards southern Mexico), with genetic differences that possibly indicate they represent more than two taxonomic entities. One possible explanation is that there could still be gene flow between these taxa, and we might be witnessing an ongoing speciation process.

Keywords
Bayesian inference, Cactaceae, chloroplast DNA, *Mammillaria haageana*, molecular phylogeny, *M.* ser. *Supertextae*, taxonomy

Introduction

Mammillaria Haw. (Cactaceae, Cactoideae, Cacteae) is the most diverse genus within the cactus family, with a broad range of recognized species, ranging from 163 (Hunt et al. 2006) to 181 (Pilbeam 1999) up to 320 species (Reppenhagen 1992). *Mammillaria* is characterized by tuberculate stems, definite dimorphic areoles not connected by a groove, flowers that arise from the base of the tubercles and not apically, and seeds with testa cell walls that are par-concave and undulated (Bravo-Hollis and Sánchez-Mejorada 1991; Lüthy 1995; Anderson 2001; Hunt et al. 2006). This genus, together with *Coryphantha* (Engelm.) Lem., *Escobaria* Britton & Rose, *Neolloydia* Britton & Rose, and *Ortegocactus* Alexander, is integrated into the Mammilloid clade (Butterworth et al. 2002). However, it has been proposed that *Mammillaria* is a polyphyletic group. Breslin et al. (2021), using plastid genomes, confirmed previous studies showing *Mammillaria* is nonmonophyletic, as currently circumscribed, so they proposed that the Mammilloid clade be circumscribed in three monophyletic genera, *Mammillaria* s.s., *Coryphantha* and *Cochemiea* s.l., as previously suggested by Vázquez-Sánchez et al. (2013). Furthermore, the taxonomy of *Mammillaria* has historically been difficult due to large morphological variability, phenotypic plasticity, sympatric distribution of species, and suspected hybridization events.

Within *Mammillaria*, there are 15 recognized series (Hunt et al. 2006), one of which is *M.* ser. *Supertextae* D.R. Hunt, distributed from western Mexico to Central America and even the Caribbean islands (Pilbeam 1999). *Mammillaria* ser. *Supertextae* is a clear example of the species delimitation problem within the genus, illustrated by the number of accepted species ranging from 8 to 27, although the most recent taxonomic proposal recognizes only 9 taxa (Table 1). Morphometric and molecular studies have attempted to assess the proposed infrageneric relationships for *Mammillaria*, but none have been specifically directed at *M.* ser. *Supertextae.* Lüthy (1995) performed a detailed morphological analysis of the genus with a phenetic approach, in which he included four species of *M.* ser. *Supertextae* (*M. albilanata* Backeb., *M. dixanthocentron* Backeb. ex Mottram, *M. haageana* Pfeiff., and *M. huitzilopochtli* D.R. Hunt), showing that *M.* ser. *Supertextae* is characterized by the presence of extracellular crystals; however, the trait is not exclusive to *M.* ser. *Supertextae*, as the *M.* ser. *Leucocephalae* Lem. ex Schumann also shows this characteristic. Butterworth and Wallace (2004) conducted a molecular study using two chloroplast markers (*rpl*16 and *psb*A-*trn*H), including five species of *M.* ser. *Supertextae* (same as Lüthy but including *M. supertexta* Mart. ex Pfeiff.); although the species were grouped together, the support values were low (BS = 63, PP = 0.99), and a phylogenetic relationship could not be established with the remainder of *Mammillaria*. More recently, the complete sequencing of the chloroplast genome of eight *Mammillaria*

Table 1. Historical account of taxonomic classifications of *M.* ser. *Supertextae* D.R. Hunt (= *Elegantes*).

Backeberg (1961)	Bravo-Hollis and Sánchez-Mejorada (1991)	Reppenhagen (1992)	Lüthy (1995)	Hunt et al. (2006)
M. crucigera Mart.	*M. huitzilopochtli* D.R.Hunt	*M. elegans*	*M. albilanata*	*M. albilanata*
M. celsiana Lem.	*M. lanata* Orcutt	*M. meissneri*	*M. columbiana*	*M. crucigera*
M. elegans DC.	*M. albilanata* Backeb.	*M. haageana*	*M. eriacantha*	*M. columbiana*
M. supertexta Mart. ex Pfeiff.	*M. supertexta*	*M. conspicua*	*M. haageana*	*M. dixanthocentron*
M. dyckiana Zucc. ex Pfeiff.	*M. crucigera*	*M. monticola* Repp.	*M. supertexta*	*M. flavicentra*
M. dealbata A.Dietr.	*M. dixanthocentron* Backeb.	*M. lanigera* Repp.	*M. crucigera*	*M. haageana*
M. haageana Pfeiff.	*M. vaupelii* Tiegel	*M. donatii*	*M. dixanthocentron*	*M. halbingeri*
M. acanthoplegma Lehm.	*M. haageana*	*M. albidula* Backeb.	*M. huitzilopochtli*	*M. huitzilopochtli*
M. meissneri Ehrenbg.	*M. collina* J.A.Purpus	*M. lanata*		*M. supertexta*
	M. donatii Berge ex K.Schum.	*M. tlalocii* Repp.		
	M. san-angelensis Sánchez-Mej.	*M. huitzilopochtli*		
	M. martinezii Backeb.	*M. crucigera*		
	M. fauxiana Backeb.	*M. flavicentra*		
	M. conspicua J.A.Purpus	*M. dixanthocentron*		
	M. halbingeri Boed.	*M. supertexta*		
	M. flavicentra Backeb.	*M. reppenhagenii*		
	M. tegelbergiana G.E.Linds.	*M. albilanata*		
	M. reppenhagenii D.R.Hunt	*M. igualensis* Repp.		
	M. ruestii Quehl	*M. tegelbergiana*		
	M. yucatanensis Orcutt	*M. igniota* Repp.		
		M. halbingeri		
		M. noureddineana Repp.		
		M. columbiana Salm-Dyck		
		M. ruestii		
		M. yucatanensis		
		M. chilapensis Repp.		
		M. eriacantha Link & Otto ex Pfeiff.		

species confirms that four *M.* ser. *Supertextae* taxa (*M. crucigera* Mart., *M. supertexta*, *M. huitzilopochtli*, *M. haageana* subsp. *san-angelensis* (Sánchez-Mej.) D.R. Hunt) represent a clade (Solórzano et al. 2019; Hinojosa-Alvarez et al. 2020).

To disentangle the evolution of *Mammillaria*, we decided to focus on elucidating the phylogenetic relationships of *M.* ser. *Supertextae*. We included all taxa proposed by Hunt et al. (2006), except for *M. halbingeri* Boed., as, according to Reppenhagen (1992), the species was not reported again. We also included 12 localities of *M. haageana* and seven of *M. albilanata*. All these species together constitute one taxonomic complex within *M.* ser. *Supertextae* (Arias et al. 2012). We chose two chloroplast markers, the *rpl*16 intron and the intergenic spacer *psb*A-*trn*H. In Cactaceae, both markers have been used to resolve phylogenetic relationships (Korotkova et al. 2010; Sánchez et al. 2014; Cruz et al. 2016; Barrios et al. 2020), including *Mammillaria* (Butterworth and Wallace 2004; Vázquez-Sánchez et al. 2013; Hernández-Hernández et al. 2014); therefore, there are many sequences available in GenBank that can be used to expand the sampling of terminals, including sister groups and outgroups essential for testing the monophyly (Korotkova et al. 2017) of *M.* ser. *Supertextae*. The main objective of this study was to test the monophyly of *M.* ser. *Supertextae* and estimate its divergence time by broadening the sample of terminals within the series.

Materials and methods

The present study included a total of 123 taxa, 111 species of *Mammillaria*, 5 closely related genera (*Escobaria*, *Pelecyphora* Ehrenb., *Coryphantha*, *Neolloydia*, and *Ortegocactus*) and three external groups (*Ferocactus haematacanthus* (Salm-Dyck) Borg ex Backeb., *Ferocactus latispinus* (Haw.) Britton & Rose, and *Stenocactus lloydii* Berger). We selected two chloroplast loci: the intron *rpl*16 and the intergenic spacer region *psb*A-*trn*H. We downloaded 95 sequences of the genus *Mammillaria* (Butterworth and Wallace 2004; Hernández-Hernández et al. 2011; Fehlberg et al. 2013) from GenBank (see Appendix 1). For *M.* ser. *Supertextae*, we obtained two sequences: *M. albilanata* subsp. *tegelbergiana* (H. E. Gates ex G. E. Linds.) D.R. Hunt and *M. columbiana* Salm-Dyck subsp. *columbiana* from Vázquez-Sánchez et al. (2013). For the remaining 28 taxa of *M.* ser. *Supertextae*, we generated new sequence data.

DNA was extracted from 40 mg of silica-dried (24 h) stems. The samples were stored at -80 °C, and 12 hours later, they were triturated in a TissueLyser II (Qiagen, Venlo, Netherlands) at 29 rpm for 25 s twice. Extraction was performed with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions, and the elution volume was 35 µl twice in Milli-Q water. The *rpl*16 intron and *psb*A-*trn*H intergenic spacer were amplified using standard PCR protocols. The *rpl*16 region was amplified using the primers from Hernández-Hernández et al. (2011), *rpl*161F (5′-GCTATGCTTAGTGTGTGACTCGTT-3′) and *rpl*163R (5′-CTTCTATTTGTCTAGGCGTGATCC-3′), by initially denaturing the DNA for 5 min at 94 °C, followed by 28 cycles of 1 min at 94 °C, 50 s at 55 °C, and 2 min at 72 °C, and a final extension of 4 min at 72 °C. The *psb*A-*trn*H intergenic spacer was amplified with primers from Korotkova et al. (2010), *CApsbA* (5′-CCGTGCTAACCTTGGTATGG-3′) and *CAtrnH* (5′-CCGCGAATGGTGGATTCACAAT-3′). PCR conditions were 2 min at 94 °C; followed by 29 cycles of 30 s at 94 °C, 30 s at 52 °C; and 1 min at 72 °C; and a final extension of 7 min at 72 °C. Amplifications were performed using 0.6 U of Platinum *Taq* polymerase according to the manufacturer's protocol (Invitrogen, Carsbad, California, USA), 4 mM mixed dNTPs (Invitrogen, Thermo Fisher Scientific, Waltham, USA), 1.5 mM MgCl2, 16 mg/mL BSA, 0.25 µM each primer, and 30–50 ng of genomic DNA in a reaction volume of 25 µL. The PCR products were sequenced in an Applied Biosystems Sequencer Model 3730xL at the Laboratorio de Biología Molecular de la Biodiversidad y de la Salud, Instituto de Biología, UNAM.

The sequences were aligned in GUIDANCE2 (v. 2.02, Sela et al. 2015) using MAFFT (v. 7.407, Katoh and Standley 2013). The algorithm was implemented with 100 iterations (–msaProgram MAFFT –MSA_Param "\–globalpair \--maxiterate 100" –bootstraps 100). The resulting matrix was imported into PHYDE (v. 0.9971, Müller et al. 2019) to manually edit ambiguously aligned sites. Both genes were concatenated, and data partitions were determined with the program PARTITIONFINDER (v. 2, Lanfear et al. 2017) using the Bayesian information criterion and greedy search. The model with the best fit for both markers was TVM + I + G. Indels and inversion were manually coded with MESQUITE (v 3.6, Maddison and Maddison 2019) using the simple coding method of Simmons and Ochoterena (2000).

Bayesian inference (BI) analysis was performed using MRBAYES (v. 3.2.1, Ronquist et al. 2012). The analysis was run with four Markov chain Monte Carlos (MCMC) (nchains = 4) and ten million generations (ngen = 10000000), sampling trees every 100 generations (samplefreq = 100) and discarding the first 25% as burn-in. All parameters were monitored with TRACER (v. 1.7.1, Rambaut 2018) until they had effective sample sizes (ESS) of greater than 200. Maximum likelihood (ML) analysis was conducted using RAXML (v. 8.2.12, Stamatakis 2014) with molecular and binary partitioning, calculating the conditional likelihood of no invariant data and considering CAT for the heterogeneity of rate. The correction was made with the Lewis (2001) method (-m ASC_MULTICAT –asc-corr=lewis -#1000). To evaluate the monophyly of the subgenera and series recognized by Hunt et al. (2006) in the tree, the Monophy package (v. 1.3, Schwery and O'Meara 2016) of the R program (v. 4.0.3, R Core Team 2018) was used.

To estimate divergence times, we used the credibility interval around the estimated age of the Mammilloid clade (5.83–12.56 Mya; Hernández-Hernández et al. 2014). We inferred a time-calibrated phylogenetic tree using a BI approach implemented in BEAST (v. 2.6.1, Bouckaert et al. 2019). Analysis of the concatenated matrix used the uncorrelated lognormal relaxed clock (Drummond et al. 2006) for a total of 20 million generations of MCMC, sampling once every 10000 trees and discarding 15% as burn-in using TREEANNOTATOR v. 2.6.0.

Results

The overall sequence matrix for the two genes included 2257 bp and 8 encoded indels. We excluded 1045 bp in *rpl*16 due to uncertain homology. The final length of the aligned matrix for *rpl*16 was 897 bp and 315 bp for *psb*A-*trn*H, with 168 and 69 potentially informative sites, respectively. The BI and ML analyses produced trees with similar topologies (Fig. 1). *Mammillaria* ser. *Supertextae* was recovered as a monophyletic group (PP = 1, BS = 84), supported by a transversion in *psb*A-*trn*H. *Mammillaria* ser. *Polyacanthae* was also recovered as a monophyletic group (PP = 1, BS = 91), supported by 2 transitions in *psb*A-*trn*H. The sister relationship between *M.* ser. *Supertextae* and *M.* ser. *Polyacanthae* (PP = 0.99, BS = 80) is supported by a deletion in *rpl*16.

A polytomy formed within *M.* ser. *Supertextae*, where four clades were formed (S1, S2, S3, and S4), three of which are defined by specific polymorphisms (i.e., clade S1 a transversion in *rpl*16, clade S3 an inversion in *rpl*16). In three clades, at least one terminal of *M. albilanata* subsp. *oaxacana* was confirmed (S1: CC044 and CC046; S2: CC040; S3: CC036); in addition, part of its geographic distribution was common to *M. haageana* (Fig. 2A, B). The 12 terminals of *M. haageana* are distributed into two clades. S1 is formed by six terminals of *M. haageana* (CC024, CDMX, CC023, CC025, CC027, and CC045), two terminals of *M. albilanata* subsp. *oaxacana* referred

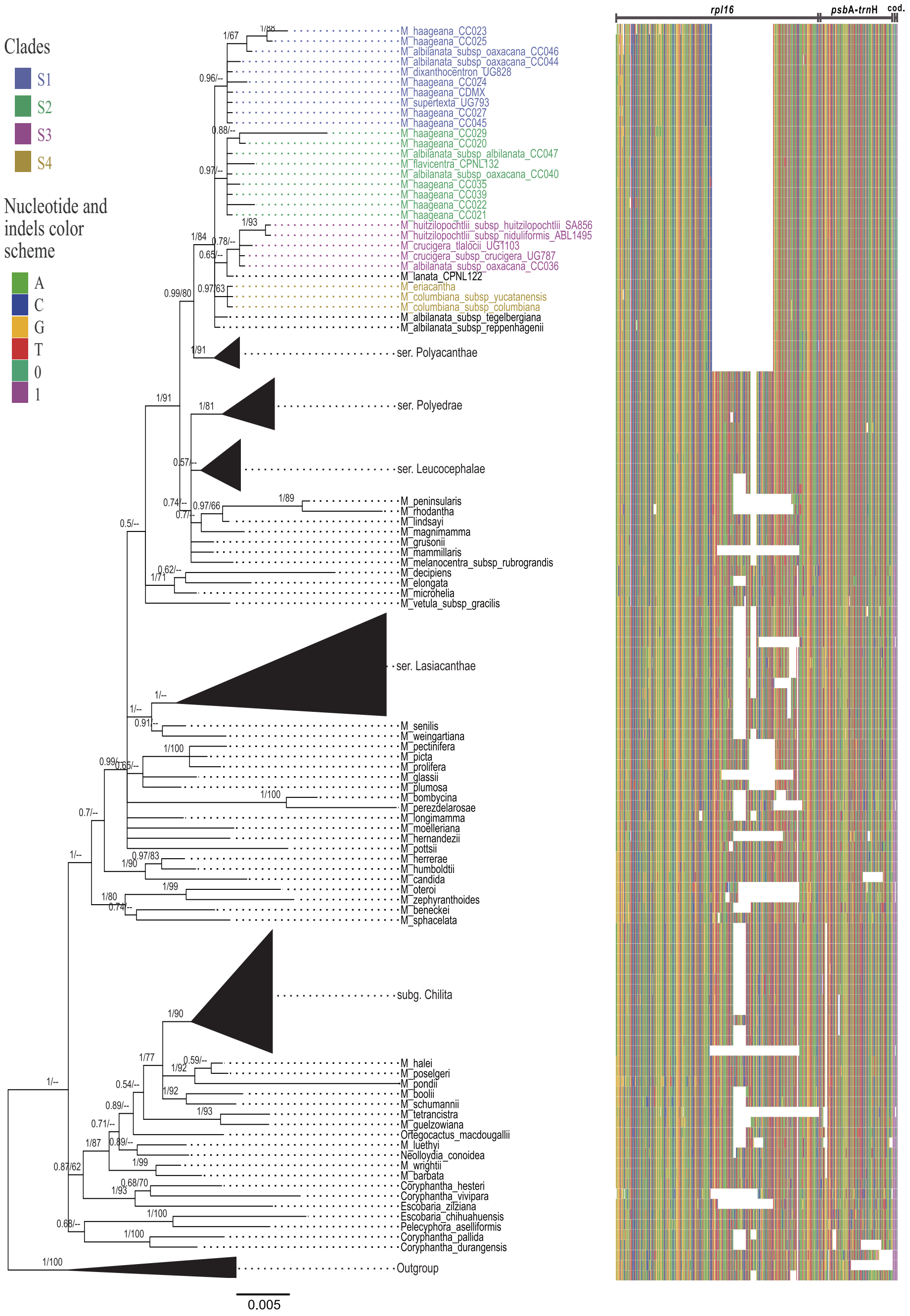


Figure 1. Phylogenetic tree of 123 taxa based on two chloroplast markers using IB. The values on the branches correspond to posterior probability (right) and ML bootstrap (left), and a dash (-) represents values of BS < 60. The left section shows a matrix with variable sites for *rpl*16 and *psb*A-*trn*H, as well as the coding of indels and inversions. Within *M.* ser. *Supertextae*, the clades are marked with colors.

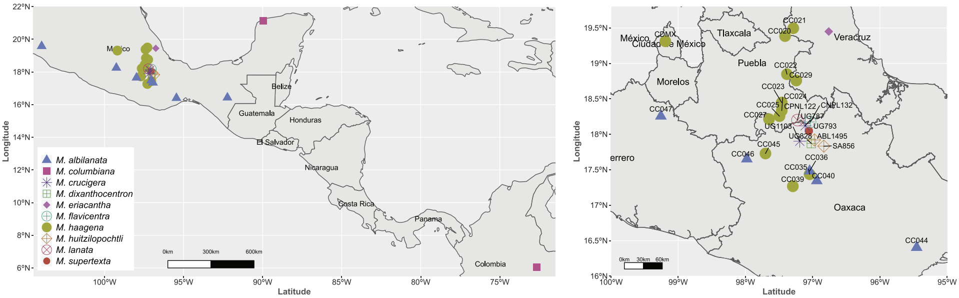


Figure 2. Left distribution of *M.* ser. *Supertextae* species sample collection localities; Right inset with southern Mexico shown in greater detail; sampling with emphasis on *M. haageana* and *M. albilanata* are shown, as well as the collection codes (Appendix 1).

to above, *M. dixanthocentron*, and *M. supertexta*, all of which display a transversion in *rpl*16. The second group consists of six terminals of *M. haageana* (CC020, CC021, CC022, CC029, CC035, and CC039), *M. flavicentra*, one terminal of M. *albilanata* subsp. *oaxacana*, and *M. albilanata* subsp. *albilanata* (CC047), all of which had a duplication of 15 bp in *rpl*16. Despite the rather small sampling of polymorphisms, these observations highlight the taxonomic problem in distinguishing *M. haageana* from *M. albilanata*, together with other sister species. The clade S3 formed by *M. huitzilopochtli* subsp. *huitzilopochtli*, *M. huitzilopochtli* subsp. *niduliformis*, *M. crucigera* subsp. *crucigera*, *M. crucigera* subsp. *tlalocii*, and one terminal of *M. albilanata* subsp. *oaxacana* (CC036) shows an inversion in *rpl*16 of 46 bp, and its sister group was *M. lanata*. Clade S4 is made up of two species, one of which corresponds to *M. columbiana*, which is distributed from Yucatan, Mexico to Colombia and Venezuela (Fig. 2A); the second species is *M. eriacantha*, which is distributed in Veracruz, Mexico (Fig. 2A, B).

The estimated crown age for *M.* ser. *Supertextae* was approximately 2.1 Mya (95% HPD = 0.91–3.47) in the Neogene-Quaternary transition (Fig. 3), whereas the *M.* ser. *Polyacanthae* crown age was estimated to be approximately 1 Mya (95% HPD = 0.15–2.22) in the mid-Pleistocene (Fig. 3). The divergence between these two groups was approximately 2.8 Mya (95% HPD = 1.46–4.73) in the late Pliocene; however, this clade has low support.

Discussion

The concatenation of two matrices (*rpl*16 and *psb*A-*trn*H) and extensive sampling (eight of nine species, according to Hunt et al. 2006; Table 1) helped to recover *M.* ser. *Supertextae* as a monophyletic group, consistent with previous molecular phylogenetic studies that included only five (Butterworth and Wallace 2004) and three taxa (Solórzano et al. 2019) of the series. The phylogenetic position of *M. eriacantha* has been

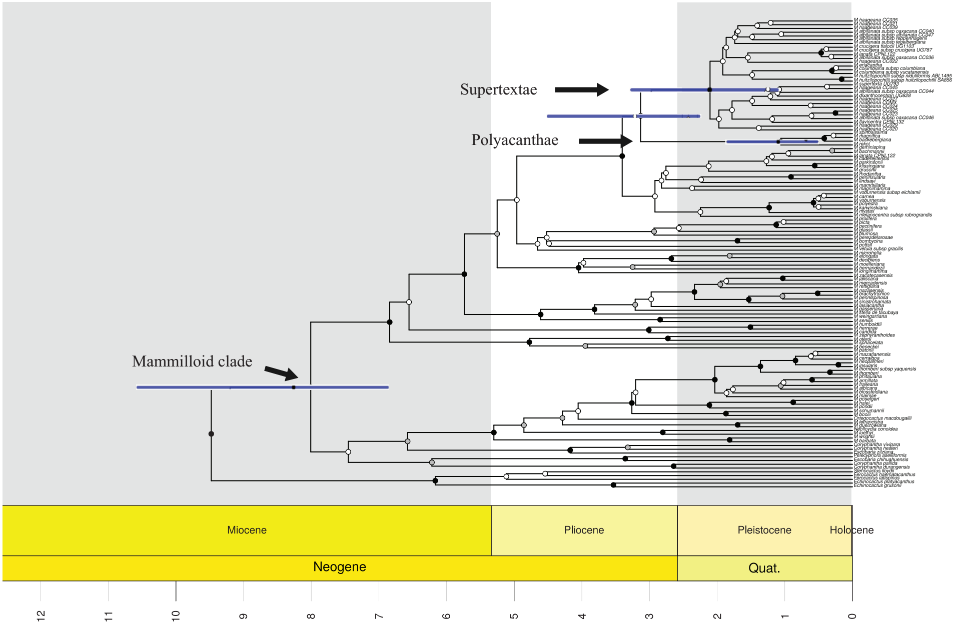


Figure 3. Divergence time estimated using BEAST based on concatenated matrix *rpl*16 and *psb*A-*trn*H. The circles on the nodes represent the PP supports: white < 0.75, gray < 0.95 and black ≥ 0.95. We show the mean divergence times (MDTs) and 95% highest posterior density (HPD) intervals (blue line) to the Mammilloid clade (MDT = 8, HPD = 5.83–11.61), *Supertextae* (MDT = 2.1, HPD = 0.91–3.47), *Polyacanthae* (MDT = 1, HPD = 0.15–2.22), and the sister group relationship (MDT = 2.8, HPD = 1.46–4.73).

uncertain, and it was placed within *M.* ser. *Polyacanthae* due to the size of its flower (Bravo-Hollis and Sánchez-Mejorada 1991; Hunt et al. 2006). Remarkably, we show that *M. eriacantha* is nested within *M.* ser. *Supertextae*, as previously proposed by Reppenhagen (1992) and Lüthy (1995) based on the presence of extracellular crystals. Our results also show that *M.* ser. *Polyacanthae* is the sister series of *M.* ser. *Supertextae* and that they are part of the *Mammillaria* sect. *Subhydrochylus* (Hunt 1987). Within *M.* ser. *Supertextae*, phylogenetic relationships were not resolved; however, both *M. haageana* and *M. albilanata* appeared in more than one clade.

Intron *rpl*16 was demonstrated to be the most variable and informative marker compared to the intergenic spacer *psb*A-*trn*H, which is consistent with previous studies in Cactaceae (Korotkova et al. 2010; Vázquez-Sánchez et al. 2013; Cruz et al. 2016). The molecular characteristics that define the monophyly of *M.* ser. *Supertextae* and *M.* ser. *Polyacanthae* were found in *psb*A-*trn*H, while a deletion in *rpl*16 supports the sister relationship. Although the deletion in *rpl*16 is partial in *M.* ser. *Supertextae* and *M.* ser. *Polyacanthae*, a total deletion has been reported in members of *M.* ser. *Stylothelae* (Butterworth et al. 2007), showing that deletions in *rpl*16 in *Mammillaria* may be a strong characteristic for the identification of infrageneric groups. It remains to be defined whether other polymorphisms, such as the inversion of another chloroplast gene, *trnF-GAA*, are also diagnostic of these clades within and between series, as recently reported for *M. crucigera*, *M. huitzilopochtli*, and *M. supertexta* (Solórzano et al. 2019).

The Mammilloid clade originated approximately 8.62 Mya (95% HPD = 5.83–12.56; Hernández-Hernández et al. 2014), and within *Mammillaria*, it is likely that *M.* ser. *Supertextae* is a recently divergent group that originated in the Neogene-Quaternary transition approximately 2.1 Mya (95% HPD = 0.91–3.47). In some geographic regions, the *M.* ser. *Supertextae* species have undergone tectonic, erosive, alluvial and volcanic changes for millions of years; during the Pleistocene, these processes continued, giving rise to the current geomorphology (Siebert and Carrasco-Núñez 2002; Medina-Sánchez et al. 2020). Paleontological and molecular evidence suggests that glacial climate cycles that occurred during the last 2.5 Mya affected the distribution, diversity, and genetic structure of plant and animal populations (Gámez et al. 2014; Scheinvar et al. 2016; Cornejo-Romero et al. 2017). The hypotheses suggest that during the Pleistocene, these species sought refuge during adverse environmental conditions and expanded again when conditions improved (Scheinvar et al. 2016). Our results show that within *M.* ser. *Supertextae*, four clades are formed, two of which have distinctive climatic and topographic characteristics: Clade S1 (*M. haageana*, *M. albialanta*, *M. dixanthocentron* and *M. supertexta*), with species that are distributed in warm zones mainly at altitudes ranging from 447 to 2318 meters in thorn and tropical deciduous forests; and Clade S2 (*M. haageana*, *M. albilanata* and *M. flavicentra*), with species that are distributed in temperate zones at altitudes that range mainly from 1285 to 2518 meters in pine-oak forests. The environmental, geological and topographic differences between closely related species produced during climatic changes suggest differential selection pressures and local adaptation, which could have driven the speciation process (Mastretta-Yanes et al. 2015; Aquino et al. 2021), as has been suggested for *Mammillaria pectinifera* (Cornejo-Romero et al. 2014), *Cephalocereus columna-trajani* (Cornejo-Romero et al. 2017) and the genus *Epithelantha* (Aquino et al. 2021). *Mammillaria haageana* and *M. albilanata* represent a complex that extends widely in southern Mexico. Our results show that the infrageneric units of *M. haageana* and *M. albilanata* can be considered independent evolutionary units. It is possible that the variation in these inhabited environments promotes divergence in these taxa, although more in-depth studies are needed to understand and corroborate the hypotheses raised here.

The chloroplast marker sequences that we used (*rpl*16 and *psb*A-*trn*H) were not sufficient to establish the relationships among the taxa within *M.* ser. *Supertextae*. This was not surprising, as chloroplast markers have been used to resolve relationships at the species level; however, they have limitations when the species are closely related (Yan et al. 2018). This is because recently diversified groups may generate complicated genetic patterns, such as incomplete lineage sorting and hybridizations and/or introgressions (Li et al. 2016; Goetze et al. 2017), which may be true for *M.* ser. *Supertextae*. In other taxa (e.g., *Petalidium* Nees, Acanthaceae; Tripp et al. 2017), these problems have been addressed using multiple-locus methods to infer genetic trees, although they require nuclear markers that are not linked with levels of sequence variation according to phylogenetic questions (Eaton and Ree 2013). To date, no effective nuclear markers have been developed for Cactaceae, and existing markers provide fewer informative sites than chloroplast markers (Cruz et al. 2016). Recently, proposals for nuclear markers have been generated through mining strategies to test hybridization in *Opuntia* species (Granados-Aguilar et al. 2020). Currently, several methodologies have been designed that allow biological questions to be answered using a reduced representation of the genome (Anderson et al. 2017; Choquet et al. 2019; David et al. 2019). This confers advantages when working with nonmodel species such as *M.* ser. *Supertextae*, since genomic markers can be genotyped in many individuals at low cost, and in most cases, it is not necessary to have a priori information such as a reference genome (da Fonseca et al. 2016).

The taxonomic proposals of *M.* ser. *Supertextae* species have been mainly based on interpretations according to the author's experience (Table 1), and their relationships have not been specifically tested under phylogenetic methods. Our methods are intended to be systematic (explicit criteria) and reproducible. Under this scheme, the results obtained show that within *M. haageana* and *M. albilanata*, there are genetic differences possibly indicating that these species comprise more than one taxonomic entity. Nevertheless, when distinguishing between *M. haageana* and *M. albilanata*, the task becomes difficult because both share similar distributions and habitats (mainly in southern Mexico; Fig. 2), and the morphological differences have not been well defined (Arias et al. 2012). A possible hypothesis is that there could still be gene flow between these taxa, and we might be witnessing an ongoing speciation process.

Conclusion

By including most of the species recognized by Hunt et al. (2006), our results show that *M.* ser. *Supertextae* is monophyletic, and we corroborate that *M. eriacantha* is part of the series as previously proposed. We find that *M.* ser. *Polyacanthae* is the sister series, as proposed by (Hunt 2011). The results also showed that *M.* ser. *Supertextae* is a recently diverged group.

This is a first approximation to understand the evolutionary processes within *M.* ser. *Supertextae*. Future work should test sequencing techniques that allow genomic markers to be genotyped in many individuals since it is possible that conflicts in the phylogeny were the result of reticulate evolution. Furthermore, disentangling this problem will require a comprehensive pool of approaches regarding morphology and ecology, opening an avenue to develop *M.* ser. *Supertextae* as a model for studying complex evolutionary processes in *Mammillaria*.

Acknowledgements

This paper is part of the first author's dissertation and is presented as a partial requirement for the Ph.D. in Biological Sciences in the Posgrado de Ciencias Biológicas (PCB), UNAM. The first author thanks CONACyT for grant No. 631251. We thank Lidia Cabrera, Andrea Jiménez-Marín, Adriana Benítez, Laura Márquez and Nelly López (Instituto de Biología, UNAM), Brenda Calderón, David Aquino and Xóchitl Granados (Jardín Botánico, UNAM), Montserrat Vázquez-Sánchez (Colegio de Posgraduados), Teresa Valverde (Facultad de Ciencias, UNAM), and Hilda Arreola (Universidad de Guadalajara). We also thank the curators of the herbaria MEXU and CICY for loaning specimens. This work was financially supported by UNAM-DGAPA-PAPIIT <IN208619> to S. A., <IN211319> to U. R., CONACyT INFR-268109.

References

Anderson EF (2001) The Cactus Family. Timber Press, Oregon, 776 pp.

Anderson BM, Thiele KR, Krauss SL, Barrett MD (2017) Genotyping-by-sequencing in a species complex of Australian hummock grasses (*Triodia*): Methodological insights and phylogenetic resolution. PLoS ONE 12(1): e0171053. https://doi.org/10.1371/journal.pone.0171053

Aquino D, Moreno-Letelier A, González-Botello MA, Arias S (2021) The importance of environmental conditions in maintaining lineage identity in *Epithelantha* (Cactaceae). Ecology and Evolution 00: 1–235. https://doi.org/10.1002/ece3.7347

Arias S, Guzmán-López L, Guzmán-Cruz U, Vázquez-Benítez B (2012) Cactaceae. In: Medina R, Sánchez G, García A, Arias S (Eds) Flora del Valle de Tehuacán-Cuicatlán. Universidad Nacional Autónoma de México 95: 1–235.

Backeberg C (1961) Die Cactaceae (Vol. 5). VEB Gustav Fischer Verlag, Jena, 911 pp.

Barrios D, González-Torres LR, Arias S, Majure LC (2020) Phylogeny and taxonomy of the Antillean endemic genus *Leptocereus* (Cactaceae) inferred from chloroplast markers and morphological evidence. Plant Systematics and Evolution 306(3): e63. https://doi.org/10.1007/s00606-020-01693-5

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, Maio ND, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, du Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu C-H, Xie D, Zhang C, Stadler T, Drummond AJ (2019) BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Computational Biology 15(4): e1006650. https://doi.org/10.1371/journal.pcbi.1006650

Bravo-Hollis H, Sánchez-Mejorada H (1991) Las Cactáceas de México (Vol. 3). Universidad Nacional Autónoma de México, 643 pp.

Breslin P, Wojciechowski MF, Majure LM (2021) Molecular phylogeny of the Mammilloid clade (Cactaceae) resolves the monophyly of *Mammillaria.* Taxon tax.12451. https://doi.org/10.1002/tax.12451

Butterworth C, Wallace RS (2004) Phylogenetic studies of *Mammillaria* (Cactaceae) insights from chloroplast sequence variation and hypothesis testing using the parametric bootstrap. American Journal of Botany 91(7): 1086–1098. https://doi.org/10.3732/ajb.91.7.1086

Butterworth C, Cota-Sánchez H, Wallace RS (2002) Molecular systematics of tribe Cacteae (Cactaceae: Cactaceae): A phylogeny based on *rpl16* intron sequence variation. Systematic Botany 27(2): 257–270.

Butterworth CA, Butterworth KM, Maurice WAF, Maurice BF (2007) A localized loss of the chloroplast *rpl16* intron in *Mammillaria* series *Stylothelae* (Cactaceae) delineates members of the *M. crinita* group. Bradleya 25(25): 187–192. https://doi.org/10.25223/brad.n25.2007.a13

Choquet M, Smolina I, Dhanasiri AKS, Blanco-Bercial L, Kopp M, Jueterbock A, Sundaram AYM, Hoarau G (2019) Towards population genomics in non-model species with large genomes: A case study of the marine zooplankton *Calanus finmarchicus.* Royal Society Open Science 6(2): e180608. https://doi.org/10.1098/rsos.180608

Cornejo-Romero A, Medina-Sánchez J, Hernández-Hernández T, Rendón-Aguilar B, Valverde PL, Zavala-Hurtado A, Rivas-Arancibia SP, Pérez-Hernández MA, López-Ortega G, Jiménez-Sierra C, Vargas-Mendoza CF (2014) Quaternary origin and genetic divergence of the endemic cactus *Mammillaria pectinifera* in a changing landscape in the Tehuacán Valley, Mexico. Genetics and Molecular Research 13(1): 73–88. https://doi.org/10.4238/2014.January.8.6

Cornejo-Romero A, Vargas-Mendoza CF, Aguilar-Martínez GF, Medina-Sánchez J, Rendón-Aguilar B, Valverde PL, Zavala-Hurtado JA, Serrato A, Rivas-Arancibia S, Pérez-Hernández MA, López-Ortega G, Jiménez-Sierra C (2017) Alternative glacial-interglacial refugia demographic hypotheses tested on *Cephalocereus columna-trajani* (Cactaceae) in the intertropical Mexican drylands. PLoS ONE 12(4): e0175905. https://doi.org/10.1371/journal.pone.0175905

Cruz MÁ, Arias S, Terrazas T (2016) Molecular phylogeny and taxonomy of the genus *Disocactus* (Cactaceae), based on the DNA sequences of six chloroplast markers. Willdenowia 46(1): 145–164. https://doi.org/10.3372/wi.46.46112

da Fonseca RR, Albrechtsen A, Themudo GE, Ramos-Madrigal J, Sibbesen JA, Maretty L, Zepeda-Mendoza ML, Campos PF, Heller R, Pereira RJ (2016) Next-generation biology: Sequencing and data analysis approaches for non-model organisms. Marine Genomics 30: 3–13. https://doi.org/10.1016/j.margen.2016.04.012

David KT, Wilson AE, Halanych KM (2019) Sequencing disparity in the genomic era. Molecular Biology and Evolution 36(8): 1624–1627. https://doi.org/10.1093/molbev/msz117

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. PLoS Biology 4(5): e88. https://doi.org/10.1371/journal.pbio.0040088

Eaton DAR, Ree RH (2013) Inferring phylogeny and introgression using RADseq data: An example from flowering plants (*Pedicularis*: Orobanchaceae). Systematic Biology 62(5): 689–706. https://doi.org/10.1093/sysbio/syt032

Fehlberg SD, Allen JM, Church K (2013) A novel method of genomic DNA extraction for Cactaceae. Applications in Plant Sciences 1(3): apps.1200013. https://doi.org/10.3732/apps.1200013

Gámez N, Escalante T, Espinosa D, Eguiarte LE, Morrone JJ (2014) Temporal dynamics of areas of endemism under climate change: A case study of Mexican *Bursera* (Burseraceae). Journal of Biogeography 41(5): 871–881. https://doi.org/10.1111/jbi.12249

Goetze M, Zanella CM, Palma-Silva C, Büttow MV, Bered F (2017) Incomplete lineage sorting and hybridization in the evolutionary history of closely related, endemic yellow-flowered

Aechmea species of subgenus *Ortgiesia* (Bromeliaceae). American Journal of Botany 104(7): 1073–1087. https://doi.org/10.3732/ajb.1700103

Granados Aguilar XC, Arias S, Granados Mendoza C, Cervantes CR, Montes JR (2020) Unraveling reticulate evolution in *Opuntia* (Cactaceae) from southern Mexico. Frontiers of Plant Science 11: e606809. https://doi.org/10.3389/fpls.2020.606809

Hernández-Hernández T, Hernández HM, De-Nova JA, Puente R, Eguiarte LE, Magallón S (2011) Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). American Journal of Botany 98(1): 44–61. https://doi.org/10.3732/ajb.1000129

Hernández-Hernández T, Brown JW, Schlumpberger BO, Eguiarte LE, Magallón S (2014) Beyond aridification: Multiple explanations for the elevated diversification of cacti in the New World succulent biome. The New Phytologist 202(4): 1382–1397. https://doi.org/10.1111/nph.12752

Hinojosa-Alvarez S, Arias S, Ferrand S, Purugganan MD, Rozas J, Rosas U, Wegier A (2020) The chloroplast genome of the pincushion cactus *Mammilllaria haageana* subsp. *san-angelensis*, a Mexican endangered species. Mitochondrial DNA. Part B, Resources 5(3): 2038–2039. https://doi.org/10.1080/23802359.2020.1757523

Hunt DR (1987) A new review of *Mammillaria* names. British Cactus and Succulent Society, Oxford, 128 pp.

Hunt DR (2011) Focus on the *Supertextae.* Huitzilopochtlia 6: 47–51.

Hunt DR, Taylor NP, Glass H (2006) The new Cactus Lexicon: Descriptions and Illustrations of the Cactus Family (Vol. 1). DH Books, Milborne Port, 375 pp.

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Korotkova N, Zabel L, Quandt D, Barthlott W (2010) A phylogenetic analysis of *Pfeiffera* and the reinstatement of *Lymanbensonia* as an independently evolved lineage of epiphytic Cactaceae within a new tribe Lymanbensonieae. Willdenowia 40(2): 151–172. https://doi.org/10.3372/wi.40.40201

Korotkova N, Borsch T, Arias S (2017) A phylogenetic framework for the Hylocereeae (Cactaceae) and implications for the circumscription of the genera. Phytotaxa 327(1): 1–46. https://doi.org/10.11646/phytotaxa.327.1.1

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34(3): 772–773. https://doi.org/10.1093/molbev/msw260

Lewis PO (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50(6): 913–925. https://doi.org/10.1080/106351501753462876

Li Q-Q, Zhou S-D, Huang D-Q, He X-J, Wei X-Q (2016) Molecular phylogeny, divergence time estimates and historical biogeography within one of the world's largest monocot genera. AoB Plants 8: plw041. https://doi.org/10.1093/aobpla/plw041

Lüthy JM (1995) Taxonomische untersuchung der gattung *Mammillaria* Haw. PhD Thesis, Universität Bern, Bern.

Maddison WP, Maddison DR (2019) Mesquite, version 3.6: A modular system for evolutionary analysis. University of Arizona, Tucson. http://www.mesquiteproject.org

Mastretta-Yanes A, Moreno-Letelier A, Piñero D, Jorgensen TH, Emerson BC (2015) Biodiversity in the Mexican highlands and the interaction of geology, geography and climate within the Trans-Mexican Volcanic Belt. Journal of Biogeography 42(9): 1586–1600. https://doi.org/10.1111/jbi.12546

Medina-Sánchez J, McLaren SJ, Ortega-Ramírez J, Valiente-Banuet A (2020) Tectono-stratigraphic basin evolution in the Tehuacán-Mixteca highlands, south western México. Heliyon 6(3): e03584. https://doi.org/10.1016/j.heliyon.2020.e03584

Müller J, Müller K, Neinhuis C, Quandt D (2019) PhyDE, version 0.9971: Phylogenetic data editor. http://www.phyde.de/download.html [Accessed on 20.03.2019]

Pilbeam J (1999) *Mammillaria*. Nuffield Press, Oxford, 376 pp.

R Core Team (2018) R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna. https://www.R-project.org/ [Accessed on 11.03.2019]

Rambaut A (2018) Tracer, version 1.7.1: MCMC trace analysis tool. University of Oxford. http://tree.bio.ed.ac.uk/software/tracer/ [Accessed on 02.05.2019]

Reppenhagen W (1992) Die gattung *Mammillaria*. Monographie (Vol. 2). Druckerei Steinhart. Titisee-Neustadt, Germany, 442 pp.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sánchez D, Arias S, Terrazas T (2014) Phylogenetic relationships in *Echinocereus* (Cactaceae, Cactoideae). Systematic Botany 39(4): 1183–1196. https://doi.org/10.1600/036364414X683831

Scheinvar E, Gámez N, Castellanos-Morales G, Aguirre-Planter E, Eguiarte LE (2016) Neogene and Pleistocene history of *Agave lechuguilla* in the Chihuahuan Desert. Journal of Biogeography 44(2): 322–334. https://doi.org/10.1111/jbi.12851

Schwery O, O'Meara BC (2016) MonoPhy: A simple R package to find and visualize monophyly issues. PeerJ. Computer Science 2: e56. https://doi.org/10.7717/peerj-cs.56

Sela I, Ashkenazy H, Katoh K, Pupko T (2015) GUIDANCE2: Accurate detection of unreliable alignment regions accounting for the uncertainty of multiple parameters. Nucleic Acids Research 43(W1): W7–W14. https://doi.org/10.1093/nar/gkv318

Siebert L, Carrasco-Núñez G (2002) Late-Pleistocene to precolumbian behind-the-arc mafic volcanism in the eastern Mexican Volcanic Belt; implications for future hazards. Journal of Volcanology and Geothermal Research 115(1): 179–205. https://doi.org/10.1016/S0377-0273(01)00316-X

Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49(2): 369–381. https://doi.org/10.1093/sysbio/49.2.369

Solórzano S, Chincoya DA, Sanchez-Flores A, Estrada K, Díaz-Velásquez CE, González-Rodríguez A, Vaca-Paniagua F, Dávila P, Arias S (2019) De novo assembly discovered novel structures in genome of plastids and revealed divergent inverted repeats in *Mammillaria* (Cactaceae, Caryophyllales). Plants 8(10): e392. https://doi.org/10.3390/plants8100392

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

Tripp EA, Tsai Y-HE, Zhuang Y, Dexter KG (2017) RADseq dataset with 90% missing data fully resolves recent radiation of *Petalidium* (Acanthaceae) in the ultra-arid deserts of Namibia. Ecology and Evolution 7(19): 7920–7936. https://doi.org/10.1002/ece3.3274

Vázquez-Sánchez M, Terrazas T, Arias S, Ochoterena H (2013) Molecular phylogeny, origin and taxonomic implications of the tribe Cacteae (Cactaceae). Systematics and Biodiversity 11(1): 103–116. https://doi.org/10.1080/14772000.2013.775191

Yan M, Xiong Y, Liu R, Deng M, Song J (2018) The application and limitation of universal chloroplast markers in discriminating east Asian evergreen oaks. Frontiers of Plant Science 9: e569. https://doi.org/10.3389/fpls.2018.00569

Appendix I

List of GenBank accession numbers and vouchers for newly published sequences for all sequences used in the analyses. Data are arranged in the following order: taxon name in bold (in alphabetical order); voucher data (country, estate, locality, collecting date, collector, collecting number, *rpl*16, *psb*A-*trn*H).

