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Research Article

Euonymus pushpagiriensis (Celastraceae), a new species from the central Western Ghats of Karnataka, India

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Abstract

Euonymus pushpagiriensis **sp. nov.**, an understorey tree species from the montane (Shola) forests of Kodagu District of Karnataka is described and illustrated. The species is morphologically distinct from all other species of *Euonymus* reported from the Western Ghats and the rest of India, in having sub-sessile, ovate leaves with rounded to sub-cordate leaf base. This species is, so far, known from the Kodagu District of the State of Karnataka.

Key words: Endemic, *Euonymus*, India, Kodagu, Western Ghats

Introduction

The genus *Euonymus* is represented by roughly 145 species of woody plants. It is distributed in the tropical and temperate regions of the Northern Hemisphere, mainly across North America, Europe, South and South East Asia. Its distribution range, however, also extends into some of the tropical regions of Southern Hemisphere including Madagascar, Papua New Guinea and north-eastern Australia (POWO 2024). The first comprehensive revision of the genus *Euonymus* was carried out by Blakelock (1951) and more recently by Ma (2001). The genus is characterised by woody and mostly erect (rarely scandent or trailing) habit, opposite or sub-opposite leaves, four or five-merous flowers produced in axillary (or rarely cauliflorous) inflorescences, stamens inserted on the periphery of the disc, loculicidal dehiscent capsules and arillate seeds (Li et al. 2024).

In India, the genus is represented by ca. 30 species (Ramamurthy 2000; Murugan and Manickam 2005; Murugan and Manickam 2006), of which ca. 20 species are concentrated in the north east India, a few of which also extending their distribution to the Western Himalayas, while two species are distributed in Andaman and Nicobar Islands. Eight species of *Euonymus* are reported from south India, all of which are distributed in the tropical wet evergreen forests of the Western Ghats and exhibit geographic distributions that are restricted to this region, with the exception of *Euonymus laxiflorus*, which shows disjunct distribution in southern China.

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Materials and methods

From year 2010 to 2014, plot-based inventory of woody flora of the evergreen forests of the Western Ghats, was carried out as part of the PhD study of the first author. Details about the sampling methodology and sampling locations are presented in Page and Shanker (2018) and Page and Shanker (2020). During this period, while compiling an inventory of the Central Western Ghats in the Kodagu District of Karnataka, we found a species of *Euonymus* that was morphologically distinct from the hitherto described species from the Western Ghats. To confirm the taxonomic novelty of the species, we compared its morphological characters with the rest of the species reported from Indo-China, based on the literature (Gamble 1915; Blakelock 1951; Ramamurthy 2000; Ma 2001; Murugan and Manickam 2005; Murugan and Manickam 2006; Li et al. 2024). We found that the population from Kodagu is morphologically distinct from all the species described so far, based on the leaf and inflorescence characters. It is, therefore, described here as a new species. The description provided is based on field observations of four individuals from two different locations. Detailed colour plates of the new species, as well as its morphologically most closely related species, are provided to aid identification in the field.

Taxonomic treatment

Euonymus pushpagiriensis **N.V.Page & T.U.Thackeray, sp. nov.**
urn:lsid:ipni.org:names:77357224-1
Figs 1–4

Type. India. • Karnataka State, Kodagu District, Mandalpatti, alt. 1240 m, 12°32'23.02"N, 75°42'10.66"E, 28 April 2013 (fl.), *N.V.Page 28413* (holotype: MH!; isotypes MH!, JCB!)

Diagnosis. *Euonymus pushpagiriensis* can be distinguished from other species of *Euonymus* from the Western Ghats based on its sub-sessile leaves (petiole ca. 1 mm long) and ovate lamina with rounded to sub-cordate base. In contrast, all the other species of *Euonymus* from the Western Ghats of south India exhibit leaves with a distinct petiole (greater than or equal to 3 mm length) and elliptic, rarely ovate lamina with obtuse, acute or cuneate base.

E. pushpagiriensis (Figs 1–4) is morphological closely related to *E. angulatus* (Figs 5, 6) in having leaf margins entire and young branches and peduncles four angled. It can be easily distinguished from the latter, based on petiole length which are less than or equal to 1 mm (as opposed to petioles more than or equal to 3 mm in *E. angulatus*), rounded to sub-cordate leaf base (leaf base acute or obtuse, but never rounded in *E. angulatus*) and inflorescences borne in the axils of terminal pair of leaves (inflorescences extra-axillary or from the axils of older leaves from the last year's growth in *E. angulatus*). Morphological differences between these two species are provided in Table 1.

Description. Understorey, evergreen shrubs or small trees, up to 3 m tall. Twigs glabrous, narrowly 4-winged, quadrangular in cross section, bud scales minute, usually persistent at nodes. ***Leaves*** opposite, lamina glabrous, thick, coriaceous, 3.5–5.5 × 1.5–2.7 cm, ovate; base rounded or subcordate; apex

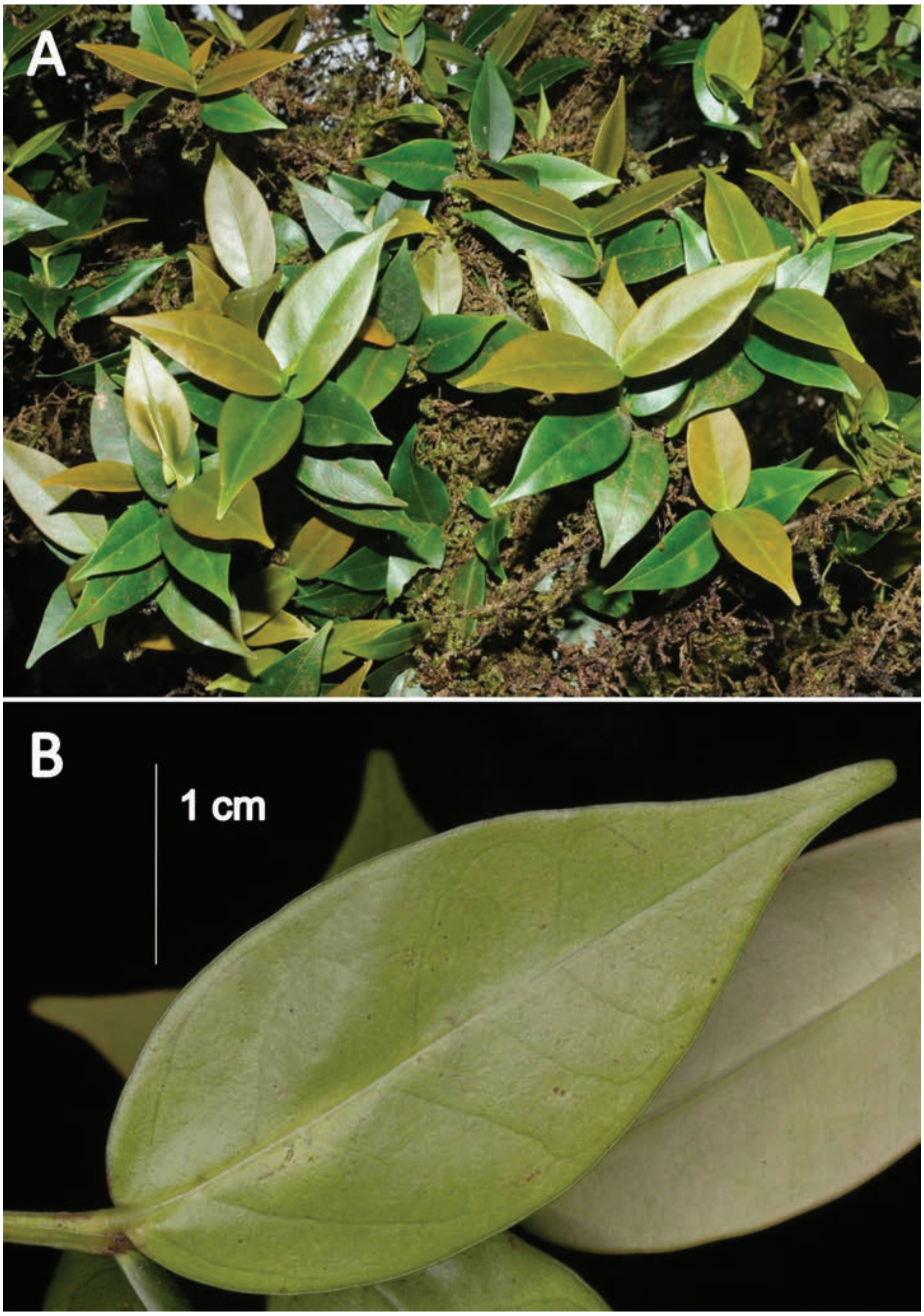

Figure 1. *Euonymus pushpagiriensis* **A** branches with light brown young and dark green mature leaves **B** abaxial surface of a leaf with sub-sessile nature, rounded leaf base, entire leaf margin, inconspicuous nerves and acuminate leaf apex with obtuse tips. Note the ducurrent nature of petiole which forms narrow wings extending along the inter-node. Photographs by Navendu Page.

acute to acuminate, rounded at the tip; margin entire, obscurely revolute; petiole stout, ca. 1 mm, decurrent in to the wings of the stem; mid-vein distinctly raised adaxially, as well as abaxially; lateral nerves inconspicuous, 4–7 on each side of mid-vein, looping at the margin. ***Inflorescences*** compound dichasium, solitary, borne in the axils of the terminal leaves; primary peduncles four angled, 1.3–1.7 cm long; secondary peduncles up to 0.5 cm long; bracts at the base of primary and secondary peduncles, lanceolate,1–1.5 mm long.

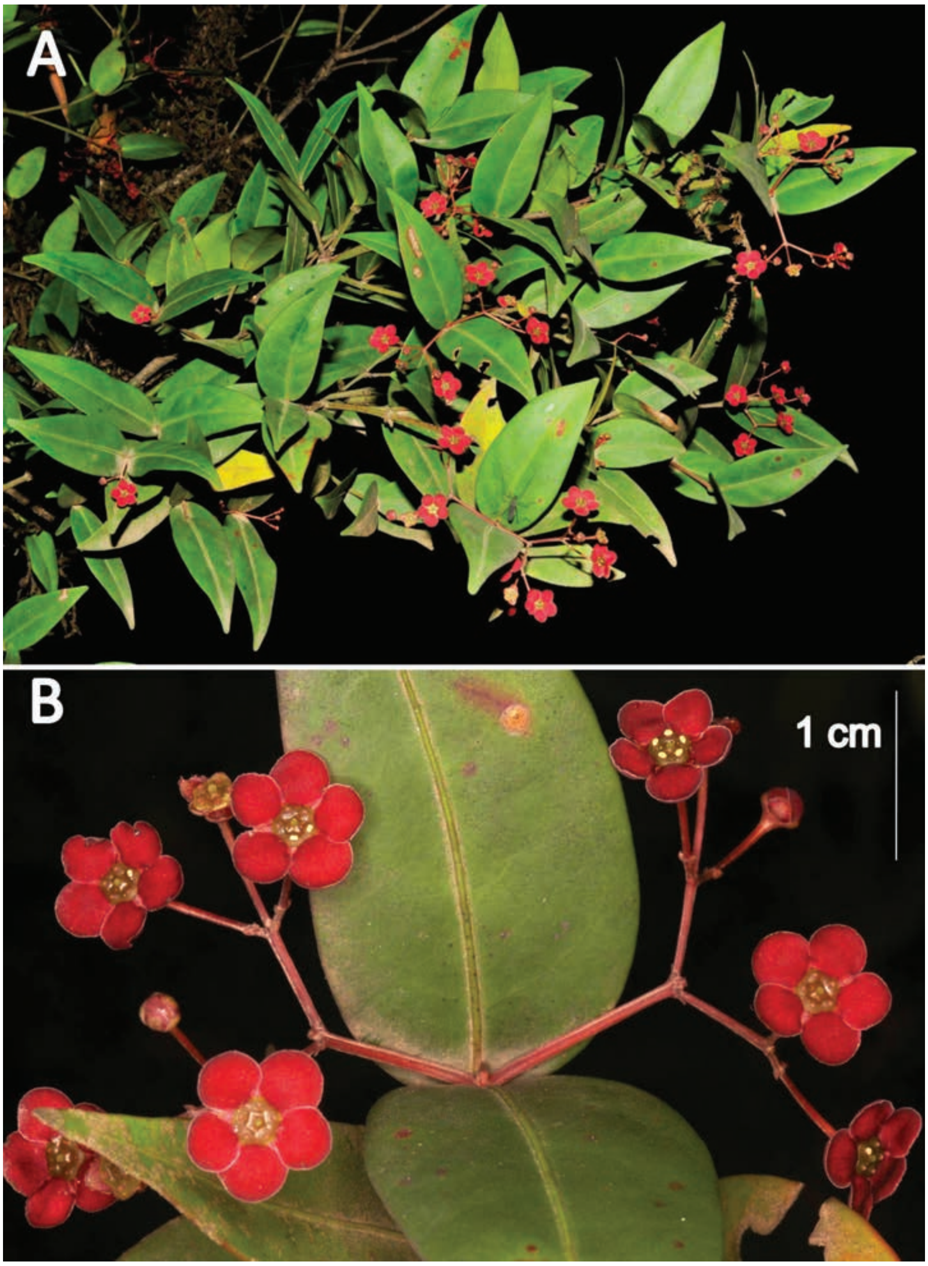

Figure 2. *Euonymus pushpagiriensis* **A** branches with inflorescences borne in the axils of terminal pairs of leaves **B** dichasial inflorescences showing the four angled primary and secondary peduncles. Photographs by Navendu Page.

Flowers 6–15 per inflorescence, 5-merous, ca. 7 mm in diameter; sepals subequal, subround, 1–1.5 × 0.5–1 mm, margin erose; petals subround, 2–2.5 × 2.5–3 mm, red, margin white, finely crenulate; disc 5-lobed, ca. 2.5 mm in diameter; stamens 5, inserted in the middle part of the lobes of the disc, filaments subsessile; ovaries superior, 5-angled, stigmas round, short; ovules 2 per cell. ***Capsules*** obovoid, with 5 angles and shallowly grooved, apex concave, 1.4–1.6 × 1.1–1.3 cm, opening into 5-lobes at maturity. ***Seeds*** (1) 2 in each cell, ellipsoid, 5–6 × 4–5 mm, orange, partially covered by orange arils at base.

Additional specimens examined. INDIA. • Karnataka State: Kodagu District, Pushpagiri Peak, Pushpagiri Wildlife Sanctuary 12°39'42"N, 75°41'05"E, alt. 1550 m, 29 xii 2015, *N.V.Page 291215* (JCB).

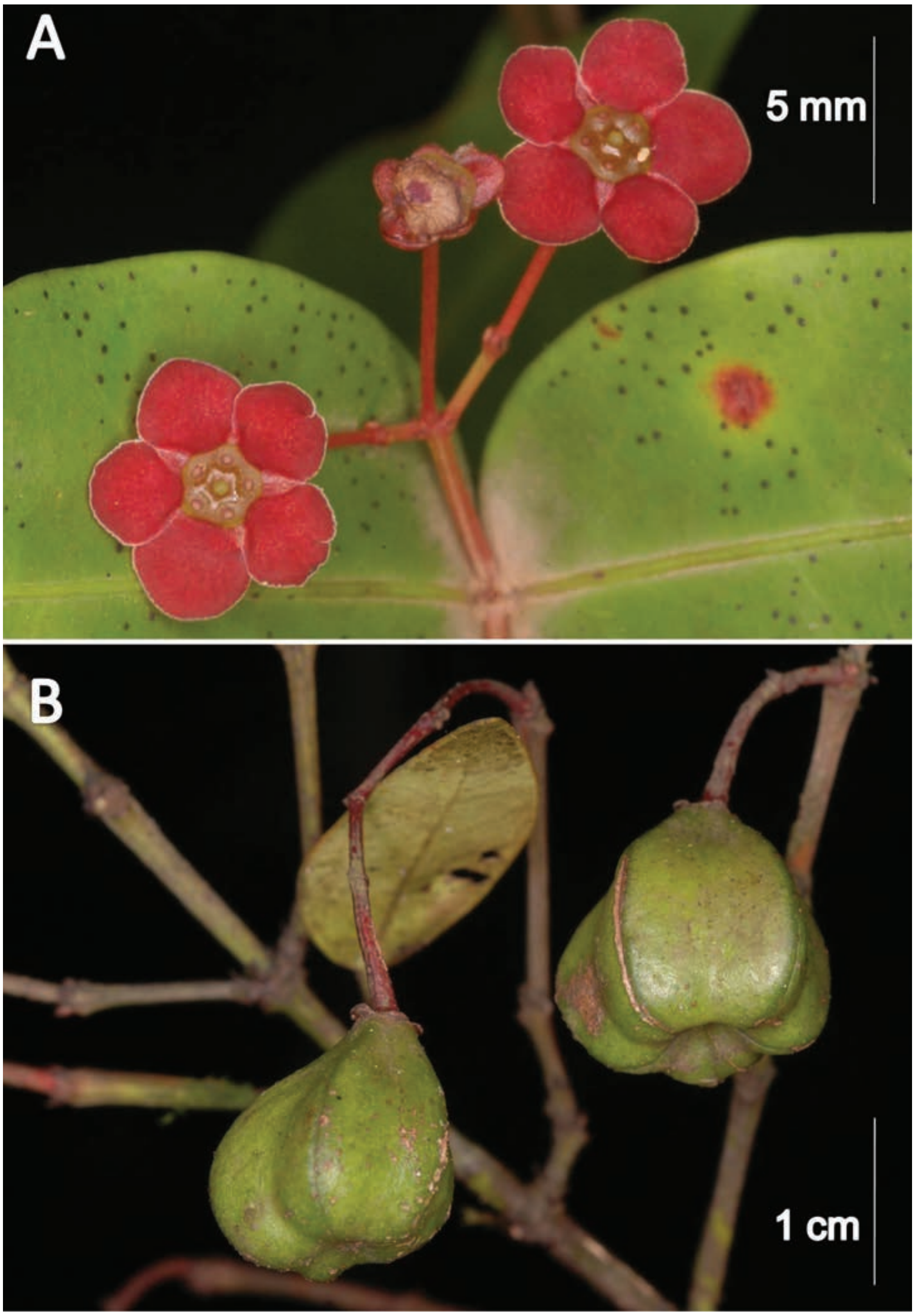

Figure 3. *Euonymus pushpagiriensis* **A** five-merous flowers with pentagonal disc, five angled ovary and stamens **B** immature capsule. Photographs by Navendu Page.

Distribution. *Euonymus pushpagiriensis* is so far known from two localities and is endemic to the Kodagu District of Karnataka.

Ecology. The species is distributed in the understorey or the edge of montane evergreen 'Shola' forests between 1200 to 1550 m elevation. The species was found to be growing in association with *Nothopegia* sp., *Actephila excelsa*, *Memecylon* sp. and *Syzygium lanceolatum*, amongst others. The species on both occasions was observed growing at the crest of the west-facing slopes of the Western Ghats.

Phenology. *Euonymus pushpagiriensis* produces young leaves in the month of January. Flowering was observed from late April to May while the fruiting period starts from June and the fruits mature in the months of December and January.

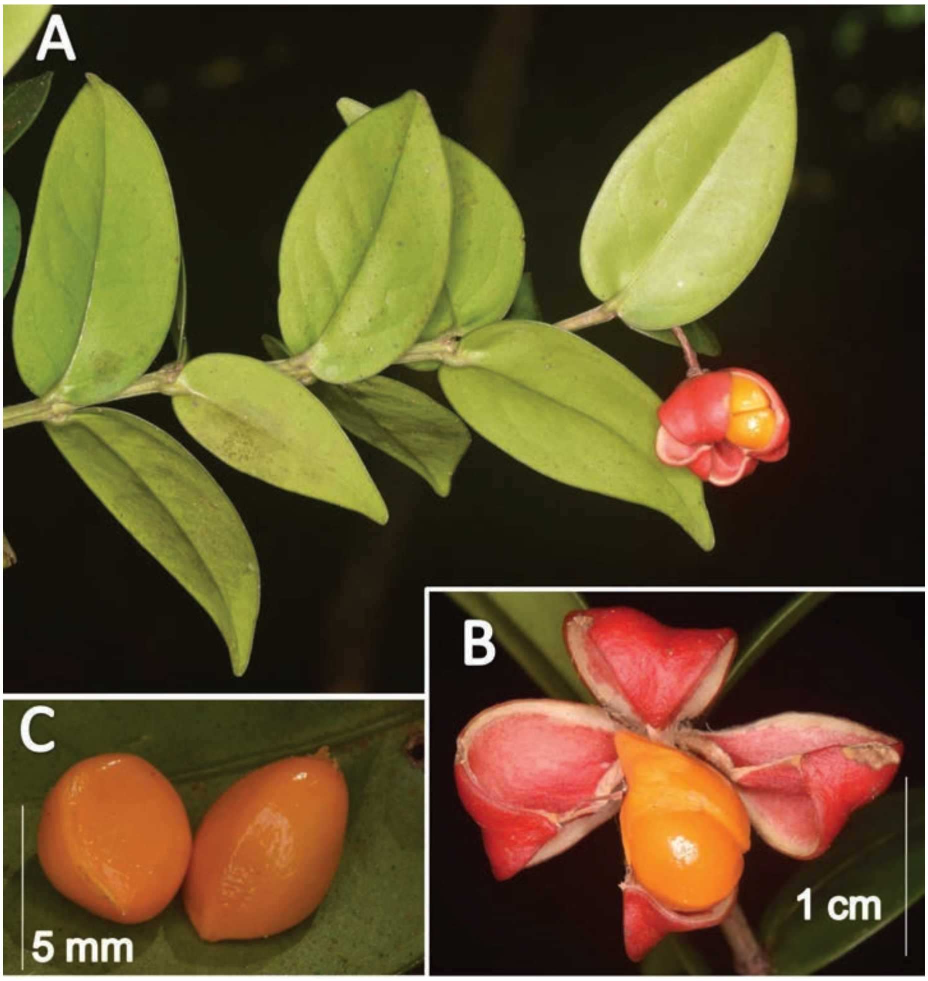

Figure 4. *Euonymus pushpagiriensis* **A** branch with mature dehisced capsule **B** dehisced capsule with two arillate seeds in a cell **C** seeds with aril removed. Photographs by Navendu Page.

Table 1. Key characters that distinguish *Euonymus pushpagiriensis* sp. nov. from its morphologically closely-related species *Euonymus angulatus*.

Character	*E. angulatus*	*M. pushpagiriensis*
Petiole	≥ 3 mm long	≤ 1 mm long
Leaf lamina shape	Elliptic	Ovate- lanceolate
Leaf base	Acute or obtuse, never rounded or sub-cordate	Rounded or sub-cordate
Leaf margin	Usually entire, rarely with a few serrations, not revolute	Always entire, obscurely revolute
Inflorescence	Borne from axils of older leaves from the last year's growth	Borne only in the axils of terminal pair of leaves
Peduncle	Usually drooping, flexuose	Erect, rigid
Pedicel	Curved upwards	Erect, not curved
Capsule	Turbinate, deeply 5-lobed, attenuate at the base	Obovoid, with 5 angles and shallow grooves
Distribution	Mid to high (1000–1600 m) elevation forests on the windward slopes of Nilgiri and south Western Ghats of Kerala State	High (1200–1550 m) elevation forests of Pushpagiri mountain range in the Kodagu District of Karnataka State

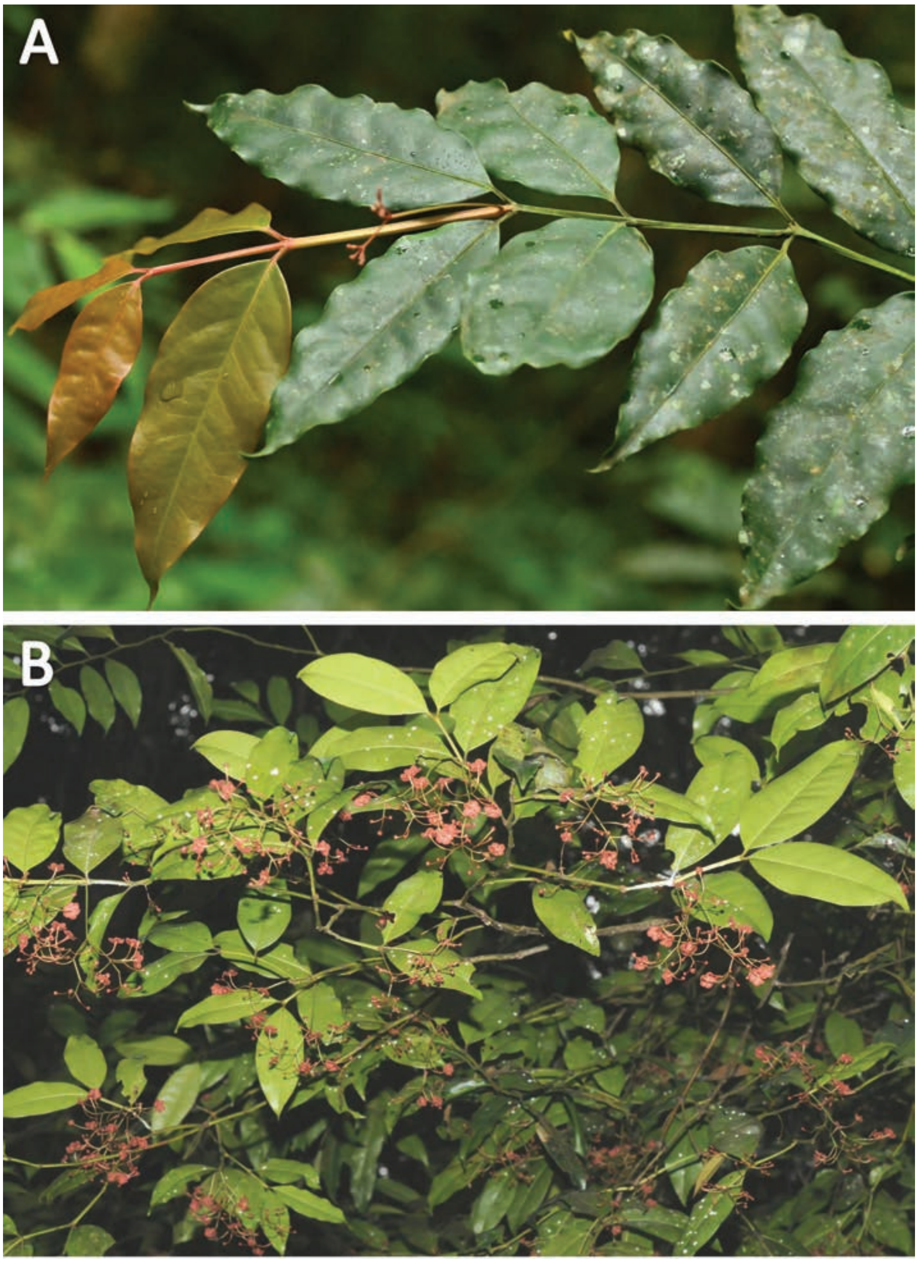

Figure 5. *Euonymus angulatus* **A** dorsal view of branch with young inflorescences **B** ventral view of branches with mature inflorescences. Photographs by Navendu Page.

Etymology. The specific epithet refers to the type locality of species – Pushpagiri which is the name of the second highest peak in Kodagu District and the fourth highest peak in the State of Karnataka and also the name of the Wildlife Sanctuary in which the peak the located. The species is, so far, known only from Pushpagiri Wildlife Sanctuary and its adjacent areas.

Provisional conservation status. The species is currently known from two locations within the Kodagu District of Karnataka State. The Area of Occupancy (AOO), as per the IUCN Red List guidelines, is estimated to be 8 km^2. Based on the geographic range (Criteria B2), the species qualifies for the Critically Endangered category. However, the species does not meet two of the three conditions required for to qualify for the threatened category. It satisfies only the condition (a) which is that of the number of locations being less than five.

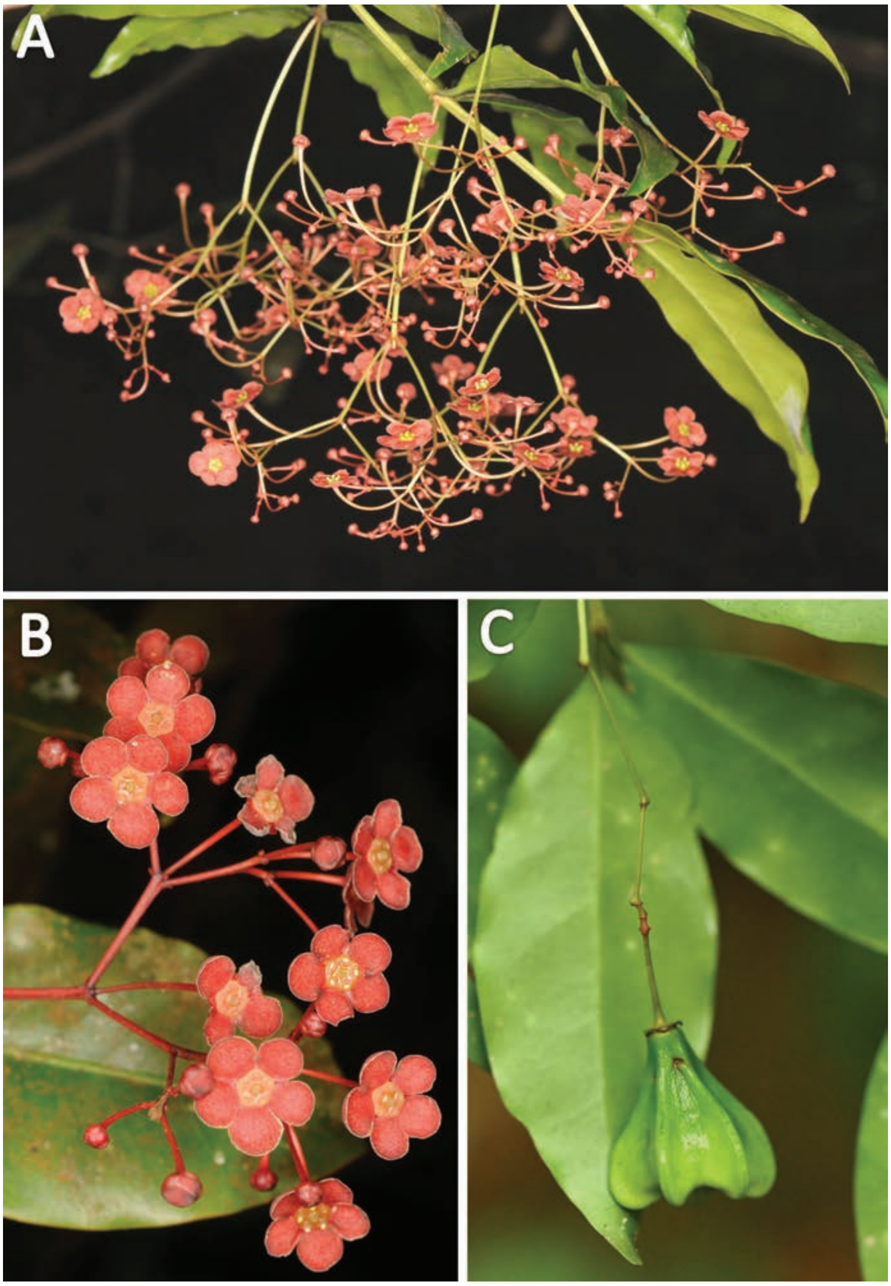

Figure 6. *Euonymus angulatus* **A** inflorescences showing the drooping or pendulous nature **B** flowers **C** fruit. Photographs by Navendu Page.

There is no evidence to suggest a continuous decline (condition b) or extreme fluctuations (condition c) in range size or number of locations. Hence, *Euonymus pushpagiriensis* is provisionally assigned 'Near Threatened' category.

Acknowledgements

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

Persicaria zhenaiguoi (Polygonaceae, Persicarieae), an overlooked new species from Dabie Mountains, central China

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Abstract

Persicaria zhenaiguoi Bo Li, a remarkable new species discovered from the summit of Tiantangzhai Peak of Dabie Mountains in Hubei Province, central China, is described and illustrated. Based on its spicate inflorescences, ciliate ocreae, and the absence of prickles, the species is placed in *P.* sect. *Persicaria*. Within this section, *P. zhenaiguoi* most resembles *P. orientalis* and *P. viscosa* in gross morphology, particularly in the presence of densely spreading villus throughout. However, the new species can be easily distinguished from these two similar taxa by its nearly sessile leaves, which are lanceolate in shape with broadly cuneate to rounded bases, membranous ocrea with a small circle of green leaf-like wing, sparse and interrupted inflorescences, glabrous peduncles, greenish tepals, and ovoid achenes with grooved surfaces. Diagnostic characteristics, along with comparative photographs of the three related species, are provided, as well as a detailed morphological description and information on the distribution and habitat of the new species.

Key words: Buckwheat family, morphology, ocrea, Polygonoideae, taxonomy

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Introduction

Persicaria Mill. is one of the largest genera in the buckwheat family (Polygonaceae) and belongs to the tribe Persicarieae, which also includes *Bistorta* Mill. and *Koenigia* L. (Galasso et al. 2009; Sanchez et al. 2011; Schuster et al. 2015). The genus includes approximately 100 species, primarily annual or perennial herbaceous plants, and is widely distributed around the world (Brandbyge 1993; Freeman 2005; Galasso et al. 2009). Within the genus, six sections have been proposed: sect. *Persicaria*, sect. *Amphibia* Tzvelev, sect. *Cephalophilon* (Meisn.) H.Gross, sect. *Echinocaulon* (Meisn.) H.Gross, and sect. *Tovara* (Adans.) H.Gross, and sect. *Truelloides* Tzvelev (Galasso et al. 2009). However, the sole species of sect. *Truelloides* Tzvelev, *P. bungeana* (Turcz.) Nakai ex Mori, has been tested to be a member of the sect. *Persicaria* in previous molecular phylogenetic analyses (Min et al. 2013; Zhai 2021) and the monophyly of the other five sections were always supported in molecular phylogenetic analyses (Kim and Donoghue 2008; Schuster et al. 2015; Cao et al. 2022, 2023).

Among these sections, species of sect. *Persicaria* can be distinguished from other *Persicaria* taxa by having a combination of characteristic features, including: usually glabrous stems without prickles, lanceolate simple leaves, tubular ocreae typically with truncate and ciliate apex, spicate inflorescences with few to many flowers, styles that are not deflexed and have a hooked apex, and *Persicaria*-type pollen grains with 20 circular pores and a reticulum (Hedberg 1946; Haraldson 1978; Brandbyge 1993; Li 1998; Li et al. 2003; Kim and Donoghue 2008). In China, 23 species were originally recorded in *Polygonum* sect. *Persicaria* (Mill.) Meisn. (≡ *Persicaria* sect. *Persicaria*) (Li 1998; Li et al. 2003). However, following the exclusion of *P. amphibia* (L.) Gray (which belongs to sect. *Amphibia*), the inclusion of *P. bungeana* (which should be transferred from sect. *Truelloides*), and the addition of two recently described species, i.e., *P. wugongshanensis* Bo Li (Li 2014) and *P. lankeshanensis* T.J.Liang & Bo Li (Liang and Li 2014), there are now 25 species of sect. *Persicaria* recognized in China.

During field surveys in the Dabie Mountains of central China from 2022 to 2023, we encountered several populations of an unknown *Persicaria* plant at the summit of Tiantangzhai Peak (Fig. 1A) in Yingshan County of Hubei Province, which is morphologically remarkable in having dense spreading hairs throughout and a small ring of green, leaf-like wing at the apex of the ocrea (Fig. 1B–E). Based on its lanceolate leaves with broadly cuneate to rounded bases, spicate inflorescences, ciliate ocreae, and the absence of prickles, we confirmed that it is a member of the sect. *Persicaria*. After thorough morphological comparisons with congeneric taxa, a review of relevant literature, and examination of herbarium specimens, we found that the plant is most similar to *P. orientalis* (L.) Spach and *P. viscosa* (Buch.-Ham. ex D.Don) H.Gross ex Nakai but different in many aspects (Fig. 2). Thus, we have concluded that this plant represents a new, previously undescribed species of *Persicaria*, namely *P. zhenaiguoi* Bo Li, which is formally reported here.

Materials and methods

Field surveys were carried out in the Dabie Mountains, located at the border between Hubei and Anhui provinces, central China, from June to September in 2022 and 2023, respectively. Morphological observations and descriptions of the putative new species were based on living plants in Yingshan County and herbarium specimens collected from the type locality. Its morphological variation was measured using a ruler and a micrometer. High-resolution images of type materials for all *Persicaria* taxa, including their synonyms, were consulted via JSTOR Plant Science (http://plants.jstor.org), and digital images of all *Persicaria* species recorded in China were examined through the Chinese Virtual Herbarium (https://www.cvh.ac.cn/). Morphological comparisons with *P. orientalis* and *P. viscosa* were critically evaluated using specimens deposited in CSH, GZTM, HBNU, HENU, HIB, IBK, IBSC, IMC, JJF, JMSM, JXCM, KUN, PE, QFNU, and SZ [acronyms according to (Thiers 2020)], as well as living plants that we have observed.

Taxonomic treatment

***Persicaria zhenaiguoi* Bo Li, sp. nov.**
urn:lsid:ipni.org:names:77357225-1
Figs 1, 2A1–A5

Diagnosis. Morphologically, *P. zhenaiguoi* is superficially most similar to *P. orientalis* and *P. viscosa* in the indumentum characteristic, but can be clearly distinguished from the latter two taxa by its nearly sessile leaves, which are lanceolate in shape with broadly cuneate to rounded bases, membranous ocrea with a small circle of green leaf-like wing, sparse and interrupted inflorescences, glabrous peduncles, greenish tepals, and ovoid achenes with grooved surfaces (Fig. 2, Table 1).

Type. China • Hubei Province, Huanggang City, Yingshan County, Tiantangzhai Town, Dabie Mountains, in the grassland at the summit of Tiantangzhai Peak, 31°06'21.44"N, 115°46'22.60"E, alt. 1712 m, 10 July 2023, *X.X. Zhu et al. ZXX23818* (***holotype*****:** HITBC0122106, ***isotype*****:** IBSC0923376).

Description. Herbs annual. Stems erect, slender, angulate, 20–50 cm tall, densely spreading villous. Petiole connate with lower parts of ocrea, nearly absent; Leaf blade lanceolate, 2.8–5.3 × 0.6–1.1 cm wide, apex acuminate, base broadly cuneate to rounded, margin densely ciliate, both surfaces densely villous, midvein slightly hollow on the adaxial surface and rise on the abaxial surface, lateral veins 8–10 pairs. Ocrea tubular, membranous, 0.6–1.1 mm long, densely villous, margin truncate with long ciliate and a small circle of green leaf-like wing. Inflorescence terminal or axillary, spicate, 2.8–5.1 cm long, slender, interrupted below, usually several spikes aggregated and panicle-like; peduncle glabrous. Bracts green, funnel-shaped, 2.8–4.6 mm long, sparsely villous, margin long ciliate, each 2–4 flowered. Pedicels slightly longer than bracts. Perianth greenish, 5-parted; tepals elliptic, 2.3–3.4 mm. Stamens 8, included. Styles 3, connate to below middle; stigma capitate. Achenes included in persistent perianth, 1.6–2.1 × 0.8–1.2 mm, brown, shiny, long ovoid, trigonous, surfaces grooved.

Phenology. Flowering and fruiting was observed synchronously from July to October.

Etymology. The specific epithet “*zhenaiguoi*” is dedicated to Professor Ai-Guo Zhen, in recognition of his significant contributions to the study of the local flora and biodiversity in Yingshan County.

Vernacular name. The Chinese name of the new species is “甄氏蓼”, and the pronunciation of the Chinese Pinyin is zhēn shì liǎo.

Distribution and habitat. *Persicaria zhenaiguoi* can be found above an altitude of 1.600 m, in the moist grassland at the summit of Tiantangzhai Peak, one of the main peaks of the Dabie Mountains, which are located on the border between Hubei and Anhui provinces (Fig. 3). This plant is typically found growing alongside species of *Dryopteris* Adanson and *Carex* L.

Preliminary conservation status. As currently known, this species has only been discovered from its type locality in the Tiantangzhai Peak of the Dabie Mountains, where it is distributed in a small area within the mountaintop region. Moreover, its habitat is increasingly threatened by the growing development of local tourism (author’s personal observation). Therefore, it should be categorised as critically endangered under criteria B and D following IUCN Red List Categories (IUCN 2012).

Taxonomic notes. Morphologically, the ocrea of all species within *P.* sect. *Persicaria* is tubular and membranous, with a truncate, mostly ciliate apex (Meisner 1856; Gross 1913; Steward 1930; Haraldson 1978; Tutin et al. 1991; Li et al. 2003; Freeman 2005). Before this, *P. orientalis* was the only species in this section known to typically have a circle of green, leaf-like wing at the apex of the ocrea (Fig. 2B3). *P. zhenaiguoi* is the second species to exhibit a similar

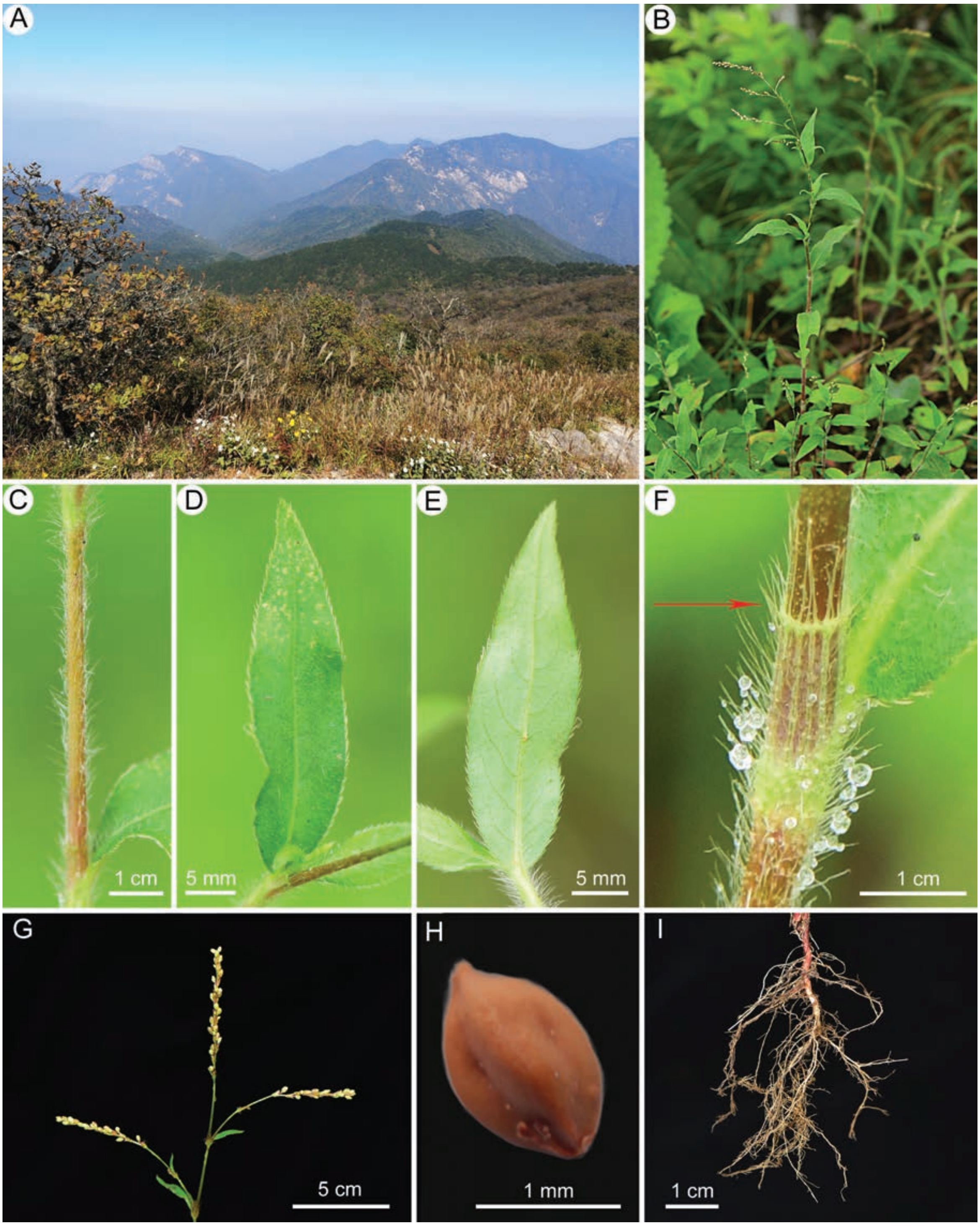

Figure 1. Habitat and morphology of *Persicaria zhenaiguoi* Bo Li, sp. nov. **A** habitat **B** habit **C** stem **D** adaxial view of leaf blade **E** abaxial view of leaf blade **F** ocrea (the red arrow shows the green leaf-like wing) **G** inflorescence **H** achene **I** roots (photographed by Dr. Xin-Xin Zhu).

structure, caused by the enlargement of the longitudinal veins at the apex of the ocrea (Fig. 2A3), although not as prominent as observed in *P. orientalis*. They also share the similar indumentum that are long spreading white hairs densely covering on stems, leaves as well as ocreae, but are clearly different from each other in plant size (Fig. 2A1, B1), leaf shape and size (Fig. 2A2, B2), inflorescence structure (Fig. 2A4, B4), as well as the fruit shape (Fig. 2A5, B5).

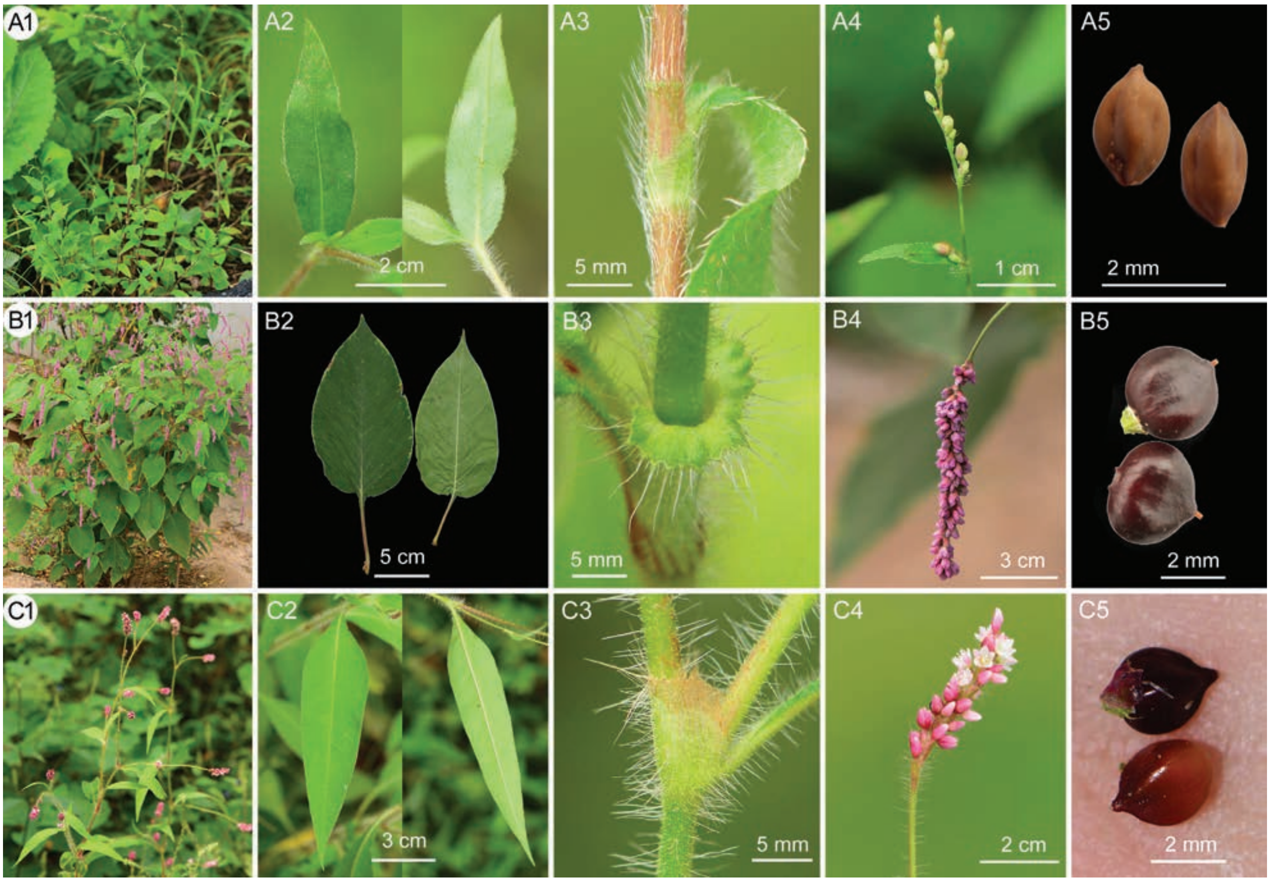

Figure 2. Morphological comparisons among *P. zhenaiguoi* (**A1–A5**), *P. orientalis* (**B1–B5**), and *P. viscosa* (**C1–C5**) **A1, B1, C1** habit **A2, B2, C2** leaves **A3, B3, C3** ocrea **A4, B4, C4** inflorescences **A5, B5, C5** achenes.

Table 1. Comparison of morphological characteristics among *P. zhenaiguoi*, *P. orientalis* and *P. viscosa*.

	P. zhenaiguoi	***P. orientalis***	***P. viscosa***
Plant height	0.2–0.5 m	0.8–2.2 m	0.4–0.9 m
Stems	slender, erect, densely spreading villous	robust, erect, densely spreading villous	ascending to erect, densely spreading villous and glandular hairy, odoriferous
Petioles	connate with lower parts of ocrea, nearly absent	1.7–11.5 cm	3.3–1.2 cm, leaf base long decurrent along petioles
Leaf blades	lanceolate, 2.8–5.3 × 0.6–1.1 cm	broadly ovate, 10.5–22.8 × 5.1–12.3 cm	lanceolate, 4.4–7.8 × 1.2–2.1 cm
Ocreae	apex with a small circle of green leaf-like wing	apex usually with large green leaf-like wing	apex truncate
Inflorescences	erect, slender, interrupted below	pendulous, densely flowered	erect, densely flowered
Peduncles	glabrous	densely hirsute	densely spreading villous and glandular hairy
Perianth	greenish	pink or white	pinkish
Achenes	long ovoid, trigonous, surfaces grooved	nearly orbicular, biconcave, surfaces grooved	broadly ovoid, trigonous, surfaces flat

Persicaria viscosa is another species having the same indumentum and much more similar to *P. zhenaiguoi* in gross morphology, but it differs from the latter in several aspects: its leaf bases are long decurrent along petioles (Fig. 2C2), the peduncles cover dense hirsute and glandular hairs (Fig. 2C1, C4), and the inflorescences are dense and pinkish (Fig. 2C4). Detailed morphological comparisons among these three taxa are listed in the Table 1.

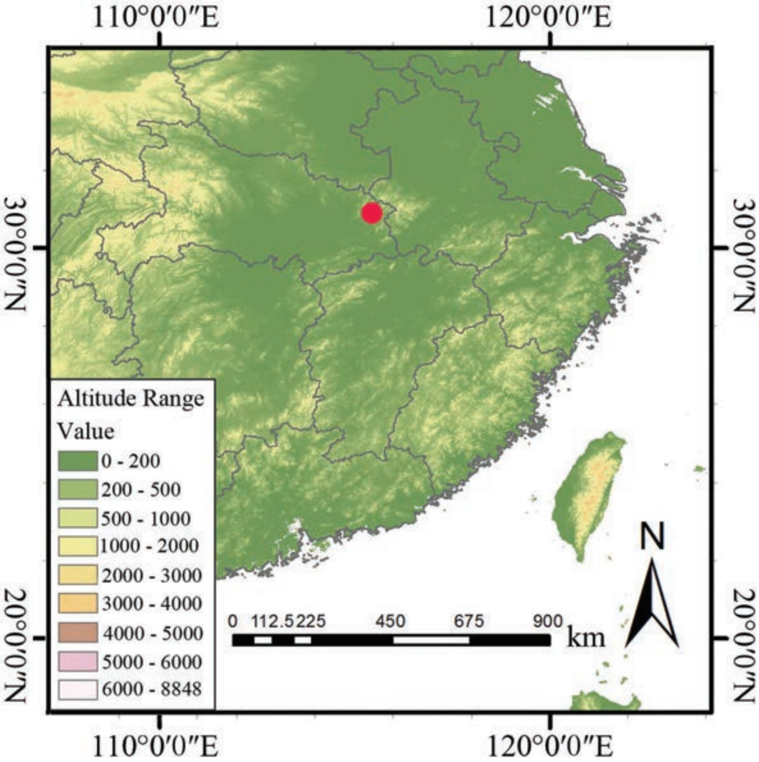

Figure 3. Distribution of *P. zhenaiguoi* (marked by the red circle).

It is worthy to mention that the habitat and distribution of *P. zhenaiguoi* are somewhat unusual, at least when comparing with other species in sect. *Persicaria* found in central and southern China. Based on our years of observation, species from sect. *Cephalophilon* and sect. *Echinocaulon*, such as *P. nepalensis* (Meisn.) H.Gross, *P. runcinata* var. *sinensis* (Hemsl.) Bo Li, and *P. thunbergii* (Siebold & Zucc.) H.Gross, are easily found in habitats like the summit of Tiantangzhai Peak (Fig. 1A). However, species from sect. *Persicaria* are rarely occurring at such high altitudes. At the same time, there has been a lack of comprehensive and in-depth surveys of the plant flora in the Dabie Mountains, especially in the mountaintop areas. This may explain why *P. zhenaiguoi* has likely been overlooked and not collected in the Dabie Mountains until now.

Additional specimens examined. *Persicaria orientalis*: CHINA • Anhui Province, Shucheng County, Xiaotian Town, 1 October 1951, *East China Workstation 4162* (PE00497378!); • Chongqing Municipality, Nanchuan County, Sanquan Village, alt. 640 m, 14 October 1985, *Z.Y. Liu 7429* (IMC0038461!); • Guangdong Province, Yangjiang City, Jiangcheng District, Hailing Town, 21°37'36.42"N, 111°58'8.87"E, alt. 27 m, 6 April 2021, *G.W. Tang et al. TangGW1343* (KUN1556765!); • Guizhou Province, Congjiang County, Doli Town, Panli Village, 25°35'14.35"N, 108°59'11.11"E, alt. 672 m, 21 September 2019, *K.T. Liu 522633190921914LY* (GZTM0096269!); • Hainan Province, Haikou City, Longhua District, Xue Village, 19°57'39.19"N, 110°20'57.89"E, alt. 15 m, 2 May 2018, *Y.T. Hou et al. 20180426580-1* (QFNU0048156!); • Hebei Province, Longhua County, Bugugou Town, alt. 993 m, 20 August 2013, *Group Six Z0272* (HBNU20001289!); • Heilongjiang Province, Qiqihar City, Longjiang County, 47°19'23"N, 123°11'41"E, alt. 131 m, 25 August 2019, *L.Y. Lin 2019082501* (JMS-

MC0000049!); • Henan Province, Xinxiang City, Huilong Village, 35°35'02"N, 113°35'57"E, alt. 369 m, 12 July 2018, *J.R. Li 368* (HENU1900368!); • Hunan Province, Nanyue District, Hengshan Nature Reserve, alt. 300 m, 1 September 2002, *Z.H. Hu 533* (PE00497445!); • Jiangsu Province, Suqian City, Siyang County, Longji Town, 33°20'40.36"N, 118°38'19.97"E, alt. 18 m, 3 August 2019, *Y.T. Hou et al. 20190803230-1* (QFNU0052420!); • Jiangxi Province, Fengchen City, Xiushi Town, grassland, 27°51'38.81"N, 115°53'15.04"E, alt. 423 m, 3 October 2019, *L. Cao 360981191003305LY* (JXCM0010118!); • Shandong Province, Zouping City, Xiyu Village, 36°47'17"N, 117°40'49"E, alt. 342 m, 4 August 2018, *J.L. Lan 201808037-1* (QFNU0047293!); • Shanxi Province, Wanrong County, Jiachun Town, 32°21'0"N, 110°37'0"E, alt. 566 m, 28 July 2020, *Y.J. Feng 201941325966* (QFNU0059553!); • Zhejiang Province, Jinyun County, Huzhen Town, Xiaxiang Village, 28°47'23"N, 120°12'58"E, alt. 194 m, 2 July 2013, *H.Y. Shou & Z.H. Wang SHY00909* (CSH0012891!).

Persicaria viscosa: China • Chongqing Municipality, Zhong County, Baishi Town, Huangjia Village, 30°20'17.78"N, 107°56'28.29"E, alt. 624 m, 30 May 2013, *Zhong County Team 500233-130530-519-03* (IMC0045792!); • Guangxi Province, Liuzhou City, Liujiang County, Jinde Town, Siliang Village, 24°15'44.59"N, 109°20'25.69"E, alt. 114 m, 14 August 2018, *Liujiang Team 450221180814022LY* (IBK00425346!); • Heilongjiang Province, Jiamusi City, Huachuan County, Shenjiadian Village, 46°34'39.68"N, 130°37'48.81"E, alt. 189 m, 8 September 2018, *C. Wang & Y.G. Peng WangCh532* (KUN1554918!); • Henan Province, Xinyang City, Shihe District, 32°6'52.15"N, 114°0'33.63"E, alt. 87 m, 8 June 2020, *X.X. Zhu et al. ZXX20942* (HIB0187735!); • Hubei Province, Hongan County, Xinhua Town, Zhangshan Village, alt. 80 m, 14 June 2019, *C.M. Tan et al. 19061418* (JJF00044259!); • Hunan Province, Shaoyang City, Dongkou County, alt. 350 m, 12 August 2004, *L.D. Duan 5337* (PE00640285!); • Jiangxi Province, Jiujiang County, alt. 250 m, 17 September 2005, *A.M. Dong 930* (SZG00002585!); • Jilin Province, Baishan City, Badaojiang District, 41°34'12.01"N, 126°34'33.24"E, alt. 311 m, 22 August 2019, *C.Q. Cao CaoChQ495* (KUN1487264!); • Yunnan Province, Baoshan City, Tengchong County, Qushi Town, 25°23'58"N, 98°50'54"E, 1820 m, 3 October 2009, *Y.F. Chen et al. 09209-3* (QFNU0056773!); • Shandong Province, Yantai City, Rizhao Village, 36°48'5"N, 121°18'55"E, alt. 18 m, 28 September 2015, *X.W. Xin Lilan859* (KUN1438272!).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

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

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Research Article

Schnabelia jiuzhaigouensis (Lamiaceae, Ajugoideae), a new species from Sichuan, China

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Abstract

Schnabelia jiuzhaigouensis C. Liu, F. Zhao & C.L. Xiang, a new species from north-eastern Sichuan, China, is described, based on both morphological and molecular phylogenetic evidence. Morphologically, the new species is mostly similar to *S. terniflora*, but can be readily distinguished by its habit, ovate to lanceolate-ovate leaf blades, the presence of 5–8 lateral veins on each side of the mid-rib and distinct characteristics of the floral structure, including oblong upper lip and lateral lobes of the lower lip, with the middle lobe being cuneate. In addition, the nutlets are puberulent and lack reticulate venation. Molecular phylogenetic analyses place the new species at a basal position within the genus *Schnabelia*. The new species is categorised as Data Deficient (DD) according to the IUCN Red List Categories and Criteria. A key to all species of *Schnabelia* is also provided.

Key words: Ajugeae, morphology, new species, *Schnabelia*, taxonomy

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Introduction

Schnabelia Hand.-Mazz. (Lamiaceae, Ajugoideae) is a small genus endemic to China. The genus was first described by Handel-Mazzetti (1921), based on specimens collected from Hunan Province in central China. The taxonomic placement and circumscription of *Schnabelia* have long been debated. Initially, in the traditional taxonomic treatment (Handel-Mazzetti 1921; Chen 1977; Chen and Gilbert 1994), the genus was placed within Verbenaceae, containing only two species (*S. oligophylla* Hand.-Mazz. and *S. tetrodonta* (Y.Z.Sun) C.Y.Wu & C.Chen), both characterised by 4-winged stems. However, based on the character of the deeply-lobed ovaries, P'ei (1932) transferred *Schnabelia* to the family Lamiaceae, associating it with *Ajuga* L. and *Teucrium* L., a classification supported by P'ei and Chen (1977). Cladistic analysis using morphological data by Cantino et al. (1999) revealed that the traditionally defined *Caryopteris* Bunge was not monophyletic and led to the transfer of three species of *Caryopteris* (i.e. *C. aureoglandulosa* (Vaniot) C.Y.Wu, *C. nepetifolia* (Benth.) Maxim. and *C. terniflora* Maxim) to *Schnabelia*. Subsequent molecular phylogenetic analyses (Huang 2002; Shi et al. 2003) further confirmed that at least the latter two species are closely related to *S. oligophylla*.

Recently, based on broad sampling and comprehensive evidence from morphological and molecular data, Xiang et al. (2018) reconstructed the backbone phylogeny of Ajugoideae. Their analyses confirmed the findings of Cantino et al. (1999), supporting the non-monophyly of the traditional circumscribed *Caryopteris* and monophyly of the re-defined *Schnabelia*. Furthermore, Xiang et al. (2018) divided *Schnabelia* into two sections. Sect. *Schnabelia* consists of two species (*S. oligophylla* and *S. tetrodonta*), characterised by perennial herb, 4-winged stems, caducous leaves and nutlets puberulent. In contrast, sect. *Cylindricaulis* C.L.Xiang & H.Peng includes three species (*S. aureoglandulosa*, *S. nepetifolia* and *S. terniflora*), characterised by subshrubs, nearly terete stems without wings, persistent leaves and densely hirsute nutlets with distinct reticulate venation.

As an endemic genus, all species of *Schnabelia* are distributed across central, northern, southern and south-western China, primarily inhabiting the slopes of mountains within subtropic forests (Wu and Li 1977; Xiang et al. 2018; Wang 2019; Zhao et al. 2021; Wang and Hong 2022). During a field expedition in Sichuan Province in 2019, we discovered an intriguing species of *Schnabelia*. Through comparative morphological studies and molecular phylogenetic analyses using plastid and nuclear DNA sequences, we determined this species as a new species of the genus *Schnabelia* and describe and illustrate it here.

Material and methods

Plant materials

Two populations of the potential new species were collected from Jiuzhaigou County, north-eastern Sichuan, in July 2019. Field photographs and phenological data were recorded during the collection. Fresh leaves were collected and dried with silica-gel for DNA extraction (Chase and Hills 1991). Mature nutlets were also collected in the field. Voucher specimens are deposited in the Herbarium of Kunming Institute of Botany (KUN) and Herbarium of Chengdu Institute of Biology (CDBI), Chinese Academy of Sciences.

Morphological study

Morphological characteristics of stems, leaves, inflorescences and flowers of the new species were photographed and measured from living plants and dried specimens. Nutlets were photographed using a Keyence VHX-700F Digital Microscope (Keyence, Osaka, Japan). All morphological features were described following the terminology of Li and Hedge (1994). In addition, specimens of all *Schnabelia* deposited in BM, CDBI, IBK, IBSC, K, KUN, NAS, NWTC, PE, SM, SZ, WCSBG and WUK were thoroughly examined for morphological comparison.

Molecular phylogenetic analyses

In order to clarify the systematic position of the new species within *Schnabelia*, we reconstructed the phylogeny of *Schnabelia* using seven DNA markers, as employed by Xiang et al. (2018): the nuclear ribosomal internal and external transcribed spacers (ITS and ETS) and five plastid DNA regions (*matK*, *rbcL*, *rps16*, *trmL-trnF* and *trnH-psbA*). Total Genomic DNA was extracted from silica-gel dried leaf tissue of two individuals of the new species using the modified CTAB method (Doyle and Doyle 1987). Primers details, Polymerase Chain Reaction (PCR) amplification, sequencing and PCR protocols followed those described by Xiang et al. (2018). In total, 112 accessions, representing all five recognised species and the potential new species of the *Schnabelia* were included as the ingroup. Six species from Teucrieae (viz. *Rubiteucris* Kudô and *Teucrium* L.) were selected as outgroup, based on previous phylogenetic frameworks (Xiang et al. 2018; Zhao et al. 2021). The accession numbers for the newly-sequenced samples have been deposited in the GenBank under PQ581109–PQ581112, PQ588101–PQ588102 and PQ594948–PQ594955 and voucher information for all species is provided in the Table 1.

Sequences were aligned using MAFFT V. 7.505 (Katoh and Standley 2013), with any ambiguous sites adjusted manually in PhyDE v.0.9971(Müller et al. 2010). Two datasets were constructed for phylogenetic reconstruction. The first dataset (5CP) combined *matK*, *rbcL*, *rps16*, *trnL-trnF* and *trnH-psbA*, while the second dataset (2NR) combined nrITS and ETS sequences.

Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) methods. The ML analysis was run on the CIPRES Science Gateway web server (http://www.phylo.org/; Miller et al. 2010) with RAxML V. 8.2.10 (Stamatakis 2014) under the GTR + Γ substitution model. The partitioned model (-q) was used for the concatenated plastid data, bootstrap iterations (-# | -N) set to 1000 and other parameters followed default settings. The BI analysis was performed in MrBayes 3.2.6 (Ronquist et al. 2012). The best-fit substitution model of each region was selected independently under the Akaike Information Criterion (AIC) using jModelTest2 (Darriba et al. 2012). For each Bayesian analysis, four MCMC chains (three heated, one cold) were run simultaneously for 20 million generations, starting with a random tree and sampled every 1000 generations. Chain convergence and estimated sample size (ESS) parameters were assessed with Tracer v.1.7.0 (Rambaut et al. 2018), with the first 25% of the trees obtained in BI analysis being discarded as burn-in and then posterior probabilities (PP) were determined from the posterior distribution. The phylogenetic trees were visualised in FigTree v.1.4.3 (Rambaut 2014; http://tree.bio.ed.ac.uk/software/figtree/).

Results and discussion

A total of 14 DNA sequences were newly generated in this study, including the seven DNA regions from two accessions of the potential new species. The combined plastid dataset had an aligned length of 4,689 bp (1,136 bp for *matK*, 1,258 bp for *rbcL*, 839 bp for *trnL-trnF*, 1008 bp for *rps16* and 448 bp for *trnH-psbA*), while the combined nuclear dataset was 992 bp (532 bp for ITS, 460 bp for ETS), respectively.

The phylogenetic topologies from Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were congruent, so only the ML trees were provided for discussion (Figs 1, 2). Both analyses strongly supported the monophyly of *Schnabelia* (ML-BS = 100%, BI-PP = 1.00; all values follow this order hereafter), with the genus *Rubiteucris* found to be sister to *Schnabelia* (100%/1.00). The phylogenetic tree constructed in this study is largely consistent with previous studies, based on the plastid DNA (Li et al. 2016; Xiang et al. 2018; Zhao et al. 2021).

Table 1. Information of the samples used for phylogenetic inference in this study. Sequences newly generated in this study are highlighted in bold font.

Taxa	Voucher	Location	*matK*	*rbcL*	*rps16*	*trnL-trnF*	*trnH-psbA*	ITS	ETS
Schnabelia tetrodonta (Y.Z. Sun) C.Y. Wu & C. Chen 1	Xiang et al., 352(KUN)	Chongqing, Nanchuan	MF801745	MF801799	MF801857	MF801949	MF801899	MF801694	MF801659
Schnabelia tetrodonta (Y.Z. Sun) C.Y. Wu & C. Chen 2	Yang et al., 001(KUN)	Yunnan, Menglun	MF801746	MF801800	MF801858	MF801950	MF801900	MF801695	MF801660
Schnabelia oligophylla Hand.-Mazz. 1	Xiang et al., 353(KUN)	Chongqing, Nanchuan	MF801738	MF801792	MF801850	MF801942	MF801892	MF801687	MF801652
Schnabelia oligophylla Hand.-Mazz. 2	Xiang et al., sn.(Cultivate)	Hubei, Enshi	MF801739	MF801793	MF801851	MF801943	MF801893	MF801688	MF801653
Schnabelia oligophylla Hand.-Mazz. 3	Liu Yanchun, 003(Cultivate)	Shanghai	MF801740	MF801794	MF801852	MF801944	MF801894	MF801689	MF801654
Schnabelia nepetifolia (Benth.) P.D. Cantino 1	Xiang et al. 590(Cultivate)	Jiangsu, Nanjing	MF801735	MF801789	MF801847	MF801939	MF801889	MF801684	MF801649
Schnabelia nepetifolia (Benth.) P.D. Cantino 2	Liu Yanchun, 002(KUN)	Shanghai	MF801736	MF801790	MF801848	MF801940	MF801890	MF801685	MF801650
Schnabelia nepetifolia (Benth.) P.D. Cantino 3	P. D. Cantino, 1428(KUN)	American	MF801737	MF801791	MF801849	MF801941	MF801891	MF801686	MF801651
Schnabelia terniflora (Maxim.) P.D. Cantino 1	Xiang et al., 079(Cultivate)	Yunnan, Kunming	MF801741	MF801795	MF801853	MF801945	MF801895	MF801690	MF801655
Schnabelia terniflora (Maxim.) P.D. Cantino 2	Fang et al., fw11146(KUN)	Gansu, Kang	MF801742	MF801796	MF801854	MF801946	MF801896	MF801691	MF801656
Schnabelia terniflora (Maxim.) P.D. Cantino 3	Xiang et al., 749(KUN)	Hubei, Shengnongjia	MF801743	MF801797	MF801855	MF801947	MF801897	MF801692	MF801657
Schnabelia terniflora (Maxim.) P.D. Cantino 4	Liu Yanchun, 001(KUN)	Shanghai	MF801744	MF801798	MF801856	MF801948	MF801898	MF801693	MF801658
Schnabelia aureoglandulosa (Vaniot) P.D. Cantino 1	Xiang et al., 345(KUN)	Chongqing, Nanchuan	MF801733	MF801787	MF801845	MF801937	MF801887	MF801682	MF801647
Schnabelia aureoglandulosa (Vaniot) P.D. Cantino 2	Liu et al., 3986(KUN)	Yunnan, Funing	MF801734	MF801788	MF801846	MF801938	MF801888	MF801683	MF801648
***Schnabelia jiuzhaigouensis* C. Liu, F. Zhao & C.L. Xiang sp. nov. 1**	**Zhang et al., 19CS18246 (KUN)**	**Sichuan, Jiuzhaigou**	**PQ594948**	**PQ594950**	**PQ581109**	**PQ581111**	**PQ594952**	**PQ588101**	**PQ594954**
***Schnabelia jiuzhaigouensis* C. Liu, F. Zhao & C.L. Xiang sp. nov. 2**	**Zhang et al., 19CS18370 (KUN)**	**Sichuan, Jiuzhaigou**	**PQ594949**	**PQ594951**	**PQ581110**	**PQ581112**	**PQ594953**	**PQ588102**	**PQ594955**
Outgroup									
Teucrium ornatum Hemsl.	Xiang et al., 332(KUN)	Chongqing, Wuxi	MF801748	MF801803	MF801862	MF801952	MF801902	MF801696	MF801662
Teucrium quadrifarium Buch.-Ham. ex D. Don	Xiang et al., s.n.(KUN)	Yunnan, Funing	MF801749	MF801804	MF801863	MF801953	MF801903	MF801697	MF801663
Teucrium viscidum Blume	Liu et al., 3083(KUN)	Gansu, Wenxian	HQ839703	MF801805	MF801864	MF801954	FJ513102	MF801698	MF801664

Taxa	Voucher	Location	*matK*	*rbcL*	*rps16*	*trnL-trnF*	*trnH-psbA*	ITS	ETS
Teucrium bidentatum Hemsl.	Xiang et al., 336(KUN)	Chongqing, Jinfoshan	MF801747	MF801802	MF801861	MF801951	MF801901	AF477790	MF801661
Rubiteucris palmata (Benth. ex Hook. f.) Kudô	Liu et al., 2998(KUN)	Sichuan, Yanyuan	MF801730	MF801784	MF801842	MF801934	MF801884	MF801679	MF801644
Rubiteucris siccanea (W.W. Sm.) P.D. Cantino 2	Xiang et al., 847(KUN)	Yunnan, Yuanjiang	MF801731	MF801785	MF801843	MF801935	MF801885	MF801680	MF801645
Rubiteucris siccanea (W.W. Sm.) P.D. Cantino 1	Xiang et al., 365(KUN)	Yunnan, Songming	MF801732	MF801786	MF801844	MF801936	MF801886	MF801681	MF801646

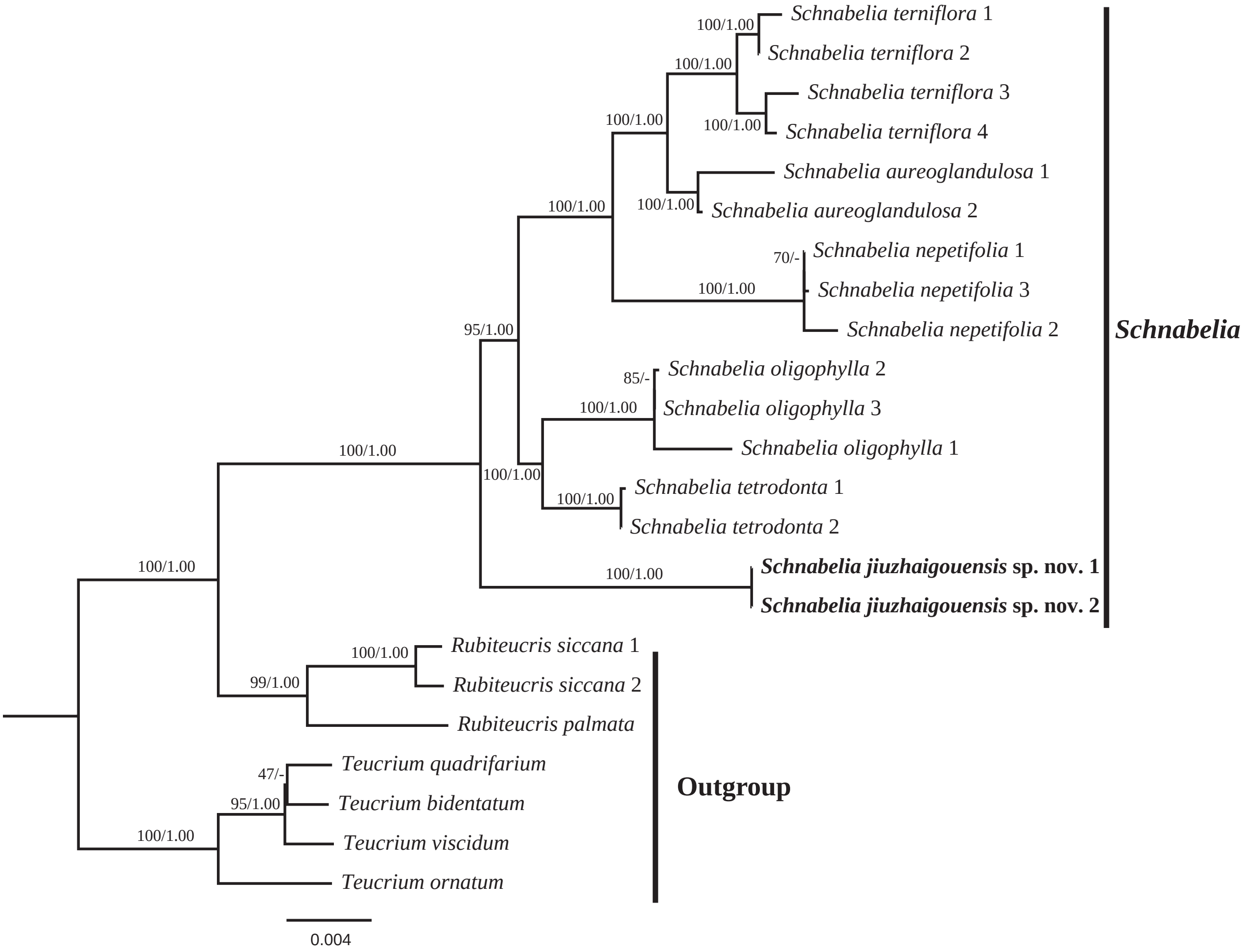

Figure 1. Phylogenetic relationship of *Schnabelia*, based on the (5CPDNA) dataset. The support values (BS/PP) indicated at branches. BS values < 50% and PP support < 90% indicated by -. The outgroup and recognised groups are marked in the right bar.

Within *Schnabelia*, the two accessions of the new species formed a clade (Fig. 1: 100/1.00; Fig. 2: 100/1.00). In the plastid phylogenetic tree, the two individuals of the new species formed a subclade sister to the remaining five species and relationships amongst these species were consistent with previous studies (Xiang et al. 2018). In addition, each species formed a monophyletic subclade (Fig. 1).

However, the nuclear phylogenetic tree revealed three subclades. The first subclade included two accessions of the new species and three individuals of *Schnabelia oligophylla*, forming a moderately supported subclade (Fig. 2. 73/0.94).

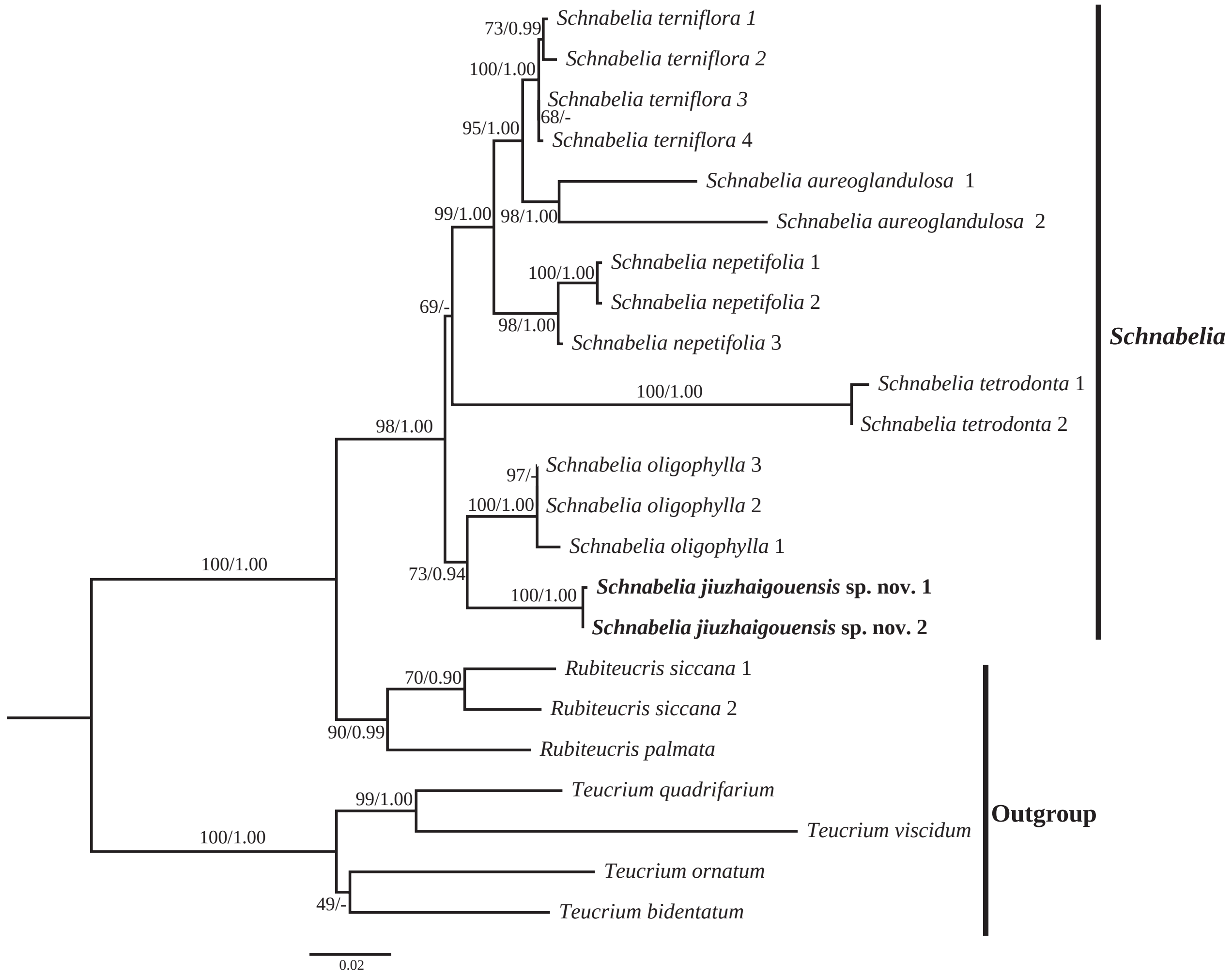

Figure 2. Phylogenetic relationship of *Schnabelia*, based on the (2NR) dataset. The support values (BS/PP) indicated at branches. BS values < 50% and PP support < 90% indicated by -. The outgroup and recognised groups are marked in the right bar.

Table 2. Morphological comparisons between *Schnabelia jiuzhaigouensis* and *S. terniflora*.

Characters	*S. jiuzhaigouensis*	*S. terniflora*
Habit	perennial herb	shrub
Lamina	ovate to lanceolate-ovate leaf blades, 2–8 × 1.5–4 cm, lateral veins 5–8	lanceolate-oblong to ovate, 1.5–4 × 1–3 cm), lateral veins 3–6
Corolla	upper lip and lateral lobes of lower lip oblong, middle lobe cuneate, corolla outside puberulent with non-glandular	upper lip and lateral lobes of lower lip broadly obovate, middle lobe subrounded, corolla outside puberulent with glandular
Nutlets	puberulent, without reticulate veins	densely hirsute, with distinctly reticulate veins

The second subclade consisted of two individuals of *S. tetrodonta* (Fig. 2. BS/PP = 69/-), while the third subclade (BS/PP = 99/1.00) consisted of the remaining three species (*S. nepetifolia*, *S. aureoglandulosa* and *S. terniflora*). The relationship amongst species within this subclade were consistent with those found in the plastid phylogenetic tree.

Morphologically, based on its non-winged stem and persistent leaves, the potential new species should be placed within sect. *Cylindricaulis*. It is most similar to *Schnabelia terniflora*, but can be distinguished by differences in habit, leaf characteristics, corolla shape and the surface ornamentation of the nutlets. Detailed morphological differences between the two species are summarised in Table 2.

Taxonomic treatment

***Schnabelia jiuzhaigouensis* C.Liu, F.Zhao & C.L.Xiang, sp. nov.**
urn:lsid:ipni.org:names:77357312-1
Fig. 3

Type. China • Sichuan Province, Jiuzhaigou County, in the vicinity of Wujiao Ranger Station of Wujiao Nature Reserve, the wet area along the stream, under the mixed forest, 32°54'42"N, 104°14'38"E, 2599 m a.s.l., 12 July 2019, flowering, *Ting Zhang, C. Liu, H. Jiang, Y.L. He & C.H. Li 19CS18246* (holotype: KUN 1630399!), (isotype: KUN 1630400!; CDBI0290980!)

Diagnosis. *Schnabelia jiuzhaigouensis* is most similar to *S. terniflora*, but can be distinguished by several morphological differences. *Schnabelia jiuzhaigouensis* is a perennial herb (vs. shrub), with ovate to lanceolate-ovate leaf blades, 2–8 × 1.5–4 cm (vs. lanceolate-oblong to ovate, 1.5–4 × 1–3 cm in *S. terniflora*), the lateral veins on each side of the mid-rib number 5–8 (vs. 3–6 in *S. terniflora*).The upper lip and lateral lobes of the lower lip are oblong in *S. jiuzhaigouensis* (vs. broadly obovate in *S. terniflora*) and the middle lobe is cuneate (vs. subrounded). The corolla is puberulent on the outside, but non-glandular (vs. puberulent and glandular in *S. terniflora*) and the nutlets puberulent (vs. densely hirsute), with *S. jiuzhaigouensis* lacking reticulate veins on the nutlets (vs. with distinctly reticulate veins in *S. terniflora*). The differences between the new species and *S. terniflora* are summarised in Table 2.

Description. Perennial herbs, erect, 20–60 cm tall. Stems 4-angled and puberulent, occasionally branched from base; internodes 1–11 cm long, puberulent. Leaves opposite, petiole 0.3–2.5 cm long, puberulent; leaf blades ovate to lanceolate-ovate, papery, 2–8 × 1.5–4 cm, puberulent on both surfaces, hairs denser along veins abaxially, base broadly cuneate to rounded or subcordate, apex acuminate, margin serrate, lateral veins 5–8 on each side of the mid-rib. Inflorescences axillary cymes, 1–3 flowered; peduncle slender, (0.5)1.5–3.5 cm, puberulent; pedicels 0.2–1 cm long; bracts lanceolate, ca. 1–2 mm long, glabrous or sparsely hairy, bracteoles lanceolate, 0.5–1 mm long. Calyx campanulate, 10-veined, outside sparsely pubescent; tube 1–1.5 mm long, lobes 5, lanceolate, ca. 2–3 × 1 mm, margin entire, apex acuminate. Corolla pink, 2-lipped, outside sparsely puberulent; tube ca. 5 mm long, both surfaces puberulent; upper lip 2-lobed, lobes oblong, ca. 3–3.5 × 1 mm; lower lip 3-lobed, lateral lobes oblong, ca. 2.5–3 × 1 mm, middle lobe larger, cuneate, 5–6 × 3–4 mm. Stamens and style strongly exserted; stamens 4, inserted near corolla throat, filaments 6–8 mm, basally hairy; style 13–16 mm, glabrous, apex subequally 2-lobed. Ovary pubescent. Nutlets 4, ovoid, puberulent, ca. 3 × 2 mm, without reticulate veins.

Phenology. Flowering from June to July, fruiting from July to September.

Distribution and habitat. Currently, *S. jiuzhaigouensis* is known from two locations in Wujiao Xiang, Jiuzhaigou County, Sichuan, China. It grows under the forest together with species of *Picea brachytyla* (Franch.) E.Pritz. (Pinaceae), *Rosa omeiensis* Rolfe (Rosaceae), *Impatiens undulata* Y.L. Chen & Y.Q. Lu (Balsaminaceae) and *Mimulus* L., at elevations from 2500 m to 2600 m.

Etymology. The specific epithet '*jiuzhaigouensis*' is derived from the type locality Jiuzhaigou County.

Chinese name. Jiǔ Zhài Gōu Sì Léng Cǎo (Chinese pronunciation); 九寨沟四棱草 (Chinese name).

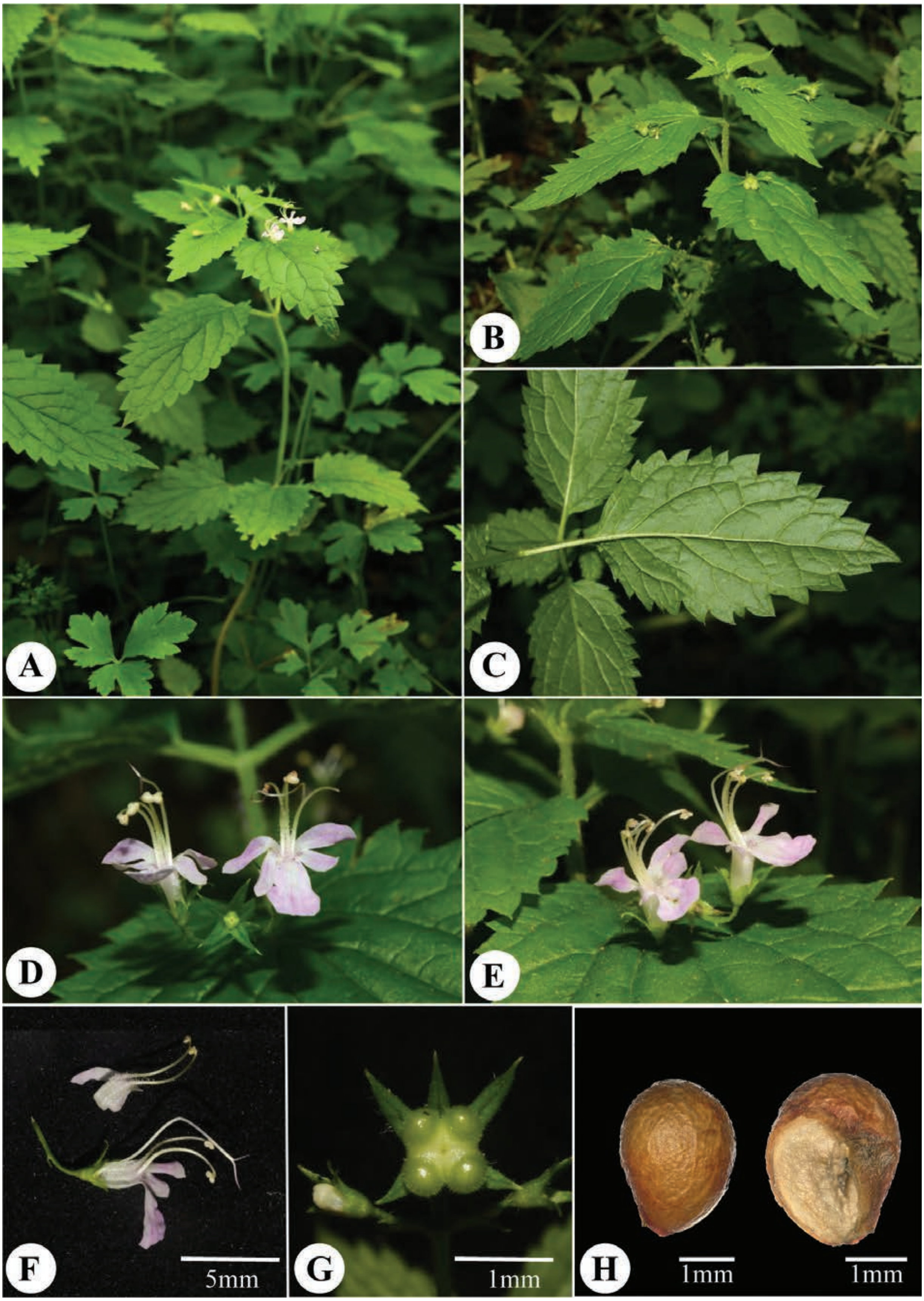

Figure 3. Morphology of *Schnabelia jiuzhaigouensis*. **A, B** habitat **C** leaf morphology **D** frontal view of inflorescence **E** lateral view of inflorescence **F** lateral view of flowers and filaments (Scale bar: 5 mm) **G** frontal view of calyces (Scale bar: 1 mm) **H** surface of the nutlets. (Scale bars: 1 mm) (Photo by Cheng Liu).

Conservation status. So far, two small populations of *Schnabelia jiuzhaigouensis* have been observed in the Wujiao Nature Reserve. These populations are geographically close enough to be considered part of a single location. Further detailed investigation of the same habitats is necessary to gain a better understanding of the species' distribution, abundance and potential threats. Therefore, this species is currently classified as Data Deficient (DD) according to the IUCN Red List Categories and Criteria (IUCN 2024).

Additional specimens examined. *Schnabelia jiuzhaigouensis* (paratypes). China • Sichuan: Jiuzhaigou County, Jiawuchi scenic spot of Wujiao Xiang, under the forest with the species of *Picea brachytyla*, 32°58'29"N, 104°09'29"E, 2551 m a.s.l., 15 July 2019, flowering, *Ting Zhang, C. Liu, H. Jiang, Y.L. He & C.H. Li 19CS18370* (KUN!).

Specimens of *S. terniflora* examined. China, Gansu • Kang County, Qujiagou, 09 Aug 2011, *W. Fang et al. fw11146* (KUN), Jia'an Town, Yuanjiawan, 01 May 1963, *Y.Q. He & C.L. Tang 145* (WUK) • Tanchang County, Hanban County, 11 Jul 1951, *T.P. Wang 14296* (PE) • Wen County, Motianling, Baishui Jiang Nature Reserve, 07 May 2007, *D.E. Boufford et al. 37468* (PE), Bikou Town, Yinchanggou, 05 Jul 1964, *Q.X. Li & X.C. Zhao 2037* (NWTC), Fanba Town, Heiyinggou, 19 Aug 1976, *J.X. Yang 3730* (IBSC); Zhouqu County, Gongbagou, 16 Jul 1998, *Baishuijiang Exped.* 064 (PE); **Hubei** • Shennongjia, on the way from Xinhua to Xiaoluoxi, 11 Jun 2013, *C.L. Xiang et al. 749* (KUN); **Shaanxi** • Mian County, Fangjiaba, 12 Apr 1942, *K.T. Fu 3529* (PE), Liushuying, 15 Apr 1938, *T.P. Wang 9065* (WUK); Nanzheng County, Near Xiaoba Village, 21 Apr 1973, *X.X. Hou 496* (WUK); Near Xiaotai Mountain, 07 May 1956, *Huanghe Exped. 521* (WUK); **Sichuan** • Dujiangyan City, Shichangwan, 19 Apr 1952, *Z. He 12165* (PE), Erwang Temple, 27 Apr 1987, *D.Z. Fu et al. 87-0276* (WCSBG), Qingcheng Mountain, 14 Apr 1930, *F.T. Wang 20395* (WUK), Yulei Mountain. 23 Aug 1987, *Z.Y. Li et al. 87-1962* (WCSBG); Maerkang County, 11 May 1957, *X. Li 70613* (IBSC), Shuadan Road, 17 May 1957, *X. Li 70662* (NAS) • Mao County, Fushun Town, Gangou, 1 Aug 1975, *Sichuan Veget. Exped. 8680* (CDBI) • Nanping (Jiuzhaigou) County; 26 Oct 1937, *T.P. Wang 7974* (PE), 17 May 1979, *Anonymous 0098* (SM) • LangZhai Village, 15 Jul 1983, *Sichuan Veget. Exped. 30420* (CDBI).

The diagnostic key for *Schnabelia*

1 Stems 4-winged; leaves caducous, blade pubescent or subglabrous, but lacking subsessile glandular trichomes; calyx deeply lobed to base, teeth 2× as long as tube .... **sect. *Schnabelia* (2)**
– Stems nearly terete, not winged; leaves persistent, blade with subsessile glandular trichomes as well as non-glandular hairs; calyx lobed nearly 1/2 its length, teeth as long as tube .... **sect. *Cylindricaulis* (3)**
2 Cymes usually reduced to 1 flower; peduncle longer than 7 mm; calyx 5-dentate .... ***Schnabelia oligophylla***
– Cymes usually 1–3-flowered; peduncle less than 2 mm; calyx 4-dentate .... ***S. tetrodonta***
3 Leaf blade irregularly sharply serrate with 1–3 teeth per side, those subtending cymes subentire; ovary and nutlets with yellow hairs .... ***S. aureoglandulosa***
– Leaf blade, including those subtending cymes, regularly serrate to crenate with 4–10 teeth or lobes per side; ovary and nutlets with white hairs....... **4**

4 Leaf blade crenate with 4–6 rounded lobes per side; flowers always solitary .... ***S. nepetifolia***

– Leaf blade serrate with more than 6 sharp teeth per side; flowers mostly in (2- or) 3–5-flowered cymes, rarely solitary **5**

5 Perennial herbs, lateral veins 5–8, upper lip and lateral lobes of lower lip oblong, middle lobe cuneate, nutlets puberulent and without reticulate veins .... ***S. jiuzhaigouensis***

– Shrub, lateral veins 3–6, upper lip and lateral lobes of lower lip broadly obovate, middle lobe subrounded, nutlets densely hirsute and with distinctly reticulate veins .... ***S. terniflora***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

CL, TZ discovered the species, CLX, FZ, CL identified the species. CL, PWG performed the experiments, FZ, PWG analysed the data and wrote the manuscript. CLX revised the manuscript. All authors read and approved the final manuscript.

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Data availability

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

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Research Article

A synopsis of *Christiana* DC. (Malvaceae, Brownlowioideae), with a new species from the Brazilian Atlantic Forest

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Abstract

A taxonomic synopsis is provided for the genus *Christiana*, with emphasis on the American species. Full synonymies, typifications, comments about distribution, and notes on main diagnostic characteristics, as well as conservation status and phenology, are provided. We describe a new species, *C. restingae* T.S. Cout., Barb.Silva & Dorr, **sp. nov**. With this addition, *Christiana* now comprises six species, with its center of richness in South America, where five species occur. The new species is endemic to Brazil where it is known only from Atlantic Forest and Restinga in the states of Espírito Santo and Rio de Janeiro, and is preliminarily assessed as Critically Endangered. Illustrations, images, a distribution map, SEM images of vegetative and reproductive structures, taxonomic comments, and information about the ecology and conservation of *C. restingae* are provided. Furthermore, the distribution and introduction of *C. africana* in the Americas is discussed. A total of eight names of *Christiana* species or synonyms described in four other genera (*Berrya*, *Carpodiptera*, *Entelea*, and *Speirostyla*) are lectotypified.

Key words: Endemism, Malvales, Restinga, taxonomy, Trans-Atlantic slave trade

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Introduction

Christiana DC. (Malvaceae, Brownlowioideae) is a small genus with six species distributed across the Americas, Africa, Madagascar, and French Polynesia (Kubitzki 1995; Bayer et al. 1999; Hernández-Gutiérrez and Magallón 2019; Colli-Silva et al. 2025). It is closely related to two other genera of the subfamily, *Berrya* Roxb. from south and southeast Asia and *Carpodiptera* Griseb. from Central America, the West Indies, and East Africa, from which it differs by having glabrous and variegated seeds (Bayer and Kubitzki 2003; Barbosa-Silva et al. 2021). *Christiana* is comprised of monoecious or dioecious trees that have reflexed stigmas, one ovule per locule, fruits that are follicles or capsules with rudimentary wings or wingless, shiny, and with crustaceous endocarp, and variegated or mottled seeds (Bayer and Kubitzki 2003).

Kubitzki (1995) provided a new concept about the genus, revisiting its taxonomy and nomenclature, and recognized five species. In Brazil, taxonomic searches in the "Tiliaceae" (i.e., Malvaceae, Brownlowioideae and Grewioideae) made in São Paulo state (southeastern region) recorded *Christiana macrodon* Toledo (Souza and Esteves 2002), and for the state of Pernambuco (northeastern region) found only *C. africana* DC. (Tschá et al. 2002). Both studies included morphological descriptions and limited data on geographic distributions. *Christiana* has its highest species diversity in Brazil, where three species now are found (Coutinho 2025). Barbosa-Silva et al. (2021) reported new collection records of *C. mennegae* (Jans.-Jac. & Westra) Kubitzki and provided molecular data, a revised geographic distribution, and identified useful new characters for its determination, including seed stomata and glandular trichomes on vegetative and reproductive organs.

The Atlantic Forest is a global hotspot and contains 371 species of Malvaceae, of which 175 or almost half are endemic (Mittermeier et al. 2005; Flora e Funga do Brasil 2024). Recent research has underscored the richness of this phytogeographic domain with the description of new species in the family (Carvalho-Sobrinho 2013; Carvalho-Sobrinho et al. 2024; Coutinho et al. 2022; de Macedo et al. 2018; Ferreira and Bovini 2020; Ferreira 2021; Costa et al. 2022). Until now, only two species of *Christiana* were recorded for the Atlantic Forest; *C. macrodon* Toledo is endemic to the state of São Paulo and occurs in regions that intersect with the Cerrado phytogeographic domain (Toledo 1952; Souza and Esteves 2002) while *C. africana* is found sporadically in various countries in northern South America and with no identifiable phytogeographic domain. The latter species also is the only species in the genus with documented human uses for both material and medicine (Diazgranados et al. 2020).

The aim of this study is to present a synopsis of *Christiana*, providing comments about taxonomy, nomenclature, and geographic distribution, as well as to describe a new species endemic to the Brazilian Atlantic Forest.

Materials and methods

The nomenclatural revision was performed by analyzing protologues and physical [housed in GH, K, MAC, MO, P, U, US, W; acronyms according to Thiers (2025)] and virtual (BISH, BM, G, HBG, JE, NY, R, RB, SP, VEN) types in herbaria, with support of JSTOR Global Plants (https://plants.jstor.org/) or physical samples.

Morphological descriptions of the new species were based on examination of material in CVRD, MO, NY, RB, US, and VIES herbaria. Exsiccatae were analyzed with a stereomicroscope to ascertain general characters. Leaves, fruits, and seeds from the specimen Lima 6114 of the species described herein were metalized and analyzed under a Scanning Electron Microscope (SEM) to examine minute morphological characters. Morphological terminology follows Harris and Harris (2001) and Radford et al. (1974) for most characters and Theobald et al. (1979) for trichomes.

The conservation status of the new species was assessed according to IUCN (2012) criteria and analyzed with support of the GeoCAT tool (Bachman et al. 2011). The distribution map for South American species was made using QGIS software v. 3.32 (QGIS Development Team 2024) with geographic coordinates taken from herbarium labels when available.

Results

Taxonomic treatment

***Christiana* DC., Prodr. 1: 516. 1824.**

Christannia Walp., Repert. Bot. Syst. 1(2): 360. 1842, sphalm. pro *Christiana* DC.
Speirostyla Baker, J. Linn. Soc., Bot. 25(171): 298. 1889. Type. *Christiana africana* DC. (as *Speirostyla tiliifolia* Baker)
Asterophorum Sprague, Bull. Misc. Inform. 1908(6): 249. 1908. Type. *Christiana eburnea* (Sprague) Kubitzki (as *Asterophorum eburneum* Sprague)
Tahitia Burret, Notizbl. Bot. Gart. Berlin-Dahlem 9(88): 609. 1926. Type. *Christiana vescoana* (Baill.) Kubitzki (as *Tahitia vescoana* Baill.)

Type. *Christiana africana* DC.

Distribution. A genus of six species found in Mexico, Central and South America, Africa, Madagascar, and French Polynesia, with Brazil where there are four species, two of which are endemic as its main center of diversity. The genus is primarily found in rainforest ecosystems.

Eponymy. Candolle named this genus in honor of Christen (Christian) Smith (1785–1816), who collected in the Canary and Cape Verde islands and in the Congo.

Key to the species of *Christiana* DC. (Malvaceae, Brownlowioideae)

1 Leaf blades with dentate margins **2**
-- Leaf blades with entire margins **3**
2 Leaf blades finely dentate on the margins, especially apically; fruits winged .... ***Christiana vescoana***
-- Leaf blades coarsely dentate on the margins; fruits not winged .... ***Christiana macrodon***
3 Leaf blades broadly ovate, bases cordate; gynoecium and capsules apocarpous .... ***Christiana africana***
-- Leaf blades narrowly elliptic, elliptic, lanceolate, or oblanceolate, bases cuneate, rounded, or subcordate; gynoecium and capsules syncarpous **4**
4 Inflorescences short peduncled; capsules conspicuously winged .... ***Christiana mennegae***
-- Inflorescences long peduncled; capsules inconspicuously winged or wingless **5**
5 Inflorescences umbellate with flowers attached to peduncles; capsules depressed-globose, inconspicuously winged .... ***Christiana restingae***
-- Inflorescences fasciculate with flowers on second order axes; capsules subturbinate to turbinate, wingless .... ***Christiana eburnea***

1. *Christiana africana* DC., Prodr. 1: 516. 1824.
Figs 1A, B, 2, 3A

Christiana cordifolia Hook. f., Niger Fl. 238. 1849. Type. Nigeria, Quorra, oppos[ite] Stirling, s.d. (fr), *T. Vogel 200* (lectotype, here designated: K

[K000241734; digital image!]; isolectotypes: K [K000241733; digital image!], K [K000241735; digital image!]).

Carpodiptera schomburgkii Baill., Adansonia 10: 181. 1872. (“*Carpodiptera? Schomburgkii*”). Type. Guyana [“British Guiana”]. Sine loc., [1840] (fl), *R.H. Schomburgk 800* [= ser. I, 800] (lectotype, here designated: P [P02143016]!; isolectotypes: B† [= F neg. no. 9254], K [K000381143]!, K [K000381144]!, P [P02143017]!, U [U 0006904]!, U [U0006905]!, W [W 0002458]!).

Christiana madagascariensis Baill., Bull. Soc. Linn. Paris 1(68): 542. 1885 (“*C[hristiana]? madagascariensis*”). Type. Madagascar. Semberano [sic], Dec 1879 (fl), *J.M. Hildebrandt 3262* (lectotype, here designated: P [P00077799; digital image!]; isolectotypes: JE [JE00003688; digital image!], K [K000241730; digital image!], P [P00077800!], W [1889-0089776]!).

Speirostyla tiliifolia Baker, J. Linn. Soc., Bot. 25(171): 299, pl. 50. 1889 (“*tiliæfolia*”). Type. Madagascar. Sembirano [sic], Dec 1879 (fl), *J.M. Hildebrandt 3262* (first-step lectotype, designated by Capuron, 1963, pg. 93, second-step lectotype, here designated: K [K000241730; digital image!]; isolectotypes: JE [JE00003688; digital image!], P [P00077799; digital image!], P [P00077800; digital image!], W [1889-0089776]!).

Type. Congo. Sine loc., s.d. (fr), *C. Smith s.n.* (lectotype designated by Mabberley in Capuron and Mabberley 1999, pg. 22): BM [BM000795022; digital image!]; isolectotypes: GH [GH00247483]!, K [K000241731; digital image], K [K000241732; digital image!], MO [MO-036957] [n.v.], P [P00368004; digital image!]).

Description. Trees, 2–16 m tall. Leaves: petioles 6–12 cm long, leaf blades 33 × 20.5–21 cm, widely ovate, concolorous to discolorous, bases cordate, margins entire, apices acuminate, stellate trichomes above and below. Inflorescences long peduncled; flowers attached on second or third order axes. Capsules apocarpous, 1.2–1.3 cm long, depressed-globose, wings absent.

Distribution and habitat (Fig. 2). Mexico, Belize, Costa Rica, Nicaragua, Venezuela, Guyana, Ecuador, and Brazil (Ceará, Maranhão, Mato Grosso, Pará, Pernambuco, Rio de Janeiro, Rondônia, Roraima and Tocantins), Central and West Africa, and Madagascar. In Brazil, Tschá et al. (2002) indicated the species occurred in Alagoas state but the specimen they cited (*M.T. Monteiro 22831*) is actually a species of Cordiaceae.

Phenology. Flowering and fruiting specimens collected throughout the year.

Conservation status. A widespread species, *Christiana africana* can be assessed as Least Concern (LC) according to IUCN (2012) criteria.

Vernacular names. Mexico: Patashtillo; Belize: Palo mulato; Nicaragua: Palo piedra; Costa Rica: Piedra; Venezuela: Cabeza de negro, however this common name is possibly misapplied as it usually refers to *Apeiba tibourbou* Aubl. (Malvaceae, Grewioideae); Ecuador: Balsa real; and Brazil: Caaguassu, coração, fruta-de-pombo, gargaúba, and jangada.

Etymology. The specific epithet refers to the African continent, where the type was collected.

Additional specimens examined. Mexico. Chiapas: La Gloria, al E de Salto de Agua, 80 m, 17 Jun 1952 (fl), *F. Miranda 7536* (US). Mpio. Ococingo, a 3 km al S de Frontera Corozoza, sobre la orilla del río Usumacinata, 120 m, 2 Oct 1984 (fl), *E. Martínez S. 7983* (NY, 2 sheets). Mpio Ocosingo, al N de la Estación Chajul, camino a la Petatillera, 25 May 1999 (fr), *S. Sinaca C. 2624* (NY).

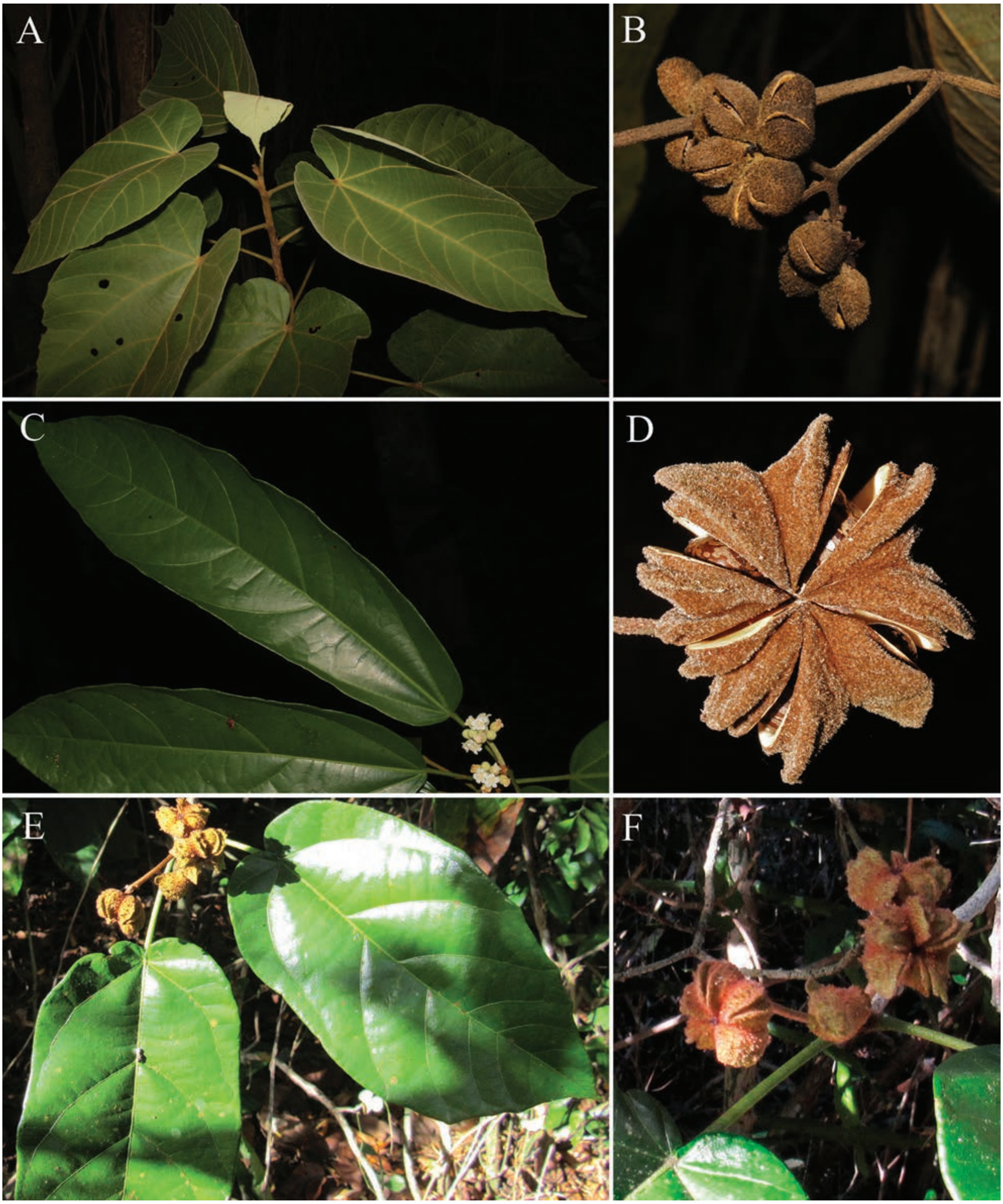

Figure 1. Several *Christiana* species found in Brazil **A** *C. africana* leaves **B** *C. africana* fruits **C** *C. mennegae* leaves **D** *C. mennegae* fruit **E** *C. restingae* leaves **F** *C. restingae* fruits. Photos: Rafael Gomes Barbosa-Silva (**A–D**), André Assis (**E–F**).

Belize ["British Honduras"]. Sine loc., 1926 (fl), *H.W. Winzerling III.7* (US). **Nicaragua. Río San Juan:** Rio San Juan, bosque situado al Oeste del Poblado de Boca de Sábalos (finca de Simeón Parrales Ulloa), 11°03'N, 084°31'W, 17 Jul 1994 (fl bud), *R. Rueda et al. 2097* (US!). **Without province:** "E. Nicaragua," 1949 (st), *P.J. Shank 118* [= *Museum Yale School of Forestry Ser. No. 46904*] (WIS). **Costa Rica.**

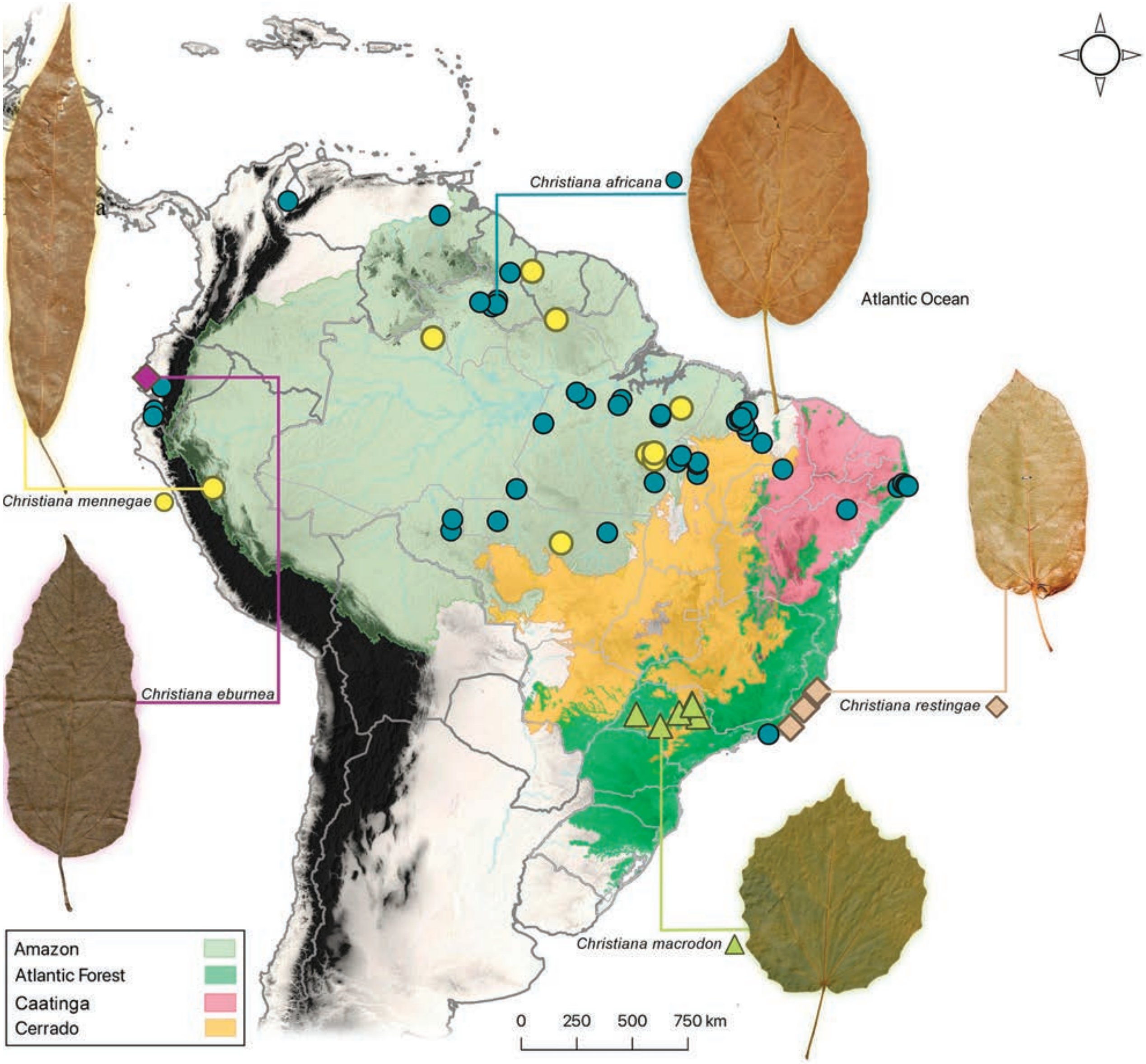

Figure 2. Geographic distribution of *Christiana* found in South America with leaf blade outlines for each species. Four phytogeographic domains (Amazonian Forest, Atlantic Forest , Caatinga, and Cerrado) are indicated for Brazil, the center of diversity for the genus.

Alajuela: Canton de Los Chiles, R.N.V.S. Caño Negro, Llanuras de Los Guatusos, Caño Negro, 10°54'50"N, 084°46'05"W, 40 m, 17 Feb 1994 (fr), *J.F. Morales et al. 2386* (K, MO, NY). R.N.V.S. Caño Negro, Los Chiles. Caño Negro, camino a Playuelas, 10°50'10"N, 084°50'02"W, 40 m, 18 Feb 1994 (fr), *V. Ramírez et al. 261* (NY, US).

Venezuela. Bolívar: Parque Caroní, San Félix-Pto. Ordaz, Sep l965 (fl, fr), *L. Aristeguieta 5872* (NY, VEN, 3 sheets). Zulia: Dtto. Colón, alrededores de Casigua El Cubo, sector Los Manueles, vía Casigua-Palmira, cerca de la aldea Querrequerre, unos 12–15 km al N de Casigua, 31 Jul 1979 (im fr), *G.S. Bunting & M. Fucci 7749* (NY, VEN). **Guyana. U. Takutu-U. Essequibo Region:** 0–4 km N of Dadanawa, 100–120 m, 02°50'N, 059°31'W, 1 Jul 1989 (fl), *L.J. Gillespie 1949* (NY, US); Kanuku Mts., Rupununi R., Bush Mouth near Witaru Falls, 90–120 m, 03°04'N, 059°28'W, 11 Feb 1985 (fr). *M.J. Jansen-Jacobs et al. 154* (US); Rupununi Distr., Dadanawa, 120 m, 9 Jun 1995 (fl), *M.J. Jansen-Jacobs et al.*

4000 (NY, U [digital image], US), ibid., 120 m, 10 Jun 1995 (fl), *M.J. Jansen-Jacobs et al. 4019* (NY, U [digital image], US); Siriuma [sic], Sep 1842 (fl), *M.R. Schomburgk 759* (A, B†); Roraima, 1842–43 (fl bud), *R.H. Schomburgk 474* (G, P, 2 sheets, W, 2 sheets). **Ecuador. Guayas:** Bosque protector Cerro Blanco, hacía la fabrica de cemento, 02°10'S, 079°58'W, 250 m, 18 Mar 2003 (fl), *X. Cornejo & C. Bonifaz 7615* (US). **El Oro:** Cerca a El Porvenir, 80 m, 15 Apr May 1979 (fr), *L. Albert de Escobar 1171* (QCA); Bosque Petrificado Puyango, al Norte Puyango, 03°52'S, 080°04'W, 450 m, 1 Jun 1995 (fr), *X. Cornejo et al. 4007* (US); Puyango and vicinity, 300–900 m, Aug 1978 (fr), *D.C. Daly 043* (NY). **Loja:** Bosque Petrificado Puyango, al Este Puyango, 03°52'S, 080°04'W, 300 m, 13 Apr 1996 (fl), *X. Cornejo & C. Bonifaz 5026* (US); Bosque Petrificado Puyango, camino a Querada Quemazones, 03°52'S, 080°04'W, 300 m, 14 Apr 1996 (fl), *X. Cornejo & C. Bonifaz 5054* (US). **Brazil. Ceará:** "M.N. Plantas da Comm. Scient. da Prov. Do Ceará," s.d. (fr/st), *Fr. Allemão & M. de Cysneiros 136* (P, 2 sheets, R, 2 sheets). **Maranhão:** Fazenda São Francisco, estrada Alto Alegre-Lago Verde km 9, Município de Lago Verde, 21 Mar 1985 (st), *A.B. Anderson et al. 2026* (NY); Fazenda São Francisco, 11 km N of Km 337 of BR 316, 04°00'S, 044°56'W, 25 Sep 1980 (fr), *D.C. Daly et al. D260* (INPA [digital image], NY, US); Codó, 18 Jun 1907 (fl), *A. Ducke HG610* (INPA [digital image]); Sine loc., BR 135, Km 41–42, 18 Feb 1979 (fr), *A. Fernandes et al. s.n.* (EAC 5580 [digital image]); Maracassumé River Region, Campo do Cusins [sic, Caixas], 9 Sep 1932 (fr), *R. Froes 1874* (A, K, MICH, MO, NY, US, WAG [digital image], WIS); Beira do Rio Itacaiuna, Surubim, 19 Jun 1949 (fr), *L. Fróes & G.A. Black 24607* (NY, US); Estreito, ao lado da agrofloresta da fazenda Balneário rio das Pedras, 22 Feb 2005 (fr), *G. Pereira-Silva et al. 9585* (CEN [digital image]); Estreito, margen direita do Rio Tocantins/ foz do Rio Feio, 14 Jan 2008 (fl), *G. Pereira-Silva et al. 12610* (CEN [digital image]); Ilha dos Bótes, a duas léguas abaixo de Carolina, Rio Tocantins, 24 May 1950 (fr), *J.M. Pires & G.A. Black 1981* (IAN [n.v.], UB [n.v.], US); Engenho, município de Vitória do Arari, Campo temporariamente alagado, Cerrado, 30 Jun 1978 (fr), *N.A. Rosa 2484* (IAN [digital image], NY, U [digital image], UFG [n.v.]). Margem do Rio Grajaú, km 285 da Red. BR-316, Campo temporiamente alagado, 15 Dec 1978 (fr), *N.A. Rosa & H. Vilar 3003* (MG [n.v.], NY). **Mato Grosso:** Aripuanã, Salto dos Dardanelos, 10°09'S, 059°27'W, 11 Dec 1999 (fl), *B. Dubs 2639* (K, NY, UFMT); Source of the Jatuarana River, Machado River region, 17 Dec 1931 (fl), *B.A. Krukoff 1571* (A, K, MICH, NY, P, U [digital image]). **Pará:** São Geraldo do Araguaia, Santa Cruz do Araguaia, margem esquerda do rio Araguaia, 13 Jul 1995 (fr), *I. Aragão & M.N. Bastos 207* (IAN [digital image], MFS [digital image]); São Geraldo do Araguaia, Parque Estadual da Serra dos Martírios-Andorinhas, 29 Aug 2018 (fr), *L. Catarino & J.C. Freitas 2760* (IAN [digital image]); Rio Vermelho, região do Tocantins, 22 Apr 1951 (fl bud), *R.L. Fróes 26955* (IAN [digital image], NY, RB [digital image]); [Santarém], Rio Curuatinga, Planalto de Santarém, onde fei feito o levantamento estatístico florestal pelo IAN, SPVEA e FAO, 11 Mar 1955 (fl), *R.L. Fróes 31618* (IAN [digital image!], NY!); Beira do Rio Itacaiuna, Surubim, 19 Jun 1949 (fr), *R.L. Fróes & G.A. Black 24607* (IAN [digital image], US); Sine loc., Rio Araguaia, região de Xambioá, 11 Mar 1961 (fr), *E. Oliveira 1368* (IAN [digital image]); Rio São Manoel a 150 km da foz, limite Pará-Mato Grosso, várzea alta, 3 Jan 1952 (fl), *J.M. Pires 3765* (IAN [n.v.], US); Alto Tapajós, frSão Raimundo, foz do Rio Cururu, margem esquerda, 16 May 1977 (fr), *N.A. Rosa & M.R. Santos 1924* (K, INPA [digital image], NY); Tucuruí, Rio Tocantins, 03 Jun

1980 (fr), *M.G. Silva 5337* (INPA [digital image]); Itaituba, São Luiz, margem do Rio Tapajós, 07 Oct 1977 (fr), *M. Silva & L. Coêlho 2307* (INPA [digital image]); Breu Branco, Tucuruí, 3 Jun 1980 (fr), *M.G. Silva & C. Rosário 5337* (IAN [digital image!], NY!). **Pernambuco:** São Lourenço da Mata, Estação Ecológica do Tapacurá, 08°00'46"S, 034°57'01"W, 17 Aug 2001 (fr), *K. Almeida 183* (IPA [n.v.], CEN [digital image], NY); Recife, Mata de Dois Irmãos, 01 Jun 1950 (fl), *D. Andrade-Lima 488* (IAN); Recife, Dois Irmãos, Mata dos Macacos, 15 Mar 2013 (fl), *M.O. Barbosa et al. 1* (UFP [digital image]); Nazaré de Mata, 4 Jan 1959 (fl), *J. Coêlho de Moraes 2036* (A); Pernambuco, 1838 (fl), *G. Gardner s.n.* (K); [São Lourenço da Mata] Tapera, 15 Apr 1967 (fl), *A. Krapovickas 12871* (P); [São Lourenço da Mata] Tapera, border of the river Tapacurá, 10 Sep 1932 (fr), *B. Pickel 3098* (US); Recife, entrada da Guabiraba, margem da mata de Dois Irmãos, 14 Apr 1962 (fl), *S. Tavares 923* (HST [n.v.], UFP [digital image], US!); Camaragibe, Aldeia, 17 Feb 2013 (fl), *J.E.L. Torres & W.B. Santos s.n.* (HST 19975 [n.v.], HUEFS [000139628, digital image]). **Rio de Janeiro:** (Rio Janeiro) [illegible], s.d. (fr), *A. Glaziou 10314* (K, NY, P); Rio de Janeiro, São Cristóvão, 16 Apr 1883 (fl), *A. Glaziou 14513* (K, NY, P, R [digital image]; Rio Janeiro, Quinta, 12 Mar 1888 (st), *A. Glaziou 16705* (BR [digital image], K, LY [digital image], P); (Rio Janeiro), Quinta, 12 Mar 1888 (fl), *A. Glaziou 16709* (P); Vicinity of Rio de Janeiro & D'Ouro, *A. Glaziou s.n.* (P); Sine loc., s.d. (fr, st), *A. Glaziou s.n.* (NY p.p., P, US). **Rondônia:** Machadinho do Oeste, Tabajara, Rio Machado, 31 May 2015 (fr), *N.C. Bigio et al. 1633* (RON [digital image], US); Sine loc., território de Rondônia, 13 Aug 1975 (fr), *M.R. Cordeiro 541* (IAN [digital image]). **Roraima:** Boa Vista, ilha no meio do Rio Branco, ilha 1, parcela 2. Floresta de várzea; 15 Mar 2021 (fr); *R.G. Barbosa-Silva 1466* (MG); Territorio do Rio Branco, Rio Branco, Fazendas São Bento, Capela e Bom Intento, 3 Sep 1951 (fr), *G.A. Black 51-13316* (IAN [n.v.], P); Boa Vista, Rio Branco, 10 Sep 1943 (fr), *A. Ducke 1387* (A, NY, US, 2 sheets); Boa Vista (near Guyana), Rio Branco, Jul 1913 (fl), *J.G. Kuhlmann 3641* (U [digital image!]); Amazonas-Expedition, bei S. Marcos, Rio Branco, Jun 1909 (fl), *E. Ule 7871* (B†, K [K001214111; digital image], L [digital image], MG [n.v.]). **Tocantins:** Araguatins, margem do Rio Araguaia, 17 Apr 1976, (fl), *J.E. de Paula 989* (UB). **Without state or definite locality:** "Brazilian Amazon," received 11 Jul 1933, *A. Ducke 189* [= *Museum Yale School of Forestry Ser. No. 23651*] (A); Altamira (PA)-Rio Xingu, Ilha Belo-Horizonte, 11 Oct 1986 (fr), *S.A. de M. Souza et al. 253* (IAN [n.v.], MO).

