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Castanopsis corallocarpus (Fagaceae), a new species from Royal Belum (Perak) in Peninsular Malaysia

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Abstract

A new species from the Fagaceae family, *Castanopsis corallocarpus* Tan & Strijk, is described from Royal Belum State Park in Peninsular Malaysia. Here, we provide technical illustrations, colour images and a description of its conservation status and the collecting locality, in addition to a comparative analysis with other species in the region. The solitary nut of *C. corallocarpus* has a morphologically unique cupule, lined with rows of thick coral-like spines not seen in other *Castanopsis* species.

Keywords

Berangan, chinquapins, flora of Peninsular Malaysia, hill dipterocarp forest, Malayan chestnut

Introduction

Castanopsis (D.Don) Spach, is the third largest genus in Fagaceae, comprising ca. 134 species (Phengklai 2008; Li et al. 2015; Strijk 2022). Apart from limestone formations, *Castanopsis* species can be found in various habitats, ranging from lowland rainforest to

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montane forest and even harsh environments, like acidic heaths and peat swamps (Soepadmo 1972). Many seem to have narrow ecological or habitat preferences though, with species often found on ridges or crests and along margins and riverbanks. All *Castanopsis* species are medium to large trees and, like other Fagaceae species, are co-dominant in the closed canopy layer (Soepadmo 1972). The wide geographical distribution of *Castanopsis* is restricted to (sub-)tropical Asia, ranging from north-eastern India (Nepal, Bhutan and Assam), parts of eastern Asia (southern China, Korea and Japan) and southeast Asia (Indochina and Malesia). The genus has two major biodiversity hotspots, namely Indochina and Malesia (Soepadmo 1972). New taxonomic discoveries of *Castanopsis* are skewed towards Indochina with eight new species having been described in the last few decades (Phengklai 2004; Chen et al. 2010; Chen et al. 2011; Vuong and Xie 2014; Hoang et al. 2018; Mitra et al. 2019). Interestingly, no new species of *Castanopsis* has been described in Malesia over the last two decades.

The dipterocarp-dominated tropical rainforests of Peninsular Malaysia are part of the megadiverse Sundaland forest range (Myers et al. 2000). It is estimated that Peninsular Malaysia has at least 9,030 vascular plant taxa comprising 248 families and 1,651 genera (Yong et al. 2021). The Fagaceae family is an important component of the rainforest in Peninsular Malaysia, with a total of 72 species comprising four genera (i.e. *Castanopsis*, *Lithocarpus*, *Quercus* and *Trigonobalanus*). Mast fruiting phenomena in the Sundaland occur on an irregular suprannual scale (2–10 years) for many plant families, resulting in long periods of crop scarcity (Medway 1972). Unlike most mast-fruiting families, tropical Fagaceae communities fruit annually at unsynchronised times throughout the year, providing an important food source for many animals during periods of low fruit availability (Kaul et al. 1986). Species in the genus are known as '*Chinquapin*' (not to be confused with two species in the North American genus of *Chrysolepis* (Fagaceae), which are also often referred to as such). Locally, the genus is known as *berangan* in Malay or the Malayan chestnut (Corner 1988). There are 20 described *Castanopsis* species in Peninsular Malaysia and, of these, five species are endemic to Malaysia (Cockburn 1972; Soepadmo 1972; Strijk 2022).

Royal Belum State Park is in the State of Perak, in the north of Peninsular Malaysia. The rainforest of Belum consists of undisturbed and pristine lowland dipterocarp, hill dipterocarp and lower montane forests. Belum is part of the larger Belum-Temenggor Forest Complex (BTFC) which has an area of ca. 3,500 km^2. The BTFC is also part of a larger forest complex, as it shares a border with two adjacent protected areas in Thailand (Hala-Bala Wildlife Sanctuary and Bang La National Park) and forms part of the Central Forest Spine of Peninsular Malaysia. A product of the geological merger between the supercontinents of southern Gondwanaland and northern Laurasia, the landscape of BTFC is estimated to be more than 130 million years old, which is older than the Amazon and Congo Basins (Malaysian Nature Society 2005). Given its unique position within the Peninsula, the rich floristic composition of BTFC is a mixture of Thai-Burmese and Malayan flora with approximately 3000 species of flowering plants recorded, many of which are endemic to northern Peninsular Malaysia (Malaysian Nature Society 2005).

During a field expedition in Royal Belum State Park, Malaysia in July 2018, we came across a specimen with a large single nut and a unique burr that does not match any described taxa of *Castanopsis*. After examining the relevant literature on Malesian Fagaceae, we report this specimen as a new species, placed within the genus *Castanopsis*.

Taxonomy

Castanopsis corallocarpus **W.H.Tan & Strijk, sp. nov.**

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Figs 1, 2

Type material. *Holotype.* Malaysia, Sungai Tiang, Royal Belum State Park, Hulu Perak District, Perak State, elevation 417 m, 11 January 2022, *W.H. Tan TWH002*, Holotype: KEP; Isotypes: IBER [IBER00000000030; IBER00000000031]. ***Paratype.*** Malaysia, Sungai Papan, Royal Belum State Park, Hulu Perak District, Perak State, elevation 290 m, *W.H. Tan TWH003*, Paratype: KEP; IBER [IBER00000000032, IBER00000000033]. Due to the small number of individuals and precarious conservation status, detailed locality information is not released here, but can be requested from the authors.

Diagnosis. *Castanopsis corallocarpus* is a medium-sized tree. It differs from similar species by its fruits which carry unique rows of basally reinforced, blunt coral-like spines on the cupule exterior, combined with singular rounded rectangular nuts which are slightly asymmetric. Currently, the species has been found in two localities, both in Royal Belum State Park and each consisting of one individual. Several additional individuals resembling *C. corallocarpus* were reported by our field staff in Temenggor Forest Reserve, Perak, but this is awaiting confirmation. Pending further discoveries, the species appears to be locally restricted to low-mid elevation forests of the BTFC.

Description. Medium size tree, approximately 16–20 m tall, no buttresses. ***Bark*** lenticellate grey. Sapwood reddish-brown to pink. ***Branches*** glabrous, densely lenticellate, dark-brown to grey-white. ***Leaves*** simple, thin-coriaceous, papery when dried, lamina elliptic, up to (11)13–17(19) × (2)3.5–5(6) cm. Leaf apex acuminate; base cuneate, occasionally somewhat asymmetric. Margin entire. Both surfaces glabrous. Leaves dark green above and glaucous below. New shoots exhibit flushing. ***Venation*** pinnately veined, secondary venation eucamptodromous. Pairs of secondary veins 9–10(11), raised on underside of leaf. Tertiary veins scalariform, but scarcely visible on underside. ***Male and female inflorescences*** not seen. ***Peduncles*** 7–11 cm long, up to 0.4 cm in diam. at the base, glabrescent, grey-brown and densely lenticellate. ***Infructescence*** a woody spike, terminal, ranging from 9–10 cm. Fruits sessile on woody peduncle, spread out on spike and not clumped. Very few fruits make it to maturity, with typically 1–3 units fully ripening. ***Acorn*** globose or ovoid when developing, globose when mature, 3.3–3.8 × 2.7–3.3 cm, covered with 4–5 eccentric ridges with blunt thick coral-like spines, originating from the style scar looping towards the suture that runs along the spine of the fruit, surface puberulous. Cupule fully enclosing the nut,

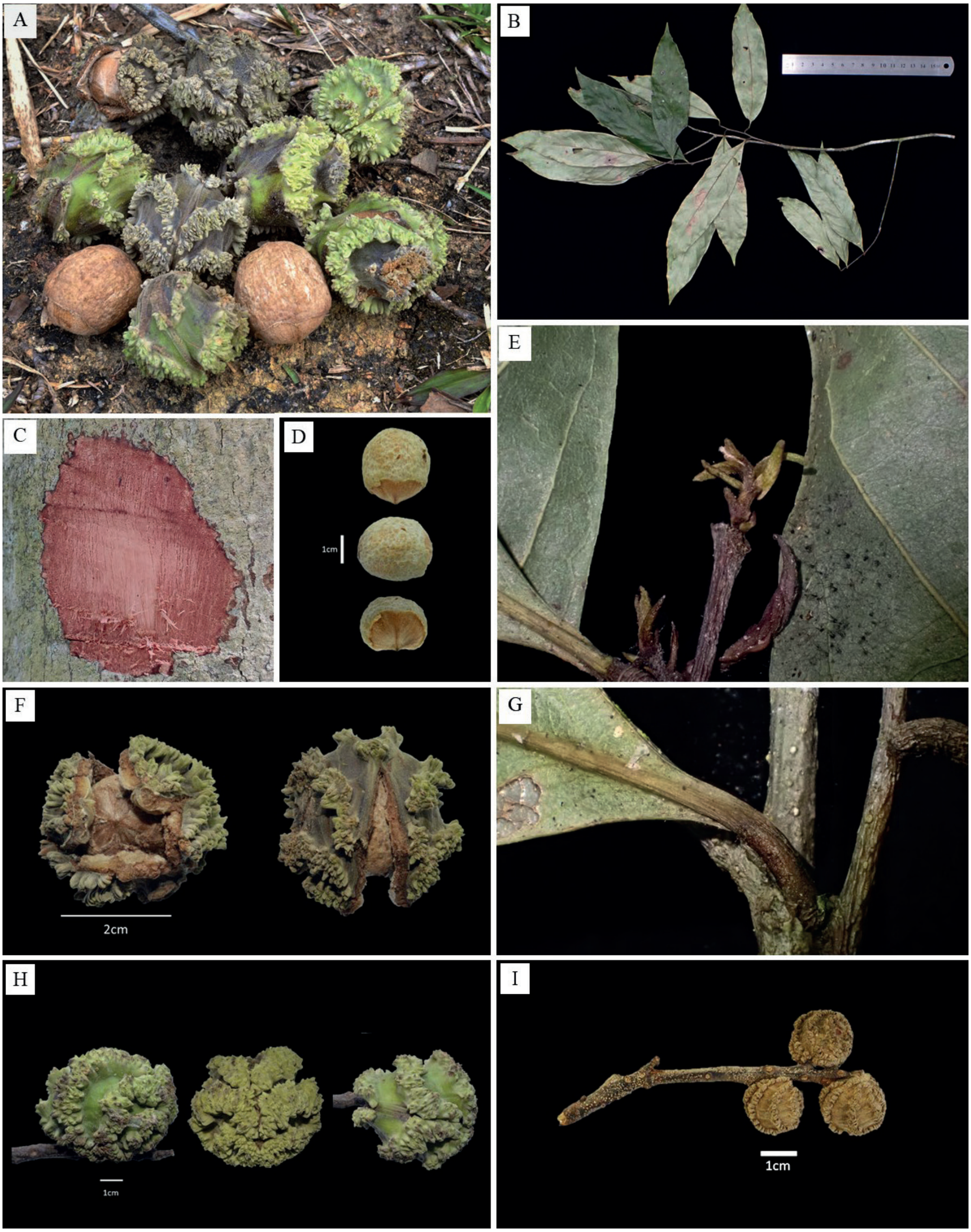

Figure 1. *Castanopsis corallocarpus* W.H.Tan & Strijk, sp. nov. *W.H.Tan TWH002* (KEP) **A** fresh fruit from field collection **B** leaves and twigs from field collection **C** bark and sapwood **D** fresh nut – top view, side view, front view **E** young emerging leaf **F** mature fruit with splitting valves on the cupule – front view, top view **G** petiole **H** fresh mature – side view, front view, top view **I** young infructescence spike. All pictures by W.H.Tan and J.S.Strijk.

Figure 2. *Castanopsis corallocarpus* W.H.Tan & Strijk, sp. nov. *W.H.Tan TWH002* (KEP) **A** habit **B** young infructescence spike **C** close-up of coral-like spine **D** mature nuts-bottom, top view and fruits-bottom, top and side view. Illustration by L. Ong.

mostly indehiscent, but occasionally dehiscent, exposing exocarp area. Fresh cupule wall bright green, suture dark grey-black. Old cupule grey-green, darker on the surface lighter on the spines. ***Nut*** 1 in each cupule, oblong in shape, flat at the bottom, 2.5–2.9 × 2.3–2.4 cm, tip pointing down. Up to 90% of the surface area of the nut comprising scar area (receptacle tissue) and up to 10% of the surface area of the nut is slightly raised and made up of vestigial exocarp layer. Nut scar pale brown-whitish with glabrous, rugose surface, adnate to the cupule, exocarp layer light brown, covered in thin layer of silvery tomentum.

Phenology. Flowering and fruiting occur annually, with flowers appearing in March and fruits maturing in July to August. Sporadic fruiting was observed in November and December 2021.

Distribution, habitat and ecology. *Castanopsis corallocarpus* is only known from the Belum-Temenggor Forest Complex, Hulu Perak District, Perak, Malaysia. Within BTFC, this species has been officially recorded in Sungai Tiang and Sungai Papan as shown in Fig. 3. This species grows in both lowland and hillside dipterocarp forests (300–450 m above sea level) with a soil type of low nutrient and high clay abundance typical of most dipterocarp forest. As Peninsular Malaysia is situated near the Equator, the climate is classified as wet equatorial, characterised by high daytime temperature and high rainfall throughout the year. According to The Malaysian Meteorological Department (2022), the District of Hulu Perak experiences an average rainfall of 1500–2000 mm annually and the daytime temperature is around 27–30 °C and 21–24 °C at night with very minimal fluctuations seasonally.

Vernacular name. Both indigenous communities of BTFC (i.e. the Jahai and Temiar) do not have a specific name in their language, instead referring to it in Malay as *Berangan*.

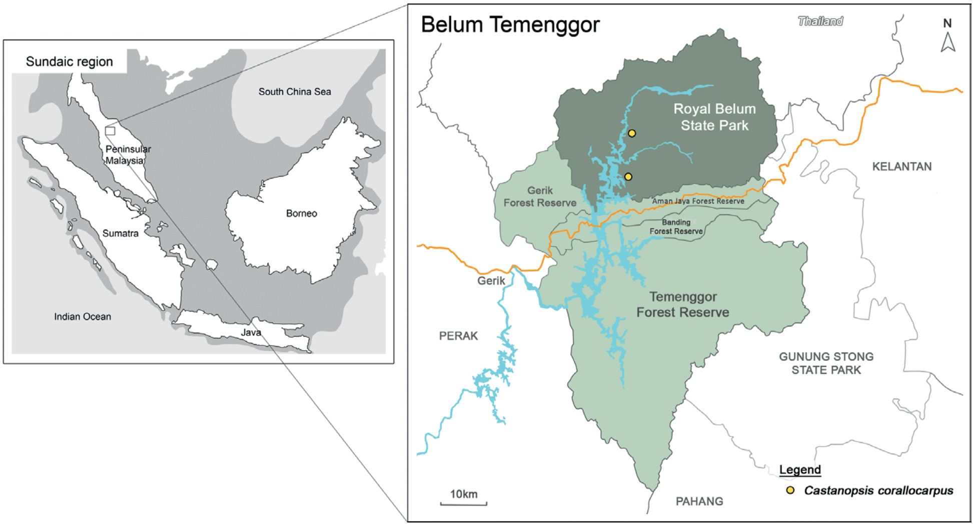

Figure 3. Collections sites of *Castanopsis corallocarpus* W.H.Tan & Strijk in Belum-Temenggor Forest Complex.

Etymology. The epithet *corallocarpus*, a noun in apposition, alludes to thick coral-like spikes arranged in undulating thickened ridges on cupule of fruit.

Conservation status. Based on the guidelines established by the IUCN Red List (IUCN 2022), we provide an initial assessment of the species here as Critically Endangered (CR B1B2ab(i,ii,iii,iv)), based on only two recorded individuals within Royal Belum State Park, small known range (BTFC) and the extensive habitat alteration and forest clearance throughout the immediately adjacent wider region. Although Royal Belum State Park is fully protected from logging, the southern part of BTFC namely Temenggor Forest Reserve is open to exploitation, further threatening to shrink its already small range.

Discussion

We report the first description of a new species, *C. corallocarpus* from BTFC, Perak, Malaysia. Peninsular Malaysia has a total of 20 species of *Castanopsis* and *C. corallocarpus* is easily distinguished by the unique rows of basally reinforced, blunt coral-like spines on the cupule. At least 10 species of *Castanopsis* species have a single nut and out of these, only two have a non-spiny cupule (i.e. *Castanopsis curtisii* King and *Castanopsis nephelioides* King ex Hook.f.). All others have either short-dense spines (*Castanopsis megacarpa* Gamble; *Castanopsis malaccensis* Gamble; *Castanopsis johorensis* Soepadmo; *Castanopsis javanica* (Blume) A.DC.; *Castanopsis tungurrut* (Blume) A.DC.; *Castanopsis ridleyi* Gamble) or thick thorns (*Castanopsis rhamnifolia* (Miq.) A.DC. and *Castanopsis acuminatissima* (Blume) A.DC.) as their main defence against seed predation.

Peninsular Malaysia and Borneo together have an estimated 103 species of Fagaceae in four genera (*Castanopsis*: 22; *Lithocarpus*: 62; *Quercus*: 18; *Trigonobalanus*: 1; Royal Botanic Gardens Kew (2021)). Numbers for the individual Bornean regions (Sabah, Sarawak, Brunei and Indonesian Kalimantan) fluctuate, depending on source and species-data considered, but it is estimated that, for the two major areas (PM and Borneo *s.l.*), endemism in Peninsular Malaysia is highest for *Castanopsis* only, whereas on Borneo, all three main genera have significant levels of endemicity (Peninsular Malaysia: C: 22%; L: 1%; Q: 0 (no endemics); Borneo *s.l.*: C: 46%; L: 91%; Q: 100% (all species endemic)). Many species in *Lithocarpus* and *Quercus* have ranges restricted to mid- or higher elevation habitat (> 600 m), which is more prevalent in Borneo (Soepadmo 1972), while occurrence and diversity of *Castanopsis* species seem to be less extremely governed by elevation, but more by the prevalence of ridges, crests, forest- and river-margins (Cockburn 1972; Soepadmo 1972).

Of the five *Castanopsis* species endemic to Peninsular Malaysia, four are found mostly in mid- to upland habitats, all first described from Perak (Larut and surrounding areas). A fifth endemic (*C. selangorensis* A.Camus) was primarily found in the lowlands, but is presumed extinct (Cockburn 1972). *Castanopsis corallocarpus*, a sixth endemic species of *Castanopsis* for Peninsular Malaysia, differs distinctly in its distribution by occurring only in the north in the lowland and hillside forest (< 450 m). Within Malaysia and the wider region, *C. corallocarpus* is unique in its combination of properties and we further outline some of the defining differences with other species in Table 1.

During our field survey, we encountered additional Fagaceae species, for example, *Lithocarpus elegans* (Blume) Hatus. ex Soepadmo, *Lithocarpus wrayi* (King) A.Camus, *Lithocarpus* cf. *kingianus* (Gamble) A.Camus, *Lithocarpus hendersonianus* A.Camus., *Lithocarpus macphailii* (M.R.Hend.) Barnett, *Lithocarpus sundaicus* (Blume) Rehder, *Castanopsis inermis* (Lindl.) Benth. & Hook.f., *Castanopsis malaccensis* and two (as of yet) unidentified species of *Quercus*.

Few studies have been done on Fagaceae in Peninsular Malaysia in the last decade. The discovery of *C. corallocarpus* in Peninsular Malaysia highlights the continued potential of new findings for this family in the region. Moreover, with only two recorded individuals of *C. corallocarpus* in BTFC, further assessment is needed to determine the extent of the species distribution for its conservation. This also extends to other Fagaceae species from *Castanopsis* and *Lithocarpus* in which many are data-defficient on the IUCN Red List (IUCN 2022).

Table 1. Morphological differences between *C. corallocarpus* and other species of *Castanopsis* of the Peninsular region.

Characters	***C. corallocarpus*** **W.H.Tan & Strijk**	***C. inermis*** **(Lindl.) Benth. & Hook.f.**	***C. purpurea*** **Barnett**	***C. pierrei*** **Hance**	***C. rhamnifolia*** **Miq. A.DC.**
1. Cupule surface	Cupule with basally reinforced, blunt coral-like spines arranged in continuous ridges. Ridges in young fruits often terminate only a few mm apart, resulting in hollow enclosures protecting the exterior inner cupule.	Cupule sparsely covered with simple, short, curled thorns set in 3–5 lines.	Cupule sparsely covered with woody, branched, curved spines.	Cupule sparsely covered with woody, branched, curved spines.	Cupule covered with tufted, erect, simple thorn-like structures.
2. Number of cupule valves	3(–4)	2(–4)	"dehiscent", #valves unreported	"dehiscent", #valves unreported	3– (4?), or indehiscent
3. Number, size of acorns (*l* × *w*)	1, 3.3–3.8 cm × 2.7–3.3 cm.	(1)2–3, 1.5–2.5 cm × 1.5–3.5 cm.	1–3 (4), 4.5–6 cm in diam.	1–3 (4), 4–6 cm in diam.	1, 1–1.5 cm × 1–1.5 cm.
4. Acorn shape (ripe), position	Acorn globose, sessile and solitary.	Irregularly globose, sessile and clustered (sometimes fused).	Globose, stalked and solitary.	Irregularly globose or bilobed, semi-stalked to sessile and solitary.	Asymmetrically depressed subglobose, sessile solitary or in pairs.
5. Acorn surface	Pustulated	Pustulated	Unreported	Pustulated	Unreported
6. Nut wall	Free	Fused	Free	Free	Fused
7. Nut indumentum	Finely adpressed silver hairs on the umbo.	Finely adpressed silver hairs on the umbo.	Sparsely covered with adpressed white hairs.	Dense white hairs, only around umbo.	Unreported.
8. Nut shape, size and scar (*l* × *w*)	Rectangular and flattened at the base, 2.5–2.9 cm × 2.3–2.4 cm, scar 2.3–2.5 × 2.3–2.4 cm.	Ovoid, emarginate, concave at the bottom, 1 cm × 1 cm, scar 0.2–0.3 × 1 cm.	Ovoid and asymmetrically compressed, 2–3 cm × 1 cm, scar unreported.	Ovoid, asymmetric and slightly curved, 3 × 1.5 cm, scar unreported.	Asymmetrically depressed subglobose, 3.5–4 cm × 2–3 cm, scar basal 1 cm diam.
9. Leaf shape, size (*l* × *w*)	Elliptic, with cuneate base and acute apex, (11)13–17(19) × (2)3.5–5(6) cm.	Obovate, obovate-oblong, oblong or lanceolate, 7–17 × 5–7 cm.	Elliptic, oblong or obovate, 10–25 × 3.2–6.3 cm.	Lanceolate or oblong, 10–20 × 3–6 cm.	Oblong, elliptic or obovate, 10–20 × 3.5–8 cm.

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RESEARCH ARTICLE

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A taxonomic revision of *Cynanchum thesioides* (Apocynaceae) with two new synonyms

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Abstract

Cynanchum thesioides, a species widely distributed in north-eastern Asia, is revised to include two new synonyms: *Vincetoxicum sibiricum* f. *linearifolium*, described from Shandong, China in 1877, but long neglected and *Cynanchum gobicum*, previously believed to be endemic to Mongolia. Typification for *C. thesioides* and all its synonyms is given, including lectotypification of *V. sibiricum* var. *australe* and *V. sibiricum* f. *linearifolium*. An updated description, three figures showing the diverse habitats, habits and variation in morphological characters, and a general distribution map are also provided.

Keywords

Asclepiadeae, China, Mongolia, taxonomy, typification, *Vincetoxicum*

Introduction

Cynanchum L. is a large genus with more than 200 species worldwide (Endress et al. 2018). Recent morphological, chemical and molecular studies (Qiu et al. 1989; Liede 1996; Liede and Täuber 2002; Khanum et al. 2016) have significantly altered the circumscription of *Cynanchum*, resulting in the inclusion of several small genera and the transfer of several species to *Vincetoxicum* Wolf.

One of the most widespread species in the genus, *Cynanchum thesioides* (Freyn) K. Schum., is found in temperate NE Asia, from eastern Kazakhstan, Mongolia, northern China or the Korean Peninsula (Fig. 1). It is distinguished by the erect/semi-erect

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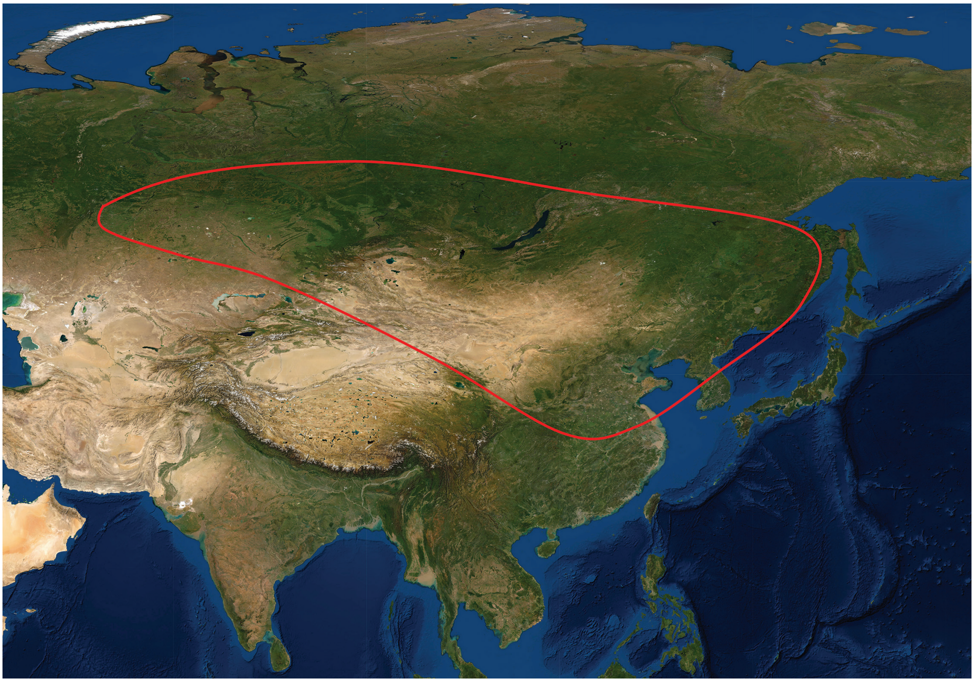

Figure 1. Distribution map of *Cynanchum thesioides* in north-eastern Asia. The base map was downloaded from the Microsoft Bing Satellite Map via QGIS 3.26 (https://qgis.org/). Map data 2022 (C) Microsoft.

stems, cuneate to rounded leaf bases and a 1-seriate corona, while most other species in *Cynanchum* display a climbing habit, cordate leaf bases and 2-seriate coronas (Khanum et al. 2016; Endress et al. 2018). As a result, some taxonomists placed it in *Vincetoxicum* (e.g. Freyn 1890; Pobedimova 1952; Kovtonyuk 1997). However, all species of the recently recircumscribed *Vincetoxicum* have clear, not white latex (Liede-Schumann et al. 2016; Endress et al. 2018), whereas the sap of *C. thesioides* is white. It had even been placed in its own genus, *Rhodostegiella* C.Y. Wu & D.Z. Li (Li et al. 1990), because of its distinctive chemical constituents. Recent molecular studies confirmed its position in *Cynanchum* (Khanum et al. 2016; Hu et al. 2020; Kang et al. 2021). It is a traditional medicinal and edible plant used by the Chinese (Tsiang and Li 1977); records of its usage can be traced back nearly one thousand years (Wu 2017: 778). Moreover, it provides good fodder resources for domestic animals (Huang and Liu 1992).

During taxonomic studies of *Cynanchum* from Central and East Asia, we found that the distinctions between *C. thesioides* and *C. gobicum* (Grubov) Grubov are questionable. The latter was considered to be endemic to Mongolia (Grubov 2000, 2002; Urgamal et al. 2014), or subendemic, meaning that it could be found in the neighbouring countries near their borders with Mongolia (Urgamal 2017). In fact, *C. gobicum* is very likely to be found in Nei Mongol (Inner Mongolia), China, since one of the localities listed by Grubov (2002: 109) lies about 5 kilometres from the border of Mongolia with China. In this study, we aim to confirm the identity of *C. gobicum* and provide an updated taxonomy of *C. thesioides*.

Materials and methods

We examined more than 1600 specimens in 73 herbaria (ABGI, ANUB, AU, B, BJFC, BJTC, BM, BNU, BRNM, BRY, CDBI, CQNM, E, FSU, GXMG, GXMI, GZAC, HBNU, HEAC, HENU, HHBG, HIB, HIMC, HNWP, HSIB, IATM, IBK, IBSC, IFP, JJF, JLSLKY, K, KUN, KUZ, L, LBG, LE, LINN, M, MO, MW, NAS, NEAU, NEFI, NMAC, NMTC, NY, P, PE, PEY, PRC, QFNU, QYTC, RSA, S, SDFGR, SM, SVER, SXTCM, SXU, SYAU, SZG, TI, TIE, VBGI, WA, WAG, WH, WIS, WUK, XBGH, YAK and Z; herbarium abbreviations follow Thiers 2022 [continuously updated]). Fresh material was collected from the National Botanical Garden (South Garden), Beijing. Fresh flowers and those kept in FAA were examined under a stereomicroscope Nikon SMZ25. This enabled us to check the micromorphology of trichomes and floral characters. Digital images from online databases were checked: the Chinese Virtual Herbarium (CVH; https://www.cvh.ac.cn/), the Integrated Digitized Biocollections (iDigBio; https://www.idigbio.org/), the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), the JACQ specimen database (https://www.jacq.org/), the JSTOR Global Plants database (https://plants.jstor.org/), the BioPortal Naturalis collections (https://bioportal.naturalis.nl/) and the online herbarium catalogues of LE, P and S were examined. More than 2000 photos from the Plant Photo Bank of China (PPBC; http://ppbc.iplant.cn/sp/27237 [accessed in October 2022]) were also checked. A full list of specimens and selected observations examined is given in Suppl. material 1.

Taxonomy

Cynanchum thesioides **(Freyn) K. Schum. in Engl. & Prantl, Nat. Pflanzenfam. 4 (2): 252 (1895).**

≡ *Vincetoxicum thesioides* Freyn, Oesterr. Bot. Z. 40: 124 (1890) ≡ *Cynanchum sibiricum* var. *thesioides* (Freyn) Kom., Trudy Imp. S.-Peterburgsk. Bot. Sada 25(1): 282 (1905) — Holotype: Russia, wüste Orte um Nerczynsk, July-Aug. 1888, *K.F. Karo 127* (BRNM [15481/36], ex herb. J. Freyn) — Fig. 2A.

= *Asclepias sibirica* L., Sp. Pl.: 217 (1753) ≡ *Cynanchum sibiricum* (L.) R. Br., Mem. Wern. Nat. Hist. Soc. 1: 48 (1811), nom. illeg., non Willd. (1799). ≡ *Vincetoxicum sibiricum* (L.) Decne. in DC, Prodr. 8: 525 (1844) ≡ *Vincetoxicum sibiricum* var. *boreale* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 23: 355 (Mar 1877), nom. illeg., as '*borealis*', ≡ *Cynanchum sibiricum* var. *boreale* (Maxim.) Kom., Trudy Imp. S.-Peterburg sk. Bot. Sada 25(1): 281 (1905), nom. illeg. ≡ *Antitoxicum sibiricum* (L.) Pobed., Fl. USSR 18: 707–708, pl. 38: 1 (1952) ≡ *Alexitoxicon sibiricum* (L.) Pobed., Taxon 11: 174 (1962) ≡ *Rhodostegiella sibirica* (L.) C.Y. Wu & D.Z. Li, Acta Phytotax. Sin. 28(6): 466 (1990) — Lectotype (designated by Grubov [2000: 138]): Russia, Siberia, *Gmelin s.n.*, Herb. Linn. No. 310.35 (LINN; image available at https://linnean-online.org/2155/ and https://plants.jstor.org/stable/10.5555/al.ap.specimen.linn-hl310-35).

= *Vincetoxicum sibiricum* var. *australe* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 23: 355 (Mar. 1877), "*australem*" ≡ *Cynanchum sibiricum* R. Br. var. *australe* (Maxim.) Kom., Trudy Imp. S.-Peterburgsk. Bot. Sada 25(1): 292 (1905). ≡ *Cynanchum thesioides* var. *australe* (Maxim.) Y. Tsiang & P.T. Li, Acta Phytotax. Sin. 12: 101 (1974) ≡ *Rhodostegiella sibirica* var. *australis* (Maxim.) C.Y. Wu & D.Z. Li, Acta Phytotax. Sin. 28: 466 (1990) — Lectotype (designated here): China. Nei Mongol, "Mongolia occidentalis, Terra Ordos, valle fl. Hoang-ho", 24 Jul – 5 Aug 1871 (fl.), *N.M. Przewalsky 298* (LE [LE01036690]); isolectotypes: K [000872724], LE [LE01036688, LE01036689], P [P03872677] — Fig. 2B.

= *Vincetoxicum sibiricum* f. *linearifolium* Debeaux, Actes Soc. Linn. Bordeaux 31(4): 235 (1877), "*linearifolia*", syn. nov. — Lectotype (designated here): China, Shandong Prov., Yantai City, "Tchéfou dunes", [1860], *O. Debeaux 79* (P [P03872669], ex herb. O. Debeaux) — Fig. 2C.

= *Cynanchum sibiricum* var. *gracilentum* Nakai & Kitag., Rep. First Sci. Exped. Manch. sect. 4, 1: 43 (1934). ≡ *Vincetoxicm sibiricum* var. *gracilentum* (Nakai & Kitag.) Kitag., Rep. Inst. Sci. Res. Manchoukuo 4(7): 85 (1940) — Holotype: China, Hebei Prov., Chengde, 19 Aug 1933 (fl.), *T. Nakai, M. Honda & M. Kitagawa s.n.* (TI [TI00204077]) — Suppl. material 2.

= *Cynanchum sibiricum* var. *gracilentum* Nakai & Kitag. f. *hypopsilum* Nakai & Kitag., Rep. First Sci. Exped. Manch., sect. 4, 1: 43 (1934) ≡ *Vincetoxicm sibiricum* f. *hypopsilum* (Nakai & Kitag.) Kitag., Rep. Inst. Sci. Res. Manchoukuo 4(7): 85 (1940) — Holotype: China, Hebei Prov., Chengde, 19 Aug 1933 (fl. & fr.), *T. Nakai, M. Honda & M. Kitagawa s.n.* (TI [TI00204078]) — Suppl. material 3.

= *Cynanchum sibiricum* var. *latifolium* Kitag., Rep. First Sci. Exped. Manch. sect. 4, 4: 90, (1936) ≡ *Cynanchum sibiricum* var. *australe* f. *latifolium* (Kitag.) Kitag., Lineam. Fl. Mansh. 363 (1939) ≡ *Vincetoxicm sibiricum* f. *latifolium* (Kitag.) Kitag., Rep. Inst. Sci. Res. Manchoukuo 4(7): 85 (1940) — Holotype: China, Liaoning Prov., Dalian, Lingshui, Lingshui Temple, 15 Aug 1930 (fl.), *M. Kitagawa s.n.* (TI [TI00204080]) — Suppl. material 4.

= *Cynanchum gobicum* Grubov, Novosti Sist. Vyssh. Rast. 32: 135 (2000), non *C. lanceolatum* Poir. (1811), syn. nov. ≡ *Antitoxicum lanceolatum* Grubov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. (Leningrad) 17: 21 (1955) ≡ *Vincetoxicum lanceolatum* (Grubov) Grubov, Novosti Sist. Vyssh. Rast. 21: 208 (1984) — Holotype: Mongolia, Dzun-Saikhan mountains, commencement of northern trail along the road from Dalan-Dzadagad to pass through Gurban-Saikhan, 22 Jul 1943 (fl.), *A. Yunatov 12902* (LE [LE01036905]) — Fig. 2D.

Description. Perennial suffrutescent sometimes lianescent herbs, usually densely shortly pubescent throughout, with white latex, arising from monopodial slightly woody creeping slender brown rhizome up to 3 m × 3 mm, with wiry horizontal offshoots. ***Stem and branches*** straight or twining above, green to dark purple; when straight 10–40 cm long, erect or ascending, simple or much divaricately branched from base, with internodes 2–30 mm long; when twining up to 2 m long, little branched, with internodes 4–8 cm long. ***Leaves*** opposite or sometimes subopposite, rarely 3- or 4-whorled, with petioles 0.5–10 (–12) mm long or subsessile; blade green, thin, linear, narrowly lanceolate, oblong-lanceolate or occasionally broadly lanceolate, 2–10.5 × 0.1–2 (–2.3) cm, apex shortly acute, obtuse or acuminate, rarely rounded, base slightly oblique, attenuate, cuneate, truncate or rounded, with colleters at middle of leaf base, margins entire, ciliolate, often revolute; mid-vein elevated abaxially, lateral veins obscure; both surfaces densely pubescent, sometimes glabrate, except the mid-veins on lower surface. ***Inflorescences*** alongside the leaf axils to terminal, with 1–10 fragrant flowers, shortly umbel- to raceme-like; ***peduncles*** 1–10 (–50) × 0.5–1.5 mm, puberulent; ***pedicels*** 1.2–10 × 0.2–0.6 mm, puberulent. ***Sepals*** ± half length of corolla, oblong, triangular or lanceolate, 1–2.8 × 0.3–0.8 mm, puberulent, ciliate, apex obtuse, acute or acuminate. ***Corolla*** white or greenish-white to yellow, 3–5 × 3–8 mm, usually glabrous, sometimes sparsely puberulent on dorsal surface and inside tube, rarely densely puberulent on both surfaces; ***tube*** 0.5–1.5 mm long; ***lobes*** 4.3–5.2 × 0.8–1.5 mm, narrowly triangular, lanceolate, oblong or oblong-ovate, apically twisted clockwise, apex ± acute or obtuse, sometimes retuse. ***Corona*** of 5 slightly fleshy lobes partly fused at bases, cupular, 0.8–1.8 mm long, shorter or longer than gynostegium; ***tube*** shorter than anthers, 0.3–0.7 mm long; ***lobes*** oval, triangular-lanceolate to linear, apices erect or incurved, acute, acuminate, obtuse or rounded, 0.5–1.4 mm long, sinuses between theses each with or without a minute triangular tooth. ***Follicles*** paired or single, ovoid-fusiform, ventricose, 4–10 × 0.8–2.5 cm, apex obtuse or attenuated, smooth or colliculate, puberulent; ***seeds*** reddish-brown, 5–10 × 3–5 mm, with white coma 1–2.4 cm long attached to micropylar end — Figs 3–5.

Vernacular names. Chinese: 地梢瓜 (dì shāo guā); Mongolian: Sibir temeen khukh; Korean: 양반풀 (Yang-ban-pul); Russian: Ластовень сибирский (Siberian Lastoven).

Distribution. China, Kazakhstan, North Korea, South Korea, Mongolia, Russia — Fig. 1.

Habitat. Thickets and/or grasses on mountain-slopes, dry valleys, sand-dunes, grasslands, roadsides, flood plains, river banks, farm land; 0–3200 m alt. — Fig. 3.

Phenology. Flowering March–September; fruiting June–October.

Notes. In some online databases, such as World Flora Online (WFO 2022), Plants of the World Online (POWO 2022), the 'accepted' name is *Vincetoxicum sibiricum* (L.) Decne. This is incorrect because phylogenetic studies confirmed this species is a member of *Cynanchum* and far from *Vincetoxicum* (Khanum et al. 2016; Hu et al. 2020; Kang et al. 2021). In addition, many online databases (Freiberg et al. 2020; Hassler 2022; POWO 2022; WFO 2022; WCVP 2022) give *C. longifolium* Decne. and/or *C. sibiricum* Willd. var. *triangularilobatum* Rassulova & B.A. Sharipova as synonyms of *C. thesioides*. They should be excluded because their types have cordate leaves and they, therefore, belong to *Cynanchum acutum* subsp. *sibiricum* (Willd.) K.H. Rech. (Tsiang and Li 1977; Rasulova and Sharipova 1984).

Freyn (1890) based *V. thesioides* on *Ferdinand K. Karo 127* with flowers and young fruits collected during July and August 1888 from desert places around Nerczynsk. Although Freyn did not give a direct indication of the herbarium, he had seen three sets of Karo's specimens (Freyn 1889: 356): the first set kept in his private herbarium which was purchased in 1905 by the Moravian Museum in Brno (BRNM, Sutorý 2012); the second set kept by Ladislav Josef Čelakovský in the National Museum in Prague (PR); the last set kept by Josef Emmanuel Kabát which is now also kept at PR

Figure 2. Type specimens **A** holotype of *Cynanchum thesioides* (BRNM [15481/36]) **B** lectotype of *Vincetoxicum sibiricum* var. *australe* (LE [LE01036690]) **C** lectotype of *Vincetoxicum sibiricum*. f. *linearifolium* (flowering plants, P [P03872669]), with fruiting plants (syntype, P [P00877371]) mounted on the same sheet: **D** holotype of *Antitoxicum lanceolatum* (LE [LE01036905]).

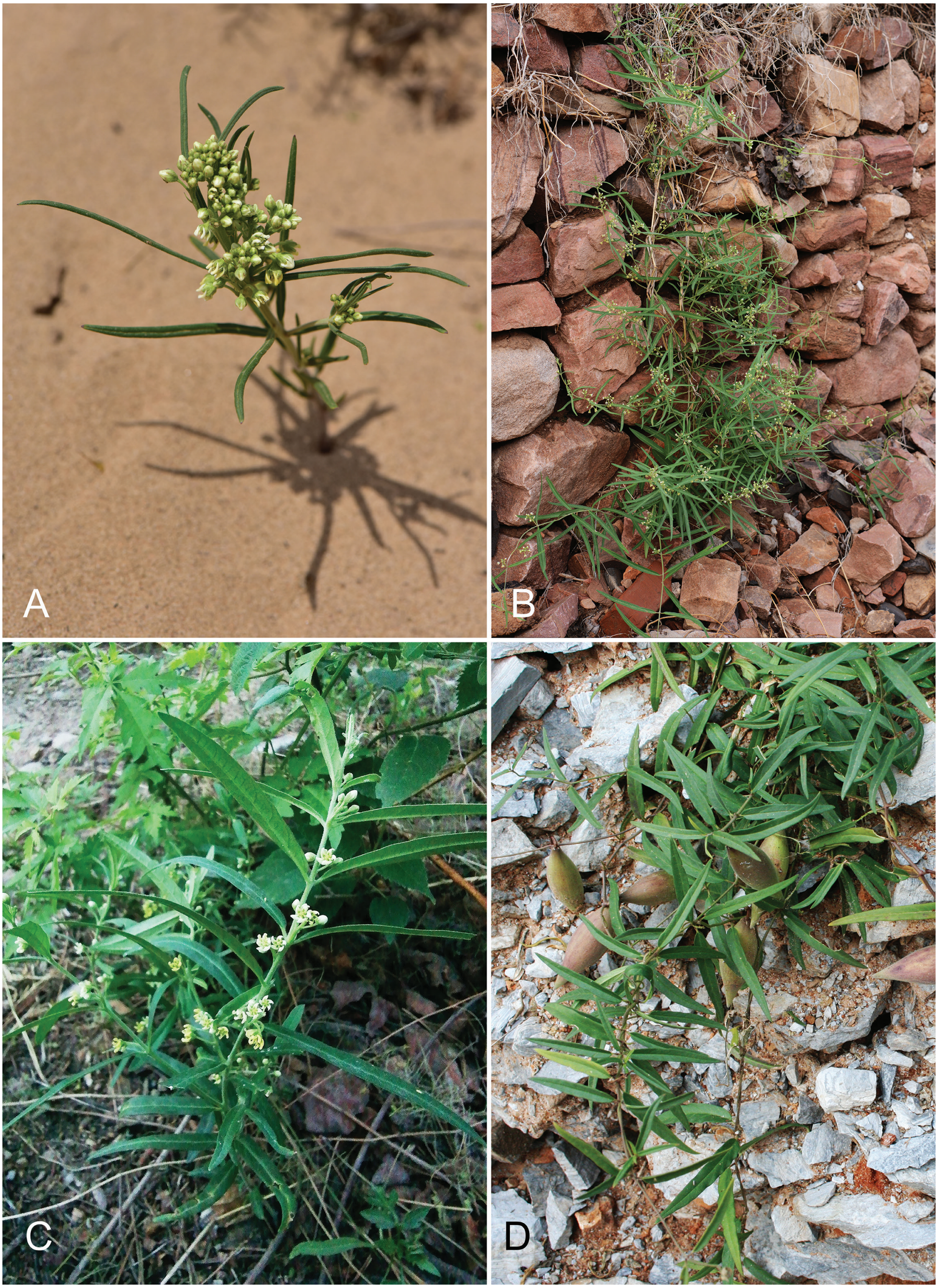

Figure 3. *Cynanchum thesioides* **A** erect plant growing in desert **B** scandent plant climbing a stony wall **C** erect plant growing on mountain slope **D** prostrate plant on roadside wasteland **A** by Xin-Xin Zhu in Xilinhot, Nei Mongol **B, D** by Lei Xie in Beijing **C** from *C.F. Zhang 5588* (HIB) and photographed by Cai-Fei Zhang in Beijing.


A
2 cm
B
2 cm
C
1 cm
a b c d e f g h i j k l m
D
2 cm
G
1 mm
E
5 mm
F
5 mm
H
1 mm
K
1 mm
I
2 mm
J
1 mm
L
1 mm
M
1 mm

(Stafleu and Cowan 1979: 482). The only specimen bearing the number *127* is that in BRNM (Fig. 2A) and is, thus, the holotype of *V. thesioides*. Another two specimens in PR (PR793598, PR793599) collected by Karo do not have the number *127* on them, but were also annotated by Freyn as *Vincetoxicum thesioides*. They may be isotypes, but equally, they may have been other gatherings made by Karo on different dates or in another place near Nerczynsk. Consequently, they are not considered here to be isotypes.

Maximowicz (1877) mentioned in the protologue of *V. sibiricum* var. *australe* a collection by *N.M. Przewalsky* from the Ordos land towards the Yellow River ("Hoang-ho") in Nei Mongol, China and a collection(s) from Beijing without any further information. We have selected Przewalsky's specimen at LE as the lectotype following unpublished annotations by N. Imkhanitzkaya (Fig. 2B).

In the protologue of *Vincetoxicum sibiricum* f. *linearifolium* Debeaux, specimens collected by Debeaux from "sables maritimes de la presqu'ile de Yan-tai" and "dunes de Fou-chan-yen" with flowers on 14 July and fruits on 23 August [1860] were cited. We have found five sheets of Debeaux's specimens at P. Of these, one sheet with flowering plants (barcode P03872669) and fruiting plants (barcode P00877371) was annotated by Debeaux as "*Vincetoxicum sibiribicum* Dec. forma *foliis augustioribus*". We designate the flowering plants from this sheet as the lectotype (Fig. 2C).

Selected specimens examined. **China:** Beijing, *C.F. Zhang 5588* (HIB); Shandong, *C.Y. Chiao 2878* (E, IBK, IBSC, NAS, PE); Shaanxi, *Y.W. Tsui 10389* (CDBI, KUN, PE); Sichuan, *Guangyuan Exped. 6001* (SM); Xinjiang, *G.L. Zhu et al. 6689* (NAS, PE, WUK). **Kazakhstan:** Lake Zaysan, *Anonymous s.n.* (E, P). **North Korea:** Pyongyang, *Pyongyang Bot. Garden s.n.* (PE [01572927]); Nampo, *U. Faurie 736* (P). **Mongolia:** Arkhangai, *I.A.Gubanov 341* (MW); Dornod, *I.A. Gubanov 5729* (MW); Dornogovi, *I.A. Gubanov 5196* (MW); Govisümber, *G.N. Ogureeva s.n.* (MW); Khentii, *I.A. Gubanov 10122* (MW). **Russia**: Far East. Amur, *E. Boyko & V. Starchenko s.n.* (RSA [RSA0286750]); Zabaykalsky, *F.K. Karo 359* (E, P, WIS). Siberia. Altai Republic, *T.S. Elias et al. 4394* (NY, PE, RSA); Irkutsk, *H.H. Iltis et al. 252* (NY, WIS); Tuva, *V.V. Nikitin et al. 1268(2)* (PE) [For a full specimens examined see Suppl. material 1].

Figure 4. *Cynanchum thesioides* **A** erect plant with part of horizontal rhizome **B** scandent plant with part of horizontal rhizome **C** leaves, **a, b, i** from the holotype of *Cynanchum sibiricum* var. *gracilentum* (TI [00204077]) **c, d** from *I.A. Gubanov & Grubov 243* (MW [MW0187936]) which had been identified as *C. gobicum*; **j** from *I.A. Gubanov 3322* (MW [MW0187934]) which had been identified as *C. gobicum* **k** from the holotype of *C. gobicum* (LE [LE01036905]) **l** from *G.M. Zhang et al. 070714* (BJFC [BJFC00062407]) **m** from the holotype of *Cynanchum sibiricum* var. *latifolium* (TI [00204080]) **D** horizontal rhizome and root **E** inflorescence with buds **F** flowering inflorescence **G** bud with glabrous corolla **H** bud with puberulent corolla **I** flower with corona shorter than anther appendages (side view) **J** flower with corona longer than anther appendages (front view) **K** flower with corona shorter than anther appendages (vertical view) **L** flower with glabrous corolla and corona longer than anther appendages (vertical view) **M** part of flower showing two corolla lobes adaxially densely puberulent (vertical view) **B, C** (**e, f**), **E, G, I, K** and **L** from *Meng Wei in C.F. Zhang 6791* (HIB) **F** from *C.F. Zhang 5588* **H** from *X.Y. Liu & F. Zhao 00283* (HIB [0101691]) **M** from *K.T. Fu 206* (HIB [0101693]) **A** by Shun-Bang Zhao in Xining; **B, C** (**e, f**), **E, I, K** and **L** by Miao Liao **C** (**g, h**) in Xilinhot and **J** in Beijing by Xin-Xin Zhu **D** by Jia-Hao Shen in Nanjing **F, G** and **H** by Cai-Fei Zhang **M** by Ye-Chun Xu in Beijing.

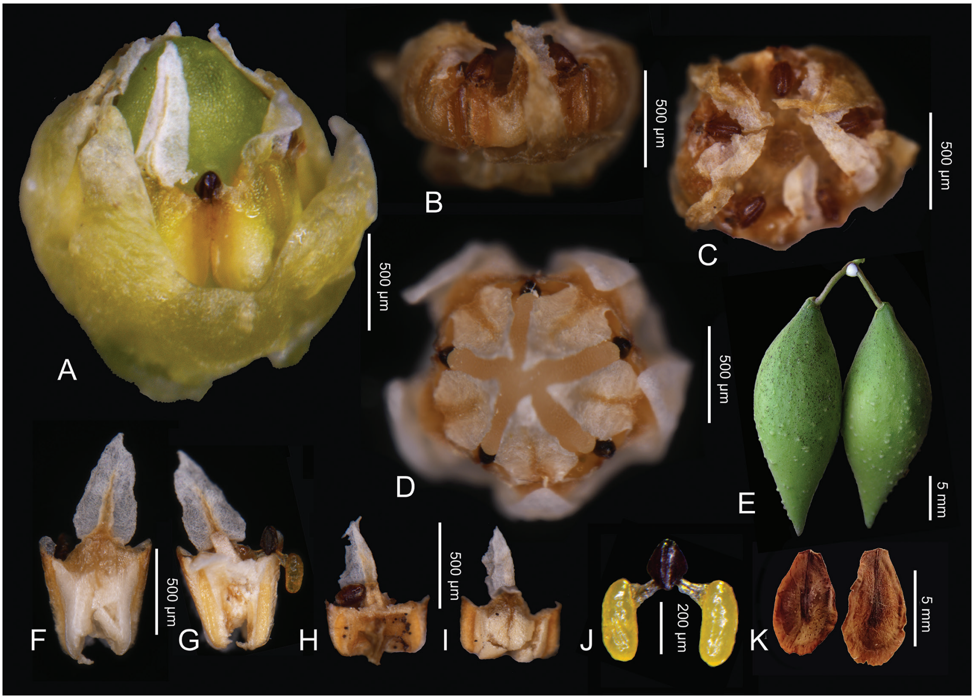

Figure 5. *Cynanchum thesioides* **A** corona and gynostegium with long style-head (front view) **B** corona and gynostegium with short style-head (front view) **C** corona and gynostegium with short style-head (vertical view) **D** corona and gynostegium with long style-head (vertical view) **E** pair of fruits **F** stamen (front view) **G** stamen (back view) **H** stamen (front view) **I** stamen (back view) **J** pollinarium **K** seeds the concave surface (left) and convex surface (right) **A, D, F, G** and **J** from *Meng Wei in C.F. Zhang 6791* (HIB); **B, C, H, I** from *Zhongxiang Pubic Health Bureau s.n.* (HIB [0101695]). All photos by Cai-Fei Zhang, except **J** by Miao Liao, **E** by Bing Liu in Beijing and **K** by Qin-Wen Lin in Beijing.

Discussion

Cynanchum gobicum was first placed in the genus *Antitoxicum* (Grubov 1955), an illegitimate replacement name for *Vincetoxicum* and was then transferred to *Cynanchum* (Grubov 2000). It was distinct from *C. thesioides* because of the long and scandent stem, broader lanceolate leaves and puberulent, but not glabrous outer surface of the corolla (Grubov 1955, 2000, 2002). However, we found those diagnostic characters to be within the range of variation of *C. thesioides*. Vegetatively, *C. thesioides* varies considerably (Figs 3, 4) over its wide range of habitats from sandy seasides to steep, crumbling, mudstone slopes at elevations of more than 3000 m (Tsiang and Li 1974: 101). This variation and wide variation also in floral parts was observed by previous taxonomists (Maximowicz 1877; Freyn 1890; Komarov 1905: 291; Tsiang and Li 1974; Ma 1980; Li et al. 1995) and reconfirmed by us (Figs 4, 5). We could not find any other significant differences separating *C. gobicum* from *C. thesioides*. Thus, we place *C. gobicum* in synonymy under *C. thesioides*.

The name *Vincetoxicum sibiricum* f. *linearifolium* Debeaux has been neglected since its publication. Debeaux (1877) described it from specimens collected in Tché-foû (now part of Yantai City, Shandong Province), China. Its narrowly linear-lanceolate leaves are narrower than the typical ones from Siberia. This form is placed here in synonymy because leaf shapes and sizes vary greatly and continuously in *Cynanchum thesioides* (Fig. 4C).

Floral dimorphism was observed in certain plants of *Cynanchum thesioides*. This dimorphism takes the form of the style-head exceeding the corona lobes (Figs 4I, K, 5A, D) or the style-head covered by the corona lobes (Figs 4J, L, M, 5B, C). In the former case, the corona lobes are erect or slightly bent over the style-head. In the latter case, the corona lobes are slightly to greatly bent towards the centre of the style-head. This is similar to distyly in simple flowers where one flower has a long style and short stamens, but other flowers have a short style and long stamens. We also found that flowers from the same inflorescence usually have the same floral morphology, though sometimes with varying colours (Fig. 5F). From the photographs in PPBC, short style-heads seem to be rarer. The purpose of these dimorphic flowers is unknown. In other Chinese species of *Cynanchum*, the lengths of corona lobes relative to the gynostegia have been described as either longer or shorter than or as long as the gynostegium; only *Cynanchum officinale* has been described with slightly variable corona lobes, as long as or slightly longer than the gynostegium (Li et al. 1995).This character had been used to distinguish sections in *Cynanchum* (Tsiang and Li 1977), but these sections were not supported by recent molecular phylogenetic studies (Liede and Täuber 2002; Khanum et al. 2016).