Coryphantha durangensis Britton & Rose, HM041405, AY545338; ***C. hesteri*** Y. Wright, AY545234, AY545342; ***C. pallida*** Britton & Rose, AY545232, AY545340; ***C. vivipara*** Britton & Rose, KC196809, KC196847; ***Escobaria chihuahuensis*** Britton & Rose, AY545233, AY545341; ***E. zilziana*** (Boed.) Backeb., AY545236, AY545344; ***Ferocactus haematacanthus*** (Salm-Dyck) Borg ex Backeb., HM041431, MH129870; ***F. latispinus*** Britton & Rose, HM041432, MH129871; ***Mammillaria albicans*** A. Berger, AY545238, AY545346; ***Mammillaria albilanata*** subsp. ***albilanata*** Backeb., México, Guerrero, 10 km east of Huitzuco, 31 October 2018, Cristian Cervantes, CC047, MT995687, MT995715; ***Mammillaria albilanata*** subsp. ***oaxacana*** D. R. Hunt, México, Oaxaca, Santiago Huauclilla-Santa Catarina Tlaxila road near the river, 1 October 2017, Cristian Cervantes, CC036, MT995698, MT995726; México, Oaxaca, 1.1 km from the junction of highway 135 Teotitlán de Flores Magón-San Fransisco Telixtlahuaca heading to San Sebastián Sedas, 2 October 2017, Cristian Cervantes, CC040, MT995689, MT995717; México, Oaxaca, Santa Maria Jalapa de Marquéz towards the microwave antenna, 22 June 2018, Cristian Cervantes, CC044, MT995678, MT995706; México, Oaxaca, 3.8 Km from Santo Domingo Tonalá to San Agustín Atenango, 24 June 2018, Cristian Cervantes, CC046, MT995677, MT995705; ***Mammillaria albilanata*** subsp. ***reppenhagenii*** (D. R. Hunt) D. R. Hunt, México, Jalisco, Tolimán, -, -, Hilda Arreola, s.n., MT995702, MT995730; ***Mammillaria albilanata*** subsp. ***tegelbergiana*** (H. E. Gates ex G. E. Linds.) D. R. Hunt, México, Chiapas, Comitán de Dominguez – 3.1 km from Comitán, 19 January 2007, Salvador Arias, SA1630, -, -; ***M. armillata*** K. Brandegee, AY545240, AY545349; ***M. bachmannii*** Boed., AY545241, AY545350; ***M. backebergiana*** Franc. G. Buchenau, AY545242, AY545351; ***M. barbata*** Engelm, AY545243, AY545352; ***M. beneckei*** Ehrenb., AY545244, AY545353; ***M. blossfeldiana*** Boed., AY545245, AY545354; ***M. bombycina*** Quehl & Quehl, AY545246, AY545356; ***M. boolii*** G. E. Linds., AY545247, AY545357; ***M. brachytrichion*** Lüthy, AY545248, AY545358; ***M. cadereytensis*** R. T. Craig, AY545249, AY545359; ***M. candida*** Scheidw., AY545250, AY545360; ***M. carnea*** Zucc. ex Pfeiff., HM041449, AY545363; ***M. cerralboa*** Orcutt, AY545254, AY545364; ***M. columbiana*** subsp. ***columbiana*** Salm-Dyck, Venezuela, Mérida, -, 2012, Teresa Terrazas, TT957, -, -; ***M. columbiana*** subsp. ***yucatanensis*** (Britton & Rose) D. R. Hunt, México, Yucatán, Municipio Dzemul, 2004, CICY, G. Carnevali & I. M. Ramírez, 7449, MT995701, MT995729; ***M. crucigera*** subsp. ***crucigera*** Mart., México, Oaxaca, 2 km from San Antonio Nahuahautipan, 9 August 1990, Ulises Guzmán, UG787, MT995697, MT995725; ***M. crucigera*** subsp. ***tlalocii*** (Repp.) D. R. Hunt, México, Oaxaca, 8 km from the rural road Santa María Tecomavaca-Santa María Ixcatlán, 9 November 1994, Ulises Guzmán, UG1103, MT995696, MT995724; ***M. decipiens*** Scheidw., AY545255, AY545369; ***M. dixanthocentron*** Backeb. ex Mottram, México, Oaxaca, km 107 highway 135 between Tecomavaca and Cuicatlán, 24 October 1990, Ulises Guzmán, UG828, MT995679, MT995707; ***M. elongate*** DC., AY545258, AY545373; ***M. eriacantha*** Link & Otto ex Pfeiff., México, Veracruz, km 305 of the Xalapa-Veracruz highway between Plan del Río and Cerro Gordo, 21 January 2012, Salvador Arias, SA2169, MT995700, MT995728; ***M. flavicentra*** Backeb. ex Mottram, México, Oaxaca, Teotitlan de Flores Magón 10 Km on the way to Huautla, 13 July 1995, Patricia Novoa, CPNL132, MT995688, MT995716; ***M. formosa*** Scheidw., AY545259, AY545376; ***M. fraileana*** (Britton & Rose) Boed., AY545260, AY545377; ***M. gasseriana*** Boed., AY545261, AY545378; ***M. geminispina*** DC., AY545262, AY545379; ***M. glassii*** R. A. Foster, AY545263, AY545380; ***M. grusonii*** Runge, AY545266, AY545383; ***M. guelzowiana*** Werderm., AY545267, AY545384; ***M. haageana*** Pfeiff., México, Puebla, 1 km over the gap from the junction with the Puebla-Xalapa highway, 15 May 2017, Cristian Cervantes, CC020, MT995686, MT995714; México, Veracruz, 7 km from Perote, 15 May 2017, Cristian Cervantes, CC021, MT995693, MT995721; México, Puebla, 1.5 km south of Esperanza, 16 May 2017, Cristian Cervantes, CC022, MT995692, MT995720; México, Puebla, 7 km west of Tehuacan, 16 May 2017, Cristian Cervantes, CC023, MT995675, MT995703; México, Puebla, near the Helia Bravo Botanical Garden, 16 May 2017, Cristian Cervantes, CC024, MT995680, MT995708; México, Puebla, 9.5 km from junction 125 to Huajolotitlán towards Los Reyes Metzontla, 16 May 2017, Cristian Cervantes, CC025, MT995676, MT995704; México, Oaxaca, km 59.5 Highway 125 then join the road to San Sebastián Frontera, 17 May 2017, Cristian Cervantes, CC027, MT995683, MT995711; México, Veracruz, In La Organera area near the Tecamalucan town, 29 September 2017, Cristian Cervantes, CC029, MT995685, MT995713; México, Oaxaca, 26 Km on the Huauclilla-El Parian dirt road, 1 October 2017, Cristian Cervantes, CC035, MT995690, MT995718; México, Oaxaca, 11.5 km from

Magdalena Jaltepec heading to Santiago Tilangongo, 1 Octuber 2017, Cristian Cervantes, CC039, MT995691, MT995719; México, Oaxaca, 7.5 km from Corral de Piedra to Santa Maria Tutla, 22 June 2018, Cristian Cervantes, CC045, MT995684, MT995712; México, CDMX, in the Reserva Ecológica del Pedregal de San Ángel (REPSA), 6 December 2018, -, -, MT995681, MT995709; ***M. halei*** K. Brandegee, AY545269, AY545386; ***M. hernandezii*** Glass & R. A. Foster, AY545270, AY545387; ***M. herrerae*** Werderm., AY545271, AY545388; ***M. huitzilopochtli*** subsp. ***huitzilopochtli*** D. R. Hunt, México, Oaxaca, 7 km northwest of San Juan Bautista Cuicatlán, 5 August 1990, Salvador Arias, SA856, MT995694, MT995722; ***M. huitzilopochtli*** subsp. ***niduliformis*** (A.B.Lau) Pilbeam, México, Oaxaca, Río Santo Domingo up the junction Rio Salado, 12 March 1983, A. B. Lau, ABL1495, MT995695, MT995723; ***M. humboldtii*** Ehrenb., AY545273, AY545390; ***M. insularis*** H. E. Gates ex Shurly, AY545275, AY545392; ***M. jaliscana*** Boed., AY545276, AY545393; ***M. karwinskiana*** Mart., AY545277, AY545394; ***M. klissingiana*** Boed., AY545278, AY545395; ***M. lanata*** Orcutt, México, Puebla, Rio Hondo cerca del puente Calapa autopista Tehuacán-Oaxaca, 19 November 1994, Patricia Novoa, CPNL122, MT995699, MT995727; ***M. lasiacantha*** Engelm., AY545279, AY545396; ***M. lindsayi*** R. T. Craig, AY545280, AY545398; ***M. longimamma*** DC., AY545281, AY545399; ***M. luethyi*** G. S. Hinton, AY545282, AY545400; ***M. magnifica*** Franc. G. Buchenau, AY545283, AY545401; ***M. magnimamma*** Haw., AY545284, AY545402; ***M. mainiae*** K. Brandegee, AY545285, AY545403; ***M. mammillaris*** H. Karst., AY545286, AY545404; ***M. mazatlanensis*** K. Schum., AY545287, AY545407; ***M. melanocentra*** subsp. ***rubrograndis*** (Repp. & A. B. Lau) D. R. Hunt, AY545288, AY545408; ***M. mercadensis*** Patoni, AY545289, AY545410; ***M. microhelia*** Werderm., AY545291, AY545411; ***M. moelleriana*** Boed., AY545292, AY545412; ***M. mystax*** Mart., AY545294, AY545414; ***M. nazasensis*** (Glass & R. A. Foster) Repp., AY545295, AY545416; ***M. neopalmeri*** R. T. Craig, AY545296, AY545417; ***M. oteroi*** Glass & R. A. Foster, AY545297, AY545418; ***M. parkinsonii*** Ehrenb., AY545298, AY545419; ***M. patonii*** Werderm. in Backeb., AY545299, AY545420; ***M. pectinifera*** F. A. C. Weber, AY545300, AY545421; ***M. peninsularis*** Orcutt, AY545301, AY545422; ***M. pennispinosa*** Krainz, AY545302, AY545423; ***M. perezdelarosae*** Bravo & Scheinvar, AY545303, AY545424; ***M. phitauiana*** Werderm. in Backeb., AY545305, AY545426; ***M. picta*** Meinsh., HM041452, AY545427; ***M. plumosa*** F. A. C. Weber in Bois, AY545307, AY545428; ***M. polyedra*** Mart., AY545308, AY545429; ***M. pondii*** Greene, HM041399, AY545431; ***M. poselgeri*** Hildm., HM041400, AY545432; ***M. pottsii*** Scheer ex Salm-Dyck, AY545312, AY545433; ***M. prolifera*** (Mill.) Haw., AY545313, AY545434; ***M. rekoi*** Vaupel, AY545314, AY545435; ***M. rettigiana*** Boed., AY545315, AY545436; ***M. rhodantha*** Link & Otto, AY545316, AY545437; ***M. schumannii*** Hildm., AY545317, AY545438; ***M. senilis*** Lodd. ex Salm-Dyck, AY545318, AY545440; ***M. sinistrohamata*** Boed., AY545319, AY545441; ***M. sphacelate*** Mart., AY545320, AY545442; ***M. spinosissima*** Lem., AY545321, AY545443; ***M. stella-de-tacubaya*** Heese, AY545322, AY545444; ***M. supertexta*** Mart. ex Pfeiff., México, Oaxaca, 0.5 km east of San Juan de los Cues, 9 August 1990, Ulises Guzmán, UG793, MT995682, MT995710; ***M. tetrancistra*** Engelm., KC196805, KC196840; ***M. thornberi*** subsp. ***thornberi*** Orcutt, AY545324, AY545447; ***M. thornberi*** subsp. ***yaquensis*** (R. T. Craig) D. R. Hunt, AY545325, AY545448; ***M. vetula*** subsp. ***gracilis*** (Pfeiff.) D. R. Hunt, AY545327, AY545449; ***M. voburnensis*** subsp. ***voburnensis*** Scheer, AY545328, AY545450; ***M. voburnensis*** subsp. ***eichlamii*** (Quehl) D. R. Hunt, AY545329, AY545451; ***M. weingartiana*** Boed., AY545330, AY545452; ***M. wrightii*** Engelm., AY545331, AY545454; ***M. zacatecasensis*** Shurly, AY545332, AY545455; ***M. zephyranthoides*** Scheidw., AY545333, AY545457; ***Neolloydia conoidea*** Britton & Rose, HM041462, AY545458; ***Ortegocactus macdougallii*** Alexander, HM041484, AY545459; ***Pelecyphora aselliformis*** C. Ehrenb., AY545336, AY545460; ***Stenocactus lloydii*** A. Berger, AY545337, AY545461.

PhytoKeys 177: 43–53 (2021)
doi: 10.3897/phytokeys.177.63401
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Chayamaritia vietnamensis (Gesneriaceae), a new species from Son La Province, northern Vietnam

Zi-Bing Xin[1,2,6,*], Long-Fei Fu[1,2,6,*], Stephen Maciejewski[2,3],
Zhang-Jie Huang[1,2], Truong Van Do[4,5], Fang Wen[1,2,6]

1 *Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006, Guilin, China* **2** *Gesneriad Conservation Center of China (GCCC), National Gesneriaceae Germplasm Bank of GXIB, Guilin Botanical Garden, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006 Guilin, China* **3** *The Gesneriad Society, 2030 Fitzwater Street, Philadelphia, PA, 19146-1333, USA* **4** *Vietnam National Museum of Nature, Vietnam Academy of Science & Technology, 18 Hoang Quoc Viet, Hanoi, Vietnam* **5** *Graduate University of Science and Technology, Vietnam Academy of Science & Technology, 18 Hoang Quoc Viet, Hanoi, Vietnam* **6** *Gesneriad Committee, China Wild Plant Conservation Association, CN-541006, Guilin, China*

Corresponding authors: Fang Wen (wenfang760608@139.com); Truong Van Do (dovantruong_bttn@yahoo.com)

Academic editor: M. Moeller | Received 20 January 2021 | Accepted 20 April 2021 | Published 12 May 2021

Citation: Xin Z-B, Fu L-F, Maciejewski S, Huang Z-J, Do TV, Wen F (2021) *Chayamaritia vietnamensis* (Gesneriaceae), a new species from Son La Province, northern Vietnam. PhytoKeys 177: 43–53. https://doi.org/10.3897/phytokeys.177.63401

Abstract

Chayamaritia vietnamensis, a new species from Son La Province, northern Vietnam, is described and illustrated. The phylogenetic study revealed that the new species is most closely related to *C. banksiae* and *C. smitinandii*. The morphological comparison suggests it as the third new species of *Chayamaritia* and distinguished from *C. banksiae* and *C. smitinandii* by a combination of morphological characters of leaf blades, bracts, calyx and corolla, especially its peltate leaf blades. This species is provisionally assessed as endangered (EN B1ab(iii), B2ab(iii)) using IUCN Categories and Criteria. Information on ecology, phenology and an identification key for the known *Chayamaritia* species are also provided.

Keywords

Cliff-dwelling, Flora of Vietnam, new taxon, taxonomy

---

[*] These authors contributed equally to this work as co-first authors.

Introduction

The genus *Chayamaritia* D.J.Middleton & Mich.Möller (Gesneriaceae) was originally established and described, based on molecular and morphological data (Middleton et al. 2015). The genus *Chayamaritia* comprises two species and is hitherto known only in Laos and Thailand. A thickened rhizomatous prostrate stem, along with alternately arranged leaves and the imbricate sepals characterise the genus (Middleton et al. 2015). The type species, *Chayamaritia smitinandii* (B.L.Burtt) D.J.Middleton, was initially placed in the genus *Chirita* Buch.-Ham. (Burtt, 2001), then transferred to the genus *Henckelia* Spreng. (Weber et al. 2011) and eventually separated as a new genus in 2015, together with the newly-described species, *Chayamaritia banksiae* D.J.Middleton (Middleton et al. 2015). *Chayamaritia banksiae* and *C. smitinandii* are endemic to Laos and Thailand, respectively (Middleton et al. 2015).

During a joint Sino-Vietnamese botanical survey for plant biodiversity in northern Vietnam in late October 2019, we collected an unknown Gesneriaceae plant. In the Xuan Nha Nature Reserve, Moc Chau District, Son La Province, northern Vietnam, we discovered this plant that looked like a *Chayamaritia* species. Detailed comparison of these specimens with the type specimens and protologues of known *Chayamaritia* species showed that these specimens neither fitted the existing protologues nor conformed to the type specimens of these species. Although, the leaf indumentum and inflorescence of the unknown plant was most similar to those of *C. banksiae* and *C. smitinandii*, it could be easily distinguished from the latter two by the combination of several morphological characters of the leaf blades, bracts, calyx and corolla, especially its peltate leaf blade. Thus, we confirmed that it represented a new species of *Chayamaritia*, which is the first *Chayamaritia* species from Vietnam. The description, illustration, information on ecology, phenology and provisional conservation assessment using IUCN (2019) of the proposed new species are provided. Furthermore, an identification key to the known *Chayamaritia* species is given.

Material and methods

Plant material

Herbarium materials were studied from the following herbaria: E, IBK, US and VNMN (herbarium acronyms according to Index Herbariorum; Thiers 2019). The macromorphological features were observed, based on the specimen sheets and notes in both the field and the conservation nursery at the Gesneriad Conservation Center of China and the National Gesneriaceae Germplasm Bank at GXIB. Micromorphological features were analysed and photographed using an optical microscope (Stemi DV4, LEICA S8 AP0, Jena, Germany).

These morphological characters of newly-proposed species were compared with those of the two known *Chayamaritia* species from protologues, type specimens and living plants. The description of the new species followed the terminology used by Harris and Harris (2001) and Wang et al. (1998). Assessment of the conservation status of the new species was according to Categories and Criteria of the IUCN (2019).

DNA extraction, PCR amplification and sequencing

Leaves were dried using silica gel for DNA extraction (Chase and Hills 1991). Genomic DNA was extracted using the CTAB protocol (Doyle and Doyle 1987). To confirm the placement of this new species, we performed phylogenetic studies of DNA sequence data obtained from the nuclear ribosomal internal transcribed spacer (ITS) region and the plastid *trnL-F* intron spacer (*trnL-F*). Given the phylogenetic studies of Middleton et al. (2015), we sampled two species (three accessions) from *Chayamaritia* and the new species as ingroup and ten species from all closely related and morphologically similar genera, including *Allostigma* (one species), *Deinostigma* (two species), *Loxostigma* (two species), *Petrocosmea* (two species), *Pseudochirita* (two varieties) and *Primulina* (two species) as outgroup (Middleton et al. 2015). DNA extraction, PCR amplification and sequencing were performed following Wei et al. (2013). The species name, voucher specimens and GenBank accession numbers of DNA sequences used in this study are listed in Table 1.

Phylogenetic analysis

The sequence data were edited and assembled using Lasergene Navigator 7.1 (DNAstar, Madison, Wisconsin, USA). Two datasets (ITS and *trnL-F*) were aligned independently using MAFFT version 7.0 (Katoh and Standley 2013) with default settings. The two best-supported tree topologies from Maximum Likelihood (ML) analyses of ITS and *trnL-F* were compared visually for topological incongruences. As there were no hard incongruences (Nishii et al. 2015), phylogenies were reconstructed, based on the combined dataset using ML and Bayesian Inference (BI). BI was performed using MRBAYES v.3.2.7 (Ronquist et al. 2012). Best-fitting models for the BI analysis were obtained independently for each gene region using MODELTEST v.3.7 (Posada and Buckley 2004). GTR+G and GTR+I were the best-fitting models for ITS and *trnL-F*, respectively. One cold and three incrementally heated Markov Chain Monte Carlo (MCMC) chains were run for five million generations and trees were sampled every 1,000 generations (5,000 trees sampled in total). The first 1250 trees (25%) were discarded as burn-in prior to calculating the BI consensus trees and posterior probabilities (PP) (See Suppl. material 1: log file). The ML analyses were performed in RAxML using raxmlGUI (Silvestro and Michalak 2012), with GTRGAMMA setting and 1,000 bootstrap replicates.

Results

The combined ITS and *trnL-F* matrix was 1,477 characters long (700 for ITS and 777 for *trnL-F*). Of the 378 variable characters, 155 (56.97%) were parsimony-informative. ML and BI analyses resulted in the same tree topology indicating the undescribed species as sister to the two known *Chayamaritia* species (BS = 97%, PP = 1), i.e. *C. banksiae* and *C. smitinandii* (Fig. 1).

Table 1. Species names, voucher specimens, and GenBank accession numbers of DNA sequences used in this study.

Species name	Voucher number	Herbarium	Origin	ITS	*trnL-F*
Allostigma guangxiense W.T.Wang	M. Möller and Y.G. Wei MMO 05-755	E, IBK	China, Guangxi, Longzhou county	HQ632977	HQ632880
Deinostigma cicatricosa (W.T.Wang) D.J.Middleton & Mich.Möller	W. B. Xu s.n. [XWB]	IBK	China, unknown locality	JX506925	JX506817
Deinostigma cyrtocarpa (D.Fang & L.Zeng) Mich.Möller & H.J.Atkins	M. Möller and Y.G. Wei MMO 06-908	E, IBK	China, Guangxi, He Zhou city	KU990889	KU990885
Pseudochirita guangxiensis (S.Z.Huang) W.T.Wang	M. Möller and Y.G. Wei MMO 06-798	E, IBK	China, Guangxi, Mashan county	HQ633003	HQ632908
Pseudochirita guangxiensis (S.Z.Huang) W.T.Wang var. *glauca* Y.G.Wei & Yan Liu	M. Möller and Y.G. Wei MMO 05-751	E, IBK	China, Guangxi, Jingxi county	HQ633004	HQ632909
Loxostigma glabrifolium D.Fang & K.Y.Pan	Y.G. Wei 709	IBK	China, Guangxi, Napo county	HQ633006	HQ632910
Loxostigma griffithii (Wight) C.B.Clarke	Kew/Edinburgh Kanchenjunga Expedition (1989) 940 [Cult. RBGE 19892473A]	E	Nepal, Yamphudin	FJ501338	FJ501508
Chayamaritia banksiae D.J.Middleton	D.J. Middleton 5220 and M. Newman et al. LAO1428	E	Laos, Khammouan, Nakai Nam Theun	KP325426	KP325433
Chayamaritia smitinandii (B.L.Burtt) D.J.Middleton & Mich.Möller	D.J. Middleton et al. 5632	E	Thailand, Nakhon Nayok, Khao Yai NP	KP325424	KP325431
Chayamaritia smitinandii (B.L.Burtt) D.J.Middleton & Mich.Möller	D.J. Middleton et al. 5652	E	Thailand, Nakhon Nayok, Khao Yai NP	KP325425	KP325432
Chayamaritia vietnamensis F.Wen, T.V.Do, Z.B.Xin & S.Maciej	F. Wen, T.V. Do, Z.B. Xin & S. Maciejewski, VMN-CN1214	IBK, VNMN	Vietnam, Son La, Moc Chau	MW458944*	MW458945*
Petrocosmea kerrii Craib	Voucher from Cult. RBGE 19715592	E	unknown origin	FJ501334	FJ501502
Petrocosmea nervosa Craib	Smithsonian Institute 78-057 [Cult. RBGE 19933232]	E, US	China, N Yunnan	FJ501335	AJ492299
Primulina tabacum Hance	Q.J. Xie and C.X. Ye s.n. [Cult. RBGE 19951540]	E	E China, Guangdong, Lian Rive	FJ501352	AJ492300
Primulina gemella (D.Wood) Yin Z.Wang	L. Averyanov 1987 [Cult. RBGE 19941913]	E	Vietnam, Hong Quang Special Region, Cat Hai	FJ501345	FJ501523

Note: newly generated sequences indicated by an asterisk (*).

Taxonomic treatment

Chayamaritia vietnamensis **F.Wen, T.V.Do, Z.B.Xin & S.Maciej, sp. nov.**

urn:lsid:ipni.org:names:77217099-1

Figs 2, 3C

Diagnosis. The new species can be easily distinguished from the known *Chayamaritia* species by its peltate leaf blades. Besides, it differs from *C. banksiae* by its leaf blades apex rounded and margin entire (vs. apex shortly acuminate and margin minutely dentate); bracts 3, apex rounded and margin entire (vs. 2, apex acuminate and margin

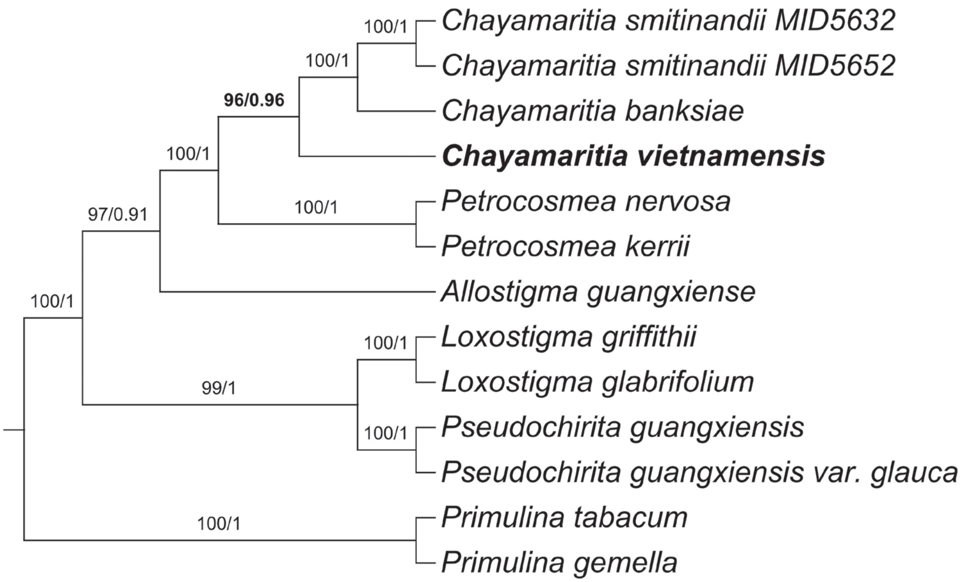


Figure 1. Phylogenetic tree of *Chayamaritia* and related genera generated from the Maximum Likelihood analysis (ML) of the combined dataset (ITS and *trnL-F*). Numbers on the branches indicate bootstrap values (≥ 50%) of the ML and the posterior probability (≥ 0.5) of the BI analyses. Created by Long-Fei Fu.

dentate); calyx lobes inside glabrous and margin entire (vs. inside with white appressed hairs in upper half, margin coarsely dentate); corolla lobes margin entire (vs. margin being minutely dentate); lateral staminodes 2.5–4 mm long (vs. 5.5–11 mm long). It also differs from *C. smitinandii* by its leaf blades apex rounded and margin entire (vs. apex acuminate and margin minutely dentate); bracts 3, ovate narrow and apex rounded (vs. 2, narrowly elliptic to lanceolate, somewhat falcate, apex acuminate); calyx lobes inside glabrous and margin entire (vs. inside densely pubescent, margin slightly toothed or appearing as large sessile glands on margin).

Type. VIETNAM. Son La Province: Moc Chau District, Xuan Nha Nature Reserve, 20°43'N, 104°40'E, elev. ca. 850 m, 31 October 2019, *F. Wen*, *T.V. Do*, *Z.B. Xin* & *S. Maciejewski*, *VMN-CN1214* (Holotype: VNMN!; Isotypes: IBK!, VNMN!).

Description. Herbs perennial, rhizomatous prostrate thickened stem. *Leaves* basal, alternately arranged, numerous; *petioles* cylindrical, 10–25 cm long, 6–8 mm in diameter, densely covered with short white appressed hairs; *leaf blade* ovate to elliptic, peltate, 12–20 × 10–15 cm, 1.2–1.3 times as long as wide, both surfaces densely covered with short white appressed hairs, base rounded, apex rounded, margin entire; lateral veins 6–9 on each side of the mid-rib, impressed on the adaxial surface, prominent on the abaxial surface. *Inflorescences* cymose, all axes and bracts pale green with red appressed hairs; cymes 4–6, axillary, 1–3-branched, 2–12-flowered; *peduncle* 15–25 cm long, 4–6 mm in diameter, scattered villous; *bracts* 3, narrow ovate, 1.3–1.6 cm long, 5–6 mm wide, adaxially sparsely villous, abaxially densely villous, margin entire, apex rounded;

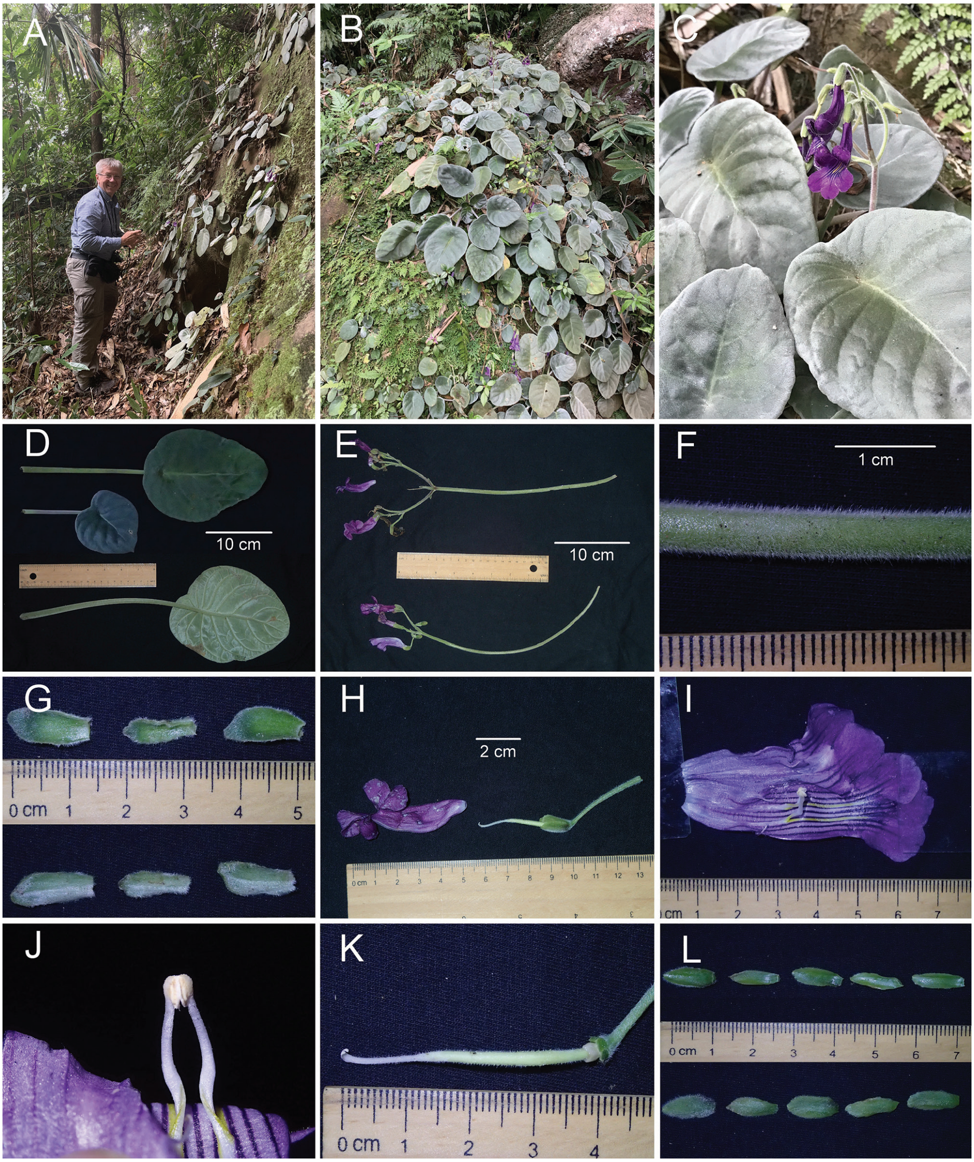


Figure 2. *Chayamaritia vietnamensis* F.Wen, T.V.Do, Z.B.Xin & S.Maciej **A, B** habitat **C** habit **D** adaxial (top) and abaxial (bottom) surface of leaf blade **E** cymes **F** peduncle **G** adaxial (top) and abaxial (bottom) surface of bracts **H** pistil, calyx and lateral view of corolla **I** opened corolla with stamens and staminodes **J** stamens with cohering anthers **K** pistil **L** adaxial (top) and abaxial (bottom) surface of calyx lobes. Photos by Fang Wen, arranged by Zi-Bing Xin.

pedicel 2.5–3.5 cm long, 1.5–2 mm in diameter, spreading puberulent. *Calyx* 5-parted nearly to the base, strongly imbricate; *lobes* ovate, ca. 1.3 cm long, ca. 6 mm wide, appressed villous outside, glabrous inside, margin entire, apex acuminate. *Corolla* 5.5–6.5 cm long, dark purple throughout outside, white to pale purple with two parallel

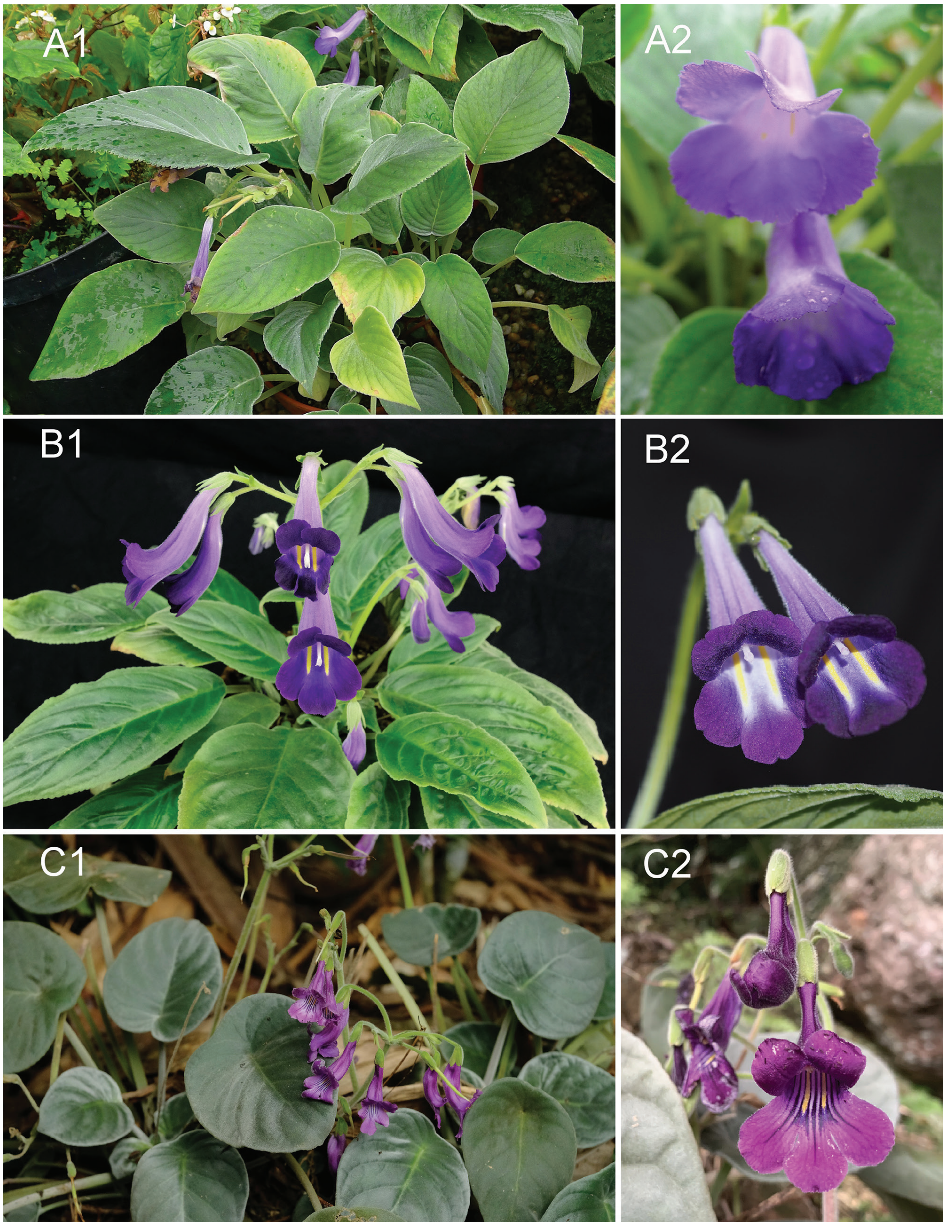


Figure 3. Three species of *Chayamaritia* **A** *C. banksiae* D.J.Middleton **B** *C. smitinandii* (B.L.Burtt) D.J.Middleton **C** *C. vietnamensis* F.Wen, T.V.Do, Z.B.Xin & S.Maciej. Photos by Fang Wen, arranged by Zi-Bing Xin.

yellow lines ventrally inside, lobes purple outside and inside, paler at base; *tube* 3.5–4 cm long, 1–1.2 cm in diameter at the mouth, 6–8 mm in diameter at the base; *limb* distinctly 2-lipped, *adaxial lip* 2-parted to over middle, lobes ca. 1 × 1 cm, orbicular; *abaxial lip* 3-parted to near the middle, lobes 1.3–1.5 × ca. 1 cm, oblong. *Stamens* 2, adnate to ca. 2.2 cm above the base of the corolla tube; *filaments* 1–1.2 cm long, white, sparsely pubescent, strongly geniculate at ca. 5 mm above the filament base, *anthers* ca. 2 mm long, sparsely pubescent. *Staminodes* 3, lateral ones 2.5–4 mm long, white, glabrous, adnate to 1.8 cm above the base of the corolla tube, the middle one ca. 0.5–1 mm long, adnate to 1.2 cm above the base of the corolla tube. *Disc* orbicular, ca. 3 mm in height, 5-crenate at the margin, glabrous. *Pistil* 4–4.5 cm long, *ovary* 2.5–2.8 cm long, 2–2.5 mm in diameter, mixed pubescent and glandular-pubescent; *style* 1–1.2 mm long, ca. 0.6 mm in diameter, mixed pubescent and glandular-pubescent; *stigma* only of lower lobe, bifid with blunt lobes, lobe ca. 3 mm long, ca. 0.5 mm in diameter. *Capsules* straight, 5.5–6.5 cm long, ca. 3.5–4 mm in diameter.

Phenology. Flowering occurs from October to December and fruiting from November to January.

Etymology. The specific epithet "*vietnamensis*" is derived from Vietnam, which holds the first discovered and only known location for the species.

Distribution and habitat. *Chayamaritia vietnamensis* is hitherto only known from the type locality, Xuan Nha Nature Reserve, Moc Chau District, Son La Province, northern Vietnam. It grows on rock surfaces surrounded by limestone areas in a subtropical evergreen seasonal rain forest.

Conservation status. *Chayamaritia vietnamensis* is known from two small-sized populations in the Xuan Nha Nature Reserve's buffer zone. The EOO and AOO of the new species are about 6.15 km^2 and 2.2 km^2, respectively. Furthermore, the natural habitat is mostly disturbed by local farmers who impose intense pressure on the remaining primary forest patches, by converting the natural habitat of the species into cornfields. Thus, following the IUCN Red List Categories and Criteria (IUCN 2019), it is provisionally assessed as endangered (EN B1ab(iii), B2ab(iii))

Identification key for the three known *Chayamaritia* species (Fig. 3)

1 Leaf blade peltate, apex rounded, margin entire .... ***C. vietnamensis***
– Leaf blade not peltate, apex acuminate, margin minutely dentate............... **2**
2 Calyx lobes 7–15 mm wide, corolla tube white ventrally........... ***C. banksiae***
– Calyx lobes 0.9–4.2 mm wide, corolla tube purple ventrally .... ***C. smitinandii***

Discussion

From the viewpoint of morphology, the newly-described species should be treated as a species of *Chayamaritia*, because it exhibits a suite of morphological characters that are diagnostic to the genus and should not be established as a distinct genus. It has a thickened rhizomatous prostrate stem, alternately arranged leaves and imbricate sepals (Middleton et al. 2015). The current molecular work also confirmed that the new species is sister to a clade comprising the two known *Chayamaritia* species (*C. banksiae* and *C. smitinandii*). A detailed morphological comparison of the new species with its

Table 2. Morphological comparison of *Chayamaritia vietnamensis* and its two relatives.

Characters	*C. vietnamensis*	*C. banksiae*	*C. smitinandii*
Leaf blade	peltate, 1.2–1.3 times as long as wide, apex rounded, margin entire	palaceous, 1.5–1.9 times as long as wide, apex shortly acuminate, margin minutely dentate	palaceous, 1.8–5.6 times as long as wide, apex acuminate, margin minutely dentate
Bracts	3, narrow ovate, 5–6 mm wide, apex rounded, margin entire	2, ovate, 19 mm wide, apex acuminate, margin dentate	2, narrowly elliptic to lanceolate, somewhat falcate, 1.8–8 mm wide, apex acuminate, margin entire
Pedicels	25–35 mm long	12–15 mm long	6.5–11 mm long
Calyx lobes	4–6 mm wide, inside glabrous, margin entire	7–15 mm wide, inside with white appressed hairs in the upper half, margin coarsely dentate	0.9–4.2 mm wide, inside densely pubescent, margin slightly toothed or appearing as large sessile glands on margin
Corolla	outside dark purple throughout, lobes margin entire	outside white ventrally, lobes being minutely dentate along the margin	outside deep purple throughout, lobes margin entire
Lateral staminodes	2.5–4 mm long	5.5–11 mm long	4–5 mm long
Disc	ca. 3 mm high	ca. 1.5 mm high	0.9–1.4 mm high

two relatives is summarised in Table 2. This new species is the first *Chayamaritia* species reported from Vietnam. In order to facilitate identification, we also provide an identification key to all known *Chayamaritia* species.

Conclusion

In the present study, we discovered and described a new species of *Chayamaritia* from Vietnam, based on both morphological and molecular evidence. This newly-described species further suggests floristic similarities amongst countries of the Indochinese Peninsula. Our new finding provides an essential addition to the ongoing project of 'Flora of Vietnam' and 'Flora of Cambodia, Laos and Vietnam'.

Acknowledgements

We want to thank the staff from Xuan Nha Nature Reserve for guiding our investigation and collecting the specimens. We also want to thank Michael LoFurno, Adjunct Professor, Temple University, Philadelphia, USA, for his editorial assistance. This study was financially supported by the Vietnam National Foundation for Science and Technology Development (NAFOSTED) (106.03-2019.308), the Foundation of Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain (19-050-6; 19-185-7), the National Natural Science Foundation (31860047), Guilin Science and Technology Foundation (20180107-6), the Key Science and Technology Research and Development Project of Guangxi (Guike AD20159091), Guangxi Natural Science Foundation (2020GXNSFBA297049), Basal Research Fund of GXIB (Guizhiye20009) and the 21st Talent project of "Ten-Hundred-Thousand" in Guangxi.

References

Burtt BL (2001) Thailand-annotated checklist of Gesneriaceae. Thai Forest Bulletin (Botany) 29: 81–109.

Chase MW, Hills H (1991) Silica gel: An ideal material for field preservation of leaf samples for DNA studies. Taxon 40(2): 215–220. https://doi.org/10.2307/1222975

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15.

Harris JG, Harris MW (2001) Plant Identification Terminology: An Illustrated Glossary (2nd ed.). Spring Lake Publishing, Payson, 216 pp.

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Middleton DJ, Nishii K, Puglisi C, Forrest LL, Möller M (2015) *Chayamaritia* (Gesneriaceae: Didymocarpoideae), a new genus from southeast Asia. Plant Systematics and Evolution 301(7): 1947–1966. https://doi.org/10.1007/s00606-015-1213-2

Nishii K, Hughes M, Briggs M, Haston E, Christie F, DeVilliers JM, Hanekom T, Roos GW, Bellstedt UD, Möller M (2015) *Streptocarpus* redefined to include all Afro-Malagasy Gesneriaceae: Molecular phylogenies prove congruent with geography and cytology and uncovers remarkable morphological homoplasies. Taxon 64: 1243–1274. https://doi.org/10.12705/646.8

Posada D, Buckley T (2004) Model selection and model averaging in phylogenetics: Advantages of Akaike Information Criterion and Bayesian approaches over likelihood ratio tests. Systematic Biology 53(5): 793–808. https://doi.org/10.1080/10635150490522304

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Silvestro D, Michalak I (2012) raxmlGUI: A graphical front-end for RAxML. Organisms, Diversity & Evolution 12(4): 335–337. https://doi.org/10.1007/s13127-011-0056-0

Thiers B (2019) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih [Accessed 10 August 2020]

Wang WT, Pan KY, Li ZY, Weitzman AL, Skog LE (1998) Gesneriaceae. In: Wu ZY, Raven PH (Eds) Flora of China (Vol. 18). Science Press, Beijing & Missouri Bot Garden, St. Louis.