Senegal. Tambacounda: Berge Gambie, 11 Dec 1948 (fr), *J.-G. Adam 2465* (MO, P [digital image]); Nieri-ko, 26 Nov 1964 (fr), *J.-G. Adam 20028* (MO). **Guinea-Bissau.** Porto de Canamine, 11°08'30"N, 015°02'55'E, 8 Nov 1995 (fr), *F. Malaisse & V. Claes 14838* (WAG [digital image]). **Guinea.** Forécariah Préfecture: Sikhourou, Moribaya, derrrièrre Kambilaya, a côté de la rivière Kitemou, 09°41'26.3"N, 012°51'39.4"W [sic], 215 m, 7 Dec 2022 (fr), *G. Konomou et al. 1040* (K [digital image]). **Mali. Kayes:** Chutes des Félou près Kayes, 28 Nov 1958 (fr), *P. Jaeger 5666* (P [digital image], WAG [digital image]). **Sierra Leone. Kabala:** Kruto, 6 Feb 1966 (st), *J.-G. Adam 23590* (MO). **Liberia. Nimba:** Certos River bridge, E of Tapeta, 8 Oct 1961 (fr), *A.G. Voorhoeve 520* (WAG, 2 sheets [digital images]). **Côte d'Ivoire.** 47 km S of Bavé, 09°19'N, 004°10'W [sic], 20 Jun 1968 (fl), *J. Bokdam* 2868 (K [n.v.], MO, WAG [digital image]); Lamto Station, riverine forest of Bandama River, 06°15'N, 005°03'W, 12 Jul 1968, *F.J. Breteler 5280* (K [n.v.], US, WAG [digital image]). **Ghana.** Kwahu Tafo-Asuboni Rd., 24 Feb 1962 (fr), *J. Deaw Sp 650* (MO, US). Ejura, Jun 1930 (fl), *C. Vigne 2030* (A, MO, US). **Togo. Plateaux Region**: Badou, sur la route Badou-Danyi konta, Nov 1986 (fr), *K. Akpagana 1155* (TOGO [digital image]). **Nigeria.** Ibadan, Hadan, Oyo Aroba Hills F.R., Line 40, 18 Oct 1943 (fr), *A.P.D. Jones F.H.I. 4061* (K, MO). **Cameroon.** 1 km S of Badékok, W of km 45 of road, Yokadouma-Moloundou, left bank Badékok R., near conjunction with Boumba R., 475 m, 14 Jul 1965 (fl), *A.J.M. Leeuwenberg 6108* (BR [digital image], MO, WAG [digital image]); Likombe-Pflanzung, 15–35 km NE von Victoria; 50–100 m, Regenwald, Dec 1928 (st), *J. Mildbraed 10748* (A). **Central African Republic.** Région de Yalinga, Haut Oubangui, 1923–34 (fl), *G. Le Testu 3887* (BR, 2 sheets [digital images], MO, P [digital image]). **Republic of the Congo.** Modzaka (Oubangui), May 1889 (fl bud), *M. Thollon 63* (A, BR [digital image], MO, P [digital image]). **Democratic Republic of the Congo. Mai-Ndombe:** Bolobo (terr. Mushi), 25 Aug 1953 (fr), *G. Gilbert 14716* (BR [digital image], NY, US). **South Sudan** [“Anglo Egyptian Sudan”]. **Equatoria:** River Sue, 40 mi NE of Yambio, 24 Aug 1938 (im fr), *J.G. Myers 9376* (A). Tanzania [“Tanganyika”]. Utete Road, mile 10, 13 Jan 1940 (fl), *J.H. Vaughan 2939* (BR [digital image]). **Angola. Uige:** Damba (Congo), Feb 1942 (fl), *J. Gossweiler 13363* (LISC [digital image], WAG [digital image]). **Madagascar. Antsiranana:** Diana Region, Diana, Ambanja, Bemanevika, Bandrakorony, près d’une rivière affluente de la grande rivière de Bandrakorony sur la Péninsule d’Ampasindava, 13°45'45"S, 047°59'09"E, 47 m, 29 Jan 2000 (fl), *C. Rakotovao et al. 4316* (TAN, US). **Mahajanga:** Près du village d’Analanambe, campement 1, direction W à 2 km, Anjiamangirana I, Antsohihy, 15°09'21"S, 047°44'09"E, 150 m, 26 May 2000 (fr), *P. Ranaivojaona et al. 323* (P [n.v.], US). **Without province:** “Chiefly from North-west Madagascar,” recd. Sep 1887 (fl), *R. Baron 5742* (syntype of *Speirostyla tiliifolia*: K, 2 sheets [K000241728, K000241729]).

Discussion. *Christiana africana* is easily distinguished from its congeners as it is the only species with a fully apocarpous gynoecium and capsule.

The African-American distribution of *Christiana africana* is an unusual biogeographic pattern. Burret (1926) postulated a natural migration of *Christiana* from Madagascar westward to Africa and eastward via the Pacific to South America but there are no obvious adaptations for such long-distance dispersal and the American collections of *C. africana* do not support an indigenous presence; *C. africana* occurs sporadically and is invariably found in either secondary vegetation or near households. Kubitzki (1995), also confronted by the odd pantropical distribution of *Christiana*, simply reiterated Burret’s argument. There are relatively few examples of flowering plant taxa with an amphi-Atlantic disjunction (Thorne 1973; Renner 2004), which mostly can be attributed to long-distance dispersal. Renner (2004) suggested that unlike family or genus level disjunctions between America and Africa that fit this long-distance dispersal hypothesis, species level disjunctions often might be anthropogenic.

An alternative hypothesis is that *Christiana africana*, at least, was introduced into the Americas by African slaves during the trans-Atlantic slave trade. Superficially, its seeds resemble in shape, color, and lack of indumentum those of castor bean (*mamona*), *Ricinus communis* L. (Euphorbiaceae) (Fig. 3), which is native to Africa, and which was brought to the Americas by slaves as a medicinal plant (see e.g., Voeks 1997, 2013; Carney 2013). This would explain its atypical distribution in the Americas and the hypothesis could be tested by a detailed genomic analysis of African and American populations. The four other South American species of *Christiana* are clearly native and although collected infrequently, they are found in undisturbed habitats.

Figure 3. Morphological comparison of *Christiana* DC. and *Ricinus* L. seed **A** *C. africana* DC. (Malvaceae) **B** *R. communis* L. (Euphorbiaceae). (Vouchers: *C. africana*, *Pires & Black 1981*, US; *R. communis*, *Smith & Klein 10502*, US). Scale bar: 1 cm (**A, B**).

Christiana africana is "pollinated" (i.e., visited) by lepidoptera (fide *Cornejo & Bonifaz 5054*, in sched.).

Hooker (1849) based *Christiana cordifolia* Hook. f. on a Vogel collection housed in Kew. In this herbarium, there are three duplicates of *Vogel 200*, and we designate here one of them (K000241734) as the lectotype of this name as it has Vogel's detailed annotations about locality according to protologue.

Carpodiptera schomburgkii Baill. was described by Baillon (1872) based on a collection by *R.H. Schomburgk* (*800*) from Guyana. The material studied by Baillon is deposited in Paris (Stafleu and Cowan 1976) where there are now two duplicates of this collection. We designate here the most complete specimen with flowering branch (P02143016) as lectotype. An isolectotype at P appears to have Baillon's notes and sketches while an isolectotype at B† was annotated by Burret.

Baillon (1885) described *Christiana madagascariensis* Baill. based on a collection by *Hildebrandt 3262* also housed in Paris. There are two duplicates of this collection now in this herbarium, and we designate one of them (P barcode P00077799) as the lectotype as it not only is representative but also has Baillon's detailed annotations about the species.

Speirostyla Baker was proposed by Baker (1889) as a new monotypic genus endemic to Madagascar. Simultaneously, he described *S. tiliifolia* Baker based on two syntypes: *Baron 5742* and *Hildebrandt 3262*. Capuron (1963) distinguished between the syntype collections when he stated that the latter was the "Typus" of this name, but he failed to distinguish between duplicates of the Hildebrandt collection. A second-step lectotype therefore is designated here.

2. ***Christiana eburnea*** **(Sprague) Kubitzki, Bot. Jahrb. Syst. 116(4): 541. 1995.** Fig. 2

Asterophorum eburneum Sprague, Bull. Misc. Inform. Kew 1908(6): 249. 1908. Type. Ecuador. Guayas: Chonona [“Chonana”] near Guayaquil, Dec 1861 (fl), *R. Spruce 6260 bis* (lectotype, here designated: K [K000381141]!; isolectotype: K [K000381140]!).

Type. Based on *Asterophorum eburneum* Sprague.

Description. Trees, 4–5 m tall. Leaves: petioles 1.8–3.7 cm long, leaf blades 15.5–40.5 × 7.5–18 cm, ovate, discolorous, bases truncate to subcordate, margins entire, apices acuminate, stellate trichomes above and below. Inflorescences long peduncled; flowers on second order axes. Capsules syncarpous, 2–2.5 cm long, subturbinate to turbinate, wings inconspicuous.

Distribution and habitat (Fig. 2). Endemic to Ecuador at 590–610 m elevation. *Christiana eburnea* occurs in areas of mangrove with influence of Savanna and Deciduous Forest. The report (Dorr 1999) of *C. eburnea* occurring in Peru was based on the misidentification of a specimen (*Schunke V. 5516*) properly referred to *C. mennegae* (Jans.-Jac. & Westra) Kubitzki as reported by Barbosa-Silva et al. (2021).

Phenology. Flowering specimens collected in December and fruiting in August.

Conservation status. *Christiana eburnea* is known from two localities, with only one specimen found within a protected area (Reserva Ecológica Manglares Churute). With an AOO of 8 km^2, this species is assessed here as Critically Endangered (CR), under B2ab (ii, iv, v) criteria, according to IUCN (2012).

Vernacular names. Unknown.

Etymology. From the Latin ‘*eburneus*, *eborinus*’ meaning ivory-white with yellow tinge, a reference to the petal color according to the protologue.

Additional specimens examined. Ecuador. Guayas: Naranjal, Reserva Ecologica Manglares – Churute, cerca a la Cumbre del Pancho Diablo de frente al Puerto de Gallo, 590––610 m, 02°25'S, 079°35'W, 13 Aug 1992 (fr), *C.E. Cerón 20141* (US [00976599]); Ad fluvium Daule prope Guayaquil, s.d. (fl, fr), *R. Spruce 6260* (BM [BM000554440; digital image], G [G00356894], MPU [MPU015290; digital image], P [P02143013], W [1889-0106457]); Guayaquil, s.d. (fr), *R. Spruce 6260* (P [P02143014]).

Discussion. *Christiana eburnea* is recognized by its fasciculate inflorescences with flowers arranged on second order axes and subturbinate to turbinate capsules, features that differentiate it from *C. restingae*.

This species was described as a novelty discovered in the Kew Herbarium (K) and its protologue states “Ecuador. Chonana [sic] near Guayaquil, *Spruce 6260*.” A specimen in Herbarium Hookerianum (K) labeled by Sprague “*Asterophorum eburneum*, Sprague nov. gen et sp. Brownlowiearum” has Sprague’s notes and sketches and the exact locality cited in the protologue but it is numbered “6260 bis.” This specimen most closely matches the information given in the protologue and is designated here as the lectotype. We imagine that Sprague either miscopied the collection number or the word “bis” was added to the label later. Another specimen in Herbarium Hookerianum (K), also labeled by Sprague, has a copied label with the locality “prope Guayaquil” and the number 6260 bis. It clearly is a duplicate of the former.

Additional Spruce material (BM, G, MPU, and P) labeled "Ad fluvium Daule prope Guayaquil" has the number "6260" as cited in the protologue but this material lacks the precise locality that was given even though Chonona, an indigenous locality, eventually was subsumed by the municipality of Daule (Jijón y Camaño 1919). Given the locality conflict, these specimens are considered original but not type material. Finally, two herbarium sheets of *Spruce 6260* in Paris (P02143014 and P02143015) lack original labels yet have Baillon's sketches and notes; the latter sheet consisting of notes only.

3. *Christiana macrodon* Toledo, Arq. Bot. Estad. São Paulo, n.s., f.m., 3: 29, pl. 8. 1952 ["1945"].

Fig. 2

Type. Brazil. São Paulo: Jardinópolis, mata à beira do Rio Pardo, 19 Nov 1947 (fl bud, fr), *M. Kuhlmann 2009* (lectotype, here designated: SP [SP001662; digital image!]; isolectotypes: HBG [HBG-512735; digital image!], HBG [HBG-512736; digital image!], MAC [MAC0055147]!, NY [01795748; digital image!], RB [RB 553263; digital image!], SP [SP001663; digital image!]).

Description. Shrubs to trees, 1.5–3 m tall. Leaves: petioles 5–7 cm long, leaf blades 10–15 × 8–12 cm, widely ovate to circular, concolorous, bases cordate, margins coarsely dentate, apices acuminate, stellate trichomes above and below. Inflorescences short peduncled; flowers attached to peduncle. Capsules syncarpous, 1–1.2 cm long, transversely ellipsoid, wings absent.

Distribution and habitat (Fig. 2). Endemic to Brazil, where it is found only in São Paulo state. This species occurs in Savanna and semi-deciduous seasonal forest (Atlantic Rainforest) at 530–600 m elevation.

Phenology. Flowering specimens collected in November, and fruiting in April and September.

Conservation status. Endangered (EN) (Fernandes and Amorim 2018).

Vernacular name. Algodoeiro.

Etymology. From the Greek '*macr*, *macro*' meaning 'long, large, great', and '*odus*, *odon*, *odontos*' meaning 'teeth', the specific ephitet probably referring to the conspicuously dentate leaf blade margins.

Additional specimens examined. Brazil. São Paulo: Adamantina, Estação Experimental do IAC, 05 Sep 1995 (fr), *L.C. Bernacci et al. 1968* (SPF [digital image]); Porto-Ferreira Reserv. Estad. Porto Ferreira, 17 Dec 1980 (fl bud), *J.E.A. Bertoni 16889* (RB [RB 312587; digital image]); Gália, 15 Jun 2005 (st), *M.R. Gorenstein 22202* (ESA [digital image]); Ribeirão Preto, margem do Córrego Labareda, 11 Nov 2001 (fl bud), *O. Kotchetkoff-Henriques & A. Furlan 623* (ESA [digital image], IAC [digital image], SPFR [digital image]); Jardinópolis, margem do Rio Pardo, s.d. (st), *M. Kuhlmann 2965* [= Herb. No. 50524] (HAS [digital image], IAN [n.v.], SP [n.v.], US [00627713]); Matão, Fazenda Cambuhy, 14 Apr 1994 (fr), *V.C. Souza et al. 5650* (SP [n.v.], SPF [digital image], UNIP [digital image]).

Discussion. Both *Christiana macrodon* and *C. vescoana* have dentate leaf blades, but the former species is distinguished by its coarsely dentate margins and fruits not winged (vs. finely dentate margins and fruits winged in the latter).

The protologue states that the "Typus" is a collection (N.° 43.987) in the herbarium at São Paulo (SP) but inasmuch as there now are two sheets with this number in that herbarium, one is designated here as the lectotype (SP barcode SP001662), as it has fruit.

4. *Christiana mennegae* (Jans.-Jac. & Westra) Kubitzki, Bot. Jahrb. Syst. 116(4): 541. 1995.

Figs 1C, D, 2

Asterophorum mennegae Jans.-Jac. & Westra, Proc. Kon. Nederl. Akad. Wetensch., C, 86(3): 377, figs. 1–4. 1983. Type. Suriname: [Sipaliwini], "Morro Grande" camp-forest island, 6 km W of "Morro Grande" dome, Sipaliwini savanna area on the Brazilian frontier, 04 Nov 1968 (lf, fl, fr), *F.H.F. Oldenburger, R. Norde, & J.P. Schulz ON415* (lectotype, designated by Barbosa-Silva et al. 2021, pg. 4, 18): U [U0006902; digital image!], isolectotypes: K [K000381142]!, MO [MO-036999]!, NY [00415374; digital image!], P [P02143012]!, U [U0006903; digital image!], VEN [VEN409940; digital image!]).

Type. Based on *Asterophorum mennegae* Jans.-Jac. & Westra.

Description. Trees, 5–17 m tall. Leaves: petioles 1.8–5.5 cm long, leaf blades 12.3–29.5 × 5–9 cm, narrowly elliptic, lanceolate or oblanceolate, concolorous, bases rounded to obtuse, rarely subcordate, margins entire, apices acuminate to cuspidate, stellate-multiangulate and glandular trichomes above and below. Inflorescences short peduncled; flowers attached to peduncle. Capsules syncarpous, 1.2–1.8 cm long, depressed-globose, wings conspicuous.

Distribution and habitat (Fig. 2). Found in Suriname, Peru, and Brazil (Amazonas, Mato Grosso, and Pará states) at 500–600 m elevation. This species grows in Amazonian Rainforest and areas of evergreen seasonal forest in Savanna (Barbosa-Silva et al. 2021).

Phenology. Flowering specimens collected in January, September, and November and fruiting in January, April, July, September, and November.

Conservation status. Least Concern (LC) (Barbosa-Silva et al. 2021).

Vernacular name. Brazil: Tartaruguinha.

Etymology. The specific epithet honors Dr. Alberta M.W. Mennega, plant taxonomist and wood anatomist (Jansen-Jacobs and Westra 1983).

Additional specimens examined. SURINAME. Area of Kabalebo Dam project, distr. Nickerie, 4o-5o NB, 57°30'-58°WL, 30–130 m, forest along trail to Wonotobo about ½ km W of road km 109, 24 Sep 1980 (st), *J.C. Lindeman et al. 589* [= Woodsample Uw 26517] (NY). **PERU. San Martín:** Prov. Mariscal Cáceres; Tocache Nuevo, nor oeste del Caserío de Bambamarca, 500–600 m, 15 Nov 1972 (fr), *J. Schunke V. 5516* (F [F1780039; digital image], MO, NY, W). **BRAZIL. Amazonas:** margem de um igarapé que nasce na Serra de Aracá, 28 Jul 1977 (fr), *N.A. Rosa & M.R. Cordeiro 1699* (IAN, 2 sheets [digital images], RB [digital image]). **Mato Grosso:** Itaúba, Resgate de Flora da UHE Colíder, lote G de supressão, 28 May 2015 (fr), *J.P. Battisti s.n.* (CNMT [7492; digital image], MBM [403702; digital image]). **Pará:** Parque Zoobotânico, 05 Nov 2019 (fl), *R.G. Barbosa-Silva et al. 1424* (MG); Paragominas, ramal principal após entrada para sede, 29 Jun 2023 (fr), *E.D. Cruz et al. 1629* (IAN [digital image]); Nova-Canaã dos Carajás [Canaã dos Carajás], 06 Jan 2001 (fl, fr), *L.C.B. Lobato 2624* (MG); Km 141 da rodovia Belém-Brasília, 19 Fev 1960 (st), *E. Oliveira 538* (IAN [digital image]); Km 167–173 da estrada Belém-Brasília, 25 Apr 1960 (fr), *E. Oliveira 565* (IAN [digital image]); Sine loc., mata da Cia. Pirelli, Fazenda Uriboca, Jul 1958 (fr), *J.M. Pires 7041* (IAN, 2 sheets [digital images]); Marabá, [Mun. Parauapebas], Serra dos Carajás, 29 Nov 1988 (fr), *N.A. Rosa & F.C. Nascimento 5084* (K, MG [n.v.]); Parauapebas, Floresta Nacional de Carajás, imediações do Parque Zoobotânico, 06 Sep 2018 (fl, fr), *D.C. Zappi et al. 4562* (MG).

Discussion. *Christiana mennegae* is recognized by its short-peduncled inflorescences.

For additional details see the extensive and detailed discussion in Barbosa-Silva et al. (2021).

5. *Christiana restingae* T.S.Cout., Barb.Silva & Dorr, sp. nov.

urn:lsid:ipni.org:names:77357319-1
Figs 1E, F, 2, 4, 5

Type. Brazil. Espírito Santo: Vila Velha, Interlagos, 20 Jun 1996 (fr), *O. Zambom & M. Fernandes 286* (holotype: VIES [VIES010759]!).

Diagnosis. *Christiana restingae* resembles *C. mennegae* but can be distinguished by its elliptic (vs. narrowly elliptic, lanceolate, or oblanceolate) leaf blades, calyces with stellate only (vs. stellate and glandular) trichomes, and capsules with inconspicuous (vs. conspicuous) wings.

Description. Trees, 4–11 m tall, functionally dioecious. Branches whitish, cylindrical, rugose, lenticels circular to oblong, 0.5–1 mm long, old branches glabrescent, trichomes stellate-multiradiate, sessile, ferrugineous, sparsely distributed, stipules caducous. Leaves alternate, spirally arranged; petioles 1.3–3 cm long, discolorous when compared to the branches, vinaceous, inconspicuously striate, not canaliculate, terete, not decurrent, sparsely pilose, trichomes stellate-multiradiate, ferrugineous, more concentrated near the branches; leaf blades entire, coriaceous, nitid when dry, concolorous to quickly discolorous, 5.5–13.5 × 3–7 cm, elliptic, bases round to subcordate, margins plane, entire, apices acuminate to cuspidate, glabrous or glabrescent above and below, but with stellate-multiradiate trichomes sparsely distributed along the veins, and glandular-sessile trichomes on the blade below; venation actinodromous, 6–8 pairs of secondary veins, 2 pairs basal, impressed above, prominent below. Inflorescences axillary, umbellate with flowers attached to peduncles; bracts caducous; peduncles whitish, striate, 5–5.5 cm long, glabrous to glabrescent, trichomes sparse. Floral buds globose, ca. 2.5 × 2.5 mm. Flowers functionally unisexual; bracteoles c. 3.5 × 0.9 mm, elliptic, abaxial surface pubescent; pedicels 1.8–2 mm long, densely pubescent, trichomes stellate-multiradiate, ferrugineous, sessile. **Pistillate flowers:** calyx gamosepalous, 5-merous, cupuliform, c. 4.5 mm long, with apical lobes free, pubescent abaxially, trichomes stellate-multiradiate, lobes c. 2.5 × 2 mm, ovate, apex acute. Corolla dialypetalous, 5-merous, white, petals c. 2.8 × 1.3 mm, obovate, glabrous, apices rounded. Androecium polystemonous, staminodes 1.4–2 mm long, filaments 1.2–1.8 mm long, glabrous, anthers c. 0.3 mm long,

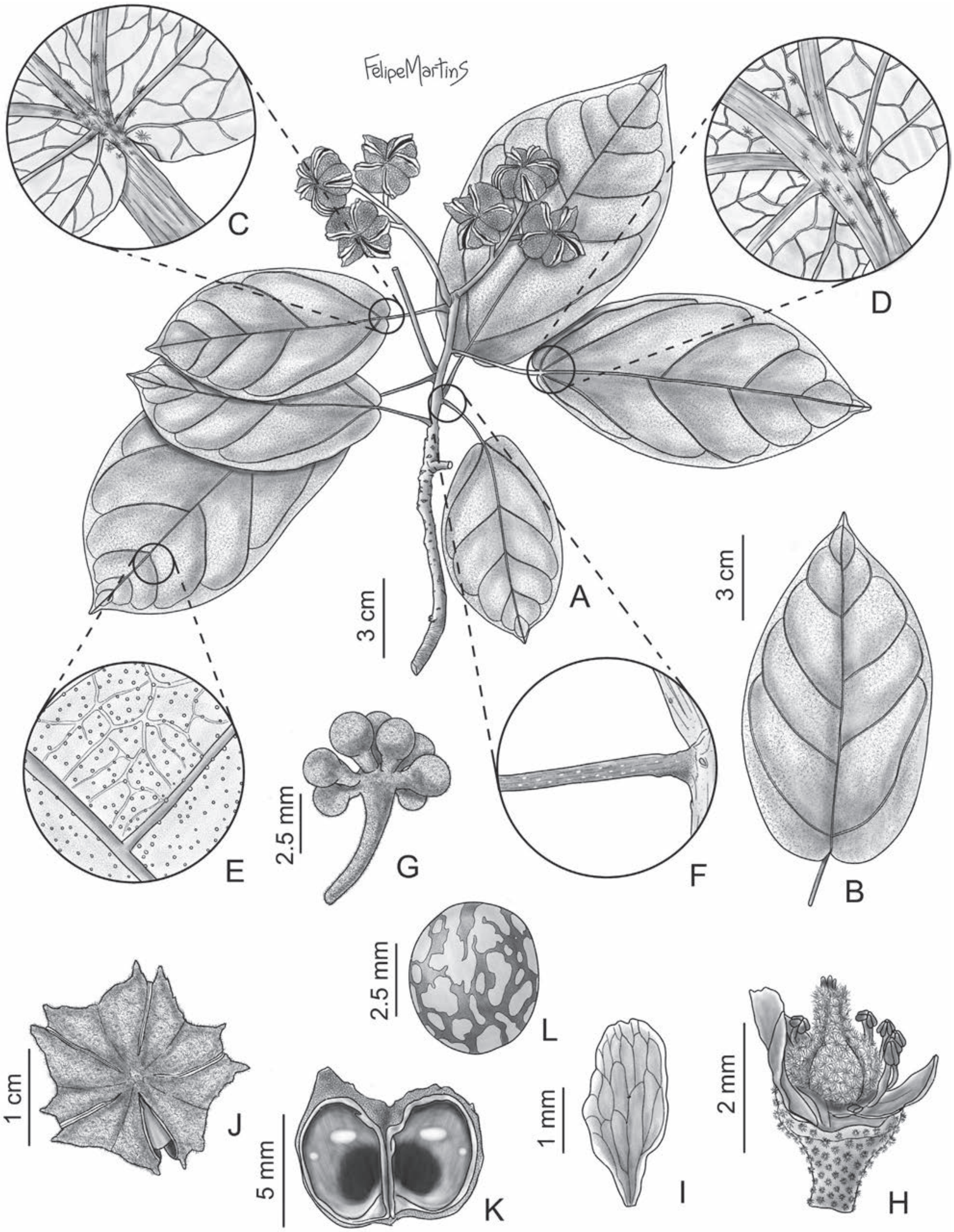

Figure 4. *Christiana restingae* T.S. Cout., Barb.Silva & Dorr **A** habit **B** leaf **C** detail of the base of the adaxial surface of the leaf blade showing concentration of stellate-multiangulate trichomes **D** detail of the base of the abaxial surface of the leaf blade showing concentration of stellate-multiangulate trichomes **E** detail of abaxial surface of the leaf blade showing glandular sessile trichomes **F** petiole **G** inflorescence with flower buds **H** gynoecium and part of androecium **I** petal **J** capsule **K** capsule opened showing shiny endocarp **L** seed.

divergent. Gynoecium 5-carpellate, ovary ca. 1.2 × 1 mm, depressed globose, densely pubescent, trichomes stellate-multiradiate, style hirsute, trichomes stellate-multiradiate, stigma not observed. **Staminate flowers:** not observed. Fruit a capsule, woody, syncarpous, c. 1.5 cm long, 1.3–1.7 cm diam., depressed-globose, 4–5-locular, inconspicuously winged, c. 0.6 × 0.6 mm, densely pubescent abaxially, glabrous, lustrous internally; seeds 1 per locule, 5 × 4 mm, ellipsoid, variegated, gray with brownish marks, glabrous.

Distribution and habitat (Fig. 2). *Christiana restingae* is known only from Espírito Santo state, in Vila Velha and Presidente Kennedy municipalities, and in the northeast of Rio de Janeiro state. This is the only species of the genus occurring in the state of Espírito Santo. The new species is found in the Atlantic Forest phytogeographic domain, where it grows in Dense Ombrophylous Forest, as well as in Restinga, at 5–300 m elevation.

The Brazilian coast has an intense history of plant collecting, especially in the coastal region of the states of Espírito Santo and Rio de Janeiro. Recently, Dutra et al. (2022) with the Espírito Santo Flora Project strengthened floristic and taxonomic studies in the state, including new collections in Restinga areas (Guarnier et al. 2022).

Phenology. Flowering specimens collected in January and fruiting in January, May, June, and August.

Conservation status. *Christiana restingae* could be assessed as Endangered (EN) because its EOO is 1,230 km^2 (< 5,000 km^2) or Critically Endangered (CR) because its AOO is 8 km^2 (< 10 km^2). The IUCN (2012) recommendation is that the taxon be classified under the highest threat category. We therefore consider the species Critically Endangered (CR) under B2ab (i, ii, iii) criteria. In addition, *C. restingae* grows in Atlantic Forest and Restinga, vegetation types with an intense history of deforestation and human occupation.

Vernacular name. Guaxumbão.

Etymology. The specific epithet refers to Restinga, vegetation typical of the Brazilian coast, characterized by sandy soil, where the new species is usually found.

Paratypes. Brazil. Espírito Santo: Presidente Kennedy, 21°16'07"S, 040°57'58"W, 5 m elev., 12 Aug 2020 (fr), *A.M. Assis & R.S. Cribari 4899* (VIES). Vila Velha, Convento da Penha, 300 m, 11 May 2007 (fr), *D.A. Folli 5755* (CVDR [digital image], US [01317134]); ibid., 300 m, 11 Sep 2009 (fr), *D.A. Folli 6409* (CDRV [digital image], US [01317133]); Vila Velha, Interlagos, 22 May 1996 (fr), *O. Zambom & M. Fernandes 283* (VIES), ibid., 31 Jan 1996 (fl, im fr), *O. Zambom et al. 222* (VIES). **Rio de Janeiro:** Armação de Búzios, 31 Aug 2003 (fr), *H.C. Lima et al. 6114* (MBM [digital image], NY [03987289], RB [digital image]); São Francisco de Itabapoana, Estação Ecológica de Guaxindiba, 17 Jul 2018 (fr), *H.C. Lima et al. 8683* (RB, 2 sheets [digital images]); Rio das Ostras, Jul 2004 (fr), *A. Oliveira & D. Oliveira 1016* (RB).

SEM. The abaxial surface of the leaves has many sparse glandular trichomes and adjacent to the veins near the base it has stellate-multiangulate trichomes (Fig. 5A, B). The abaxial surface of the epidermis has cells shaped like irregular polygons (Fig. 5B). The epicarp has stellate multiangulate trichomes (Fig. 5C).

The seed has several openings and crevices (Fig. 5D, E) and its surface has small sparse papillae (Fig. 5F).

Discussion. *Christiana restingae* is described here three decades after it was first collected by O. Zambom and M. Fernandes. Ironically, it is worth mentioning

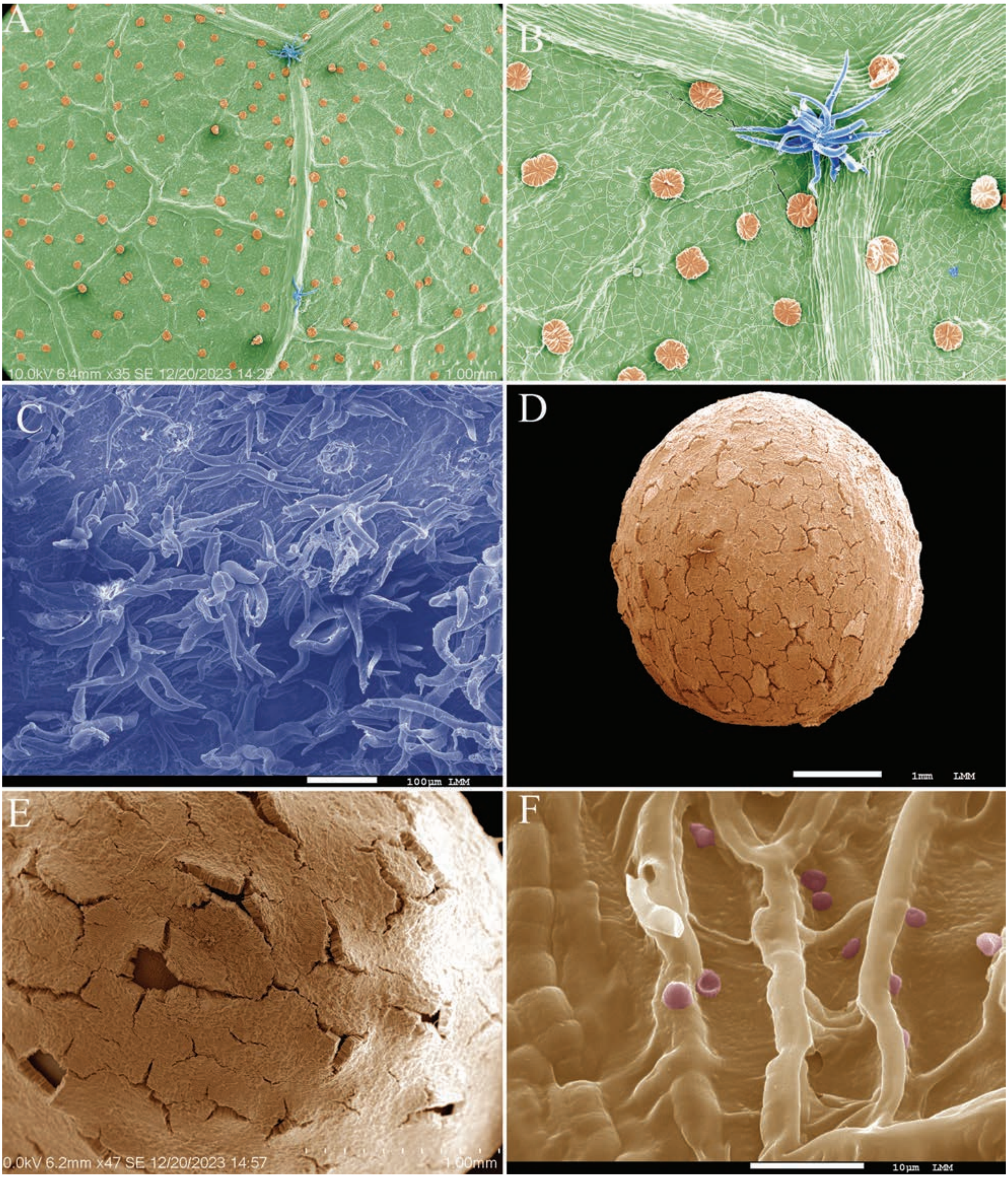

Figure 5. SEM images of *Christiana restingae* T.S. Cout., Barb.Silva & Dorr **A** abaxial leaf surface showing glandular trichomes (orange) and stellate-multiangulate trichomes (blue) **B** detail of the abaxial leaf surface **C** epicarp **D** seed **E** seed surface displaying the openings and fissures characteristic of this species **F** detail of scattered micropapillae on the seed surface.

that most of the large botanical research centers in Brazil are concentrated in the central region of the Atlantic Forest, and this is where most Brazilian plant taxonomists are based. This underscores the lack of attention *Christiana* has received in recent years (Barbosa-Silva et al. 2021) and the paucity of specialists knowledgeable about certain groups of plants.

Christiana is a genus with homogeneous morphology, sharing stellate trichomes on the vegetative and reproductive parts including inflorescences and flowers. Using a Scanning Electron Microscope (SEM), Barbosa-Silva et al. (2021) discovered the occurrence of simple, two-armed, and glandular trichomes on the petioles and leaf blades of *C. mennegae*, characters known only from this species. Leaf shape and capsule morphology can be useful to distinguish the different species. *Christiana africana*, the most widespread species of the genus, has an apocarpic gynoecium and fruit, which is an apomorphy. On the other hand, *C. macrodon* is the only species with leaf blades that are serrate along the entire length of their margins. Analyzing the type of *C. vescoana*, it was observed that in a few specimens the leaf blades near the apex also have this leaf margin characteristic, albeit less pronounced.

Christiana restingae is characterized especially by its elliptic leaf blades and fruits with inconspicuous wings. It has the shortest leaf length among the species of the genus, with mature leaf blades as small as 5.5 cm long. The new species differs from *C. africana* and *C. macrodon* by its elliptic leaf blade with rounded to subcordate (vs. widely cordate and cordate) bases. It also is distinguished from *C. africana* by its syncarpous (vs. apocarpous) capsules and from *C. macrodon* by leaf blades with entire (vs. dentate) margins. Although, morphologically, the new species is more similar to *C. mennegae* in having nitid leaves when dried, glabrescent, and with trichomes especially on the veins, *C. restingae* is distinguished by having smaller leaf blades (5.5–13.5 × 3–7.5 vs. 12.3–29 × 5–9 cm) that are elliptic (vs. narrowly elliptic, lanceolate or oblanceolate), and capsules 1.3–1.7 cm in diam. and with inconspicuous wings (vs. 3.8 cm in and conspicuous wings).

The analysis of structures in SEM brings new insights into understanding the genus, which exhibits various characteristics that can aid in species differentiation. For instance, the leaves of *Christiana restingae* possess more glandular trichomes than *C. mennegae* and have stellate-multiangulate trichomes, whereas *C. mennegae* only has stellate rotate trichomes on its leaves (Barbosa-Silva et al. 2021). Additionally, with SEM, the cell walls of the epidermis of *C. restingae* are visible, a character not seen in *C. mennegae*. The epicarp of *C. restingae* also exhibits a high concentration of stellate-multiangulate trichomes similar to *C. mennegae*. The seed of *C. restingae* also has maculae that are medium brown with darker irregular marks like other species in the genus; however, only *C. restingae* has these openings and crevices (Fig. 5E), which even can be observed in herbarium material without the aid of magnification. Although these openings and fissures have been found in all fruit-bearing material, we are not sure if they are found in fresh material or if this character occurs only during the drying process of specimens. The seed of *C. restingae* does not have stomata, a character that was found to be very interesting in *C. mennegae* and is also present in other Malvaceae species, although it is rare in Angiosperms (Paiva et al. 2006; Barbosa-Silva et al. 2021).

Regarding geographic distribution, *Christiana restingae* is endemic to Espírito Santo and Rio de Janeiro states, occurring in Atlantic Forest and Restinga, sharing the vegetation type with *C. africana* (Amazonia and Atlantic Forest) and *C. macrodon* (Atlantic Forest and Cerrado) (Coutinho 2025). *Christiana mennegae* and *C. restingae* do not occur sympatrically since the first species occurs in Brazil only in the Amazonian Domain (Secco 2000; Barbosa-Silva et al. 2021). With the discovery of *Christiana restingae*, the number of species of the genus in Brazil reaches four, making the country the center of diversity. Of the six known species of the genus, two are endemic to Brazil and its Atlantic Forest.

It is worth noting that with the Flora do Brasil 2020 project (BFG 2021), various taxonomists were encouraged to monograph different groups. Consequently, plant groups that had long gone without taxonomic revisions, that were neglected, or that were known to be of little interest, were revised. Thus, numerous results have been published in recent years as a result of this careful process of revision in these groups (Giulietti 2020; Andrino et al. 2022; Antar et al. 2022; Asprino et al. 2024; Barbosa-Silva 2024). The same factor also has driven recent studies on the genus *Christiana* (Barbosa-Silva et al. 2021), as well as the data presented here.

6. *Christiana vescoana* (Baill.) Kubitzki, Bot. Jahrb. Syst. 116(4): 541. 1995.

Berrya vescoana Baill., Adansonia 10: 240. 1872. Type. Tahiti. Sine loc., 1847 (fr), *J.N.E. Vesco s.n.* (lectotype, here designated: P [P00637093; digital image!]; isolectotypes: BISH [BISH1003216; digital image!], P [P00637094; digital image!], P [P00637095; digital image!], P [P04756685; digital image!], P [P04756686; digital image!]).

Entelea tahitensis Nadeaud, Énum. Pl. Tahiti 69. 1873. Type. Tahiti, [Ravins de Papaihonu, 600 m.], s.d. (fr), *J. Nadeaud 439* (lectotype, here designated: P [P04756684; digital image!]; isolectotypes: BISH [BISH1003217; digital image!], G, 3 sheets [G00393886; digital images!], P [P04756683; digital image!], P [P00637089; digital image!], P [P00637090; digital image!], P [P00637091; digital image!], P [P00637092; digital image!]).

Berrya tahitensis (Nadeaud) Drake, Ill. Fl. Ins. Pacif.: 125. 1890 ["1886"] ("*B.* (?) *Tahitensis*"). Type. Based on *Entelea tahitensis*.

Tahitia vescoana (Baill.) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 9: 607, 610. 1926. Type. Based on *Berrya vescoana*.

Tahitia tahitensis (Nadeaud) S.L. Welsh, Fl. Societensis: 282. 1998. Type. Based on *Entelea tahitensis*.

Type. Based on *Berrya vescoana* Baill.

Description. Trees, 5–8 m tall. Leaves: petioles 2.5–6.5 cm long, leaf blades 11–21 × 7.3–11 cm, widely ovate, concolorous to slightly discolorous, bases cordate, margins slightly dentate apically, apices acuminate, stellate trichomes above and below. Inflorescences short peduncled; flowers attached to peduncle. Capsules syncarpous, c. 1 cm long, depressed-globose, wings conspicuous.

Distribution and habitat. Found only on the islands of Moorea and Tahiti in French Polynesia at 100–280 (–600) m elevation. The species is poorly known with relatively few recent collections.

Phenology. Fruiting specimens collected in April, May, and June.

Conservation status. *Christiana vescoana* has a restricted and endemic population and presents an AOO of 20 km^2 and EOO of 248.140 km^2. It is assessed here as Critically Endangered (EN), under D1 criterion as it has a reduced number of mature individuals, according to IUCN (2012).

Vernacular names. Unknown.

Etymology. The specific epithet honors Jean Nicolas Eugène Vesco, Naval surgeon and botanist, who collected the type.

Additional specimens examined. French Polynesia. Moorea: Vallée de Maharepa, 23 Apr 2004 (fr), *J.F. Butaud 439* (P, 2 sheets [P05253217, P05253221;

digital images]); Mt Raaiu [sic], 16 Apr 1898 (fr), *J. Nadeaud s.n.* (P [P05253216; digital image]). **Tahiti:** Vallée du Panaruu, 21 May 1896 (fr), *J. Nadeaud s.n.* (P, 3 sheets [P05253218, P05253219, P05253220; digital images]); Sine loc., 1870 (fr), *M. Pancher s.n.* (P [P05253224; digital image]); Vallée de Faataua, 09 May 2005 (st), *W. Teamotuaitau 26* (P [P05253226; digital image]); Punaruu, 02 Jun 2005 (fr), *W. Teamotuaitau 35* (P [P05253222; digital image]). Sine loc., sine coll. (P [P05253225; digital image]); Sine loc., 1855 (fr), *M. Vieillard & M. Pancher s.n.* (P [P05253227; digital image]).

Discussion. *Christiana vescoana* shares dentate leaf margins with *C. macrodon*, but it is distinguished by characters previously mentioned (and also given in the key).

For additional details see Florence (2004).

The description of *Berrya vescoana* was based on an unnumbered collection made by M. Vesco in Tahiti: this collection, including duplicates, is now housed in the herbarium in Paris (P). Kubitzki (1995) noted the type was in P, but only wrote "*Vesco a. 1847* (P)" where "1847" refers to the year of collection, not a collection number. Five duplicates of this unnumbered collection are found now in P, none of them have the "a" noted by Kubitzki, and consequently, we designate the most complete specimen with fruits and seeds (P barcode P00637093) here as the lectotype. It is also the same specimen that Florence (2004) considered to be the "holotype."

When Nadeaud (1873) described *Entelea tahitensis* he associated it with a single collection (*Nadeaud 479*) for which he also indicated there were duplicates ("un nouvel examination de mes échantillons …"). There therefore is no holotype as indicated by Florence (2004) who stated that one was deposited in G. Additionally, Florence's statement cannot be interpreted as designating a lectotype since it contravenes the rules of the ICN (Turland et al. 2018; Arts. 7.3, 9.23). Here, we designate as lectotype the only specimen in P (P barcode P04756684) with fruits.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: TSC, RGBS, LJD. Data curation: TSC, LJD, RGBS. Formal analysis: LJD, RGBS, TSC. Investigation: RGBS, LJD, TSC. Methodology: RGBS, LJD, TSC. Project administration: TSC. Supervision: TSC, LJD. Validation: TSC, LJD. Visualization: RGBS, LJD, TSC. Writing - original draft: TSC, RGBS, LJD. Writing - review and editing: TSC, RGBS, LJD.

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Data availability

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

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Research Article

Columnea golondrinensis (Gesneriaceae), a new species from Cerro Golondrinas in the northern Andes of Ecuador

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Abstract

Exploratory field expeditions to the Chocó forests in the northern Andes of Ecuador resulted in the discovery of a new species of *Columnea* (Gesneriaceae). *Columnea golondrinensis* J.L.Clark, **sp. nov.**, is described as a narrow endemic from the cloud forests of Cerro Golondrinas in the Carchi Province near the northern Ecuadorian border with Colombia. The oval leaves with a rust-colored multicellular hispid indumentum, terrestrial subwoody habit and deeply bilabiate dark purple corollas with glandular trichomes differentiate this taxon from all other congeners. Based on IUCN guidelines, a preliminary conservation status of Vulnerable (VU) is provided for *C. golondrinensis*.

Resumen

Las expediciones de campo exploratorias a los bosques del Chocó en los Andes del norte de Ecuador resultaron en el descubrimiento de una nueva especie de *Columnea* (Gesneriaceae). *Columnea golondrinensis* J.L.Clark, **sp. nov.**, se describe como una endémica restringida a los bosques nublados del Cerro Golondrinas, en la provincia de Carchi, cerca de la frontera norte de Ecuador con Colombia. Las hojas ovaladas con un indumento híspido multicelular de color óxido, el hábito subleñoso terrestre y las corolas profundamente bilabiadas de color púrpura oscuro con tricomas glandulares diferencian a este taxón de todos sus congéneres. Según las directrices de la UICN, se proporciona un estatus preliminar de conservación de Vulnerable (VU) para *C. golondrinensis*.

Key words: Chocó, Colombia, *Columnea*, Ecuador, Gesneriaceae, taxonomy

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Introduction

The Gesneriaceae family, part of the order Lamiales, comprises more than 3,900+ species across 150 genera (Weber 2004; Weber et al. 2013, 2020; GRC 2025). The family is organized into three subfamilies and seven tribes, each representing monophyletic lineages (Weber et al. 2013, 2020; Ogutcen et al. 2021). In the New World, the majority of species belong to the subfamily Gesnerioideae, encompassing over 1,200 species and 77 genera (Clark et al. 2020). Within this group, *Columnea* L. is classified in the tribe Gesnerieae and the subtribe Columneinae (Weber et al. 2013, 2020). A defining generic character of

Columnea is indehiscent berries, which contrast with the fleshy, bivalved capsules of closely-related genera.

Columnea ranges from Mexico south to Bolivia and is most diverse in the northern Andes of Colombia and Ecuador. With over 220 species (Clark et al. 2020; GRC 2025), *Columnea* is the largest genus in the subfamily Gesnerioideae (Weber et al. 2013, 2020). *Columnea* is strongly supported as a monophyletic genus, based on molecular phylogenetic studies (Smith et al. 2013; Schulte et al. 2014). Most subgeneric ranks are artificially defined and not supported by phylogenetic studies (Smith and Carroll 1997; Smith 2000; Clark and Zimmer 2003; Clark et al. 2006; Clark et al. 2012; Smith et al. 2013; Schulte et al. 2014). Thus, the new species is not classified or assigned to a subgeneric rank.

Materials and methods

Plants were photographed in the field and subsequently pressed and dried. Specimens are currently deposited at the herbarium at the Pontificia Universidad Católica del Ecuador (QCA). Additional specimens will be distributed to the Field Museum (F), Conservatoire et Jardin Botaniques de la Ville de Genève (G), Missouri Botanical Garden (MO), Marie Selby Botanical Gardens (SEL), New York Botanical Garden (NY), and the United States National Herbarium (US). Photographs were taken of live specimens in the field using a Nikon D100 DSLR with a Nikon 105 mm lens. Morphological observations and measurements were made from live collections, alcohol-preserved material, and digital images using the ImageJ program (https://imagej.nih.gov/ij/).

The extinction risk was assessed following the IUCN Red List Categories and Criteria (IUCN 2012) and updated criteria in the IUCN Standards and Petitions Committee (IUCN 2024). Field observations and collection sites from fieldwork were used to evaluate the IUCN category. The extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the software program GeoCAT (Bachman and Moat 2012) with the default setting of 2 km, which is a 4 km^2 grid cell.

Taxonomic treatment

Columnea golondrinensis **J.L.Clark, sp. nov.**
urn:lsid:ipni.org:names:77357320-1
Fig. 1

Type. Ecuador. • Carchi: cantón Tulcan, parroquia Chical, Cerro Golondrinas, ridgeline(s) between campsite #1 (sector Río Verde) to campsite #2 (La Laguna), 0°52'20.07"N, 78°12'25.61"W, 1800–2225 m alt., 26 Jan 2024, *John L. Clark, Luis Micanquer, Milton Cantincuz, Mia Johnson & Nolan Exe 18185* (holotype: QCA; isotypes: F, G, MO, NY, SEL, US).

Diagnosis. Vegetatively similar to *Columnea suffruticosa* J.F. Sm. & L.E. Skog due to the presence of ovate leaves with a rust-colored multicellular hispid indumentum, but differing in the terrestrial habit (vs. epiphytic habit in *C. suffruticosa*) and deeply bilabiate corolla (vs. uniformly tubular corolla in *C. suffruticosa*). The deeply bilabiate corolla, dark purple corolla tube, and glandular trichomes

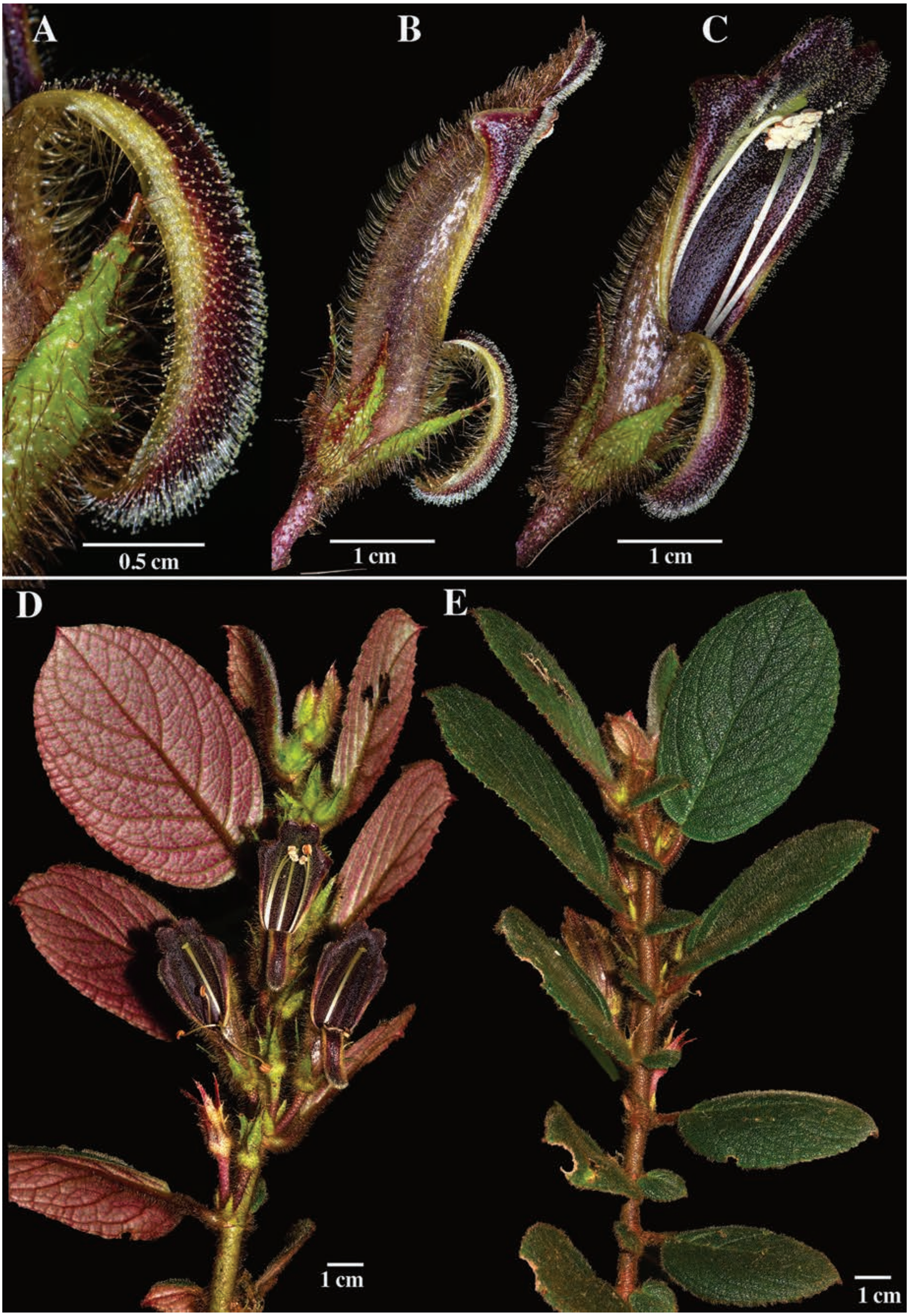

Figure 1. *Columnea golondrinensis* J.L.Clark **A** recurved lower lip of bilabiate corolla **B, C** lateral views of flower **D** abaxial surface of flowering shoot **E** adaxial surface of flowering shoot (**A–E** from *J.L. Clark et al. 18185*). Photos by J.L. Clark.

throughout the upper and lower lobes are unique characters not found in any other known species of *Columnea*.

Description. Terrestrial subshrub with dorsiventral shoots, 1.0–1.5 m tall, stems green with densely pilose rust to gold-colored multicellular hispid indumentum; internodes 1.0–2.5 cm long. Petioles 1.0–2.5 cm long, red, with densely pilose to gold-colored multicellular hispid indumentum; leaves opposite, pairs strongly anisophyllous, larger leaf 9.0–15.0 cm long, 4.0–7.0 cm wide, ovate-elliptic, apex acuminate, base rounded and slightly oblique, lateral veins 5–9 per side, adaxially light-green, with multicellular hispid indumentum, abaxially uniformly-red, with multicellular hispid indumentum, more densely pubescent on veins, margin entire; smaller leaf 1.0–2.0 cm long, 0.9–1.5 cm wide, lateral veins 2–3 per side, petiole 1–2 mm long, otherwise similar to larger leaf. Inflorescence reduced to 1–3 axillary flowers; bracts triangular, green, 2–3 mm at base, apex broadly acuminate. Pedicels 1.0–1.8 cm long, dark red, densely pilose with multicellular rust-colored hispid indumentum. Calyx lobes uniformly green or green suffused with red, 1.0–1.7 cm long, 0.5–0.7 cm wide at base, oblong, apex acuminate, exterior pilose, with multicellular rust-colored hispid indumentum, interior glabrous, margin mostly entire or with 1–3 serrations. Corolla 5.0–6.2 cm long, 2.0 cm at widest (apex) point, deeply bilabiate, lower lobe recurved, 1.8–2.2 cm long, 3–4 mm wide, lateral and upper lobes fused into a hood, lateral lobes reflexed, rounded, 5 mm at base with acuminate apex, upper lobes fused, 1.0 cm wide, 1.3 cm long, apex bilobed, each lobe rounded, densely pubescent with multicellular rust-colored trichomes, interior uniformly dark purple, covered with glandular trichomes, occasionally with yellow margins, especially along the lower lobes, outer surface dark purple to dark purple suffused with yellow. Filaments ca. 3.5 cm long, connate at base for 0.3 cm and adnate to corolla, anthers ca. 3.0 mm long, 3.0 mm wide, included in the corolla throat, quadrangular. Ovary ca. 4.0 mm long, conical, glabrescent; style 3.5–4.0 cm long, glabrescent, stigma rounded. Nectary comprised of one large dorsal and two smaller lateral glands. Fruit not observed.

Phenology. Collected in flower in January.

Etymology. The specific epithet reflects the type locality, Cerro Golondrinas, where this species is presumably endemic.

Distribution and preliminary assessment of conservation status. *Columnea golondrinensis* is only known from a single population on a ridgeline in Cerro Golondrinas. The region is protected by the recent acquisition and purchase of forest by Fundacion EcoMinga. The forest corresponds to the Chocó Biogeographic Region for the relatively high levels of precipitation and epiphytic diversity. Based on the available information and according to the IUCN Red List criteria (IUCN 2012; IUCN Standards and Petitions Committee 2024), *C. golondrinensis* is preliminarily assessed as Vulnerable (VU) based on a limited area of occupancy (IUCN criterion D2 where AOO < 20 km^2) and limited number of locations (< 5).

Comments. Most *Columnea* are epiphytic and terrestrial with primary shoots that are characterized as erect, horizontal, dorsiventral (associated with facultative epiphytes), or pendent. The species described here was observed as a multibranched terrestrial subshrub with dorsiventral shoots. It was not observed growing epiphytically and was only observed on a ridgeline

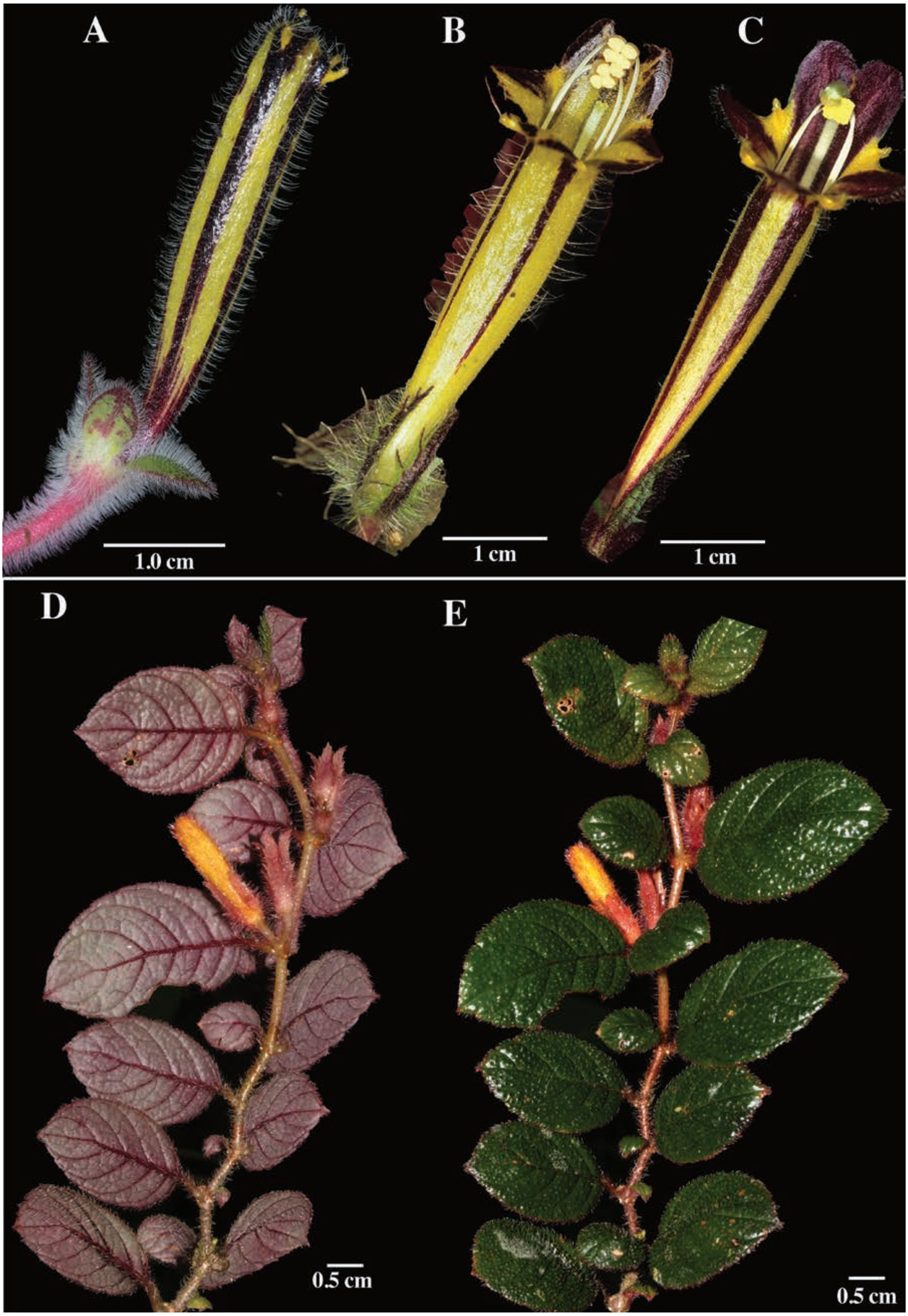

Figure 2. **A** *Columnea formosa* (C.V.Morton) C.V.Morton **B** *Columnea illepida* H.E.Moore **C** *Columnea purpureovittata* (Wiehler) B.D.Morley **D, E** *Columnea suffruticosa* J.F.Sm. & L.E.Skog (**A** from *J.L. Clark et al. 19154* **B** from *J.L. Clark et al. 9500* **C** from *L. Jost 3224* **D, E** from *J.L. Clark et al. 19448*). Photos **A, B, D** and **E** by J.L. Clark. Photo **C** by Lou Jost.

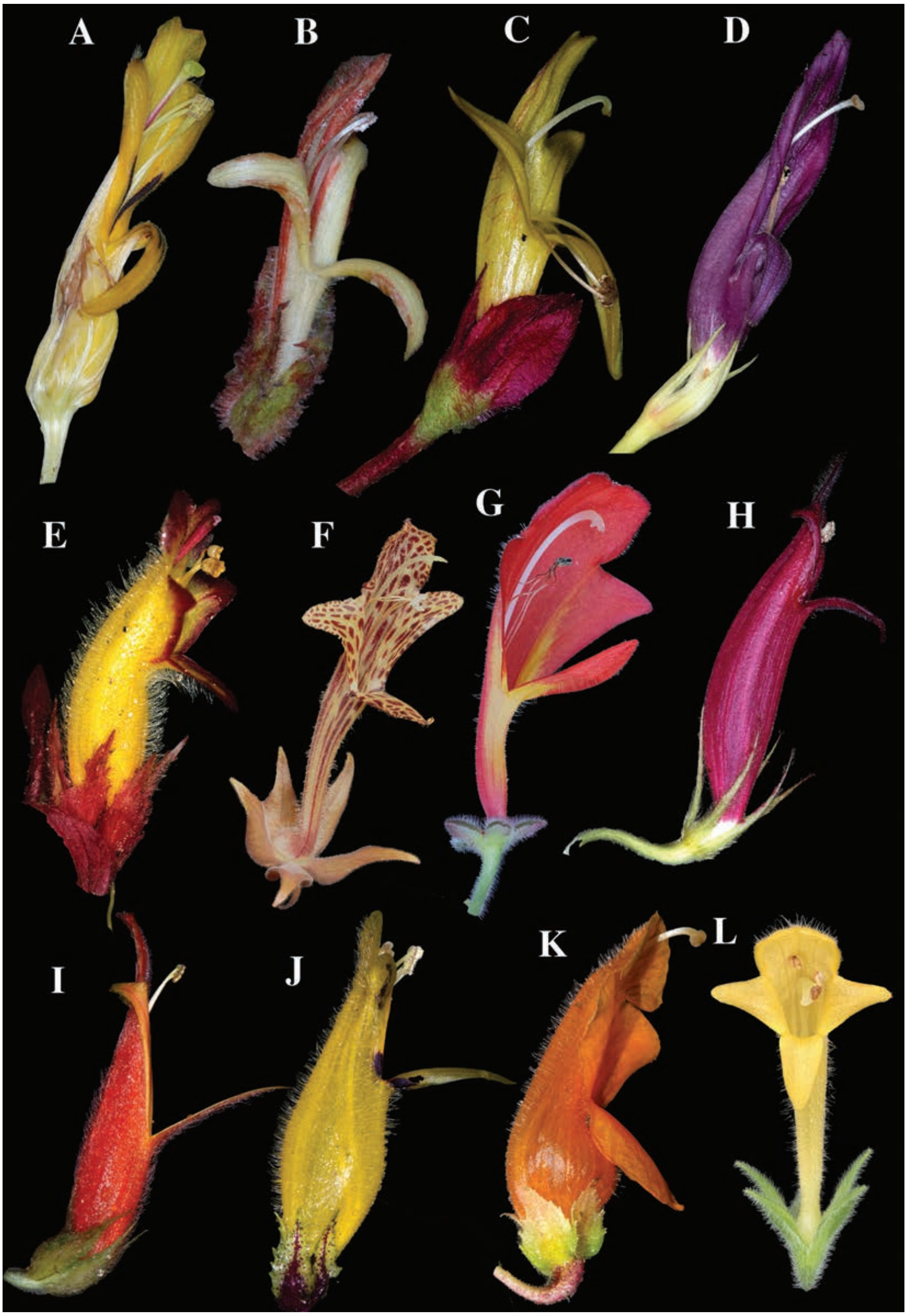

Figure 3. Examples of bilabiate corollas in *Columnea* **A** *Columnea karsteniana* R.Kr.Singh **B** *C. fawcettii* (Urb.) C.V.Morton **C** *C. tincta* Griseb. **D** *C. stilesiana* M.Amaya & L.P.Kvist **E** *C. eubracteata* Mansf. **F** *C. schiedeana* Schltdl. **G** *C. florida* C.V.Morton **H** *C. ferruginea* J.F.Sm. & J.L.Clark **I** *C. ceticeps* J.L.Clark & J.F.Sm. **J** *C. kucyniakii* Raymond **K** *C. strigosa* Benth. **L** *C. hirsuta* Sw. (**A** from *J.L. Clark 13159*, **B** from *J.L. Clark 11321*, **C** from *J.L. Clark 12775*, **D** from *J.L. Clark 19470*, **E** from *J.L. Clark 7686*, **F** from *J.L. Clark 18639*, **G** from *J.L. Clark 17645*, **H** from *J.L. Clark 19439*, **I** from *J.L. Clark 17737*, **J** from *J.L. Clark 16303*, **K** from *J.L. Clark 17611*, **L** from *J.L. Clark 17737*). Photos **A–E, H–K** by J.L. Clark. Photos **F, G** and **L** by Wade Collier.

with a low canopy and low-growing shrubs where epiphytic diversity was lower. Thus, surrounding forests with higher canopies could host *C. golondrinensis* as an epiphyte.

Several species of *Columnea* have purple-brownish coloration on the corolla tube, but these are consistently mostly yellow with narrow bands of horizontal purple-brownish stripes (Fig. 2). In contrast, the corolla color in *C. golondrinensis* is mostly dark purple to brown with yellow margins on the lower lip. The corolla colors in *C. golondrinensis* are unique amongst all known members of *Columnea*.

Corolla lobes in *Columnea* are always fused and either shallowly bilabiate or nearly radial (Fig. 2C) to bilabiate (Figs 1, 3). The more common form of bilabiate corolla tubes in *Columnea* is shallowly bilabiate (Fig. 3E, F, H, L) where the lower lip is about the same size as the lateral lobes. The least common form of bilabiate corolla tubes in *Columnea* is deeply bilabiate (Fig. 3A–D) where the lower lip is half the length of the lateral lobes. The corolla tube in *C. golondrinensis* corresponds to deeply bilabiate (Fig. 1), the least common corolla form in *Columnea*. Some examples of *Columnea* with deeply bilabiate corollas include *Columnea karsteniana* R.Kr.Singh (Fig. 3A), *C. fawcettii* (Urb.) C.V.Morton (Fig. 3B), *C. tincta* Griseb. (Fig. 3C), *C. stilesiana* M.Amaya & L.P.Kvist (Fig. 3D), and *C. strigosa* Benth. (Fig. 3K). The presence of dense clusters of glandular trichomes covering the inner surface of the corolla (especially the lower lip) in *C. golondrinensis* (Fig. 1A) is also relatively uncommon in *Columnea*. Two species with glandular trichomes on the lower corolla lip include *C. karsteniana* (Fig. 3A) and *C. stilesiana* (Fig. 3D), but the glandular trichomes are less apparent and more sparsely distributed. The combination of glandular trichomes on the inner corolla surface (Fig. 1A), deeply bilabiate corollas (Fig. 1B, C), dark purple corollas (Fig. 1), and ovate leaves with rust-colored multicellular hispid indumentum (Fig. 1D, E) are unknown in any other species of *Columnea*. The combination of these characters are remarkable and support *C. golondrinensis* as unique and distinct from all other congeners.

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

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Data availability

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

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Research Article

The genus *Plagiothecium* (Plagiotheciaceae) in Europe — current state of knowledge, checklist and key to taxa

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Abstract

This manuscript presents current knowledge of the taxonomy, variability and distribution of taxa of the genus *Plagiothecium* in Europe. Currently the genus comprises 31 taxa: 17 species and 14 varieties. In this study I designated 10 lectotypes and proposes six new synonyms for the described taxa, in addition five new nomenclatural combinations: *P. denticulatum* var. *pseudosylvaticum*, *P. denticulatum* var. *pungens*, *P. laetum* var. *hercinicum*, *P. succulentum* var. *cryptarum*, and *P. sylvaticum* var. *immersum*. Detailed descriptions and distribution data for each taxon, illustrations highlighting key taxonomic features and a diagnostic key are also provided to facilitate the identification of individual taxa.

Key words: Distribution, lectotype, new combinations, new synonyms, new taxa, resurrection

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Introduction

Plagiothecium Schimp. is a pleurocarpous genus with a global distribution, with the most frequently recorded and most widespread species being in the Northern Hemisphere (e.g., Jedlička 1948, 1950, 1961; Sakurai 1949; Ireland 1969, 1985, 1992; Iwatsuki 1970; Lewinsky 1974; Ireland and Buck 1994; Ochyra et al. 2008; Wynns et al. 2017; Wolski et al. 2020, 2021a, 2022a, b, 2024). In the Southern Hemisphere, there are significantly fewer species, but as recent studies indicate, this is still an area with an under-recorded number of taxa of this genus (Wolski et al. 2024).

This genus was first described in *Bryologia Europea* (Bruch et al. 1851). Since then, due to its usually medium to large size and very characteristic, flattened habit, it has been an included element of all bryological revisions and monographs (e.g., Paris 1894–1898; Dixon 1904; Brotherus 1923; Mönkemeyer 1927; Grout 1932; Podpěra 1954; Szafran 1960) and has never been omitted by bryologists.

Throughout history, the genus *Plagiothecium* has also undergone a relatively large number of national or continental revisions (Jedlička 1948, 1950, 1961; Sakurai 1949; Greene 1957; Ireland 1969, 1985, 1992; Iwatsuki 1970; Lewinsky 1974; Buck and Ireland 1989; Ireland and Buck 1994; Buck 1998; Li and Ireland 2011; Ignatova et al. 2019; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2022a, b, 2024). An attempt to revise this genus on a global scale was also made (Wynns 2015). However, such a broad approach will not provide an accurate picture of the relations between individual taxa, because, as recent years of research have shown, almost every epithet in this genus, and every complex, requires verification of its taxonomic status (Wolski and Nowicka-Krawczyk 2020; Wolski and Proćków 2020, 2021; Wolski et al. 2021a, 2022a-b, 2024).

Revisions by earlier scientists (Jedlička 1948, 1950, 1960; Sakurai 1949; Greene 1957; Ireland 1969, 1985, 1992; Iwatsuki 1970) had a great influence on later generations of bryologists, shaping in a certain way the perceptions of the genus. Most importantly, the above-mentioned articles also influence our current perception of individual taxa of *Plagiothecium* (e.g., Lewinsky 1974; Noguchi 1994; Smith 2001; Cano 2018; Li and Ireland 2011).

Revisions made in the previous century resulted in the fact that in the history of this genus we can distinguish two periods — the first one connected with the multiplication of the number of individual taxa (e.g., Jedlička 1948, 1950, 1960; Sakurai 1949), and the second one, initiated independently by Ireland (1969, 1985) and Iwatsuki (1970) — the reductionist period. The reduction of the number of taxa was connected with the mass synonymization of individual names in *Plagiothecium*. It led to the fact that in Europe, out of 117 taxa distinguished by Jedlička (1948, 1950), within about 25 years, Lewinsky (1974) reported only 11 species. This idea and reductionist approach was adopted by subsequent researchers and for decades was widely accepted by bryologists (Noguchi 1994; Smith 2001; Iwatsuki 2004; Suzuki 2016; Cano 2018).

This overly broad treatment of individual taxa of *Plagiothecium* resulted in individual researchers very often pointing out that species within the genus are highly variable and cause a number of taxonomic difficulties (Nyholm 1965; Noguchi 1994; Smith 2001; Wolski 2017, 2018; Cano 2018).

The latest literature (Wynns et al. 2017; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2020, 2021b, 2022a, b, c, 2024) presents a balanced approach, which does not align very closely with the reductionist vision of most predecessors, nor with the synonymizations proposed by them (e.g., Ireland 1969, 1985; Iwatsuki 1970; Lewinsky 1974). Thus, the aforementioned studies not only resurrected a number of previously synonymized taxa, but also allowed for the description of new species. This clearly indicates that the number of taxa from individual continents is greatly under-estimated (Wynns et al. 2017; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2020, 2021b, 2022a, b, c, 2024).

Taking into account the above and the relatively rapid changes in the taxonomy of *Plagiothecium*, the aim of the following manuscript is to collect all current knowledge on the genus in Europe, to create a checklist of the accepted infrageneric taxa and to present a key for the identification of European taxa.

Materials and methods

The following study, including the data contained therein, is part of the results obtained from my ongoing revision of the genus *Plagiothecium* since 2016. The results below are a compilation of my published works (Wolski 2020; Wolski and Nowicka-Krawczyk 2020; Wolski and Proćków 2020, 2021, 2022; Wolski et al. 2020, 2021a, 2022 a-d) as well as my unpublished data.

The conducted research and revision were based on herbarium collections from 52 world herbaria (AAU, B, BG, BM, BRA, BRNU, C, CP, E, F, FH, G, GB, H, HBG, JE, IBL, KRAM B, LBL, LOD, M, MANCH, MICH, MO, MU, NTNU, NY, OXF, PL, POZG-B, PC, PR, PRC, S, SLO, SOSN, SZUB-B, TAA, TALL, TAM, TRH, TROM, TU, TUB, TUR, UBC, UME, UPS, YU, VLA, WRSL), including the study of 90 nomenclature types of this genus.

The division of species according to cell areolation was made according to the width of the cells from the middle part of the leaf. Whereby when the cells were 7–9 µm wide, areolation was recognized as tight; cells 11–15 µm wide are termed quite loose; cells 16–19 µm are referred to as loose; while with cells above 20 µm wide, areolation was considered as very loose.

Data on the geographical distribution of individual taxa were taken from the labels of herbarium specimens and were supported by literature data.

Results

Currently, in Europe, within the genus *Plagiothecium*, 31 taxa can be distinguished, belonging to eight sections. The most speciose are the sections *Orthophyllum* Jedl. (11 taxa) and *Leptophyllum* Jedl. (nine). On the other hand, the least speciose are four sections: *Philoscia* (Berk.) Ochyra, *Rectithecium* (Hedenäs and Huttunen) J.T.Wynns, *Pseudo-Neckera* (Kindb.) J.T.Wynns and *Lycambium* Jedl. (each with a single species).

The results of this research not only allows for the proposal of five new combinations, the designation of 10 lectotypes and the proposal of six new synonyms, but also shows that the diversity of *Plagiothecium* in Europe is still under-estimated.

Detailed description of individual taxa

Sect. *Plagiothecium*

Plagiothecium denticulatum var. ***denticulatum*** (Hedw.) Schimp., Bryologia Europea 5: 190, 501, Tab. VIII. 1851.

≡ *Hypnum denticulatum* Hedw., Species Muscorum Frondsorum 237. 1801 ≡ *Stereodon denticulatus* (Hedw.) Brid., Bryologia Universa 2: 824. 1827 ≡ *Pancovia denticulata* (Hedw.) J.Kickx f., Flore Cryptogamique des Flandres 1: 93. 1867. Lectotype (designated by Ireland 1969): Germany, *Starke*, G 000420240!

= *Plagiothecium denticulatum* var. *bullulae* Grout, North American Musci Perfecti 450 1942. Lectotype (designated here): U.S.A., Idaho, Elmore Co., Boise National Forest, on soil and base of saplings by small water course above cemetery, 22 Sep. 1942, *F. A. MacFadden*, C-M-9386! Isolectotypes: MO-406576, NY 505676, NY 507145.

= *Plagiothecium sylvaticum* var. *rupestre* Warnst. *ex* Grav., Bulletin de la Société Royale de Botanique de Belgique 19: 31. 1880. Lectotype (designated here): Germany, Bavar. Australis, ad rupes silic. umbros. montium editiorum Silvae Gabretae, parietes verticals investiens, ca. 800–1000 m, Aug 1879, sub “*P. silvaticum* var. *rupestre* Progel”, *Progel*, PC 0132568! Isolectotypes: Germany Baiern, Waldmünchen am Böhmerwald, auf Gneissfelsen im Juni, *Progel*, PC 0132569! syn. nov.

Description. Plants medium-sized, light to dark green, with metallic luster; stems 2–5 cm long; leaves complanate, more julaceous in lower part of stem, concave, ovate, asymmetrical, with two rounded sides, rounded asymmetric, 1.5–3.0 × 0.5–2.0 mm (Fig. 1A); the apex acute to acuminate; margins denticulate near the apex; laminal cells 80–130 × 10–14 µm at midleaf (Fig. 1D), cell areolation quite loose; decurrencies well developed, consisting of 4–5 rows of spherical, inflated cells; capsule inclined.

Distribution. Asia (Azerbeijan, Bangladesh, China, Democratic People's Republic of Korea, Iraq, India, Islamic Republic of Iran, Japan, Kazakhstan, Kyrgystan, Mongolia, Nepal, Pakistan, Republic of Korea, Russian Federation); Europe (Albania, Andorra, Armenia, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Kosovo, Latvia, Lichtenstein, Lithuania, Luxembourg, Montenegro, Netherlands, North Macedonia, Norway, Poland, Portugal, Romania); North America (Canada, U.S.A.).

Plagiothecium denticulatum **var.** ***obtusifolium*** **(Turner) Moore, Proceedings of the Royal Irish Academy 1: 424. 1873.**

≡ *Hypnum denticulatum* var. *obtusifolium* Turner, Muscologiae Hibernicae Spicilegium 146, T. 12, f. 2. 1804 ≡ *Hypnum obtusifolium* (Turner) Brid., Muscologiae Recentiorum Supplementum 2: 93. 1812 ≡ *Stereodon denticulatus* var. *obtusifolius* (Turner) Brid., Bryologia Universa 2: 824. 1827 ≡ *Plagiothecium obtusifolium* (Turner) J.J.Amann, Mémoire de la Société Vaudoise des Sciences Naturelles 3: 61. 1928. Holotype: figure 2, tabela 12 "T. 12, f. 2", Turner 1804: 237. Epitype (designated by Wolski et al. 2022d): [Ireland,] in summo montis Bulbein jugo, ab oculatissimo *D. Brown* lectam, benigne communicavit *D. Templeton*, BM 000890810!

= *Plagiothecium sandbergii* Renauld & Cardot, Contributions from the United States National Herbarium 3: 274. 1895. Lectotype (designated by Wolski et al. 2022d): U.S.A., Idaho, Kootenai County, Hope, *J. H. Sandberg*, *D. T. Macdougal*, *A. A. Heller 1174*, August 1892, PC 0132604! Isolectotypes: NY 507114! (available online), US 70396! (available online), FH 220148. Additional original material from *locus classicus* (not signed "*No. 1174*"), NY 507115! (available online); additional *Sandberg* material, potentially from *locus classicus* PC 0132605! and *Sandberg* material FH 220147.

= *Plagiothecium denticulatum* var. *auritum* Kern, Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur 91(Abt. 2b): 97. 1914. Lectotype (designated by Wolski et al. 2022d): [Italy,] South Tirol, Ortler, Martelltal, in Felshöhlungen oberhalb der Cevedalehütte, 2350 m, 30 July 1913, *F. Kern s.n.*, herb. *I. Thériot*, PC 0132639!

Description. Plants small, light green, with metallic luster; stem 0.9–2.5 cm; leaves julaceous, very concave, ovate-elliptical, gently asymmetrical, 1.0–2.2 × 0.5–1.2 mm (Fig. 1B); the apex obtuse, not denticulate; laminal cells linear, 50–140 × 10–21 µm at midleaf (Fig. 1E), cell areolation quite loose; decurrencies broad, alar cells rounded.

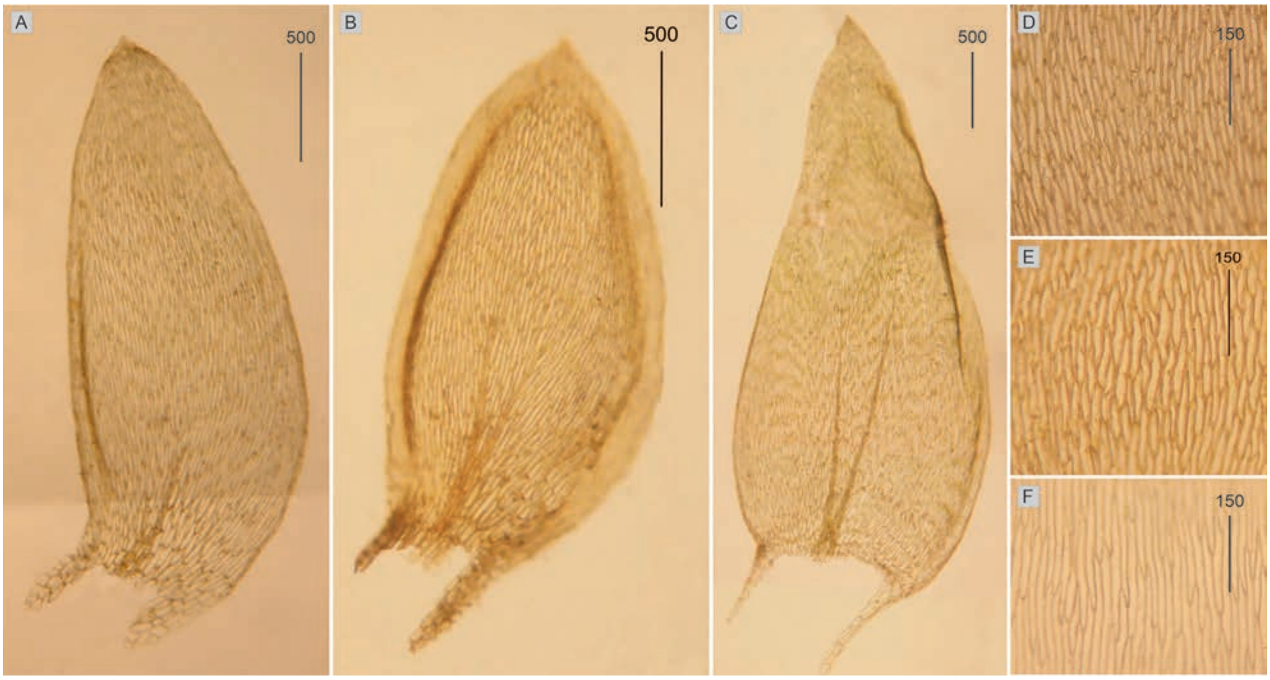

Figure 1. Selected, most important taxonomic features of taxa from the *Plagiothecium denticulatum* complex **A–C** shape and dimensions of the leaves **D–F** shape and dimensions of cells from the middle part of the leaves **A**, **D** *P. denticulatum* var. *denticulatum* (from type of *P. denticulatum* var. *bullulae*, *F. A. MacFadden*, C-M-9386!) **B**, **E** *P. denticulatum* var. *obtusifolium* (from epitype of *P. denticulatum* var. *obtusifolium*, *D. Templeton*, BM 000890810!) **C**, **F** *P. denticulatum* var. *undulatum* (from samples of *P. ruthei*, *S. Lisowski*, POZN-B 12388!).

Distribution. Asia (China, Islamic Republic of Iran, Japan, Nepal, Russian Federation, Turkey); Europe (Austria, Bulgaria, Czech Republic, Finland, France, Germany, Hungary, Iceland, Ireland, Italy, Kosovo, Luxembourg, Montenegro, Netherlands, Poland, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

Plagiothecium denticulatum **var.** ***undulatum*** **R.Ruthe *ex* Geh., Revue Bryologique 4: 42. 1877.**

≡ *Plagiothecium ruthei* Limpr., Die Laubmosse Deutschland, Oesterreichs und der Schweiz 3: 217. 1897 ≡ *Plagiothecium denticulatum* var. *majus* fo. *undulatm* (R.Ruthe *ex* Geh.) C.E.O.Jensen, Skandinaviens Bladmossflora 494. 1939 ≡ *Plagiothecium ruthei* subsp. *eu-ruthei* Giacomini, Istituto Botanico della R. Università R. Laboratorio Crittogamico Pavia, Atti 4: 278. 1947, nom. inval. Type: près de Barwalde, dans la Nouvelle-Marche, *R. Ruthe*, 1873.

Description. Plants medium-sized, light green, glossy; leaves complanate, transversely undulate, ovate to ovate-lanceolate, asymmetric, with one rounded and one flattened side, shrunken when dry, 2.0–2.5 × 1.0–1.2 mm (Fig. 1C); the apex acute to acuminate; margins denticulate near the apex or not; laminal cells 100–160 × 10–17 μm at the midleaf (Fig. 1F), cell areolation quite loose; decurrencies very long, consisting of 2–3 rows of rounded to rounded-rectangular and inflated cells; capsule inclined.

Distribution. Asia (China, Japan, Russian Federation); Europe (Austria, Belarus, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lichtenstein, Lithuania, Luxembourg, Montenegro, Netherlands, Poland, Romania, Slovakia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada).

Plagiothecium denticulatum **var.** ***pseudosylvaticum*** **(Warnst.** ***in*** **Schiffner) G.J.Wolski comb. nov.**

≡ *Plagiothecium pseudosylvaticum* Warnst. *in* Schiffner, Österreische Botanische Zeitschrift 48: 428. 1898. Lectotype (designated by Wynns 2015): [Germany,] Brandenburg, Neuruppin, an dem Waldwege zwischen Rottstiel und dem “Stern” auf von einer schwachen Humusdecke überlagertem Sandboden, 24 July 1897, *C. Warnstorf*, C-M-9394! Isolectotype: PC 0132600! Syntypes: [Poland,] in einer etwas schwächeren, bei Swinemünde, *R. Ruthe*; [Germany,] bei Schönebeck a.d. Elbe, Aug. 1892, *Fromm*. Apparent topotypes: [Germany,] Neuruppin, Osterwald auf Sand, zwischen Rottstiel und dem Stern, 22 July 1900, *C. Warnstorf*, S-B 160601; Sand., auf Waldboden, bei Rottstiel, July 1898, *C. Warnstorf*, PC 0132601!

Description. Plants medium-sized, light green to yellow green, glossy; stems 2.0–2.5 cm; two types of leaves: symmetrical and asymmetrical, the symmetrical ones: ovate-lanceolate, concave, with two rounded sides, rounded symmetric, asymmetrical ones: ovate-lanceolate, concave, with one rounded and one flattened side, both types of leaves identical in size, 2.0–2.5 × 0.8–1.3 mm (Fig. 2A); the apex acuminate, denticulate; laminal cells 100–130 × 15–20 μm at midleaf (Fig. 2C), cell areolation loose; decurrencies long, consisting of 3–5 rows of rounded and inflated cells; capsule inclined.

Distribution. Europe (Czech Republic, Germany, Poland), but the range of this taxon still requires research.

Plagiothecium denticulatum **var.** ***pungens*** **(Mönk.) G.J.Wolski, comb. nov.**

≡ *Plagiothecium sylvaticum* fo. *pungens* Mönk., Die Laubmoose Europas 865. 1927 ≡ *Plagiothecium denticulatum* fo. *pungens* (Mönk.) C.E.O.Jensen, Skandinaviens Bladmossflora 494. 1939. Lectotype (designated here): [Denmark,] Bornholm, an feuchten im Echotale bei Almindingen, sub *Plagiothecium Roeseanum* var. *orthocladon* fo. *pungens*, July 1910, *W. Mönkemeyer*, C-M-9396! Isolectotypes: [Denmark,] Bornholm, an feuchten im Echotale bei Almindingen, sub. *Plagiothecium silvatiucm* fo. *pungens*, July 1910, *W. Mönkemeyer*, HBG-021135!

Description. Plants medium-sized, yellow green to dark green; stems 1.0–2.0 cm, julaceous-foliate; leaves imbricate, concave, ovate, symmetrical, with two rounded sides, rounded symmetric, 2.0–2.5 × 1.0–1.2 mm (Fig. 2C); the apex acute to acuminate; margins denticulate near the apex; laminal cells 110–160 × 15–20 μm at midleaf (Fig. 2D), cell areolation loose; decurrencies well developed, consisting of 4–5 rows of spherical, inflated cells; capsules unknown for now.

Distribution. Europe (Denmark), but the range of this taxon still requires research.

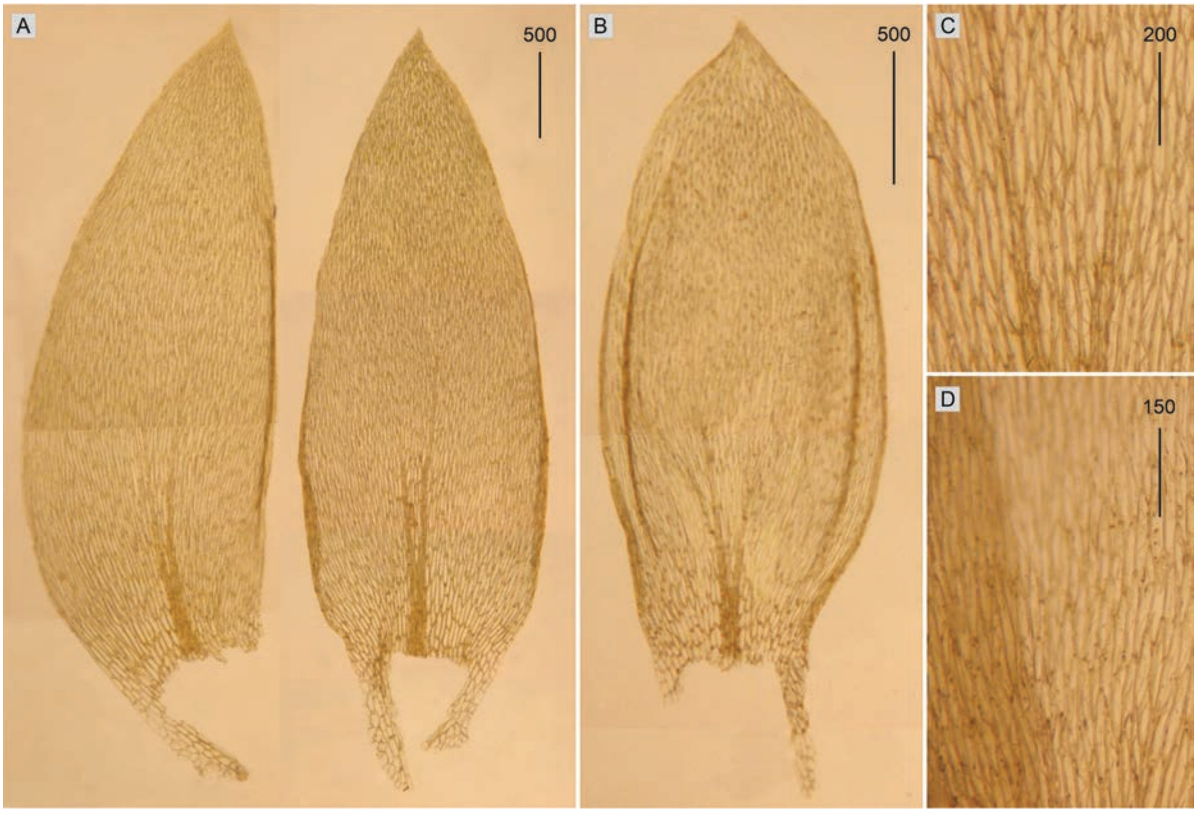

Figure 2. Selected, most important taxonomic features of taxa from the *Plagiothecium denticulatum* complex **A, B** shape and dimensions of the leaves **C, D** shape and dimensions of cells from the middle part of the leaves **A**, **C** *P*. *denticulatum* var. *pseudosylvaticum* (from lectotype of *P*. *pseudosylvaticum*, *C*. *Warnstorf*, C-M-9394!) **B**, **D** *P*. *denticulatum* var. *pungens* (from lectotype of *P*. *silvaticum* fo. *pungens*, *W*. *Mönkemeyer*, C-M-9396!).

Sect. *Rostriphyllum* Jedl.

Plagiothecium sylvaticum var. *sylvaticum* (Brid.) Schimp., Bryologia Europea 5: 192, 503. 1851.

≡ *Hypnum sylvaticum* Brid., Muscologiae Recentiorum 2(2): 53, 1 f. 5. 1801 ≡ *Hypnum denticulatum* var. *sylvaticum* (Brid.) Turner, Muscologiae Hibernicae Spicilegium 146. 1804 ≡ *Stereodon sylvaticus* (Brid.) Brid., Bryologia Universa 2: 825, 1827 ≡ *Hypnum denticulatum* subsp. *sylvaticum* (Brid.) Boulay, Muscinées de la France, Mousses 85. 1884 ≡ *Plagiothecium denticulatum* subsp. *sylvaticum* (Brid.) Dixon, Student's Handbook of British Mosses 437. 1896. Lectotype (the clump at the top of the sheet, selected by Iwatsuki 1970): [Germany,] saltus Thuringicus in paluda, *ex* herb. Brid., B 31091501!

= *Plagiothecium sylvaticum* var. *flavescens* Warnst., Allegmeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie 5(1): 34. 1899. Lectotype (designated here): [Germany,] am Gaisriegl Dreitannenriegel, Bayr Wald, in Quellsümpfen, 1887, *M. Lickleder*, PC 0132583! syn. nov.

= *Plagiothecium platyphyllum* Mönk., Die Laubmoose Europas 866, 207b. 1927 ≡ *Plagiothecium sylvaticum* var. *platyphyllum* (Mönk.) F.Koppe, Abhandlungen und Berichte der Naturwissenschaftlichen Abteilung der Grenzmärkischen Gesellschaft zur Erforschung und Pflege der Heimat, Schneidemühl 1931 ≡ *P*. *neglectum* subsp. *platyphyllum* (Mönk.) Szafran, Flora Polska Mchy (Musci) 2: 288, 1961, *comb*. *inval*. Type: Germany, bei Gersfeld in der Rohn 1906, ferner mir aus Thüringen unddem sächsischen Vogtlande unter anderer Bezeichnung bekannt geworden; The Czech Republic, ferner 1911 im Böhmerwalde bei Eisenstein gesammelt. Lectotype (designated by Wolski et al. 2024): Germany, Thüringien, Finsteres Loch, 26 June 1916, *R. Schmidt*, HBG!

= *Plagiothecium ruthei* fo. *submersum* Bizot, *in sched*. Basis: France, Vosges, Hohneck, immergé dans le lac du Frankenthal, *M. Bizot 2910*, PC 0132598!

= *Plagiothecium ruthei* var. *rivulare* Mayl. *in sched*. Basis: Switzerland, Uri, entre Göschenen et Andermatt, Sep., 1903, *Thériot*, *J. J. Amann*, PC 0132602! syn. nov.

Description. Plants medium-sized to large, light green, dull, without metallic luster; leaves complanate, more or less flat, ovate, not imbricate and not julaceous, symmetrical, 2.0–3.0 × 1.0–1.6 mm (Fig. 3A); the apex acute and denticulate, often eroded; laminal cells 75–160 × 12.5–20 μm at midleaf (Fig. 3D), cell areolation loose; decurrencies long, consisting of 3–4 rows of rounded and inflated cells; capsule inclined.

Distribution. Asia (China, Democratic People's Republic of Korea, Georgia, Islamic Republic of Iran, Japan, Republic of Korea, Russian Federation, Turkey); Europe (Andorra, Austria, Bulgaria, Croatia, Czech Republic, Denmark, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Kosovo, Lithuania, Luxembourg, Montenegro, North Macedonia, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

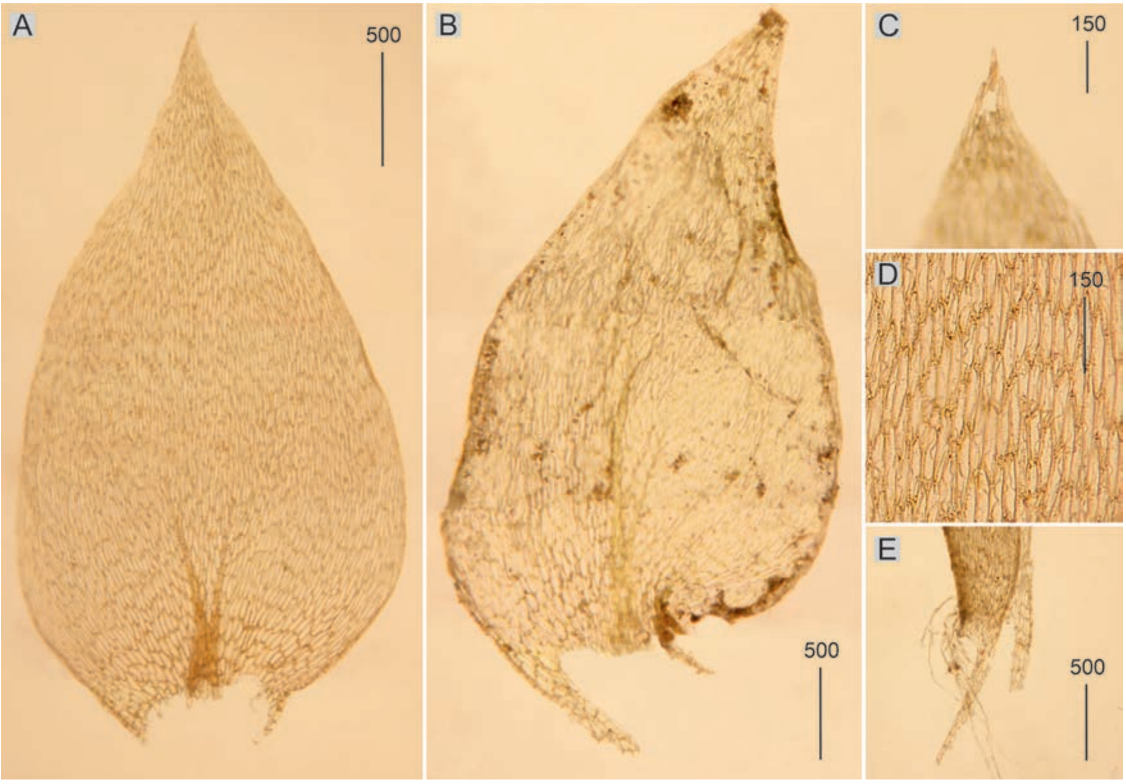

Figure 3. Selected, most important taxonomic features of taxa from the *Plagiothecium sylvaticum* complex **A, B** shape and dimensions of the leaves **C** eroded leaves apex **D** apex and dimensions of cells from the middle part of the leaves **E** rhizoids on the dorsal side of the leaf **A**, **D** *P. sylvaticum* var. *sylvaticum* (from lectotype of *H. sylvaticum*, *S. É. Bridel*, B 31091501!, based on Wolski et al. 2024, changed) **B**, **C**, **E** *P. sylvaticum* var. *immersum* (from lectotype of *P. platyphyllum* fo. *immersa*, *Lorrens*, HBG-021127!).

Plagiothecium sylvaticum var. *immersum* (Mönk.) G.J.Wolski, comb. nov.

≡ *Plagiothecium platyphyllum* fo. *immersa* Mönk., Die Laubmoose Europas 867. 1927. Type: [Germany,] Aus dem Harze, Thüringen, der Rhön, dem Fichtelgebirge, aus Böhmen, dem Bayerischen Walde, Mähren, der Schweiz (Kanton Uri), Norditalien (Provinz Como) und Bulgarien mir bekannt geworden. Lectotype (designated here): [Switzerland,] Kanton Uri, Schöllenen, 1100–1400 m, 18 August 1884, *Lorrens*, HBG-021127!

Description. Plants large, dark green, dull, without metallic luster; leaves asymmetrical, complanate, ovate, not imbricate and not julaceous, 3.4–3.6 × 1.4–2.0 mm (Fig. 3B), often with rhizoids on the dorsal side of the leaf (Fig. 3E); the apex acute and denticulate, often eroded (Fig. 3C); laminal cells 90–150 × 8–16 µm at midleaf, cell areolation loose; decurrencies long, consisting of 3–5 rows of rounded and inflated cells; capsule unknown so far.

Distribution. Europe (Bulgaria, Czech Republic, Italy, Switzerland), but the range of this taxon still requires research.

Sect. *Orthophyllum* Jedl.

Plagiothecium nemorale (Mitt.) A.Jaeger, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1876–1877: 451. 1878.

≡ *Stereodon nemoralis* Mitt., Journal of the Proceedings of the Linnean Society, Botany, Supplement 1(2): 104. 1859 ≡ *Plagiothecium silvaticum* var. *nemorale* (Mitt.) Paris, Index Bryologicus 967. 1898. Type: *Hab*. in Himalayae orient. reg. temp., Sikkim, in monte Tonglo (ad radicem filicis cujusdam), *J. D. Hooker*. Lectotype (designated by Wolski et al. 2020): Herb. ind or *Hook*. Fil. & *Thomson Stereodon nemorale* m. Hab. Sikkim, Tonglo Regio temp. Alt. – *J.D.H*., BM 1030713! Isolectotype: NY 913349!

= *Plagiothecium neglectum* Mönk., Die Laubmoose Europas 866. 1927. Lectotype (designated by Wolski and Proćków 2022): figure 207c excluding a part of the figure with the top of the leaf (Mönkemeyer 1927: 862). Epitype (designated by Wolski and Proćków 2022): [Germany,] Wesergebirge, in Erlenbrüchen bei Eschershausen, Juli 1900, *W. Mönkemeyer s.n.* B 300105646! The remaining original material according to Walter and Martienssen (1976) was confirmed to have been lost at HBG: Thüringen: Eisenach, Annatal, 26.7.1898, u. Wartburg, 2.5.1915 (*J. Bornmüller s.n.*); Wesergebirge: Bodenwerder, Königszinne, Juli 1901 (*W. Mönkemeyer s.n.*); Hessen, Rhön: Gr. Nallen, Juli 1906 (*W. Mönkemeyer s.n.*); Vogtland: Plauen, Triebtal, 25.07.1904 (*E. Stolle s.n.*); Bayern: Allgäu, Hinterstein, Sauwald, Aug. 1906, u. Regensburg, U-Lichtenwald, Schindelmacherhänge, Nov. 1906 (*I. Familler s.n.*); Prien/Chiemsee: 500 m, Juni 1911 (*T. Linder s.n.*); Mähren: Oppafall, Juli 1904 (*J. Podpěra s.n.*); Ostpreuβen: Labiau, Juli 1864 (*H. v. Klinggräff s.n.*); Kurland: Usmaitensee, Moritzholm, Mengwald, 3.8.1913 (*K. R. Kupffer s.n.*); sine loc. et dat. (*Wüstnei 380*).

= *Plagiothecium saxicola* Sakurai, Botanical Magazine, Tokyo 48: 395. 1934. Type: [Japan,] Honshu, Prov. Aki, 4 Jan 1933, *Y. Doi 3282*, PC 0132573!

Description. Plants medium-sized, dark green, dull, without metallic luster; stems to 1.5–3.0 cm long; leaves complanate, in dry condition shrunken, concave, symmetrical, ovate, those from the middle of the stem 2.2–2.4 × 1.0–1.5 mm (Fig. 4A); the apex acuminate, apiculate and denticulate; laminal cells hexagonal in transverse rows, 50–90 × 17–20 µm at mid-leaf (Fig. 4D), cell areolation loose; decurrencies of 3 rows of rectangular cells; capsule inclined.

Distribution. Asia (Azerbeijan, Bhutan, China, Democratic People's Republic of Korea, Georgia, India, Islamic Republic of Iran, Japan, Myanmar, Nepal, Pakistan, Philippines, Republic of Korea, Russian Federation, Taiwan, Turkey, Vietnam); Europe (Albania, Andorra, Armenia, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Italy, Ireland, Kosovo, Latvia, Lichtenstein, Lithuania, Luxembourg, Montenegro, Netherlands, North Macedonia, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

Plagiothecium longisetum **Lindb., Contributio ad Floram Cryptogamam Asiae Boreali-Orientalis 232. 1872 [1873].**

= *Plagiothecium roeseanum* var. *heterophyllum* Warnst., Kryptogamenflora der Mark Brandenburg, Laubmoose 814. 1906 ≡ *Plagiothecium roeseanum* fo. *heterophyllum* (Warnst.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 40. 1948. Type: Germany, Brandenburgia, Neurippen, Ruppin, auf Waldboden, Böschungen im "Flössergrunde", *C. Warnstorf*; Westprignitz, Forsthaus "Alte Eiche", auf Waldboden am Standort von *Osmunga regalis*, *Janzen* und *C. Warnstorf*; Wittenberge, Westprignitz, am Grunde eines Baumstammes, "Krauses Brack", *C. Warnstorf*; Ratzburg, Buchenwälder, Prahl. Poland, Świnoujście, Weg nach Corswant, *R. Ruthe* (*n.v.*).

= *Plagiothecium mauiense* Broth., Bernice P. Bishop Museum Bulletin 40: 28. 1927. Lectotype (designated by Wolski and Proćków 2021): [United States,] Hawaii, E. Maui, Haleakala, 8000 ft., in damp ravines, fertile, June 1876, *D. D. Baldwin 221*, NY 01256708! Isolectotype: FH 00220142!, MU 000000546!, YU 233890!

= *Plagiothecium sylvaticum* var. *neglectum* fo. *orthocladum* Barkman, nom. inval., Buxbaumia, 11: 23. 1957. Type: no type was specified.

Type. [Japan,] ad Nikosan ins. Kiusiu, [fertile], 16 Junii 1863, *S. O. Lindberg*. Lectotype (designated by Wolski and Proćków 2020): H-SOL 1563011! Isolectotype: S-B 160017, PC 0132572!

Description. Plants medium-sized to large, green to yellowish, without metallic luster; stems 2–3 cm long; leaves complanate, concave, strongly asymmetrical, ovate to lanceolate, 3.0–4.0 × 1.6–2.0 mm (Fig. 4B); the apex acute to acuminate, not denticulate; laminal cells elongate-hexagonal, in irregular transverse rows, 94–150 × 17–34 µm at midleaf (Fig. 4E), cell areolation very loose; decurrencies of 3 rows of rectangular cells; capsule inclined.

Distribution. Asia (China, Georgia, India, Islamic Republic of Iran, Japan, Nepal, Russian Federation, Turkey); Europe (Austria, Belgium, Denmark, Estonia, Finland, France, Germany, Norway, Poland, Spain, Sweden, Switzerland, United Kingdom); North America (Canada, U.S.A.).

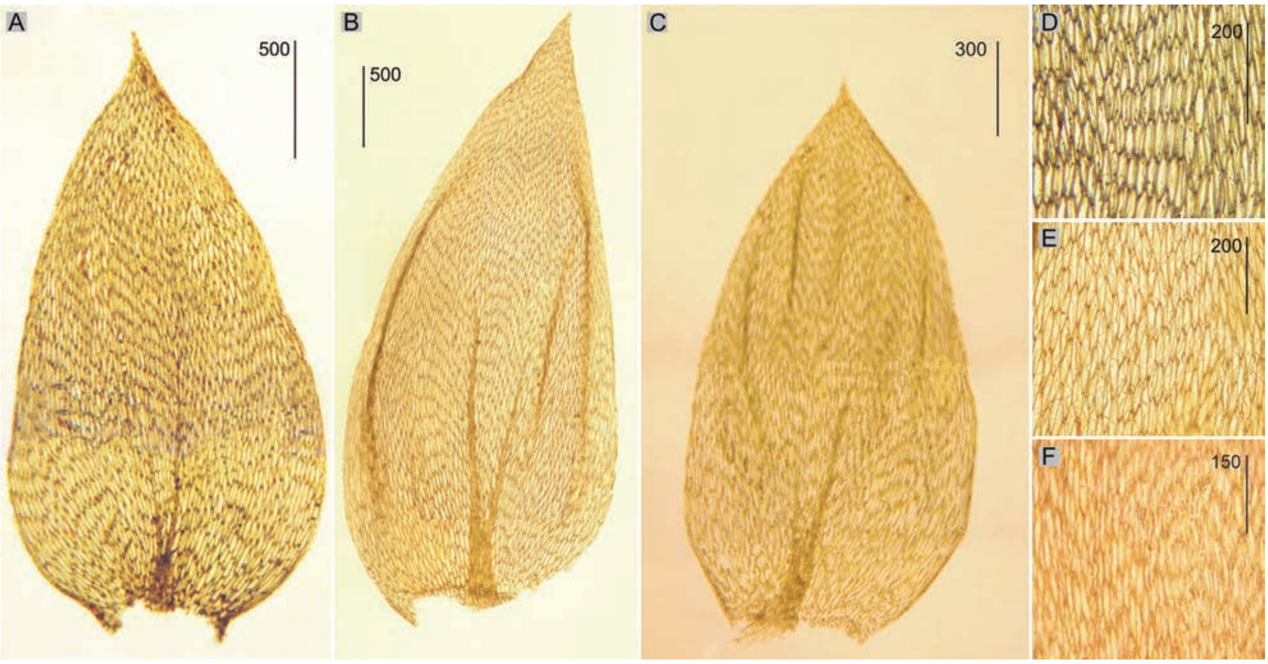

Figure 4. Selected, most important taxonomic features of taxa from the *Plagiothecium nemorale* complex **A–C** shape and dimensions of the leaves **D–F** shape and dimensions of cells from the middle part of the leaves **A**, **D** *P. nemorale* (from lectotype of *S. nemoralis*, *J. D. Hooker*, BM 1030713!, based on Wolski et al. 2020 changed) **B**, **E** *P. longisetum* (from lectotype of *P. longisetum*, *S. O. Lindberg*, H-SOL 1563011!) **C**, **F** *P. angusticellum* (*B. Goffinet*, *11,795*, NY 02331429, based on Wolski 2020, changed).

Plagiothecium angusticellum **G.J.Wolski & P.Nowicka-Krawczyk, PLoS ONE 15(3): e0230237. 2020.**

Holotype. Poland, łódzkie Voivodeship, Grądy nad Moszczenicą reserve, 51°55'N, 19°29'E, at the base of *Carpinus betulus* in *Fraxino-Alnetum* forest, 11 Dec. 2017, *G. J. Wolski*, LOD 14927! Isotype: LOD 14937!

Description. Plants medium-sized, light to dark green, dull, without metallic luster; stems 2–4 cm long; leaves julaceous and imbricate mainly on lower part of the stem, concave, folded, asymmetrical, ovate to lanceolate, 3.1–3.4 × 1.3–1.5 mm (Fig. 4C); the apex acuminate, short, often gently curved; margins not denticulate near the apex; laminal cells narrowly elongate-hexagonal, 113–143 × 15–19 µm at midleaf (Fig. 4F), cell areolation loose; decurrencies of 3 rows of rectangular to quadrate cells; capsule inclined.

Distribution. Europe (Czech Republic, Estonia, Hungary, Latvia, Lithuania, Poland); North America (U.S.A.).

Plagiothecium succulentum **var.** ***succulentum*** **(Wilson) Lindb., Botaniska Notiser 43: 143. 1865.**

≡ *Hypnum denticulatum* var. *succulentum* Wilson, Bryologia Britannica 407. 1855 ≡ *Hypnum succulentum* Wilson, Bryologia Britannica 407. 1855, nom. inval. ≡ *Plagiothecium sylvaticum* var. *succulentum* (Wilson) Spruce, Journal of Botany, British and Foreign 18: 357. 1880 ≡ *Plagiothecium denticulatum* var. *succulentum* (Wilson) Dixon, The Student's Handbook of British Mosses 437. 1896

≡ *Plagiothecium sylvaticum* ssp. *succulentum* (Wilson) Amann & Meyl., Flore des Mousses de la Suisse 1: 174. 1919 ≡ *Plagiothecium laetum* subsp. *succulentum* (Wilson) Szafran, Flora Polska Mchy (Musci) 2: 281. 1961. Type: [Great Britain,] Winwick Stone Quarry, near Warrington, *Wilson*; near Todmorden, *J. Nowell*.

= *Plagiothecium succulentum* fo. *flavescens* Mönk. *in sched*. Basis: [Denmark,] Insel Bornkolm, bei Helligdommen, Juli 1910, *W. Mönkemeyer*; [Germany,] Fichtelgebirge, unten Bischofsgrün, Juli 1903, *W. Mönkemeyer*; Leipzig, Eilenburg bei Gantsch. Oct. 1905, *W. Mönkemeyer*, HBG! syn. nov.

Description. Plants medium-sized to large, usually yellowish gold, golden green, golden, very glossy; stems to 3 cm long; leaves spreading, in dry condition not shrunken, complanate, symmetrical, ovate, 2.50–3.00 × 0.80–1.40 mm (Fig. 5A); apex acuminate and not denticulate; laminal cells 130–240 × 10–18 µm at midleaf (Fig. 5D), cell areolation quite loose; decurrencies of 2–3 rows of rectangular cells; capsule inclined.

Distribution. Asia (China, Democratic People's Republic of Korea, Georgia, Islamic Republic of Iran, Republic of Korea, Russian Federation, Turkey); Europe (Albania, Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iceland, Ireland, Italy, Kosovo, Latvia, Lithuania, Luxembourg, Montenegro, Netherlands, North Macedonia, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada and U.S.A.).

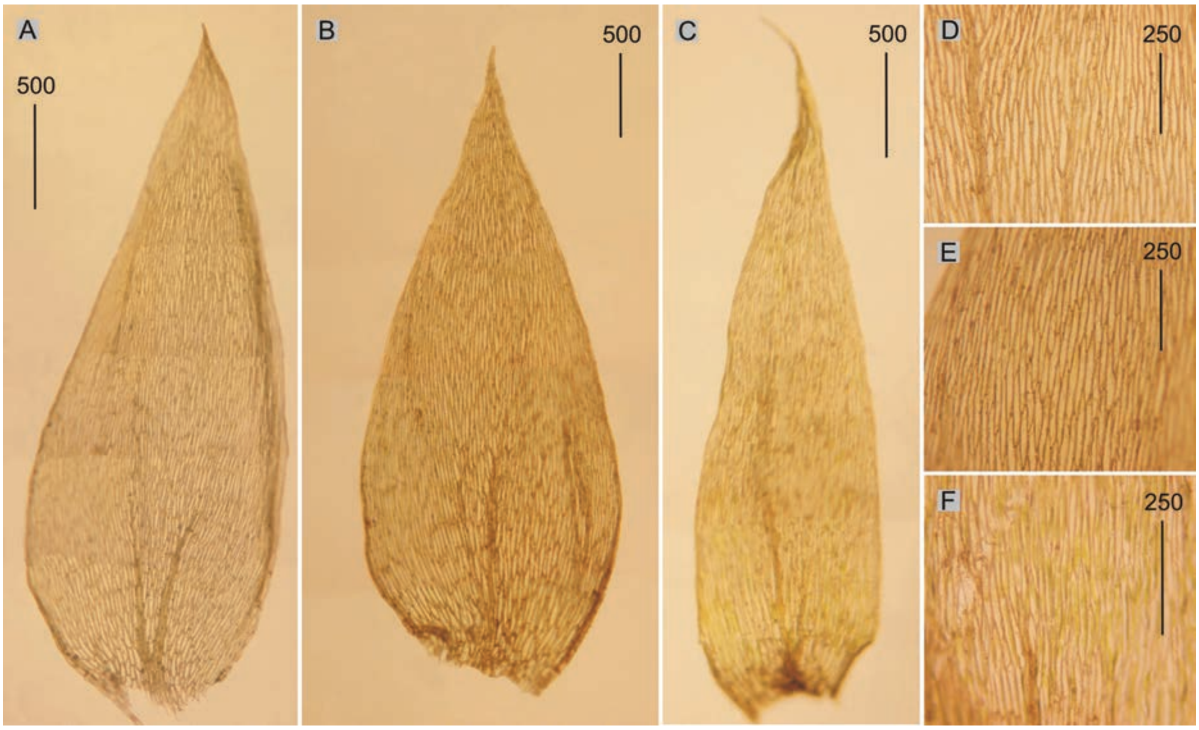

Figure 5. Selected, most important taxonomic features of taxa from the *Plagiothecium succulentum* complex **A–C** shape and dimensions of the leaves **D–F** shape and dimensions of cells from the middle part of the leaves **A**, **D** *P. succulentum* var. *succulentum* (*H. N. Dixon*, *B. M. Sutton*, BM 001007959!) **B**, **E** *P. succulentum* var. *propaguliferum* (from lectotype of *P. succulentum* fo. *propaguliferum*, *F. V. Schiffner*, C-M-9395!) **C**, **F** *P. succulentum* var. *cryptarum* (from the lectotype of *P. succulentum* var. *longifolium* fo. *splendens*, *W. Mönkemeyer*, JE 04004213!).

