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Research Article

New taxa of *Plagiothecium* (Plagiotheciaceae) from Pakistan

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Abstract

A revision of specimens of *Plagiothecium* deposited in the herbarium of Pakistan Museum of Natural History (PMNH) collected during a Japanese lead project on Cryptogams in the Western Himalaya (Pakistan) shows that the material consists of five taxa. Of the studied samples, the most common taxa were from the *P. denticulatum* complex, including *Plagiothecium denticulatum* var. *obtusifolium*, new to Pakistan. Examination of the rest of the collection showed that it consists of specimens with a unique combination of qualitative and quantitative characteristics of their gametophyte. For example, for small plants, with small asymmetrical, folded leaves, gradually tapering into long, acuminate, not denticulate apex, whose leaf cells are long and narrow, making the cell areolation tight, the name *Plagiothecium filifolium* is proposed. For other plants with large leaves, loosely arranged on the stem, concave, symmetrical to slightly asymmetrical, with denticulate apex and long decurrency composed of rectangular and spherical, inflated cells, the name *Plagiothecium higuchii* is proposed. However, within this material, specimens differ in terms of the length and width of the leaf cells and therefore, within this taxon, two varieties are distinguished: *Plagiothecium higuchii* var. *higuchii* and *Plagiothecium higuchii* var. *brevicellum*.

Key words: Bryophyta, new taxa, Pakistan, Plagiotheciaceae, South Asia, taxonomy



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Introduction

The northern part of Pakistan has a suitable climate and ambience for bryophytes, while the southern part of this country is nearly unexplored because it is far drier, having hot weather and some parts with arid and desert ecosystems. Thereby, due to difficult fieldwork, geographic and climatic conditions, this country is generally still poorly studied bryologically but mainly due to the lack of a resident bryologist. The scattered literature principally covers northern Pakistan and Western Himalaya (Asghar 1957; Froehlich 1963; Karczmarz 1980; Higuchi 1992; Nishimura et al. 1993a, b; Townsend 1993, 1994; Nishimura and Higuchi 2001; Higuchi and Nishimura 2003; Sollman 2008; Gruber and Peer 2012; Khan et al. 2020; Khan et al. 2021; Koponen et al. 2022).

The first checklist of mosses of Pakistan based on previous literature, and herbarium specimens, from Punjab and Khyber Pakhtunkhwa provinces was

provided by Asghar (1957). Later, Higuchi and Nishimura (2003) presented a detailed list, primarily covering the moss flora of Northern part of this country and a few cities of Punjab province, which is currently considered the most valuable and authoritative source regarding the moss flora of this country. There is still a lot to be done to explore the moss flora because new studies have shown that there is a huge potential for new reports (Sollman 2008; Gruber and Peer 2012; Koponen and Higuchi 2020; Koponen et al. 2022).

Currently, the moss flora of Pakistan is represented by 319 species, with the largest family (Pottiaceae) consisting of 79 species (Sollman 2008; Gruber and Peer 2012; Koponen and Higuchi 2020; Koponen et al. 2022). According to investigations of the bryophytes by Higuchi and Nishimura (2003), nearly 45% of the species show a circumboreal distribution, with 32% belonging to an Eurasian element. The Eurasian element is further sub-divided into six components: East Asian taxa (with 30 species), European-Pakistani taxa (13), Himalayan taxa (11), Indian taxa (five), Eurasian taxa (six) and endemic (42; 13%). Additionally, 23 taxa are palaeotropical, nine are East Asiatic-North American, 14 are pantropical and 43 are cosmopolitan in distribution. There is a possibility that some of the endemic species are synonyms (Higuchi and Nishimura 2003; Gruber and Peer 2012).

The earliest mentions of *Plagiothecium* Schimp. in Pakistan go back to the 19th century, when Brotherus (1898a, b) first reported *P. denticulatum* (Hedw.) Schimp. and *P. nemorale* (Mitt.) A.Jaeger. Later, Noguchi (1954) again reported *P. nemorale* from Pakistan. Karczmarz (1980) reported *Plagiothecium cavifolium* (Brid.) Z.Iwats. from the Indian-administrated area of Kashmir. Subsequent studies (Higuchi 1992; Nishimura et al. 1993a, b) brought several new discoveries, thus increasing the number of species described in the genus. Thus, at the turn of the 20th and 21st centuries, four *Plagiothecium* species were recorded in Pakistan: *P. cavifolium*, *P. denticulatum*, *P. latebricola* Schimp. and *P. nemorale* (Higuchi and Nishimura 2003). These species are included in the checklist of *Plagiothecium* in Eurasia (Wolski et al. 2021).

The current initiative is to update the moss flora of Pakistan, by taxonomically revising the dominant families and the addition of new records to the moss flora of Pakistan. This self-funded project was started by Mr. Aamir Shehzad Khan, after his master's work on the Bryopsida in Pakistan (Khan 2019; Khan et al. 2020; Khan et al. 2021; Koponen et al. 2022).

However, comparing these data with data from other countries in this region (e.g., Iran and India [nine species], or China [20 taxa]) we can see that the *Plagiothecium* flora of this country is extremely poor (Wolski et al. 2021). Taking these facts into account, research was undertaken to revise the *Plagiothecium* specimens available from Pakistan.

Materials and methods

The current study is based exclusively on the Pakistani material, on the specimens deposited at the herbarium of Botanical Sciences Division, Pakistan Museum of Natural History (herbarium PMNH). This collection was made by Japanese bryologists during their Cryptogamic Expedition in Pakistan, which was organized through the collaboration of the National Science Museum (National Museum of Nature and Science), Tokyo, Japan (herbarium TNS) and the Pakistan Museum of Natural History (Higuchi 1992; Nishimura et al. 1993b). All the studied herbarium specimens were collected from the Nanga Parbat base camp and Mazeno base camp in 1990. The studied specimens have also been deposited at the herbarium of University of Lodz (LOD), Poland.

In addition, the investigated herbarium collection was supplemented by field research carried out by the second author from August 2018 to July 2020 in the northern areas of Pakistan, including Murree (Punjab Province), Galiyat-region, Swat Valley, Lower Dir (Khyber Pakhtunkhwa Province), and some selected areas of Azad Jammu and Kashmir (Pakistan).

Measurements were made in accordance with the methodology proposed by Wolski (2017, 2019). Both the qualitative and quantitative characteristics of the gametophyte were studied. Measurements were obtained from leaves that were torn off from the central part of the stem. Leaf cells were measured in all leaf zones, randomly selecting 30 cells from each leaf zone. Furthermore, a cross-section of the stem was made to measure the width of epidermal and parenchymal cells. Results were summarized, giving the minimum, maximum and average (M) value for each feature – these data were used to describe individual taxa.

The features of two similar specimens – later named *Plagiothecium higuchii* var. *higuchii* and *Plagiothecium higuchii* var. *brevicellum* – were statistically compared to see whether the differences are significant. However, due to the lack of normality in the distributions of individual variables, a non-parametric U-Mann-Whitney test was performed.

Results and discussion

The conducted revision shows that the entire analyzed material is not very diverse. Most of the tested specimens belong to the *Plagiothecium denticulatum* complex. Thus, *P. cavifolium*, *P. latebricola* and *P. nemorale*, previously reported from this area, were not identified in the samples surveyed. The *P. denticulatum* complex dominated the examined material, within which the largest number of samples was represented by *P. denticulatum* var. *denticulatum*, the remaining specimens belonged to a new taxon, not previously recorded from Pakistan, *P. denticulatum* var. *obtusifolium* (Turner) Moore (*M. Higuchi 20499*).

Taxonomic treatment

Plagiothecium denticulatum (Hedw.) Schimp.

- *Plagiothecium denticulatum* (Hedw.) Schimp., Bryologia Europaea 5: 190, 501, Tab. VIII (1851).
- = *Hypnum denticulatum* Hedw., Species Muscorum Frondosorum 237 (1801). **Lectotype** (fide Ireland 1969): "St. Cr. 4. p. t. 30", leg. *Starke*, Germany?, G (*n.v.*).

Description. Plants green to yellowish green, with metallic luster; stem in cross section rounded, $200-250 \mu m$ in diameter; leaves not folded, julaceous, elliptical-ovate, asymmetrical; leaves $2.2-3.0 \times 1.0-1.3$ (M 2.6×1.1) mm, shortly tapering to acute, denticulate apex; costae two, extending usually to ½ of the leaf length, ranging 440-810 (M 625) μm ; cell areolation loose; length and width of cells very variable, but dependent on location: $85-140 \times 15-28$ (M 113×22) μm at the apex; $120-210 \times 15-30$ (M 165×23) μm at midleaf; $116-205 \times 18-37$



Figure 1. The most important taxonomic features of *Plagiothecium denticulatum* **A** shape of apex **B**, **C** dimension of cells (**B** from the middle **C** basal part of the leaf) **D** decurrent cells **E** leaf shape (from *M. Higuchi 20462*).

(M 160 × 28) µm toward insertion; broad decurrency 400–700 (M 555) µm; alar cells rounded, clearly inflated, 45–90 × 20–50 (M 68 × 35) µm; sporophytes not found in this material (Fig. 1). In these studies, *Plagiothecium denticulatum* has been recorded on soil and boulders.

Plagiothecium denticulatum var. obtusifolium (Turner) Moore

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).
- Plagiothecium obtusifolium (Turner) J.J.Amann, Mémoire de la Société Vaudoise des Sciences Naturelles 3: 61 (1928). Holotype: fig. 2, tabela 12 "T. 12, f. 2" (Turner 1804: 237) (fig. 3). Epitype (selected by Wolski et al. 2022) [Ireland], in summo montis Bulbein jugo, ab oculatissimo D. Brown lectam, benigne communicavit D. Templeton, BM000890810! (fig. 10).
- Plagiothecium sandbergii Renauld & Cardot, Contributions from the United States National Herbarium, 3: 274 (1895), Lectotype (selected by Wolski et al. 2022): U.S.A., Idaho, Kootenai County, Hope, J.H. Sandberg, D.T. Macdougal, A.A. Heller 1174, August 1892 (PC0132604!); isolectotypes: NY507114!, available online; US70396!, available online; FH220148. Additional original material from locus classicus (not signed "No. 1174"): 456 NY507115!, available online. Additional Sandberg material, potentially from locus 457 classicus: PC0132605! Additional Sandberg material: FH220147.
- Plagiothecium denticulatum var. auritum Kern, Jahresbericht der Schlesischen Gesellschaft für Vaterländische Cultur 91(Abt. 2b): 97 (1914).
 Lectotype (selected by Wolski et al. 2022): [Italy] South Tirol, Ortler, Martelltal, in Felshöhlungen oberhalb der Cevedalehütte, F. Kern s.n., 2350 m, 30 July 1913, herb. I. Thériot (PC0132639!).

Description. Plants light green, with metallic luster; stem in cross section rounded, $150-200 \mu m$ in diameter; the central strand well developed, epidermal cells $12-20 \times 15-31 (M \ 16 \times 23) \mu m$, the parenchyma thin-walled, $25-43 \times 21-39 (M \ 34 \times 30) \mu m$; leaves very concave, not folded, julaceous, elliptical-ovate, very slightly asymmetrical, $1.6-1.7 \times 0.8-0.95 (M \ 1.65 \times 0.87) mm$; the apex obtusely-apiculate; costae two, extending usually up to 1/3 or $\frac{1}{2}$ of the leaf length, ranging $250-530 (M \ 390) \mu m$; cell areolation loose; length and width of cells very variable, but dependent on location: $85-140 \times 15-18 (M \ 113 \times 17) \mu m$ at the apex; $95-170 \times 12-18 (M \ 133 \times 15) \mu m$ at midleaf; $98-200 \times 15-25 (M \ 150 \times 20) \mu m$ toward insertion; broad decurrency $260-400 (M \ 330) \mu m$; alar cells rounded-rectangular, $51-98 \times 21-31 (M \ 75 \times 26) \mu m$; sporophytes not found in this material (Fig. 2). In these studies, *Plagiothecium denticulatum* var. *obtusifolium (M. Higuchi 20499*) has been recorded on soil.

The next two samples (*M. Higuchi 20460* and *M. Higuchi 20479*) were characterized by a unique combination of qualitative and quantitative features of their gametophytes. They did not match any of the taxa of the genus currently known in the Northern and Southern Hemispheres.

The specimen collected by M. Higuchi (*M. Higuchi 20460*) represents two morphotypes that are microscopically very different from each other. This material differs in the length and width of the leaf, the shape of the apex, the length and width of the cells of the top, middle and basal part of the leaf – which are one of the most important taxonomic features for the whole genus. In addition, the result of the U Mann-Whitney test showed that the length and width of the cells of the leaf of these morphotypes differ statistically significantly (p<0.001) from each other. Thus, it was proposed to recognise two varieties – *Plagiothecium higuchii* var. *higuchii* and *P. higuchii* var. *brevicellum*.

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Figure 2. The most important taxonomic features of *Plagiothecium denticulatum* var. *obtusifolium* **A** leaf shape **B**–**D** dimension of cells (**B** from the apex **C** the middle **D** basal part of the leaf) **E** decurrent cells (from *M*. *Higuchi* 20499).

Plagiothecium higuchii G.J.Wolski, sp. nov.

Type. Pakistan, Mt. Nanga Parbat, Mazeno Base Camp, 4000 m alt, on soil, 15 September 1990, *M. Higuchi 20460*, *holotype* L0D15016, *isotype* PMNH.

Description. Plants green-yellow to golden-gold, without metallic luster; stems complanate-foliate, 3.0-4.0 cm long, in cross-section rounded, with a diameter of 290-360 (M 325) µm, the central strand well developed, epidermal cells $11-22 \times 13-32$ (M 16×22) µm, the parenchyma thin-walled, $26-50 \times 23-45$ (M 38×34) µm; leaves quite loosely arranged on the stem, concave, symmetrical to asymmetrical, ovate, those leaves from the middle of the stem $3.4-4.3 \times 1.2-1.9$ (M 3.8×1.5) mm; the apex acuminate and denticulate; cos-



Figure 3. The most important taxonomic features of *Plagiothecium higuchii* var. *higuchii* A apex serration B, C dimension of cells (B from the middle C basal part of the leaf) D decurrent cells E, F leaf shape (from *M. Higuchi 20460*).

tae two, thick and strong, usually to 1/2 of the leaf length, reaching 0.5–1.2 mm; laminal cells symmetrical, in unregulated transverse rows, the length and width very variable, but dependent on location: $107-250 \times 16-24$ (M 178 × 20) µm at apex, $139-266 \times 21-33$ (M 203 × 27) µm at mid-leaf and $139-266 \times 21-33$ (M 203 × 27) µm towards insertion, cell areolation very loose; decurrency long, 300-500 (M 400) µm, composed of 4–6 rows of rectangular and spherically inflated cells, $48-144 \times 26-70$ (M 96 × 48) µm. Sporophytes so far unknown (Fig. 3). In these studies, *Plagiothecium higuchii* var. *higuchii* (*M. Higuchi 20460*) has been recorded on soil.

Etymology. The present species is named in honor of Professor Masanobu Higuchi, who participated in the Studies on Cryptogams in the Western Himalayas in Pakistan project, and who collected the specimen (*Higuchi 20460*) chosen here as the holotype of *Plagiothecium higuchii*.

Plagiothecium higuchii var. brevicellum G.J.Wolski, var. nov.

Type. Pakistan, Mt. Nanga Parbat, Mazeno Base Camp, 4000 m alt, on soil, 15 September 1990, *M. Higuchi 20460pp*, *holotype* LOD 15017, *isotype* PMNH.

Description. Plants green-yellow to golden-gold, without metallic luster. Stems complanate-foliate, 3.0-4.0 cm long, in cross-section rounded, with a diameter of $310-388 \mu$ m, epidermal cells $10-16 \times 21-33$ (M 13×27) μ m, the parenchyma thin-walled, $14-58 \times 18-51$ (M 34×35) μ m; leaves quite loose-ly arranged on the stem, concave, symmetrical to gently asymmetrical, ovate, those leaves from the middle of the stem $2.9-3.2 \times 1.0-1.2$ (M 3.1×1.1) mm; the apex acute and apiculate, denticulate; costae two, thick and strong, usually to 1/2 of the leaf length, reaching 0.5-1.5 (M 1.0) mm; laminal cells symmetric



Figure 4. The most important taxonomic features of *Plagiothecium higuchii* var. *brevicellum* **A** apex serration **B**, **C** dimension of cells (**B** from the middle **C** basal part of the leaf) **D** decurrent cells **E**, **F** leaf shape (from *M*. *Higuchi* 20460).

cal to slightly asymmetrical, the length and width very variable, but dependent on location: $70-170 \times 10-19$ (M 120×15) µm at apex, $100-200 \times 14-26$ (M 150×20) µm at mid-leaf and $100-200 \times 19-36$ (M 150×28) µm towards insertion, cell areolation loose; decurrency long, 390-650 (M 520) µm, composed of 4-6 rows of rectangular and spherically inflated cells, $36-116 \times 18-67$ (M $76 \times$ 43) µm. Sporophytes unknown so far (Fig. 4). In these studies *Plagiothecium higuchii* var. *brevicellum* (*M. Higuchi* 20460) has been recorded on soil.

Etymology. The variety name *brevicellum* refers to breve- [Lat.] short; -cellus [Lat.] cells and indicates the most distinctive features between varieties – leaves with short cells.

Plagiothecium filifolium G.J.Wolski, sp. nov.

Type. Pakistan, Mt. Nanga Parbat, Mazeno Base Camp, 4000 m alt, on boulder, 15 September 1990, *M. Higuchi 20479*, *holotype* LOD 15018, *isotype* PMNH.

Description. Plants green-yellow, without metallic luster; stems complanate-foliate, 1.0-1.5 cm long; cross-section rounded, with a diameter of 200–300 µm, the central strand well developed, epidermal cells $9-13 \times 11-15$ (M 11×13) µm, the parenchyma thin-walled, $15-21 \times 16-28$ (M 18×22) µm; leaves folded, most strongly in the upper part of leaves, concave, asymmetrical, those leaves from the middle of the stem $1.6-2.2 \times 0.5-0.8$ (M 1.9×0.66) mm; leaves gradually tapering to long, acuminate, not denticulate apex; costae two, very thin and delicate, extending up to 1/2 of the leaf length, reaching 140-423 (M 282) µm; laminal cells rather symmetrical, the length and width very variable,



Figure 5. The most important taxonomic features of *Plagiothecium filifolium* **A**, **B** leaf shape **C** leaf apex **D** folding of the apex **E**, **F** dimension of cells (**E** from the middle **F** basal part of the leaf) (from *M*. *Higuchi* 20479).

but dependent on location: $97-160 \times 7-10$ (M 127×8) µm at apex, $105-180 \times 7-9$ (M 150×8) µm at mid-leaf and $70-165 \times 8-11$ (M 118×9) µm towards insertion, cell areolation tight; decurrency short, 220-530 µm, composed of 3 rows of gently inflated, rectangular cells, $47-147 \times 12-21$ (M 97×16) µm. Sporophytes unknown so far (Fig. 5). In these studies, *Plagiothecium filifolium* (*M. Higuchi 20479*) has been recorded on boulders.

Etymology. Filum- [Lat.] thread; -folium [Lat.] leaf. The present species is named in reference to the most distinctive feature – its threadlike leaf apex.

Discussion

Previously, only four species had been reported from Pakistan: *Plagiothecium cavifolium*, *P. denticulatum*, *P. latebricola* and *P. nemorale* (Brotherus 1898a, b; Noguchi 1954; Karczmarz 1980; Higuchi 1992; Nishimura et al. 1993b; Higuchi and Nishimura 2003). Noguchi (1954) also reported *P. sylvaticum* (Brid.) Bruch and Schimp., but this is now considered to be a synonym of *P. nemorale* (Wolski et al. 2022). The current research revealed five taxa belonging to this genus, including three new to science and one new to Pakistan. Thus, the conducted research added another four *Plagiothecium* taxa to the known flora of Pakistan.

Compared to neighboring countries, the four species previously reported from Pakistan (*Plagiothecium cavifolium*, *P. denticulatum*, *P. latebricola* and *P. nemorale*) were considered a very low number (Wolski et al. 2021). Of course, the higher numbers of species of *Plagiothecium* recorded from China (20 taxa) (e.g. He and Redfearn 1995; Redfearn et al. 1996; Wynns 2015; Zuo et al. 2011; Wolski, Nowicka-Krawczyk 2020) or India (nine taxa) (e.g. Gangulee 1980; Dandotiya et al. 2011; Asthan and Sahu 2015; Wolski and Nowicka-Krawczyk 2020) result from the larger size of these countries, greater diversity of habitats, but also from a longer history of bryological research. On the other hand, ten taxa have been reported from Iran (Wolski et al. 2021), which has a similar climate and habitats to Pakistan.

As indicated by Wolski et al. (2021) in the Northern Hemisphere, the *Plagiothecium denticulatum* is the most frequently recorded. This was also the case in the above studies. Most of the specimens studied represented this species. It is also not surprising to find *Plagiothecium denticulatum* var. *obtusifolium*, which is new to Pakistan, in the examined material, not only because it is recorded in many neighboring countries, including China or Iran (Wolski et al. 2021), but also because it is a montane taxon (Wolski et al. 2022) and all specimens studied were collected between 3.430 m to 4.000 m.

This research showed that some of the specimens have unique combinations of qualitative and quantitative gametophytic features. A specimen with complanate-foliate stems; folded, concave, asymmetrical leaves gradually tapering to long, acuminate, not denticulate apex, with a decurrency composed of gently inflated, rectangular cells has been named *Plagiothecium filifolium*. There is no species in the Northern Hemisphere with this set of features. The most similar to this taxon is *P. latebricola*, which, however, is characterized by a symmetrical leaf, narrow decurrency with non-inflated cells (e.g. Nyholm 1965; Lewinsky 1974; Wolski et al. 2021). *Plagiothecium filifolium* is also different from *Plagiothecium subulatum*, recently transferred to *Vesicularia* (Müll. Hal.) Müll. Hal. (Müller and Wynns 2020) and now known as *Vesicularia subulata* (Broth.) J.T. Wynns & Frank Müll. The aforementioned can be characterized as medium-sized plants, complanate or fluffy, leaves weakly overlapping, flat, short, broad, ovate, asymmetric, with erect margins and gemmae produced in dense clusters at leaf tips (Wolski et al. 2021).

Specimens with leaves quite loosely arranged on the stem, concave, symmetrical to asymmetrical, ovate, with a denticulate apex, loose cell areolation and wide decurrency, composed of rectangular and spherically inflated cells have been named *Plagiothecium higuchii*. These specimens also represent a unique set of features hitherto unknown in the Northern or Southern Hemispheres (Ireland 1986, 1992, 2001; Buck and Ireland 1989; Buck 1998; Wolski et al. 2021). Decurrencies, composed of spherically inflated cells, asymmetric, concave leaf or the dimensions of the cells distinguish *P. higuchii* from the common Northern Hemisphere *P. nemorale* (Wolski 2020; Wolski and Nowicka-Krawczyk 2020). On the other hand, this feature indicates a similarity with representatives of *Plagiothecium* section *Plagiothecium*, because taxa from this section usually have a wide decurrency with a group of cells more or less clearly inflated (Wynns et al. 2018).

The taxa from the Northern Hemisphere most similar to *P. higuchii* would be: *P. denticulatum*, *P. platyphyllum* Mönk. or *P. ruthei* Limpr., however, they differ in the arrangement of the leaves on the stem, in the shape and dimensions of the leaf, and the dimensions of the leaf cells, which shows the striking distinctiveness of the examined material against the previously described taxa (Ireland 1986, 1992; Buck 1998; Wolski 2020; Wolski and Nowicka-Krawczyk 2020; Wolski et al. 2021).

As studies of *Plagiothecium* indicate (e.g. Ireland 1969; Iwatsuki 1970; Lewinsky 1974; Wynns et al. 2018; Wolski and Nowicka-Krawczyk 2020) the dimensions of the leaf cells are one of the most important taxonomic features of these plants. The conducted research, confirmed by statistical analyses, shows that the material of *P. higuchii* represents two different morphotypes, therefore two varieties were proposed within this species, *Plagiothecium higuchii* var. *higuchii*, with long leaf cells, and *P. higuchii* var. *brevicellum*, with short leaf cells.

The present study describes three taxa, *Plagiothecium higuchii* var. *higuchii*, *P. higuchii* var. *brevicellum*, and *P. filifolium*, as new to science and reports another taxon, *P. denticulatum* var. *obtusifolium*, as new to Pakistan. With the four species reported earlier this brings the number of recognized species and infraspecific taxa of *Plagiothecium* in Pakistan to eight.

On the basis of herbarium specimens and literature analysis, it was possible to determine the range of the described species of the genus in Pakistan:

- *Plagiothecium cavifolium* has been recorded so far from: Khyber Pakhtunkhwa, Kaghan Valley, Lake Saif Ul Maluk, 3150 m (*Higuchi 19888, Higuchi 19891*, Higuchi 1992) (Fig. 6).
- Plagiothecium denticulatum has been recorded so far from: Khyber Pakhtunkhwa, Chitral, Ziarat, 7400 m and Gilgit-Baltistan, Minimarg, Burzil Pass, 10 000 to 11 000 m (Brotherus 1898a, b); Gilgit-Baltistan, Nanga Parbat Base camp 3430 m, and Mazeno Base camp, 4000 m (*Higuchi 20462*, 20475, Higuchi 1992); Khyber Pakhtunkhwa, Mansehra, Sikyan near Nadi, 2020 m (Nishimura et al. 1993b) and Nanga Parbat Base Camp and Nanga Parbat Mazeno Base Camp, at 3430–4000 m (*M. Higuchi 20462*; *M. Higuchi 20464*; *M. Higuchi 20479*; *M. Higuchi 20510*) (Fig. 6).



Figure 6. A distribution map showing all the currently known localities of Plagiothecium species in Pakistan.

- *Plagiothecium denticulatum* var. *obtusifolium* has been recorded so far from: Gilgit-Baltistan, Nanga Parbat, Base Camp, at 3430 m (*M. Higuchi 20499*) (Fig. 6).
- *Plagiothecium filifolium* has been recorded so far from: Gilgit-Baltistan, Nanga Parbat, Mazeno Base Camp, at 4000 m (*M. Higuchi 20479*) (Fig. 6).
- Plagiothecium higuchii var. higuchii has been recorded so far from: Gilgit-Baltistan, Nanga Parbat, Mazeno Base Camp, at 4000 m (*M. Higuchi* 20460) (Fig. 6).
- Plagiothecium higuchii var. brevicellum has been recorded so far from: Gilgit-Baltistan, Nanga Parbat, Mazeno Base Camp, at 4000 m (M. Higuchi 20460) (Fig. 6).
- Plagiothecium latebricola has been recorded so far from: Khyber Pakhtunkhwa, Mansehra, Shogran – Sali Hut, 2710 m (Nishimura et al. 1993b) (Fig. 6).
- Plagiothecium nemorale has been recorded so far from: Gilgit-Baltistan, Minimarg, Burzil Pass, 9000 to 10 000 m and 10 000 to 11 000 m (Brotherus 1898a); Azad Jammu and Kashmir, Shekh Bela, between Shardi and Kel, alt. 2000–2100 m (Noguchi 1954) (as *P. sylvaticum*); Khyber Pakhtunkhwa, Mansehra, Sharan Forest, 2400 m (Nishimura et al. 1993b) (Fig. 6).

A key to the species of the genus Plagiothecium from Pakistan

- 1 Angular cells of decurrency rounded, inflated, forming distinct auricles...2
- Angular cells of decurrency rectangular, not inflated, not forming distinct
- auricles......5
- 2 Leaves asymmetrical; apex acute and denticulate P. denticulatum
- Leaves symmetrical or slightly asymmetric; apex denticulate or not.......3

- 3 Plants with acuminate, denticulate apex......4
- Plants with obtuse, not denticulate apex..... P. denticulatum var. obtusifolium
- 4 Cells from the middle part of the leaves long and wide $(139-266 \times 21-$
- 33)P. higuchii var. higuchii

- 6 Cells from the middle part of the leaves < than 10 µm wide..... *P. latebricola*
- Cells from the middle part of the leaves > than 10 µm wide......7
- 7 Stem julaceus; leaves strongly concave; apex not denticulateP. cavifolium

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: GJW. Investigation: GJW, ASK. Project administration: GJW. Supervision: GJW. Visualization: ASK, GJW. Writing – original draft: GJW, BP, ASK. Writing – review and editing: ASK, BP, GJW.

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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

Raw data of new taxa from Pakistan

Authors: Grzegorz J. Wolski, Aamir Shehzad Khan, Beata Paszko Data type: xlsx

- Explanation note: The raw data contains two sheets, with morphological data and statistical test results.
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Research Article

Gelidocalamus albozonatus (Poaceae, Bambusoideae), a new species from the southeast of Chongqing, China, and analysis of the morphological diversity in the core group of *Gelidocalamus*

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Abstract

Gelidocalamus albozonatus W. G. Zhang, S. R. Yi & Y. L. Li, a new species of *Gelidocalamus*, collected from Pengshui County of Chongqing City in China, was described and illustrated herein. In this study, key morphological characters were compared between the new species and other eight "gelido-" members of *Gelidocalamus*. By using scanning electron microscopy (SEM), its leaf epidermal characters were observed in comparison with those of another three *Gelidocalamus* representatives. Our results show that the new taxon has the typical characteristics of the genus *Gelidocalamus*, both macromorphologically and micromorphologically. Moreover, it was most similar to *G. tessellatus*, but differed by a ring of white tomenta below per node, culm sheath base with densely purple verrucous setae and foliage leaf blades mesophyll.

Key words: Arundinarieae, Bambusoideae, leaf epidermis, Poaceae, SEM

Introduction

Gelidocalamus T. H. Wen, is a genus of the temperate woody bamboos (Poaceae, Bambusoideae, Arundinarieae) with only two species (i.e., *G. stellatus* T. H. Wenand *G. tessellatus* T. H. Wen) (Wen 1982). Its typical characteristics include leptomorph rhizomes, each node with many branches (up to 20), terminal branch usually with solitary foliage leaf, semelauctant inflorescence and three stamens. Phenologically, new shoots usually appear in autumn-winter (Wen 1982; Li et al. 2006). However, as the taxon number increased, e.g., nine species in Keng and Wang (1996) and 13 species in Yi et al. (2008), the genus has become more diverse. Particularly, some "spring-shoot" species, e.g., *G. rutilans* T.H Wen, *G. subsolidus* W. T. Lin & Z. J. Feng, *G. solidus* C. D. Chu & C. S. Chao, and *G. longiinternodus* W. T. Wen & S. C. Chen (Wang et al. 2023), expanded the boundary of *Gelidocalamus*.

Recently, Guo et al. (2021) provided a robust phylogenetic tree based on double digest restriction-site associated DNA (ddRAD) sequences of the tribe



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Arundinarieae in consistence with the analysis of morphological data, revealed that six "gelido-" members (i.e. core members of shooting in autumn and winter) of Gelidocalamus were clustered into a monophyletic clade, while other "springshoot" members were scattered and grouped with other genera. The "gelido-" taxa have identical micromorphological characters (i.e., prominent stomata apparatus surrounded by 8-12 short papillae and a dense waxy covering) (Wang et al. 2023), including G. stellatus T. H. Wen, G. tessellatus T. H. Wen & C. C. Chang, G. annulatus T. H. Wen, G. latifolius Q. H. Dai & T. Chen, G. multifolius B. M. Yang, and G. monophyllus (Yi et B. M. Yang) B. M. Yang, as well as three recently reported species, i.e. G. xunwuensis W. G. Zhang & G. Y. Yang (Zhang et al. 2017), G. fengkaiensis N. H. Xia & Z. Y. Cai (Cai et al. 2021), and G. zixingensis W. G. Zhang, G. Y. Yang & C. K. Wang (Wang et al. 2023). Moreover, except for G. monophyllus (a taxon of the high-elevation distribution, ca. 1250 m), all above taxa were distributed below 1000 m (Li et al. 2016), and have similarly micromorphological characteristics of foliage leaf epidermis, i.e., prominent stomata apparatuses covered with dense wax, and surrounded by 8 to 12 short papillae (Wu et al. 2014; Long et al. 2015; Liu et al. 2017; Nie et al. 2018; Wang et al. 2023).

During a botanical expedition in the southwest of China in 2019, a distinctive "Gelidocalamus-like" collection with many branches per node and solitary foliage leaf on each ultimate branch was found from the Wu-Ling Mountain of Chongqing. Then, a complete morphological characterization, including scanning electron microscope (SEM) images of the abaxial leaf epidermis, had been done, and its key features have been also compared with these of other allied species of *Gelidocalamus*. By all the evidence obtained, we believe that this collection is a new species, herein formally described and illustrated.

Materials and methods

In the study, eight "gelido-" taxa of *Gelidocalamus* were selected (see Table 1 in detail), and morphologically compared with each other. Key morphological characters, e.g., bamboo shoot, culm and culm leaf, branch and foliage leaf, were surveyed and photographed by DSLR camera (Canon, EOS 60D) with microscope lens (Canon, EF 60mm f/2.8 USM). By using Origin 2021 (OriginLab 2021), foliage leaf blade size has been measured and analyzed based on 30 randomly selected blades of each species, and foliage leaf blade shape of each representative has been drawn based on herbarium specimens. SEM: After washing by using ultrasonic cleaner BRANSON 2800, the middle portion (ca. 5mm × 5mm) of foliage leaf blades was dried at room temperature, mounted on stubs, then sputter-coated with gold powder (3 nm), and observed by using Hitachi S-4800 or Nova NanoSEM 450. Terminologies of the epidermis appendages follows Ellis (1979), Zhang et al. (2014), and Leandro et al. (2019). All voucher specimens were deposited at the herbarium of the College of Forestry, Jiangxi Agricultural University, China (JXAU).

Results and discussion

Eight "gelido-" species (Table 1), including *G. albozonatus*, were observed and compared in detail. We found that the genus has quite rich diversity in the morphology of culm node, culm internode, culm leaf sheath, and the number of

branches (Fig. 3). Among them, the ring of white tomenta below the culm nodes and the number of branches of 5–10 in *G. albozonatus* can be distinguished from the other seven taxa. It was also found that *G. albozonatus* resembles *G. tessellatus* most by the number of branches, culm sheath purple patches, and foliage leaf blade size. Thus, it was further found that the new taxa could be distinguished from the latter by glabrous (vs. sparsely setose) internode, densely purple hairs of culm leaf sheath base (vs. smooth), 2–4 pairs of oral setae (vs. hairless), and hairless (vs. densely pubescent) midvein base of foliage leaf (Fig. 4). In a word, based on morphological traits, the above species were easily distinguished (see "Key to nine "gelido-" taxa of the genus *Gelidocalamus*"; Wang et al. 2023).

Interestingly, *Gelidocalamus* showed a rich diversity in terms of foliage leaf blade size and shape (Fig. 5). Based on foliage leaf blade size, eight taxa of the genus can be categorized into three types (Ellis et al. 2009), i.e. mesophyll (including *G. albozonatus*, *G. latifolius* and *G. multifolius*), notophyll (including *G. annulatus*, *G. stellatus*, *G. tessellatus* and *G. xunwuensis*), and microphyll (only *G. monophyllus*). Furthermore, based on foliage leaf blade shape, these taxa also can be divided into two types, i.e. lanceolate (including *G. annulatus*, *G. stellatus* and *G. xunwuensis*) and elliptic-lanceolate (including *G. albozonatus*, *G. latifolius*, *G. multifolius* and *G. tessellatus*). Thus, it was obvious that foliage leaf blade of *G. albozonatus* was the largest, belonging to the type Mesophyll usually between 77 cm² and 153 cm².

Besides, to reveal the properties of *G. albozonatus* in terms of micromorphological characteristics, its abaxial leaf epidermis was observed by SEM together with three other species (Fig. 6), and referring to previous research (Wu et al. 2014; Zhang et al. 2014; Long et al. 2015; Liu et al. 2017; Zhang et al. 2017; Nie et al. 2018; Wang et al. 2023). Leaf epidermis characters of *G. albozonatus* was identical to that of *G. tessellatus* (Fig. 6B) and *G. annulatus* (Fig. 6C): short papillae scattering on the leaf vein and stomatal zone; stomatal apparatus (usually in 5 to 6 rows between the veins) exposed, surrounded by 8–10 short papillae, but not covered with wax; two types of trichomes (i.e., microhairs and prickles) on the abaxial leaf epidermis, but both sparsely distributed on the abaxial leaf epidermis; silica bodies saddle-shaped, distributed on the veins (Table 2).

Species	Voucher information
G. albozonatus	Pengshui County, Chongqing, China, 108°13'42"N, 29°18'55"E, alt 268 m, S.R. Yi et al. CQPS01 (JXAU!)
G. annulatus	Chishui City, Guizhou, China, 105°95′80″N, 28°47′61″E, alt 809 m, <i>W.G. Zhang et al. 20151122001</i> (JXAU!)
G. latifolius	Rongshui County, Guangxi, China, 109°10'44"N, 25°13'52"E, alt 229 m, <i>W.J. Li & Y.G. Liu RS203</i> (JXAU!)
G. monophyllus	Ningyuan County, Hunan, China, 111°98'80"N, 25°23'77"E, alt 1200 m, <i>W.G. Zhang et al. 20161023</i> (JXAU!)
G. multifolius	Ningyuan County, Hunan, China, 111°57'44"N, 25°19'40"E, alt 346 m, W.G. Zhang et al. JYS026(JXAU!)
G. stellatus	Jinggangshan City, Jiangxi, China, 114°11'32"N, 26°31'48"E, alt 468 m, W.G. Zhang et al. JGS003(JXAU!)
G. tessellatus	Libo City, Guizhou, China, 108°07'04"N, 25°20'58"E, alt 526 m, <i>W.G. Zhang et al. SJJ033</i> (JXAU!)
G. xunwuensis	Xunwu County, Jiangxi , China, 115°28'02"N, 24°54'01"E, alt 526 m, W.G. Zhang et al. 1107(JXAU!)

Table 1. Voucher information of eight species in the study.

Taxon	Main features	Plates
G. albozonatus	prickles, sparse; 8–10 short papillae without dense wax, around the stomata; stomata visible, usually in 5 to 6 rows between the veins	Fig. 2A
G. tessellatus	prickles, sparse; 8–10 short papillae with dense wax, around the stomata; stomata visible, usually in 3 rows between the veins	Fig. 2B
G. annulatus	prickles, dense; 8–10 short papillae with dense wax, around the stomata; stomata visible, usually in 3 rows between the veins	Fig. 2C
G. monophyllus	prickles, dense; short papillae with dense wax; stomata invisible, usually in 3 rows between the veins, totally covered by papillae	Fig. 2D

Table 2. Micromorphology of the abaxial leaf epidermis examined in the present study.

Currently, *G. albozonatus* is the northernmost distributed species of *Gelido-calamus*, so its discovery has updated the northward distribution line of the genus *Gelidocalamus*.

Taxonomic treatment

Gelidocalamus albozonatus W.G.Zhang, S.R.Yi & Y.L.Li, sp. nov.

urn:lsid:ipni.org:names:77331500-1 Figs 1, 2

Type. CHINA, Chongqing, Pengshui County, Luduhu Village, under the forest, 29°18'55.38"N, 108°13'42.14"E, elev. ca. 268 m, 6 Mar. 2019, *S.R. Yi et al. CQPS01* (holotype: JXAU!).

Diagnosis. *G. albozonatus* is similar to *G. tessellatus*, but differed by having a ring of white (vs. brownish) tomenta below each culm node, culm sheath base densely purple setulose (vs. yellowish pubescence) and foliage leaf blades mesophyll (vs. notophyll).

Description. Rhizomes leptomorph. Culms up to 5.5 m tall, ca. 6–15 mm in diam., erect, apically slightly nodding; internodes glabrous, 11–54 cm long, wall 1.5–3 mm thick; a ring of white tomenta below each node. Branching intravaginal, arising from the 6th node above ground, ca. 5–10 branches per node; branches equal or subequal, ca. 25–55 cm long, 2–4 mm in diam. Culm leaf sheaths tardily deciduous, 15–25 cm long, abaxially sparsely wine-red or purple hispidulous when young, purple patches densely distributed between transverse veins, sheath base densely purple setulose, ca. 1–3 mm long, margins with wine-red cilia, ca. 1–2 mm long; auricles absent or tiny; oral setae erect or slightly curved, 2–4 pairs, ca. 3–8 mm long; ligule less than 1 mm or absent; blade deciduous, linear or linear-lanceolate, 2–4.5 × 1.7–2.6 mm, erect or recurved, apex acuminate, base constricted with densely short setae, 1/3–1/2 as wide as sheath apex. Ultimate branches usually with one foliage leaf; branch sheath fragile; ligule absent or weak; auricles absent or tiny; blade broadly lanceolate to narrowly oblong, usually 19–42 × 4–7 cm, secondary veins 7–9 pairs, basally cuneate and asymmetrical, abaxially hairless, margins serrulate.

Distribution and habitat. *G. albozonatus* occurs under evergreen broad-leaved forests, along the ravine to the east of Luduhu Village, at elev. ca. 200–600 m. It grows together with *Cupressus funebris* Endl. (Cupressaceae), *Bambusa emeiensis* L. C. Chia & H. L. Fung (Poaceae), and *Nymphanthus calcicola* S. R. Yi & Gang Yao, 2022 (Phyllanthaceae), and so on. So far, *G. albozonatus* is only known from one small population (lessthan 1000 m²) in the Pengshui County of Chongqing, China.

Chinese vernacular name. péng-shuǐ-duǎn-zhī-zhú (彭水短枝竹).



Figure 1. *Gelidocalamus albozonatus* sp. nov. A habitat B individual C rhizome D branches E culm node of new shoots F transection of culm and pith-cavity G dry new shoot H–L culms and culm leaves M foliage leaf blade. Scale bars: 1 m (A); 10 cm (B); 1 cm (C–E, G–L); 5 mm (F); 5 cm (M).



Figure 2. Illustration of *Gelidocalamus albozonatus* A culm and culm sheath B new shoot C details of culm sheath D culm leaf E oral setae details of culm leaf F–G branches and foliage leaves H details of foliage leaf sheath. Drawn by Rong Guo.



Figure 3. Comparison of key morphological characters between *G. albozonatus* and other seven species. Scale bars: as shown in the figure.



Figure 4. Comparison of morphological characters between *G. albozonatus* (A–F) and *G. tessellatus* (G–L) A, G branches B, H clum sheath base C, I internode D, J oral setae of culm leaf E, K margin of clum sheath F, L midvein. Scale bars: 1 cm (A–L).



Figure 5. Comparison of foliage leaf blade size and outline between G. albozonatus and other seven species.



Figure 6. SEM images of the abaxial leaf epidermis **A** *G. albozonatus* (Pengshui, Chongqing, China) **B** *G. tessellatus* (Libo, Guizhou, China) **C** *G. annulatus* (Chishui, Guizhou, China) **D** *G. monophyllus* (Ningyuan, Hunan, China).

Phenology. New shoots Sep-Nov, Inflorescence unknown.

Etymology. The specific epithet indicates the ring of white tomenta below the node.

Leaf micromorphology. Stomatal apparatuses are embossed outwards and smooth without appendages, ca. 27 $(25-30) \times 13 (11-14) \mu m$. The short papillaes are scattered on the leaf vein and stomatal zone. The exposed stomatal apparatus is surrounded by 8–10 short papillae, but not covered with wax. There are two types of trichomes (i.e., microhairs and prickles) on the abaxial leaf epidermis, but both are sparsely distributed on the abaxial leaf epidermis. The saddle-shaped silica bodies are clearly distributed on the veins. Microhairs are composed of two cells with the apical cell withered, and only occur on the intercostal regions of the abaxial leaf epidermis.

Conservation status. Based on the field investigations in Pengshui County and adjacent regions (e.g., Shizhu, Qianjiang and Youyang). As the type locality is a mountain with steep terrain, only a population is found on the hillside on both sides of a valley. Therefore, before carrying out further investigations, this species should be assessed as "Data Deficient" (DD), according to the IUCN standards (IUCN 2022).

Key to nine "gelido-" taxa of the genus Gelidocalamus

1	Culm internodes glabrous2
-	Culm internodes hairy5
2	Culm leaf sheaths glabrous
_	Culm leaf sheaths pubescent with sparse setae Gelidocalamus zixingensis
3	Culm sheaths glabrous; oral setae of culm leaves 1-2 pairs, weak; branch
	sheath margins hairless
_	Culm sheaths covered with setae; oral setae of culm leaves 3-5 pairs;
	branch sheath margins with ciliate4
4	Culm sheaths base covered with densely purple verrucous setulose
	Gelidocalamus albozonatus
-	Culm sheaths base glabrous Gelidocalamus multifolius
5	Culm sheaths with densely brown short setae5
-	Culm sheaths with white erect small setae7
6	Culms up to 5m tall, greater than 1cm in diam Gelidocalamus tessellatus
-	Culms less than 4m, less than 1cm in diam6
7	Culm sheaths with white villus, margins with ciliate
	Gelidocalamus monophyllus
-	Culm sheaths hairless, margins hairless
8	Culm sheath margins densely ciliate, oral setae 1 pair; leaves 1(or 2) per
	ultimate branch, lateral veins 6–9 pairs Gelidocalamus latifolius
-	Culm sheath margins hairless, oral setae 2-3 pairs; leaves 1-3 per ultimate
	branch, lateral veins 4–6 pairsGelidocalamus annulatus

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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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PhytoKeys

Research Article

Melanoseris kangdingensis (Lactucinae, Cichorieae, Asteraceae), a new species reported from western Sichuan, China

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Abstract

Melanoseris kangdingensis, a new species native to western Sichuan, China, is firstly described and illustrated, and its conservation status is also assessed. It bears resemblance to *M. macrantha* and *M. bracteata* in terms of morphology; however, there are distinguishing characteristics in terms of their leaf structure, presence of bracts, hairiness of involucre, number of florets, and length of both stamen tube and achene's beak.

Key words: *Melanoseris bracteata, Melanoseris macrantha,* morphology, new taxon, taxonomy

Introduction

Melanoseris Decne. is a genus belonging to the subtribe Lactucinae, tribe Cichorieae of the Asteraceae family. This genus was first established by Decaisne (1843) based on two species, namely *M. lessertiana* (Wall. ex DC.) Decne. and *M. lyrata* Decne., but it has now become the largest genus of the subtribe Lactucinae in China. After extensive research conducted by plant taxonomists (Decaisne 1843; Edgeworth 1846; Shih 1991, 1997; Zhu 2004; Zhu et al. 2004, 2006; Bano 2009; Bano and Qaiser 2009, 2010, 2011; Kilian et al. 2009, 2017; Wang et al. 2009; Deng et al. 2011; Shih and Kilian 2011; Zhang et al. 2011; Wang et al. 2013, 2015, 2020; Abid et al. 2017; Yin et al. 2018), there has been a significant improvement in our understanding of the morphological characteristics of *Melanoseris* species and their relationships within the genus. According to the most recent delimitation of the genus and species (Wang et al. 2013, 2015, 2020; Yin et al. 2018), there are currently 19 accepted species of *Melanoseris* known to occur in China.

During a thorough examination of all the *Melanoseris* specimens in the herbaria, the corresponding author discovered scans of two intriguing specimen images (Gao Yundong et al. THP–KD–2024 at CDBI). These particular specimens had previously been identified as *M. macrantha* (C.B.Clarke) N.Kilian & J.W.Zhang, but what caught their attention was the presence of densely covered long white trichomes on the involucre, setting it apart from all other known *Melanoseris* species. To investigate the stability of this unique characteristic, a field



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investigation was conducted based on the collection information obtained from the specimens. Two populations of this species were discovered, and all the observed plants in the flowering and fruiting stages exhibited densely covered involucres with these long white trichomes. This confirmed that the indumentum of the involucre is indeed a stable and distinct feature. Further morphological studies and analysis revealed similarities between this plant and *M. macrantha* and *M. bracteata* (Hook.f. & Thomson ex C.B.Clarke) N.Kilian, but also distinct differences. Therefore, the authors concluded that this plant represents a new species, which is described and illustrated in detail in this study.

Materials and methods

The morphological description of the new species was conducted based on live plants that were observed and photographed in the field. Additionally, herbarium collections (KUN, GTZM) from these occasions were utilized. To compare the morphology, we referred to the keys and descriptions for the genus and species in Flora Reipublicae Popularis Sinicae (Shih 1997) and Flora of China (Shih and Kilian 2011). To facilitate further comparison, we examined specimens and photographs in the herbaria of Chengdu (CDBI), Kunming (KUN), and Beijing (PE). The morphology of trichomes and pappus, as well as the length of ligules, anther tubes, and achenes, were observed or measured using anatomy microscope (OD500H) or light microscope (Olympus DP72) on fresh or pickled flowers or achenes. Photographs were taken using a Canon EOS 77D and a Dell E2014Hf camera. Figures were edited, arranged, and merged using Adobe Illustrator CS4. The conservation status is determined based on the actual population size observed in the field and the assessment criteria of the IUCN.

Results

Taxonomy

Melanoseris kangdingensis Ze H.Wang, sp. nov.

urn:lsid:ipni.org:names:77331502-1 Fig. 1

Type. CHINA, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding City, Pusharong Town, Kuxirong Village. 29°25.63'N, 101°18.39'E, alt. 2848 m, 22 Aug 2023, Wang Zehuan, Zhong Qianqian & Xu Jiaju wzh20230801 (holotype: KUN!, isotypes: KUN!, LBG!).

Diagnosis. *Melanoseris kangdingensis* most closely resembles *M. bracteata* in the presence of subequal phyllaries, and numerous peduncle bracts grading into the narrow outer phyllaries, but differs from the latter in basal leaves persistent (vs. wither) during flowering, leaves noticeably pinnatipartite (vs. typically entire), phyllaries densely covered with multiseriate glandular hairs (vs. glabrous), length of anther tubes 5.5–6.4 mm (vs. 3.7–4.6 mm), achenes 10–11 mm (vs. 7.9–8.5 mm), beak ca. 4 mm, about 1/2 length of the achene's body (vs. ca. 6.5 mm, nearly equal in length to the achene's body).

Description. Perennial herb, 30–80 cm tall. Roots about 1–2 cm in diameter, fleshy, cylindrical, often branched. Stems erect, rather robust. Basal leaves 21–



Figure 1. *Melanoseris kangdingensis* **A**, **B** habitat **C** plant **D** surface of leaves **E** petiole base **F** lateral view of the capitulum **G** bracts on peduncular branches and one capitulum **H** phyllaries of each layer **I** upper view of the capitulum **J** ray floret **K** trichomes on the outer phyllary **L** microscope photos of trichomes, to show its type (multiseriate glandular hairs) **M** achene **N** the apex of beak. Photographed by Zehuan Wang.

45 × 10−19 cm, persist in flowering, elongated oblong, lyrately pinnatipartite; terminal lobes 5.5-22 × 5-19 cm, broadly triangular or broadly ovate, apex acuminate; lateral lobes 2-3 pairs, 5.2-10.3 × 3.4-6 cm, triangular, ovate or rectangular, apex obtuse or truncate. Leaf margins coarsely dentate, green on both sides, sparsely covered with multiseriate glandular hairs; petiole 5-10 cm long, sparsely covered with multiseriate glandular hairs. Middle and lower stem leaves 8-28 × 3.5-12 cm, homomorphic with basal leaves, pinnatipartite; terminal lobes 3-9 × 3.5-12 cm, elongated triangular, apex acuminate; lateral lobes 2-4 pairs, 2-6.5 × 1.7-5.2 cm, triangular, semicircular or rectangular, apex obtuse or truncate, leaf margins coarsely dentate, green on both sides, sparsely covered with multiseriate glandular hairs; petiole base auriculately clasping, with wings 0.5-3 cm wide. Stem leaves gradually decrease upward, transitioning into bract-like structures on the branches of the capitulescence. Lower leaves on the branches of capitulescence 7-17 × 2.6-7.5 cm, elongated oblong or lanceolate, deeply or shallowly pinnatilobed, or entire, apex long acuminate, leaf margins coarsely dentate, sparsely hairy. Bracts on a capitulescence branches 4-7, 1.5-5.5 × 0.1-1.5 cm, lanceolate or linear, gradually receding to involucral bracts, margin entire, green on both sides, dorsal and margin densely covered with white flattened multiseriate glandular hairs. Capitulescence corymbiform, branches slender, peduncle 2-9.5 cm long, densely covered with long multiseriate glandular hairs. Capitula 4-10, pendulous in flowering, with 22–27 florets. Involucre 1.9–2.2 × 1.3–1.8 cm, broadly campanulate, densely covered with long white multiseriate glandular hairs abaxially and along the margin. Phyllaries 5-seriate, subequal, apical acute or obtuse, margin entire. Outer phyllaries ca. 16 × 2 mm, oblong, slightly shorter than inner phyllaries, purple or purplish-green, densely covered with broadly flat multiseriate glandular hairs abaxially or along the margin, trichomes up to ca. 2 mm long; middle phyllaries ca. 16 × 1.5 mm, broadly linear, green or apically purplish, with multiseriate glandular hairs gradually decreasing from the outer to inner layers; innermost phyllaries linear, ca. 16 × 1 mm, light green, subapical sparsely with multiseriate glandular hairs. Florets ligulate, tube ca. 9 mm long, white; ligules ca. 17 × 2 mm, 5-toothed at the apex, light blue. Stamens synantherous, anther tube 5.5–6.4 mm long, light blue. Ovary inferior, flattened, ellipsoid, style ca. 22 mm long, apically bifid, stigmatic branches ca. 1.5 mm long, long and acuminate, evenly coated with elongate collecting hairs. Achenes 10-11 × 1.5-2 mm, fusiform, dark brown, compressed, lateral ribs slightly thickened, each side with 3 slightly raised ribs, surface sparsely hairy, and apex contracted into ca 4 mm beak, beak discolorous, with the top half being white. Pappus ca. 8 mm long, white, consisting of a single layer, finely serrated.

Distribution and habitat. *Melanoseris kangdingensis* is currently known from two localities in western Sichuan, China. It has been observed growing on the slope and at the foot of cliffs by the roadside at elevations ranging from 2800–2900 m. The dominant species of the community include *Dasiphora fruticosa* (L.) Rydb. (Rosaceae), *Gentiana tibetica* King ex Hook.f. (Gentianaceae), *Heracleum candicans* Wall. ex DC. (Apiaceae), *Paraceterach vestita* (Hooker) R.M. Tryon (Pteridaceae), and *Cheilanthes chusana* Hook. (Pteridaceae).

Phenology. Flowering and fruiting from July to September.

Etymology. The specific epithet *'kangdingensis'* refers to Kangding City in the Sichuan Province, which is the locality of the type collection.

Vernacular name. Simplified Chinese: 康定毛鳞菊; Chinese Pinyin: Kāngdìng Máolínjú.

Conservation status. Currently, two populations of *Melanoseris kangdingensis* have been discovered, each with approximately 20 mature individuals. These plants grow on slopes and at the foot of cliffs by the roadside, making them vulnerable to disturbance from human activities. Additionally, the habitat and dispersal environment for reproduction are steep and harsh, making it challenging for the species to expand its distribution area. Based on the IUCN Red List criteria (IUCN 2012, 2022), this new species should be classified as Endangered (EN; criteria B1ac(iii)+2ac(iii); C2a(i); D). However, we recognize that further assessments are required as additional populations are identified.

Additional specimens examined. CHINA, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding City, Pusharong Town, Binggu Village, 29°28.18'N, 101°18.84'E, alt. 2939 m, 22 Aug 2023, Wang Zehuan, Zhong Qianqian & Xu Jiaju wzh20230802 (KUN!, GTZM!); CHINA, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding City, Pusharong Town, Kuxirong Village, 29°25.07'N, 101°18.02'E, alt. 2800–3000 m, 04 Aug 2017, Gao Yundong, Deng Hengning & Li Huaicheng THP–KD–2024 (CDBI!).