Weber A, Middleton DJ, Forrest A, Kiew R, Lim CL, Rafidah AR, Sontag S, Triboun P, Wei YG, Yao TL, Möller M (2011) Molecular systematics and remodelling of *Chirita* and associated genera (Gesneriaceae). Taxon 60(3): 767–790. https://doi.org/10.1002/tax.603012

Wei YG, Wen F, Zhao B, He SZ (2013) *Anna rubidiflora* (Gesneriaceae), a new species from Guizhou, the southern part of China. Plant Ecology and Evolution 146(2): 203–211. https://doi.org/10.5091/plecevo.2013.731

Supplementary material 1

Log file

Authors: Zi-Bing Xin, Long-Fei Fu, Stephen Maciejewski, Zhang-Jie Huang, Truong Van Do, Fang Wen

Data type: phylogenetic

Link: https://doi.org/10.3897/phytokeys.177.63401.suppl1

PhytoKeys 177: 55–61 (2021)
doi: 10.3897/phytokeys.177.63878
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Primulina papillosa (Gesneriaceae), a new species from limestone areas of Guangxi, China

Zi-Bing Xin[1,2,3,4*], Wei-Chuen Chou[4*], Stephen Maciejewski[3,4,5],
Long-Fei Fu[1,2,3,4], Fang Wen[1,2,3,4]

1 *Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006, Guilin, China* **2** *National Gesneriaceae Germplasm Resources Bank, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006, Guilin, China* **3** *Gesneriad Committee, China Wild Plant Conservation Association, CN-541006, Guilin, China* **4** *Gesneriad Conservation Center of China (GCCC), Guilin Botanical Garden, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, CN-541006, Guilin, China* **5** *The Gesneriad Society, 2030 Fitzwater Street, Philadelphia, PA. 19146-1333, USA*

Corresponding author: Fang Wen (wenfang760608@139.com)

Academic editor: E. Fischer | Received 3 February 2021 | Accepted 27 April 2021 | Published 12 May 2021

Citation: Xin Z-B, Chou W-C, Maciejewski S, Fu L-F, Wen F (2021) *Primulina papillosa* (Gesneriaceae), a new species from limestone areas of Guangxi, China. PhytoKeys 177: 55–61. https://doi.org/10.3897/phytokeys.177.63878

Abstract

Primulina papillosa Z.B. Xin, W.C. Chou & F. Wen, a new species from limestone areas of Guangxi, China, is described and illustrated here. It morphologically resembles *P. linearifolia* (W.T. Wang) Yin Z. Wang and *P. pseudolinearifolia* W.B. Xu & K.F. Chung, but can be easily distinguished by some combined characters, especially its leaf blades densely papillose-hispid. We found only one population at the type locality with no more than 200 individuals, so that this new species is provisionally assessed as Critically Endangered (CR) using IUCN Criteria.

Keywords

Cliff-dwelling, flora of Guangxi, limestone flora, new taxon, taxonomy

---

[*] These authors contributed equally to this work as co-first authors.

Introduction

By the end of 2020, the genus *Primulina* Hance (1883) of the family Gesneriaceae comprised 201 species and 27 varieties (IPNI 2021; Tropicos 2021). It is mainly distributed throughout southern, south-western China and northern Vietnam (Wang et al. 2011; Weber et al. 2011). China is the centre of diversity for *Primulina* with at least 183 species and 27 varieties occurring there at present, especially in limestone areas (e.g. Wei 2018; Wen et al. 2019, 2021; Ge et al. 2020; Liu et al. 2020; Xin et al. 2020a, b, c). The tropical and subtropical karst limestone mountainous areas of Guangxi are the centres of species diversity and differentiation of this genus (Li et al. 2019). An acceleration of *Primulina* species discovery has been seen over the last five years, with an average of over ten new species per year (Wen et al. 2019, 2021). Assuming this trend persists, more new *Primulina* species from China will most likely be discovered (Möller 2019).

A Gesneriaceae enthusiast from Guangxi found this unknown plant species in the wild on 6 April 2020. One of authors, W.C. Chou, went to the type locality and collected the specimens for it. At the same time, some living plants were introduced and cultivated in the gardens of the Gesneriad Conservation Center of China (GCCC) and National Gesneriaceae Germplasm Resources Bank for further study. Detailed comparisons of the specimens and living plant materials with the type specimens and protologues of some related known *Primulina* species revealed that these specimens neither fit the existing protologues nor conform to the type specimens of these species. Nevertheless, its leaf shape and rhizome are most similar to those of *P. linearifolia* (W.T. Wang) Yin Z. Wang (Wang and Pan 1982; Wang et al. 2011) and *P. pseudolinearifolia* W.B. Xu & K.F. Chung (Xu et al. 2011, 2012) and it can be easily distinguished from the latter two by the combination of several morphological characters (Table 1), especially its leaf blades densely papillose-hispid. Thus, we confirmed that it represents a new species of *Primulina* and describe it here.

Taxonomic treatment

Primulina papillosa Z.B. Xin, W.C. Chou & F. Wen, sp. nov.

urn:lsid:ipni.org:names:77217100-1
Figs 1, 2E–F

Diagnosis. The new species resembles *Primulina linearifolia* (Fig. 2A, B) and *P. pseudolinearifolia* (Fig. 2C, D), but can be easily distinguished from the latter two by both surfaces of its leaf blades being densely papillose-hispid. It differs from *P. linearifolia* by its 1–2-flowered per cyme (vs. 4–7-flowered); pedicel 20–35 mm long (vs. 5–12 mm); calyx lobes 7.5–9 mm long (vs. 3.2–4 mm); disc ca. 1.2 mm high, margin entire (vs. ca. 0.5 mm, margin repand); capsule 5–6.5 cm long (vs. 2.2–3.6 cm). It also differs from *P. pseudolinearifolia* by its 1–2-flowered per cyme (vs. 4–12-flowered); pedicel

Table 1. Detailed comparison of *Primulina papillosa* and its two relatives.

Characters	*P. papillosa*	*P. linearifolia*	*P. pseudolinearifolia*
Leaf blades	densely papillose-hispid	densely appressed pubescent	densely appressed pubescent
Cymes	1–2-flowered	4–7-flowered	4–12-flowered
Pedicel	20–35 mm long	5–12 mm long	7–15 mm long
Calyx lobes	7.5–9 × ca. 2 mm	3.2–4 × 0.6–1.1 mm,	5–6 × ca. 1 mm
Central staminodes	ca. 0.5 mm long	none	ca. 3 mm long
Disc	ca. 1.2 mm high, margin entire	ca. 0.5 mm high, margin repand	ca. 2.5 mm high, margin repand
Flowering time	September to November	April	April to May
Capsule	5–6.5 cm long	2.2–3.6 cm long	3–4.5 cm long

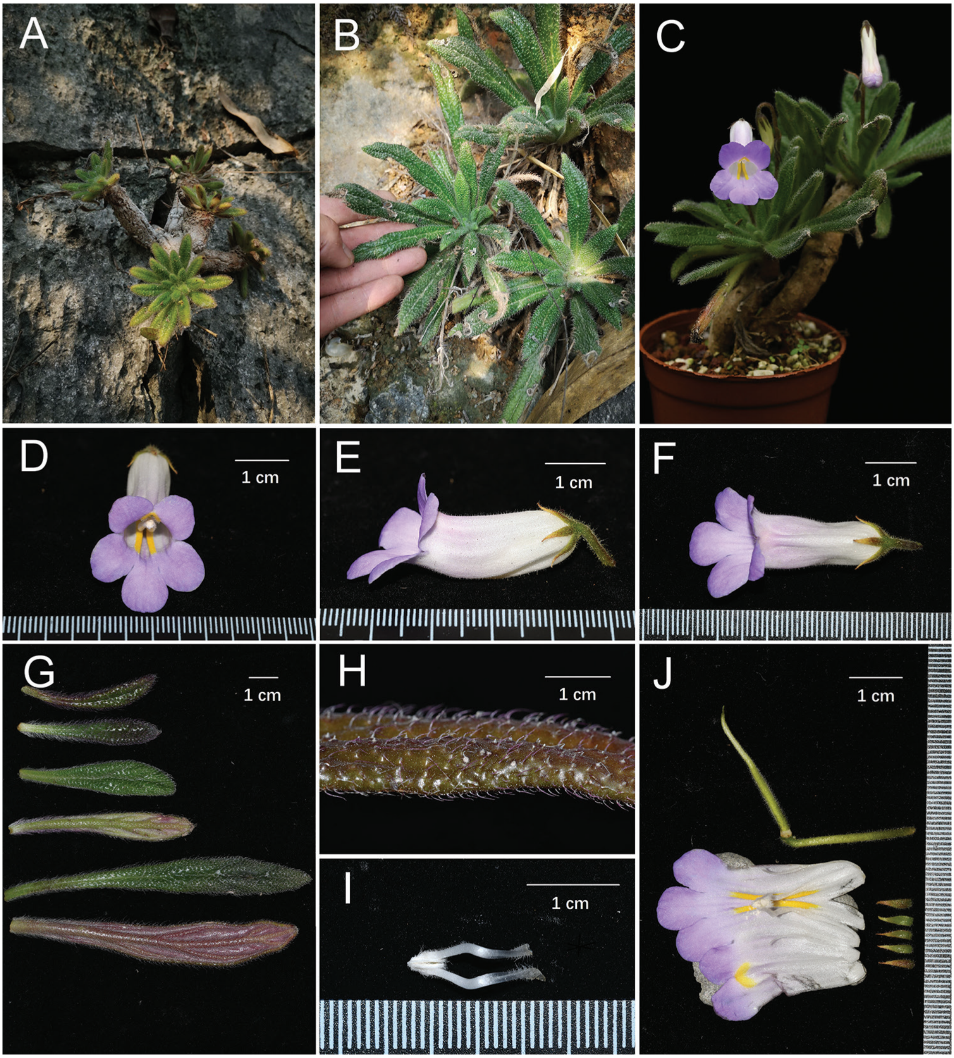


Figure 1. *Primulina papillosa* **A, B** habitat **C** habit **D** front view of the corolla **E** lateral view of the corolla **F** top view of the corolla **G** adaxial and abaxial surface of leaf blades **H** papillose-hispid hairs on leaf blade surface **I** stamens **J** pistil, calyx and opened corolla with stamens and staminodes. (**A, B** photos by W.C. Chou, **C–J** photos by F. Wen; arranged by Z.B. Xin).

20–35 mm long (vs. 7–15 mm); central staminodes ca. 0.5 mm long (vs. ca. 3 mm); disc ca. 1.2 mm high, margin entire (vs. ca. 2.5 mm, margin repand).

Type. China. Guangxi: cultivated material in the Gesneriad Conservation Center of China and National Gesneriaceae Germplasm Resources Bank, harvested on 24 October 2020, wild-collected, from Dingdang Town, Longan County, Nanning City, 23°07'N, 107°57'E, 9 April 2020, *W.C. Chou 20200409-01* (Holotype, IBK!; Isotypes, IBK!).

Description. Herbs perennial. ***Rhizome*** thickened, woody, subterete, 10–15 cm long, 1.5–2 cm in diameter, internodes inconspicuous, commonly branched at the apex of the rhizome or not branched. ***Leaves*** 15–25, congested at the apex of the rhizome, subsessile; ***leaf blade*** fleshy, linear-lanceolate, 5–15 × 0.9–1.8 cm, densely papillose-hispid on both surfaces, apex obtuse to round, base attenuate, margin entire, lateral veins 2–4 on each side of the mid-rib, conspicuous on the abaxial surface, inconspicuous on the adaxial surface. ***Cymes*** 2–5, axillary, 1–2-flowered; peduncle 4–8 cm long, ca. 2 mm in diameter, glandular-pubescent and sparsely pilose; ***bracts*** 2, opposite, linear-lanceolate, 6–8 × 1–1.5 mm, apex acute, margin entire, pubescent on both surfaces, pedicel 2–3.5 cm long, ca. 2 mm in diameter, glandular-pubescent. ***Calyx*** 5-parted from the base, segments equal, lanceolate, 7.5–9 × ca. 2 mm, abaxially glandular-pubescent, adaxially sparsely glandular-pubescent to glabrous, apex acute, margin entire. ***Corolla*** purple, throat with two yellow stripes inside, 3.5–4.5 cm long, outside puberulent with both glandular and eglandular hairs, inside glabrous, tube 2.5–3 cm long, orifice 0.8–1.5 cm in diameter; limb distinctly 2-lipped, adaxial lip 2-parted to the middle, with a yellow patch between the two adaxial lobes, lobes ovate, 6–7 × 8–9 mm, abaxial lip 3-parted to near the base, lobes ovate, 8–9 × 9–10 mm. ***Stamens*** 2, adnate ca. 1.2 cm above the corolla base; filaments 1.3–1.5 cm long, geniculate near the middle, sparsely pubescent; anthers reniform, 3.5–4 mm long, bearded; ***staminodes*** 3, lateral ones linear, glabrous, ca. 9 mm long, apex capitate, sparsely pubescent, adnate to ca. 1 cm above the corolla tube base, the central one ca. 0.5 mm long, apex capitate, adnate to 3.5 mm above the corolla tube base. ***Disc*** annular, ca. 1.2 mm high, margin entire, glabrous. ***Pistil*** 2.5–3 cm long, ***ovary*** 1.4–1.6 cm long, ca. 2 mm in diameter, densely glandular-pubescent and eglandular-pubescent; ***style*** 0.9–1.2 cm long, 1.5 mm in diameter, glandular-pubescent and eglandular-pubescent; ***stigma*** obtrapeziform, ca. 2 mm long, apex shallowly 2-lobed. ***Capsule*** linear, 5–6.5 cm long, 2–3 mm in diameter, puberulent with both glandular and eglandular hairs.

Phenology. Flowering from September to November, fruiting from October to December.

Etymology. The specific epithet '*papillosa*' is derived from the leaf blade densely papillose-hispid on both surfaces.

Vernacular name. The Chinese name '刺疣报春苣苔' (Cì Yóu Bào Chūn Jù Tái) is newly coined for this species because of its special leaf blades surface full of densely papillose-hispid hairs.

Distribution and habitat. *Primulina papillosa* is only known from the type locality, Dingdang Town, Longan County, Nanning City, Guangxi, China. It only grows in

Figure 2. Comparison of three species of *Primulina* **A, B** *P. linearifolia* **C, D** *P. pseudolinearifolia* **E, F** *P. papillosa*. (photos by F. Wen; arranged by Z.B. Xin).

crevices of the cliff near the top of limestone hills in a subtropical evergreen seasonal rain forest.

Conservation status. *Primulina papillosa* is only found from the type population with less than 200 individuals. The EOO and AOO of the new species are about 1.05 km^2 and 0.01 km^2, respectively. The beautiful flowers, thickened rhizomatous woody stem and leaves with dense papillose-hispid hairs, have led to its over-harvesting by local people who have sold it as an ornamental plant. Furthermore, the natural habitat is mostly disturbed due to local farmers imposing intense pressure on the remaining patches of primary forest. Thus, following the IUCN Red List Categories and Criteria (IUCN 2019), it is temporarily assessed as Critically Endangered [CR B1+B2ab (iii, v)].

Acknowledgements

We wish to thank Michael LoFurno, an Adjunct Professor from Temple University, Philadelphia, the USA, for his editorial assistance. This study was financially supported by the Foundation of Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain (19-050-6; 19-185-7), the National Natural Science Foundation (31860047), Guilin Science and Technology Foundation (20180107-6), the Key Science and Technology Research and Development Project of Guangxi (GuikeAD20159091), Guangxi Natural Science Foundation (2020GXNSFBA297049), Basal Research Fund of GXIB (Guizhiye20009) and the 21st Talent project of "Ten-Hundred-Thousand" in Guangxi.

References

Ge YZ, Xin ZB, Fu LF, Chou WC, Huang Y, Huang ZJ, Maciejewski S, Wen F (2020) *Primulina hochiensis* var. *ochroleuca* (Gesneriaceae), a new variety from a limestone area of Guangxi, China, and errata on five new species of *Primulina*. PhytoKeys 152: 111–120. https://doi.org/10.3897/phytokeys.152.50968

Hance HF (1883) New Chinese Cyrtandreae. Le Journal de Botanique 21: 165–170.

IPNI (2021) The International Plant Names Index. http://www.ipni.org [accessed: 28 January 2021]

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee of the IUCN Species Survival Commission. http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf

Li S, Xin ZB, Chou WC, Huang Y, Pan B, Maciejewski S, Wen F (2019) Five new species of the genus *Primulina* (Gesneriaceae) from Limestone Areas of Guangxi Zhuangzu Autonomous Region, China. PhytoKeys 127: 77–91. https://doi.org/10.3897/phytokeys.127.35445

Liu K, Meng DC, Huang ZJ, Maciejewski S, Xin ZB (2020) *Primulina jiuyishanica* (Gesneriaceae), a new species from Hunan, China. PhytoKeys 162: 37–44. https://doi.org/10.3897/phytokeys.162.53763

Möller M (2019) Species Discovery in Time: An Example from Gesneriaceae in China. Guangxi Sciences 26(1): 1–16.

Tropicos (2021) Tropicos.org. Missouri Botanical Garden. http://www.tropicos.org [accessed: 28 January 2021]

Wang WT, Pan KY (1982) Notulae de Gesneriaceis Sinensibus III. Bulletin of Botanical Research 2(2): 121–152.

Wang YZ, Mao RB, Liu Y, Li JM, Dong Y, Li ZY, Smith JF (2011) Phylogenetic reconstruction of *Chirita* and allies (Gesneriaceae) with taxonomic treatments. Journal of Systematics and Evolution 49(1): 50–64. https://doi.org/10.1111/j.1759-6831.2010.00113.x

Weber A, Middleton DJ, Forrest A, Kiew R, Lim CL, Rafidah AR, Sontag S, Triboun P, Wei YG, Yao TL, Möller M (2011) Molecular systematics and remodelling of *Chirita* and associated genera (Gesneriaceae). Taxon 60(3): 767–790. https://doi.org/10.1002/tax.603012

Wei YG (2018) The Distribution and Conservation Status of Native Plants in Guangxi, China. China Forestry Publishing House, Beijing, 876 pp.

Wen F, Li S, Xin ZB, Fu LF, Cai L, Qin JQ, Pan B, Hong X, Pan FZ, Wei YG (2019) The Updated Plant List of Gesneriaceae in China against the Background of Newly Chinese Naming Rules. Guangxi Sciences 26(1): 37–63.

Wen F, Wei YG, Fu LF, Xin ZB, Li S, Huang ZJ, Ge YZ, Meng DC (2021) The Checklist of Gesneriaceae in China. http://gccc.gxib.cn/about–46.aspx. [accessed: 28 January 2021]

Xin ZB, Fu LF, Huang ZJ, Chou WC, Huang Y, Wen F (2020a) *Primulina titan* sp. nov. (Gesneriaceae) from a Limestone Area in Northern Guangxi, China. Journal of Botanical Research 2(3): 1–4. https://doi.org/10.30564/jrb.v2i3.1994

Xin ZB, Huang ZJ, Chou WC, Huang Y, Meng DC, Wen F (2020b) *Primulina qintangensis* (Gesneriaceae), A new species from limestone areas of Guangxi, China. Xibei Zhiwu Xuebao 40(8): 1424–1427. https://doi.org/10.30564/jrb.v2i3.1994

Xin ZB, Huang ZJ, Fu LF, Li S, Wang BM, Wen F (2020c) *Primulina spiradiclioides* (Gesneriaceae), a new species from limestone areas in Guangxi, China. Annales Botanici Fennici 57(4–6): 245–248. https://doi.org/10.5735/085.057.0408

Xu WB, Huang YS, Wu L, Liu Y (2011) *Chirita luochengensis* (Gesneriaceae), a new species from limestone areas in northern Guangxi, China. Brittonia 63(2): 314–317. https://doi.org/10.1007/s12228-010-9175-8

Xu WB, Zhang Q, Wen F, Liao WB, Pan B, Chang H, Chung KF (2012) Nine new combinations and one new name of *Primulina* (Gesneriaceae) from South China. Phytotaxa 64(1): 1–8. https://doi.org/10.11646/phytotaxa.64.1.1

PhytoKeys 177: 63–75 (2021)
doi: 10.3897/phytokeys.177.57725
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Taxonomic Identity of *Carpinus dayongina* Franchet (Betulaceae)

Qianqian He[1], Runan Zhao[1], Anguo He[2], Zunling Zhu[1,3], Yihua Tong[4]

1 *College of Landscape Architecture, Nanjing Forestry University, Nanjing 210037, China* **2** *Zhejiang Dapanshan National Natural Reserve, Pan'an 322300, China* **3** *College of Art & Design, Nanjing Forestry University, Nanjing 210037, China* **4** *Key Laboratory of Plant Resources Conservation & Sustainable Utilization/Key Laboratory of Digital Botanical Garden of Guangdong Province, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*

Corresponding authors: Zunling Zhu (zhuzunling@njfu.edu.cn); Yihua Tong (yh-tong@scbg.ac.cn)

Academic editor: Norbert Holstein | Received 19 August 2020 | Accepted 21 April 2021 | Published 12 May 2021

Citation: He Q, Zhao R, He A, Zhu Z, Tong Y (2021) Taxonomic Identity of *Carpinus dayongina* Franchet (Betulaceae). PhytoKeys 177: 63–75. https://doi.org/10.3897/phytokeys.177.57725

Abstract

Carpinus polyneura and *C. dayongina* are recognised as separate species in *Flora of China*. In this study, the results of an examination of literature, morphological comparison and phenetic clustering of nuclear ITS sequences suggest that *C. dayongina* is conspecific with *C. polyneura*. Thus, we propose reducing *C. dayongina* to a synonym of *C. polyneura*.

Keywords

Hornbeam, new synonym, taxonomy

Introduction

Carpinus (Linnaeus 1753) is a large genus in the family Betulaceae. It contains about 50 species distributed across the Northern Hemisphere (Asia, Europe, North America) (Li and Skvortsov 1999; Holstein and Weigend 2017), 36 of which occur in China (including 30 endemic species) (Li and Skvortsov 1999; Tong et al. 2014; Lu et al. 2017; Lu et al. 2018; Lu 2020). Although some *Carpinus* species have been studied (Hu 1948; Hu 1964; Li 1979; Ill and Chang 1997; Li and Skvortsov 1999), this genus is still taxonomically problematic because of the lack of comprehensive field investigations and analyses of morphological characters for some species.

Carpinus polyneura Franchet was described, based on collections (*Farges*, *s.n.*) (Fig. 1A) from Chengkou County, Sichuan Province (now Chengkou County, Chongqing City) (Franchet 1899). Although there are some morphological variations amongst populations of this species due to its wide distribution, the higher density of leaf veins and setiform serrate leaf margin make it clearly distinguishable from the other species of *Carpinus* (Hu 1964).

In the protologue, *Carpinus polyneura* is described as having lanceolate or ovate-lanceolate with a long-acuminate apex and simply serrate margin and nutlets that are mainly villous at the apex. *Carpinus dayongina* K. W. Liu & Q. Z. Lin was described, based on several collections (Fig. 1B–D) from Tianmenshan, Dayong County, Hunan Province (now Tianmenshan, Zhangjiajie City, Hunan Province) (Liu and Lin 1986). Liu and Lin (1986) stated that *C. dayongina* was similar to *C. polyneura*, but could be distinguished by its narrower leaves, shorter infructescence, smaller bracts and narrower leaves. They cited two collections, i.e. *K. W. Liu 33359* and *Y. T. Xiao 40700*, with the former designated as holotype. The collection, *Y. T. Xiao 40700*, contains a total of six specimens (here considered as duplicates). The specimen with the barcode CSFI017465 (Fig. 1C) bears leaves that are clearly wider in shape (ovate-lanceolate) than those of the other five specimens (narrow-lanceolate) and it was identified as *C. polyneura* previously (by Qi Cheng Jing in June 1984).

Li and Skvortsov (1999) pointed out that *C. polyneura* has leaves with doubly setiform serrate margin and nutlets that are pubescent, while *C. dayongina* has narrower leaf blades with simply setiform serrate margin and nutlets that are only villous at the apex (Table 1).

When revising the species of *Carpinus* in China, we noticed that these two species are very similar to each other. This made us speculate that the two are possibly conspecific, although Li and Skvortsov (1999) followed Liu and Lin (1986) and treated them as separate species in *Flora of China*.

Materials and methods

Morphological analysis

Specimens of *C. polyneura* and *C. dayongina* deposited in the herbaria CSFI, HHBG, HIB, HNWP, IBK, IBSC, IFP, KUN, LBG, NAS, P, PE, SHM, SZ and WUK were studied and field investigations in Guizhou, Hubei, Hunan and Zhejiang to study *C. polyneura* and *C. dayongina* had been conducted in recent years. The morphological characteristics of the two species were also documented via photography and some of the physical features were measured (Table 2). Abbreviations for the names of herbaria in this study refer to the Herbarium Index Database (http://sweetgum.nybg.org/science/ih/).

Table 1. Differences between *Carpinus polyneura* and *C. dayongina* indicated by Li and Skvortsov (1999).

Species	Leaf	Length × width (cm)	Margin of leaf	Nutlet
C. polyneura	Elliptic-lanceolate or oblong-lanceolate	4–8 × 1.5–2.5	Doubly setiform serrate	Pubescent
C. dayongina	Lanceolate or ovate-lanceolate	2.5–4.5 × 1–1.5	Simply setiform serrate	Only villous at apex

Table 2. Specimens used for measurement of morphological characters of *Carpinus polyneura* and *C. dayongina*.

Species	Collector	Collection number	Collection site	Herbarium
C. polyneura	T. L. Dai	104469	Chengkou, Chongqing	PE
	H. F. Zhou	26421	Fengjie, Chongqing	KUN
	H. F. Zhou	26317	Fengjie, Chongqing	KUN
	Z. R. Zhang	25054	Fengjie, Chongqing	KUN
	Y. Liu	668	Shennongjia, Hubei	KUN
	P. C. Cai	20297	Shimen, Hunan	CSFI
	C. L. Long	87290	Shimen, Hunan	CSFI
	J. R. Zheng	80108	Shimen, Hunan	CSFI
	P. C. Cai	20442	Zhangjiajie, Hunan	CSFI
	P. Y. Li	8277	Langao, Shaanxi	KUN
	T. P. Soong	39145	Baoxing, Sichuan	KUN
	G. H. Yang	57149	Emeishan, Sichuan	KUN
	W. P. Fang	7546	Emeishan, Sichuan	PE
	W. P. Fang et al.	31110	Emeishan, Sichuan	IBK
	W. P. Fang et al.	32888	Emeishan, Sichuan	IBSC
	G. H. Yang	54569	Emeishan, Sichuan	IBSC
	S. G. Wu	394	Sichuan	KUN
	G. R. Chen	2383	Tiantai, Zhejiang	KUN
	Anonymous	2759	Without precise locality	KUN
	S. Y. Hu	1906	Without precise locality	KUN
C. dayongina	Y. T. Xiao	40700	Tianmenshan, Hunan	CSFI
	K.W. Liu	33359	Tianmenshan, Hunan	CSFI, PE
	Q. P. Zhang	2020072801	Tianmenshan, Hunan	NF
	Q. P. Zhang	2020072802	Tianmenshan, Hunan	NF

Molecular analysis based on nuclear ribosomal ITS sequences

Twelve individuals from five populations of the two species (Table 3), including nine individuals of *C. polyneura* (P1–P9) and three individuals from the type locality of *C. dayongina* (D1–D3), respectively, were sampled. Fresh leaves were collected from each individual. Coordinates and altitude information were recorded by using a hand-held GPS. All voucher specimens were stored in Nanjing Forestry University (NF).

DNA was extracted using the modified CTAB method (Doyle and Doyle 1990). PCR amplifying and sequencing of the ITS fragment refer to Lu et al. (2016). We made an alignment of 12 newly-sequenced ITS fragments and 10 ITS sequences of *C. polyneura*, *C. mollicoma* (Hu 1949), *C. rupestris* (Camus 1929) and *C. tschonoskii* (Maximowicz 1881b) that were downloaded from NCBI (Table 4). We used Mega X (Kumar et al. 2018) to construct a neighbor-joining (NJ) tree (Saitou and Nei 1987) using pairwise deletion and the *P*-distance model. Bootstrap values were set to 1000 to calculate the support values.

Table 3. Geographical information of four populations of *Carpinus polyneura* and one population of *C. dayongina* used for phylogenetic analyses of ITS sequences.

Species	Number of individuals	Collection site	Latitude (N) / Longitude (E)	Altitude (m)
C. polyneura	4 (P1–P4)	Hupingshan, Hunan	30°0'42.1"N, 110°36'20.5"E	350
	3 (P5–P7)	Dapanshan, Zhejiang	29°12'33.4"N, 120°43'56.6"E	600
	1 (P8)	Liujiaping, Hubei	30°6'27.9"N, 110°43'56.6"E	1380
	1 (P9)	Caoyuan, Guizhou	26°18'43.9"N, 106°54'39.6"E	1460
C. dayongina	3 (D1–D3)	Tianmenshan, Hunan	29°3'5.8"N, 110°28'30.3"E	1335

Table 4. ITS sequences used in this study are from NCBI; a dash (–) indicates missing data.

Species	Location	Voucher	ITS from NCBI
C. polyneura (P1)	Hupingshan, Hunan	Z.F. Chen 20200601	MW882972
C. polyneura (P2)	Hupingshan, Hunan	Z.F. Chen 20200603	MW882973
C. polyneura (P3)	Hupingshan, Hunan	Z.F Chen 20200605	MW882974
C. polyneura (P4)	Hupingshan, Hunan	Z.F. Chen 20200607	MW882975
C. polyneura (P5)	Dapanshan, Zhejiang	A.G. He 20200710	MW882976
C. polyneura (P6)	Dapanshan, Zhejiang	A.G. He 20200715	MW882977
C. polyneura (P7)	Dapanshan, Zhejiang	A.G. He 20200717	MW882978
C. polyneura (P8)	Liujiaping, Hubei	Z.Q. Lu LJP-1	MW882979
C. polyneura (P9)	Caoyuan, Guizhou	Z.Q. Lu CY-1	MW882980
C. dayongina (D1)	Tianmenshan, Hunan	Q.P. Zhang 2020072801	MW893478
C. dayongina (D2)	Tianmenshan, Hunan	Q.P. Zhang 2020072802	MW893479
C. dayongina (D3)	Tianmenshan, Hunan	Q. P. Zhang 2020072803	MW893480
C. polyneura	Xingshan, Hubei	Chen et al. 961325	AF081517
	–	Liu 631	FJ011726
	Tiantai Mt., Zhejiang	–	JF796533
	Qinling Mt.	SZH 454	MH703152
	Qinling Mt.	Q875	MH711693
C. mollicoma	Daba Mt. Shaanxi	–	KX946977
C. rupestris	Daba Mt. Shaanxi	–	KX946978
C. tschonoskii	Hangzhou Bot. Gard., Zhejiang	W 97-30	AY006369
	–	Lee s. n.	FJ011733
	Qinling Mt.	HZ 283	MH710986

Results and discussion

Re-collections of material from the type localities and further field investigation showed that the leaf shapes are quite variable in the same area, from ovate-lanceolate to lanceolate, then narrow-lanceolate (Fig. 2). After a thorough examination of more specimens, we found that, not only leaf blade shape, but also infructescence length and bract size of *C. dayongina*, are all within the limits of *C. polyneura* (Table 5). After review of the type specimens, we found the leaf margins of *C. polyneura* and *C. dayongina* have both simply and doubly setiform serration (Table 5). In addition, by carefully searching for comprehensive and extensive groups of specimens, performing field investigations and measuring morphological characteristics, we found that the indumentum of their nutlets is also variable, from being villous at the apex and glabrous, sparsely villous or pubescent in the remaining part (Fig. 3, Table 5). Therefore, this character can also not be regarded as a useful character to differentiate these two taxa.

Phenetic comparison of ITS sequences showed that the samples of *C. dayongina* from Tianmenshan population and those of *C. polyneura* from other regions are mixed with each other (Fig. 4).

We therefore conclude that *C. dayongina* and *C. polyneura* are conspecific. According to ICN (McNeill et al. 2018), the earlier published *C. polyneura* has priority over *C. dayongina* and thus, *C. dayongina* is reduced to a synonym of *C. polyneura* herein.

Taxonomic treatment

***Carpinus polyneura* Franch., J. Bot. 13: 202. 1899.**

≡ *Carpinus turczaninovii var. polyneura* (Franch.) H. J. P. Winkl., Das Pflanzenreich IV 61 (Heft 19): 38 (Winkler 1904). – Type: China, Su-tchuen [Sichuan], in District de Tchen kéou tin [Chengkou County], *P. G. Farges s. n.* (lectotype: P06811144!, designated by Holstein and Weigend 2017; isolectotypes: P06811145!, P06811146!) (Fig. 1A).

= *Carpinus dayongina* K. W. Liu & Q. Z. Lin, Bull. Bot. Res., Harbin 6(2): 143. 1986. syn. nov. – Type: China, Hunan, Dayong [now Zhangjiajie], Tianmenshan, 1100 m a.s.l., 28 July 1985, *K. W. Liu* [*Liu Ke Wang*] *33359* (holotype: CSFI050241!; isotype: PE01843387!) (Fig. 1B). – Additional original material: ibid., 25 August 1984, *Y. T. Xiao* [*Xiao Yu Tan*] *40700* (paratypes: CSFI017465!, CSFI017535!, CSFI017536!, CSFI017538!, CSFI017539!, CSFI017542!) (Figs. 1C and D).

Description. A deciduous tree, up to 15 m tall. Bark grey. Branchlets slender, dark purplish, covered with white roundish lenticels, densely villous and soon glabrous. Petiole 5–11 mm, 0.5–0.8 mm in diameter; leaf blade ovate-lanceolate to narrow-lanceolate, sometimes oblong or ovate, 2.5–8 × 1–3 cm, base broadly sub-rounded or slightly cordate, margin doubly setiform serrate, sometimes simply setiform serrate at the apex or simply setiform serrate, upper surface sparsely villous, densely villous along the veins, glabrescent, lower surface densely villous along the veins, sometimes bearded in axils of lateral veins, lateral veins 15–20 on each side of the mid-vein. Infructescence 1.4–6.5 cm long, pendent, peduncle slender, densely villous with white roundish lenticels; bracts semi-ovate-lanceolate, 5–15 × 3–6 mm, outer margin dentate, without basal lobe, inner margin entire with small, inflexed basal auricle. Nutlets broadly ovoid, 2–4 × 1.5–3 mm, villous at apex, glabrous or sparsely villous or pubescent on the remaining part, ribbed.

Distribution and habitat. China: Chongqing, Gansu, Shaanxi, Sichuan, Guizhou, Hubei, Hunan, Jiangxi and Zhejiang. This species grows in subtropical broad-leaved forests or thickets at altitudes of 400–1900 m.

Additional specimens examined. *Carpinus polyneura*: Chongqing, Chengkou, 5 September 1958, *T. L. Dai 104405* (IBSC, NAS, PE, SZ); Chongqing, Chengkou, 6 September 1956, *T. L. Dai 104469* (IBSC, NAS, PE, SZ); Chongqing, Chengkou, 14 September 1958, *T. L. Dai 104783* (IBSC, NAS, PE, SZ); Chongqing, Chengkou, 20 September 1958, *T. L. Dai 104961* (IBK, NAS, PE); Chongqing, Fengjie, 1 June

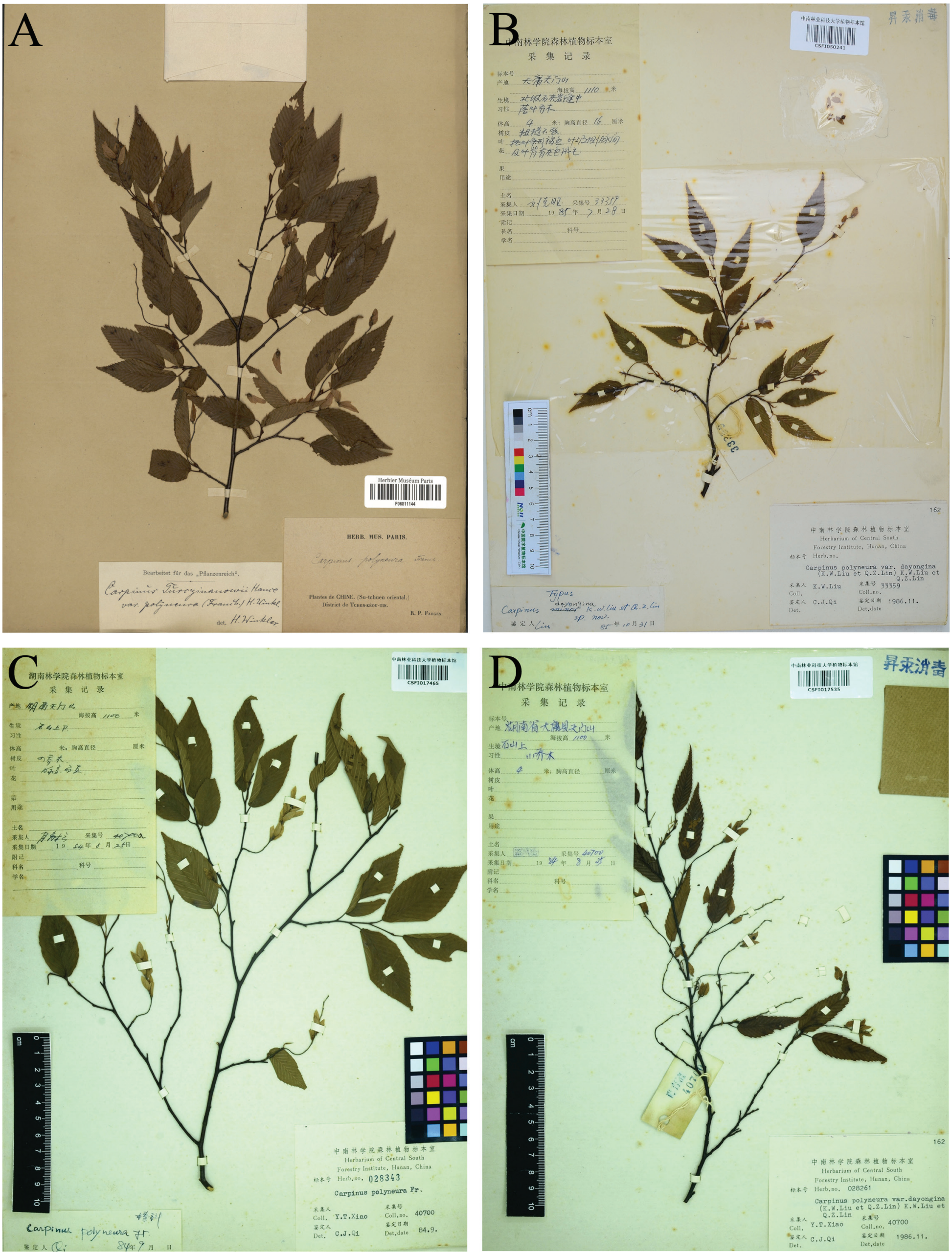


Figure 1. Specimens of *Carpinus polyneura* Franchet **A** lectotype of *C. polyneura* (*P. G. Farges s.n.*, P06811144) **B** holotype of *C. dayongina* K. W. Liu & Q. Z. Lin (*K. W. Liu 33359*, CSFI050241) **C** paratype of *C. dayongina* (*Y. T. Xiao 40700*, CSFI017465) **D** paratype of *C. dayongina* (*Y. T. Xiao 40700*, CSFI017535).

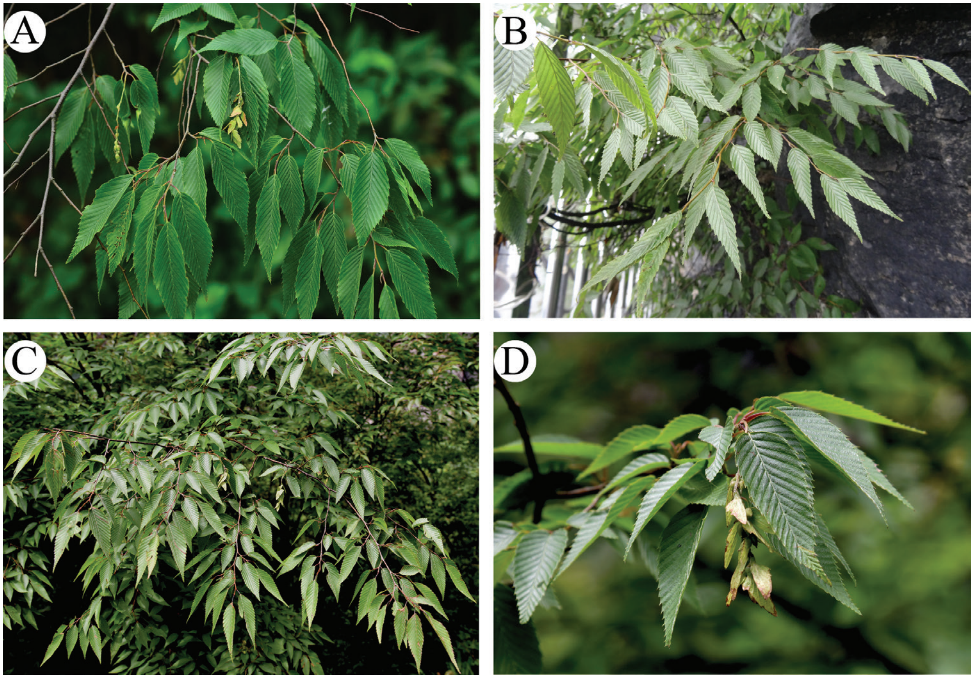


Figure 2. *Carpinus polyneura* **A, B** population from Tianmenshan, Zhangjiajie City (type locality of *C. dayongina*) (**A** photographed by H. Zhou **B** photographed by W. Q. Qin) **C, D** population from Wushan, Chongqing City (near the type locality of *C. polyneura*) (**C, D** photographed by H. L. Zhou).

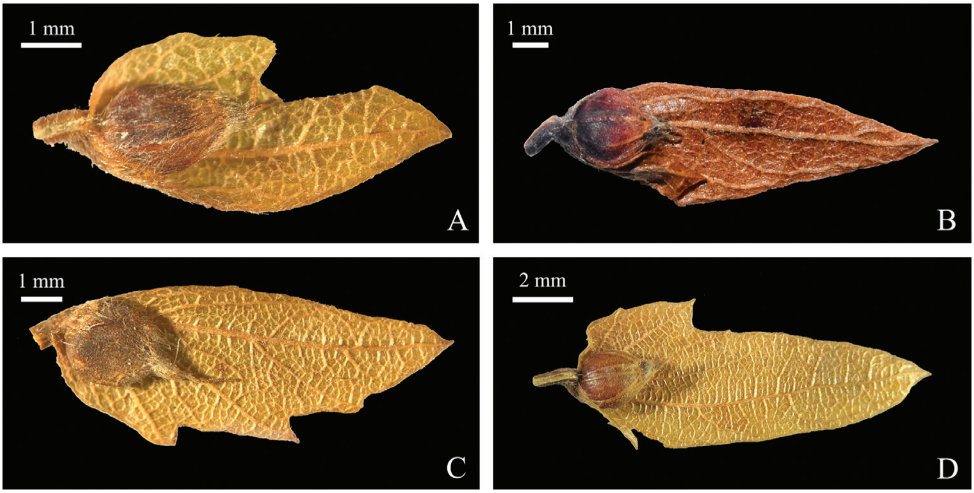


Figure 3. Nutlet trichomes of *C. polyneura* **A** from isotype of *C. dayongina* (*K. W. Liu 33359*, PE01843387) **B** from paratype of *C. dayongina* (*Y. T. Xiao 40700*, CSFI017539) **C** from *T. L. Dai 104469*, PE00818275 **D** from *W. P. Fang 7546*, PE00818253. **A, C, D** photographed by Q. Q. He **B** photographed by X. Li.

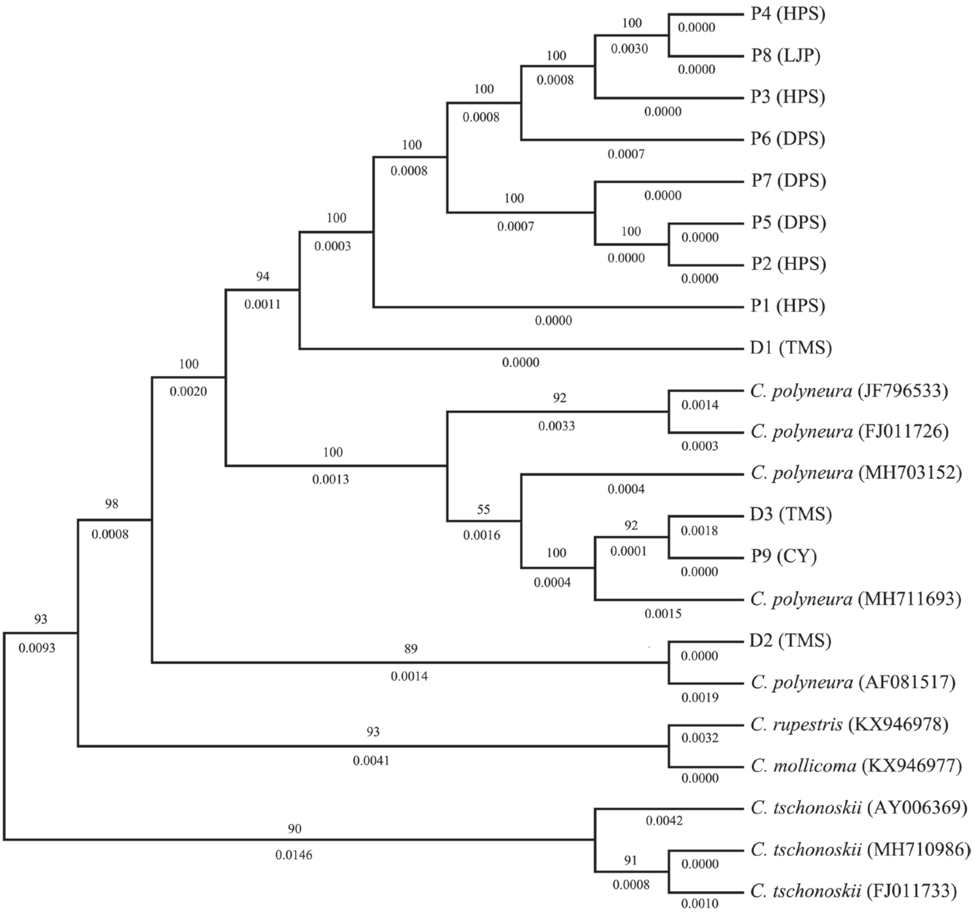


Figure 4. The neighbor-joining (NJ) tree, based on ITS sequence data. *Carpinus mollicoma*, *C. rupestris* and *C. tschonoskii* as related species; **P1–P4** are samples of *C. polyneura* from Hupingshan (HPS), Shimen, Hunan, China; **P5–P7** are samples of *C. polyneura* from Dapanshan (DPS), Panan, Zhejiang, China; **P8** is a sample of *C. polyneura* from Liujiaping (LJP), Wufeng, Hubei, China; **P9** is a sample of *C. polyneura* from Caoyuan (CY), Longli, Guizhou, China; **D1–D3** are samples of *C. dayongina* from Tianmenshan (TMS), Zhangjiajie, Hunan, China. The numbers above the branch are bootstrap values (%), and the numbers below the branch are branch length.