***Plagiothecium succulentum* var. *propaguliferum* (E.Bauer) G.J.Wolski, com. nov.**

≡ *Plagiothecium succulentum* fo. *propaguliferum* E.Bauer, Deutsche Botanische Monatsschrift 20: 2. 1902. Lectotype (designated here): [Germany,] an Erlenstöcken in Erlbruche am Schiessniger Teiche bei B. Leipa, 250 m, ü. d. adr. M. *V. Schiffner*, *Bryotheca Bohemica 259*, 7 Aug. 1900, C-M-9395!

Description. Plants medium-sized, dark golden to brown, very glossy; stems to 2.0–2.5 cm long; leaves spreading, in dry condition shrunken, complanate, symmetrical, ovate-lanceolate, 3.0–3.60 × 1.40–1.60 mm (Fig. 5B); apex acuminate, not denticulate; laminal cells linear-rhomboidal, linear-hexagonal, 180–260 × 17.0–20.0 µm at mid-leaf, (Fig. 5E), cell areolation loose; decurrencies of 2–3 rows of rectangular cells; capsule inclined.

Distribution. Europe (Austria, Czech Republic, Denmark, Germany, Latvia); North America (Canada, U.S.A.).

***Plagiothecium succulentum* var. *cryptarum* (Renauld & Hérib. *in* Héribaud) G.J.Wolski, comb. nov.**

≡ *Plagiothecium denticulatum* var. *cryptarum* Renauld & Hérib. *in* Héribaud, Mémoires de l'Académie des Sciences, Belles-lettres et Arts de Clermont-Ferrand, Deuxième Série 14: 229, 1899 ≡ *Plagiothecium sylvaticum* var. *cryptarum* (Renauld & Hérib.) P.Syd., Botanischer Jahresbericht 27(1): 200. 1904 ≡ *Plagiothecium roeseanum* fo. *cryptarum* (Renauld & Hérib.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 37. 1948. Type: [France,] Central, près l'hôtel de Cournillou, Vallée de la Rue, sur le sol d'une grotte, Aug. 1894 & 1895, *J. Héribaud*. Lectotype (designated here): PC 0132577! Isolectotypes: PC 0132578!, PC 0132579!, PC 0132580!, PC 0132581!, PC 0132582!, PC 0132586!

= *Plagiothecium succulentum* var. *longifolium* fo. *splendens* Mönk., Die Laubmoose Europas 863. 1927. Lectotype (designated here): [Germany.] Kreuzenberg, bei Nieder Feer. Juli 1908, *W. Mönkemeyer*, JE 04004213! syn. nov.

Description. Plants medium-sized to large, dark golden to golden brown; stems to 3–5 cm long; leaves spreading, not overlapping, in dry condition not shrunken, complanate, symmetrical or almost symmetrical, lanceolate, 1.9–3.5 × 0.6–1.0 mm (Fig. 5C); apex acuminate, filiform, and not denticulate; laminal cells 150–260 × 16–22 µm at mid-leaf (Fig. 5F), cell areolation loose; decurrencies of 2–3 rows of rectangular cells; capsule unknown so far.

Distribution. Europe (France, Germany), but the range of this taxon still requires research.

***Plagiothecium cavifolium* (Brid.) Z.Iwats., Journal of the Hattori Botanical Laboratory 33: 360. 1970.**

≡ *Hypnum* (*Stereodon*) *cavifolium* Brid., Bryologia Universa 2: 556. 1827 ≡ *Stereodon cavifolius* (Brid.) Brid., Bryologia Universa 2: 824. 1827. Type: [Canada,] in terra habitat in insula Terre Neuve, *La Pylaie*, B-Brid 915!

= *Plagiothecium roeseanum* Hampe *ex* Schimp., Bryologia Europea 5: 193, 504, table X. 1851 ≡ *Hypnum roeseanum* Hampe *in* Bruch, Schimper and W.Gümbel, Bryologia Europea 5: 193, 504. 1851, nom. inval. ≡ *Plagiothecium sylvaticum* var. *roeseanum* (Hampe *ex* Schimp.) A.W.H.Walther & Moldendo, Die Laubmoose Oberfrankens 177. 1868 ≡ *Plagiothecium denticulatum* var. *roeseanum* (Hampe *ex* Schimp.) Hérib., Mémoires de l'Académie des Sciences, Belles-lettres et Arts de Clermont-Ferrand, Deuxième Série, 14: 228. 1899 ≡ *Plagiothecium denticulatum* subsp. *roeseanum* (Hampe *ex* Schimp.) Grout, Moss Flora of North America 3: 158. 1932. Type: [Germany,] Ad terram arenosam sub *Fagis* in monte Inselberg Thuringiae cl. *A. Roese* legit atque nobiscum benevole communicavit, JE 04004196!, JE 04004197!, JE 04004198!, JE 04004199!, HBG-021130!

= *Plagiothecium orthocladium* Schimp., Bryologia Europea 5: 193, 504, table X. 1851 ≡ *Plagiothecium sylvaticum* var. *orthocladium* (Schimp.) Schimp., Corollarium Bryologiae Europaeae 115. 1856 ≡ *Hypnum sylvaticum* var. *orthocladium* (Schimp.) Husn., Flore Analytique et Descriptive des Mousses du Nord-Ouest, 2 Edition 149. 1882 ≡ *Plagiothecium roeseanum* var. *orthocladium* (Schimp.) Limpr., Die Laubmoose Deutschlands, Oesterreichs und der Schweiz 3: 262. 1897 ≡ *Plagiothecium denticulatum* var. *orthocladium* (Schimp.) Hérib., Mémoires de l'Académie des Sciences, Belles-lettres et Arts de Clermont-Ferrand, Deuxième Série, 14: 229. 1899 ≡ *Plagiothecium sylvaticum* fo. *orthocladium* (Schimp.) Barkman, Phytosociology and Ecology of Cryptogamic Epiphytes 619. 1958, *comb. inval.* ≡ *Plagiothecium cavifolium* var. *orthocladium* (Schimp.) Z.Iwats., Journal of the Hattori Botanical Laboratory 33: 371. 1970. Type: In m. Donnersberg Vogesi inferioris, *Th. Gumbel* legit auno 1842 (*n.v.*).

= *Plagiothecium attenuatirameum* Kindb., Catalogue of Canadian Plants, Part VI, Musci 277. 1892 ≡ *Plagiothecium laetum* subsp. *attenuatirameum* (Kindb.) Kindb., Canadian Record of Science 6(2): 72. 1894. Type: Canada, Québec, Chelsea in Gilmour's Park, on rock, *J. Macoun 417*, 6 September 1889, herb. *I. Thériot*, PC0132687!

= *Plagiothecium roeseanum* var. *angustirete* Warnst., Verhandlungen des Botanischen Vereins der Provinz Brandenburg 42: 214. 1900 ≡ *Plagiothecium roeseanum* fo. *angistirete* (Warnst.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 39. 1948. Type: Germany, Brandenburg, Chorin (Mark), Hohlweg am Bach, am Waldhohlwege im „Forstarten" mit *Eurhynchium schleicheri*, *L. Loeske*, 10 Sep. 1899, herb. *H. Dohl*, JE 4004200!

= *Plagiothecium roeseanum* var. *japonicum* Cardot, Bulletin de la Société Botanique de Genève, sér. 2, 4: 385. 1912. Type: Japan, Aomori Pref., *Faurie 408* ("*P. silvaticum* var. *orthocladum* Sch."), herb. *J. Cardot*, PC 0132574!; idem, *Faurie 418*; Kanita, *Faurie 1812*; Hirosaki, *Faurie 1878*; Osorezan, *Faurie 2104*; château d'Akita, *Faurie 2904*; Nayoro, *Faurie 3078* in parte; Sambongi, *Faurie 3190*; Otaru, *Faurie 3753*; Tobetsu, *Faurie 3761*, KYO.

Description. Plants small-sized, yellowish-green to light green; stems 2–4 cm long; leaves julaceous, concave, imbricate, symmetrical, more or less folded, 1.2–2.5 × 0.6–1.0 mm (Fig. 6A); the apex not denticulate; laminal cells 100–150 × 10–12 µm at midleaf (Fig. 6B), cell areolation quite loose; decurrencies of 2–3 rows of rectangular to quadrate cells; setae 1.8–2.5 cm; capsule inclined.

Distribution. Europe (Czech Republic, Denmark, Finland, Germany, Italy, Lithuania, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine, United Kingdom).

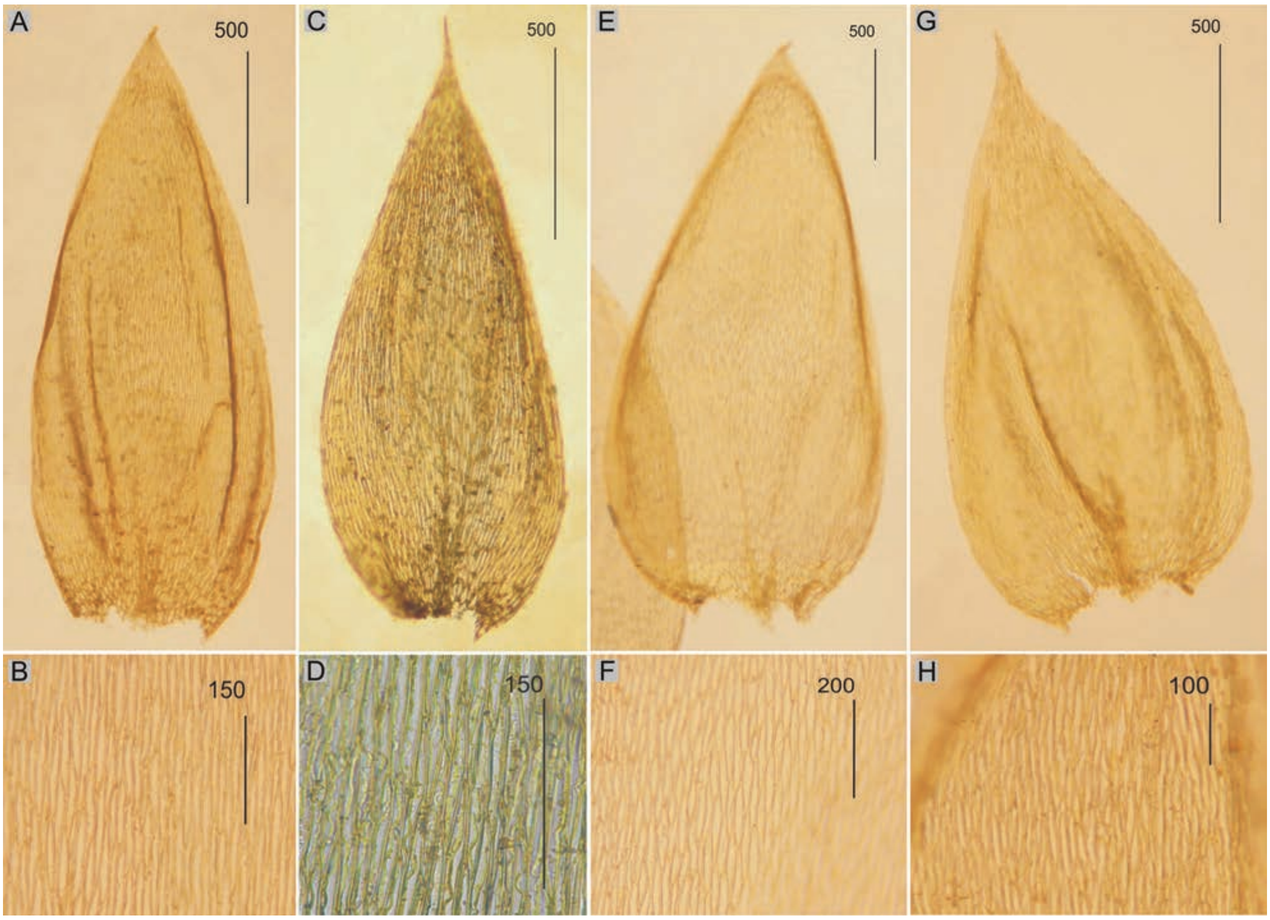

Figure 6. Selected, most important taxonomic features of taxa from the *Plagiothecium cavifolium* complex **A**, **C**, **E**, **G** shape and dimensions of the leaves **B**, **D**, **F**, **H** shape and dimensions of cells from the middle part of the leaves **A, B** *P. cavifolium (*from type of *Hypnum roeseanum*, *A. Roese*, JE4004197!) **C, D** *P. ikegamii* (from type of *P. propaguliferum*, *Y. Iishiba*, PC 0132610!) **E, F** *P. subjulaceum* (from type of *P. roeseanum* fo. *umbrosa*, *R. Schmidt*, HBG 021131!) **G, H** *P. flaccidum* (from type of *Leskea flaccida*, *J. Torrey*, B 31076701!), based on Wolski et al. 2022b changed.

Plagiothecium ikegamii **Sakurai, Botanical Magazine (Tokyo) 62: 113, f. 3. 1949.**

= *Plagiothecium roeseanum* var. *alpinum* Kern, Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur 91(2b): 64. 1914 ≡ *Plagiothecium roeseanum* fo. *alpinum* (Kern) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 37. 1948 ≡ *Plagiothecium alpinum* (Kern) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 318: 5, 1950. Type: Italy, Felsritzen des Cruschettapasses an der Schweizer Grenze, 2300 m, 30 July 1913, *F. Kern*, PC 0132603!

= *Plagiothecium roeseanum* fo. *rigidum* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 37. 1948. Type (authentic specimens cited in Jedlička 1961): Moravia, Jeseníky, Švýcárna, 1300 m, ster., *J. Podpěra*, H.M.B.; Brno, Bílovice, cfr., *K. Doležal*, H.U.B., as. *P. denticulatum*; Adamov, in conc. riv. Kateřinský, ster., *J. Jedlička*, H.J.; Slovakia, Vysoké Tatry, Štrbské Solisko, in *Calamagrostideto villosae*, solo granitico, 1385 m, ster., Krajina, H.U.P., sub *P. denticulatum* (*n.v.*).

= *Plagiothecium roeseanum* fo. *subdentatum* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 38. 1948 ≡ *Plagiothecium subdentatum* (Jedl.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University

318: 5. 1950. Type (authentic specimens cited in Jedlička 1961): Moravia, Jeseníky, ster. cum Desmatodon, *Frank*, H.P., Inter. p. Dalečín et Jimramov, 500 m, ster., *J. Podpěra*, H.P.; Carp. occid., Rožnov, s.m. Radhošt, versus Kluzov, ster., *J. Podpěra*, H.P.; Turcia, Salonichi, Kartaš-dagh, 1200 m, ster., *J. Podpěra*, H.P. (*n.v.*).

= *Plagiothecium propaguliferum* Broth., *in sched*. Basis: Japan, Sendai, *Y. Iishiba*, July 1907, herb. *J. Cardot*, *I. Thériot*, PC 0132610!

= *Plagiothecium apiculatum* Sakurai, *in sched*. Basis: Japan, Niigata Pref., Toyanao, 2 Apr. 1942, *Y. Ikegami 4256*, MAK B115140!

Type. Japan, Etigo Prov., Mt. Renge, ad terram, ca. 2200 m, *Y.Ikegami 11270*, herb. *K. Sakurai 16336*, August 1949; Shinano Prov., Mt. Shirouma, 2500 m, *N. Takaki in herb*. *K. Sakurai 16368*, August 1949 (*n.v.*).

Description. Plants medium-sized, yellowish-green; stems 2–4 cm long; leaves julaceous, concave, imbricate, symmetrical, more or less folded, 1.3–2.0 × 0.5–1.2 mm (Fig. 6C); the apex denticulate; laminal cells 100–150 × 10–12 µm at midleaf (Fig. 6D), cell areolation quite loose; decurrencies of 1–2 rows of rectangular to quadrate cells; capsule inclined.

Distribution. Asia (Japan); Europe (Czech Republic, Italy), but the range of this taxon still requires research.

Plagiothecium subjulaceum **(Meyl.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 318: 5. 1950.**

≡ *Plagiothecium roeseanum* var. *subjulaceum* Meyl. *in* J.J.Amann, Flore des Mousses de la Suisse 2: 328. 1918 ≡ *Plagiothecium roeseanum* fo. *subjulaceum* (Meyl.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 38. 1948. Type: (authentic specimens cited in Jedlička 1961): Typus secundum specimina a *J. Podpěra* in Moravia orientali (Rajnochovice) collecta, descriptus est. ČSSR – Rapotice, ster. (*Doležal*, H.U.B.). Carp. occident.: Bašta pr. Rajnochovice, ad rup. arenac., ster. (*Podpěra*, H.M.B.). – Slovakia. Bratislava: in conv. Pajštúnska dolina, ster. (*Podpěra*, H.P.) (hygromorphosa).

= *Plagiothecium sylvaticum* var. *cavifolium* Jur. *in* Rabenhorst, Bryotheca Europaea 16: 765. 1864. Type: *Bryotheca europaea 765*, Auf nacktem Boden in Buchenwäldern auf Nagelfluhe am Mönchsberge bei Salzburg, Sauter (als. *Plag. Lucens Sauter* n. sp.), distrib. *L. Rabenhorst*, FH 220150, MO 406590, PC 00132571!

= *Plagiothecium silvaticum* var. *latifolium* Röll, Deutsche Botanische Monatsschrift 9: 131. 1891, *non* Cardot, Bulletin de la Société Botanique de Genève, sér. 2, 4: 385. 1912, *hom. illeg.* ≡ *Plagiothecium sylvaticum* var. *latifolium* Röll, Hedwigia 56: 229. 1915, *hom. illeg*. Type: Germany, Thuringia, im Werrthal bei Plankenburg an der hohen Schlaufe bei Ilmenau, *J. Röll*, HBG 21134!

= *Plagiothecium roeseanum* fo. *umbrosa* Mönk., Die Laubmoose Europas 863. 1927. Type: Germany, Thüringen, Finsteres Loch, *Rich Schmidt Lips.*, 20 June 1916, HBG 021131!

= *Plagiothecium succulentum* var. *longifolium* Mönk., Die Laubmoose Europas 863, f. 206b. 1927 ≡ *Plagiothecium sylvaticum* fo. *longifolium* (Mönk.) C.E.O. Jensen, Skandinaviens Bladmossflora 495. 1939 ≡ *Plagiothecium succulentum* fo. *longifolium* (Mönk.) Jedl., Spisy Vydávané Přírodovědeckou Fakultou

Masarykovy University 308: 42. 1948. Lectotype (designated by Wolski et al. 2022b): Germany, Thüringen Wald, am Simmetsberg im Ungeheuren Grund, Hess, Aug. 1872, JE 4004211! Isolectotype: Germany, Thüringen, Annathal bei Eisenach, Hess, Aug. 1872, JE 4004212!

= *Plagiothecium fujiyamae* Sakurai, *in sched*. Basis: Japan, Aokigahara, Fuji, Yamanashi Pref., *T. Maede 1462*, 9 Nov. 1950, herb. *K.Sakurai*, MAK 57198!

= *Plagiothecium nakajimae* Sakurai, *in sched*. Basis: Japan, Chichinu, Nagano, 6 Nov. 1951, herb. *K. Sakurai 761*, MAK B57158!

Description. plants medium-sized, yellowish-green to green, stems 2–4 cm long; leaves julaceous, concave, imbricate, symmetrical, more or less folded, 1.3–2.6 × 0.6–1.2 mm (Fig. 6E); the apex acuminate, not denticulate; laminal cells 60–100 × 10–16 µm at midleaf (Fig. 6F), cell areolation quite loose; decurrencies of 2–3 rows of rectangular cells; capsule inclined.

Distribution. Asia (Japan); Europe (Germany), but the range of this taxon still requires research.

Plagiothecium flaccidum (Brid.) G.J.Wolski & W.R.Buck, Diversity 14(8): 633. 2022.

≡ *Leskea flaccida* Brid., Bryologia Universa 2: 308. 1827. Type: In Republica Massachusets Americae Foedewatae circa Noveboracum in rupis habitat, caespitosa, caespitum basi e congerie caulium veterarnorum marcescentium constante, *Torrey 67*, 1820, B 31076701!

= *Hypnum sullivantiae* Schimp. *ex* Sull., A Manual of the Botany of the Northern United States. Second Edition 680. 1856 ≡ *Plagiothecium sullivantiae* (Schimp. *ex* Sull.) Schimp. *ex* A.Jaeger, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1876–77: 450. 1878 ≡ *Plagiothecium sylvaticum* var. *sullivantiae* (Schimp. *ex* Sull.) Renauld & Cardot, Revue Bryologique 20: 22. 1893. Type: Ohionis et Novae Angliae, in rupium fissuris terra impletis, *Musci Boreali-Americani 355*, PC 0132606!, PC 0132607!; idem herb. *M.Bizot 13157*, PC 0132608!

= *Plagiothecium roeseanum* var. *orthocladon* fo. *propaguliferum* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 39. 1948, *hom*. *illeg*., *non* (R.Ruthe) Jaap, Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, ser. 3, 7: 36. 1900 ≡ *Plagiothecium roeseanum* var. *orthocladon* fo. *moravicum* Pilous *in* Jedlička, Spisy Přírodovědecké Fakulty University v Brně 422: 214. 1961, nom. nov. Type: Moravia, conv. flum. Oslava, ster., *Latzel*, H.L., observavi (*n.v*.).

Description. Plants small-sized, yellowish-green to light green; stems 2–3 cm long; leaves julaceous, concave, imbricate, symmetrical, more or less folded, 1.5–1.8 × 0.7–0.8 mm (Fig. 6G); the apex not denticulate; laminal cells 75–130 × 10–12 µm at midleaf (Fig. 6H), cell areolation quite loose; decurrencies of 1–2 rows of rectangular to quadrate cells; capsule erect.

Distribution. Europe (Czech Republic); North America (U.S.A.), but the range of this taxon still requires research.

Plagiothecium tenue **(Jedl.) G.J.Wolski and W.R.Buck, Divesity, 14(8): 633 [16]. 2022.**

≡ *Plagiothecium roeseanum* fo. *tenue* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 38. 1948. Type (authentic specimens cited in Jedlička 1961): Silesia, Cuidowa, Steinberg, ster. *Paul*, H.M.B.; Bohemia, Beroun, Skryje, in decl. Vosník col. ster., *Šmerda*, H.Š. (sub *P. denticulatum*); Moravia, Jeseníky, Quarklöcher, pr. Brummlitz, ster. una cum *Barbula rigida* et *Fissidens pusillus*, *Latzel*, H.L.; Voskovice, in silva umbrosa pr. oppid, 300 m, ster., *Doležal*, H.P.; Brno, Kuřím, ad col. Baba, ster. *Doležal*, H.M.B. (sub *P. denticulatum*); Kůňku pr. Obora, str., *Podpěra*, H.P.; Mor. Krumlov, ad rup. perm., 300 m, ster. *Podpěra*, H.M.B.; Carp. occid., in m. Ondřejník, pr. Frýdlant, ster., *Podpěra* H.P.; in m. Lysá in conv. riv. Mazák, ster., *Podpěra*, H.P.; Rajnochovice, Pomsko, ster., *Podpěra*, H.P.; Rychtářov, in conv., V. Haná, ster., *Podpěra*, H.P.; Unčov, cataract. Řešovský, ster., *Podpěra*, H.P. Austria. Koralpe, Theisseneppergraben, solo granit., 800 m, ster., *Latzel*, H.L.; Pressinggraben, ster. *Latzel*, H.L. (s. *P. Roeseanum gracile*). Jugoslavia, Surdulica, in conv. Vrla reka, ster. *Podpěra*, H.P.; Vrane-Kazandžol, ster., Podpěra, H.P (*n.v*.).

= *Plagiothecium roeseanum* fo. *tenue* subfo. *propaguliferum* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 38. 1948, *hom. illeg*. ≡ *Plagiothecium roeseanum* subfo. *gemmicladum* Pilous, Spisy Přírodovědecké Fakulty University v Brně 422: 212. 1961. Type (authentic specimens cited in Jedlička 1961): Suecia, Skåne, Bokeberg, ster., *Möller*, H.M.B.; Germania, Sachsen, Plauen, ad saxa umber. in conv. Elstertal, ster., *Stolle*, H.P. (planta pulcherima!!); Austria, Saualpe, Pöllinggraben, cfr., *Latzel*, H.L.; Wien, ad arcem Greifenstein, 300 m, cfr., Baumgartner, Krypyog. exsicc. M.N. no. *1788a*, H.M.P.; Bohemia, Praha, Hasenburg, 250 m, ster., *Bauer*; Musc. eur. exsicc. no. *1311*, H.P., H.M.B., H.M.P., H.U.B. (sub *P. Roeseanum* fo. *gracilescens*) *Bauer in sched*.; Řevnice, ster. *Podpěra*, H.P. (sub *P. denticulatum*); Nové Mešto n. Met. ad rup. fyllit. Peklo, ster., *Šmaeda*, H.Š.; Berno, Skryje, ster., cum *Anomodon attenuatus* et *Mnium cuspidatum*, *Šmaeda*, H.Š. (sub *P. denticulatum propaguliferum*); Tusset, 1000 m, ster., *Podpěra*, H.P. (sub *P. denticulatum*); Moravia, Jeseníky, Švýcárna, ster. 1300 m, *Podpěra*, H.P.; Hokšár, ster., *Podpěra*, H.P.; Brno, pr. arcem Veveří, ster., *Podpěra*, H.P.; in conv. Bílý potok, sup. Hluboké, ster. *Podpěra*, H.P. (sub *P. Roeseanum umbrosum*); Adamov, in conv. riv., Josefovský, ster., *Podpěra*, H.P.; in conv. rivuli Kateřinský potok, ster., *J.Müller*, H.U.B.; ad rup. syenit. in conv. flum. Svitava, inter Adamov et Blansko, ster., *Podpěra*, H.P.; Rousínov, Vítocický žleb, *Podpěra*, H.P. (sub *P. Roeseanum gracile* fo. *tenullum*) *Podpěra in sched*.; Mor. Krumlov, ad rup. perm., 300 m, ster., *Podpěra*, H.P.; Carp. occid., ad ped. m. Lysá Hora, pr. Staré Hamry, ster., *Podpěra*, H.P.; in m. Hostýn, ster., *Podpěra*, H.P. (*n.v*.).

= *Plagiothecium roeseanum* fo. *acuminatum* Jedl., Spisy Vydávané Přírodovědeckou Fakultou Masarykovy University 308: 40. 1948 ≡ *Plagiothecium cavifolium* fo. *acuminatum* (Jedl.) Z.Iwats., Journal of the Hattori Botanical Laboratory 33: 363. 1970. Type (authentic specimens cited in Jedlička 1961): Austria, Arlingsgraben, ster., *Latzel*, H.L. Bohemia, Praha, ad rup. lydit., 200 m, ster., *Šmarda*, H.Š.; Babka pr. Řevnive, 400 m, Bauer, Bryoth. Bohem. no *255*, H.U.P., H.Š., H.M.P. (sub *P. roeseanum typicum*); Mladá Boleslav, in conv. Choboty, cfr., *Podpěra*, H.P., Moravia, Jeseníky, Dolní Lipová, ster., *Latzel*, H.L.; in conv.

riv. Seifen pr. Vernířovice, 800 m, ster., *Podpěra*, H.P.; Znajmo, Eisleiten pr. Varanoc, ster., *Podpěra*, H.P.; Senohrady, ad rup., ster., *Podpěra*, H.P.; Unčov, ad cataract. Řešovský, 400 m, ster., *Podpěra*, H.P.; Slovakia, Babia Góra, ad lignus putr., ster., *Šmerda*, H.Š. (sub *P. silvaticum longifolium*); Bielské Tatry, in conv. Havran, 1100 m, cum *Blepharostoma trichophyllum*, ster., *Šmerda*, H.Š (*n.v.*).

Description. Plants small, yellowish-green to light green; stems 0.5–1.5 cm; leaves not julaceous; flat, not imbricate, asymmetrical, ovato-lanceolate, 1.2–1.8 × 0.6–0.8 mm (Fig. 7A, B); the apex acuminate, long (Fig. 7C), not denticulate; laminal cells 70–100 × 10–12 μm at midleaf (Fig. 7D), cell areolation quite loose; decurrencies of 2–3 rows of rectangular cells; capsule inclined.

Distribution. Europe (Austria, Czech Republic, Germany, Poland, Serbia, Slovakia, Sweden), but the range of this taxon still requires research.

Sect. *Leptophyllum* Jedl.

Plagiothecium berggrenianum Frisvoll, Lindbergia 7: 96, f. 2: a–i. 1981.

Type material. Holotype: Norway, Svalbard, Haakonvii Land, Krossfjorden, Kollerfjorden, below bird cliff in Christian Michelsenfjell W, 50 m, 22 July 1974, *A. A. Frisvoll*, TRH B-19507! Isotype: C-M-20077! Paratypes: Lilliehöökfjorden, bird cliff in Nilsfjellet N, 50 m, 22 July 1974 (TRH); Bellsund, Vårsolbukta, by Camp Miller, 25 m, 29 July 1980, *Olsen*; S of Ingeborgfjellet, 10 m, 13 July 1980, *Olsen* (TRH); Sjuøyane; Parryya, 80°40'N, below brid cliff, 1868, *Berggren*, TRH.

Description. Plants small, dense, yellowish green to green, glossy, with metallic luster; stems erect, 3–9 cm long; leaves very crowded on stem, julaceous, imbricate, symmetrical and very concave, thus the leaves often cracked, plicate, 1.5–3.1 × 0.7–1.1 mm (Fig. 8A); the apex acuminate, recurved, hook-shaped; margins denticulate or not near the apex; laminal cells 120–170 × 12–15 μm at midleaf (Fig. 8C), cell areolation quite loose; decurrencies well developed, consisting of 3–4 rows of rectangular cells.

Distribution. Asia (Russian Federation); Europe (Norway); North America (Canada, U.S.A.).

Plagiothecium svalbardense Frisvoll, Norsk Polarinstitutt Skrifter, Part 2. Bryophytes 198: 103. 1996.

Type material. Holotype: Norway, Svalbard, Krossfjorden, Kollerfjorden, below a bird cliff in Christian Michelsenfjella W, 50 m, 22 July 1974, *A. A. Frisvoll*, TRH B-19481! Isotypes: O, S, TRH.

Description. Plants medium-sized, dark green, dull, without metallic luster; stems 2–4 cm long, more or less julaceous; leaves concave, two types of leaves: symmetrical and asymmetrical, ovate, 2.4–2.8 × 1.2–1.5 mm (Fig. 8B); the apex acuminate, often gently curved; margins not denticulate near the apex; laminal cells narrowly elongate-hexagonal, asymmetric, 80–120 × 7–10 μm at midleaf (Fig. 8D), cell areolation tight; decurrencies of 3 rows of rectangular to quadrate cells.

Distribution. Asia (Russian Federation); Europe (Norway, Sweden).

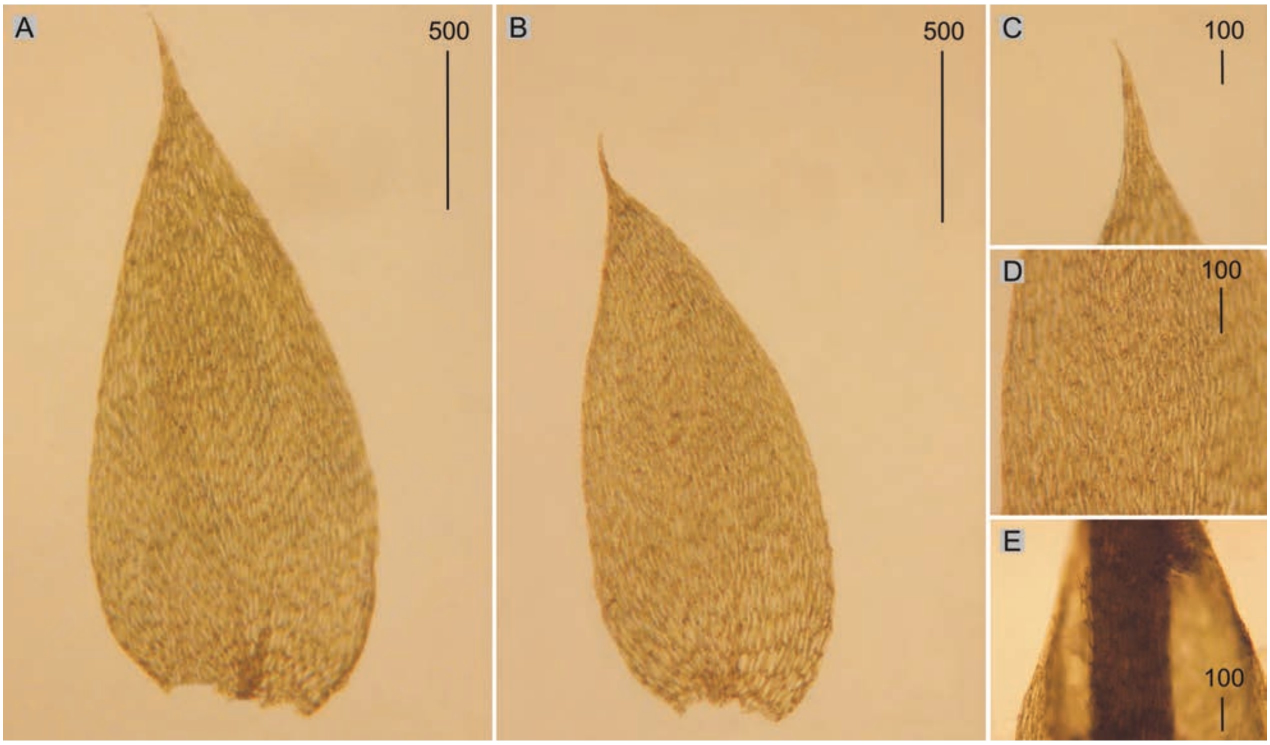

Figure 7. Selected, most important taxonomic features of taxa from the *Plagiothecium cavifolium* complex **A, B** shape and dimensions of the leaves **C** leaves apex **D** shape and dimensions of cells from the middle part of the leaves **E** decurrencies on the stem. **A–E** *Plagiothecium tenue* (from *P. roeseanum* fo. *tenue*, herb. *A. Baros*, det. *J. Jedlička*, BRNU 592!).

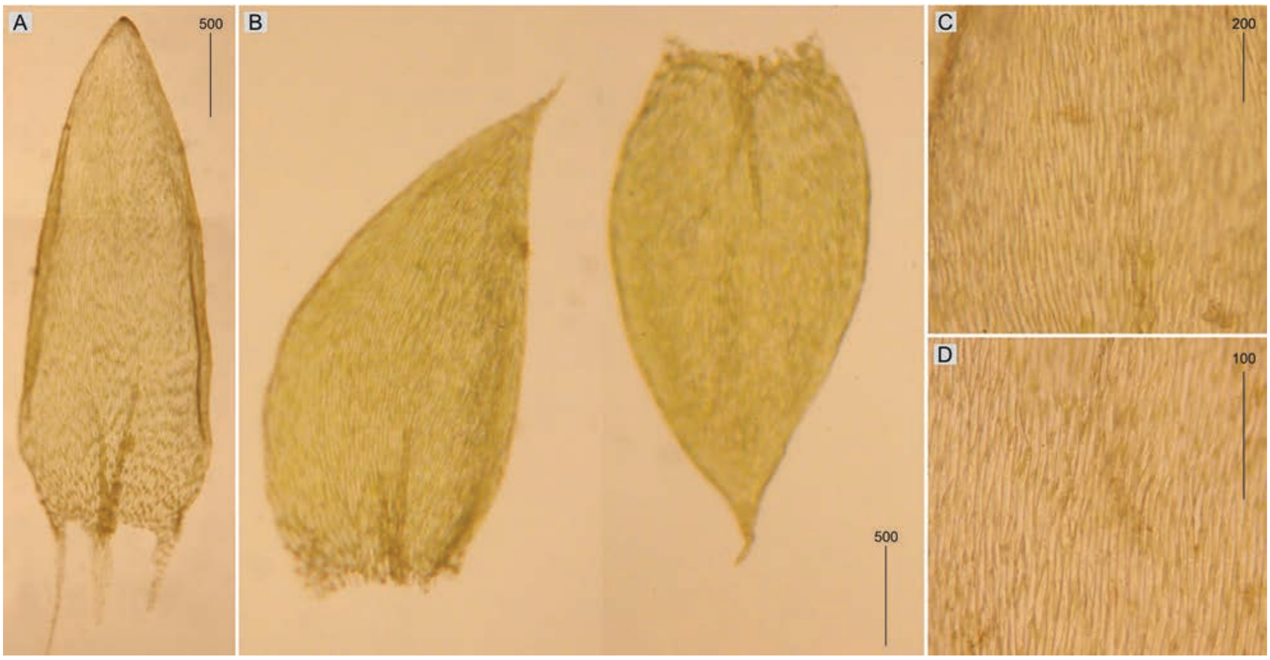

Figure 8. Selected, most important taxonomic features of *Plagiothecium berggrenianum* and *Plagiothecium svalbardense* **A, B** shape and dimensions of the leaves **C, D** shape and dimensions of cells from the middle part of the leaves **A**, **C** *P. berggrenianum* (from holotype, *A. A. Frisvoll*, TRH B-19507!) **B**, **D** *P. svalbardense* (from holotype, *A. A. Frisvoll*, TRH B-19481!).

***Plagiothecium curvifolium* var. *curvifolium* Schlieph. *ex* Limpr., Die Laubmoose Deutschlands, Oesterreichs und der Schweiz 3: 269. 1897.**

Type material. Lectotype (designated by Wolski et al. 2022a): Germany, Thuringia, in feuchten Nadelwäldern, Schmücke, 29 July 1880, *D. K. Schliephacke*, JE 04004091! Isolectotypes: HBG 02115!, PC 01322640!, WRSL!, G!, DUKE 155945.

Description. Plants medium-sized, yellow-green to green; stems 1.5–2.5 cm long, complanate-foliate; leaves symmetrical or almost symmetrical, gently imbricate, lanceolate to ovate-lanceolate, concave, slightly curved towards the ground, 1.7–2.7 × 0.7–1.5 mm (Fig. 9A); margin incurved, delicately on both sides or strongly on one side; the apex acuminate, not denticulate; laminal cells linear-vermicular, 110–155 × 8–9 µm at midleaf (Fig. 9C), cell areolation tight; decurrencies of 2–3 rows of rectangular cells forming semi-distinct auricles, some cells from external row inflated; capsules inclined to horizontal.

Distribution. Asia (Georgia, Russia); Europe (Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany, Great Britain, Hungary, Latvia, Netherlands, Poland, Romania, Spain, Sweden); North America (Canada, U.S.A.).

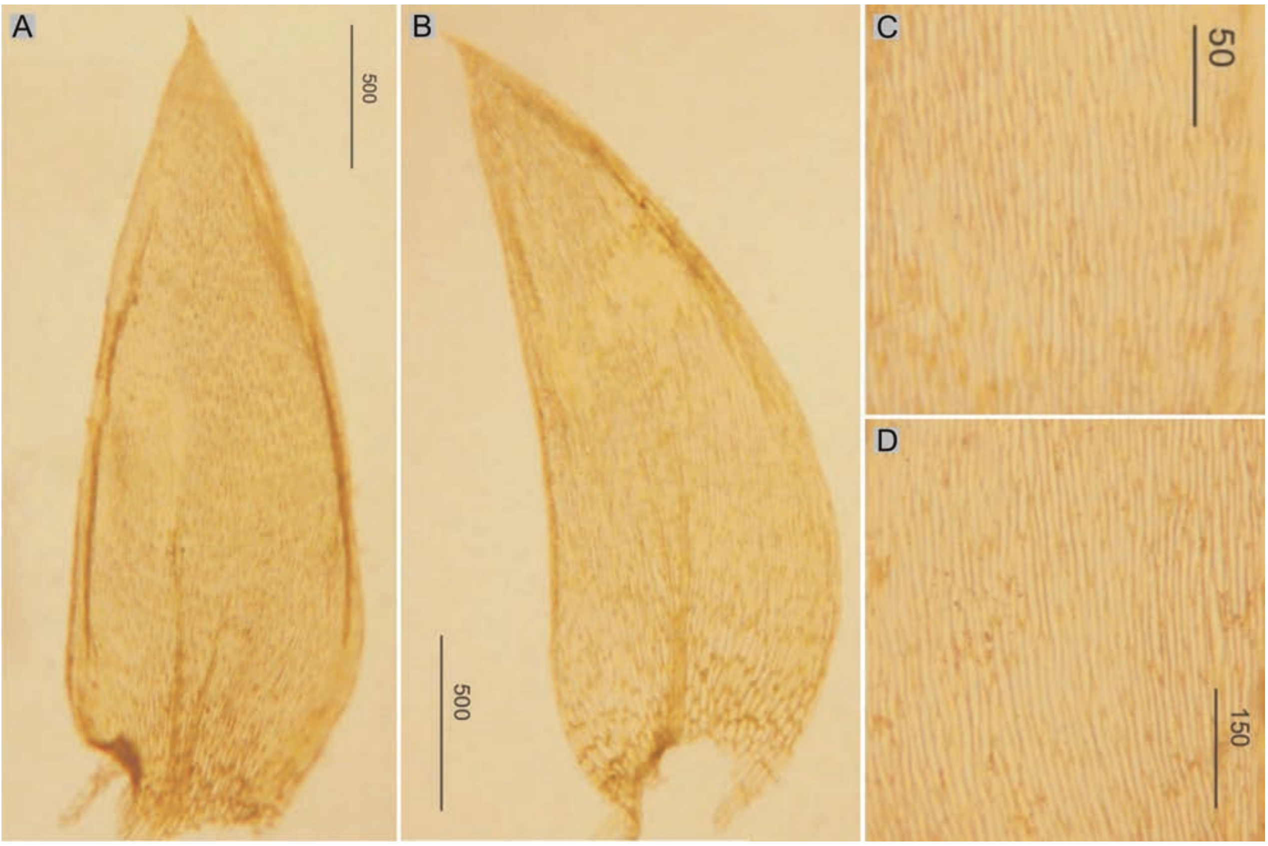

Figure 9. Selected, most important taxonomic features of taxa from the *Plagiothecium curvifolium* complex **A, B** shape and dimensions of the leaves **C, D** shape and dimensions of cells from the middle part of the leaves **A**, **C** *P. curvifolium* var. *curvifolium* (from lectotype of *P. curvifolium*, *K. Schliephacke*, JE 04004091!) **B**, **D** *P. curvifolium* var. *recurvum* (from lectotype of *P. denticulatum* var. *recurvum*, *C. Warnstorf*, JE 04004201!), based on Wolski et al. 2022a changed.

***Plagiothecium curvifolium* var. *recurvum* (Warnst.) G.J.Wolski & W.R.Buck, PLoS ONE 17(11): e0275665. 2020.**

≡ *Plagiothecium denticulatum* var. *recurvum* Warnst., Verhandlungen des Botanischen Vereins für die Provinz Brandenburg und die Angrenzenden Länder 27: 73. 1885. Lectotype (designated by Wolski et al. 2022a): Germany, prov. Brandenburg, auf nacktem Bodem in Kiefernschonungen vor Altruppin, Neuruppin, *C. Warnstorf*, JE 04004201! Isolectotypes: G!

= *Plagiothecium curvifolium* var. *hypnophyllum* Ukrainskaya, Novosti Sistematiki Nizaikh Rastenii 31: 183, f. 12–14. 1996. Type: [Russia,] Prov. Mosquensis, distr. Krasnogorskensis, 2 km ad austro-occidentem a Krasnogorsk. Ad Betulam in silva, 28 VII 1986, *Ignatov*. In herbario bryologico Horti Botanici Publici Mosquae conservatur, MHA, VLA!

Description. Plants medium-sized, bright-green to green; stems 1.5–2.0 cm long; leaves complanate, strongly asymmetrical, hooked, lanceolate, concave, curved towards the ground, 1.7–2.2 × 0.6–0.9 mm (Fig. 9B); margin sometimes incurved; the apex acuminate, usually denticulate by 2–3 teeth; cells linear-vermicular, 60–120 × 7–9 µm at midleaf (Fig. 9D), cell areolation tight; decurrencies forming semi-distinct auricles, of 2–3 rows of rectangular, sometimes inflated cells; capsules inclined.

Distribution. Asia (Russia); Europe (Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Great Britain, Hungary, Latvia, Poland, Slovakia, Sweden); North America (Canada).

***Plagiothecium decursivifolium* Kindb. *in* Macoun & Kindberg, Catalogue of Canadian Plants, Part VI, Musci 277. 1892.**

= *Plagiothecium curvifolium* fo. *julaceum* Culm. *in* E.Bauer, Musci Europaei Exsiccati 27: 1307. 1915. Lectotype (designated by Wolski et al. 2022a): Switzerland, auf Tannenwurzeln ini der Nähe der oberen Waldgrenze, Burgfeld ob Beatenberg, Kanton Bern, 1630–1700 m, 31 July 1912, *Musci eur. exs. 1307*, *P. Culman*, C-M-9120! Isolectotype: MO 3974490!

Type material. Lectotype (designated by Wolski et al. 2022a): Canada, Ontario, Belleville, on cedar (*Thuja occidentalis*) stump in a swamp, 5 miles west of Belleville, Ont. *J. Macoun*, *N. C. Kindberg*, PC 0132686! Kindberg Canadian types should be at S with duplicates at CANM

Description. Plants medium-sized to small, yellow to yellow-green; stems 0.5–1.5 cm long; leaves gently julaceous and imbricate, folded, ovate to ovate-lanceolate, asymmetrical, concave, often cracked at the base, 1.3–2.5 × 0.4–1.8 mm (Fig. 10A); the apex acuminate, not denticulate or rarely with one tooth; cells linear-vermicular, 95–190 × 6–10 µm at midleaf (Fig. 10D), cell areolation tight; decurrencies of 3–5 rows of rectangular, quadrate, often inflated cells forming semi distinct auricles.

Distribution. Asia (China); Europe (Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Hungary, Latvia, Netherlands, Poland, Slovakia, Sweden, Switzerland); North America (Canada).

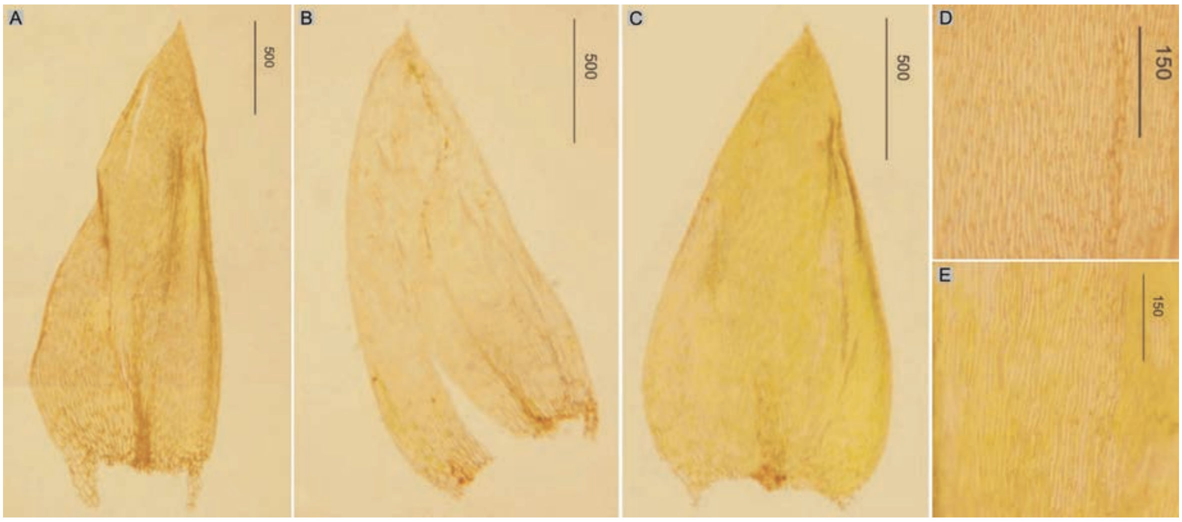

Figure 10. Selected, most important taxonomic features of taxa from the *Plagiothecium curvifolium* complex **A–C** shape and dimensions of the leaves **D, E** shape and dimensions of cells from the middle part of the leaves **A**, **D** *P. decursivifolium* (from lectotype, *P. Culmann*, C-M-9120!) **B, C**, **E** *P. imbricatum* (from holotype, *G. J. Wolski*, LOD 15015!), based on Wolski et al. 2022a changed.

Plagiothecium imbricatum G.J.Wolski & W.R.Buck, PLoS ONE, 17(11): e0275665. 2020.

Type material. Holotype: Poland, kujawsko-pomorskie Voivodeship, surroundings of Dolina rzeki Brdy reserve, slope near the river on soil in mixed forest, 13 July 2020, *G. J. Wolski 424*, LOD 15015! Isotypes: NY 04688394!, SZUB-B 00001!

Description. Plants small, bright-green to green; stems 0.7–1.5 cm long, densely foliate; leaves julaceous and imbricate, two types of leaves: symmetrical and asymmetrical, the symmetrical ones: folded, lanceolate, concave, sometimes strongly cracked at the base, asymmetrical ones: ovate, slightly concave or flat, both types of leaves identical in size, 1.2–2.3 × 0.7–1.0 mm (Fig. 10B, C); the apex acuminate, not denticulate; cells linear-vermicular, 80–190 × 5–9 µm at midleaf (Fig. 10E), cell areolation tight; decurrencies of 3–4 rows of rectangular, quadrate often inflated cells forming semi distinct auricles; capsules unknown so far.

Distribution. Europe (Great Britain, Netherlands, Poland); North America (Canada).

Plagiothecium laetum var. *laetum* Schimp., Bryologia Europea 5: 184, 495, Tab. II. 1851.

≡ *Leskea laeta* (Schimp.) Berggr., Acta Universitatis Lundensis, 2 Afd., 3(7): 8. 1866 = *Plagiothecium denticulatum* var. *laetum* (Schimp.) Lindb., Animadversiones de Hypno elegante 31. 1867 ≡ *Plagiothecium denticulatum* subsp. *laetum* (Schimp.) Kindb., Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar 7(9): 46. 1883 ≡ *Hypnum denticulatum* var. *laetum* (Schimp.) Lindb. *in* Lesquereux & James, Manual of the Mosses of North America 367. 1884. Type: [Switzerland,] in Rhaetic Alpe Albula, ubi in regione sylvatica versus Ponte in logno putrido, et supra hanc reionem prope Weissenstein, in rupium fissuris Dicrano gracilescenti intermixtum, *W. P. Schimper* aestate 1845 detexit. Nusquam alias adhuc observatum est. Syntype: PC 0132699!, PC0132701!

Description. Plants small, light green, glossy; leaves forming 20–70° angle with stem, complanate, more or less concave, asymmetrical, ovate-lanceolate, with one side almost flat, 1.0–2.0 × 1.1–1.3 mm (Fig. 11A); the apex acute, denticulate near the apex or not; laminal cells linear, 80–150 × 6–8 μm at midleaf (Fig. 11D), cell areolation dense; decurrencies of 1–3 rows of rectangular cells; setae 1.3–1.8 cm, capsule straight.

Distribution. Asia (Azerbaijan, China, Democratic People's Republic of Korea, Georgia, Islamic Republic of Iran, Japan, Kazakhstan, Kyrgystan, Mongolia, Republic of Korea, Russian Federation, Taiwan, Turkey); Europe (Albania, Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Kosovo, Latvia, Lichtenstein, Lithuania, Luxemburg, Montenegro, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

***Plagiothecium laetum* var. *hercinicum* (Jur. *ex* Grav.) G.J.Wolski, comb. nov.**

≡ *Plagiothecium denticulatum* var. *hercynicum* Jur. *ex* Grav., Bulletin de la Société Botanique de Belgique 13: 430. 1874. Type: Belgium, Loutte-Saint-Pierre, sur les rochers ombragés et au pied des arbres dans les bois humides. Lectotype (designated here): Belgium, Loutte-Saint-Pierre, rochers ombragés, Oct. 1872, *F. Gravet*, C-M-9387!

Description. Plants medium-sized, yellowish to yellowish golden; stems 1.5–2.0 cm long; leaves complanate, asymmetrical, lanceolate, concave, not curved towards the ground, 2.0–2.4 × 0.7–1.0 mm (Fig. 11B); margin incurved; the apex acuminate, denticulate by 2–3 teeth; cells linear-vermicular, 120–170 × 6–10 μm at midleaf (Fig. 11E), cell areolation tight; decurrencies of 2–3 rows of rectangular, quadrate cells; capsule straight.

Distribution. Europe (Belgium), but the range of this taxon still requires research.

***Plagiothecium rossicum* Ignatov & Ignatova, Arctoa 28: 33. 2019.**

Type material. Holotype: Russia, Pskov Province, Nevel'sk Distr., vicinities of Ustavnoe Settl. (near Yazno Lake), pine forest, at base of pine trunk, 26.IX.2001, Zolotov P504, MHA9041611.

Description. Plants small, light green; stems 0.6–1 cm long; leaves forming 40–100° angle with stem, distinctly complanate, spreading, asymmetrical, ovate-lanceolate, 0.7–1.6 × 0.3–0.6 mm (Fig. 11C); the apex acute to acuminate; margins flat, denticulate or not near the apex; laminal cells narrow, 70–130 × 6–7 μm at midleaf (Fig. 11AF), cell areolation tight; decurrencies of 2–3 rows of rectangular cells; setae 1.0 cm, capsules more or less slightly inclined.

Distribution. Asia (Russian Federation); Europe (Poland), but the range of this taxon still requires research.

Figure 11. Selected, most important taxonomic features of taxa from the *Plagiothecium laetum* complex **A–C** shape and dimensions of the leaves **D–F** shape and dimensions of cells from the middle part of the leaves **A**, **D** *P. laetum* var. *laetum* (from syntype, *W. P. Schimper*, PC 0132699!) **B**, **E** *P. laetum* var. *hercinicum* (from lectotype of *Plagiothecium denticulatum* var. *hercynicum*, *F. Gravet*, C-M-9387!) **C**, **F** *P. rossicum* (from the original collection of *P. rossicum*, *M. S. Ignatov*, MHA9041632!).

Sect. *Rectithecium* (Hedenäs & Huttunen) J.T.Wynns

Plagiothecium piliferum (Sw.) Schimp., Bryologia Europea 5: 186, 496, Tab. III. 1851.

≡ *Leskea pilifera* Sw. *in* C.J.Hartman, Handbok i Skandinaviens Flora 419. 1820 ≡ *Hypnum denticulatum* var. *piliferum* (Sw.) Wahlenb., Flora Suecica (Wahlenberg) 2: 710. 1826 ≡ *Neckera pilifera* (Sw.) Spruce, Musci Pyrenaici 66. 1847 ≡ *Isopterygium piliferum* (Sw.) Loeske, Studien zur Vergleichenden Morphologie und Phylogenetischen Systematik der Laubmoose 169. 1910 ≡ *Plagiotheciella pilifera* (Sw.) M.Fleisch. *in* Brotherus, Die natürlichen Pflanzenfamilien, Zweite Auflage, 11: 466. 1925 ≡ *Dolichotheca pilifera* (Sw.) M.Fleisch. *ex* Podp., Conspectus Muscorum Europaeorum 683. 1954 ≡ *Rectithecium piliferum* (Sw.) Hedenäs & Huttunen, Botanical Journal of the Linnean Society 171(2): 344. 2013. Type: In rupe praerupta cujus totam parietem verticalem obducit horti regalis Haga-Park prope Holmiam cl. Swartz detexit ibidemque serius legerunt *Lindberg*, *Thedenius*, *Angström*, *W. P. Sch*., e.a; ex Ostrogothiae monte Halberget cl. Holmgren, e Pyrenaeorum umbrosissima valle *de Jéret* ubi ad latera scopulorum graniticorum terram versus spectantia laete viget cl. *R.Spruce* misit.

Description. Plants small to medium sized, light green to yellowish green; leaves more or less complanate, ovate to lanceolate, concave, symmetrical, 0.8–1.5 × 0.4–0.8 (Fig. 12A), abruptly narrowed to a long filform acumen; the apex denticulate; laminal cells linear, 40–110 × 5–7 μm at midleaf (Fig. 12C), cell areolation tight; decurrencies of 2–3 rows of cells; setae 0.8–1.5 cm, capsule erect.

Distribution. Asia (China, Democratic People's Republic of Korea, Japan, Republic of Korea, Russia Federation, Turkey); Europe (Andorra, Denmark, Finland, France, Ireland, Italy, Latvia, Norway, Portugal, Romania, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

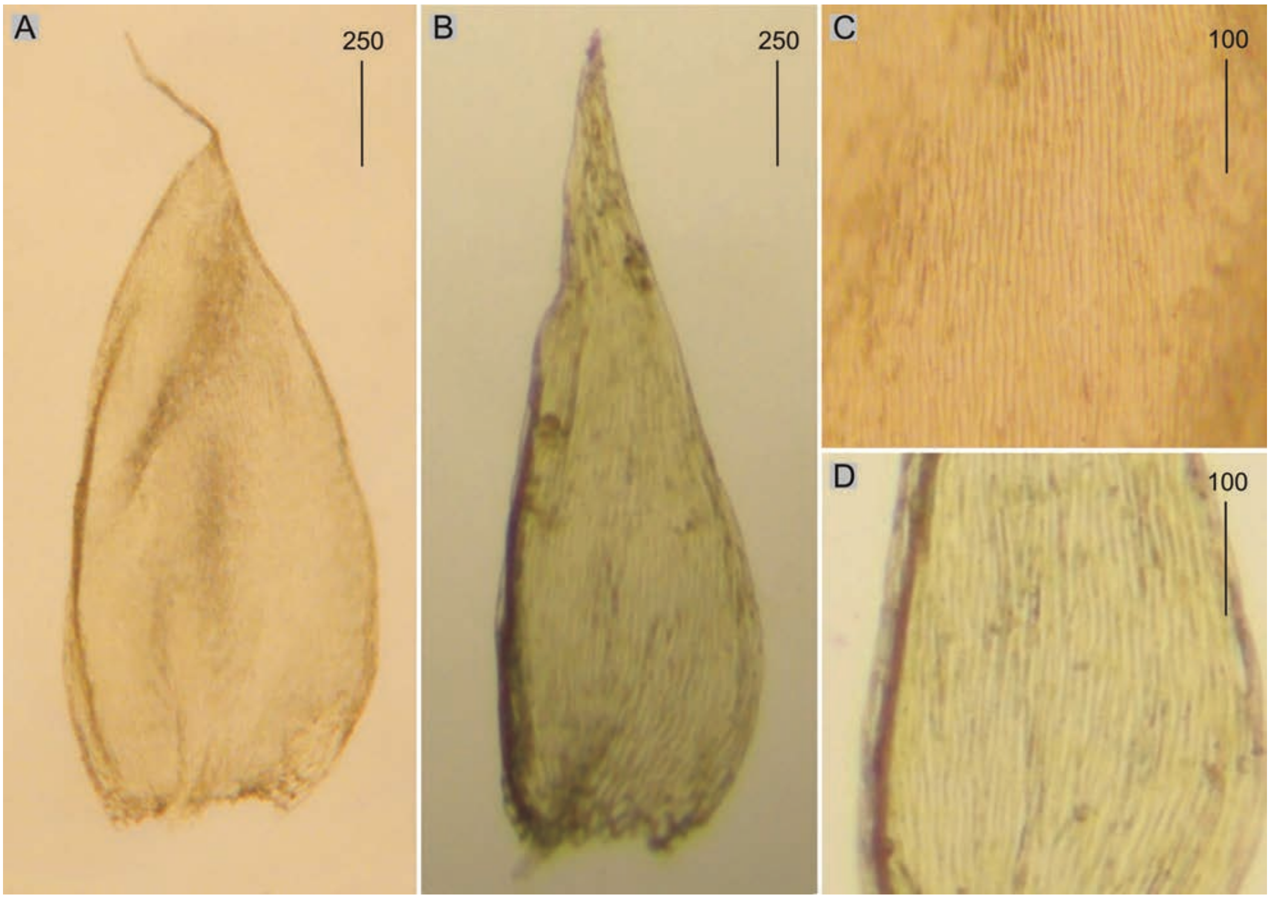

Figure 12. Selected, most important taxonomic features of the *Plagiothecium piliferum* and *Plagiothecium latebricola* **A, B** shape and dimensions of the leaves **C, D** shape and dimensions of cells from the middle part of the leaves **A**, **C** *P. piliferum* (*U. Laine*, TUR!) **B**, **D** *P. latebricola* (from lectotype of *P. latebricola* var. *gemmascens*, PC 0132685!).

Sect. *Philoscia* (Berk.) Ochyra

Plagiothecium latebricola Wilson *ex* Schimp., Bryologia Europea 5: 184, 494, Tab. I. 1851.

≡ *Leskea latebricola* (Schimp.) Wilson, Bryologia Britannica 329, 54. 1855 ≡ *Philoscia latebricola* (Schimp.) Berk., Handbook of British Mosses 146. 1863 ≡ *Hypnum latebricola* (Schimp.) Lindb., Bidrag till Sydöstra Tavastlands Flora 154. 1870 ≡ *Isopterygium latebricola* (Schimp.) Delogne, Annales de la Société Belge de Microscopie 9: 141. 1885 ≡ *Plagiotheciella latebricola* (Schimp.) M.Fleisch. *in* Brotherus, Die natürlichen Pflanzenfamilien, Zweite Auflage, 11: 466. 1925. Type: [Great Britain,] in truncis Alnorum semiputridis prope Hurstpierpoint (Sussex) ubi el. *Mitten* primus parcissime legit; prope Warrington (Wilson).

= *Plagiothecium latebricola* var. *gemmascens* Ryan & I.Hagen, Kongelige Norske Videnskabers Selskabs Skrifter 1896(1): 135. 1896 [1897] ≡ *Plagiothecium latebricola* fo. *gemmascens* (Ryan & I.Hagen) Correns, Untersuchungen über die Vermehrung der Laubmoose 248. 1899 ≡ *Plagiotheciella latebricola* fo. *gemmascens* (Ryan & I.Hagen) Podp., Conspectus Muscorum Europaeorum 682. 1954. Type: Nordlands ved Åle i Onsø (oktober 1889: R.) også funden ved vejen malle Larvik og Fredriksvaern, på rådne orestubber i en myr, (1/8

1890: kand. E. Nyman) og ved Rognan i Saltdalen, under dryppet fra tagskjaegger på vaeggen af et bådnøst (30/8 1892: H.). Lectotype (designated here): Nordlands amt, Salten, Saltdalen, Rognanm ad lignum vetustum in stillicides, 67°5'N, 30/8 1892, Musci Norvegici ex. herb. *I. Hagen*, PC 0132685!

Description. Plants small, slender, bright green to yellowish-green; leaves complanate, narrowly ovate-lanceolate, symmetrical, 0.7–1.2 × 0.3–0.5 mm (Fig. 12B); the apex long acuminate; margins denticulate near the apex or not, gemmae often present on apex or leaf axils; laminal cells very narrow, 80–130 × 5–7 μm at midleaf (Fig. 12D), cell areolation tight; decurrencies of 2–3 rows of rectangular cells; setae 0.8–1.2 cm, capsule erect.

Distribution. Asia (China, Georgia, Japan, Kyrgystan, Pakistan, Russian Federation, Sri Lanka, Turkey); Europe (Austria, Belarus, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

Sect. *Pseudo-Neckera* (Kindb.) J.T.Wynns

Plagiothecium neckeroideum Schimp., Bryologia Europea 5: 194, 505, Tab. XII. 1851.

≡ *Stereodon neckeroideus* (Schimp.) Mitt., Journal of the Proceedings of the Linnean Society, Botany, Supplement 1(2): 103. 1859 ≡ *Hypnum neckeroideum* (Schimp.) Lindb., Animadversiones de Hypno elegante 28. 1867, nom. inval. Type: [Austria], Loco praerupto umbroso ad viam supra catarractum Krimml-Fall dicta Alpinum salisburgensium, ubi. *W. P. Sch.* Julio 1843 detexit.

Description. Plants large, light green to yellowish green; stems 2–4 cm long; leaves of two types: ventral and dorsal symmetrical and asymmetrical, lateral ones distinctly asymmetrical, ovate, concave, undulate, 1.5–2.8 × 0.9–1.8 mm (Fig. 13A); apex acute; margins denticulate near the apex; laminal cells linear, 70–100 × 5–7 μm at midleaf (Fig. 13C), cell areolation tight; decurrencies of 3–4 rows of rectangular to quadrate cells; setae 1.5–2.0 cm; capsules inclined or almost erect.

Distribution. Asia (Bhutan, China, Democratic People's Republic of Korea, India, Indonesia, Japan, Malaysia, Nepal, Philippines, Republic of Korea, Russian Federation, Taiwan, Thailand); Europe (Austria, Czech Republic, Germany, Romania, Slovenia, Switzerland, Ukraine).

Sect. *Lycambium* Jedl.

Plagiothecium undulatum (Hedw.) Schimp., Bryologia Europea 5: 195, 506, Tab. XIII. 1851.

≡ *Hypnum undulatum* Hedw., Speciorum Muscorum Frondsorum 242. 1801 ≡ *Stereodon undulatus* (Hedw.) Mitt., Journal of the Linnean Society, Botany 8: 39. 1865 [1864] ≡ *Pancovia undulata* (Hedw.) J.Kickx f., Flore Cryptogamique des Flandres 1: 93, 1867 ≡ *Neckeropsis undulata* (Hedw.) Kindb. *ex* J.A.Allen, Mosses of the Cascade Mountains, Washington 117. 1900, *hom. illeg.*, *non* (Hedw.)

Reichardt ≡ *Buckiella undulata* (Hedw.) Ireland, Novon 11(1): 55. 2001. Type: Ad terram humidiusuclam sylvarum umbrosarum planitiei et montium totius Europae. Lectotype (designated by Ireland 1969): In silvis densis acerosis ad terram, in cavernosis saxosis Europae, in Hercynia, Franconia, G 00040241!

= *Plagiothecium menziesii* Thér. *ex* J.T.Wynns, *in sched*. Based on: New Zealand, *A. Menziesi*, *ex hab. P. E. Boissier*, cum *Hypnum molluscum*, *ex herb. I.Thériot*, PC 0132669! syn. nov.

Description. Plants large, whitish-green; stems 3–9 cm long, more or less complanate-foliate; leaves transversely undulate, symmetrical to slightly asymmetrical, imbricate, ovate, 2.5–4.5 × 1.3–2.5 mm (Fig. 13B); the apex acute to obtuse, denticulate or not; laminal cells papillose, 90–175 × 7–10 µm at midleaf (Fig. 13D), cell areolation tight; decurrencies of 1–3 rows of rectangular to quadrate cells; setae 2.5–4.5 cm, capsule inclined.

Distribution. Asia (Azerbaijan, China, Islamic Republic of Iran, Russian Federation, Turkey); Europe (Austria, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Hungary, Ireland, Italy, Latvia, Lichtenstein, Lithuania, Luxembourg, Montenegro, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Ukraine, United Kingdom); North America (Canada, U.S.A.).

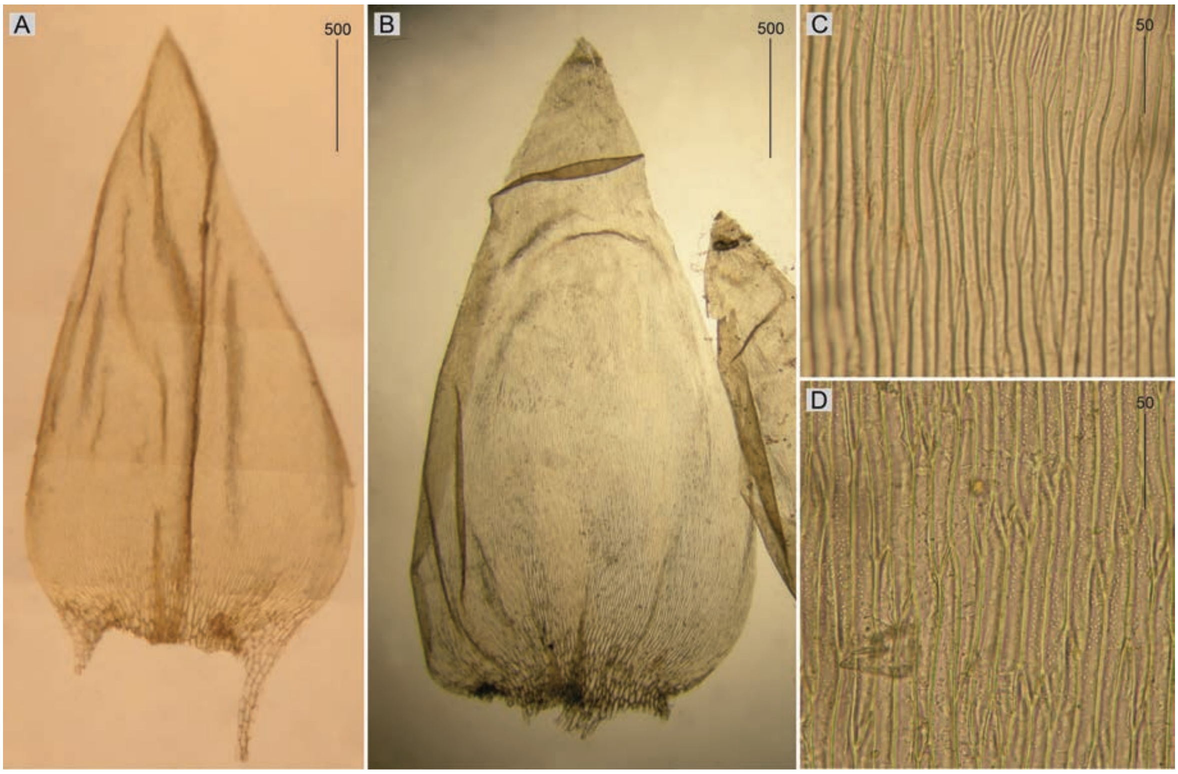

Figure 13. Selected, most important taxonomic features of the *Plagiothecium neckeroideum* and *Plagiothecium undulatum* **A, B** shape and dimensions of the leaves **C, D** shape and dimensions of cells from the middle part of the leaves **A**, **C** *P. neckeroideum* (from lectotype of *P. neceroideum* var. *mureum*, *Holler*, C-M-9389! and syntype of *P. neceroideum* var. *javense*, *M. Fleischer*, PC 0132631!, PC 0132632!) **B**, **D** *P. undulatum* (based of *P. menziesii*, *A. Menziesi*, PC 0132669!).

Key to European taxa of *Plagiothecium*

1 Decurrencies narrow or very narrow, wedge-shaped, composed only of square and rectangular cells, very often remaining attached to stem on dissection........**2**
– Decurrencies wider, forming distinct or semidistinct auricles, composed of square, rectangular, rounded and inflated cells or only rounded and inflated cells, decurrencies usually attached to the leaf on dissection......**22**
2 The cells of the middle part of the leaves narrow, 10 µm or less, cell areolation tight........**3**
– The cells of the middle part of the leaves narrow to wide, 10 µm or more, cell areolation tight to loose........**10**
3 Leaves symmetrical or almost symmetrical, but always one type of leaves........**4**
– Leaves asymmetrical or two types of leaves – symmetrical and asymmetrical........**6**
4 Plants small size, 2–6 cm long........**5**
– Plants large size, 5–13 cm long........***P. undulatum***
5 Leaves gradually tapering to apex........***P. latebricola***
– Leaves abruptly narrowed to long, filiform acumen........***P. piliferum***
6 Leaves asymmetrical........**7**
– There are two types of leaves on the stem, symmetrical and asymmetrical........**9**
7 Plants small size, 1.5–2.0 cm long; leaves lanceolate, concave; apex often denticulate by 2–3 teeth........***P. laetum* var. *hercinicum***
– Plants small or even smaller, 0.6–2.0 cm long; leaves ovate-lanceolate, rather flat; apex rather entire........**8**
8 Leaves forming 40–100° angle with stem, flat, short and narrow, 0.6–1.6 × 0.3–0.6 mm; setae short, about 1 cm, capsules more or less slightly inclined........***P. rossicum***
– Leaves forming 20–70° angle with stem, concave, longer and wider, 1.0–2.0 × 1.1–1.3 mm; setae longer, 1.3–1.8 cm; capsules erect................***P. laetum* var. *laetum***
9 Plants dark green; leaves not undulate and not folded; the apex often gently curved; margins not denticulate near the apex........***P. svalbardense***
– Plants light green to yellowish green; leaves undulate and folded; the apex straight; margins denticulate near the apex........***P. neckeroideum***
10 Leaves symmetrical........**11**
– Leaves asymmetrical or gently asymmetrical........**20**
11 Stems erect........***P. berggrenianum***
– Stems creeping........**12**
12 Leaves flat or slightly concave........**13**
– Leaves clearly concave........**16**
13 The cells of the middle part of the leaf short and wide, 50–90 × 17–20 µm........***P. nemorale***
– The cells of the middle part of the leaf long, very long and wide, 130–260 × 10–22 µm........**14**

14 Plant usually yellowish gold, golden green, golden; leaves large, 2.50–3.00 × 0.80–1.40 mm; laminal cells 130–240 × 10–18 µm at mid-leaf.. ***P. succulentum* var. *succulentum***

– Plant usually dark golden to brown; leaves and laminal cells of other dimensions **15**

15 Leaves ovate, in dry condition shrunken, not folded, long and wide, 3.0–3.60 × 1.40–1.60 mm; apex acuminate... ***P. succulentum* var. *propaguliferum***

– Leaves lanceolate, not shrunken in dry condition, folded, long and narrow, 1.9–3.5 × 0.6–1.0 mm; apex abruptly narrowed to long filiform acumen ....***P. succulentum* var. *cryptarum***

16 Leaves with an eroded apex .... ***P. sakuraii***

– Leaves without an eroded apex...**17**

17 Leaves serrate .... ***P. ikegamii***

– Leaves not serrate..**18**

18 Capsules inclined **19**

– Capsules erect..***P. flaccidum***

19 The cells from the middle part of the leaf to 101 µm in length...***P. cavifolium***

– The cells from the middle part of the leaf more than 101 µm in length .... ***P. subjulaceum***

20 Plants medium-sized to large; leaves large, 3–4 × 1.6–2 mm, distinctly concave, very asymmetrical; cells very wide, 17.0–34.0 µm, cell areolation very loose..***P. longisetum***

– Plants with a different combination of these features **21**

21 Plants medium-sized, stems 2–4 cm long; leaves concave, folded, julaceous and imbricate mainly on lower part of the stem, quite large, 3.1–3.4 × 1.3–1.5 mm; the apex acuminate, short; laminal cells quite long and wide, 113–143.3 × 15.1–19.3 µm at midleaf ....***P. angusticellum***

– Plants small, stems 0.5–1.5 cm long; leaves flat, not folded or imbricate and not julaceous, very small, 1.2–1.8 × 0.6–0.8 mm; the apex acuminate, long; laminal cells short and quite narrow, 70–100 × 10–12 µm at midleaf...***P. tenue***

22 Decurrencies quite narrow but not wedge-shaped, forming semidistinct auricles, composed of square, rectangular, rounded and inflated cells, however, square and rectangular cells clearly dominate..........................**23**

– Decurrencies forming clear, wide, shorter or longer auricles, composed of rounded and inflated cells **26**

23 Plants rather medium-sized; leaves complanate, not cracked at the base **24**

– Plants medium-sized or small; leaves julaceous and imbricate, mainly in lower part of the stem, often cracked at the base **25**

24 Leaves symmetrical, long and wide, 1.7–2.7 × 0.7–1.5 mm; apex not hooked, and not curved towards the ground, usually not denticulate; cells from midleaf 110–151 × 8–9 µm................ ***P. curvifolium* var. *curvifolium***

– Leaves asymmetrical, long and narrow, 1.7–2.2 × 0.6–0.9 mm; apex hooked, curved towards the ground, usually denticulate by 2–3 teeth; cells from midleaf 60–120 × 7–9 µm......................***P. curvifolium* var. *recurvum***

25 Plants medium-sized, leaves julaceous and imbricate mainly in lower part of the stem; leaves asymmetrical; cells from midleaf 95–190 × 6–10 µm. .... ***P. decursivifolium***

– Plants small, clearly julaceous and imbricate; two types of leaves, symmetrical and asymmetrical; cells from midleaf 80–190 × 5–9 µm............. .... ***P. imbricatum***

26 Two types of leaves on the stem, the symmetrical ones: rounded symmetric, with two rounded sides, and asymmetrical ones: with one rounded and one flattened side.......................... ***P. denticulatum* var. *pseudosylvaticum***

– Only symmetrical or only asymmetrical leaves on the stem.................... **27**

27 Only symmetrical leaves on the stem **28**

– Only asymmetrical leaves on the stem **29**

28 Plants medium-sized; leaves imbricate, julaceous, concave; apex not eroded.. ***P. denticulatum* var. *pungens***

– Plants large; leaves not imbricate and not julaceous, more or less flat; apex often eroded .... ***P. sylvaticum* var. *sylvaticum***

29 Plants medium-size to large, stems 2–5 cm long; leaf apex acute to acuminate, usually denticulate; leaves long and wide, 1.4–3.0 × 0.5–3.6 mm 30

– Plants small, stems 0.9–2.5 cm long; leaf apex obtuse, not denticulate; leaves short and narrow, 1.0–2.2 × 0.5–1.2 mm .... ***P. denticulatum* var. *obtusifolium***

30 Leaves not shrunken when dry, not transversely undulate, ovate, with two rounded sides **31**

– Leaves shrunken when dry, transversely undulate, ovate to ovate-lanceolate, with one rounded and one flattened side ....***P. denticulatum* var. *undulatum***

31 Leaves more or less complanate-foliate, julaceous in lower part of stem, 1.5–3.0 × 0.5–2.0 mm; the apex not eroded .... ***P. denticulatum* var. *denticulatum***

– Leaves not overlapping, not imbricate and not julaceous, 3.4–3.6 × 1.4–2.0 mm; the apex often eroded .... ***P. sylvaticum* var. *immersum***

Discussion

The ambiguous taxonomic status of individual species of the genus *Plagiothecium* which have been widely described in the literature over the last decades (Nyholm 1965; Lewinsky 1974; Noguchi 1994; Smith 2001) results from several facts. First of all, from the too hasty synonymization of many names, which in later years led to a reduction in the number of distinguished species and to an overly broad treatment of the remaining ones (Ireland 1969, 1985; Iwatsuki 1970).

The perception of *Plagiothecium* by subsequent generations of bryologists was also significantly influenced by which taxonomic features were considered diagnostic. At the same time, each of the commonly recognized studies considered the width of the cells of the middle part of the leaf as one of the first and most important taxonomic features distinguishing individual species (e.g., Greene 1957; Nyholm 1965; Smith 2001). Thus, in the narrow-cell group there were, e.g., *P. laetum* and *P. curvifolium* and in the wide-cell group, among others, *P. nemorale* and *P. denticulatum*. However, the latter two (*P*. *nemorale* and *P*. *denticulatum*) are sometimes difficult to distinguish in poorly prepared leaves, without preserved and analyzed decurrencies, and consequently errors of determination of individual taxa are quite frequent (Wolski and Nowicka-Krawczyk 2020).

The above-mentioned decurrencies and their significant role in the discrimination of individual species, including the division of the genus into sections, were already indicated by Jedlička (1948, 1950), although subsequent keys and revisions did not attach such great importance to this feature.

An equally important issue, very rarely mentioned, which Wolski et al. (2022a) noticed recently, is the possibility of two types of leaves existing on one plant — symmetrical and asymmetrical. This, together with other qualitative and quantitative features, allowed the description of a new species – *Plagiothecium imbricatum* (Wolski et al. 2022a) and, in this study, to propose a new taxon within the *P*. *denticulatum* complex: *P*. *denticulatum* var. *pseudosylvaticum*.

The new combinations proposed here are justified because not only are they easily distinguished from other closely related taxa, but also their presence and subsequent separation within individual complexes explains the outstanding variability of these taxa described in the literature (Lewinsky 1974; Noguchi 1994; Smith 2001; Cano 2018). Thus, *P*. *denticulatum* var. *pseudosylvaticum* and *P*. *denticulatum* var. *pungens* differ from other members of the *P*. *denticulatum* complex, e.g., by shape, concavity, symmetry of leaf and dimensions of the cells from the middle part of the leaf. *Plagiothecium laetum* var. *herciniicum* is distinguished within the *P*. *laetum* complex, e.g., by plant size, shape, size, concavity of leaf, apex serration, and dimensions of the cells from the middle part of the leaf. *Plagiothecium succulentum* var. *cryptarum* differs from other taxa within the *P*. *succulentum* complex, e.g., by the color of the plant, the shape, dimensions, leaf folding, and the shape and length of the apex. On the other hand, *P*. *sylvaticum* var. *immersum* differs from *P*. *sylvaticum* var. *sylvaticum* in the color of the turf, the symmetry and dimensions of the leaves, as well as the dimensions of the cells from the middle part of the leaf. Due to these features, as well as the descriptions given above, these taxa can be quite easily distinguished macroscopically and microscopically from other closely related species.

Plagiothecium ruthei is a taxon morphologically and genetically distinct from other representatives of the *P*. *denticulatum* complex (Wynns 2015; Wynns et al. 2017). This name (*P*. *ruthei*) is widely recognized by many bryologists and easily associated with features associated with this species. But, contrary to the cited literature (Wynns 2015; Wynns et al. 2017), I propose, as suggested by Hill et al. (2006) and Blockeel et al. (2020), to treat it as a variety of *P*. *denticulatum* — *P*. *denticulatum* var. *undulatum*. This is related to the availability of the oldest name referring to this taxon. A similar situation has been documented, e.g., by Iwatsuki (1970) in the context of *P*. *cavifolium* (= *P*. *roeseanum*) or by Wolski et al. (2024) in the context of *P*. *sylvaticum* (= *P*. *platyphyllum*).

In the current list, given from Europe by Wynns and Schröck (2018), *Plagiothecium handelii* Broth. was not included as a member of the European flora, because the material presented by these authors deviates from the type specimens of this species (isolectotype CP0132634!, syntype CP0132633!) and is more similar to *P*. *angusticellum* which was described in 2020 (Wolski and Nowicka-Krawczyk 2020).

In this article ten lectotypes are designated for: *P. denticulatum* var. *bullulae*, *P. denticulatum* var. *hercynicum*, *P. latebricola* var. *gemmascens*, *P. platyphyllum* fo. *immersum*, *P. succulentum* fo. *propaguliferum*, *P. succulentum* var. *longifolium* fo. *splendens*, *P. sylvaticum* fo. *pungens*, *P. sylvaticum* var. *cryptarum*, *P. sylvaticum* var. *flavescens* and *P. sylvaticum* var. *rupestre*, formally ending the taxonomic revision of these names (Wolski and Proćków 2021).

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Data availability

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

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Research Article

A digital multi-access key for easy identification of large tree species of ebony wood in Madagascar

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Abstract

In 2013, all populations of the precious wood genera *Dalbergia* (Fabaceae) and *Diospyros* (Ebenaceae) from Madagascar were placed on CITES Appendix II in an effort to combat unsustainable and illicit over-exploitation and illegal exportation for the international market. The accompanying Action Plan adopted by CITES identified several information and capacity gaps, which undermine the sustainable and equitable management of these valuable resources. These gaps include the lack of practical, reliable tools to identify species along the entire value chain, from standing trees to cut wood and finished products. To address this need, we developed simple, user-friendly, multi-access keys for the two genera in Madagascar using the Lucid application. This new tool provides highly accurate identification of standing and felled trees to assist actors in the forestry, regulatory, and natural resource management sectors, including customs officials and law enforcement authorities as well as conservationists and protected area managers. In this paper, we focus on the development of the *Diospyros* identification tool. This interactive, electronic key employs 109 informative characters, including morphological features, emphasizing vegetative structures such as bark, stems, and leaves that are present even in the absence of flowers and fruits, in conjunction with eco-geographic characters (bioclimate, elevation, and geography). The key is supplemented with photos, illustrations, and a comprehensive glossary, to deliver accurate identification of the 88 *Diospyros* species that are large enough to be potential sources of commercially valuable ebony wood (≥ 20 cm DBH and/or ≥ 20 m height). This is the first use of Lucid to develop an identification key for species in Madagascar, paving the way for its application to other taxa for which practical electronic field identification is needed.

Key words: CITES, *Diospyros*, ebony, Lucid 4, Madagascar, multi-access key, precious woods

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Introduction

Over the last two decades, members of the precious wood genera *Diospyros* (Ebenaceae) and *Dalbergia* (Fabaceae) have faced rapidly growing pressure and worsening threats due to unsustainable levels of illicit exploitation, primarily within legally protected areas. Most of the ebony and rosewood timber obtained from them has been harvested illegally and exported for the international market, primarily to China (Global Witness & Environmental Investigation Agency 2009, 2010; Schuurman and Lowry 2009; Wilmé et al. 2009; Randriamalala and Liu 2010; Ballet et al. 2011; Randriamalala et al. 2011; Waeber et al. 2015; Andriamanana 2019).

As part of Madagascar's obligations under the Convention on Biological Diversity (CBD) signed in Rio de Janeiro in 1992 (Stone 1996) and the Convention on International Trade of Endangered Species (CITES 1978), the government is responsible for ensuring the sustainable management and protection of all its species and for guaranteeing that their utilization does not threaten their survival. Measures to achieve a permanent halt to illegal exploitation in order to establish policies for rational and sustainable management of precious woods as well as for the equitable sale of these valuable resources have recently been initiated (Innes 2010; Pepke et al. 2015). Furthermore, in 2013, all Malagasy species of both *Diospyros* (which produces ebony wood) and *Dalbergia* (the primary source of rosewood) were listed on CITES Appendix II in an attempt to reduce over-exploitation and commercial trafficking (Andriambololonera et al. 2013; CITES 2013a, b). That same year, at the 16th CITES Conference of Parties, an Action Plan was adopted (Decision 16.152 and subsequently Decision 17.203) requiring the establishment of an embargo on the export of wood stockpiles that had accumulated following seizure by the Malagasy authorities and prohibiting commercial exchange of ebony and rosewood (Andriamanana 2019). Yet despite these efforts, exploitation has continued (Ballet et al. 2011; Mason et al. 2016; Ratsimbazafy et al. 2016). Moreover, significant gaps were identified regarding the scientific knowledge base of these precious wood genera, which prompted a series of recommendations in the Action Plan to address them (CITES 2018).

One of the most important issues identified in the Action Plan was the inability to provide correct scientific names and reliable identifications for species, which are the principal unit of CITES management and a key element of biodiversity. This situation is due in large part to the lack of efficient identification tools (Delaunay 2020). Moreover, actors involved in the Malagasy forestry sector use generalized designations for various types of precious wood, either in the form of common (vernacular) names (which vary regionally) or commercial names based on the color and other characteristics of the wood being exploited. However, these names often apply to two or more distinct species, and they are frequently used inconsistently. For example, all species of *Diospyros* with black heartwood are called 'ebony' or 'hazomainty' in Malagasy, and species of *Dalbergia* with red or deep pink-violet heartwood are called 'rosewood', or 'andramena'. Consequently, commercial and scientific names represent fundamentally different concepts in the context of the sustainable management of these important resources and the species from which they are sourced (Rakotovao et al. 2012). Addressing the challenges associated with the accurate identification and naming of species is a major hurdle for the eventual relaxation or lifting of the current embargo on these two genera by means of establishing a non-detriment finding (NDF) for a species whose exploitation would be possible without compromising its survival (Mason et al. 2016) or by removing them for CITES Appendix II. Therefore, it is crucial to develop methods and tools that allow for the accurate, precise, and unambiguous identification of species. This is particularly important when evaluating and managing populations of precious wood species, as it informs decision-making regarding their conservation, management, and exploitation.

To help address the objectives of the CITES Action Plan for Madagascar, a consortium was established in 2017 to develop scientific knowledge and tools in support of the sustainable management of the country's precious wood genera *Dalbergia* and *Diospyros* (the consortium is known by its French acronym G3D – Gestion Durable des bois précieux *Dalbergia* et *Diospyros* de Madagascar). The management and control of these species requires reliable identification along the entire value chain, from standing trees and cut logs in the forest to sawn wood and finished products, and each of these stages requires its own methods and tools. A multi-disciplinary approach was therefore adopted that comprises four complementary components:

- Taxonomy (documentation of populations, field collection of representative samples, and clarification of species delimitation).
- Development of practical, reliable identification tools for standing trees and for specimens with leaves, flowers and/or fruits.
- Establishment of forensic identification methods based on the study of a) comparative wood anatomy, b) DNA sequencing (barcoding), and c) near infrared spectroscopy.
- Development of effective management strategies for the conservation of wild populations.

Collectively the main objective of these components is to establish a solid scientific base of research material and associated knowledge to inform accurate delimitation and identification of potentially exploitable species of *Diospyros* and *Dalbergia* for their effective management and for forensics. As part of this initiative, work was undertaken to develop practical identification tools for both genera based on morphological and eco-geographic characters, as part of the G3D taxonomy component led by the Missouri Botanical Garden's Madagascar Program.

Identification keys are generally based on morphological characters of plant organs and are primarily used to distinguish species based, as far as possible, on easily observed features. Keys primarily make use of the inflorescence structure and of characteristics of the flowers and fruits, often complemented by characters of the leaves as well as other aspects such as the plant's growth form or habit. They are nearly always dichotomous and are generally structured for publication in scientific articles or in floras and guidebooks. In this type of key, the sequence in which information is presented to the user is pre-determined by the author, usually by offering the user two mutually exclusive choices (a "couplet") at each step by means of a text description of one or more alternative diagnostic characters (Judd et al. 1999; Hagedorn et al. 2010; Griffing 2011), leading either to another couplet or to an identification. However, when attempting to make an identification in the field, and especially if confronted with a sterile individual (lacking flowers and fruits, which is often the case when conducting forest inventories), dichotomous keys based primarily or exclusively on reproductive organs are difficult if not impossible to use. Even when flowers and/or fruits are available, a key that employs specialized terminology can present problems that render it impractical to users not familiar with technical jargon. Moreover, published dichotomous keys cannot easily be modified or updated if new information becomes available or new, morphologically similar species are recognized (Hardisty and Roberts 2013; Mangold 2013; Zuquim et al. 2017).

One way to overcome these constraints is to develop keys that combine traditionally used characters with new, informative features that have been underutilized or ignored, such as those involving vegetative structures, which are more likely to be observable regardless of the phenological stage, even in the absence of flowers and fruits. Leaf features are particularly pertinent in that they often enable recognizing and distinguishing among closely related taxa (Hickey et al. 1999, Ellis et al. 2009). Similarly, while the utility of bark features for recognizing tree species is well known in temperate areas for genera such as *Acer*, *Betula*, *Picea*, *Populus*, and *Quercus*, among others (Biswas et al. 2016; Carpentier et al. 2018; Wu et al. 2021; Juola et al. 2022), bark characters have not been used widely in tropical regions and very little in Madagascar. Although bark characters have not been utilized previously for species delimitation and recognition of Malagasy *Diospyros*, field observations have clearly revealed significant variation among species, suggesting that they are of potential use for field identification. Likewise, eco-geographic characters such as bioclimate, vegetation type, and elevation, which have proven to exhibit species-specific patterns and to be highly informative for species delimitation (Lowry et al. 1999; Vences et al. 2009; Rabarimanarivo et al. 2015; Crameri et al. 2022), are also of potential value for informing accurate identification.

In the age of global access to information via the internet and the rapid development of bioinformatics tools and technologies, it is now possible to build interactive and richly illustrated, multi-access identification keys that are simple, practical, and efficient. Moreover, these keys can be accessed through portable platforms that function independently, without needing an internet connection. This is precisely the type of tool that is required to enable reliable identification of Malagasy *Diospyros* and *Dalbergia*, employing a data matrix (or character/species) multi-access type of key, a model that is now being widely used (Begum et al. 2012; Wati et al. 2018). Early multi-access keys were based on the punch card approach (Hansen and Rahn 1969), in which an array of characters with two or more states that are not necessarily mutually exclusive are presented to the user, who is not required to follow a pre-determined sequence of steps (in contrast to conventional keys), but which can instead be used to select features in the order that best corresponds to the material being identified. This type of key is particularly advantageous when dealing with incomplete material (Judd et al. 1999, 2002). Several computer programs have recently been developed to produce interactive, matrix-based, multi-access identification keys (Dallwitz 2007; Gaubert et al. 2008; Hagedorn et al. 2010) such as DELTA and INTKEY (Dallwitz 1993), FRIDA (Martellos 2010), LINNAEUS (Wati et al. 2018), Lucid (Norton et al. 2000), and Xper versions 2 et 3 (Ung et al. 2010; Vignes-Lebbe et al. 2016; Lombard et al. 2021). They all exploit practical and flexible methods for coding characters, and some can incorporate illustrations (photos, drawings, and maps), as well as videos, links to internet sites, and a glossary. The major advantages of these keys are that they facilitate identification even when material is incomplete and are accessible for a wide range of users, including those less familiar with the organisms being identified than professional taxonomists.

One of the main objectives of the taxonomic component of the G3D project is to produce a tool that can be used at the beginning of the precious wood value chain to obtain a reliable species identification for each potentially exploitable tree of *Diospyros* and *Dalbergia*, a required step for the sustainable management of these resources. To meet this need, the identification tool must work reliably for trees that are still standing or that were recently felled, even if flowers or fruits are absent. After a careful comparison of the advantages and drawbacks of each of the applications mentioned above, Lucid was considered to be the best adapted to meet Madagascar's current needs for accurate field identification. Lucid has already proven to be effective for the development of practical identification keys for a wide diversity of objects, ranging from minerals to fossil bacteria and living animals, such as certain insect groups, as well as algae and vascular plants (many examples in these and other groups can be found on the Lucid website: http://lucidcentral.org/).

The work presented in this paper summarizes the development of a practical key using Lucid 4 to facilitate the accurate and reliable identification of Malagasy species of *Diospyros* that are potential sources of commercially valuable ebony wood. As for large tree species of *Dalbergia* (Phillipson et al. 2023), a separate key has been developed using the same software and following the same principles and methods but is not discussed further in this paper.

Diospyros comprises an estimated 903 species of which 763 have been described to date, distributed across the main tropical regions (see the following for examples of recent taxonomic accounts of *Diospyros* spp. from various parts of the world: Tang et al. 2019; Schatz et al. 2021b; Puglisi et al. 2022; Hassler 2023; POWO 2023) and the remainder are currently in the process of being formally described. Madagascar represents one of the main centers of diversity for the genus, as indicated by the first comprehensive revision for the island published by Perrier de la Bâthie (1952a, b), who recognized a total of 97 species. However, collections and field observations made over the following decades clearly revealed the presence of far greater species diversity, and this catalyzed a new effort to document and describe Malagasy *Diospyros* starting some 15 years ago. This has led to the recognition of an estimated 285 species on the island, 151 of which have now been described and all but two of which are endemic to Madagascar (Schatz and Lowry 2018; Schatz and Lowry 2020; Schatz et al. 2020, 2021a, 2021b; Linan et al. 2021; Rakouth et al. 2023; Linan et al. 2024; Mestre et al. 2024), while an additional ca. 140 endemic species remain to be described (Madagascar Catalogue 2024). Field work conducted as part of the G3D project has contributed significantly to the available collection base, whose taxonomic component has now clarified the delimitation and completed the description of all 88 'large tree' species (CITES 2024; Lowry et al. 2024), each of which is regarded as a potential source of commercially valuable ebony wood by virtue of the fact that it has been documented to reach a diameter at breast height (DBH) of ≥ 20 cm and/or a height of ≥ 20 m (Schatz et al. 2021b).

Species of *Diospyros* are found throughout all regions of Madagascar, but depending on a given species' ecological preferences (altitude, substrate, habitat, etc.), they will generally be found in just one or two of Madagascar's principal native vegetation types, including evergreen humid forest in the east, woodland or shrubland in the west, and deciduous dry forest in the north (often on karstic limestone, known as 'tsingy') or the south, as well as spiny thickets in the south and southwest (species of *Diospyros* are rare in montane vegetation). Some have wide geographical ranges, occurring across a large proportion of one or two of the island's main bioclimatic regions, as defined by Cornet (1974) and simplified by Schatz (2000), while others have highly restricted ranges (Madagascar Catalogue 2024). A species' eco-geographic preferences comprise valuable information that can complement morphological characters for developing identification keys (Wati et al. 2018; Lombard et al. 2021). With this in mind, we tested the value of including eco-geography in building our identification tool for large tree *Diospyros* species using the Lucid platform.

The tool we present here was designed primarily to assist an array of actors involved in various aspects of the management and control of Madagascar's forestry sector, in particular with regard to inventories of standing trees. These stakeholders include forestry agents, operators involved in wood harvest (including both landowners and concession holders), managers of protected areas and other conservation sites, customs officials, and officers of the judiciary police, among others. Moreover, because the key we have developed enables users to identify dried collections (i.e., herbarium specimens) as well as living material, it will also be of value to researchers, field botanists, and students to improve their knowledge of the Malagasy species that are potential sources of commercially valuable ebony wood and strengthen their ability to recognize them.

Materials and methods

Lucid 4 software

For an identification tool to perform well and respond to Madagascar's needs for managing precious woods by enabling accurate identification of standing trees and dried specimens, it must be simple, practical, interactive, and portable. Among the various programs available to produce electronic, matrix-based or multi-access keys, we selected Lucid version 4.0.4 (https://www.lucidcentral.org), which meets all of Madagascar's needs for identifying large tree species of *Diospyros* in the field and herbarium. To our knowledge, Lucid keys have never been used before in Madagascar for species-level identification, even though keys can be distributed free of charge; only the developers are required to obtain a license to produce an operational tool. Utilization of a Lucid-based key does not require internet access, and as a key it can easily be modified, corrected, and updated with little effort by the developer. However, the main reason we opted to employ this program is because it is simple to use and functions without an internet connection, making it particularly well suited for field identification in Madagascar, where there is usually no internet access. Moreover, Lucid keys can easily be shared and transferred (by e-mail, USB key, on-line download, etc.) and can be used freely in any browser and on a wide range of platforms (laptops and tablets, or smartphones via a mobile application). Lucid is also practical and intuitive, allowing users to access a wide range of visual and text-based descriptors as well as species profiles (Vignes-Lebbe et al. 2016; Pinel et al. 2017). The developer is provided with an efficient interface containing all the tools and functionality needed to organize and deliver supplementary information to the user (photos, line drawings, links to on-line sites, glossaries, etc.) for each species and for important or difficult-to-interpret characters, greatly increasing the user's ability to grasp and understand terminology, thus improving their ability to obtain an accurate identification. To optimize the functionality and utility of the Lucid-based tool we have developed, it was designed to perform well even in the absence of flowers and fruits and to remain robust and reliable even if the user misinterprets some characters. The tool thus provides efficient, multi-access entry according to the user's needs and can deliver rapid and accurate identifications as well as valuable diagnostic information.

Taxa

Among the ca. 285 species of *Diospyros* recognized in Madagascar, 88 develop into large enough trees to be potentially exploitable for ebony wood (CITES 2024; Lowry et al. 2024) and are therefore included in the Lucid key we have developed. Each species has its own particular geographic and bioclimatic distribution range, reflecting its ecological preferences. For example, within the island's humid bioclimatic zone, *D. squamosa* is widely distributed in dense, humid, evergreen forests of the northwest and along the eastern escarpment (Schatz and Lowry 2020), whereas *D. littoralis* is restricted to littoral forests on sand near the eastern coastline (Schatz et al. 2021a). Other species have narrow ranges and are known from only a few sites, such as *D. lowryi* and *D. ultima*, both from low elevation humid forests in the northeast and known from only 2 and 4 localities, respectively (Schatz and Lowry 2018; Schatz et al. 2021a; Madagascar Catalogue 2024). Some species of *Diospyros* occur in dry, semi-deciduous forest on karstic limestone in the extreme north of the island, such as *D. vescoi* (which has a rather large range) and *D. crassifolia* (much more narrowly distributed) (Linan et al. 2021). Still other species occur in areas with similar vegetation in the west, such as *D. tropophylla* and *D. sakalavarum*, which have fairly large ranges, and *D. subtrinervis*, known from a single locality. The risk of extinction for each of the 88 large tree species was assessed between 2018 and 2024 according to the IUCN Red List criteria (IUCN SSC 2012, 2024). A total of 45 species (51%) were assessed as threatened, including 5 that were found to be Critically Endangered (CR), 18 Endangered (EN), and 22 Vulnerable (VU), whereas 11 species were assessed as Near Threatened (NT), and 31 were regarded as Least Concern (LC). One species was Data Deficient (DD) (IUCN 2024).

Building the key

The key was constructed in four steps, implemented in the application's key-building interface (Lucid Builder), which comprises three tabs at the base of the tree panels, [Tree View], [Spreadsheet Scoring] and [Score Analyser], as follows:

1. Data compilation within the [Tree View] tab.
2. Data coding and entry within the [Spreadsheet Scoring] tab.
3. Development of the key.
4. Testing, feedback, and improvement.

The [Score Analyser] tab provides analyses of character differences and species polymorphism to assess and indicate where improvements can be made to the key.

Data compilation within the [Tree View] tab

Taxonomic entities backbone

The first tab [Tree View] enables the developer to view the structure (sequence and hierarchy) of characters and character states in the 'features' panel as well as a list of the species in the 'entities' panel. The taxonomic entities backbone was established by alphabetically entering the names of the 88 large tree *Diospyros* species in the [TreeView] tab. The species for which the key was developed are listed in Appendix 1 and can also be found on a dedicated page via the Catalogue of the Plants of Madagascar (Lowry et al. 2024).

Features backbone

The initial step of selecting characters and scoring character states involved preparing a list of potentially informative features of the stems, leaves, flowers, and fruits that vary among the large tree species of Malagasy *Diospyros*. Additional characters that could facilitate reliable field identification were then incorporated, in particular those that can only be observed in fresh material, including macroscopic features of vegetative organs such as the bark, which are easily observable throughout the year, even when an individual tree is sterile. For a key based exclusively on morphological data, the assumption is usually that any given species can occur anywhere within the geographic area being considered. This is clearly not the case, however, for *Diospyros* in Madagascar. We therefore compiled additional information on the ecological preferences of each species (bioclimate, altitudinal range, and vegetation type) as well as the potential geographic range for each species, to improve ease of identification by reducing the list of candidate species for a given site (Wati et al. 2018). The final selection of character features and the corresponding terminology included those that were determined to be the most pertinent for discriminating among the species and the easiest for users to interpret. The list of characters and states was entered into the 'features' panel on the [TreeView] tab of Lucid Builder. The features backbone of the key for the 88 species comprises data for morphological and eco-geographic characters, including a total of 109 characters and 356 character states (Appendix 2).

Compilation of data on morphological characters

Data on morphological character states exhibited by each species were primarily collected from descriptions available in the literature, complemented and refined based on examination of specimens available in the herbaria of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar (TAN), the Missouri Botanical Garden, St. Louis, Missouri, USA (MO), and the Muséum National d'Histoire Naturelle (MNHN), Paris, France (P), as well as scans of selected specimens available online. This was further enriched with field observations recorded by collectors on specimen labels (Lombard et al. 2021) and photos of living material, notably taken as part of the G3D project, showing details of habit, branching, bark, leafy branches, flowers, and fruits, which provide more precise information on character states seen on standing trees, whereas information obtained from the literature and pressed specimens is more informative for making identifications of herbarium material (Fig. 1, Appendix 2).

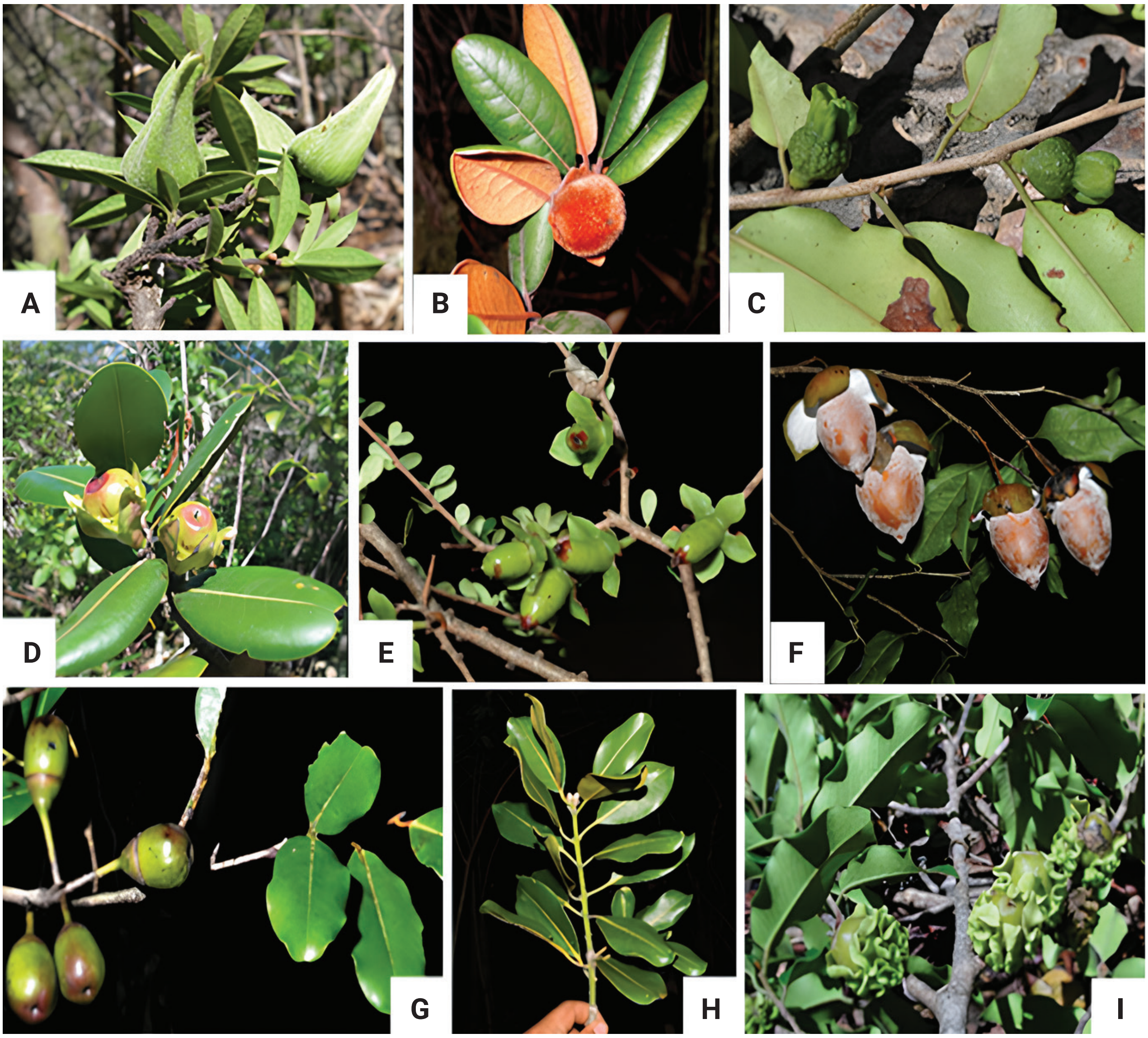


Figure 1. Photographs of selected large tree species of *Diospyros*, showing various morphological features of their leaves, fruit, and fruiting calyx **A** *D. aculeata*, leaf apices terminating in a spine and fruiting calyx completely enclosing the fruit (photograph by F. Ratovoson) **B** *D. antsirananae*, densely pubescent leaves and fruit, with reddish brown to ferruginous trichomes (photograph by S. Rakotonandrasana) **C** *D. bernieriana*, margins of the leaves undulate and fruiting calyx expanding to enclose the fruit completely and form a prominent collar (photograph by G.E. Schatz) **D** *D. crassifolia*, coriaceous, elliptic leaves and erect fruiting calyx lobes (photograph by S. Rakotonandrasana) **E** *D. humbertiana*, small, obovate leaves and fruiting calyx with 4 or 5 spreading lobes (photograph by P. Lowry) **F** *D. labatiana*, fruit surface and inner portion of calyx lobes covered by a white waxy substance (photograph by S. Andrianarivelo) **G** *D. maculata*, glabrous leaves and fruit with an entire (unlobed), cupuliform calyx (photograph by P. Lowry) **H** *D. parifolia*, subopposite to opposite, coriaceous, glabrous leaves (photograph by S. Andrianarivelo) **I** *D. plicaticalyx*, lenticellate, gray/grayish twigs and fruiting calyx with undulate and plicate margins (photograph by G.E. Schatz).

As mentioned above, bark characters have been shown to be of value for species identification in temperate genera but have been less widely used in the tropical areas, including Madagascar, where scientists have only rarely used bark features. In the absence of a standard method for describing bark characters, we drew from the works of several authors (Letouzey 1969; Junikka 1994; Rakotovao et al. 2012; Biswas et al. 2016; Carpentier et al. 2018) to identify those of potential value for Malagasy *Diospyros*.

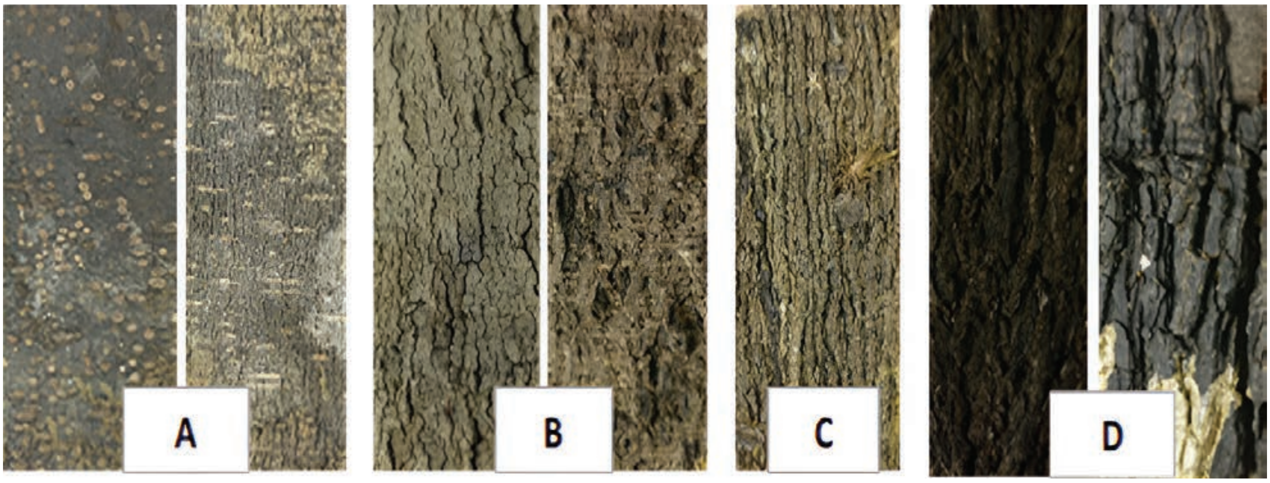


Figure 2. Examples of the three bark characters utilized in the Lucid key for Malagasy *Diospyros* (texture, presence of distinctive structures, and color) **A** smooth, lenticellate, gray/grayish bark of *D. ferrea* **B** smooth, fissured, gray/grayish to light brown bark of *D. chitoniophora* (left) and *D. bardotiae* (right) **C** rugose, light brown bark with longitudinal striations of D. *brevipedicellata* **D** rugose, deeply fissured, cracked, dark brown to black/blackish bark of *D. clusiifolia* (left) and *D. toxicaria* (right) (all photographs by H.N. Rakouth).

Three types of easy-to-observe characters were retained: bark surface texture (smooth, fissured, scaly, rugose), the presence of distinctive structures (lenticels, fissures, longitudinal and transverse striations, scales, a crust, crevasses, etc.), and overall color, both *in vivo* and *in sicco* (Fig. 2). To compile information on these characters for each species, we examined photos of tree trunks and bark samples taken in the field, along with high resolution images of dried bark material associated with herbarium specimens (Fig. 2). High resolution photos were taken at the Scientific Imaging Workshop (UAR 2700 2AD, BAOBAB facilities, DIM-MAP Île-de-France, CNRS and MNHN) located at the Muséum in Paris. For Madagascar, the use of bark features to identify species for the development of a practical identification tool represents pioneering work.

Compilation of data on eco-geographical characters

Information on ecological preferences and geographic distribution is also useful for facilitating the identification of Malagasy species of *Diospyros* given that each of them has its own distinctive specificities. We used QGIS (3.16.8 with GRASS 7.8.5) to visualize distribution data for each species (as a .kml points layer) and to record their eco-geographic characteristics using three key descriptors:

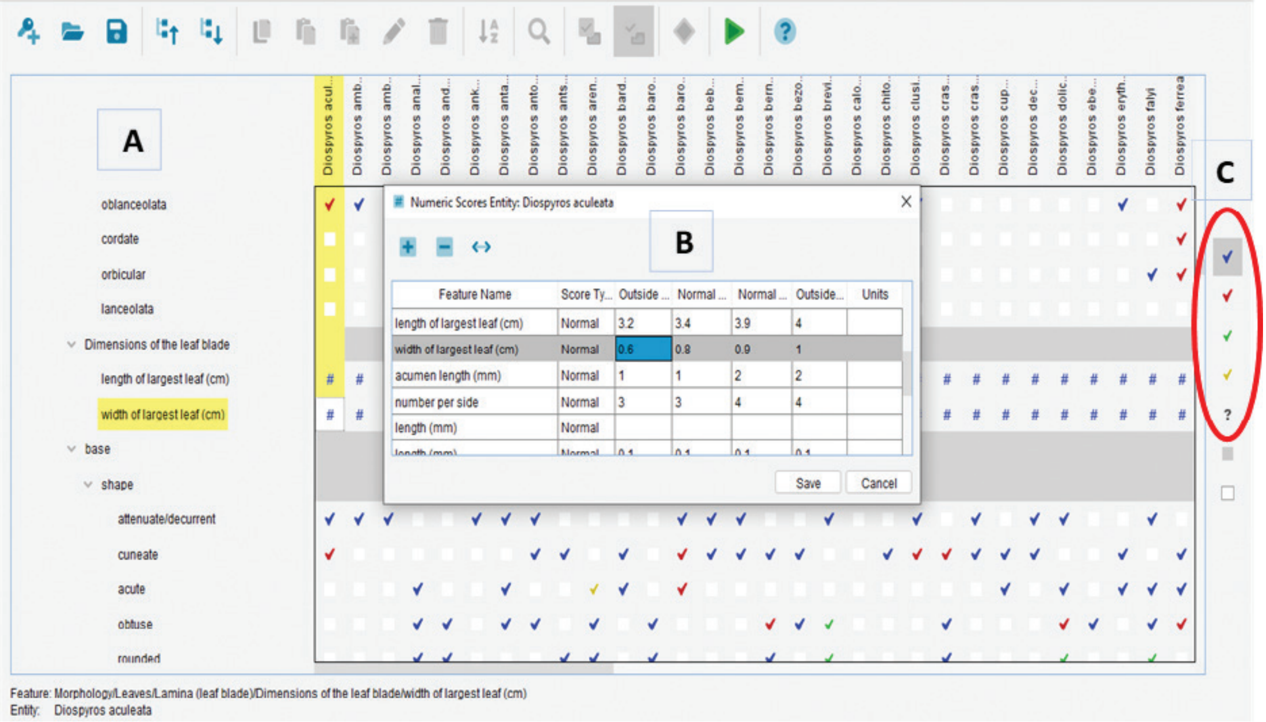
- Madagascar's five main bioclimatic regions (humid, subhumid, dry, subarid, and montane), based on the bioclimatic map of Cornet (1974) as simplified by Schatz (2000).
- Five altitudinal classes between 0 and 2500 m (in 500 m increments); < 500 m, < 1000 m, < 1500 m, < 2000, and 2000 m or more.
- Potential geographic distribution: actual and potential presence in Madagascar was recorded in cells of 1°×1° resolution; potential presence was extrapolated from known occurrence points.

Data scoring within the [Spreadsheet Scoring] tab

Scoring of features and states that correspond to each species was done for both qualitative and quantitative characters using the second tab in the key-building interface [Spreadsheet Scoring], which contains the data matrix of characters and species. Those that can potentially be misinterpreted, e.g. certain leaf shapes (elliptic, oblong, ovate, etc.), can be recorded in Lucid in a way that accommodates for potential user error. By using this feature, species are retained in the final list of potential results that would otherwise have been excluded due to the incorrect selection of a character state that is in fact not found in material belonging to the taxon. This is a helpful option since the interpretation of character states is not always straightforward and can vary between users. For a species that exhibits morphological variability, all possible character states are coded, enabling the user to select more than one state for a polymorphic feature. On the other hand, even if certain character states have not actually been observed on material of a given species, the person building the key can nevertheless select states that could reasonably be expected to be expressed and could therefore be encountered by a user or could be inadvertently selected due to a misinterpretation. To record information on the reliability of the states known for a particular character, a blue symbol is selected when the interpretation is verified and unambiguous, whereas a red symbol is chosen in situations where misinterpretation by the user is possible or likely. Rare or exceptional character states are indicated by a green symbol and those that are both rare and prone to misinterpretation are indicated in yellow. Finally, a question mark is used for characters whose state(s) is (are) uncertain or for which data are unavailable (Fig. 3). The Lucid tool for Malagasy *Diospyros* has thus been designed to function regardless of which plant organs are available for identification and to be reliable even when there is a risk of potential errors for certain characters due to user misunderstanding or misinterpretation.

Quantitative characters were counted or measured to code numerical values (#) in the data matrix table. This information was recorded in a table comprising four columns: outside minimum value, normal minimum value, normal maximum value, and outside maximum value, in which the normal values are calculated as the most frequent class of observations [normal min – normal max] in all measured samples. For example, in Fig. 3, the normal values are comprised in the class [0.8–0.9 cm] of the character "width of the largest leaf", among 10 measured leaves. Counts or measurements were systematically made on an organ or structure regarded as being fully mature, and in order to standardize and facilitate comparison, the largest values were always used. For example, leaf dimensions were measured on the largest leaf on a leafy branch (Fig. 3).

To score the potential geographic distribution of each species treated in the key, a grid comprising 75 cells, each with an area of 1°×1°, was superimposed over a map of Madagascar, which is situated between 11° to 25° S latitude and 43° to 50° E longitude. Taking into consideration the known range of each of the 88 *Diospyros* species as well as its eco-geographic preferences, the potential geographic range was scored in the appropriate cells. The convention used to name a given cell was based on the degree values for longitude and latitude corresponding to the points it encompasses. For example, the cell containing the coordinates of a population of *D. aculeata* located at 45°16'23"E longitude



Numeric Scores Entity: Diospyros aculeata

Feature Name	Score Ty...	Outside ...	Normal ...	Normal ...	Outside...	Units
length of largest leaf (cm)	Normal	3.2	3.4	3.9	4	
width of largest leaf (cm)	Normal	0.6	0.8	0.9	1	
acumen length (mm)	Normal	1	1	2	2	
number per side	Normal	3	3	4	4	
length (mm)	Normal					
length (mm)	Normal	0.1	0.1	0.1	0.1	

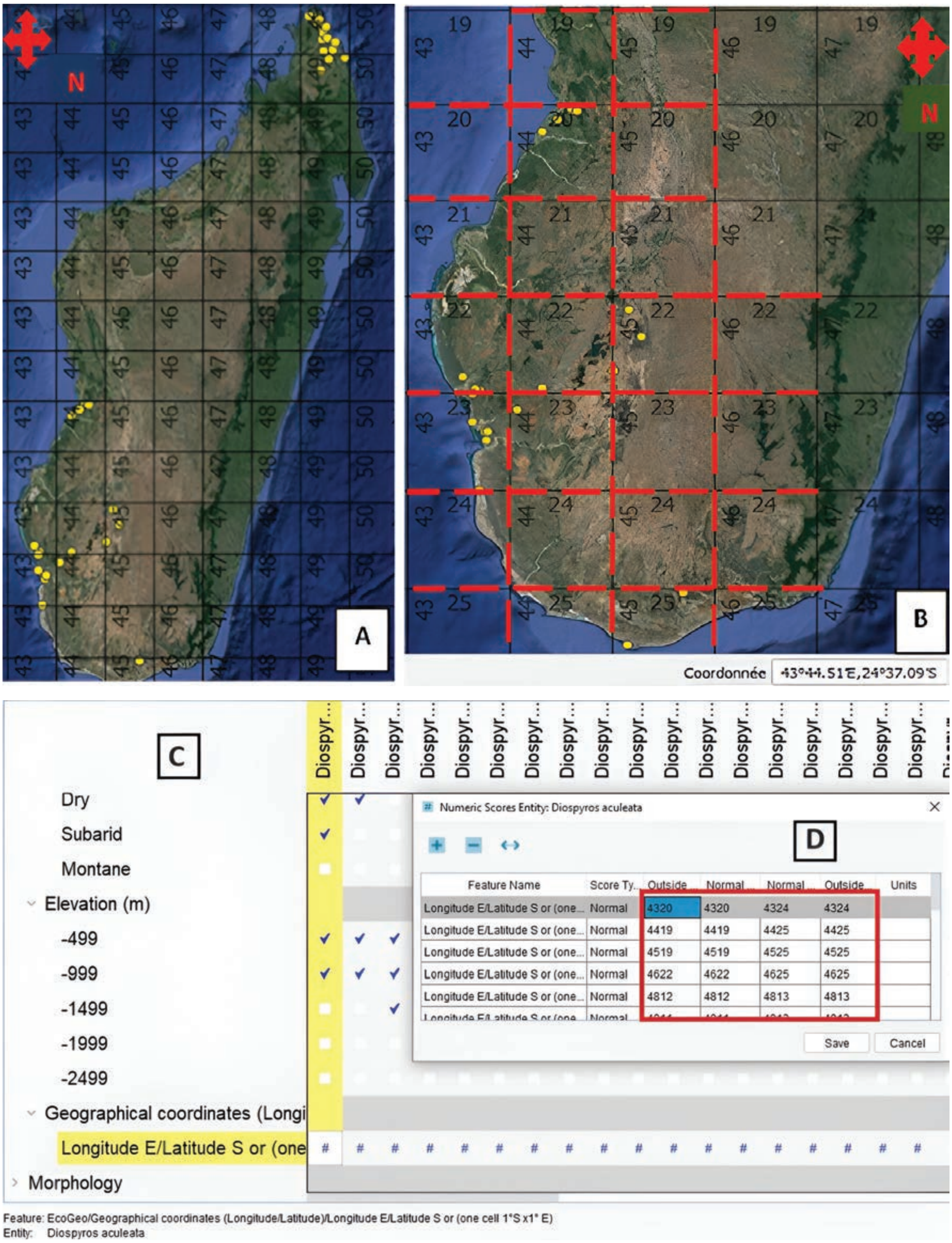
Feature: Morphology/Leaves/Lamina (leaf blade)/Dimensions of the leaf blade/width of largest leaf (cm)
Entity: Diospyros aculeata

Figure 3. A screenshot of the *Diospyros* Lucid key-builder showing the data matrix table and the methods for scoring character data **B** inner pop-up table for numeric scores (#) of quantitative characters (here, width of largest leaf in cm). **C** The 5 types of usable interpretation scores for qualitative characters colored differently depending on the level of the character's certainty: verified and unambiguous (blue), possible or likely to be misinterpreted (red), rare (green), rare and prone to misinterpretation (yellow), uncertain (?).

and 22°54'05"S latitude was labeled 4522, as shown in Fig. 4A–D. This allowed for scoring of longitudinal bands of presence, which, given the shape of Madagascar, were comparatively fewer in number than the alternative, using latitudinal bands of presence. Hence, the potential distribution of each species was characterized as a range within one or more longitudinal bands, and these were entered into Lucid as a quantitative variable with multiple independent ranges. We intentionally used a conservative approach for the process of estimating potential range, including all grid cells in which the species could reasonably be anticipated to occur. The resulting potential distribution was then systematically reviewed and validated by comparison with expert information provided by field botanists and taxonomists working on Malagasy *Diospyros*.