Discussion

The main distinguishing feature between *Melanoseris kangdingensis* and *M. bracteata* is the dense coverage of flat, long multiseriate glandular hairs on the back and margins of the outer phyllaries (Fig. 2). Another species, *M. macrantha*, also possesses similar flat trichomes on the outer phyllaries. However, *M. kangdingensis* can be easily differentiated by its numerous and conspicuous bracts gradually transitioning into the outer phyllaries, fewer florets in the capitulum, subequal phyllaries densely covered with multiseriate glandular hairs abaxially, longer anther tube length, and beak. A summary of the main morphological differences between *M. kangdingensis*, *M. macrantha*, and *M. bracteata* is provided in Table 1. In fact, *M. kangdingensis* is the species with the hairiest

	Table 1	1. M	Iorpholo	gical	com	oarison	between	М.	kangdingensi	is, M	. macrantha	and	М.	bracteata
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Characters	M. kangdingensis	M. macrantha	M. bracteata
Leaves	basal leaves persistent during flowering; leaves pinnatipartite	basal leaves wither during flowering; leaves pinnatipartite	basal leaves wither during flowering; leaves usually entire
Bracts	numerous and conspicuous, grading into the narrow outer phyllaries	absent	numerous and conspicuous, grading into the narrow outer phyllaries
Capitula	with 22-27 florets	with ca. 40 florets	with usually 20-30 florets
Involucres	phyllaries subequal, narrow, densely covered with long white multiseriate glandular hairs abaxially and along the margins, trichomes gradually decreased from the outer to inner phyllaries	phyllaries imbricate, outer phyllaries wide, margin white densely fimbriate, glabrous abaxially; inner phyllaries narrow, completely glabrous	phyllaries subequal, narrow, all completely glabrous
Anther tube length	5.5-6.4 mm	3.7-4.3 mm	3.7-4.6 mm
Achene length	10–11 mm	10-11 mm	7.9-8.5 mm
Achene beak	ca. 4 mm long, about 1/2 length of the achene's body	ca. 1.8 mm long, about 1/3 length of the achene's body	ca. 6.5 mm long, nearly equal in length to the achene's body



Figure 2. Photographs of the plants and capitula of *Melanoseris kangdingensis*, *M. bracteata* and *M. macrantha* **A1**, **A2** *M. kangdingensis* **B1**, **B2** *M. bracteata* **C1**, **C2** *M. macrantha*. Photographed by Zehuan Wang.

involucre among the *Melanoseris* genus. Fluffy and hairy involucre may be related to the specific growing environment of *M. kangdingensis*. Most *M. kangdingensis* plants grow on wind-exposed cliffs without tall vegetation, and the dense hairy involucre serves to better protect the smooth development of the achenes inside.

During field surveys, it was observed that in the type population, which is situated on relatively shady slopes, only 1–2 mature achenes developed in each capitulum of several fruiting plants, while the majority of achenes or a few entire capitula were found to be sterile. Furthermore, we also discovered insect eggs inside some nearly matured achenes of the capitula, indicating that *Melanoseris kangdingensis*, like *Sinoseris muliensis* (Y.S.Chen, L.S.Xu & R.Ke) Ze H.Wang, N.Kilian & H.Peng (Wang et al. 2020), is susceptible to seed parasitism by certain insects. *M. kangdingensis* exhibits the longest anther tube length (5.5–6.4 mm) among the *Melanoseris* genus. The longer anther tubes have the potential to release a greater quantity of pollen, theoretically. A higher quantity of pollen can increase the probability of successful fertilization of the ovary, enhance seed maturation, and ultimately improve seed reproduction success. However, due to limited distribution information, further investigation into its growth and reproductive mechanisms is necessary to gain a better understanding of the adaptability and conservation requirements of this plant.

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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

A new species of *Cotoneaster* (Rosaceae) from western Sichuan, China

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Abstract

Cotoneaster densiflorus, a new species of Rosaceae from western Sichuan, China, is described and illustrated. Morphologically, we inferred that the new species belongs to *Cotoneaster* Ser. *Salicifolii* sensu Yü et al. (1974) in the Flora of China and Fryer and Hylmö (2009). This species is most similar to *C. salicifolius*, but differs in its leaf blade of ovate-lanceolate to obovate shape (vs. elliptic-oblong to ovate-lanceolate), smaller lengthwidth ratio of 2.37 ± 0.31 (vs. 3.17 ± 0.32), slightly conduplicate (vs. not conduplicate), less lateral veins of 6-8 pairs (vs. 12-16 pairs), upper surface slightly rugose (vs. rugose), leaf margin plane (vs. revolute), lower surface densely grey tomentose (vs. grey tomentose, with bloom), greater corolla diameter of 7-9 mm (vs. 5-6 mm), styles 2 (vs. 2-3), pyrenes 2 (vs. 2-3), larger pollen grains P/E values of 2.05 ± 0.12 (vs. 1.19 ± 0.05) and leaf epidermis type W (vs. type I). Based on phylogenetic analysis of the whole chloroplast genome, *C. densiflorus* is sister to *C. rhytidophyllus*, but distantly related to *C. salicifolius*.

Key words: Anatomical, chloroplast genome, leaf epidermis, palynological, Ser. Salicifolii

Introduction

Cotoneaster Medik. (Rosaceae, Maloideae) is a morphologically highly variable genus that is naturally distributed in Europe, North Africa and the temperate areas of Asia except Japan. The Himalayas and neighboring mountains in Yunnan and Sichuan of China are species diversity and distribution centers for this genus (Fryer and Hylmö 2009). Due to the frequent occurrence of hybridization and polyploidisation, together with apomixis, its infrageneric classification is controversial and unstable (Campbell et al. 2007; Lo and Donoghue 2012; Li et al. 2014, 2017a; Meng et al. 2021). The number of species in the genus ranges from about 50 to more than 400 according to different (and often contradictory) species concepts and traits (Flinck and Hylmö 1966; Yü et al. 1974; Phipps et al. 1990; Lu et al. 2003; Fryer and Hylmö 2009; Dickore and Kasperek 2010). In the Flora of China, the genus was divided into three sections (Sect. *Densiflos*, Sect. *Cotoneaster* and Sect. *Uniflos*), based on the number of flowers in the inflorescence



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(Yü et al. 1974). However, more studies supported the conclusion of two major sections/subgenera: *Chaenopetalum* and *Cotoneaster* (Koehne 1893; Flinck and Hylmö 1966; Phipps et al. 1990; Fryer and Hylmö 2009), which was also proved by molecular phylogenetic studies, based on nuclear ITS, chloroplast or low-co-py nuclear genes in the last decade (Li et al. 2012, 2014; Lo and Donoghue 2012; Meng et al. 2021). For species in Subg. *Chaenopetalum*, the flowers in a cyme open simultaneously, within white spreading (rarely pink) petals, white filaments and purple to black anthers. While for species in Subg. *Cotoneaster* species, the flowers in a cyme open continuously over an extended period, within red (rarely pink) erect (less suberect) petals, red, pink or white filaments and white anthers.

Within the sections/subgenera, the further division into 7–39 series was mainly based on morphology of stems, branches, leaves, number of pyrenes and resistance (Flinck and Hylmö 1966; Yü et al. 1974; Phipps et al. 1990; Fryer and Hylmö 2009). The Ser. *Salicifolii* included 5–7 species and about three varieties, whose name was derived from the mostly lanceolate and willow-like leaves. In Fryer and Hylmö (2009) and Flora of China (Yü et al. 1974), the important morphological features that distinguished the Ser. *Salicifolii* species from other series include evergreen or semi-evergreen shrub, leaf blade leathery, mostly lanceolate, abaxially persistently densely tomentose, veins impressed, white spreading petals, and pyrenes 2–4 (–5). Multiple phylogenetic trees of *Cotoneaster*, based on low-copy nuclear and chloroplast genes showed that these series, as smaller taxonomic units under subgenera, were not monophyletic (Lo and Donoghue 2012; Meng et al. 2021), which agreed with our recent phylogenetic study results on Ser. *Salicifolii* (unpublished study).

During our field survey in western Sichuan Province, an interesting population that shares morphological affinities with Ser. Salicifolii species was discovered. These affinities are based on evergreen or semi-evergreen shrub, leathery leaf blade, dense inflorescence and white spreading petals. However, this taxon was not completely similar to any species that has been described worldwide. Furthermore, the individuals of this species were distributed in Baoxing County, which is located in Siguniang and Jiajin Mountains at the eastern edge of the Hengduan Mountains, a biodiversity hotspot in southwest China (Zhang and Ma 2008, 2009; Li et al. 2017b). Interestingly, this county was also the type specimen collection site of C. salicifolius and C. moupinensis. Over the past 10 years, approximately 10 new plant species were discovered and illustrated in Baoxing County, such as Youngia baoxingensis Y.S. Chen (Chen 2018), Primula luteoflora X.F. Gao & W.B. Ju (Ju et al. 2018), Berberis jinwu Y.K. Li, Harber, Y.W. Xing & C.C. Yu (Li et al. 2022) and several others. From 2016 to 2023, after detailed morphological examination, specimen collection and comparison with herbarium specimens sampled in this region, we identified this shrub as a new species and determined its phylogenetic position in the genus of Cotoneaster through whole chloroplast genome data. Our study not only enriched the diversity of Cotoneaster species in China, but also highlighted the importance of the basic survey of biodiversity in this area of Sichuan and the Hengduan Mountains.

Material and methods

Plant morphological features and habits were recorded and photographed in the field during the flowering and fruiting periods of the putative new species. The characteristics and measurements were compared with those of its related species naturally occurring in Sichuan Province (i.e. *C. salicifolius* and *C. rhytidophyllus*) as described in the Flora of China (Yü et al. 1974) and related taxonomic literature of *Cotoneaster* (Fryer and Hylmö 2009). Voucher specimens were deposited in the Herbarium of SunYat-sen University (SYS) in China.

For scanning electron microscopy (SEM) observations, pollen grains of this putative new species and two related species were collected from specimens (*M.W. Li 20230617007, Q.Fan 15682-01* and *Q.Fan 15643* (SYS)). For scanning electron microscopy (SEM) observation, the pollen grains were transferred onto metal stubs with double-sided adhesive tape and sputter-coated with technical gold (Li et al. 2017b; Xiong et al. 2019). Approximately 20 randomly selected pollen grains were scanned and photographed by the SEM (S-3400, Hitachi, To-kyo, Japan) at 5 kV accelerating voltage and SE detector, then the pollen grains were measured and the polar axis (P), equatorial axis (E) and the ratio of polar axis length to equatorial axis length (P/E) were calculated. The nomenclature for pollen morphology mainly followed Erdtman (1943, 1952) and the terminology of ornamentation mainly followed Ueda and Tomita (1989).

Leaf epidermal materials were prepared from mature leaves and macerated in 1:1 (by volume) hydrogen dioxide solution and glacial acetic acid and then were boiled in a water bath for 1.5–2 h. After being rinsed with water, leaf materials were transferred to Schultze's solution for 30 minutes. Finally, pieces of leaf epidermis were stained with a solution of 1% safranin prior to mounting in glycerine gel. Prepared cuticles were observed using a SY100 light microscope and JSM-6330F SEM. The nomenclature of stomatal types and leaf epidermis is mainly based on the descriptions of Wilkinson (1979), Prabhakar (2004) and Ding et al. (2008).

Total genomic DNA was extracted using the Plant Genomic DNA Kit (DP305, Tiangen Biotech Co., Ltd., Beijing, China) and DNA quality was measured using a NanoDrop 2000 spectrophotometer (NanoDrop Technologies; Thermo Fisher Scientific, Inc., Wilmington, DE, USA). The qualified DNAs (≥50 ng) were sent to Novogene Bioinformatics Technology Co., Ltd. (Beijing, China) for pairedend (PE) library construction and genome-skimming sequencing. The generated reads were assembled by the GetOrganelle (Jin et al. 2020) pipeline. In this pipeline, the chloroplast genome of C. salicifolius (KY419943.1; Zhang et al. (2017)) was set as a reference. The genome annotation was performed with CpGAVAS (Liu et al. 2012), then the inverted repeat (IR) boundaries were manually adjusted and confirmed on geneious prime2023.0.4 (https://www. geneious.com/). In order to determine the phylogenetic position of this species in Cotoneaster, complete chloroplast genomes of 64 accessions downloaded from NCBI and seven unpublished Ser. Salicifolii taxa were obtained to reconstruct the phylogenetic trees with Rhaphiolepis bibas and Rhaphiolepis prinoides as outgroups (Table 1). The sequences were aligned using MAFFT version 7 (https://mafft.cbrc.jp). The best-fit nucleotide substitution model was determined by ModelFinder (Kalyaanamoorthy et al. 2017). The maximum-likelihood (ML) phylogenetic tree was constructed using RAxML-HPC Blackbox Software (Stamatakis 2014) with the GTRGAMMAI model and 1000 bootstrap replicates to assess the support for each branch. Bayesian inference (BI) was conducted using MrBayes v.3.2.7 (Ronquist et al. 2012) with Markov chains for at least 10,000 generations and sampled every 10 generations. After the

Table 1. Taxa, voucher information, and GenBank accession numbers of the chloroplastgenome sequences used in this study (a. This study, b. Meng et al. 2021, c. Liu et al.2020, d. Chen et al. 2022, e. unpublished study).

Taxon	Voucher	Accession numbers	
Cotoneaster Subg. Chaenopetalum			
Cotoneaster densiflorus	14924	OR478167ª	
C. argenteus	13466-1	MK578683 ^b	
C. astrophoros	17073	MK650065 ^ь	
C. conspicuus	15902	MK638987 ^ь	
	17912	MK650062 ^b	
C. coriaceus	13462-12	MK650049 ^b	
	13462-10	MK561974 ^b	
	_	NC_060440 ^b	
C. dammeri spp. songmingensis	17091	MK605511 ^b	
C. delavayanus	17148-5	MK605518 ^b	
C. fulvidus	17168	MK614792 ^ь	
C. glaucophyllus	15960-1	MK561976 ^b	
C. hebephyllus	14669	MK638988 ^b	
C. lacteus	17153-5	MK605517 ^ь	
C. marginatus	17082	MK605510 ^b	
C. multiflorus	YZSP	MK650060 ^b	
C. pannosus	16009	MK605509 ^b	
C. rockii	17155-5	MK605515 ^ь	
C. salicifolius	16911-2	MK638989 ^b	
	_	NC_060455 ^b	
C. salicifolius var. henryanus	2241	MN577863°	
C. serotinus	15962-2	MK578685 ^ь	
C. sherriffii	17178-2	MK614794 ^b	
C. soongoricus	ZGE-1	MK650057 ^ь	
C. submultiflorus	MYS-1	MK650061 ^b	
C. turbinatus	16900	MK650054 ^b	
C. vandelaarii	17186-1	MK544858 ^b	
C. angustus	14996	_e	
C. coriaceus	B15184	_e	
C. hylmoei	15219	_e	
C. rhytidophyllus	15661	_e	
C. rugosus	15270	_e	
C. turbinatus	B15045	_e	
C. glabratus	14989	_e	
Cotoneaster Subg. Cotoneaster			
Cotoneaster acuminatus	324-64*B	MK650045 ^b	
C. acutifolius	13755-27	MK638990 ^b	
C. adpressus	12388	MK638993 ^b	
C. affinis	14662-06	MK650051 ^b	
C. bullatus	17157-8	MK614791 ^b	

Taxon	Voucher	Accession numbers	
C. cf_chengkangensis	17145	MK638992 ^b	
	17145-1	MK605514 ^b	
C. cinerascens	17136-1	MK638991 ^b	
C. cochleatus	14835	MK524400 ^b	
C. dielsianus	15959-2	MK614800 ^b	
C. foveolatus	860-84*E	MK650046 ^b	
C. franchetii	17191	MK638985 ^b	
C. frigidus	14650-10	MK561975 ^₅	
C. gamblei	14663-09	MK650052 ^b	
C. horizontalis	1981-65	MK561973 ^b	
C. huahongdongensis	17187-8	MK614796 ^b	
C. integerrimus	1234*82C	MK614799 ^b	
C. langei	17181-2	MK605516 ^b	
C. leveillei	17122-8	MK544857 ^b	
C. melanocarpus	13756-19	MK561977 ^b	
C. microphyllus	17028_25	MK544856 ^b	
C. moupinensis	628*97C	MK614797 ^b	
C. obscurus	1231-82*C	MK614798 ^b	
C. perpusillus	PZXY4-8	MK638994 ^b	
C. praecox	Cnanshan	MK638986 ^b	
C. qungbixiensis	17138-1	MK605513 ^b	
C. reticulatus	WMXZ	MK650055 ^b	
C. rotundifolius	17029-1	MK650063 ^b	
C. rubens	17175-1	MK614793 ^b	
C. schantungensis	SD1	MK650053 ^b	
C. shansiensis	SS-1	MK650064 ^b	
C. subadpressus	17167	MK650058 ^b	
C. tenuipes	7276*C	MK650047 ^b	
C. vellaeus	17179-7	MK614795 ^ь	
C. verruculosus	17137-1	MK605512 ^b	
C. villosulus	13165*B	MK650048 ^b	
C. zabelii	XB3	MK650056 ^b	
Outgroups			
Rhaphiolepis bibas	201819	MN577877°	
R. prinoides	-	MT876398 ^d	

average standard deviation of split frequencies (ASDFs) was assessed and reached < 0.01, the first 25% trees were discarded as burn-in.

Flow cytometry was used to estimate the genome size and to determine the ploidy level. Samples were prepared by a modified method according to Rothleutner et al. (2016). Approximately 1 cm² of fresh leaf tissue was chopped with maize as the internal standard using a blade in cold (4 °C) Otto I buffer (0.1 M citric acid, 0.5% (v/v) Tween 20) for 90 s before being filtered through a 50-µm nylon mesh. The suspension was stained with Otto II buffer (0.4 M Na₂HPO₄·12H₂O), β-mercaptoethanol, Rnase and PI fluorochrome. An Accuri C6 flow cytometer (BD Biosciences, San Jose, CA, USA) equipped with 488-nm laser, was employed with a sample flow rate 14 μ l min⁻¹. Fluorescence measurements were obtained using the FL2 (585/40 nm) optical filter, capturing 10 000 events and utilizing the FL2-A values for the 2C peak.

Result and discussion

Taxonomic treatment

Cotoneaster densiflorus M.W. Li, Q. Fan & W. B. Liao, sp. nov. urn:lsid:ipni.org:names:77331508-1

Type. CHINA. Sichuan Province, Baoxing County, Qiaoqi Town, Zegen Village, on the cliff of steep slopes, 30°43'N, 102°45'E, 2180 m a.s.l., 7 Dec 2016, *Q. Fan & M.W. Li 14925* (holotype: SYS; isotype: SYS) (Figs 1, 2)

Diagnosis. Morphologically, *Cotoneaster densiflorus* is similar to *C. salicifolius*, but differs in its leaf blade of ovate-lanceolate to obovate shape (vs. elliptic-oblong to ovate-lanceolate), smaller length-width ratio of 2.37 ± 0.31 (vs. 3.17 ± 0.32), slightly conduplicate (vs. not conduplicate), fewer lateral veins of 6–8 pairs (vs. 12–16 pairs), upper surface slightly rugose (vs. rugose), leaf margin plane (vs. revolute), lower surface densely grey tomentose (vs. grey tomentose, with bloom), greater corolla diameter of 7–9 mm (vs. 5–6 mm), styles 2 (vs. 2–3) and pyrenes 2 (rarely 3). Although there is a closer phylogenetic relationship between the new species and *C. rhytidophyllus*, it is easy to distinguish them by the indumentum color of branchlets, leaves and inflorescences, rugose leaf upper surface, fruit shape and pyrenes number. See Table 2, Figs 1, 2 for a detailed comparison.

Description. Evergreen shrubs, rarely semi-evergreen, up to 5 m tall, with spreading to erect branches; stems 5 cm in diameter; branchlets terete, stout, reddish-brown, initially sparsely tomentose, glabrous when old. Petiole red, robust, 4-7 mm long, tomentose; stipules linear, 4-7 mm, tomentulose, caducous; leaf blades ovate-lanceolate to obovate, 25-72 × 12-33 mm, leathery, lightly conduplicate along the mid-vein, mid-vein conspicuously raised abaxially and deeply impressed adaxially, lateral veins 6-8 pairs, rarely 5 or 9, impressed, lower surface densely grey tomentose, apex acute or obtuse, rarely abruptly mucronate, base cuneate, margin entire, plane, upper surface initially sparsely pilose, subglabrous when old, slightly rugose. Compound corymbs 25-40 mm long, 17-43 mm diam., with (5-)10- to 50-(61)-flowered per inflorescence; rachis and pedicels densely white pilose; peduncles 2-3 cm; bracts linear, tomentulose, caducous, 2-4 mm long; pedicel 2-4 mm. Flowers 7-9 mm diam.; hypanthium campanulate, abaxially densely white tomentose; sepals triangular, apex acute, pilose; petals spreading, white, glabrous, suborbicular, ca. 3-4 mm and nearly as broad, apex obtuse, base shortly clawed; stamens 20, slightly longer than or subequal to petals, anthers purple, filaments white; styles 2, free, slightly shorter than stamens; carpels 2, ovary apically pilose. The ripe pome obovoid or subglobose, 5-7 mm diam., red, sparsely pilose; 2 pyrenes per fruit.

Pollen morphology. The pollen grains of *C. densiflorus* are tricolpate. Polar axis (P) = $46.15 \pm 3.09 \mu$ m, equatorial axis (E) = $22.64 \pm 1.28 \mu$ m, the P/E value (proportion of polar axis to equatorial axis length) = 2.05 ± 0.12 . The P/E values



Figure 1. Cotoneaster densiflorus **A** habit **B** leaf, adaxial surface **C** leaf, abaxial surface **D** flowers **E** vertical section of flower **F** petals **G** stamens **H** styles I fruiting branch **J** pome **K** transverse section of pome **L** pyrenes. Illustration by Zhengmeng Yang based on living field-collected materials (*Q. Fan & M.W. Li 14925, M.W. Li 20230617007*).



Figure 2. Cotoneaster densiflorus sp. nov. A habitat B habit C branchlets D petal, stamen, style, and vertical section of flower E ovate-lanceolate to obovate shape of leaves F leaf, abaxial surface G 2 pyrenes per fruit H inflorescence I fruiting branch.

	C. densiflorus	C. salicifolius	C. rhytidophyllus	
Leaf shape	ovate-lanceolate to obovate	elliptic-oblong or ovate- lanceolate	elliptic-oblong or ovate-oblong to oblong-lanceolate	
Leaf size (mm)	25-72×12-33	40-85×15-25	40-70 ×18-30	
Leaf apex	acute or obtuse, rarely abruptly mucronate	acute or acuminate	acuminate, rarely acute	
Leaf length-width ratio	2.37 ± 0.31	3.17 ± 0.32	3.19 ± 0.48	
Leaf conduplicate state	slightly conduplicate	not conduplicate	not conduplicate	
Lateral veins number (pairs)	6-8	12-16	5-8	
Leaf upper surface indumentum	initially sparsely pilose	initially sparsely pilose	initially sparsely villous	
Upper surface rugose state	slightly rugose	rugose	extremely rugose	
Margin revolute state	plane	revolute	revolute	
Leaf lower surface indumentum	densely gray tomentose	gray tomentose, with bloom	yellow tomentose-floccose	
Inflorescence number of flowers	(5-)10- to 50-(61) flowers	10- to 50- flowers	10- to 40(-50) flowers	
Corolla diameter (mm)	7-9	5-6	7-8	
Patal indumentum	glabrous	glabrous	adaxially slightly pilose near base	
Styles number	2	2-3	2-3	
Fruits shape	obovoid or subglobose	subglobose pyriform		
Fruits size	5–7 mm in diam	5–7 mm in diam	4 mm in diam, 5–6 mm long	
Pyrenes number	2	2-3	2-3, rarely 4	

Table 2. Diagnostic macro-morphological characteristic of Cotoneaster densiflorus, C. salicifolius and C. rhytidophyllus.

of the new species is obviously larger than C. salicifolius (1.19 ± 0.05) . The surface is mainly striate-foveolate ornamentation (Fig. 3, Table 3).

Leaf epidermis morphology. According to previous studies on leaf epidermis type of *Cotoneaster* species (Ding et al. 2008), the leaf epidermis of this species could be classified as type W, with irregular stomata surrounded by 4–5 corneous papillae, while *C. salicifolius* and *C. rhytidophyllus* are presented as type I, with irregular stomata surrounded by various ridges protruding from the stratum corneum (Fig. 3, Table 3).

Phenology. Flowering from June to July, fruiting from November to December. **Etymology.** The specific epithet refers to the compact compound corymbs with (5-)10- to 50-(61)-flowered per inflorescence.

Distribution and habitat. *C. densiflorus* is currently known only from the type locality, Zegen Village, Baoxing County, Sichuan Province, China. This population includes nearly 60 individuals, with about 40 densely distributed individuals and 20 scattered shrubs on a steep slope of sunny sparse forest along the National Highway at altitudes of about 2180 m a.s.l. The associated tree species include *C. dielsianus, Coriaria nepalensis, Indigofera szechuensis, Desmodium elegans*, and *Elaeagnus bockii*.

Phylogenetic analysis. The complete chloroplast genome of *C. densiflorus* exhibited characteristic quadripartite structure with 159,759 bp in total length, including a pair of inverted repeat (IRA and IRB) region of 26,371 bp, separated by a larger single-copy (LSC) region of 87,807 bp and a small single-copy (SSC) region of 19,210 bp with an overall GC content of 36.60%. A total of 111 unique genes were encoded, including 78 protein-coding genes (PCGs), 29 transfer RNA (tRNA) genes and four ribosomal RNA (rRNA) genes, while 17 genes duplicated in the IR regions.



Figure 3. SEM micrographs of pollen grains of *Cotoneaster densiflorus* (**A**–**C**), light microscope and SEM micrographs of leaf epidermis of *C. densiflorus* (**D**–**F**) **A** equatorial view **B** polar view **C** striate-foveolate ornamentation **D** upper epidermis **E** under epidermis **F** stomata and corneous papillae of under epidermis.

	C. densiflorus	C. salicifolius	C. rhytidophyllus
Polar axis length (µm)	46.15 ± 3.09	24.31 ± 1.07	37.39 ± 7.35
Equatorial axis length (µm)	22.64 ± 1.28	20.51 ± 0.16	18.47 ± 3.03
P/E values	2.05 ± 0.12	1.19 ± 0.05	2.02 ± 0.23
Type of leaf epidermis	type W	type I type I	
2C DNA (pg)	2.33 ± 0.19	0.19 1.57 ± 0.15 1.55 ± 0.10	

Table 3. Diagnostic micro-morphological characteristic and 2C DNA of *Cotoneaster densiflorus*, *C. salicifolius* and *C. rhytidophyllus* (values $M \pm SD \mu m$).

Phylogenetic analyses constructed from 72 *Cotoneaster* chloroplast genomes resulted in the ML tree topology as shown in Table 1. Two main clades (*Cotoneaster* and *Chaenopetalum*) with well-supported values are presented in Fig. 4, which was consistent with the previous phylogenetic studies. The new species was placed in Clade *Chaenopetalum* and clustered with *C. rhytidophyllus* of Ser. *Salicifolii*, but with weak support values (BS = 44, BI = -).

Chromosome ploidy analysis. The results of flow cytometry analysis displayed a mean genome size (2C-value) of 2.33 ± 0.19 pg for *C. densiflorus* (Table 3). Comparing with ploidy levels and genome sizes of *Cotoneaster* species reported in the previous studies (Rothleutner et al. 2016; Ksinan et al. 2021), this species was inferred as tetraploid (2n = 4x =68), while its closely-related species, *C. salicifolius* (2C-value = 1.13 ± 0.16 ; unpublished data) and *C. rhytidophyllus* (2C-value = 1.55 ± 0.10 ; unpublished data) were diploid (2n = 2x = 34) (Fryer and Hylmö 2009).

Conservation status. Only one large population was found with nearly 60 mature and juvenile individuals on steep slopes about 2 km along the highway. Its habitat is affected and threatened by the violent geological, climate



Figure 4. The phylogenetic tree of 65 *Cotoneaster* taxa based on 72 whole chloroplast genomes showing the position of *Cotoneaster densiflorus* (bold and highlighted with green) in the genus. Numbers near the branches are ML and BI bootstrap values. GenBank accessions were provided after underlines.

and artificial activities with frequent construction of highways, mud-rock flows, landslides, and even earthquakes in the last few decades. Therefore, the species could be considered as CR (Critically Endangered) status according to IUCN Red List Criteria (IUCN 2022).

Additional specimens examined (paratypes). China. Sichuan: Baoxing County, Qiaoqi Town, Zegen Village, 30°43'N, 102°45'E, 2180 m a.s.l., 17 June 2023, *M.W. Li 20230617007* (SYS).

Conclusions

We described and illustrated a new species of *Cotoneaster* genus (Rosaceae) in western Sichuan Province of China and provided evidence for its phylogenetic position through whole chloroplast genome data. After detailed field research, we found *Cotoneaster densiflorus* M.W. Li, Q. Fan & W. B. Liao, sp. nov. is distributed in a narrow range of Baoxing County, which is located in the Hengduan Mountains. Only one large population of nearly 60 individuals was observed, with about 40 densely distributed individuals and 20 scattered shrubs on a steep slope of sunny sparse forest along the National Highway. Morphologically, this shrub is

most similar to *C. salicifolius*, but obviously differs in leaf upper surface rugose state, margin revolute state, number of lateral veins, styles and pyrenes, pollen grains P/E values and leaf epidermis type. Our study not only enriched the diversity of *Cotoneaster* species in China, but also highlighted the importance of the basic survey of biodiversity in this area of Sichuan and the Hengduan Mountains.

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: QF. Data curation: ML. Formal analysis: SM. Funding acquisition: SD. Investigation: YC. Methodology: YL. Project administration: WL. Resources: DZ. Writing - original draft: DL. Writing - review and editing: ML.

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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

Eugenia sarahchazaroi (Myrtaceae, Myrteae), a new species from the cloud forest of Mexico

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Abstract

Following the description of *Eugenia naraveana* in 2016 from the cloud forest of the Cofre de Perote volcano, Mexico, the doubt about the existence of another unlocalized and sympatric species of *Eugenia* remained. After years of searching, the second endemic species of the Cofre de Perote volcano, *Eugenia sarahchazaroi*, is presented here. It belongs to the section *Umbellatae*, and is described, illustrated, and compared with *E. naraveana* and *E. coetzalensis*, recently described from Veracruz, the second state with the highest diversity of *Eugenia* in Mexico. The species is only known from the type locality and is classified in the Critically Endangered CR B1+B2(a,biii) category of the IUCN Red List conservation assessments.

Key words: Cloud forest, Cofre de Perote, endemic species, *Eugenia naraveana*, *Umbellatae*, Veracruz

Introduction

Myrtaceae Juss. is a diverse family with ca. 6000 species distributed in tropical and subtropical regions (Lucas et al. 2019). It is classified into the subfamilies Psiloxyloideae (with two tribes) and Myrtoideae (with 17 tribes) (Wilson et al. 2005; Wilson 2010; Giaretta et al. 2019; Uc-Gala et al. 2023). From the latter, the tribe Myrteae is the most diverse within the family, with 2690 species (Stevens 2023). About 109 species of Myrtaceae are distributed in Mexico, of which 87 correspond to *Eugenia* L. (Uc-Gala et al. 2023), a monophyletic genus, one of the most hyperdiverse genera with 1218 species (Giaretta et al. 2022; POWO 2023), and the second largest genus of tree species in the world (Beech et al. 2017; Uc-Gala et al. 2023).

Eugenia currently circumscribes ca. 1218 species (POWO 2023). They are distributed mainly from Mexico to northern Argentina and Uruguay (including the Caribbean), with fewer species in New Caledonia, the Philippines, India, Sri Lanka, Madagascar, Mauritius, and Comores. Based on phylogenetic analyses, *Eugenia* has been classified into nine sections: *Eugenia*, *Hexachlamys*, *Phyllocalyx*, *Pilothecium*, *Pseudeugenia*, *Racemosae*, *Schizocalomyrtus*, *Speciosae*, and



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Copyright: © Antonio Francisco-Gutiérrez et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). *Umbellatae*, which can be determined with morphological characters (Mazine et al. 2016; Giaretta et al. 2021).

This year, Uc-Gala et al. (2023) performed the most comprehensive checklist of *Eugenia* species from Mexico. They reported 87 species of *Eugenia*, 46 endemic to this country. Veracruz is the second state with the highest *Eugenia* species richness in Mexico, with 31 of them (Uc-Gala et al. 2023). Also, *Eugenia* occupies the fourth place among the richest tree genera in Mexico (Téllez et al. 2020; Uc-Gala et al. 2023). The species of *Eugenia* from Veracruz were studied in the taxonomic treatment of Myrtaceae for the Flora of Veracruz series (Sánchez-Vindas 1990). In the last decade, two new and endemic species of *Eugenia* were described from the same state, *E. naraveana* Cházaro & Franc.Gut. (Cházaro-Basáñez and Francisco-Gutiérrez 2016), and *E. coetzalensis* Durán-Esp. & Cast.-Campos (Durán-Espinosa et al. 2018).

After botanical explorations in the Cofre de Perote Volcano in Veracruz, Mexico, a new suspected species of *Eugenia* is studied here. The aims of this work are: 1) to describe a new species of *Eugenia*; 2) to compare it with the sympatric and endemic *E. naraveana*; and 3) to evaluate the conservation status of the species.

Materials and methods

Field work

In 2014, during the fieldwork for describing E. naraveana, Macario Córdova-Cortina guided the authors to one population of trees with morphological characters similar to the species collected by Miguel Cházaro-Basáñez in 1987, known as "guayabo" (guajava), but with a different vernacular name, "guayabillo" (small guajava), but it was not explored because it was decided to find the species first collected three decades ago, since both populations were considered to belong to the same taxon, the differences in fruit size being attributed to phenotypic variation. After having described and published the species (Cházaro-Basáñez and Francisco-Gutiérrez 2016), the work of the author mainly focused on the description of the species of Agave (Arzaba-Villalba et al. 2018, 2023) and parasitic Orobanchaceae (Francisco-Gutiérrez et al. 2019, 2023a). In July 2021, during the lockdown of the coronavirus pandemic, the fieldwork was resumed with an expedition by Miguel Cházaro-Basáñez and Héctor Narave-Flores. Finally, the species was found in the locality of Encinal II, municipality of Acajete, Veracruz, Mexico, and subsequent visits were made to collect biological and photographic material.

Taxonomic determination

Fresh specimens of the species were collected, photographed, and dried or preserved in a solution 1:1 of ethanol and water. Measurements were made on living and preserved specimens. Voucher specimens are deposited in the cited herbaria, these cited by the acronyms following Thiers (2023). The sectional placement was determined following the sectional key provided by Mazine et al. (2016). The checklist of accepted species of *Eugenia* in Mexico (Uc-Gala et al. 2023), the taxonomic treatment of Myrtaceae in Veracruz (Sánchez-Vindas

1990), and articles of recently described species in the state (Cházaro-Basáñez and Francisco-Gutiérrez 2016; Durán-Espinosa et al. 2018) were consulted for taxonomic determination and morphological comparisons.

Conservation assessments

Geographic coordinates were obtained in the field with a Garmin eTrex10 GPS. The data were used to estimate the geographic ranges of the extent of occurrence (EOO) and area of occupancy (AOO) with the Geospatial Conservation Assessment Tool (GeoCAT, Bachman et al. 2011) at the website http://geocat. kew.org/. The obtained values and literature on threats in the species' distribution area were weighted to evaluate the conservation status following the Categories and Criteria of the IUCN Red List of Threatened Species (IUCN Standards and Petitions Committee 2022).

Distribution map

The polygon of the Cofre de Perote Volcano National Park was extracted from the World Database on Protected Areas and Other Effective Area-based Conservation Measures (WDPA–WDOECM) of the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC and IUCN 2021), available at https://www.protectedplanet.net/en. Digital elevation models correspond to the layer provided by WorldClim 2.1 (Fick and Hijmans 2017) with resolution of 2.5 min, and the model Continuo de Elevaciones Mexicano 3.0 of the Instituto Nacional de Estadística y Geografía (INEGI) of Mexico with resolution of 130 m, available at https://www.inegi.org.mx/app/geo2/elevacionesmex/. Map was designed in QGIS 2.15 (QGIS Development Team 2016).

Taxonomic treatment

Eugenia sarahchazaroi Cházaro, Franc.Gut. & J.R.Carral, sp. nov. urn:lsid:ipni.org:names:77331910-1

Diagnosis. Eugenia sarahchazaroi is morphologically similar to *E. naraveana* but differs by having shorter and smaller leaves $(37.3-59.7 \times 14.4-21.3 \text{ mm} \text{ vs. } 57-116 \times 22-55 \text{ mm} \text{ in } E. naraveana)$, reduced number of flowers per fascicle (4-6 vs. 3-16), absence of bracteoles (vs. presence), shorter pedicels (1-1.7 × 0.6-1 mm vs. 6-12 × 1-2.6 mm), smaller staminal disc (1.6-2 mm vs. 3-5 mm wide), presence of central cavity in staminal disc (vs. absence), shorter style (3.4-7 mm vs. 7.5-9.7 mm), and shorter fruits (1.4-1.8 cm vs. 1.1-4.3 cm). The species is also similar to *E. coetzalensis* but it can be distinguished by its inflorescence (axillary fascicles vs. axillary racemes in *E. coetzalensis*).

Type. MEXICO. Veracruz: Municipio Acajete, Paraje La Cieneguilla, cerca del Encinal II, 19.517372, -97.043692, elev. 2400 m, 01 July 2021, fl., *M. Cházaro-Basáñez & H. Narave-Flores 11226* (holotype: XAL!; isotypes: CIB!, CITRO!, ENCB!, IBUG!, MEXU!, XALU!).

Description. *Tree* 4.5–20 m tall. *Bark* exfoliating, the outer layer fissured and covered by lichens, the inner layer smooth and pink to reddish. Twigs terete,

some covered by lichens, apical leaves paired. Internodes 15.8-21.6 mm long, 1.1-2.1 mm in diam., not exfoliating, shortly lanose to glabrescent in apical leaves. Cataphylls absent. Leaves opposite, petioles curved and adpressed, later the terminal petioles parallel to the main axis of the branches, sometimes straight and perfectly aligned one in front of the other, simulating a cross, 2.4-7.2 × 0.9-1 mm, shortly lanose. Blades 37.3-59.7 × 14.4-21.3 mm, lanceolate or elliptical, chartaceous and glossy, discolorous when dry, glabrous adaxially and abaxially, oil glands present; base cuneate, apex acuminate, 5.6-10.7 mm long, margin entire and sinuate; midvein slightly impressed adaxially, prominent abaxially, glabrous in both surfaces; secondary veins 7-14 at each side, leaving the midvein at angles of 53-76°, slightly conspicuous adaxially; one marginal vein, 0.6-1.4 mm from the margin. Inflorescences axillary fascicles, frequently 2 per node, rarely 1, 4-6 flowers each, bracts, and bracteoles absent. Pedicels of floral buds: 1.0-1.7 × 0.6-1 mm, straight to slightly curved, sometimes thickened at the base. 2-ribbed, pubescent, trichomes strigose. Flower buds ovoid to spherical, 1.1-3 mm diam., hypanthium campanulate, 1.2-2.3 × 1.5-2.2 mm, light green, shortly pubescent, trichomes simple. Flowers at anthesis with hypanthium, 1.08-1.5 × 1.4-1.9 mm, glabrous, pale green to reddish. Calyx lobes 4, free, one pair slightly less developed than the other, lobes 0.44-0.77 × 1.2-1.91 mm, widely triangular or orbicular, apex obtuse, abaxially, and adaxially glabrous, margin ciliate, trichomes 0.04-0.07 mm long, green to reddish. Petals 4, 2.4-3.2 × 2.7-2.9 mm, orbicular to elliptical, with few circular brown glands, apex widely rounded, glabrous. Staminal disc a circular ring, sometimes square with rounded corners, 1.6 mm in diameter or 1.6-2.0 mm in diameter, central cavity with no stamens inserted, 0.79-1 mm in diameter, glabrous. Stamens 31-76, deciduous, filaments 2.1-5 × 0.16-0.18 mm, glabrous; anthers 0.38-0.51 × 0.31-0.64 mm, oblong to ellipsoid, glabrous. Style 3.4-7 × 0.33-0.44 mm, glabrous, white, sometimes reddish, deciduous. Ovary locules 2, 2 ovules each. Fruit a drupe; peduncles straight or slightly curved, 4.2-4.7 × 1.9-3.8 mm; immature fruit globose to ellipsoid with some prominent and longitudinally parallel veins, 9-17.9 × 11.3-14.8 mm, smooth to reticulate, partially green, yellow or red-tinged, glabrous, not crowned at the apex with calyx lobes, pulp yellow with red granules; ripe fruit globose to ellipsoid with no veins, 14.1-18.2 × 14.7-17.2 mm, smooth, dark purple to black, glabrous; mesocarp 3.1 mm wide, salmon to dark purple; one seed per fruit, spherical to elliptical, $13.5-13.8 \times 12-12.5$ mm, testa smooth (Fig. 1).

Phenology. The species was collected with floral buds, flowers, and mature fruits from April to July.

Etymology. The specific epithet honors Sarah Magyari Cházaro-Hernández, the beloved daughter of Miguel Cházaro-Basáñez, who has accompanied him on numerous botanical expeditions. As a child, Sarah Cházaro developed an interest in botany by learning to identify several plant genera on field trips with her father (Fig. 4). This new species is the third dedicated to his children, with *Agave paskynnellchazaroi* Arzaba, Cházaro & Franc.Gut. (Arzaba-Villalba et al. 2023), and *Valeriana rudychazaroi* Cházaro, Franc.Gut. & J.R.Carral (Francisco-Gutiérrez et al. 2023b). These eponyms were the last will of Miguel Cházaro before he passed away on April 04, 2023. The obituary with a review of his life and work can be found in Francisco-Gutiérrez and Vázquez-García (2023).



Figure 1. *Eugenia sarahchazaroi* **A** inflorescence **B** twig with fruits **C** detail of flowers **D** fascicles **E** floral buds **F** staminal disc **G** adaxial surface of a leaf **H** abaxial surface of a leaf **I** immature fruit **J** ripe fruit, and **K** seedling. All photographs were taken by Rodrigo Carral-Domínguez and edited by Antonio Francisco-Gutiérrez.

Distribution and habitat. The Cofre de Perote volcano, has been botanically explored since 1804 by Humboldt & Bonpland and many subsequent botanists. The mountain and its periphery house rare and new species recorded and described since the 1980's (for a detailed review, see Cházaro et al. 2016). Eugenia sarahchazaroi is only known from the type locality. Other species inhabiting the cloud forest near the new species are Quercus corrugata Hook., Q. acherdophylla Trel. (Fagaceae), Eugenia naraveana Cházaro & Franc.Gut., Myrsine penduliflora A.DC. (Primulaceae), Ilex discolor Hemsl., Peperomia tenerrima Schltdl. & Cham. (Piperaceae), Lamourouxia xalapensis Kunth, Pedicularis canadensis L. (Orobanchaceae), Oreomunnea mexicana (Standl.) J.-F.Leroy (Juglandaceae), Echeveria secunda Booth ex Lindl., E. rosea Lindl. (Crassulaceae), Turpinia occidentalis (Sw.) G.Don (Staphyleaceae), Ocotea disjuncta Lorea-Hern. (Lauraceae), Citharexylum hidalgense Moldenke (Verbenaceae), Cestrum fasciculatum Miers (Solanaceae), Symplocos coccinea Bonpl. (Symplocaceae), Oreopanax flaccidus Marchal (Araliaceae) and Aporocactus flagelliformis (L.) Lem. (Cactaceae), among many other species. It is close to the also endemic E. naraveana, which was only known from the type locality. Recent data allow for the expansion of its distribution, reported in the municipality of Zongolica, Veracruz (David Jimeno-Sevilla, curator of ZON herbarium, pers. comm.). An updated distribution map of E. sarahchazaroi and related species is provided in Fig. 3.

Vernacular name. "Guayabillo" (Macario Córdova-Cortina and Héctor Narave-Flores, pers. comm.).

Paratypes. MEXICO. Veracruz: Municipio Acajete, Rancho de Martín Sangabriel, camino El Zapotal – El Encinal 2, km 1.52, 19.512869, -97.04118, 2320 m, 18 April 2022, fr., *R. Carral-Domínguez, L. Islas-Tello, I. Gómez-Escamilla & B. Téllez-Baños RCD-852* (IBUG!, MEXU!, XAL!); Municipio Acajete, Rancho de Martín Sangabriel, camino El Zapotal – El Encinal 2, km 1.52, 19.512974, -97.040498, 2312 m, 18 April 2023, *R. Carral-Domínguez, E. Marinero-Sobal & L. Abrajan-Cortés RCD-853* (XAL!, MEXU!); Municipio Acajete, Rancho de Martín Sangabriel, camino El Zapotal – El Encinal 2, km 1.52, 19.513025, -97.040499, 2306 m, 07 May 2023, *R. Carral-Domínguez, D. Canales-Suardíaz & A. Seedorf-Anaya RCD-854* (XAL!, MEXU!, IBUG!).

Conservation status. The species has geographic ranges of Extent of Occurrence (EOO) of 0 km², and Area of Occupancy of 4 km². The species grows in the foothills of the Cofre de Perote Volcano, about 7.5 km from the limit of the protected area under the national park category (Fig. 3), a location that threatens it because the vicinity of the volcano has experienced constant overexploitation of forests and illegal logging since the 20th century (Hoffmann 1989). Because of EOO < 100 km², AOO < 10 km², number of locations = 1, and continuing decline observed in the extent and quality of habitat, we evaluate the new species *E. sarahchazaroi* in the category critically endangered CR B1+B2(a,biii). This species is currently the target of conservation efforts being reproduced in the greenhouses of the Secretary of Environment and Natural Resources (SEDEMA) of Veracruz.

Discussion. Eugenia sarahchazaroi belongs to the section Umbellatae through having bracteoles and calyx lobes not foliaceous, calyx open in the bud, and flowers 4-merous arranged in fascicles. This section has the largest species richness in Eugenia, with about 680 species (Mazine et al. 2016).

The species of *Eugenia* from Veracruz, Mexico, were studied in the issue of Myrtaceae of the Flora of Veracruz series (Sánchez-Vindas 1990). These species were considered for the morphological comparisons with *E. naraveana* (Cházaro-Basáñez and Francisco-Gutiérrez 2016), the most similar species. Besides, only the species *E. coetzalensis* was later described for Veracruz. Because of it, the new species presented here is compared with both.

Eugenia sarahchazaroi is distinguished from *E. coetzalensis* mainly by the type of inflorescence (fascicle vs. racemes, respectively). The paratype of *E. coetzalensis, E. Guízar-N. & J.C. Echeverría 5688* (MEXU1075426) can be electronically consulted at https://datosabiertos.unam.mx/IBUNAM:MEXU:1075426. *Eugenia sarahchazaroi* is similar to *E. naraveana* but it differs in several morphological characters, which can be analyzed in the Table 1. Overall, this new species' leaves, pedicels, hypanthium, staminal discs, and fruits are smaller than those of the *E. naraveana*. Additionally, the number of leaves and fruits are notably higher than in *E. naraveana*, as seen in photographs of Fig. 2. The staminal disc also shows a suppressed central area with no stamens where the style inserts, which is lacking in the staminal discs of *E. naraveana*. These features allow us to determine this taxon as a different species.

Character	E. sarahchazaroi	E. naraveana	E. coetzalensis
Leaf size (mm)	37.3-59.7 × 14.4-21.3	57-116 × 22-55	23-60 × 18-33
Petiole orientation	Curved and adpressed or sometimes straight	Straight	Straight
Number of secondary veins per side	7–14	7–13	11–16
Angle of secondary veins	53-76°	60-70°	40°
Indumentum of leaf surfaces	Glabrous	Glabrous	Adpressed-strigose when newly formed, glabrescent when mature
Inflorescence and number of flowers	Axillary fascicles, frequently 2 per node, rarely 1; 4–6 flowers	Axillary fascicles, 1–2 per node; 3–16 flowers	Axillary racemes, 1 per axil, 2 per node; 2–4 flowers
Bracteoles shape	Absent	Ovate	Lanceolate
Pedicels size (mm)	1.0−1.7 × 0.6−1.0	6-12×1.0-2.6	8−17 × 0.4−0.5
Hypantium length (mm)	1.08-2.3	2.6-3.4	1.6-2.6
Staminal disc shape	Rounded, sometimes square with rounded corners	Quadrangular	Square
Staminal disc size	1.6 mm in diameter or 1.6–2.0 mm per side	3−5 × 3−5 mm	2 × 2 mm
Central cavity in staminal disc	Present	Absent	Unknown
Number of stamens	31-76	70-131	60-100
Style length (mm)	3.4-7	7.5-9.7	3.4-5.6
Fruit shape	Globose to ellipsoid	Subglobose	Globose
Fruit size (cm)	1.4-1.8 × 1.4-1.7	1.1-4.3 × 0.9-3.4	1.3 × 2
Fruit indumentum	Glabrous	Glabrous	Faintly strigose
Source	This study	Cházaro-Basáñez and Francisco-Gutiérrez (2016)	Durán-Espinosa et al. (2018)

Table 1. Morphological comparison among Eugenia sarahchazaroi and similar species E. naraveana and E. coetzalensis.



Figure 2. Morphological comparison between *Eugenia sarahchazaroi* and *E. naraveana*. All photographs of *E. sarahchazaroi* aroi were taken by Rodrigo Carral-Domínguez; photographs of *E. naraveana* were taken by Antonio Francisco-Gutiérrez, except for the branch with fruits by Jose Luis Ramírez-Pacheco.



Figure 3. Distribution map of *Eugenia sarahchazaroi* and similar species in Mexico. The colored square corresponds to the Cofre de Perote volcano and its natural protected area under the category of National Park, delimited with the yellow line.



Figure 4. Miguel Cházaro and his beloved daughter, Sarah M. Cházaro-Hernández **A** learning her first botanical knowledge at three years old at home **B** botanical expedition in El Chico National Park, Hidalgo, Mexico, in 2018. Photographs taken by Patricia Hernández-Romero.

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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: MCB, HNF. Data curation: RCD, LIT, AFG, MCB. Formal analysis: AFG. Funding acquisition: MCB. Methodology: AFG, RCD. Project administration: MCB. Visualization: RCD, AFG. Writing - original draft: AFG. Writing - review and editing: HNF.

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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

Research Article

Rhynchospora mesoatlantica (Cyperaceae), an imperiled new species of beaksedge from eastern U.S.A.

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Abstract

Rhynchospora mesoatlantica **sp. nov.** (Cyperaceae) is described, illustrated, and compared with morphologically similar species. *Rhynchospora mesoatlantica* is known only from southern Delaware, southeastern Maryland, and southern New Jersey, all within the Mid-Atlantic region of the U.S.A. It inhabits sunny, wet margins of natural, shallow, nutrient-poor, seasonal ponds of the Coastal Plain. Narrow leaf blades; fruits obpyriform in outline; faces of mature fruits possessing a central, pale, well-demarcated disk; and fruit tubercle margins denticulate for most of their lengths indicate *R. mesoatlantica* is most similar to *R. filifolia* and *R. harperi. Rhynchospora mesoatlantica* is unique in its fruit dimensions, scales intermediate in length between *R. filifolia* and *R. harperi*, and relatively long fruit stipe. The NatureServe rank of Critically Imperiled and the IUCN rank of Endangered appear warranted for *R. mesoatlantica* because only six populations are known to be extant, most quite small and isolated; all populations occur within a small geographic area; populations have declined; and serious threats confront the survival of the species.

Key words: Mid-Atlantic, morphometric analysis, *Rhynchospora filifolia*, *Rhynchospora harperi*, *Rhynchospora* section *Fuscae*, sedge

Introduction

Rhynchospora Vahl section *Fuscae* (C.B.Clarke ex Gale) Kük., as circumscribed by Gale (1944) and Kral (1996), is a group of sedges characterized by perianth bristles antrorsely barbed, fruit bodies widest in distal half and with smooth faces, and tubercle margins denticulate. Six species belong to *Rhynchospora* section *Fuscae: R. crinipes* Gale, *R. curtissii* Britton, *R. filifolia* A.Gray, *R. fusca* (L.) W.T.Aiton, *R. harperi* Small, and *R. pleiantha* (Kük.) Gale. These species occur from eastern North America south to northeastern South America, with *R. fusca* also occurring in Europe. The center of diversity is the southeastern U.S.A.

The most recent phylogenetic analysis that included members of *Rhyn-chospora* section *Fuscae* indicated the section was polyphyletic (Budden-



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hagen et al. 2017). This analysis indicated the four included members of *Rhynchospora* sect. *Fuscae* (*R. curtissii*, *R. filifolia*, *R. fusca*, and *R. pleiantha*) belonged to three clades separated from each other by multiple clades composed of species from other sections of *Rhynchospora*, e.g. *R. ciliaris* (Michx.) C. Mohr, *R. fascicularis* (Michx.) Vahl, and *R. lindeniana* Griseb. However, this analysis is based on DNA sequence data from only one marker, *trnL/F*. Future analyses with more ample taxon and molecular sampling will be necessary to settle questions of monophyly of *Rhynchospora* section *Fuscae* and relationships of taxa within it.

Several previous authors have included Delaware and Maryland within the range of *R. harperi* (Kral 1996, 2002; LeBlond 1997; McMillan 2007; McAvoy 2013; Maryland Natural Heritage Program 2016, 2021; Knapp and Naczi 2021). In addition, McMillan (2007) included New Jersey within the range of this species. Both Kral (1996: 396) and LeBlond (1997: 278) reported northern plants (from Delaware and Maryland) resembled *R. filifolia* in aspect, but had fruits resembling *R. harperi* plants from the southeastern U.S.A. These authors contended that the northern plants fit within the concept of *R. harperi* and included them within this species.

Among plants previously identified as *Rhynchospora harperi*, we observed substantial differences between plants of the Mid-Atlantic (Delaware, Maryland, and New Jersey) and plants from farther south, including characters not noted by previous authors. Our observations led us to hypothesize that the Mid-Atlantic plants were a species distinct from *R. harperi*. We tested this hypothesis with field work, herbarium work, and morphometric analyses. The purpose of this paper is to report our results, which supported our hypothesis. Accordingly, we also describe the new species *Rhynchospora mesoatlantica*.

Materials and methods

We studied the morphology, geography, and ecology of *Rhynchospora* through herbarium work and field work. For herbarium work, we borrowed specimens from, or studied specimens during, visits to DOV, GA, GH, MO, NCU, NY, PH, US (abbreviations as in Thiers 2023). We directly examined all specimens cited in this paper.

The measurements we report in this paper are ones we made directly from specimens. For morphometric analyses, we selected a representative set of 68 specimens of *Rhynchospora filifolia* and *R. harperi* to measure. We chose mature, ample specimens from throughout the geographic ranges of these species that exhibited their full range of morphologic variation. Among these specimens, we measured type specimens. All measured specimens are from different populations. We considered populations to be different if their localities are at least 1 km apart and separated by unsuitable habitat. For each of these measured specimens (Appendix 1), we measured eight continuous characters and calculated one ratio of measured characters (Table 1). The characters we studied morphometrically are those suggested to be diagnostic for species and infraspecific taxa by previous authors (Gale 1944; Kükenthal 1950; Kral 2002; McMillan 2007; Naczi and Moyer 2016; Ciafré and Naczi 2022), as well as additional ones we suspected to be diagnostic based on our observations from field and herbarium work.

 Table 1. Morphologic characters, with their abbreviations, measured on herbarium specimens of *Rhynchospora*.

1. SPKLTL	spikelet length, measured from base of lowest scale or its scar to apex of distalmost scale
2. SCLL	scale length, measured for scale from middle of spikelet, from its base to its apex, including awn when present
3. FRL	fruit length, measured from base of fruit to apex of tubercle
4. FRW	fruit width, measured at widest point
5. STPL	stipe length, measured from base of fruit to point at which it widens
6. LBRL	longest perianth bristle length, measured from base of fruit to apex of bristle
7. FRBDYL	fruit body length, measured from base of fruit to summit of fruit body
8. TL	tubercle length, measured from summit of fruit body to apex of tubercle
9. RTLFRL	tubercle length/fruit length

We plotted measurements of characters that were not highly correlated with each other (r < 0.7, thus probably not genetically redundant) in order to detect groups within the morphometric dataset. We then used ANOVA to test for differences among the groups. We performed all statistical analyses with SYSTAT version 11 (SYSTAT Software 2004).

Field work furnished geographic and ecologic data. To determine the geographic range of *Rhynchospora mesoatlantica*, we used specimen collection data to map all known occurrences. For each population of *Rhynchospora* that we studied in the field, we noted vascular plant taxa growing in close association with the target species. We considered closely associated plant taxa to be those growing within 10 meters of *R. mesoatlantica*.

Results

Within *Rhynchospora* section *Fuscae*, *R. crinipes*, *R. curtissii*, *R. filifolia*, and *R. harperi* comprise a group characterized by four features: cespitose habit, fruit body compressed, mature fruit body with well-demarcated pale disk on center of each face, and fruit with tubercle margins denticulate for most of their lengths (both proximally and distally). The other members of *Rhynchospora* sect. *Fuscae*, *R. fusca* and *R. pleiantha*, have a long-creeping rhizomatous habit, fruit bodies biconvex, mature fruit body uniformly brown, and tubercles denticulate only in the proximal half.