1958, *Z. R. Zhang 25054* (HIB, IBSC, IFP, KUN, NAS, PE); Chongqing, Fengjie, 16 June 1958, *H. F. Zhou 26317* (HIB, IBSC, IFP, KUN, NAS, PE); Chongqing, Fengjie, 25 June 1958, *H. F. Zhou 26421* (HIB, IBSC, IFP, KUN, PE); Chongqing, Nanchuan, 8 June 1957, *J. H. Xiong & Z. L. Zhou 91297* (HIB, IBSC); Chongqing, Nanchuan, 29 June 1957, *J. H. Xiong & Z. L. Zhou 91753* (HIB); Chongqing, Wushan, 15 October 1958, *G. H. Yang 59826* (IBSC, PE, SHM); Chongqing, Wushan, 20 August 1964, *H. F. Zhou & H. Y. Li 110088* (IBSC, PE, SZ); Chongqing, Wuxi, 8 August 1958, *M. Y. Fang 23898* (HIB, IBSC, IFP, KUN, PE, SZ); Chongqing, Wuxi, 30 June 1958, *G. H. Yang 58658* (IBK, IBSC, PE, SHM); Gansu Province, Chengx-

Table 5. Measurements of morphological characteristics of *Carpinus polyneura* and *C. dayongina*. A dash (–) indicates missing data.

Species	Specimen	Leaf length × width (cm)	Leaf size ratio	Leaf margin	Infructescence length (cm)	Bract size (cm)	Nutlet indumentum
C. polyneura	T. L. Dai 104469, PE00818275	5–5.9 × 1.7–1.8	2.9–3.3	Simply setiform serrate	2.6–2.9	1 × 0.35	Villous at apex
	H. F. Zhou 26421, KUN0590808	5.1–5.9 × 1.9–2.3	2.5–2.8	Simply setiform serrate	3.2–5.6	1.3 × 0.5	Villous at apex
	H. F. Zhou 26317, KUN0590809	5.5–6.2 × 1.7–1.9	3–3.4	Simply setiform serrate at apex, doubly setiform serrate in the rest	1.8–3.2	1.2 × 0.45	Villous at apex
	Z. R. Zhang 25054, KUN0590804	5.8–6.5 × 2.1–2.5	2.3–3.1	Simply setiform serrate	4.4–4.9	1.5 × 0.6	Villous at apex
	Y. Liu 668, KUN0590794	3.9–4.1 × 1.2–1.3	3–3.3	Simply setiform serrate	2.1	1 × 0.3	Pubescent
	P. C. Cai 20297, CSFI017457	5.3–6 × 1.8–2.1	2.8–3	Doubly setiform serrate	2.6–3.9	1.2 × 0.4	Pubescent
	C. L. Long 87290, CSFI017461	5.4–6.1 × 1.6–2.2	2.5–3.4	Doubly setiform serrate	3.9–4.3	1.2 × 0.5	Villous at apex
	J. R. Zheng 80108, CSFI017456	6.7–7.1 × 2.3–2.5	2.8–3	Doubly setiform serrate	–	–	–
	P. C. Cai 20442, CSFI017455	5.1–5.7 × 1.8–1.9	2.7–3	Simply setiform serrate at apex, doubly setiform serrate in the rest	2.2–2.7	1.2 × 0.5	Villous at apex
	P. Y. Li 8277, KUN0590814	5.9–7.3 × 2.2–2.7	2.4–3	Simply setiform serrate	4.4–4.8	1.4 × 0.6	Villous at apex
	T. P. Soong 39145, KUN0590798	5.5–6.5 × 2.4–2.7	2.2–2.7	Doubly setiform serrate	2–3.6	1.2 × 0.4	Villous at apex
	G. H. Yang 57149, KUN0590811	6–7.4 × 2.1–2.5	2.8–3	Simply setiform serrate, sometimes doubly setiform serrate	4.1–5.5	1.4 × 0.5	Pubescent
	W. P. Fang 7546, PE00818253	5–6.2 × 1.8–2.5	2.5–2.8	Simply setiform serrate	2.8	1.2 × 0.5	Villous at apex
	W. P. Fang et al. 31110, IBK00079496	6.7–7.5 × 1.9–2.1	3.2–3.7	Simply setiform serrate	3.1	1 × 0.3	Pubescent
	W. P. Fang et al. 32888, IBSC0368122	5.4–6.6 × 2.5–3	2–2.3	Doubly setiform serrate	3.2	1.5 × 0.5	Villous at apex
	G. H. Yang 54569, IBSC0368131	6–7.2 × 2–2.5	2.4–3.3	Doubly setiform serrate	3.9	1.4 × 0.5	Villous at apex
	S. G. Wu 394, KUN0590803	4.8–5.6 × 1.5–1.8	2.7–3.2	Simply setiform serrate	2.2–3.5	1.1 × 0.4	Villous at apex
	G. R. Chen 2383, KUN0590815	5.1–5.8 × 1.7–1.9	2.8–3	Doubly setiform serrate	2.8–4.1	1.1 × 0.4	Pubescent
	Anonymous 2759, KUN0590800	5.7–6.4 × 1.8–2.1	2.9–3.5	Doubly setiform serrate	3.1	1.3 × 0.4	Pubescent
	S. Y. Hu 1906, KUN0590797	6–6.6 × 2–2.2	2.7–3	Simply setiform serrate, sometimes doubly setiform serrate	5–6.5	1.5 × 0.6	Villous at apex
C. dayongina	Y. T. Xiao 40700, CSFI017539 (paratype of *C. dayongina*)	5.1–5.7 × 1.2–1.5	3.4–3.8	Simply setiform serrate	3.5–4.2	1.1 × 0.35	Villous at apex
	Y. T. Xiao 40700, CSFI017465 (paratype of *C. dayongina*)	5.7–6.5 × 2.3–2.8	2.2–2.7	Doubly setiform serrate	3.6–3.8	1 × 0.4	Villous at apex
	K.W. Liu 33359, CSFI050241 (holotype of *C. dayongina*)	4.3–4.7 × 1.4–1.6	2.9–3.6	Simply setiform serrate	2.5	0.7 × 0.4	Pubescent
	K. W. Liu 33359, PE01843387 (isotype of *C. dayongina*)	4.4–5 × 1.3–1.7	2.8–3.5	Simply setiform serrate	2.1	0.7 × 0.4	Pubescent
	Q. P. Zhang 2020072801, NF	5–5.6 × 1.6–1.8	2.7–3.3	Simply setiform serrate	–	–	–
	Q. P. Zhang 2020072802, NF	4.5–4.9 × 1.4–1.8	2.7–3.7	Simply setiform serrate, sometimes doubly setiform serrate	2	0.9 × 0.3	Villous at apex

ian, 31 August 1958, *Z. P. Wei 2245* (HHBG, HNWP, SZ, WUK); Guizhou Province, Tungtze, 27 May 1930, *Y. Tsiang 5177* (IBSC, NAS, PE); Hubei Province, Badong, 31 October 1958, *S. X. Fu 1228* (HIB); Hubei Province, Hefeng, 27 August 1958, *H. J. Li 5874* (HIB, IBSC, KUN, PE, SZ); Hubei Province, Shennongjia, 29 August 1976, *Hubei Shennongjia Botanical Expedition 32766* (HIB, PE); Hubei Province, Shennongjia, 10 August 1976, *Hubei Shennongjia Botanical Expedition 31451* (HIB, PE); Hubei Province, Shennongjia, 19 June 1976, *Hubei Shennongjia Botanical Expedition 30417* (HIB, PE); Hubei Province, Shennongjia, 12 August 1976, *Hubei Shennongjia Botanical Expedition 11239* (HIB, PE); Hubei Province, Shennongjia, 26 August 1976, *Hubei Shennongjia Botanical Expedition 22775* (HIB); Hubei Province, Shennongjia, 3 June 1987, *Y. Liu 00668* (HIB, NAS, PE); Hubei Province, Shennongjia, August – September 1959, *Z. E. Zhao 113* (HIB); Hubei Province, Xingshan, 3 June 1957, *Y. Liu 668* (KUN, NAS, PE); Hunan Province, Anhua, 2 October 1978, *Z. H. Shen 1669* (CSFI); Hunan Province, Baojing, 8 August 1991, *X. L. Yu 91547* (CSFI); Hunan Province, Chengbu, 14 July 1981, *T. R. Cao 032* (CSFI); Hunan Province, Chengbu, August 1981, *Q. Z. Lin 11152* (CSFI); Hunan Province, Cili, 1 September 1984, *Xiangxi Expedition 0066* (PE); Hunan Province, Longshan, 10 August 1957, *B. M. Yang 2041* (IBSC, PE); Hunan Province, Luxi, 12 April 1982, *K. W. Liu 30079* (CSFI); Hunan Province, *Qianyang Expedition 122207* (IBK); Hunan Province, Sangzhi, 24 August 1988, *Beijing Expedition 3922* (PE); Hunan Province, Sangzhi, October 1976, *Sangzhi Expedition 960* (CSFI); Hunan Province, Shimen, 30 June 1979, *P. C. Cai 20297* (CSFI); Hunan Province, Shimen, 24 May 1987, *C. L. Long 87290* (CSFI); Hunan Province, Shimen, 4 May 1980, *J. R. Zheng 80108* (CSFI); Hunan Province, Yongshun, 31 May 1988, *Beijing Expedition 00571* (PE); Hunan Province, Yongshun, 5 June 1988, *Beijing Expedition 01123* (PE); Hunan Province, Yongshun, 22 August 1991, *X. L. Yu 91751* (CSFI); Hunan Province, Yongshun, 27 August 1991, *X. L. Yu 91854* (CSFI); Hunan Province, Yuanling, 23 June 1988, *Zhang et al. 512* (PE); Hunan Province, Yuanling, 23 June 1988, *G. C. Zhang et al. 510* (PE); Hunan Province, Yuanling, 15 June 1988, *Zhang et al. 380* (PE); Hunan Province, Zhangjiajie, 18 August 1979, *P. C. Cai 20442* (CSFI); Jiangxi Province, *anonymous 0470* (SHM); Jiangxi Province, Quannan, 27 June 1958, *anonymous 01184* (PE); Jiangxi Province, Shangrao, 21 June 1982, *anonymous 518* (LBG); Jiangxi Province, Xiushui, 4 September 1963, *S. K. Lai 03449* (LBG, SHM); Jiangxi Province, Zixi, 11 October 1985, *S. K. Lai & D. F. Huang 319* (LBG); Jiangxi Province, Zixi, 7 November 1957, *M. J. Wang et al. 2561* (NAS); Shaanxi Province, Langao, 27 July 1959, *P. Y. Li 8277* (KUN); Shaanxi Province, Zhenping, 13 May 1989, *G. Y. Xu 4899* (WUK); Shaanxi Province, Zhenping, 20 July 1991, *J. S. Ying et al. 217* (WUK); Sichuan Province, without date, *anonymous 20574* (IBK); Sichuan Province, without date, *anonymous 6255* (IBK); Sichuan Province, without date, *E. H. Wilson 5191* (IBSC); Sichuan Province, without date, *S. Y. Hu 1906* (KUN); Sichuan Province, without date, *S. G. Wu 394* (KUN); Sichuan Province, 23 November 1935, *W. G. Hu 8842* (IBK); Sichuan Province, 23 November 1935, *W. G. Hu 8832* (IBK, SZ); Sichuan Province, Baoxing, 1954, *Z. P. Song 39145* (IBSC, KUN, PE, WUK); Sichuan Province, Baoxing, 9 May 1954, *Z. P.*

Song 38130 (IBSC, KUN, PE, SHM, SZ); Sichuan Province, Dujiangyan, 29 October 1956, *Q. Li 47102* (IBSC, PE, SZ); Sichuan Province, Ebian, 28 October 1938, *T. N. Liou 12651* (WUK); Sichuan Province, Emeishan, 18 May 1929, *W. P. Fang 14651* (IBSC); Sichuan Province, Emeishan, 6 May 1931, *W. P. Fang 18625* (IBSC, SZ); Sichuan Province, Emeishan, 15 June 1952, *W. P. Fang et al. 31110* (IBK, IBSC, NAS); Sichuan Province, Emeishan, 13 September 1952, *W. P. Fang et al. 32478* (IBK, PE); Sichuan Province, Emeishan, 26 September 1952, *W. P. Fang et al. 32888* (IBK, IBSC, NAS, SHM); Sichuan Province, Emeishan, 6 September 1957, *G. H. Yang 57149* (HIB, IBSC, KUN, NAS, PE); Sichuan Province, Emeishan, without date, *Sichuan University Biology Department Expedition 54569* (HIB, IBSC, KUN, NAS, PE, SZ); Sichuan Province, Emeishan, without date, *Sichuan University Biology Department Expedition 52273* (HIB); Sichuan Province, Emeishan, without date, *Sichuan University Biology Department Expedition 51243* (HIB); Sichuan Province, Emeishan, 25 April 1940, *S. L. Sun 1711* (KUN, PE); Sichuan Province, Emeishan, 1 May 1940, *S. L. Sun 1800* (KUN); Sichuan Province, Emeishan, 17 May 1940, *S. L. Sun 1993* (KUN); Sichuan Province, Emeishan, 21 May 1940, *S. L. Sun 2127* (KUN, PE); Sichuan Province, Emeishan, 6 June 1931, *F. T. Wang 23224* (IBSC, PE, WUK); Sichuan Province, Emeishan, without date, *J. H. Xiong et al. 31690* (IBSC); Sichuan Province, Emeishan, sin.dat. *J. H. Xiong et al. 31790* (IBK); Sichuan Province, Emeishan, 10 May 1957, *G. H. Yang 54569* (IBSC, KUN, NAS, PE, SZ); Sichuan Province, Emeishan, 6 September 1957, *G. H. Yang 57149* (HIB, IBSC, KUN, NAS, PE, SZ); Zhejiang Province, Jiande, 4 July 1986, *C. R. Wu L8413260* (IBSC); Zhejiang Province, Tiantai, 1958, *G. R. Chen 2383* (KUN, PE); Zhejiang Province, Zhuji, 21 June 1984, *Y. J. Gao et al. 823-068* (IBSC).

Acknowledgements

This work was supported financially by the National Natural Science Foundation of China (31770752) and the Fifth Stage Funded Research Projects of 333 in Jiangsu Province (BRA2018065). The authors are grateful to the curators of many herbaria (CSFI, HIB, IBK, IBSC, KUN, NAS, P, PE and WUK) for permission to access and study the specimens, as well as the staff of Central South University of Forestry and Technology for providing the holotype photos of *Carpinus dayongina*. Thanks also to Ms. Hui Zhou from Central South University of Forestry and Technology, Mr. Weiqing Qin of Jishou University and Mr. Houlin Zhou of Forestry Bureau of Wushan for providing living plant images. In addition, we appreciate Hunan Tianmenshan National Forest Park, Mr. Zhenfa Chen from Hunan Hupingshan National Natural Reserve, Mr. Guoqian Hao from Emeishan and Mr. Zhiqiang Lu from Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for collecting samples. We thank LetPub (www.letpub.com) for its linguistic assistance during the preparation of this manuscript. We are equally grateful to reviewers for their helpful comments on how to improve the manuscript, especially Editor N. Holstein.

References

Camus A (1929) Espèces asiatiques nouvelles du genre *Carpinus*. Bulletin de la Société botanique de France 76: 966–969. https://doi.org/10.1080/00378941.1929.10836320

Doyle JJ, Doyle JL (1990) Isolation of plant DNA from fresh tissue. Focus 12: 13–15. https://doi.org/10.2307/2419362

Franchet A (1899) Plantarum sinensium ecloge tertia. Le Journal de Botanique 13(7): 198–208.

Holstein N, Weigend M (2017) No taxon left behind? – a critical taxonomic checklist of *Carpinus* and *Ostrya* (Coryloideae, Betulaceae). European Journal of Taxonomy 375: 1–52. https://doi.org/10.5852/ejt.2017.375

Hu HH (1948) The silva of China (Vol. 2). The Fan Memorial Institute of Biology and the National Forestry Research Bureau Ministry of Agriculture and Forestry, Beijing, 83–197.

Hu HH (1949) Four new species of *Carpinus* from Yunnan. Bulletin of the Fan Memorial Institute of Biology n.s. 1(3): 213–218.

Hu HH (1964) The materials on the monography of gen. *Carpinus* Linn. of China. Acta Phytotaxonomica Sinica 9(3): 281–298.

Ill JJ, Chang SC (1997) Reconsideration of *Carpinus* L. (Betulaceae) of Korea primarily based on quantitative characters. Korean Journal of Plant Taxonomy 27(2): 157–187. https://doi.org/10.11110/kjpt.1997.27.2.157

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Li PC (1979) Betulaceae (Vol. 21). Science Press, Beijing, 58–89. https://doi.org/10.2307/25157899

Li PC, Skvortsov AK (1999) Betulaceae. In: Wu ZY, Raven PH (Eds) Flora of China (Vol. 4). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.

Linnaeus C (1753) Species Plantarum. Laurentius Salvius, Stockholm 2: 998. https://www.biodiversitylibrary.org/page/358012

Liu KW, Lin QZ (1986) A new species of *Carpinus* from Hunan. Bulletin of Botanical Research, Harbin 6(2): 143–145.

Lu ZQ (2020) *Carpinus gigabracteatus*, a new species from southeast Yunnan, China. PhytoKeys 145: 47–56. https://doi.org/10.3897/phytokeys.145.49488

Lu ZQ, Zhang D, Liu SY, Yang XY, Liu X, Liu JQ (2016) Species delimitation of Chinese hophornbeams based on molecular and morphological evidence. Ecology and Evolution 6(14): 4731–4740. https://doi.org/10.1002/ece3.2251

Lu ZQ, Liu SY, Yang XY, Liang QL, Yang YZ, Zhang D, Milne R, Liu JQ (2017) *Carpinus langaoensis* (Betulaceae), a new hornbeam species from the Daba Mountains in Shaanxi, China. Phytotaxa 295(2): 185–193. https://doi.org/10.11646/phytotaxa.295.2.6

Lu ZQ, Li Y, Yang XY, Liu JQ (2018) *Carpinus tibetana* (Betulaceae), a new species from southeast Tibet, China. PhytoKeys 98: 1–13. https://doi.org/10.3897/phytokeys.98.23639

Maximowicz CJ (1881b) Diagnoses plantarum novarum asiaticarum IV. Bulletin de l'Academie impériale des sciences de St.-Pétersbourg 27: 425–460.

McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'Homme Van Reine WF, Smith GF, Wiersema JH, Turland NJ (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code).

Saitou N, Nei M (1987) The Neighbor-joining method: A new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4(4): 406–425. https://doi.org/10.1093/oxfordjournals.molbev.a040454

Tong YH, Pang KS, Xia NH (2014) *Carpinus insularis* (Betulaceae) A new species from Hong Kong, China. Journal of Tropical and Subtropical Botany 22(2): 121–124.

Winkler HJP (1904) Betulaceae. In: Engler HGA (Ed.) Das Pflanzenreich IV 61 (Heft 19). Wilhelm Engelmann, Berlin.

PhytoKeys 177: 77–116 (2021)
doi: 10.3897/phytokeys.177.64465
https://phytokeys.pensoft.net

MONOGRAPH

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Taxonomic revision of *Martinella* Baill. (Bignonieae, Bignoniaceae)

Eric Y. Kataoka[1], Lúcia G. Lohmann[1]

1 *Laboratório de Sistemática Vegetal, Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 277, 05508-090, São Paulo, SP, Brazil*

Corresponding authors: Eric Y. Kataoka (erickataoka@alumni.usp.br); Lúcia G. Lohmann (llohmann@usp.br)

Academic editor: Eberhard Fischer | Received 15 February 2021 | Accepted 21 April 2021 | Published 13 May 2021

Citation: Kataoka EY, Lohmann LG (2021) Taxonomic revision of *Martinella* Baill. (Bignonieae, Bignoniaceae). PhytoKeys 177: 77–116. https://doi.org/10.3897/phytokeys.177.64465

Abstract

Martinella Baill. is a genus of Neotropical lianas in tribe Bignonieae (Bignoniaceae). The genus is monophyletic and well supported by morphological and molecular characters. Members of *Martinella* are characterized by a continuous interpetiolar ridge surrounding the stem, bilobed or 4–5-parted calyces, and minute triangular prophylls of the axillary buds. Generic circumscription remained unchanged since the description of the genus, although unclear species limits remained. Based on extensive fieldwork, herbarium work, and a molecular phylogenetic hypothesis for the genus, we here recognize five species of *Martinella*. Of these, three were recognized in earlier treatments for the genus, while two represent new species described here, *Martinella lanuginosa* Kataoka & L.G.Lohmann, **sp. nov.** and *Martinella tomentosa* Kataoka & L.G.Lohmann, **sp. nov.** *Martinella iquitoensis* A.Samp. is treated as a synonym of *M. insculpta* Sprague & Sandwith. In addition, one second-step lectotype is designated for *Bignonia martini* DC., and neotypes are designated for *Doxantha longisiliqua* Miers and *Martinella gollmeri* K.Schum. This work provides a full taxonomic treatment for *Martinella*, including a complete list of synonyms, morphological descriptions, illustrations, photographs, distribution maps, conservation status, and comments for all five species recognized.

Keywords

Amazon, lianas, Neotropical flora, taxonomy

Introduction

Martinella Baill. (Bignonieae, Bignoniaceae) is a genus of Neotropical lianas, whose monophyly is supported by molecular phylogenetic studies (Lohmann 2006) and by morphological features. Namely, minute triangular prophylls of the axillary buds and interpetiolar ridges surrounding the stems are thought to represent morphological synapomorphies of the genus (Lohmann and Taylor 2014). Additionally, silvery or whitish leaflets on the abaxial surface, bilobed or 4–5-parted calyces, and corollas with a constricted basal portion and an upper campanulate portion also characterize species of *Martinella*.

Baillon (1888) described *Martinella* based on reproductive characters such as the irregularly 2–4-lobed calyces, bilabiate corollas with a wide tube (presumably referring to what was named *Martinella*-type flower nearly a century later; see Gentry 1974), stipitate ovary that sits on a large nectariferous disk, and glabrous, flattened and narrow fruits. The genus was described based on *Bignonia martini* DC. [= *Martinella obovata* (Kunth) Bureau & K.Schum.], and the new combination *Martinella martini* (DC.) Baill. was proposed. Schumann (1894) described the new species, *Martinella gollmeri* K.Schum. [= *Martinella obovata*] based on the shallow and bowl-shaped nectariferous disk and frizzy calyces. Two years later, Bureau and Schumann (1896) transferred *Spathodea obovata* Kunth into *Martinella*, proposing the new combination *Martinella obovata* (Kunth) Bureau & K.Schum., which became the accepted name for *Martinella martini*.

Sprague and Sandwith (1934) described *Martinella insculpta* Sprague & Sandwith, while Sampaio (1935) described *M. iquitoensis* A.Samp. and *M. manaosiana* A.Samp. (Sampaio 1936); both of these names are synonyms of *M. insculpta*. More recently, Zuntini and Lohmann (2014) published a new species endemic to the Atlantic Forest, *M. insignis* A.H.Gentry ex Zuntini & L.G.Lohmann, expanding the distribution of this predominantly Amazonian genus.

The circumscription of *Martinella* remained very stable over the years (Lohmann and Taylor 2014). Despite the generic stability, delimitation of the Amazonian species remained confusing, which led some authors to consider the Amazonian *Martinella* as part of a species complex due to overlapping morphological characters (e.g., MacBride 1961, Zuntini and Lohmann 2014). Alwyn Gentry treated *M. insculpta* as a synonym of *M. obovata* in the floristic treatments of several Neotropical countries such as Panama (Gentry 1973), Ecuador (Gentry 1977), and Venezuela (Gentry 1982).

In the most recent synopsis of the genus (Zuntini and Lohmann 2014), three species were recognized: *M. insignis*, *M. iquitoensis* [= *M. insculpta*], and *M. obovata*. A recent molecular phylogeny of *Martinella* (Kataoka and Lohmann in prep.) recovered five main clades that are easily diagnosed by morphological features. Each of these clades is here recognized as a distinct species. Of these, three correspond to species treated in the recent synopsis of the genus (Zuntini and Lohmann 2014), i.e., *Martinella insculpta*, *Martinella insignis*, and *Martinella obovata*, while two correspond to taxa that are newly described here, i.e., *Martinella lanuginosa* Kataoka & L.G.Lohmann and *Martinella tomentosa* Kataoka & L.G.Lohmann.

Methods

The taxonomic revision of *Martinella* was based on living specimens and observations made on fresh material during field expeditions and the analyses of herbarium specimens deposited in the following herbaria: IAN, INPA, MG, MO, NY, QCA, QCNE, R, RB, SPF, and UFACPZ (acronyms follow Thiers, continuously updated). All specimens were examined either physically or digitally through high quality photographs of herbarium specimens. In many cases we accessed specimens' photographs that were available in virtual herbaria via the JSTOR Global Plants (https://plants.jstor.org/), the Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/), or websites of individual herbaria.

Field expeditions were conducted between June and December 2016 in the Brazilian states of Acre, Amazonas, Mato Grosso, Pará, and Roraima. All specimens were deposited at SPF. All accepted names are listed in alphabetical order. Nomenclatural discussions follow the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) (Turland et al. 2018). Citations of type specimens are followed by the herbarium acronym and barcode, unless otherwise stated between brackets.

We used a molecular phylogeny (Kataoka and Lohmann in prep.) and morphological data to circumscribe species. We treated separately evolving lineages as species, following De Queiroz (2007). In addition, only taxa diagnosable by unique combinations of morphological features were recognized as species (Cracraft 1983). Therefore, we recognized species as separately evolving lineages that share a unique combination of morphological characters.

Morphological descriptions follow the general terminology of Lohmann and Taylor (2014). Additional terms follow Radford et al. (1974) for general morphology, Hickey (1973) for leaf shape and venation, Weberling (1992) for inflorescence type, Nogueira et al. (2013) for trichome type, and Gentry and Tomb (1979) or Halbritter et al. (2018) for pollen morphology. All measurements were carried out on dried specimens and/or rehydrated material. In addition, pollen from herbarium specimens were analyzed using scanning electron microscopy (SEM) on a Zeiss DSM 970 scanning electron microscope. Rare character conditions are shown in parentheses in the species descriptions.

Distributions maps were produced in QGIS 2.18 (QGIS Development Team 2018) using a dataset that included a combination of two separate datasets: (i) a newly generated distribution dataset with approximately 150 records from collections made in the field and from digitized specimen labels, and (ii) a dataset with approximately 500 records compiled during the past 25 years (Lohmann unpublished data, described in Meyer et al. 2017).

Preliminary conservation status assessments were performed using the complete distribution dataset using the Geospatial Conservation Assessment Tool (GeoCAT; http://geocat.kew.org/) (Bachman et al. 2011). This tool considers the metrics Extent of Occurrence (EOO) and Area of Occupancy (AOO) for 4 km^2 grids to objectively estimate conservation status based on the IUCN's criterion B (IUCN 2012; IUCN Standards and Petitions Subcommittee 2017). We only considered EOO to estimate conservation status of each species as this criterion is less prone to extinction risk overestimation.

The list of examined specimens was produced using the R package monographaR (Reginato 2016).

Geographic distribution

Members of *Martinella* are distributed in wet forests of Central America, northern South America, the Amazon and the Atlantic Forest of Brazil, between 0–1700 m above sea level (a.s.l.) (Zuntini and Lohmann 2014). Among the five *Martinella* species recognized in this study, *M. obovata* is the most frequent and broadly distributed, occurring from southern Mexico to the southern Amazon, reaching as far south as Bolivia and the Brazilian state of Mato Grosso do Sul. *Martinella insculpta* is also broadly distributed in Central America and Amazonia, but is less common when compared to the sympatric *M. obovata*. The other three species in the genus are rare, with narrow distribution ranges. The only known records of *M. tomentosa* are from Central Brazilian Amazon (Amazonas state), while *M. lanuginosa* is only known from western Brazil (Acre state), Peru, and northern Colombia. Lastly, *M. insignis* is the only member of *Martinella* that is restricted to the Atlantic Forest, occurring in the states of Espírito Santo and Bahia, in eastern Brazil.

Habitat

Species of *Martinella* occur in wet Neotropical forests. *Martinella insculpta*, *M. lanuginosa*, and *M. tomentosa* predominantly occur in *terra firme* (non-flooded) forests in the Amazon, with some reports of *M. insculpta* growing in white-sand soils. *Martinella obovata* preferentially occurs along riverbanks of the Amazonian white-water rivers, where many individuals were found during field expeditions, and where many collections were made over the years. *Martinella insignis* is restricted to sandy soils of the Brazilian Atlantic Forest, growing close to the shore (Zuntini and Lohmann 2014).

Reproductive biology

All species of *Martinella* share the flower morphology described by Gentry (1974) as *Martinella*-type flower. This floral morphology is characterized by spathaceous, tubular or urceolate calyces, and by tubular, infundibuliform, or urceolate corollas that are straight and coriaceous, varying in color from red to magenta, or white (Gentry 1974; Alcantara and Lohmann 2010). These traits suggest hummingbird pollination.

All Amazonian species of *Martinella* fit the pollination syndrome suggested by their floral morphology, which is supported by field observations, although Euglossini bee visitation was also observed (Gentry 1974). Conversely, *M. insignis* has a yellow corolla that is unique in the genus. This corolla color suggests bee pollination, although field studies are needed to confirm this prediction.

Economic and ethnobotanical uses

Bignoniaceae species are traditionally used for timber, handicraft, and medication (Gentry 1992). *Martinella* species are broadly used by Amazonian indigenous peoples to treat eye inflammation and conjunctivitis (e.g., Gentry and Cook 1984; Alexiades 1999). Extracts are made using the root's outer bark, which is scraped, macerated with water, filtered and used as eye drops (e.g., Gentry and Cook 1984; similar reports are available in herbarium specimens' labels, e.g., G.T. Prance 15557 deposited at INPA and Lewis 14026 deposited at QCNE).

The widespread use of *Martinella* extracts for medicinal purposes throughout the Amazon motivated chemical analyses, which led to the discovery of the alkaloids Martinelline and Martinellic acid from organic extracts of *M. iquitoensis* [= *M. insculpta*] (Witherup et al. 1995). Further studies have been conducted attempting to synthesize these compounds (e.g., Davies et al. 2013).

Cytology

Chromosome counts for *Martinella obovata* is $2n = 40$ (Goldblatt and Gentry 1979), which also corresponds to the most common chromosome number in the tribe Bignonieae as a whole (Cordeiro et al. 2017).

Morphology

Habit. All species of *Martinella* are lianas, although seedlings are self-supporting shrubs up to 70 cm tall (see Fig. 1A–C).

Stems. Mature stems of *Martinella* bear lenticels and solid pith with four phloem wedges in cross section. Stems with four phloem wedges predominate within tribe Bignonieae and are also found in *Adenocalymma*, *Callichlamys*, *Cuspidaria*, *Fridericia*, *Lundia*, *Manaosella*, *Neojobertia*, *Tanaecium*, *Tynanthus*, *Pachyptera*, *Pleonotoma*, and *Stizophyllum* (Lohmann 2006, Lohmann and Taylor 2014). Young stems are cylindrical and generally remain cylindrical at maturity, becoming tetragonal in *Martinella insculpta*. A continuous ring surrounds the interpetiolar regions of stems (see Fig. 1E). The stem surface is smooth, sparsely to densely covered with trichomes. Stems over ca. 4 cm in diameter often have sparse lenticels. Non-lenticelled parts of the stem are pale to dark green, often with dark blotches.

Prophylls of the axillary buds. Structures traditionally referred to as pseudostipules (Gentry 1980) were subsequently shown to represent well-developed prophylls of the

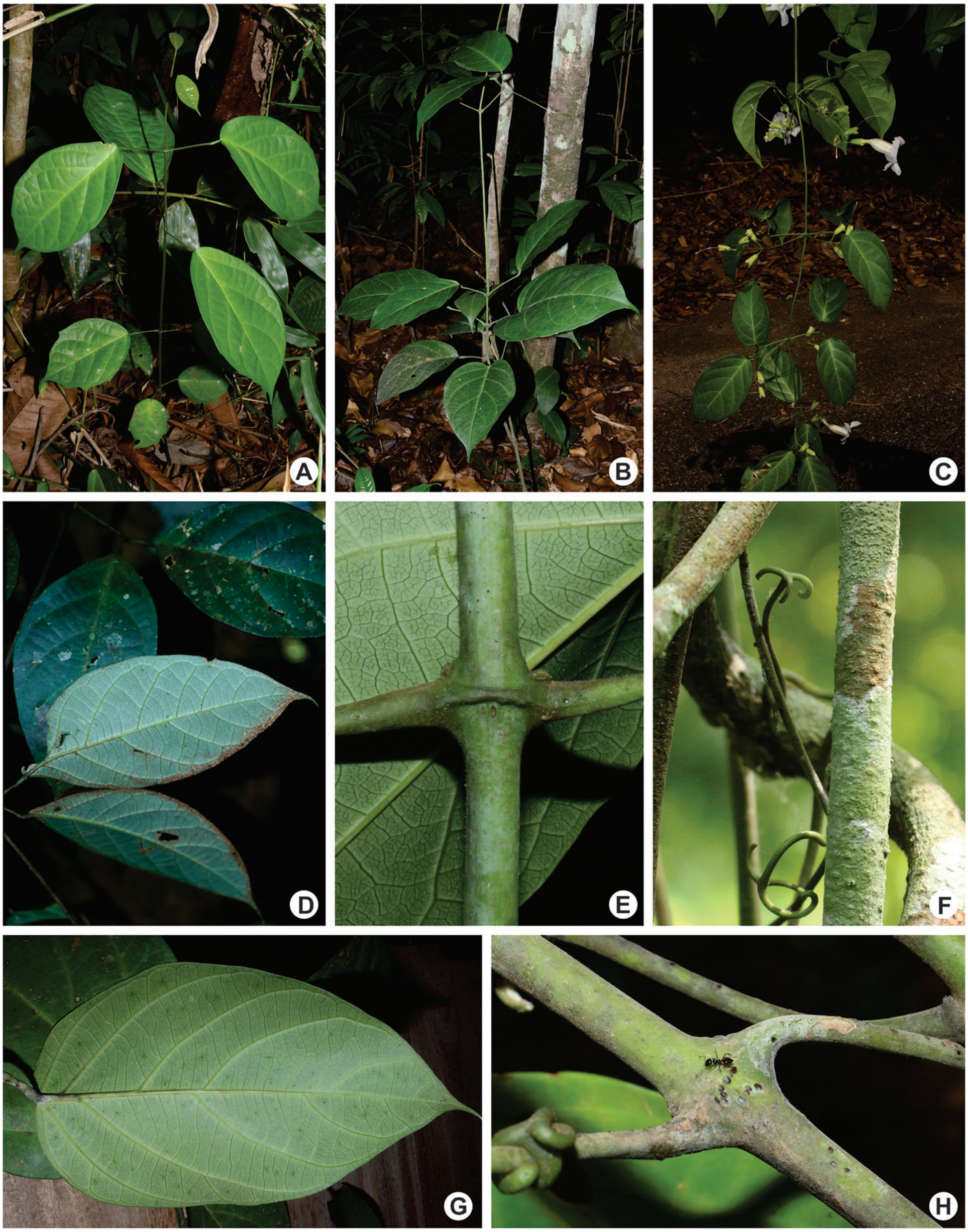


Figure 1. Vegetative characters of *Martinella* Baill **A, B** young individuals of *M. obovata* and *M. insculpta* bearing unifoliolate leaves **C** branch of *M. obovata* **D** discolor leaflets of *M. insculpta* **E** interpetiolar ridge of *M. obovata* **F** trifid tendril of *M. insculpta* **G** abaxial side of leaflets of *M. insculpta* with patelliform glandular trichomes **H** interpetiolar region of *M. insculpta* with patelliform glandular trichomes being visited by ants. Photos taken by E.Y. Kataoka, except from photo **D** taken by R. Foster.

axillary buds (Lohmann and Taylor 2014). Prophylls are very useful structures for the identification of genera and species in tribe Bignonieae, often representing morphological synapomorphies of generic-level clades (Lohmann and Taylor 2014). All species of *Martinella* have minute triangular prophylls, a putative morphological synapomorphy of the genus (Lohmann 2006) (see Fig. 1E, H).

Leaves. In Bignonieae, leaves are commonly 2-foliolate or 3-foliolate with the terminal leaflet modified in a tendril (Gentry 1980; Lohmann and Taylor 2014). In mature individuals of *Martinella*, leaves are exclusively 2-foliolate, bearing a trifid tendril, with discolor leaflets that bear glandular trichomes on the abaxial side (see Fig. 1C, D, F, G). Young individuals of *M. insculpta* and *M. obovata* show unifoliolate leaves at first and lack tendrils (see Fig. 1A, B). In some taxonomic treatments, *Martinella* was described as bearing simple or trifid tendrils (MacBride 1961; Gentry 1977; Zuntini and Lohmann 2014). However, careful examination of herbarium specimens revealed that most seemingly simple tendrils corresponded to trifid tendrils with missing parts. Trifid tendrils represent the ancestral character state within tribe Bignonieae and were maintained in *Martinella* (Sousa-Baena et al. 2014). Leaf venation is brochidodromous in all species of *Martinella*. Leaf domatia is only found in *M. insignis*, as pocket-like structures at the axil of the midvein with the secondary veins, on the abaxial side of leaflets, mainly at the basal portion.

Trichomes. Four main types of trichomes are found in tribe Bignonieae: (i) non-glandular (eglandular) trichomes, (ii) peltate glandular trichomes, (iii) stipitate glandular trichomes, and (iv) patelliform/cupular glandular trichomes (Nogueira et al. 2013). Trichome distribution on the plant body is highly variable, although some genera of tribe Bignonieae are readily recognized by diagnostic patterns of trichome distribution, e.g., *Adenocalymma*, with patelliform glandular trichomes on the prophylls of the axillary buds, floral bracts, calyces, bracteoles, and fruits (Lohmann and Taylor 2014; Fonseca and Lohmann in prep.), and *Pachyptera*, with a field of patelliform glandular trichomes at the interpetiolar region and petiole apex (Francisco and Lohmann 2018). In species of *Martinella*, three trichome types are found: (i) non-glandular trichomes (referred to as simple eglandular trichome hereafter), (ii) stipitate glandular trichomes, and (iii) patelliform glandular trichomes (commonly referred to as "glands" in the literature). The simple eglandular trichomes are distributed throughout the plant, often with density variation in different plant organs; stipitate glandular trichomes are found in high density on the whole plant of *M. insignis* and *M. lanuginosa* and in variable density at different parts of the plant in other species; patelliform glandular trichomes are found on the whole plant of all members of *Martinella*, mainly at the interpetiolar region, and at the base of the abaxial surface of leaflets (see Fig. 1E, H). The patelliform glandular trichomes can also be found on stems, inflorescences, and calyces of *M. insculpta* and *M. obovata*.

Inflorescences. Flowers of *Martinella* are organized in axillary and/or terminal inflorescences that bear six to 26 flowers, although only a few flowers open at a time. Botryoid inflorescences are found in *M. insculpta*, racemes are found in *M. obovata*, and thyrses are found in *M. insignis*, *M. tomentosa*, and *M. lanuginosa*. Botryoid and racemose inflorescences (see Fig. 2A, B) are lax, contrasting with the congested thyrses, which show higher levels of branching and a higher number of flowers per inflorescence.

Figure 2. Reproductive characters of *Martinella* Baill **A–C** flowers of *M. obovata* in frontal (**A**) and lateral view (**B, C**) **B** irregularly 3-parted calyces, and corolla narrowly-tubular at base and campanulate at upper portion **C** euglossini bee visiting the flower of *M. obovata* **D** lateral view of *M. insignis* flower showing the typical corolla shape and 5-parted calyx **E** scanning electron micrograph showing tricolpate and reticulate pollen grains of *M. obovata* **F** dried seeds of *M. obovata* with greenish wings **G** flat, narrow, and long (≤ 1.5 m) fruit of *M. obovata*. All photos taken by E.Y. Kataoka, except from photo **C** taken by G. Gerlach, and **D** taken by A.R. Zuntini.

Calyx. Calyx morphology is highly variable within Bignonieae (Lohmann and Taylor 2014). However, this trait is quite constant within *Martinella*, with the tubular-campanulate and irregularly 2–4-lobed calyx (or regularly 5-lobed in *M. insignis*) representing a diagnostic character (Lohmann 2006; Lohmann and Taylor 2014) (see Fig. 2B–D).

Corolla. Corolla shape is an additional distinctive feature in *Martinella*. All species show tubular-campanulate corollas, with a tubular basal portion that is long and much narrower than the markedly campanulate upper portion, giving an inflated appearance compared to the basal portion (see Fig. 2A–D). This distinctive corolla morphology was described by Gentry as the *Martinella*-type flower (Gentry 1974). Corolla color varies from pale lilac (*M. obovata*) to dark magenta (*M. insculpta*) or yellow (*M. insignis*). Corolla color in *Martinella lanuginosa* and *Martinella tomentosa* is unknown, but seems to vary from lilac to magenta, as in other Amazonian species.

Androecium. Members of *Martinella* have four didynamous stamens and one very reduced staminode (ca. 1 mm long). The stamens are inserted at the inferior portion of the corolla tube, at approximately 1/4 of the corolla length. Anthers are included, bearing straight and divaricate thecae, and showing glabrous filaments and thecae.

Pollen. Gentry and Tomb (1979) highlighted the usefulness of pollen morphology to generic-level identification of members of Bignonieae, although this trait shows convergent evolution. In *Martinella*, pollen is quite constant, tricolpate with reticulate exine (see Fig. 2E) in all species. Similarly, reticulate pollen grains are also found in *Bignonia*, *Mansoa*, *Pachyptera*, and *Pyrostegia* (Gentry and Tomb 1979, Francisco and Lohmann 2018).

Gynoecium. As in most Bignonieae, *Martinella* has a bilocular ovary with two fused carpels with axillary placentation (Gentry 1980), a single style with lanceolate and bilamellate stigma. The ovary is terete, with a glabrous and smooth surface.

Fruits. Species of *Martinella* have linear, flattened, septicidal capsules with two valves. Capsules of *Martinella* are among the longest fruits in Bignonieae, reaching up to 1.5 m long and 3 cm wide (Fig. 2G), only comparable to *Dolichandra* fruits (Fonseca et al. 2017). In addition, the capsules are glabrous to puberulent.

Seeds. Seeds of *Martinella* are symmetrically winged, oblong, and thin (Fig. 2F). The seed body is chartaceous, opaque and brown or green, even when dried (in *M. obovata*). The seed wings are membranous and translucent, brown or green-colored. Like several other clades of Bignoniaceae, seeds are wind-dispersed (Gentry 1979; Gentry 1980).

Taxonomic treatment

Martinella Baill., Hist. Pl. 10: 30. 1888

Type. *Martinella martini* (DC.) Baill. [= *Martinella obovata* (Kunth) Bureau & K.Schum.].

Description. Lianas. ***Roots*** with swollen portions. ***Branches*** green or light brown, terete, tetragonal, glabrous, puberulous or pubescent, eglandular trichomes simple, glandular trichomes stipitate or patelliform, with a continuous ridge at the interpetiolar region, with few interpetiolar patelliform trichomes; prophylls of the axillary buds minute, glabrous, puberulous or pubescent. ***Leaves*** 2-foliolate with the terminal leaflet generally modified in a trifid tendril; leaflets membranous, chartaceous or coriaceous, glabrous to pubescent, margins entire, revolute, more conspicuously when dried, with or without mite-domatia, with patelliform glands on the adaxial surface. ***Inflorescences*** axillary, botryoid, racemose, or a thyrse. ***Flowers*** with calyces tubular-campanulate, irregularly 2–4(–5)-lobed, lobe apices mucronate or aristate, chartaceous, with scattered patelliform glands; corolla deep purple, lilac, dark magenta or yellow, narrowly tubular at basal portion and wide campanulate at upper portion, straight to slightly curved, membranous, outer surface glabrous, inner surface glabrous with eglandular trichomes concentrated at stamen insertion; stamens included, glabrous, pollen tricolpate and reticulate; ovary terete, smooth, glabrous, with a single series of ovules per placenta, style glabrous, stigma rhombic, glabrous. ***Capsules*** drying brown, linear, flattened, smooth, glabrous, with calyx normally persistent; seeds oblong, winged, with wings opaque, green or beige.

Discussion. The nomenclatural type of *Martinella* has been indicated as *Martinella martinii* (DC.) Baill. ex K.Schum. in earlier treatments of the genus (e.g., Lohmann and Taylor 2014; Zuntini and Lohmann 2014) because Schumann (1894) was the first to explicitly associate the genus name with a species epithet. However, Baillon (1888) provided a footnote that says "Generis typus est *Bignonia Martini* DC.," representing a valid reference to a previously published basionym, and validly publishing the name *Martinella martini* (DC.) Baill. (see Art. 41.3 and 38.13 of Turland et al. 2018).