Acknowledgements

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Supplementary material 1

A full list of specimens and selected observations of *Cynanchum thesioides* examined

Authors: Cai-Fei Zhang, Dong-Juan Zhang, Miao Liao, Guang-Wan Hu

Data type: occurrence and distribution

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Link: https://doi.org/10.3897/phytokeys.219.93514.suppl1

Supplementary material 2

Holotype of *Cynanchum sibiricum* var. *gracilentum* (TI [TI00204077])

Authors: Cai-Fei Zhang, Dong-Juan Zhang, Miao Liao, Guang-Wan Hu

Data type: image (jpg file)

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Supplementary material 3

Holotype of *Cynanchum sibiricum* f. *hypopsilum* (TI [TI00204078])

Authors: Cai-Fei Zhang, Dong-Juan Zhang, Miao Liao, Guang-Wan Hu

Data type: image (jpg file)

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Link: https://doi.org/10.3897/phytokeys.219.93514.suppl3

Supplementary material 4

Holotype of *Cynanchum sibiricum* var. *latifolium* (TI [TI00204080])

Authors: Cai-Fei Zhang, Dong-Juan Zhang, Miao Liao, Guang-Wan Hu

Data type: image (jpg file)

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RESEARCH ARTICLE

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Liparis tianchiensis (Orchidaceae), a new species from Gansu, China

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Abstract

Liparis tianchiensis (Orchidaceae, Epidendroideae), a new species from Wenxian County, Gansu Province, China, is described and illustrated, based on morphological characters. *Liparis tianchiensis* is morphologically similar to *L. damingshanensis*, *L. pauliana* and *L. mengziensis* with erect, lax flowered-inflorescences, small persistent floral bracts, small greenish-purple flowers, spreading sepals, free reflexed and linear petals, a lip with 2 calli near the base and an arcuate column. *Liparis tianchiensis* differs from *L. pauliana* by the single and much smaller leaf, shorter sepals and petals, smaller and reflexed oblong lip. It differs from *L. mengziensis* by having fewer and larger flowers and not connate lip apex. The novelty mostly resembles *L. damingshanensis*, but can be readily identified by having longer sepals and a reflexed oblong lip. *Liparis tianchiensis* only occurs in evergreen broad-leaved forest around a mountain lake in Wenxian County, Gansu Province, China.

Keywords

Malaxideae, morphology, new species, Wenxian County

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Introduction

The genus *Liparis* Richard (1817: 21) belongs to tribe Malaxideae (subtribe Malaxidinae) of the subfamily Epidendroideae (Chase et al. 2015) and comprises approximately 424 species (Plants of the World Online (https://powo.science.kew.org/)) with cosmopolitan distribution from the tropics and subtropics to the temperate and alpine regions. Most species in this genus occur in Southeast Asia as well as in Africa, Australia and the Americas (Pridgeon et al. 2005). *Liparis* is easily distinguished from its allies, *Malaxis* Sol. ex Sw. (Swartz 1788: 119), *Oberonia* Lindley (1830: 15) and *Hippeophyllum* Schltr. in Schumann and Lauterbach (1905: 107), based on its floral morphology (viz. resupinate flowers with narrow linear petals and a curved, slightly winged column lacking a foot) (Pearce and Cribb 2002; Chen et al. 2009). The taxonomy of the genus is very confused and inconsistent (Margońska and Szlachetko 2001, 2004; Pridgeon et al. 2005; Liu et al. 2008) and some research indicated that *Liparis* were polyphyletic. Tang et al. (2015) performed molecular and morphological analyses to establish the phylogenetic relationships within Malaxideae, the results supporting the division of *Liparis* into 11 genera, but the intergeneric relationships remain unclear and the genus definition is considerably controversial. Therefore, we tentatively opted to maintain *Liparis* as a broad concept for the present taxonomic treatment. There are approximately 70 species of *Liparis* in China, including many recently described taxa (see Chen et al. (2009); Feng and Jin (2010); Jin (2010, 2011); Wu et al. (2012); Hsu (2013); Li and Yan (2013); Su et al. (2014); Su et al. (2015); Tang et al. (2015); Li et al. (2019); Ya et al. (2021)).

Wenxian County, Gansu Province, is situated in the northwest of China, in a transitional zone between the north subtropical and warm temperate regions. The altitudes vary from 595 to 4072 m. Variations in climate combined with complex topography have resulted in high plant diversity (Li 2014). Although being a biodiversity hotspot in China, the flora of this area is still unknown despite many years of directed fieldwork and research. Several new species have been described in the last decades, such as *Cardamine tianqingiae* Al-Shehbaz & Boufford in Ihsan (2008: 89) (Brassicaceae), *Spiranthes sunii* Boufford & Wen H.Zhang (2008: 261) (Orchidaceae), *Vitis wenxianensis* W.T.Wang (2010: 288) (Vitaceae), *Clematis austrogansuensis* W.T.Wang & L.Q.Li (2011: 285) (Ranunculaceae) and, more recently, *Oreocharis wenxianensis* XiaoJ.Liu & X.G.Sun (2021: 182) (Gesneriaceae) and *Saxifraga sunhangiana* T.Deng, X.J.Zhang & J.T.Chen in Zhang et al. (2022: 197) (Saxifragaceae).

Tianchi Lake in Wenxian County is a famous mountain lake in China, covering an area of nearly 1 km^2, surrounded by mountains, rich in plant diversity. During our field trip around Tianchi Lake in 2021, we collected nearly 20 orchid species, including an unknown *Liparis*. Further examination by means of morphological comparison indicated that it represented a new species, which is described and illustrated here.

Material and method

Specimens from the single known subpopulation of the putative new species were collected during field expeditions in 2021. Morphological characters of five living plants, including three flowering and two non-flowering individuals, were observed, measured and photographed under an Olympus stereozoom microscope. Specimens were deposited in the Forestry Herbarium of Gansu Agricultural University (**GAUF**), located in Lanzhou City, Gansu Province, China.

After consulting relevant literature (Pearce and Cribb 2002; Pridgeon et al. 2005; Liu et al. 2008; Chen et al. 2009; Yang et al. 2009; Feng and Jin 2010; Jin 2010, 2011; Wu et al. 2012; Hsu 2013; Li and Yan 2013; Su et al. 2014; Su et al. 2015; Tang et al. 2015; Li et al. 2019; Ya et al. 2021) and examining scans of type specimens and other relevant herbarium specimens of *Liparis* available online from AMES, BM, E, L, K, P and PE (acronyms following Thiers, continuously updated), JSTOR Global Plants (http://plants.jstor.org), China National Specimen Information Infrastructure NSII (http://www.nsii.org.cn/2017/home-en.php) and The Chinese Virtual Herbarium NPSRC (http://www.cvh.ac.cn), the taxonomic status of the putative new species and morphologically similar species were investigated.

Taxonomic treatment

***Liparis tianchiensis* X.J.Liu & X.G.Sun, sp. nov.**
urn:lsid:ipni.org:names:77312597-1
Figs 1, 2

Type. China. Gansu Province, Longnan City, Wenxian County, Tianchi Lake, growing on moss in evergreen broad-leaved forest, elev. 1680 m, 15 July 2021, X.J. Liu & H. Lin, WX20210715001 (holotype: GAUF!, isotype: GAUF!).

Diagnosis. *Liparis tianchiensis* is similar to *L. damingshanensis* with single small leaf, erect, lax flowered-inflorescences, small greenish purple flowers, spreading sepals, free reflexed and linear petals, a lip with 2 calli near the base and an arcuate column. It, however, differs from the latter by having a longer dorsal sepal (9.0–11.0 mm vs 6.0–8.0 mm) and a longer (8.0–10.0 vs 5.0–7.0 mm) and oblong (vs obovate-triangular) lip.

Description. Terrestrial herbs. Pseudobulbs ovoid or oblong-ovoid, 0.5–1.5 cm long, 0.4–1.0 cm in diameter, covered with white membranous remnant sheaths. Leaf single, green, glabrous, petiole sheath like, 0.5–1.0 cm long, amplexicaul, not articulate; blade ovate, 1.2–3.0 cm × 1.0–2.0 cm, contracted and decurrent into petiole at base and acute or obtuse at apex, margin entire and flat or slightly undulate. Inflorescence 4.0–9.0 cm long; peduncle slightly compressed cylindrical, narrowly winged on either side; rachis laxly 2–4-flowered; floral bracts ovate-triangular, 2.0–3.0 mm long, membranous, greenish-white. Flowers fully opening, greenish-purple, 1.6–2.2 cm across; pedicel and ovary greenish-purple, twisted, 1.0–1.2 cm long. Dorsal sepal

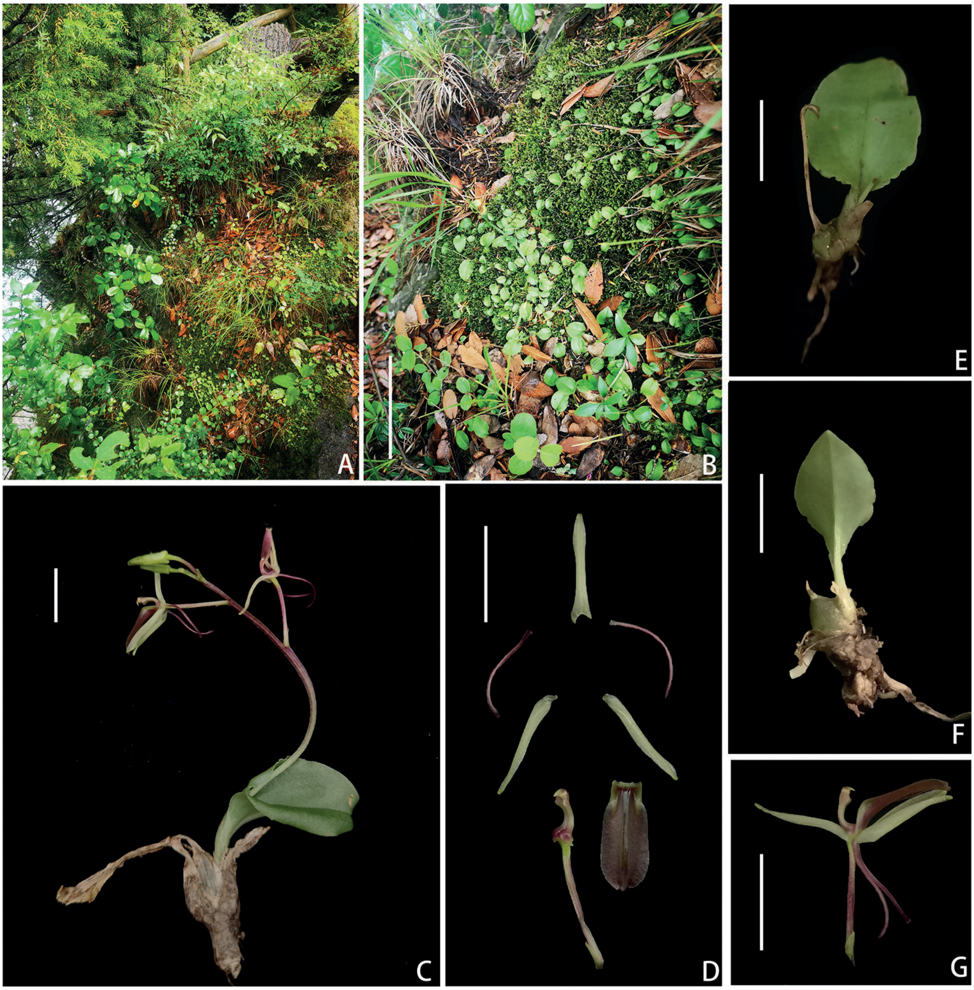

Figure 1. *Liparis tianchiensis* sp. nov. **A** habit **B** non-flowering plants *in situ* **C** flowering individual **D** dissected floral parts **E** leaf, adaxial view **F** leaf, abaxial view **G** flower, lateral view. Scale bars: 10 cm (**B**); 1 cm (**C–G**).

ovate-oblong, margins often revolute, apex obtuse, 9.0–11.0 mm × ca. 1.0 mm, translucent greenish-white. Lateral sepals parallel under the lip, obliquely ovate-elliptic, margins often revolute, apex obtuse, 8.0–11.0 mm × ca. 1.0 mm, translucent greenish-white. Petals deflexed, narrowly oblong-falcate, margins revolute, 8.0–10.0 mm × 0.3–0.5 mm, purple. Lip oblong, 8.0–10.0 mm × 3.0–5.0 mm, pale purple, with 2 short longitudinal triangular lamellae at the shallowly concave base, mucronate at apex; mid-vein dull-purple, broad and stout, conspicuous from the base up to the apex. Column conspicuously incurved, 4.0–5.0 mm long, ca. 1 mm in diameter, apex with 2 short, triangular wings, base purple and swollen; anther-cap obovate, glabrous; pollinia four in two pairs, yellow. Fruit not observed.

Etymology. The specific epithet is derived from the type locality Tianchi Lake, Wenxian County, Gansu Province, China.

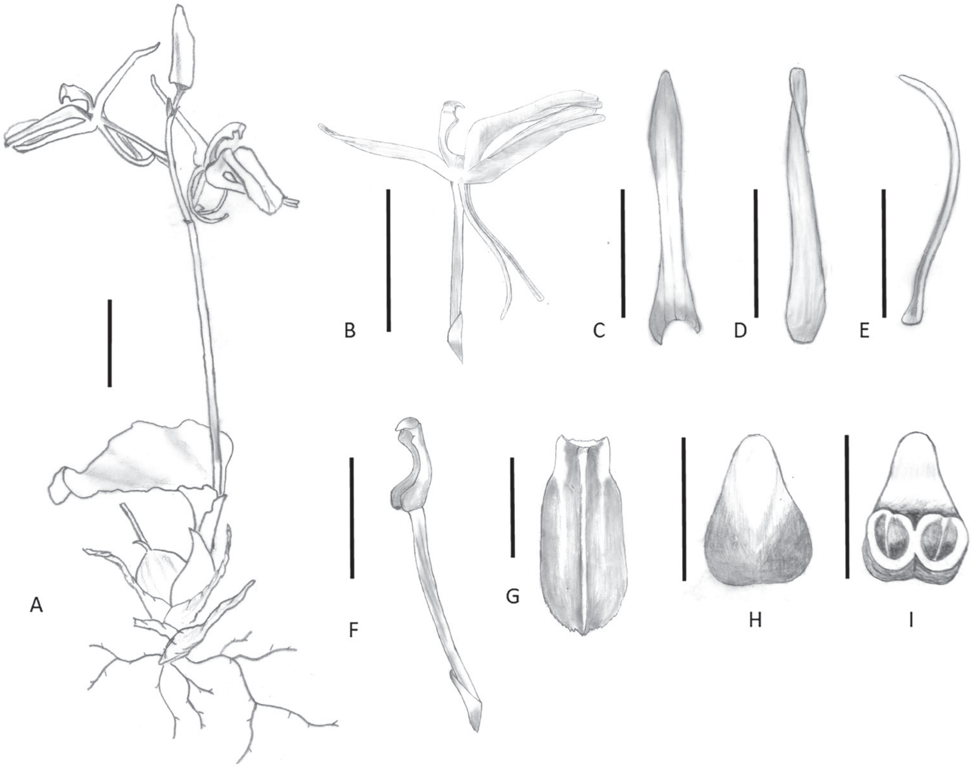

Figure 2. *Liparis tianchiensis* sp. nov. **A** individual in bloom **B** flower, lateral view **C** dorsal sepal **D** lateral sepal **E** petal **F** pedicel, ovary and column **G** lip **H** anther-cap, abaxial view **I** anther-cap, adaxial view. Scale bars: 1 cm (**A, B**); 0.5 cm (**C–G**); 1 mm (**H, I**). Drawn by Hui Lin from the holotype.

Distribution and habitat. *Liparis tianchiensis* is terrestrial and grows in shaded and damp moss-covered areas in evergreen broad-leaved forest, forming scattered colonies on the slopes of Tianchi Lake at 1680 m a.s.l. For the time being, *Liparis tianchiensis* is only known from the type locality. The subpopulation is small, with less than 200 individuals.

Flowering phenology. June and July.

Key to *Liparis tianchiensis* and its related species

1 Pedicel and ovary shorter than 1.0 cm, lip apex connate along the margins... .... ***Liparis mengziensis***
– Pedicel and ovary longer than 1.0 cm, lip apex flat........ **2**
2 Flower size larger than 1.0 cm, leaf 2, very rarely 1 .... ***Liparis pauliana***
– Flower size not larger than 1.0 cm, leaf 1 .... **3**
3 Lip obovate-triangular, 5.0–7.0 × 5.0–6.0 mm, dorsal sepal 6.0–8.0 mm long .... ***Liparis damingshanensis***
– Lip oblong, 8.0–10.0 × 3.0–5.0 mm, dorsal sepal 9.0–11.0 mm long........ ***Liparis tianchiensis***

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RESEARCH ARTICLE

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Allium sunhangii – a new species from section *Brevidentia* F.O.Khass. & Iengal. (Amaryllidaceae) from Southern Pamir-Alay, Uzbekistan

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Abstract

A new species, *Allium sunhangii* **sp. nov.**, of the Middle Asiatic section *Brevidentia* F.O.Khass. & Iengal., (subgenus *Allium*, tribe Allioideae, Amaryllidaceae) is described. The species is a small plant from the Babatag Ridge in the Surkhandarya province of Uzbekistan. It is morphologically close to *Allium brevidens* Vved. in having initially dark violet filaments and three-cuspidate inner filaments, but differs by its small size and visibly unequal tepals as well as in the phylogenetic analysis based on ITS data.

Keywords

Allium, *Brevidentia*, Middle Asia, new taxon, phylogeny, taxonomy

Introduction

Allium Linnaeus (1753), one of the largest genera in the Amaryllidaceae (Friesen et al. 2006; Li et al. 2010), has more than 1100 species worldwide (Govaerts et al. 2021). Members of the genus, such as garlic, leek, onion and shallot, are used as food, medicine and ornament (Herden et al. 2016) and are characterized by bulbs enclosed in a membranous, fibrous or reticulate tunic, free or basally connate tepals and often a subgynobasic style (Friesen et al.

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2006). *Allium* has two probable diversity centers, one in South-Western and Middle Asia and in the Mediterranean region, and a smaller center is in western North America (Friesen et al. 2006; Nguyen et al. 2008). The most recent classification of *Allium*, by Friesen et al. (2006), based on molecular phylogenetic analyses, includes 15 subgenera and 72 sections.

Subgenus *Allium*, with more than 375 species and 35 subspecies, is the largest subgenus within *Allium*, and is one of three main evolutionary lines within the genus (Friesen et al. 2006; Fritsch and Friesen 2002). Subgenus *Allium* consists of two main groups (Hanelt 1992; Friesen et al. 2006); one has simple inner filaments while the other has three-cuspidate inner filaments. The newly described sections are supported by nuclear molecular data (Friesen et al. 2006) and have revealed the presence of centers of recent speciation in the Middle Asia, Pakistan, Iran, Afghanistan and the Middle East (Khassanov 2018). Also, results from whole chloroplast genome analyses are continuing and being compared with morphology to determine whether morphology-based taxonomy corresponds well to molecular data (Munavvarov et al. 2022)

Section *Brividentia* F.O.Khass. & Iengal. was previously treated as a part of section *Allium* of subgenus *Allium*. Khassanov et al. (1997) divided section *Allium* into six sections (*Allium* s. str., *Crystallina* F.O.Khass. & Iengal., *Filidentia* F.O.Khass. & Iengal., *Brevidentia* F.O.Khass. & Iengal., *Spathulata* F.O.Khass. & R.M.Fritsch and *Multicaulea* F.O.Khass. & Iengal.). According to the last revised and updated classification of subgenus *Allium* (Khassanov 2018), section *Brevidentia* includes 12 species, most of which are in Middle Asia and adjacent areas. The main characteristics are purple filaments, the inner ones three-cuspidate, as well as a rounded purplish ovary with pocket-like mounds of the nectary tubes. Most species show S-to U-type, U-type anticlinal walls and (globular) convex periclinal walls of seeds (Yusupov et al. 2022).

In 2021, during grid mapping of the flora of the Surkhandarya province (Babatag Ridge, Zarkasa peak in Uzbekistan), we collected an interesting species of *Allium*. Comparisons of molecular and morphological characteristics showed it as a member of sect. *Brevidentia*. Morphologically, it resembles *A. brevidens* in its purple, three-cuspidate inner filaments, but differs in unequal tepals, which showed that it was a previously unknown characteristic for the species of *Allium*. Here, we propose it as new species and provide a comprehensive description based on morphological and molecular approaches.

Materials and methods

Plant material

A total of 14 specimens were collected in the summer of 2021. Material from the new species was collected in the Zarkasa (Babatag Ridge) peak, Surkhandarya province, Uzbekistan.

DNA extraction, PCR amplification and sequencing

Leaves for molecular analysis were dried in silica gel upon collecting. Total DNA was isolated by the CTAB protocol (Doyle and Doyle 1987) from 1 g of well-dried leaves.

ITS1 and ITS4 primers were from White et al. (1990). Polymerase chain reaction (PCR) was performed under the following conditions: 5 min of initial denaturation at 94 °C, 35 cycles of denaturation for 45 secs at 94 °C, annealing for 45 secs at 55 °C, and extension for 1–1.5 min at 72 °C, then a final extension at 72 °C for 5 min. PCR products were visualized using electrophoresis on 1.5% agarose TAE gel and sent to Beijing Genomics Institute (Shenzhen, China) for sequencing.

Phylogenetic analyses

To assemble and edit complementary strands, we used Sequencher 4.1.4 software (Burland 2000). Clustal X (Jeanmougin et al. 1998) was used to align DNA sequences, which were then manually adjusted using MEGA 7.0 (Kumar et al. 2016). Analysis of parsimony was conducted in PAUP* 4.0b10 (Swofford and Sullivan 2003) using heuristic searches with TBR and 1000 random addition sequence replicates. Bootstrap support (BS) was estimated with 1000 replicates, each with 100 random addition sequence searches according to Felsenstein (1985). The major consensus trees constructed from a maximum of 1000 trees were saved. RAxML v 8.2.8 (Stamatakis 2014). The best-fitting nucleotide substitution model GTR + G model was determined for each dataset and 1000 bootstrap replicates were used for performing Maximum Likelihood (ML) analyses. Based on the Akaike information criterion (AIC) implemented in jModelTest2 on XSEDE (www.phylo.org). For Bayesian inference (BI) analyses, MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) was utilized, with 10,000,000 generations with random trees sampled every 1000 generations. In the latter analysis, after discarding the first 25% of trees as burn-in, and in order to estimate posterior probabilities (PP) we constructed a 50% majority-rule consensus tree from the remaining trees.

A total of 28 ITS sequences were downloaded from NCBI and used for phylogenetic reconstruction. In order to confirm the systematic position of the new species we selected 8 sections of subgen. *Allium* and two species from subgen. *Rhizirideum* (see Appendix 1). The classification system in this study follows the nuclear-based molecular phylogenetic classification of Friesen et al. (2006).

Results

Taxonomic treatment

Allium sunhangii **F.O.Khass., Tojibaev & Yusupov, sp. nov.**
urn:lsid:ipni.org:names:77311234-1
Figs 1–3

Type. Uzbekistan. Surkhandarya province, Babatag Ridge, Zarkasa peak, 37.986537, 68.166650, 2251 m a.s.l., 22 June 2021, *S. O. Pulatov and O.A. Turdiboev 22062021001*. (TASH109001!, holotype; TASH109002! and TASH111001!, isotypes).

Figure 1. Holotype of *Allium sunhangii* F.O.Khass., Tojibaev & Z.Yuss., sp. nov.

Description. Bulbs 0.4–0.8 cm wide, 0.7–0.9 cm long, ovoid, solitary tunics reticulate, light brown, bulblets several, smooth, brownish. Scape terete, erect, 4.5–10 cm high, 1.0–1.2 mm wide. Spathe bivalved, persistent, ca 4 mm long, with short beak.

Leaves 2–4, narrowly linear, longer than inflorescence, 6–12 cm long, 1.0–1.5 mm wide, semi-terete. Inflorescence lax, umbellate, hemispheric, 10 to 15-flowered. Flowers widely cup-shaped, nearly star-like, ca 5 mm long. Pedicels 2–3 times longer than tepals, at base with bracts. Tepals lanceolate-ovate, smooth, whitish with a dirty greenish-purple midvein, 2.5–4 mm long, outer tepals slightly longer than inner ones. Filaments 1.5–2.0 times longer than tepals, inner ones 3-cuspidate, filament bearing cusp 2 times longer than basal teeth. Style exerted from flowers. Capsule 2 mm in diam.

Diagnosis. This species is most similar to *Allium brevidens* Vved. (Fig. 1), from which it differs in a more compact habit, remaining small spathe with a short beak, unequal tepals and strongly exserted, dark violet filaments (Fig. 2).

Distribution and habitat. *Allium sunhangii* is known from one population occurring to the south in the northwestern part of the Zarkasa peak, at 2251 m a.s.l. (Figs 3, 4). New species grows in continental and drier *Juniperus* forests (Fig. 4B$_1$– B$_2$)

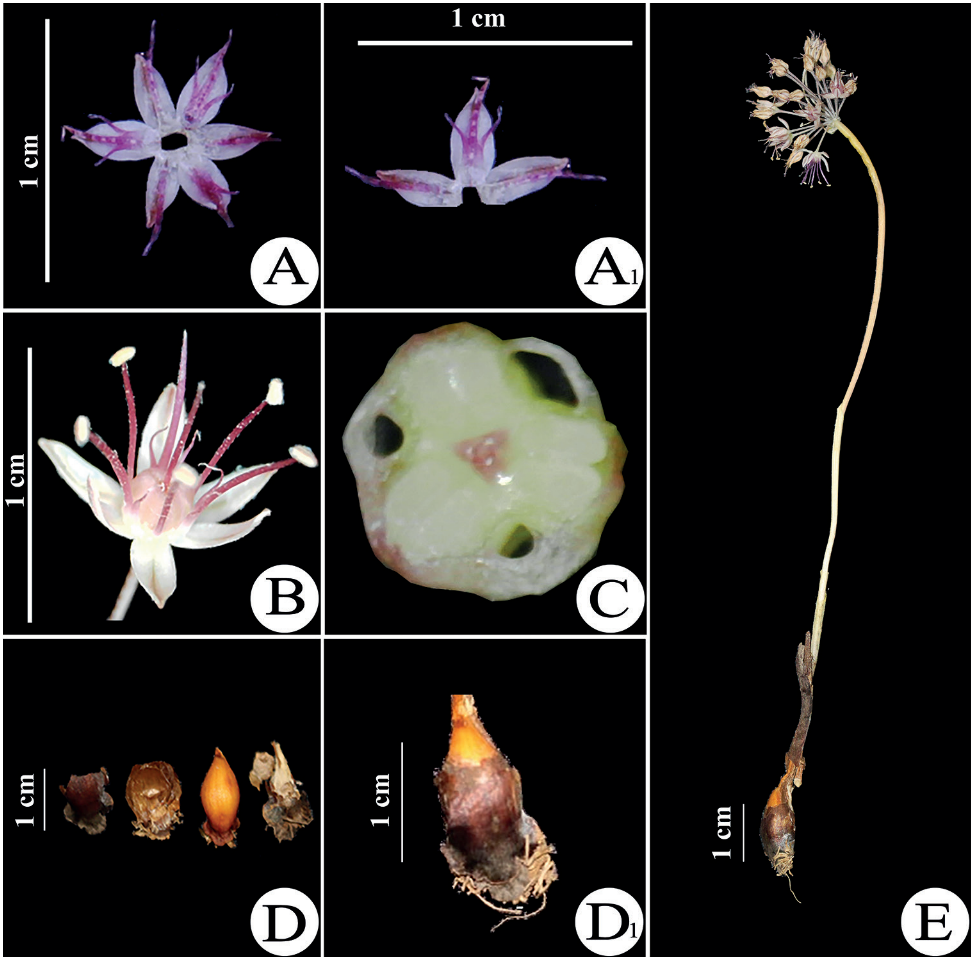

Figure 2. *Allium sunhangii* **A–A$_1$** whole and longitudinal section of flower with teeth **B** view of single flower **C** cross section of pistil **D–D$_1$** bulb tunic and bulb **E** general view of species without leaves.

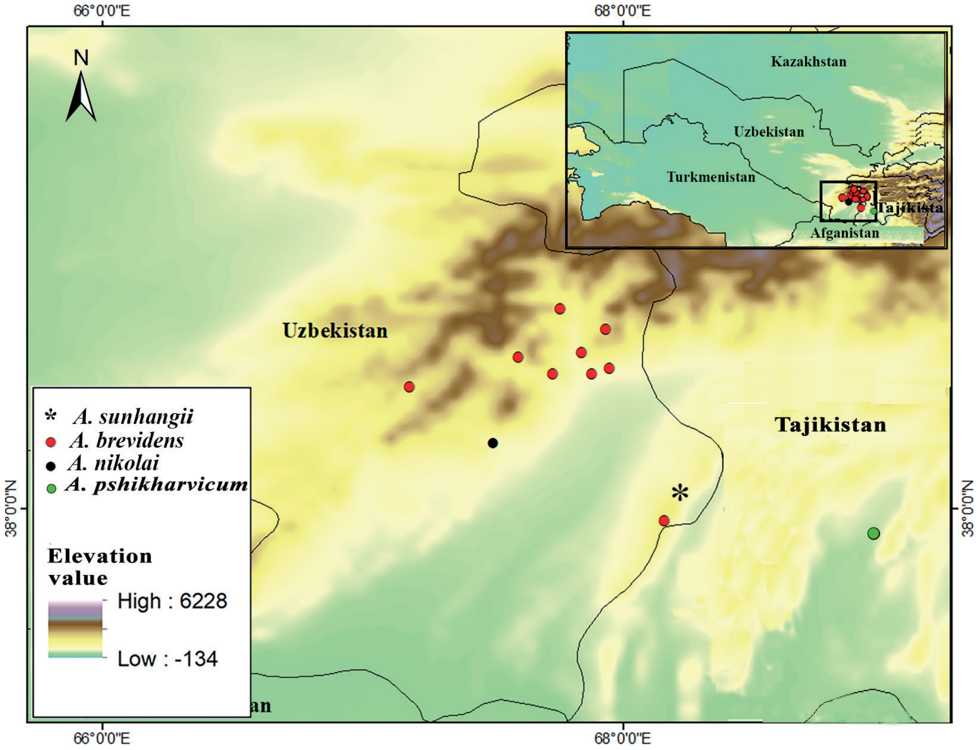

Figure 3. Distribution of *Allium sunhangii*, *A. brevidens*, *A. nikolai* and *A. pshikharvicum*.

(*Juniperus seravschanica* Kom.) primarily on loamy soil, with shrubs (*Cotoneaster nummularius* Fisch. & C.A.Mey., *Lonicera nummulariifolia* Jaub. & Spach, *Rosa canina* L., *Rosa ecae* Aitch.), perennial (*Convolvulus lineatus* L., *Dianthus tetralepis* Nevski & Schischk., Eremurus *olgae* Regel, *Gentiana olivieri* Griseb., *Hypericum scabrum* L., *Malva neglecta* Wallr., *Phlomis olgae* Regel, *Primula baldshuanica* B. Fedtsch., *Ziziphora pamiroalaica* Juz.), annual and biennial (*Cousinia candicans* Juz., *C. microcarpa* Boiss., *Daucus carota* L., *Lactuca serriola* L., *Lappula microcarpa* (Ledeb.) Giirke, *Veronica cardiocarpa* (Kar. & Kir.) Walp.,) herbs and is always with dominance by *Carex pachystylis* J.Gay.

Etymology. *Allium sunhangii* is named after Prof. Sun Hang, one of the leading botanists at the Kunming Institute of Botany, Chinese Academy of Sciences, China, who actively promotes several projects within Central Asia.

Phenology. *Allium sunhangii* was flowering (Fig. 4 A_1–A_2) on 22 June, 2021 when we found its fruits began to mature at the same time. It is supposed that flowering starts in about late May and/or early June. As we visited this area only once, we are not sure when fruiting finishes.

Conservation status. *Allium sunhangii* is so far only known from two closely spaced localities. The total distribution area of this species is around 5 km^2. The total

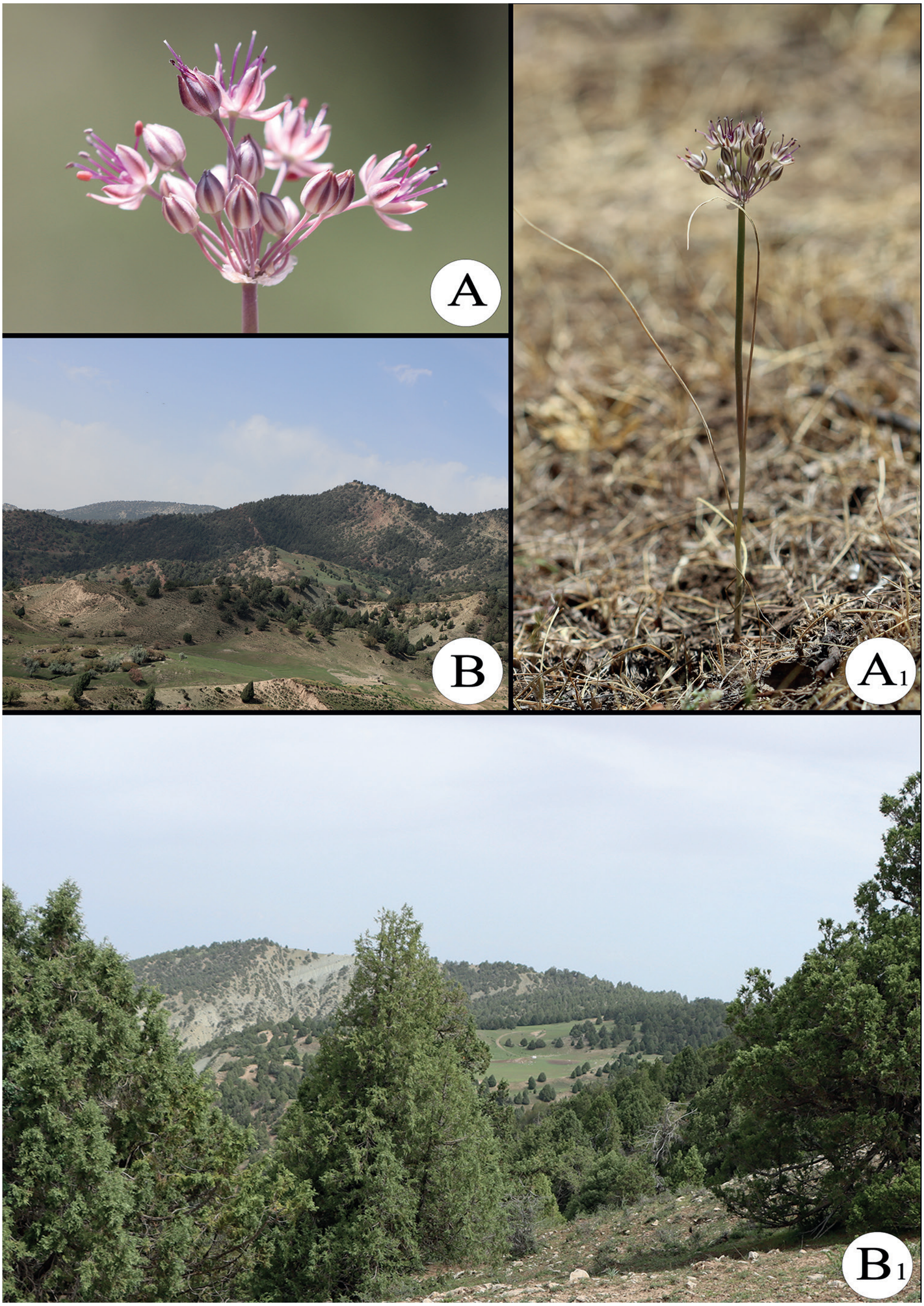

Figure 4. **A_1–A_2** inflorescence and general view of growing *Allium sunhangii* **B_1–B_2** Zarkasa peak and habitat landscape.

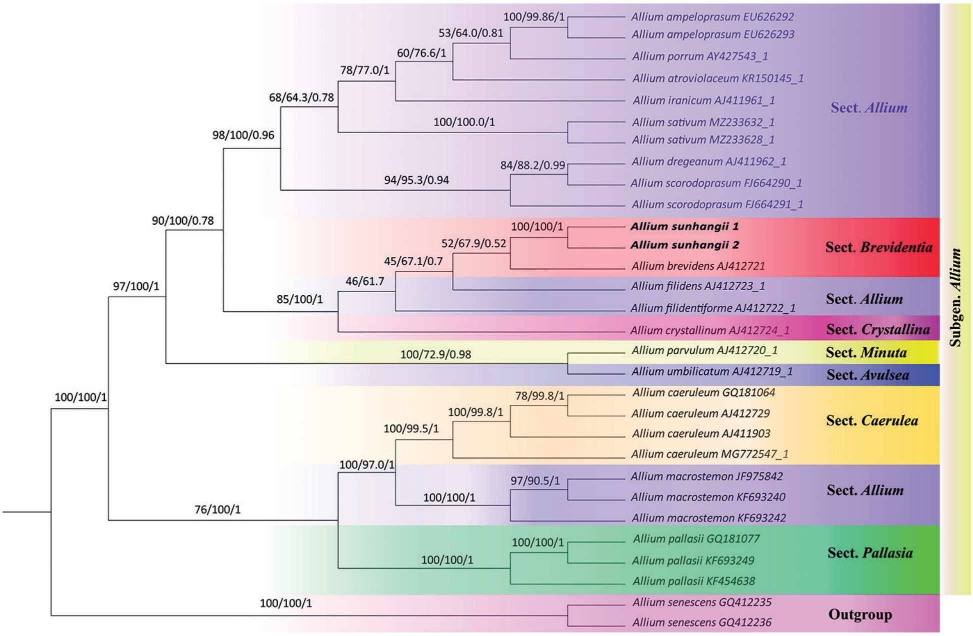

Figure 5. Phylogenetic tree inferred from MP, ML and BI (bootstrap support and posterior probabilities are given on branches, respectively), showing location of the *Allium sunhangii*.

number of individuals does not exceed 41. However, the new species is categorized as 'Data Deficient' (DD) according to IUCN (2019) criteria.

Phylogenetic analysis

Allium sunhangii was placed in the section *Brevidentia* (subgen. *Allium*) in all phylogenetic analyses (MP, ML and BI) (Fig. 5). Phylogenetic tree based on ITS data suggests that the new species closely related to *A. brevidens*.

Discussion

Allium sunhangii is morphologically close to *A. brevidens* in having initially dark violet filaments. However, it differs in a more compact habit, remaining small spathe with a short beak, unequal tepals and strongly exserted, dark violet filaments. Compared to all known species of *Allium* sect. *Brevidentia*, the new species differs by having leaves longer than scape, spathe with rather small beak ca. 3 mm long; tepals whitish with greenish midvein. Most significantly, the new species has lax (vs dense) and umbellate (vs globose) inflorescence, and also fewer flowers, 10–25 (vs 30–50) (Table 1). In phylogenetic tree the new species and *A. brevidens* were placed along with the species of sect. *Allium*. Similarly, according to some unsolved reasons, species of the section *Allium* were placed in different positions in the previous studies (Friesen et al. 2006; Li

Table 1. Comparison in morphology between *Allium sunhangii* sp. nov. and *A. brevidens*.

Characters	*A. sunhangii*	*A. brevidens*
Bulb	smooth	reticulate
Scape	4.5–10 cm	20–30 cm
Leaf	longer than scape	shorter than scape
Pedicels	2–3 times longer than tepals	3–8 times longer than tepals
Spathe	remaining	falling
Tepals	unequal (inners – 2 mm lg., outers – 3 mm lg.)	equal (inners and outers – 3.5–4.0 mm lg.)
Filaments	1.5–2.0 times longer than tepals	slightly longer than tepals

et al. 2010). Accordingly, our phylogenetic analysis was also consistent with those phylogenetic analyses. However, *A. sunhangii* can be distinguished morphologically and geographically from the representatives of sect. *Allium*. In consistence of morphologic evidence, the position of *A. sunhangii* and *A. brevidens* in the phylogenetic tree supports that they are most relative and the new species belongs to sect. *Brevidentia*. Also, the distribution of the new species and the related species may also slightly support this arrangement. Thus, current molecular and morphological data support the recognition of *A. sunhangii* as a new species of *Allium* sect. *Brevidentia*.

Key for determination of species belonging to sect. *Brevidentia*

1 Inner filaments simple, triangular-subulate .... ***A. miserabile***

– Inner filaments 3 (or 5) cuspidate, the lateral sterile cusps shorter than the median anther- bearing cusp **2**

2 Outer filaments with two obtuse teeth at base .... ***A. hedgei***

– Outer filaments simple **3**

3 Leaves normally twisted **4**

– Leaves normally straight **6**

4 Perianth (6)7 mm long .... ***A. ophiophyllum***

– Perianth 3.0–4.5 mm long **5**

5 Perianth lilac with purple midvein; filaments violet, twice as long as tepals ... . ***A. circumflexum***

– Perianth lilac-greenish with green midvein; filaments whitish, shorter than tepals .... ***A. michaelis***

6 Filaments ciliate at the base, bracteoles present 7

– Filaments glabrous, bracteoles absent **11**

7 Bulblets with subcrystalline tunic .... ***A. brevidentiforme***

– Bulblets without subcrystalline tunic **8**

8 Plants to 60–80 cm tall; inflorescence dense, globose, flowers 30–50 .... **9**

– Plants 10–30 cm tall; inflorescence lax, umbellate, flowers 10–25 .... **10**

9 Scape ca 80 cm tall; inflorescence dense, tepals greenish red with green midvein, ... ***A. pshikharvicum***

– Scape ca 30 cm tall; infloresscene loose, tepals white with purple midvein...... .... ***A. brevidens***

10 Leaves shorter than scape; spathe with beak to 1 cm long; tepals rose colored, with purple midvein .... ***A. nikolai***
– Leaves longer than scape; spathe with beak ca 3 mm long; tepals whitish with greenish midvein.. ***A. sunhangii***
11 Outer tunic reticulate-fibrous; perianth urceolate-campanulate, whitish .... ***A. ionandrum***
– Outer tunic coriaceous; perianth, widely bell-shaped, purple or viole........... .... ***A. micranthum***

Members of *Allium* sect. *Brevidentia*

Sect. ***Brevidentia*** F.O.Khass. & Yengal. in Ozturk, Sećmen & Gork (Eds.) Plant Life in South West Asia. Ege Univ. Press, Izmir:147 (1996).

1. ***A. brevidens*** Vved. in Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 5: 89 (1924). Holotype: Uzbekistan. Bukhara Khanate, Hissar distr., hills on the southern slopes of Hissar range, near Karatag, (in Russian). 20 May 1913, *A.I. Michelson 1721* (lectotype LE; designated by Khassanov in Flora of Uzbekistan 1: 61 (2017)). Distribution: Middle Asia (Southern Pamir-Alai): Tajikistan, Uzbekistan (Fig. 6A).
2. ***A. brevidentiforme*** Vved. in Opred. Rast. Sred. Azii 2: 315, 78 (1971). Holotype: Uzbekistan. Kashkadarja valley, Igri-su river, right bank, Juniper forests (in Russian), 6 July 1955, fl., *Pjataeva*, *Tsukerwanik 1617* (TASH000341!). Distribution: Western Pamir Alay (Hissar Range): Uzbekistan.
3. ***A. circumflexum*** Wendelbo in Acta Horti Gothob. 28: 22 (1966). Type: Iran. Prov. Bamian, Band-e-Amir, rich limestone steppe vegetation, 2900 m, 29 June 1962, leg. *Hedge & Wendelbo 4803* (holotype BG, isotypes E; TASH000348!). Distribution: Afghanistan.
4. ***A. hedgei*** Wendelbo in Acta Horti Gothob. 28: 20 (1966). Type: Afghanistan. Prov. Mazar-i-Sharif, Takht-i-Rustam, near Samangan (Aybak), dry slopes, 1200 m, 10 June 1962, leg. *Hedge & Wendelbo 3990* (holotype BG, isotypes E; TASH000390!). Distribution: Afghanistan.
5. ***A. ionandrum*** Wendelbo in Bot. Not. 121: 270 (1968). Type: Afghanistan, Urgun. 35 km NW Urgun, 32°27'N, 69°07'E, versus Surmat, 33°27'N, 69°02'E, 2200–2400 m. 10 June 1967, Per Wendelbo *35915* (holotype W, isotype B, MUN). Distribution: Afghanistan.
6. ***A. michaelis*** F.O.Khass. & Tojibaev in Linzer Biol. Beitr. 41(2): 1059 (2009). Holotype: Uzbekistan. Western Tian-Shan, Kurama Range, near Ujgursaj village, 40°54'54"N, 71°03'27"E, 563 m, 24 May 2009, *Khassanov*, *Tojibaev*, *Keusgen* (TASH000424!). Distribution: Ferghana valley (Uzbekistan, Kyrgyzstan) (Fig. 6C).
7. ***A. micranthum*** Wendelbo in Biol. Skr. 10, No. 3 (Symb. Afghan. 4): 178 (1959) (as cited in Nasir 1975, 22. p). Type: Afghanistan. Kurram valley, Afghanistan, December 1879, *Dr. J.R.T. Aitchison 228*, (holotype K). Distribution: Afghanistan.

8. ***A. miserabile*** Wendelbo in Nytt Mag. Bot., Oslo xiv. 104 (1967). Type: Pakistan. Flora of West Pakistan, Kohat, Kohat to Thal, c. 20 km from Kohat, Rocky slope on a small hillock, c. 675 m. 26 May 1965, *Jennifer Lammond 1549* (holotype E). Distribution: Afghanistan.

9. ***A. nikolai*** F.O.Khass. & Achilova in Opred. Rast. Sred. Azii 11: 497 (2015). Neotype: Uzbekistan. 25 km eastern Bajssun town, gypsaceous slopes under the shrubs, 23 July 2013, *Yusupov et al. s. n.* (TASH). Distribution: Uzbekistan (Kelif-Sherabad mountain range). Uzbekistan (Fig. 6D).

10. ***A. ophiophyllum*** Vved. in Trudy Sredne-Aziatsk. Gosud. Univ., Ser. 8b, Bot. 3: 8 (1928) (as cited in Khassanov and Yusupov 2022, 415. p). Type: Uzbekistan. Montes Meridionales: Sogdiano-transoxanae. Ad declivia argilloso-arenosa gypsacea, elevationis Chaudak-tau haud procul a pago Dzharkurgan, 30 April 1928, *Vvedensky s. n.* (TASH000440!, isotype K, W, MBG, LE, MW). Distribution: Southern Pamir-Alay (Uzbekistan, Tajikistan).

11. ***A. pshikharvicum*** (R.M. Fritsch & F.O.Khass.) F.O. Khass & Z.Yuss. in M.Ozturk et al. Biodiversity, Conservation and Sustainability in Asia. Volume 2: Prospects and Challenges in South and Middle Asia. Springer, 2022, p. 415. Type: Tajikistan, Darvaz Range, the road from pass Khoburabot between Robot and soldier post, steep stony-loamy slopes, in SE to SW exposition; 2200 m, 38°33'17"N,

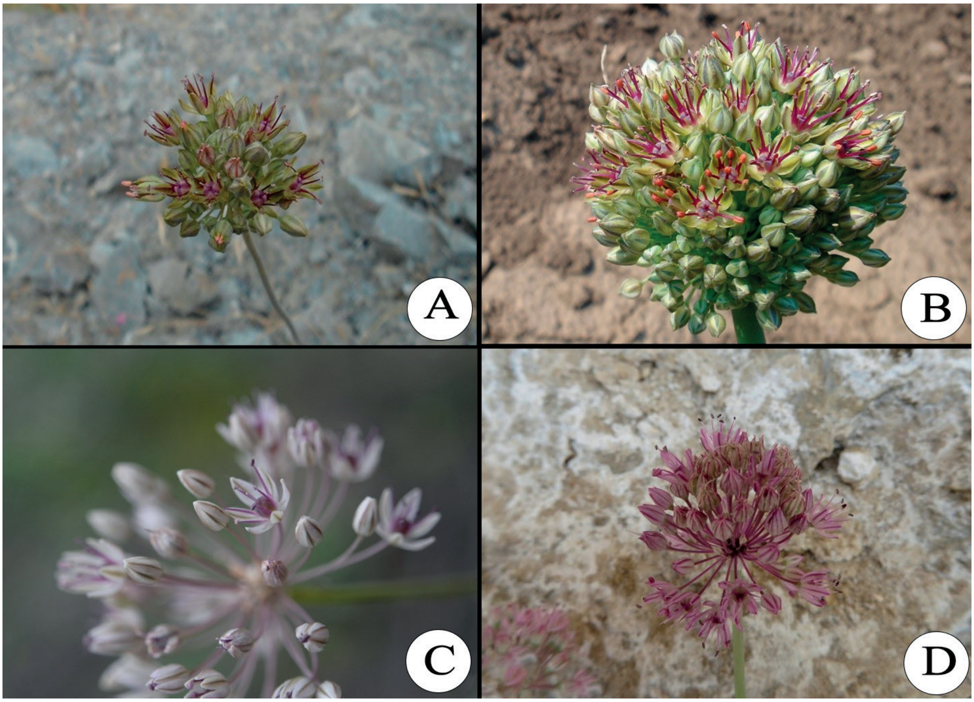

Figure 6. The species of section *Brevidentia* **A** *A. brevidens* **B** *A. pshikharvicum* **C** *A. michaelis* **D** *A. nikolai*.

70°48'07"E, leg. *Fritsch*, *Keusgen*, *Hissoriev*, *Kudratov 6199*, (Holotype GAT!, isotypes GAT!, TAD!). Distribution: Southern Pamir Alay (Darwaz Range): Tajikistan (Fig. 6B).

12. ***A. sunhangii*** F.O.Khass., Tojibaev & Yusupov sp. nov. Holotype: Uzbekistan. Surkhandarya province, Babatag Ridge, Zarkasa peak, 37.986537, 68.166650, 2251 m, 22 June 2021, *S.O. Pulatov and O.A. Turdiboev 22062021001* (TASH109001!, Holotype). Distribution: Middle Asia: Southern Pamir-Alay (Babatag ridge). Uzbekistan.

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Appendix 1

Table A1. List of the GenBank accession numbers of the ITS sequences of sampled species in this study. Sequences generated in this study are marked with asterisks (*).

Species	Location, collector, herbarium voucher /Reference	GenBank Accession Number
Allium ampeloprasum L.	Spain, collected by C. M. Messiaen,BF-ALL-015/ Hirschegger et al. 2009	EU626292
Allium ampeloprasum L.	Argentina, BF-ALL-001/ Hirschegger et al. 2009	EU626293
Allium atroviolaceum Boiss.	Iran: N khorasan. collected by Yousef Saeedi/ Ghorbani et al. 2015 (unpubl. res.)	KR150145.1
Allium dregeanum Kunth	South Africa, Tax 5772/Friesen et al. 2016	AJ411962.1
Allium iranicum (Wendelbo) Wendelbo	Iran:Elburz range, Karaj valley, Asara, Tax 3969/Friesen et al. 2016	AJ411961
Allium macrostemon Bunge	China: Shanxi, collected by Li Qinqin, He Xingjin, Hexj0473/Li et al. 2011	JF975842
Allium macrostemon Bunge	China: Yunnan, Hutiaoxia, collected by D.Q Huang, H11100509/He X and Huang D 2013 (unpubl. res.)	KF693240
Allium macrostemon Bunge	China: Yunnan, Kunming, collected by Q.Q Li, L20081102/He and Huang 2013 (unpubl. res.)	KF693242
Allium porrum L.	NVRS 01 4549/Ricroch et al. 2005	AY427543.1
Allium sativum L.	Iran: Hamadan/Fakhrfeshani et al. 2021 (unpubl. res.)	MZ233628.1
Allium sativum L.	Iran: Hamadan/Fakhrfeshani et al. 2021 (unpubl. res.)	MZ233632.1
Allium scorodoprasum L.	Slovenia, collected by P. Hirschegger, BF-ALL-042/ Hirschegger et al. 2009	FJ664290.1
Allium scorodoprasum L.	Slovenia, collected by P. Hirschegger, BF-ALL-044/ Hirschegger et al. 2009	FJ664291.1
Allium umbilicatum Boiss.	Iran:Teheran, Tax 2646/Friesen et al. 2001 (unpubl. res.)	AJ412719.1
Allium brevidens Vved.	Uzbekistan:Hissar Mts, Tax 5037/Friesen et al. 2001 (unpubl. res.)	AJ412721
Allium caeruleum Pall.	Russia:B. G. Moscow, Tax 1525/Friesen et al. 2001 (unpubl. res.)	AJ411903
Allium caeruleum Pall.	Kazakhstan:Chu-Ili Mts., Tax 3735/Friesen et al. 2001 (unpubl. res.)	AJ412729
Allium caeruleum Pall.	Collected by He XJ & Zhang XL, 97609/Li et al. 2010	GQ181064
Allium caeruleum Pall.	Kazakhstan, ipbb_2.1.12.1/Turuspekov et al. 2018 (unpubl. res.)	MG772547.1
Allium filidens Regel	Kazakhstan:Karatau Mts., Tax 3674/Friesen et al. 2001 (unpubl. res.)	AJ412723.1
Allium filidentiforme Vved.	Tajikistan:Schakhristan Pass, Tax 2573/Friesen et al. 2001 (unpubl. res.)	AJ412722.1
Allium crystallinum Vved.	Uzbekistan:Chakchar Mts., Tax 3662/Friesen et al. 2001 (unpubl. res.)	AJ412724.1
Allium parvulum Vved.	Kyrgyzstan:Tallas Mts., Tax 5055/Friesen et al. 2001 (unpubl. res.)	AJ412720.1
Allium pallasii Murray	Collected by He XJ & Zhang XL, 97603/Li et al. 2010	GQ181077
Allium pallasii Murray	654026120714039/Li and Fan 2013 (unpubl. res.)	KF454638
Allium pallasii Murray	654026120714039/He and Huang 2013 (unpubl. res.)	KF693249
Allium senescens L.	Collected by H.J.Choi, 070001 (KH)/Jang et al. 2009 (unpubl. res.)	GQ412235
Allium senescens L.	Collected by H.J.Choi et al., 010009 (CBU)/Jang et al. 2009 (unpubl. res.)	GQ412236
Allium sunhangii **F.O.Khass., Tojibaev & Yusupov sp. nov.**	Uzbekistan, Babatag Ridge: Zarkasa peak, collected by S.O. Pulatov and O. Turdiboev, 22062021001	**OP642456***
Allium sunhangii **F.O.Khass., Tojibaev & Yusupov sp. nov.**	Uzbekistan, Babatag Ridge: Zarkasa peak, collected by S.O. Pulatov and O. Turdiboev, 22062021002	**OP642457***

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RESEARCH ARTICLE

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Astragalus bashanensis (Leguminosae), a new species from Central China

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Abstract

A new species *Astragalus bashanensis*, from western Hubei Province, Central China is described and illustrated. The new species is morphologically similar to *Astragalus sinicus* and *A. wulingensis*, but differs from both by its spreading pubescent indumentum on stems and petioles, longer petioles, white bracts, whitish or yellow corolla, longer claw of the keel-petal, hairy pods and smaller seeds.

Keywords

Astragalus bashanensis, Central China, new species, taxonomy

Introduction

Astragalus L., consisting of ca. 2500 species, is one of the largest genera of vascular plant (Lewis et al. 2005). *Astragalus sinicus* L. (Chinese milk vetch) is native to the Yangtze River Basin of China and has been introduced to many countries as green manure, forage or ornamental plants and became widely naturalised, especially in Japan (Ohashi 2001, 2021; Shimizu 2003). The corolla of *Astragalus sinicus* is usually purple, sometimes pink or pure white, but some scholars enlarged the colour range of the corolla to orange (Ho 1993), creamy-yellow or yellow (Xu and Podlech 2010). In the spring of 2022, during field investigations in Zhuxi County, the authors discovered an unknown *Astragalus* species. After comparing with several *Astragalus* species,

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we found that these specimens with yellow flowers are similar to *A. sinicus* L. and *A. wulingensis* J.X. Li & X.L. Yu by having a prostrate stem, umbellate racemes, outer surface of the calyx sparsely appressed white-pubescent and blackish pod. However, they differ from *A. sinicus* and *A. wulingensis* in habit and morphology of stem, leaf, stipule, bract, flower, fruit and seed (Table 1). Later, we found similar specimens with yellow flowers collected in western Hubei, Central China and stored under the name of *Astragalus sinicus* in some herbaria, which were also different from *A. sinicus*. After carefully checking specimens and literature (Ho 1993; Ohashi 2001, 2021; Zhu et al. 2007, 2015; Xu and Podlech 2010), we conclude that the *Astragalus* specimens collected in Zhuxi County and the aforementioned yellow-flowered herbarium specimens stored under the name of *Astragalus sinicus* represent a new species placed in *Astragalus* subgen. *Astragalus* sect. *Lotidium* Bunge and we describe and illustrate it here.