Rhynchospora curtissii is quite distinctive in having the perianth bristles long [longest perianth bristle (3.0-)3.5-4.2 mm long in *R. curtissii* vs. 1.5-2.7(-3.1) mm long in other members of *Rhynchospora* sect. *Fuscae*]. In addition, in *R. curtissii*, the fruit body is narrowly oblong-obovate in outline (vs. obovate or obpyriform in other members of *Rhynchospora* sect. *Fuscae*).

Rhynchospora crinipes is distinctive in having relatively wide leaves (widest leaf blade per plant 2.2–3.8 mm wide in *R. crinipes* vs. 0.6–1.9 mm wide in other members of *Rhynchospora* section *Fuscae*). Also, *R. crinipes* has relatively long fruits [fruits, including tubercles, 2.6–2.9 mm long in *R. crinipes* vs. 1.5–2.6(–2.8) mm long in other members of *Rhynchospora* sect. *Fuscae*] with a long stipe (stipe 0.45–0.83 mm long in *R. crinipes* vs. 0.11–0.38 mm long in other members of *Rhynchospora* sect. *Fuscae*).

The remaining species of *Rhynchospora* sect. *Fuscae*, *R. filifolia* and *R. harperi*, are more similar to each other than they are to other species of the section. A plot of scale length (SCLL) vs. fruit width (FRW) for these two species reveals three clusters of points (Fig. 1). Inclusion of measurements from type specimens enables identification of these groups. These clusters correspond to *R. filifolia*, another to *R. harperi*, and a third corresponds to plants from Delaware, Maryland, and New Jersey that we propose as a new species and describe below as *R. mesoatlantica*. For this plot, all of the clusters of points are separate and non-overlapping.

Most characters measured are statistically significantly different among *Rhynchospora filifolia*, *R. harperi*, and *R. mesoatlantica* (Table 2). The characters that best differentiate the species, judging by ANOVA *F* scores, are scale length (SCLL), spikelet length (SPKLTL), tubercle length (TL), fruit width (FRW), and fruit length (FRL), in descending order of discriminatory power. For every one of these five characters, *R. filifolia* has the lowest values, *R. harperi* has the highest values, and *R. mesoatlantica* has intermediate values. For measurements of one character, stipe length (STPL), *R. mesoatlantica* has greater values than both *R. filifolia* and *R. harperi* (Table 2, Fig. 2). For fruit body length (FRBDYL) and longest perianth bristle length (LBRL), *R. mesoatlantica* have very similar measurements, and both have larger values than in *R. filifolia*.

We observed syntopy of *Rhynchospora filifolia* and *R. mesoatlantica* at one site in Sussex County, Delaware. At this site, we discovered the two species growing within 5 meters of each other (*R. filifolia: Treher 84a, Naczi 12060A; R. mesoatlantica: Treher 84, Naczi 12060*).



Figure 1. Scale length vs. fruit width for *Rhynchospora filifolia*, *R. harperi*, and *R. mesoatlantica*. Asterisked symbols indicate lectotype of *R. filifolia*, holotype of *R. harperi*, and holotype of *R. mesoatlantica*.

Character	R. filifolia (N = 29)	R. harperi (N = 27)	R. mesoatlantica (N = 12)	ANOVA F
1. SPKLTL	3.3° ± 0.44 (2.5-4.3)	5.9 ^b ± 0.58 (5.0-7.2)	4.2° ± 0.31 (3.6-4.7)	220
2. SCLL	2.5° ± 0.20 (2.1-3.0)	4.3 ^b ± 0.40 (3.8-5.0)	3.2° ± 0.17 (3.0-3.4)	260
3. FRL	1.7° ± 0.11 (1.5−1.9)	2.4 ^b ± 0.19 (2.1-2.8)	2.2° ± 0.055 (2.1-2.3)	140
4. FRW	0.70° ± 0.058 (0.55-0.81)	0.97 ^b ± 0.071 (0.83-1.1)	0.90° ± 0.022 (0.85-0.93)	150
5. STPL	0.24ª ± 0.046 (0.16-0.34)	0.26° ± 0.044 (0.20-0.35)	0.33 ^b ± 0.030 (0.29-0.38)	21
6. LBRL	1.8° ± 0.20 (1.5-2.3)	2.3 ^b ± 0.29 (1.5−2.9)	2.2 ^b ± 0.10 (2.0-2.4)	31
7. FRBDYL	1.2° ± 0.098 (1.1-1.4)	1.5 ^b ± 0.15 (1.2−1.8)	1.6 ^b ± 0.067 (1.5-1.7)	56
8. TL	0.51° ± 0.052 (0.39-0.62)	0.85 ^b ± 0.087 (0.70-0.99)	0.63° ± 0.050 (0.56-0.70)	180
9. RTLFRL	0.29° ± 0.028 (0.24-0.34)	0.36 ^b ± 0.028 (0.30-0.45)	0.29ª ± 0.022 (0.26-0.32)	48

Table 2. Means \pm 1 SD and ranges for morphologic characters measured for *Rhynchospora*. Character abbreviations correspond to those in Table 1. All measurements are in millimeters. *N* = sample size. Within a row, means with different superscripts differ significantly (ANOVA, *P* < 0.01).

Discussion

Comparative morphology and morphometric analyses support the hypothesis that *R. mesoatlantica* is distinct from all other *Rhynchospora* species. Multiple morphologic features clearly place *Rhynchospora* mesoatlantica in *Rhynchospora* sect. *Fuscae*: perianth bristles antrorsely barbed, fruit bodies widest in distal half and with smooth faces, and tubercle margins denticulate. Additional features place *R. mesoatlantica* as most similar to *R. filifolia* and *R. harperi*: habit cespitose, widest leaf blade < 2.0 mm wide, longest perianth bristle < 3.0 mm long, fruit body compressed and with a well-demarcated pale disk on the center of each face, and tubercle margins denticulate for most of their lengths.

Several morphologic characters distinguish *Rhynchospora mesoatlantica* from *R. filifolia* and *R. harperi*. A plot of SCLL vs. FRW provides complete separation of *R. mesoatlantica* from both *R. filifolia* and *R. harperi* (Fig. 1). In addition, ANOVA reveals *R. mesoatlantica* is statistically significantly different from both *R. filifolia* and *R. harperi* in six of the nine characters studied in the morphometric analysis: SPKLTL, SCLL, FRL, FRW, STPL, and TL. Two additional characters distinguish *R. mesoatlantica* from *R. filifolia* (FRBDYL, LBRL), and one other character distinguishes *R. mesoatlantica* from *R. harperi* (RTLFRL). All these diagnostic characters are from fruits, scales, and spikelets.

Syntopy of *Rhynchospora filifolia* and *R. mesoatlantica* is another line of evidence supporting species status for *Rhynchospora mesoatlantica*. Despite *R. mesoatlantica* growing in close proximity to *R. filifolia*, the two species maintain their morphologic distinctions at the syntopic site, as well as in all known populations. This naturally occurring syntopy provides a strong test of species distinctions for *R. filifolia* and *R. mesoatlantica*. However, the geographic ranges of *Rhynchospora mesoatlantica* and *R. harperi* do not overlap, making syntopy of these two species impossible.

Specimens of *Rhynchospora mesoatlantica* collected prior to our work had been determined as *R. filifolia* or *R. harperi*. Now that we have presented support for species status for *R. mesoatlantica*, we name and describe this species in order to clarify its status and bring attention to it as a species of conservation concern.

Taxonomic treatment

Rhynchospora mesoatlantica A.Eberly & Naczi, sp. nov.

urn:lsid:ipni.org:names:77332119-1 Figs 2–4

Type. U.S.A., Delaware: Sussex County, 2 mi E of Bayard, Assawoman Wildlife Area, 29 Sep 2007, *A. Treher 84 & R. Naczi* (holotype: NY [measured for morphometric analyses]; isotypes: DOV, PH, US).

Diagnosis. *Rhynchospora mesoatlantica* is similar to *R. filifolia* and *R. harperi*, but *R. mesoatlantica* differs by its fruit dimensions, scales intermediate in length between *R. filifolia* and *R. harperi*, and relatively long fruit stipe. In *R. mesoatlantica*, scales are 3.0–3.4 mm long, and tubercles are 0.6–0.7 mm long and 26–32% of fruit length, in contrast to *R. harperi*, which has scales 3.8–5.0 mm long, and tubercles 0.7–1.0 mm long and (30–)33–39(–45)% of fruit length. In *R. mesoatlantica*, scales are 3.0–3.4 mm long, and fruits are 2.1–2.3 mm long and 0.9 mm wide, in contrast to *R. filifolia*, which has scales 2.1–3.0 mm long, and fruits 1.5–1.9 mm long and 0.6–0.8 mm wide. *Rhynchospora mesoatlantica* has fruit stipes 0.29–0.38 mm long, in contrast to *R. filifolia* (0.16–0.34 mm long) and *R. harperi* (0.20–0.35 mm long).

Description. Culm (2-)3-9 dm tall, 0.4-1.2 mm wide at midpoint, erect. Leaves filiform, flexuous; proximal leaf blades 7-25 cm long, 0.2-0.6 times the culm height, 0.5-0.8 mm wide, margins involute; cauline leaf blades 9-21 cm long, 0.5-1.5 mm wide, margins involute. Infructescence composed of 1-3 (-4) compound fascicles per culm. Fascicles hemispheric to occasionally turbinate, 1.0-2.0 cm wide, composed of 5-75 spikelets, branches of subfascicle 0.3-0.9 cm long, 0.2-0.3 mm wide; distalmost fascicle bracts 1-3, 2-13 cm long, 1-1.5 mm wide. Spikelets 3.6-4.7 mm long, proximal scales 1.5-2 mm long, scales from middle of spike 3.0-3.4 mm long, cinnamon brown with darker brown central nerve. Perianth bristles 6, the longest per fruit 2.0-2.4 mm long, 0.8–1.1 times as long as fruit (including tubercle), antrorsely barbellate. Fruit (including the tubercle) 2.1-2.3 mm long, 0.85-0.93 mm wide, bearing persistent perianth bristles; body 1.5-1.7 mm long, obpyriform in outline, surface shiny, smooth, brown or reddish-brown except for whitish and well-demarcated central disk on each face, central disk occupying 0.4-0.8 of fruit width; tubercle with straight or slightly concave margins, 0.56-0.70 mm long, 0.26-0.32 of fruit length, 0.6-0.7 mm wide at base; stipe 0.29-0.38 mm long.

Etymology. We name *Rhynchospora mesoatlantica* for the Mid-Atlantic region of the U.S.A., the region in which all known populations occur.

Geographic distribution. *Rhynchospora mesoatlantica* is a narrow endemic of a portion of the Mid-Atlantic U.S.A. (Fig. 5). It is known only from southern New Jersey, southern Delaware, and southeastern Maryland, where it occurs on the Coastal Plain physiographic province. Specimens document its occurrence from a total of 12 populations, each separated by at least 1 km from other populations. Two of the populations in the vicinity of Ellendale, Delaware [E of Ellendale, *Commons s.n.* (PH); S of Ellendale, *McAvoy 6333* (DOV) and later collections] are sufficiently close (3 km apart) that they map as one population (Fig. 5). Other populations are separated by greater distances. The greatest distance separating nearest neighbors among populations



Figure 2. Representative mature fruits of *Rhynchospora* species. Left to right: *Rhynchospora* filifolia [Naczi 12060A & Treher (NY)], *R. harperi* [Naczi 16347 (NY)], and *R. mesoatlantica* [Naczi 12060 & Treher (NY)]. Scale bar: 1.0 mm.

(*Moyer G0272* in Cape May County, New Jersey, and *Commons s.n.* in Sussex County, Delaware) is 70 km.

Habitat. Rhynchospora mesoatlantica grows on the sunny, moist upper portions of natural, shallow, nutrient-poor, seasonal ponds and depressions with gently sloping shorelines and sandy-peaty soils (Fig. 6). Surrounding these wetlands are dry-mesic forests or pine plantations. Water levels are typically highest in winter and spring, which is characteristic of Coastal Plain ponds (Phillips and Shedlock 1993). By the time of fruiting, the ponds are usually devoid of standing water, and the plants grow in soils that are merely moist. At most sites we visited, natural seasonal fluctuations in water levels were disrupted by extensive ditching and draining that apparently lowered the water table. Drier soils throughout the year have provided favorable growing conditions for woody vegetation, which is slowly overgrowing and shading some of the sites. The least disturbed site had few trees and shrubs (Fig. 6). In the absence of the natural disturbance of fluctuating water levels, management appears necessary to maintain a sunny environment. Rhynchospora mesoatlantica may persist vegetatively or in the seed bank during periods of unfavorable conditions, but research is needed to understand its persistence and dormancy.

Close plant associates (those growing within 10 m) of *Rhynchospora mesoatlantica* are *Acer rubrum* L., *Boltonia asteroides* (L.) L'Hér. (*Treher 75 & Naczi*, DOV), *Cladium mariscoides* (Muhl.) Torr. (*Treher 74 & Naczi*, DOV), *Coelorachis rugosa* (Nutt.) Nash (*Naczi 12056 & Treher*, DOV, PH; *Treher 72 & Naczi*, DOV), *Coleataenia longifolia* (Torrey) Soreng ssp. *longifolia*, *Dichanthelium spretum* (Schult.)



Figure 3. *Rhynchospora mesoatlantica* **A** habit **B** distal portion of infructescence **C** spikelet **D** distal scale **E** immature fruit **F** mature fruit, lateral view, with detail of perianth bristle (left) and top view (below). From *Treher 84 & Naczi* (Holotype, NY). Scale bars: 2 cm (**A**); 1 cm (**B**); 1 mm (**C**, **D**, **E**); 0.5 mm (**F**).


Figure 4. Habit of *Rhynchospora mesoatlantica*. Amanda T. Eberly with *R. mesoatlantica* rooted in habitat at type locality (*Treher 84 & Naczi*).

Freckmann (Naczi 12057 & Treher, NY, PH), Eleocharis tenuis Schult., Hypericum denticulatum Walter (Naczi 12058 & Treher, DOV), Juncus canadensis J.Gay in Laharpe (Naczi 12064 & Treher, NY; Treher 82 & Naczi, DOV), Juncus repens Michx. (Naczi 12062 & Treher, NY; Treher 78 & Naczi, DOV), Kellochloa verrucosa (Muhl.) Lizarazu, Nicola, & Scataglini (Treher 116 & Naczi, DOV), Proserpinaca pectinata Lam. (Treher 79 & Naczi, DOV), Rhexia aristosa Britton (Naczi 12065 & Treher, DOV), Rhexia virginica L. (Treher 118 & Naczi, DOV), Rhynchospora chalarocephala Fernald & Gale (Naczi 12086 & Treher, NY; Treher 112 & Naczi, DOV), Rhynchospora filifolia (Naczi 12060A & Treher, NY; Treher 84a & Naczi, DOV), Rhynchospora gracilenta A.Gray (Treher 113 & Naczi, DOV), Rhynchospora inundata (Oakes) Fernald (Naczi 12061 & Treher, DOV), Saccharum giganteum (Walter), Scleria reticularis Michx. (Naczi 12063 & Treher, NY; Treher 77 & Naczi, DOV), Sclerolepis uniflora (Walter) Britton, Sterns, & Poggenb. (Naczi 12059 & Treher, DOV; Treher 73 & Naczi, DOV), and Sphagnum macrophyllum Bernh. ex Brid. Pers.

Preliminary conservation assessment. *Rhynchospora mesoatlantica* is at a high risk of extinction due to a restricted geographic range, small number of occurrences, small population sizes, and historic and ongoing declines due to numerous threats. All historic and current populations total 12. Six of the populations have not been seen for over 20 years, despite repeated, more recent surveys at most of the sites. Three of these populations had been documented in the 1990s, yet we could not relocate them. Thus, declines are apparent in



Figure 5. Known geographic distribution of Rhynchospora mesoatlantica. Based on all known collections.

number of populations and number of plants. We are sufficiently familiar with some of these sites to identify likely causes for extirpations: habitat destruction for some and, for others, habitat degradation, including changes to hydrology.

Only six populations are known to be extant. Populations are typically small, ranging from 25 to a maximum of 200–300 plants at the population northwest of Belleplain (R. Moyer, pers. comm.). Only three populations contain more than 100 plants. Our estimate of the total number of mature plants present in extant populations is 700.

Five of the six populations known to be extant are in protected areas. Most of these protected areas are state forests that allow resource extraction and consequent habitat alteration.

Most extant and historic occurrences are/were in Coastal Plain ponds in Delaware and Maryland, one of the most threatened habitats on the Delmarva Peninsula and host to many rare species (McAvoy and Bowman 2002). Most of these ponds and surrounding forests are highly degraded due to direct and indirect anthropogenic impacts. Land-use changes resulting in habitat fragmen-



Figure 6. Representative habitat of Rhynchospora mesoatlantica. At type locality (Treher 84 & Naczi).

tation, conversion of forest to pine plantations, destructive forestry practices like clear-cutting, and hydrologic alterations due to extensive ditching and draining are among the threats contributing to past and ongoing declines (McAvoy and Bowman 2002). Quantifying declines in *Rhynchospora mesoatlantica* is challenging; the historic record is sparse, with only four populations documented prior to 1990. Landscape changes are evident throughout the Delmarva Peninsula, including the extent of ditching and draining. In Delaware alone, there are over 2,000 miles of ditches intended to redirect normal water flows across the land and sustain productive agricultural lands (DE DNREC 2023). Unfortunately, these ditches negatively impact natural plant communities hosting *R. mesoatlantica* by interrupting seasonal water-level fluctuations that suppress woody vegetation. Habitat restoration with ongoing maintenance, especially for natural hydrologic cycles, appears to be warranted at most sites, including those on public lands.

Also noteworthy is the fact that *R. mesoatlantica* plants usually occupy only a portion, and often a small portion, of the Coastal Plain ponds that host this species. For example, the area of one pond is 0.008 km^2 ($8,000 \text{ m}^2$), yet plants of *R. mesoatlantica* occupy only 0.004 km^2 ($4,000 \text{ m}^2$) of the pond. Our estimate of the area occupied by all known *R. mesoatlantica* populations, historic and extant, is 0.031 km^2 ($31,000 \text{ m}^2$). For *R. mesoatlantica* populations known to be extant, our estimate of area occupied is 0.017 km^2 ($17,000 \text{ m}^2$).

Due to decades-long recognition of Coastal Plain ponds as centers of rare plant diversity (e.g., Hirst 1983; Boone et al. 1984; McAvoy and Bowman 2002) and our own extensive field efforts to rediscover formerly documented populations of *Rhynchospora mesoatlantica* and discover new ones, we regard the likelihood of discovery of new populations as low. Simply, most Coastal Plain ponds within the geographic range of *R. mesoatlantica* have been botanically explored, many very extensively during multiple years and multiple seasons.

We recommend a NatureServe Global Rank of Critically Imperiled (G1, Faber-Langendoen et al. 2012) for *Rhynchospora mesoatlantica*, based on considerations of rarity, threats, and trends (Master et al. 2012). There are 12 known occurrences (6 historic and 6 extant), a Range Extent (Extent of Occur-

rence, EOO) of 4,495 km², and an Area of Occupancy (AOO) of 44 km². Threat impact is estimated at very high, and short-term trends and long-term trends are estimated to be at least 10% and 40%, respectively, based on declines in AOO, population size, and number of occurrences.

As a preliminary assessment, we consider the IUCN category Endangered (IUCN Standards and Petitions Committee 2022) to apply to *Rhynchospora mesoatlantica* for the following reasons: EOO of 4,495 km² is < the 5,000 km² threshold (B1); AOO of 44 km² is < the 500 km² threshold (B2); and we have observed continuing decline in AOO, habitat quality, and number of populations (Bb). Tentatively, we assess the metapopulation as severely fragmented since at least 50% of the populations are isolated and small (< 50 plants) and occurring in a very rare and localized habitat surrounded by unsuitable habitats and with limited capacity for dispersal between distant extant populations 11–70 km apart (Ba).

Due to the severity of conservation threats, few known extant populations, small population sizes, and apparent necessity of human-mediated intervention to maintain habitats, we recommend *Rhynchospora mesoatlantica* for protection under the U.S.A. Endangered Species Act.

Additional specimens examined. (* = specimen measured for morphometric analyses)-U.S.A. Delaware: Sussex Co., Population 1: E of Bayard, 26 Sep 1986, Hirst 459 (DOV); Assawoman Wildlife Area, 8 Sep 1991, McAvoy s.n. (US); E of Bayard, Assawoman Wildlife Area, 31 Nov 1991, Hirst 449 (DOV); Assawoman Wildlife Area, 22 Nov 1992, McAvoy 243 (DOV); Assawoman Wildlife Area, 1.7 mi E of Bayard, 11 Nov 1993, Hirst 309 (DOV); Assawoman Wildlife Area, 16 Aug 1995, McAvoy 1234 (DOV); 2 mi E of Bayard, Assawoman Wildlife Area, 29 Sep 2007, Naczi 12060 & Treher (MO, NY, PH). Population 2: E of Ellendale, 17 Aug 1899, Commons s.n. (PH*). Population 3: S of Ellendale, Redden State Forest tract, N side of Saw Mill Road, E of Spicer Road, 29 Oct 2007, 6333 McAvoy (DOV); Redden State Forest, N side of Saw Mill Road, E of Spicer Road, SE of Ellendale, 5 Aug 2008, McAvoy 6417 (DOV); 4.5 mi W of Milton, 25 Sep 2008, Treher 373 & McAvoy (DOV*); S of Ellendale, N side of Saw Mill Road, 21 Aug 2013, McAvoy 7220 (NY). Population 4: 1.8 mi NNE of Whitesville, 12 Sep 1992, Hirst 415 & Wilson (DOV); 1.8 mi NNE of Whitesville, 12 Sep 1992, Hirst 416 & Wilson (DOV); 1.5 mi N of Whitesville, 27 Jul 1993, Hirst 409 & Wilson (DOV*); SE of Pepperbox, 30 Jul 1997, McAvoy 2765 (DOV). Population 5: 1.8 mi SW of Woodland, 28 Aug 1993, Hirst 410 & Wilson (DOV*). Maryland: Dorchester Co., Population 6: 1.7 mi NW of Reids Grove, 21 Aug 1998, Hirst 1198 & Wilson (DOV); 0.2 mi SE of junction of Centennial and Kraft Roads, 21 Aug 1998, Hirst 1200 & Wilson (DOV); NW of Reids Grove, 28 Aug 1998, McAvoy 3994 (DOV); 3.4 mi SW of Brookview, 1.8 mi NW of Reids Grove, 29 Aug 1998, Hirst 1208 & Wilson (DOV); 1.8 mi NW of Reids Grove, 3.4 mi SW of Brookview, 29 Aug 1998, Hirst 1209 & Wilson (DOV); 3.3 mi SW of Brookview, 1 Oct 2008, Treher 377 & Knapp (DOV*). Population 7: 1.5 mi SW of Brookview, 20 Sep 1997, Hirst 1189 & Wilson (DOV); W of Brookview, 4 Oct 1997, McAvoy 3160 (DOV*); S of Brookview, 28 Aug 1998, McAvoy 4002 (DOV); 1.4 mi SSW of Brookview, 2.0 mi NNE of Reids Grove, 29 Aug 1998, Hirst 1207 et al. (DOV). Wicomico Co., Population 8: NE of Mardela Springs, 17 Sep 2000, Hirst 1234 & Wilson (DOV*). Population 9: 1.5 mi W of Wango, 2 Oct 2007, Treher 110 & Naczi (DOV), 1.5 mi W of Wango, SW of junction of Twilleys Bridge Road and Fooks Road, 2 Oct 2007, Naczi 12087 & Treher (NY); S of Twilley's Bridge Road, W of Powellville, 30 Sep 2014, McAvoy 7465 (DOV*). Worcester Co., Population 10:

5 mi N of Pocomoke, Pocomoke State Forest, 6 Oct 1984, *Hirst 418* (DOV*); N of Pocomoke, Pocomoke State Forest, 22 Aug 1986, *Hirst 439* (DOV). **New Jersey:** Cape May Co., **Population 11:** Woodbine, 30 Aug 1900, *S. Brown 4289* (NY, PH*); Between Belleplain and Woodbine, 4 Sep 1960, *B. Hirst s.n.* (PH). **Population 12:** NW Belleplain, 24 August 2015, *R. Moyer G0272* (NY*).

Identification key to Rhynchospora section Fuscae

This key is for specimens bearing mature fruits. Measurements of fruit length include the tubercle, but not perianth bristles. Scale length is for scales from middle of spikelets.

2a Fruit 2.3–3.0 mm long, 0.9–1.3 mm wide; longest perianth bristle 2.7–3.	.8 ;a .8
	.8
mm long	.8
2b Fruit 1.6–2.0 mm long., 0.6–0.8 mm wide; longest perianth bristle 2.1–2.	12
mm long R. pleianth	Ia
1b Plants cespitose; fruit body with pale disk on center of each face, con	n-
pressed; tubercle margins denticulate for most of their lengths3	3a
3a Fruit body narrowly oblong-obovate in outline; longest perianth brist	le
(3.0–)3.5–4.2 mm long R. curtiss	sii
3b Fruit body obovate or obpyriform in outline; longest perianth bristle 1.5	<u>;</u> —
2.7(-3.1) mm long4	la
4a Widest leaf blade per plant 2.2–3.8 mm wide; fruit 2.6–2.9 mm long; fru	ıit
stipe 0.5–0.8 mm long R. crinipe	es
4b Widest leaf blade per plant 0.6-1.9 mm wide; fruit 1.5-2.6(-2.8) mi	m
long; fruit stipe 0.1–0.4 mm long5	ja
5a Spikelet 5.0–7.2 mm long; scale 3.8–5.0 mm long; tubercle 0.7–1.0 mi	m
long, (30–)33–39(–45)% of fruit length R. harpe	ri
5b Spikelet 2.5–4.7 mm long; scale 2.1–3.4 mm long; tubercle 0.4–0.7 mi	m
long, 24–34% of fruit length6	ba
6a Scale 2.1–3.0 mm long; fruit 1.5–1.9 mm long, 0.6–0.8 mm wide; fru	ıit
stipe 0.2–0.3 mm long R. filifol	ia
6b Scale 3.0-3.4 mm long; fruit 2.1-2.3 mm long, 0.9 mm wide; fruit stip	be
0.3–0.4 mm long R. mesoatlantic	a

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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

Conceived project: RN; conducted fieldwork: AE, RN; conducted herbarium work: AE, RN; conducted analyses: RN, AE; generated figures: RN, AE; wrote manuscript: RN, AE; reviewed and commented on manuscript prior to submission: RN, AE; revised manuscript in response to peer review: RN, AE.

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Data availability

All of the data that support the findings of this study are available in the main text and Appendix 1.

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Appendix 1

Selected Specimens Examined of *Rhynchospora filifolia* and *R. harperi*. Asterisked specimens are those measured for morphometric analyses.

Rhynchospora filifolia-BELIZE. Belize District: ca. 6 mi SE of La Democracia, along Coastal Highway, ca. 6 mi SE of its junction with Western Highway, 29 Nov 2005, Naczi 11210 et al. (BRH, DOV*, NY); 1.6 air mi N of junction of Old Northern Highway and Northern Highway, 0.15 mi E of Old Northern Highway, 15 Mar 2008, Treher 176 & Gibson (DOV). Toledo District, 6.8 mi NNE of Medina Bank, 2.2 mi S of southern boundary of Belize Foundation for Research and Environmental Education (BFREE), Deep River Forest Reserve, 25 Mar 2006, Naczi 11315 (BRH, DOV*, NY). CUBA. [Isla de la Juventud Municipality]: Vivijagua Savanna, 28-29 Feb 1916, Britton 15018 et al. (NY*, US). Pinar Del Rio Province: Herradura, 2 & 4 Dec 1904, Baber & Abarca 4195 (NY*, US). MEXICO. Tabasco: km 44.4 rumbo de Huimanguillo a Francisco Rueda, 6 Aug 1979, Cowan 2237 (NY*). NICARAGUA. Comarca del Cabo: Puente Pozo Azul, Kornuk Creek near Bilwaskarma, 14 Mar 1971, Svenson 4758 (NY*). U.S.A. Alabama: Covington Co., Route 7, ca. 9 mi S of Red Level and 3 mi S of Loango, 20 Jun 1967, Clark 14462 (NCU*). Houston Co., Route 4, ca. 4 mi W Chattahoochee State Park entrance, 5 Jun 1972, Kral 47253 (NCU*). Delaware: Sussex Co., East of Bayard, Assawoman Wildlife Management Area, 14 Sep 1998, Hirst 1221 (DOV*), 2 mi E of Bayard, Assawoman Wildlife Area, 29 Sep 2007, Naczi 12060A & Treher (NY), Treher 84a & Naczi (DOV). Florida: Bay Co., NW of Panama City, 3.55 mi E of route 79 on route 388, 27 Aug 2000, Abbott 13938 & Carlsward (DOV*). Duval Co., 1-2 mi ENE of Bryceville, E of route 301, Cary State Forest, 2 Jun 2000, Anderson 19290 (NY*). Martin Co., SE of Hobe Sound, Jonathan Dickinson State Park, 7 Jul 2008, Treher 306 et al. (DOV). Okeechobee Co., Okeechobee Prairie, North of Lake Okeechobee, 1 May 1919, Small 9093 (NY*). Palm Beach Co., W of Jupiter, N of Indiantown Road/route 706, Hungryland Environmental and Wildlife Area, 7 Jul 2008, Treher 273 et al. (DOV). Sarasota Co., Myakka River State Park, 0.25 mi S of State Rd 72, Treher 317 et al. (DOV*). Saint Lucie Co., 18 mi E of Okeechobee City, 8 Dec 1919, Small 9305 (NY*). Wakulla Co., Along route 372, SE of Sopchoppy, 9 Jun 1960, Godfrey 59702 (NCU*). Georgia: Bacon Co., 4 mi E of Nicholls by route 32, 25 Jun 1993, Kral 82714 & Carter (NCU, NY*). Bartow Co., 4.8 mi E, 28 degrees S of Adairsville, 14 July 1951, Duncan 12730 (NY*). Charlton Co., ca. 2 mi SW of Folkston, along W side of route 121, 28 Aug 2001, Naczi 8768 (DOV*). Louisiana: Allen Parish, end of dirt road running S from Parish Road 2-36, 12 Jun 1996, Sorrie 8904 (NCU*). Mississippi: Harrison Co., 3-4 mi N of Biloxi, 24 Jul 1971, Rogers 6829 (NCU*). Jackson Co., Ocean Springs, 29 Jul 1952, Demaree 32463 (PH*). New Jersey: Cape May Co., Lower Fishing Creek, Oliver's Bog, 18 Sep 1914, Brown s.n. (PH*). North Carolina: [No locality, no date], Curtis s.n. (Lectotype, designated by Gale [1944: 175]: NY00277848*). Carteret Co., Croatan National Forest, 1.8 mi NE of Ocean, 20 Aug 2008, Treher 356 (DOV*). South Carolina: Dillon Co., 3.5 mi SW of Latta, 11 Jul 1949, Godfrey SC49004 (PH, NCU, NY*, US). Georgetown Co., 4 mi NW of North Santee, 13 Jun 1957, Radford 25128 (NCU*). Texas: Burleson Co., 4.6 air mi WSW of Caldwell and 2.4 air mi NW

of junction of Routes 21 and 908, 7 Jun 1989, *Orzell 10431 & Bridges* (NCU, NY*). Waller Co., Hempstead, 10 Jun 1872, *Hall 717* (US*, NY). Virginia: Sussex Co., Airfield Millpond, SW of Wakefield, 11–12 Sep 1945, *Fernald 14908 & Long* (GH, NY, PH*, US).

Rhynchospora harperi-BELIZE. Belize District: 1.6 air mi N of junction of Old Northern Highway and Northern Highway, 0.15 mi E of Old Northern Highway, 15 Mar 2008, Treher 173 & Gibson (DOV*); ca. 1 mi W of Hattieville, 0.1 mi S of Western Highway, 15 Apr 2008, Naczi 12266 (BRH, DOV*, NY, US, W); 4.7 km (2.9 mi) NNW of Sand Hill village, 16 Apr 2016, Naczi 16347 (BRH, NY). GUYANA. 5°37'5.6"N, 60°40'58.1"W, 491 m, 19 May 2009, Wurdack 5101 et al. (NY, US*). U.S.A. Alabama: Baldwin Co., Gulf Shores State Park, NE of Little Lake, 24 Sep 1996, Sorrie 9050 & LeBlond (GH, NCU*). Florida: Franklin Co., 0.4 mi W of route 65, Apalachicola National Forest, generally S of Sumatra, 14 Jul 1989, Godfrey 83360 & Gholson (GA*, GH, NY); by route 65, 2.2 mi N of junction US route 98, 3 Jul 1993, Kral 82800 (GA, GH, MO*, NY, US); 2 mi drive E of route 65 along S side of Buck Siding Road, 14 Jul 1988, Anderson 11611 (MO, NY*). Gulf Co., By Florida route 71, 6-7 mi S of Wewahitchka, 20 Jul 1993, Kral 82854 & Moore (GH, MO, NY*); 4.3 mi drive S of route 22, 5.5 air mi SW of Wewahitchka, 20 Jul 1989, Anderson 12,170 (MO, NY*). Liberty Co., By route 65, ± 5 mi N of Sumatra, 26 Jul 1993, Godfrey 84647 (GA*, GH, MO, NY, US); E of route 65 a few mi NE of Wilma, 10 Jul 1992, Anderson 13,706 (NY*). Martin Co., S side Stuart off US route 1, 18 Sep 1973, Kral 51780 (MO*); Hypericum-Taxodium pond by Willoughby Ave., 0.25 mi. N jct. county route 722, 8 Jul 1994, Kral 83706 (MO, NCU*, NY); SE of Hobe Sound, Jonathan Dickinson State Park, 7 Jul 2008, Treher 307 et al. (DOV*). Palm Beach Co., W of Jupiter, N of Indiantown Road/route 706, Hungryland Environmental and Wildlife Area, 7 Jul 2008, Treher 272 et al. (DOV*). Polk Co., 2.5 air mi SW of Hesperides, 11 May 1991, Orzell 16650 & Bridges (GA, NY*, US); 1.7-2.0 mi air mi N of junction FL 630, ca. 1 air mi SW of Lake Weohyakapka, 12 May 1991, Orzell 16666 & Bridges (NY*). Sarasota Co., 0.7 mi S of Myakka River State Park and Manatee County line, 0.3 mi S of FL 72 at a point ca. 5 mi E of Myakka River bridge, 9 May 1991, Orzell 16565 & Bridges (NY*, US); Myakka River State Park, 0.25 mi S of State Rd 72, Treher 315 et al. (DOV). Wakulla Co., just E of Sopchoppy, St. Mark National Wildlife Refuge, Orzell 13967 & Bridges (MO*). Walton Co., Florida route 20, 1.1 mi E of Bruce, 18 Jul 1995, Kral 85337 (GH, MO, NY*, US). Washington Co., 0.5-1 mi W of Bay County line by Florida route 20 just E of Ebro, 19 Jul 1993, Kral 82820 & Moore (GH, MO, NY*, US). Georgia: Long Co., ca. 6 mi NE of Ludowici on W side of US route 82, 3 Nov 1993, Sorrie 7777 et al. (GA*, NCU). Pulaski County, ca. 3 mi E of Hawkinsville, 26 June 1902, Harper 1377 (Holotype: NY00051395*; Isotype: US00087005). Sumter Co., Wet pine barrens, 23 Aug 1900, Harper 467 (GH, NY*, US). Mississippi: Jackson Co., Between route 613 and railroad, 0.25 mi N of Frank Snell Road, 10 Nov 1997, Sorrie 9632 (NCU). North Carolina: Brunswick Co., Hog Branch Ponds Natural Area, 13 Sep 1993, LeBlond 3623A (NCU*). Carteret Co., Croatan National Forest, 1.4 mi NE of Ocean, 20 Aug 2008, Treher 362 & LeBlond (DOV*). South Carolina: Berkeley Co., S of Route 45, S of Honey Hill, 4 Aug 1997, McMillan 2632 (NCU*).

PhytoKeys

Research Article

An integrative approach to species delimitation sinks three Chinese limestone karst *Elatostema* (Urticaceae) species

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Abstract

Elatostema is recognized as a taxonomically difficult group due to the reduced nature of the tiny flowers and inflorescences, also the large number of species (ca 650 to 700). Different opinions on morphological species delimitation have resulted in instability, which is problematic in such a speciose group. In this paper, the taxonomic status of three putative species, E. robustipes, E. scaposum, E. conduplicatum and their hypothetical closest relatives, was revised using morphological and molecular observations. Morphological comparison suggested high similarity between E. robustipes & E. retrohirtum, E. scaposum & E. oblongifolium, E. conduplicatum & E. coriaceifolium, respectively. Phylogenetic analyses of four universal DNA barcodes (ITS, trnH-psbA, matK and rbcL) suggested that each species pair represents a single evolutionary lineage. Taking these two findings together, we propose E. robustipes to be a synonym of E. retrohirtum, E. scaposum a synonym of E. oblongifolium, and E. conduplicatum a synonym of E. coriaceifolium. Our results recover the number, shape and size of the bracts and bracteoles to be relatively stable characters, and the disposition of the male inflorescences on modified stems to be an unstable character, unsuitable for species delimitation in Elatostema.

Key words: DNA barcoding, integrative taxonomy, phylogenetically informative morphological characters, phylogeny, point-endemics

Introduction

Elatostema J.R.Forst. & G.Forst. is one of the most species-rich genera in the Urticaceae, comprising ca 650 to 700 species of mainly succulent herbs that grow in dense shade of forest, stream sides, gorges, and caves (Wang 2014; POWO 2023). *Elatostema* is distributed throughout tropical and subtropical Africa, Madagascar, Asia, Australia and Oceania (Lin et al. 2003). Recent phylogenetic studies suggest that *Elatostema* is a monophyletic group that includes taxa hitherto attributed to *Pellionia*, but excludes those attributed to *Elatostema* atoides, *Procris*, and *Pellionia repens* (Tseng et al. 2019).

Southwest China and Southeast Asia are renowned biodiversity hotspots, in part due to extensive limestone karst present in both (Xu 1995; Clements



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et al. 2006; Wei 2018; Wei et al. 2022). Southwest China is the center of both Elatostema species diversity and morphological variation within the genus, which suggests that it may be a center of diversification for the genus (Wang 2014). This diversity is associated with limestone karst, a fragile habitat characterized by substantial exposed rock, shallow soils deficient in N and P, excessive Ca, Mg, seasonal droughts (Hao et al. 2015), high species diversity and point-endemism (Clements et al. 2006). Karst has been subject to extensive human intervention (mining, agriculture) and is very sensitive to climate change and water pollution (Parise et al. 2009; Jiang et al. 2014). Documenting this biodiversity is a high priority if species are to be conserved or their extinction threat assessed (Clements et al. 2006; Wang 2014). Collecting in karst is, however, very difficult as there are few roads and the terrain is irregular and steeply dissected. A consequence of the above is that there are relatively few collections from such areas and undescribed species are frequently represented by one or two collections only (Fu et al. 2019). Describing species based on few collections is problematic and carries the risk of over-describing species (Fu et al. 2019). Furthermore, considering the information lacking on pistillate inflorescence (21%) and staminate inflorescence (29%) of Chinese Elatostema species (Wang 2014), as well as the extensive occurrence of apomixis in Elatostema (Fu et al. 2017), it is likely that many new species are described from populations that comprise a single sex, further increasing the risk of over-description, whereby male and female populations can be described as different species.

Over the past two decades, there has been some instability in *Elatostema* species delimitation in China with several *Elatostema* species being placed in synonymy or reduced to ranks below that of species (Duan and Lin 2003; Lin and Duan 2003; Duan et al. 2006; Lin et al. 2011) and then raised back to species rank (Wang 2010a, 2014) because of different opinions on the importance of specific morphological characters. Wang (2010a) studied bract and bracteole morphology of *Elatostema* and concluded that their number, shape and size are relatively constant. More recently, additional morphological characters, such as male inflorescences borne on modified stems, were identified and used to delimitate species (Yang et al. 2011; Wang 2014). The phylogenetic informativeness of these characters has not, however, been evaluated (Lin et al. 2011). Controversy in species delimitation cannot, therefore, be resolved by morphological evidence alone.

Phylogenetic analyses of DNA barcodes can provide a means to use paraphyly to identify conspecific groupings and it has been successfully applied to delimit *Elatostema setulosum* W.T.Wang (Fu et al. 2019).

In this study we evaluate the taxonomic status of three putative *Elatoste-ma* species, *E. robustipes* W.T.Wang, F.Wen & Y.G.Wei, *E. scaposum* Q.Lin & L.D.Duan, *E. conduplicatum* W.T.Wang. To do so, we employed four universal DNA barcodes (ITS, *trnH-psbA*, *matK* and *rbcL*) (Hollingsworth et al. 2009, 2011; China Plant BOL Group et al. 2011) and visual morphological comparison. We aimed to use a phylogenetic framework to evaluate the phylogenetic informativeness of several morphological characters (see Wells et al. 2021) that have previously been used for species delimitation in the above species, as well as assess their monophyly.

Materials and methods

Taxon sampling

Fieldtrips in SW China and northern Vietnam were conducted between 2009 and 2023 to collect specimens and DNA materials of Elatostema robustipes, E. scaposum, E. conduplicatum and their closest relatives for morphological and molecular studies. Our sampling strategy of molecular analysis aimed to sample all putative species and their closest relatives, using material collected from type localities or, where this was not possible, to sample material that exhibited the diagnostic morphological characters for those species. Elatostema robustipes and E. conduplicatum were collected from type localities and E. scaposum from a specimen with key characters. The studied material covered the main distribution range of the respective species in SW China to northern Vietnam. In total, seven species with 11 accessions represented by three putative species and their closest relatives with the exception of E. shanglinense W.T.Wang (DNA material is not available) were ingroups. Elatostema radicans (Siebold & Zucc.) Wedd. and E. heterolobum (Wedd.) Hallier f. were selected as outgroups based on previous phylogenetic analyses (Tseng et al. 2019). Materials for molecular analysis are listed in Table 1. The morphological comparison between putative species and their closest relatives were based on consulting protologues, checking type specimens and other specimens as well as observing field individuals. Specimens used for morphological studies are listed in Appendix 1.

Morphological examination

A morphological species concept was employed to compare the taxa based on Wei et al. (2011). Specimens were examined using dissecting microscopy following Fu et al. (2019). The selection of morphological characters was

Species name	Accession	Voucher specimen	Locality	ITS	trnH-psbA	matK	rbcL
Elatostema balansae	C098	L.F. Fu & S.L. Huang FL0001 (IBK)	Yunnan, Guangxi	OR733575*	OR730813*	OR730814*	OR730815*
E. conduplicatum	C038	L.F. Fu FLF042 (IBK)	Guangxi, China	OR577332*	OR568594*	OR568577*	OR591476*
E. coriaceifolium	C696	F. Wen 0097 (IBK)	Guizhou, China	OR577335*	OR568595*	OR568585*	OR591473*
	C140	F. Wen WF0070 (IBK)	Guizhou, China	OR577334*	OR568596*	OR568583*	OR591468*
	J078	Z.B. Xin XZB20180128-01 (IBK)	Guangxi, China	OR577333*	OR568597*	OR568584*	OR591475*
E. heterolobum	C775	Y.G. Wei Wei054 (IBK)	Guangxi, China	OR577343*	OR568593*	OR568587	OR591474*
E. oblongifolium	C199	Y.G. Wei & F. Wen 1147 (IBK)	Guizhou, China	OR577338*	OR568588*	OR568582*	OR591469*
	C067	Y.G. Wei & L.F. Fu 068 (IBK)	Guangxi, China	OR577336*	OR568589*	OR568581*	OR591478*
E. radicans	C694	F. Wen 0111 (IBK)	Guizhou, China	OR577342*	OR568599*	OR568586*	OR591472*
E. retrohirtum	C598	A.K. Monro &Y.G. Wei AM6801 (IBK)	Guangxi, China	OR577340*	OR568591*	OR568579*	OR591470*
	C610	L.F. Fu & S.L. Huang FL0026 (IBK)	Yunnan, China	OR577341*	OR568592*	OR568580*	OR591471*
E. robustipes	C041	Y.G. Wei & L.F. Fu 002 (IBK)	Guangxi, China	OR577339*	OR568598*	OR568578*	OR591477*
E. scaposum C085 F. Wen WF0068 (IBK)		Guizhou, China	OR577337*	OR568590*	/	OR591479*	

Table 1. Species name, voucher specimen of *Elatostema* and their accession numbers of ITS, *trnH-psbA*, *matK* and *rbcL* used in this study (*denoted newly generated sequences).

made based on the morphological diagnosis of three putative species distinguishing from their closest relatives (Wang 2010b; Yang et al. 2011; Wei et al. 2012).

Genomic DNA extraction, PCR amplification & sequencing

Four universal barcodes: the nuclear ribosomal internal transcribed spacer (ITS) region, the *trnH-psbA* intergenic spacer, *matK* and *rbcL* were used to establish hypotheses of phylogenetic relationship based on their ability to detect variation at the species level (China Plant BOL Group et al. 2011; Gao et al. 2012). The primers used to amplify four universal barcodes were those developed by the Kress et al. (2005), China Plant BOL Group et al. (2011) and Gao et al. (2012). Total genomic DNA was isolated from dried plant material using a modified CTAB protocol (Chen et al. 2014). PCR amplification protocols followed Gao et al. (2012) and Fu et al. (2019).

Sequence alignment and phylogenetic analysis

Sequence data were edited and assembled using Lasergene Navigator (DNAStar, Madison, Wisconsin, USA). Cleaned sequences were then aligned with the MEGA 5.1 (Tamura et al. 2011) with additional manual refinements where necessary. Phylogenetic analyses for the aligned matrix were performed by maximum parsimony (MP), Bayesian inference (BI) and maximum likelihood (ML) methods. MP analyses were carried out using PAUP* 4.0b10 (Swofford 2002). All characters were unordered and equally weighted, and gaps were coded as missing data. Heuristic searches were performed using a starting tree built from stepwise addition with tree bisection-reconnection (TBR) branch swapping and 1,000 random addition replicates. To assess confidence in clades, 1,000 bootstrap replicates (maximum parsimony bootstrap; MPBS) with 10 random additions per replicate were used. The ML analyses were constructed in IQtree v1.6.12 (Nguyen et al. 2015) with 1,000 bootstrap replicates (MLBS) and HKY+G selected as the best model. The BI analyses were done using Mr-Bayes v3.2.7a (Ronquist et al. 2012). The model of best fit (TIM+F+G4) was determined based on Bayesian information criterion (BIC) (Aho et al. 2014) in jModelTest2 v. 2.1.7 (Darriba et al. 2012). Two independent runs were performed, each consisting of four Markov Chain Monte Carlo (MCMC) chains. The beginning 25% of trees were discarded as burn-in while the remaining trees were used for generating a consensus tree to estimate posterior probabilities (PP). The convergence of the MCMC chains of each run was determined when the average standard deviation of split frequencies (ASDSF) achieved ≤ 0.01 .

Estimates of support

We adopted the same criteria of ML, MP and BI analyses as Tseng et al (2019): For ML and MP analyses, 70–79%, 80–89%, and 90–100% bootstrap supports were considered as weakly, moderately, and strongly supported, respectively, and values lower than 70% were considered as providing no support. For BI analyses, the posterior probabilities of < 0.9, 0.9–0.94, 0.95–0.99, and 1.0 were considered as providing no, weak, moderate, and strong support, respectively.

Results

Morphological comparison

After consulting protologues, checking type specimens and other specimens as well as observing field individuals, a suite of morphological characters was confirmed and used to compare three putative species and their closest relatives. Characters used were plant height, stem indumentum, leaf shape, leaf indumentum, leaf venation, stipule shape, male inflorescence insertion, male inflorescence peduncle length, male bract appendage, male bracteole shape and male flower sepal number. Specifically, Elatostema robustipes had densely hispid stem comprising weakly curved to crooked, appressed hairs, broader half auriculate leaf basal, 3.5-4.5 mm male inflorescence peduncle length, 5 longitudinal ribs outer bracts and 1 longitudinal rib inner bracts, and oblanceolate or obovate male bracteoles that can be easily distinguished from E. balansae Gagnep., but showed no significant difference to E. retrohirtum Dunn (Table 2). Elatostema scaposum presented 50-90 cm plant height, male inflorescence borne on modified or unmodified stems and 5-15 mm male inflorescence peduncle length showing no significant difference to E. oblongifolium Fu ex W.T.Wang (Table 3). Elatostema conduplicatum had glabrous leaf blade, semitriplinerve leaf venation, triangular stipule, broadly triangular and corniculate male bract, linear-cymbiform and corniculate male bracteoles and 5-merous male flower which can be easily distinguished from E. shanglinense, but showed no significant difference to E. coriaceifolium W.T.Wang (Table 4).

Molecular analysis

The combined matrix had a length of 2,526 characters (ITS: 652, *trnH-psbA*: 375, *matK*: 800, *rbcL*: 699). Including indels, 289 (11.4%) were variable and 205 (8.1%) were parsimoniously informative. Phylogenies reconstructed using ML, MP and BI methods recovered consistent topologies for all samples of the ingroup taxa, which formed a monophyletic clade with strong supports (MLBS

Table 2. Morphological comparison of Elatostema robustipes, E. balansae and E. retrohirtum.

Characters	E. robustipes	E. balansae	E. retrohirtum		
Stem indumentum	densely hispid, weakly curved to crooked	glabrous or pubescent	densely hispid, weakly curved to crooked		
Leaf shape	broader-half auriculate	broader-half broadly cuneate or rounded	broader-half auriculate		
Male inflorescence peduncle length	3.5–4.5 mm	1.0-2.0 mm	4.0-6.0 mm		
Male bract appendage	outer bracts bearing 5 longitudinal ribs; inner bracts bearing 1 longitudinal rib	outer bracts bearing 3 inconspicuous longitudinal ribs; inner bracts not bearing rib	outer bracts bearing 5–6 longitudinal ribs; inner bracts bearing 1–3 longitudinal ribs		
Male bracteoles shape	oblanceolate or obovate	linear	Oblanceolate		

 Table 3. Morphological comparison of Elatostema scaposum and E. oblongifolium.

Characters	E. scaposum	E. oblongifolium
Plant height	50–90 cm	20-90 cm
Disposition of male inflorescence	borne on modified or unmodified stems	borne on unmodified stems
Male inflorescence peduncle length	5–15 mm	0.5–10 mm

Characters	E. conduplicatum	E. shanglinense	E. coriaceifolium
Leaf indumentum	glabrous	shortly ciliated	Glabrous
Leaf venation	semitriplinerve	triplinerve	Semitriplinerve
Stipule shape	triangular	narrowly lanceolate	triangular or narrowly ovate
Male bract shape	broadly triangular, conduplicate	oblong-cymbiform, not conduplicate	broadly ovate, conduplicate
Male bracteoles shape	linear-cymbiform, corniculate	narrowly linear, not corniculate	linear-cymbiform, corniculate
Male flower merism	5	4	5

Table 4. Morphological comparison of Elatostema conduplicatum, E. shanglinense and E. coriaceifolium.

100, MPBS 100, PP 1.0) sister to the outgroup taxa. The ingroup taxa were recovered as three subclades (A–C), each of which comprised the putative species and its most morphologically similar congener in a paraphyletic grouping (Fig. 1). In detail, clade A comprised three species including *Elatostema balansae*, *E. retrohirtum* and *E. robustipes* with strong supports (MLBS 100, MPBS 100, PP 1.0). *Elatostema balansae* was sister to a clade consist of *E. retrohirtum* and *E. robustipes* was nested in this clade including a paraphyletic *E. retrohirtum*, with strong supports in BI analysis (PP = 1). Similar situations also occurred in clade B and clade C that *E. scaposum* and *E. conduplicatum* were nested in the paraphyletic *E. oblongifolium* and *E. coriaceifolium*, respectively with strong supports (MLBS 98/100, MPBS 100/100, PP 1.0/1.0).

Discussion

Elatostema robustipes was described based on a single collection with two duplicate specimens that displayed only male inflorescences, with reference to *E. balansae* (Wei et al. 2012). It was argued that *E. robustipes* could be distinguished from *E. balansae*, based on leaf shape, male inflorescence peduncle length, bract appendage and bracteole shape (Table 2). At the time of





description, E. robustipes was not compared to another morphologically similar species, E. retrohirtum, as no description of the male inflorescence for the latter was known, limiting the basis of a comparison. During subsequent fieldtrips to Yunnan and northern Vietnam, we collected several specimens of E. retrohirtum bearing male inflorescences (Fu et al. 2014). These suggested that E. robustipes was, in fact, most similar to E. retrohirtum. A detailed morphological comparison of E. robustipes and E. retrohirtum showed that they share several diagnostic morphological characters: a densely hispid stem comprising weakly curved to crooked, appressed hairs; a male inflorescence with an involucre comprising six bracts, the outer two of which are larger and bear five longitudinal ribs, the four inner of which are smaller and bear a single longitudinal rib (Table 2; Fig. 2). Our phylogenetic analyses suggest that E. robustipes is nested in a clade A, which includes a paraphyletic E. retrohirtum, with strong supports in BI analysis (PP 1.0), and which itself is sister to a morphologically distinct, E. balansae. Based on the morphological and molecular evidence, we consider that E. robustipes and E. retrohirtum represent the same species. The latter name has priority.

Elatostema scaposum was described with reference to *E. oblongifolium*, based on 12 duplicate specimens (Yang et al. 2011). The diagnostic characters in the diagnosis were plant height, male inflorescence peduncle length and the disposition of the male inflorescences (Yang et al. 2011). Based on our extensive field observations and collections across Guizhou and Yunnan, plant height and male inflorescence peduncle length for both groupings overlapped, and a single population of *E. scaposum* being recovered which comprises individuals bearing male inflorescences on both modified and unmodified stems (Table 3; Fig. 2) suggesting that the character of modified stem is not stable for the species. Our phylogenetic analyses recovered *E. scaposum* nested in clade B, which includes a paraphyletic *E. oblongifolium*, with strong support (MLBS 98, MPBS 100, PP 1.0). Based on the morphological and molecular evidence, we consider that *E. scaposum* and *E. oblongifolium* represent the same species. The latter name has priority.

Elatostema conduplicatum was described from two duplicate specimens of a single collection comprising only male inflorescences, with reference to E. shanglinense (Wang 2010b). Elatostema conduplicatum can easily be distinguished from E. shanglinense by a suite of characters, including leaf indumentum and venation, stipule shape, male bract shape and conduplicate arrangement, male bracteole shape, and male flower merism (Table 4). Elatostema conduplicatum was not, however, compared with another species, E. coriaceifolium, presumably as the male inflorescences of the latter were unknown at the time. Wang (2010c) later provided a supplementary description of the male inflorescences of E. coriaceifolium, which suggested that E. conduplicatum was most similar to E. coriaceifolium, from which it could be distinguished by the conduplicate bract arrangement. Our field observations, however, clearly showed that the male bract of E. coriaceifolium is also conduplicate (Table 4, Fig. 2). In addition, our phylogenetic analyses suggest that E. conduplicatum is nested within clade C, which includes a paraphyletic E. coriaceifolium, with strong supports (MLBS 100, MPBS 100, PP 1.0). Based on the morphological and molecular evidence, we consider that E. conduplicatum and E. coriaceifolium represent the same species. The latter name has priority.

Based on the above, we present the following detailed taxonomic treatments for the species.

Taxonomic treatment

Elatostema coriaceifolium W.T.Wang, Acta Phytotax. Sin. 31(2): 170. 1993.

= Elatostema conduplicatum W.T.Wang, Guihaia 30(1): 3. 2010. Syn. nov. Type: Сніма. Guangxi: Donglan County, Bala, Y.M. Shui & W.H. Chen B2004-171A (holotype: PE [PE01842427]; isotype: KUN!).

Type. CHINA. Guizhou: Libo, Wengangmogan, 29 April 1984, *Q.H. Chen et al.* 2289 (holotype: HGAS).