As circumscribed here, *Martinella* comprises five species distributed from southern Mexico to eastern Brazil. A key to all species recognized is given below:

Key to species of *Martinella*

1	Abaxial surface of leaflets with pocket domatia on the axils of the primary and secondary veins; calyx 5-lobed; corolla yellow; eastern Brazil (Atlantic Forest)	***M. insignis***
–	Abaxial surface of leaflets without pocket domatia; calyx irregularly 2–4-lobed; corolla lilac to deep purple or dark magenta; southern Mexico, the Antilles, Central America and South America (Amazon basin)	**2**
2	Inflorescence racemose	***M. obovata***
–	Inflorescence botryoid or a thyrse	**3**
3	Mature stem quadrangular in cross section; leaflet coriaceous; inflorescence botryoid	***M. insculpta***
–	Mature stem cylindrical in cross section; leaflet chartaceous; inflorescence a thyrse	**4**
4	Branches densely covered with simple eglandular trichomes; leaflets tomentose abaxially	***M. tomentosa***
–	Branches densely covered with stipitate glandular trichomes; leaflets lanuginose abaxially	***M. lanuginosa***

1. *Martinella insculpta* Sprague & Sandwith, Bull. Misc. Inform. Kew 1934(3): 101. 1934

Fig. 3

Martinella iquitoensis A.Samp., Ann. Acad. Bras. Sci. 7: 123. 1935. [*Martinella iquitosensis*, orth. var.]. TYPE: PERU. Loreto: Iquitos, 23 Feb 1924, *J.G. Kuhlmann 1492* (holotype: RB-00536899!; isotypes: RB-00537289!, K-000449503 image!, MO-074501 image!).

Martinella manaosiana A.Samp., Bol. Mus. Nac. RJ. 12(3–4): 84. 1936. TYPE: BRAZIL. Amazonas: Manaus, Capuêra de terra firme, Villa Belizario, 25 Jul 1931, *A. Ducke* s.n. [RB 24095] (holotype: RB-00536900!; isotypes: K-000449502 image!, MO-074517 image!, R-000028732!, RB-00537290!).

Type. Guyana. Unknown locality, s.d., *Drake* s.n. (holotype: K-000449501 image!).

Description. Lianas; ***branches*** with solid pith, tetragonal when mature, cylindrical when young, green with dark blotches, drying brown or black, smooth, glabrescent, with simple eglandular trichomes and scattered patelliform glandular trichomes in higher densities at interpetiolar region; prophylls of the axillary buds covered with simple eglandular trichomes, with few patelliform glands. ***Leaves*** 2-foliolate, with the terminal leaflet generally modified into a trifid tendril; petioles terete, pulvinated, 31–73 mm long, glabrous, with few patelliform glandular trichomes; petiolules terete, pulvinated, 23–65 mm long, glabrous, with few patelliform glandular trichomes; leaflets discolor, with abaxial surface lighter than the adaxial surface, coriaceous, ovate, apex acuminate, base cuneate or truncate, margins entire and slightly revolute, 15–32 × 8.2–23.5 cm, adaxial surface glabrous with simple eglandular trichomes at canaliculi of veins, abaxial surface glabrescent, with patelliform glandular trichomes concentrated near base and scattered along the midvein. ***Inflorescences*** botryoid, 8.7–22.3 cm long, puberulent with simple eglandular trichomes, and stipitate and patelliform glandular trichomes; bracts linear, 1.1–1.2 mm long, puberulent, with simple eglandular trichomes and stipitate glandular trichomes; pedicels terete, 11.1–15.2 mm, puberulent, with simple eglandular trichomes and stipitate glandular trichomes. ***Flowers*** with calyx green, chartaceous, campanulate, 11.8–16.8 × 5.5–8 mm, densely covered with simple eglandular trichomes and stipitate glandular trichomes, with few patelliform glandular trichomes, lobes 2–4, apex mucronate, puberulent; corolla dark magenta, membranous, 41.3–69.4 mm long, narrowly tubular basal portion 15–27.4 long × 2.9–4.3 mm wide, upper campanulate portion 26.3–41.9 long × 12–16.6 mm wide, slightly curved, lobes subcircular, ca. 8.7 × 12.7 mm; stamens in two lengths, longer ones 16–21.2 mm, shorter ones 9.8–14 mm, thecae 2.9–3.1 mm, glabrous; staminode ca. 1.8 mm, glabrous; gynoecium 34.8–45.2 mm long; ovary glabrous; style glabrous; stigma lanceolate, glabrous; nectariferous disk ca. 4.3 × 0.9 mm. ***Capsules*** linear, 70–88 × 1.1–1.6 cm, glabrous. *Seeds* ca. 4.7 × 0.9 cm.

Distribution and habitat. *Martinella insculpta* is widely distributed through Amazonian *terra firme* forests and Central American wet forests (Fig. 4). This species occurs from 59–650 m a.s.l.

Etymology. The specific epithet means carved, engraved, referring to the aspect of leaflet venation on both sides, but especially on the adaxial surface.

Phenology. Flowering specimens were collected from February to November, while fruiting specimens were collected from August to December.

Conservation status. Least Concern (LC) based on the EOO of 4,002,910 km^2.

Discussion. Here we synonymize *Martinella iquitoensis* under *Martinella insculpta*. Gentry (1973) synonymized *Martinella insculpta* A.Samp. under *M. obovata*, a circum-

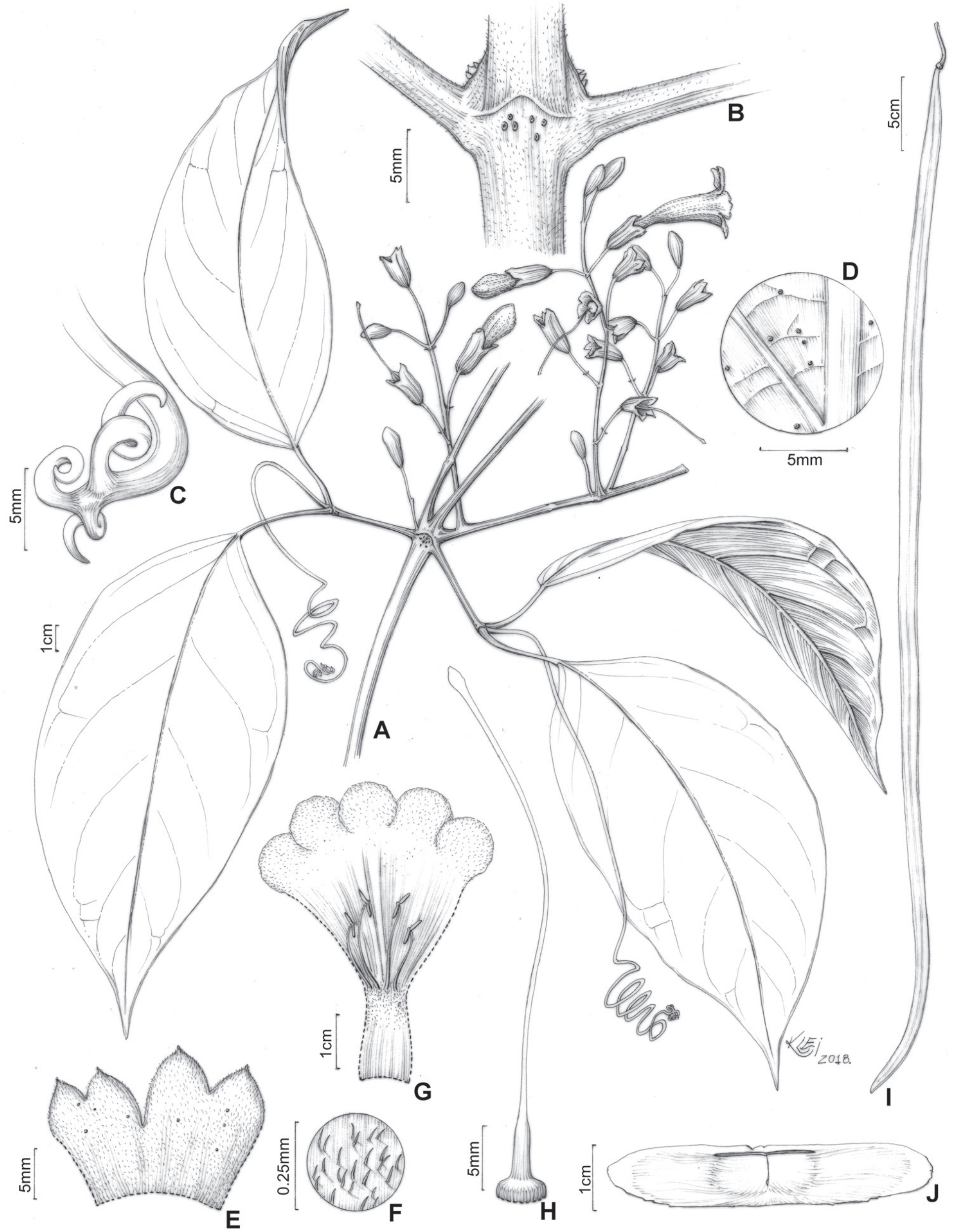


Figure 3. *Martinella insculpta* Sprague & Sandwith **A** flowering branch **B** interpetiolar region with patelliform glandular trichomes and minute and triangular prophylls **C** trifid tendril **D** abaxial side of leaflet with patelliform glandular trichomes **E** calyx external view **F** calyx indumentum **G** open flower showing stamens, trichome distribution, and reduced (ca. 1 mm) staminode **H** gynoecium **I** fruit, flattened with a smooth surface **J** winged seed. Illustrated by Klei Sousa, based on B.L. Stannard 423 (**A, E, G, H**), SPF; E.Y. Kataoka 372 (**B**) and 407 (**C, D**), SPF; G.T. Prance 14914 (**I, J**), INPA; L.O.A. Teixeira 958 (**F**), INPA.

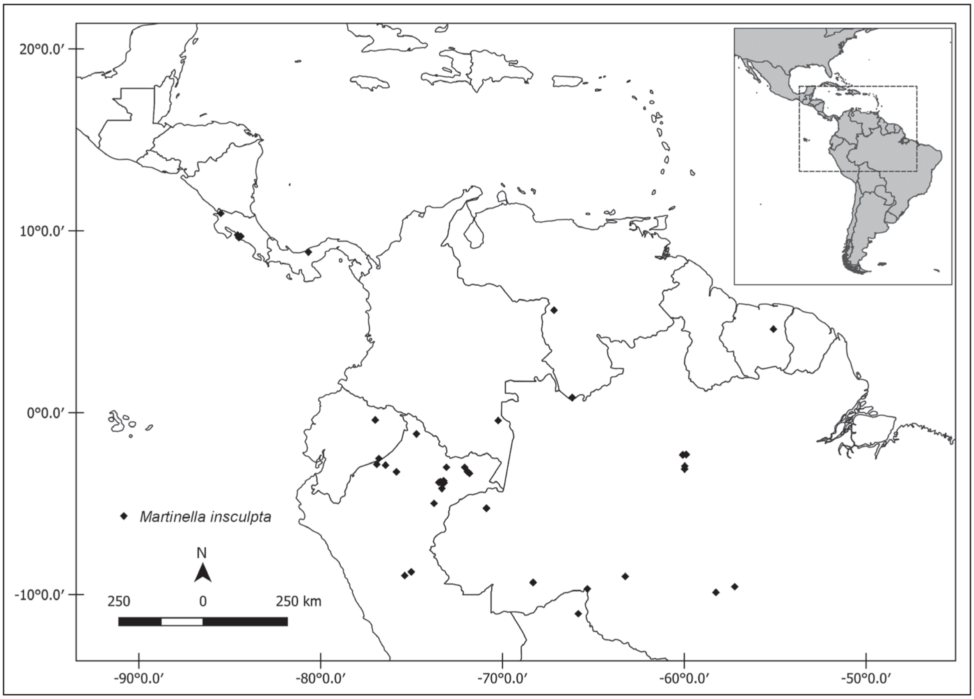


Figure 4. Distribution map of *Martinella insculpta*.

scription that was followed in subsequent taxonomic studies (e.g., Gentry 1977; Gentry 1982). However, the analysis of a large number of living and herbarium specimens of these taxa indicated that the original description and type specimen of *M. insculpta* actually match the circumscription of *M. iquitoensis*. Therefore, *M. iquitoensis* A.Samp. (published in 1935), is here treated as a synonym of *Martinella insculpta* Sprague & Sandwith (published in 1934).

Previous taxonomic studies (Gentry 1982; Zuntini and Lohmann 2014) treated *M. insculpta* and *M. obovata* as part of a species complex due to overlapping morphological characters. However, new collections made in the field and a comprehensive analysis of herbarium specimens collected throughout the known geographic range of this species indicated that these two taxa indeed represent distinct units. Our decision to treat these taxa as separate species was based on the following morphological traits: (i) shape of mature stems in cross section (quadrangular in *M. insculpta* versus cylindrical in *M. obovata*), (ii) apex of petioles and petiolules (pulvinated in *M. insculpta* versus non-pulvinated in *M. obovata*), (iii) leaflet texture and size (coriaceous and consistently larger in *M. insculpta* versus chartaceous and smaller in *M. obovata*), and (iv) inflorescence structure (botryoid in *M. insculpta* and racemose in *M. obovata*). The combination of these distinctive morphological features allows for the correct identification of specimens that are often misidentified in herbarium sheets. In addition, a densely sampled phylogeny of *Martinella* revealed that *M. insculpta* and *M. obovata* represent distinct evolutionary lineages (Kataoka and Lohmann in prep.) providing further support for the recognition of these two taxa as separate species.

Common uses. The bark of the roots of *M. insculpta* and *M. obovata* is used in traditional medicine.

Local names. *Martinella insculpta* and *M. obovata* are known by the popular names *raiz dos olhos* (Brazil), *yuquilla toxju* (Peru), *raíz de ojo*, and *uarakú-manaté* (Venezuela).

Specimens examined. Bolivia. Beni: Province of Vaca Diez, 17 km from the road between Riberalta and Guayaramerín on the old road to Cachuela Esperanza, ca. 18 km E of Riberalta, primary forest, 230 m, 11°3'S, 65°50'W, 4 Sept 1981, *J.C. Solomon 6108* (MO). **Brazil. Acre:** Bujari, estrada de acesso à área da Floresta do Antimary sem atividade de manejo florestal, 196 m, 9°19'46.1"S, 68°18'56.2"W, 10 Dec 2016, *E.Y. Kataoka 404* (SPF); Lado direito da entrada da trilha de acesso à torre de observação, 226 m, 9°20'5.3"S, 68°19'13.1"W, 12 Dec 2016, *E.Y. Kataoka 407* (SPF). **Amapá:** Rio Falsino, approx. 10 km upstream of confluence with rio Araguari, west bank, primary forest on terra firme, undulating terrain, 0°50'S, 51°45'W, 29 Sept 1983, *B.V. Rabelo 2386* (SPF). **Amazonas:** Rainforest, vicinity of Maturacá Mission, near rio Maturacá, on trail to heliport, 19 Oct 1970, *J.A. Steyermark 104035* (IAN); Rio Cuieiras just below mouth of rio Branquinho, capoeira, 26 Sept 1971, *G.T. Prance 14914* (INPA, MG, R); Rio Purus, rio Ituxi, serra near Namorado Novo between rio Curuquetê and rio Madeira at Abunã, forest on Terra Firme, 5 Aug 1971, *G.T. Prance 14717* (INPA, MG, R); Barcelos, rio Negro, próximo ao rio Arara, 1 May 1973, *A. Loureiro 37901* (INPA, SPF); Humaitá, Estrada Humaitá-Lábrea, km 59, a 6 km ao norte, mata de terra firme, com muito Babassu, 6 Jun 1982, *L.O.A. Teixeira 958* (INPA, MG); Manaus, 22 Jun 1882, *Schwacke 3610* (RB); A partir da entrada da Reserva pela AM-010 (km 26), estrada sentido alojamento, lado esquerdo na bifurcação entre estrada de acesso ao alojamento e estação meteorológica, 139 m, 2°55'59"S, 59°58'31.9"W, 21 Sept 2016, *E.Y. Kataoka 344* (SPF); Bosque da Ciência do INPA, próximo ao Paiol da Cultura, subindo pela escadaria larga, 84 m, 3°5'56.5"S, 59°59'10.5"W, 20 Sept 2016, *E.Y. Kataoka 342* (SPF); Bosque da Ciência do INPA, próximo ao tanque dos peixes-boi, 69 m, 3°5'50.6"S, 59°59'15.1"W, 20 Sept 2016, *E.Y. Kataoka 339* (SPF); Estrada do Aleixo, km 7, 7 Jul 1977, *W.A. Rodrigues 9707* (INPA, SPF); Estrada do Aleixo, near Manaus, turnoff to rio Negro at km 11 past INPA, 2 Dec 1974, *A.H. Gentry 13024* (INPA); Grounds of INPA at Manaus, 5 Apr 1974, *A.H. Gentry 11208* (INPA); Igapó, 14 Jun 1882, *C.A.W. Schwacke 425* (R); Igapó, 22 Jun 1882, *C.A.W. Schwacke 463* (R); Sede do INPA, estrada do Aleixo, 30 Jul 1973, *P.L. Lisboa 6* (INPA); Presidente Figueiredo, Vila de Balbina, Represa da UHE de Balbina, mata de beira de rio, 27 Jun 2007, *J.A.C. da Silva 1294* (INPA); Rio Preto da Eva, estrada Manaus-Itacoatiara, km 90, rio Preto, terra firme, solo arenoso, 30 Jul 1961, *W. Rodrigues 2203* (INPA); Santa Isabel do Rio Negro, rio Uneiuxi, Makú indian village, 300 km above mouth, indian plantation, 23 Oct 1971, *G.T. Prance 15557* (INPA). **Mato Grosso:** Apiacás, Margem da estrada de acesso Paranaíta – Apiacás, 233 m, 9°33'53.3"S, 57°13'44.5"W, 12 Nov 2016, *E.Y. Kataoka 370* (SPF); Cotriguaçu, Margem da estrada de acesso Nova Bandeirante – Cotriguaçu, ca. 10 Km após travessia do rio Juruena, 251 m, 9°52'40.4"S, 58°15'47.1"W, 13 Nov 2016, *E.Y. Kataoka 372* (SPF). **Rondônia:** Rio Machado, curso inferior, igapó, Feb 1981, *M. Goulding 1324* (MG); Porto Velho, Represa Samuel southern end of E dike near quarry by road, ca. 2 km S of end of main dike, upland hillside forest, 9°00'S, 63°15'W, 7 Jun 1986, *W. Thomas 4974* (INPA). **Colombia. Antioquia:** Primary/old secondary forest on west bank of river, 2 km N of Quebrada La Tirana, tropical Wet/Very Wet Forest Transition zone, rainfall approx. 4400 mm/year, Vic. Planta Providencia 28 km SW of Zaragoza, valley of Río Anorí in areas surrounding the confluence of Quebrada La Tirana and Río Anorí, approx. 3 km upriver from Planta Providencia, 24 Mar 1977, *W.S. Alverson 266* (MO); San Luis, Autopiste Medellín – Bogotá, sector Río Samaná – Río Claro, San Luis – Antioquia, 500 m, 3 Dec 1981, *J.J. Hernandez 99* (QCA). **Costa Rica. Guanacaste:** Liberia, P.N. Guanacaste, cuenca del Tempisque, volcán Orosí, Estación Biológica Maritza, trail to Cacao Station, ca. 1 km from Maritza comedor, ~ 100 km into first patch of primary forest, N side of trail, 0.1 ha Transect Maritza, premontane moist forest, 650 m, 10°57'19.1748"N, 85°29'29.6432"W, 12 Mar 2003, *B. Boyle 7052* (MO). **Puntarenas:** Cantón de Garabito, R.B. Carara, cuenca del Tárcoles, sector Bijugual, entrando a los bosques poco intervenidos, 600 m, 9°46'0"N, 84°34'0"W, 14 May 1998, *A. Rodríguez 3367* (MO). **San José:** Turrubares, San Juan De Mata, area no protegida, Montelimar, 85 m, 9°37'24"N, 84°29'55"W, 15 Oct 2001, *A. Estrada 3072* (MO); Z.P. La Cangreja, Mastatal de Puriscal, bosque primario en parches remanentes, 300 m, 9°41'45"N, 84°23'47"W, 21 Oct 1992, *J.F. Morales 910* (MO). **Ecuador. Napo:** Coca (Puerto Francisco de Orellana), 8 km al N de Coca, bosque humedo tropical, suelo aluvial fertil, bosque secundario, 250 m, 0°24'S, 77°0'W, 8 Apr 1985, *W. Palacios 272* (MO, QCA, QCNE); **Pastaza:** Kapawi, Río Pastaza, village area, secondary and primary forests, and pastures, 235 m, 2°31'S, 76°48'W, 25–29 Jul 1989, *W.H. Lewis 14026* (QCNE). **Panama.** Colón, Teck Cominco Petaquilla mining concession, forest along road, 220 m, 8°49'39"N, 80°40'28"W, 20 Feb 2008, *G. McPherson 20083* (MO). **Peru. Huanuco:** Carretera marginal (in construction) km 4–12 south from Km. 86 of Pulcallpa-Tingo Maria road, 270 m, 8°45'S, 75°1'W, 1 Jun 1983, *A.H. Gentry 41384* (MO). **Loreto:** Pampa hermosa and vicinity, Río Corrientes, 1 km S of junction with Río Macusari, low rainforest, mostly terra firma with scattered white sand, 160 m, 3°15'S, 75°50'W, 3–20 Dec 1985, *W.H. Lewis 9975* (MO); Alto Amazonas, Puranchim, río Sinchiyacu, rainforest, terra firma and palm lowlands, 200 m, 2°50'S, 76°55'W, 3–7 Dec 1988, *W.H. Lewis 14389* (MO); Alto Amazonas, Andoas, Capihuari, 5 km NE of Andoas on Río Capihuari, near Ecuador border along oil pipeline, lateritic uplands alternating with Mauritia swamps, 240 m, 17 Nov 1979, *A.H. Gentry 28200* (MO); Primary forest behind Brillo Nuevo, Pebas, Río Yaguasyacu, Brillo Nuevo, 11 Sept 1981, *R. Hahn 123* (MO). **Maynas:** Iquitos, Carretera de Peña Negra, ca. 7 km de Quisto Cocha, en terreno arenoso, monte despejado, 150 m, 12 Jul 1982, *M. Rimachi Y. 6180* (MO); Carretera Iquitos-Nauta, km 45, bosque primario, 120 m, 4°10'S, 73°20'W, 12 Jun 1987, *R. Vásquez 9172* (MO); Iquitos, trail between extension of Yavari and Versailles, mostly highly disturbed upland scrub area, 11 Feb 1974, *M. Rimachi Y. 835* (MO); Puerto Almendras, Río Nanay, bosque primario en suelo con arena blanca, 122 m, 3°48'S, 73°25'W, 18 Jul 1988, *R. Vásquez 10977* (MO); Río Nanay, Carretera de Picuruyacu, trocha de la granja de la marina, en terreno arenoso, 160 m, 26 Jul 1982, *M. Rimachi Y. 6270* (MO); Río Momon, Momoncillo (Caserio), borde de pastizal de ganado, 17 Aug 1976, *J. Revilla 979* (MO); Santo Tomas (Iquitos), 100 m, 3°51'S, 73°13'W, 14 Apr 1979, *F. Ayala 1793* (MO); Napo, Environs of Río Santa María, collected one hour upstream of the Secoya village of "Vencedor", 4 hours by outboard from the mouth of the Santa Maria river, 100 m, 1°10'S, 74°44'W, 15 May 1982, *S.R. King 492* (MO). **Suriname. Brokopondo:** Brownsweg, near Brownsweg Nature Park, little disturbed high mesophytic rain forest on slope, gravelly clay soil, 240 m, 4°35'41.28"N, 55°6'0"W, 1 Oct 2005, *K. Van Kerckhove MVK 114* (SPF). **Venezuela. Amazonas:** Atures, transecto desde bosque alto denso con tatucos a orillas de río Cataniapo, hasta bosque medio ralo en parte alta de colina, a 1 km al oeste de San Pedro de Cataniapo, a unos 60 km al sur-este de Puerto Ayacucho, 100 m, 5°38'N, 67°10'W, 7 Mar 1981, *F. Guanchez 923* (MO); Río Negro, 0 to 2 km west of Cerro de La Neblina base camp, which is on Río Mawarinuma, 140 m, 0°50'N, 66°10'W, 7 Feb 1984, *R. Liesner 15711* (MO); Near Cerro de La Neblina base camp, which is on Río Mawarinuma, 140 m, 0°50'N, 66°10'W, 25 Mar 1984, *R. Liesner 16956* (MO); Río Negro, Neblina Massif, bongo (dugout) trip down rio Mawarinuma for c. 2 km + NW from base camp at mouth of canyon, 140 m, 0°50'N, 66°10'W, 31 Mar 1984, *B.L. Stannard 423* (SPF).

2. *Martinella insignis* A.H.Gentry ex Zuntini & L.G.Lohmann, Phytokeys 37: 17–21. 2014

Fig. 5

Type. Brazil. Bahia: Itamaraju, Rodovia Itamarajú-Teixeira de Freitas, 3 km de Itamarajú (BR-101). Fazenda Chapadão, 3 Nov 1983, *R. Callejas, A.M. de Carvalho & L.M. Silva 1629* (holotype: MBM-94960 image!; isotypes: K-000977667 image!, MO-074484 image!, NY-00483568 image!, RB-00058792!, CEPEC-00034725 not seen).

Description. Lianas; ***branches*** with solid pith, cylindrical, green, drying brown, striated, pubescent, densely covered with stipitate glandular trichomes; prophylls of the axillary buds densely covered with stipitate glandular trichomes. ***Leaves*** 2-foliolate, with the terminal leaflet generally modified into a trifid tendril; petioles terete, not pulvinated, 34.6–48.4 mm long, covered with stipitate glandular trichomes; petiolules terete, not pulvinated, 13.9–26.4 mm long, covered with stipitate glandular trichomes; leaflets discolor, with abaxial surface lighter than the adaxial surface, membranous, ovate, apex acuminate to caudate, base cordate, margins entire and slightly revolute, 6.4–8.8 × 3.6–5.2 cm, adaxial surface glabrous, with stipitate glandular trichomes on the margins and at the canaliculi of main veins, abaxial surface pubescent, densely covered with stipitate glandular trichomes at main veins, pocket domatia on the axils of primary and secondary veins, few patelliform glandular trichomes concentrated near base

Figure 5. *Martinella insignis* A.H. Gentry ex Zuntini & L.G. Lohmann **A** flowering branch **B** interpetiolar region **C** stipitate glandular trichomes **D** flower in lateral view **E** calyx (opened) and gynoecium **F** fruit **G** roots with swollen portions. Illustration reproduced from Zuntini and Lohmann (2014); illustrated by Klei Sousa, based on *A.R. Zuntini 151* (**A–E**) and *321* (**G**), SPF; *D. Sucre 5519* (**F**), RB.

and scattered along the midvein. ***Inflorescences*** in compound thyrses, 7.5–11.5 cm long, sparsely to densely covered with stipitate glandular trichomes; bracts linear to narrowly elliptic, 5.2–20.2 × 0.6–2.5 mm, pubescent, densely covered with stipitate

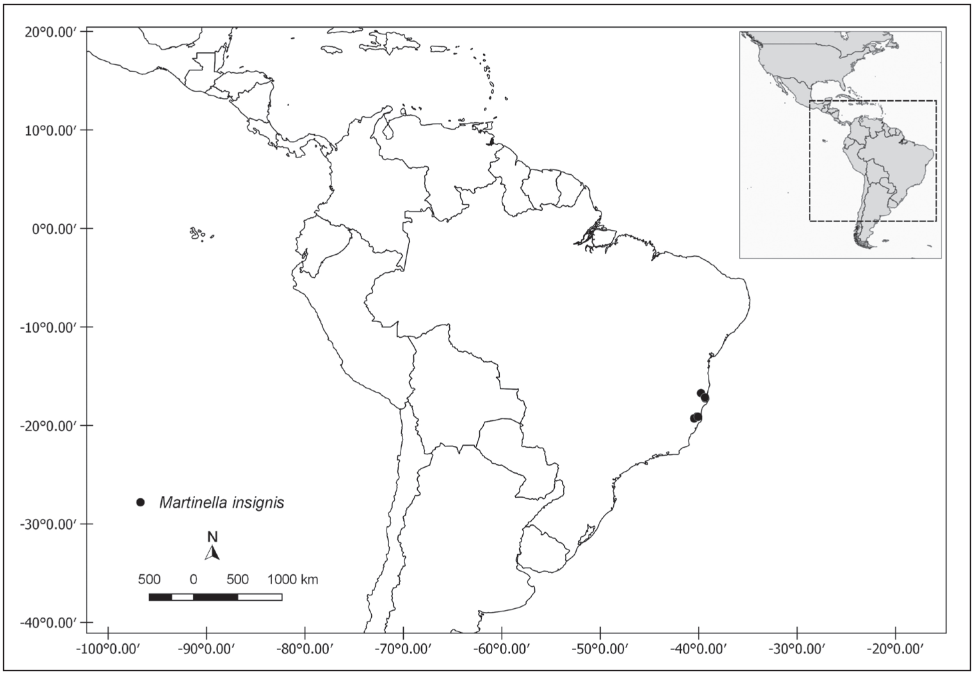


Figure 6. Distribution map of *Martinella insignis*.

glandular trichomes; pedicels terete, 6.3–11.2 mm, sparsely to densely covered with stipitate glandular trichomes. ***Flowers*** with calyx pale green, chartaceous, campanulate, 13.1–17.2 × 6.1–11.9 mm, densely covered with stipitate glandular trichomes, lobes 5, apex aristate, aristae 1.8–4.3 mm long, pubescent, densely covered with stipitate glandular trichomes; corolla yellow, membranous, 41.5–47.3 mm long, narrowly tubular basal portion 15.8–18.5 mm long × 2.5–4.9 mm wide, upper campanulate portion 23.1–32 mm long × 12.5–15.2 mm wide, slightly curved, lobes subcircular, 7.5–9.1 × 8.6–9.5 mm; stamens in two lengths, longer ones 12.4–13.3 mm, shorter ones 12.0–12.5 mm, thecae 2.5–2.7 mm, glabrous; staminode 1.3–3.4 mm, glabrous; gynoecium 30.9–35 mm long; ovary glabrous; style glabrous; stigma lanceolate, glabrous; nectariferous disk 2.3–3.1 × 1.0–1.2 mm. ***Capsules*** linear, 40.2–90 × 1.1–1.5 cm, pubescent when immature, glabrous when developed. ***Seeds*** ca. 4.5 × 1.2 cm.

Distribution and habitat. *Martinella insignis* is endemic to the Atlantic Forest of Eastern Brazil (see Fig. 6), where it grows in sandy soils, in areas between 62–590 m a.s.l.

Etymology. The specific epithet means conspicuous, readily distinguishable, referring to the contrasting corolla color when compared to other species.

Phenology. Flowering specimens were collected between October and February, while fruiting specimens were collected in January and November.

Conservation status. Vulnerable (VU) based on the EOO of 12,721 km^2.

Discussion. *Martinella insignis* is the only representative of the genus that occurs in the Atlantic Forest, where it is rare, with only a few herbarium collections available to date. In addition, *M. insignis* is remarkably distinctive from its congeneric species due to the membranous leaflets with pocket-shaped domatia on the abaxial surface, 5-lobed and aristate calyces, and yellow corollas.

Specimens examined. Brazil. Bahia: RPPN Fazenda Riacho das Pedras, prop. Gersino Antônio Bronzon, Mata de Tabuleiro com pequenos distúrbios (extração seletiva), 78 m, 17°8'48"S, 39°21'53"W, 12 Feb 2007, *R.A.X. Borges 825* (RB, SPF). **Espírito Santo:** Governador Lindemberg, Pedra de Santa Luzia, prop. Firmino Sottele, 420–590 m, 19°17'17"S, 40°27'56"W, 7 Nov 2007, *V. Demuner 4481* (SPF); Linhares, Reserva Natural Vale. MME, 5 Oct 2011, *A.R. Zuntini 321* (SPF); Sooretama, Reserva Natural da Companhia Vale do Rio Doce ("Reserva de Linhares"), 62 m, 19°6'59.7"S, 40°4'21.7"W, 14 Dec 2007, *A.R. Zuntini 151* (SPF).

3. *Martinella lanuginosa* Kataoka & L.G.Lohmann, sp. nov.

urn:lsid:ipni.org:names:77217116-1

Fig. 7

Type. Peru. Madre de Dios: Tambopata, Dist. Puerto Maldonado, Fundo Concepción, bosque ribereño, 200 m, 12°32'S, 69°03'W, 22 Aug 2003, *I. Huamantupa*, *J. Vargas & J. Quispe*, *3698* (holotype: SPF-240817!; isotypes: MO-2981780 not seen, AMAZ not seen, CUZ not seen, HUT not seen, USM not seen).

Diagnosis. *Martinella lanuginosa* differs from other Amazonian species of *Martinella* by the lanuginose leaflets on the abaxial surface and inflorescences arranged in lax thyrses, contrasting with the glabrous or tomentose leaflets on the abaxial surface and inflorescences botryoid or racemose found in all other Amazonian species.

Description. Lianas; ***branches*** with solid pith, cylindrical, green, drying light brown, smooth, pubescent, densely covered with stipitate glandular trichomes, with scattered patelliform glandular trichomes more frequently at interpetiolar region; prophylls of the axillary buds densely covered with stipitate glandular trichomes. ***Leaves*** 2-foliolate with the terminal leaflet generally modified into a trifid tendril; petioles terete, not pulvinated, 40–83.7 mm long, densely covered with stipitate glandular trichomes with few scattered patelliform glandular trichomes; petiolules terete, not pulvinated, 19.4–70.1 mm long, densely covered with stipitate glandular trichomes and occasional patelliform glandular trichomes; leaflets discolor, with abaxial surface lighter than the adaxial surface, chartaceous, ovate, apex acuminate, base cordate, margins entire and slightly revolute, 6.5–14.4 × 5.2–11.2 cm, adaxial surface glabrous, with simple eglandular trichomes and stipitate glandular trichomes at canaliculi of veins, abaxial surface lanuginose, densely covered with simple eglandular trichomes with few patelliform glandular trichomes distributed along the midvein. ***Inflorescences*** in thyrses, 6.5–11 cm long, densely covered with simple eglandular trichomes and stipitate glandular trichomes, with few patelliform glandular trichomes; bracts linear, 1.5–3 mm long, puberulent, densely covered with stipitate glandular trichomes; pedicels terete, 6.5–15.5 mm, densely covered with stipitate glandular trichomes. ***Flowers*** with

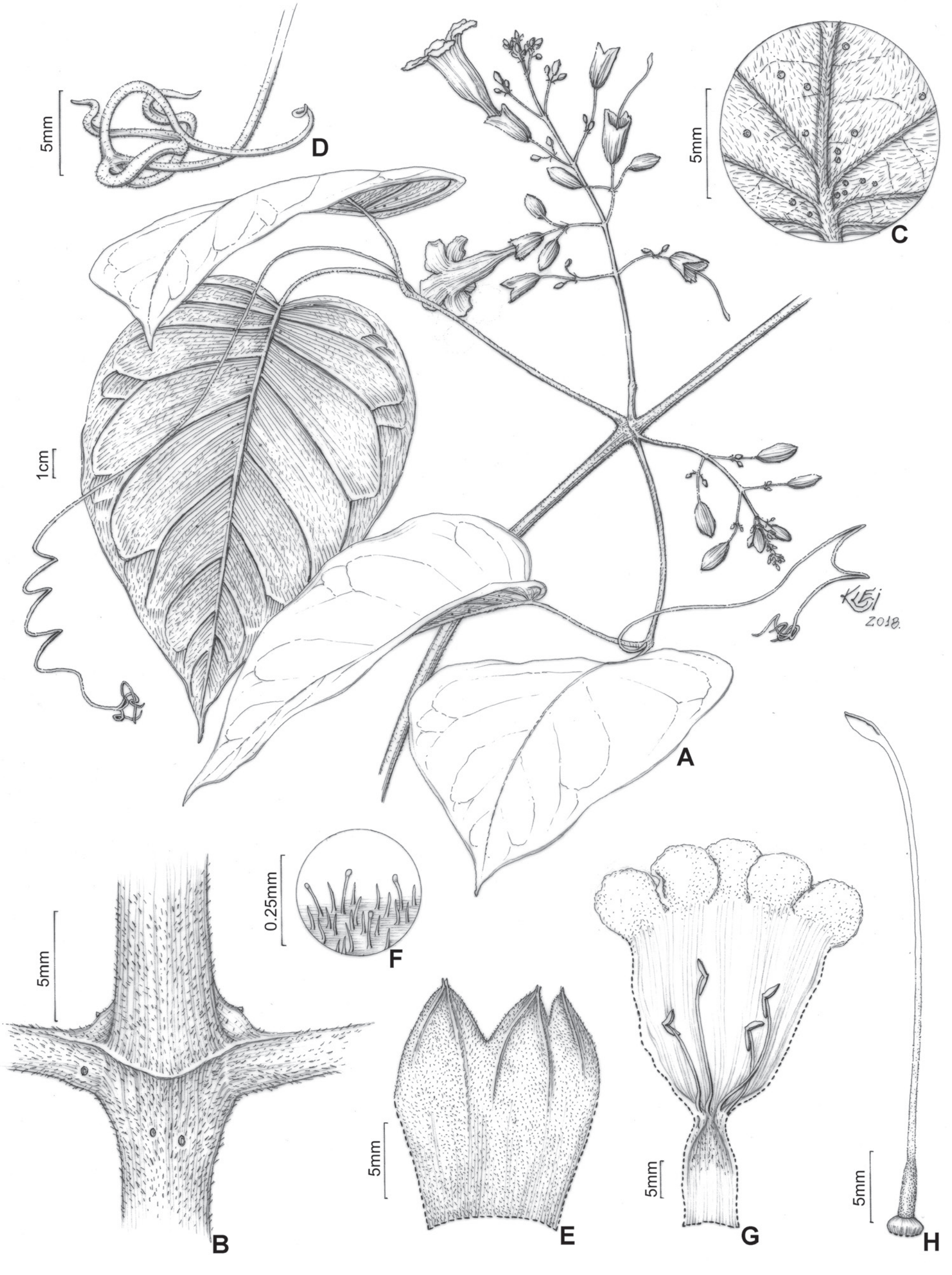


Figure 7. *Martinella lanuginosa* Kataoka & L.G. Lohmann **A** flowering branch **B** interpetiolar region with patelliform glandular trichomes **C** abaxial side of leaflet with lanuginose indumentum and patelliform glandular trichomes **D** trifid tendril **E** calyx external view **F** detail of calyx indumentum **G** open flower showing anthers, trichome distribution, and reduced (ca. 1.5 mm) staminode **H** gynoecium. Illustrated by Klei Sousa, based on *A.H. Gentry 27233* (**B, D**), MO; *I. Huamantupa 3698* (**A, E, F–H**), *R. Rueda 414* (**C**), SPF.

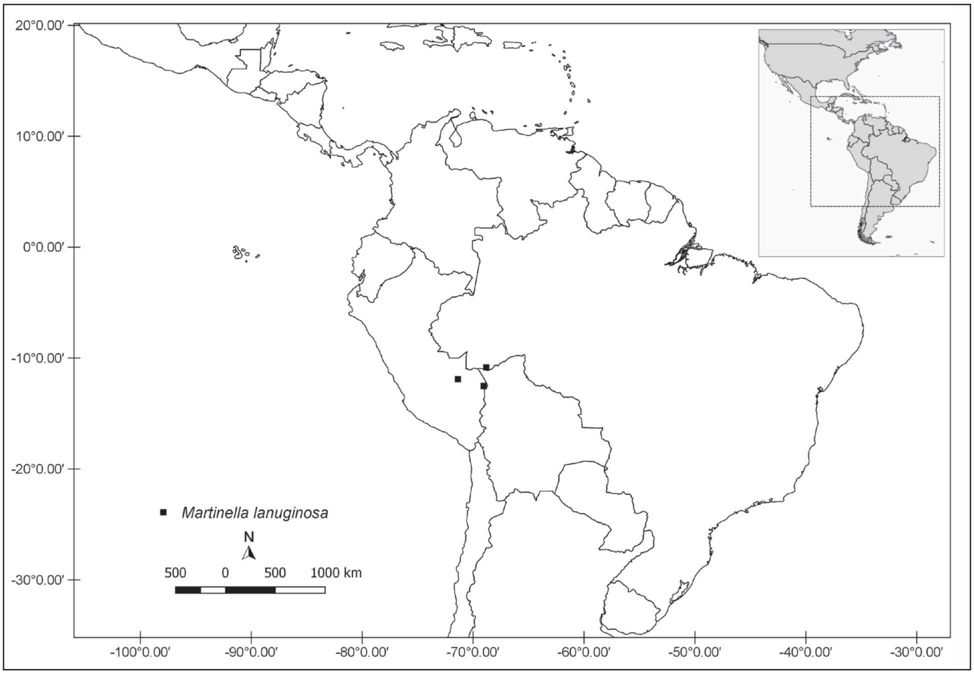


Figure 8. Distribution map of *Martinella lanuginosa*.

calyx chartaceous, campanulate, 18–21.6 × 8.9–12.3 mm, puberulent, covered with simple eglandular trichomes and stipitate glandular trichomes, lobes 2–4, apex mucronate, puberulent; corolla lilac, membranous, 62.6–69.6 mm long, narrowly tubular basal portion 20.6–21.9 mm long × 5.3–6.2 mm wide, upper campanulate portion 42–47.7 mm long × 16.9–20.7 mm wide, lobes subcircular, 7.3–8.3 × 12.4–13 mm; stamens in two lengths, longer ones 17.9–18.6 mm, shorter ones 12.3–13.3 mm, thecae 3–3.2 mm, glabrous; staminode ca. 1.2 mm, glabrous; gynoecium ca. 42 mm long; ovary glabrous; style glabrous; stigma lanceolate, glabrous; nectariferous disk 3.3–3.4 × 1.1–1.15 mm. ***Fruits and seeds*** not seen.

Distribution and habitat. *Martinella lanuginosa* is restricted to *terra firme* (non-flooded) forests of western Amazon (see Fig. 8), with known occurrences in Brazil (Acre state) and eastern Peru.

Etymology. The specific epithet relates to the lanuginose indumentum on the abaxial surface of leaflets that confers a wool-like feel when touched.

Phenology. Flowering specimens were collected in late October.

Conservation status. Near Threatened (NT) based on the EOO of 24,543 km^2.

Discussion. *Martinella lanuginosa* is a new taxon discovered based on morphology and confirmed to represent an independent lineage based on molecular phylogenetic data (Kataoka and Lohmann in prep.). This new taxon is sister to *M. insculpta* and *M. obovata*. *Martinella lanuginosa* is readily distinguished from its Amazonian sister-taxa by the leaflets lanuginose on the abaxial side (versus glabrescent in *M. insculpta*), and glabrous in *M. obovata* (versus tomentose in *M. tomentosa*). The inflorescence is a lax thyrse that is easily distinguished from the densely arranged thyrse of *Martinella tomentosa*. Very few specimens of *M. lanuginosa* have been collected, none of which bear fruits and/or seeds.

Specimens examined. BRAZIL. Acre: Brasileia, Reserva Extrativista Chico Mendes, seringal Porongaba, colocação Dois Irmãos, terra firme, 10°51'N, 68°48'W, 28 Oct 1991, *L. Ferreira 109* (NY). **COLOMBIA. Bolívar:** Turbaco, Fundación Jardín Botánico "Guillermo Piñeres" y alrededore, 130 m, 23 May 1992, *R. Rueda 414* (MO). **PERU. Loreto:** Alto Amazonas, Yurimaguas Estación Experimental de North Carolina State, 10 years old second growth dominated by *Cecropia*, on sandy and yellow lateritic soil, 180 m, 9 Oct 1985, *A.H. Gentry 52144* (MO). **Madre de Dios:** Cocha Cashu camp, Manú National Park, Río Manú, mature forest on alluvial soil, 380 m, 24 Oct 1979, *A.H. Gentry 27233* (MO); Manú, Parque Nacional Manú, Estación Biologica de Cocha Cashu. Mature floodplain, 150 m, 11°54'S, 71°22'W, 6 Jun 2001, *L.G.Lohmann 616* (MO).

4. *Martinella obovata* (Kunth) Bureau & K.Schum., in Mart., Fl. Bras. 8(2):161, tab. 84. 1896

Fig. 9

Spathodea obovata Kunth, Nov. Gen. Sp. (quarto ed.) 3: 147. 1819 [1818]. *Bignonia obovata* (Kunth) Spreng., Syst. Veg. 2:830. 1825. *Macfadyena obovata* (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 200. 1863. TYPE. Colombia. Magdalena: Turbaco, s.d., *F.W.H.A. von Humboldt & A.J.A. Bonpland 1391* (holotype: P-00670823 image!).

Bignonia fockeana Miq., Linnaea 18: 609. 1844. *Macfadyena fockeana* (Miq.) Miers, Proc. Roy. Hort. Soc. 3: 200. 1863. TYPE. Suriname. Paramaribo, Aug 1844, *H.C. Focke 924* (lectotype, designated by Gentry 1974 [1973], p. 877: U-0000750 image!).

Tabebuia cordata Benth., Bot. Voy. Sulphur 129. 1845 [1844]. TYPE. Panama. Isthmus of Darién, s.d., G.W. *Barclay s.n.* (lectotype, designated by Gentry 1974 [1973]: K-000449504 image!).

Bignonia martini DC., Prodr. 9: 152. 1845. [as Martini]. *Martinella martini* (DC.) Baill. ex K.Schum. In Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894. TYPE. French Guiana. Cayenne, s.d., J. *Martin s.n.* (lectotype, first-step designated by Gentry 1974 [1973], p. 877 [as "type"], second-step designated here: P-00481520 image!; isolectotypes: P-00481521 image!, P-00481522 image!, U-0000749 image!, US-00125833 image!).