Materials and methods

Astragalus specimens were collected in Shennongjia and Zhuxi County of Hubei Province. Comparisons with its relatives were made by consulting specimens stored in PE and HIB, fresh material in the field and some virtual specimen databases (CCAU, KUN, IBK, IBSC, CVH and JSTOR). All morphological characters were measured with dissecting microscopes and were described using the terminology suggested by Harris and Harris (1994).

Taxonomic treatment

Astragalus bashanensis Q.L.Gan, X.W.Li & S.Z.Xu, sp. nov.

urn:lsid:ipni.org:names:77312598-1
Figs 1, 2

Diagnosis. *Astragalus bashanensis* Q.L.Gan, X.W.Li & S.Z.Xu is similar to *Astragalus sinicus* L. and *A. wulingensis* J.X. Li & X.L. Yu, but the new species can be easily distinguished from both by its spreading pubescent indumentum on stems and petioles, petioles longer than the leaf rachis, white bracts, whitish or yellow corolla, longer claw of the keel-petal, persistent pubescence on both sides of pods and smaller seeds.

Type. China. Hubei Province: Zhuxi County, Quanxi Town, Hongyangou Village, on Hengduan Mountain, alt. 840 m, 32°4'8.5"N, 109°39'26.33"E, June 2022, Q. L. Gan 3295 (holotype: PE!; isotype: HIB!).

Paratypes. China. Hubei: Zhuxi County, Jiangjiayan Town, Yanjiajie Village, Piaoshiyan, 3 June 2022, Qi-Liang Gan 3294 (PE!); Quanxi Town, Hongyangou Village, Hengduan Mountain, 7 June 2022, alt. ca. 840 m, Qi-Liang Gan 3295 (PE!); Biaohulinchang, at the foot of Piantou Mountain, alt. 1200 m, Qi-Liang Gan 3287 (PE!); Shennongjia, Dashennongjia, south slopes, alt. 2800 m, flower white, 5 July 1976, Shennongjia Exped. 10718 (PE!, HIB!); Guanmenshan, Shibangou, alt. 2160 m, slopes, 5 August 1976, Shennongjia Exped. 10790 (PE!, HIB!); Guanmenshan, alt. 2150 m, under forests, 5 August 1976, Shennongjia Exped. 10835 (PE!, HIB!); Songluoxiang, Longchahe, Huilongsi, alt. 2000 m, roadside grassland, 2 September 1976, Shennongjia Exped. 22834 (PE!, HIB!).

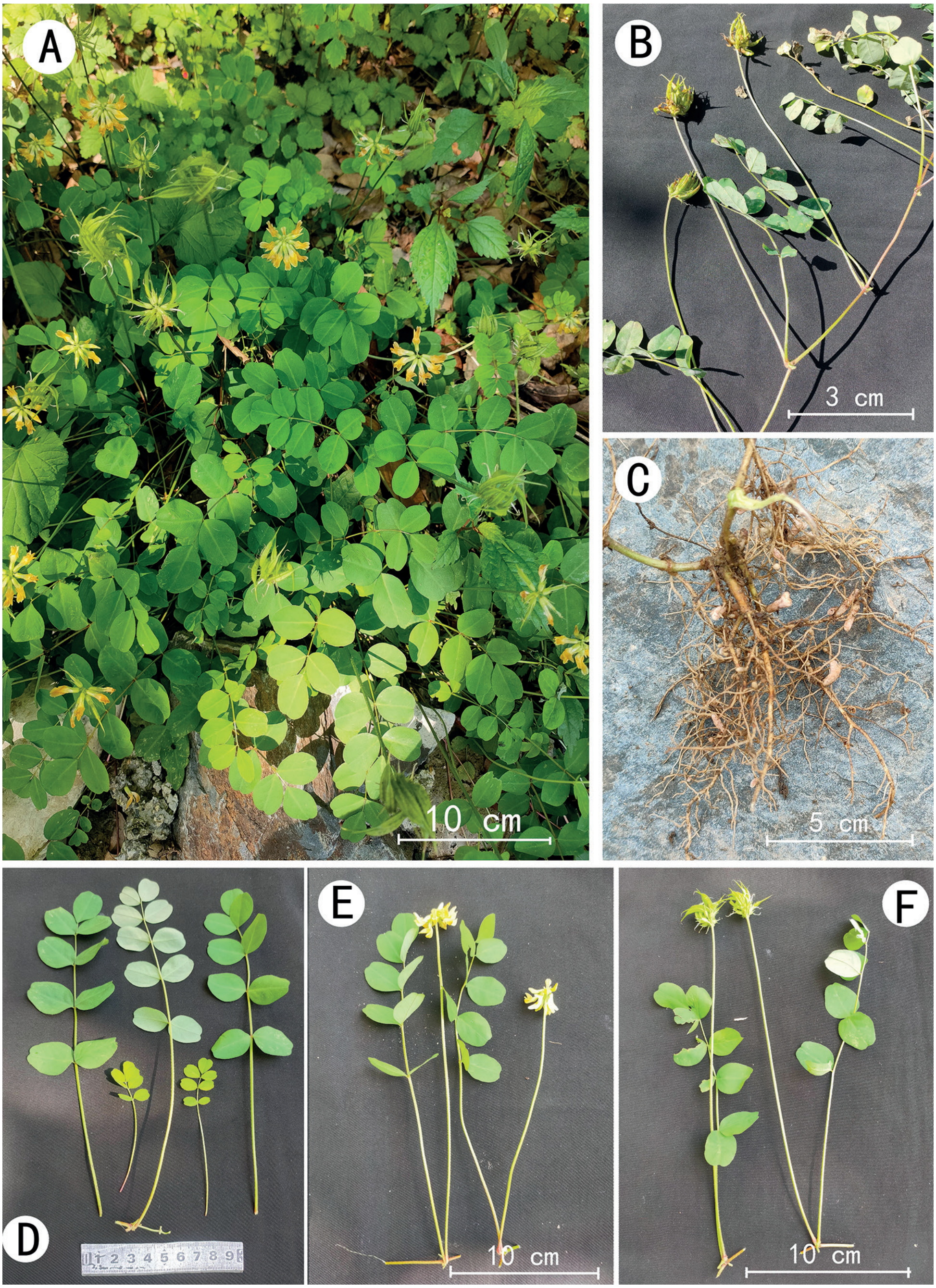

Figure 1. *Astragalus bashanensis* sp. nov. **A** population **B** branches **C** root **D, E, F** leaves.

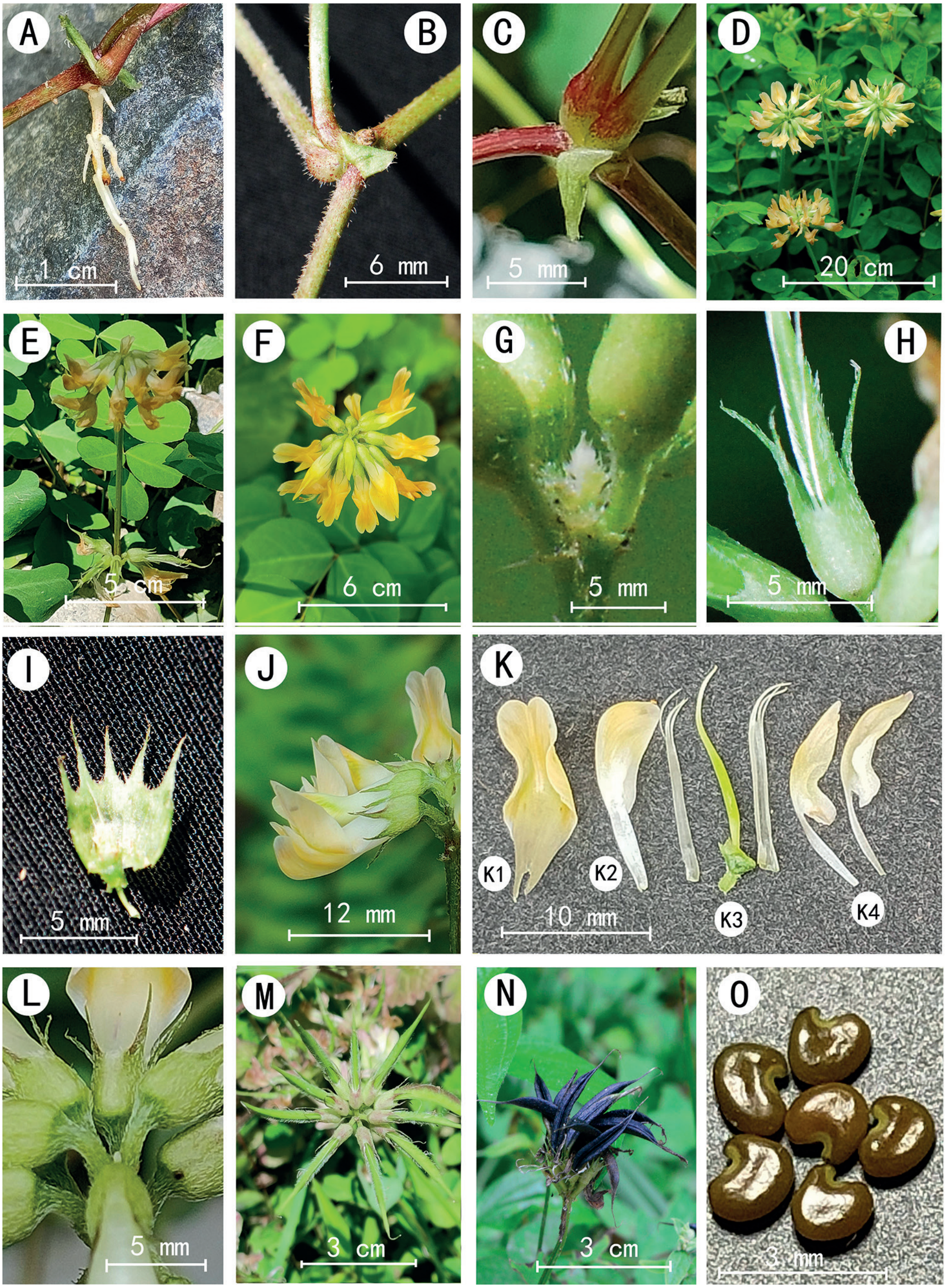

Figure 2. *Astragalus bashanensis* sp. nov. **A** adventitious roots **B** petioles **C** stipules **D** flowering plant **E, F** umbellate racemes **G** bracts **H** calyx **I** opened calyx **J, K** corolla **K1** standard **K2** keel-petal **K3** ovary and stamens **K4** wings **L** pedicels **M** young fruits **N** mature fruits **O** seeds.

Description. Herbs annual or biennial. Primary root slender, 8–12 cm long, yellowish; nodules sparsely on lateral roots. Stem 20–70 cm long, spreading white pubescent; branches from base, prostrate or decumbent, rooting at nodes, internodes 3–8 cm long. Stipules free, triangle-ovate, 3–5 mm long, base 3–4 mm wide, glabrous or with few hairs at apex. Petioles 5–13 cm long, longer than the leaf rachis, spreading-white-pubescent, thickened at base. Leaves odd-pinnate, 7–9-foliolate, rarely even-pinnate 10-foliolate, 5–13.5 cm long, 2.5–6.3 cm wide; rachis sparsely pubescent; leaflets broadly elliptic or broadly obovate, 0.8–3.1 cm long, 0.7–2.4 cm wide, apex emarginate, base rounded or broadly cuneate, margin entire, adaxial surface glabrous, abaxial surface sparsely appressed white-pubescent, the hairs on nerves denser; petiolules less than 1 mm long, densely pubescent. Racemes umbellate, 6–20-flowered, in one, rarely two umbels; peduncles axillary, erect, 10–20 cm long, up to 15–26 cm in fruit, sparsely pubescent; bracts ovate ca. 0.5 mm long, ciliate, white, deciduous after anthesis; pedicels 0.5–1.5 mm long, white-pubescent; flowers spreading or nutant. Calyx tubular, out surface sparsely appressed white-pubescent; tube ca. 3 mm long; lobes 5, subulate, 2.6–3.2 mm long, lower two shorter than the tube, upper three longer than or as long as the tube. Corolla whitish, creamy-yellow, yellowish or deep yellow; standard obovate, 10–13 mm long, 4–5 mm wide, apex emarginate, base broadly cuneate with short claw; wings 8–10 mm long, claw scarcely shorter than the limb, limb oblique-oblong; keel-petal 7–9 mm long, limb crescent-shaped, base auriculate, claw ca. 2/3 of limb length. Stamens (9) + 1, white, ca. as long as the keel-petal. Ovary narrowly linear, both sides white pubescent; style filiform, glabrous. Pod linear, lateral oblate and green when young; mature pod swelling into boat-like, blackish, 2.5–3 cm long, ca. 4 mm wide, both sides persistent white-pubescent, apex with a thicker beak ca. 1 cm long. Seed dark green-brown, lustrous, orbicular-reniform or reniform, 1.5–1.8 mm long.

Phenology. Flowering from late May to early July; fruiting from mid-June to late August.

Distribution and habitat. Populations of *Astragalus bashanensis* are known from Quanxi Town, Zhongfeng Town, Longba Town, Jiangjiayan Town, Piantoushan National Forest Park and Baguashan Provincial Nature Protection Area of Zhuxi County and it is also widely distributed in Shennongjia National Forest Park, western Hubei, Central China. It grows in roadside grassland, on mountain slopes, forest edges or under forest canopy at elevations from 600 to 2160 m.

Etymology. The specific epithet is derived from the type locality of the new species. Bashan is an abbreviation for Dabashan or Daba Mountains.

Vernacular name. Ba Shan Huang Qi (Chinese).

Conservation assessment. During our field investigations in 2021 and 2022, many populations of *A. bashanensis* have been found in Zhuxi County and Shennongjia Forest Region. The numbers of individuals of each population ranges from dozens to thousands. In addition, it is distributed along roadsides as a weed. We believe that it should have a much wider distribution than what is now known. Due to its wide distribution range and large population size, *A. bashanensis* is here recommended as Least Concern (LC) (IUCN 2022).

Results. *Astragalus bashanensis* is most similar to *A. sinicus* and *A. wulingensis* in having prostrate stems, simple hairs, umbellate racemes, outer surface of calyx sparsely appressed white-pubescent and blackish and boat-like pods, but it can be easily distinguished from both by its spreading-pubescent indumentum on stems and petioles (vs. ascending-pubescent in *A. sinicus*; appressed-puberulent in *A. wulingensis*), long petioles (5–13 cm long), longer than the leaf rachis (vs. much shorter than the leaf rachis), white bracts (vs. green or flushed purplish), corolla whitish or yellow (vs. purple, pink to white or yellowish flushed purplish at apex), longer claw of the keel-petal (vs. much shorter), both sides of pods persistent pubescent (vs. glabrous or glabrate) and smaller seeds 1.5–1.8 mm long (vs. 2–3 mm long). The diagnostic features between *A. bashanensis*, *A. wulingensis* and *A. sinicus* are summarised in Table 1.

Table 1. Morphological comparisons of *Astragalus bashanensis*, *A. wulingensis*, and *A. sinicus*.

Characters	*A. wulingenesis*	*A. bashanensis*	*A. sinicus*
Stems	30–80 cm long	20–70 cm long	10–30 cm long
Stipules	ciliate	glabrous or with few hairs at apex	ciliate
Petioles	3–5 cm long, much shorter than the leaf rachis	5–13 cm long, longer than the leaf rachis	0.5–4 cm long, much shorter than the leaf rachis
Indumentum on stems and petioles	sparsely appressed-pubescent	spreading-pubescent	sparsely ascending-pubescent
Leaflets	1.5–2.8 × 0.8–1.1 cm	0.8–3.1 × 0.7–2.4 cm	0.5–1.7 × 0.3–1.3 cm
Bracts	green or flushed purplish	white	green or flushed purplish
Calyx	tubular, ca. 7 mm long	tubular, 5–6 mm long	campanulate, 3–5 mm long
Lobes of calyx	subulate, 3–4 mm long	subulate, 2.6–3.2 mm long	lanceolate, 1–2 (–3) mm long
Corolla colour	white or yellow, apex flushed purplish	whitish, creamy yellow, yellowish or deep yellow	purple, pink to pure white
Claw of keel-petal	ca. as long as the limb	ca. 2/3 length of the limb	ca. 1/3 length of the limb
Wings	10–13 mm long, claw as long as the limb	8–10 mm long, claw scarcely shorter than the limb	7–11 mm long, claw ca. 1/3 length of the limb
Pods	3–4 cm long, glabrous	2.5–3 cm long, both sides persistent-pubescent	1.2–2 cm long, glabrous or glabrate
Seeds	orbicular-deltoid, 2–2.2 mm long, red-brown	orbicular-reniform or reniform, 1.5–1.8 mm long, dark green-brown	reniform, 2–3 mm long, green-brown

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RESEARCH ARTICLE

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Ranunculus jiguanshanicus (Ranunculaceae), a new species from Sichuan, China

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Abstract

Ranunculus jiguanshanicus (Ranunculaceae), a new species from Chongzhou in Sichuan province, China, is here described and illustrated. The new species is easily distinguishable from other Chinese members of the genus by an array of characters, including small stature, glabrous and prostrate stems, 3-foliolate leaves with obvious petiolules (3–5 mm long), unequally 3-sected leaflets, lanceolate to linear ultimate leaflet segments, small flowers (5.2–6 mm in diameter), and long styles in the carpels and achenes (ca. 0.8 mm long). A distribution map of this new species is also provided.

Keywords

Asia, buttercups, Ranunculales, *Ranunculus glareosus*, *Ranunculus pegaeus*

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Introduction

Ranunculus L., comprising approximately 600 species, is the largest genus in the Ranunculaceae and is widely distributed in all continents (Tamura 1995; Hörandl et al. 2005; Paun et al. 2005; Hörandl and Emadzade 2012). In China, one of the centers of species diversity of *Ranunculus*, more than 150 species and 30 varieties are currently recognized in the genus (Wang 1995a, b, 1996, 2007, 2008, 2013, 2015, 2016, 2018, 2019a, b, 2022; Yang 2000; Wang and Gilbert 2001; Wang and Liao 2009; Luo and Zhao 2013; Wang and Chen 2015; Wang et al. 2016; Yuan and Yang 2017a, b, c; Zhang et al. 2020; Fei et al. 2022, 2023a, b).

During a survey of herbarium specimens of *Ranunculus* from China for the first author's Ph.D. dissertation project, one gathering, *W.B. Ju, L. Zhang & D.K. Chen AZH01290* (CDBI) (Fig. 1), from Jiguan Shan in the Anzihe Nature Reserve in Chongzhou, Sichuan province, China, caught our attention. This gathering had been previously identified on the determination slips as *R. glareosus* Hand.-Mazz., a species distributed in China's Qinghai, Sichuan, Xizang (Tibet) and Yunnan (Handel-Mazzetti 1931; Liou 1980; Wang and Gilbert 2001). The plants on the two sheets of the gathering, which have unique leaf morphology and very small flowers, certainly do not belong to *R. glareosus* or any other members of *Ranunculus* currently known for China.

During a botanical expedition to Sichuan from June to July 2022, we successfully discovered a flowering population of this species in early June on Jiguan Shan in Chongzhou, where the gathering *W.B. Ju*, *L. Zhang & D.K. Chen AZH01290* was made. Moreover, we discovered a fruiting population in early July on Xiling Xue Shan in Dayi, a mountain closely adjacent to Jiguan Shan. Based on our observations of living plants in the wild, we confirmed all the diagnostic characters of the new species observed from the herbarium specimens and determined that the gathering and the two populations in question represent a new species. Morphologically, this new species is somewhat similar to *R. pegaeus* Hand.-Mazz., a species occurring in southwestern China (Sichuan, Xizang, Yunnan), India (Sikkim) and Nepal (Handel-Mazzetti 1939; Liou 1980; Wang and Gilbert 2001), but differs by an array of characters. It is described below as *R. jiguanshanicus*.

Materials and methods

For morphological comparison, we critically examined specimens or high-resolution specimen images of *Ranunculus glareosus*, *R. jiguanshanicus* and *R. pegaeus* at CDBI, E, KUN, PE, and WU (acronyms according to Thiers 2022). We also observed living plants in one population each in *R. glareosus* (Menyuan in Qinghai province) and *R. pegaeus* (Maoxian in Sichuan province) and those in two populations of *R. jiguanshanicus* (Chongzhou and Dayi in Sichuan province). The morphological description of *R. jiguanshanicus* was based on observations of both herbarium specimens and living plants in the wild.

Taxonomy

Ranunculus jiguanshanicus **W.Q.Fei, Q.Yuan & Q.E.Yang, sp. nov.**
urn:lsid:ipni.org:names:77312739-1
Figs 1–5

Diagnosis. *Ranunculus jiguanshanicus* is readily distinguishable from all other Chinese species of *Ranunculus* by a unique array of characters, including small stature, glabrous and prostrate stems, 3-foliolate leaves with obvious petiolules (3–5 mm long), unequally 3-sected leaflets, lanceolate to linear ultimate leaflet segments, small flowers (5.2–6 mm in diameter), and long styles in the carpels and achenes (ca. 0.8 mm long).

Type. China. Sichuan province: Chongzhou, Anzihe Nature Reserve, Jiguan Shan, 30°46'5.8"N, 103°10'21.93"E, alt. 2998 m, among moss on rocks or rocky cliffs in moist places in fir forests, 10 June 2022, *W.Q. Fei 581* (holotype: IBSC; isotypes: IBSC, PE).

Description. ***Herbs*** perennial, terrestrial or rupicolous. ***Roots*** 2–5, 6–10 cm long, fibrous, slender, slightly thickened at base. ***Stems*** 7–15 cm long, prostrate, glabrous, unbranched to few-branched. ***Basal leaves*** 2–5, 3-foliolate, long-petiolate; petioles 2–4 cm long, glabrous; blades 0.8–1 × 0.8–1.3 cm, suborbicular, thinly chartaceous, adaxially green, abaxially light green, both sides glabrous; leaflets 3, unequally 3-sected,

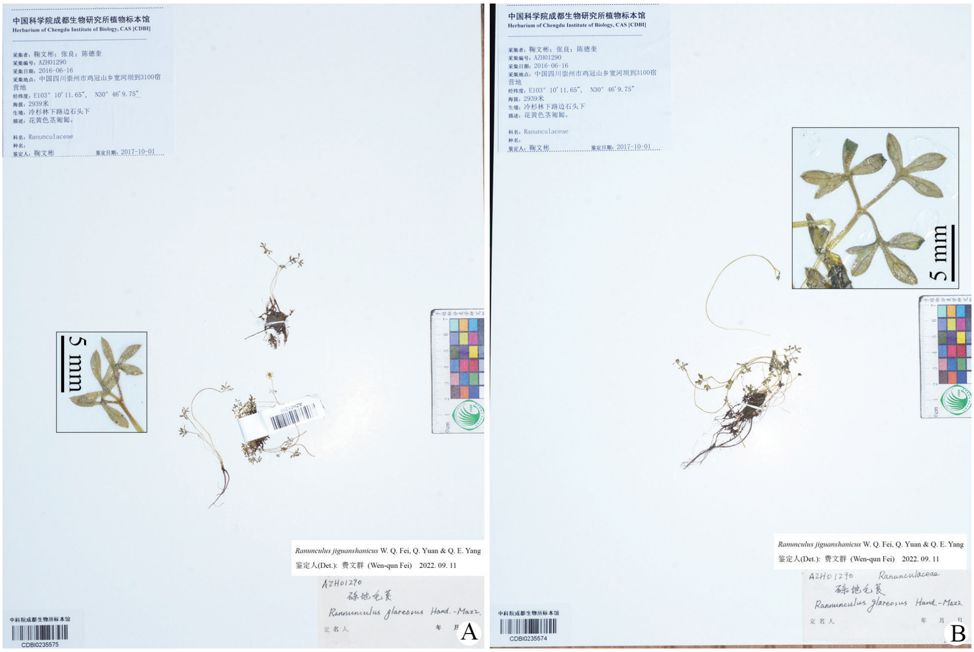


Figure 1. Two specimens of *Ranunculus jiguanshanicus* sp. nov. (**A, B**) previously misidentified as *R. glareosus*. China, Sichuan province, Chongzhou, Anzihe Nature Reserve, Jiguan Shan, 30°46'9.75"N, 103°10'11.65"E, alt. 2939 m, on rocks in fir forest, 16 June 2016, *W.B. Ju, L. Zhang & D.K. Chen AZH01290* (CDBI). Insets: leaf blades.

Figure 2. *Ranunculus jiguanshanicus* sp. nov. in the wild **A, B** habitat **C** habit. The left plant (at fruiting stage) in **B** photographed by De-Chang Meng from Xiling Xue Shan in Dayi, Sichuan province, and the right two plants (at flowering stage) photographed by Wen-Qun Fei from Jiguan Shan in the Anzihe Nature Reserve in Chongzhou, Sichuan province.

petiolulate, petiolules 3–5 mm long, ultimate leaflet segments 3–4 × 0.8–1.2 mm, narrowly lanceolate to linear, margin entire, apex 1–2-denticulate to 1–2-cleft. ***Lower cauline leaves*** 2–3, similar to basal ones but smaller. ***Upper cauline leaves*** 1–2, 3-foliolate, subsessile or sessile, adaxially glabrous or sparsely puberulous, abaxially glabrous, central leaflet 4.5–5 × 1–1.2 mm, narrowly lanceolate to linear, margin entire, lateral leaflets

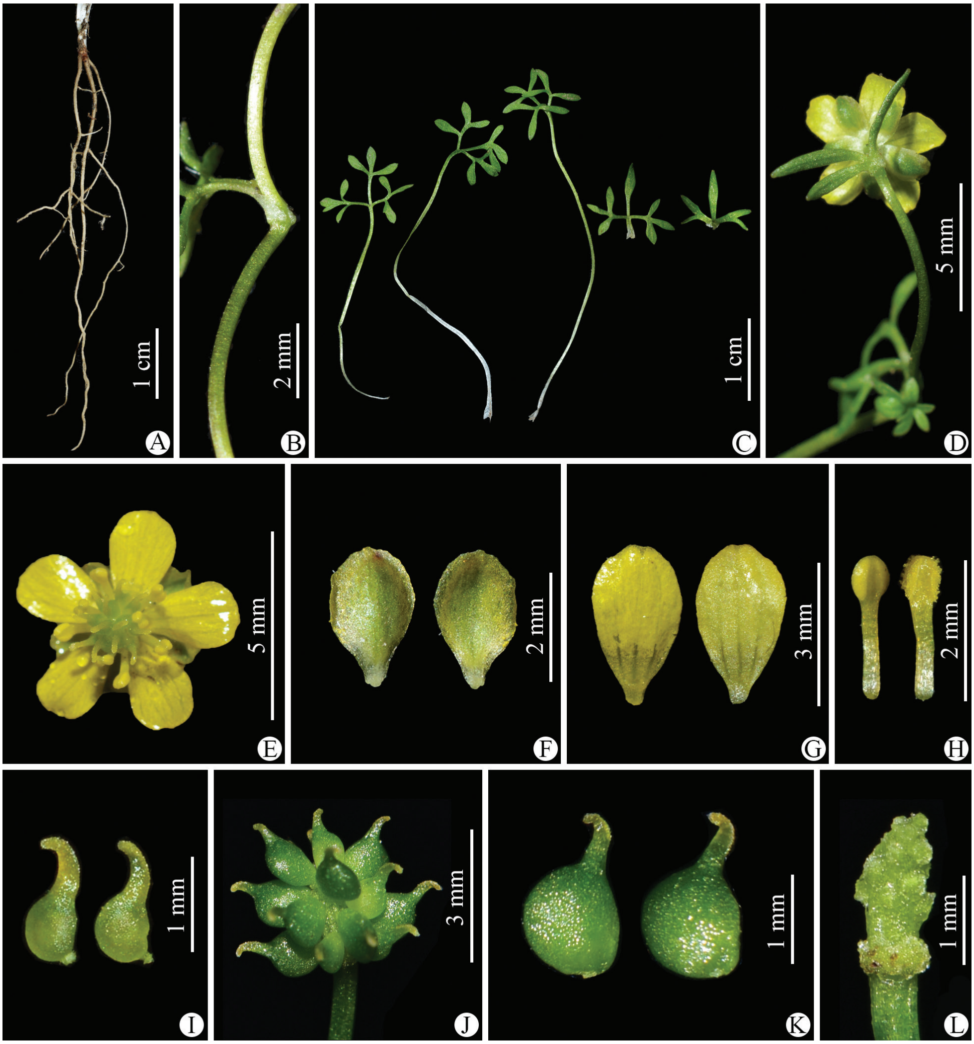
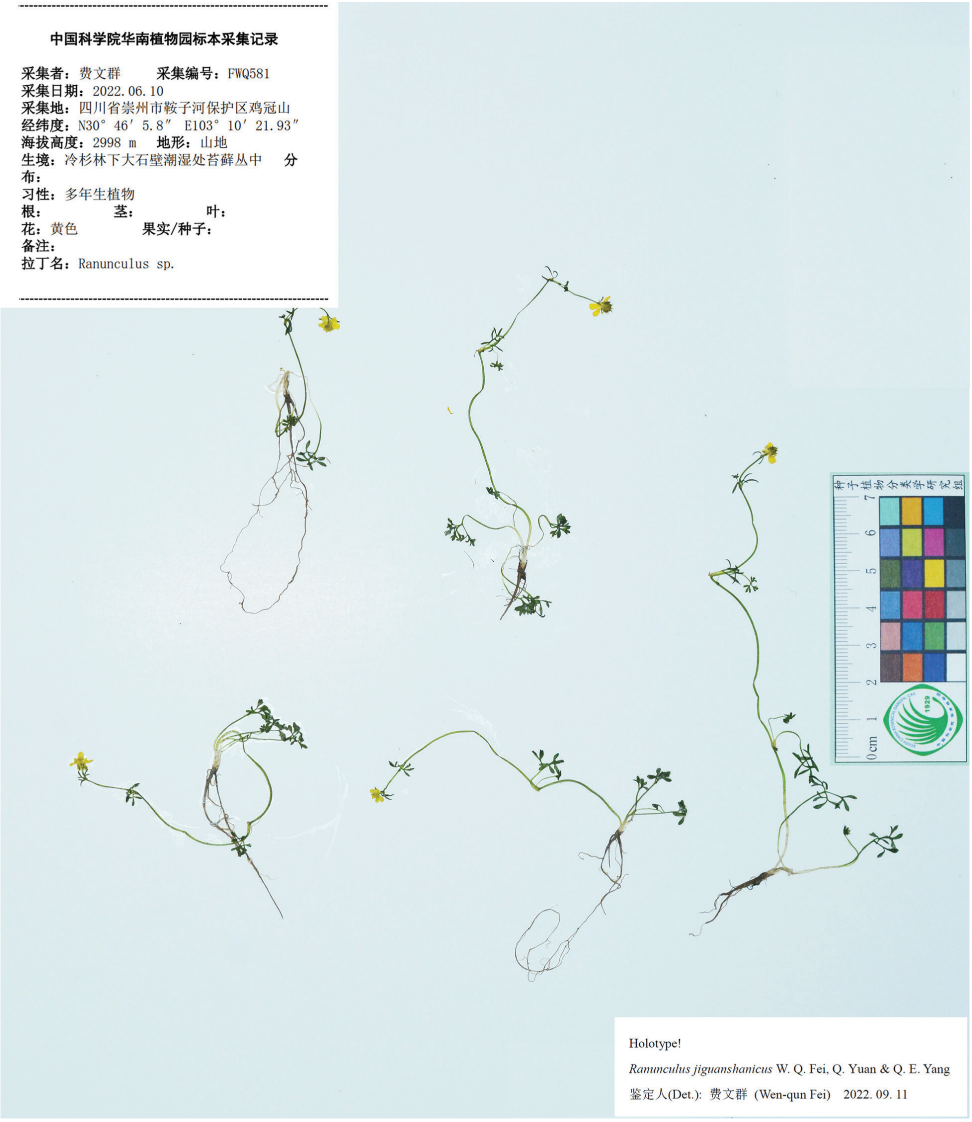


Figure 3. *Ranunculus jiguanshanicus* sp. nov. in the wild **A** roots **B** portion of stem **C** leaves **D** flower (lateral view) **E** flower (top view) **F** sepal (left: abaxial side; right: adaxial side) **G** petal (left: adaxial side; right: abaxial side) **H** stamens **I** carpels **J** aggregate fruit **K** achenes **L** receptacle. **A–H** photographed by Wen-Qun Fei from the population on Jiguan Shan in Chongzhou, Sichuan province and **I–L** photographed by De-Chang Meng from the population on Xiling Xue Shan in Dayi, Sichuan province.

entire, 1–2-lobate or 2–3-sected, ultimate leaflet segments 3–3.5 × 1–1.2 mm, narrowly lanceolate to linear. ***Inflorescences*** terminal, 1(–2)-flowered. ***Flowers*** 5.2–6 mm in diameter; pedicels 1–2 cm long, glabrous or sparsely puberulous; receptacles ca. 1.2 mm long, clavate, glabrous; sepals 5, 2.2–2.5 × 1.5–1.8 mm, elliptic to obovate, patent, green tinged with yellowish, concave, both sides glabrous; petals 5(–6), 3.2–3.5 × 1.8–2 mm, obovate, yellow, glabrous, apex rounded, nectary pit without



中国科学院华南植物园标本采集记录

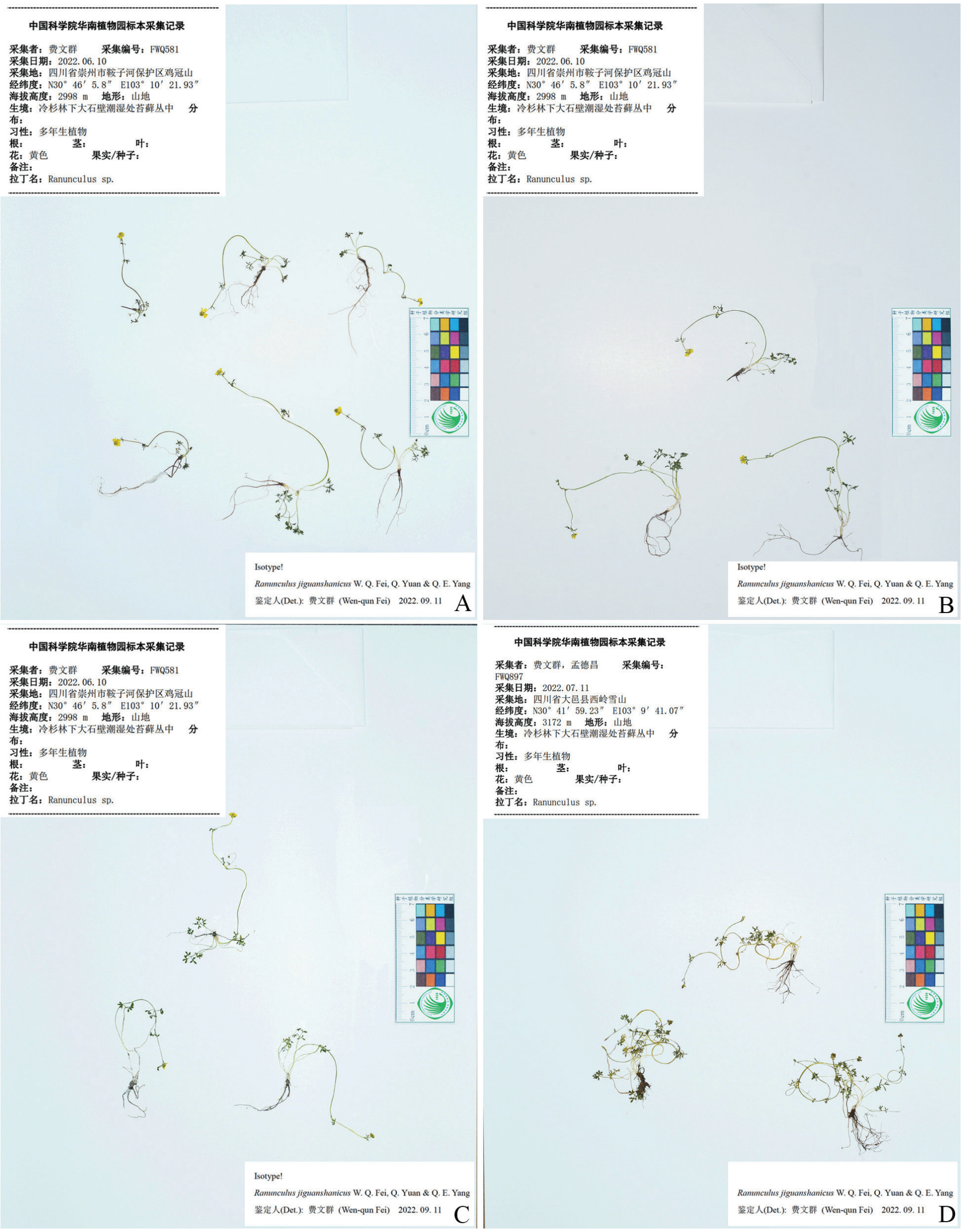
采集者：费文群　　**采集编号：**FWQ581
采集日期：2022.06.10
采集地：四川省崇州市鞍子河保护区鸡冠山
经纬度：N30° 46′ 5.8″ E103° 10′ 21.93″
海拔高度：2998 m　**地形：**山地
生境：冷杉林下大石壁潮湿处苔藓丛中　**分布：**
习性：多年生植物
根：　**茎：**　**叶：**
花：黄色　**果实/种子：**
备注：
拉丁名：Ranunculus sp.

Holotype!
Ranunculus jiguanshanicus W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 11

Figure 4. Holotype sheet of *Ranunculus jiguanshanicus* sp. nov.

a scale, claws ca. 0.4 mm long; stamens 6–8, ca. 2 mm long, filaments ca. 1.5 mm long, narrowly linear, anthers ca. 0.5 mm long, oblong; gynoecium subglobose; carpels 8–12, ovaries ca. 0.8 × 0.6 mm, ovoid, laterally flattened, biconvex, glabrous, styles ca. 0.8 mm long, glabrous, apex recurved. ***Aggregate fruit*** ca. 4 × 4.2 mm, subglobose; achenes ca. 1.2 × 1 mm, widely ovoid, laterally flattened, biconvex, glabrous, styles ca. 0.8 mm long, persistent, glabrous, apex recurved.

Etymology. The specific epithet refers to the type locality of the new species, i.e. Jiguan Shan in the Anzihe Nature Reserve in Chongzhou, Sichuan province, China.



中国科学院华南植物园标本采集记录
采集者：费文群　　采集编号：FWQ581
采集日期：2022.06.10
采集地：四川省崇州市鞍子河保护区鸡冠山
经纬度：N30° 46′ 5.8″ E103° 10′ 21.93″
海拔高度：2998 m　地形：山地
生境：冷杉林下大石壁潮湿处苔藓丛中　分布：
习性：多年生植物
根：　茎：　叶：
花：黄色　果实/种子：
备注：
拉丁名：Ranunculus sp.

Isotype!
Ranunculus jiguanshanicus W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 11

中国科学院华南植物园标本采集记录
采集者：费文群　　采集编号：FWQ581
采集日期：2022.06.10
采集地：四川省崇州市鞍子河保护区鸡冠山
经纬度：N30° 46′ 5.8″ E103° 10′ 21.93″
海拔高度：2998 m　地形：山地
生境：冷杉林下大石壁潮湿处苔藓丛中　分布：
习性：多年生植物
根：　茎：　叶：
花：黄色　果实/种子：
备注：
拉丁名：Ranunculus sp.

Isotype!
Ranunculus jiguanshanicus W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 11

中国科学院华南植物园标本采集记录
采集者：费文群　　采集编号：FWQ581
采集日期：2022.06.10
采集地：四川省崇州市鞍子河保护区鸡冠山
经纬度：N30° 46′ 5.8″ E103° 10′ 21.93″
海拔高度：2998 m　地形：山地
生境：冷杉林下大石壁潮湿处苔藓丛中　分布：
习性：多年生植物
根：　茎：　叶：
花：黄色　果实/种子：
备注：
拉丁名：Ranunculus sp.

Isotype!
Ranunculus jiguanshanicus W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 11

中国科学院华南植物园标本采集记录
采集者：费文群，孟德昌　　采集编号：FWQ897
采集日期：2022.07.11
采集地：四川省大邑县西岭雪山
经纬度：N30° 41′ 59.23″ E103° 9′ 41.07″
海拔高度：3172 m　地形：山地
生境：冷杉林下大石壁潮湿处苔藓丛中　分布：
习性：多年生植物
根：　茎：　叶：
花：黄色　果实/种子：
备注：
拉丁名：Ranunculus sp.

Ranunculus jiguanshanicus W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 11

Figure 5. Isotype (**A–C**) and paratype (**D**) sheets of *Ranunculus jiguanshanicus* sp. nov.

Phenology. Flowering in early June; fruiting at the end of June.

Distribution and habitat. *Ranunculus jiguanshanicus* is currently known from its type locality, i.e., Jiguan Shan in the Anzihe Nature Reserve in Chongzhou, and from the closely adjacent Xiling Xue Shan in Dayi, both in Sichuan province, China (Fig. 6).

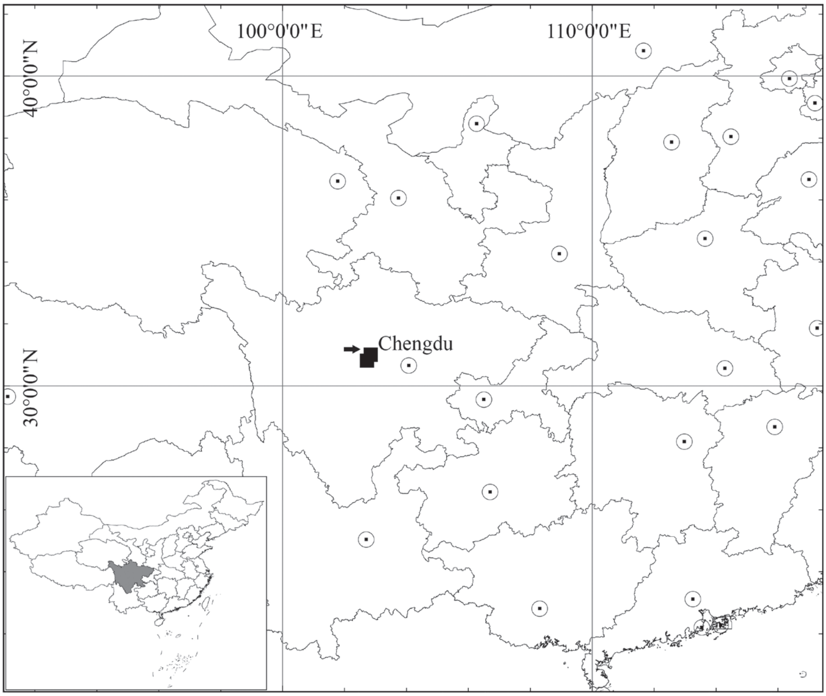


Figure 6. Distribution of *Ranunculus jiguanshanicus* sp. nov. (black square). Arrow indicates the type locality.

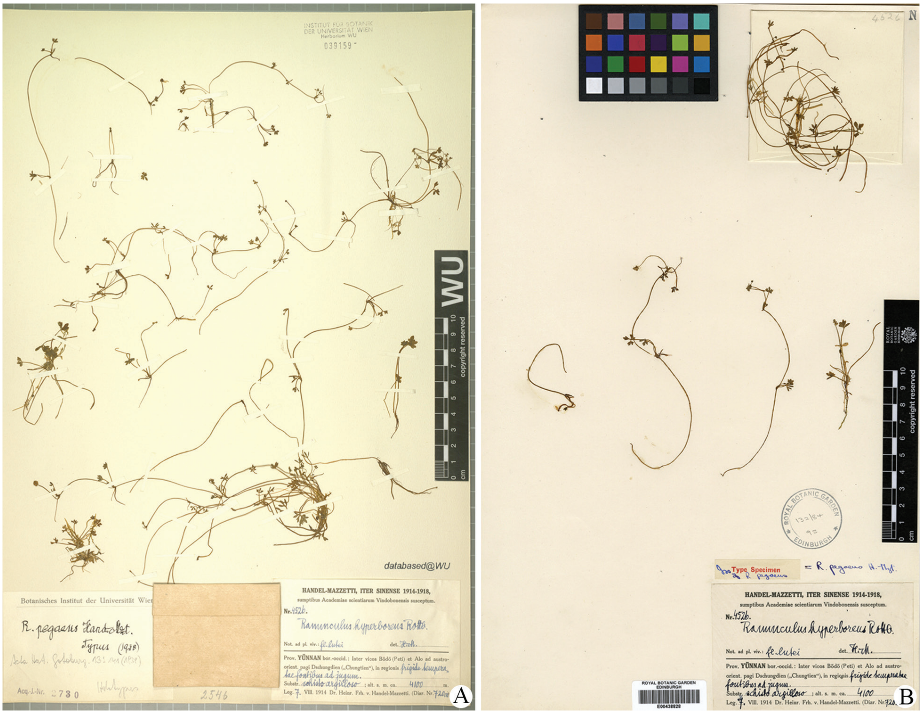


Figure 7. Type sheets (**A, B**) of *Ranunculus pegaeus*.

Figure 8. *Ranunculus pegaeus* in the wild (China, Sichuan, Maoxian) **A, B** habitat **C** habit. Photographed by Wen-Qun Fei.

It grows among moss on rocks or rocky cliffs in moist places in fir forests at altitudes of 2900–3150 m above sea level.

Conservation status. *Ranunculus jiguanshanicus* is currently known only from two populations in Sichuan province, China. The Chongzhou population consists of ca. 150 individuals within an area of less than 10 m^2. The size of the Dayi population remains unknown. The conservation status of *R. jiguanshanicus* should better be categorized as "Data Deficient (DD)" before adequate information of this species is acquired (IUCN Standards and Petitions Committee 2022).

Discussion. *Ranunculus jiguanshanicus* is readily assigned to *R.* sect. *Ranunculus* due to its swollen achenes with a distinct beak and receptacles hardly enlarged after anthesis. In his infrageneric classification of the Chinese *Ranunculus*, Wang (1995a, b) placed almost all the alpine species within this section under the name *R.* sect. *Auricomus* (Spach) Schur.

Morphologically, *Ranunculus jiguanshanicus* is somewhat similar to *R. pegaeus* (Figs 7–10), also a member of *R.* sect. *Ranunculus*, in having prostrate and glabrous stems (Figs 2A, B, 8A, B), small flowers (Figs 3D, 9D), subglobose aggregate

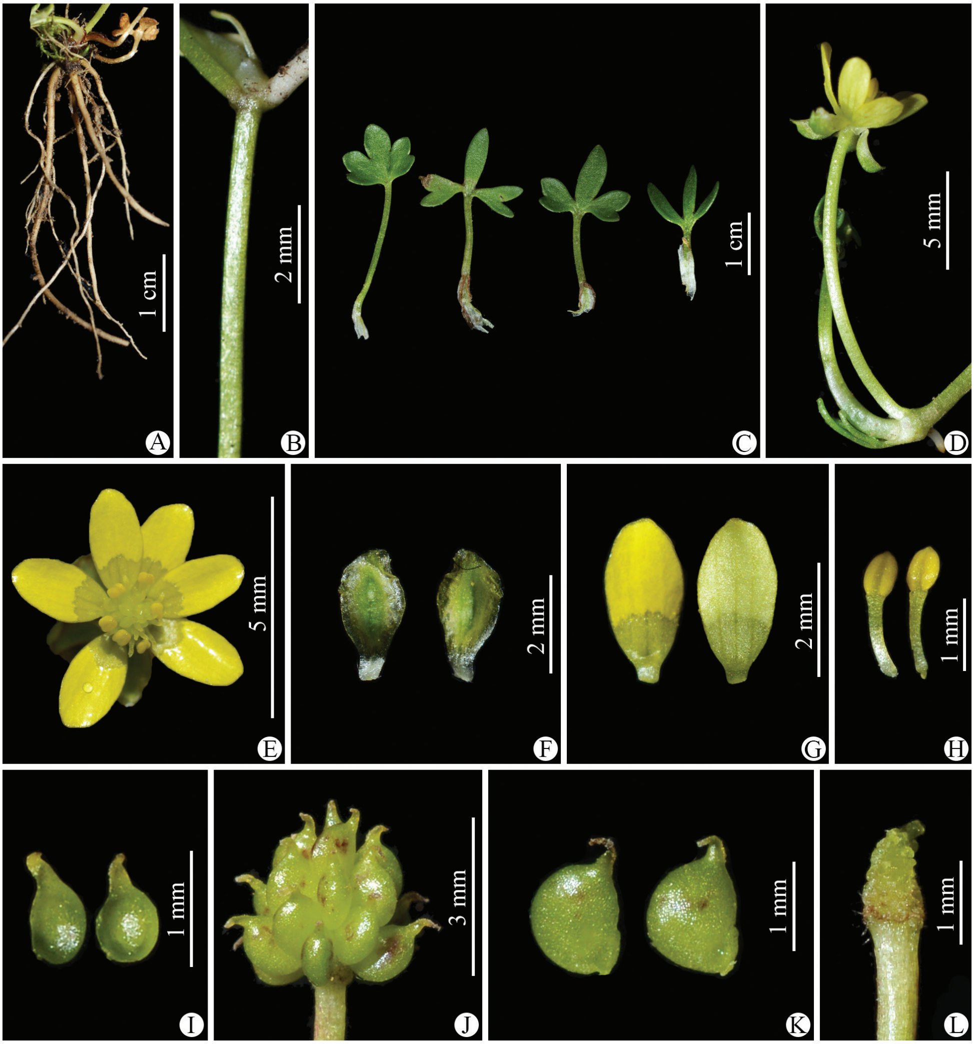
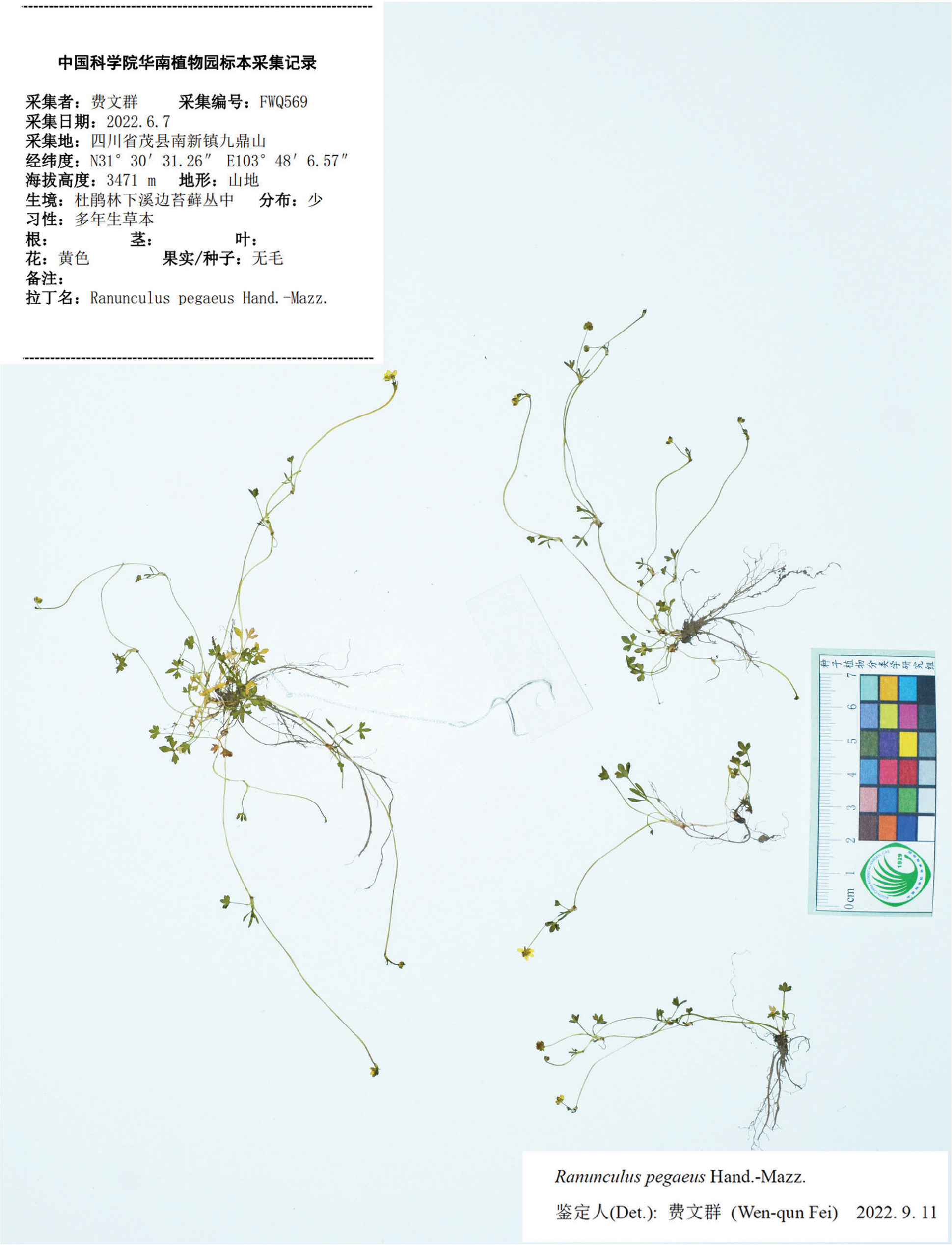


Figure 9. *Ranunculus pegaeus* in the wild (China, Sichuan, Maoxian) **A** roots **B** portion of stem **C** leaves **D** flower (lateral view) **E** flower (top view) **F** sepal (left: abaxial side; right: adaxial side) **G** petal (left: adaxial side; right: abaxial side) **H** stamens **I** carpels **J** aggregate fruit **K** achenes **L** receptacle. Photographed by Wen-Qun Fei.



中国科学院华南植物园标本采集记录

采集者：费文群 采集编号：FWQ569
采集日期：2022.6.7
采集地：四川省茂县南新镇九鼎山
经纬度：N31° 30′ 31.26″ E103° 48′ 6.57″
海拔高度：3471 m 地形：山地
生境：杜鹃林下溪边苔藓丛中 分布：少
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：无毛
备注：
拉丁名：Ranunculus pegaeus Hand.-Mazz.

Ranunculus pegaeus Hand.-Mazz.
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022. 9. 11

Figure 10. *Ranunculus pegaeus*. China, Sichuan, Maoxian, *W.Q. Fei 569* (IBSC).

fruit (Figs 3I, 9I), and glabrous carpels (Figs 3H, 9H), achenes (Figs 3G, 9G) and receptacles (Figs 3K, 9K). However, it differs by having 3-foliolate leaves with obvious petiolules (3–5 mm long), unequally 3-sected leaflets, lanceolate to linear, entire or 1–2-denticulate to 1–2-cleft ultimate leaflet segments (Fig. 3C), and styles

Figure 11. Type sheet of *Ranunculus glareosus*.

Figure 12. *Ranunculus glareosus* in the wild (China, Qinghai, Menyuan) **A, B** habitat **C** habit. Photographed by Wen-Qun Fei.