Description. Perennial herb. Stems 140-185(-270) × 1.0-1.5 mm, erect, simple, fasciculate, furfuraceous, glabrous; stipules 2, triangular or narrowly ovate, $0.8-1.8 \times 0.4-1.0$ mm, without cystoliths. Leaves sessile or shortly petiolate, glabrous; laminae $12-24(-40) \times 8-11(-14)$ mm, obliquely elliptic or rhombic-elliptic, chartaceous or thinly coriaceous, semitriplinerve; cystoliths densely scattered; base asymmetrical, broader-half auriculate, narrower-half cuneate; margin denticulate; apex acute. Staminate inflorescences solitary, capitate; sessile; receptacle inconspicuous, subtended by marginal bracts; the bracts 6, unequal, outer 2 bracts major, broadly ovate, conduplicate, $4-4.5 \times ca$. 3 mm, abaxial surface with 1 longitudinal rib, ribbed extending apically as a corniculate protuberance, inner 4 bracts minor, oval, ca. 3 × 2-2.8 mm, abaxial surface with 1 longitudinal rib, ribbed extending apically as a corniculate protuberance, glabrous; staminate flowers pedicellate; bracteoles 2 per flower, subequal, ca. 2.4 × 1.0 mm, linear-cymbiform, subapical appendage, corniculate, shortly ciliate; tepals 5, broadly ovate, subapical appendage 0.8-1.1 mm, corniculate, pubescent. Pistillate inflorescence solitary, capitate; peduncle ca. 1 mm, glabrous; receptacle broadly rectangular, 3-3.5 mm, glabrous, subtended by marginal bracts, the bracts ca. 20, unequal, outer 6 bracts major, triangular or broadly ovate, ca. 1.1 × 0.4–2 mm, subapical appendage, inner bracts minor, narrowly triangular or linear, sparsely ciliate or glabrous; pistillate flowers pedicellate; bracteoles 2 per flower, equal, 0.9-1.5 × 0.1-0.4 mm, linear, ciliate or glabrous; achenes ca. 0.8 mm, narrowly ellipsoidal, ca. 6-8-ribbed.

Distribution. This species is endemic to China (Guangxi, Guizhou).

Elatostema oblongifolium Fu ex W.T.Wang, Bull. Bot. Lab. N. E. Forest. Inst., Harbin 7: 26. 1980.

- ≡ Pellionia bodinieri H. Lév., Repert. Spec. Nov. Regni Veg. 11: 551. 1913.
- ≡ Elatostema bodinieri (H.Lév.) Hand.-Mazz., Symb. Sin. Pt. 7: 144. 1929, nom. illeg., non H.Lév. 1913. Type: CHINA. Guizhou: Gan-pin, 29 April 1897, Bodinier 1547 (syntype E); Ou-la-gay, 9 April 1898, Seguin s.n. (syntype: E).
- = Elatostema schizocephalum W.T.Wang, Bull. Bot. Lab. N. E. Forest. Inst., Harbin 7: 82. 1980. Type: Сніма. Hunan: Yizhang, 22 January 1942, S.Q. Chen 73 (holotype: PE [PE00023194!]). = Elatostema multicanaliculatum B.L.Shih & Yuen P. Yang, Bot. Bull. Acad. Sin. 36: 268. 1995. Type: Сніма. Taiwan: Taoyuan Co., Mt. Lala, 23 October 1994, B.L. Shih 3226 (isotypes: HAST, TAI!, TAIF).
- = Elatostema scaposum Q. Lin & L.D. Duan, Nordic J. Bot. 29: 420. 2011. Syn. nov. Type: CHINA. Guizhou: Libo County, Jialiang Baibidong, alt. 800 m, 26

October 2003, *Q. Lin & L.D. Duan 1023* (holotype: PE [PE01863021!]; isotypes E!, GH, HUH [HUH A00293663!], K, L, NY, PE [PE01863023!, PE01863023!], TUS, US, WU).

Description. *Perennial herb.* Stems $20-90 \times 0.5-12$ mm, ascending or erect, branched or simple, with 5 or more longitudinal canals, glabrous; stipules 2, narrowly triangular to subulate or narrowly lanceolate, $2.5-12 \times 0.2-2.0$ mm,



Figure 2. Elatostema spp. A E. retrohirtum B E. robustipes C E. oblongifolium D E. scaposum E E. coriaceifolium F E. conduplicatum 1 habit 2 male inflorescence.

glabrous. Leaves sessile or short petiolate; laminae 50-220 × 14-50(-80) mm, obliquely oblong or elliptic, chartaceous, pinnately nerved; cystoliths densely scattered; base asymmetrical, broader-half rounded to cordate, narrower-half cuneate; margin serrulate to coarsely serrate; apex acuminate or long acuminate. Staminate inflorescences borne on modified or unmodified stems, solitary, cymiferous, shortly pedunculate, subglabrous; bracts membranous, ovate, lanceolate or linear, 2-12 mm, glabrous; staminate flowers pedicellate, glabrous; tepals 5, narrowly elliptic, ca. 2 mm, subapical appendage, shortly corniculate. Pistillate inflorescence paired, capitate; peduncle ca. 3 mm, glabrous; receptacle rectangle or broadly ovate, deeply divided into two lobes, lobe further weakly divided into two lobes, $2-10 \times 3$ mm, glabrous, subtended by marginal bracts, the bracts 25 or more, unequal, outer bracts major, triangular, 0.6-1.0 × 0.4-0.8 mm, glabrous, inner bracts minor, linear or lanceolate, sparsely ciliate; pistillate flowers pedicellate; bracteoles 2 per flower, subequal, 0.5-1.5 mm, linear, narrowly obovate or cymbiform; achenes 0.6-0.9 × 0.3-0.5 mm, broadly ellipsoidal or ovoid, ca. 6-ribbed.

Distribution. This species is distributed in China (Chongqing, Hubei, Hunan, Guangxi, Guizhou, Sichuan, Taiwan, Yunnan) and Vietnam (Ha Giang).

Elatostema retrohirtum Dunn, Bull. Misc. Inform. Kew, Addit. Ser. 10: 249. 1912.

= Elatostema robustipes W.T.Wang, F.Wen & Y.G.Wei, Ann. Bot. Fenn. 49: 188. 2012. Syn. nov. Type: CHINA. Guangxi: Huanjiang County, Mulun National Reserve, Hongdong, alt. 308–512 m, 24°43'N, 108°18'E, 26 April 2009, Y.G. Wei 124 (holotype: IBK!; isotypes: IBK!, PE [PE01843378!, PE01843379!]).

Type. CHINA. Guangdong: near Yit-hai Han valley, *Dunn's Han Exped., Herb. Hongk. no. 6288* (holotype: K!).

Description. Perennial herb. Stems 150-350 × 1.8-2.5 mm, ascending or erect, branched, densely hispid, the hairs weakly curved to crooked, appressed; stipules 2, linear-lanceolate, 4-8 × 1.0-2.0 mm, cystoliths sparsely scattered, glabrous. Leaves sessile or short petiolate, petioles 0-1(-4.5) mm, densely hispid, the hairs weakly curved to crooked, appressed; laminae 40-60(-100) × 15-20(-50) mm, obliquely elliptic, herbaceous or chartaceous, triplinerve; cystoliths densely scattered; base asymmetrical, broader-half rounded or auriculate, narrower-half cuneate; margin denticulate; apex short acuminate or acute, rarely acuminate. Staminate inflorescences solitary, capitate; peduncle 3.5-6.0 × 0.3-0.8 mm, sparsely hispid, the hairs weakly curved, appressed; recepta $cle 2-4 \times 3-5$ mm, rectangle or oblong, glabrous, subtended by marginal bracts; the bracts ca. 6, unequal, outer 2 bracts major, broadly ovate, 2-2.5 × 4-5 mm, abaxial surface sparsely hispid, the hairs weakly curved, appressed, with 5 or 6 longitudinal ribs, each ribbed extending apically as a corniculate protuberance, inner 4 bracts minor, obovate, ca. 2 × 3 mm, abaxial surface with 1-3 longitudinal ribs, at least one ribbed extending apically as a corniculate protuberance, glabrous; staminate flowers pedicellate, glabrous; bracteoles 2 per flower, equal, 2.5-4.0 × 1.0-1.5 mm, oblanceolate or obovate, glabrous; tepals 4, ovate, 0.9-1.2 × 0.7-0.9 mm, subapical appendage ca. 0.5 mm, corniculate, glabrous. Pistillate inflorescence solitary, capitate; peduncle ca. 1 × 0.5 mm, glabrous;

receptacle subrounded, 3–3.5 mm in diam., glabrous, subtended by marginal bracts, the bracts numerous, subequal, triangular, $0.6-1.2 \times 0.4-0.6$ mm; pistillate flowers pedicellate; bracteoles 2 per flower, subequal, ca. $0.6-1.2 \times 0.3$ mm, spatulate-linear; achenes 0.5-0.6 mm, ovoid or ellipsoidal, ca. 6-ribbed.

Distribution. This species is distributed in China (Guangdong, Guangxi, Guizhou, Sichuan, Yunnan) and Vietnam (Bac Kan, Gia Lai, Ha Giang, Ha Noi, Hai Phong, Hoa Binh, Lam Dong, Nghe An, Ninh Binh, Son La, Tuyen Quang).

Conclusions

We conclude that the three species studied are conspecific to earlier described taxa that have priority under the International Code of Nomenclature for Algae, Fungi and Plants and place them in synonymy with these names. Our results emphasize that some morphological characters, such as the number, shape and size of bract and bracteole, are relatively constant (Wang 2010a), whilst the bearing of male inflorescences on modified stems is unstable and ill-suited to delimit species in *Elatostema*. More importantly, our results provide further support for the need to integrate multiple lines of evidence when describing new species based on very small numbers of individuals, as is frequently the case for point-endemic species (Hong 2016; Fu et al. 2021).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: RFW. Funding acquisition: LFF. Investigation: AKM, ZBX, RFW. Project administration: LFF. Writing – original draft: ZBX, LFF. Writing – review and editing: AKM, LFF.

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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

Specimens used for morphological studies.

- *Elatostema conduplicatum* W.T.Wang, CHINA. Guangxi: Donglan County, Bala, *Y.M. Shui & W.H. Chen B2004-171A* (KUN, PE [PE01842427]).
- Elatostema coriaceifolium W.T.Wang, CHINA. Guangxi: Fengshan County, Yangzi cave, 28 January 2018, *Z.B. Xin XZB20180128-01* (IBK); Guizhou: Libo County, Jiarong Town, 21 October 2012, *F. Wen 0097* (IBK); Dushan County, Jichang Town, 19 October 2012, *F. Wen 0070* (IBK).
- Elatostema oblongifolium Fu ex W.T.Wang, CHINA. Guizhou: Anlong County, 29 October 2010, F. Wen 1082 (IBK); Dushan County, Jichang Town, 19 October 2012, F. Wen 0068 (IBK); Yunnan: Guangnan County, Sanla waterfall, 08 November 2011, F. Wen WFLTC111108 (IBK); Malipo County, Xiajinchang village, 23 October 2023, C. Xiong & X.Y. He XC20231023-06 (IBK).
- *Elatostema retrohirtum* Dunn, CHINA. Guangdong: near Yit-hai Han valley, Dunn's Han Exped., Herb. Hongk. no. 6288 (K); Guangxi: Longzhou County, 20 May 2010, A.K. Monro & Y.G. Wei 6801 (IBK); Yunnan: between Malipo County and Babu Village, alt. 931 m, 23°14'52"N, 104°46'37"E, 2 May 2013, L.F. Fu & S.L. Huang FL0015 (IBK).
- *Elatostema robustipes* W.T.Wang, F.Wen & Y.G.Wei, CHINA. Guangxi: Huanjiang County, Mulun National Reserve, Hongdong, alt. 308–512 m, 24°43'N, 108°18'E, 26 April 2009, Y.G. *Wei 124* (IBK, PE[PE01843378, PE01843379]).
- *Elatostema scaposum* Q.Lin & L.D.Duan, *CHINA. Guizhou:* Libo County, Jialiang Baibidong, alt. 800 m, 26 October 2003, *Q. Lin & L.D. Duan 1023* (E, HUH [HUH A00293663], PE [PE01863021, PE01863023]).

PhytoKeys

Research Article

A new species of *Casearia* Jacq. (Salicaceae) from Central Panama and insights into its phylogenetic position within the genus

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Abstract

We describe here a new species of *Casearia* from Panama based on both morphological and molecular data. *Casearia isthmica* **sp. nov.** is restricted to the mid-elevation cloud forests of Central Panama and presents morphological similarities with two more widespread species, *C. sanchezii* from high elevation areas of El Salvador and Mexico and *C. tremula* from the Caribbean, Central America, and Northern South America. *Casearia isthmica* differs in presenting pedunculated and congested inflorescences with up to 20 flowers, as well as flowers with 12 stamens and a pubescent style. Phylogenetic analysis based on selected plastid (*petD*, *trnK-matK*, *rpl16* and *rps4-trnLF*) and nuclear (GBSSI and ITS) markers shows that the new species belongs to subclade B3 of *Casearia*, a lineage that encompasses species from Central America, Mexico and the Caribbean. Results of the morphological and molecular analysis were congruent and allowed a broader understanding of this new taxon, especially regarding its relationships to other *Casearia*.

Key words: Molecular phylogeny, Neotropics, new species, Samydeae



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Introduction

Casearia Jacq. is a pantropical genus of more than 200 species, therefore being the most species rich genus of the subfamily Samydeae (Salicaceae). In the Neotropics, it is widely distributed and reported from every biome, such as the Amazonian rainforests, the Brazilian Cerrado, the Caribbean and the savannas (Sleumer 1980; Correll and Correll 1982; Liogier 1994; Gutiérrez 2000). Sleumer (1980) provided a taxonomical revision of the whole family Flacourtiaceae (within which *Casearia* was then placed) for the Neotropics, therefore providing insights into its morphological variability. He divided the genus, based on morphological characters, into six sections which were not found to be monophyletic by a recent molecular study (Mestier et al. 2022). Nevertheless, the study showed nine monophyletic subclades. Recently, many new taxa have been described

in the Neotropical regions from both South America (Marquete and Mansano 2010, 2013; Alford 2015; Marquete and Torres 2022) and Mesoamerica (Castillo-Campos and Medina Abreo 2003; Linares and Angulo 2005). Here, we describe a new species of *Casearia* from Central America, endemic to Central Panama. *Casearia* species are trees or shrubs that present pellucid dots or lines on the leaves. The limb possesses a pinnate nervation and mostly serrate, crenate, or subentire margins. Flowers are apetalous, with four to five sepals, sometimes more, and mostly uniseriate stamens, alternating with staminodes. *Casearia* usually presents eight to ten stamens, although some species possess a higher number (Warburg 1895; Hutchinson 1967; Sleumer 1980).

Speciation processes are often associated with morphological changes (Losos and Miles 1994; Givnish 2010) and traditionally, species have been described following a morpho-species concept (Stuessy 2009). Nevertheless, providing a phylogenetic framework for a newly described taxon provides valuable insights regarding its relationships with species of the same genus and support for the accuracy of the species delimitation (Padial and De La Riva 2010). Here, we described a new species of *Casearia* endemic to Panama and establish a phylogenetic tree of the genus with the newly described taxa, therefore providing insights into its phylogenetic position within *Casearia*.

Materials and methods

Taxon sampling and field work documentation

The description of the new species was based on collections that were carried out in Panama between 1992 and 2022 in Panama and Panama Oeste provinces. The documentation of the plant in the field was carried out in April and June 2022, using a Nikon D3100 digital camera with a Nikon DX AF-S Nikkor 18–55 mm lens. Illustrations were made using Adobe Photoshop 2023 software and the PhotoRoom app.

We sampled new sequence data from the proposed new species (two individuals) and from *Casearia sanchezii* J. Linares & Angulo, through a specimen of the Berlin herbarium coming from El Salvador, since the new taxon bears a certain morphological resemblance to this species. Those newly generated sequences were added to the published alignment by Mestier et al. (2023) of the plastid regions: *petD*, *rpl16*, *rps4-trnLF* and *trnK-matK*, as well as a nuclear data set based on GBSSI and ITS. Fresh silica-dried material and corresponding vouchers of the new species were deposited at B, PMA and SCZ herbaria. Voucher information can be found in Suppl. material 1.

Herbarium work and morphological descriptions

Herbarium specimens, including types, were studied from B, PMA, SCZ, and UCH. Also, scanned images from GBIF, JACQ, JSTOR and TROPICOS were examined. In addition to reviewing the types and protologues of other *Casearia* species, the suspected new species were investigated following taxonomic treatments by Sleumer (1980), Pool (2001) and Gonzalez (2007). The descriptions are based on fertile and vegetative material.

Conservation status

The conservation status assessment was based on the criteria of the International Union for Conservation of Nature (IUCN Standards and Petitions Committee 2019), using the parameters of number of locations (the number of geographical or ecological areas of occurrence), extent of occurrence (EOO), and/or area of occupancy (AOO). Calculations of EOO and AOO values were computed with GeoCAT (Bachman et al. 2011).

Phylogenetic analysis

Wet laboratory procedure followed the protocol of Mestier et al. (2023). We added the newly generated sequences to the alignment by Mestier et al. (2023). A motif-based alignment approach (Löhne and Borsch 2005) in PhyDE v. 0.9971 (Müller et al. 2010) was used (see Suppl. material 1 for the plastid alignment and Suppl. material 2 for the nuclear alignment). Short regions of uncertain homology (hotspots) were excluded, and gaps were coded following the simple indel coding method (Simmons and Ochoterena 2000), as implemented in SeqState v.1.4.1 (Müller 2005) (see Suppl. material 3 for the plastid matrix and Suppl. material 4 for the nuclear matrix).

Bayesian inference was computed using MrBayes v.3.2.7.a (Ronquist et al. 2011) in the high-performance computer cluster "Curta" of the Freie Universität Berlin. Optimal nucleotide substitution models were selected under the Akaike Information Criterion (AIC) with jModelTest v.2.1.7 (Darriba et al. 2012). The summary of character statistics and evolutionary models can be found in Suppl. material 5. Indels were coded with the F81 model, as suggested by Ronquist et al. (2011). We performed four runs each with four chains, sampling every 10,000 generations with 80 million generations for the plastid dataset and 20 million for the nuclear dataset. The average standard deviation of split frequencies and post burn-in effective sampling size (ESS) was used to verify the convergence of the runs. Finally, 10% of the trees were discarded as a burn-in and a 50% majority-rule consensus tree was constructed.

Maximum Likelihood analysis was performed with RAxML v.8.2.12 (Stamatakis 2014) in CIPRES (Miller et al. 2011). The majority-rule consensus tree from 1000 pseudo-replicates with 200 searches was used to estimate rapid bootstrap support (BS). Parsimony analysis was executed using PAUP v.4.0b10 (Swofford 2008) in the high-performance computer cluster "Curta" of the Freie Universität Berlin, using the commands obtained from the parsimony ratchet as implemented in PRAP (Nixon 1999). It allows the inclusion of all characters with equal weight and treat gaps as missing characters. Ratchet settings included 200 iterations, unweighting 25% of the positions randomly and (weight=2) and 100 random additional cycles. Finally, we obtained Jackknife support (JK) values with a single heuristic search within each of 10,000 JK pseudo-replicates, tree bisection-reconnection branch swapping, and 36.79% of characters being deleted in each replicate with PAUP v.4.0b10 (Swofford 2008). We used TreeGraph 2 (Stöver and Müller 2010) to process the trees and added node support values for all inference methods on the Bayesian majority rule topology.

Results

Phylogenetic analysis

We generated new sequences from plastid and nuclear regions for this study, which we added to the alignment provided by Mestier et al. (2023). The resulting alignment had 7724 positions of which *rps4-trnLF* contributed to 2126, *trnK-matK* 3137, *petD* 1333 and *rpl16* 1128 (Suppl. material 2). The final matrix had 8017 positions including the indels (Suppl. material 3). Unfortunately, ITS could not be amplified for *C. laetioides* (*=Zuelania guidonia* (Sw.) Britton & Millsp), the species resolved as sister in the plastid tree to the putative new species, focus of this investigation. To test if the nuclear genomic partition would support the same relationships, we included information of another nuclear marker, GBSSI. The nuclear alignment (GBSSI and ITS) had 1711 positions (Suppl. material 4) and the final matrix 1647 positions, including the indels (Suppl. material 5).

The plastid and nuclear phylogenies presented in Figs 1 and 2 respectively, are highly congruent and similar to previous molecular studies (Mestier et al. 2022, 2023), recovering the same nine *Casearia* subclades. The newly sequenced individuals of *Casearia isthmica* are retrieved together in subclade B3 both in the plastid (PP: 0.51. BS: [100], JK: [99,99]) and the nuclear tree (PP: 1, BS: 1, JK: 98.99). In both trees, *C. isthmica* is also retrieved as direct sister to *C. laetioides* (A. Rich.) Northr., to which a lineage of *C. tremula* (Griseb.) Griseb. ex C. Wright and *C. sanchezii* J. Linares & Angulo is sister. In both trees, subclade B4 including the more widespread *C. corymbosa* Kunth and subclade B5 containing the exclusively Caribbean taxa of the genus are resolved as close relative to the subclade B3.

Taxonomic treatment

Casearia isthmica de Mestier & O.Ortiz, sp. nov.

urn:lsid:ipni.org:names:77332275-1 Figs 3, 4

Type. PANAMA. Distrito de Capira: Parque Nacional Altos de Campana, sendero La Rana Dorada, ca. 100 m desde la entrada, 8°41'32"N, 79°55'34"W, 839 m, 27 April 2022, *E. Campos & J. Sumich 1329* (SAL302) (holotype: PMA-127644!; isotypes: B-101233230!, SCZ! two sheets, barcodes: 20033 and 20034).

Casearia isthmica shares morphological similarities with *C. laetioides* (=*Zuelania guidonia* (Sw.) Britton & Millsp), *C. sanchezii* and *C. tremula*. From both the plastid and nuclear trees, *C. laetioides* can be hypothesized as sister species to the newly discovered *C. isthmica*. In terms of morphology, this new taxon differs from *C. laetioides* (A. Rich.) Northr. by having essentially glabrous leaf blades (vs. pubescent), a prominent style (vs. absent or sometimes poorly developed), greenish-white sepals (vs. yellowish), 12 staminodia and stamens (vs. 15–20 staminodia and 20–40 stamens), and glabrous fruits (vs. pubescent). Furthermore, *C. sanchezii* differs morphologically from *C. isthmica* in presenting sessile inflorescence, crenate to subentire leaf blade and a longer petiole of 1 to 2.5 cm. *C. isthmica* differs from *C. tremula* in having congested inflorescences with 12–20 flowers (vs. 15 to 24 stamens in two



Figure 1. Bayesian 50% majority-rule consensus tree based on four plastid markers (*rps4-trnLF, trnK-matK, rpl16* and *petD*). Values above branches in bold are posterior probabilities (PP), values in italic are bootstrap support (BS) and Jackknife support (JK) is below the branches. Values in square brackets represent a conflict in the topology of the Bayesian analysis with maximum likelihood or Bayesian analysis with parsimony. The species name at the tip of the node is preceded by its DNA number and followed by the country of origin of the sample.



Figure 2. Bayesian 50% majority-rule consensus tree based on two nuclear markers (GBSSI and ITS). Values above branches in bold are posterior probabilities (PP), values in italic are bootstrap support (BS) and Jackknife support (JK) is below the branches. Values in square brackets represent a conflict in the topology of the Bayesian analysis with maximum likelihood or Bayesian analysis with parsimony. The species name at the tip of the node is preceded by its DNA number and followed by the country of origin of the sample.

rows), and pubescent styles (vs. glabrous). The discriminating morphological characteristics between *C. isthmica* and its congeners were listed in Table 1. *C. sanchezii* is found in the cloud forest of Mexico and El Salvador at elevation of 1600 to 2000 m, whereas *C. isthmica* is endemic to Central Panama and occurs at 800 m.



Figure 3. *Casearia isthmica* de Mestier & O. Ortiz **A** flowering branch **B** inflorescence **C** flowers at anthesis **D** fruiting branch **E** leaves **F** ripe fruit **G** bark. Photos **A**, **C**, **E** (back side of the leaf) by Carmen Galdames (Galdames 6153). Photos **D**, **E** (front side of the leaf) by Carmen Galdames (Galdames 6642). Photo B by Ernesto Campos (Sumich 151). Photos **G**, **E** by Ernesto Campos Plate by Marco Cedeño-Fonseca.



Figure 4. *Casearia isthmica* de Mestier & O. Ortiz **A** branches **B** twig and stipules **C** trunk base and roots **D** lenticellate bark. Photos **A**, **B** by Carmen Galdames (Galdames 6642). Photo **C** by Ernesto Campos (Campos 1087). Photo **D** by Ernesto Campos. Plate by Marco Cedeño-Fonseca.

	1			1
	C. isthmica	C. laetioides	C. sanchezii	C. tremula
Elevation (m)	(600-)800-900	0-500	1600-2200	0-600
Habitat	cloud forests	wet or dry lowland forests	cloud forests	wet or dry lowland forests
Petiole	caniculate	non-caniculate	caniculate	non-caniculate
Petiole size (cm)	0.5-0.8	1-2 cm	(0.4-)1-2.5 cm	(0.5-)1-1.8(-2.4)
Leaf blade	glabrous	pubescent	glabrous	glabrous
Leaf base	asymmetrical, rounded to acute	asymmetrical, obtuse to rotundate	symmetrical, obtuse, cuneate or subcordate	asymmetrical, cuneate to rounded
Leaf margins	serrate to crenate	serrate	crenate to subentire	serrate-crenulate
Leaf apex	subcaudate to acuminate	acuminate	acute to acuminate	attenuate to subacuminate
Inflorescence type	pedunculate, umbelliform	sessile, fascicle	sessile, umbelliform	pedunculate, fascicle or corymb
Flower number per inflorescence	12-20	15	15-20	3-10
Stamens	12	20-40	12-15	15-24
Style	present, pubescent	absent	present, glabrous	present, glabrous
Stamens in the same row as staminodia	yes	yes	yes	no
Sepals	5	4-5	5	(5-)6-9
Sepal color	greenish-white	yellow	white	greenish-white
Fruit pubescence	glabrous	pubescent	glabrous	glabrous
Fruit color	red pinkish	yellowish-green	red to dark red	purple red

Table 1. Comparison of the morphological characteristic of the newly described species and its closest relatives.

Description. Tree, up to 15–20 m tall; trunk straight, with bark cream, highly lenticellate; linear lenticels, arranged horizontally and vertically; branches zig-zag in shape, brownish, glabrous, with white lenticels. Stipules 4.0-6.8 × 2.5-4 mm, glabrous, ovate or triangular, persistent on the upper part (distally) and then deciduous. Leaves alternate, simple, deciduous when flowering; petiole 0.5-0.8 cm, canaliculate, glabrous; leaf blade 3.5-8.8 × 0.7-2.6 cm, subcoriaceous or coriaceous, drying brownish or blackish, lanceolate to obovate, asymmetrical, rounded or sometimes acute at the base, subcaudate-acuminate at the apex, densely pellucid punctate, glabrous on both sides, although slightly puberulous on the major abaxial veins; margins slightly serrate to crenate, marginal teeth more frequent in the upper half of the leaf blade; venation pinnate, lateral secondary veins in 5-10 ascending pairs, higher-order veins forming a dense reticulation, prominent on the abaxial surface. Inflorescences pedunculate, congested, umbeliform, each unit 12-20 flowered; peduncle 3 mm; bracts ca. 3.2 mm, coriaceous, ovate-lanceolate, greenish; pedicels ca. 8 mm, terete, basally articulate, green, glabrous. Floral buds oblong-obovate; flowers bisexual; sepals 5, ca. 4.0×1.6 mm, seemly free, oblong-obovate, glabrescent, greenish-white, white internally and greenish externally; staminodia 12, white, ligulate, white-hirsute; stamens 12 on the same row as the smaller staminodia and alternating with them, densely pubescent; filaments equal, free, white-hirsute; anthers elliptic, creamy, white-hirsute externally; ovary greenish, ovate, white-hirsute; style undivided, white-hirsute; stigma capitate, creamy. Fruits fleshy, orbicular, up to 5 cm diameter, very glossy, green during development, turning black-purple externally and pinkish or red internally when ripe, covered on the lower part by the sepals, dehiscent by 3 valves; seeds many, creamy-white, aril orange.

Distribution and habitat. Endemic to Central Panama (Panamá and Panamá Oeste provinces) (Fig. 5), documented only from cloud forests at elevations between (600–)800–900 m, in the premontane rain forest life zone.



Figure 5. Geographic distribution of Casearia isthmica.

Phenology. Flowering in April, May. Fruiting in June, July.

Etymology. The specific epithet refers to the geographic distribution of the new species, which is restricted to the Isthmus of Panama.

Preliminary conservation status. *Casearia isthmica* is known from ten collections made in two locations (Altos de Campana and Altos de Pacora). These collections were made within or very close to the external limits of protected areas (Altos de Campana National Park and Chagres National Park). Although they are protected areas, both locations face moderate anthropic disturbances, mainly in the borders such as Altos de Pacora (Chagres National Park). The highest threat facing this taxon is the loss of habitat caused by new road constructions and building of housing, as well as destructive tourist activities that are not environmentally sustainable, such as clandestine motorcycle races through the forest. Because this species has a limited distribution (EOO: 220 km²; AOO: 16 km²), the effect on its natural habitat may be extremely critical and may compromise its conservation. *Casearia isthmica* must be considered as Endangered [EN B1ab(iii)+2ab(iii)].

Selected specimens examined. PANAMA Panamá Oeste Province: Parque Nacional Altos de Campana; Sendero de Interpretación; 1 km del campamento de los guardaparques de INRENARE; bosque muy húmedo tropical premontano; Camino Zamora; 8°40'N, 79°55'W; 800-900 m; fl; 21 May 1992; M.D. Correa et al. 8944 (PMA) • Parque Nacional Altos de Campana; colectado a 5 m de la orilla de la carretera dentro del parque; 8°40'N, 79°55'W; 800-900 m; fr; 24 June 1993; M.D. Correa & E. Montenegro 9622 (PMA) • Parque Nacional Altos de Campana; Finca García; 8°40'N, 79°55'W; 800–900 m; fr; 28 July 1994; M.D. Correa & E. Montenegro 10717 (PMA) • Parque Nacional Altos de Campana; 3 agosto 1995; E. Montenegro 1112 (SCZ) • Parque Nacional Altos de Campana; Las Nubes; División Continental entre Finca de Tomás Herrera; 600-700 m; 3 May 1997; M.D. Correa et al. 11430 (F; MO PMA) • Parque Nacional Altos de Campana; Sendero El Tigre; bosque nuboso; 8°40'N, 79°55'W; 900 m; fr; 11 Jul 1998; C. Galdames; E. Montenegro & H. Valdéz 4317 (F; PMA; SCZ) • Distrito de Capira; Parque Nacional Altos de Campana; colectado en el sendero de la Rana Dorada; ca. A 100 m de la entrada; 8°41'32"N, 79°55'34"W; 839 m; fl; 3 May 2018; E. Campos & C. Galdames 1087 (B; SCZ) • Distrito de Capira; Parque Nacional Altos de Campana; sendero La Rana Dorada; ca. 100 m desde la entrada; 8°41'32"N, 79°55'34"W; 839 m; fl; 27 April 2022; J. Sumich & E. Campos 151 (SCZ) • Distrito de Capira; Parque Nacional Altos de Campana; 27 April 2022; sendero La Rana Dorada; J. Sumich 127 (SCZ). Panamá Province: Cerro Pelón; finca del Sr. Rodrigo Coba; reserva boscosa privada; adyacente a Cerro Jefe; 9°12'29"N, 79°22'33"W; 825 m; fr; 29 June 2010; C. Galdames; R. Vergara & F. Rodríguez 6642 (PMA; SCZ).

Discussion

Results of both the molecular and morphological analysis highly support the recognition of *Casearia isthmica* as a new species. Based on the molecular trees (Figs 1, 2), *C. isthmica* can be hypothesized as sister to *C. laetioides* (A. Rich.) Northr. (*=Zuelania guidonia* (Sw.) Britton & Millsp) and both are related to taxa with a largely central American distribution such as *C. tremula* (Griseb.) Griseb. ex C. Wright, and *C. sanchezii* J. Linares & Angulo.

Morphologically, *Casearia laetioides*, *C. tremula*, and *C. sanchezii* share similarities with *C. isthmica*, such as the general shape of the leaves, the presence of more than ten stamens with pubescent filaments, and the size of the fruit. However, *C. laetioides* differs from *C. isthmica* in many aspects, mainly in the petiole, leaf blades, inflorescences, fruits, and other floral aspects related to the style and number of stamens and staminodia (Table 1). Character states such as essentially glabrous leaves (sometimes puberulent along the major veins), glabrous and glossy fruits shared between *C. isthmica*, *C. tremula* and *C. sanchezii* (Table 1) could be of plesiomorphic nature but the latter two differ mainly in the type of inflorescence, number of flowers per inflorescence and the number of stamens. Taken together, morphological differences support the recognition of *C. isthmica* as a new species.

Casearia laetioides was historically classified within the genus *Zuelania* A. Rich., which has recently been shown to be nested within *Casearia*, on the basis of morphological and molecular characters (Samarakoon and Alford 2019; Mestier et al. 2022). *C. laetioides* is widely distributed in the Caribbean region, in Mexico, in Central America and Northern South America (Sleumer 1980). *Zuelania* was distinguished from *Casearia* by having a high number of stamens and a sessile and peltate stigma, whereas most *Casearia* species possess up to 12 stamens and a capitate stigma with a style. However, it seems that the high number of stamens is a homoplastic character state, as within clade B3, *C. isthmica* is the only species presenting 12 stamens.

From a geographical and ecological viewpoint, *Casearia isthmica* and *C. laetioides* are both present in Panama, although not in the same ecosystem as *C. isthmica*, which occurs at higher elevation in cloud forest, whereas *C. laetioides* occurs at lower elevation, below 600 m, usually in wet or dry habitats such as seasonal forests (Table 1). Further research will be needed to clarify if *C. laetioides* is monophyletic and a vicariant to *Casearia isthmica* and to clarify the position of the lineage including *C. isthmica* and *C. laetioides* within subclade B3 of *Casearia*. It will be relevant to a better understanding of the speciation history of *C. isthmica* as an example for the origin of cloud forest species in Panama, but also with respect to the origin of the flora of the Caribbean, for which studies in recent years underscored the close affinities between Central America, Mexico and the Caribbean islands (Cervantes et al. 2016; Mestier et al. 2022).

Some specimens from Panama previously identified as *C. tremula* were re-identified and included in this work as *Casearia isthmica* (*Galdames et al.* 4317 and *Correa et al.* 11430). However, there is currently a representative specimen (*Carrasquilla* 2072 MO, PMA) that confirms the occurrence of *C. tremula* in the country, which was collected in the dry seasonal lowland forests from the Pacific slope of Panama.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

All authors contributed to and accepted the final manuscript. Conceptualization: AM, ECP, MCP, 000; Formal analysis: AM, ECP, MCP, 000; Acquisition of material in the field: ECP, 000; Writing – Original draft: AM; Writing – Review and Editing: AM, ECP, MCP, 000.

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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 used for molecular analysis

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: docx

- Explanation note: Accessions are listed in alphabetic order. Name and author, lab number, DNA bank number, locality, collector and collector number, herbarium voucher and NCBI accession number for *rps4-trnLF*, *trnK-matK*, *rpl16*, *petD*, GBSSI and ITS respectively. Species names follow Sleumer (1980). ¹Korotkova et al. (2009), ²Li et al. (2019), ³Alford (2005), all others are newly sequenced for this study; "–" indicates missing sequences.
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Link: https://doi.org/10.3897/phytokeys.236.108651.suppl1

Supplementary material 2

Annotated alignment of five concatenated plastid regions (*rps4-trnL-F*, *trnK-matK*, *rpl16*, *petD*)

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: fas

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Link: https://doi.org/10.3897/phytokeys.236.108651.suppl2

Supplementary material 3

Matrix of five concatenated plastid regions (*rps4-trnL-F*, *trnK-matK*, *rpl16*, *petD*) including the indel partition

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: fas

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Supplementary material 4

Annotated alignment of nuclear region (GBSSI and ITS)

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: fas

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Supplementary material 5

Matrix of nuclear regions (GBSSI and ITS) including the indel partition

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: fas

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Supplementary material 6

Summary of characters and tree statistics and evolutionary models for each dataset

Authors: Astrid de Mestier, Ernesto Campos Pineda, Marco Cedeño Fonseca, Orlando O. Ortiz

Data type: xlsx

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PhytoKeys

Research Article

Vaccinium chaozhouense (Ericaceae), a new species from East Guangdong, China

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Abstract

Vaccinium chaozhouense (Ericaceae), a new species from East Guangdong Province, China is described and illustrated. This new species is morphologically similar to *V. wrightii* by having flowers with persistent and leaf-like bracts, long pedicels, and white spherical-urceolate corollas, but is distinguished by having glandular trichomes on the abaxial surface of the leaf blade, shorter pedicels, sparsely pilose corolla ridges, and anther thecae longer than the tubules. A key to the new species and morphologically similar species is also provided.

Key words: Endangered species, morphology, taxonomy, Vaccinieae, *Vaccinium* sect. *Bracteata*

Introduction

With 470 accepted species, *Vaccinium* L. is the largest genus of the subfamily Vaccinioideae Rchb. (Ericaceae) (POWO 2023). In the account of Flora of China, 92 *Vaccinium* species were recorded (Fang and Stevens 2005). As several new species have been described in recent years, the number of *Vaccinium* species has now reached 100 for this country (Tong and Xia 2015; Tong et al. 2018, 2020, 2021a, b, 2022; Huang et al. 2022; Qin et al. 2023). Some preliminary molecular phylogenetic studies showed that *Vaccinium* is polyphyletic, with many sections considered more distinct than some genera (Stevens 1985; Kron et al. 2002; Predraza-Peñalosa and Luteyn 2011; Argent 2019). However, a comprehensive sampling is not easy for such a cosmopolitan genus, as it will need full international cooperation to make it possible.

Recently, one of the co-authors (J.-H. Ding) found an interesting *Vaccinium* in Chao'an Fenghuangshan Provincial Nature Reserve, Guangdong Province, China. It resembles *V. wrightii* A. Gray, a species endemic to Taiwan and the Ryukyu Islands, in having leaf-like floral bracts and white spherical-urceolate corollas (Li 1978; Yamazaki 1993; Li et al. 1998). However, after careful comparison of this plant to other similar species similar, we confirmed that it represents a species new to science and is here described and illustrated.



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Materials and methods

Flowering and fruiting materials were collected from Fenghuangshan, Chaozhou City, Guangdong Province, China, during several field trips from 2022 to 2023. The description was based on dried herbarium specimens. The online specimen photos (including type specimens) of *V. wrightii* in GH, K, and W were consulted, as well as physical herbarium specimens deposited at IBSC and PE. Measurements were obtained with a ruler, and small plant parts were observed and measured under a stereo microscope (Mshot-MZ101).

Taxonomic treatment

Vaccinium chaozhouense Y.H.Tong & J.H.Ding, sp. nov.

urn:lsid:ipni.org:names:77332387-1 Fig. 1

Type. CHINA. Guangdong Province: Chaozhou City, Chao'an Fenghuangshan Provincial Nature Reserve, 980 m a.s.l., 10 May 2023 (fl.), *Yi-Hua Tong et al. TYH-2699* (holotype: IBSC, isotypes: KUN, PE).

Diagnosis. The new species is most similar to *V. wrightii* A. Gray (including its variety with smaller habit and leaf blades, *V. wrightii* var. *formosanum* (Hayata) H. L. Li) by having flowers with persistent and leaf-like bracts, and white spherical-urceolate corollas, but is distinguished by the presence of glandular trichomes on the abaxial surface of the leaf blade (vs. glabrous), shorter pedicels (4–6 mm vs. 5–15 mm), sparsely pilose (vs. glabrous) ridges of the corolla, and anther thecae longer than the tubules (vs. equal to or shorter than the tubules). A more detailed comparison of the two species is provided in Table 1.

Description. Evergreen shrubs, 0.3–1.5 m tall. Young branchlets densely pubescent, glabrescent. Leaves dense, spirally alternate; blades leathery or thickly leathery, elliptic or ovate, 1.5-3.1 × 0.7-1.8 cm, apex acute, base cuneate to broad cuneate, margin serrate, each serra tipped with a gland, abaxially with evenly distributed glandular trichomes throughout, adaxially glabrous, midvein raised abaxially, slightly impressed adaxially, lateral veins 4-7 on each side, slightly conspicuous abaxially, inconspicuous adaxially; petiole 2-3 mm long, initially pubescent, glabrescent at maturity. Racemes pseudoterminal and axillary, 1.5-4 cm long, with 3-7 flowers, rachis pubescent or sometimes glabrous; bracts persistent, leaf-like, ovate, elliptic or obovate, 3.5-8 × 2-4 mm, nearly glabrous on both sides, margin with (1-)5-15 glandular teeth per side, occasionally ciliolate at the apex; pedicel glabrous or sparsely pubescent on upper part, 4-6 mm long; bracteoles 2, caducous, usually borne at the middle and lower part (towards rachis) of the pedicel, occasionally at the upper part (towards hypanthium), lanceolate, $1.5-3 \times 0.5-1$ mm wide, glabrous on both sides, margin with (0-)1-2 glandular teeth, occasionally ciliolate at the apex. Hypanthium obconical, densely white-pubescent or sometimes glabrous; calyx limb 5-lobed to near base, calyx lobes triangular or broadly triangular, 1-1.5 × 1.2-1.5 mm, glabrous on both sides or sparsely pubescent abaxially, often with glandular teeth on the margin, apex acuminate, sometimes ciliolate. Corolla white, spherical-urceolate, slightly 5-ridged, 5-6 × 4-5 mm, sparsely pilose on the ridges abaxially, otherwise glabrous, pilose adaxially, apex shallowly



Figure 1. Vaccinium chaozhouense A habitat B habit and flowering branchlets C flowering branch D fruiting branches E abaxial surface of leaf blade showing glandular trichomes F flower G bracts, adaxial (left) and abaxial (right) surfaces H bracteoles, adaxial (left) and abaxial (right) surfaces I stamens, ventral (left), lateral (middle) and dorsal (right) view J hypanthium (with calyx lobes removed), showing disk and style K disk, top view L ovary cross-section, showing the pseudo-10-locular ovary. Scale bars: 5 mm (F–G, J); 3 mm (H); 2 mm (I, L); 1.5 mm (E, K). Photographs by Yi-Hua Tong, except D by Jian-Hong Ding.

lobed, lobes recurved, triangular, ca. 1.2×1.2 mm; stamens 10, 4.5-4.8 mm long, filaments 2–2.2 mm long, densely white-villous, anthers 2.5–2.7 mm long, thecae 1–1.2 mm long, tubules 1.5-1.7 mm long, spurs present, borne at the base of tubules, obliquely projected, ca. 0.8 mm long; style 4–5.5 mm long, stigma truncate, ovary pseudo-10-locular, each with several ovules, disk

Table 1. Morphological comparison of *Vaccinium chaozhouense* and *V. wrightii*. The data for *V. wrightii* are from Li (1978), Fang and Stevens (2005), and Yamazaki (1993) as well as the examination of the specimens listed in the text.

Characters	V. chaozhouense	V. wrightii	
Abaxial surface of leaf blade	With evenly distributed glandular trichomes	Glabrous	
Inflorescence length (cm)	1.5-4	5-8.5	
Indumentum of inflorescence rachis	Pubescent or sometimes glabrous	Glabrous	
Pedicel length (mm)	4-6	5-15	
Indumentum of calyx	Pubescent or sometimes glabrous	Glabrous	
Indumentum of abaxial surface of corolla	Sparsely pilose on edges, otherwise glabrous	Glabrous	
Anther thecae Longer than tubules		Equal to or shorter than tubules	
Indumentum of disk	White-pubescent or sometimes nearly glabrous	Usually glabrous	

white-pubescent or sometimes nearly glabrous. Fruit globose, 4–4.5 mm in diameter, black when ripe; fruiting pedicel 4–6 mm long.

Etymology. The species epithet is named after the type locality, Chaozhou City. The Chinese name is given as 潮州越橘 (Chinese pinyin: cháo zhōu yuè jú).

Distribution, habitat and conservation status. This species is currently known only from the type locality, i.e., Fenghuangshan, the highest mountain in the Chaoshan district (an area of nearly 16,000 km² in East Guangdong) with an elevation of 1497.8 m at the summit. *Vaccinium chaoanense* grows among shrubs on sunny volcanic rocks at an elevation of ca. 980 m. This kind of habitat where this species grows is actually a little unusual in Fenghuangshan, as most of Fenghuangshan area is covered with evergreen broadleaf forests. Only one population with < 30 individuals was found despite a careful search in the area. Thus, it is assigned a status of 'Critically Endangered' (CR, criterion D) following the IUCN Red List categories and criteria (IUCN 2012) and guidelines (IUCN Standards and Petitions Committee 2022). Because its distribution area is under the protection of Chao'an Fenghuangshan Provincial Nature Reserve, and it is not economically valuable, the threat risk seems low.

Phenology. Flowering in May and fruiting in October–November.

Additional specimens examined. Vaccinium chaozhouense: the same locality as the type, 18 May 2022 (fl), Jian-Hong Ding s.n. (IBSC); ibid., 31 October 2022 (fr.), Jian-Hong Ding s.n. (IBSC); ibid., 10 May 2023 (fl.), Yi-Hua Tong et al. TYH-2700 (IBSC).

Vaccinium wrightii: JAPAN. Ryukyu: without precise locality, without date, *C. Wright 170* (holotype GH00015982, image, isotypes K000780593, image, NY00010772, image); without precise locality, 1887, *O. Warburg s.n.* (W, image); Gneka-Kesaji, 9 June 1930, *K. Kondo 1975* (PE00245894); Higashi-son, Gaji, in windy scrubs, 100 m a.s.l., 12 October 1990, *T. Yamazaki 6486* (PE00197326); Iriomote Island, Shirahama, on the seaside, 29 April 1980, *K. Inoue 1469* (IBSC0457605, PE00197336); Iriomote Island, on the way from Ootomi to Mt. Goza, in evergreen forest, 20–200 m a.s.l., 4 August 1981, *N. Fukuoka & M. Ito 180* (IBSC0457604); Iriomote Island, valley of Yuchin-gawa River, on rocky cliff at shady riverside, 6 April 2004, *K. Yonekura et al. 11346* (IBSC0741637); Iriomote Island, along Shirahama Forest Road, ca. 1 km from the entrance, on sunny slope around a marsh in a small valley, 120–130 m a.s.l., 3 April 2004, *Koji Yonekura 11213* (PE); Iriomote Island, in evergreen forest, 50 m a.s.l., 8 November 1985, *Toshiyuki Nakaike s.n.* (PE00197345); Nago-shi, NW slope of the Mt. Nago-dake, 200 m a.s.l., 11 March 1978, *J. Murata* 4717 (PE00438051). CHINA. Taiwan: Hualien, Hsiaochingshui, 350 m a.s.l., 17 April 2002, *Tien-Tsai Chen* 11872 (PE); Taipei, Taluntoushan, 13 June 1997, *Her-Long Chiang* 496 (PE00197448).

Discussion. Vaccinium chaozhouense can be assigned to V. sect. Bracteata Nakai according to Sleumer's or Vander Kloet & Dickinson's infrageneric classification system (Sleumer 1941; Vander Kloet and Dickinson 2009) by its terrestrial habit, pinninerved leaf blade with a serrate margin, persistent and leaf-like floral bracts, pseudo-10-locular ovary and black fruit, which match the characters of that section. Two other species are also similar to this new species in having the same leathery leaf texture, persistent, large, and leaf-like floral bracts, and similar urceolate or spherical-urceolate corolla shape, i.e., V. eberhardtii Dop from Vietnam and Thailand, which has also been recently reported from Guangxi, China (Tong et al. 2018), and V. boninense Nakai endemic to the Bonin Islands (also known as Ogasawara Islands). A key to the four species is provided below summarizing the morphological differences among them. Although these four species were assigned to V. sect. Bracteata for now, they bear unusual urceolate shape of corolla, while many other species in this section have tubular corolla. Meanwhile, a continuous coastal distribution from western Pacific Ocean islands to Indochina is presented by the four species. Thus, according to their morphological characteristics and distribution pattern, these four species may represent a distinct lineage in V. sect. Bracteata, and studies on their biogeography and speciation seem warranted.

Key to V. chaozhouense and similar species

1	Pedicel 2–4 mm; anther spurs oriented nearly straight upward, ca. 1.2 mm
	long, longer than half of anther tube; China (South Guangxi), Vietnam, and
	Thailand
-	Pedicel 4-15 mm; anther spurs oriented obliquely upward, 0.3-0.8 mm
	long, shorter than or equal to half of anther tube2
2	Leaf blade margin entire or nearly so, obscurely dentate; corolla urceolate;
	Japan (Bonin Islands) V. boninense
-	Leaf blade margin evidently serrate; corolla spherical-urceolate3
3	Abaxial surface of leaf blade with evenly distributed glandular trichomes;
	pedicels 4-6 mm long; corolla ridges sparsely pilose abaxially; anther the-
	cae longer than tubules; China (East Guangdong)
-	Abaxial surface of leaf blade glabrous; pedicels 5-15 mm long; corolla
	glabrous throughout abaxially; anther thecae equal to or shorter than tu-
	bules; China (Taiwan) and Japan (Ryukyu Islands)

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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. Data curation: PZY. Funding acquisition: PZY. Investigation: PZY, WH, YHT, JBN, JHD, WCH. Resources: JHD. Writing - original draft: JHD, YHT.

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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

Research Article

Molecular and morphological evidence for a new species of *Stachys* (Lamiaceae) from Hunan, China

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Abstract

Stachys yingzuijieensis, a new species from western Hunan, China, is described and illustrated. Molecular phylogenetic analyses based on three nuclear ribosomal DNA loci (ETS, ITS and 5S-NTS) recovered *S. yingzuijieensis* within the *Stachys* clade and as a sister group of *S. arrecta*. The two species can be easily distinguished by the morphology of lamina, corolla and nutlet. A key to all species of Stachydeae from China is also provided.

Key words: Eurystachys clade, Lamioideae, micromorphology, Stachydeae, taxonomy

Introduction

As one of the largest genera in Lamiaceae, Stachys L. comprises over 365 species distributed worldwide (Bhattacharjee 1980; Harley et al. 2004; POWO 2023). Together with other 11 genera, Stachys belongs to the largest tribe in subfamily Lamioideae, i.e. Stachydeae (Zhao et al. 2021). However, the intergeneric relationship within the tribe is taxonomically challenging and Stachys has been continuously shown to be non-monophyletic in previous molecular phylogenetic studies. While exploring the phylogenetic position of the Hawaiian endemic mints with respect to Stachys, Lindqvist and Albert (2002) showed that three genera endemic to Hawaii (Haplostachys (A. Gray) Hillebr., Phyllostegia Benth. and Stenogyne Benth.), as well as Prasium L., Phlomidoschema (Benth.) Vved. and Sideritis L., were embedded within Stachys. Scheen et al. (2010) and Bendiksby et al. (2011) further added the Asian genera Chamaesphacos Schrenk ex Fisch. & C.A. Mey., Hypogomphia Bunge, Suzukia Kudô and Thuspeinanta T. Durand to the list of taxa nested within Stachys in their lamioid-wide studies. The most comprehensive phylogenetic analyses of Stachydeae were performed by Salmaki et al. (2013, 2019), based on multiple nuclear ribosomal and plastid DNA loci. Salmaki et al. (2019) recognised 12 well-supported clades within the Eurystachys clade, a name suggested by Salmaki et al. (2013) to include all genera of Stachydeae, except the monotypic genus Melittis L. Though the synapomorphies for Stachydeae remain unclear, members of the tribe usually share



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Copyright: © Ling Xue et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). campanulate or weakly 2-lipped calyx with spiny lobes and hairy throat, strongly 2-lipped corolla and apically rounded nutlets (Scheen et al. 2010).

A total of 18 species of *Stachys* are recorded from China and eight of them are endemic (Li and Hedge 1994). Except for *Stachys*, China also accommodates another three genera of Stachydeae, i.e. *Chamaesphacos* (1 sp.), *Sideritis* (2 spp.) and *Suzukia* (2 spp.) (Li and Hedge 1994; Liu and Zhang 2004). Recently, a potential new species of *Stachys* was discovered during our field investigation in western Hunan Province, China. By carrying out comprehensive molecular phylogenetic and morphological studies, we confirmed its status as a species new to science. It was, thus, named *Stachys yingzuijieensis* L. Wu & Y.P. Chen and described below.

Materials and methods

Molecular phylogenetic analyses

The phylogenetic placement of the new species within Stachydeae was evaluated based on the framework of Salmaki et al. (2019). A total of 90 accessions representing 88 taxa from all 12 clades and 11 genera of *Eurystachys*, as well as *Melittis melissophyllum* L., were sampled as the ingroups. Two genera that are closely related to Stachydeae – *Betonica* L. and *Galeopsis* L. – were selected as the outgroups. Except for one accession of the new species and one accession for each of eight species of *Stachys* from China that were newly sequenced here, all remaining sequences were downloaded from GenBank. Voucher information for newly-sequenced samples and GenBank accession numbers for all sequences are listed in Appendix 1.

Total genomic DNA was extracted from silica-gel-dried leaf material using the modified CTAB method (Doyle and Doyle 1987). According to Salmaki et al. (2019), three nuclear ribosomal DNA loci, i.e. the internal and external transcribed spacers (ITS and ETS) and the 5S non-transcribed spacer (5S-NTS), were used to reconstruct the phylogenetic relationships. Polymerase chain reaction primers and protocols of ITS and ETS followed those used by Chen et al. (2019) and that of 5S-NTS followed Roy et al. (2013).

Raw sequences were assembled and edited using Geneious v.11.0.3 (Kearse et al. 2012). Data matrices were aligned using MUSCLE (Edgar 2004) and then manually adjusted in Geneious. After removing the ambiguously aligned regions in the ITS dataset, the three DNA loci were concatenated for phylogenetic reconstruction. Partitioned Bayesian Inference (BI) and partitioned Maximum Likelihood (ML) analyses were performed on the web server Cyberinfrastructure for Phylogenetic Research Science (CIPRES) Gateway (http://www.phylo. org/; Miller et al. 2010), using RAxML-HPC2 (Stamatakis 2014) and MrBayes v.3.2.2 (Ronquist et al. 2012), respectively. Detailed settings for the two analyses followed those described in Chen et al. (2019). The resulting trees were visualised in TreeGraph 2 (Stover and Müller 2010).

Morphological studies

Morphological similarities and differences between the new species and other taxa of Stachydeae were compared, based on our previous field investigations and specimen examination. Images of specimens (including type specimens) and living plants of Stachydeae from JSTOR (https://www.jstor.org/), Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/) and Plant Photo Bank of China (PPBC, http://ppbc.iplant.cn/) were examined. Protologues and other taxonomic and floristic literature related to Stachydeae (Knorring 1954; Ball 1972; Nelson 1981; Bhattacharjee 1982; Codd 1985; Li and Hedge 1994; Turner 1994; Paton et al. 2009; Salmaki et al. 2012) was also reviewed.

Trichomes on the lamina and calyx, as well as the nutlet and pollen morphology of the new species, were investigated using scanning electron microscopy (SEM). All materials were directly mounted on to stubs and sputter-coated with gold for 90 s at 20 mA. Micromorphological observations were conducted using a Zeiss EVO LS10 scanning electron microscope (Carl Zeiss NTS, Oberkochen, Germany) at 10 kV. Terminologies used for trichome, nutlet and pollen description followed those of Salmaki et al. (2008a, 2008b, 2009), Karaismailoğlu and Güner (2019, 2021) and Totmaj and Salmaki (2022).

Results

Phylogenetic results

The aligned length of the combined nuclear dataset was 1,381 bp (589 bp for ITS, 456 bp for ETS and 336 bp for 5S-NTS). The topologies of the BI and ML trees were largely consistent with each other, but the BI tree provided higher resolution. Thus, only the Bayesian 50% majority-rule consensus tree was presented (Fig. 1), the posterior probabilities (PP) and Bootstrap support (BS) values being superimposed on the nodes.

Our molecular phylogenetic result (Fig. 1) revealed that *Melittis* was sister to the remaining Stachydeae, i.e. the *Eurystachys* clade (PP = 0.99, BS = 58%). Two large clades were resolved within the *Eurystachys* clade: the first one (PP = 0.91, BS = 71%) mainly included temperate North American, Hawaiian and several Old World taxa and the second one (PP = 0.99, BS = 61%) only comprised Old World (mostly Mediterranean) taxa. Twelve robustly supported small clades (PP = 1.00, BS > 90%) can be further recognised, with two clades (*Eriostomum* clade and *Stachys* clade) in the first *Eurystachys* clade and the remaining (*Burgsdorfia* clade, *Distantes* clade, *Empedoclia* clade, *Hesiodia* clade, *Marrubiastrum* clade, *Olisia* clade, *Prasium* clade, *Setifolia* clade, *Sideritis* clade and *Swainsoniana* clade) in the second *Eurystachys* clade. Species distributed in China were mostly recovered in the *Stachys* clade were poorly resolved, *Stachys yingzuijieensis* was strongly supported as sister to *Stachys arrecta* L.H. Bailey (PP = 0.99, BS = 81%).