Doxantha longisiliqua Miers, Proc. Roy. Hort. Soc. 3: 190. 1863. *Bignonia longisiliqua* Bertero ex Spreng., Syst. Veg. 2: 830. 1825, non Jacq. 1780 nec Vell. 1829. TYPE: Colombia. S. Martha, s.d., C.L.G. *Bertero s.n.* (neotype, designated here: G-DC-00133287 image!).

Martinella gollmeri K.Schum. Engler & Prantl, Nat. Pflanzenf. 4(3b): 216. 1894. TYPE: Venezuela, s.d., J. Gollmer s.n. (B probably destroyed); Amazonas, road from San Fernando de Atabapo to Santa Barbara, 12–40 Km from San Fernando, 24 Mar 1974, A.H. Gentry & S.S. Tillet 10864 (neotype, designated here: MO-074427!).

Anemopaegma leptosiphon Rusby, Mem. New York Bot. Gard. 7: 354. 1927. TYPE. Bolivia. Ixiamos, 245 m, 15 Dec 1921, *M. Cardenas 1926* (holotype: NY-00313067 image!; isotype: BKL-00002909 image!).

Arrabidaea duckei A.Samp., Bol. Mus. Nac. Rio de Janeiro 12(3–4): 81. 1936. *Periarrabidaea duckei* (A.Samp.) A.Samp., Ann. Acad. Bras. Sci. 12: 91. 1936. TYPE. Brazil. Manaus, s.d., A. *Ducke s.n.* (holotype [two sheets]: sheet 1, RB-00536852!, sheet 2, RB-00536853!; isotype: R-28626 [accession number]!).

Description. Lianas; ***branches*** with solid pith, cylindrical, green, drying brown, smooth, puberulent, covered with few stipitate glandular trichomes, with scattered patelliform glandular trichomes more frequently at interpetiolar region; prophylls of the axillary buds covered with simple eglandular trichomes. ***Leaves*** 2-foliolate, with the terminal leaflet generally modified into a trifid tendril; petioles terete, not pulvinated, 8.5–66 mm long, covered with stipitate glandular trichomes, with few scattered patelliform glandular trichomes; petiolules terete, not pulvinated, 5–40.4 mm long, covered with stipitate glandular trichomes, with occasional patelliform glandular trichomes; leaflets discolor, with abaxial surface lighter than the adaxial surface (silver-like color), chartaceous, ovate, apex acuminate, base cordate, margins entire and slightly revolute, 7.9–13.2 × 3.0–9.4 cm, adaxial surface glabrous, with simple eglandular trichomes and stipitate glandular trichomes at canaliculi of veins, abaxial surface glabrescent, with patelliform glandular trichomes concentrated near the base and scattered along the midvein. ***Inflorescences*** racemose, 11.9–15.5 cm long, sparsely covered with simple eglandular trichomes and stipitate and patelliform glandular trichomes; bracts linear, 1.5–2 mm long, puberulent, densely covered with simple eglandular trichomes and stipitate glandular trichomes; pedicels terete, 4–12.7 mm, puberulent, with simple eglandular trichomes and stipitate glandular trichomes. ***Flowers*** with calyx green, chartaceous, campanulate, 11.9–17.6 × 4.8–9.6 mm, puberulent, sparsely covered with simple eglandular trichomes and stipitate glandular trichomes, with few patelliform glandular trichomes, lobes 2–4, apex mucronate, puberulent; corolla light lilac to dark magenta, membranous, 55.2–58.5 mm long, narrowly tubular basal portion 15.6–17.2 long × 4.2–5.3 mm wide, upper campanulate portion 16.1–18.7 mm long × 14–15 mm wide, lobes subcircular, 10.5–11.7 × 12.7–15.7 mm; stamens in two lengths, longer ones 16–20 mm, shorter ones 12–12.6 mm, thecae 2.5–3.1 mm, glabrous; staminode 0.8–1 mm, glabrous; gynoecium 34–36.3 mm long; ovary glabrous; style glabrous; stigma lanceolate, glabrous; nectariferous disk 3.2–3.6 × 1.3 mm. ***Capsules*** linear, 20.5–116 × 1.1–2 cm, glabrous. ***Seeds*** ca. 4 × 1.1 cm.

Distribution and habitat. *Martinella obovata* is widely distributed through Amazonian *terra firme* forests and wet forests of southern Mexico and Central America (Fig. 10). This species occurs between 0–1700 m a.s.l., in a wide range of forested habitat types.

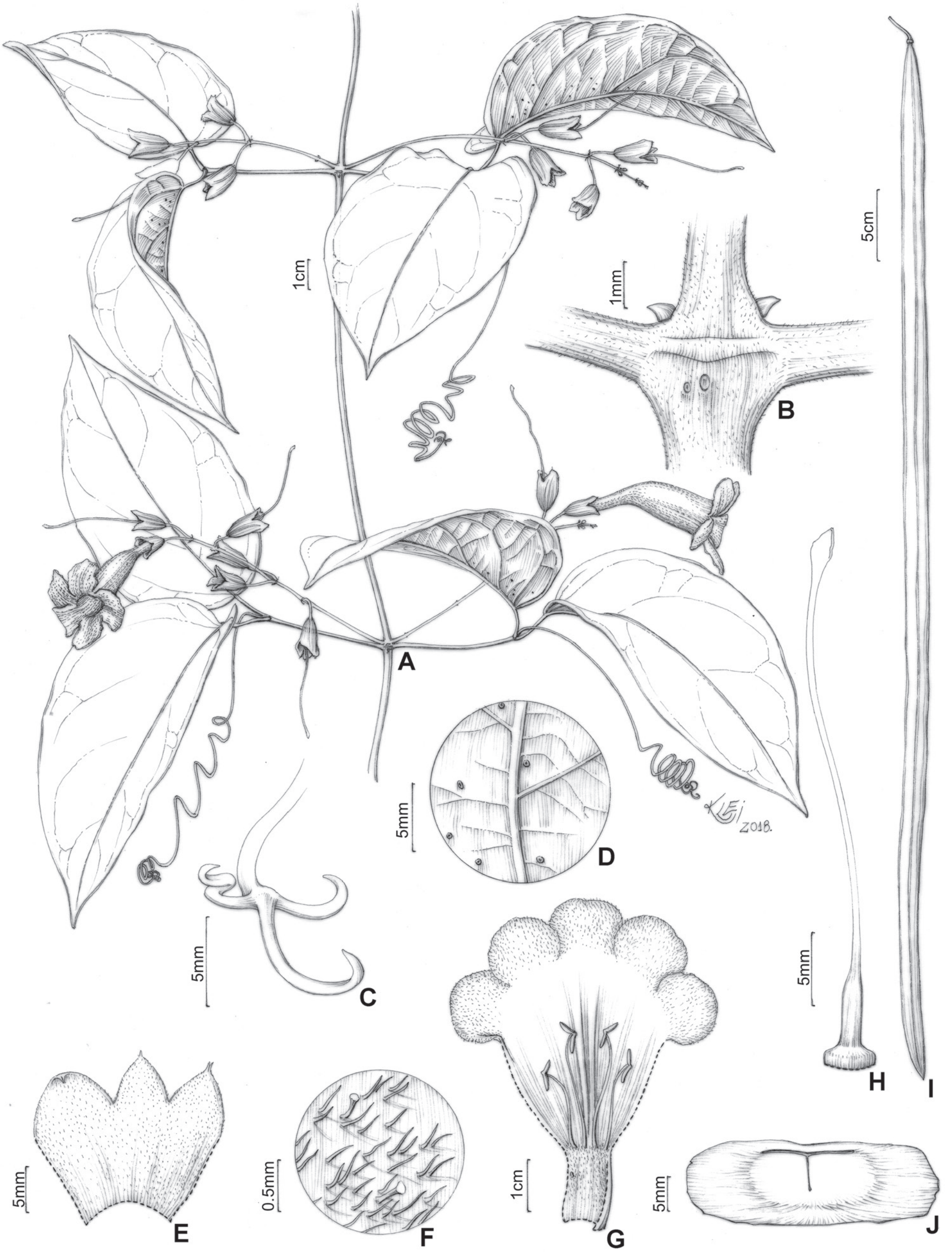


Figure 9. *Martinella obovata* (Kunth) Bureau & K. Schum **A** flowering branch **B** interpetiolar region with minute and triangular prophylls **C** trifid tendril **D** abaxial side of leaflet with patelliform glandular trichomes **E** calyx external view **F** detail of calyx indumentum **G** open flower showing anthers, trichome distribution, and reduced (ca. 1 mm) staminode **H** gynoecium **I** fruit flattened with a smooth surface **J** winged seed. Illustrated by Klei Sousa, based on *E.Y. Kataoka 309* (B), *329* (**C, J**) and *360* (**A, D–I**), SPF.

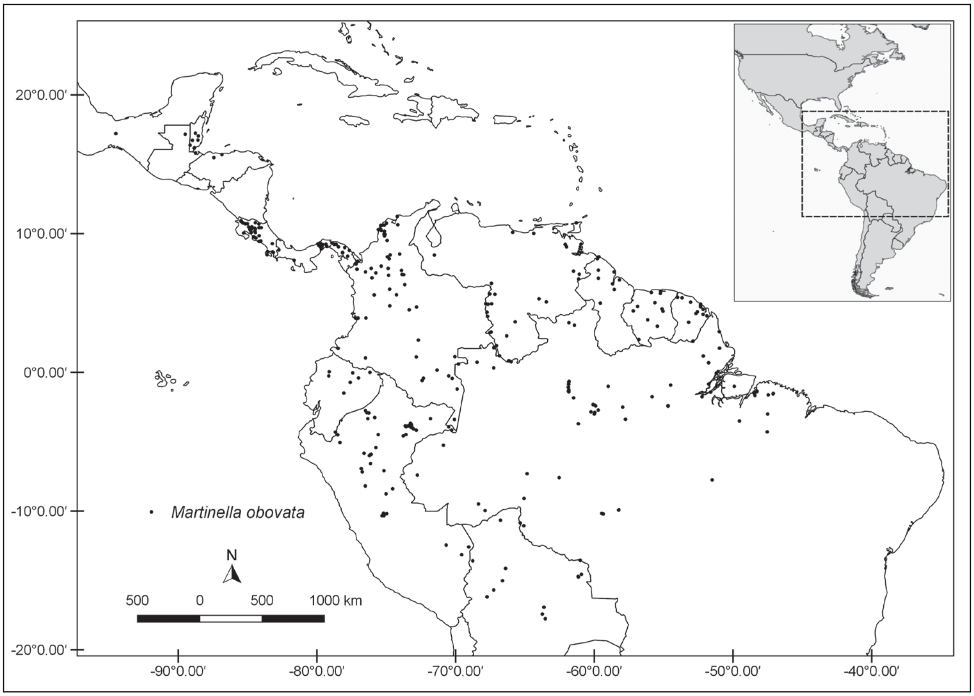


Figure 10. Distribution map of *Martinella obovata*.

Phenology. Flowering and fruiting specimens were collected throughout the year.

Conservation status. Least Concern (LC) based on the EOO of 10,477,635 km^2.

Discussion. *Martinella obovata* is diagnosable by a combination of cylindrical stems in cross section, glabrous leaflets, racemose inflorescence, and calyx covered with simple eglandular and stipitate glandular trichomes. *Martinella obovata* is the most widely distributed species in the genus and occurs from southern Mexico to the southern Amazon in a wide altitudinal range. Despite the wide geographic and elevational range, no clear morphological discontinuities were identified in our study. However, as expected, we did find some variation especially considering plasticity to local environmental conditions, such as thicker leaves in specimens collected at localities associated with rocky outcrops. Based on the morphological evidence and robust molecular phylogenetic data (Kataoka and Lohmann in prep.), we recognize a broadly distributed *M. obovata*.

The widespread *M. obovata* recognized here includes multiple synonyms, several of which required the designation of lectotypes or neotypes. During Alwyn Gentry's prolific career, he published many taxonomic treatments and Floras in which he listed several types and unintentionally designated lectotypes. For example, Gentry (1973) unintentionally designated lectotypes for *Bignonia fockeana* Miq. and *Tabebuia cordata* Benth. The specimens designated as lectotypes are in good condition, allowing for an accurate identification of these taxa, representing good lectotypes.

Some of Gentry's unintentional lectotypes were first-step lectotypifications (see Art. 9.17 of Turland et al. 2018), requiring second-step lectotypes. When appropriate, the required second-step lectotypes are proposed here. For example, in the protologue of *Bignonia martini*, De Candolle (1845) specifically cited a specimen collected by Martin in Cayenne (French Guiana). Gentry (1973) cited as "type" collections made by J. Martin in French Guiana deposited at U and US. We found additional collections made by J. Martin in Cayenne that were annotated as "Type" and "Isotype" deposited at P. One of those specimens bears flowers, is in good condition and has a stamp that indicates "Type". This material is here selected as a second-step lectotype. Duplicates (isolectotypes) of the type collection are deposited at P, U and US.

Bignonia longisiliqua Bertero ex Spreng. (Sprengel 1825) and *Bignonia longisiliqua* Vell. (Vellozo 1825 [1829]) are illegitimate homonyms of *Bignonia longisiliqua* Jacq. (Jacquin 1780). While *B. longisiliqua* Bertero ex Spreng. is a synonym of *M. obovata*, *Bignonia longisiliqua* Vell. is a synonym of *Catalpa longissima* (Jacq.) Dum. Cours., and *Bignonia longisiliqua* Jacq. is a synonym of *Stizophyllum perforatum* (Cham.) Miers. *Bignonia longisiliqua* Bertero ex Spreng. was described based on a specimen from "Ad fl. Magdalen." (Magdalena river, Colombia) collected by C.L.G. Bertero. However, the referred specimen was never mentioned in subsequent taxonomic studies and could not be located. Instead, a specimen collected by C.L.G. Bertero in Santa Martha (Colombia) was cited by De Candolle (1845). *Doxantha longisiliqua* Miers is a new name subsequently published based on a specimen from "Sa. Martha" (Colombia), also collected by C.L.G. Bertero, with explicit reference to the specimen cited in De Candolle (1845). We found two specimens collected by Bertero in Santa Martha, one deposited at G-DC and the other deposited at MO. These specimens were identified as types of *Bignonia longisiliqua* Bertero ex Spreng., with the specimen at MO (barcode MO-074584) including a "Type Specimen" stamp. However, we did not find any publication citing the MO specimen as a nomenclatural type. In addition, it is likely that the specimen from Magdalena river that Sprengel used to describe *B. longisiliqua* was destroyed at B, where many specimens were held after 1890, including some of those collected by Bertero (Stafleu and Cowan 1976). Therefore, we designate the well-preserved specimen deposited at G-DC as a neotype for *Bignonia longisiliqua* Bertero ex Spreng. Lastly, the collection year written on the label "1822" is likely wrong because C.L.G. Bertero's travels in the West Indies were from 1816–1821 (Stafleu and Cowan 1976). Given this information, we could not confidently assign the MO specimen as a duplicate (isoneotype).

In the original description of *Martinella gollmeri*, a specimen collected in Venezuela by J. Gollmer is cited. This specimen was most likely destroyed at B; no isotypes or illustrations have been found, and a neotype from Venezuela that matches the original description is here designated as a neotype.

The holotype of *Arrabidaea duckei* A.Samp. is interpreted to be mounted in two sheets, as both sheets have the same accession number (24094) written on their labels. Sheet 1 (RB-00536852) is a better material with leaves and an immature fruit.

Specimens examined. Belize. Cayo: Hummingbird highway, south of Belmopan, vicinity of mile 28, premontane wet forest, 70 m, 14 Jun 1973, *A.H. Gentry*

8250 (MO); Vicinity of Grano de Oro lumber camp south of Millionario, disturbed forest and roadside, 500 m, 2 Jun 1973, *A.H. Gentry 7767* (MO). **Bolivia. Beni:** José Ballivián, Comunidad Galilea, Canchon Tierra Negra, 200 m, 14°30'S, 66°37'W, 21 Oct 1994, E. Rivero 183 (SPF); Isla de Espiritu, Prov. Ballivian, Espiritu en la zona de influencia del río Yacuma. Sabana húmeda, 200 m, 13 Apr 1981, *St.G. Beck 5372* (MO). **La Paz:** Franz Tamayo, Madidi, Chalalan, Sendero Silvador, bosque amazonico preandino estacional, 350 m, 14°25'23"S, 67°55'26"W, 24 Nov 2004, A. Araujo-M 1532 (SPF); Prov. Nor Yungas, 4.1 km N of (below) Yolosa on road to Caranavi, secondary growth, roadside, 1200 m, 16°11'S, 67°44'W, 6 Oct 1984, *J.C. Solomon 12474* (MO). **Santa Cruz:** Prov. Ichilo, Parque Amboró, Río Semayo, Nueva Palestina, a 35 km al E de la Ciudad de Santa Cruz, 480 m, 17°45.5'S, 63°32'W, 4 Mar 1990, *R.C. Quevedo S. 51* (MO); Sara, Camino de Santa Rosa del Sara a Buen Retiro, 274 m, 17°13'57"S, 63°39'1"W, 7 Jan 2009, *G.A. Parada 1394* (SPF). **Brazil. Acre:** Bujari, margem direita do rio Antimary, sentido jusante a partir da ponte da BR-364, 154 m, 9°28'52.3"S, 68°20'55"W, 11 Dec 2016, *E.Y. Kataoka 406* (SPF); Mâncio Lima, São Domingos, Campina, solo arenoso humoso, 7°23'57"S, 72°45'41"W, 23 Oct 1998, *C.A.C. Ferreira 11751* (INPA); Rio Branco, próximo ao prédio do Herbário UFACPZ, ca. 60 m após fim da trilha de acesso do campus ao herbário, 182 m, 9°57'26.5"S, 67°52'27.8"W, 06 Dec 2016, *E.Y. Kataoka 390* (SPF). **Amapá:** Coastal Region survey, right bank of rio Flechal, 1°45'N, 50°58'W, 13 Aug 1962, *J.M. Pires 52504* (IAN, MG); Rio Araguarí, terra firme, baixa, 22 Jul 1951, *R.L. Fróes 27594* (IAN, R); Rio Araguari, along river between Mongubas and Serra do Navio, 0°42'N, 51°45'W, 25 Sept 1961, *J.M. Pires 51176* (IAN, INPA, MG); Rio Araguari, porto Platon, 18 Sept 1961, *J.M. Pires 51057* (IAN, MG); Matapi, mata baixa, terra firme, solo argiloso e úmido, 28 Dec 1976, *B.G.S. Ribeiro 1645* (MG); Porto Grande, Fazenda Governador, Aporema, 10 Nov 1982, *M. Dantas 1428* (IAN); Oiapoque: Amapá, Parque Nacional do Cabo Orange, igarapé Cova da Onça, 2°56'26.24"N, 50°59'3.147"W, 3 Aug 2006, S.R.M. Silva 62 (MG). **Amazonas:** Estrada Manaus-Caracaraí km 39, Reserva Experimental de Silvicultura Tropical, terra firme, solo arenoso, campina, 12 Sept 1977, *J. Ribamar 189* (INPA); Km 65, on road from Manaus to Boa Vista, manioc plantation, sandy soil, 22 Jul 1974, *A. Lasseign P21164* (INPA); Mindu, em capoeira, 5 Sept 1947, *T. Guedes 14* (IAN, RB); Rio Negro, próximo ao rio Arara, 2° acampamento da SIDERAMA, mata de terra firme, solo arenoso, 2 May 1973, *A.A. Loureiro 37946* (INPA, RB, SPF); Barcelos, Parque Nacional do Jaú, margem direita do Rio Negro, 35 m, 1°49'59.8"S, 61°29'38.5"W, 6 Jun 2016, *E.Y. Kataoka 247* (SPF); Rio Negro, between Ilha da Silva & Tapuruquara, 15 Oct 1971, *G.T. Prance 15281* (INPA); Humaitá, Estrada Humaitá-Lábrea, km 77, igarapé na beira da estrada, latossolo, 11 Jun 1982, *L.O.A. Teixeira 1076* (INPA); Itapiranga, Rio Uatumã, em frente ao igarapé Sta. Lizia, 1 km da margem direita do rio, mata de terra firme, solo argiloso, 16 Aug 1979, *C.A. Cid 448* (INPA); Lábrea, Rio Ituxi, vicinity of Boca do Curuquete, 8 Jul 1971, *G.T. Prance 14014* (INPA); Manaus, banks of rio Tarumã and Praia Dourada, sandy substrate, 14 Dec 1974, *A.H. Gentry 13292* (INPA); BR 17, igarapé da Bolívia, terra firme, arenoso, capoeira, 3 Jun 1955, *J. Cha-*

gas s.n. (INPA, MG); Cabeceira do igarapé da Cachoeira Alta, terreno arenoso, capoeira, 28 Nov 1960, *W. Rodrigues 1956* (IAN, INPA); Campos Sales, igarapé da Cachoeira Alta do Tarumã, terra úmida, 22 Sept 1954, *J.C. de Almeida s.n.* (INPA); Campos Sales, km 10 da BR-17, terreno alagadiço, 30 Aug 1954, *J. Chagas s.n.* (INPA); Estrada da Forquilha solo arenoso, capoeira fechada, terra úmida, 11 Oct 1956, *J. Chagas s.n.* (INPA); Estrada do Aleixo, km 7 entrada à esquerda, terra firme, arenoso, capoeira aberta, 24 Aug 1956, *F. Mello s.n.* (INPA); Igarapé da Cachoeira Alta do Tarumã, terra firme, solo arenoso, capoeira, 17 Sept 1962, *W. Rodrigues 4635* (INPA); Igarapé da Cachoeira Alta, solo arenoso, úmido, capoeira, 11 Dec 1961, *W. Rodrigues 3846* (INPA); Km 10 da estrada do Aleixo, terra firme, arenoso, capoeira aberta, 14 Sept 1955, *D. Coelho s.n.* (INPA); Margem do igarapé da Bolívia, estrada da BR – 17, terra firme, arenosa, capoeira, 3 Jun 1955, *J.C. de Almeida s.n.* (INPA); Margem do igarapé da Bolívia terra firme, arenoso, capoeira baixa, aberta, 27 Jul 1956, *D. Coelho s.n.* (INPA); Margem do igarapé do Binda, terreno firme, arenoso, capoeira baixa, aberta, 27 Jul 1956, *D.F. Coelho 4001* (IAN); Margem do igarapé do Mariano terra firme, arenoso, capoeira, alta, 31 Jul 1956, *F.C. Mello 4016* (IAN, INPA); Margem do igarapé do parque 10, terra firme, arenoso, capoeira grossa, 6 Sept 1955, *F.C. Mello 1830* (INPA, MG); Parque 10 de Novembro, terra firme, úmido, arenoso, capoeira fechada, alta, 29 Feb 1956, *J. Chagas s.n.* (INPA); Ponta Negra, 11 Feb 1977, *M. Silva 2089* (INPA); Ponta Negra, campina de solo arenoso, 22 Jun 1961, *W. Rodrigues 2059* (INPA); Praia de Lajes, opposite meeting of the waters, Manaus, 11 Feb 1977, *G.T. Prance 24374* (INPA); Ramal Pau Rosa, na margem de um pequeno igarapé, 52 m, 02°50'42"S, 60°14'12"W, 11 Jun 2011, *R. Goldenberg 1554* (INPA); Reserva Florestal Adolpho Ducke, rodovia Manaus-Itacoatiara, km 26, lateral Oeste-Acará, floresta de baixio, 2°53'S, 59°58'W, 9 Aug 1995, *C.A. Sothers 558* (INPA, SPF); Reserva Florestal Adolpho Ducke, rodovia Manaus-Itacoatiara, km 26, saída do Igarapé Acará, área alterada, solo argiloso, próximo ao baixio/igarapé, 02°53'S, 59°58'W, 6 Jun 1997, *C.A. Sothers 1013* (INPA); Trilha próxima à entrada da Reserva Ducke pela AM-010 (km 26), ca. 300 m a partir da portaria da Reserva, trilha paralela à rodovia, 80 m, 2°54'49.72"S, 59°58'50.24"W, 22 Sept 2016, *E.Y. Kataoka 346* (SPF); Maués, rio Maués-Assu, lado oposto à cidade de Maués, capoeira de terra firme, solo argilo-arenoso, 3°23'S, 57°45'W, 21 Jul 1983, *C.A. Cid 4244* (INPA); Presidente Figueiredo, Balbina 193 km de Manaus, 12 Aug 1986, *C.A.A. Freitas 156* (INPA); Entorno, entrada à direita na estrada indo para a vila, depois da entrada para o CPPMA, 1°00'S, 59°00'W, 29 Nov 2006, *J.G. de Carvalho-Sobrinho 1246* (INPA, SPF); Entorno, picada da Suçuarana, 11 Jul 2007, *S. Sakagawa 435* (INPA, SPF); Rio Preto da Eva, 2–5 km N of Manaus-Itacoatiara road at Km 79 near Rio Preto da Eva, 100–200 m, 24 Nov 1974, *A.H. Gentry 12836* (INPA); São Gabriel da Cachoeira, road Camanaús-Uaupés near Camanaús, caatinga on white sand, terra firme, 1 Nov 1971, *G.T. Prance 15986* (INPA); Tabatinga, próximo ao aeroporto, sub-base do projeto RADAM/BRASIL, quadrícula SB-19xA, ponto 02, 1 May 1976, *C.D.A. Mota 358* (INPA, MG). **Goiás:** Alto Horizonte, Estrada para o trevinho, na ponte do rio Formiga, mata de galeria, 324 m, 14°9'1"S, 49°17'9"W, 1 May 2012, *J.E.Q. Faria* 2653 (SPF). **Maranhão:** Viana, Jan 1960, *O. de Carvalho 13* (RB); **Mato Grosso:** Aripuanã, Margem direita do rio Aripuanã, acesso pelo 'Balneário Oásis', acima da cachoeira, 224 m, 10°9'53.1"S, 59°27'44.9"W, 14 Nov 2016, *E.Y. Kataoka 380* (SPF); Cotriguaçu, Margem esquerda do rio Juruena, sentido montante, a partir da área de embarque da balsa, 192 m, 9°55'13.6"S, 58°15'4.2"W, 15 Nov 2016, *E.Y. Kataoka 381* (SPF); Rio Juruena, ilha próximo à margem esquerda do rio, 199 m, 9°54'2.8"S, 58°13'38.8"W, 15 Nov 2016, *E.Y. Kataoka 383* (SPF); Juara, margem direita do rio Apiacás, junto à primeira cachoeira, salto Apiacás, solo arenoso úmido, floresta aluvial, 26 May 1988, *M. Macedo 1918* (INPA). **Pará:** Aramanahy, low and high land, 11 Jan 1932, M.D. Cost 255 (IAN); Approx. 18 km east of Tucurui and rio Tocantins, by BR 263, white-sand campina and campina forest (campinarana), 3°30'S, 49°32'W, 28 Oct 1981, *D.C. Daly 1016* (INPA, MG); Beira do rio Mapuá, várzea, entre Vila Emilia e Boca do Mapuá, 18 Jul 1950, *G.A. Black 50-9804* (IAN); Beira do rio Mojú, fábrica e cereanías, 1 Jun 1954, *G.A. Black 54-16288* (IAN); Cacaual Grande, lado W do Canal Novais Filho, capoeira de várzea, 4 Jul 1952, *G.A. Black 52-15399* (IAN, RB); Km 15, Belem Brasilia highway E of Belem, near check point, 9 Dec 1974, *A.H. Gentry 13159* (IAN, INPA, MG); Km 56 da BR-163, *O.H. Knowles 1476* (MG); Região do Anapú, rio Pracajaí, Portel, 16 Sept 1956, *R.L. Fróes 32723* (IAN); Afuá, Rio Cajuuna, mata de várzea, margem inundável, 12 a 02 Sept – Oct 1992, *U.N. Maciel 1899* (MG); Alemquer, várzea, Amazonian Costa Rica, 28 Jul 1903, *A. Ducke s.n.* (MG); Anajás, Jun 1900, *A. Ducke s.n.* (MG); Aramanai, Belterra, Jan 1932, *R.C. Monteiro da Costa 255* (R); Aveiro, orla da mata firme, rio Tapajós, 2 Apr 1924, *J.G. Kuhlmann 1887* (R, RB); Barcarena, Itupanema, quintal, 23 Oct 1985, *M.C. Amorozo 220* (MG); Belém, Baixa da Pedreira, 3 Nov 1960, *E. Oliveira 1146* (IAN); Capoeira do Black, 25 m, 1°26'11.1"S, 48°26'37"W, 04 Nov 2016, *E.Y. Kataoka 360* (SPF); Capoeira do Black, 25 m, 1°26'11.1"S, 48°26'37"W, 04 Nov 2016, *E.Y. Kataoka 361* (SPF); Embrapa Amazônia Oriental, capoeira do Black, *A.C. da S. Andrade 141* (IAN); IPEAN grounds, forest edge and roadside second growth, alt. near sea level, 7 Dec 1974, *A.H. Gentry 13123* (IAN, INPA, MG); On lands of Instituto Agronômico do Norte, 2 K SO of Administration Building, near Rio Guamá, 15 Feb 1944, *A. Silva 117* (IAN); Parque do Utinga, aproximadamente 1,5 km da entrada do parque à direita, três metros da beira da estrada, 8 Jul 2011, *F.F.P. Castro s.n.* (MG); Benevides, rua na beira da BR316, no balneário Olho d'água, 1°21'19"S, 48°15'47"W, 31 Oct 2012, *M.P. do Nascimento 521* (IAN); Breves, local onde foi feito um inventário florestal, Oct-Nov 1957, *J.M. Pires 6653* (IAN); Gurupa, rio Moju, afluente do rio Amazonas, próximo ao porto de Gurupa, várzea alta, 8 Dec 1991, *G. dos Santos 314* (MG); Rio Moju, afluente do rio Amazonas, próximo ao porto de Gurupa, várzea alta, 8 Dec 1991, *G. dos Santos 317* (MG); Monte Alegre, Rio Maicurú, várzea, 12 Sept 1953, *R.L. Fróes 30203* (IAN); Oriximiná, rio Paru do oeste, mata de beira de rio, solo argiloso, 5 Sept 1980, *C.A. Cid 2155* (INPA, MG, RB); Ourém, 1°32'51"S, 47°6'36"W, Oct 2011, *F.C.A. Lucas 228* (IAN); Capoeira, 5 Dec 1903, *R.S. Rodr. s.n.* (MG); Paragominas, Rodovia Belém-Brasília. Rio Uraim, beira do rio, terreno alagado, 18 Jan 1966, *M. Silva 452* (MG);

Porto Trombetas, mineração rio do norte, 1991, *E. Soares 545* (INPA); Mineração rio do norte, 1991, *E. Soares 766* (INPA); Mineração rio do norte, restinga do rio Trombetas 1991, *E. Soares 345* (INPA); Mineração rio do norte, restinga do rio Trombetas, 3 Jul 1991, *O.H. Knowles 1732* (INPA); Primavera, Subindo o rio Quatipuru, aproximadamente 5 km da ilha de Maçaranduba, capoeira baixa, 24 Nov 1993, *R. Lisboa 2992* (MG); Santarém, Km 35 da estrada do Palhão, arredores do acampamento do igarapé Curupira, capoeira, beira do igarapé, 30 Aug 1969, *M. Silva 2446* (MG); Rio Curuaúna, várzea inundável, região do planalto de Santarém onde foi feito o levantamento estatístico florestal pelo IAN, SPVEA e FAO, Oct 1954, *R.L. Fróes 31360* (IAN); Tapeirinha para Santarém, terra firme, 25 Dec 1958, *F. Markgraf 3872* (RB); Vitória do Xingu, Usina Hidrelétrica de Belo Monte, 19 Jun 2012, *L.S. Lima 417* (MG). **Rondônia:** Porto Velho, BR 364, Rio Novo próximo ao acesso à UHE de Samuel, mata secundária, solo argilo-arenoso, 16 Aug 1987, *A. Vasques 18* (INPA); Mata ciliar, UHE – Samuel, Rio Jamari, montante da UHE, margem direita, 10 May 1988, *M. Pereira 230* (RB). **Roraima:** Boa Vista, T.F. de Roraima, terra firme, beira do rio, 20 Feb 1964, *M. Silva 16* (IAN, MG); Caracaraí, margem direita do Rio Branco, 26 m, 1°2'50.3"S, 61°52'6.7"W, 8 Jun 2016, *E.Y. Kataoka 273b* (SPF); Rorainópolis, confluência Rio Negro/Rio Branco, margem esquerda do Rio Branco, 33 m, 1°23'30.2"S, 61°50'20.7"W, 7 Jun 2016, *E.Y. Kataoka 250* (SPF); Foz do rio Branco no rio Negro, mata de igapó com interferência da água branca do rio Branco, 1°23'27.1"S, 61°50'31.6"W, 13 May 2015, *B.M. Gomes 647* (SPF); Margem a jusante do rio Branco, borda de mata de várzea, 22 m, 1°4'41.92"S, 61°51'7.33"W, 8 Jun 2016, *A. Frazão 267* (SPF); Margem esquerda do Rio Branco, 27 m, 1°17'42.2"S, 61°51'1.7"W, 10 Jun 2016, *E.Y. Kataoka 330* (SPF); Margem esquerda do Rio Branco, 28 m, 0°38'47.7"S, 61°49'15.3"W, 9 Jun 2016, *E.Y. Kataoka 309* (SPF); Margem esquerda do Rio Branco, 28 m, 0°38'47.9"S, 61°49'15.5"W, 9 Jun 2016, *E.Y. Kataoka 310* (SPF); Margem esquerda do Rio Branco, 28 m, 0°38'54.1"S, 61°49'18.2"W, 9 Jun 2016, *E.Y. Kataoka 311* (SPF); Margem esquerda do Rio Branco, 28 m, 0°38'54.1"S, 61°49'18.2"W, 9 Jun 2016, *E.Y. Kataoka 312* (SPF); Margem esquerda do Rio Branco, 28 m, 0°50'30.3"S, 61°51'4.6"W, 8 Jun 2016, *E.Y. Kataoka 289* (SPF); Margem esquerda do Rio Branco, 28 m, 0°50'30.3"S, 61°51'4.6"W, 8 Jun 2016, *E.Y. Kataoka 290* (SPF); Margem esquerda do Rio Branco, 28 m, 1°16'41.8"S, 61°50'13.9"W, 10 Jun 2016, *E.Y. Kataoka 329* (SPF); Margem esquerda do Rio Branco, 28 m, 1°5'46.9"S, 61°52'7.4"W, 10 Jun 2016, *E.Y. Kataoka 324* (SPF); Margem esquerda do Rio Branco, 29 m, 1°23'9.4"S, 61°50'54.4"W, 7 Jun 2016, *E.Y. Kataoka 251* (SPF); Margem esquerda do Rio Branco, 30 m, 0°39'20.1"S, 61°49'32.1"W, 9 Jun 2016, *E.Y. Kataoka 313* (SPF); Margem esquerda do Rio Branco, 31 m, 1°23'2.8"S, 61°51'3.7"W, 7 Jun 2016, *E.Y. Kataoka 252* (SPF); Margem esquerda do Rio Branco, 31 m, 1°23'22.9"S, 61°50'38"W, 10 Jun 2016, *E.Y. Kataoka 332* (SPF); Margem esquerda do Rio Branco, 33 m, 0°40'57.1"S, 61°50'37.8"W, 8 Jun 2016, *E.Y. Kataoka 302* (SPF); Margem esquerda do Rio Branco, 34 m, 1°20'39.7"S, 61°52'5.2"W, 7 Jun 2016, *E.Y. Kataoka 262* (SPF); Margem esquerda do Rio Branco, 37 m, 0°50'32.4"S, 61°51'5.7"W, 8 Jun 2016, *E.Y. Kataoka 288* (SPF). **COLOMBIA. Amazonas:** Leticia, Parque Nacional Natural Amacayacu, cerca de la Cabaña en la boca del río Amacayacu, bosque secundario, 14 Jun 1992, *R. Rueda 525* (MO). **Antioquia:** Cáceres, 10–15 km NE de Cáceres en la Troncal de la paz, 180 m, 7°40'N, 75°22'W, 6 Nov 1987, *R. Callejas 5380* (MO). **Bolivar:** Isla de Barú, entre Santa Ana y Playa Mojana, 20 m, 25 Aug 1986, *H. Cuadros 3070* (MO); Road to Pta. Barú, W of Cartagena across Canal de Dique, scrubby (dry) forest remnants, 20 m, 10°18'N, 75°35'W, 4 Jul 1984, *A.H. Gentry 47648* (MO); Cartagena, Along road ca. 7 km SW of Arroyo Grande, old secondary vegetation, 70 m, 10°36'N, 75°24'W, 31 Jul 1985, *J.L. Zarucchi 3901* (MO); Morales, Cgto Norosí, caminoa Tiquisionuevo, 200 m, Apr 1985, *H. Cuadros 2126* (MO); San Juan, Loma de los colorados, 2 km S of San Juan, disturbed moist forest, 300 m, 9°58'N, 75°10'W, 27 Oct 1989, *A.H. Gentry 68258* (MO); Turbaco, Camino al depositario, 100 m, 8 Jun 1982, *H.C. Villalobos 1373* (MO). **Córdoba:** Ayapel, Carreteable a Ayapel de la Carretera Caucasia – Nechi, Finca del diamante, 50 m, 8°12'N, 74°47'W, 5 May 1999, *F.J. Roldán 2807* (MO); Junction of río Tigre and río manso, Paramillo National Park, transect no. 6, 200 m, 7°30'N, 76°5'W, 28 Jul 1988, *A.H. Gentry 63841* (MO). **Caquetá:** Solano, Sitio Araracuara, pista de aterrizaje, colecciones sobre afloramiento rocoso, 200 m, 0°35'S, 72°25'W, 10–25 May 1998, *M.V. Arbeláez 1088* (MO). **Chocó:** Riosucio, Peye, orillas del río Peye, 30 m, 5 Jun 1976, *E. Forero 1874* (INPA). **Sucre:** San Onofre, corregimiento “Las Brisas”, clto de “Salas”, Arroyo “Mambú”, 11 Sept 1996, *A. Realpe 229* (SPF). **Valle:** Bajo Calima, pluvial forest, road to Juanchaco Palmeras, 100 m, 3°55'N, 77°2'W, 10 Jul 1984, *A.H. Gentry 47843* (MO). **Costa Rica**. **Alajuela:** San Isidro de San Ramón, 1259 m, 10°4'46"N, 84°26'30"W, 25 Oct 1986, *G. Herrera 123* (MO); Cantón de Upala, Z.P. Tenorio, cordillera de Guanacaste, Bijagua, primary forest on a ridge at Volcán Tenorio, premontane rainforest, 1000–1500 m, 10°43'0"N, 85°1'0"W, 20 Apr 1995, *D. Penneys 485* (MO). **Guanacaste:** Liberia, P.N. Guanacaste, cuenca del Tempisque, estación Cacao, alrededores de la estación, 1100 m, 10°55'36"N, 85°28'6"W, 7 Aug 2007, *A. Soto 1822* (MO); P.N. Guanacaste, cordillera de Guanacaste, Estación Cacao, Sendero Maritza, 1100 m, 10°55'43"N, 85°28'10"W, 9 Feb 1995, *L. Angulo 42* (MO); P.N. Guanacaste, cuenca del Tempisque sector Cacao, hacia la estacíon de 1.5 km, después del río Góngora, 650 m, 10°53'10.421"N, 85°28'19"W, 30 Apr 2000, *L. Acosta 1057* (MO); P.N. Rincón de la Vieja, cuenca del Tempisque, sendero hacia el cráter, 1004 m, 10°47'19.3"N, 85°20'57"W, 31 May 2011, *L.D. Vargas 4556* (MO); Parque Nacional de Guanacaste estación Cacao, 1100 m, 10°55'45"N, 85°28'15"W, 31 Oct 1993, *C. Chávez 332* (MO); Parque Rincón de La Vieja, del mirador siguiendo la fila al volcán Santa María, 1100 m, 10°46'N, 85°49'W, 22 Nov 1987, *G. Herrera 1364* (MO). **Heredia:** La Selva, Río Sarapiqui near Puerto Viejo, tropical wet forest, junction SSO and LOC trails, 100 m, 10°26'N, 84°1'W, 8 Jan 1993, *A.H. Gentry 78642* (MO). **Puntarenas:** Monteverde, Pacific slope forest, 1450 m, 8 Aug 1985, *W.A. Haber 2204* (MO); Monteverde, Pacific slope forest, 1450 m, 8 Aug 1985, *W.A. Haber 2211* (MO); Golfito, P.N. Corcovado, peninsula de Osa, Estacion Sirena, sendero Espaveles, 0 m, 8°28'51"N, 83°35'42"W, 16 Jan 1997, *R. Aguilar 4986* (MO); Refugio de Vida Silvestre Golfito, camino a la

Gamba, 94 m, 8°40'56"N, 83°11'50"W, 9 Oct 2008, R. Aguilar 11418 (MO, SPF); San Luis, Monteverde, camino a Veracruz, 1050 m, 10°16'35"N, 84°47'45"W, 16 Oct 1992, *A. Fernández 440* (MO). **San Jose:** Reserva Biológica Carara, sector Bijagual, sitio Sendero Bijagual-Quebrada Bonita, 550 m, 9°46'20"N, 84°33'50"W, 1 Nov 1990, *R. Zúñiga 327* (MO); Cantón de Dota, faja costeña del Valle de Parrita, faldas Cerro Narra, quebrada Salitrillo, bosque primario cerca del cauce, 200 m, 9°28'55"N, 84°2'50"W, 19 Jul 1995, *J.F. Morales 4572* (MO). **Ecuador. Cantón Archidona:** Napo, Faldas al sur del Volcán Sumaco, carretera Hollin-Loreto, km 31, comuna Challua Yacu, bosque pluvial pre montano, suelos de origen volcánico, 1200 m, 0°43'S, 77°36'W, 15–17 Nov 1988, *A. Alvarado 46* (MO). **Los Ríos:** Hacienda Los Ocho, km 50 on road from Santo Domingo to Quevado, wet Forest, 200 m, 4 Feb 1974, *A.H. Gentry 9640* (QCA). **Napo:** Archidona Cantón, faldas al sur del Volcán Sumaco, carretera Hollin-Loreto, km 31, comuna Challua Yacu, bosque pluvial pre montano, suelos de origen volcánico, 1200 m, 0°43'S, 77°36'W, 15–17 Nov 1988, *A. Alvarado 46* (QCNE). **Orellana:** Along MAXUS (YPF) road at Km 50, Yasuni National Park, 250 m, 16 Mar 1997, *R.J. Burnham 1493* (QCNE). **Pastaza:** Shell, Vicinity of Shell, 1.2 km N of town, disturbed virgin forest in swampy area, 1092 m, 1°29'33"S, 78°3'57"W, 9 May 2003, *T.B. Croat 88873* (QCNE). **Pichincha:** Quito Cantón, Parroquia Puerto Quito, reserva Florestal de ENDESA, 10 km al norte de Alvaro Pérez Intriago, bosque muy húmedo premontano, bosque primario, transectos, 650–800 m, 00°03'N, 79°07'W, 11 Jun 1990, *C.E. Cerón 10140* (MO, QCNE). **Sucumbíos:** Lago Agrio Cantón, Reserva Cuyabeno, laguna Grande, bosque húmedo tropical, bosque primario sobre suelo bien drenado alrededor de cabañas de Neotropic, 230 m, 0°0'S, 76°11'W, 15 Nov 1991, *W. Palacios 9153* (QCNE). **Zamora-chinchipe:** Nangaritza Cantón, Mizai, in río Nangaritza valley, forest on slope above military post, 850 m, 4°18'S, 78°40'W, 31 Jul 1993, *A.H. Gentry 80967* (QCNE). **French Guiana**. Montagne de Kaw, borde de piste forestière, 40 m, 4°33'N, 52°9'W, 25 Mar 1988, *G. Cremers 9827* (MO); Cayenne, Ile de Cayenne, bord de route, la rocade, entre les ronds points Baduel et la Madeleine à proximité du croisement avec la route Raban, 7 m, 4°56'N, 52°20'W, 9 Mar 2009, *C. Delnatte 1693* (MO). **Saül:** La Fumée Mountain, Antenne Nord, non-flooded moist forest, 400 m, 3°37'N, 53°12'W, 14 May 1986, *S.A. Mori 17998* (MO). **Guyana**. Bords de la Rivière du Maroni 1861, *M. Melinon 13* (R); Kariako village, Barama river, North-West District Mora riparian forest around Kariako village, 145 m, 7°22'N, 59°42'W, 23 Dec 1995, *T. van Andel 680* (MO). **Honduras**. **Atlántida:** Campamento Quebrada Grande ca. 10 km south west of La Ceiba, at base of north slope of Pico Bonito, from camp to 2 km east of camp, upland forest on slope, 80 – 180 m, 15°42'N, 86°51'W, 10 May 1993, *R.L. Liesner 26180* (MO). **Yoro:** Cordillera Nombre de Dios, hills S of San José de Texíguat, evergreen rainforest on steep slopes, 350 m, 15°29'N, 87°26'W, 17 May 1991, *G. Davidse 34509* (MO). **Mexico. Veracruz:** Hidalgotitlán, afluente O del río Las Cuevas, +/- 7–9 horas a pie al S del de La Laguna, área arriba de las cascadas donde el arroyo corre en direccíon E-O, entre lomas con suelos prof., selva alta perenifolia con mucha jimba, 350 m, 17°13'30"N, 94°30'30"W, 17 Apr 1982, *T.*

Wendt 3865 (MO). **Peru. Amazonas:** Bagua, Distrito Imaza, Comunidad de Yamakat, bosque primario, 600 m, 5°3'24"S, 78°20'17"W, 6 Jun 1997, *R. Vásquez 23907* (MO). **San Martín:** Prov. Mariscal Caceres, Dtto Tocache Nuevo, al sud oeste del Aeropuerto de Tocache Nuevo, en bosque secundario, 400 m, 12 Jan 1970, *J. Schunke V. 3691* (INPA). **Loreto:** Km 22 Yurimaguas-Tarapoto road, remnant patch of mature forest on white sand and adjacent scrub, 190 m, 6°S, 76°13'W, 10 Oct 1985, *A.H. Gentry 52177* (MO); Iquitos, Laguna Quistococha, ca. 15 km SW of Iquitos, 8 July 1977, *J.C. Solomon 3448* (MO). **Madre de Dios:** Tobapata Province, Cuzco Amazónico Lodge, lago Sandobal and río Madre de Dios, lake edge, aguajal, 200 m, 12°35'S, 69°3'W, 14 Apr 1990, *P. Núñez 12071* (MO). **Maynas:** Alpahuayo (km 25, carretera Iquitos-Nat.), Estacíon IIAP, bosque primario, 19 Oct 1984, *R. Vásquez 5769* (MO); Iquitos, Río Itaya, Sanangal, restinga over silty clay mostly disturbed, 110 m, 17 May 1980, *S. McDaniel 23739* (MO); Río Nanay, Carretera de Picuruyacu, en terreno arenoso, 160 m, 23 Sept 1981, *M. Rimachi Y. 5720* (MO); Nauta, Carretera a Iquitos, bosque inundable estacional, 150 m, 4°29'S, 75°35'W, 12 Dec 1986, *R. Vásquez 8604* (MO); Pebas, Río Ampiyacu, 19 Jul 1976, *J. Revilla 924* (MO). **Pasco:** Oxapampa, Dist. Palcazú, comunidad nativa Alto Lagarto – Reserva Comunal Yanesha, remanente de bosque primario, 584 m, 10°9'7"S, 75°23'32"W, 30 Oct 2009, *R. Rojas 7122* (SPF); Distrito Palcazú. Comunidad Nativa Centro Connás, bosque primario remanente en borde de carretera, 373 m, 10°9'59"S, 75°16'5"W, 14 May 2010, *R. Vásquez 36497* (SPF). **Tocache Nuevo:** San Martín, al sud oeste del Aeropuerto de Tocache Nuevo, en bosque secundario, 400 m, 12 Jan 1970, *J. Schunke V. 3691* (IAN). **Suriname. Brokopondo:** NW of Brokopondo Stuwmeer Lake (E of Brownsberg Nature Reserve), Tonka island, trail west from main compound, high forest on laterite soil, 15 m, 4°35'N, 55°7'W, 4 Feb 1999, *B. Hoffman 5299* (MO); Brownsweg, near Brownsweg Nature Park, scarcely disturbed high mesophytic rain forest on slope, gravelly clay soil, 240 m, 4°35'41.28"N, 55°6'0"W, 7 Oct 2005, *S. Ruysschaert SRU 728* (SPF). **Paramaribo:** Bakboord farm and lake property, just within NE corner of Paramaribo city limits, ca. 1 km N of Kwattaweg, ca. 1/2 km E of Henri Fernandesweg, secondary forest patch bordering fairly recently abandoned pastureland, 5°50'60"N, 55°12'59.97"W, 25 Nov 1996, *R.J. Evans 2591* (MO, RB). **Sipaliwini:** Kwamalasemutu village vicinity, 50 m, 2°22.5'N, 56°47.3'W, 23 Feb 1999, *M.J. Plotkin 1359* (MO). **Venezuela.** Delta Amacuro, cienega de selva húmeda caliente y selva de galería, carretera Caño Guará – La Horqueta, 30–31 Jan 1982, *B. Stergios 3982* (MO). **Amazonas:** Road from San Fernando do Atapabo to Santa Barbara 12–40 km from San Fernando, thickets and forest, mostly on white sand, 110 m, 24 Mar 1974, *A.H. Gentry 10964* (MO); Atures, bosque húmedo del río Cataniapo entre San Pedro de Cataniapo y comunidad El Milagro, 95 m, 6°25'N, 67°25'W, 12 Aug 1986, *A. Castillo 2179* (MO); Primary rainforest, along road between Paso el Diablo and Caño de Culebra, 25–30 km southeast of Puerto Ayacucho, 100 m, 12 May 1980, *J.A. Steyermark 122336* (MO). **Bolivar:** Reserva Florestal Itamaca, selva pluvial del bajo río Botanamo, entre su desemboque al río Cuyuni hasta la boca del río Guarapín, 16–17 Jul 1983, *B. Stergios 6108* (MO).