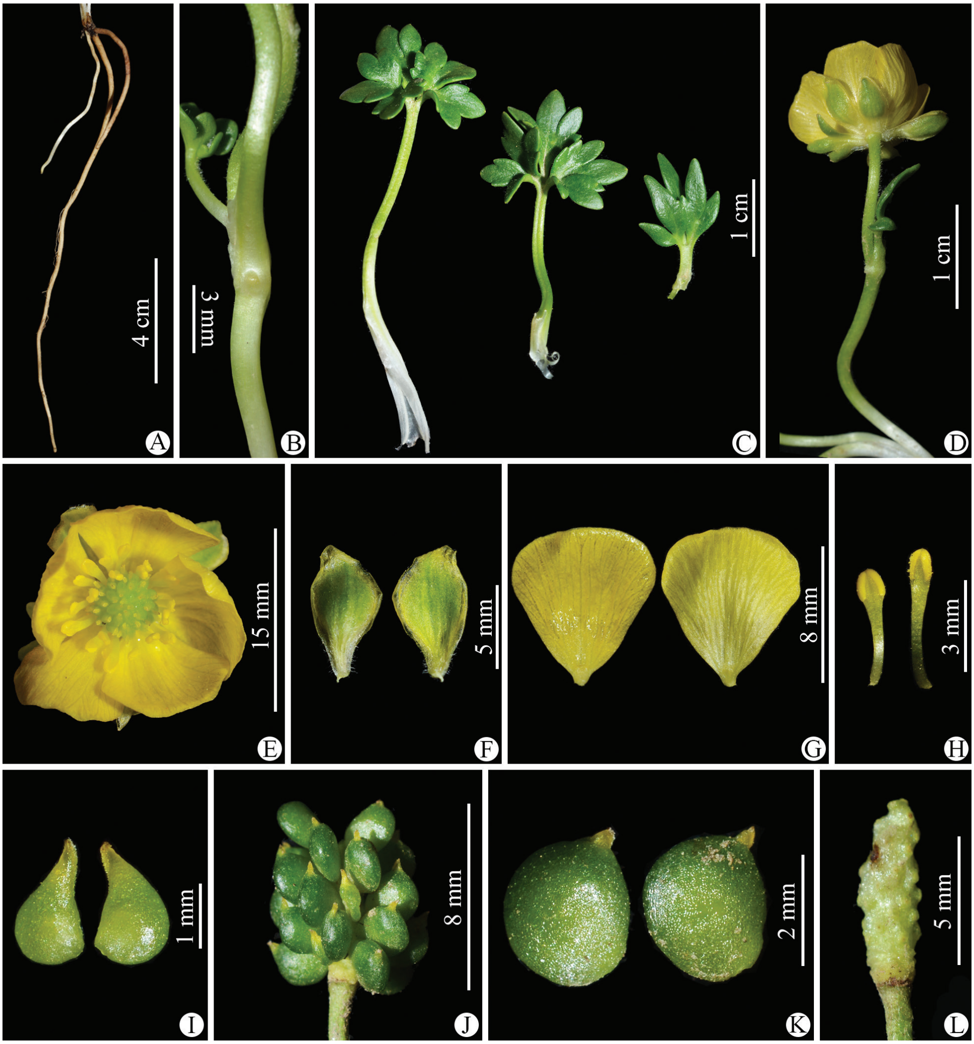


Figure 13. *Ranunculus glareosus* in the wild (China, Qinghai, Menyuan) **A** roots **B** portion of stem **C** leaves **D** flower (lateral view) **E** flower (top view) **F** sepal (left: abaxial side; right: adaxial side) **G** petal (left: adaxial side; right: abaxial side) **H** stamens **I** carpels **J** aggregate fruit **K** achenes **L** receptacle. Photographed by Wen-Qun Fei.

in the carpels and achenes ca. 0.8 mm long (Fig. 3H, G). In *R. pegaeus*, the leaves are 3-partite, 3-sected or 3-foliolate with the central segment/leaflet rhombic or oblong, entire or 3-denticulate and the lateral segments/leaflets obliquely flabellate, entire or unequally 2-cleft (Figs 9C, 10), and styles in the carpels and achenes ca. 0.3 mm long (Fig. 9H, G). A detailed morphological comparison between *R. jiguanshanicus* and *R. pegaeus* is given in Table 1.

中国科学院华南植物园标本采集记录

采集者：费文群　　**采集编号：**FWQ623
采集日期：2022.6.26
采集地：青海省门源县达坂山
经纬度：N37° 20′ 12.24″　E101° 24′ 8.97″
海拔高度：4004 m　**地形：**山地
生境：流石滩　**分布：**少
习性：多年生草本
根：　　**茎：**　　**叶：**
花：黄色　　**果实/种子：**无毛
备注：
拉丁名：Ranunculus glareosus Hand.-Mazz.

Ranunculus glareosus Hand.-Mazz.
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022.9.11

Figure 14. *Ranunculus glareosus*. China, Qinghai, Menyuan, *W.Q. Fei 623* (IBSC).

Table 1. Morphological comparison of *Ranunculus glareosus*, *R. jiguanshanicus* sp. nov. and *R. pegaeus*.

	R. glareosus	*R. jiguanshanicus*	*R. pegaeus*
Roots	2–5, more than 15 cm long	2–5, 6–10 cm long	5–10, 8–12 cm long
Stems	sparsely puberulous	glabrous	glabrous
Basal leaves	3-sected or 3-foliolate, fleshy, adaxially glabrous or sparsely puberulous, abaxially glabrous, central segment/leaflet ovate or rhombic, entire or 3-lobate, lateral segments/leaflets flabellate, unequally 2-partite	3-foliolate, thinly chartaceous, both sides glabrous, leaflets unequally 3-sected, with ultimate leaf segments narrowly lanceolate to linear, entire or 1–2-denticulate to 1–2-cleft	3-partite, 3-sected or 3-foliolate, thinly chartaceous, both sides glabrous, central segment/leaflet rhombic or oblong, entire or 3-denticulate, lateral segments/leaflets obliquely flabellate, entire or unequally 2-cleft
Flowers	terminal, 1–4, 15–17 mm in diameter	terminal, 1(–2), 5.2–6 mm in diameter	terminal or axillary, 3–7, 5.5–8 mm in diameter
Receptacles	3–5 mm long, clavate, glabrous	ca. 1.2 mm long, clavate, glabrous	ca. 1 mm long, clavate, glabrous
Sepals	adaxially glabrous, abaxially puberulous	both sides glabrous	both sides glabrous
Petals	9–10 × 7–8 mm, widely obovate	3.2–3.5 × 1.8–2 mm, obovate	3–3.5 × 1.5–1.7 mm, obovate
Carpels	20–35; ovaries ovoid, glabrous; styles ca. 0.2 mm long, straight	8–12; ovaries ovoid, glabrous; styles ca. 0.8 mm long, apex recurved	18–22; ovaries ovoid, glabrous; styles ca. 0.3 mm long, apex recurved
Aggregate fruit	ellipsoid	subglobose	subglobose
Achenes	widely ovoid, glabrous, styles ca. 0.2 mm long, straight	widely ovoid, glabrous, styles ca. 0.8 mm long, apex recurved	widely ovoid, glabrous, styles ca. 0.3 mm long, apex recurved

As mentioned earlier, a gathering of *Ranunculus jiguanshanicus*, *W.B. Ju*, *L. Zhang & D.K. Chen AZH01290* (CDBI), from Chongzhou in Sichuan, the type locality of this species, had been previously misidentified as *R. glareosus* (Figs 11–14). Morphologically, *R. jiguanshanicus* is very easily distinguishable from *R. glareosus* by having glabrous stems (vs. sparsely puberulous) (Figs 3B, 13B), thinly chartaceous leaves (vs. fleshy), leaflets of the 3-foliolate leaves with obvious petiolules (3–5 mm vs. 0.5–2 mm long), unequally 3-sected, with the ultimate leaflet segments narrowly lanceolate to linear, entire or 1–2-denticulate to 1–2-cleft (vs. 3-sected or 3-foliolate, central segment/leaflet ovate or rhombic, entire or 3-lobed, and lateral segments/leaflets flabellate, unequally 2-partite) (Figs 3C, 13C), smaller flowers (5.2–6 mm vs. 15–17 mm in diameter) (Figs 3D, E, 13D, E), abaxially glabrous sepals (vs. puberulous) (Figs 3F, 13F), smaller (3.2–3.5 × 1.8–2 mm vs. 9–10 × 7–8 mm) and obovate petals (vs. widely obovate) (Figs 3G, 13G), subglobose aggregate fruit (vs. ellipsoid) (Figs 3J, 13J), and longer styles in the carpels and achenes (ca. 0.8 mm vs. ca. 0.2 mm long) (Figs 3I, K, 13I, K). In habitat, *R. jiguanshanicus* grows among moss on rocks or rocky cliffs in moist places in fir forests at altitudes of 2900–3150 m above sea level, whereas *R. glareosus* grows on alpine scree slopes at altitudes of 3900–4800 m above sea level. A detailed morphological comparison between *R. glareosus* and *R. jiguanshanicus* is given in Table 1.

Additional specimens examined (paratypes). China. **Sichuan:** Chongzhou, *W.B. Ju*, *L. Zhang & D.K. Chen AZH01290* (CDBI); Dayi, *W.Q. Fei 897* (IBSC).

Acknowledgements

We are grateful to Dr. Andrey Erst, Dr. Andriy Novikov, and Dr. Marco Pellegrini, for their valuable comments on the manuscript. We thank the curators of CDBI, E, KUN, PE, and WU for allowing us to use their scanned images of specimens and for research facilities. We also thank Jun Li and De-chang Meng for their assistance with the fieldwork. This work was supported by the National Natural Science Foundation of China (grant nos. 31870184, 31770218, 31970210).

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RESEARCH ARTICLE

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Ranunculus maoxianensis (Ranunculaceae), a new species from northwestern Sichuan, China, with an emended description of *R. chongzhouensis*, the putative closest ally of the new species

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Abstract

Ranunculus maoxianensis (Ranunculaceae), a new species from Jiuding Shan in Maoxian county, northwestern Sichuan province, China, is here illustrated and described. The species is morphologically similar to *R. chongzhouensis*, a species also occurring in Sichuan, in having reniform leaves and puberulous receptacles, carpels and achenes, but differs by having leaves adaxially puberulous with shorter appressed hairs 0.16–0.28 mm long (vs. longer appressed hairs 0.55–0.85 mm long), larger flowers (1.8–2 cm vs. 1.4–1.6 cm in diameter), larger (8–10 × 5.5–6.5 mm vs. 6–7 × 4.5–5 mm) and widely obovate petals (vs. obovate), more numerous stamens (35–55 vs. 12–18), and subglobose gynoecium and aggregate fruit (vs. ellipsoid). The two species are also different in chromosome number and chromosome morphology. *Ranunculus chongzhouensis* has a karyotype of $2n = 2x = 16 = 10m + 6sm$ while *R. maoxianensis* has a karyotype of $2n = 4x = 32 = 16m + 16sm$. An emended description of *R. chongzhouensis* is provided, and its geographical distribution is largely extended.

Keywords

Asia, buttercups, chromosome number, *Ranunculus* sect. *Ranunculus*

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Introduction

Ranunculus L., comprising approximately 600 species, is the largest genus in the Ranunculaceae and is widely distributed in all continents (Tamura 1995; Hörandl et al. 2005; Paun et al. 2005; Hörandl and Emadzade 2012). In China, one of the centers of species diversity in *Ranunculus*, more than 150 species and 30 varieties are currently recognized in the genus (Wang 1995a, b, 1996, 2007, 2008, 2013, 2015, 2016, 2018, 2019a, b, 2022; Yang 2000; Wang and Gilbert 2001; Wang and Liao 2009; Luo and Zhao 2013; Wang and Chen 2015; Wang et al. 2016; Yuan and Yang 2017a, b, c; Zhang et al. 2020; Fei et al. 2022, 2023a, b). Many taxa in the genus occur in the Hengduan Mountains region in southwestern China, including mainly southeastern Gansu, eastern Qinghai, western Sichuan, southeastern Xizang (Tibet) and northwestern Yunnan, one of the most important biodiversity hotspots worldwide (Zhang et al. 2009; Sun et al. 2017). In total, 56 species and nine varieties of *Ranunculus* are known from that region (Wang 1993, 1995a, b, 2008, 2013, 2015, 2022; Yang 2000; Wang and Gilbert 2001; Wang and Liao 2009; Wang and Chen 2015; Yuan and Yang 2017c).

During a botanical expedition to the Hengduan Mountains region from June to August 2022 for the first author's Ph.D. dissertation project, we discovered an unusual population (Figs 1, 2) of *Ranunculus* on Jiuding Shan in Maoxian county, northwestern Sichuan province, China. The plants are somewhat similar to *R. chongzhouensis* W.T. Wang (Figs 3–10), a species also occurring in Sichuan, in having reniform leaves and puberulous receptacles, carpels and achenes, but differ by an array of characters, such as the length of hairs on the adaxial side of leaf blades, size of flowers, size and shape of petals, number of stamens, and shape of the gynoecium and aggregate fruit. Moreover, our chromosomal examination revealed that the Maoxian population in question has a chromosome number of $2n = 16$ (Fig. 11A), while *R. chongzhouensis* has a chromosome number of $2n = 32$ (Fig. 11B). Therefore, we determined that this population represents a hitherto undescribed species, which we describe as *R. maoxianensis* below. Furthermore, we found that *R. chongzhouensis*, the putative closest ally of *R. maoxianensis*, is much more widely distributed than documented before and that its original description is not complete, lacking a description of root and floral characters, with the description of indumentum of leaf blades, receptacles and achenes being also incorrect. Based on our critical observations of herbarium specimens and living plants in the wild, the description of this species is here emended. We also largely extended its geographical distribution.

Materials and methods

For morphological comparison, we critically examined specimens or high-resolution specimen images of *Ranunculus* at CDBI, KUN, PE, and WCSBG (acronyms according to Thiers 2022). We also observed living plants in three populations of *R. chongzhouensis* from Sichuan and one population of the new species *R. maoxianensis* (Table 1) at flowering and fruiting time (June to July). We observed characters of roots, stems, leaves, pedicels, flowers, receptacles, petals, stamens, gynoecium, carpels,

Table 1. Information about three populations of *Ranunculus chongzhou*ensis and one of *R. maoxianensis* sp. nov. observed in the wild. Populations with an asterisk were used for SEM observation of the leaf epidermis and chromosomal examination.

Taxon	Voucher	Locality
R. chongzhouensis	*W.Q. Fei 915* (IBSC)	China, Sichuan, Chongzhou, Jiguan Shan
	W.Q. Fei 577 (IBSC)*	China, Sichuan, Dayi, Xiling Xue Shan
	W.Q. Fei & H.S. Wu 395 (IBSC)	China, Sichuan, Xiaojin, Siguniang Shan
R. maoxianensis	W.Q. Fei 565 (IBSC)*	China, Sichuan, Maoxian, Jiuding Shan

aggregate fruit and achenes, paying special attention to the indumentum of basal leaves, size of flowers, size and shape of petals, number of stamens, and the shape of gynoecium and aggregate fruit.

For scanning electron microscopy (SEM), dry leaves were taken from herbarium specimens (Table 1) and mounted directly onto stubs using double-sided sellotape, gold-coated, and then observed and photographed under a JSM-6360LV scanning electron microscope.

For chromosomal examination, living plants of *Ranunculus chongzhouensis* from Xiling Xue Shan in Dayi, Sichuan, and *R. maoxianensis* from its type locality, i.e., Jiuding Shan in Maoxian, Sichuan (Table 1), were cultivated in pots in the experimental garden of South China Botanical Garden, Chinese Academy of Sciences. Root tips were pretreated in 0.1% colchicine for 2.5 h, fixed in Carnoy I (glacial acetic acid: absolute ethanol = 1: 3), then macerated in 1 M HCl at 37 °C for 45 min, and stained and squashed in Carbol fuchsin. Karyotype formulas were based on the data of measurements of mitotic-metaphase chromosomes of three cells taken from photographs. We followed the acronyms proposed by Levan et al. (1964) to describe the karyotypes.

Results and discussion

Our critical observations on herbarium specimens and living plants in the wild indicate that *Ranunculus maoxianensis* (Figs 1, 2) is morphologically similar to *R. chongzhouensis* (Figs 3–10) in having reniform leaves and puberulous receptacles, carpels and achenes, but differs by having leaves adaxially puberulous with shorter appressed hairs 0.16–0.28 mm long (vs. longer appressed hairs 0.55–0.85 mm long) (Fig. 12A, C), larger flowers (1.8–2.0 cm vs. 1.4–1.6 cm in diameter), larger (8–10 × 5.5–6.5 mm vs. 6–7 × 4.5–5 mm) and widely obovate petals (vs. obovate), more numerous stamens (35–55 vs. 12–18), and subglobose gynoecium and aggregate fruit (vs. ellipsoid). The difference in the indumentum of leaves between the two species is further confirmed by our SEM results (Fig. 12B, D). A detailed morphological comparison between *R. maoxianensis* and *R. chongzhouensis* is given in Table 2.

Our chromosomal examination reveals that *Ranunculus maoxianensis* is a diploid species with $2n = 2x = 16 = 10m + 6sm$ (Fig. 11A, C), while *R. chongzhouensis* is a tetraploid with $2n = 4x = 32 = 16m + 16sm$ (Fig. 11B, D). This result lends strong support to the description of *R. maoxianensis* as a new species.

Table 2. Morphological comparison between *Ranunculus chongzhouensis* and *R. maoxianensis* sp. nov.

	R. chongzhouensis	*R. maoxianensis*
Stems	10–25 cm tall	25–55 cm tall
Basal leaves	5–8, blades 2.2–3.1 × 3.1–3.7 cm, chartaceous, adaxially appressed puberulous with hairs 0.55–0.85 mm long, abaxially glabrous or sometimes appressed puberulous	2–5, blades 2.2–3.2 × 3.8–5.2 cm, herbaceous, adaxially appressed puberulous with hairs 0.16–0.28 mm long, abaxially appressed puberulous
Flowers	terminal, 4–10, 1.4–1.6 cm in diameter	terminal, 4–10, 1.8–2 cm in diameter
Receptacles	3–5 mm long, clavate, puberulous	3.5–4 mm long, clavate, puberulous
Petals	6–7 × 4.5–5 mm, obovate	8–10 × 5.5–6.5 mm, widely obovate
Stamens	12–18	35–55
Gynoecium	ellipsoid	subglobose
Carpels	20–40; ovaries ovoid or widely ovoid puberulous, styles ca. 0.9 mm long, glabrous, slightly recurved at apex	16–22; ovaries ovoid or widely ovoid, puberulous, styles ca. 0.9 mm long, glabrous, straight or apex recurved
Aggregate fruit	ellipsoid	subglobose
Achenes	ca. 2 × 1.5 mm, obliquely or widely ovoid, puberulous, styles ca. 1 mm long, straight or apex recurved.	ca. 2.5 × 2 mm, obliquely or widely ovoid, puberulous, styles ca. 1 mm long, straight or apex recurved.

Our literature consultation and critical observations on herbarium specimens and living plants in the wild reveal that *Ranunculus chongzhouensis*, the putative closest ally of *R. maoxianensis*, lacks the description of root and floral characters, with the description of indumentum of leaf blades, receptacles and achenes by Wang (2015) being also incorrect. Wang (2015) described this species based on a single specimen, *Z.B. Feng*, *D.H. Zhu & X.J. Li 4171* (PE; Fig. 3A), from Jiguan Shan in the Anzihe Nature Reserve in Chongzhou city, Sichuan province, China. The three plants on the sheet are all fruiting, lacking roots and flowers. Therefore, the number of basal leaves and floral morphology were not mentioned in the original description of *R. chongzhouensis*. We traced two isotype sheets of *R. chongzhouensis* from WCSBG (Fig. 3B, C), which Wang (2015) did not see when he described this species as new. Wang (2015) described the basal leaves of *R. chongzhouensis* as adaxially glabrous and abaxially appressed puberulous, and the receptacles and achenes as glabrous. However, the basal leaves of this species are adaxially appressed puberulous (Fig. 3D, E) and abaxially glabrous (Fig. 3F, G), and the receptacles (Fig. 3H) and achenes (Fig. 3H, I) are puberulous. These results are further confirmed by our observations of living plants in three populations of *R. chongzhouensis*, respectively, from Chongzhou (type locality), Dayi, and Xiaojin, all in Sichuan province (Figs 4–9). In addition, we found that the indumentum on the abaxial side of the leaf blades of *R. chongzhouensis* is somewhat variable between populations. The leaf blades are often abaxially glabrous (Figs 4E, 6E), but sometimes abaxially puberulous (Fig. 8E).

From our survey of herbarium specimens and fieldwork, we found that *Ranunculus chongzhouensis* is much more widely distributed than reported by Wang (2015). In addition to its type locality, this species is also distributed in Baoxing, Dayi, Heishui, Luding, Songpan, and Xiaojin counties. Selected specimens from Baoxing (Fig. 10A), Heishui (Fig. 10B), Luding (Fig. 10C) and Songpan (Fig. 10D) are shown in Fig. 10.

Ranunculus maoxianensis is readily assigned to *R.* sect. *Ranunculus* due to its swollen achenes with a distinct beak and receptacles hardly enlarged after anthesis. Wang (2015) also included *R. chongzhouensis* in this section. We accept the sectional placement of this species.

Taxonomic treatment

***Ranunculus maoxianensis* W.Q.Fei, Q.Yuan & Q.E.Yang, sp. nov.**

urn:lsid:ipni.org:names:77313248-1
Figs 1, 2

Diagnosis. *Ranunculus maoxianensis* is similar to *R. chongzhouensis* in leaf blade shape and indumentum of the receptacles, carpels and achenes. However, it is easily distinguishable by having leaves adaxially puberulous with shorter appressed hairs 0.16–0.28 mm long (vs. longer appressed hairs 0.55–0.85 mm long), larger flowers (1.8–2 cm vs. 1.4–1.6 cm in diameter), larger (8–10 × 5.5–6.5 mm vs. 6–7 × 4.5–5 mm) and widely obovate petals (vs. obovate), more numerous stamens (35–55 vs. 12–18), and subglobose gynoecium and aggregate fruit (vs. ellipsoid).

Type. China. Sichuan: Maoxian, Nanxin town, Jiuding Shan, 31°30'36.28"N, 103°46'52.01"E, alt. 3274 m, in *Rhododendron* forests, 7 June 2022, *W.Q. Fei 565* (holotype: IBSC; isotypes: CDBI, IBSC, PE).

Description. ***Herb*** perennial, terrestrial. ***Roots*** fibrous, slender. ***Stems*** 25–55 cm tall when in bloom, branched, erect, sparsely puberulous. ***Basal leaves*** 2–5, long petiolate; petioles 7–20 cm long, sparsely puberulous; blades 2.2–3.2 × 3.8–5.2 cm, reniform, 3-lobed or 3-partite, herbaceous, adaxially green, appressed puberulous with hairs 0.16–0.28 mm long, abaxially light green, puberulous with hairs 0.65–1.1 mm long, base truncate or cordate, central segment 1.2–1.5 × 0.8–1.2 cm, rhombic or rhombic-obovate, margin crenulate, lateral segments 1.5–1.8 × 2–2.6 cm, obliquely flabellate, unequally 2-partite, margin crenulate. ***Lower cauline leaves*** 1–2, similar to basal ones but smaller. ***Upper cauline leaves*** 2–4, subsessile or sessile, 3-sected, segments 1.5–3 × 0.3–0.8 mm, obtriangular, lanceolate or linear, entire or 3–5-lobed. ***Inflorescences*** terminal, 4–10-flowered. ***Flowers*** 1.8–2 cm in diameter; pedicels 5–10 cm long, appressed puberulous; receptacles 3.5–4 mm long, clavate, puberulous; sepals 5, 4.6–5 × 2–3 mm, elliptic to obovate, green tinged with yellowish, adaxially glabrous, abaxially puberulous; petals 5(–6), 8–10 × 5.5–6.5 mm, widely obovate, yellow, glabrous, apex rounded or subtruncate, nectary pit without a scale, claw ca. 0.6 mm long; stamens 35–55, filaments 1.5–2 mm long, narrowly linear, anthers 1–1.2 mm long, oblong; gynoecium subglobose; carpels 16–22, ovaries ca. 0.9 × 0.8 mm, ovoid or widely ovoid, laterally flattened, biconvex, puberulous, styles ca. 0.9 mm long, glabrous, straight or apex recurved. ***Aggregate fruit*** ca. 7 × 7 mm, subglobose; achenes ca. 2.5 × 2 mm, obliquely or widely ovoid, laterally flattened, biconvex, puberulous, styles ca. 1 mm long, persistent, glabrous, straight or apex recurved.

Etymology. The specific epithet refers to the type locality of the new species, i.e. Maoxian county in northwestern Sichuan province, China.

Phenology. Flowering from June to July; fruiting from July to August.

Distribution and habitat. *Ranunculus maoxianensis* is currently known only from its type locality, i.e., Jiuding Shan in Maoxian county, northwestern Sichuan province, China (Fig. 13). It grows in *Rhododendron* forests at altitudes of 3200–3400 m above sea level.

Conservation status. Although *Ranunculus maoxianensis* is currently known only from its type locality, i.e., Jiuding Shan in Maoxian county, northwestern Sichuan province, China, our observations on living plants at its type locality revealed that this species is very common in *Rhododendron* forests at altitudes of 3200−3400 m above sea level. It should better be categorized as "Least Concern (LC)", following the IUCN Standards and Petitions Committee (IUCN 2022).

Additional specimens examined (paratype). China. **Sichuan**: Maoxian, *W.Q. Fei & H.S. Wu 397* (IBSC).

Ranunculus chongzhouensis W.T. Wang, Bull. Bot. Res., Harbin 35(5): 645. 2015

Figs 3−10

Type. China. Sichuan: Chongzhou city, Anzihe Nature Reserve, Jiguan Shan, alt. 3000 m, in forests, 27 July 2007, *Z.B. Feng, D.H. Zhu & X.J. Li 4171* (holotype: PE!; isotypes: WCSBG!).

Description. ***Herbs*** perennial, terrestrial. ***Roots*** fibrous, slender. ***Stems*** 10−25 cm tall, ascending or erect, branched, puberulous. Basal leaves 5−8, 3-lobed or 3-partite, long petiolate; petioles 4−10 cm long, sparsely puberulous; blades 2.2−3.1 × 3.1−3.7 cm, reniform, chartaceous, adaxially green, appressed puberulous with hairs 0.55−0.85 mm long, abaxially light green, glabrous, sometimes puberulous, base cordate, central segment 0.6−1 × 0.9−1.4 cm, obtrapezoid or obovate-obtrapezoid, margin 3-crenulate, lateral segments 0.8−1.2 × 1.5−2.3 cm, obliquely flabellate, unequally 2-lobed, margin crenulate. ***Lower cauline leaves*** 1 or absent, similar to basal ones but smaller. ***Upper cauline leaves*** 2−3, 3-sected, subsessile, segments 1.1−1.5 × 0.3−0.9 mm, obliquely flabellate, lanceolate to linear, margin entire or 3−4-lobed. ***Inflorescences*** terminal, 4−10-flowered. ***Flowers*** 1.4−1.6 cm in diameter; pedicels 5−10 cm long, appressed puberulous; receptacles 3−5 mm long, clavate, puberulous; sepals 5, 3.9−4.5 × 2.5−3 mm, elliptic to obovate, green tinged with yellowish, adaxially glabrous, abaxially puberulous; petals 5(−6), 6−7 × 4.5−5 mm, obovate, yellow, glabrous, apex truncate or subtruncate, nectary pit without a scale, claw ca. 0.5 mm long; stamens 12−18, filaments ca. 2 mm long, narrowly linear, anthers ca. 1 mm long, oblong; gynoecium ellipsoid; carpels 20−40, ovaries ca. 0.9 × 0.8 mm, ovoid or widely ovoid, laterally flattened, biconvex, puberulous, styles ca. 0.9 mm long, glabrous, apex slightly recurved. ***Aggregate fruit*** ca. 7 × 5 mm, ellipsoid; achenes ca. 2 × 1.5 mm, obliquely or widely ovoid, laterally flattened, biconvex, puberulous, styles ca. 1 mm long, persistent, straight or apex recurved.

Phenology. Flowering from June to July; fruiting from July to August.

Distribution and habitat. *Ranunculus chongzhouensis* is distributed in Baoxing, Chongzhou, Dayi, Heishui, Luding, Songpan, and Xiaojin in Sichuan province, China (Fig. 13). It grows in forests or meadows at elevations of 2900−4150 m above sea level.

Additional specimens examined. China. **Sichuan**: Baoxing, *W.Q. Fei & H.S. Wu 371* (IBSC); Chongzhou, *W.Q. Fei 915* (IBSC), *W.B. Ju, L. Zhang & D.K. Chen AZH01296* (CDBI); Dayi, *W.Q. Fei 577* (IBSC), *J.P. Luo & H.M. Li 613* (IBSC), *Y.P. Zeng, Y.F. Luo & Y.Q. Tao 149* (IBSC); Heishui, *W.Q. Fei 719* (IBSC); Luding, *W.Q. Fei 754* (IBSC); Songpan, *W.Q. Fei 725* (IBSC); Xiaojin, *W.Q. Fei & H.S. Wu 395* (IBSC).

Figures

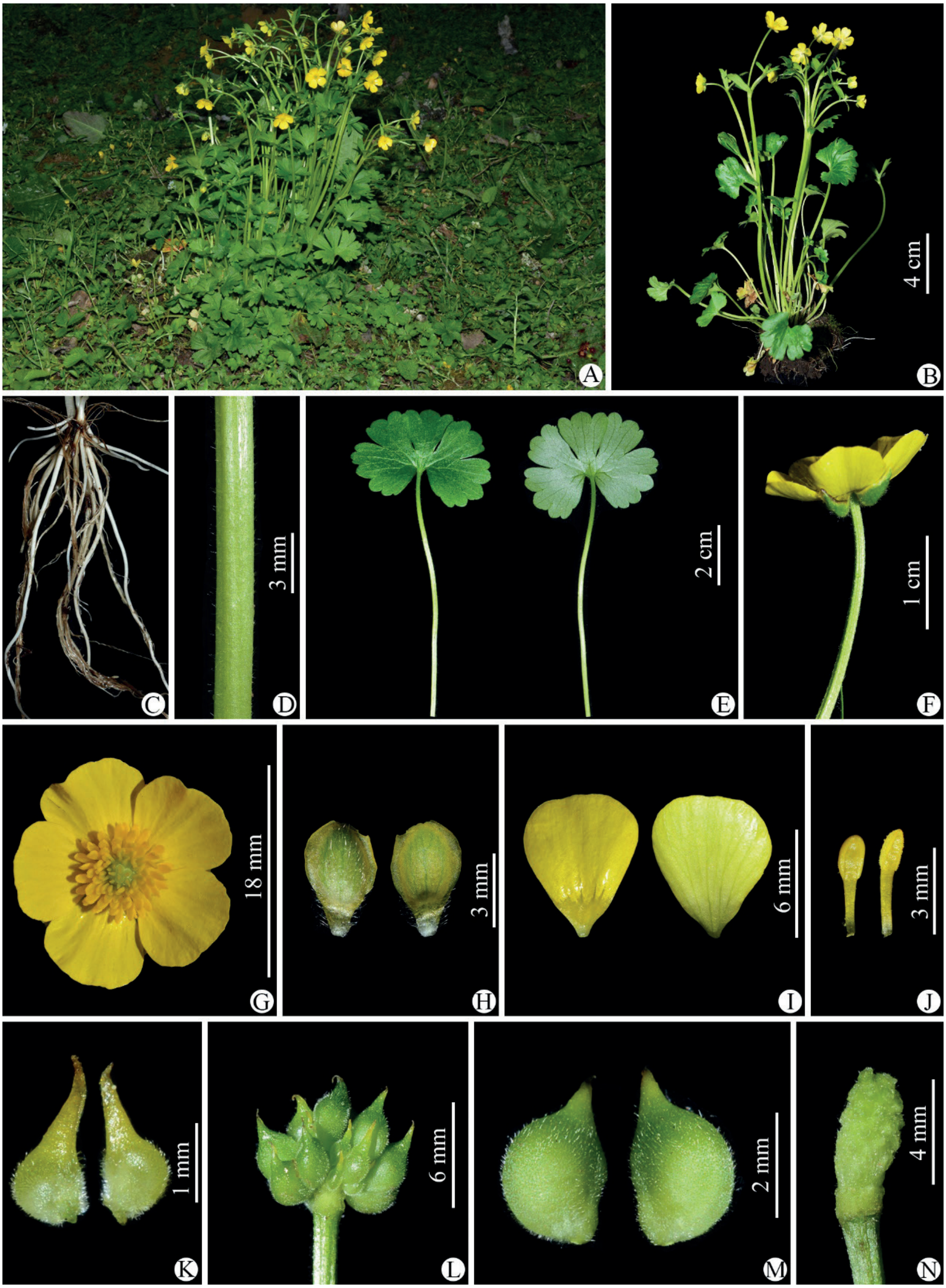
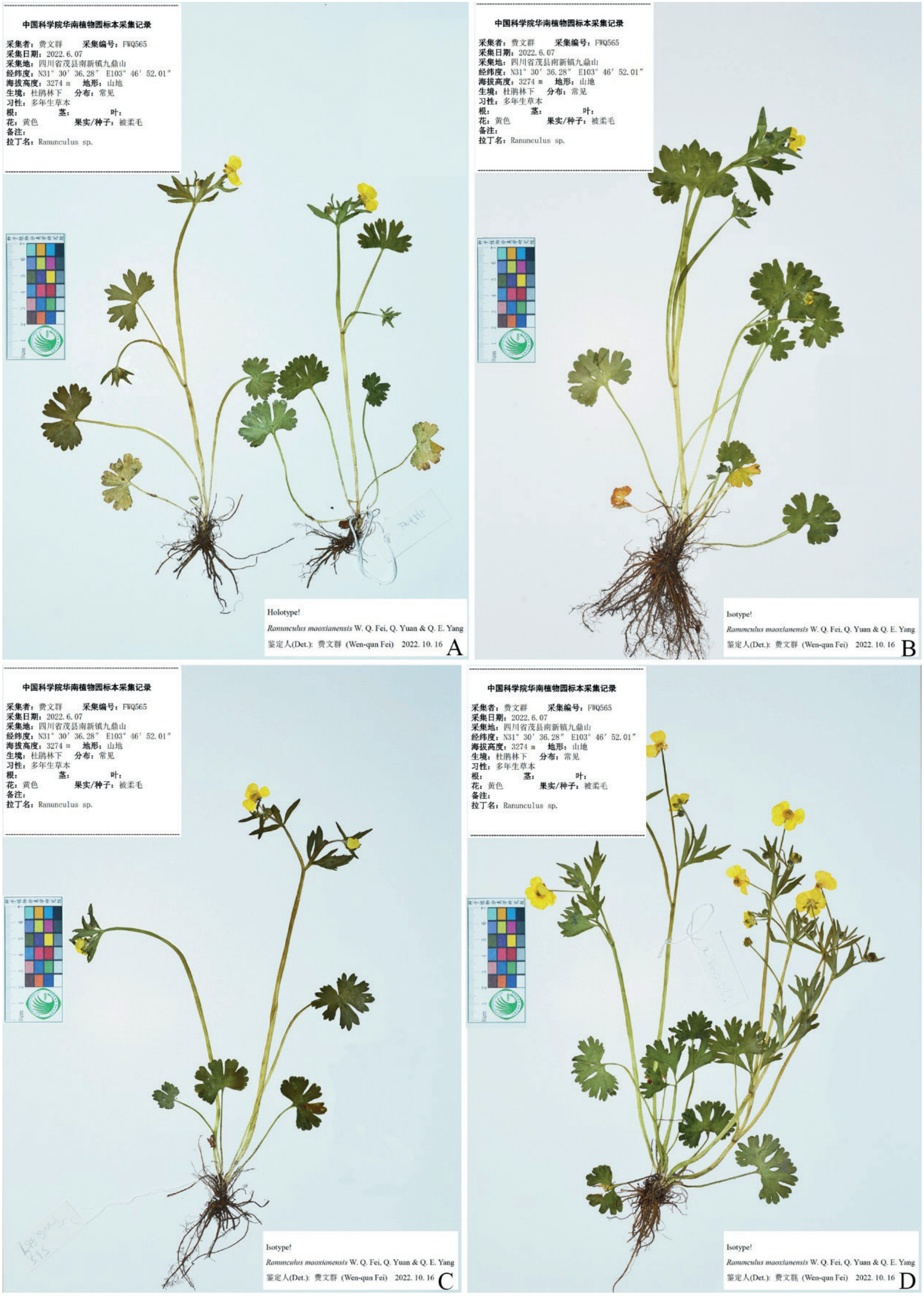


Figure 1. *Ranunculus maoxianensis* sp. nov. in the wild (China, Sichuan, Maoxian) **A** habitat **B** habit **C** roots **D** portion of stem **E** leaf blade (left: adaxial side; right: abaxial side) **F** flower (lateral view) **G** flower (top view) **H** sepal (left: abaxial side; right: adaxial side) **I** petal (left: adaxial side; right: abaxial side) **J** stamens **K** carpels **L** aggregate fruit **M** achenes **N** receptacle. Photographed by Wen-Qun Fei.



中国科学院华南植物园标本采集记录
采集者：费文群 采集编号：FWQ565
采集日期：2022.6.07
采集地：四川省茂县南新镇九鼎山
经纬度：N31° 30′ 36.28″ E103° 46′ 52.01″
海拔高度：3274 m 地形：山地
生境：杜鹃林下 分布：常见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus sp.

Holotype!
Ranunculus maoxianensis W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022. 10. 16

中国科学院华南植物园标本采集记录
采集者：费文群 采集编号：FWQ565
采集日期：2022.6.07
采集地：四川省茂县南新镇九鼎山
经纬度：N31° 30′ 36.28″ E103° 46′ 52.01″
海拔高度：3274 m 地形：山地
生境：杜鹃林下 分布：常见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus sp.

Isotype!
Ranunculus maoxianensis W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022. 10. 16

中国科学院华南植物园标本采集记录
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Ranunculus maoxianensis W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022. 10. 16

中国科学院华南植物园标本采集记录
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采集日期：2022.6.07
采集地：四川省茂县南新镇九鼎山
经纬度：N31° 30′ 36.28″ E103° 46′ 52.01″
海拔高度：3274 m 地形：山地
生境：杜鹃林下 分布：常见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus sp.

Isotype!
Ranunculus maoxianensis W. Q. Fei, Q. Yuan & Q. E. Yang
鉴定人(Det.)：费文群 (Wen-qun Fei) 2022. 10. 16

Figure 2. Holotype (**A**) and isotype (**B–D**) sheets of *Ranunculus maoxianensis* sp. nov.

Figure 3. Holotype (**A**) and isotype (**B, C**) sheets of *Ranunculus chongzhouensis*, showing the general morphology and indumentum of leaf blade (**D–G**), aggregate fruit (**H, I**) and receptacle (**H**) **D, E** portion of adaxial side of leaf blade (appressed puberulous with longer hairs) from **A** and **B** respectively **E, G** portion of abaxial side of leaf blade (glabrous) from **A** and **B** respectively **H, I** portion of aggregate fruit (puberulous) from **A** and **C** respectively **H** portion of the receptacle (puberulous) from **A**.

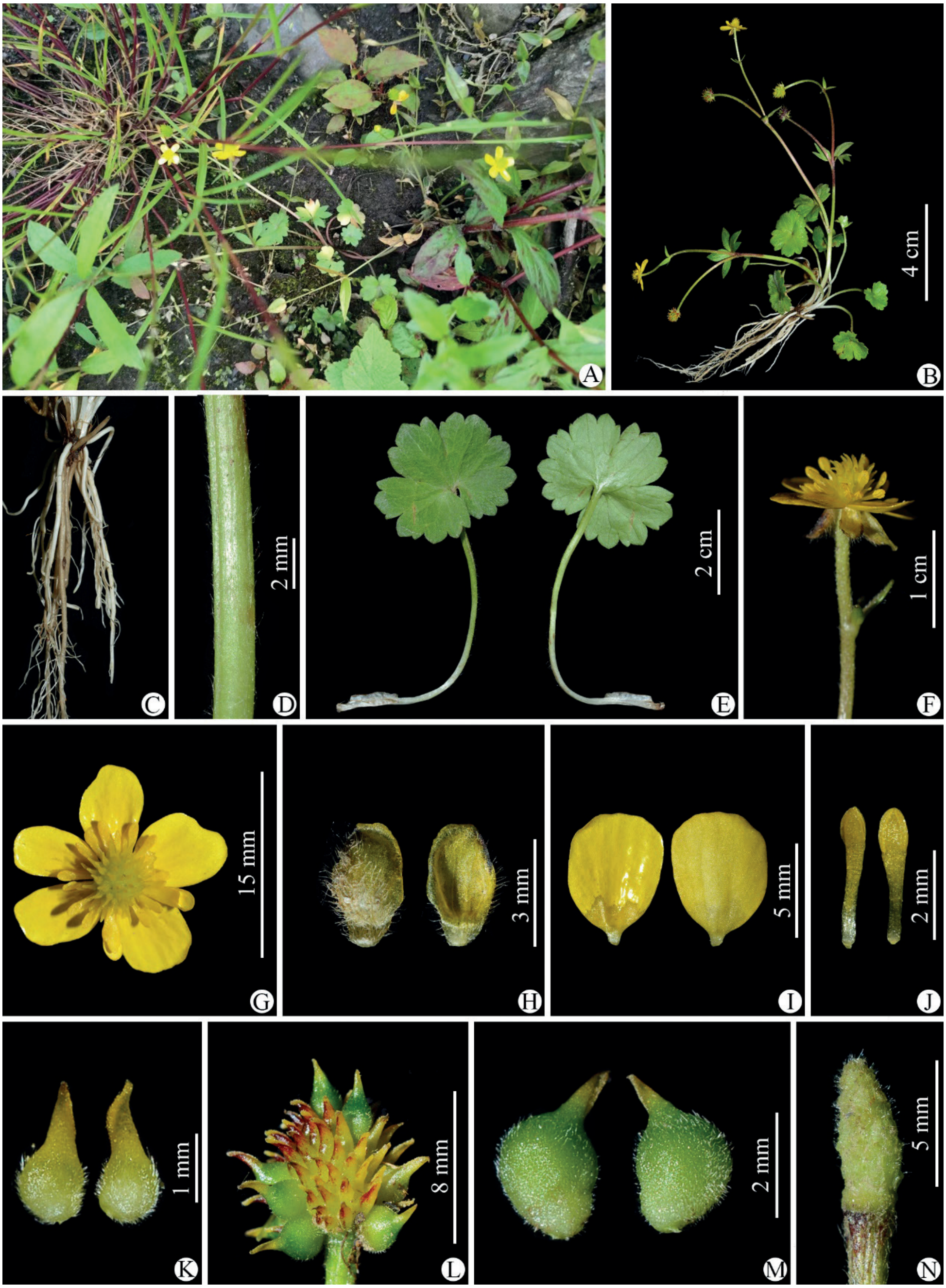


Figure 4. *Ranunculus chongzhouensis* in the wild (China, Sichuan, Chongzhou, the type locality) **A** habitat **B** habit **C** roots **D** portion of stem **E** leaf blade (left: adaxial side; right: abaxial side) **F** flower (lateral view) **G** flower (top view) **H** sepal (left: abaxial side; right: adaxial side) **I** petal (left: adaxial side; right: abaxial side) **J** stamens **K** carpels **L** aggregate fruit **M** achenes **N** receptacle. Photographed by Wen-Qun Fei.

中国科学院华南植物园标本采集记录
采集者：费文群　　采集编号：FWQ915
采集日期：2022.7.15
采集地：四川省崇州市鞍子河保护区鸡冠山
经纬度：N30° 46′ 17.55″ E103° 10′ 8.24″
海拔高度：2975 m　　地形：山地
生境：林下、山坡草丛　　分布：少见
习性：多年生草本
根：　　茎：　　叶：
花：黄色　　果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

Figure 5. Selected specimens of *Ranunculus chongzhouensis* from its type locality, i.e., Chongzhou city in Sichuan province, China **A, B** *W.Q. Fei 915* (IBSC).

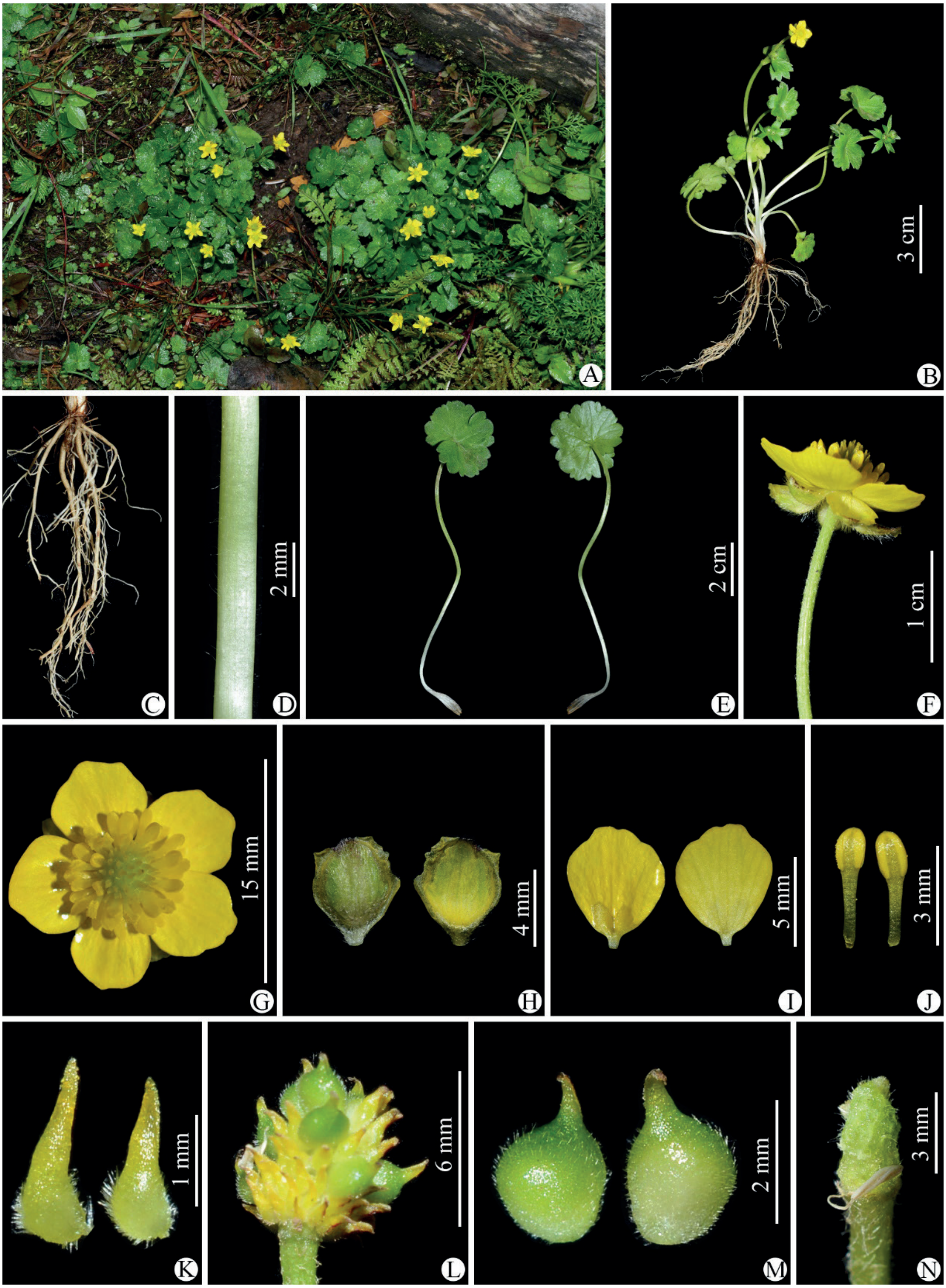


Figure 6. *Ranunculus chongzhouensis* in the wild (China, Sichuan, Dayi) **A** habitat **B** habit **C** roots **D** portion of stem **E** leaf blade (left: adaxial side; right: abaxial side) **F** flower (lateral view) **G** flower (top view) **H** sepal (left: abaxial side; right: adaxial side) **I** petal (left: adaxial side; right: abaxial side) **J** stamens **K** carpels **L** aggregate fruit **M** achenes **N** receptacle. Photographed by Wen-Qun Fei.

中国科学院华南植物园标本采集记录

采集者：费文群　采集编号：FWQ577
采集日期：2022.6.10
采集地：四川省大邑县西岭雪山
经纬度：N30° 41′ 59.23″ E103° 9′ 41.07″
海拔高度：3172 m　地形：山地
生境：林下、山坡草丛　分布：常见
习性：多年生草本
根：　茎：　叶：
花：黄色　果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

中国科学院华南植物园标本采集记录

采集者：费文群　采集编号：FWQ577
采集日期：2022.6.10
采集地：四川省大邑县西岭雪山
经纬度：N30° 41′ 59.23″ E103° 9′ 41.07″
海拔高度：3172 m　地形：山地
生境：林下、山坡草丛　分布：常见
习性：多年生草本
根：　茎：　叶：
花：黄色　果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

Figure 7. Selected specimens of *Ranunculus chongzhouensis* from Dayi county in Sichuan province, China **A, B** *W.Q. Fei 577* (IBSC).

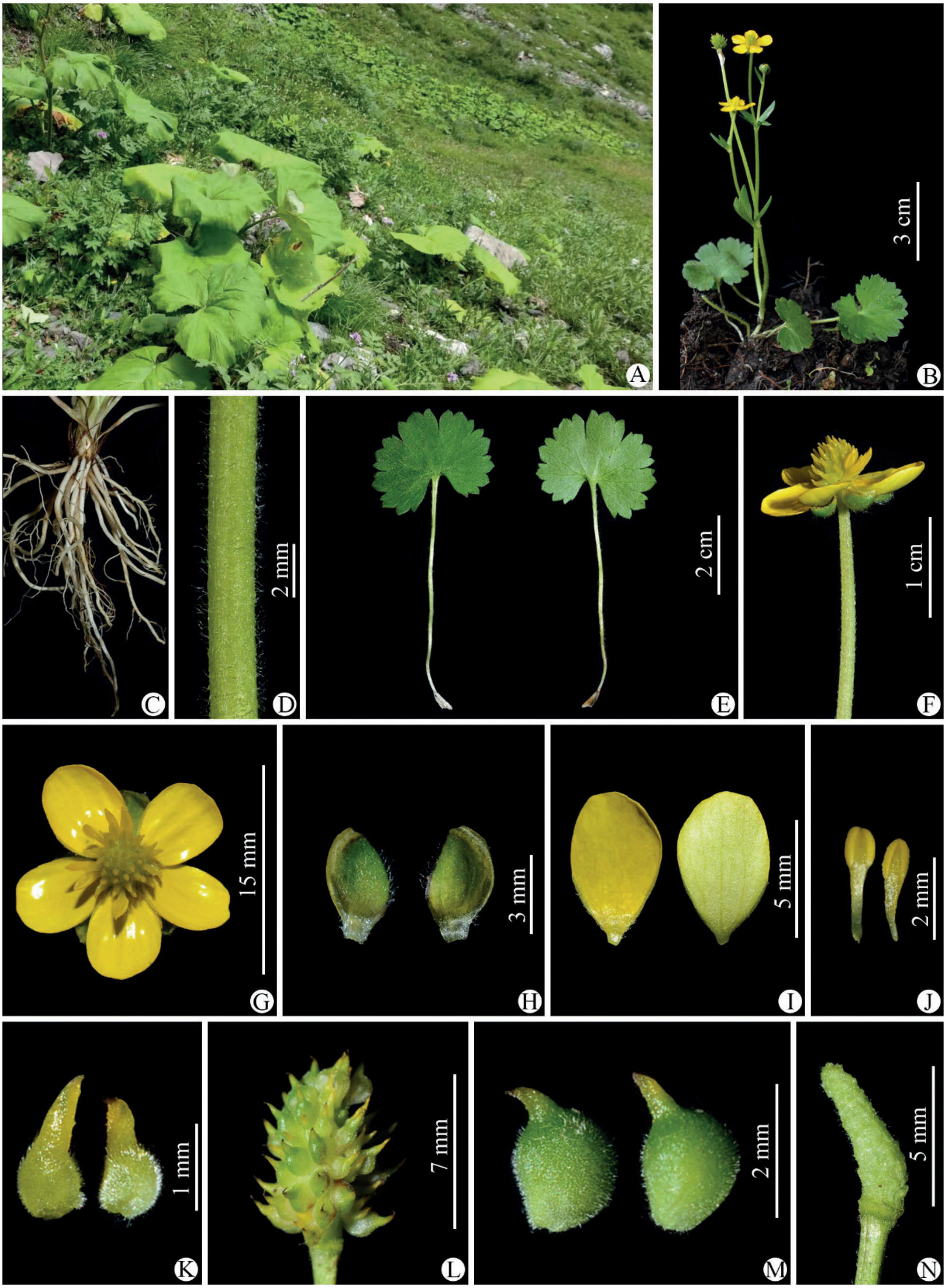


Figure 8. *Ranunculus chongzhouensis* in the wild (China, Sichuan, Xiaojin) **A** habitat **B** habit **C** roots **D** portion of stem **E** leaf blade (left: adaxial side; right: abaxial side) **F** flower (lateral view) **G** flower (top view) **H** sepal (left: abaxial side; right: adaxial side) **I** petal (left: adaxial side; right: abaxial side) **J** stamens **K** carpels **L** aggregate fruit **M** achenes **N** receptacle. Photographed by Wen-Qun Fei.