Development of the key

The process of developing the *Diospyros* key involved making changes and fine-tuning it to enhance both its functionality and visual aspects in an effort to make it as user-friendly and straight forward as possible while retaining the ability to incorporate various types of supplementary information to improve identification accuracy. As English is the default language for Lucid, it was utilized in the development of the prototype *Diospyros* key. Considering the varying levels of botanical knowledge and familiarity with terminology among users in Madagascar, the key was designed to employ concise terminology for characters (features) while avoiding complex technical terms. Nevertheless, certain



Dry
Subarid
Montane
Elevation (m)
-499
-999
-1499
-1999
-2499
Geographical coordinates (Longi
Longitude E/Latitude S or (one
Morphology

Numeric Scores Entity: Diospyros aculeata

Feature Name	Score Ty...	Outside ...	Normal ...	Normal ...	Outside ...	Units
Longitude E/Latitude S or (one...	Normal	4320	4320	4324	4324	
Longitude E/Latitude S or (one...	Normal	4419	4419	4425	4425	
Longitude E/Latitude S or (one...	Normal	4519	4519	4525	4525	
Longitude E/Latitude S or (one...	Normal	4622	4622	4625	4625	
Longitude E/Latitude S or (one...	Normal	4812	4812	4813	4813	

Feature: EcoGeo/Geographical coordinates (Longitude/Latitude)/Longitude E/Latitude S or (one cell 1°S x1° E)
Entity: Diospyros aculeata

Figure 4. A, B screenshot from QGIS 3.16.8 **C, D** screenshot of Lucid key builder **A** current distribution map visualized on QGIS within Madagascar **B** map of the southern part of Madagascar showing grid cells (red dashes) encompassing the potential range visualized on QGIS **C** some of the eco-geographic features employed (elevation and geographic coordinates) **D** coordinate position coding system using the degree values of each 1 × 1-degree cell.

scientific terms were retained to maintain precision. For example, the technical term "brochidodromous" was used to define leaf venation in which secondary veins do not terminate at the margin but join to form a series of prominent arches, which form a sub marginal nerve (Ellis et al. 2009).

Media tool function

To augment the utility of the key, images were incorporated for each species, including photos of living plants as well as details of particular organs and distinctive features, accompanied by scans of herbarium specimens and line drawings as exemplars. Using the image viewer function of Lucid, the user can thus scroll among images and zoom in as needed to facilitate comparison with the material being identified. Selected images were recomposed to highlight key characters and character states in the ‘features’ window, and photos were taken of informative structures from herbarium specimens (e.g., leaves, fruits, bark samples, etc.) using the high-resolution imaging equipment at the MNHN in Paris (a Nikon D7100 camera with a Nikkor AF-S 60 mm macro lens mounted on a Kaiser light stand equipped with a Cognisys StackShot Macro rail). Two methods were employed. For two-dimensional objects such as leaves, photos were taken using the macro mode in the Nikon Camera Control software (ver. 2.0), whereas for large objects such as fruits or those with significant relief (e.g., bark), z-stacking was done using the Helicon Remote program (ver. 3.9.12) and Helicon Focus (ver. 8.1.1), which creates a final image with unlimited depth of field by electronically superimposing the in-focus portions of a series of shots taken at distinct levels and combining them into a single image that clearly shows the entire structure being photographed. A total of ca. 4,500 images were taken from 200 bark samples representing 40 of the 88 large tree species of *Diospyros* (bark material was not available for the other 48 species).

An integrated glossary provides quick access to clear definitions of all technical terms, often accompanied by photos and/or illustrations. The definitions presented to the user were compiled from several widely used sources, including Beentje (2016) and Harris and Harris (2001) for general terminology, and Ellis et al. (2009) for features relating to leaf architecture. The utility of the *Diospyros* key was further strengthened by providing links to internet sources for each species, including the corresponding pages in the Madagascar Catalogue (2024) and the IUCN Red List (IUCN 2024), although these can only be accessed when connected to the internet. However, because precise information on the distribution of precious wood species is potentially sensitive, access to maps and full data on known occurrences is limited in these on-line sources and is not available to the general public.

Testing the key and integrating feedback

Early iterations of the *Diospyros* key underwent thorough evaluation and testing by botanists familiar with Madagascar’s precious woods, particularly *Diospyros*, as well as by non-specialists. This was done during a series of working sessions in which participants provided feedback through evaluation forms. The results were utilized to enhance and fine-tune both the structure and content of the key. Subsequently, three initial trial identification workshops using herbarium specimens were held (in June and September 2021, and October 2022) for groups of participants with varying levels of knowledge and experience. The main objectives were to:

1. Review and discuss the multi-access structure of the key and ease of interpretation of the characters.

2. Determine which of the morphological and eco-geographic characters were the most informative for making accurate species-level identifications.
3. Test the overall performance of the key and identify problems or gaps.

In April 2022, an additional test workshop was conducted for students participating in the Madagascar precious woods project at the University of Antananarivo, and six regional training workshops were organized between November 2022 and August 2023 for various important stakeholder groups such as customs agents, members of the judiciary police, police officers, forestry agents, and conservation site managers. The purpose of these workshops was to introduce the key to the participants and gather their comments and suggestions.

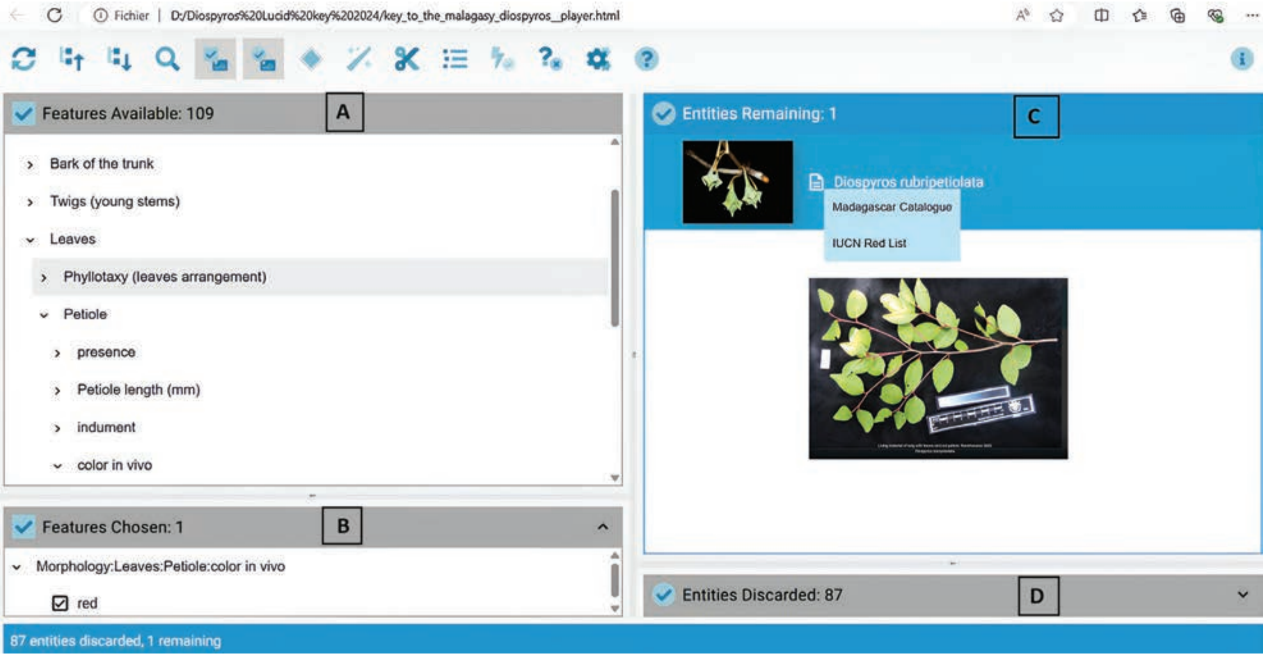
Results

Key efficacy, character performance, and limits

During the initial test sessions, participants were able to achieve correct identifications from 65–75% of the time. The feedback received after each workshop was then used to make improvements to the *Diospyros* key. Specifically, adjustments were made regarding the organization and structure of characters and character states. The presentation to the user was also modified based on the logical progression from basal to apical organs and from macro- to microscopic features. Additionally, the characters were re-categorized into two main groups within the key, “Morphology” and “EcoGeo”.

The results obtained from the trials indicated that the initial versions of the key were highly successful at leading users to the correct identification. The fact that the key is designed to allow multi-access utilization was clearly a strength because it enabled users to follow their intuition when selecting the order of characters to be entered. The botanists who tested the key made several suggestions for its improvement and for how it can be used most efficiently. They recommended that a user first note any obvious and striking features of the material being identified. For example, one of the most evident characters in fresh material of *Diospyros rubripetiolata* is the red tinge of the petiole, and if the user goes directly to the ‘features’ window and selects Morphology/Leaves/Petiole/Color_in_vivo/Red, the number of ‘discarded entities’ that do not express this particular character state (which is indicated in the lower left of the window) is indicated as 87, while the number of ‘remaining entities’ is indicated as 1 in the upper right, corresponding to *D. rubripetiolata* (Fig. 5). By clicking on the first photo in the species profile, the ‘image viewer’ displays all the images corresponding to the species, several of which clearly show the red petioles, thereby rapidly facilitating verification of the identification.

The second suggestion made during the test phase was that, in the absence of obvious and informative morphological characters, the user should start by focusing on eco-geographic parameters. In particular, they should begin by entering the geographic coordinates (longitude and latitude) of the location where the sample was obtained, which provides an efficient way to reduce the number of candidate species. For example, when one enters the coordinates corresponding to the 1°×1° cell for localities with a longitude starting with 46°E and a latitude starting with 15°S (using the format called for in the key, ‘4615’), 74



Morphology:Leaves:Petiole:color in vivo
☑ red

87 entities discarded, 1 remaining

Figure 5. Screenshot of the deployed key in the Lucid player interface showing use of the characters that are most obvious when examining a sample with the naked eye. The example shown here assumes that the key had already been used to identify a sample taken from a tree in the field whose leaves have a red petiole **A** by selecting the character state "red" for petiole color *in vivo*, a single candidate species is retained **B** window showing the number of selected features and the chosen path **C** window showing the number of remaining entities after one or more characters have been selected, in this case, the single entity corresponding to *Diospyros rubripetiolata*; the image viewer can be accessed by clicking on the first image displayed **D** window indicating the number of discarded entities; in this case, the 87 species that did not meet the selected identification criterion 'red petioles *in vivo*'.

entities are excluded and only 14 candidate species are retained (i.e., just 16% of the 88 large tree species of *Diospyros* occurring in Madagascar).

A third suggestion was that, when using vegetative characters, leaf features should be considered first because they are often the most effective for distinguishing species from one another. For example, the cordate leaf shape of *Diospyros vescoi* combined with the presence of indument on both surfaces of the leaf blade are uniquely diagnostic for this species. When reproductive organs are available, the fruit is often useful and informative, especially features of the fruiting calyx, such as the degree to which it covers the fruit surface and the presence/absence of lobes. As an example, if the initial entry of characters indicates *D. mapingo* and *D. tropophylla* as the two remaining candidate species, they can easily be distinguished based respectively on the presence or absence of lobes on the fruiting calyx.

Regarding characters seen as difficult to interpret or not particularly useful or pertinent for identification in the field or the herbarium (and thus rarely chosen during testing), the participants mentioned that subjective or ambiguous features requiring the user to make a personal interpretation, such as color (for both fresh or dried material) and leaf texture, were frequently scored differently by different persons. Likewise, it can be challenging to select the correct character state for features such as trichome type and length, which often requires using a hand lens or microscope, and is thus not always possible or practical in the field, especially for someone who is not familiar with the corresponding technical terminology. These characters are therefore more appropriate for identifying herbarium specimens and for use by experienced botanists.

After incorporating user feedback and remarks to improve the overall accuracy, appearance, and user-friendliness of the *Diospyros* key, it is now fully operational, enabling error-free identification of species 90–100% of the time.

Several practical aspects should be considered when developing and refining Lucid keys such as the one we have prepared for Malagasy *Diospyros*. The use of English could be an issue for some users not intimately familiar with terminology in this language. Several participants suggested during the testing phase that it would be helpful to have a version in French or even in Malagasy (which would be more challenging to develop as many technical terms do not exist in this language). It would also be helpful to have a version developed for use on smartphones, which are more portable and would facilitate use at remote field sites lacking internet access. Conversion of the Lucid tool into a mobile application for Android or iOS can be done, but publication of a fully functional key would involve an additional 5-step development phase requiring paid services that can only be provided by the Lucid team.

Conclusions and perspectives

As part of a coordinated effort to promote the sustainable and equitable use of precious woods resources in Madagascar in response to the CITES Action Plan regarding the genera *Diospyros* and *Dalbergia*, and in particular with respect to the development of practical and reliable identification tools for species that are of potential commercial interest, we have developed a key using Lucid that can be employed to identify standing and recently felled trees as well as herbarium specimens. This powerful, interactive, multi-access key can be used without an internet connection and is accessible to a broad group of users, ranging from non-specialists to experienced botanists. Moreover, since most trees encountered during forest inventories lack flowers and fruits, the key was designed specifically to enable accurate identification of sterile material using characters that can be observed in the field throughout the year. Special attention was given to incorporating vegetative characters, including bark features, which have been shown to be useful and informative for distinguishing *Diospyros* species in the field (further work is being conducted to explore the taxonomic value of bark characters). Eco-geographic features were also used to develop the key and were found to be particularly valuable for increasing the speed and accuracy of identifications by returning only candidate species that are known or inferred to occur within a given 1°×1° cell.

The morphological and eco-geographic characters employed in our key enable accurate identification of all 88 species of *Diospyros* in Madagascar that form large enough trees to be potential sources of commercially valuable ebony wood. Each species is accompanied by its own set of images to help verify initial identifications, along with links to additional information available online, and most technical terms are likewise illustrated to facilitate accurate comprehension and interpretation. Lucid is a tried and tested platform that is flexible and offers many useful options, enabling regular improvements and updates, including the addition of new species and informative characters. For example, as work progresses on developing a comprehensive understanding of characters based on anatomy, spectroscopy, and even DNA barcoding of Malagasy *Diospyros*, taxonomically informative features can be incorporated into our key. As part of the G3D project focusing on precious woods in Madagascar, a key has also been developed for the 56 large tree species of *Dalbergia* from which rosewood and palisander are obtained.

There remain some aspects that could be refined for further improvement of the current version of the key. Additional field testing encompassing multiple populations of each species (especially those that exhibit significant morphological variation) would be valuable. This could improve our knowledge of character variation, add new features while removing those that are less informative or more difficult to interpret, and fill gaps in character states for some species (notably for bark features), identifying and correcting errors that may have inadvertently been introduced into the character data matrix. After an ongoing round of improvements now being completed, as part of the second phase of the G3D project, the key will be translated into French to render it more accessible for francophone users, which should be finalized during 2025. In parallel, we will seek support to develop and test a stand-alone, portable version for smartphones. Lucid's flexibility and wide range of functionality make it possible to design and develop practical, multi-access digital keys that can easily be updated as new information becomes available. Finally, the methods and approach used to develop this practical identification tool for potentially exploitable Malagasy *Diospyros* species could easily be expanded to include all ca. 285 members of the genus occurring on Madagascar and all 83 species of *Dalbergia* (Madagascar Catalogue 2024) as well as to other groups (genera and even families) of plants and animals of commercial and/or scientific interest.

Key security and accessibility

Because many of the *Diospyros* species harvested in Madagascar as sources of ebony wood are threatened by over-exploitation and illegal logging, information relating to their characterization and distribution is potentially sensitive. To ensure that access to and use of the prototype key presented here for identifying large tree species can be adequately controlled, we have opted to host it on a password protected server (https://www.mobot.org/sci/), making it available to appropriate users when a request is sent to the first author. Upon obtaining a password, the user will be able to download a stand-alone version of the key or access an html link that can be opened on any web browser, both online or offline.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

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

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Appendix 1

Table A1. The 88 large tree species included in the *Diospyros* key (in alphabetical order) and their IUCN Red List status. CR: Critically endangered; DD: Data Deficient; EN: Endangered; LC: Least Concern; NT: Near Threatened; VU: Vulnerable (from Lowry et al. 2024).

Species	IUCN Red List status
Diospyros aculeata H. Perrier	LC
Diospyros ambanjensis G.E. Schatz & Lowry	EN
Diospyros amborelloides G.E. Schatz & Lowry	VU
Diospyros analamerensis H. Perrier	EN
Diospyros andohahelensis G.E. Schatz & Lowry	CR
Diospyros ankaranensis Mas, G.E. Schatz & Lowry, ined.	EN
Diospyros antakaranae Capuron ex G.E. Schatz & Lowry	VU
Diospyros antongilensis G.E. Schatz & Lowry	NT
Diospyros antsiranana G.E. Schatz & Lowry	VU
Diospyros arenicola A.G. Linan, G.E. Schatz & Lowry	VU
Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry	VU
Diospyros baroniana H. Perrier	LC
Diospyros baronii (H. Perrier) H.N. Rakouth & Lowry	NT
Diospyros beberonnii G.E. Schatz & Lowry	EN
Diospyros bemarivensis H. Perrier	VU
Diospyros bernieriana (Baill.) H. Perrier	LC
Diospyros bezofensis H. Perrier	EN
Diospyros brevipedicellata G.E. Schatz, Lowry & Mas, ined.	LC
Diospyros calophylla Hiern	LC
Diospyros chitoniophora Capuron ex A.G. Linan, G.E. Schatz & Lowry	VU
Diospyros clusiifolia (Hiern) G.E. Schatz & Lowry	NT
Diospyros crassifolia A.G. Linan, G.E. Schatz & Lowry	VU
Diospyros crassipedicellata G.E. Schatz & Lowry	VU
Diospyros cupulifera H. Perrier	LC
Diospyros decaryoides G.E. Schatz & Lowry	VU
Diospyros dolichopoda G.E. Schatz, Lowry & Mas, ined.	VU
Diospyros ebenifera (H. Perrier) G.E Schatz & Lowry	EN
Diospyros erythrosperma H. Perrier	LC
Diospyros falyi G.E. Schatz & Lowry	EN
Diospyros fuscovelutina Baker	NT
Diospyros gracilipes Hiern	LC
Diospyros grandiflora G.E. Schatz & Lowry	EN
Diospyros haplostylis Boivin ex Hiern	LC
Diospyros hazomainty H. Perrier	DD
Diospyros humbertiana H. Perrier	LC
Diospyros implexicalyx H. Perrier	EN
Diospyros labatiana Mas, G.E. Schatz & Lowry, ined.	LC
Diospyros lanceolata Poir.	NT
Diospyros lewisiae Mas, G.E. Schatz & Lowry, ined.	VU
Diospyros littoralis Capuron ex G.E. Schatz & Lowry	VU
Diospyros lowryi G.E. Schatz	EN
Diospyros maculata G.E. Schatz & Lowry	LC

Species	IUCN Red List status
Diospyros madagascariensis (A.DC.) E. Mestre & H.N. Rakouth	LC
Diospyros mahaboensis G.E. Schatz, Lowry & Mas, ined.	EN
Diospyros malandy H.N. Rakouth, G.E. Schatz & Lowry	EN
Diospyros manampetsae H. Perrier	LC
Diospyros mandenensis H.N. Rakouth, G.E. Schatz & Lowry	VU
Diospyros mapingo H. Perrier	LC
Diospyros masoalensis H. Perrier	NT
Diospyros meeusiana (H. Perrier) G.E. Schatz & Lowry	EN
Diospyros melanocarpa G.E. Schatz & Lowry	VU
Diospyros micrograciIipes G.E. Schatz, Lowry & Mas, ined.	EN
Diospyros mimusops G.E. Schatz & Lowry	EN
Diospyros myriophylla (H. Perrier) G.E. Schatz & Lowry	LC
Diospyros myrtifolia H. Perrier	LC
Diospyros occlusa H. Perrier	LC
Diospyros olacinoides (H. Perrier) G.E. Schatz & Lowry	LC
Diospyros olivieri A.G. Linan, G.E. Schatz & Lowry	CR
Diospyros orbicularis G.E. Schatz & Lowry	VU
Diospyros parifolia H. Perrier	NT
Diospyros parvifolia Hiern	LC
Diospyros perrieri Jum.	NT
Diospyros platycalyx Hiern	LC
Diospyros plicaticalyx A.G. Linan, G.E. Schatz & Lowry	EN
Diospyros pubiramulis A.G. Linan, G.E. Schatz & Lowry	VU
Diospyros quadrangularis G.E. Schatz & Lowry	LC
Diospyros rakotovaoi G.E. Schatz & Lowry	VU
Diospyros ramisonii G.E. Schatz & Lowry	VU
Diospyros randrianasoloi G.E. Schatz, Lowry & Mas, ined.	LC
Diospyros ranirisonii G.E. Schatz, Lowry & Phillipson	VU
Diospyros retusa H.N. Rakouth, G.E. Schatz & Lowry	EN
Diospyros rubripetiolata G.E. Schatz & Lowry	LC
Diospyros sakalavarum H. Perrier	LC
Diospyros sclerophylla H. Perrier	VU
Diospyros sennenii G.E. Schatz & Lowry	LC
Diospyros sphaerosepala Baker	NT
Diospyros squamosa Bojer ex A. DC.	LC
Diospyros subenervis (H. Perrier) G.E. Schatz & Lowry	VU
Diospyros subtrinervis H. Perrier	CR
Diospyros taikintana G.E. Schatz & Lowry	CR
Diospyros tampolensis H.N. Rakouth, G.E. Schatz & Lowry	CR
Diospyros torquata H. Perrier	NT
Diospyros toxicaria Hiern	LC
Diospyros tropophylla (H. Perrier) G.E. Schatz & Lowry	LC
Diospyros ultima G.E Schatz & Lowry	EN
Diospyros urschii H. Perrier	NT
Diospyros velutipes (H. Perrier) G.E. Schatz & Lowry	LC
Diospyros vescoi Hiern	LC

Appendix 2

Table A2. Eco-geographic and morphological available features, with the 109 characters and 356 character states used in the Lucid key for Malagasy *Diospyros*.

"Eco-geography" or Eco-geographic available features		
Features	**Characters**	**Character states**
Eco-geography	Bioclimate	Humid, Subhumid, Dry, Subarid, Montane
	Elevation (m)	-499, -999, -1499, -1999, -2499
	Longitude E/ Latitude S coordinates coded with 4 digit number	Numerical values (#). The first pair of digit corresponds to the degree longitude, and the second pair to the degree latitude. For example: if the relevant coordinates are **16°** 77719 S and **46°** 85432 E or **16**°46'37"S and **46**°51'15"E, the observed value should be entered as (longitude first and latitude second) : **4616**
"Morphology" or Morphological available features		
Organs features	**Characters**	**Character states**
WHOLE PLANT	Growth form	Shrub (woody, 1–7 m tall), tree over 7 m tall, usually single stem
BARK OF THE TRUNK	Surface texture	Smooth, fissured (=cracked), flaky (rhytidom), rugose
	Structure present	Lenticels, blisters, elongate striations, transverse striations, flakes, shallow cervices
	External bark	
	Color. *In vivo*	white/whitish, gray/grayish, light brown, dark brown, black/blackish
	Color. *In sicco*	white/whitish, gray/grayish, light brown, dark brown, black/blackish
TWIGS (YOUNG STEMS)	Cross section	Terete, flattened, square
	Surface structures on twigs bark	Lenticels, blisters, elongate striations, transverse striations, fissures or cracks (including microfissure), flakes/thin flakes, micro-spines
	Indument on twigs (young stems)	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi appressed, appressed, curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Trichomes (hairs). *Color*	White/whitish, gray/grayish, brown/ light brown, golden/yellowish, tawny (yellowish brown)/ferruginous, orange/reddish brown
	Twigs. Color (*in sicco*)	White/whitish/light gray, brownish-green, brown/light brown, dark brown/ reddish-brown, dark gray, black/blackish
LEAVES	Phyllotaxy	Alternate, spiral, opposite (subopposite), whorled (verticillate)
PETIOLE	Presence	Absent (leaf sessile), present (leaf petiolate)
	If present. *Length* (in mm)	Numerical values (#)
	Indument on petiole	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi appressed, appressed, curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Indument. Trichomes (hairs). *Color*	White/whitish/light gray, brown/ light brown, golden/yellowish, tawny (yellowish brown)/ferruginous, orangish/reddish brown
	Color of the petiole. *In vivo*	Green, yellowish-green, brownish-green, light (pale) brown, red, glaucous
	Color of the petiole. *In sicco*	Gray/grayish/glaucquescent, brownish-green, light brown/ yellowish-brown, dark brown/reddish, black/blackish

Morphology		
Features	**Characters**	**Character states**
LAMINA (LEAF BLADE)	Texture	Coriaceous, subcoriaceous, chartaceous, membranaceous
	Shape	Elliptic to largely elliptic, oblong, ovate, obovate, oblanceolate, cordate, orbicular, lanceolate
	Dimensions of the largest leaf. *Length* (in cm)	Numerical values (#)
	Dimensions of the largest leaf. *Width* (in cm)	Numerical values (#)
	Leaf base	
	Shape	Attenuate/decurrent, cuneate, acute, obtuse, rounded, truncate, subcordate/cordate
	Symmetry of the base in relation to the midvein	Symmetric, asymmetric
	Margin	Flat (thin), revolute, minutely revolute, undulate, slightly undulate, slightly thickened on the leaf blade below surface
	Apex	
	Mucron presence	Absent, present
	Shape	Acute, acuminate, obtuse, rounded, emarginate/retuse;
	Acumen of the apex	
	Presence	Absent, present
	if present, *length* (in mm)	Numerical values (#)
	Shape of the acumen tip	Retuse, apiculate, rounded, acute
	Primary vein/ midvein	
	Upper surface	Distinctly raised, flat, slightly impressed, sunken/impressed or distinctly depressed
	Lower surface	Distinctly raised, slightly raised, flat
	Secondary veins. Upper surface	
	Visibility/appearance	Obscure/indistinct, weakly visible, raised, slightly raised, flat, sunken/ impressed,
	Number per side	Numerical values (#)
	Tertiary veins /intersecondaries presence	Absent, present
	Secondary veins. Lower surface	
	Visibility/appearance	Obscure/indistinct, weakly visible, raised, slightly raised, flat, sunken/ impressed
	Venation type	Brochidodromous, craspedodromous, semicraspedodromous, reticulodromous, eucamptodromous, cladodromous
	Indument on leaf blade. Upper surface	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Disposition*	Throughout the lamina except on venation, all over venation, on midvein only, on the margin or on the edge of leaf blade
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi-appressed, appressed, irregular/messy or confused/curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Indument. Trichomes (hairs). *Color*	White/whitish, gray/grayish (silvery), brown/ light (pale) brown, golden/yellowish, tawny/fauve/orange (yellowish-brown)/ferruginous, brown/reddish brown
	Indument on leaf blade venation. Lower surface	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Disposition*	Throughout the lamina except on venation, all over venation, on midvein only, on the margin or on the edge of leaf blade

Morphology		
Features	**Characters**	**Character states**
LAMINA (LEAF BLADE)	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi-appressed, appressed, irregular/messy or confused/curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Indument. Trichomes (hairs). *Color*	White/whitish/gray, brown/ light (pale) brown, dark-brown/brown, golden/yellowish, tawny/fauve/orange (yellowish-brown)/ferruginous, reddish brown
FEMALE FLOWERS	Position and place of birth	Axillary, borne on twigs (ramiflorous), on stem (cauliflorous), on trunk (trunkiflorous), or on short shoots (on brachyblasts)
	Inflorescence types	Solitary, born in 2 s or 3 s, glomerules, fascicules, cymes, umbels, or branched/multiple
PERSISTENT FRUITING CALYX	Degree of enclosure of the fruit	Fully enclosed (100% fruit surface obscured), largely enclosed (at least 50%), partially enclosed (< 50%)
	Total height (incl. lobes if present)	Height (in mm) Numerical values (#)
	Calyx lobes	
	Presence	Absent (calyx entire), present (calyx lobed)
	Number	3, 4, 5, 6
	Degree of fusion	Partially united, entirely united (calyx accrescent at the base), entirely free (rare)
	Dimensions. *Length* (in mm)	Numerical values (#)
	Dimensions. *Width* (in mm)	Numerical values (#)
	Shape	Oblong, elliptic, obovate, semi-ovate warhead shaped, orbicular, triangular, linear
	Orientation	Erect, spreading, reflexed
	Margins (shape)	Flat, revolute, minutely revolute, involute, plicate-undulate, lacerate
	Apex (shape)	Acute, obtuse, rounded, retuse
	Venation, striations presence	Absent (indistinct), present (distinct)
	Calyx indument. Outer surface	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Disposition*	Throughout, apical portion, basal portion
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi appressed, appressed, curly); color
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Trichomes (hairs). *Color*	White/whitish, gray/grayish, brown/ light brown, brownish-orange/ reddish brown, golden/yellowish, fauve/orange/tawny (yellowish brown)/ferruginous/rusty, dark-brown/blackish
	Calyx indument. Inner surface	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Disposition*	Throughout, apical portion, basal portion
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi appressed, appressed, curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Trichomes (hairs). *Color*	White/whitish, gray/grayish, brown/ light brown, brownish-orange/ reddish brown, golden/yellowish, fauve/orange/tawny (yellowish brown)/ferruginous/rusty, dark-brown/blackish
FRUIT BODY	Shape	Ellipsoid, obloid, ovoid, spherical (globose), subspherical (subglobbose)
	Height (in mm)	Numerical values (#)
	Apex shape	Acute, apiculate/rostrate, rounded, flat/depressed
	External texture	Smooth and matte, smooth and shiny, rugose/rough, verrucose (warty), pubescent

Morphology		
Features	**Characters**	**Character states**
FRUIT BODY	**Indument on the fruit body**	
	White waxy substance. *Presence*	Absent, present
	Trichomes (hairs). *Presence*	Absent, present
	Trichomes (hairs). *Persistence*	Persistent, not persistent
	Trichomes (hairs). *Density*	Dense, moderately dense, sparse
	Trichomes (hairs). *Disposition*	Throughout, apical portion, basal portion
	Trichomes (hairs). *Orientation*	Erect, semi-erect, semi appressed, appressed, curly
	Trichomes (hairs). *Length* (in mm)	Numerical values (#)
	Trichomes (hairs). *Color*	White/whitish, gray/grayish, brown/ light brown, brownish-orange/ reddish brown, golden/yellowish, fauve/orange/tawny (yellowish brown)/ferruginous/rusty, dark-brown/blackish
	Color of the fruit body. *In vivo*	Green, yellow/yellowish-green, orange, red, light brown/beige, white (due to white waxy substance), dark brown;
	Color of the fruit body. *In sicco*	Light brown/yellowish-brown, white (due to persistent white waxy substance), dark brown/ferruginous, black blackish

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Research Article

Bambusa rushunii (Poaceae, Bambusoideae, Bambuseae), a new bamboo species from Guangdong, China

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Abstract

A new bamboo species, *Bambusa rushunii*, from Yangjiang City, Guangdong Province, China, is described and illustrated in this paper. The new species resembles *B. gibba* and *B. dissimulator* in having branchlets specialised into weak thorns at the lower nodes of culms, but can be easily distinguished from the latter two by having one or two extremely shortened internodes at the culm base, glabrous internode, culm leaf sheath being dark brown strigose on the central part and with a nearly truncate or slightly obliquely truncate apex, relatively high culm leaf ligule, culm leaf blade base not narrowed, extending outwards and contiguous with auricles and the glabrous foliage leaf with a ciliate ligule margin.

Key words: *Bambusa*, Guangdong, morphology, woody bamboo

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Introduction

Bamboos, belonging to the subfamily Bambusoideae of Poaceae, are of great ecological, social and economic value as building material, household utensils, vegetables, raw material for making paper and musical instruments (Zhang et al. 2012; Ahmad et al. 2023). There are nearly 1700 species in 136 genera of bamboos worldwide, classified into three tribes, tropical Bambuseae Kunth ex Dumort., temperate Arundinarieae Asch & Graebn and herbaceous Olyreae Kunth ex Spenn (Sungkaew et al. 2009; Kelchner and Bamboo Phylogeny Group 2013; Clark and de Oliveira 2018; Soreng et al. 2022).

The genus *Bambusa* Schreber is the most widely cultivated woody bamboo genus with more than 150 species, of which about 80 species are distributed in southern and south-western China (Xia et al. 2006; Vorontsova et al. 2016; Clark and de Oliveira 2018). It forms the BDG complex (*Bambusa-Dendrocalamus-Gigantochloa* complex), which is considered to be the "core Bambusinae" by Goh et al. (2013), together with *Dendrocalamus* Nees, *Gigantochloa* Kurz ex Munro and other closely-related genera (Zhou et al. 2017; Liu et al. 2020). The paraphyly of *Bambusa* was confirmed by much phylogenetic research based on plastome and nuclear DNA data (Yang et al. 2010; Zhou et al. 2017; Liu et al. 2020). Moreover, none of the four subgenera within *Bambusa* was supported as monophyletic (Yang et al. 2010; Liu et al. 2020). Although there are intractable phylogenetical problems due to a history of rapid diversification and putative introgression events, it is now generally believed that some floral characters, such as morphology of rachillas, lodicules and filaments can be used to distinguish *Bambusa*, *Dendrocalamus* and *Gigantochloa*, which also possess phylogenetic signals (Loh et al. 2000; Goh et al. 2010; Liu et al. 2020). Specifically, disarticulated rachillas, 2–3 lodicules and free filaments could serve as suitable diagnostic characters to distinguish *Bambusa* from the other two genera (Wong 1995; Chia et al. 1996; Xia et al. 2006; Qin et al. 2022).

Guangdong, with more than 60 *Bambusa* species, is one of the provinces that harbour the highest biodiversity of *Bambusa* in China (Xia and Lin 2009). It belongs to the East Asian monsoon region, with subtropical and tropical climates from north to south, respectively. The annual average temperature in Guangdong Province is 18–22 °C and the rainfall in Guangdong Province is mainly concentrated from April to September, with an average precipitation from 1500 mm to 2000 mm each year. Thus, the hydrothermal condition of Guangdong is very suitable for the growth of *Bambusa* species. During several field investigations in Yangchun County, Yangjiang City, Guangdong Province, we found three populations of an unknown species of *Bambusa*. This species bears extremely shortened internodes at the basal culm, which is very rare in *Bambusa*. After comparison with morphologically similar species, it is concluded that this unknown species has not been described before. Therefore, it is described as a new species in this paper.

Materials and methods

Specimens of this new species were collected during two field surveys to Dongping Town, Yangdong District, Yangjiang City, Guangdong Province in 2016 and Tanshui Town, Yangchun County, Yangjiang City, Guangdong Province in 2023. Voucher specimens were deposited in the Herbarium of the South China Botanical Garden (IBSC), Chinese Academy of Sciences. Flowering materials were dissected under a stereomicroscope (Mshot-MZ101) and small parts were measured and photographed with the camera attachment (Mshot-MSX2). The specimens kept in SYS and specimen photos from A, CAS, ISC, K, L, P and US were examined. Herbarium acronyms follow Thiers (2024). Terminology follows McClure (1940), Li et al. (2006) and Beentje (2016).

Taxonomic treatment

Bambusa rushunii **J.B.Ni & Y.H.Tong, sp. nov.**
urn:lsid:ipni.org:names:77357415-1
Figs 1, 2

Type. China. • Guangdong Province: Yangjiang City, Yangchun County, Tanshui Town; 22°4'52.71"N, 111°36'6.80"E; alt. 28 m; 18 September 2023; *Jing-Bo Ni et al. NJB-004* (holotype: IBSC!).

Diagnosis. *Bambusa rushunii* resembles *B. gibba* McClure and *B. dissimulator* McClure, but can be easily distinguished from *B. gibba* by having a thicker culm wall (ca. 1.5 cm vs. 3–5 mm), extremely shortened basal internode present (vs. absent), culm leaf sheath without (vs. with) a protuberance on higher shoulder and dark brown strigose on the central part (vs. glabrous wholly), higher culm leaf ligule (4–8 mm vs. 2–3 mm) and glabrous (vs. abaxially densely pubescent) foliage leaf and is different from *B. dissimulator* by the extremely shortened basal internode present (vs. absent), nearly truncate or slightly obliquely truncate (vs. asymmetrically convex) culm leaf sheath apex, culm leaf auricle contiguous (vs. not contiguous) with the blade base, culm leaf blade base not narrowed (vs. narrowed), foliage leaf ligule margin ciliate (vs. glabrous) and glabrous (vs. abaxially pubescent) foliage leaf.

Description. Arborescent bamboo. Rhizome pachymorph, short-necked. Culm 8–10 m tall, 5–7.5 cm in diameter, erect, basal part slightly zigzag, apex slightly pendulous; internode terete, 35–45 cm long, 2nd and/or 3rd and/or 4th internodes usually extremely shortened, only ca. 1 cm long; initially white powdery, glabrous, basal internodes green with many pale yellow stripes, stripes sometimes not inconspicuous; wall ca. 1.5 cm thick; supranodal ridge inconspicuous, sheath scars raised; culm bud round, branches developing from 5th node upwards, nearly horizontally spreading, branch complements with several branches per node, central 3 dominant, branchlets usually specialised into weak thorns. Culm leaf sheath deciduous, thickly leathery, 30–40 cm long, 9–12 cm wide at apex, 20–32 cm wide at base, with yellow-green stripes, stripes inconspicuous when dry, sparsely dark brown strigose on central part, longitudinal ribs conspicuous when dry, apex nearly truncate or slightly obliquely truncate, without protuberance on shoulder; auricles unequal, oblong to lanceolate, contiguous with the base of blade, slightly wrinkled, margin densely with ca. 8 mm long and curved oral setae; larger auricle 1–2 cm long, 4–6 mm wide, not slanted; smaller auricle 3–8 mm long, 2–5 mm wide; ligule 4–8 mm high, margin serrate, densely with 2–3 mm long cilia; blade erect, narrowly triangular, 10–13 cm long, 5–8 cm wide, 1/2–3/5 as long as culm sheath, glabrous on both sides, apex involute and acuminate, base slightly extending outwards and joined with auricles, 3/5–4/5 as wide as sheath apex. Foliage leaves 7–11 per ultimate branchlet, sheath ca. 6 cm long, glabrous; auricles elliptic, ca. 2 mm long, ca. 1 mm wide, oral setae deciduous, ca. 8 mm long; inner ligules ca. 1 mm high, entire, margin ciliate; pseudopetioles ca. 2 mm long, ca. 1 mm wide; blades linear-lanceolate, papyraceous, 15–20 cm long, 1.4–1.7 cm wide, both surfaces glabrous, apex acuminate, base subrounded to cuneate, secondary veins 6 pairs, transverse veins inconspicuous. Pseudospikelets sessile, usually several to many fasciculate at nodes of flowering branches, green when fresh, yellow when dry, linear-lanceolate, 4–6 cm long, 5–8 mm wide, basally subtended by several gemmiferous bracts; prophylls ovate, 3–4 mm long, 2–keeled, apex densely ciliolate; gemmiferous bracts 1–3, ovate, 4–9 mm long, glabrous, 10–14-veined, apex acuminate and muronate; florets several to many, apical 1–2 sterile, rachilla segments flat, ca. 4 mm long, puberulous, slightly grooved, apex enlarged, with a ring of white hairs, disarticulating below each floret; glumes 1 or 2, broadly ovate, 5–6 mm long, glabrous, 10–12-veined, apex acute; lemma lanceolate, ca. 13 mm long, glabrous, 10–12-veined, apex acute; palea lanceolate, ca. 12 mm long, slightly shorter than lemma, apex acute, abaxially 2-keeled, keels densely ciliolate at apex, with 6 veins between keels and 4 veins on each side; lodicules 3, subequal, fleshy, white, ca. 2 mm long, margin with long cilia; stamens 6, filaments free,

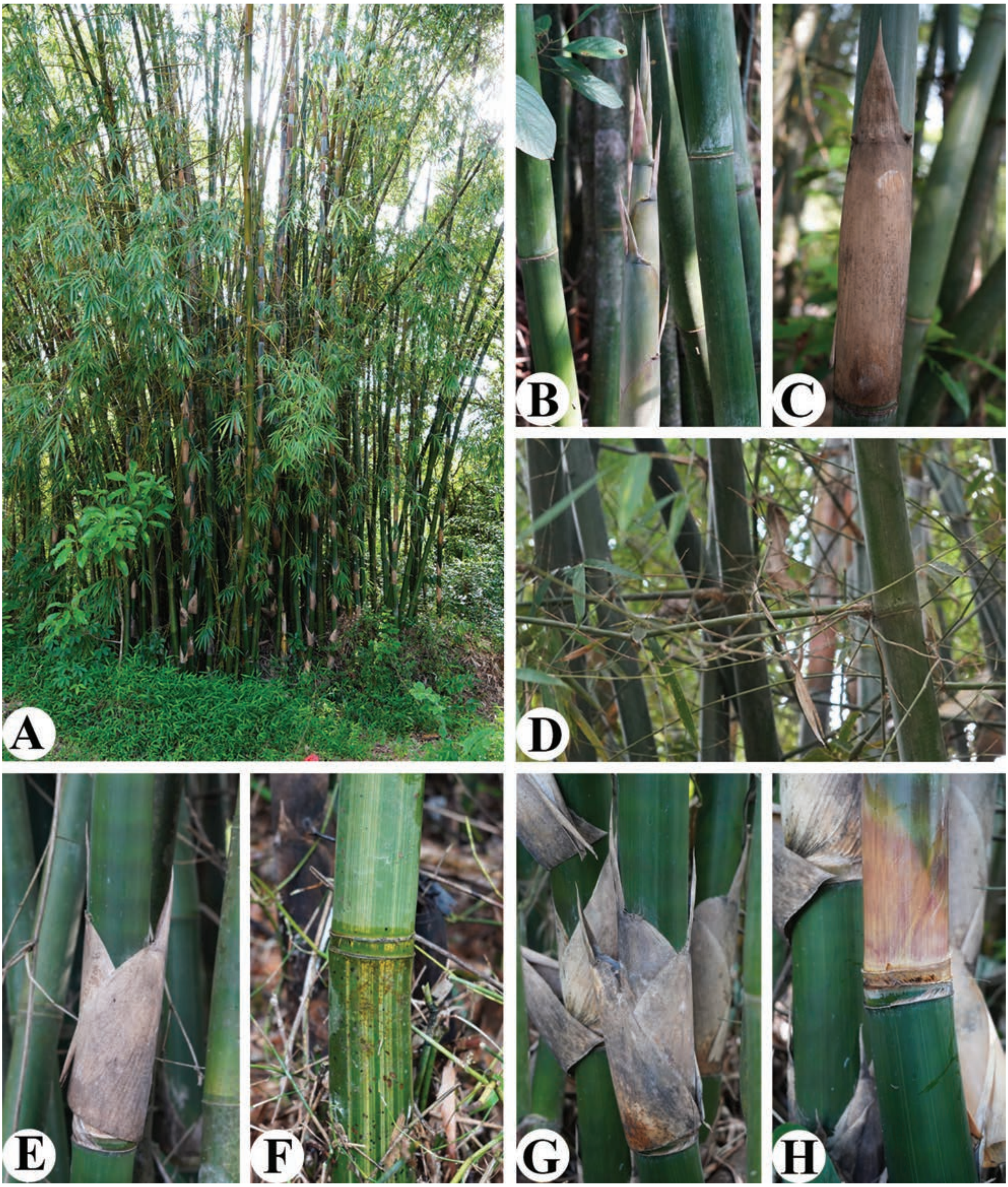

Figure 1. *Bambusa rushunii* J. B. Ni & Y. H. Tong **A** habit **B** new shoot **C** culm leaf **D** branch complement **E–H** extremely shortened internodes. Photos by Meng-Ling Li.

ca. 2 cm long, white; anthers initially green-yellow, later yellow-brown, ca. 5 mm long, apex retuse; ovary obovoid, ca. 1 mm long, apex hispidulous, style short, ca. 0.3 mm long, sparsely hispidulous at base; stigmas 3, 2–3 mm long, slender and plumose. Mature caryopsis fusiform, yellow, ca. 8 mm long.

Phenology. New culm shoots produced from July to September, flowering in September.

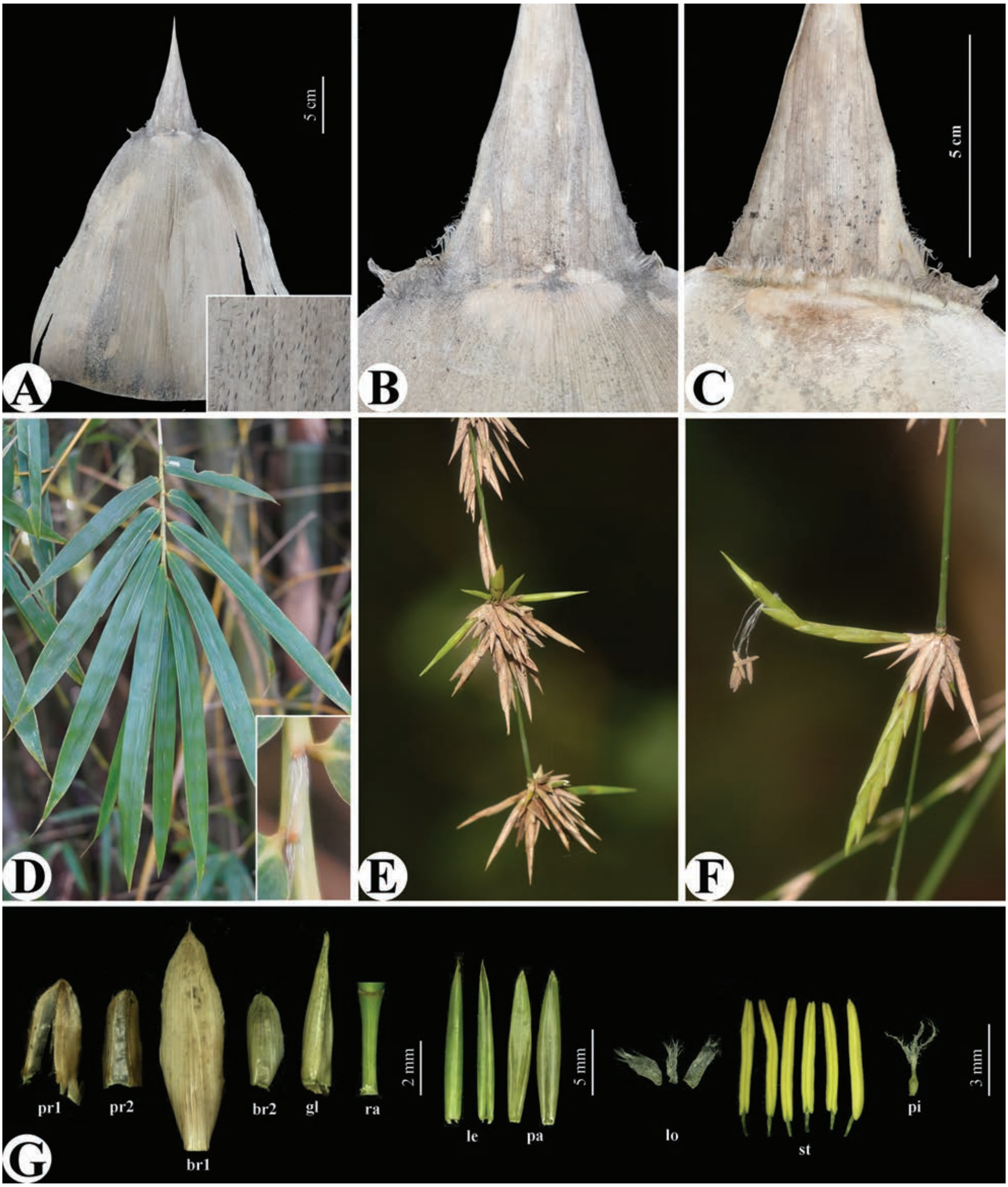

Figure 2. *Bambusa rushunii* J. B. Ni & Y. H. Tong **A** abaxial view of culm leaf, with a close-up view of the strigose hairs on the central part **B** abaxial view of culm leaf sheath apex, showing auricles **C** adaxial view of culm leaf sheath apex, showing ligule **D** foliage leafy branchlet **E** flowering branches **F** pseudospikelets **G** dissection of pseudospikelet, pr1 and pr2 = prophylls, br1 and br2 = gemmiferous bracts, gl = glume, ra = rachilla segment, le = lemma, pa = palea, lo = lodicules, st = stamens, pi = pistil. Photos **A–D, G** by Meng-Ling Li; **E, F** by Shu-Peng Dong.

Distribution and habitat. This new species is found in Yangjiang City, Guangdong Province, China and cultivated in South China Botanical Garden. It usually occurs near villages and streams at elevations of 20–120 m.

Etymology. The species epithet honours Mr. Ru-Shun Lin, a retired employee from South China Botanical Garden, Chinese Academy of Sciences, who has made more than 600 living collections of bamboos and contributed a lot to the development of the Bamboo Garden of South China Botanical Garden. Its Chinese name is given as 汝顺坭簕竹(Pinyin: rǔ shùn ní lè zhú).

Discussion. In "Flora of China", the genus *Bambusa* was further classified into four subgenera: subg. *Bambusa*, subg. *Dendrocalamopsis* L. C. Chia & H. L. Fung, subg. *Leleba* (Rumph. ex Nakai) Keng ex L. C. Chia & H. L. Feng and subg. *Lingnania* (McClure) L. C. Chia & H. L. Fung (Xia et al. 2006). *Bambusa rushunii* possesses typical characteristics of subg. *Bambusa*, such as the relatively thick culm wall, persistent culm leaf blade with a broad base that is 1/2–3/4 as wide as sheath apex and the branchlets usually specialised into weak thorns. Thus, it is placed into that subgenus.

Amongst the species of *B.* subg. *Bambusa*, *B. rushunii* is most similar to *B. gibba* and *B. dissimulator* in the branchlets of lower branches which are usually specialised into weak thorns and the relatively small culm leaf auricles. The detailed morphological comparison of the three species is shown in Table 1 and the diagnosis section. The most unique morphological character of *B. rushunii* is the extremely shortened internodes at the culm base. As far as we know, this characteristic also occurs to another species of *Bambusa* subg. *Dendrocalamposis*, viz. *B. bicicatricata* (W. T. Lin) L. C. Chia & H. L. Fung. However, except this character, *B. rushunii* is very different from *B. bicicatricata* in many other characters, such as morphology of culm leaves, pseudospikelet length and number of stigmas, since they belong to different subgenera (Chia et al. 1996; Xia et al. 2006).

Additional specimens examined. *Bambusa rushunii* J. B. Ni & Y. H. Tong: China. • Guangdong Province, Guangzhou City, Tianhe District, introduced from the type locality, cultivated in Bamboo Garden of South China National Botanical Garden, 5 September 2024, *J. B. Ni 005* (paratype: IBSC).

Bambusa dissimulator McClure: China. • Guangdong Province, Guangzhou City, Panyu District [Haizhu District], Lingnan University campus (now the campus of Sun Yat-Sen University), 26 September 1939, *F. A. McClure 20861* (K000854766, image); • ibid., 30 April 1931, *H. Fung A-674/BG2348* (A00023169, image, L0043812, image, SYS00095355, US00130308, image, US00130310, image, US00130311, image, US00130312, image); • ibid., 18 November 1929, *H. Fung LU18499* (SYS00011949, US00391111, image); • ibid., 30 April 1931, *H. Fung LU19079* (isotypes: CAS0027955, image, ISC-v-0000942, image, ISC-v-0000943, image, K000854765, image, L0043812, image); • ibid., 15 March 1932, *H. Fung 20003* (two sheets: SYS00011892 & SYS00011893); • ibid., Lingnan University, Primary School, 30 October 1936, *H. Fung 20987* (US0050544, image).

Bambusa dissimulator var. *albonodia* McClure: China. • Guangdong Province, Guangzhou City, Honam Island [Haizhu District], west end of same island of land, Lingnan University Agriculture workmen’s barracks, 13 December 1937, *F. A. McClure 20719* (holotype: two sheets US00130313 & US0034812, image); • ibid., Honam Island [Haizhu District], Ng Ts’uen, 18 May 1921, *F. A. McClure LU18552* (two sheets: US 00034813 & US0034814, image).

Bambusa dissimulator var. *hispida* McClure: China. • Guangdong Province, Guangzhou City, Panyu District [Haizhu District], growing on edge of small knoll, east. of Lingnan University campus (now the campus of Sun Yat-Sen University), 26 September 1939, *F. A. McClure 20861* (holotype US00130315,

Table 1. Morphological comparisons of *Bambusa rushunii*, *B. gibba* and *B. dissimulator*.

Characters	***B. rushunii***	***B. gibba***	***B. dissimulator***
Culm wall thickness	ca. 1.5 cm	3–5 mm	ca. 1.5 cm
Internode			
extremely shortened basal internodes	Present	Absent	Absent
indumentum	Glabrous	Sparsely stiffly grey-white or brown strigose, glabrescent	Glabrous or hairy
Culm leaf			
sheath indumentum	Dark brown strigose on the central part	Glabrous	Subglabrous or inconspicuously strigose
sheath apex	Truncate or slightly obliquely truncate	Obliquely truncate	Asymmetrically convex
protuberance on higher shoulder	Absent	Present	Absent
auricle	Contiguous with the base of the blade	Contiguous with the base of the blade	Not contiguous with the blade
ligule height	4–8 mm	2–3 mm	5–7 mm
blade	Base not narrowed 3/5–4/5 as wide as sheath apex	Base not narrowed ca. 2/3 as wide as sheath apex	Base cordately narrowed 1/2–3/5 as wide as sheath apex
Foliage leaf ligule margin	Ciliate	Ciliate or glabrous	Glabrous
Foliage leaf indumentum	Glabrous	Abaxially densely pubescent	Abaxially sparsely pubescent

image; isotypes A00023170, image, ISC-v-0000944, image, K00854764, image, K00854766, image, L0043813, image, P00800933, image).

Bambusa gibba McClure: China. • Kiangsi [Guangxi], south of Kanchow [Qinzhou], cultivated in Lingnan University Bamboo Garden (now in the campus of Sun Yat-Sen University), 30 September 1933, *H. Fung 20709* (holotype: three sheets US00065370, US00065371 & US00065372, image; isotype: three sheets US00289540, US00289541 & US00289542, image); • ibid., March 1929, *F. A. McClure LU18518* (A00023177, image, K000854759, image, L0043815, image, L0043816, image, P00800942, image SYS00095349); • ibid., 23 February 1937, *H. Fung 21001* (SYS00095350, SYS00095351).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Jing-Bo Ni and Meng-Ling Li participated the field investigation and manuscript writing; Shu-Peng Dong performed some fieldwork; Yi-Hua Tong provided funds, supervised this work and revised the manuscript.

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Data availability

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

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Research Article

Viola xinchengensis (Violaceae), a new species from central Guangxi, China

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Abstract

Viola xinchengensis (Violaceae), a new species from Guangxi, China, is established on the basis of morphological and molecular evidence. This new species resembles *V. lucens*, but differs from the latter by its stipules margin long fimbriate-dentate (vs. fimbriate-dentate), stolon absent (vs. stolon slender, often producing a new plant at the top) and sepals 4–6 mm, glabrous (vs. 2.5–3 mm, villous). *Viola xinchengensis* is similar to *V. fargesii*, but it can be easily distinguished by its pedicels sparsely white villous (vs. densely spreading white puberulous), stolon absent (vs. stolon longer, elongated, puberulous, sometimes stem-like) and sepals 4–6 mm, glabrous (vs. 7–9 mm, puberulous). Our morphology analysis confirms that the new species belongs to *V.* sect. *Plagiostigma* subsect. *Diffusae*. Photographs, an illustration, a distribution map and comparisons with the most similar species are also provided.

Key words: Morphology, new species, sinkhole, taxonomy, *Viola*

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Introduction

Viola L. is the largest genus of the family Violaceae, with approximately 664 species that are classified in two subgenera, 31 sections and 20 subsections around the world (Marcussen et al. 2022). This genus has a high level of morphological differentiation and there are hybridisation and horizontal evolution amongst its sections and species (Marcussen et al. 2015). However, the delimitation of the species with stolons distributed in southern and south-western China remains highly problematic and new species are still being discovered (Zhou and Xing 2007; Chen and Yang 2009; Dong et al. 2009; Ning et al. 2012; Huang et al. 2021; Li et al. 2022; Huang et al. 2023a; Huang et al. 2023b).

Guangxi is located in the southwest of China and is a biodiversity hotspot where many new species or new species records have been recently found (Hu et al. 2019; Luo et al. 2020; Feng et al. 2021; Huang et al. 2022; Nong et al. 2023; Nong et al. 2024). During our field surveys in Xincheng County, Guangxi in April 2024, we found a special *Viola* population in flowers and fruits that was morphologically similar to the species *V. fargesii* H. Boissieu and *V. lucens* W. Becker in having rhizomes erect, leaves basal, stipules margin fimbriate-dentate and ovaries glabrous. After careful comparisons and verifications, we carried out one more field survey to confirm that the unusual plant is a species of *Viola* new to science and we describe it below. Photographs, an illustration, a distribution map and a table of comparisons with the most similar species are also provided.

Materials and methods

Morphology

The new species was described, based on field observations made in April 2024 and examination of herbarium specimens. Other related *Viola* species were examined, based on online images from the Kew Herbarium Catalogue (http://apps.kew.org/herbcat/gotoHomePage.do) and JSTOR Global Plants (http://plants.jstor.org/) and specimens from GXMI. We also observed living plants of the new species at flowering and fruiting time (April and May). We observed characters of stems, leaves, pedicels, flowers, receptacles, petals, stamens, gynoecium and capsule.

Descriptions were based on observations from herbarium specimens. Measurements were made with a tape measure and calipers. The structure of the indumentum and its distribution were observed and described under a dissecting microscope at magnifications of more than 20×. Additional information on locality, habitat, plant form and fruits was collected in the field and taken from herbarium labels. We followed the IUCN Categories and Criteria (IUCN 2022) to assess the provisional conservation status of the new species.

Molecular phylogenetic analysis

Leaf material of the putative new species was collected and stored with silica gel in zip-lock plastic bags until use for comparisons and taxonomical treatment. In this study, molecular phylogenetic analysis, based on the ITS dataset, was firstly conducted to resolve the phylogenetic position of the new species. 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). 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). Another 42 sample sequences were obtained from NCBI (Gong et al. 2010; Liang and Xing 2010). The specimen information of samples and GenBank accession numbers for all sequences are listed in Table 1.

All sequences were assembled and edited using Geneious v.7.06 (Kearse et al. 2012) 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). Phylogenetic construction was conducted by Maximum Likelihood with MEGA 6.0 (Tamura et al. 2013), selecting the best-fit model of Jukes-Cantor with 2000 bootstraps. The resulting trees with posterior probabilities (PP) and Bootstrap support (BS) values were visualised and annotated in TreeGraph 2 (Stöver and Müller 2010). 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. *Melicytus chathamicus* (F.Muell.) Garn.-Jones. was used as outgroup.

Results and discussion

The ITS dataset comprises 34 accessions representing 34 species, including the outgroup (Table 1). The aligned matrix of ITS sequences was 656 bp in total. The result of ML is shown in Fig. 1. The samples of the putative new species (red background) clustered into a strongly supported monophyletic lineage, forming a weak sister relationship with a clade composed of *V. yunnanensis*, *V. davidii* and *V. philippica*. Based on morphological characters and phylogenetic results, we recognise this unfamiliar violet as a distinct species and describe it here as *V. xinchengensis* Y.Nong & G.Y.Wei.

Table 1. Vouchers of specimens and GenBank accession number.

Accession no.	Taxon	Voucher
EF660538.1	*Melicytus chathamicus*	–
JQ950556.1	*Viola albida*	Fengcheng, Liaoning, Chen Y. S. 01819036 (PE)
JF830900.1	*Viola amamiana*	–
OQ848672.1	*Viola austroyunnanensis*	–
MN493162.1	*Viola baoshanensis*	Hunan, Liu W. SYS00142785 (SYS)
LC669903.1	*Viola betonicifolia*	Jingxi, Guangxi, Qin H. N. 01990960 (PE)
DQ787768.1	*Viola chaerophylloides*	Fengcheng, Liaoning, Chen Y. S. 01840427 (PE)
OP935155.1	*Viola changii*	Guangdong, Liang G. X. 0765177 (IBSC)
JQ950563.1	*Viola dactyloides*	Daxinganling, Heilongjiang, Chen Y. S. 01840253 (PE)
MH711664.1	*Viola davidii*	Leishan, Guizhou, Chen Y. S. 01840420 (PE)
MH711723.1	*Viola diffusa*	Leibo, Sichuan, He M. Y. 02093842 (PE)
FJ002914.1	*Viola diffusoides*	Sichuan, Y.C.Yang 00025459 (PE)
JQ950564.1	*Viola dissecta*	Zhenan, Shanxi, Zhang C. F. 02247331 (PE)
JQ950567.1	*Viola eizanensis*	Janpan, Miyoshi Furuse 01207914 (PE)
AY928297.1	*Viola hirtipes*	Tonghua, Jilin, Chen Y. S. 01840415 (PE)
AY928295.1	*Viola japonica*	Pengzhe, Jiangxi, Qin H. N. 01861607 (PE)
MT923897.1	*Viola kunawarensis*	Hejing, Xinjiang, Chen Y. S. 02038258 (PE)
FJ002913.1	*Viola lucens*	Lechang, Guangdong, Chen Y. S. 01840441 (PE)
OR483796.1	*Viola nanlingensis*	Nanling, Guangdong, Wang G. F. 0765184 (IBSC)
AY928298.1	*Viola patrinii*	Hengren, Liaoning, Chen Y. S. 01840394 (PE)
MH710789.1	*Viola phalacrocarpa*	Taian, Shandong, Chen Y. S. 01861292 (PE)
MH711011.1	*Viola philippica*	Fangshan, Beijing, Shi L. 02112316 (PE)
JQ950572.1	*Viola pinnata*	Beijing, Wang J. W. PEY0004742 (PEY)
AY928279.1	*Viola raddeana*	Janpan, Miyoshi Furuse 01220858 (PE)
AY928301.1	*Viola seoulensis*	Korea, G.-N.Jeon,B.-S.Kim 020407329 (PE)
DQ787772.1	*Viola sieboldiana*	–
AB828325.1	*Viola sieboldii*	Janpan, Miyoshi Furuse 00159231 (PE)
FJ002912.1	*Viola triangulifolia*	Lingui, Guangxi, Liu B. 01990939 (PE)
KC330744.1	*Viola variegata*	Tonghua, Jilin, Chen Y. S. 01840188 (PE)
AY928283.1	*Viola verecunda*	Xingan, Guangxi, Chen Y. S. 01819105(PE)
AY928308.1	*Viola violacea*	Jiujiang, Jiangxi, Chen Y. S. 01840530 (PE)
AY928291.1	*Viola woosanensis*	–
PV089292	*Viola xinchengensis*	Xincheng, Guangxi, Nong Y. 051188 (GXMI)
FJ002915.1	*Viola yunnanensis*	Lingshui, Hainan, Chen Y. S. 01819675 (PE)

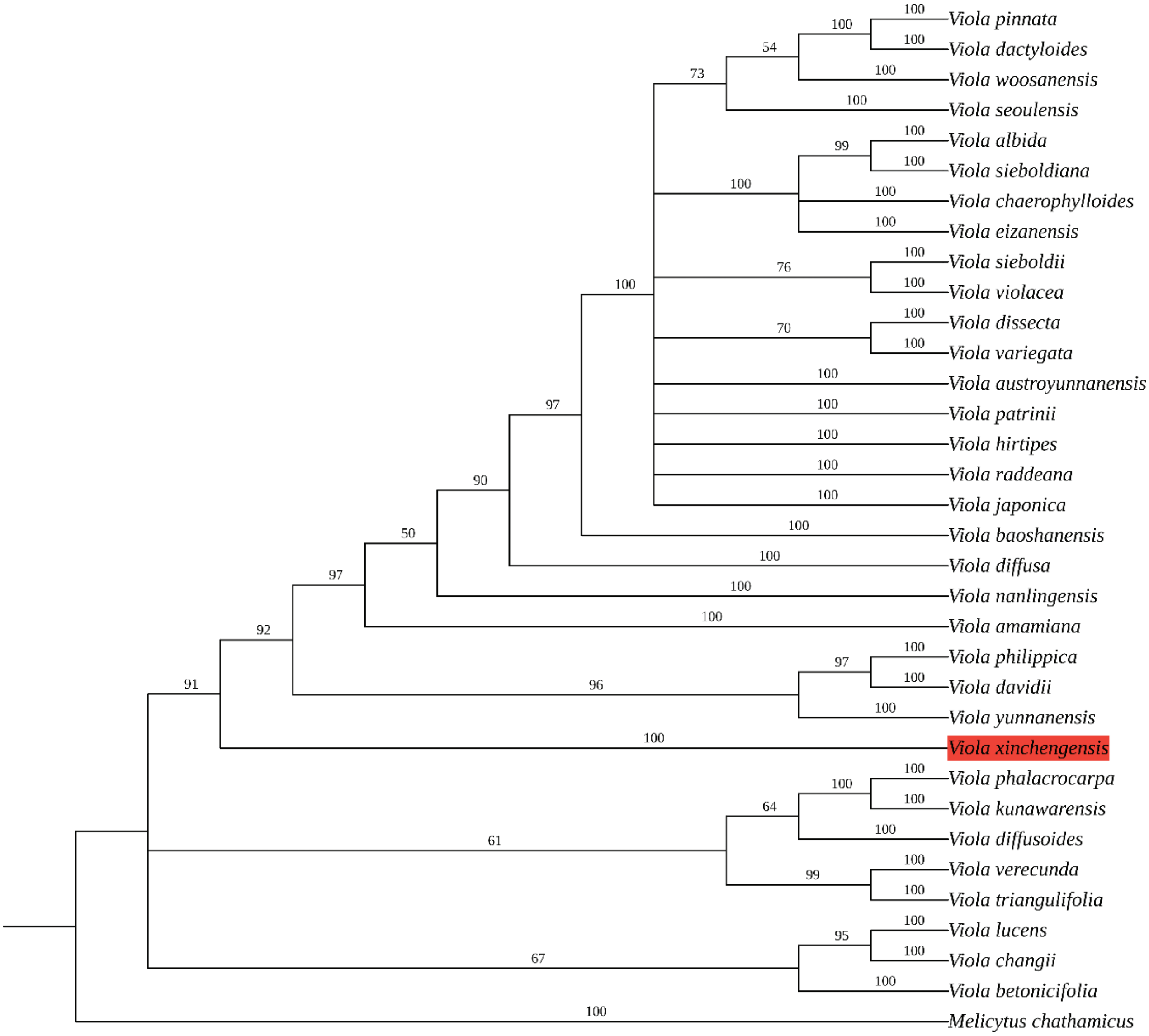

Figure 1. ML tree of the new species *Viola xinchengensis* sp. nov. and its related species, based on the ITS dataset. Bootstrap values of the Maximum Likelihood are shown along the branches.

Taxonomic treatment

***Viola xinchengensis* Y.Nong & G.Y.Wei, sp. nov.**
urn:lsid:ipni.org:names:77357572-1
Figs 1–4

Chinese name. xīn chéng jǐn cài (忻城堇菜).

Diagnosis. *Viola xinchengensis* is most similar to *V. lucens*, but differs from the latter by its stipules margin long fimbriate-dentate (vs. fimbriate-dentate), stolon absent (vs. stolon slender, often producing a new plant at the top) and sepals 4–6 mm, glabrous (vs. 2.5–3 mm, villous). *Viola xinchengensis* is similar to *V. fargesii*, but it can be easily distinguished by its pedicels sparsely white villous (vs. densely spreading white puberulous) and sepals 4–6 mm, glabrous (vs. 7–9 mm, puberulous). More detailed morphological differences amongst the three similar species are shown in Table 2.

Table 2. Main morphological differences amongst *Viola xinchengensis*, *V. lucens*, and *V. fargesii*.

Morphological traits	*Viola xinchengensis*	*V. lucens*	*V. fargesii*
Stolon	absent	slender, often producing new plant at top	longer, elongated, puberulous, sometimes stem-like
Stipules	margin long fimbriate-dentate	margin fimbriate-dentate	margin long fimbriate-dentate
Petiole	villous, narrowly winged only in upper part	densely villous, wingless	densely villous, wingless
Leaf blade	ovate, 1.5–2.5 cm × 1.5–2 cm, base cordate	oblong-ovate, ovate or oblong, 1–2(–3) × 0.5–1.3 cm, base cordate or rounded	ovate or broadly ovate, sometimes suborbicular, 2–6 × 2–4.5 cm, base shallowly cordate
Flowers	purplish	light bluish violet	white
pedicels	sparsely white villous	sparsely puberulous	densely spreading white puberulous
Sepals	narrowly ovate-lanceolate or lanceolate, 4–6 mm, glabrous	narrowly lanceolate, 2.5–3 mm, villous	narrowly ovate-lanceolate or lanceolate, 7–9 mm, puberulous
Petals	oblong-obovate, 6–10 mm, lateral ones bearded	narrowly lanceolate, 2.5–3 × ca. 1 mm, lateral ones glabrous	oblong-obovate, 1–1.5 cm, lateral ones slightly bearded
Spur	1.5–2 mm	ca. 1.5 mm	2–2.5 mm
Ovary	ovoid, glabrous	globose, glabrous	conic, glabrous
Styles	base slightly geniculate, slightly flat at apex, conspicuously margined on lateral sides, shortly beaked in front, with a stigma hole open upwards at tip of beak	base geniculate, thickened at apex; stigmas narrowly margined on lateral sides, apex shortly beaked	base slightly geniculate, slightly flat at apex, conspicuously margined on lateral sides, shortly beaked in front, with a stigma hole open upwards at tip of beak
Capsule	narrowly orbicular, 5 mm, glabrous	ovoid-orbicular, 5 mm, glabrous	narrowly orbicular, 8 mm, glabrous

Type. China • Guangxi: Xincheng, 23°59'42"N, 108°44'28"E, alt. 370 m, on the cliff at the bottom of a sinkhole, 20 April 2024, *Y. Nong NY2024042002* (holotype GXMI! 051188; isotypes IBK!).

Description. Perennial herbs, small, 5–10 cm tall; rhizome erect, sometimes elongate, with short internodes, ca. 2 mm, lateral stem and stolon absent. Leaves nearly basal; stipules adnate to petioles for about 1/8 at base, brown, lanceolate, 5–7 mm × 1–2 mm, margin long fimbriate-dentate, apex acuminate. Petiole 1.5–3.5 cm, villous, narrowly winged only in the upper part. Leaf blade ovate, 1.5–2.5 cm × 1.5–2 cm, apex acute, base cordate, margin crenate, both surfaces densely villous. Pedicels much exceeding the leaves, glabrous or sparsely villous, 2-bracteolate above middle; bracteoles opposite, linear, 6–8 mm, margin villous. Sepals ovate-lanceolate, entire, 4–6 mm, apex acuminate, basal auricles short, ca. 2 mm, glabrous. Flower 1.0–1.5 cm in diameter, petals 5, white with purple or purplish, posterior and lateral ones oblong-obovate, ca. 7–8 mm × 3–5 mm, narrow at the base, lateral petals white with purple, lateral ones bearded, anterior one boat-shaped, 5–8 mm (spur included); spur saccate, short, 1.5–2 mm, ca. 2 mm in diam. Anthers ca. 1.2 mm, connective appendages ca. 0.5 mm; nectariferous glands broadly triangular, ca. 0.5 mm. Ovary ovoid, glabrous; style clavate, base slightly geniculate, thickened upwards, slightly flat at the apex, conspicuously margined on lateral sides, shortly beaked in front, with a stigma hole open upwards at the tip of the beak. Cleistogamous flowers ca 1.5 mm long; bracteoles linear, 6–8 mm, margin villous, acuminate at the apex. Sepals green, entire, 4–6 mm, apex acuminate. Petal 1, ovate, white with purple, 1.0–1.5 cm long. Capsule ovoid, dehiscence explosive, ca. 5 mm, glabrous. Seeds brown, ovoid, 1 mm, densely covered with tubercles.

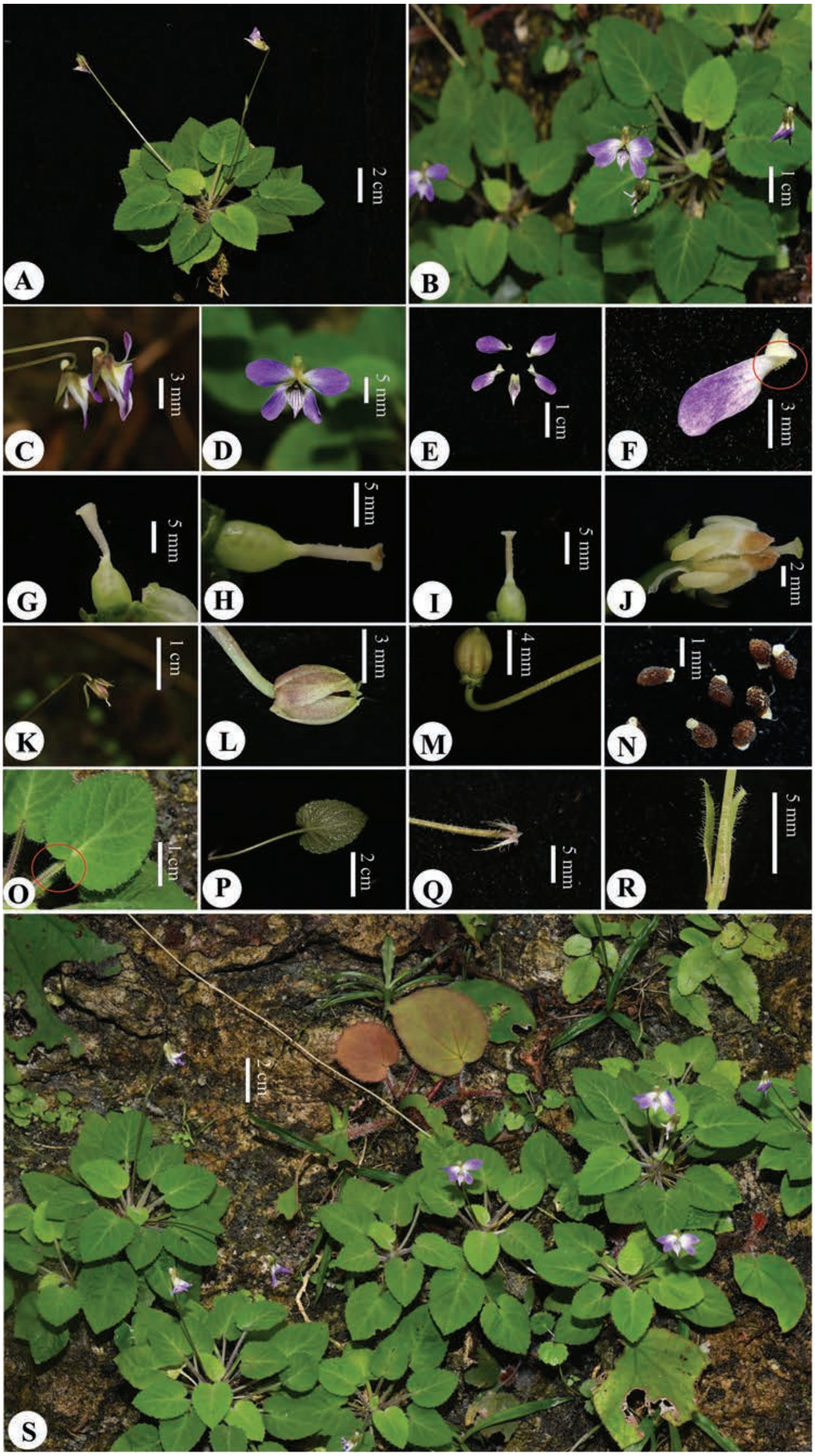

Figure 2. *Viola xinchengensis* Y.Nong & G.Y.Wei **A** plant (top view) **B** plant (flowering) **C** flowers (lateral view) **D** flower (front view) **E** petals **F** lateral petal **G–I** ovary and style **J** stamens **K–M** capsule **N** seeds **O** leaf (adaxial surface) **P** leaf (abaxial surface) **Q** stipules **R** bract **S** habitat (Photographed and edited by You Nong).

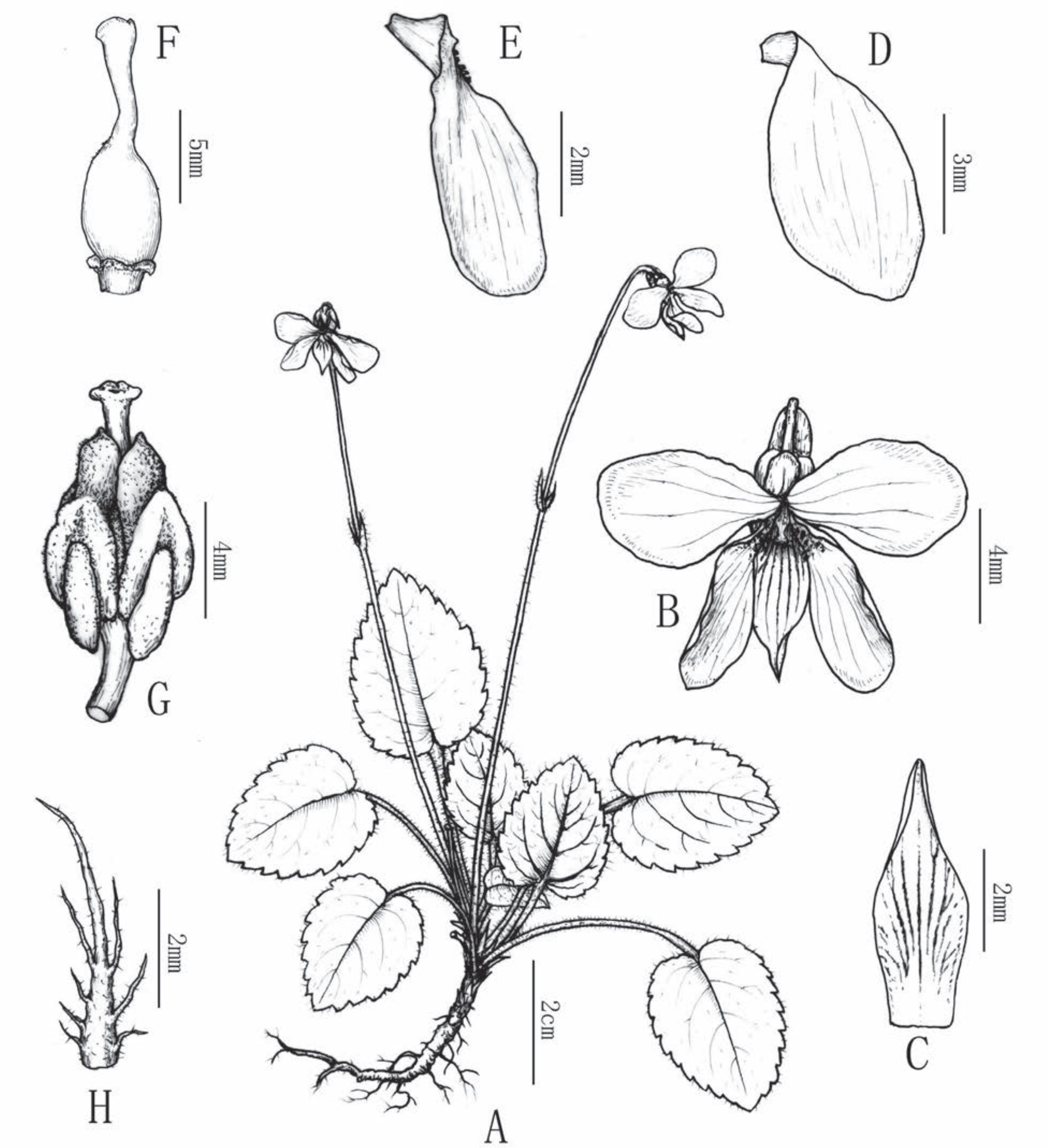

Figure 3. Line drawing of *Viola xinchengensis* Y.Nong & G.Y.Wei **A** flowering plant **B** flower **C** anterior petal **D** upper petal **E** lateral petal **F** ovary and style **G** stamens and pistil **H** stipule. Drawn by Xin-cheng Qu.

Phenology. Flowering and fruiting from April to June.

Etymology. The specific epithet "xinchengensis" refers to the type locality, Xincheng County (忻城县), which is situated in central Guangxi, southwest China.

Distribution and habitat. The new species is known only from central Guangxi, China (Fig. 5). It has been found mainly on the cliff at the bottom of a sinkhole at elevations of 370 m. It usually grows with *Begonia pseudoleprosa* C. I Peng & al. and *Primulina sclerophylla* (W. T. Wang) Yan Liu on the damp cliffs.

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),

标本采集记录签(Record label)
采集号(No.)：NY2024042002
标本份数(Number of specimens)：2 份
采集人(Collector)：农友，韦贵元
采集日期(Date)：2024 年 4 月 20 日
采集地点(Location)：广西忻城县加沙屯附近天坑
环境(Environment)：天坑崖壁
出现多度(Abundance)：少
生活型(Life-form)：草本
株高(Height)：
枝、叶(Branches and leaves)：
花(Flower)：紫色
果实及种子(Fruits and seeds)：
科名(Family)：
植物名（Name）：
备注（Remark）：堇菜属

采集号：NY2024042002 堇菜科
忻城堇菜
Viola xinchengensis Y Nong & G.Y. Wei
鉴定人：农友
鉴定日期：2024.6.3

Figure 4. The holotype specimen of *Viola xinchengensis* Y.Nong & G.Y.Wei.

it is considered Data Deficient (DD) until more information becomes available. Although *Viola xinchengensis* currently has relatively good growth, further collection and monitoring are necessary to allow more conclusive estimations about the rarity and vulnerability of the species.

Figure 5. The distribution of *Viola xinchengensis* Y.Nong & G.Y.Wei (red circle) in Guangxi (blue triangle in insert map), China.

Additional specimens examined (paratypes). CHINA • Guangxi: Xincheng, 23°59'42"N, 108°44'28"E, alt. 370 m, at the bottom of a sinkhole, 26 April 2024 *Y. Nong NY20240042602*(GXMI) • Xincheng, 23°59'42"N, 108°44'28"E, alt. 370 m, at the bottom of a sinkhole, 12 June 2024 *G. Y. Wei WGY20240061201*(GXMI).

Taxonomic notes. *Viola xinchengensis* lacks bulbils, lateral stems and stolons. Stipules are adnated to petioles for about 1/8 at base, membranous, glandular-lacerate. Bottom petal is 7–12 mm long, including the spur. Style apex margined and flattened. According to the study of *Viola* (Marcussen et al. 2022), *V. xinchengensis* belongs to *V.* sect. *Plagiostigma* subsect. *Diffusae* W. Becker.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

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Author contributions

Data curation: YN. Funding acquisition: YN, XCQ. Investigation: YN, CGX, YGW. Methodology: YN, QMH, YGW. Project administration: YN, FB. Supervision: BF, LYL. Visualisation: YN, YGW, CY. Writing – original draft: YN. Writing – review and editing: YN.

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Data availability

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

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Research Article

Grewia kentingensis (Malvaceae, Grewioideae), a new species from Taiwan

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Abstract

Grewia kentingensis Y.H. Tseng, Chih Y.Chang & C.Y.Lin, **sp. nov.**, a new species found on elevated coral reefs in southern Taiwan, is described. The species was previously misidentified as *G. piscatorum* Hance. *Grewia kentingensis* differs from *G. piscatorum* in its habit (procumbent vs. erect to ascending shrub), leaf length (<2 cm vs. up to 7 cm), breeding system (gynodioecious vs. trioecious), smaller flower diameter, fewer stamens, and smaller pollen grains. Color photographs, line drawings, and pollen images of the new species are provided. Additionally, a lectotype for *G. piscatorum* is designated and an identification key for the *Grewia* taxa of Taiwan is presented.

Key words: Critically endangered, *Grewia piscatorum* Hance, pollen morphology, southern Taiwan, taxonomy

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Introduction

Grewia L. (Malvaceae: Grewioideae) is comprised of 280–300 species, which are distributed in the Old World tropics (Chung et al. 2003, 2005; Randrianasolo et al. 2013). The genus includes trees, shrubs, and climbers, which are characterized by leaves that are 3- to 5-nerved from the base; solitary, cymose, or umbellate inflorescences that are axillary, leaf-opposed, or terminal; and numerous free stamens, an androgynophore, and unlobed or 2- to 4-lobed drupaceous fruits (Liu and Lo 1993; Kubitzki and Bayer 2003; Tang et al. 2007). According to Liu and Lo (1993), four species have been recorded in Taiwan; *G. biloba* G. Don, *G. eriocarpa* Juss., *G. piscatorum* Hance, and *G. rhombifolia* Kaneh. & Sasaki. Chang et al. (2018) later reported an occurrence of *G. tiliifolia* Vahl.

On the basis of floral and fruit morphology, Burret (1926) subdivided *Grewia* into four sections but his classification system is probably artificial (Dorr, pers. comm.). Nonetheless, the Taiwanese taxa can be placed in two of Burret's sections. *Grewia eriocarpa* and *G. tiliifolia*, which are characterized by axillary inflorescences, bisexual flowers, entire stigmas lobes, and often unlobed fruits, can be assigned to sect. *Axillares* Burret while *G. biloba*, *G. piscatorum*, and *G. rhombifolia*, characterized by leaf-opposed, terminal, or rarely axillary inflorescences, unisexual or bisexual flowers, stigmas lobes with filamentary divisions, and usually 4-lobed fruits can be assigned to sect. *Glomeratae* Burret (see also Chang et al. 2018).

During recent field and herbarium investigations, we noticed that populations of *Grewia* growing on elevated coral reefs in Hengchun Peninsula, Taiwan had been identified as *G. piscatorum* based on sparse hairs on both leaf surfaces and white sepals. However, individuals in this locality diverged from *G. piscatorum* in several characters, including their procumbent habit, smaller stipules, leaves with fewer serrations, smaller flowers, shorter pedicels, and fewer stamens. After careful comparison, we concluded that the material from Hengchun represents a new species, which is described here as *G. kentingensis*.

Materials and methods

Morphological comparison

We compared our unknown taxon to *Grewia piscatorum*. Additionally, we compared it to the Taiwanese taxa *G. rhombifolia* and *G. biloba* var. *biloba* as well as to the non-Taiwanese taxa *G. biloba* var. *parviflora* (Bunge) Hand.-Mazz. and *G. biloba* var. *microphylla* (Maxim.) Hand.-Mazz., all of which can be assigned to sect. *Glomeratae*. Morphological measurements were conducted using both fresh and dried material. Quantitative characters were measured using fresh material, while dry specimens only were used for qualitative character observations and descriptions. For each taxon, at least three individuals were used for measurements and statistical tests. Morphological descriptions follow Liu and Lo (1993); Wahlert et al. (2015); and Barrett (2019).

Herbarium resources

Herbarium acronyms from Index Herbariorum were used in this study (Thiers 2024, continuously updated). Voucher specimens collected for the current study were deposited in the herbarium of the Department of Forestry, National Chung Hsing University, Taiwan (TCF). Physical and digital specimens in several herbaria also were examined; physical specimens: Department of Forestry and Natural Resources, National Chia-Yi University, Taiwan (CHIA), Provincial Pingtung Institute (PPI), National Taiwan University, Taiwan (TAI), Endemic Species Research Institute, Taiwan (TAIE), Taiwan Forestry Research Institute (TAIF), TCF, and National Museum of Natural Science, Taiwan (TNM); and digital specimens: School of Life Sciences, Xiamen University (AU), The Natural History Museum (BM), South China Botanical Garden, Chinese Academy of Sciences (IBSC), and the Royal Botanic Gardens, Kew (K).

Pollen morphology

Pollen grains were acetolyzed following the method established by Erdtman (1960). Grains were sequentially dehydrated in ethanol and then critical point dried. The dried pollen grains were mounted on a stub and sputter-coated with gold in a Quorum SC7620 sputter coater (Quorum Technologies, Laughton, UK) for 120 s. Subsequently, the grains were observed under a Hitachi S-3400N scanning electron microscope (Hitachi, Ltd, Tokyo, Japan). At least thirty pollen

Table 1. Voucher material for the *Grewia* L. pollen morphology.

Taxon	Location	Coordinate	Altitude	Date	Voucher
G. kentingensis	Taiwan. Pingtung County, Hengchun Township, Fongchueisha	21°56'57.8"N, 120°50'16.5"E	73 m	3 May 2024	*C. Y. Lin et al. 69* (TCF)
	Taiwan. Pingtung County, Hengchun Township, Sheding Formosan Sika Deer Restoration Area	21°57'53.0"N, 120°49'39.2"E	154 m	26 June 2024	*C. Y. Lin et al. 93* (TCF)
G. piscatorum	Taiwan. Kinmen County, Jincheng Township, Zhaishan Tunnel	24°23'20.0"N, 118°19'07.1"E	20 m	25 May 2024	*C. Y. Lin et al. 80* (TCF)
	Taiwan. Kinmen County, Jinsha Township, Mashan Observation Post	24°31'39.3"N, 118°24'37.9"E	4 m	29 May 2023	*C. Y. Lin 24* (*TCF*)
	Taiwan. Lienchiang County, Nangan Township, Guanmaoshan	26°08'23.7"N, 119°55'44.3"E	15 m	13 June 2023	*C. Y. Lin 26* (TCF)
G. rhombifolia	Taiwan. New Taipei City, Wanli Dist., Yehliu Geopark	25°12'32.2"N, 121°41'38.2"E	1 m	22 April 2023	*C. Y. Lin et al. 7* (TCF)
	Taiwan. New Taipei City, Ruifang Dist., Nanyaqiyan	25°07'11.4"N, 121°53'33.1"E	2 m	12 May 2024	*C. Y. Lin 79* (TCF)
	Taiwan. New Taipei City, Ruifang Dist., Bat cave park	25°07'39.2"N, 121°50'05.1"E	4 m	27 June 2024	*C. Y. Lin 96* (TCF)
G. biloba var. *biloba*	Taiwan. Hualien County, Xiulin Township, Chongde trail	24°11'34.4"N, 121°39'45.3"E	24 m	26 March 2023	*C. Y. Lin 6* (TCF)
	Taiwan. Kaohsiung City, Mituo Dist., Ta-di Mountain Natural Park	22°46'05.8"N, 120°14'58.7"E	47 m	23 July 2023	*C. Y. Lin 31* (TCF)
	Taiwan. Pingtung County, Chunri Township, Dahan forest road	22°25'13.0"N, 120°40'51.4"E	953 m	11 August 2024	*C. Y. Lin 105* (TCF)

grains were observed and measured for each taxon. The terminology for the morphological descriptions of pollen grains is in accordance with the terminology used by Erdtman (1952) and Halbritter et al. (2018). Information on voucher specimens is provided in Table 1.

Distribution map

A distribution map for this species was generated using QGIS ver. 3.24.2 (QGIS.org 2024) with the package developed by Lin (2018).

Data analysis

Quantitative morphological characters of taxa were measured and means and standard deviations were calculated (Table 2). Differences among taxa were analyzed using one-way analysis of variance, followed by Tukey's Honestly Significant Difference (HSD) multiple-range test ($p \leq 0.05$) (Oliveira 2013). All statistical analyses were conducted using SPSS ver. 20 (Jasrai 2020).

Results and discussion

Macromorphological differences

Grewia kentingensis can be assigned to sect. *Glomeratae* in the infrageneric classification system proposed by Burret (1926), as can *G. piscatorum*, *G. rhombifolia*, and *G. biloba* var. *biloba*. The species assigned to sect. *Glomeratae* in Taiwan have three different habits: 1) *G. biloba* var. *biloba* is a small tree that is ca. 3–5 m tall and usually has a distinct main trunk, 2) *G. piscatorum* and *G.*

rhombifolia are erect to ascending shrubs 1–2 m tall, 3) *G. kentingensis* is a procumbent shrub that is clearly distinct from other taxa (Fig. 1, Table 2). Both leaf surfaces in *G. rhombifolia* are densely covered with stellate hairs, whereas both leaf surfaces in *G. kentingensis*, *G. piscatorum*, and *G. biloba* var. *biloba* are nearly glabrous (Table 2). The leaf blades of *Grewia* taxa in Taiwan have distinct shapes: *G. kentingensis* has broadly elliptic to elliptic leaves, *G. piscatorum* displays elliptic, obovate, ovate, and rhomboid-ovate leaves, *G. biloba* var. *biloba* features ovate, elliptic, and rhomboid-ovate leaves, and *G. rhombifolia* has rhomboid, broadly rhomboid, and obtrullate leaves (Table 2). Among the *Grewia* taxa in Taiwan, *G. kentingensis* has the smallest leaves ($p \leq 0.05$). The leaves of *G. kentingensis* measure 0.4–1.6 × 0.3–1.3 cm. The leaves of *G. piscatorum* measure 0.7–7.8 × 0.5–5.5 cm. The leaves of *G. rhombifolia* measure 1.6–6.7 × 1.1–7.0 cm. The leaves of *G. biloba* var. *biloba* measure 2.1–13.9 × 1.3–7.4 cm (Table 2). *Grewia piscatorum* exhibits considerable variation in leaf size, partially overlapping with *G. kentingensis* (Table 2). The leaf margin in *G. kentingensis* is serrate, and that of *G. piscatorum* and *G. biloba* var. *biloba* are serrulate to biserrulate. The leaf margin in *G. rhombifolia* is irregularly serrulate or biserrulate to dentate. *Grewia kentingensis* features significantly fewer leaf serrations (9–20) ($p \leq 0.05$) than *G. piscatorum* (23–82), *G. rhombifolia* (26–88), or *G. biloba* var. *biloba* (29–132) (Table 2).

Significant differences also were observed in the length of peduncles and pedicels among the *Grewia* taxa measured ($p \leq 0.05$). *Grewia kentingensis* features significantly shorter peduncles and pedicels (peduncles: 0.7–2.7 mm, pedicels: 0.9–4.9 mm) ($p \leq 0.05$) compared with *G. piscatorum* (peduncles: 3.1–17.2 mm, pedicels: 3.5–8.8 mm), *G. rhombifolia* (peduncles: 3.0–13.1 mm, pedicels: 3.8–8.6 mm), and *G. biloba* var. *biloba* (peduncles: 3.7–14.3 mm, pedicels: 4.4–9.3 mm) (Table 2). Regarding the sexual or breeding system, *G. kentingensis* is gynodioecious, whereas the other taxas are all trioecious (Table 2). Flower diameter in *G. kentingensis* (7.2–11.7 mm in bisexual flowers and 5.2–7.8 mm in female flowers) is significantly smaller ($p \leq 0.05$) than it is in *G. piscatorum* (14.8–18.5 (–20.2) mm in bisexual flowers and 9.4–14.6 mm in female flowers), *G. rhombifolia* (13.9–17.8 mm in bisexual flowers and 8.9–13.8 mm in female flowers), or *G. biloba* var. *biloba* (13.9–18.7 mm in bisexual flowers and 8.8–11.3 mm in female flowers) (Table 2). Moreover, the sepals and petals in *G. kentingensis* are notably shorter than those in *G. piscatorum*, *G. rhombifolia*, or *G. biloba* var. *biloba* (Table 2). *Grewia kentingensis* also features significantly fewer stamens (25–34 in bisexual flowers and 14–23 in female flowers) ($p \leq 0.05$) compared with *G. piscatorum* (103–118 in bisexual flowers and 58–102 in female flowers), *G. rhombifolia* (64–103 in bisexual flowers and 51–80 in female flowers), and *G. biloba* var. *biloba* (65–121 in bisexual flowers and 55–98 in female flowers (Table 2). Additionally, the filaments and styles of bisexual flowers in *G. kentingensis* are significantly shorter ($p \leq 0.05$) than those in other taxa (Table 2).

Finally, although all the taxa assigned to sect. *Glomeratae* in Taiwan exhibit 4-lobed fruits with nearly glabrous surfaces that turn red after maturation, drupelet size in *Grewia kentingensis* (4.1–5.2 mm) is significantly smaller ($p \leq 0.05$) than those in *G. piscatorum* (4.4–6.4 mm), *G. rhombifolia* (4.7–6.3 mm), or *G. biloba* var. *biloba* (4.5–5.6 mm) (Table 2).

Other taxa that are morphologically similar to *Grewia kentingensis* and assigned to sect. *Glomeratae* but not found in Taiwan include *G. biloba* var. *parviflo-*

Table 2. Summary of diagnostic characters of *Grewia* sect. *Glomeratae* Burret in Taiwan.

Characters		***G. kentingensis***	***G. piscatorum***	***G. rhombifolia***	***G. biloba* var. *biloba***
Habit		procumbent shrub, ca. 5 cm tall	erect to ascending shrub, ca. 1–2 m tall	erect to ascending shrub, ca. 1–2 m tall	small tree, ca. 3–5 m tall
Leaves					
shape		broadly elliptic to elliptic	elliptic, obovate, ovate to rhomboid-ovate	rhomboid, broadly rhomboid to obtrullate	ovate, elliptic to rhomboid-ovate
size (cm)		0.76 ± 0.28^{c} × 0.60 ± 0.25^{c}	3.93 ± 1.82^{b} × 2.67 ± 1.31^{b}	4.12 ± 1.32^{b} × 3.01 ± 1.23^{b}	6.56 ± 2.36^{a} × 3.64 ± 1.26^{a}
margin		serrate	serrulate to biserrulate	irregularly serrulate, biserrulate to dentate	serrulate to biserrulate
surfaces		Both surfaces nearly glabrous	Both surfaces nearly glabrous	Both surfaces densely covered with stellate hairs	Both surfaces nearly glabrous
number of serrations		13.83 ± 2.57^{c}	47.87 ± 16.00^{b}	49.69 ± 17.66^{b}	65.48 ± 24.75^{a}
stipule length (mm)		0.78 ± 0.19^{b}	3.84 ± 0.73^{a}	3.99 ± 0.60^{a}	4.02 ± 0.79^{a}
Sexual system		Gynodioecy	Trioecy	Trioecy	Trioecy
Inflorescences					
position		terminal	leaf-opposed, rarely axillary	leaf-opposed, rarely axillary	leaf-opposed, rarely axillary
per inflorescence flower number		2.39 ± 1.17^{c}	9.49 ± 2.63^{a}	7.41 ± 2.01^{b}	8.42 ± 2.19^{ab}
peduncle length (mm)		1.49 ± 0.60^{b}	6.63 ± 2.61^{a}	6.90 ± 2.64^{a}	7.87 ± 2.19^{a}
pedicel length (mm)		2.59 ± 1.21^{b}	6.05 ± 1.46^{a}	6.23 ± 1.35^{a}	6.57 ± 1.50^{a}
Flowers					
flower diameter (mm)	Bisexual flower	9.49 ± 1.34^{c}	16.88 ± 1.71^{a}	15.39 ± 1.22^{b}	16.25 ± 1.52^{ab}
	Female flower	6.75 ± 0.84^{c}	11.65 ± 1.29^{a}	11.49 ± 1.23^{a}	10.09 ± 0.75^{b}
sepal number		(3)4–5	(4)5(6)	(4)5(6)	(4)5(6)
sepal size (mm)	Bisexual flower	5.34 ± 0.46^{c} × 1.84 ± 0.27^{c}	8.70 ± 0.83^{a} × 3.03 ± 0.44^{a}	8.15 ± 0.73^{b} × 2.54 ± 0.43^{b}	7.89 ± 0.57^{b} × 2.46 ± 0.27^{b}
	Female flower	3.94 ± 0.49^{c} × 1.29 ± 0.23^{c}	5.09 ± 0.34^{b} × 1.63 ± 0.13^{a}	5.47 ± 0.46^{a} × 1.51 ± 0.13^{b}	5.12 ± 0.46^{b} × 1.62 ± 0.12^{ab}
petal size (mm)	Bisexual flower	1.32 ± 0.13^{d} × 0.75 ± 0.08^{c}	2.65 ± 0.28^{a} × 1.01 ± 0.08^{a}	2.32 ± 0.24^{b} × 1.00 ± 0.06^{a}	1.79 ± 0.19^{c} × 0.92 ± 0.11^{b}
	Female flower	1.37 ± 0.10^{c} × 0.79 ± 0.07^{a}	1.93 ± 0.24^{a} × 0.78 ± 0.13^{a}	1.64 ± 0.20^{b} × 0.78 ± 0.12^{a}	1.87 ± 0.53^{a} × 0.86 ± 0.20^{a}
stamens number	Bisexual flower	29.88 ± 3.09^{c}	110.86 ± 4.93^{a}	82.89 ± 15.88^{b}	87.09 ± 18.74^{b}
	Female flower	17.55 ± 2.58^{c}	79.53 ± 12.30^{a}	64.77 ± 8.18^{b}	80.67 ± 19.16^{a}
filaments length (mm)	Bisexual flower	1.92 ± 0.56^{b}	4.02 ± 0.96^{a}	3.87 ± 1.16^{a}	3.61 ± 0.83^{a}
	Female flower	0.76 ± 0.12^{c}	1.00 ± 0.27^{ab}	0.90 ± 0.28^{bc}	1.05 ± 0.37^{a}
style length (mm)	Bisexual flower	2.44 ± 0.32^{c}	4.18 ± 0.58^{a}	3.65 ± 0.22^{b}	3.71 ± 0.53^{b}
	Female flower	1.83 ± 0.28^{c}	2.25 ± 0.22^{ab}	2.46 ± 0.21^{a}	2.02 ± 0.24^{bc}
Druplet size (mm)		4.60 ± 0.22^{b}	5.39 ± 0.50^{a}	5.43 ± 0.45^{a}	5.11 ± 0.36^{a}
Pollen					
polar axis (μm)		37.61 ± 1.62^{b}	45.32 ± 1.34^{a}	45.93 ± 1.65^{a}	44.65 ± 1.27^{a}
equatorial axis (μm)		28.35 ± 2.47^{bc}	29.07 ± 1.05^{ab}	29.90 ± 1.38^{a}	26.89 ± 1.74^{c}
P/E ratio		1.33 ± 0.10^{c}	1.56 ± 0.06^{b}	1.54 ± 0.11^{b}	1.67 ± 0.11^{a}
shape		subprolate to prolate	prolate	prolate	prolate
lumen size (μm)		1.98 ± 0.56^{b}	2.47 ± 0.77^{a}	2.40 ± 0.53^{a}	2.24 ± 0.72^{ab}
muri width (μm)		0.68 ± 0.06^{a}	0.56 ± 0.09^{b}	0.55 ± 0.07^{b}	0.54 ± 0.06^{b}
perforation size (μm)		0.11 ± 0.05^{a}	0.11 ± 0.06^{a}	0.11 ± 0.06^{a}	0.12 ± 0.08^{a}
Distribution		Endemic to Taiwan; restricted to elevated coral reefs and coastal grasslands of the eastern coast of Hengchun Peninsula.	Distributed along the coast in Fujian and Hainan provinces in China. In Taiwan, found in Kinmen and Lienchiang counties.	Endemic to Taiwan; distributed along the coast and hills of northern to central Taiwan.	Distributed in central and southern China. At altitudes of ca. 10–1000 m in southern and eastern Taiwan.

^{abcd} Means in the same row followed by the same letter are not significantly different ($p \leq 0.05$; Tukey's HSD test).

Figure 1. Habit of taxa assigned to *Grewia* sect. *Glomeratae* Burret in Taiwan. **A** *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin **B** *Grewia piscatorum* Hance **C** *Grewia rhombifolia* Kaneh. & Sasaki **D** *Grewia biloba* G. Don var. *biloba*.

ra, which is distributed from northern to southern China and the Korean Peninsula (Chang 1989; Tang et al. 2007; Chang et al. 2014) and *G. biloba* var. *microphylla*, which is distributed in Sichuan and Yunnan provinces in China (Chang 1989; Wu et al. 1995; Tang et al. 2007). They all exhibit common characteristics such as white sepals, unisexual or bisexual flowers, and 4-lobed drupes that turn red upon maturation (Chang 1989; Tang et al. 2007). However, these two varieties are shrubs or trees 1–4-m tall (Chang 1989; Tang et al. 2007), whereas *G. kentingensis* is a procumbent shrub (Table 3). In addition, *G. kentingensis* can be readily dis-

Table 3. Summary of diagnostic characters of *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin and two non-Taiwanese species of sect. *Glomeratae* Burret.

Characters	***G. kentingensis***	***G. biloba var. microphylla*** [a]	***G. biloba* var. *parviflora*** [b]
Habit	procumbent shrub, ca. 5 cm tall	shrub or tree, ca. 1–4 m tall	shrub or tree, ca. 1–4 m tall
Leaves			
shape	broadly elliptic to elliptic	ovate	ovate
size (cm)	0.4–1.6 × 0.3–1.3	1.0–2.5 × 0.9–1.5	3.0–11.5 × 2.0–7.0
margin	serrate	biserrulate	biserrulate
surfaces	Both surfaces nearly glabrous	adaxial surface nearly glabrous, abaxial surface covered with stellate hairs	adaxial surface nearly glabrous, abaxial surface covered with stellate hairs
Inflorescences	solitary to cyme	umbel	umbel
Adaxial surface of petals	glabrous	tomentose	glabrous
Distribution	Endemic to Taiwan; restricted to elevated coral reefs and coastal grasslands of the eastern coast of Hengchun Peninsula.	Distributed in Sichuan and Yunnan provinces in China.	Distributed in northern to southern China and the Korean Peninsula.

[a] Character states from Maximowicz (1889), Chang (1989) and Tang et al. (2007).
[b] Character states from Bunge (1835), Chang (1989) and Tang et al. (2007).

tinguished from *G. biloba* var. *parviflora* by its broadly elliptic to elliptic (vs. ovate) leaf blade shape, smaller leaf blade size (0.4–1.6 × 0.3–1.3 cm vs. 3.0–11.5 × 2.0–7.0 cm), nearly glabrous (vs. abaxial surface covered with stellate hairs) leaf surfaces, and solitary to cymose (vs. umbellate) inflorescences (Bunge 1835; Chang 1989; Tang et al. 2007) (Table 3). The leaf blade size in *G. biloba* var. *microphylla* is smaller (1.0–2.5 × 0.9–1.5 cm), and its range overlaps with that of *G. kentingensis* (0.4–1.6 × 0.3–1.3 cm) (Table 3). *Grewia biloba* var. *microphylla* has ovate leaf blades with an acute to obtuse apex, stellate hairs covering the abaxial surface of leaves, and tomentum on the adaxial surface of its petals (Maximowicz 1889; Chang 1989; Tang et al. 2007). *Grewia kentingensis* features broadly elliptic to elliptic leaf blades with a rounded to obtuse apex, nearly glabrous leaf surfaces, and glabrous adaxial surface on its petals (Table 3).

Pollen morphology

Pollen grains of taxa assigned to sect. *Glomeratae* in Taiwan are medium-sized and tricolporate, subprolate, or prolate (Fig. 3, Table 2). These observations are consistent with those provided by Huang (1972) and Hsieh and Huang (1983). *Grewia kentingensis* has a significantly shorter polar axis ($p \leq 0.05$) (35.8–41.4 μm) than *G. piscatorum* (42.8–47.8 μm), *G. rhombifolia* (42.8–48.2 μm), or *G. biloba* var. *biloba* (42.5–46.9 μm) (Fig. 3, Table 2). The P/E ratio in *G. kentingensis* is the smallest (1.1–1.5) and is significantly lower ($p \leq 0.05$) than that in the other species (Fig. 3, Table 2). In addition, pollen grains of *G. kentingensis* are subprolate to prolate in shape, whereas those of the other taxa are prolate (Fig. 3, Table 2). The exine in all these taxa is reticulate, with perforations in the lumen (Fig. 3). Perforation size is not significantly different among the four species (Fig. 3, Table 2). Lumen size in *G. kentingensis* (1.0–2.9 μm) is significantly smaller ($p \leq 0.05$) than that in *G. piscatorum* (1.1–4.0 μm) or *G. rhombifolia* (1.4–3.5 μm). However, no significant difference was observed in the lumen size between *G. kentingensis* and *G. biloba* var. *biloba* (1.1–3.6 (–4.0) μm) (Fig. 3, Table 2). Muri width in *G. kentingensis* (0.6–0.8 μm) is significantly larger ($p \leq$

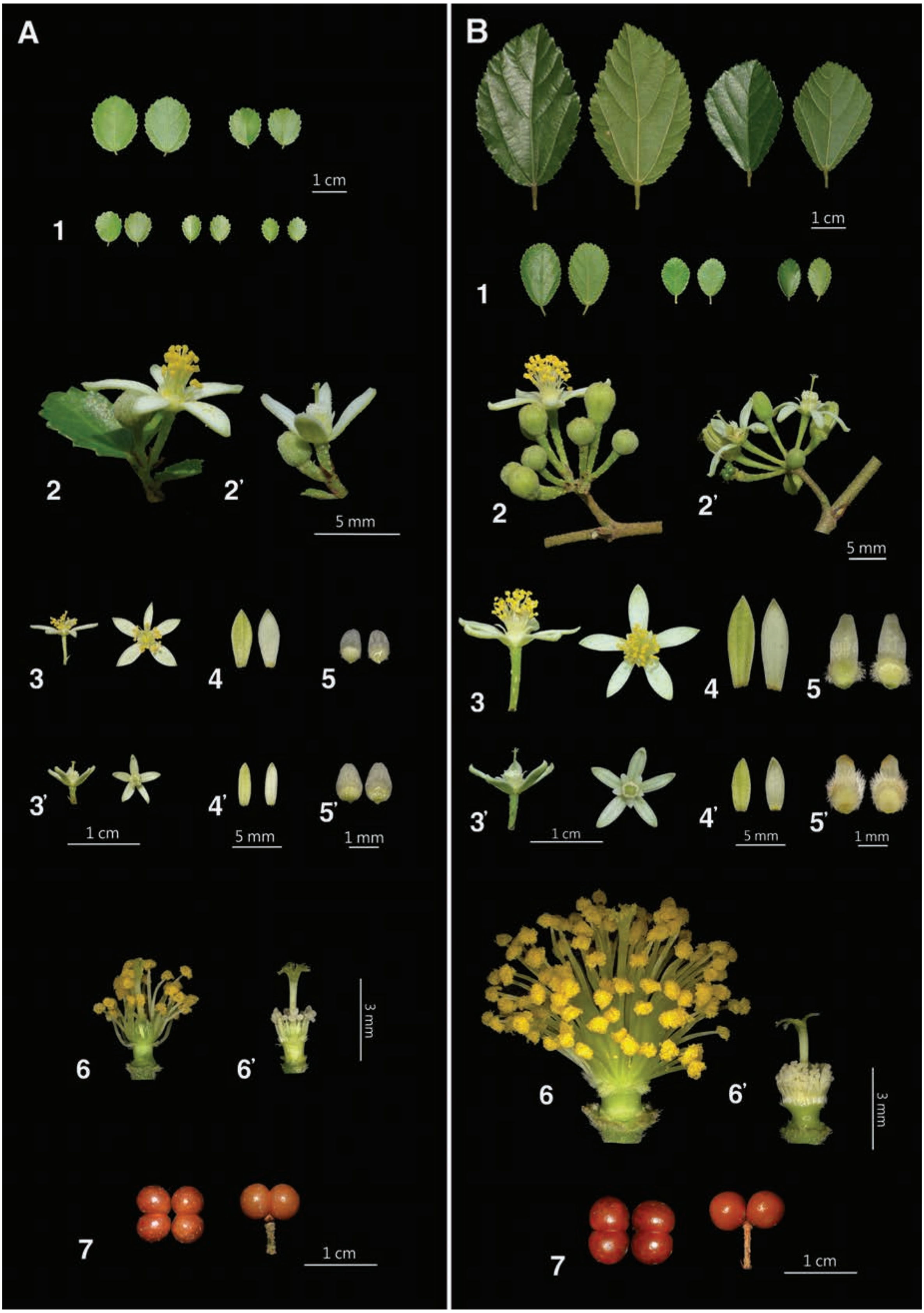


Figure 2. Comparison of morphological characters. **A** *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin **B** *Grewia piscatorum* Hance **1** leaves **2** bisexual inflorescence **2'** female inflorescence **3** bisexual flower **3'** female flower **4** sepal (bisexual) **4'** sepal (female) **5** petal (bisexual) **5'** petal (female) **6** bisexual flower (sepals and petals removed) **6'** female flower (sepals and petals removed) **7** fruit (left: overhead view; right: side view).

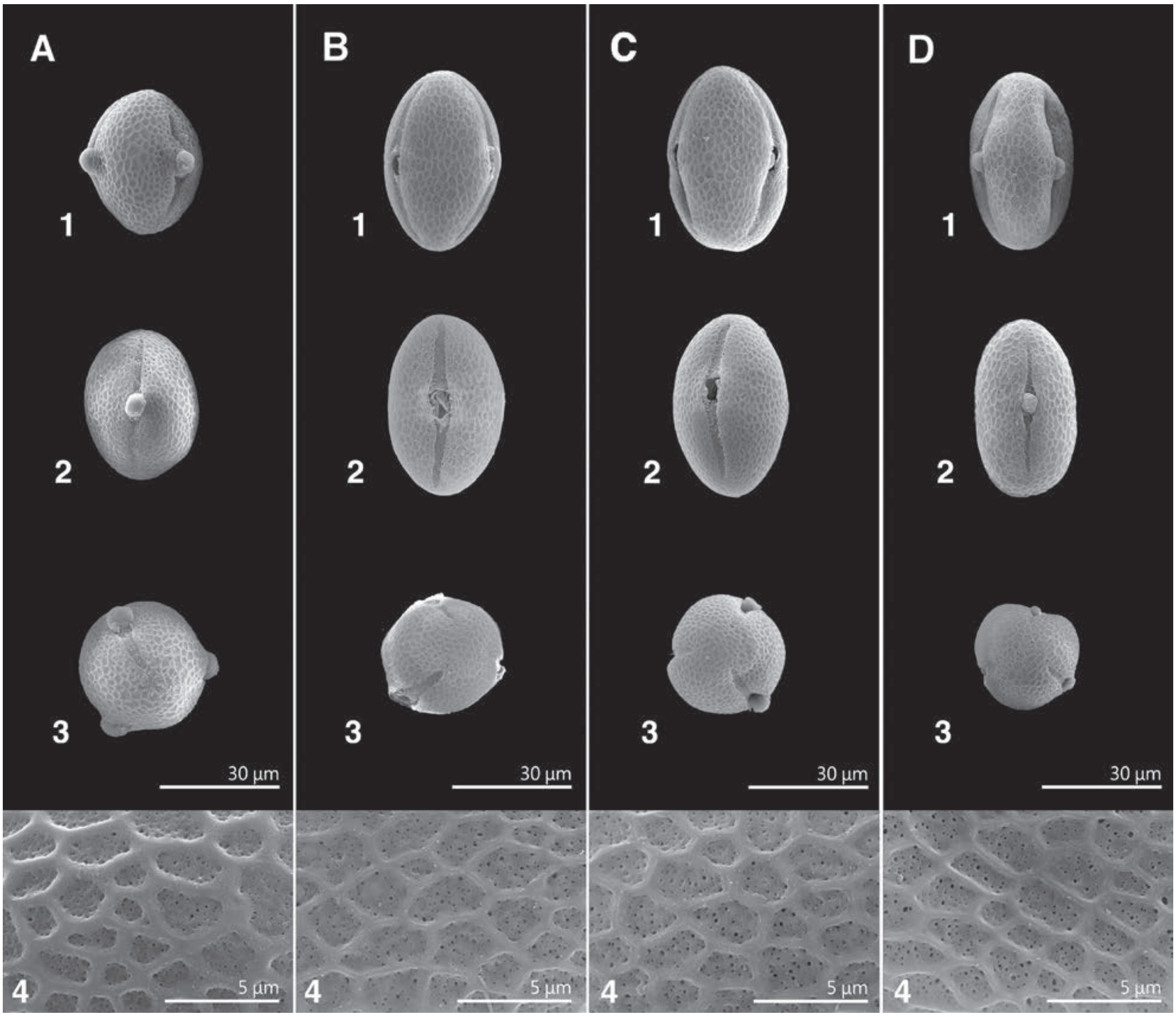


Figure 3. Comparison of pollen morphology of four *Grewia* taxa. **A** *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin **B** *Grewia piscatorum* Hance **C** *Grewia rhombifolia* Kaneh. & Sasaki **D** *Grewia biloba* G. Don var. *biloba* **1** equatorial view **2** colporate view **3** polar view **4** surface sculpture.

0.05) than that in *G. piscatorum* (0.4–0.7 µm), *G. rhombifolia* (0.4–0.7 µm), or *G. biloba* var. *biloba* (0.4–0.7 µm) (Fig. 3, Table 2). In conclusion, *G. kentingensis* pollen can be distinguished from that of other taxa by its shape, smaller polar axis, smaller P/E ratio, smaller lumen size, and wider muri.

Re-evaluation of *Grewia piscatorum* in Kinmen and Lienchiang counties, Taiwan

Grewia piscatorum was described by Hance (1866), who based the name on a collection by Swinhoe made on Lamyet Island (Nanjeih Island) in Fujian Province, China (*Swinhoe* in Herb. Hance *6527*). During our field trip to Kinmen and Lienchiang counties in Taiwan and based on examination of specimens, we found that the *Grewia* in Kinmen and Lienchiang counties closely resembled the type specimen of *G. piscatorum*. Additionally, the *Grewia* populations found in Kinmen and Lienchiang counties are geographically close to the type locality of *G. piscatorum*; both counties located on islands along the coast of Fujian Province.

In previous studies, the *Grewia* in Kinmen and Lienchiang counties was identified as *G. rhombifolia* (Kuo 2004; Lu 2011). However, we found that this *Grewia* has nearly glabrous leaf surfaces on both sides, with sparse stellate hairs on the veins. Thus, it differs from *G. rhombifolia*, which is characterized by a dense covering of stellate hairs on both leaf surfaces. Hance (1866) stated that *G. piscatorum* has a small leaf blade size. After measuring the type specimen, we determined the leaf blade size to be 0.7–2.5 cm. Nevertheless, based on field observations, we found that leaf blade size varies greatly within an individual plant, differing by leaf position on the branchlet (Fig. 4). On the same branchlet, leaves near the distal end of a branchlet are usually larger, reaching 3–7 cm, whereas leaves near the proximal end of a branchlet are smaller, with a size of 0.5–2 cm. This latter leaf blade size matches that of the type specimen of *G. piscatorum* (Fig. 4). This variation in leaf size has also been found in Bombacoideae (Malvaceae) (Carvalho-Sobrinho et al. 2024). Additionally, such variation in leaf morphology has been observed in *G.*

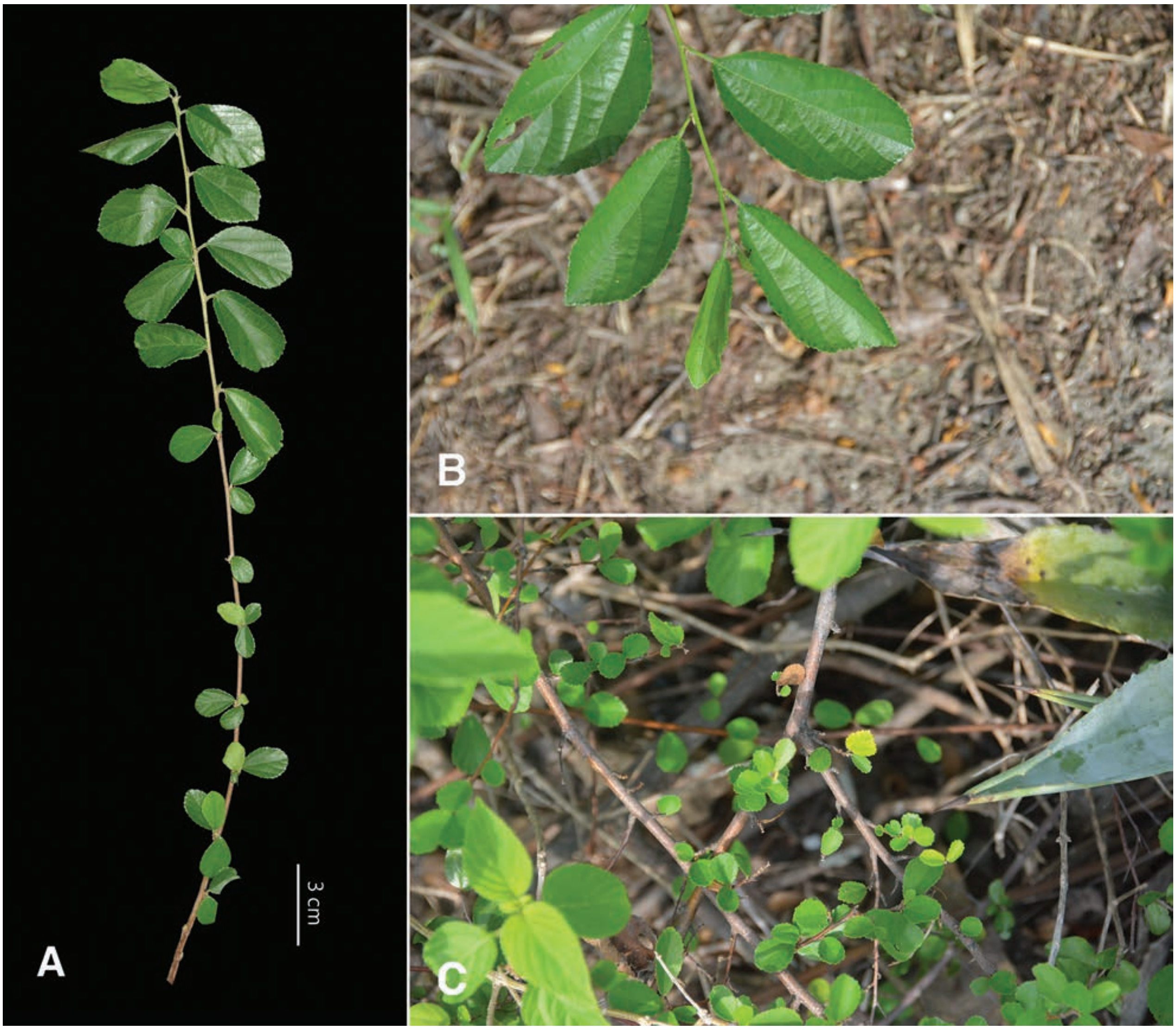


Figure 4. Variation in leaf size of *Grewia piscatorum* Hance. **A** variation in leaf size at different positions on the same branchlet **B** leaves near the distal end of a branchlet **C** leaves near the proximal end of a branchlet.

rhombifolia. Smaller leaf blade forms of *G. rhombifolia* in Taiwan have been identified as *G. piscatorum* (Sasaki 1928; Kanehira 1936; Li 1963; Liu and Lo 1993). In previous studies, leaf blade size was often used for identification (Li 1963; Liu et al. 1988; Liu and Lo 1993; Liu et al. 1998). However, variation in leaf blade size can contribute to overlap in size measurements among different taxa thereby rendering the identification of closely related taxa by this criterion alone challenging. In addition to leaf blade size, other characters such as habit, leaf vestiture, and floral morphology should be considered in comparisons for identification (Table 2).