5. *Martinella tomentosa* Kataoka & L.G.Lohmann, sp. nov.

urn:lsid:ipni.org:names:77217117-1

Fig. 11

Type. Brazil. Amazonas: Manaus, Reserva Florestal Adolfo Ducke, Rodovia Manaus Itacoatiara, km 26, 02°53'S, 59°58'W, 19 Jun 1995, *M.A.D de Souza & C.F. da Silva, 39* (holotype: SPF-102015!; isotypes: INPA-179938!, MO not seen).

Diagnosis. *Martinella tomentosa* differs from other Amazonian species of *Martinella* by the tomentose leaflets and branches, and inflorescences arranged in thyrses, as opposed to the glabrous to lanuginose leaflets and inflorescences arranged in racemes or lax thyrses of all other Amazonian species.

Description. Lianas; ***branches*** with solid pith, cylindrical, green, drying brown, smooth, tomentose, densely covered with simple eglandular trichomes and stipitate glandular trichomes, with scattered patelliform glandular trichomes more frequently at interpetiolar region; prophylls of the axillary buds densely covered with simple eglandular trichomes and stipitate glandular trichomes. ***Leaves*** 2-foliolate, with the terminal leaflet generally modified into a trifid tendril; petioles terete, not pulvinated, 38.1–58.6 mm long, densely covered with simple eglandular trichomes and stipitate glandular trichomes with few scattered patelliform glandular trichomes; petiolules terete, pulvinated, 27–31.5 mm long, densely covered with simple eglandular trichomes and stipitate glandular trichomes with occasional patelliform glandular trichomes; leaflets concolorous, chartaceous, ovate, apex acuminate, base cordate, margins entire and slightly revolute, 16.5–19.0 × 12.0–14.0 cm, adaxial surface glabrescent with simple eglandular trichomes and stipitate glandular trichomes at the canaliculi of veins, abaxial surface tomentose, densely covered with simple eglandular trichomes and stipitate glandular trichomes, and patelliform glandular trichomes concentrated near the base and few scattered along the midvein. ***Inflorescences*** in thyrses; 10–19.5 cm long, tomentose, densely covered with simple eglandular trichomes and stipitate and few patelliform glandular trichomes; bracts linear, ca. 2 mm long, pubescent, densely covered with simple eglandular trichomes and stipitate glandular trichomes; pedicels terete, 4.3–9.4 mm, pubescent, with simple eglandular trichomes and stipitate glandular trichomes. ***Flowers*** with calyx green, chartaceous, campanulate, 14–21.8 × 18.1–21.3 mm, densely covered with simple eglandular trichomes and stipitate glandular trichomes, with few patelliform glandular trichomes, lobes 2–4, apex acuminate, pubescent; corolla white to lilac, membranous, 44.9–48.7 mm long, narrowly tubular basal portion 14.5–14.9 mm long × 2.9–3.2 mm wide, upper campanulate portion 28.4–30.2 mm long × 12.1–14.9 mm wide, lobes subcircular, 6.5–7.8 × 11.8–12.1 mm; stamens in two lengths, longer ones 14.4–15.4 mm, shorter ones 10.3–10.5 mm, thecae 2.6–3.1 mm, glabrous; staminode not seen; gynoecium 28.4–36.3 mm long; ovary glabrous; style glabrous; stigma lanceolate, glabrous; nectariferous disk 2.3–2.5 × 1–1.1 mm. ***Fruits and seeds*** not seen.

Distribution and habitat. *Martinella tomentosa* is restricted to the central portion of Amazonia (Fig. 12), where it occurs in *Terra Firme* forests from Brazil (state of Manaus).

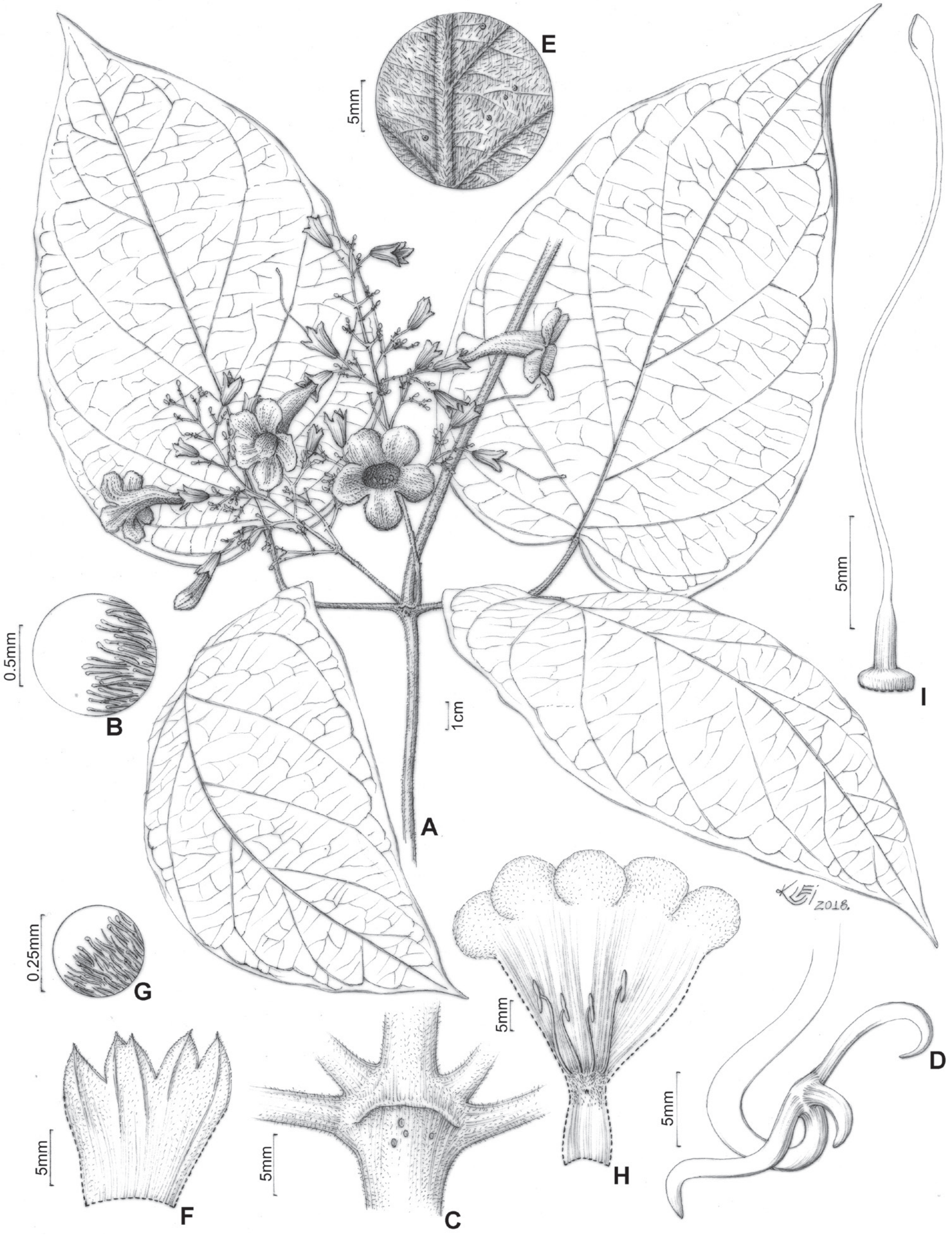


Figure 11. *Martinella tomentosa* Kataoka & L.G. Lohmann **A** flowering branch **B** leaflet indumentum **C** ridge at the interpetiolar region and patelliform glandular trichomes **D** trifid tendril **E** abaxial side of leaflet with patelliform glandular trichomes **F** calyx external view **G** calyx indumentum **H** open flower showing anthers, trichome distribution, and reduced (ca. 1 mm) staminode **I** gynoecium. Illustrated by Klei Sousa, based on *M.A.D. de Souza 39* (**A–C, F–I**), SPF; *W. Rodrigues 4444* (**E**), *M.F. Silva 855* (**D**), INPA.

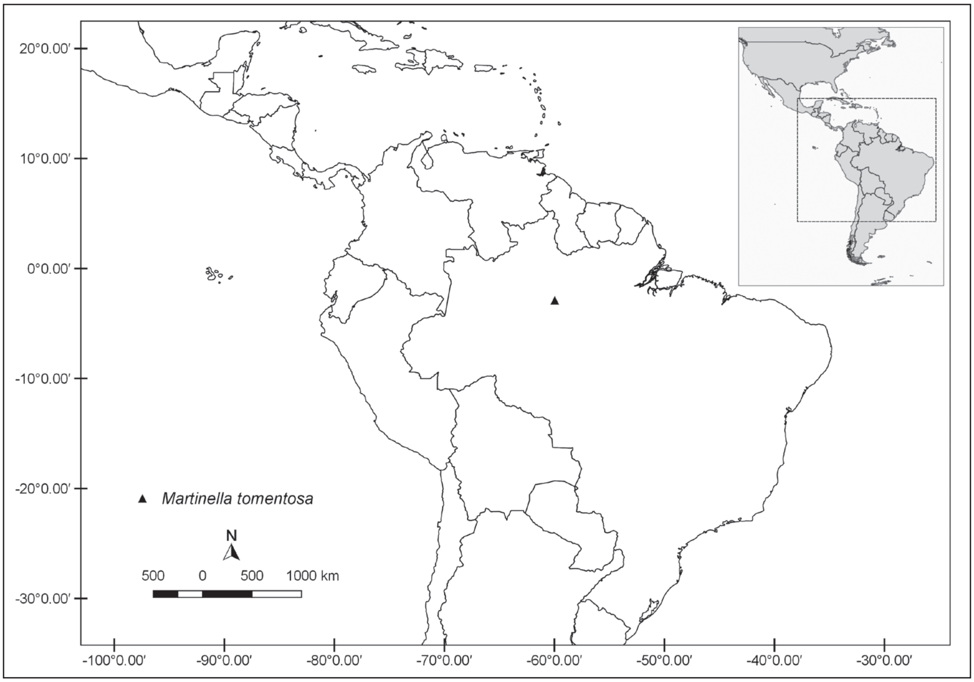


Figure 12. Distribution map of *Martinella tomentosa*.

Etymology. The species epithet relates to the distinguished tomentose indumentum in leaves and branches of *M. tomentosa*.

Phenology. Flowering specimens were collected in June.

Conservation status. Data deficient (DD); known from only three specimens of two localities.

Discussion. *Martinella tomentosa* is a new species whose description is strongly supported by morphological and molecular phylogenetic data (Kataoka and Lohmann in prep). The tomentose leaves and branches are the most striking characteristics that easily distinguish *M. tomentosa* from all other species of Amazonian *Martinella*. This new taxon is only known from very few collections from Central Amazonia, none of which was collected during the fruiting season.

Specimens examined. Brazil. Amazonas: Estrada Castanho-Tupana, entre o km 50–40, solo argiloso, margem da estrada sempre alagada, 18 Jul 1972, *M.F. Silva 855* (INPA); Manaus, Igarapé do Passarinho, terreno firme, argiloso, capoeira grossa, 15 May 1962, *W. Rodrigues 4444* (INPA); Reserva Florestal Adolfo Ducke, Manaus Itacoatiara, km 26, 2°53'S, 59°58'W, 28 Sept 1995, *C.D. Leme 39* (INPA).

Acknowledgements

We thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for a graduate scholarship to E.Y.K. (2016/04143-9), a regular research grant (2011/50859-

2) and a collaborative FAPESP-NSF-NASA grant (2012/50260-6) to L.G.L. We also thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a Pq-1B grant to L.G.L. (310871/2017-4). We are indebted to the curators of the herbaria listed in this taxonomic revision for allowing us to examine the specimens deposited at their Institutions. We also thank Klei Sousa for preparing the illustrations, as well as Adenor Lima, Ananias Reis, Annelise Frazão, Antenor Nicácio, Beatriz Gomes, Maila Beyer, Martin Acosta, Osmar Ferreira, and Ricardo S. Ribeiro for their assistance during fieldwork, and Juan Pablo Narváez-Gómez and Luiz Henrique Fonseca for taking photos of many herbarium specimens. We thank Gustavo Shimizu, Maria Claudia Pacheco Medeiros, Marcelo Reginato, Miriam Kaehler, and Eberhard Fischer for insightful comments and suggestions on the manuscript.

References

Alcantara SF, Lohmann LG (2010) Evolution of floral morphology and pollination system in Bignonieae (Bignoniaceae). American Journal of Botany 97(5): 782–796. https://doi.org/10.3732/ajb.0900182

Alexiades MN (1999) Ethnobotany of the Ese Eja: plants, health, and change in an Amazonian society. PhD thesis, 464 pp.

Bachman S, Moat J, Hill AW, Torre J, Scott B (2011) Supporting Red List threat assessment with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Baillon HE (1888) Bignoniaceae. Histoire des plantes 10(53). Libraire Hachette & Co., Paris, 58 pp.

Bureau E, Schumann KM (1896) Bignoniaceae. In: von Martius CFP, Eichler AG, Urban I (Eds) Flora Brasiliensis. Frid. Fleischer in Comm. Monachii (Leipzig) 8(2) [1897]: 1–452.

Cordeiro JMP, Kaehler M, Souza G, Felix LP (2017) Karyotype analysis in Bignoniaeae (Bignoniaceae): Chromosome numbers and heterochromatin. Anais da Academia Brasileira de Ciências 89(4): 2697–2706. https://doi.org/10.1590/0001-3765201720170363

Cracraft J (1983) Species concepts and speciation analysis. Current Ornithology 1: 159–187. https://doi.org/10.1007/978-1-4615-6781-3_6

Davies SG, Fletcher AM, Lee JA, Lorkin TJA, Roberts PM, Thomsom JE (2013) Asymmetric synthesis of (–)-Martinellic Acid. Organic Letters 15(8): 2050–2053. https://doi.org/10.1021/ol4007508

De Candolle AP (1845) Bignoniaceae. In: de Candolle AP (Ed.) Prodromus Systematis Naturalis Regni Vegetabilis. Fortin, Masson (Paris) 9: 142–248.

De Queiroz K (2007) Species concepts and species limits. Systematic Biology 56(6): 879–886. https://doi.org/10.1080/10635150701701083

Fonseca LHM, Cabral SM, Agra M de F, Lohmann LG (2017) Taxonomic revision of *Dolichandra* (Bignonieae, Bignoniaceae). Phytotaxa 301(1): 1–70. https://doi.org/10.11646/phytotaxa.301.1.1

Francisco JNC, Lohmann LG (2018) Taxonomic revision of *Pachyptera* (Bignonieae, Bignoniaceae). PhytoKeys 92: 89–131. https://doi.org/10.3897/phytokeys.92.20987

Gentry AH (1973) [1974] Bignoniaceae. In: Woodson RE, Schery RW (Eds) Flora of Panama. Annals of the Missouri Botanical Garden 60: 781–997. https://doi.org/10.2307/2395026

Gentry AH (1974) Coevolutionary patterns in Central American Bignoniaceae. Annals of the Missouri Botanical Garden 61(3): 728–759.

Gentry AH (1977) Bignoniaceae. Flora of Ecuador (7). University of Gothenburg, Stockholm, 173 pp.

Gentry AH (1979) Distribution patterns of Neotropical Bignoniaceae: Some phytogeographical implications. In: Larsen K, Holm-Nielsen L (Eds) Tropical Botany. Academic Press, London, 339–354.

Gentry AH (1980) Bignoniaceae. Part I (tribes Crescentieae and Tourretieae). Flora Neotropica Monographs 25: 1–131.

Gentry AH (1982) Bignoniaceae. Flora de Venezuela (8). Instituto Botánico de Venezuela, Caracas, 7–433.

Gentry AH (1992) Bignoniaceae. Part II (Tribe Tecomeae). Flora Neotropica Monographs 25: 1–370.

Gentry AH, Cook K (1984) *Martinella* (Bignoniaceae): A widely used eye medicine of South America. Journal of Ethnopharmacology 11(3): 337–343. https://doi.org/10.1016/0378-8741(84)90079-5

Gentry AH, Tomb AS (1979) Taxonomic implications of Bignoniaceae palynology. Annals of the Missouri Botanical Garden 66(4): 756–855. https://doi.org/10.2307/2398917

Goldblatt P, Gentry AH (1979) Cytology of Bignoniaceae. Botaniska Notiser 132: 475–482.

Halbritter H, Ulrich S, Grímsson F, Weber M, Zetter R, Hesse M, Buchner R, Svojtka M, Frosch-Radivo A (2018) Illustrated pollen terminology. Springer, Wien, 483 pp. https://doi.org/10.1007/978-3-319-71365-6

Hickey LJ (1973) Classification of the architecture of dicotyledonous leaves. American Journal of Botany 60(1): 17–33. https://doi.org/10.1002/j.1537-2197.1973.tb10192.x

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Cambridge. https://www.iucn.org/content/iucn-red-list-categories-and-criteria-version-31

Jacquin NJ (1780) Selectarum Stirpium Americanarum Historia 89. Ex officina Krausiana, Vienna.

Lohmann LG (2006) Untangling the phylogeny of Neotropical lianas (Bignonieae, Bignoniaceae). American Journal of Botany 93(2): 304–318. https://doi.org/10.3732/ajb.93.2.304

Lohmann LG, Taylor CM (2014) A new generic classification of Tribe Bignonieae (Bignoniaceae). Annals of the Missouri Botanical Garden 99(3): 348–489. https://doi.org/10.3417/2003187

MacBride JF (1961) Bignoniaceae. Flora of Peru. Publications of the Field Museum of Natural History, Botany Series 13 (5C/1): 3–101.

Meyer L, Diniz-Filho JAF, Lohmann LG (2017) A comparison of hull methods for estimating species ranges and richness maps. Plant Ecology & Diversity 10(5–6): 389–401. https://doi.org/10.1080/17550874.2018.1425505

Nogueira A, El-Ottra JHL, Guimarães E, Machado SR, Lohmann LG (2013) Trichome structure and evolution in Neotropical lianas. Annals of Botany 112(7): 1331–1350. https://doi.org/10.1093/aob/mct201

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Radford AE, Dickison WC, Massey JR, Bell CR (1974) Vascular plant systematics. Harper Collins, 891 pp.

Reginato M (2016) monographaR: An R package to facilitate the production of plant taxonomic monographs. Brittonia 68(2): 212–216. https://doi.org/10.1007/s12228-015-9407-z

Sampaio AJ (1935) Novas especies de Bignoniaceas. Annaes da Academia Brasileira de Sciencias 7: 111–127.

Sampaio AJ (1936) Boletim do Museu Nacional do Rio de Janeiro 12(3–4): 81–85.

Schumann K (1894) Bignoniaceae In: Engler A, Prantl K (Eds) Die natürlichen Pflanzenfamilien Teil 4 (Abt. 3b). Wilheim Engelmann, Leipzig, 189–252.

Sousa-Baena MS, Sinha NR, Lohmann LG (2014) Evolution and development of tendrils in Bignonieae (Lamiales, Bignoniaceae). Annals of the Missouri Botanical Garden 99(3): 323–347. https://doi.org/10.3417/2011018

Sprague TA, Sandwith NY (1934) Decades Kewensis. Plantarum Novarum in Herbario Horti Regii Conservatarum. Decas CXXX. Bulletin of Miscellaneous Information Kew 1934(3): 99–107. https://doi.org/10.2307/4111598

Sprengel CPJ (1825) Systema Vegetabilium, editio decima sexta 2: e830.

Stafleu FA, Cowan RS (1976) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Vol. I: A–G. Second edition. Bohn, Scheltema and Holkema, Utrecht. https://doi.org/10.5962/bhl.title.48631

Standards IUCN, Petitions Subcommittee (2017) 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

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF [Eds] (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code). Regnum Vegetabile, 159 pp. https://doi.org/10.12705/Code.2018

Vellozo JM (1825) Florae Fluminensis. Typographia Nationali, Rio de Janeiro.

Weberling F (1992) Morphology of flowers and inflorescences. Cambridge University Press, 344 pp.

Witherup KM, Ransom RW, Graham AC, Bernard AM, Salvatore MJ, Lumma WC, Anderson PS, Pitzenberger SM, Varga SL (1995) Martinelline and Martinellic Acid, novel G-protein linked receptor antagonists from the tropical plant *Martinella iquitosensis* (Bignoniaceae). Journal of the American Chemical Society 117(25): 6682–6685. ttps://doi.org/10.1021/ja00130a005

Zuntini AR, Lohmann LG (2014) Synopsis of Martinella Baill. (Bignonieae, Bignoniaceae) with the description of a new species from the Atlantic Forest of Brazil. PhytoKeys 37: 15–24. https://doi.org/10.3897/phytokeys.37.6940

Supplementary material 1

Index to numbered collections

Authors: Eric Y. Kataoka, Lúcia G. Lohmann

Data type: Index to numbered collection.

Explanation note: The file contains a list of all numbered collections analysed for the taxonomic revision

Link: https://doi.org/10.3897/phytokeys.177.64465.suppl1

PhytoKeys 177: 117–124 (2021)
doi: 10.3897/phytokeys.177.64764
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

On a noteworthy habitat type in the savannahs of Central Cuba and a remarkable new species of *Elytraria* (*Acanthaceae*)

Werner Greuter[1], Rankin Rodríguez[2]

1 *Botanischer Grten und Botanisches Museum Berlin, FU Berlin, Germany* **2** *Jardín Botánico Nacional, Universidad de La Habana, La Habana, Cuba*

Corresponding author: Werner Greuter (w.greuter@bgbm.org)

Academic editor: E. Fischer | Received 21 February 2021 | Accepted 14 April 2021 | Published 13 May 2021

Citation: Greuter W, Rodríguez R (2021) On a noteworthy habitat type in the savannahs of Central Cuba and a remarkable new species of *Elytraria* (*Acanthaceae*). PhytoKeys 177: 117–124. https://doi.org/10.3897/phytokeys.177.64764

Abstract

A peculiar habitat type found in the savannahs of Central Cuba, Villa Clara Province and characterised by the presence of a surface gravel layer of “perdigones”, an assemblage of small ferralitic concretions, upon the “mocarrero” soil prevailing in the area, is described. On sterile gravel patches, only one species grows: *Elytraria serpens*, a new species described and named here. It is noteworthy for possessing long and wide creeping, stoloniform subterranean peduncles with apical gemmae developing into rooting leaf rosettes enabling vegetative propagation. The new species is close to *E. shaferi* and considered to derive from the latter by adaptive evolution, enabling it to survive in its hostile habitat, sheltered from the competition of other plant species. Small soil insects, for example, ants, are believed to act as pollinators.

Resumen

Se describe un hábitat particular encontrado en la provincia Villa Clara, caracterizado por la presencia de una capa superficial de perdigones (pequeñas concreciones ferralíticas) que recubre el suelo mocarrero de aquella área. En los parches estériles con grava solo crece *Elytraria serpens*, nueva especie aquí descrita, notable por tener pedúnculos subterráneos largamente rastreros y reproducirse vegetativamente por yemas apicales que forman rosetas satélites que luego se enraízan. La nueva especie es afín a *E. shaferi* y se considera derivada de esta por evolución adaptativa, permitiéndole la colonización de un hábitat desfavorable, abrigada de la competencia de otras especies vegetales. Se opina probable la polinización por pequeños insectos terrícolas, p. ej. hormigas.

Keywords

Acanthaceae, Cuba, *Elytraria*, “mocarrero” soil, myrmecophyly, new species, “perdigón”, vegetative propagation, Villa Clara Province

Introduction

Amongst many interesting Cuban localities that the authors visited in March 2019, under the expert guidance of botanists of the Botanical Garden, Universidad Central "Marta Abreu" of Las Villas, the one that we want to present here stands out, not only for hosting a species new to science that we are going to describe hereunder, but also by the particular aspect of its soil. Villa Clara botanists were already familiar with that very locality because of the presence in it of a small population of *Paspalum edmondii* León, a rare endemic species, listed as Critically Endangered (González Torres et al. 2016). This site is located in the Corralillo Municipality, at 22°50'55" latitude North and 80°28'22" longitude West, at an elevation of ca. 65 m a.s.l., between the Las Cañas and Clarita Rivers (or brooks). According to Borhidi's (1991: 344) phytogeographic typology, it situated within the "Sagüense District" that encompasses the hills and plains of the northern coastal strip of Las Villas.

The soils of the area are of the "mocarrero" type, which, according to Bennett and Allison (1928: 67), is characterised by the presence of a 10–25 cm thick ferralitic rock layer ("ironstone") at a depth of 25 to 100 cm, a layer that inhibits drainage and causes the lands, very arid in the dry season, to become swampy in the rainy season. This, added to the general soil oligotrophy, results in the prevailing of savannah plant formations (Bennett and Allison 1928; Borhidi 1991: 149). Borhidi (1991: 162) believes that the savannahs have replaced an original scrub vegetation, following an alternation of fire and grazing events.

"Mocarrero" soils cover large areas in the Cuba lowlands. The particular locality to which we refer is, moreover, characterised by the presence of a dense and homogeneous surface layer of ferralitic glomeruli, conditioning a very open vegetation interrupted by sterile gravel patches (Fig. 1). In Cuba, ± globular concretions of this type are found in various types of soil, including "mocarrero". In pedology, they are known as "perdigón" or pellets (Bennett and Allison 1928: 4–6); they are thought of as matching the "mocarrero" ironstone's mineral composition (Bennett and Allison 1928: 78–80) and they are considered as resulting from in situ concretion, not as alluvial deposits.

It would be interesting, although exceeding the purpose of this paper, to study the microclimatic properties of the pellet surface layer in our locality. We surmise that the thermal and hydric conditions inside and below the gravel layer will be found to differ markedly from those at the soil surface and in the overlying air.

No exhaustive inventory of the flora present in that locality was made, but a good sample of the flora was collected, including the following taxa (listed alphabetically with, in parentheses, the collecting number of the voucher specimens [kept in the herbaria PAL-Gr, B, HAJB and ULV]): *Angelonia pilosella* J. Kickx f. (29683), *Aniseia martinicensis* (Jacq.) Choisy (29684), *Byrsonima crassifolia* (L.) Kunth (29696), *Caesalpinia pinnata* subsp. *oblongifolia* (Urb.) A. Barreto & Beyra (29681), *Cuphea parsonsia* (L.) R. Br. (29693), *Evolvulus minimus* Ooststr. (29685), *Metastelma cubense* Decne. (29686), *Rauvolfia cubana* A. DC. (29689), *Paspalum edmondii* (29695), *Phyla stoechadifolia* (L.) Small (29692), *Pisonia rotundata* Griseb. (29691), *Sideroxylon salicifolium* (L.) Lam. (29694), *Stachytarpheta angustifolia* (Mill.) Vahl

(29682), *Tabebuia lepidota* (Kunth) Britton (29690) and *Viguiera dentata* (Cav.) Spreng. (29688). According to Borhidi's (1991: 613) classification, that plant community would seem to belong to the class *Curatello-Byrsonimetea* Borhidi and perhaps to the order *Byrsonimo-Andropogonetalia teneris* Bal.-Tul.: low-grass savannahs with scattered palms, on seasonally flooded "mocarrero" soil.

Scattered on the gravel patches of that locality, we noticed a very curious plant, a species of the genus *Elytraria* Michx. (*Acanthaceae*) that did not match any of the known Cuban representatives of this genus: stemless perennial herbs, with all leaves flat on the ground, forming a basal rosette. The inflorescences, solitary or paired spikes, emerge from the soil at a distance from their rosette and are connected with it by a slender axis (the peduncle) winding below or inside the top layer of gravel. These peduncles, which mimic underground stolons, are pale, yellow or yellowish-brown in colour and covered with dense scales or sterile bracts. In the flowering season, they are devoid of adventitious roots, but at their apex, below the inflorescence(s), they frequently produce buds that develop into small foliar rosettes, destined to take root and give rise to new plants in the subsequent rainy season (Fig. 2). The spikes, surrounded by densely imbricate bracts, produce few tiny, white, unspectacular flowers that open one at a time. It is hard to believe that they are apt to attract pollinating flying insects; which is why it is likely that pollination, when performed, is the work of small terrestrial animals, for example, ants. It is obvious that reproduction is mostly vegetative, a hypothesis that explains the scarcity of well-developed fruits and the low efficiency of the seed dispersal mechanism.

Taxonomy

Elytraria serpens Greuter & R. Rankin, sp. nov.

urn:lsid:ipni.org:names:77217118-1

Type. Cuba central, Prov. Villa Clara, "Municipio Corralillo: entre Las Cañas y el arroyo Clarita, alt. 85 m, 22°50'55"N, 80°28'22"W. Sabana en suelo mocarrero (con capa superficial de glomérulos ferralíticos)", 4-III-2019, *Greuter 29687*, *R. Rankin*, *I. Castañeda & A. Pérez Obregón* (holotypus PAL-Gr, isotypi: B #101145054 [Fig. 3], HAJB, JE, ULV).

Planta perennis herbacea acaulis,foliis omnibus basalibus in rosulam humo accumbentem congestis. Folia anguste spatulata, 2–4 cm longa et 0.6–0.8 mm lata, subplana vel saepius transverse undulata, glabra vel praecipue in latere abaxiali ad costam ± villosa, petiolo brevi (2–3 mm) pallide brunneo-villoso. *Pedunculi* graciles, 3–12 ex axillis rosulae basalis orientes, unus alterve brevis arcuate adscendens folia vix superans, praecipui autem tortuosi, stolonorum modo longe (20 cm vel ultra) subterranee repentes, omnes dense bracteis sterilibus squamiformibus subimbricatis obsiti. *Bracteae steriles* sessiles, amplexicaules, subterraneae, extus glabrae, margine antrorsum ciliolatae, intus apicem versus minutissime glanduloso-papillosae; inferiores (subterraneae) ovato-triangulares, subacutae, stramineae, minimae (1–2 mm longae), superiores (aer-

Figure 1. *Elytraria serpens*, a plant at the locus classicus, with six inflorescences (one of them with a flower, bottom right) emerging from the ground around it (photo R. A. Pérez Obregón).

eae) gradatim majors, 2–3 mm longae, acuminatae, virentes. Ad apicem pedunculorum nonnullorum *gemmae* jam florendi tempore foliiferae sed nondum radicantes conspiciuntur. *Inflorescentiae* spiciformes, densae, 1–2 cm longae, bracteis imbricatis indutae, ad apicem pedunculorum singulae vel binae ternaeve congestae. *Bracteae floriferae* bracteis sterilibus superioribus non dissimiles sed majores, virides, ca. 6 mm longae et 2.5 mm latae, ovato-triangulares, acuminatae et breviter aristatae, infra glabrae sed apicem versus sub lente retrorso-pubescentes, margine cuncto antrorse ciliatae, intus minute glanduloso-papillosae. *Flores* pauci, singulatim florentes. *Calyx* ca. 5 mm longus, bracteolis binis suffultus. *Bracteolae* bracteis conformes sed minores et angustiores, ca. 4 mm longae et 0.7 mm latae. *Sepala* 4 (sed sepalum abaxiale binerve et apice bidentatum), bracteolis majora, ca. 5 mm longa et 1.2 mm lata, extus glabra, margine apicem versus fimbriato-ciliata, intus minute antrorso-puberula. *Corolla* parva (ca. 3 mm longa), hypocrateriformis, albida, tubo subrecto, inconspicue sigmoideo, ca. 2.5 mm longo et 0.6 mm crasso, limbo subregulari, 1.5 mm diámetro, lobis expansis truncato-retusis. *Capsulae* (paucae perfectae) lineari-obpyriformes, ca. 4 mm longae et 1.2 mm latae, bivalvatae, valvis post dehiscentiam basi connatis apice arcuatim di-

Figure 2. *Elytraria serpens*, a plant at the locus classicus with a dozen unearthed stoloniform peduncles, showing several subapical buds (rosettes in formation) and one fully developed daughter rosette, already rooted (photo R. A. Pérez Obregón).

vergentibus. *Semina* (submatura?) ca. 12, quae dehiscencia peracta in capsula inclusa manent, pallide brunnea, glabra (etiamsi in acua inmersa), subanguloso-ellipsoidea, ca. 0.6 mm longa et 0.4 mm lata, sub lente rugulosa.

Amongst Cuban *Acanthaceae*, the two genera *Elytraria* and *Stenandrium* Nees stand out, being small stemless herbs with basal leaves forming a rosette and flowers in terminal spikes borne on scapiform peduncles that emerge directly from the basal rosette. According to Alain (1957) and other authors, these genera are best distinguished by the number of fertile stamens, 2 in the first and 4 in the second; but this character is not easily observed even when flowers are present. More obvious is the difference in the scapes or peduncles, which are naked in *Stenandrium*, but densely beset with small scaly bracts in *Elytraria*. In addition, the inflorescences of the latter genus are compact, surrounded by densely imbricate bracts, whereas, in *Stenandrium*, at least the lower flowers of each spike are distant from each other and their bracts do not overlap. Both genera have a major centre of diversity in the Caribbean. According to Greuter and Rankin Rodríguez (2017), seven taxa (species and subspecies) of *Elytraria* were known from Cuba, all endemic and 11 taxa of *Stenandrium*, nine endemic. Worldwide (PoWo 2021), 22 taxa are accepted in *Elytraria*: the seven Cuban ones, plus one from Hispaniola, eight from continental America, four from the African continent (one of them also grows in eastern India) and two from Madagascar. The genus *Stenandrium* is larger (65 taxa) and less homogeneous, as it includes several species with elongated stems and opposite leaves; it presents a very similar distribution and diversification

Acanth

Werner Greuter & al. – Plantae e Cuba insula

29687 *Elytraria* serpens ~~*cf. shaferi* (P. Wilson)~~ Greuter & R. Rankin
~~Leonard~~ ISOTIPO

Prov. Villa Clara, Munic. Corralillo: entre Las Cañas yel arroyo Clarita, alt. 85 m.
22°50´55´´N, 80°28´22´´W.
Sabana en suelo mocarrero (con capa superficial de glomérulos ferralíticos).

W. Greuter, R. Rankin, I. Castañeda
& A. Pérez Obregón 4 Marzo 2019

Figure 3. Isotype of *Elytraria serpens* (B).

pattern: 15 taxa from the Caribbean islands, 11 of them present and nine endemic in Cuba, more than 31 species from the American continent (22 from South America); and 19 African species, 10 of them endemic to Madagascar (PoWo 2021).

Most of the seven Cuban endemics of *Elytraria* have restricted ranges and five of the six species are threatened; one of them (*E. filicaulis*) is considered as Critically Endangered (González-Torres et al. 2016). Borhidi and Muñiz (1978), who proposed a determination key for the six taxa known at that time, distinguish species with papery leaves and 5-merous calyx from the others, with membranous leaves and 4-merous calyx. However, our data and the descriptions of other authors (Leonard 1934; Dietrich 1982) suggest that the calyx always consists of four free sepals, but with the abaxial one slightly wider, 2-nerved and apically bidentate, that takes the place of two concrescent sepals. According to label data and protologue indications, at least four of the Cuban taxa of *Elytraria* grow on ophiolitic substrates and can be considered serpentinophytes: *E. cubana*, *E. filicaulis*, *E. planifolia* subsp. *planifolia* and *E. planifolia* subsp. *acunae*. *E. bissei* and *E. spathulifolia* are considered calcicolous, while the habitat of *E. shaferi*, according to the collector, is an arid cliff-face in a serpentine area of Holguín (Sierra de Nipe, Woodfred mines).

In its vegetative features, *Elytraria serpens* is very similar to *E. bissei* of limestone areas of southern Guantánamo (Abra de Mariana), which, however, has leaves hairy on both sides and subsessile spikes not exceeding the basal rosette; and it is akin to *E. shaferi*, with which it shares the pubescence of the outer face of the flower bracts. The species most closely related to ours is *E. cubana*, for which the collector, on the label of the type specimen (*Shafer 2948*, NY), noted: "Lvs. flat on ground, among rocks in red soil, stony hillsides". In this species, with leaves of similar dimensions and shape to ours, the peduncles are decumbent and flexuous, but much shorter than in *E. serpens*, never subterranean, and the flower bracts, on the outside, are glabrous rather than pubescent.

In our opinion, *Elytraria serpens* evolved from plants similar to *E. cubana* by adapting itself to the particular edaphic conditions of its habitat. It takes advantage of the loose granular structure of the gravel layer that enables it to push its developing peduncles through it, hiding them underground, sheltered from the extreme drought and radiation at the surface, to produce apical buds at an appreciable distance from its origin, thus ensuring its vegetative spread. The specimens at hand suggest that fruit set is poor, perhaps due to inadequate pollination and that the explosive capsule dehiscence, normally ensuring seed dispersal in this family (Greuter and Rankin Rodríguez 2010), is not fully functional.

Acknowledgements

We are grateful to Rosalina Berazaín Iturralde for advice and information on ecology and habitat; to Idelfonso Castañeda Noa, who led us to the type locality of the new species and offered information on the locality studied; to Rafael Alejandro Pérez Obregón, who, at our behest, took for us the photographs of Fig. 1; and to Sigrid Liede-Schumann, Bayreuth, who identified our *Metastelma* gathering.

References

Alain (1957) Flora de Cuba, 4. Dicotiledóneas: *Melastomataceae* a *Plantaginaceae*. Contribuciones Ocasionales del Museo de Historia Natural del Colegio "De La Salle" 16.

Bennett HH, Allison RV (1928) The Soils of Cuba. Washington.

Borhidi A (1991) Phytogeography and Vegetation Ecology of Cuba. Budapest.

Borhidi A, Muñiz O (1978) Notas sobre Acantáceas cubanas I. *Oplonia* y *Elytraria*. Acta Biologica Academiae Scientiarum Hungaricae 23: 303–317.

Dietrich H (1982) *Acanthaceae* cubanae novae I. *Elytraria bissei* H. Dietrich, spec. nov. Revista del Jardín Botánico Nacional, Universidad de La Habana 3(2): 39–51.

González-Torres LR, Palmarola A, González-Oliva L, Bécquer ER, Testé E, Barrios D [Eds] (2016) Lista roja de la flora de Cuba. Bissea 10, Núm Espec: 1–1.

Greuter W, Rankin Rodríguez R (2010) Notes on some endemic Cuban species of *Ruelliinae* (*Acanthaceae*), on their seeds, pollen morphology and hygroscopic features. Willdenowia 40(2): 285–304. https://doi.org/10.3372/wi.40.40210

Greuter W, Rankin Rodriguez R (2017) Plantas vasculares de Cuba: inventario preliminar. Segunda edición, actualizada, de Espermatófitos de Cuba con inclusión de los Pteridófitos. Vascular plants of Cuba: a preliminary checklist. Second updated edition of The *Spermatophyta* of Cuba with *Pteridophyta* added. Berlin & La Habana. https://doi.org/10.3372/cubalist.2017.1

Leonard EC (1934) The American species of *Elytraria*. Journal of the Washington Academy of Sciences 24: 443–447.

PoWo (2021) PoWo, Plants of the World online. Kewscience. http://www.plantsoftheworldonline.org/

PhytoKeys 177: 125–138 (2021)
doi: 10.3897/phytokeys.177.63116
https://phytokeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
PhytoKeys
Launched to accelerate biodiversity research

Lagenophora (Asteraceae, Astereae) in New Caledonia

Guillaume Lannuzel[1,2], Gildas Gâteblé[1], Anthony R. Bean[3], Jian Wang[3]

1 *Institut Agronomique néo-Calédonien, Equipe ARBOREAL, BP 711, 98810, Mont-Dore, New Caledonia* **2** *Endemia, Plant Red List Authority, BP 4682, 98847, Nouméa, New Caledonia* **3** *Queensland Herbarium, Department of Environment and Science, Brisbane Botanic Gardens, Mt Coot-tha Road, Toowong, Queensland 4066, Australia*

Corresponding authors: Guillaume Lannuzel (lannuzel@iac.nc); Jian Wang (jian.wang@des.qld.gov.au)

Academic editor: P. de Lange | Received 14 January 2021 | Accepted 10 March 2021 | Published 13 May 2021

Citation: Lannuzel G, Gâteblé G, Bean AR, Wang J (2021) *Lagenophora* (Asteraceae, Astereae) in New Caledonia. PhytoKeys 177: 125–138. https://doi.org/10.3897/phytokeys.177.63116

Abstract

The genus *Lagenophora* Cass. is taxonomically revised for New Caledonia with two species recognised. *Lagenophora sinuosa* Lannuzel, Gâteblé & Jian Wang ter, **sp. nov.** is endemic to New Caledonia and the other, *L. sublyrata* (Cass.) A.R.Bean & Jian Wang ter occurs there and in many other countries from the region. Both are fully described and illustrated. An identification key is provided, as are notes on the distribution (including maps), habitat, phenology and conservation status. The generic placement of the new species is also discussed.

Keywords

Asteroideae, Compositae, identification key, *Lagenophora sinuosa*, *Lagenophora sublyrata*, Lagenophorinae, New Caledonia flora, new species

Introduction

Lagenophora Cass. belongs to subfamily Asteroideae (Cass.) Lindl., tribe Astereae Cass. and subtribe Lagenophorinae G.L.Nesom and is found mainly in the southern hemisphere (Nesom and Robinson 2007). Presently, there are 12 species in Australia (Wang and Bean 2019), nine species in New Zealand (Breitwieser et al. 2012), three species in southern South America (Cabrera 1966; Pruski 2017), two in New Guinea (Wang and Bean 2020) and two in New Caledonia (Munzinger et al. 2020+). The genus also extends to Indonesia, and as far as Sri Lanka and southern Japan (Walker 1976;

Wang and Bean 2019, 2020). The genus is considered non-monophyletic as species of *Solenogyne* Cass. are nested between the two main clades of *Lagenophora* retrieved by Sancho et al. (2015).