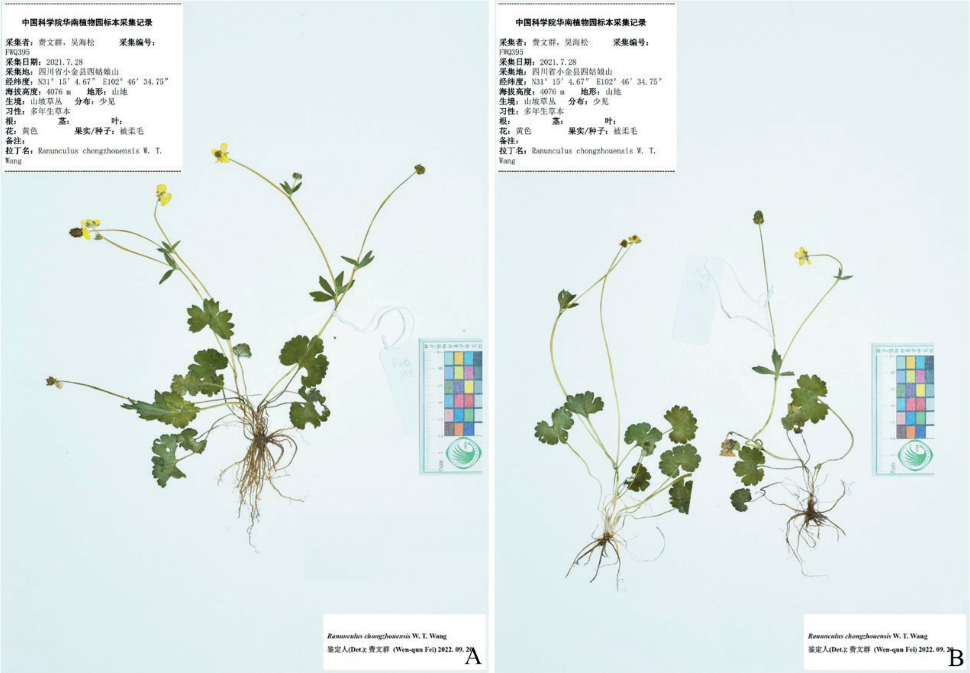
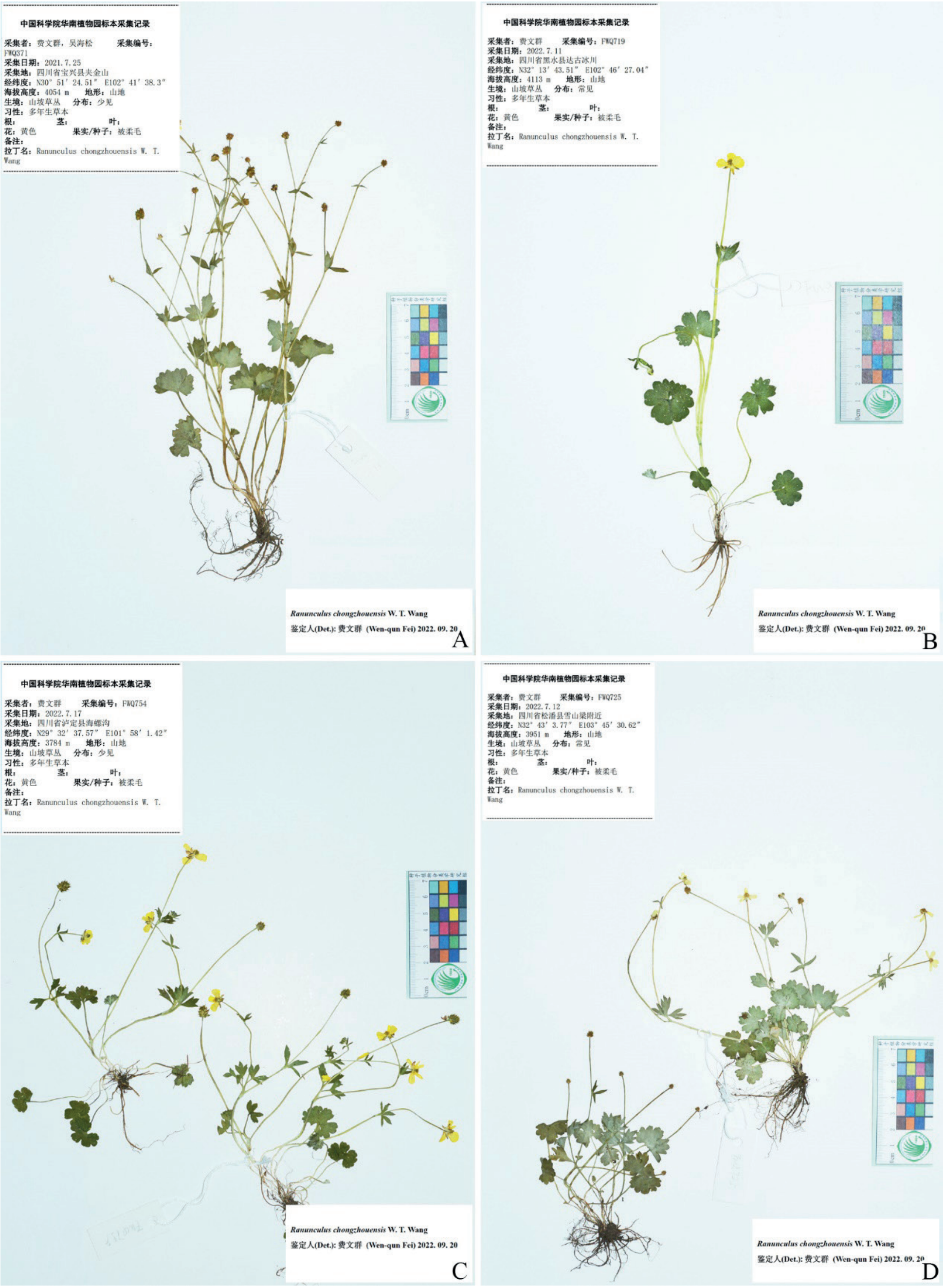


Figure 9. Selected specimens of *Ranunculus chongzhouensis* from Xiaojin county in Sichuan province, China **A, B** *W.Q. Fei 395* (IBSC).



中国科学院华南植物园标本采集记录
采集者：费文群，吴海松 采集编号：FWQ371
采集日期：2021.7.25
采集地：四川省宝兴县夹金山
经纬度：N30° 51′ 24.51″ E102° 41′ 38.3″
海拔高度：4054 m 地形：山地
生境：山坡草丛 分布：少见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

中国科学院华南植物园标本采集记录
采集者：费文群 采集编号：FWQ719
采集日期：2022.7.11
采集地：四川省黑水县达古冰川
经纬度：N32° 13′ 43.51″ E102° 46′ 27.04″
海拔高度：4113 m 地形：山地
生境：山坡草丛 分布：常见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

中国科学院华南植物园标本采集记录
采集者：费文群 采集编号：FWQ754
采集日期：2022.7.17
采集地：四川省泸定县海螺沟
经纬度：N29° 32′ 37.57″ E101° 58′ 1.42″
海拔高度：3784 m 地形：山地
生境：山坡草丛 分布：少见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

中国科学院华南植物园标本采集记录
采集者：费文群 采集编号：FWQ725
采集日期：2022.7.12
采集地：四川省松潘县雪山梁附近
经纬度：N32° 43′ 3.77″ E103° 45′ 30.62″
海拔高度：3951 m 地形：山地
生境：山坡草丛 分布：常见
习性：多年生草本
根： 茎： 叶：
花：黄色 果实/种子：被柔毛
备注：
拉丁名：Ranunculus chongzhouensis W. T. Wang

Ranunculus chongzhouensis W. T. Wang
鉴定人(Det.): 费文群 (Wen-qun Fei) 2022. 09. 20

Figure 10. Selected specimens of *Ranunculus chongzhouensis* from Baoxing (**A**), Heishui (**B**), Luding (**C**) and Songpan (**D**) in Sichuan province, China **A** *W.Q. Fei 371* (IBSC) **B** *W.Q. Fei 719* (IBSC) **C** *W.Q. Fei 754* (IBSC) **D** *W.Q. Fei 725* (IBSC).

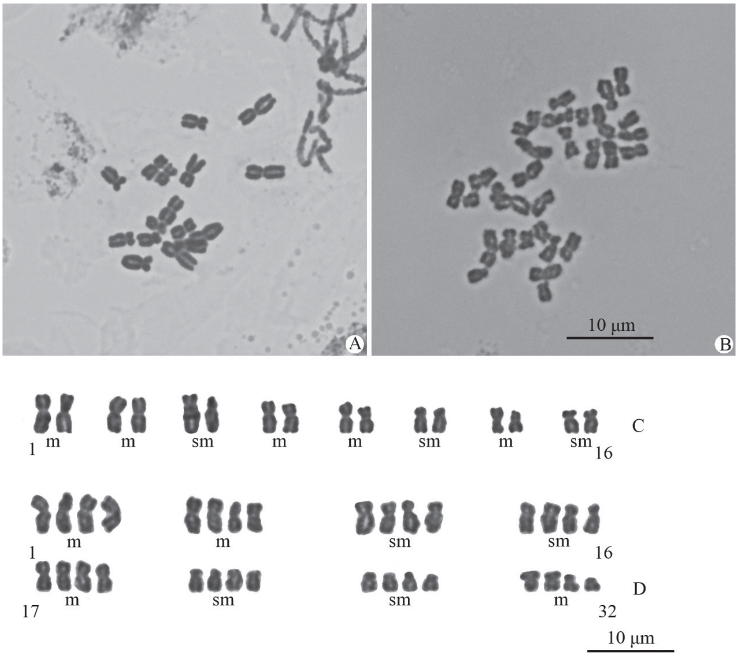


Figure 11. Mitotic metaphase chromosomes (**A, B**) and karyotypes (**C, D**) of *Ranunculus maoxianensis* sp. nov. (**A, C**) and *R. chongzhouensis* (**B, D**), with m = median-centromeric chromosome, sm = submedian-centromeric chromosome.

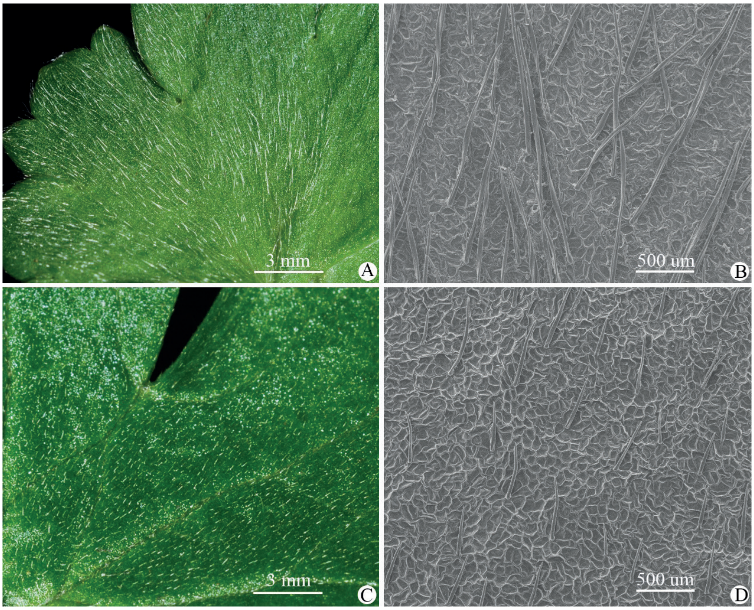


Figure 12. Portion of the adaxial side of the leaf blade of *Ranunculus chongzhouensis* (**A, B**) and *R. maoxianensis* sp. nov. (**C, D**), showing the difference in length of hairs. The hairs on the adaxial side of the leaf blade in *R. chongzhouensis* are 0.55–0.85 mm long, and those in *R. maoxianensis* are 0.16–0.28 mm long **A, C** photographed in the wild and **B, D** photographed with SEM.

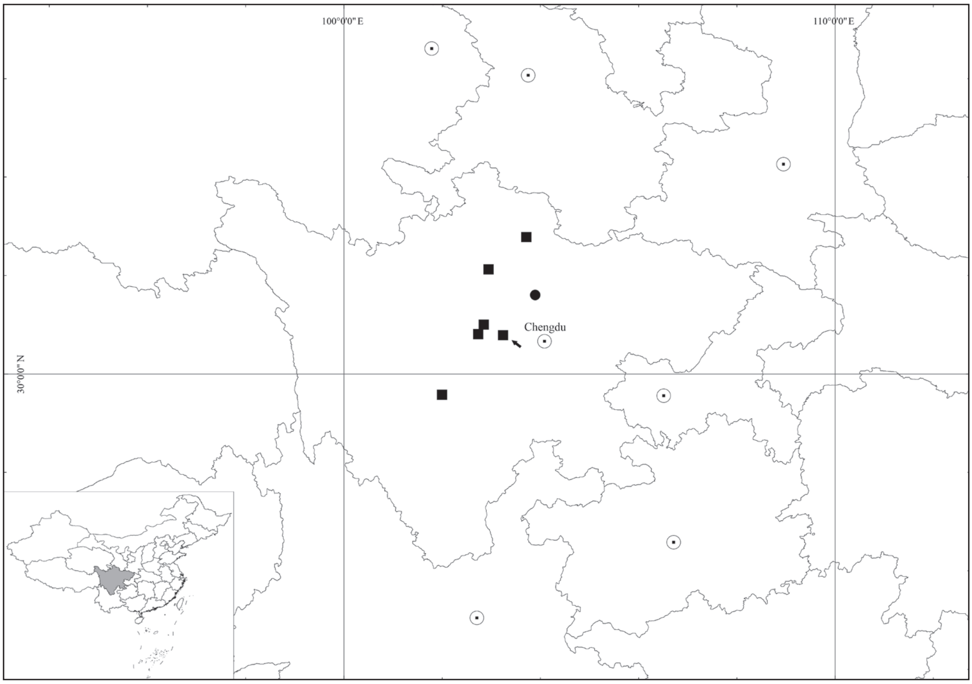


Figure 13. Distribution of *Ranunculus chongzhouensis* (■) and *R. maoxianensis* (●). Black arrow indicates the type locality of *R. chongzhouensis*, i.e., Chongzhou city in Sichuan province, China.

Acknowledgements

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doi: 10.3897/phytokeys.219.94275
https://phytokeys.pensoft.net

RESEARCH ARTICLE

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Epimedium longnanense (Berberidaceae), a new species from Gansu, China

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Abstract

Epimedium longnanense, a new species of *Epimedium* (Berberidaceae) from Longnan Prefecture, Gansu Province, China, is here proposed and illustrated. *E. longnanense* has large flowers with petals possessing long spur and obvious basal lamina, and thus should be grouped into series *Davidianae*. The species closely resembles *E. flavum* of ser. *Davidianae* in morphology. However, it can be easily distinguished by its elongated rhizome (vs. compact), trifoliolate leaves (vs. five leaflets, sometimes trifoliolate), pale pink or purplish-red inner sepals with 6–8 × 2–3 mm (vs. pale sulphur-yellow, ca. 11 × 4 mm).

Keywords

Epimedium, IUCN Red List, morphology, taxonomy

Introduction

Epimedium Linnaeus, the largest herbaceous genus of Berberidaceae, is a relatively primitive group of angiosperms (Stearn 2002; Zhang et al. 2007). Currently, there are about 62 known species of *Epimedium* (Zhang et al. 2022b). They are widely

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and intermittently distributed in a narrow strip between Japan in Asia and Algeria in northern Africa (Ying 2002). With about 52 species, China is the center of diversity and distribution for *Epimedium* (Ying et al. 2011; Zhang et al. 2022b). *Epimedium* plants are excellent horticultural crops due to their beautiful and diverse leaves and flowers (Li et al. 2020). *Epimedium* has also been reported to have important medicinal values, such as strengthening the kidneys, curing rheumatism, and helping to fight osteoporosis, and tumors (Zhang and Yang 2021; Zhao et al. 2022).

In June 2021, we collected an unusual plant of *Epimedium* from Kangnan Forest District, Longnan Prefecture, Gansu province, China. In June 2022, we went to the forest district on two further occasions to investigate this plant of *Epimedium*. The plant is a low-growing herb with a height of 15–20 cm, bearing slender and elongated rhizomes. Its leaves are trifoliolate, and the leaflets are broadly ovate or almost orbicular and relatively small (2.4–4 × 2.3–4 cm). Furthermore, the plant possesses large yellow flowers and its petals are long spurred with an obvious basal lamina, and thus should be a member of ser. *Davidianae* Stearn. However, this plant has obvious morphological differences from other species of ser. *Davidianae* by its elongated rhizome, leaflet number, leaflet morphology, leaf arrangement on the flowering stem, flower color, and shape and size of inner sepals and petals. We confirmed that the plant should be a new species, which we describe below.

Materials and methods

We have been engaged in taxonomic research of Chinese *Epimedium* since 2004. We examined all the specimens of *Epimedium* from the main herbaria of China (BCMM, CDCM, CDBI, GXMI, GZTM, HGAS, HGCM, HIB, HNNU, HNWP, HWA, IBK, IMD, KUN, PE, SAU, SM and SZ). Other *Epimedium* herbaria of China were examined from the Chinese virtual herbarium (http://www.cvh.ac.cn/). We also investigated the images of specimens of *Epimedium* from K, P, WU and WUK obtained by email or their network databases. In total, about 1700 *Epimedium* specimens have been intensively studied. Furthermore, our field investigations covered most of the distribution regions of Chinese *Epimedium*, including the following provinces, Anhui, Chongqing, Gansu, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangxi, Jilin, Liaoning, Shanxi, Shaanxi, Sichuan and Zhejiang of China. Almost all of the Chinese species of *Epimedium* were collected and transplanted to Wuhan Botanical Garden, the Chinese Academy of Sciences, for further study and conservation. For the new species of *Epimedium*, we compared its morphological characters with other species of the genus based on the specimen review and cultivation observation, as well as investigating its distribution and habitat. The morphological characters were described using the terminology used by Stearn (2002), Ying et al. (2011) and Zhang et al. (2022b).

Resulsts

Epimedium longnanense **Y.J.Zhang, sp. nov.**
urn:lsid:ipni.org:names:77313386-1
Figs 1, 2

Type. China, Gansu, Longnan Prefecture, Kangxian County, Kangnan Forest District, 32°59'N, 105°38'E, alt. 2000 m, 15 June 2022, *Yanjun Zhang 709* (holotype, HIB!; isotypes, HIB!).

Diagnosis. *Epimedium longnanense* is closely similar to *E. flavum* Stearn in morphology, but can be easily distinguished by its elongated rhizome, trifoliolate leaves, and relatively smaller and pale pink or purplish-red inner sepals.

Description. Perennial herbs 15–20 cm tall. Rhizome ca. 15 cm or longer, ca. 1 mm in diam., elongated. Leaves basal and cauline, trifoliolate. Leaflets 2.4–4 × 2.3–4 cm, broadly ovate or almost orbicular, membranous, adaxially glabrous, abaxially sparsely pubescent, base deeply cordate with usually rounded lobes, those of lateral leaflets unequal, margins spinous-serrulate, apex usually acute or obtuse. Flowering stem with one leaf, or occasionally two alternate leaves, glabrous. Inflorescence compound or simple, 5–15-flowered, 10–15 cm long, glandular, pedicels 1.5–3.5 cm long. Flowers 3–5 cm in diam., yellow. Outer sepals ovate, soon falling; inner sepals 6–8 × 2–3 mm, narrowly ovate, pale pink or purplish-red. Petals 1.5–2.5 cm, much longer than inner sepals, horn-shaped, yellow, spurs slender; basal lamina 6–8 mm high, distinct. Stamens ca. 4 mm long, included, anthers ca. 3 mm long, anthers and pollen pale yellow. Capsules ca. 2 cm long.

Phenology. Flowering in June; fruiting in late June and early July.

Etymology. Longnan is located in the southeast of Gansu Province, the intersection of Qinba Mountain, Loess Plateau and Qinghai Tibet Plateau in China. Longnan is a biodiversity hotspot where many new species or new species records have been found (Liu et al. 2018; Qin et al. 2020; Zhang et al. 2022a). The new species, *E. longnanense*, is found in this region and is named after the geographic name.

Distribution and habit. At present, *Epimedium longnanense* is only known from its type locality, i.e. Kangnan Forest District, Kangxian County, Longnan Prefecture, Gansu Province, China. The new species mainly occurs in thickets at elevations of 1800–2300 m and is usually together with *Fargesia nitida* (Mitford) Keng f. ex Yi, *Rubia cordifolia* L., *Smilax stans* Maxim., *Cardamine tangutorum* O. E. Schulz and *Veratrum nigrum* L. It often grows in stone crevices with barren soil, and its elongated and slender rhizome might be an adaptive characteristic of its living environment. Except for *E. longnanense*, there are two other species of *Epimedium*, *E. brevicornu* Maxim. and *E. pubescens* Maxim., in Gansu Province, China. In the type locality of *E. longnanense*, we also found *E. pubescens* at elevations of 300–1500 m, but no sympatric distribution of these two species was found.

Chinese name. Long nan yin yang huo (陇南淫羊藿).

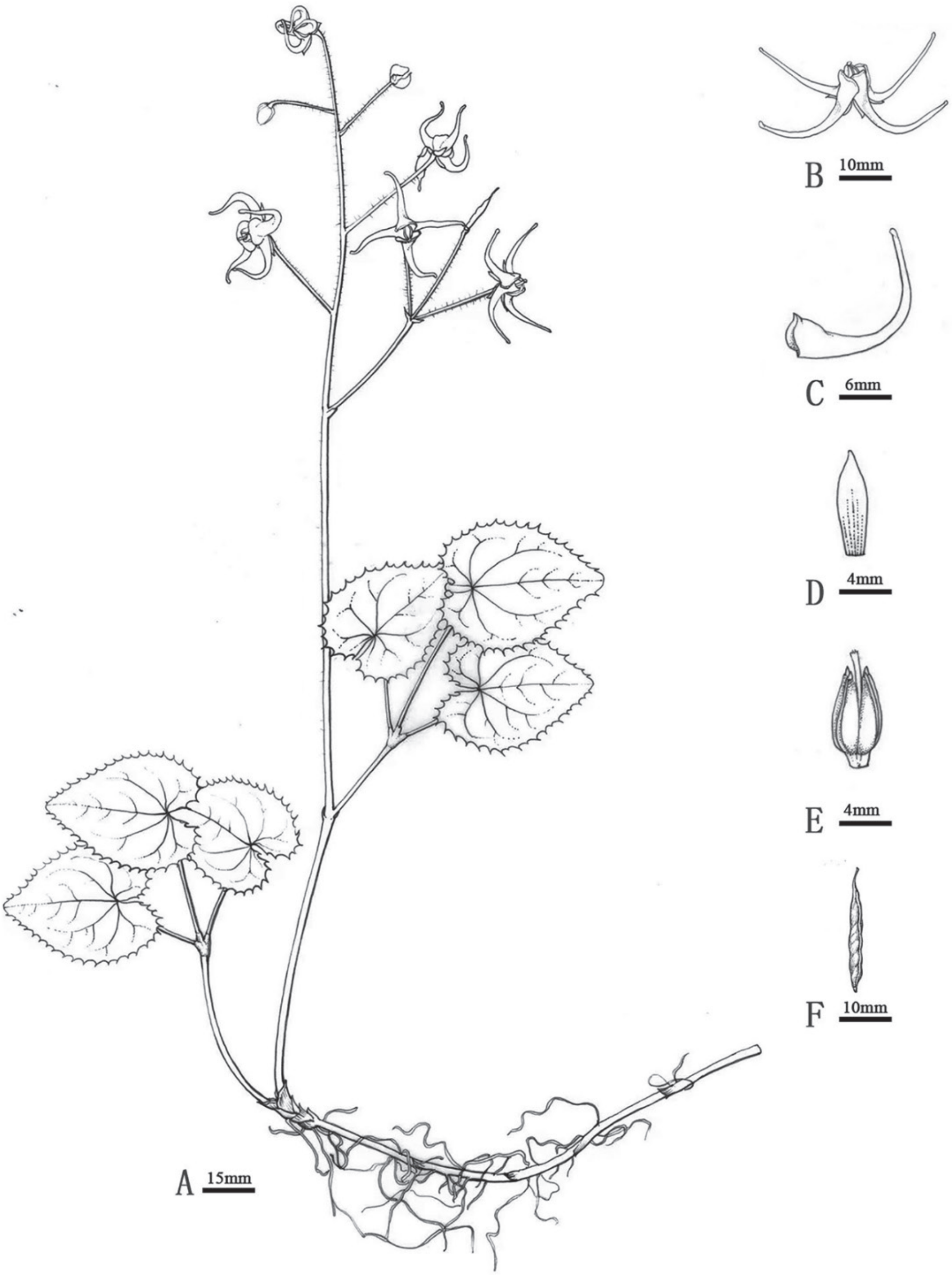

Figure 1. *Epimedium longnanense* **A** plant **B** flower **C** petal **D** inner sepal **E** stamen and gynoecium. Drawn by Nan Jia.

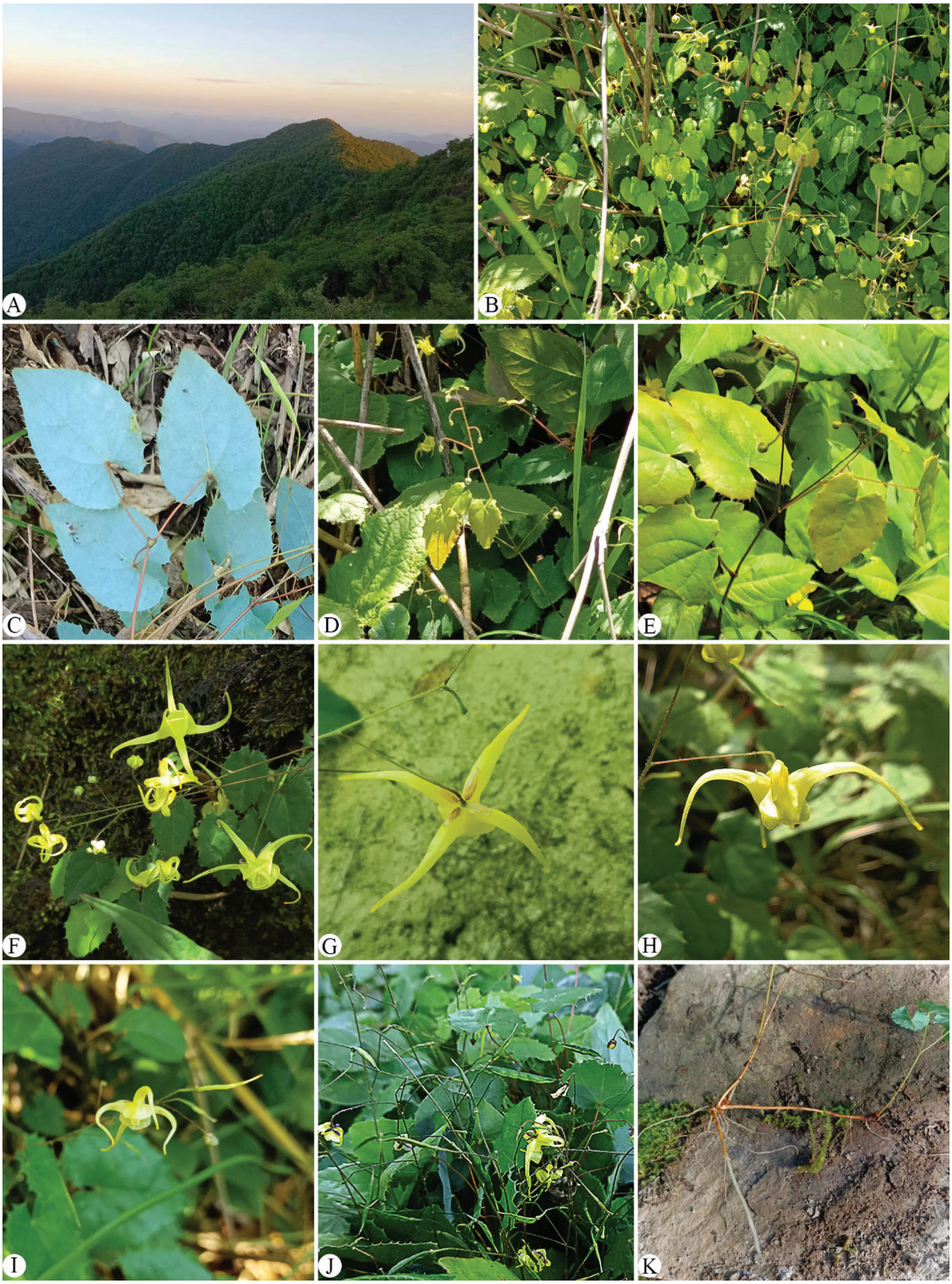

Figure 2. *Epimedium longnanense* **A** habitat **B** plant **C** leaves (abaxial sides) **D** simple inflorescence with a flowering stem bearing one leaf **E** compound inflorescence with a flowering stem bearing two alternative leaves **F** flowers (adaxial view) **G** flower (abaxial view) **H** flower (Side view) **I** flower (Side view) and immature capsules **J** mature capsules **K** rhizome. Photographed by Yanjun Zhang and Ying Ji.

Additional specimens examined (Paratypes). China, Gansu Province, Longnan Prefecture, Kangxian County, Kangnan Forest District, alt. 2270 m, 20 June 2021, *Yanjun Zhang 699* (HIB!); loc. cit., alt. 1900 m, 30 June 2022, *Yanjun Zhang 710* (HIB!).

IUCN Red list category. Data available for the new species are still insufficient to assess its conservation status. According to the IUCN criteria (IUCN 2022), it is considered Data Deficient (DD) until more information becomes available. Although *E. longnanense* currently has relatively good growth and protection status, we would like to elaborate that many other species of *Epimedium* have severely suffered from destructive excavation due to their huge medicinal values. Therefore, special attention should be given to the conservation of the new species of *Epimedium*.

Key to species of *Epimedium* ser. *Davidianae*

1 Leaves biternate, or leaflets 7, 5, 3 .... **2**

– Leaflets 3 .... **4**

2 Inner sepals pale sulphur-yellow, ca. 11 × 4 mm .... **1. *E. flavum* Stearn**

– Inner sepals purple red, 4–6.5 mm long **3**

3 Leaves biternate, or leaflets 7, 5, rarely 3; inner sepals ovate, 5.5–6.5 × ca. 3 mm; petal spurs horizontally spreading with basal lamina 6–7 mm high .... **2. *E. xichangense* Y. J. Zhang**

– Leaflets 5, or 3; inner sepals narrowly ovate, ca. 4 × 1 mm; petal spurs downward-curved with basal lamina 7–13 mm high .... **3. *E. davidii* Franch.**

4 Inflorescences racemose or compound **5**

– Inflorescences paniculate **13**

5 Rhizome long-creeping, 1–3 mm in diam **6**

– Rhizome compact. **10**

6 Leaflets broadly ovate or almost orbicular. **7**

– Leaflets ovate or narrowly ovate **8**

7 Inflorescences simple, 3–4-flowered, flowers white, inner sepals 8–10 × ca.2.5 mm, spurs of petals ca. 1.2 cm long .... **4. *E. pauciflorum* K. C. Yen**

– Inflorescences compound or sometimes simple, 5–15-flowered, flowers yellow, inner sepals 6–8 × 2–3 mm, spurs of petals much longer than inner sepals, 1.5–2.5 cm long .... **5. *E. longnanense* Y. J. Zhang**

8 Leaflets ovate, 4–5.5 × 2–2.5 cm .... **6. *E. shuichengense* S. Z. He**

– Leaflets narrowly ovate, 4–8 × 2–5.5 cm. **9**

9 Inner sepals white, ovate, ca. 13 × 9 mm; petals purple, spurs a little longer than inner sepals, 15–16 mm long .... **7. *E. epsteinii* Stearn**

– Inner sepals reddish, cymbiform, ca. 6 × 2.5 mm; petals pale yellow, spurs much longer than inner sepals, ca. 22 mm long .... **8. *E. fangii* Stearn**

10 Inner sepals white, petals white **11**

– Inner sepals white or pale pinkish-lilac, petals purple or chestnut-brown **12**

11 Inner sepals lanceolate, 16–19 × 7–8 mm, apex acuminate; petals white, spurs almost as long as inner sepals, 15–18 mm long .... **9. *E. ogisui* Stearn**

– Inner sepals elliptic, ca. 16 × 8–9 mm, apex shortly acuminate; petals as long as inner sepals .... **10. *E. latisepalum* Stearn**

12 Inner sepals narrowly ovate, white, petals deep purple, slightly shorter, or nearly as long as inner sepals............... **11. *E. shengnongjiaense* Y. J. Zhang & J. Q. Li**

– Inner sepals ovate, pale pinkish-lilac, petals chestnut-brown, a little longer than inner sepal, inner sepals pale pinkish-lilac .... **12. *E. stearnii* Ogisu & Rix**

13 Petals with obvious basal lamina 7–8 mm high **14**

– Petals with slight base lamina 2–3.5 mm high.. **15**

14 Leaflets oblong-elliptic or narrowly ovate, 10–13 × ca. 6 cm; inner sepals broadly elliptic, 5–6 × 3–4 mm ....**13. *E. hunanense* (Hand.-Mazz.) Hand.-Mazz.**

– Leaflets lanceolate or narrowly lanceolate, 9–23 × 1.8–4.5 cm; inner sepals ovate, ca. 12 × 6–8 cm ....**14. *E. wushanense* T. S. Ying**

15 Inner sepals ovate or broadly ovate, 8–13 × 4–8 mm; spurs of petals slightly longer than inner sepals, 10–15 mm long .... **15. *E. pseudowushanense* B. L. Guo**

– Inner sepals ovate, 11–12 × 4–5.5 mm; spurs of petals obviously longer than inner sepals, 17–20 mm long ....**16. *E. mikinorii* Stearn**

Discussion

The floral trait is one of the most stable taxonomic characters in *Epimedium*, which has abundant diversities and is the focus of evolution studies of the genus (Ying 2002; Zhang et al. 2014; Guo et al. 2022). In the updated taxonomic system of *Epimedium* (Stearn 2002), all species endemic to China were classified into section *Diphyllon* Stearn of subgenus *Epimedium* Stearn. The section was divided into four series according to the flower morphology: ser. *Campanulatae* Stearn is characterized by campanulate flowers and flat petals without spur; ser. *Davidianae* Stearn bears large flowers and long spurred petals with obvious basal lamina; ser. *Dolichocerae* Stearn possesses large flowers and long spurred petals with no basal lamina; and ser. *Brachycerae* Stearn is characterized by short and spurred or saccate petals that are much shorter than the inner sepals. *Epimedium longnanense* has large flowers with petals possessing long spur and obvious basal lamina, and thus should be grouped into ser. *Davidianae*.

So far, in total, there are 16 species in ser. *Davidianae* (Stearn 2002; Guo et al. 2007; Zhang and Li 2009; Ying et al. 2011; Zhang et al. 2016, 2022b). Among these 16 species of *Epimedium* ser. *Davidianae*, *E. longnanense* is the most closely similar to *E. flavum* Stearn in morphology. However, *E. longnanense* can be easily distinguished by its rhizome, leaf and flower characters (Table 1). *E. longnanense* has a slender and elongated rhizome ca. 1 mm in diameter, while *E. flavum* has a compact rhizome 2–4 mm

Table 1. Comparison of morphological characters of *E. longnanense*, *E. flavum* and *E. membranaceum*.

Characters	*E. longnanense*	*E. flavum*	*E.membranaceum*
Plant height	15–20 cm	13–30 cm	20–65 cm
Rhizome	Elongated, ca. 1 mm	Compact, 2–4 mm	Compact or occasionally elongated, 2–4 mm
Number of leaflets	3	(3–)5	3
Leaves on the flowering stem	1 leaf or occasionally 2 alternate leaves	1 leaf or 2 opposite or alternate leaves	2 opposite or sometimes alternate leaves
Leaflets	Broadly ovate or almost orbicular, the tip acute or obtuse, 3.5–5.5 × 2.5–4.5 cm	Broadly ovate, the tip obtuse, ca. 4 × 3 cm	Broadly ovate or narrowly ovate, the tip acute or short-acuminate, 3–10 × 2–6 cm
Inflorescence	Compound or simple, 10–15 cm, 5–15-flowered	Simple or compound, 13 cm, 3–10-flowered	Compound, 16–30 cm, 5–35-flowered
Inner sepals	Pale pink or purplish-red, 6–8 × 2–3 mm	Pale sulphur-yellow, ca. 11 × 4 mm	Pale pink, 6–7 × 2.5–3 mm
Spur length of petals	1.5–2.5 cm	ca. 1.3 cm	1.5–2.5 cm
Basal lamina height of petals	6–8 mm	8 cm	–

in diameter. Although their leaflets are similar in shape and size, *E. longnanense* has trifoliolate leaves, and *E. flavum* bears leaves usually with five leaflets, sometimes three leaflets. Furthermore, *E. longnanense* has smaller and pale pink or purplish-red inner sepals (6–8 × 2–3 mm), and its petals have spurs much longer than inner sepals (1.5–2.5 cm), while *E. flavum* has pale sulphur-yellow and larger sepals (ca. 11 × 4 mm), and its spurred petals are slightly longer than its inner sepals (ca. 1.3 cm).

Among the other three series of Chinese *Epimedium* sect. *Diphyllon*, *E. longnanense* closely resembles *E. membranaceum* in morphology, a species in ser. *Dolichocerae*. *Epimedium membranaceum* was treated as a synonym of *E. davidii* Franchet in Flora Reipublicae Popularis Sinica (Ying 2001) and Flora of China (Ying et al. 2011). However, *E. membranaceum* and *E. davidii* are two distinct species with obvious differences in leaflet number and floral characters (Stearn 2002; Zhang et al. 2015). Both *E. longnanense* and *E. membranaceum* have large yellow flowers, and their petals possess long, slender and slightly-curved spurs. However, *E. longnanense* is only 15–20 cm high with shorter inflorescence (10–15 cm), while *E. membranaceum* is taller (20–65 cm) with longer inflorescence (16–30 cm). Furthermore, *E. longnanense* has petals possessing an obvious basal lamina and is a member of ser. *Davidianae*, while *E. membranaceum* has petals with no lamina and is a member of ser. *Dolichocerae* (Table 1).

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RESEARCH ARTICLE

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Paraphlomis yingdeensis (Lamiaceae), a new species from Guangdong (China)

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Abstract

Paraphlomis yingdeensis (Lamiaceae), a new species from the limestone area in northern Guangdong Province, China, is described and illustrated. Phylogenetic analyses, based on two nuclear DNA regions (ITS and ETS) and three plastid DNA regions (*rpl32-trnL*, *rps16* and *trnL-trnF*), suggest that *P. yingdeensis* represents a distinct species in *Paraphlomis*. Morphologically, *P. yingdeensis* is similar to *P. foliata* subsp. *montigena* and *P. nana*, but can be distinguished from the former by its densely villous lamina and calyx, not decurrent base of lamina and bristle-like-acuminate apex of calyx teeth, and distinguished from the latter by its significantly taller plant (15–20 cm vs. 1–5 cm) and larger lamina (6.2–16.5 × 4–11.5 vs. 2–7 × 1.5–4 cm), densely villous stem, lamina and calyx and yellow corolla.

Keywords

endemics, limestone, new taxon, Paraphlomideae, phylogeny

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* These authors contributed equally to this work.

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Introduction

As a member of tribe Paraphlomideae (Lamiaceae, Lamioideae) (Bendiksby et al. 2011; Zhao et al. 2021), the genus *Paraphlomis* Prain is characterised 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; Chen et al. 2021). A total of 36 species and seven varieties are recognised within *Paraphlomis*, most of which are distributed in southern China (Chen et al. 2022b; Yuan et al. 2022), with several species occurring in the Himalayas, Korea and Southeast Asia (Li and Hedge 1994; Ko et al. 2014; Chen et al. 2021). Many species of *Paraphlomis* are endemics of limestone soils, including the recently described *P. kuankuoshuiensis* R.B. Zhang, D. Tan & C.B. Ma (Zhang et al. 2020), *P. longicalyx* Y.P. Chen & C.L. Xiang (Chen et al. 2022a) and *P. hsiwenii* Y.P. Chen & X. Li (Chen et al. 2022b). This shows species richness of *Paraphlomis* has been quite underrated and more field investigations are needed to infer its diversity in limestone areas.

The botanical expedition to the Shimentai National Nature Reserve in Guangdong Province, China in October 2021, showed an unknown species of *Paraphlomis*. Based on other field observations (from May to August in 2022), morphological comparisons with congeneric species, as well as molecular phylogenetic studies, we confirmed that it represented a new species, here described and illustrated.

Materials and methods

Morphological study

Field observations and collections of the new species were carried out from May to August in 2022 in Boluo Town of Yingde City in northern Guangdong Province, China. Morphological comparisons of the putative new species with other *Paraphlomis* species were conducted firstly by consulting relevant taxonomic literature, included “Flora of China” (Li and Hedge 1994), “Flora of Guangdong” (Luo 1995) and other recently described species and infraspecies of *Paraphlomis* (Yan and Fang 2009; Ding et al. 2019; Zhang et al. 2020; Chen et al. 2021, 2022a, b, c; Zhao et al. 2022). We also carried out a check of herbarium specimens deposited in LBG, AU, IBK, FJFC, PE, ANUB, KUN, FJSI and SYS (herbarium acronyms following Thiers 2022). All morphological characters were measured using dissecting microscopes.

Phylogenetic analyses

Previous molecular phylogenetic study revealed genus *Paraphlomis* is not monophyletic, because species of *Matsumurella* were recovered within it (Chen et al. 2021; Chen et al. 2022b). Thus, *Matsumurella* was also included in our phylogenetic analyses. A total of 37 accessions, representing 20 species and four varieties/subspecies of *Para-*

phlomis and two *Matsumurella* species were selected as ingroups. One species each of *Phlomis* L. and *Phlomoides* Moench were included as outgroups following Chen et al. (2022a, b). Except for the three accessions of the new species that were newly sampled here, sequences of the remaining accessions were all retrieved from our previous studies (Chen et al. 2021, 2022a, b, c). Genomic DNA of the potential new species was extracted from silica-gel-dried leaves using the modified 2× CTAB procedure of Doyle and Doyle (1987). We selected five DNA markers for the phylogenetic reconstruction, including two nuclear ribosomal regions (internal and external transcribed spacers, i.e. ITS and ETS) and three plastid DNA regions (*rpl32-trnL*, *rps16* and *trnL-trnF*). Primers used for the polymerase chain reaction (PCR) amplification and sequencing were the same as those of Chen et al. (2021), while PCR procedures followed those described in Chen et al. (2016). The specimen information of samples and GenBank accession numbers for all sequences are listed in Appendix 1.

Raw sequences were assembled and edited using Sequencher 4.1.4 (Gene Codes, Ann Arbor, MI, USA) and then aligned using MUSCLE (Edgar 2004) and manually adjusted in MEGA 6.0 (Tamura et al. 2013). Bayesian Inference (BI) (Ronquist et al. 2012) and Maximum Likelihood (ML) (Stamatakis 2014) analyses were used for phylogenetic reconstruction and detailed settings for the two analyses followed those described in Chen et al. (2021). The resulting trees with posterior probabilities (PP) and Bootstrap support (BS) values were visualised and annotated in TreeGraph 2 (Stöver and Müller 2010). The combined nuclear dataset and the combined plastid dataset were initially analysed separately. Topological incongruence between the two reconstructions was visually inspected, based on the thresholds of PP ≥ 0.95 and/or BS ≥ 70%. After excluding the taxa that exhibited strong conflicts between the nuclear tree and the plastid tree, the combined nuclear dataset and the combined plastid dataset were then concatenated for phylogenetic analyses.

Results and discussion

The aligned length of the combined nuclear dataset was 1254 bp (810 bp for ITS, 444 bp for ETS) and that of the combined plastid dataset was 2479 bp (850 bp for rpl32-trnL, 812 bp for rps16, 817 bp for trnL-trnF). Since the placements of three taxa, *Paraphlomis albiflora* (Hemsl.) Hand.-Mazz., *P. nana* Y.P. Chen, C. Xiong & C.L. Xiang and *P. javanica* var. *pteropoda* D. Fang & K.J. Yan, showed hard incongruences in the nuclear tree (Appendix 2) and the plastid tree (Appendix 3), these taxa were excluded prior to the combination of the nuclear and plastid datasets. All the resulting trees (Fig. 1; Appendices 2–3) were topologically consistent with those in previous study (Chen et al. 2021). With the two species of *Matsumurella* deeply nested within *Paraphlomis*, both genera were shown to be non-monophyletic. The three individuals of the putative new species formed a strongly supported clade (Fig. 1: PP = 1.00 / BS = 100%), but its relationship with other species of *Matsumurella-Paraphlomis* was not resolved.

Our morphological study revealed that the new species *P. yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan is most similar to *P. foliata* subsp. *montigena* X.H. Guo & S.B. Zhou and *P. nana* for some morphological characters as they have short habits and triangular-laceolate calyx teeth with apices acuminate or bristle-like-acuminate. *Paraphlomis foliata* subsp. *montigena* was classified by Guo (1993) as a subspecies of *P. foliata* (Dunn) C.Y. Wu & H.W. Li. However, previous molecular phylogenetic studies (Chen et al. 2022b, c) and our present analyses (Fig. 1; Appendices 2–3) indicated that *P. foliata* subsp. *montigena* might represent an independent species within the genus as it is distantly related to *P. foliata* subsp. *foliata*. The new species can be distinguished from *P. foliata* subsp. *montigena* in the morphology and indumentum of laminae and calyces. Both the laminae and calyces are densely villous in *P. yingdeensis*, but are sparsely strigose in *P. foliata* subsp. *montigena*; the base of lamina is broadly cuneate and not decurrent in the new species, but is cuneate and decurrent in *P. foliata* subsp. *montigena*; *P. yingdeensis* has bristle-like-acuminate apex of calyx teeth, in contrast, the apex of calyx teeth of *P. foliata* subsp. *montigena* is acuminate. The phylogenetic placement of *P. nana* was conflicting in the nuclear tree and plastid tree, but it was consistently sister to *P. albiflora* (Appendices 2–3). Both *P. nana* and *P. yingdeensis* have translucent and membranous calyces with bristle-like-acuminate apex of calyx teeth. The two species mainly differ in the height of plants, size and indumentum of laminae, as well as colour of corollae. Specifically, plants of *P. nana* are 1–5 cm tall, whereas those of *P. yingdeensis* are 10–20 cm tall. The stems and laminae are densely villous in *P. nana*, but are densely strigose in *P. yingdeensis*. Moreover, *P. yingdeensis* has significantly larger laminae than *P. nana* (6.2–16.5 × 4–11.5 cm vs. 2–7 × 1.5–4 cm) and the corollae of *P. yingdeensis* are yellow, differing from the white corollae of *P. nana*. Detailed morphological comparisons amongst the three taxa were summarised in Table 1.

Geographically, *P. foliata* subsp. *montigena* is restricted to the Qingliangfeng Nature Reserve at the border area of Zhejiang and Anhui Provinces in eastern China (Guo 1993) and *P. nana* is now only known from Chongqing City in central China (Chen et al. 2022c). Both the two species are not karst-adapted. In contrast, the new species is distributed in the limestone area in Guangdong Province, southern China.

Taxonomic treatment

***Paraphlomis yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan, sp. nov.**

urn:lsid:ipni.org:names:77313387-1
Figs 2–4
Chinese name: 英德假糙苏

Type. China. Guangdong Province: Yingde City, Boluo Town, on the way from Xinzhai Village to Changshan Village, on the limestone cliff at the roadside, 24°24'N, 113°0'E, alt. 61 m, 29 May 2021, *Zhao Wan-Yi*, *Li Yuan-Qiu*, *Pan Jia-Wen & Yang Ling-Han ZWY-2092* (holotype: SYS00236856! isotypes: KUN!, SYS00236857!, SYS00236858!, SYS00236859!)

Diagnosis. *Paraphlomis yingdeensis* is morphologically similar to *P. foliata* subsp. *montigena* and *P. nana*, but differs from the former in its lamina and calyx densely villous (vs. sparsely strigose), base of lamina not decurrent (vs. decurrent) and apex

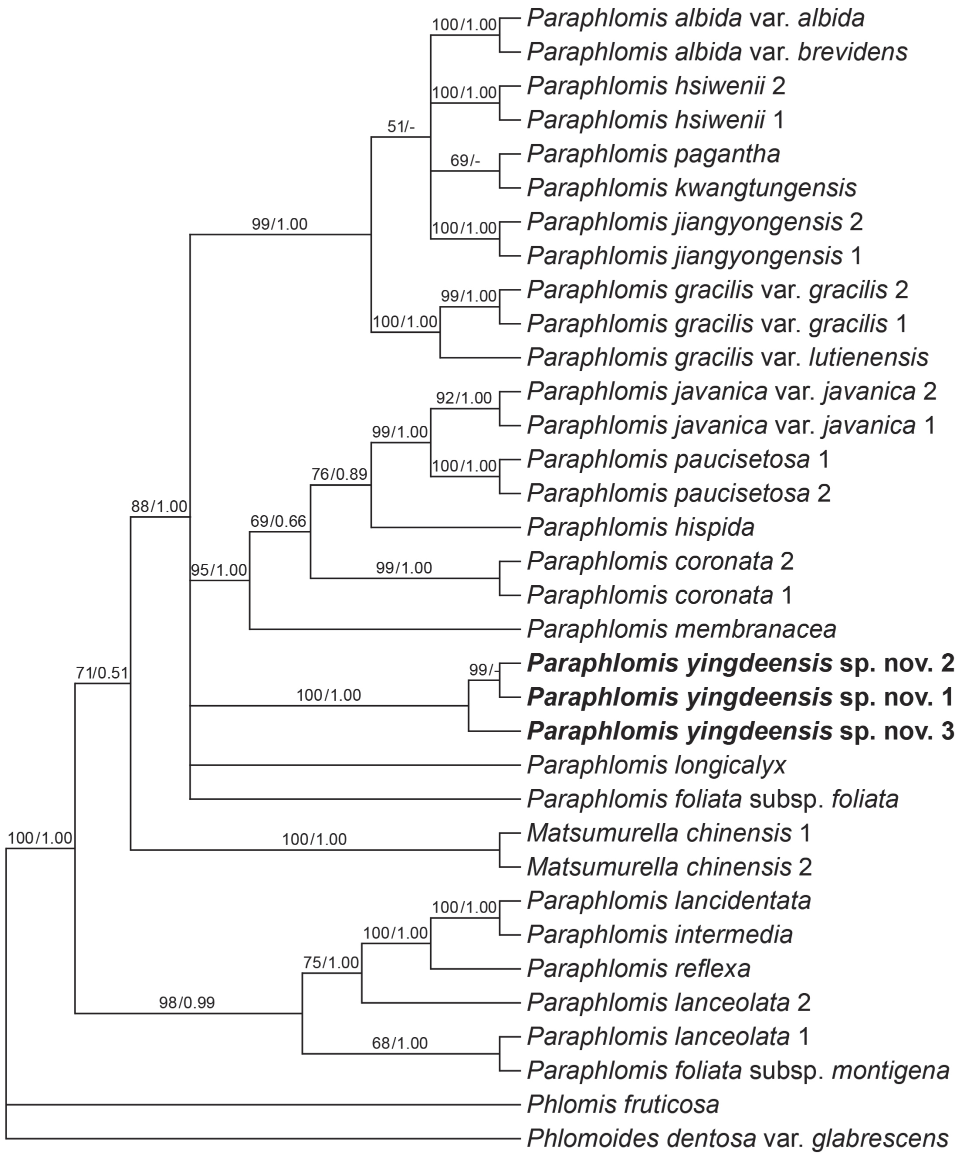

Figure 1. Optimal Maximum Likelihood tree of *Paraphlomis* inferred from combined nuclear (ETS and ITS) and plastid (*rpl32-trnL*, *rps16* and *trnL-trnF*) dataset. Support value ≥ 50% BS or 0.50 PP are displayed above the branches ("-" indicates a support value < 0.50 PP).

Table 1. Morphological comparisons amongst *Paraphlomis yingdeensis*, *P. foliata* subsp. *montigena* and *P. nana*.

Characters	*P. yingdeensis*	*P. foliata* subsp. *montigena*	*P. nana*
Stem	10–20 cm tall, densely villous	15–20 cm tall, densely villous	1–5 cm tall, densely retrorse strigose
Lamina	6.2–16.5 × 4–11.5 cm, base broadly cuneate, not decurrent, densely villous	5–16 × 2.5–6.5 cm, base cuneate, decurrent, sparsely strigose	2–7 × 1.5–4 cm, base cuneate to broadly cuneate, decurrent, densely to sparsely strigose
Calyx	Densely villous outside, teeth 3–4 mm long, apex bristle-like-acuminate	Sparsely strigose outside, teeth ca. 2.5 mm long, apex acuminate	Appressed strigose outside, teeth ca. 3 mm long, apex bristle-like-acuminate
Corolla	yellow	yellow	white

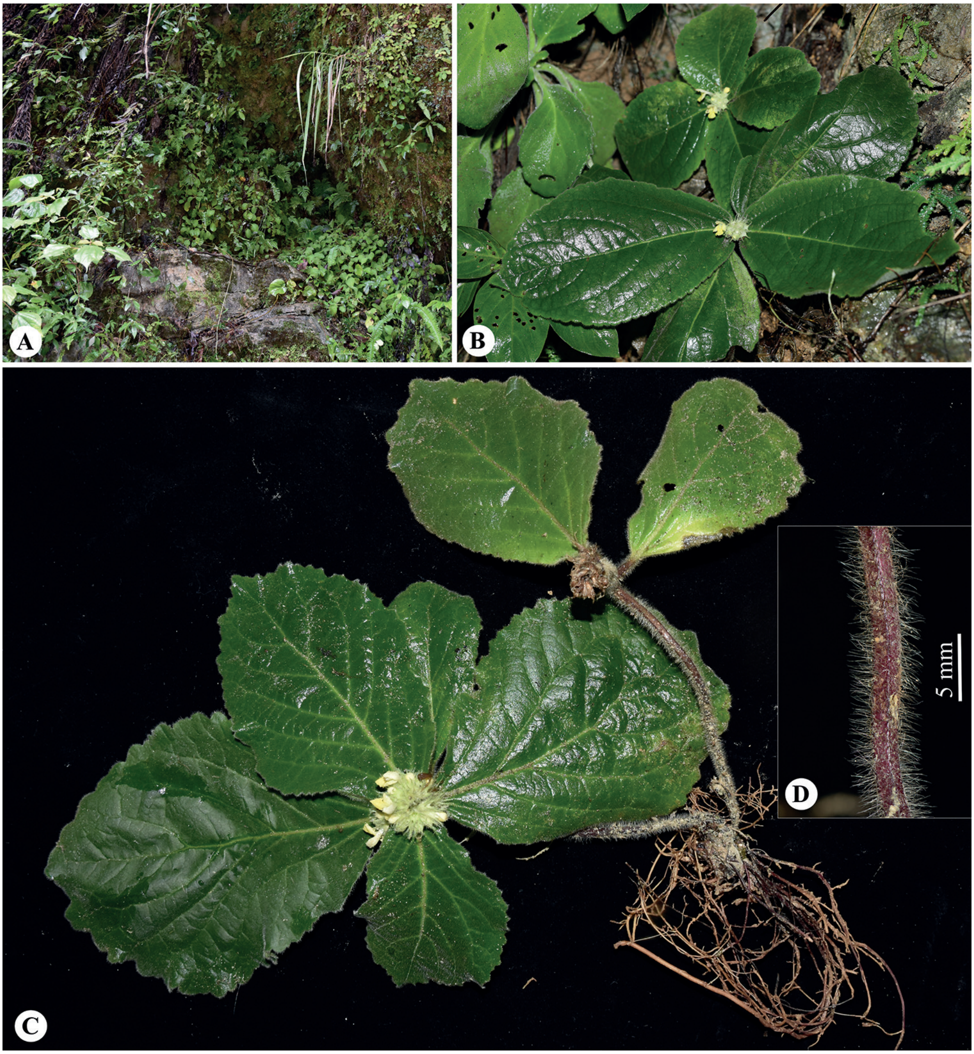

Figure 2. *Paraphlomis yingdeensis* from the type locality **A** habitat **B, C** plants **D** stem. (Photographs: **A, C, D** by W.-Y. Zhao; **B** by Y.-Q. Li).

of calyx teeth bristle-like-acuminate (vs. acuminate) and from the latter in its plants 10–20 cm tall (vs. 1–5 cm tall), lamina 6.2–16.5 × 4–11.5 cm and densely villous (vs. 2–7 × 1.5–4 cm and densely strigose) and corolla yellow (vs. white).