Morphological results

Stalked glandular and simple non-glandular trichomes were found on both surfaces of the lamina as well as the calyx of the new species (Fig. 2A–C). The abaxial surface of lamina and the outside surface of the calyx were more densely covered with longer trichomes. Pollen grains of *Stachys yingzuijieensis* were tricolpate with reticulate exine sculpturing (Fig. 2D–F), while nutlets were ovate with glabrous and reticulate surface (Fig. 2G–I).



Figure 1. Bayesian 50% majority-rule consensus tree of Stachydeae based on combined nuclear (ITS, ETS and 5S-NTS) dataset. Support values ≥ 0.50 PP or 50% BS are displayed above the branches (an "*" indicates a support value = 1.00 PP or 100% BS and a "-" indicates a conflicting node in the BI and ML trees). Species marked in bold represent samples newly sequenced in the present study. Multiple accessions of the same species are numbered according to Appendix 1.



Figure 2. Trichome, pollen, and nutlet micromorphology of *Stachys yingzuijieensis* **A** trichomes on the adaxial surface of lamina **B** trichomes on the abaxial surface of lamina **C** trichomes on the outside surface of calyx **D** polar view of pollen **E** equatorial view of pollen **F** surface sculpturing of pollen **G** dorsal view of nutlet **H** ventral view of nutlet **I** surface sculpturing of nutlet.

Discussion

The backbone of Stachydeae in the present study and the 12 clades recovered in the *Eurystachys* clade (Fig. 1) were consistent with that of Salmaki et al. (2019). The *Stachys* clade, which was referred to as the "*Stachys* core clade" in Salmaki et al. (2013) and the *Stachys* s.s. clade in Lindqvist and Albert (2002), is one of the largest monophyletic groups in the *Eurystachys* clade and comprises five genera (*Haplostachys*, *Phyllostegia*, *Stachys*, *Stenogyne* and *Suzukia*) and over 100 species. No synapomorphy has been found for this clade due to large morphological and geographical diversity (Salmaki et al. 2019). Next-generation sequencing data and comprehensive morphological studies are needed to further clarify the synapomorphies and relationships within this taxonomically problematic and important group.

Only several representatives of Stachydeae from China had been included in previous molecular phylogenetic studies and no morphological study had been carried out for Chinese *Stachys*. In this study, nine species of *Stachys* from China were newly sequenced and included in the phylogenetic analyses. Our results showed that most species that were collected from or reported to be occurring in China were recovered within the *Stachys* clade, including the new species (Fig. 1). *Stachys yingzuijieensis* was further revealed to be sister to *Stachys arrecta*, a species distributed in the evergreen broad-leaved forests at altitudes of 1500–2000 m in central China.

Characters	S. yingzuijieensis	S. arrecta Cordate, 2.5–6.5 × 1.5–3 cm, margin coarsely serrate		
Lamina	Oblong to oblong-lanceolate, 10−16 × 4−6 cm, margin crenulate			
Calyx	Approximately 7 mm long, teeth ca. 3 mm long, ovate-lanceolate	Approximately 5 mm long, teeth 2–2.5 mm long, narrowly triangular		
Pedicel	Absent	Approximately 1 mm long		
Corolla	White without spots, ca. 1 cm long, tube included in calyx	Pink with purple spots, ca. 1.2 cm long, tube exerted from calyx		
Nutlet	Surface smooth	Surface verrucate		

Table 1. Morphological comparisons between Stachys yingzuijieensis and S. arrecta.

Stachys yingzuijieensis differs from all other Chinese Stachydeae in its densely villosus and glandular pubescent plants, as well as the white corollas with tube included in the calyces (Figs 3, 4). For example, the corollas of *Stachys arrecta* are pink with purple spots and the corolla tubes are exerted from the calyces (Li and Hedge 1994). Except for above differences, *Stachys yingzuijieensis* also has oblong to oblong-lanceolate laminae with crenulate margin, whereas the laminae of *Stachys arrecta* are cordate with coarsely serrate margin. Moreover, they can be distinguished in the nutlet surface, which is smooth in the new species (Fig. 2), but verrucate in *Stachys arrecta*. More detailed differences between the two species are listed in Table 1. Here, we also provided a key to all species of Stachydeae from China below.

Key to the species of Stachydeae from China

1	Creeping herbs2
-	Erect herbs
2	Middle lobe of lower corolla lip entire
-	Middle lobe of lower corolla lip irregularly incisedSuzukia luchuensis
3	Lamina spinescent-aristate Chamaesphacos ilicifolius
-	Lamina not spinescent-aristate4
4	Calyx tubular-campanulate; corolla included in calyx5
_	Calyx campanulate; corolla exserted from calyx6
5	Corolla yellow, middle lobe of lower lip incised Sideritis montana
_	Corolla purple, middle lobe of lower lip entire Sideritis balansae
6	Annual herbs Stachys arvensis
-	Perennial herbs7
7	Bracteoles over half as long as calyx8
_	Bracteoles less than half as long as calyx, early deciduous9
8	Plants densely sericeous-lanate; verticillasters in compact spikes
-	Plants pilose; verticillasters in widely spaced spikes Stachys melissifolia
9	Lamina oblong, lanceolate to oblong-lanceolate10
-	Lamina ovate, ovate-oblong, or cordate16
10	Corolla white
_	Corolla pink, purple to red-purple11
11	Lamina densely villous-tomentose abaxiallyStachys oblongifolia
_	Lamina hispid, puberulent, or glabrous abaxially12

Stems densely retrorse villous Stachys palustri	is
Stems spreading hispid, glabrous, or subglabrous1	3
Calyx densely villous-hispid outsideStachys baicalensi	is
Calyx sparsely villous-hispid or glandular puberulent outside1	4
Calyx teeth obtuse at apex; corolla tube long exserted from ca	Э-
lyxStachys adulterina	9
Calyx teeth spinescent at apex; corolla tube included in calyx1	5
Lamina sparsely minutely hispid or subglabrous adaxially; calyx sparsel	y
villous-hispid along veins outsideStachys chinensi	s
Lamina glabrous adaxially; calyx glandular puberulent outside	•••
Stachys japonic	а
Corolla white or yellow1	7
Corolla pink or purple1	8
Corolla white; calyx teeth triangular, less than 2 mm long	•••
	S
Corolla yellow; calyx teeth ovate-triangular, over 2 mm long	•••
	а
Rhizomes not enlarged or succulent1	9
Rhizomes enlarged, succulent2	1
Lamina over 8 cm longStachys sylvatic	a
Lamina less than 5 cm long	0
Calyx teeth ovate-lanceolate	'a
Calyx teeth triangular	S
Calyx teeth linear-lanceolate, reflexed Stachys pseudophlomi	S
Calyx teeth narrowly triangular to triangular, straight	2
Lamina ovate-oblong; nutlet smooth Stachys geobombyci	S
Lamina ovate to cordate; nutlet tuberculate	3
Lamina cordate; calyx ca. 5 mm long Stachys arrect	a
Lamina ovate to oblong-ovate; calyx ca. 9 mm long Stachys siebold	П

Taxonomic treatment

Stachys yingzuijieensis L.Wu & Y.P.Chen, sp. nov.

urn:lsid:ipni.org:names:77332759-1 Figs 3, 4

Type. CHINA, Hunan, Huitong County, Yingzuijie National Nature Reserve, alt. 300–800 m, 26°56'N, 109°54'E, 3 Aug 2022, L. Wu et al. YZJ0145 (holotype: CSFI079941!; isotype: CSFI!).

Diagnosis. *Stachys yingzuijieensis* is most closely related to *S. arrecta*, but differs in its lamina oblong to elliptic-lanceolate (vs. cordate) with margin crenulate (vs. coarsely serrate), corolla white (vs. pink with purple spots) with tube included in calyx (vs. exerted from calyx) and nutlet surface smooth (vs. verrucate).

Herbs perennial. Rhizomes white, densely glandular pubescent. Stems erect, simple, 50–75 cm long, quadrangular, densely villous and glandular pubescent. Leaves opposite; petioles 2–4 cm long, densely villous and glandular pubescent; lamina oblong to oblong-lanceolate, papery, $10-16 \times 4-6$ cm, apex acute, margin crenulate, base cordate, adaxially green, sparsely villous and glandular pubescent, abaxially light green, densely villous and glandular pubescent, lateral veins



Figure 3. Morphology of *Stachys yingzuijieensis* from the type locality **A** habitat **B** habit **C–D** inflorescence **E** adaxial view of lamina **F** abaxial view of lamina **G** roots and rhizomes **H** frontal view of corolla **I** lateral view of calyces **J** dissected corolla **K** nutlets (**A–J** photographed by Lei Wu **K** photographed by Ya-Ping Chen).

4–5-paired, conspicuously elevated abaxially. Verticillasters 6-flowered, flowers sessile; bracts leaf-like, upper ones sessile, lanceolate, densely villous and glandular pubescent on both surfaces, longer than verticillasters; bracteoles linear, 1–2 mm long. Calyx campanulate, ca. 7 mm long, 10-veined, densely villous and glandular pubescent outside, glandular pubescent inside, fruiting calyx dilated, ca. 9 mm long; teeth 5, subequal, ovate-lanceolate, ca. 3 mm long, apex spinescent. Corolla white, ca. 1 cm long, tube ca. 7 mm long, ca. 1.5 mm wide, pubes-



Figure 4. Holotype specimen of Stachys yingzuijieensis.

cent annulate inside at 1/3 distance from base; 2-lipped, upper lip erect, concave, subcircular, ca. 3 mm in diam., densely pubescent and glandular pubescent outside, glabrous inside, lower lip spreading, sparsely pubescent and glandular pubescent to glabrescent outside, glabrous inside, ca. 6 mm long, 3-lobed, medium lob largest, trapeziform, ca. 3 mm long, ca. 4 mm wide, apex entire or emarginate, lateral lobs oblong, ca. 2 mm long, ca. 1 mm wide. Stamens 4, straight, included, filaments pubescent and glandular pubescent, anther cells 2, divergent. Style included, glabrous, apex subequally 2-lobed, lobes subulate. Ovary rounded at apex, glabrous. Nutlets 4, dark brown, ovoid, ca. 1.5 mm in diam., smooth and glabrous.

Phenology. Flowering from July to September, fruiting from August to October.

Distribution and habitat. Currently, *S. yingzuijieensis* is only known from the Yingzhuijie National Nature Reserve and a total of 50 mature plants were found during our field investigation. The new species usually grows in shady and moist places in evergreen broad-leaved forests at an altitude of 300–800 m.

Etymology. The specific epithet is derived from the type locality of the new species, i.e. the Yingzuijie National Nature Reserve in western Hunan Province, China.

Chinese name (assigned here). yīng zhuǐ jiè shuǐ sū (鹰嘴界水苏).

Additional specimen examined. CHINA. Hunan: Huitong County, Yingzuijie National Nature Reserve, 8 Aug 2022, L. Wu et al. YZJ0654 (CSFI!).

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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

LX, LW and Y-PC conceptualized the study. LW, J-HC and X-PL collected the samples. LX, MZ and Y-PC conducted the analyses. LX drafted the manuscript. Y-PC and LW 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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Appendix 1

Specimen information (taxon, voucher, herbarium, country) for samples newly sequenced in the present study with GenBank accession numbers for ITS, ETS and 5S-NTS, respectively. A "-" indicates a missing sequence. Herbarium abbreviations are listed after the vouchers. The accession numbers marked with an asterisk represent sequences newly generated. Only GenBank accession numbers are listed for sequences downloaded from NCBI.

Betonica officinalis L., KF529533, MK909580, MK909684; Betonica scardica Griseb., KF529534, MK909581, -; Chamaesphacos ilicifolius Schrenk ex Fisch. & C.A. Mey., KF529540, MK909585, MK909689; Galeopsis angustifolia Ehrh. ex Hoffm, KF529535, -, MK909685; Galeopsis pubescens Besser, KF529536, -, MK909686; Haplostachys haplostachya (A. Gray) H.St. John, KF529541, -, MK909690; Hypogomphia bucharica Vved., KF529542, MK909587, MK909691; Hypogomphia turkestana Bunge, KF529543, MK909588, MK909692; Melittis melissophyllum L., KF529544, KF235787, MK909693; Phyllostegia velutina (Sherff) H.St. John, KF549547, KF235809, AF308212; Phyllostegia waimeae Wawra, KF529548, KF235811, KF235752; Prasium majus L. 1, KF529549, MK909590, MK909694; Prasium majus L. 2, KF529550, MK909591, AF501919; Sideritis canariensis L., AF335605, MK909593, MK909695; Sideritis clandestina (Bory & Chaub.) Hayek, AF335616, MK909595, -; Sideritis endressii subsp. emporitana Willk, AF335627, MK909598, MK909698; Sideritis incana L., AF335634, MK909601, -; Sideritis leucantha Cav., AF335636, MK909603, MK909700; Sideritis macrostachys Poir., AF335609, -, AF501920; Sideritis montana L. 1, AF335612, -, MK909701; Sideritis montana L. 2, KF529551, -, MK909702; Sideritis nutans Svent., DQ900767, MK909604, MK909703; Sideritis perfoliata L., AF335618, -, MK909705; Sideritis romana L. 1, AF335614, -, MK909706; Sideritis romana L. 2, KF529552, -, AF501922; Sideritis scardica Griseb., AF335619, MK909606, MK909707; Sideritis syriaca L., AF335620, -, MK909708; Sideritis tragoriganum Lag., AF335639, MK909608. MK909710: Stachys aculeolata Hook. f., KF529556. KF235814. AF501924; Stachys aethiopica L., KF529559, KF235815, KF235753; Stachys affinis Bunge, MH703287, KF235816, AF501925; Stachys albens A. Gray, KF529560, MK909613, AF501928; Stachys alpigena T.C.E. Fr., KF529561, KF235822, KF235755; Stachys arabica Hornem., KF529564, MK909616, MK909711; Stachys arenaria Vahl, KF529566, MK909618, -; Stachys arrecta L.H. Bailey, H.J. Dong et al. HGNU-0485 (KUN), Hubei, China, OR878465*, OR887616*, OR887626*; Stachys arvensis (L.) L., KF529567, MK909619, MK909712; Stachys baicalensis Fisch. ex Benth., Y.P. Chen & Y. Zhao EM1459 (KUN), Hebei, China, OR878468*, OR887619*, OR887629*; Stachys bullata Benth., KF529576, KF235831, KF235759; Stachys burchelliana Launert, KF529574, MK909624, MK909713; Stachys byzantina K. Koch, KF529577, KF235832, AF501938; Stachys chinensis Bunge ex Benth.,

B. Liu et al. 7252 (PE), Beijing Botanical Garden (cultivated), China, OR878467*, OR887618*, OR887628*; Stachys chrysantha Boiss. & Heldr., KF529580, MK909628, AF501939; Stachys circinata L'Hér., KF529581, MK909629, -; Stachys corsica Pers., KF529582, KF235836, KF235762; Stachys cretica L., KF529583, KF235838, AF501948; Stachys debilis Kunth, KF529584, KF235839, KF235763; Stachys distans Benth., KF529585, MK909630, MK909716; Stachys dregeana Benth., KF529586, MK909631, MK909717; Stachys durandiana Coss., KF529587, MK909632, MK909718; Stachys eriantha Benth., KF529589, KF235842, AF501951; Stachys floridana Shuttlew. ex Benth, KF529590, KF235843, AF501952; Stachys graeca Boiss. & Heldr., KF529595, MK909636, MK909719; Stachys grandidentata Lindl., KF529596, KF235845, KF235766; Stachys grandifolia E. Mey., KF529597, MK909637, -; Stachys heraclea All., KF529598, MK909638, MK909720; Stachys hildebrandtii Vatke, KF529599, MK909639, MK909721; Stachys hyssopoides Burch. ex Benth, KF529600, MK909640, MK909722; Stachys inflata Benth., KF529601, MK909641, MK909723; Stachys ionica Halácsy, KF529602, MK909642, MK909724; Stachys kouyangensis (Vaniot) Dunn, Y.P. Chen et al. EM482 (KUN), Yunnan, China, OR878463*, OR887614*, OR887624*; Stachys lamioides Benth., KF529607, KF235852, KF235773; Stachys latidens Small, KF529608, KF235854, AF501956; Stachys lavandulifolia Vahl, KF529609, MK909646, MK909725; Stachys macraei Benth., KF529611, KF235857, KF235774; Stachys maritima Gouan, KF529612, MK909647, MK909726; Stachys melissifolia Benth., Y.P. Chen et al. EM1206 (KUN), Xizang, China, OR878466*, OR887617*, OR887627*; Stachys natalensis Hochst., KF529619, MK909654, -; Stachys nigricans Benth., KF529622, MK909657, -; Stachys oblongifolia Wall. ex Benth., H. Peng et al. FJ881 (KUN), Guizhou, China, OR878472*, OR887623*, OR887632*; Stachys ocymastrum (L.) Brig., KF529623, MK909658, MK909727; Stachys palustris L., KF529624, MK909659, MK909728; Stachys pilosa Nutt., KF529628, KF235861, MK909730; Stachys pubescens Ten., KF529629, MK909663, MK909731; Stachys reptans Hedge, KF529632, MK909664, MK909732; Stachys rupestris Montbret & Aucher ex Benth., KF529633, MK909665, MK909733; Stachys saxicola Coss. & Balansa, KF529634, MK909666, MK909734; Stachys schtschegleevii Sosn. ex Grossh., KF529637, MK909667, MK909736; Stachys setifera subsp. iranica (Rech. f.) Rech. f., KF529636, -, MK909735; Stachys setifera subsp. setifera C.A. Mey., KF529635, -, AF501976; Stachys sieboldii Miq., Y.P. Chen & Y. Zhao EM1492 (KUN), Ningxia, China, OR878469*, OR887620*, OR887630*; Stachys subaphylla Rech.f., KF529641, MK909671, MK909737; Stachys swainsonii Benth., KF529642, KF235871, AF501977; Stachys sylvatica L., KF529643, MK909672, MK909738; Stachys tenuifolia Willd., OR392565, -, AF501981: Stachys tetragona Boiss. & Heldr., KF529646, MK909673, MK909739; Stachys trinervis Aitch. & Hemsl., KF529647, MK909674, MK909740; Stachys turcomanica Trautv., KF529649, MK909676, MK909742; Stachys xanthantha C.Y. Wu, Y.P. Chen & H.M. Li EM620 (KUN), Chongging, China, OR878464*, OR887615*, OR887625*; Stachys vingzuijieensis L. Wu & Y.P. Chen, L. Wu et al. YZJ0654 (CSFI), Hunnan, China, OR878471*, OR887622*, OR887613*; Stenogyne bifida Hillebr., KF529652, KF235876, AF308221; Suzukia luchuensis Kudô, KF529653, MK909678, MK909744; Suzukia shikikunensis Kudô, KF529655, KF235889, KF235782; Thuspeinanta brahuica (Boiss.) Brig., KF529656, MK909679, MK909745; Thuspeinanta persica (Boiss.) Brig., KF529657, MK909681, MK909746.



Research Article

Primula lizipingensis (Primulaceae), a new species from Sichuan, China

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Abstract

A new species, *Primula lizipingensis* W.B.Ju, L.Y.He & X.F.Gao, found in Shimian County, Sichuan, China, is described and illustrated. It is morphologically similar to *P. rhodochroa* and *P. socialis*, but can be distinguished from them in having shorter plants covering with white farinose, leaf margin sharply dentate above the middle, the leaf blade becomes papery after drying, scapes obsolete, the bract linear-lanceolate to subulate, solitary at the base of the pedicel, and the white hairs present inside the corolla tube.

Key words: Aleuritia, Hengduan Mountains, Primula sect, taxonomy



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Introduction

The genus Primula L. is one of the largest genera in the Primulaceae with more than 500 species, and widely distributed in the temperate and alpine regions of the Northern Hemisphere with its major concentration in the Sino-Himalayan regions and in western China, with only a few occurring on mountains in Ethiopia, tropical Asia and South America (Hu 1990, 1994; Hu and Kelso 1996; APG 2016). In China, more than 300 species of Primula have been recorded, which are concentrated in the southwestern and northwestern provinces, with only a few species distributed in other regions (Hu and Kelso 1996; Richards 2003). Sichuan Province is a particularly important biodiversity hotspot in China. The southwestern area of Sichuan Province belongs to the Hengduan Mountains, which is recognized as one of the 36 biodiversity hotspots in the world. Moreover, this region serves as a center of diversity for Primula (Hu 1994; Hu and Kelso 1996). Since the publication of the Flora of China, numerous new species of Primula have been discovered and described in the region (Hu and Geng 2003; Wu et al. 2013; Xu et al. 2014, 2015a, 2015b, 2016, 2017, 2019; Ju et al. 2018, 2021; Yuan et al. 2018; Li et al. 2023).

In May 2023, during field expeditions in Liziping National Nature Reserve, an unusual *Primula* population was discovered. Upon observing its morphological characteristics, such as its mealy, deciduous perennials, and overwintering through an above-ground mealy resting bud, along with bracts that are typically smaller and somewhat swollen or thick, calyx prominently 5-veined, corolla narrow tube and lobes apex deeply emarginate, we have identified this species as belonging to the *Primula* section *Aleuritia*. After consulting relevant literature (Smith and Word 1926; Smith and Fletcher 1944; Hu 1986, 1990; Fang 1994, 2003; Hu and Kelso 1996; Wu 1999; Richards 2003) and herbarium specimens (BM, E, K, KUN, and US), we have concluded that this species is indeed unique and previously undescribed, and similar to *Primula rhodochroa* W.W.Sm. and *P. socialis* F.H.Chen & C.M.Hu. Therefore, it is described here as a new species.

Materials and methods

The descriptions and illustrations presented here were based on an analysis of the habits and characteristics observed in fresh material during field surveys, as well as the examination of type specimens deposited in CDBI. The morphological features of this new species, as well as those of its similar species, were described using the terminology outlined in the Flora of China (Hu and Kelso 1996). To supplement our examination, we accessed digital specimens online through various platforms, including the Chinese Virtual Herbarium (http://www.cvh.ac.cn/), JSTOR Global Plants (https://plants.jstor.org/), the Global Biodiversity Information Facility (https://www.gbif.org/), and Europeana (https://www.europeana.eu), with particular emphasis on type specimens from BM, E, K, KUN, and US. The regional conservation status was assessed following the IUCN guidelines (IUCN Standards and Petitions Committee 2022).

Taxonomic treatment

Primula lizipingensis W.B.Ju, L.Y.He & X.F.Gao, sp. nov.

urn:lsid:ipni.org:names:77332792-1 Figs 1-3

Diagnosis. *Primula lizipingensis* is morphologically similar to *P. rhodochroa* and *P. socialis.* However, the new species can be easily distinguished from *P. rho-dochroa* by its leaf margin sharply dentate above the middle, scape absent, flower solitary subtended by a single, linear-lanceolate to subulate bract, the calyx lobes split to the middle, the corolla tube longer than the calyx, and its interior has white hairs. Compared with *P. socialis*, the new species is covered with white farinose (vs. glabrous), leaf oblanceolate to spathulate, and papery when dry (vs. obovate-elliptic to oblanceolate, membranous when dry), bracts linear-lanceolate to subulate (vs. linear), calyx lobes split to the middle (vs. split to the middle or below), and corolla tube hairy inside (vs. glabrous).

Type. CHINA. Sichuan: Shimian county, Liziping National Nature Reserve, growing in moist rock crevices covered with moss; 29°00'N, 102°11'E, 4318 m alt., 18 May 2023 (fl.), *Liuyang He J-1201* (holotype CDBI!; isotypes KUN!)

Description. A dwarf farinose tufted perennial herb, at most 2.5 cm tall, with a short stout rhizome and covered at the base by the withered remains of old



Figure 1. Habitat of the Primula lizipingensis sp. nov. (A-D).

leaves of the previous year. *Leaves* forming a dense tuft, papery when dry, including the petiole 5–12 mm long, 2.5–5.5 mm broad, oblanceolate to spathulate, rounded or acute at apex, tapering into the papery winged petiole which when fully developed is as long as the leaf blade, margin sharply dentate above the middle, green above with a thin covering of potentially white farinose glands, thickly covered below with white farina, the midveins and lateral veins are prominent at abaxially. *Scape* almost obsolete, bearing one flower. *Bracts* solitary, at base, linear-lanceolate to subulate, more or less white farinose, 1–2.8 mm long. *Flower* solitary, heterostylous. *Pedicels* 1.5–5.0 mm long, cover the white farinose, not extended in fruit. *Calyx* green, campanulate, 5–5.5 mm long, farinose both within and without, prominently 5-veined, split to the middle, lobes narrowly triangular to lanceolate, apex acute. *Corolla* obscurely annulate, with sparsely white farinose glands abaxially; limb 14–18 mm across, funnelform; tube deep purple, 1.3–1.8 times the length of the calyx and a few white hairs Wen-Bin Ju et al.: Primula lizipingensis (Primulaceae), a new species from Sichuan, China



Figure 2. *Primula lizipingensis* sp. nov. **A** fresh plants **B** leaves **C** pin flower (showing flower side and front, the position of anthers and styles in the tube) **D** thrum flower (showing flower side and front, the position of anthers and styles in the tube) **E** plants base **F** calyx, capsule and mature fruit that has already split **G** bracts. Photographs by W-BJ.



Figure 3. *Primula lizipingensis* sp. nov. **A** habit **B** leaves **C** inflorescence and front of the flower **D** bracts **E** pin flowers (left) and thrum flowers (right) **F** calyx and pistil of pin flowers (left) and thrum flowers (right). Drawn by Z-LL.

adaxially; lobes pale purple with a white eye, spreading, $6.5-8.2 \times 4.5-6.0$ mm, broadly obovate, deeply emarginate. **Pin flowers:** corolla tube 7–8 mm long, widely ampliated above the insertion of stamens; stamens ca. 1.5 mm above base of corolla tube; style ca. 2/3 as long as tube. **Thrum flowers:** corolla tube ca. 8 mm long, widely ampliated above insertion of stamens; stamens inserted slightly above the middle of corolla tube; style ca. 2 mm. **Capsule** oblong, slightly shortly than the calyx.

Phenology. Flowering occurs in May, fruiting is unknown.

Distribution and habitat. *Primula lizipingensis* is only known from the type locality Liziping National Nature Reserve, Shimian County, Sichuan, China. It grows in moss-covered limestone crevices at an altitude of 4300–4400 meters.

Etymology. The specific epithet 'lizipingensis' refers to the type locality where the new species occurs, Liziping National Nature Reserve, Sichuan, China.

Conservation status. Data Deficient (DD). Due to insufficient field investigations, we do not yet have a clear understanding of its natural distribution and population status, nor do we have enough information to directly or indirectly assess its risk of extinction. Therefore, we temporarily categorize this species as Data Deficient according to the International Union for Conservation of Nature Red List Categories (IUCN Standards and Petitions Committee 2022). Further field investigations in the high-altitude areas of western Sichuan in the future can provide more information about its abundance and distribution.

Discussion. The section *Aleuritia* was originally considered by Duby (1844) with citation of type species *P. farinosa* L. This section is a large group having more than 80 species with wide distribution. The distribution is almost throughout the range of the genus *Primula*, spanning across circum-arctic regions and major mountain systems in Europe, North America, and Asia (Hu 1990, 1994; Hu and Kelso 1996). Notably, this is the sole section of the *Primula* genus that includes representative species in South America (Hu 1994; Basak et al. 2014). In this study, we followed Hu's (1990) taxonomic treatment of the *Primula* in China.

Further research indicates that this new species is similar to P. rhodochroa and P. socialis in that they have dwarf farinose plant, possess short rhizomes, and produce solitary flowers emerging from basal rosettes. P. rhodochroa, distributed in southeast Xizang, thrives in wet moss on boulders or rock faces at altitudes of 4000-5000 meters. P. socialis, found in western Yunnan, flourishes in shady crevices of mountain rocks at an altitude of 2950 m. P. lizipingensis, found in Shimian County, Sichuan Province, on the eastern edge of the Hengduan Mountains, grows in moss-covered limestone crevices at an altitude of 4300-4400 m. Despite all three growing in limestone dam crevices with moss, prolonged geographical isolation has led to morphological differentiation, resulting in the emergence of distinct species. The same situation also occurs in the morphological and habitat similarities between P. kialensis Franchet and P. yunnanensis subsp. membranifolia (Franchet) Halda. These species are both covered with yellow farinose and showing resemblances in leaf morphology, and inflorescence. The main difference is that P. yunnanensis subsp. membranifolia has a corolla tube length 2-4 times that of the calvx, and its leaves texture is membranous, whereas P. kialensis has a corolla tube length 1–2 times that of the calyx and chartaceous leaves. The former is distributed in counties such as Jiulong, Kangding, and Lixian, located in the eastern part of the Hengduan Mountains, and belongs to a unique species in Sichuan. The latter is distributed in counties such as Dali, Yangbi, and Fengging, located in the

Charactera	Species				
Characters	Primula lizipingensis	P. rhodochroa	P. socialis		
Farinose color White		white	yellow		
Leaf shape	oblanceolate to spathulate	oblanceolate to narrowly obovate	obovate-elliptic to oblanceolate		
Leaf blade	margin sharply dentate above the middle	margin denticulate to dentate	margin dentate above the middle		
	papery when dry	papery when dry	membranous when dry		
	rounded or acute at apex	obtuse to rounded at apex	obtuse to rounded at apex		
Scape	Absent	present but less than 1 cm	absent		
Inflorescence	flowers solitary	1-2(4)-flowered umbel	flowers solitary		
Bracts	1, linear-lanceolate to subulate 2-3, linear		1, linear		
Calyx lobes	split to the middle of the calyx	plit to the middle of the calyx split to 1/3 of the calyx			
Corolla	tube longer than the calyx, and white hairs adaxially	tube ca. as long as calyx, glabrous adaxially	ig as calyx, glabrous tube longer than the calyx, glabrous daxially adaxially		

Table 1. Comp	arison of mor	phological	characters among	Primula liziping	ensis, P. rhodo	ochroa and P. socialis.
				, , , , ,	,	

central and western parts of the Hengduan Mountains, and belongs to a unique species in Yunnan. The new species differs from *P. rhodochroa* in the characteristic of leaf margin teeth, the presence or absence of scape, the characteristic and numbers of bracts, the split degree of calyx lobes, and the presence of hairs inside the corolla tube. Morphologically, the new species is more closely related to *P. so-cialis* because both are characterized by having solitary flower and bract, without a scape, but easily recognized by the present of white farina covering the whole plant, leaves smaller and papery after drying with margin sharply dentate, the bract linear-lanceolate to subulate, and hairy with white hairs inside the corolla tube. A detailed comparison of the three species is shown in Table 1.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Writing – original draft: WBJ. Investigation: LYH, QL, YHW. Methodology: XJH, BX. Project administration: XFG. Writing – review: BX.

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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 first epiphytic species of *Valeriana* in the world: *Valeriana rudychazaroi* (Caprifoliaceae)

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Abstract

The currently known species of *Valeriana* are herbs, shrubs, small trees and vines. After 20 years without new species of *Valeriana* in Mexico, here is described and illustrated the first epiphytic species in the genus. The species was found growing on *Quercus glabrescens* trees of the cloud forests from central Veracruz in eastern Mexico. It is known and described from very few specimens in the type locality. The most morphologically similar Mexican species are the vines *V. naidae* and *V. subincisa*, it was compared. Conservation assessment classifies this species under the Critically Endangered CR B1+B2ab(ii,v) category of the IUCN Red List Criteria.

Key words: Cloud forest, Dipsacales, endemic species, epiphytic species, Mexico

Introduction

Valeriana L. (Dipsacales, Caprifoliaceae, Valerianoideae) is a genus of ca. 270 species distributed in southern Africa, the Americas and Eurasia. Its species are annual or perennial rhizomatous herbs, often semi-rosulate or rosulate, shrubs or subshrubs, small trees or lianas (Weberling and Bittrich 2016; Rabuske-Silva et al. 2020). Barrie (2003) states North American valerians are rhizomatous or tap-rooted perennial herbs, while South American species are herbs, shrubs and vines. The highest species richness, centres of origin and centres of diversification of *Valeriana* are in the southern Andes (Bell and Donoghue 2005; Bell et al. 2012; Luebert and Weigend 2014).

Recent phylogenetic and phylogenomic analyses classify *Valeriana* into the Valerianoideae clade of Caprifoliaceae and suggest the polyphyly of the genus (Bell and Donoghue 2005; Hidalgo et al. 2010; Lee et al. 2021; Wang et al. 2021). Further studies are needed to reveal the internal relationships in *Valeriana*. As a result of this, the morphological classification is followed to maintain a coherent group, *Valeriana* s.l., to avoid multiple generic segregations until most species be sequenced, as proposed by Christenhusz et al. (2018).

The most significant contribution to the knowledge of the Mexican Valeriana species was performed by Barrie (2003), where seven species and one variety



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Copyright: © Antonio Francisco-Gutiérrez et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). were described, including a key for 39 species. In the same issue of the former publication, Rzedowski and Calderón de Rzedowski (2003a) published another two new endemic species from Mexico. Later, the taxonomic treatment for *Valeriana* species of the Bajío Region in central-western Mexico was published by the same authors (Rzedowski and Calderón de Rzedowski 2003b). Since that date, no new species for Mexico have been described. The only update to the known diversity of the genus in Mexico was the addition of *V. insignis* (Suksd.) Christenh. & Byng, with distribution from California to Washington, Arizona, US and Baja California, Mexico.

In contrast, in the last five years, many Valeriana species from South America have been described: V. plateadensis Á.J.Pérez, C.H.Perss. & J.N.Zapata, V. yacuriensis Sklenář & B.Eriksen, V. xenophylloides Sklenář & B.Eriksen (Persson et al. 2023), V. praecipitis A.E.Villarroel & Menegoz (Villarroel et al. 2022), V. caparaoensis Rabuske, Sobral & Iganci (Rabuske-Silva et al. 2020), V. nahuelbutae Penneck. (Penneckamp 2020), V. sobraliana Rabuske & Iganci (Rabuske-Silva and Vieira-Iganci 2019), V. iganciana Rabuske & J.Külkamp (Rabuske-Silva and Külkamp 2018) and V. vilcabambensis Sylvester & Barrie (Sylvester et al. 2018). Recently, the medicinal species V. officinalis gained great importance for being an important alternative in the treatment of anxiety disorders, insomnia and stress caused during the Covid-19 pandemic around the world (Frost et al. 2021; Pessolato et al. 2021; Bertuccioli et al. 2022).

Current botanical research has discovered striking and remarkable new species with evolutionary innovations for the genus to which they belong, like *Pinanga subterranea* Randi & W.J.Baker, the first known palm species flowering and fruiting underground (Randi et al. 2023; Kuhnhäuser et al. 2023) or *V. rupi-cola* Pansarin & E.L.F.Menezes, the first Neotropical rupicolous species of *Vanilla* (Pansarin and Fernandes-Menezes 2023). This paper describes the first epiphytic member of the genus *Valeriana* (Caprifoliaceae) in the world found in Mexico. The aims of this study are: 1) to describe and illustrate a new species of *Valeriana*; 2) to compare the new taxon with the known species from Mexico and 3) to evaluate the conservation status of the new species.

Materials and methods

This species was discovered in 2012 during botanical expeditions of Dr Miguel Cházaro-Basáñez (1949–2023), Dr Pablo Carrillo-Reyes and MSc David Jimeno-Sevilla in the Municipality of Tlacolulan, central Veracruz, Mexico. Miguel Cházaro determined this species as a new taxon and brought preserved specimens to Dr Jerzy Rzedowski (1926–2023) to confirm the status, obtaining the confirmation of this being a new species. A new collection was made by Miguel Cházaro-Basáñez and Rodrigo Carral-Domínguez in September 2020 to obtain specimens, geographic data and photographic evidence of the habit of this species.

Taxonomic determination

A literature revision was carried out to identify the taxon. The species was determined following the dichotomic key of the Mexican species of *Valeriana*, published by Barrie (2003) and compared with the species described by Rzedowski and Calderón de Rzedowski (2003a). Since that date, novelties and nomenclatural changes of species distributed in Mexico have been looked for. Only the nomenclatural change of *V. insignis* (Suksd.) Christenh. & Byng, based on the basionym *Aligera insignis* Suksd. (Christenhusz et al. 2018), was found. The synonym of the latter, *Plectritis ciliosa* var. *insignis* (Suksd.) Dempster was treated by Moore (2012) in the Jepson eFlora of California as distributed in Baja California, Mexico. Morphological comparisons of similar species were made with the descriptions included in Barrie (2003) and Rzedowski and Calderón de Rzedowski (2003b).

Conservation assessment

Geographical coordinates were obtained in the field with a Garmin eTrex 10 GPS. Data were used for calculating geographic ranges of Area of Occupancy (AOO) and Extent of Occurrence (EOO) in the Geospatial Conservation Assessment Tool (GeoCAT, Bachman et al. (2011)), available at http://geocat.kew.org. Both estimates are required by the guidelines of the IUCN (IUCN Standards and Petitions Committee 2022) for conservation assessments. Scientific literature about threats in the distribution area was searched to select the risk category accurately.

English language revision

The artificial intelligence tool Grammarly Premium was used to corroborate the grammar and syntaxis of the manuscript.

Taxonomic treatment

Valeriana rudychazaroi Cházaro, Franc.Gut. & J.R.Carral, sp. nov. urn:lsid:ipni.org:names:77332878-1

Diagnosis. *Valeriana rudychazaroi* can be distinguished from all the known species of the genus by its epiphytic habit on trees of *Quercus glabrescens* Benth. (vs. herbs, shrubs, subshrubs, small trees or climbing vines in the rest of the genus). It is morphologically similar to *V. naidae* Barrie and *V. subincisa* Benth., from which it differs by having thinner stems (0.25–0.6 cm vs. up to 2 cm in diameter in both species), leaves elongately spatulate (vs. ovate to elliptic or narrowly ovate to elliptic, respectively), inflorescence corymboid (vs. paniculoid in both species), inserted stamens in flowers (vs. exserted in both species), different shape of fruits (ovate vs. oblong to lanceolate in both species) and longer fruits (3–5 mm vs. 2–3 mm in both species).

Type. MEXICO. Veracruz: Municipio Tlacolulan, Cerro de la Magdalena, 19°43'21"N, 96°59'09"W, 2900–2950 m elev., 20 September 2020, fl., fr., *R. Carral-Domínguez & M. Cházaro-Basáñez 766* (holotype: XAL!).

Description. *Perennial gynodioecious epiphyte*, growing on branches of *Quercus glabrescens*, 45–80 cm tall. *Roots* fibrous. *Stems* terete, decumbent, 20–45 \times 0.25–0.6 cm, branched in the basal portion, glabrous until the insertion of the central axis of the inflorescence, where is shortly pubescent with trichomes simple, trichomes up to 0.5 mm long. *Leaves* cauline and clasping, simple, opposite and decussate, persistent near the inflorescence, deciduous in late phenophases, elongately spatulate, 5.7–10.8 \times 0.6–2.1 cm, apex obtuse, base

largely decurrent 1.5-3.5 cm long, slightly canaliculate, margin entire, one main nerve, slightly conspicuous on adaxial surface, prominent on abaxial surface, glabrous on both surfaces and margins. Inflorescence terminal, corymboid, dichotomously divided, each terminal corymb scorpioid without rotation, being less developed one of the lateral sides, 17-24 × 13-25.5 cm from the first division to the top and considering the lateral extremes of the inflorescence, main axis $10.1-21 \times 0.11-0.25$ cm measured from the base until the first bifurcation. Secondary axes 2, 2.9-6.0 × 0.05-0.2 cm, tertiary axes 4, 0.33-034 × 0.1 cm, decreasing dimensions as dichotomies increase, 31-85 flowers and less than five mature fruits per terminal corymb. Bracts narrowly lanceolate to lanceolate, 2.0-2.9 × 0.45-0.8 cm, base cuneate, apex acute, margin entire, glabrous, one main nerve. Bractlets of first division linear, longer than the fruits, 0.7-0.8 × 1-1.5 mm, base narrowly clasping, apex acute, margin entire, glabrous. Bractlets of corymbs linear, equal or shorter than the fruits, $1.5-5 \times 0.5-0.8$ mm. Staminate flowers white, 1.5 × 0.5 mm, calyx reduced, glabrous, corolla infundibuliform, tube 2-2.7 × 2 mm (opened), 5-lobed, corolla lobes elliptic to widely triangular, 0.5-0.8 × 0.4-0.5 mm, internally and externally glabrous, stamens 3, 1 mm long, adnate to the corolla in the middle of the length, anthers globose, 0.5-0.8 mm long, bithecal, glabrous; pistilodium 1.6 mm long, included, glabrous. Pistillate flowers white, 2 × 0.7 mm, calyx reduced, glabrous, corolla infundibuliform, tube 1.0-2.2 mm long, 5-lobed, corolla lobes orbicular, 1 mm in diameter, main style 2.7-5 mm long, exserted, glabrous; secondary styles reminiscent, inserted near 1/3 corolla length. Fruit a cypsela, ovate, 12 plumose limbs derived from calyx, $3-5 \times 1-1.3$ mm, with 3 veins on the abaxial side 1 on the adaxial side and 2 along the margins, glabrous on all surfaces (Figs 1-3).

Phenology. Flowering and fruiting recorded only in September.

Distribution and habitat. Valeriana rudychazaroi is only known from the type locality in cloud forests from central Veracruz in eastern Mexico (Fig. 4). There are no specimens deposited in major Mexican herbaria because of the rarity of the individuals and the difficult access to the branches of the hosts. The first collections of the species (previous to 2017) have been lost due to the death of Miguel Cházaro. During one decade of botanical explorations in the Cerro de la Magdalena Mountain and adjacent regions for floristic inventories and species descriptions (Lascurain-Rangel et al. 2017; Francisco-Gutiérrez et al. 2023a), very few specimens have been found and collected in the same locality of the type, some of them preserved as sterile material. The new species grows on very tall Quercus glabrescens (Fagaceae) trees, at altitudes of 3-6 m. It is distributed in the remnants of very humid pine-oak forests at elevations from 2,900 to 2,950 m. This species inhabits a zone of cloud forests on cliffs with strong winds rising from the Sierra de Chiconquiaco, Veracruz. The Sierra de Chiconquiaco is a biodiverse basin, home to 3016 species, the type localities of 72 species and 36 endemic species (Castillo-Campos et al. 2005; Lascurain-Rangel et al. 2017). The species is only known from the Volcán de la Magdalena Mountain in Tlacolulan, State of Veracruz, in eastern Mexico. From this mountain, the narrowly endemic species Salvia chazaroana B.L.Turner (Lamiaceae), Lobelia biflora Rzed. (Campanulaceae) and Castilleja eggeri Franc.Gut. & Cházaro were described. Species sharing the habitat are Beschorneria yuccoides K.Koch (Asparagaceae, Agavoideae), Ageratina chazaroana B.L.Turner (Asteraceae, Eupatorieae) and the epiphytic Nelsonianthus tapianus (B.L.Turner) C.Jeffrey (Asteraceae, Senecioneae).

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Etymology. Miguel Cházaro dedicates the name of the species to Rudy Miguel Cházaro-Hernández, his beloved son, who, since an early age, has accompanied him on numerous botanical trips (Fig. 5). This is the second of a series of new species that Miguel Cházaro wished to dedicate to his children before he died on 4 April 2023. First, the species *Eugenia sarahchazaroi* Cházaro, Franc. Gut. & J.R.Carral was dedicated to his daughter, Sarah M. Cházaro-Hernández (Francisco-Gutiérrez et al. 2023b). A sketch of the life of Miguel Cházaro can be consulted in his obituary (Francisco-Gutiérrez and Vázquez-García 2023).

Conservation status. The new species has an Area of Occupancy (AOO) of 4 $\rm km^2$ and Extent of Occurrence (EOO) of 0 $\rm km^2$. A worrying situation for



Figure 2. Valeriana rudychazaroi on Quercus glabrescens trees in the field. Photograph taken by Rodrigo Carral-Domínguez.



Figure 3. *Valeriana rudychazaroi* in the field. **A** habitat at an altitude of 3–6 m on *Quercus glabrescens* trees **B** detail of inflorescence with flowers and fruit **C** hosts in cloud forests from central Veracruz, Mexico. Photographs taken by Rodrigo Carral-Domínguez.



Figure 4. Distribution map of the epiphytic species Valeriana rudychazaroi in Mexico.

the conservation of this remarkable species is the overexploitation of oak trees that have been felled for charcoal production since the 1930's decade (Flores 1938). Besides, the cloud forest is the most endangered ecosystem in Mexico, with projections of high vulnerability in the face of climate change scenarios (Ponce-Reyes et al. 2012). That is why, given the reduced values of



Figure 5. Author and eponymy of the new species **A** Miguel Cházaro showing a specimen of *Valeriana rudychazaroi* next to its host, a *Quercus glabrescens* tree in Tlacolulan, Veracruz, Mexico (Author: Rodrigo Carral-Domínguez) **B** Rudy Miguel Cházaro-Hernández, son of Miguel Cházaro, during a botanical expedition at Barranca de Ramírez, 1981 **C** Miguel Cházaro and his son, to whom he dedicates the name of this new species (Author of **B** and **C**: Patricia Hernández-Romero).

A00 < 100 km², E00 < 10 km², number of locations = 1 and observed decline in quality of habitat, *Valeriana rudychazaroi* is classified under the Critically Endangered CR B1+B2ab(ii,v) category.

Discussion. Valeriana rudychazaroi is the first recorded epiphytic species in the genus. Previous works on worldwide Valeriana species reported habits of small trees, herbs, subshrubs, shrubs or lianas (Weberling and Bittrich 2016). Barrie (2003) reported five species of suffruticose or herbaceous vines in the country, while the checklist of Mexican lianas reported one, V. subincisa (Ibar-

Character	V. rudychazaroi	V. naidae	V. subincisa		
	Gynodioecious	Dioecious	Gynodioecious		
Habit	Epiphytic herbs	Suffrutescent herbs or climbing vines	Herbs or climbing vines		
Stems length	Up to 0.8 m	Up to 15 m	1-2 m (up to 10 m when climbing)		
Stems diameter	0.25-0.6 cm	Up to 2 cm	Up to 2 cm		
Leaves shape	Elongately spatulate	Ovate to elliptic	Narrowly ovate to elliptic		
Leaves size	5.7-10.8 × 0.6-2.1 cm	1.5-8.7 × 0.8-4.1 cm	2-8 × 0.8-4 cm		
Leaves apex	Obtuse	Acute	Acute		
Leaves base	Largely decurrent	Connate	Cuneate to truncate		
Inflorescence type	Corymboid mostly dichotomous with terminal branchlets scorpioid.	Paniculoid with terminal branchlets scorpioid.	Panicles mostly dichotomous with terminal branchlets scorpioid.		
Stamens position	Inserted	Weakly to strongly exserted	Exserted		
Fruit shape	Ovate	Oblong to lanceolate	Oblong to lanceolate		
Fruit length	3–5 mm	2.2-2.7 mm	2-3 mm		
Phenology	Flowering and fruiting only known from September	Flowering and fruiting October-May (Flowering March-June, fruiting May-July in Nevado de Colima.	Flowering November-July		
Habitat and distribution	Quercus glabrescens cloud forests from central Veracruz	Fir forests, cloud forests from the Trans-Mexican Volcanic Belt	<i>Quercus</i> and <i>Pinus</i> humid forests, cloud forests from Tamaulipas and Nuevo León south to Veracruz (growing along the ground), also in Chiapas and Guatemala (generally scandent).		
Source	This study	Barrie (2003)	Rzedowski and Calderón de Rzedowski (2003b), Barrie, pers. comm.		

Table 1. Comparison of morphological characters and phenology amongst the two climbing vines and the new epiphytic species of *Valeriana* from Mexico.

ra-Manríquez et al. 2015). Unlike the *Valeriana* species that are lianas, this species has short stems that are rooted on the branches of *Q. glabrescens* trees, flowering and fruiting without contact with the ground. Further studies on seed dispersal and the biology of the species are needed.

Barrie (2003) stated that there are seven species of *Valeriana* vines in the Americas, four endemic to the northern Andes, one endemic to Panama and Costa Rica and two in Mexico: *V. naidae* and *V. subincisa*. Following the dichotomic key provided in Barrie (2003) and considering the habit of this new species, it is closest related to this group, compared to the herbaceous species. Due to the absence of twining stems, the key for species showed the new species to be most similar to *V. naidae* and *V. subincisa*, to which it was compared. A detailed comparison is provided in Table 1. The contrasting differences in morphological characters and ecological features allow us to separate *V. rudy-chazaroi* from other species that overlap its distribution in western Veracruz in the Cofre de Perote Volcano (Barrie 2003).

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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: AFG, MCB. Data curation: AFG. Funding acquisition: MCB. Investigation: RCD. Supervision: MCB. Visualization: RCD, AFG. Writing – original draft: AFG. Writing – review and editing: MCB.

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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

Erica L. (Ericaceae): homonyms amongst published names for African species and proposed replacement names

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Abstract

In support of ongoing taxonomic work on the large and complex flowering plant genus Erica (Ericaceae), we document nineteen pairs of homonyms representing currently used illegitimate names. We provide replacements for thirteen names and new typifications for five. We relegate five names to synonymy: Erica aemula Guthrie & Bolus under Erica distorta Bartl.; Erica armata Klotzsch ex Benth. under Erica umbrosa H. A. Baker; Erica capensis T.M. Salter under Erica turbiniflora Salisb.; Erica lanata Andrews under Erica flaccida Link; and Erica tomentosa Salisb. under Erica velutina Bartl. Finally, we suggest conservation of Erica aristata Andrews. The new names are: Erica adelopetala E.C. Nelson & E.G.H. Oliv. replacing Erica insignis E.G.H. Oliv.; Erica bombycina E.C. Nelson & Pirie replacing Erica niveniana E.G.H. Oliv.; Erica concordia E.C. Nelson & E.G.H. Oliv. replacing Erica constantia Nois. ex Benth.; Erica didymocarpa E.C. Nelson & E.G.H. Oliv. replacing Erica rugata E.G.H. Oliv.; Erica galantha E.C. Nelson & E.G.H. Oliv. replacing Erica perlata Benth.; Erica mallotocalyx E.C. Nelson & E.G.H. Oliv. replacing Erica flocciflora Benth.; Erica notoporina E.C. Nelson & E.G.H. Oliv. replacing E. autumnalis L.Bolus; Erica oliveranthus E.C. Nelson & Pirie replacing Erica tenuis Salisb.; Erica oraria E.C. Nelson & E.G.H. Oliv. replacing Erica spectabilis Klotzsch ex Benth.; Erica oresbia E.C. Nelson & E.G.H. Oliv. replacing Erica demissa Klotzsch ex Benth.; Erica poculiflora E.C. Nelson & E.G.H. Oliv. replacing Erica stenantha Klotzsch ex Benth.; Erica rhodella E.C. Nelson & E.G.H. Oliv. replacing Erica rhodantha Guthrie & Bolus; Erica supranubia E.C. Nelson & Pirie replacing Erica praecox Klotzsch.

Key words: Cape heaths, *Erica*, Hans Dulfer, International register of heather names, nineteenth-century English nursery catalogues, nomenclature

Introduction

The nomenclatural history of the genus *Erica* L. *sensu lato* (Oliver 2000, 2012) is complicated by the extraordinary fashion in western Europe for cultivating "Cape heaths", the English name generally given to plants derived from the *Erica* species endemic to southern Africa. *Erica*-mania commenced in the last decade of the 18th century, burgeoned in the early 1800s and petered out in the middle of that century (Nelson and Pirie 2022). A consequence of the

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horticultural interest was a proliferation of names, applied often in a haphazard manner by nurserymen and gardeners, as well as by botanists. Many names were first published in nurserymen's and gardeners' catalogues and in horticultural periodicals, often with accompanying descriptions or diagnoses (Nelson and Oliver 2004; Nelson and Small 2004–2005; see also Reveal (2012)).

Work carried out between 1995 and 2004 by ECN for The Heather Society (established in 1963, formally dissolved in 2020) on the second volume of the International Register of Heather Names (Nelson and Small 2004-2005) necessarily included an extensive survey of nineteenth-century horticultural publications, resulting in the accumulation of more than 6,000 names, at all ranks and many times that number of bibliographic citations, for Erica taxa of African origin. This information was collated in a database, complementing a similar one for the so-called "hardy heaths" - Andromeda L., Calluna Salisb., Daboecia D. Don and species of Erica endemic in Europe, Macaronesia and western Asia (Nelson and Small 2000). We are currently working to make this resource openly accessible, particularly through integration with the World Flora Online (WFO 2023; Elliot et al. in prep.). The database provides an invaluable bibliographic tool, much more comprehensive and, for a genus of more than 800 species, more practical and detailed than any existing botanico-bibliographic indexes including such standard publications as "Index Kewensis" which only provided publication information for protologues. Inevitably a database of such a comprehensive nature revealed a scattering of hitherto unsuspected, or inadvertently overlooked, problems with the established and currently accepted names of African Erica species.

Some of these problems do not arise, in fact, from the unearthing of long-buried names (most of the binomials discussed here were recorded by Dulfer (1965)), but rather from a better understanding of the history of certain publications and more accurate information about dates of publication of, for example, George Bentham's (1839) treatment of *Erica* and related genera (Nelson 2005) and Henry Cranke Andrews's multi-volume works, Coloured Engravings of Heaths (Cleevely and Oliver 2002) and The Heathery (Cleevely et al. 2003).

Although changes in current names are rarely welcomed, particularly outside the taxonomic community, by following the rules set out in the International Code of Nomenclature for Algae, Fungi and Plants (Shenzhen Code) 2018 (Turland et al. 2018) (hereafter ICN (Shenzhen Code) 2018), we can reflect the state of knowledge in the field and maintain overall stability in nomenclature. In this paper, we provide replacement names for homonyms and clarify typifications where necessary.

Homonyms in Erica

The Heather Society's database revealed pairs of homonyms within *Erica* where the one in current use (compare Oliver and Oliver (2003); Oliver (2012)) is not the earliest published. The need to replace these later names was signalled in the four published parts of the International Register of Heather Names, volume 2, African Species, Hybrids and Cultivars (Nelson and Small 2004–2005). These names are listed (as summarised in Table 1) and discussed and, where necessary, replacements are provided when an alternative validly published name is not available.

Specific epithet	Author(s) and date of currently accepted binomial	Author(s) and date(s) of earlier binomial
aemula	Guthrie and Bolus (1905)	Rollisson (1855)
aristata	Andrews (1807)	Salisbury (1796)
armata	Klotzsch ex Bentham (1839)	Sprengel (1825)
autumnalis	L. Bolus (1923)	Hort. ex Bentham (1839)
capensis	Salter (1935)	Regel (1842)
constantia	Noisette ex Bentham (1839)	Hort. ex Sinclair (1825)
demissa	Klotzsch ex Bentham (1839)	Hort. ex Sinclair (1825)
flocciflora	Bentham (December 1839)	Tausch (October 1839)
insignis	Oliver (1981)	Hort. (1853)
lanata	Andrews (1806)	Wendland (1798)
niveniana	Oliver (2000)	Hort. ex Loudon (1830)
perlata	Bentham (1839)	Sinclair (1825)
praecox	Klotzsch (1838)	Hort. ex Sinclair (1825)
rhodantha	Guthrie and Bolus (1905)	Regel (1842)
rugata	Oliver (2000)	Hort. ex Sinclair (1825)
spectabilis	Klotzsch ex Bentham (1839)	Waitz (1805)
stenantha	Klotzsch ex Bentham (1839)	Sweet (1830)
tenuis	Salisbury (1802)	Moench (1802)
tomentosa	Salisbury (1802)	Masson (1776)

Table 1. Homonym pairs in Erica in alphabetic order with dates of publication.

It should be noted that nurserymen's catalogues during the 19th and 20th centuries were usually annual publications, reissued with minor amendments, deletions and additions, year after year, decade after decade. The dated catalogues noted in this paper are examples only – they must not be assumed to be the first, the last or the only issue containing a particular name.

1. Erica aemula Rollisson (1855), non Guthrie and Bolus (1905)

This binomial first appeared in print within an advertisement inserted by Messrs William Rollisson & Sons of Tooting, London, in "The Gardeners' Chronicle": 218 (7 April 1855). A brief description, noting the "fine bright crimson" flowers, was included that validates the name. Subsequently, it was published in several other English nurserymen's catalogues (see Nelson and Small (2004: pt 1: 11)): for example, in William Rollisson and Sons' catalogue for 1877, which company claimed it as a hybrid raised and sent out by them; James Fraser, Lea Bridge Road Nursery, for 1866–1867; E. G. Henderson and Son for Autumn 1871; James Veitch and Sons for 1873–1874; and B. S. Williams for 1881. Compilers of gardening dictionaries soon included this heath in their works including Hereman (1868: 217) and Wright (ca. 1907: 325).

