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Research Article

Petrocodon liboensis (Gesneriaceae), a new species from Guizhou, China

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Abstract

Petrocodon liboensis Sheng H.Tang & Jia W.Yang is a new species of Gesneriaceae from Guizhou, southwestern China. The new taxon has a pale-yellow corolla and is most similar to *P. luteoflorus*. However, it differs from the latter by having a urceolate (vs. cannulate) corolla tube, an abaxial corolla lip 0.8–1.1 mm (vs. 2–2.2 mm) long, and filaments 1.5–1.7 mm (vs. ca. 7 mm) long that are straight (vs. S-shaped or geniculate near the middle). The new taxon is assessed as “Data Deficient” (DD) according to the IUCN standards.

Key words: Didymocarpoideae, flora of China, Guizhou, karst flora, new taxon

Introduction

The genus *Petrocodon* Hance belongs to the family Gesneriaceae and subfamily Didymocarpoideae (Weber et al. 2013). *Petrocodon* was established in 1883 with a single species, *P. dealbatus* Hance (Hance 1883). Molecular studies have recently redefined the genus (Möller et al. 2011; Wang et al. 2011; Weber et al. 2011), which currently comprises 50 species and one variety (GRC 2024; IPNI 2024). This genus mainly occurs in China (POWO 2024).

During a field survey conducted in early July 2020 in Libo County, Guizhou Province, China, a population belonging to the genus *Petrocodon* (Gesneriaceae) was identified. Live plants with flower buds were cultivated in the Guizhou Botanical Garden. In late July 2020, they bloomed with pale-yellow flowers and for the first time, a corolla with straight filaments was observed. As the newly published species, viz., *P. luteoflorus* Lei Cai & F. Wen (Fan et al. 2020), which also has pale-yellow corollas, occurs in Libo County too, they were misidentified as *P. luteoflorus*. In late July 2021, they bloomed again, but only one picture of a flowering plant was captured by us because of the misidentification. In August 2022, the plants bloomed for the third time, and straight filaments were observed again. In September 2022, a field survey was conducted in Libo County to collect wild type plant specimens. The flowers of the cultivated and wild plants were identical.

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In April 2017, live plants of *P. luteoflorus* (published in 2020) were introduced from Limingguan town, Libo County, which is its type locality, and bloomed in 2017 and 2018. In 2019, they perished due to inadequate care. Fortunately, we had already meticulously photographed the blossoms in 2017. In September 2022, we photographed the flowers at their original location with great care. The flowers of both cultivated and wild plants were indistinguishable. In November 2022, a second population without flowers was found in Yongkang Town, Libo County, and the shape and size of the leaf blades were the same as those of the plants from its type locality. Therefore, the leaf blade characteristics were stable.

The misidentified plants have stable characteristics different from *P. luteoflorus*, e.g., urceolate (vs. cannulate) corolla tube, abaxial corolla lip 0.8–1.1 mm (vs. 2–2.2 mm) long, and filaments straight (vs. S-shaped or geniculate near middle). Therefore, we conclude that the plants represent a new species.

Materials and methods

One corolla was observed in 2020, and approximately 15 corollas of cultivated plants and 30 corollas of wild plants were observed in 2022. All observed corollas were pale-yellow and contained urceolate corolla tubes and straight filaments. Ten flowers in the field and ten flowers of cultivated plants were measured. A microscope (Olympus SZ61; Tokyo, Japan) was used for microscopic observations. The plants were described according to the terminology used by Wang et al. (1998). Relevant literature (e.g., Wei 2007; Jiang et al. 2011; Li and Wang 2015; Cen et al. 2017; Liu et al. 2020), especially those of the 12 accepted taxa of *Petrocodon* recorded in Guizhou, China (Wen et al. 2012; Guo et al. 2016; Li et al. 2019; Zhang et al. 2019; Fan et al. 2020; Xin et al. 2020; Pan et al. 2021; Zhang et al. 2023) was consulted. Specimen images of *Petrocodon* available in virtual herbaria and databases, including E (https://data.rbge.org.uk/search/herbarium/), K (http://apps.kew.org/herbcat/navigator.do), P (https://science.mnhn.fr/all/search), iPlant (containing specimen images of most herbaria in China, e.g., PE, IBSC, IBK, KUN) (http://www.iplant.cn/), and Global Plants (https://plants.jstor.org/) were examined. Specimens stored in CSH and the Guizhou Botanical Garden were also consulted.

Results

Taxonomic treatment

***Petrocodon liboensis* Sheng H.Tang & Jia W.Yang, sp. nov.**
urn:lsid:ipni.org:names:77343416-1
Fig. 1

Diagnosis. The new taxon has a nearly actinomorphic corolla and one nearly globose stigma. This combination of characters is shared by eight species and one variety of *Petrocodon*. The new taxon closely resembles *P. luteoflorus* (Fig. 2) in its pale-yellow corolla, two stamens, and divaricate thecae. However, it can be easily distinguished from the latter by the leaf blade being lanceolate or oblong (vs. narrowly elliptic or oblanceolate), lateral veins 2–3 (vs. 4–6) on each side of midrib, calyx segments 2.1–3.7 × 0.5–0.6 mm (vs. 6–8 × 1.5–2 mm) with entire (vs. entire to denticulate) margin, urceolate (vs. cannulate) corolla tube, abaxial corolla lip 0.8–1.1 mm (vs. 2–2.2 mm) long, and filaments 1.5–1.7 mm (vs. ca. 7 mm) long and straight (vs. S-shaped or geniculate near middle).

Type. China. Guizhou Province: Libo County, Daqikong Scenic Spot, 25°16'N, 107°45'E, ca. 450 m elev., September 1, 2022, *Sheng-Hu Tang 202209001* (holotype: CSH! CSH0192992; isotype: the Guizhou Botanical Garden!)

Description. Herbs, perennial, stemless. ***Rhizome*** terete, 5–55 mm long, 3.9–6.5 mm in diameter. ***Leaves*** 8–30, basal or crowded at rhizome apex; petiole 8.2–32 mm long, 0.9–1.8 mm in diameter, short strigose; leaf blade lanceolate or oblong, 26.4–82 × 11.3–19 mm, chartaceous, adaxially sparsely short strigose, abaxially densely short strigose along veins, base cuneate or broadly cuneate, margin entire to dentate or slightly repand, apex acute; lateral veins 2–3 on each side of midrib, adaxially inconspicuous or slightly impressed, abaxially slightly prominent. ***Cymes*** 1–4, axillary, 2–7 flowers per cyme; peduncle 35.8–59.2 mm long, 0.9–1 mm in diameter, densely short strigose; bracts 3, free, margin slightly crenulate, outside short strigose, inside sparsely short strigose, central one linear-lanceolate, 4.2–4.5 × 0.6–0.8 mm, lateral ones oblanceolate, 5.9–7.3 × 1.3–2 mm; bracteoles 3, same indumentum and shape as bracts, and slightly smaller than bracts in size, 2.5–3 × 0.9–1.2 mm. Pedicel 2.8–9.3 mm long, 0.3–0.4 mm in diameter, densely short strigose. ***Calyx*** nearly actinomorphic, 5-parted from base; segments equal or subequal, 2.1–3.7 × 0.5–0.6 mm, linear, both outside and inside short strigose, margin entire. ***Corolla*** pale-yellow, 5.3–8 mm long, outside puberulent, inside glabrous, 5-parted to 1/5, segments slightly converged; tube urceolate, 4.5–6.9 mm long, 2.1–3 mm in diameter at base, 1.7–2.1 mm in diameter at mouth; limb indistinctly 2-lipped, adaxial lip 2-parted from base, segments triangular, equal, 0.5–0.8 × 0.9–1.2 mm, abaxial lip 3-parted from base, segments triangular, subequal, 0.8–1.1 × 1.5–1.7 mm. ***Stamens*** 2, adnate to abaxial side of corolla tube 2.8–3.1 mm above base, included; filaments 1.5–1.7 mm long, ca. 0.2 mm in diameter, straight, glabrous; anthers dorsifixed, coherent at apex, elliptic, 1.3–1.7 × 0.8–0.9 mm, glabrous; thecae divaricate, confluent at apex, dehiscing longitudinally; connective not projecting; staminodes 3, central one inconspicuous, adnate to adaxial side of corolla tube 1.6–2 mm above base, ca. 0.1 mm long, lateral ones conspicuous, adnate to adaxial side of corolla tube 2.3–2.5 mm above base, 0.7–0.8 mm long. ***Disc*** ring-like, pale yellow, 0.2–0.3 mm high, margin entire or repand. ***Pistil*** 7.9–12 mm long; ovary linear, 2.8–4.5 mm long, 0.5–0.6 mm in diameter, glabrous or short strigose, 1-loculed, placentas 2, parietal, projecting inward, 2-cleft; style 5.1–7.5 mm long, ca. 0.3 mm in diameter, glabrous or sparsely short strigose; stigma 1, terminal, nearly globose, undivided. ***Capsule*** straight, linear, 10.3–17.8 mm long, 0.8–0.9 mm in diameter, dehiscing loculicidally to base; valves 2, straight, not twisted. ***Seeds*** unappendaged, fusiform, 0.4–0.6 mm long.

Phenology. Flowering occurs from late July to early September, and fruiting in the wild is unknown; only capsules from the previous year were observed.

Etymology. The new taxon was named after its locality in Libo County, China.

Vernacular name. The Chinese name is “Lì Bō Shí Shān Jù Tái” (荔波石山苣苔).

Distribution and habitat. Only one population was found at the Daqikong Scenic Spot, Libo County, Guizhou Province, China. Plants were found growing on wet shady rocks in the valley, along with mosses, weeds, and shrubs.

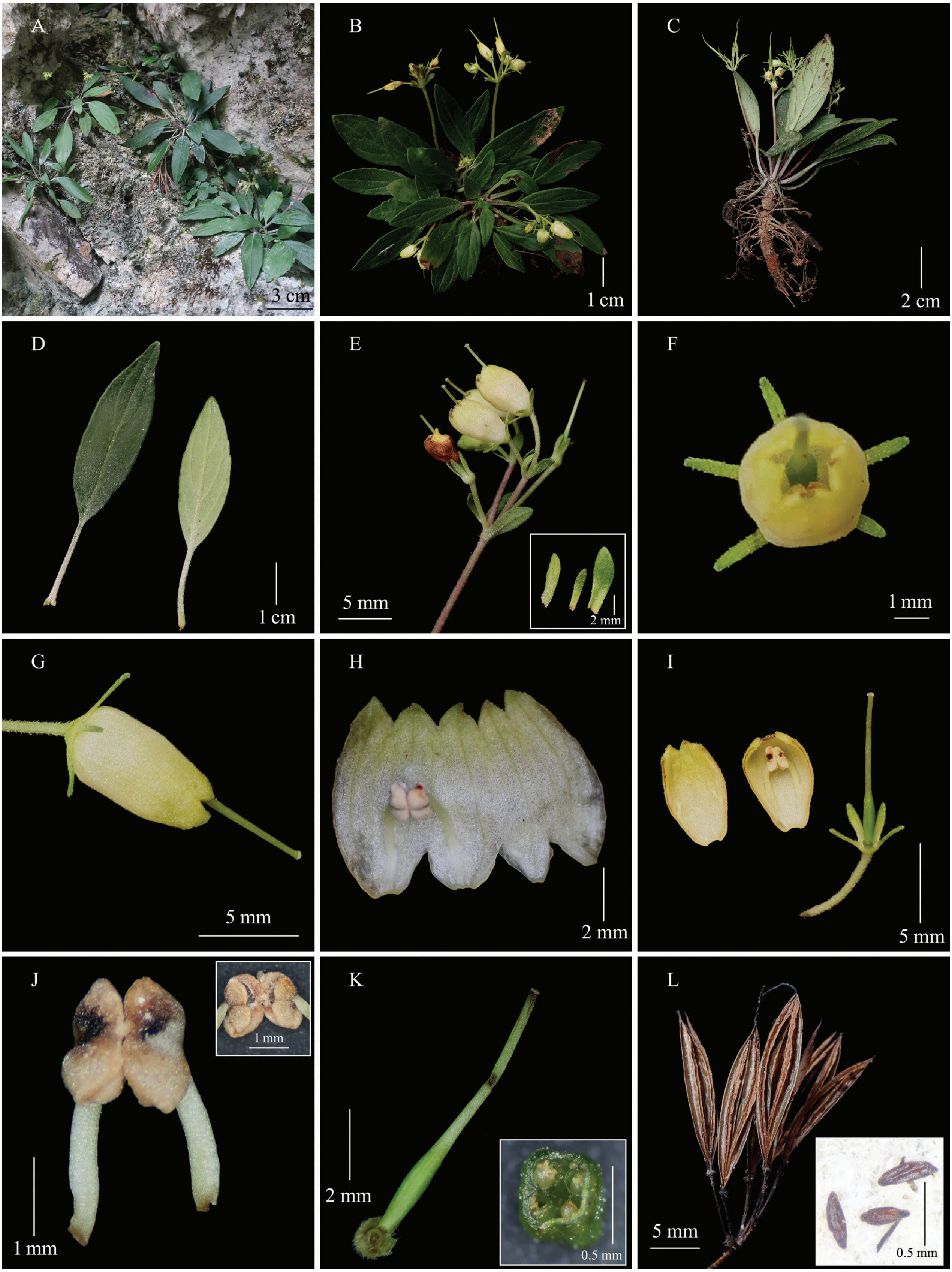

Figure 1. *Petrocodon liboensis* **A** habitat **B, C** flowering plant **D** adaxial and abaxial surfaces of leaf blade **E** cymes, and bracts (inset) **F** flower in front view **G** flower in side view **H, I** opened corolla **J** stamens, and anthers (inset) **K** pistil, and cross section of ovary (inset) **L** capsules, and seeds (inset) (Photographs by Sheng-Hu Tang).

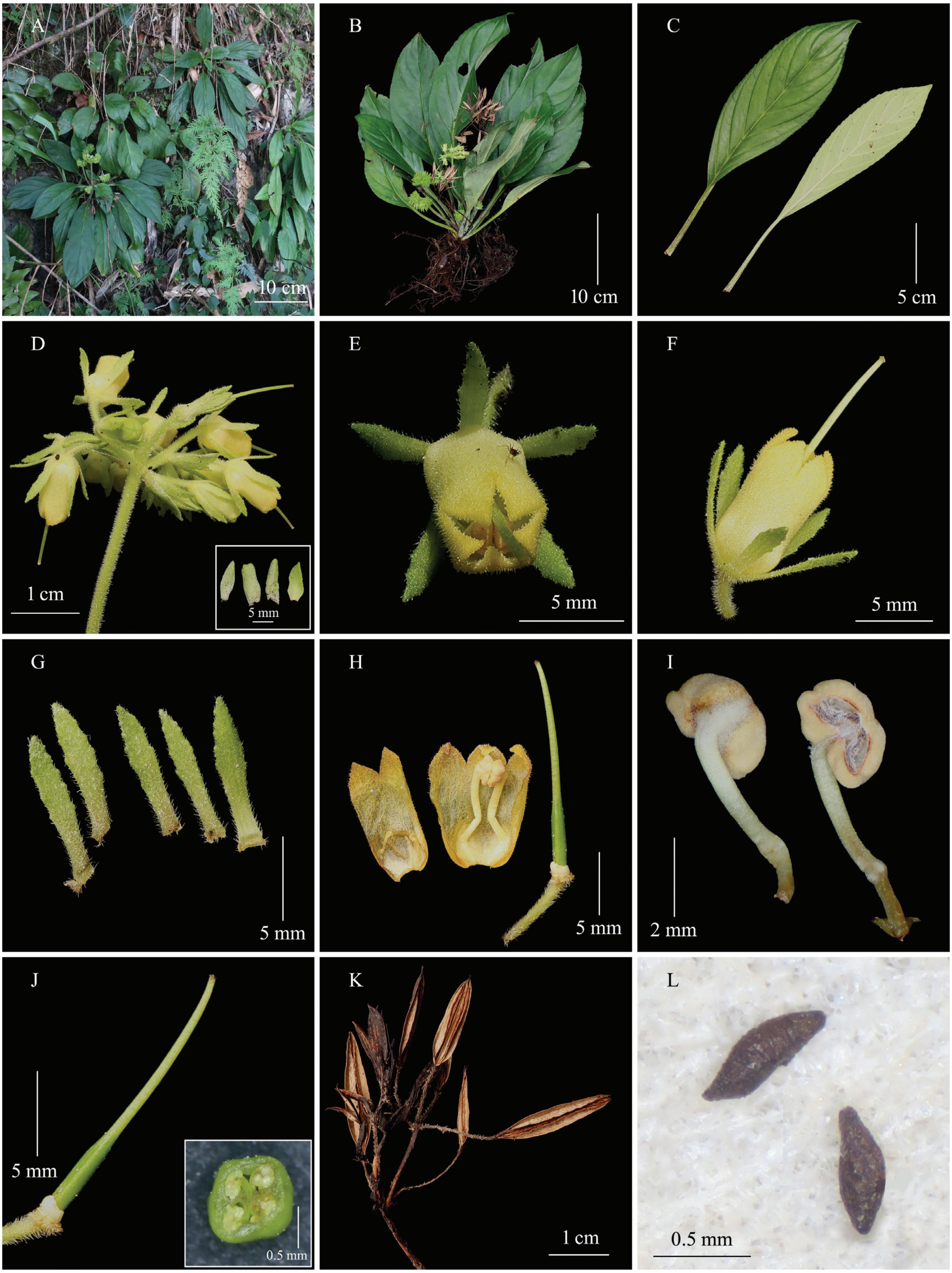

Figure 2. *Petrocodon luteoflorus* **A** habitat **B** flowering plant **C** adaxial and abaxial surfaces of leaf blade **D** cymes, and bracts (inset) **E** flower in front view **F** flower in side view **G** calyx segments **H** opened corolla **I** stamens **J** pistil, and cross section of ovary (inset) **K** capsules **L** seeds (Photographs by Sheng-Hu Tang).

Table 1. Detailed comparisons between *Petrocodon liboensis* and *P. luteoflorus*.

Character	*P. liboensis*	*P. luteoflorus*
Leaf blade	lanceolate or oblong	narrowly elliptic or oblanceolate
Lateral veins	2–3 on each side of midrib	4–6 on each side of midrib
Calyx segments size	2.1–3.7 × 0.5–0.6 mm	6–8 × 1.5–2 mm
Calyx segments margin	entire	entire to denticulate
Corolla tube shape	urceolate	cannulate
Abaxial corolla lip length	0.8–1.1 mm	2–2.2 mm
Filaments	1.5–1.7 mm long and straight	ca. 7 mm long and S-shaped or geniculate near middle

Preliminary conservation assessment. Only one population of approximately 200 mature individuals was found in the type locality. It is highly likely that more populations were present in this area. Until further investigation, the species should be designated as “Data Deficient” (DD) according to the IUCN standards (IUCN 2022).

Taxonomic notes. The new taxon is similar to eight species and one variety of *Petrocodon* in nearly actinomorphic flowers and one stigma. Its corolla tube is urceolate, similar to *P. scopulorum* (Chun) Yin Z. Wang (Chun 1946; Wang et al. 2011) and *P. urceolatus* F. Wen, H. F. Cen & L. F. Fu (Cen et al. 2017). The new taxon differs from *P. scopulorum* in its pale-yellow (vs. white) corolla, corolla parted to 1/5 (vs. 1/3), stamens 2 (vs. 4), and anthers coherent (vs. free). The new taxon is different from *P. urceolatus* by bracts 3 (vs. 2), pale-yellow (vs. white) corolla, puberulent (vs. glabrous) corolla outside, slightly constricted (vs. constricted) corolla mouth, and 1.7–2.1 mm (vs. ca. 0.9 mm) in diameter at corolla mouth. The new taxon was most similar to *P. luteoflorus* in terms of corolla color. The detailed morphological comparisons between *P. liboensis and P. luteoflorus* are presented in Table 1.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Sheng-Hu Tang and Qi-Fei Ren conceived of the study. All the authors collected the samples. Sheng-Hu Tang and Ming-Zhu Ou conducted the measurements of the morphological characteristics, data analysis, and microscopic observations. Sheng-Hu Tang and Jia-Wen Yang wrote the original manuscript. Qi-Fei Ren reviewed and edited the manuscript. All the authors approved the final version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Short Communication

A new synonym of *Rhododendron leishanicum* (subg. *Hymenanthes*) from China (Ericaceae)

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Abstract

Based on a critical examination of type specimens, images of living plants, and the literature has shown *Rhododendron oligocarpum* to be conspecific with *R. leishanicum*. Although slight variations in corolla colour exist amongst different populations of *R. oligocarpum*, it does not serve as a key distinguishing trait. Therefore, we reduced *R. oligocarpum* to a synonym of *R. leishanicum*, and recommend placing it in Subsection *Maculifera*.

Key words: Morphology, new synonym, *Rhododendron*, *Rhododendron leishanicum*

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Rhododendron L. which contains ca. 1200 species, is the largest genus of Ericaceae (Chamberlain et al. 1996; MacKay and Gardiner 2017). This genus is widely distributed in Asia, Europe and North America, of which the great majority (ca. 900) occurs in China and the Malaysian archipelago, the centres of diversity being in the Himalayas and South East Asia (Fang et al. 2005; Brown et al. 2006; Gibbs et al. 2011; Liu et al. 2020). When we examined the type specimens of *Rhododendron* from Guizhou Province, China, *R. leishanicum* W. P. Fang et S. S. Chang ex D. F. Chamb. and *R. oligocarpum* W. P. Fang et S. S. Chang were found to be morphologically very similar and identified as very confusing in terms of leaf, flower, and fruit characters.

Rhododendron leishanicum was originally described by Chamberlain (1982), based on a single collection, Austro-Guizhou Exped 909, from Leigong mountain in Lei Shan Xian, Guizhou Province, China (Fig. 1A). In the protologue, Chamberlain placed *R. leishanicum* in the Subsection *Williamsiana*. The next year, *R. oligocarpum* was described by Fang (1983), based on six collections (including Z. S. Zhang et al. 401557 (Types: HGAS0088928, IBSC0481928, PE01297915, PE01297916), Z. S. Zhang 58 (HGAS007915), T. H. Tu 31739 (SZ0036179), from Fanjing Mountain; Austro-Guizhou Exped 1411 (PE00312607, PE00313389, KUN540382), from Leigong Mountain and G. Z. Li 6211 & 11277 (IBK00187538, IBK00187539 & IBK00187541, IBK00187559), from Maoer Mountain) from three different origins in China (Fig. 1B–D). According to the protologue, Fang placed *R. oligocarpum* in the Subsection *Maculifera*. Meanwhile, *R. leishanicum* was again described as a new species by Fang in the same protologue. It is worth noting that a paratype of *R. oligocarpum*, Austro-Guizhou Exped 1141, was collected from Leigong Mountain (Fig. 1C). However, the relationship between *R. oligocarpum* and *R. leishanicum* was not mentioned by Fang when he described *R. leishanicum* as a new species again in the publication in 1983.

According to critical examination of the type specimens and morphological comparisons of *R. leishanicum* and *R. oligocarpum*, we found that both species have setose young branches and petioles, with small apiculate leathery leaves, racemose-umbellate inflorescences, corolla campanulate, with deep purple basal spots, pedicel, ovary and filament with identical indumentum (Fig. 2). It is worth noting that during our field surveys of populations of these two species, we observed a certain difference in colour of the corolla between the Guangxi population of *R. oligocarpum* and those in Guizhou. However, variation in corolla colour is known to occur within species of the genus *Rhododendron* (Jin 2006; Zhou 2008); hence, the differences in corolla colour between them fall within a normal range of variation. Therefore, we place *R. oligocarpum* in synonymy with *R. leishanicum* according to ICN rules (Turland et al. 2018).

Based on the setose branchlets and petioles, the small apiculate leaves, the campanulate corolla and the glabrous style, we suggest placing *R. leishanicum* in the Subsection *Maculifera*.

Taxonomy treatment

Rhododendron leishanicum **W. P. Fang & S. S. Chang ex D. F. Chamb.**

Type. China. Guizhou province: Leishan Xian, Leishan, 1850 m elev, 29 April 1959, Austro-Guizhou Exped 909 (holotype: SZ; isotype: HGAS007912!; KUN0540381!).

Rhododendron oligocarpum **W. P. Fang & S. S. Chang, syn. nov.**

Type. China. Guizhou province: Yinjiang county, Sanduodian, 2070 m elev, 14 april 1964, Z. S. Zhang et al. 401557 (holotype: HGAS0088928!; isotypes: IBSC0481928!; PE01297915!, PE01297916!; paratype: HGAS007915!; IBK00187538!, IBK00187539!, IBK00187541!, IBK00187559!; PE00312607!, PE00313389!; KUN540382!; SZ0036179!).

Description. Shrubs or small trees, 3–6 m tall; bark grey, dehiscent on drying; **branchlets** terete, setose when young, gradually glabrescent. **Petiole** rounded abaxially, furrowed adaxially, 5–15 mm, densely setose; **leaf** blade leathery, elliptic or obovate, 4–8 × 2–4 cm; base rounded or subcordate; margin revolute, apex rounded, with small apiculate; adaxial surface green, abaxial surface pistachio; mid-rib impressed abaxially, grooved adaxially, glabrous or sometimes sparsely hairy; lateral veins 11–15-paired, slightly conspicuous on both surfaces. **Inflorescence** racemose-umbellate, 3–5-flowered; rachis 5–7 mm, tomentose. **Pedicel** 1–2 cm, densely setose-tomentose; **Calyx** small, discoid, lobes 5, triangular, tomentose, 1–2 mm. **Corolla** campanulate, purple-red to rose-red, with deep purple basal spots, 3–3.5 cm; lobes 5, suborbicular, ca. 1.5 × 2 cm, apex emarginate; **stamens** 10, unequal, 1–3 cm, filaments puberulent at base;

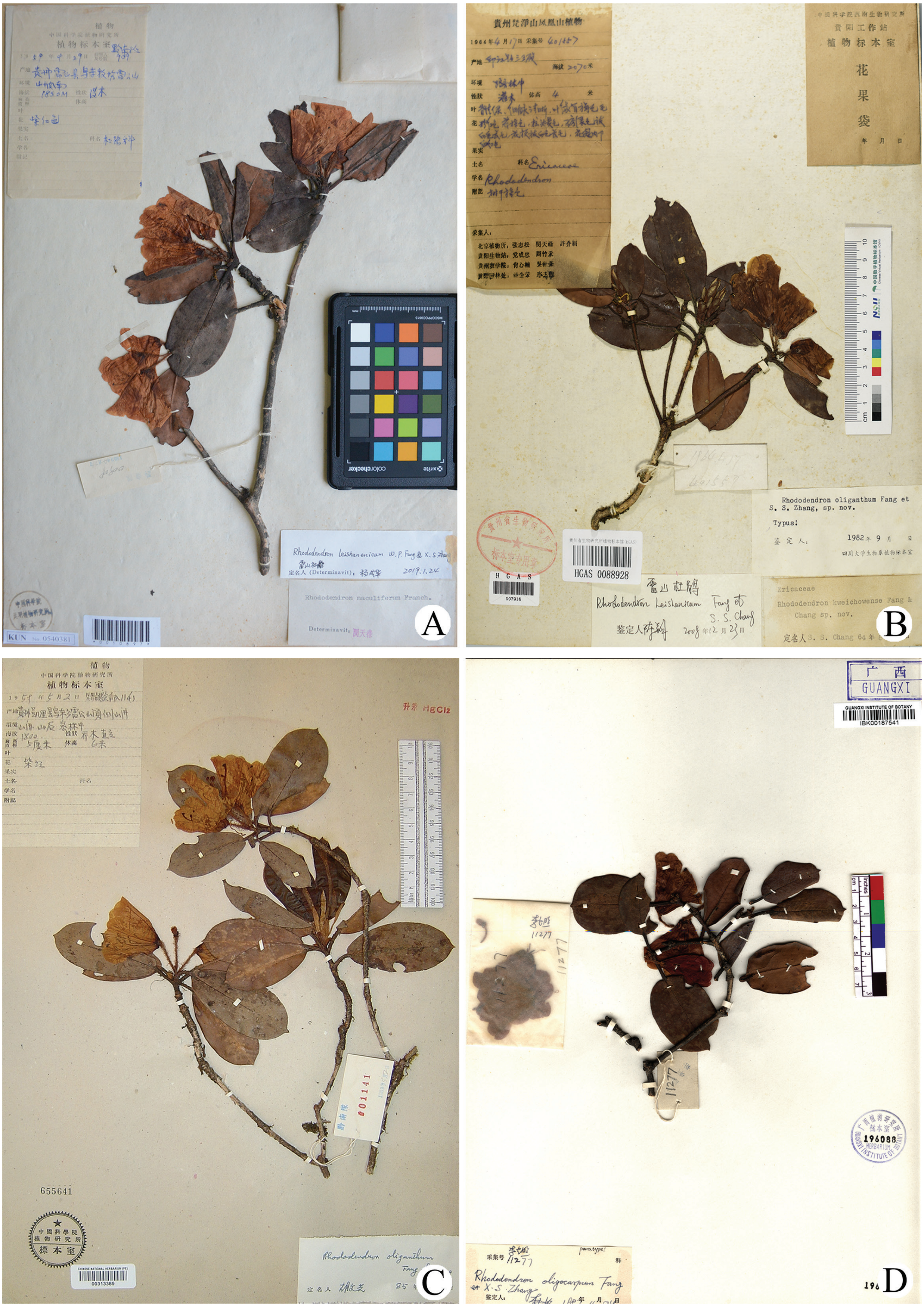

Figure 1. *Rhododendron leishanicum* and *R. oligocarpum* **A** isotype of *R. leishanicum* **B** holotype of *R. oligocarpum* **C, D** paratype from Leigong Mountain and Maoer Mountain of *R. oligocarpum*, respectively.

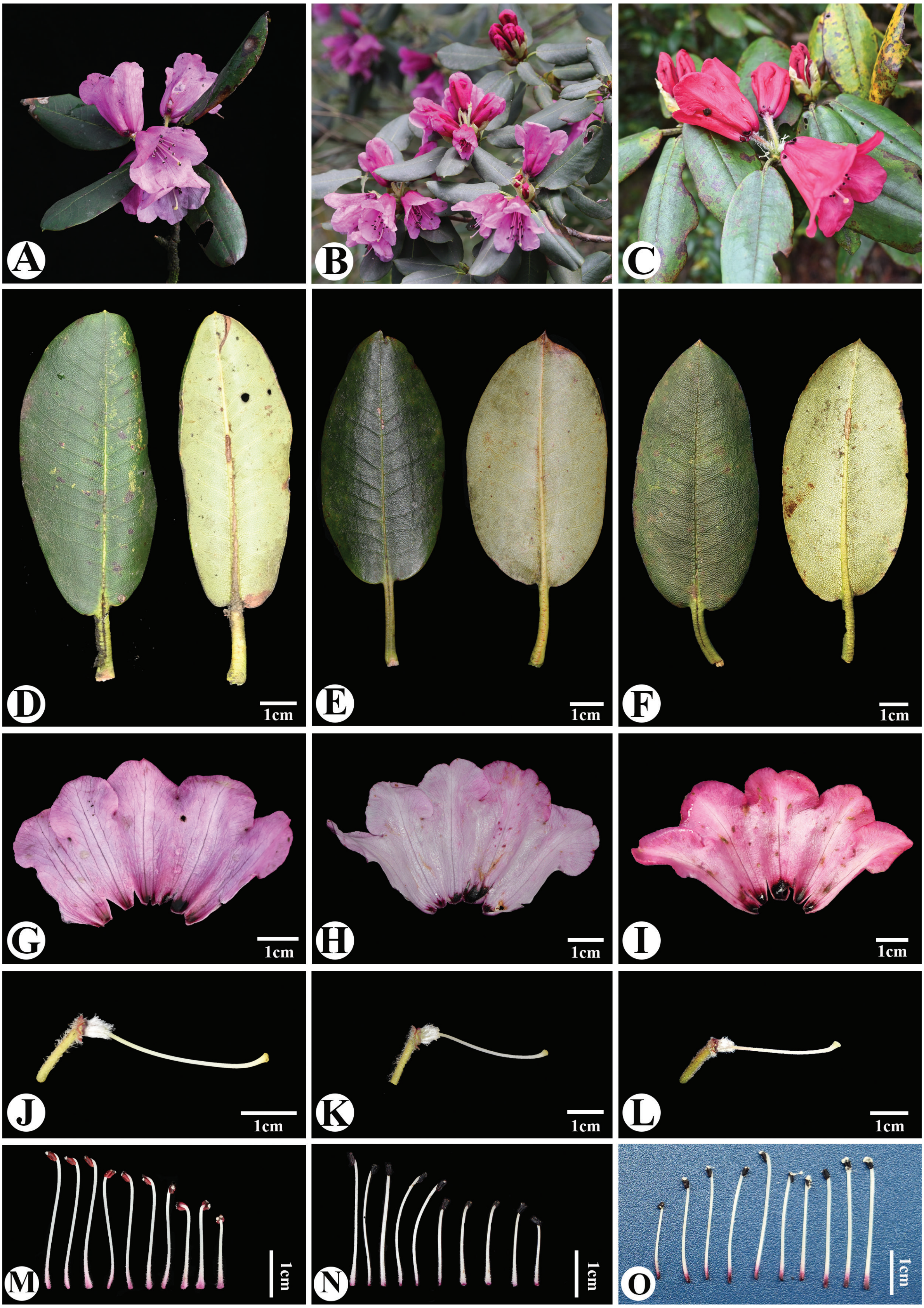

Figure 2. Comparison of *Rhododendron leishanicum* and *R. oligocarpum* **A, D, G, J, M** *R. leishanicum* from Leigong mountain **B, E, H, K, N** *R. oligocarpum* from Fanjing mountain **C, F, I, L, O** *R. oligocarpum* from Maoer mountain **A–C** branchlets with flowers **D–F** adaxial and abaxial surface of leaf **G–I** corolla with deep purple basal spots **J–L** pedicel, Calyx, ovary and style indumentum **M–O** stamens side view.

ovary cone-shaped, 4–5 mm, densely densely setose and tomentose; **style** 2.5–3 cm, glabrous, stigma slightly expanded. **Capsule** cylindrical, 20–25 × 7 mm, rough. Flowering from April to May and fruiting from September to October.

Distribution and habitat. *Rhododendron leishanicum* is distributed in Eastern Guizhou and North-eastern Guangxi. It grows in Thickets at 1800–2500 m a.s.l.

Specimens examined. China. Guizhou: Qiandongnan Prefecture, Leigong Mountain, *P. L. Song 1016* (GYBG barcode 0002282, 0002283), *4407* (CCNU barcode 9018123), *4717* (CCNU barcode 9018122); Tongren City, Fanjing Mountain, Z. S. Zhang et al. 401673 (IBSC barcode 0481934), *401317* (HGAS barcode 0088940, IBSC barcode 0481929), *400681* (HGAS barcode 0088933), *400610* (HGAS barcode 0088939), *Z. P. Jian 32039* (HGAS barcode 0088938), *Wuling Mountain Expedition 731* (GFS barcode 0007355, KUN barcode 0339467, 0339468, PE barcode 00258535), *1348* (GFS barcode 0007356, KUN barcode 0339469). **Guangxi:** Guilin City, Maoer Mountain, *G. Z. Li 11272* (IBK barcode 00187540), *12378* (IBK barcode 00187542), *12084* (IBK barcode 00187561), *F. X. Jin 1066* (HTC barcode 0010523, 0010524, 0010525), *J. X. Zhong 83311* (IBK barcode 00187551, 00187552, IBSC barcode 0481913), *83523* (IBK barcode 00187560), *81647* (IBK barcode 00187566, 00187567), *L. M. Gao 20077* (KUN barcode 0767388, 0767389).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualisation: XC, LH, SC. Data curation: YHD, CHY, JMY, JXL, YSH. Writing – original draft: SC, LH, XC. Writing – review and editing: SC, XC.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Carex recondita Muñoz-Schüler, Martín-Bravo & Jim.Mejías (Carex section *Junciformes* Kük., Cyperaceae), a new sedge species from the Andes of central Chile

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Abstract

Carex section *Junciformes* is one of the most diverse groups of the genus in South America, consisting of approximately 30 species. Here we describe a new species, *Carex recondita*, belonging to this section. We studied its placement within a molecular phylogeny of the group and found it to constitute an independent lineage. The new species is morphologically very close to *C. austroamericana*, from southern Patagonia, despite being phylogenetically divergent to the rest of Patagonian species of sect. *Junciformes*. So far, this species is known only from a few specimens recently collected in its type locality, despite growing in a well-collected area in the Andes of Metropolitana Region of Santiago, the most populated administrative region of Chile. We provide a detailed morphological description, comments on its relationship with other Southern Cone species of sect. *Junciformes* and relevant ecological notes.

Key words: Andes, *Carex*, Chile, Cyperaceae, South America, taxonomy

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Introduction

With about 96 species, *Carex* is among the three most biodiverse genera of the flora of Chile (Rodriguez et al. 2018; Muñoz-Schüler et al. 2023). However, the taxonomic knowledge of the genus in the country is fragmentary, as it is in the rest of South America. Recently, a series of works focusing on particular groups of *Carex* are shedding light on the taxonomic structure and systematic relationships of these understudied groups (e.g. Benítez-Benítez et al. 2021; Jiménez-Mejías et al. 2021a; García-Moro et al. 2022). The relatively large number of new species that are being steadily described from the continent in the last few years (e.g., Jiménez-Mejías and Escudero 2016; Jiménez-Mejías and Roalson 2016; Poindexter et al. 2017; Jiménez-Mejías and Reznicek 2018; Jiménez-Mejías et al. 2020, 2021a, 2021b) depicts how much is still to be done before a comprehensive understanding of the genus in South America is reached.

Carex section *Junciformes* Kük (subgenus *Psyllophorae*), with over 25 species in the continent (Roalson et al. 2021; Morales-Alonso et al. in press), is one of the most diversified *Carex* groups of South America. It is almost entirely endemic to the continent, with only four species in the SW Pacific and a clear center of diversity in Patagonia (Barros 1935, 1969; Moore 1968, 1983). The evolutionary history of the group has been recently studied by Benítez-Benítez et al. (2021). They showed that the section includes two main lineages, namely “Junciformes clade” and “Aciculares clade” -as these were formerly considered independent sections due to several diagnostic morphological characters (Wheeler 1989)- plus three isolated lineages (*C. camptoglochin* V.I.Krecz., *C. phalaroides* Kunth s.l., and *C. vallis-pulchrae* Phil.). Benítez-Benítez et al. (2021) also showed that the ancestral area and diversification cradle of the group was centered in South America, with several migrations out of the Southern Cone to the Tropical Andes, Brazil, and the SW Pacific. However, the circumscription of this section is still under study, as a recent phylogenetic framework excluded the geographically isolated Pampean *C. herteri* G.A.Wheeler from sect. *Junciformes* (Morales-Alonso et al. in press).

During a fieldtrip in Chile in January 2023 we collected material of an undetermined acaulescent *Carex* sect. *Junciformes* taxon in the Andes of Metropolitana region of Santiago (see Taxonomic Treatment for details on the collection). In a preliminary assessment using the available identification keys (Barros 1969; Moore 1983; Wheeler 1986, 1988) the specimen was determined as *C. austroamericana* G.A. Wheeler, a Patagonian species belonging to the Junciformes clade (Benítez-Benítez et al. 2021). The strong disjunction of this undetermined specimen population regarding its tentative species distribution (>700 km north) raised the question of whether it could be a different species. Accordingly, we proceeded with a molecular phylogenetic and morphological study to resolve the taxonomic identity and systematic affinities of the problematic specimen, and to warrant its taxonomic recognition if required.

Materials and methods

Molecular analyses

Silica-dried leaves of the undetermined taxon collected on the field in January 2023 were used for DNA extraction and PCR amplification.

The DNA extraction was performed using a modified CTAB procedure (Doyle and Doyle 1987). We amplified the loci ETS and ITS (nuclear ribosomal DNA, nrDNA) and *mat*K and *rps*16 (plastidial DNA, ptDNA) since these have been previously used for the study of the systematics of sect. *Junciformes*, following the protocols in Benítez-Benítez et al. (2021). The amplified products were externally sequenced by Macrogen (Madrid, Spain). The sequence chromatograms were edited and revised with Geneious v.2022.0.1 (Biomatters Ltd., Auckland, New Zealand). The resulting sequences were concatenated and included in the complete multiaccession matrix built by Benítez-Benítez et al. (2021).

The alignment was made with MUSCLE v.3.8.425 (Edgar 2004), and the best substitution models for each DNA region were selected with JModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012) as implemented in CIPRES Science Gateway v3.3 (www.phylo.org/portal2; Miller et al. 2010). The concatenated matrix contained 106 accessions, 96 belonging to species of subg. *Psyllophorae* of which 17 are representatives of the South American species of sect. *Junciformes*. Thus, all but five species -if *C. phalaroides* is considered in a broad sense (Morales-Alonso and Jiménez-Mejías 2021)- from the section were included in the study. The missing species are *C. boelckeiana* Barros, *C. moorei* G.A.Wheeler, and *C. nelmesiana* Barros, which are morphologically close to the Junciformes s.s. clade, and *C. sanctae-marthae* L.E.Mora & J.O.Rangel and *C. transandina* G.A.Wheeler, putatively belonging to the Aciculares clade. It is worth saying that the samples determined as *C. nelmesiana* and *C. transandina* in Benítez-Benítez et al. (2021) were re-identified here as *C. austroamericana* (P.J.-M., pers. obs.). Additionally, the former species named *C. lateriflora* Phil. has been here corrected to *C. trichodes* Steudel ex Boott (Penneckamp 2022).

The phylogenetic reconstructions analysis were run employing Maximum Likelihood (ML) in RAxML v.8.2.12 (Stamatakis 2014), and Bayesian Inference (BI) using MrBayes v.3.2 (Ronquist and Huelsenbeck 2003; Ronquist et al. 2012) as implemented in the CIPRES Science Gateway v3.3 (Miller et al. 2010) and in the Scientific Computer Center of Andalucía supercomputing cluster (CICA). ML analysis was set with default parameters and 1000 replicates. BI analysis was set with 10 million generations and 4 simultaneous Monte Carlo Markov chains (MCMC) runs, with a sample frequency of one tree every 1000 generations. After checking for the analysis to reach stationarity, a burn-in threshold of 25% was applied and the consensus tree was built using the 50% majority rule. Strong clade support was considered above 75% for bootstrap (BS) and above 0.90 for posterior probability (PP) (Gehrke et al. 2010).

Morphological study

Three collections of the undetermined taxon were located and studied: the original collection from the 2023 fieldwork campaign, a second collection by M.T.K.A. in 2022, and a last voucher located in CONC collection, determined as *Carex andina* Phil., and collected in 2007. These vouchers were determined using the available keys and thoroughly compared against descriptions (Barros 1969; Moore 1983; Wheeler 1986, 1988; see Results).

Direct comparisons were also carried out against material (including type material -herbarium specimens or high-resolution images of them-) belonging to the other three Junciformes clade acaulescent species: *C. argentina* Barros, *C. austroamericana*, and *C. nelmesiana*. In total, we studied 17 vouchers housed at BAB, CONC, SI, and UPOS.

Conservation status

Since our results showed that the undetermined taxon constitutes an undescribed species with a very restricted known distribution, a preliminary conservation status for it was assessed. We followed the criteria provided in the IUCN Red List Categories and Criteria Version 13 (IUCN 2017) manual.

Results

Molecular analyses

The multiaccession matrix consisted of 606 bp for ETS, 624 bp for ITS, 572 bp for *mat*K, and 937 bp for *rps*16. The length of obtained sequences for the problematic specimen were 493 bp for ETS, 603 bp for ITS, 503 bp for *matK*, while for *rps*16 marker only 285 bp could be obtained. The obtained BI tree topology (Fig. 3) was highly in concordance with the one recovered in Benítez-Benítez et al. (2021) and Morales-Alonso et al. (unpublished results). The best resolved topology was obtained with BI with no indels coded. ML and BI analyses resulted in very similar topologies. The main incongruences were mostly minor and retrieved at shallow branch levels of the tree.

The sample of the undetermined taxon (Fig. 3) was nested within the Junciformes clade with maximum BS and PP support. It was placed as sister to a well-supported clade containing the caulescent *C. sorianoi* Barros and the acaulescent *C. austroamericana* (BS = 100; PP = 1,00). The sample shared up to 98.6% pairwise nucleotide identity with *C. austroamericana* and *C. sorianoi* while 96.5% of identical sites were reached for this clade.

Morphological analyses

The samples of the undetermined specimen share a number of morphological affinities with *C. austroamericana*, such as an acaulescent growing habit, stiff leaves that surpass the entire inflorescence, and stipitate utricles. However, it can be distinguished from this and any other species of sect. *Junciformes* by having the following combination of characters: leaves up to 9 cm long, spikes ≤ 3.5 mm wide, and utricles ellipsoid, ovoid or sub-obovoid, glabrous to sparsely hispidulous, with -usually weakly- raised nerves on the faces and a stipitate base often flattened. A detailed morphological comparison between these problematic specimens, *C. austroamericana* and the other three acaulescent species of sect. *Junciformes* from the Southern Cone is provided in Table 1.

From the other three Junciformes clade species not included in the phylogeny (*C. boelckeiana*, *C. moorei* and *C. nelmesiana*) the undetermined taxon is readily distinguished because the two first species have well-developed stems, longer than leaves, as well as larger utricles (see Barros 1969, Wheeler 1988), and *C. nelmesiana* has utricles with faces entirely nerveless. The undetermined taxon is also readily distinguished from the closely related *C. sorianoi* (Fig. 3) because this latter has culms exceeding its leaves, that are usually flexuose, and also by having two stigmatic female flowers (instead of three; see the Description section below).

Discussion

The set of evidence presented here makes it clear that the studied specimens should be treated as a new species. Even though it is morphologically very similar to *C. austroamericana*, the molecular data by itself is compelling enough to support its status as a different taxon (Fig. 2). Moreover, the differences in key -but subtle- traits (such as rachilla shape and utricle venation; see Table 1) and its disjunct distribution with respect to the other three phylogenetically

Table 1. Variation in diagnostic morphological characters of *C. recondita* and morphologically related Patagonian species of sect. *Junciformes*. Characters listed for *C. austroamericana* and *C. nelmesiana* are based largely on Wheeler (1986) and complemented with personal observations and measurements. Given the low sampling sizes, the natural variation of these characters might be underestimated and could be wider.

Character	*Carex austroamericana*	*Carex nelmesiana*	*Carex argentina*	*Carex recondita*
Leaf length	0.5–5 cm	1–5 cm	8–12 cm	2.9–9 cm
Spike width	3.5–6 mm	5–6 mm	5 mm	2.8–3.5 mm
Number of female flowers/utricles	Four to six	Four to seven	Five to seven	Four to five
Utricle shape	Obovoid	Sub-globose	Ovate to lanceolate	Elliptical, sub-fusiform or sub-obovate
Utricle indurnenturn	Glabrous, but scaberulent on the beak and the margins of the distal third of the body	Puberulent, margins hispidulous	Flocculent	Glabrous to hispidulous, the margins scaberulent on the distal half of the body or beyond
Utricle venation	Faintly or prominently veined, up to 6–8 prominent veins abaxially and 4–6 veined adaxially	Faintly veined or with 4–7 prominent veins in the proximal third of the abaxial side	Veinless	Weakly 2–5 veined adaxially and 1–4 veined abaxially
Utricle base	Stipitate, rounded or flattened in cross section	Shortly stipitate	Truncate to stipitate	Stipitate and flattened in cross section
Utricle margins	Rounded	Rounded	Rounded	Flattened
Beak	Conical, bidentate	Shortly conical and obscurely bidentate	Longly conical and strongly bidentate	Conical, short and bidentate
Rachilla	Subulate	Ovate	Lanceolate	Linear

related species of southern South America (i.e., *C. austroamericana*, *C. nelmesiana* and *C. sorianoi*) reinforces treating the studied specimens as a new species. Morphologically similar species, such as the species here described, are prevalent within sect. *Junciformes* despite many of its lineages having deep times of divergence (dating back to Miocene; Benítez-Benítez et al. 2021). The relatively reduced diversification rate estimated for subgen. *Psyllophorae* suggests that its diversity stems from the progressive accumulation of morphological changes (disparification) and thus might have resulted in lower levels of morphological diversity than the expected by means of evolutionary radiations (Benítez-Benítez et al. 2021). This overall morphological resemblance has led to the misuse of names in quite a few cases for Patagonian taxa (Barros 1969, Wheeler and Muñoz-Schick 1990), a recurrent phenomenon in *Carex* that hinders its already problematic taxonomy (Jiménez-Mejías et al. 2014). Likewise, Wheeler (1986) highlighted the resemblance of *C. austroamericana* with *C. argentina* and *C. nelmesiana*, but the morphological differences between those three species were clearer than that existing between the new species and *C. austroamericana* (Table 1).

Wheeler (1986) described the phytogeography of *C. austroamericana* as growing primarily on Patagonian steppe, forming “*small, dense tufts in moist depressions of the steppe, which is often dominated by Festuca gracillima*”. For *C. nelmesiana* he said that it “*grows on Patagonian steppe and occur primarily on moderate to steep slopes, where they form dense tufts in dry, exposed sites*”. Currently, both species are known only from stepparian environments in southern Patagonia, ranging from Río Negro to Tierra del Fuego provinces

(Argentina), and Magallanes region (Chile) for *C. austroamericana*, and Chubut to Santa Cruz provinces (Argentina), and Aysén region (Chile) for *C. nelmesiana* (Fig. 4). Another tuft-forming acaulescent species, *C. argentina*, also grows in the Patagonian steppe, but extends its distribution further north through the Andes, reaching the north of Mendoza province (Argentina) and Metropolitana region of Santiago (Chile), and being reported as south as Santa Cruz province (Argentina) and Araucanía region (Chile). The species here described, however, is only known from the Andes of Metropolitana region of Santiago, where it grows in a lower altitudinal vegetation belt than *C. argentina* (2750–2880 vs 3200 m; Fig. 4), and at least 1300 km north of the northernmost population of any of the two other Patagonian species (Fig. 4).

Andean-Patagonian disjunctions are not uncommon within and between closely related species of *Carex* (e.g. South American sect. *Racemosae*, Wheeler 1990, Jiménez-Mejías et al. 2021b; *C. melanocystis* É.Desv., Villaverde et al. 2017, Jiménez-Mejías et al. 2021a; Muñoz-Schüler et al. 2023; *C. microglochin* Wahlenb., Wheeler and Guaglianone 2003) and sect. *Junciformes* is not an exception (e.g. *C. camptoglochin*, *C. phalaroides*, *C. vallis-pulchrae* var. *vallis-pulchrae*; Wheeler and Guaglianone 2003; Wheeler 1989; Benítez-Benítez et al. 2021). This apparent gap might be either due to the lack of suitable environments in the territory between the two groups of known populations, or a reflection of the undersampling in Andean steppe-like environments in south-central Southern Cone in general, and of *Carex* species in particular.

Taxonomic treatment

Carex recondita **Muñoz-Schüler, Martín-Bravo & Jim.Mejías, sp. nov.**
urn:lsid:ipni.org:names:77343736-1

Diagnosis. *Carex recondita* is similar to *C. austroamericana*, from which it is distinguished by its longer leaves up to 9 cm long (versus 5 cm long in *C. austroamericana*), narrower spikes up to 3.5 mm wide (versus 3.5–6 mm wide), and weakly veined ellipsoid, obovoid or suborbicular utricles, with a flattened stipitate base (versus strongly veined obovoid utricles, with a rounded or flattened stipitate base).

Type. Chile. Región Metropolitana de Santiago: Provincia de Santiago, Farellones, camino al centro de ski Valle Nevado, Tres Puntas, 2750 m.a.s.l., 33°21.39183'S, 70°15.45538'W, 16 January 2023, *P. Jiménez Mejías, J.I. Márquez Corro, S. Martín Bravo & P. Muñoz Schüler 12PJM-CL23* (holotype: CONC 193519; isotypes: EIF 17307, UPOS).

Description. Plants low-growing, densely caespitose 3–10.2 cm tall from the base of the shoots to the tip of the leaves, acaulescent or nearly so. Leaves numerous, up to eight per shoot, much longer than the flowering shoots and concealing them, 2–8.2 cm long, canaliculate but flattish distally, stiff to slightly flexuose. Flowering shoots elevated on erect stalks of 1.2–4.4 cm long formed by the basal leaf sheaths, with the portion between the insertion of the distal-most leaf and the proximal-most bract inconspicuous, up to 1.2 mm long. Inflorescence a single, terminal, androgynous, subglobose spike, 4.3–6.2 mm long and 2.8–3.5 mm wide, subtended by an involucral bract, with a glumaceous base and prolonged into a 5.8–9.1 mm long antrorsely scabrid or smooth setaceous portion. Staminate part concealed by the pistillate portion, 2-flowered. Pistillate part 4–5 flowered, sometimes with an extra infertile flower borne by the involucral bract; glumes ovate to widely elliptical, 3.1–4.1 mm long and 1.4–2.3 mm wide, glabrous, with wide hyaline margins contrasting with a narrow green middle strip, veinless, attenuated distally into an awn, the 2-proximalmost glumes with a 1.9–3.3 mm long awned portion that usually surpasses the whole inflorescence, distalmost glumes with a 0.6–0.9 mm long mucronate apex. Utricles 2.4–3 mm long and 1.2–1.8 mm wide, ellipsoid, suborbicular, ovoid or sub-obovoid, obscurely trigonous in cross section, green to pale green, with 2 prominent lateral veins dark greenish, contrasting with the rest of the body, veinless or 2–5 weakly veined adaxially and 1–4 veined abaxially, glabrous to sparsely hispidulous on its distal half, with the lateral veins hispidulous to ciliolate on its distal ⅔ portion, attenuated or constricted proximally into a sub-stipitate base 0.4–0.8 mm long, often flattened in cross section, constricted distally into a short, bidentate, and pale beak 0.3–0.6 mm long. Achenes 1.9–2.2 long and 1.2–1.6 mm wide, broadly elliptical to sub-obovoid, obscurely trigonous, often flattened, greenish, more or less constricted proximally into a sub-stipitate base and attenuated distally into a short beak. Rachilla often absent, when present 0.6–0.9 mm long, linear, margins smooth. Stigmas 3. Anthers 3.

Phenology. The phenology of this species is poorly understood. A fully flowering specimen with some ripe utricles was collected in mid-late December, while a specimen with entirely ripe utricles bearing some female flowers was collected in mid-January. According to these observations we infer that the flowering period for the new species is likely to range from mid-November to late December with mature individuals bearing ripe utricles from mid-late December onwards. This agrees with the plant community peak flowering period at 2935 m.a.s.l. (late-December to early-January) in an adjacent high Andean valley (Arroyo et al. 1981), thus our species should flower during the first half of the flowering season.

Etymology. The specific epithet *recondita* (female) refers to the Latin word *recondito* (male), meaning something hidden or occult, apropos the acaulescent inflorescence and low-growing habit of this species.

Distribution and habitat. *Carex recondita* occurs in the area of La Parva and Farellones-Valle Nevado ski circuits, in the Andes of the Metropolitana region of Santiago (see Fig. 4), and has been reported to grow between 2750–2880 m.a.s.l. The new species occurs in the central Chilean Andes, in an area characterized by a semi-arid Mediterranean-type influence climate (Arroyo et al. 1981) and it grows in the alpine cushion plant belt (Cavieres et al. 2000), on steep slopes around 650 m of elevation above a climatically depressed *Kageneckia angustifolia* D.Don treeline. Phytogeographically, this area and elevation in the high Andes falls in the Cuyano-Pikumche district of the Altoandean Province of the southern Andes (Biganzoli et al. 2022). Snow is received from May-June to October-November, depending on the year. *Carex recondita* was growing on a south-facing slope next to an important road leading from Farellones mountain town to Valle Nevado ski resort, forming dense tufts in a habitat dominated by the cushion-forming umbellifer *Azorella ruizii* G.M. Plunkett & A.N. Nicolas (Fig. 1). Other common species in the area include *Acaena pinnatifida* Ruiz & Pav., *Adesmia corymbosa* Clos, *Anarthrophyllum cumingii* (Hook. & Arn.) F. Phil., *Chaetanthera euphrasioides* (DC.) F. Meigen, *Haplopappus scrobiculatus* (Nees) DC.,

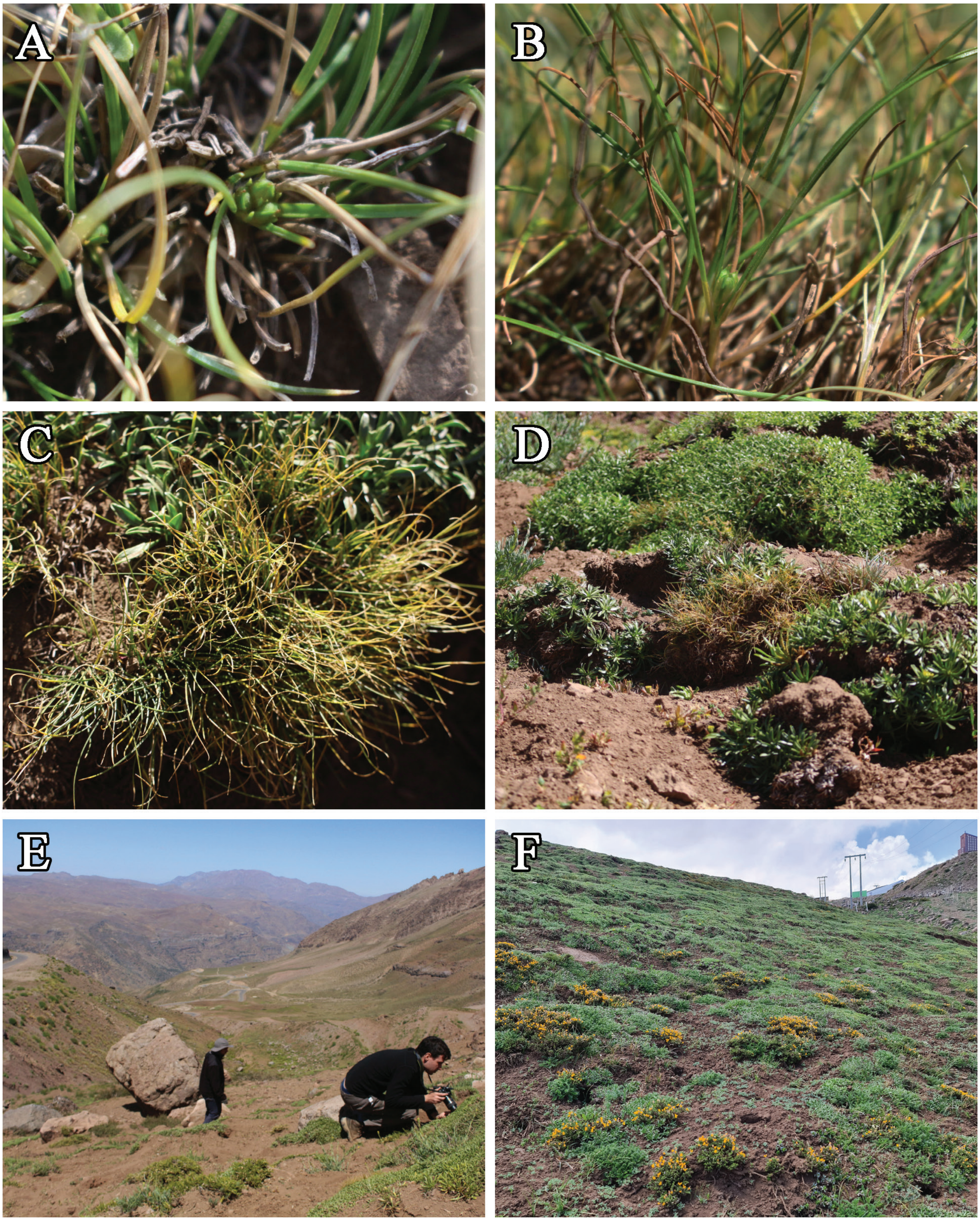

Figure 1. *Carex recondita* Muñoz-Schüler, Martín-Bravo & Jim.Mejías **A, B** aerial and frontal view of the plant and a spike **C, D** habit **E** two of the authors looking for more specimens of *C. recondita* on its habitat, the road can be seen at the upper-left portion of the picture **F** habitat of *C. recondita*, showing dominant *Azorella ruizii* (green cushions) and *Anarthrophyllum cumingii* (prostrate shrub with orange-yellow flowers). Photos by P M-S (**A–E**) and MTKA (**F**).

Hypochaeris clarionoides (J. Remy) Reiche, *Hordeum comosum* J. Presl, *Noccaea magellanica* (Comm. ex Poir.) Holub, *Perezia carthamoides* (D. Don) Hook. & Arn., *Poa holciformis* J. Presl, *Quinchamalium chilense* Molina, *Rytidosperma pictum* (Nees & Meyen) Nicora and *Senecio pentaphyllus* Phil. The exotic *Taraxacum officinale* F.H. Wigg., an invasive Palearctic species at high elevations in the central Chilean Andes (Cavieres et al. 2008), can also be locally common. This plant is currently known from only three points. Two are located on two contiguous slopes, with approximately 280 meters of distance between each other, while the third point is located approximately 3 km Northwest in a straight line from the closest known point (Fig. 4). Further fieldwork might expand its known presence within the area by searching in environmentally similar localities.

Vernacular name. We propose the common name for this species to be "Carex de las nieves".

Conservation status. *C. recondita* has an area of occupancy (AOO) smaller than 10 km^2, and only a single population (three subsets) of approximately < 200 individuals has been reported. Although the entire known individuals of this species are located in protected land (Yerba Loca Nature Sanctuary), the management of the area that is effectively being protected only includes the watershed of the La Yerba Loca stream, which is located 4 km west (in straight line) and approximately 1000 m below the area in which *C. recondita* grows. Notwithstanding this, the new species grows within one of the most crowded ski circuits of Chile (La Parva and Farellones-Valle Nevado circuit), on an area contiguous to one of its main roads, which has also been affected by exotic plant invasions (Cavieres et al. 2008). Road construction and maintenance works seem like a plausible threat to the future conservation of the population. The scarcity of observed individuals and the lack of previous reports or collections for this area suggests that *C. recondita* might be extremely rare and thus vulnerable to disturbances. The real extent of its natural distribution is unknown, and its area of occurrence might be greater than estimated by current data. However, and according to our data and observations, we propose that this species is better assessed as 'Critically Endangered' (CR; B2ab (ii-iv) + C2a (i)), according to the IUCN Red List criteria (IUCN 2017). Further searching of this species will contribute to expanding the knowledge about its presence and might help proposing a more robust assessment.

Notes. *C. recondita* is a tuft-forming species with stiff leaves and an acaulescent spike burrowed between the leaves, a type of growth form shared with many other Patagonian species of sect. *Junciformes* and recurrent in South American *Carex* species (see Jiménez-Mejías et al. 2021b). This type of growth might be an adaptation to harsh environments such as the high Andes or the Patagonian steppe (Körner 2021, pp. 37–38). This made *C. recondita* remain unnoticed until now, despite growing just beside a busy road in a popular skiing holiday area barely over one hour by road from Santiago, the most populated city of Chile. Some of the studied material included inflorescences with involucral bracts bearing -apparently- infertile female flowers.

Additional specimens examined (*paratypes*). CHILE. Región Metropolitana de Santiago: Provincia de Santiago, camino entre Farellones y Valle Nevado, laderas por debajo de la curva 14, piso altoandino, 2853 m a.s.l., 33°21.46188'S, 70°15.32352'W, 20 December 2022, *M.T.K. Arroyo, V. Robles, K. Robles, M. Acevedo & L. Retamal 29576* (CONC). Provincia de Santiago, Farellones, a 1 km de la Parva. 2674 m a.s.l., 33°20'S, 70°17'W, 1 March 2007, *M. Mihoc 777* (CONC 178536).

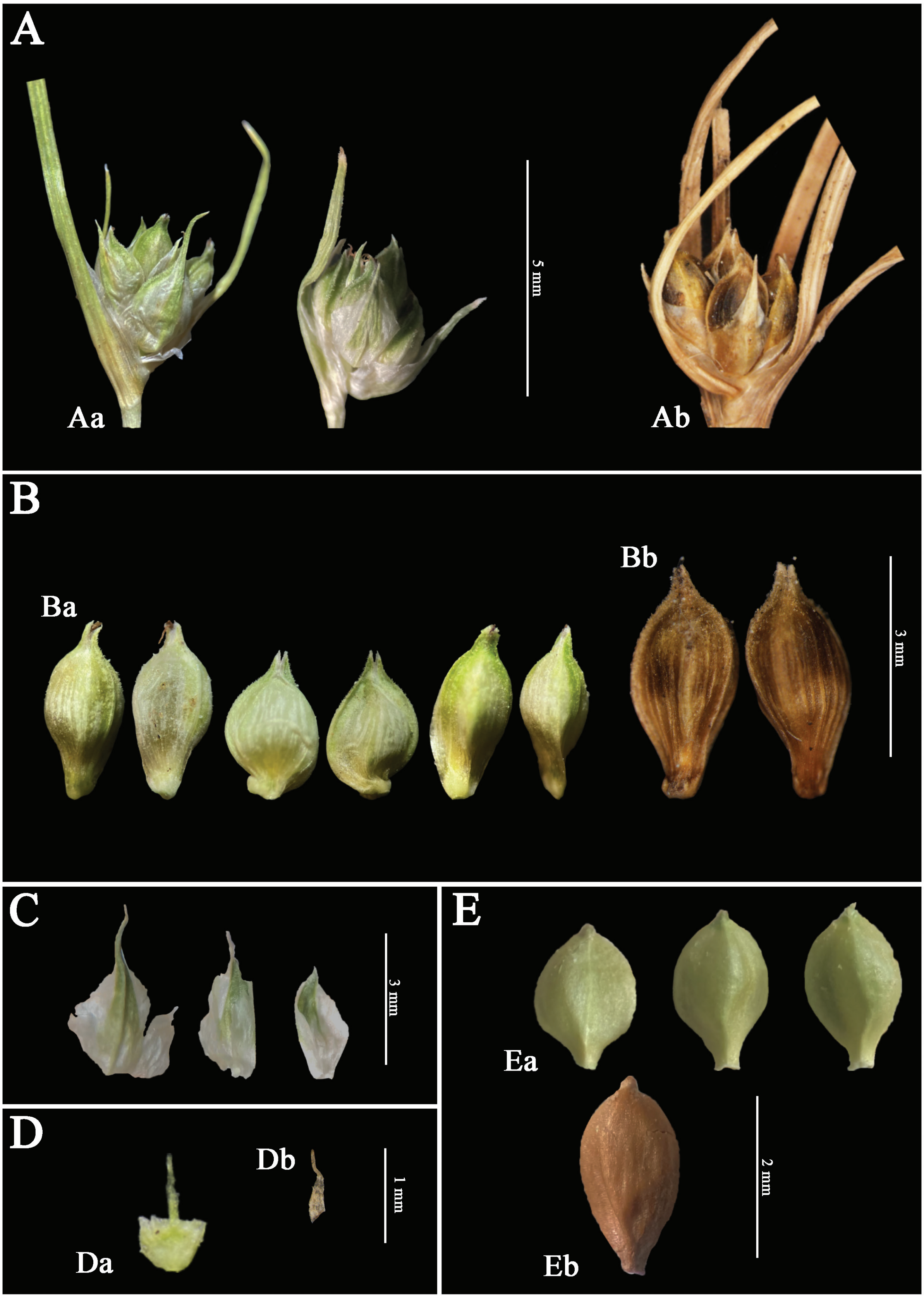

Figure 2. Detailed comparison between *C. recondita* and *C. austroamericana* **A** spikes of *C. recondita* (Aa) and *C. austroamericana* (Ab) **B** utricles of *C. recondita* (Ba) and *C. austroamericana* (Bb) **C** glumes of *C. recondita* **D** rachillas of *C. recondita* (Da) and *C. austroamericana* (Db). Note that the rachilla of *C. recondita* is attached to the utricle base **E** achenes of *C. recondita* (Ea) and *C. austroamericana* (Eb).

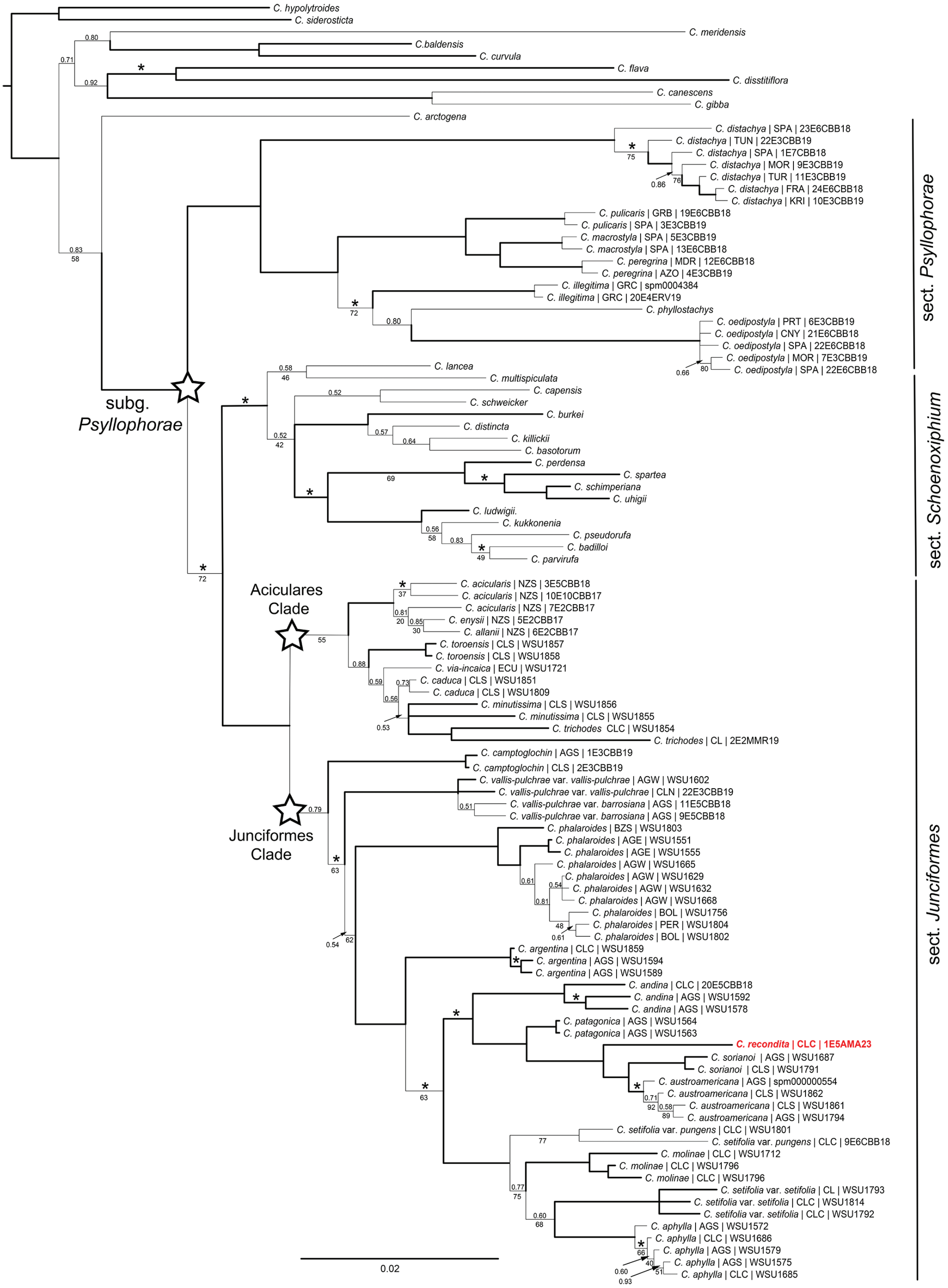

Figure 3. Phylogram resulting from BI analysis using MrBayes of the multiaccession matrix for *Carex* subg. *Psyllophorae*. Branch support is not indicated when PP=1.00/BS = 100. Posterior probability (PP) support is given above branches while ML BS support is given below branches. Asterisks above branches indicate BI 100 > PP ≥ 0.95. Bold thick branches indicate nodes supported by ML BS ≥ 80 and/or BI PP ≥ 0.95. ML support BS ≤ 80 is given below branches. The newly sequenced voucher of *C. recondita* is displayed in bold red letters. Tip labels include the geographical origin of the specimen using TDWG level 3 regions abbreviations (“botanical countries”; Brummitt 2001).

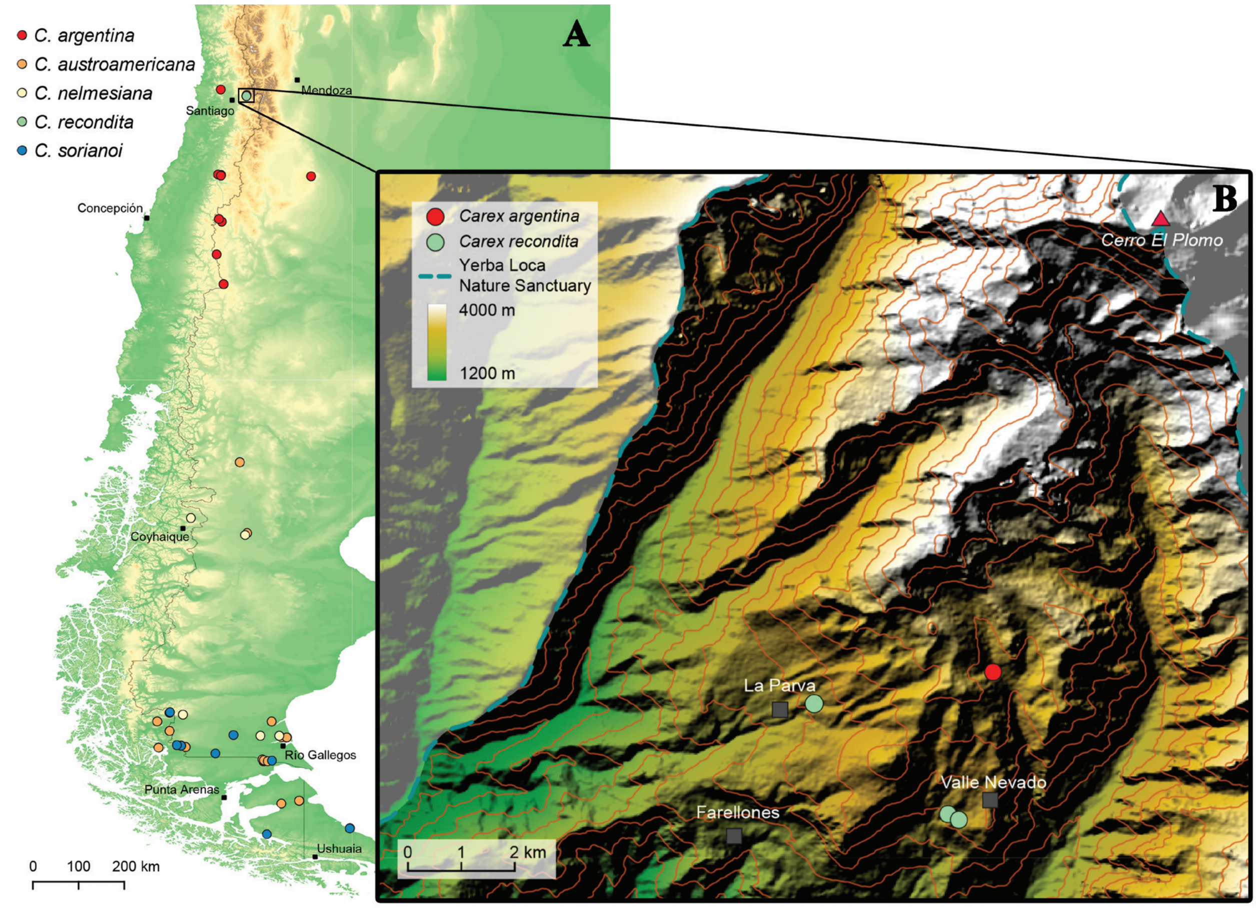

Figure 4. Occurrence map of *Carex* sect. *Junciformes* species cited in this work **A** occurrence map of five Patagonian species of *Carex* sect. *Junciformes*. Species locations are depicted in colored circles and some cities are represented as black squares **B** detailed map of the area of occurrence of *C. recondita* (light-green circles). Another species occurring in the area, *C. argentina*, is depicted by red circles. The highlighted region corresponds to the Yerba Loca Nature Sanctuary. Altitude was represented by a color palette and contour lines, representing elevation every 200 meters. For orientation purposes, some landmarks were depicted on the map.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Methodology: AM-A, PJ-M, PM-S. Writing – original draft: PM-S, PJ-M. Review and editing: SM-B, PJ-M, JIM-C, AM-A, MTKA, PM-S.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

A new combination for a neglected member of *Linaria* subsect. *Versicolores* (Plantaginaceae, Antirrhineae) endemic to the Algarve, Portugal

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Abstract

Linaria bimaculata **comb. et stat. nov.**, from the overlooked Central Algarve plant endemism centre, is here lectotypified and redescribed as a full species based on *Linaria viscosa* var. *bimaculata*, which was historically misidentified under allopatric *L. spartea* and *L. viscosa*. Traditional herbarium taxonomy and citizen science observations were combined to document the geographical range of the four species of *Linaria* subsect. *Versicolores* in the Algarve and amend an identification key for the Iberian clade of this subsection. Geographical patterns and morphological similarity suggest a sister relationship between *L. bimaculata* and *L. algarviana*, unveiling a new possible example of parallel speciation linked to a purple to yellow shift in corolla colour. Besides the yellow flowers, *L. bimaculata* differs from *L. algarviana* in the more elongate fertile stems and the invariably erect-patent corolla tube. It is assessed as Vulnerable (VU) according to the IUCN Categories and Criteria.

Key words: Flower colour, Iberian Peninsula, iNaturalist, lectotypification, Mediterranean flora, plant taxonomy, endemic to the Algarve, stone pine, toadflax

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Introduction

The Iberian clade of *Linaria* subsect. *Versicolores* (Benth.) Wettst. comprises eight currently accepted taxa, being keyed out from the other Iberian congeners by their distinctly bifid stigma (Fernández-Mazuecos et al. 2018a). Corolla colour divergence between parapatric or sympatric sister species and convergence in allopatric species are a hallmark of this clade (Fernández-Mazuecos et al. 2018b). As an example, and doing justice to this subsection's name (i.e., colour-changing), a colour shift of the corolla from purple to yellow has occurred independently twice in the Iberian Peninsula, namely in the common ancestor of *L. viscosa* (L.) Chaz. and *L. onubensis* Pau in southwestern Iberia, and in the common ancestor of *L. spartea* (L.) Chaz. and *L. incarnata* (Vent.) Spreng. in central Iberia (Fernández-Mazuecos et al. 2018b). Here, we resuscitate an overlooked taxon from coastal central Algarve, in southernmost Portugal, which has been confused with yellow-flowered *L. viscosa* and *L. spartea*. It probably represents an additional case of corolla colour convergence and a purple-yellow shift coupled with speciation, considering that we here infer *L. algarviana* Chav. as its hypothetical sister.

Linaria viscosa, the type of subsection *Versicolores*, is endemic to Southern and Eastern Spain, while *Linaria spartea* is widespread in Iberia and southwestern France (Fernández-Mazuecos et al. 2018a). The latter is renowned for accommodating significant morphological variation (Sutton 1988, Sáez 2009), which is reflected in the existence of 10 heterotypic synonyms (POWO 2024), including *Linaria praecox* Hoffmanns. & Link (Hoffmannsegg and Link 1811: 234). The type of *L. praecox* was collected in the "*champs sablonneux de l'Algarve*", with no mention of a precise locality, certainly during the voyage of Johan Centurius von Hoffmannsegg and Johann Heinrich Friedrich Link to the Algarve in February–March 1799. Most of the type material was probably included in Link's personal herbarium, which was destroyed during the bombing of the Berlin Herbarium in 1943 (Medina and Aedo 2022). The surviving original material at Berlin, consisting of a single flower (B-W11283-010), which was part of Hoffmannsegg's herbarium bequeathed to Willdenow, and the associated colour plate in the *Flore Portugaise* (Hoffmannsegg and Link 1811: t37), agree well with *L. spartea*. This taxon is still namely present in the sand fields west from the mouth of the Guadiana (Domingues de Almeida et al. 2024) together with plants tentatively identified as *L. viscosa* (Domingues de Almeida et al. 2024). This area was visited by the two German botanists during their sojourn in Vila Real de Santo António (Gomes Oliveira 2015). After the original description, the name *L. praecox* – transferred to *Antirrhinum* L. by Brotero (1828) – and its recombination *Linaria spartea* var. *praecox* (Hoffmanns. & Link) Willk. & Lange, were first applied to plants collected around Faro, in central Algarve (Willkomm and Lange 1861; Henriques 1889), but later the use of this name – including the synonym *Linaria juncea* var. *praecox* Hoffmanns. & Link ex Samp. (Sampaio 1913: 111) – changed to encompass other early-blooming populations of *L. spartea* in Portugal (e.g., Coutinho 1906; Sampaio 1946; Viano 1973, 1978).