Description. ***Herbs*** perennial, 10–20 cm tall. ***Rhizomes*** short; roots fibrous, yellowish-brown, glabrous. ***Stems*** erect or prostrate, 4-angled, green (young branch) to purplish-red, densely villous. ***Leaves*** opposite, leafless towards base, upper two pairs crowded and rosulate; petiole 0.3–2.5 cm long, densely villous; lamina obovate, papery, 6.2–16.5 cm long, 4–11.5 cm wide, apex obtuse, base broadly cuneate, margin crenate-serrate; adaxially green, abaxially light green, densely villous on both sides; lateral veins 5–7-paired, obviously raised abaxially. ***Verticillasters*** in compact, sometimes capitate-like

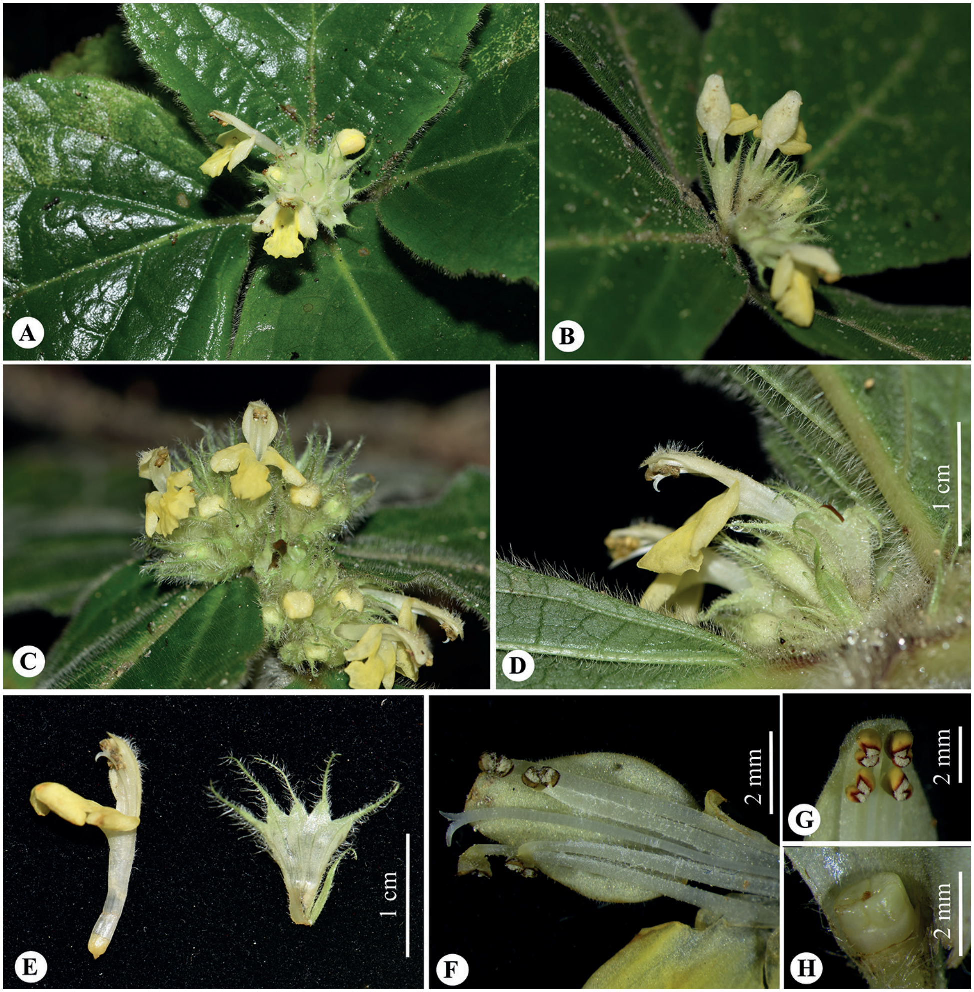

Figure 3. Floral traits of *Paraphlomis yingdeensis* **A, B** inflorescences **C** frontal view of flower **D** lateral view of flower **E** corolla and dissected calyx (inner view) **F** pistil and stamens **G** anthers **H** ovary. (Photographs: **A, B** by Y.-Q. Li; **C–H** by W.-Y. Zhao).

inflorescences, 8–16-flowered, 2.2–3.0 cm in diam.; bracteoles lanceolate to linear, 7–8 mm long, densely villous. ***Calyx*** light green, translucent, membranous, campanulate, 6–7 mm long, densely villous outside, glabrous inside, conspicuously 10-veined; teeth 5, subequal, triangular lanceolate, 3–4 mm long, apex bristle-like-acuminate. ***Corolla*** yellow, 1.5–1.8 cm long; tube 1.0–1.1 cm long, ca. 1.5 mm in diam., straight, pubescent annulate in throat inside; 2-lipped, villous outside, upper lip oblong, margin entire, erect, ca. 6 mm long, ca. 3.5 mm wide; lower lip spreading or reflexed, 4–5 mm long, 3-lobed, medium lobe suborbicular, apex emarginate, lateral lobes oblong, apex obtuse. ***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. ***Ovary*** 4-loculed, glabrous. ***Nutlets*** not seen.

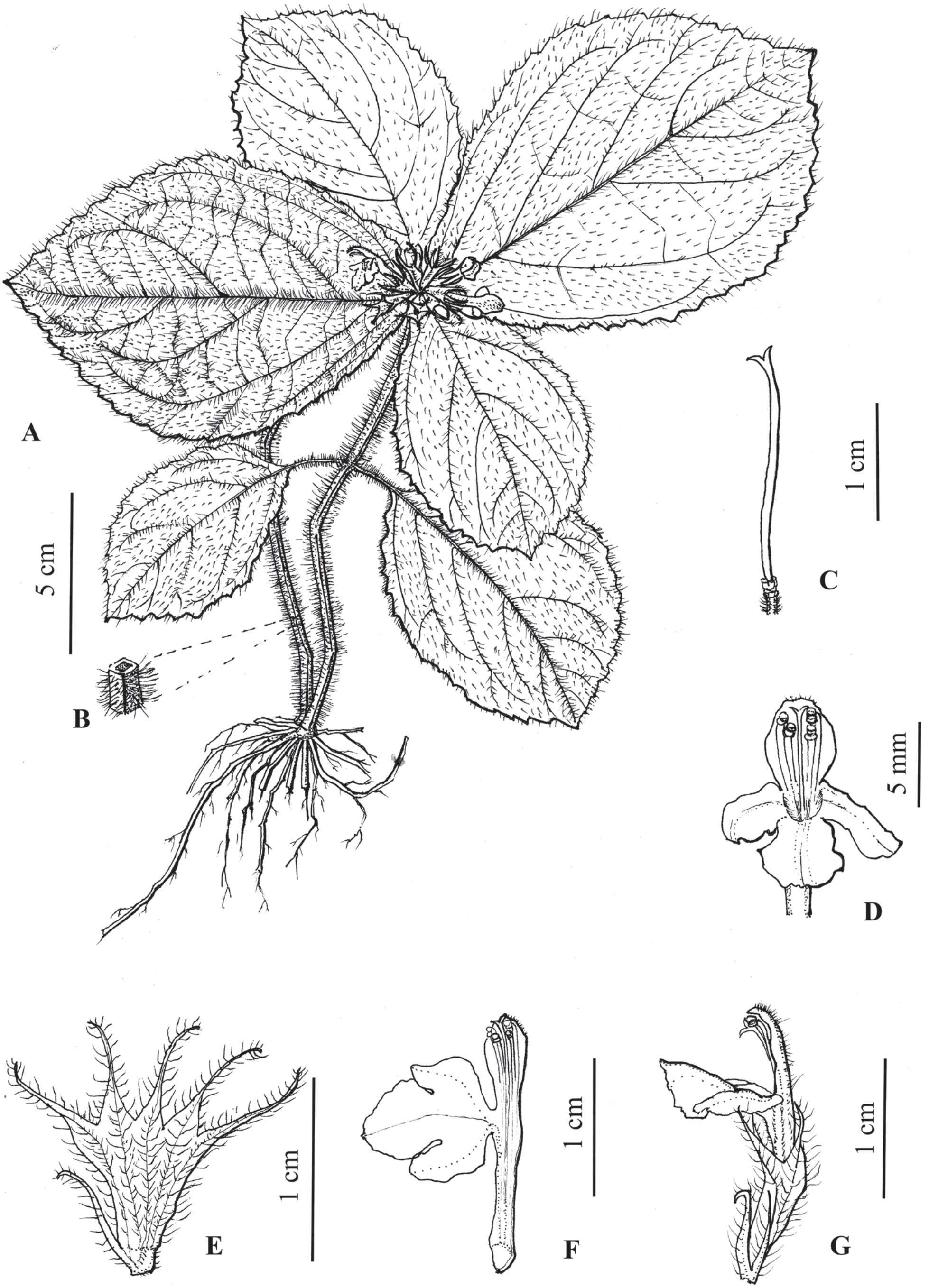

Figure 4. Line drawing of *Paraphlomis yingdeensis* **A** plant **B** transverse section of stem **C** pistil **D** frontal view of flower **E** dissected calyx (outside view) **F** dissected corolla **G** lateral view of flower. (Drawn by Rong-En Wu).

Distribution and habitat. Currently, only one population of *P. yingdeensis* was found in Boluo Town, Yingde City, in northern Guangdong Province. This town was located in the subtropical monsoon climate region, with development of a large area of karst landform. *Paraphlomis yingdeensis* usually grows on moist limestone cliffs in evergreen broad-leaved forests in association with *Tectaria devexa* Copel., *Primulina yingdeensis* Z.L. Ning, M. Kang & X.Y. Zhuang, *Begonia leprosa* Hance and *Ficus* spp.

Phenology. Flowering from May to June and fruiting from June to August.

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

Additional specimens examined (paratypes). China. Guangdong Province: Yingde City, Boluo Town, on the way from Xinzhai Village to Changshan Village, 24°24'N, 113°0'E, alt. 61 m, 9 June 2021, *Q. Fan 19013* (SYS); *ibid.*, 5 June 2022, *Li Yuan-Qiu ZWY-2020* (SYS); *ibid.*, 14 August 2022, *Ye Fan ZWY-2032* (SYS).

Specimens of *P. foliata* subsp. *montigena* examined. China. Anhui Province: Xi County, Qingliangfeng, alt. 1300 m, 29 October 1980, *Guo Xin-Hu 800023* (ANUB 13030926); *ibid.*, 16 July 1989, *Guo Xin-Hu & Zhou Shou-Biao 89011* (KUN 778733).

Specimens of *P. nana* examined. China. Chongqing: Chongkou County, Mingzhong Town, Jinchi Village, Longmenxi, Dabashan National Natural Reserve, on the moist cliff, alt. 996 m, 7 July 2021, *Chi Xiong XC21097* (holotype: KUN; isotypes: CQNM, IBK); Wushan County, Zhuxian Town, Shizhuzi Village, Daguling, Wulipo National Natural Reserve, in the moist valley, alt. 1310 m, 18 July 2021, *Chi Xiong & Hou-Lin Zhou XC21126* (KUN); *ibid.*, 11 September 2021, *Hou-Lin Zhou s.n.* (KUN).

Acknowledgements

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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	*rpl32-trnL*	*rps16*	*trnL-trnF*
Matsumurella chinensis (Benth.) Bendiksby 1	Y. Yang OYY00316 (KUN)	Pingxiang, Jiangxi, China	MW602147	MW602117	MW602021	MW602053	MW602084
Matsumurella chinensis (Benth.) Bendiksby 2	Y. Yang OYY00131 (KUN)	Guilin, Guangxi, China	MW602148	MW602118	MW602022	MW602054	MW602085
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	MW601996	MW602028	MW602060
Paraphlomis albida var. *brevidens* Hand.-Mazz.	Y.P. Chen EM312 (KUN)	Hezhou, Guangxi, China	MW602130	MW602098	MW602003	MW602035	MW602067
Paraphlomis albiflora (Hemsl.) Hand.-Mazz.	C.M. Tan et al. 1806393 (JJF)	Jiujiang, Jiangxi, China	/	MW602101	MW602006	MW602038	MW602069
Paraphlomis coronata (Vaniot) Y.P. Chen & C.L. Xiang 1	E.D. Liu et al. 3043 (KUN)	Emeishan, Sichuan, China	MW602137	MW602107	MW602012	MW602044	MW602075
Paraphlomis coronata (Vaniot) Y.P. Chen & C.L. Xiang 2	C.L. Xiang 358 (KUN)	Jiangkou, Guizhou, China	MW602123	MW602090	MW601995	MW602027	MW602059
Paraphlomis foliata (Dunn) C.Y. Wu & H.W. Li subsp. *foliata*	S.P. Chen s.n. (KUN)	Jiangle, Fujian, China	/	MW602097	MW602002	MW602034	MW602066
Paraphlomis foliata subsp. *montigena* X.H. Guo & S.B. Zhou	Y.C. Dai s.n. (KUN)	Hangzhou, Zhejiang, China	OM836064	OM884453	OM884456	OM884459	OM884462
Paraphlomis gracilis (Hemsl.) Kudô var. gracilis 1	A. Liu LK0931 (CSFI)	Changsha, Hunan, China	MW602134	MW602104	MW602009	MW602041	MW602072
Paraphlomis gracilis (Hemsl.) Kudô var. *gracilis 2*	C.L. Xiang XCL1315 (KUN)	Chongqing, China	MW602141	MW602111	MW602016	MW602048	MW602079
Paraphlomis gracilis var. *lutienensis* (Y.Z. Sun) C.Y. Wu	C.L. Xiang XCL881 (KUN)	Shibing, Guizhou, China	MW602131	MW602099	MW602004	MW602036	MW602068
Paraphlomis hispida C.Y. Wu	X. Li LX200702 (GXF)	Napo, Guangxi, China	MW602132	MW602102	MW602007	MW602039	MW602070
Paraphlomis hsiwenii Y.P. Chen & Xiong Li 1	W.H. Wu et al. DD426 (KUN)	Jingxi, Guangxi, China	OP605346	OP609841	OP609848	OP609855	OP609862
Paraphlomis hsiwenii Y.P. Chen & Xiong Li 2	W.H. Wu et al. DD426 (KUN)	Jingxi, Guangxi, China	OP605347	OP609842	OP609849	OP609856	OP609863
Paraphlomis intermedia C.Y. Wu & H.W. Li	X. Zhong et al. ZX16823 (CSH)	Suichang, Zhejiang, China	MW602135	MW602105	MW602010	MW602042	MW602073
Paraphlomis javanica (Blume) Prain var. *javanica* 1	Y.P. Chen s.n. (KUN)	Kunming, Yunnan, China	MW602121	MW602088	MW601993	MW602025	MW602057
Paraphlomis javanica (Blume) Prain var. *javanica* 2	L.B. Jia et al. JLB0029 (KUN)	Maguan, Yunnan, China	MW602143	MW602113	MW602017	MW602049	MW602080
Paraphlomis javanica var. *pteropoda* D. Fang & K.J. Yan	X. Li 2020090501 (GXF)	Jingxi, Guangxi, China	MW602140	MW602110	MW602015	MW602047	MW602078
Paraphlomis jiangyongensis X.L. Yu & A. Liu 1	A. Liu et al. LK1104 (CSFI)	Jiangyong, Hunan, China	MW602128	MW602095	MW602000	MW602032	MW602064
Paraphlomis jiangyongensis X.L. Yu & A. Liu 2	A. Liu et al. LK1104 (CSFI)	Jiangyong, Hunan, China	MW602129	MW602096	MW602001	MW602033	MW602065
Paraphlomis kwangtungensis C.Y. Wu & H.W. Li	Y.P. Chen & Y. Zhao EM1391 (KUN)	Huaiji, Guangdong, China	MW602126	MW602093	MW601998	MW602030	MW602062
Paraphlomis lanceolata Hand.-Mazz. 1	C.Z. Huang s.n. (KUN)	Guidong, Hunan, China	MW602145	MW602115	MW602019	MW602051	MW602082
Paraphlomis lanceolata Hand.-Mazz. 2	A. Liu et al. LK0825 (CSFI)	Ningyuan, Hunan, China	MW602146	MW602116	MW602020	MW602052	MW602083
Paraphlomis lancidentata Y.Z. Sun	X. Zhong et al. ZX16824 (CSH)	Suichang, Zhejiang, China	MW602136	MW602106	MW602011	MW602043	MW602074
Paraphlomis longicalyx Y.P. Chen & C.L. Xiang	Y.P. Chen et al. EM583 (KUN)	Huanjiang, Guangxi, China	OK104771	OK104774	OK104778	OK104780	OK104783
Paraphlomis membranacea C.Y. Wu & H.W. Li	M.S. Nuraliev 1057 (MW)	Thanh Son, Phu Tho, Vietnam	/	MW602100	MW602005	MW602037	/
Paraphlomis nana Y.P. Chen, C. Xiong & C.L. Xiang 1	C. Xiong XC21097 (KUN)	Chengkou, Chongqing, China	OM836062	OM884451	OM884454	OM884457	OM884460
Paraphlomis nana Y.P. Chen, C. Xiong & C.L. Xiang 2	C. Xiong & H.L. Zhou XC21126 (KUN)	Wushan, Chongqing, China	OM836063	OM884452	OM884455	OM884458	OM884461
Paraphlomis pagantha Dunn	L.X. Yuan et al. s.n. (KUN)	Qionghai, Hainan, China	OP605345	OP609840	OP609847	OP609854	OP609861
Paraphlomis paucisetosa C.Y. Wu 1	X.X. Zhu s.n. (KUN)	Malipo, Yunnan, China	MW602125	MW602092	MW601997	MW602029	MW602061
Paraphlomis paucisetosa C.Y. Wu 2	X. Li LX200704 (GXF)	Napo, Guangxi, China	MW602133	MW602103	MW602008	MW602040	MW602071
Paraphlomis reflexa C.Y. Wu & H.W. Li	Z.Z. Yang et al. s.n. (HIB)	Tongshan, Hubei, China	MW602122	MW602089	MW601994	MW602026	MW602058
***Paraphlomis yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan 1**	**Q. Fan et al. 19013 (SYS)**	**Yingde, Guangdong, China**	**OP605348**	**OP609843**	**OP609850**	**OP609857**	**OP609864**
***Paraphlomis yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan 2**	**Q. Fan et al. 19013 (SYS)**	**Yingde, Guangdong, China**	**OP605349**	**OP609844**	**OP609851**	**OP609858**	**OP609865**
***Paraphlomis yingdeensis* W.Y.Zhao, Y.Q.Li & Q.Fan 3**	**Q. Fan et al. 19013 (SYS)**	**Yingde, Guangdong, China**	**/**	**OP609845**	**OP609852**	**OP609859**	**OP609866**
Phlomis fruticosa L.	Y. Tong s.n. (KUN)	Shanghai, China (cultivated)	MW602119	MW602086	MW601991	MW602023	MW602055
Phlomoides dentosa var. *glabrescens* (Danguy) C.L. Xiang & H. Peng	Y.P. Chen EM360 (KUN)	Beijing, China (cultivated)	MW602120	MW602087	MW601992	MW602024	MW602056

Appendix 2

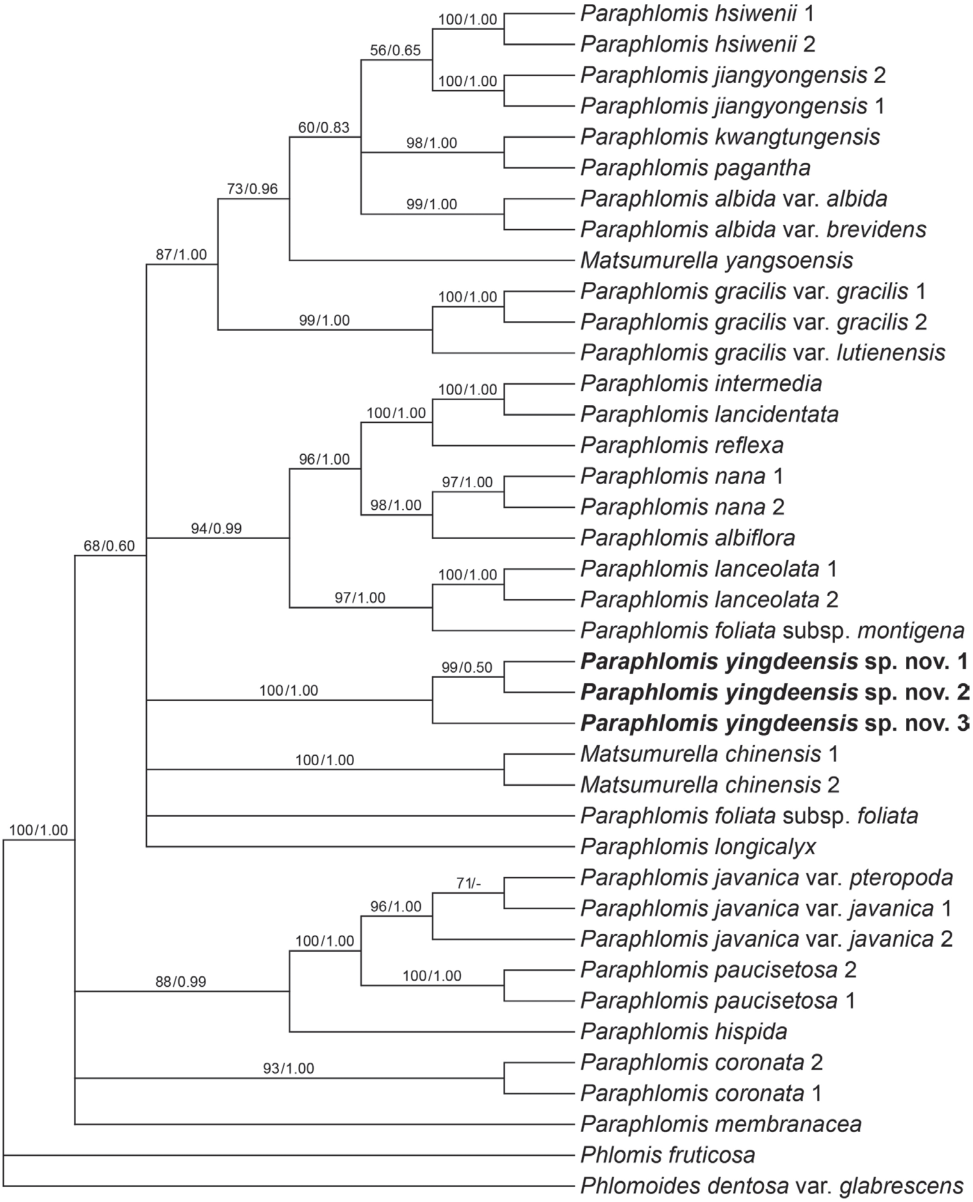

Figure A1. Optimal Maximum Likelihood tree of *Paraphlomis* inferred from combined nuclear (ITS and ETS) dataset. Support value ≥ 50% BS or 0.50 PP are displayed above the branches ("-" indicates a support value < 0.50 PP).

Appendix 3

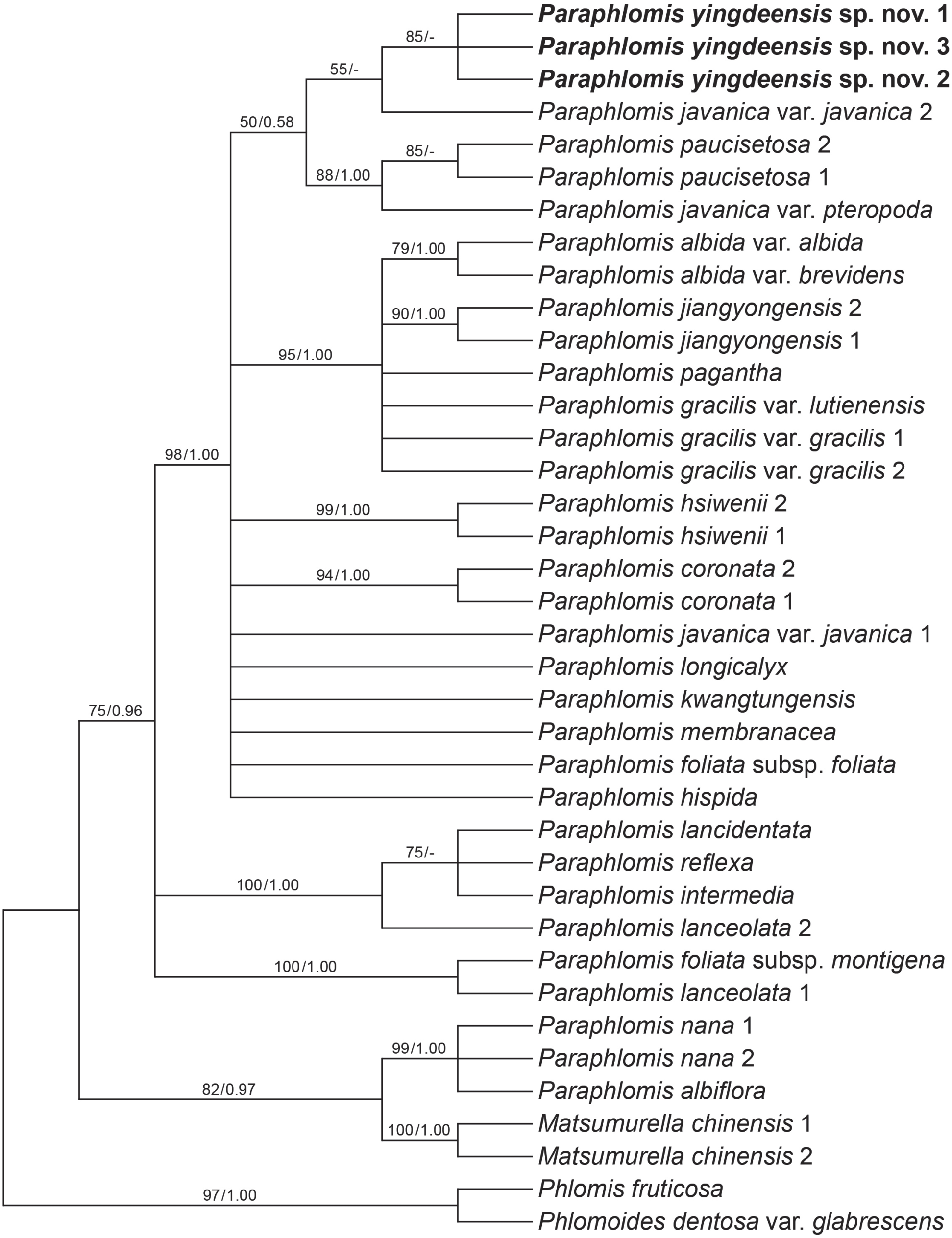

Figure A2. Optimal Maximum Likelihood tree of *Paraphlomis* inferred from combined plastid (*rpl32-trnL*, *rps16* and *trnL-trnF*) dataset. Support value ≥ 50% BS or 0.50 PP are displayed above the branches ("-" indicates a support value < 0.50 PP).

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A new, disjunct species of *Bahiana* (Euphorbiaceae, Acalyphoideae): Phytogeographic connections between the seasonally dry tropical forests of Peru and Brazil, and a review of spinescence in the family

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Abstract

Bahiana is expanded from 1 to 2 species with the description of *B. occidentalis* K. Wurdack, **sp. nov.** as a new endemic of the seasonally dry tropical forests (SDTFs) of Peru. The disjunct distribution of *Bahiana* with populations of *B. occidentalis* on opposite sides of the Andes in northwestern Peru (Tumbes, San Martín) and *B. pyriformis* in eastern Brazil (Bahia) adds to the phytogeographic links among the widely scattered New World SDTFs. Although *B. occidentalis* remains imperfectly known due to the lack of flowering collections, molecular phylogenetic results from four loci (plastid *matK*, *rbcL*, and *trnL-F*; and nuclear ITS) unite the two species as does gross vegetative morphology, notably their spinose stipules, and androecial structure. Spinescence in Euphorbiaceae was surveyed and found on vegetative organs in 25 genera, which mostly have modified sharp branch tips. Among New World taxa, spines that originate from stipule modifications only occur in *Bahiana* and *Acidocroton*, while the intrastipular spines of *Philyra* are of uncertain homologies.

Keywords

Biogeography, Huancabamba Depression, molecular phylogeny, SDTF, spines, taxonomy

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Introduction

Seasonally dry tropical forest (SDTF) is a biome broadly characterized by a pronounced dry season in addition to low mean annual precipitation, flora with diverse drought adaptations (e.g., deciduousness, succulence), fertile non-acidic soils, fire intolerance, and sparse herb layers with few grasses (Pennington et al. 2000, 2009; Banda-R et al. 2016). SDTFs have attracted much recent attention and research due to their rich endemism, interesting historical biogeography, and conservation concern (Pennington et al. 2009). In the New World they range from northwestern Mexico, through the Caribbean, and across South America, roughly encircling the Amazon basin. Within this range they are patchy, especially along the Pacific side and inter-Andean valleys of South America, and are broken into floristic "nuclei" which display patterns of regional endemism and a strong geographic component to floristic relatedness. Taxa that are widespread or disjunct across their breadth are rare, but some distribution patterns and modeling suggest SDTF formations were more continuous across South America during the Pleistocene (Pleistocene Arc Theory; see Werneck et al. 2011). The processes of SDTF flora assembly and species diversification are thought to revolve around relatively long biome stability, dispersal limitations, and phylogenetic niche conservatism (Pennington et al. 2009).

Euphorbiaceae are an important component of SDTF floras and in terms of diversity are among the top six most species-rich families in woody plant inventories (Banda-R et al. 2016). The family is represented by diverse endemics including *Bahiana* spp., *Croton* spp., *Gymnanthes boticario* Esser, M.F.Lucena & M.Alves, and a small species radiation of stem-succulent *Euphorbia* spp. in eastern Brazil (Hurbath et al. 2021). *Bahiana* J.F.Carrión was recently described as a monotypic genus and narrow SDTF endemic, with a population of ca. 20 plants at the type locality in central Bahia of eastern Brazil (Carrión et al. 2022). A cryptic plant from the Peruvian SDTF, here described as a new species of *Bahiana*, that was first collected 40 years ago (1982) and is now represented by 35 collections, has lain unidentified to genus (or misidentified) among Euphorbiaceae in the Missouri Botanical Garden herbarium. The principal impediment to recognition of this taxon has been that many of those collections which were made for plot studies are sterile, and the reproductive collections are either fruiting or else in very young staminate buds. I recognized five years ago that these collections were united by leaf architecture and spinose stipules, and represented an unusual, potentially undescribed Euphorbiaceae-Acalyphoideae. However, an initial analysis of plastid *trnL-F* sequence data within the context of the family-wide phylogeny of Wurdack et al. (2005) only yielded placement with New World members of Acalyphoideae tribe Bernardiaeae (clade A7; Bernardia clade, Carrión et al. 2022; Bernardieae pro parte, Radcliffe-Smith 2001; Webster 2014), with no clear generic affiliation. The phylogenetic analysis and description of *Bahiana pyriformis* by Carrión et al. (2022) expanded the sampling for the Bernardia clade and provided critical context for the Peruvian plant. The four genera comprising the Bernardia clade are diverse, even in habitat, where species of *Adenophaedra* (Müll.Arg.) Müll.Arg. and *Caryodendron* H.Karst. are in rainforests, *Bahiana* are in SDTF, and *Bernardia* Houst. ex Mill. are wide ranging from rainforests to dry-adapted taxa, including SDTF endemics.

Although the Peruvian plants remain incompletely known, morphological similarities and new molecular phylogenetic results indicate that they should be recognized as a second species of *Bahiana*. Hopefully its description will spur further efforts to secure flowering collections and additional localities. Moreover, it adds an unusual floristic connection among the SDTFs of South America. Given the fragmented and sometimes erroneous information on spinescence in Euphorbiaceae and its relevance to ecology (i.e., understanding the evolution anti-herbivory defenses), the character was reviewed for the entire family, with special emphasis on spinose stipules to enable comparisons with *Bahiana*.

Materials and methods

Molecular methods for DNA extraction with modified Qiagen DNeasy Plant kits, then amplification and fluorescent Sanger sequencing with BigDye Terminator v3.1 chemistry (Thermo Fisher Scientific, Waltham, Massachusetts) on an ABI 3730xl DNA Analyzer (Thermo Fisher Scientific) followed prior studies (i.e., Wurdack et al. 2005; Wurdack and Davis 2009; Cardinal-McTeague et al. 2019; van Welzen et al. 2021). The 2-marker (plastid *rbcL*, *trnL-F*) data set of Carrión et al. (2022) was largely derived from Wurdack et al. (2005) by restricting the taxon sampling to Acalyphoideae and adding *Bernardia* clade representatives, and then further modified here by my addition of three tips (two of the Peruvian *Bahiana* and previously published *Adelia cinerea* [Wiggins & Rollins] A.Cerv., V.W.Steinm. & Flores Olv., GenBank DQ997801, HG971805). *Adelia* may not be monophyletic (De-Nova and Sosa 2007; Cervantes et al. 2016), and the addition of *A. cinerea* to the 2-marker data set provides better context for the use of that outlier species as an outgroup in the 4-marker data set. The 4-marker data set of Carrión et al. (2022) included *Bernardia* clade representatives for plastid *matK* (including 3' *matK-trnK*), *petD*, and *trnL-F*, and nuclear ribosomal ITS, and was modified here by my addition of the Peruvian *Bahiana* (two tips). Laboratory work on each of the two Peruvian samples occurred at very different times and under contamination-control protocols developed for degraded museum samples. The visually best-preserved ("greenest") of the 35 collections (*A. Gentry et al. 37824*, MO) yielded DNA of sufficient quality to sequence *matK* (partial), *rbcL*, *trnL-F*, ITS, and ETS (GenBank OP900956, OP900955, OP900957, OP879622, OP901195, respectively); more degraded DNA from another collection (*C. Díaz S. et al. 6545*, US) yielded sequences for *trnL-F*, ITS, and ETS (GenBank OP900958, OP879623, OP901196). Due to the lack of differences in ITS between the new species accessions, a 400 bp fragment of ETS was sequenced to further explore population variation. Nuclear ribosomal ETS has been a useful rapid-evolving complement to ITS for fine-scale resolution of many clades of Euphorbiaceae (e.g., Cardinal-McTeague et al. 2019; van Welzen et al. 2021). For new data, I amplified and/or sequenced the genetic markers using mostly standard primers for *matK* (400f, 1159r, 1053f, K2r), *rbcL* (1f, 724r, 626f, 1360r), *trnL-F* (c, d, e, f, intF), ITS (5a, P3, U2, U4), and ETS (F2; 18s_5pr, newly published here, CTGGCAGGATCAACCAGGTAGCA).

The reads were assembled with Sequencher v5.2.4 (Gene Codes, Ann Arbor, Michigan, U.S.A.) and consensus sequences were manually inserted into the multiple sequence alignments (MSAs) of Carrión et al. (2022), followed by alignment refinements based on a sequence similarity criterion. Preliminary analyses showed that my minor MSA improvements and various stringencies in the masking of ambiguously aligned regions had limited impact on resolution or support values, thus a limited exclusion set of select indel hotspots was implemented (details in the archived MSAs). The 2-marker data set had 418 columns excluded (original length 3230 bp) and 24.7% missing data; the 4-marker data set had 260 columns excluded (original length 6560 bp) and 22.2% missing data. Maximum likelihood (ML) analyses used IQ-TREE v1.6.11 under GTR+F+I+G4 and clade support estimated by 1000 rapid bootstrap replicates (Trifinopoulos et al. 2016). Bayesian inference (BI) was with MrBayes v3.2.7a (Ronquist et al. 2012) as implemented on CIPRES XSEDE with two concurrent runs, each with four chains and sampling every 1000 generations over 50 000 000 generations, a 0.2 temperature coefficient, a conservative 25% burn-in, and an Effective Sample Size (**ESS**) > 200 verified with Tracer v1.6.0 (Rambaut et al. 2013).

Scanning electron microscopy (**SEM**) used a Zeiss EVO MA15 (Carl Zeiss SMT, Inc., Peabody, Massachusetts) at 3 kV after sputter-coating herbarium specimen fragments with Au/Pd over C (11 nm total) using a Leica EM ACE600 (Leica Microsystems GmbH, Wetzlar, Germany). Staminate inflorescences were rehydrated and buds microdissected before critical point drying (**CPD**) from an ethanol transition. A leaf was cleared in 5% sodium hydroxide followed by saturated chloral hydrate, and then stained with basic fuchsin (1% in absolute ethanol). Light microscopy (**LM**) was with a Leica DM6 B (Leica Microsystems Inc., Deerfield, IL) or an Olympus DSX100 (Olympus Corp., Tokyo, Japan). Spinescence was assessed based on literature reports (mostly confirmed with collections), surveys of herbarium specimens (primarily MO, NY, US, and type images in JSTOR Global Plants, https://plants.jstor.org/), and observations of living plants. Words pertaining to spinescence were searched for in literature treatments (e.g., Webster 2014) of Euphorbiaceae as leads to additional taxa. Not considered here were trichomes, spines (or horns) associated with reproductive structures such as fruit pericarps (e.g., *Hancea* Seem., *Mallotus* Lour., *Microstachys* A.Juss., *Sclerocroton* Hochst.) and bracts (e.g., *Dalechampia* Plum.), or sub-spinose branch tips that appear to be the result of weathering (e.g., *Bernardia obovata* [Chodat & Hassl.] Pax & K.Hoffm.) rather than developmental processes. Many pericarp spinose structures appear more ornamental in nature in being few (1–2 per valve), short, and/or blunt. Spinose species estimates are uncertain in *Euphorbia* L., and there is some subjectivity in the distinctions between spinose and sub-spinose structures (e.g., variations in *Erythrococca* spp. stipules).

Phylogenetic results

The two geographically widely separated samples of the Peruvian *Bahiana* have identical ITS and *trnL-F* sequences, but differ at four positions in ETS (1.0% difference); slower evolving *matK* and *rbcL* were not compared because sequences were not generated for both samples. These two samples also provide molecular evidence to unite staminate and pistillate collections. Within the context of the modified Carrión et al. data sets, the new species is strongly supported (posterior probabilities, PP = 1.0; bootstrap percentages, BP = 100%) as sister to *Bahiana pyriformis* within a similarly supported *Bernardia* clade, and branch lengths (not shown) indicate considerable sequence divergence between the two species (Figs 1, 2).

Data resources

The data underpinning the phylogenetic analyses reported in this paper are deposited in GenBank and the Dryad Data Repository at https://doi.org/10.5061/dryad.wstqjq2r6.

Taxonomy

Bahiana occidentalis **K. Wurdack, sp. nov.**
urn:lsid:ipni.org:names:77314428-1
Figs 3, 5

Diagnosis. Differs from *Bahiana pyriformis* in leaves smaller (3.5–6[8.1] × 2.1–3.9[4.6] versus 6–12 × 3–6 cm), staminate cymules 1-flowered (versus usually 3-flowered), fruits smaller and subglobose (ca. 9 × 14 mm versus 18–28 × 17–23 mm and usually obovoid to pyriform), fruit pedicels longer (10–18 versus up to 5 mm), and seeds smaller (6.9–7.3 long × 6.4–6.5 wide × 6.8–7.4 thick versus 10–15 long × 8–11 wide × 8–13 thick mm).

Type. Peru. Tumbes: Zarumilla Province, Matapalo, zona "El Caucho-Campo Verde", Parcela 2 × 500 m (evaluación florística) paralela a parcela "V" de evaluación forestal permanente, desde 420 m hasta 500 m, 03°50'29"S, 080°15'30"W (-3.8413800, -80.2583300), 500 m, 11 Feb 1993 (fr), *C. Díaz S. et al. 6288* (holotype: MO sheet 7004543; isotypes: K, NY, US, USM; 13 reported duplicates).

Description. Small trees, 4–10 m, trunk to 12 cm dbh, probably dioecious (collections unisexual); bark of branches smooth, lenticellate; lateral leafy branchlets 1–6 cm long, 1–2 mm wide, terete, sometimes as brachyblasts with numerous compressed nodes, or with zones of compressed nodes (long shoot/short shoot transitions on same axis), sparsely pubescent when young. ***Indumentum*** simple, pale, to 0.5 mm long. ***Stipules*** free, persistent, paired; when young appressed to stem, triangular 1.5–2.5 × 1 mm, with prominent midrib and narrow membranous margins extending ca.

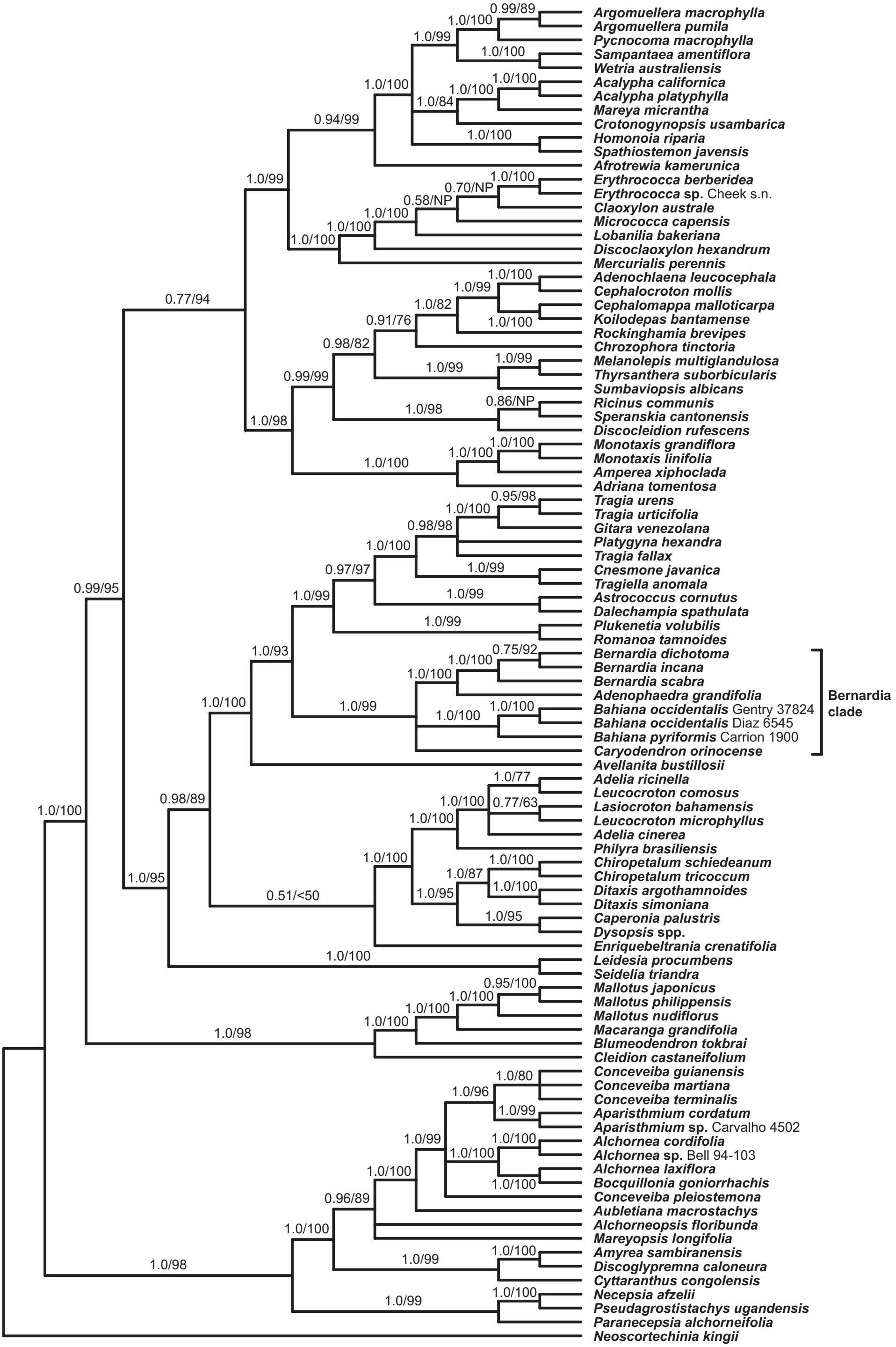

Figure 1. Phylogenetic relationships of *Bahiana* and its Acalyphoideae relatives. Bayesian 50% majority-rule consensus tree based on the combined 2-marker (*rbcL*, *trnL-F*), 96-tip data set with posterior probability/ML bootstrap values indicated, respectively. NP = an edge not present with ML.

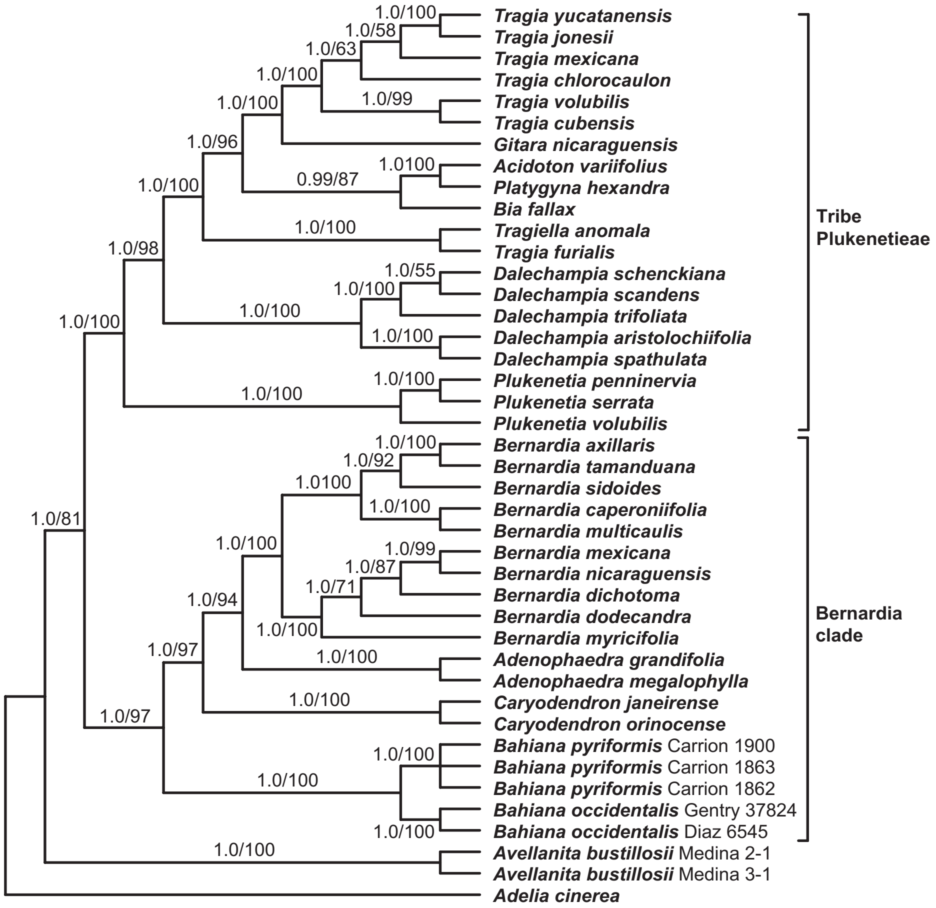

Figure 2. Phylogenetic relationships of *Bahiana* and its Bernardia clade relatives. Bayesian 50% majority-rule consensus tree based on the combined 4-marker (*matK*, *petD*, *trnL-F*, ITS), 42-tip data set with posterior probability/ML bootstrap values indicated, respectively.

triangular, navicular. ***Leaves*** alternate, simple, petiolate. ***Petioles*** 3–7(11) mm long, 0.5–0.7 mm tall × 0.7–1 mm wide (mid-length cross section), slightly dorsiventrally flattened (rarely terete), adaxially moderately pubescent and abaxially distinctly less pubescent to nearly glabrous. ***Leaf blades*** elliptic, 3.5–6(8.1) × 2.1–3.9(4.6) cm, length:width ratio 1.45–2.91:1 (mean = 2.00, SD = 0.313, n = 55, 5 leaves each from 11 collections); base obtuse to acute; apex obtuse to acute, tip minutely retuse and tipped by a globose gland as on marginal teeth; chartaceous, margins subentire proximally (near base obscurely crenate with little evidence of teeth) to distinctly toothed (crenate) distally, tooth depth varying 0.2–0.5 mm, 7–15 well-defined teeth per side, tooth tip bearing persistent sub-globose glandular knob to 0.2 mm diam. that terminates principal (tertiary) vein; laminar glands (cicatricose-crateriform glands sensu Cervantes et al. 2009) abaxial, scattered, 5–20 glands per leaf, elliptic, 0.1–0.2 × 0.1–0.25 mm, associated with tertiary or quaternary veins; other laminar or petiolar glands

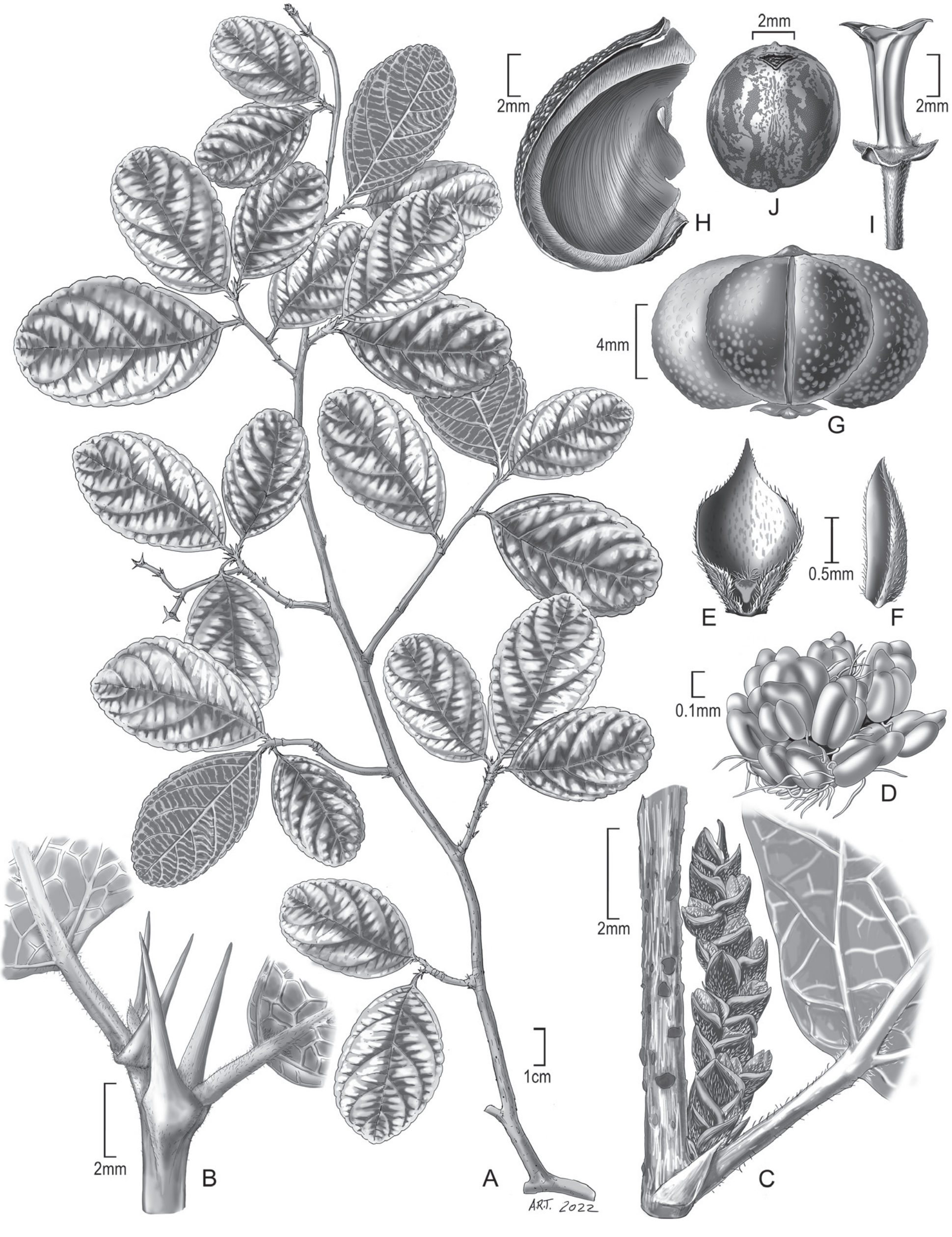

Figure 3. Illustration of *Bahiana occidentalis* **A** habit **B** shoot tip with spinose stipules **C** staminate inflorescence in bud **D** androecium **E** staminate bract **F** staminate bractlet **G** fruit **H** fruit valve (coccus) **I** columella **J** seed (ventral). Sources: **A, B, H–J** *C. Díaz et al. 6288*, US **C–F** *C. Díaz et al. 6148*, MO **G** *C. Díaz et al. 7340*, MO.

0.1 mm, sparsely short puberulent; with age spinose, stiff, accrescent to 5–6 mm long, base with shield-like attachment zone to stem, projecting 45–90° from stem, glabrescent; resting buds with multiple series of spines and scales; bud scales 1.5 × 1 mm, absent; trichomes abaxially usually only associated with major veins (rarely uniformly pubescent, *A. Gentry et al. 37824*), sparsely present along midvein but more densely as acarodomatial tufts in axils of primary/secondary vein junctions; acarodomatia with narrow flaps of vein tissues extending to 0.1 mm from vein junctions, not coincident with laminar glands; adaxial surface micropustulate (likely an artifact of drying around subsurface crystals), pustules mostly tracing vein fabric. ***Venation*** pinnate, agrophic veins absent, major secondaries bronchidodromous, 5–7 secondary veins per side, intersecondaries absent, tertiary and quaternary veins mixed percurrent. ***Staminate inflorescences*** axillary and appearing terminal, 6–11 mm long in young bud, racemose, simple, ca. 20+ cymules in 3 anticlockwise spirals, cymules each containing 1 bud, subtended by a bract and 2 lateral bractlets; bract 1.5 × 1 mm, navicular, tip acuminate; bractlets navicular, 1.7 × 0.4 mm, glabrous internally and hirsute externally. ***Staminate flowers*:** sepals 5?, densely hirsute externally, glabrous internally; receptacle glandular, hirsute; stamens 12–15, filaments free; anthers dorsifixed, introrse, pollen sacs unequal with dorsal pair longer than ventral, connective with protrusion; petals and disc segments absent. ***Pistillate infructescences*** axillary, with 1–2 nodes, dichotomously branched, 1–2 fruits per inflorescence; proximal internode (peduncle) 10–40 mm long; ultimate branches (pedicels) 10–18 mm long, 0.5–0.6 mm diam., articulated and often bent at middle but not detaching there, proximal segment (relative to articulation) 3–9 mm long, distal segment 4–8 mm long, slightly thicker and usually darker colored; nodes subtended by navicular bract to 2 mm long. ***Pistillate flowers*** (details inferred from fruits) sepals 5, 1.5 × 1–1.5 mm, triangular, slightly unequal in size, interior glabrous, disk annular, thin, densely hirsute; locules 3, styles 3, undivided, thin, to 2.5 mm long, not connate into a column, glabrous. ***Fruits*** schizocarps, subglobose, trilobed, ca. 9 (long) × 14 (wide) mm, splitting septicidally and loculicidally into 3 equal 2-valved mericarps; valve segments ca. 13 × 5 mm; sepals and styles persistent; sparsely pubescent, pericarp dry; endocarp woody, 0.8–1 mm thick (equatorial at dorsal dehiscence suture); epicarp ca. 0.2 mm thick, separating when dry, inner surface vascularized, colliculate internally and externally; septa of mericarps thin, nearly complete except for distal funicular gap, shallow basal triangle 4 × 1 mm; columella 5–6 mm long, 1.2–1.3 mm wide (middle), trigonous, tip retaining arms to 1–1.5 mm long, persistent. ***Seeds*** 1 per chamber, ellipsoid, laterally slightly compressed, 6.9–7.3 (long) × 6.4–6.5 (wide) × 6.8–7.4 (thick) mm, minutely apiculate for 0.2–0.4 mm; testa ca. 0.2 mm thick, dry, smooth, obscurely brown-marbled; ecarunculate, raphe ventral; hilum near top, triangular, ca. 1.5–2 × 1.5–2 mm; embryo axile spathulate, straight, stalk 1.2 × 0.6 mm, cotyledons ovate, 4.5 (long) × 4 (wide) × 0.1 (thick) mm, with midrib and higher order veins evident, nearly filling seed profile; endosperm firm, oily; central cavity absent.

Etymology. The specific epithet *occidentalis* refers to western, and indicates the distribution of the new species in western South America, in contrast to *B. pyriformis*, which grows on the eastern side of the continent.

Distribution and ecology. The populations of *Bahiana occidentalis* in Tumbes and San Martín are separated by more than 520 km and represent two (equatorial and eastern, respectively) of the three SDTF subunits defined for Peru (Linares-Palomino

Figure 4. Distribution of *Bahiana* in northern South America (triangle, *B. occidentalis*; circle, *B. pyriformis*). Each marker represents multiple collections. Southern limit of the Amotape–Huancabamba zone is beyond the boundary of lower map.