The leaf blade size in *Grewia kentingensis* is much more consistent, with a leaf blade size of 0.5–1.5 cm. Leaves do not exceed 2 cm, which is significantly different from leaves of *G. piscatorum*. In summary, based on the similarity to the type specimen and description of *G. piscatorum* by Hance (1866), we consider the *Grewia* previously identified as *G. rhombifolia* in Kinmen and Lienchiang counties to be *G. piscatorum*.

Comparison of the distributions of *Grewia kentingensis* and *G. piscatorum*

Grewia kentingensis is only found along the eastern coastline of Hengchun Peninsula. This species grows on elevated coral reefs and open coastal grasslands with intense sunlight. By contrast, *G. piscatorum* is found in coastal hills or islands in Fujian and Hainan provinces in China (Chun and Chang 1965; Chang 1987; Chang 1989; Tang et al. 2007). In Taiwan, *G. piscatorum* is only found in Kinmen and Lienchiang counties (Fig. 5).

Key to *Grewia* in Taiwan modified from Liu and Lo (1993) and Chang et al. (2018)

1a Leaf bases cordate to rounded, usually oblique; inflorescences axillary; flowers bisexual only; sepals reflexed; fruits unlobed or 2-lobed **2**
2a Abaxial surface of leaves tomentose; petals and stamens turn from yellow to orange before withering; fruit surface tomentose ....***G. eriocarpa***
2b Abaxial surface of leaves nearly glabrous; petals and stamens turn from yellow to red before withering; fruit surface pubescent ....***G. tiliifolia***
1b Leaf bases cuneate, obtuse to rounded, seldom oblique; inflorescences terminal or rarely axillary; flowers unisexual or bisexual; sepals erect or slightly reflexed; fruits usually 2- to 4-lobed **3**
3a Procumbent shrubs; leaf blade length < 2 cm; gynodioecious; inflorescences terminal, 1–3(4–6) flowers per peduncle; stamens < 40 per flower ....***G. kentingensis***
3b Trees or erect to ascending shrubs; leaf blade length often > 2 cm; trioecious; inflorescences leaf-opposed, 4–15 flowers per peduncle, rarely axillary; stamens > 50 per flower...**4**
4a Leaves densely covered with stellate hairs above and below....***G. rhombifolia***
4b Leaves surfaces nearly glabrous above and below **5**
5a Small trees ca. 3–5 m tall; leaf blades ovate to elliptic, sometimes rhomboid-ovate, maximum length > 10 cm...........................***G. biloba* var. *biloba***
5b Erect to ascending shrubs ca. 1–2 m tall; leaf blades elliptic, obovate, or ovate to rhomboid-ovate, maximum length < 10 cm .... ***G. piscatorum***

Figure 5. Distribution map of *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin (white star) and *G. piscatorum* Hance (black triangle) in Taiwan.

Taxonomic treatment

Grewia kentingensis Y.H.Tseng, Chih Y.Chang & C.Y.Lin, sp. nov.

urn:lsid:ipni.org:names:77357855-1
Figs 1A, 2A, 3A, 6, 7, 8

Diagnosis. *Grewia kentingensis* is similar to *G. piscatorum* but can be distinguished by its procumbent (vs. erect to ascending) habit, smaller leaf size, serrate (vs. biserrulate) leaf margin, terminal (vs. often leaf-opposed) inflorescences, gynodioecious (vs. trioecious) breeding system, smaller flowers, fewer stamens, smaller fruits, and smaller pollen grains.

Type. Taiwan. Pingtung County • Hengchun Township, Sheding Formosan Sika Deer Restoration Area, 154 m alt., 21°57'53.0"N, 120°49'39.2"E, 26 June 2024, *C. Y. Lin et al. 93* (holotype: TCF; isotype: TNM).

Description. Procumbent shrubs to ca. 5 cm tall, stems rooting at the nodes; young branchlets puberulent, older branchlets nearly glabrous. Leaf blades broadly elliptic to elliptic, 0.4–1.6 cm long, 0.3–1.3 cm wide, apex rounded to obtuse, base cuneate to rounded, 3-nerved, margin serrate, nearly glabrous, stellate hairs sparsely distributed along the veins on both surfaces; petioles

0.4–1.3(–1.7) mm long, stellate hairs sparse; stipules linear, 0.4–1.2 mm long. Inflorescences terminal, cymose or flowers solitary; peduncles 0.7–2.7 mm long, 1 to 3(4 to 6) flowers, pedicels 0.9–4.9 mm long; bracts linear, 0.7–1.4(–1.8) mm long. Flowers bisexual or functionally unisexual (female), bisexual flowers 7.2–11.7 mm diam., female flowers 5.2–7.8 mm diam. Sepals (3)4 to 5, narrowly oblong to oblong, bisexual flowers 4.5–6.0 mm long, 1.4–2.3 mm wide; female flowers 3.2–4.8 mm long, 0.9–1.9 mm wide, apex acute, abaxial surface yellowish green, stellate–pubescent, adaxial surface white, glabrous. Petals (3)4 to 5, oblong to ovate, apex rounded, bisexual flowers 1.1–1.5 mm long, 0.6–0.9 mm wide, female flowers 1.2–1.6 mm long, 0.7–0.9 mm wide; nectaries present at the base of adaxial surface, 0.6–0.9 mm diam., surrounded by ciliate hairs. Androgynophore cylindrical, bisexual flowers 0.7–0.9 mm long; female flowers 0.8–0.9 mm long, glabrous, ciliate hairs only at the apex. Ovary globose to oblate, pubescent, bisexual flowers 0.8–1.0 mm diam.; female flowers 0.8–1.0 mm diam. Bisexual flowers with stamens 25 to 33, filaments white, glabrous, 1.2–3.2 mm long, anthers dehiscing longitudinally; style (1.8–)2.3–2.7 mm long, glabrous, stigma 4-lobed, each lobe dentate at apex. Female flowers with 15–20 stamens, filaments white, glabrous, 0.6–1.1 mm long, anthers white, always indehiscent; style 1.3–2.2 mm long, glabrous, stigma 4-lobed, each lobe dentate at apex. Fruits drupaceous, usually 4-lobed, fruit lobe 4.1–5.2 mm diam., globose, puberulent to nearly glabrous, red when mature.

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

Distribution and habitat. The species is endemic to Taiwan. *Grewia kentingensis* is sparsely distributed only on the elevated coral reefs and the coastal open grasslands at 50–200 m alt. along the eastern coastline of the Hengchun Peninsula. Commonly associated species include *Maytenus diversifolia* (Maxim.) Ding Hou (Celastraceae), *Pandanus odorifer* (Forssk.) Kuntze. (Pandanaceae), *Phoenix loureiroi* Kunth var. *loueiroi* (Palmae), *Rostellularia hayatae* (Yamam.) S.S.Ying (Acanthaceae), *Galactia tashiroi* Maxim. (Fabaceae), and *Cirsium albescens* Kitam. (Compositae).

Chinese name. kěn-dīng-bǔ-yú-mù (墾丁捕魚木)

Etymology. The species epithet *kentingensis* refers to the type locality of Kenting in Hengchun Peninsula, Pingtung County, Taiwan.

Palynology. Pollens grains are tricolporate, subprolate to prolate, 35.8–41.4 × 24.1–33.4 μm. Exine reticulate, with muri 0.6–0.8 μm wide and lumen 1.0–2.9 μm. Perforations present in the lumen, 0.04–0.24 μm.

Conservation status. *Grewia kentingensis* has an extremely limited distribution on the Hengchun Peninsula and is known from 12 collections representing three populations. It has a geographic range in the form of an estimated EOO of 8 km^2 (adjusted upward from 1.423 km^2 following IUCN 2024) and an AOO of 8 km^2. Even though the distribution of the species is located within the areas of Kenting National Park, its habitat is threatened by grazing, wildfires, and invasive plant species (*Cuscuta campestris* Yunck., *Stachytarpheta jamaicensis* (L.) Vahl, and *Bidens pilosa* var. *radiata* (Sch. Bip.) J.A. Schmidt). Given these ongoing threats, we infer a continuing decline in the area, extent and quality of habitat. With respect to the most serious plausible threat of wildfire, the three occurrences represent one location, which falls within the limits for “Critically Endangered” status. *Grewia kentingensis* is therefore preliminarily assessed as “Critically Endangered” [CR B1ab(iii)+2ab(iii)] in accordance with the IUCN Red

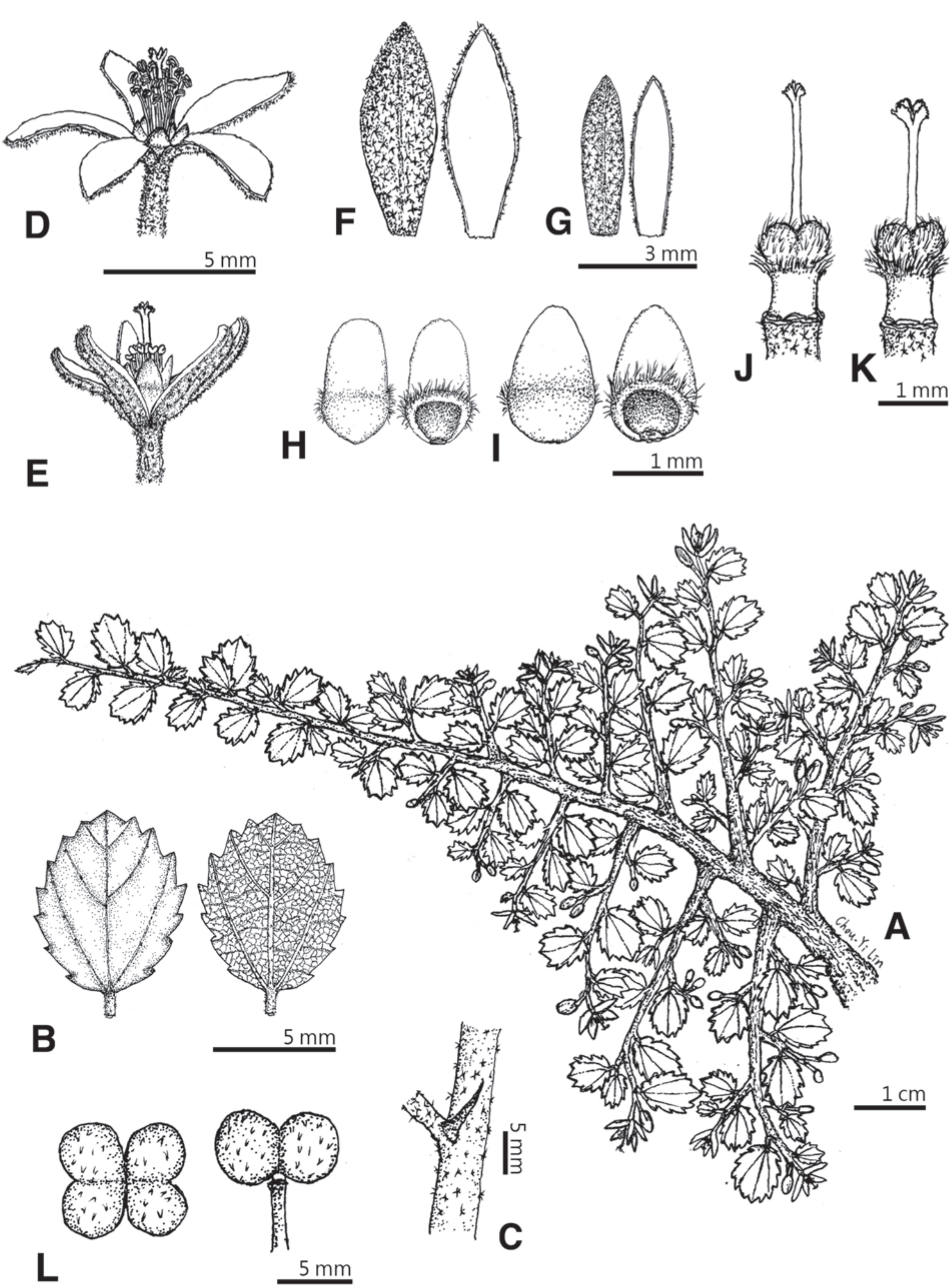


Figure 6. *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin. **A** habit **B** leaves **C** stipule **D** bisexual flower **E** female flower **F** sepals (bisexual) **G** sepals (female) **H** petals (bisexual) **I** petals (female) **J** gynoecium (bisexual) **K** gynoecium (female) **L** fruit (left: overhead view; right: lateral view).

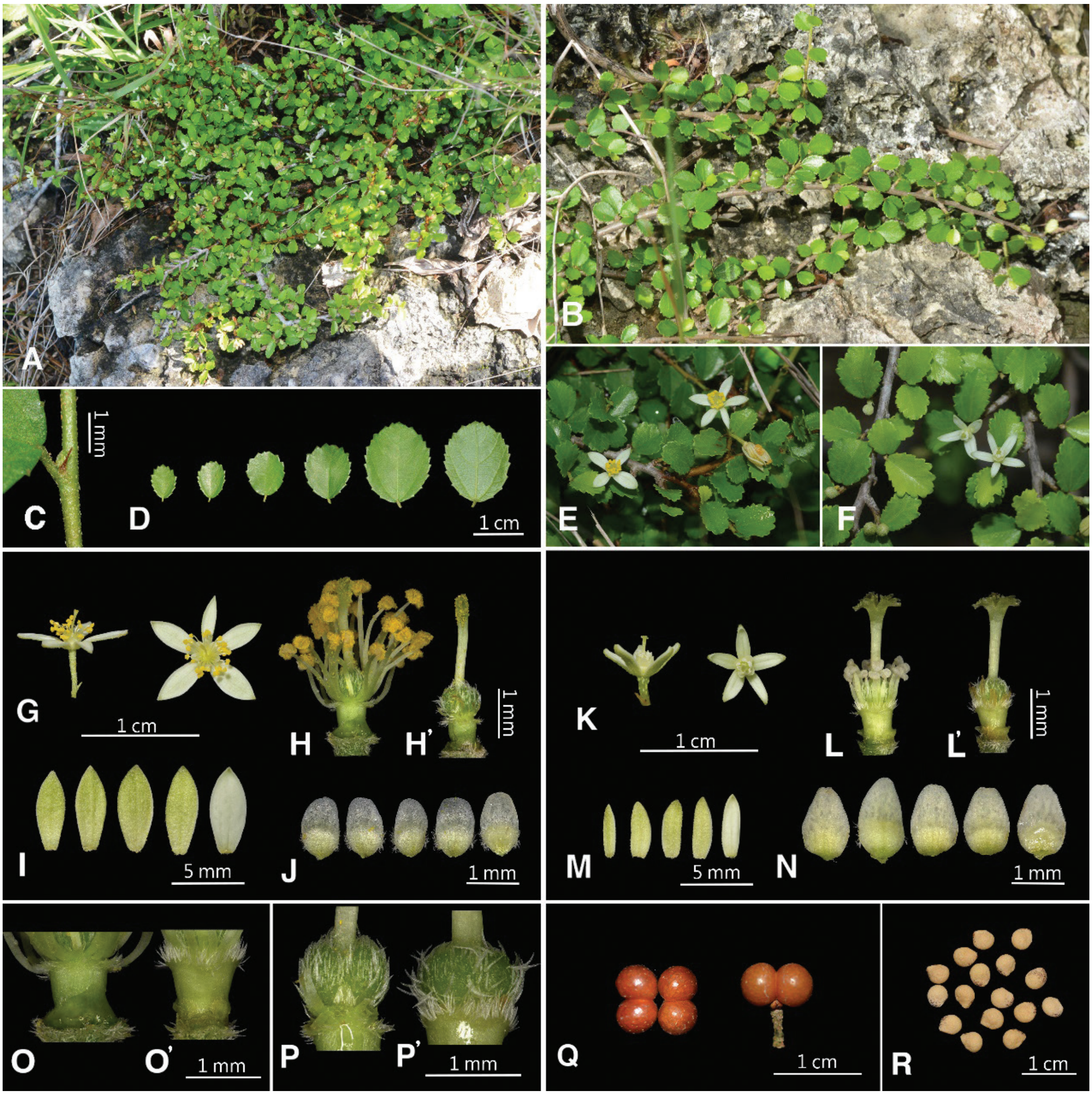
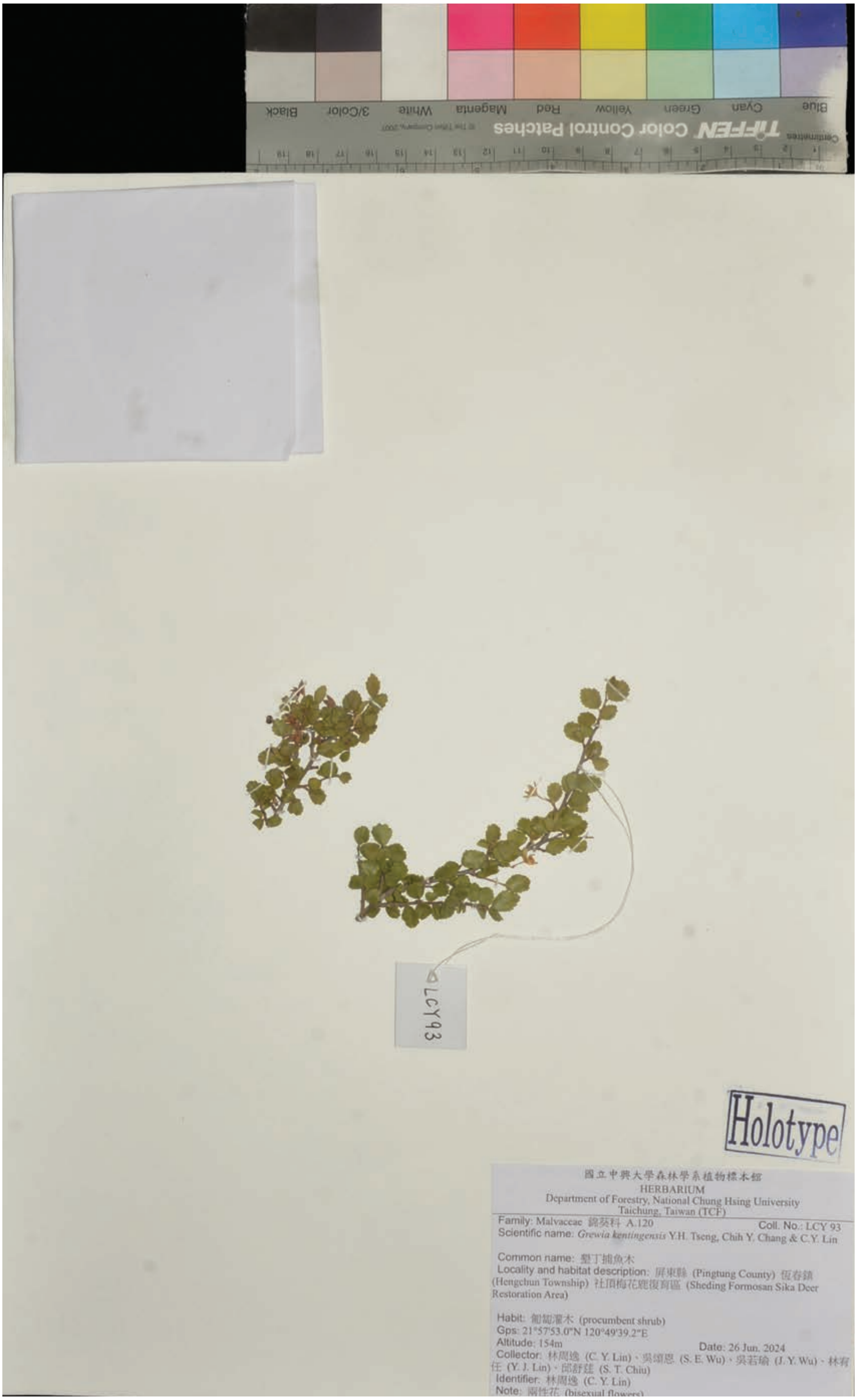


Figure 7. *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin. **A** habitat **B** habit **C** stipule **D** leaf blade variation **E** inflorescence (bisexual) **F** inflorescence (female) **G** bisexual flowers **H** bisexual flower (sepals and petals removed), **H'** gynoecium (bisexual) **I** sepals (bisexual) **J** petals (bisexual) **K** female flowers **L** female flower (sepals and petals removed), **L'** gynoecium (female) **M** sepals (female) **N** petals (female) **O** androgynophore (bisexual) **O'** androgynophore (female) **P** ovary (bisexual) **P'** ovary (female) **Q** fruit (left: overhead view; right: lateral view) **R** pyrenes.

List Categories and Criteria (IUCN 2024). The above analysis is based on the specimens cited and georeferenced as shown in Table 4.

Specimens examined. TAIWAN. Pingtung County • Fongchueisha, 28 Jun 1988, *T. C. Huang & S. F. Huang 13542* (TAI) • Ibid., 23 Jul 2013, *K. C. Chang 4893, 4894* (CHIA) • Ibid., 29 Mar 2015, *C. Y. Chang & C. H. Liu 397* (TNM) • Ibid., 3 May 2024, *C. Y. Lin et al. 69* (TCF) • Longzaipu, 6 Sep 2008, *P. F. Lu 16921* (TAIF) • Ibid., 17 Sep 2008, *T. C. Hsu 1743* (TAIF) • Ibid., 23 Jul 2013, *C. M. Wang et al. 15470* (TNM) • Ibid., 14 Aug 2013, *C. F. Chen 4697* (TAIF) • Ibid., 12 Apr 2014, *C. Y. Chang 30* (PPI) • Sheding, 12 Aug 1995, *Y. H. Yu 7968* (TAIF) • Sheding Formosan Sika Deer Restoration Area, 15 Jan 2021, *C. Y. Chang et al. 3236* (TNM).



Holotype

國立中興大學森林學系植物標本館
HERBARIUM
Department of Forestry, National Chung Hsing University
Taichung, Taiwan (TCF)

Family: Malvaceae 錦葵科 A.120 Coll. No.: LCY 93
Scientific name: *Grewia kentingensis* Y.H. Tseng, Chih Y. Chang & C.Y. Lin

Common name: 墾丁捕魚木
Locality and habitat description: 屏東縣 (Pingtung County) 恆春鎮 (Hengchun Township) 社頂梅花鹿復育區 (Sheding Formosan Sika Deer Restoration Area)

Habit: 匍匐灌木 (procumbent shrub)
Gps: 21°57'53.0"N 120°49'39.2"E
Altitude: 154m Date: 26 Jun. 2024
Collector: 林周逸 (C. Y. Lin)、吳緒恩 (S. E. Wu)、吳若瑜 (J. Y. Wu)、林宥任 (Y. J. Lin)、邱舒廷 (S. T. Chiu)
Identifier: 林周逸 (C. Y. Lin)
Note: 兩性花 (bisexual flowers)

Figure 8. Holotype of *Grewia kentingensis* Y.H.Tseng, Chih Y.Chang & C.Y.Lin, *C. Y. Lin et al. 93* (TCF).

Table 4. Specimens and coordinates used for the analysis of the conservation status.

Latitude / Longitude	Specimens
21°56'52.3"N, 120°50'18.3"E	*T. C. Huang & S. F. Huang 13542*; *K. C. Chang 4893*, *4894*; *C. Y. Chang & C. H. Liu 397*; *C. Y. Lin et al. 69*
21°56'31.1"N, 120°49'37.9"E	*P. F. Lu 16921*; *T. C. Hsu 1743*; *C. M. Wang et al. 15470*; *C. F. Chen 4697*; *C. Y. Chang 30*
21°57'53.0"N, 120°49'39.2"E	*Y. H. Yu 7968*; *C. Y. Chang et al. 3236*; *C. Y. Lin et al. 93*

***Grewia piscatorum* Hance in Ann. Sci. Nat., Bot., sér. 5, 5. 208. 1866.**
Figs 1B, 2B, 3B, 4, 9

Type. China • Fokien province: Lamyet island, 1860, *Swinhoe s.n.* in Herb. Hance 6527 (lectotype, designated here: BM [barcode BM000795018 as image!]; isolectotype, K [barcode K000686751 as image!]).

Notes. In the protologue, Hance (1866) cited a Swinhoe collection that he assigned one of his own collection numbers ("Herb. propr., no. 6527"). Hance (1866) did not unequivocally state that he based the name on a single specimen and since there are duplicates of this Hance number in BM (BM000795018) (Fig. 9) and K (K000686751), we designate a lectotype for *Grewia piscatorum*. The sheet selected is in Hance's herbarium (BM), and it is the duplicate with relatively more leaves and flowers.

Description. Erect to ascending shrubs, ca. 1–2 m tall; young branchlets scabrous, older branchlets nearly glabrous. Leaf blades elliptic, obovate, ovate to rhomboid-ovate, 0.7–7.8 cm long, 0.5–5.5 cm wide, apex acute, obtuse to rounded, base cuneate to obtuse, 3-nerved, margin serrulate to biserrulate, nearly glabrous, stellate hairs sparsely distributed along the veins on both surfaces; petioles 1.3–13.4 mm, sparsely stellate hairy; stipules linear, 2.4–5.1 mm long. Inflorescences leaf-opposed or rarely axillary, umbellate; peduncles 3.1–17.2 mm long, 6 to 15 flowers, pedicels 3.5–8.8 mm long; bracts linear, 1.4–2.6(–3.0) mm long. Flowers bisexual, functionally unisexual male or functionally unisexual female; bisexual flowers 14.8–18.5(–20.2) mm diam.; male flowers 14.2–18.8 mm diam.; female flowers 9.4–14.6 mm diam. Sepals (4)5(6), narrowly oblong to oblong, bisexual flowers 7.5–10.8 mm long, 2.4–4.1 mm wide, male flowers 7.3–8.4 mm long, 2.1–3.0 mm wide, female flowers 4.5–5.7 mm long, 1.4–2.0 mm wide, apex acute, abaxial surface yellowish green, stellate–pubescent, adaxial surface white, glabrous. Petals (4)5(6), oblong to ovate, apex rounded, bisexual flowers 2.2–3.3 mm long, 0.9–1.2 mm wide, male flowers 2.1–2.9 mm long, 0.9–1.2 mm wide, female flowers 1.5–2.5 mm long, 0.6–1.0 mm wide; nectaries present at the base of adaxial surface, 0.8–1.3 mm diam., surrounded by ciliate hairs. Androgynophore cylindrical, bisexual flowers 1.1–1.6 mm long; male flowers 1.1–1.5 mm long; female flowers 0.9–1.2 mm long, glabrous, ciliate hairs only at the apex. Ovary globose to oblate, pubescent, bisexual flowers 1.2–1.4 mm diam.; male flowers 1.2–1.5 mm diam.; female flowers 0.9–1.3 mm diam. Bisexual flowers with 103–118 stamens, filaments white, glabrous, 2.4–6.8 mm long, anthers dehiscing longitudinally; style 3.6–5.4 mm long, glabrous, stigma 4-lobed, each lobe dentate at apex. Male flowers with 70–88 stamens, filaments white, glabrous, 2.1–4.7 mm long, anthers dehiscing longitudinally; style 3.1–4.1 mm long, glabrous, stigma 4-lobed, each lobe dentate at apex. Female flowers with 58–102 stamens, filaments white, glabrous, 0.5–1.5 mm long, anthers white, always inde-

Figure 9. Lectotype of *Grewia piscatorum* Hance, *Swinhoe s.n.*in Herb. Hance 6527 (BM000795018).

hiscent; style 1.8–2.6 mm long, glabrous, stigma 4-lobed, each lobe dentate at apex. Fruits drupaceous, usually 4-lobed, fruit lobe 4.4–6.4 mm diam., globose, puberulent to nearly glabrous, red when mature.

Phenology. Flowering from May to September and fruiting from June to October.

Distribution and habitat. Distributed in Fujian Province and Hainan Province in China and in Taiwan on the coastal areas of Kinmen and Lienchiang Counties.

Palynology. Pollens grains are tricolporate, prolate, 42.8–47.8 × 27.4–31.0 μm. The exine is reticulate, with muri 0.4–0.7 μm wide and lumen size 1.1–4.0 μm. Perforations present in the lumen, 0.04–0.26 μm.

Specimens examined. China. Fujian Province • Fuzhou City, Tangyu, 24 May 1964, *T. H Chen 493* (AU) • Fuzhou City, Yemayu, 31 May 1964, *T. H Chen 515* (AU); Fuzhou City, Zhuyu, 17 May 1963, *T. H Chen 1561* (AU) • Xiamen City, Nanputuo, 20 Jul 1954, *J. C. Lin 3857* (AU). **Hainan Province** • Dongfang City, seacoast of Dingjiao village, 20 Aug 1936, *S. K. Lau 27727*, *27730* (IBSC); Sanya City, Xigu island, 3 Aug 2018, *H. L. Hou 92038* (AU). **Taiwan. Kinmen County** • Brave Fortress, 24 Jun 2017, *S. W. Chung 12988* (TAIF) • Caicuo Trail, 2 Jun 2019, *C. T. Lu et al.* 2515 (TNM) • Doumen to Taiwu Mountain, 22 Jul 2007, *C. M. Wang 10497* (TNM) • Fengshang, 20 May 2009, *J. S. Shiu & Y. L. Hsueh H315* (CHIA) • General's Spring, 28 May 2023, *C. Y. Lin 22* (TCF) • Jiugong Pier, 25 May 2002, *C. M. Wang 5611* (TNM) • Ibid., 7 Sep 2021, *C. Y. Chang et al. 3539* (TNM)Ibid., 28 May 2023, *C. Y. Lin 17* (TCF) • Jiugong Tunnel to shore-line road, 28 May 2023, *C. Y. Lin 20* (TCF) • Liaoluo, 22 May 2017, *T. C. Hsu 9131* (TAIF) • L36 Fortress, 25 May 2024, *C. Y. Lin et al. 85* (TCF) • Mashan Observation Post, 26 Aug 2015, *C. Y. Chang et al.* 724 (TCF, TNM) • Ibid., 29 May 2023, *C. Y. Lin 24* (TCF) • Paichushan to Huotou, 10 Jun 1999, *S. T. Chiu 5386* (TNM) • Qilinshan, 25 May 2024, *C. Y. Lin et al. 86* (TCF) • Qingyuan Lake, 9 Aug 2002, *I. H. Chiang 120* (TAI) • Shuitou Pier, 28 May 2023, *C. Y. Lin 21* (TCF) • Taiwu Mountain, 27 Jul 2005, *K. C. Chen s.n.* (TAIF) • Ibid., 15 Jun 2006, *C. H. Chen 7283* (TNM) • Ibid., 4 Jun 2016, *S. W. Chung 12534* (TAIF) • Taiwu nursery, 22 Jul 2007, *C. M. Wang 10519* (TNM) • Tashan, 14–17 May 2010, *F. Y. Lu et al. H2794* (CHIA) • Tzuhu, 25 Jul 2005, *K. C. Chen s.n.* (TAIF) • Tzuti, 25 Jul 2005, *K. C. Chen s.n.* (TAIF) • Wuhu Mountain, 13–16 Jul 2009, *F. Y. Lu et al. 1015* (CHIA) • Xiyuan beach to Chengkung Fortress, 29 May 2023, *C. Y. Lin 23* (TCF) • Zhaishan Tunnel, 25 May 2024, *C. Y. Lin 80* (TCF). **Lienchiang County** • Beihai Tunnel, 19 Jul 2008, *C. M. Wang 12180* (TNM) • Chengkungshan, 27 Aug 2007, *T. W. Hsu 13020* (TAIE) • Chiukueishan, 27 Aug 2001, *Y. L. Huang et al. 816* (TAI) • Daping to lighthouse, 30 May 1994, *T. Y. Liu & H. L. Ho 653* (TNM) • Dapu Inscription, 9 Sep 2007, *C. M. Wang & C. P. Lu 10690* (TNM) • Fuzheng, 30 Jul 1999, *S. H. Su 624* (TAI) • Jinsha, 1 Jul 1999, *S. H. Su 352* (TAI) • Dawo Mountain, 16 Sept 2014, *S. W. Chung 11782* (TAIF) • Kunqiu Trail, 17 Oct 2017, *C. Y. Chang 1473* (TCF, TNM) • Leishan, 29 Aug 2007, *T. W. Hsu 13079* (TAIE).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: YHT, CYC, CMW, CYL. Data curation: CYL. Formal analysis: CYL. Funding acquisition: YHT. Investigation: CYC, CYL. Methodology: CYL, CYC. Project administration: YHT, CYL. Resources: CMW, CYL, CYC, HYT. Software: HYT. Supervision: YHT, HYT. Validation: CMW, CYL. Visualization: CYL. Writing – original draft: CYL. Writing – review and editing: CYC, CMW, YHT, HYT, CYL.

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Data availability

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

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PhytoKeys

PhytoKeys 253: 177–187 (2025)
DOI: 10.3897/phytokeys.253.147019

Research Article

The rediscovery of *Ohwia luteola* (Fabaceae, Papilionoideae) after 50 years and comparative analysis of *Ohwia* species in plastid genome sequence

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Abstract

Ohwia luteola (H. Ohashi & T. Nemoto) H. Ohashi is only known from one collection in Yunnan Province, China. It has not been recollected since its last collection in 1972. Here, we report the rediscovery of the species that means the first new record in Hunan Province, China. Based on fresh material, we present a revised morphological description of *O. luteola* and conducted sequencing and assembly of the plastid genome. Morphologically, *O. luteola* is similar to *O. caudata*, but the former can be easily distinguished by leaflets length/width ratio ranging from 2.5 to 3.6, leaflets apex acute (with an angle of 50°–80°), terminal inflorescences, wings distinctly auriculate at base and inner side indistinctly rugose, and hilum center not over 3/5 length of seed. Molecular phylogenetic analysis confirmed *O. luteola* is sister to *O. caudata*.

Key words: Desmodieae, morphology, *Ohwia luteola*, phylogeny, plastome

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Introduction

Fabaceae (or Leguminosae), the third largest family of angiosperm, comprises more than 19,500 species in ca. 765 genera, 36 tribes, and 6 currently recognized subfamilies (Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae, and Papilionoideae) (Azani et al. 2017). The legume plants have highly diversified in growth forms including trees, shrubs or herbs, sometimes climbing or decumbent, and ca. 88% of legume species have the ability to establish associations with nitrogen-fixing bacteria (Sprent et al. 2017; Zhang et al. 2020). Many legume species are economically and ecologically important (Yahara et al. 2013).

Ohwia H. Ohashi, is a small genus within the tribe Desmodieae of subfamily Papilionoideae containing two species, i.e., *O. luteola* (H.Ohashi & T.Nemoto) H. Ohashi and *O. caudata* (Thunb.) Ohashi (Huang and Ohashi 2010). Members of this genus are characterized by their shrub or subshrub growth habit, featuring pinnately trifoliolate leaves, persistent stipules, and winged petioles. *Ohwia luteola* is endemic to Yunnan Province (China) and characterized by

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corolla pale yellow, while *O. caudata* widely distributed in East Asia, and corolla greenish or yellowish white (Huang and Ohashi 2010). *Ohwia luteola* was described in 1998 based on a single number collection from northeastern Yunnan Province (China) in 1972 (Ohashi and Nemoto 1998), but additional specimens of *O. luteola* have not been recorded for more than 50 years.

In a recent exploration of Zhangjiajie city (Hunan Province, China), we collected an unknown *Ohwia* species with similar morphological characteristics to *O. caudata*. However, they have smaller leaflets with obtuse apex, which are obviously different from *O. caudata*. After having a determination of the material by Hiroyoshi Ohashi, one of the original authors of *Ohwia luteola* as *Desmodium luteolum* H.Ohashi & T.Nemoto, we made a morphological comparison of our material with the images of the type of *O. luteola* (KUN) and habitat description and confirmed that they belong to *O. luteola*. Therefore, the purpose of our research described here was to provide an insight into the taxonomic status of the *O. luteola* by comparing morphological features and analyzing the plastome.

Material and methods

Morphology observation and measurement

In total, 9 individuals of the *O. luteola* and 6 individuals of *O. caudata* were examined and herbarium voucher specimens deposited in the herbariums of the Department of Biology, Jishou University (JIU) and the Kunming Institute of Botany (KUN). Fourteen morphological characters were selected for the morphometric analysis. The characters include terminal leaflet length; terminal leaflet width; lateral leaflet length; lateral leaflet width; petiole width; terminal leaflet petiole length; lateral leaflet petiole length; number of inflorescences per branch; number of flower nodes per inflorescence; flower stipe length; wing base (1-slightly auriculate, 2-distinctly auriculate); terminal leaflet length/width ratio; lateral leaflet length/width ratio. We performed a principal component analysis (PCA) using R v.4.0.2 (R Core Team 2020) to project and visualize trends in morphological variability across our samples.

DNA extraction and sequencing

Total genomic DNA was extracted from silica gel-dried materials and herbarium material (three individuals of *O. luteola* and one individual of *O. caudata*) using the Plant Genomic DNA Kit (TianGen Biotech, Beijing, China) following the manufacturer's protocol. DNA libraries were constructed with paired-end reads (PE150) were generated using an Illumina NovaSeq 6000 platform. Library construction and sequencing were carried out at Novogene Co., Ltd. in Beijing, China. Approximate 4 Gb of raw-reads were obtained for each sample.

Plastid genome assembly, annotation, and comparison

Plastomes were assembled using GetOrganelle (Jin et al. 2020) based on the clean reads. The plastome of *O. caudata* (MG867572) was selected as a reference (Jin et al. 2019). We detected the boundaries of large single-copy (LSC), small single-copy (SSC), and two inverted repeats (IRs) using RepeatFinder v.1.0.1 (Volfovsky et al. 2001). The final annotation was conducted in GENEIOUS v. 11.1.4 (Kearse et al. 2012). A circular plastome map was drawn in OGDraw v.1.3.1 (Greiner et al. 2019). SSRs are tandem repeats of one to six nucleotide long DNA motifs with high variability, multi-allelic nature, codominant inheritance, repeatability, relative abundance, and other traits that hold great promise in evolutionary and population genetics studies. The MISA program (http://pgrc.ipk-gatersleben.de/misa/) was used to identify the SSR, with a minimum number of repeat units of 10, 5, 4, 3, 3, and 3 for mono-, di-, tri-, tetra-, penta-, and hexa-nucleotides, respectively.

Phylogenetic analyses

We failed to obtain a complete plastid genome of the sample of '*O. caudata* 928' (isotype) because the DNA of this sample was extracted from herbarium material collected over 50 years ago. To determine the phylogenetic position of *O. caudata*, a total of 34 plastid CDS were extracted using GENEIOUS v.11.1.4. The outgroups and other Leguminosae species were selected based on the work of Jin et al. (2019). Voucher information and GenBank accession numbers were provided in Appendix 1. Sequences were aligned with MAFFT (Katoh and Standley 2013). The concatenated plastid CDS dataset is deposited in DRYAD (https://doi.org/10.5061/dryad.4qrfj6qn5). Maximum likelihood (ML) analysis was performed using RAxML-HPC v.8.2.4 (Stamatakis 2014), with the GTR + I + G model and run for 1000 bootstrap iterations. The phylogenetic trees were visualized using FigTree v.1.4.2 (Rambaut 2014).

Results and discussion

The aligned plastid CDS matrix contained 34,582 sites. The ML tree is shown in Fig. 1. Our results showed that *O. luteola* from Hunan Province and isotype from Yunnan Province were clustered together and strongly supported *O. luteola* sister to *O. caudata* (BS = 100%, Fig. 1). This sister relationship is also supported by morphological characters. Morphological synapomorphies of *O. luteola* and *O. caudata* included pinnately 3-foliolate, stipules persistent, calyx campanulate and 4-lobed (Huang and Ohashi 2010).

Morphologically, most leaflets of *O. caudata* are lanceolate or oblong (Fig. 2D) (Ohashi 2005), terminal leaflets have a length/width ratio of up to 6.7, and leaflets apex acuminate. In contrast, *O. luteola* has oblong-elliptic leaflets, the terminal leaflet length/width ratio ranges from 2.9 to 3.6, and the leaflets apex is acute (Fig. 2H). The wings of *O. luteola* are distinctly auriculate at the base, and the inner side is indistinctly rugose (Fig. 2E) (vs. wings slightly auriculate at the base and inner side distinctly rugose). Also, it differs by its hilum at the center of the axis and not over 3/5 length of seeds (Fig. 2G) (vs. hilum off-center and over 1/2 length of seeds). More importantly, *O. luteola* grows on limestone along the river, and *O. caudata* usually grows under the forest. It is noteworthy that the corolla of *O. luteola* is described as pale yellow (Ohashi and Nemoto 1998), and the flowers observed from fresh materials collected in Hunan province are greenish-white to yellowish-white. Additionally, the flowers of the specimen turn yellow after drying. Morphological traits from 15 specimens were explored using PCA (Fig. 3). The first two principal components identified by PCA

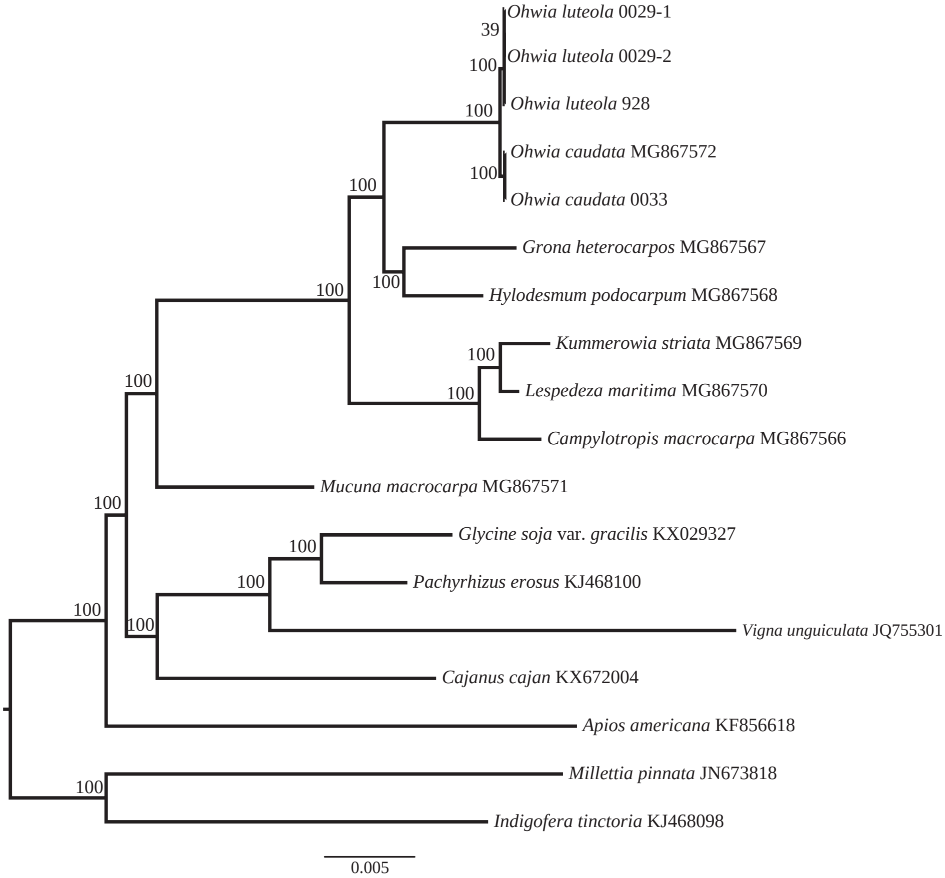

Figure 1. Maximum likelihood (ML) analysis based on the 34 plastid protein-coding genes. ML bootstrap (BS) values are given above the branches.

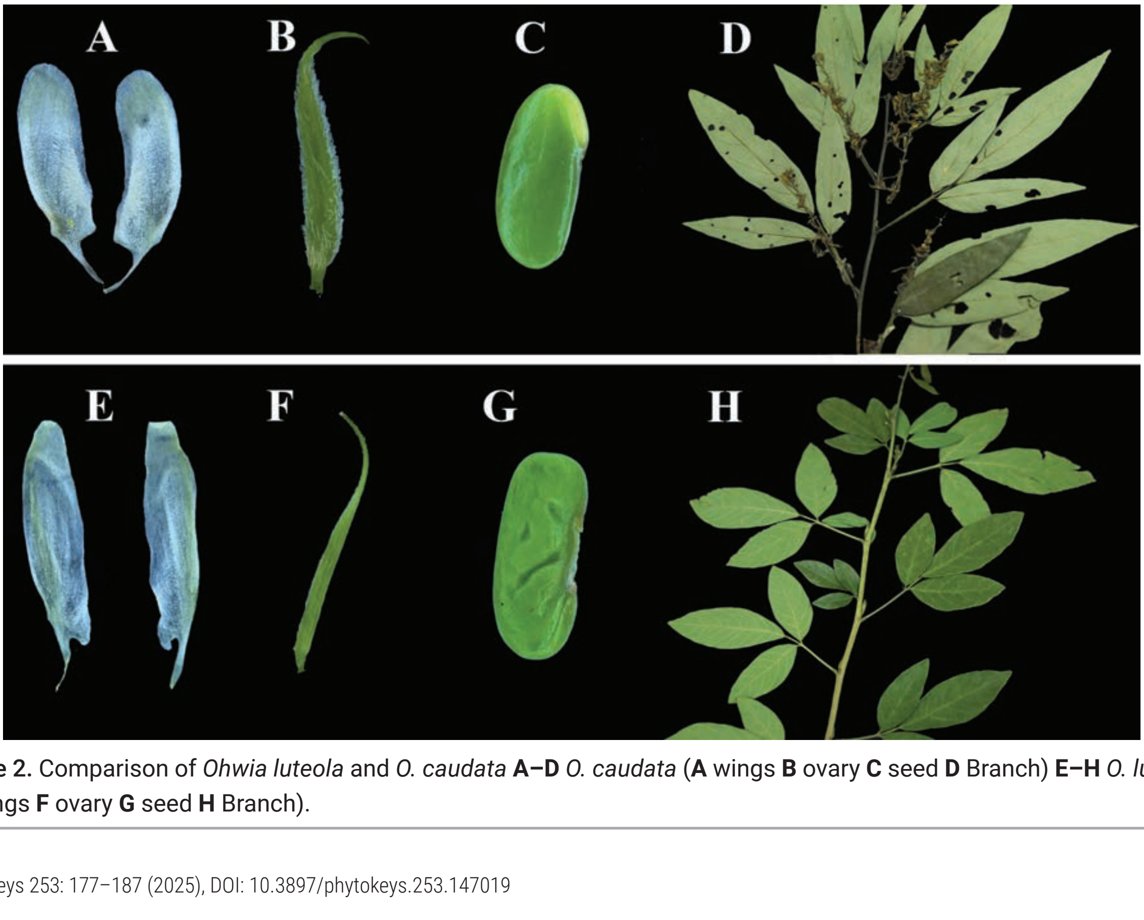

Figure 2. Comparison of *Ohwia luteola* and *O. caudata* **A–D** *O. caudata* (**A** wings **B** ovary **C** seed **D** Branch) **E–H** *O. luteola* (**E** wings **F** ovary **G** seed **H** Branch).

accounted for 66.08% of the variation across all characters. The PCA results showed that individuals of *O. luteola* and *O. caudata* formed distinct clusters.

We sequenced, assembled, and annotated three plastomes representing *O. luteola* (two individuals) and *O. caudata* (one individuals). The features of these plastomes are summarized in Table 1. Plastome map for the *O. luteola* is shown in Fig. 4. Consistent with previous studies in legumes, the plastomes were highly conserved, with no structural variations or content rearrangements (Jin et al., 2019). The plastome sizes of the *Ohwia* species ranged from 150,217 bp for *O. luteola* to 150,250 bp for *O. caudata*. All the two species presented a classical quadripartite structure, a LSC, an SSC, and two IRs. The length of the LSC region ranged from 83,227 bp to 83,242 bp. The SSC region varied from 18,442 bp to 18,480 bp in length, and that of the IR regions ranged from 24,264 bp to 24,274 bp (Table 1). A total of 128 genes were identified, including 83 protein-coding genes, 37 transfer RNA (tRNA) genes, and 8 ribosomal RNA (rRNA) genes. The GC content of the two species was identical in the whole chloroplast genome (35.1%), with the GC content in the IR regions (42.0%) noticeably higher than that in the SSC (28.3%) and LSC (32.6%) regions in each chloroplast genome. Our study identified a total of 384 SSRs in the two *Ohwia* species (Fig. 5). The number of SSRs in *Ohwia caudata* is 95, while the number of simple repeats in *O. luteola* is 97. Among them, the A/T mononucleotide SSRs are the most abundant.

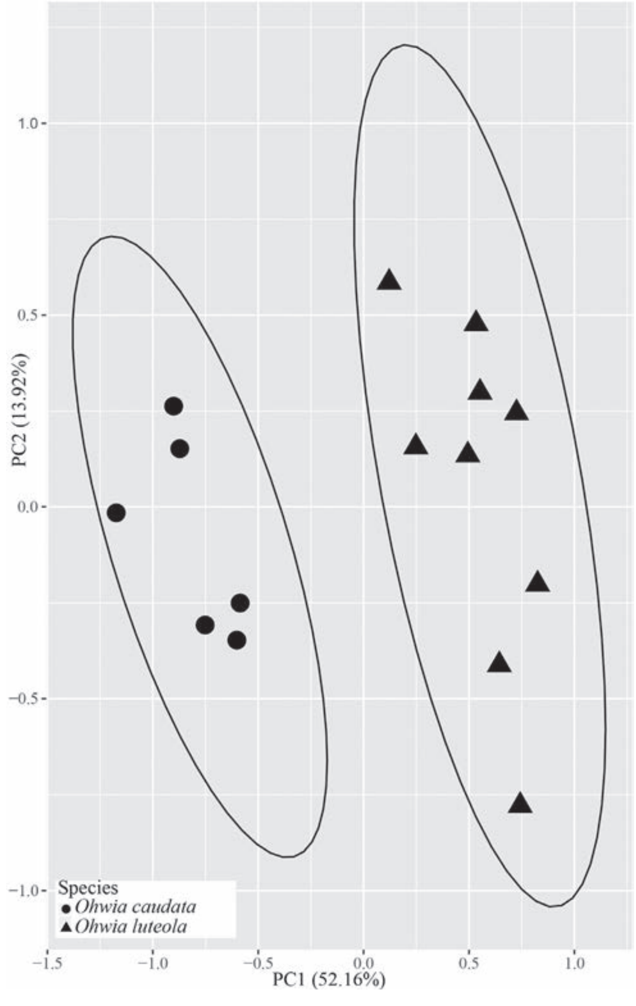

Figure 3. Principal components plots based on fourteen morphological characters.

Table 1. Plastome characteristics of *Ohwia luteola* and *O. caudata*.

Species	Total size (bp)	Length of LSC (bp)	Length of SSC (bp)	Length of IRs (bp)	GC content (%)	No. of genes
O. luteola 0029-1	150,217	83,227	18,442	24,274	35.1%	128
O. luteola 0029-2	150,217	83,227	18,442	24,274	35.1%	128
O. caudata 0033	150,250	83,242	18,480	24,264	35.1%	128
O. caudata	150,249	83,241	18,480	24,264	35.1%	128

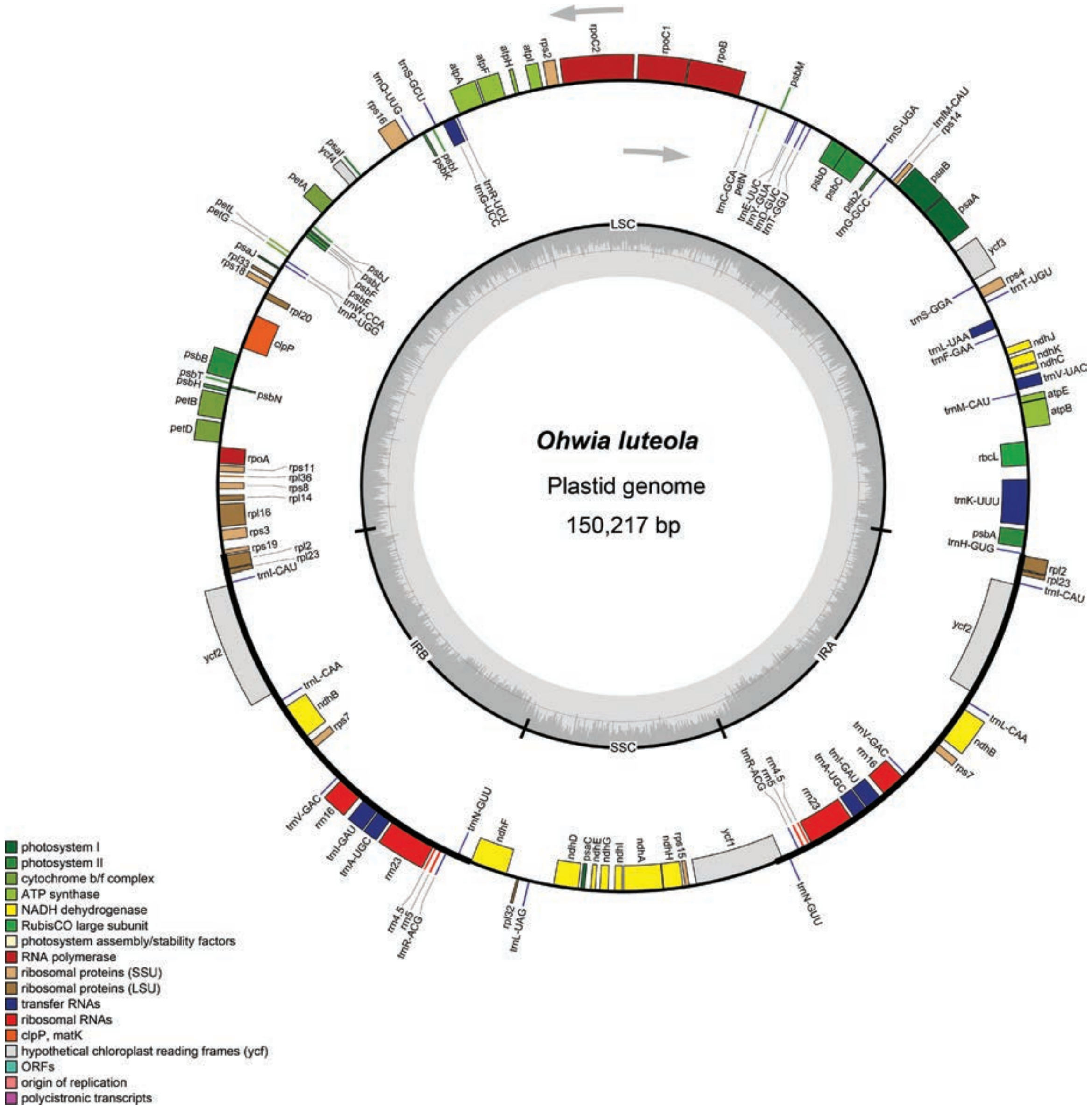

Figure 4. Plastid genome map of *Ohwia luteola*.

Taxonomy

Ohwia luteola **(H. Ohashi & T. Nemoto) H. Ohashi**

Fig. 6

Diagnosis. *Ohwia luteola* resembles *O. caudata* but differs from the latter by having terminal leaflets length/width ratio rang from 2.9 to 3.6 (vs. terminal leaflets length/width ratio rang from 4.2 to 6.7), leaflets apex acute (vs. acuminate)

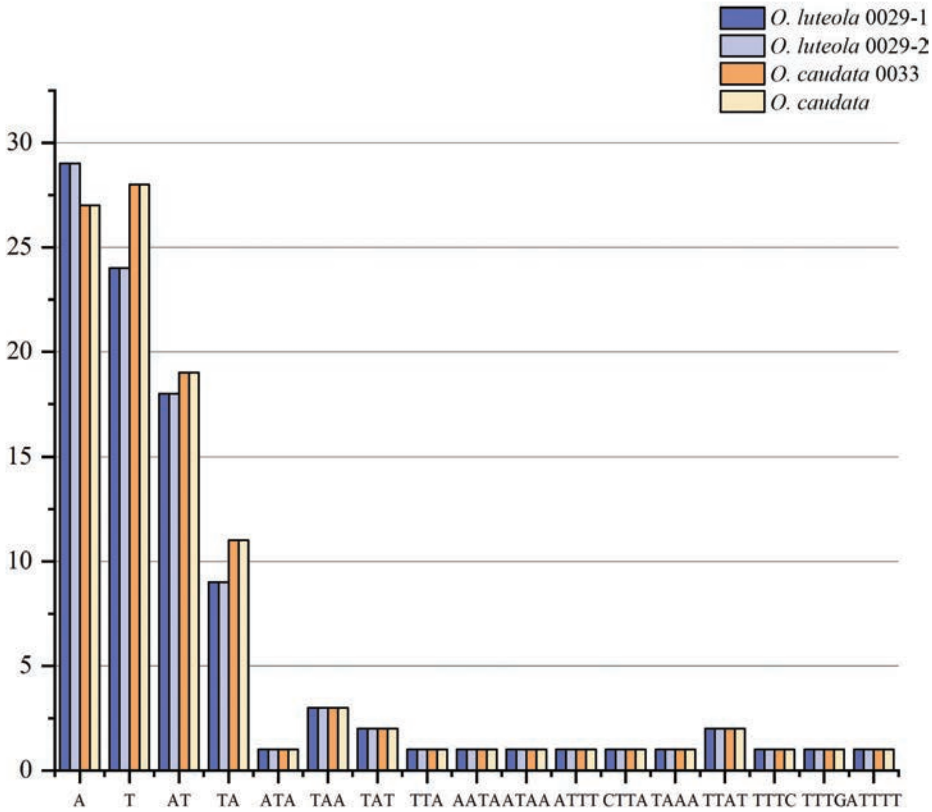

Figure 5. Specific forms of SSRs in 4 genomes from *Ohwia*.

terminal inflorescences (vs. terminal and axillary), wings with distinctly auriculate at base, inner side indistinctly rugose (vs. wings with slightly auriculate at base, inner side distinctly rugose), hilum center, not over 3/5 length of seed (vs. hilum off-center, over 1/2 length of seed).

New record. Populations of *Ohwia luteola* are known from Xixiping Street, Yaping village, and Bamaoxi village of Zhangjiajie. It is growing on limestone along the Lishui River. The companion species mainly including *Adina rubella* Hance, *Distylium buxifolium* (Hance) Merr., and *Cornus quinquenervis* Franch.

Specimens examined. CHINA • Hunan: Zhangjiajie City, Yongding District, Sanjiaguan Township, Yaping village, under Zhanghua Lishui Large Bridge, on limestone areas along Lishui River, alt. 218 m, 29.111375°N, 110.258679°E, 31 Aug. 2023, *M. H. Zhang et al. 0029* (JIU); • Yunnan: Jinping County, Laomeng River, alt. 750 m, 20 May 1974, *Lüchun Exped. 944* (KUN 0608532); • Yiliang County, Niujie, alt. 450 m, 23 Sep. 1972, *Northeast Yunnan Exped. 928* (KUN 0608538).

Revised description. Shrubs, erect, 1–2 m tall, main stem ca. 1 cm in diam at base, much branched. Leaves 3-foliolate, thickly papery to subleathery, both surfaces pilose and more densely hairy on raised veins, margin entire. Petiole 2–3 cm long, with narrowly winged on both, 0.2–0.3 mm wide. Terminal leaflet oblong-elliptic, widest near the middle part, 4–7.1 × 1.5–2.4 cm, principal veins 10–14 pairs, reaching the leaf margin, apex acute, base cuneate, small petiole 0.8–1.2 cm long, pubescent. Lateral leaflets smaller, 3.7–6.4 × 1.1–1.8 cm, small stipe 0.2–0.3 cm long, widest near the middle part, principal veins 6–12 pairs, reaching the leaf margin, apex acute, base cuneate, small petioles 0.2–0.3 cm long, densely pubescent. Stipules 3–7 mm long, ca. 1.0 mm wide at the base, densely pubescent, persistent. Inflorescences terminal, 7–19 cm long, rachis

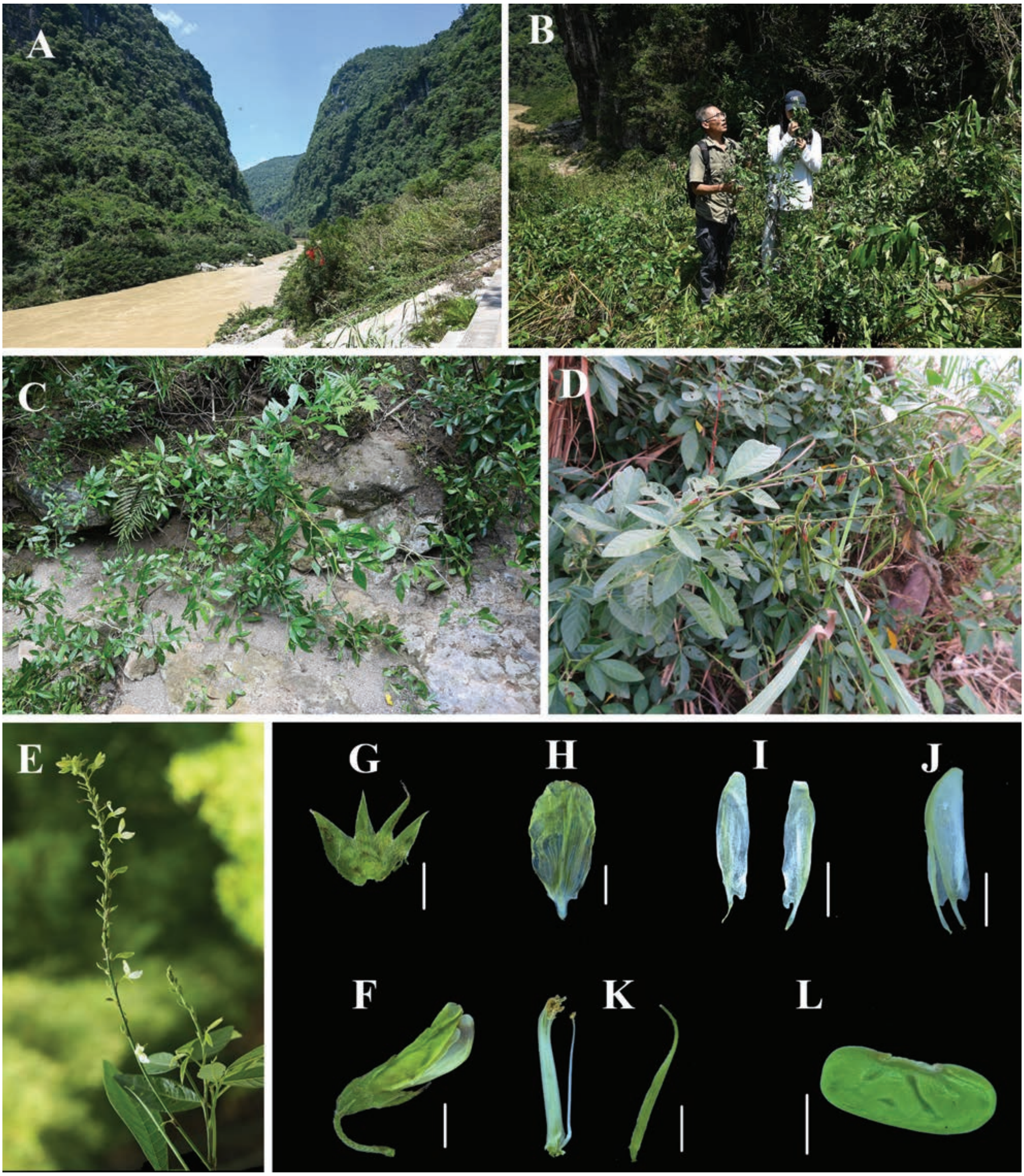

Figure 6. *Ohwia luteola* **A** habitat **B, C** habit **D** fruits **E** inflorescence **F** flower **G** calyx **H** standard **I** wings **J** keel-petal **K** ovary and stamens **L** seed.

densely pubescent intermixed with minute uncinate and appressed or spreading longer hairs, 2–4-flowered at each node; bracts subulate, ca. 0.3 cm long. Pedicels 0.4–0.6 cm long, densely pubescent. Calyx campanulate, 0.8–1.2 cm long, outside densely appressed pubescent, 4-lobed, lobes united for ca. 1/2 length, lobes ca. 0.5 cm long, longest one linear-lanceolate. Corolla greenish-white or yellowish-white, ca. 1.5 cm long, distinctly veined; standard elliptic, 0.8–1.7 × 0.5–1.0 cm, claw ca. 2.5 mm, slightly auriculate at base, apex slightly retuse; wings shorter than keel, 1.3–1.6 cm long, apex obtuse, lamina narrowly elliptic, distinctly auriculate at base, claw ca. 3 mm, keel 0.8–1.8 cm long, apex rounded, slightly auriculate at base, claw ca. 3 mm. Vexillary stamen slightly connate at base from other 9, ca. 1.6 cm long, puberulent at upper part; remaining 9 stamens connate for 4/5 or more of length, puberulent at upper part. Style curved upward, ovary densely ap-pressed pilose on both sutures. Disk present at base of pistil. Legume linear, flat, 3.5–7 cm long, stipe ca. 5 mm long, 3–6-jointed; articles nearly rectangle, 1–1.3 × 0.5–0.7 cm, with dense, transparent to brown, uncinate hairs. Seeds compressed, reniform, ca. 12 × 5 mm; hilum center, not over 3/5 length of seed. Flowering from July to early September; fruiting from September to November.

Conservation status. During our field investigations in 2022 and 2024, many populations of *O. luteola* were found in Zhangjiajie. The number of individuals of each population ranges from tens to hundreds. In addition, it is distributed along the river. We believe that it should have a much wider distribution than is currently known. Due to its wide distribution range and large population size, *O. luteola* is here recommended as Least Concern (LC) (IUCN 2022).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Funding acquisition: DGZ, MHZ, QZ. Methodology: LP, YJZ, YYX, XL, CYX. Project administration: MHZ, QZ. Resources: DGZ, WQQ. Writing – original draft: LP, YJZ, YYX, MHZ. Writing – review and editing: ZLN, MHZ.

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Data availability

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

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Appendix 1

Table A1. Species sequence information downloaded from the GenBank.

Taxon	Locality	Voucher information	GenBank number
Apios americana			KF856618
Cajanus cajan			KX672004
Campylotropis macrocarpa	Mt. Hwanghak, Chilgok-gun, Gyeongsangbuk-do, Korea	109901	MG867566
Desmodium heterocarpon	Sallokdoro, Seogwipo-si, Jeju-do, Korea	98555	MG867567
Glycine gracilis			KX029327
Hylodesmum podocarpum	Mt. Geomdan, Gwangju-si, Gyeonggi-do, Korea	169505	MG867568
Kummerowia striata	Mt. Geomdan, Gwangju-si, Gyeonggi-do, Korea	DP167901	MG867569
Lespedeza maritima	Peak Gyeokja, Bogil-myeon, Wando-gun, Jeollanam-do, Korea	DP149121	MG867570
Mucuna macrocarpa	Kunigami, Okinawa, Japan	15001	MG867571
Ohwia caudata	Jeju-do, Korea	NIBR378625	MG867572
Ohwia caudata	Zhangjiajie, Hunan	M.H. Zhang et al., 0033 (JIU)	*
Ohwia luteola	Zhangjiajie, Hunan	M.H. Zhang et al., 0029-1 (JIU)	*
Ohwia luteola	Zhangjiajie, Hunan	M.H. Zhang et al., 0029-2 (JIU)	*
Ohwia luteola	Yiliang County, Yunnan	Northeast Yunnan Exped. 928 (KUN).	#
Pachyrhizus erosus			KJ468100
Vigna unguiculata			JQ755301
Outgroups			
Indigofera tinctoria			KJ468098
Millettia pinnata			JN673818

An asterisk (*) indicates newly generated plastomes; a hashtag (#) indicates plastid genome assembly failed and extracted protein-coding genes can be obtained in DRYAD (https://doi.org/10.5061/dryad.4qrfj6qn5).

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Research Article

Rorippa daguanensis (Brassicaceae), a new species from eastern China

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Abstract

Rorippa daguanensis W.Zhang & K.Zhao (Brassicaceae), a new species from Anhui and Hubei Provinces of eastern China, is described. Its floral morphology resembles *R. dubia*, with its fruit morphology similar to *R. cantoniensis*. However, it can be readily distinguished from *R. dubia* by its inconspicuous stems, oval silicle and from *R. cantoniensis* by the absence of petals and bracts on its flowers. The complete plastid genome of this new species is 155,594 bp in length. Phylogenetic analyses, based on whole plastid genome sequences of *Rorippa* species, revealed that *R. daguanensis* is sister to *R. cantoniensis*.

Key words: Morphology, new species, phylogenomics, *Rorippa*, taxonomy

Introduction

Brassicaceae is one of the largest angiosperm families, encompassing approximately 340 genera and more than 4140 species (İlçim 2008; Al-Shehbaz 2015; German et al. 2023). The genus *Rorippa* Scop. belongs to the Brassicaceae family, comprising approximately 86 species (Zheng et al. 2021; Han et al. 2024). These species are primarily distributed in the Northern Hemisphere and are found on every continent, except Antarctica (Stuckey 1972; Han et al. 2024; Ren et al. 2024).

According to the Flora of China, nine *Rorippa* species were recognised in China (Zhou et al. 2001). However, recent studies have documented new species and expanded distribution records for Chinese *Rorippa* (Zhang et al. 2009; Zheng et al. 2021). Currently, 11 *Rorippa* species are known to occur in China. The majority of these species are primarily found in subtropical lowland areas. Notably, *Rorippa elata* and *Rorippa hengduanshanensis* are exceptions, being endemic to high-altitude regions of the Hengduan Mountains (HDM) (Zhou et al. 2001; Zheng et al. 2021).

During a field investigation in Qili Lake (QLH), Daguan District, Anqing City, Anhui Province, China, in April 2022 (Fig. 1), a novel *Rorippa* species was discovered. This unique plant exhibits inconspicuous stems, rosulate leaves, apetalous flowers lacking bracts and oval silicle. A comprehensive review of existing literature revealed no prior records of a *Rorippa* species possessing this combination of characteristics (Stuckey 1972; Al-Shehbaz 1991, 2015;

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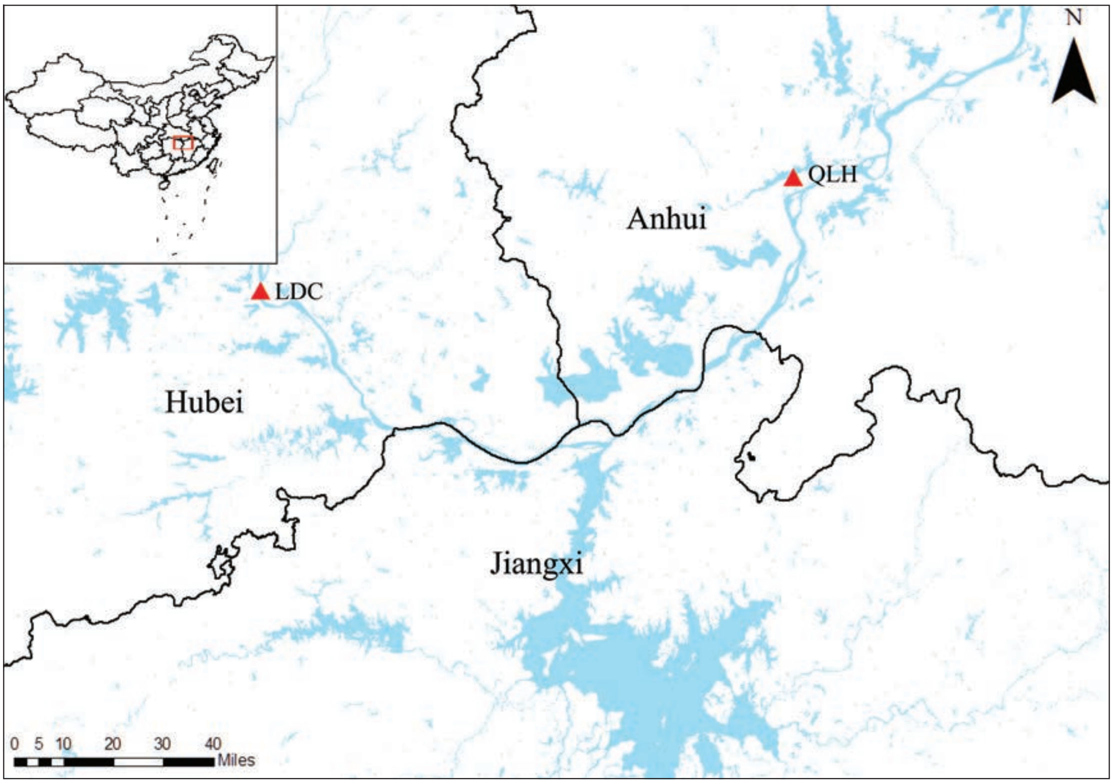


Figure 1. Known geographical distribution of *R. daguanensis* in China (red triangle).

Zhou et al. 2001; İlçim 2008). Careful morphological examination, coupled with molecular evidence, confirmed the discovery of a new species. This paper reports the results of this investigation and formally describes the new species as *Rorippa daguanensis* W.Zhang & K.Zhao.

Materials and methods

Sampling, morphological feature observation and comparison

Type specimens of the potential new species were collected in Qili Lake (QLH), (30°29'33.22"N, 116°54'31.27"E, alt. 7 m), Daguan District, Anqing City, Anhui Province (Fig. 1). They are deposited in the Herbarium of Anhui Normal University (ANUB). Morphological comparisons were performed between the new species and its closest relatives, *R. dubia* and *R. cantoniensis*. We examined both fresh materials and images from online resources, including the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/), the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and the Plant Photo Bank of China (PPBC, http://ppbc.iplant.cn/). A total of seven diagnostic characteristics were used for the comparisons (Table 1).

DNA extraction, chloroplast genome sequencing, assembly and annotation

Genomic DNA was extracted from silica gel-dried leaves using a modified CTAB protocol (Doyle and Doyle 1987). The DNA library construction and 150 bp paired-end sequencing were performed on the Illumina NovaSeq 6000

Table 1. Morphological features comparison between *R. daguanensis* sp. nov. and its morphologically similar species.

Characters	*R. daguanensis*	*R. dubia*	*R. cantoniensis*
Plant height	3–8 cm	10–30 cm	10–30 cm
Stems	Inconspicuous	Conspicuous	Conspicuous
Basal leaves	Basal leaves do not wither during the flowering period	Basal leaves wither during the flowering period	Basal leaves wither during the flowering period
Petals	Absent	Absent	Obovate to narrowly spatulate, 2–3 (–3.5) × 0.5–1 mm
Bracts	Absent	Absent	Present throughout the raceme
Fruits	Silicle oval 5.5–6.5 mm × 2.5–3.5 mm	Silique linear 2.5–4 cm × 0.7–0.9 mm	Silicle oblong 4.5–8.5 mm × 1.5–2.5 mm
Pericarps	Wrinkled	Smooth	Smooth

platform (Novogene, Tianjin, China), generating approximately 5 GB of raw data. The chloroplast genome of *R. daguanensis* was assembled using GetOrganelle v.1.7.5 (Jin et al. 2020), with *R. cantoniensis* chloroplast genome (ON892592) as a reference. The assembled chloroplast genome of *R. daguanensis* was annotated with Plastid Genome Annotator (PGA) (Qu et al. 2019). The CPGVIEW (www.1kmpg.cn/cpgview/) (Liu et al. 2023) was used to draw the circular map of the chloroplast genome. The sequences generated in this study were submitted to the NCBI database under accession numbers PQ159268 and OR992090.

Phylogenetic analyses

To determine the phylogenetic position of the new species within the *Rorippa* genus, we downloaded 19 accessions of cp genome sequences of *Rorippa* species from NCBI for phylogenetic analysis. All sequences were aligned with MAFFT v.7 (Katoh and Standley 2013) with the default settings. A Maximum Likelihood (ML) phylogenetic tree was constructed using MEGA version 11.0.13 (Tamura et al. 2021) with 1000 bootstrap replicates. *Nasturtium officinale* (MK045962) and *Cardamine hirsuta* (MK637681) were used as outgroup taxa. The GTR+G+I model was selected as the best-fit substitution model.

Results

Characteristics of the complete plastid genome

The chloroplast genome of *R. daguanensis* was 155,594 bp in length and exhibited a typical quadripartite structure (Fig. 2). It comprised a large single-copy region (LSC of 84,507 bp), a small single-copy region (SSC of 18,015 bp) and a pair of inverted repeat regions (IRs of 26,536 bp in each) (Fig. 2). The GC content of the whole chloroplast genome was 36.3%. The *R. daguanensis* chloroplast genome encoded 130 genes, including 85 protein-coding genes (PCGs), 37 transfer RNA genes (tRNAs) and eight ribosomal RNA genes (rRNAs).

Molecular phylogenetic relationship

Phylogenetic analysis of the whole plastid genome using Maximum Likelihood (ML) revealed the phylogenetic relationship of the new species and its congeners. The results placed the new species within the genus *Rorippa* and

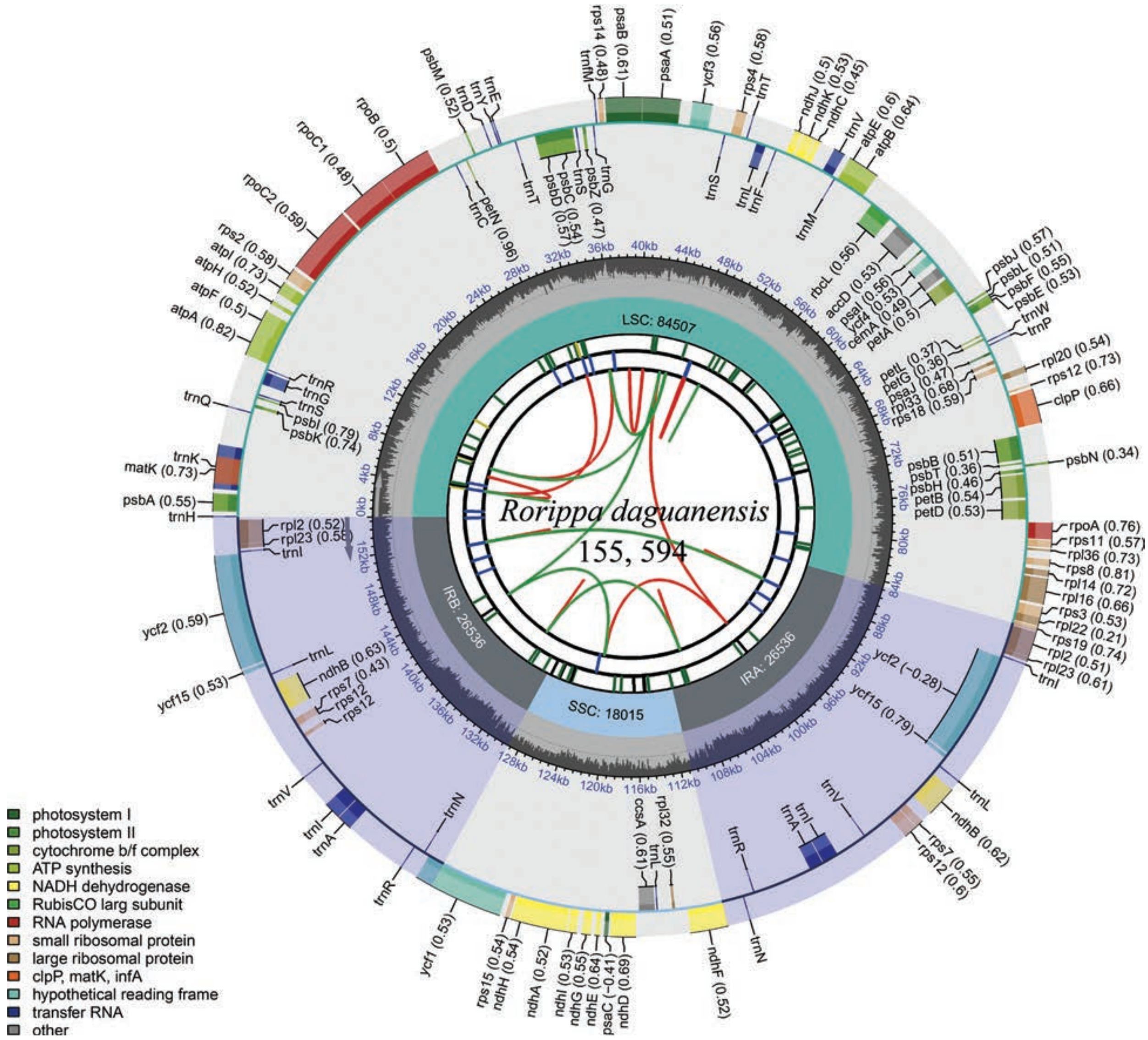


Figure 2. The complete chloroplast genome map of *R. daguanensis* sp. nov. The boxes of different sizes and colours on the outermost circle represent genes and their lengths. The inner and outer boxes of the outermost circle represent genes transcribed clockwise and counter-clockwise. The grey area in the middle circle represents the changes in GC content at different positions and the regions and lengths represented by the tetrad structure (LSC, SSC, IRa and IRb) are drawn in different colours on the inner circle.

the overall topology of *Rorippa* was congruent with previous studies (Nakayama et al. 2014, 2018; Zheng et al. 2021; Han et al. 2024). *R. daguanensis* was identified as the sister species of *R. cantoniensis*, with both species forming a well-supported monophyletic group (bootstrap support (BS) = 100%) (Fig. 3).

Morphological comparison

In morphology, this new species resembles *R. dubia* in floral characters and is similar to *R. cantoniensis* in fruit characters. However, it can be readily distinguished from *R. dubia* by its inconspicuous stems, oval silicle and from *R. cantoniensis* by the absence of petals and bracts on its flowers. Detailed morphological comparisons between the new species and its morphologically similar species are summarised in Table 1.

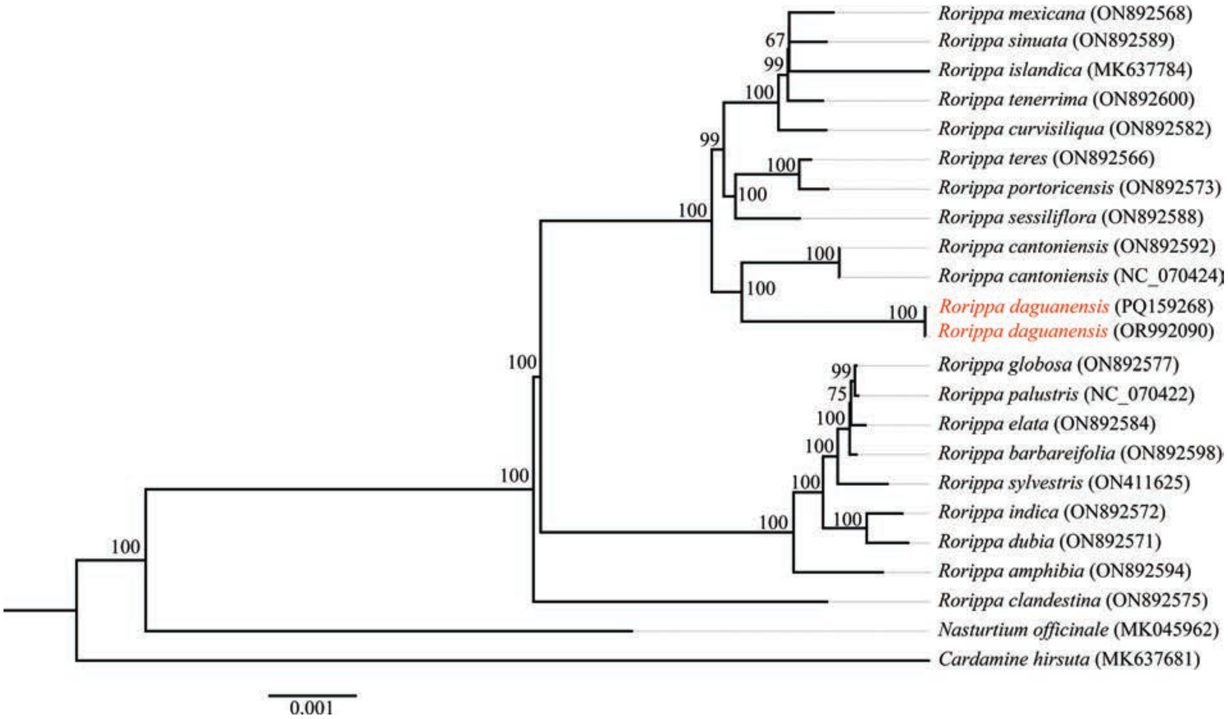


Figure 3. Phylogenetic placement of *R. daguanensis* using the Maximum Likelihood (ML) method, based on the whole plastid genome; bootstrap supports (BS) are shown on branches. NCBI accession numbers are shown in parentheses.

Taxonomic treatment

Rorippa daguanensis **W.Zhang & K.Zhao, sp. nov.**
urn:lsid:ipni.org:names:77358194-1
Figs 4, 5

Type. China • Anhui, Anqing City, Daguan District, Qili Lake, 30°29'33.22"N, 116°54'31.27"E, alt. 7 m, 18 April 2022, *Wei Zhang & Kai Zhao* ZW20220418 (holotype: ANUB!; isotypes: ANUB!; isotypes: CSH!) (Fig. 5).

Diagnosis. *Rorippa daguanensis* is similar to *R. dubia* and *R. cantoniensis*, but it can be readily distinguished from *R. dubia* by inconspicuous stems (vs. conspicuous stems), oval silicle 5.5–6.5 mm × 2.5–3.5 mm (vs. linear silique 2.5–4 cm × 0.7–0.9 mm) and can be differentiated from *R. cantoniensis* by the absence of petals and bracts on the flowers (vs. flowers with petals and bracts) and wrinkled pericarps (vs. smooth pericarps).

Description. Herbs annual, 3–8 cm tall, glabrous throughout. Stems mostly inconspicuous, with a few erect or decumbent. Leaves petiolate, 10–20, forming an open rosette, pinnatisect or almost bipinnatisect, 2–10 × 1–2 cm, lateral lobes 3–10 on each side of mid-vein, 2–10 × 1–4 mm, incised, dentate or entire. Racemes ebracteate. Fruiting pedicels stout, ascending, 1–4 mm. Sepals purple or green, ascending, oblong or subelliptic, 0.8–1.2 × 0.2–0.4 mm. Petals absent. Filaments 0.8–1.2 mm; anthers oblong, 0.1–0.3 mm. Ovules 100–200 per ovary. Fruit broadly or narrowly oblong, 5.5–6.5 × 2.5–3.5 mm; pericarp wrinkled, valves thin papery, veinless; style 1–1.4 mm. Seeds reddish-brown, ovate or oblate, foveolate, 0.2–0.4 × 0.2–0.4 mm.

Phenology. Flowering and fruiting from February to November.

Chinese name. Dà Guān Hān Cài (大观蔊菜).

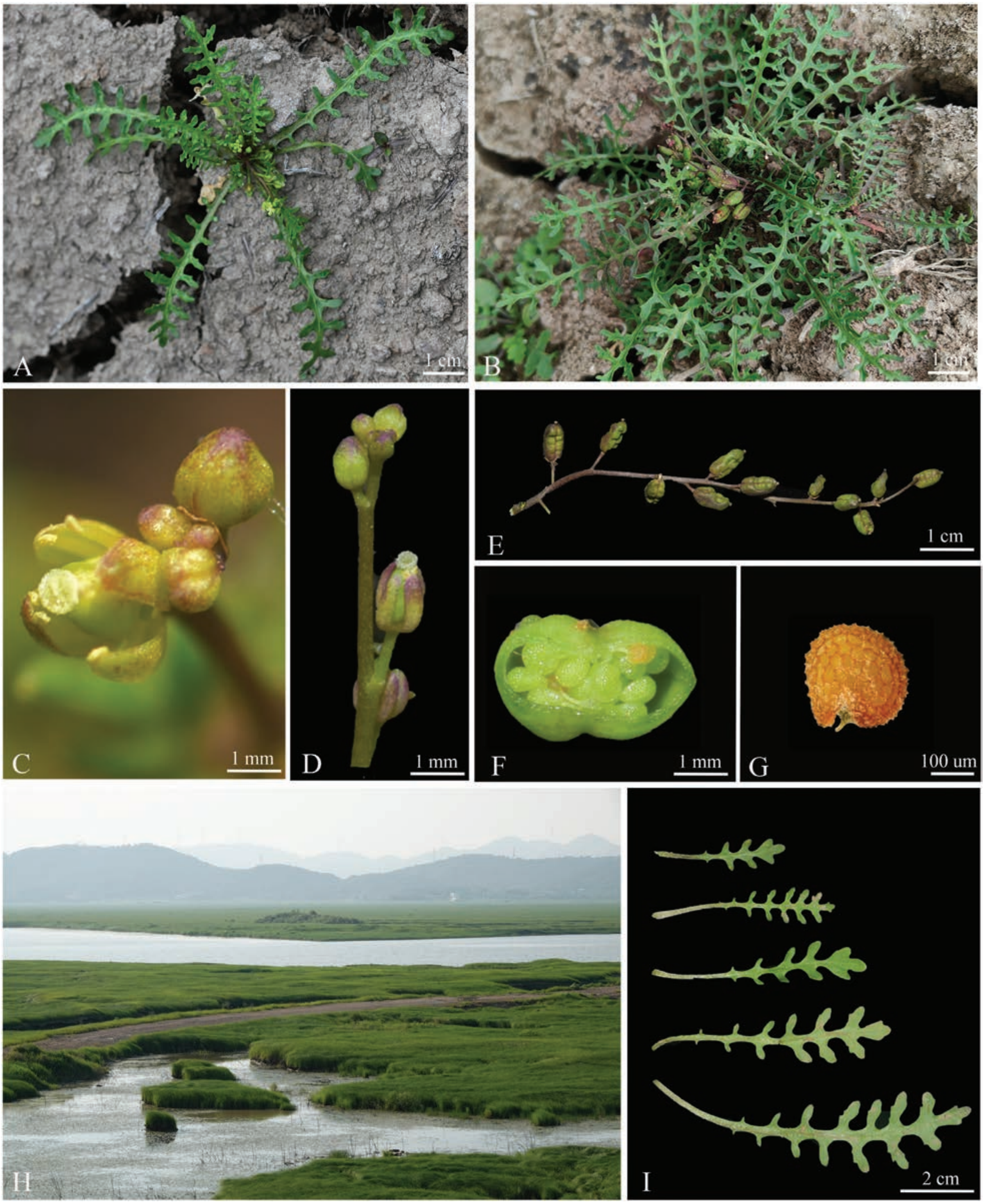
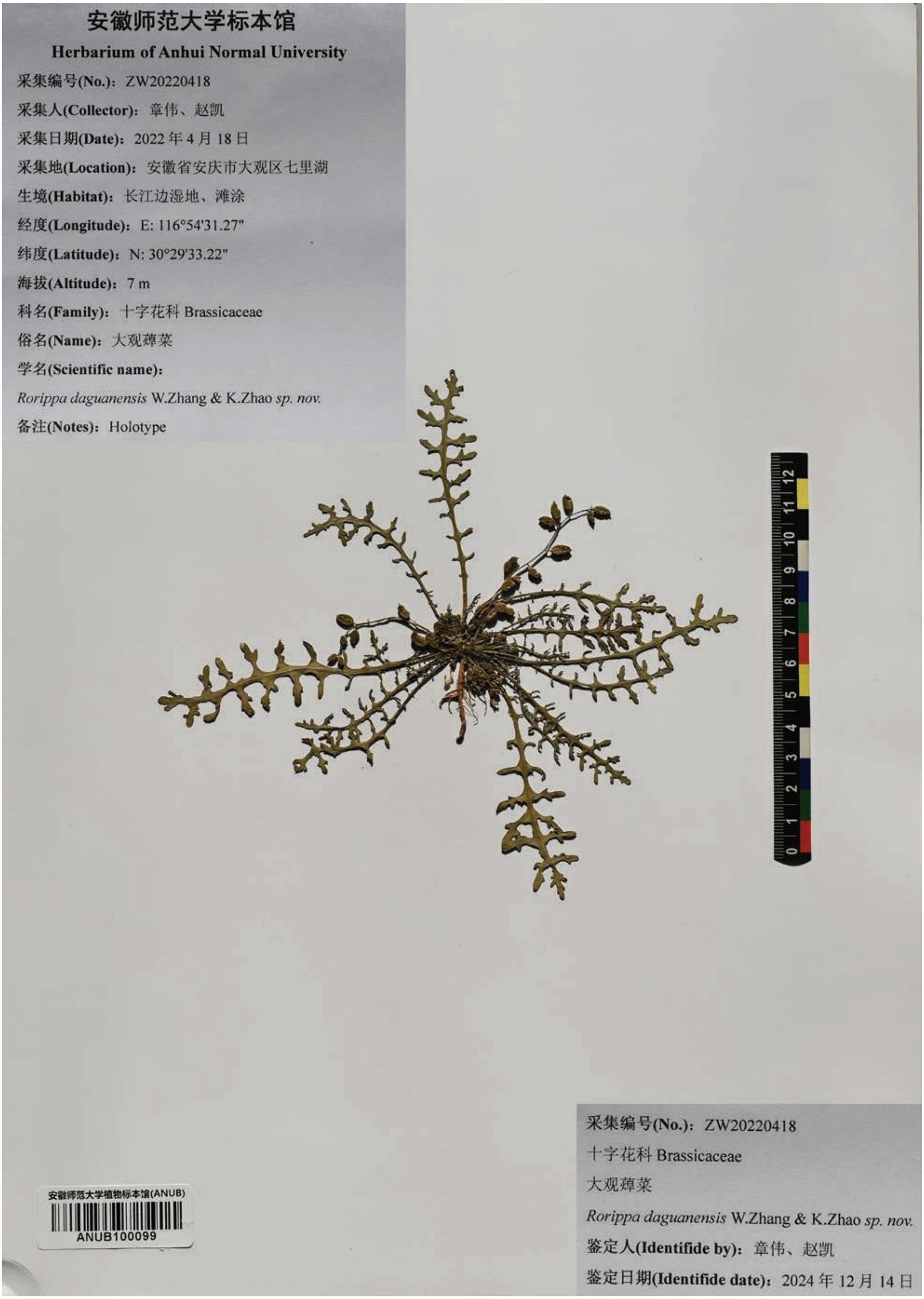


Figure 4. Morphological characters of *R. daguanensis* sp. nov. **A** plant in flowering **B** plant in fruiting **C** apetalous flower **D** inflorescence **E** infructescence **F** transection of fruits **G** seed **H** habitat **I** leaf morphology.

Etymology. The specific epithet ‘*daguanensis*’ refers to the type specimen collection locality, Daguan District, Anqing City, Anhui, China.

Distribution and ecology. Based on our field survey, *Rorippa daguanensis* is currently known only from two populations: one located in Qili Lake (QLH), Daguan District, Anqing City, Anhui Province and the other in Lidu Village



安徽师范大学标本馆
Herbarium of Anhui Normal University
采集编号(No.)： ZW20220418
采集人(Collector)： 章伟、赵凯
采集日期(Date)： 2022 年 4 月 18 日
采集地(Location)： 安徽省安庆市大观区七里湖
生境(Habitat)： 长江边湿地、滩涂
经度(Longitude)： E: 116°54'31.27"
纬度(Latitude)： N: 30°29'33.22"
海拔(Altitude)： 7 m
科名(Family)： 十字花科 Brassicaceae
俗名(Name)： 大观蔊菜
学名(Scientific name)：
Rorippa daguanensis W.Zhang & K.Zhao *sp. nov.*
备注(Notes)： Holotype

安徽师范大学植物标本馆(ANUB)
ANUB100099

采集编号(No.)： ZW20220418
十字花科 Brassicaceae
大观蔊菜
Rorippa daguanensis W.Zhang & K.Zhao *sp. nov.*
鉴定人(Identifide by)： 章伟、赵凯
鉴定日期(Identifide date)： 2024 年 12 月 14 日

Figure 5. Holotype of *R. daguanensis* sp. nov. (ANUB100099).

(LDC), Xishui County, Huanggang City, Hubei Province (Fig. 1). It grows in wetlands and mudflats along the Yangtze River, at elevations between 7 m and 13 m. This characteristic results in making *R. daguanensis* a well-defined obligate wetland indicator in its native area.

Preliminary conservation assessment. Currently, only two populations of *Rorippa daguanensis* were recognised in eastern China, each consisting of approximately 300 individuals. The estimated Extent of Occurrence (EOO) for this species is 15 km^2 and the Area of Occupancy (AOO) is 0.05 km^2. In addition, its living environment has been significantly impacted by seasonal floods and human activities over an extended period. Therefore, based on IUCN Red List Categories and Criteria (IUCN 2024), the conservation status of this new species is evaluated as 'Vulnerable' (VU) as it meets criteria D1 and D2.

Key to the species of *Rorippa* in China

1 Racemes bracteate throughout or rarely along lowermost third **2**
– Racemes ebracteate, rarely lowermost 1 or 2 flowers bracteate............... **3**
2 Fruiting pedicels slender, 3–6.5(-8) mm; fruit linear, 7–17(-21) × 1.2–1.6 mm; seeds colliculate .... ***R. benghalensis***
– Fruiting pedicels stout, (0.3-)0.7–2(-3) mm; fruit oblong, (3-)4.5–8.5(-10) × 1.5–2.5 mm; seeds foveolate .... ***R. cantoniensis***
3 Fruiting pedicels erect to erect-ascending, subappressed to rachis; fruit valves with a distinct mid-vein; seeds 1.1–1.5 × 0.7–1.1 mm .... ***R. elata***
– Fruiting pedicels ascending, divaricate or reflexed, not appressed to rachis; fruit valves not veined; seeds 0.4–0.9 × 0.3–0.6 mm **4**
4 Fruit globose, oblong, ellipsoid or oblong-ovoid, length less than 3× width... **5**
– Fruit linear, rarely linear-oblong, length more than 4 × width **9**
5 Fruit oblong, ellipsoid or oblong-ovoid **6**
– Fruit globose or subglobose **8**
6 Petals absent, Fruiting pedicels shorter than fruit .... ***R. daguanensis***
– Petals present, Fruiting pedicels longer than fruit **7**
7 Leaves dentate, Fruit not curved .... ***R. amphibia***
– Leaves pinnatisect, Fruit often slightly curved .... ***R. palustris***
8 Fruit valves 2, papery; sepals (1-)1.3–1.8(-2) mm; petals 0.7–1.3(-1.5) × 0.3–0.8 mm .... ***R. globosa***
– Fruit valves (3 or)4(-6), leathery; sepals 1.6–2.8 mm; petals (1.5-)1.8–3(-3.5) × 0.7–1.8(-2) mm .... ***R. barbareifolia***
9 Perennials; middle cauline leaves deeply pinnatisect; fruit rarely producing seeds; seeds colliculate .... ***R. sylvestris***
– Annuals; middle cauline leaves lyrate-pinnatipartitite or undivided; fruit producing numerous seeds; seeds foveolate **10**
10 Seeds biseriate; fruit often 1–2.5 cm long, 1–1.5 mm wide .... ***R. indica***
– Seeds uniseriate; fruit often 2–3.5 cm long, 0.5–1 mm wide **11**
11 Petals mostly absent, if present, often shorter than sepals, 1.5–2.5 mm long, 0.2–0.7(–1) mm wide; fruit straight, (1.5–) 2.5–3.5(–4) cm long, 0.7–0.9 (–1) mm wide .... ***R. dubia***
– Petals present, petals longer than sepals or equal to the sepals, (1.5–)2–3(–3.5) mm long, 1–2 mm wide; fruit often curved, (1.5–)2–3(–3.5) cm long, 0.5–0.7 (–8) mm wide .... ***R. hengduanshanensis***

Acknowledgements

We would like to thank Dr. Xin-Xin Zhu (Xinyang Normal University) for providing the site information of *Rorippa daguanensis*.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Investigation: ZW, ZK. Conceptualisation: ZK. Formal analysis: ZW, XXY, SJW. Writing-original draft: ZW. Writing-review and editing: HTS, SJW. Funding acquisition: ZW, ZK.

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Data availability

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

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PhytoKeys 253: 199–259 (2025)
DOI: 10.3897/phytokeys.253.138216

Monograph

A revision of the endemic Brazilian *Solanum hexandrum* group (Leptostemonum, *Solanum*, Solanaceae)

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Abstract

The Leptostemonum Clade, or the 'spiny solanums', represents half of the species diversity of the large cosmopolitan genus *Solanum* (Solanaceae). Brazil is a centre of both species and lineage diversity in 'spiny solanums' with a number of lineages occurring mostly only there. Here, we treat the *Solanum hexandrum* group, a monophyletic species group that is part of the larger and unresolved Erythrotrichum clade *sensu lato*. The six species treated here are all robust very prickly shrubs with amongst the largest and showiest flowers in *Solanum* and accrescent calyces in fruit that often completely cover the mature berry. All six species are endemic to the coastal Atlantic forests of south-eastern and north-eastern Brazil. We describe one new species, *S. phrixothrix* Gouvêa & S.Knapp, **sp. nov.**, known only from two collections made 200 years apart. Many of the species in the group occur in very small populations around isolated gneissic/granitic inselbergs, a highly threatened habitat in the region. We provide complete nomenclatural details for all recognised species and their synonyms, complete descriptions, distributions including maps, illustrations, common names and uses and preliminary conservation assessments.

Resumo

O clado Leptostemonum, ou dos 'solanums aculeados', representa metade da diversidade de espécies do hiperdiverso e cosmopolita gênero *Solanum* (Solanaceae). O Brasil é um centro de diversidade de espécies e linhagens de *Solanum* aculeados, com uma série de linhagens ocorrendo principalmente no país ou restritas a ele. Aqui apresentamos o tratamento do grupo *Solanum hexandrum*, uma linhagem que faz parte do clado maior e ainda não resolvido, chamado de *Erythrotrichum sensu lato*. As seis espécies tratadas aqui são todas arbustos robustos e armados, algumas portando flores entre as maiores e mais vistosas de *Solanum*, com cálices tipicamente acrescentes que muitas vezes cobrem completamente os frutos maduros. Todas as seis espécies são endêmicas das Floresta Atlântica brasileira, ocorrendo nas regiões Sudeste e Nordeste do país. Descrevemos uma nova espécie, *S. phrixothrix* Gouvêa & S.Knapp, **sp. nov.**, conhecida apenas por duas coletas feitas com 200 anos de diferença. Muitas das espécies do grupo ocorrem em populações muito pequenas ao redor de inselbergs de graníticos e gnáissicos isolados, um habitat altamente ameaçado na região. Fornecemos detalhes nomenclaturais completos para todas as espécies reconhecidas e seus sinônimos, descrições, informação sobre sua distribuição, incluindo mapas, ilustrações, nomes comuns e usos, e avaliação preliminar de seu *status* de conservação.

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Key words: Atlantic Forest, Brazil, endemism, fruit morphology, prickles

Introduction

Solanum L. is one of the ten most species-rich genera of flowering plants (Frodin 2004; Moonlight et al. 2024), with 1,245 currently accepted species occurring on all temperate and tropical continents (Hilgenhof et al. 2023). The highest diversity of both groups and species is in tropical South America, concentrated around the Amazon Basin (see Knapp (2002)), with hotspots of species diversity in the north-central Andes and south-eastern Brazil. Species of *Solanum* have flowers with fused sepals and petals that are usually 5-merous, stellate to pentagonal to rotate or somewhat campanulate corollas, stamens with short filaments and anthers opening by terminal pores. Despite this apparent uniformity, the genus as currently recognied has not always been treated as a monophyletic group (Spooner et al. 1993; Bohs 2005). Phylogenetic reconstruction using DNA sequence data has shown that previously segregated genera such as *Lycopersicon* Mill. and *Cyphomandra* Sendtn. (amongst others) are part of a larger monophyletic *Solanum* with strong support (Weese and Bohs 2007; Särkinen et al. 2013; Gagnon et al. 2022). Thirteen major clades are recognised in *Solanum* (see Gagnon et al. (2022); Hilgenhof et al. (2023)), the largest of which is the monophyletic Leptostemonum clade or the 'spiny solanums', characterised by the presence of prickles on the plant body (e.g. Satterlee et al. (2024)) and tapering, usually attenuate anthers.

The 'spiny solanums' comprise approximately half the species diversity of the genus (ca. 600 species), but unlike the rest of *Solanum*, where species diversity is concentrated in the Americas, the clade has significant diversity in Africa, Asia, Australia (incl. New Guinea) and the Pacific (Bean 2004, 2016; McClelland 2012; Knapp and Vorontsova 2016; Vorontsova and Knapp 2016; Echeverría-Londoño et al. 2020; McClelland et al. 2020). Species outside the Americas largely fall into a single monophyletic 'minor' clade that has been called the Eastern Hemisphere Spiny clade (Gagnon et al. 2022), except for some members of the otherwise American Torva and Lasiocarpa clades (see Aubriot et al. (2016)). Group diversity in the Americas is more complex, with 18 'minor' clades of spiny solanums occurring across the continent (Hilgenhof et al. 2023). Brazil is a hot spot of both species and clade diversity of spiny solanums; to date, 112 species in ten of the 'minor' clades of the Leptostemonum clade are recorded as native to Brazil and many taxa identified as new to science have also been identified and are awaiting description. Ongoing work on the Flora e Funga do Brasil (BFG 2021b) coupled with increased sampling of the many Brazilian species in molecular studies (e.g. Gouvêa (2020)), has revealed a number of morphologically coherent species groups within the spiny solanums that warrant monographic treatment.

The six species treated here comprise one such small monophyletic group (see discussion of phylogeny below). All these species are endemic to the south-eastern Brazilian forests, with one species (S. *sublentum*) extending to central Brazil (Fig. 1, Table 1) and share strongly accrescent fruiting calyces, large repand leaves often with decurrent bases and large, robust flowers. We here treat this group as part of the wider effort to provide a monograph of *Solanum* at a global

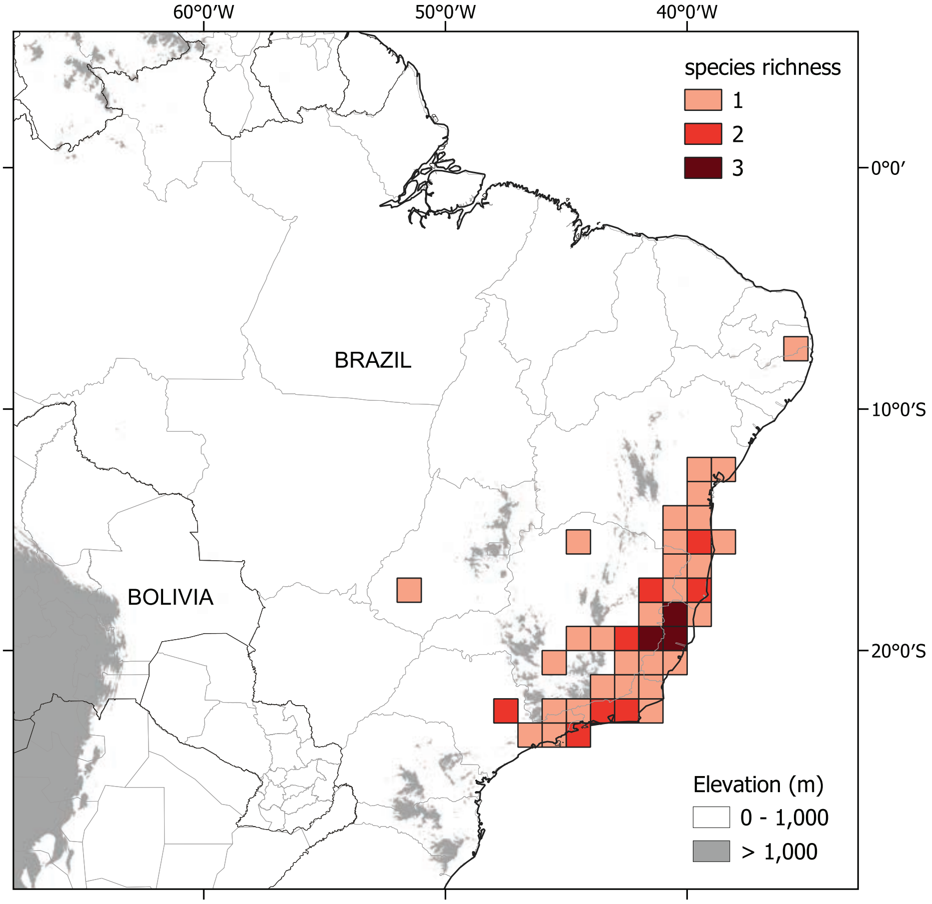

Figure 1. Map of distribution of the entire *S. hexandrum* group. Darker squares indicate higher species richness.

Table 1. Distribution of species of the *S. hexandrum* group. All species are endemic to Brazil.

Species	State(s)
Solanum aciculare Sw.	Bahia, Minas Gerais
Solanum hexandrum Vell.	Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo
Solanum hydroides Gouvêa & Giacomin	Espírito Santo, Minas Gerais
Solanum phrixothrix Gouvêa & S.Knapp	Espírito Santo, [Minas Gerais?]
Solanum stagnale Moric.	Bahia, Minas Gerais, Paraíba
Solanum sublentum Hiern	Bahia, Espírito Santo, Goiás, Minas Gerais, Rio de Janeiro, São Paulo

scale (Knapp et al. 2004) with detailed descriptions, keys and conservation assessments to aid understanding of Brazilian plant diversity and spur botanists to further collect and study the rare and fascinating species of this endemic group.

Taxonomy and relationships

Species of the *Solanum hexandrum* group were not described until the early 19th century, despite their large, showy flowers. *Solanum aciculare* Sw. was the first species to be described in the group; Roemer and Schultes (1819) published a name and description they attributed to Olaf Swartz, based on a collection made by Georg Freyreiss who travelled with the prolific collector of Brazilian plants, Frederich Sellow (see description of *S. aciculare*). Roemer and Schultes (1819) had not seen the specimen itself, they only used Swartz's name and description. *Solanum hexandrum* Vell., although possibly the earliest member of the group to be collected and recognised scientifically, was only published after *S. aciculare* in Brother José Mariano da Conceição Vellozo's Flora Fluminensis (Vellozo 1829); Vellozo's illustration (Vellozo 1831) is unambiguous and clearly shows the 6-parted corolla from which the epithet is derived. Vellozo (1829) also described *S. multiangulatum* Vell. that, from the illustration, was also possibly a member of this group, but the illustration and description are so rudimentary that the name is now suppressed (Knapp et al. 2015; See Names "designations" not validly published).

Solanum stagnale Moric. was described by Etienne Moricand (Moricand 1836) from the collections of the Swiss diplomat and botanist Jacques Samuel Blanchet. Blanchet was the Swiss consul resident in Bahia from 1826–1856 and collected many novelties in the region. *Solanum stagnale* was so named from the collection data stating "Hab. in stagnis circa Bahiam" ("habitat in [around] ponds near Bahia [probably Salvador]"). He did not contrast his new species with any other from Brazil.

In the treatment of *Solanum* in Flora Brasiliensis (Sendtner 1846), *S. aciculare*, *S. hexandrum* and *S. stagnale* were included in the large group of spiny solanums with straight prickles, lateral inflorescences and leaves that were not geminate, together with species with large, repand leaves now recognised as members of the Crinitum clade (*S. macranthum* Dunal = *S. crinitum* Lam.) and the Lasiocarpa clade (*S. sessiliflorum* Dunal) along with several other distinct clades of spiny solanums. Dunal (1852) included all three of the Brazilian species in his treatment of *Solanum* for the Prodromus (Dunal 1852), placing them in a group of spiny solanums distinguished by their more or less 5-parted corollas and more or less plicate corollas ("Corollis plus minusve 5-fidis, plus minusve plicatis" Dunal 1852: 30). He placed them in proximity with large-leaved species now considered part of the Crinitum clade, as had Sendtner (1846) before him.

Solanum sublentum Hiern was described some years later in a paper detailing species of *Solanum* occurring in central Brazil (Hiern 1878) described up to that time. It was compared to *S. sisymbriifolium* Lam., based on its prickliness and differing from it in shallowly lobed leaves, but not to the more closely-related *S. hexandrum* (treated by Hiern as *S. maroniense* Poit.).

Seithe (1962, 1979) developed a classification scheme for *Solanum*, based on hair types and included only *S. hexandrum* (as *S. maroniense*) in her system. She did not suggest affinities, but merely placed *S. hexandrum* as a member of her "subgenus Stellatipilum" (i.e. species with stellate trichomes). Danert (1970) followed Seithe's sectional classification, although he based his descriptions on branching patterns rather than pubescence; he did not mention any of the species of the *S. hexandrum* group. D'Arcy (1972), in his lectotypification of the sections of *Solanum*, did not indicate where he thought these species belonged; he only indicated types for the subdivisions of *Solanum* and did not place any of these species in his system.

Whalen (1984) developed a species-group classification for the spiny solanums treating all species worldwide. He placed *S. hexandrum* and *S. stagnale* in his *S. polytrichum* species-group together with a miscellaneous set of taxa, based on their bristly pubescence and prickly accrescent calyces (*S. polytrichum* Moric., *S. hasslerianum* Chodat, *S. laniflorum* Sendtn. (= *S. polytrichum*), *S. rupincola* Mart. and *S. urticans* Dunal). These are all now considered more closely related to other species groups (Hilgenhof et al. 2023). Earlier (Whalen et al. 1981), he had treated *S. stagnale* as a member of section *Lasiocarpa* (Dunal) D'Arcy (= Lasiocarpa clade, called in Whalen (1984) the *S. quitoense* group) and in his conspectus (Whalen 1984) suggested it "bridges the gap in some respects between the *polytrichum* and *quitoense* groups" and that those two groups were probably closely related. He also suggested a relationship with his *S. erythrotrichum* group, based on decurrent leaves and reddish-brown pubescence (Whalen 1984: fig. 5).

Child (1998) formalised Whalen's (1984) informally named group, typifying it with *S. polytrichum* (Child 1998; Child and Lester 2001). He excluded *S. urticans* from the group as he circumscribed it, but included *S. aciculare*; Child was the first to recognise *S. aciculare* as related to other species of the *S. hexandrum* group. Nee (1999) followed Whalen (1984), but excluded *S. hasslerianum* and *S. urticans* and added several poorly-known bristly Caribbean species (*S. gundlachii* Urb., *S. lomense* Britton & Wilson [= *S. gundlachii*], *S. schulzianum* Urb., *S. urens* Dunal). He suggested section *Polytrichum* A.Child as circumscribed by him "may not form a natural group" (Nee 1999: 317).

More recently and with increased interest and collecting associated with the Flora of Brazil project (BFG 2015, 2021a, 2021b), two taxa were described and associated with those three species that had been known and whose circumscription had remained essentially unchanged at the species level since the 19th century. Remnant forests around granite inselbergs in Minas Gerais and Bahia states harboured *S. kollastrum* Gouvêa & Giacomin (now recognised as *S. aciculare*, see species treatment) and *S. hydroides* Gouvêa & Giacomin (Gouvêa et al. 2018, 2020).

Phylogenetic analysis of DNA sequence data has clarified monophyletic groups within *Solanum* (Levin et al. 2006; Gagnon et al. 2022) and strongly confirmed the monophyly of the large Leptostemonum clade, within which 19 minor clades were recognised. The highest lineage diversity in the spiny solanums is in the Americas (Särkinen et al. 2013); 18 of the 19 clades are from the Americas. All spiny species from the Eastern Hemisphere (i.e. Africa, Asia, Australia, Europe and the Pacific) grouped in one poorly-resolved clade (termed the EHS clade) comprising half of the spiny solanum diversity.

Only two species of the group (*S. hexandrum* and *S. stagnale*) were sampled in the first large scale molecular phylogeny of the spiny solanums (Stern et al. 2011); they resolved as sister and, together with *S. robustum* H.Wendl., formed a moderately supported clade sister to species previously recognised (Agra 2004, 2007) as section *Erythrotrichum* A.Child. Särkinen et al. (2013) and Gagnon et al. (2022) recovered the same relationship. These studies made clear that the previously postulated close affinities of *S. hexandrum* and *S. stagnale* to other spiny solanum species with large, repand leaves like *S. sessiliflorum* Dunal (Lasiocarpa clade) and *S. crinitum* Lam. (Crinitum clade) were more likely due to convergence in leaf shape than to evolutionary relationship.

A study employing full plastome sequences and focusing on Brazilian spiny solanums included all of the taxa recognised here, except *S. hydroides* and *S. phrixothrix* (i.e. *S. aciculare*, *S. hexandrum*, *S. stagnale* and *S. sublentum*) and further clarified monophyletic species groups in Brazilian spiny solanums (Gouvêa 2020). In these analyses, all sampled species formed a monophyletic group that was sister to a set of closely-related groups including species such as *S. jussiaei* Dunal, *S. rupincola* Sendtn., *S. cordifolium* Dunal and *S. oocarpum* Sendtn. *Solanum robustum*, considered a member of the *S. hexandrum* group by Stern et al. (2011), resolved as sister to a group containing the poorly-known species *S. schizandrum* Sendtn. and an undescribed species (Gouvêa 2020). Together, the *S. hexandrum* group and these additional groups were sister to members of the Erythrotrichum clade s.s. and the Thomasiifolium clade, forming a group Gouvêa (2020) called "Erythrotrichum s.l.". Based on these results, we have not included *S. robustum* in our treatment of the *S. hexandrum* group. As many of the species in these groups are undescribed and poorly characterised, it is clear that more studies are needed, employing both nuclear markers and morphology, to untangle these largely Brazilian groups of spiny solanums.

Morphology

Habit

Members of the *Solanum hexandrum* group are all medium- to large-sized shrubs. Amongst the largest plants are *Solanum aciculare* and *S. hexandrum*, both often reach 3 metres tall in shaded environments with considerably robust stems (to 2–3 cm diameter at base in some populations of *S. hexandrum*), that are nevertheless soft-wooded. The strongly-branched stems that are fully covered with very long, straight prickles in *Solanum aciculare* give it an extremely robust appearance, even when quite small (Fig. 2C). *Solanum stagnale* and some populations of *S. hexandrum* are shorter plants, reaching no more than 2–2.5 m. *Solanum hydroides* and *S. sublentum* are more delicate plants, with relatively slender stems. No rhizomatous growth is reported in the group.

Stems

The stems in the *Solanum hexandrum* group are organised as a typical *Solanum* sympodium, with a 2/5 phyllotaxic spiral with inflorescences emerging laterally (internodal) or subopposite to the leaves (Danert 1958). All species of the clade have monochasial branching (Danert 1958). Plants from shaded environments, like some populations of *S. hexandrum*, are commonly observed in flower with a single unbranched stem with robust and showy flowers easily seen from a considerable distance. The sympodial units are mostly difoliate and the leaves usually not geminate, but unifoliate sympodial units are occasional in *S. hexandrum* and *S. aciculare* and *S. phrixothrix* have plurifoliate sympodial units. The exact nature of the sympodial unit in these plants, however, can be difficult to see, as the plants are large and herbarium specimens often consist of very few leaves and a single inflorescence.