Plants from a narrow coastal strip centred in Faro, between Albufeira and Olhão, were later described as *Linaria viscosa* var. *bimaculata* Cout. (1916:10) based on the presence of two conspicuous longitudinal brownish red stripes on the throat of the corolla, and later accepted under this name by Coutinho (1935, 1939) and Viano (1973, 1976, 1978). These plants may correspond to what Hoffmannsegg and Link (1811: 256) designated as "*Linaria bipunctata* var. *bipunctata*", collected in the "(…) *Algarve, aux lieux sablonneux entre Villanova et Lagôa*", in February–March 1799, described as having the "*Palais à 2 points pourpres-noirâtres*". Unfortunately, no material of *Linaria bipunctata* var. *bipunctata* sensu Hoffmannsegg & Link has survived at the Berlin Herbarium. More recently, Sutton (1988: 436), while advocating for further studies, reassigned plants from the vicinity of Faro to *L. praecox*, including *L. v.* var. *bimaculata*, describing them as somewhat intermediate between *L. spartea* and *L. viscosa*, and characterised by a well-developed basal rosette of sterile shoots, relatively small leaves, a sparsely glandular inflorescence and small flowers. Yet, the latest monographic works on *Linaria* subsect. *Versicolores* from the Iberian Peninsula (Sáez 2009; Fernández-Mazuecos et al. 2018a) did not recognise this taxon, including it implicitly within *L. spartea*. As a result of all the different views on its taxonomic status, plants ascribable to *Linaria viscosa* var. *bimaculata* were also identified as *L. spartea* (Costa et al. 1996; Pereira et al. 2007) or *L. viscosa* in floristic studies (Carapeto 2020), and correspond to most records of *L. spartea* in the Algarve uploaded on iNaturalist between 2015 and 2023, one of them (i.e., 1694064) being selected as the thumbnail image for *L. spartea*. However, these plants differ in multiple morphological characters from *L. spartea* and *L. viscosa*, or from any other *Linaria*, being most similar to *L. algarviana*, endemic to western Algarve, with which they share the typically decumbent fertile stems and broadly ovate, divergent and slightly reflexed upper petals. Accordingly, we here raise *L. v.* var. *bimaculata* to full species and provide an updated taxonomic account for this narrow endemic, including a risk of extinction assessment, together with an amended key to the Iberian clade of *Linaria* subsect. *Versicolores*.

Material and methods

We applied standard herbarium practices to study the variation of plants ascribable to *Linaria* subsect. *Versicolores* in the Algarve, namely material referable to *L. algarviana*, *L. spartea* and *L. viscosa*, including *L. viscosa* var. *bimaculata*, at ALGU, COI, LISE, LISI, LISU, PO (incl. PO-GS) and MA (acronyms following Thiers, continuously updated). Additionally, we examined all scans of *Linaria* subsect. *Versicolores* from southwestern Iberia and northwestern Africa published on GBIF (2024), including those facilitated at the online catalogue of P (https://science.mnhn.fr/institution/mnhn/collection/p/item/search). This enabled us to locate additional specimens of *L. viscosa* var. *bimaculata* at BR, P, W and WAG. No records of *L. viscosa* var. *bimaculata* were found outside the Algarve. Herbarium specimens of *L. viscosa* var. *bimaculata* were photographed with a scale and, subsequently, the acquired images were utilised to score multiple quantitative characters to the nearest 0.1 mm with the "Measure" tool from ImageJ v.1.52.d. Specimens of *L. viscosa* var. *bimaculata* were described following recent taxonomic references on Iberian *Linaria* (Sáez 2009; Fernández-Mazuecos 2018a; Blanca et al. 2023), and the chromosome number for this taxon was retrieved from Viano (1973). Seeds were examined under an Emspira 3 digital microscope (Leica Mycrosystems) and photographed with Application Suite X (LAS X). The key to the Iberian clade of *L.* subsect. *Versicolores* by Fernández-Mazuecos et al. (2018a) was amended, from couplet number 9, to accommodate the newly reappraised taxon.

We combined herbarium taxonomy with a review of iNaturalist (2024) records of *Linaria* in the Algarve, uploaded until January 31, 2024. A total of 78 occurrences of *L. viscosa* var. *bimaculata* were identified (Appendix 1). No observations of similar plants were found in other botanical provinces of Portugal, Spain or Morocco.

Herbarium and iNaturalist records, together with occurrence data available through Flora-On (Pereira et al. 2016), were used to plot the distribution of the different taxa of *Linaria* subsect. *Versicolores* (viz. *L. algarviana*, *L. spartea*, *L. viscosa* and *L. viscosa* var. *bimaculata*) in the Algarve, on ArcGis 10.4. A risk of extinction assessment was prepared following Carapeto et al. (2020) and using the IUCN Red List guidelines (IUCN Standards and Petitions Committee 2022). Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCAT (Bachman et al. 2011).

Taxonomic treatment

Identification key (amendment to Fernández-Mazuecos et al. 2018a)

9a Corolla tube erect-patent; throat with 2 longitudinal brownish red to blackish brown stripes .... ***L. bimaculata***

9b Corolla tube erect; throat with no markings or with multiple darker veins ... **10**

10a Inflorescence predominantly lax, glabrous, sparsely glandular-pubescent or densely glandular-pubescent, fruit pedicels porrect................ ***L. spartea***

10b Inflorescence predominantly dense, corymbiform at anthesis, generally densely glandular-pubescent, fruit pedicels appressed **10**

11a Pedicels ± adnate in his basal part to the inflorescence axis; calyx lobes 0.4–0.9 mm wide ....***L. salzmannii***

11b Pedicels not adnate to the inflorescence axis; calyx lobes 0.9–1.8 mm wide.. ***L. viscosa***

Linaria bimaculata **(Cout.) Farminhão & Carapeto, comb. et stat. nov.**
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Figs 1, 2

Basionym. *Linaria viscosa* var. *bimaculata* Cout., Notas Fl. Portugal III: 10 (1916).

Type. Portugal. Algarve: Faro, February 1915, *R. Palhinha & F. Mendes s.n.* (***lectotype*** LISU [LISU33258!], designated here, Fig. 1; isolectotypes LISE [LISE83092!], PO [PO20408!]).

Description. Annual herb; somewhat glaucous, glabrous, except for glandular-pubescent inflorescence, hairs 0.4–0.5 mm. Fertile stems 1–3(–8), (4.6–)18–33.3(–41.8) cm long, decumbent to ascending or erect, simple or 2–4(–10)-branched; sterile stems (1–)4–10(–29), (1.6–)3.9–8.5(13.6) cm long, prostrate to decumbent, simple, sometimes forming a dense rosette. Leaves of fertile stems (3.3–)6–13.9(–30.6) × (0.4–)0.7–1.3(–2.5) mm, linear, flat to revolute, obtuse to ± acute, alternate, sometimes the intermediate in whorls of 3; leaves of sterile stems (1.8–)3.4–8.6(–17.8) × (0.3–)1–2.1(–3.1) mm, linear to ovate, flat, in whorls of 3(–4). Inflorescence racemose, rachis up to (2–)2.6–4.3(–6.2) cm long in fruit, green or red, with (1–)4–7(–14) flowers, lax in flower and fruit. Bracts (2–)2.3–2.8(–3.4) × 0.2–0.4 mm, linear, acute, glabrous or glandular. Pedicels (3.7–)5.2–7.8(–9.6) mm long in flower, (3.4–)6–9.4(–12.9) mm long in fruit, erect, not adnate to the inflorescence axis, red. Calyx lobes (2.2–)2.3–2.9(–3) × (0.4–)0.7–0.9(–1.1) mm in flower and (2.4–)2.9–3.5(–4.1) × (0.6–)0.8–1.1 mm in fruit, subequal, glandular-pubescent, linear-lanceolate, acute, green sometimes red-tinged with whitish scarious margin. Corolla personate, spurred, (13.1–)14.8–17.6(–19.8) mm long, deep yellow with 2 longitudinal brownish red to blackish brown stripes on the throat, and an orangey palate, sometimes with brownish red spots or reticulate markings, without conspicuous dark veins; tube (1.9–)2.4–3.2(–3.7) mm broad in dorsiventral section, erect-patent; upper petals broadly ovate, divergent, slightly reflexed; spur (5.7–)7.9–9.6(–10.9) × 1–1.6(–1.9) mm (the width measured at the base), straight or slightly curved, equalling to slightly shorter than the rest of the corolla. Capsule (2.1–)2.4–3.1 × (1.6–)2–2.8 mm, globose, glabrous, loculi equal; style 2.1–2.5(–3.2) mm long,

Figure 1. Lectotype of *Linaria bimaculata* (Cout.) Farminhão & Carapeto (*Palhinha & Mendes s.n.*, LISU33258).

persistent, bifid at apex. Seeds (0.5–)0.6–0.7 × 0.4–0.5(–0.6) mm, wingless, pyriform-triquetrous, transversely ridged, alveolate, black. 2*n* = 12.

Habitat and distribution. *Linaria bimaculata* is endemic to coastal central Algarve, from Galé (Albufeira) in the west to Pinheiro (Tavira) to the east, up to 50 m a.s.l (Fig. 3). Its distribution is centred on the Plio-Pleistocene medium to coarse grain siliceous sands and gravels of the Ludo Formation (Moura and Boski 1994) in central Algarve. It occurs mostly on clearings and at fringe of *Pinus pinea* L. and *P. pinaster* Aiton woods and scrubland with *Ulex argenteus* subsp. *subsericeus* (Cout.) Rothm., *Stauracanthus* spp. and *Cistus* spp. (Costa et al. 1996; Pereira et al. 2007; Carapeto 2020). *Linaria bimaculata* integrates psammophilic communities protected from the direct influence of sea spray, where characteristic species include mostly ephemeral annuals, namely *Tuberaria guttata* (L.) Fourr., *Tolpis barbata* (L.) Gaertn., *Briza maxima* L., *Silene scabriflora* Brot., *Plantago bellardii* All., *Rumex bucephalophorus* L., *Marcus-kochia triloba* (L.) Al-Shehbaz and *Ornithopus pinnatus* (Mill.) Druce, described as the association *Tolpido barbatae-Tuberarietum bupleurifoliae*, endemic to the Algarve (Costa et al. 1996).

Phenology. Flowering from December to June (September), peaking between January and April. Fruits develop mostly from March to June.

Conservation assessment. *Linaria bimaculata* presents a restricted distribution range in coastal central Algarve. The EOO comprises 271.8 km^2 and the AOO is 152 km^2. The population faces several threats, including urban and touristic development, agricultural intensification, and the expansion of alien plants and nitrophilous communities as result of human disturbance. These ongoing threats are responsible for continued declines in the area and quality of the habitat. A continued decline in population size and AOO can also be inferred from the habitat loss and from disappearance from historical collection sites (e.g. near Faro). Considering the urban/touristic expansion within its distribution range as the main cause of habitat loss and fragmentation, only eight locations are identified, therefore this plant is assessed as Vulnerable, fulfilling the criteria B1ab(ii,iii,v)+2ab(ii,iii,v).

Notes. Coutinho (1916) does not cite any type material in the protologue of *Linaria viscosa* var. *bimaculata*, but only one gathering, *R. Palhinha & F. Mendes s.n.* from Faro, can be regarded as original material, with duplicates at LISE, LISU and PO. The duplicate at LISU is labelled with a Latin diagnosis in Coutinho's handwriting matching the protologue in Portuguese, therefore being here selected as the lectotype. Besides the type collection, the only other specimen determined as *Linaria viscosa* var. *bimaculata* by Coutinho, *R. Palhinha & F. Mendes s.n.* (LISU) from Ilha das Lebres (Olhão), was only collected after the original publication of this taxon. The reticulate pattern of the palate (Fig. 2E) described in the type material (Fig. 1) is absent from most individuals observed in the field, which present an immaculate palate, being absent altogether in some populations. The apparent absence of spatial structure of this trait (i.e.reticulate vs immaculate palate) suggests it is best interpreted as polymorphism.

Linaria algarviana, hypothetically the closest relative of *L. bimaculata* based on flower and habit similarity, presents multiple, although rare, colour morphs (Fig. 4), which are here illustrated for the first time. Darker flowers (Fig. 4A, B) occur on the western part of its range (Aljezur, Vila do Bispo). Flowers with an erect-patent corolla tube, similar to those of *L. bimaculata*, occur sporadically

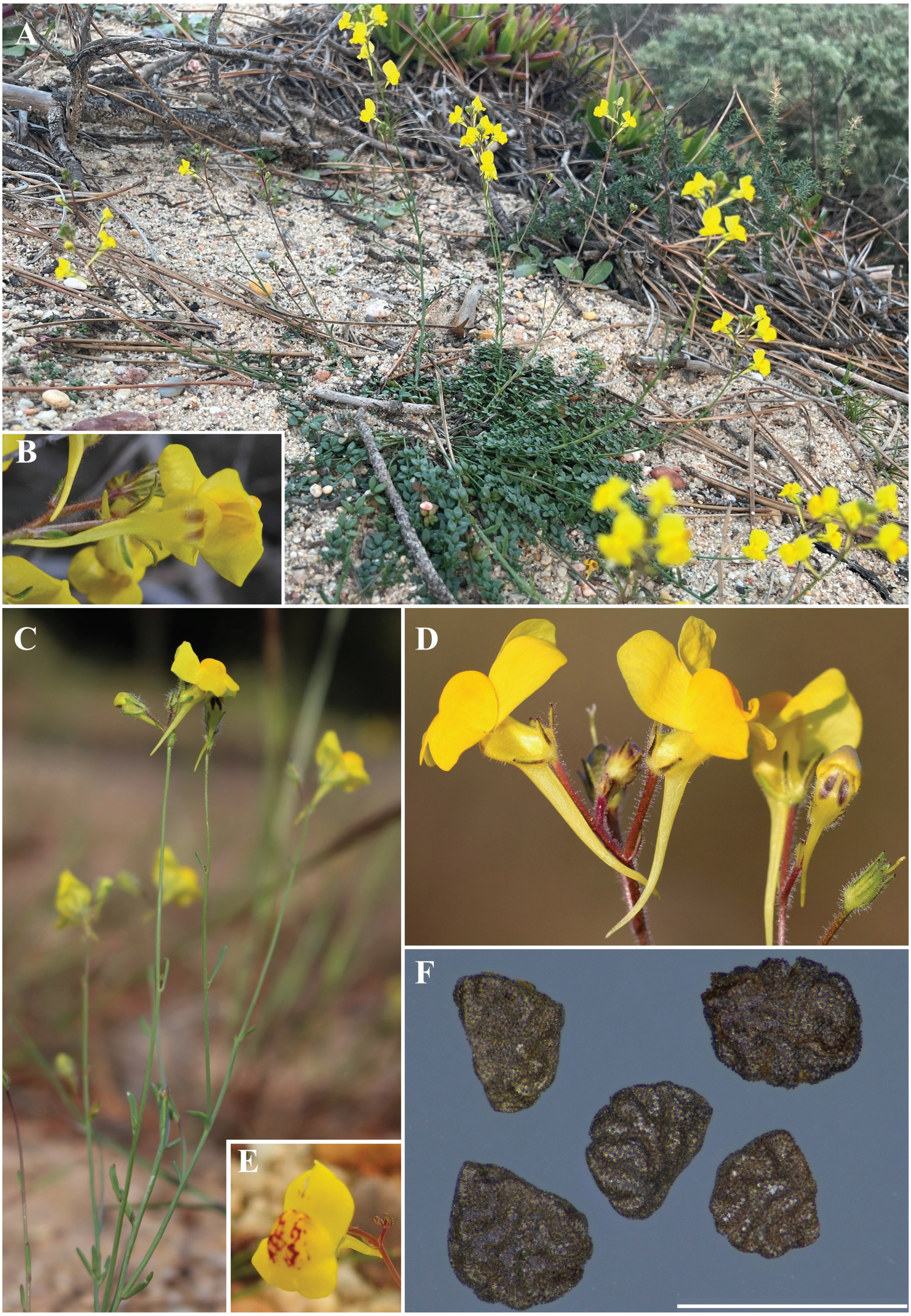

Figure 2. Overview of *Linaria bimaculata* (Cout.) Farminhão & Carapeto **A** habit (ascending form) and habitat **B** underside of flower with visible stripes **C** habit (erect form) D flowers with erect-patent corolla tube, immaculate palate and stripes visible on the underside of flower bud **E** flower with reticulate palate **F** seeds (*A. Moller s.n.*, COI), scale bar 1 mm. Photos by M. Hansch (**A**), D. Frade (**B, E**), V. Dvořák (**C**), J. Neiva (**D**) and A. Coelho (**F**).

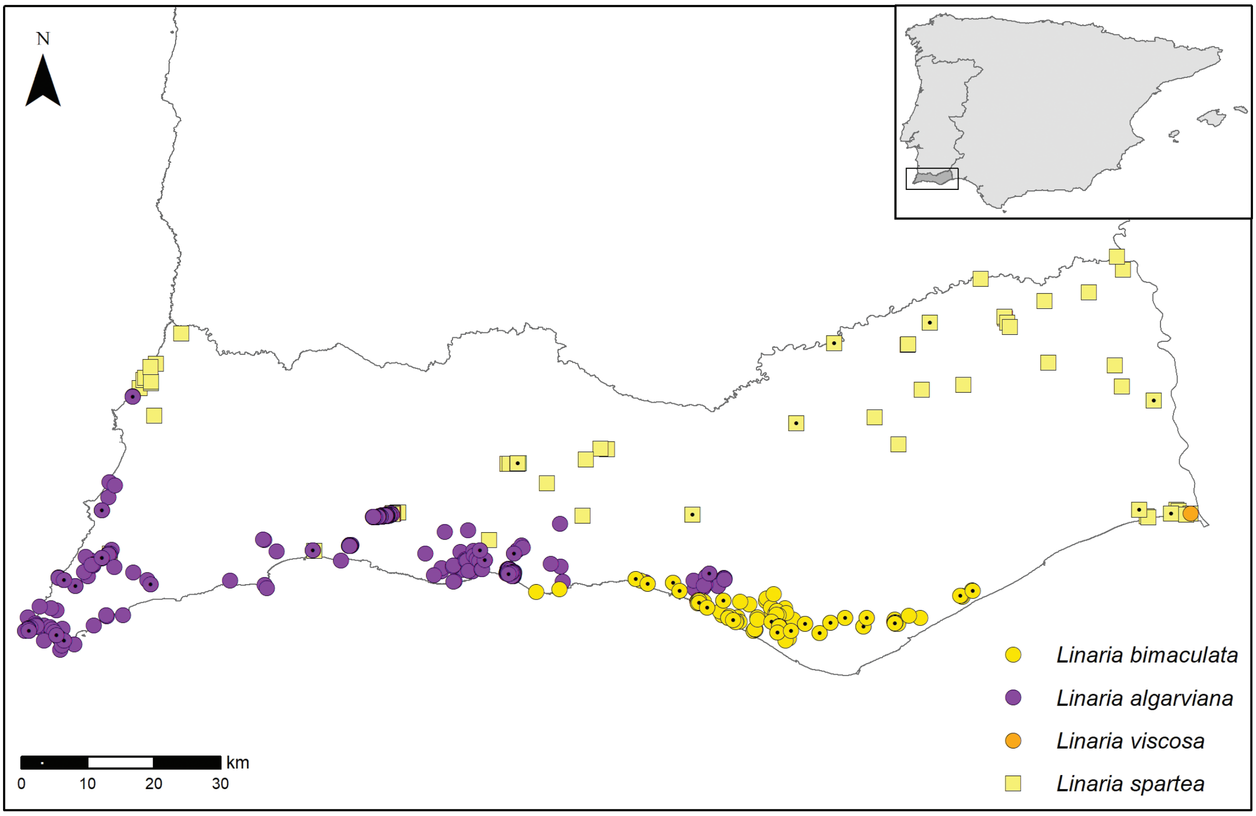

Figure 3. Distribution of *Linaria algarviana* Chav., *Linaria bimaculata* (Cout.) Farminhão & Carapeto, *Linaria spartea* (L.) Chaz. and *Linaria viscosa* (L.) Chaz. in the Algarve, in southwesternmost Iberia. Plain symbols indicate observation records and dotted symbols indicate herbarium specimens.

towards the eastern part of its range (Loulé). Also, there are yellow-flowered individuals of *L. algarviana* (Fig. 4G), that can be distinguished from *L. bimaculata* by the erect corolla tube and the paler throat stripes. This colour polymorphism, involving purple, yellow and bicolour morphs is similar to the one reported in *Linaria salzmannii* Boiss., another Iberian species of *Linaria* subsect. *Versicolores* (Fernández-Mazuecos et al. 2018a).

Differences between *L. bimaculata* and other *Linaria* subsect. *Versicolores* present in the Algarve are summarised in Table 1. *Linaria bimaculata* differs from *L. algarviana* in the more elongate fertile stems and the yellow flowers, with an invariably erect-patent corolla tube.

Additional specimens examined. PORTUGAL. Algarve: Albufeira, Pinhal do Concelho, próximo da praia da Falésia, terreno arenoso em pinhal, 25 Feb 1968, *A. Fernandes, J. Paiva & J. Matos 10115* (COI); Albufeira, estrada da Rocha Baixinha, Olhos de Água, 23 Feb 2019, *M.J. Correia s.n.* (ALGU); Loulé, Vilamoura, pinhal em substrato arenoso, 19 Mar 1995, *M.D. Espírito Santo & J.C. Costa s.n.* (LISI); Loulé, Vilamoura, Borjaca [aldeamento de], areias do Pliocénico, subbosque de pinhal manso, com *Oxalis pes-caprae*, *Malcolmia gracilima*, 9 Feb 1982, *J. Gomes Pedro, A.M. Medeiros & J.P. Simões 22792* (ALGU); Loulé, east of Quarteira, 7 Apr 1992, *F. Billiet 127* (BR); Loulé, praia do Porto Novo, 1 Mar 2008, *M.D. Espírito Santo & R. Caraça s.n.* (LISI); Loulé, foz do Almargem, 18 Feb 2023, *A. Carapeto s.n.* (COI); Loulé, Trafal, 18 Feb 2023, *A. Carapeto s.n.* (COI); Loulé; entre Almancil e Vale de Lobo, pinhal, 19 Mar 1995, *M.D. Espírito Santo & J.C. Costa s.n.* (LISI); Loulé, near Formosa Park Hotel, exist to the beach,

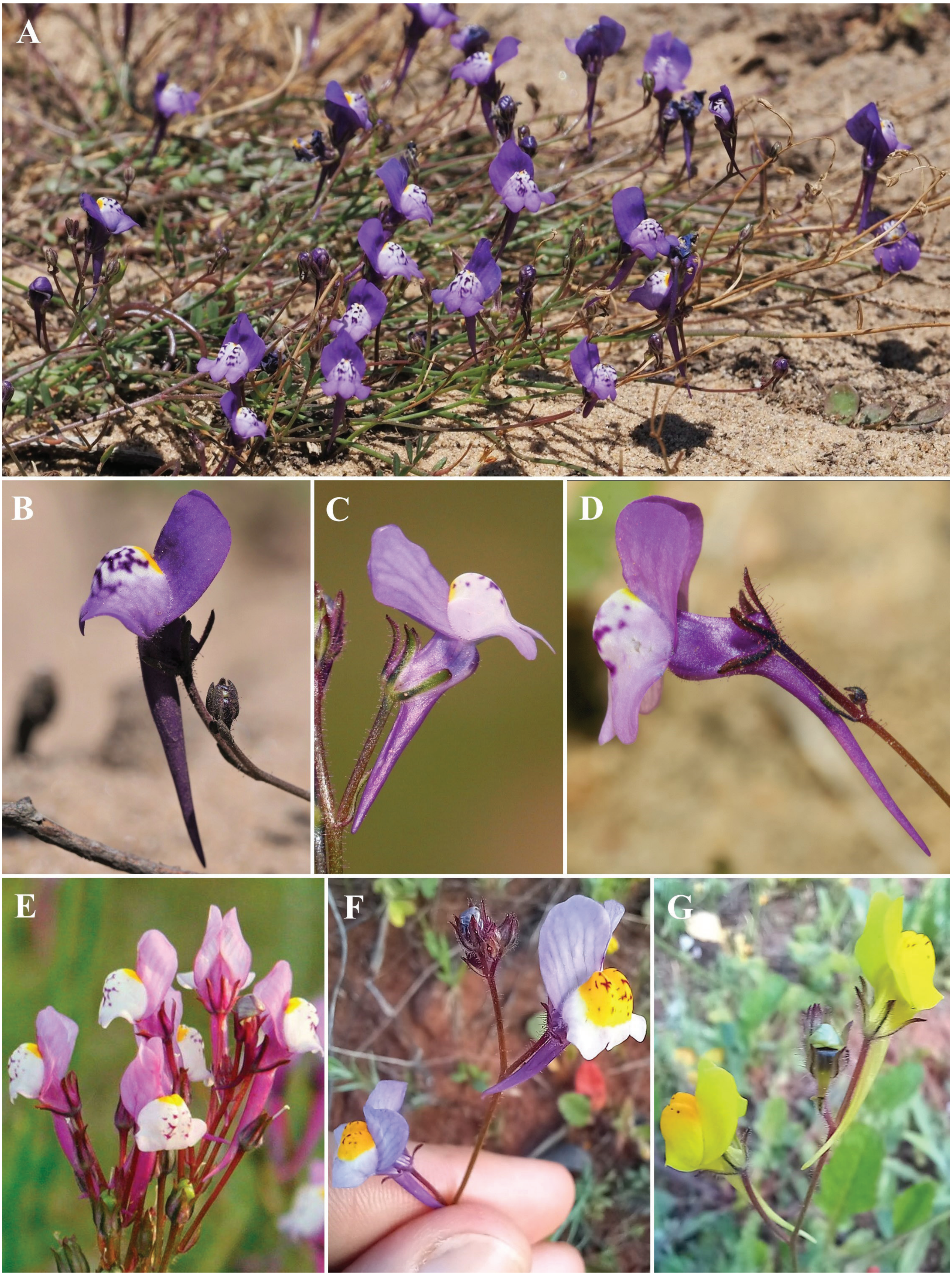

Figure 4. Overview of *Linaria algarviana* **A** habit **B** dark purple morph (Aljezur) typical of the westernmost populations **C** light purple morph (Loulé) **D** flower with erect-patent corolla tube (Loulé) **E** pink morph **F** bicolorous morph (Portimão) **G** yellow morph (Portimão). Photos by V. Achterberg (**A, B**), J. Neiva (**C**), J.T. Tavares (**D**), A.J. Pereira (**E**) and S. Lobo Dias (**F, G**).

Table 1. Synopsis of key traits in *Linaria* subsect. *Versicolores* present in the Algarve.

	L. bimaculata	***L. algarviana***	***L. viscosa***	***L. spartea***
Fertile stem length (cm)	5–42	14–25	5–80	15–55
Fertile stem position	decumbent to ascending or erect	decumbent to ascending or erect	erect or sometimes ascending	erect or sometimes ascending, rarely decumbent
Inflorescence	lax, densely glandular-pubescent	lax, densely glandular-pubescent	dense, densely glandular-pubescent	lax, sparsely to densely glandular-pubescent
Corolla tube position	erect-patent	erect, rarely erect-patent	erect	erect
Corolla colour (typical)	deep yellow with 2 longitudinal brownish red stripes on the throat, and an orangey palate, sometimes with brownish red spots or reticulate markings	violet-purple, the palate whitish with yellow spot and usually reticulated with violet	deep yellow	deep yellow
Upper petals	broadly ovate, divergent and slightly reflexed	broadly ovate, divergent and slightly reflexed	ovate, connivent and markedly reflexed	ovate, connivent and markedly reflexed

pine grove on white and brown-ochre sand dunes with *P. pinea* and *P. pinaster*, 28 Mar 2004, *L.J.G. van der Maesen 7873* (WAG); Loulé, Ancão, solo arenoso sob pinhal, 5 Feb 2000, *J. Rosa Pinto 436/A* (ALGU); Loulé, Ancão, entre Faro e Ferreiras, base de morro areno-calcáreo com pinhal degradado, 10 Mar 1987, *A. Moura 3079* (MA); Loulé, Quinta do Lago, pinhal, 28 Abr 1989, *J.C. Costa s.n.* (LISI); Faro, Ludo, 22 Feb 1986, *J. Rosa Pinto 436* (ALGU); *ibid. loc.*, 22 Feb 2000, *J. Rosa Pinto s.n.* (ALGU); Faro, S. Pedro, Monte Negro, pinhal de pinheiro-manso em solo arenoso, 3 Feb 1988, *J.C. Costa s.n.* (LISI); Faro, cerca de Gambelas, 11 Apr 2017, *P. Escobar García s.n.* (W); Faro, Marchil, a caminho de Armação de Arábia (salinas), pousio, areias, 2 May 1945, *A.R. Pinto da Silva, C. Fontes, M. Myre & B. Rainha 904* (LISE); Faro, Pinhal de Arábia, solo arenoso-argiloso, 13 Mar 1953, *C. Romariz & E.J. Mendes s.n.* (COI, LISE, LISI, LISU); Faro, entre a cidade e a praia, 13 Jun 1961, *J. Malato-Beliz & J.A. Guerra 5099* (MA); Faro, 3 Feb 1846, *H.M. Willkomm 1377* (COI-WILLK, P [P04057111 (specimen on the right), P04057154]); Faro, Champs sablonneux à Faro, 11 Mar 1853, *E. Bourgeau 1975* (COI-WILLK, P [P03440695, P03440739, P03440744, P04057189]); *sin. loc.*, *E. Bourgeau s.n.* (BR); Faro, in siccis/sabulosis collinis Algarbiae prope Faro, May 1847, *F.M. Welwitsch 257* (COI, LISU, P [P03440692 (3 lowermost specimens), P03440734, P03440742, P03440743, P03440745]); Faro, arredores de Faro, Apr 1889, *A. Moller 707* (COI, P [P03950057, P04057181]); Faro, *s.d.*, *G. Sampaio s.n.* (P-GS); Faro, estrada da Senhora da Saúde, Mar 1883, *J.d'A. Guimarães s.n.* (COI); Faro, Santo António do Alto, Mar 1883, *J.d'A. Guimarães s.n.* (COI); Faro, Areal Gordo, Mar 1891, *J. Brandeiro s.n.* (COI); Olhão, Joinal, areias, Jan 1888, *J. Brandeiro s.n.* (COI); Olhão, Ilha das Lebres, Apr 1917, *R. Palhinha & F. Mendes s.n.* (LISU); Olhão, in pinetis siccis, solo arenoso, 3 Feb 1939, *W. Rothmaler 14383* (LISE); Olhão, Belamandil, pinhal, 17 Feb 2019, *M.J. Correia s.n.* (ALGU); Olhão, Quinta de Marim, no solo greso-calcário do pinhal, 23 Feb 1986, *A. Moura 2864* (COI); *ibid. loc.*, 24 May 1986, *A. Moura 3021* (COI, MA); *ibid. loc.*, pinhal em areias, 3 Feb 1988, *J.C. Costa s.n.* (LISI); *ibid. loc.*, 12 Feb 1993, *J.C. Costa s.n.* (LISI); Olhão, cercanias del centro de educación ambiental de Marim, claros de pinar sobre arenas, 11 Apr 2017, *P. Escobar García 1160/2017* (NY [not seen], W); entre Olhão e Tavira, Quintal de P. Pimentel, junto à estrada, 21

Apr 1956, *J. Malato-Beliz 2849* (MA); Olhão [Tavira], Fuzeta, pr. Livramento, 16 Apr 1963, *B. Rainha 6005* (LISE); Tavira, Livramento, 3 Apr 2024, *A. Carapeto s.n.* (COI); Tavira, Pinheiro, 3 Apr 2024, *A. Carapeto s.n.* (COI).

Discussion

Although there is overlap among the differential character states (i.e. stem length and position, corolla tube position) of *Linaria bimaculata* and other species of *Linaria* subsect. *Versicolores*, the combination of a conspicuously striped yellow corolla and a relatively narrow erect-patent tube, not found anywhere else in the Iberian clade of *L.* subsect. *Versicolores*, allows for unambiguous identification of *L. bimaculata* both in live and herbarium specimens. This phenotypic singularity, stable in all investigated populations and not found as part of the intraspecific variability of any closely-related taxa, in association with a well-defined geographic range and habitat requirements, support the recognition of *L. bimaculata* as a *bona fide* taxon, and not as a mere morph. The full species status should be molecularly tested to ascertain its position within the least inclusive clade comprehending *L. algarviana* and *L. spartea* (Fernández-Mazuecos et al. 2018a, b). Future DNA sampling should also target plants of *L. bimaculata* with immaculate (Fig. 2D) and reticulate (Fig. 2E) palates, along with key variants of *L. algarviana*, notably plants with erect-patent corolla tubes (Fig. 4D) similar in shape to *L. bimaculata*, to screen for hybridisation events involving *L. algarviana* and explore additional untapped diversity.

With the recognition of *Linaria bimaculata*, the Iberian clade of *L.* sect. *Versicolores* now includes nine species (viz. *L. algarviana*, *L. becerrae* Blanca, Cueto & J.Fuentes, *L. bimaculata*, *L. clementei* Haens. ex Boiss., *L. incarnata*, *L. onubensis*, *L. salzmannii*, *L. spartea* and *L. viscosa*). The hypothetical sister relationship between *L. bimaculata* and *L. algarviana* is supported by the observation that closely related species in the Iberian clade of *Linaria* subsect. *Versicolores* tend to have close geographical ranges and strikingly divergent floral characters, such as corolla colour (Fernández-Mazuecos et al. 2013, 2018b). Distribution of the four taxa in the Algarve (Fig. 3) conforms to the patterns of corolla colour distribution already described in other areas of the Iberian Peninsula and northwestern Africa for *L.* subsect. *Versicolores* (Fernández-Mazuecos et al. 2013, Fernández-Mazuecos et al. 2018b), whereby the hypothetical sisters *L. algarviana*/*L. bimaculata* present a purple-yellow divergence in parapatry and the yellow flowers of *L. bimaculata* are convergent to allopatric *L. viscosa* and *L. spartea*. *Linaria algarviana* sporadically co-occurs with *L. spartea*, but it is never syntopic with *L. bimaculata*, even in areas of close population proximity (e.g. Quarteira). This geographically structured variation is unlike the distribution pattern of purple and yellow morphs of *Linaria salzmannii*, from southeastern Iberia, which occur mixed in the same populations, and therefore do not correspond to *bona fide* taxa (Fernández-Mazuecos et al. 2018a). However, an integrative approach, combining molecular phylogenetics with statistical morphometrics, following previous studies on *Linaria* subsect. *Versicolores* (Vigalondo et al. 2015; Fernández-Mazuecos et al. 2018a, b), will be instrumental to confirm the hypothesised close affinity between parapatric *L. bimaculata* and *L. algarviana* inferred from morphology and biogeography, and thus confirm another instance of parallel speciation linked to colour shifts in *Linaria*. Pollinator shifts are probably coupled with the evolution of these purple-yellow species pairs, but observation studies are long overdue to investigate this niche dimension.

The geographically structured variation of corolla colour in *L. algarviana*/*L. bimaculata* is reminiscent of the pattern found in *Linaria amethystea* Hoffmanns. & Link [*Linaria* sect. *Diffusae* (Benth) Wettst] in Western Portugal, where yellow-flowered *L. amethystea* subsp. *multipunctata* (Brot.) Chatter & D.A. Webb presents a marginal distribution to the more widespread *L. amethystea* subsp. *amethystea* (Blanca et al. 2023). Arguably, the small differences between *L. bimaculata* and *L. algarviana*, the most prominent being corolla colour, could also be accommodated at subspecies level within *L. algarviana*. However, we prefer not to adopt such treatment for three reasons: 1) the exact phylogenetic position of *L. bimaculata* relative to *L. algarviana* is unknown, 2) no subspecies are currently accepted within *L.* sect. *Versicolores* (Fernández-Mazuecos et al. 2018a), 3) the empirical and philosophical merits of recognising subspecies are questionable (Burbrink et al. 2022).

Linaria bimaculata is one of the three angiosperms endemic to the red sandstone derived soils of Central Algarve, which represent an overlooked centre of plant endemism, obscured by recent taxonomic deflation. The other two endemics, *Tuberaria major* (Willk.) P.Silva & Rozeira (Cistaceae) and *Scilla odorata* Link (Asparagaceae) were reduced to synonyms in the respective generic treatments of *Flora iberica* (Gallego 2005; Almeida da Silva and Crespi 2013), but they are likely best treated as full species in need of renewed conservation attention (Carapeto et al. 2020). The distribution of *L. bimaculata* largely overlaps with that of *Tettigettalna mariae* (Quartau & Boulard, 1995) in the Algarve, a narrow endemic cicada (Nunes et al. 2014). Both species are mostly restricted to stone pine (*Pinus pinea*) coastal woodlands on sands, which have been largely degraded by urban and tourism encroachment in the last decades. This unfavourable conservation scenario is an extra argument not to postpone the recognition of *L. bimaculata* as a distinct taxon, even if future research would support its treatment as a subspecies of another closely-related species. *Linaria bimaculata*, as a Vulnerable narrow endemic, should be added to the Portuguese register of classified natural values (*Cadastro Nacional dos Valores Nacionais Classificados*) to ensure its long-term conservation.

Finally, this study also illustrates the potential of citizen science platforms such as iNaturalist to accelerate the pace of taxonomic work in groups in which diagnostic traits, such as colour (Fritz and Ihlow 2022), have been neglected or considered as unreliable in the past, due to poor preservation in natural history collections.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: AC, JF. Data curation: AC, JF. Funding acquisition: JF. Investigation: JF. Methodology: JF. Software: AC. Validation: AC. Writing – original draft: JF. Writing – review and editing: AC.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

List of iNaturalist records of *Linaria bimaculata* (Cout.) Farminhão & Carapeto uploaded until January 31, 2024

https://www.inaturalist.org/observations/1694064; 1694065; 9152467; 15234186; 15234630; 15234663; 20429494; 33551548; 35569286; 37998325; 38132618; 38263852; 39248890; 42943045; 60163625; 66782895; 69008325; 69045725; 69884823; 70056054; 70280873; 70441524; 71180571; 71501177; 102937835; 105059203; 105655088; 105730603; 106400463; 107103481; 107568403; 107653944; 107657034; 107885110; 108528642; 108836648; 111447319; 112011577; 113006724; 117444569; 144378343; 144762023; 144762024; 146982475; 146983199; 147882882; 148209938; 149340056; 149720631; 149971359; 149993357; 150971013; 151540180; 151635619; 152600749; 152659979; 152962235; 153950334; 154956346; 155000038; 155000128; 155000146; 155014589; 155014835, 163207488, 196153706; 196153746; 196153752; 196235055; 196235079; 196235089; 196266826; 196283753; 196431724; 196587295; 197400046; 197717962; 198040564.

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Research Article

Myrsine cirrhosa (Primulaceae), a distinctive new shrub species from Kaua'i, Hawaiian Islands

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Abstract

Myrsine cirrhosa Lorence & K.R.Wood (Primulaceae), a new single-island endemic shrub species from Kaua'i, Hawaiian Islands, is described and illustrated. Notes on its distribution, ecology and conservation status are included. The new species is known from an area with ca. 45 individuals, where it is restricted to the remote central windward region of Kaua'i in open bogs and along open windy ridges. Suggested IUCN Red List status is CR (Critically Endangered). It differs from its Kaua'i congeners by its longer petals and narrowly elliptic leaves with strongly undulate margins and tendril-like apex. Phylogenetic analysis using RADseq data supports the recognition of this new species.

Key words: Conservation, Hawaiian Islands, Kaua'i endemism, *Myrsine*, Primulaceae

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Introduction

Myrsine L., in the family Primulaceae, is a pantropical to subtropical genus comprising ca. 200 species of shrubs and trees occurring throughout Africa, Asia and most of the Pacific Basin (Appelhans et al. 2020; Lorence and Wagner 2020). Although *Rapanea* Aubl. and *Suttonia* A.Rich. were previously recognised as distinct genera, both morphological (Hosaka 1940) and molecular phylogenetic studies (Appelhans et al. 2020) confirm they are nested within a monophyletic *Myrsine*. The genus is taxonomically complex, certain species are morphologically variable and the differences between species are mostly vegetative and often subtle (Wagner et al. 1999; Lorence and Wagner 2020).

Myrsine species range from small shrubs to medium-sized trees reaching 8 m tall or more, with simple, alternate leaves punctate with secretory canals. Inflorescences are in fascicles, umbels or glomerules produced along the branches on short woody knobs (spurs), either axillary or often below the leaves. Flowers are either perfect or unisexual (and then the plants dioecious) and fruits are subglobose, 1-seeded drupes (Wagner et al. 1999). In the Hawaiian Islands, species of *Myrsine* are associated with insect pollination and seed dispersal by forest birds (Sakai et al. 1995).

Hosaka (1940) wrote a revision of the Hawaiian *Myrsine* and recognised 25 species, based on morphological characters, whereas Wagner et al. (1999) recognised 20 species. Currently there are 19 recognised species in the Hawaiian Islands, with *M. emarginata* (Rock) Hosaka now being a synonym of *M. lessertiana* A.DC. (Wagner et al. 2023; POWO 2024). The Hawaiian group was resolved as monophyletic, based on their ITS/ETS phylogeny (Appelhans et al. 2020) ranking it amongst the ten largest Hawaiian plant radiations. The greatest species diversity occurs on Kaua‘i, the oldest of the main Hawaiian Islands at 4.7 mya (Price and Clague 2002). During the course of fieldwork on high summit regions of Kaua‘i, a distinctive new species of *Myrsine* was collected at three localities; it is described below and subsequently referred to as *Myrsine cirrhosa*. This new species is most similar morphologically to *M. helleri* (O.Deg. & I.Deg.) H.St.John and *M. fosbergii* Hosaka from which it differs by its longer petals and leaves with a combination of strongly undulate margins and tendril-like, cirrhose apices. With the inclusion of this new species, Kaua‘i now harbours 15 species, of which 12 are single island endemics. Unfortunately, material of the new species was not available for study by Appelhans et al. (2020), who studied Hawaiian *Myrsine* using RADseq. We, therefore, sequenced two specimens of the new species plus additional samples of Kaua‘i species in the framework of this project in order to evaluate its phylogenetic position.

Methods

RADseq: Taxon sampling

This study is largely based on Appelhans et al. (2020). In addition to that dataset, we added two samples of the new species collected from spatially separated individuals in the same (Wai‘ahi) population, as well as one sample each of *M. fosbergii*, *M. helleri* and *M. linearifolia* Hosaka (Suppl. material 5). With the exception of the O‘ahu endemic *M. degeneri* Hosaka, all currently accepted species of Hawaiian *Myrsine* have now been included in a phylogenomic study based on RADseq. Appelhans et al. (2020) used two species of *Ardisia* Sw. as outgroups. In order to have more closely-related taxa as outgroups, we omitted the *Ardisia* samples and rooted the phylogenetic trees with the earliest branching clade of Hawaiian *Myrsine* that consists of *M. lanaiensis* Hillebr. and two specimens of the polyphyletic *M. lessertiana* (Clade C in Appelhans et al. 2020). The final dataset included 31 samples (Suppl. material 5).

RADseq: DNA Extraction, Library Preparation and Sequencing

Genomic DNA was extracted from silica-dried leaf material using the Qiagen DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer’s instructions. A Qubit 3.0 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) in combination with the Qubit dsDNA Broad Range assay kit was used to measure the quality and quantity of the DNA extractions. The normalised samples (30 ng/µl) were sent to Floragenex (Eugene, OR, USA) for library preparation using the restriction enzyme *Sfb*I and for sequencing on an Illumina HiSeq machine, which produced 2 × 150 bp paired-end reads. De-multiplexed raw reads for all samples have been deposited at the Sequence Read Archive (SRA; https://www.ncbi.nlm.nih.gov/sra; Suppl. material 5) under the BioProject number PRJNA614459 together with the sequence reads from Appelhans et al. (2020).

RADseq: Bioinformatics and Phylogenetic Reconstruction

All steps, from demultiplexing to the calculation of the alignments of RAD loci, were carried out using ipyrad 0.9.52 (Eaton and Overcast 2020). One mismatch in the barcode sequence was allowed for demultiplexing. Adapters were removed and read filtering was done by deleting reads with more than five low-quality bases (< 20), a phred Q score offset of 33 and removing trimmed reads shorter than 35 bp. RAD loci were assembled *de novo* using clustering thresholds of 85% for within and amongst sample clustering. Appelhans et al. (2020) tested two different clustering thresholds (85% and 90%) and did not record any significant differences, so that only the 85% threshold – which is the default setting – is used here. As a trade-off between number of RAD loci included and missing data, five datasets were assembled that differed in the minimum number of samples recovered per RAD locus. This minimum number was set to either > 25% (min8; a RAD locus was only included in the alignment in case a sequence had been recovered for at least eight of the 31 samples), > 33% (min11), > 50% (min16), > 66% (min21) or > 75% (min24). With increasing “min” numbers, the numbers of RAD loci, but also the amount of missing data, were expected to drop. The resulting alignments were used for phylogenetic reconstruction using RAxML 8.2.4. (Stamatakis 2014), applying the GTR + Γ model and calculating 100 bootstrap replicates.

All ipyrad and RAxML analyses were computed on the high-performance computing cluster of the “*Gesellschaft für wissenschaftliche Datenverarbeitung Göttingen*” (GWDG), Germany (https://gwdg.de/en/hpc/services/).

Morphological analyses

Herbarium specimens of the new species have been deposited at PTBG and other herbaria listed under specimens examined and in Suppl. material 5 (acronyms according to Thiers (2018)). All measurements were taken from dried herbarium specimens and field notes and are presented in the descriptions as follows: length × width, followed by units of measurement (m, mm or cm). The authors have examined all specimens cited. We assessed the extinction risk for the new species following the IUCN Red List Categories and Criteria (IUCN 2012) and guidelines of the IUCN Standards and Petitions Committee (IUCN 2022). The extent of occurrence and area of occupancy were calculated by using ArcMap 10.6.1 (ESRI 2011) in relation to coordinates recorded while collecting herbarium specimens and making field observations. The coordinates latitude and longitude have been truncated to protect the exact holotype location from unauthorised access.

Results and discussion

Sequencing and RADseq datasets

The sequencing runs yielded an average of 4,425,834 raw reads per sample of which an average of 4,422,490 reads remained after trimming. This is less compared to the sequence reads from the Appelhans et al. (2020) study (5,505,232 raw reads, 5,281,476 reads after filtering; Suppl. material 5), but the newly-generated sequences had more bp overall because they were sequenced with the 2 × 150 bp paired-end chemistry instead of single end 100 bp in the previous study. Despite the higher number of bp in the newly-sequenced samples, the numbers of retained RAD loci was much lower for the new samples (18× lower in the min8 dataset; 19× lower in min11; 16× lower in min16; 5× lower in min21; 2× in min24 dataset), which might be due to the different sequencing strategies (2 × 150 bp vs. 1 × 100 bp) and the different fragment size selection during library preparation in particular.

As expected, the assembled datasets varied greatly in numbers of RAD loci, alignment length and amount of missing data. The min8 dataset contained 55,048 loci with a concatenated alignment length of 4,832,837 bp and 49.87% missing data, while the min24 dataset contained only 317 loci with an alignment length of 35,821 bp and 35.78% missing data (Suppl. material 5).

Phylogeny

Despite the large differences in the datasets, the consensus trees showed a congruent backbone, in which the same three main clades (Clades A, B and C) and the division of Clade A in two subclades (Subclades A1 and A2) are inferred as in Appelhans et al. (2020) (Fig. 1, Suppl. materials 1–4). However, average branch support differs amongst the datasets. The min16 and min8 consensus trees had the highest average branch support of 89.2% bs and 88.9% bs, respectively, followed by the min11 consensus tree with 84.2% bp, the min21 consensus tree with 79.9% bs and the min24 consensus tree with only 60.0% bs. Due to the higher support values, we discuss the consensus tree, based on the min16 dataset (Fig. 1, Suppl. materials 1–4) and the other consensus trees are mentioned in case of supported differences.

The two samples of the new species *M. cirrhosa* and the specimens of *M. helleri* and *M. linearifolia* are resolved within Subclade A2 (Fig. 1). This subclade consists of species endemic to Kaua‘i. With the exception of *M. denticulata* (Wawra) Hosaka, which has small leaves with a dentate margin, all species in this subclade are characterised by linear, narrowly elliptic to narrowly lanceolate leaves (Wagner et al. 1999; Appelhans et al. 2020). The new species *M. cirrhosa* fits well into this clade regarding its distribution and morphology.

Myrsine cirrhosa is resolved as the closest relative of *M. helleri*. In the min21 and min24 phylogenies, the two species are resolved as monophyletic sister species (Suppl. materials 3, 4). The other phylogenies did not resolve *M. helleri* as monophyletic. In the min11 and min16 phylogenies, *M. helleri* forms a grade at the base of *M. cirrhosa* (Suppl. material 2, Fig. 1). In the min8 phylogeny, one sample of *M. helleri* is sister to a clade that consists of the second *M. helleri* sample as well as *M. cirrhosa*, *M. fosbergii* and *M. linearifolia* (Suppl. material 1). A denser taxon sampling is needed to address the correct placement and potential polyphyly of *M. helleri*.

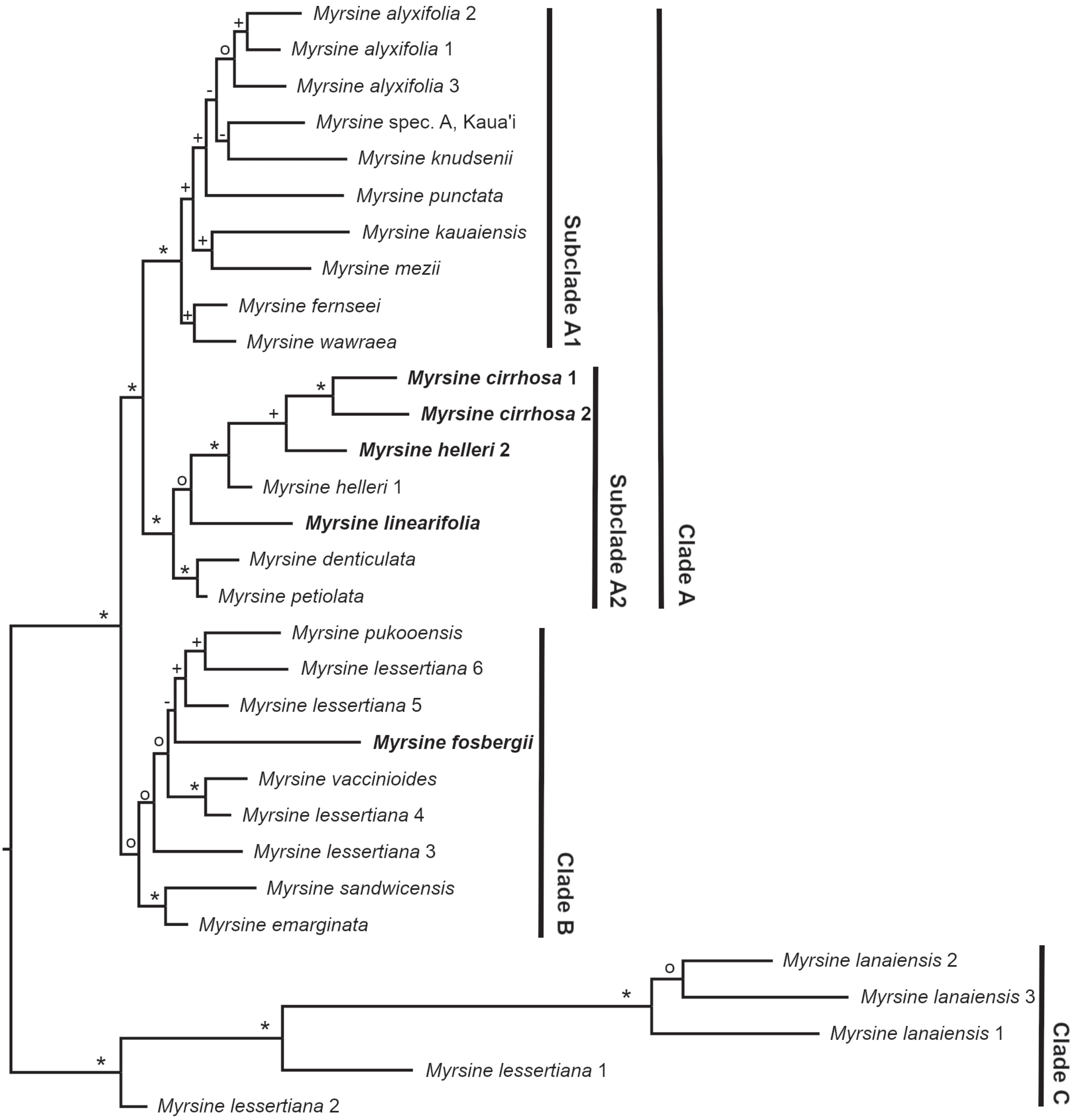

Figure 1. RADseq phylogeny of Hawaiian *Myrsine* based on the min16 dataset. Samples with newly-generated sequence data are highlighted in bold. Symbols at branches represent bootstrap support (bs) values (*: maximum bs; +: bs of 90 or higher; °: bs of 70 or higher; -: bs < 70).

Myrsine fosbergii (Kaua'i, O'ahu) is part of Clade B in all analyses, except the phylogeny of the min8 dataset (Suppl. material 1), where it also belongs to subclade A2. In all, but the min8 phylogeny, the backbone support of Clade B is rather low, which is potentially caused by the *M. fosbergii* specimen. In the min8 phylogeny, bootstrap support values of Clade B are generally higher and also the placement of *M. fosbergii* in Subclade A2 as sister to *M. linearifolia* is highly supported. The placement of *M. fosbergii* in Subclade A2 is highly supported by morphology and the species is characterised by narrowly elliptic leaves. The different phylogenetic placements of this species might be due to the low number of recovered RAD loci instead of a biological reason such as introgression or hybridisation. The number of loci is the second lowest after *M. lanaiensis* 3 for the min8, min11, min16 and min21 datasets and is the third lowest after *M. lanaiensis* 3 and *M. knudsenii* (Rock) Hosaka for the min24 dataset (Suppl. material 5). On the other hand, the estimated heterozygosity, which is indicative of introgression and hybridisation, in the *M. fosbergii* sample is only slightly above the average (Suppl. material 5).

Taxonomic treatment

Myrsine cirrhosa **Lorence & K.R.Wood, sp. nov.**
urn:lsid:ipni.org:names:77343738-1
Figs 2, 3A, B

Diagnosis. *Myrsine cirrhosa* is most similar morphologically to both *M. helleri* and *M. fosbergii*, from which it differs by its longer petals and leaves with a combination of strongly undulate margins and tendril-like, cirrhose apex.

Type. USA. Hawaiian Islands: Kauaʻi: Līhuʻe District, Kapalaoa, peak north of Wahiawa drainage, 21.99 N; -159.50 W, 930 m elev., 15 May 1991, *K. R. Wood et al. 835*, (holotype: PTBG-barcode 1000096825; isotypes (to be distributed): BISH, MO, NY, UC, US).

Description. Moderately branched shrubs 0.7–2 m tall; branches slender, glabrous, erect-spreading, bark brown or with orange- to reddish-brown tinge. ***Leaves*** clustered towards branch tips, blades linear-lanceolate to linear-elliptic, 4–8(–10.5) cm long, 0.9–1.5 cm wide, glabrous, adaxial surface medium green, yellow-green near base, not or sparsely black punctate, sometimes with longitudinal black streaks, abaxial surface light green, usually with several inconspicuous parallel black streaks 2.5–3.0 cm long on either side of the costa, not or scarcely black punctate, costa scarcely raised above, prominulous below, secondary veins 9–12 on each side, higher order venation conspicuously reticulate, venation prominulous on both surfaces especially below, submarginal vein present, margins entire, revolute and slightly thickened, strongly undulate in distal 2/3–3/4, apex long-acuminate, curved and hooked, base narrowly cuneate, subsessile, tapering to a winged petiole (1–)3–5 mm long. ***Flowers*** apparently perfect, 4–7 in bracteate fascicles in leaf axils or occasionally on leafless nodes, bracts broadly ovate-triangular, ca. 1.8 mm long, 1.5 mm wide, margins erose; pedicels 5–7 mm long, glabrous; calyx lobes 1.5–2.0 mm long, 0.9–1.1 mm wide, triangular-ovate, glabrous, black-streaked, margins entire; petals linear-elliptic or linear-lanceolate, 4–5 mm long, 1.3–1.5 mm wide, black-streaked, apex acute, margins slightly incurved, finely glandular ciliate towards apex; anthers 1.5–1.7 mm long, apex with slightly hooked appendage, glabrous; ovary ovoid, 1.0–1.5 mm long including the capitate stigma 0.6–0.7 mm wide. ***Drupes*** longitudinally dark streaked when immature, when ripe purple-black, globose, 7–8 mm in diameter, glabrous; pedicel 5–7 mm long.

Etymology. Specific epithet refers to the curved or hooked, tendril-like leaf apices. However, the plant is shrubby and non-climbing.

Specimens examined (*paratypes*). USA, Hawaiian Islands, Kauaʻi: Hanalei District, Waiʻaleʻale summit area, 1524 m elev., 2 May1992, *K. R. Wood et al. 1846* (BISH, PTBG); 1524 m elev., 2 May 1992, *S. Perlman & K. R. Wood 12747* (PTBG); 1524 m elev., 28 Dec 1994, *K. R. Wood 3896* (BISH, PTBG); 1487 m elev., 29 Dec 1994, *S. Perlman et al. 14606* (PTBG, US); 1554 m elev., 30 Dec 2005,

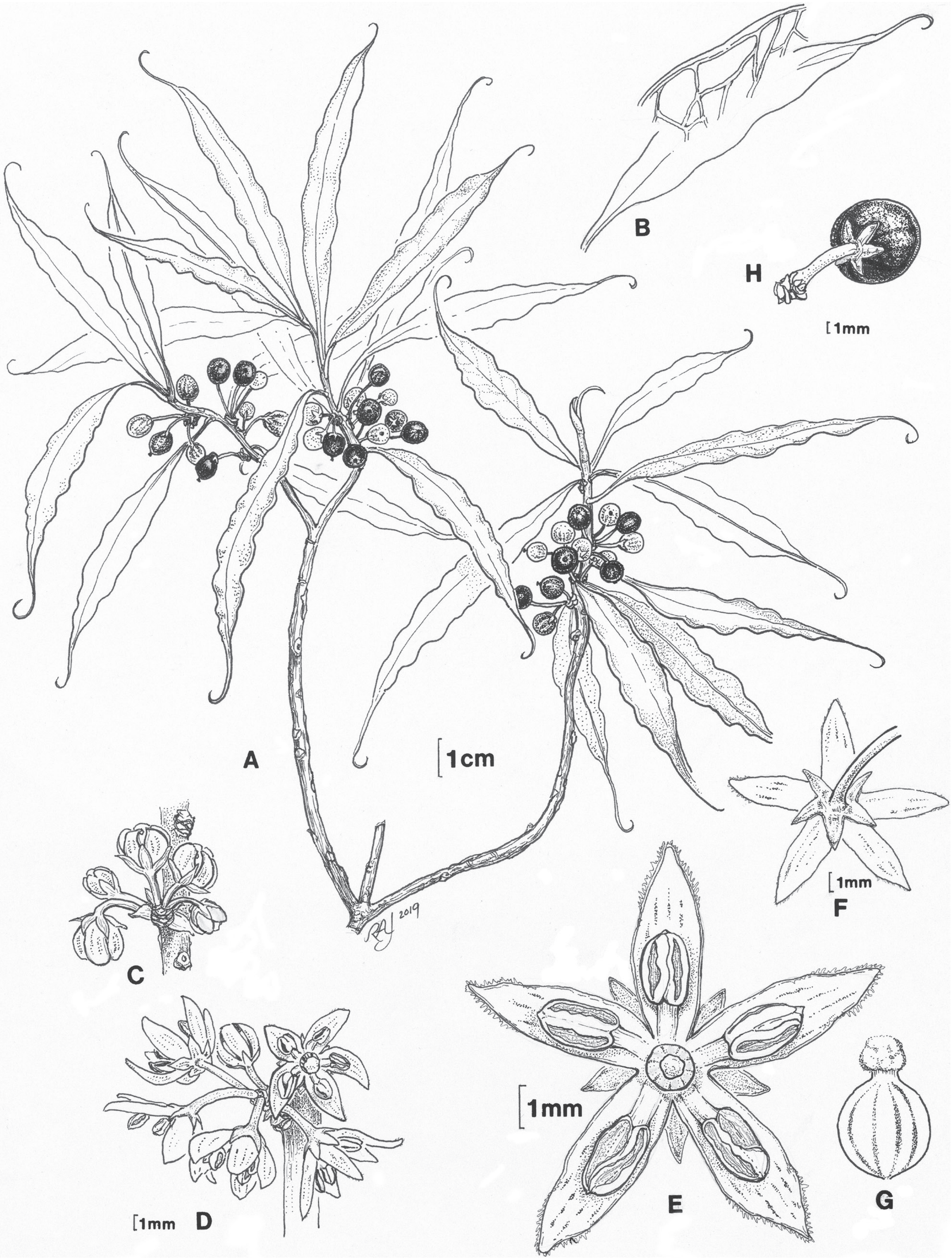

Figure 2. *Myrsine cirrhosa* Lorence & K.R.Wood **A** habit, fruiting branch **B** leaf showing cirrhose apex and detail of intramarginal venation **C** inflorescence in bud **D** inflorescence, flowers at anthesis **E** flower at anthesis, view from apex **F** flower at anthesis, view from base **G** pistil **H** mature drupe. **A, B** drawn from *Wood et al. 835* (PTBG), **C** drawn from *Wood & Query 12824* (PTBG), **D–G** drawn from *Wood et al.18139* (PTBG), **H** drawn from *Perlman & Wood 12747* (PTBG). Illustration by Robin Jess.

Figure 3. *Myrsine cirrhosa* **A** habit showing leaves with characteristic undulate margins and cirrhose apex (from Kamo‘oloa headwater below Kapalaoa Kaua‘i, *Wood & Query 12824*) **B** twig with leaves and flowers (from Wai‘ahi, Kaua‘i *Wood 18139*) **C** open exposed wind-swept summit ridges of Wai‘ale‘ale, Kaua‘i representing the habitat for *Myrsine cirrhosa*. All photos by K.R. Wood.

K. R. Wood 11662 (PTBG, US); 1500 m elev., 30 Dec 2005, *K. R. Wood 11683* (BISH, PTBG); 1553 m elev., 6 Dec 2013, *A. Williams & V. Caraway AMW 27* (BISH, PTBG); Lihue District, Kamoʻoloa headwater drainage below Kapalaoa, 975 m elev., 4 Oct 1996, *K. R. Wood 5692* (PTBG); 905 m elev., 21 Feb 2008, *K. R. Wood & M. Query 12804* (BISH, PTBG); 884 m elev., 21 Feb 2008, *K. R. Wood & M. Query 12824* (BISH, PTBG); Waiʻahi, upper central headwaters, 790 m elev., 4 Apr 2019, *K. R. Wood et al. 18139* (NY, PTBG, UC); Waiʻahi, upper northern headwaters, 884 m elev., 25 Nov 2013, *K. R. Wood et al. 15744* (BISH, CAS, PTBG).

Phenology. *Myrsine cirrhosa* has been collected with flowers from December to April, and with fruit in May and December.

Distribution and ecology. *Myrsine cirrhosa* has only been documented along the central windward summit ridges and peaks of Kauaʻi, preferring lowland to predominantly montane wet ecosystems at 784–1554 m (2572–5098 ft) elevation (Fig. 4). The two plant communities where the new species has been observed include open montane bogs and also exposed windswept ridges dominated by low statured shrubs and ferns. To date, only 45 plants of *M. cirrhosa* have been documented, including ca. 20 plants within the summit bogs of Waiʻaleʻale, renowned for being one of the wettest places on earth; ca. 20 plants in the general area of Kapalaoa peak and the very northern reaches of Wahiawa (ca. 9 km to the south of Waiʻaleʻale); and ca. five plants found midway between those peaks along the windswept ridges of Waiʻahi.

The open montane bog vegetation around the Waiʻaleʻale population of *Myrsine cirrhosa* is characterised by gently contoured wet slopes dominated by a mixed composition of native sedges, grasses, herbs, shrubs and ferns. Generally, lichens and mosses are prevalent wherever pig disturbance is minimal. The low-stature vegetation (ca. < 1 m) of these open bogs is occasionally interspersed with small islands of taller (1–5 m) shrubs and trees or dissected with headwater streams of riparian vegetation bordered with forest dominated by species of *Metrosideros* Banks ex Gaertn. and *Cheirodendron* Nutt. ex Seem. In addition to the small stunted trees of *Metrosideros* and *Cheirodendron*, these remote bogs are typically composed of endemic taxa, including grass and sedge genera such as *Carex* L., *Deschampsia* P.Beauv., *Dichanthelium* (Hitchc. & Chase) Gould, *Gahnia* J.R.Forst. & G.Forst., *Machaerina* Vahl, *Oreobolus* R.Br. and *Rhynchospora* Vahl. Genera of herbs and shrubs include *Astelia* Banks & Sol. ex R.Br., *Bidens* L., *Coprosma* J.R.Forst. & G.Forst., *Drosera* L., *Dubautia* Gaudich., *Geniostoma* J.R.Forst. & G.Forst., *Geranium* Juss., *Kadua* Cham. & Schltdl., *Keysseria* Lauterb., *Melicope* J.R.Forst. & G.Forst., *Myrsine*, *Nertera* Banks ex Gaertn., *Peperomia* Ruiz & Pav., *Perrottetia* Kunth, *Plantago* L., *Stenogyne* Benth., *Vaccinium* L. and *Viola* L. Fern genera typically include *Adenophorus* Gaudich., *Asplenium* L., *Cibotium* Kaulf., *Dryopteris* Adans., *Elaphoglossum* Schott ex J.Sm., *Odontosoria* (C.Presl) Fée, *Huperzia* Bernh. and *Sadleria* Kaulf.

Exposed windswept ridges where individuals of *Myrsine cirrhosa* have been observed at the Kapalaoa, Wahiawa and Waiʻahi sites are also dominated by endemic tree species of *Metrosideros* and *Cheirodendron* along with other shrub and tree genera, such as *Dubautia*, *Hydrangea* Gronov. ex L., *Ilex* Tourn. ex L., *Kadua*, *Leptecophylla* C.M.Weiller, *Lobelia* Plum. ex L., *Melicope*, *Polyscias* J.R.Forst. & G.Forst., *Pritchardia* Seem. & H.Wendl., *Psychotria* L., *Vaccinium*; sedges including *Machaerina*; and scrambling ferns *Dicranopteris* Bernh. and *Diplopterygium* (Diels) Nakai.

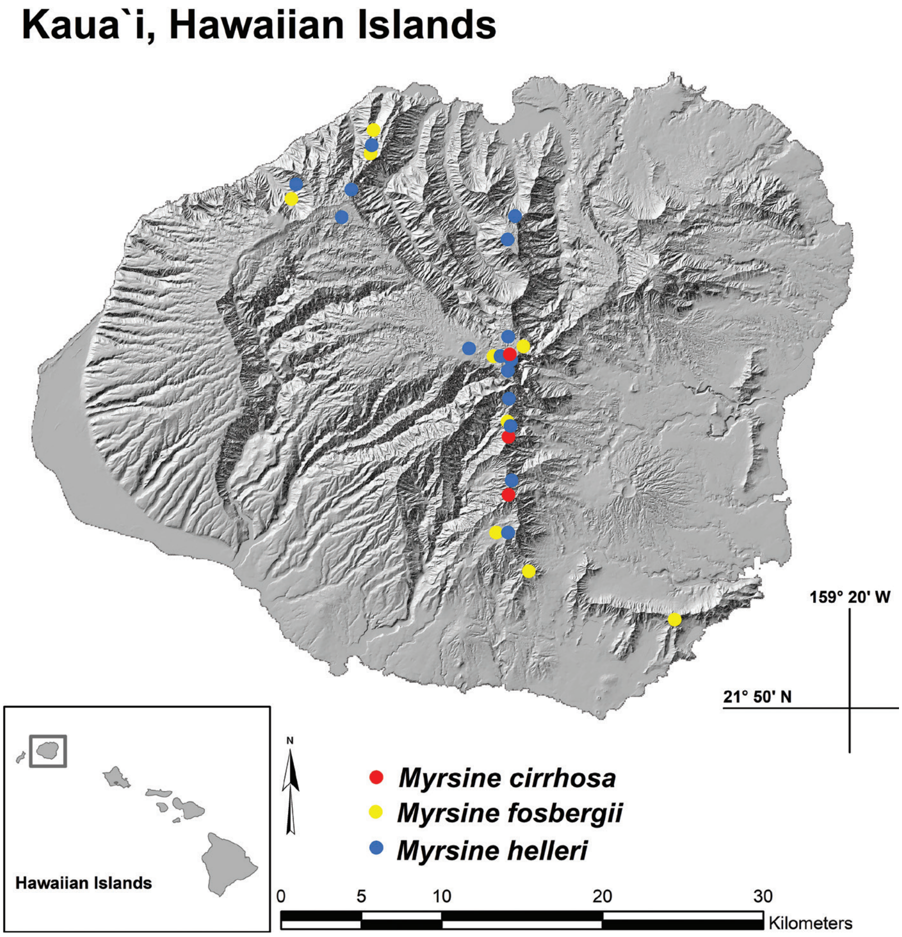

Figure 4. Distribution map with dots representing known locations for three *Myrsine* species on Kaua'i, Hawaiian Islands.

Modification to existing key to Hawaiian *Myrsine* (Wagner et al. 1999)

To accommodate *Myrsine cirrhosa*, the following couplets can be inserted into the beginning of the existing key to Hawaiian *Myrsine* (in Wagner et al. (1999, p. 935)). Note: K = Kaua'i; O = O'ahu.

1 Leaves linear, narrowly elliptic to narrowly lanceolate, apex attenuate to long-attenuate or long-acuminate and falcate or cirrhose-hooked............**2**

– Leaves variable in shape, apex short-acuminate, acute to obtuse or rounded, ± emarginate...**5**

2(1) Leaves narrowly elliptic, 8–13(–14) cm long, 1–2(–3.3) cm wide, margins plane, not undulate, apex straight or slightly hooked; flowers 4–8 per fascicle; K, O..***M. fosbergii***

– Leaves linear, linear-elliptic to narrowly lanceolate or rarely narrowly elliptic, 1.5–9(–13) cm long, 0.25–1.4 cm wide, margins plane, slightly revolute or undulate, apex straight, falcate, slightly hooked or strongly cirrhose-hooked; flowers 1–7 per fascicle; K **3**

3(2) Leaves linear, 5–9 cm long, 0.25–0.4 cm wide; petals ca. 2.2–2.5 mm long...***M. linearifolia***

– Leaves linear-lanceolate, linear-elliptic, narrowly lanceolate or rarely narrowly elliptic, 1.5–7(–13) cm long, 0.5–1.4(–1.5) cm wide; petals 2–5 mm long...**4**

4(3) Leaves with margins strongly undulate, apex strongly cirrhose-hooked, tendril-like; flowers 4–7 per fascicle; petals 4–5 mm long .... ***M. cirrhosa***

– Leaves with margins plane to slightly revolute, apex straight, falcate or slightly hooked; flowers 1–3 per fascicle; petals 3.5 mm long **5**

5(3) Leaves glabrous, 4–7 cm long, subsessile; pedicels 2–4 mm long; bogs .. .. ***M. helleri***

– Leaves glabrous, except sparsely pubescent with minute rectangular, glandular hairs at the very base, especially on younger leaves, 1.5–4(–13) cm long, petioles (0–)1–3 mm long; pedicels 3–7 mm long; bogs and forest .... ***M. petiolata***

Preliminary conservation assessment

According to the guidelines set by the World Conservation Union (IUCN 2012, 2022), *Myrsine cirrhosa* is classified as Critically Endangered (CR), indicating a very high risk of extinction in its natural habitat. This assessment, summarised by the IUCN alphanumeric criteria (CR B1ab(i,ii,iii,v); B2ab(i,ii,iii,v); C2a(i); D), is based on the fact that the species has a severely limited Extent of Occurrence (EOO) of only 2 km^2, an Area of Occupancy (AOO) of approximately 1 km^2 and population size of fewer than 50 individuals. Threats to the habitat of *Myrsine cirrhosa* include introduced non-native animals that destroy native vegetation such as pigs (*Sus scrofa*), rats (*Rattus* spp.), slugs (*Meghimatium striatum*) and occasional goats (*Capra hircus*) and black-tailed deer (*Odocoileus hemionus*). Remote island ecosystems have low resistance to non-native competitors, especially introduced animals and plants which can be devastating to native species that have evolved in their absence (Carlquist 1974; Weller et al. 2011, 2018). Invasive non-native plant species that compound habitat degradation around *M. cirrhosa* include *Andropogon virginicus* L., *Axonopus fissifolius* (Raddi) Kuhlm., *Miconia crenata* (Vahl) Michelang. (syn. *Clidemia hirta* (L.) D.Don), *Cyperus meyenianus* Kunth, *Erechtites valerianifolius* (Link ex Spreng.) DC., *Juncus planifolius* R.Br., *Paspalum conjugatum* P.J.Bergius, *P. urvillei* Steud., *Pterolepis glomerata* (Rottb.) Miq., *Rhodomyrtus tomentosa* (Aiton) Hassk., *Rubus argutus* Link, *R. rosifolius* Sm., *Sacciolepis indica* (L.) Chase, *Setaria parviflora* (Poir.) Kerguélen, and *Sphaeropteris cooperi* (Hook. ex F.Muell.) R.M.Tryon. Landslides after heavy rains also can be a very serious threat, especially along the windswept ridge colonies of *M. cirrhosa* where a single landslide could destroy large sections of native habitat.

Relationships and similar taxa

Myrsine cirrhosa most closely resembles *M. helleri*. RADseq resolved this as its closest relative (Fig. 1, Suppl. materials 1–4), but the new species can be consistently distinguished from the latter species by its strongly undulated leaf margins (Table 1, Figs 2, 3A, B). One collection was initially identified as *M. helleri* and distributed under that name (i.e. *Perlman 14606*), but it clearly represented *M. cirrhosa* on critical examination. Leaves of *M. cirrhosa* tend to be comparatively larger than those of *M. helleri* and have a combination of undulate margins and a cirrhose apex, in addition to the inflorescences having more numerous (4–7) flowers per fascicle and longer petals. Populations of *M. helleri* from Wahiawa and Namolokama may have leaves with a slightly hooked apex, but the margins are

Table 1. Distinguishing characters of four Kaua‘i *Myrsine* species.

Character	*M. cirrhosa*	*M. helleri*	*M. fosbergii*	*M. linearifolia*
Height	0.7–2 m	2–5 m	2–4 m	2.5–8 m
Lamina length	4–8(–10.5) cm	4–7 cm	8–13(–14) cm	5–9 cm
Lamina width	0.9–1.5 cm	0.5–1.4 cm	1–2(–3.3) cm	0.25–0.4 cm
Petiole length	(1–)3–5 mm	0–4 mm	0	1–2 mm
Leaf margin	undulate	plane	plane	slightly revolute
Apex	cirrhose-hooked	straight ± curved	straight	falcate ± hooked
Flowers/fascicle	4–7	1–3	4–8	1–3
Petal length	4–5 mm	3.5 mm	2.8–3.5 mm	2–2.5 mm
Pedicel length	5–7 mm	2–4 mm	5–8 mm	1–4.2 mm

not undulate and inflorescences have fewer (1–3) flowers per fascicle. The type of *Myrsine helleri* is from the headwaters of the Wahiawa Stream area on Kaua‘i, where it may grow sympatrically with *M. cirrhosa* (see Wagner et al. (1999) for synonymy and Wagner and Shannon (1999) for typification). *Myrsine cirrhosa* also was observed to grow sympatrically with *M. helleri* at Wai‘ale‘ale summit (*Wood & Nishek 11683*, BISH, PTBG). However, the two species remain distinct morphologically. One collection from Wai‘ale‘ale summit (*Wood 3894*, PTBG, US) is intermediate, having larger leaves with undulate margins, but lacking a cirrhose apex. It likely represents a hybrid between *M. cirrhosa* and either *M. helleri* or *M. fosbergii*, which is also sympatric here, but needs further investigation.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

David H. Lorence / lead author and field research; Kenneth R. Wood / co-author and field research; Marc S. Appelhans / co-author, RADseq, phylogenetic analyses; Warren L. Wagner / co-author and additional RADseq project preparation.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

RADseq phylogeny of Hawaiian *Myrsine* based on the min8 dataset

Authors: David H. Lorence, Kenneth R. Wood, Marc S. Appelhans, Warren L. Wagner
Data type: tif

Link: https://doi.org/10.3897/phytokeys.234.123694.suppl1

Supplementary material 2

RADseq phylogeny of Hawaiian *Myrsine* based on the min11 dataset

Authors: David H. Lorence, Kenneth R. Wood, Marc S. Appelhans, Warren L. Wagner
Data type: tif

Link: https://doi.org/10.3897/phytokeys.234.123694.suppl2

Supplementary material 3

RADseq phylogeny of Hawaiian *Myrsine* based on the min21 dataset

Authors: David H. Lorence, Kenneth R. Wood, Marc S. Appelhans, Warren L. Wagner
Data type: tif

Link: https://doi.org/10.3897/phytokeys.234.123694.suppl3

Supplementary material 4

RADseq phylogeny of Hawaiian *Myrsine* based on the min24 dataset

Authors: David H. Lorence, Kenneth R. Wood, Marc S. Appelhans, Warren L. Wagner
Data type: tif

Link: https://doi.org/10.3897/phytokeys.234.123694.suppl4

Supplementary material 5

Herbarium voucher information, SRA accession numbers and sequencing statistics of specimens used for RADseq

Authors: David H. Lorence, Kenneth R. Wood, Marc S. Appelhans, Warren L. Wagner
Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.234.123694.suppl5

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Short Communication

Revisiting the infrageneric classification of *Garcinia* L. (Clusiaceae): an updated sectional name and new, legitimate names in *Garcinia* for *Allanblackia gabonensis* (Pellegr.) Bamps and *A. parviflora* A.Chev.

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Abstract

In a recent publication dealing with the sectional-level taxonomy of *Garcinia*, an illegitimate superfluous sectional name and two illegitimate homonyms were published. Herein we choose a legitimate sectional name, *Garcinia* section *Rheediopsis* Pierre, for the superfluous name *Garcinia* section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney; and create two new legitimate names in *Garcinia* for *Allanblackia gabonensis* (Pellegr.) Bamps and *A. parviflora* A.Chev.

Key words: Homonym, nomenclature, priority, taxonomy

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Introduction

In Gaudeul et al. (2024), *Garcinia* sect. *Rheedia* (L.) S.W.Jones ex P.W.Sweeney was recognized to include species placed by Jones (1980) into *G.* sect. *Rheedia* (L.) S.W.Jones *nom. inval.*, *G.* sect. *Rheediopsis* Pierre, and *G.* sect. *Teracentrum* Pierre. However, *Garcinia* section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney is an illegitimate name (superfluous as per Art. 52.1, Turland et al. 2018) due to the two previously published sectional names being included within it. Instead, we here choose the name *Garcinia* section *Rheediopsis* Pierre for this section.

In Gaudeul et al. (2024), the genus *Allanblackia* was placed into synonymy under *Garcinia* section *Allanblackia* (Oliv.) P.W. Sweeney and new combinations and names were created in *Garcinia* for the former *Allanblackia* species. Two of these new names are illegitimate later homonyms (Art. 53.1 Turland et al. 2018). Here we provide new legitimate names for these species.

Nomenclature

Garcinia section *Rheediopsis* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5 (1883). Clade 2 in Gaudeul et al. (2024).

Type. *Garcinia smeathmannii* (Planch. & Triana) Oliv., Fl. Trop. Afr. 1: 168 (1868), designated by Gaudeul et al. (2024).

Synonyms. *Rheedia* L., Sp. Pl.: 1193 (1753).

Garcinia section *Teracentrum* Pierre, Fl. Forest. Cochinch. 1, Fasc. 5 (1883).

Garcinia section *Rheedia* (L.) S.W.Jones ex P.W.Sweeney, *nom. illegit*., PhytoKeys 239: 86 (2024).

Species. *Garcinia albuquerquei* (M.E.Berg) Bittrich; *G. ambrensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. anjouanensis* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aphanophlebia* Baker; *G. apostoloi* Mouzinho; *G. arenicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. aristata* (Griseb.) Borhidi; *G. bakeriana* (Urb.) Borhidi; *G. barkeriana* (Urb. & Ekman) Alain; *G. benthamiana* (Planch. & Triana) Pipoly; *G. brasiliensis* Mart.; *G. calcicola* (Jum. & H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. cincta* (Urb.) Borhidi; *G. clarensis* Borhidi; *G. commersonii* (Planch. & Triana) Vesque; *G. cubensis* (Borhidi) Borhidi; *G. dalleizettei* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. decussata* C.D.Adams; *G. floribunda* Miq.; *G. fluviatilis* Mouzinho & L.Marinho; *G. gabonensis* Sosef & Dauby; *G. gardneriana* (Planch. & Triana) Zappi; *G.* × *guacopary* (S.Moore) M.Nee; *G. hessii* (Britton) Alain; *G. humilis* (Vahl) C.D.Adams; *G. intermedia* (Pittier) Hammel; *G. kingaensis* Engl.; *G. leptophylla* Bittrich; *G. livingstonei* T.Anderson; *G. macrophylla* Mart.; *G. madruno* (Kunth) Hammel; *G. magnifolia* (Pittier) Hammel; *G. magnophylla* (Cuatrec.) Hammel; *G. mangorensis* (R.Vig. & Humbert) P.W.Sweeney & Z.S.Rogers; *G. martinii* (Maguire) Govaerts; *G. megistophylla* P.W.Sweeney & Z.S.Rogers; *G. moaensis* (Bisse) Borhidi; *G. obliqua* Sosef & Dauby; *G. ophiticola* (Borhidi) Borhidi; *G. ovalifolia* Oliv.; *G. pachyclada* N.Robson; *G. parviflora* Benth.; *G. pervillei* (Planch. & Triana) Vesque; *G. polyneura* (Urb.) Borhidi; *G. portoricensis* (Urb.) Alain; *G. pulvinata* (Planch. & Triana) Hammel; *G. pungens* Borhidi; *G. revoluta* (Urb.) Borhidi; *G. robsoniana* Bamps; *G. ruscifolia* (Griseb.) Borhidi; *G. semseii* Verdc.; *G. serpentini* Borhidi; *G. smeathmannii* (Planch. & Triana) Oliv.; *G. spruceana* (Engl.) Mouzinho; *G. staudtii* Engl.; *G. thouvenotii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. tsimatimia* P.W.Sweeney & Z.S.Rogers; *G. urschii* (H.Perrier) P.W.Sweeney & Z.S.Rogers; *G. verticillata* Alain.