2006). The new species is expected also to occur in adjacent Ecuador, which contains extensions of the Tumbesian SDTF, and perhaps also in the Marañón inter-Andean STDF that is in between the two populations, although it is isolated from them and mostly at a higher elevation. It occurs in lowland SDTF (500–720 m in Tumbes, 350 m in San Martín). Seasonal rains typically fall (Dec-) Jan to Apr (85% of annual precipitation; Cueva-Ortiz et al. 2020), after critically dry Sep to Nov. Flowering appears to coincide with the start of the rainy season (young staminate inflorescences present until mid-Nov) and mature fruit by Feb. The collections, although not diagnostic due to having only very young inflorescences or fruits, appear unisexual, which probably indicates dioecy as has been documented for *B. pyriformis* (Carrión et al. 2022). The Tumbesian SDTF appears to have few other endemic Euphorbiaceae (e.g.,

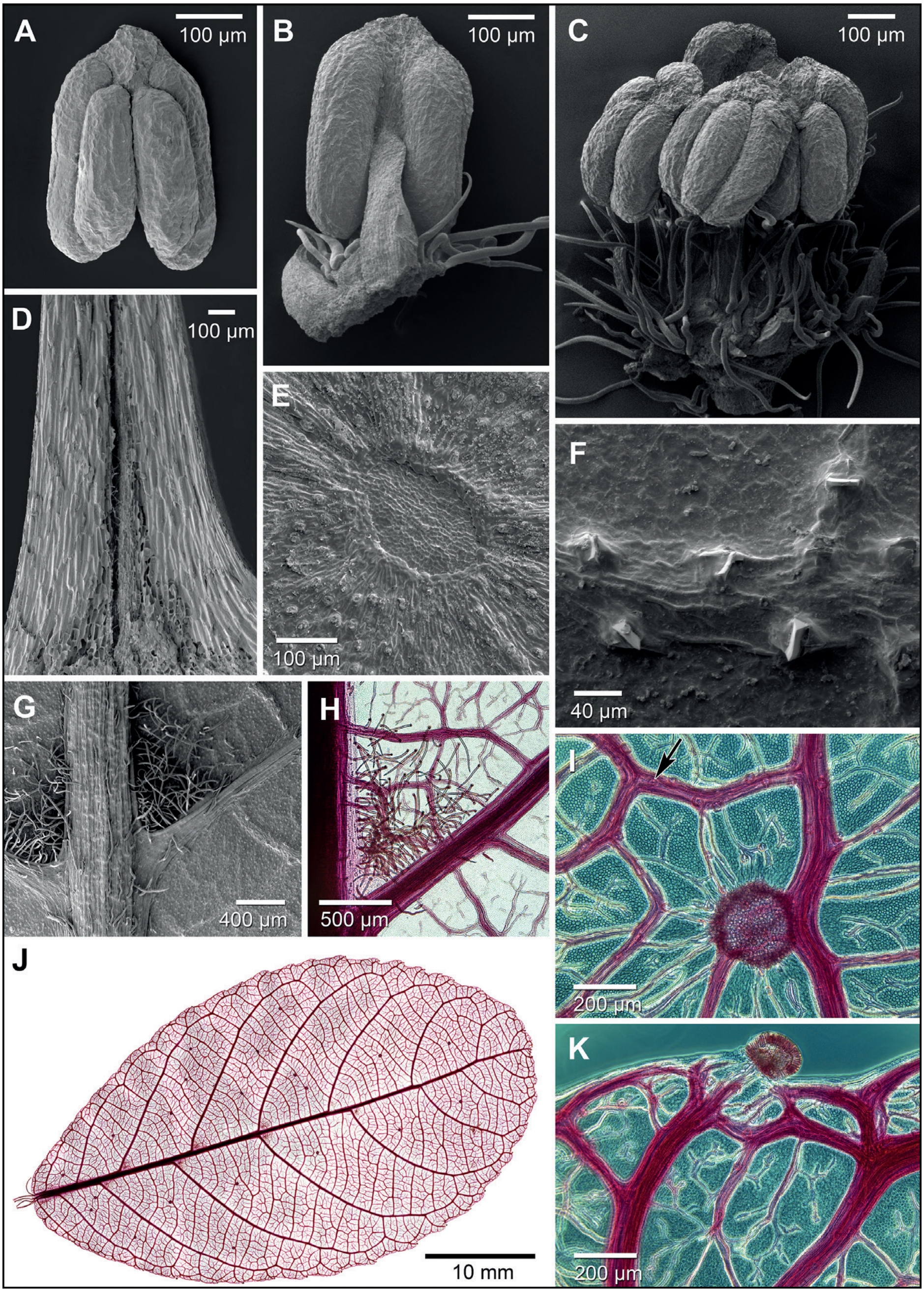

Figure 5. Morphology of *Bahiana occidentalis* **A** anther ventral **B** stamen dorsal **C** androecium with outer stamens removed to show hirsute receptacle (young bud) **D** stipule inner structure (split longitudinally) **E** leaf gland (abaxial) **F** leaf surface with prismatic crystals poking through epidermis along veins (adaxial) **G** leaf acarodomatia bounded by primary and secondary veins (abaxial) **H** leaf acarodomatium (clearing) **I** leaf gland with crystal along vein indicated by arrow (clearing) **J** whole leaf (clearing; tiled from 418 images) **K** glandular tooth at leaf margin (clearing) **A–G** SEM **H, J** brightfield LM **I, K** darkfield LM; sources **A–C** *C. Díaz S. et al. 5522*, MO **D** *C. Díaz S. et al. 6148*, MO **E–K** *C. Díaz S. et al. 6288*, US.

Acalypha delicata Cardiel, *Croton tumbesinus* Riina) (Cardiel 2006; Linares-Palomino et al. 2010; Feio et al. 2018).

Conservation status. Following the criteria and categories of IUCN (2012), *B. occidentalis* is given a preliminary status of Vulnerable (VU) under geographic range criteria B2 area of occupancy < 2000 km^2 (B2a, known to exist at no more than 10 locations; B2b, continuing decline projected). The Tumbes population is within the Reserva Nacional de Tumbes, a protected area of relatively pristine forest and will ensure long term conservation of the taxon. However, the eastern SDTFs in San Martín are fragmented due to farming, including in the area around the Gentry collection locality (fide Google Earth imagery). *Bahiana pyriformis* is presently known from a single, small population in a mostly deforested region that is not protected and still at risk.

Additional specimens examined. Peru. San Martín: 31 km S of Tarapoto, dry forested slopes overlooking Río Huallaga, Transect 1, 06°35'S, 076°25'W (-6.5833333, -76.4166667), 350 m, 18 Jul 1982, *A.H. Gentry et al. 37732* (MO sheet 3029763); *ibid. loc.*, Transect 3, 20 Jul 1982 (stam infl), *A.H. Gentry et al. 37824* (MO sheet 3211186). **Tumbes:** Zarumilla, Matapalo. Entre P.C. "El caucho" y P.C. "Campoverde", Bosque Nacional de Tumbes, Reserva de Biósfera del Noroeste, Arbol #326, 03°50'29"S, 080°15'33"W (-3.8413889, -80.2591667), 720 m, 21 Jul 1992, *C. Díaz S. et al. 5009* (MO sheet 5564626); *ibid. loc.*, Arbol #359, 22 Jul 1992, *C. Díaz S. et al. 5072* (MO sheet 6060058). Parcela "V" de evaluación permanente, No. 393, 03°50'29"S, 080°15'33"W (-3.8413800, -80.2591600), 720 m, 27 Oct 1992, *C. Díaz S. et al. 5176* (MO sheet 6060054); *ibid. loc.*, No. 427, 27 Oct 1992, *C. Díaz S. et al. 5201* (MO sheet 6060056); *ibid. loc.*, No. 641, 27 Oct 1992 (stam infl), *C. Díaz S. et al. 5390* (MO sheet 5707417); *ibid. loc.*, No. 658, 31 Oct 1992 (stam infl), *C. Díaz S. et al. 5432* (MO sheet 5707423); *ibid. loc.*, No. 666, 31 Oct 1992 (stam infl), *C. Díaz S. et al. 5438* (MO sheet 5707422); *ibid. loc.*, No. 679, 31 Oct 1992 (stam infl), *C. Díaz S. et al. 5472* (MO sheet 5707421); *ibid. loc.*, No. 719, 2 Nov 1992 (stam infl), *C. Díaz S. et al. 5486* (MO sheet 5707420); *ibid. loc.*, No. 720, 2 Nov 1992, *C. Díaz S. et al. 5487* (MO sheet 5707415); *ibid. loc.*, No. 732, 2 Nov 1992, *C. Díaz S. et al. 5489* (MO sheet 5707416); *ibid. loc.*, No. 735, 2 Nov 1992, *C. Díaz S. et al. 5491* (MO sheet 5707419); *ibid. loc.*, No. 721, 2 Nov 1992, *C. Díaz S. et al. 5520* (MO sheet 5707428); *ibid. loc.*, No. 725, 2 Nov 1992, *C. Díaz S. et al. 5521* (MO sheet 6060063); *ibid. loc.*, No. 729, 2 Nov 1992 (stam infl), *C. Díaz S. et al. 5522* (MO sheet 6060062); *ibid. loc.*, No. 743, 2 Nov 1992, *C. Díaz S. et al. 5537* (MO sheet 5707424); *ibid. loc.*, No. 326, 10 Nov 1992, *C. Díaz S. et al. 5957* (MO sheet 6060061); *ibid. loc.*, No. 359, 10 Nov 1992, *C. Díaz S. et al. 5979* (MO sheet 6060060). Parcela de evaluación florística (2 mt. × 500 m) paralela a la parcela "V", orientación Este-Oeste, 03°50'29"S, 080°15'33"W (-3.8413800, -80.2591600), 500 m, 12 Nov 1992, *C. Díaz S. et al. 6007* (MO sheet 6060059); *ibid. loc.*, 12 Nov 1992, *C. Díaz S. et al. 6127* (MO sheet 6060052); *ibid. loc.*, 12 Nov 1992 (stam infl), *C. Díaz S. et al. 6148* (MO sheet 5707407); *ibid. loc.*, 12 Nov 1992, (stam infl), *C. Díaz S. et al. 6149* (MO sheet 6060065); *ibid. loc.*, 12 Nov 1992, *C. Díaz S. et al. 6151* (MO sheet 6060064). Entre P.C. "El caucho" y P.C. "Campoverde," Bosque Nacional de Tumbes, Reserva de Biósfera del Noroeste, Arbol 326, 03°50'29"S, 080°15'33"W

(–3.8413800, –80.2591600), 720 m, 21 Jul 1992, *C. Díaz S. et al. 5009* (MO sheet 5564626); Arbol #359, 22 Jul 1992, *C. Díaz S. et al. 5072* (MO sheet 6060058). Zona “El Caucho-Campo Verde”. Parcela 2 × 500 m (evaluación florística) paralela a parcela “V” de evaluación forestal permanente, 03°50'29"S, 080°15'30"W (–3.8413800, –80.2583300), 500 m, 11 Feb 1993, *C. Díaz S. et al. 6272* (MO sheet 6060051); *ibid. loc.*, 11 Feb 1993, *C. Díaz S. et al. 6277* (MO sheet 6060053); *ibid. loc.*, 11 Feb 1993, *C. Díaz S. et al. 6282* (MO sheet 6060057). Zona “El Caucho-Campo Verde”, Parcela “E” evaluación permanente, No. 326, 03°50'29"S, 080°15'30"W (–3.8413800, –80.2583300), 500 m, 16 Feb 1993 (fr), *C. Díaz S. et al. 6545* (MO, US); *ibid. loc.*, 17 Feb 1993, *C. Díaz S. et al. 6575* (MO sheet 6060055); *ibid. loc.*, No. 359, 17 Feb 1993, *C. Díaz S. et al. 6605* (MO sheet 6060066); *ibid. loc.*, 17 Jan Feb 1995 (fr), *C. Díaz S. et al. 7430* (MO sheet 5707408).

Discussion

Despite being relatively well-collected, *Bahiana occidentalis* remains imperfectly known due to the lack of flowering specimens and limitations with inferring floral details from buds and fruits. Pistillate flowers are unknown, and the anthers are too underdeveloped for pollen comparisons. Characteristics shared by both *Bahiana* spp., which in combination are not in any other genus of Euphorbiaceae, include persistent spinose stipules, staminate bracts of two orders, 12–15 free stamens with dorsifixed apiculate anthers, and slender undivided styles (see generic comparisons in Carrión et al. 2022: table 2). Especially distinctive are the spinose stipules, a feature present in only five genera of Euphorbiaceae, of which only *Bahiana* and unrelated *Acidocroton* (Crotonoideae) have spiny species in the Neotropics (see below). Other *Bernardia* clade genera have stipules that are sheathing and caducous (*Caryodendron*); or mostly small, triangular, sometimes thickened, and persistent or tardily deciduous (*Adenophaedra*, *Bernardia*).

Beyond biogeography there are clear morphological differences in staminate cymules, fruits, and leaves that serve to distinguish the two species of *Bahiana*, and additional differences may be discovered when flowering collections become available. Dissection of young staminate inflorescences found each cymule of *B. occidentalis* contained a single bud, while *B. pyriformis* is described as “cymules usually 3-flowered” with an early-developing central flower (Carrión et al. 2022). Within the *Bernardia* clade, the fruits (and seeds) of *B. occidentalis* are closer in size to small-fruited *Adenophaedra* and most *Bernardia* (*B. macrocarpa* A.Cerv. & Flores Olv. is also large-fruited), rather than large-fruited *Bahiana pyriformis* and *Caryodendron* spp. The leaves of both species of *Bahiana* are similar in details of simple indument type, abaxial leaf glands, gland-tipped teeth, and paracytic stomata (Fig. 5E–K; Carrión et al. 2022: Fig. 3). They notably differ in leaf size and some anatomical characters, with *B. pyriformis* possessing numerous relatively large crystalline druses that do not trace the vein fabric, whereas *B. occidentalis* has small epidermal prismatic crystals that follow the venation (Fig. 5I). The crystals in *B. occidentalis* often pierce the surface of the dried leaves (Fig. 5F) and cause rough, finely pustulate adaxial surfaces; similar crystals occur in *Acalypha* L.

(Cardiel et al. 2020). Each tooth is capped by a sub-globose marginal gland with a palisade epidermis that resembles a colleter of the standard (S) type, but is not elongate or stalked (Fig. 5K) as seen in other Euphorbiaceae (Thomas 1991; Vitarelli et al. 2015). There is little morphological distinction between the Tumbes and San Martín collections of *B. occidentalis*, except for more pronounced brachyblasts in the latter. While one San Martín collection (*A. Gentry 37824*) is noteworthy in abaxially uniformly pubescent leaves, a second collection (*A. Gentry 37732*) from the same locality is typical of the species with sparse pubescence (except the defined hirsute acarodomatia). Associated with the acarodomatia along the primary vein are hairs, but almost no pocket (merely a narrow flange from the bounding veins), and no pits or glands (Fig. 5G, H).

The biogeography of *Bahiana* is notable due to its substantial disjunction (Fig. 4). The two species are nearly 4000 km apart at their closest locations in Peru and Brazil, and the populations of *B. occidentalis* in Tumbes and San Martín are separated by more than 520 km. The known distribution of *B. occidentalis* is within the floristically unusual Amotape–Huancabamba zone (see Weigend 2002), and the two populations are on opposite sides of the Andes across the Huancabamba Depression which is in the center of the zone. The Huancabamba Depression, the lowest point in the Andean chain (2145 m at Abra de Porculla), is a dispersal impediment to montane species but has been considered an opportunity for lowland SDTF taxa (e.g., *Bahiana*) to cross the Andes (Linares-Palomino et al. 2003; Quintana et al. 2017). Estimates of diversification histories for taxa in this region have been varied. Pennington et al. (2010) found the SDTF endemic *Cyathostegia matthewsii* (Benth.) Schery (Fabaceae) had relatively high sequence divergences among inter-Andean populations, which indicated an older diversification history and in particular, populations (Loja and Marañón) spanning the Huancabamba Depression were isolated 2.8 (+/- 0.6) million years. In *B. occidentalis*, the low genetic divergences (0–1% across three fast-evolving loci) between the two populations suggest recent dispersal; however, broader genomic comparisons are needed. While undercollecting in the region limits our full understanding of the distribution of *B. occidentalis*, it is likely discontinuous due to altitude barriers and the patchy nature of SDTF. Its dispersal ability via ballistochory is limited, and its seeds even lack caruncles which are often implicated in Euphorbiaceae secondary seed dispersal by ants. Disjunctions across South America are known within and among closely related SDTF taxa, and in particular the legume species pair *Pithecellobium diversifolium* Benth. and *P. excelsum* (Kunth) Benth. resembles the transcontinental distribution of *Bahiana* (Lewis et al. 2006; Colli-Silva et al. 2021). Other legumes display stepping stone patterns either through southern SDTFs or northern connections. Patterns of Euphorbiaceae distribution and diversification across the SDTFs are largely unstudied beyond *Euphorbia*. A disjunct *Euphorbia* species pair – *E. heterodoxa* Müll.Arg. of eastern Brasil SDTF and *E. lagunillarum* Croizat of the dry Venezuelan Andes – with a distribution pattern approaching that of *Bahiana* suggests northern connections (Hurbath et al. 2021). *Gymnanthes boticario* and *Croton laceratoglandulosus* Caruzo & Cordeiro have disjunct distributions that follow the southern SDTF ecosystems from eastern Brazil to Bolivia (de Oliveira et al. 2013).

Spinescence in Euphorbiaceae

Many Euphorbiaceae have well-developed intrinsic physical and/or chemical anti-herbivory defenses that include latex, toxic secondary chemistry, stinging trichomes, and spinescence. Escalation of plant defenses through multiple defense types rather than just refinements of a single type may be a recurring pattern in Euphorbiaceae (e.g., *Dalechampia*, Armbruster et al. 2009). Spinescence is generally associated with drier and more open habitats that can have abundant mammal herbivores (Charles-Dominique et al. 2016). Here, spinescence is considered broadly to include all sharp, hardened structures, thereby avoiding the inconsistent usage and not always clear distinctions among traditional definitions of spines (modified leaves or stipules), thorns (reduced branches), and prickles (emergences with epidermal-subepidermal origin and usually detachable) (see Bell 2008). My survey found vegetative spines in 25 genera of Euphorbiaceae scattered in subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae (Table 1). Their distribution is phylogenetically dispersed (relative to trees in Wurdack et al. [2005] and not explicitly mapped here) such that each genus has evidently evolved spines one or more times. Of the ca. 590 spiny species, 500+ are in *Euphorbia* L., the largest genus in the family, and the remaining genera mostly have a few spiny taxa each. The other two large genera of Euphorbiaceae, *Croton* and *Acalypha*, are notable for their paucity of spines despite considerable diversification in arid and open environments.

The spines in Euphorbiaceae have diverse origins (homologies) and positions on the plant, including modified branch tips (stem spines), stipules, peduncles, leaf margins, and stem emergences (Fig. 6). Leaf spines (i.e., an entire leaf taking the form of a spine) appear to be absent. The short leafless axillary spines in *Croton* L. (and *Doryxylon* Zoll.) could represent modified prophylls of axillary buds, but the replacement of spines with inflorescences on *Croton bispinosus* C.Wright specimens (e.g., *C. Morton & J. Acuña 2964*, US) suggests they are fundamentally shoot axes. Most spiny taxa occur in dry and/or open environments (i.e., SDTF, scrub, and deserts), with the exceptions of *Hura* L. and *Macaranga* Thouars which are primarily in wet forests and *Caperonia* A.St.-Hil. in wetlands. When considering habit, nearly all spiny genera are woody shrubs or trees, with the exceptions being many *Euphorbia* spp. that are succulent (sometimes also woody), and *Caperonia* that are herbaceous. Stem spines, widely distributed across 12 genera, can be very plastic in their occurrence on individual plants, from terminating all lateral short shoots to an erratic distribution (sparse or sometimes with varying degrees of sharpness). The spines along the trunk and/or branches of *Hura* (Fig. 6G; Lefebvre et al. 2022) and *Macaranga* spp. (Jeník and Harris 1969; Whitmore 2008) need further study on their development; in the former they are considered cork-spines derived from suber and the latter derived from roots. Emergences, as sharp structures with epidermal-subepidermal origin (Bell 2008) on stems or leaves, are prominent in species of at least three genera. While toothed leaf margins occur widely across the family, strongly spinose teeth appear rare, although subspinose or mucronate intermediates exist (e.g., the teeth

Table 1. Taxa of spinescent Euphorbiaceae. Taxonomy follows World Checklist of Selected Plant Families (WCSP 2018), except as noted, and the species of *Sebastiania* and *Gymnanthes* listed here are known to need generic adjustments.

Genus	# spinescent species/ total species	Spinescent species	Distribution of spinescent species	Spine location or origins	Additional references
Subfamily Acalyphoideae					
Acalypha	3/ca. 500	*baretiae* I.Montero & Cardiel, *echinus* Pax & K.Hoffm., *sonderiana* Müll.Arg.	Madagascar, tropical East Africa	Leafy branch tips; possibly result of weathering	Muñoz et al. 2018
Acidoton	2/5	*microphyllus* Urb., *variifolius* Urb. & Ekman	Hispaniola	Lateral leafy branch tips	
Adelia	6/10	*barbinervis* Schltdl. & Cham., *brandegeei* V.W.Steinm., *membranifolia* (Müll.Arg.) Chodat & Hassl., *ricinella* L., *triloba* (Müll.Arg.) Hemsl., *vaseyi* (J.M.Coult.) Pax & K.Hoffm.	USA (Texas), Caribbean, Mexico, Central & South America	Branch tips	
Alchornea	1/51	*ilicifolia* (Js.Sm.) Müll.Arg.	Australia	Leaf margins	
Bahiana	2/2	*occidentalis* K.Wurdack, *pyriformis* J.F.Carrión	Brazil, Peru	Stipules	Carrión et al. 2022
Bernardia	1/80	*hamadryadica* J.F.Carrión & Cordeiro	Brazil	Lateral leafy branch tips	Carrión et al. 2017
Caperonia	3/34	*aculeolata* Müll.Arg., *buettneriacea* Müll.Arg., *heteropetala* Didr.	Brazil	Emergences as prickles along stems and abaxial midveins; well-developed in listed species but as small prickles or glandular trichomes in others	
Doryxylon	1/1	*spinosum* Zoll.	Malesia (Philippines, Lesser Sunda Islands)	Leafless axillary shoots	Welzen 1999
Enriquebeltrania	2/2	*crenatifolia* (Miranda) Rzed., *disjuncta* De-Nova & Sosa	Mexico	Lateral leafy branch tips; stipules are indurated, persistent but sub-spinose	
Erythrococca	ca. 10/41	Most members of sects. *Deflersia*, *Tristis*, *Lasiococcae* including: *E. anomala* (Juss. ex Poir.) Prain, *berberidea* Prain, *bongensis* Pax, *fischeri* Pax, *laurentii* Prain, *natalensis* Prain, *poggeophyton* Prain, *pubescens* Radcl.Sm., *subspicata* Prain, *zambesiaca* Prain	Africa	Stipules	Prain 1911; Uhlarz 1978
Lasiocroton	1/26	*microphyllus* (A.Rich.) Jestrow	Cuba	Lateral leafy branch tips	
Macaranga	18/ca. 260	*angolensis* (Müll.Arg.) Müll.Arg., *assas* Amougou, *barteri* Müll.Arg., *beillei* Prain, *capensis* (Baill.Sim, *heterophylla* (Müll.Arg.) Müll.Arg., *heudelotii* Baill., *klaineana* Pierre ex Prain, *longipetiolata* De Wild., *monandra* Müll.Arg., *occidentalis* (Müll.Arg.) Müll.Arg., *paxii* Prain, *pierreana* Prain, *poggei* Pax, *saccifera* Pax, *schweinfurthii* Pax, *spinosa* Müll.Arg., *staudtii* Pax	Africa (especially tropical west Africa)	Along trunk and branches as simple or divided structures	Whitmore 2008
Philyra	1/1	*brasiliensis* Klotzsch	Argentina, Brazil, Paraguay	Intrastipular structures; stipules are not spinose	

Genus	# spinescent species/ total species	Spinescent species	Distribution of spinescent species	Spine location or origins	Additional references
Subfamily Crotonoideae					
Acidocroton (including *Ophellantha*)	12/14	*acunae* Borhidi & O.Muñiz, *adelioides* Griseb., *ekmanii* Urb., *gentryi* Fern.Alonso & R.Jaram., *horridus* Urb. & Ekman, *litoralis* Urb. & Ekman, *lobulatus* Urb., *montanus* Urb. & Ekman, *oligostemon* Urb., *spinosus* (Standl.) G.L.Webster, *trichophyllus* Urb., *verrucosus* Urb.	Caribbean (especially Hispaniola), Central America	Stipules	Uhlarz 1978
Croton	2/1200+	*bispinosus* C.Wright, *brittonianus* Carabia	Cuba	Axillary leafless shoots. Spines on *C. bispinosus* can be 0–2 per axil	
Jatropha	ca. 10/174	Sects. Collenucia and Spinosa, including: *collina* Thulin, *dichtar* J.F.Macbr, *ellenbeckii* Pax, *glauca* Vahl, *humifusa* Thulin, *inaequispina* Thulin, *marginata* Chiov., *nogalensis* Chiov., *paradoxa* (Choiv.) Chiov., *rivae* Pax, *rosea* Radcl.-Sm., *tetracantha* Chiov.	East Africa (especially Somalia)	Stipules as simple or branched structures	Hemming and Radcliffe-Smith 1987; Thulin 1993
Subfamily Euphorbioideae					
Bonania	2/7	*domingensis* (Urb.) Urb., *elliptica* var. *spinosa* (Urb.) Borhidi	Cuba, Hispaniola	Lateral leafy branch tips	
Euphorbia	ca. 500+/2200	Parts of sects. *Goniostema*, *Monadenium*, *Euphorbia*, *Tirucalli* (*E. stenoclada* Baill.), *Espinosae* (*E. espinosa* Pax), *Articulofruticosae*	Old World xerophytes (especially Africa)	Stipules, leafy branch tips, tubercules (spine shields), and/or persistent peduncles	White et al. 1941; Uhlarz 1974; Yang et al. 2012; Dorsey et al. 2013; Peirson et al. 2013
Gymnanthes	3/25	*guyanensis* Müll.Arg., *hirsuta* Esser, *microphylla* Esser	Bolivia, Columbia, Guyana	Lateral leafy branch tips	
Hippomane	2/3	*horrida* Urb. & Ekman, *spinosa* L.	Hispaniola	Leaf margins	
Hura	2/2	*crepitans* L., *polyandra* Baill.	Mexico, Caribbean, Central & South America	Along trunk and branches, where they begin developing in young saplings and emerge by piercing the bark from subsurface (endogenous) origins	Lefebvre et al. 2022
Pachystroma	1/1	*longifolium* (Nees) I.M.Johnst.	Bolivia, Brazil, Peru, Paraguay	Leaf margins, variable 0–15 spines per side	
Sebastiania	8/56	*chaetodonta* Müll.Arg., *klotzschiana* (Müll.Arg.) Müll.Arg., *mosenii* Pax & K.Hoffm., *obtusifolia* Pax & K.Hoffm., *picardae* Urb., *schottiana* (Müll.Arg.) Müll.Arg., *serrata* (Baill. ex Müll.Arg.) Müll. Arg., *vestita* Müll.Arg.	South America, Caribbean (Hispaniola)	Branch tips. Spines well-developed in *S. picardae* and erratic in other species on leafy lateral branches	
Spegazziniophytum	1/1	*patagonicum* (Speg.) Esser	Argentina (Patagonia)	Branch tips (stems photosynthetic and leaves ephemeral)	
Tetraplandra (united with *Algernonia*, but the species here has yet to be transferred)	1/13	*anomala* Pax & K.Hoffm. (poorly known and possibly extinct species)	Brazil	Rarely present as leafless lateral branch tips (*Glaziou 8323*, K)	

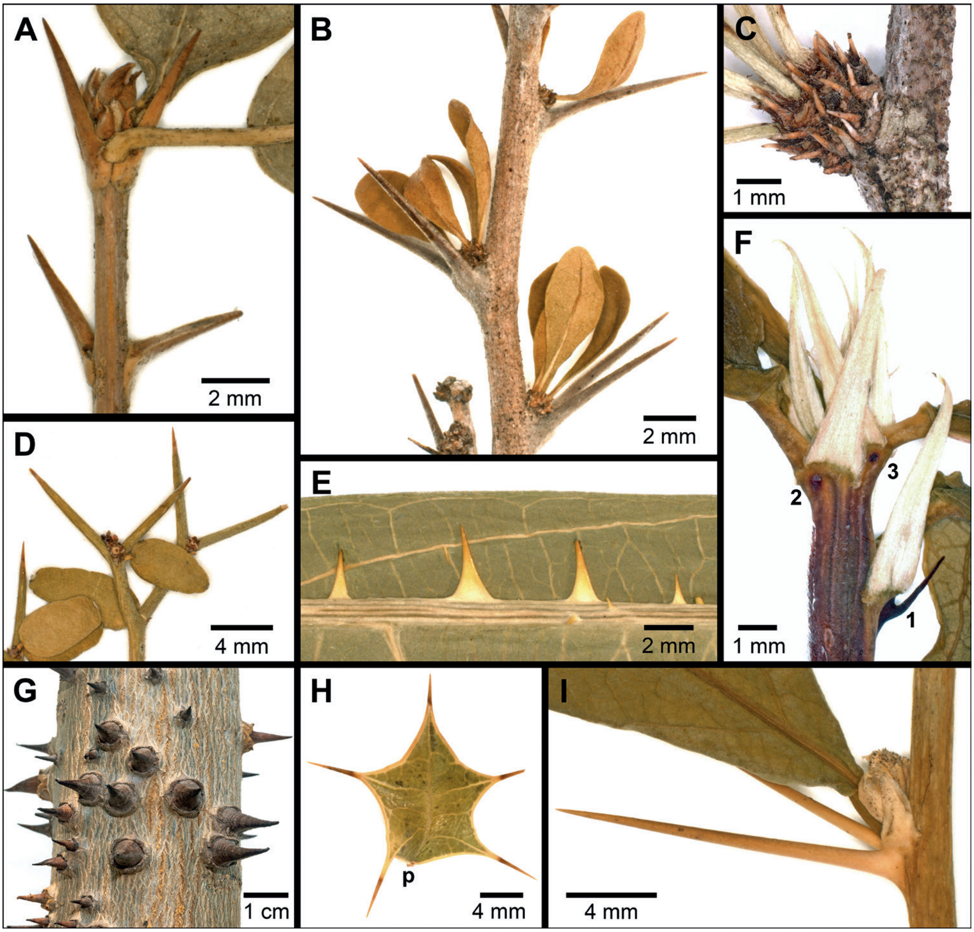

Figure 6. Diversity of spiny structures on Euphorbiaceae **A** spinose stipules and protected terminal resting bud (*Bahiana occidentalis*, *C. Díaz S. et al. 5072*, MO) **B** spinose stipules subtending leafy fascicles (*Acidocroton litoralis*, *G. Proctor 10991*, US) **C** spinose stipules as clear pairs associated with each fascicle leaf (*Acidocroton verrucosus*, *G. Webster et al. 8463*, US) **D** spinose branch tips (*Sebastiania picardae*, *E. Ekman 2229*, US) **E** spiny emergences along primary vein (abaxial, *Caperonia buettneriacea*, *G. Hatschbach 6394*, US) **F** intrastipular spine development (sequentially 1–3) in *Philyra* below stipule pairs at shoot tip (*P. brasiliensis*, *A. Gentry et al. 51884*, MO) **G** spiny emergences on trunk (*Hura crepitans*) **H** spiny leaf margins, p = site of petiole attachment below gland (*Hippomane horrida*, *A. Liogier 14212*, US) **I** intrastipular spines mature and lignified in *Philyra* (same branch as **F**).

of *Alchornea castaneifolia* [Humb. & Bonpl. ex Willd.] A.Juss. sometimes resemble less spinose margins of *A. ilicifolia* [J.Sm.] Müll.Arg.). Trichomes are not treated here; however, I note that they can be substantial and spinose in *Cnidoscolus* (e.g., *C. quercifolius* Pohl) (see Maya-Lastra and Steinmann 2019). In some South American *Cnidoscolus* (e.g., *C. bahianus* [Ule] Pax & K.Hoffm., *C. pavonianus* [Müll.Arg.]

Fern.Casas, *C. ulei* [Pax] Pax) bark forms around the trichome base as a turbinate collar and permanently anchors the usually detachable stinging arm. Spines of stipular origin, of special focus here and further detailed below, occur in five genera (*Acidocroton* Griseb., *Bahiana*, *Erythrococca* Benth., *Euphorbia*, *Jatropha* L.). *Acidocroton* and *Bahiana* are restricted to the New World, while the other three genera either are restricted to the Old World (*Erythrococca*) or have spiny species only there (*Euphorbia*, *Jatropha*).

Acidocroton (including *Ophellantha*) has paired spines of stipular origin that are usually 1–2× the length of the leaves (to 15 mm) in the microphyllous Caribbean species and much shorter (to 5 mm) in the large leaved taxa referred to sect. *Ophellantha*. A node subtended by a pair of long, strongly attached primary spines (i.e., those subtending the fascicle and that are usually larger) typically contains a cluster of fascicled leaves (up to 11 leaves per fascicle in *A. oligostemon* Urb.), long trichomes, and tiny spines which represent stipules for the other leaves (Fig. 6B). The spines precociously develop and well arm the branch tips (sometimes before the leaves expand) and then continue to enlarge and lignify. The spines in Jamaican *A. verrucosus* Urb. often show less dimorphism where the primary spines are often of similar short length (<1.5 mm) to those in the fascicle; they also show spine pairings with fascicle leaves that clearly indicate stipular origins (Fig. 6C).

Bahiana has paired spines of stipular origin that elongate, lignify, and often spread with age (Fig. 6A). Their prominence varies across collections in length and degree of spreading. Resting buds usually have nested sets of scales with spinose tips and overlapping papery basal margins. In *B. occidentalis* the spine core contains thin walled-cells and can be hollow towards the base (Fig. 5D).

The paired stipules of *Erythrococca* can be spinose and 1–5 mm long, but there is much variation among species as well-summarized by Prain (1911: 848) as "stipules cartilaginous, glabrous, often accrescent and modified into umbonate mammillae or weakly conical thorns, rarely into wide-based pungent spines, sometimes minute, subulate and unaltered". In spinose *E. anomala* (Juss. ex Poir) Prain, they are asymmetric horns resembling rose thorns to 3 mm long, and they easily detach due to their basally hollow structure (see Uhlarz 1978).

Euphorbia spp. with their remarkable variation in xerophytic growth forms have equally diverse and complex spines, including stipules, modified branch tips, persistent peduncles, and tubercules (spine shields) bearing single, paired, or clustered spines of sometimes unclear origins (White et al. 1941; Uhlarz 1974). The spines can reach 7.5 cm long and be simple or elaborated with short branches. Uhlarz (1974) studied *Euphorbia* spine structure and ontogeny, and noted that "dorsal spines" (on the dorsal side of the leaf base) develop after the stipules and their formation is influenced by environmental factors such as light. There are an estimated 500+ spiny species, especially in subgen. *Euphorbia* sect. *Euphorbia* with more than 340 species, mostly with spine shields and spinose stipules. Spines (non-stipular) have evolved in subgen. *Athymalus* (sects. *Lyciopsis*, *Anthacanthae*) and subgen. *Chamaesyce* (sects. *Espinosae*, *Articulofruticosae*), but they are apparently absent in subgen. *Esula* (Yang et al. 2012; Dorsey et al. 2013; Peirson et al. 2013).

The stipules of *Jatropha* spp. are typically glandular (or reduced) but can be variously elaborated as spines in the northeast African species; they are not spinose in South African, Malagasy, or New World taxa. These stipular spines are stout and simple, up to 5 cm long (e.g., *J. dichtar* J.F.Macbr.), or thin and branched so as to cover the stems in spiny thickets (e.g., *J. marginata* Chiov.). Somalia contains an especially rich diversity of spiny-stipuled *Jatropha*, although some species distributed there are clearly not spinose (Hemming and Radcliffe-Smith 1987; Thulin 1993).

The paired intrastipular spines of *Philyra brasiliensis* Klotz. are outgrowths on each side of the petiole base just below (and distinctly separate when young) the persistent stipules. The spines usually develop (sometimes starting as a pigmented spot) near the shoot tips after the young leaves have begun to expand, and then lignify and elongate up to 3 cm (Fig. 6F, I). There is considerable plasticity in presence and mature spine length across branches and collections, and sometimes the spines are scarcely evident. While not stipular in origin, their homologies are unclear. They appear to be similar to intrastipular spines described in some legumes and suggested to be either modified short shoots (Sharma and Kumar 2012; Juárez et al. 2018) or emergences (Bell 2008).

Conclusions

Bahiana occidentalis is a distinct new species that broadens the character states for the genus, notably in inflorescence structure details and in fruit more typical of Euphorbiaceae in size and shape. The distribution of *Bahiana* is unusual and adds to emerging patterns of SDTF flora disjunctions, although its transcontinental nature is not informative as to whether this arose from northern or southern dispersal routes. While legumes are the most species-rich and investigated component of SDTF floras, Euphorbiaceae deserve further study, and *Bahiana* demonstrates that surprises remain. Spines in Euphorbiaceae are diverse in origin, and with relatively few exceptions occur in woody or succulent taxa from dry or open environments. While the focus here is on spines from a family perspective, their occurrence in the SDTF flora deserves further study and quantification (legumes and cacti are notable spiny components).

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RESEARCH ARTICLE

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A taxonomic revision of *Keraunea*, including three new species and its phylogenetic realignment with Ehretiaceae (Boraginales)

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Abstract

Keraunea is an enigmatic genus of lianescent shrubs endemic to Brazil and found within the Caatinga and Mata Atlântica phytogeographic regions. When first published, *Keraunea* was included in the Convolvulaceae and there has been considerable recent disagreement about its true family placement on the Angiosperm tree of life. Based on further assessment of morphology and a new comprehensively-sampled combined phylogenetic analysis of nuclear and plastid genes from recently published DNA sequence data, we settle the position of the genus within the Ehretiaceae as sister to the Australian genus *Halgania* Gaudich. and provide an expanded family description. We recognize five species within *Keraunea*, three of them newly described here: *K. brasiliensis* Cheek & Simão-Bianchini, *K. bullata* Moonlight & D.B.O.S.Cardoso, **sp. nov.**, *K. capixaba* Lombardi, *K. confusa* Moonlight & D.B.O.S.Cardoso, **sp. nov.** and *K. velutina* Moonlight & D.B.O.S.Cardoso, **sp. nov.** We also provide a full taxonomic revision of the genus, including a key, descriptions, map of geographical distribution and provisional IUCN threat assessments for all species.

Keywords

Boraginales, Brazil, Caatinga, Ehretiaceae, *Keraunea*, Mata Atlantica

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Introduction

In spite of its short taxonomic history, the small Brazilian genus *Keraunea* Cheek & Simão-Bianchini (Cheek and Simão-Bianchini 2013) has caused considerable taxonomic confusion. In 2013, three specimens of lianescent shrubs with a highly unusual inflorescence structure were published as a new genus and species: *Keraunea brasiliensis* Cheek & Simão-Bianchini (Cheek and Simão-Bianchini 2013). The authors "confidently" placed the genus within the Convolvulaceae because its fruits (with the pedicels adnate to a large leaf-like bracteole) resembled the African lianas of the genus *Neuropeltis* Wall. Additional flowering, fruiting and vegetative characters were used to support this family placement (Cheek and Simão-Bianchini 2013). In 2014, a second species of *Keraunea* was described, *K. capixaba* Lombardi (Lombardi 2014). This was based upon four specimens, all collected after 2012 in Jaguaré and Sooretama municipalities, Espírito Santo, Brazil.

The first molecular phylogenetic study that sampled *Keraunea* was published in 2022 by authors working on the Convolvulaceae of the Americas (Muñoz-Rodríguez et al. 2022). The authors produced DNA sequence data for an isotype (*Passos et al. 5263* [K]) and paratype (*Lombardi & Salino 1819* [K]) of *K. brasiliensis* and a paratype of *K. capixaba* (*Siqueira 893* [K]). Rapid phylogenetic inference was carried out with IQ-Tree (Nguyen et al. 2015), which conclusively demonstrated that all samples fell outside of the Convolvulaceae. More surprisingly, the isotype of *K. brasiliensis* was resolved within the Malpighiaceae while the paratype of *K. brasiliensis* and the paratype of *K. capixaba* was resolved within the Ehretiaceae. It is worth noting, however, that the primary motivation for this study was demonstrating that *Keraunea* does not belong within the Convolvulaceae, and the authors suggested further comprehensive studies were required to correctly place *Keraunea* in the right family (Muñoz-Rodríguez et al. 2022). The placements within the Malpighiaceae and Ehretiaceae were well supported but the authors did not formalise the taxonomic changes because of their conflicting results and the sparse phylogenetic sampling within the Ehretiaceae. The placement with *Keraunea* nested in Malpighiaceae has more recently shown to be erroneous, possibly caused by Muñoz-Rodríguez et al. (2022) extracting DNA from an errant Malpighiaceae leaf, likely *Masgania cordifolia* (A.Juss.) Griseb., found within the capsule of the Kew specimen of *Passos et al. 5236* (de Almeida et al. 2023). While we note that Muñoz-Rodríguez et al. (2022) did re-extract and re-sequence the specimen *Passos et al. 5236* (K), it is unclear whether this was from the same leaf sample.

During general collecting in the Caatinga of southwestern Bahia and northern Minas Gerais, the second author of this paper collected several specimens of two closely related species but was unable to determine them to family with confidence. These were identified subsequently as *Keraunea* with reference to the specimens in HUEFS but, like the authors of Muñoz-Rodríguez et al. (2022), we were unconvinced by placement in the Convolvulaceae. Furthermore, one of our yet undescribed species was a close match for the type of *K. brasiliensis* (*Passos et al. 5263*) but the second was a close match for a paratype of that species (*Lombardi & Salino 1819*). This led us to conclude that the original generic description and illustration of *K. brasiliensis* (Cheek and Simão-Bianchini 2013) were based upon two separate species, both of which were distinct from *K. capixaba*. We then conducted a thorough survey and revision of the material held in several Brazilian herbaria (ALCB, HUEFS, RB) and online during which we were able to recognise five species of *Keraunea*.

It came to our attention after the submission of our article that a preprint had been filed with bioRxiv, also placing *Keraunea* within the Ehretiaceae and providing a taxonomic revision of the group (Cheek et al. 2023). While not effectively published, this article includes the description of "*K. lombardiana* Cheek", whose type specimen falls within our concept of *K. confusa* Moonlight & D.B.O.S.Cardoso but also includes material from our concept of *K. bullata* Moonlight & D.B.O.S.Cardoso (*Rose & Russell 19979*, *Mori et al. 11534*). The article also included "*Keraunea* sp. A" whose concept matches our *K. velutina* Moonlight & D.B.O.S.Cardoso, and "*Keraunea* sp. B" whose concept falls clearly within our concept of *K. capixaba*.

In this article we assemble a more comprehensive and taxonomically vetted molecular dataset based on four genes to settle the family-level placement and generic relationships of *Keraunea*. We also provide an expanded description of the Ehretiaceae and the genus *Keraunea*. We further provide a full taxonomic revision of the genus, including a key to all five species, and the publication of three undescribed species. For each species, we include a description, provisional IUCN Red List assessment, and identification notes.

Methods

Taxonomic treatment

We performed a thorough search of specimens available in several Brazilian herbaria (all herbarium acronyms follow *Index herbariorum*, Thiers 2016) supplemented with searches of the online databases CRIA Species Link (http://splink.cria.org.br/, February 2023) and Flora do Brasil (http://floradobrasil.jbrj.gov.br/reflora/herbarioVirtual/, February 2023). We searched for all Brazilian data of *Keraunea* and Ehretiaceae as well as undetermined material in the families Boraginaceae, Dichapetalaceae, and Nyctaginaceae (all families into which *Keraunea* specimens had previously been thought to belong). All descriptions are based upon direct measurements of herbarium specimens and our own field collections, with some macro-morphological characters measured from images of herbarium specimens using the ruler tool in Adobe Photoshop CS5 v.12.0 ×64.

Phylogenetic analyses

Previously published molecular phylogenetic analyses have suggested that the genus *Keraunea* is a member of the Boraginales and more closely related to the Ehretiaceae than to Malpighiacae (Muñoz-Rodríguez et al. 2022; de Almeida et al. 2023). As such, we assembled a new, more comprehensively-sampled combined molecular dataset of the plastid regions *matK*, *rbcL* and *trnL-F* and the nuclear ribosomal internal transcribed spacer (*ITS*), with focus on members of the Ehretiaceae. The molecular data were downloaded from the GenBank sequence repository (http://www.ncbi.nlm.nih.gov/Genbank), including one published *Keraunea* sample (Muñoz-Rodríguez et al.

2022). We supplemented these data with eight samples representing families in the Boraginales *sensu* Luebert et al. (2016). All sequences were retrieved with a custom R script using functions from ape package (Paradis and Schliep 2019). Details of all sequenced samples and their GenBank accession numbers are available in Table 1.

The individual DNA matrices were subjected to automatic multiple alignments in AliView v.1.26 (Larsson 2014), using the Muscle algorithm, but with subsequent manual editing to improve homology in more variable sites. Individual DNA alignments were combined into a concatenated dataset using the R package catGenes (https://github.com/DBOSlab/catGenes; Cardoso et al. 2020). The custom R script uses catGenes functions to automatically build the concatenated dataset by maximising the inclusion of taxa that are incomplete or with missing data (Wiens 2003, 2006).

A maximum likelihood (ML) phylogeny was inferred using RAxML (Stamatakis 2006) using the graphical user interface raxmlGUI v.2.0 (Edler et al. 2020), with the following settings: best-scoring ML tree starting with a random seed and utilizing the GTR + GAMMA nucleotide substitution model, with the gamma distribution and invariants sites estimated during the run; and 500 rapid bootstrap (BS) replicates to determine branch support. The phylogeny was rooted based on a clade including the Wellstediaceae, Boraginaceae *s.str.* and Codonaceae following Luebert et al. (2017).

Results

Phylogenetic analyses

Our four-gene ML phylogenetic analysis resolve the genus *Keraunea* as nested within the Ehretiaceae sister to the Australian endemic genus *Halgania* Gaudich. (Fig. 1). This placement is well supported (BS: 94) and consistent with previous analyses placing samples of the genus as nested within the Ehretiaceae (Muñoz-Rodríguez et al. 2022; Cheek et al. 2023). The topology within the Ehretiaceae is largely congruent with that found in previous analyses (e.g. Luebert et al. 2017) and the monophyly of the Ehretiaceae, including *Keraunea*, is well supported (BS: 97). The Ehretiaceae is resolved as sister to the Lennoaceae (BS: 96).

Discussion

The phylogenetic realignment of the genus *Keraunea* as nested within the Ehretiaceae requires a slightly emended description of the family. *Keraunea* represents the first lianescent member of a family that otherwise includes trees, shrubs and perennial herbs (Luebert et al. 2016). The inflorescence structure of *Keraunea* is also unique not just within the Ehretiaceae but in the Boraginales as a whole. *Keraunea* does, however, present the only character believed to hold together the Ehretiaceae, bifid styles with two stigmatic branches (Luebert et al. 2016). We provide an emended family description below (see Taxonomic treatment) and a discussion of the unique inflorescence of *Keraunea*.

Table 1. Details of all sequenced samples used in the phylogenetic analysis (Fig. 1), including species names, voucher information and GenBank accession numbers.

Family	Species	Voucher	*trnL-F*	*rbcL*	*matK*	ITS
Boraginaceae	*Pentaglottis sempervirens* (L.) L.H.Bailey	*Weigend 9065* (B)	KF158194	KF158095	NA	NA
Codonaceae	*Codon royenii* L.	*Greuter 21551* (B)	KC542572	KF158090	NA	NA
Cordiaceae	*Coldenia procumbens* L.	*Jongkind 1973* (MO)	KF158207	KF158128	DQ197227	DQ197284
Heliotropiaceae	*Heliotropium stenophyllum* Hook. & Arn.	*Luebert* 1990 (SGO)	EF688847	KF158148	NA	EF688899
Hydrophyllaceae	*Eriodictyon trichocalyx* A.Heller	*Fraga 2209*	KX929271	KX929185	NA	NA
Lennoaceae	*Pholisma arenarium* Nutt. ex Hook.	*Hilger 1992/62* (B)	KF158216	KF158155	DQ197226	DQ197283
Wellstediaceae	*Wellstedia somalensis* Thulin & A.Johanss.	*Thulin 10084* (UPS)	KF158198	KF158105	NA	NA
Ehretiaceae	*Bourreria apetala* (J.S.Mill.) J.S.Mill. & Gottschling	*Jongkind 3280* (MO)	NA	NA	NA	KF673262
Ehretiaceae	*Bourreria bosseri* (J.S.Mill.) J.S.Mill. & Gottschling	*Miller 6182* (MO)	NA	NA	NA	KF673265
Ehretiaceae	*Bourreria croatii* (J.S.Mill.) J.S.Mill. & Gottschling	*Miller 4514* (MO)	NA	NA	NA	KF673263
Ehretiaceae	*Bourreria exsucca* Jacq.	*Ramirez 2744* (MO)	KF673291	NA	NA	KF673264
Ehretiaceae	*Bourreria havanensis* (Willd. ex Roem. & Schult.) Miers	*Abbott 23888* (FLAS)	NA	KJ773317	KJ772588	NA
Ehretiaceae	*Bourreria littoralis* Urb.	*BioBot00944*	NA	JQ590874	JQ587063	NA
Ehretiaceae	*Bourreria moaensis* Britton	*Beurton s.n.* (B)	KF158205	KF158116	NA	KF673250
Ehretiaceae	*Bourreria mollis* Standl.	*Wallnöfer 9717* (MO)	KF673283	NA	NA	AF385780
Ehretiaceae	*Bourreria petiolaris* (Lam.) Thulin	*Hilger s.n.* (B)	NA	NA	NA	KF673248
Ehretiaceae	*Bourreria pulchra* Millsp.	*Sima 2101* (F)	KF673288	NA	NA	KF673259
Ehretiaceae	*Bourreria quirosii* Standl.	*Gomez 18666* (MO)	KF673290	NA	NA	KF673261
Ehretiaceae	*Bourreria spathulata* (Miers) Hemsl.	*Cedillo 1415* (MO)	KF673289	NA	NA	KF673260
Ehretiaceae	*Bourreria succulenta* Jacq.	*Olmstead 96/114* (WTU)	NA	NA	DQ197229	DQ197285
Ehretiaceae	*Ehretia acuminata* R.Br.	*Anonymous B227*	EU599919	EU599831	EU599655	NA
Ehretiaceae	*Ehretia amoena* Klotzsch	*Maurin 1123*	NA	JF265404	JF270754	NA
Ehretiaceae	*Ehretia anacua* (Terán & Berl.) I.M.Johnst.	*Cultivated HB Adelaide*	EU600009	EU599833	EU599657	AF385796
Ehretiaceae	*Ehretia aquatica* (Lour.) Gottschling & Hilger	*Jongkind 2517* (MO)	EU600011	EU599835	EU599659	AF385791
Ehretiaceae	*Ehretia aspera* Willd.	*Rechinger 29501* (B)	KF673273	NA	NA	AF385787
Ehretiaceae	*Ehretia bakeri* Britten	*Chen 28823*	NA	ON950787	ON981999	NA
Ehretiaceae	*Ehretia coerulea* Gürke	*Anonymous 1969* (B)	KF673274	NA	NA	KF673249
Ehretiaceae	*Ehretia cymosa* Thonn.	*De Wilde 4230* (B)	EU600012	EU599836	EU599660	AF385790
Ehretiaceae	*Ehretia dicksonii* Hance	*TNM S159846*	NA	MF623374	MF651973	NA
Ehretiaceae	*Ehretia glandulosissima* Verdc.	*Chen 29046*	NA	ON950788	ON982000	NA
Ehretiaceae	*Ehretia grahamii* Randell	*Anonymous 300101051*	NA	KU564793	KU564569	NA
Ehretiaceae	*Ehretia latifolia* DC.	*Roitman 18x96* (B)	KF673282	NA	NA	AF385797
Ehretiaceae	*Ehretia longiflora* Champ. ex Benth.	*King s.n.* (B)	EU600010	EU599834	EU599658	AY331400
Ehretiaceae	*Ehretia macrophylla* Wall.	*XA010*	NA	MH657238	MH658814	MH712731
Ehretiaceae	*Ehretia microcalyx* Vaupel	*Crosby 1027*	KX929266	KX929180	NA	NA
Ehretiaceae	*Ehretia microphylla* Lam.	*Cultivated HB Singapore*	KF158204	KF158114	NA	AF469166
Ehretiaceae	*Ehretia obtusifolia* Hochst. ex. A.DC.	*Ehrobt 419*	NA	NA	NA	AY331401
Ehretiaceae	*Ehretia philippinensis* A.DC	*P2300*	NA	LC604229	LC604260	NA
Ehretiaceae	*Ehretia resinosa* Hance	*TNM S159880*	NA	MF623351	MF651953	NA
Ehretiaceae	*Ehretia rigida* (Thunb.) Druce	*Schwerdtfeger s.n.* (B)	KF673278	NA	NA	AF385788
Ehretiaceae	*Ehretia saligna* R.Br.	*Walter s.n.* (B)	KF673272	NA	NA	AF385786
Ehretiaceae	*Ehretia tinifolia* L.	*Anonymous 439*	HQ286270	KF158115	NA	AF385793
Ehretiaceae	*Ehretia wallichiana* Hook.f. & Thomson ex C.B.Clarke	*Ehrwal 1362*	NA	NA	NA	AY331402

Family	**Species**	**Voucher**	***trnL-F***	***rbcL***	***matK***	**ITS**
Ehretiaceae	*Halgania anagalloides* Engl.	*Strid 21757* (B)	MF423321	NA	NA	MF423308
Ehretiaceae	Halagnia *andromedifolia* Behr. & F.Muell. ex F.Muell.	*Strid 21146* (B)	KF673280	NA	NA	AF402584
Ehretiaceae	*Halgania bebrana* Oldfield & F.Muell.	*Lewis s.n.* (B)	MF423323	NA	NA	MF423312
Ehretiaceae	*Halgania brachyrhyncha* P.G.Wilson	*Streimann 820* (A)	NA	NA	NA	MF423313
Ehretiaceae	*Halgania cyanea* Lindl.	*Greuter 18801* (B)	KF158209	KF158130	NA	KF673254
Ehretiaceae	*Halgania glabra* J.M.Black	*Broadbent 2042* (A)	NA	NA	NA	MF423307
Ehretiaceae	*Halgania integerrima* Endl.	*Strid 21282* (MO)	MF423324	NA	NA	MF423315
Ehretiaceae	*Halgania andromedifolia* Behr. & F.Muell. ex F.Muell.	*Eichler 19328* (B)	NA	NA	NA	KF673255
Ehretiaceae	*Halgania solanacea* F.Muell.	*Mitchell 1090* (B)	NA	NA	NA	MF423311
Ehretiaceae	*Lepidocordia punctata* Ducke	*Steyermark 88509* (NY)	KF673287	NA	NA	KF673257
Ehretiaceae	*Lepidocordia williamsii* (I.M.Johnst.) J.S.Mill.	*Nee 27982* (M)	NA	NA	NA	KM893038
Ehretiaceae	*Rochefortia acanthophora* (DC.) Griseb.	*Liogier 23240* (NY)	NA	NA	NA	KM893039
Ehretiaceae	*Rochefortia barloventensis* Irimia & Gottschling	*Liogier 32280* (MO)	NA	NA	NA	KM893065
Ehretiaceae	*Rochefortia cubensis* Britton & P.Wilson	*Maxon 1720* (US)	NA	NA	NA	KM893049
Ehretiaceae	*Rochefortia cuneata* Sw.	*Correll 51418* (F)	NA	NA	NA	KM893048
Ehretiaceae	*Rochefortia oblongata* Urb. & Ekman	*Ekman 9224* (G)	NA	NA	NA	KM893061
Ehretiaceae	*Rochefortia spinosa* (Jacq.) Urb.	*Hilger 99/20* (B)	KF673276	NA	NA	KF673251
Ehretiaceae	*Rochefortia stellata* Britton & P.Wilson	*Areces 30714* (JE)	NA	NA	NA	KM893070
Ehretiaceae	*Tiquilia canescens* (DC.) A.T.Richardson	*Moore 239* (TEX)	NA	NA	DQ197230	DQ197312
Ehretiaceae	*Tiquilia conspicua* (I.M.Johnst.) A.T.Richardson	*Moore 294* (TEX)	NA	NA	DQ197250	DQ197586
Ehretiaceae	*Tiquilia cuspidata* (I.M.Johnst.) A.T.Richardson	*Moore 223* (TEX)	NA	NA	DQ197247	DQ197540
Ehretiaceae	*Tiquilia darwinii* (Hook.f.) A.T.Richardson	*Tye 573* (CDS)	NA	NA	DQ197248	DQ197541
Ehretiaceae	*Tiquilia elongata* (Rusby) A.T.Richardson	*Moore 289* (TEX)	NA	NA	DQ197251	DQ197588
Ehretiaceae	*Tiquilia gossypina* (Wooton & Standl.) A.T.Richardson	*Moore 134* (TEX)	NA	NA	DQ197233	DQ197337
Ehretiaceae	*Tiquilia greggii* (Torr. & A.Gray) A.T.Richardson	*Moore 133* (TEX)	NA	NA	DQ197231	DQ197325
Ehretiaceae	*Tiquilia hispidissima* (Torr. & A.Gray) A.T.Richardson	*Moore 131* (TEX)	NA	NA	DQ197240	DQ197423
Ehretiaceae	*Tiquilia latior* (I.M.Johnst.) A.T.Richardson	*Moore 216* (TEX)	NA	NA	DQ197244	DQ197538
Ehretiaceae	*Tiquilia mexicana* (S. Watson) A.T.Richardson	*Moore 245* (TEX)	NA	NA	DQ197236	DQ197372
Ehretiaceae	*Tiquilia nuttallii* (Benth. ex Hook.) A.T.Richardson	*Moore 218* (TEX)	NA	NA	DQ197254	DQ197579
Ehretiaceae	*Tiquilia palmeri* (A.Gray) A.T.Richardson	*Moore 197* (TEX)	NA	NA	DQ197252	DQ197581
Ehretiaceae	*Tiquilia paronychioides* (Phil.) A.T.Richardson	*Moore 300* (TEX)	NA	NA	DQ197249	DQ197564
Ehretiaceae	*Tiquilia plicata* (Torr.) A.T.Richardson	*Moore 196* (TEX)	NA	NA	DQ197246	DQ197570
Ehretiaceae	*Tiquilia purpusii* (Brandegee) A.T.Richardson	*Moore 109* (TEX)	NA	NA	DQ197245	DQ197409
Ehretiaceae	*Tiquilia tuberculata* A.T.Richardson	*Moore 98* (TEX)	NA	NA	DQ197239	DQ197407
Ehretiaceae	*Tiquilia turneri* A.T.Richardson	*Moore 89* (TEX)	NA	NA	DQ197237	DQ197398
Ehretiaceae	*Keraunea confusa* Moonlight & D.B.O.S.Cardoso	*Lombardi 1819* (BHCB)	NA	NA	submitted	OP034981

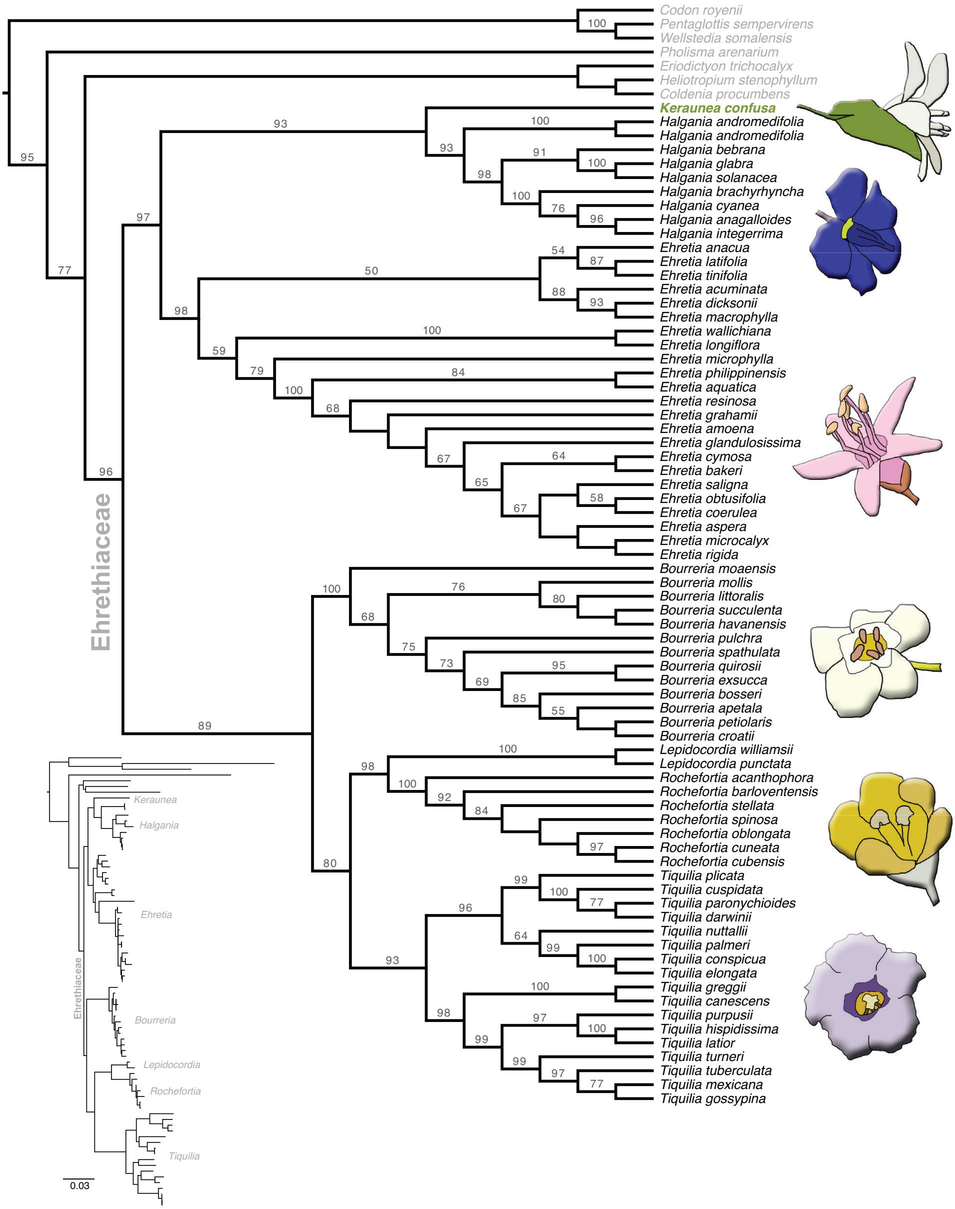

Figure 1. RAxML bootstrap tree based on nuclear ribosomal (ITS) and plastid (*matK*, *rbcL*, *trnL-F*) DNA sequence data resolving *Keraunea* within the Ehretiaceae. Node labels indicate nodes with bootstrap support values above 50. Inset phylogram (bottom left) indicates branch lengths. Outgroup taxa from representatives of other Boraginales families are in light grey. Illustrations are (top to bottom): *Keraunea*, *Halgania*, *Ehretia*, *Bourreria*, *Rochefortia* and *Tiquilia*.