Leaves

All species of the *Solanum hexandrum* group have large, simple repand leaves that are elliptic to ovate in outline and usually lobed to some extent (see Figs 2, 4, 5, 7, 9, 11, 13). Most of these leaves are membranous, but look thicker due to the dense pubescence; in live plants, they are somewhat floppy and soft. It is important to observe that great variation in leaf size and width is observed between young and mature plants and when comparing plants from shaded and sunny environments in all species, with larger leaves reported in young individuals from shaded environments (Gouvêa et al. 2020). The greatest variation, nevertheless, is found in species that can be found associated with granitic outcrops (inselbergs), such as *S. hydroides* and *S. hexandrum* (especially the glabrous individuals of the latter), with much smaller leaves observed in specimens growing on the rocks of outcrops as compared to those from shaded forest edges. As leaves of members of the clade can be quite large, reaching 45 cm or more long, it is common to find herbarium specimens with leaf sizes that do not represent what is observed in nature. Stem apices are preferentially collected so that they fit in a standard herbarium sheet (ca. 45 × 30 cm) and because this is where flowers are fruits are borne.

Leaf bases can be decurrent on to the petiole in *S. hexandrum*, *S. hydroides* and *S. stagnale* (see Figs 4B, 11C), not or rarely decurrent in *S. sublentum* (Fig. 13F, G) or not at all decurrent (*S. aciculare*, *S. phrixothrix*). Leaf margins can be entire (e.g. *S. hexandrum*), shallowly to deeply lobed or lobed with few to many secondary lobes. Young individuals and resprouts of most species produce more deeply-lobed leaves, often with more abundant and prominent secondary lobing. As the plants develop, more distally produced leaves are more shallowly lobed, with sparser and usually less pronounced secondary lobing or with this secondary lobing completely absent. *Solanum sublentum* is the only species in the group whose leaves retain numerous secondary lobes in more developed and older individuals (Fig. 13F, G).

Leaf texture also varies greatly and is mostly related to the environment and type of trichome developed. Species growing in open environments, such as *S. hydroides* and some populations of *S. hexandrum* tend to have trichomes with multiseriate bases that can be rough to the touch, especially when growing on rocky outcrops or exposed forest clearings. The leaves of *S. sublentum* are quite soft to the touch, but sticky due to the presence of glandular trichomes. *Solanum aciculare* is strongly glandular pubescent (Fig. 2), but a single specimen (*Magalhães 17651*, IAN) appears to be less glandular pubescent than other collections we have seen; we have, however, only seen this as an image and the glandular nature of the stellate trichomes of *S. aciculare* is hard to see unless resolution is high.

Inflorescences

The inflorescences of members of the *Solanum hexandrum* group, as in most Solanaceae species, are developmentally terminal (Lippman et al. 2008), but they can appear lateral due to subsequent branch elongation from the subtending axillary bud. Most species in the group have unbranched inflorescences, but we have seen one specimen of *S. hexandrum* with a forked inflorescence, perhaps due to injury. Inflorescences of *S. hydroides* and *S. sublentum* usually have relatively short axes (Figs 7C, 13H) bearing only a few flowers and more robust axes than are found in *S. aciculare* and *S. hexandrum*. *Solanum phrixothrix* has a long, slender inflorescence axis with flowers borne only near the tip (Fig. 9A).

The number of flowers per inflorescence varies greatly amongst species of the clade, ranging from a few (3–6) in *S. sublentum* and *S. hydroides*, to many (up to 35) in *S. aciculare* and *S. phrixothrix*. There are commonly only one or two flowers open at a time, even in species like *S. sublentum* that is not markedly andromonoecious (see Breeding systems below).

Pubescence

Like all members of the Leptostemonum clade, members of the *S. hexandrum* group have stellate trichomes, composed of a stalk of varying lengths (including absent and the trichomes sessile), lateral rays and a central mid-point (see Roe (1971); Vorontsova and Knapp (2016)). Some of these hairs can appear simple, due to loss of the lateral rays, but are derived from stellate trichomes (Roe 1971; Nee 1979) and are here and in the descriptions described as stellate or modifications thereof. Pubescence in the group is variable, particularly in *S. hexandrum* (see below). Most species of the group have stalked trichomes, with multiseriate stalks composed of 2-many rows of cells. Stalks with more rows of cells are more robust and generally stiffer. Rays (lateral branches) are usually single-celled, porrect and all in a single plane (Fig. 7E), but are sometimes multangulate and pointing in different planes (see Fig. 2I). The mid-point is 1-2(3) cellular and is often shorter (e.g. *S. hexandrum*, *S. hydroides*) than the ray cells, but, in *S. aciculare*, the mid-point can be much longer than the rays. The trichomes of *S. aciculare*, *S. sublentum* and *S. stagnale* are gland-tipped; those of *S. aciculare* are unusual in *Solanum* in having glandular tips on not only mid-points. but also on all of the ray cells (Fig. 2I).

Solanum phrixothrix and *S. sublentum* have apparently simple uniseriate trichomes that appear to be modified stellate trichomes like those that occur in the Acanthophora clade (Nee 1979; Hilgenhof et al. 2023), in *S. sublentum*, these are accompanied by a subtending layer of sessile rayed stellate trichomes and, in the few specimens seen, all trichomes of *S. phrixothrix* lack rays (Fig. 9B). Some populations of *S. hexandrum* appear to be completely glabrous, lacking trichomes altogether. In others, plants are pubescent, but with apparently simple trichomes like those of *S. phrixothrix*, with the rays lost such that the multiseriate stalk appears to be an unbranched multiseriate trichome topped with a 1-celled mid-point, this is often bent at right angles to the stalk making the trichome a distinctive L-shape (Fig. 5L). These are often characterised as bristles. Pubescence density in *S. hexandrum* is extremely variable, but the distinctive bent trichomes are consistent across the species range.

Most species of this group have dense pubescence on all parts, except for some populations of *S. hexandrum* (see species description and discussion). In general, pubescence of abaxial leaf surfaces is denser than that of adaxial surfaces; in *S. stagnale*, the leaf lamina is not visible on either surface due to the dense covering of long-stalked trichomes subtended with a lower layer of sessile stellate trichomes. Field observations of several species indicate that trichomes can be purple-tinged (e.g. *S. aciculare*, *S. hexandrum* and *S. hydroides*) and those of *S. stagnale* are usually characterised as reddish-brown or red, but can also be somewhat purple-tinged in live plants (Fig. 11C).

Prickles

In *Solanum*, prickles are considered to be modified trichomes (Whalen 1984) as can be seen by them often having apical stellae (Vorontsova and Knapp 2016). They have been lost in several groups and species; all losses are due to modifications in a single gene (Satterlee et al. 2024). There is a fine gradation between bristles and prickles (Vorontsova and Knapp 2016; see descriptions of *S. setaceum* Dammer and *S. schumannianum* Dammer), with less sturdy structures being termed bristles (e.g. in this group *S. phrixothrix*, Fig. 9B) and more robust structures called prickles. In species of the *S. hexandrum* group, prickles can be distinguished from bristle-like trichomes by their pointed tips, which lack rays and mid-points. Bristle-like trichomes, on other hand, always have a unicellular or 2–3-celled uniseriate mid-point of varying lengths, which leaves a scar when deciduous.

In the *S. hexandrum* group, prickles occur throughout the plant, but are most prominent on stems and along the leaf venation. Prickles also occur on inflorescence axes and calyces in most species, but are generally smaller than those of stems. Prickles in the spiny solanums are either needle-like (acicular) or laterally flattened (Hilgenhof et al. 2023); in this group, stem prickles are usually laterally compressed and widest at the base, although *S. phrixothrix* has acicular bristles that are not markedly flattened (Fig. 9B). Straight stem prickles are found in *S. aciculare*, *S. hexandrum* and *S. phrixothrix*, but those of *S. hydroides*, *S. stagnale* and *S. sublentum* are moderately to strongly curved (Figs 2I, 5B, 7C, 11E, 13E).

Prickle density and size varies both between and within species. Most stem prickles in this group are between 0.5 and 1 cm long, whereas prickles along leaf venation are usually shorter. *Solanum aciculare* and *S. phrixothrix* are consistently densely prickly/bristly, whereas *S. stagnale* is quite variable. Some individuals of *S. stagnale* have large, densely-spaced recurved prickles along the stems.

Pedicels

Flower and fruit pedicels in the *S. hexandrum* group are usually quite robust and vary from being almost absent (*S. stagnale*, Fig. 11C, F) to 2 cm long (e.g. *S. hexandrum*, Fig. 5B). *Solanum hydroides* and *S. phrixothrix* have the most delicate pedicels in the group (Figs 7C, 9C). They usually have at least some prickles, especially in the lower flowers that are co-sexual (see below and species descriptions). Pedicels are usually spreading to erect at anthesis, whereas in fruit, they are usually somewhat deflexed from the weight of the large berries (Fig. 5J).

Calyx

Calyces in members of the *S. hexandrum* group are typically sympetalous and 5-merous as most species of *Solanum* (although as the specific epithet implies that those of *S. hexandrum* are often 6-merous). The shape of the sepals and how they develop in fruit can be informative for species recognition. In *S. hydroides* and *S. hexandrum*, the sepals are generally deltate to lanceolate (Figs 4, 5, 7), they are somewhat tongue-shaped to spathulate in *S. stagnale* (Fig. 11C) and expanded at the base and somewhat cordate in *S. aciculare* (Fig. 2E) and *S. sublentum* (Fig. 13G). The calyx in fruit is usually to some degree inflated and accrescent, often covering half or more of the mature berry, only in *S. hydroides*, *S. stagnale* and some populations of *S. hexandrum* does the calyx remain closely appressed to the developing berry (Figs 4J, 7E, 11F). In *S. aciculare*, *S. sublentum* and some populations of *S. hexandrum*, the calyx in both flower and fruit is strongly inflated (Figs 5J, 13J) and the base is invaginate. In *S. hexandrum*, this accrescent condition can vary (e.g. Fig. 4J) and is often not visible in flower. In some populations of *S. hexandrum*, the calyx appears to be fused throughout development, opening only just before anthesis (Fig. 5C–E); this state occurs more often in glabrous or sparsely pubescent individuals.

Calyces of all these species are often dark purple or purple-tinged in fruiting plants. Ants of the genus *Camponotus* have been seen foraging on exudate from the abaxial surface of the calyx of *S. hexandrum* (YFG, pers. obs.); this has only observed in the glabrous to sparsely hairy plants, but may be more common as has been seen in other groups of spiny solanums (e.g. Lasiocarpa clade, Anderson and Symon (1985); Falcão et al. (2003)).

Corolla

The corolla in members of the *S. hexandrum* group is sympetalous and 5(6)-merous and relatively large compared to most other members of the Leptostemonum clade. The smallest corollas are found in *S. hydroides* (2.4–3 cm in diameter) and the largest in *S hexandrum* (3–6 cm in diameter). Most species have somewhat stellate corollas, lobed up to halfway to the base, with deltate to broadly triangular lobes. *Solanum phrixothrix* has a rotate to rotate-pentagonal corolla with only very tiny, minutely apiculate lobes (Fig. 9C, E, F).

Corollas in these species are usually various shades of purple, fading to paler shades with age. In *S. aciculare*, the corollas are dark purple at the onset of anthesis (Fig. 2F, G), becoming white when old. *Solanum sublentum* is polymorphic, with individuals with white corollas (Fig. 13H inset) and others with purple (Fig. 13G, H). *Solanum hydroides* and *S. phrixothrix* have uniformly white corollas.

Where abaxial petal tissue is exposed in bud, it is usually pubescent with stellate trichomes like those of the rest of the inflorescence (Fig. 4G); interpetalar tissue, however, is always thin and glabrous. Adaxial petal surfaces are usually glabrous, but sparse stellate trichomes (e.g. *S. aciculare*) and sometimes minute straight prickles (e.g. *S. sublentum*) occur along the petal mid-veins and apices. The tips of the corolla lobes are often somewhat apiculate (Fig. 2G, uppermost corolla lobe).

Androecium

As in all species of *Solanum*, anthers are borne on short filaments and are poricidal at the tips. In all species of the *S. hexandrum* group, the androecium is monomorphic, with stamens and anthers are of equal size (e.g. Fig. 2F). Anthers are loosely connivent and colour is uniformly recorded as yellow on herbarium labels. The anthers of members of the group are somewhat plump in the lower half and not as attenuate as in other groups with large flowers (e.g. *S. crinitum* or *S. lycocarpon* A.St.-Hil., both of the Crinitum clade), but in common with other members of the Leptostemonum clade, they are narrowed apically. The abaxial surfaces are swollen (making the anthers somewhat gibbous) and sometimes papillate, but this is not constant within a species. The apical pores do not lengthen to slits with age or drying and are usually directed distally and somewhat extrorsely.

Gynoecium

The ovary in members of this group is 2–4-locular with axile placentation. The ovary is usually somewhat pubescent apically with a tuft of stellate trichomes, these being deciduous or mostly deciduous throughout fruit development. The style is cylindrical, straight and glabrous; in long-styled flowers, it is exserted from the anther tube, whereas in short-styled flowers (usually distal on the inflorescence), it is held well-within the anther tube (see Fig. 9D). The stigma is usually large, clavate or globose-capitate and is occasionally bilobed; stigmas in live plants are bright green (see Figs 2G, 7D, 11E, 13I).

Fruit

The fruit of all members of the *S. hexandrum* group is a 2–4-locular berry, usually enclosed in the accrescent calyx (Fig. 7F). Mature berries of most species are completely enclosed in the accrescent calyx, but those of *S. hydroides* and *S. stagnale* are only partially enclosed with approximately half of the mature berry exposed (Figs 7E, 11F). The berries of these species are green, greenish-white or white at maturity with a fleshy pale white mesocarp and many small seeds (> 100 per berry); medium-sized greenish-white berries have been shown to be ancestral in *Solanum* (Messeder et al. 2024).

A single collection of *S. hexandrum* (*Magnago 467*, MBML) has been recorded as having a purple fruit, but it is probable that this observation refers to the accrescent calyx and not the berry itself (the specimen is in early fruit with completely accrescent calyces). A mild sweet scent has been recorded for *S. aciculare* (Gouvêa et al. 2018), but scent has not been recorded for any other species. Fruits are not known for *S. phrixothrix*.

Seeds

The seeds of these species are dark brown, relatively small within the Leptostemonum clade (ca. 2–2.6 mm long) and flattened reniform or somewhat ovoid with minutely-pitted testal cells (Fig. 7F). The testal cells are usually pentagonal or only slightly sinuate in outline, but *S. aciculare* and *S. sublentum* have testal cells that are markedly sinuate in outline.

Chromosomes

Chromosome numbers in *Solanum* are based on a base number of x = 12 (Chiarini et al. 2018). *Solanum stagnale* is the only one of the species treated that has a chromosome count. Bernardello et al. (1994) recorded a sporophytic count of 2n = 24 for *S. stagnale* (treated as a member of section *Lasiocarpa*) and showed that, morphologically, its karyotype was similar to that of *S. quitoense* (Lasiocarpa clade) with a formula of 10 m + 2 sm chromosomes.

Ecology and natural history

Habitats

All of these species are endemic to Brazil (Fig. 1, Table 1). Members of the *Solanum hexandrum* group are associated with a wide range of habitats, from wet shaded forests to outcrops, mostly restricted to the Atlantic Forest domain in eastern Brazil, from the States of São Paulo to Paraíba. *Solanum sublentum*, however, also occurs in patches of seasonally dry forest (SDTF of Murphy and Lugo (1986); Pennington et al. (2009)) within a savannah matrix in the Cerrado domain at the limits of Cerrado vegetation in central and south-eastern Brazil in the

States of Minas Gerais and Goiás (see Table 1 for the distribution of all species). Species are recorded from evergreen and seasonally semi-deciduous wet forests, in clay soils, to more open sandy coastal lowland vegetation (restinga, see Araújo (1992)) or associated with forest patches at the base of gneiss or granite inselbergs, where sandy or leached shallow soils are more common. *Solanum sublentum* is also found growing in soils with high levels of calcium and magnesium associated with limestone outcrops. but is not exclusive to this soil type.

Solanum hexandrum is the most widely distributed species ranging from São Paulo to southern Bahia State and has been collected both in and at the edges of evergreen and seasonal forests. *Solanum aciculare* and *Solanum hydroides* are restricted to gneissic/granitic outcrops together with some populations of *S. hexandrum*, but *S. aciculare* can also be found in disturbed restinga vegetation. *Solanum phrixothrix* is found in wet evergreen and semi-deciduous forests in the Rio Doce drainage, sometimes associated with forests on sandy soils known as “tabuleiro” (tableland) formations (Peixoto et al. 2008). All species have also been collected in anthropogenically disturbed habitats, by roads or in forest clearings.

Sex expression and breeding systems

Like many other members of the Leptostemonum clade, some species of the *S. hexandrum* group exhibit andromonoecy where the first (proximal) “long-styled” flower(s) have styles that protrude beyond the anthers (e.g. Figs 4G, 13I) and go on to develop fruits and the later (distal) “short-styled” flowers have partly developed styles and do not normally develop fruits (Fig. 2D, F)). Andromonoecy has been extensively studied in *Solanum* (e.g. Dulberger et al. (1951); Whalen and Costich (1986); Anderson and Symon (1989); Miller and Diggle (2003); Diggle and Miller (2013)) and is believed to be an adaptation to limited resources which allows the plant to restrict the number of costly fruits without decreasing pollen production. In the spiny solanums, there is a continuum from weakly andromonoecious species with a low proportion of staminate flowers (i.e. many co-sexual flowers, for example, *S. sublentum*) to strongly andromonoecious species with a high proportion of staminate flowers and only one hermaphroditic flower that sets fruit. A statistically significant correlation has been found between the strength of andromonoecy, larger fruit size, larger ovary size and larger size of long-styled flowers (Miller and Diggle 2003). Our phylogenetic studies across *Solanum* indicate that andromonoecy does not define monophyletic groups (Vorontsova et al. 2013; Aubriot et al. 2016). Breeding systems in the *S. hexandrum* group have not been studied in the field or laboratory and are postulated here, based on morphology.

Pollination and dispersal

Members of the *S. hexandrum* group have been the subject of little ecological study in the field. Based on the poricidal dehiscence and anther robustness, the main pollinators of these species are likely to be medium- to large-sized bees that gather pollen by buzzing the anthers (Bowers 1975; Buchmann et al. 1977; Vallejo-Marín 2019, 2022). A study of pollination networks in the forests around the inselberg of Itaoca (Rio de Janeiro State) recorded visits of bees from the families Apidae [*Bombus morio* (Swederus), *Eulaema cingualata* (Fabricius), *Oxaea flavescens* Klug), Halictidae (*Augochloropsis* sp., *Pseudaugochloropsis graminea* (Fabricius)] and Megachilidae (*Megachile* sp.) to plants of *S. hexandrum* (Marques et al. 2018). It is likely that only the larger of these bees were effective pollinators. Species of *Bombus*, for example, are effective pollinators of *Solanum* in other habitats (Knapp 1986; Messinger et al. 2016). Smaller bees such as *Augochloropsis* often glean pollen from anther pores and may be less important in pollination of these large-flowered species (Whalen 1979; Solís-Montero and Vallejo-Marín 2017; Vallejo-Marín 2019).

Berries of members of the *S. hexandrum* group are variable in size (from 1–3.5 cm in diameter); they usually hang below the foliage on short or long inflorescence axes and are enclosed in an accrescent calyx. This combination of characteristics, coupled with the white or greenish-white colour at maturity and sweet smell (observed in *S. aciculare*) suggest dispersal by bats (Van der Pijl 1972; Valenta and Nevo 2020). Messeder et al. (2024) suggest that correlation of the emergence of medium-sized green fruits and the most diverse family of fruit-eating bats (Phyllostomatidae) is evidence for bat dispersal being ancestral in the genus. In the Brazilian Atlantic Forest, *Solanum* species have been shown to be important components of bat diets (Aguiar and Marinho Filho 2007; Mello et al. 2008) and the role of bats as dispersal agents for some *Solanum* species is well-documented (Iudica and Bonaccorso 1997; Paulino-Neto et al. 2014).

Conservation status

Most species of the *Solanum hexandrum* group are found in small populations with individuals growing close to each other, often in isolated forest patches at the base of granitic or other rocky outcrops. No vegetative reproduction has been reported for any species of the group. Although some species were previously informally assessed as threatened (*S. aciculare* as EN, Gouvêa et al. (2018); *S. hydroides* as VU, Gouvêa et al. (2020)), we assess all species of the group here for the first time (see Table 2 and species descriptions). Using AOO (Area of Occupancy), all of these species are identified as Endangered (see species treatments), but EOO (Extent of Occurrence) estimates suggest only *S. aciculare* and *S. hydroides* are of significant conservation concern (*S. phrixothrix* is Data Deficient due to scarcity of collections). All these species are probably subject to population size fluctuations or area of occupancy reductions due to anthropogenic landscape change. Urban centre expansion and conversion of native vegetation to alternative land uses, such as pastures or *Pinus/Eucalyptus* plantations for cellulose production (Ribeiro et al. 2009), are resulting in rapid fragmentation of the Atlantic Forest (Tabarelli et al. 2004). Half of the species treated here (e.g. *S. aciculare*, *S. hydroides* and *S. phrixothrix*) are found in the central Brazilian Atlantic Forest, where botanical knowledge gaps are known to exist (Stehmann et al. 2009; Oliveira et al. 2016). Rock outcrops in these regions harbour the last remnants of forest fragments (Martinelli 2007) and every remnant of native vegetation of rocky outcrops, no matter the size, is worth preserving and should be inspected. Except for *Solanum hexandrum*, most of these species have not been recorded from any or only a single protected area (see Preliminary Conservation Assessments for each species), suggesting they are all vulnerable to some degree.

Table 2. Preliminary conservation status of members of the *S. hexandrum* group.

Species	EOO (km^2)	AOO (km^2)	Preliminary status
Solanum aciculare Sw.	38, 227 (NT)	56 (EN)	Endangered
Solanum hexandrum Vell.	327,280 (LC)	460 (EN)	Near Threatened
Solanum hydroides Gouvêa & Giacomin	12,549 (VU)	24 (EN)	Endangered
Solanum phrixothrix Gouvêa & S.Knapp	--	--	Data Deficient
Solanum stagnale Moric.	157,059 (LC)	68 (EN)	Vulnerable
Solanum sublentum Hiern	642,872 (LC)	72 (EN)	Near Threatened

Materials and methods

Our taxonomic treatment is based on study of herbarium specimens and plants in the field. Delimitation and descriptions are based on fieldwork and examination (physical and virtual) of 749 [= 460 collections] herbarium specimens from 64 herbaria: A, ALCB, BH, BHCB, BM, BR, C, CEPEC, CESJ, CORD, CVRD, E, EFC, ESA, F, FUEL, FURB, G, G-DC, GH, GOET, HAS, HCF, HRCB, HSTM, HUEFS, IAC, IAN, IBGE, ICN, JPB, K, L, LE, M, MA, MBM, MBML, MCCA, MG, MO, NIT, NY, OXF, P, RB, RFA, RFFP, S, SI, SP, SPF, SPSF, TCD, U, UCPB, UEC, UNOP, UPCB, US, UT, VIC, W and WU. Some of these specimens were examined digitally through individual herbarium portals; we include only those specimens which we have been able to unequivocally identify from these images or that are duplicates of collections we have personally examined.

Measurements were made from dried herbarium material supplemented by measurements and observations from living material. Colours of vegetative organs (e.g. leaves, prickles and trichomes) and seeds are described from dried herbarium collections (and living plants when available) and for corollas, fruits etc., are described from living material or from herbarium label data. Specimens with latitude and longitude data on the labels were mapped directly. Most species had few or no georeferenced collections; here, we retrospectively georeferenced the collections using available locality data. Maps were constructed with the points in the centres of degree squares in a 1° square grid. Conservation threat status was assessed following the guidelines for the IUCN Red List Categories and Criteria (IUCN 2020) using the GIS-based method of Moat (2007) as implemented in the online assessment tools in GeoCat (http://geocat.kew.org; Bachman et al. (2007)). The Extent of Occurrence (EOO) measures the range of the species and the Area of Occupancy (AOO) represents the number of occupied points within that range, based on the default grid size of 2 km^2. We have taken a pragmatic approach in the threat assessments for most species, especially where assessments based on EOO and AOO differ widely; AOO is very sensitive to georeferencing bias and collecting effort, but the extreme vulnerability of these habitats is clear.

Where specific herbaria have not been cited in protologues, we have followed McNeill (2014) and designated lectotypes rather than assuming holotypes exist. We cite page numbers for all previous lectotypifications. In general, we have lectotypified names with the best preserved or, in some cases, with the only herbarium sheet we have seen; in these cases, we have not outlined our reasoning for the lectotypifications. Where there has been difficulty or where the choice may not be obvious, we detail our reasoning at the end of the species discussions. For names that have been “inadvertently” lectotypified (*sensu* Prado et al. (2015)), we indicated what the original author cited (e.g. “type”, “holotype”) after the lectotype citation.

Type specimens with sheet numbers are cited with the herbarium acronym followed by the sheet number (e.g. SD [acc. # 6543]); barcodes are written as a continuous string in the way they are read by barcode readers (e.g. G00104280, MO-1781232). For those herbaria (e.g. A, GH, NY, US) where the barcode consists of only a number, we cite only the number string. Where herbaria have both barcodes and accession numbers, we always cite the barcode first, followed by the accession number (e.g. MO-503846, acc. # 3783069); this citation will allow users to access individual sheets where barcode numbers are not human-readable.

Identities of all collections seen for this study are presented in Suppl. materials 1, 2 with full searchable specimen details available in Suppl. material 1 and all collection events in Suppl. material 2. All these files of specimens used for this study are also deposited in the Natural History Museum Data Portal (https://doi.org/10.5519/vv8f8pkx).

Citation of literature follows BPH-2 (Bridson 2004) with alterations implemented in IPNI (International Plant Names Index, http://www.ipni.org) and Harvard University Index of Botanical Publications (http://kiki.huh.harvard.edu/databases/publication_index.html). Following Knapp (2013), we have used the square bracket convention for publications in which a species is described by one author in a publication edited or compiled by another (the traditional “in” attributions), as, for example, Dunal in DC. for those taxa described by Dunal in Candolle’s *Prodromus Systematis Naturalis Regni Vegetabilis*. This work is cited here as Prodr. [A.P. de Candolle] and the names are thus attributed only to Dunal. For “ex” attributions, we cite only the publishing author, as suggested in the *Code* (Turland et al. 2018). Standard forms of author names are according to IPNI (International Plant Names Index, http://www.ipni.org).

Species concepts

Our goal for this treatment has been to provide circumscriptions for the members of this morphologically variable group of species, while also clearly highlighting areas, taxa and populations where further in-depth research would be useful. Delimitation of species here basically follows what is known as the “morphological cluster” species concept (Mallet 1995; Knapp 2008): i.e. “assemblages of individuals with morphological features in common and separate from other such assemblages by correlated morphological discontinuities in a number of features” (Davis and Heywood 1963). Biological (Mayr 1982), phylogenetic (Cracraft 1989) and the host of other finely-defined species concepts (see Mallet (1995)) are almost impossible to apply in practice and are, therefore, of little utility in a practical sense (see Knapp (2008)). It is important, however, to clearly state the criteria for the delimitation of species, rather than dogmatically follow particular ideological lines (see Luckow (1995); Davis (1997)). We have relied on clear and consistent morphological discontinuities to define species. Specific characters used for recognition are detailed with each species description and in the key. In this revision, we have tried to emphasise similarities between populations instead of differences, which so often reflect incomplete collecting or local variation. We have been conservative in our approach, recognising as distinct entities those population systems (sets of specimens) that differ in several morphological characteristics. We describe and illustrate variation occurring within more variable species (e.g. *S. hexandrum*) realising that others may wish to interpret it differently.

Taxonomic treatment

The *Solanum hexandrum* group

Solanum hexandrum clade, sensu Stern et al. (2011) pro parte.
Solanum subsection *Asterotrichotum* Dunal, Prodr. [A.P. de Candolle] 13(1): 30. 1852, pro parte.
Solanum polytrichum species group of Whalen, Gentes Herb. 12: 248. 1984, pro parte (excl. *S. hasslerianum* Chodat, *S. polytrichum* Moric., *S. urticans* Dunal).
Solanum quitoense species group of Whalen, Gentes Herb. 12: 249. 1984, pro parte.
Solanum section *Polytrichum* (Whalen) A.Child, Feddes Repert. 109: 422. 1998, pro parte (excl. type species *S. polytrichum*).

Description. Shrubs, erect, sparsely to densely armed. Stems terete, glabrous to densely pubescent and/or bristly, usually prickly; trichomes porrect-stellate or multangulate, eglandular or glandular, sessile to long-stalked, the stalks multiseriate and usually robust, the rays (2)-4-20, often deciduous or missing and the trichomes appearing simple; prickles straight or recurved, acicular or laterally compressed, often widest at the base and with scattered stellate trichomes on the prickle itself. Sympodial units unifoliate, difoliate or plurifoliate, the leaves not geminate. Leaves simple, usually shallowly lobed, repand; blades glabrous to densely stellate-pubescent, usually prickly, the trichomes eglandular or glandular, porrect or multangulate, sometimes the stellate trichomes without rays and appearing simple, the prickles generally along the mid-rib and veins, smaller than those of the stems; base attenuate to truncate or cordate, often decurrent on to the stem; margins usually shallowly lobed, sometimes secondarily so, the basiscopic lobes, if present, rounded to angular; apex acute to acuminate; petioles winged or not. Inflorescences internodal or subopposite the leaves, unbranched (a single specimen of *S. hexandrum* seen with a furcate inflorescence), with 3–30 or more flowers, usually only a few open at a time, glabrous to densely stellate-pubescent and/or bristly, often prickly; peduncle usually elongate; pedicels very short to ca. 2 cm long, glabrous to stellate-pubescent and/or bristly, articulated at the base, the trichomes glandular or eglandular. Flowers 5-merous (sometimes 6-merous in *S. hexandrum*), actinomorphic, heterostylous, co-sexual (long-styled) flowers either along the entire inflorescence or borne near the base, staminate (short-styled) flowers borne distally, the plants varyingly andromonoecious; calyx with the tube often enlarged and saccate, sometimes plicate at the junction of the lobes, glabrous or more usually variously stellate-pubescent, prickly or bristly, the lobes narrowly to broadly triangular to spathulate, often foliose, usually enclosing the bud until just before anthesis, sometimes completely fused until just before anthesis; corolla large, usually purple, but, in some species, white, stellate to rotate, the lobes usually planar at anthesis, but, in *S. phrixothrix*, somewhat campanulate, interpetalar tissue absent to copious; stamens 5 (or sometimes 6 in *S. hexandrum*); filaments equal, glabrous; anthers equal, plump and tapering, connivent, abaxially often papillate and swollen in the lower half, dehiscing by apical pores; ovary 2–4-locular, glabrous or with a few apical glandular or eglandular stellate trichomes; styles straight or slightly curved, usually white, glabrous, in short-styled flowers held within the anther tube. Fruit a berry, usually 4-locular, up to 3.5 cm in diameter, often somewhat compressed, pale green to white at maturity, the mesocarp fleshy, the pericarp glabrous or with a few scattered stellate trichomes near the apex; fruiting pedicels usually deflexed from the weight of the berry; fruiting calyx variously accrescent, partially or completely enclosing the berry, appressed or saccate and invaginate; seeds many per berry, flattened reniform or somewhat ovoid, the surfaces minutely pitted, the lateral testal cell walls straight or sinuate; stone cells always absent. Chromosome number: n = 12 (Bernardello et al. 1994).

Distribution and ecology. Members of the *S. hexandrum* group are mostly endemic to eastern Brazil, ranging from São Paulo State in the south to Paraíba State as the northern limit, with a single species, *S. sublentum*, extending to the State of Goiás in central region of the country (see Fig. 1). All species occur in the Mata Atlântica, or Atlantic Rainforest, in a variety of environments, from shaded forest environments in clay soils to open exposed environments in sandy soils, often in association with gneissic/granitic inselbergs.

Discussion. This small group of species, all endemic to Brazil, is morphologically distinctive in having large, repand leaves, usually copious bristly pubescence on all parts, large flowers and accrescent fruiting calyces enclosing pale green to white mature berries. There is considerable morphological variation in some species (*S. hexandrum*) that needs further study. Most of these species have only rarely been collected, are found in small populations mostly outside of protected areas and are likely to be of conservation concern.

The spiny, shrubby Brazilian species of the Crinitum clade (e.g. *S. crinitum* Lam., *S. falciforme* Farruggia and *S. medusae* Gouvêa; Gouvêa et al. (2019)) can also have large, showy purple flowers, large leaves and bristly pubescence. However, species of the *S. hexandrum* group are easily distinguishable from these by their robust, abaxially glabrous anthers (rather than slender, stellate-pubescent anthers) and medium-sized fruits up to 3.5 cm in diameter enclosed or partially covered by accrescent calyces (as opposed to large fruits over 5 cm in diameter that are not covered by the calyces).

Other somewhat robust, large-leaved, spiny species occur within the range of the *S. hexandrum* group and can be superficially confused with them (e.g. *S. asterophorum* Mart., Asterophorum clade; *S. robustum* H.Wendl., Erythrotrichum clade). Although species of both the Asterophorum clade and the *S. hexandrum* group have accrescent fruiting calyces, they can be easily distinguished by their leaves, which are geminate (paired at the same node) in species of the Asterophorum clade, but not geminate in species of the *S. hexandrum* group. The leaves of *S. robustum* are similarly decurrent to those of some species of the *S. hexandrum* group, but in that species, the fruiting calyces are not accrescent and berries are densely pubescent at maturity, whereas in members of the *S. hexandrum* group, fruiting calyces are markedly accrescent and berries are not densely pubescent at maturity.

Artificial key to the species of the *S. hexandrum* group

1 Leaf bases cordate to hastate or sagittate-hastate with angular to rounded basiscopic lobes, not decurrent onto the petiole, rarely with a short and narrow attenuate extension < 1/2 the length of the petiole; leaf margins usually with secondary lobing **2**

– Leaf bases rounded, obtuse, attenuate or truncate, strongly decurrent onto all or most of the petiole; leaf margins without secondary lobing **4**

2 Pubescence mostly glandular of stellate or a mixture of simple and stellate trichomes; calyx tube plicate from expanded lobe bases, especially in fruit; corollas shallowly to deeply stellate with deltate lobes **3**

– Pubescence eglandular of long, bristle-like trichomes; calyx tube not plicate; corollas rotate-apiculate .... ***Solanum phrixothrix***

3 Stem and petiole trichomes strictly stellate, long-stalked and multiglandular; corolla stellate, lobed to half of its length; leaf bases rounded-cordate, with basal-most lobes touching or overlapping each other over the petiole; leaf lobe apices rounded to obtuse in fully developed leaves of adult plants.. ***Solanum aciculare***

– Stem and petiole trichomes mostly or strictly without rays and uniseriate, any stellate trichomes (when present) eglandular, sessile to short-stalked and less abundant; corolla pentagonal to very shallowly stellate, lobed to one quarter of its length; leaf bases cordate-angular to hastate or sagittate-hastate, with basal-most lobes never touching or overlapping each other over the petiole; leaf lobe apices acute with straight or concave margins in fully developed leaves of adult plants...............***Solanum sublentum***

4 Mature leaves with both surfaces glabrous or very sparsely pubescent adaxially, the stellate trichomes lacking rays, bristle-like and bending; stems glabrous or with scattered stellate trichomes; calyx lobes in bud fused, enclosing the corolla almost to anthesis; calyces glabrous or with scattered trichomes, prickles and/or bristles............. ***Solanum hexandrum***

– Mature leaves with both surfaces pubescent, the trichomes stellate or robust and bristle-like on the adaxial surface; stems pubescent with stellate trichomes or with a mix of stellate and unbranched bristle-like trichomes; calyx lobes in bud splitting before anthesis; calyces moderately to densely pubescent, also with prickles and/or bristles... **5**

5 Pedicels at anthesis up to 0.5 cm long, usually shorter; leaves and stems densely pubescent with multi-rayed trichomes; calyx lobes spathulate ....***Solanum stagnale***

– Pedicels at anthesis > 0.5 mm long, usually 1–2 cm long (if < 0.5 cm long, then the flowers white); leaves and stems glabrous to pubescent or bristly, at least some trichomes, when present, few-rayed, or bristle-like and unbranched; calyx lobes triangular to deltate.. **6**

6 Corollas purple, 3–6 cm in diameter, often 6-merous; plants robust, usually > 1 m tall; blades of fully developed leaves > 13 cm long in adult plants; fruiting calyx accrescent, completely to almost completely covering the berry, inflated or loosely investing the berry, the lobes overlapping; berry 2–3.5 cm in diameter.. ***Solanum hexandrum***

– Corollas white, 2.4–3 cm in diameter; plants delicate, usually < 1.5 m tall; blades of fully developed leaves ≤ 13 cm long in adult plants; fruiting calyx partially accresent, not completely covering the berry, tightly appressed, the lobes not overlapping; berry 0.9–1.8 cm in diameter...... ***Solanum hydroides***

Synoptic character list for members of the *S. hexandrum* group

Leaf bases decurrent on to petiole and stem: *hexandrum*, *stagnale*, *hydroides*.
Leaf bases cordate: *aciculare*, *sublentum*, *phrixothrix*.
Stellate trichomes apparently absent: *hexandrum*, *phrixothrix*.

Trichomes glandular: *aciculare*, *sublentum*.
Trichomes unbranched (modified stellate trichomes without rays): *hexandrum*, *phrixothrix*, *sublentum*.
Prickles broad-based: *hexandrum*, *stagnale*.
Corolla rotate to pentagonal: *phrixothrix*.
Fruiting calyx invaginate (plicate, sometimes only obvious on immature fruits): *aciculare*, *sublentum*.

Species descriptions

1. *Solanum aciculare* Sw., Syst. Veg., ed. 15 bis [Roemer & Schultes] 4: 647. 1819

Fig. 2

Solanum kollastrum Gouvêa & Giacomin, PhytoKeys 111: 105. 2018. Type. Brazil. Minas Gerais: Ataléia, povoado de Canaã do Brasil, estrada não pavimentada que liga o município de Ouro Verde de Minas ao povoado de Canaã do Brasil, 18°00'19"S, 41°12'17"W, 313 m alt., Jun 2018, *Y.F Gouvêa 280* (holotype: BHCB [BHCB190863]; isotype: RB [RB1411895, acc. # 787650]).

Type. Brazil. “Ex Brasilia” [probably collected in Mucuri River drainage in the State of Bahia, see discussion], no date, *G.W. Freyreiss s.n.* (lectotype, designated here: S [acc. # S-R-5812]).

Description. Shrubs up to 3.5 m, erect, moderately branched. Stems terete, densely glandular-pubescent and prickly, the trichomes porrect-stellate or somewhat multangulate, sessile to long-stalked, the stalks to 1 mm long, the rays 5–20, 2–3-celled, unequal in length, distally glandular, the mid-point 2–3-celled, equal to or twice the length of the longest ray, distally glandular, the prickles to 1.7 cm long, 2–3 mm in diameter at the base, straight, acicular or only slightly flattened, yellowish-red, basally somewhat pubescent with stellate trichomes like those of the stems and some small, stalked, uniseriate glandular trichomes; new growth densely glandular pubescent with long-stalked stellate or multangulate trichomes and acicular prickles like those of the stems; bark of older stems greyish-dark brown. Sympodial units difoliate to plurifoliate, the leaves not geminate. Leaves simple, lobed; blades (10)20–42 cm long, (8)20–38 cm wide, ca. 1–1.2 times as long as wide, broadly elliptic to broadly ovate, membranous, discolorous, prickly on both surfaces along the veins, the prickles to 1 cm long, straight; adaxial surface densely glandular pubescent, the lamina always visible, the larger trichomes porrect-stellate or multangulate, short- to long-stalked, the stalks to 1 mm long, the rays 4–11, unequal in length, eglandular and 1-celled or 2–3-celled and gland-tipped, the mid-points 2–3-celled, usually longer than the rays, these mixed with smaller sessile to short-stalked porrect-stellate eglandular trichomes, the stalks if present to 0.1 mm long, the rays 2–5, 1-celled, ca. 0.5 mm long; abaxial surface densely glandular-pubescent, the lamina barely visible, the trichomes porrect-stellate to multangulate like those of the adaxial surface, but denser and much more delicate; principal veins 5–7 pairs; sparsely to moderately armed on both surfaces, the prickles 1–1.7 cm long, 1.3–1.8 mm in diameter at the base, straight, somewhat laterally compressed, usually larger abaxially; base cordate, not decurrent, the two major basal lobes 2.5–7 cm long at the longest point, obtuse to rounded, often

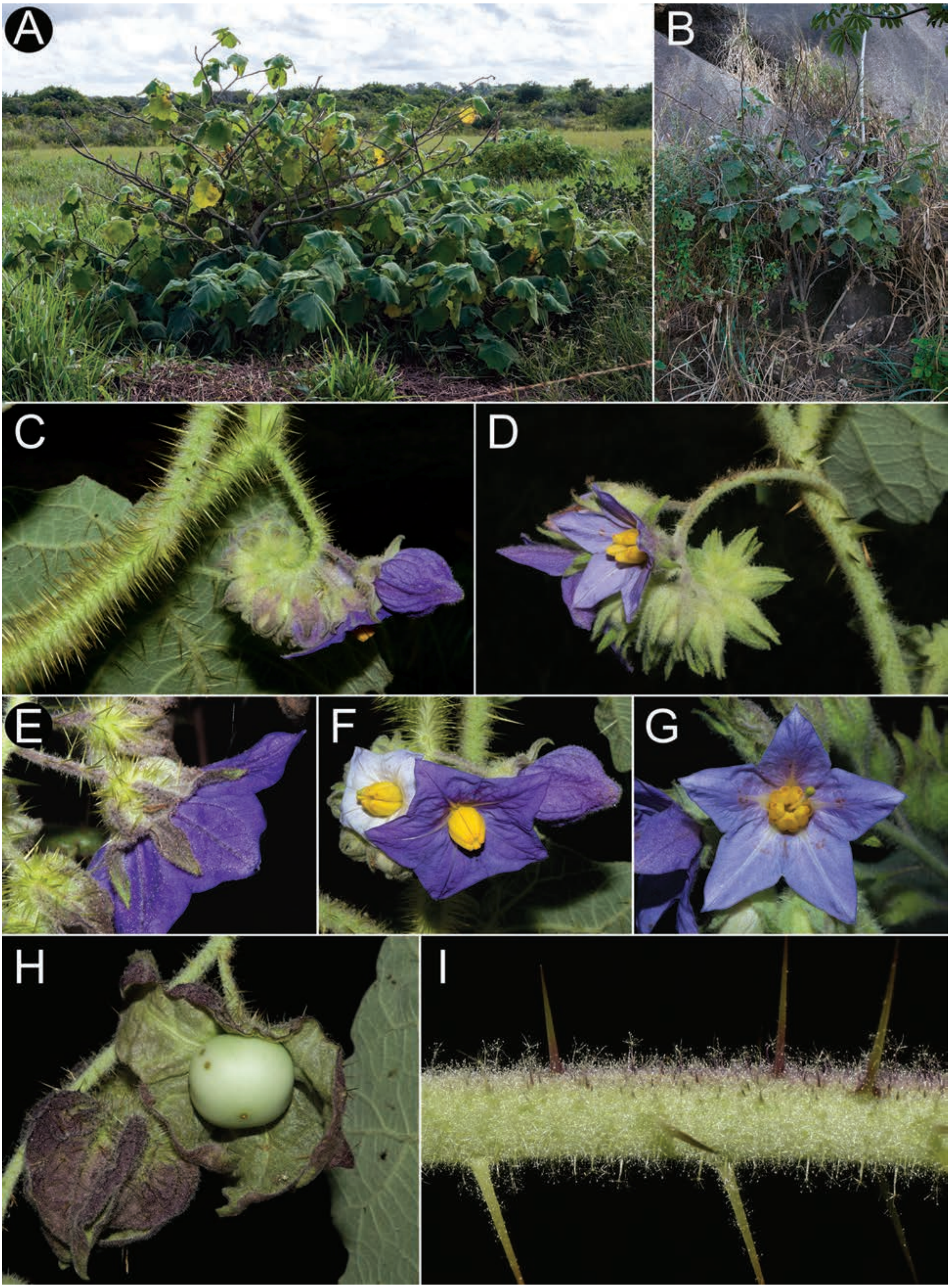

Figure 2. *Solanum aciculare* **A** habit in open area **B** habit along rock face **C** inflorescence with bud **D** inflorescence with open short-styled flower **E** calyx at anthesis **F** short-styled flowers (note colour change over anthesis) **G** long-styled flower **H** mature berry with calyx removed **I** stem section with glandular long-stalked stellate and multangulate trichomes and straight acicular prickles (**A**, **D**, **G** *Gouvêa 283*; **B**, **H** *Gouvêa 281*; **C**, **E**, **F**, **I** *Gouvêa 280*). Photos: Yuri F. Gouvêa .

overlapping each other across the petiole; margins lobed, the lateral lobes 1.5–4.8 cm long, 4–9 cm wide at base, obtuse or rounded or less often acute at the apex, both basal and lateral lobes sometimes with small secondary lobes; apex obtuse or rounded or less often acute; petioles 4.5–19.5 cm long, densely stellate-pubescent with trichomes like those of the stems, usually densely prickly. Inflorescences subopposite the leaves or internodal, 4.5–12 cm long, usually unbranched, rarely forked or trifurcate, with 11–35 flowers, up to 3 open at a time; axes densely glandular-pubescent and prickly, the trichomes porrect-stellate to multangulate, hyaline to yellowish-brown like those of the stems, the prickles ca. 1 mm long, straight, like those of the stems and leaves ; peduncle 2.6–6 cm long; pedicel scars generally unequally spaced, closely packed to spaced 2.3 cm apart; pedicels 4.8–18 mm long, densely pubescent and prickly with trichomes and prickles like those of the stem, but these often purple-tinged, articulated at base. Buds ellipsoid to globose-ellipsoid, the corolla ca. halfway exserted from the calyx tube before anthesis, but enclosed in the calyx lobes. Flowers 5-merous, heterostylous, with basal long-styled co-sexual flowers and functionally staminate short-styled flowers that vary in proportion between inflorescences, the plants andromonoecious. Calyx with the tube 4.5–8.2 mm long, 9.4–15.2 mm in diameter, broadly cup-shaped to somewhat urceolate, inflated, purple-tinged (mainly along the margins and apex of the calyx lobes) to green, armed, densely pubescent with trichomes like those of the stem, but these sometimes purple and with some eglandular rays, the lobes 7.5–15.6 mm long, 6–9 mm wide, triangular, the margins plane to strongly undulate and revolute, the apices acute to caudate. Corolla 2.3–3.9 cm in diameter, purple to lilac or bluish-lilac, white in some stages of development, shallowly stellate to stellate, lobed 2/5 to 1/2 the way to the base, interpetalar tissue absent, the lobes 10.9–15 mm long, 8.8–13.4 mm wide, deltate to triangular, spreading at anthesis, abaxially glandular stellate-pubescent with trichomes like those of the leaves, adaxially almost glabrous with only a few stellate trichomes sparsely distributed along the veins and near the tips, the apex acute, slightly apiculate. Stamens equal; filament tube 1–2.1 mm long; free portion of the filaments 1.3–2.9 mm long, glabrous; anthers 7.5–10 mm long, 2.8–4.3 mm wide, broadly lanceolate and tapering, connivent, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, slightly extrorse, not elongating to slits with age. Ovary conical to somewhat cupuliform, densely stellate-pubescent and glandular at the apex, becoming glabrous with age, the trichomes porrect-stellate, sessile, 2–7-rayed, with a 2–4-celled, eglandular or glandular mid-point longer than the 1-celled rays; style 13.7–15.9 mm long in long-styled flowers, 1.2–3.7 mm long in short-styled flowers, straight, glabrous; stigma large-capitate to clavate, up to 1.4 mm long in long-styled flowers, the surface papillose, green when fresh. Fruit a globose to somewhat compressed globose berry, 1–1.1 cm long, 1.2–2.3 cm wide, pale green to white, glabrous, but with scattered stellate trichomes at the apex, the pericarp somewhat shiny when dry, the berry almost completely enclosed in the saccate fruiting calyx; fruiting pedicels 1.4–2.2 cm long, 1.5–2 mm in diameter at the base, woody and somewhat deflexed from the weight of the fruit, armed with sparse straight prickles like those of the flowering pedicels; fruiting calyx strongly accrescent and inflated, completely enclosing the berry, the tube 1.6–2.1 cm long, 1.9–3.4 cm in diameter at the widest point, the base somewhat plicate and invaginate, the lobes 1.1–2.2 cm long, 1.3–1.9 cm wide, usually somewhat overlapping, densely glandular-pubescent with porrect-stellate to multangulate trichomes. Seeds ca. 230 per berry, ca. 2 mm long, 2.4 mm wide, flattened-reniform, dark brown, the testal cells sinuate in outline; stone cells absent. Chromosome number: not known.

Distribution (Fig. 3). *Solanum aciculare* is endemic to eastern Brazil. Records are mostly concentrated along the Mucuri River watershed, ranging from the Municipality of Teófilo Otoni, in north-eastern Minas Gerais State, to Mucuri on the southern coast of Bahia. A single collection (*J.G. Jardim et al. 3151*; CEPEC, NY) is known from further north, in Mun. Caatiba of the south-central region of Bahia State.

Ecology. *Solanum aciculare* inhabits edges of small forest fragments, especially those at the base or on granitic outcrops (inselbergs) or in disturbed sites near these rock outcrops, such as borders of unpaved roads and pastures. It is also found in herbaceous to arboreal vegetation growing along the Brazilian sandy coastal lowlands (restinga *sensu* Araújo (1992)), where plants grow in open disturbed areas dominated by grasses and at the edge of forest fragments (Fig. 2A). Habitats vary from environments subject to periods of drought (e.g. the edge of small seasonal semi-deciduous forest fragments or vegetation islands on inselbergs) to constantly wetter environments, at the edge of coastal evergreen forests, where the climate is under a strong oceanic influence. Plants have been collected from sea level to about 900 m elevation.

Common names and uses. None recorded.

Preliminary conservation assessment (IUCN 2020). EOO (38,277 km^2, NT); AOO (56 km^2, EN). Despite the relatively large range of *S. aciculare*, all collections are from only three broad localities and all are outside protected areas; vulnerability of the habitats in which the species occurs and the small number of localities suggest *S. aciculare* should be considered Endangered using the criteria B2 a, b (ii, iii, iv).

Discussion. The name *Solanum aciculare* has not been used previously in treatments of Brazilian *Solanum* (Sendtner 1846) and, until recently, had been considered an 'unassigned' name (Flora e Funga do Brazil 2024). Examination of the type specimen and analysis of the collecting trajectory of Georg Freyreiss (see below or in Taxonomy) make clear that this plant is identical to that described as *S. kollastrum* (Gouvêa et al. 2018). Sendtner (1846) had not seen the specimen on which *S. aciculare* was based and his description was of another plant (*Sellow s.n.*) that he admitted did not completely correspond to Swartz's description ("Solano subscandenti non dissimile in unico specimine suppetente a diagnosi Swartziana paullisper recedens. Proferamus descriptionem nostro specimini accomadatam, momenti, quo discrepat Swarztius haud immemores" - Not dissimilar to Solano subscandens in the only specimen available, departing for a moment from the Swartzian diagnosis. Let us present the description attached to our specimen, the importance of which Swartzius disagrees, not unmindful of it: transl. SK). The specimen described by Sendtner as *S. aciculare* is *S. cordifolium* Dunal, a member of the Erythrotrichum clade.

Amongst the species in this group, only *S. aciculare* and *S. sublentum* have cordate leaf bases coupled with glandular trichomes throughout the stems and leaves. Decurrent leaf bases of *S. aciculare* are only seen in the first leaves of the seedlings, with the subsequent leaves gradually changing shape to become

Figure 3. Distribution of *S. aciculare*.

cordate and non-decurrent. In contrast, the leaf bases in *S. hexandrum* and *S. stagnale* remain decurrent throughout plant development, varying in shape from attenuate to truncate.

Solanum aciculare closely resembles *S. sublentum*, from which it can be readily distinguished by the robust long-stalked (up to 1 mm) stellate-glandular trichomes with all rays having a glandular distal cell (some rays may lose the glandular cell through breakage or by the disruption of the gland wall) on young stems, petioles and inflorescence axis; trichomes in *S. sublentum* are usually simple. *Solanum aciculare* and *S. sublentum* have very similar floral morphologies, sharing well-developed calyces that are strongly accrescent in fruits, showy purple to lilac corollas and robust anthers. Fruits of *S. aciculare* are completely enclosed in the accrescent calyx, whereas those of *S. sublentum* are exposed. Their leaves also resemble each other: both are lobed (with secondary lobes or not), elliptic to ovate (or broadly ovate in *S. aciculare*) and have cordate bases (varying from truncate to cordate or sagittate in *S. sublentum*). In the field, *S. aciculare* has notably larger leaves than those of *S. sublentum*; however, usually only the apices of the branches are collected, with the fully developed leaves not represented in herbarium material, so this character is often not apparent from herbarium specimens. Although *S. aciculare* and *S. sublentum* occur in similar environmental conditions (associated with outcrops or at edges of lowland forests), they have not been observed in sympatry.

Both *S. aciculare* and *S. phrixothrix* have densely bristly stems and elongate slender inflorescences. They can be distinguished by the glandular long-stalked stellate pubescence of *S. aciculare* (versus eglandular bristles and lack of long-stalked stellate trichomes in *S. phrixothrix*) and flower shape and colour (purple and stellate in *S. aciculare* versus white and rotate in *S. phrixothrix*).

The German collector Georg Freyreiss (also sometimes spelled Freyreis), who was principally an ornithologist and Friedrich Sellow, a botanist, travelled and collected in Brazil in the first decade of the 19th century. Sellow's botanical collections comprise many hundreds of specimens and were the basis for many new species (Urban 1893; Moraes 2023). In 1815, Freyreiss and Sellow were planning a trip to the north of Rio de Janeiro. They joined forces with Prince Maximilian of Wied, a member of the German aristocracy who was interested in natural history and had been inspired by Baron Alexander von Humboldt to travel to South America, particularly to Brazil (Moraes 2009, 2011). Wied was keen to travel via the, at the time, relatively unexplored coast and, with Freyreiss (Sellow having stayed in what is now the State of Espirito Santo), reached the Rio Mucuri near the border of Espirito Santo and Bahia States, then continued to Salvador in today's State of Bahia. The type specimen of *S. aciculare* was probably collected by Freyreiss in the Mucuri River drainage during this voyage.

2. *Solanum hexandrum* Vell., Fl. Flumin. 88. 1829.

Figs 4, 5

Solanum hexandrum Vell. var. *minax* Sendtn., Fl. Bras. (Martius) 10: 71. 1846. Type. Brazil. São Paulo: "primaevis sulvis supra Serra do Mar, Prov. Sebastianopolit.", Dec, *C.F.P. van Martius s.n.* (lectotype, designated here: M [M-0171650]).

Solanum maroniense Poit. var. *hexandrum* (Vell.) Dunal, Prodr. [A. P. de Candolle] 13(1): 319. 1852. Type. Based on *Solanum hexandrum* Vell.

Solanum echidniforme Dunal, Prodr. [A. P. de Candolle] 13(1): 324. 1852, as "*echidnaeforme*". Type. Brazil. Sin. loc., *J. Lhotsky s.n.* (holotype: G-DC [G00131228]).

Solanum polytrichum Moric. var. *enoplocalyx* Dunal, Prodr. [A. P. de Candolle] 13(1): 324. 1852. Type. Brazil. Rio de Janeiro: Serra dos Orgãos ["circa de Rio de Janeiro" – protologue], *C. Gaudichaud 500* (lectotype, second step designated here; first step designated by Nee 1996, pg. 32 [as "holotype"]: P [P00368655]; isolectotype: P [P00368656]).

Solanum maroniense Poit. forma *hexandrum* (Vell.) Voss, Vilm. Ill. Blumengartn., ed. 3, 1: 719. 1894. Type: Based on *Solanum hexandrum* Vell.

Type. BRAZIL. [Rio de Janeiro]: "habitat silvis nondum cultis"; (lectotype, designated by Knapp et al. (2015), pg. 831: [illustration] Original parchment plate of Flora Fluminensis in the Manuscript Section of the Biblioteca Nacional, Rio de Janeiro [cat. no.: mss1198651_125] and later published in Vellozo, Fl. Flumin. 2: tab. 122. 1831).

Description. Shrubs (0.5-)1–2.5 m tall, erect or occasionally somewhat spreading, strongly armed. Stems terete, glabrous to densely pubescent and/or bristly, sparsely to densely prickly, the stellate trichomes long-stalked, eglandular, porrect-stellate or less often appearing simple due to the complete lack

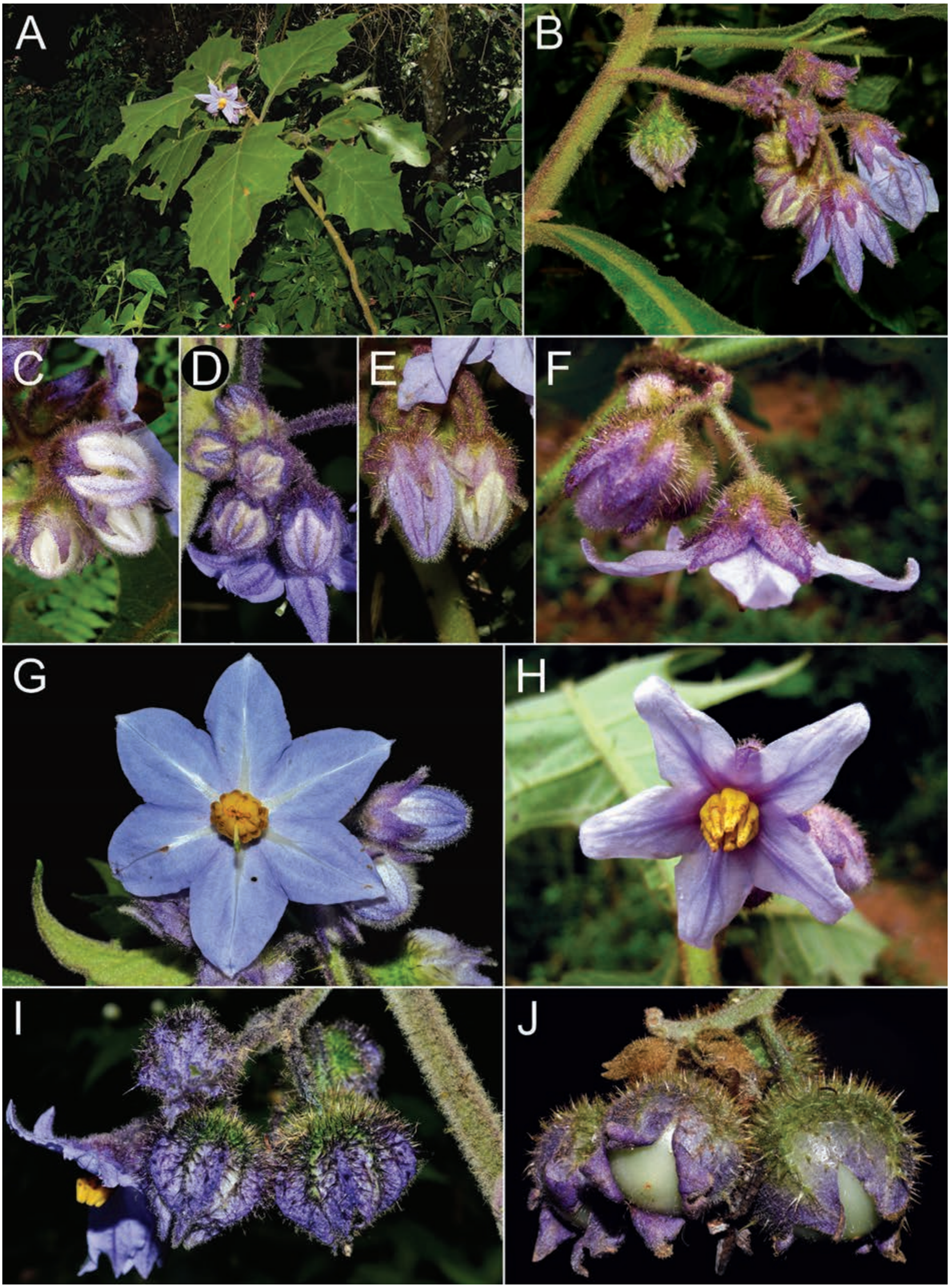

Figure 4. *Solanum hexandrum* (pubescent individuals) **A** habit **B** inflorescence **C–E** buds showing differences in colour and shape **F** open flower **G** long-styled flower with 6 lobes **H** short-styled flower with 5 lobes **I** developing fruits enclosed in purple-tinged calyx **J** mature berries with tightly appressed accrescent calyx (**A**, **B** *Stehmann et al. 4513*; **C** *Giacomin et al. 875*; **D**, **G**, **I** *Agra et al. 7359*; **E**, **F**, **H** *Giacomin et al. 1827*; **J** *Gouvêa & Salino 514*). Photos: **A, B** João R. Stehmann **D**, **G**, **I** Leandro L. Giacomin **E**, **F**, **H** Lynn Bohs **J** Yuri F. Gouvêa.

of rays, the stalks 1–5 mm long, multiseriate, the rays 4–7, ca. 1 mm long, the mid-point ca. 0.5 mm long, always shorter than the lateral rays, with age the trichomes becoming thicker and the stems then densely bristly, the bristles often tipped with stalks and rays, underlying pubescence of minute papillate trichomes dense, more apparent on more glabrous individuals, the prickles 0.3–2 cm long, yellowish-golden, broad-based, the base 1.5–2 mm in diameter; new growth glabrous to densely stellate-pubescent and bristly, the multiseriate stalks of stellate trichomes usually shorter than the rays, but lengthening with leaf expansion; bark of older stems dark brownish-black in herbarium specimens, dark brown in live plants. Sympodial units unifoliate or difoliate, the leaves not geminate. Leaves simple or shallowly lobed (in some specimens, for example, *de Paula 641*, *Giacomin 1827* deeply lobed) and repand, the blades 12–35(-40) cm long, 8–26(-30) cm wide, ca. 1.3–1.5 times as long as wide, broadly elliptic to narrowly obovate, usually widest in the basal half, membranous, concolorous, usually prickly on both surfaces with scattered straight prickles to 0.4–1.5 cm long, the prickles occasionally absent; adaxial surface glabrous to sparsely to moderately and evenly pubescent with long-stalked porrect-stellate trichomes, the stalks 1–1.5 mm long, multiseriate and arising from an expanded base, the rays 4–7, 1–2 mm long, the mid-point 0–1 mm long, always shorter than the rays, in some individuals, the rays often lost and the trichomes then appearing to be composed of a multiseriate base 1–1.5 mm long with a single celled tip often bent at 90° to the leaf surface; abaxial surfaces glabrous to evenly and densely pubescent with similar porrect-stellate long-stalked trichomes, but the stalks thinner and shorter than those on the adaxial surfaces and the rays occasionally more numerous, the trichomes denser along the veins, the surface densely dotted with crystal sand (inclusions of calcium oxalate, this not visible on the upper surfaces); principal veins 4–6 pairs, prickly or not, the prickles, if present, 0.4–1.5 cm long, on both surfaces; base attenuate on the petiole with a wing of ca. 2 mm wide along half the petiole length, sometimes to base of petiole; margins entire to 6-lobed, the lobes usually shallow, the sinuses less than 1/4 of the distance to the mid-rib; apex acute to attenuate; petiole (0.1-)2–10 cm long, glabrous to densely stellate pubescent and bristly, usually sparsely prickly. Inflorescences opposite the leaves or internodal, (1.5-)2.5–6(-8) cm long, unbranched (rarely furcate), with 3–10 flowers; axes glabrous to densely stellate-pubescent and prickly like the rest of the plant, the bristles and trichomes grading into each other and not distinct in morphology; peduncle (0.5-)2–7 cm long; pedicels 1–2 cm long, 1–1.5 mm in diameter at the base, 1.5–2 mm at the apex (excluding trichomes), erect to spreading, glabrous to densely stellate-pubescent and bristly, if prickly, the prickles ca. 1 mm long and thinner than those of stems and leaves, articulated at the base; pedicel scars more or less evenly spaced 5–7 mm apart on mature inflorescences, more tightly packed distally. Buds globose to broadly elliptic, the corolla completely included in the saccate calyx tube until just before anthesis, the younger buds less bristly and prickly than older ones. Flowers 5–6-merous, mostly co-sexual, but a few distal flowers are sometimes short-styled and probably functionally staminate. Calyx with the tube 4–7 mm long, 7–10 mm in diameter, cup-shaped and often completely closed in bud sometimes until just before anthesis, green or purple-tinged, the lobes 5–10 mm long, irregularly tearing at anthesis, but generally broadly triangular to deltate, acute to acuminate apically, glabrous

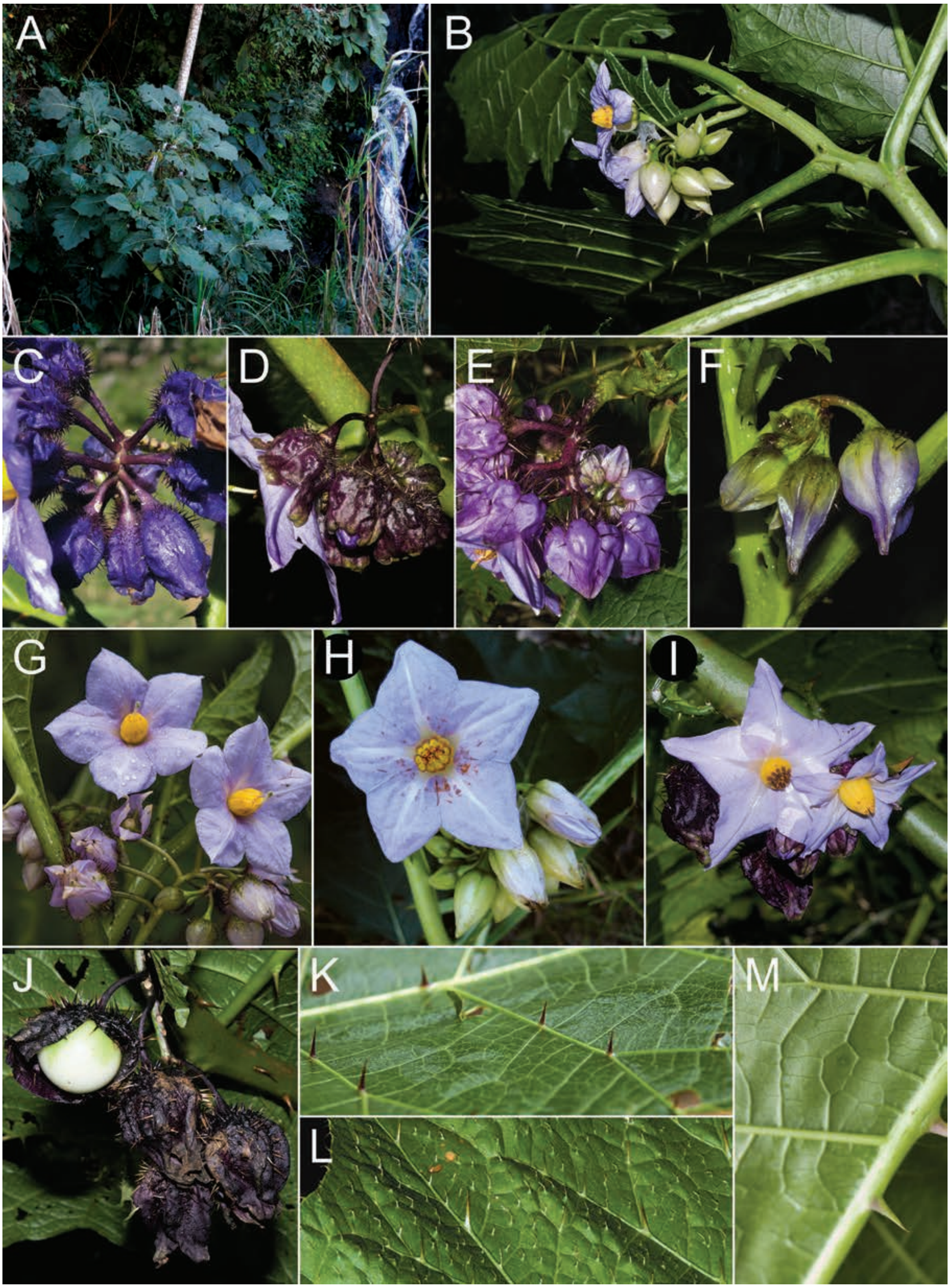

Figure 5. *Solanum hexandrum* (glabrous individuals) **A** habit at forest edge **B** inflorescence **C–F** buds showing variation in fusion of calyx during development **G** open long-styled flowers **H** open short-styled flower **I** open short-styled flowers showing corolla expansion (enlargement) during flowering **J** mature berry with calyx removed **K** upper leaf surface with prickles and no stellate trichomes **L** upper leaf surface with prickles and rayless stellate trichomes with bent mid-points **M** lower leaf surface with broad-based prickles along the veins (**A**, **B**, **H** *Giacomin et al. 1833*; **C** *Giacomin et al. 1844*; **D, I, J** *Gouvêa & Falcão 137*; **E**, **L** *Gouvêa & Falcão 135*; **F** *Gouvêa & Stehmann 158*; **G, K, M** *Gouvêa & Stehmann 159*). Photos: **A, C** Lynn Bohs **B**, **H** Leandro L. Giacomin **D**, **E**, **I**, **J**, **L** Yuri F. Gouvêa **F**, **G**, **K**, **M** João R. Stehmann.

to bristly and prickly with long-stalked bristles/trichomes, these with or lacking rays, the multiseriate stalk often purple-tinged. Corolla 3–6 cm in diameter, purple (rarely white), stellate, lobed halfway to the base, interpetalar tissue thin, glabrous, the lobes 15–21 mm long, 8–15 mm wide, deltate, spreading at anthesis, abaxially sparsely to densely pubescent with long-stalked porrect stellate trichomes, the stalks to 1 mm long, these denser at the tips and along the petal mid-vein, pubescence of corollas often purple-tinged, adaxially glabrous or with a few weak stellate trichomes on the mid-vein, the mid-veins often white adaxially. Stamens equal; filament tube minute to 0.5 mm long, glabrous; free portion of the filaments 1–1.5 mm long, glabrous; anthers (7-)9–11 cm long, 2–3 mm wide, broadly lanceolate and tapering, connivent, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, not elongating to slits with age. Ovary conical, sparsely to densely pubescent with sessile stellate trichomes with rays 2–3 mm long, these soon deciduous; style 10–15 mm long in long-styled flowers (in rare short-styled flowers, the style 3.5–7 mm long), straight, glabrous; stigma clavate or broadly capitate, the surface minutely papillose. Fruit a globose to flattened globose berry, 2–2.5(-3.5) cm in diameter, green or pale whitish-green, glabrous, the pericarp somewhat shiny when dry, the berry almost completely enclosed in the accrescent saccate calyx; fruiting pedicels 1.8–2.3 cm long, 1.7–2.5 mm in diameter at the base, woody and spreading to somewhat deflexed from the weight of the fruit; fruiting calyx strongly accrescent, inflated or not, almost completely enclosing the berry, the tube 1.5–2 cm long, the lobes 1.5–2 cm long, irregular, usually overlapping, glabrous to sparsely to densely bristly and prickly with multiseriate bristles occasionally topped with porrect rays. Seeds ca. 100 per berry, 2–3.5 mm long, 1.5–2 mm wide, flattened reniform to somewhat ovoid, unwinged, reddish-brown or dark brown when dry, the surface minutely pitted, the testal cells pentagonal in outline, equal in size over the entire seed surface; stone cells absent. Chromosome number not known.

Distribution (Fig. 6). *Solanum hexandrum* is endemic to the south-eastern region of Brazil and is known from the States of São Paulo, Rio de Janeiro, Minas Gerais, Espirito Santo and Bahia.

Ecology and habitat. *Solanum hexandrum* grows in the wet forests of the Mata Atlântica, often in openings and along roads and streams; it occurs from almost sea level to 1,600 m elevation.

Common names and uses. Brazil. Minas Gerais: juá-bravo (a widely used vernacular name for any spiny solanum in Brazil). No uses have been recorded.

Preliminary conservation status (IUCN 2020). EOO (327,280 km^2, LC); AOO (460 km^2, EN). *Solanum hexandrum* is the most collected of any of these species and all forms of the variation are known from many localities, several of which are within protected areas (e.g. Parque Nacional da Serra dos Orgãos, Parque Nacional do Caparaó, Parque Estadual da Pedra Selada in Rio de Janeiro State; Parque Estadual da Serra do Brigadeiro in Minas Gerais State; RPPN Cafundó, Parque Estadual Mata das Flores in Espírito Santo State; RPPN Serra do Teimoso and RPPN Serra Bonita in Bahia State; Estação Ecológica de Bananal in São Paulo State). Nevertheless, given its high degree of variability that needs further study, we suggest it be assigned a preliminary status of Near Threatened based on criteria (B 2 a, b (ii,iii,iv).

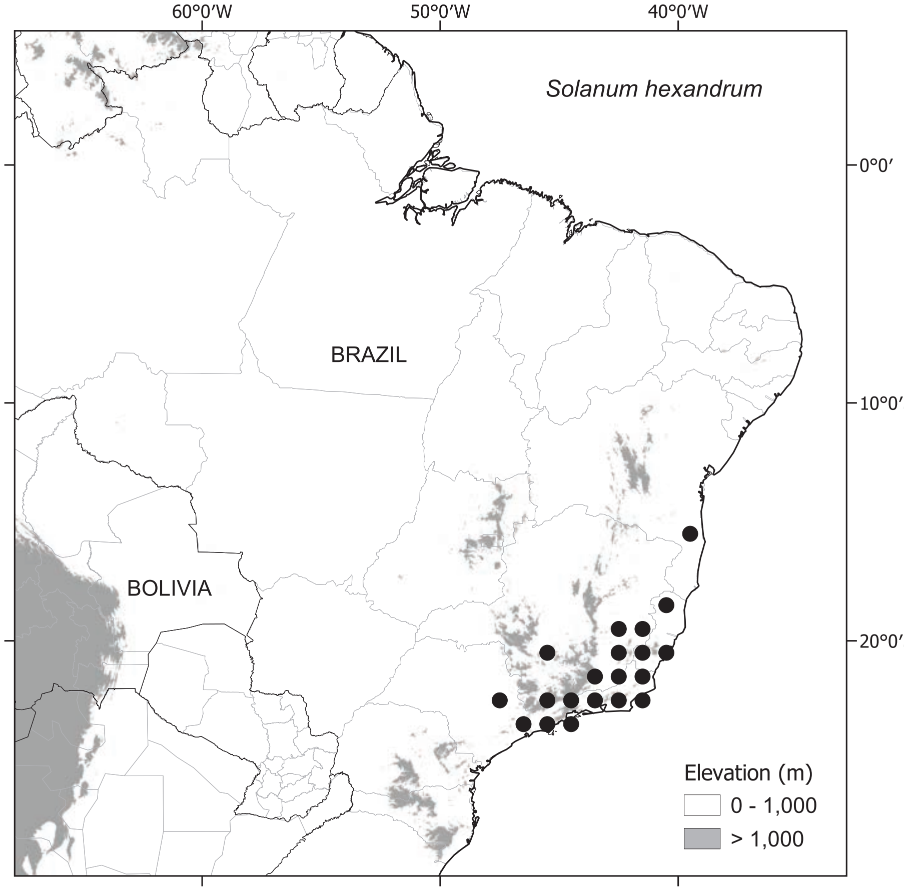

Figure 6. Distribution of *S. hexandrum*.

Discussion. *Solanum hexandrum* is the most variable species in the clade in terms of calyx and corolla shape and degree of pubescence, but is otherwise remarkably uniform. More glabrous individuals from the more northerly part of the species range have been called *S. echidniforme* Dunal, although the type of that species (G00131228) is a sparsely bristly plant and fits within the overall circumscription as we treat this species here. The more glabrous individuals of *S. hexandrum* (mostly from the State of Espirito Santo) are strikingly different looking morphologically from more pubescent individuals (see Fig. 5), but there is a continuous gradation from glabrous to densely pubescent when specimens from across the range are examined. In several localities, individuals of both types are found and it is not clear if the differences are due to environmental or genetic factors.

The pubescence variability in *S. hexandrum* is extreme, with glabrous and pubescent individuals at first glance appearing to be completely different morphologically. Some other variation seems to be correlated with lack of rayed stellate trichomes; glabrous plants often have the calyx lobes fused until just before anthesis (see Fig. 5B, D), but this is not completely consistent (see Fig. 5C). The calyx in these glabrous plants is also often more saccate than in populations from elsewhere in the range (Fig. 5J versus Fig. 4J), but this also varies and is difficult to assess on herbarium sheets when all reproductive stages are not present. The single specimen of *S. hexandrum* which we have seen with a branched inflorescence (*Brotto et al. 3265*, MBM) comes from amongst these glabrous plants.

The unusual stellate trichomes with the single-celled mid-point bent at an approximately 90° angle to the multiseriate base (see Fig. 5L) are found on the leaves in many populations of *S. hexandrum*, even if very sparsely. Leaf shape also varies across the range, with some populations from Rio de Janeiro having very narrow, more deeply lobed leaves (e.g. *Giacomin 1827*). The range of variation in trichome morphology in *S. hexandrum* warrants further study at a population and genetic level to determine if these variants represent distinct entities. Loss of prickles (derived from stellate trichomes) has been shown to be common across spiny solanums (Satterlee et al. 2024) and it may be that the extremes seen in *S. hexandrum* could be genetically quite simple.

Solanum hexandrum was described and illustrated in the late 18th century by Brother José Mariano Conceição da Vellozo (1742–1811) for his "*Flora Fluminensis*". Vellozo was a parish priest in Rio De Janeiro and completed his work in 1790, but, unfortunately, this work was not published until long after he had died in 1811 (Carauta 1969, 1973). The somewhat telegraphic descriptions of *Solanum* (Vellozo 1829) referred to original illustrations now held in the library of the Biblioteca Nacional, Rio de Janeiro; printed illustrations, based on these originals, were published several years later (Vellozo 1831). Typification of names of Solanaceae in *Flora Fluminensis* was treated by Knapp et al. (2015); the original illustration that is the lectotype for *S. hexandrum* is unambiguous and clearly shows the 6-parted corolla that inspired the specific epithet.

Many herbarium specimens of *S. hexandrum* are annotated as *S. maroniense* Poit., a species described only a year after (Poiteau 1830). The description of *S. maroniense* is of a cultivated plant and is quite telegraphic, but is clearly stated to come from “fleuve Maroni” (the River Maroni) in French Guiana. Although, from the description alone, *S. maroniense* could correspond to *S. hexandrum*, the locality suggests it represents a plant of *S. crinitum* Lam. *Solanum crinitum* is common in the Guianas and a neotype will be selected as part of upcoming monographic work on the Crinitum clade.

Sendtner (1846) described a variety (“β minax”) citing a manuscript name of Martius, citing several specimens from various collectors, as well as plants from the garden in Munich. A sheet at Munich (M-0171650) exactly matches the very precise locality information and date given in the protologue for a specimen collected by C.F.P. von Martius and we select this as the lectotype; it is the most unambiguous of the syntypes and appears to have been annotated by Sendtner. Another sheet at Munich (M-0171847) has a description and the annotation “*Solanum minax*” in Martius’ hand is probably also a syntype; this sheet was collected in “Oct” while the lectotype was collected in “Dec” – the protologue states “Octobri ad Decembrem florens”. Other collections cited have no or less unambiguous localities (see Suppl. materials 1, 2). Sendtner (1846) suggested that *S. latifolium* Poir. (= *S. rigidum* Lam.) might be a synonym of *S. hexandrum*; this species is endemic to the Cape Verde Islands and related to the brinjal eggplant (Knapp and Vorontsova 2013).

Dunal (1852: 324) cited *Gaudichaud 501* from Rio de Janeiro in “h. Mus. Paris” in his circumscription of *S. polytrichum* Moric. var. *longifolium* along with *Blanchet 602* from Bahia in “h. DC”. *Solanum polytrichum* var. *longifolium* is illegitimate and superfluous as he (Dunal 1852: 324) cited an earlier name at the varietal level, *S. polytrichum* var. *grandifolium* Sendtn. (Sendtner 1846), in synonymy. The three specimens of *Gaudichaud 501* in P (P00368657, P00368658, P00368659) are of a plant of *S. hexandrum* and, although P00368657 has been annotated as an "Isosyntype of Solanum polytrichum Moric. var. longifolium Dunal", this collection has no status as a type. Both collections (*Gaudichaud 500*, 501) cited by Dunal (1852) may actually have been collected by Frederich Sellow (see Moraes (2023)).

Gaudichaud 500 in "h. Mus. Paris" was the only element cited in the protologue of *S. polytrichum* var. *enoplocalyx* (Dunal 1852). Nee (1996) cited as "holotype" *Gaudichaud 500* in P and cited two photographs taken by C.V. Morton (Morton neg. 8300, 8301, both held in US). Two sheets of this collection are in P, one bears the original locality label (P00368655), while the other (P00368656) has an undated label in what appears to be Dunal's hand. Both are scrappy specimens with tiny apical leaves, but P00368655 has two inflorescences, one in flower and one in early fruit. As the more complete specimen, we select the sheet P00368655 of *Gaudichaud 500* as the second step lectotype for *S. polytrichum* var. *enoplocalyx*. This sheet is labelled as an isotype. Both of these sheets are very similar morphologically to those labelled *Gaudichaud 501* and may have been collected together.

3. *Solanum hydroides* Gouvêa & Giacomin, PhytoKeys 139:66. 2020.

Fig. 7

Type. Brazil. Minas Gerais: Mun. Teófilo Otoni, afloramento rochoso lado esquerdo da MG 418, cerca de 30 km norte de Teófilo Otoni, 560 m alt., 17°51'22"S, 41°15'39"W, 27 Jan 2014, *L.F.A. de Paula*, *L. Azevedo*, *R. Fernandes & J.R. Stehmann 669* (holotype: BHCB [BHCB053358] ; isotype: RB [RB01472905]).

Description. Shrubs 1–1.5 m tall, erect, armed. Stems terete, directed upwards and spreading, moderately to densely pubescent and sparsely to moderately prickly, the trichomes eglandular, porrect-stellate, variably short- to long-stalked, the stalks 0.5–1.5 mm long, the rays 4–8, 0.5–1 mm long, the mid-points 1– to 2–celled, always shorter than the rays, the prickles 4–6 mm long, 2–6 mm wide at the base, broad-based and recurved; new growth densely stellate pubescent and sparsely prickly, the trichomes pale yellow to dark brownish-red; bark of older stems glabrescent, drying greenish-brown to dark brown. Sympodial units plurifoliate, the leaves not geminate. Leaves simple, nearly entire to shallowly lobed; blades 2.8–12.1(21.8) cm long, 2.2–7.5(10.1) cm wide, ca. 1.2 to 2 times as long as wide, elliptic to ovate, membranous, slightly discolorous, both surfaces prickly along the mid-rib and veins; adaxial surface densely to moderately stellate-pubescent and prickly, brown to dark green when dry, the trichomes like those of the stem, but with (1–)4–6 rays, the prickles along the mid-rib and major veins to 5.5 mm long and 1 mm wide at the base, straight and laterally compressed; abaxial surface more densely stellate-pubescent than the adaxial surface, whitish-green when dry, the trichomes like those of the adaxial surface, the prickles like those of the adaxial surface, but to 6.5 mm long and 2 mm wide at the base; base attenuate to truncate or rounded, less often with 1 or 2 basiscopic lobes, decurrent on to the petiole, sometimes asymmetrical; margins shallowly lobed, the lobes (0)3–5 on each side, 1–12(14.8) mm long, 3.2–11(23) mm wide at base with usually acute, sometimes rounded or obtuse apices, the sinuses 3.2–8.5 mm deep; apex acute to acuminate; principal veins 4–6 pairs, more prominent beneath, prickly on both surfaces, the prickles 5–6 mm long, straight;

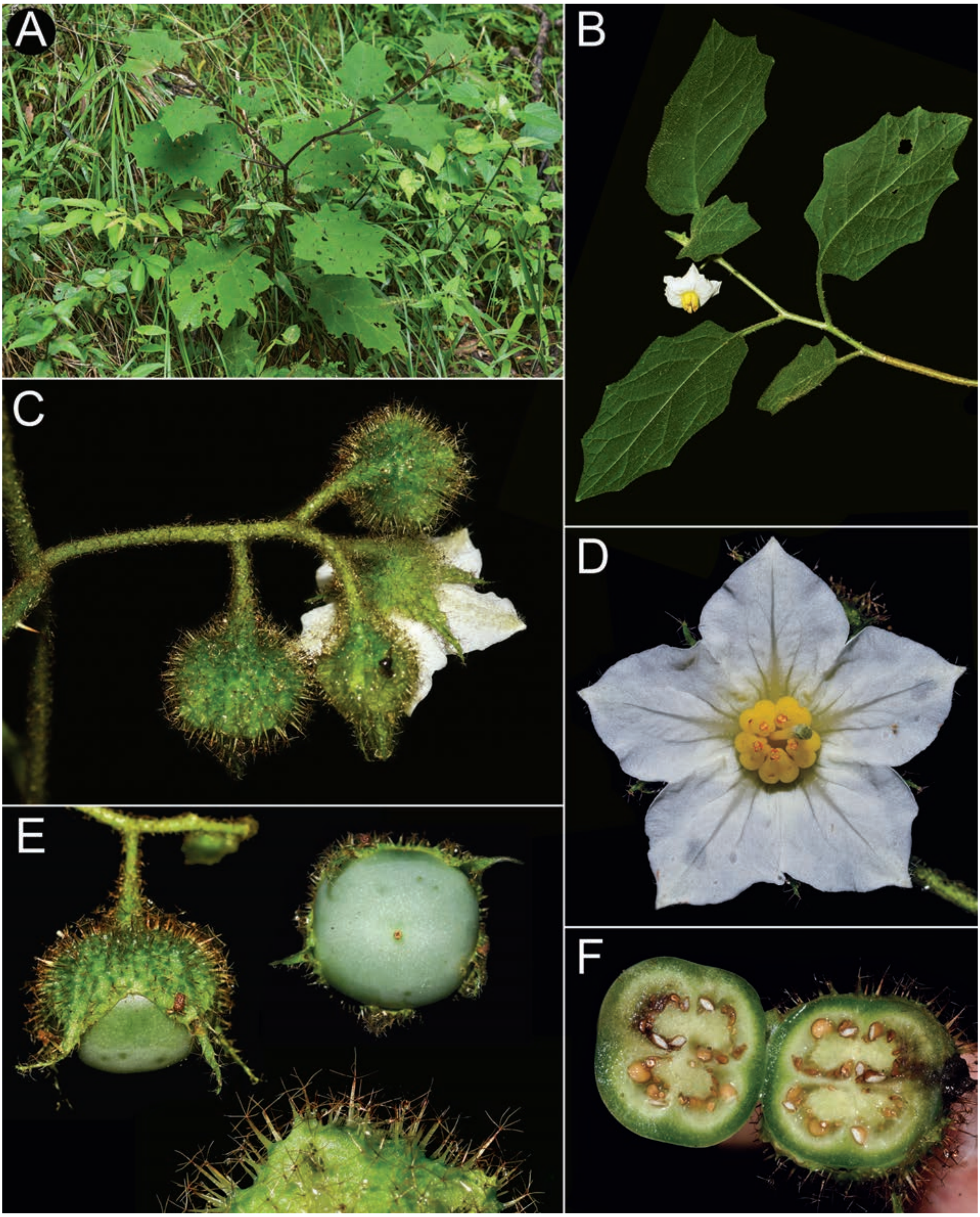

Figure 7. *Solanum hydroides* **A** habit **B** flowering branch **C** inflorescence **D** open long-styled flower **E** mature berry with only partially accrescent calyx **F** cross-section of 4-locular mature berry showing fleshy mesocarp and brown seeds (**A**, **C–F** *Gouvêa et al. 492*; **B** *Gouvêa & Santos 325*). Photos: Yuri F. Gouvêa.

petioles 0.6–3.3 cm long, densely to moderately pubescent with porrect-stellate trichomes like those of the leaves, usually armed with 1–5 prickles. Inflorescence internodal, to 6 cm long, unbranched, with 4–10 flowers, up to 2 flowers open at a time; axes glabrescent to densely pubescent, usually unarmed, the stellate trichomes like those of the stem, but these sometimes with the mid-point as long as the rays; peduncles 0.4–2.3 (-3.8) cm long; pedicels 3–17 mm long, 0.5–0.8 mm in diameter at the base, to 1.5 mm in diameter at the apex, spreading to slightly deflexed, pubescent with trichomes like those of the inflorescence axes, unarmed, articulated at the base; pedicel scars evenly spaced 1–7 mm apart. Buds ovoid to ellipsoid, with the corolla enclosed in the calyx until just before anthesis. Flowers 5-merous, heterostylous with long-styled flowers (co-sexual) at the base of inflorescence, short-styled (functionally staminate) flowers more distally, the plants andromonoecious. Calyx with the tube 2.6–4.3(6) mm long, 6.5–8 mm in diameter, broadly obconical to cupuliform, the lobes 3–7 mm long, 3–5.5 mm wide, triangular to deltate, with acute to acuminate apices, glabrous adaxially, densely pubescent abaxially with bristly purple-tinged, hyaline or reddish-brown porrect to multangulate long-stalked stellate trichomes, the stalks 1.1–3.8 mm long, rays 4–8, to 1.5 mm long, the mid-points 1–2 celled, shorter than or the same length as the rays, armed or unarmed, if present, the prickles 2.8–4 mm long, 0.5–1 mm in diameter at the base, straight, acicular. Corolla 2.4–3 cm in diameter, white, often with a greenish-yellow star at the base, shallowly stellate, lobed ca. halfway to the base, interpetalar tissue nearly absent, the lobes 5.9–8.8 mm long, 9.9–12.2 mm wide, pubescent abaxially on the petal mid-vein and/or apices with sparse delicate short-stalked porrect-stellate trichomes with stalks to 0.9 mm long, the apices acute to apiculate. Stamens equal; filament tube to 1 mm long; free portion of the filaments 0.7–1 mm long, glabrous; anthers 6.5–8 mm long, 2.5–3 mm wide, broadly lanceolate and tapering, connivent or slightly divergent at the tips, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, slightly extrorse, not lengthening to slits with age. Ovary somewhat conical, glabrous; style 8–10 mm long in long-styled flowers, ca. 3 mm long in short-styled flowers, straight, glabrous; stigma clavate to bilobed, the surface papillose and irregular, the style and stigma poorly developed in short-styled flowers. Fruit a globose berry, 0.9–1.8 cm in diameter, green to whitish-green at maturity, drying dark brown, glabrous, the pericarp matte; fruiting pedicels 1–1.5 cm long, 1–2 mm in diameter at the base, usually unarmed, deflexed from the weight of the fruit; fruiting calyx partially accrescent, the tube tightly investing 1/2–3/4 of the fruit at maturity, the lobes 5.8–8 mm long, 7–9.6 mm wide, not overlapping, pubescent with long-stalked porrect-stellate trichomes often with the base of the stalks markedly expanded and bristly, the stalks to 4.8 mm long. Seeds ca. 250 per berry, 2.2–2.6 mm long, 1.6–2 mm wide, pyriform to reniform, not markedly flattened, the surface irregularly pitted, the testal cells pentagonal in outline; stone cells absent. Chromosome number not known.

Distribution (Fig. 8). *Solanum hydroides* is endemic to the south-eastern region of Brazil, with records in four localities in north-eastern Minas Gerais (Mun. Teófilo Otoni and Conselheiro Pena) and northern (Mun. Nova Venécia) and central (Mun. Santa Teresa) Espírito Santo States.

Ecology and habitat. *Solanum hydroides* grows at the edge of seasonal semi-deciduous tropical rainforests associated with granitic or gneissic rock outcrops (inselbergs) and somewhat disturbed sites at their bases, such as roadsides and clearings; from 300 to 600 m elevation. It also occasionally grows in epilithic vegetation patches lying on the flatter parts of inselbergs.

Common names and uses. None recorded.

Figure 8. Distribution of *S. hydroides*.

Preliminary conservation status (IUCN 2020). EOO (12,549 km^2, VU); AOO (24 km^2, EN). *Solanum hydroides* is known from only four disjunct localities in vegetation remnants associated with inselbergs: these rock outcrops harbour the last remnants of forest fragments (Martinelli 2007) in areas where they occur. Only one of these localities is within a protected area (APA Pedra do Elefante, Espiríto Santo State). Although we have seen a few more collections than were used in the original assessment (Gouvêa et al. 2020), we concur with their evaluation of *S. hydroides* as Endangered (B 2 a,b ii,iii,iv).

Discussion. *Solanum hydroides* is a comparatively smaller plant than other species of the group, except *S. sublentum*; its smaller leaves and thinner stems, petioles and inflorescence axes give it a more delicate overall aspect. *Solanum hydroides* can, however, be readily distinguished from *S. sublentum* by its pubescence of stellate eglandular trichomes (Fig. 7A, B) and by the widely obconical to cupuliform shape of the calyx at anthesis. In *S. sublentum*, the indumentum is of both conspicuous simple glandular trichomes and stellate eglandular trichomes (Fig. 13E–G), with the stellate trichomes usually much less numerous than the simple ones and often early deciduous (i.e. present only in new growth). Calyces of *S. sublentum* are somewhat urceolate, inflated and prominently plicate at the top of the calyx tube (Fig. 13J), whereas, in *S. hydroides*, calyces are tightly adherent to the berry at maturity and not notably plicate, especially in live plants.

Although being a markedly less robust plant, *S. hydroides* can be very similar to some specimens of *S. hexandrum*, the most variable species in the clade, with which it shares the indumentum of few-rayed stellate eglandular trichomes on the stems, leaves, inflorescence axis and calyces. *Solanum hydroides* differs from *S. hexandrum* in its white and smaller corollas (13–21.5 mm total length), shorter corolla lobes (5.9–8.8 mm long; Fig. 7D) and accrescent, but not inflated, fruiting calyces that only partially cover the mature fruit (Fig. 7E). *Solanum hexandrum* has corollas in various shades of lilac to purple and are larger (24.3–40 mm long), with longer corolla lobes (12.6–25 mm long; Figs 4G, H, 5G, H, I) and the fruiting calyces are accrescent and inflated, completely enclosing the mature fruit (Figs 4J, 5J). The corollas of *S. hydroides* are thin and membranous and easily tear apart between the lobes during the drying process, which can make the lobes on herbarium specimens seem longer than they really are. Care is needed to ensure correct measurements from herbarium specimens.

Leaf measurements are also useful for distinguishing *S. hydroides* from *S. hexandrum*. The leaves of *S. hydroides* are usually smaller (7.5–13.6 cm long and 5–8.7 cm wide) than those of *S. hexandrum* (17–45 cm long and 10.5–32 cm wide). Nevertheless, leaves of *S. hydroides* are larger in plants growing in shade and in young individuals (see Roe (1966) for other examples in *Solanum*) and we have seen plants with leaves to 22 cm long and 11 cm wide. Specimens of *S. hydroides* growing in shade are less densely pubescent, with less robust (i.e. stalks with fewer series of cells) and slightly shorter trichomes on stems, leaves and calyx. Corollas of these shade plants are usually larger in relation to the other flower parts (e.g. stamens and calyx).

Trichome morphology in *S. hydroides* is not particularly variable within individual plants and amongst plants of the same population; however, there is a significant variation in the number of trichome rays between some populations, as is seen also in *S. hexandrum*. Trichomes of specimens from the southernmost-known population (in Santa Teresa Municipality, Espirito Santo State) are mostly 6- to 8-rayed and usually denser, whereas those of plants from the other populations (Teófilo Otoni and Nova Venécia Municipalities of Minas Gerais State) are mostly 4-rayed. Within individual plants, the variation in trichome morphology is limited to a reduction in the number of rays and is especially evident in plants with four-rayed trichomes. In these plants, the trichomes may lack one to almost all rays, sometimes with only the mid-point or a lateral ray remaining and the trichome appearing to be unbranched, but with a basal multiseriate stalk, as is also seen more dramatically in *S. hexandrum*. This kind of variation has been reported in other *Solanum* groups, such as the Brevantherum clade or members of the Acanthophora clade (Nee 1991; Levin et al. 2005; Stern et al. 2013).

4. ***Solanum phrixothrix*** **Gouvêa & S.Knapp, sp. nov.**

urn:lsid:ipni.org:names:77358212-1
Fig. 9

Diagnosis. *Solanum phrixothrix* differs from all other members of the *S. hexandrum* group in its rotate, white corollas. It is similar to *S. aciculare* and *S. sublentum* in its cordate non-decurrent leaf bases, but differs from both in its eglandular pubescence. The eglandular bristle-like trichomes completely lacking lateral rays distinguish it from *S. aciculare* and its densely bristly stems distinguish it from *S. sublentum*. It differs from *S. hexandrum*, *S.hydroides* and *S. stagnale* in its cordate non-decurrent leaf bases and from *S. stagnale*, it is acicular, rather than broad-based and usually curved prickles.

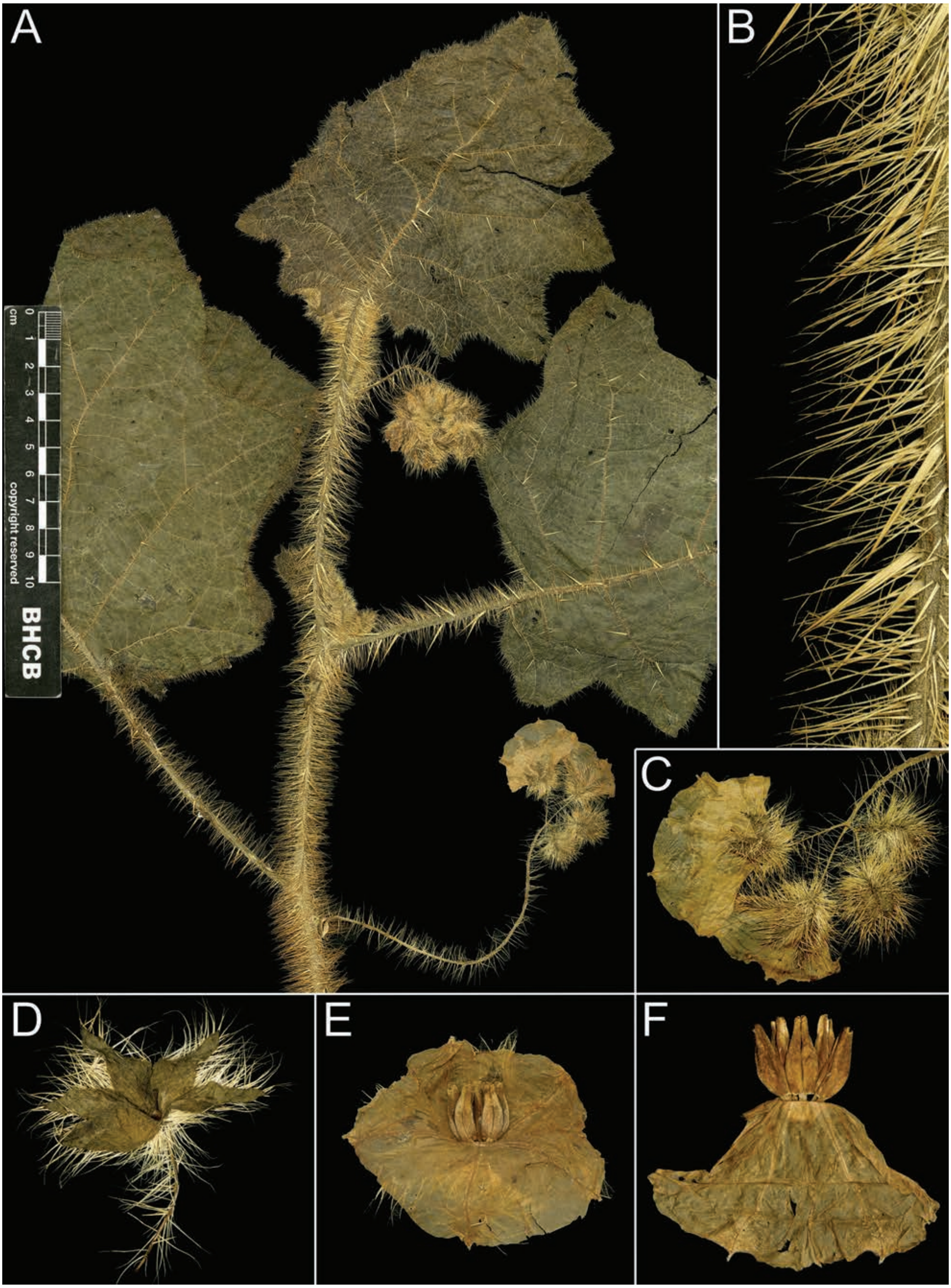

Figure 9. *Solanum phrixothrix* **A** flowering branch **B** section of stem with copious bristles **C** inflorescence with two open flowers **D** adaxial surface of calyx **E** open short-styled flower **F** short-styled flower with corolla bent back to expose the tapering anthers (**A–F** *Folli 7560*, BHCB). Photos: Yuri F. Gouvêa.

Type. BRAZIL. Espirito Santo: Mun. Linhares, bairro Bebedouro, mata de tabuleiro, estrada ES-245, sentido a Regência, mata de cabruca (Cacau), UTM: 394627, 7851005 [19°25'57.1"S, 40°00'13.5"W], 12 Jun 2017, *D.A. Folli 7560* (holotype: BHCB [BHCB221244]; isotype: CVRD [acc. # 15743]).

Description. Shrubs to ca. 2 m tall, erect to somewhat spreading, strongly armed and bristly. Stems terete, conspicuously fistulose (at least the younger ones), densely bristly and prickly; the bristle-like trichomes simple, 3.4–19.2 mm long, with a long multiseriate stalk and a shorter uniseriate mid-point at the tip, the stalks 2.5–16 mm long, the mid-points 0.9–3.2 mm long, 1–2-celled, underlying pubescence of sparse, very tiny papillate trichomes, these drying golden yellow; the prickles 0.5–1.2 cm long, the base ca. 1 mm in diameter, straight to retrorse, somewhat laterally compressed, yellowish-golden at base, becoming yellowish-brown towards the tip; the epidermis densely dotted with crystal sand (inclusions of calcium oxalate); new growth densely bristly and prickly, with simple bristle-like trichomes and prickles like those of the stems; bark of older stems not known. Sympodial units plurifoliate, the leaves not geminate. Leaves lobed, the blades 21–30 cm long, 20–24 cm wide, ca. 1–1.25 times as long as wide, broadly ovate to broadly elliptic, usually widest in the basal half, membranous, concolorous, sparsely to moderately prickly on the mid-rib and major veins of both surfaces with prickles like those of the stems, but usually smaller; adaxial surface densely to moderately pubescent to hirsute with simple bristle-like trichomes similar to those of the stems, but smaller, 0.8–6.5 mm long, the stalks 0.2–4.5 mm long, the mid-points 0.7–2 mm long; abaxial surfaces more sparsely pubescent with trichomes like those of the adaxial surface, these restricted to the mid-rib, major and minor veins and usually smaller and thinner-walled; principal veins 5–7 pairs; base cordate to angular-cordate often with a prominent pair of basiscopic lobes, not decurrent on to the petiole, symmetrical; margins 4–6-lobed, leaves of young plants or new growth also with secondary lobing, the sinuses 1/3–1/5 of the distance to the mid-rib; apex acute to obtuse; petiole 4.8–9.5 cm long, densely bristly, moderately to densely prickly with trichomes and prickles like those of the stems. Inflorescences opposite the leaves or internodal, 12–15 cm long, unbranched, with 19–25 flowers; axes densely to moderately bristly and prickly with trichomes and prickles like those of the stems, but the prickles sometimes thinner; peduncle 2.7–3.6 cm long; pedicels 1–2 cm long, 0.6–0.9 mm in diameter at the base, same diameter at the apex (excluding trichomes), erect to directed downwards, moderately to densely bristly with bristle-like trichomes like those of the stems, prickly or not, articulated at the base; pedicel scars more or less evenly spaced 1–5 mm apart on mature inflorescences, more closely packed distally. Buds ellipsoid to narrowly ellipsoid, the calyx lobes soon splitting, exceeding the length of the corolla until just before anthesis. Flowers 5-merous, heterostylous, the proximal flowers long-styled (co-sexual) and distal ones short-styled (functionally staminate), the plants andromonoecious. Calyx with the tube 4.3–7.5 mm long, 4–8 mm in diameter, shallowly cup-shaped to obconical, the lobes 4.5–11.3 mm long, triangular to somewhat lanceolate, sometimes varying in size in a single flower, densely bristly with trichomes like those of the stems, prickly or not. Corolla 3–3.6 cm in diameter, white, rotate, shallowly campanulate or tubular, lobed less than 1/8 of the way to the base, interpetalar tissue indistinguishable from the rest of the lobe or nearly so, copious and reaching nearly to the tips, the lobes 3.8–5 mm long, 16.5–25 mm wide, rounded to retuse, glabrous with pubescence restricted to the lobe apices on both surfaces, the trichomes minute, simple. Stamens equal; filament tube 1.5–1.7 mm long, glabrous; free portion of the filaments 1.4–1.8 mm long, glabrous; anthers 6.5–10 mm long, 2.2–3 mm wide, broadly lanceolate and tapering, connivent, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, not elongating to slits with age. Ovary cup-shaped, moderately to densely pubescent, the trichomes simple, glandular, very tiny papillate and sessile to 0.6 mm long, 1–5-celled, thin-walled, the longer ones less abundant, pubescence sometimes restricted to the ovary apex; style 8.8–12 mm long in long-styled flowers, 1.2–3.6 mm long in short-styled flowers, straight, sparsely to moderately puberulent with very tiny papillate trichomes; stigma clavate, the surface minutely papillose. Fruit and seeds not known. Chromosome number not known.

Distribution (Fig. 10). *Solanum phrixothrix* is endemic to the south-eastern region of Brazil and known only from two collections; one with a specific locality from Espírito Santo State and another made by A. St.-Hilaire that is likely to be from Minas Gerais State (see Dwyer (1955)).

Ecology and habitat. The only known collection with locality and vegetation type information of *S. phrixothrix* is from wet evergreen forests of the lower Rio Doce drainage, at approximately 13 m elevation. This collection is from a “cabruca” (cacao plantation). These cacao plantations retain the upper strata of the forest for shade, but the understorey is significantly damaged by shrub and herb removal, along with significant cacao leaf litter.

Common names and uses. None recorded.

Etymology. The species epithet is derived from the Greek, meaning with bristling (or horrid) hairs.

Preliminary conservation status (IUCN 2020). *Solanum phrixothrix* is known from only two collections, gathered 200 years apart and so must have a preliminary assessment of Data Deficient. That said, however, it is imperative that more populations be sought to better assess its range and population density. It is likely to be of conservation concern, as the single collection with an accurate locality (*Folli 7506*) is from a highly disturbed anthropogenic site (cacao plantation), not within a protected area. It is near the Floresta Nacional de Goytacazes in Espiríto Santo State and should be sought there. Other protected areas close to this collection, such as Reserva Biológica de Sooretama and Reserva Natural Vale are well-inventoried and we have seen no specimens of *S. phrixothrix* from them in any of the many herbaria we consulted.

Discussion. *Solanum phrixothrix* is a distinctive, densely bristly plant that has only been collected twice, once by Auguste St. Hilaire in the early 19th century and more recently in 2017 (*Folli 7506*) along the Rio Doce in Espiríto Santo State. It differs from other taxa in the group in its rotate to rotate-pentagonal corollas (Fig. 9E, F) and densely bristly stems with no stellate trichomes present (Fig. 9B). The long inflorescences and somewhat delicate pedicels are similar to those of *S. aciculare*, but that species has copious glandular stellate to multangulate pubescence and stellate corollas (Fig. 2F, G, I). It is surprising that this species has escaped notice for so long, but members of the *S. hexandrum* group often occur in very small populations at the bases of rocky outcrops and may easily overlooked despite their large size and fearsome appearance.

Figure 10. Distribution of *S. phrixothrix*.

Solanum phrixothrix shares dense bristly stems with *S. aciculare* but can be easily distinguished from that species by its lack of copiously glandular pubescence of long-stalked stellate trichomes. *Solanum phrixothrix* appears to lack long-stalked stellate trichomes on any part. White flowers are also found in *S. hydroides* (Fig. 7D) and *S. sublentum* (Fig. 13H), as well as occasionally in *S. aciculare* (Fig. 2F). Corollas in these three species are always stellate with variously deltate to triangular lobes, whereas those of *S. phrixothrix* are rotate and somewhat campanulate with the lobes reduced to tiny apiculae.

5. ***Solanum stagnale*** **Moric., Pl. Nouv. Amer. 34, tab. 23. 1837.**

Fig. 11

Solanum moricandii Dunal, Prodr. [A. P. de Candolle] 13(1): 319. 1852, nom. illeg. superfl. Type: Based on *Solanum stagnale* Moric.

Solanum moricandii Dunal var. *majus* Dunal, Prodr. [A. P. de Candolle] 13(1): 319. 1852. Type: Based on *Solanum stagnale* Moric.

Solanum moricandii Dunal var. *minus* Dunal, Prodr. [A. P. de Candolle] 13(1): 320. 1852. Type; Brazil. Bahia: Ilheus, 1840, *J.S. Blanchet 3095A* (lectotype, designated by Whalen et al. (1981), pg. 69: G-DC [G00131269]; isolectotypes: G [G00343734], P [P00371688], W [acc. # 0004133]).

Solanum moricandii Dunal var. *echinocalyx* Dunal, Prodr. [A. P. de Candolle] 13(1): 320. 1852. Type: Brazil. Sin. loc., *J.J. Lalande s.n.* (holotype: P [P00371692]).

Solanum nolitangere Salzm. ex Dunal, Prodr. [A. P. de Candolle] 13(1): 320. 1852. Type: Brazil. Bahia: "in maritimis", 1830, *P. Salzmann s.n.* (lectotype, designated by Whalen et al. (1981), pg. 69: G-DC [G00131246]; isolectotypes: C [C10019308], K [K000590187, K000590188], LE [LE00016989], P [P00366831, P00366832, P00366833, P00366834], W [acc. # 1889-0293774]).

Solanum nolitangere Dunal var. *ochraceo-ferrugineum* Dunal, Prodr. [A. P. de Candolle] 13(1): 320. 1852. Type: Brazil. Bahia: sin.loc., 1832, *J.S. Blanchet 710* (lectotype, designated by Whalen et al. (1981), pg. 69: G-DC [G00131245]).

Type. Brazil. Bahia: sin. loc., *J.S. Blanchet 2085* (lectotype, designated by Whalen et al. (1981), pg. 69 [as holotype]: G [G00343733]; isolectotypes: BM [BM000617832], G-DC [G00131205], P [P00371689, P00578808, P00371690]).

Description. Large, soft-wooded perennials 0.3 - several m tall. Stems terete, usually somewhat winged from the decurrent leaf bases, densely pubescent and sparsely prickly, the pubescence of whitish or reddish-cream porrect-stellate or occasionally multangulate (*Agra 617*) trichomes with multiseriate stalks 0.2–0.8 (-2.5) mm long, the lateral rays 4–9, 0.4–0.6 (-1) mm long, the mid-points much shorter than the rays, 0.05–0.2 mm long, the hairs densely interwoven and entirely concealing young stems, the prickles 1–2 cm long, 0.3–0.5 cm wide at the base, straight or recurved (e.g. *Blanchet 2085*) broad-based and strongly laterally compressed, often densely stellate-pubescent basally. Sympodial units difoliate, the leaves of a pair not geminate. Leaves shallowly lobed and coarsely repand; blades 9.5–30 cm long, 8–15 cm wide, ca. 1–1.5 times as long as wide, broadly elliptic to ovate, slightly discolorous, membranous or somewhat chartaceous, prickly on both surfaces along the veins with straight prickles to 15 mm long; adaxial surfaces densely pubescent with eglandular short- to long-stalked porrect stellate trichomes, the stalks 0.5–0.8 (-1) mm long, the rays 4–8, 0.5–0.7 mm long, the mid-points minute or equal in length to the rays, the lamina visible under the microscope; abaxial surfaces densely woolly-pubescent with stalked porrect stellate trichomes, the stalks 0.5–1 mm long, the rays 6–10, 0.5–1 mm long, often not in a single plane, the mid-points 0.2–0.4 mm long, much shorter than the rays; principal veins 4–5 pairs, with scattered straight prickles to 1.3 mm long, the prickles longer and larger on the mid-rib; base strongly decurrent along a winged petiole, the wing of laminar tissue to 0.5 cm wide on each side, often decurrent on to stem; margin lobed, the lobes 4–5, 1.5–3 cm long, 2–3 cm wide, deltate, acute- or round-tipped, often with irregular secondary lobing, the sinuses reaching less than halfway to the mid-rib ; apex acute or obtuse; petioles 0.8–5 cm, usually 1/4–1/3 the length of the blades and winged, stellate-pubescent like the stems, prickly. Inflorescences 2–7 cm long, extra-axillary or leaf-opposed, unbranched, with ca. 10 flowers, the axes densely stellate-pubescent, unarmed; peduncle 1–2 cm; pedicels 2–5 mm, 1–2.5 mm in diameter at the base, 2–2.6 mm diameter at the apex, articulated at the base; pedicel scars closely spaced 2–7 mm apart. Flowers 5-merous, heterostylous, with the lowermost long-styled (co-sexual) and the distalmost short-styled (functionally staminate), the plants probably andromonecious. Calyx with the tube 5–10 mm long, 8–10 mm in diameter, broadly obconical, the lobes 10–15 mm long, 5–8 mm wide, ovate-lanceolate or somewhat spathulate or tongue-shaped, obtuse or round apically, densely stellate-pubescent on both

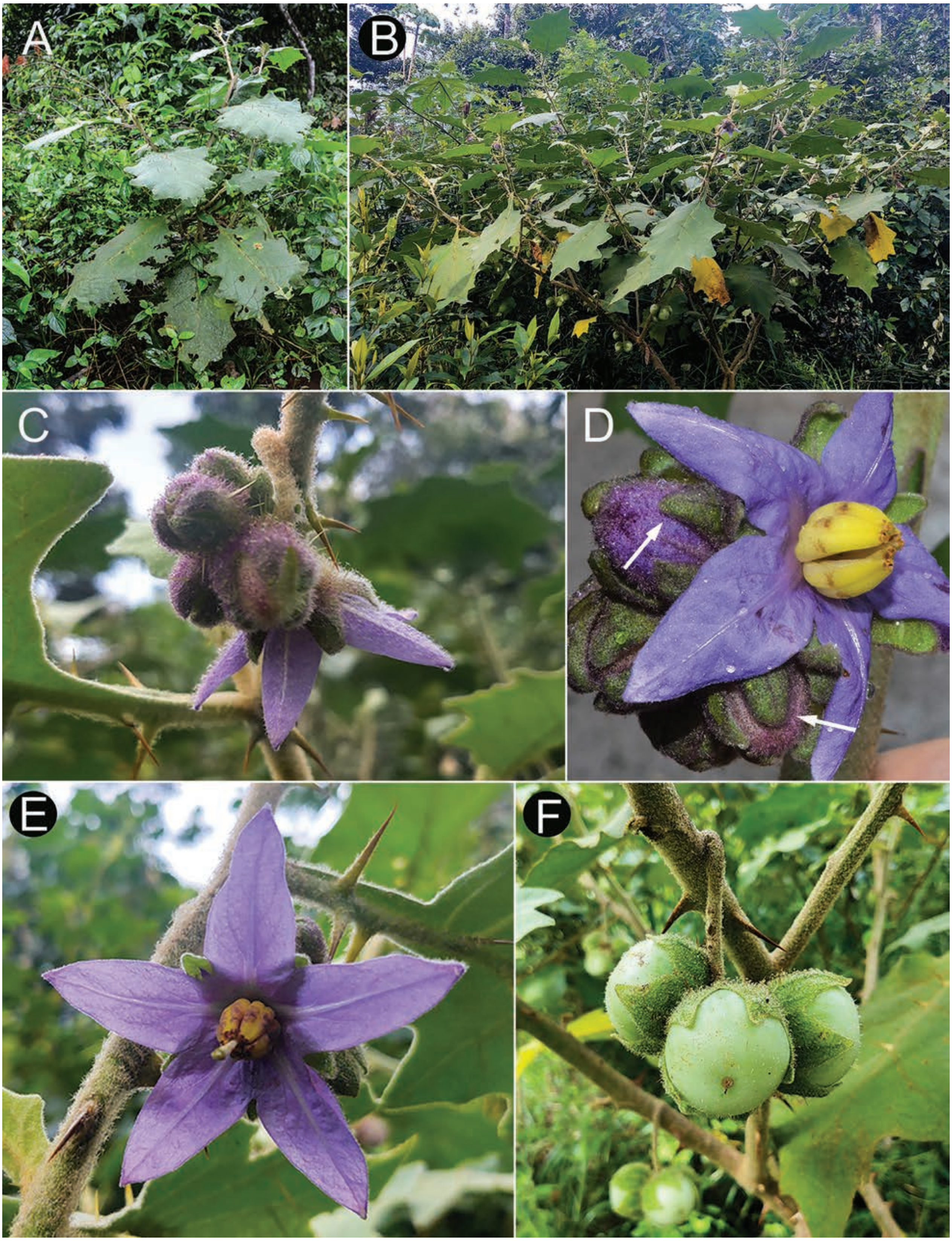

Figure 11. *Solanum stagnale* **A** habit of a young plant **B** habit of an older reproductive plant **B, C** inflorescence congested with flowers clustered due to extremely short pedicels **D** flower buds and short-styled flower (arrows point to spathulate calyx lobes) **E** long-styled flower and leaf base markedly decurrent on to the petiole **F** berries (almost mature) with appressed, only partially accrescent fruiting calyces (**A**, **D** *Giacomin & Stehmann 1930*, BHCB; **B**, **C**, **E**, **F** unvouchered field photograph, Bahia State [12°32'23"S, 38°03'08"W]). Photos: **A**, **D** Leandro L. Giacomin **B**, **C**, **E**, **F** Wagner Nogueira.

surfaces, often with scattered prickles on both surfaces near the mid-vein, often purple-tinged distally. Corolla 2.5–4.5 cm in diameter, white or lilac with a paler central star, stellate, lobed 2/3 to 3/4 of the way to the base, interpetalar tissue a thin edge on the lobes, the lobes 13- 20 mm long, 10–12 mm wide, ovate-lanceolate, densely stellate-pubescent abaxially, the trichomes with robust mid-points equal to or longer than the rays, glabrous adaxially, but the acute tips stellate-pubescent, the interpetalar tissue thin, glabrous. Stamens equal; filament tube minute; free portion of the filaments ca. 1 mm long, glabrous; anthers 7–10 mm long, ca. 3 mm wide, broadly lanceolate and tapering, connivent, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, slightly extrorse, not elongating to slits with age. Ovary conical, densely stellate-pubescent, the trichomes with well-developed lateral rays; style 10–14 mm long, glabrous or sparsely stellate-pubescent in the lower half; stigma large and capitate. Fruit a globose to flattened-globose berry, 2–2.5 cm in diameter, whitish-green at maturity, sparsely stellate-pubescent, ultimately glabrous, the pericarp matte or slightly shiny; fruiting pedicels 0.5–1 cm long, usually less than 0.5 cm long, 3–5 mm in diameter at the base, ca. 6 mm in diameter at the apex; fruiting calyx only partially accrescent, tightly investing. but not completely covering fruit, the tube ca. 1.5 cm long, the lobes ca. 15–20 mm long, ca. 10 mm wide, not overlapping. Seeds ca. 100 per berry, ca. 2.5 mm long, ca. 1.5 mm wide, flattened reniform, dark brown, the surfaces minutely pitted, the testal cells pentagonal in outline. Chromosome number; 2n = 24 (Bernardello et al. 1994; voucher (grown in Indiana and, therefore, should be in IND, but not seen) *Carvahlo 3213*, possibly a misprint for *Carvalho 3219*).

Distribution (Fig. 12). *Solanum stagnale* is endemic to eastern Brazil; it has been recorded from the States of Bahia and adjacent northern Minas Gerais and disjunctly in Paraíba State. This disjunct distribution is unusual, the single collection from Paraíba is from the northern side of the São Franscisco River, the site of the Pernambuco area of endemism.

Ecology and habitat. *Solanum stagnale* occurs in sandy coastal vegetation (restinga) habitat, in sand dunes, forests, forest edges and somewhat open habitats, from sea level to 300 m elevation.

Common names and uses. None recorded.

Preliminary conservation status (IUCN 2020). EOO (157,059 km^2, LC); AOO (68 km^2, EN). *Solanum stagnale* is known from more than five localities, even if the widely disjunct collection from Paraíba State is not included. Only one of these is within a protected area (Estação Ecológica de Cotegipe in Mun. Salvador, Bahia). The fragmented nature of the habitat and the absence of state or national level of protection for areas where it occurs suggests it should be assigned a preliminary conservation status of Vulnerable, based on criteria B 2 a,b i,ii,iii,iv.