Guthrie and Bolus (1905), presumably unaware of the previous publication of the epithet *aemula* within *Erica*, used the same epithet for a white-blossomed species that inhabits rocky, coastal slopes and inland, marshy, high mountain plateaux in the Western Cape, from Bainskloof to the Steenbras Mountains (Oliver and Oliver 2000: 429). The species was illustrated by Schumann et al. (1992: 104) and is listed amongst the recognised plant species of southern Africa by Oliver and Oliver (2003). However, it was subsequently treated as a local variant from Gordon's Bay of *E. distorta* Bartl. (Oliver and Forshaw 2012). We follow the latter taxonomic opinion and treat *E. aemula* as a heterotypic synonym of *E. distorta* without providing a replacement name.

Erica distorta Bartl., Linnaea 7: 644. 1832 wfo-0000671898

Erica aemula Guthrie & Bolus, Fl. Capensis 4,1: 118. 1905 [wfo-0000671313], nom. illeg., non Erica aemula Rollisson, Gard. Chron. 1855: 218 (1855) [wfo-1200040659]. Type. South Africa. "Bains Kloof" [Bainskloof], Cummings 171 BOL [BOL137142 [https://plants.jstor.org/stable/10.5555/al.ap.specimen. bol137142], syntype; "Fish Hoek, Gordon's Bay", Guthrie 3108 BOL (BOL137141) [https://plants.jstor.org/stable/10.5555/al.ap.specimen.bol137141], syntype.

Type. South Africa, "Auf Felsenrücken in der Kluft nach der Platte des Tafelberges in vierter Höhe" (lectotype †GOET destroyed, *fide* annotation by N. E. Brown on K000314148; isolectotype [fragments only], "ad Cap. b. Spei in monte tabulari leg. Ecklon. Hb. Bg. 1841" K [K000314148].

2. *Erica aristata* Salisb. (1796) [wfo-1000053511], non Andrews (1807) [wfo-0000671412]

Richard Anthony Salisbury's (1761–1829) catalogue (Salisbury 1796) of the plant collection in his own garden at Chapel Allerton, outside Leeds in Yorkshire, England, gave the name *Erica aristata* for a plant from the Cape of Good Hope, introduced by the nurseryman James Lee (1715–1795). The accompanying diagnosis validates the binomial, but is quite inadequate to identify the species, which evidently had not bloomed (there is no description of the flowers, only the ternate, linear leaves). Guthrie and Bolus (1905) and Dulfer (1965) placed Salisbury's name in synonymy under *E. banksii* Andrews. No herbarium specimens, determined by Salisbury, of his *E. aristata* are known so that equation is extremely dubious, especially given the brevity of the protologue.

A decade later the same binomial was employed by Henry Cranke Andrews (fl. 1794–1830) when he illustrated and described the plant that currently bears this name, an inhabitant of the Kleinrivier Mountains (Andrews 1807: t. 152; 1809a: t. 147). It is an erect, semi-spreading shrublet, to 0.5 m tall, producing large (to 25 mm long), tubular-inflated flowers that are very sticky and have spreading lobes; the corolla is longitudinally striped dark and light pink (Oliver and Oliver 2000).

This species was illustrated by Schumann et al. (1992: 80) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003; Oliver 2012: 489). This species is a very well-known plant due to its striking floral morphology. It is the first *Erica* species for which pollination by long-proboscid flies has been demonstrated (Lombardi et al. 2021). Changing its name would cause considerable confusion, so a proposal will be submitted for the conservation of *E. aristata* Andrews over *E. aristata* Salisb.

3. Erica armata Spreng. (1825), non Benth. (1839)

Erica armata was validly published by Sprengel (1825: 2: 184), but Guthrie and Bolus (1905: 86) and Dulfer (1965: 53) placed it in synonymy under *E. sparrmanii* L.f., despite upholding *E. armata* Klotzsch ex Benth. (1839) as a distinct species. Thus, *Erica armata* Klotzsch ex Benth. (1839: 672) is an illegitimate later homonym. The species to which the binomial is currently applied (see Oliver and Oliver (2003: 427); Schumann et al. (1992: 100); Oliver (2012: 489)) is an erect shrublet, to 0.5 m tall, bearing broadly urn-shaped to tubular, hairy, pink flowers with exserted anthers; it occurs on rocky slopes. Fortunately, a later synonym for it is available, *Erica umbrosa* (Baker 1961).

Erica umbrosa H.A.Baker, J. S. Afr. Bot. 27: 267. 1961 wfo-0000673499

E. armata Klotzsch ex Benth., Prodr. [A. P. de Candolle] 7(2): 672. 1839 [wfo-0000671419], nom. illeg., non Spreng., Syst. Veg. 2: 184. 1825 [wfo-0000671418]; Guthrie and Bolus, Fl. Capensis 4,1: 113. 1905; Dulfer, Ann. Naturhist. Mus, Wein 68: 67. 1965; Oliver, Strelitzia 29: 489. 2012. Type. South Africa. "in herb. reg. Berol. ... in montibus prov. Worcester et Stellenbosch", Masson, Niven, Drège (lectotypes B destroyed; isolectotype K [*Niven 158*] (det. E.G.H. Oliver) K000314208).

Note. Specimens in other herbaria collected by Masson and Drège are variously labelled as syntypes or isosyntypes, but their identity has not been confirmed: GDC (Masson, F., s.n., G00494351 https://plants.jstor.org/stable/10.5555/al.ap.specimen.g00494351); GDC (Drège, J.F., s.n., G00494352 https://plants.jstor.org/stable/10.5555/al.ap.specimen.g00494352); HBG (Drège, J.F., s.n., HBG515307 https://plants.jstor.org/stable/10.5555/al.ap.specimen.hbg515307); TUB (Drège, J.F., s.n., TUB003182 left-hand specimen only https://plants.jstor.org/stable/10.5555/al.ap.specimen.tub003182); S (Drège, J.F., s.n., S08-5237 https://plants.jstor.org/stable/10.5555/al.ap.specimen.s08-5237).

Type. South Africa. "Caledon, Elandskloof, Villiersdorp, on a steep S-facing slope in shade in kloof with a large waterfall, 3 April 1961, *E.G.H. Oliver 1423* (holotype: BOL; isotype: NBG-0199392-1 [https://plants.jstor.org/stable/10.5555/al.ap.specimen.nbg0199392-1].

4. Erica autumnalis Hort. ex Benth. (1839), non L.Bolus (1923)

This binomial was published under the entry for *Erica formosa* Thunb. with a validating diagnostic phrase by Bentham (1839) who attributed the name to horticulturists. Bentham appended an asterisk indicating that he deemed it to be a horticultural hybrid. Regel (1842) attributed the same name to English gardeners. It was not included in "Index Kewensis", nor was it taken up or listed by Guthrie and Bolus (1905). On the other hand, Dulfer (1965) included the name, for a hybrid, following Regel.

Bolus (1923) probably overlooked Bentham's use of the binomial and published it for a Western Cape species found on moist slopes at middle altitude distributed from the Hottentots Holland Mountains to Kogelberg (Dulfer 1964: 146; 1965: 92; Oliver and Oliver 2000: 430; Sieben et al. 2004; Oliver 2012: 490). This species was illustrated by Schumann et al. (1992: 146) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 427; Oliver 2012: 490).

A new name is required for the taxon and the new epithet alludes to the autumn, which is the species' main, Southern-Hemisphere flowering season.

Erica notoporina E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327519-1 wfo-1000053505

pro Erica autumnalis L.Bolus, Ann. Bolus Herb. 3: 178. 1923 [wfo-0000671451], nom illeg., non E. × autumnalis Hort. ex Benth., Prodr. [A. P. de Candolle] 7(2): 659 (1839) [wfo-1000053512]; Regel, Verh. Vereins Beförd. Gartenbaues Königl. Preuss. Staaten 16: 307. 1842; Regel, Kult. Aufz. Eriken, 147. 1843; Dulfer, Ann. Naturhist. Mus, Wein 68: 151 (1965).

Type. South Africa, "Bought in Adderly St., Cape Town", 2 February 1922, *N.S. Pillans 16784*: (holotype: BOL [BOL-137249 (https://plants.jstor.org/sta-ble/10.5555/al.ap.specimen.bol137249); isotype BOL [BOL-137250]).

5. Erica capensis Regel (1842), non T.M.Salter (1935)

In his monograph on *Erica*, Eduard August von Regel (1815–1892) described a plant named *E. capensis* (Regel 1842: 318, 1843: 158) and the binomial has had a sporadic existence since the mid-19th century. Guthrie and Bolus (1905) did not list Regel's use of the epithet *capensis*. The binomial reappeared in the early 20th century in, for example, the seed-list of the French nursery Vilmorin Andrieux & Cie for 1922–1923 and was recorded by Dulfer (1965: 151) who opined that Regel's name was synonymous with *E. pelviformis* Salisb. (= *E. mauritanica* L.).

Salter (1935) employed the same binomial for a species found in marshes at low altitude on the Cape Peninsula (Dulfer 1964: 145, 146; 1965: 90; Oliver and Oliver 2000; Oliver 2012: 493). This species was illustrated by Schumann et al. (1992: 144), and is listed amongst the currently recognised plant species of southern Africa by Oliver and Oliver (2003: 429).

Oliver and Oliver (2003: 429, 447) placed Salter's name in synonymy under *Erica turbiniflora* Salisb. (wfo-0000673478). As that name was validly published and pre-dates Salter's by more than a century, it is the correct name for the taxon.

Erica turbiniflora Salisb., Trans Linn. Soc. 6: 377. 1802 wfo-0000673478

Erica capensis T.M.Salter, J. S. Afr. Bot. 1: 34. 1935 [wfo-0000671621], nom. Illeg., non Regel, Verh. Vereins Beförd. Gartenbaues Königl. Preuss. Staaten 16: 318 (1842) [wfo-1000053513], 158. 1843. Type: South Africa. "Cape Peninsula, marshes on lower Hout and Klaasjager River", 14 February 1934, T.M. Salter 4292 (holotype: BOL-137252 [https://plants.jstor.org/stable/10.5555/ al.ap.specimen.bol137252]).

Type. Without locality, *Hibbert ex herb. Salisbury* (lectotype, designated here: K [K-314663]).

6. Erica constantia Hort. Ex G.Sinclair (1825), non Nois. Ex Benth. (1839)

A Cape heath named "Erica Constantia" was included by Messrs Lee & Kennedy in a manuscript list of species that had been introduced into cultivation by the firm up to 1808 (see Nelson and Oliver (2004: 138)). The binomial has been traced in print in Conrad Loddiges & Sons' 1818 catalogue and, three years later, in Johann Heinrich Friedrich Link's (1767–1851) list of plants in Berlin Botanic Garden (Link 1821: 374). Neither of those publications contained a description, but George Sinclair's (1787-1834) catalogue of the heaths (Sinclair 1825) grown in the Duke of Bedford's garden at Woburn, Bedfordshire, England, did include a description (based on at least one living plant, although Sinclair had not observed this in bloom and a herbarium specimen). Sinclair (1825) attributed the name to "Hortulanis" (gardeners) and described the heath as having leaves in threes, with bell-shaped flowers in terminal inflorescences, with awnless anthers. He did not provide (as he usually did) the colour of the corolla because he had only seen a dried specimen. The name is also known from at least eight other 19th-century works, including those of Bentham (1839: 666), Regel (1842: 300) who remarked "Die als E. constantia in deutschen Gärten gehende Pflanze gehört zur E. trivialis" and Hereman (1868: 218) whose description indicated that the cultivated plant bore purple flowers.

However, Bentham (1839: 672) also described a species, stated to have been named *Erica constantia* by Noisette – presumably the French horticulturist Jean Claude Noisette (1772–1849) – on the basis of one of Klotzsch's specimens, then in the Berlin Herbarium and destroyed during the Second World War. Guthrie and Bolus (1905: 115) accepted this name, having seen the type material in Berlin "ex horto [Lee &] Kennedy, 1816", but overlooked the earlier usage, whereas Dulfer (1964: 108, 137; 1965: 67) chose to ignore the other use of the same binomial (including as a synonym for his *E. simulans* var. *trivialis* (Klotsch ex Benth.) Dulfer [wfo-0000673262]) and accepted Bentham's second application of the name, citing a specimen collected by Esterhuysen (*28188*) from "Oudensberg" [sic. Audebsberg], Worcester District, Western Cape, as matching Bentham's protologue.

Erica constantia Nois. ex Benth. is currently applied to a white-flowered heath from rocky slopes at high altitude, ranging from the Hex River Mountains to Klein Swartberg (Oliver and Oliver 2000, 2003: 430; Oliver 2012: 492). It is clearly not the purple-flowered taxon cultivated in European gardens during the 19th century.

Here, we designate the Esterhuysen collection cited by Dulfer (1965) as neotype to fix the application of the name in its current sense and provide a replacement name for the species. One meaning of the Latin word *constantia* is harmony, although whether that was also the intended meaning of Lee & Kennedy's epithet cannot be determined. *Concordia* also means harmony.

Erica concordia E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327521-1 wfo-1000053500

pro *E. constantia* Nois. ex Benth., Prodr. [A. P. de Candolle] 7(2): 672. 1839 [wfo-0000671735], nom. illeg., non Hort. ex G.Sinclair, Hort. eric. woburn.: 6, 32. 1825 [wfo-1000055091]; Guthrie and Bolus, Fl. Capensis 4,1: 115–116. 1905; Dulfer, Ann. Naturhist. Mus, Wein 68: 67–68. 1965.

Type. Without locality or collector, *Herb. Klotzsch* (holotype: B, destroyed). South Africa, Audensberg, S slopes. 15 February 1959, *E.E. Esterhuysen 28188* (neotype, designated here, NBG [NBG-0265661-0]).

7. Erica demissa Hort. ex G.Sinclair (1825), non Klotzsch ex Benth. (1839)

"Dwarf green-flowered heath" was the English name used by Sinclair (1825) when he described a plant cultivated in England in the early 19th century under the name *Erica demissa*. The name (as "*demisa*") was included in Messrs Lee and Kennedy's manuscript list, mentioned above (see Nelson and Oliver (2004: 138)), of Cape heaths that had been introduced into cultivation by the firm up to 1808. Within a year of this, the name was printed by Donn (1809), Cushing (1814: 210) and in Conrad Loddiges and Sons' catalogue for 1818.

Sinclair's description (1825) is more than adequate to validate the name, which Dulfer (1965: 29) noted, perhaps correctly, as a synonym of *Erica coccinea* L., no doubt following Sinclair's grouping of the species (Sinclair 1825: 35). There is a specimen so named in LIV, but we have not examined it.

Meanwhile, Bentham (1839) chose to adopt a name proposed by Klotzsch and, thus, published the same binomial for an entirely different species with white to rosy-pink flowers. This is distributed on the lower to middle slopes of the Swartberg as far east as Grahamstown (Oliver and Oliver 2000). This species was illustrated by Schumann et al. (1992: 137) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 432), but clearly is not the "dwarf, green-flowered" heath known to Sinclair.

A new epithet, derived from the Greek compound ορεσβιος (*oresbios*) meaning living on mountains (Stearn 1973), is published here and alludes to the species' habitat in "rocky veld on the Swartberg" (Schumann et al. 1992: 137).

Erica oresbia E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327522-1 wfo-1000053507

pro *E. demissa* Klotzsch ex Benth., Prodr. [A. P. de Candolle] 7(2): 666. 1839 [wfo-0000671862], nom illeg., non Hort. ex G. Sinclair Hort. eric. woburn.: 8. 1825 [wfo-0000671861]; Benth., Prodr. [A. P. de Candolle] 7(2): 621. 1839; Guthrie and Bolus, Fl. Capensis 4,1: 47. 1905; Dulfer, Ann. Naturhist. Mus, Wein 68: 86–87. 1965. **Type.** South Africa. "Uitenhaag [Uitenhage], in monitbus Vanstadensrivier", 1000–4000[ft], *C.F. Ecklon and C.L.P. Zeyher s.n.* (syntype: not traced); South Africa, "flum. Camtoo [Gamtoos]", *Masson s.n.* (syntype: not traced), *Burchell* 4709 (syntype: HAL [https://plants.jstor.org/stable/10.5555/al.ap.specimen.hal0135770]).

8. Erica flocciflora Tausch (1839), non Benth. (1839)

This is an instance of two names published within weeks of each other. Tausch's binomial was published on 28 October 1839, more than a month before Bentham's and, thus, has priority. Unfortunately, Dulfer (1965) consistently misquoted (as 1838) the publication date of Bentham's treatment of *Erica* published in the second part of volume 7 of Augustin Pyramus de Candolle's *Prodromus*. Late December 1839 is accepted as being the correct publication date for volume 7 part 2, although standard sources (e.g. Stafleu and Cowan (1976)) contain contradictory dates (for discussion, see Nelson (2005)). The first part of volume 7 was issued in 1838, but it does not contain the Ericeae.

Given the fact he had an incorrect (earlier) date of publication, Dulfer (1965: 98, 140) maintained Bentham's binomial as the correct name for the taxon and disregarded Tausch's name (which he stated was synonymous with *Erica daphniflora* Salisb.).

Erica flocciflora, as described by Bentham, occurs on the dry, lower slopes and rocky foothills of the Kouga Mountains and has a cream corolla with a distinctive woolly calyx (Oliver and Oliver 2000). This species was illustrated by Schumann et al. (1992: 157) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 434).

Irrespective of synonymy, Bentham's binomial is illegitimate because it is a later homonym. The new epithet that we provide below continues the allusion to *floccus* (Latin: tuft of woolly hairs) by adopting a Greek equivalent, $\mu\alpha\lambda\lambda\omega\tau\sigma\varsigma$ (*mallotos*), fleecy.

Erica mallotocalyx E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327523-1 wfo-1000053504

pro *E. flocciflora* Benth., Prodr. [A. P. de Candolle] 7(2): 660. 1839 (late December) [wfo-0000672068], nom. illeg., non Tausch, Flora Bot. Zeit. Regensb. 22: 629. 1839 (28 October) [wfo-0000672067]; Guthrie and Bolus, Fl. Capensis 4,1: 310 (1905); Dulfer, Ann. Naturhist. Mus, Wein 68: 98 (1965).

Type. South Africa. "In colonia capensi" (cit. Bentham 1839) ['on a rocky hill near Groot River, Uniondale Div.'], 14 March 1814, *W.J. Burchell* 4992 (lectotype, here designated, K (K-314571 [https://plants.jstor.org/stable/10.5555/al.ap. specimen.k000314571]; isolectotype, G)

9. Erica insignis Hort. (1853), non E.G.H. Oliv. (1981)

This binomial, overlooked by the compilers of "Index Kewensis", has been traced in no fewer than six publications issued during the latter half of the 19th century

including the "Journal of the Royal Horticultural Society" (1853: **8**: xl) and "Revue horticole" (1882: **54**: 219–220). Accompanying descriptions indicated it was applied to a scarlet-blossomed heath. It was also traced in catalogues issued by the following British and New Zealand nurseries: James Fraser, Lea Bridge Road Nursery for 1866–1867; William Rollisson & Sons for 1877; B. S. Williams for 1881; James Dickson & Sons, Newton Nurseries, for 1884; Nairn & Sons, Christ-church (New Zealand) for 1896. It is highly improbable that the plant cultivated at least until the end of the 19th century in European and New Zealand gardens was the same species as that first collected by Stokoe in 1935 and described by Oliver (1981). It inhabits rock crevices on upper, north-facing slopes of mountains including the Anysberg and Groot Swartberg and has remarkable flowers with a very small corolla (\pm 5 mm) concealed within a greatly extended calyx (\pm 20 mm). It was illustrated by Schumann et al. (1992: 215) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 436).

The new epithet alludes to the concealed corolla (from Greek: $\alpha\delta\epsilon\lambda\sigma\varsigma$ (adelos = unseen), $\pi\epsilon\tau\alpha\lambda\sigmav$ (petalon = leaf, i.e. petal)) and echoes the name of the section to which this species and *E. nabea* Guthrie and Bolus were assigned.

Erica adelopetala E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327524-1 wfo-1000053498

pro *E. insignis* E.G.H. Oliv., Bothalia 13: 446. 1981 [wfo-0000672329], nom. illeg., non hort. in J. Roy. Hort. Soc. 8: xl. 1853 [wfo-1000053515]; Rev. hort. 54: 219–220. 1882.

Type. South Africa, "Swartberg, north slopes below Kangoberg", 1,400 m, 11 December 1979, *E.G.H. Oliver* 7469 (holotype, NBG [as STE] [https://plants.jstor. org/stable/10.5555/al.ap.specimen.nbg0133788-0]; isotypes K, PRE).

10. Erica lanata J.C. Wendl. (1798), non Andrews (1806)

Messrs Lee & Kennedy had employed the name "Erica lanata" in the manuscript list, mentioned previously (see Nelson and Oliver (2004: 138)), of species that had been introduced into cultivation by the firm before 1808. Andrews (1806: t. 121) was undoubtedly using this binomial for the same plant. However, the binomial had been published eight years earlier by Johann Christoph Wendland (1755–1828) for a different species (Wendland 1798: 45). The persistent use of Andrews's binomial, despite the priority of Wendland's, is inexplicable. As noted by Dulfer (1965: 44), Wendland's name was a synonym of Erica conspicua Sol., which Dulfer relegated to a variety of E. curviflora L. (var. splendens (J.C. Wendl.) Dulfer = E. splendens J.C. Wendl., non Andrews), but is currently regarded as a distinct species (Oliver and Oliver 2000, 2003; Oliver 2012). There is a later name available to replace Erica lanata Andrews and that is E. flaccida Hort. ex Link; Sinclair (1825: 10) was the first to make this equation in print. *Erica flaccida* has been traced in print in several publications (e.g. Anonymous (1808: 191); Cushing (1812: 224; 1814, 224)) and in Conrad Loddiges & Sons' catalogue for 1811, before it was taken up by Link (1821: 1: 367), who cited

English gardeners as his source. None of the sources published prior to 1821 included a diagnosis or description.

Erica flaccida Hort. ex Link, Enum. hort. berol. alt.: 367. 1821 wfo-0000672048

Erica lanata Andrews, Heathery, 3: t. 121 (1806); Col. engr. heaths, 3, t. 179.
1809b [wfo-0000672411], nom. illeg., non *E. lanata* J.C. Wendl., Bot. Beobach.: 45. 1798 [wfo-0000672410]; Salisb., Trans. Linn. Soc. 6: 360 (1802); Guthrie and Bolus, Fl. Capensis 4,1: 73. 1905; Dulfer, Ann. Naturhist. Mus, Wein 68: 112 (1965); Oliver, Strelitzia 29: 499. 2012. Type. Icontype (illustration in Andrews, Heathery, 3: t. 121. 1806 [cit. Dulfer (1965): 112]).

Type. South Africa. "Hab. in Pr. b. sp. [Promontorium Bonae Spei = Cape of Good Hope] ... *Hort. angl.*" (B destroyed). Neotype (here designated). South Africa. Western Cape, George Dist., Outeniqua Pass. June 1960. *E.G.H. Oliver* 1596 NBG [NBG0112414-0].

11. Erica niveniana Hort. ex Loudon (1830), non E.G.H.Oliv. (2000)

This binomial appeared in print two centuries ago (Donn 1804: 69) and was repeated four years later (Anonymous 1808: 193); neither publication contained a diagnosis. However, Loudon (1830: 147) provided a description and explicitly attributed it to Andrews's "heaths 2" (i.e. "Coloured Engravings of Heaths" 2: t. 112. 1802). The name also occurs in at least two mid-19th century publications: M'Intosh (1855: 709) and Hereman (1868: 219).

Andrews (1802) did not employ the termination *-iana* (adjectival), but published *E. nivenia* (an incorrect variant of the substantive form *nivenii*) (see Nelson and Oliver (2004: 140)). These epithets are deemed (under ICN (Shenzhen Code) (2018, Art. 61.1 and 61.2); Turland et al. (2018)) to be simple orthographical variants, with the same type, of *E. nivenii*. Regrettably, this means that Oliver's binomial, proposed when *Syndesmanthus nivenii* N.E. Br. was transferred into *Erica* (Oliver 2000: 225), is an illegitimate later homonym.

The new name alludes to the silky hairs that give the inflorescences a fluffy appearance (Oliver 2012: 486).

E. bombycina E.C.Nelson & Pirie, nom. nov.

urn:lsid:ipni.org:names:77327525-1 wfo-1000053499

pro *E. niveniana* E.G.H.Oliv., Contrib. Bolus Herb. 19: 225. 2000 [wfo-0000672716], nom. Illeg., non *E. nivenii* Hort. Ex Loudon (as "*nivenia*"), Hort. Brit.: 147. 1830 [wfo-1000053516] (see Nelson and Oliver (2004)).

Type. South Africa. Without locality ["Erica N95 on elevated Situations"], *J. Niven 95* (holotype K (K-000225736 [https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:1017329-1]).

12. Erica perlata G.Sinclair (1825), non Benth. (1839)

It appears that no-one has hitherto noticed the inconsistency pertaining to the application of the binomial *Erica perlata* (meaning "beset with pearls") (Baker and Oliver 1967: 74). Twentieth-century works consistently attribute the name to Sinclair (1825) and apply it to an erect shrublet, up to 0.6 m tall, with small, urn- to bell-shaped, hairy, white flowers, possessing partly exserted anthers (Baker and Oliver 1967: t. 67; Schumann et al. 1992: 115; Oliver and Oliver 2000, 2003; Oliver 2012: 504). However, Sinclair's protologue (1825: 18) clearly applies to a different species. He wrote:

Fol.	Bractea.	Anth.	Pistill.	Inflorescentia	Color. Corol.	T. Flor.
4	rem.	sub. ex.	ex.	term. br. umbel.;	R.P.1-3. Anthers	Spring,
		mut.		corol. glob.	R.R.O.7.	Autumn.

In other words: leaves ternate; bracts remote; anthers subulate, exserted, muticous; pistil exserted, inflorescences terminal, branching, umbellate; corolla globose, pink-madder; anthers red (between scarlet and Indian red); flowering [in Northern Hemisphere] spring and autumn.

No herbarium specimens from the Duke of Bedford's Woburn collection, the basis of Sinclair's descriptions, are known that could be considered as type material, so the protologue is paramount. At least the colour of the flower signals that the protologue does not match the current application of the binomial. Sinclair's colour codes were very precise, being determined using a specially constructed "diagram of colours" (a colour-wheel) (Sinclair 1825: [39]–41; see Nelson (2011: 8), fig. 5).

Dulfer (1965: 74–75, 77, 141, 153) succeeded in making the various 19th-century applications of the binomial more confusing, although he correctly accorded priority to Sinclair, albeit quoting an incorrect publication date ("1816?") for "Hortus ericaeus Woburnensis" (see Nelson (2003)), an error inadvertently repeated in Baker and Oliver (1967: 74).

According to Dulfer (1965: 74), the disparate species that were identified under this name by various authors included the European *Erica lusitanica* Rudolph (Regel 1843: 162) and his own *E. sphaeroidea* Dulfer ("Lee sec KI[otzsch] sec Benth. [1839: 672]") (illustrated by Schumann et al. (1992: 119)). In synonymy under *E. perlata* G.Sinclair, Dulfer (1965: 75) placed *E. barbata* var. *minor* Andrews, *E. pura* Lodd., *E. procumbens* Lodd., *E. ephemera* Tausch, *Gypsocallis* procumbens G.Don and *Ericodes minus* Kuntze. He concluded (Dulfer 1965: 75): "*E. perlata* ist eigentlich nur eine in allen Teilen kleinere Form von *E. pannosa* und daher kaum eine Art, sondern eine Var. von *E. pannosa*."

Baker and Oliver (1967: 74–75) were not in any doubt that *Erica perlata* possessed "pearly-white flowers", inhabited the Riviersonderend Range and was allied to *E. barbata* Benth., but considering Sinclair's protologue (1825: 18), his name cannot apply to that plant. In fact, the white-blossomed Riviersonderend heath appears to have no valid name because Sinclair's is not applicable and renders Bentham's illegitimate. *Erica pura* Loddiges (1817: t. 72) is a *nomen nudum*, while Loddiges's *E. procumbens* (1833: t. 1993) is

another illegitimate later homonym (contrary to Taylor (2016: 1127) who was not aware of the homonymy).

We propose the replacement name *Erica galantha* for the Riviersonderend species, in allusion to the white, pearl-like flowers. *Galanthos*, from $\gamma \dot{\alpha} \lambda \alpha$ (gala = milk) and $\ddot{\alpha} \nu \theta_{0} \varsigma$ (anthos = flower), means with a milk-white flower (as in *Galanthus* L., Amaryllidaceae, the Eurasian snowdrop).

Erica galantha E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327526-1 wfo-1000053503

pro *E. perlata* Benth., Prodr. [A. P. de Candolle] 7(2): 670. 1839 [wfo-1000053517], nom. Illeg., non *E. perlata* G.Sinclair, Hort. Eric. woburn.: 18 (1825) [wfo-0000672873].

Type. South Africa, "In colonia capensi", *Drège s.n.* (lectotype W, effectively designated by Dulfer (1965: 75)) [https://plants.jstor.org/stable/10.5555/al.ap. specimen.w0008571].

13. Erica praecox Hort. Ex G.Sinclair (1825), non Klotzsch (1838)

This binomial was printed, without accompanying descriptions, in Conrad Loddiges & Sons' catalogue for 1807 and in at least two other pre-1825 publications (Anonymous 1808: 195; Cushing 1814: 210). The next publication, that of Sinclair (1825: 22), is the significant one. As he often did, Sinclair attributed this name to horticulturists, in this case specifically to one, "Hortul. Cormack", undoubtedly the English nurseryman John Cormack of New Cross, Kent, with whom Sinclair was to enter partnership in 1827 (Harvey 1973, 1981). Messrs Lee & Kennedy had employed the name "Erica praecox" in the manuscript list of species, mentioned previously (Nelson and Oliver 2004: 138), that the firm had introduced into cultivation.

Sinclair's (1825: 19) accompanying description is, like the majority of his descriptions, precise and accurate, sufficient to validate the binomial and render Klotzsch's one illegitimate.

Klotzsch (1838) described a quite different species under this same binomial. His name is currently applied to a spreading, compact shrublet, to 0.2 m tall, bearing urn-shaped to tubular urn-shaped, pink flowers between December and February (Oliver and Oliver 2000, 2003: 443; Oliver 2012: 505). It inhabits mountain summits and ridges between the Du Toitskloof Mountains and Villiersdorp and was illustrated by Schumann et al. (1992: 88, 89).

Dulfer (1965: 60) placed *Erica praecox* Klotzsch in synonym under *E. ventricosa* var. *meyeriana* Dulfer and noted *E. behen* E.Mey. ex Klotzsch as a synonym. However, Klotzsch (1838), noting *E. behen* as a name used in Drège's Herbarium, gave it as synonymous with *E. savileae* Andrews.

Our replacement epithet refers to the species' occurrence high in the mountains – above the clouds.

Erica supranubia E.C.Nelson & Pirie, nom. nov.

urn:lsid:ipni.org:names:77327527-1 wfo-1000053510

pro *E. praecox* Klotzsch, Linnaea 12: 517. 1838 [wfo-0000672980], nom. illeg., non Hort. ex G.Sinclair, Hort. eric. woburn.: 19, 32. 1825 [wfo-1200010024]; Benth., Prodr. [A. P. de Candolle] 7(2): 678. 1839.

Type. South Africa. "Dutoitskloof", *Drège 1147* (lectotype P (P-00110863), designated here (det. E.G.H. Oliver) [https://plants.jstor.org/stable/10.5555/al.ap. specimen.p00110863]; isolectotype W [https://plants.jstor.org/stable/10.5555/ al.ap.specimen.w18890186298, https://plants.jstor.org/stable/10.5555/al.ap. specimen.w18890158225].

14. Erica rhodantha Regel (1842), non Guthrie and Bolus (1905)

Regel (1842, 1843) published this name for a plant which Dulfer (1965: 154) equated with *Erica pelviformis* (= *E. mauritanica*) (see above no. 4). The later publication of the same binomial by Guthrie and Bolus (1905) is illegitimate.

The plant described and named by Guthrie and Bolus (1905) is poorly represented in herbaria, but is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 444). The type locality was Garcia's Pass and the taxon has recently also been collected on the lower, northern slopes of the Langeberg (Oliver and Oliver 2003: 444). *Erica rhodantha* Guthrie and Bolus resembles *E. gillii* Benth., but can be distinguished from that species by its unridged, brown anthers (ridged and black in *E. gillii*) (Oliver and Oliver 1994: 27). It is an erect shrublet with small, subcalycine, cup-shaped, rose-coloured flowers (Oliver and Oliver 2000).

The new epithet continues the allusion to the rose-red (*rhodellus*) flowers.

Erica rhodella E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327528-1 wfo-1000053509

pro *E. rhodantha* Guthrie and Bolus, Fl. Capensis 4,1: 288. 1905 [wfo-0000673111], nom. illeg., non Regel, Verh. Vereins Beförd. Gartenbaues Königl. Preuss. Staaten 16: 318. 1842 [wfo-1000053518], Regel, Kult. Aufz. Eriken, 158 (1843); Dulfer, Ann. Naturhist. Mus, Wein 68: 154. 1965.

Type. South Africa. Riversdale Div.; Garcias Pass, 1200 ft, *Galpin 3706* (lectotype BOL, effectively designated by Dulfer (1965: 131) [https://plants.jstor.org/ stable/10.5555/al.ap.specimen.bol137442]; isolectotypes K [https://plants. jstor.org/stable/10.5555/al.ap.specimen.k000314992], NBG [https://plants. jstor.org/stable/10.5555/al.ap.specimen.nbg0199737-0], PRE [https://plants. jstor.org/stable/10.5555/al.ap.specimen.pre0309255-0], SAM [https://plants. jstor.org/stable/10.5555/al.ap.specimen.sam0010474-0], W [https://plants. jstor.org/stable/10.5555/al.ap.specimen.w19610016719].

15. Erica rugata Hort. ex G.Sinclair (1825), non E.G.H.Oliv. (2000)

This binomial was printed, without accompanying descriptions, in Conrad Loddiges & Sons' catalogue for 1811 and in at least two other pre-1825 publications (Cushing 1814: 227; Link 1821: 374). The next publication, that of Sinclair (1825: 22), is, as before, the significant one. Sinclair attributed this name to gardeners ("Hortulanis"), noting it in synonymy under the entry for *Erica rugosa* Andrews; there is a cryptic (cf. ICN (Shenzhen Code) (2018, Art. 38.14); Turland et al. (2018)) reference to Andrews's publication "Heaths, vol. iv." (i.e. "Coloured Engravings of Heaths" 4: t. 267 (post 1809; see Cleevely and Oliver (2002))). Andrews's *E. rugosa* is regarded as a horticultural hybrid.

Unaware of the previous use of this binomial – it is not listed in botanical indexes such as "Index Kewensis", nor was it noted by Dulfer (1965) – Oliver (2000: 368) chose and published the same binomial when transferring *Coccosperma rugosum* Klotzsch into *Erica*. The new epithet alludes to the rugose ovary of this species which is always bi-locular (fide Oliver (2000: 369)).

Erica didymocarpa E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327529-1 wfo-1000053501

pro *E. rugata* E.G.H.Oliv., Contrib. Bolus Herb. 19: 368 (2000) [wfo-0000673157], nom. illeg., non Hort. ex G.Sinclair, Hort. eric. woburn.: 22 (1825) [wfo-1000053519] (= *E. × rugosa* Andrews [wfo-0000673159]).

Type. South Africa. "Cap, im Gebirge bei der Kapstadt" [mountains near Cape Town] [loc. 84], *Zeyher s.n.* (lectotype K, designated by Oliver 2000); isolectotype MEL [https://plants.jstor.org/stable/10.5555/al.ap.specimen.mel623226]).

16. Erica spectabilis C.F. Waitz (1805), non Klotzsch ex Benth. (1839)

The name *Erica spectabilis* appeared in print more than thirty years before its publication by Bentham (1839). Under his *E. spectabilis*, Waitz (1805: 220) quoted Andrews's description making *E. formosa* Andrews a synonym, an equation he reinforced in the "Alphabetisches Verzeichniß der Heidenarten" (Waitz 1805: 324). Andrews's name was illegitimate, because of the prior publication of *E. formosa* Thunb. and the plant concerned, which possessed vermilion-coloured flowers, is regarded as being a horticultural hybrid (it was claimed by Messrs Rollisson of Tooting).

As the variant "spectabilia", the binomial has been traced in the 1804 catalogue issued by Conrad Loddiges & Sons who corrected the spelling to "spectabilis" in 1818.

The handsome, variable, white-, cream- to green-flowered species for which Bentham (1839: 659) published the same binomial is restricted to the limestone hills near the coast from Bredasdorp to Gouritsmond, whilst

a similar species, *E. syngenesia* Compton, with larger cream-white flowers occurs inland, from the Witteberg to Swartberg (Oliver 2012) and Kammanassie Mountains (Oliver et al., in prep.). Both species were illustrated by Schumann et al. (1992: 156), *E. syngenesia* from the Klein Swartberg (Schumann et al. 1992: 156, figs 12, 13 and 14) and *E. oraria* (as *E. spectabilis*) from coastal habitats near Still Bay (Schumann et al. 1992: 156, figs 10 and 11). *E. syngenesia* and *E. oraria* (as *E. spectabilis*) are included amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 445; Oliver 2012).

The new epithet, from the Latin *ora* (edge or sea coast), reflects the coastal distribution of the species.

Erica oraria E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77330003-1 wfo-1000056203

pro E. spectabilis Klotzsch ex Benth., Prodr. [A. P. de Candolle] 7(2): 659. 1839 [wfo-0000673283], nom. illeg., non Waitz, Beschreibung der Gattung und Arten der Heiden: 220. 1805 [wfo-0000673282]; Guthrie and Bolus, Fl. Capensis 4,1: 57. 1905.

Type. South Africa. "in Strandweld [Strandveld]", Drège s.n. (syntypes: †B, GDC [https://plants.jstor.org/stable/10.5555/al.ap.specimen.g00465165],
HBG [https://plants.jstor.org/stable/10.5555/al.ap.specimen.hbg507932], K, W [https://plants.jstor.org/stable/10.5555/al.ap.specimen.w18890186305, https://plants.jstor.org/stable/10.5555/al.ap.specimen.w18890321973, https://plants.jstor.org/stable/10.5555/al.ap.specimen.w0005951]).

17. Erica stenantha Sweet (1830), non Klotzsch ex Benth. (1839)

Sweet (1830: 340) published this binomial with a reference to the fourth volume of Andrews's "heath." and also the synonym "tenuiflora γ carnea. A. H. v. 4." (i.e. "Coloured Engravings of Heaths" 4: t. 281 (post 1824)); this indirect reference to a previously published description validates Sweet's binomial (ICN (Shenzhen Code) (2018, Art. 38.13); Turland et al. (2018)). Thus, Sweet was raising Andrews's *Erica tenuiflora* var. carnea to the rank of a species with this binomial.

As noted by Dulfer (1965: 61), following Andrews's *Erica tenuiflora, E. stenantha* Sweet is a synonym of *E. cylindrica* Thunb. Dulfer (1965) did not recognise that Bentham's binomial (1839: 685) was a later, illegitimate homonym. The species named *E. stenantha* by Bentham (1839) inhabits the upper slopes of the Langeberg; it is an erect shrub, with small, calycine, cupshaped, dark pink flowers (Oliver and Oliver 2000) and is listed amongst the currently recognised plant species of southern Africa (Oliver and Oliver 2003: 446).

The new epithet is derived from Latin *poculus* (cup) and alludes to the cupshaped flowers.

Erica poculiflora E.C.Nelson & E.G.H.Oliv., nom. nov.

urn:lsid:ipni.org:names:77327531-1 wfo-1000053508

pro *E. stenantha* Benth., Prodr. [A. P. de Candolle] 7(2): 685. 1839 [wfo-0000673321], nom. illeg., non Sweet, Hort. Brit.: 340. 1830 [wfo-0000673320] (= *E. cylindrica* Thunb.).

Type. South Africa. "Berge bei Zwellendam", *C.F.Ecklon and C.L.P. Zeyher 221* (lectotype W, effectively designated by Dulfer 1965: 130) [https://plants.jstor. org/stable/10.5555/al.ap.specimen.w0005950]; isolectotypes MEL [https://plants.jstor.org/stable/10.5555/al.ap.specimen.mel2384382]; S [https://plants.jstor.org/stable/10.5555/al.ap.specimen.s08-6141]).

18. Erica tenuis Moench (1802), non Salisb. (1802)

According to Stafleu and Cowan (1981), the supplementary volume to Moench's "Methodus plantas Horti Botanici et Agri Marburgensis" was issued on 2 May 1802, a little more than three weeks before Salisbury's paper was published in "Transactions of the Linnean Society" between 24 and 27 May 1802. Thus, Moench's binomial renders Salisbury's illegitimate.

Mysteriously, Dulfer (1965: 141) stated that Moench's name was a synonym of "*Ceramia tenuis* G. Don sec. Benth., Pr. 693 (1838) [sic]". However, Don's publication contains no such name, nor is there any reference on p. 693 in Bentham (1839) to this synonymy. The identity of the plant described by Moench, therefore, remains unknown.



Figure 1. *Erica oliveranthus* E.C. Nelson and Pirie, renamed in honour of E.G.H. (Ted) Oliver and Inge M. Oliver (photo: MDP; https://www.inaturalist.org/observations/19098927).

Erica tenuis Salisb. is the current name for a white-flowered heath (Fig. 1) that occurs in the Western Cape from Clanwilliam to Humansdorp (Schumann et al. 1992: 172), but it must now be replaced.

The new epithet published here is a tribute to our co-author, Dr E.G.H. ('Ted') Oliver, pre-eminent authority on the taxonomy of *Erica*, and to his late wife and collaborator, Inge Magdalene Oliver (1947–2003), who was an authority on *Erica* in her own right. They have previously been honoured separately in *E. ingeana* E.G.H. Oliv. and *E. oliveri* H.A.Baker (Schumann et al. 1992: 131).

Erica oliveranthus E.C.Nelson & Pirie, nom. nov.

urn:lsid:ipni.org:names:77327532-1 wfo-1000053506

pro *E. tenuis* Salisb., Trans. linn. Soc 6: 329. 1802 [wfo-0000673389], nom. illeg., non Moench, Methodus: 17. 1802 [wfo-0000673388].

Type.Without locality or collector, Ex herb. R. A. Salisbury (lectotypeK[K000314799][https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:329729-1]).

19. E. tomentosa Masson (1776), non Salisb. (1802)

Masson only published one account of his botanical explorations at the Cape of Good Hope (Masson 1776) and, in this, he recorded that on 30 December 1773, during his second journey (Masson 1776: 298–299; see Bradlow (1994: 124)), he reached:

... the hot bath, which is situated at the foot of a ridge of dry mountains: ... Next morning, we went up to the top of this ridge of mountains ... We found here a species of heath remarkable for having its branches and leaves all covered with a fine hoary down or nap, which we thought singular in that genus: we called it *Erica tomentosa*.

Bradlow (1994: 157 n. 212) identified the "hot bath" as the spring situated 4 km east of the southern entrance to Toorwater Poort, in the Groot Swartberg Range. Thunberg was with Masson on this occasion and his corresponding specimen became the type of *Erica passerina* Montin (1775) (fide J.P. Rourke, in Bradlow (1994: 157 n. 212)).

It is often difficult to decide whether a sentence such as Masson's constitutes a diagnosis as defined in the International Code of Nomenclature: '... a statement of that which, in the opinion of its author, distinguishes the taxon from others' (ICN (Shenzhen Code) 2018, Art. 38.2; Turland et al. 2018). Given that, at this time, the early 1770s, only about fifty *Erica* species from the Cape Region had been described (Oliver 2000: 4, figure 1; Nelson and Oliver 2004) and that Masson was, by then, familiar with many more undescribed species in their wild habitats, the clause "which we thought singular in that genus" suggests that this is precisely what Masson wrote. Thus, his binomial was validly published. However, it is a junior synonym of *E. passerina*. It follows that Salisbury's binomial is illegitimate and has to be replaced. The heterotypic synonym, *Erica velutina* Bartl. (fide Dulfer (1965: 67)), may be employed for this taxon. It is found on the rocky, lower, southern slopes of the Riviersonderend Mountains (Oliver and Oliver 2000, 2003: 446). An erect shrublet, to 0.5 m tall, *E. velutina* bears small, urn-shaped, finely hairy, lilac or dark pink flowers.

Erica velutina Bartl., Linnaea 7: 645. 1832.

Erica tomentosa Salisb., Trans. Linn. Soc. 6: 327. 1802 [wfo-0000673425], nom. illeg., non Masson, Phil. Trans. 66: 299. 1776 [wfo-1000053520] (= *E. passerina* Montin). Type. South Africa. "Hottentots Holland", *I. Mulder s.n. ex herb. Salisbury* (not located).

Note. A label identifying the specimen labelled "C.B.S. *Niven 16*" (K-000314197) [https://plants.jstor.org/stable/10.5555/al.ap.specimen. k000314197] as a lectotype is incorrect as the protologue cited only a collection from Hottentots Holland by I. Mulder and the Niven collection is, therefore, not original material.

Type. South Africa. "Am Fusse des Babylonschenthurmbergen [Babilonstoring]", *Ecklon s.n.* (holotype GOET-003270 [https://plants.jstor.org/stable/10.5555/al.ap.specimen.goet003270]).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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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

Lectotypification of two names of *Carex buekii* hybrids (Cyperaceae) and notes on their morphology, ecology and distribution

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Abstract

Lectotypes are designated for two *Carex buekii* hybrid names. The typification is supplemented with notes on their morphology, ecology, and distribution.

Key words: Carex ×ligniciensis, Carex ×vratislaviensis, section Phacocystis, typification, WRSL herbarium

Introduction

Carex L. (Cyperaceae) is one of the most species-rich angiosperm genera with more than 2,000 species distributed worldwide (POWO 2023). In a large genus like *Carex* hybridisation is especially frequent, however most of the *Carex* hybrids are restricted to a few sections, e.g. *Ceratocystis* Dumort., *Glareosae* G.Don, *Phacocystis* Dumort., and *Vesicariae* Heuff. (Cayouette and Catling 1992, Wallnöfer 2006, Więcław and Koopman 2013, Pedersen et al. 2016).

Carex buekii Wimm. belongs to the section *Phacocystis*, one of the largest and taxonomically most complex sections within the genus *Carex*, with about 110 species distributed worldwide. Furthermore, hybridisation is frequent in *Phacocystis*, and several species are of hybrid origin (Roalson et al. 2021). *Carex buekii* has hybridised with four other *Phacocystis* species so far: *C. acuta* L., *C. cespitosa* L., *C. elata* All., and *C. nigra* (L.) Reichard (Koopman 2022), all these four hybrids were described by Figert (1900, 1907).

Ernst Figert (1848–1925), a German (Prussian) teacher and botanist from Liegnitz (nowadays named Legnica, Poland) collected plants mainly from Lower Silesia, paying attention to difficult genera, e.g. *Carex, Salix* L., *Mentha* L., and their hybrids. Figert (1900) described the first two hybrids of *C. buekii*, *C. × ligniciensis* Figert [*C. buekii* × *C. nigra*] and *C. × vratislaviensis* Figert [*C. acuta* × *C. buekii*], based on plants collected on the same date and at the same site in Silesia (Poland). Figert (1900) did not select a type specimen or provide an illustration for *C. × ligniciensis*. Neither did he do so for *C. × vratislaviensis* when



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Copyright: © Helena Więcław et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0). he named and described these two hybrids. Original material of *C*. × *ligniciensis* and *C*. × *vratislaviens* was found in the herbarium of WRSL (Poland). Both sheets were originally labelled by Figert. These hybrids are usually intermediate to the parental species and exhibit a wide range of morphological variability. *Carex buekii* hybrids, especially *C*. × *vratislaviensis* may be fertile and backcrosses appearing in populations are difficult to identify. These issues can lead to no-menclatural and taxonomic confusion and a lack of clarity in limits between parental species and hybrids. The lectotype of *C. buekii* has been designated (Jiménez-Mejías et al. 2014), the next step is the typification of its hybrids.

Material and methods

Taxonomic literature, including protologues, as well as fresh collections from parts of the Czech Republic and Poland, were examined. We also examined dried specimens deposited at the herbaria of BRNM, BRNU, JE, PR, PRC, and WSRL (acronyms based on Thiers 2023, continuously updated) and used the online database (JACQ Virtual Herbaria 2023) to check for type specimens. We have designated lectotypes, by comparing specimens with protologues, and selecting the most complete ones, in accordance with Art. 9.3 of the "Shenzhen Code" (Turland et al. 2018).

Results and discussion

Carex ×ligniciensis Figert, Allg. Bot. Z. Syst. 6: 38 (1900) [C. buekii × C. nigra].

Lectotype (designated here). POLAND. Flora von Schlesien. Liegnitz: Parchwitz, auf einer Wiese an der Katzbach unter den Stammarten. 10/6/99. Leg. Figert (WRSL barcode WR GS 066846; isolectotype WRSL barcode WR GS 058738) (Fig. 1).

Morphology. The hybrid is mostly intermediate between the parental species and characterised by the following traits: ± tussocks 25-40 cm high, with numerous, shorter or longer creeping rhizomes; stems slender, with reddish brown to purple scale-like, non-reticulate basal sheaths, rough on the edges in the lower half; leaf blades 3-4 mm wide, with very long acuminate, bristle-like tip, very rough on the margin, dark green to grey-green; male spikes 1-2, oblong-cylindrical, glumes brown-black to black, obtuse, with a light central stripe, female spikes 3(-4), narrow, short cylindrical, proximate, lowermost slightly distant, lax at base, ca 4 cm long, pedunculate; female glumes ovate, shorter than utricles, dark brown; utricles empty, small, non-deciduous, green, without veins; lower bract shorter than inflorescence (Grulich et al. 2023). Wallnöfer (2006) stated that this hybrid has amphistomatic leaves (stomata on both sides of the leaves). This trait makes this hybrid impossible to confuse with the other C. buekii hybrids, which have only stomata on the lower surface of the leaves (hypostomatic). The first of the parental species, C. buekii, is hypostomatic while in the second one, C. nigra, the stomata are found on the upper (adaxial) side of the leaves (epistomatic).

Ecology. This hybrid was found in floodplains of large rivers where both parental species could meet. However, *C. nigra* avoids warm areas with the exception of isolated lowland fen sediments in previously flooded meadows, which corresponds to all known finds of this hybrid so far.


Figure 1. The lectotype of *Carex × ligniciensis* Figert (WRSL barcode WR GS 066846). Photo: Herbarium, Museum of Natural History University of Wrocław, Poland.

Distribution. *Carex ×ligniciensis* is relatively rare and has been found so far in Poland, the Czech Republic and Italy (Koopman 2022). The specimens in BRNL, BRNM, CB, PR, and PRA were collected in the Czech Republic between 1921 and 1995, and they lack field verification. Therefore, we could consider it missing or even extinct at this locality. On the other hand, *C. ×ligniciensis* is a very inconspicuous and apparently overlooked plant. In the Czech Republic, only one recent locality is known from the floodplain of the River Morava near the town of Kroměříž. As far as we know there are no recent findings of this hybrid in Poland, while its occurrence in Italy is at least questionable, as *C. buekii* is extremely rare in this country (Koopman et al. 2018).

The sterility of *C*. *×ligniciensis* limits it dispersal, however, the persisting of hybrid populations probably depends on vegetative reproduction, like with other sterile hybrids in *Carex* (Pedersen et al. 2016). The spontaneous recurrence and survival of hybrids under natural conditions are a driving force of plant speciation (e.g. Mallet 2007, Soltis 2013).

Carex ×vratislaviensis Figert, Allg. Bot. Z. Syst. 6: 39 (1900) [C. acuta × C. buekii].

= C. buekii Wimmer var. melanostachya R. Uechtr., Jahresber. Schles. Ges. Vaterl. Cult. 43: 236 (1865, publ. 1866).

Lectotype (designated here). POLAND. Flora von Schlesien. Liegnitz: Parchwitz, auf Wiesen an der Katzbach unter den Stammarten. 10/6/99. Leg. Figert (WRSL barcode WR GS 066847; isolectotypes: WRSL barcode WR GS 058739; JE barcode JE 00021673, barcode JE 00026167, barcode JE 00026168, barcode JE 00026169) (Fig. 2).

Morphology. This hybrid is very variable, often intermediate between the parental species, but also tends to be morphologically closer to one of the parents. The utricles are very different in shape and size, from small ones similar to C. buekii, to more often closer in size to C. acuta. The leaf sheaths vary with the gene flow of the parental species: from reddish brown, robust, scale-like, shiny, reticulate, to intermediate types with smaller and slender sheaths than C. buekii, dark reddish brown, in spring with distinctive reticulate sheaths and in summer without. In the field, this hybrid is striking for its vegetative traits being close to C. acuta, but it has narrow and long female spikes (longer than those of C. acuta), especially the lowest one, which is pedunculate, interrupted at the base down to individual flowers and often pendent. The lowest bract sometimes exceeds the inflorescence, a character inherited from C. acuta (Koopman et al. 2018), but it is often shorter than, or as long as, the inflorescence. Carex ×vratislaviensis is usually partially or fully fertile, less often sterile. In the field, backcrosses from the hybrid swarm are fertile and their traits match the variability of either parent. These plants are morphologically indistinguishable in the field from parental species. The only distinctive trait of this hybrid is the persistent small or larger red-brown scale-like basal sheaths.

Ecology. Both parental species are relatively commonly found, most often in the floodplains of large rivers, where both find suitable habitats (*C. buekii*: gravel-sand terraces covered with clay and littoral embankments; *C. acuta*: oxbows, reservoirs, eutrophic wetlands in floodplains with nutrient-rich sediments) (Kaplan et al. 2018). Most localities of *C. ×vratislaviensis* correspond with the distribution



Figure 2. The lectotype of *Carex ×vratislaviensis* Figert (WRSL barcode WR GS 066847). Photo: Herbarium, Museum of Natural History University of Wrocław, Poland.

of *C. buekii*, however, it was also found on banks of lakes and in adjacent marshes where *C. acuta* usually grows (Koopman et al. 2018). Řepka (2023) recently described large populations of the hybrid on the banks of the River Elbe near the town of Děčín (northern Bohemia), and at the edge of the field, a unique habitat completely outside the requirements of both parental species.

Distribution. It has been recorded so far in Austria, Czech Republic, Germany, Hungary, Italy, Poland, and Slovakia (Koopman 2022).

Carex ×*vratislaviensis* is an independent hybridogenous taxon (nothospecies) living autonomously in nature, mostly fully or partially fertile, and spreads spontaneously in the landscape. In the Czech Republic, it is currently documented in approximately 400 extensive populations. Based on current knowledge, it is now the most abundant hybrid (nothospecies) of the genus *Carex* in the Czech Republic. It has an excellent ability of clonal reproduction, and its utricles are spread by water birds to other habitats. At some habitats, especially in older meadows in the floodplains of large rivers, it can strongly dominate over the parental species or grow completely independently without their presence. In our opinion it can be compared with the hybridogenous *C. recta* Boott, also from the section *Phacocystis*, which has originated from hybridisation between *C. aquatilis* Wahlenb. and *C. paleacea* Schreb. Ex Wahlenb. (Standley 1990). It is presumed that *C. ×vratislaviensis* influences other species and hybrids by its gene flow and forms triple hybrids or at least simply affects their fertility in situ (and the subsequent formation of empty utricles and thus empty spikes); however, this process needs further research.

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Conceptualization: HW, RŘ. Formal analysis: JK, HW. Project administration: HW. Visualization: HW. Writing – original draft: HW. Writing – review and editing: RŘ, JK.

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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

Research Article

Vaccinium usneoides (Ericaceae), a new species from Yunnan, China

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Abstract

Vaccinium usneoides (Ericaceae), a new species from Fugong County of Yunnan Province, China is described and illustrated. This new species belongs to *Vaccinium* sect. *Calcicolus* and is most similar to *V. brachyandrum*, but differs in its branches hanging down, much smaller leaf blades, shorter inflorescences and pedicels, non-glandular tomentellate or densely pubescent inflorescence rachis and pedicels, densely white-pubescent hypanthium and pilose filaments.

Key words: Gaoligong Mountain, morphology, Vaccinieae, Vaccinium arbutoides

Introduction

The genus *Vaccinium* L. (Ericaceae), with about 450–500 species distributed worldwide, is the largest genus of the blueberry tribe (Fang 1991; Fang and Stevens 2005; Vander Kloet and Dickinson 2009). This genus is a morphologically diverse group, which was divided into 33 (Sleumer 1941) or 30 sections (Vander Kloet and Dickinson 2009) with most sections of this genus allopatric. In China, 100 species of *Vaccinium* have been recorded, including the very recently published *V. jiuwanshanense* Ying Qin, Yan Liu & Y. H. Tong and *Vaccinium bangliangense* Y. S. Huang & Y. H. Tong (Huang et al. 2022; Qin et al. 2023). Yunnan Province, with 47 species of *Vaccinium*, harbours the highest diversity of this genus in China (Fang 1986; Huang and Fang 1991).