New names for species included in *Garcinia* sect. *Allanblackia* (Oliv.) P.W. Sweeney

Garcinia alepensis P.W.Sweeney, nom. nov.

urn:lsid:ipni.org:names:77339326-1

≡*Allanblackia parviflora* A.Chev., Vég. Ut. Afr. Trop. Franç. 5: 163 (1909). Type. Côte d’Ivoire: Alépé, *Chevalier 16239*. non *Garcinia parviflora* Benth., London J. Bot. 2: 370 (1843).

≡*Garcinia guineensis* P.W.Sweeney, PhytoKeys 239: 87 (2024), *nom. illeg.* non *Garcinia guineensis* (G.Don) Vesque, Monogr. Phan. [A.DC. & C.DC.] 8: 335 (1893).

Note. A replacement name, *Garcinia alepensis*, is created here for *Allanblackia parviflora*, because the epithet *parviflora* was used previously in *Garcinia* for a different species. The epithet *alepensis* is chosen in reference to the type locality of the species, Alepe, Côte d'Ivoire.

Garcinia agnoume **P.W.Sweeney, nom. nov.**
urn:lsid:ipni.org:names:77341601-1

≡*Allanblackia gabonensis* (Pellegr.) Bamps, Bull. Jard. Bot. Natl. Belg. 39: 356 (1969). Type. Gabon: between Moubighou and Nzoundou, *Le Testu 6001*. non *Garcinia gabonensis* Sosef & Dauby, PhytoKeys 17: 52 (2012).
≡*Garcinia ngouniensis* P.W.Sweeney, PhytoKeys 239: 88 (2024), *nom. illeg.*
non *Garcinia ngouniensis* Pellegr., Bull. Mus. Natl. Hist. Nat. 27: 195 (1921).

Note. A replacement name, *Garcinia agnoume*, is created here for *Allanblackia gabonensis*, because the epithet *gabonensis* was used previously in *Garcinia* for a different species. The epithet *agnoume*, constructed as a noun in apposition, is in reference to a vernacular name *agnoumé* used for this species within parts of its range (Eyog Matig et al. 2006).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

All authors have contributed equally.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Checklist

A taxonomic backbone for the Plumbaginaceae (Caryophyllales)

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Abstract

A taxonomic backbone of the Plumbaginaceae is presented and the current state of knowledge on phylogenetic relationships and taxon limits is reviewed as a basis for the accepted taxon concepts. In total, 4,476 scientific names and designations are treated of which 30 are not in the family Plumbaginaceae. The Plumbaginaceae are subdivided in three tribes with 26 genera and 1,179 accepted species. Two subgenera, 17 sections, two subsections and 187 infraspecific taxa are accepted. At the species and infraspecific level 2,782 synonyms were assigned to accepted taxa, whereas 194 names were excluded from the core checklist (i.e., unplaced taxa, infrageneric subdivisions with still uncertain application, names of verified uncertain application, invalid horticultural names, excluded names from other families, other excluded designations, and unresolved names). The EDIT Platform for Cybertaxonomy was utilized as the tool to compile and manage the names and further taxonomic data under explicit taxon concepts. Secundum references are given in case taxon concepts were taken from the literature, whereas this study serves as reference for newly circumscribed taxa. The family's division into the tribes Aegialitideae, Limonieae, and Plumbagineae departs from earlier two-subfamily classifications, prompted by recent phylogenetic findings that challenge the subfamilial affinity of *Aegialitis*. The genus *Acantholimon* was extended to include *Gladiolimon*, as currently available phylogenetic and morphological data support this merger. In *Limonium*, all accepted species could be assigned to sections and subsections or the "Mediterranean lineage", respectively, making use of the phylogenetic distribution of their morphological characters and states. A new combination and/or status is proposed for *Dyerophytum socotranum*, *Limonium thymoides*, *Limonium* × *fraternum*, *Limonium* × *rossmaessleri*, and *Limonium* sect. *Jovibarba*. Special attention is given to nomenclatural issues, particularly for *Statice nomen ambiguum* to resolve the names under accepted names. The use of artificial groupings like "aggregates", "complexes" and "species groups" in alpha-taxonomic treatments is discussed. The taxonomic backbone will receive continued updates and through the Caryophyllales Taxonomic Expert Network, it contributes the treatment of the Plumbaginaceae for the World Flora Online.

Key words: Caryophyllales, EDIT Platform, phylogenetic relationships, *Statice*, taxon concept, World Flora Online

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Introduction

The Plumbaginaceae Juss. is a nearly cosmopolitan family of the order Caryophyllales that is most diverse in the northern hemisphere. The majority of its species are halophytes or psammophytes, growing on salty soils or in coastal habitats, while another large group of species are cold-adapted orophytes of arid regions. The generic concepts in this family have varied over time. The last family-wide synopsis accepted 29 genera (Hernández-Ledesma et al. 2015) compared to Kubitzki's (1993) treatment with 27 accepted genera. Most of the species are concentrated in the large genera *Limonium* Mill. (ca. 600 spp.), *Acantholimon* Boiss. (ca. 200 spp.) and *Armeria* Willd. (ca. 100 spp.), whereas the other genera are small or monotypic, segregate genera (Kubitzki 1993).

Plumbaginaceae are monophyletic and sister to Polygonaceae (Lledó et al. 1998; Cuénoud et al. 2002; Schäferhoff et al. 2009; Yang et al. 2015; Yao et al. 2019). Plumbaginaceae has been divided into two subfamilies, Plumbaginoideae Burnett and Limonioideae Reveal (= Staticoideae), and three tribes, Plumbagineae Dumort. belonging to Plumbaginoideae, and Aegialitideae Z.X.Peng and Limonieae Reveal belonging to Limonioideae, based on molecular phylogenies (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018). Compared to the Plumbagineae and Aegialitideae, the Limonieae stands out by more than 90 percent of the species diversity of the family. Among the large genera of Limonieae the monophyletic status of *Limonium* and *Armeria* was confirmed by investigations with dense taxon sampling (Lledó et al. 1998, 2005a; Malekmohammadi et al. 2017a; Koutroumpa et al. 2018), whereas *Acantholimon* turned out to be non-monophyletic as currently classified (Moharrek et al. 2017; Koutroumpa et al. 2018). *Plumbago*, the largest genus of the Plumbagineae, also appears as non-monophyletic (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018).

The Plumbaginaceae are primarily perennial herbs and shrubs, rarely climbers, characterized by flowers that have stamens opposite the petals, a single basal anatropous ovule with curled funicle, an endotrophic transmitting tissue projecting inward from the base of the style, and salt (chalk) glands on leaves and stems (known as 'Licopoli' or 'Mettenius' organs). These traits are regarded as synapomorphies for the family (Labbe 1962; Kubitzki 1993; De Laet et al. 1995). Figures 1, 2 as well as two links of herbarium images of *Aegialitis annulata* R. Br. illustrate a segment of the morphological and ecological variability found within the family (https://herbarium.bgbm.org/object/B100518467; https://herbarium.bgbm.org/object/B100745686).

Estimates of species diversity have varied considerably, ranging from about 650 species (Kubitzki 1993) to 1000 (Hernández-Ledesma et al. 2015) or over 1000 species (Lledó et al. 1998), with the differences ascribed primarily to species number estimates in large genera with numerous microspecies. For example, estimated species numbers in *Limonium* vary from 350 (Hernández-Ledesma et al. 2015), 400–500 (Erben 1993; Brullo and Erben 2016), up to about 600 (Koutroumpa et al. 2018; Hassler 2023), and 708 (Govaerts 2023). Many of the recently described species in *Limonium* are small-ranged apomictic polyploids, for which taxonomic circumscriptions are particularly challenging. A prominent example of a significant increase in species number is found in a recent monograph of *Limonium* in Greece (Brullo and Erben 2016) that almost doubled the

Figure 1. Morphological and habitat diversity in the family Plumbaginaceae. Limonieae: **A** *Acantholimon pterostegium* Bunge **B** *Armeria pungens* (Brot.) Hoffmanns. & Link **C** *Bakerolimon plumosum* (Phil.) Lincz. **D** *Ceratolimon feei* (Girard) M.B.Crespo & Lledó **E** *Ceratolimon weygandiorum* (Maire & Wilczek) M.B.Crespo & Lledó **F** *Limoniastrum monopetalum* (L.) Boiss. **G** *Limonium bonduellei* (T.Lestib.) Kuntze **H** *Limonium virgatum* (Willd.) Fourr. Photos **A** by Hossein Akhani **B, F, G** by Mario Martínez-Azorín **C** by Sergio Ibáñez **D, E** by José Quiles **H** by Konstantina Koutroumpa.

number of species previously known for the country by describing many new apomictic polyploid morphospecies.

This species backbone is part of the Global Caryophyllales Synthesis initiative, which aims at generating and maintaining a dynamic synthesis of data and knowledge on the species diversity of this order of flowering plants in a single open-access portal (Borsch et al. 2015, 2020; Arias et al. 2016). The Caryophyllales Network functions as a Taxonomic Expert Network dedicated to Caryophyllales within the World Flora Online (WFO) (http://www.worldfloraonline.org/) which acts as a community-driven authoritative source of information for the world's plants (Wyse-Jackson and Miller 2015; Borsch et al. 2020). The WFO Plant List (https://wfoplantlist.org) now serves as the taxonomic backbone of the WFO and has replaced The Plant List (TPL 2013) that was the first consistent global species list for angiosperms, which is no longer curated (Schellenberger-Costa et al. 2023). Among the taxonomic backbones already

Figure 2. Morphological and habitat diversity in the family Plumbaginaceae. Limonieae: **A** *Limonium thymoides* (Girard) M.B.Crespo **B** *Psylliostachys leptostachya* (Boiss.) Roshkova **C** *Psylliostachys spicata* (Willd.) Nevski **D** *Saharanthus ifniensis* (Caball.) M.B.Crespo & Lledó. Plumbagineae: **E** *Dyerophytum africanum* (Lam.) Kuntze **F** *Plumbago auriculata* Lam. **G** *Plumbago europaea* L. Photos **A, E, G** by Mario Martínez-Azorín **B, C, F** by Hossein Akhani **D** by José Quiles.

published by the Caryophyllales Taxonomic Expert Network are the families Nepenthaceae (Berendsohn et al. 2018), Cactaceae (Korotkova et al. 2021), Aizoaceae (Berendsohn 2022), and the genus *Dianthus*, Caryophyllaceae (Fassou et al. 2022). The current work started with treatment of the names of *Limonium*. Considering that *Statice* is a rejected name with the respective species mostly belonging to *Limonium* or *Armeria* (Kuntze 1891) and that a considerable part of *Statice* names were still unresolved, it was mandatory to work in a broader scope including the subfamily Limonioideae to resolve these names. Finally, to accommodate recent phylogenetic results that inform changes at the circumscriptions of major taxonomic units below the family level (e.g., subfamilies and tribes), we extended the taxonomic treatment to the entire family.

The classification presented in this taxonomic backbone is built upon monophyletic groups, where possible. Our approach was to evaluate the available phylogenetic literature on the Plumbaginaceae. A detailed review on the state of knowledge as well as the evolution and diversity of Plumbaginaceae is provided.

The taxonomic backbone aims at including all validly published names and assigning them to the status as accepted names or synonyms. To be comprehensive, it also comprises (invalid) designations published in the literature or covered by online databases. This was deemed important when using the taxonomic backbone as a reference for name matching in meta-analysis of biodiversity data which also have to handle taxonomically less accurate sources.

Materials and methods

Informatics tools

The EDIT Platform for Cybertaxonomy (Ciardelli et al. 2009; Berendsohn 2010; BGBM 2011+, 2016+, Luther et al. 2019) (https://cybertaxonomy.eu/) was used to manage the taxonomic data, and to present them online as well as in text document format. The platform unites a set of open-source software tools that have been developed over the past 25 years at the Botanic Garden and Botanical Museum Berlin. This platform aims at including all aspects of taxonomic treatments and the workflows to create and maintain them (Borsch et al. 2015; Kilian et al. 2015; Henning et al. 2018). It provides the database system, editing tools, the online portal, and publication pipelines for this treatment. All sources of information can be cited for almost any item in the database, so that the information is transparent and appropriately credited.

The database component is structured according to the Common Data Model (CDM), a fully standard-based object-oriented data-model covering in detail the entire scope of taxonomic data (Müller et al. 2017). The principal software tool used in the context of the work presented here was the Taxonomic Editor, an operating-system independent frontend used to input and edit the taxonomic data in the online CDM database.

The appended taxonomic backbone was generated from an output of the EDIT platform using the functionalities of MS Access and MS Word processing software (Berendsohn et al. 2018). The contribution to the World Flora Online taxonomic backbone will be accomplished by submitting a WFO-DwCA (Darwin Core Archive) file generated from the EDIT platform.

Data entry, sources of taxonomic information and editorial workflows

The terminology, editorial approaches, and the handling of source citations in the EDIT Platform are applied here as described in Berendsohn et al. (2018), Korotkova et al. (2021) and The Caryophyllales Network (2024+; https://caryophyllales.org/Editorial).

A list of Plumbaginaceae names was received from the World Flora Online (WFO 2017). This list was based on The Plant List 1.1 (TPL 2013) and included 2925 names with a unique WFO-identifier. The list was uploaded to the Tropicos (1991+) name matching service to obtain publication details, author and literature abbreviations were standardized and the names then matched with and imported into the EDIT Platform, resulting in a dataset comprising 2990 names. The first author then preliminarily placed the imported names not yet classified as either taxon names or synonyms. Afterwards, the names from the World Checklist of Vascular Plants (WCVP, obtained from Kew in December 2019) were matched with the records already present in the database and further names covered in the Euro+Med PlantBase were added manually. Newly published names or names that were missing from other databases were also entered manually.

Botanical literature, both in print and online, online databases, phylogenetic studies, monographs, regional or species group treatments and checklists as well as personal taxonomic knowledge of the authors were used to evaluate the taxon concepts at species level.

The taxonomic backbone includes a core part with accepted names and their synonyms. Names excluded from the core checklist were assigned to the following categories: "Unplaced taxa" currently contains only 2 invalidly published hybrid designations that were described by Pignatti and used in later publications. "Unplaced generic subdivisions" contains names of sections and subsections that we refrained from classifying awaiting further evidence from phylogenetic studies. "Names of verified uncertain application" lists names that probably will never be placed. The categories "Invalid horticultural names and combinations" and "Excluded designations" list designations that have been in use but which we did not want to include in the synonymy (e.g. erroneous author citations). "Excluded names" contains names outside the Plumbaginaceae that were erroneously part of the original WFO backbone. In contrast, the "unresolved names" offers a provisional category for practical reasons to accommodate names for which the correct application or status has yet to be determined. To classify the unresolved names in the correct place, further literature and/or herbarium revisions are required but this investigation exceeds the scope of this study. The circumscription of taxa is always indicated by a secundum "sec." reference (Berendsohn 1995), a reference that indicates the circumscription of a taxon and its distinction from other taxa. The sec. references are either literature references, or original work done here, and then are referred as this publication. The "syn. sec." reference of the synonyms refers to a reference stating the synonymy to the accepted name or to one of its synonyms. The sec. reference of the names that are excluded from the core taxonomic backbone is normally the source of the name, i.e., the dataset from where the name has been imported.

The authors collaborated both by exchange of corrections in the formatted output produced by the EDIT Platform and by using a preliminary password-protected online portal that gave direct access to the CDM database.

Key literature sources

The Euro+Med Plant Base (2006+) as a continental-level checklist was used as primary source for taxon concepts at species level for many of the European, Mediterranean and North African Plumbaginaceae species (Plumbaginaceae treatment by Domina 2011+). The taxonomic treatment by Erben (1993) in the Flora Iberica was further considered for the species from the Iberian Peninsula and the Balearic Islands. Different literature was reviewed for the Italian species (e.g., Brullo 1988; Arrigoni 2015; Peruzzi et al. 2015; Brullo and Guarino 2017). A checklist of vascular plants of Greece (Dimopoulos et al. 2013, 2016) as well as the treatment by Brullo and Erben (2016) were the main source for species from Greece. Sell (2018) is used as the principal reference for the species of Great Britain.

The African species were treated based on the African Plant Database (http://africanplantdatabase.ch), floras and other literature (e.g., Lobin et al. 1995; Mucina and Hammer 2019).

Taxa from SW and Central Asia and Russia were treated according to relevant literature (e.g., Linczevski 1952; Rechinger and Schiman-Czeika 1974; Bokhari and Edmondson 1982) but also based on the personal knowledge of the first author on taxa from the Caucasus and Middle East.

The accepted species from SE Asia and China are based on literature and the online version of Flora of China (Peng and Kamelin 1996) (http://www.efloras.org).

The taxon concept of American taxa at species level were adopted from the Vascular Plants of the Americas online database (Ulloa Ulloa et al. 2018+) (https://www.tropicos.org/Project/VPA), Flora of North America (Morin 1993) (http://floranorthamerica.org/Plumbaginaceae) and the treatments by Luteyn (1976, 1990).

The majority of the *Statice* species were transferred to *Armeria*, *Limonium* or other Plumbaginaceae genera by Kuntze (1891). His treatment is the main source of nomenclatural information for *Statice* in our database together with other literature.

A total of 198 different literature references or online databases were used as secundum reference or in notes for Plumbaginaceae.

Infrageneric taxa

Below the genus, we included the subgenera and sections of *Limonium* that had been revised in recent studies (e.g., Malekmohammadi et al. 2017a; Koutroumpa et al. 2018). A large group of *Limonium* species forming a well-supported clade were mostly not circumscribed at the sectional level due to the low internal phylogenetic resolution (Koutroumpa et al. 2018) and the difficulty in identifying diagnostic morphological characters that would be required to characterize sections. These species are currently classified under the non-formal "Mediterranean lineage" until further molecular and morphological data will allow their assignment to sections.

Though sections have been also described for *Armeria*, *Acantholimon* and *Goniolimon* (Boissier 1848; Bunge 1872; Linczevski 1952; Sauvage and Vindt 1952), only a small part of their species have been assigned into them. Furthermore, phylogenetic studies have shown that these sections are non-monophyletic (e.g., Fuertes Aguilar and Nieto Feliner 2003 for *Armeria*, and Moharrek et al. 2017 for *Acantholimon*). Therefore, sectional classifications of these genera were not included in the core checklist but were assigned to the "Unplaced generic subdivisions" category. Finally, aggregates, complexes and species groups that represent informal taxonomic units are not included in the checklist, but are mentioned in notes.

When necessary, all references to official herbaria of the type information follow the acronyms in Thiers (2024+).

Phylogenetic analysis

We utilised Koutroumpa et al.'s (2018, 2021) ITS dataset (nrDNA) of the largest Plumbaginaceae phylogeny and added recently generated GenBank sequences for the two *Aegialitis* species to test the sister relationship of Aegialitideae. A Bayesian approach was employed using MrBayes v.3.2.7 (Ronquist et al. 2012), following the methodology described in Koutroumpa et al. (2018). The results from the nrDNA dataset were compare to previous phylogenetic inferences that relied only on chloroplast data for the genus (*rbcL*, *trnL-F* and *matK*; Lledó et al. 2001, 2005a; Koutroumpa et al. 2018, 2021). The new phylogenetic insights regarding the position of *Aegialitis* inform the subfamilial division of Plumbaginaceae.

Results

Taxonomic backbone

The taxonomic backbone, encompassing the taxa in the family and their synonyms as the core checklist, along with the lists of names and taxa not included in the core, is provided in the Suppl. material 1 as a static treatment. This list offers a snapshot reflecting the current state of knowledge. An online version is accessible through the Caryophyllales portal (https://caryophyllales.org). The taxonomic backbone comprises scientific names (both taxonomically accepted names and synonyms), author names standardized according to IPNI (2000+), and standardized nomenclatural citations. The URL of the protologue is provided where available, preferably connecting to the specific page of the protologue (e.g., links available online through the Biodiversity Heritage Library, BHL 2005+), otherwise a link to the entire publication is provided. Additional information, such as distribution area, common names, types, and the source of nomenclatural status, will be available for some taxa in the online portal. Discussion notes provide details on decisions regarding the status of a taxon, classifications into groups or aggregates by certain authors, and additional data like hybrid parents.

The taxonomic backbone is divided into a core part, encompassing all accepted taxa and their synonyms, and lists of names that could not be resolved or are excluded from the core part ("names of verified uncertain application", "unresolved names", "unplaced taxa", "invalid horticultural names and combinations", "excluded designations", "excluded names non Plumbaginaceae" and "unplaced generic subdivisions").

The Plumbaginaceae, as presented here, comprises 3 tribes, 26 accepted genera, 2 subgenera, 17 sections, 2 subsections, 1,179 accepted species, 105 subspecies, 79 varieties, 3 forms and 37 nothotaxa. The core checklist in the taxonomic backbone assigns 2,782 synonyms to accepted names, whereas 30 homotypic synonyms are found in non-core sections. A total of 4,446 scientific name records for Plumbaginaceae are included, incorporating 94 invalid designations and 70 illegitimate names). Table 1 shows the core database statistics including the number of taxa and synonyms assigned to each accepted genus.

Through a review of both old and recent literature, numerous hitherto unresolved names, could be placed. Some names require further revision, notably 45 names mostly from *Statice*. Five *Limonium* names are of verified uncertain application. A separate list contains 46 horticultural designations, including 19 synonyms, identified as *nomina nuda*. Twenty-eight names from the original WFO data set were excluded as they do not belong to the Plumbaginaceae. Most of these names are *Phlox* names from the Polemoniaceae family, relocated to a genus named *Armeria* in that family (with reference to Linnaeus 1737) by Kuntze (1891), with the argument that *Armeria* Willd. was an invalid synonym of *Statice*. The rest belong to other taxa, *Aegialitis* Trin. and *Plumbago esquirolii* H.Lév., members of the Poaceae and Linaceae families, respectively.

New combinations for three *Limonium* names are implemented in the taxonomic novelties section of this paper, together with the new combinations *Limonium* sect. *Jovibarba* and *Dyerophytum socotranum*.

Table 1. Statistics of names in the core Plumbaginaceae database.

Genus	Taxa[1]	Accepted species	Accepted infraspecies[2]	Synonyms[3]	Names total[4]	Generic synonyms
Plumbaginaceae tribe Aegialitideae	*3	2	-	4	*7	1
Aegialitis R.Br.	2	2	-	4	6	1
Plumbaginaceae tribe Limonieae	*1370	1146	182	2699	*4069	**67
Acantholimon Boiss.	357	310	47	313	670	5
Armeria Willd.	186	108	78	879	1065	4
Bakerolimon Lincz.	2	2	-	3	5	-
Bamiania Lincz.	1	1	-	1	2	-
Bukiniczia Lincz.	1	1	-	4	5	1
Cephalorhizum Popov & Korovin	4	4	-	2	6	-
Ceratolimon M.B.Crespo & Lledó	5	3	2	9	14	3
Chaetolimon (Bunge) Lincz.	2	2	-	4	6	1
Dictyolimon Rech.f.	3	3	-	9	12	2
Ghaznianthus Lincz.	1	1	-	1	2	-
Goniolimon Boiss.	28	21	7	118	146	3
Limoniastrum Heist. ex Fabr.	2	2	-	14	16	2
Limoniopsis Lincz.	2	2	-	2	4	-
Limonium Mill.	**737	668	48	1283	**2020	**38
Muellerolimon Lincz.	1	1	-	3	4	-
Myriolimon Lledó, Erben & M.B.Crespo	2	2	-	9	11	4
Neogontscharovia Lincz.	3	3	-	3	6	1
Popoviolimon Lincz.	1	1	-	1	2	-
Psylliostachys (Jaub. & Spach) Nevski	9	9	-	35	44	1
Saharanthus M.B.Crespo & Lledó	1	1	-	4	5	2
Vassilczenkoa Lincz.	1	1	-	2	3	-
Plumbaginaceae tribe Plumbagineae	*40	31	5	79	*119	8
Ceratostigma Bunge	7	7	-	12	19	1
Dyerophytum Kuntze	4	4	-	13	17	1
Plumbagella Spach	3	1	2	2	5	-
Plumbago Tourn. ex L.	22	19	3	52	74	6
Sum: 26 accepted genera	**1413	1179	187	2782	*4195	**76

[1] Including accepted genera, subgenera, sections, subsections, species and infraspecies. [2] Including subspecies, varieties, forms and autonyms. [3] Synonym of species and infraspecies. [4] Excluding generic synonyms. * Including accepted generic names. **Including infrageneric ranks. Seven synonymy names at the family and tribe rank are not included in this table.

Phylogenetic position of *Aegialitis* in the ITS tree

In the ITS Bayesian tree, representatives of *Aegialitis* (Aegialitideae) form a well-supported clade (posterior probability [pp] = 1; Suppl. material 2) sister to the genera of Plumbagineae (Fig. 3; Suppl. material 2). However, the sister relationship between Plumbagineae and Aegialitideae received low support (pp = 0.63; Suppl. material 2). Plumbagineae and Limonieae are reciprocally monophyletic with the highest support (pp = 1; Suppl. material 2).

Discussion

Overall relationships and the division of Plumbaginaceae into three tribes

Molecular phylogenetic studies have shown that Plumbaginaceae are well supported as monophyletic and sister to Polygonaceae (e.g., Lledó et al. 1998; Cuénoud et al. 2002; Yang et al. 2015; Yao et al. 2019; Baker et al. 2022). Several studies provided insights into the phylogenetic relationships within Plumbaginaceae. The main ones include Lledó et al. (1998, 2001, 2005a), Fuertes Aguilar and Nieto Feliner (2003), Akhani et al. (2013), Moharrek et al. (2017), Malekmohammadi et al. (2017a) and Koutroumpa et al. (2018).

The family was divided into two well-supported clades assigned to subfamilies Plumbaginoideae and Limonioideae (= Staticoideae) (Lledó et al. 1998, 2001, 2005a; Malekmohammadi et al. 2017a; Koutroumpa et al. 2018). Plumbaginoideae comprised the tribe Plumbagineae, whereas Limonioideae was further divided into the tribes Limonieae and Aegialitideae, with the monogeneric Aegialitideae (genus *Aegialitis*) sister to the Limonieae clade with high support according to molecular phylogenies employing the chloroplast markers *rbcL*, *trnL-F* and *matK* (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018, 2021). However, in a recent phylogenomic study for the angiosperm tree of life using the 353 nuclear bait set, *Aegialitis* was recovered sister to Plumbagineae clade, comprising *Plumbago* and *Ceratostigma* Bunge, with highest support (Baker et al. 2022). These results challenge the subfamilial classification of *Aegialitis* contradicting previous molecular studies that used two or three chloroplast markers for the genus (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018, 2021). In order to explore whether there is an incongruence between chloroplast and nuclear data or the position of *Aegialitis* was affected by the very limited taxon sampling in Baker et al.'s (2022) phylogenomic study (only 11 genera of Plumbaginaceae), we inferred an ITS phylogeny adding *Aegialitis* to Koutroumpa et al.'s (2018, 2021) dataset of the largest Plumbaginaceae phylogeny. Our results confirmed Baker et al.'s (2022) topology, placing *Aegialitis* sister to the Plumbagineae genera (Fig. 3; Suppl. material 2), yet with low support, showing a conflict between nuclear and chloroplast genomes regarding the placement of *Aegialitis*. These results further indicate that either incomplete lineage sorting or reticulate evolution may have been implicated in the emergence of this lineage. *Aegialitis* was regarded as the "most primitive" and aberrant genus of Plumbaginaceae (Prakash and Lim 1995). It exhibits several autapomorphies, namely fleshy corolla, basifixed anthers, elongated fruit (capsule)

Figure 3. Topological incongruence in the sister relationships of the three tribes in Plumbaginaceae, using Polygonaceae as outgroup **A** plastid cpDNA tree (*rbc*L, *trn*L-F, *mat*K; Lledó et al. 2001, 2005a; Koutroumpa et al. 2018) **B** nrDNA tree, ITS (see Suppl. material 2), and 353 low copy nuclear loci (Baker et al. 2022).

with spongy mesocarp and seed two or three times longer than the calyx (e.g., Kubitzki 1993; Lledó et al. 2001). *Aegialitis* also exhibits intermediate features between the tribes Limonieae and Plumbagineae. Specifically, it has similar vegetative and chemical features to Limonieae (Boissier 1848; Maury 1886; Harborne 1967; Hanson et al. 1994; Lledó et al. 2001), but the same breeding system (‘Plumbago-type’ pollen and monomorphic stigma) and similar anatomical characters to Plumbagineae (Maury 1886; Weber-El Ghobary 1984; Lledó et al. 2001). Taken together, in the present taxonomic treatment, we accept the classification of Plumbaginaceae into three distinct and monophyletic tribes: Aegialitideae, Limonieae and Plumbagineae. We abstain from dividing the family into the two subfamilies Limonioideae and Plumbaginoideae due to the incongruent placement of *Aegialitis* observed in phylogenetic studies. Our decision is also informed by the need for additional investigations including analyses of complete chloroplast and nuclear genomes, coupled with detailed morphological studies.

Intergeneric relationships within Limonieae

Limonieae currently comprises 21 genera, namely *Acantholimon*, *Armeria*, *Bakerolimon* Lincz., *Bamiania* Lincz., *Bukiniczia* Lincz., *Cephalorhizum* Popov & Korovin, *Ceratolimon* M.B.Crespo & Lledó, *Chaetolimon* (Bunge) Lincz., *Dictyolimon* Rech.f., *Ghaznianthus* Lincz., *Goniolimon* Boiss., *Limoniastrum* Fabr., *Limonium*, *Limoniopsis* Lincz., *Myriolimon* Lledó, Erben & M.B.Crespo, *Muellerolimon* Lincz., *Neogontscharovia* Lincz., *Popoviolimon* Lincz., *Psylliostachys* (Jaub. & Spach) Nevski, *Saharanthus* M.B.Crespo & Lledó and *Vassilczenkoa* Lincz. These genera constitute five well-supported subclades in Limonieae: i) *Limonium*, ii) *Ceratolimon-Limoniastrum*, iii) *Armeria-Psylliostachys*, iv) *Bakerolimon-Muellerolimon-Myriolimon-Saharanthus*, and v) *Goniolimon-Acantholimon s.l.* with *Acantholimon s.l.* comprising the small genera *Bamiania*, *Bukiniczia*, *Chaetolimon*, *Cephalorhizum*, *Dictyolimon*, *Gladiolimon*, *Popoviolimon* and *Vassilczenkoa* (Malekmohammadi et al. 2017a; Moharrek et al. 2017; Koutroumpa et al. 2018). The sister relationships between these subclades remained largely unresolved (Koutroumpa et al. 2018). However, in the recent angiosperm phylogeny by Baker et al. (2022), the authors sampled representatives of eight Limonieae genera belonging to four out of the five aforementioned subclades (except iv) and found *Ceratolimon-Limoniastrum* sister to a clade comprising *Goniolimon-Acantholimon s.l.*, *Limonium* and *Psylliostachys-Armeria*, with *Limonium* sister to *Psylliostachys-Armeria* subclade. All these relationships were highly supported, yet further sampling of genera under a phylogenomic approach is essential to draw clear conclusions regarding sister relationships within Limonieae. In addition, three small genera (*Ghaznianthus*, *Limoniopsis* and *Neogontscharovia*) have not been sampled yet in a phylogenetic framework.

Morphological data corroborate some of the inferred sister relationships of the genera within the five subclades. Specifically, *Ceratolimon* and *Limoniastrum* have stamen filaments adnate to the corolla up to the apex of the corolla tube, which is a synapomorphy within Plumbaginaceae (Lledó et al. 2000). *Armeria* and *Psylliostachys* share a unique calyx trait in which the rib-like tissue fuses at the base of the calyx limb and is absent along the calyx tube

(Crespo and Lledó 2000; Lledó et al. 2001). *Muellerolimon* and *Bakerolimon* (Malekmohammadi et al. 2017a; Koutroumpa et al. 2021) share distinctive pollen morphology and shrub habit with articulate, almost leafless stems (Baker 1953), whereas similar stem morphology is present in *Myriolimon* belonging to the same subclade (Lledó et al. 2003; Lledó et al. 2005b). The majority of small genera in Limonieae are found in the *Goniolimon-Acantholimon s.l.* subclade and several of them have been previously segregated from these two genera. The monospecific genus *Ikonnikovia* Lincz., previously segregated from *Goniolimon* by Linczevski (1952), was found nested in *Goniolimon* and synonymised by Koutroumpa et al. (2018) on the basis of molecular and morphological data (i.e., styles free from the base, papillose or hairy in the lower part and capitate stigmata distinguish *Goniolimon* including *Ikonnikovia*, from the rest of Plumbaginaceae; Boissier 1848; Siebert and Voss 1896). The well-supported *Acantholimon s.l.* clade comprise representatives of *Acantholimon s.s.* placed in two subclades with small genera branching in-between them (Moharrek et al. 2017; Koutroumpa et al. 2018). One of the two subclades (clade B sensu Moharrek et al. 2017) is highly supported with the oligospecific genera *Dictyolimon* and *Bukiniczia* forming a monophyletic group sister to *Acantholimon s.s.* species. The other subclade (clade A sensu Moharrek et al. 2017) is not highly supported and consists of the oligospecific genera *Vassilczenkoa*, *Chaetolimon*, *Popoviolimon*, *Cephalorhizum* and *Bamiania*, with the latter three forming a monophyletic group sister to *Acantholimon s.s.* that includes *Gladiolimon* (Moharrek et al. 2017). The sister relationships between the lineages *Vassilczenkoa-Chaetolimon*, *Popoviolimon-Cephalorhizum-Bamiania* and *Acantholimon s.s.* are not well resolved (Moharrek et al. 2017). Considering the phylogenetic results of Moharrek et al. (2017), Beshko et al. (2019) changed the circumscription of *Acantholimon* for Flora of Uzbekistan to include *Chaetolimon*, *Vassilczenkoa* and *Cephalorhizum*, and provided recombinations for their species under *Acantholimon*. Although a wider circumscription for *Acantholimon* including the smaller genera could avoid naming a non-monophyletic assemblage, the absence of morphological diagnostic characters for *Acantholimon s.l.*, the unresolved relationships between *Acantholimon s.s.* and some of the smaller genera, the non-comprehensive taxon sampling, and the few (two or three) molecular markers used in the phylogenetic studies hinder a formal revision in the circumscription of the genus. Therefore, in this taxonomic backbone, we adopt a more conservative approach by keeping *Bamiania*, *Bukiniczia*, *Chaetolimon*, *Cephalorhizum*, *Dictyolimon*, *Popoviolimon* and *Vassilczenkoa* separate from *Acantholimon* pending further molecular data and a detailed morphological analysis. However, we merge the previously segregated monospecific genus *Gladiolimon* following Rechinger and Schiman-Czeika (1974) back into *Acantholimon* as it is found nested into *Acantholimon s.s.*, at a shallow phylogenetic node, in a well-supported clade sister to two species of *Acantholimon* sect. *Acmostegia* Bunge, with which it shares the morphological traits that were used for its segregation (Moharrek et al. 2017). Finally, in the *Limonium* clade of Limonieae, *Afrolimon* Lincz. and *Eremolimon* Lincz., two genera previously separated from *Limonium*, were found nested in the genus (Lledó et al. 2005a; Akhani et al. 2013; Malekmohammadi et al. 2017a) and were formally synonymised by Malekmohammadi et al. (2017a), and Akhani et al. (2013), respectively.

Infrageneric relationships and genus concepts within Limonieae

The accepted name or synonym status and number of genera in Limonieae varied in different studies. Kubitzki (1993) accepted 22 genera in Limonieae including *Acantholimon*, *Armeria*, *Bakerolimon*, *Bamiania*, *Bukiniczia*, *Chaetolimon*, *Cephalorhizum*, *Dictyolimon*, *Ghaznianthus*, *Gladiolimon*, *Goniolimon*, *Ikonnikovia*, *Limoniastrum*, *Limoniopsis*, *Limonium*, *Muellerolimon*, *Neogontscharovia*, *Popoviolimon*, *Psylliostachys*, *Vassilczenkoa*, as well as *Afrolimon* and *Eremolimon*. The three genera *Ceratolimon*, *Myriolimon* and *Saharanthus* were described after the publication of Kubitzki (1993). *Ceratolimon* and *Saharanthus* were described by Crespo and Lledó (2000) based on phylogenetic results of Lledó et al. (2000). Lledó et al. (2005b) proposed the new name *Myriolimon* to replace their illegitimate *Myriolepis* (Boiss.) Lledó, Erben & M.B.Crespo, a combination that they had published before (Lledó et al. 2003), but that was considered homonymous with the earlier *Myrialepis* Becc. (Arecaceae) by the Committee for Spermatophyta and thus ratified at the XVII International Botanical Congress held in Vienna in July 2005 (Brummitt 2005). Molecular support for separation of *Myriolimon* was argued by Lledó et al. (2005a).

Hernández-Ledesma et al. (2015) accepted 24 genera in this tribe including the genera accepted by Kubitzki (1993) and the three described genera at that time, whereas *Eremolimon* was considered nested in *Limonium*. The 21 accepted genera in the current taxonomic backbone differ from Kubitzki (1993) with *Ikonnikovia* and *Afrolimon* being synonyms of *Goniolimon* (Koutroumpa et al. 2018) and *Limonium* (Malekmohammadi et al. 2017a), respectively. *Gladiolimon* is merged here in *Acantholimon* following Rechinger and Schiman-Czeika (1974) and the latest phylogenetic studies (Moharrek et al. 2017; Koutroumpa et al. 2018). Genera that are well supported as monophyletic are *Armeria* (e.g., Lledó et al. 1998, 2005a; Moharrek et al. 2017; Koutroumpa et al. 2018), *Ceratolimon* (e.g., Lledó et al. 2000, 2005a; Koutroumpa et al. 2018), *Dictyolimon* (Moharrek et al. 2017), *Goniolimon* (e.g., Moharrek et al. 2017; Koutroumpa et al. 2018), *Limoniastrum* (e.g., Lledó et al. 2000, 2005a; Koutroumpa et al. 2018), *Limonium* (e.g., Lledó et al. 2005a; Malekmohammadi et al. 2017a; Koutroumpa et al. 2018), *Myriolimon* (Malekmohammadi et al. 2017a) and *Psylliostachys* (Moharrek et al. 2017; Koutroumpa et al. 2018), *Acantholimon* is non-monophyletic (e.g., Moharrek et al. 2014, 2017; Koutroumpa et al. 2018). Monophyly has not been tested yet for *Bakerolimon*, *Cephalorhizum* and *Chaetolimon* as only one species per genus is sampled in available phylogenetic studies (e.g., Moharrek et al. 2017; Koutroumpa et al. 2018). *Limoniopsis*, *Ghaznianthus* and *Neogontscharovia* have not been sampled yet phylogenetically, and *Bamiania*, *Bukiniczia*, *Muellerolimon*, *Popoviolimon*, *Saharanthus* and *Vassilczenkoa* are monospecific genera. Below we discuss the infrageneric classifications and give some examples of recent studies on species delimitation within the large genera of Limonieae.

Acantholimon

It is the second largest genus in Plumbaginaceae and is highly diverse in the Irano-Turanian area. Fifteen sections were recognized by Rechinger and Schiman-Czeika (1974) based on morphological characteristics such as scape length and leaf and flower morphology (Rechinger and Schiman-Czeika 1974; Moharrek et al. 2017) and most of them were not monophyletic in the molecular phylogenetic trees (Moharrek et al. 2017; Koutroumpa et al. 2018). *Acantholimon* species and its related genera form a well-supported clade that is divided into two main subclades without recognized morphological synapomorphic characters (Moharrek et al. 2017; Koutroumpa et al. 2018). The moderately supported subclade A (sensu Moharrek et al. 2017) includes species from two large sections *Acantholimon* and *Armeriopsis* Boiss. as well as species from the small genera *Bamiania*, *Chaetolimon*, *Cephalorhizum*, *Popoviolimon* and *Vassilzenkoa*. The well-supported subclade B (sensu Moharrek et al. 2017) comprises species from *Acantholimon* sections *Acantholimon* and *Armeriopsis*, along with representatives from 12 other sections and *Gladiolimon speciosissimum* (Aitch. & Hemsl.) Mobayen that is deeply nested in this clade and therefore merged in *Acantholimon* as mentioned above. In subclade B, sister to *Acantholimon s.s.* are the small genera *Dictyolimon* and *Bukiniczia*. The monotypic section *Bromeliopsis* Rech.f. & Schiman-Czeika is missing from the phylogenetic sampling. The phylogenetic trees constructed from sampling of 197 individuals corresponding to a large part of the species of *Acantholimon* by Moharrek et al. (2017) only confirmed monophyly of sections *Platystegia* Rech.f. & Schiman-Czeika and *Pterostegia* Bunge, each with two species that appear in highly supported internal clades within subclade B. All other sections were non-monophyletic or their monophyly could not be tested, since only a single representative per section was sampled.

Regarding species monophyly in *Acantholimon*, 38 out of 121 species in the phylogeny were represented by multiple accessions (Moharrek et al. 2017), so that their monophyly could be tested. Seventeen of them were recovered as monophyletic, 16 were placed in polytomies with representatives of other species, and five species were non-monophyletic (Moharrek et al. 2017). Highly supported non-monophyly was found in only *Acantholimon festucaceum* (Jaub. & Spach) Boiss. The authors did not present a corresponding matrix of morphological characters to further test species limits and to check for proper identification and application of names. However, their results show that species delimitations within this genus need a much more comprehensive taxon and character sampling to resolve evolutionary relationships at species level. In the absence of comprehensive phylogenetic studies at species level, we followed the morphology-based taxon concepts available through regional floras (e.g., Rechinger and Schiman-Czeika 1974, Flora Iranica; and Bokhari and Edmondson 1982, Flora of Turkey) and monographs (Mobayen 1964; Bunge 1872) as secundum references for the species of *Acantholimon*. The sectional classification within *Acantholimon* is not applied in this taxonomic backbone, as the sections mostly do not represent monophyletic entities. The expanded *Acantholimon* including *Gladiolimon* is consistent as to the variation of morphological characters. All species are pulvinate to densely branched cespitose subshrubs with linear acuminate leaves (Linczevski 1952; Kubitzki 1993). An expanded morphological description of *Acantholimon* to include *Gladiolimon* is given in the nomenclature novelty part of this paper.

Armeria

It is a diploid genus (2*n* = 2x = 18) (Nieto Feliner 1990; Tiburtini et al. 2023) with high diversity in the Mediterranean region, especially in the western Mediterranean, and it has been found to be monophyletic in all phylogenetic studies so far (Lledó et al. 1998, 2005a; Fuertes Aguilar and Nieto Feliner 2003; Moharrek et al. 2017; Koutroumpa et al. 2018). The estimated number of species has varied from just a few to about 120 species (Fuertes Aguilar and Nieto Feliner 2003). Bernis (1950) even proposed a single species with many subspecies, varieties and forms in the Iberian Peninsula. There are few comprehensive taxonomic or phylogenetic studies on this genus and most of the studies focused on certain geographic regions, for example the Iberian Peninsula (Bernis 1954; Nieto Feliner 1990). Other investigations addressed assumed species complexes such as *Armeria arenaria* (Pers.) F.Dietr. and allies (Tauleigne-Gomes and Lefèbvre 2005), *A. maritima* Willd. (Lefèbvre and Vekemans 1995), *A. pubigera* Boiss. (Blanco-Dios 2007), or the *Armeria canescens* aggregate, examined by Scassellati et al. (2013) with morphometrics. Hybridization, introgression, and reticulate evolution have been frequently considered as the major reason of complex and gradual morphological variation in *Armeria* (Bernis 1954, 1957; Pinto da Silva 1972; Nieto Feliner 1990, 1997; Nieto Feliner et al. 2001; Tauleigne-Gomes and Lefèbvre 2005, 2008; Villa-Machío et al. 2023) that resulted in describing artificial taxa and ecotypes and there are often conflicting views on which taxa to accept (Fuertes Aguilar and Nieto Feliner 2003; Tiburtini et al. 2023). From an evolutionary point of view, *Armeria* stands out as one of the groups of angiosperms with frequent homoploid hybrid speciation (Tauleigne-Gomes and Lefèbvre 2008; Nieto Feliner et al. 2017).

Fuertes Aguilar and Nieto Feliner (2003) generated an ITS data set of 133 accessions from 71 species, covering most of the geographical distribution of the genus *Armeria*. They found nine clades comprising species from mostly specific geographical areas, among others a southern Iberian Sierra Nevada clade, a Sardinia-Corsica clade, and a West-Mediterranean clade including the highest number of species among all these clades. In contrast, the *A. maritima-A. alpina* clade was found to unite plants from the European mountains, temperate to subarctic coastal areas in the northern hemisphere as well as the Mediterranean climate regions of California and Chile. Unlike the other clades that are not linked to hitherto recognized entities, all members of this *A. maritima-A. alpina* clade sensu Fuertes Aguilar and Nieto Feliner (2003) belong to the *A. maritima* and *A. alpina* species complexes (Lawrence 1940; Moore and Yates 1974; Lefèbvre and Vekemans 1995; Tauleigne-Gomes and Lefèbvre 2005, 2008). Based on morphological similarities, *A. alpina* was even considered a synonym of *A. maritima* by different authors (Bernis 1954; Pinto da Silva 1972). Through the consistent presence of additive polymorphic sites in certain taxa, Fuertes Aguilar and Nieto Feliner (2003) concluded that ancient hybridization events as earlier suggested (Nieto Feliner 1997; Fuertes Aguilar et al. 1999a, 1999b) indeed played a major role in the evolution of the genus. However, the ITS trees remained largely unresolved within these nine clades. Two sections have been described in this genus, *A.* sect. *Macrocentron* Boiss. with three subsections (*Astegiae* Boiss., *Microstegiae* Boiss. and *Macrostegiae* Boiss.) and *A.* sect. *Plagiobasis* Boiss. with two subsections (*Holotricae* Boiss. and *Pleurotrichae* Boiss.) (Boissier 1848), but none of them were monophyletic in the phylogenetic trees (Fuertes Aguilar et al. 1999a, 1999b; Fuertes Aguilar and Nieto Feliner 2003).

Recently, Tiburtini et al. (2023) employed an integrative taxonomic approach on the species of *Armeria* in Sardinia and Corsica and recognized five well-delimited, monophyletic and also geographically distinct endemic species on the basis of molecular phylogenetic trees, chromosome data and morphology. Based on their results, the authors for example suggested merging *A. multiceps* Wallr. and its subspecies into *A. leucocephala* Salzm. ex W.D.J.Koch, and disregarding recognition of the subspecies described in *A. leucocephala* and *A. sardoa* Spreng. This research demonstrates a significant taxonomic knowledge turnover (from 11 taxa formerly described for the islands only five could be upheld with altered circumscription) and underscores the value of detailed analyses of species limits using phylogenetic methods.

In our taxonomic backbone we build upon the published morphological or phylogenetic results and also regional Flora treatments that often offer insights from comprehensive investigations of specimens (e.g., Nieto Feliner 1987, *Armeria* in the Iberian Peninsula, and Pinto da Silva 1972, Flora Europaea; Tiburtini et al. 2023) as secundum references for the species of *Armeria* whereas the sectional classification is not applied here.

Goniolimon

This genus has been explored in the context of phylogenetic studies dedicated to other genera (Lledó et al. 2005a; Koutroumpa et al. 2018), confirming its monophyly with *Ikonnikovia* nested within it (Koutroumpa et al. 2018). Despite the extensive geographical distribution of this genus, ranging from North Africa (Algeria) and southeastern Europe to Mongolia and China, few studies on species limits have been undertaken. Recent research addressed *G. tataricum* (L.) Boiss. and allies in southeastern Europe (i.e., in Serbia: Buzurović et al. 2013 and in Croatia: Buzurović et al. 2016), and *G. speciosum* (L.) Boiss. of the Asian steppe (Volkova et al. 2017). In the latter phylogenetic study, monophyly of *G. speciosum* was either not resolved (ITS tree) or not supported (cpDNA tree). Buzurović et al. (2020) reconstructed a phylogenetic tree for seven species of this genus in the Balkans and Apennines using plastid loci and sampling multiple individuals per species. The resulting phylogenetic tree revealed two major unsupported clades with few well-supported subclades. Notably, three of these subclades included individuals from more than one species (sub-clades 2, 4, and 5 sensu Buzurović et al. 2020). Using morphological and phylogenetic data, Buzurović et al. (2020) presented a novel taxonomic classification for three closely related species: *G. italicum* Tammaro, Pignatti & G.Frizzi, *G. tataricum* and *G. dalmaticum* Rchb.f. that had been frequently confused with *G. tataricum* in Croatia. Buzurović et al. (2020) included *G. italicum* within *G. tataricum* and delineated four subspecies within *G. tataricum*. The relationships of *G. besserianum* (Schult.) Kusn. and *G. incanum* (L.) Hepper remained unclear due to lack of morphological data and statistical support in the presented phylogenetic trees.

Considering the non-monophyletic status of three out of the seven species studied by Buzurović et al. (2020) within a relatively small area in comparison to the extensive distribution range of *Goniolimon*, further investigations aiming at defining species boundaries within this genus appear necessary.

Although two sections and two subsections have been described for *Goniolimon* (Linczevski 1952), they only encompass a fraction of the currently recognized species. Also, due to the limited taxon sampling in existing phylogenetic studies, proposed infrageneric division cannot be adequately tested. Therefore, the sectional classification is not applied in this study. Here, we use the morphology-based treatments in Floras (e.g., Linczevski 1952) as well as the protologues from newly described species based on morphological (Buzurović et al. 2016) or molecular and morphological evidence (Buzurović et al. 2020) as secundum references.

Limonium

It is the largest and most diverse genus of the family Plumbaginaceae distributed worldwide (Kubitzki 1993) with c. 70% of its species being endemic in the Mediterranean area (Koutroumpa et al. 2018). The monophyly of *Limonium* is confirmed by multiple molecular phylogenetic studies (Lledó et al. 1998, 2005a; Malekmohammadi et al. 2017a; Koutroumpa et al. 2018). *Limonium* contains two well-supported monophyletic subgenera *L.* subg. *Limonium* and *L.* subg. *Pterocladus* (Spach) H.Arnaud (Lledó et al. 2005a; Malekmohammadi et al. 2017a; Koutroumpa et al. 2018). Twenty-five species are here classified under *L.* subg. *Pterocladus* and the rest are assigned to *Limonium* subg. *Limonium*.

Boissier (1848) provided the first infrageneric treatment for *Limonium* (under *Statice*) recognizing 13 sections and 10 subsections, which were mostly transferred to *Limonium* by Sauvage and Vindt (1952). Since Boissier (1848), some of the subsections were raised to sectional rank (e.g., *Statice* sect. *Limonium* subsect. *Sarcophyllae* raised to *L.* sect. *Sarcophylla* by Linczevski 1952), several new sections were described (e.g., *L.* sect. *Limoniodendron* Sventenius (1960), *L.* sect. *Nephrophyllum* Rech.f. by Rechinger and Schiman-Czeika 1974), whereas some of Boissier's sections were segregated from *Limonium* as independent genera (namely *Dictyolimon* by Rechinger and Schiman-Czeika (1974), *Psylliostachys* by Nevski (1937) and *Myriolimon* by Lledó et al. (2003, 2005b)). Sectional classification has been updated recently following molecular phylogenetic studies (Malekmohammadi et al. 2017a; Koutroumpa et al. 2018). The new *Limonium* sect. *Iranolimon* M.Malekm., Akhani & Borsch was described by Malekmohammadi et al. (2017a) to accommodate species of an Irano-Turanian subclade previously classified under *L.* sect. *Sarcophylla* (Boiss.) Lincz. The latter section was originally described based on the woody habit of its species, which turned out to have convergently evolved in two unrelated lineages (Malekmohammadi et al. 2017a). Also, the new *Limonium* sect. *Circinaria* (Boiss.) M.Malekm. was validated to include species previously assigned to *Afrolimon* that were found nested within *Limonium* (Lledó et al. 2005a; Malekmohammadi et al. 2017a). Koutroumpa et al. (2018) described the new monospecific section *L.* sect. *Tenuiramosa* Koutr. (*L. anthericoides* (Schltr.) R.A.Dyer) which is sister to *L.* sect. *Pterocladus* (Spach) Bokhari and both constitute *L.* subg. *Pterocladus*. Furthermore, Koutroumpa et al. (2018) amended *L.* sect. *Limonium*, *L.* sect. *Nephrophyllum* and *L.* sect. *Sarcophylla*, and published new combinations for *L.* sect. *Pruinosa* (Batt.) Koutr. and *L.* sect. *Pterocladus* subsect. *Nobilia* (Boiss.) Koutr.

The extensive sampling of Mediterranean endemics of *Limonium* in Koutroumpa et al.'s (2018) study of Plumbaginaceae revealed that they all belong to a large, well-supported internal clade, namely the "Mediterranean lineage". Nevertheless, species relationships within the lineage remained largely unresolved. Only few species of the "Mediterranean lineage" were assigned to four morphologically well-defined sections (i.e., *L.* sect. *Polyathrion* (Boiss.) Sauvage & Vindt, *L.* sect. *Pruinosa*, *L.* sect. *Siphonantha* (Boiss.) Sauvage & Vindt and *L.* sect. *Schizhymenium* (Boiss.) Sauvage & Vindt), two of which were represented by multiple species in the phylogeny and recovered as monophyletic (Koutroumpa et al. 2018). A sectional classification for the remaining species within this lineage at the moment is difficult. Species of this lineage have diversified very recently (mostly during the Pleistocene; Lledó et al. 2005a; Koutroumpa et al. 2021) and to resolve their phylogenetic relationships, many molecular characters will be required. In addition, combined effects of polyploidy, apomixis and hybridization may have blurred species limits and make the identification of diagnostic morphological characters a difficult task. Therefore, all these species are provisionally assigned to the phylogenetically well-defined “Mediterranean lineage”. Apart from causing taxonomic complexity, polyploidy, apomixis and hybridization have been considered as the main factors for promoting speciation of *Limonium* in the Mediterranean region (Ingrouille 1984; Kubitzki 1993; Palacios et al. 2000; Lledó et al. 2005a). Indeed, Koutroumpa et al. (2021) found a significant shift in diversification rates for the “Mediterranean lineage” and showed that the turbulent geological history and climatic oscillations in the Mediterranean, combined with the significant role of apomixis triggered species radiation in *Limonium*.

We follow the mentioned recent advances in the infrageneric classification of *Limonium* and assign taxa to major clades corresponding to the two subgenera, and further classify them to one of the 17 accepted sections and two subsections or the “Mediterranean lineage”. We achieved this by combining information from the latest phylogenetic analyses (Malekmohammadi et al. 2017a; Koutroumpa et al. 2018) with other data (e.g., morphology, chromosome counts, geographic distributions) obtained from an extensive literature search for *Limonium* taxa that were not yet sampled in a phylogenetic framework (see for example table S3 in Koutroumpa et al. 2018). As a result, we can summarize *Limonium* subg. *Pterocladus* to comprise *L.* sect. *Tenuiramosa* (one species) and *L.* sect. *Pterocladus* (24 species) that is further divided into *L.* subsect. *Nobilia* (18 species) and *L.* subsect. *Odontolepidea* (six species) (Fig. 4). *Limonium* subg. *Limonium* is divided into three distinct well-supported clades (B1, B2 and B3 sensu Koutroumpa et al. 2018; Fig. 4), with *L.* sect. *Limoniodendron* (one species; clade B1) being sister to a clade comprising mostly non-Mediterranean taxa (clade B2) and the “Mediterranean lineage” (clade B3). Clade B2 includes ten morphologically and phylogenetically well-defined sections (Fig. 4), namely *L.* sect. *Circinaria* (eight species), *L.* sect. *Ctenostachys* (Boiss.) Sauvage & Vindt (11 species), *L.* sect. *Iranolimon* (nine species), *L.* sect. *Jovibarba* (Boiss.) M.Malekm. & Koutr. (three species), *L.* sect. *Limonium* (25 species), *L.* sect. *Nephrophyllum* (16 species), *L.* sect. *Plathymenium* (Boiss.) Lincz. (28 species), *L.* sect. *Sarcophylla* (12 species), *L.* sect. *Siphonocalyx* Lincz. (12 species) and *L.* sect. *Sphaerostachys* (Boiss.) Bokhari (four species). The “Mediterranean lineage” (clade B3) comprise four small sections (Fig. 4) *L.* sect. *Polyarthrion* (four species), *L.* sect. *Pruinosa* (six species), *L.* sect. *Schizhymenium* (two species) and *L.* sect. *Siphonantha* (four species), whereas 479 species are assigned to this lineage but not classified further into sections or subsections due to the reasons explained above.

Only a few studies explore species limits and relationships in *Limonium* at shallow phylogenetic levels. A recent example is the phylogenomic investigation by Pina-Martins et al. (2023) on seven representatives of *Limonium* sect. *Limonium*. The authors sampled multiple individuals per species and analyzed

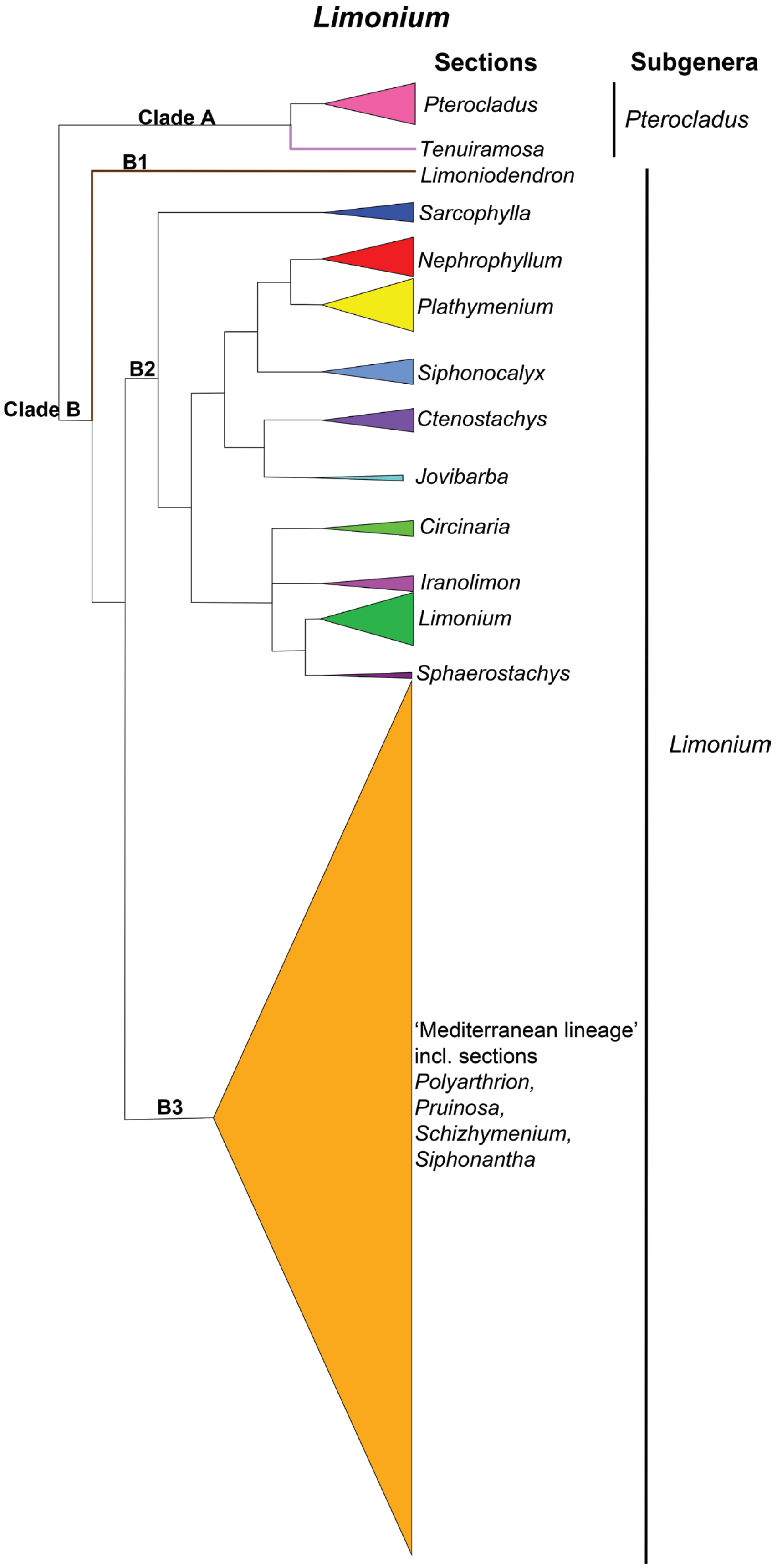

Figure 4. Phylogenetic relationships of the major clades in *Limonium* and the corresponding infrageneric units, following Koutroumpa et al. (2018). The size of triangles is proportional to the number of species assigned to the different sections and the "Mediterranean lineage".

more than 10,000 SNPs obtained from genotyping by sequencing (GBS). The large amount of molecular data employed in the study could resolve species relationships that were previously mostly unresolved when only few molecular markers were used (see e.g., Malekmohammadi et al. 2017a, 2017b; Koutroumpa et al. 2018). Pina-Martins et al.'s (2023) phylogeny recovered *L. brasiliense* (Boiss.) Kuntze, *L. californicum* (Boiss.) A.Heller, *L. carolinianum* (Walter) Britton, *L. humile* Mill. and *L. narbonense* Mill. as monophyletic with high support. The widespread *L. vulgare* Mill. formed a large, well-supported clade with *L. maritimum* Caperta, Cortinhas, A.P.Paes, Guara, Esp.Santo & Erben nested in it. *Limonium maritimum*, represented by a single population although it is widely distributed along the Portuguese coast (Cortinhas et al. 2015), differed from *L. vulgare* only by 34 out of 10,000 SNPs. Moreover, the populations of *L. vulgare* across its distributional range showed high genetic structure based on the phylogenetic and clustering analyses (Pina-Martins et al. 2023). *Limonium maritimum* was described as separate species based on morphometric data, in which few diagnostic traits had slightly smaller yet largely overlapping size ranges compared to the closely related *L. vulgare* (Cortinhas et al. 2015). Taken together, the nested phylogenetic position of *L. maritimum* within *L. vulgare* and the low genetic and morphometric differentiation of *L. maritimum* compared to *L. vulgare*, question the recognition of the former as a separate species. Therefore, we consider *L. maritimum* as a synonym of *L. vulgare*.

Iamonico et al. (2022) examined species boundaries in four endemic species along the Tyrrhenian coast and Ponziane Archipelago (central Italy) combining molecular and morphometric data. They analyzed ITS sequences and found the same ribotype in all populations of the four species, except for two populations displaying individuals with dual ribotypes. This suggests a possible hybrid origin, though not addressed in the study. Morphometric analyses revealed that individuals from the two populations with dual ITS ribotypes were differentiated in morphospace, and at species level, *L. pandatariae* Pignatti was distinguished from *L. circaei* Pignatti, while *L. amynclaeum* Pignatti and *L. pontium* Pignatti occupied a central position relative to the other species, with considerable overlap among individuals. The authors proposed merging all species under *L. pontium* and recognizing the populations with mixed ITS genotypes as two different subspecies. However, considering the potential hybrid nature of these populations and the limitations of using a single molecular maker for species resolution within the "Mediterranean lineage" (see e.g., Koutroumpa et al. 2018), we suggest maintaining the four previously recognized species separate until further molecular studies provide clarity. Additionally, we propose synonymizing the newly described *L. pontium* subsp. *terracinense* Iberite, Iamonico, De Castro & Nicolella under *L. amynclaeum*.

We used phylogenetic studies for the circumscription of taxa in *Limonium*, where available (e.g., Akhani et al. 2013; Pina-Martins et al. 2023). As many species are of restricted range, in the absence of such studies it was considered adequate to use morphological circumscriptions from regional floras (e.g., Erben 1993, 2012), regional monographs (e.g., Brullo and Erben 2016, *Limonium* in Greece; Doğan et al. 2020, *Limonium* in Turkey), taxonomic revisions of specific species groups (e.g., Bogdanović and Brullo 2015, *Limonium cancellatum* group), and protologues (Pignatti 1955, 1982) as secundum references for the taxa of *Limonium*.

Intergeneric relationships within Plumbagineae

The tribe Plumbagineae comprises *Ceratostigma*, *Dyerophytum* Kuntze, *Plumbagella* Spach and *Plumbago*. *Ceratostigma* is sister to the rest of the genera (Koutroumpa et al. 2018). *Plumbago* is polyphyletic (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018) with *Plumbago europaea* L., the type species of the genus, sister to the monotypic *Plumbagella* and the tropical/subtropical species of *Plumbago* sister to *Dyerophytum*. All phylogenetic relationships within Plumbagineae are highly supported (Koutroumpa et al. 2018). *Plumbago* and *Plumbagella* are characterised by glandular calyces, a distinct diagnostic feature for the family (Kubitzki 1993). Although *Plumbago* forms a non-monophyletic assemblage, a formal revision of its generic circumscription would require a comprehensive taxon sampling in a phylogenetic framework (currently four out of 19 *Plumbago* species sampled in Koutroumpa et al. 2018) and a revision of the diagnostic characters of the well-supported phylogenetic groups and corresponding genera. Therefore, no changes in generic circumscriptions are advisable for the time being.

Infrageneric relationships and genus concepts within Aegialitideae and Plumbagineae

The Aegialitideae comprise *Aegialitis* which is recovered as monophyletic with high support in our phylogenetic analysis in which we included sequences for its two species *A. annulata* (two accessions) and *A. rotundifolia* (four accessions) that are also recovered as reciprocally monophyletic with high support (Suppl. material 2). In Plumbagineae, highly supported monophyly is inferred for *Ceratostigma* (Koutroumpa et al. 2018; Zhao et al. 2023) and *Dyerophytum* (Koutroumpa et al. 2018). *Plumbago* is non-monophyletic (Lledó et al. 2001, 2005a; Koutroumpa et al. 2018) and *Plumbagella* is a monospecific genus, therefore, monophyly at the genus level cannot be tested.

To our knowledge, very few phylogenetic studies have explored species limits within the genera of Plumbagineae. Zhao et al. (2023) sampled whole plastid genomes of multiple individuals from five *Ceratostigma* species in China in a phylogenomic framework and tested for species limits. The inferred phylogeny resolved the interspecific relationships within *Ceratostigma* with high support in almost all clades and species' monophyly was confirmed for four out of the five species, namely *C. griffithii* C.B.Clarke, *C. plumbaginoides* Bunge, *C. ulicinum* Prain and *C. willmottianum* Stapf. *Ceratostigma minus* Stapf ex Prain was not monophyletic with its individuals found in two distinct clades corresponding to their geographical ranges. Individuals from Hengduan Mountains were sister to *C. plumbaginoides* and *C. willmottianum* and individuals from the Qinghai-Tibet Plateau were sister to *C. griffithii*. The authors attributed the non-monophyletic clustering of *C. minus* to genetic divergence promoted by geographical barriers in the two mountainous regions but they did not exclude a potential impact of hybridization and introgression to the observed topology. They also highlighted the necessity of comparing chloroplast genome phylogenies with those from nuclear genomes to further understand the evolutionary relationships between and within species.

Graham (2014) investigated the systematics of *Dyerophytum* using morphometric and molecular data (ITS and two cpDNA regions). She found *D. africanum*

(Lam.) Kuntze highly supported as monophyletic and sister to a clade comprising *D. indicum* (Gibbs ex Wight) Kuntze, which was monophyletic in the ITS tree, *D. pendulum* (Balf.f.) Kuntze, and *D. socotranum*. The latter taxon was originally described as a variety of *D. indicum* (under the former generic name *Vogelia* Lam., i.e., *Vogelia indica* var. *socotrana* Balf.f.), but it was later unofficially raised to species level by J.R. Edmondson. This taxon was monophyletic in the ITS tree but formed a polytomy with *D. pendulum* in the cpDNA tree. In the morphometric analysis, individuals of all four *Dyerophytum* taxa were largely distinct. Consequently, we uphold all four taxa at the species level in this study and formally propose the new combination and status for *Dyerophytum socotranum* (see Taxonomic and nomenclatural novelties).

For Plumbagineae and Aegialitideae, we follow floras and e-floras (e.g., Peng and Kamelin 1996, Flora of China) in addition to the recent phylogenetic studies (e.g., Zhao et al. 2023) as secundum references.

Taxonomic history and nomenclature of *Statice* L. nom. rej.

Our current understanding of phylogenetic relationships and generic concept in the tribe Limonieae show that *Armeria* and *Limonium* are two well differentiated entities (e.g., Koutroumpa et al. 2018). However, the classification of these two genera is still historically linked via the name *Statice* and the names have been in part intermingled. Since the whole Plumbaginaceae were approached in this study, we also revisited the “Statice problem” and a few names could be resolved, resulting in three new combinations (see taxonomic and nomenclatural novelties below).

Tournefort (1694) considered *Limonium* and *Statice* as two distinct genera of sea-lavenders and thrifts, respectively. Linnaeus 1737, in his Genera Plantarum) and Species Plantarum (1753), combined them in the single genus *Statice* L. and regarded *Limonium* Tourn. as its synonym. Miller (1754, 1768) used the names *Limonium* Tourn. for sea-lavenders and *Statice* Tourn. for thrifts, based on the pre-Linnaean treatments. Willdenow (1809) separated the thrifts in the genus *Armeria* Willd. and called the sea-lavenders *Statice* L. (p.p.). This caused confusion in the circumscription of the three genera *Armeria*, *Limonium*, and *Statice* because following Willdenow’s publication, the names *Armeria* and *Statice* were both applied to the thrifts by different authors (Lawrence 1940) that led to the rejection of the name *Statice* as a *nomen ambiguum*. The name *Armeria* was conserved for the thrifts and *Limonium* for sea-lavenders in the International Botanical Congress of Cambridge 1930, following the report of the Editorial Committee for Nomenclature (see Bricquet 1935).

Rejection of *Statice* in favour of *Armeria* and *Limonium* caused part of the taxonomic and nomenclatural complexities in Plumbaginaceae. Only 18 species of *Statice* were described by Linnaeus (1753, 1762, 1767), 11 of which refer to species of *Limonium* and seven species are now synonyms of accepted species in *Acantholimon*, *Armeria*, *Goniolimon*, *Limoniastrum*, *Myriolimon* and *Psylliostachys*. Many new species were described under *Statice* before its rejection that are currently mostly synonyms of *Limonium* or *Armeria* but *Statice* names are spread over the Plumbaginaceae and can be found in synonymy status under 11 out of 26 genera of the family. This resulted in a multitude of required taxonomic recombination that is continuing even in this study. Kuntze (1891) recombined most of the described *Statice* species to their correct generic name. Despite several other works (Greuter and Raus 1987, 1989; Erben 2012), there are still 31 *Statice* names that have not yet been recombined or their status remains unresolved (classified under "unresolved names" in the database).

The comprehensive treatment in this study, attempting to completely cover *Statice* names, to clarify nomenclatural status and to highlight the still unresolved taxonomic and/or nomenclatural questions will facilitate future investigations.

Classification of closely related and often apomictic species

Besides the accepted taxonomic subdivisions above species rank (e.g., subgenus, section, subsection), several informal terms are used by different authors to categorize species or infraspecies of similar morphology (Tutin et al. 1972; Greuter et al. 1984). These informal classifications mostly reflect the taxonomic complexity of species groups in which biological processes, such as apomixis, polyploidy and hybridization, play an important role in their speciation as demonstrated for example in *Limonium* (Koutroumpa et al. 2021).

Greuter et al. (1984) defined the term "aggregate" as an informal grouping for easily confused and morphologically allied and (probably) closely related species, the so-called "segregate species". The following rule is given for naming aggregates: "an aggregate is designated by the oldest name, in terms of nomenclatural priority, of an included species, but without author citation", yet this is not a formal rule and is not included in the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). In the Flora Europaea (Tutin et al. 1972), the term "group" was used for the same purpose, i.e., to group similar species that are difficult to distinguish. These groups, and not the individual species, were keyed out in the main identification key. A key to the component species within each group was provided along with descriptions for further study and identification. Furthermore, the term "complex" has also been used in literature, especially for *Limonium* and *Armeria* (e.g., Pignatti 1982; Baumbach and Hellwig 2007; Róis et al. 2018), to refer to morphologically related taxa, but its application sometimes lacks a global context.

Aggregates, complexes, and groups have been mostly used for *Limonium* in Plumbaginaceae due to the highly variable nature of its species, with several of them being polyploid and apomictic. These informal subdivisions contain many sexual and apomictic microspecies with narrow geographical distributions. For example, the *Limonium binervosum* aggregate is a complex assemblage of nine species and over 40 infraspecies in the British Isles (Ingrouille and Stace 1986) that are mostly raised to species level by Sell (2018) (e.g., *L. anglicum* (Ingr.) P.D.Sell), whereas Pignatti (1972) considered it as a group with only five species. *Limonium binervosum* (G.E.Sm.) C.E.Salmon is a widespread, apomictic, and variable species (Domina 2011+) but, has not been studied throughout its entire distribution area (Ingrouille and Stace 1986). Further examples of informal subdivisions in *Limonium* include the aggregates adopted by Greuter et al. (1989) to classify several Mediterranean species, the complexes recognized by Brullo and Guarino (2017) to classify species occurring in Italy and the groups adopted by Brullo and Erben (2016) for the Greek taxa.

All aggregates, complexes, and groups in *Limonium* are essentially regional classifications that refer to morphologically similar species and infraspecies in a restricted geographical area without considering the wider distribution of the group. It is therefore unclear which species should belong to a group, complex or aggregate when the range is expanded. In addition, the monophyly of these informal subdivisions in a phylogenetic framework has not yet been explored. Therefore, in our global Plumbaginaceae backbone we refrained from using aggregates, complexes or groups as ranks since they lack nomenclatural and phylogenetic status. A note is given in the database for each taxon that is part of a literature-based aggregate or group. These notes highlight the existing alpha-taxonomic confusion associated with the respective taxa.

Comparison of different online sources

This database encompasses a total of 4,301 scientific names in the family Plumbaginaceae, surpassing the count in other online databases: Tropicos (1991+) assigns 2,067 names to Plumbaginaceae, IPNI (2000+) lists 3,200 names, the World Checklist of Vascular Plants (Govaerts 2023) 3,727 names, and the Catalogue of Life Checklist (COL 2024) contains 3,769 names. The Global Biodiversity Information Facility's (GBIF) backbone largely follows COL (using a 2023 version).

With respect to the taxonomy, the Catalogue of Life (COL 2024), sourced from Hassler (2023) includes two subfamilies, 23 genera, 1,149 species, 100 subspecies, and 30 varieties in the accepted names and 166 names are considered "ambiguous synonyms", of these 158 are unambiguously placed as synonyms in our treatment and four as misapplied names.

Future updates and interaction with the World Flora Online

The database will be updated continuously according to newly published results of taxonomic and phylogenetic studies and published online in the Caryophyllales portal (https://caryophyllales.org). Future versions that significantly differ from this one will be published as further stable and citable versions. Adding further information such as distribution, common names, protologue link, type species, morphological description, species keys, molecular data, photographs or link to the photographs, cytological data, conservation status, etc. is a future goal for the Plumbaginaceae database, with the initial priority set to nomenclatural types, protologue links and geographical distribution.

Following publication, this information will be stored in ChecklistBank (Döring et al. 2022) (https://www.checklistbank.org/) and shared with the WFO Plant List, contributing to the development of the WFO Backbone. Regular updates will be consistently incorporated into WFO to keep the information current.

Taxonomic and nomenclatural novelties

Dyerophytum socotranum **(Balf.f.) J.R.Edm., M.Malekm. & Koutr., comb. et stat. nov.**
urn:lsid:ipni.org:names:77343843-1

≡ *Vogelia indica* var. *socotrana* Balf.f. in Proc. Roy. Soc. Edinburgh 12(113): 406. 1884, basionym. Lectotype (designated here by J.R. Edmondson): Yemen, Socotra, *Balfour 416* (E00068915); isolectotypes: E00068913, E00068914.

Limonium thymoides **(Girard) M.B.Crespo, comb. nov.**
urn:lsid:ipni.org:names:77343844-1

≡ *Statice thymoides* Girard in Mém. Sect. Sci. Acad. Sci. Montpellier 1: 189. 1848, basionym. Lectotype (designated here by M.B. Crespo): Algéria. Alger [Algeria, Algiers], *Durieu* (MPU021644).
= *Statice asparagoides* Coss. & Durieu ex Batt., Fl. Algérie Dicot.: 727. 1890, **syn. nov.**
≡ *Limonium asparagoides* (Coss. & Durieu ex Batt.) Maire in Bull. Soc. His. Nat. Afrique N. 22: 55. 1931, **syn. nov.** Lectotype (designated here by M.B. Crespo): Algeria. Rochers maritimes à Nemours, ouest de Prov. d'Oran, June 1856, [Plantes d'Alger n° 131], *E. Bourgeau* (MPU 007820); isolectotypes: FI 000898, MPU 007818, MPU 007819.

Limonium ×fraternum **(Sennen & Pau) M.B.Crespo, comb. nov.**
urn:lsid:ipni.org:names:77343845-1

≡ *Statice ×fraterna* Sennen & Pau in Bull. Acad. Int. Geogr. Bot. 23: 47. 1913, pro sp., basionym. Lectotype (designated here by M.B. Crespo): Spain. Catalogne, [Lérida], Llano de Urgel au Prado de Monsoa [sic], 1 September 1911, Pl. Espagne n° 1222, *Sennen* (BC 54018); isolectotypes: ABH 42341, BC 54017; DAO 00455905, M, MA, FR, G, JE, RNG, etc.

Notes. This name applies to the hybrid *L. hibericum* × *L. viciosoi*, sec. Erben (1993).

Limonium ×rossmaessleri **(Willk.) M.B.Crespo, stat. nov.**
urn:lsid:ipni.org:names:77343846-1

≡ *Statice insignis* var. *rossmaessleri* Willk. in Linnaea 30: 123. 1859, basionym.
≡ *Limonium insigne* var. *rossmaessleri* (Willk.) Pignatti in Collect. Bot. (Barcelona) 6: 295. 1962. Lectotype (designated here by M.B. Crespo): Spain. "H. M. Willkommii herbar. hispan. *Statice Rossmaessleri* n. sp." [Regno Murcico apud Willkomm], Legit. *Rossmaessler* [Anno] 1853 (COI 00043402).

Notes. This name applies to the hybrid *L. insigne* × *L. caesium*, sec. Erben (1993).

Limonium **sect. *Jovibarba* (Boiss.) M.Malekm. & Koutr., comb. nov.**
urn:lsid:ipni.org:names:77343907-1

≡ *Statice* sect. *Jovibarba* Boiss. in Candolle, Prodr. 12: 665. 1848, basionym. Type: *Limonium jovibarba* (Webb ex Boiss.) Kuntze, Revis. Gen. Pl. 2: 395. 1891.

***Chaetolimon* (Bunge) Lincz. in Trudy Tadzikisk. Bazy 8: 586. 1940.**

Type (designated here by M.Malekmohammadi). *Chaetolimon limbatum* Lincz. in Trudy Tadzikisk. Bazy 8: 595. 1940.

***Acantholimon* Boiss., Diagn. Pl. Orient. ser. 1, 7: 69. 1846, nom. cons.**

= *Gladiolimon* Mobayen, Rev. Taxon. Acanthol.: 296. 1964. Type: *Gladiolimon speciosissimum* (Aitch. & Hemsl.) Mobayen, Rev. Taxon. Acanthol.: 297. 1964

Type. *Acantholimon glumaceum* (Jaub. & Spach) Boiss., Diagn. Pl. Orient. ser. 1, 7: 75. 1846.