The placement of *Keraunea* as sister to the Australian endemic genus *Halgania* presents a biogeographical conundrum but is ecologically and morphologically coherent. *Halgania* is a dry adapted group (Holstein and Gottschling 2017), and *Keraunea* is primarily found in dry forest within the Caatinga phytogeographic domain or in and around rock outcrops in the Mata Atlântica phytogeographic domain. Insights from recent biogeographical studies with dated molecular phylogenies of transcontinentally disjunct plant clades have suggested that long distance dispersal and phylogenetic niche conservatism may explain why closely related lineages are ecologically confined to the same dry forest biome no matter how much geographic distance separates them (Gagnon et al. 2019; Ringelberg et al. 2020). An assessment of the diversification history of Ehretiaceae in the context of biome conservatism seems an important issue to explore in the future to better understand the evolution of the interesting geographical disjunction, yet similar ecologies of *Keraunea* and *Halgania*.

The flowers of *Halgania* are buzz-pollinated "solanum-type" flowers (Holstein and Gottschling 2018) that at first glance seem highly distinct from those of *Keraunea* (Fig. 1). The androecium of the two groups is very similar, with both genera having five stamens with short filaments fused at the base to the corolla tube, long anthers and conspicuous, extended connectives. The two genera differ in that the anthers of *Halgania* dehisce by opening into a small chamber formed by protrusions of the connective and appear to be poricidally dehiscent while those of *Keraunea* dehisce via longitudinal slits along the entire length of the anther, and in *Halgania* the anthers are held together in a cone by long, interlaced trichomes while in *Keraunea* they are held apart and are glabrous (Holstein and Gottschling 2018). Further, the fruits of the two genera are very similar. Cheek and Simão-Bianchini (2013) dissected a fruit of *K. brasiliensis* and characterised it as bilocular with four ovules, though two of those may be aborted. We characterise this fruit as a drupe, and bilocular, drupaceous fruits with four ovules are the most common character state in the Ehretiaceae (Luebert et al. 2016) and one shared with *Halgania* (Holstein and Gottschling 2018).

Taxonomic treatment

We recognise five species of *Keraunea*, which are all endemic to Brazil, including three newly described species.

Ehretiaceae Mart., Nov. Gen. Sp. Pl. 2: 136, 138. 1827, nom. cons.

Type genus. *Ehretia* P.Browne.

Description. [differences from Luebert et al. (2016) in bold] Trees, shrubs, **lianas**, perennial herbs, rarely with thorns (*Rochefortia* Sw.); indumentum variable, hirsute to glabrescent. Leaves alternate, entire, petiolate; lamina variable in shape, strongly dissected in the halophytic *Cortesia* Cav. Inflorescences terminal or axillary thyrses, sometimes congested, **or few-flowered corymbs (*Keraunea*)**. Flowers pentamerous, cosexual or unisexual and dioecious in *Lepidocordia* Ducke and *Rochefortia*, **sometimes inserted on the centre of an accrescent bracteole (*Keraunea*)**; calyx lobes united in a tube or distinct nearly to the base, tubular to campanulate; aestivation imbricate (mostly quincuncial); corolla sympetalous, generally tubular with spreading lobes, rotate, or campanulate to urceolate, white, red or blue (*Halgania*, some species of *Bourreria* P.Browne); stamens 5, the filaments generally adnate to the corolla tube at least at the base, sometimes puberulent at the point of insertion, the anthers usually exerted; gynoecium bicarpellate, the ovary uni- to tetralocular from secondary subdivision, style terminal, the stigma clavate to capitate with 1(2) branches; nectar disc usually present at base of the ovary. Fruits drupaceous, often drying and separating into two two-seeded pyrenes, or 4 1-seeded pyrenes or schizocarps, or 4 nutlets.

Distribution. Ehretiaceae is a broadly distributed family found throughout tropical and subtropical Asia, Australia, sub-Saharan Africa. In the Americas, its distribution encompasses the eastern United States, Florida, Central America, the Caribbean, the Guyana shield and the Andes. In Brazil, the Ehretiaceae was previously only known from the single species *Lepidocordia punctata* Ducke (Stapf 2023), found in lowland Amazonian forests in Pará and Roraima states. Our treatment therefore represents new records of the family from the Caatinga and Mata Atlântica phytogeographic regions in Brazil, and from the states of Bahia, Minas Gerais, Espírito Santo and Rio de Janeiro (Fig. 1).

Included genera. The family includes the following eight genera: *Bourreria*, *Cortesia*, *Ehretia*, *Halgania*, *Keraunea*, *Lepidocordia* Ducke, *Rochefortia* and *Tiquilia* Pers. (Luebert et al. 2016).

Notes. Our morphological concept of the Ehretiaceae is little changed from that of Luebert et al. (2016). The characters that differ are included in bold in the description above. The first of these is that the four species of *Keraunea* are the first lianescent species included within the family (versus perennial herbs, shrubs, or trees). Lianas are elsewhere found in the Boraginales in the Cordiaceae (*Cordia* L.) and Heliotropiaceae (*Tournefortia* L.). Secondly, we have expanded the concept of the Ehretiaceae to include species with a few-flowered corymb inflorescence structure and where the flower and later fruit are inserted at the centre of an accrescent bracteole. To our knowledge, these characters are unique among not just the Ehretiaceae but the Boraginales, whose members are known for their characteristic scorpioid cymose inflorescences. We suggest the few-flowered inflorescence of *Keraunea* is the result of secondary reduction rather than a retained ancestral form. Within the Boraginales, reductions to few-flowered inflorescences are present elsewhere in the Boraginaceae, Codonaceae and Wellstediaceae (Luebert et al. 2016).

***Keraunea* Cheek & Simão-Bianchini, Nord. J. Bot. 31: 454. 2013.**

Type species. *Keraunea brasiliensis* Cheek & Simão-Bianchini.

Description. Scandent shrubs or lianas. Stems woody, cylindrical, hollow, lacking lenticels. Stipules lacking. Leaves on the main stems alternate, simple, petiolate;

margins entire; venation pinnate, camptodromous or brochododromous. Side shoots with 2–4 aborted leaves, then 2–6 progressively larger leaves along the shoot. Inflorescences terminal on side shoots, determinate, corymbose, with 3–6 flowers; bracteoles one per flower or rarely lacking, leaf-like, inserted halfway along the pedicel. Flowers 5-merous, cosexual. Calyx campanulate, fused at the base, alternating with the petals; aestivation imbricate. Corolla with the tube campanulate, fused at the base; aestivation imbricate. Stamens epipetalous, inserted at the base of the corolla tube, alternating with the petals; filaments free; anthers basifixed, introrse, dehiscing via lateral slits; connectives extended. Nectary disk present, at base of the ovary. Ovary superior, subglobose, 2-locular, the locules biovulate, each with one functional and one aborted ovule. Style single, with two apical stigmas. Fruit a dry, indehiscent drupe, usually inserted in the centre of the persistent and accrescent bracteole; calyx persistent; corolla caducous; style persistent.

Distribution. *Keraunea* is endemic to Brazil and thus far known from the states of Bahia (3 spp.), Espírito Santo (1 sp.), Minas Gerais (1 sp.) and Rio de Janeiro (1 sp.). Each of the species is restricted to a single state except for *K. capixaba*, which is found in both Bahia and Espírito Santo (Fig. 2).

Habitat. Two species are known from seasonally dry forest within the Caatinga domain (*K. brasiliensis* and *K. confusa*); two from humid forests within the Mata Atlântica domain (*K. capixaba* and *K. velutina*); and a fifth from transitional, semi-deciduous forests between the Caatinga and Mata Atlântica domains (*K. bullata*). The genus has a marked preference for rock outcrops or forest on rocky soils. Both *K. brasiliensis* and *K. confusa* are found mostly on karstic outcrops, while *K. capixaba* and *K. velutina* have both been collected at the base of granitic inselbergs.

Etymology. The epithet derives from the Greek, keraunos, or lightning bolt. This was intended to signify the unexpected but now disproven appearance of a neuropeltoid genus of the Convolvulaceae in the Americas.

Notes. Cheek and Simão-Bianchini (2013) treated the flower and fruit of *Keraunea* as being inserted at the centre of a large, leaf-like bract. This 'bract' is inserted halfway up and adnate to the pedicel, so we instead follow Lombardi (2014) and treat it as a bracteole rather than a bract.

Identification notes. *Keraunea* species are distinctive in being semi-scandent shrubs or lianas with simple, alternate, exstipulate leaves and inflorescences terminal on foliose side shoots. The flowers and fruits are highly unusual in being inserted at and appearing to arise from the centre of an accrescent bracteole.

Several specimens of *Keraunea* were erroneously identified as *Bougainvillea* Comm. ex Juss. (Nyctaginaceae), which is understandable, as both genera have exstipulate leaves, a semi-lianescent habit, and flowers and fruits associated with showy bracts or bracteoles. *Keraunea* spp. are however never spinescent, and the flowers and fruits are inserted directly onto the bract, whereas in *Bougainvillea* several flowers or fruits are clustered on a pedunculate inflorescence surrounded by two or more bracts.

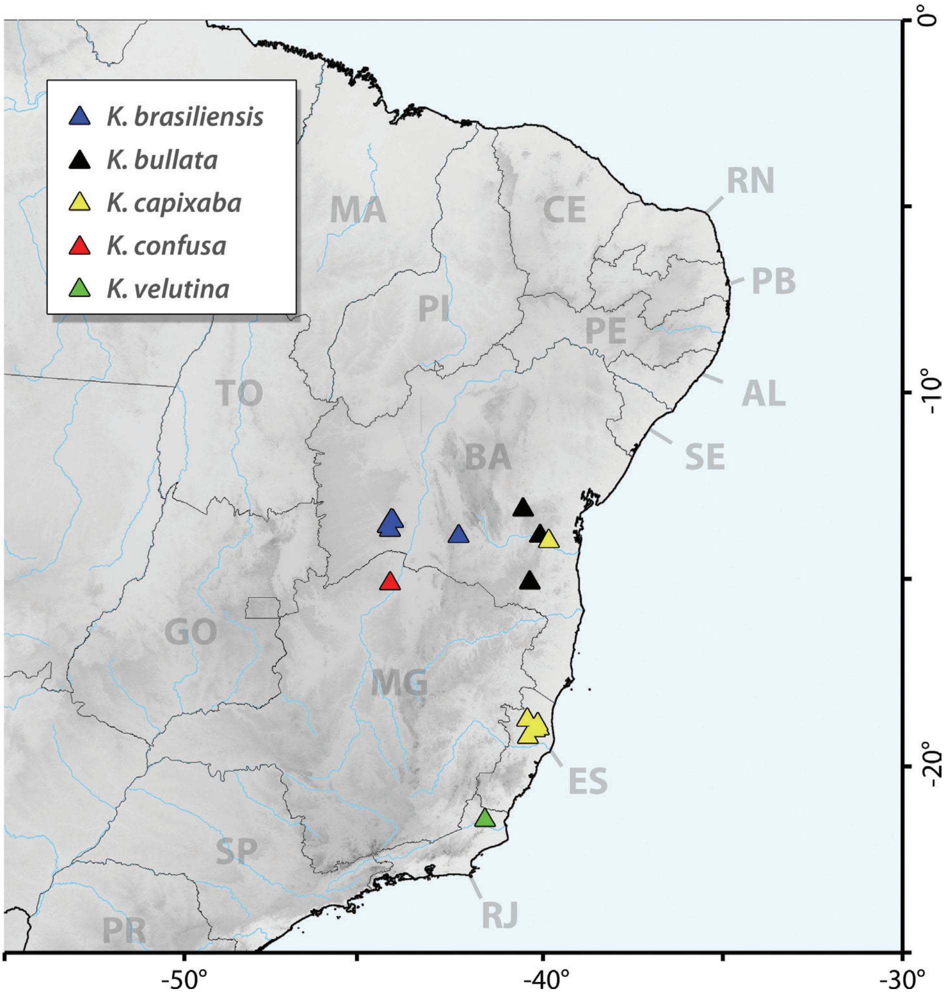

Figure 2. Distribution of species of the genus *Keraunea*. Shading denotes elevation; two letter codes represent the standardised two letter codes for the states of Brazil. Species are coloured as follows: **blue**, *K. brasiliensis* Cheek & Simão-Bianchini; **black**, *K. bullata* Moonlight & D.B.O.S.Cardoso; **yellow**, *K. capixaba* Lombardi; **red**, *K. confusa* Moonlight & D.B.O.S.Cardoso; **green**, *K. velutina* Moonlight & D.B.O.S.Cardoso.

Key to the species of *Keraunea*

1 Leaf base rounded, truncate, or subcordate; leaf venation brochidodromous **2**

– Leaf base attenuate, acuminate, or obtuse; leaf venation camptododromous...... **3**

2 Tertiary veins plane with the lower leaf surface, not raised; leaf blades to 18 × 12 cm, rugose .... ***Keraunea confusa***

– Tertiary veins raised from the lower leaf surface; leaf blades to 10.5 × 7.5 cm, bullate.. ***Keraunea bullata***

3 Leaves on side shoots elliptic with attenuate apices; leaf blades conspicuously velutinous below .... ***Keraunea velutina***

– Leaves on side shoots ovate to broadly ovate with acute to obtuse apices; leaf blades glabrescent to hirtellous below **4**

4 Main stem frequently branching, rugose; stems and leaves hirtellous; leaves membranous to papyraceous, dull green above; secondary veins raised abaxially .... ***Keraunea brasiliensis***

– Main stem rarely branching, smooth; stems and leaves glabrous; leaves chartaceous, glossy green above; secondary veins not raised abaxially ...... ***Keraunea capixaba***

1. *Keraunea brasiliensis* Cheek & Simão-Bianchini, Nord. J. Bot. 31: 454. 2013.
Fig. 3

Type. Brazil. Bahia: Mun. Caetité, caminho da Fazenda Boa Vista para Urânio, 13°59'35"S, 42°12'27"W, 560 m, 8 Feb 1997, *L. Passos*, *M.L. Guedes*, *B. Stannard & E. Saar 5263* (holotype: SPF; isotypes ALCB, CEPEC [CEPEC00077827], HRCB [acc. #38156], HUEFS [HUEFS000058973], K [K000979156]).

Description. Scandent shrub or liana, to 7 m tall. Stems cylindrical, hollow, 3–9 mm in diameter, frequently branching, sericeous-pubescent with silky hairs; internodes 0.7–11 cm long; side shoots 4–9 cm long, hirtellous-pubescent with minute, rigid hairs. Leaves of main stem with the blades 5.0–6.5 × 3.1–3.6 cm, ovate, hirtellous-pubescent with minute, rigid hairs, the venation pinnate, camptodromous, with 4–6 secondary veins; the base acute, the margins entire, ciliate, the apex obtuse; petioles of leaves on main stem ca. 8 mm long, distinctly curved to 90° ⅓ of the way along their length. Side shoots with 3–5 leaves, these progressively larger along the shoot; blades 5.1–7.2 × 2.3–3.9 cm, ovate, hirtellous-pubescent, the venation as on leaves of the main stem, the base acute, the margins entire, ciliate, the apex obtuse; petioles 5.7–6.1 mm long, straight, hirtellous-pubescent like the leaves. Inflorescence corymbose, with 2–4 flowers; free portion of the peduncle ca. 3.5 mm long, 2.5 cm long, the remainder adnate to the bracteole, hirtellous-pubescent; bracteole 5.1–8.1 × 2.4–3.8 cm, inserted ca. ¼ of the way along the pedicel, ovate, hirtellous-pubescent, the venation as the leaves, the base acute, the margins entire, ciliate, the apex obtuse. Flowers incompletely known, 5-merous. Calyx with the tube campanulate, ca. 3.5 mm long, the lobes ca. 12 × 1.5 mm, lanceolate, velutinous-pubescent. Corolla unknown; androecium and gynoecium unknown. Fruit inserted on the accrescent bracteole; calyx persistent, expanding to 14 mm long.

Distribution. *Keraunea brasiliensis* is endemic to Brazil and is known only from the state of Bahia (Coribe, São Félix do Coribe and Caetité municipalities) (Fig. 2).

Habitat. *Keraunea brasiliensis* has primarily been collected scrambling over exposed rocks and vegetation in karst formations supporting Caatinga seasonally dry tropical forest vegetation. The two most easterly collections of the species (*Pereira-Silva et al. 9111*, *Passos et al. 5263*) were collected in Caatinga vegetation but far from any known karst outcrops.

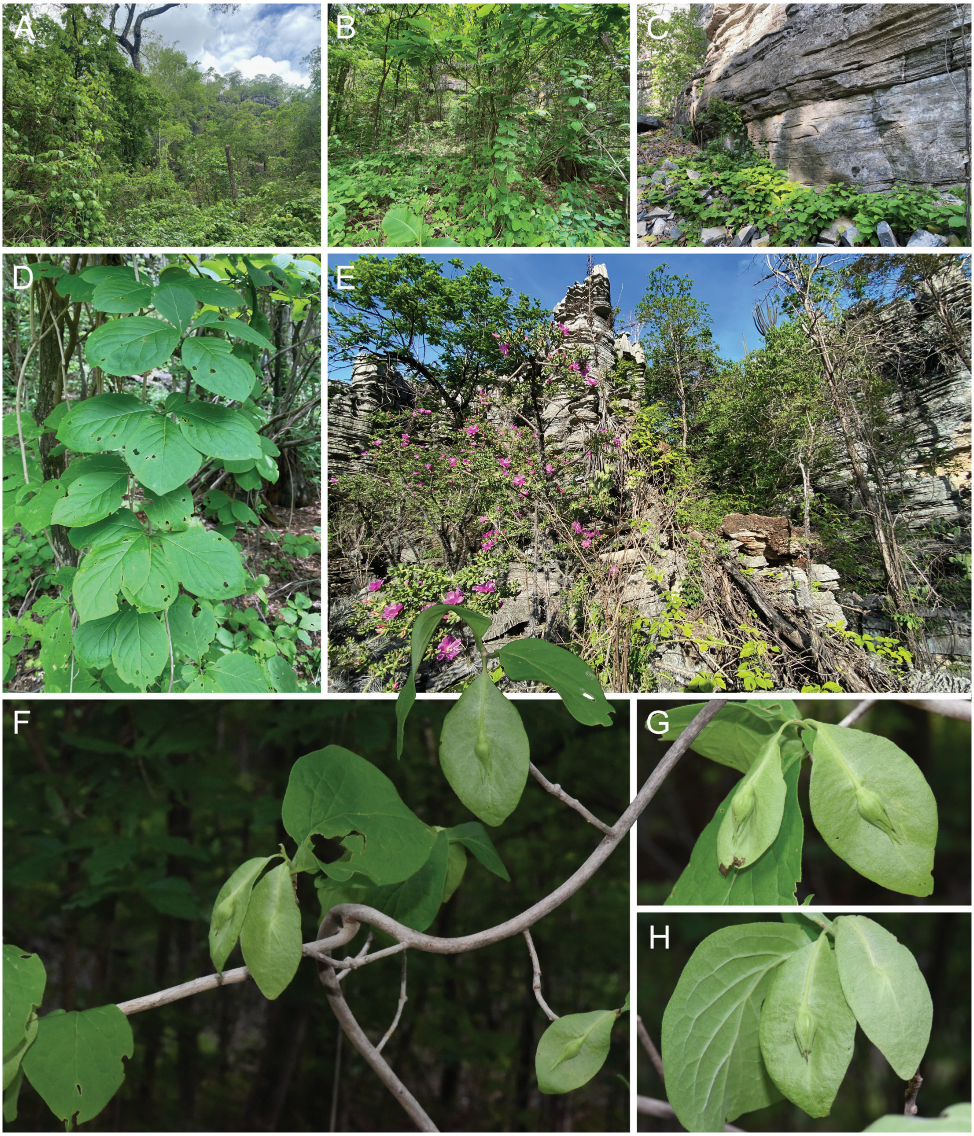

Figure 3. Habitat and morphology of *Keraunea brasiliensis* Cheek & Simão-Bianchini **A–C** karstic Caatinga in southwestern Bahia **D** stem and leafy side shoots **E** habit **F** main shoot and side shoots with fruits **G–H** close up of developing fruits and accrescent bracteole. All photos by Domingos Cardoso.

Conservation status. *Keraunea brasiliensis* was provisionally assessed by Cheek and Simão-Bianchini (2013) as Endangered (EN B2 a b iii) under IUCN Criteria (IUCN 2019). We alter this assessment as it covered specimens now known to be of two different species. Our narrower concept includes plants from four localities and has an EOO of 4,550 km^2. None of the known localities are in protected areas. Accordingly, we still assess *K. brasiliensis* as EN (EN B2 a b iii) under IUCN criteria (IUCN 2019).

Etymology. Named for the country of Brazil.

Notes. The protologue of *K. brasiliensis* cited individuals we now recognise as two different species and both paratypes collected in Minas Gerais fall under our circumscription of *K. confusa*. The authors of *K. brasiliensis* did, however, note the unusual intraspecific morphological variation within the species and speculated that the material collected in Bahia and Minas Gerais may have represented two different species. The original illustration in the protologue (Cheek and Simão-Bianchini 2013) included individuals of both of the species we recognise here so only the subfigures (B, H–I) represent *K. brasiliensis*. Muñoz-Rodríguez et al. (2022) also published sequence data for *K. brasiliensis* and *K. confusa* and a member of the family Malpighiaceae under the name *K. brasiliensis*.

Our emended description of *K. brasiliensis* reflects our much narrower circumscription of this species. The specimens we cite represent a morphologically homogenous group of specimens all collected at a similar phenological state, i.e. with fruits but lacking flowers. As such, our description lacks some floral traits. The floral description of *K. brasiliensis* provided by Cheek and Simão-Bianchini (2013) was made using a dissected bud from *Lombardi & Salino 1819* (K), which we now consider as an isotype of *K. confusa* (see below).

Identification notes. Within its range, *K. brasiliensis* is most likely to be confused with *K. confusa*, but the two species can be distinguished with ease based entirely upon vegetative characters. The leaves of *K. confusa* are larger (to 18 × 12 cm versus to 7.5 × 4 cm) with brochidodromous venation and a rugose texture (versus camptodromous venation and smooth texture in *K. brasiliensis*). *Keraunea brasiliensis* is most similar to *K. capixaba* (though this species is also similar to *K. velutina*), from which it can be distinguished by its rugose stems (versus smooth) and membranous, dull green leaves (versus chartaceous, glossy green) with indistinct secondary veins (versus raised above the lower leaf surface).

Additional specimens examined. Brazil. Bahia: Mun. Coribe, BA-172 sentido São Félix do Coribe, entrada a direita em Colônia do Formoso por estrada de terra até afloramento de calcário a ca. 2.5 km de Ponta d'Água, 13°41'28"S, 44°15'33"W, 4 Dec. 2022, 4 Dec 2022, *D. Cardoso et al. 4902* (ALCB, RB, TCD), *D. Cardoso et al. 4904* (ALCB, HUEFS, RB, TCD), *D. Cardoso et al. 4906* (ALCB, HUEFS, RB, TCD; Mun. São Félix do Coribe, BA-172 sentido Coribe, afloramento de calcário do lado esquerdo, 13°26'6"S, 44°13'5"W, 4 Dec. 2022, *D. Cardoso et al. 4909* (ALCB, HUEFS, RB, TCD), *D. Cardoso et al. 4910* (ALCB, HUEFS, RB, TCD), *D. Cardoso et al. 4912* (ALCB, HUEFS, RB, TCD); Mun. Caetité, Distrito de Maniaçu, Estrada para São Timóteo, km 6, 13°51'18"S, 42°20'45"W, 870 m alt., 22 May 2004, *G. Pereira-Silva et al. 9111* (HUEFS [HUFES000117294]); Mun. Santa Maria da Vitória, c. 7.7 km S de Santa Maria da Vitória na Estrada para Lagoinha, extremidade septentrional da Serra do Ramalho, 13°27'0"S, 44°10'16"W, 13 Feb 2000, *L.P. de Queiroz et al. 5972* (CEPEC [CEPEC00113512]; HUEFS [HUEFS000110252]); Mun. Coribe, c. 5 km S em estrada de terra que cruza pequeno ramal que sai a 5.1 km E de Ponta d'Água, a 24.4 km S de São Félix do Coribe na estrada para Coribe, 13°35'10"S, 44°19'12"W, 14 Apr. 2007, *L.P. de Queiroz et al. 12707* (CEN [CEN00113310], HUEFS [HUEFS000117258]).

2. *Keraunea bullata* Moonlight & D.B.O.S.Cardoso, sp. nov.

urn:lsid:ipni.org:names:77314429-1

Fig. 4

Diagnosis. Most similar to *K. confusa* with relatively broad leaves with brochidodromous venation but differing from it in smaller leaves (reaching 10 × 7.4 cm versus 18 × 12 cm) with a bullate texture (versus rugose) and by its tertiary veins, which are raised from the lower leaf surface (versus not raised).

Type. Brazil. Bahia: Mun. Jequié, Bairro Suíça, 13°51'S, 40°5'W, *M.L. Guedes*, *D.M. Loureiro & D.L. Santana 9176* (holotype: ALCB [acc. #55929, ALCB075866, 3 sheets]).

Description. Scandent shrub or liana, to 2 m. Stems cylindrical, hollow, 2–5 mm in diameter, frequently branching, glabrescent to sparsely pubescent; internodes 2.9–8.2 cm long; side shoots 3.0–4.5 cm long, sericeous. Leaves of main stem unknown. Side shoots with 3–4 leaves, these progressively larger along the shoot; blades 4.2–10.5 × 2.4–7.4 cm, ovate to broadly ovate, velutinous-pubescent, the venation pinnate, brochidodromous, with 4–6 secondary veins; the base rounded to truncate, the margins entire, ciliate, the apex obtuse; petioles 8–19 mm long, straight, velutinous-pubescent. Inflorescence corymbose, with 2–6 flowers; free portion of the peduncle 4–6 mm long, 1.8–2.1 cm long, the remainder adnate to the bracteole, sericeous-pubescent; bracteoles 5.0–5.7 × 2.7–3.1 cm, inserted ca. ¼ of the way along the pedicel or rarely lacking, ovate, velutinous-pubescent, the venation as the leaves, the base short-rounded, the margins entire, ciliate, the apex attenuate. Flowers incompletely known, 5-merous. Calyx with the tube campanulate, ca. 1.5 mm long, the lobes ca. 1.5 × 10–12 mm, ensiform, sericeous-pubescent. Corolla unknown; androecium and gynoecium unknown. Fruit inserted on the accrescent bracteole; calyx persistent, expanding to 12 mm long.

Distribution. Endemic to the state of Bahia (Fig. 2).

Habitat. *Keraunea bullata* is a species of forests in the transition from humid forests in the coastal Mata Atlântica phytogeographic domain and seasonally dry forests in the inland Caatinga domain. This forest is described on labels as “Caatinga arborea” (*Guedes et al. 9176*) and (*Mori et al. 11534*) as growing on rocky soils. This area has a metamorphic bedrock (often called crystalline in the literature, de Queiroz et al. 2017) and is quite edaphically distinct from the karstic outcrops that are home to *K. brasiliensis* and *K. confusa*.

Conservation status. *Keraunea bullata* is known from only three localities with a combined EOO of ca. 6,300 km^2. We know of no specific conservation threats to this species so provisionally assess it as Vulnerable (VU D2) under IUCN Red List criteria (IUCN 2019).

Etymology. Named for the bullate texture of the leaves and bracteoles.

Identification notes. *Keraunea bullata* is highly distinct within its range. Despite also occurring in the same Mata Atlântica phytogeographic domain as *K. capixaba*, their habitat does not overlap. *Keraunea bullata* can be morphologically distinguished by its leaf venation (brochidodromous versus camptodromous) and texture (bullate and dull green versus smooth and glossy green).

Figure 4. Holotype of *Keraunea bullata* Moonlight & D.B.O.S.Cardoso, *M.L. Guedes*, *D.M. Loureiro & D.L. Santana 9176* (ALCB [ALCB075855, acc. #55929, sheet 1]).

Additional specimens examined. Brazil. Bahia: Mun. Itambé, rod. BA-265, trecho Itapatinga/Caatiba, Faz. Serra Verde a 17 km da Rod. BR-415, [15°6'S, 40°22'W], 14 Mar. 1979, *S.A. Mori et al. 11534* (CEPEC [CEPEC00016207], NY

[03147645], RB [00725192]). Mun. Juraci, Vicinity of Machado Portela [13°10'S, 40°46'W], 19–23 Jun 1915, *J.N. Rose & P.G. Russell 19979* (US [01341072, acc. # 762304).

3. *Keraunea capixaba* Lombardi, Phytotaxa 181: 54. 2014.

Fig. 5

Type. Brazil. Espírito Santo: Mun. Jaguaré, perto da Comunidade São Jorge de Paduá, sentido para Fátima, 18°54'29.0"S, 40°8'44.9"W, 26 Sep. 2013, *G.S. Siqueira 891* (holotype: CVRD [acc. # 14565]; isotypes HRCB [acc. # 76196], SP [SP003725]).

Description. Scandent shrub or liana, to ca. 4 m. Stems cylindrical, hollow, 2–4 mm in diameter, glabrescent, rarely branching, internodes 2.4–11.5 cm long; side shoots 1.3–5.5 cm long, glabrescent. Leaves of main stem with the blades 7.0–13.5 × 2.1–4.5 cm, elliptic, glabrescent, the venation pinnate, camptodromous, with 4–6 secondary veins; the base cuneate, the margins entire, ciliate, the apex attenuate; petioles 5–6.5 mm long, straight. Side shoots with 4–6 leaves, these progressively larger along the shoot; blades 1–9.5 × 0.5–6.5 cm, ovate, rarely obovate or broadly ovate, glabrescent, the venation as on leaves of the main stem, the base cuneate to rounded, the margins entire, rarely crenulate toward the apex (*Siqueira 891*), ciliate, the apex acute to rounded; petioles 5.5–12 mm long, straight, glabrescent. Inflorescence corymbose, with 2–4 flowers; free portion of the pedicel, 8–14 mm long, 1.8–2.6 cm long, the remainder adnate to the bracteole, sericeous-pubescent with silky hairs; bracteole 3.3–3.5 × 1.9–2.4 cm, inserted ca. ½ of the way along the pedicel or rarely lacking, ovate, glabrescent, the venation as the leaves, the base short acute, margin entire, not ciliate, the apex acute. Flowers 5-merous. Calyx with the tube campanulate, ca. 3.5 mm long, the lobes 6.5–18 × 1.5–2.5 mm, ensiform, glabrescent to minutely pubescent. Corolla with the tube campanulate, ca. 6.5 mm long, the lobes 19–26 × 7.5–11.5 mm, elliptic to oblong, glabrous. Stamens epipetalous, inserted at the base of the corolla tube, the filaments 2–3 mm long, the anthers ca. 9 mm long, connective extending to 3.2 mm. Ovary subglobose, 2-locular, the locules biovulate; style single, conduplicate, unbranched; stigmas 2, truncate. Fruit inserted on the accrescent bracteole; calyx persistent, expanding to 18 mm long.

Distribution. Endemic to Espírito Santo state and known from the municipalities of Jaguaré, Sooretama and Nova Venécia (Fig. 2).

Habitat. Collections of *Keraunea capixaba* have primarily been made in "mata tabuleiro" or flat, semi-deciduous forests found within the coast of the Mata Atlântica domain of Brazil. A more recent collection (*Gurtler & Dutra 371*) was made growing over rocks in forest understory at the base of a granitic outcrop. Specimen labels describe the species as scandent or lianescent.

Conservation status. *Keraunea capixaba* was provisionally assessed by Lombardi (2014) as Endangered because it was at that time known from four collections made

Figure 5. Morphology of *Keraunea capixaba* Lombardi **A** habit **B** inflorescence, front view **C** inflorescence, side view. For photograph of fruit with accrescent bracteole see Lombardi (2014). All photographs by Geovane Siqueira.

within disturbed forest patches adjacent to the Sooterama Biological Reserve. We add five collections to the known distribution, including one collected within the Sooterama Biological Reserve (*Covre s.n.*), two collected at the base of inselbergs > 30 km from the reserve (*Gurtler & Dutra 371*, *Demuner et al. 3799*), and a gathering made a remarkable 500 km to the north near Ipauí, Bahia. The species is now known from six localities with a collective Extent of Occurrence (EOO) of ca. 11,000 km^2. The species is known from < 10 localities and has a EOO of < 20,000 km^2, so we assess *K. capixaba* as Vulnerable (VU B1 a b iii) under IUCN criteria (IUCN 2019).

Etymology. The epithet is an indigenous term referring to people or objects from Espírito Santo state.

Identification notes. *Keraunea capixaba* is most morphologically and ecologically similar to the newly described *K. velutina*, the two species of the genus that are associated with more humid settings in the Mata Atlântica phytogeographic region, yet they were never found growing sympatrically. *Keraunea capixaba* differs in lacking an indumentum on the stems, side shoots and lower leaf surface (versus a velutinous-pubescent in *K. velutina*), and its ovate leaves on the side shoots (versus elliptic to narrowly-lanceolate). Its range is close to that of *K. confusa*, from which it is readily distinguished by its camptodromous venation (versus brochidodromous).

Additional specimens examined. Brazil. Bahia: Rod Ipiau-Ibirataia, [14°6'S, 39°41'W], 13 Nov. 1971, *T.S. Santos 2139* (HUEFS). **Espírito Santo:** Mun. Sooretama, Reserva Biológica de Sooretama, [19°1'S, 40°7'W], 19 May 2015, *C. Covre s.n.* (SAMES [SAMES03696]); Mun. Rio Bananal, Alto Bananal, 19°14'56"S, 40°24'59"W, 300–600 m alt., 25 Apr. 2007, *V. Demuner et al. 3799* (BHCB [BHCB017211]); Mun. Jaguaré, Perto da Comunidade São Jorge de Paduá, 25 Sep. 2013, *D.A. Folli 7117* (CVRD [acc. #14563]; HRCB [acc. #16194], NY [02687787], RB [00895205]); Mun. Sooretama, Barro Roxo a Córrego Rodrigues, 19°4'35"S, 40°13'25"W, 156 m alt., 8 Oct. 2014, *D.A. Folli 7273* (CVRD [acc. #15122]; RB [01103439]); Mun. Nova Venécia, fazenda Santa Rita, ao pé da pedra da torre (P3), 18°47'7"S, 40°26'29"W, 2 Feb. 2018, *J. Gurtler & S.C. Dutra 371* (VIES [VIES036853]); Mun. Sooretama, Rodovia ES 358, distrito de Bom Jardim, 19°2'20.31"S, 40°14'48.23"W, 1 Sep. 2012, *A. Moreira de Assis & J. Freitas 3340* (HRCB [acc. #76193], MBML [2 sheets: MBML00016754, MBML00016755]); Mun. Jaguaré, perto da Comunidade São Jorge de Paduá, 18°54'29.0"S, 40°8'44.9"W, 6 Oct. 2013, *G.S. Siqueira 893* (CVRD [acc. #14570], HRCB [acc. #76199], K [K001275507], MBML [MBML00016491], NY [02687786], RB [00895202])

4. *Keraunea confusa* Moonlight & D.B.O.S.Cardoso, sp. nov.

urn:lsid:ipni.org:names:77314430-1
Fig. 6

Diagnosis. Most similar to *K. brasiliensis* but differing in its larger leaves (to 18 × 12 cm versus to 7.5 × 4 cm) with brochidodromous (versus camptodromous) leaf venation and a rugose (versus flat) leaf texture and by its leaves and stems with a sericeous (versus hirtellous) indumentum.

Type. Brazil. Bahia: Mun. Januária, distrito de Fabião, junto ao Abrigo do Malhador, 15°7.85'S, 44°15.17'W, 25 May 1997, *J.A. Lombardi & A. Salino 1819* (holotype: BHCB [BHCB017209]; isotypes: HRCB [acc. #26438]; K [K001395055], UEC [UEC117783]).

Description. Scandent shrub or liana, to 4 m tall. Stems cylindrical, hollow, 2–5 mm in diameter, rarely branching, sericeous-pubescent with silky hairs; internodes 3.8–16.5 cm long; side shoots 2.6–3.5 cm long, sericeous-pubescent. Leaves of the main stem with the blades 9.5–17 × 5.6–13.5 cm, ovate, velutinous-pubescent, the venation pinnate, brochidodromous, with 5–7 secondary veins, the base truncate to subcordate, the margins entire, ciliate, the apex attenuate to acute; petioles of leaves on main stem 10–16 mm long, distinctly curved to 90° ¼ of the way along their length. Side shoots with 2–5 leaves, these progressively larger along the shoot; blades 2.1–18 × 3.0–12 cm, velutinous-pubescent, the venation as on leaves of the main stems, the base rounded to truncate, the margins entire, ciliate, the apex obtuse; petioles 3–25 mm long, sericeous-pubescent. Inflorescence corymbose, with 2–4 flowers; free portion of the peduncle 5–13 mm long, 2.2–2.8 cm long, the remainder adnate to the bracteole, sericeous-pubescent; bracteole 4.9–5.6 × 2.7–5.1 cm, inserted ca. ⅓ of the way along the pedicel or rarely lacking, ovate, sericeous-pubescent,

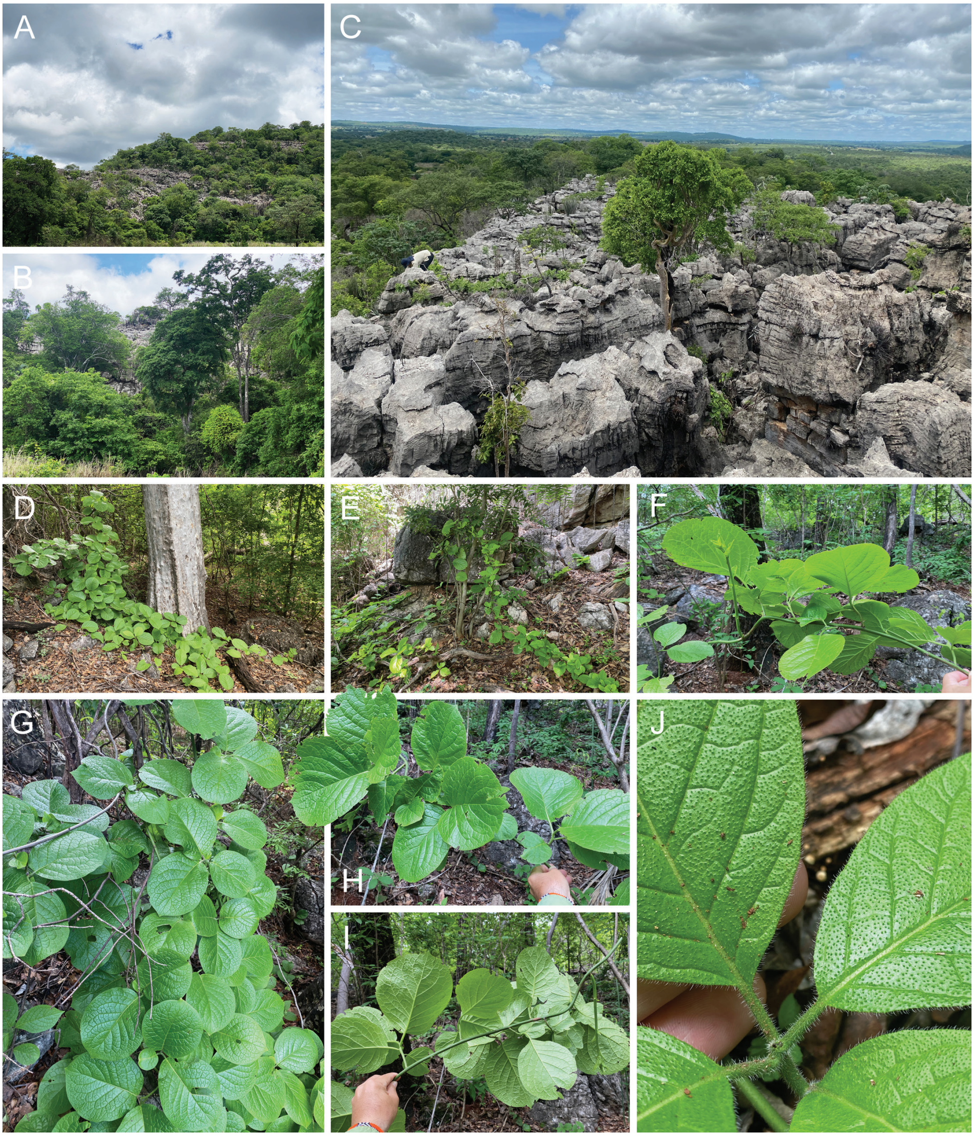

Figure 6. Habitat and morphology of *Keraunea confusa* Moonlight & D.B.O.S.Cardoso **A–C** karstic Caatinga seasonally dry tropical forest in northern Minas Gerais **D–G** habit **H–I** branching pattern **J** close up of side shoot. All photographs by Domingos Cardoso.

the venation as the leaves, the base short cuneate, the margins entire, ciliate, the apex attenuate. Flowers incompletely known, 5-merous. Calyx with the tube campanulate, ca. 1.5 mm long, the lobes ca. 7–9 × 1.5 mm, ensiform, sericeous-pubescent. Corolla unknown; androecium and gynoecium unknown. Fruit inserted on the accrescent bracteole; calyx persistent, expanding to 9 mm long.

Distribution. *Keraunea confusa* is endemic to Brazil and to the state of Minas Gerais (Fig. 2).

Habitat. All collections of *K. confusa* are from karstic (limestone) areas, where plants have been collected growing over rocks and vegetation in the understory of Caatinga seasonally dry tropical forest vegetation.

Conservation status. *Keraunea confusa* is known from two localities and has an AOO of ca. 12 km^2. Two of the known collections (*Lombardi & Salino 1819*, *Lombardi 2107*) were made within Parque Nacional Cavernas do Peruaçu, which includes extensive karst limestone habitat suitable for the species. We know of no specific threats to this species but provide a preliminary assessment as Vulnerable (VU D2) because of the species' few known localities (IUCN 2019).

Etymology. The epithet refers to the confusion that has surrounded the taxonomic history of this species, which was both included within the original circumscription of the type species and the placement of the genus in the wrong family by Cheek and Simão-Bianchini (2013).

Identification notes. *Keraunea confusa* is one of two species of the genus with brochidodromous venation, the other of which is *K. bullata*. It is distinguished from *K. bullata* by its generally bigger leaves measuring 9.5–17 cm long (versus 4.2–10.5 cm long), rugose (versus bullate) leaf texture and by the tertiary veins, which are plane to the lower leaf surface (versus raised).

Additional specimens examined (paratypes). Brazil. Minas Gerais: Mun. Manga, BR-135, entre Montalvânia e Manga, afloramento de calcário do lado esquerdo a ca. 400 m da rodovia sentido Manga-Januária, 14°30'44.8"S, 44°10'31.8"W, 5 Dec. 2022, *D. Cardoso et al. 4916* (ALCB, HUEFS, TCD, RB), *D. Cardoso et al. 4918* (ALCB, HUEFS, TCD, RB); Mun. Januária, distrito de Fabião, junto ao Abrigo do Malhador, 15°7'16"–15°8'57"S, 44°15'20"–44°14'13"W, 26 Oct. 1997, *J.A. Lombardi 2107* (BHCB [BHCB017210], K [K000593363]).

5. *Keraunea velutina* Moonlight & D.B.O.S.Cardoso, sp. nov.

urn:lsid:ipni.org:names:77314431-1
Fig. 7

Diagnosis. Most similar to *Keraunea capixaba* but differing in its velutinous indumentum on the stems, side shoots and lower leaf surface (versus glabrescent); its strigose indumentum on the upper leaf surface (versus glabrescent); its elliptic to narrowly lanceolate leaves on the side shoots (versus ovate).

Type. Brazil. Rio de Janeiro: Mun. Cardoso Moreira, Santíssimo, Fazenda Borges, [21°29'S, 41°37'W], 10 Sep. 2013, *J.G. Costa 257* (holotype: RB [00852871]).

Description. Scandent shrub or liana, size unknown. Stems cylindrical, hollow, 2–3 mm in diameter, rarely branching, velutinous-pubescent; internodes 2–5.9 cm long; side shoots 2.2–4.7 cm long velutinous-pubescent. Leaves of the main stem with the blades 7.9–8.1 × 2.7–3.1 cm, lanceolate, velutinous-pubescent, the venation pinnate, camptodromous, with 6–8 secondary veins; the base obtuse, the margins entire, ciliate, the apex attenuate; petioles of leaves on main stem 10–11 mm long, distinctly curved to 90° ¼ of the way along their length. Side shoots with 6–8 leaves, these pro-

HERBÁRIO RB
596863
JARDIM BOTÂNICO
DO
RIO DE JANEIRO

DADOS DE COLETA

Família: Solanaceae

Procedência: RJ - Cardoso moreira, Santíssimo, em fragmento de mata, Fazenda Borges.

Observações: planta trepadeira volúvel; corola branca, ca. 2.5 cm.

Coletor: J.G. Costa 257

Data: 10/09/2013

Figure 7. Holotype of *Keraunea velutina* Moonlight & D.B.O.S.Cardoso, *J.G. Costa 257* (RB [00852871]).

gressively larger along the shoot; blades 0.5–3.5 × 0.3–1.7 cm, elliptic, rarely or lanceolate or obovate, strigulose-pubescent above, velutinous below, the base cuneate to rounded, the margins entire, ciliate, the apex rounded to attenuate. Inflorescence corymbose, with 2–4 flowers; free portion of the peduncle 3–5 mm long; pedicel 0.5–1.5 cm long, the remainder adnate to the bracteole, sericeous-pubescent; bracteole 2–3.8 × 0.7–1.6 cm, inserted ca. ⅓ of the way along the pedicel or rarely lacking, ovate, velutinous- pubescent, the venation as the leaves, the base short-cuneate, margin entire, ciliate, the apex attenuate. Flowers 5-merous. Calyx with the tube campanulate, ca. 1.5 mm long, the lobes 0.7–1.4 × 6.7–12 mm, ensiform, velutinous-pubescent. Corolla with the tube campanulate, 5–5.9 mm long, the lobes 14 × 7 mm, elliptic, glabrous. Stamens epipetalous, inserted at the base of the corolla tube, filaments 3–4 mm long, anthers ca. 7 mm long, connective extending to 1.3 mm; ovary subglobose, 2-locular, the locules biovulate; style single, conduplicate, unbranched; stigmas 2, truncate. Fruit inserted on the accrescent bracteole; calyx persistent, expanding to 15 mm long.

Distribution. *Keraunea velutina* is endemic to Brazil and known only from the type from Cardoso Moreira municipality in the state of Rio de Janeiro (Fig. 2).

Habitat. The single specimen known of *K. velutina* was collected within a forest fragment around isolated inselbergs. Cardoso Moreira municipality includes several granitic inselbergs and deforestation appears reduced around these compared to the surrounding land. We suspect that, like the similar *Keraunea capixaba*, this species was collected scrambling over rocks at the base of an inselberg.

Conservation status. *Keraunea velutina* is known from a single specimen collected within a small forest fragment. Forest cover within Cardoso Moreira municipality declined from 5.2% in 1985 to 4.0% in 2012 before recovering to 4.6% by 2021 (Mapbiomas 2022). This picture is however complex, with Google Earth imagery showing that deforestation of primary forest is continuing in some areas, but forest is recovering in other areas (Google Earth Pro 2020). As such, due to single collection with imprecise locality information from a largely deforested municipality, we provisionally assess *K. velutina* as Critically Endangered (CR B1 B2 a b ii) under IUCN criteria (IUCN 2019).

Etymology. Named for the plant's velvety indumentum.

Identification notes. *Keraunea velutina* is a distinct species easily distinguished from all others in the genus by the dense, velvety indumentum of the stems and lower leaf surfaces. It is also distinctive in its side shoots with more numerous leaves than other members of the genus (6–8 versus 2–5), which are almost all elliptic (versus variously ovate to broadly ovate).

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Appendix 1

Index to collections

Only first collectors are cited.

Cardoso, D. 4902, 4904, 4909, 4910, 4912 (brasiliensis); 4916, 4918 (confusa)
Costa, J.G. 257 (velutina)
Covre, C. s.n. (capixaba)
Demuner, V. 3799 (capixaba)
Folli, D.A. 7117, 7273 (capixaba)
Guedes, D.M. 9176 (bullata)
Gurtler, J. 371 (capixaba)
Lombardi, J.A. 1819, 2107 (confusa)
Moreíra de Assis, A. 3340 (capixaba)
Mori, S.A. 11534 (bullata)
Passos, L. 5263 (brasiliensis)
Pereira-Silva, A. 9111 (brasiliensis)
de Queiroz, L.P. 5972, 12707 (brasiliensis)
Rose, J.N. 19979 (bullata)
Santos, T.S. 2139 (capixaba)
Siqueira, G.S. 891, 893 (capixaba)