Discussion. Like all members of this group, *S. stagnale* has large, repand leaves. Most collections have strongly winged petioles with a wing extending fully to the base, but occasionally the wing becomes very narrow basally (*Rosas 1* from Salvador). The pedicels in both flower and fruit of *S. stagnale* are the shortest in the group, rarely reaching 5 mm long. *Solanum stagnale* is easily distinguished from *S. hexandrum*, with which it is most similar, by its pubescence

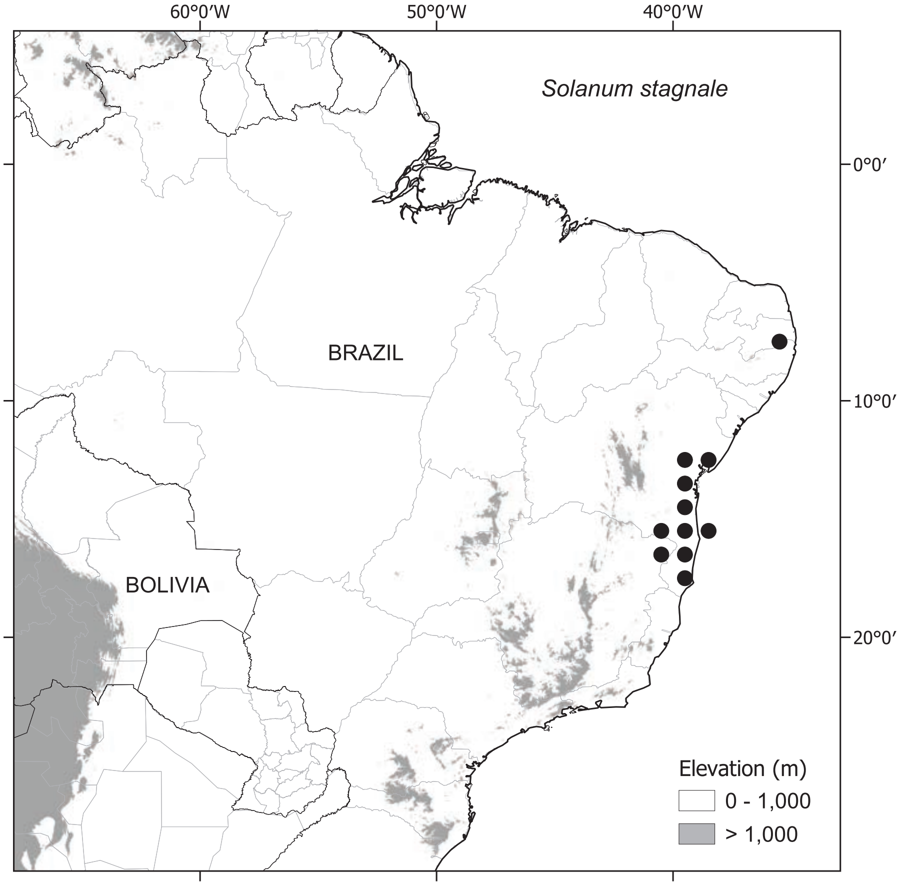

Figure 12. Distribution of *S. stagnale*.

of porrect-stellate trichome with usually more than 5 lateral rays, usually curved prickles, short, stubby pedicels usually less than 0.5 cm long, spathulate calyx lobes with rounded apices and berry that is not completely enclosed in an accrescent calyx. The trichomes of *S. stagnale* usually have mid-points that are shorter than or equal to the rays in length; in contrast, other species of the group have longer mid-points.

Whalen et al. (1981) treated *S. stagnale* as a member, albeit anomalous, of section *Lasiocarpa* (Dunal) D'Arcy and Whalen (1984) later included it in his equivalent *S. quitoense* Lam. species group. Both groups were composed of species, with the exception of *S. stagnale*, which are now recognised (Gagnon et al. 2022) as the Lasiocarpa clade; they share with members of the *S. hexandrum* group large repand leaves. Molecular data (Gouvêa 2020; Gagnon et al. 2022), however, clearly show that *S. stagnale* is related to *S. hexandrum* and other Brazilian endemic species of this group, not to the largely Andean members of the Lasiocarpa clade.

Dunal (1852) changed the name *S. stagnale* to *S. moricandii* because he felt it was inappropriate ("Blanchet in schedis non dicit hanc specimen crescere in stagnis, ut putat Moricand, et hâc ratione, nomen *stagnale* mutavi" – Blanchet does not say this specimen grows in ponds, as Moricand thinks, for this reason I have changed the name *stagnale*": Dunal 1852: 319) rendering the name *S. moricandii* illegitimate and superfluous.

6. *Solanum sublentum* Hiern., Kjoeb. Vidensk. Meddel. 1877–78: 53. 1878.
Fig. 13

Solanum wettsteinianum Witasek, Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 79 (advance separate): 50. 1910. Type. Brazil. São Paulo: prope "Fazenda Bella Vista" in districtu urbis S. Cruz ad flumen Rio Pardo, 500 m alt., Jul 1901, *R. von Wettstein s.n.* (lectotype, designated here: WU [acc. # 0038006]).

Type. BRAZIL. Minas Gerais: Lagoa Santa, [24 Feb 1863], *E. Warming s.n.* (lectotype, designated here: C [C10019316]; possible isolectotype: [note date on sheet is 1866] S [acc. # S04-2985]).

Description. Shrubs 1–3 m, erect or sometimes somewhat prostrate, armed. Stems terete, densely glandular-pubescent and sparsely prickly, the trichomes weak, simple uniseriate ca. 0.5 mm long with glandular tips, mixed with sparse short-stalked porrect stellate trichomes with 6–7 rays to 1 mm long, the mid-point to 1 mm long, gland-tipped or eglandular, the prickles 0.5–1.2 cm long, slightly to strongly curved and broad-based, ca. 0.5–1 cm in diameter at the base; new growth densely glandular pubescent with mixed simple and stellate trichomes like the stems; bark of older stems pale greyish-brown, somewhat glabrescent. Sympodial units difoliate, the leaves not geminate. Leaves shallowly lobed and repand, much smaller in younger branches; blades (5)8.5–17 cm long, (3)6–13 cm wide, ca. 1.3–1.6 times as long as wide, broadly elliptic or ovate, widest at or just below the middle, membranous, concolorous, sparsely prickly on both surfaces along the veins with straight prickles 0.3–1 cm long; adaxial surface densely pubescent with a mix of short-stalked porrect stellate trichomes with 5–7 rays ca. 1 mm long, trichomes consisting of solely unicellular or multicellular gland-tipped mid-points to 1.2 mm long (probably derived from stellate trichomes) and sessile, papillate glands composed of 4 cells; abaxial surface pubescent like the adaxial surface, but lacking the sessile papillate glands, also with delicate sessile porrect stellate trichomes with 4–5 rays ca. 0.3 mm long and mid-points shorter than the rays, these underneath the dense layer of larger short-stalked trichomes; principal veins 4–5 pairs, usually sparsely prickly on both surfaces with straight prickles to 0.9 cm long; base somewhat cordate-angular to hastate or sagittate-hastate from the basiscopically directed lowest leaf lobes, occasionally acute to abruptly attenuate, usually not decurrent on to the petiole; margins shallowly and broadly lobed, the lobes 4–5, 1–2.5 long, 2–4 cm wide, apically acute to acuminate, sometimes minutely secondarily lobed, the sinuses less than 1/4 of the way to the mid-rib; apex acute to acuminate; petiole (1-) 1.5–7 cm long, prickly with straight prickles to 1 cm long, densely glandular pubescent like the stems with a mix of simple trichomes apparently consisting of unicellular or multicellular mid-points with glandular tips and sparse porrect stellate trichomes. Inflorescences internodal, 2–9 cm long, unbranched, with 3–6 flowers. but only one open at a time; axes densely glandular pubescent like the stems with a mix of unicellular and multicellular gland-tipped simple uniseriate trichomes (derived from mid-points of stellate trichomes) and sparse porrect stellate trichomes with glandular mid-points; peduncle 1.5–5 cm long; pedicels 1.2–1.5 cm long, ca. 1 mm in diameter at the base, ca. 2.5 mm in diameter at the apex (excluding trichomes), erect to spreading, densely glandular pubescent like the inflorescence axes and stems and occasionally with a few

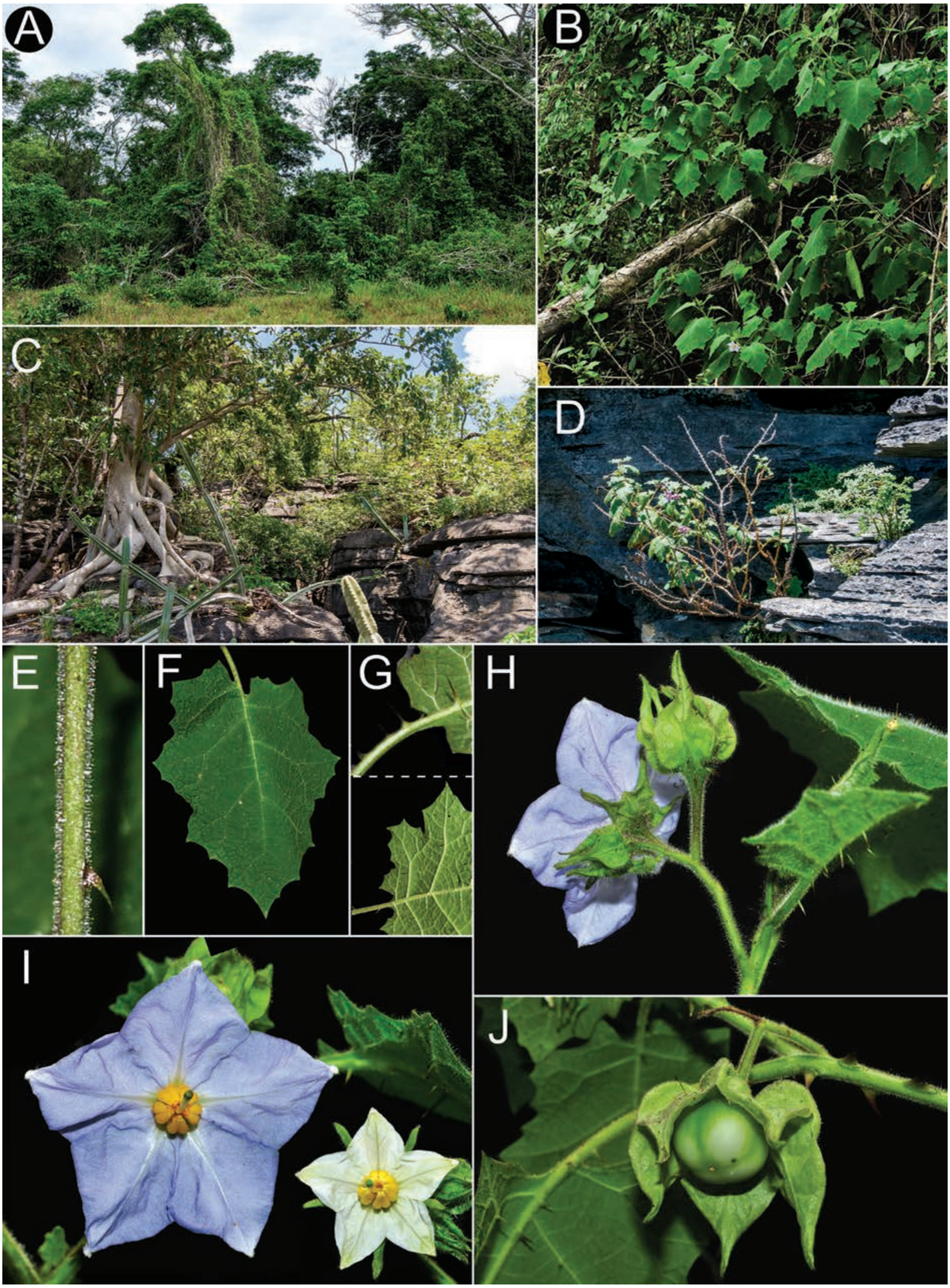

Figure 13. *Solanum sublentum* **A** habitat of arboreal restinga (coastal scrub-forest transition) forest edges **B** habit **C** habitat in seasonally dry deciduous forests **D** habit in rocky inselberg **E** stem with recurved prickles and unbranched glandular pubescence **F** leaf with cordate base and secondary lobing **G** variation in leaf bases and lobing **H** inflorescence **I** long-styled flowers showing colour polymorphism **J** mature berry with accrescent invaginate calyx (**B**, **F, H–J** *Gouvêa & Guerrero* 452; **D** *Stehmann et al. 6370*; **E, G** *Stehmann et al. 6372*). Photos: **A**, **B**, **H–J** Yuri F. Gouvêa **C**, **D, E, G** João R. Stehmann.

straight prickles, articulated at the base; pedicel scars more or less evenly spaced 4–5 mm apart, further apart in fruit, distally and, in young inflorescences, more tightly packed. Buds globose to ovoid, the corolla ca. halfway exerted from the calyx tube just before anthesis. Flowers 5-merous, co-sexual or perhaps a few distal flowers short-styled and functionally staminate, the plants only weakly andromonoecious. Calyx with the tube 3.5–4 mm long, 5–6 mm in diameter, deeply to shallowly broadly cup-shaped, plicate from the fused bases of adjacent lobes, usually invaginate at the base, the lobes 7–10 mm long, 2.3–5 mm wide, long-triangular, apically acuminate, densely glandular pubescent with a mix of simple uniseriate (mid-points?) and sparse short-stalked or sessile stellate trichomes, often with a few straight prickles 0.2–1.5 mm long on the main veins abaxially. Corolla 3.5–5 cm in diameter, purple to pale violet or white, shallowly stellate, lobed ca. 1/4 of the way to the base, interpetalar tissue thin, glabrous, the lobes 9–12 mm long, 11–19 mm wide, spreading to slightly cupped, densely pubescent abaxially where exposed in bud with short-stalked and sessile stellate trichomes, these occasionally glandular, glabrous adaxially, but occasionally with a few minute prickles along the veins. Stamens equal; filament tube minute; free portion of the filaments 0.5–1 mm long, glabrous; anthers 8.5–9 mm long, 2.6–3 mm wide, broadly lanceolate and tapering, connivent, glabrous, yellow, abaxially swollen in the lower half (gibbous) and somewhat papillate, poricidal at the tips, the pores directed distally, not elongating to slits with age. Ovary conical, glabrous; style 14–16 mm long, glabrous, widening markedly distally; stigma clavate or broadly capitate, the surface minutely papillate. Fruit a globose berry, 1.4–2 cm in diameter, green or pale whitish-green, glabrous, the pericarp matte when dry, opaque, the berry completely enclosed in the accrescent saccate calyx; fruiting pedicel 1.6–2.5 cm long, 1–1.5 mm in diameter at the base, 3–5 mm in diameter at the apex, spreading or pendent from the weight of the fruit; fruiting calyx strongly accrescent, inflated and invaginate, exceeding the length of the berry, but not completely enclosing it, the tube 1.5–2 cm long, saccate (invaginate) at the base, the lobes 0.8–0.9 cm long, often broken in dried specimens, not overlapping, densely glandular pubescent and occasionally prickly like the calyx in flower. Seeds 80–100 per berry, ca. 2.5 mm long, ca. 2 mm wide, flattened reniform, reddish-brown when dry, the surface minutely pitted, the testal cells thick-walled and sinuate in outline. Chromosome number not known.

Distribution (Fig. 14). *Solanum sublentum* is recorded to south-eastern and central Brazil, in the States of Espírito Santo, Goiás, Minas Gerais, Rio de Janeiro and São Paulo. The collection from Goiás is discontinuous from the rest of the species range (see discussion).

Ecology and habitat. *Solanum sublentum* occupies primarily forest understory, edges and clearings of wet coastal and semi-deciduous forests in the Atlantic Forest domain (Mata Atlântica; Fig. 13A, B), as well as semi-deciduous and deciduous seasonally dry tropical forests (Fig. 13C, D) in ecotonal zones or within savannah matrices in the Cerrado domain. The forests where S. sublentum occurs can be associated with granite/gneiss (wet and semi-deciduous forests in coastal and sub-coastal regions) and limestone or basaltic (inland seasonally dry tropical forests in savannah matrices) outcrops, it is the only species in the group and one of the few American species of *Solanum* found in STDFs associated with limestone outcrops. *Solanum sublentum* grows both in deep soils and in rock cavities, in fissures and in small, shallow soil patches that accumulate on bare rocks (Fig. 13D); from sea level to 800 m elevation.

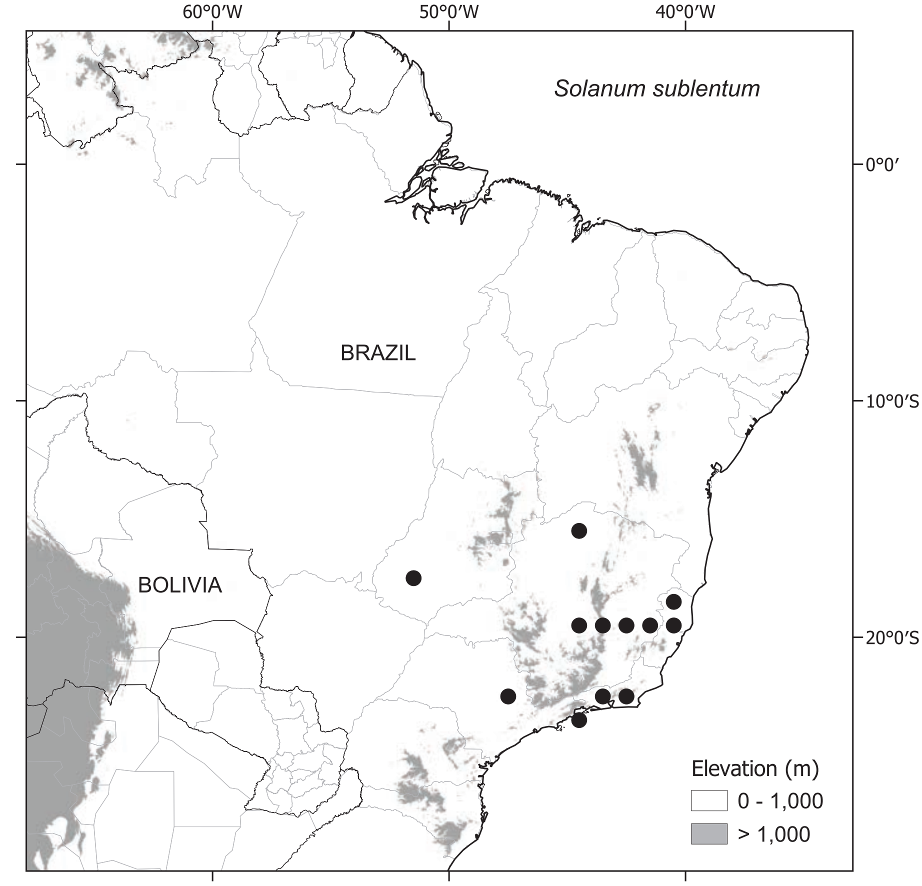

Figure 14. Distribution of *S. sublentum*.

Common names and uses. None recorded.

Preliminary conservation status (IUCN 2020). EOO (642,872 km^2, LC); AOO (72 km^2, EN). *Solanum sublentum* is known from eight localities (including the extremely disjunct occurrence in the State of Goiás), at least three of which are in protected areas (Parque Nacional Cavernas do Peruaçu, Estação Biológica de Caratinga in Minas Gerais State; Parque Municipal Sombra da Tarde in Espirito Santo State) with other collections from the mountains near Rio de Janeiro in what is now Parque Nacional da Serra dos Orgãos (e.g. "Organ Mount"). Even with the disjunct occurrence in Goiás excluded, *S. sublentum* has the largest extent of occurrence of any of the species of the *S. hexandrum* group. Nevertheless, due to the extreme level of habitat alteration in the region where it occurs and the paucity of recent collections (most of those used in calculating the EOO are more than a century old), we consider it of some conservation concern and suggest a preliminary status of Near Threatened, based on criteria B 2 a,b ii,iii, iv.

Discussion. *Solanum sublentum* is easily distinguishable from other members of this group in its markedly plicate accrescent calyces that exceed, but do not completely enclose the berries and simple, glandular pubescence with a mix of much less abundant stellate trichomes.

The majority of trichomes of *S. sublentum* are simple, uniseriate and unicellular or multicellular. Their shape and overall morphology suggest they are structurally analogous to mid-points of stellate trichomes without rays, like those that occur in the Acanthophora clade (Nee 1979; Hilgenhof et al. 2023) and most members of the Gonatotrichum group of the Brevantherum clade (Stern et al. 2013).

The single collection of *S. sublentum* from Goiás (*Hatschbach 34747*) is from Mun. Jataí, in the extreme southwest of the State. The habitat is stated as "clareiras da mata" (forest clearings) and the area in which it was collected was a remnant of the now very restricted Atlantic Forest. The southernmost portion of Goiás State is the original limit of the Atlantic Rainforest domain in central Brazil and an ecotonal zone with the Cerrado domain, where contiguous forested formations were found in the past (IBGE 2012). These mostly semi-deciduous forests were either considered part of the Cerrado ("Cerradão") or the Atlantic Rainforest itself. They have been largely converted first to cattle farming and later to soy and corn plantations (Oliveira 2007). No recent collections from this locality have been seen, so recollection there is a priority.

Solanum sublentum is similar to *S. aciculare* in possessing glandular indument and strongly accrescent, inflated and invaginate fruiting calyx lobes. The pubescence of *S. sublentum* is of unbranched trichomes (the bases and mid-points of modified stellate trichomes), while that of *S. aciculare* is of long-stalked stellate trichomes with glands on each ray tip. Prickles in *S. sublentum* are sparse and recurved, whereas those of *S. aciculare* are straight and denser especially on stems. The calyx completely covers the berry in *S. aciculare* (Fig. 2H) while, in *S. sublentum*, the berry is clearly visible (Fig. 13J).

Many different collecting dates are written on the Warming collections at C used by Hiern (1878) to describe *S. sublentum*. We have chosen the only sheet with both flowers and fruits (C10010316), showing the characteristic saccate calyx in fruit of *S. sublentum*. The many syntype collections in Copenhagen and sent elsewhere by Hiern have a confusing panoply of dates and some may be isolectotypes, but, in the absence of unambiguous dates on these sheets, we do not recognise them as such. The sheet we here cite as a possible isolectotype at S (acc. # S04-2985) has a label stating 1866, so it too is likely not a duplicate, but it is the only original material we have seen outside of Copenhagen.

"Names" (designations) not validly published

Solanum minax Mart. ex Sendtn., Fl. Bras. (Martius) 10: 71. 1846. Not intended as a new name, cited as a manuscript name under *Solanum hexandrum* Vell. "β minax" = *S. hexandrum*

Solanum multiangulatum Vell., Fl. Flumin. 91. 1829 [1825], nom. utique rej. = *S. hexandrum* (as = *S. echidnaeforme* Dunal in Knapp et al. 2015).

Solanum tubiflorum Dunal, Prodr. [A. P. de Candolle] 13(1): 318. 1852, pro syn. *Solanum maroniense* Poit. = *S. hexandrum* (herbarium name on *Sellow s.n.* in BM [BM000935474]).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: LLG, YFG, SK. Data curation: LLG, SK, YFG. Formal analysis: LLG, SK, YFG. Funding acquisition: YFG, LLG, SK. Investigation: LLG, YFG, SK. Methodology: SK. Visualization: YFG. Writing - original draft: SK. Writing - review and editing: LLG, YFG.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information. Supplementary files can also be found on the Natural History Museum's Data Portal (https://doi.org/10.5519/vv8f8pkx).

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Appendix 1

Index to numbered collections

For collections made by two or more collectors, only primary (first listed) collector is presented here. Collections by anonymous collectors without date or other identifying features are not listed. Full collector strings can be found in the Suppl. materials 1, 2. This index and the searchable files are also available on the NHM Data Portal (https://doi.org/10.5519/xuvrw79j).

Agra, MF 617 (*stagnale*); 7216, 7234, 7254, 7359 (*hexandrum*).
Aguiar, MIH 446 (*hexandrum*).
Aleixo, S sp28-1 (*hexandrum*).
Almeida-Lafetá, RC 78 (*hexandrum*).
Amorim, AM 2706 (*stagnale*); 7124 (*hexandrum*).
Andrade, IR 147 (*hexandrum*).
Araujo, D 801, 1399 (*hexandrum*).
Arbo, MM 7792 (*sublentum*).
Arbocz, GF 160, 1446 (*hexandrum*).

Azevedo, IFP 28 (*hexandrum*).
Bandeira, BC 147 (*hexandrum*).
Barbosa, MR 1508 (*hexandrum*).
Barth, OM P-11 (*hexandrum*).
Belém, RP 1078 (*stagnale*).
Bernardi, L. 32 (*hexandrum*).
Blanchet, JS 32, 179, 370, 710, 1843, 2085, 3095A, 3095 (*stagnale*).
Boechat, SL 17 (*hexandrum*).
Bovini, MG 658, 1072, 2128 (*hexandrum*).
Brade, AC 11018 (*sublentum*) 18190, 18312 (*hexandrum*).
Braga, JMA 677, 874, 1451, 6244 (*hexandrum*).
Brotto, ML 3269 (*hexandrum*).
Bünger, MO 531 (*hexandrum*).
Burchell, WJ 1157 (*sublentum*).
Callejas, R 1582 (*stagnale*).
Campos Porto, P 776 (*hexandrum*).
Campos, WG 55 (*hexandrum*).
Campos, MTVA 150 (*hexandrum*).
Carauta, JPP 2348, 2780, 2803, 3282, 4592, 5330 (*hexandrum*).
Cardoso, LJT 694, 1382 (*hexandrum*).
Carrijo, TT 1490, 1827, 2015 (*hexandrum*).
Carvalho, AM de 452, 1490, 3219 (*stagnale*); 6866 (*hexandrum*).
Castellar, A 6, 14 (*hexandrum*).
Ceccantini, GCT 2812 (*sublentum*).
Clarissa, C 3 (*hexandrum*).
Colletta, GD 166 (*hexandrum*).
Cordeiro, J 6030 (*hexandrum*).
Costa, APL 16985 (*hexandrum*).
Costa, IG 543 (*hexandrum*).
Costa, LV 89 (*sublentum*); 199 (*hexandrum*); 200 (*sublentum*); 865 (*hexandrum*).
Couto, DR 690, 1661 (*hexandrum*).
Davis, PH D. 59826 (*hexandrum*).
Demuner, V 2922, 4131, 4944 (*hexandrum*).
Duarte de Barros, W 1121 (*hexandrum*).
Duarte, AP 1573 (*hexandrum*); 5002 (*sublentum*).
Duarte, C 8 (*hexandrum*).
Dusén, P 5135 (*hexandrum*).
Egler, W 105 (*hexandrum*).
Eiten, G 7914 (*hexandrum*).
Emygdio, L RB- 38680 (*hexandrum*).
Erickson, HT 1 (*hexandrum*).
Esteves, GL 2634 (*hexandrum*).
Faria, ALA 120 (*hexandrum*).
Farney, C 161 (*hexandrum*).
Ferreira, LA 69108 (*hexandrum*).
Fiaschi, P 1987 (*hexandrum*).
Flores, TB 1465, 1705, 1717 (*hexandrum*).
Folli, DA 1943 (*stagnale*); 7560 (*phrixothrix*).
Fontana, AP 3051, 5440 (*hexandrum*).

Forzza, RC 5029, 5125, 8803 (*hexandrum*).
Fraga, CN 1899 (*hydroides*); 2012 (*hexandrum*).
França, GS 348, 548 (*hexandrum*).
Freire de Carvalho, L d'A 559, 662 (*hexandrum*).
Freitas, L 587 (*hexandrum*).
Frutuoso, LCF 108 (*hexandrum*).
Furlan, A 1445 (*hexandrum*).
Galland, Y 13 (*hexandrum*).
Gardner, G 533 (*hexandrum*); 799 (*sublentum*); 800 (*hexandrum*).
Gaudichaud, C 500, 501 (*hexandrum*).
Gemtchújnicov, ID de 250 (*hexandrum*).
Gentry, AH 49340 (*hexandrum*).
Giacomin, LL 499 (*sublentum*); 875, 1689, 1827, 1833, 1844 (*hexandrum*); 1930 (*stagnale*).
Giordano, LC 392, 517 (*hexandrum*).
Glaziou, AFM 338 (*sublentum*); 3777, 5960, 8848 (*hexandrum*); 8879 (*sublentum*); 13082 (*hexandrum*).
Glocker, EF von 42, 102 (*stagnale*).
Góes, OC 228, 976, 1019, 1181 (*hexandrum*).
Goldenberg, E 32388 (*hexandrum*).
Gouvêa, YF 102 (*aciculare*); 135, 137, 158, 159 (*hexandrum*); 280, 281, 282, 283, 284 (*aciculare*); 492 (*hydroides*).
Guedes, ML 3649, 6553 (*stagnale*); 19611 (*sublentum*).
Harley, RM 17932 (*stagnale*).
Hatschbach, GG 34747 (*sublentum*); 46667 (*hexandrum*); 47806 (*aciculare*); 48677, 57934 (*hexandrum*); 62938 (*hydroides*); 63105 (*stagnale*).
Herb. Richard 533 (*hexandrum*).
Heringer, EP 879 (*hexandrum*); 6455 (*sublentum*).
Hoehne, FC SP-42651, SP-42653 (*hexandrum*).
Horst, MIA 16, 150 (*hexandrum*).
Hottz, D 290 (*hexandrum*).
Ichaso, CLF 154 (*hexandrum*).
Irwin, HS 2076 (*hexandrum*).
Isern, J 6467 (*hexandrum*).
Jardim, JG 1743 (*hexandrum*); 3151 (*aciculare*).
Jascone, CES 1111 (*hexandrum*).
Jouvin, PP 468 (*hexandrum*).
Kirizawa, M 1889 (*hexandrum*).
Kollmann, L 3459 (*sublentum*); 10314 (*hexandrum*); 11385 (*hydroides*).
Kreiger, L (*hexandrum*).
Krieger, L (Padre) 1073, 7453, 7515, 8845, 11769, 13395 (*hexandrum*).
Kuhlmann, M 2678 (*hexandrum*).
Kuntz, J 645 (*hexandrum*).
Leitão Filho, HF 1373, 1379 (*hexandrum*).
Leoni, LS 524, 3116, 7341, 7345, 7346 (*hexandrum*).
Liene, D 3912 (*hexandrum*).
Lima, JR 35, 39, 42, 83 (*hexandrum*).
Lira Neto, JA 164, 648 (*hexandrum*).
Lobão, A 1676 (*hexandrum*).

Loefgren, A CGG-1868, 3129 (*hexandrum*).
Lombardi, JA 1280 (*hexandrum*); 1814, 2355 (*sublentum*); 2388, 3120 (*hexandrum*); 5076, 5326 (*stagnale*); 8215, 8951 (*hexandrum*).
Lopes, MA 417 (*sublentum*).
Luber, J 101 (*hydroides*).
Lucas, EJ 625 (*hexandrum*).
Lund, PW 621 (*sublentum*).
Machado, TM 298 (*hexandrum*); 673 (*hydroides*).
Magalhães, MG 17651 (*aciculare*).
Magnago, LFS 467 (*hexandrum*); 579 (*sublentum*).
Manhães, VC 172 (*hexandrum*).
Mantovani, W 138 (*hexandrum*).
Marcolino, F 152 (*hexandrum*).
Marquete Ferreira da Silva, N 93, 242 (*hexandrum*).
Marquete, R 802 (*hexandrum*); 1092 (*sublentum*).
Martinelli, G 13, 3558, 8860 (*hexandrum*).
Martius, CFP 253 (*sublentum*).
Mattos Silva, LA 833 (*stagnale*); 4152 (*aciculare*).
Mattos, J 15755 (*hexandrum*).
Mauad, L.P. 6 (*hexandrum*).
Mautone, L 274, 422, 1356 (*hexandrum*).
Mello-Silva, R 1727 (*hexandrum*).
Mexia, Y 4118, 4731, 5033 (*hexandrum*).
Miers, J 2731 (*hexandrum*); 3601, 3656 (*sublentum*).
Mori, SA 10459 (*aciculare*); 14066 (*stagnale*).
Mosén, CWH 2540 (*hexandrum*).
Moura, R 1198 (*hexandrum*).
Nadruz, M 2795 (*hexandrum*).
Nardin, CF 40 (*hexandrum*).
Nee, M 3373 (*sublentum*).
Neves, PT 45 (*hexandrum*).
Oliveira, A 1107 (*hexandrum*).
Oliveira, CAL de 261 (*hexandrum*).
Oliveira, SA 1 (*hexandrum*).
Ostenfeld, CH 5560 (*hexandrum*).
Pabst, G 5216 (*hexandrum*).
Paula, LFA de 148, 247, 388, 581, 669 (*hydroides*); 972, 1180 (*aciculare*).
Pedroni, F 2454 (*hexandrum*).
Pereira, E 1258, 2271, 3912 (*hexandrum*).
Pereira, FB 45/ 35 (*hexandrum*).
Pereira, LA 1557 (*hexandrum*).
Pereira, OJ 829 (*hexandrum*); 6545 (*hydroides*).
Pinheiro, RS 2115 (*aciculare*).
Pinto, HV 496 (*hydroides*).
Pinto, LJS 246 (*hexandrum*).
Pirani, JR 803, 1032 (*hexandrum*).
Pizziolo, W 119 (*sublentum*).
Plowman, TC 2753 (*sublentum*).
Pohl, JBE 108 (*hexandrum*); 5488 (*sublentum*).

Ponte, ACE 29801 (*hexandrum*).
Queiroz, LP de 15302 (*aciculare*).
Queiroz de Melo 63 (*hexandrum*).
Quinet, A 23/55, 97, 32/140 (*hexandrum*).
Raben, FC 19 (*sublentum*); 308 (*sublentum*); 310 (*hexandrum*).
Ramalho, RS 1190, 1255, 1309 (*hexandrum*).
Regnell, AF Rio-164, Rio-342 (*sublentum*).
Reidel, L 32 (*sublentum*); 197 (*stagnale*).
Rosa, M 213 (*hexandrum*).
Rosa, P 1017 (*hexandrum*).
Saint-Hilaire, A de A1-393 (*sublentum*); A1-379, B-13 (*hexandrum*); B1-1046 (*phrixothrix*); B2-33, C-48 (*hexandrum*).
Salgado, CS 79 (*hexandrum*).
Salino, A 3259 (*sublentum*); 3513, 4112, 5885, 14662 (*hexandrum*).
Sampiao, AJ 3340 A (*hexandrum*).
Santos, HGP dos 352 (*hexandrum*).
Santos, MCF dos 1966 (*hexandrum*).
Schott, HW 5439 (*sublentum*); 5444 (*hexandrum*).
Schüch, G 5438 (*hexandrum*).
Sellow, F 70, 120 (*hexandrum*); 120[a] (*sublentum*).
Sellow, F (*hexandrum*).
Sellow, F Silva, JM 58677 (*hexandrum*).
Sobral, M 6769 (*stagnale*); 8250 (*hexandrum*).
Souza, JP 641 (*hexandrum*).
Souza, TP 16 (*hexandrum*).
Stehmann, JR 3839 (*stagnale*); 4513 (*hexandrum*); 6370, 6372 (*sublentum*); 6387 (*aciculare*).
Sucre, D 6245, 7487, 8923 (*hexandrum*); 9668 (*sublentum*).
Tsuji, R 1119 (*hexandrum*).
Vasconcellos Neto, J 6625 (*sublentum*; 9265 (*hexandrum*).
Verdi, M 3136 (*hexandrum*).
Vermelho 18 (*hexandrum*).
Vervloet, RR 3372 (*hexandrum*).
Vidal, MRR 259 (*hexandrum*).
Vieira, MF 406 (*hexandrum*).
Vimercat, JM 239 (*hexandrum*).
Vinha, PC 1380 (*hexandrum*).
Völtz, RR 2289, 2549a (*hexandrum*).
Webster, GL 25426 (*sublentum*).
Weddell, HA 435, 678 (*hexandrum*).
Weyland, MC 333 (*hexandrum*).
Widgren, JF 141 (*hexandrum*).
Wied-Neuwied, M 1[25], 4 (*hexandrum*).
Without collector 156, 12010 (*hexandrum*).

Supplementary material 1

All specimens of members of the *Solanum hexandrum* group examined

Authors: Sandra Knapp, Yuri F. Gouvêa, Leandro L. Giacomin

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.253.138216.suppl1

Supplementary material 2

All collection events of members of the *Solanum hexandrum* group seen

Authors: Sandra Knapp, Yuri F. Gouvêa, Leandro L. Giacomin

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.253.138216.suppl2

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Research Article

Pternopetalum shunhuangensis (Apiaceae), a new species from Hunan, China

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Abstract

Based on field investigations, morphological and molecular systematic studies, a new species, *Pternopetalum shunhuangensis* (Apiaceae) from Hunan Province, China is described. Diagnostic morphological characters, full description and a detailed illustration are provided. The differences between *P. shunhuangensis* and morphologically similar species *P. tanakae* are presented and discussed. Since no population assessment of this species in its whole distribution area is made, it is best to assign a conservation status of 'Data Deficient' (DD) for this species.

Key words: Apiaceae, China, new species, *Pternopetalum*

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Introduction

Pternopetalum Franch. (Apiaceae), including ca. 25 species, is endemic to East Asia (Shan and Pu 1978; Pu 1985; Wu et al. 2006). Typical characteristics of this genus are petals saccate at base, umbellules with 2–5 flowers, and rays reflexed in fruit. In Wang's revision (Wang 2007), the shape of the underground part, leaf morphology, the position of umbels, and the characteristics of flowers and fruits are important traits for delimiting *Pternopetalum* species.

With 23 species, 21 of which are endemic (Pu and Phillippe 2005), China is undoubtedly the center of diversity and endemism for *Pternopetalum*. Wang (2012) recognized only 15 species in the genus, while Pimenov (2017) considered it the eighth largest genus of Apiaceae in China, comprising 21 species. After Wang's revision, three new species and one new combination of *Pternopetalum* were described from China (Tan et al. 2014, 2015; Zhong et al. 2018; Ye et al. 2020). Even the species *P. arunachalense* Bhaumik & P. Satyanar. which was published by Indian scholars Bhaumik and Satyanarayana (2014) was found in Southern Xizang according to the officially claimed boundary.

Species of *Pternopetalum* are mainly distributed in the southwest area of China, especially in Sichuan and Yunnan (Su and Sheh 2001). However, Hunan Province in Central China is also one of the concentrated distribution areas of this genus. There are ten species of *Pternopetalum* in Hunan, making it the largest genus of Apiaceae in the province (Sun et al. 2010).

During an arduous journey to the Hunan Dong'an Shunhuang Mountain National Nature Reserve in April 2024, we found an interesting population of *Pternopetalum* with flowers and young fruits. The species possesses unusual cauline leaves that are homomorphic with the basal leaves, sometimes even larger. In July and October, we returned to the locality and collected specimens with mature fruits. According to the characters of fruit, the species obviously belongs to *P.* sect. *Pteridophyllae* Wolff due to its minute calyx teeth and filiform ribs, but the homomorphic basal and cauline leaves differentiate it from all the other species of the section. Its relatively small habit and distinct fruit characteristics, also distinguish it from all the species in the other section, i.e., sect. *Denterioideae* Wolff.

After thorough consultation of the relevant literature and herbarium investigations, and comparison with morphologically similar species, we are confident that this is a new species of *Pternopetalum*.

Materials and methods

Morphological observation

Specimens were collected from Dong'an County in three field trips during April, July and October 2024. The habitat of the new species was investigated in the field. Descriptions are based on dried collections, except for flower colour.

DNA extraction, amplification and sequencing

We collected fresh green leaves of this new species from Hunan, China. Total genomic DNA was extracted from silica-dried leaves with a plant genomic DNA kit (Tiangen Biotech Co., Ltd., Beijing, China). We used the nuclear ribosomal DNA internal transcribed spacer (ITS) for phylogenetic analyses. The universal primers ITS4 and ITS5 (White et al. 1990) were used to amplify the nuclear ribosomal ITS region. Amplification was undertaken using a volume of 25 μl with 20 μl Green Taq Mix (Novogene, China), 1.5 μl forward primer, 1.5 μl reverse primer, and 2 μl total DNA. The amplification of the ITS region was obtained by initial denaturation for 2 min at 98 °C, followed by 35 cycles of 10 s at 98 °C,15 s at 52 °C, and 15 s at 72 °C, and then a final extension of 5 min at 72 °C. All PCR products were separated using a 1.5% (w/v) agarose TAE gel and sent to Sangon (Nanjing, China) for sequencing.

Phylogenetic analysis

To confirm the phylogenetic position of this species, 28 ITS belonging to 15 species with accession numbers were obtained from GenBank. A total of 29 taxa were sampled for phylogenetic analysis, including 27 taxa and 14 species from *Pternopetalum*. Two species *Oenanthe hookeri* C. B. Clarke and *Sium suave* Walter, served as outgroups.

We used SeqMan7 (Burland 2000) to assemble ITS sequences. The sequences were aligned using MAFFT v7.221 (Katoh and Standley 2013). The alignment was employed to reconstruct the phylogenetic tree using Maximum-Likelihood

(ML) and Bayesian Inference (BI) methods. For ML analyses, the software RAxML v8.2.8 (Stamatakis 2014) was used to construct the phylogenetic trees with the GTR model and 1000 bootstrap (BS) replicates. Bayesian inference (BI) analyses were conducted by MrBayes version 3.2.7 (Ronquist et al. 2012) with the best-fit substitution model (GTR+G+I) determined by Modeltest v3.7 (Posada and Crandall 1998). Markov Chain Monte Carlo (MCMC) search was performed for 1×10^8 generations, sampling every 1000 generations.

Results and discussion

Molecular phylogenetic analyses based on the internal transcribed space (ITS) region showed that *P. shunhuangensis* is sister to *P. tanakae* (Franch. & Sav.) Hand.-Mazz. and *P. gracillimum* (H. Wolff) Hand.-Mazz. (Fig. 4). Thus, both morphological and phylogenetic evidence suggested that *P. shunhuangensis* is a distinct species of *Pternopetalum*.

After examining of herbarium specimens, we found that two other collections of the same species were collected in 1962 and 1984 respectively from Ziyun Mountain, which is part of the Shunhuang Mountain. However, they were misidentified as *P. heterophyllum* Hand.-Mazz. and *P. filicinum* (Franch.) Hand.-Mazz respectively. Both of the two species have already been treated as synonym of *P. tanakae* (Franch. & Sav.) Hand.-Mazz by Wang (2012). This treatment is widely accepted. The new species resembles *P. tanakae* in possessing the minute calyx teeth and filiform ribs, but differs from the latter by roots without tubercles at nodes, fewer basal leaves, cauline leaves and stems and elongate styles (Fig. 3F). In fact, the length of ultimate segments of the cauline leaves in the two species are distinctly different (3–5 mm in *P. shunhuangensis* vs.10–25 mm in *P. tanakae*; Fig. 3D).

As no population assessment has been conducted for this species in its entire range, it is best to assign a conservation status of 'Data Deficient' (DD) for this species (IUCN Standards and Petitions Committee 2022).

Taxonomic treatment

***Pternopetalum shunhuangensis* W.Zhou & L.Wu, sp. nov.**
urn:lsid:ipni.org:names:77358254-1
Figs 1–3

Type. China • Hunan Province, Yongzhou City, Dong'an County, Hunan Dong'an Shunhuang Mountain National Nature Reserve, on rocks densely covered with moss in forests, at an altitude ca 1600 m a.s.l., 23 Apr. 2024, *Lei WU*, *Yan-Jie Yang*, *Zi-Lin Feng SHS0001* (holotype NAS); 19 July 2024, *Lei WU*, *D. Deng*, *Zi-Lin Feng SHS1749* (paratype CSFI).

Etymology. The species epithet is derived from the type locality, Shunhuang Mountain. Its Chinese name is given as 舜皇囊瓣芹 [Pinyin: shùn huáng náng bàn qín].

Diagnosis. *Pternopetalum shunhuangensis* differs from *P. tanakae* (Franch. & Sav.) Hand.-Mazz. by its roots without tubercles at nodes, fewer basal leaves, unelongated ultimate segments of cauline leaves, elongate styles and terminal umbels. A more detailed comparison between the two species is presented in Table 1.

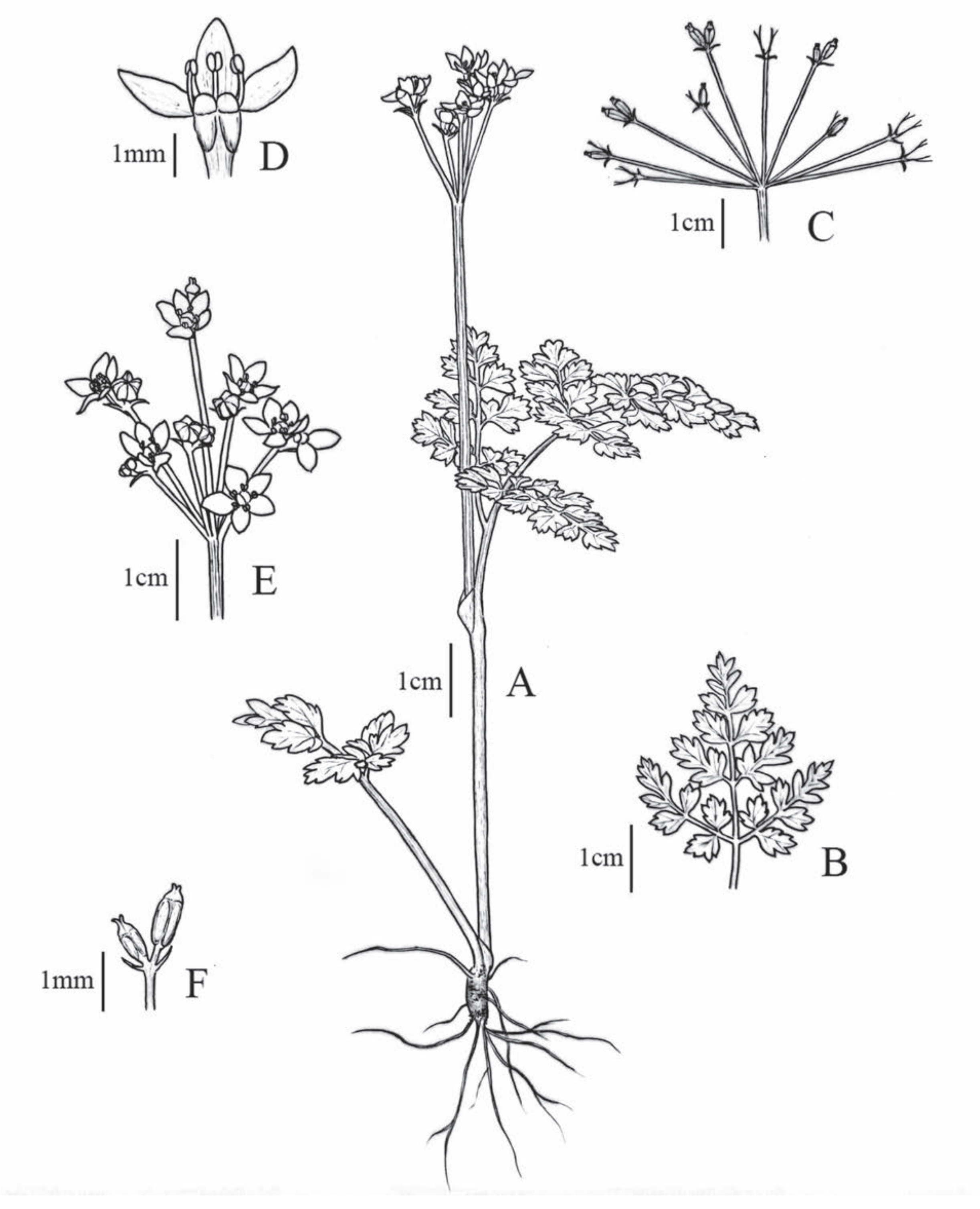

Figure 1. Illustration of *Pternopetalum shunhuangensis* W. Zhou & L. Wu **A** habit **B** another type of basal leaf **C** umbel in fruit **D** flower with two petals removed to show stamens and stylopodium **E** umbel in flower **F** mericarps. (Drawn by B. S. Li).

Plants 12–16 cm high. Taproot fusiform. Stem 1, erect, slender, unbranched, glabrous. Basal leaves 0–1(2), petiolate; petioles 3–5 cm; blade ovate-triangular, 1.5–3 × 2.5–3 cm, ternate or ternate-2-pinnate; ultimate segments flabelliform or diamond, 3–8 × 2–7 mm. Cauline leaves 1, ternate-2-pinnate, petioles 0.5–4 cm; 2–4.5 × 3–6 cm, ultimate segments flabelliform or diamond, 2–5 × 2–6 mm. Umbels 1–3 cm across in flower, to 5 cm in fruit; bracts absent; rays

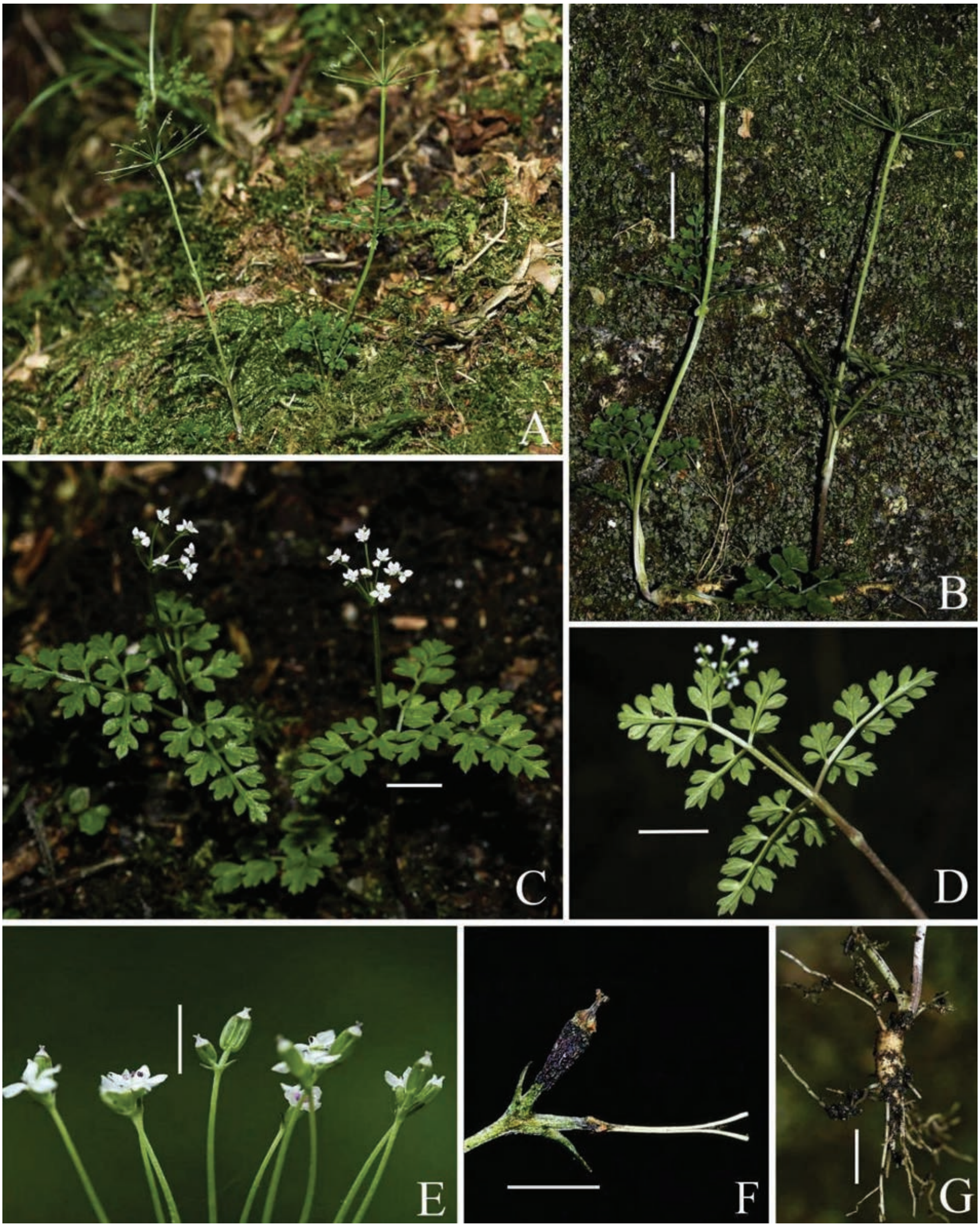

Figure 2. *Pternopetalum shunhuangensis* W. Zhou & L. Wu **A** microhabitat **B** habit **C** flowering plant **D** abaxial surface of cauline leaf **E** umbels in fruit **F** mature fruit **G** root. Scale bars: 2 cm (**B**); 1 cm (**C**–**D**, **G**); 2 mm (**E**–**F**).

6–20, 1.5–2.5 cm; bracteoles 2–3; umbellules 2-flowered; pedicels 0.2–1 mm long. Calyx teeth minute, or obsolete. Petals white, broad ovate, 1.5–1.8 × 1.2–1.5 mm; stylopodium conic; styles elongate, erect, longer than the stylopodium; stylopodium plus style ca 0.8mm, styles ca. 0.5 mm. Fruit oblong ovoid, 2–2.5 × 1–1.5 mm; ribs filiform; vittae 1–2 in each furrow, 2 on commissure.

Figure 3. Type specimens of *Pternopetalum shunhuangensis*, *P. heterophyllum*, *P. filicinum* and *P. tanakae*. **A** holotype of *P. shunhuangensis* (NAS) **B** holotype of *P. heterophyllum* (E00265241) **C** isotype of *P. filicinum* (P00432458) **D** holotype of *P. tanakae* (P00495952).

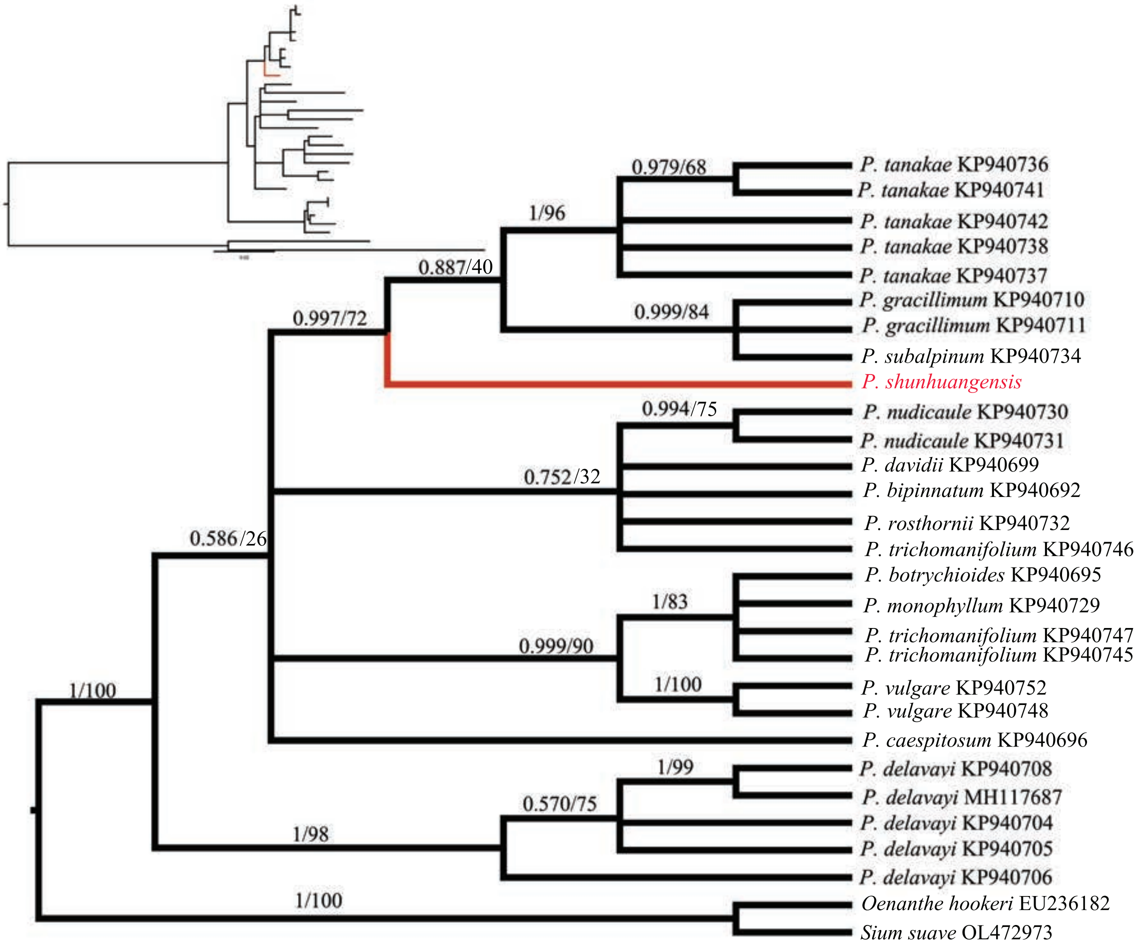

Figure 4. Phylogenetic tree inferred from the nrDNA ITS sequences. Bayesian posterior probability values (PP) / Bootstrap support values (BS) are shown on the branches. Only branches with PP > 0.5 are shown.

Table 1. Comparison of *Pternopetalum shunhuangensis* and *P. tanakae*. Morphological data for *P. tanakae* are obtained from Pu and Phillippe (2005).

Characters	*P. shunhuangensis*	*P. tanakae*
Height (cm)	12–16	10–40
Root	without tubercles at nodes	with tubercles at nodes
Stem	1, unbranched	1–2, 1–2 branched or unbranched.
Basal leaves	0–2	2–4
Cauline leaves	1, ultimate segments flabelliform or diamond	1–3, ultimate segments lanceolate or elongate-linear
Position of umbels	terminal	lateral and terminal
Number of flowers in each umbellule	2	1–3
Style	longer than stylopodium	shorter than stylopodium

Phenology. *Pternopetalum shunhuangensis* is flowering from April to May, and fruiting from June to July.

Additional specimens examined. *Pternopetalum shunhuangensis* (paratypes): China • Hunan Province: Xinning County, 21 Oct. 1962 *Lin-Han Liu 15250* (NAS, WUK); Xinning County, Ziyun mountain, 9 Sep. 1984 *Ziyunshan Team 301*, *981* (PE).

P. tanakae: Japan • Silvis montis ignivomi, Fudsi Yama, Jun. 1874 *Savatier 3436* (holotype P, image).

P. heterophyllum: CHINA • Hunan Province: Xinning County, Huping mountain, 10 Jul. 1987 *Hupingshan Team 1318* (PE); Sichuan Province: Baoxing County, 7 Agu. 1936 *Gui-ling Qu 3454* (holotype E, image).

P. filicinum: CHINA • Hubei Province: Ichang City, *A. Henry 6600* (isotype P, image).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Wei Zhou: Writing – Original draft; Wei Zhou and Lei Wu: Writing – Review and Editing; Zi-Lin Feng and Bao-cheng Wu: Data Curation; Lei Wu, Long-Ping Tang and Du Deng: Investigation.

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Data availability

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

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Supplementary material 1

Supplementary data

Authors: Wei Zhou, Zi-Lin Feng, Long-Ping Tang, Du Deng, Bao-cheng Wu, Lei Wu
Data type: fasta

Link: https://doi.org/10.3897/phytokeys.253.142516.suppl1

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Research Article

A new species of *Sedum* (Crassulaceae) from eastern China based on morphological and molecular evidence

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Abstract

Sedum orientalichinense, a new species of Crassulaceae from eastern China, is described and illustrated here. Phylogenetic analysis based on the internal transcribed spacer (ITS) region of nrDNA suggests that the new species belongs to *S.* sect. *Sedum* sensu Fu and Ohba (2001) in the "Flora of China", and is sister to *S. makinoi* with high support values (BS = 100, PP = 1). The new species was previously always misidentified as *S. makinoi*, *S. emarginatum* or *S. baileyi*, due to its opposite leaves. *Sedum emarginatum* can be easily distinguished by its leaf blades with the apex emarginate in which it differs from the other three species. *Sedum orientalichinense* usually has 2-branched cymes, unlike *S. makinoi* which is 2- to 4-branched. The new species further differs from *S. makinoi* in its obovate to obovate-rhombic leaf blades (vs. obovate to obovate-spatulate in the latter) and has shorter stems (6–18 cm vs. 11–28 cm) with less internodes. It can also be easily distinguished from *S. baileyi* by its slender to sub-woody suberect stems (vs. slender and erect stems) and larger plant height (6–18 cm vs. 3–7 cm).

Key words: Eastern China, morphology, nr-ITS, *Sedum* sect. *Sedum*

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Introduction

Sedum L. is the largest genus of the family Crassulaceae, including approximately 470 species of predominantly succulent plants (Thiede and Eggli 2007). The genus is predominantly distributed in temperate and subtropical areas of the Northern Hemisphere with diversity centers in the Mediterranean Region, Central America, the Himalayas, and East Asia (Stephenson 1994; Thiede and Eggli 2007). The succulent leaves and stems of *Sedum* allow them to store water and tolerate dry conditions, making them adapted to harsh environments such as deserts, cliffs, rocky or sandy areas, and meadows (Thiede and Eggli 2007).

According to Fu and Ohba (2001) in the "Flora of China", the genus has three sections in the area, *S.* sect. *Sedum*, *S.* sect. *Oreades* (Fröd.) K.T. Fu, and *S.* sect. *Filipes* (Fröd.) S.H. Fu. Section *Sedum* can be separated from sections *Oreades* and *Filipes* by adaxially gibbous carpels and follicles, while sect. *Oreades* differs from sect. *Filipes* in having a spurred (vs. spurless) leaf base and petals that are mainly yellow (vs. white).

During the past 20 years, 18 new species have been published from China, including *S. hoi* X.F. Jin & B.Y. Ding (Wang et al. 2005), *S. fanjingshanense* C.D. Yang et X.Y. Wang (Yang et al. 2012), *S. kuntsunianum* X.F. Jin, S.H. Jin & B.Y. Ding (Jin et al. 2013), *S. plumbizincicola* X.H. Guo et S.B. Zhou ex L.H. Wu (Wu et al. 2012), *S. tarokoense* H.W. Lin & J.C. Wang (Lu et al. 2013), *S. spiralifolium* D.Q. Wang, D.M. Xie & L.Q. Huang (Xie et al. 2014), *S. peltatum* M.L. Chen et X.H. Cao (Chen et al. 2017), *S. ichangensis* Y.B. Wang (Wang and Xiong et al. 2019), *S. kwanwuense* H.W. Lin, J.C. Wang & C.T. Lu (Lu et al. 2019), *S. lipingense* R.B. Zhang, D. Tan & R.X. Wei (Zhang et al. 2019), *S. taiwanalpinum* H.W. Lin, J.C. Wang & C.T. Lu (Lu et al. 2019), *S. nanlingense* Yan Liu & C.Y. Zou (Zou et al. 2020), *S. danxiacola* S.Y. Meng & B. Chen (Meng and Chen et al. 2023), *S. jinglanii* Yan S. Huang & Q. Fan (Huang et al. 2023), *S. matsuense* C.T. Lu & W.Y. Wang (Lu and Wang et al. 2023), *S. yangjifengensis* B. Chen & Z.W. Zhu (Zhu et al. 2023), *S. fluviale* B. Chen & Z.W. Zhu (Zhu et al. 2024) and *S. xunvense* Y.L. Xu & P. Li (Chai et al. 2024). According to the Flora of China records by Fu and Ohba (2001), China originally documented 121 *Sedum* species with 91 endemics. The listed additional records (as of 2024) have updated these figures to 139 recognized species, including 109 endemic taxa.

During extensive field investigations in eastern China (Jiangxi, Zhejiang, and Anhui Provinces), we found a unique *Sedum* species growing on a rocky slope with opposite leaves, and usually 2-branched cymes. Through comprehensive literature studies, morphological comparison with related species and molecular analysis, we confirmed that it was a new species and provide a detailed description and illustration of it here.

Methods

We conducted detailed field investigations and observations of the putative new species during its flowering and fruiting stages, and cultivated some plants in the laboratory for the study of its morphology. Morphological data were obtained by measurements based on abundant living samples from three different localities: Matoushan of Jiangxi Province (MTS), and Baizhangji (BZJ) and Daciyan (DCY) of Zhejiang Province (Fig. 5). Morphologically related species were collected from Lushan Mountain (LS) of Jiangxi Province (*S. baileyi*), Huangshan Mountain (HS) of Anhui Province and Yuyao (YY) of Zhejiang Province (both *S. emarginatum*). Additionally, numerous digital specimens were studied from online resources: Chinese Virtual Herbarium CVH (https://www.cvh.ac.cn/); Vascular Plants Herbarium of the Komarov Botanical Institute RAS—Herbarium LE (https://en.herbariumle.ru/); Global Biodiversity Information Facility GBIF (https://www.gbif.org/); Kagoshima University Museum KAG (https://dbs.kaum.kagoshima-u.ac.jp/musedb/s_plant/s_plant.php); and Kagoshima University Museum TSN (https://db.kahaku.go.jp/webmuseum/search?cls=col_b1_01) to obtain morphological data for related species. Data of *S. makinoi* were obtained from 33 specimens, and data of the putative new species were from 33 individuals. We measured the plant height and selected three mature leaf blades from each individual to measure the length and width of the leaf blade and calculated the average value. Since the Shapiro-Wilk test results showed that the three data sets did not follow a normal distribution, the two-sample Mann-Whitney U test was performed using SPSS 27.0.1.0 (2020). Type specimens were collected in the Matoushan National Nature Reserve, Jiangxi Province, China, and were deposited in the Herbarium of Sun Yat-sen University (SYS!).

The putative new species was sampled at three localities: Matoushan of Jiangxi Province (MTS, 3 individuals, *Xiong Y. 23062901*), and Daciyan (DCY, 1 individual, *Dai J.M. 24040701*) and Baizhangji (BZJ, 1 individual, *Dai J.M. 24040302*) of Zhejiang Province. Fresh leaves of the five individuals were collected and stored with silica gel in zip-lock plastic bags until use. Total DNA was extracted using the modified CTAB method (Doyle and Doyle 1987). For the amplification of the partial internal transcribed spacer 1, the 5.8S ribosomal RNA gene and the partial internal transcribed spacer 2 region we used the primers ITS1 and ITS4 (White et al. 1990). PCR amplifications were performed following Huang et al. (2021).

In order to explore the phylogenetic position of the putative new *Sedum* species, we downloaded ITS sequences of 56 accessions representing 46 *Sedum* taxa and three outgroup species from the Genbank database at the National Center for Biotechnology Information (NCBI) (Suppl. material 1). The selection of the three outgroup species (*Greenovia aizoon*, *Aeonium lancerottense*, *A. viscatum*) followed Huang et al. (2023). The sequences were aligned using MAFFT v. 7.520 (Katoh and Standley 2013). Based on Maximum likelihood (ML) and Bayesian Inference (BI), phylogenetic reconstructions were run by IQ-TREE v. 2.0.3 (Nguyen et al. 2015, Minh et al. 2020) with 2000 bootstraps (Hoang et al. 2018), and MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001), respectively. BI analysis used random starting trees and four Markov Chain Monte Carlo (MCMC) simulations were run simultaneously and sampled every 1000 generations for 30 million generations. Bayesian posterior probabilities (PP) were calculated as the majority consensus of all sampled trees with the first 25% discarded as burn-in. Figtree v. 1.4.3 (Rambaut 2016) was employed to visualize the tree.

Result and discussion

The ITS sequences were aligned to a length of 732 bps, and 349 positions were parsimony-informative. The best-fit nucleotide substitution model was determined as SYM+I+G4 based on the Bayesian Information Criterion (BIC). The 5 samples of the new species had 5 variable sites within itself. There were 18 variable sites between the new species and *S. makinoi*, and 56 variable sites between the new species and *S. baileyi* and *S. emarginatum*, respectively.

According to the topology produced (Fig. 1), the five accessions of the new species formed a clade well supported by ML (BS = 92%, PP = 0.93). It was resolved as a well-supported sister (BS = 100%, PP = 1) to a robust (BS = 99%, PP = 1) *S. makinoi* clade. As shown in the ML phylogenetic tree, the morphologically similar species *S. baileyi* and particularly *S. emarginatum* placed (widely) separate the new species from *S. makinoi*.

Morphologically, the putative new species is similar to *S. makinoi*, but can be distinguished by its usually 2-branched (rarely 3-branched) cymes (vs. 2–4-branched in the latter), the shape of the leaf blades (obovate to obovate-rhombic vs. obovate to obovate-spatulate), and its plant height (6–18 cm

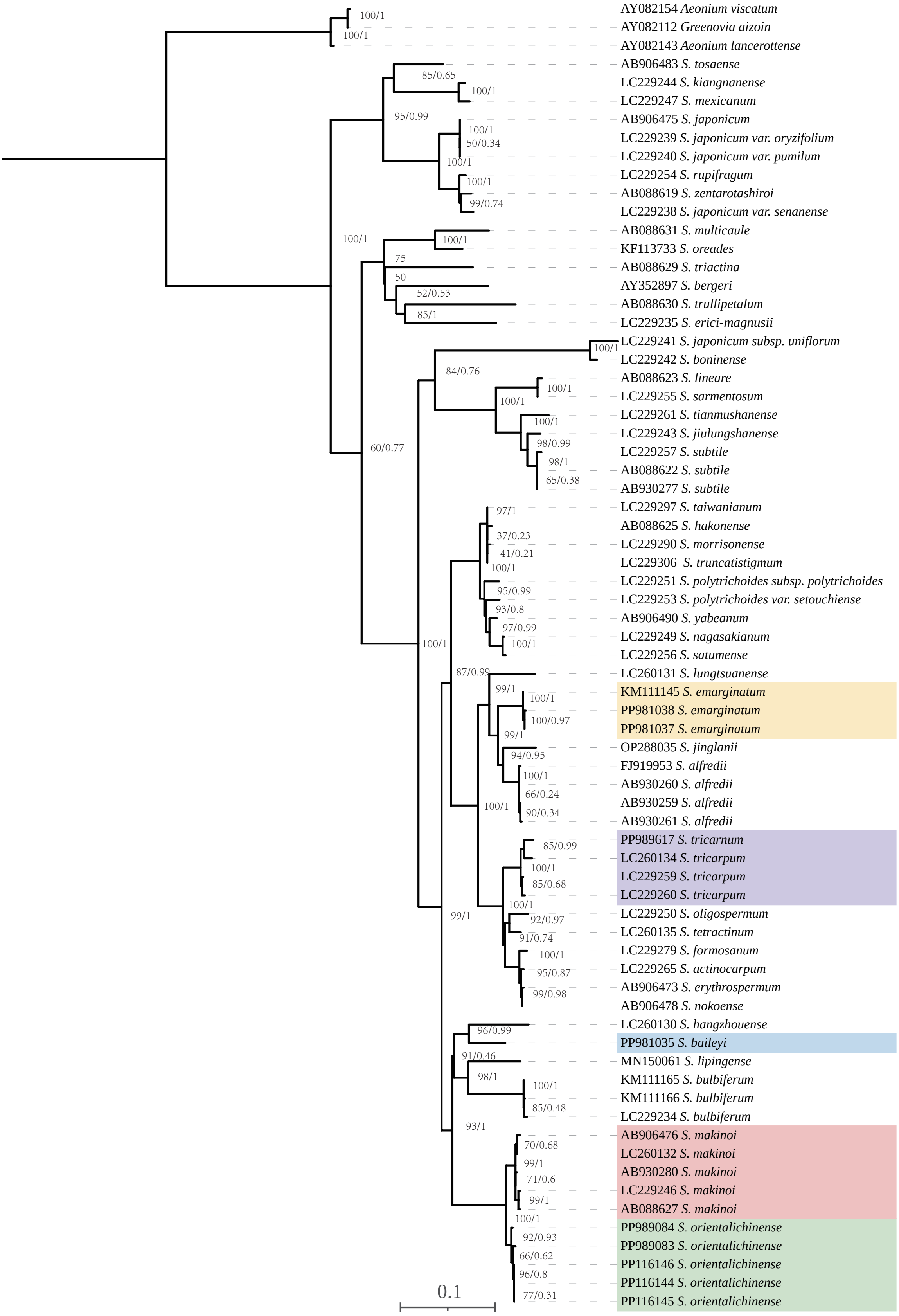

Figure 1. Maximum Likelihood (ML) tree based on ITS sequences of *Sedum orientalichinense* and related species. Bootstrap values of the ML and BI posterior probabilities are shown at the nodes. Three outgroups were used: *Greenovia aizoon*, *Aeonium lancerottense*, and *A. viscatum*. The new species is shaded in green. *Sedum makinoi*, *S. emarginatum*, and *S. baileyi* are shaded in red, yellow and blue, and *S. tricarpum* in purple, respectively.

vs. 11–28 cm) (Table 1). Although the new species was previously often misidentified as *S. baileyi* due to its opposite leaves, it can be easily distinguished from the latter by its slender to sub-woody stems (vs. slender stems), usually larger plant height (6–18 cm vs. 3–7 cm) (Table 1). Additionally, the Mann-Whitney U test results showed that the median plant height of *S. makinoi* was 16 (12.3, 20) and that of *S. orientalichinense* was 9.5 (7.875, 16.85), with statistically significant differences between the two groups (Z = 3.633, p = 0.01). The same conclusion can be drawn from the calculation results of leaf width (Table 2). These morphological differences support classifying *S. orientalichinense* as a new species. *Sedum makinoi* was previously given as distributed in Zhejiang and Anhui Province in China as well as Japan (Fu and Fu 1984; Fu and Ohba 2001). Supporting specimens were sampled from Huangshan, Anhui Province (Production practice team of Department of Biology of FDU 0338,

Table 1. Morphological comparisons between *Sedum orientalichinense*, *S. baileyi*, *S. makinoi* and *S. emarginatum*.

Character*	**Species**			
	S. orientalichinense	***S. makinoi***	***S. baileyi***	***S. emarginatum***
Plant height	6–18 cm	11–28 cm	3–7 cm	10–27 cm
Flowering stems	Suberect, slender to sub-woody, 4–8 internodes	Erect to suberect, slender to sub-woody, 8–12 internodes	Erect, slender	Suberect, slender
Phyllotaxy	Opposite	Opposite	Opposite	Opposite
Leaf blade	Obovate to obovate-rhombic, base tapered and shortly spurred, apex obtuse	Obovate to obovate-spatulate, base cuneate and shortly spurred, apex subacute	Obovate to obovate-rhombic, base tapered and shortly spurred, apex subacute	Spatulate-obovate to broadly obovate, base attenuate and shortly spurred, apex rounded and emarginate
Leaf length × width	1.3–2.7 × 0.6–2.4 cm	1.0–2.5 × 0.6–0.8 cm	Ca. 1.5 × 0.6 cm	1.5–2 × 0.5–1 cm
Inflorescence	Cymes usually 2-branched, rarely 3-branched	Cymes 2–4-branched	Cymes 1–2-branched, few flowered	Cymes usually 3-branched
Inflorescence diam.	3–10 cm	3–15 cm	1.5–3.5 cm	3–6 cm
Sepal shape	Spatulate-obelliptic, base shortly spurred, apex obtuse	Linear-spatulate, base shortly spurred, apex obtuse	Oblong-linear, basal spur broad and obtuse	Lanceolate to narrowly oblong, base shortly spurred, apex obtuse
Sepal length × width	2–4 × 1–1.5 mm	3–4 × 0.7–1 mm	1.5–2 × ca. 1 mm	2–5 × 0.7–2 mm
Petal length × width	3–5 × ca. 1 mm	4–6 × 1–2 mm	4–5 × ca. 1.5 mm	6–8 × 1.5–2 mm
Stamen size	Antesepalous ones subequaling petals; antepetalous ones shorter than petals	Antesepalous ones subequaling petals; antepetalous ones shorter than petals	Shorter than petals	Shorter than petals
Nectar scales	Broadly cuneate to sub-quadrangular	Oblong-spatulate	Oblong-spatulate	Oblong to broadly cuneate
Flowering	June–July	June–July	April	May–June
Fruiting	July	July	July	July
Distribution	China (Jiangxi, Zhejiang)	Japan	China (Guangdong, Guangxi, Hunan, Jiangxi)	China (Anhui, Gansu, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Yunnan, Zhejiang)

Abbrevistions: *Data of *S. orientalichinense* were from 33 individuals, data of *S. makinoi* were from 33 specimens and the “Flora of China”, data of *S. baileyi* and *S. emarginatum* were from the “Flora of China” (Fu and Ohba 2001).

Table 2. Quantitative characteristics and significance difference analysis of the species *Sedum makinoi* and *Sedum orientalichinense*.

Value	Species	M (P25, P75)	Mann-Whitney U test	
			Z	P
ph (cm)	*S. makinoi*	16 (12.3, 20)	3.633	0.001*
	S. orientalichinense	9.5 (7.875, 16.85)		
ll (cm)	*S. makinoi*	1.5 (1.3,1.9)	1.745	0.081
	S. orientalichinense	1.7 (1.588,1.863)		
lw (cm)	*S. makinoi*	0.55 (0.47,0.7)	3.821	0.001*
	S. orientalichinense	0.83 (0.67,0.95)		
ll/lw	*S. makinoi*	2.6 (2.16, 3)	3.056	0.002*
	S. orientalichinense	2.07 (1.8, 1.46)		

Abbreviations: ph = plant height; ll = leaf length; lw = leaf width. Independent-Sample Mann-Whitney Test was used, pl and lw representing significant differences at the 0.5% nominal level. M(P25, P75) means Median and Interquartile range, * means P < 0.05.

PE00914380), and Siming Mountain, Zhejiang Province (*Siming Mountain 0577*, PE00914382, PE00914383). Based on morphology and phylogeny, the specimen collected from Huangshan is *Sedum tricarpum* Makino (Figs 1, 7). Xia and Liu et al. (2011) first recorded *S. tricarpum* from Anhui Province, China. This finding supports that the specimen (Production practice team of Department of Biology of FDU 0338, PE00914380, CVH) is misidentified as *S. makinoi* due to its occasionally opposite leaves. We could not find specimens of *S. makinoi* in Siming Mountain, Zhejiang, as was indicated by the specimens (*Siming Mountain 0577*, PE00914382, PE00914383). We believe the specimen from Siming Mountain and the new species are conspecific based on careful comparison of the morphology, such as 2-branched cymes and short stems (6.5–14.5 cm).

Although *S. makinoi* had not been found on Siming Mountain, as was indicated by the specimen cited above, some specimens morphologically closely related to *S. makinoi* were collected from other sites in Zhejiang Province (*Dai J.M. 24040302*, *Dai J.M. 24040701*). These specimens clustered together with *S. orientalichinense* (Fig. 1) and shared a similar morphology with it. This finding may suggest that the species previously misidentified as *S. makinoi* in China was actually *S. orientalichinense*, and that *S. makinoi* is absent from China and restricted in its distribution to Japan.

Taxonomic treatment

***Sedum orientalichinense* Q.Fan & P.Li, sp. nov.**
urn:lsid:ipni.org:names:77358282-1
Figs 2–6

Type. China • Jiangxi Province, Fuzhou City, Mount Matoushan, Baishakeng, on rocky cliff, 27.77°N, 117.23°E, 424 m a.s.l., 29 June 2023, *Xiong Y. 23062901* (holotype: SYS00236991).

Diagnosis. The new species differs from *S. makinoi* in its usually 2-branched cymes. *S. makinoi* also has longer, more erect stems with more internodes (8–12 vs. 4–8), resulting in denser foliage, whereas the new species has fewer leaves. Key differences include the shape and width of the leaf blades of

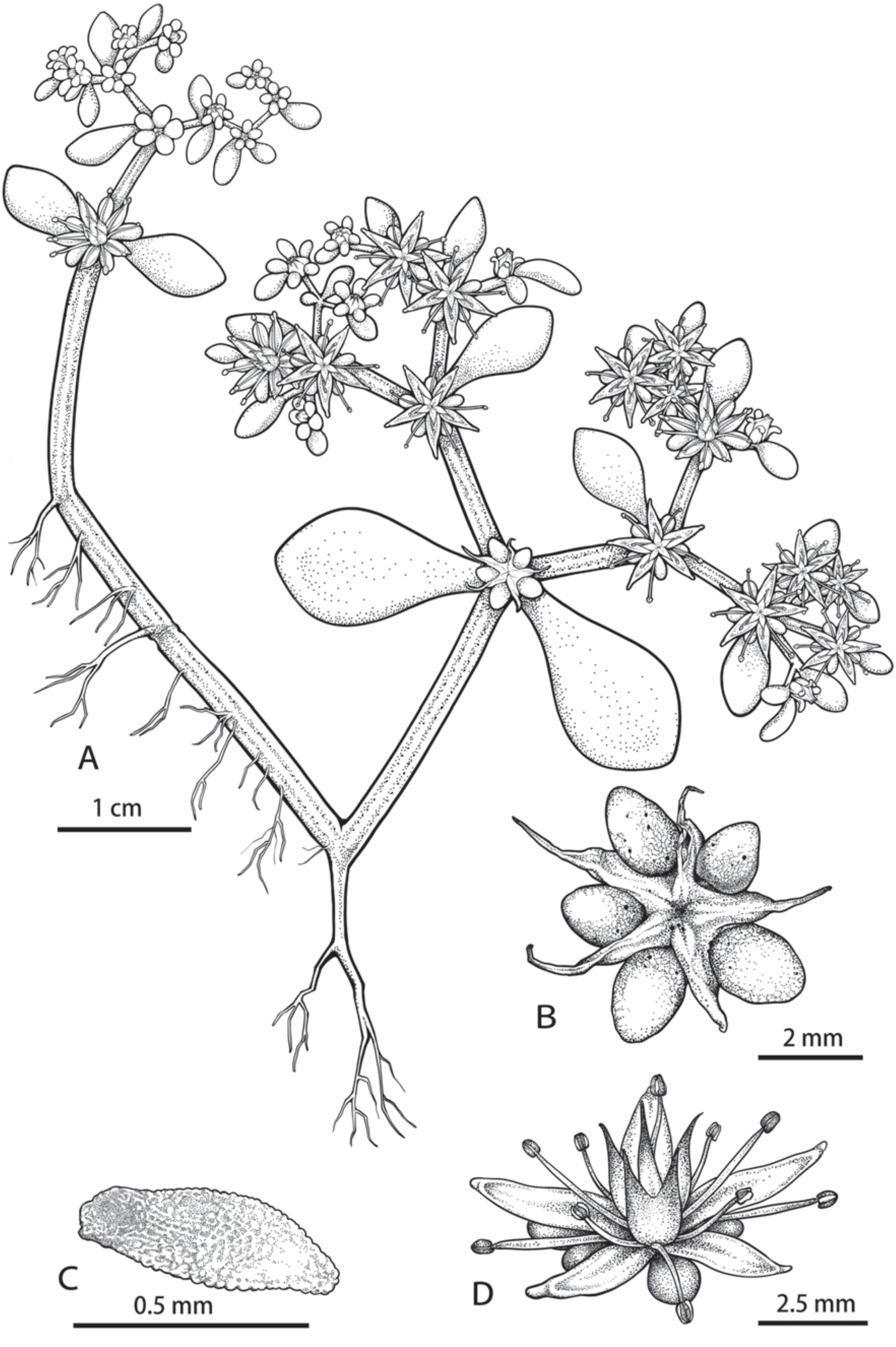

Figure 2. *Sedum orientalichinense* **A** habit: Flowering stem with inflorescences **B** unripe follicles with sepals **C** seed **D** flower.

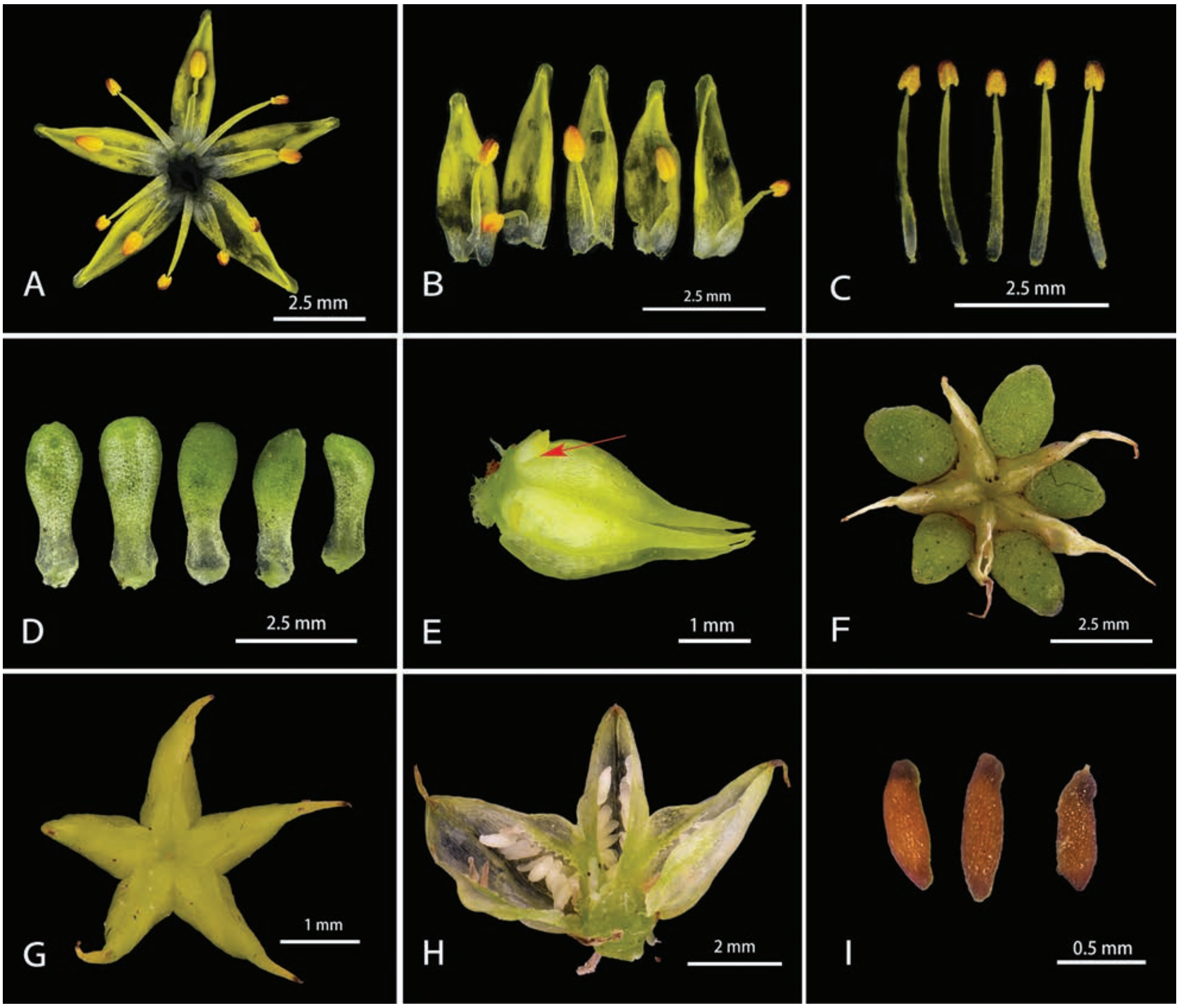

Figure 3. *Sedum orientalichinense* **A** flower **B** petals and epipetalous stamens **C** episepalous stamens **D** sepals **E** carpels with nectar scale (marked with red arrow) **F** unripe follicles with sepals **G** unripe follicles **H** opened unripe follicles **I** seeds (photographs taken from plants cultivated at Sun Yat-sen University, Guangzhou Province, with **A–E** in June 2023, **F–H** in July 2023, **I** in July 2024, from the collection *Xiong Y. 23062901*).

S. orientalichinense and *S. makinoi* (obovate to obovate-rhombic vs. obovate to obovate-spatulate; 0.6–2.4 cm vs. 0.6–0.8 cm), shorter stems (6–18 cm vs. 11–28 cm), and a usually smaller inflorescence diameter (3–10 cm vs. 3–15 cm). The new species also has distinct sepals (spatulate-obelliptic vs. linear-spatulate) and nectar scales (broadly cuneate to sub-quadrangular vs. oblong-spatulate). Additionally, our research indicates that *S. makinoi* is endemic to Japan, which helps to distinguish the two species geographically. The new species can be distinguished from *S. baileyi* by its robust, slender to sub-woody stems (vs. slender stems) and greater height (6–18 cm vs. 3–7 cm) (Table 1). Lastly, *S. emarginatum* is easily identified by its emarginate leaf apex, a feature not found in the other three species (Table 1).

Description. Perennial herbs, fleshy, glabrous, roots fibrous, stems slender to sub-woody, basally prostrate and rooting at nodes, apically erect, usually branched, rarely single, flowering stems sub-erect, with 4–8 internodes, usually

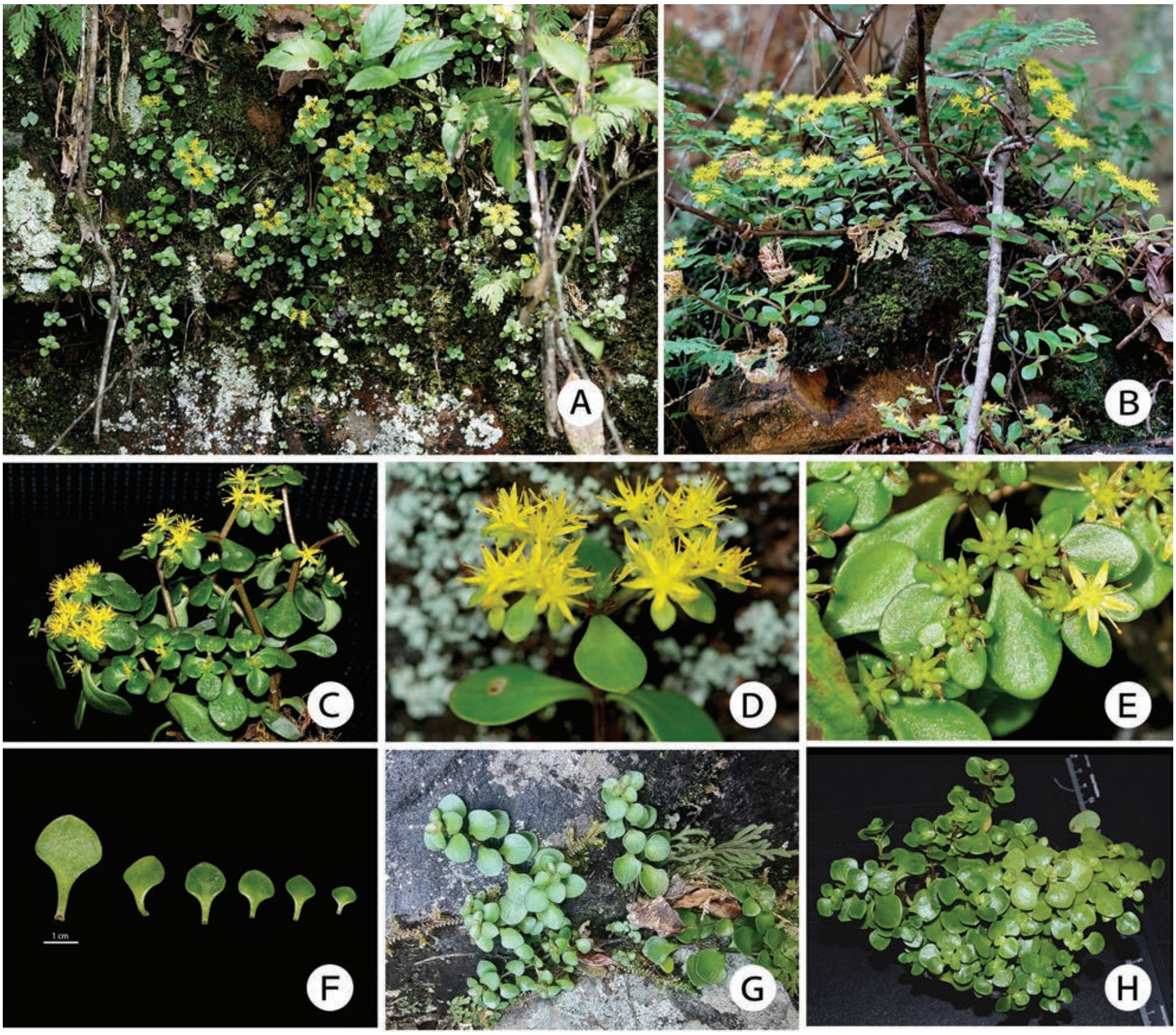

Figure 4. *Sedum orientalichinense* **A** habitat **B, C** habit showing the sub-erect, 2-branched stems **D** side view of a cyme **E** cyme with unripe follicles **F** leaves from a single stem of *S. orientalichinense* **G** sterile stems in the wild **H** vegetative growth of *S. orientalichinense* under artificial light in cultivation (**A, B, D, E, G** were photographed by Yu Xiong in Matoushan, Jiangxi Province in June 2023; **C, F, H** were photographed by Jing-Min Dai cultivated at Sun Yat-sen University, Guangzhou Province, with **F, H** in December 2023, and **C** in July 2024).

2-branched, rarely 3-branched, 6–18 cm high. Leaves opposite, glabrous, pseudopetiolate; leaf blade obovate to obovate-rhombic, margin entire, 1.3–2.7 × 0.6–2.4 cm, base tapered and shortly spurred, apex obtuse. Cymes usually 2-branched, rarely 3-branched, many flowered, 3–10 cm in diam. Bracts resembling stem leaves but obovate and smaller, 0.3–2.1 × 0.1–1.2 cm. Flowers sessile, equally 5-merous. Sepals 5, usually equal, rarely subequal, spatulate-obelliptic, 2–4 × 1–1.5 mm, base shortly spurred, apex obtuse. Petals yellow, base connate for ca. 0.3 mm, 3–5 × ca. 1 mm, lanceolate, apex acuminate, hooded. Stamens 10, in 2 whorls, both antesepalous ones and antepetalous ones shorter than petals, the antepetalous stamens fused at base for about 0.5 mm with the petal base, and the antepetalous ones slightly shorter the than antesepalous ones (1.3–1.4 vs. 0.9–1 cm). Nectar scales broadly cuneate to sub-quadrangular,

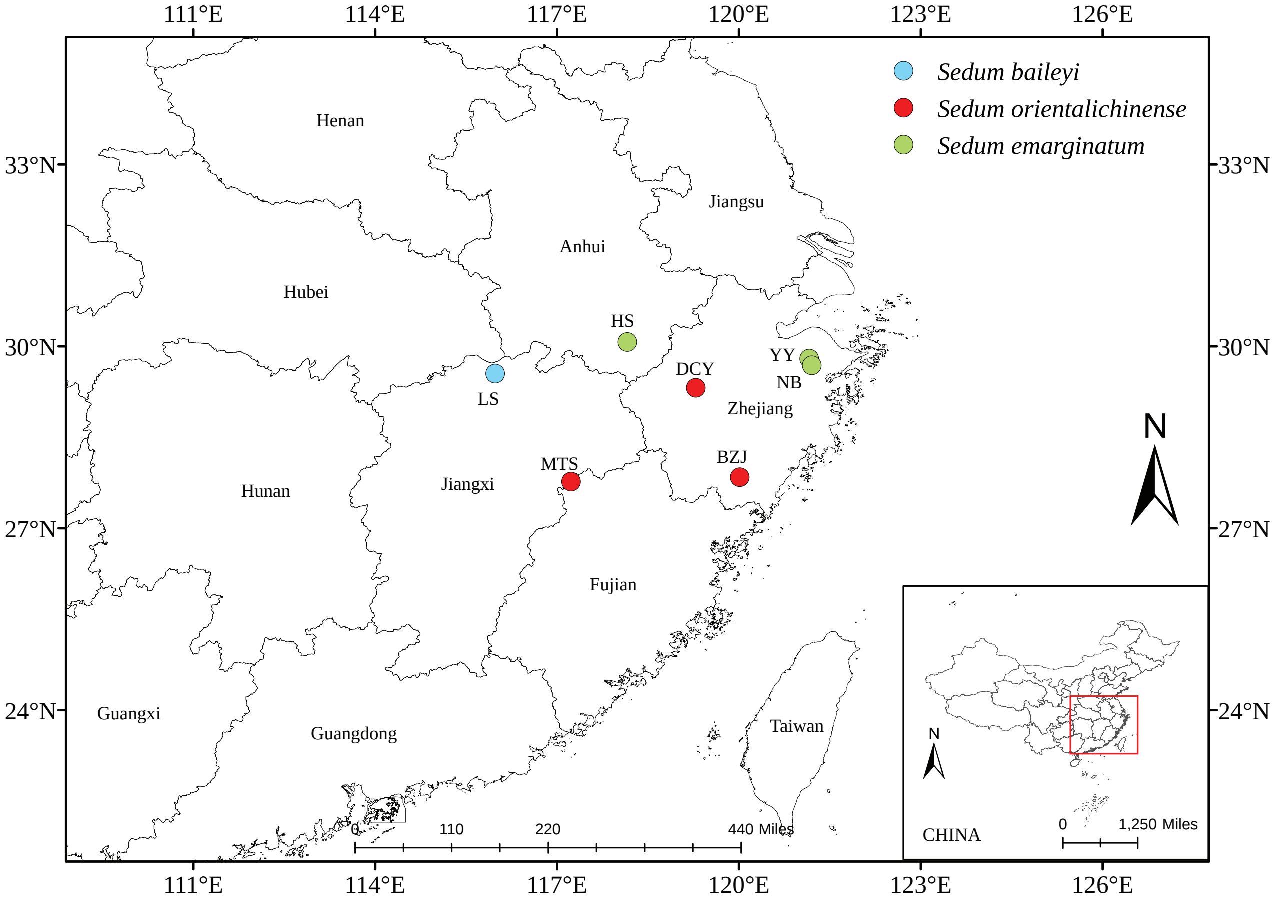

Figure 5. Distribution of *Sedum orientalichinense* and sampling sites of morphologically similar species. *Sedum orientalichinense* was sampled at its three known localities Matoushan (MTS, Jiangxi Province), Baizhangji (BZJ, Zhejiang Province), and Daciyan (DCY, Zhejiang Province). *S. baileyi* was sampled at the type locality Lushan Mountain (LS), Jiangxi Province. *S. emarginatum* was sampled at three sites: Yuyao (YY) and Ningbo (NB) in Zhejiang Province, and Huangshan (HS) in Anhui Province.

ca. 0.5 mm long. Carpels 5, lanceolate, 4–5 mm long, connate at base for ca. 1 mm, apically usually divergent, sometimes closely connivent. Follicles obliquely divergent, stellate, many seeded, placentation marginal. Styles ca. 1 mm long. Seeds sub-ovoid, mammillate, brown when mature, 0.3–0.5 mm long.

Phenology. Flowering from June to July, fruiting in July.

Etymology. The specific epithet refers to the distribution area of the species.

Vernacular name. We propose a Chinese name, Huá dōng Jǐng Tiān (华东景天).

Distribution and habitat. The new species is distributed in eastern China in Jiangxi and Zhejiang, provinces. It grows in rocky crevices and soil slopes in valleys at altitudes of 300–600 m a.s.l.

IUCN conservation status. Due to its wider distribution and numerous individuals at each of the three investigation sites, *S. orientalichinense* should be considered as least concern (LC) (IUCN Standards and Petitions Subcommittee 2022).

Additional specimens examined. *Sedum orientalichinense* (paratypes): CHINA • Jiangxi Province, Mount Matoushan, Baishakeng, on rocky cliff, 27.77°N, 117.23°E, 424 m a.s.l. 21 May 2024, *Xiong Y. 240521* (SYS00236993) • Longjing, in soily slope, 27.79°N, 117.24°E, 375 m a.s.l., *Xiong Y. s.n.*, *Li*

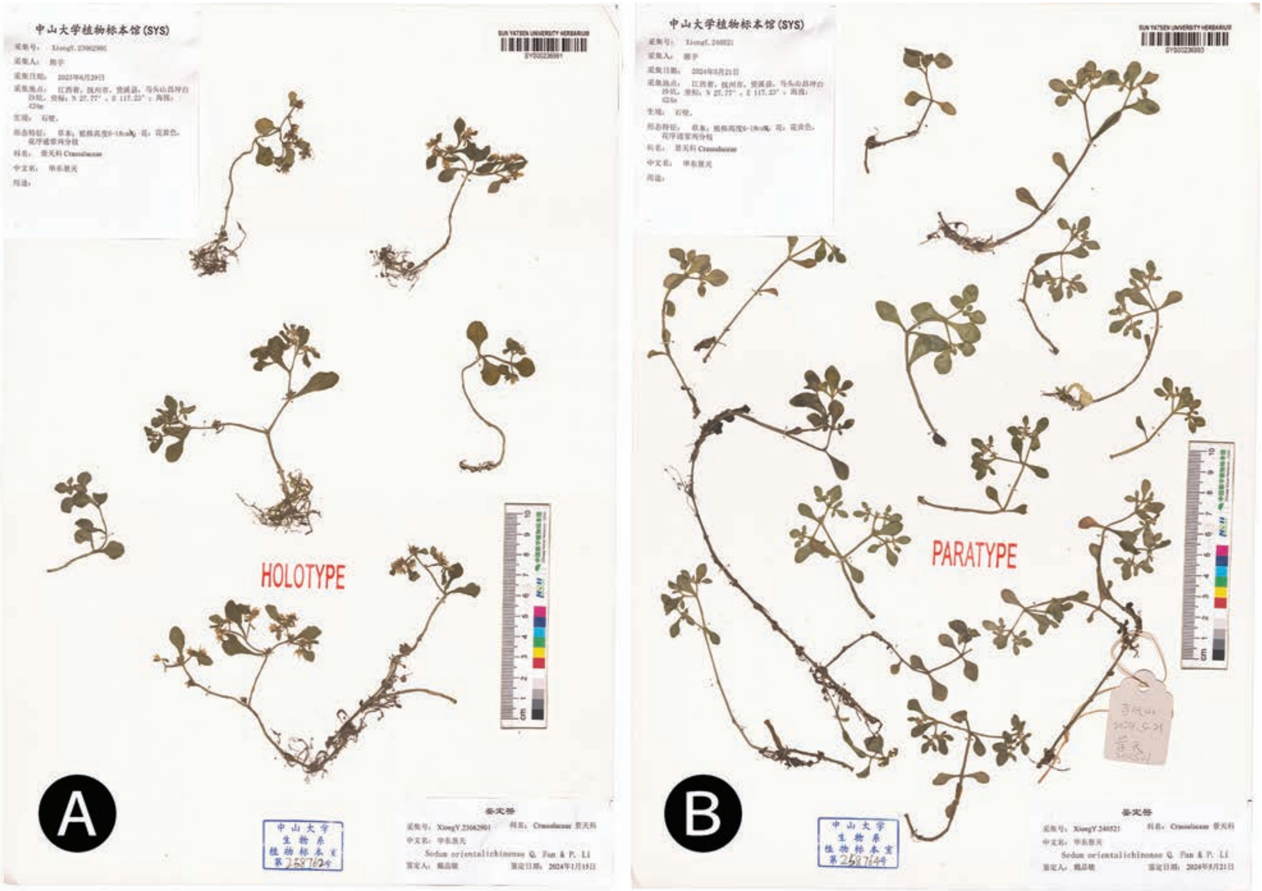

Figure 6. Type specimens of *Sedum orientalichinense* **A** the holotype (*Xiong Y. 23062901* [SYS00236991]) **B** a paratype (*Xiong Y. 240521* [SYS00236993]).

E.X & Li, *J.X. NCU2016MTS0221* (JXU0017056) • Zhejiang Province, Jiande City, Daciyan, *Dai J.M 24040701* (SYS00237017), Wenzhou City, Baizhangji, *Dai J.M*. (SYS00237018). ***Sedum emarginatum*:** CHINA • Zhejiang Province, *Migo H. s.n.* (ZNAS00332278, NAS00071019, NAS00332264). ***Sedum baileyi***: China • Jiangxi Province, Lushan Mountain, *Peng Y.S. 21051101* (SYS). ***Sedum makinoi***: JAPAN • Nanokawa, Tosa, *Makino T. 93* (LE01014732, LE01014733), *Watanabe, K. s.n.* (HUH01989208) • Nagasaki, *Anonymous s.n.* (K000732545) • Okayama, *Furuse M. 52653* (PE01135685, PE01135684), *Furuse M. 51887* (PE01135678), *Furuse M. 52825* (PE01135672), *Furuse M. 52653* (PE01135686) • Yamaguchi, *Saito, S. 3173* (PE01458488), *Nikai J. s.n.* (TNS-VS-48304) • Tochigi, *Furuse M. 14896* (PE01135683), *Furuse M. 54759* (PE01135687), *Nakamura s.n.* (KAG046500), *Yoshi K. 14896* (KAG175186) • Kumamoto, *Sumihiko H. 44370* (KAG046490) • Saga, *Bajou I. s.n.* (KAG046495) • Shizuoka, *Hideaki N. 4493* (KAG046499) • Oita, *Sumihiko H. 44371* (KAG046504) • Hiroshima, *Taizo M. 165* (KAG046497) • Saitama, *Shigeki K. 1171* (KAG046502) • Hyogo, *Fukuoka N. 13638* (TNS-VS-564993) • Oity, *Yamaki N.*, *Herb. H. Koidzumi 97349* (TNS-VS-480622), *Herb. H. Koidzumi 97536* (TNS-VS-480623) • Tokushima, *Akiyama S. 20808* (TNS-VS-775554) • Ehime, *Koidzumi H. 99692* (TNS-VS-480618).

Figure 7. *Sedum tricarpum* from Huangshan **A** specimen from the Herbarium of the Institute of Botany, Chinese Academy of Sciences (Production practice team of Department of Biology of FDU 0338, PE00914380, Beijing, photographed by Bin-bin Liu) **B–D** living samples of *S. tricarpum* from Huangshan, Anhui province **B** habit **C** the leaves may occasionally be opposite which leads to misidentifications **D** leaf blade shape. (3 July 2024, photographed and collected by Jing-Min Dai, **B–D** were from a cultivated individual, *Dai J.M.2403221*).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: PL. Data curation: JMD, YLX. Formal analysis: YX, JMD. Funding acquisition: PL, QF. Investigation: YX. Methodology: YLX, JMD. Project administration: QF. Resources: YX. Supervision: QF. Visualization: YX, YLX. Writing – original draft: JMD. Writing – review and editing: PL, QF.

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Data availability

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

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Supplementary material 1

Taxa, voucher information, GenBank accession numbers and references for ITS sequences of *Sedum* (*S.*) species and three outgroups used for phylogenetic analyses in this study

Authors: Jing-Min Dai, Yu Xiong, Pan Li, Yue-Liang Xu, Qiang Fan

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Link: https://doi.org/10.3897/phytokeys.253.119922.suppl1

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Research Article

Neotrinia kurramica (Poaceae, Stipeae), a new species from Parachinar (Khyber Pakhtunkhwa, Pakistan)

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Abstract

The family of grasses (Poaceae) is one of the most diverse plant families, with the tribe Stipeae representing an ecologically significant group of more than 600 species primarily distributed in arid and semi-arid regions. The genus *Neotrinia*, a lesser-known member of this tribe, is characterised by unique morphological traits, including distinctive patterns of lemma epidermis. During field studies in the upper Kurram Valley, Pakistan, we found a new species, *Neotrinia kurramica*, which is described here. This perennial grass exhibits distinct morphological features, that differentiate it from previously known species. It is characterised by having up to 8.5 mm long ligules of cauline leaves, up to 15 cm long panicles bearing up to 41 spikelets, subequal glumes, lemma bearing two apical lobes, palea almost equal to lemma, 0.9–1.2 mm long obtuse callus and 50–70 mm long scabrid awns. Figures illustrating the new taxon and a comparison of distinguishing characters of the species representing the genus *Neotrinia* are presented.

Key words: Lemma micromorphology, Pakistan, Stipeae, taxonomy

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Introduction

The family Poaceae is among the most diverse and ecologically important plant families, encompassing more than 789 recognised genera (Soreng et al. 2022). They dominate diverse ecosystems ranging from tropical savannas and temperate grasslands to croplands (Hodkinson and Parnell 2007). Within Poaceae, the tribe Stipeae represents ecologically significant lineage comprising more than 600 species distributed across 34 genera (Soreng et al. 2022). Members of Stipeae are primarily distributed in arid and semi-arid regions, where they play critical roles in stabilising soils, providing forage, and maintaining ecological balance. The tribe is characterised by its unique morphology, including distinctive awned florets and complex seed dispersal mechanisms. The evolutionary history of Stipeae suggests an origin in Eurasia with Central Asia as its species diversity hotspot, with subsequent diversification influenced by climate shifts and habitat specialisation (Nobis et al. 2019, 2020; Vintsek et al. 2022; Krzempek et al. 2024; Sinaga et al. 2024).

The genus *Neotrinia*, is a relatively little-known member of tribe Stipeae, established to accommodate species with specific morphological traits that differentiate them from closely related genera such as *Stipa*, *Achnatherum*, *Piptatherum*, *Ptilagrostis*, *Stipellula* or *Trikeraia* (Nobis et al. 2019, 2020, Peterson et al. 2019). The most characteristic features of the members of *Neotrinia* are as follows: plants rather tall, from 50 to 250 cm high, densely tufted, panicle axis and branches covered by very dense short hairs, glumes abaxially covered by sparsely distributed and short prickles, lemma with two permanent apical unawned lobes (tithes) terminated by persistent, uni-geniculate or indistinctly bent scabrous awn, from 6 to 70 mm long, lemma epidermal pattern with elongated fundamental (long) cells (several times longer than wide) with deeply sinuous side walls; silica bodies rounded with adjacent cork cells and sparse and scattered hooks, prickles and macrohairs scattered throughout the entire lemma surface (Nobis et al. 2019; Nobis et al. 2020).

To date, only two species were included in the genus *Neotrinia*, *N. splendens* (Trin.) M. Nobis, P.D. Gudkova & A. Nowak and *N. chitralensis* (Bor) M. Nobis. *Neotrinia splendens* has a rather wide distribution range (from southern Russia throughout Mongolia, China, Japan, Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, Turkmenistan, Afghanistan, Iran, and Pakistan up to India (Nobis et al. 2019) and holds particular interest in its adaptations to harsh environments. Whereas *N. chitralensis* is treated as an endemic to Chitral Mts in Pakistan (Cope 1982). During field studies conducted in Khyber Pakhtunkhwa (upper Kurram Valley, western Pakistan), we found interesting specimens representing the tribe Stipeae, and described below as a new species belonging to the genus *Neotrinia*. This new taxon exhibits unique morphological characters that distinguish it from previously described species within the genus. Its discovery highlights the rich but under-documented biodiversity of the region and emphasises the need for continued botanical exploration in the mountains of Asia.

Methods

During recent field expeditions carried out in Parachinar (upper Kurram valley) in April-May, 2024 by Amir Sultan, Amjad Khan and Murtaza Hussain, interesting specimens of *Neotrinia* were collected from Malakyar Tangay area of Zerhan. Herbarium specimens of this species have been deposited at RAW and KRA (herbarium codes follow Thiers 2025). Morphological revision of herbarium material of all species representing the genus *Neotrinia* and allies, preserved at BM, CAL, COLO, E, K, KRA, KUN, LE, M, MO, MSB, PE, W herbaria was carried out by Marcin Nobis.

Micromorphological details of the lemma epidermis, leaf surfaces and awn were studied directly under both a stereomicroscope (Olympus 605371; Tokyo, Japan), JEOL-5910 scanning electron microscope (Tokyo, Japan) installed at the Centralized Resource Laboratory Department of Physics, University of Peshawar and Hitachi S-4700 scanning electron microscope at Jagiellonian University in Krakow. The dried material was coated with gold and then photographed under various magnifications.

Taxonomy

Neotrinia kurramica **A.Sultan, M.Nobis & Amjad Khan, sp. nov.**
urn:lsid:ipni.org:names:77358342-1
Figs 1–3

Type. Pakistan • Khyber Pakhtunkhwa, Upper Kurram Valley, Parachinar, Zerhan, Malakyar Tangai above Mulla Bagh, grassland on calcareous rocks, 33°56'47.4"N, 70°10'03.4"E, 2220 m, 6 May 2024, *Amir Sultan, Amjad Khan & Murtaza Hussain* s.n. (***holotype*** RAW [barcode 103365], ***isotype*** KRA00639009).

Description. Plant perennial, densely tufted with numerous culms and vegetative shoots (Fig. 1). ***Culms*** 40–80 cm tall, with 2 nodes, nodes pilose or pubescent. ***Leaves of vegetative shoots*****:** sheaths glabrous to sparsely and shortly pilose with white edge, scabrid at margins; ligules membranous, 2–3.5 mm long, acute to acuminate, apex shortly ciliate, and pubescent on the back; blades convolute, pale green, 20–55 cm long, 0.6–0.8(–1.0) mm in diameter, adaxial surface covered by dense and up to 0.15 mm long hairs (Fig. 3f), while abaxial surface glabrous to minutely scabrous along the midrib. ***Cauline leaves*****:** lower sheaths scabrous whereas the uppermost glabrous to minutely scabrous, the margins white and sparsely pubescent; ligules 3.5–8.5 mm long, acute or acuminate, at apex and the back shortly ciliate (Fig. 2d); blades convolute, pale green, up to 25 cm long, adaxial surface densely covered by short hairs, while abaxial surface glabrous to minutely scabrid along the midrib and margins. ***Panicle*** 10–15 cm long, contracted, with (15–)29–41 spikelets, exserted (sometimes lower branches enclosed by sheath of upper cauline leaf), branches erect (basal branches often spreading), hirsute with up to 0.5 mm long hairs, lower ones in threes (apical branches single, paired or sometimes up to 4 branches per node), the lower ones up to 18 mm long (Fig. 2c). ***Glumes*** subequal, pale green with hyaline membranous margins and at

Figure 1. Habitat and general habit of *Neotrinia kurramica* in northwestern Pakistan.

Figure 2. Main morphological characters of *Neotrinia kurramica*: glumes (**a**), florets (**b**), panicle (**c**), ligule of culm leaf (**d**), generative elements of flower, three anthers and two styles of ovary (**e**). Scale bars: 3 mm (**a, b, d**); 2 cm (**c**).

the top taper into a long hyaline tip, lower glume 14–15 mm long, three nerved, somewhat shorter than the upper glume, which is 5–7 nerved, lanceolate, 15–16 mm long, abaxially sparsely covered by scattered short prickles (Fig. 2a). ***Floret*** (anthecium = callus + lemma) 9–10.5 mm long (including apical lobes of lemma), ca. 1 mm wide (Fig. 2b). ***Callus*** 0.9–1.2 mm long, densely and long-pilose, hairs 0.5–1 mm long; peripheral ring 0.1–0.25 mm in diameter elliptic, scar circular (Fig. 3c). ***Lemma*** pale green to purple, dorsal surface with elongated basal (long) cells, rounded silica bodies with adjacent cork cells and sparse and scattered hooks, prickles and ascending hairs 0.75–1 mm long (Fig. 3a, b); apical lobes of lemma 0.6–1.0 mm long and covered by short hairs, the top of the lemma with

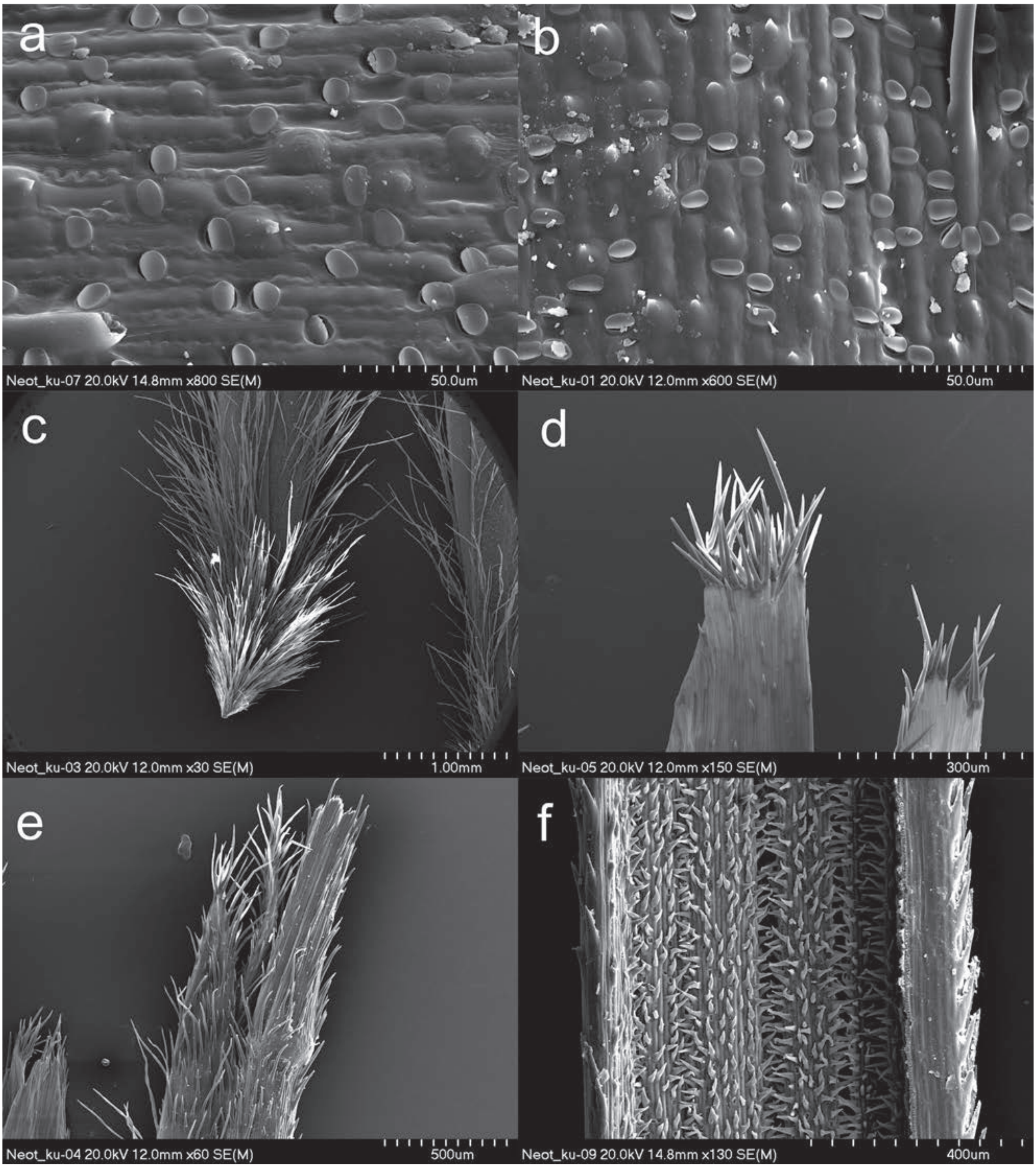

Figure 3. Micromorphological characters of *Neotrinia kurramica*: abaxial surface of lemma (**a, b**), callus (**c**), palea apex (**d**), lemma lobes (**e**), indumentum of the adaxial surface of leaf (**f**).

0.15–0.2 mm long hairs forming corolla (Figs 2b, 3e). ***Awn*** 50–70 mm long, unigeniculate; column 18–21 mm long, twisted, straw-coloured, covered by 0.2 mm long hairs, gradually decreasing in length towards geniculation; seta straight 30–50 mm long, hairs in lower part of seta 0.1–0.2 mm long, gradually decreasing in length towards apex. ***Palea*** equal to lemma in length, with a dorsal line of hairs and a ring of short hairs at the apex (Fig. 3d). ***Anthers*** yellow, glabrous, 6 mm long, filaments ca. 1 mm long (Fig. 2e). ***Lodicules*** 3, linear-lanceolate, 2–2.4 mm long, 0.3 mm wide. ***Ovary*** with 2 styles (Fig. 2e). ***Caryopsis*** not seen.

Table 1. A comparison of the main characters distinguishing *Neotrinia kurramica* from other members representing the genus occurring in Pakistan.

Character	*N. kurramica*	*N. chitralensis*	*N. splendens*
Floret (anthecium)	9–10.5 mm	9–11 mm	4.0–7.2 mm
Apical lemma teeth	0.6–1.0 mm, pilose	2–2.5 mm, glabrous	0.5–1.2 mm, pilose
Callus	0.9–1.2 mm	0.5–0.6 mm	0.3–0.5 mm
Awn	50–70 mm	16–21 mm	5–12 mm
Glumes	14–16 mm long, subequal, the lower slightly shorter than the upper, at the top tapering into long hyaline tips	9.5–12 mm long, subequal, the lower slightly shorter than the upper, at the top without long hyaline tips	5–8.5 mm long, lanceolate, distinctly unequal, the lower 1–1.7 mm shorter than the upper, at the top without long hyaline tips

Distribution and ecology. *Neotrinia kurramica* is so far only known from the type locality in Upper Kurram, Khyber Pakhtunkhwa Province (Fig. 1), occurring at an elevation of about 2220 m. The population of *N. kurramica* was found growing along stony/gravelly slopes leading to the edges of a mountain stream. While these slopes are dominated by grasses, oak (*Quercus baloot* Griff.) forests dominate the hilltops above these slopes. *Neotrinia kurramica* grows in association with *Isodon rugosus* (Wall. ex Benth.) Codd, *Duthiea oligostachya* (Munro ex Aitch.) Stapf, *Sophora mollis* (Royle) Graham ex Baker, *Piptatherum* sp. and *Cirsium falconeri* (Hook. f.) Petr. It is expected to have a distribution in similar habitats of Upper Kurram valley. Further explorations in the area are needed, to determine its population size, distribution range and to evaluate conservation status of this new species.

Paratype. Pakistan • Khyber Pakhtunkhwa, Upper Kurram, Parachinar, Zerhan, Malakyar Tangay above Mulla Bagh, 22 May 2021, *Amir Sultan, Asif Mehmood, Waqar Hassanain & Noor Ali Shah* s.n. (RAW [barcode 101893]).

Etymology. The name of the new species originates from Kurram Valley.

Similar species. *Neotrinia kurramica* differs significantly from all the remaining species representing the genus by having awns 50–70 mm long vs. 5–12 or 16–21 mm long in *N. splendens* and *N. chitralensis* respectively (Table 1). The new species is slightly similar also to *Achnatherum jacquemontii*, however differs in having longer lemmas, longer glumes, longer awns, and completely different patterns of the lemma morphology sow-like vs. maize-like respectively (cf. Nobis et al. 2020).