Emended diagnosis of *Acantholimon* (including *Gladiolimon*). Laxly or densely branched, often with chalk protuberances, hemispherical or subspherical pulvinate subshrubs, usually forming thorny pincushions. Leaves, alternate, frequently spiny, linear-triangular, subcylindrical or linear, rarely flat and fairly broad, acuminate at apex. Inflorescence simple or branched spike, elongate or short, compact and capitate, paniculate, or subsessile. Spikes with one to numerous flowered spikelets, forming simple or compound panicles. Calyx broadly to narrowly infundibular or tubular, scarious, glabrous or hairy. Corolla longer than the calyx, petals slightly connate at base, white, pink, purple or red. Filaments of stamens distinct except at base, glabrous. Styles distinct from base, glabrous or rarely verrucose. Stigma capitate or oblong-capitate. Ovary narrowly linear-cylindrical or sub-ovoid. Fruit oblong-linear, not enlarged at the top, opening with a small round lid and with valves.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

MM: taxonomic and nomenclatural investigations based on the available literature, herbarium revisions and field studies, as well as data entry. WGB: preparation of the data for the initial imports and checks, nomenclatural issues, transformation of the EDIT Platform's generic output to the document provided in Supplementary Material online, statistics and data quality control. MM, KK, NK and WGB: editorial control of the database. MBC, GD, HA, and KK: taxonomic and nomenclatural revisions of the draft checklist. MM, KK and TB: design of the structure of the manuscript. MM and KK: writing of the manuscript with inputs from TB. SvM provided initial software training for MM and contributed to the database and to an early version of the manuscript. All authors contributed to the text and approved its final version.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Plumbaginaceae taxonomic backbone

Authors: Maryam Malekmohammadi, Konstantina Koutroumpa, Manuel B. Crespo, Gianniantonio Domina, Nadja Korotkova, Hossein Akhani, Sabine von Mering, Thomas Borsch, Walter G. Berendsohn

Data type: pdf

Link: https://doi.org/10.3897/phytokeys.243.122784.suppl1

Supplementary material 2

Phylogenetic relationship of Plumbaginaceae using Polygonaceae outgroups

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Data type: pdf

Explanation note: Phylogenetic relationship of Plumbaginaceae using Polygonaceae outgroups: Bayesian analysis of ITS sequences from Koutroumpa et al. (2018, 2021) with additional Aegialitis sequences from GenBank (highlighted in pink). Tree nodes display posterior probabilities.

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Research Article

Lappula effusa (Boraginaceae), a new species from Xinjiang, China

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Abstract

Lappula effusa D.H.Liu & W.J.Li, a new species of Boraginaceae from Xinjiang, China, is described and illustrated in this study. The new species is morphologically similar to *Lappula himalayensis* and *L. tadshikorum*. However, it can be distinguished from the compared species by several characteristics, such as: stem single, erect, frequently branched at middle and above, densely spreading hispid, hairs discoid at base; corolla white or blue; fruit compressed, heteromorphic nutlets with two rows of marginal glochids, nutlets acute ovoid, disc narrowly ovate-triangular. The diagnosis of the new species is supported with comprehensive investigation including photographs, detailed description, notes on etymology, distribution and habitat, conservation status, as well as comparisons with morphologically similar species.

Key words: Boraginaceae, China, *Lappula*, new taxon, taxonomy

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Introduction

The genus *Lappula* Moench, belonging to the Boraginaceae family within the Rochelieae tribe, encompasses approximately with 50–70 species (Ovczinnikova 2005; Weigend et al. 2016). These species are predominantly distributed in Eurasia, North Africa, North and South America and Australia, with the centre of species diversity lying in Central Asia (Wang 1981; Ovczinnikova 2005, 2021; Huang et al. 2013). *Lappula* is characterised by prickly cauline leaves, blue/white corollas that each bear five throat appendages, a subulate gynobase, nutlets four, homomorphic or heteromorphic and nutlets with either one/more rows of marginal glochids or marginal wings tipped with anchor-like spines (Popov 1953; Riedl 1967; Zhu et al. 1995; Huang et al. 2013; Weigend et al. 2016; Khoshsokhan-Mozaffar et al. 2018).

Initially, *Lappula* had been treated as a member of *Myosotis* L. (Linnaeus 1753), with Moench (1794) later distinguishing and circumscribing *Lappula* as a separate genus. In the taxonomy of *Lappula* originating from Candolle (1846), there were 38 species in the *Prodromus* and these species were classified into three sections, based on the morphology of nutlets. In the Flora USSR, Popov

(1953) identified 39 species and improved the infrageneric classification of *Lappula* by introducing two sections and 14 series. Ovczinnikova (2005) recognised 70 species and proposed an updated infrageneric classification of *Lappula*, based on corolla, nutlets and gynobase morphology. She classified the 70 species into eight sections and 14 series. Recent molecular phylogenetic studies showed that *Lappula* was polyphyletic and some species were transferred to the *Rochelia* and *Pseudolappula* (Huang et al. 2013; Khoshsokhan-Mozaffar et al. 2018; Liu et al. 2021). In China, the genus *Lappula* had 31–36 species and was highly diversified in north-western China, especially in Xinjiang Province (Wang 1981; Zhu et al. 1995).

During field investigations in Xinjiang Province, China, an unknown population of *Lappula* was discovered in Balikun County. It appeared to be similar to *L. himalayensis* Ching J.Wang and *L. tadshikorum* Popov in general habit and fruit morphology. However, the unknown population showed great differences in an array of characters: stem single, frequently branched at middle and above, spreading; style surpassing the fruit by ca. 0.5 mm, fruit compressed, nutlets acute ovoid and disc narrowly ovate-triangular (Figs 1, 3). After conducting a comprehensive review of relevant literature (Gürke 1894; Brand 1931; Popov 1953; Vvedensky 1961; Sharashova 1962; Goloskokov 1964; Riedl 1967; Chukavina 1984; Nasir 1989; Zhu et al. 1995; Ovczinnikova 2009) and examining specimens of *Lappula* from the Herbaria of Royal Botanic Garden Edinburgh (E), Muséum National d'Histoire Naturelle (P), Komarov Botanical Institute of RAS (LE), Moscow University (MW), Central Siberian Botanical Garden SB RAS (NS), Institute of Botany, Chinese Academy of Sciences (PE), North-western Institute of Botany (WUK), Northwest Institute of Plateau Biology, Chinese Academy of Sciences (HNWP), National Herbarium of Uzbekistan (TASH) and Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences (XJBI), we concluded that it did not match morphologically with any known species of *Lappula*. Based on these distinctive morphological features, we confirmed that it was a new species, which we describe and illustrate here as *Lappula effusa* D.H.Liu & W.J.Li.

Materials and methods

The voucher specimens of the new species in this study were collected during our field expedition to Xinjiang Province in 2023. Photographs were captured using a Nikon Z7 II digital camera (Tokyo, Japan), while morphological observations and measurements were conducted on living plants in the field and herbarium specimens deposited at XJBI. For morphological comparison, we critically examined available digitised specimens of *Lappula* stored in the E (https://data.rbge.org.uk/search/ herbarium/), LE (https://plant.depo.msu.ru/), MW (https://en.herbariumle.ru/), NS (http://herb.csbg.nsc.ru:8081/) and P (https://science.mnhn.fr/institution/mnhn/collection/p/item/search), as well as physical herbarium specimens deposited at PE, HNWP, TASH, WUK and XJBI. Additionally, we compared the morphological characteristics of the new species with those of similar species, relying on online or physical specimens. The conservation status was assessed following the IUCN guidelines (IUCN 2022). In this study, we employed the morphological species concept (Davis and Heywood 1963; Mallet 1995), which defines species solely by their morphological differences.

Results

Taxonomy

Lappula effusa **D.H.Liu & W.J.Li, sp. nov.**
urn:lsid:ipni.org:names77343947-1
Figs 1–3

Diagnosis. The new species is morphologically similar to *Lappula himalayensis* and *L. tadshikorum*, but differs from the *L. himalayensis* primarily in the following characteristics: stem single (vs. stems 4–6, cespitose), erect (vs. ascending or erect), frequently branched at middle and above (vs. branched above), densely spreading hispid, hairs discoid at base (vs. densely appressed pubescent); corolla white or blue (vs. blue); fruit compressed (vs. fruit globose), nutlets acute ovoid, ca. 2.5 mm long, 1 mm wide, 0.5 mm thickness (vs. ovoid, ca. 2.5 mm long, 1.5 mm wide, 1 mm thickness), the inner glochids erect (vs. often curved), disc narrowly ovate-triangular (vs. ovoid) (Figs 2, 3). Furthermore, compared to the *L. tadshikorum*, the new species is 12–28 cm tall (vs. 30–50 cm tall), stem single (vs. stems 2–3), densely spreading hair (vs. appressed or semi-appressed hair), fruit compressed (vs. fruit globose-ovoid), nutlets acute ovoid, 0.5 mm thickness (vs. ovoid, 1 mm thickness), disc narrowly ovate-triangular (vs. oblong or ovate), inner glochids erect, ca. 0.5 mm long (vs. curved, 1–1.2 mm long), style surpassing nutlets and glochids (vs. style slightly surpassing nutlets, but not surpassing glochids) (Figs 2, 3).

Type. China. Xinjiang: Balikun County, Dahongliuxia Village, growing on the gravel desert, 44°47'26.17N, 91°30'9.55E, alt. 842 m, 18 June 2023, *D.H.Liu, Y.X.Zhou, S.J.Shang et al. 2023EH908* (holotype: XJBI00135936!).

Description. Annual herbs. ***Stems*** erect, single, frequently branched at middle and above, 12–28 cm tall, with spreading white hispid, hairs discoid at base (Fig. 3I). ***Basal leaves*** forming a rosette; leaf blade spatulate, 1.5–2.5 cm long, 2–4 mm wide, densely spreading white hirsute, hairs discoid at base; withered in fruit; ***Stem leaves*** linear-lanceolate, 1–2 cm long, 2–4 mm wide, abaxially densely spreading white hispid, adaxially sparsely hispid or glabrous, hairs discoid at base. ***Inflorescences*** elongated to 5–10 cm long in fruit, with oval bracts near 3–5 mm long, 1.5–2.5 mm wide. ***Pedicels*** short, ca. 1 mm long in flowering and elongated from 2.5–3 mm long in fruit. ***Calyx*** lobes oblong, ca. 1.5 mm long, 1 mm wide, slightly elongated ca. 2 mm long in fruit, spread, abaxially densely spreading hispid, adaxially sparsely hispid or glabrous. ***Corolla*** blue and white (plants with either all blue or all white corollas), campanulate, corolla tube ca. 1.5 mm long; limb as long as tube, ca. 1.5 mm wide, lobes obtuse; throat appendages white or light yellow, trapeziform, ca. 0.3 mm high; stamens five, included in the corolla tube, filament short, inserted at the middle of tube, anthers brown. ***Gynobase*** narrowly subulate (Fig. 3J), with a style surpassing the nutlets by ca. 0.5 mm. ***Coenobium*** laterally compressed ovoid (Fig. 3L), with glochids 2.5–3 mm in diameter. ***Nutlets*** four, heteromorphic, easily separated from gynobase, acute ovoid; 2.5–3 mm long, ca. 1.2 mm wide, disc narrowly ovate, adaxially granulose, centre-line keeled, with a single row glochids, glochids erect; marginal glochids in 2 rows, erect, two nutlets with the inner glochids 0.5–1 mm long, outer glochids 0.2–0.5 mm long (Fig. 3N); two other nutlets with short glochids, inner glochids less than 0.5 mm long,

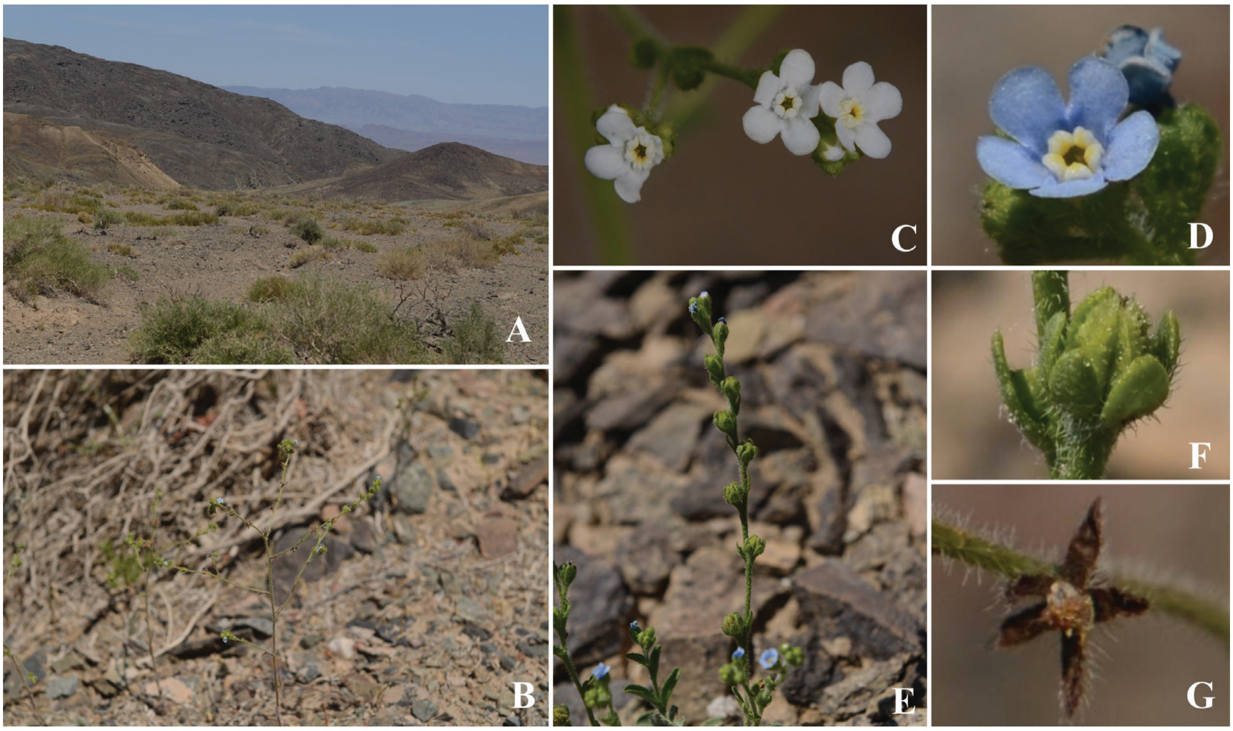

Figure 1. *Lappula effusa* D.H.Liu & W.J.Li, sp. nov. **A** habitat **B** habit **C, D** flower morphology **E** inflorescences **F** fruit **G** spreading calyx in fruit.

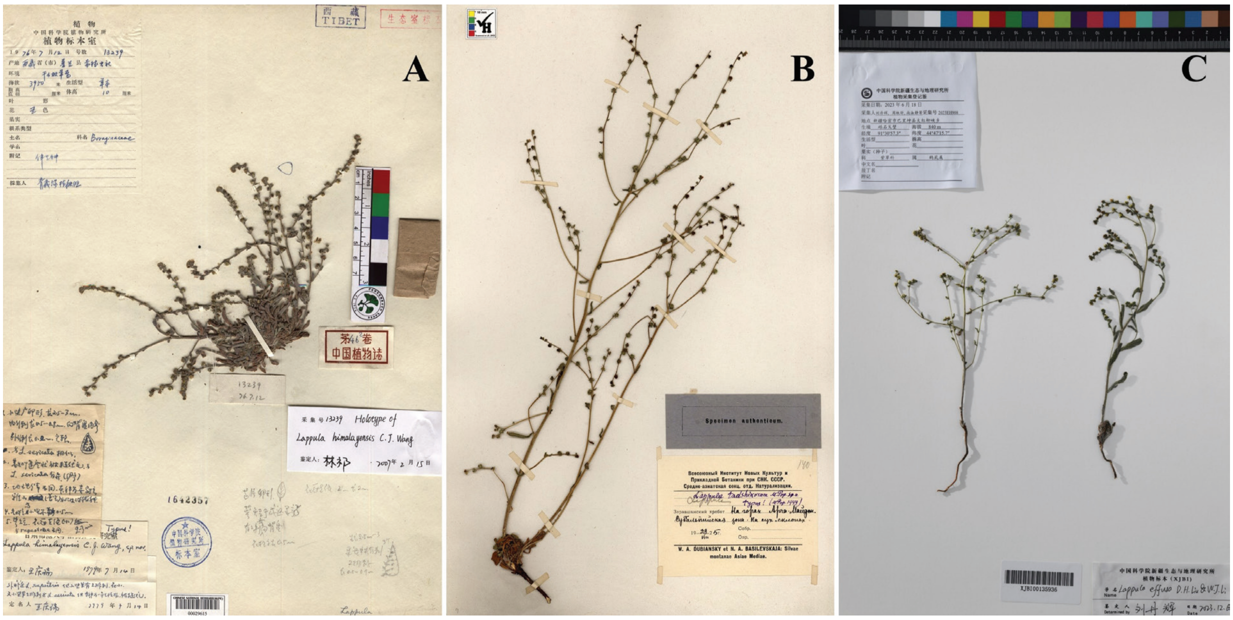

Figure 2. Type specimens of *L. himalayensis*, *L. tadshikorum* and *L. effusa* **A** holotype of *L. himalayensis* (PE00029615!) **B** lectotype of *L. tadshikorum* (LE 140!) **C** holotype of *L. effusa* (XJBI00135936!).

outer glochids reduced to 0.1–0.2 mm or tuberculate (Fig. 3M); nutlets thin, ca. 0.5 mm thickness (Fig. 3O); abaxially granulose, cicatrix narrow lanceolate, ca. 1 mm long, located in the base of nutlets, adaxial keel ca. 1.5 mm long (Fig. 3P).

Distribution and ecology. The new species is currently known only from its type locality in Dahongliuxia Village, Balikun County, Xinjiang Province, China. It grows in gravel desert at an elevation of 840 m above sea level.

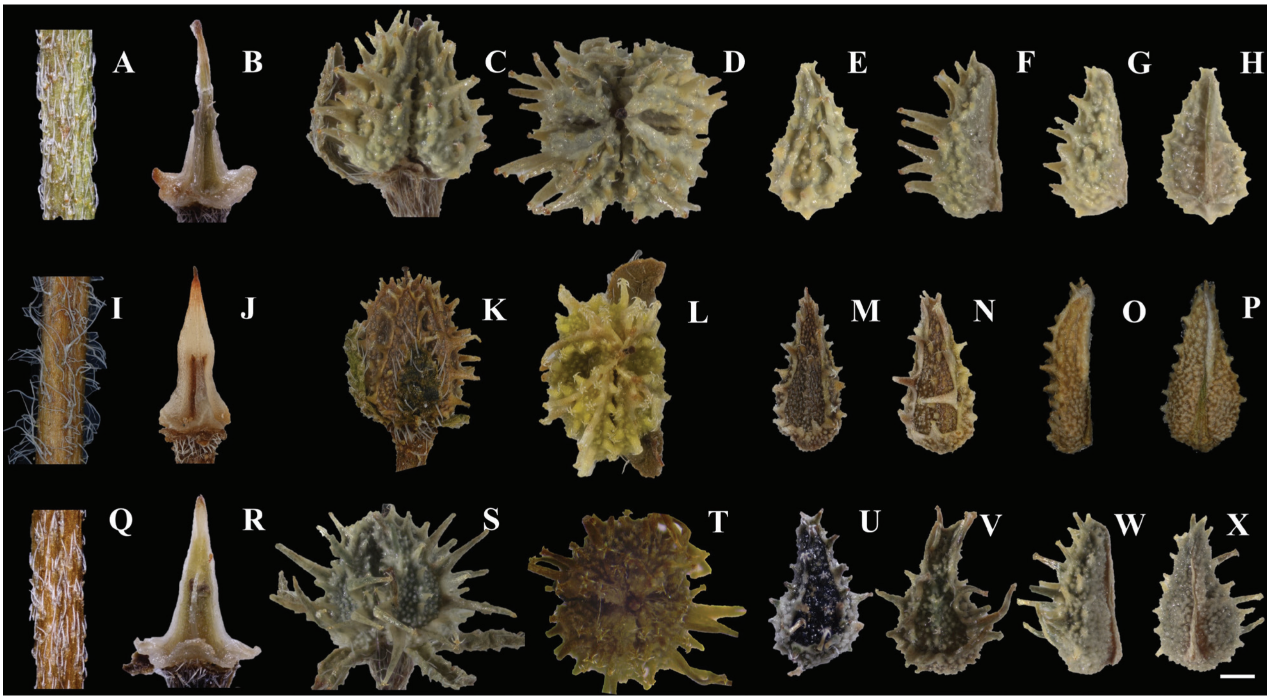

Figure 3. Morphological comparisons of *L. himalayensis*, *L. effusa* and *L. tadshikorum*. *L. himalayensis* **A** stem indumentum **B** gynobase **C** fruit lateral view **D** fruit polar view **E** nutlet abaxial view (with short glochids) **F** nutlet lateral view (with long glochids) **G** nutlet lateral view (with short glochids) **H** nutlet adaxial view. *L. effusa* **I** stem indumentum **J** gynobase **K** fruit lateral view **L** fruit polar view **M** nutlet abaxial view (with short glochids) **N** nutlet abaxial view (with long glochids) **O** nutlet lateral view **P** nutlet adaxial view. *L. tadshikorum* **Q** stem indumentum **R** gynobase **S** fruit lateral view **T** fruit polar view **U** nutlet abaxial view (with short glochids) **V** nutlet abaxial view (with long glochids) **W** nutlet lateral view **X** nutlet adaxial view. Scale bar represents 0.5 mm.

Phenology. Flowering and fruiting from May to July.

Etymology. The specific epithet refers to the appearance of new species, stems frequently branched at middle and above and nearly horizontal spreading.

Vernacular name. Simplified Chinese: 展枝鹤虱 (Chinese pinyin: zhǎn zhī hè shī).

Conservation status. Based on the current survey data, we have only found a single population of the new species at its type locality, Dahongliuxia Village, Balikun County, Xinjiang Province, China. Data for the *Lappula effusa* were still insufficient to assess its conservation status. According to the IUCN Criteria (IUCN 2022), the conservation status of this new species is temporarily assessed as Data Deficient (DD) until more information becomes available.

Notes. Based on the classification of *Lappula* by Ovczinnikova (2005), the new species *L. effusa* should belong to the sect. *Microcarpae* (M. Pop.) Ovczinnikova, ser. *Tianschanicae* M. Pop. ex Ovczinnikova, which is characterised by the narrowly subulate gynobase, style surpassing the nutlets by ca. 0.5–1 mm, heteromorphic nutlets with two rows of marginal glochids, disc with centre line keel. Amongst this series, there are approximately seven species (*Lappula aktaviensis* Popov & Zakirov; *L. himalayensis*; *L. pratensis* Ching J.Wang; *L. sericata* Popov; *L. subcaespitosa* M Popov ex Golosk.; *L. tadshikorum*; *L. tianschanica* Popov & Zakirov). *L. effusa* most resembles *L. himalayensis* and *L. tadshikorum*, sharing similar corolla and gynobase morphology. However, nutlets are always important for identification and classification of *Lappula* (Popov 1953; Riedl 1967; Zhu et

Table 1. Morphological comparisons of *L. effusa L. himalayensis* and *L. tadshikorum*.

Characters	*L. effusa*	*L. himalayensis*	*L. tadshikorum*
Habit	12–28 cm	7–15 cm	30–50 cm
Stem	stem single, erect, branched from middle and above, with spreading hair	stems 4–6, cespitose, ascending or erect, branched from above, with appressed hair	stems 2–3, erect, branched from above, with (semi-) appressed hair
Leave indumentum	abaxial densely spreading hispid, adaxially sparsely hispid or glabrous	abaxial densely appressed pubescent, adaxially sparsely pubescent	abaxial densely spreading hair, adaxially sparsely
Inflorescences	5–10 cm in fruit	3–7 cm in fruit	3–7 cm in fruit
Pedicel	2–3 mm long in fruit	1.5–2 mm long in fruit	1–3 mm long in fruit
Calyx	ca. 2 mm and shorter than the nutlets	ca. 2 mm and shorter than the nutlets	ca. 2 mm and shorter than the nutlets
Corolla	blue or white	blue	blue
Style	surpassing the fruit ca. 0.5 mm and surpassing glochids	surpassing the fruit ca. 0.5 mm and surpassing glochids	surpassing the fruit, but not surpassing glochids
Nutlets	heteromorphic; acute ovoid	heteromorphic; ovoid	heteromorphic; ovoid
Marginal glochids	two rows; 0.5–1 mm long inner glochids erect	two rows; 1.5 mm long; inner glochids often curved	two rows; 1–1.2 mm long; inner glochids curved
Disc of nutlets	narrowly ovate-triangular	ovoid	ovoid
Flowering and fruiting	May to July	June to August	June to July
Elevation	840 m	3700–4200 m	1800–3000 m

al. 1995; Ovczinnikova 2005) and the new species exhibits distinctive nutlet morphology from the compared species: i.e. relatively compressed fruit, acute ovoid nutlets, narrowly ovate disc and short marginal glochids. Additionally, *L. himalayensis* and *L. tadshikorum* are distributed in the mountain areas of Xizang and western Xinjiang (Himalaya and Pamir, usually 1800–4000 m a.s.l.), while *L. effusa* occurs in the gravel desert of eastern Xinjiang (lower than 1000 m a.s.l.). The detailed differences amongst these three species are provided in Table 1.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Investigation: DHL, XYZ, SJS, JJW. Data curation: DHL, XYZ, SJS, JJW. Formal analysis: DHL, XYZ. Writing-original draft: DHL. Writing-review and editing: DHL, WJL.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Impatiens karenensis (Balsaminaceae), a new tiny flowered species from Myanmar

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Abstract

Impatiens karenensis (*I.* sect. *Semeiocardium*) from Kayin State, Myanmar is described and illustrated here. It is most similar to *I. micromeris*, but differs in having lower petals with outer margins strongly undulate in the lower half (vs. lower petals entire), apex of upper petals acute to obtuse (vs. apex rounded), short stout spur, ± as long as the depth of lower sepal, ca. 2.5 mm long (vs. long attenuate spur, twice as long as the depth of lower sepal, ca. 5 mm long). Its conservation status is also assessed as Critically Endangered.

Key words: Critically endangered, endemic, Kayin State, limestone species, Southeast Asia

Introduction

A total of 69 native *Impatiens* species have been documented in Myanmar (Kress et al. 2003; Tanaka et al. 2015, 2018, 2022; Ruchisansakun et al. 2017, 2018a, 2018b; Akiyama et al. 2018; Ding et al. 2019; Dakaw Phong San and Ruchisansakun 2022; Myo Min Latt et al. 2023). Amongst these, eight of them belong to *Impatiens* sect. *Semeiocardium* (Zoll.) S.X.Yu & Wei Wang which is characterised by a 4-lobed capsule and predominantly fused lateral united petals (Ruchisansakun et al. 2015, 2018b; Yu et al. 2015). In August 2022, the first author discovered an unknown species during his expedition in the Kayin State of Myanmar. Here, we present a detailed description, along with colour photographs and additional information, to document this finding.

Materials and methods

The new *Impatiens* specimens were collected in Kayin State, Myanmar. The living plants were grown and seeds collected for ex-situ conservation at the Chit Win Sein Farm, while the dried specimen was deposited in the Herbaria (RAF, RANG). The description and line drawings were made from living specimens. The distribution map was made by SimpleMappr (Shorthouse 2010). To determine the IUCN conservation status, the extent of occurrence (EOO) as

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well as area of occupancy (AOO) were calculated using the GeoCAT (Bachman et al. 2011) and then compared to the IUCN guidelines (IUCN Standards and Petitions Committee 2024).

Taxonomy

Impatiens karenensis Chit Soe Paing & Ruchis., sp. nov.

urn:lsid:ipni.org:names:77343949-1
Figs 1–3

Diagnosis. *Impatiens karenensis* resembles *I. micromeris*, but differs in having lower petals with outer margins strongly undulate in the lower-half (vs. lower petals entire), apex of upper petals acute to obtuse (vs. rounded), short stout spur, ± as long as the depth of lower sepal, ca. 2.5 mm long (vs. long attenuate spur, twice as long as the depth of lower sepal, ca. 5 mm long).

Type. Myanmar. Kayin State (Karen State), Hpa-an, Ta Yoke Hla (Kawt Kyaik), 16°50'31.4"N, 97°37'10.4"E, 100–150 m a.s.l., 16 Oct 2023, *Chit Soe Paing 002* (holotype RAF!, isotype RAF, RANG).

Description. Lithophytic annual herbs, 50–70 cm tall. ***Stems*** erect, laxly branched near the top, green to red to purple with red dots, glabrous; hypocotyl elongate, 1–2 cm in diam., epicotyl slightly zigzag in the upper parts. ***Leaves*** spirally arranged, congested on the top when young; petiole ca. 2 cm long, ca. 1.3 mm in diameter, green to reddish-green; lamina ovate, 4–5 × 2.3–2.5 cm, apex acute, base cuneate, green above, paler green below, glabrous, margin serrate with teeth, with a pair of linear glands at the margin near the base, lateral main veins 4–6 pairs. Inflorescence axillary, 2-flowered fascicle; bracts linear-lanceolate, ca. 2 mm long. Flowers white with yellow patch and two yellow streaks at the lip base, 19–19.5 × 6–7 mm, 7–8 mm deep; pedicel 1.6–1.7 cm long, green to reddish-green, glabrous. Lateral sepals 4; inner pair ovate, 0.6–0.7 × 0.5–0.6 mm, apex round, green, glabrous; outer pair free, ovate, ca. 3 × 2 mm, apex acute, green, glabrous. Lower sepal navicular, 7–9 × 5–5.5 mm, 2–3 mm deep, light green, apex acute and mucronate, abruptly constricted into a short strait green spur, ca. 2.5 mm long. Dorsal petal 5.4–5.6 × 6.5–7.5 mm, broadly ovate to broadly obovate to suborbicular, green at the margin and apex, apex emarginate-mucronate, mid-vein crested, ca. 0.5 mm high. Lateral united petals connate, white with yellow mark in the middle at ca. ¼ from the base, clawed to 2–3 mm long; upper petals, 3–3.5 × 1.5–2 mm, ovate to triangular, apex acute to obtuse; lower petals 1.4–1.52 × 0.34–0.35 cm, narrowly ovate in outline, apex obtuse-slightly bilobed, base with two small triangular projections, outer margins strongly undulate in the lower half. Stamens ca. 3 mm long. Ovary 4-loculate, ca. 3 mm long, green, glabrous. ***Fruits*** clavate, 4-lobed, ca. 9 mm long, green, glabrous with green to red pedicel. Seeds unknown.

Habitat and phenology. Grows in open areas on small limestone mountains, 100–400 m a.s.l. Flowering. August–October, fruiting October–November.

Distribution. Endemic to Myanmar. This species is only known from the two localities, around 2 km apart (Fig. 3).

Etymology. The specific epithet is derived from the former name of the state of its type locality “Karen”.

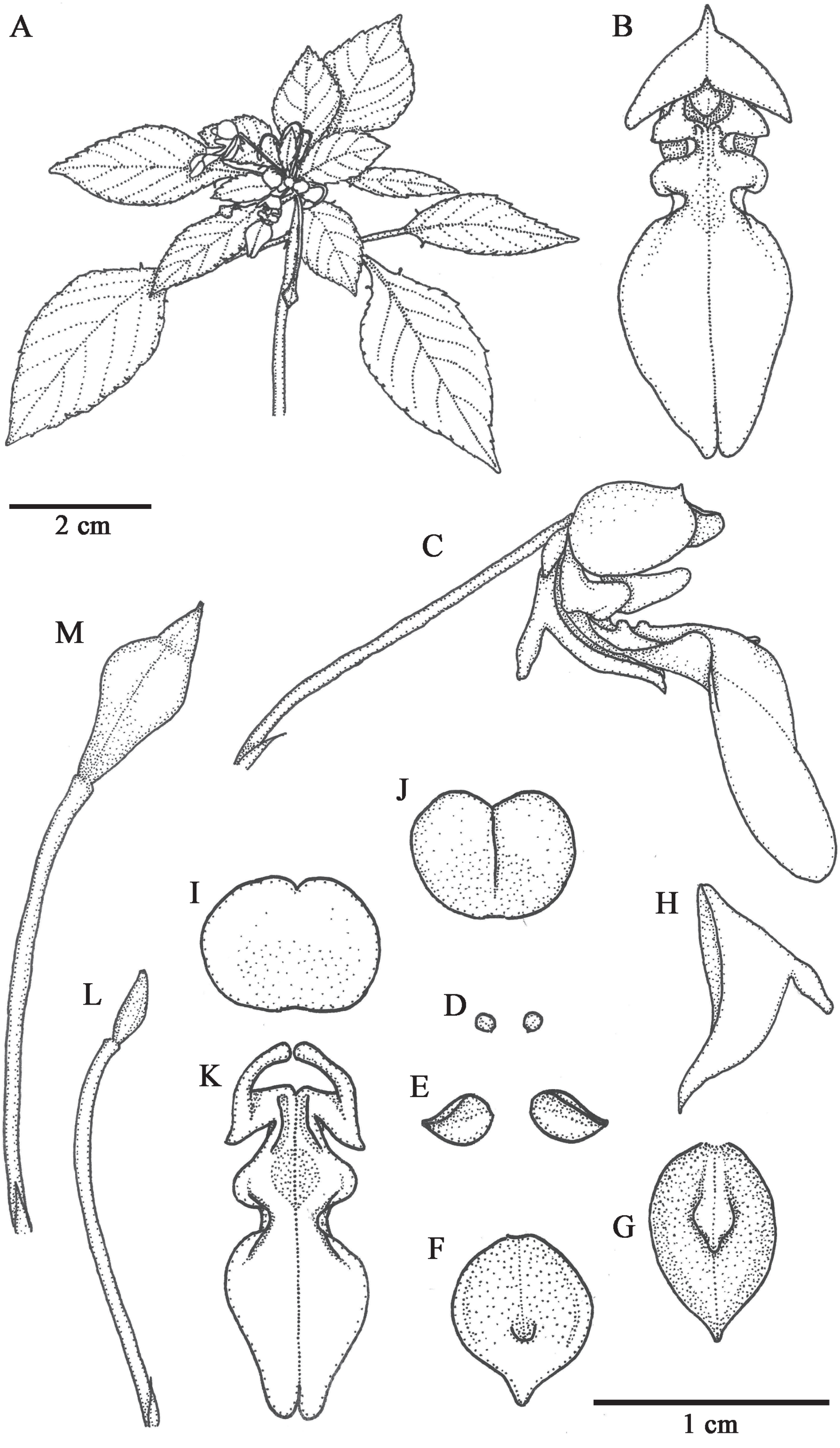

Figure 1. *Impatiens karenensis* Chit Soe Paing & Ruchis **A** habit **B** flower, front view **C** flower, side view **D** inner lateral sepals **E** outer lateral sepals **F–H** lower sepal **I–J** dorsal petal **K** lateral united petals **L** ovary, pedicel and bract **M** fruit (from *Chit Soe Paing 002*). Drawn by S. Ruchisansakun.

Figure 2. *Impatiens karenensis* Chit Soe Paing & Ruchis. *in vivo* **A** flower, front view **B** flowers, side view **C** habit. Photographed by Chit Soe Paing.

Conservation status proposed. *Impatiens karenensis* is currently found at two locations outside of the protected area. This species has a limited extent of occurrence (EOO) and area of occupancy (AOO), spanning less than 10 km^2 (GeoCAT, Bachman et al. (2011)). The population of mature individuals is known to fluctuate. Moreover, the habitat quality is consistently declining because of warmer and drier conditions, particularly by El Niño, coupled with invasive species encroachment. Based on these significant threats, we strongly recommend designating *Impatiens karenensis* as Critically Endangered (CR; B1+B2ac(iv)) according to the IUCN Categories and Criteria (IUCN Standards and Petitions Committee 2024).

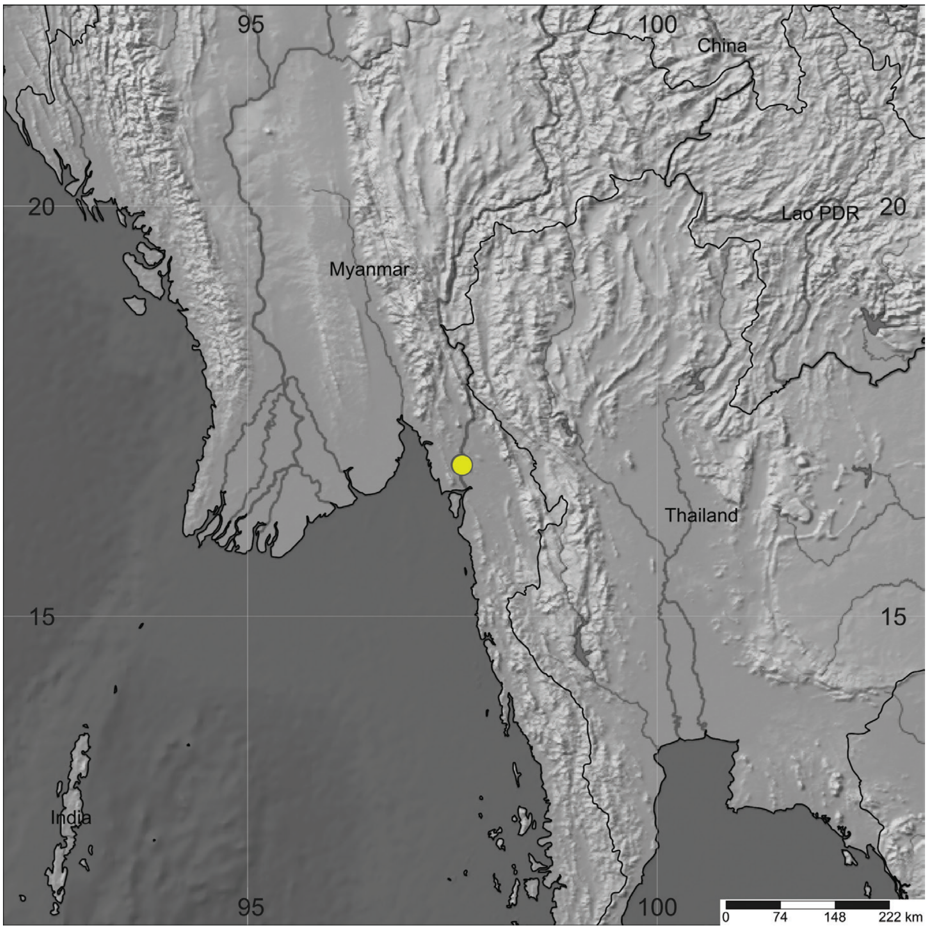

Figure 3. The distribution of *Impatiens karenensis* Chit Soe Paing & Ruchis. (SimpleMappr, Shorthouse 2010).

Note. *Impatiens karenensis* shares similarities with *I. micromeris* and other small *Semeiocardium* species. It also bears resemblance to *I. suksathanii*, but differs in having undulate margin lower petals (vs. entire margin lower sepals), white flower (vs. pink or yellow flower), ovate leaves (vs. linear to narrowly elliptic leaves) (Suksathan and Ruchisansakun 2022).

Key to species of *Impatiens* sect. *Semeiocardium* in Myanmar

1 Flower very small, less than 2 cm long **2**
– Flower much larger, more than 3 cm long **4**
2 Flowers non-resupinate, very small, up to 10 mm, spur facing upwards and incurved .... ***I. capillipes***
– Flowers resupinate, larger than 10 mm, spur downwards, incurved or straight **3**
3 Lower petals with outer margins strongly undulate in the lower half; upper petals apex acute .... ***I. karenensis***
– Lower petals with entire outer margins; upper petals apex rounded .... ***I. micromeris***
4 Lateral united petals free; upper pair of lateral sepals linear ...... ***I. laevigata***
– Lateral united petals connate; upper pair of lateral sepals ovate to elliptic or absent **5**

5 Perennial shrub, (45–)150–300 cm tall; basal part of stems grey, 10–80 mm in basal diam **6**

– Annual herb, 15–40(–100) cm tall; stem light green to red to purple, 2–7(–22) mm diam **7**

6 Pedicels shorter than petioles of the subtending leaves; lower petals without orange to red longitudinal lines .... ***I. parishii***

– Pedicels longer than petioles of the subtending leaves; lower petals with orange to red longitudinal lines .... ***I. kerriae***

7 Lower sepal navicular .... ***I. lobbiana***

– Lower sepal deeply bucciniform **8**

8 Flowers zygomorphic; pedicel pendulous; spur hooked, shorter than 6 mm .... ***I. psittacina***

– Flowers asymmetric; pedicel erect; spur curved, longer than 10 mm .... ***I. tanintharyiensis***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Chit Soe Paing: Collecting sample, photograph. Saroj Ruchisansakun: Draft the manuscript, Drawing, Write a description. Piyakaset Suksathan: Draft the manuscript, Drawing, Write description.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Curating an online checklist for *Erica* L. (Ericaceae): contributing to and supporting global conservation through the World Flora Online

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Abstract

To support the work of the Global Conservation Consortium for *Erica* and update the *Erica* checklist in the World Flora Online (WFO), we have curated the taxonomic backbone in the WFO by expanding it to include updated nomenclatural information from the International Plant Name Index, missing names present in the World Checklist of Vascular Plants (WCVP), the Botanical Database of Southern Africa (BODATSA), and from the “International register of heather names” database, a data source not readily available online. The result is the most robust database of *Erica* names to date, including 851 species, 111 subspecies, 244 varieties, and 2787 synonyms, which is a reliable reference for initiatives such as the *Erica* identification aid, conservation prioritisation, and gap analyses. We disambiguate common orthographic variants within the database and present an overview of these. We also comment on the correct orthography of *E. heleophila* Guthrie & Bolus and *E. michellensis* Dulfer and the validity of *E. tegetiformis* E.G.H.Oliv. are discussed, and the use of *E. adunca* Benth. for a South African species rather than *E. triceps* Link, which is here regarded as insufficiently known and of uncertain application, is clarified.

Key words: *Erica*, International register of heather names, World Flora Online

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Introduction

Erica L., with 851 accepted species (WFO Plant List June 2024), is the second most diverse genus in the Ericaceae after *Rhododendron* L. and is listed amongst the most species-diverse genera of flowering plants (Frodin 2004). The Global Conservation Consortium (GCC) for *Erica* (https://www.globalconservationconsortia.org/gcc/erica/) was established in 2021 (Pirie et al. 2022) to bring together the complementary skills and resources of the world’s *Erica* experts, conservationists, and the botanic garden community for effective

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† Deceased.

conservation to prevent species extinctions. Part of the consortium's role is to maintain a checklist of accepted species as a baseline to inform and prioritise conservation work. To do this the GCC-*Erica* contributes to the World Flora Online's (WFO) Ericaceae Taxonomic Expert Network (TEN).

Building and maintaining a checklist of names in a species-rich plant group is rarely trivial, and plants with a history of horticultural innovation present particular challenges. During the nineteenth and the early twentieth centuries, there was often no clear distinction between names given to naturally occurring species and subspecific taxa and the names (often in Latin form) applied in horticulture to plants that would now be regarded as selected cultivars. The problem is exacerbated in *Erica* by the often undocumented and unacknowledged artificial and accidental hybridization of plants in European gardens (Nelson and Pirie 2022). As a result, there are many more validly published names within *Erica* than there are accepted taxa, and the origins of the oldest names can be obscure.

Prior to this work, the most comprehensive checklist of *Erica* names was published in the International Register of Heather Names (IRHN; Nelson and Small 2000; 2004–2005), derived from a highly curated Access 2000® database maintained by The Heather Society and not available online. Many names listed and documented in this work had not been represented in openly accessible databases, and some nomenclatural issues were flagged, but remained unaddressed. During the current work, we resolved several outstanding cases of current use of later homonyms (Nelson et al. 2023). There remains inconsistency in nomenclature between important sources of information, such as conservation threat assessments (Raimondo et al. 2009) and commonly used databases (POWO 2024), and a lack of consensus on synonymy and on numbers of species and subspecific taxa that poses an obstacle to conservation prioritisation, for example in attempts to map taxa from GBIF records or to assign threat status to currently accepted names (Pirie et al. 2024).

The main aim of this work was to create a global checklist for the GCC-*Erica* as part of the World Flora Online. We set out to curate the classification in the WFO backbone, comparing and integrating online resources of BODATSA, IPNI, WCVP, and names data from the IRHN database. We clarify some points of outstanding nomenclatural confusion, including inconsistent use of orthographic variants (Nelson and Oliver 2004) and how these may be impacted by current proposals to amend the botanical code of nomenclature (Mabberly 2020; Van Rijckevorsel 2020).

Methods

Initial curation

As part of the formation of the WFO TEN for Ericaceae in 2020, the family backbone was supplied by the WFO (WFO Consortium 2019) as a Darwin Core Archive. This seeded a dataset (Elliott et al. 2020), managed in Padme, a taxonomic database system developed by the Royal Botanic Garden Edinburgh. The family data, provided by WFO, was largely based on "The Plant List" (2013) v1.1. For *Erica*, updated nomenclatural records were compared to the "International Plant Names Index" (IPNI). Additional names published since 2012 were added to the backbone. Taxonomic placement of species was checked mainly using literature sources for the “Flora of Southern Africa” region (FSA) (Oliver 1984, 1987, 2000; Oliver and Oliver 2002, 2005; Pirie et al. 2017) and online resources, namely Catalogue of the Plants of Madagascar (Rabarimanarivo et al. 2015) and the Botanical Database of Southern Africa (BODATSA) (South African National Biodiversity Institute 2016). Although the South African data was chiefly accessed through the frontend user interface, the yearly checklist data is available in an archived version (South African National Biodiversity Institute 2024).

In 2022, the WFO’s Rhakhis tool (Hyam et al. 2022; Hyam and Elliott 2023) became available, and data in the WFO taxonomic backbone was synced to the Ericaceae classification from Padme. Curation for Ericaceae then transferred from Padme to Rhakhis.

Global conservation consortium for *Erica*

The initial checklist created for the formation of the Global Conservation Consortium for *Erica* (GCC-*Erica*), based on the World Checklist of Vascular Plants (WCVP; Govaerts 2022), was compared to the WFO backbone in Rhakhis. Missing names were added to the WFO backbone and conflicts in classification were highlighted and resolved by referring to the literature or the IRHN.

The international register of heather names

In 1970, The Heather Society undertook the role of International Cultivar Registration Authority (ICRA) for the genera *Andromeda* L., *Bruckenthalia* Rchb., *Calluna* Salisb., *Daboecia* D.Don, and *Erica* [these formed a denomination class as defined by the “International code of nomenclature of cultivated plants” 1995 (*ICNCP*) under the International Commission for the Nomenclature of Cultivated Plants]. The published volumes (Nelson and Small 2000, 2004–2005) were derived from a database that included more details of the names, including bibliographic references to descriptions and illustrations, history, and etymology of the individual scientific and horticultural (cultivar) names. To preserve these data, the entire IRHN database has been archived (see below).

The first volume of the “International Register of Heather Names” (IRHN; Nelson and Small 2000) was published in four parts and contained all cultivar and botanical names that had then been traced within the genera *Andromeda*, *Bruckenthalia*, *Calluna*, *Daboecia*, and *Erica* in the broad sense. This list covered species and subspecific taxa of *Erica* species indigenous in Europe, Asia Minor, the Atlantic islands (Azores, Madeira, and the Canary Islands), and Africa north of the Tropic of Cancer, and their natural and man-made hybrids and their cultivars. These are generally known colloquially as “hardy heaths” or “hardy heathers” because the majority can tolerate the relatively cool climate of the northern hemisphere, north of the Tropic of Cancer.

The second volume (Nelson and Small 2004–2005), also published in four parts, contained names for *Erica* species and subspecific taxa indigenous to Africa south of the Tropic of Cancer and the islands of the southern Atlantic and Indian Oceans. Many of these are colloquially known (especially in horticulture) as “Cape heaths” although many do not occur within the Cape provinces of South Africa. This volume also included the names of subspecific taxa, natural and artificial hybrids, and cultivars of the Cape heaths. With the re-circumscription of *Erica* to include previously separate "minor" genera (Oliver 2000), a list of these synonymised genera was included as Annex 1 of Volume 2, and their names, now being synonyms of *Erica* taxa, were also included in that checklist.

Compilation of the IRHN was a major collaborative effort involving members of The Heather Society (1963–2020), particularly its designated registrars, and sister societies in western Europe and North America. Research and publication of the checklist was funded by The Heather Society with additional financial support from the Stanley Smith Horticultural Trust (UK).

Names data from The Heather Society's Access 2000® database, used to produce the IRHN (Nelson and Small 2000, 2004–2005), were matched against the WFO backbone. Names data were extracted from this database. To aid in name matching, authorships were modified to reflect standard author abbreviations according to Biodiversity Information Standards (TDWG) (formerly the Taxonomic Databases Working Group), and names without an author string were initially excluded. Natural and artificial hybrid names were added to the WFO when missing as these can have nomenclatural significance. Natural hybrids were placed in the classification where appropriate following the IRHN. Artificial hybrids are unplaced and deprecated, as these are outside the scope of the WFO. The status of "deprecated" was introduced primarily as an internal device in the WFO. It is meant in the modern sense of the word, particularly regarding software: "to withdraw official support for or discourage the use of". Cultivar names were not processed as they also are beyond the scope of the WFO. This process of bringing in historic names from IRHN raised homonym issues among Latin binomials that were known but not yet resolved. The required replacement scientific names have been dealt with by Nelson et al. (2023). These new names were registered with IPNI (2023) as part of the pre-publication process and subsequently added to the WFO database.

An IRHN archive (Elliott et al. 2023) has been created in Zenodo (the general-purpose open repository developed under the European OpenAIRE program). This contains the complete, unedited IRHN database, the two volumes (eight parts) as published by The Heather Society (in pdf format), and a csv file containing WFO IDs linked to botanical names in the IRHN.

Correctable orthographic variation

Orthographic variation (particularly in the terminations employed in eponyms and toponyms) has been prevalent in the historic literature for *Erica* (Nelson and Oliver 2004; Turner 2016). Existing WFO records were corrected in accordance with the "International Code of Nomenclature for algae, fungi, and plants" (*ICN*, Shenzhen Code; Turland et al. 2018). Some variants that have featured in botanical and horticultural literature and databases (including SANBI's Red List of South African Plants for threat status; http://redlist.sanbi.org/genus.php?genus=1820) were added and linked to the currently accepted name. We further considered the future consequences of proposals currently under consideration to modify Article 60.8 of the *ICN* with regard to restricting the correction of names (Proposal 023 by Mabberly 2020; and proposal 024 by Van Rijckevorsel 2020).

Unplaced names

In the context of the WFO, unplaced names are those not associated with any taxon as an accepted name or synonym. This could be due a taxonomist having not expressed an opinion on its placement, or the name cannot be resolved to anything in the classification. These records can be found by searching the name parts but are not found by browsing the classification's hierarchy.

Cultivars

Modern cultivar names as defined under the *ICNCP* (Brickell et al. 2009), used in the horticultural industry and in gardens lie beyond the scope of the WFO and were therefore omitted from the checklist. Historic Latin form names applied to horticultural selections were removed from the classification and deprecated when there was little doubt that they did not refer to wild species.

Data on cultivar names published before 2001 can be found in the original Access database format and as a csv file in the Zenodo archive (https://zenodo.org/doi/10.5281/zenodo.10255787) (Elliott et al. 2023). The cultivar list will be added to the Catalogue of Life's Checklist Bank.

For comparison, the number of accepted species, subspecies, varieties, and synonyms were recorded from the "World Checklist of Vascular Plants" (WCVP; v.11.0) (Govaerts 2023), the "Synonymic Checklists of the Vascular Plants of the World" (v.16.4, Sep 2023) (Hassler 2023), and "The Leipzig Catalogue of Vascular Plants" (v.3.01) (Freiberg et al. 2020) using datasets deposited in the Catalogue of Life Checklist Bank (https://www.checklistbank.org/).

Results

The *Erica* checklist, as published in the WFO June 2024 data release, available in a human readable form at https://wfoplantlist.org/, has 851 accepted species (the 852 in the December 2023 release wrongly included *E. perlata* G.Sinclair as Accepted instead of as Unplaced following Nelson et al. 2023). Table 1 compares the number of accepted species, subspecies, and varieties, as well as the number of synonyms and unplaced name records against "The Plant List" v1.1 and the two previous "WFO Plant List" releases.

Since the beginning of curation of *Erica* names in early 2023 for GCC-*Erica* and WFO, the number of *Erica* and related synonymised names in Rhakhis has increased by 1012. Removal of the names of artificial (horticultural) hybrids and duplicate name records has reduced the number of accepted species by 208. The process has added more than 800 synonyms by resolving the unplaced names from now synonymised genera and the addition of historic names from the IRHN database. Following published taxonomic accounts and incorporating infraspecific names from BODATSA and IRHN has increased the number of accepted subspecific taxa when comparing the December 2022 to June 2024 WFO release. There are now 111 accepted subspecies compared to 56, an increase of 55 and 244 accepted varieties compared to 44, an increase in 200. The number of unplaced names has also increased.

Table 1. Accepted species, subspecies, varieties, and synonyms within *Erica* across versions of “The Plant List” and the “WFO Plant List”.

Version	Species	Subspecies	Varieties	Synonyms	Unplaced names
The Plant List v.1.1 (2012)	1 044	37	37	1 948	178
WFO Plant List (December 2022)	1 061	56	44	2 540	677
WFO Plant List (June 2023)	853	104	199	2 619	729
WFO Plant List (June 2024)	851	111	244	2787	1413

As of June 2024 there are 1413 unplaced name in the WFO backbone. Unplaced names are mostly historic and still need to be placed in the classification or deprecated within the WFO. These names, especially those of horticultural origin, may not be useful, especially to ecologists and conservationists who are the primary end-users of the WFO. By maintaining these records, however, the wider WFO names database allows for them to be accounted for by those using the data for taxonomic or historical research purposes. Most of these names could not be readily placed using the IRHN database and were deprecated. To reduce confusion, deprecated names are maintained in the WFO database but are not made visible in the public checklist.

Number comparison to other Global Lists

Table 2 shows the comparison of numbers of taxa represented across the “World Checklist of Vascular Plants” (WCVP; v.11.0), the “Synonymic Checklists of the Vascular Plants of the World” (v.16.4, Sep 2023), and “The Leipzig Catalogue of Vascular Plants” (v.3.01). There is great variation in the number of names across all taxonomic ranks among these lists, especially in terms of infraspecific taxa and synonym names.

Orthographic variants

Table 3 lists species and hybrid names in *Erica* with orthographic variants that have appeared in botanical and horticultural literature and databases, as well as their currently accepted orthography. An indication is also given for names where the acceptance at the Madrid Nomenclature Section of the International Botanical Congress (IBC; July 2024) of current proposals to amend Article 60.8 of the *ICN*, would result in a reversion to the original spelling as published in the protologue of each name.

Table 2. Accepted species, subspecies, varieties, and synonyms within *Erica* across the four major global checklists.

Global list	Species	Subspecies	Varieties	Synonyms
GCC-Erica Checklist in WFO Plant List (June 2024)	851	111	244	2787
Leizpig Catalogue of Vascular Plants v.3.01 (November 2020)	893	79	116	1196
Synonymic Checklists of the Vascular Plants of the World v.16.4 (September 2023)	839	112	143	2782
World Checklist of Vascular Plants v.11 (20 April 2023)	859	97	247	2688

Table 3. Orthographic variants of species and hybrid names in *Erica* that have appeared in botanical and horticultural literature and databases [as discussed in Nelson and Small (2004–2005) and in Nelson and Oliver (2004) where numerous other orthographic variations are also listed] that were added to WFO and linked to the currently accepted name and spelling [#If Proposals 023 (Mabberly 2020) and 024 (Van Rijckevorsel 2020) to emend the *ICN* is ratified at the IBC 2024 the spelling will revert to that given in the 'Original orthography' column.].

Correct orthography	WFO ID	Original orthography#	WFO ID	Other orthographic variants	WFO ID
Erica aitonii Masson ex Andrews, non Willd.	wfo-1000061246	*Erica aitonia*	wfo-0000671323	*Erica aitoniana*	wfo-0000671324
Erica argyraea Guthrie & Bolus	wfo-0000671411	*Erica argyrea*	wfo-1000055018		
Erica banksii Andrews, non Willd.	wfo-0000671465	*Erica banksia*	wfo-1000057523		
Erica banksii subsp. *comptonii* (T.M.Salter) E.G.H.Oliv. & I.M.Oliv.	wfo-0000671466	*Erica banksia* subsp. *comptonii*	wfo-0001440938		
Erica baueri Andrews	wfo-0000671485	*Erica bauera*	wfo-1200068674		
Erica beaumontiae Andrews	wfo-1000057504	*Erica beaumontia*	wfo-0000671488	*Erica beaumontiana*	wfo-0000671489
Erica blandfordii Andrews	wfo-0000671517	*Erica blandfordia*	wfo-1000054989		
Erica bonplandiana Sims	wfo-0000671531	*Erica bonplandii*	wfo-0000671530		
Erica bowieana G.Lodd.	wfo-0000671543	*Erica bowia*	wfo-0000671542		
Erica coventryi Andrews	wfo-0000671767			*Erica coventrya*	wfo-1000054990
Erica etheliae L.Bolus	wfo-0000671983	*Erica ethelae*	wfo-1000056273	*Erica ethelii*	wfo-1000055005
Erica eweriana Dryand.	wfo-1000057515			*Erica ewerana*	wfo-0000671987
Erica fastigiata var. *coventryi* Bolus	wfo-1200011362			*Erica fastigiata* var. *coventryana*	wfo-1200068673
Erica gordoniae J.Forbes	wfo-1000057514	*Erica gordonia*	wfo-0000672178	*Erica gordonii*	wfo-1000055024
Erica heleophila Guthrie & Bolus	wfo-0000672224			*Erica heliophila*	wfo-1000056274
Erica hendricksei H.A.Baker	wfo-0000672226			*Erica hendricksi*	wfo-1000056275
Erica hibbertii Andrews	wfo-0000672237			*Erica hibbertia*	wfo-1000054992
Erica irbyana Andrews	wfo-0000672344			*Erica irbyana*	wfo-1000057513
Erica lawsonii Sims	wfo-0000672436	*Erica lawsonia*	wfo-1000056276	*Erica lawsoniana*	wfo-1000056277
Erica leei Andrews	wfo-1000054993	*Erica leea*	wfo-1000057512		
Erica linnaei Andrews	wfo-0000672483	*Erica linnaea*	wfo-1000057511		
Erica massonii L.f.	wfo-0000672581	*Erica massonia*	wfo-0000672580		
Erica maximilianii Guthrie & Bolus	wfo-0000672585			*Erica maximiliani*	wfo-1000057510
Erica michellensis Dulfer	wfo-1000056285			*Erica mitchellensis*	wfo-1000056285
				Erica mitchelliensis	wfo-0000672628
Erica monsoniana L.f.	wfo-0000672640	*Erica monsoniae*	wfo-1000055014		
Erica newdigateae Dulfer	wfo-0000672700			*Erica newdigatei*	wfo-1000057505
Erica nivenii Andrews	wfo-1000055003	*Erica nivenia*	wfo-0000672714	*Erica nivenia*	wfo-0000672714
Erica patersonii Andrews	wfo-0000672833	*Erica patersonia*	wfo-1000056281	*Erica patersonia*	wfo-1000056281
Erica petiveri L.	wfo-0000672890	*Erica petiveriana*	wfo-0000672895	*Erica petiveriana*	wfo-0000672895
Erica plukenetii L.	wfo-0000672951			*Erica plukenetiana*	wfo-0000672950
				Erica plukenetia	wfo-1000057848
Erica plukenetii subsp. *penicillata* (Andrews) E.G.H.Oliv. & I.M.Oliv.	wfo-0000672958			*Erica plukenetii* subsp. *penicellata*	wfo-0001441063
Erica priorii Guthrie & Bolus	wfo-0000672992			*Erica priori*	wfo-1000057509
Erica sainsburyana Andrews	wfo-0000673173			*Erica sainsburya*	wfo-1000057507
Erica salisburii Andrews	wfo-1000054995	*Erica salisburia*	wfo-0000673176		
Erica savileae Andrews	wfo-0000673184	*Erica savilea*	wfo-1000057506	*Erica savilliae*	wfo-0000673187
				Erica savileana	wfo-0000673185
Erica shannonii Andrews	wfo-0000673248	*Erica shannonea*	wfo-1000056279		
Erica solandri Andrews	wfo-0000673268	*Erica solandra*	wfo-1000054997		
Erica sparrmannii L.f.	wfo-1000055043			*Erica sparrmanni*	wfo-0000673276
Erica thunbergii Montin	wfo-0000673417			*Erica thunbergia*	wfo-1000056283
Erica uhrii Andrews	wfo-1000057518	*Erica uhria*	wfo-0000673487		
Erica walkeri Andrews	wfo-0000673622	*Erica walkeria*	wfo-1000056280		
Erica wendlandiana Klotzsch	wfo-0000673627			*Erica wendlandii*	wfo-1000055071
Erica zeyheri Bartl.	wfo-0000673654			*Erica zeyheriana*	wfo-0000673655

Nomenclatural notes

Nomenclatural issues have been dealt with by Nelson et al. (2023) as part of the systematics, natural history, and conservation of the *Erica* (Ericaceae) collection. The following three species are further clarified:

***Erica tegetiformis* E.G.H.Oliv. in Bothalia 20(1): 46. 1990.**
IPNI: urn:lsid:ipni.org:names:941276-1
WFO: wfo-0000673371

Replaced synonym: *Erica senilis* var. *australis* Dulfer in Ann. Naturhist. Mus. Wien 66: 32. 1963.
IPNI: urn:lsid:ipni.org:names:77251074-1
WFO: wfo-0000673222

Oliver (1990) raised *E. senilis* var. *australis* Dulfer to species level since it is significantly different from *E. senilis* Klotzsch ex Benth. The epithet '*australis*' was not available for this taxon at species level because of the earlier name *E. australis* L. (in Mant. Pl. Altera: 231. 1771) that remains the valid name for one of the European species. Therefore, Oliver (1990) published the new name *E. tegetiformis* E.G.H.Oliv. for this taxon. We consider this name to be validly published. In other lists it is considered to be not validly published due to the omission of the full reference of the replaced synonym. There is an indirect reference made with the combination "*E. senilis* Klotzsch ex Benth. var. *australis* Dulfer: 32 (1963)". There is only one Dulfer reference in the bibliography of the article by Oliver (1990). While the *ICN* recommends refraining from this practice (see Rec. 41A.1; Turland et al. 2018), it is permissible to have the full and direct reference separate from the newly published name or combination. The year of the journal volume for the Dulfer reference is cited as 1964 (instead of 1963), but we consider this to be a correctable error under Art. 41.6 (Turland et al. 2018). For these reasons, we treat *E. tegetiformis* (in Bothalia 20: 46. 1990) as validly published.

***Erica heleophila* Guthrie & Bolus in Fl. Cap. (Harvey) 4(1.1): 110. 1905.**
IPNI: urn:lsid:ipni.org:names:328833-1
WFO: wfo-0000672224

This orthographic issue was dealt with in Nelson and Small (2004–2005) but is revisited here. In the key to species and the protologue (Guthrie and Bolus 1905: 19, 110), the species epithet was published as '*heliophila*'. However, in the Addenda and Corrigenda preceding the Index and the Corrigenda following the Index in the same volume and section of the "Flora Capensis" (Thiselton-Dyer 1909: 1126, 1168), the epithet was amended to '*heleophila*', changing the meaning of the epithet to "of the marsh" rather than "of the sun". In the Index (Thiselton-Dyer 1909: 1146), both epithets are listed. It is unclear why this amendment has been largely overlooked. The original publication date of part 1 of volume 4 of "Flora Capensis" was May 1905 (Stafleu and Cowan 1979: 76) and the correction was published in February 1909 (part 6 of the volume), albeit in the same volume and section (volume 4 section 1). The correction of the name *E. heleophila* is an orthographic (potentially, typographic; Nelson and Small 2004–2005) error permissible under Art. 60.1 (Turland et al. 2018).

The WFO ID of the original orthographic variant can be found in the Table 3.

***Erica michellensis* Dulfer in Ann. Naturhist. Mus. Wien 67: 85. 1963.**
IPNI: urn:lsid:ipni.org:names:329124-1
WFO: wfo-1000055012

Erica saxatilis L.Bolus in Ann. Bolus Herb. 3: 177. 1924. nom illeg. hom. non *Erica saxatilis* Salisb., Prodr. Stirp. Chap. Allerton: 295. 1796.
IPNI: urn:lsid:ipni.org:names:329562-1
WFO: wfo-0000673189

This orthographic issue was also dealt with by Nelson and Small (2004–2005) but is revisited here. The name *E. saxatilis* L.Bolus (in Ann. Bolus Herb. 3: 177. 1923) is an illegitimate later homonym of the earlier name *E. saxatilis* Salisb. (in Prodr. Stirp. Chap. Allerton: 295. 1796) (= *E. carnea* L.). Dulfer (1963) therefore published a new name for this taxon, namely *E. mitchelliensis*, with that original spelling. The type collection of *E. saxatilis* L.Bolus was given as "Cape Province; South-Western Region; Ceres Div., Mitchells Peak, Mitchells Pass, "growing on rocks, rare," alt. 4500 ft., fl. Dec. 1920, *T.P. Stokoe 66*" (Bolus 1923: 177). The peak and pass commemorate Charles Cornwallis [baptised Collier] Michell (1793–1851) (Richings 2006), Surveyor-General of the Cape of Good Hope and Superintendent of Works in 1848 when the pass was originally opened (Raper et al. 2014). Dulfer (1963) chose 'mitchelliensis' as his epithet, using the "Mitchell" spelling as it was found in the *E. saxatilis* protologue (Bolus 1923), and derived from the label on Stokoe's specimens.

Dulfer (1963) also constructed the name with an additional "i" before the -ensis. This has been considered a correctable error in previously published works. The corrected orthography, *E. mitchellensis*, is used in the South African National Plant Checklist (South African National Biodiversity Institute 2024) and Red List of South African Plants (Turner 2008).

The IRHN (Nelson and Small 2004–2005) further corrected the name to *E. michellensis* due to the incorrect spellings of "Mitchell's Peak" and "Mitchell's Pass", when they should have been Michell's Peak and Michell's Pass as on modern maps of the region. The correction in the IRHN has not been widely adopted or used, but there is nothing in the *ICN* to suggest that Nelson's entry in the IRHN is incorrect. We therefore suggest that *E. michellensis* is the correct orthography to follow for this name. Both orthographic variants are in the WFO as separate entries and synonymised to *Erica michellensis*.

The WFO IDs for the orthographic variants can be found in the Table 3.

Resolving the application of the name *Erica adunca* Benth. (1839), rather than *Erica triceps* Link (1821)

***Erica triceps* Link in Enum. Hort. Berol. Alt. 1: 371. 1821.**
IPNI: urn:lsid:ipni.org:names:329771-1
WFO: wfo-0000673442

Erica adunca Benth. in Prodr. 7: 618. 1839.
IPNI: urn:lsid:ipni.org:names:328152-1
WFO: wfo-0000671312

Although previously treated as separate species (e.g., in Schumann et al. 1992: 193 and 195), Oliver (in Oliver 2012 and in Oliver and Forshaw 2012) treated these two names as synonymous. The name *E. triceps* is the older of the two names and thus has priority (Art. 11.1; Turland et al. 2018). However, a note in the ID aid from Oliver (Oliver and Forshaw 2012) stated that any type in Berlin was destroyed during the Second World War and the description in the protologue (Link 1821: 371) is insufficient to definitely associate it morphologically with *E. adunca* or any other known species. No type was explicitly designated in the protologue, but original material derived from the plant cultivated at the Berlin Botanical Garden in 1808 can be assumed to have been in Herb. B. We have not traced other original material. Dulfer (1964: 116 no. 370) noted that the habitat of the species was the Cape of Good Hope ("Hab. in promont. bon. sp."), repeating information published by Link (1821: 371 no. 3731: "Hab. in Pr. b. sp.") in the protologue. However, Dulfer (1964) did not directly cite any extant specimen as a type.

Nomenclatural resolution depends on the relative use of *E. triceps* and *E. adunca* for the species as currently circumscribed. Use of the older name, *E. triceps*, and its application is uncertain due to the lack of original material and the ambiguity of the description in the protologue (Link 1821: 371). Should *E. triceps* and *E. adunca* be regarded as synonymous, unequivocal use of the younger name, *E. adunca*, would require formal rejection of the older *E. triceps* under Art. 56 (Turland et al. 2018). Such action at this stage would be premature as further investigation might reveal information that can clarify the application of *E. triceps*. We believe the best course of action is to regard *E. triceps* as an insufficiently known name that cannot be applied to any extant taxon with certainty, and we do not treat it as a synonym of *E. adunca*. We apply only the name *E. adunca* to the South African taxon that has previously been treated as either *E. adunca* or *E. triceps*, the latter probably a misapplication.

Discussion

The WFO's Rhakhis tool, which is made available for use by Taxonomic Expert Networks to curate and produce classification, has allowed for a hybrid approach to curate the *Erica* checklist. A mix of batch processing of csv files and manual edits to records through the user interface has allowed multiple collaborators to contribute to the process.

While the number of unplaced names has increased with the inclusion of IRHN data these are mostly historic names that may never be adequately placed in the generic classification due to incomplete descriptions, the absence of supporting herbarium specimens or competent scientific illustrations. Many have been treated by previous authors as, for example, "imperfectly known species" or "supposed hybrids" (Guthrie and Bolus 1905: 310–315) or "Ungenügend bekannte Arten [insufficiently known species]" or putative hybrids (Dulfer 1964: 139–148). Some of the unplaced names can be accounted for by this ambiguity created by the historic usage of Latin names for plants of horticultural origin. Gradually all unplaced names will be re-assessed, and either placed where appropriate in the classification, or deprecated from the main checklist.

While we corrected orthography in the WFO checklist to follow previously corrected versions in the literature, and corrected others (Table 3), we are aware that Proposals 023 (Mabberly 2020) and 024 (Van Rijckevorsel 2020), if passed at the 2024 IBC, may impact those changes. If that is the case, then these will revert to the original author's spelling (as indicated in Table 3).

Through the inclusion of the names data from IRHN, the resolution of homonym issues by Nelson et al. (2023), and the nomenclatural work highlighted in this paper, we believe the current checklists in the WFO's December 2023 release is the most robust global checklist for *Erica*. The need to maintain and update the checklist is essential if it is to be the baseline for conservation efforts. We feel that the most sustainable way to achieve this is through continued collaborative contributions to the WFO using the Rhakhis tool.

Future work

Immediate work is required to reduce the number of unplaced names, by placing names that can be traced to wild plants in the classification and deprecating those of horticultural origin.

As of June 2024, many names have a taxonomic reference, i.e. the citation from where the taxonomic concept or circumscription is derived (see Berendsohn 1995) but more references are needed. These references are currently omitted because the relevant publications lack a doi or stable URL to link with, which is a requirement for references in Rhakhis. Use of a taxonomic concept reference is implemented throughout the Ericaceae TEN and follows the best practice adopted by the Caryophyllales TEN (Fassou et al. 2022; Korotkova et al. 2021).

The *Erica* checklist will be continually edited, when appropriate, via the WFO Rhakhis tool to contribute to the Ericaceae TEN, the wider WFO project and support various activities of the GCC-*Erica*. The six-monthly releases, apart from providing achievable deadlines for incremental improvements, also allow for a stable citable taxonomy that can be referenced and compared across time through the WFO Plant List API.

The *Erica* classification was extracted from the December 2023 WFO Plant List release to synchronise the classification in the *Erica* identification aid (Oliver et al. 2024). Synchronisation to future WFO Plant List releases will continue.

In working through the developing WFO pipeline with Catalogue of Life (CoL), the *Erica* checklist will be incorporated into the annual CoL Checklist and from there can be utilised by the Global Biodiversity Information Facility (GBIF).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Author contributions

ACE: Data Curation, Investigation, Writing - Original draft, Writing - Review and Editing. SPB: Data Curation, Writing - Review and Editing. RRK: Data Curation, Writing - Review and Editing. ECN: Data Curation, Investigation, Writing - Review and Editing. MDP: Data Curation, Investigation, Writing - Review and Editing.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Clarifying the nomenclature of *Strychnos bredemeyeri* and *Lasiostoma* (Loganiaceae)

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Abstract

Strychnos (Loganiaceae, Gentianales) is a large and pantropical genus of woody plants, ethnobotanically important as a source of many toxic alkaloids, including strychnine. Unfortunately, the status of numerous names at various ranks of *Strychnos* remains unresolved, including that of many specific or infraspecific taxa in the Neotropics. In this study, we address *Strychnos bredemeyeri* (basionym *Lasiostoma bredemeyeri*), a species described in 1827 based on type material collected in Venezuela during the poorly documented Austrian Märter expedition (1783–1788). *Strychnos bredemeyeri* is an unarmed liana with solitary tendrils and axillary inflorescences that occurs in Neotropical rainforests and savannas in Brazil, Guyana, Trinidad and Tobago, and Venezuela. We clarify here the nomenclatural status of *Lasiostoma* Schreb., an illegitimate and superfluous genus currently in synonymy under *Strychnos*, and its former species *Lasiostoma bredemeyeri* [= *Strychnos bredemeyeri*]. Also, we lectotypify *S. pedunculata* and *S. trinitensis*, both taxa currently synonyms of *S. bredemeyeri*.

Key words: Classification, Gentianales, Neotropics, nomenclature, Strychneae, systematics

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Introduction

Strychnos L. is a pantropical genus of lianas, shrubs, or trees with ca. 200 spp., making it the largest genus in Loganiaceae (Gentianales; Struwe et al. 2018). It is well-known for its poisonous properties, including being the source of the toxic alkaloid strychnine (Setubal et al. 2021). Many of the ca. 80 species from the Americas were named and described by naturalists and explorers of the Neotropics of the 18th century and onward, who sought the ingredients of the indigenous dart poison *curare* (Krukoff 1972). This interest resulted in the description of new genera, including *Rouhamon* Aubl. and *Lasiostoma* Schreb., both names now placed in synonymy under *Strychnos* (Krukoff and Monachino 1942), and more than a hundred new species or infraspecific taxa, many of which are currently in synonymy or remain in a doubtful taxonomic status among American *Strychnos* (Krukoff and Monachino 1942; Krukoff 1972; Krukoff 1979a).

Rouhamon was published by the French pharmacist and botanist Jean Baptiste C. F. Aublet based only on the type species *R. guianensis* Aubl. (Aublet 1775: 93). *Rouhamon guianensis* [= *Strychnos guianensis* (Aubl.) Mart.] was collected during Aublet's trip to French Guyana in 1762–1764 and described as being part of the preparation of curare by the indigenous tribe of the Galibis. Schreber (1789: 85) published *Lasiostoma* as an avowed substitute (replacement name) of *Rouhamon* (i.e., the protologue of *Lasiostoma* explicitly cited *R. guianensis* as the only species included in the new genus). Not many botanists followed Schreber, but a few species were eventually published under *Lasiostoma*, including *L. bredemeyeri* Schult. & Schult.f. (1827: 64) [= *Strychnos bredemeyeri* (Schult. & Schult.f.) Sprague & Sandwith], an unarmed liana with solitary tendrils and axillary inflorescences that occurs in Neotropical rainforests and savannas in Brazil, Guyana, Trinidad and Tobago, and Venezuela (Krukoff 1972).

Lasiostoma bredemeyeri was published based on material collected by Franz Bredemeyer, a gardener who traveled from Austria to Martinique, Puerto Rico, and Venezuela on the poorly documented Franz Joseph Märter expedition during 1783–1788 (von Jacquin 1797; Stafleu 1972). Bredemeyer stayed in Venezuela between 1786–1788 (Lindorf 2004) and the eventual type material of *L. bredemeyeri* was taken back to Austria and distributed to personal herbaria such as those of Carl L. von Willdenow and Nicolaus J. von Jacquin [later incorporated into herbaria in Berlin, Germany (B) and Vienna, Austria (W), respectively]. The protologue of *L. bredemeyeri* presents scarce information about the species, including the name of Willdenow and a short and controversial diagnosis associating the herbarium designation "Lasiostoma glabrum" with the description "*corollis fauce glabris*".

After the publication of *Lasiostoma bredemeyeri*, De Candolle (1845a: 18), Progel (1868: 284), Sprague and Sandwith (1927: 128), and Krukoff and Monachino (1942: 321; 1946: 192) treated *L. bredemeyeri* as a doubtful species, not being able to locate its type material. Krukoff (1965: 50) finally located Bredemeyer's specimen deposited in Jacquin's herbarium at W (*Bredemeyer s.n.*, W0078191) due to a suggestion made by another specialist of *Strychnos*, Noel Y. Sandwith, noting that "Franz Bredemeyer was probably a gardener sent out to Venezuela by Jacquin". The Bredemeyer's specimen at W was identified by Krukoff as *Strychnos pedunculata* (A.DC.) Benth. (1964), based on the pilose inner surface of the corolla tube. Because of the morphological contradiction between the pilose inner surface of the corolla in Bredemeyer's specimen at W and the diagnosis of *L. bredemeyeri* (mouth of the corolla glabrous), Krukoff kept this material in doubt as the possible lost type specimen of *S. bredemeyeri*. Later, Krukoff and Barneby (1969b: 181) attempted to locate Bredemeyer's specimen deposited in Willdenow's herbarium at B (*Bredemeyer s.n.*, BW02865000, BW02865010), but the material was not found at the time probably because Willdenow's herbarium is still kept separate from the main collection of B since 1943 (B–W), when it was removed in an attempt to avoid being destroyed by bombing during WWII (Hiepko 1987). Therefore, Krukoff and Barneby (1969b) designated Bredemeyer's specimen at W as the lectotype of *Lasiostoma bredemeyeri*, citing *S. bredemeyeri* as the accepted name with priority of use, and placing *S. pedunculata* and *S. trinitensis* Griseb. (an old synonym of *S. pedunculata*; Sandwith 1933: 397) in its synonymy.

Rouhamon pedunculatum A.DC. [= *S. pedunculata*] was published in De Candolle (1845b: 561) based on material collected by the brothers Robert and Richard Schomburgk during their expedition to Guyana and vicinities in 1840–1844 (*R.H. Schomburgk 482*, BM [BM000952958], F [V0062158F, V0062159F], G [G00368309, G00368310, G00132188], GH [GH00076757], NY [NY00297387], P [P00647601, P00647602], TCD [TCD0000695], US [US00112974], W [W0078192, W0196054]). *Strychnos pedunculata* was cited by the brothers Schomburgk as being part of the preparation of curare by the indigenous tribe of the Macusis (Schomburgk 1848a: 179). The type material of *S. trinitensis* (*H. Crueger s.n.*, GOET [GOET005464], K [K000573430], NY [NY00297487], TRIN [Catalog Nos. 258, 1529], US [US01100481, US00112982]) was collected by Hermann Crueger, a German-born apothecary who settled in Trinidad and Tobago in 1841, becoming a government botanist and director of the Botanical Garden during 1857–1864 (Stafleu and Cowan 1976). This material was distributed to other herbaria by the Trinidad Botanical Garden, and eventually formed the basis for Grisebach's (1861: 407) new species *S. trinitensis*, which at the time was thought to be endemic to Trinidad.

No further information about the correct nomenclatural status of the genus *Lasiostoma* Schreb., the basionym of *S. bredemeyeri*, and the location of Bredemeyer's specimen at B was published by Krukoff in his subsequent publications (Krukoff 1972; Krukoff and Barneby 1973, 1974; Krukoff 1976, 1977, 1978, 1979a, 1979b, 1980, 1982a, 1982b). Also, there is no publication updating the location and typification of the type materials of *S. pedunculata* and *S. trinitensis*, both taxa currently in synonymy under *S. bredemeyeri*. Thus, we clarify the nomenclature of *Lasiostoma* and its former species *L. bredemeyeri*, describe the location of the type materials of all the names involved, and lectotypify its synonyms *S. pedunculata* and *S. trinitensis*.

Material and methods

We examined herbarium material from 13 herbaria; seen in-person at F, GH, NY, and US; or seen online as digital images from B, BM, G, GOET, K, P, TCD, TRIN, and W (acronyms according to Thiers, updated continuously). All nomenclatural actions follow the Shenzhen Code (Turland et al. 2018).

Results and discussion

Notes on *Lasiostoma* and *Rouhamon*

Schreber (1789: 85) validly published the monospecific genus *Lasiostoma* as an avowed substitute (replacement name) for *Rouhamon* witnessed by the fact that the only species included in *Lasiostoma* was *Rouhamon guianensis* (Turland et al. 2018: Art. 6.11). However, *Rouhamon* (Aublet 1775: 93) is legitimate and has priority, making *Lasiostoma* an illegitimate and superfluous name (Turland et al. 2018: Art. 52.1, 52.2). Later, Bentham (1843: 224) published the homonym *Lasiostoma* Benth. in Rubiaceae (type species: *L. loranthifolium* Benth.), but this name is also illegitimate because *Lasiostoma* Schreb. had already been described (Turland et al. 2018: Art. 53.1). The illegitimacy of *Lasiostoma* Schreb. does not affect the legitimate status of species effectively published under it, unless the publications of these species are in disagreement with other rules of the Code (Turland et al. 2018: Art. 55.1). *Rouhamon* and *Lasiostoma* are correctly placed as synonyms of *Strychnos*.

Notes on *Strychnos bredemeyeri*

We found two specimens of the type material of *Lasiostoma bredemeyeri*, the lectotype designated by Krukoff and Barneby (1969b: 181) at W (Jacquin's herbarium; *Bredemeyer s.n.*, W0078191; Fig. 1A) and an isolectotype at B (Willdenow's herbarium; *Bredemeyer s.n.*, BW02865000, BW02865010; Fig. 1B, C). Both specimens have the names "Bredemeyer" and "Caracas" annotated, but only the isolectotype at B has an original label containing the same diagnosis used in the protologue of the species: "Lasiostoma glabra, *corollis fauce glabris*" (Fig. 1B).