The genus was apparently first recorded in a publication for New Caledonia by Schlechter (1906) who identified his own specimen (*Schlechter 14804*) as *L. billardierei* Cass. An earlier specimen (*Pancher 473*, P03292495) collected during the 1860s was, however, also identified as a *Lagenophora* by its collector. Other early specimens from this period by Balansa, Baudouin, Deplanche, Germain and Vieillard were either unidentified at the genus level or identified as *Strongylosperma reptans* Benth. [now synonymous to *Leptinella reptans* (Benth.) D.G.Lloyd & C.J.Webb]. In his catalogue of the plants of New Caledonia, Guillaumin (1911: 177) identified most of these early specimens as *L. billardierei*. Later, Moore (1921: 345) also identified some Compton specimens as *L. billardierei* and described a new species under *L. neocaledonica* S.Moore. Guillaumin maintained the two aforementioned names under *Lagenophora* in his revision of New Caledonian Asteraceae (Guillaumin 1937) and in his flora of New Caledonia (Guillaumin 1948) while the name *L. neocaledonica* was excluded from *Lagenophora* by Cabrera (1966: 307) and then placed in the synonymy of *Pytinicarpa sarasinii* (Däniker) G.L.Nesom by Nesom (2001). In addition, Cabrera (1966) listed two species of *Lagenophora* for New Caledonia viz. *L. lanata* A.Cunn. for the Schlechter specimen and *L. gracilis* Steetz for all the other specimens, *L. billardierei* being synonymous with *L. stipitata* (Labill.) Druce, an Australian taxon not present in New Caledonia. Wang and Bean (2019) put *L. lanata* into synonymy under *L. sublyrata* (Cass.) A.R.Bean & Jian Wang ter and narrowed the definition of *L. gracilis* as a Western Australian endemic species. After searches and studies over years, we recognise two species for New Caledonia – one is the indigenous *L. sublyrata*, the other one being a new endemic species described here.

Materials and methods

This revision is based on morphological examination of *Lagenophora* material from the following herbaria: BRI, CANB, L, MEL, NOU, NSW and P (acronyms following Thiers 2020+). Images of type specimens held at BM, FI, G, HAL, K, M, NY, P and W have also been examined. An exclamation mark (!) is used for the specimens physically seen while “image!” is used for specimens seen only by means of digitized images. In January 2017, a whole shipment of loaned *Lagenophora* specimens from P was destroyed at the Australian border before they could be examined by the borrowing botanists. These specimens were examined by means of scans and are marked with a † symbol. Some nomenclatural typifications were made subsequent to this event, including that of *L. sublyrata*, discussed here (Bean and Wang 2017; Bean and Jabbour 2018). Morphological descriptions and terminology follow Harris and Harris (2001). In addition to dried specimens, live specimens were collected by the first two authors and Christian Laudereau and subsequently cultivated at the nursery of Institut

Agronomique néo-Calédonien in Païta, Port-Laguerre, to make finer measurements and facilitate observations. As much as possible, localities recorded on older specimens were visited to recollect the plants and to assess the ecology where they were found. Most measurements are based on live cultivated material under binocular Olympus SZ2-ILST equipped with a camera. When dried material was used, the dimensions are based on material (i.e. florets) reconstituted with boiling water. Specimen locations were mapped with QGIS 3.10 (QGIS Development Team 2020) to generate the distribution maps and to help for IUCN (2019) evaluation assessments. The occurrence data have been uploaded to the Global Biodiversity Information Facility (**GBIF**) via the Pensoft Data Hosting Center at the GBIF's Integrated Publishing Toolkit (**IPT**) (https://doi.org/10.15468/zkjcfx).

Taxonomic treatment

Key to the New Caledonia species of *Lagenophora*:

1 Trichomes on scape patent, 0.2–0.5 mm long. Cypsela with beak 0.1–0.3 mm long; oval in cross section, longitudinal ribs on both surfaces, base with no trichome .... ***L. sinuosa***

– Trichomes on scape appressed, c. 0.1 mm long. Cypsela with a beak 0.4–0.5 mm long; laterally flattened, smooth on both surfaces, base usually with 1–3 trichomes more or less caducous .... ***L. sublyrata***

Lagenophora sinuosa **Lannuzel, Gâteblé & Jian Wang ter, sp. nov.**

urn:lsid:ipni.org:names:77217119-1
Figs 1, 2

Type. **New Caledonia.** **North Prov.:** Pouembout, Ouaté, 500 m, 21°9'52.43"S, 165°7'1.5"E, 26 Mar 2019, G. *Gâteblé, S. Liede-Schumann, U. Meve &D. Fleurot 1091* (***Holotype*****:** P!, ***isotype*****:** NOU107482!).

Diagnosis. *Lagenophora sinuosa* Lannuzel, Gâteblé & Jian Wang ter differs from all other species in the genus with its usually deeply lobed leaf margins and ribbed cypsela surface. It resembles *L. queenslandica* Jian Wang ter & A.R.Bean with its very short cypsela beak.

Description. ***Perennial rhizomatous herb***; roots and rhizomes fibrous; stem usually absent (leaves in basal rosette); leaves and scapes firmly attached to stem and/or rootstock. ***Leaves*** 5–10, oblanceolate to spathulate, 1.5–4 cm long by 0.5–1.5 cm wide (1.5–3 × longer than wide), winged petiole-like base 0.1–3 cm long; leaf apex obtuse to rounded; leaf margins more or less deeply lobate, sinuate to crenate, usually with 4–10 deep lobes, each lobe 2–5 mm deep; upper leaf surface greyish green; with 4–10 trichomes per mm^2, each 0.3–1 mm long ; lower leaf surface pale green, with 1–6

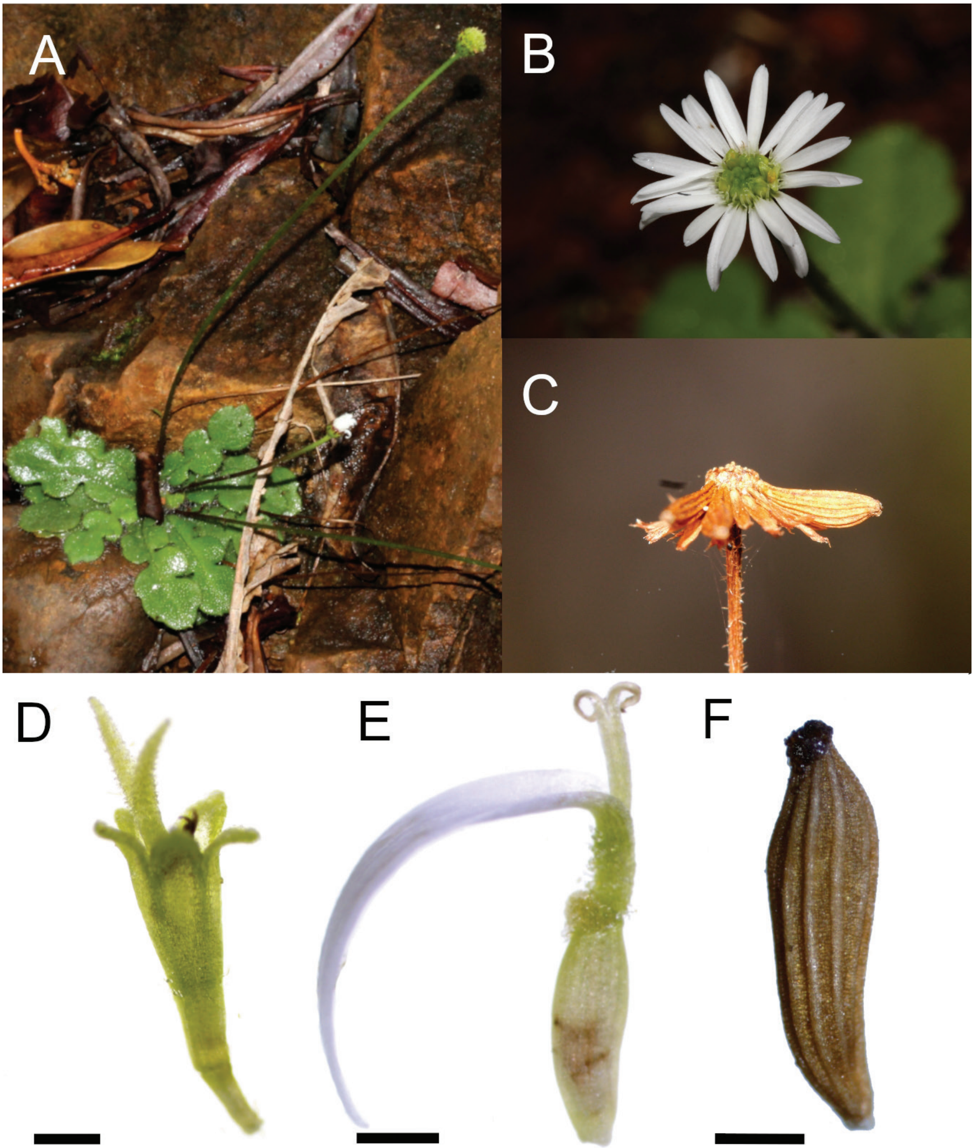


Figure 1. *Lagenophora sinuosa* Lannuzel, Gâteblé & Jian Wang ter, sp. nov. **A** plant in natural conditions **B** capitula **C** capitula with mature cypsela **D** disc floret **E** ray floret **F** cypsela **A–D** from *Gâteblé 1184* **E, F** from *Gâteblé 1187*. Photos from G. Lannuzel. Scale bars: 0.5 mm.

trichomes per mm^2, each 0.2–0.6 mm long; leaf margins with 6–14 trichomes per mm, each 0.7–1 mm long; secondary veins obscure on upper leaf surface, but sometimes obvious on lower leaf surface. ***Scapes*** channelled or not, 1–4 per tuft, 3–25 cm long, c. 0.5 mm diameter; bracts 2–7, upper ones c. 4 × 0.5 mm, lower ones c. 5.0 × 1.5 mm; trichomes 0.2–0.5 mm long, patent or retrorse, erect; 10–15 trichomes per mm^2 at midpoint of scape, 15–30 trichomes per mm^2 towards apex; papillae to c. 0.01 mm long, 5–15 per mm^2 at midpoint of scape, but very densely distributed towards apex. ***Capitula*** 3–6 mm long, 2–5 mm diameter; involucral bracts c. 25 in 2–3 rows, with trichomes c. 0.3 mm occasionally along midrib on outer surface, linear to lanceolate, apex purple, acute to acuminate, with fringed margins on distal half, outer bracts 1.3–2.1 × 0.5 mm, inner bracts 2–3.5 × 0.3–0.7 mm. ***Receptacle*** convex, 2.8–4.2 mm diameter and 1.4–2.5 mm high. ***Ray florets*** 20–30 in 1 or 2 rows; tube 0.1–1 mm long, c. 0.3 mm wide, glandular pilose; style branches c. 0.5 mm long; ligules 1.9–4.2 × 0.4–0.9 mm, with longitudinal veins obscure, white or very occasionally pink, apex obtuse and bidentate. ***Disc florets*** 10–30, corolla greenish or yellow, tubular, 1.5–2 mm long, outer surface covered with papillae; corolla lobes 4–5, deltate, 0.4–0.6 × 0.3 mm; stamens 4–5, anthers 0.6–0.8 mm long; style branches 0.4–0.9 mm long; sterile ovary 2.2–2.5 mm long; pappus scales absent. ***Cypselae*** oval in cross section, oblanceolate, 2.3–3.2 × 0.5–0.8 mm excluding beak, uniformly brown at maturity; surfaces with 2–4 longitudinal ribs on each side; no trichome at the base; beak 0.1–0.3 mm long, densely covered by glands, without a thickened white annular collar at its apex.

Additional specimens examined. New Caledonia. North Prov.: Haute rivière de Voh, 250 m, 12 Mar 1951, *Guillaumin & Baumann-Bodenheim 12112* (P03292561image!†); Haute rivière de Voh, 250 m, 12 Mar 1951, *Guillaumin & Baumann-Bodenheim 12154* (P03292559image!†); Vallée de la Moindah (branche nord), 150 m, 3 Oct 1965, *MacKee 13515* (P04427664image!†); Mt Paéoua, contrefort nord-est, 600–900 m, 4 Jul 1967, *MacKee 17004* (P04427667image!†); Pouembout, 30 m, 26 May 1971, *MacKee 23675* (NOU054762!, P04234038image!); Pouembout, 30 m, 16 Feb 1972, *MacKee 25003* (P03276832image!); Pouembout, 30 m, 16 Apr 1981, *MacKee 38956* (P04427671image!†); Poya, forêt de Nékoro, 2 m, 26 May 1983, *MacKee 41502* (CANB718870.1image!, NOU054761!, P04427669image!†); Poya, forêt de Nékoro, 2 m, 16 Aug 1984, *MacKee 42136* (NOU072073!, P04295155image!†); Poya nord, entre le creek Hervouet et son affluent nord au dessus de la RT1, 40–50 m, 14 Oct 1998, *Veillon 8135* (NOU072074!); Cap Devert, 1861–1867, *Vieillard 816 (Deplanche? 109)* (P03292531image!†). **South Prov.**: Mont Dore, 800 ft., 3 Apr 1914, *Compton 675* (BM013867015image !); Tontouta, 1 Nov 1924, *Däniker 414* (P03292449image!†); Prony, 2 m, 22°19'31.5"S, 166°49'34.44"E, 17 Mar 2020, *Gâteblé, Lannuzel & Ititiaty 1184* (NOU107485!, P!); Cap N'Doua, Kô Mwâ Nirê, 20 m, 22°22'33.78"S, 166°56'28.1"E, 17 Mar 2020, *Gâteblé, Lannuzel & Ititiaty1187* (BRI!, K!, MPU!, NOU107484!, P!); Prony, Îlot Casy, 5 m, 22°21'20.84"S, 166°50'46.77"E, 14 Aug 2020, *Gâteblé 1224* (BRI!, K!, MPU!, NOU107486!, P!); Prony, Sep 1910, *Godefroy s.n.* (P03292558image!, left plant); Ouipouin, 21°41'18.96"S, 165°59'25.08"E, 14 Dec 2018, *Laudereau 1236* (NOU091404!); Sommet de la Table Unio (1000 m), 21 Sep 1965, *MacKee 13414* (P04427666image!†); Plateau sommital de la Table Unio, 1000 m, 14 Nov 1970, *MacKee 22908* (NOU072308!, NSW935348, P04427668image!†); Mont Nakada, 1000 m, 21°37'50"S, 166°3'35"E, 18 Apr 2001, *Munzinger & McPherson 814* (P00217314image!); Ouaménie, 1 Jul 2006, *Munzinger et al. 3488* (NOU013890!); Poya, sud-est de Mépouiri, 10 m, 9 Jul 1991, *Veillon 7390* (NOU072081!); Colline à M'bée, 1855–1860, *Vieillard 816* (P03292447image!†).

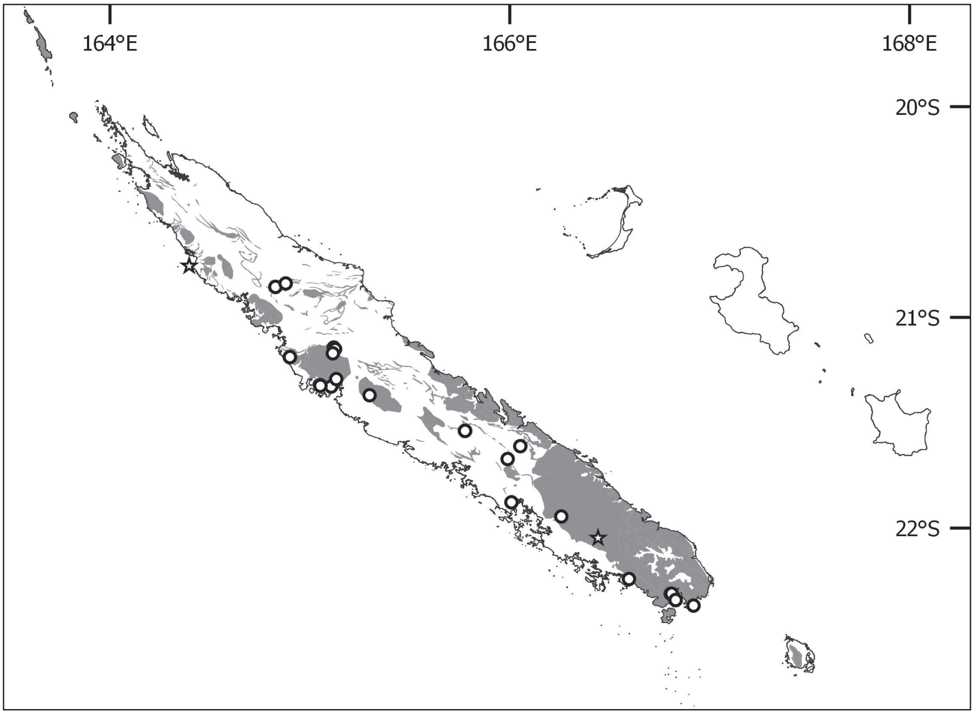


Figure 2. Distribution of *Lagenophora sinuosa* Lannuzel, Gâteblé & Jian Wang ter, sp. nov. Dots represent reliable localities and stars doubtful ones, grey shaded areas represent ultramafic outcrops.

Probable additional specimen. Haute Tipindje, Contrefort Sud du massif Oua Tilou, 400 m, 28 Jun 1970, *MacKee 22128* (P03292503image!†). We were not able to conclusively identify this specimen as the image apparently bears no cypsela. Regarding morphology and ecology, it may be a *L. sinuosa* but further field work is needed to acquire certitude on that locality.

Distribution and habitat. *Lagenophora sinuosa* is an endemic species to New Caledonia. It grows only on mainland Grande Terre from the southern tip to Kaala-Gomen as the northernmost locality. As with *L. sublyrata*, the species has a relatively broad altitudinal distribution ranging from 2 to 1000 m above sea level (Fig. 2). It inhabits the wet forests and open scrublands (maquis minier), mainly on serpentinic alluvium but has been recorded also on peridotitic derived soils at higher altitude and on vertisols at low altitudes.

Phenology. Both flowers and fruits were recorded from February through November from herbarium specimens.

Etymology. The specific epithet *sinuosa* refers to the sinuate leaf margins, by which the species differs from *L. sublyrata*. Some immature plants or populations bear crenate leaves in natural conditions, but showed ability to produce deeply lobed leaves in greenhouse conditions.

Conservation status. The species is largely distributed on the mainland, though often neglected by collectors, perhaps because it is an inconspicuous herb and maybe considered as an "exotic" or weedy species. The number of localities where it occurs may then be underestimated through herbarium records. The ecology of the species being rainforests floors and maquis on both ultramafic and non-ultramafic substrates at low to medium altitudes tend to consider the invasive introduced Rusa deer (*Rusa timorensis*) as the major threat both by grazing and by trampling. The fire threat is another issue, especially for open maquis populations. Nevertheless, with over ten localities (sensu IUCN 2019) recorded, *L. sinuosa* does not meet the requirements for a threatened species and qualifies for the Least Concern (LC) status.

Notes. *Lagenophora sinuosa* has variable leaf shapes. Although its leaf margins are usually deeply lobed, there are two populations growing in the understory of coastal *Araucaria* forests showing crenate leaf margins. These two populations were considered at one stage as a different species. However, further examinations of their fertile aspects showed there were no significant differences between these two and all other populations. Moreover, some individuals of two of the populations that were cultivated in greenhouse conditions with fertilizers can occasionally produce lobed leaves. Therefore, these two populations have been included in *L. sinuosa*.

Generic placement of the new species is subject to debate, and consideration was given to making it a new monotypic genus. However, as pointed out by Saldivia et al. (2020), rank redundancy with monotypic genera is already relatively high (36%) in Asteraceae. Thus, considering existing genera in the region, this new species is here included in the genus *Lagenophora* because of the involucres with 1 to 2–seriate ray florets, the disc florets with 4–5 corolla lobes, and cypselae with a glandular beak. The new species is atypical in the genus because of its distinctive but variable leaf shapes and more importantly its cypselae that have longitudinal ribs on both surfaces. Its characteristics were also compared with other genera in the subtribe *Lagenophorinae*, including the closely related genera in the region, viz. *Pytinicarpa* G.L.Nesom, *Solenogyne* Cass., *Keysseria* Lauterb. and *Myriactis* Less., or the morphologically similar *Brachyscome* Cass. in Brachyscominae. In Table 1 also a comparison with other members of the genus is made. Further molecular based studies among these related genera, and including New Caledonian samples, are highly recommended to clarify its position.

Table 1. Comparison of the diagnostic characters of *Lagenophora sinuosa* and related genera with data modified from Hind (2004).

Taxon	Marginal florets	Disc florets	Cypselae	Pappus
Lagenophora sinuosa	1–2–seriate with ligule	4–or 5–lobed, functionally male	ribbed, with glandular beak	absent
Lagenophora (other species)	2–5–seriate with ligule	4– or 5–lobed, functionally male	smooth, with glandular beak	absent (except scales on disc florets of *L. sublyrata*)
Brachyscome	uniseriate with ligule	4– or 5–lobed, fertile or sterile	ribbed or not, no glandular beak	present
Keysseria	2– or 3–seriate with ligule	4–lobed, sterile	smooth, with glandular beak	absent
Myriactis	2–5(–10) –seriate with ligule	4– or 5–lobed, fertile or sterile	smooth, with glandular beak	absent
Pytinicarpa	uniseriate with ligule	5–lobed, sterile	ribbed, no glandular beak	present (barbellate)
Solenogyne	3– or 4–seriate without ligule	4–lobed, functionally male	smooth, no glandular beak	absent

Lagenophora sublyrata (Cass.) A.R.Bean & Jian Wang ter, Austrobaileya 10: 435. 2019.

Figs 3, 4

Ixauchenus sublyratus Cass. in F.Cuvier, Dict. Sci. Nat. 2nd ed. 56: 176. 1828. Type: New South Wales. Port Jackson, Nov.-Dec. 1819, *C. Gaudichaud* (Lectotype: P 00742955, image only extant, fide Bean and Wang (2017).

Ixauchenus lyratus Less., Syn. Gen. Compos. 193. 1832, *nomen nudum*.

Lagenophora billardierei var. *media* DC., Prodr. 5: 307. 1836. Type: Nova Hollandia, 1823, *F.W. Sieber 505* (Syntypes: G 00454010!, HAL, NY 00180436!).

Lagenophora billardierei var. *glabrata* DC., Prodr. 5: 307. 1836. Type: Nova Hollandia, without locality, 1816, from Lambert's herbarium (Syntype: G 00454009!).

Lagenophora lanata A.Cunn., Ann. Nat. Hist. 2: 126. 1838. Type: New Zealand. Between the Waitangy and Keri-Keri Rivers, 1834, *R. Cunningham 437* (Lectotype: K000890104!, *fide* Allen 1961: 606).

Type. Australia. New South Wales: Port Jackson, November–December 1819, *C. Gaudichaud* (***Lectotype*:** P 00742955†, image only extant; designated by Bean and Wang 2017) ; **Australia. New South Wales:** Hornsby, April 1914, *W.F. Blakely s.n.* (***Epitype*:** NSW 10275!, designated by Bean and Wang 2017).

Description. ***Perennial rhizomatous herb***; roots fleshy, 0.2–1 mm diameter; no obvious stem; leaves and scapes firmly attached to rootstock. ***Leaves*** 4–9(–11), obovate, oblanceolate, elliptical or spathulate, 1–6 cm long by 0.6–1.6 cm wide (c. 2.5 ×longer than wide), sessile or with a winged petiole-like base to 1 cm long; leaf apex obtuse; leaf margins toothed, crenate to sinuate, with 2–10 teeth, each tooth c. 1 mm long; upper leaf surface green, with 2–7 trichomes per mm^2, each 0.3–0.6 mm long; lower leaf surface pale green, with 3–7 trichomes per mm^2, each 0.1–0.4 mm long; leaf margins with 6–12 trichomes per mm, each 0.1–0.4 mm long; net veins usually obscure on dried material on both surfaces. ***Scapes*** channelled or not, 1–6 per tuft, 5–11(–22) cm long, 0.5–0.8 mm diameter; bracts 2–4, upper ones c. 1.1 × 0.2 mm, lower ones 1.1–2.9 × 0.4 mm; trichomes c. 0.1 mm long, antrorse, more or less appressed; 10–30 trichomes per mm^2 at midpoint of scape, slightly denser towards apex. ***Capitula*** 3.1–3.5 mm long, 1.8–4 mm diameter; involucral bracts 15–20 in 2–3 rows, glabrous, lanceolate, oblong to obovate, apex green or purple, obtuse to acute, ciliate on distal part, outer bracts 1.3–1.9 × 0.6 mm, inner bracts 2.1–2.7 × 0.7–0.8 mm. ***Receptacle*** convex, 0.6–0.8 mm diameter and 0.5–0.8 mm high. ***Ray florets*** 20–30 in 2 rows; tube c. 0.4 mm long, 0.1–0.2 mm wide, glandular pilose; style branches c. 0.4 mm long; ligules 1.8–2.6 mm × 0.5–0.6 mm, with obscure longitudinal veins, white, creamy, or purple with age, apex obtuse or bidentate. ***Disc florets*** 6–11, corolla light yellow, tubular, 1.5–1.8 mm long, outer surface with sparse glandular trichomes; corolla lobes 5, deltate, 0.2–0.3 × 0.4–0.5 mm; stamens 5, anthers c. 0.6 mm long; style branches 0.3–0.6 mm long; sterile ovary 0.6–0.7 mm long; pappus scales 1 or 2, c. 0.1 mm long. ***Cypselae*** laterally compressed, lanceolate or obliquely oblanceolate,

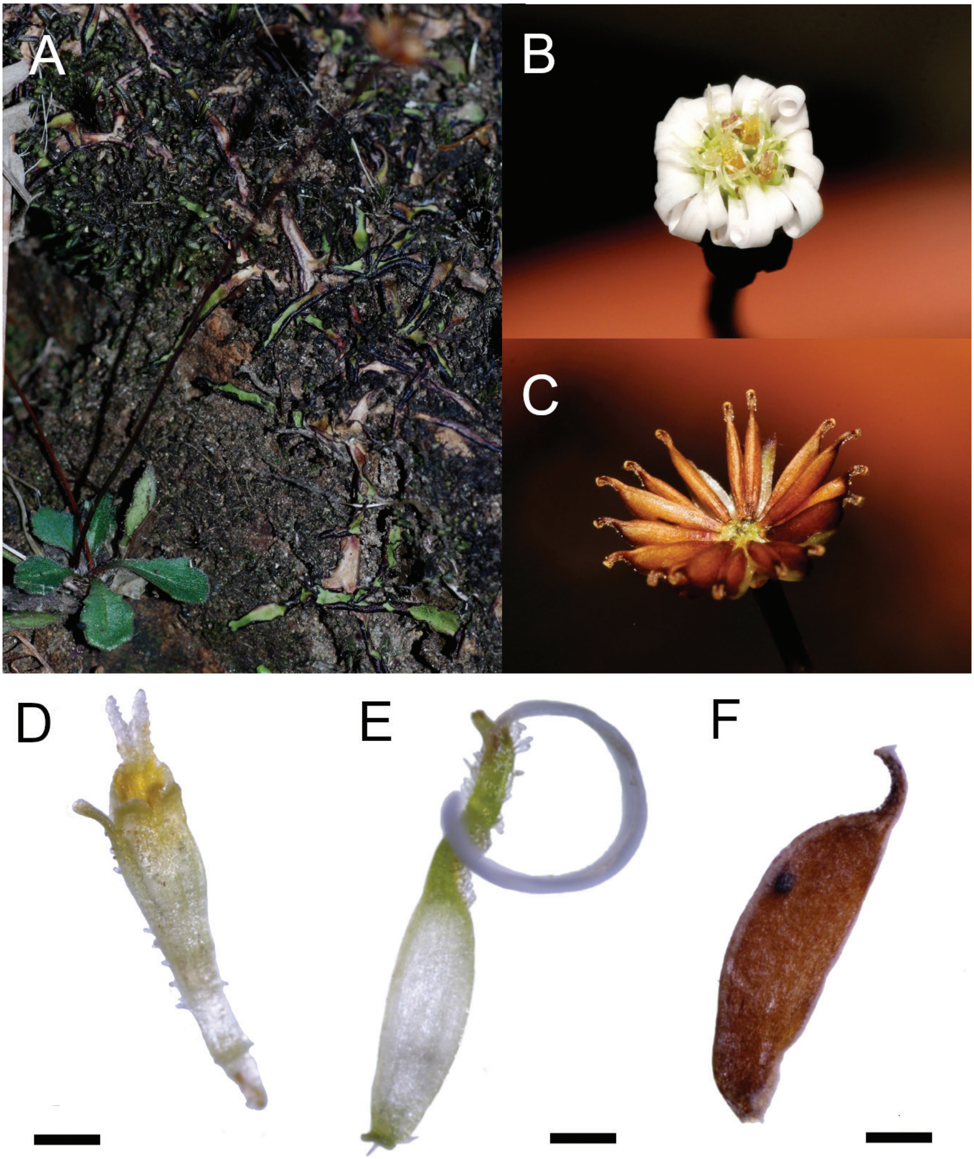


Figure 3. *Lagenophora sublyrata* (Cass.) A.R.Bean & Jian Wang ter. **A** plant in habitat **B** capitula **C** capitula with mature cypsela **D** disc floret **E** ray floret **F** cypsela **A–F** from *Lannuzel 348*. Photos from G. Lannuzel. Scale bars: 0.5 mm.

2.2–2.4 × 0.4–0.8 mm excluding beak, light brown to dark brown at maturity; cypsela edges more or less thickened, smooth; with 1–3 eglandular more or less caducous trichomes present usually at base of cypsela; cypsela glands confined to dorsal side of beak and adjacent area of cypsela; cypsela beak 0.4–0.5 mm long, with a thickened white annular collar at its apex, 0.15–0.2 mm diameter.

Specimens examined. **New Caledonia. North Prov.:** Mont Mi, 9 Mar 1869, *Balansa 1023* (P03292499image!†); Col des Roussettes, 537 m, 15 Sep 1964, *Blanchon 963* (NOU072076!); Ouaté, 21°9'19.98"S, 165°9'6.98"E, 15 Apr 2019, *Laudereau 1268* (NOU091405!); Diahoué, 20°28'53.11"S, 164°41'33.29"E, 28 Jul 2019, *Laudereau 1286* (NOU091406!); Mt Pouitchate between upper Tipindjé and upper Kamendoua above Ateu, 1000 m, 29 Aug 1956, *MacKee 5139* (L1815294image!, P03292522image!†); Contrefort de la roche Ouaième, 400 m, 27 Dec 1964, *MacKee 11865* (P03292502image!†); Haute Diahot, forêt de Tendé, exploitation forestière Frouin, 500 m, 31 Mar 1969, *MacKee 20470* (NOU072078!, P03276833image!, P04234036image!); Tiwaka, Moindip, 550 m, 31 Mar 1974, *MacKee 28455* (P04427679image!†); Col Maré, Amoa-Tiwaka, 500 m, 13 Aug 1977, *MacKee 33612* (CANB718871.1!, NOU072079!, P04427665image!†); Pouébo, Ouangati, 700 m, 20 Oct 1978, *MacKee (legit Cherrier)35947* (P04427672image!†); Néhoué, vallée de la Rade, 50 m, 8 Mar 1979, *MacKee 36698* (NOU072077!, P04427673image!†); Piémont sud du Kantalupaik, 300 m, 20°51'6.012"S, 165°0'36"E, 1 Nov 2017, *Pignal, Munzinger & Bruy 5263* (P01073109image!); Région de Pouembout au nord de Forêt Plate, 25 Mar 1981, *Suprin 1079* (NOU072080!); Plateau de Tango, 650 m, 20 Oct 1981, *Veillon 4555* (NOU072082!, P04427674image!†); Cap Tonnerre, 1861–1867, *Vieillard 816* (P03292525image!†); sur la montagne à Balade, 1855–1860, *Vieillard 817* (P03292446image!†, P03292497image!†); Gatope, 1861–1867, *Vieillard 817* (P03292496image!†). **South Prov.**: Dumbéa, *Baudouin 498* (P03292450image!†); Mont Mou summit, 3500 ft, 15 Mar 1914, *Compton 574* (BM013867014image!, P03292498image!†); Mts Koghis, 300 m, 25 Jan 1927, *Franc 486* (P03292501image!†); 1874–1876, *Germain s.n.*(P03292500image!†); Mé Aoui, 500 m, 8 Feb 1951, *Guillaumin & Baumann-Bodenheim 10444* (P03292560image!†); Cultivated plant at IAC Port-Laguerre, 11 Jun 2020, originally collected at Cascade de Dogny, 915 m, 21°37'04.2"S, 165°53'18.8"E, 21 Jan 2019, *Lannuzel 348* (NOU107487!); Cultivated plant at IAC Port-Laguerre, 5 Jan 2021, originally collected at Monts Koghis, sur le chemin du Pic Malaoui, 670m, 22°10'52.2"S, 166°30'43.2"E, 15 May 2020, *Lannuzel 427* (NOU107488!); Ouipouin, 21°41'17.88"S, 165°59'13.56"E, 13 Dec 2018, *Laudereau 1235* (NOU091403!); Vallée de la Thy, 400 m, 7 Jan 1956, *MacKee 3741* (L1815296image!, P03292451image!†, P03292523image!†); Slope of Mt Koghi toward Vallée de la Thy (St Louis), 400–500 m, 24 May 1956, *MacKee 4651* (L1815293image!, P03292520image!†); Col d'Amieu, Mont Pembai, 600 m, 15 Apr 1976, *MacKee 31018* (NSW935344!, P04427663image!†); Dogny, la cascade, 26 Oct 2007, *Munzinger 4621* (NOU030729!); Monts Koghis, propriété Lavoix, 11 Mar 1966, *Nothis 67* (NOU072075!); Ile des Pins, 1860s, *Pancher 473* (P03292495image!†); Auf den Hügeln bei Yaouhé, 150 m, 25 Sep 1902, *Schlechter 14804* (L1815295image!, P03292494image!†).

Probable additional specimen. Some plants on *Vieillard 817*, sur la montagne à Balade, 1855–1860 (P03292448image!†), see notes.

Distribution and habitat. *Lagenophora sublyrata* is the most widespread species in the genus ranging from India and Sri Lanka to south-east Asia (e.g. Vietnam), China,

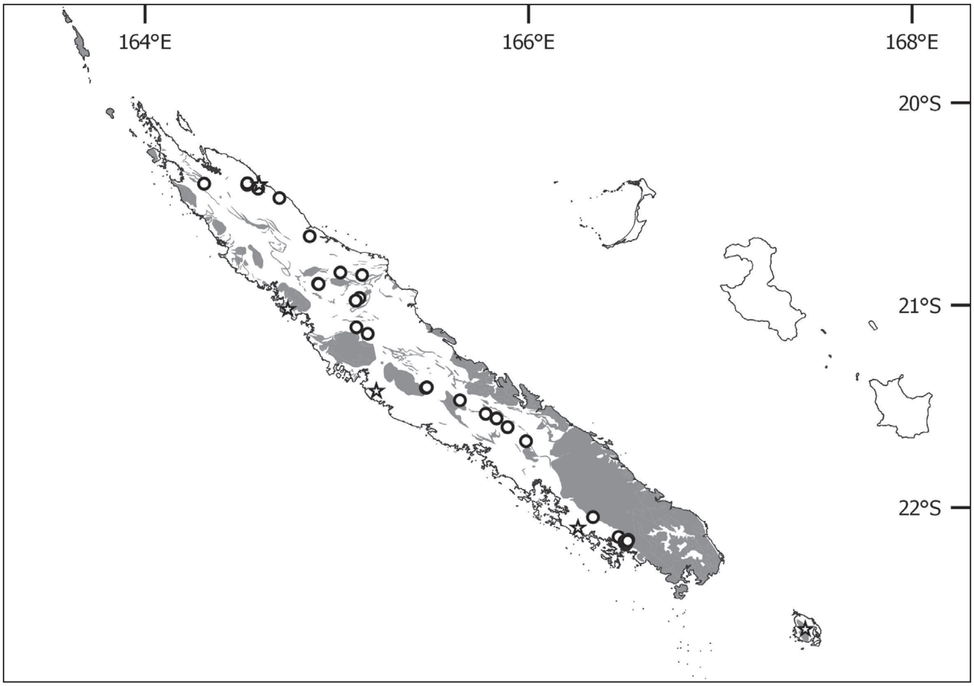


Figure 4. Distribution of *Lagenophora sublyrata* in New Caledonia. Dots represent reliable localities and stars doubtful ones, greyed areas represent ultramafic outcrops.

Taiwan, Japan, Indonesia (e.g. Java), New Guinea, Australia and New Zealand. In New Caledonia, it has a widespread distribution (Fig. 4) on mainland Grande-Terre with only one old specimen on the outer island of Île des Pins (if the *Pancher* locality is correct). It mainly inhabits the wet grounds of rainforests or rainforests margins though some specimens are collected in more open conditions (e.g. *Franc 486*, *Lannuzel 348*, *MacKee 33612*& *35947*). The species seems to avoid soils derived from ultramafic substrate, except for *Compton 574* which was recorded on ultramafic outcrop (Fig. 4) and is recorded from 50 m to 1200 m above sea level but is usually growing at medium altitudes (400–600 m a.s.l.).

Phenology. Flowers and fruits have been recorded almost all year round with a peak of specimens in March but this could be an artefact. In cultivation, the species seems to flower throughout the year.

Conservation status. The species is relatively common on mainland, though often neglected by collectors, perhaps because it is inconspicuous or considered to be an exotic or weedy species. Hence, the number of localities where it occurs, judging by herbarium records, may be underestimated. The ecology of the species is rainforest on non-ultramafic substrates at low to medium altitudes. The invasive-introduced Rusa deer (*Rusa timorensis*) may represent a major threat through overgrazing or by trampling of herbaceous vegetation. Nonetheless, with over ten localities (sensu IUCN

2019) recorded, *L. sublyrata* does not meet the requirements for a threatened species and qualifies for the Least Concern (LC) status.

Notes. *Lagenophora sublyrata* is a widespread species with variable leaf shape, indument and plant size. New Caledonia specimens are usually smaller in stature than typical plants from eastern Australia, but features of the roots, cypselae, scapes and involucral bracts are consistent with it. The specimen *MacKee11865* bears two numbers on it; 11864 on the Paris herbarium label and on the wrapper and 11865 on a manuscript label by MacKee himself. MacKee's field notebook (held at NOU herbarium) shows that 11864 is a *Mitrasacme* Labill., and 11865 is a *Lagenophora* sp. The correct collection number is therefore 11865. The specimen *Vieillard 817* (P03292448image!†) is a mixed specimen with plants of both *L. sublyrata* and *L. sinuosa*. Vieillard used a confusing system of numbering of herbarium specimens and mixed specimens are well-known (see Hopkins and Bradford 2009; Morat 2010). An additional problem is the mounting of several plants on the same sheet, probably done by Sébastien-René Lenormand at Institut Botanique de Caen (CN) before the New Caledonian collection was sent to P.

Acknowledgements

We acknowledge the curators of CANB, L, MEL, NOU, NSW and P for the loan of herbarium specimens and especially Marc Pignal (P) and David Bruy, the curator of NOU. Ranee Prakash (BM) provided high resolution images of Compton specimens. Jérôme Munzinger and the P herbarium team are also acknowledged for the transmission of the destroyed herbarium list. Christian Laudereau (www.endemia.nc) and Dominique Fleurot (www.endemia.nc) shared their valued photos and observations, Daniel Lemaître for access to his estate and Giliane Karnadi-Abdelkader (IAC) for fieldwork. The authors are most thankful to the South and North Province authorities for providing collecting permits and to the South Province rangers Catherine Geoffray and Sophie Raillard for fieldwork on Îlot Casy. This study was partly supported through a grant aiming at identifying rare and threatened species in the *Lagenophora*/*Pytinicarpa* complex from the Kaala massif (funded by Société des Mines de la Tontouta, Lannuzel et al. 2019) and by a grant (CSF n°4PS2017-CNRT.IAC/ERMINE) from "CNRT Nickel et son Environnement, Nouméa, New Caledonia"to study rare species threatened by nickel mining. Finally, we wish to thank Filip Verloove and Gustavo Heiden for their careful reading and constructive remarks on a previous version of this manuscript.

References

Allen HH (1961) Flora of New Zealand (Vol. 1). Indigenous Tracheophyta. RE Owen Government Printer, Wellington, 1085 pp.

Bean AR, Jabbour F (2018) The typification of *Lagenophora sundana* Miq. (Asteraceae). Adansonia 40(1): 43–45. https://doi.org/10.5252/adansonia2018v40a2

Bean AR, Wang J (2017) The identity and typification of *Ixauchenus sublyratus* Cass. (Asteraceae). Adansonia 39(2): 167–170. https://doi.org/10.5252/a2017n2a7

Breitwieser I, Brownsey PJ, Garnock-Jones PJ, Perrie LR, Wilton AD (2012) Phylum Tracheophyta – vascular plants. In: Gordon DP (Ed.) New Zealand Inventory of Biodiversity (Vol. 3), Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi. University of Canterbury Press, Christchurch, 411–459.

Cabrera AL (1966) The genus *Lagenophora* (Compositae). Blumea 14: 285–308.

Guillaumin A (1911) Catalogue des Plantes phanérogames de la Nouvelle-Calédonie et dépendances (Îles des pins et Loyalty). Annales du Musée Colonial de Marseille, série 2 9: 77–290.

Guillaumin A (1937) Matériaux pour la flore de la Nouvelle-Calédonie. XLIII. Révision des Composées. Bulletin de la Société Botanique de France 84: 54–61. https://doi.org/10.1080/00378941.1937.10833036

Guillaumin A (1948) Flore Analytique et Synoptique de la Nouvelle-Calédonie, Phanérogames. Office de la Recherche Scientifique coloniale, Paris, 371 pp.

Harris JG, Harris MW (2001) Plant identification terminology, an illustrated glossary (2nd edn.). Spring Lake Publishing, Spring Lake, 206 pp.

Hind DJN (2004) Novaguinea (*Compositae*: *Astereae*: *Lagenophorinae*), a new endemic genus to Papua, Indonesia. Contributions to the Flora of Mount Jaya, XIII. Kew Bulletin 59(2): 177–188. https://doi.org/10.2307/4115848

Hopkins HCF, Bradford JC (2009) Nomenclature and typification of names in the endemic genus *Pancheria* (Cunoniaceae) from New Caledonia. Adansonia, sér. 3 31(1): 103–135. https://doi.org/10.5252/a2009n1a6

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf [Accessed on 8 July 2020]

Lannuzel G, Gâteblé G, Fogliani F (2019) Etude d'espèces micro-endémiques et rares présentes sur les sites miniers de la SMT. Technical report n°1-EcoRCE/2019. IAC, Païta, 109 pp.

Moore (1921) A Systematic account of the plants collected in New Caledonia and the Isle of Pines by Prof. R. H. Compton, M.A., in 1914 – Part I. Flowering Plants (Angiosperms). Compositae. Botanical Journal of the Linnean Society 45: 345–347. https://doi.org/10.1111/j.1095-8339.1921.tb00125.x

Morat P (2010) Les botanistes récolteurs en Nouvelle-Calédonie de 1774 à 2005. Adansonia sér. 3 32(2): 159–216. https://doi.org/10.5252/a2010n2a1

Munzinger J, Morat P, Jaffré T, Gâteblé G, Pillon Y, Rouhan G, Bruy D, Veillon JM, Chalopin M (2020+) [continuously updated] FLORICAL: Checklist of the vascular indigenous flora of New Caledonia. http://publish.plantnet-project.org/project/florical [Accessed on 8 July 2020]

Nesom GL (2001) Taxonomic notes on *Keysseria* and *Pytinicarpa* (Asteraceae : Astereae, Lageniferinae). SIDA, Contributions to Botany 19: 513–518.

Nesom GL, Robinson H (2007) Tribe Astereae. In: Kubitzki K (Ed.) The Families and Genera of Vascular Plants 8. Springer-Verlag, Berlin, 284–342.

Pruski JF (2017) Compositae of Central America – IX. *Talamancaster* (Astereae), a new grangeoid genus from Guatemala, Costa Rica, Panama, and Venezuela. Phytoneuron 61: 1–35.

QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.org [Accessed on 8 July 2020]

Saldivia P, Wood KR, Orlovich DA, Lord JM (2020) *Pacifigeron indivisus* (Asteraceae: Astereae), a new species endemic to Rapa, Austral Islands, and a new delimitation of the *Celmisia* group. Phytotaxa 442(4): 239–266. https://doi.org/10.11646/phytotaxa.442.4.1

Sancho G, de Lange PJ, Donato M, Barkla J, Wagstaff SJ (2015) Late Cenozoic diversification of the austral genus *Lagenophora* (*Astereae*: *Asteraceae*). Botanical Journal of the Linnean Society 177(1): 78–95. https://doi.org/10.1111/boj.12224

Schlechter (1906) Beiträge zur Kenntnis der Flora von Neu-Kaledonien. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 39: 1–274.

Thiers B (2020+) Index herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's virtual herbarium. http://sweetgum.nybg.org/science/ih [Accessed on 8 July 2020]

Walker EH (1976) Flora of Okinawa and the Southern Ryukyu Islands. Smithsonian Institution Press, Washington, 1159 pp.

Wang J, Bean AR (2019) A taxonomic revision of *Lagenophora* Cass. (Asteraceae) in Australia. Austrobaileya 10(3): 405–442.

Wang J, Bean AR (2020) A taxonomic revision of *Lagenophora* Cass. (Asteraceae) in New Guinea. Austrobaileya 10(4): 576–582.