During several field trips to Gaoligong Mountain, we encountered an interesting *Vaccinium* species. This species is epiphytic on large trees with long hanging-down branches, which looks just like beard lichens from a distance. The inflorescence of this species is very hairy and shorter than and shaded by leaf blades, suggesting a close relationship with *V. brachyandrum* C. Y. Wu & R. C.



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Fang, another sympatrically distributed species in Gaoligong Mountain. However, *V. brachyandrum* owns scrambling branches and much larger leaf blades, which are totally different from this unknown species. After a careful comparison of morphology with similar congeneric species from China and adjacent Myanmar (Kress et al. 2003; Fang and Stevens 2005), it was confirmed that this plant represents a new species, which is described and illustrated below.

Material and methods

Flowering and fruiting materials were collected from Gaoligong Mountain during three field trips in May 2022, October 2022 and March 2023. Descriptions were based on both living and dried collections. The voucher specimens were deposited at the Herbaria of Kunming Institute of Botany, Chinese Academy of Sciences (KUN) and South China Botanical Garden, Chinese Academy of Sciences (IBSC). Measurements were performed with a ruler and small plant parts were observed and measured under a stereomicroscope (Mshot-MZ101).

Taxonomic treatment

Vaccinium usneoides Y.H.Tong, Y.J.Guo & Ting Zhang, sp. nov.

urn:lsid:ipni.org:names:77333175-1 Figs 1, 2

Type. CHINA. Yunnan Province: Fugong County, Shiyueliang Xiang, Yaduo Village, Nihajiadi (also called "Shibagongli" unofficially), Gaoligong Mountain, epiphytic on trees in evergreen and deciduous broad-leaved mixed forest, 27°9'55.0"N, 98°46'44.2"E, 2497 m a.s.l., 27 May 2022 (fl.), *Ting Zhang, Ji-Dong Ya & Wei Zhang 22CS21979* (holotype: KUN, barcode no. 1584163 (Fig. 3), isotypes: IBSC, barcode no. 1003856, KUN, barcode no. 1584164).

Diagnosis. This new species is close to *V. brachyandrum* in the short and hairy inflorescences (less than 3.5 cm) with many flowers and the abaxially glandular leaf blades with one basal gland per side and a caudate-acuminate apex, but can be immediately distinguished by its hanging-down (vs. scrambling) branches, much smaller leaf blades ($2.5-5.5 \times 0.9-1.8$ cm vs. $8.5-11 \times 4-6$ cm) with fewer pairs of secondary veins (3-4 vs. 6-7), shorter inflorescence (1-1.5 cm vs. 1.5-3.5 cm), non-glandular tomentellate or densely pubescent (vs. glandular pubescent) inflorescence rachis and pedicel, shorter pedicel (0.7-1 mm vs. ca. 2 mm), densely white-pubescent (vs. glabrous) hypanthium and pilose (vs. glabrous) filament. A detailed morphological comparison between the two species is presented in Table 1.

Description. Evergreen shrubs, epiphytic on tree trunks, sparsely branched; roots creeping firmly on tree trunks or branches; stems 0.5–3 m long, without swollen basal tuber or root swellings. Branches hanging down, young shoots brownish or greenish, terete or slightly angled, without lenticels, densely pubescent; old ones more or less glabrescent, brownish or greyish, often obviously angled in sicco. Perennating buds dimorphic (floral perennating buds at least twice the size of vegetative perennating buds). Leaves alternate; petiole short, curved, 2–5 mm long, 1–1.5 mm wide, densely pubescent, glabrescent when mature; blade narrowly ovate to oblong, 2.5–5.5 (including caudate apex)



Figure 1. *Vaccinium usneoides* sp. nov. A habitat, the red ovals indicating this species B habit C leafy branches, the arrow showing the indumentum on young branchlets and leaf blades D flowering branchlets with young inflorescences E flowering branchlet F fruiting branchlet. A, B taken by Yi-Hua Tong C, F taken by Yong-jie Guo D taken by Ji-Dong Ya E taken by Ting Zhang.

 \times 0.9–1.8 cm, thickly leathery, adaxially more or less transversely wrinkled when dry, especially for young ones, abaxially with evenly distributed and caducous appressed black glandular trichomes, trichome base papillate, both sides pu-



Figure 2. Vaccinium usneoides sp. nov. A flowering branchlet B trichomes on abaxial surface of leaf blades C fruiting branchlet D flower E flower with corolla and calyx limb removed, showing androecium and gynoecium F stamens, adaxial (left), abaxial (middle) and lateral (right) view G seeds. Illustrated by Ding-Han Cui.

bescent when young, glabrous when mature, base rounded to broadly cuneate, with 1 basal gland per side at ca. 1 mm distance from the junction of leaf blade base and petiole, margin entire, revolute, with a ca. 0.5 mm broad, cartilaginous edge, apex caudate-acuminate; veins impressed adaxially, more so when dry, obscure abaxially, secondary veins 3–4 per side, tertiary veins slightly promi-



Figure 3. Holotype of Vaccinium usneoides (Ting Zhang, Ji-Dong Ya & Wei Zhang 22CS21979, KUN, barcode no. 1584163).

Table 1. A morphological comparison of *Vaccinium usneoides* and *V. brachyandrum*. The character information of the latter species is taken from Fang and Wu (1987), Fang and Stevens (2005) and its type specimens.

Characters	V. usneoides	V. brachyandrum
Branches	Hanging down	Scrambling
Leaf blade	2.5-5.5 × 0.9-1.8 cm	8.5−11 × 4−6 cm
Pairs of secondary veins	3-4	6-7
Inflorescence length	1-1.5 cm	1.5-3.5 cm
Indumentum on inflorescence and pedicel	Non-glandular tomentellate or densely pubescent	Glandular pubescent
Hypanthium	Densely white-pubescent	Glabrous
Pedicel length	0.7–1 mm	ca. 2 mm
Filament	Pilose	Glabrous

nent. Inflorescence short racemose, 1-1.5 cm long, axillary on biennial branches, shorter than and shaded by leaf blades, 8-14-flowered. Peduncle very short, inflorescence rachis 0.7-1 cm long, white-tomentellate or densely white-pubescent; bracts red on exposed part, greenish on covered part, broadly obovate, cucullate, $5-6 \times 6-7$ mm, abaxially more or less white-pubescent on mid-vein, more so on lower half, adaxially glabrous, margin ciliate, caducous; bracteoles 2, inserted at base of pedicel, greenish, sometimes tinged with red, obovate, 3.5-4 × 2-2.5 mm, indumentum similar to bracts, caducous. Pedicels greenish, very short, 0.5–1 mm long, densely white-pubescent, articulate with the hypanthium. Hypanthium greenish, obconical, $1-1.5 \times 1-1.5$ mm, densely white-pubescent, more so at base; calyx limb lobed nearly to base, lobes 5, green, more or less tinged with red, triangular, ca. 2 × 1.5 mm, abaxially white-pubescent at apex, otherwise glabrous, adaxially glabrous, apex acuminate, margin ciliate. Corolla red, urceolate-campanulate, slightly angled when young, 3.5-4 × ca. 3 mm, tube glabrous on both sides; lobes 5, ovate-triangular, reflexed, ca. 0.8 × 1 mm, abaxially white-pubescent at apex, otherwise glabrous, adaxially papillose, apex acuminate. Stamens 10, 2.8-3 mm long; filaments flat, slightly S-shaped, 1-1.2 mm long, papillose on both sides, margin pilose; anthers 1.8-2 mm long, thecae slightly longer than or nearly as equal as tubules; spurs 2, borne at abaxial base of tubules, 0.7–0.8 mm long, spreading. Disc yellowish-green, annular, glabrous; style cylindrical, slightly angled in sicco, 2.7-3 mm long, glabrous, stigma truncate; ovary pseudo-10-locular, each locule with several ovules. Fruiting pedicels 1-3.5 mm long; berries pale green to green when young, yellowish-green to purplish-red or dark purple when mature, globose, 4.5–6 mm in diam., densely white-pubescent, with persistent calyx lobes appressed at apex, ripe berries a little bitter. Seeds ovoid, $0.7-0.8 \times 0.5-0.7$ mm, testa brownish, reticulate.

Etymology. The species epithet is derived from the genus of beard lichen "Usnea" and the suffix "-oides", which means the habit of this new species looks very much like beard lichen on trees from a distance. Chinese name is given as 松萝越橘 (Pinyin: song luó yuè jú).

Distribution and habitat. This species is currently known only from the type locality, i.e. the part of the Gaoligong Mountain in Fugong County. It grows on trees in mountainous evergreen and deciduous broad-leaved mixed forests at elevations of 2400–2800 m a.s.l.

Conservation status. *Vaccinium usneoides* is not rare in the type locality and the whole distribution area is under the protection of Gaoligongshan National Nature Reserve. Thus, the threat risk seems to be low. Since the type locality is very near the border of China and Myanmar, this species is probably also distributed in the adjacent area of Myanmar. Thus, it is best to assign a status of 'Data Deficient' (DD) for this species following the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022).

Phenology. Flowering in May–June and fruiting in October–November.

Additional specimens examined. Vaccinium usneoides (paratypes): the same locality with holotype: 27°9'57.78"N, 98°46'14.91"E, 2661 m a.s.l., 27 October 2022 (fr.), Yong-Jie Guo, Zhou-Dong Han & Xiu-Ying Shen 22CS22598 (IBSC, barcode no. 1003853, KUN, barcode nos. 1584165 & 1584166); 27°9'56.89"N, 98°46'14.63"E, 2652 m a.s.l., 27 October 2022 (fr.), Yong-Jie Guo, Zhou-Dong Han & Xiu-Ying Shen 22CS24002 (IBSC, barcode no. 1003856, KUN, barcode nos. 1584167 & 1584168); 27°9'46.08"N, 98°46'39.98"E, 2544 m a.s.l., 27 October 2022 (fr.), Yong-Jie Guo, Zhou-Dong Han & Xiu-Ying Shen 22CS24003 (IBSC, barcode no. 1003856, KUN, barcode nos. 1584167 & 1584168); 27°9'46.08"N, 98°46'39.98"E, 2544 m a.s.l., 27 October 2022 (fr.), Yong-Jie Guo, Zhou-Dong Han & Xiu-Ying Shen 22CS24003 (IBSC, barcode no. 1003855, KUN, barcode no. 1584169); 27°9'39.6"N, 98°46'56.06"E, 2444 m a.s.l., 10 March 2023, Yi-Hua Tong, Jing-Bo Ni, Bing-Mou Wang & Wei-Hao Pan TYH-2637 (IBSC).

Examined specimens of Vaccinium brachyandrum. CHINA. Yunnan Province: Tengchong, Houqiao, 2720 m a.s.l., 18 May 1964, *Su Kung Wu* 6629 (holotype KUN1209465, isotype KUN1209466); ibid., 25°24'16.700"N, 98°8'43.869"E, 2564 m a.s.l., 22 August 2022, Yong-Jie Guo & Zhong-Lan Yang 22CS22523 (IBSC, KUN); Lushui, Pianma, Fengxueyakou, 25°59'12.779"N, 98°40'3.828"E, 2691 m a.s.l., 23 May 2022, *Ting Zhang, Ji-Dong Ya & Wei Zhang 22CS21913* (IBSC, KUN); ibid., 25°59'12.72"N, 98°40'3.9"E, 2705 m a.s.l., 28 October 2022, *Yong-Jie Guo & Zhou-Dong Han 22CS22599* (IBSC, KUN); ibid., 25°59'0.76"N, 98°40'5.03"E, 2782 m a.s.l., 11 March 2023, *Yi-Hua Tong, Jing-Bo Ni, Bing-Mou Wang & Wei-Hao Pan TYH-2643* (IBSC) & TYH-2644 (IBSC).

Discussion

In the key to Vaccinium in "Flora of China" (Fang and Stevens 2005), V. usneoides is keyed out to be close to V. arbutoides C. B. Clarke and V. brachvandrum (item 47). However, we found that the description of V. arbutoides in "Flora of China" is inconsistent with that in the protologue (although the description made by Clarke (1881-1882) is brief) on some important characters, such as the length of petiole (6-9 mm in "Flora of China" vs. 3.2-5.1 mm in the protologue, the same order for the following comparison), inflorescence (1.5-3 cm vs, 6.35 cm), pedicel (1-3 mm vs. 4.2 mm) and calyx lobe (ca. 2.5 mm vs. 3.2 mm), which made us suspect that the Chinese material of this species (the only one collection, Tse-Tsun Yu 20963 (SZ) from Gongshan County, Yunnan Province) may be misidentified. However, due to incomplete information on floral morphology of the type collection (Griffith 3469 (K) from northeast India) and the Chinese material, the relationship between these two collections remains uncertain, whether they belong to the same species or not needs further study. Nonetheless, compared to the large leaf blades (ca. 12.7 × 6.35 cm) of V. arbutoides (Clarke 1881-1882), the leaf blades of V. usneoides are so much smaller (2.5-5.5 × 0.9–1.8 cm) that they can hardly be recognised as conspecifics.

According to Vander Kloet and Dickinson's infrageneric classification of *Vaccinium*, *V. usneoides* fits well with the circumscription of *V.* sect. *Calcicolus* Kloet, which is characterised by an evergreen habit, dimorphic perennating buds (i.e. floral perennating buds at least twice the size of vegetative perennating buds), racemose inflorescences with large caducous bracts, pseudo-10-locular ovary, berry with 2–5 seeds per locule and soft seed testa (Vander Kloet and Dickinson 2005, 2009). This new species usually grows on large trees (e.g. *Acer campbellii* Hook. f. & Thomson ex Hiern, *Quercus saravanensis* A. Camus etc.) trunks covered with mosses, orchids, ferns and some other ericaceous species like *Agapetes pensilis* Airy Shaw, *Vaccinium leucobotrys* (Nutt. ex Hook.) G. Nicholson and *V. dendrocharis* Hand.-Mazz.

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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

YJG: Investigation; Writing manuscript. TZ: Investigation; Funding acquisition. JDY, WZ, XYS, ZDH, JBN, JYS: Investigation. YHT: Investigation; Writing manuscript; Supervision; Funding acquisition.

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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

Distribution and morphology of the diatom genus *Olifantiella* Riaux-Gobin & Compère in Indonesian and Australian waters, including the description of *O. gondwanensis* sp. nov.

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Abstract

Samples from coastal tropical waters of Central Sulawesi, Bangka Island and Bawean Island in Indonesia and from the Great Barrier Reef at Fitzroy Island in Queensland, Australia were analysed for species composition of diatom assemblages with a focus on *Olifantiella*. Whereas samples from Fitzroy Island littoral in Australia retrieved only one species of *Olifantiella*, in Poso Bay, Indonesia, we observed at least six species. All established taxa were documented with light (LM) and scanning electron microscope (SEM) and principal component analysis (PCA) analysis was used to compare the species, based on the basic valve parameters of length, width, length to width ratio and striae density. A new species of the genus *Olifantiella*, *O. gondwanensis* is described from Australia. In addition, we showed the distinct nature of *O. pilosella* var. *rhizophorae* permitting to species status. Particular attention is placed on girdle bands in this genus.

Key words: Bacillariophyta, buciniportula, Diadesmidaceae, marine coasts, new combination, new species, taxonomy

Introduction

Olifantiella Riaux-Gobin and Compère is a relatively recently described diatom genus consisting mainly of small, marine naviculoid diatoms (Riaux-Gobin and Compère 2009). To date, 12 taxa have been described within the genus, 11 at the species rank (Riaux-Gobin and Compère 2009; Riaux-Gobin and Al-Handal 2012; Van de Vijver et al. 2016; Kaleli et al. 2018; Van de Vijver et al. 2018; Jung and Park 2019; Wetzel and Ector 2020) and one variety (Riaux-Gobin 2015). The major characters of the genus are marginal elevated ridge, parallel to slightly radiate striae, composed of single transapically elongated macroareola with fine-

ly perforated hymenate occlusions which are not interrupted under the elevated ridge, simple raphe slit, several girdle bands and presence of a trumpet-like ('olifant') internal tubular process called buciniportula after which the genus is named (Riaux-Gobin and Al-Handal 2012). The exact function of the buciniportula is still unclear, but probably may have a function in excretion of metabolites (Riaux-Gobin 2015). Due to the small size of the cells and the mainly very dense striation, the identification of individual *Olifantiella* taxa is currently only possible using SEM. In addition, due to only single molecular sequences being available, genetic sequencing does not allow identification of most known taxa.

The genus Olifantiella exhibits high morphological similarity to other genera that possess a central isolated process, such as Labellicula Van De Vijver and Lange-Bertalot, Luticola D.G. Mann and Luticolopsis Levkov, Metzeltin & Pavlov. Olifantiella can be discriminated from Labellicula, based on differences in isolated pores (Riaux-Gobin and Compère 2009). Furthermore, both genera differ in the presence of a longitudinal channel in Olifantiella, but which is absent in Labellicula (Majewska et al. 2017). Additionally, the genus Olifantiella shows a small, heavily silicified nodule, placed between the proximal raphe endings (similar to Neidium Pfitzer), but which is absent in Labellicula. Moreover, the genus Labellicula shows curved T-shaped grooves on distal raphe endings, while in Olifantiella, the distal raphe endings are simple or only curved on one side. In contrast to Olifantiella, the monotypic genus Luticolopsis shows strongly apically twisted valves and striae composed of two rows of areolae (Levkov et al. 2013). The genus Luticola differs from Olifantiella mainly by its larger size, punctate striae and less tubular internal opening of the isolated process (Levkov et al. 2013). Luticola is also different in its ecological preferences, as the genus contains mainly freshwater and terrestrial species with only few taxa known from marine habitats (Levkov et al. 2013; Rybak et al. 2021). Han et al. (2018), based on molecular data of a Chinese O. muscatinei culture (strain DB21-1), confirmed that Olifantiella and Luticola are not only similar, but also closely related genera. Unfortunately, molecular data for Labellicula and Luticolopsis are currently not available and, hence, the degree of their evolutionary relationship with Olifantiella and Luticola remains unclear.

The genus seems to occur in various climatic zones of the world ocean, including temperate waters of the North Atlantic, South Atlantic and North West Pacific (Van de Vijver et al. 2016; Kaleli et al. 2018; Jung and Park 2019). However, most species have been described from the tropical Indian and Pacific Oceans. The first *Olifantiella* species was formally described from coral sands of Mascarenes in the Western Indian Ocean (Riaux-Gobin 2015), but retrospectively, it was realised that the first documented *Olifantiella* originated from the Gulf of Eilat in the Red Sea and originally characterised as *Navicula muscatinei* Reimer and Lee = *Olifantiella muscatinei* (syn. *O. pseudobiremis* Riaux-Gobin) present as an endosymbiont from the foraminiferan *Amphistegina lessonii* (Reimer and Lee 1988). Interestingly, *O. muscatinei* has also been isolated from foraminiferans of the Great Barrier Reef within which Fitzroy Island, the type habitat of our newly-described *Olifantiella* species, is located. A few *Olifantiella* species have been described from the tropical South Pacific (Riaux-Gobin 2015).

During our recent studies of the coastal diatom floras of Australia and Indonesia, a large number of *Olifantiella* were observed. Amongst them, an unknown species was recorded necessitating its description as a new species – *O. gondwanensis* M.Rybak, A.Witkowski & C.Riaux-Gobin, sp. nov. Additionally, updated information about the distribution and morphology of established taxa are given.

Methods

Diatom samples were cleaned with 10% hydrochloric acid and washed thereafter with deionised water, followed by boiling with 30% hydrogen peroxide (H_2O_2) for a few hours and washed with deionised water. Cleaned diatom material was pipetted on to coverslips and dried and then mounted on glass slides using Naphrax mounting medium (Brunel Microscopes Ltd, Wiltshire, U.K.). Identification, counting and the measurements of diatom basic morphological features were performed under a Nikon ECLIPSE 80i light microscope (LM), equipped with a 100× Planapochromatic objective with differential interference contrast (DIC) for oil immersion (NA 1.4) and captured with a Nikon DS-Fi1c camera. For the observations in scanning electron microscope, the samples were applied to a polycarbonate membrane filter with a 3 μ m mesh, attached to aluminium stubs and sputtered with 20 nm of gold using a turbo-pumped Quorum Q 150T ES coater. Diatoms were observed using a Hitachi SU 8010 SEM at University of Rzeszów, Poland. Diatom terminology follows Round et al. (1990) and Riaux-Gobin and Compère (2009).

The following samples were used in the present work:

- SZCZ 27565 Bangka Island near the SE coast of Sumatra, 2°4'52.55"S, 105°8'14.65"E, 22 June 2022, sandy sediment.
- SZCZ 27652 Bawean Island, North of Surabaya in the Central Sea of Java, 5°50'57.5"S, 112°43'3.6"E, 07 January 2021, the sample was taken from mangrove roots, temperature – 29 °C, salinity – 31‰.
- SZCZ 28814 Indonesia, Sulawesi, Poso Regency, Tanjung Perak, 1°18'2.974"S, 120°37'37.009"E, 29 September 2022, the sample was collected during low tide as a scrape from exposed rock (depth ± 10–20 cm), temperature approximately above 30 °C, salinity – 28.5‰, pH – 7.76.
- SZCZ 28526 Fitzroy Island, Australia, 16°55'38"S, 149°59'24"E, 15 August 2022, the sample was taken from green algae *Chlorodesmis* sp. exposed on the Great Barrier Reef during the low tide.

To determine the similarity and/or dissimilarity of newly-described species (based on basic morphological features: length, width, length-to-width ratio and number of striae) with other members of the genus, Principal Component Analysis (PCA) was performed using Canoco 5.03 software (Ter Braak and Šmilauer 2012). Prior to analysis, diatom data were square-root transformed. Comparison was made, based on data from current observations and from the following publications: Riaux-Gobin and Compère (2009); Riaux-Gobin and Al-Handal (2012); Riaux-Gobin (2015); Kaleli et al. (2018) and Riaux-Gobin et al. (2019). Data for the following number of specimens were used for the analysis: *O. gondwanensis* sp. nov. (n = 42), *O. gorandiana* (n = 94), *O. infirmitata* (n = 7), *O. mascarenica* (n = 21), *O. muscatinei* (n = 15), *O. cf. muscatinei* (n = 25), *O. onnuria* (n = 7), *O. paucistriata* (n = 5), *O. pilosella* (n = 46), *O. rhizophorae* stat. nov.



Figure 1. Locality of the sampling sites 1 Bangka Island 2 Bawean Island 3 Poso Pesisir, Sulawesi Island 3a, b view of the sampling site, photo. S. Arsad 4 type locality of *Olifantiella gondwanensis* sp. nov. in Fitzroy Island, Queensland, Australia 4a view of the type locality 4b green algae *Chlorodesmis* sp. from which sample was taken, photo. A. Witkowski.

(n = 27), *O. rodriguensis* (n = 22), *O. seblae* (n = 33), *O. societatis* (n = 32) and *O. visurgis* (n = 26). In the case of *Olifantiella onnuria*, data obtained from photographs included in their original description were used (Jung and Park 2019).

Results

Description of new species

Class: Bacillariophyceae Haeckel, 1878 Subclass: Bacillariophycidae D.G.Mann in Round et al. (1990) Order: Naviculales Bessey, 1907 Suborder: Neidiineae D.G.Mann in Round et al. (1990) Family: Diadesmidaceae D.G.Mann in Round et al. (1990) Genus: *Olifantiella* Riaux-Gobin & Compère

Olifantiella gondwanensis M.Rybak, A.Witkowski & C.Riaux-Gobin, sp. nov. Fig. 2A-X

LM. Valves small, elliptic to linear-lanceolate with broadly rounded apices, $6.3-13.7 \mu m$ long and $2.7-3.4 \mu m$ in width. Striae barely resolvable with LM, 26-31 in 10 μm , an isolated pore (buciniportula) visible near the central area.



Figure 2. Holotype population of *Olifantiella gondwanensis* sp. nov. from Fitzroy Island A-P valves in size diminution series viewed by light microscopy Q-X SEM micrographs Q, R external view of the valve, white arrowhead indicates the girdle band S opened frustule T details of valve central part in external view U detail of valve apex in internal view V internal view of valve W details of valve central part in internal view X detail of valve apex in internal view. = indicates a valves of the same specimen. Scale bars: 10 µm (A-P); 5 µm (Q, R); 4 µm (S); 3 µm (V); 1 µm (T, U, W, X).

SEM. Striae composed of macroareolae, equidistant, with finely perforated hymen. At the junction of the valve face and the mantle, a ridge runs over the striae and opens to the exterior by round to oblong fenestrae, bordered by long thin spines – pili. Near the buciniportula, 1–2 shortened striae are present. Buciniportula located on opposite side of valves. Macroareolae on mantle the same as on valve and possessing long thin spines. Apical slits are few and small-sized without spines in their lumen. External raphe slits are straight and filiform.

Table 1. Compariso	n of Olifantiella gondwa	inensis sp. nov. with mos	t similar <i>Olifantiell</i>	a taxa based on valve m	lorphology.		
	0. gondwanensis sp. nov.	0. gorandiana	0. 1	nuscatinei	0. pilosella	0. rhizophorae stat. nov.	0. paucistriata
shape	linear-lanceolate	elliptical, slightly elongated apices	elliptic-lanceolate	variable, depending on size, linear-lanceolate, lanceolate or elliptic-lanceolate	elliptical to oblong-elliptical, slightly elongate apices	elliptical with slightly acuminate apices	naviculoid
length (µm)	6.3-13.7	4.0-9.0	2.5-6.0	3.6-11.7	7.4–11	5.4-7.8	6.0-8.0
width (µm)	2.7-3.4	0.7-3.0	2.0-2.5	1.3-3.4	1.8–3	1.4–2.3	1.8-2.0
striae (in 10 μm)	26-31	52-70	28-30	37-52	30-41	40-47	31–37
macroareolae structure	occluded by finely perforated hymen, bordered by long thin spines	occluded by finely perforated hymen	no data	occluded by finely perforated hymen	occluded by finely perforated hymen, bordered by long thin spines	occluded by finely perforated hymen	occluded by finely perforated hymen
external process opening	Round to elliptical, deeply depressed	trapezoidal, deeper split into four sectors, close to margin	no data	single foramen-like opening	tear-like, in mid-stria	round, near the margin	round, small-sized, close to central area
external central raphe endings	expanded and deflected to the external opening of buciniportula	inflated, slightly deflected away from process opening	no data	expanded and deflected away from the external opening of buciniportula	slightly inflated, deflected away from the foramen	deflected away from foramen	slightly inflated, not deflected
external terminal raphe endings	strongly deflected to buciniportula opening side	simple, straight	no data	expanded and in the same direction as central raphe endings	simple, deflected opposite foramen	simple, deflected opposite to foramen	simple, slightly deflected opposite foramen
buciniportula	double, slightly raised, closed	multiple, flattened, (not erected), with two satellites	no data	double, each covered by finely perforated, domed thickening	double, raised, closed	double, raised, closed	no data
modified or shortened striae	7	4	no data	2–3	-	-	2
Type locality	Australia, Fitzroy Island	Western Indian Ocean (Rodrigues Island)	Gulf of Eilat (Israel)		Western Indian Ocean (Rodrigues Island)	Moorea Island (South Pacific)	Western Indian Ocean (Rodrigues Island)
source	this study	Riaux-Gobin and Al-Handal 2012; Riaux-Gobin et al. 2019	Reimer and Lee 1988	Riaux-Gobin and Al-Handal 2012; Jung and Park 2019	Riaux-Gobin and Al-Handal 2012; Riaux-Gobin 2015	Riaux-Gobin 2015	Riaux-Gobin and Al- Handal 2012

External proximal raphe endings slightly bent towards buciniportula bearing side, terminal raphe endings strongly hooked to the same side. Buciniportula opening sunken in the valve face connected with central raphe endings by small grooves. Small silica warts present externally along the raphe slits. Girdle bands numerous without ornamentation. Internally proximal raphe endings simple, terminal raphe endings forming small helictoglossae. Small siliceous warts present near the proximal raphe endings. Internally double buciniportula, slightly raised and closed. Longitudinal channels visible internally along the valve margin.

Type locality. Fitzroy Island, the Great Barrier Reef, Queensland, NE Australia, 16°55'38"S ,149°59'24"E (Fig. 1).

Type material. *Holotype*: Slide SZCZ 28526 and unmounted material with the same number in the collection of Andrzej Witkowski at the University of Szczecin. Holotype population is depicted in Fig. 2A–X.

Isotype: Slide number 2022/64 at the Diatom Collection at the University of Rzeszów.

Etymology. The species epithet is derived from Gondwana, a super continent of which Australia was part of during the Paleozoic and Mesozoic Era.

Distribution. So far observed only from the Australian type locality.

Morphological characteristics of observed taxa

Olifantiella gorandiana C.Riaux-Gobin

Fig. 3A-F

Description. Valves elliptic to lanceolate with rounded to sub-rostrate apices, $4.8-6.8 \mu m \log$, $1.5-2.3 \mu m$ wide and with 58-67 striae in 10 μm . Buciniportula complex, internally with two short not raised tubular strctures flanked by two small satelites, external opening shifted near the valve margin. Buciniportula on both valves located on the same side of the frustule. Externally proximal raphe endings straight and slightly tear-drop-shaped, distal raphe endings with small, hooked grooves on site opposite to buciniportula. Internally proximal raphe endings rounded, distal raphe endings with small helictoglossa. Two types of girdle bands are present. The first one, wide with two rows of perforations (120–133 perforations in 10 μm) and second, thin without any perforations. Internally, this species shows a lack of longitudinal channel.

Distribution. Newly observed from coastal waters of Sulawesi Island (sample SZCZ 28814). Originally reported from Rodrigues Island and also observed in French Polynesia, Western Indian Ocean (Riaux-Gobin 2015; Riaux-Gobin et al. 2019), Galapagos Island and West Coast of United States (Witkowski – unpublished data).

Comments. All observed specimens represent the morphotype 'b' following Riaux-Gobin et al. (2019).

Olifantiella mascarenica C.Riaux-Gobin & Compère Fig. 4G–J

Description. Valves linear with capitate apices, 6.4–11.8 μ m in length, 2.0–2.3 μ m in width and with 41–55 striae in 10 μ m. Buciniportula complex,



Figure 3. SEM documentation of *Olifantiella gorandiana* from Sulawesi Island coast (sample SZCZ 28526). Scale bars: 3 μm (**B**, **D**); 2 μm (**A**, **E**, **F**); 1 μm (**C**).

internally with a single raised tubular process. A single shortened stria is present near the valve margin on the side of the buciniportula. Apical slits narrower than macroareola. Girdle bands with two rows of perforations (ca. 110 pores in 10 μ m). Externally proximal raphe endings straight and tear-drop-shaped, distal raphe endings slightly bent towards buciniportula site. Narrow longitudinal channels visible internally along the valve margin.

Distribution. Newly observed from coastal waters of Sulawesi and Bawean Islands (samples SZCZ 28814 and SZCZ 27652). Originally reported from Rodrigues Island, also observed in Moorea Island (Riaux-Gobin 2015) and coast of Turkey (Kaleli 2022).

Olifantiella paucistriata C.Riaux-Gobin Fig. 5A

Description. Valves small, elliptic with rounded apices, 6.1 μ m in length, 2.7 μ m in width and 31 striae in 10 μ m. Striae composed of macroareolae, equidistant, with finely perforated hymen. External buciniportula opening sunken in

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Figure 4. SEM documentation of *Olifantiella rodriguensis* (**A**–**F**) and *Olifantiella mascarenica* (**G**–**J**) **B**–**J** population from Sulawesi Island coast (sample SZCZ 28814) **A** specimen from Bangka Island (sample SZCZ 27565). Scale bars: 3 μm (**E**); 2 μm (**A**–**D**, **H**); 1 μm (**E**, **F**, I, J).

the valve face connected with central raphe endings by small grooves. On the buciniportula-bearing side, 1–2 shortened striae are present. External proximal raphe endings straight with small grooves, terminal raphe endings strongly hooked towards buciniportula side.



Figure 5. SEM documentation of *Olifantiella paucistriata* (**A**) and *Olifantiella pilosella* (**B**–**F**) from from Sulawesi Island coast (sample SZCZ 28814). Scale bars: 3 μm (**A**–**D**); 2 μm (**E**); 1 μm (**F**).

Distribution. Newly observed from coastal waters of Sulawesi Island (sample SZCZ 28814). Originally reported from Rodrigues Island (Riaux-Gobin and Al-Handal 2012).

Olifantiella pilosella C.Riaux-Gobin Fig. 5B-F

Description. Valves elliptic to linear-elliptic with rounded apices, $5.4-8.2 \mu m$ in length, $2.3-2.8 \mu m$ in width and with 38-43 striae in 10 μm . Macroareolae, both on valve face and valve mantle bordered by thin siliceous spines (pili) and small siliceous plates (flabella). Between buciniportula opening and valve margin, one shortened stria is present. Apical slits small, without silica projections. Buciniportula complex, internally with two short raised tubular processes. Externally, both proximal and distal raphe endings are tear-drop-shaped and slightly bent opposite to the buciniportula opening with elongate grooves on buciniportula site. Internally raphe endings are straight and simple, forming small helictoglossae at distal endings. Girdle bands numerous with barely visible perforations. Internally, small silica warts between proximal raphe endings are present. Broad longitudinal channels visible internally along the valve margin.

Distribution. Newly observed from coastal waters of Sulawesi Island (sample SZCZ 28814). Originally described from Rodrigues Island and afterwards observed in Moorea Island (Riaux-Gobin and Al-Handal 2012; Riaux-Gobin 2015). Additionally observed in Mariana Islands, Guam (Lobban et al. 2012).

Olifantiella rodriguensis C.Riaux-Gobin Fig. 4A-F

Description. Valves linear with capitate apices, $9.0-12.8 \mu m$ in length, $2.0-2.3 \mu m$ in width and with 41-43 striae in $10 \mu m$. Buciniportula complex, internally with two short raised tubular processes. Two shortened striae are present near the valve margin on the side of the buciniportula. Apical slits narrower than macroareola. Girdle bands with two rows of perforations (ca. 100 perforations in $10 \mu m$). Externally proximal raphe endings straight and tear-drop-shaped, distal raphe endings slightly bent towards buciniportula location. Broad longitudinal channels visible internally along the valve margin.

Distribution. Newly observed from coastal waters of Sulawesi and Bangka Island (samples SZCZ 28814 and SZCZ 27565). Originally reported from Rodrigues Island and later observed from Galapagos Islands (Riaux-Gobin and Al-Handal 2012; Riaux-Gobin 2015; Witkowski et al. – unpublished data).

Olifantiella societatis C.Riaux-Gobin

Fig. 6A-F

Description. Valves elliptic to linear-elliptic with rounded apices, $3.9-10.3 \mu m$ in length, $2.2-2.8 \mu m$ in width and with 31-34 striae in 10 μm . Macroareolae are present at valve face and valve mantle. External buciniportula opening elongate, internally in form of singular tubular process, with a "*Nepenthes*-like" plug (Fig. 6F) as in *O. mascarenica* (Riaux-Gobin and Compère 2009; Riaux-Gobin and Al-Handal 2012). A short macroareola (not observed in *O. societatis* type) is present at the prolongation of the buciniportula aperture. At the junction of the valve face and the mantle, a ridge runs over the striae and opens to the exterior by round to oblong fenestrae. Externally, both proximal and distal raphe endings are straight and tear-drop-shaped. Internally raphe endings are straight and simple, forming small helictoglossae at distal endings. Small silica warts are present externally along raphe slits. Internally two broad longitudinal channels and small silica warts between proximal raphe endings are present.

Distribution. Newly observed from the coast of Sulawesi Island (sample SZCZ 28814), Bangka Island (SZCZ 27565) and Bawean Island (SZCZ 27652). Originally reported from Moorea Island (Riaux-Gobin 2015).

Comparison of basic morphological characters of known taxa

Principal component analysis (PCA) revealed considerable variability in the morphological characters of the *Olifantiella* species considered. The gradient length in analysis was 0.4. The first ordination axis eigenvalue was 0.95 and the second 0.04 (Fig. 6). The newly-described species clearly distinguished itself



Figure 6. SEM documentation of *Olifantiella societatis* from Sulawesi Island coast (sample SZCZ 28814). Scale bars: 5 μm (**A**); 4 μm (**D**); 3 μm (**B**, **C**, **E**); 1 μm (**F**).

from the others. Additionally, based on the results of the PCA analysis showing the separation of the *O. pilosella* group from the group of its variety, we propose the following taxonomic change:

Olifantiella rhizophorae (C.Riaux-Gobin) M.Rybak, A.Witkowski & C.Riaux-Gobin, stat. nov.

Olifantiella pilosella var. *rhizophorae* C.Riaux-Gobin 2015: Botanica Marina 58(4): 255–258, figs 9–16. Basionym.

Discussion

Despite its small size and more than a dozen of species discriminated, the genus *Olifantiella* presents great morphological diversity. This manifests itself in the shape of the valves, the number and structure of the internal buciniportula openings, the structure of the areolae and in the details of the distal and proximal raphe endings.

Amongst known *Olifantiella* taxa, the newly-described *O. gondwanensis* sp. nov. is characterised by the lowest striae density (Fig. 7), which makes it the only species that can be easily identified using light microscopy. The greatest



Figure 7. PCA ordination of all currently known *Olifantiella* taxa, based on their basic morphological features L length W width L/W length/width ratio S stria density **nov** *O. gondwanensis* sp. nov. **rhi** *O. rhizophorae* stat. nov. **vis** *O. visurgis* **gor** *O. gorandiana* **mas** *O. mascarenica* **cfm** *O.* cf. mascarenica **inf** *O. infirmitata* **seb** *O. seblae* **pil** *O. pilosella* **rod** *O. ro-driguensis* **soc** *O. societatis* **pau** *O. paucistriata* **mus** *O. muscatinei* **onn** *O. onnuria.*

similarity to the newly-described species is shown by *O. pilosella*, *O. rhizophorae*, *O. paucistriata*, *O. gorandiana* and *O. muscatinei* (Reimer and J.J.Lee) Van de Vijver, Ector and C.E.Wetzel. Interestingly, *O. muscatinei* has also been isolated from foraminiferans of the Great Barrier Reef within which Fitzroy Island, the type habitat of our newly-described *Olifantiella* species, is located.

Olifantiella pilosella like the newly-described species, has areolae bearing long thin spines (pili), but in contrast to *O. gondwanensis* sp. nov., it has additional siliceous plates (flabella) in the areolae lumen (Riaux-Gobin and Al-Handal 2012; Riaux-Gobin 2015) which are absent in our newly-described species (Fig. 2Q–U). Additionally, both species can be separated, based on the external opening of the buciniportulae, which are positioned midway between the valve centre and valve margin in *O. pilosella*, but positioned in a small depression close to the proximal raphe endings in *O. gondwanensis* sp. nov. Internal views also show that *O. pilosella* possesses wider longitudinal channels when compared to the whole valve than *O. gondwanensis* sp. nov. (Fig. 2V–X vs. Fig. 5E, F). Another fea-

ture that allows the two species to be distinguished is the more elliptical shape of the vales in the newly-described species when compared to *O. pilosella*.

In addition, due to the elliptical shape of the valves, it is possible to distinguish *O. gondwanensis* sp. nov from the similar *O. rhizophorae* stat. nov. The latter species is also characterised by the simpler structure of areolae that show only short warts on the margin, instead of long and thin pili. Moreover, the external opening of buciniportula is shifted near the valve margin in *O. rhizophorae* stat. nov. (Riaux-Gobin 2015), but not positioned almost in the valve centre like in *O. gondwanensis* sp. nov. Additionally, *O. rhizophorae* stat. nov. possesses simpler raphe branches, which have both proximal and distal endings gently bent to the side opposite to the buciniportula (Riaux-Gobin 2015). This feature distinguishes this species from both *O. gondwanensis* sp. nov. and *O. pilosella* which have shallow depressions at both raphe endings (Riaux-Gobin and Al-Handal 2012; Riaux-Gobin 2015, Fig. 5B–D)

Olifantiella paucistriata is the least known member of the genus, with fewer than 10 individuals of this species documented so far (Riaux-Gobin and Al-Handal 2012). Despite that fact and despite the similar shape of the valve to *O. gondwanensis* sp. nov., both species can be easily discriminated. The main distinguishing characters are the striae density (higher in *O. paucistriata*, see Table 1) and presence of the pili in the areolae lumen in *O. gondwanensis* sp. nov. However, similar structures of the raphe, location of the external opening of the buciniportula near the valve centre and the presence of small warts in the areolae lumen in *O. paucistriata* indicate its close relationship to *O. gondwanensis* sp. nov. This requires further research supported by better documentation for the first of these species.

Olifantiella muscatinei (syn. *O. pseudobiremis* Riaux-Gobin) not only has a valve similar in shape to the newly-described species, but also overlapping size dimensions including length, width and striae density (see Table 1). Nevertheless, the distinction of both species is possible on the basis of morphological features of its valves and girdle bands. *O. muscatinei* is the only known member of the genus showing well-developed external perforated areola occlusions, both on the valve face and vale mantle (Riaux-Gobin and Al-Handal 2012; Jung and Park 2019). Additionally, the external opening of the buciniportula is shifted more towards the edge of the valve than with *O. gondwanensis* sp. nov. An additional difference between the two species is their girdle bands. They are hyaline in *O. gondwanensis* sp. nov. (Fig. 1R, S), while *O. pseudobiremis* has girdle bands with double rows of pores (Riaux-Gobin and Al-Handal 2012; Jung and Park 2019).

Of the five described morphotypes of *O. gorandiana* (Riaux-Gobin et al. 2019), the greatest similarity to *O. gondwanensis* sp. nov. is shown by the morphotypes 'a' and 'b'. However, based on morphological characterss of the valves, both species are easily separated. Regardless of the morphotype, *O. gorandiana* has definitely denser striae (see Table 1), composed of simple areolae without any silica projections (Fig. 3A–D; Riaux-Gobin and Al-Handal 2012; Riaux-Gobin et al. 2019). In addition, the external opening of the buciniportula is strongly shifted to the edge of the valve face in *O. gorandiana* and not centrally positioned like in the case of *O. gondwanensis* sp. nov.

Olifantiella gorandiana is the only species in the genus within which several morphotypes have been distinguished, based on the shape of the valves. Based

on the observation of a population developing epizoic on sea turtle (Chelonia mydas Linnaeus, 1758), five morphotypes have been distinguished (Riaux-Gobin et al. 2019). In the population documented in this work, all observed individuals represented the 'b' morphotype. However, the observed population showed a polymorphism in the construction of girdle bands. Most of them showed two rows of puncta (Fig. 3B-D), while some specimens also possessed plain girdle bands without any pores (Fig. 3C). The presence of two different types of girdle bands in a single species, even in single specimens, has not been observed so far in the genus Olifantiella. Most species within the genus have girdle bands with clearly visible two rows of pores, which were originally considered to be a characteristic feature of the genus (Riaux-Gobin and Compère 2009). However, later described species showed some plasticity in this character. For example, the here-described O. gondwanensis sp. nov. and O. rhizophorae stat. nov. have girdle bands without pores (Fig. 2R, S; Riaux-Gobin 2015). Additionally, O. pilosella also shows girdle bands which are not typically with two rows of areolae, but possess small and poorly visible pores (Fig. 4C). It seems that the morphology of the girdle bands is not a good criterion for defining members of this genus.

Studies focusing on *Olifantiella* have been conducted in Mascarenes (La Réunion, Rodrigues), Tahiti and Moorea Islands and coastal waters of the Mediterranean, Red, Baltic and North Seas. Until now, the occurrence of this genus has not been observed in the coastal waters of south-east Asia as well as in Australia, except the Great Barrier Reef area. Despite the great morphological diversity of representatives of the genus *Olifantiella*, only a few species are known, which may be due to their small size and, thus, difficulties in their observation and even detection in the studied materials. Future studies of coastal waters may result in descriptions of further members of this elusive genus. Additionally, further research (including molecular methods) is required to determine the relationships within the genus and with the other isolated pore-bearing members of family Diadesmidaceae, especially with the morphologically similar genus *Labellicula*.

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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

Mateusz Rybak: collecting data, preparing manuscript; Sulastri Arsad: field work, collecting data; Catherine Riaux-Gobin: collecting data, manuscript verification; Oktiyas Muzaki Luthfi: field work, collecting data; Gustaaf Hallegraeff: field work, manuscript verification Renata Ciaś: field work; Agnieszka Kierzek: field work; Andrzej Witkowski: field work, collecting data, preparing manuscript, manuscript verification.

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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 History and introduction of the Daurian Lily Lilium pensylvanicum and the new combination L. pensylvanicum var. alpinum (Liliaceae)

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Abstract

Manuscripts in the Archives of the Academy of Sciences in St. Petersburg reveal the first recorded observations and introductions of *Lilium pensylvanicum* Ker-Gawl. from Siberia to European Russia. The naming of *Lilium pensylvanicum* and its attempted renaming to *L. dauricum* Ker-Gawl. is fully outlined. Lectotypes are designated here for the names *Lilium pseudodahuricum* M.Fedoss. & S.Fedoss., *L. dauricum* var. *alpinum* N.I.Kuznetsov and *L. pensylvanicum* f. *praecox* Vrishcz. The new combination *L. pensylvanicum* var. *alpinum* (N.I.Kuznetsov) J.Compton & Sytin is made and a key is provided to the varieties of *L. pensylvanicum*.

Key words: Amman, Catesby, Collinson, Demidov, Dillwyn, Gmelin, Heydenreich, Ker Gawler, *Lilium dauricum*, *Lilium pensylvanicum* var. *alpinum*, Messerschmidt, nomenclature, Steller, typification

Introduction

Species of the genus *Lilium* L. with scattered leaves, upright-facing, cup or bowl-shaped flowers and tepals that narrow to a basal claw are found in North America, Europe and east Asia. *Lilium catesbaei* Walter and *L. philadelphicum* L., the only two North American species with that morphology, are endemic to that continent. *Lilium bulbiferum* L. is European and *L. concolor* Salisb., *L. pen-sylvanicum* Ker-Gawl. and *L. maculatum* Thunb. occur across east Asia and Japan. The first of the upright, bowl-flowered, Asian species of *Lilium* to be introduced to western Europe was almost certainly *L. pensylvanicum*, described with a pre-Linnaean phrase name by Johann Georg Gmelin (1709–1755) from Siberia. Gmelin cited a paper by the Prussian physician, chemist and mineral-ogist Johann Friedrich Henckel (1678–1744) discussing a collection of the lily by the metallurgist Johann Gottfried Heydenreich. This species was collected by Heydenreich from Siberia in the late 1720s and introduced into what was then Saxony shortly thereafter (Henckel 1733: 354; Gmelin 1747: 41).



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Due to their morphological similarities, all the above-mentioned Lilium species have been considered to be closely related (e.g. Baker (1871); Wallace (1873)). Phylogenetic analyses of molecular sequence data from nuclear DNA ITS, however, (e.g. Du et al. (2014); Huang et al. (2018); Givnish et al. (2020)), as well as from both cpDNA and nuclear DNA (Watanabe et al. 2021), have shown that the two North American species L. catesbaei and L. philadelphicum are more distantly related to the others and belong in Lilium sect. Pseudolirium (Endl.) Spach (Spach 1846: 277) typified on L. catesbaei (Wilson 1925: 50), whereas L. bulbiferum, L. concolor, L. maculatum and L. pensylvanicum all belong in sect. Sinomartagon H.F.Comber typified on L. davidii Duch. (Comber 1949: 101). Lilium concolor, known as the morning star lily, has terete, glabrous stems, rather than ribbed or papillose-scarious stems in L. bulbiferum, L. maculatum and L. pensylvanicum, the flowers are stellate in appearance as opposed to bowl-shaped and the tepals are shorter, ca. 3-4 cm as opposed to 5-9 cm long in the other species. Although native in China, Japan, Korea and Russian Far East, L. concolor is not part of the discussion in this paper.

There is no doubt that the closest relative of *L. pensylvanicum* is *L. macula-tum* from Honshu, Japan. This species, is distinguished from *L. pensylvanicum* by its lacking the floccose pubescence on its stems and leaf axils. The stems of *L. maculatum* are instead papillose and scarious and the germination mode is epigeal as opposed to hypogeal (Hayashi 2016: 112). Recent molecular data also confirm the segregation of these species (Watanabe et al. 2021: 192, 193).

The two North American species are distinguished from *L. bulbiferum*, *L. maculatum* and *L. pensylvanicum* by their glabrous stems and leaves and narrower tepals. In *L. catesbaei*, these are 1.2–1.9 cm wide (Skinner 2003: 179), whereas in *L. philadelphicum*, they are 2–3.2 cm wide (Skinner 2003: 180). The American species also have longer claw-like tepal bases which partly enclose the nectar guides near the base of the tepal lamina. *Lilium philadelphicum* frequently has at least one whorl of leaves subtending the inflorescence and characteristically long seed capsules which attain 2.2–7.7 cm in length (Skinner 2003: 180).

The European species *L. bulbiferum* was known to very early writers and was frequently discussed and illustrated in several works across Europe, for example by Dodoens (1553: 237; 1583: 198); L'Obel (1576: 84); Clusius (1583: 139–141) and Caspar Bauhin (1623: 75–76). Bauhin's *Pinax* was much cited by subsequent botanists who usually indicated reference to his work simply by citing his initials. *Lilium bulbiferum* was so named for the production of small bulbils in the leaf axils along the inflorescence axis; however, plants lacking such axillary bulbils were also included within the circumscription of this species (Linnaeus 1753: 302). Those plants which lacked bulbils were later segregated as *L. croceum* Chaix (Villars 1786: 322). These two taxa which are restricted to Europe and have more or less glabrous leaves and stems are undoubtedly closely related to *L. pensylvanicum*, but are not the focus of this paper.

This paper looks closely at the history and nomenclature of *L. pensylvanicum* (see Fig. 1) along with notes on its introduction from Siberia and references to the people who were associated with it. The mistaken belief that its origin was in North America is carefully scrutinised along with its journey from Dauria


Figure 1. Sydenham Edwards illustration of *Lilium pensylvanicum* in Curtis's Botanical Magazine 22 t. 872 (1805).

in east Siberia to the herbaria and gardens of Imperial Russia and thence to England. Literary, archival and illustrated materials were used to track its route from Siberia to northern Europe. The attempt to rename it *L. dauricum* Ker Gawl. (Ker Gawler 1809b) is also fully examined. A proposal to conserve *L. dauricum* against *L. pensylvanicum* by Y-D. Gao in Taxon 70: 1139–1140 (2021), has been rejected (Taxon 72: 908–922 (2023)), meaning that *L. pensylvanicum* is maintained as the correct name for the Daurian lily.

Messerschmidt's Siberia Expedition 1720–1727

The first collector in the Russian service to explore the natural history of Siberia was Daniel Gottlieb Messerschmidt (1685–1735). Originally from Danzig [Gdansk], Messerschmidt, having been introduced to Tsar Peter I of Russia in 1716 by Johann Philipp Breyne, had been asked by him to explore the nature of the great majesty of the Russian Empire. Two years later, he was tasked to collect medicinal and other plants on an expedition that he undertook from 1720 to 1727 across Russia to Siberia (Sytin 2004; Koroloff 2014).

Messerschmidt sent a large box full of seeds and an herbarium back to the Aptekarskiy Ogorod or Apothecary Gardens in St. Petersburg founded by Tsar Peter in 1714 on Aptekarskiy Ostrov [Aptekarsky Island] (Koroloff 2014: 126). This site which now houses the Komarov Botanical Institute, would have been the main botanical collection point for new introductions until the founding of the botanic garden of the Academy of Science in the mid-1730s (Sokoloff et al. 2002: 147). The seeds would have been tended by the director of the garden Johann Christian Buxbaum (1693–1730). Evidence of the lily's cultivation in the garden, however, does not exist, in large part due to a disastrous fire that occurred in the Medical Chancellery in 1737 which destroyed the entire archive of the Apothecary Garden (Koroloff 2014: 138).

While in Siberia, in September 1724, Messerschmidt's expeditionary detachment travelled from Chita to Irkutsk skirting around the southern end of the enormous Lake Baikal. During a severe snowstorm, they lost their bearings and went too far south. They ended up between the Onon and Ulz Rivers in Mongolian China where their arrival was brought to the attention of the local Chinese authorities. Messerschmidt and his retinue had to remain in Selenginsk throughout the winter months until March 1725 when they were able to continue to Udinsk (now Ulan Ude). During that period, Messerschmidt wrote a dictionary of the Mongolian and Tangut language with assistance from several local teachers. In that list, he cited as entry 67b.8 "Ssaranà Lilium purpurocroceum feüer Lilien" with the word Ssaranà also written in Khalkha Mongolian (Sizova et al. 2022: 98). Messerschmidt's citation of Bauhin's "Lilium purpurocroceum" (Bauhin 1623: 77) and the German "feüer lilien", meaning fire lily, both terms often used for the morphologically similar *L. bulbiferum*, indicate that he had already encountered *L. pensylvanicum* in Siberia.

Further evidence of Messerschmidt's finding of the Daurian lily is found in his unpublished journal: "*Pinacis simplicium regnum vegetabile seu plantae medicae*" in which 1290 medicinal and useful plants are included (Messerschmidt 1720–1727). He listed as number 502: *Lilium purpuro-croceum majus* along with a note: "In Russia in exterorum quorundam botanophilon hortis Moscuae. Ejus species minor in Sibiria, in Chatanga, Lena, Angara, Ingoda, Schilka, Argun et Onon fluviorum montanis et apricis, sat abunde" [In Russia, it is found in the Moscow gardens of those who love botany. Its smaller Siberian species is found abundantly in sunny places and in the mountains alongside the rivers Khatanga, Lena, Angara, Ingoda, Shilka, Argun and Onon].

Gmelin and the Great Northern Expedition 1733–1743

Johann Georg Gmelin (1709–1755), born in Tübingen, moved to St. Petersburg in 1727 where he assisted in the Kunstkammer, the first public Museum in Rus-

sia, which had been founded by Tsar Peter I in 1704. Gmelin became an adjunct of the Academia Scientiarum Imperialis Petropolitanae [Imperial St. Petersburg Academy] in 1730 and was employed by the Academy from 1731 as Professor of chemistry and natural history (Sokoloff et al. 2002: 154). The Second Kamchatka Expedition also known as the Great Northern Expedition, one of the largest exploration enterprises in human history, took place from 1733 to 1743 and was instigated under the aegis of Tsarina Anna Ivanovna. The distance covered was phenomenal, from St. Petersburg to Okhotsk on the east coast is more than 3400 miles or 5500 km. Gmelin, as one of three professors sent out by the Academy, led the Natural History deputation, accompanied by his assistant Stepan Petrovich Krascheninnikov (1711–1755). Their mission was to join the Danish sailor in the Russian service, Vitus Jonassen Bering in order to ascertain if Kamchatka and Alaska were linked and to collect and record all forms of natural and cultural history along the way.

During the third year of the expedition in November 1736, a drastic fire broke out in Yakutsk in central Siberia which burnt Gmelin's collections, drawings and part of his library. As a result, he had to remain in the Yakutian part of Siberia to gather new collections and this prevented him from ever reaching the Pacific (Sokoloff et al. 2002: 158). In 1737, Gmelin and the Academy Professor of ethnology and natural history, Gerhard Friedrich Müller (1705–1783) sent Krascheninnikov on to Okhotsk on the Pacific coast and then to the Kamchatka Peninsula where he remained collecting natural history material for the next four years.

Steller an adjunct of the Academy

Georg Wilhelm Steller (1709–1746), originally from Bad Windsheim, Bavaria, arrived in St. Petersburg in November 1734. He was introduced to the Swiss botanist Johann Amman (1707–1741), who was, at that time, a recently appointed Assistant Director of the Kunstkammer or Cabinet of Curiosities, the first public museum in Russia, officially the Museum Imperialis Petropolitani. Steller also met Daniel Messerschmidt shortly before the latter's death in 1735. Steller then subsequently married his widow Birgitta and was hired as an adjunct of the Academy in February 1737 specifically to join the Great Northern Expedition.

Ernest Wilson, in the introduction to his monographic book The Lilies of Eastern Asia, stated that Steller had discovered the Daurian lily in 1737 in the region of the river Lena (Wilson 1925: 7). Steller, in fact, only set off east from Moscow in March 1738 for Tobolsk (Engel and Willmore 2020: 180). He left his wife behind and was accompanied by the illustrator Johann-Cornelis Dekker. He eventually met the Academy Professors Gmelin and Müller in the Siberian city of Yeniseysk on 7 December 1738 (Krascheninnikov 1764: v; Engel and Willmore 2020: 180). It is highly probable that Wilson had confused Gmelin's collection (mentioned below) with Steller's.