Krukoff never mentioned Bredemeyer's specimen at B (BW02865000, BW02865010) in any of his subsequent works (Krukoff 1972; Krukoff and Barneby 1973, 1974; Krukoff 1976, 1977, 1978, 1979a, 1979b, 1980, 1982a, 1982b), but we found a photograph of this specimen housed in the type photograph collection of the New York Botanical Garden (Negative No. 1163; sheet without barcode or access number and not available online; Fig. 2). The photograph was identified as *S. bredemeyeri* by Krukoff in 1975 and contains a typewritten and a handwritten note made by Krukoff (Fig. 2B, C). In these notes, Krukoff stated that the diagnosis "Lasiostoma glabra, *corollis fauce glabris*" (BW02865000; Fig. 1B) was probably proposed by Willdenow, but the epithet 'glabrum' was deliberately altered by Schultes and Schultes (1827: 64) to 'bredemeyeri' because a glabrous corolla throat was not diagnostic of the species based on the pilose inner surface of the corolla in Bredemeyer's specimen. The etymology of *Lasiostoma* is about the hairy, woolly (lasio- from Greek) mouth (-stoma from Greek), probably referring to the characteristic whitish-woolly inner surface of the corolla tube of *S. guianensis* that extends from the near base to the lower half of the corolla lobes (Sandwith 1933: 400; Krukoff 1972: 236). Schultes and Schultes (1827: 64) perhaps changed the epithet 'glabrum' to 'bredemeyeri' to avoid a contradictory combination such as "Lasiostoma glabrum", however, the contradictory diagnosis was kept the same (glabrous corolla throat). "Lasiostoma glabrum" was cited as part of the diagnosis of *L. bredemeyeri*, and therefore this cannot be considered as a name because the new taxon described was *L. bredemeyeri*. Consequently, "L. glabrum" is not a potential homonym of *Strychnos glabra* Sagot ex Progel (Progel 1868: 275) as also expressed in Krukoff's notes (Fig. 2B, C). "Lasiostoma glabrum" was eventually cited by De Candolle (1845a: 18), but is a nomen nudum (Turland et al. 2018: Art. 38.1, 38.2, 38.8).

Despite the illegitimacy of *Lasiostoma* Schreb. and considering that a validating description need not be diagnostic of the new taxon (Turland et al. 2018: Art. 38.1), *L. bredemeyeri* was validly published and its nomenclatural application is correct due to priority over the other taxa currently in its synonymy (see below). Sprague and Sandwith (1927: 128) were the first authors to validly publish the new combination of *Strychnos bredemeyeri* (Turland et al. 2018: Art. 41.3) as mostly cited in all subsequent publications of Krukoff, except in Krukoff and Barneby (1969a: 45) when it was incorrectly attributed to Badillo (1947: 247).

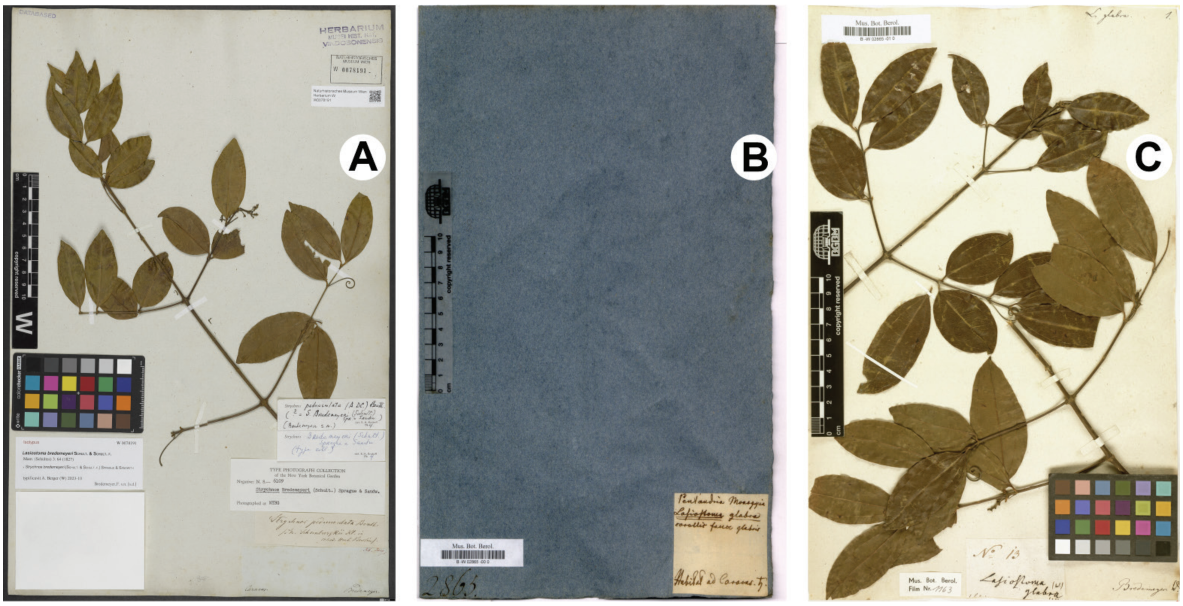
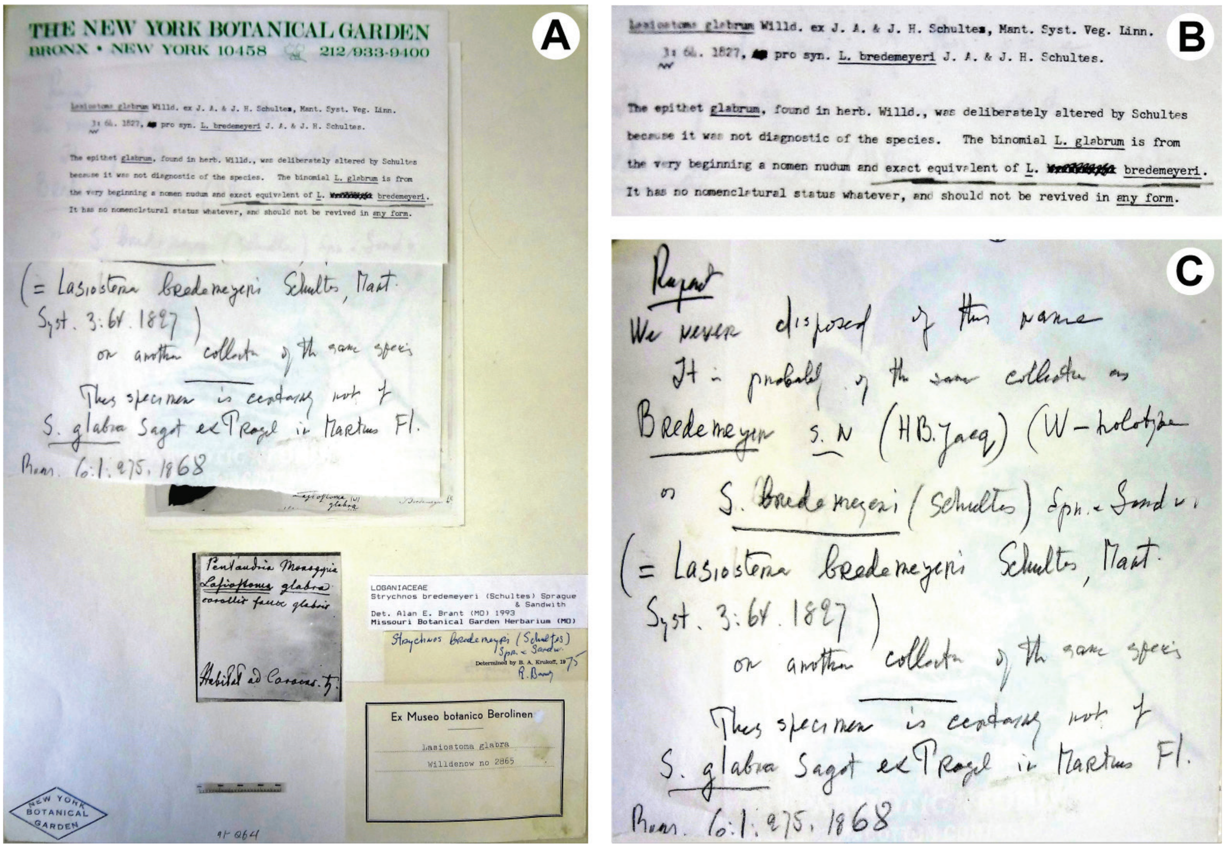


Figure 1. Type specimens of *Lasiostoma bredemeyeri* Schult. & Schult.f **A** lectotype conserved in the Jacquin herbarium at W (*Bredemeyer s.n.*; W barcode W0078191) **B, C** isolectotype conserved in the Willdenow herbarium at B (*Bredemeyer s.n.*; B barcodes BW02865000 and BW02865010, respectively).



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Lasiostoma glabrum Willd. ex J. A. & J. H. Schultes, Mant. Syst. Veg. Linn. 3: 64. 1827, pro syn. L. bredemeyeri J. A. & J. H. Schultes.

The epithet glabrum, found in herb. Willd., was deliberately altered by Schultes because it was not diagnostic of the species. The binomial L. glabrum is from the very beginning a nomen nudum and exact equivalent of L. bredemeyeri. It has no nomenclatural status whatever, and should not be revived in any form.

Repeat
We never disposed of this name
It is probably of the same collection as
Bredemeyer s. N (HB. Jacq) (W-holotype
or S. bredemeyeri (Schultes) Spr. & Sandw.
(= Lasiostoma bredemeyeri Schultes, Mant.
Syst. 3: 64. 1827)
on another collection of the same species
This specimen is certainly not of
S. glabra Sagot ex Progel in Martius Fl.
Bras. 6:1: 275. 1868

Pentandria Monogynia
Lasiostoma glabra
corollis fauce glabris
Habitat ad Caracas.

LOGANIACEAE
Strychnos bredemeyeri (Schultes) Sprague & Sandwith
Det. Alan E. Brant (MO) 1993
Missouri Botanical Garden Herbarium (MO)

Strychnos bredemeyeri (Schultes) Spr. & Sandw.
Determined by B. A. Krukoff, 1975
R. Brant

Ex Museo botanico Berolinensi
Lasiostoma glabra
Willdenow no 2865

NEW YORK BOTANICAL GARDEN

Figure 2. A–C sheet deposited in the type photograph collection of the New York Botanical Garden (Negative No. 1163; sheet without barcode or access number and not available online) containing a photograph of the isolectotype of *Lasiostoma bredemeyeri* Schult. & Schult.f. conserved in the Willdenow herbarium at B (*Bredemeyer s.n.*; Fig. 1B,C) and two overlapping notes made by Krukoff **A** overview; note the detail of the original label containing the description "Lasiostoma glabra, *corollis fauce glabris*" (at center) and Krukoff's identification tag made in 1975 (at right) **B** detail of the uppermost typewritten note made by Krukoff **C** detail of the basalmost handwritten note made by Krukoff (all images made by R. B. Setubal).

Notes on *Strychnos pedunculatum*

The type material of *Rouhamon pedunculatum* was collected during the brothers Robert (R.H. Schomburgk) and Richard Schomburgk's (M.R. Schomburgk) expedition to Guyana in 1840–1844. While the protologue of the species mentions the type locality as "In Guyana brit. ad Roraima", the route indicated on the map and the respective text in Schomburgk (1922: 140; Map. 5) suggests that the type material was collected during the passage through the confluence of the Surumu and Cotingo Rivers, close to "Mount Piriwai" in October 1842, in the State of Roraima, Brazil. The holotype of *R. pedunculatum* was not indicated, and the lectotype selected here (G barcode G00132188) has the indication "Herb. Prodr. (G–DC)", suggesting it to be part of the original material seen by De Candolle (Turland et al. 2018: Art. 9.3, 9.4). We also verified the existence of a second specimen identified as *R. pedunculatum* housed at G–DC (G barcode G00132189), but this sheet does not have any label or information about this collection. We contacted herbarium G about the origin of this second specimen, but the staff responded that there is not enough information to accurately tell whether these two images containing two different barcodes might be interpreted as two or only one gathering (Fred Stauffer, curator of herbarium G, pers. comm). Therefore, we did not include this specimen in the type material of *R. pedunculatum*.

Three specimens without original labels but bearing written indications of "Schomburgk" and "Br. Guiana" have the alternative collector number "792" (photograph of specimen at F, Catalog No. 620082; not available online – not to be confused with F barcode V0044336F; see further) or "792.B" (K barcodes K000573484 and K000573485; Fig. 3). This number led to different citations of the type material of *R. pedunculatum* by different authors: "*R.H. Schomburgk 482* and *792B*" (Bentham 1857: 105; Progel 1868: 275), "*R.H. Schomburgk 482=792B*" (Sandwith 1933: 397, 1935: t. 3225), and "*R.H. Schomburgk 482* and *M.R. Schomburgk 792B"* (Krukoff and Monachino 1942: 291). The F specimen with only the number "792" (Fig. 3B) consists of a single fragment taken from an original specimen housed at B that unfortunately appears not to have been photographed by J. Francis McBride of the Field Museum and was probably destroyed during WWII. While this specimen is not available online, we verified the existence of a second collection labeled as "R.H. Schomburgk 792", available online at F, but this is not a specimen of *Strychnos*, and is identified as type material of *Lecythis schomburgkii* O.Berg (F barcode V0044336F).

The two K specimens (Fig. 3C, D) are the only material that have both numbers ("482" and "792.B") written juxtaposed, and a possibility is that the letter "B" was added to the number "792" to represent the existence of the collection number "792" written in the label of the B specimen destroyed in WWII. Due to the lack of evidence to confirm if these three specimens represent true duplicates of "*R.H. Schomburgk 482*", we excluded these specimens from the type material of *R. pedunculatum*, at least until new evidence is available.

We also examined two additional specimens labeled *M.R. Schomburgk s.n.* (BR barcode BR0000005859795; GH, sheet without barcode or access number and not available online) without date, locality or collection number, and with label and handwriting that clearly differs from all other specimens. This material was cited as additional material examined and not type collection by Progel

Figure 3. Comparison of labels on four specimens of *Rouhamon pedunculatum* A.DC **A** lectotype showing original label "*Schomburgk 482*" (G barcode G00132188) **B–D** specimens of *R. pedunculatum* without original labels and containing alternative numbers **B** specimen with the alternative number "792" (F Catalog No. 620082; not available online; image from R. B. Setubal) **C, D** specimens with the numbers "482" and "792.B" written juxtaposed (K barcodes K000573484 and K000573485, respectively).

(1868: 275) and Sandwith (1933: 397), a position that we also share. Finally, the specimens BR0000005859795 and W0078192 also have the designation "*Strychnos schomburgkiana* Klotzsch" (Schomburgk 1848b: 1144), which is a *nomen nudum* (Turland et al. 2018: Art. 38.1, 38.2, 38.8).

Notes on *Strychnos trinitensis*

The protologue of *S. trinitensis* notes "Trinidad, *Crueger* at Caura", indicating that the type material was collected by Herman Crueger (past director of the Trinidad Botanical Garden) at the Caura or Tacarigua River, a tributary of the Caroni River in the Northern Range of Trinidad Island. All the type material examined has the information "Caura, Sept. 1849", and the name "Crueger" written with different legibility (Fig. 4). The protologue of *S. trinitensis* did not indicate the holotype, and the lectotype selected here (GOET barcode GOET005464) has the stamp of "Herbarium Grisebachianum", suggesting that it is part of the original material seen by Grisebach (1861: 407; Turland et al. 2018: Art. 9.3, 9.4).

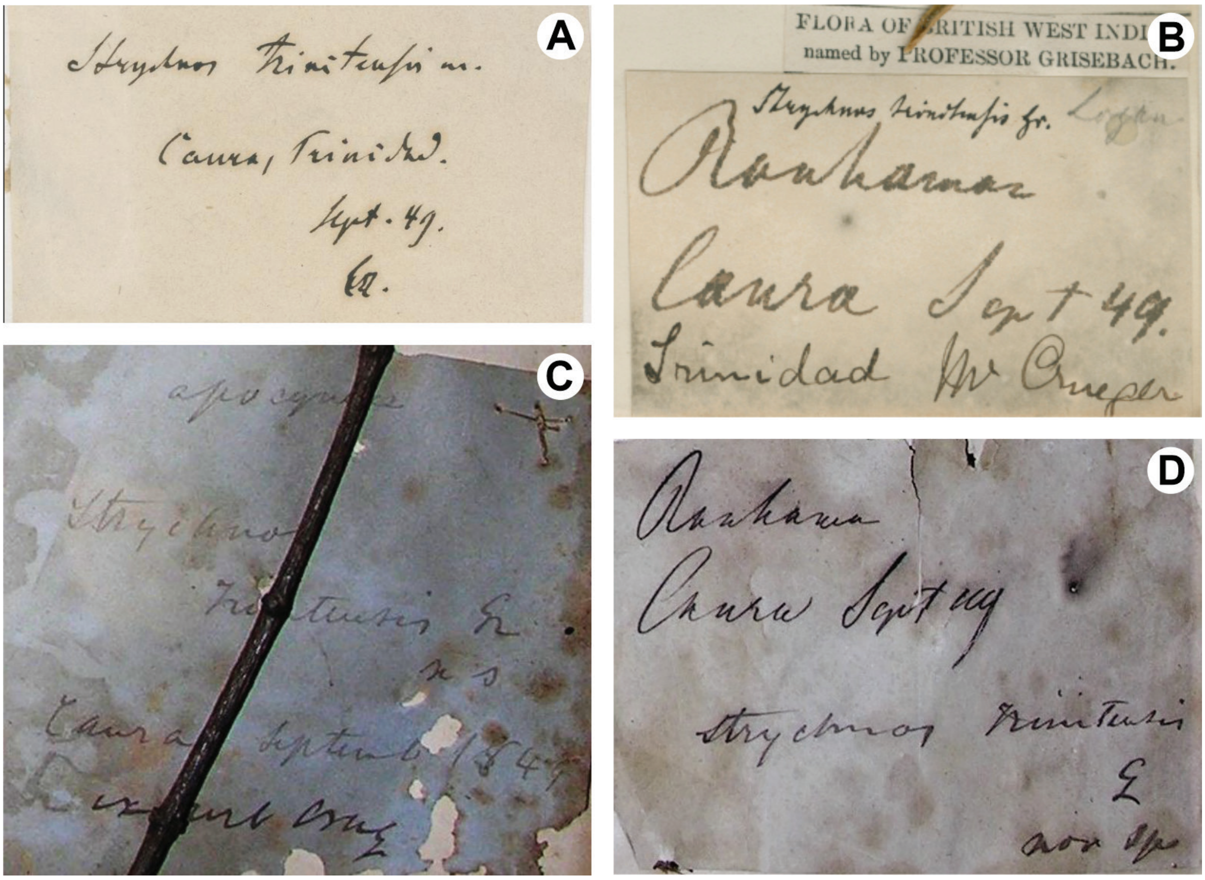

Figure 4. Comparison of labels on four type specimens of *Strychnos trinitensis* Griseb **A** lectotype (*H. Crueger s.n.*, GOET barcode GOET005464) **B–D** isolectotypes **B** K barcode K000573430 **C** TRIN Catalog No. 258 **D** TRIN Catalog No. 1529.

***Strychnos bredemeyeri* (Schult. & Schult.f.) Sprague & Sandwith, Bull. Misc. Inform. Kew 3: 128. 1927. Type: Venezuela. Caracas, [1786–1788] (fl.), *F. Bredemeyer s.n.* Lectotype (designated by Krukoff & Barneby [1969b: 181]): W [W0078191]; isolectotype: B [BW02865000, BW02865010].**

≡ *Lasiostoma bredemeyeri* Schult. & Schult.f., Mant. 3: 64. 1827.
≡ *Rouhamon bredemeyeri* (Schult. & Schult.f.) DC. in A.P. De Candolle, Prodr. 9: 18. 1845.
≡ *Lasiostoma glabrum* Willd. ex DC. in A.P. De Candolle, Prodr. 9: 18. 1845. nom. nud.
= *Rouhamon pedunculatum* A.DC. in A.P. De Candolle Prodr. 9: 561. 1845. Type: British Guiana [Brazil]. [Roraima]: ad Roraima, [Oct] 1842 (fl.), *R.H. Schomburgk 482*. Lectotype (designated here): G [G00132188]; isolectotypes: BM [BM000952958], F [V0062158F, V0062159F], G [G00368309, G00368310], GH [GH00076757], NY [NY00297387], P [P00647601, P00647602], TCD [TCD0000695], US [US00112974], W [W0078192, W0196054]).
≡ *Strychnos schomburgkiana* Klotzsch, Reis. Br.-Guiana [Ri. Schomburgk] 3: 1144. 1848. nom. nud.
≡ *Strychnos pedunculata* (A.DC.) Benth., J. Proc. Linn. Soc., Bot., 1: 105. 1857.
= *Strychnos trinitensis* Griseb., Fl. Brit. W.I.: 407. 1861. Type: Trinidad and Tobago. Caura, Sep 1849 (fl.), *H. Crueger s.n.* Lectotype (designated here): GOET [GOET005464]; isolectotypes: K [K000573430], NY [NY00297487], TRIN [Catalog Nos. 258, 1529], US [US01100481, US00112982]).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: RCF, RBS, JP, LS. Data curation: JP, RCF, RBS, LS. Formal analysis: RBS, JP, RCF, LS. Funding acquisition: RBS, LS, RCF. Investigation: JP, LS, RCF, RBS. Methodology: RCF, JP, RBS. Project administration: RBS, RCF. Resources: RBS, LS, RCF. Supervision: RCF. Validation: JP, LS, RCF. Writing - original draft: RBS. Writing - review and editing: LS, RBS, RCF, JP.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

The polyphyletic Caucasus-centred *Campanula* subg. *Scapiflorae* (Campanulaceae) revisited with a newly circumscribed *C.* sect. *Tridentatae* for its core clade

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Abstract

Campanula L. is among the genera with the highest number of endemics in the Caucasus ecoregion. A group of attractive alpine and subalpine perennial rosette plants with short single-flowered stems centred in the Caucasus has been treated as *Campanula* subg. *Scapiflorae* or at other ranks, with considerably varying circumscription and classification. Molecular phylogenetic analysis of three plastid DNA regions (*trnK/matK*, *petD*, *rpl16*) of a strongly extended sampling, comprising 23 of the 27 commonly accepted taxa (85%) with 330 accessions built on and guided by the results of our previous study of the group, confirmed the polyphyly of *C.* subg. *Scapiflorae* in any of its circumscriptions. The core clade of the group comprises exclusively endemics and near-endemics of the Caucasus and is treated here as *C.* sect. *Tridentatae* in a revised circumscription. The phylogenetic relationships of the disparate other elements of the *Scapiflorae* group are outlined.

Key words: Bellflower family, Caucasus range, molecular phylogenetics, taxonomy

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Introduction

With approximately 600 species (Lammers 2007; Mansion et al. 2012; Jones et al. 2017), *Campanula* in the wide sense is among the one hundred largest plant genera (Frodin 2004), representing also the largest genus in the family Campanulaceae (order Asterales). Although *Campanula* was formally established by Linnaeus, it was first described more than 200 years earlier by Fuchs (1542), based on the species later named *C. trachelium* L. *Campanula* includes mostly perennial herbs with alternate leaves, bell-shaped, mostly purplish blue, pentamerous, bee-pollinated flowers and capsule fruits (Candolle 1830; Boissier 1875; Fedorov 1957). The members of the genus are found in forests, meadows, steppes and semi-deserts in temperate and subtropical zones of the northern hemisphere and is most abundant and diverse in the subalpine and alpine zones of mountain ranges (Fedorov 1957; Kovačić 2004, Jones et al. 2017). In the Caucasian flora, *Campanula* is one of the 17 genera with the highest number of endemic species (Dolukhanov 1966; Zazanashvili and Mallon 2009).

One group of species in *Campanula*, hitherto recognized as *C.* subg. *Scapiflorae* (Boiss.) Oganesian, is mainly endemic to the Caucasus. The group is characterised by single flowers, basal leaf rosettes and preference of alpine and subalpine habitats with rocky substrate (Silakadze et al. 2019). Sharing reflexed appendages between the calyx lobes and 3-locular capsules dehiscing down to the base led Fedorov (1957) to conclude that they belong to the core of *Campanul*a. This core group corresponds to the large clade CAM 17 found by Mansion et al. (2012) in their overall analysis of *Campanula* and allies, which also includes *C. latifolia* L., the type of the name *Campanula*. In contrast, the genus in any of its current wider circumscriptions is excessively paraphyletic to a number of segregate genera mostly differing in floral traits (Mansion et al. 2012; Xu and Hong 2020).

The *Scapiflorae* group is an example of a complex species group in *Campanula* in the sense that different authors arrived at very different conclusions on the numbers and boundaries of the taxa to be recognized in this group. Whereas Ruprecht (1867), Boissier (1875) and Fomin (1905) had recognized 13, eight and 12 species, respectively, Fedorov (1957) and Kharadze (1949, 1976) recognized many more species (26 and 24, respectively). Oganesian (2000) accepted a similar number of taxa (25), of which 20 were at the species level and five additional subspecies. Seven of the species accepted by Fedorov (1957) and Kharadze (1976) were treated by her as synonyms, whereas, on the other hand, she added eight more species not included to the *Scapiflorae* before. In the most recent treatment Victorov (2001, 2002) recognized 11 species with seven subspecies. Whereas Mansion et al. (2012) just placed several of these species in one of the major *Campanula* clades (CAM 17), the addition of further molecular characters by Jones et al. (2017) and Silakadze et al. (2019) revealed many of them as part of a well-supported subclade of CAM 17, whereas others appeared distantly. However, several species hitherto classified in *Scapiflorae* remained unsampled.

The majority of species that were considered as part of the *Scapiflorae* group are endemics of the Caucasus. The distribution area of two species *Campanula ledebouriana* Trautv. and *C. minsteriana* Grossh. extends from the Caucasus into Anatolia and adjacent mountains south-eastwards; two species, *C. bornmuelleri* Nábělek and *C. pulvinaris* Hausskn. & Bornm., occur in Anatolia only, and two further are European, of which one (*C. alpina* Jacq.,) is restricted to the eastern Alps and the Carpathians, the other (*C. orbelica* Pančić) to the mountains of the central and eastern Balkans (Ronikier and Zalewska-Gałosz 2014); two species, *C. capusii* (Franch.) Fed. and *C. lehmanniana* Bunge, occur in middle Asia and two species, *C. chamissonis* Fed. and *C. dasyantha* M. Bieb., are distributed in North-East Asia. Moreover, recent phylogenetic studies (Silakadze et al. 2019) revealed that *C. ciliata* Steven, the type of the name *C.* subg. *Scapiflorae*, is only distantly related to the core clade of this group, and more closely related to *C. latifolia*, the type species of the name *Campanula*.

The present paper has three aims: Based on a considerably increased sampling of *Campanula* species in the Caucasus region and species previously assigned to *C.* subg. *Scapiflorae* (1) to further evaluate the composition of the *Scapiflorae* clade (in the sense of Silakadze et al. 2019), (2) to update the classification of the *Scapiflorae* group at the supraspecific level; and (3) to further examine phylogenetic relationships within this clade.

Materials and methods

Taxon sampling

We densely sampled the species diversity of *Campanula* subg. *Scapiflorae* across its entire geographical range. Samples were collected during fieldwork in Armenia, Georgia, and Russia, and additional material from various countries was examined from the herbaria of B, DAG, ERE and TBI (Appendix 1). Compared to our previous study (Silakadze et al. 2019), we added nine more taxa with multiple accessions and covering a wider geographical range of the Caucasus region. These include eight Caucasian endemics, i.e., *C. anomala* Fomin, *C. ardonensis* Rupr., *C. besenginica* Fomin, *C. doluchanovii* Kharadze, *C. fominii* Grossh., *C. kadargavanica* Amirkh. & Komzha, *C. kryophila* Rupr. *C. sosnowskyi* Kharadze and the Caucasian and East Anatolian *C. ledebouriana* (see Suppl. material 3). One accession previously identified as *C.* cf. *aucheri* A. DC. (CAM217) was excluded from our extended dataset, as we were not sure about the accuracy of the sequences. For *C. doluchanovii* and *C. meyeriana* Rupr., we were able to include sequences from type material. We also included additional accessions of two species *C. ciliata* and *C. petrophila* Rupr., to test with material from different localities if these species are indeed not part of the *Scapiflorae* clade.

Our sampling of the *Scapiflorae* group contained 23 of the 27 commonly accepted taxa (85%) with 330 (271 newly included) accessions. In addition, we increased the sampling of other Caucasian *Campanula* species, located in the CAM 17C clade (Mansion et al. 2012; Jones et al. 2017; Silakadze et al. 2019), by 54 new accessions, some species from multiple localities. Overall, our sampling of *Campanula* was increased by 325 additional sequences representing three genomic regions of the plastid DNA (*trnK/matK*, *petD* and *rpl16*), more than doubling the sampling of our previous study (Silakadze et al. 2019).

DNA extraction, amplification, sequencing, and alignment

DNA extraction, amplification, sequencing and alignment followed Silakadze et al. (2019). For newly generated sequences from the leaf tissue of older herbarium specimens, we used a CTAB protocol with extraction of three fractions for each plant sample (Borsch et al. 2003). As DNA was often much degraded and also contained secondary metabolites, we combined fractions I, II and III of each sample and cleaned them using DNeasy PowerClean Pro Cleanup Kit. DNA size (bp) and concentration (ng/µl) were checked using Fragment Analyser (www.aati-us.com), and 10 ng/µl was considered as ideal for the polymerase chain reaction (PCR). DNA samples were diluted with purified water depending on the concentration; if the concentration was less than 10 ng/µl, the amount of DNA was duplicated in the PCR mix. DNA stocks were kept at −20 °C.

For amplification and sequencing, we mostly used the same primers as in our previous study (Silakadze et al. 2019). For *petD* we used shorter primers designed by Schäferhoff (unpublished), and, in addition, we designed new, shorter internal primers for *rpl16* and *trnK/matK* (see Suppl. material 4). Primer design was carried out using the *Campanula* alignment published in Silakadze et al. (2019), using the program Seqstate 1.4.1 (Müller 2005).

All pherograms were checked using PhyDE version 0.9971 (Müller et al. 2010) and manually assembled using the motif-based alignment approach for non-coding plastid DNA (Kelchner 2002; Borsch et al. 2003; Löhne and Borsch 2005). Indels were coded as binary characters using the Simple Indel Coding approach (Simmons and Ochoterena 2000) as implemented in SeqState version 1.4.1 (Müller 2005). Consensus DNA sequences were submitted to ENA (European Nucleotide Archive) (www.ebi.ac.uk/ena/), using the software tool EMBL2checklists (Gruenstaeudl and Hartmaring 2019).

Phylogenetic analysis

We used the matrix including the same plastid DNA regions (*trnK*/*matK*, *petD* and *rpl16*) as in Silakadze et al. (2019). Phylogenetic analyses were performed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) approaches.

Maximum parsimony (MP) analysis was done in PAUP version 4.0b10 (Swofford 2002), using the parsimony ratchet settings (Nixon 1999) conducted in PRAP version 2.0b3 (Müller 2004). As ratchet parameters, we selected 1,000 iterations, unweighting 25% of the positions randomly (weight = 2), and 100 additional random cycles. Jackknife (JK) support was derived through a single heuristic search in PRAP with 10,000 replicates using tree bisection-reconnection (TBR) branch swapping and in each replicate, 36.79% of the characters were deleted.

Maximum likelihood (ML) analyses were executed with RAxML version 8.2.12 (Stamatakis 2014) on the CIPRES Science Gateway V 3.3 (Miller et al. 2011), using the CAT approximation (Stamatakis 2006) of the GTR model of the DNA partitions and BINCAT for the binary indel partitions (Stamatakis 2014). Rapid bootstrap analyses (BS) were conducted with 1,000 iterations integrated with a thorough ML search.

For Bayesian inference, the nucleotide dataset was divided into six partitions and the likelihood scores of models of sequence evolution were calculated for each using jModelTest version 2.1.7 (Darriba et al. 2012), choosing the best-fitting model under Akaike's Information Criterion (AIC). Three partitions represented *trnK/matK* (*trnK* 5' intron = GTR+G, *matK* gene = TVM+G, and *trnK* 3' intron = GTR+G), two partitions *petD* (*petB-petD* intergenic spacer = TVM+I+G and *petD* exon/intron = TVM+G), and one partition the *rpl16* intron (TVM+I+G). The indel matrices were added using the restriction site model (Ronquist and Huelsenbeck 2003).

Bayesian inference analyses was carried out in MrBayes v.3.2.7.a (Ronquist et al. 2011) on CIPRES (Miller et al. 2011), with four runs and four chains each performed for 20 million generations, sampling every 5000th generation. We checked convergence of the runs into stationarity by examining the average standard deviation of split frequencies and post-burn-in effective sampling size (ESS). The first 10% of trees were discarded as burn-in; the remaining trees were used to construct a 50% majority-rule consensus tree.

Additionally, Maximum parsimony (MP) and Maximum likelihood (ML) were applied to a matrix with two further species, *Campanula kadargavanica*, and *C. pulvinaris*, for which only *petD* and *rpl16* sequences were available.

Results

Phylogenetic analysis

The final alignment of three combined plastid genomic regions (*trnK/matK*, *petD*, and *rpl16*) containing 536 concatenated sequences (325 newly generated) had a total length of 5,361 positions, of which *trnK/matK* had 2,854, *petD* 1,099 and *rpl16* 1408. To document intraspecific variation, multiple samples for the same taxa were maintained in the alignment. In the multiple sequence alignment of *trnK/matK*, we excluded six hotspots of uncertain homology or poly-A/T microsatellites [positions 633–738; 746–779; 785–788; 2539–2627; 2754–2763; 2769–2773]. In *petD* one hotspot was excluded with poly-A [position 3681–3684] and in *rpl16* ten hotspots were excluded, including some poly A/T microsatellites or other sequence elements [positions 3962–3969; 4066–4083; 4123–4132; 4239–4249; 4380–4390; 4417–4419; 4463–4470; 4811–4820; 4835–4846; 5219–5252]. The final concatenated plastid matrix contained 4,984 bases (2,606 bp of *trnK/matK*, 1,095 bp of *petD*, and 1,283 bp of *rpl16*, respectively). Simple Indel Coding provided further 270 binary characters (104 of *trnK/matK*, 61 of *petD*, and 105 of *rpl16*).

Bayesian inference, maximum likelihood, and maximum parsimony analyses of the concatenated plastid dataset produced largely identical topologies and revealed significant statistical support values for various nodes at PP > 0.95 and BS and JK values > 70%, and strong support values at PP > 0.99 and BS and JK values > 90%.

Twelve species hitherto considered as members of the *Scapiflorae* group were found distantly related to the core *Scapiflorae* clade (Fig. 1; see also Suppl. materials 1, 2, 3).

Campanula alpina, which is sister to *C. hofmanii* (Pant.) Greuter & Burdet and *C. takhtadzhianii* Fed. with strong support (PP = 1, BS = 100, JK = 99.84), was resolved in clade CAM 17A2.

Campanula bornmuelleri, *C. ledebouriana* and *C. minsteriana* were found related to each other in a polytomy with good support (PP = 0.99, BS = 75, JK = 56.76), all nested in clade CAM 17B3.

Campanula ciliata, *C. dasyantha*, *C. chamissonis* and *C. dzaaku* Albov were resolved in the clade CAM 17C1 with good support (PP = 1, BS = 75, JK = 70.61). The various *C. ciliata* samples appear all in one clade which forms a trichotomy with *C. mirabilis* Albov and a clade including the remainder of CAM 17C1. In the last clade, *C. dasyantha* and *C. chamissonis* formed a sister-group with strong support (PP = 1, BS = 92, JK = 83.01), and the two *C. dzaaku* samples emerged in a separate subclade of their own with strong support (PP = 0.99, BS = 100, JK = 69.64).

Campanula petrophila was found sister to *C. raddeana* Trautv. with strong support (PP = 1, BS = 91, JK = 96.6), nested in clade CAM 17C2. Notably, *C. latifolia*, the type of the genus name, fell in the same clade as *C. petrophila*.

Campanula hypopolia Trautv. (Clade CAM 17C6) and *C. andina* Rupr., forming a trichotomy (Clade CAM 17C8) with *C. suanetica* Rupr. and *C. ossetica* M. Bieb., were found nested in the polytomy with the *C. pendula* (Clade CAM 17C7) and the core *Scapiflorae* clade (CAM 17C9).

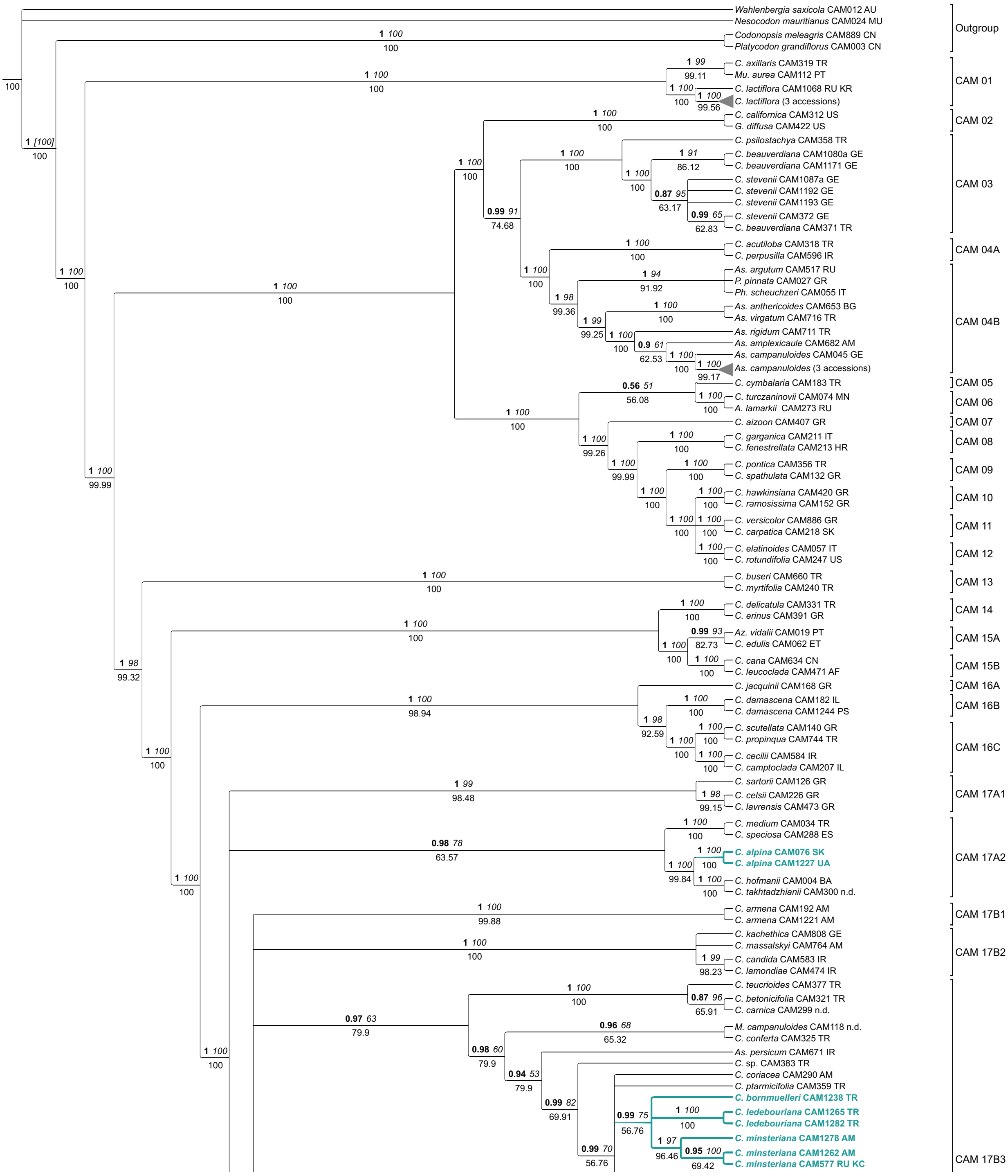

Figure 1. Bayesian 50% majority-rule consensus tree of the combined dataset of the Caucasian *Campanula* species based on three plastid markers (*trnK/matK*, *petD* and *rpl16*). Values above nodes indicate posterior probabilities (bold) and maximum likelihood bootstrap support (italic), values below nodes indicate maximum parsimony jackknife support, values in square brackets indicate conflicting topologies. Sample designations include the taxon name, DNA lab code, and ISO (international organization for standardization) country code, in case of the Russian part of the Caucasus also the TDWG (Biodiversity Information Standards) code of the territory (n.d. – sample not documented); for DNA lab codes and ISO codes of collapsed terminals with multiple accessions, see Suppl. materials 1, 2. Abbreviations in species names: *A.* – *Adenophora*, *As.* – *Asyneuma*, *Az.* – *Azorina*, *C.* – *Campanula*, *G.* – *Githopsis*, *M.* – *Michauxia*, *Mu.* – *Musschia*, *P.* – *Petromarula*, *Ph.* – *Phyteuma*. Sample designations in bold (in black) indicate species from the core *Scapiflorae* clade, sample designations in blue indicate *Scapiflorae* group members phylogenetically distant from the core clade. Subdivision of the *Scapiflorae* clade by numbered terminal clades (1-17) and geographical distribution of the lineages.

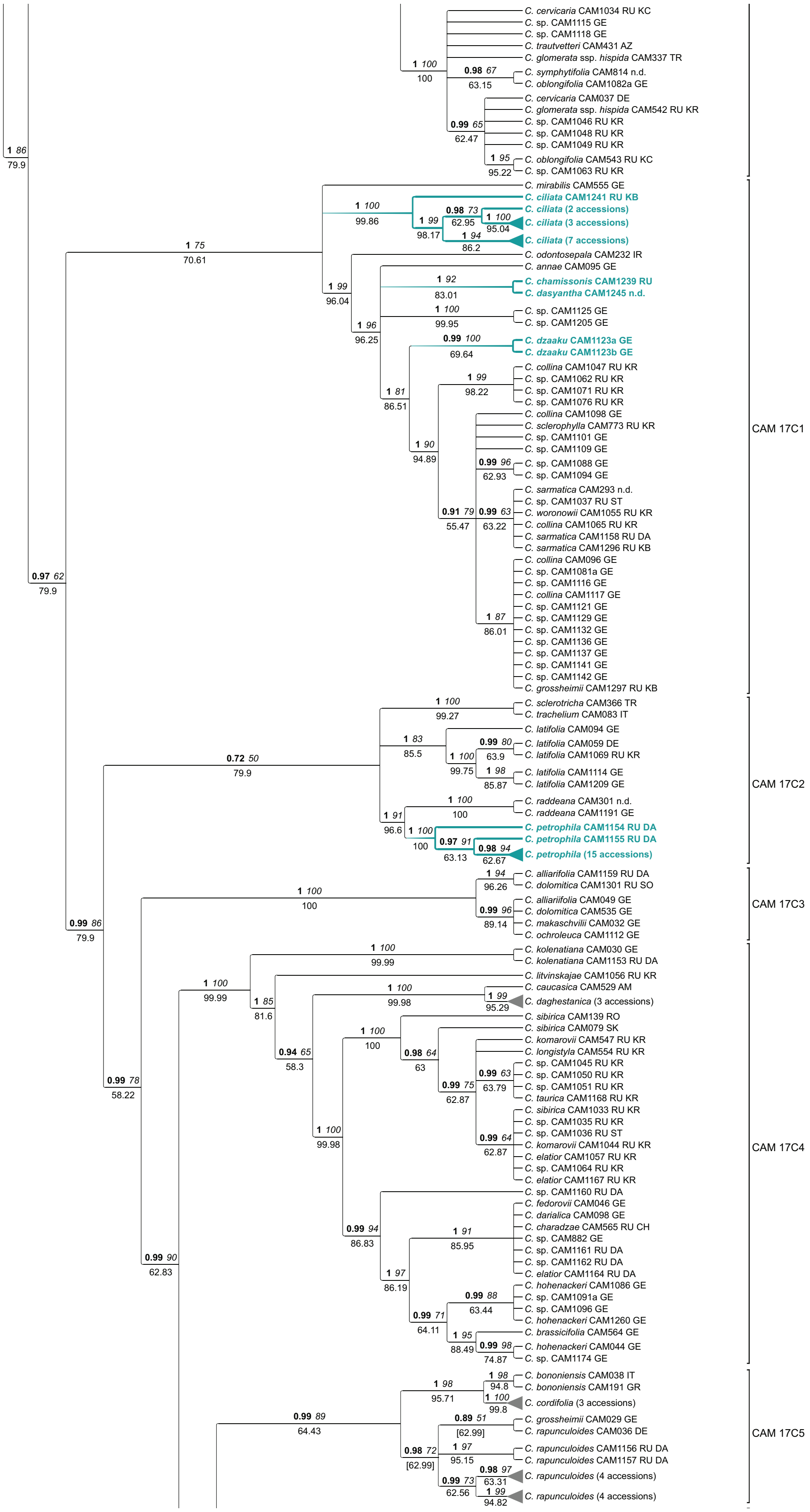

Figure 1. Continued.

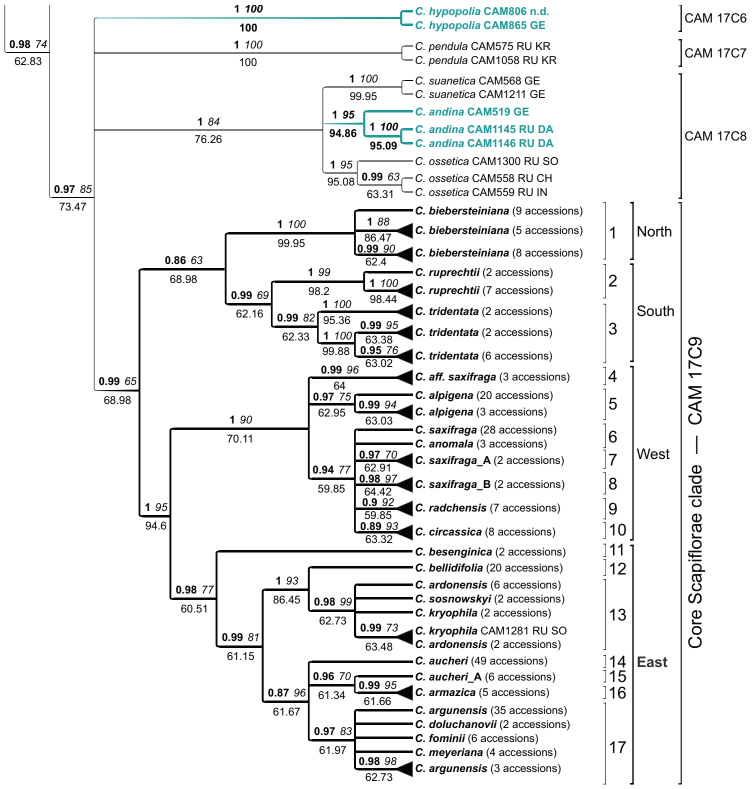

Figure 1. Continued.

The additional tree (see Suppl. material 2; ML and MP), including further species of which only *petD* and *rpl16* sequences were available, revealed that also *Campanula pulvinaris* is not part of the *Scapiflorae* clade and instead nested in clade CAM 17B3 with *C. bornmuelleri*, *C. ledebouriana* and *C. minsteriana*, although without support. Notably, *C. latifolia*, the type of the genus name, fell in the same clade as *C. petrophila*, being sister in a polytomy to two clades, one containing *C. petrophila* and *C. raddeana* and another *C. sclerotricha* Boiss. and *C. trachelium*; all are nested in clade CAM 17C2, which is, however, weakly supported (PP = 0.72, BS = 50, JK = 79.9).

The majority of the taxa of the *Scapiflorae* group were resolved in clade CAM 17C9, here considered the core *Scapiflorae* clade. Within the well-supported *Scapiflorae* core clade (PP = 0.99, BS = 65, JK = 68.9; Fig. 1, see also Suppl. material 1) 17 terminal clades were resolved, which form two larger lineages and sister clades: the lineage A or north/south clade (PP = 0.86, BS = 63, JK = 68.98; Fig. 1, see also Suppl. material 1) and the strongly supported lineage B or west/east clade (PP = 1, BS = 95, JK = 94.6; Fig. 1, see also Suppl. material 1).

The clade A1 corresponds to the *C. biebersteiniana* Roem. & Schult. accessions from the Greater Caucasus, extending to the northern part of the Caucasus region, and hence clade A1 is also referred to as north (N) clade, exhibiting strong supported (PP = 1, BS = 100, JK = 99.95).

The clade A2 contains the terminal clades 2 and 3 with the accessions of *C. ruprechtii* Boiss. and *C. tridentata* Schreb., all from the Lesser Caucasus, extending to the southern part of the Caucasus, and so this clade was also referred to as south (S) clade, likewise moderately supported (PP = 99.69, BS = 69, JK = 62.16).

The clade B1 received strong support (PP = 1, BS = 90, JK = 70.11) and comprises the terminal clades 4 through 10, including the accessions of *C. alpigena* K. Koch, *C. anomala*, *C. circassica* Fomin, *C. radchensis* Kharadze, *C. saxifraga* M. Bieb. and *C.* aff. *saxifraga*, all from the western part of the Caucasus and hence referred to as the west (W) clade.

Finally, the clade B2, which received moderate support (PP = 0.98, BS = 77, JK = 60.51), consists of the terminal clades 11 through 17 and includes the accessions of *C. ardonensis*, *C. argunensis* Rupr., *armazica* Kharadze, *C. aucheri*, *C. bellidifolia* Adams, *C. besenginica*, *C. doluchanovii*, *C. fominii*, *C. kryophila*, *C. meyeriana* and *C. sosnowskyi*, all originating from the eastern part of the Caucasus, and hence referred to as the east (E) clade.

The terminal clade 1 contains 22 accessions of *C. biebersteiniana* and shows strong support (PP = 1, BS = 100, JK = 99.95). Clade 2 covered nine accessions of *C. ruprechtii*, strongly supported (PP = 1, BS = 99, JK = 98.2). Clade 3 includes ten accessions of *C. tridentata* with good support (PP = 0.99, BS = 82, JK = 62.33; Fig. 1, see also Suppl. material 1). Clade 4 with strong support (PP = 0.99, BS = 96, JK = 64) consists of three accessions of uncertain identifications, two labelled *C. besenginica* and one *C. saxifraga*, which we all treat as *C.* aff. *saxifraga*. Clade 5 contains 23 accessions of *C. alpigena* with moderate support (PP = 0.97, BS = 75, JK = 62.95), whereas clade 6 includes three accessions of *C. anomala* and 48 of *C. saxifraga* with weak support (PP = 0.94, BS = 77, JK = 59.85). Clades 7, 8, 9 and 10 are all nested within clade 6, encompassing *C. saxifraga* A with two accessions with moderate support (PP = 0.97, BS = 70, JK = 62.91), *C. saxifraga* B also with two accessions with good support (PP = 0.98, BS = 97, JK = 64.42), *C. radchensis*, comprising seven accessions with moderate support (PP = 0.9, BS = 92, JK = 59.85), and *C. circassica* with eight accessions, also with moderate support (PP = 0.89, BS = 93, JK = 63.32; Fig. 1, see also Suppl. material 1). Clade 11 consists of two accessions of *C. besenginica*, forming a polytomy relative to all other terminal clades in this area of the tree. Clade 12 includes 20 accessions of *C. bellidifolia* and has good support (PP = 1, BS = 93, JK = 86.45), whereas clade 13, nested within clade 12, covered eight accessions of *C. ardonensis*, three of *C. kryophila* and two of *C. sosnowskyi* with good support (PP = 0.98, BS = 99, JK = 62.73). The next terminal clade 14 included 49 accessions of *C. aucheri* with moderate support (PP = 87, BS = 96, JK = 61.67), with clades 15 and 16 nested within clade 14, consisting of six accessions of *C. aucheri* A and five of *C. armazica*, with moderate or good support, respectively (PP = 0.96, BS = 70, JK = 61.34; PP = 0.99, BS = 95, JK = 61.66). Finally, clade 17, also nested within clade 14, included 38 accessions of *C. argunensis*, two of *C. doluchanovii*, six of *C. fominii* and four of *C. meyeriana*, overall with moderate support (PP = 0.97, BS = 83, JK = 61.97; Fig. 1, see also Suppl. material 1).

Discussion

Revised classification of the core *Scapiflorae* clade

The re-circumscription and infrageneric re-classification of the iconic bell-flower genus, *Campanula*, is still in progress (Mansion et al. 2012; Jones et al. 2017; Xu and Hong 2020). It is evident from these and further analyses that applying a phylogeny-based genus concept to *Campanula* will inevitably shatter the genus as it is known traditionally but a detailed analysis of a representative spectrum of morphological characters in a phylogenetic context will be needed to evaluate if conspicuous floral differences are not just caused by adaptive shifts as part of pollination syndromes. What applies to the genus as a whole is also true for the *Scapiflorae* group on a small scale. Silakadze et al. (2019) and the present study revealed that *C.* subg. *Scapiflorae* is an artificial assemblage but resolved a well-supported core lineage, the core *Scapiflorae* clade (Fig. 1, see also Suppl. material 1). Compared to Silakadze & al. (2019), the present study provides a much more in-depth analysis of this group, based on 330 accessions, representing 85% of the taxa of this group. The present study also fully corroborates the results of the previous study by Silakadze et al. (2019) that the core *Scapiflorae* clade and all other elements of the polyphyletic *C.* subg. *Scapiflorae* belong to the core of *Campanula* (Fig. 1, see also Suppl. material 1) defined by inclusion of *C. latifolia* as the type of the generic name in the clade CAM 17 (sensu Mansion et al. 2012 and later authors). We can thus postulate with certainty that the group will remain in *Campanula* also after a future reorganisation of the genus.

Based on research conducted by Silakadze et al. (2019), the *Scapiflorae* clade can be clearly defined and differentiated based on a combination of morphological, distributional and ecological characteristics. These include the presence of calyx appendages, leaf rosettes with a single-flowered stem, and its members typically grow in rocky habitats within the (sub)alpine zone and occur in the Caucasus region and adjacent areas to the south. One of the main results of our studies is that *Campanula ciliata*, the designated lectotype (Fedorov 1957: 256) of the name *Campanula* ser. *Scapiflorae* Boiss. and all combinations based on it, falls far outside the core *Scapiflorae* clade. Consequently, the name *Scapiflorae* is not available for a formal taxonomic recognition of the core clade. Among the authors treating the *Scapiflorae* group, only Fedorov (1957), Kharadze (1976) and Victorov (2002) formally subdivided *C.* subg. *Scapiflorae*. Fedorov (1957) and Kharadze (1976) recognized eleven and ten series, respectively, Victorov (2002) recognized seven sections and his treatment is the one most congruent with our result. Our core clade is represented in his treatment by only two species: *C. tridentata* and *C. bellidifolia*, the latter with five subspecies. They form *C.* sect. *Tridentatae* (Kharadze) Victorov, which also comprises, contrary to our results, the north-east Asian *C. dasyantha* with *C. chamissonis* as its subspecies, and the Caucasian *C. petrophila* and *C. andina*. At section rank the infrageneric epithet *Tridentatae* has priority over any other name; at series rank it is one of nine series names of equal priority for the core clade (Fedorov 1957; Kharadze 1976). Considering the phylogenetic position of the core *Scapiflorae* clade within clade CAM17, we have chosen the rank of section for the core clade, applying the name *C.* sect. *Tridentatae* in our revised circumscription restricted to the Caucasian members only. The choice of the rank, of a section, may appear a bit of a long shot given the unsettled circumscription and classification of a monophyletic genus *Campanula*. However, subgenera may likely be applied at a more inclusive level to name major clades such as CAM 1 to CAM 17, also depending if these can be recognized by morphology. For the time being it should best serve the needs of an unambiguous classification to handle the *Scapiflorae* clade at the level of a section.

Campanula sect. *Tridentatae* (Kharadze) Victorov ≡ *Campanula* ser. *Tridentatae* Kharadze in Zametki Sist. Geogr. Rast. 15: 25. 1949. – Type: *Campanula tridentata* Schreb.
= *Campanula* ser. *Anomalae* Fed. in Komarov (ed.), Fl. SSSR 24: 197. 1957. – Type: *Campanula anomala* Fomin
= *Campanula* ser. *Ardonenses* Fed. in Komarov (ed.), Fl. SSSR 24: 198. 1957. – Type: *Campanula ardonensis* Rupr.
= *Campanula* ser. *Argunenses* Fed. in Komarov (ed.), Fl. SSSR 24: 192. 1957. – Type: *Campanula argunensis* Rupr.
= *Campanula* ser. *Aucherianae* Kharadze in Zametki Sist. Geogr. Rast. 15: 25. 1949 [“*Aucheri*”]. – Type: *Campanula aucheri* A. DC.
= *Campanula* ser. *Bellidifoliae* Fed. in Komarov (ed.), Fl. SSSR 24: 194. 1957. – Type: *Campanula bellidifolia* Adams
= *Campanula* ser. *Besenginicae* Fed. in Komarov (ed.), Fl. SSSR 24: 199. 1957. – Type: *Campanula besenginica* Fomin
= *Campanula* ser. *Kryophilae* Kharadze in Zametki Sist. Geogr. Rast. 15: 25. 1949. – Type: *Campanula kryophila* Rupr.
= *Campanula* ser. *Saxifragiformes* Fed. in Komarov (ed.), Fl. SSSR 24: 190. 1957. – Type: *Campanula saxifraga* M. Bieb.

In our circumscription, the section includes all taxa belonging to the core *Scapiflorae* clade. These are: *Campanula alpigena*, *C. argunensis* (incl. *C. doluchanovii*, *C. fominii*, *C. meyeriana*), *C. armazica*, *C. aucheri*, *C. bellidifolia* (incl. *C. ardonensis C. sosnowskyi*, *C. kadargavanica*, *C. kryophila*), *C. besenginica*, *C. biebersteiniana*, *C. radchensis*, *C. ruprechtii*, *C. saxifraga* (incl. *C. anomala*, *C. circassica*) and *C. tridentata*. They are Caucasian endemics, or near endemics extending into southerly adjacent mountain ranges, growing on rocky to soil-rich substrates predominantly in the subalpine to alpine zone and are morphologically characterised by the presence of calyx appendages, leaf rosettes with short and strictly single-flowered stems. However, the combination of these characters does not represent an exclusive synapomorphy for the core *Scapiflorae* clade but has evolved independently also in the single case of *C. ciliata* (Silakadze et al. 2019), nested in the distant clade CAM 17C1 (see below).

A revised classification of the members of *Campanula* sect. *Tridentatae* will be substantiated and elaborated in two further contributions (Silakadze et al. in prep.; Silakadze and Kilian in prep.).

Phylogenetic position of the *Scapiflorae* members excluded from *Campanula* sect. *Tridentatae*

According to our analysis, 12 species do not belong to the *Tridentatae* clade (Fig. 1, see also Suppl. material 1). These are *Campanula alpina*, *C. andina*, *C. bornmuelleri*, *C. chamissonis*, *C. ciliata*, *C. dasyantha*, *C. dzaaku*, *C. hypopolia*, *C. minsteriana*, *C. ledebouriana*, *C. petrophila* and *C. pulvinaris*. Their phylogenetic positions are briefly discussed in the following.

The *Tridentatae* clade CAM 17C9 is part of a polytomy of exclusively Caucasian endemics, together with the three clades CAM 17C6, C7 and C8 (Fig. 1, see also Suppl. material 1). The first of these clades is represented by *Campanula hypopolia*, which was placed by Victorov in *C.* sect. *Hypopolion* (Fed.) Ogan. of his *C.* subg. *Scapiflorae*, the second is represented by *C. pendula* M. Bieb. The third includes *C. andina*, which was described from the "Andi" range of Dagestan and placed by Victorov (2002) in his *C.* sect. *Tridentatae*, together with *C. suanetica* and *C. ossetica* in an unresolved clade. Notably, none of them except the members of the *Tridentatae* clade have unbranched single flowered stems.

Campanula ciliata is resolved as member of clade CAM 17C1, far distant from the *Tridentatae* clade. All seven authors who have studied the *Scapiflorae* group agreed that *Campanula ciliata* belongs to that group (see Suppl. material 3) as defined by a set of mostly convergent morphological characters. The name *Scapiflorae*, with its type *C. ciliata*, thus applies to the clade CAM 17C1 (Fig. 1, see also Suppl. material 1), also containing the *Scapiflorae* members *C. chamissonis*, *C. dasyantha* and *C. dzaaku*, and the other Caucasian species *C. annae* Kolak., *C. collina* Sims, *C. grossheimii* Kharadze, *C. mirabilis*, *C. odontosepala* Boiss., *C. sarmatica* Ker Gawl., *C. sclerophylla* (Kolak.) Ogan. and *C. woronowii* Kharadze. At subgenus rank, *C.* subg. *Annae* (Kolak.) Ogan. is also available but does not have priority over *Scapiflorae*, whereas at sectional rank, *C.* sect. *Annae* would have priority for clade CAM 17C1. Within this clade, multiple accessions of the Caucasian *C. ciliata* form a trichotomy with *C. mirabilis* and the remainder of the clade, which also includes, besides the Caucasian members, *C. odontosepala* from Iran and the north-east Asian *C. dasyantha* and *C. chamissonis*. These *Scapiflorae* species and the closely related and sympatric *C. aldanensis* Fed. & Karav. were treated by Fedorov (1957) and Victorov (2002) as *C.* ser. *Dasyanthae* Fed. However, Victorov recognised only *C. dasyantha*, in which he included *C. chamissonis* as a subspecies (*C. dasyantha* subsp. *chamissonis*) and sank *C. aldanensis* in the synonymy of the typical subspecies, a treatment we fully agree with. The placement of *C. dzaaku*, a species without calyx appendages and unusual coriaceous leaves with cartilagineously denticulate margin, was disputed. Kharadze (1949) and Fedorov (1957) placed it close to *C. ciliata*, Victorov (2002) placed it distant to the latter but as a member of *Scapiflorae*, and Oganesian (2000) did not at all include it in the *Scapiflorae*. The lack of calyx appendages was identified by Silakadze & al. (2019: fig. 4) as a synapomorphy of a subclade including *C. dzaaku* together with *C. collina*, *C. sclerophylla*, *C. woronowii* and, with a reversal in this state, *C. sarmatica*. As it turns out, clade CAM 17C1 is morphologically heterogenous and its internal relationships and character evolution require further study.

The Central to S European *Campanula alpina*, still included by Oganesian (2000) and Victorov (2002) in the *Scapiflorae* group (see Suppl. material 3), is resolved very distantly to the *Tridentatae* clade, in the CAM 17A2 clade, sister to *C. hofmanii* and *C. takhtadzhianii*, and these in turn sister to *C. medium* L. and *C. speciosa* Pourr. (Fig. 1, see also Suppl. material 1). The morphological similarity of *C. alpina* to the *Tridentatae* members is only by convergent evolution to similar habitats and its inflorescence can, moreover, also be few-flowered (Silakadze et al. 2019). Another species closely related to *C. alpina* but not included in our study is the Balkan endemic *C. orbelica* (Ronikier and Zalewska-Gałosz 2014).

The former *Scapiflorae* species *Campanula bornmuelleri*, *C. ledebouriana*, *C. minsteriana* and *C. pulvinaris* are nested in CAM 17B3 is (Fig. 1, see also Suppl. material 1; for the *C. pulvinaris* see Suppl. material 2). They are distributed mainly in Anatolia (Turkey) and the Armenian Highlands. *C. karakuschensis* was included in the *Scapiflorae* group only by Victorov (2002) (see Suppl. material 3) and as a synonym of *C. minsteriana*, in line with Oganesian (2000), who classified that species under *C.* subg. *Theodorovia* (Kolak.) Ogan. *C. minsteriana* according to our phylogeny, is closely related to *C. ledebouriana*, corroborating the view of Fedorov (1957) and Kharadze (1976), who placed *C. minsteriana* with *C. ledebouriana* into *C.* ser. *Ledebourianae* Fed. of the *Scapiflorae* group. Also, Oganesian (2000) recognized *C. ledebouriana* as a member of the *Scapiflorae*, and additionally included *C. bornmuelleri* and *C. pulvinaris*. Our phylogenetic results confirm these to belong to one lineage together with *C. coriacea* P. H. Davis, *C. ptarmicifolia* Lam. and the members of the clade of *C. glomerata* L. (Fig. 1, see also Suppl. materials 1, 2). For unknown reasons, Fedorov (1957) and Kharadze (1976) treated *C. karakuschensis* not as conspecific with *C. minsteriana* but as a quite different species and outside the *Scapiflorae* group in *C.* ser. *Saxicolae* (Boiss.) Kharadze, together with *C. lehmanniana* and *C. capusii*. These two species are distributed in Kirgizistan and Tadzhikistan and were considered only by Victorov to belong to *C.* subg. *Scapiflorae*. They were not included in our phylogenetic analyses but with their branched inflorescences and Middle Asian distribution we postulate that they are certainly not closely related to the *Tridentatae* lineage.

The Caucasian endemic *Campanula petrophila* is nested in clade CAM 17C2 sister to *C. raddeana*, another Caucasian endemic species, and together with *C. latifolia*, the type of the name *Campanula*, *C. trachelium* and *C. sclerotricha* (Fig. 1, see also Suppl. material 1). *C. petrophila* and *C. raddeana* have similar ecological patterns like growing only in vertical rocks, but somewhat differ in leaf shape and develop slightly branched inflorescence.

Campanula czerepanovii Fed. is a little known local endemic of Dagestan with branched inflorescences and was included in the *Scapiflorae* group only by Kharadze (1949). It has not been included in any phylogenetic study but is certainly no member of *C.* sect. *Tridentata*e, because of its different stem morphology.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

TB and NK designed the project; NS did the fieldwork, generated the data and analysed, assisted by NK, the data; NS and NK with contribution by TB and MM wrote the text; all authors have revised and finally approved the text.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Appendix 1

Sample list. Taxon sampling, voucher data and INSDC (International Nucleotide Sequence Database Collaboration, including GenBank/EMBL/DDBJ) accession numbers. The data are arranged in the following order: taxon name in italics in alphabetical order; unique sample identifier as used in the trees and, in square brackets where applicable, unit ID of preserved DNA sample in the GGBN data portal (Droege et al. 2014); abbreviated voucher data (country, locality, collecting date, collectors and collecting number, specimen barcode with stable URI to the digitised specimen, if available, or herbarium code and accession number); INSDC accession numbers in the following order: *trnK/matK*, *petD*, *rpl16*.

Asyneuma campanuloides (M. Bieb. ex Sims) Bornm.: CAM1126 [DB 41545]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Askhi Mountain, 1990 m, 42.55675°N, 42.62668°E, 23 July 2016, *N. Silakadze & al. 51* (B 10 1052266), PP004711, PP004386, PP004060; CAM1128 [DB 41564]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Samegrelo), Martvili district, Taleri village, Chegola Mountain, 2430 m, 42.42293°N, 42.77655°E, 26 July 2016, *N. Silakadze & al. 53* (B 10 1052274), PP004719, PP004394, PP004068.

Campanula alpigena K. Koch: CAM1144b [DB 41648]: Georgia, S Caucasus, On the border of Imereti and Samckhe-Javakheti, Adigeni district, Abastumani, Meskheti Range, Zekari Pass, 2200 m, 42.8731°N, 41.82823°E, 13 August 2016, *N. Silakadze 69b* (B 10 1052332), PP004759, PP004434, PP004108; CAM1144c [DB 41649]: *N. Silakadze 69c* (B 10 1052333), PP004760, PP004435, PP004109, from the same population as *69b*; CAM1144d [DB 41650]: *N. Silakadze 69c* (B 10 1052334), PP004761, PP004436, PP004110, from the same population as *69b*; CAM1144e [DB 41651]: Georgia, S Caucasus, On the border of Imereti and Samckhe-Javakheti, Adigeni district, Abastumani, Meskheti Range, Zekari Pass, 2160 m, 42.88198°N, 41.82453°E, 13 August 2016, *N. Silakadze 69e* (B 10 1052335), PP004762, PP004437, PP004111; CAM1144f [DB 41652]: *N. Silakadze 69f* (B 10 1052336), PP004763, PP004438, PP004112, from the same population as *69e*; CAM1144g [DB 41653]: *N. Silakadze 69g* (B 10 1052337), PP004764, PP004439, PP004113, from the same population as *69e*; CAM1144h [DB 41654]: Georgia, S Caucasus, On the border of Imereti and Samckhe-Javakheti, Adigeni district, Abastumani, Meskheti Range, Zekari Pass, 2170 m, 42.86617°N, 41.82565°E, 13 August 2016, *N. Silakadze 69h* (B 10 1052338), PP004765, PP004440, PP004114; CAM1144i [DB 41655]: *N. Silakadze 69i* (B 10 1052339), PP004766, PP004441, PP004115, from the same population as *69h*; CAM1144k [DB 41657]: *N. Silakadze 69k* (B 10 1052341), PP004767, PP004442, PP004116, from the same population as *69h*; CAM1144l [DB 41658]: *N. Silakadze 69l* (B 10 1052342), PP004768, PP004443, PP004117, from the same population as *69h*; CAM1144m [DB 41659]: *N. Silakadze 69m* (B 10 1052343), PP004769, PP004444, PP004118, from the same population as *69h*; CAM1144o [DB 41661]: *N. Silakadze 69o* (B 10 1052345), PP004770, PP004445, PP004119, from the same population as *69h*; CAM1195b [DB 41746]: Georgia, S Caucasus, On the border of Imereti and Samckhe-Javakheti, Adigeni district, Abastumani, Meskheti Range, Zekari Pass, 2250 m, 42.85592°N, 41.82845°E, 17 June 2017, *N. Silakadze & K. E. Jones 96b* (B 10 1052408), PP004825, PP004501, PP004175; CAM1217b [DB 41806]: Georgia, S Caucasus, Adjara, Shuakhevi district, Gogadzeebi village, Tbeti Mountain, 2260 m, 42.18222°N, 41.53198°E, 23 July 2017, *N. Silakadze & al. 118b* (B 10 1052468), PP004872, PP004548, PP004222; CAM1217c [DB 41807]: *N. Silakadze & al. 118c* (B 10 1052469), PP004873, PP004549, PP004223, from the same population as *118b*; CAM1217d [DB 41808]: Georgia, S Caucasus, Adjara, Shuakhevi district, Gogadzeebi village, Tbeti Mountain, 2240 m, 42.1841°N, 41.53018°E, 23 July 2017, *N. Silakadze & al. 118d* (B 10 1052470), PP004874, PP004550, PP004224; CAM1218a [DB 41809]: Georgia, S Caucasus, Guria, Chokhatauri district, daba Bakhmaro, Sakornia Mountain, 2100 m, 42.31428°N, 41.84426°E, 24 July 2017, *N. Silakadze & al. 119a* (B 10 1052471), PP004875, PP004551, PP004225; CAM1218c [DB 41811]: Georgia, S Caucasus, Guria, Chokhatauri district, daba Bakhmaro, Sakornia Mountain, 2130 m, 42.31405°N, 41.84333°E, 24 July 2017, *N. Silakadze & al. 119c* (B 10 1052473), PP004876, PP004552, PP004226; CAM1219 [DB 41812]: Georgia, S Caucasus, Adjara, Tivnari, Gomi Mountaun, 1920 m, 42.10991°N, 41.56324°E, 24 June 2017, *Z. Asanidze 120*

(B 10 1052474), PP004905, PP004553, PP004227; CAM1235 [DB 41831]: Turkey, S Caucasus, Province Coruh (Artvin), Tiryal dag, above Murgul, 2150 m, 23 June 1957, *Davis & Hedge D29908* (ERE 56071), PP004910, PP004563, PP004237.

Campanula andina Rupr.: CAM1146 [DB 41663]: Russian Federation, Dagestan, N Caucasus, Botlikhskiy raion, slopes above the road at the border to the Tsumadinskiy rayon, 860 m, 46.14317°N, 42.62853°E, 9 August 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004771, PP004446, PP004120.

Campanula anomala Fomin: CAM1271 [DB 41864]: Russian Federation, N Caucasus, Karachay-Cherkessia, Klukhor pass, 26 August 1954, *L. Khintibidze* s.n. (TBI 1037305), PP004923, PP004592, PP004302; CAM1286 [DB 41879]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Shoda Mountain, 2300–2500 m, 20 August 1965, *R. Gagnidze & I. Mikeladze* s.n. (TBI 1037304), PP004931, PP004604, PP004278; CAM1289 [DB 41882]: Russian Federation, N Caucasus, Karachay-Cherkessia, Klukhor pass, 26 August 1954, *L. Khintibidze* s.n. (TBI 1037303), PP004933, PP004606, PP004280.

Campanula ardonensis Rupr.: CAM1177g [DB 41710]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Dariali gorge, 1310 m, 44.62899°N, 42.73897°E, 7 June 2017, *N. Silakadze & K. E. Jones 78g* (B 10 1052372), PP004798, PP004473, PP004147; CAM1228 [DB 41825]: Russian Federation, N Caucasus, North Ossetia-Alania, River Ardon, Buron, 9 June 1985, *Yu. L. Menitsky* s.n. (ERE 69614), PP004906, PP004558, PP004232; CAM1280 [DB 41873]: Russian Federation, N Caucasus, North Ossetia-Alania, Bass. R. Ardon, near the glacier Tsey, 9 August 1954, *K. Qimeridze & D. Ochiauri* s.n. (TBI 1037311), PP004928, PP004600, PP004273; CAM1287 [DB 41880]: Russian Federation, N Caucasus, North Ossetia-Alania, Ardon, 4000 ?, 17 July 1902, *I.J. Akinfiev* s.n. (TBI 1037309), PP004932, PP004605, PP004279; CAM1299 [DB 40126]: Russian Federation, N Caucasus, North Ossetia-Alania, Fiagdon valley, 1135 m, 44.32638°N, 42.88166°E, 22 July 2019, *G. Parolly & al. 15795* (B 10 1118223), PP004942, PP004616, PP004290; CAM1302 [DB 40138]: Russian Federation, N Caucasus, North Ossetia-Alania, Sadon valley, just above the first tunnel, 1090 m, 44.02444°N, 42.84222°E, 23 July 2019, *G. Parolly & al. 15815* (B 10 1118229), PP004945, PP004619, PP004293; CAM1304 [DB 40143]: Russian Federation, N Caucasus, North Ossetia-Alania, Arkhon-Don valley, 1090 m, 44.10333°N, 42.84277°E, 23 July 2019, *G. Parolly & al. 15818* (B 10 1118227), PP004946, PP004620, PP004294.

Campanula argunensis Rupr.: CAM1089k [DB 41396]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2130 m, 45.56724°N, 42.45041°E, 7 July 2016, *N. Silakadze & al. 12k* (B 10 1052213), PP004667, PP004342, PP004016; CAM1092 [DB 41414]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, between villages Bochorna and Dochu, 2370 m, 45.57093°N, 42.40428°E, 8 July 2016, *N. Silakadze & al. 16* (B 10 1052217), PP004671, PP004346, PP004020; CAM1100 [DB 41433]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dartlo village, 1910 m, 45.58929°N, 42.4276°E, 9 July 2016, *N. Silakadze & al. 25* (B 10 1052228), PP004681, PP004356, PP004030; CAM1104p [DB 41471]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, road to Chesho village, 1940 m, 45.54396°N, 42.47186°E, 9 July 2016, *N. Silakadze & al. 29p* (B 10 1052233), PP004686, PP004361, PP004035; CAM1108a [DB 41478]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2290 m, 45.52758°N, 42.29441°E, 10 July 2016, *N. Silakadze & al. 33a* (B 10 1052237), PP004688, PP004363, PP004037; CAM1108b [DB 41479]: *N. Silakadze & al. 33b* (B 10 1052238), PP004689, PP004364, PP004038, from the same population as *33a*; CAM1110p [DB 41496]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2140 m, 45.50213°N, 42.25535°E, 10 July 2016, *N. Silakadze & al. 35p* (B 10 1052240), PP004691, PP004366, PP004040; CAM1148 [DB 41665]: Russian Federation, Dagestan, N Caucasus, Charodinsky raion, surroundings of village Gochob, in river gorge, eastern slope, 2050 m, 46.64914°N, 42.23283°E, 19 August 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004772, PP004447, PP004121; CAM1149 [DB 41666]: Russian Federation, Dagestan, N Caucasus, Rutulskiy raion, Vug river gorge, below village Djinykh, northern rocky slope, 1810 m, 47.05497°N, 41.66447°E, 26 July 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004773, PP004448, PP004122; CAM1169a [DB 41684]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Mutso village, 1570 m, 45.20378°N, 42.62°E, 1 June 2017, *N. Silakadze & al. 70a* (B 10 1052346), PP004778, PP004453, PP004127; CAM1169b [DB 41685]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Mutso village, 1500 m, 45.20465°N, 42.62017°E, 1 June 2017, *N. Silakadze & al. 70b* (B 10 1052347), PP004779, PP004454, PP004128; CAM1169c [DB 41686]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Mutso village, 1520 m, 45.20511°N, 42.62004°E, 1 June 2017, *N. Silakadze & al. 70c* (B 10 1052348), PP004780, PP004455, PP004129; CAM1169d [DB 41687]: *N. Silakadze & al. 70d* (B 10 1052349), PP004781, PP004456, PP004130, from the same population as *70c*; CAM1169e [DB 41688]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Mutso village, 1480 m, 45.20398°N, 42.61689°E, 1 June 2017, *N. Silakadze & al. 70e* (B 10 1052350), PP004782, PP004457, PP004131; CAM1170a [DB 41689]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), between Ardoti and Mutso villages, 1600 m, 45.21127°N, 42.59964°E, 1 June 2017, *N. Silakadze & al. 71a* (B 10 1052351), PP004783, PP004458, PP004132; CAM1170b [DB 41690]: *N. Silakadze & al. 71b* (B 10 1052352), PP004784, PP004459, PP004133, from the same population as *71a*; CAM1170c [DB 41691]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), between Ardoti and Mutso villages, 1700 m, 45.19035°N, 42.57224°E, 1 June 2017, *N. Silakadze & al. 71c* (B 10 1052353), PP004785, PP004460, PP004134; CAM1170d [DB 41692]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), between Ardoti and Mutso villages, 1710 m, 45.19025°N, 42.57221°E, 1 June 2017, *N. Silakadze & al. 71d* (B 10 1052354), PP004786, PP004461, PP004135; CAM1170e [DB 41693]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), between Ardoti and Mutso villages, 1910 m, 45.21297°N, 42.60002°E, 1 June 2017, *N. Silakadze & al. 71e* (B 10 1052355), PP004787, PP004462, PP004136; CAM1200 [DB 41759]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 1620 m, 45.49331°N, 42.2392°E, 27 June 2017, *N. Silakadze & al. 101* (B 10 1052421), PP004837, PP004513, PP004187; CAM1201b [DB 41761]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Kvavlo village, 2120 m, 45.58375°N, 42.44753°E, 28 June 2017, *N. Silakadze & al. 102b* (B 10 1052423), PP004838, PP004514, PP004188; CAM1202a [DB 41762]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2180 m, 45.56667°N, 42.45°E, 28 June 2017, *N. Silakadze & al. 103a* (B 10 1052424), PP004839, PP004515, PP004189; CAM1202b [DB 41763]: *N. Silakadze & al. 103b* (B 10 1052425), PP004840, PP004516, PP004190, from the same population as *103a*; CAM1203a [DB 41764]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, road to Chesho village, 1970 m, 45.54361°N, 42.4755°E, 28 June 2017, *N. Silakadze & al. 104a* (B 10 1052426), PP004841, PP004517, PP004191; CAM1203b [DB 41765]: *N. Silakadze & al. 104b* (B 10 1052427), PP004842, PP004518, PP004192, from the same population as *104a*; CAM1203c [DB 41766]: *N. Silakadze & al. 104c* (B 10 1052428), PP004843, PP004519, PP004193, from the same population as *104a*; CAM1203d [DB 41767]: *N. Silakadze & al. 104d* (B 10 1052429), PP004844, PP004520, PP004194, from the same population as *104a*; CAM1204a [DB 41768]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2410 m, 45.49041°N, 42.26998°E, 29 June 2017, *N. Silakadze & al. 105a* (B 10 1052430), PP004845, PP004521, PP004195; CAM1204b [DB 41769]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2370 m, 45.49472°N, 42.26881°E, 29 June 2017, *N. Silakadze & al. 105b* (B 10 1052431), PP004846, PP004522, PP004196; CAM1204c [DB 41770]: *N. Silakadze & al. 105c* (B 10 1052432), PP004847, PP004523, PP004197, from the same population as *105b*; CAM1204d [DB 41771]: *N. Silakadze & al. 105d* (B 10 1052433), PP004848, PP004524, PP004198, from the same population as *105b*; CAM1229 [DB 41826]: Russian Federation, Dagestan, N Caucasus, Akhtynsky District, Kurush village, 23 July 1986, *Y. L. Menitsky & al.* s.n. (ERE 69616), PP004907, PP004559, PP004233; CAM1231 [DB 41828]: Azerbaijan, Oghuz district, Bash-Dashagil village, 28 June 1973, *J. Hashimov* s.n. (ERE 66955), PP004908, PP004560, PP004234; CAM1274 [DB 41867]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Parsma village, 2000 m, 16 August 1987, *D. Chelidze & Sh. Shetekauri* s.n. (TBI 1038261), PP004899, PP004594, PP004267; CAM1291 [DB 41884]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Etelta village, the river Gometsris Alazani, 2000 m, 7 August 1986, *Sh. Shetekauri* s.n. (TBI 1038260), PP004935, PP004608, PP004282.