A key to genera of the tribe Stipeae in Pakistan

1 Lemma lobes awn-like, 2–3 mm long, setaceous .... ***Trikeraia***
– Lemma without awn-like lobes, lobes (if present) usually less than 2.5 mm long **2**
2 Surface of lemma epidermis covered by numerous and rounded silica bodies, basal cells as wide as long or wider than longer, hooks usually absent, at least in the middle part of lemma (lemma epidermal pattern maize-like) **3**
– Surface of lemma epidermis covered with square, rectangular or elongated basal cells (2–11 times longer than wider), silica bodies usually associated with cork cells, hooks usually present and more or less densely distributed (lemma epidermal pattern sow-like) **4**
3 Plants annual .... ***Stipellula***
– Plants perennial .... ***Achnatherum***

4 Awns straight, scabrous. Floret (anthecium) usually dorsally compressed. Callus short, up to 0.3 mm long .... ***Piptatherum***

– Awns geniculate, scabrous or variously pilose. Floret (anthecium) terete or laterally compressed. Callus longer than 0.3 mm **5**

5 Callus stiff, usually acute at the apex, (0.5–)1–4(–6) mm long. Lemma epidermis with square or rectangular cells associated with numerous hooks (visible under high magnification) and reniform to ovate silica bodies ....***Stipa***

– Callus blunt, usually rounded at the apex, (0.3–)0.5–1(–1.2) mm long. Lemma epidermis with elongated cells 4–11 times longer than wider, associated with ovate or elongated silica bodies and rather sparse or absent, at least in the middle part of the lemma, hooks (visible under high magnification) **6**

6 Glumes glabrous or with sparse cilia along the middle vein, lower segment of awn pilose, with hairs over 0.3 mm long. Surface of lemma epidermis with elongated, 1–3-constricted silica bodies, without or with very sparse hooks ....***Ptilagrostis***

– Glumes scabrous or densely covered by short prickles, lower segment of awn scabrous, with prickles up to 0.3 mm long. Surface of lemma epidermis with ovate to rounded silica bodies and sparse hooks ....***Neotrinia***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Data availability

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

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Research Article

Broad-ranged, highly disjunct, locally rare and severely endangered: the challenging risk assessment and a global conservation strategy for *Erica sicula* Guss. *sensu lato* (Ericaceae)

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Abstract

The distribution range of *Erica sicula* Guss. *sensu lato* spans the central and eastern Mediterranean Basin, but shows a significantly fragmented pattern, and its populations are locally subject to multiple threats inducing continuous regression. The species is distributed across five countries, Italy, Libya, Cyprus, Türkiye and Lebanon, and includes two subspecies, subsp. *sicula* and subsp. *bocquetii*, currently represented by 31 and 8 stands, respectively. This study provides an updated overview of the distribution, ecology, and conservation status of both subspecies. New distribution data and ecological information were gathered through fieldwork, literature, and herbarium specimens. In Sicily (Italy), unmanned aerial systems and high-resolution digital elevation models were employed to perform a detailed census of the last extant stand, mapping its distribution and calculating its 3D occupation surface. Based on our analyses, *Erica sicula* is evaluated as Least Concern (LC) at the global level, even though each subspecies and subpopulation are nationally endangered. In fact, 19 locations of *E. sicula* subsp. *sicula* were not confirmed recently, and this subspecies should be considered as Critically Endangered (CR) in Italy and Vulnerable (VU) in Lebanon, Cyprus and Türkiye. In Libya, *E. sicula* subsp. *sicula* is VU due to severe habitat degradation. *E. sicula* subsp. *bocquetii*, formerly known from a few locations in the mountains of SW Anatolia, Türkiye, has been found at lower altitudes in several new locations and is also assessed as VU. Further fieldwork is recommended to better assess the demographic trends of the different subpopulations. Genetic analyses are needed to clarify the taxonomic value of infraspecific taxa previously described and to guide future conservation efforts of the most unique and genetically rich stands, both in-situ and ex-situ. Improving the conservation strategies for taxa like *Erica sicula s. l.* requires the collaboration of specialists from all involved countries, making it crucial to maintain networks of experts in the Mediterranean.

Key words: Biogeography, cliff vegetation, conservation biology, ecological field surveys, international partnership, red listing, unmanned aerial systems

Introduction

Biogeographic interest of the heathers of *Erica sicula* group

Extreme geographical disjunction is a very rare and fascinating phenomenon among Mediterranean plants living in vertical environments. In fact, very disjunct subpopulations usually have been isolated long enough to have differentiated into distinct species (Davis 1951). Nevertheless, there are notable examples of significant disjunction, particularly among Paleogene relict species which did not evolve into distinct species despite their populations being presumably separated for a long time, such as isolated populations of *Zelkova abelicea* on the Cretan Mountains (Christe et al. 2014), or the strikingly disjuct populations of *Rhododendron ponticum* in the Iberian Pensinsula and Georgia (Mejías et al. 2006). The large majority of these vulnerable taxa persist only in habitats that provide environmental conditions enabling their survival, such as north-facing cliffs and sheltered gulleys, where anthropogenic disturbance (e.g., overgrazing, fire) is low. These areas also experience reduced interspecific plant competition and lower drought stress due to particularly favourable microclimatic conditions (Thompson 2020).

In some cases, differentiation among disjunct populations of a given species led to the description of taxa that are formally recognised at the varietal or subspecific level, as is the case in *E. sicula*. These heathers form a rather distinct and isolated group (Ojeda et al. 1998), nested within *Erica* (McGuire and Kron 2005; Mugrabi de Kuppler et al. 2015; Pirie et al. 2024), and in the past they were classified under a distinct genus, *Pentapera* (Klotzsch 1838) due to their pentamerous flowers, in contrast to the tetramerous flowers of all other *Erica* species of the world. However, most scholars have argued against recognising this group of heathers as a separate genus or subgenus, in part due to the lack of other strikingly distinctive traits (see Bentham 1839; Boissier 1875; Bentham and Hooker 1876; Drude 1897; Webb and Rix 1972; McClintock 1980 and 1989; Meikle 1985 and, more recently, Nelson 2011; Elliott et al. 2024; Oliver et al. 2024).

Variation within *E. sicula* may be significantly influenced by local abiotic factors, such as substrate and climate, as well as disturbances. A taxonomic synthesis of the epithets referring to the *Erica sicula* group is presented in Table 1.

An additional aspect of interest in this puzzling study case is the extremely small area occupied by the stands of these taxa in each country (Fig. 1). Apart from the Italian one, all other subpopulations of *E. sicula* subsp. *sicula* are situated in countries of the eastern Mediterranean. The subpopulations growing in Lebanon, Cyprus and SW Anatolia were previously considered as a separate taxon, *E. sicula* subsp. *libanotica* (Yaltırık 1967; Browicz 1983). Similarly, the subpopulation of N Libya has been referred to as subsp. *cyrenaica* (Brullo and Furnari 1979). Concerning *E. sicula* subsp. *bocquetii* (Peşmen 1968), it is documented to occur in the Antalya region in W Taurus (SW Anatolia, Türkiye).

The minimum geographic distances between the populations are remarkable (Fig. 1): c. 850 km between SW Anatolia and N Libya, c. 1000 km between NW Sicily and N Libya, c. 1600 km between NW Sicily and SW Anatolia, c. 300 km between SW Anatolia and N Cyprus, c. 550 km between SW Anatolia and Lebanon and c. 250 km between N Cyprus and Lebanon.

Table 1. Taxonomic and synonymic prospects of the epithets referring to the *Erica sicula* group. In bold: accepted names according to POWO (2025) and adopted in this paper.

***Erica sicula* Guss., Cat. Pl. Hort. Boccadifalco: 74. 1821 (subsp. *sicula*)**
Pentapera sicula (Guss.) Klotzsch, Linnaea 12: 498. 1838
Erica gussonei Schouw (unpublished manuscript)
Pentapera sicula (Guss.) Klotzsch var. *libanotica* Barb.-Boiss. & Barbey, Herb. Levant: 144. 1882
Erica sicula Guss. var. *libanotica* (Barb.-Boiss. & Barbey) Holmboe, Stud. Veg. Cyprus: 142. 1914
Pentapera sicula (Guss.) Klotzsch subsp. *libanotica* (Barb.-Boiss. & Barbey) Yalt., Notes Roy. Bot. Gard. Edinburgh, 28: 13. 1967
Erica sicula Guss. subsp. *libanotica* (Barb.-Boiss. & Barbey) P.F. Stevens, Fl. Türkiye & East Aegean Islands, 6: 97. 1978
Erica sicula Guss. subsp. *cyrenaica* Brullo & Furnari, Webbia, 34: 164. 1979
Pentapera bocquetii Peșmen, Candollea, 23. 271. 1968
Erica bocquetii (Peșmen) P.F. Stevens, Fl. Türkiye 6: 97. 1978
***Erica sicula* Guss. subsp. *bocquetii* (Peșmen) E.C. Nelson, Hardy Heathers: 299. 2011**

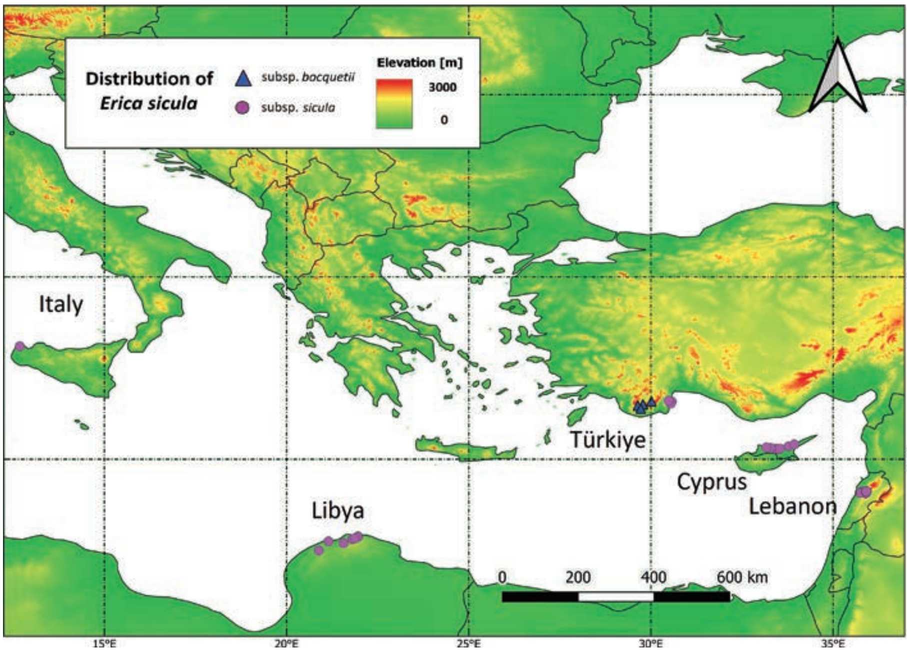

Figure 1. Distribution range of the two subspecies of *Erica sicula* Guss.

Aims of the paper

Based on data gathered from the literature, herbarium records and field surveys, we present an updated synthesis of the distribution and ecology of the known populations within the *Erica sicula* group. Additionally, we assessed the extinction risk of both subspecies at global and national scales, identifying key knowledge gaps and outlining critical conservation actions required to enhance the status of extant populations.

Methods

Researchers from four of the five countries where these taxa are found collaborated on this study. We analysed and combined historical and recent first-hand field data to trace the past and present distribution and to clarify the ecological requirements of the different populations of *Erica sicula sensu lato* (*s.l.*).

Literature survey

To begin, we meticulously analysed the extensive scientific and horticultural literature available on these taxa, including regional floras, such as the floras of Lebanon (Mouterde 1983), Syria, Palestine, and Sinai (Post and Dinsmore 1932), Turkey and the East Aegean Islands (Stevens 1978), Cyprus (Meikle 1985) and Europe (Webb and Rix 1972).

Herbarium specimens

We then examined the specimens preserved in various European herbaria (AMD, B, BM, BOLO, C, CAT, COI, E, FI, G, K, L, LD, LM, MHNF, NAP, P, PAL, PAV, PI, RO, S, W, WAG, WSY), as well as in the non-European herbaria of the countries where the taxa are found, namely Cyprus (NEUN), Lebanon (BEI), Libya (ULT) and Türkiye (AEF, AKDU, ANK, EGE, GAZI, HUB, ISTE, ISTF, NGBB). The acronyms of the above listed herbaria follow the standard abbreviations of the Index Herbariorum (Thiers 2025). We also referred to the national database of Turkish master's and doctoral theses (Republic of Türkiye, Council of Higher Education, Thesis Center, https://tez.yok.gov.tr/UlusalTezMerkezi/giris.jsp) to gather occurrence data related to the Antalya province. Additionally, we compiled an inventory of specimens kept in the European herbaria. Geographic coordinates were assigned wherever possible to facilitate mapping of both literature records and dry specimens.

Field work

Field surveys were conducted in Italy, Lebanon, Türkiye and Cyprus to revisit historical localities where the species had previously been reported, to discover new occurrences in potential habitats, to accurately map its distribution, to collect additional information on its ecology and threats, and to accurately assess extinction risk. In Italy, we utilised the data previously collected between 2017 and 2020 by one of the authors (LDS) from the sole remaining locality where *E. sicula* subsp. *sicula* occurs, namely Mt. Cofano (de Simone 2020). Additional explorations in the neighbouring mountains were carried out between 2019 and 2022. In Lebanon, the Nahr Ibrahim Valley, or Adonis River, where the taxon occurs, was thoroughly surveyed by one of the authors (HEZ) in 2022 and 2023. In Cyprus, fieldwork was conducted in 2020 by one of the authors (SG) through the Kyrenia mountain range to map the entire extent of occurrence of the species on the island. In Türkiye, several localities with *E. sicula* subsp. *sicula* were visited and confirmed in the province of Antalya. As for *E. sicula* subsp. *bocquetii* in Türkiye and *E. sicula* subsp. *sicula* in Libya, fieldwork could not be conducted; therefore, herbarium specimens and literature data were used, with the most recent records being considered. For all countries, we deemed it appropriate to map the localities of unconfirmed historical records. The names of the localities as well as the information provided on the specimen labels were used to estimate their position on the maps. However, risk assessments were performed based only on confirmed and extant stands.

Unmanned aerial systems

During field activities, in Italy it was also possible to exploit unmanned aerial systems (UAS) to perform a detailed census of its only extant stand. Using UAS-derived 3D models of target areas where the species was present and high-resolution digital elevation models of the entire study area, it was possible to perform a detailed census of the stand, map in detail its distribution and calculate its 3D occupation surface.

We carried out separate aerial surveys for each sampled area in spring 2019. We used a DJI Phantom 4 (hereafter drone) along vertical transects parallel to the cliff. The drone has a built-in GPS and a gimbal mounting a 12 MP camera that was manually triggered by a remote radio controller. The drone never exceeded a Ground Sampling Distance of 0.3 cm/pixel. Prior to the flight, two to four ground control points (GCPs) were positioned on the cliff wall. A Bosch laser distance meter (Bosch GLM 50) was used to measure the distance between GCPs centres.

Following the pipeline documented in de Simone (2020), the geo-referenced photos were used for the creation of a point cloud and a 3D model. For this purpose, the dataset was processed using Agisoft Metashape (Agisoft LLC, St. Petersburg, Russia). The general workflow suggested in the software user manual was followed. Photo alignment was performed using “high” as accuracy settings. The resulting point cloud was manually cleaned from homologous points and artefacts.

Subsequently, the GCPs positioned on the cliff were manually marked in each photo, and their distance was added to the software as a scale bar-based information for optimizing the results of photo alignment. Both the dense cloud and 3D model were performed using “medium” quality settings. Then, the whole photo dataset was manually scrutinized to detect each individual of *E. sicula* subsp. *sicula*. When an individual was detected, we marked its spatial position by placing a marker (i.e., a point of the dense cloud, with its X, Y, Z embedded information) on its centroid. The photo identification of *E. sicula* subsp. *sicula* was straightforward because it was in full bloom and literally covered with pale pink-white flowers. For logistic reasons, UAS could not be used in Cyprus, Türkiye or Lebanon.

Mapping

Spatial data were all mapped using the software QGIS (version 3.28). Geographic coordinates, provided in decimal degrees using the WGS84 coordinate system (EPSG: 4326) were made available on the GBIF platform (https://doi.org/10.15468/8dk2qz) and will therefore be accessible to users in future updates of the Erica Identification Aid (Oliver et al. 2024).

Extinction risk assessment

The extinction risk for each subspecies of *E. sicula* was assessed separately in each country according to the International Union for Conservation of Nature Red List categories and criteria (IUCN Standards and Petitions Committee 2024). The Extent of Occurrence (EOO) was calculated as the minimum convex hull based on the taxon occurrence records. The Area of Occupancy (AOO) was calculated using a cell width of 2 km, equivalent to a 4 km^2 grid cell.

When existing, previous assessments were reviewed and updated, as it was the case for Italy (Domina et al. 2012) and Lebanon (Stephan et al. 2017). Finally, the comprehensive global assessment of both taxa of the *E. sicula* group was carried out by consolidating the data provided by each national assessment.

The terms 'population' and 'subpopulation' are used according to the definitions provided by IUCN (2012). More specifically, the populations of both subspecies encompass all stands where these taxa are found, while subpopulations are defined as geographically or otherwise distinct groups in the population (characterised by minimal demographic or genetic exchange, typically no more than one successful migrant individual or gamete per year; we do not currently have data to confirm this).

Results

Morphological variability within the *Erica sicula* group

We collated all available information on the morphology, ecology and biology of the two subspecies from the literature. The main distinctive morphological traits among the populations of the *E. sicula* group are summarised here below (Table 2).

Table 2. Summary of the intra- and inter-specific morphological and phenological variability within the *Erica sicula* group.

E. sicula* subsp. *sicula
Sicilian (Italian) subpopulation (Figures 2a-c): erect 20-60 cm tall cushion-shaped shrub, with robust woody erect to ascending branches; the young twigs are subterete, densely pubescent in their upper side due to small patent glandular hairs; evergreen leathery leaves densely pubescent when young, linear, patent, 1 × 5-6 mm, in whorls of 4(-5), glossy dark green above, whitish beneath, with incompletely revolute and contiguous margins, concealing the lower surface forming a whitish line; flowers actinomorphic, 5-merous, grouped in terminal umbels of 4-6(10); pedicels 2 × 4 mm with 3 pink lanceolate bracteoles near the middle; 5 sepals ovate-lanceolate, pubescent, pink, 4 mm (2/3 of the corolla); 5 petals entirely welded forming a white or very pale pink urceolate, sparsely pubescent corolla, 4 × 6-8 mm; stamens 10, dark purple, anthers without appendages, included; ovary 5-locular, pubescent; stigma capitate (from Pignatti 2018). Plants start to flower in December, but the usual blooming period begins in February; its acme is between April and May and lasts until June (LDS, pers. obs.), whilst the fruits ripe during the summer season. The blooming time of the congeneric *Erica multiflora* L., often co-occurring in close vicinity with *E. sicula*, is autumn (September to November), hence the two heathers are probably visited by different pollinators (LDS, pers. obs.).
Lebanese subpopulation (Fig. 2d, e): according to Mouterde (1983) *[Erica] sicula* is a shrub, 30-150 cm or more, very branched, with young branches pubescent and slightly velvety leaves, whorled in fours, often very deciduous during drying. Flowers in small umbels of 4-5, terminal, fairly large, borne on pedicels with three bracts, longer than the calyx. Sepals lanceolate, obtuse, slightly tomentose, three times shorter than the tomentose corolla itself. Corolla with lobes shorter than the tube, folded. Ovary white, tomentose. Mouterde (1983) adds these distinctive traits for var. *libanotica*: the entire plant is glabrous, except for the pedicels, which are puberulent; the terminal flowers are often more than five, and also lateral flowers are present, either solitary or in short fascicles. Flowering takes place all year round, except possibly from June to November.
Turkish subpopulation: according to Stevens (1978), local plants, previously referred as to *E. sicula* subsp. *libanotica*, would differ from those of the type (Sicilian) locality for several traits, like the size of the individuals (up to 150 cm), their almost glabrous twigs, the longer and narrower leaves (8.5-13 × 0.8-1.3 mm), the lack of a whitish mucrone on the leaf tip, the bigger and less hairy flower parts (pedicels 7-15 mm, sepals 6.5 mm, petals 7.5-9 × 5-5.5 mm) and the colour of the corolla (usually bright pink instead of pale pink-white).
Cypriot subpopulation (Figures 2f-g): local plants are smaller than the Turkish ones, probably because of stressful conditions induced by overgrazing and frequent fire disturbance. According to Viney (1994): "spreading shrub to 60 cm with tough, brown, flaking stems, needle leaves c. 7 mm long with edges rolled over, in close whorls of 4; flowers in umbels of 3-8 or more at the end of branches; corolla in various shades of pink (even to white), 7-8 mm long, bell-shaped-cylindrical, with 5 tiny-ended lobes; dark purple anthers inside the bell, but style shortly protruding. Flowering: March-July" (until August according to Meikle 1985).
Libyan subpopulation: according to Brullo and Furnari (1979), who described these plants as belonging to *E. sicula* subsp. *cyrenaica*, the plants growing in Cyrenaica differ from the type for their dwarfed habit, mostly growing as subshrubs (but Trotter 1915 observed well-developed individuals reaching 1 m), and for having 4.5-5 × 1.5-1.8 mm sepals, a 6 mm long corolla inflated in the lower part and evidently constricted in the upper one, the teeth up to 1 mm long, stamens 5 mm long, anthers 1.5-1.8 mm long, styluses 4.5 mm long hairy only in the upper part and rarely in the lower one.
E. sicula* subsp. *bocquetii
Small, 25-40 cm high, irregularly branched shrub that differs from the other taxa of the group for its overall dwarfed size: the flowers are smaller (Fig. 2h), the leaves are 3-4(-5) mm long, typically arranged in whorls of 3 rather that 4, and anthers lack spurs. The terminal inflorescence bears 1-4 purplish flowers, reduced leaves at the base (pedicels 8-13 mm, bracts and bracteoles 1.3-2 mm). Sepals 3-4 mm. Pale purple urceolate corolla 5-6(8)3 × 2-4 mm, somewhat pubescent. Filaments 2.4-4 mm, bent; anthers 2-2.5 mm, impressed styles 3.5-4 mm. Seeds compressed ovoid 0.5 × 0.3 mm (Peşmen 1968; Yaltırık 1971; Stevens 1978).

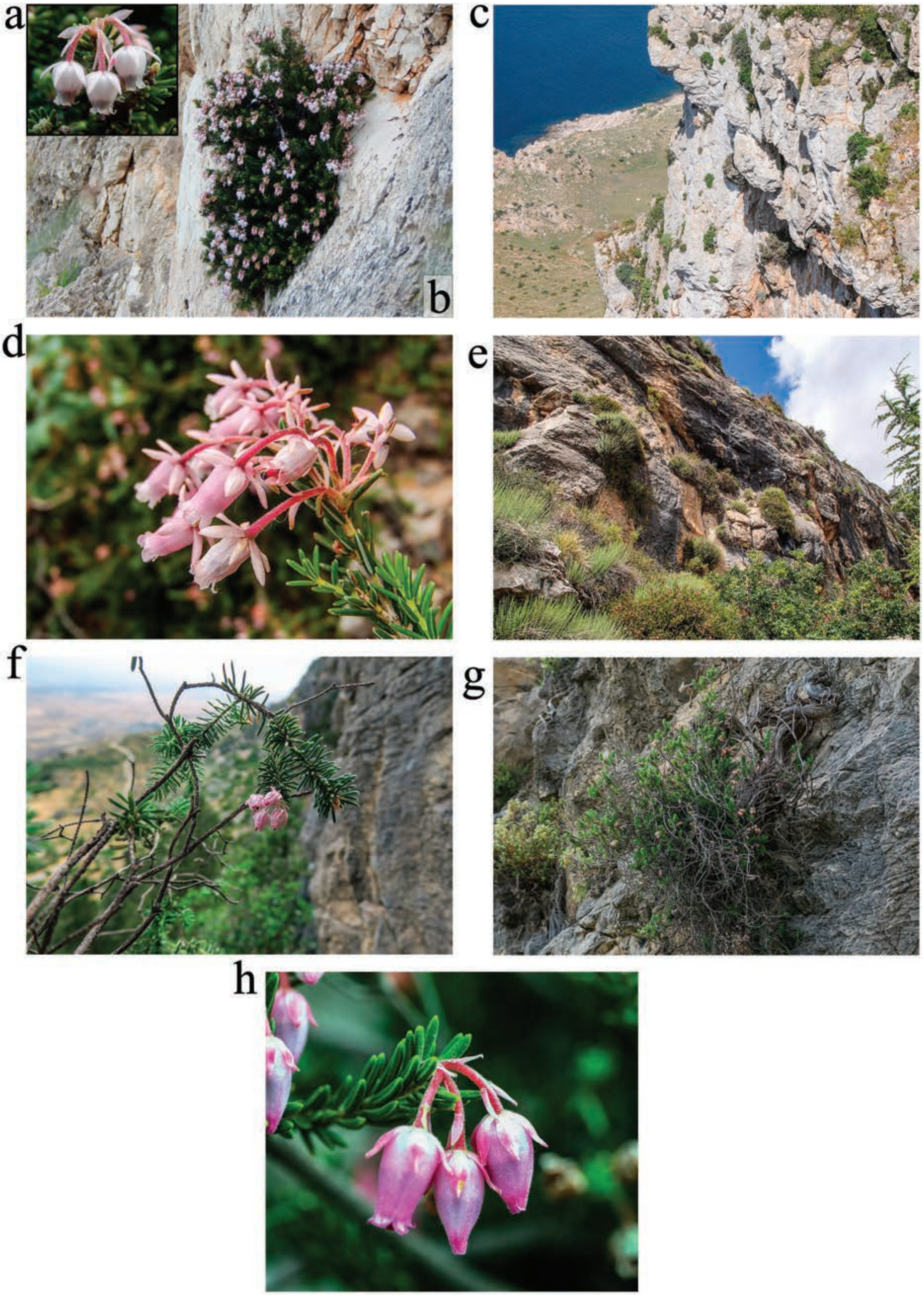

Figure 2. *Erica sicula* subsp. *sicula* in its type locality, Monte Cofano (NW Sicily, Italy): flowers and overall habit (**a, b**: photo credit D. Salemi) and habitat (**c**: photo credit L. de Simone); *E. sicula* subsp. *sicula* at Aaqoura, Byblos District, Lebanon: flowers and habitat (**d, e**: photo credit: H. El Zein); *E. sicula* subsp. *sicula* at Buffavento, Cyprus: flowers and habitat (**f, g**: photo credit S. Cambria); *E. sicula* subsp. *bocquetii* at Kaş, Province of Antalya Türkiye: flowers (**h**: photo credit: Z. Aytaç).

Table 3 provides a list of the available drawings related to *Erica sicula s.l*. These illustrations help to better understand the morphological characteristics and habitus of the plants in question.

Past and present distribution of *Erica sicula s.l.*

To provide a clear and updated distribution map of the stands in each country, we compiled a comprehensive list in Suppl. material 1. It contains detailed information retrieved from the literature and from the labels of the 212 herbarium specimens examined, such as the names of the collection localities, collectors, dates, specimen numbers, the herbarium where the specimen is housed, bibliographic references, geographic coordinates (estimated or provided by the sources), as well as the information on the stands observed or collected during recent field surveys. Nearly half of the specimens of *E. sicula* subsp. *sicula* were collected in Italy (88), followed by Libya (35), Türkiye (25), Cyprus (22) and Lebanon (20), while *E. sicula* subsp. *bocquetii* accounted for 22 specimens. Field surveys performed in Italy, Lebanon and Cyprus confirmed most of the historical occurrences. However, two of the three historical stands reported for Sicily, along with two from Lebanon and four from Cyprus, became extinct. Additionally, field surveys carried out in Türkiye during spring 2024 (i.e. after the submission of the first version of the manuscript) allowed the discovery of two stands of *E. sicula* subsp. *sicula* very close to historical collection sites. Detailed information for each country is provided in the following text.

Italy (and Malta)

The Sicilian subpopulation of *E. sicula* subsp. *sicula* currently occurs only on Mt. Cofano in NW Sicily, where it was first observed growing on its N-facing cliffs ("al Crocefisso": Gussone 1821; "al Passo della Zita": Ponzo 1900). Claims about the occurrence of other NW Sicilian stands date back to the early XIX century and have never been confirmed afterwards (Fig. 3). On Marettimo Island it was reported as extremely rare by Gussone (1832, 1843) with no further details on the exact location of the stand. No specimen has been found to confirm its past occurrence on the island, where it seems to have long since disappeared (Francini and Messeri 1956; Scuderi 2003; Gianguzzi et al. 2006; Gianguzzi et al. 2011; Domina et al. 2019; LDS, pers. obs.). However, Pignatti and Pignatti-Wikus (1990) reported observing it on a north-facing cliff below the summit of Pizzo Falcone, and Osti (2009) also claimed to have seen it on the island. It was observed on Monte Erice solely by Gasparrini during his field collections in Sicily between 1828 and 1831 (Alippi Cappelletti 1999). Its past presence there, reported by Lojacono-Pojero (1907) but not by Ponzo (1900), is documented by a single specimen collected by Gasparrini and preserved in PAL. Furthermore, extensive field investigations conducted in recent years on the nearby and ecologically similar cliffs of the adjacent mountains (namely Mt. Monaco, Mt. Palatimone and Mt. Passo del Lupo) were unsuccessful (LDS, L. Scuderi, SP, pers. obs.).

The occurrence of *E. sicula* in Malta was communicated by G. Gulia to C. F. Nyman during his visit to the island in 1844. In his subsequent report on Malta's vegetation, Nyman (1846) only cited *Erica multiflora* L., whilst the first official mention of *E. sicula*

Table 3. Inventory of the available iconographic sources concerning the *Erica sicula* group (in chronological order).

Erica sicula* subsp. *sicula
Gussone, Ic. Fl. Sic. T. 197 (not found, Authors' note)
C.F. Schmidt in Klotsch (1841-1844): table 19
http://plantillustrations.org/illustration.php?id_illustration=187541&SID=0&mobile=0&code_category_taxon=2&size=0
M. Smith in Hooker (1888): table 7030
http://plantillustrations.org/illustration.php?id_illustration=4516&SID=0&mobile=0&code_category_taxon=2&size=0
J. Weathers (1874-1955): fig. 45, p. 335
http://plantillustrations.org/illustration.php?id_illustration=384340&SID=0&mobile=0&code_category_taxon=2&size=0
Fiori and Paoletti (1899-1904): fig. 2649, p. 312
Lojacono-Pojero (1907): fig. 1, plate I
Trotter (1915) fig. 91, p. 243
Siddiqi (1978): fig. 2, p. 5
A. Zizza in Brullo and Furnari (1979): fig. 7, p. 165 (as *Erica sicula* subsp. *cyrenaica*)
Mouterde (1983), Plate II, n° 4 (as *Pentapera sicula*)
Nelson (2011), figs. A-T, p. 298
Erica sicula* subsp. *bocquetii
Peşmen (1968): fig. 3 a and c, p. 272 (as *Erica bocquetii*)

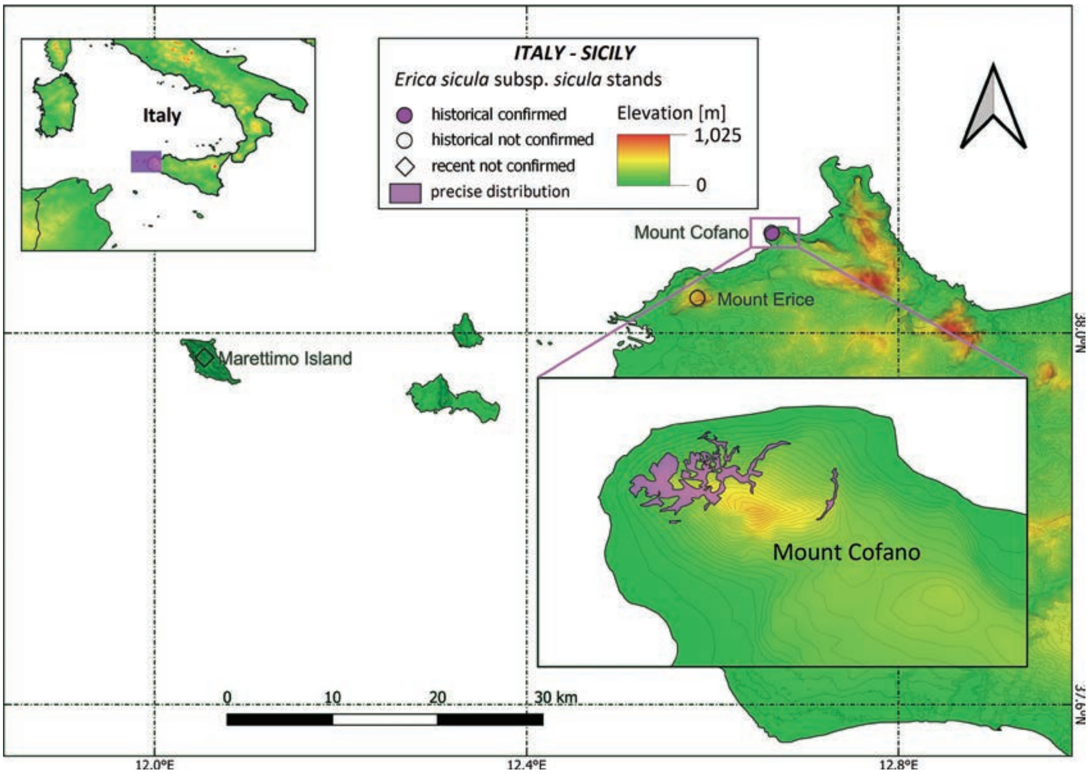

Figure 3. Past and present distribution of *Erica sicula* subsp. *sicula* in Sicily (Italy) based on literature data and herbarium specimens; below: detailed distribution on Mt. Cofano (from de Simone 2020, modified).

came from Duthie (1875) and was later cited by several other authors (Nyman 1879; Caruel 1889; Fiori and Paoletti 1898). However, Sommier and Caruana-Gatto (1915) pointed out the absence of herbarium specimen, and more recently, this record has been considered a misidentification, leading to the exclusion of the species from the Maltese vascular flora (Brullo 1982; Lanfranco 1982).

Lebanon

In Lebanon, *E. sicula* subsp. *sicula* occurs in the Nahr Ibrahim Valley, historically known as the River of Adonis, located in the central part of Mount Lebanon. This taxon shows a scattered distribution as it occurs in two separated areas in the lower and the upper part of the valley (Fig. 4). The first is a canyon known as the Gorges of Yahchouch, the other includes several steep cliffs overlooking Aqoura and Afqa.

In the following lines we present a diachronic overview of the finds of *E. sicula* subsp. *sicula* in Lebanon. The taxon was first collected at Belhos in 1880 (also known as Billa, Billaa, Bil'âs, or Balhas), below the bridge between Machnaqa and Qartaba, by L.C.É. Lortet. The specimen was subsequently given to W. Barbey, who made the first description of the taxon *Pentapera sicula* var. *libanotica* (Barbey-Boissier and Barbey 1882). The plant was later collected in the surrounding areas: at Ehmej (also Ihmish and Ehmège) by T. Boutros in 1890 (Mouterde 1983), Qartaba (also Kartaba) by E. Hartmann in 1898 (Browicz 1983), at Frat and at Milassa by G. Post in 1908 (Post and Dinsmore 1932). The taxon was also collected in the gorges of Yahchouch and at Aaqoura (also Aakoura and Akoura) by R. Gombault, J. Louis and J. Thiébaut in 1932 (Mouterde 1983). It was collected for the first time at Afqa (also Afka) under the river catchment, by P. Mouterde in 1935 (Mouterde 1983). H.A. Pabot also collected a specimen in the gorges of Yahchouch in 1953 (Mouterde 1983). *E. sicula* subsp. *sicula* was recently observed at Chouwen, which is located within the buffer zone of the Jabal Moussa Biosphere Reserve (Tohmé and Tohmé 2014) and at Janna (Stephan et al. 2017).

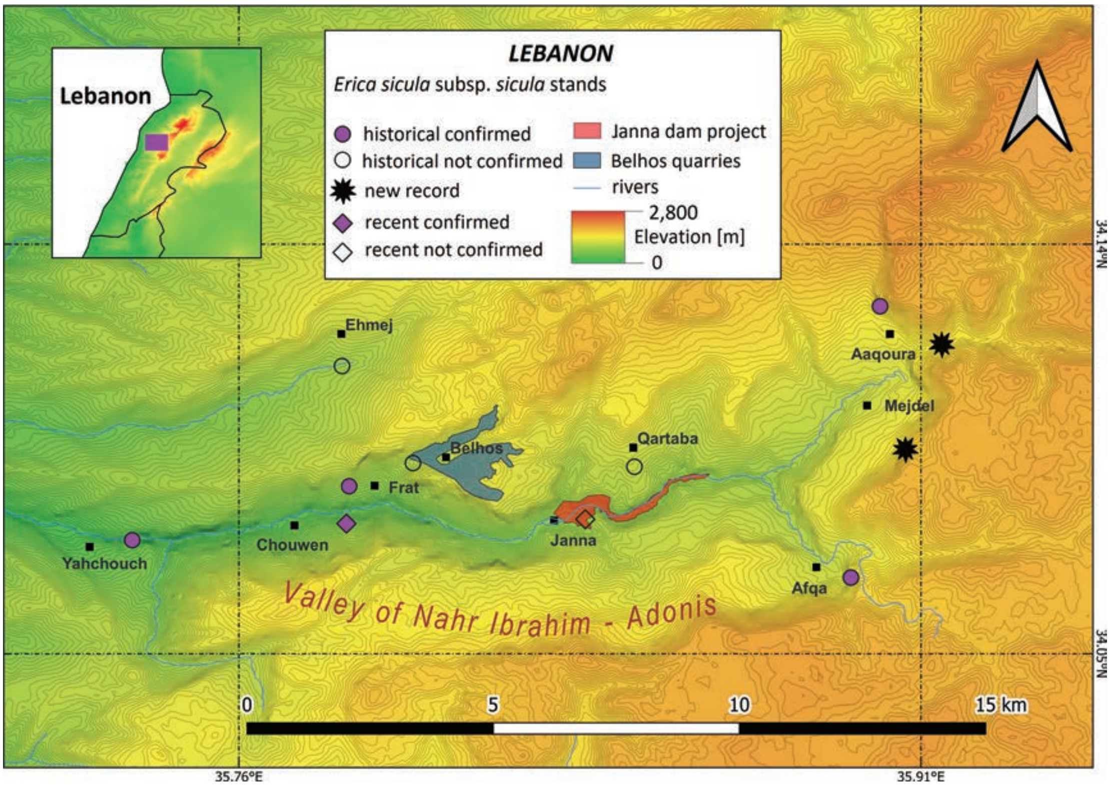

Figure 4. Past and present distribution of *Erica sicula* subsp. *sicula* in Lebanon based on literature data and herbarium specimens and on field data collected between 2022 and 2023 by one of the authors (HEZ). Belhos quarries and Janna dam correspond to the areas where the local stands were recently wiped out due to habitat destruction.

Our field surveys enabled the mapping of seven extant stands. The locality of Milassa could not be located and the specimen remains untraceable. Actually, there is no village named Milassa in Lebanon. The most similar toponym is Lassa, but we chose to exclude this unplaced occurrence recorded by Post. We confirmed the destruction of two stands: the stand once located in Belhos was destroyed approximately 20 years ago by quarrying activities (Stephan et al. 2017), which resulted in the loss of about 302 ha of suitable habitat. The second stand, formerly located on the cliffs of the canyon in Janna, was destroyed by the construction of a dam that began in 2014. The entire locality, covering an area of 85.66 ha, was excavated and the adjacent cliffs were stripped up to a height of 50 metres. Despite extensive and repeated surveys in the area, the nucleus of Ehmej could not be located. This area, intensely exploited by stone quarries, has experienced significant degradation of its cliff habitats. The specimen labelled as collected in Qartaba was probably collected on the road between Qartaba and Janna, as no nucleus was observed in Qartaba. The stands of Yahchouch, Chouwen and Frat were confirmed in the lower part of the canyon. The stand of Afqa was confirmed, found just above the cave where the river of Ibrahim-Adonis begins its flow. Two additional stands were found in the upper part of the valley, in Mejdel and East Aqoura. The four nuclei of the upper valley, namely Afqa, Mejdel, Aqoura and East Aqoura are the largest in terms of size.

Cyprus

Eight stands of *E. sicula* subsp. *sicula* occur in Cyprus, all within the Kyrenia Mountain range (Fig. 5). Meikle (1985) provides a detailed list of historical records: the taxon was first found by Kotschy at Pentadaktylos in April 1859 and at Agios Khrysostomos in 1862 (Unger and Kotschy 1865). The nucleus of Buffavento, first noted by Kotschy (1862), has been repeatedly observed in the recent years, including by Syngrassides in 1937 (Meikle 1985), by S. Brullo and G. Giusso del Galdo in September 2013 (Wagensommer 2017), and by S. Cambria in June 2019 (pers. comm.). Other early records refer to a nucleus near Akanthou (‘Sintenis and Rigo Iter Cyprium 1880’, ‘Merton 1967’ in Meikle 1985) and in the gorges west of Saint Hilarion (‘Hartmann 1904–1905’, ‘Casey 1951’ in Meikle 1985); recent surveys confirm the species persists at both sites (SG, pers. obs.). Additional stands were recorded between the 1930s and 1960s: at Yaïlá (district Alevkaya-Halevga) by Kennedy and Davis between 1938 and 1941, at Halevga by Davis between 1940 and 1949, and above Phamoudhi (district of Kyrenia) by Merton in 1967. In 2006, a new stand was found at Karpaz Zeytinburnu and another close to a historical collection site at Alevkaya on the road to Esentepe. Two additional new sites were discovered in 2020 on the highest peaks of the Kyrenia Mountains at 1,024 m a.s.l. at Kyparissovouno (= Selvilitepe, authors’ note) and at Kantara Kaplica.

The only historical record from the Troodos Mountain range is from Mount Afamis (c. 1,050 m a.s.l.) in the Limassol-Lemesos District, reported by Kennedy in 1937 (Meikle 1985). However, this stand has not been confirmed despite repeated *ad hoc* expeditions carried out between 2003 and 2007.

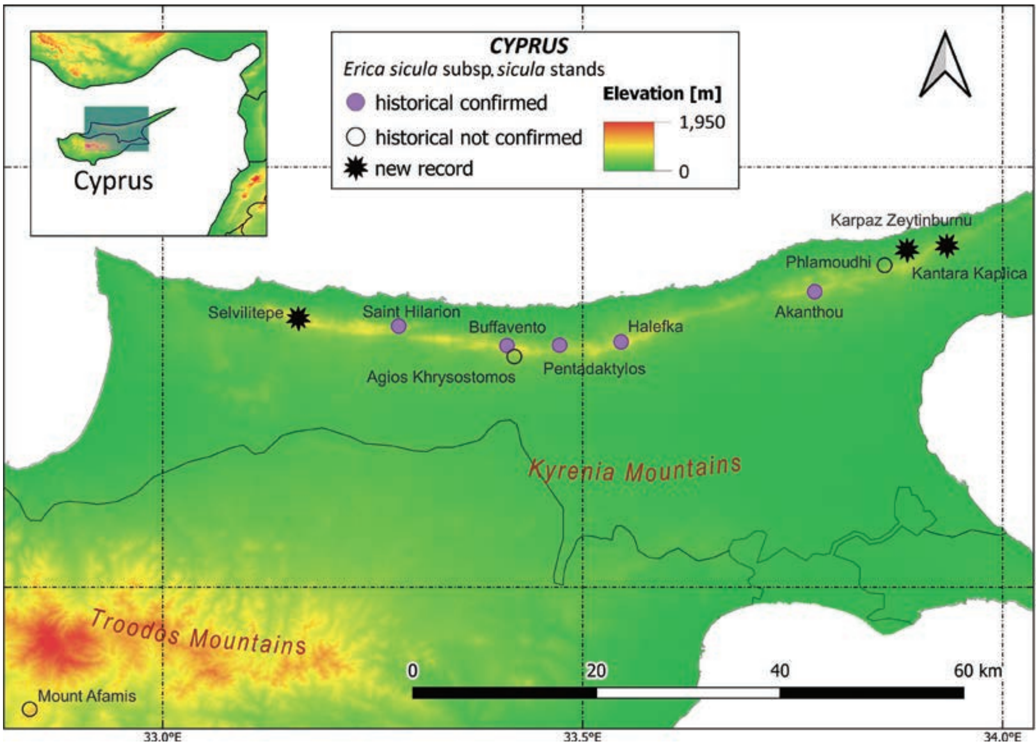

Figure 5. Past and present distribution of *Erica sicula* subsp. *sicula* in Cyprus Island based on literature data and herbarium specimens (Meikle 1985) and on the occurrence data collected during the field surveys carried out in 2022 by one of the authors (SG).

Türkiye

E. sicula subsp. *bocquetii*, locally known as 'yılgun çalısı' (OŞ, pers. comm.), was discovered and described by Peşmen (1968). Its type locality is located at about 1,750 m a.s.l. in a clearing of *Cedrus libani* A. Rich. forest at Çiğlikara, Dokuzgöl Mevkii, in western Taurus (SW Anatolia, province of Antalya, district of Elmalı; see Fig. 6). A specimen in the herbarium of J. Bornmüller at Berlin suggests this taxon was collected in the same area in 1938. More recently, it has been observed growing under similar ecological conditions and repeatedly collected between 1,600 and 1,850 m a.s.l., close to the type locality, within the Elmalı Cedar Research Forest (Yaltırık 1971; McClintock 1990, 1991; Kendir 2005; Kendir and Güvenç 2008; Ari et al. 2014).

Another stand was found by Burton (1995) at approximately 1,200 m a.s.l. growing under warmer climatic conditions on the steep limestone outcrops of an area dominated by *Pinus brutia* Ten., located between Sinekçibeli and Kaş (province of Antalya).

During the last 15 years *E. sicula* subsp. *bocquetii*, previously thought to grow exclusively in mountainous areas, has been found at much lower altitudes; in fact, a stand located at 250 m a.s.l. was discovered in 2009 near Bayındır-Kaş (Z. Aytaç, pers. comm.). Ten years later, Dilek (2018 and 2020) reported three more stands, located near Enişdibi and close to Üçağız Cemetery (both near Demre, Antalya) and on Kekova Island, whilst Fener (2018) and Fener and Aykurt (2019) reported its occurrence at 762 m a.s.l. at Çığlıkara Püreni, and there is an herbarium specimen ("Gülkokan 1871") collected in the roadsides between Akçay and Kemer.

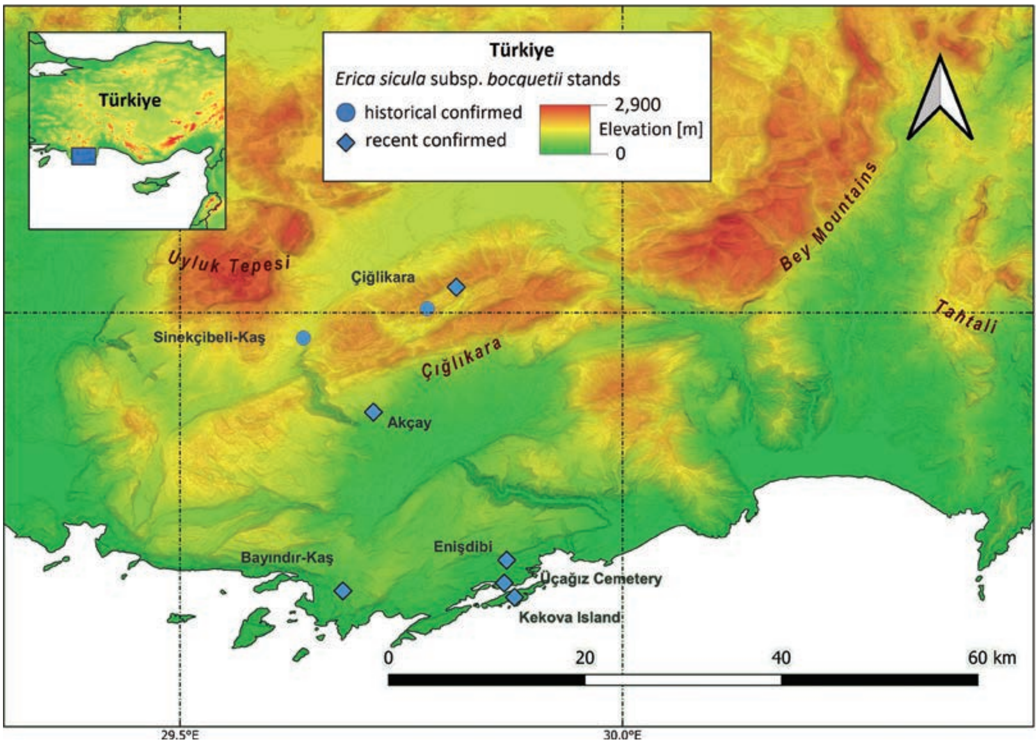

Figure 6. Current distribution of *Erica sicula* subsp. *bocquetii* in Türkiye based on literature data and herbarium specimens and on recently recorded occurrence data.

E. sicula subsp. *sicula* has been reported from several localities in the southeastern sector of the Antalya province in southwestern Anatolia (Fig. 7). Eight collection sites have been documented. Specifically, it was first observed at Kezme Boğazi, south of Kemer, in 1947 and at Göynük Canyon (Stevens 1978; Browicz 1983). A third stand was observed in 1960 at Tahtalı Dağ, followed by Hisarçandır-Karlıktepe in 1978, around Phaselis Bay in 1979, around the coast of Kemer in 1980, and above the ruins of Phaselis in 1995. More recently, a stand was found by Gülkokan et al. in 2015 (Fener 2018; Fener and Aykurt 2019; Gülkokan is the surname of D. Fener prior to her marriage, Authors' note) on the calcareous stony slopes near Kemerköy, although the exact collection site could not be localised. Finally, recent field surveys led to the discovery of two stands very close to the historical collection sites of Kesme Boğazı and Phaselis Bay.

Libya

E. sicula subsp. *sicula*, locally known as 'hamra' (Siddiqi 1978), occurs in the hilly regions of N Cyrenaica subject to Mediterranean climatic conditions, namely in the districts of Al Hizam Al Akhdar, Al Marj, Jabal Al Akhdar, Al Qubbah and Derna. The distribution map (Fig. 8) of the Libyan population was based on literature data (e.g., Durand and Baratte 1910; Béguinot and Vaccari 1913a, 1913b, 1913c; Pampanini 1931; Brullo and Furnari 1979, 1994; Siddiqi 1978) and herbarium specimens. It shows the location of seven stands considered still extant, and of five historical collection sites not confirmed since the 1970s. *E. sicula* subsp. *sicula* was first observed near the city of Derna/Darnah ('Haimann 1881' and 'Taubert 1887' in Durand and Baratte 1910), at Wadi Sarak ('quite common in the woods') and Wadi Naga ('mountains at the north

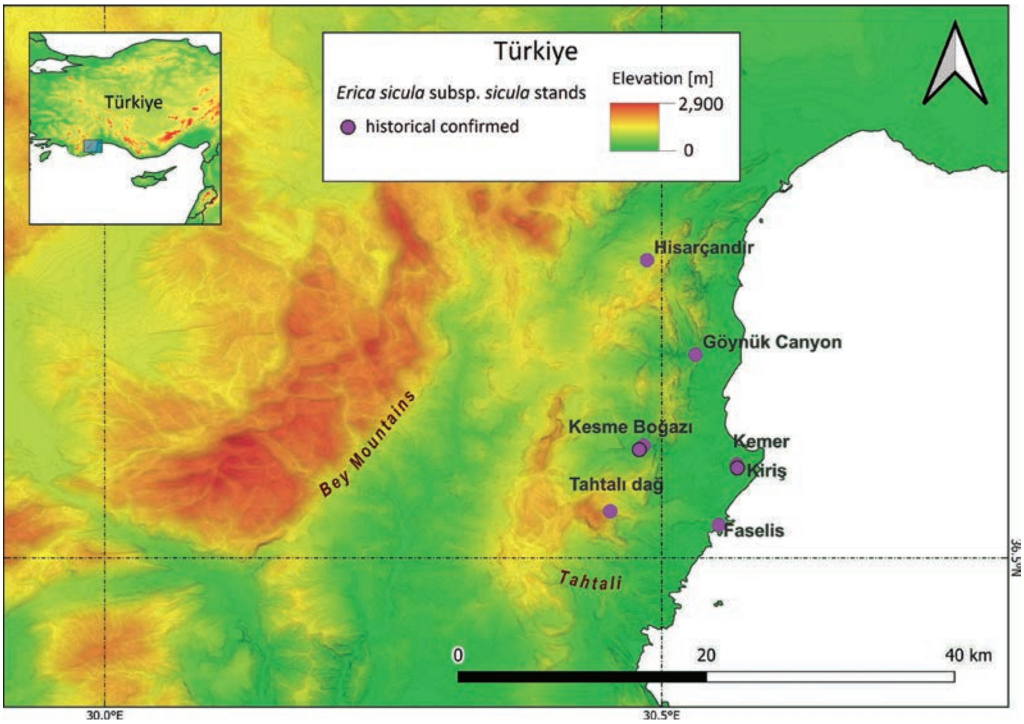

Figure 7. Current distribution of *Erica sicula* subsp. *sicula* in Türkiye based on literature data and herbarium specimens and on recently recorded occurrence data.

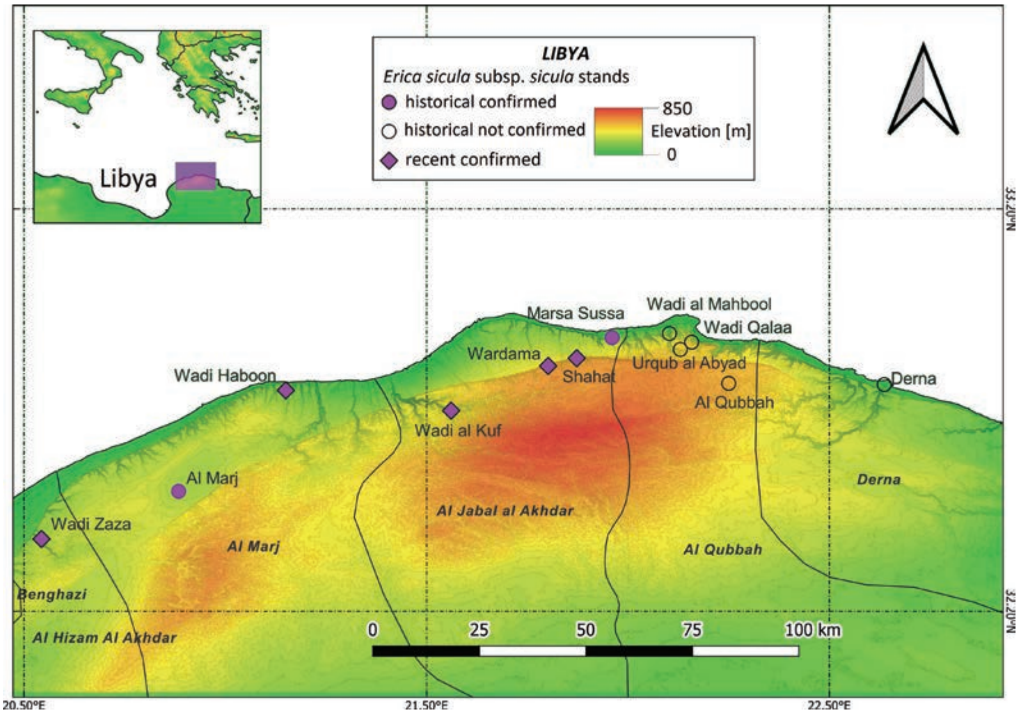

Figure 8. Distribution of *Erica sicula* subsp. *sicula* in Libya based on literature data and herbarium specimens.

of the valley': 'Taubert 1887' in Durand and Baratte 1910). Both Haimann and Taubert sent numerous specimens to European herbaria, quickly disseminating their discovery to the scientific community (e.g., Hooker 1888). In the following decades, additional stands were sampled at Barca (also Barqa or Barce, today's Al Marj: Arcangeli 1894), Gouba (also El Gubba, Quba, Al Qubbah) and

Wadi Derna (‘Vaccari 1912’ in Béguinot and Vaccari 1913a, ‘Longa 1912’ in Pampanini 1912), Marsa Susa (ancient Apollonia, Authors’ note; ‘Vaccari 1913’ in Béguinot and Vaccari 1913b), and ‘in the valley of the aqueduct’ (‘Vaccari 1913’ in Béguinot and Vaccari 1913c). More recently, *E. sicula* subsp. *sicula* was observed at Wadi Zaza (El-Barasi et al. 2003), Wadi Haboon (El Rabiai and Al Tira 2015), whilst Omar (2019a) reported its occurrence in the maquis at Marsa Susa (180–195 m a.s.l.), the forest at Wardamah (500–550 m a.s.l.) and at Shahhat (500–550 m a.s.l.).

Ecology of *Erica sicula s.l.*

Italy

In NW Sicily, *E. sicula* subsp. *sicula* grows on dolomitic cliffs and ledges between 100 and 630 m a.s.l. and may be considered a primary chasmophyte. This taxon is a characteristic species of a plant community rich in endemic taxa only occurring on Mt. Cofano, described as the phytosociological subassociation *Scabioso limonifoliae-Centauretum ucriae* subass. *ericetosum siculae* (Brullo and Marcenò 1979; Gianguzzi and La Mantia 2008). Near the ledges, it may co-occur with other woody species, such as *Quercus ilex* L., *Arbutus unedo* L., *Pistacia lentiscus* L., *P. terebinthus* L. and *Erica multiflora* L. or with the tussock grass *Ampelodesmos mauritanicus* (Poir.) Dur. & Schinz. Field surveys by de Simone (2020) found *E. sicula* subsp. *sicula* absent on S-facing slopes, but present on all other orientations. A plot-based analysis showed that it has an ecological preference for east- and west-facing cliffs with inclinations between 60° and 90°. Moreover, it prefers ridges exposed to cool and humid breezes rather than cliff bases (de Simone 2020).

Lebanon

E. sicula subsp. *sicula* typically grows between 400 and 1600 m a.s.l. (Mouterde 1983; Browicz 1983; Mugrabi de Kuppler 2013), preferring N-facing rocky slopes and cool, shady microclimates at the bottom of gullies (Gombault 1946; Bou Dagher-Kharrat et al. 2013). According to the zonation of Abi-Saleh (1982), it ranges within the meso- to supra-Mediterranean levels. Field surveys reported it growing in at least five habitat types, co-occurring with diverse species. In the lower Ibrahim Valley, on both N- and S-facing slopes, near Yahchouch, Chouwen and Frat, it occurs in meso-Mediterranean *Quercus coccifera* woodlands and *Pinus brutia* woodlands (habitat types T213_LB1 and T3A5 according to El Zein et al. 2022). Typically accompanying species are *Pinus brutia*, *Arbutus andrachne* L., *Ptilostemon chamaepeuce* (L.) Less, *Rosularia sempervivum* subsp. *libanotica* (Labill.) Eggli, *Sedum* spp., and *Dryopteris pallida* (Bory) Maire et Petitm. subsp. *libanotica* (Rosenst.) E. Nardi (Stephan et al. 2017). In the upper Ibrahim Valley, the plant occurs on N- and W-facing cliffs between 1,400 and 1,600 m a.s.l., in scattered supra-Mediterranean *Quercus coccifera* L. woodlands (habitat T213_LB2), *Ostrya carpinifolia* Scop. woodlands (habitat T19B1_LB1) and *Juniperus deltoides* R.P. Adams thickets (habitat S2314), with scattered individuals of *Pistacia terebinthus* L., *Potentilla libanotica* Boiss., *Onosma frutescens* Lam. and *Hirtellina lobelii* DC.

Cyprus

E. sicula subsp. *sicula* occurs between 275 and 975 m a.s.l., mostly growing on N-facing sites, but on S-facing slopes at its highest location at Buffavento. It typically thrives in the crevices of hardly accessible cliffs, occasionally in sclerophyllous maquis and within gaps among natural or artificial conifer woodlands of *Pinus brutia* Ten. and *Cupressus sempervirens* L. on mountain slopes (Meikle 1985; Viney 1994; Hand et al. 2011; Wagensommer 2017).

Türkiye

According to Stevens (1978), *E. sicula* subsp. *bocquetii* grows on N-facing limestone cliffs within *Cedrus libani* woodlands in the montane-Mediterranean vegetation belt in Çığlıkara Nature Reserve. More recently this taxon has been recorded also under fully thermo- and meso-Mediterranean conditions, always on N-facing limestone cliffs, ledges and cracks.

The Turkish stands of *E. sicula* subsp. *sicula* are located near the coast between 60 and 100 m a.s.l., under fully thermo-Mediterranean climatic conditions, often accompanied by *Globularia davisiana* O. Schwarz (Stevens 1978).

Libya

In Cyrenaica *E. sicula* subsp. *sicula* grows on the cliffs and ledges of steep calcareous slopes along seasonal streamsides (called ‘widien’, plural of ‘ouadi/wadi’), between (100)250 and 500 m a.s.l. (Browicz 1983; Brullo and Furnari 1994). According to Brullo and Furnari (1994), it participates in various chamaephytic communities, including garrigue formations such as the *Asperulo tragacanthoidis-Rosmarinetum offinalis* (Susa and el-Hilal, 180–310 m a.s.l.), and chasmophilous assemblages like the *Origano cyrenaici-Putorietum calabricae* in a wadi beneath Susa and el-Hilal (100–310 m a.s.l.), and the *Telephio barbeyani-Darnielletum cyrenaicae* in Wadi Derna (260–300 m a.s.l).

Biology of *Erica sicula s.l.*

Concerning the vegetative growth, Raunkiær (1934) probably observed the behaviour of an individual of *Pentapera sicula* cultivated in the Botanic Garden of Copenhagen, noting that the plant was able to produce dwarfed and denser foliage on shorter shoots under stressful conditions. Vegetative propagation trials with woody cuttings of *E. sicula* subsp. *sicula* from Türkiye, harvested in February, showed low rooting success (43.5%). Success was even lower (<20%) during harvesting periods and for subsp. *bocquetii* (Ari et al. 2015). Green cuttings from NW Sicily also showed low success, suggesting the need for improved techniques (A. Cristaudo, pers. comm.).

Information on reproductive biology (e.g., breeding system, seed duration and seedling survival) is scarce. Accessions collected for the Genmedoc and Semclimed Projects in the 2000s and stored in the germplasm bank of the Department of Biological, Geological and Environmental Sciences of the University of Catania (BGS-CT) contained no viable seeds. This fact may be due to low reproductive performance, particularly in plants growing on the foothills of Mt. Cofano (A. Cristaudo, pers. comm.).

Germination tests on Lebanese *E. sicula* subsp. *libanotica* (now considered part of *E. sicula* subsp. *sicula*) at the University Saint Joseph of Beirut showed that seeds are orthodox, with a germination rate of approximately 25% after 30 days at 16 °C on agar with alternating 12 h light/12 h dark cycles (Lebanon Flora 2020). In contrast, another Lebanese accession studied at Kew achieved 100% germination after 63 days at 10 °C on 1% agar under an 8 h light/16 dark regime (source: SER INSR-RBGK 2023; https://ser-sid.org/species/5dc3038b-0eb7-4a23-b665-3cec9a4aacc8 and https://ser-sid.org/species/1aed0b53-1f32-4a6f-9df8-c9036134337c).

Both subspecies of *Erica sicula* possess pollen tetrads, as verified in Lebanese (Haddad 1969) and Cypriot (Sarwar 2007) stands of *E. sicula* subsp. *sicula*, as well as in *E. sicula* subsp. *bocquetii* (Pınar and Oybak 1995).

Moreover, neither the pollination ecology nor the dispersal strategies of the species complex have been properly investigated yet. Within the genus *Erica* pollination is often by insects (Rebelo et al. 1985; Ballantyne et al. 2015; Bouman et al. 2017; Moquet et al. 2017; Heystek and Pauw 2014). The seeds of the pentamerous heathers are very light 0.5–0.9 mg), small (0.5–0.8 × 0.3–0.5 mm) and winged (Fagúndez and Izco 2011), suggesting wind dispersal, although the distance they might travel before landing on suitable habitat remains unknown.

Census and measure of AOO and EOO at the global and national scale

The overall EOO of *Erica sicula s.l.* (i.e., including both subspecies) exceeds 715,000 km^2, whilst the AOO is only 140 km^2. Fig. 2 displays the extent of the species' range throughout the Mediterranean Basin.

Italy

A UAS census at Mt. Cofano precisely located 985 individuals (Fig. 9) in four sampled areas in suitable habitat, covering a total cliff surface of 5.91 ha (de Simone 2020). Considering the cliff inclination within the grid cells where the taxon was confirmed, and using a 2 × 2 m digital model, we calculated a real AOO of 57.84 ha, while the projected AOO was only 25.12 ha. Consequently, when using the minimum convex polygon method, the EOO was found to be 100.63 ha.

Assuming the surveyed areas represent the total stand and considering the total extent of the cliffs where the species was observed, the total subpopulation in Sicily is estimated between 4,186 and 9,638 individuals, with the oldest and largest ones (crown > 2 m) growing at higher altitudes (de Simone 2020). However, this may be an overestimate of the actual subpopulation size, as the cliffs are not homogeneously colonized due to micro-topographic preferences (de Simone 2020). Indeed, the assumption of homogeneous occupation may underestimate the impact of local abiotic (e.g., slope, rockiness) and biotic (e.g., competition with other rupicolous species) factors.

Lebanon

Fieldwork carried out between 2022 and 2023 enabled a more precise calculation of the EOO and AOO of *E. sicula* subsp. *sicula*, whose values are 55.067 km^2 and 28 km^2, respectively.

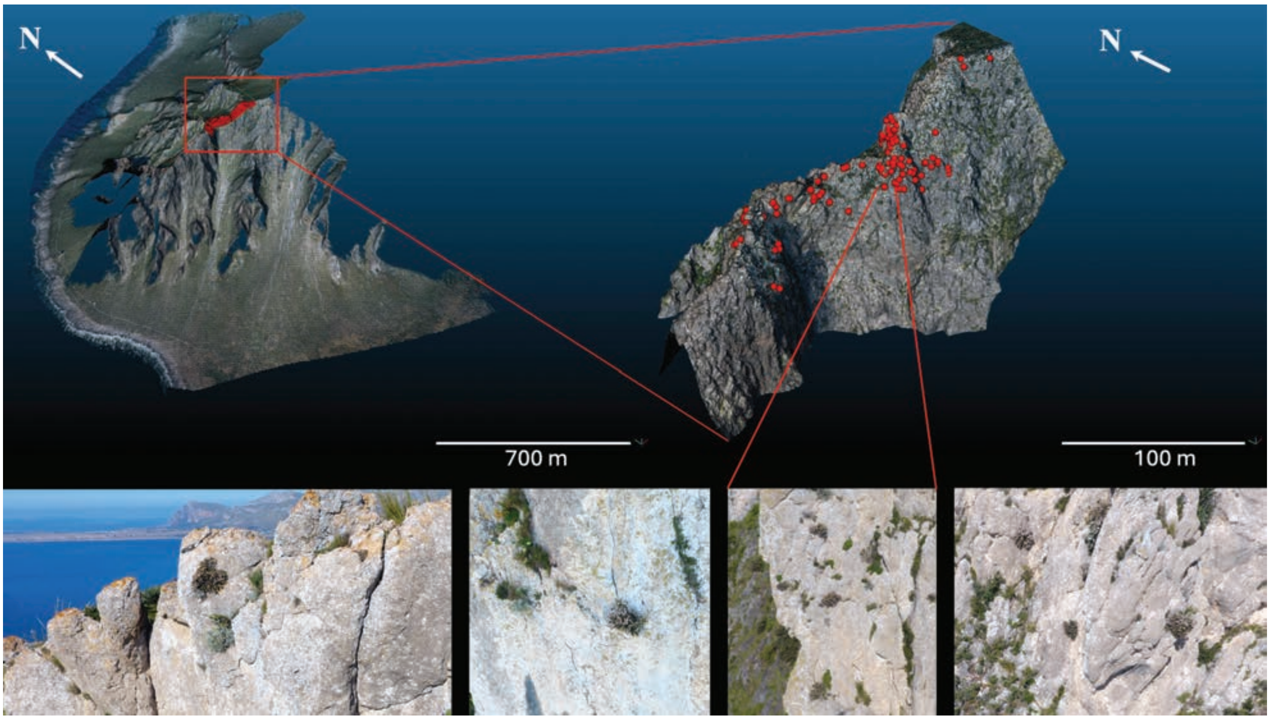

Figure 9. Results of UAS-based monitoring of the Italian subpopulation. The red surface in the upper left image points out a target site hosting *E. sicula* subsp. *sicula* located on Mt. Cofano (Sicily); the red points in the point cloud of the upper right image correspond to the individuals growing on the cliff, whose identity and exact position was recorded through the photos taken by the drone (see image sequence below).

Cyprus

Recent surveys have provided detailed information about the 8 subpopulations inhabiting the island. Based on 2 × 2 km wide cells, the EOO of the Cypriot subpopulations is around 327.1 km^2, with an AOO of 32 km^2.

Türkiye

For the 8 subpopulations for *E. sicula* subsp. *bocquetii*, we estimated an EOO of 595.6 km^2 and an AOO of 32 km^2.

Based on the location of the 8 subpopulations of *E. sicula* subsp. *sicula* in Antalya province, the EOO of the Turkish subpopulations is about 153.6 km^2, with an AOO of 24 km^2.

Libya

Based on the geographic coordinates of the herbarium specimens, we were able to map most of the historical records of *E. sicula* subsp. *sicula* in Libya. Seven stands were confirmed, which allowed us to estimate an EOO of 1,464 km^2 and an AOO of 28 km^2.

Current conservation, main threats and demographic trends

The minimum viable value for *E. sicula* was estimated to be 500–1000 mature individuals per subpopulation (Commission of the European Communities 2009).

Italy

Most likely, two out of three Sicilian stands have disappeared during the last two centuries. The whole population falls within the Special Area of Conservation of the Natura 2000 network ITA010016 "Monte Cofano e littorale" and in the regional nature reserve 'Monte Cofano". Mt. Cofano is also an Important Plant Area (hereinafter IPA; Blasi et al. 2010). *E. sicula* is featured in all the Italian (Conti et al. 1992; Conti et al. 1997; Scoppola and Spampinato 2005; Rossi et al. 2013) and Sicilian (Raimondo et al. 1994; Raimondo et al. 2011) red lists. The increasingly frequent wildfires which recently affected Mt. Cofano represent the only factor currently affecting this local subpopulation. Another threat is the oversampling of plant specimens. In fact, more than 80 specimens collected in the *locus classicus* of Mt. Cofano are found in European herbaria (see Suppl. material 1), suggesting that, even if most plants are safe from collectors, the more accessible portion of the local subpopulation has been systematically damaged for two centuries by botanists eager to possess their own specimen. Additionally, the fast spread in the adjacent municipalities of the invasive alien perennial grass *Cenchrus setaceus* (Forssk.) Morrone (Scuderi and Pasta 2009), may soon pose a serious threat to the Italian subpopulation.

Lebanon

E. sicula subsp. *sicula* is severely threatened by the increasing impact of human activities. In fact, the primary threats to most of the Lebanese subpopulations are quarrying, urban sprawl and the construction of built infrastructure such as dams and roads. The increasingly frequent fires severely affect some of the stands, especially in the lower parts of the canyon and constitute a secondary threat. Overgrazing occurs in the upper part of the valley and may hinder the expansion of the few remnant nuclei in cliff areas accessible to goats. The total subpopulation size in Lebanon is estimated at 5,000 individuals, with 4,000 distributed in the areas of Afqa, el Mejdel and Aaqoura, and 1,000 in the area of Yahchouch Chouwen and Frat. At least two of the known subpopulations were destroyed in the two last decades by quarrying and the construction of the dam of Janna. Only a small part (<10%) of the subpopulations fall into the territory of Jabal Moussa Biosphere Reserve. Although the entire Nahr Ibrahim Valley has been identified as an IPA according to two studies (Radford et al. 2011; Bou Dagher-Kharrat et al. 2018) and as a Key Biodiversity Area (El Zein et al. 2018), only the small area included in Jabal Moussa is a protected area. Hence a total of 7 location were identified, 6 of them being currently threatened.

Cyprus

E. sicula subsp. *sicula* grows in areas of high conservation interest, but these sites currently are not yet protected by law. The most recent field census suggests an overall number of approximately 4,700 individuals forming seven distinct subpopulations, whose number and size are expected to shrink in the long term due to goat overgrazing and to increasingly frequent wildfires (SG, pers. comm.). Although some of its stands became extinct during the last decades, this taxon is not included in the Red Data Book of the Flora of Cyprus (Tsintides et al. 2007).

Türkiye

In the IUCN Red Data Book of the Turkish Vascular Flora (Ekim et al. 2000), both *E. sicula* subsp. *bocquetii* and *E. sicula* subsp. *sicula* (under subsp. *libanotica*, Authors' note) were classified as Vulnerable (VU), while Tezel et al. (2020) cite *E. sicula* subsp. *bocquetii* as Critically Endangered (CR) with no further details.

Moreover, the type locality of *E. sicula* subsp. *bocquetii* falls within the Çığlıkara Tabiat Koruma Alanı (= Çığlıkara Nature Reserve) (OŞ, *pers. obs*.), while some of the Turkish subpopulations of *E. sicula* subsp. *sicula* fall within the Beydağları Sahil Milli Parkı (= Beydağları Coastal National Park) and/or the Kaş-Kekova Special Environmental Protection Area.

Libya

The lack of recent updates concerning this country does not allow us to evaluate the exact number and the size of local subpopulations. All of them grow in the Jabal Al Akhdar Region, a territory that has been designated as IPA by El-Rtaib (2010) and by Radford et al. (2011), but that is not protected by law. Threats to vegetation in the massif of Jabal Al Akhdar are well documented. Human activities were relatively more restricted in this area in the past, aimed at protecting the forests. However, the situation has changed during the last decade following the political instability, which led to civil unrest and movement of human populations. The main threats are firewood collection, charcoal production, over-harvesting of medicinal and aromatic plants, bush fires, quarrying, urban sprawl, overgrazing, agriculture expansion and uncontrolled camping (Saaed et al. 2022). The habitat extent and quality are still declining now. Several dams were built along Wadi Derna in the 1970s to prevent seasonal floods and to collect water for irrigation purposes. These dams sadly hit the headlines in September 2023 because of their collapse after an intense rainstorm, causing thousands of human casualties. Many Libyan subpopulations of *E. sicula* subsp. *sicula*, which were concentrated within the catchment area of this seasonal stream might have been severely affected by this event.

Discussion

Ecology

Both subspecies *Erica sicula* group grow exclusively on vertical cliffs (chasmophytes) or in ledges and large fractures (comophytes). Such ecological behaviour proves to be a globally rare feature among heathers. Additionally, they grow only on limestones and dolomias, whereas most Ericaceae thrive on acid or very acid soils (Webb and Rix 1972; Oliver 1991). Although these very unusual edaphic requirements are intriguing, there is currently no available information on the soil biota (e.g., ericoid mycorrhizae capable of capturing phosphorus and nitrogen) connected with *Erica sicula s.l.*

Although they all share the same habitat, the different populations of *E. sicula* subsp. *sicula* differ in terms of altitudinal range strikingly enough to raise taxonomic questions. For instance, the Italian, Turkish and Libyan populations of

Erica sicula subsp. *sicula* only occur under strictly thermo-Mediterranean climate, whereas the Cypriot and Lebanese populations grow only on mountain ranges subject to meso- and supra-Mediterranean climatic conditions.

The remarkably wide altitudinal range of *E. sicula* subsp. *bocquetii* probably induces striking differences in the blossoming times between its lowland and the mountain subpopulations (June to September), thus causing significant reproductive isolation between them (McClintock 1980). Moreover, the finding of *E. sicula* subsp. *bocquetii* at lower altitudes makes it necessary to verify its biological distinction from subsp. *libanotica*, with which it is sympatric.

Extinction risk assessment

Table 4 provides a synthetic overview of the thresholds, and the criteria followed to perform the extinction risk assessment both at the global/species scale and at the subspecies-regional scale.

At the global/species scale *E. sicula sensu lato* was evaluated as of Least Concern (LC). On the one hand, the EOO is rather extensive, with 715,366 km^2; on the other hand, the AOO is of 140 km^2 and a continuing decline was observed (b) in EOO (i), AOO (ii), area, extent and/or quality of habitat (iii) and number of subpopulations or locations (iv). Although each subpopulation is capable of surviving within the five countries, the global distribution pattern is severely fragmented. Considering the considerable distances between *E. sicula* subpopulations, only those in Cyprus may be interconnected with those of Lebanon and Türkiye. However, the potential for long-distance dispersal by pollinators allowing effective gene flow, as well as the requirements for seed dispersal, remain unproven. It is likely that no subpopulation is sufficiently close to allow regular gene flow, except under exceptional circumstances, which raises concerns about genetic depletion as a significant threat. The situation of *Erica sicula* subsp. *sicula* is worrying, because it has undergone substantial population decline over the past fifty years across its entire distribution range. In fact, two of the three known stands in northwest Sicily (Italy) are now definitively extinct; in Lebanon, two new stands were discovered, along with five confirmed and four unconfirmed, including two that have been proven extinct. Similarly, Cyprus has three new stands, five confirmed and three unconfirmed, while in Türkiye, there are two new, two confirmed and five extinct stands.

Italy

Based on 2 × 2 km wide cells, Domina et al. (2012) previously estimated the EOO and AOO at 4 km^2 each, considering the surface effectively occupied by *E. sicula* subsp. *sicula* around 25 ha. These authors listed the species as Critically Endangered (CR) based on the subcriterion B1ab(i,ii,iv,v). Based on the data collected during the fieldwork by de Simone (2020), we are able to confirm the risk level assigned to this subspecies; yet, we applied different and additional sub-criteria - B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv) - to support the previous assessment: the EOO (4 km^2) and AOO (4 km^2) are very restricted (B1 + B2), there is one sole location (a) and a continuing decline observed (b) in EOO (i), AOO (ii), area, extent and/or quality of habitat (iii), number of subpopulations or locations (iv).

Table 4. Overview of the thresholds and criteria followed for the extinction risk assessment of the taxa of the *Erica sicula* group at the species-global scale and at the subspecies-national scale; n.a. = not assessed. AOO = Area of Occupancy; EOO = Extent of Occurrence.

Taxon	**Country**	**Nb. of Stands**	**EOO (km^2)**	**AOO (km^2)**	**Estimated subpopulation size (nr)**	**Severely fragmented (Y/N)**	**Threats**	**Criteria**	**Status**
E. sicula subsp. *sicula*	Italy	1	4	4	4,186-9,638	N	wildfires, invasive alien plants	B1ab(i,ii,iii,iv) + 2ab(i,ii,ii,iv)	CR
E. sicula subsp. *sicula*	Libya	7	1,464	28	n.a.	N	firewood collection for charcoal production, overharvesting for medicinal purposes, wildfires, quarrying, urban sprawl, overgrazing, dam construction	B1ab(iii) + 2ab(iii)	VU
E. sicula subsp. *sicula*	Cyprus	8	327.1	32	4,700	N	overgrazing, wildfires	B1ab(i,ii,iii,iv) + 2ab(i,ii,ii,iv)	VU
E. sicula subsp. *sicula*	Türkiye	8	153.6	24	n.a.	N	urban sprawl	B1ab(i,ii,iii,iv) + 2ab(i,ii,ii,iv)	VU
E. sicula subsp. *sicula*	Lebanon	7	55.1	28	5,000	N	quarrying, dam construction, road construction, urban sprawl, wildfires	B1ab(i,ii,iii,iv) + 2ab(i,ii,ii,iv)	VU
E. sicula subsp. *bocquetii*	Türkiye	8	595.6	32	n.a.	N	overgrazing, wildfires	B1ab(iii) + 2ab(iii)	VU
E. sicula sensu lato	Global	39	715,366	140	n.a.	Y		B2ab(i,ii,iii,iv)	LC

Lebanon

The discovery of additional subpopulations led to larger values for EOO and AOO compared to the previous assessment (Stephan et al. 2017), which were 45 km^2 and 20 km^2, respectively.

The updated data collected during surveys on distribution, number of subpopulations and threats have allowed us to review the EN status previously evaluated in the initial assessment (Stephan et al. 2017). We assessed the taxon as VU at the national scale of Lebanon under the subcriteria B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv): the EOO (55.067 km^2) and AOO (28 km^2) are very restricted (B1 + B2), there are seven locations (a) and a continuing decline observed (b) in EOO (i), AOO (ii), area, extent and/or quality of habitat (iii), number of subpopulations or locations (iv).

Cyprus

The data yielded during the recent field investigations allowed us to assess *E. sicula* subsp. *sicula* as VU at the island scale under the subcriteria B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv): both the EOO (327.1 km^2) and the AOO (32 km^2) are very restricted (B1 + B2), there are eight locations (a) and a continuing decline observed (b) in EOO (i), AOO (ii), area, extent and/or quality of habitat (iii), number of subpopulations or locations (iv).

Türkiye

E. sicula subsp. *bocquetii* was previously evaluated as Critically Endangered (CR) according to the criteria B1a+2a, as already suggested by AKS Planlama Mühendislik Ltd Şti. (2010). Following updated analyses, we assessed the taxon as VU at the global scale under the subcriteria B1ab(iii) + 2ab(iii): EOO (595.6 km^2) and AOO (32 km^2) are restricted (B1 + B2), there are eight locations (a) and a constant decline (b) in the (iii) area, extent and/or quality of habitat was observed.

E. sicula subsp. *sicula* was evaluated as nationally VU under the subcriteria B1ab(i,ii,iii,iv) + 2ab(i,ii,iii,iv): the EOO (153.6 km^2) and AOO (24 km^2) are very restricted (B1 + B2), there are six locations (a) for eight stands, and a continuing decline observed (b) in EOO (i), AOO (ii), area, extent and/or quality of habitat (iii), number of subpopulations or locations (iv).

Libya

E. sicula subsp. *sicula* was assessed as VU at the national scale under the subcriteria B1ab(iii) + 2ab(iii): the EOO (1,464 km^2) and the AOO (28 km^2) are restricted (B1 + B2), there are seven locations (a) and a continuing decline observed (b) in the area, extent and/or quality of habitat observed (iii). It is worth underlining that the Libyan stands are currently affected by many severe and synergic threats (Alawamy et al. 2020).

Conclusions

The information provided in this paper may be used to enhance the protection of all known and threatened subpopulations of the taxa referred to *Erica sicula sensu lato*. Identifying knowledge gaps is a crucial step for effective plant conservation. By pinpointing missing information, efforts can be directed to address those gaps in order improve our understanding of ecological requirements of the target species and to develop effective mid- and long-term protection measures.

The global conservation status of a taxon is influenced by the conditions and challenges it faces in the countries where it occurs. However, as illustrated by the case of *Erica sicula*, the global status may not accurately reflect the distinct risks of extinction in each individual country. This observation could also underscore a potential flaw in the guidelines and criteria of the IUCN Red List. Consequently, it is essential to carefully consider the regional assessments when evaluating species with many subspecies and subpopulations scattered across extensive ranges. To accurately understand and mitigate species extinction risk, a careful examination of the status and threats faced by each subspecies is required.

All taxa within this group inhabit very steep slopes, exhibit extremely low reproductive performance, have narrow ranges and show fragmented and declining population at the national scale. These characteristics, coupled with low competitivity and ongoing population shrinkage, are probably triggered by multiple factors. Therefore, future investigations should adopt a multifaceted approach.

For instance, we need to record detailed diachronic data on the microclimatic requirements of the pentamerous taxa using data-loggers (Marcenò et al. 2022). In fact, these heathers likely benefit from favourable climatic conditions, such as cool summers at higher altitudes, and microclimatic factors, such as overnight moisture near the coasts or riverbeds, which help reduce seasonal water stress. Notably, de Simone (2020) recorded consistent air humidity and daily temperature values in the north-facing cliffs of Mt. Cofano (Sicily). This finding helps explain why attempts to plant *E. sicula* subsp. *sicula* at lower altitudes on Cyprus Island were unsuccessful (SG, pers. comm.). The use of drones to monitor the subpopulations can facilitate better understanding of the auto- and synecology of these cliff-dwelling taxa in otherwise inaccessible contexts (de Simone 2020; Reckling et al. 2021; Li et al. 2022). When combined with detailed climatic data, occurrence records and ecological data, these efforts can significantly improve the quality of IUCN risk assessments and the precision of niche models (e.g., Bazan et al. 2012).

Intensive prospections and increased sampling effort are needed, particularly for the less investigated subpopulations of Türkiye and Libya, to assess the genetic diversity within and among all members of the *Erica sicula* group. Sampling material from cliff-dwelling individuals is crucial to capture the whole genetic variability of each taxon. This could enable the identification of evolutionarily significant units and genetic diversity hotspots, ultimately supporting future *in-situ* and *ex-situ* conservation projects.

Our study highlights the fact that UAS are tools that allow a significant refinement of demographic estimates, calculating more precise EOO and AOO. In particular, the role of the Z dimension, i.e. the cliff inclination, is of paramount importance when dealing with plant species tied to rupestrial habitats, and ignoring this fact may lead to a sensitive underestimation of the AOO.

Studies on population genetics, pollination biology and seed dispersal would be invaluable to assess the potential threat of fragmentation, especially given the reduced fecundity previously reported in this species (Commission of the European Communities 2009).

Furthermore, enhancing our knowledge about the physical, chemical, and biological properties of the soils where the pentamerous heathers grow is proving to be crucial. For instance, soil microbiota may host mycorrhizae useful for inoculation that may facilitate the establishment of the saplings during plant translocation initiatives.

Ad hoc research on reproductive biology, namely on plant-insect interactions (pollinators, predators), seed dispersal strategies and seedling or sapling establishment rates, is needed to address the problems of low reproductive fitness likely affecting all populations of the species.

As for *ex situ* conservation, the first known attempt to cultivate *E. sicula* outside its native range has been carried out at Kew (T. Freeth, pers. comm.). In 1952 the Royal Botanic Gardens hosted a plant grown in open ground, whose provenance and identity remain uncertain. In 1984, Kew hosted many individuals of *E. sicula* subsp. *sicula* grown from seeds collected by J.J. Archibald near Kemer (Türkiye). These plants, cultivated in pots, alpine houses, and more recently on the rock garden once their hardiness in UK climate was assured, have persisted through hostile weather conditions, including warm, wet, regularly frozen winters, and long summer droughts (T. Freeth, pers. comm.).

Along with the above-mentioned multifaceted research needed, some concrete interventions should be carried out as soon as possible. For instance, considering the clear preference of *Erica sicula s. l.* for shady and humid habitats, the increasing frequency of extreme heat, drought events, and wildfires in the coming decades will probably affect the survival of this group across its entire distribution range (MedECC Members 2019). Hence, to fight against the ongoing decline of many subpopulations, translocation initiatives should be encouraged (e.g., Abeli et al. 2021; Godefroid et al. 2025), especially in Italy, Libya, Lebanon, and Cyprus, where local disturbances are expected to persist or intensify in the next future.

In the specific case of *E. sicula* subsp. *sicula*, much more efforts should made to prevent and fight against the spread of invasive alien plants like the tussock alien grass *Cenchrus setaceus*, rapidly spreading along the disturbed coastal areas of NW Sicily and getting every year closer to Mt. Cofano (Pasta et al. 2010).

Contacts with the large number of scientists involved in this study were greatly facilitated by networks of Mediterranean specialists such as the IUCN/SSC/Mediterranean Plant Specialist Group and GENMEDA (http://www.genmeda.net/members/current_members/iucn). For this purpose, this study represents a paradigmatic case of international collaboration. Similar efforts should be encouraged and multiplied to strengthen the relationship between countries and improve knowledge, data sharing and produce effective and long-lasting conservation policies, going beyond the political and administrative borders of the countries hosting broad-ranged endangered plants (Pirie et al. 2022, 2024; Elliott et al. 2024).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Author contributions

SP led the research and the writing of the manuscript; HEZ, OŞ, SG and SP collected and curated data from herbarium, literature and/or unpublished field reports; HEZ, SG and LDS conducted field surveys respectively in Lebanon, Cyprus and Italy; HEZ produced the maps and supported risk assessments using GIS software; the additions and remarks of HEZ and LDS significantly improved the final quality of the first draft. BDM supervised the whole process, including E. Charles Nelson who handled the initial reviews and provided constructive feedback. All the co-authors revised, improved, and accepted the manuscript before submission, and declare that there is no potential conflict of interest among them. Both SP and HEZ should be considered first co-authors.

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Data availability

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

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Supplementary material 1

Detailed information retrieved from the literature and from the labels of the 212 herbarium specimens examined

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Research Article

Chelonopsis guchengensis, a new species of Lamiaceae from Hubei Province in Central China

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Abstract

Chelonopsis is a small genus endemic to East Asia. In this study, a new species, *C. guchengensis*, from Nanhe National Nature Reserve, Gucheng County, Hubei Province is described and illustrated. Molecular phylogenetic analyses based on two nuclear ribosomal DNA regions (ETS and ITS) and five plastid DNA markers (*trnL* intron, *trnL-trnF*, *trnS-trnG*, *psbA-trnH*, and *rps16*) were carried out to explore the phylogenetic position of the new species. A close relationship between the new species and *C. giraldii* is supported by molecular phylogenetic and morphological evidence. However, the two species can be easily distinguished from each other by mostly leaf and inflorescence morphology.

Key words: Central China, Gomphostemmateae, Lamioideae, molecular phylogeny, taxonomy

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Introduction

Chelonopsis Miq. (Lamiaceae, Lamioideae) is a genus of herbs and shrubs endemic to East Asia (Mabberley 1997). The genus comprises 14 species and three varieties, with most species endemic to China, and southwest China (Xizang, Yunnan and Sichuan) is a center of species diversity for the genus (Li and Hedge 1994; Xiang and Peng 2008; Xiang et al. 2009, 2013; Weckerle et al. 2009). The genus was originally placed within subtribe Melittinae Briq. (Bentham 1848, 1876; Cantino 1985). However, molecular phylogenetic study (Scheen et al. 2010) utilizing chloroplast *rps16* and *trnL-trnF* sequences revealed that it forms a monophyletic group with *Bostrychanthera* Benth. and *Gomphostemma* Wall. ex Benth. Based on this finding, Scheen et al. (2010) established tribe Gomphostemmateae to elucidate the phylogenetic position of these genera, and the tribe was supported by a subsequent study (Bendiksby et al. 2011). Later, a molecular phylogenetic analysis using two nuclear regions and five plastid loci based on comprehensive taxon sampling has confirmed the monophyly of Gomphostemmateae and *Bostrychanthera* was synonymized under *Chelonopsis* (Xiang et al. 2013).

Based on calyx morphology and habit, *Chelonopsis* was divided into two subgenera: subg. *Aequidens* C. Y. Wu & H. W. Li and subg. *Chelonopsis* (Wu et al. 1965; Wu 1977). Subgenus *Aequidens* was further divided into sect. *Microphyllum* C. Y. Wu & H. W. Li and sect. *Aequidens* on the basis of leaf blade morphology. Meanwhile, sect. *Microphyllum* was subdivided into ser. Roseae C. Y. Wu and H. W. Li (with glandular trichomes) and ser. *Lichiangenses* C. Y. Wu and H. W. Li (without glandular trichomes), a classification system supported by the anatomical studies of the trichomes (Xiang et al. 2010). The infrageneric classification system based on morphology was supported by molecular evidence (Xiang et al. 2013).

During a biological survey of Nanhe National Nature Reserve in Hubei Province, we found a unique species of *Chelonopsis* distributed in Gucheng County. By comparing it with herbarium specimens of *Chelonopsis*, we observed that this species differs from all known species within the genus. We further confirmed its status as a distinct new species based on morphological and molecular phylogenetic evidence, and designate it as *C. guchengensis*.

Material and methods

Phylogenetic analyses

DNA was extracted from silica-dried leaves using a modified CTAB method (Porebski et al. 1997), and it was then placed at -20 °C for storage. Two nuclear ribosomal regions (ETS, ITS) and five chloroplast regions (*trnL* intron, *trnL-trnF*, *trnS-trnG*, *psbA-trnH*, *rps16*) were amplified by using universal primers, and the sequences of specific primers are shown in Suppl. material 1: table S1 (Taberlet et al. 1991; Wen and Zimmer 1996; Oxelman et al. 1997; Baldwin and Markos 1998; Hamilton 1999; Beardsley and Olmstead 2002). Polymerase chain reaction (PCR) used the following protocol: 2×Super Pfx MasterMix 25 μL; forward primer 2.5 μL (10 μmol/L); reverse primer 2.5 μL (10 μmol/L); template DNA 2 μL (50 ng/μL) and ddH_2O 18 μL. The program was set as follows: pre-denaturation at 94 °C for 5min, 35 cycles of 30 s at 94 °C, 30 s at 53 °C, 1 min at 72 °C, and a final extension of 7 min at 72 °C (Xiang et al. 2013). After amplification, the PCR products were electrophoresed in a 1% agarose gel stained with GelRed at 200V for 20 min, and then the results were observed under a UV analyzer, and finally the PCR products with the right size and bright bands were used for sequencing (Applied Biosystems 3730xl, Tsingke Biotechnology Co., Ltd.).

To explore the phylogenetic position of the putative new species in *Chelonopsis*, 202 sequences representing 12 genera of Lamiaceae (Xiang et al. 2013) were downloaded from the GenBank (https://www.ncbi.nlm.nih.gov/). *Holmskioldia sanguinea* Retz. was selected as the outgroup. All sequences used in this study together with their accession numbers in GenBank were listed in Suppl. material 1: table S2. All DNA sequences newly obtained were edited and spliced using SeqMan (DNASTAR package. Seqman User Manual. USA: 2020). The edited sequences were concatenated in PhyloSuite v. 3.2.6 (Ronquist et al. 2012) in the order of *trnS-trnG*, *psbA-trnH*, *trnL* intron, *trnL-trnF*, *rps16*, ITS, and ETS, and the sequence alignment was performed in MAFFT v. 7.402 (Katoh and Standley 2013). IQ-Tree

v. 2.0.3 (Nguyen et al. 2015) was used to find the optimal model and construct a phylogenetic tree using the maximum likelihood (ML) method (1000 replications) (Felsenstein 1981). The phylogenetic tree was displayed using the online website Interactive Tree Of Life (iTOL) v5 (https://itol.embl.de/) (Letunic and Bork 2021).

Morphological observations

Living plants and vouchers of *C. guchengensis* were examined in Yujiagou, Nanhe National Nature Reserve in Hubei Province. The length and width of the leaves were measured using a digital vernier caliper, and a magnifier was used to check the leaf pubescence. A detailed comparison of *C. guchengensis* with other species of the genus was made based on descriptions and herbarium specimens housed in the following herbaria: ANUB, CDBI, CSFI, CSHH, HHBG, HITBC, IBK, IBSC, ISCB, JF, KUN, NWP, LBG, NAS, PE, WUK, XBGH, SYS, and SZG.

Distribution and mapping

Collection sites of specimens representing *C. guchengensis* and *C. giraldii* were located with the software of “2bulu” APP V7.8.8 (https://www.2bulu.com/) to determine the known range of each species. Maps were produced in ArcGIS vers. 10.8.2 (Redlands, California, USA) using the free vector and raster map data available through GeoJSON (https://geojson.cn/).

Results

Sequences and alignment characterization

A total of 272 sequences were used, which included 70 sequences newly generated in this study and 202 sequences downloaded from the GenBank (see Suppl. material 1: table S2). Sequence lengths were 470–523 nucleotides (nt) in *Chelonopsis* (349–510 nt in the other included taxa) for the *trnL* intron, 286–347 nt (185–309 nt in the other included taxa) for the *trnL*-*trnF* spacer, 470–569 nt (449–572 nt in the other included taxa) for the *trnS*-*trnG* spacer, 303–361 nt (168–424 nt in the other included taxa) for the *psbA*-*trnH* spacer, 822–908 nt (802–916 nt in the other included taxa) for the *rps16* intron, 582–653 nt (481–626 nt in the other included taxa) for the ITS1-5.8S-ITS2 region, and 342–483 nt (374–448 nt in the other included taxa) for the ETS region. The resulting combined and aligned sequence matrix contained 4146 positions (including gaps), of which 548 positions belong to the *trnL* intron partition, 375 to the *trnL*-*trnF* intergenic spacer partition, 457 to the *psbA*-*trnH* partition, 614 to the *trnS*-*trnG* partition, 946 to the *rps16* partition, 704 to the ITS partition, and the ETS region contributed 502 bp.

Phylogenetic analyses

As the ML phylogenetic tree (Fig. 1) shows that *C. guchengensis* is a new species in the genus *Chelonopsis*, which could be further placed in subg. *Aequidens* sect. *Microphyllum* ser. Roseae. *Chelonopsis guchengensis* and *C. giraldii* formed a subclade with a high support value (SH-aLRT = 100) and is clearly distinguished from other species of the genus.

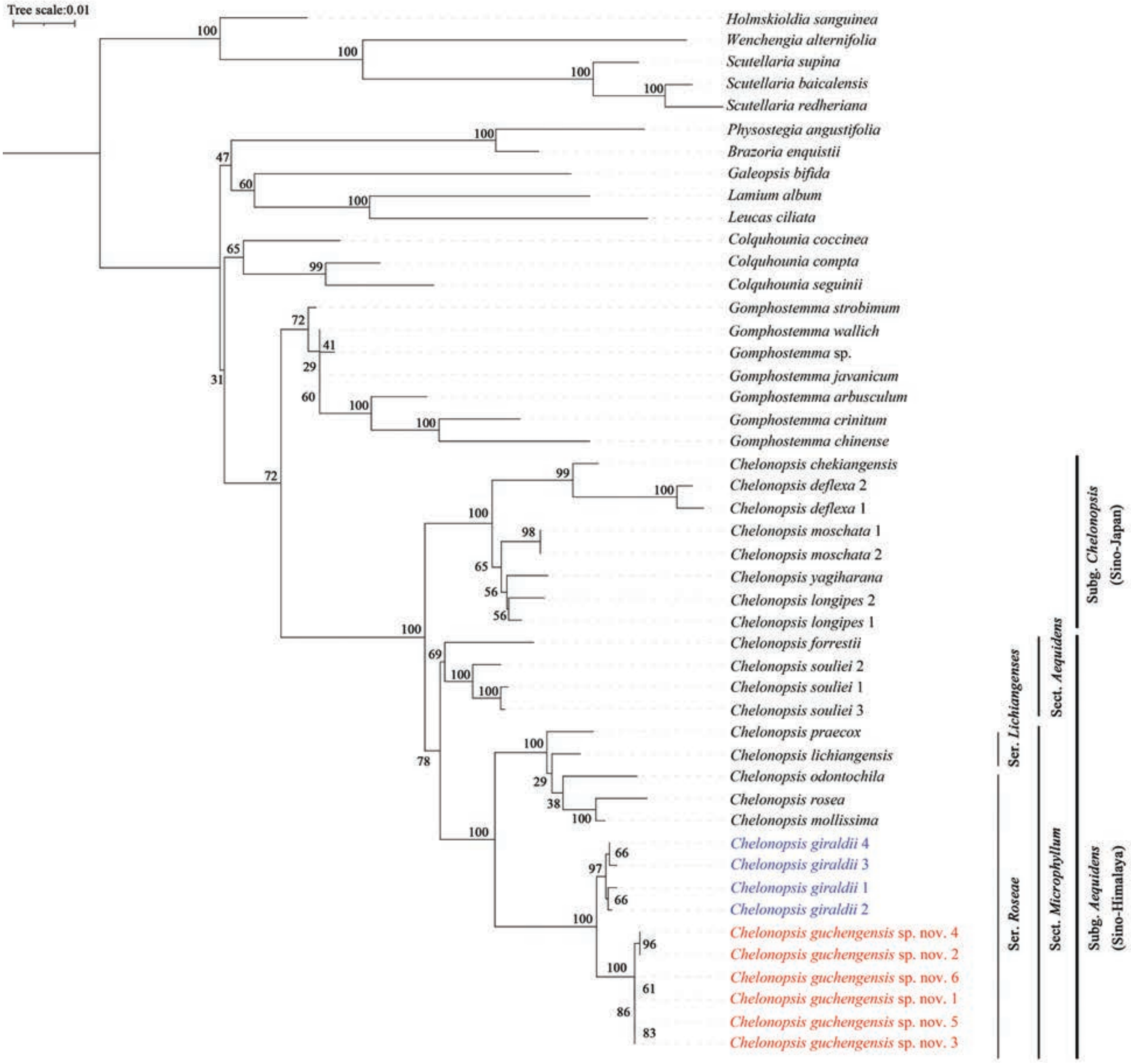

Figure 1. Phylogenetic tree showing the relationship and position of *C. guchengensis* and *C. giraldii* in *Chelonopsis*. Bootstrap values are shown above branches.

Table 1. Morphological comparisons of *C. guchengensis* and *C. giraldii*.

Characters	*C. guchengensis*	*C. giraldii*
Life form	semi shrub, high ca.1–2 m	shrubs, high ca.0.3–1.0 m
Size of leaves	ca. 2–10 × 1–5 cm	ca. 2.5–4 × 1.8–2.5 cm
Leaf shape characters	leaf shape oblong-ovoid, base attenuate, margin serrate, apex caudate	leaf shape ovate, base truncate, margin crenate, apex obtuse
Lateral veins	5–7 pairs, impressed above, elevated below	3–4 pairs, impressed above, elevated below
Leaf stalk	ca.1–3 cm, slender, subterete, densely puberulent.	ca.1–2 cm, slender, subterete, densely puberulent.
Stem	terete, striate, much branched, densely white tomentose, greenish or purplish red.	subterete, striate, densely puberulent, much branched, branches slender, leafy.
Inflorescence	cymes axillary, usually 2-flowered.	cymes axillary, 1–3-flowered, usually 1-flowered.
Pedicel	ca.1–2 cm	ca.1–1.4 cm
Bracteole	ca.1–1.5 × 1–2 mm	ca.1 × 1.5 mm
Altitude	570 m	750 m
Distribution	Hubei Province	Shaanxi, Gansu provinces

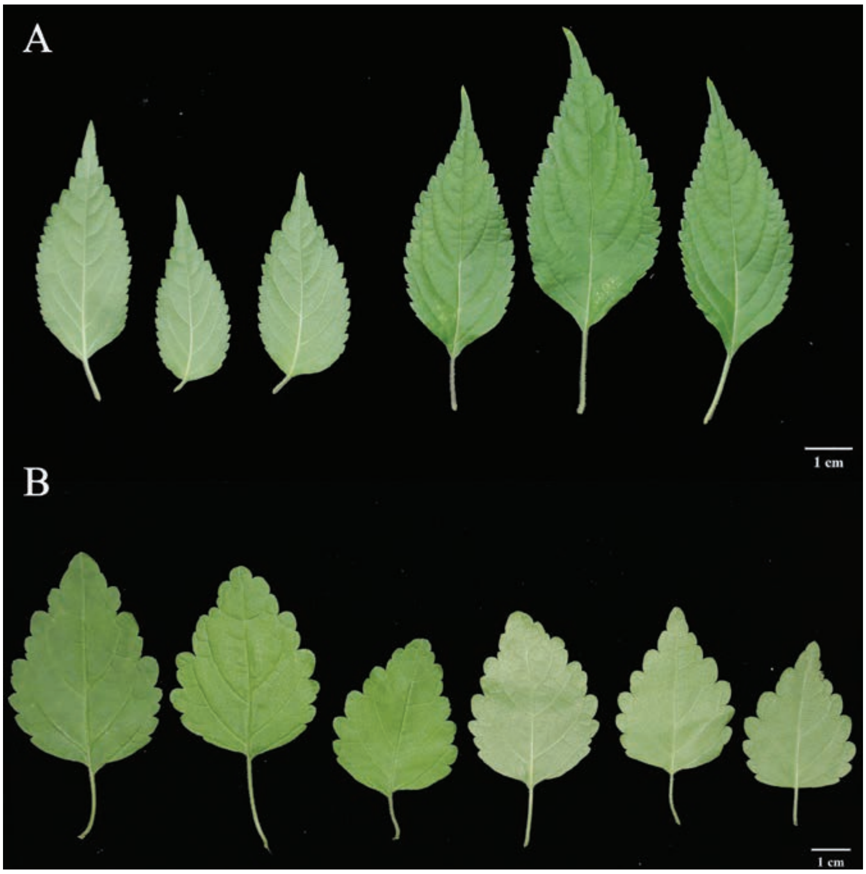

Figure 2. Comparison of *C. guchengensis* and *C. giraldii* in leaf morphology **A** *C. guchengensis* **B** *C. giraldii*.

Morphological comparisons

We compared in detail the morphological differences between *C. guchengensis* and *C. giraldii* because of its close phylogenetic relationships. They showed significant morphological differences (size, shape, lateral veins of leaves) (Table 1, Fig. 2).

Taxonomy

Chelonopsis guchengensis **X.Q.Liu, Z.C.Wei, Y.H.Xu, Y.X.Chen & J.Wen, sp. nov.**
urn:lsid:ipni.org:names:77358663-1
Figs 3, 5, Zhang et al. 2012: fig. 1

Type. China. Hubei • Gucheng County, Nanhe National Nature Reserve, valley nearby Nanhe River, 32°2'8"N, 111°23'48"E, 592 m, 23 October 2023, in ff., *X.Q. LIU 1200* (holotype: CCAU!; isotypes: CCAU!).

Diagnosis. The new species is morphologically similar to *C. giraldii* but differs in having longer and wider leaves (ca. 2–10 cm × 1–5 cm vs ca. 2.5–4 cm × 1.8–2.5 cm), and different leaf shapes (leaf shape oblong-ovoid, base attenuate, margin serrate, apex caudate vs leaf shape ovate, base truncate, margin crenate, apex obtuse in *C. giraldii*) (Fig. 4). The main differences between *C. guchengensis* and other plants in the genus are as follows: leaf shape oblong-ovoid (vs lanceolate in *C. chekiangensis* and ovate in *C. rosea* and *C. mollissima*); usually 2-flowered, pedicel length 1.5 cm (vs 3-flowered or more, pedicel tight and nearly sessile in *C. abbreviata*); bracteoles linear-lanceolate, ca. 1.5 cm long (vs bracteole conspicuous, leaf lanceolate, ca. 2.5 cm long in *C. bracteata*); corolla purplish red (vs yellow in *C. lichiangensis*, *C. odontochila* and milky yellow in *C. souliei*); and calyx apex acuminate (vs gradually aristate in *C. forrestii*).

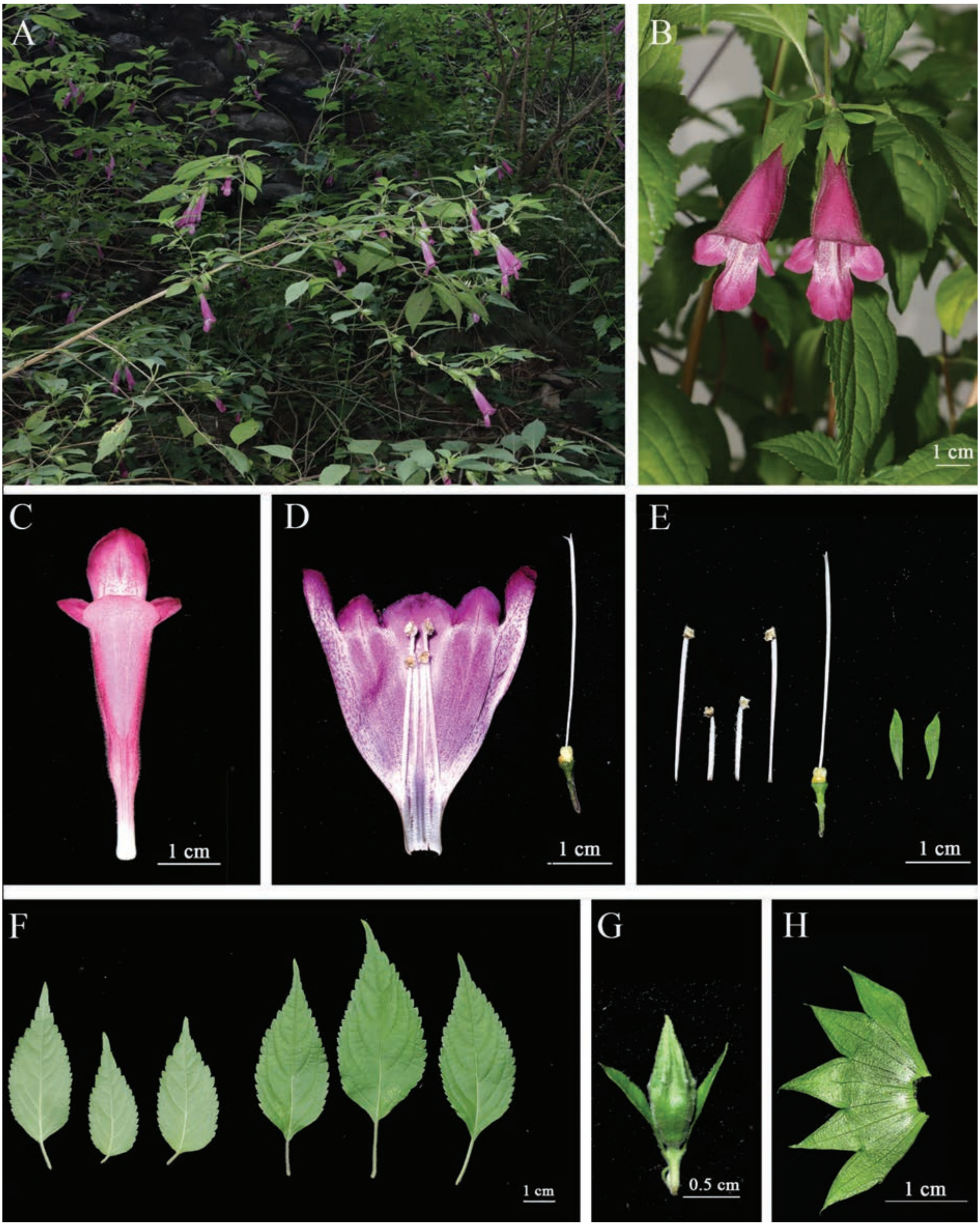

Figure 3. *Chelonopsis guchengensis* **A** habit **B** flower **C** front view of flower **D** internal view of corolla **E** pistil, stamens and bracteoles **F** front and back views of the blades **G** flower bud **H** front view of sepal.

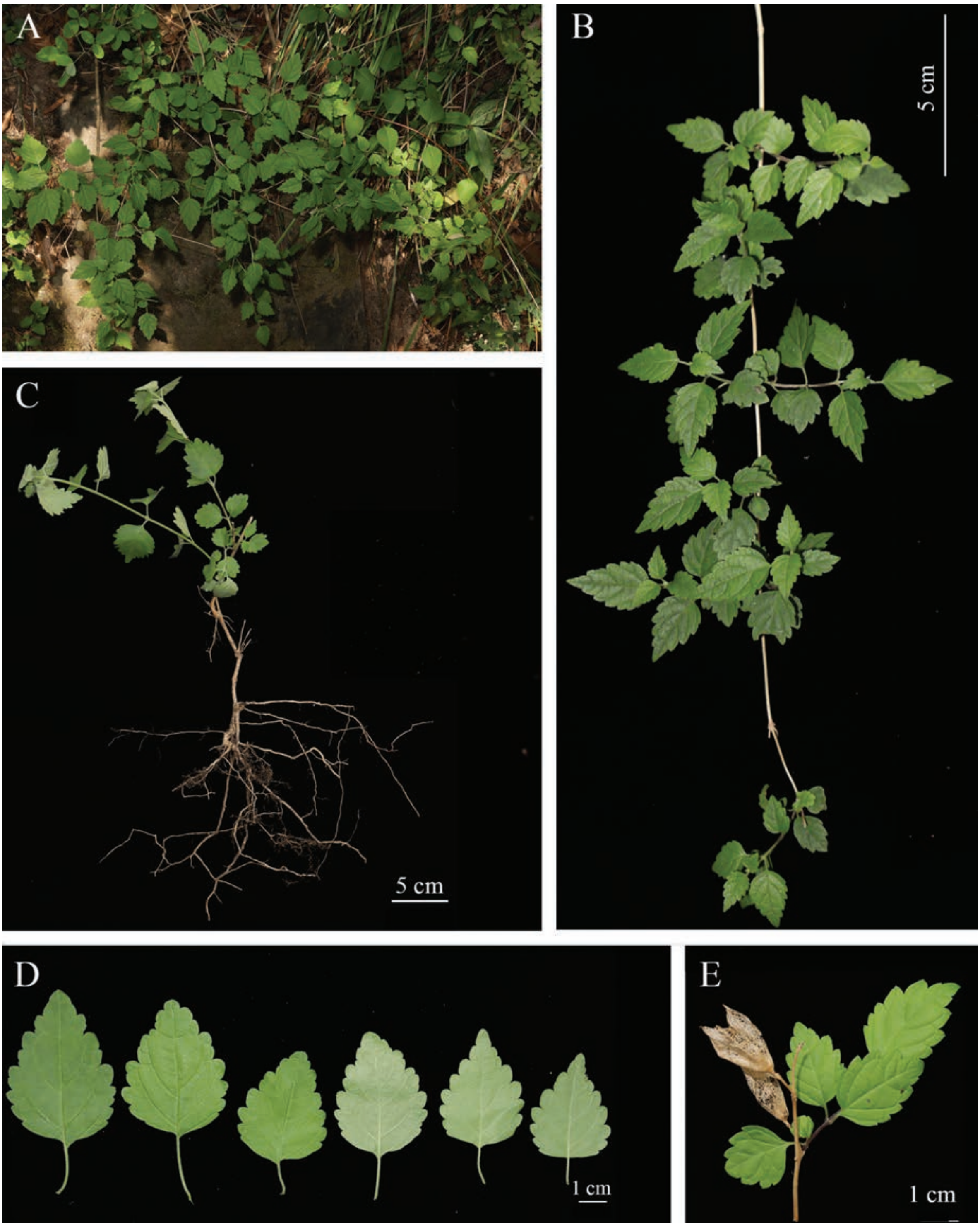

Figure 4. *Chelonopsis giraldii* **A** habit **B** branch **C** plant **D** front and back views of the blades **E** persistent calyxes.

Description. Semi shrubs, ca. 1–2 m tall. ***Stem:*** terete, striate, much branched, densely white tomentose, lime green or purple-red. ***Leaves:*** ca. 2–10 cm × 1–5 cm, opposite, lanceolate to ovate, apex acuminate, base cuneate, margins doubly serrate, green above, paler below, leaves all cauline, finely punctate, adjacent leaves cruciform, leaf surfaces white bristly, leaf abaxial surfaces glabrous, lateral veins 5–7 pairs, impressed above, elevated below; petiole slender, subterete, ca. 1–3 cm long, densely puberulent. ***Inflorescence:*** Cymes axillary,

华中农业大学园艺林学学院
植物标本采集记录

采集人：徐玉晗　　采集号：LIU1200
地点：湖北省襄阳市谷城县南河自然保护区
日期：2023 年 10 月 20 日；海拔 570 米
经纬度：E 111.39661059；N 32.03574564
生境：平地、石壁
分布：偶见
性状：半灌木
根：主根粗壮，多须根
茎：茎直立，多分枝，高 1-2 米
叶：披针形，长 2-10 厘米，宽 1-5 厘米
花：聚伞状花序，几全部生叶腋中，通常为 2 花
物候期：花期 9-10 月；果期 10-11 月
科名：唇形科 Lamiaceae　中文名：谷城铃
学名：*Chelonopsis guchengensis*
土名：
备注：

襄阳谷城
南河铃子香
2023.10.20

植物标本鉴定签

学　　名：*Chelonopsis guchengensis*
科　　名：唇形科 Lamiaceae
属　　名：铃子香属 Chelonopsis
中 文 名：南河铃子香
采 集 号：LIU1200
采集时间：2023 年 10 月 20 日
采集地点：湖北省襄阳市谷城县南河自然保护区
采 集 人：徐玉晗　　鉴 定 人：刘秀群

Figure 5. Holotype of *C. guchengensis* sp. nov. X. Q. Liu, Z. C. Wei, Y. H. Xu, Y. X. Chen & J. Wen (*LIU 1200*).

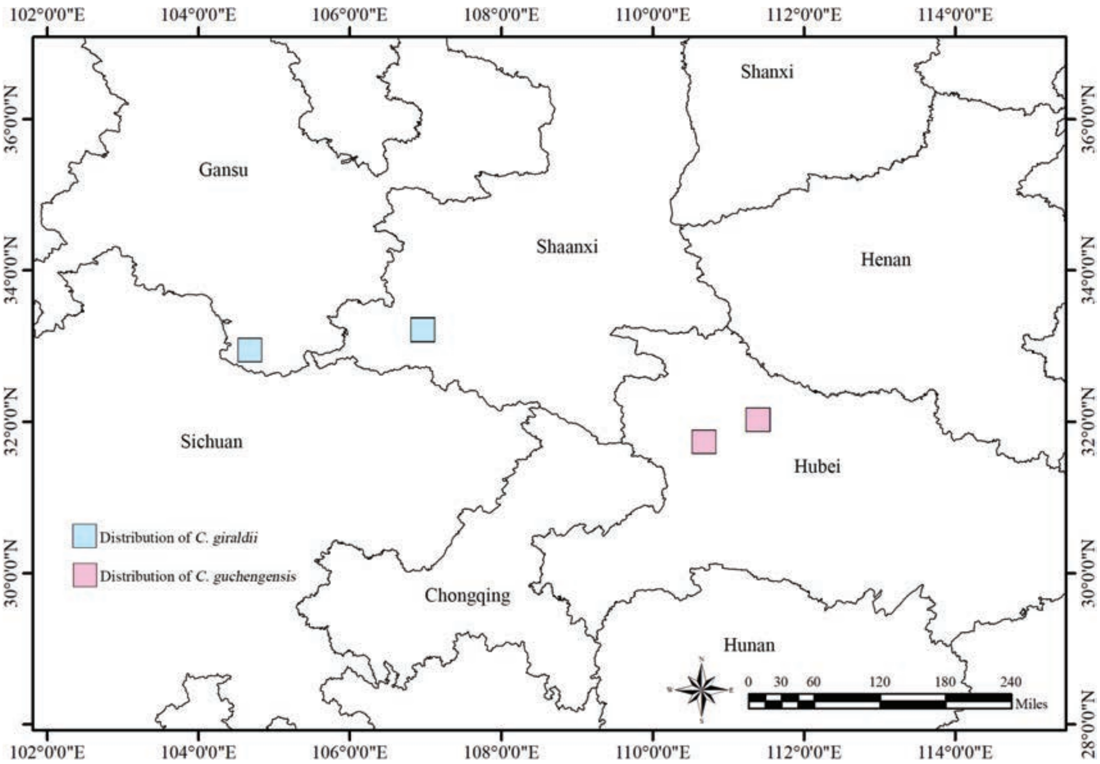

Figure 6. Distribution of *C. guchengensis* and *C. giraldii*. The pink boxes show the distribution areas of *C. guchengensis* and the blue boxes show the distribution areas of *C. giraldii*.

usually 2-flowered. ***Bracteoles:*** 2, linear-lanceolate, ca. 1–1.5 cm × 1–2 mm. ***Flowers:*** purplish red; calyx with 5 regular, very large, triangular teeth, calyx tube outside white pilose, inside glabrous, apex acuminate, reticulate veins conspicuous, purplish red when young, the same color as the stem, turning green at maturity; corolla ca. 5 cm, upper and lower lips unequal, lower lip obviously longer than upper lip; corolla tube ca. 3 cm, projecting much beyond calyx tube, throat inflated, exterior densely white tomentose, interior glabrous, irregularly spotted along lower lip axis; stamens didynamous, anterior pair longer, filaments filiform, flattened, puberulent, anthers ovoid, whiskered; styles filiform, glabrous, projecting beyond apothecia, apex equally 2-lobed.

Phenology. Flowering from September to October.

Distribution and habitat. At present, this species is only found in the mountainous area of Nanhe National Nature Reserve, Gucheng County, Hubei Province, China and Shennongjia Forest District, which is commonly found in the valleys near water sources at an altitude of 432–673 m, as well as in moist and fertile thickets (Fig. 6).

Etymology. The new species is named after Gucheng County in Hubei, China where it is distributed. The Chinese name is given as“谷城铃子香”.

Discussion

The phylogenetic study placed *Chelonopsis guchengensis* in subg. *Aequidens* sect. *Microphyllum* ser. Roseae. Within the genus, *Chelonopsis guchengensis* was supported to be sister to *C. giraldii* (Fig. 1). Morphologically, *C. guchengensis* is significantly different from other species in the genus, mainly in its larger leaves and purplish red flowers (Fig. 3). It could be identified by its oblong-ovoid leaf shape, base attenuate, margin serrate, apex caudate and purplish red flowers. Overall, the status of the new species of *C. guchengensis* was clearly established.

The genus *Chelonopsis* was first recorded in Central China (Shennongjia Forest District, Hubei Province) in 2012, and the species was then identified as *C. giraldii* (Zhang et al. 2012). However, the plant from Shennongjia Forest District was clearly different from *C. giraldii*. The leaf shape of the former was oblong-ovoid, base attenuate, margin serrate and apex caudate (fig.1 in Zhang et al. 2012), and that of the latter was ovate, base truncate, margin crenate and apex obtuse. So we identified the plant from Shennongjia Forest District as *C. guchengensis* based on its leaf morphology. As the new species is recorded in Shennongjia Forest District and Gucheng County, Xiangyang City, we speculate that *C. guchengensis* is mainly distributed in the Northwestern part of Hubei Province in Central China. *Chelonopsis giraldii* is however distributed in Shaanxi and Gansu provinces of Northwestern China.

Acknowledgements

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Investigation: QF, YC, HL. Resources: ZW, ZD. Supervision: XL. Writing – original draft: YX. Writing – review and editing: CX, JW.

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Data availability

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

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Supplementary material 1

Supplementary data

Authors: Yuhan Xu, Zhengcai Wei, Qiang Fu, Chunlei Xiang, Zhengqun Deng, Houchao Liu, Yuxing Chen, Jun Wen, Xiuqun Liu

Data type: docx

Explanation note: **table S1.** Universal primer sequences for amplification of target DNA regions; **table S2.** Species, voucher information, and GenBank accession numbers of the sequences used in this study. Sequence data generated for this study are indicated with an asterisk (*). Missing data are indicated with an n-dash (–).

Link: https://doi.org/10.3897/phytokeys.253.145834.suppl1