Campanula armazica Kharadze: CAM1078b [DB 41321]: Georgia, S Caucasus, Mtskheta-Mtianeti, Mtskheta district, between Mtskheta and Karsan, 790 m, 44.70372°N, 41.83316°E, 24 June 2016, *N. Silakadze & Z. Janiashvili 1b* (B 10 1052201), PP004659, PP004334, PP004008; CAM1175a [DB 41700]: Georgia, S Caucasus, Mtskheta-Mtianeti, Mtskheta district, between Mtskheta and Karsan, 750 m, 44.70372°N, 41.83316°E, 3 June 2017, *N. Silakadze & al. 76a* (B 10 1052362), PP004791, PP004466, PP004140; CAM1175b [DB 41701]: *N. Silakadze & al. 76b* (B 10 1052363), PP004792, PP004467, PP004141, from the same population as *76a*.

Campanula aucheri A. DC.: CAM1079a [DB 41325]: Georgia, S Caucasus, Kvemo Kartli, Tsalka district, Cholmani village, Didi Kldekari Mountain, 2040 m, 44.21004°N, 41.74328°E, 29 June 2016, *N. Silakadze 2a* (B 10 1052202), PP004660, PP004335, PP004009; CAM1079b [DB 41326]: *N. Silakadze 2b* (B 10 1052203), PP004661, PP004336, PP004010, from the same population as *2a*; CAM1135a [DB 41622]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2400 m, 43.51897°N, 41.69375°E, 10 August 2016, *N. Silakadze 62a* (B 10 1052306), PP004740, PP004415, PP004089; CAM1135b [DB 41623]: *N. Silakadze 62b* (B 10 1052307), PP004741, PP004416, PP004090, from the same population as *62a*; CAM1135c [DB 41624]: *N. Silakadze 62c* (B 10 1052308), PP004742, PP004417, PP004091, from the same population as *62a*; CAM1135d [DB 41625]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2210 m, 43.51307°N, 41.70018°E, 10 August 2016, *N. Silakadze 62d* (B 10 1052309), PP004743, PP004418, PP004092; CAM1135e [DB 41626]: *N. Silakadze 62e* (B 10 1052310), PP004744, PP004419, PP004093, from the same population as *62d*; CAM1143a [DB 41636]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2410 m, 43.36113°N, 41.72723°E, 11 August 2016, *N. Silakadze 68a* (B 10 1052320), PP004752, PP004427, PP004101 PP004101 ; CAM1143c [DB 41638]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2480 m, 43.36077°N, 41.72632°E, 11 August 2016, *N. Silakadze 68c* (B 10 1052322), PP004753, PP004428, PP004102; CAM1143e [DB 41640]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2500 m, 43.36038°N, 41.726°E, 11 August 2016, *N. Silakadze 68e* (B 10 1052324), PP004754, PP004429, PP004103; CAM1143g [DB 41642]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2510 m, 43.3602°N, 41.72592°E, 11 August 2016, *N. Silakadze 68g* (B 10 1052326), PP004755, PP004430, PP004104; CAM1143h [DB 41643]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2540 m, 43.3604°N, 41.72565°E, 11 August 2016, *N. Silakadze 68h* (B 10 1052327), PP004756, PP004431, PP004105; CAM1143j [DB 41645]: *N. Silakadze 68j* (B 10 1149579), PP004757, PP004432, PP004106, from the same population as *68h*; CAM1143k [DB 41646]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2570 m, 43.36072°N, 41.7253°E, 11 August 2016, *N. Silakadze 68k* (B 10 1052330), PP004758, PP004433, PP004107; CAM1179a [DB 41716]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Sioni village, Kabarjina Mountain, 2190 m, 44.58766°N, 42.57445°E, 8 June 2017, *N. Silakadze & K. E. Jones 80a* (B 10 1052378), PP004804, PP004479, PP004153; CAM1179b [DB 41717]: *N. Silakadze & K. E. Jones 80b* (B 10 1052379), PP004805, PP004480, PP004154, from the same population as *80a*; CAM1180 [DB 41719]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Sioni village, Kabarjina Mountain, 2190 m, 44.59061°N, 42.57493°E, 8 June 2017, *N. Silakadze & K. E. Jones 81* (B 10 1052381), PP004807, PP004482, PP004156; CAM1187a [DB 41728]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2120 m, 43.50328°N, 41.70553°E, 13 June 2017, *N. Silakadze & K. E. Jones 88a* (B 10 1052390), PP004814, PP004490, PP004164; CAM1187c [DB 41730]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2380 m, 43.51889°N, 41.69384°E, 13 June 2017, *N. Silakadze & K. E. Jones 88c* (B 10 1052392), PP004815, PP004815, PP004815; CAM1188 [DB 41731]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2550 m, 43.36107°N, 41.72514°E, 13 June 2017, *N. Silakadze & K. E.*

Jones 89 (B 10 1052393), PP004816, PP004492, PP004166; CAM1190b [DB 41734]: Georgia, S Caucasus, Samckhe-Javakheti, daba Aspindza, Vardzia, 1260 m, 43.27569°N, 41.37382°E, 14 June 2017, *N. Silakadze & K. E. Jones 91b* (B 10 1052396), PP004817, PP004493, PP004167; CAM1190c [DB 41735]: *N. Silakadze & K. E. Jones 91c* (B 10 1052397), PP004818, PP004494, PP004168, from the same population as *91b*; CAM1190d [DB 41736]: *N. Silakadze & K. E. Jones 91d* (B 10 1052398), PP004819, PP004495, PP004169, from the same population as *91b*; CAM1190e [DB 41737]: *N. Silakadze & K. E. Jones 91e* (B 10 1052399), PP004820, PP004496, PP004170, from the same population as *91b*; CAM1194a [DB 41742]: Georgia, S Caucasus, Samckhe-Javakheti, Akhalkalaki district, Abuli Mountain, 2370 m, 43.65961°N, 41.40294°E, 16 June 2017, *N. Silakadze & K. E. Jones 95a* (B 10 1052404), PP004822, PP004498, PP004172; CAM1194b [DB 41743]: Georgia, S Caucasus, Samckhe-Javakheti, Akhalkalaki district, Abuli Mountain, 2370 m, 43.65981°N, 41.40407°E, 16 June 2017, *N. Silakadze & K. E. Jones 95b* (B 10 1052405), PP004823, PP004499, PP004173; CAM1194c [DB 41744]: Georgia, S Caucasus, Samckhe-Javakheti, Akhalkalaki district, Abuli Mountain, 2390 m, 43.65968°N, 41.40417°E, 16 June 2017, *N. Silakadze & K. E. Jones 95c* (B 10 1052406), PP004824, PP004500, PP004174; CAM1196a [DB 41747]: Georgia, S Caucasus, Kvemo kartli, Manglisi district, Birtvisi Mountain, 1010 m, 44.54022°N, 41.604°E, 21 June 2017, *N. Silakadze & al. 97a* (B 10 1052409), PP004826, PP004502, PP004176; CAM1196b [DB 41748]: *N. Silakadze & al. 97b* (B 10 1052410), PP004827, PP004503, PP004177, from the same population as *97a*; CAM1196c [DB 41749]: *N. Silakadze & al. 97c* (B 10 1052411), PP004828, PP004504, PP004178, from the same population as *97a*; CAM1196d [DB 41750]: *N. Silakadze & al. 97d* (B 10 1052412), PP004829, PP004505, PP004179, from the same population as *97a*; CAM1197b [DB 41752]: Georgia, S Caucasus, Kvemo kartli, Tsalka district, Akhalshenari village, 1680 m, 44.07125°N, 41.6725°E, 22 June 2017, *N. Silakadze & al. 98b* (B 10 1052414), PP004830, PP004506, PP004180; CAM1197c [DB 41753]: *N. Silakadze & al. 98b* (B 10 1052415), PP004831, PP004507, PP004181, from the same population as *98b*; CAM1198 [DB 41754]: Georgia, S Caucasus, Kvemo kartli, Tsalka district, Kaburi village, 2000 m, 44.01223°N, 41.71483°E, 22 June 2017, *N. Silakadze & al. 99* (B 10 1052416), PP004832, PP004508, PP004182; CAM1199a [DB 41755]: Georgia, S Caucasus, Kvemo kartli, Tsalka district, Khachkoi village, Arjevani Mountain, 1980 m, 43.97305°N, 41.71371°E, 22 June 2017, *N. Silakadze & al. 100a* (B 10 1052417), PP004833, PP004509, PP004183; CAM1199b [DB 41756]: *N. Silakadze & al. 100b* (B 10 1052418), PP004834, PP004510, PP004184, from the same population as *100a*; CAM1199c [DB 41757]: *N. Silakadze & al. 100c* (B 10 1052419), PP004835, PP004511, PP004185, from the same population as *100a*; CAM1199d [DB 41758]: *N. Silakadze & al. 100d* (B 10 1052420), PP004836, PP004512, PP004186, from the same population as *100a*; CAM1222a [DB 41816]: Armenia, S Caucasus, Gegharkunik Province, Lake Sevan, Surroundings of Sevan lake, on the old road, 1990 m, 44.99379°N, 40.57617°E, 22 August 2017, *N. Silakadze & M. Oganesian 123a* (B 10 1052478), PP004878, PP004555, PP004229; CAM1222b [DB 41817]: *N. Silakadze & M. Oganesian 123b* (B 10 1052479), PP004879, PP004556, PP004230, from the same population as *123a*; CAM1223b [DB 41819]: Armenia, S Caucasus, Gegharkunik Province, Gegha Mountain, 2480 m, 44.91523°N, 40.42012°E, 22 August 2017, *N. Silakadze & M. Oganesian 124b* (B 10 1052481), PP004880, PP004557, PP004231; CAM1233 [DB 41829]: Azerbaijan, S Caucasus, Kalbajar raion, Surroundings Istisu village, 19 June 1985, *Yu. L. Menitsky* s.n. (ERE 66880), PP004881, PP004561, PP004235; CAM1234 [DB 41830]: Turkey, S Caucasus, Province Kars, South-West side of Kisir dag, 2700 m, 3 July 1957, *Davis & Hedge D30499B* (ERE 56333), PP004909, PP004562, PP004236; CAM1252 [DB 41848]: Armenia, S Caucasus, Kotayk Province, Mountain Arayi Lerr, surroundings of the Monastery Gharghavank (Spitakavor Monastery), 6 July 1989, *E. Gabrielian & M. Oganesian* s.n. (ERE 141517), PP004917, PP004579, PP004253; CAM1254 [DB 41850]: Armenia, S Caucasus, Shirak Province, Amasia district, 1 km W of village Bandivan, 1850 m, 43.8°N, 40.96666°E, 21 June 2003, *M. Oganezian & al.* s.n. (ERE 152386), PP004891, PP004580, PP004254; CAM1266 [DB 41859]: Georgia, S Caucasus, Samckhe-Javakheti, Tetrobi range, 24 July 1967, *L. Khintibidze* s.n. (TBI 1036646), PP004895, PP004587, PP004261; CAM1310 [DB 41889]: Iran, S Caucasus, In monte Chalil Kuh prope Razhan [Rajan Khalil, Mountain], 2600-3200 m, 2 July 1974, *W. Rechinger & J. Renz 48816* (B 10 1015488), PP004948, PP004622, PP004296; CAM1311 [DB 41890]: Iran, S Caucasus, West Azerbaijan Province, Urma, Darband [Urmia, darband, silvaneh], 2000 m, 3 June 1994, *S. Narimisa 410* (B 10 0626006), PP004949, PP004623, PP004297.

Campanula bellidifolia Adams: CAM1172b [DB 41696]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Shatili village, 1570 m, 45.14587°N, 42.67244°E, 2 June 2017, *N. Silakadze & al. 73b* (B 10 1052358), PP004788, PP004463, PP004137; CAM1172c [DB 41697]: *N. Silakadze & al. 73c* (B 10 1052359), PP004789, PP004464, PP004138, from the same population as *73b*; CAM1177a [DB 41704]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Tsdo village, 1660 m, 44.63317°N, 42.68351°E, 7 June 2017, *N. Silakadze & K. E. Jones 78a* (B 10 1052366), PP004793, PP004468, PP004142; CAM1177b [DB 41705]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Tsdo village, 1670 m, 44.63321°N, 42.68466°E, 7 June 2017, *N. Silakadze & K. E. Jones 78b* (B 10 1052367), PP004794, PP004469, PP004143; CAM1177c [DB 41706]: *N. Silakadze & K. E. Jones 78c* (B 10 1052368), PP004795, PP004470, PP004144, from the same population as *78b*; CAM1177d [DB 41707]: *N. Silakadze & K. E. Jones 78d* (B 10 1052369), PP004796, PP004471, PP004145, from the same population as *78b*; CAM1177e [DB 41708]: *N. Silakadze & K. E. Jones 78e* (B 10 1052370), PP004797, PP004472, PP004146, from the same population as *78b*; CAM1177h [DB 41711]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Dariali gorge, 1280 m, 44.62981°N, 42.7387°E, 7 June 2017, *N. Silakadze & K. E. Jones 78h* (B 10 1052373), PP004799, PP004474, PP004148; CAM1177i [DB 41712]: *N. Silakadze & K. E. Jones 78i* (B 10 1052374), PP004800, PP004475, PP004149, from the same population as *78h*; CAM1177j [DB 41713]: *N. Silakadze & K. E. Jones 78j* (B 10 1052375), PP004801, PP004476, PP004150, from the same population as *78h*; CAM1177k [DB 41714]: *N. Silakadze & K. E. Jones 78k* (B 10 1052376), PP004802, PP004477, PP004151, from the same population as *78h*; CAM1178 [DB 41715]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Gveleti village, Devdoraki gorge, 1810 m, 44.59435°N, 42.7246°E, 7 June 2017, *N. Silakadze & K. E. Jones 79* (B 10 1052377), PP004803, PP004478, PP004152; CAM1179c [DB 41718]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Sioni village, Kabarjina Mountain, 2190 m, 44.58766°N, 42.57445°E, 8 June 2017, *N. Silakadze & K. E. Jones 80c* (B 10 1052380), PP004806, PP004481, PP004155; CAM1182 [DB 41722]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Sioni village, Kabarjina Mountain, 2110 m, 44.58824°N, 42.57915°E, 8 June 2017, *N. Silakadze & K. E. Jones 83* (B 10 1052384), PP004809, PP004484, PP004158; CAM1184 [DB 41725]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Gergeti Church, Sabertse, 2440 m, 44.59739°N, 42.66365°E, 9 June 2017, *N. Silakadze & K. E. Jones 85* (B 10 1052387), PP004904, PP004487, PP004161; CAM1186 [DB 41727]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Elia Mountain, 1880 m, 44.65625°N, 42.65376°E, 9 June 2017, *N. Silakadze & K. E. Jones 87* (B 10 1052389), PP004813, PP004489, PP004163; CAM1292 [DB 41740]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), Devdoraki gorge, 1 August 1967, *E. Khutsishvili* s.n. (B 10 1052402), PP004936, PP004609, PP004283.

Campanula besenginica Fomin: CAM1236 [DB 41832]: Russian Federation, N Caucasus, Kabardino-Balkaria, Sovet raion, 5 km from Bezengi village to north, 6 June 1985, *Yu. L. Menitsky* s.n. (ERE 70791), PP004911, PP004564, PP004238; CAM1261 [DB 41854]: Russian Federation, N Caucasus, Kabardino-Balkaria, Bezengi glacier, July 1893, *I. J. Akinfiev* s.n. (TBI 1033286), PP004920, PP004584, PP004258.

Campanula biebersteiniana Roem. & Schult.: CAM1070 [DB 41299]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, just S of lake Psenodakh, 1950-2000 m, 39.9°N, 44.00833°E, 29 July 2015, *E. von Raab-Straube & al. 6932* (B 10 1052542), PP004652, PP004327, PP004001; CAM1072c [DB 41303]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, near lake Psenodakh, at the N foot of Mt. Pshekho-Su, 1950-2000 m, 39.9°N, 44.00833°E, 30 July 2015, *E. von Raab-Straube & al. 6941c* (B 10 1052545), PP004654, PP004329, PP004003; CAM1072g [DB 41307]: *E. von Raab-Straube & al. 6941g* (B 10 1052545), PP004655, PP004330, PP004004, from the same population as *6941c*; CAM1074a [DB 41309]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, just S of Fisht-Oshtenskiy pereval [= Pass between Mts. Fisht and Oshten], 2200 m, 39.91388°N, 43.99055°E, 30 July 2015, *E. von Raab-Straube & al. 7001a* (B 10 1052547), PP004656, PP004331, PP004005; CAM1074f [DB 41314]: *E. von Raab-Straube & al. 7001f* (B 10 1052547), PP004657, PP004332, PP004006, from the same population as *7001a*; CAM1084a [DB 41358]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2310 m, 45.512033°N, 42.28488°E, 6 July 2016, *N. Silakadze & al. 7a* (B 10 1052208), PP004663, PP004338, PP004012; CAM1131b [DB 41585]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2730 m, 42.70793°N, 43.08657°E, 28 July 2016, *N. Silakadze & al. 56b* (B 10 1052295), PP004731, PP004406, PP004080; CAM1131t [DB 41603]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2750 m, 42.703°N, 43.08707°E, 28 July 2016, *N. Silakadze & al. 56t* (B 10 1052296), PP004732, PP004407, PP004081; CAM1133b [DB 41607]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Tetnuldi Mountain, 3040 m, 42.91712°N, 43.0287°E, 30 July 2016, *N. Silakadze & al. 60b* (B 10 1052299), PP004734, PP004409, PP004083; CAM1133d [DB 41609]: *N. Silakadze & al. 60d* (B 10 1052301), PP004735, PP004410, PP004084, from the same population as *60b*; CAM1133e [DB 41610]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Tetnuldi Mountain, 3070 m, 42.91907°N, 43.02922°E, 30 July 2016, *N. Silakadze & al. 60e* (B 10 1052302), PP004736, PP004411, PP004085; CAM1133k [DB 41616]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Tetnuldi Mountain, 3190 m, 42.9172°N, 43.03205°E, 30 July 2016, *N. Silakadze & al. 60k* (B 10 1052304), PP004737, PP004412, PP004086; CAM1173 [DB 41698]: Georgia, N Caucasus, Mtskheta-Mtianeti (Khevsureti), Datvijvari gorge, 1970 m, 45.10094°N, 42.5773°E, 2 June 2017, *N. Silakadze & al. 74* (B 10 1052360), PP004790, PP004465, PP004139; CAM1181b [DB 41721]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Sioni village, Kabarjina Mountain, 2230 m, 44.59172°N, 42.57534°E, 8 June 2017, *N. Silakadze & K. E. Jones 82b* (B 10 1052383), PP004808, PP004483, PP004157; CAM1183a [DB 41723]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Gergeti Church, Sabertse, 3020 m, 44.55905°N, 42.66031°E, 9 June 2017, *N. Silakadze & K. E. Jones 84a* (B 10 1052385), PP004810, PP004485, PP004159; CAM1185 [DB 41726]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Gergeti Church, 2260 m, 44.61147°N, 42.66489°E, 9 June 2017, *N. Silakadze & K. E. Jones 86* (B 10 1052388), PP004812, PP004488, PP004162; CAM1298 [DB 40121]: Russian Federation, N Caucasua, Kabardino-Balkaria, Mt. Elbrus, S slopes, E of lift station “Mir”, 3450 m, 42.46472°N, 43.28944°E, 20 July 2019, *G. Parolly & al. 15769* (B 10 1118233B), PP004903, PP004615, PP004289.

Campanula chamissonis Fed.: CAM1239 [DB 41835]: Russia, Sakhalin, Karakulchan range, 500 m, 26 July 1968, *G. Pomomarczuk* s.n. (ERE 55255), PP004882, PP004566, PP004240.

Campanula ciliata Steven: CAM1038f [DB 41220]: Russian Federation, N Caucasus, Karachay-Cherkessia, Karachayevsky rayon, Skalistyy khrebet, SE slopes of Mt. Gumbashi, 2000 m, 42.20556°N, 43.77972°E, 25 June 2015, *T. Borsch & al. 5790f* (B 10 1052498), PP004631, PP004306, PP003980; CAM1038o [DB 41229]: *T. Borsch & al. 5790o* (B 10 1052498), PP004632, PP004307, PP003981, from the same population as *5790f*; CAM1039c [DB 41232]: Russian Federation, N Caucasus, Karachay-Cherkessia, Karachayevsky rayon, Skalistyy khrebet, SE slopes of Mt. Gumbashi, 2100 m, 42.20556°N, 43.77972°E, 25 June 2015, *T. Borsch & al. 5802c* (B 10 1052501), PP004633, PP004308, PP003982; CAM1039n [DB 41243]: *T. Borsch & al. 5802n* (B 10 1052501), PP004634, PP004309, PP003983, from the same population as *5802c*; CAM1039s [DB 41248]: *T. Borsch & al. 5802s* (B 10 1052501), PP004635, PP004310, PP003984, from the same population as *5802c*; CAM1067c [DB 41296]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, N slopes of Mt. Pshekho-Su, ca. 1 km S of lake Psenodakh, 2200 m, 39.895°N, 44.00194°E, 30 July 2015, *E. von*

Raab-Straube & al. 6969c (B 10 1052538), PP004649, PP004324, PP003998; CAM1183b [DB 41724]: Georgia, N Caucasus, Mtskheta-Mtianeti (Kazbegi), daba Stepantsminda, Gergeti Church, Sabertse, 3020 m, 44.55905°N, 42.66031°E, 9 June 2017, *N. Silakadze & K. E. Jones 84b* (B 10 1052386), PP004811, PP004486, PP004160; CAM1240 [DB 41836]: Russian Federation, N Caucasus, Krasnodar Krai, Oshten Mountain, 2500-2700 m, 14 July 1981, *Yu. L. Menitsky & al. 414* (ERE 66937), PP004883, PP004567, PP004241; CAM1241 [DB 41837]: Russian Federation, N Caucasus, Kabardino-Balkaria, Zapadnyy Kinzhal mountain, 30 July 1981, *Yu. L. Menitsky & al. 431* (ERE 66938), PP004884, PP004568, PP004242; CAM1243 [DB 41839]: Azerbaijan, N Caucasus, Qusar, The right side of river Kusarchay, village Laza, Karadan Mountain, 12 July 1978, *Yu. L. Menitsky & al. 105* (ERE 70849), PP004886, PP004570, PP004244.

Campanula circassica Fomin: CAM1130e [DB 41570]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2630 m, 42.7113°N, 43.08155°E, 28 July 2016, *N. Silakadze & al. 55e* (B 10 1052280), PP004721, PP004396, PP004070; CAM1130k [DB 41576]: *N. Silakadze & al. 55k* (B 10 1052286), PP004724, PP004399, PP004073, from the same population as *55e*; CAM1130q [DB 41582]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2750 m, 42.703°N, 43.08707°E, 28 July 2016, *N. Silakadze & al. 55q* (B 10 1052292), PP004729, PP004404, PP004078; CAM1130r [DB 41583]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2750 m, 42.70257°N, 43.08717°E, 28 July 2016, *N. Silakadze & al. 55r* (B 10 1052293), PP004730, PP004405, PP004079; CAM1242 [DB 41838]: Russian Federation, N Caucasus, Krasnodar Krai, Adler raion, Cochi, surroundings village Krasnaya Polyana, Aibga Ridge, 23 July 2011, *B. S. Tuniev* s.n. (ERE 80037), PP004885 PP004569, PP004243.

Campanula aff. *collina* Sims: CAM1062 [DB 41289]: *E. von Raab-Straube & al. 6830* (B 10 1052532), PP004645, PP004320, PP003994, from the same population as *6832*; CAM1037 [DB 41214]: *T. Borsch & al. 5812* (B 10 1052495), PP004630, PP004305, PP003979, from the same population as *5810*; CAM1071 [DB 41300]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, near lake Psenodakh, at the N foot of Mt. Pshekho-Su, 1950-2000 m, 39.9°N, 44.00833°E, 30 July 2015, *E. von Raab-Straube & al. 6935* (B 10 1052543), PP004653, PP004328, PP004002; CAM1076 [DB 41316]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, N slopes of Mt. Pshekho-Su, ca. 1 km S of lake Psenodakh, 2200 m, 39.895°N, 44.00194°E, 30 July 2015, *E. von Raab-Straube & al. 6981* (B 10 1052549), PP004658, PP004333, PP004007; CAM1081a [DB 41337]: Georgia, S Caucasus, Kvemo Kartli, Tsalka district, Cholmani village, Didi Kldekari Mountain, 1960 m, 44.2051°N, 41.74266°E, 29 June 2016, *N. Silakadze & al. 4a* (B 10 1052205), PP004662, PP004337, PP004011; CAM1088 [DB 41385]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2150 m, 45.56757°N, 42.45046°E, 7 July 2016, *N. Silakadze & al. 11* (B 10 1052212), PP004666, PP004341, PP004015; CAM1094 [DB 41417]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dochu village, 2230 m, 45.5544°N, 42.39217°E, 8 July 2016, *N. Silakadze & al. 19* (B 10 1052220), PP004674, PP004349, PP004023; CAM1101 [DB

41434]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dartlo village, 1910 m, 45.58929°N, 42.4276°E, 9 July 2016, *N. Silakadze & al. 26* (B 10 1052229), PP004682, PP004357, PP004031; CAM1109 [DB 41480]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2290 m, 45.52758°N, 42.29441°E, 10 July 2016, *N. Silakadze & al. 34* (B 10 1052239), PP004690, PP004365, PP004039; CAM1116 [DB 41504]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1650 m, 43.40138°N, 42.48907°E, 21 July 2016, *N. Silakadze & al. 41* (B 10 1052248), PP004697, PP004372, PP004046; CAM1121 [DB 41509]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Khvamli Mountain, 1880 m, 42.72087°N, 42.50805°E, 22 July 2016, *N. Silakadze & al. 45* (B 10 1052253), PP004700, PP004375, PP004049; CAM1129 [DB 41565]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Samegrelo), Martvili district, Taleri village, Chegola Mountain, 2430 m, 42.42293°N, 42.77655°E, 26 July 2016, *N. Silakadze & al. 54* (B 10 1052275), PP004720, PP004395, PP004069; CAM1132 [DB 41605]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2480 m, 42.71327°N, 43.07747°E, 28 July 2016, *N. Silakadze & al. 59* (B 10 1052297), PP004733, PP004408, PP004082; CAM1136 [DB 41627]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2400 m, 43.51897°N, 41.69375°E, 10 August 2016, *N. Silakadze 2* (B 10 1052311), PP004745, PP004420, PP004094; CAM1137 [DB 41628]: *N. Silakadze 63-2* (B 10 1052312), PP004746, PP004421, PP004095, from the same population as *63-1*; CAM1141 [DB 41634]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2390 m, 43.36105°N, 41.72778°E, 11 August 2016, *N. Silakadze 66* (B 10 1052318), PP004750, PP004425, PP004099; CAM1142 [DB 41635]: *N. Silakadze 67* (B 10 1052319), PP004751, PP004426, PP004100, from the same population as *66*; CAM1296 [DB 40117]: Russian Federation, N Caucasua, Kabardino-Balkari-a, on Mountain road between Chegem and Baksan valley ("Aktaprak"), 1900 m, 43.08889°N, 43.40694°E, 19 July 2019, *G. Parolly & al. 15730* (B 10 1118230), PP004940, PP004613, PP004287. CAM1297 [DB 40119]: Russian Federation, N Caucasua, Kabardino-Balkaria, Baksan valley, between Azau village and Azau waterfall, 2360 m, 42.47528°N, 43.265°E, 19 July 2019, *G. Parolly & al. 15742* (B 10 1118222), PP004941, PP004614, PP004288.

Campanula cordifolia K. Koch: CAM1043 [DB 41271]: Russian Federation, N Caucasus, Krasnodar Kra, Novorossiysk district, khrebet Markotkh above Novorossiysk bay, near pereval Andreevskiy (= Sem' Vetrov), 450-550 m, 37.86667°N, 44.72556°E, 20 July 2015, *E. von Raab-Straube & al. 6730* (B 10 1052507), PP004636, PP004311, PP003985.

Campanula damascena Labill.: CAM1244 [DB 41840]: Palestinian Territory, Wadi Tawahin (Safad), 3 May 1942, *P. H. Davis 4538* (ERE 33388), PP004913, PP004571, PP004245.

Campanula dasyantha M. Bieb.: CAM1245 [DB 41841]: Russia, Buryatia, Khentei-Chikoy Highlands, Chikokonskiy Khrebet, "Golets" (mountain summit), along the watershed of the Goronkova and Bystrinsky valleys, *M. Maksimova & A. Maksimova* s.n. - *1967-06-30* (ERE 30106), PP004887, PP004572, PP004246.

Campanula daghestanica Fomin: CAM1150 [DB 41667]: Russian Federation, Dagestan, N Caucasus, Akushinskiy raion, surroundings of village Akusha, slope of Mt. Maara, 1770 m, 47.30439°N, 42.24453°E, 13 June 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004774, PP004449, PP004123.

Campanula dolomitica E.A. Busch: CAM1301 [DB 40131]: Russian Federation, N Caucasua, North Ossetia-Alania, Fiagdon valley, 1135 m, 44.32639°N, 42.88167°E, 22 July 2019, *G. Parolly & al. 15800* (B 10 1118226), PP004944, PP004618, PP004292.

Campanula doluchanovii Kharadze: CAM1273 [DB 41866]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Chesho village, 2000 m, 21 August 1926, *D. Mtskhvetadze & M. Pataraia* s.n. (TBI 1038259), PP004898, PP004593, PP004266; CAM1329 (Type) [DB 45126]: Georgia, N Caucasus, Lagodekhi reserve, Khochal-dag tract, to the west from marker 9289' (according 5-mile map), 2700 m, 27 Jul 1938, *A. Doluchanov* s.n. (TBI 1024822), PP004951, PP004625, PP004299.

Campanula fominii Grossh.: CAM1246 [DB 41842]: Azerbaijan, N Caucasus, Qusar, At the foot of the Mountain Qızılqaya, 6 August 1952, *A. A. Fedorov* s.n. (ERE 69605), PP004914, PP004573, PP004247; CAM1247 [DB 41843]: Azerbaijan, N Caucasus, Qusar, River Qusar, eastern of village Laza, Mountain Qızılqaya, 2400 m, 26 August 1976, s.n. (ERE 69623), PP004915, PP004574, PP004248; CAM1267 [DB 41860]: Azerbaijan, N Caucasus, At the foot of the Mountain Qızılqaya, 6 August 1952, *A. A. Fedorov* s.n. (TBI 1038314), PP004896, PP004588, PP004262; CAM1268 [DB 41861]: Azerbaijan, N Caucasus, between village Laza and Mountain Shahdagh, along the right side of the valley, 18 July 1966, *A. Kharadze* s.n. (TBI 1035163), PP004897, PP004589, PP004263; CAM1284 [DB 41877]: Azerbaijan, N Caucasus, Laza village, 1850 m, 17 July 1966, *N. Cholokashvili & A. Kharadze* s.n. (TBI 1038315), PP004902, PP004602, PP004276; CAM1285 [DB 41878]: Azerbaijan, N Caucasus, between village Laza and Mountain Shahdagh, along the right side of the valley, 18 July 1966, *A. Kharadze* s.n. (TBI 1035165), PP004930, PP004603, PP004277.

Campanula aff. *glomerata* L.: CAM1046 [DB 41274]: *E. von Raab-Straube & al. 6834* (B 10 1052511), PP004638, PP004313, PP003987, from the same population as *6832*; CAM1048 [DB 41276]: *E. von Raab-Straube & al. 6838* (B 10 1052513), PP004639, PP004314, PP003988, from the same population as *6832*; CAM1049 [DB 41277]: *E. von Raab-Straube & al. 6839* (B 10 1052514), PP004640, PP004315, PP003989, from the same population as *6832*; CAM1063 [DB 41290]: *E. von Raab-Straube & al. 6828* (B 10 1052533), PP004646, PP004321, PP003995, from the same population as *6832*; CAM1115 [DB 41503]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1920 m, 43.41615°N, 42.5066°E, 21 July 2016, *N. Silakadze & al. 40* (B 10 1052247), PP004696, PP004371, PP004045; CAM1118 [DB 41506]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1650 m, 43.40138°N, 42.48907°E, 21 July 2016, *N. Silakadze & al. 42* (B 10 1052250), PP004698, PP004373, PP004047.

Campanula kadargavanica Amirkh. & Komzha: CAM546, [DB 16536]: Russian Federation, N Caucasus, North Ossetia-Alania, 24 June 1982, *Amijanov* s.n (LE), *petD* JX915017, *rpl16* PP004301.

Campanula kryophila Rupr.: CAM1248 [DB 41844]: Russian Federation, N Caucasus, North Ossetia-Alania, River Ardon, Tsey, 14 July 1983, *Yu.*

L. Menitsky et al. s.n. *1983-07-14* (ERE 69613), PP004916, PP004575, PP004249; CAM1279 [DB 41872]: Russian Federation, N Caucasus, North Ossetia-Alania, Bass. R. Ardon, near the glacier Tsey, 9 August 1954, *A. Kharadze & R. Gagnidze* s.n. (TBI 1037313), PP004927, PP004599, PP004272; CAM1281 [DB 41874]: Russian Federation, N Caucasus, North Ossetia-Alania, Glacier Tsey, 5 July 1915, *N. Vvedensky 1309* (TBI 1034882), PP004929, PP004627, PP004274.

Campanula lactiflora M. Bieb.: CAM1068 [DB 41297]: Russian Federation, N Caucasus, Republic of Adygea, Apsheronskiy rayon, road to Lagonaki plateau ca. 1.5 km S of Bol'shaya Azishskaya peshchera [= big Azish cave], 1500 m, 40.01944°N, 44.10833°E, 28 July 2015, *E. von Raab-Straube & al. 6909* (B 10 1052539), PP004650, PP004325, PP003999; CAM1139 [DB 41630]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, on the road from Tskhratskaro Pass to Bakuriani, 1820 m, 43.49492°N, 41.72062°E, 10 August 2016, *N. Silakadze 64-2* (B 10 1052314), PP004747, PP004422, PP004096.

Campanula latifolia L.: CAM1069 [DB 41298]: Russian Federation, N Caucasus, Republic of Adygea, Maikopskiy rayon, Lagonaki plateau, just S of lake Psenodakh, 1950-2000 m, 39.9°N, 44.00833°E, 29 July 2015, *E. von Raab-Straube & al. 6926* (B 10 1052540), PP004651, PP004326, PP004000; CAM1114 [DB 41502]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1920 m, 43.41615°N, 42.5066°E, 21 July 2016, *N. Silakadze & al. 39* (B 10 1052246), PP004695, PP004370, PP004044.

Campanula ledebouriana Trautv.: CAM1265 [DB 41858]: Turkey, S Caucasus, Kars Province, the ridge between the Araks and the Upper Euphrates, 19 July 1886, *W. Massalski* s.n. (TBI 1035047), PP004894, PP004586, PP004260; CAM1282 [DB 41875]: Turkey, S Caucasus, Kars Province, Digor-chay valley, 15 July 1886, *W. Massalski* s.n. (TBI 1035046), PP004901, PP004601, PP004275.

Campanula meyeriana Rupr.: CAM1249 [DB 41845]: Azerbaijan, N Caucasus, Qusar, Right side of the river Qusar, Kuzun village, 10 July 1978, *Yu. L. Menitsky & al. 170* (ERE 70847), PP004888, PP004576, PP004250; CAM1269 [DB 41862]: Azerbaijan, N Caucasus, Prov. Baku, distr. Kuba, prope pag. Kryz, 15 July 1929, *M. Sachokia* s.n. (TBI 1035166), PP004921, PP004590, PP004264; CAM1330 (Type) [DB 45127]: Azerbaijan, N Caucasus, between village Laza and Mountain Shahdagh, along the right side of the valley, 18 July 1966, *A. Kharadze* s.n. (TBI 1024863), PP004952, PP004626, PP004300.

Campanula minsteriana Grossh.: CAM1262 [DB 41855]: Armenia, in districtu Daralakhez (in the district of Daralakhez), Meridiem versus a pago Chaczik (facing south from the village of Chaczik), 21 July 1950, *A. Takhtadzhian & S. Czerepanov 4186b* (TBI 1034828), PP004893, PP004585, PP004259; CAM1278 [DB 41871]: Azerbaijan, S Caucasus, Nakhchivan, in monte Karakusch prope pag. Aznabyurt (In the mountains of Karakusch near the village of Aznabyurt), 8 July 1947, *A. Grossheim & al. 4186a* (TBI 1034827), PP004900, PP004598, PP004271.

Campanula ossetica M. Bieb.: CAM1300 [DB 40130]: Russian Federation, N Caucasus, North Ossetia-Alania, Fiagdon valley, 1135 m, 44.32638°N, 42.88166°E, 22 July 2019, *G. Parolly & al. 15799* (B 10 1118224), PP004943, PP004617, PP004291.

Campanula petrophila Rupr.: CAM1085a [DB 41376]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Abano Pass, 2310 m, 45.51258°N, 42.28558°E, 6 July 2016, *N. Silakadze & al. 8a* (B 10 1052209), PP004664, PP004339, PP004013; CAM1090a [DB 41397]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2140 m, 45.5661°N, 42.4508°E, 7 July 2016, *N. Silakadze & al. 13a* (B 10 1052214), PP004668, PP004343, PP004017; CAM1090o [DB 41411]: *N. Silakadze & al. 13o* (B 10 1052215), PP004669, PP004344, PP004018, from the same population as *13a*; CAM1093a [DB 41415]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, between villages Bochorna and Dochu, 2230 m, 45.55618°N, 42.3945°E, 8 July 2016, *N. Silakadze & al. 18a* (B 10 1052218), PP004672, PP004347, PP004021; CAM1093b [DB 41416]: *N. Silakadze & al. 18b* (B 10 1052219), PP004673, PP004348, PP004022, from the same population as *18a*; CAM1095a [DB 41418]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, between villages Dochu and Begelta, 2190 m, 45.54946°N, 42.40073°E, 8 July 2016, *N. Silakadze & al. 20a* (B 10 1052221), PP004675, PP004350, PP004024; CAM1095g [DB 41424]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, between villages Dochu and Begelta, 2020 m, 45.53849°N, 42.40451°E, 8 July 2016, *N. Silakadze & al. 20g* (B 10 1052222), PP004676, PP004351, PP004025; CAM1095k [DB 41428]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, between villages Dochu and Begelta, 1980 m, 45.53567°N, 42.40676°E, 8 July 2016, *N. Silakadze & al. 20k* (B 10 1052223), PP004677, PP004352, PP004026; CAM1097 [DB 41430]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Begelta village, 1980 m, 45.53567°N, 42.40676°E, 8 July 2016, *N. Silakadze & al. 22* (B 10 1052225), PP004679, PP004354, PP004028; CAM1099 [DB 41432]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dartlo village, 1910 m, 45.58929°N, 42.4276°E, 9 July 2016, *N. Silakadze & al. 24* (B 10 1052227), PP004680, PP004355, PP004029; CAM1102 [DB 41435]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dartlo village, 1840 m, 45.55722°N, 42.44881°E, 9 July 2016, *N. Silakadze & al. 27* (B 10 1052230), PP004683, PP004358, PP004032; CAM1103j [DB 41445]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, road to Chesho village, 1920 m, 45.54597°N, 42.47004°E, 9 July 2016, *N. Silakadze & al. 28j* (B 10 1052231), PP004684, PP004359, PP004033; CAM1103t [DB 41455]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, road to Chesho village, 1940 m, 45.54396°N, 42.47186°E, 9 July 2016, *N. Silakadze & al. 28t* (B 10 1052232), PP004685, PP004360, PP004034; CAM1105a [DB 41472]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Kvavlo village, 2180 m, 45.58342°N, 42.44753°E, 9 July 2016, *N. Silakadze & al. 30a* (B 10 1052234), PP004687, PP004362, PP004036; CAM1154 [DB 41671]: Russian Federation, Dagestan, N Caucasus, Rutulskiy raion, Vug river gorge, below village Djinykh, northern rocky slope, 1810 m, 47.05497°N, 41.66447°E, 26 July 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004775, PP004450, PP004124.

Campanula radchensis Kharadze: CAM1111b [DB 41498]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, Kvagakhetkila, 1660 m, 43.39915°N, 42.51237°E, 21 July 2016, *N. Silakadze & al. 36b* (B 10 1052242), PP004692, PP004367, PP004041; CAM1111c [DB 41499]: *N. Silakadze & al. 36c* (B 10 1052243), PP004693, PP004368, PP004042, from the same population as *36b*; CAM1206b [DB 41774]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, Kvagakhetkila, 1660 m, 43.3993°N, 42.51266°E, 5 July 2017, *N. Silakadze & al. 107b* (B 10 1052436), PP004849, PP004525, PP004199; CAM1207a [DB 41775]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Ambrolauri district, Zemo Tlughi village, Mountain Satsalike, 1900 m, 43.19407°N, 42.40336°E, 6 July 2017, *N. Silakadze & al. 108a* (B 10 1052437), PP004850, PP004526, PP004200.

Campanula rapunculoides L.: CAM1032 [DB 41209]: Russian Federation, N Caucasus, Stavropol Krai, Pyatigorsk, NE slopes of Mt. Mashuk, 620 m, 43.11139°N, 44.05389°E, 25 June 2015, *T. Borsch & al. 5779* (B 10 1052484), PP004628, PP004303, PP003977; CAM1053 [DB 41280]: Russian Federation, N Caucasus, Krasnodar Krai, Mostovskiy rayon, Skalistyy khrebet, NW of Psebay, khrebet Gerpegem, 1100 m, 40.77778°N, 44.13972°E, 27 July 2015, *E. von Raab-Straube & al. 6867* (B 10 1052518), PP004643, PP004318, PP003992; CAM1061 [DB 41288]: Russian Federation, N Caucasus, Krasnodar Krai, Mostovskiy rayon, Skalistyy khrebet, Shakhan mountain between Malaya Laba and Bol'shaya Laba ca. 4 km E of Andryuki, 1150 m, 40.88833°N, 44.105°E, 25 July 2015, *E. von Raab-Straube & al. 6831* (B 10 1052531), PP004644, PP004319, PP003993; CAM1066 [DB 41293]: Russian Federation, N Caucasus, Krasnodar Krai, Apsheronskiy rayon, ca. 1 km S of Mezmay, verkhneye Kurdzhipskoye ushchel'ye [= gorge of upper Kurdzhips river], 700 m, 39.96306°N, 44.18861°E, 28 July 2015, *E. von Raab-Straube & al. 6903* (B 10 1052537), PP004648, PP004323, PP003997; CAM1113 [DB 41501]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1920 m, 43.41615°N, 42.5066°E, 21 July 2016, *N. Silakadze & al. 38* (B 10 1052245), PP004694, PP004369, PP004043; CAM1119 [DB 41507]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Oni district, Shkmeri village, 1850 m, 43.343716°N, 42.51512°E, 21 July 2016, *N. Silakadze & al. 43* (B 10 1052251), PP004699, PP004374, PP004048.

Campanula ruprechtii Boiss.: CAM1255 [DB 41851]: Armenia, S Caucasus, Kapan region, Kaputjugh Mountain, 22 August 1989, *M. Oganesian* s.n. (ERE 118764), PP004918, PP004581, PP004255; CAM1257 [DB 41853]: Armenia, S Caucasus, Syunik province, Near lake Tsakhkar, 3100 m, 46.074°N, 39.061°E, 21 July 2008, *M. Aghabalyan & A. Malkhasian* s.n. (ERE 182056), PP004919, PP004582, PP004256; CAM1276 [DB 41869]: Armenia, S Caucasus, Zangezur, Bargushat range, 3000 m, 1 August 1951, *Akhverdov & Mirzoeva* s.n. (TBI 1036558), PP004925, PP004596, PP004269; CAM1293 [DB 41886]: Armenia, S Caucasus, Zangezur, Bargushat range, 3000 m, 1 August 1951, *Akhverdov* s.n. (TBI 1036645), PP004937, PP004610, PP004284; CAM1294 [DB 41887]: Armenia, S Caucasus, East spur of Mountain Soyukh, (Soyugdagh Mountain), 2500 m, 7 June 1947, *A. A. DoluChanov* s.n. (TBI 1036647), PP004938, PP004611, PP004285; CAM1295 [DB 41888]: Azerbaijan, S Caucasus, Nakhchivan, Peak of Soyukh (Soyugdagh Mountain), 3100 m, 9 August 1968, *D. Mtskhvetadze & D. Kapanadze* s.n. (TBI 1036648), PP004939, PP004612, PP004286.

Campanula saxifraga M. Bieb.: CAM1122a [DB 41510]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Khvamli Mountain, 1920 m, 42.71693°N, 42.50947°E, 22 July 2016, *N. Silakadze & al.*

46a (B 10 1052254), PP004701, PP004376, PP004050; CAM1122l [DB 41521]: *N. Silakadze & al. 46l* (B 10 1052255), PP004702, PP004377, PP004051, from the same population as *46a*; CAM1122m [DB 41522]: *N. Silakadze & al. 46m* (B 10 1052256), PP004703, PP004378, PP004052, from the same population as *46a*; CAM1122n [DB 41523]: *N. Silakadze & al. 46n* (B 10 1052257), PP004704, PP004379, PP004053, from the same population as *46a*; CAM1124a [DB 41538]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Askhi Mountain, 1930 m, 42.5564°N, 42.6281°E, 23 July 2016, *N. Silakadze & al. 49a* (B 10 1052259), PP004705, PP004380, PP004054; CAM1124b [DB 41539]: *N. Silakadze & al. 49b* (B 10 1052260), PP004706, PP004381, PP004055, from the same population as *49a*; CAM1124c [DB 41540]: *N. Silakadze & al. 49c* (B 10 1052261), PP004707, PP004382, PP004056, from the same population as *49a*; CAM1124d [DB 41541]: *N. Silakadze & al. 49d* (B 10 1052262), PP004708, PP004383, PP004057, from the same population as *49a*; CAM1124e [DB 41542]: *N. Silakadze & al. 49e* (B 10 1052263), PP004709, PP004384, PP004058, from the same population as *49a*; CAM1124f [DB 41543]: *N. Silakadze & al. 49f* (B 10 1052264), PP004710, PP004385, PP004059, from the same population as *49a*; CAM1127a [DB 41546]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Samegrelo), Martvili district, Taleri village, Chegola Mountain, 2500 m, 42.42575°N, 42.77593°E, 26 July 2016, *N. Silakadze & al. 52a* (B 10 1052267), PP004712, PP004387, PP004061; CAM1127b [DB 41547]: *N. Silakadze & al. 52b* (B 10 1052268), PP004713, PP004388, PP004062, from the same population as *52a*; CAM1127c [DB 41548]: *N. Silakadze & al. 52c* (B 10 1052269), PP004714, PP004389, PP004063, from the same population as *52a*; CAM1127d [DB 41549]: *N. Silakadze & al. 52d* (B 10 1052270), PP004715, PP004390, PP004064, from the same population as *52a*; CAM1127e [DB 41550]: *N. Silakadze & al. 52e* (B 10 1052271), PP004716, PP004391, PP004065, from the same population as *52a*; CAM1127f [DB 41551]: *N. Silakadze & al. 52f* (B 10 1052272), PP004717, PP004392, PP004066, from the same population as *52a*; CAM1127g [DB 41552]: *N. Silakadze & al. 52g* (B 10 1052273), PP004718, PP004393, PP004067, from the same population as *52a*; CAM1130g [DB 41572]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2630 m, 42.7113°N, 43.08155°E, 28 July 2016, *N. Silakadze & al. 55g* (B 10 1052282), PP004722, PP004397, PP004071; CAM1130j [DB 41575]: *N. Silakadze & al. 55j* (B 10 1052285), PP004723, PP004398, PP004072, from the same population as *55g*; CAM1130l [DB 41577]: *N. Silakadze & al. 55l* (B 10 1052287), PP004725, PP004400, PP004074, from the same population as *55g*; CAM1130m [DB 41578]: *N. Silakadze & al. 55m* (B 10 1052288), PP004726, PP004401, PP004075, from the same population as *55g*; CAM1130n [DB 41579]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2690 m, 42.70922°N, 43.08383°E, 28 July 2016, *N. Silakadze & al. 55n* (B 10 1052289), PP004727, PP004402, PP004076; CAM1130p [DB 41581]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Mestia district, Mestia-Koruldi Lake, 2720 m, 42.7081°N, 43.08475°E, 28 July 2016, *N. Silakadze & al. 55p* (B 10 1052291), PP004728, PP004403, PP004077; CAM1208a [DB 41778]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Khvamli Mountain, 1910 m, 42.71736°N, 42.50833°E, 8 July 2017, *N. Silakadze & al. 109a* (B 10 1052440), PP004851, PP004527, PP004201; CAM1208b [DB 41779]: *N. Silakadze & al. 109b* (B 10 1052441), PP004852, PP004528, PP004202, from the same population as *109a*; CAM1208c [DB 41780]: *N. Silakadze & al. 109c* (B 10 1052442), PP004853, PP004529, PP004203, from the same population as *109a*; CAM1208d [DB 41781]: *N. Silakadze & al. 109d* (B 10 1052443), PP004854, PP004530, PP004204, from the same population as *109a*; CAM1210b [DB 41784]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Lechkhumi), Tsageri district, Zemo Lukhvano village, Tsekuri Mountain, 2270 m, 42.62859°N, 42.69225°E, 12 July 2017, *N. Silakadze & al. 111b* (B 10 1052446), PP004855, PP004531, PP004205; CAM1210c [DB 41785]: *N. Silakadze & al. 111c* (B 10 1052447), PP004856, PP004532, PP004206, from the same population as *111b*; CAM1212a [DB 41787]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Kvemo Svaneti), Lentekhi district, between Rhobi and Zeskho villages, 1530 m, 43.16454°N, 42.85818°E, 13 July 2017, *N. Silakadze & al. 113a* (B 10 1052449), PP004857, PP004533, PP004207; CAM1212b [DB 41788]: *N. Silakadze & al. 113b* (B 10 1052450), PP004858, PP004534, PP004208, from the same population as *113a*; CAM1214a [DB 41790]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Ushguli village, Shkhara Glacier, 2510 m, 43.08811°N, 42.96178°E, 15 July 2017, *N. Silakadze & al. 115a* (B 10 1052452), PP004859, PP004535, PP004209; CAM1214b [DB 41791]: *N. Silakadze & al. 115b* (B 10 1052453), PP004860, PP004536, PP004210, from the same population as *115a*; CAM1214c [DB 41792]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Ushguli village, Shkhara Glacier, 2470 m, 43.08767°N, 42.9605°E, 15 July 2017, *N. Silakadze & al. 115c* (B 10 1052454), PP004861, PP004537, PP004211; CAM1215a [DB 41794]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Kvemo Svaneti), Lentekhi district, Zeskho village, Shavi Utsnobi Mountain, 2120 m, 43.21659°N, 42.90786°E, 16 July 2017, *N. Silakadze & al. 116a* (B 10 1052456), PP004862, PP004538, PP004212; CAM1215b [DB 41795]: *N. Silakadze & al. 116b* (B 10 1052457), PP004863, PP004539, PP004213, from the same population as *116a*; CAM1215c [DB 41796]: *N. Silakadze & al. 116c* (B 10 1052458), PP004864, PP004540, PP004214, from the same population as *116a*; CAM1216a [DB 41797]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Kvemo Svaneti), Lentekhi district, Koruldashi village, Ailama Mountain, 2390 m, 43.15861°N, 42.92956°E, 17 July 2017, *N. Silakadze & al. 117a* (B 10 1052459), PP004865, PP004541, PP004215; CAM1216b [DB 41798]: *N. Silakadze & al. 117b* (B 10 1052460), PP004866, PP004542, PP004216, from the same population as *117a*; CAM1216c [DB 41799]: *N. Silakadze & al. 117c* (B 10 1052461), PP004867, PP004543, PP004217, from the same population as *117a*; CAM1216d [DB 41800]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Kvemo Svaneti), Lentekhi district, Koruldashi village, Ailama Mountain, 2430 m, 43.15974°N, 42.93037°E, 17 July 2017, *N. Silakadze & al. 117d* (B 10 1052462), PP004868, PP004544, PP004218; CAM1216f [DB 41802]: *N. Silakadze & al. 117f* (B 10 1052464), PP004869, PP004545, PP004219, from the same population as *117d*; CAM1216g [DB 41803]: *N. Silakadze & al. 117g* (B 10 1052465), PP004870, PP004546, PP004220, from the same population as *117d*;

CAM1216h [DB 41804]: *N. Silakadze & al. 117h* (B 10 1052466 PP004871, PP004547, PP004221, from the same population as *117d*; CAM1237 [DB 41833]: Russian Federation, N Caucasus, Kabardino-Balkaria, North side of Elbruzi Mountain, Massive of the river Malka, 29 July 1981, *Yu. L. Menitsky et al. 430* (ERE 70768), PP004912, PP004565, PP004239; CAM1250 [DB 41846]: Russian Federation, N Caucasus, Karachay-Cherkessia, Top of the Bol'shaya Laba river, on the hill of Zakan, 8 July 1979 *T. Zaikonnikova et al.* s.n. (ERE 70757), PP004889, PP004577, PP004251; CAM1251 [DB 41847]: Russian Federation, N Caucasus, Karachay-Cherkessia, Karachayevsky raion, the right side of river Kuban, village Khurzuk, 1600-1800 m, 7 August 1989, *N. Khandilyan* s.n. (ERE 70759), PP004890, PP004578, PP004252; CAM1270 [DB 41863]: Georgia, N Caucasus, Samegrelo-Zemo Svaneti (Zemo Svaneti), Gorges of Tsaneri, Khozheri, 2800 m, 1 September *B. Zurebiani* s.n. (TBI 1038399), PP004922, PP004591, PP004265; CAM1277 [DB 41870]: Russian Federation, N Caucasus, Karachay-Cherkessia, Uchkulan village, right side of river Kuban, 14 August 1956, *A. Kharadze et al.* s.n. (TBI 1033287), PP004926, PP004597, PP004270; CAM1290 [DB 41883]: Georgia, N Caucasus, Racha-Lechkhumi and Kvemo Svaneti (Racha), Ghebi village, 2400- 2600 m, 5 August 1982, *Sh. Shetekauri* s.n. (TBI 1037294), PP004934, PP004607, PP004281; CAM1312 [DB 41891]: Russian Federation, N Caucasus, Kabardino-Balkaria, Elbrus Mountain, 3800 m, September 1980, *W. Heller* s.n. (B 10 0507479), PP004950, PP004624, PP004298.

Campanula aff. *sibirica* L.: CAM1036 [DB 41213]: Russian Federation, N Caucasus, Stavropol Kray, Predgorny rayon, W side of Podkumok river valley ca. 8 km N of Kislovodsk on road (A157) to Yessentuki, 670-700 m, 42.79417°N, 43.99583°E, 25 June 2015, *T. Borsch & al. 5810* (B 10 1052494), PP004629, PP004304, PP003978; CAM1045 [DB 41273]: Russian Federation, N Caucasus, Krasnodar Krai, Mostovskiy rayon, Skalistyy khrebet, Shakhan mountain between Malaya Laba and Bol'shaya Laba ca. 4 km E of Andryuki, 1150 m, 40.88833°N, 44.105°E, 25 July 2015, *E. von Raab-Straube & al. 6832* (B 10 1052510), PP004637, PP004312, PP003986; CAM1050 [DB 41278]: *E. von Raab-Straube & al. 6840* (B 10 1052515), PP004641, PP004316, PP003990, from the same population as *6832*; CAM1051 [DB 41279]: *E. von Raab-Straube & al. 6841* (B 10 1052516), PP004642, PP004317, PP003991, from the same population as *6832*; CAM1064 [DB 41291]: *E. von Raab-Straube & al. 6827* (B 10 1052534), PP004647, PP004322, PP003996, from the same population as *6832*.

Campanula aff. *sibirica* subsp. *hohenackeri* (Fisch. & C. A. Mey.) Damboldt: CAM1091a [DB 41412]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2140 m, 45.5661°N, 42.4508°E, 7 July 2016, *N. Silakadze & al. 15a* (B 10 1052216), PP004670, PP004345, PP004019; CAM1096 [DB 41429]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Begelta village, 1980 m, 45.53567°N, 42.40676°E, 8 July 2016, *N. Silakadze & al. 21* (B 10 1052224), PP004678, PP004353, PP004027; CAM1161 [DB 41678]: Russian Federation, Dagestan, N Caucasus, Levashinskiy raion, surroundngs of village Tsudarakh, 1250 m, 47.16505°N, 42.32419°E, 13 July 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004776, PP004451, PP004125; CAM1162 [DB 41679]: Russian Federation, Dagestan, N Caucasus, Dakhadayevsky raion, Urkarakh - Kubachi, on rocky places along the port side at the bridge over the river Khulakherk, 910 m, 47.61794°N, 42.12358°E, 28

July 2016, *R. Murtazaliyev* s.n. (herb. Murtazaliyev), PP004777, PP004452, PP004126; CAM1260 [DB 27374]: Georgia, N Caucasus, Kakheti, Akhmeta district, Tusheti, Tusheti Protected Area, Upper Omalo road, below Omalo Castle, 2040 m, 8 July 2016, *G. Parolly & al. 15045* (B 10 0518297 PP004892, PP004583, PP004257.

Campanula stevenii M. Bieb.: CAM1087a [DB 41382]: Georgia, N Caucasus, Kakheti (Tusheti), Akhmeta district, Dano village, 2150 m, 45.56757°N, 42.45046°E, 7 July 2016, *N. Silakadze & al. 10a* (B 10 1052211), PP004665, PP004340, PP004014; CAM1193 [DB 41741]: Georgia, S Caucasus, Samckhe-Javakheti, On the way to Akhalkalaki Diago village, 1940 m, 43.49905°N, 41.60252°E, 16 July 2017, *N. Silakadze & K. E. Jones 94* (B 10 1052403), PP004821, PP004497, PP004171.

Campanula sosnowskyi Kharadze: CAM1275 [DB 41868]: Russian Federation, N Caucasus, North Ossetia-Alania, Environs of village Chmi, left side of Didneua-kom gorge, 13 July 1947, *A. Kharadze & K. Khutsishvili* s.n. (TBI 1036039), PP004924, PP004595, PP004268; CAM1306 [DB 40158]: Russian Federation, N Caucasua, North Ossetia-Alania, Alagir district, middle course of the Fiagdon river, Kadargavan canyon, 1085 m, 44.32583°N, 42.88111°E, 28 July 2013, *D. S. Shilnikov,* s.n. (*D. S. Shilnikov* n.s), PP004947, PP004621, PP004295.

Campanula tridentata Schreb.: CAM1134a [DB 41620]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Bakuriani, Tskhratskaro Pass, 2460 m, 43.51987°N, 41.68785°E, 10 August 2016, *N. Silakadze 61a* (B 10 1052305), PP004738, PP004413, PP004087; CAM1134b [DB 41621]: *N. Silakadze 61b*, PP004739, PP004414, PP004088, from the same population as *61a*; CAM1140a [DB 41631]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2390 m, 43.36105°N, 41.72778°E, 11 August 2016, *N. Silakadze 65a* (B 10 1052315), PP004748, PP004423, PP004097; CAM1140c [DB 41633]: Georgia, S Caucasus, Samckhe-Javakheti, Borjomi district, Tsikhisjvari village, Kodiani Mountain, 2410 m, 43.36113°N, 41.72723°E, 11 August 2016, *N. Silakadze 65c* (B 10 1052317), PP004749, PP004424, PP004098; CAM1220a [DB 41813]: Armenia, S Caucasus, Aragatsotn Province, Aragats Mountain, surroundings of the Kari lake, 3210 m, 44.17857°N, 40.47334°E, 21 August 2017, *N. Silakadze & al. 121a* (B 10 1052475), PP004877, PP004554, PP004228.

Supplementary material 1

Bayesian 50% majority-rule consensus tree of the combined dataset of the Caucasian *Campanula* species based on three plastid markers (*trnK/matK*, *petD* and *rpl16*)

Authors: Nana Silakadze, Marine Mosulishvili, Thomas Borsch, Norbert Kilian

Data type: pdf

Link: https://doi.org/10.3897/phytokeys.243.120908.suppl1

Supplementary material 2

Maximum parsimony tree of the combined dataset of the Caucasian *Campanula* species based on three plastid markers (*trnK/matK*, *petD* and *rpl16*)

Authors: Nana Silakadze, Marine Mosulishvili, Thomas Borsch, Norbert Kilian
Data type: pdf

Link: https://doi.org/10.3897/phytokeys.243.120908.suppl2

Supplementary material 3

Taxonomy of the *Scapiflorae* group by the different authors

Authors: Nana Silakadze, Marine Mosulishvili, Thomas Borsch, Norbert Kilian
Data type: docx

Link: https://doi.org/10.3897/phytokeys.243.120908.suppl3

Supplementary material 4

Primers are used for amplification and sequencing reactions

Authors: Nana Silakadze, Marine Mosulishvili, Thomas Borsch, Norbert Kilian
Data type: docx

Link: https://doi.org/10.3897/phytokeys.243.120908.suppl4

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Research Article

Molecular and morphological evidence supports the resurrection of *Chrysosplenium guangxiense* H.G.Ye & Gui C.Zhang (Saxifragaceae)

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Abstract

Chrysosplenium guangxiense H.G.Ye & Gui C.Zhang was first described as a new species in 1994 but later synonymized in the Flora of China treatment with *C. glossophyllum* H.Hara. Plastid genomes and nrDNA sequences were used to infer the phylogenetic relationships of selected taxa in *Chrysosplenium*. Our phylogenetic analyses revealed that *C. guangxiense* belongs to sect. *Alternifolia*, is closely related to *Chrysosplenium Hydrocotylifolium* H.Lév. & Vaniot but distant from *C. glossophyllum*. Morphologically, *C. guangxiense* could be easily distinguished from *C. glossophyllum* by having robust rhizomes, basal leaves with a long cuneate base and fewer teeth in the margin, curled sepal margins, and red, larger seeds. It could also be easily distinguished from *C. hydrocotylifolium* by possessing long elliptic leaves and a long cuneate leaf base. Along with the phylogenetic studies, the complete plastid genome of *C. guangxiense* was also reported. The plastid genome was 154,004 bp in length and comprised two inverted repeats (IRs) of 28,120 bp, separated by a large single-copy of 80,646 bp and a small single-copy of 17,118 bp. A total of 111 functional genes were discovered, comprising 78 protein-coding genes, 29 tRNA genes, and four rRNA genes. Based on assessment of morphological and molecular data *Chrysosplenium guangxiense* H.G.Ye & Gui C.Zhang is resurrected from *C. glossophyllum* H.Hara at species level. A global conservation assessment classifies *C. guangxiense* as Vulnerable (VU).

Key words: *Chrysosplenium*, phylogeny, plastid genome, Saxifragaceae, taxonomy

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Introduction

Chrysosplenium L. (Saxifragaceae) comprises more than 70 species of perennial herbs (Kim et al. 2019; Fu et al. 2020, 2021). *Chrysosplenium* is distributed throughout Asia, America and Europe (Pan and Ohba 2001; Soltis 2007). The latest checklist of Chinese *Chrysosplenium* included 35 species (Pan and Ohba 2001). Their earlier revisions classified the genus into two subgenera (subg. *Chrysosplenium* and subg. *Gamosplenium*) based on leaf arrangement (Pan 1986a, b). This

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character was also considered by Hara, who divided *Chrysosplenium* into two sections, namely sect. *Alternifolia* and sect. *Oppositifolia* (Hara 1957). The following molecular analyses (Soltis et al. 2001; Fu et al. 2021) demonstrated that these two subgenera/sections are monophyletic and sister to each other, further confirming that leaf arrangement is a good indicator of the relationships within the genus. However, a recent systematic study based on a complete chloroplast genome and nrDNA data challenged this relationship as their results recovered an additional clade composed of two species with alternate leaves (as members of sect. *Alternifolia*). The newly defined clade was recognized as a basal clade sister to the rest of the species of *Chrysosplenium* (Yang et al. 2023).

Chrysosplenium guangxiense H.G.Ye & Gui C.Zhang was first described as a new species in 1994 by having ovate-elliptic leaves, an acuminate apex, a cuneate base, fewer dentate margins, and a depressed sepal apex, enabling it to be distinguished from its similar species, *C. glossophyllum* H.Hara (Ye and Zhang 1994). Subsequently, it appeared as a synonym of the latter in *Flora of China* without additional explanation (Pan and Ohba 2001). We assumed that the authors considered these differences were insufficient to distinguish them. It is possible that the scarcity of *C. glossophyllum* species in China, with its only population in Sichuan Province, may have led to this misinterpretation. Molecular data, however, could provide a means to confirm the systematic position of morphological similarities and to evaluate the phylogenetic informativeness of morphological characters (Scotland et al. 2003).

In 2019, we conducted an extensive investigation in Tianlin County, Baise City, Guangxi, China, the type locality of *Chrysosplenium guangxiense*. We collected a plant of *Chrysosplenium*, which was then confirmed as *C. guangxiense*. Following a thorough literature survey (Hara 1957; Pan 1992; Pan and Ohba 2001; Liu et al. 2016; Wei 2018; Kim et al. 2019; Fu et al. 2020, 2021; Wei et al. 2022), along with the molecular evidence, it was confirmed that *C. guangxiense* is a different species from *C. glossophyllum*.

Materials and methods

Morphology observations and conservation assessments

All morphological characters were studied based on the material from field and herbarium specimens using a dissecting microscope (SMZ171, Motic, China). For seed morphology, we also undertook scanning electron microscope (SEM) observations; seeds were collected from the field and dried with silica gel. The pre-treatments, including impurity removal, air-drying, and gold-coating, were performed following Fu et al. (2020). Observations and photographs were taken under a Hitachi SU8010 scanning electron micrograph. At least 15 seeds were used to determine their size and ornamentation. A conservation assessment was undertaken following the IUCN (2019).

Genomic DNA extraction, sequencing, plastid genome and nrDNA assembly and annotation

The genomic DNA was extracted using the modified CTAB method (Doyle and Doyle 1987). The short-insertion library (300 bp) was constructed and then sequenced to obtain 2×150 bp paired-end data using the Illumina NovaSeq platform at Majorbio Company (Shanghai, China). The raw data was filtered through Trimmomatic v. 0.39 (Bolger et al. 2014) to obtain clean data, and then the clean data were quality-controlled using FastQC v. 0.11.9 (Simon 2020). The complete plastid genome and nrDNA sequence were assembled using GetOrganelle v. 1.7.5 (Jin et al. 2020), and annotation was performed using CPGAVAS2 (Shi et al. 2019) and PGA (Qu et al. 2019).

Phylogenetic analysis

To confirm the phylogenetic placement of *Chrysosplenium guangxiense*, we undertook phylogenetic studies using the chloroplast (CP) genomes and nrDNA sequences obtained in a previous study (Yang et al. 2023). Forty-seven species of *Chrysosplenium* as in-group, and two species from other genera in Saxifragaceae and *Itea chinensis* Hook. & Arn. from Iteaceae as an out-group were sampled. The species names and GenBank accession numbers are listed in Table 1.

The chloroplast protein-coding genes (cpPCGs) were extracted from the CP genome using PhyloSuite v.1.2.3 (Zhang et al. 2020). These cpPCGs and nrDNA sequences were aligned by MAFFT v. 7.4 (Katoh and Standley 2013), and concatenated using PhyloSuite v.1.2.3 (Zhang et al. 2020) to form the cpPCGs+nrDNA matrix. The phylogenetic analyses of *Chrysosplenium* based on cpPCGs, nrDNA and cpPCGs+nrDNA matrices were performed using maximum likelihood (ML) and Bayesian inference (BI), respectively. The ML analyses were conducted using IQ-TREE v. 2.1.2 (Nguyen et al. 2015) with 1,000 bootstrap replicates and the default ModelFinder (Kalyaanamoorthy et al. 2017) to find GTR+F+I+G4 as the best-fit substitution model. Tree visualization was achieved in Figtree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). For BI analysis, MrBayes v. 3.2.6 (Ronquist et al. 2012) was employed to obtain a maximum clade credibility (MCC) tree. BI analysis was performed using one million generations, two runs, 25% trees discarded as burn-in, and trees sampled every 1,000 generations (1,000 trees sampled in total) with the GTR model.

Results

Characteristics of the complete chloroplast genome

The CP genome of *Chrysosplenium guangxiense* comprised 154,004 bp (Fig. 1). The characteristics and statistics of the CP genome are summarized in Tables 4, 5.

Molecular phylogenetic studies

The cpPCGs matrix length was 71,919 bp, including 6,392 parsimony informative sites, 13,645 variable sites, and 55,865 conserved sites. The nrDNA matrix was 6,738 bp in length, with 765 parsimony informative sites, 1,200 variable sites, and 5,231 conserved sites. The cpPCGs+nrDNA matrix was 78,657 bp in length, with 7,157 parsimony informative sites, 14,845 variable sites, and 61,096 conserved sites. The phylogenetic tree of the cpPCGs matrix exhibited high confidence, while the phylogenetic tree of the nrDNA matrix had some branches with low support, and was significantly different from the former (Suppl. materials 1, 2). However, *Chrysosplenium guangxiense* was consistently related to

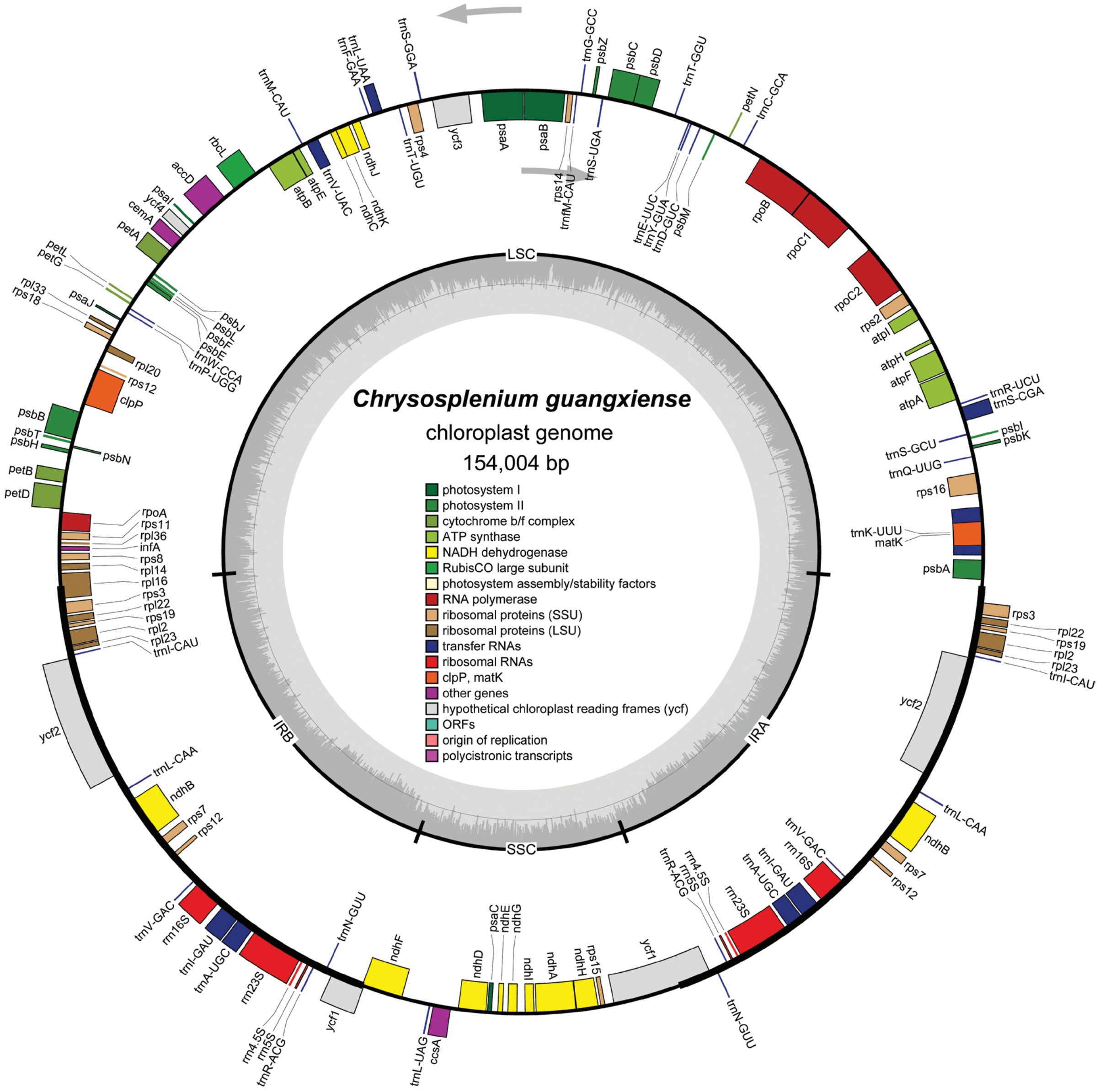

Figure 1. Plastid genome map of *Chrysosplenium guangxiense*. The thick lines on the outer complete circle identify the inverted repeat regions (IRa and IRb). The innermost track of the plastome shows the GC content. Genes on the outside and inside of the map are transcribed in clockwise and counter directions, respectively.

C. hydrocotylifolium H.Lév. & Vaniot in both chloroplast and nuclear gene trees (Suppl. materials 1, 2). The phylogenetic tree of the cpPCGs+nrDNA matrix received a higher confidence value compared to trees generated from subsets (cpPCGs and nrDNA). Topologies obtained from BI and ML methods were congruent and showed that *Chrysosplenium* species clustered in a strongly supported clade (BS = 100%, PP = 1) which was further divided into three well-supported clades (defined as A-C clades; Fig. 2). *Chrysosplenium guangxiense* was recognized as a member of clade B and fell in its basal clade (BS = 100%, PP = 1; Fig. 2), which also included *C. macrophyllum* Oliv., *C. zhangjiajieense* X.L.Yu, Hui Zhou & D.S.Zhou, *C. hydrocotylifolium*, *C. flagelliferum* F.Schmidt, and *C. zhouzhiense* Hong Liu. Of these, *C. guangxiense* was most closely related to *C. hydrocotylifolium* (BS = 100%, PP = 1; Fig. 2). Although *C. glossophyllum* was also a member of clade B, it fell into a much more distant clade from *C. guangxiense* (Fig. 2).

Table 1. Species names and GenBank accession numbers of plastid genomes and nrDNA sequence used in this study (* newly generated sequences).

Species	Location	Voucher specimens	Herbarium	Plastid GenBank number	nrDNA GenBank number
Chrysosplenium album Maxim.	Nikkou-shi, Japan	HSN09815	HSN	OK336556	OP154009
Chrysosplenium aureobracteatum Y.I.Kim & Y.D.Kim	Gangwon Province, South Korea	KYI-2009032	(Kim et al. 2018)	MG878089	MK989509
Chrysosplenium biondianum Engl.	Shanxi, China	HZ2017050107362	HSN	OK336542	OP154015
Chrysosplenium carnosum Hook.f. et Thoms.	Sichuan, China	HSN013113	HSN	OK336564	OP154016
Chrysosplenium davidianum Decne. ex Maxim.	Sichuan, China	HSN06442	HSN	OK336537	OP154017
Chrysosplenium delavayi Franch.	Sangzhi, Hunan, China	SZ2016080907105	HSN	OK336539	OP154018
Chrysosplenium dubium J. Gayex DC.	Georgia	P03_WF11	(Folk et al. 2019)	–	OP154019
Chrysosplenium echinus Maxim.	Nikkou-shi, Japan	HSN09817	HSN	OK336557	OP154020
Chrysosplenium fauriae Franch.	Nikkou-shi, Japan	HSN09823	HSN	OK336561	OP154021
Chrysosplenium flagelliferum Fr. Schmidt.	Nikkou-shi, Japan	HSN09816	HSN	OK336541	OP154022
Chrysosplenium forrestii Diels	Nikkou-shi, Japan	HSN7797	HSN	OK336565	OP154024
Chrysosplenium giraldianum Engl.	Sichuan, China	JZ2018042507981	HSN	OK336548	OP154025
Chrysosplenium glossophyllum H. Hara	Sichuan, China	QCS2017102608035	HSN	OK336544	OP154026
Chrysosplenium grayanum Maxim.	Nikkou-shi, Japan	HSN09810	HSN	OK336555	OP154027
Chrysosplenium griffithii Hook.f. et Thoms.	Shanxi, China	HSN7760	HSN	OK336547	OP154028
Chrysosplenium guangxiense H.G.Ye & Gui C.Zhang	Guangxi, China	HSN13356	HSN	OP093635*	OR941245*
Chrysosplenium henryi Franch.	Sangzhi, Hunan, China	HSN7505	HSN	OK336532	OP154030
Chrysosplenium hydrocotylifolium H. Lév. & Vaniot	Hubei, China	HSN09188	HSN	OK336540	OP154031
Chrysosplenium japonicum (Maxim.) Makino	Zhejiang, China	HSN7909	HSN	OK336554	OP154032
Chrysosplenium kamtschaticum Fisch. ex Seringe	Shimane-ken, Japan	DG2019032310004	HSN	MT371065	OP154033
Chrysosplenium kiotense Ohwi.	Nikkou-shi, Japan	HSN09818	HSN	OK336558	OP154034
Chrysosplenium lanuginosum Hook.f. et Thoms.	Anhui, China	BD2017030507343	HSN	OK336534	OP154035
Chrysosplenium lectus-cochleae Kitagawa	Jilin, China	HSN7379	HSN	OK336550	OP154036
Chrysosplenium macrophyllum Oliv.	Hubei, China	BD2017030507344	HSN	MK973001	OP154037
Chrysosplenium macrospermum Y.I.Kim & Y.D.Kim	Jilin, China	CBS2016062406656	HSN	OK336562	OP154038
Chrysosplenium macrostemon Maxim. ex Franch. et Sav.	Nikkou-shi, Japan	HSN09820	HSN	OK336560	OP154039
Chrysosplenium microspermum Franch.	Jinfo Mountain, Chongqing, China	HSNTG025	HSN	OK336546	OP154040
Chrysosplenium nepalense D.Don	Tengchong, Yunnan, China	GLGH20170607375	HSN	OK336535	OP154043
Chrysosplenium nudicaule Bunge	Gansu, China	HSN07772	HSN	MZ424445	OP154044
Chrysosplenium oppositifolium L.	Wales, UK	BGN_RN_W	(Folk et al. 2019)	OR397749	OP154057
Chrysosplenium pilosum Maxim.	Nikkou-shi, Japan	HSN09819	HSN	OK336559	OP154045
Chrysosplenium valdepilosum (Ohwi) S.H.Kang & J.W.Han	Jilin, China	HSN09819	HSN	OR397753	OP154046
Chrysosplenium qinlingense Z.P.Jien ex J.T.Pan	Sichuan, China	HSN7980	HSN	OK336549	OP154047
Chrysosplenium ramosum Maxim.	Jilin, China	SJH2017052107372	HSN	MK973002	OP154048
Chrysosplenium sedakowii Turcz.	Irkutsk, Russia	P02_WC8	(Folk et al. 2019)	–	OP154049

Species	Location	Voucher specimens	Herbarium	Plastid GenBank number	nrDNA GenBank number
Chrysosplenium serreanum Hand.-Mazz.	Jilin, China	SJH2017052107371	HSN	OK336538	OP154050
Chrysosplenium sinicum Maxim.	Hunan, China	TPS2017042407504	HSN	MT362051	OP154051
Chrysosplenium taibaishanense J.T.Pan	Shanxi, China	HSN7761	HSN	OK336552	OP154052
Chrysosplenium uniflorum Maxim.	Tibet, China	HSN7380	HSN	OK336533	OP154053
Chrysosplenium zhouzhiense Hong Liu	Shanxi, China	HSN13356	HSN	OK336551	OP154055
Chrysosplenium alternifolium L.	Shimane-ken, Japan	DG2019032310003	HSN	OK336545	OP154010
Chrysosplenium tetrandrum (N. Lund) Th. Fries	Nunavut, Canada	Brysting_01-065_CAN	CAN	OR397750	OP154052
Chrysosplenium wrightii Franch. & Sav.	Yukon, Canada	Bennett_08-125_CAN	CAN	OR397751	OP154059
Chrysosplenium valdivicum Hook.	Chile	P04_WG8	HSN	OR397752	OP154060
Chrysosplenium zhangjiajieense X.L.Yu, Hui Zhou & D.S.Zhou	Hunan, China	ZJ2016031506369	HSN	OK336563	OP154054
Peltoboykinia tellimoides (Maxim.) Hara	Henan, China	PT210814	(Yang et al. 2022)	MZ779205	JQ895246
Saxifraga stolonifera Curt.	Hubei, China	S313	(Chen et al. 2022)	NC_037882	MK092506
Itea chinensis C.K.Schneider	Hunan, China	S371	–	NC_037884	MG730867

Morphological observations

A suite of morphological characters including rhizome size, leaf shape, leaf margin dentate, sepal apex shape, and seed size of *Chrysosplenium guangxiense* and *C. glossophyllum* was consulted or observed. *Chrysosplenium guangxiense* had a robust rhizome, basal leaves with a long cuneate base and fewer teeth in the margin, curled sepal margins, and red, larger seeds that make it easily distinguished from *C. glossophyllum* (Table 2). Considering the phylogenetic results, a morphological comparison between *C. guangxiense* and *C. hydrocotylifolium* was also conducted. *Chrysosplenium guangxiense* had long elliptic leaves and a long cuneate leaf base, which can be easily distinguished from *C. hydrocotylifolium* (Table 3).

Table 2. Diagnostic comparison of *Chrysosplenium guangxiense* and *C. glossophyllum*.

Characters	*C. guangxiense*	*C. glossophyllum*
Rhizome	Rhizome thick, crossed and nodular	absent
Basal leaves	base long cuneate, margin 10–20-crenate	base rounded to subcordate; margin 20–36-crenate
Sepals	margin curl	margin uncurl
Seed	red, 0.59–0.85 × 0.48–0.63 mm	black, 0.50 × 0.40 mm

Table 3. Diagnostic comparison of *Chrysosplenium guangxiense* and *C. hydrocotylifolium*.

Characters	*C. guangxiense*	*C. hydrocotylifolium*
Basal leaves and cauline leaves	Isophyllous	heterophyllous
Basal leaves	long elliptic, margin 14–24-crenate; base long cuneate	orbicular, margin 34–39-crenate; base reniform

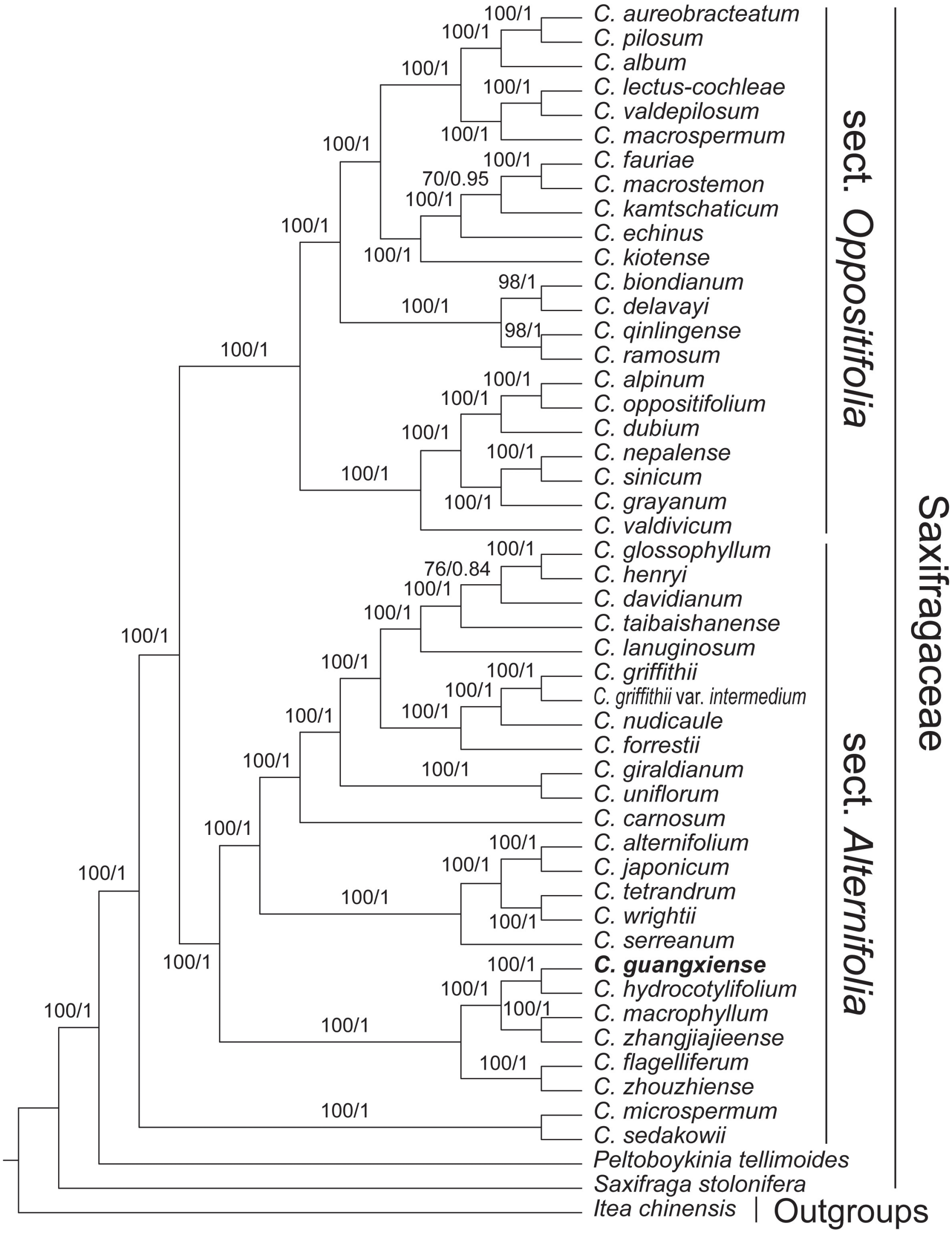

Figure 2. Phylogenetic tree of *Chrysosplenium* generated from maximum likelihood (ML) and Bayesian inference of cpPCGs+nrDNA dataset. Numbers below the branches indicate bootstrap values (≥50%) of the ML analyses and the posterior probability (≥0.5) of Bayesian analyses.

Discussion

Our phylogenetic result supported the monophyly of *Chrysosplenium* (Soltis et al. 2001; Fu et al. 2021; Yang et al. 2023). Besides two well-defined clades (denoted as sect. *Oppositifolia* and sect. *Alternifolia*), our result also revealed a third clade comprising two species from sect. *Alternifolia*, the topology of which is consistent with the previous study (Yang et al. 2023). This phylogenetic relationship indicated a non-monophyletic status of sect. *Alternifolia* and suggested that a deeper morphological character evolution across this phylogenetic framework is needed to evaluate the phylogenetic informativeness of characters.

Table 4. Summary of the complete plastid genome of *Chrysosplenium guangxiense*.

Characteristic	***Chrysosplenium guangxiense***
Size (base pair, bp)	154,004
LSC length (bp)	80,646
SSC length (bp)	17,118
IR length (bp)	28,120
Number of genes	111
Protein-coding genes	78
rRNA genes	4
tRNA genes	29
GC content	37.51%

Table 5. The gene statistics of the plastid genome of *Chrysosplenium guangxiense*. [Genes with one or two introns are indicated by one (*) or two asterisks (**), respectively. Genes in the IR regions are followed by the (×2) symbol].

Group of Genes	Gene Name	Number
tRNA genes	_trnK_-UUU, _trnQ_-UUG, _trnS_-GCU, _trnG_-GCC, _trnR_-UCU, _trnC_-GCA, _trnD_-GUC, _trnY_-GUA, _trnE_-UUC, _trnT_-GGU, _trnS_-UGA, _trnS_-CGA, _trnfM_-CAU, _trnS_-GGA, _trnT_-UGU, _trnL_-UAA*, _trnF_-GAA, _trnV_-UAC*, _trnM_-CAU, _trnW_-CCA, _trnP_-UGG, _trnR_-ACG(×2), _trnN_-GUU(×2), _trnI_-GAU*(×2), _trnA_-UGC*(×2), _trnL_-UAG, _trnI_-CAU(×2), _trnL_-CAA(×2), _trnV_-GAC(×2)	29
rRNA genes	_rrn16_(×2), _rrn23_(×2), _rrn4.5_(×2), _rrn5_(×2)	4
Ribosomal small subunit	_rpsl6_, _rps2_, _rps14_, _rps4_, _rps18_, _rps12_(×2), _rps11_, _rps8_, _rps3_(×2), _rps19_(×2), _rps7_(×2), _rps15_	12
Ribosomal Large subunit	_rpl33_, _rpl20_, _rpl36_, _rpl14_, _rpl16_, _rpl22_(×2), _rpl2_(×2), _rpl23_(×2)	8
DNA-dependent RNA polymerase	_rpoC2_, _rpoC1*_, _rpoB_, _rpoA_	4
Photosystem I	_psaB_, _psaA_, _psaI_, _psaJ_, _psaC_	5
Large subunit of rubisco	_rbcL_	1
Photosystem II	_psbA_, _psbK_, _psbI_, _psbM_, _psbD_, _psbC_, _psbZ_, _psbJ_, _psbL_, _psbF_, _psbE_, _psbB_, _psbT_, _psbN_, _psbH_	15
NADH dehydrogenase	_ndhJ_, _ndhK_, _ndhC_, _ndhB*_(×2), _ndhF_, _ndhD_, _ndhE_, _ndhG_, _ndhI_, _ndhA*_, _ndhH_	11
Cytochrome b/f complex	_petN_, _petA_, _petL_, _petG_, _petB_, _petD_	6
ATP synthase	_atpA_, _atpF*_, _atpH_, _atpI_, _atpE_, _atpB_	6
Maturase	_matK_	1
Subunit of acetyl-CoA carboxylase	_accD*_	1
Envelope membrane protein	_cemA_	1
Protease	_clpP**_	1
Translational initiation factor	_infA_	1
c-type cytochrome synthesis	_ccsA_	1
Conserved open reading frames(_ycf_)	_ycf3**_, _ycf4_, _ycf2_(×2), _ycf1_(×2)	4

In our phylogenetic tree, *Chrysosplenium guangxiense* was recovered as a member of sect. *Alternifolia*, most closely related to *Chrysosplenium hydrocotylifolium* (BS = 100%, PP = 1) but had a distant relationship with *C. glossophyllum*. It was easy to distinguish *C. guangxiense* from *C. hydrocotylifolium* by the long elliptic leaves and long cuneate leaf bases (Table 3). Our morphological comparison between *C. guangxiense* and *C. glossophyllum* also showed a suite of characters, including having a robust rhizome, basal leaves with a long cuneate base and fewer teeth in margin, and larger seeds in *C. guangxiense* which helped distinguish it from *C. glossophyllum* (Table 2). Furthermore, there was a typical viviparous phenomenon of *C. guangxiense*; the mature seeds were able to germinate directly in the opening capsule (Figs 3E, 4G, H). This feature has not been reported in any other *Chrysosplenium* species so far. Therefore, our molecular and morphological evidence supports *C. guangxiense* as a distinct species that resurrected from *C. glossophyllum*. We presented the following detailed taxonomic treatment for *C. guangxiense*.

Taxonomic treatment

***Chrysosplenium guangxiense* H.G.Ye & Gui C.Zhang in Acta Bot. Austro Sin. 9: 57, f. 1 (1994)**
Figs 3, 4

Type. Tian Lin, 11 Oct. 1989, South China Exped. 2458 (holotype: IBSC!; isotype: IBSC!).

Description. Perennial herbs, 5.5–17 cm high. ***Root*** fibrous and robust. Long creeping ***rhizome*** developed, thick, crossed and nodular, 1–2 cm between each node, without stolons and bulbs. ***Flowering stem(s)*** always 1, erect, branched, 10–17 cm high, sparsely pilose, green, squared. ***Sterile branches*** arise from all basal leaves. ***Isophyllous, Basal leaves*** 3–6, alternate and clustered; petiole 1–6.5 cm long, white pilose; leaf blade long elliptic, 2.2–10.3 × 1.8–3.3 cm, abaxially glabrous, light green, adaxially with sparse long hispid, dark green, apex rounded, margin 14–25-crenate, base long cuneate. ***Cauline leaves*** always 1, petiole 1.3–2.2 cm long; blade 2.2–4.0 × 1.2–1.9 cm, long elliptic, glabrous in the abaxial side and with sparse hispid in the adaxial side; apex obtuse; margin obtusely dentate (9–13 teeth); base broadly cuneate; veins obvious in adaxial. ***Pleiochasium*** 9–16 cm wide, 10–15 cm high, extremely diffused, with 5–20-flowered cyme, branches sparsely hispid, surrounded by bracts; ***bracteal leaves*** green, elliptic to broadly ovate or round, glabrous. ***Flowers*** tetramerous, actinomorphic; ***sepals*** 4 (2 pairs), flat, green, 0.9–1.2 × 2.1–4.3 mm, broadly ovate, apex acute, with margin curls outward in fruiting time; disk obvious; ***stamens*** 8, ca. 0.2 mm long, shorter than sepals; anthers orange, 2-locular, longitudinally dehiscent; ova-

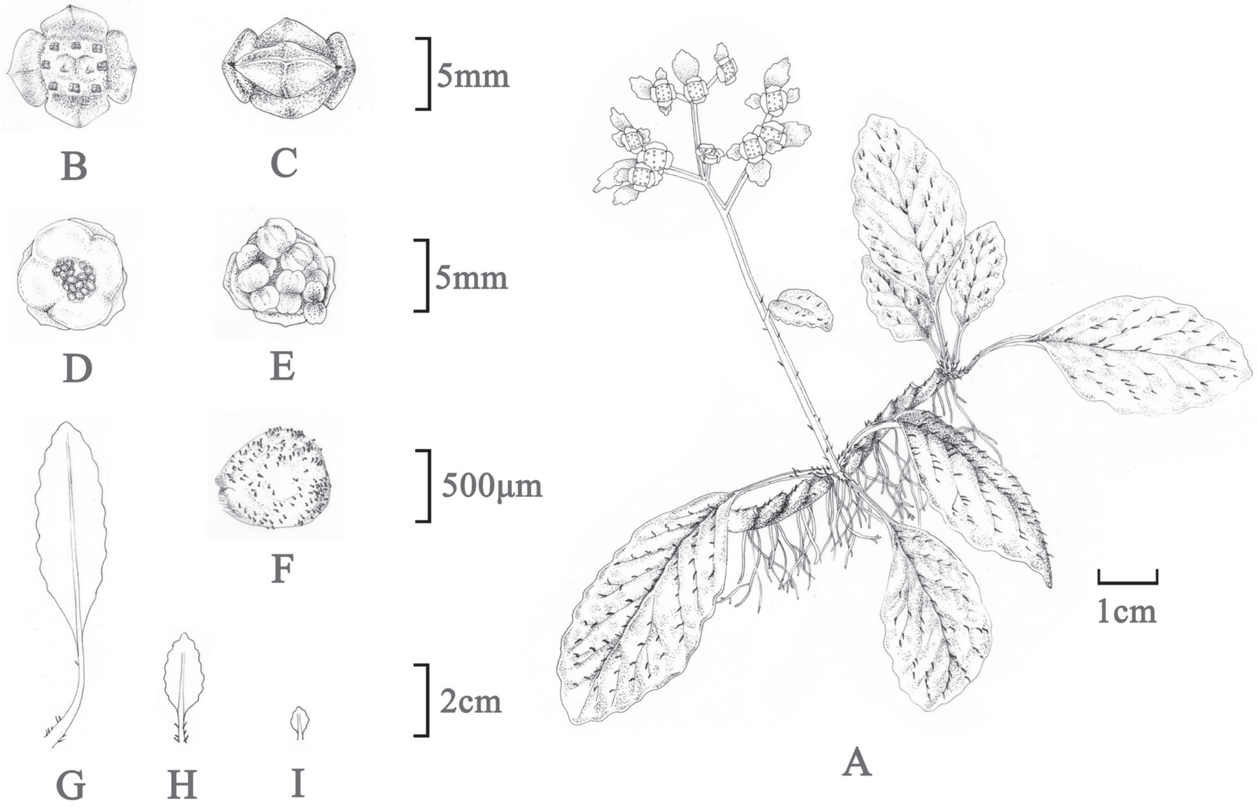

Figure 3. Illustration of *Chrysosplenium guangxiense* H.G.Ye & Gui C.Zhang **A** habit in flowering phase **B** flower **C** indehiscent capsule **D** dehiscent capsule and seeds **E** germinated seeds in capsule **F** seeds **G** caulline leaf **H, I** bracteal leaf.3

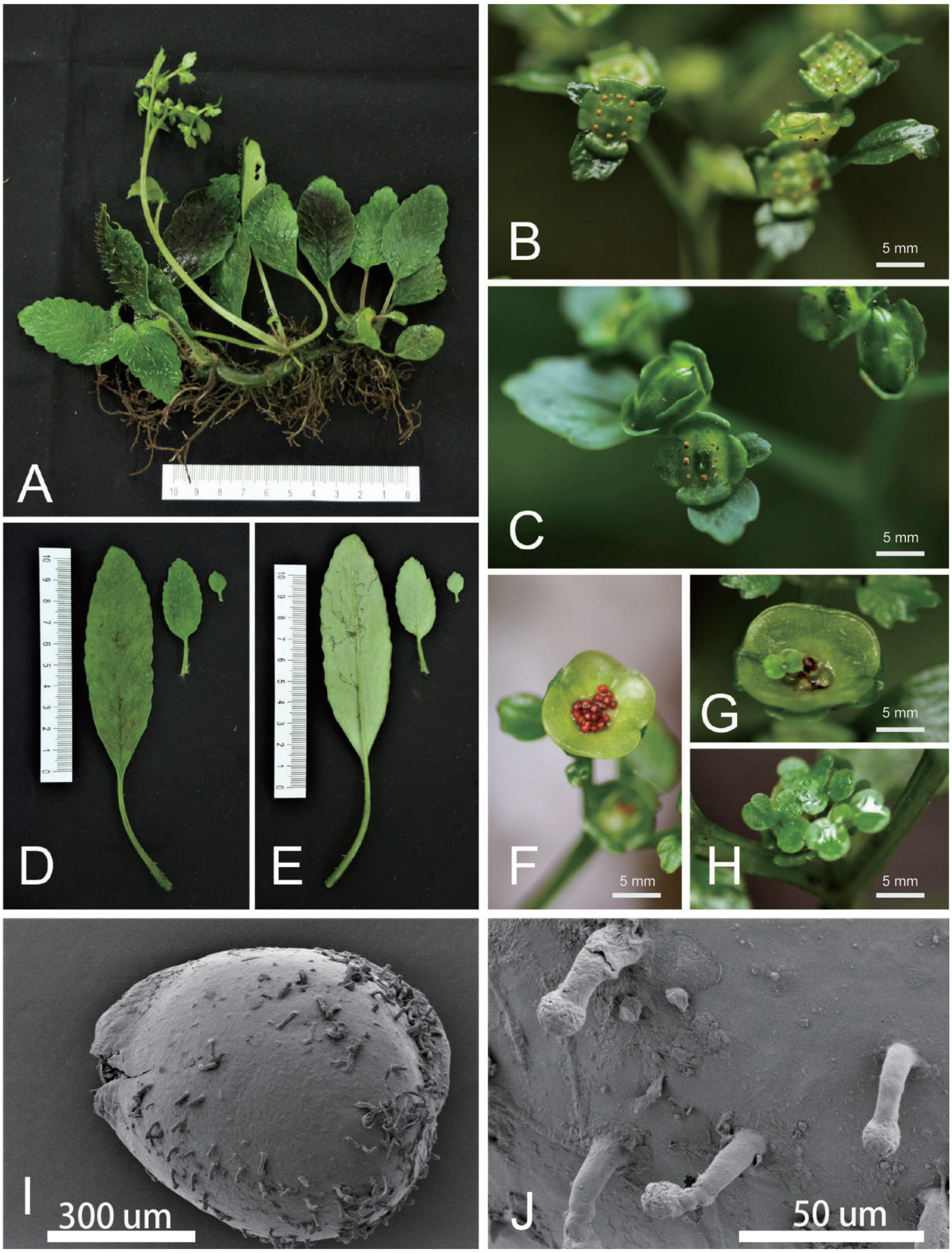

Figure 4. Plate of *Chrysosplenium guangxiense* H.G.Ye & Gui C.Zhang **A** habit **B, C** inflorescence with flowers **D, E** basal leaves **F** fruit and seed **G, H** germinated seeds and seedlings in capsule **I, J** SEM of seed (Photos by Hong Liu).

ry 2-locular, semi-inferior; stigma 2; styles erect, ca. 0.2 mm long. ***Fruit*** a capsule, 5–7 mm long, green, smooth, 2-lobed (horn-shaped), equal, dehiscent along the adaxial suture; seeds numerous, red or reddish brown, obovoid, a raphe on one side, 594.19–855.33 × 475.41–625.7 µm, long papillose. Viviparous.

Additional specimen examined. *Chrysosplenium glossophyllum*. CHINA. Sichuan: Kuan County (Dujiangyan City), 19 April 1930, F. T. Wang 20553 (PE!, NAS!); same locality, 6 May 1987, Xintang Ma & Zhilong Zhao 87-0521 (WCSBG!); same locality, 15 April 2013, LiXJ 353 (KUN!); same locality, 24 May 2016, Hong

Liu, HSN06644 (HSN!); same locality, 26 October 2017, Hong Liu, HSN08105 (HSN!). *Chrysosplenium guangxiense*. China. Guangxi: Lingyun County, Baise City, 6 March 2014, Lingyun team 451027140305005 (GXMG!); Tianlin County, Baise City, 27 November 2019, Hong Liu HSN13356 (HSN!).

Conservation status. *Chrysosplenium guangxiense* is only known from two localities (IUCN criterion D2). At these two localities, the populations included ca. 200 mature individuals (IUCN criterion D1) growing in several patches. Using the IUCN methodology, *C. guangxiense* is classified as Vulnerable (VU) based on criteria D1 and D2: population size and the number of locations, combined with a plausible future threat that could drive this taxon to Critically Endangered or Extinct in a very short time. However, the vivipary of *C. guangxiense* may strengthen its adaptability to cope with future climate and environmental changes. The future threat is mainly due to grazing.

Conclusions

The phylogenetic analyses using plastomes and nuclear gene sequences of *Chrysosplenium guangxiense* reveal that *C. guangxiense* belongs to the sect. *Alternifolia*, is closely related to *Chrysosplenium hydrocotylifolium*, but distant from *C. glossophyllum* based on leaf morphology and other traits. Our findings support the resurrection of *C. guangxiense* as a distinct species and provide a detailed taxonomic treatment for its identification. The phylogenetic analyses confirm the monophyly of *Chrysosplenium* and reveal a non-monophyletic status of sect. *Alternifolia*. Further systematic studies of *Chrysosplenium* should focus on finding additional morphological characters with phylogenetic informativeness to disentangle the non-monophyletic sect. *Alternifolia*, and propose a new infrageneric classification and provide a stable framework for answering broader questions in evolutionary biology.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: TGY. Funding acquisition: LH, LFF. Investigation: HL, DQL, XTC. Project administration: HL, LFF. Writing – original draft: LFF, TGY, HL. Writing – review and editing: LFF, TGY, HL.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Phylogenetic tree of *Chrysosplenium* generated from maximum likelihood (ML) of cpPCGs dataset

Authors: Long-Fei Fu, Tian-Ge Yang, De-Qing Lan, Xi-Tang Chen, Hong Liu

Data type: jpg

Explanation note: Numbers on the branches indicate bootstrap values (left) of the ML analyses and the posterior probability (right) of Bayesian analyses.

Link: https://doi.org/10.3897/phytokeys.243.125742.suppl1

Supplementary material 2

Phylogenetic tree of *Chrysosplenium* generated from maximum likelihood (ML) of nrDNA dataset

Authors: Long-Fei Fu, Tian-Ge Yang, De-Qing Lan, Xi-Tang Chen, Hong Liu

Data type: jpg

Explanation note: Numbers on the branches indicate bootstrap values (left) of the ML analyses and the posterior probability (right) of Bayesian analyses.

Link: https://doi.org/10.3897/phytokeys.243.125742.suppl2

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DOI: 10.3897/phytokeys.243.127579

Research Article

Cyrtomium adenotrichum (Dryopteridaceae), a new species from Guangxi, China

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Abstract

Cyrtomium adenotrichum Y. Nong & R.H. Jiang (Dryopteridaceae), a new species from Guangxi, China, is described and illustrated. This new species is similar to *C. nephrolepioides* (Christ) Copel., *C. obliquum* Ching & K. H. Shing ex K. H. Shing, *C. sinningense* Ching & K. H. Shing ex K. H. Shing and *C. calcis* Liang Zhang, N.T.Lu & Li Bing Zhang in having erect rhizomes, dense, leathery lamina and rounded sori, but it can be easily distinguishable by its stipe sparsely glandular, base obvious oblique, basiscopic base truncate, acroscopic base auriculate or ovate.

Key words: Gully, limestone, Nandan, new species, taxonomy

Introduction

Cyrtomium (Presl 1836) was founded upon the basis of *Polypodium falcatum* (Linnaeus 1781), originating from Japan. It comprises approximately 40 recognized species, the majority of which are found in East Asia, with a particular concentration of diversity centered in Southwest China. Within this group, 31 species are native to China (Zhang and Barrington 2013). *Cyrtomium* ser. *Falcata* Ching & Shing (Shing 1965), which was not confirmed as monophyletic in an earlier molecular study conducted (Lu et al. 2005), is distinguished by its leathery leaves and pinnae, which possess intact (occasionally repand) and thickened margins. Notably, all species belonging to this series can be located in China, except for *C. elongatum* S.K.Wu & P.K.Lôc (Wu et al 2005) and most of them are naturally distributed in limestone regions. Within the past decade, more new species of *Cyrtomium* have been discovered in Vietnam and China (Lu et al 2023; Nong et al. 2023).

During our field surveys conducted in Nandan County, Guangxi, in March 2024, we encountered a unique population of *Cyrtomium* that exhibited morphological similarities to the species *C. nephrolepioides* (Christ) Copel.(Copeland 1929), *C. obliquum* Ching & K. H. Shing ex K. H. Shing (Shing 1965), *C. sinningense* Ching & K. H. Shing ex K. H. Shing (Shing 1965) and *C. calcis* Liang

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Zhang, N.T.Lu & Li Bing Zhang (Lu et al 2023) in having erect rhizomes, dense, leathery lamina, and rounded sori, but it can be easily distinguished by its stipe sparsely glandular, base obvious oblique, basiscopic base truncate, acroscopic base auriculate or ovate. We hypothesize that this unique population may represent a previously unrecognized species due to these distinct morphological characteristics. To further validate our findings, we conducted additional observations and examined numerous specimens of *Cyrtomium* housed in various herbaria. We also consulted relevant literature to ensure the accuracy of our identification and to gain a deeper understanding of the taxonomic status of this potential new species (Lu et al 2023; Nong et al. 2023). We describe this population as a new morphologically distinct species.

Materials and methods

The new species was described based on field observations made in March and examination of herbarium specimens at GXMI. Other related *Cyrtomium* species were examined based on online images from Kew Herbarium Catalogue (http://apps.kew.org/herbcat/gotoHomePage.do) and JSTOR Global Plants (http://plants.jstor.org/) and PE, IBK and KUN. Morphological characters that distinguish it from all other species in the genus of *Cyrtomium* are used. We also observed living plants of the new species. We observed characters of rhizome, leaves, pedicels, stipe, lamina, scales, sori, indusia.

Descriptions were written from herbarium specimens. Measurements were made with a tape–measure and callipers. The structure of the indumentum and its distribution was observed and described under a dissecting microscope at magnifications of more than 20×. Additional information on locality, habitat, ecology, plant form and fruits were collected in the field and taken from herbarium labels. Conservation threat assessment followed IUCN Categories and Criteria (IUCN 2022).

Results and discussion

Taxonomy

***Cyrtomium adenotrichum* Y.Nong & R.H.Jiang, sp. nov.**
urn:lsid:ipni.org:names:77344264-1
Figs 1–4
Chinese name: xiàn máo guàn zhòng (腺毛贯众)

Diagnosis. *Cyrtomium adenotrichum* is similar to *C. nephrolepioides*, *C. obliquum*, *C. sinningense* and *C. calcis*, but differs in its stipe sparsely glandular (vs. glabrous). In addition, it can be distinguished from *C. sinningense* by its scale margins fimbriate (vs. dentate), lateral pinnae 5–10 pairs (vs. 1–4 pairs), indusia margins dentate (vs. subentire); it can also be distinguished from *C. nephrolepioides* by its lateral pinnae 5–10 pairs (vs. 10–26 pairs), base obvious oblique (vs. cordate or sometimes obliquely cordate). It differs from *C. obliquum* by its scale margins fimbriate

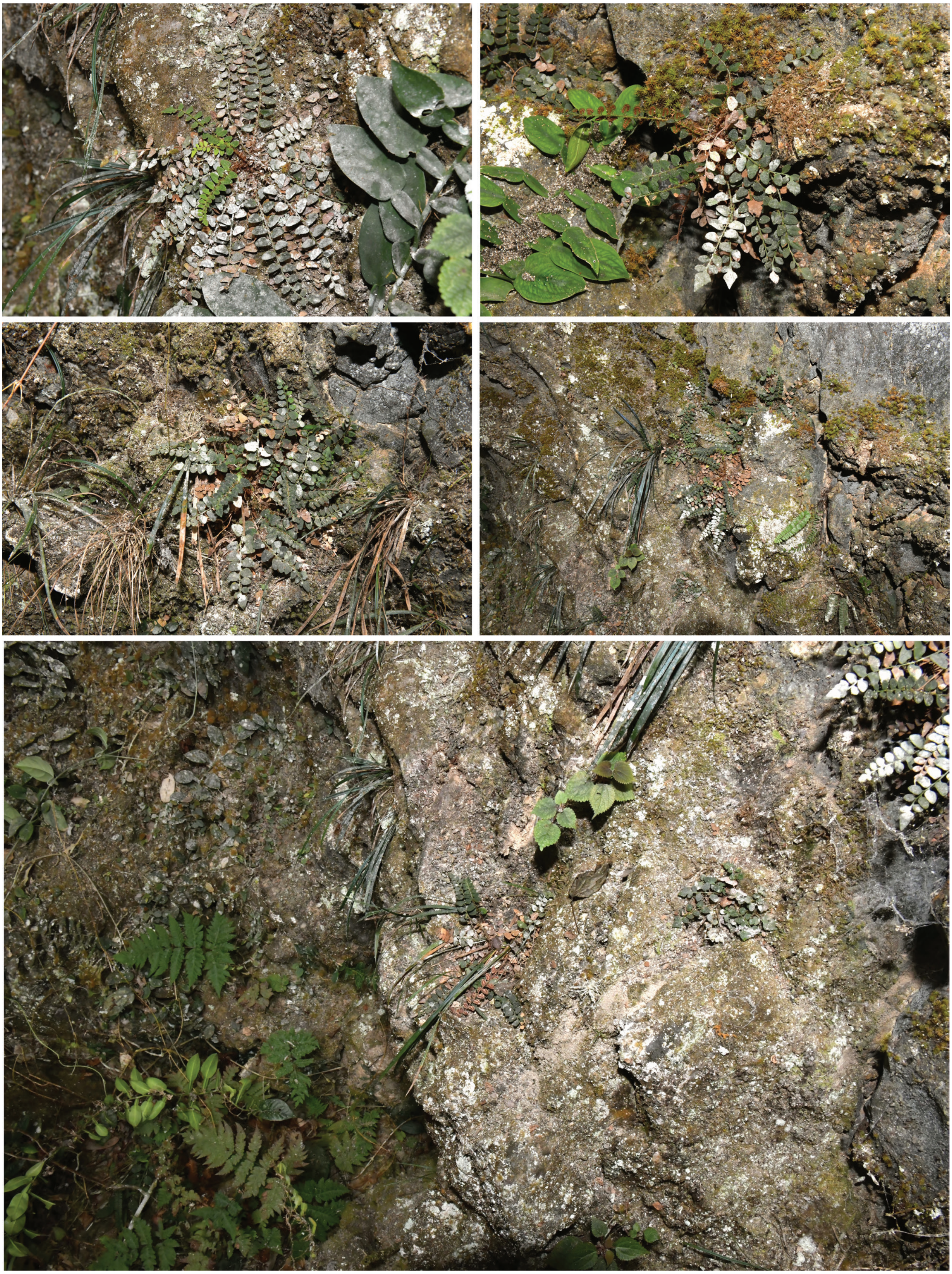

Figure 1. Habitat of *Cyrtomium adenotrichum* Y. Nong & R.H. Jiang on cliffs at a gully (Photographed by YN).

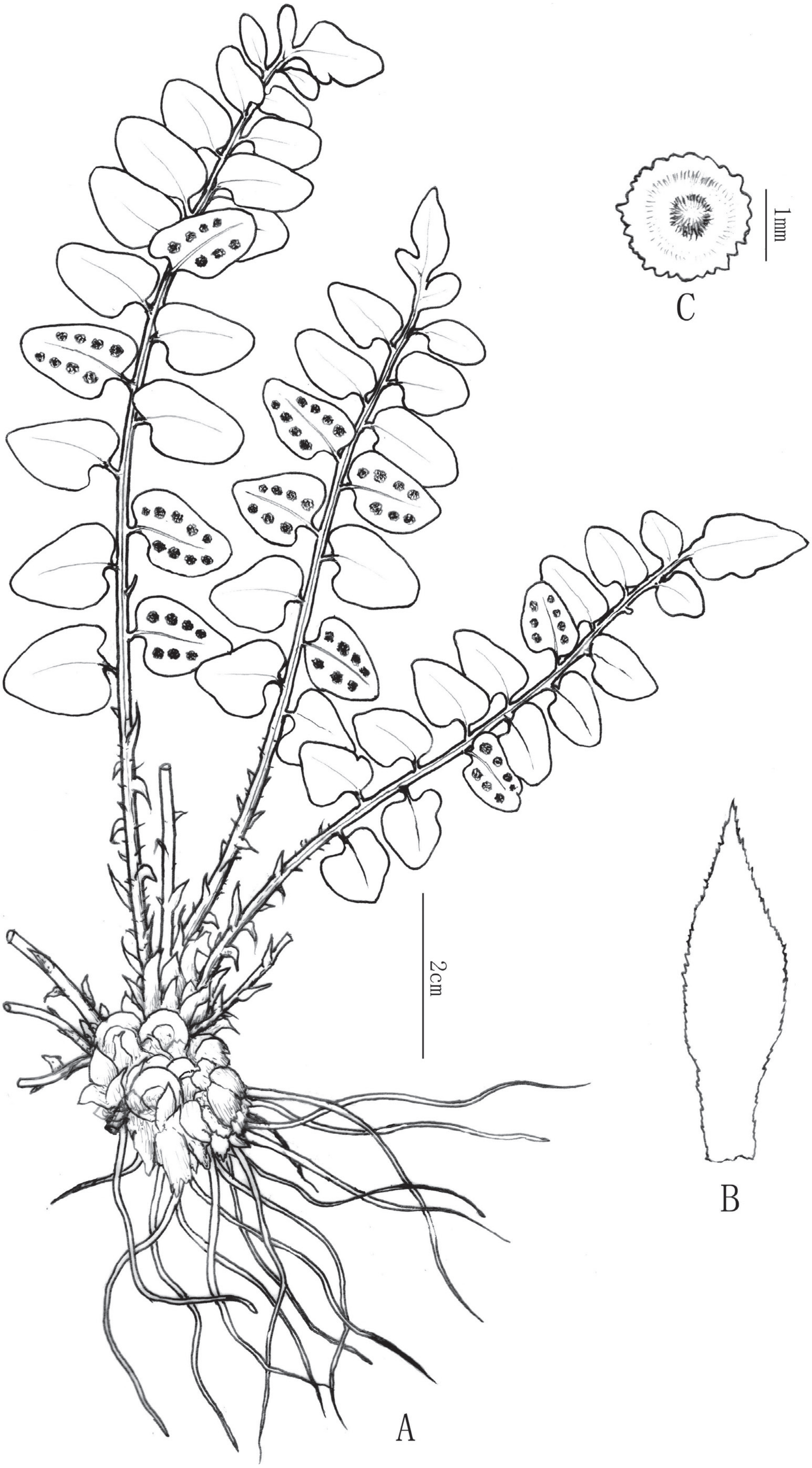

Figure 2. Line drawing of *Cyrtomium adenotrichum* Y. Nong & R.H. Jiang **A** plant **B** scale **C** indusium (Drawn by Xin–Cheng Qu).

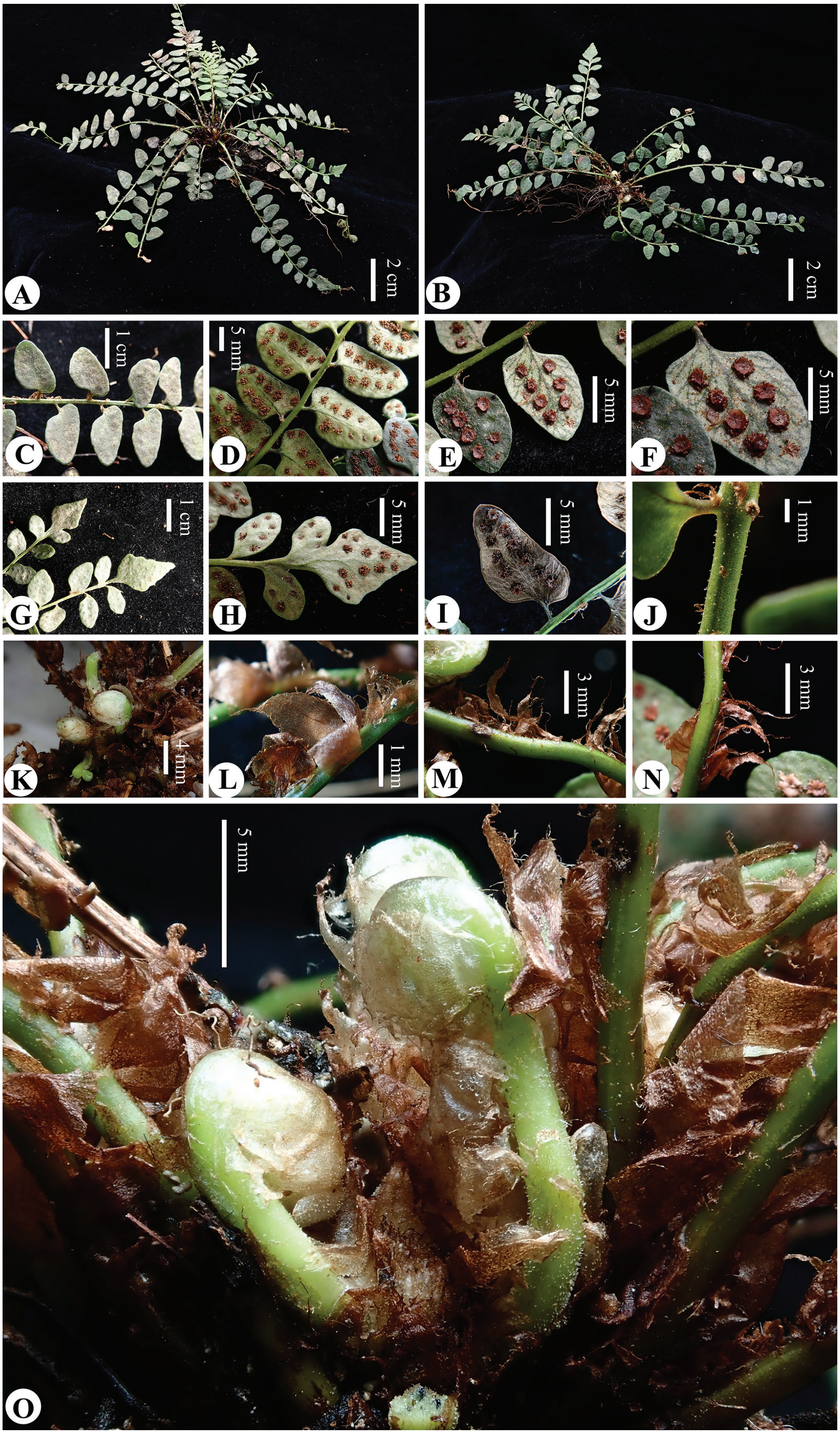

Figure 3. *Cyrtomium adenotrichum* Y. Nong & R.H. Jiang **A, B** plant **C, D** lamina (adaxially and abaxially view) **E, F** sori and indusia **G, H** terminal pinna (adaxially and abaxially view) **I** lateral pinnae (abaxially view, showing: margins entire and often slightly reflexed) **J** stipe (sparsely glandular) **K** curled leaves **L, M, N** scales **O** curled leaves (sparsely glandular) (Photographed and edited by You Nong).

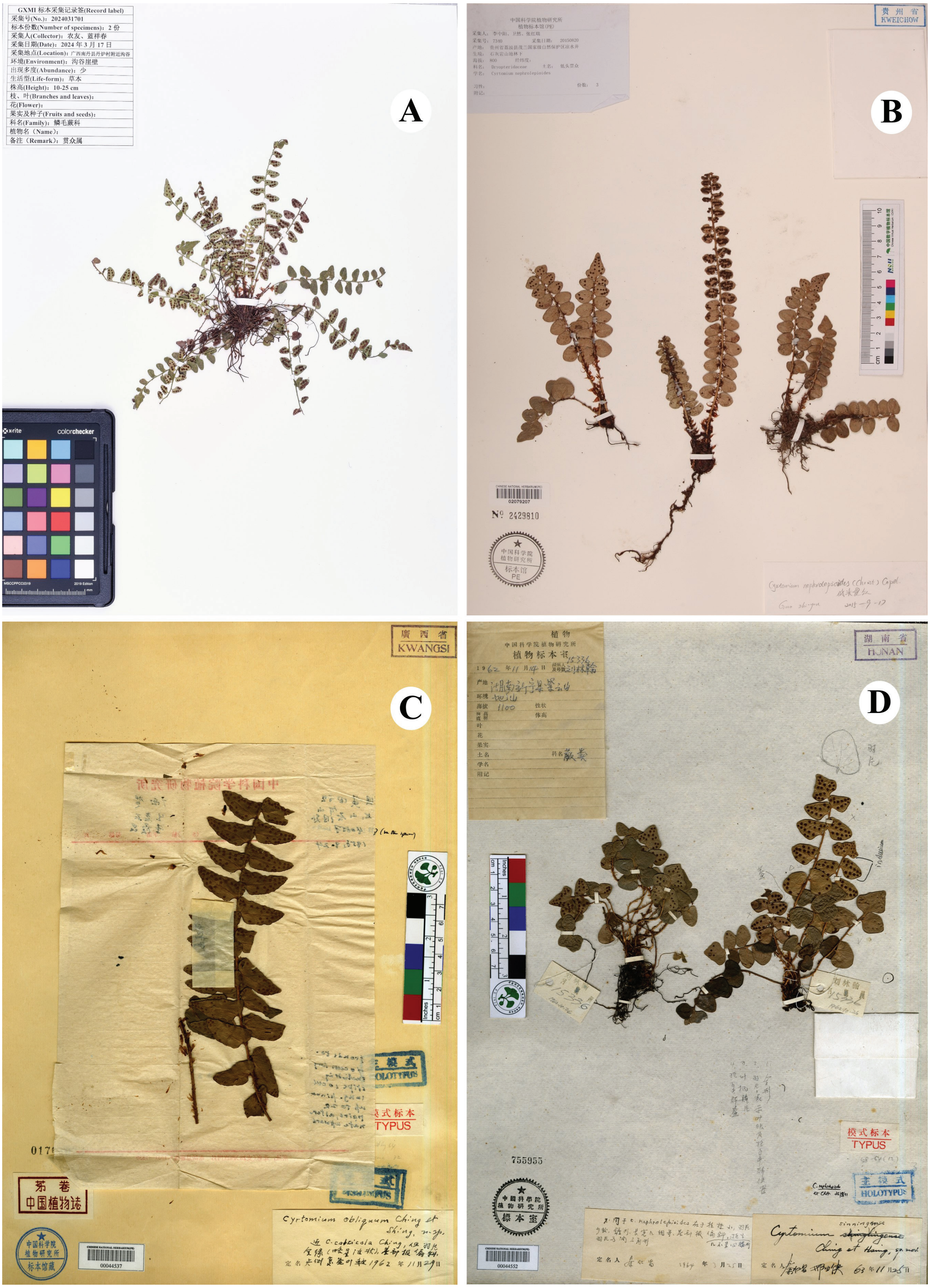

Figure 4. *Cyrtomium* specimens of the new taxon and three morphologically related species **A** type specimen of *Cyrtomium adenotrichum* **B** *C. nephrolepioides* **C** type specimen of *C. obliquum*, and **D** type specimen of *C. sinningense*.

(vs. dentate), lateral pinnae 5–10 pairs (vs. 12–21 pairs), indusia margins dentate (vs. entire). It can be distinguished from *C. calcis* by its base obvious oblique (vs. cordate to hastate), lateral pinnae thin leathery (vs. thick leathery). Comparative morphological differences among all five species are presented in Table 1.

Holotype. China. Guangxi: Nandan, 24°48'47"N, 107°27'12"E, alt. 470 m, on the cliff at a gully; 17 March 2024; *Y Nong NY2024031701* (GXMI!). (holotype: GXMI!; isotypes: IBK!).

Description. Plants perennial, evergreen, 5–15 cm tall. Rhizome short and erect, together with basal stipe densely scaly. Scales brown, ovate; Leaves clustered, petiole 1–3 cm, stipe stramineous, 3–10 cm, 1 mm in diam, sparsely glandular, densely scaly; scales brown, ovate or lanceolate, margins fimbriate. scales on stipe base brown, ovate or lanceolate, membranous, ca. 8–12 × 1–3 mm, margin minutely denticulate and slightly long ciliate, upword gradually narrowed, subulate, linear-lanceolate. Lamina linear-lanceolate, 5–10 × 1.5–2 cm, base not contracted, 1-imparipinnate; Lateral pinnae 5–10 pairs, crowded, alternate, spreading or slightly ascendant, shortly stalked, ovate or rarely deltoid-lanceolate; lower and middle pinnae 8–10 × 4–6 mm, respectively, subopposite or alternate, apex rounded, base obvious oblique, basiscopic base truncate, acroscopic base auriculate or ovate, margins entire and often slightly reflexed, sparse hairlike scales adaxially and abaxially; terminal pinna ovate, with 1 or 2 connate lobes at base, 20–35 × 15–25 mm; rachis c. 1 mm in diam, sparsely glandular, grooved adaxially, scaly abaxially; scales on rachis brown, linear to subulate, margins sparsely toothed or fimbriate; frond texture thin leathery; venation pinnate, midrib flat or slightly concave on abaxially and adaxially, lateral vein connection, indistinct, lateral veins anastomosing to form 1 or 2 rows of areoles on each side of midrib. Sori 1 row on each side of midrib; indusia margins dentate.

Etymology. The specific epithet refers to the stipe sparsely glandular of the new species.

Distribution and habit. Known only from the north of Guangxi, China (Fig. 5). It has been mainly found on cliffs at a gully at elevations of 470 m. We found

Table 1. Main morphological differences amongst *Cyrtomium adenotrichum* and *C. nephrolepioides*, *C. obliquum*, *C. sinningense* and *C. calcis*.

Morphological traits	*C. adenotrichum*	*C. nephrolepioides*	*C. obliquum*	*C. sinningense*	*C. calcis*
Plant height	5–15 cm	12–28 cm	20–35 cm	8–12 cm	13–23 cm
Stipe	3–10 cm, 1 mm in diam., sparsely glandular	3–10 cm, 1–2 mm in diam., glabrous	6–10 cm, 1–2 mm in diam., glabrous	5–7 cm, 1 mm in diam., glabrous	15 cm, 1–3 mm in diam., glabrous
Scales margins	fimbriate	fimbriate	dentate	Dentate	fimbriate-dentate
Lamina	linear-lanceolate, 5–10 × 1.5–2 cm	linear-lanceolate, 10–25 × 2–5 cm	lanceolate, 13–35 × 3–5 cm	ovate or oblong-lanceolate, 3–7 × 2.5–3 cm	lanceolate-oblong, 13–23 × 1.9 cm
Lateral pinnae	5–10 pairs	10–26 pairs	12–21 pairs	1–4 pairs	9–14 pairs
Pinnae	0.8–1 × 0.4–0.6 cm	1–2.5 × 0.6–1.2 cm	2–3 × 1–1.5 cm	1.2–1.6 × 1–1.2 cm	1.5–3.5 × 1.2–1.9 cm
Base	obvious oblique	cordate or sometimes obliquely cordate	oblique	broadly cuneate	cordate to hastate
Texture	thin leathery	thick- leathery	leathery	Leathery	thick leathery
Venation	midrib flat or slightly concave on both surfaces	midrib concave on both surfaces	slightly raised abaxially, slightly concave adaxially	indistinct on both surfaces	obscure
Rows of areolae	1 or 2	2 or 3	2	2 or 3	2, 3, rarely to 4
Indusia margins	dentate	subentire	entire	subentire	dentate

Figure 5. The distribution of *Cyrtomium adenotrichum* (red circle) in Guangxi, China.

only one population with 10 individuals, and the habitat of *Cyrtomium adenotrichum* is fragile because it could be submerged during the rainy season.

IUCN Red List Category. Only one population with 10 individuals of *Cyrtomium adenotrichum* is currently known from Nandan County, Guangxi China. Due to its rarity, the low number of individuals and habitat vulnerability, *C. adenotrichum* is considered to be Critically Endangered (CR), according to the IUCN (IUCN 2022).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: YN. Funding acquisition: YN, CGX. Investigation: YN, CGX, YGW. Methodology: YN, LQL, ZYZ, YGW. Project administration: YN, BF. Supervision: XCQ, RHJ. Visualization: YN, LQL, XCQ. Writing–original draft: YN. Writing–review and editing: YN.

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Data availability

All of the data that support the findings of this study are available in the main text.

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PhytoKeys

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DOI: 10.3897/phytokeys.243.119707

Research Article

Astragalus liuaiminii, a new species of *Astragalus* (Fabaceae) from Xinjiang, China

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Abstract

A new species, *Astragalus liuaiminii* Z. Z. Yang & Q. R. Liu (Fabaceae), is described and illustrated from Xinjiang Province, China. The new species is close to *A. wenquanensis* S. B. Ho, but differs from the latter by leaves having a single leaflet (vs. 3–5 leaflets), and inflorescences with 1–2 flowers (vs. inflorescences with 5–7 flowers). It is also similar to *A. monophyllus* Maxim in leaf shape, but differs by its calyx expanding to become saccate and totally enveloping the pod (vs. calyx tubular, and ruptured by pod after flowering).

Key words: *Astragalus* sect. *Laguropsis*, new species, taxonomy, Xinjiang

Introduction

The genus *Astragalus* Linnaeus is the largest genus of flowering plants, containing about 2500 to 3000 species, with ca. 2350 species in the Old World and ca. 500 species in the Americas (Chang et al. 2007). Species of the genus are mainly distributed in arid and semi-arid mountainous regions of the Northern Hemisphere, as well as in South America and Africa (Zhai and Yan 2010; Podlech and Zarre 2013). China is one of the largest centres of diversity for the genus with 388 species, of which 210 are endemic (Ho 1993; Chang et al. 2007; Xu and Podlech 2010). While conducting field work in June 2023, in the Habahe Region, we collected some interesting *Astragalus* specimens that have distinct characters including being acaulescent or nearly so, leaves with only one leaflet, inflorescence 1- to 2-flowered, and the calyx at first being tubular and enlarging after anthesis becoming saccate. After critical study of the specimens and comparison with other existing species in the surrounding area, we confirmed that these specimens were new to science. The new species belongs to *Astragalus* sect. *Laguropsis* (Podlech and Zarre 2013), and is described and illustrated below.

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Materials and methods

Specimens were collected from Habahe County of Xinjiang Province. Morphological studies of the new species were based on observation of living individuals. Comparisons of the new species with other related specimens were conducted by checking materials from PE and XJBI, as well as virtual specimen databases (CCAU, KUN, IBK, IBSC, CVH and JSTOR). Measurements were carried out under a stereomicroscope (Olympus SZX2, Tokyo, Japan) using a ruler and a metric vernier caliper.

Taxonomy

Astragalus liuaiminii **Z.Z.Yang & Q.R.Liu, sp. nov.**
urn:lsid:ipni.org:names:77344331-1
Figs 1–3

Diagnosis. *Astragalus liuaiminii* belongs to *Astragalus* sect. *Laguropsis* (*A.* subg. *Calycocystis*) by its acaulescent, densely caespitose, with only white hairs. The calyx expands to become saccate, enveloping the pod.

Type. China. XinJiang Province. Habahe County. Mt. Talede, 1050 m elev., 9 June 2023, on dry gravelly slopes, *A. M. Liu, Z. Z. Yang 2388* (Holotype BNU!)

Paratypes. China. Xinjiang: Habahe County, 1000 m elev., 11 June 2023, *A. M. Liu, Z. Z. Yang 2398* (BNU!).

Figure 1. Plants and habitat of *Astragalus liuaiminii* Z. Z. Yang and Q. R. Liu **A** Mr. Aimin Liu and the distribution area **B** habitat **C** plant **D** side view of the plant.

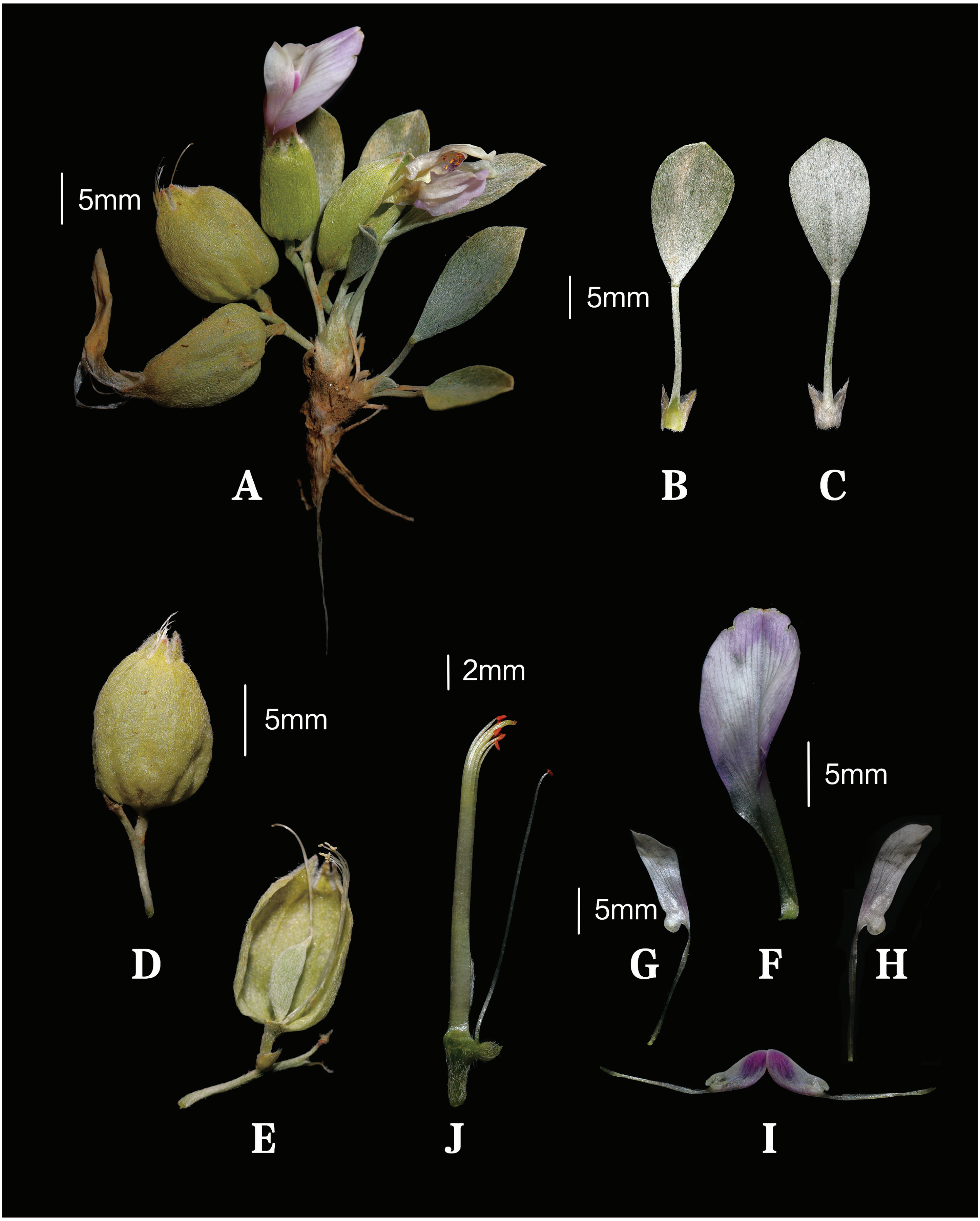

Figure 2. Habit and plant structures of *Astragalus liuaiminii* Z. Z. Yang & Q. R. Liu **A** habit **B** leaf, adaxial view **C** leaf, abaxial view **D** mature saccate calyx **E** half calyx removed exposing immature fruit **G–H** wings **I** keel **J** pistils and stamens.

Description. Plants perennial, 3–5 cm tall, acaulescent or nearly so, densely caespitose, covered with white medifixed hairs. Caudex with a pluricipital root crown. Stipules whitish membranous, 3–5 mm long, triangular, adnate to the petiole

Figure 3. *Astragalus liuaiminii* sp. nov. **A** plants **B** standard **C** keel **D** wings **E** leaf, adaxial view **F** mature saccate calyx **G** half calyx removed exposing immature fruit **H** pistils and stamens.

for ca. 2 mm, densely covered with appressed white hairs. Leaves with single leaflet, 2–3.5 cm long, rhomboid, petiole 0.8–1.5 cm long, very densely covered with appressed white hairs; leaflets obovate to elliptic, subacute at apex, rather densely covered with appressed hairs on both surfaces. Racemes 1–2 flower, 1.2–2.2 cm. Bracts whitish membranous, narrowly triangular, ca. 2 mm long, anther densely covered with short appressed hairs. Pedicels very short, with white hairs. Calyx tubular at anthesis, ca. 9 mm, later enlarged and becoming saccate, spherical-ovoid, 15–17 mm, densely covered with white appressed hairs, and denser towards the margins of teeth; teeth triangular, 2–3 mm long. Petals whitish or pinkish. Standard 25–27 mm long; limb oblong, 6.5–8 mm wide, emarginate, constricted below the middle, gradually narrowing into the claw. Wings 23–24 mm long; limbs narrowly oblong, obtuse, ca. 10–11 × 1.2 mm; claw ca. 13 mm long. Keel ca. 19–20 mm long; limbs narrowly elliptic, with widely-curved lower edge and straight upper edge, pink-purple at apex, ca. 13–14 × 2.2 mm; claw ca. 6 mm long. Ovary sessile, white hairy; style glabrous. Mature legumes not seen.

Phenology. Flowering in June.

Distribution and habitat. *Astragalus liuaiminii* is currently known only from Habahe County in northwest Xinjiang Province, China, where it grows at an altitude of 1000–1100 m, on dry gravel slopes.

Etymology. The species is named in honour of Mr. Aimin Liu, who collected the type specimens.

Chinese name. 爱民黄芪 (Ai Min Huang Qi).

Preliminary conservation status. *Astragalus liuaiminii* has a restricted distribution area. It is only known from the upstream region of Habahe County, where there is no natural protection area. The total population size of the species is estimated no more than 100 individuals. According to the IUCN (2022), this new species should be considered as “Critically Endangered” (CR).

Results. The new species is close to *A. wenquanensis* S. B. Ho, but differs chiefly in leaves having single leaflet (vs. 3–5 leaflets) and inflorescences with 1–2 flowers (vs. 5–7 flowers). It is also similar to *A. monophyllus* Maxim in leaf shape, but differs in its calyx expanding into a sac-like and totally enveloping the pod (vs. calyx tubular, and ruptured by pod as it matures). *Astragalus monophyllus* is distributed in the northeastern and southern regions of Xinjiang, and belongs to subg. *Cercidothrix*, while *A. liuaiminii* is only found in Habahe County of the Altai Mountains in the northern part of Xinjiang, belonging to subg. *Calycocystis*. The calyx is an important taxonomic characteristic of the genus *Astragalus*, these two species have distinctly different calyces representative of different subgenera. The differences between *A. liuaiminii*, *A. wenquanensis* and *A. monophyllus* are summarised in Table 1.

Table 1. Morphological comparisons among *Astragalus liuaiminii*, *A. wenquanensis* and *A. monophyllus*.

Characters	***A. liuaiminii***	***A. wenquanensis***	***A. monophyllus***
Subgenera	subg. *Calycocystis*	subg. *Calycocystis*	subg. *Cercidothrix*
leaf	Single leaflet	3–5 leaflets	1–3 leaflets
inflorescence	1–2 flowers	5–7 flowers	1–2 flowers
calyx	light green suffused, covered with white hairs, expanding to become saccate and enveloping the pod after flowering	red suffused, covered with white and black hairs, expanding to become saccate and enveloping the pod after flowering	calyx tubular, not expanding and becoming saccate, and ruptured by pod after flowering

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Eriotheca paganuccii (Bombacoideae, Malvaceae), a new endangered species from montane forests in the Atlantic Forest of Bahia, northeastern Brazil

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Abstract

A new species of *Eriotheca* (Bombacoideae, Malvaceae) from montane wet forests in the Atlantic Forest of Bahia, northeastern Brazil, is described and illustrated. It is known from only three populations situated between 750 m and 850 m in elevation on mountain summits and categorized as Endangered (EN) based on IUCN criteria. *Eriotheca paganuccii* is distinct from all congeners by the combination of coriaceous to strongly coriaceous leaves and remarkable few-seeded, globose to subglobose woody capsules that contain scanty kapok and the largest seeds known in the genus to date. The affinities of *E. paganuccii* to morphologically similar species as well as the importance of obtaining phenologically complete collections are discussed.

Key words: Bahian southern Atlantic Forest, 'Bombacaceae', 'embiruçú', endemism, plant taxonomy

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Introduction

Eriotheca Schott & Endl. (Bombacoideae, Malvaceae), a genus comprised predominantly of trees, is restricted to South America. It includes 28 species of which 22 occur in Brazil mainly in Atlantic Forest and Cerrado areas (Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2015, 2020; Macedo et al. 2018; Yoshikawa and Duarte 2021; Duarte and Yoshikawa 2024). Three species, *E. discolor* (Kunth) A.Robyns, *E. ruizii* (K.Schum.) A.Robyns, and *E. vargasii* (Cuatrec.) A.Robyns, inhabit seasonally dry tropical forests (SDTF) reaching 3,000 m in elevation (Robyns 1963; Tropicos.org); however, no species of *Eriotheca* is known to occur in Caatinga vegetation (Duarte and Yoshikawa 2024) within the largest SDTF nucleus in South America (Pennington et al. 2009; Queiroz et al. 2017).

The current taxonomy of *Eriotheca* is grounded in studies published by Robyns (1963, 1968, 1979) and Robyns and Nilsson (1975, 1981), whose work was based mainly on analysis of herbarium collections. Robyns' (1963) principal contribution to this genus appeared in his revision of *Bombax* L. *s.l.*, in which he accepted 20 species and four infraspecific taxa. Subsequently, the Brazilian taxa of *Eriotheca* were treated by Martins (1993) in a master's thesis. She followed Robyns' taxonomy but added leaf surface anatomical studies. Despite detecting some anatomical differences among taxa, she did not propose formal taxonomic changes to the genus in what remains an unpublished work.

The most recent comprehensive study on the taxonomy of Brazilian *Eriotheca* was by Duarte (2010), who in her doctoral thesis proposed taxonomic changes based on macromorphological characters and the micromorphology of scales on leaves. Her innovations were published in Duarte and Esteves (2011, 2012). Since then, several additional nomenclatural novelties from Brazil have been published, including five new species and three infraspecific taxa elevated to species rank (Duarte and Esteves 2011, 2012; Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2015, 2020; Macedo et al. 2018; Yoshikawa and Duarte 2021).

Historically, the taxonomy of *Eriotheca* has been challenging for several reasons: i) Individual trees often reach 40 m in height and making herbarium specimens requires climbing equipment or tree climbers; ii) Wet forest species often have supra-annual flowering; iii) Leaf morphology is highly variable within species and within individuals (even on the same branch) as well as between vegetative and reproductive branches; iv) Reproductive branches are often leafless resulting in herbarium collections consisting of separate branches and often including much larger leaves from young individuals; v) A lack of standardization in the collection and description of leaves, including proximal and distal leaflets; vi) Fruit and seed are seldom included on herbarium sheets and rarely linked to well-curated carpological collections; vii) Type material of *Eriotheca* species is typically incomplete phenologically and often comprised of poorly preserved reproductive and vegetative parts with loose bits such as fragments of leaflets, flowers, capsules, and seeds.

Except for a few species (see e.g., Robyns 1968; Carvalho-Sobrinho et al. 2015, 2020; Yoshikawa and Duarte 2021), protologues of *Eriotheca* characteristically lack either illustrations or descriptions of fruit and seed (or both). In Robyns' (1963) revision, seven taxa of *Eriotheca* were described without fruit and seed descriptions. Despite a doctoral thesis on the Brazilian species of *Eriotheca* (Duarte 2010), the morphology of fruit and seed of many Brazilian species is still unknown. This hampers a thorough understanding of the taxonomy of the genus. Nonetheless, taxonomic decisions including the synonymizing of taxa have been undertaken without a complete knowledge of the morphology of the fruit and seed of the taxa involved (e.g., Duarte 2010; Duarte and Esteves 2012) and new species have been described based on phenologically incomplete material (e.g., Fernández-Alonso 2003; Duarte and Esteves 2011; Macedo et al. 2018).

Thus, long-term monitoring of populations of Neotropical Bombacoideae in the field has been undertaken, especially in northeastern Brazil, and has produced phenologically complete herbarium collections including fruit and seed (see e.g., Carvalho-Sobrinho 2013; Carvalho-Sobrinho and Queiroz 2008, 2010; Carvalho-Sobrinho et al. 2012, 2013a, b, 2014, 2015, 2020, 2021; Carvalho-Sobrinho and Dorr 2017, 2020).

The Atlantic Forest of northeastern Brazil, particularly the southern Atlantic Forest of Bahia, harbors remarkable levels of plant richness and endemism (Amorim et al. 2005, 2008, 2009; Thomas et al. 2008; Amorim and Matos 2009). Recent field efforts in this region have revealed specimens of *Eriotheca* that are noteworthy due to their capsules containing scanty kapok and relatively few seeds that are much larger than those occurring in other species of the genus. These specimens have flowers typical of *Eriotheca*, which differ morphologically from the phylogenetically related genus *Pachira* Aubl. *Eriotheca* flowers are consistently smaller with reniform (vs. oblong-linear) anthers and they lack (vs. possess) phalanges on the androecium (Carvalho-Sobrinho et al. 2016).

Careful study of these collections has led to the recognition of a new species, which is described and illustrated here. None of the collections has been cited previously in the literature including in the last taxonomic treatment of *Eriotheca* for Brazil by Duarte (2010). Notes on the distribution and phenology of this new species, along with comments on morphologically similar species, and an assessment of the conservation status of this novelty, are provided. Also highlighted is the importance of having phenologically complete collections for studies in this and closely related genera.

Material and methods

This study was based on examination of herbarium collections, digital images of specimens, and field observations. Specimens were studied by visits to or loans from the following herbaria: ALCB, ASE, BAH, CEPEC, F, G, HRB, HUEFS, IPA, K, M, MBM, MO, NY, P, PEUFR, R, RB, SP, SPF, UESC, UFPB, UFPE, UFRN, and US (acronyms according to Thiers 2021). A comprehensive analysis of images of herbarium specimens was studied through the following websites: INCT – Herbário Virtual da Flora e dos Fungos (http://inct.splink.org.br/), JSTOR Global Plants (https://plants.jstor.org/), and Reflora Virtual Herbarium (https://reflora.jbrj.gov.br). Descriptions and measurements were based on dry herbarium specimens unless otherwise clearly stated. The distribution map was prepared using the free and open source QGIS software. A preliminary extinction risk assessment of the new species was made based on the IUCN criterion B (IUCN 2024). Georeferenced specimen data were imported into GeoCAT (Bachman et al. 2011) to estimate the extent of occurrence (EOO) and the area of occupancy (AOO) using 2 × 2 km grid cells.

Taxonomic treatment

***Eriotheca paganuccii* Carv.-Sobr., A.C.Mota & Dorr, sp. nov.**
urn:lsid:ipni.org:names:77344361-1
Figs 1–3, Table 1

Diagnosis. Similar to *Eriotheca obcordata* A.Robyns due to its absence of buttresses, obcordate leaflets, oblong to oblanceolate flower buds, oblanceolate petals, and stamens c. 80 in number, but differing in its caducous (vs. often persistent) bracteoles, larger calyces (7 × 7–9 mm vs. 5–5 mm), globose to subglobose (vs. obovoid) capsules, scanty (vs. abundant) kapok, seed number (c. 10 vs. numerous) per fruit, seed size (10–19 mm vs. 5–7 mm) long, and marcescent, lignified calyces that often split into patent lobes (in herbarium collections, at least).

Type. Brazil. Bahia: Castro Alves, Serra da Jiboia (=Serra da Pioneira), Mata higrófila, 12°51'11"S, 39°28'19"W, 22 Dec 1992 (lf, fr), *L.P. Queiroz* & *T.S.N. Sena 3008* (Holotype: HUEFS barcode 000132176! Isotype: SP barcode 057771!).

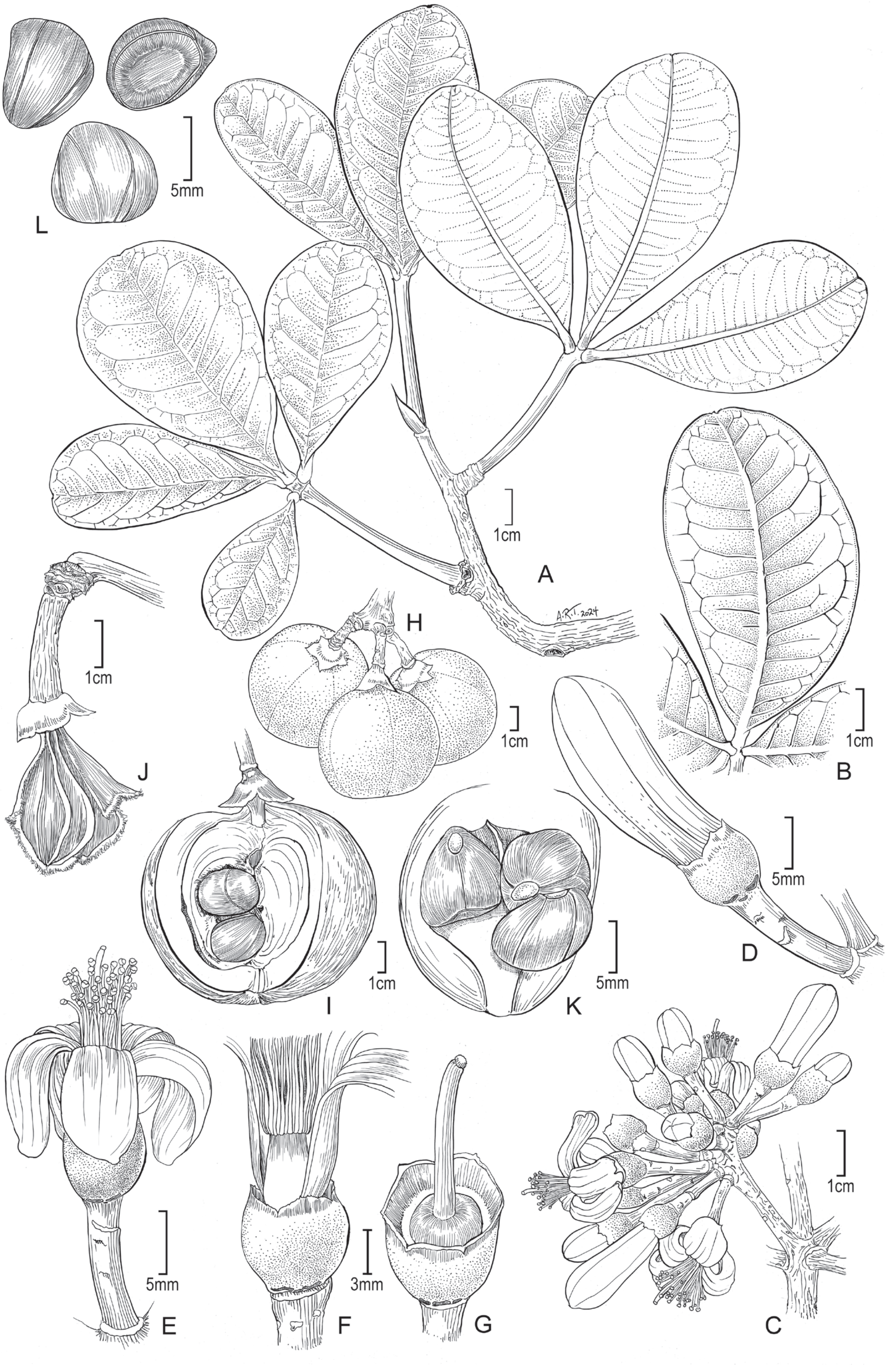

Figure 1. *Eriotheca paganuccii* **A** vegetative branch from the top of the tree canopy **B** details of a leaflet also from the top of the tree canopy **C** leafless branch with umbelliform cymes **D** flower bud (note the glands on receptacle) **E** flower at anthesis (note the unilaterally apiculate petals) **F** staminal tube (detached from the receptacle and slightly pulled up) **G** gynoecium **H** globose woody capsules before dehiscence **I** capsule with one valve detached showing scanty kapok and large seeds **J** dehisced fruit with marcescent calyx, exposing the columella and remaining kapok after seed dispersal **K** seeds relative to a fruit valve **L** angulate, striated seeds; each seed with two plane and one concave sides. **A, B, I–L** drawn from *J.G. Carvalho-Sobrinho 4040*, **C–G** drawn from *J.G. Carvalho-Sobrinho & A.C. Mota 4022*.

Description. Trees 2.5–5(–8) m tall, lacking buttresses; branches glabrous, often lenticellate; fertile branches often suberized. Terminal bud often persistent at branch apex, 11–15 mm long, acute at apex of mature branches, often curved at apex of younger branches. Leaves palmately compound; petiole doubly-pulvinate, (15–)40–65 × 2–3 mm, cylindric, swollen at base when fresh; petiolule greatly reduced; leaflets 3–5 (often 1–2-foliolate on canopy branches), coriaceous to strongly coriaceous, glabrous on both surfaces, discolorous, margin entire, revolute, the adaxial surface covered by dense indumentum of scales with irregular outline, the abaxial surface light green when fresh, the midrib yellowish adaxially, strongly prominent abaxially, secondary veins 10–13, prominent on abaxial surface, impressed on adaxial surface, the tertiary veins impressed on abaxial surface; leaflets often naviculate when young, distal leaflets 48–190 × 35–88 mm, length-to-width ratio 1.4–2.7, obovate, obcordate, widely-elliptic, or rarely elliptic, apex obtuse, truncate to retuse, base acute, decurrent or obtuse, rarely falcate; proximal leaflets 24–161 × 15–79 mm, length-to-width ratio 1.4–2, elliptic to widely-elliptic or elliptic-obovate, apex apiculate, base acute, decurrent, or obtuse. Inflorescences 1–8-flowered umbelliform cymes, borne on terminal, often suberized, leafless branches; pedicels 11–25 × 2.5(–4 at apex) mm, with sparse scales, green to blackish-green when fresh, the bracteoles ovate, caducous. Flower buds oblongoid when young to narrowly obovoid just before anthesis, receptacle c. 1–2 mm long, glandular, rarely eglandular; calyx 7–8 × 7–8 (–10 mm when compressed on herbarium sheets), glabrous except for sparse scales, urceolate when fresh, cupuliform to campanulate on herbarium sheets, apex inconspicuously crenulate to shortly 5-lobed, the lobes irregularly-shaped to triangular, marcescent in fruit, the outer surface green to blackish-green covered with sparse ferruginous indumentum; petals 23–26 (31–32 when fresh) × 4 mm at the base to 8 mm at the apex, cream-colored to pale yellow on both faces when fresh, greyish-brown when dried, reflexed by the distal length, oblanceolate, unilaterally apiculate and curved, tomentose on both faces, internally with longitudinal lines of longer trichomes on one longitudinal half (sericeous); stamens c. 80, reddish-brown when fresh, the staminal tube 7 × 4 mm, slightly enlarged at ovary height, slightly constricted at apex, producing free filaments 20 mm long; ovary globose, densely ferruginous indument at the distal half, style white, glabrous, stigma light-green. Loculicidal capsules woody, globose to subglobose, 35–50 mm long (–70 mm, when fresh), length-to-width ratio 0.8–0.9, externally ferruginous when young, the indument caducous at maturity, the kapok scanty, golden, the marcescent, lignified calyces often splitting into patent lobes on herbarium sheets. Seeds c. 10 per fruit, (11–)14(–19) × (10–)11(–14) × (9–)10(–12) mm (L×W×H), brown, glabrous, angulate, three-sided (two plane and one concave), 5-striate, three striae often coinciding with seed corners, two striae on dorsal (opposite the hilum) side, striae the same color as the testa.

Phenology. *Eriotheca paganuccii* was collected in flower in September (very young flower buds) and December, and in fruit in October (very young fruits), December to February.

Distribution and habitat. *Eriotheca paganuccii* is endemic to montane wet forests found between 750 m and 850 m in elevation near granitic-gneissic rock outcrops on summits of mountains in the Atlantic Forest of Bahia, northeastern Brazil (Fig. 3). Remnants of Montane Forest in the Atlantic Forest of

Figure 2. Habitat and morphological aspects of *Eriotheca paganuccii* **A** crown of *E. paganuccii* individuals in the canopy **B** detail of leaves at the top of the tree canopy showing smaller, more rigid leaves that are comprised of 1–2 leaflets oriented upward **C** bark of *E. paganuccii* **D** leaves with less exposure to the sun that have 5 leaflets, which are larger, less rigid, and patent (not oriented upward) unlike those in the canopy **E** flower at anthesis **F** seeds relative to a fruit valve and scanty kapok.

Bahia are known for their outstanding diversity and include several endemic angiosperm taxa in *Bertolonia* Raddi, *Dichorisandra* J.C.Mikan, *Macrocarpaea* (Griseb.) Gilg, and *Quesnelia* Gaudich. (Coelho and Amorim 2014). In particular, the Serra da Jiboia is also the type locality of several species of algae (e.g., *Diplocladiella cornitumida* F.R.Barbosa et al.), fungi (e.g., *Anteaglonium brasiliense* D.A.C.Almeida et al.; *Diplococcium variegatum* S.S.Silva et al.; *Thozetella submersa* F.R.Barbosa & Gusmão), and angiosperms (e.g., *Heteropterys jardimii* Amorim, *Maranta villosovaginata* N.Luna & E.M.Pessoa, and *Passiflora jiboiaensis* M.A.Milward de Azevedo). These latter three species are endemic to the state of Bahia. Additional angiosperms endemic to Bahia that occur in Serra da Jiboia include *Eugenia altissima* Sobral & Faria (Endangered – EN category), *Inga conchifolia* L.P.Queiroz (Endangered – EN category), *Ormosia timboensis* D.B.O.S.Cardoso et al. (Critically Endangered – CR category), and *Senna bahiensis* A.G.Lima & V.C.Souza (Critically Endangered – CR category), all of which are threatened with extinction according to CNCFlora (2024).

Conservation status. *Eriotheca paganuccii* is known only from seven collections made at three different localities (IUCN B2a criterion), which qualifies it for the Endangered (EN) category. The extent of occurrence (EOO) of this species has been calculated to be 1,738 km^2, which qualifies the species for the Endangered (EN) category, and the area of occupancy (AOO) was estimated to be 12 km^2, which also qualifies it for the Endangered (EN) category according to B1 criterion (IUCN 2024). Two of the three known populations of *E. paganuccii* inhabit legally protected Reserves: one population occurs within a federal level Reserve “Parque Nacional Serra das Lontras” and one population within the state level protected “Área de Proteção Ambiental Lagoa Encantada”. However, the Atlantic Forest habitat has been lost at an accelerated rate due to anthropogenic pressures (B2b criterion). Therefore, due to the very restricted extent of the habitat of this species (montane wet forests on mountain summits), the rapid rate of deforestation of the surrounding Atlantic Forest, and the small AOO (12 km^2) and EOO (1,738 km^2) of *E. paganuccii*, we consider this species to be Endangered belonging to the EN B1ab(i,iii), B2ab(ii,iii) category based on available data and IUCN criteria (IUCN 2024).

Etymology. The specific epithet honors Luciano Paganucci de Queiroz, a distinguished Brazilian taxonomist who was the first to collect this new species and one of the first to promote and undertake floristic efforts on Serra da Jiboia, Bahia, its type-locality.

Additional specimens examined. Brazil. Bahia: **Arataca**, RPPN do IESB, Serra do Peito de Moça, Rod. Arataca/Una, entrada 9,5 km da cidade, mais 8,9 km da entrada, topo da serra, 15°10'27"S, 39°20'22"W, 20 Dec 2008 (lf, fr), *A.B. Jardim et al. 168* (CEPEC 127300!, RB barcode 00734410). **Barro Preto**, estrada de terra para Pedra Lascada, cume da serra, 14°46'17"S, 39°32'10"W, 841 m alt., 13 Feb 2011 (lf), *J.G. Carvalho-Sobrinho & A.C. Mota 2902* (HUEFS barcode 000132932!). **Santa Terezinha**, Serra da Jiboia, c. 4 km de Pedra Branca, Mata Higrófila, 12°51'11"S, 39°28'19"W, 27 Sept 2000 (lf, fl buds), *L.P. Queiroz 6370* (CESJ 44810, HUEFS barcode 000132068!, SP barcode 057770!). Same municipality, 14,5 km na rod. Elísio Medrado/Santa Terezinha, Torre da Embratel, c. 7 km do distrito de Pedra Branca, Serra da Jiboia, Campos de Altitude, 12°51'13"S, 39°28'33"W, 750 m alt., 24 Feb 2000 (lf, fr), *J.G. Jardim et al. 2808* (ALCB barcode 062988, BAH 5228, CEPEC 88453!, HUEFS barcode 000138269!,

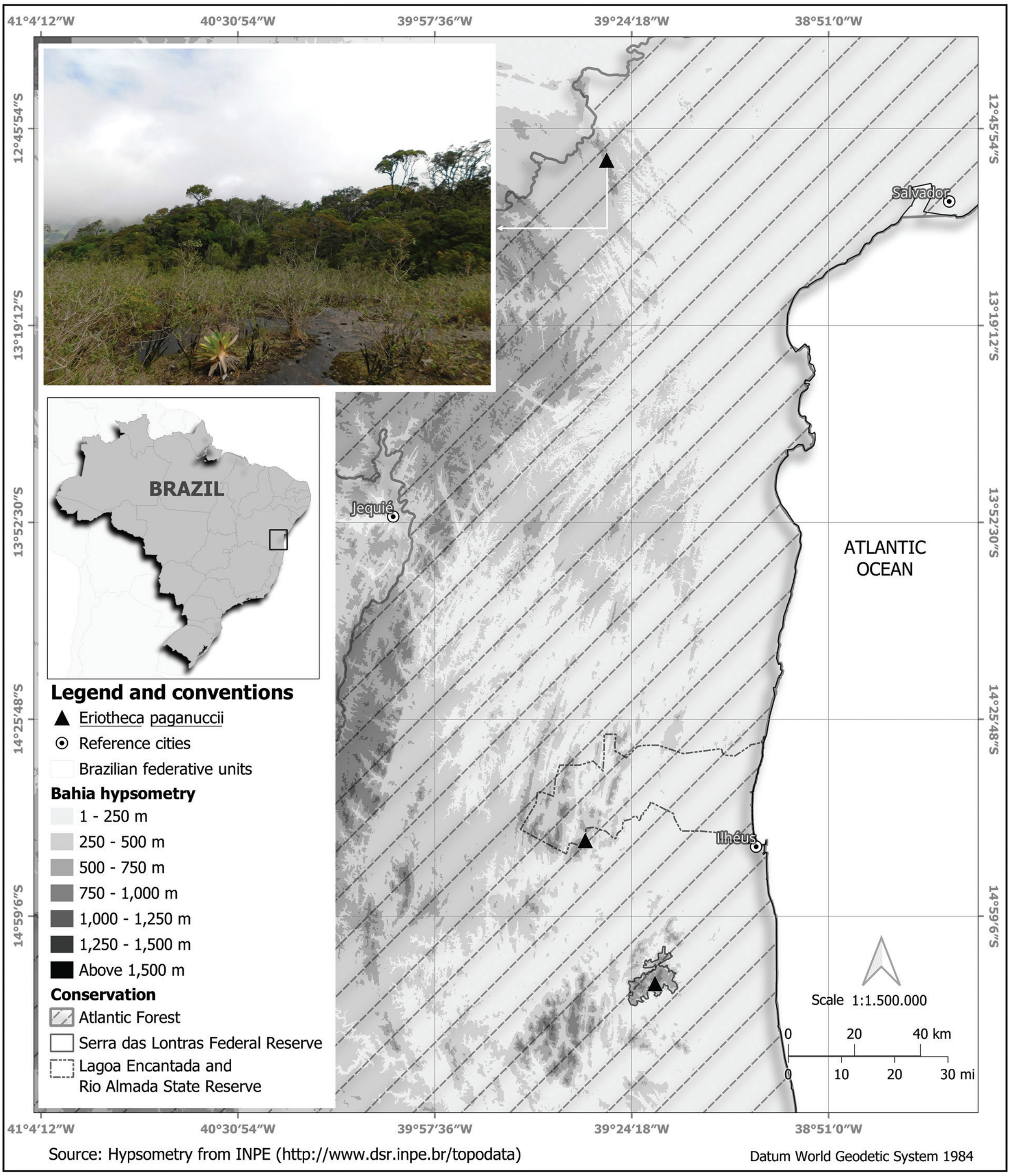

Figure 3. Distribution map of *Eriotheca paganuccii* and type-locality with montane wet forest between 750 m and 850 m in elevation near granitic-gneissic rock outcrops on the summit of Serra da Jiboia in the Atlantic Forest of Bahia, northeastern Brazil.

NY barcode 00566377!, RB barcode 00778244!, SPF barcode 00161825, UESC 7099, UFRN 13793!); same municipality, Serra da Jiboia, Morro da Pioneira, cume, 12°51'18"S, 39°28'33"W, 817 m alt., 28 Oct 2023 (lf, fl), *J.G. Carvalho-Sobrinho & A.C. Mota 4022* (CEPEC, HUEFS, IPA, RB, SP, SPF); same locality, 28 Oct 2023 (lf, very young fruits), *J.G. Carvalho-Sobrinho & A.C. Mota 4023* (HUEFS,

Table 1. Comparison of *Eriotheca paganuccii* to morphologically similar species in the state of Bahia, northeastern Brazil.

Trait	*E. alversonii*	*E. macrophylla*	*E. obcordata*	*E. paganuccii*
Buttresses	present	present	absent	absent
Outline of scales on leaves	unknown	regular outline (Duarte 2010)	regular outline (Duarte 2010)	irregular outline (Duarte 2010)
Glands on receptacle	absent	present	absent	present, rarely absent
Bracteoles	caducous	caducous	often persistent	caducous
Flower bud shape	oblong	widely-elliptic	oblong	oblanceolate
Calyx dimensions (mm)	3–4 × 3–5	5–6 × 7–9	5 × 5	7 × 7–9
Calyx apex	truncate to crenulate	crenate to crenulate	truncate	inconspicuously to shortly 5-lobed
Petal dimensions (mm)	15–23 × 3–6	30 × 10–12	21–25 × 7	23–26 × 4–6
Number of stamens	c. 70	c. 140	c. 80	c. 80
Staminal tube length (mm)	4–5	4 × 3.5	5–6 × 1.5–1.7	7 × 4
Fruit kapok	abundant	abundant	abundant	scanty
Fruit length (mm)	15–21	38–60	28–60	35–50(–70, when fresh)
Fruit shape	globose to subglobose	obovoid to subglobose	obovoid	globose to subglobose
Seed length (mm)	c. 5	c. 10	c. 5	(11–)14(–19)
Seed number per fruit	numerous	numerous	numerous	c. 10
Flowering period	July to September	October to December	November to April	September (very young flower buds); December
Fruiting period	August to October, December to February	December to February	February	October (very young fruits); December to February

IPA); same locality, 25 Jan 2024 (lf, fr), *J.G. Carvalho-Sobrinho 4038* (HUEFS barcode 000100270218!); same locality, 25 Jan 2024 (lf), *J.G. Carvalho-Sobrinho 4039* (HUEFS barcode 000100270219!); same locality, 25 Jan 2024 (lf, fr), *J.G. Carvalho-Sobrinho 4040* (HUEFS barcode 000100270220!).

Discussion

Taxonomic affinities of *Eriotheca paganuccii*

Eriotheca paganuccii is characterized by flowering branches with caducous leaves, often suberized, leaflets coriaceous to strongly coriaceous (chartaceous when young), leaves 3(–5)-foliolate, and fruit globose to subglobose that are 35–50 mm long (–70 mm when fresh). The woody capsules with scanty kapok enclosing few seeds (c. 10 per capsule) are unique characteristics among species of *Eriotheca*. Moreover, the seeds that are 11–19 mm long are the largest in the genus encountered to date.

Among species found in Bahia, *Eriotheca paganuccii* is similar to *E. obcordata* due to its absence of buttresses, obcordate leaflets, oblanceolate petals, stamens c. 80 in number, and staminal tube length-to-width ratio of c. 1.5, but it differs by the presence (vs. absence) of glands on the receptacle, caducous (vs. often persistent) bracteoles, larger (7 × 7–9 mm vs. 5–5 mm) calyces, and globose to subglobose (vs. obovate) capsules (Table 1).

Eriotheca paganuccii has been misidentified in herbaria as *E. macrophylla* (K.Schum.) A.Robyns. Both species share inflorescences borne on branches that are often leafless and modified as brachyblasts, caducous bracteoles, and glands on the receptacles (Table 1). However, *E. paganuccii* can be readily distinguished from *E. macrophylla* by its oblanceolate (vs. widely-elliptic) flower buds, short (c. 1 mm vs. 2–5 mm long) receptacles, oblanceolate (vs. obovate) petals that are 4–8 mm (vs. 10–12 mm) wide and with a length-to-width ratio of 5 (vs. 3), fewer (c. 80 vs. c. 140) stamens, and staminal tube length-to-width ratio of 1.5–2 (vs. up to 1.2).

Eriotheca paganuccii differs from the two aforementioned species also by the presence of scales with an irregular outline on leaves (vs. scales with regular outline according to Duarte and Esteves 2011). Moreover, *E. paganuccii* is endemic to montane wet forests near 800 m in elevation whereas *E. macrophylla* and *E. obcordata* inhabit mainly low altitudinal areas in the Atlantic coast.

Eriotheca paganuccii is also morphologically similar to *E. alversonii* because the two species may present 3-foliolate leaves with obovate leaflets, oblong flower buds, oblanceolate petals, and globose to subglobose capsules. However, *E. paganuccii* can be distinguished by its leafless (vs. leafy) flowering branches, very coriaceous (vs. chartaceous) leaflets, glabrous (vs. with sparse, darkish indumentum) pedicels, receptacles and calyces, larger calyces (7 × 7–9 mm vs. 3–4 × 3–5 mm), larger capsules (35–50 mm vs. 15–21 mm), scanty (vs. abundant) kapok, and seeds c. 14 mm (vs. c. 5 mm) long.

Eriotheca paganuccii is morphologically similar to *E. pentaphylla* (Vell.) A.Robyns, a species endemic to the southeastern Atlantic Forest in the states of Rio de Janeiro and São Paulo (Duarte and Yoshikawa 2024), both species with relatively large seeds, 7–14 mm vs. (11–)14–18 mm long, respectively. Additionally, herbarium specimens of these two species often present marcescent, lignified calyces that split into patent lobes. However, *E. paganuccii* differs from *E. pentaphylla* in its smaller calyces (7 × 7–9 mm vs. 8–12 × 13 mm) that are inconspicuously to shortly 5-lobed (vs. distinctly lobed), narrower petals (4–8 mm vs. 11–15 mm wide), white (vs. often pinkish) filaments, and globose to subglobose (vs. obovoid) capsules that are c. 35–50(–70) mm long (vs. 80–100 × 45 mm). Furthermore, *E. paganuccii* flowers from November to December and fruits from December to February whereas *E. pentaphylla* flowers from April to July and fruits from August to November.

Leaf morphology variation and the importance of phenologically complete collections

Typically, species of *Eriotheca* and other Bombacoideae present distal and proximal leaflets that are distinct in shape and size. This can be observed in *E. paganuccii*, in which distal leaflets can be longer (length-to-width ratio of 1.4–2.7) than proximal ones (length-to-width ratio of 1.4–2). *Eriotheca paganuccii* also presents great variation in its leaves according to their position on the tree (Fig. 2D, F). During fieldwork, we observed that leaves on branches at the top of the tree canopy are generally distinct from leaves on branches with less exposure to the sun: they are smaller and consist of fewer (often one or two), more rigid leaflets that are oriented upwards (Fig. 2D). This high plasticity in leaf morphology has also been observed on herbarium specimens of other

Eriotheca from the Atlantic Forest and can make taxonomic identification difficult, especially for taxa originally described based on few or only one specimen, as is frequently observed in the genus.

This idiosyncratic way in which Bombacoideae herbarium specimens are made (Carvalho-Sobrinho and Queiroz 2008, 2010; Carvalho-Sobrinho et al. 2013a, b, 2014) also highlights the taxonomic importance of the morphology of reproductive organs especially fruit and seed as demonstrated by recent studies (Carvalho-Sobrinho et al. 2020; Yoshikawa and Duarte 2021). Regrettably, morphological descriptions of both fruit and seed of ten species of *Eriotheca* have not yet been published including the following six species known from the Atlantic Forest: *E. bahiensis* M.C.Duarte & G.L.Esteves, *E. crenulaticalyx* A.Robyns, *E. dolichopoda* A.Robyns, *E. longipes* (A.Robyns) M.C.Duarte & G.L.Esteves, *E. macrophylla*, and *E. platyandra* A.Robyns.

As a consequence, a number of herbarium specimens of *Eriotheca* represented by only fruit continue to have inaccurate taxonomic identifications. *Eriotheca paganuccii* can serve to illustrate this situation: it was first collected in 1992 with only fruits, and again with only fruits in 2000 and 2008. These incomplete specimens were tentatively identified as *E. globosa*, *E. macrophylla*, and *E. obcordata*. The morphology of flowers, however, collected in October 2023 allowed *E. paganuccii* to be clearly distinguished from these *Eriotheca* species as demonstrated above.

An additional example of the impact of phenologically complete collections for plant taxonomy and conservation can been observed in *Eriotheca platyandra* (Robyns 1963) whose identity remains doubtful to the point of its being overlooked in the treatment of the genus for “Flora e Funga do Brasil” (Duarte and Yoshikawa 2024).

Here we provide further evidence for the importance of fruit and seed characters to the taxonomy of *Eriotheca* especially for circumscribing species from Atlantic Forest that present fairly conservative floral morphologic traits and represent the major taxonomic challenge remaining in the genus (Carvalho-Sobrinho, pers. observ.). The greater morphological and taxonomic diversity of *Eriotheca* observed in the Atlantic Forest demands further efforts toward resolving the taxonomy of the genus and eventually may be linked to complex dynamics of speciation, as observed in *Eriotheca* from the Brazilian Cerrado. The existence of polyploid populations associated with distinct fruit and seed traits has been linked to reproductive strategies in Cerrado lineages. Such findings have revealed the existence of a species complex (Mendes-Rodrigues et al. 2019; Marinho et al. 2020) and can help us understand the origins of the high morphological variability observed in *Eriotheca* species of the Cerrado.

Cytogenetic and cytomolecular data also have revealed noteworthy biogeographic and species richness patterns in *Eriotheca* and allied genera that shed light on its evolutionary history as well as on the relationship of *Eriotheca* with the closely related genus *Pachira* (Costa et al. 2017). Furthermore, these data have been analyzed in a phylogenetic framework and indicated neopolyploidy may be involved in speciation of *Eriotheca* lineages from the Atlantic Forest (Costa et al. 2017).

Therefore, in order to improve the taxonomy of *Eriotheca* and facilitate the production of cytogenetic and cytomolecular data, it is critical to obtain phenologically complete herbarium collections including fruit and seed of each species and, whenever possible, each population. Such efforts will enhance the systematics of *Eriotheca* allowing the evaluation of the evolutionary processes underpinning the diversity in this group especially in Atlantic Forest lineages that are threatened with extinction.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

Conceptualization: JCS. Data curation: JCS, LJD, ACCM. Formal analysis: JCS, ACCM. Funding acquisition: JCS, LJD. Investigation: JCS. Methodology: ACCM, JCS. Resources: JCS, LJD. Supervision: LJD. Validation: LJD, JCS. Visualization: ACCM. Writing – original draft: ACCM, JCS, LJD. Writing – review and editing: JCS, LJD.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

Herbarium specimens examined of two *Eriotheca* species in Bahia morphologically similar to *E. paganuccii*

Eriotheca macrophylla (K.Schum.) A.Robyns

Brazil. Bahia. Ilhéus, on road to Vila Brasil, 10 km West of junction with BA001, the junction c. 40 km south of Ilhéus, just north of the Rio Acuípe, 15°06'S, 39°04'W, 10 May 1993 (lf, fl), *W. Thomas et al. 9843* (CEPEC, NY barcode 00998006, SP, US barcode 01220017). Itacaré, entre a Praia do Farol e a Praia da Ribeira, 14 Dec 1992 (lf, fl), *A. Amorim et al. 951* (CEPEC, HUEFS barcode 000138305, NY barcode 00402470, US barcode 01226959). Itapebi, Faz. Dois Irmãos, Rodovia para Potiraguá, 10 Nov 1970 (lf, fl), *R.S. Pinheiro* & *T.S. Santos 419* (CEPEC). Jequié, Fazenda Brejo Novo, a 10,5 km da Av. Otávio Mangabeira entrado pela Exupério Miranda no Bairro do Mandacaru, 13°56'53.6"S, 40°06'42"W, 716 m, 08 Dec 2004 (st), *G.E.L. Macedo & J.L. Paixão 1499* (HUEFS). Porto Seguro, parte sul entre os municípios de Ajuda e Porto Seguro, 08 Nov 1963 (lf, buds), *A.P. Duarte 7999* (RB barcode 00059485, SP barcode 057769). Santa Cruz de Cabrália, Res. Bio. Pau-Brasil, 11 Dec 1971 (lf, fl), *A. Eupunino 94* (CEPEC). **Espírito Santo.** Conceição da Barra, Área 157 da Aracruz Celulose S.A., 28 Oct 1993 (lf, buds) *O.J. Pereira et al. 5163* (VIES). Linhares, Reserva Natural da CVRD, estrada Flamengo, km 08, 03 Dec 2004 (lf, buds), *D.A. Folli 4999* (CVRD); *ibidem,* Reserva Natural da CVRD, estrada Flamengo, km 07, próximo ao pátio, 14 Jan 1994 (lf, fr), *D.A. Folli 2170* (CVRD). **Pernambuco.** Brejo da Madre de Deus, Mata do Bituri, Serra do Prata, próximo do mirante, 08°12'27"S, 36°23'32"W, 920–1030 m, *L.M. Nascimento 195* (HUEFS barcode 000132032, PEUFR, RB barcode 00059255).

Eriotheca obcordata A.Robyns

Brazil. Bahia. Buerarema, estrada São José da Vitória-Buerarema, ramal à direita, estrada de acesso a Pedra Branca, 15°05'S, 39°19'W, 15 Oct 2003 (lf, fl), *P. Fiaschi et al. 1709* (CEPEC, HUEFS barcode 000138548, MO barcode 2256429, NY barcode 01092733, SPF barcode 162815). Entre Rios, Fazenda Mangueira, 11°53'8"S, 37°57'13"W, 90–100 m, 26 Feb 2005 (lf, fr), *J.G. Carvalho-Sobrinho 365* (HUEFS barcode 000138548). Entre Rios, Fazenda Mangueira, 27 Feb 2010 (lf, fr), *J.G. Carvalho-Sobrinho et al. 2660* (HUEFS barcode 000138053). Entre Rios, Fazenda Mangueira, 28 Feb 2010 (lf, fl, fr), *J.G. Carvalho-Sobrinho et al. 2711* (HUEFS barcode 000138584). Ilhéus, Ribeirão da Fortuna, 23 June 1944 (lf, fl), *H.P. Velloso* (HUEFS barcode 000138053).

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Research Article

Two new species of *Paraphlomis* (Lamiales, Lamiaceae) from limestone karsts in Guangdong Province, China

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Abstract

Paraphlomis qingyuanensis and *P. baiwanensis* (Lamiaceae), two new species from the limestone area in Guangdong Province, China, are described. Morphologically, both species belong to *P.* ser. Subcoriaceae C.Y. Wu & H.W. Li. A close relationship between the two new and *P. subcoriacea* was revealed by molecular phylogenetic analyses based on ETS and ITS. Further morphological and population genetic evidence indicated that they are distinct species in *Paraphlomis*. According to the IUCN Red List Categories and Criteria, *P. qingyuanensis* and *P. baiwanensis* were assessed as Endangered (EN) and Deficient (DD), respectively.

Key words: IUCN, limestone, new taxon, Paraphlomideae, phylogeny, Qingyuan, RAD-seq

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Introduction

Paraphlomis (Prain) Prain is a member of the tribe Paraphlomideae Bendiksby (Lamiaceae, Lamioideae) (Bendiksby et al. 2011; Li et al. 2016; Zhao et al. 2021). Most species of *Paraphlomis* are distributed in southern China, with several species occurring in the Himalayas, Korea and Southeast Asia (Li and Hedge 1994; Wu and Li 1997; Ko et al. 2014; Chen et al. 2021). Previous molecular phylogenetic studies of *Paraphlomis* revealed that the genus was not monophyletic, because species of *Matsumurella* were recovered within it (Chen et al. 2021; Chen et al. 2022b; Guo et al. 2023). In general, *Paraphlomis* is characterized by its herbaceous habit, actinomorphic calyx with five lobes less than half as long as the tube, corolla 2-lipped (1/3) with hairy upper lip but hardly bearded along the margin, included stamens and an apically truncate ovary (Wu and Li 1977; Bendiksby et al. 2011; Ko et al. 2014; Chen et al. 2021).

As currently circumscribed, a total of 37 species and seven varieties are recognised within *Paraphlomis* (Li and Hedge 1994; Chen et al. 2022a, 2022b;

Yuan et al. 2022; Guo et al. 2023; Yan et al. 2023). China is the distribution center of *Paraphlomis*, with 23 species documented in the Flora of China (Li and Hedge 1994). In recent years, a number of new species and infraspecies of *Paraphlomis* were reported in China, including *P. javanica* var. *pteropoda* D. Fang & K.J. Yan and *P. javanica* var. *angustifolia* f. *albinervia* D. Fang & K.J. Yan (Yan and Fang 2009); *P. breviflora* B.Y. Ding, Y.L. Xu & Z.H. Chen (Ding et al. 2019); *P. kuankuoshuiensis* R.B. Zhang, D. Tan & C.B. Ma (Zhang et al. 2020); *P. jiangyongensis* X.L. Yu & A. Liu and *P. coronata* (Vaniot) Y.P. Chen & C.L. Xiang (Chen et al. 2021); *P. nana* Y.P. Chen, C. Xiong & C.L. Xiang (Chen et al. 2022c); *P. longicalyx* Y.P. Chen & C.L. Xiang (Chen et al. 2022a); *P. hsiwenii* Y.P.Chen & XiongLi (Chen et al. 2022b); *P. strictiflora* J.C.Yuan, B.Chen & C.L.Xiang (Yuan et al. 2022); *P. jinggangshanensis* Boufford, W.B. Liao & W.Y. Zhao (Zhao et al. 2022); *P. yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan (Guo et al. 2023), *P. caloneura* K.J.Yan, Y.P.Chen & Y.Feng Huang (Yan et al. 2023).

During a botanical expedition of the limestone area in Qingyuan city, Guangdong Province in 2023, we discovered two unknown species of *Paraphlomis*. The calyx teeth of the two unknown species extended into wings from veins, which are consistent with the characteristics of *Paraphlomis* ser. Subcoriaceae C.Y. Wu et H.W. Li (Li 1965; Wu and Li 1977). However, their morphological characters differ from the two known two species of the series, *P. subcoriacea* C. Y. Wu ex H. W. Li and *P. brevifolia* C. Y. Wu & H. W. Li. Thus, we suspected both of them were undescribed species. After careful field observations, morphological comparisons with other species of *Paraphlomis*, and molecular phylogenetic studies, we confirmed that they were new species and named them as *P. qingyuanensis* W.Y. Zhao, R.M. Wu & Q. Fan and *P. baiwanensis* W.Y. Zhao, Y.P. Chen & Q. Fan.

Materials and methods

Morphological study

The flowering and fruiting plants of the two new species were examined in the field from August to December in 2023 and compared with herbarium specimens deposited in IBSC, KUN, GCMI and SYS (herbarium acronyms follow Thiers 2023). The two putative new species were most similar to *Paraphlomis subcoriacea* and *P. brevifolia*. We have carried out several field work trips to the collection site of the type specimens of these two species from December 2023 to April 2024. Unfortunately, we did not find *P. brevifolia* in the field due to a lack of detailed collection site information (Li 1965). Therefore, the morphological features contrasting with those of *P. brevifolia* were based on its type specimens (IBSC0005124). All morphological characteristics were measured using dissecting microscopes.

Phylogenetic analyses

The nuclear ribosomal internal and external transcribed spacers (ITS and ETS) were used for reconstructing the phylogeny of the suspected new species and related taxa based on previous study (Chen et al. 2021; Zhao et al. 2022).

Most sequences were downloaded from GenBank, except for the two nuclear ribosomal DNA (nrDNA) sequences of the two new species and *Paraphlomis subcoriacea*, which were newly sequenced in the present study. Genomic DNA of the suspected new species was extracted from silica-gel-dried leaves using the modified 2× CTAB procedure of Doyle and Doyle (1987). The ITS and ETS sequences were amplified with primer pairs 17SE/26SE (Sun et al. 1994) and ETSB/IGS (Beardsley and Olmstead 2002), respectively, with PCR amplification and sequencing following Chen et al. (2016). A total of 49 accessions representing 30 species and four varieties/subspecies of *Paraphlomis* and two species of *Matsumurella* were sampled in the phylogenetic study. *Phlomoides bracteosa* (Royle ex Benth.) Kamelin & Makhm. and *Phlomis fruticosa* Sieber ex C. Presl were selected as the outgroups. The GenBank accession numbers are listed in Appendix 1.

Nucleotide sequences were aligned using MAFFT 7 (Katoh and Standley 2013). After removing aligned columns with more than 70% missing data using Phyx (Brown et al. 2017), the two nrDNA regions were concatenated for phylogenetic reconstruction. The phylogenetic relationships were assessed using the Bayesian inference (BI) and maximum likelihood (ML) methods, and both were implemented on the online server Cyberinfrastructure for Phylogenetic Research Science (CIPRES) Gateway (http://www.phylo.org/; Miller et al. 2010). The BI analysis was carried out using MrBayes 3.2.7a (Ronquist et al. 2012) and the ML analysis using RAxML-HPC2 (Stamatakis 2014), with detailed settings following that of Chen et al. (2021). The resulting BI tree with posterior probabilities (PP) and best-scoring ML tree with bootstrap support (BS) values were visualized and annotated using TreeGraph 2 (Stover and Müller 2010).

Population genetic structure analyses

To investigate the phylogenetic relationship between the two newly discovered species and their close relatives, we further conducted an analysis of their population genetic structure. A total of 84 individuals were sampled from seven populations of the two putative *Paraphlomis* new species and its close relative *P. subcoriacea* (Appendix 2). The fresh leaves were dried and stored with silica gel, and then sent to JieRui BioScience Co. Ltd. (Guangzhou, China) for DNA extraction, ddRAD-seq library preparation, and Illumina sequencing. The produced raw data was processed with the software Stacks 2.55 (Catchen et al. 2013). The procedure “process_radtags” was used to demultiplex RAD tags, “denovo_map.pl” to process all the fastq files, and “populations” to filter the data by setting “--min-maf 0.05 --max-obs-het 0.7 -R 0.8 –write-random-snp –vcf”. The produced vcf file was transformed to ped file using bed file using software vcftools 0.1.16 (Danecek et al. 2011), and to bed file using the software Plink v1.90 (Chang et al. 2015). The produced bed file was used to perform Bayesian cluster analysis with the software ADMIXTURE v1.3.0 (Alexander et al. 2009), in which the number of groups (K) was set from 1–6 and the optimal K was determined by the minimum value of cross-validation error (CV). Principal coordinate analysis (PCA) was performed with Plink, and python script were used to draw the scatter diagram.

Results and discussion

The combined nuclear data set was 1211 bp (773 bp for ITS, 438 bp for ETS) in length, including 347 variable sites (165 for ITS, 182 for ETS) and 200 parsimony-informative characters (87 for ITS, 113 for ETS). The resulting phylogenetic tree of *Paraphlomis* in this study was similar to that in previous studies (Chen et al. 2021; Zhao et al. 2022). The two accessions of *P. baiwanensis* grouped together (Fig. 1: BS = 100%/PP < 0.50) and this new species was sister to *P. subcoriacea* (Fig. 1: BS = 100%/PP = 1.00). The *P. baiwanensis-P. subcoriacea* clade was further sister to another new species, *P. qingyuanensis* (Fig. 1: BS = 99%/PP = 1.00). All three species were nested within the previously suggested "Clade III" by Chen et al. (2021) (Fig. 1: BS = 78%/PP = 1.00). Species of "Clade III" (marked in blue in Fig. 1) are characterized by hairy nutlets/ovaries (Chen et al. 2021; 2022b). The nutlets of both new species are sparsely hispid and densely glandular at apex (Figs 2M, 5I, 6H), which confirmed the significance of nutlet morphology for the infrageneric classification of *Paraphlomis* (Chen et al. 2021).

The close relationships among the two new species and *P. subcoriacea* are also supported by morphological evidence. In morphology, the two putative new species are most similar to *Paraphlomis brevifolia* C. Y. Wu et H. W. Li and *P. subcoriacea* C. Y. Wu ex H. W. Li. They share the features such as conspicuously extended calyx teeth, and the fact that they are also growing in a limestone habitat. A comparison of their morphological features is presented in Table 1 and Fig. 4.

The putative new species *Paraphlomis qingyuanensis* differs from *P. brevifolia* by its slender and much branched stem (vs. unbranched) (Figs 2C, 4A), leaves without glandular (vs. abaxially golden glandular) (Table 1). Furthermore, the reticulate veins and pilose indumentum on leaves of *P. brevifolia* are more obvious (Fig. 4B). *P. qingyuanensis* could also be easily distinguished from *P. subcoriacea* by its papery leaves (vs. thin leathery), fewer leaf veins, 2–4 pairs (vs. 5–6 pairs), and smaller leaf size (Table 1, Fig. 4A, D).

Paraphlomis baiwanensis is most similar to *P. subcoriacea*. They share such features as leaves lanceolate, 5–7 lateral vein pairs, and leaf base shape (Table 1). However, *P. baiwanensis* could be easily distinguished from the latter by its stout stem (diam. 3.6–5.3 mm vs. ca. 3.6 mm), leathery leaves (vs. thin leathery), and larger leaves size (12.5–18.7 cm × 2.6–4.8 cm vs. 7–15 cm × 1.5–3.2 cm) (Table 1, Fig. 4C, D). Furthermore, the distribution areas of the two species are separated by a distance of approximately 45 km, exhibiting complete non-overlap (Fig. 7A). The results of population genetic analysis also confirmed significant differences in their genetic structure (Fig. 7B).

Bayesian cluster analysis showed lowest CV value as $K = 3$, each of the three species *P. baiwanensis* (P1), *P. subcoriacea* (P2–4), and *P. qingyuanensis* (P5–7) possesses a unique gene pool, and no gene admixture is observed in any individuals (Fig. 7B). PCA analysis reveals similar results in which the 84 individuals are assigned into three groups and individuals of the same species are clustered into the same group (Fig. 7C). These results showed that individuals of the three species can be separated clearly from each other based on genomic data, strongly supported their species status and no obvious gene flow was observed among the three species.

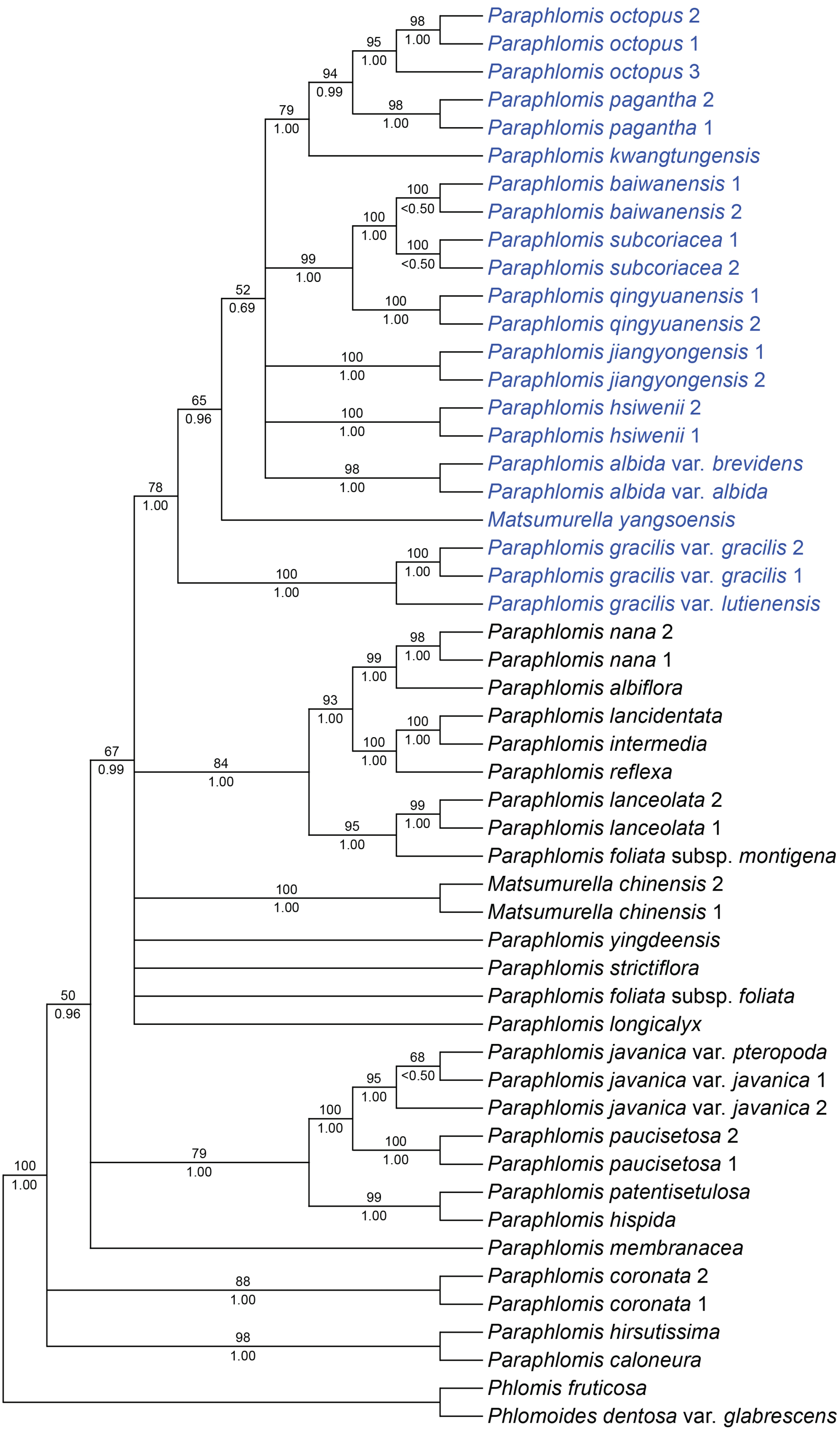

Figure 1. The best-scoring maximum likelihood tree of *Paraphlomis* inferred from concatenated nrDNA (ETS and ITS) dataset. Support values ≥ 50% BS or 0.50 PP are displayed above and below the branches, respectively. Multiple accessions of the same species are numbered according to Appendix 1.

Table 1. Morphological comparisons among *Paraphlomis baiwanensis*, *P. brevifolia*, *P.qingyuanensis*, and *P. subcoriacea*.

Characters	*P. qingyuanensis*	*P. baiwanensis*	*P. subcoriacea*	*P. brevifolia*
Stem	50–90 cm, slender, 1.4–3.1 mm in diam	50–80 cm tall, erect, stout, 3.6–5.3 mm in diam	ca. 60 cm, ca. 3.6 mm in diam	ca. 40 cm, ca. 2.5 mm in diam
Stem branching	much branched	unbranched or 2–3 branched	unbranched or 2–3 branched	unbranched
Length of petiole	0.4–1.6 cm	0.6–1.3 cm	1.0–1.3 cm	0.3–0.6 cm
Leaf size	2.7–9.5 cm long, 1.2–2.5 cm wide	12.5–18.7 cm long, 2.6–4.8 cm wide	7–15 cm long, 1.5–3.2 cm wide	5–8 cm long, 2.4–3.4 cm wide
Leaf base	cuneate, not decurrent	cuneate or abruptly obtuse, not decurrent	attenuate or abruptly obtuse, not decurrent	obtuse to rounded, not decurrent
Leaf texture	papery	leathery	thin leathery	thin leathery
Leaf vein	2–4 (-5) pairs	5–7 (-8) pairs	5–6 pairs	4–5 pairs
Calyx teeth	subtruncate, extended into wings from veins	subtruncate, extended into wings from veins	subtruncate, extended into wings from veins	triangular, conspicuously extended into wings from veins
Corolla	upper lip yellow, lower lip red with purple spots	white	white or purple-white	unknown

Taxonomic treatment

Paraphlomis qingyuanensis **W.Y.Zhao, R.M.Wu & Q.Fan, sp. nov.**
urn:lsid:ipni.org:names:77344362-1
Figs 2, 3, 4A
清远假糙苏

Type. China. Guangdong Province: Yingde City, Huanghua Town, near Hegushi, on the limestone valley, 24°13'N, 112°56'E, alt. 135 m, 7 September 2023, *Xiong Qin-Dai ZWY-3793* (holotype: SYS00236954! isotypes: KUN, SYS00236955!, SYS00236968!, SYS00236969!).

Diagnosis. *Paraphlomis qingyuanensis* is morphologically similar to *P. brevifolia* and *P. subcoriacea*, but differs from the latter two species by its slender and much branched stem, papery leaves, inconspicuous reticulate veining, and fewer leaf veins.

Description. ***Herbs*** perennial, 50–90 cm tall; stoloniferous, with sparsely villous. **Stems** erect or decumbent, slender and much branched, 4-angled, diameter 1.4–3.1 mm, densely retrorse pilose. ***Leaves*** opposite; lamina ovate to oblong, papery, 2.7–9.5 cm long, 1.2–2.5 cm wide, apex obtuse, base cuneate, margin crenate-serrate; adaxially green, abaxially light green, sparsely pilose on both sides, more densely on viens; lateral veins 2–4 (-5)-paired; petiole 0.4–1.6 cm long, densely pilose. ***Verticillasters*** born in upper leaf axils, cymes 1–4-flowered; bracteoles inconspicuous, ca. 0.5 mm long, early deciduous; pedicels ca. 1 mm long, sparsely pilose. ***Calyx*** light green, obconical, 4.5–5 mm long, outside with sparsely pilose and white glandular, glabrous inside, conspicuously 10-veined; teeth 5, inconspicuous so that calyx mouth appears subtruncate, extended into wings from veins as 1.5–2.0 mm long. ***Corolla*** 1.0–1.2 cm long; tube ca. 0.3 cm long, ca. 1 mm in diam., straight, inside of throat dark purple, with pubescent annulate; 2-lipped, villous outside, upper lip oblong, erect and galeate, apex undulate or bilobate, ca. 8 mm long, ca. 4 mm wide; lower lip reflexed, ca. 4.5 mm long, 3-lobed, medium lobe largest, suborbicular, ca. 5 mm long, ca. 4.5 mm wide, apex emarginate, white, dotted with purplish-red

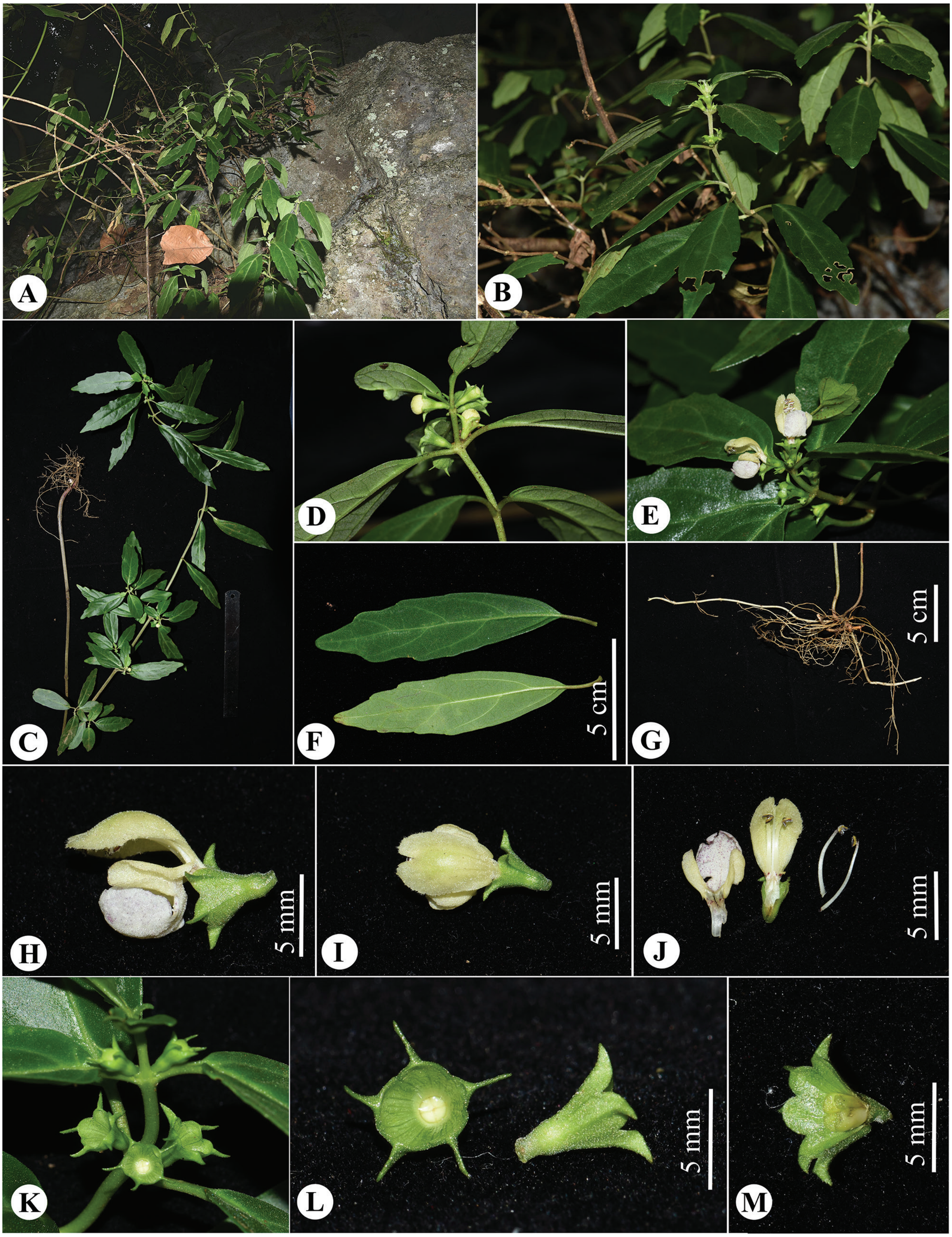

Figure 2. *Paraphlomis qingyuanensis* **A** habitat **B** plants **C** individual **D** inflorescences with unopened flowers **E** opening flowers **F** leaves **G** stolons and roots **H** lateral view of flower **I** upper lip of flower **J** dissected corolla and stamens **K** infructescence **L** frontal and lateral view of calyx **M** dissected calyx and seeds. (Photographs: **A, B** by Qin-Dai Xiong; **C–G** by Wan-Yi Zhao).

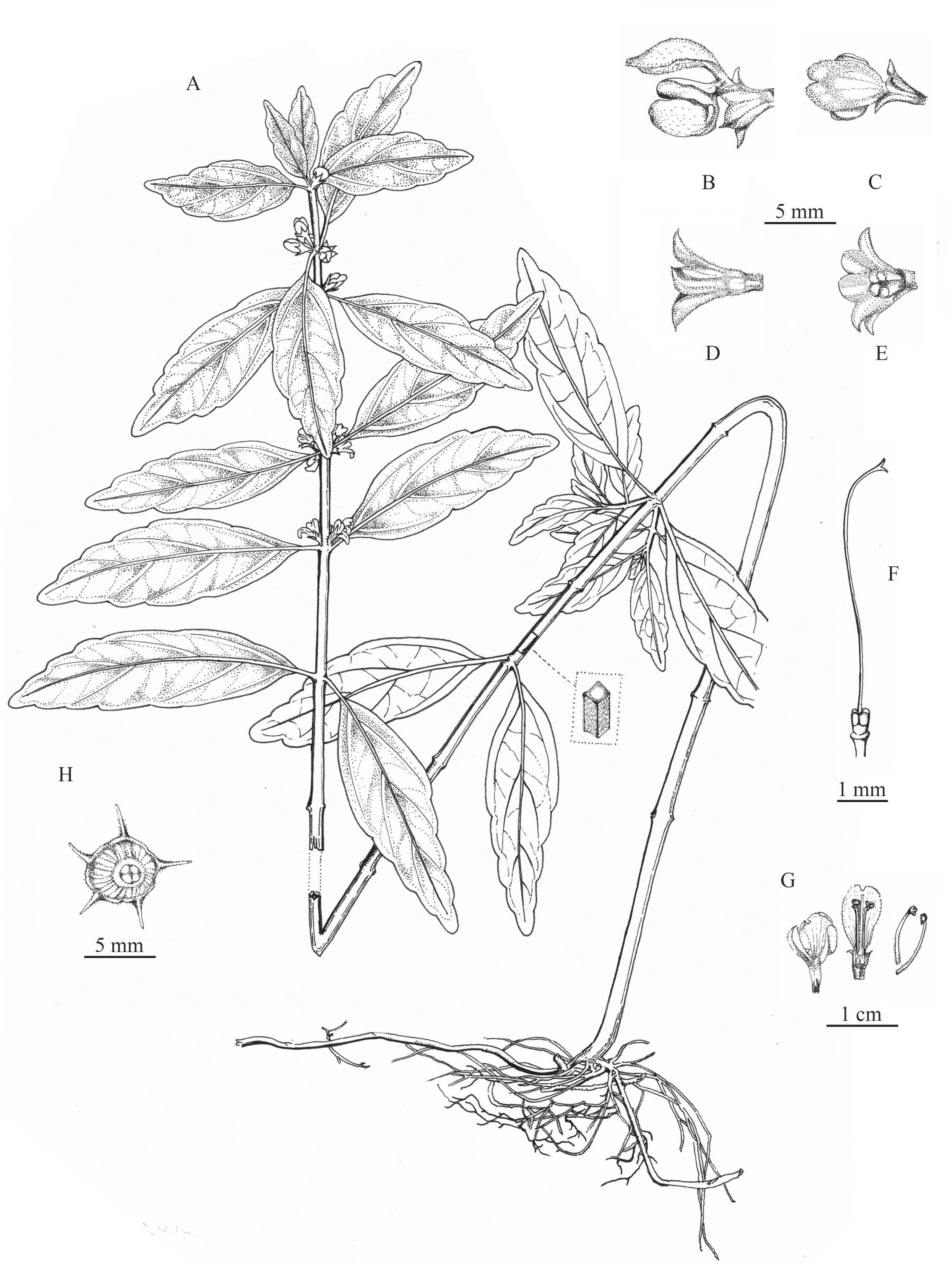

Figure 3. Line drawing of *Paraphlomis qingyuanensis* **A** plant **B** lateral view of flower **C** upper lip of flower **D** lateral view of calyx **E** inner view of calyx **F** style **G** dissected corolla and stamens **H** front view of calyx (Drawn by Zhong-Jin Wang).

spots, lateral lobes ovate, ca. 3.5 mm long, ca. 3 mm wide, apex obtuse, yellow. ***Stamens*** 4, inserted above middle and upper of corolla tube, straight, included, filaments flat, sparsely puberulent-villous, anther cells 2, ovoid, glabrous. ***Style*** filiform, included, glabrous, apex subequally 2-lobed, ca. 1 cm long.

Ovary 4-loculed, truncate at apex. ***Nutlets*** triquetrous-oblong, ca. 2.5 mm long, apex sparsely hispid and glandular.

Distribution, habitat and conservation status. Currently, only three populations of *Paraphlomis qingyuanensis* were found in Huanghua Town of Yingde City, Qingyuan City in Guangdong Province (Fig. 7A). These populations were located in the subtropical monsoon climate region, in a large area of karst landform. The distribution area of *P. qingyuanensis* is extremely fragmented, and it is not within a protected area. Human activity, such as forestry production and tourism, have a negative effect on population regeneration. Thus, *P. qingyuanensis* is here suggested to be endangered (EN) according to IUCN categories guidelines B2(a, b(iii)) (AOO < 500 km^2, number of locations <5, and habitat affected by human activities) (IUCN Standards and Petitions Subcommittee 2022).

Phenology. Flowering was observed from August to December, and fruiting from September to December.

Etymology. The specific epithet "*qingyuanensis*" is derived from the type locality of the new species, i.e. Qingyaun City in Guangdong Province, China.

Additional specimens examined. *Paraphlomis qingyuanensis* (paratypes): China. Guangdong Province: Qingyuan City, Yingde City, Huanghua Town, near Hegushi, on the limestone valley, 24°13'N, 112°56'E, alt. 132 m, 6 September 2023, *Qin-Dai Xiong QYK-HH-156* (SYS); Yingde city, Huanghua town, Hegushi, 24°13'35.7"N, 112°56'08.97"E, alt. 114 m, 16 December 2023, *Qiang Fan 20255* (SYS); Yingde city, Huanghua town, near Hegushi, 24°13'22.71"N, 112°56'05.71"E, alt. 159 m, 26 December 2023, *Qiang Fan & Qin-Dai Xiong QYK-HH-1904* (SYS); Yingde city, Huanghua town, Huanghua park, 24°12'03.46"N, 112°54'10.05"E, alt. 205 m, 25 December 2023, *Qiang Fan & Qin-Dai Xiong QYK-HH-1882* (SYS).

Paraphlomis baiwanensis W.Y.Zhao, Y.P.Chen & Q.Fan, sp. nov.

urn:lsid:ipni.org:names:77344363-1
Figs 4C, 5, 6
白湾假糙苏

Type. China. Guangdong Province: Qingyuan city, Qingxin district, Baiwan town, Hecang village, on the limestone cliff, 24°15'09.40"N, 112°46'47.32"E, alt. 310 m, 15 December 2023, *Qiang Fan 20251* (holotype: SYS00236952!; isotypes: KUN, SYS00236953!).

Diagnosis. *Paraphlomis baiwanensis* is morphologically similar to *P. subcoriacea*, but differs from the latter by its stout stem, larger and leathery leaves, and larger flower.

Description. ***Herbs*** perennial, 50–80 cm tall; stoloniferous, with villous indumentum. ***Stems*** erect, stout, unbranched or 2–3 branched, 4-angled, diameter 3.6–5.3 mm, with densely retrorse pilose hairs. ***Leaves*** opposite; lamina long ovate to lanceolate, leathery, 12.5–18.7 cm long, 2.6–4.8 cm wide, apex acuminate, base cuneate or abruptly obtuse, margin serrulate; adaxially dark green, with densely pilose, abaxially light green with densely brown glandular, sparsely pilose, more densely on veins; lateral veins 5–7 (-8)-paired, raised abaxially and deeply impressed adaxially, anastomosing at leaf margin; petiole 0.6–1.3 cm long, densely pilose. ***Verticillasters*** borne in upper leaf axils, cymes (2-) 5–9-flowered; bracteoles inconspicuous, early deciduous; pedicels ca. 1.2–2.0 mm long,

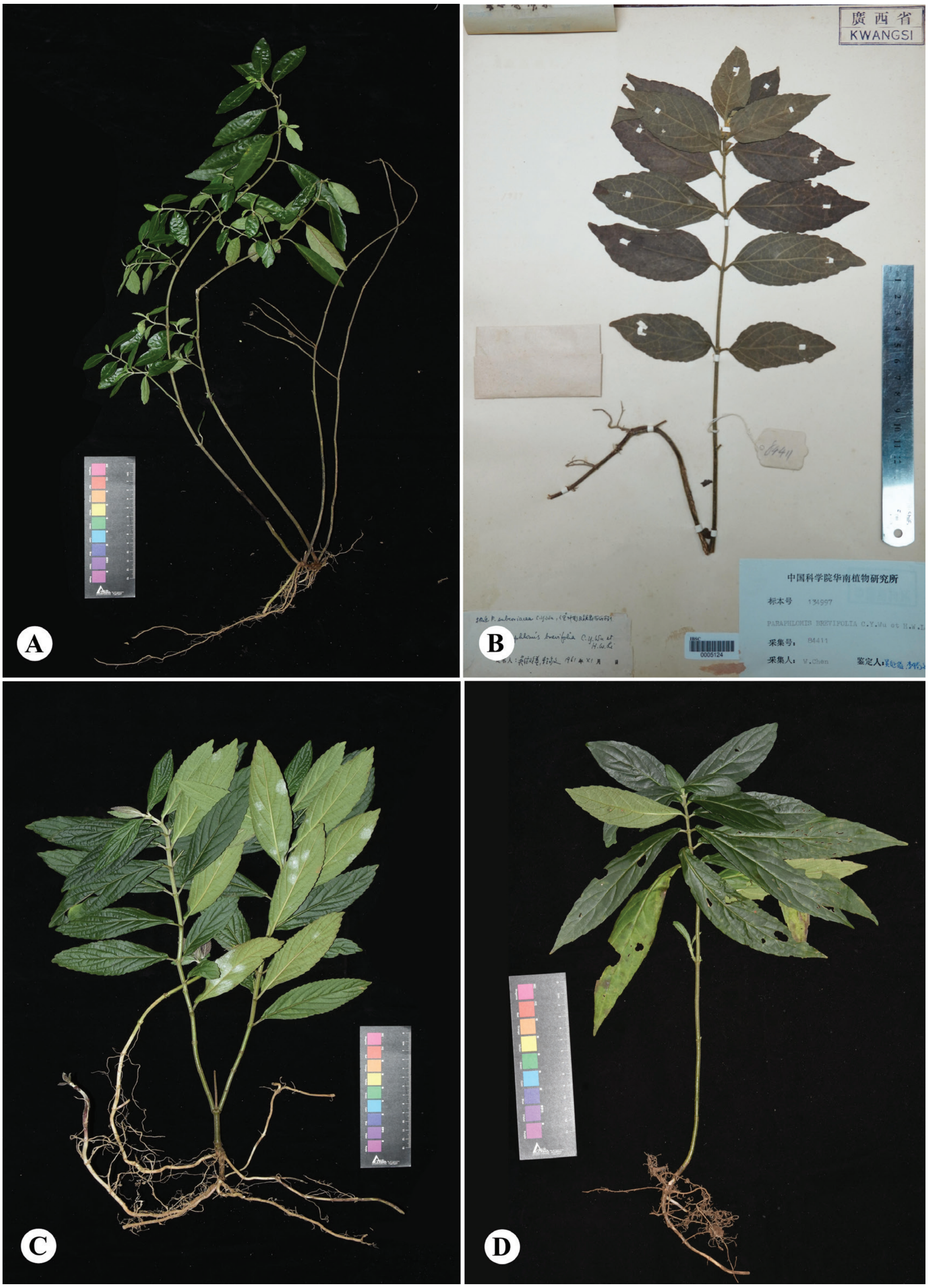

Figure 4. Morphological comparison of *Paraphlomis qingyuanensis*, *P. brevifolia*, *P. baiwanensis*, and *P. subcoriacea*. *Paraphlomis qingyuanensis* **A** plant of *P. qingyuanensis* **B** plant of *P. brevifolia* **C** plant of *P. baiwanensis* **D** plant of *P. subcoriacea* (Photographs by Wan-Yi Zhao; photographs of *P. brevifolia* from isotype *W. Chen 84411*, IBSC0005124).

densely pilose. ***Calyx*** light green, obconical, 5.2–5.7 mm long, glabrous inside, outside with densely retrorse pilose, conspicuously 10-veined; calyx teeth 5, inconspicuous, throat appearing subtruncate, calyx veins extended into wings as 2.5–3.0 mm long. ***Corolla*** 1.5–2.1 cm long, white; tube ca. 7 mm long, ca. 2 mm

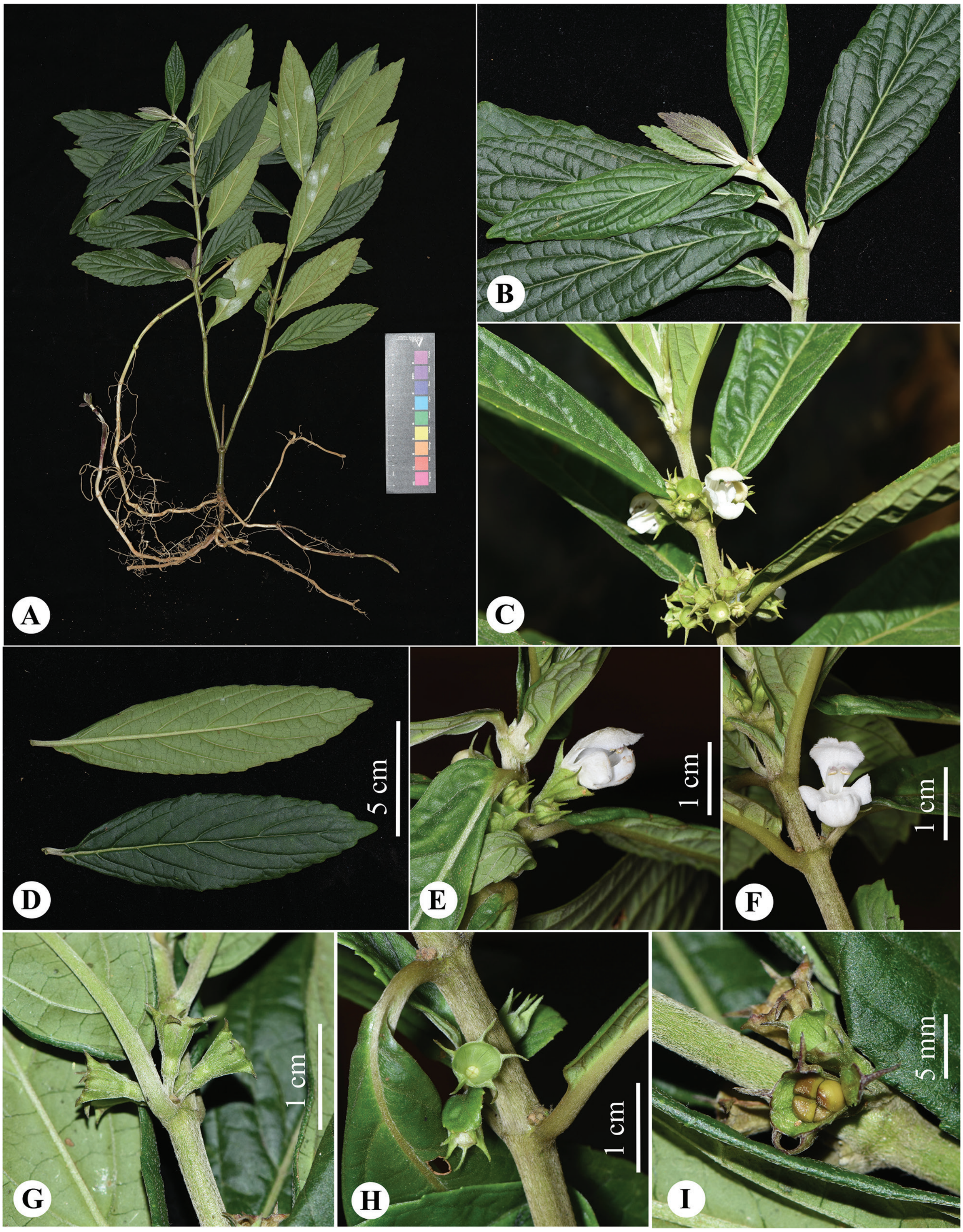

Figure 5. *Paraphlomis baiwanensis* **A** plant **B** young branch and leaves **C** flowering branch **D** leaves **E** lateral view of flower **F** front view of flower **G** lateral view of calyx **H** front view of calyx **I** seeds (Photographs: **A, B, D, G, I** by Wan-Yi Zhao; **C** by Qin-Dai Xiong; **E-F, H** by Qiang Fan).

in diam., straight, inside of throat with pubescent annulate; 2-lipped, villous outside, upper lip oblong, galeate, apex undulate, ca. 8–10 mm long, ca. 3.8–5.5 mm wide; lower lip reflexed, ca. 7 mm long, 3-lobed, medium lobe largest, suborbicular, ca. 6.5 mm long, ca. 6 mm wide, apex emarginate, lateral lobes ovate, ca.

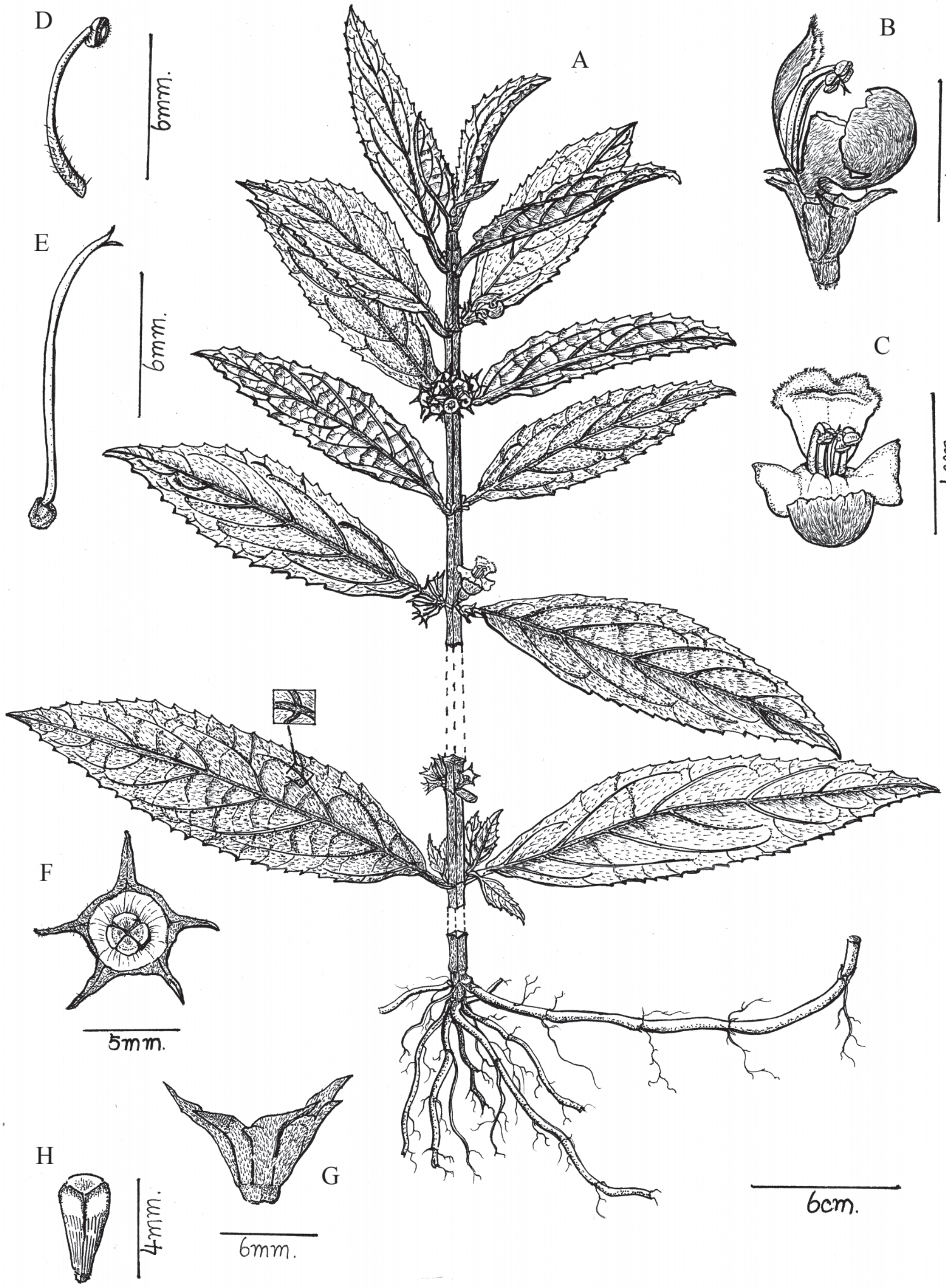

Figure 6. Line drawing of *Paraphlomis baiwanensis* **A** plant **B** lateral view of a flower **C** frontal view of corolla **D** stamen **E** style **F** front view of calyx **G** lateral view of calyx tube **H** seed (Drawn by Rong-En Wu).

4.5 mm long, ca. 3.2 mm wide, apex obtuse. ***Stamens*** 4, inserted above middle and upper of corolla tube, straight, included, filaments flat, 7–9 mm long, sparsely puberulent-villous, anther cells 2, ovoid, glabrous. ***Style*** filiform, included, glabrous, apex subequally 2-lobed, ca. 1 cm long. ***Ovary*** 4-loculed, truncate at apex. ***Nutlets*** triquetrous-oblong, ca. 3.8 mm long, apex sparsely hispid.

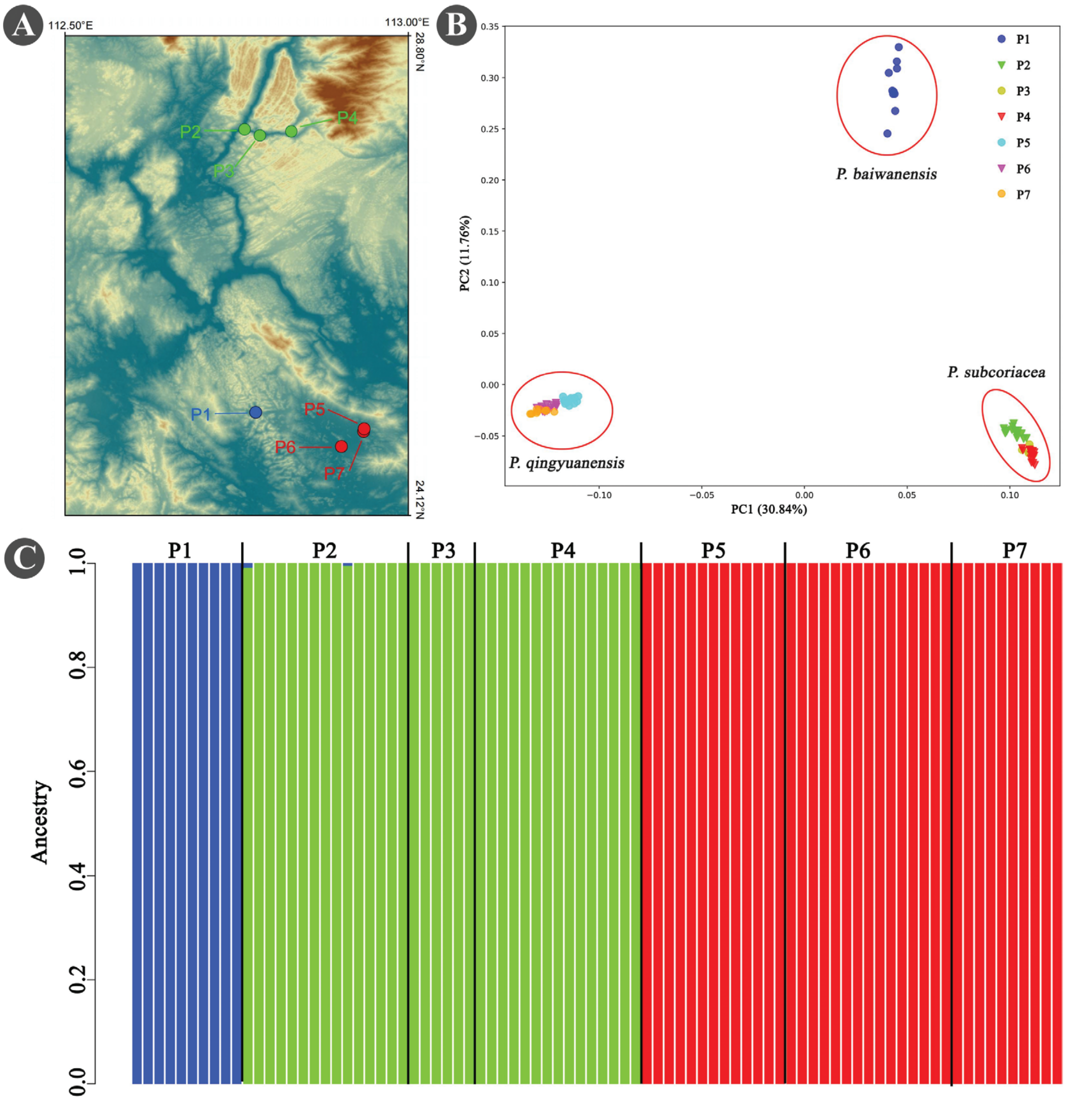

Figure 7. Geographic distribution and population genetic structure of *Paraphlomis baiwanensis* (P1), *P. subcoriacea* (P2–4), and *P. qingyuanensis* (P5–7) based on Admixture analysis **A** geographic distribution of the seven populations used for analysis **B** two-dimensional clustering of genetic variation from seven populations obtained via principal component analysis **C** Populations genetic structure result based on Admixture analysis.

Distribution, habitat and conservation status. *Paraphlomis baiwanensis* is currently known to occur only in Baiwan town, Guangdong in one population numbering less than one hundred individuals. It was observed to grow on limestone cliffs at altitudes about 300 m. Its known population was located in Qingxin Baiwan Provincial Nature Reserve of Guangdong which is well-protected. More field investigations are needed to determine its wild distribution. Therefore, the Protection level of *Paraphlomis baiwanensis* was suggested as Data Deficient (DD) based on the IUCN Red List Criteria (IUCN Standards and Petitions Subcommittee 2022).

Phenology. Flowering was observed from June to September, and fruiting from August to December.

Etymology. The specific epithet "*baiwanensis*" is derived from the type locality of the new species, i.e. Qingxin Baiwan Provincial Nature Reserve of Guangdong, Qingyuan, China.

Additional specimens examined. *Paraphlomis baiwanensis* (paratypes): CHINA. Guangdong Province: Qingyuan city, Qingxin district, Baiwan town, Hecang village, on the limestone cliff, 24°15'09.40"N, 112°46'47.32"E, alt. 310 m, 23 August 2023,*Yi-Wen Liu QYK-BW-1470* (SYS).

Paraphlomis brevifolia: CHINA. Guangxi Province: Luocheng City, 1939, *Wen Chen 84411* (IBSC0005124, isotype).

Paraphlomis subcoriacea: CHINA. Guangdong Province: Qingyuan City, Yangshan City, Chengjia country, Wuyuan village, Baizhushan, 20 June 1956, *Liang Deng 1572* (IBSC0005130, isotype); Yangshan City, Dalang Town, Chakeng village, 7 August 1936, *Liang Deng 263* (IBK00059958; IBSC0585118); Yangshan City, Lingbei Town, Xiatianxia, 24°39'48.99"N, 112°45'41.73"E, alt. 295 m, 21 December 2023, *Qiang Fan 20257* (SYS); Yangshan City, Lingbei Town, Yanzidong, 24°39'16.92"N, 112°46'59.95"E, alt. 156 m, 27 December 2023, *Qiang Fan & Qin-Dai Xiong QYK-LB-1920* (SYS); Yangshan City, Chengjia Town, Baizhuling (collection site of type specimen), 24°39'39.56"N, 112°49'45.69"E, alt. 387 m, 27 December 2023, *Qiang Fan & Qin-Dai Xiong QYK-CJ-1911* (SYS).

Acknowledgements

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Q.F conceptualized and led the project. Field investigation and sample collection were conducted by Q.D.X, Q.F, R.M.W, Y.H.Z, and Z.B.X. W.YZ, and Q.D.X examined and detailed the fine structure of the species represented in the study. The phylogenetic analysis and population genetic analysis were carried out by Y.P.C, and Q.F. The initial draft of the manuscript was prepared by W.YZ and Y.P.C. All the authors approved the final manuscript.

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Data availability

The newly-obtained ITS and ETS sequences have been submitted to the NCBI (accession number: PP897029–PP897034; PP897950–PP897955). RAD raw data was deposited to the NCBI SRA database with BioProject PRJNA1107389. All of the other data that support the findings of this study are available in the main text.

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Appendix 1

Table A1. Sequence information for all samples used in present study. A "/" indicates a missing sequence. Herbarium abbreviations are listed after the vouchers. The accession numbers marked in bold represent sequences newly generated.

Taxon	Voucher	Country	ITS	ETS
Matsumurella chinensis (Benth.) Bendiksby 1	Y. Yang OYY00316 (KUN)	Pingxiang, Jiangxi, China	MW602147	MW602117
Matsumurella chinensis (Benth.) Bendiksby 2	Y. Yang OYY00131 (KUN)	Guilin, Guangxi, China	MW602148	MW602118
Matsumurella yangsoensis (Y.Z. Sun) Bendiksby	L. Wu & W.B. Xu 10965 (IBK)	Yangshuo, Guangxi, China	MW602142	MW602112
Paraphlomis albida Hand.-Mazz. var. *albida*	A. Liu et al. LK0841 (CSFI)	Ningyuan, Hunan, China	MW602124	MW602091
Paraphlomis albida var. *brevidens* Hand.-Mazz.	Y.P. Chen EM312 (KUN)	Hezhou, Guangxi, China	MW602130	MW602098
Paraphlomis albiflora (Hemsl.) Hand.-Mazz.	C.M. Tan et al. 1806393 (JJF)	Jiujiang, Jiangxi, China	/	MW602101
***Paraphlomis baiwanensis* 1**	**Y.S. Chen et al. QY20230302 (IBSC)**	**Qingyuan, Guangdong, China**	**PP897029**	**PP897950**
***Paraphlomis baiwanensis* 2**	**Q. Fan et al. 20251 (SYS)**	**Qingyuan, Guangdong, China**	**PP897030**	**PP897951**
Paraphlomis caloneura K.J. Yan, Y.P. Chen & Y.F. Huang	W.H. Wu et al. LHT1841 (KUN)	Napo, Guangxi, China	OQ627454	OQ628080
Paraphlomis coronata (Vaniot) Y.P. Chen & C.L. Xiang 1	E.D. Liu et al. 3043 (KUN)	Emeishan, Sichuan, China	MW602137	MW602107
Paraphlomis coronata (Vaniot) Y.P. Chen & C.L. Xiang 2	C.L. Xiang 358 (KUN)	Jiangkou, Guizhou, China	MW602123	MW602090
Paraphlomis foliata (Dunn) C.Y. Wu & H.W. Li subsp. *foliata*	S.P. Chen s.n. (KUN)	Jiangle, Fujian, China	/	MW602097
Paraphlomis foliata subsp. *montigena* X.H. Guo & S.B. Zhou	Y.C. Dai s.n. (KUN)	Hangzhou, Zhejiang, China	OM836064	OM884453
Paraphlomis gracilis (Hemsl.) Kudô var. gracilis 1	A. Liu LK0931 (CSFI)	Changsha, Hunan, China	MW602134	MW602104
Paraphlomis gracilis (Hemsl.) Kudô var. *gracilis 2*	C.L. Xiang XCL1315 (KUN)	Chongqing, China	MW602141	MW602111
Paraphlomis gracilis var. *lutienensis* (Y.Z. Sun) C.Y. Wu	C.L. Xiang XCL881 (KUN)	Shibing, Guizhou, China	MW602131	MW602099
Paraphlomis hirsutissima C.Y. Wu & H.W. Li	F. Zhao & G. Chen XCL2115 (KUN)	Malipo, Yunnan, China	OQ627453	OQ628079
Paraphlomis hispida C.Y. Wu	X. Li LX200702 (GXF)	Napo, Guangxi, China	MW602132	MW602102
Paraphlomis hsiwenii Y.P. Chen & Xiong Li 1	W.H. Wu et al. DD426 (KUN)	Jingxi, Guangxi, China	OP605346	OP609841
Paraphlomis hsiwenii Y.P. Chen & Xiong Li 2	W.H. Wu et al. DD426 (KUN)	Jingxi, Guangxi, China	OP605347	OP609842
Paraphlomis intermedia C.Y. Wu & H.W. Li	X. Zhong et al. ZX16823 (CSH)	Suichang, Zhejiang, China	MW602135	MW602105
Paraphlomis javanica (Blume) Prain var. *javanica* 1	Y.P. Chen s.n. (KUN)	Kunming, Yunnan, China	MW602121	MW602088
Paraphlomis javanica (Blume) Prain var. *javanica* 2	L.B. Jia et al. JLB0029 (KUN)	Maguan, Yunnan, China	MW602143	MW602113
Paraphlomis javanica var. *pteropoda* D. Fang & K.J. Yan	X. Li 2020090501 (GXF)	Jingxi, Guangxi, China	MW602140	MW602110
Paraphlomis jiangyongensis X.L. Yu & A. Liu 1	A. Liu et al. LK1104 (CSFI)	Jiangyong, Hunan, China	MW602128	MW602095

Taxon	Voucher	Country	ITS	ETS
Paraphlomis jiangyongensis X.L. Yu & A. Liu 2	A. Liu et al. LK1104 (CSFI)	Jiangyong, Hunan, China	MW602129	MW602096
Paraphlomis kwangtungensis C.Y. Wu & H.W. Li	Q. Fan et al. 19738 (SYS)	Qujiang, Guangdong, China	PP713070	PP706067
Paraphlomis lanceolata Hand.-Mazz. 1	C.Z. Huang s.n. (KUN)	Guidong, Hunan, China	MW602145	MW602115
Paraphlomis lanceolata Hand.-Mazz. 2	A. Liu et al. LK0825 (CSFI)	Ningyuan, Hunan, China	MW602146	MW602116
Paraphlomis lancidentata Y.Z. Sun	X. Zhong et al. ZX16824 (CSH)	Suichang, Zhejiang, China	MW602136	MW602106
Paraphlomis longicalyx Y.P. Chen & C.L. Xiang	Y.P. Chen et al. EM583 (KUN)	Huanjiang, Guangxi, China	OK104771	OK104774
Paraphlomis membranacea C.Y. Wu & H.W. Li	M.S. Nuraliev 1057 (MW)	Thanh Son, Phu Tho, Vietnam	/	MW602100
Paraphlomis nana Y.P. Chen, C. Xiong & C.L. Xiang 1	C. Xiong XC21097 (KUN)	Chengkou, Chongqing, China	OM836062	OM884451
Paraphlomis nana Y.P. Chen, C. Xiong & C.L. Xiang 2	C. Xiong & H.L. Zhou XC21126 (KUN)	Wushan, Chongqing, China	OM836063	OM884452
Paraphlomis octopus Q. Fan, Y.P. Chen & Ying Liu 1	Y.P. Chen & Y. Zhao EM1391 (KUN)	Huaiji, Guangdong, China	MW602126	MW602093
Paraphlomis octopus Q. Fan, Y.P. Chen & Ying Liu 2	Q. Fan et al. 19752 (SYS)	Fengkai, Guangdong, China	PP713071	PP706068
Paraphlomis octopus Q. Fan, Y.P. Chen & Ying Liu 3	Q. Fan et al. 19760 (SYS)	Pingle, Guangxi, China	PP713072	PP706069
Paraphlomis pagantha Dunn 1	L.X. Yuan et al. s.n. (KUN)	Qionghai, Hainan, China	OP605345	OP609840
Paraphlomis pagantha Dunn 2	X.Y. Jiang et al. HN001 (SYS)	Wenchang, Hainan, China	PP713073	PP706070
Paraphlomis patentisetulosa C.Y. Wu	C.L. Su et al. XY015 (KUN)	Xinyi, Guangdong, China	OQ627455	OQ628081
Paraphlomis paucisetosa C.Y. Wu 1	X.X. Zhu s.n. (KUN)	Malipo, Yunnan, China	MW602125	MW602092
Paraphlomis paucisetosa C.Y. Wu 2	X. Li LX200704 (GXF)	Napo, Guangxi, China	MW602133	MW602103
***Paraphlomis qingyuanensis* 1**	**Q. Fan et al. QYK-HH-1904 (SYS)**	**Yingde, Guangdong, China**	**PP897031**	**PP897952**
***Paraphlomis qingyuanensis* 2**	**Q. Fan et al. 20255 (SYS)**	**Yingde, Guangdong, China**	**PP897032**	**PP897953**
Paraphlomis reflexa C.Y. Wu & H.W. Li	Z.Z. Yang et al. s.n. (HIB)	Tongshan, Hubei, China	MW602122	MW602089
Paraphlomis strictiflora J.C. Yuan, B. Chen & C.L. Xiang	B. Chen et al. CB05956 (CSH)	Yinjiang, Guizhou, China	/	OP609839
***Paraphlomis subcoriacea* 1**	**Q. Fan et al. QYK-CJ-1911 (SYS)**	**Yangshan, Guangdong, China**	**PP897033**	**PP897954**
***Paraphlomis subcoriacea* 2**	**Q. Fan et al. QYK-LB-1920 (SYS)**	**Yangshan, Guangdong, China**	**PP897034**	**PP897955**
Paraphlomis yingdeensis W.Y. Zhao, Y.Q. Li & Q. Fan	Q. Fan et al. 19013 (SYS)	Yingde, Guangdong, China	OP605348	OP609843
Phlomis fruticosa L.	Y. Tong s.n. (KUN)	Shanghai, China (cultivated)	MW602119	MW602086
Phlomoides dentosa var. *glabrescens* (Danguy) C.L. Xiang & H. Peng	Y.P. Chen EM360 (KUN)	Beijing, China (cultivated)	MW602120	MW602087

Appendix 2

Table A2. Populations information for PCA and Admixture analysis used in this study.

Population ID	Species	Voucher	GPS	Number of individual
P1	*Paraphlomis baiwanensis*	Q. Fan 20251 (SYS); Hecang village, Baiwan town, Qingyuan city, Guangdong, China	24°15'09.40"N, 112°46'47.32"E	10
P2	*Paraphlomis subcoriacea*	Q. Fan 20257 (SYS); Xiatianxia, Lingbei town, Yangshan city, Guangdong, China	24°39'48.99"N, 112°45'41.73"E	15
P3	*Paraphlomis subcoriacea*	QYK-LB-1920 (SYS); Yanzidong, Lingbei town, Yangshan city, Guangdong, China	24°39'16.92"N, 112°46'59.95"E	6
P4	*Paraphlomis subcoriacea*	QYK-CJ-1911 (SYS); Baizhuling, Chengjia country, Yangshan city, Guangdong, China	24°39'39.56"N, 112°49'45.69"E	15
P5	*Paraphlomis qingyuanensis*	Q. Fan 20255 (SYS); Hegushi, Huanghua town, Yingde city, Guangdong, China	24°13'35.7"N, 112°56'08.97"E	14
P6	*Paraphlomis qingyuanensis*	QYK-HH-1882 (SYS); Huanghua park, Huanghua town, Yingde city, Guangdong, China	24°12'03.46"N, 112°54'10.05"E	15
P7	*Paraphlomis qingyuanensis*	QYK-HH-1904 (SYS); near Hegushi, Huanghua town, Yingde city, Guangdong, China	24°13'22.71"N, 112°56'05.71"E	10