Steller however, collected plants of the lily in Siberia later and sent back plants or seeds to Amman in St. Petersburg. In a letter that Steller wrote on 24 December 1739 from Irkutsk to Johann Daniel Schumacher, Secretary of the Russian Academy of Sciences and Director of the Academy's Library, he mentions sending back to Amman his collection of seeds and plants (Engel and Willmore 2020: 186). Amman had been appointed the first director of the Academy's new botanic garden in 1735 (Sokoloff et al. 2002: 151). This despatch to St. Petersburg apparently contained six boxes of herbarium specimens, seeds, plants and other natural history items. The Russian authorities temporarily impounded the collection for some time in Yeniseysk (Sokoloff et al. 2002: 155). Amman, however, received several boxes of plants from Siberia sent by Steller on 30 May 1740 (Sytin 2022: 190).

Steller wrote about his encounters with a Siberian lily. On 18 June 1740, he wrote in his journal from the Lena River near Yakutsk "Walking back I noticed a wild growing blood red lily which Dr Gmelin had noticed on the Irtysh River and I had found among the dried plants Mr Rosing the pharmacist in Kyakhta had collected around the Kyakhta River" (Engel and Willmore 2020: 116). On 3 July 1740, he wrote from near the Amga River, the largest tributary of the Aldan: "Today I noticed a wild Iris, northern Indian paint-brush with white and red flowers, a cinquefoil with long runners, the wild blood-red Siberian lily and a species of lousewort" (Engel and Willmore 2020: 126). It is possible that he was referring to *L. pensylvanicum*, but equally to *L. pumilum*.

Steller was given instructions by Gmelin in 1739 to continue his journey onwards to Kamchatka. He was accompanied by the archaeology student Aleksei Petrovich Gorlanov and the painter and scientific illustrator Johann Christian Berckhan (1709–1751). On their onward journey south-east from Yeniseysk towards Lake Baikal, Steller and his companions were delayed for almost a year in Irkutsk near the western shore of Lake Baikal. They explored the flora, minerals and fauna around Barguzin during the summer for six weeks on the eastern shores of Lake Baikal until September 1739 (Engel and Willmore 2020: 180). During that time, Steller wrote his unpublished manuscript Flora Irkutensis in which he listed 1152 plant names including as number 495 the name Lilium minii colore cruentum, a reference to the Daurian lily (see below). They continued first to Kyakhta on the Siberia-Mongolian border (then part of China), then along the River Lena to Yakutsk in March 1740, then overland to Okhotsk where they met up with Vitus Bering on 14 August 1740 (Engel and Willmore 2020: 181). Berckhan, Gorlanov and Steller then joined up with the Academy student Stepan Krascheninnikov who was already in Kamchatka.

Gmelin's Flora Sibirica and Heydenreich

Gmelin published his finding of the upright Daurian lily in the first volume of Flora Sibirica (Gmelin 1747: 41–42) as "Lirium number 8". He described the plant using Linnaeus's phrase name for *Lilium bulbiferum*: "foliis sparsis, corollis campanulatis, erectis, intus scabris, Linn" (Gmelin 1747: 41). Gmelin stated that the phrase name was taken directly from Linnaeus's Hortus Cliffortianus (Linnaeus 1738: 120). This same phrase name was later used by Linnaeus in the validating description of *L. bulbiferum* (Linnaeus 1753: 302). Linnaeus had catalogued the morphologically similar European *L. bulbiferum* growing in the garden of the rich Dutch East India Company merchant George Clifford III at de Hartekamp in the Netherlands (Linnaeus 1738: 120). Linnaeus later, in his protologue for *L. bulbiferum*, also included the reference Gmel. Sibir. 1 p. 41 (Linnaeus 1753: 302) believing that the Siberian plant was in fact *L. bulbiferum*. Both Linnaeus and Gmelin each included a reference to Adriaan van Royen's Flora Leydensis prodromus (van Royen 1740: 31). After his work for George Clifford, Linnaeus went to Leiden in 1737 where he helped the Leiden garden's

Director, van Royen, to compile his volume on the plants cultivated there. Clearly both Gmelin and Linnaeus believed they were dealing with a single widely dispersed species occurring in both Europe and east Asia.

In the dissertation presented to Linnaeus on 15 May 1766 with the title: Necessitas Historiae Naturalis Rossiae by the Russian student of metallurgy at Moscow University, Alexander Matwejewitsch von Karamyschew, he referred to the immense value of Gmelin's Flora Sibirica (Karamyschew 1769: 443). In the list of useful plants from Siberia under the heading 'Flora Sibirica', Karamyschew lists under *Hexandria* four lily names: number 59, *Lilium bulbiferum*; 60, *L. pomponium*; 61, *L. martagon* and 62, *L. kamschat*. (Karamyschew 1769: 461). His number 59 was without doubt *L. pensylvanicum*, but was categorically recognised by Linnaeus as *L. bulbiferum*.

In his Flora Sibirica treatment, Gmelin divided this upright-flowering Siberian Lilium species into the modern-day equivalent of two varieties: 1. Folia latioribus, plants with broad leaves and 2. Folia angustioribus, narrow-leaved plants, the latter divided further into the equivalent of two formae: a. Flore miniato, plants with red flowers and β . Flore luteo, yellow-flowered plants (Gmelin 1747: 41). Gmelin included additional information about these taxa, stating that they were found everywhere between the Yenisey River eastwards to Okhotsk on the Pacific coast, especially in fields and near rivers and streams. He added that, where they grew in the wild, they frequently had only one, two or three flowers and the leaves often had marginal hairs. Gmelin further stated that the var. 2 a with narrow leaves and red flowers, was most commonly found in regions around the Rivers Lena, Aldan, Maya and Yudoma and the var. 1 with broad leaves was found throughout. Gmelin went on to state that, apart from their height and the width of their leaves, var. 1 and var. 2 were very similar. He added that the narrow-leaved and yellow-flowered var. 2 ß was collected by his adjunct Steller who had written to him to say that he had found it growing below the City of Yakutsk near the Lena and Aldan Rivers and that the leaves were whitish underneath, whereas he, i.e. Gmelin, had always observed that those of the red-flowered forma α were green on both sides (Gmelin 1747: 42).

Gmelin's next entry "Lirium number 9" was another species of *Lilium* found in Siberia which he described as "radice tunicata, foliis sparsis, floribus reflexis, corollis revolutis" (Gmelin 1747: 42). He added "Lilium reflexum montanum, humile, angustifolium, aurantium, Sarana Mungulis in Dauria Mess. Amm. Ruth. No. 138" and "Bauhin Lilio byzantine miniato", a direct reference to the scarlet-flowered European *Lilium chalcedonicum* L. to which he compared the species as being very similar (Gmelin 1747: 43). It was almost certain that this Siberian scarlet turkscap species was listed without any description in 1812 as *L. tenuifolium* on page eight in the Catalogue of plants growing in the garden of Count Alexis Razoumoffsky (1748–1822) at Gorenki Palace, Balashikha near Moscow. It was, however, first validly described and depicted by the famous botanical illustrator Pierre-Joseph Redouté as *L. pumilum* Redouté in Paris later that same year.

In addition to the information on the Daurian lily number 8, Gmelin added three references to his broad-leaved var 1: *Lilium purpureo-croceum maius* (Bauhin 1623: 76), *Lilium purpureum maius* (Dodoens 1583: 198) and the query "? *Lilium floris rubro-lutei, Tangunensibus Sarana polevvaga appellatum* Act. Nat. Cur vol. iii p. 355", followed by the comment "Videtur. Auctor relationis

populum nominans Tungusos intelligit. Nomen Tungusis adscriptum Russicum est, legendum sarana polevvaja (Lilium campestre) [Apparently, the author of the report understands that the people who gave this name are the Tungus. The Tungusic name is attributed in Russian as sarana polevvaja (лилия полевая or lily of the field)] (Gmelin 1747: 41). The first two of these references undoubtedly refer to the Daurian lily unequivocally as the European L. bulbiferum. The third one, which Gmelin included with a guestion mark, was the reference Act. Nat. iii p. 355. This refers to a short paper presented by the Prussian physician, mineralogist and metallurgist Johann Henckel in "Acta physico-medica Academiae Caesareae Leopoldino Carolinae Naturae" vol. 3: 355 (1733). Henckel's paper, dated Dresden 28 March 1732, was entitled 'Plantis Sinensium, ad confinia Siberiae australis nuper observantis' [Chinese plants recently observed on the borders of southern Siberia]. Henckel stated that his great friend and fellow metallurgist Johann Gottfried Heydenreich had recently returned [to Saxony] with 37 collections of seeds that he had collected along the Chinese - Siberian border. In fact, this was the border with modern-day Mongolia. Heydenreich had presented these to the King (Henckel 1733: 354). It is difficult to ascertain to which king Henckel was referring, but it was probably to Augustus II (1670–1733) known as Augustus the Strong, King of Poland and who was also Freidrich Augustus I, Elector of Saxony.

Heydenreich [also Heidenreich] was a mining specialist from Saxony who was initially employed to work for Tsar Peter I's recently formed Berg-kollegia or Collegium of Mining in 1722 alongside Vilim Ivanovich de Gennin (né Georg Wilhelm Henning). In May 1728, he was sent to examine silver deposits near Nerchinsk in southern Siberia as a chief technical specialist. He returned to Saxony in 1730 (N. Koparenov in Enzyklopädie der Russlanddeutschen https:// enc.rusdeutsch.eu/articles/5560 accessed 2 Jan 2023).

Four of Heydenreich's collections were of lilies of which number eleven on the list stated simply "Lilium cujus folia Mongalenses coquunt cum carnibus [Lilium the leaves of which the Mongolians cook with meat]. Number 12 on the list included the information "Lilium, floris rubro-lutei, Tangunensibus Sarana polevvaga appellatum: radicem siccatam loco pannis edunt, partier et carnibus coquendis addunt" [the lily with red-yellow flowers is called by the Tanguts sarana polevvaga: they eat the dried roots instead of bread and as an addition when they cook meats] (Henckel 1733: 355). There is a potential confusion here between the Tungusic peoples [the Evenki] mentioned by Gmelin, who inhabited the lands between the Yenissei River and Lake Baikal in Siberia and the Tanguts of northern China. Although the name sarana polevvaga may have been that used by the Tungus, it was from the Tangut/Mongolian Region that Heydenreich had collected his seeds. Gmelin, in fact, also discussed the virtues of sarana, adding that it was known under that name by the Tungus, Buryats and Yakuts where it was boiled up with milk. He added that the Russians either referred to it as "toothed" because of the scales on the bulbs or "of the plains" due to its habitat and that it was also called by the Yakuts "Korun" (Gmelin 1747:42).

Gmelin believed that his broad-leaved variant of the lily was probably the same as that described earlier by Henckel from seeds collected in Siberia by Heydenreich. There is no record of where or, indeed, by whom the lily was cultivated when it arrived in Saxony, but it could have been to Freiberg where Henckel was living as a physician and was made Councillor of Mining from 1732. Henckel stated that the plant was given to the King, perhaps this plant was cultivated at the royal palace of Dresden Castle or in the garden of the summer palace at Schloss Pillnitz on the River Elbe outside Dresden; however, this is conjecture.

There is an interesting herbarium specimen of L. pensylvanicum in the Herbarium of Lomonosov Moscow State University [MW0044033] with a label for the Imperial Moscow University and Herbarium Genning (Fig. 2). The Imperial Moscow University was founded in 1755 by Tsarina Elizaveta Petrovna. During the French invasion of Russia in 1812 under Napoleon, the University of Moscow building was razed to the ground, but many natural history specimens had already been evacuated to Nizhny Novgorod 270 miles (440 km) to the east. On this Moscow sheet, there is another much older label with the annotation in ink "neguit seperare a L. spectabile Link h. Berol. in horto Fintelmanniano sub nomen Lilium camchatkense colitur" [this cannot be separated from L. spectabile Link in the Hortus Berolinensis and is cultivated in the Fintelmann Garden under the name Lilium camchatkense]. The reference to the garden of Fintelmann is likely to be that of one of the descendants of Heinrich Fintelmann (d. 1733) whose progeny were gärtners and hofgärtners at Charlottenburg Palace in Berlin. The reference to L. spectabile Link is to a superfluous synonym of L. pensylvanicum. A possible cultivator of the plant, therefore, is Joachim Anton Ferdinand Fintelmann (1774–1863), hofgärtner at Charlottenburg, who may have sent the specimen to Moscow from the royal garden in Berlin. Again, this can only be conjecture.

Gmelin (1747: 41) also included two references to his narrow-leaved var. 2: *Lilium purpureo-croceum minus* (Bauhin 1623: 77) and *Lilium purpureum minus* (Dodoens 1583: 198). These references also both refer equally to the European *L. bulbiferum*, but in this context to the lily's counterpart in Siberia which, according to him, in one of the variants, is smaller and has narrower leaves than those described in var. 1. No specimen has been found to confirm this variety's identity, but Gmelin could have been referring to what was later described as *L. dauricum* var. *alpinum* N.I.Kuznetsov.

The Daurian lily's first records and illustrations

Over a decade after Messerschmidt's death in 1735, records of the dispatch of *L. pensylvanicum* as a living plant from Siberia to St. Petersburg are to be found in Amman's published and unpublished catalogues. These were a survey of the plants grown in the garden of the Academy of Science on Vasilevsky Ostrov [Vasilevsky Island] prepared shortly before his death. *Lilium pensylvanicum* is found in Amman's unpublished catalogue as number 863 under the name: *"Lilium minii colore cruentum"*, citing Gmelin as the collector and the River Lena as its place of origin (Amman 1739–1740: 41).

One of the many people accompanying Gmelin on the Great Northern Expedition was the scientific illustrator Johann Christian Berckhan. In the archives of the Academy of Sciences in St Petersburg is a watercolour of *L. pensylvanicum* painted by Berckhan t. LXXII online as http://ranar.spb.ru/rus/vystavki/id/710/ (Fig. 3). The painting is annotated "Berkhan del." in his hand and in ink above in Gmelin's hand "Lilium purpuro-croceum C.B.", the



Figure 2. Moscow University specimen MW0044033 of L. pensylvanicum bearing 'In horto Fintelmanniano' label.

initials C. B. referring to the name Lilium purpuro-croceum in Caspar Bauhin's *Pinax*, the name of the morphologically similar *L. bulbiferum* (Bauhin 1623: 76). According to Gmelin's own unpublished notes: Index vegetablium ad Lenam fluvium nascentium, annis 1736–1737 (or Index Lenensis) in the archives of the Academy, this painting was made by Berckhan near the River Lena during the summer of 1736 or 1737 and numbered with Roman

numerals (Gmelin 1736–1737). In Gmelin's MS, this species is described under number 443 on sheet 32v-33 as "Lilium minii colore cruentum Licet cum Lilio purpuro-croceo majore C.B.P". The draft MS later had added to it "Tab. LXXII" (see Fig. 3) corresponding to the number on Berckhan's watercolour. Gmelin added in his MS with respect to the location and habit of the plant in the watercolour: "Floret sub medium Junii ad omnem Lenam ad Schiganensia usque hibernacula" [It blooms from the middle of June and grows throughout the Lena to Zhigansk Districts until winter]. Berckhan did not return to St. Petersburg until 1746, several years after his colleagues had all returned and was, therefore, not involved in the preparation of the 297 illustrations for the four volumes of Gmelin's Flora Sibirica. No illustration of the lily featured in that work.

The drawing t. 72 by Berckhan was copied by Georg Steller who wrote in his unpublished Flora Irkutensis: "495. Lilium minii colore cruentum, cuius Iconem procuravit D. D. Gmelin vidi Tab. LXXII" [I have seen the flame-blood coloured lily, whose icon t. LXXII the illustrious Dr Gmelin procured] (Steller 1739a: 90v, 91). Steller then lists references to L'Obel (1581: 169, t. 208) and Bauhin (1623: 78), although, both these references are to the red-flowered turkscap European species L. chalcedonicum. Steller continues with additional information about the species "Planta haec perennis sub initium Junii in montosis apricis ad Angaram et circum lacum Baikal abunde florens" [This perennial plant blooms profusely at the beginning of June in the sunny mountains by the River Angara and around Lake Baikal] (Steller 1739a: 104, t. 91-91v.). He alludes to its production of underground stolons [....] "facile e bulbo veluti vagina extrahitur, qua parte e bulbo prominent terrae legitur, fibras albas tenues emittit, terrae inhaerentes, iisque prossus similes, quae bulbo inferius ad haerescunt [....it sends out thin prostrate stems which adhere to the earth and which remain attached to the bulb]. Finally, Steller alludes to the edible qualities of the bulb of this species "Russis et Tataris accredit Сарана, quam Russi addito distinguere solent a priori, quoad radicem Glava, in cibo utrorumque" [The Russians and the Tartars both value Sarana, the Russians distinguish their food from that of the Tartars by the addition of the root Glava]. Steller's still unpublished Flora Irkutensis with 1152 plant descriptions was completed by December 1739 (Engel and Willmore 2020: 180).

Steller also produced a seed list from his collecting activities in Siberia, from around Barguzin in Buryatia, Irkutsk and Lake Baikal (Steller 1739b). On page 15 of this list, Steller included as number 200 "Semen Lilii Cat. Pl. no. 495. In tribus chartis Horum liliorum etiam bulbi siccati-mitturitur" [Seed of lilies in the Catalogue of Plants. number 495. In the three papers of these lilies will also be sent the dried bulbs]. The number 495 was the same number for *L. pensylvanicum* as that which he had used in his Flora Irkutensis MS.

Amman the Academy's Garden Director

Gmelin, his student Krascheninnikov and the Academy adjunct Steller all sent seeds to the Swiss Johann Amman (1707–1741), the Academy Botanic Garden's first Director and Professor of Botany (Koroloff 2014: 134; Sytin 2022: 171). During his earlier time in England as an assistant to Sir Hans Sloane, Amman had forged contacts with several eminent botanical and horticultural



Figure 3. Watercolour of L. pensylvanicum by Johann Christian Berckhan t. LXXII ca. 1736-1737.

figures. Amongst these were Peter Collinson in Peckham and most significantly Mark Catesby for whom he was a subscriber to his Natural History of Carolina (Catesby 1731–1743) and to whom he donated and inscribed his name in a copy of his published catalogue of the St. Petersburg Academy Garden, *Stirpium rariorum* (Amman 1739). This copy is in the Smithsonian Institution Library. After Müller's visit to London, in 1733, Amman joined the Academy of Sciences in St. Petersburg. Müller, meanwhile, was to leave St. Petersburg in 1736 to join up with Gmelin on The Great Northern Expedition. Amman's health began to seriously decline in St. Petersburg where he died aged only 34 on 4 December 1741. Before his death, Amman produced an unpublished descriptive list of the plants cultivated in the Academy Botanic Garden. The phrase name for Gmelin's Siberian lily *Lilium minii colore cruentum* was included in this list as number 863: with the citation of Gmelin and the River Lena (Amman 1739–1740: 41). This name was not included in the published Catalogue of the plants in the garden, but Amman did include two other lilies, also with phrase names, which had been collected by Messerschmidt in Siberia (Amman 1739: 105–106). These lilies, cited later by Gmelin (1747: 43), would eventually be described as *Lilium martagon* L. and *L. pumilum* Redouté. With reference to the latter, he refers to Messerschmidt and the use of Sarana:

138. LILIUM reflexum, montanum, humile, angustifolium, aurantium, Sarana Mungulis in Dauria, Messersschm [138. The low growing, reflexed, orange, mountain lily, Sarana of the Mongolians in Dauria, Messerschmidt] (Amman 1739: 105). In the same text, he also provided additional information that more than one lily was known by the name Sarana, translated from Latin "[....] both these Lilies of Russia should be called Sarana, borrowed from the Tartars; the Tunguts and Burats dig up and eat the bulbs; both lilies come from the plains as well as from the mountains of Dauria" (Amman 1739: 105).

Following Amman's early death in 1741, the Academy Botanic Garden was placed first under Johann Siegesbeck, then briefly in 1747 to Gmelin and later Krascheninnikof from 1747 to 1749, who was subsequently appointed Professor of the Academy in 1750. The Academy Garden was finally closed in 1812 (Sokoloff et al. 2002: 151). In 1823, the Apothecary Garden became the Imperial Botanical Garden and is now the Vladimir Komarov Botanical Institute's Botanical Garden of Peter the Great.

Herbarium specimens of the Daurian lily

The Academy purchased Amman's herbarium and drawings in 1743; however, his possessions were already being kept in the Kunstkammer in 1741 at the very end of his life. The bulk of the Kunstkammer Herbarium, including an Herbarium bought by Tsar Peter I in 1717 from Frederik Ruysch and which was compiled by Amman, was largely destroyed by a fire on 5 December 1747 with additional damage to the specimens caused by the water which was used to put the fire out. Amongst the collections that were destroyed were many plants from Messerschmidt, Gmelin and Steller (Sytin 2022: 180). Much of Gmelin's Herbarium was in fact incorporated into the Kunstkammer in 1757, two years after his death, while many Siberian specimens were sold in 1808 (see below).

Another of Gmelin's botanical companions in Siberia was Alexander Wilhelm Martini (1702–1781). Martini travelled with Gmelin across much of Siberia from 1740 to 1743 collecting botanical specimens and copying his notes (Sebald 1983: 1). These were deposited in the Herbarium of the Natural History Museum of Stuttgart (Staatliches Museum für Naturkunde, STU). Any material of *L. pensylvanicum* collected by Martini in STU would have been destroyed by bombing during World War Two (Anette Rosenbauer pers. comm.) A thorough search through the collections of *Lilium* in the Komarov Botanical Institute Herbarium (LE), where any possible specimens of *L. pensylvanicum* collected by Gmelin, Krascheninnikov or Steller would have been deposited, did not yield any such material. It is possible that any specimens collected during the Great Northern Expedition could have been destroyed as a result of the disastrous fire in the Kunstkammer of 1747. There are, however, in the Herbarium still some unopened bundles of specimens from the Kunstkammer collections that have not yet been incorporated into the general collections. Part of Steller's collections were sold by Pallas at auction and were bought by the British botanist Aylmer Bourke Lambert in 1808 along with Pallas's own collections, but none of Steller's specimens of *Lilium* has been located. Lambert's Herbarium was sold and dispersed after his death in 1842. There is also no lily specimen to be found in BM amongst the Amman collections which Amman had sent to his former employer Sir Hans Sloane.

There is one specimen of interest amongst the pre-Linnaean G-PREL collections of the Geneva Herbarium [G00818223]. This sheet (Fig. 4), listed as SIB 567883/1, clearly represents a single flowering specimen of L. pensylvanicum. It has a label with "Herbier Delessert collection Burman" printed in ink and also in ink written on the same label by hand "Siberie Demidoff Burman". The Herbarium of the Dutch botanists Johannes Burman (1706-1779) and his son Nicolaas Laurens Burman (1734-1793) was acquired in 1810 after the death of the latter's widow by the French banker and naturalist [Jules Paul] Benjamin Delessert (1773-1847). In 1869, the city of Geneva acquired Delessert's Herbarium including the Burman Herbarium from his daughters. This specimen of L. pensylvanicum possibly originated from one of the collectors on the Great Northern Expedition. There is no date or additional information on the sheet as to which of the Demidov brothers (see below) had acquired the sheet or how the specimen had then been incorporated into the Burman collections. One possibility is that it may have been sent initially by Grigory Demidov to Linnaeus who then distributed it to either Johannes or his son in Amsterdam.

Unconnected with these earlier collections, the German Naturalist Peter Simon Pallas (1741–1811) also visited Siberia having joined the St. Petersburg Academy of Sciences in 1767. Under the instructions of Tsarina Catherine II, Pallas led an expedition for the Academy across Russia from 1768–1774 as far as Lake Baikal. In his Corrigendum (Ker Gawler 1809b: sub t. 1210), Gawler cites a specimen collected by Pallas from this expedition. There is a sheet in BM (Fig. 7) with four collections of the Daurian lily on one sheet, three are in flower and one in fruit [BM000551418]. Three labels on the sheet attest to this having been a collection by Pallas, one has "Lilium bulbiferum spontan. e Dauria', another has "Herb. Pallas" and the third has "Lilium bulbiferum spontan. Sibir.". There is however, no evidence that Pallas sent back to St. Petersburg any living plants.

The Demidovs, amateur botanists and garden makers

The wealthy salt, iron and steel mining and manufacturing family of Demidov (or Demidoff) created a botanic garden in the village of Krasnoe near Solikamsk, west of the Ural Mountains in ca. 1730 near the family's salt mines (Sokoloff et al. 2002: 161). Three brothers, Prokofy Akinfievich Demidov (1710–1786), Grigory Akinfievich Demidov (1715–1761) and Nikita Akinfievich Demidov



Figure 4. Burman Herbarium specimen G00818223 of L. pensylvanicum labelled 'Siberie Demidoff'.

(1724–1787) were all keen amateur botanists involved with the creation of that garden. Prokofy exchanged plants with Amman in St. Petersburg and with the Moscow Apothecary Garden, moving in 1756 to Neskuchny on the Moskva River, which was then just outside Moscow, to start his own private botanic garden. He was later visited by the plant collector Peter Simon Pallas in 1773 who, in

1781, published a catalogue of the plants cultivated there (Sokoloff et al. 2002: 163). The Daurian lily was not included in that catalogue. The palace and garden were sold after his death to Count Alexei Orlov-Chesmensky.

Grigory Demidov remained in Solikamsk where he exchanged plants and corresponded with Amman in St. Petersburg, as well as with Traugott Gerber (1710-1743) who, from 1735, was Director of the Apothecary Garden in Moscow. Grigory was visited by Gerhard Müller and Johann Gmelin in 1743 on their return from Siberia bringing with them their collection of Siberian plants destined for the St. Petersburg Academy Botanic Garden (Elina 2022). Grigory was also visited by Steller and the adjunct ethnographer J. E. Fischer in April 1746, only a few months before Steller's death in Tyumen on 12 November that year (Elina 2022). Steller who was suffering from illness, stayed for several months having brought with him his large collection of frozen Siberian plants which he planted to defrost in Demidov's garden for safekeeping. The intention was for the plants to be given a temporary home before being sent on to St. Petersburg. These plants and an herbarium were collected from across Siberia; near the Lena River, around Lake Baikal and near Irkutsk. Following Steller's death, his collections were eventually sent on to St. Petersburg by Grigory arriving there on 11 March 1748 (Elina 2022). It is clear, however, that many of Steller's living plants remained in Solikamsk. Having moved to his house fronting the Moyka River in St. Petersburg, leaving the Solikamsk garden in the hands of a reliable gardener, Grigory wrote his first letter to Linnaeus (L0877) on 26 February 1748 (Elina 2022). In this letter, he included 62 packets of seeds of Siberian plants from Steller's collections, followed on 28 October 1748 (L0969) by ten more sets of seeds (Savage 1945: vii; Elina 2022). It is not known how large his garden was in St. Petersburg, but he was believed to have used it as a temporary repository for growing plants. No specific mention of any lilies was made in these letters. Despite several additional letters in which Steller's Herbarium was sent to Linnaeus for determining the contents and which were later returned to Grigory (L0915; L0946; L1359), there was no mention of any Lilium.

It is still likely that it had been Grigory Demidov who had sent the specimen of *L. pensylvanicum* to the older Burman from Steller's original Siberian collections (Fig. 4). There are other specimens from Siberia in G that simply bear the label "Demidoff, Siberie" (Martin Callmander, pers. comm.). Many of Grigory Demidov's living Siberian collections eventually went to his brother Prokofy's garden at Neskuchny near Moscow after the sale of the Solikamsk estate in 1772 (Elina 2022).

How the Daurian lily acquired an American name

After the arrival of the Daurian lily in Europe, it was confused with *L. philadelphicum*, one of the two upwards-facing bowl-shaped lilies from North America. A lily that was believed to have come from North America was painted by Mark Catesby (1683–1749) in the Appendix (Fig. 5) of his The Natural History of Carolina, Florida and the Bahama Islands (Catesby 1747: App. t. 8). The Appendix comprised twenty additional plates prepared after the ten original parts published in two volumes. It is known that, after Catesby's return to England in 1726 from his own collecting in Carolina, many plants he depicted in the Appendix were sent from John Clayton and John Bartram in North America to either his friend Peter Collinson (1694–1768) or to Catesby himself (Dandy 1958: 111).



Figure 5. Watercolour of *L. pensylvanicum* as '*Lilium angustifolium*, *flore rubro singulari*' in the Appendix to Mark Catesby's The Natural History of Carolina, Florida and the Bahama Islands (Catesby 1747: App. t. 8).

Catesby described the lily which he depicted in the Appendix with the name *"Lilium angustifolium, flore rubro singulari*, Le Lys rouge de Pensylvanie" (Catesby 1747: App. t. 8). In an Advertisement for this Appendix (of which only two copies are known to exist), the lily was called *Lilium rubrum minimum* (Overstreet 2015: 164). When these additional plates were presented to the Royal Society, the Society's Second Secretary and Sir Hans Sloane's Medical Assistant Cromwell Mortimer, added the statement regarding plate eight of the Appendix: *"Lilium angustifolium, flore rubro singulari*. The red Pensylvanian Lily. This lily comes from Pensylvania. It agrees with our climate" (Mortimer 1748: 161).

Catesby stated in his text to this eighth plate in the Appendix that the flower consists of six deep scarlet petals spotted with very dark red or purple. He also added that the upper part of the stem and underside of the tepals were roughly hairy and that it was a native of Pennsylvania and that, in 1743, he saw it in flower in the garden of Mr. Collinson in Peckham (Catesby 1747: App. t. 8). Peter Collinson, a rich cloth merchant who traded extensively with North America, had very strong connections with Catesby, being his principal sponsor for the publication of the Natural History and having given him a very substantial interest-free loan. The question concerning the identity of the plant portrayed in this painting is – did Catesby actually portray a North American lily? Catesby referred to the plant unequivocally as the Pennsylvania lily; however, the illustration is undoubtedly one of Catesby's least convincing portraits (see Fig. 5). The image of the lily and its brief description were eventually published only two years before Catesby's death at a time when his eyesight was alleged to have been failing, according to Linnaeus's apostle Pehr Kalm (Nelson 2015: 17).

In 1747, Catesby presented his final illustrations for the Appendix to the Royal Society (Overstreet: 2015: 158). The only North American lily species that Catesby's description and image could refer to is the species *L. philadelphicum* and it has naturally been identified as that species (Reveal 2015: 341; M. Skinner, pers. comm.). There is, however, a huge "**but**" here - *L. philadelphicum* usually has at least one whorl of leaves subtending the emergence of the peduncle, whereas Catesby's image has scattered leaves throughout. Although scattered leaves can, however, occasionally occur on young or small plants of *L. philadelphicum*, there is also Catesby's comment to consider concerning the presence of rough hairs on the upper stem and on the reverse of the tepals. Any such pubescence does not occur on *L. philadelphicum* whose stem, leaves and tepals are glabrous and occasionally glaucous.

There is an herbarium specimen in BM [BM001047104] originally with the unpublished name *Lilium collinsoniae* written on it. The name, written by an unknown hand, was probably designed to honour Peter Collinson's wife Mary. This is readily recognised to be the other North American species with upright flowers and has been correctly identified as *Lilium catesbaei*. It has narrower tepals than those in *L. philadelphicum*, each tepal has longer and narrower claw-like bases and scattered rather than whorled leaves. This sheet is conserved in the Catesby collection within the Sloane Herbarium. Another specimen also of *L. catesbaei* is conserved in OXF [Sher-0708.14] in the Sherard Herbarium number 700 and is labelled simply "Mr Catesby S. Carolina 1723".

There is a specimen of L. pensylvanicum in BM [BM014605092] with the annotation on one label attached on to the sheet simply with "Hort. Collinson" in ink and with an indecipherable initial in pencil which could be an entwined JG, possibly representing John Gawler (Fig. 6). At the bottom of the sheet are written a succession of references which, reading chronologically are: "Lilium dauricum G. in Bot. Mag. 1210!" in ink with "sub t." added in pencil above, then immediately under that in pencil "----- pensylvanicum Gawl. Bot. Mag. t. 872!", the dashed line indicating Lilium from the ref. above it; above that is "Lilium [empty space, possibly with angustifolium, but now rubbed out] Catesby car. III. p. 8. t. 8" in pencil and, at the top, "Lilium collinsonii G. in Bot. Mag." also in pencil. The specimen has been cut out from its original mount and remounted and consists of an inflorescence with a single upright flower with distinct spotting and an unopened flower bud. There are several narrowly lanceolate leaves scattered along the stem. There is a noticeable presence of pubescence at the junction where the leaves join the stem i.e. in the leaf axils, and along the upper parts of the pedicel and hairs are scattered loosely on the outside of the tepal surfaces. These characters are consistent with Catesby's description of the species and are to be found on L. pensylvanicum i.e. the Daurian lily from east Asia, not on L. philadelphicum from North America. There is no date to indicate from which of Collinson's gardens this specimen was taken, but it could have been the specimen from which Catesby had made his painting.

The Daurian lily in Collinson's catalogue

From the year 1722, Peter Collinson began to compile a catalogue or list of plants growing in his garden in Peckham, which was then merely a village south of London. On the death of his wife's father in 1749, he inherited Ridgeway



Figure 6. The Hort. Collinson specimen of L. pensylvanicum BM014605092.

House in Mill Hill with a much larger garden of eight acres. There he continued to contribute to his catalogue which, from the start, included his own additional memoranda on the origin and performance of his plants. Many of these memoranda he added either as interleaved additions within his original text or, in some cases, as separate pages. The catalogue remained unpublished during his lifetime. It was, however, published posthumously by the Quaker Lewis

Weston Dillwyn (1778-1855) of Sketty Hall, owner of the Cambria Pottery near Swansea, naturalist, abolitionist and Whig politician. Dillwyn basically edited Collinson's catalogue and rearranged Collinson's polynomial phrase names into what he perceived to be the correct Linnaean binomials. The named entries listed by Dillwyn as "Not in Catalogue" were largely based on the Linnaean names he had found in Loudon's Hortus Brittanicus (Loudon 1830; Dillwyn 1843: 1). Moreover, Dillwyn applied to the list of names in Collinson's catalogue those of Collinson's memoranda that he surmised to be correctly associated with them (Dillwyn 1843: vi). Many relevant dates of introduction into Collinson's garden were included in Collinson's catalogue and subsequent memoranda. Thus, Lilium philadelphicum, according to Collinson, was introduced into the garden in 1730, L. pensylvanicum in 1740 and L. carolinianum (i.e. L. catesbaei) before 1743 and the Siberian scarlet-flowered turkscap L. pumilum in 1748 (Dillwyn 1843: vi). In our context, Dillwyn's identifications based on Collinson's catalogue and memoranda beg the question as to what Collinson's L. pensylvanicum might have been?

Dillwyn included what he believed to have been *Lilium philadelphicum* with the statement "Not in Catalogue" adding Collinson's memorandum: "1730, *June* 16, *J. Bartram sent me some very elegant red lily roots, flowered in 1740, it rises a foot high; the leaves set round the joints of the stem in tiers, one above another; the flower is the smallest of all the Lilies that I have seen; it consists of six leaves, set wide from each other, of a deep fire or flame colour; one half of the leaf or petal clear, the other half spotted, with very large deep purple brownish spots; one single flower on a stalk, but in the year 1746 it had two flowers from one stalk; from Pensylvania" (Dillwyn 1843: 30). It is clear that Collinson is referring to <i>L. philadelphicum* sent to him by John Bartram and that Dillwyn had correctly identified this species.

Another lily which Dillwyn attributed to "L. pensylvanicum of Bot. Mag." was mentioned in Collinson's catalogue with the phrase and reference "Lilium acadiense pumilum flore rubro punctato. Dodart's Mem." (Dillwyn 1843: 29). Collinson's reference is to the phrase name in the work of Dionys Dodart with illustrations by Nicolas Robert (Dodart 1686: 91). Dodart, in turn, stated that the Acadian lily was sent from Cayenne by Monsieur Richer of the Académie Royale des Sciences. This would have been Jean Richer who visited Canada [Acadia] on an astronomical expedition in 1670 for the French Académie Française and who went, in 1672, on a similar expedition to French Guyana. Collinson's two memoranda referring to this lily are: "1740. Received from J. Bartram a new Orange Lily, with hoariness on flower and leaves, figured by Catesby". The second memorandum read: "1750, a Pensylvanian Lily, that bears but one flower, dotted with purple, is well described in Dodart's Memoire des Plantes, and well figured. Since, I have raised many crimson coloured Martagons from Pensylvania seed; all new species". The description by Dodart and the illustration by the French royal painter Robert is without doubt also that of L. philadelphicum. This lily then was clearly Dillwyn's "L. pensylvanicum of Bot. Mag." (Dillwyn 1843: 29), but the statement "hoariness of flower and leaves" is not correct for L. philadelphicum, whose parts are glabrous.

Collinson was obviously very keen on the genus *Lilium* as he grew 18 more lilies listed in his catalogue. He included as postscripts various memoranda relating to them. The majority of these lilies are not relevant for this paper,



Figure 7. Peter Simon Pallas's specimens of *L. pensylvanicum* from Siberia that may have been in Aylmer Bourke Lambert's Herbarium BM000551418.

but at least one clearly is. Dillwyn listed "Lilium pomponium Var.?" Collinson had written "Lilium purpuro-croceum majus an floris rubro lutei. Act. Nat. iii., p. 155; this orange or red Lily I raised in plenty, sent me by Dr. Amman, of Petersburgh, sent from Siberia, and the roots are there eat(en) for bread" (Dillwyn 1843: 30). The descriptive phrase name reflects the name that was used for L. bulbiferum by Casper Bauhin in his Pinax i.e. "Lilium purpurocroceum majus"

(Bauhin 1623: 76). As we have already seen, the Siberian lily is very closely related to the European *L. bulbiferum* and the Siberians' use of eating sarana polyvega has already been discussed above.

The reference which Collinson gave i.e. Act. Nat. iii p. 155, refers to the same paper by Henckel (Henckel 1733: 354) as that which was also cited by Gmelin (Gmelin 1747: 41), although the pagination of 155 should have been 355 (Jacek Wajer, pers. comm.). As discussed above, this species was introduced from Siberia by 1733 at the latest and it seems likely that seeds or even bulbs may have been cultivated by Amman in St. Petersburg before being sent on to Collinson in Peckham. It would strongly suggest that Collinson's "Lilium pomponium var.?" was indeed the Daurian lily i.e. *L. pensylvanicum* Ker Gawl.

Why it was that Dillwyn had doubtfully suggested this could be a variety of the western Mediterranean turkscap *Lilium pomponium* L. with its scarlet, highly recurved tepals is possibly explained by his confusing it with the Siberian *L. pumilum*, which does, indeed, have pendent, scarlet flowers with reflexed segments like the European species. Collinson's description, however, is almost certainly of *L. pensylvanicum* not *L. pumilum* as the latter bears no similarities with Bauhin's *Lilium purpurocroceum*.

Immediately above this entry, Dillwyn had listed another lily also with the name *Lilium pomponium* Var.? He attributed to it Collinson's memorandum *"Lilium Martagon sibiricum, petalium quasi fistalosum flore purpureo nigricante; sent from Moscow"*. Collinson's memorandum also stated *"1756 sent to me by Mr Demidoff, proprietor of the Siberian Iron Mines, some roots of Siberian Martagon; flowered for the first time May 24 1756; the flower is but little reflexed, and is, I think, the nearest black of any flower I know" (Dillwyn 1843: 30). This, according to the description, refers to <i>Fritillaria camschatcensis* (L.) Ker-Gawl., a species with deep reddish-black flowers from east Siberia and which also occurs across the Bering Strait in Alaska and the western USA. This was evidently cultivated much later in Collinson's garden in Mill Hill. Linnaeus had originally called this species *Lilium camschatcense* L. (Linnaeus 1753: 303).

Dillwyn had added two further entries which are somewhat confusing. The first simply is *L. pumilum* with Collinson's phrase "Lilium sibiricum pumilum cruente". Collinson's memorandum added "1748, July, flowered orange or yellow lily, I raised seed from Daurica, called Saranna; can perceive very little difference from those we had before, except they grow not so high, or produce so many flowers". Then another memorandum "Called Sarana by the Tartars; they dry and powder the roots, and mix for bread in their broths, for they grow no corn" (Dillwyn 1843: 30).

This appears to be another collection of *L. pensylvanicum* which was identified incorrectly as *L. pumilum*. Both these lilies, as well as *Fritillaria camschatcensis*, are known under the name Sarana and all three species have been used as food in Siberia (Ståhlberg and Svanberg 2006). The second entry has "*L. pumilum* Var. Lilium sibiricum pumilum novum, flore rubro nigro quatuor unciarum altitudinem, new" [A new Siberian lily, four inches high, with reddish-black flowers]. This is probably only a variant of *Fritillaria camschatcensis*.

As Amman had died in 1741, Collinson's memorandum on the lily that he described as *Lilium purpuro-croceum majus an floris rubro lutei* reveals that Amman did, indeed, already have the Siberian lily now known as *L. pensylvanicum* in cultivation well before that date. It is also possible that he was cultivating

the lily shortly after 1733 when it may have arrived in Germany. The Collinson herbarium specimen now in BM [BM014605092] with distinct pubescence in its upper parts might have originated from one of the plants sent by Amman to Collinson and which was subsequently painted by Catesby (Catesby 1747: App. t. 8). There is, however, no indication of a date on the sheet and it may have been from a later introduction. Nor is there any indication by Collinson as to whether he grew the lily in his garden in Peckham or later in the larger one in Mill Hill of eight acres that he moved into in 1749, thereby ruling out Catesby's involvement.

Ker Gawler's Lilium pensylvanicum

The amateur botanist John Bellenden Ker Gawler, later Bellenden Ker (1764-1842 cited here as Ker Gawler), having seen Catesby's illustration (Fig. 5) and description, unwittingly described the Siberian lily with an illustration under the name Lilium pensylvanicum Ker Gawl. (Fig. 1), citing Catesby's Appendix (as volume three of his Natural History) as a reference (Ker Gawler 1805: t. 872). Ker Gawler clearly believed that he was giving Catesby's lily from North America a valid binomial; however, the illustration painted by Sydenham Edwards and the description without doubt represents the Asian species. The lanate peduncle, outside of the corolla "floccoso-lanata" and pubescence at the junction of the leaves with the stem and along the leaf margins are not characters found on the North American species (Mark Skinner, pers. comm.). As Ker Gawler himself admitted "The only mention of this species that we have been able to find, is in the above quoted work of Catesby" (Ker Gawler 1805: t. 872 text), adding that it had flowered in Peter Collinson's garden in 1745 and that a specimen from that collection was deposited in the Banksian Herbarium [now in the General Herbarium BM]. Additionally, of note is Ker Gawler's comment "The affinity with Lilium bulbiferum is so great that we can hardly bring ourselves to consider it specifically distinct" (Ker Gawler 1805: t. 872 text). Ker Gawler mentioned that the four or five upper leaves are whorled, a character found sometimes in the Asiatic species and frequently L. philadelphicum, but he went on to say that the bulb sends out numerous creeping shoots, a character typical of the Asian plants, but not of *L. philadelphicum*.

The illustration accompanying the written description, however, was prepared by Sydenham Edwards from a plant cultivated by the London nursery of Whitley & Brames of Old Brompton and was dated 1 September 1805 and published by the late William Curtis's brother Thomas in the Botanical Magazine. The large nursery of Whitley & Brames covering eight acres next to Gloucester Road and Old Brompton Road was founded in 1784 by Frank Thoburn. Between 1801 and 1810, it was run by partners Reginald Whitley (1754–1835) and Peter Brames (? -1834), specialising in hardy herbaceous and alpine plants (Harvey 1973: 186). The error that Ker Gawler made as to the origin of the lily was compounded by the fact that one of the proprietors of the nursery had informed Ker Gawler that the plant in the nursery had also come originally from North America. Nowhere in Ker Gawler's text is the name of the provider of the lily to the nursery mentioned.

Could the provider of the Daurian lily to Whitley and Brames have been the botanist Richard Anthony Salisbury (1761–1829)? Salisbury was one of the founding members in 1804 of the Horticultural Society of London [later RHS], but was also the Society's first secretary from 1805 to 1816. After Peter Collinson's death in 1768, Ridgeway House passed to his son Michael, another amateur

botanist, who died in 1795. Michael's son Charles Streynsham Collinson sold Ridgeway House and its fine garden to R. A. Salisbury in 1801. Salisbury lived at Ridgeway House until 1806 and had befriended the Burchell family, nurserymen of Kings Road, Fulham. In his will he left the bulk of his estate to the son of Matthew Burchell, the South African explorer William John Burchell (1781–1863). The Burchell nursery was acquired in 1810 by Reginald Whitley, Peter Brames and Thomas Milne. In the absence of any nursery records of the time, it is not beyond the realms of possibility that Salisbury could have grown the Daurian lily from Collinson's collection and that either Whitley or Brames had acquired it from him for Ker Gawler to describe and Sydenham Edwards to paint.

First doubts on the lily's origin

Ker Gawler cast doubt on his own assertion that the illustration and description of his *L. pensylvanicum* originated from North America three years later. In a discussion under his depiction of *Pancratium rotatum* Ker Gawl. [now *Hymenocallis rotata* (Ker Gawl.) Herb.], in which he propounded correctly that Linnaeus had erred in his identification of *Pancratium carolinianum* L., mistakenly as a North American species instead of the European *P. maritimum* L., he again discussed *Lilium pensylvanicum* (Ker Gawler 1808: t. 1082). In that work, he stated that he believed the lily's origin was not from North America, but possibly from China or Japan and that the lily was likely to be the same as what Thunberg had called either *L. philadelphicum* or *L. bulbiferum* from Japan. In neither case was Thunberg referring to either *L. philadelphicum* L. or *L. bulbiferum* L. (Ker Gawler 1808: t. 1082).

Ker Gawler stated the following year, after his diagnosis of the differences between *L. pensylvanicum* and his depiction and description of *L. concolor* (Ker Gawler 1809a: t. 1165), that he still needed to ascertain the country of origin of his original description of *L. pensylvanicum*. He added too that he had yet to establish how it differed from *L. bulbiferum* and that Reginald Whitley, upon reflection, believed it to have been a plant from Russia. Ker Gawler continued to fan the flames of confusion by stating that perhaps Catesby had only guessed that the plant growing in Peter Collinson's garden and which Catesby had painted (Fig. 5) was from North America, inferring that it was the same as that figured by Ker Gawler. Crucially though, Ker Gawler then posited two questions – was this the variety 2 foliis angustioribus – (a) flore miniato of the *Lilium bulbiferum* of Gmelin's Flora Sibirica; and a Siberian plant? Or was it from China? He stated categorically, however, that it was not a native of North America (Ker Gawler 1809a: t. 1165).

The Corrigendum and renaming

Ker Gawler finally added a Corrigendum later that year in which he attempted to rename *L. pensylvanicum* Ker Gawl. as *L. dauricum* Ker Gawl. (Ker Gawler 1809b: sub t. 1210). His Corrigendum read: "No. 872. For Lilium pensylvanicum. Pensylvanian Lily, read Lilium dauricum, Siberian Lily". Ker Gawler renamed the lily after the land of the Daur peoples in Dauria or Dahuria, a mountainous region once located near Lake Baikal encompassing modern-day Transbaikal and comprising Buryatia, Zabaykalsky Krai and the Amur River region. This renaming has, of course, subsequently engendered a great deal of confusion and has subsequently been formally rejected.

In Ker Gawler's protologue for *L. dauricum* (Ker Gawler 1809b: sub t. 1210), he included three synonyms:

Lilium bulbiferum. Pallas. Herb. penes Dom. A. B. Lambert
L[ilium]. 2 foliis angustioribus (α) flore miniato Gmel. Sib. 1. 41
L[ilium]. angustifolium flore rubro singulari. Catesby Carol. 3 p. 8. t. 8. false ab auctore pro Americae indigena datum: tabula a planta in Horto Londini

suburbano florida desumpta fuit. [Narrow-leaved lily with a single red flower in Catesby's Carol. 3, page 8 t. 8 falsely provided by the author as a native American plant: the illustration was made from a flowering plant in a garden in the suburbs of London].

Ker Gawler added the statement "In Pallas's Herbarium at Mr. A. B. Lambert's, there are several very perfect specimens of the species, gathered in the eastern parts of Siberia" (Ker Gawler 1809b: sub t. 1210). The specimens collected by Pallas in BM [BM000551418] have already been discussed above (Fig. 7). These specimens may well have been at one time in Aylmer Bourke Lambert's Herbarium as they do, indeed, perfectly represent the Siberian species; however, even though Ker Gawler attempted to change the name of the species to *L. dauricum*, they were not included in the original protologue. Only material cited within the protologue of *L. pensylvanicum*, however, would be eligible as type (Art. 7.4, Turland et al. 2018). The available elements for typification, therefore, are Edwards's illustration which accompanies the description, the Catesby illustration t. 8 in his Appendix discussed above and a specimen in the Banksian Herbarium in BM (Ker Gawler 1805: t. 872). The illustration accompanying the protologue (Ker Gawler 1805: t. 872) was chosen by Y-D. Gao in Taxon 70(5): 1139 (2021) as the lectotype.

Ker Gawler's conclusion

Ker Gawler later reiterated his conclusion that *L. pensylvanicum* was, indeed, from Siberia in a note under the description of the North American lily *L. philadelphicum* var. *andinum* (Nutt.) Ker Gawl. (Ker Gawler 1821: sub. t. 594). It is worth reiterating his note verbatim for clarity:

"Owing to a mistake originating with Catesby, a species of this genus is given by Messrs. Pursh and Nuttall to America, while in fact it does not belong to that quarter of the globe. Lilium angustifolium flore rubro singulari of the Natural History of Carolina was described and figured from a plant in Mr. Peter Collinson's garden at Peckham, and being conceived in the recollection of Catesby to be the same with one he had seen in America, was published by him in the above History as such. A sample of that plant from the same garden is also preserved in the Banksian Herbarium. Many years after it was published by ourselves in Curtis's Magazine (No. 872), under the title of L. pensylvanicum, upon this authority; but having subsequently detected the mistake, we corrected it in No. 1210 (over-leaf) of the same work; where we republished the species by the name of L. dauricum, having ascertained its Siberian origin from native samples in the Lambertian Herbarium. This emendation however, having been overlooked in the works of Messrs. Pursh and Nuttall, as well as in the Hortus Kewensis, it may not be useless to restate the whole correction. The species Catesby mistook it for was probably Lilium Catesbaei, if not philadelphicum" (Ker Gawler 1821: sub t. 594).

Ker Gawler added under his list of synonyms another short note: "*Mr. Nuttall* seems to have been puzzled in adopting the plant as American; and suggests the possibility of its being a hybrid produced during culture, because of its occasionally wanting the pistil in our gardens; an effect more probably of luxuriance, as the pistil is usually perfect with us and frequently fertile. The species is in fact, very close to bulbiferum, but we believe it nevertheless to be truly distinct" (Ker Gawler 1821: sub. t. 594).

Taxonomic treatment

The distribution of *L. pensylvanicum* covers a large area in eastern Asia and, as such, also encompasses some morphological variation mainly in differences of stem stature, flower colour and leaf width. These might best be regarded as of horticultural rather than botanical significance as evidenced in the synonymy. The significantly shorter stature and narrower leaf width of the alpine forms of this species found in Sakhalin Island and in alpine meadows of the Amur Region and the Primorye Mountains we believe merit varietal recognition. We have, therefore, considered that the typical taller more robust, wider leaved variety and the alpine variety are worthy of taxonomic recognition.

Species description for Lilium pensylvanicum

Description. Bulb ovoid-globose, $2-4 \times 2-4$ cm with numerous white, fleshy, convex, lanceolate, acute scales, stoloniferous bearing small subterranean bulbils; stems (5 -) 30-75 (- 120) cm tall, green, sometimes purple spotted, more or less ribbed, partly or entirely covered with white floccose pubescence especially in upper leaf axils and along inflorescence axis; leaves scattered, sessile, blades linear-lanceolate to lanceolate, 1-3 (- 5) veined, 4-10 × 0.2-2 cm, apex acuminate, margins entire or finely papillose; inflorescence 1-3 (- 6) flowered, buds frequently covered in floccose hairs; pedicels erect 1-9 cm long, frequently covered in floccose hairs; flowers erect, red, orange, rarely vellow, spotted or unspotted with dark brown spots, more or less openly campanulate, perianth of six tepals, obovate-spathulate to oblanceolate 3-6 (- 8) × 1-3 cm, inner three equal in size and shape to outer three, all narrowing to a claw-like base, tepals gently recurving at apex, nectariferous sinus densely pubescent along margins; stamens shorter than tepals, filaments glabrous, reddish, anthers 1 cm long, pollen red; pistil slightly longer than filaments, stigma capitate, 3-lobed; capsule oblong-ovoid, obtusely angled $4-5 \times 2-3$ cm.

Habitat. Forest clearings, meadows, riverbanks and sandy areas.

Key to the varieties of Lilium pensylvanicum

- Stems 30-75 (-120) cm; leaves 3-5 veined, lanceolate, 6-10 × 0.5-2 cm; perianth segments 6-9 cm longL. var. pensylvanicum
- Stems (5-) 10-20 cm; leaves 1-3 veined, linear-lanceolate, 4-5 × 0.2 0.5 cm; perianth segments 5-6 cm long...... L. var. alpinum

Lilium pensylvanicum var. *pensylvanicum* Ker Gawl., Bot. Mag. 22 t. 872 (1805). Lectotype designated by Y-D Gao in Taxon 70(5): 1139 (2021) [icon] Bot. Mag. 22 t. 872 (1805)

- \equiv L. dauricum Ker Gawl. Bot. Mag. 30 corrigendum sub t. 1210 (1809).
- \equiv L. bulbiferum subsp. davuricum Baker, Gard. Chron. 1871(2): 1034 (1871).
- ≡ L. maculatum subsp. davuricum (Baker) H.Hara, J. Jap. Bot. 38(8): 249 (1963).
- = L. maculatum var. davuricum (Baker) Ohwi, Fl. Japan: 297 (1965).
- = *Lilium dauricum* [as *L. davuricum*] var. *tigrinum* Regel, Gartenfl. 21: 295 (1872) no ref. or type cited, merely the statement "compare with Gawler t. 872".
- = *Lilium dauricum* [as *davuricum*] var. *costatum* Regel, Gartenfl. 21: 295 (1872) no. ref. or type cited, merely the statement "compare with Gawler t. 872".
- = Lilium pseudodahuricum M.Fedoss. & S.Fedoss., Acta Comment. Imp. Univ. Jurjev. 7(2) Delectus Plantarum Exsiccatarum: 45 (1899). Type: Hubelmann 50 (TU) [Tartu, Estonia] not located. Lectotype designated here: Russia, Chitinskaya Oblast, Dauriya, forest meadows and thickets around the city of Nerchinsk, 20 June 1898, M.Gubelmann 50 (lecto. KFTA!) [KFTA0003266].
- = Lilium sachalinense Vrishcz, Novosti Sist. Vyssh. Rast. 5: 48 (1968). Holotype: Russia Far East, Sachalin [Sakhalin], "litus occidentale, prope opp. Alexandrovsk, western coast between Niarmi and Chirkumnay. 22 June 1916, O.A. Derbek s.n. (holo. LE!) [LE01010710].
- Lilium pensylvanicum f. praecox Vrishcz, Spisok Rast. Gerb. Fl. S.S.S.R. Bot. Inst. Vsesoyuzn. Akad. Nauk 18(90–102): 38. (1970) Lectotype designated here from isotypes: Russia, Siberia, Promorje Prov. [Primorsky Krai] Anuchinsky distr. In pratis varie herbosis 12 June 1967, *D.L.Vrishcz 3104* ex Fl. SSSR 4961(lecto. LE!) [LE01075423]; isolectotypes: (BM!) [BM013719281]; (DAO!) [DA0000466238]; (E!) [E01184390]; (ERE) [ERE0004422]; (JE!) [JE00009931]; (L!) [L1451491]; (L!) [L1451492]; (LE!) [LE01075422]; (MO!) [M03459011]; (MW!) [MW0043937]; (PE!) [PE01713340]; (TK).

Note. Dina Lukinichna Vrishcz did not designate a holotype for the name *L. pen-sylvanicum* f. *praecox* and we, therefore, designate a lectotype here from an isotype in LE.

- Lilium sibiricum Willd., Enum. Pl. Hort. Berol., Suppl.: 17 (1814), nom. nud.
- Lilium dahuricum Reuthe, Gartenflora 40: 476 (1891), nom. nud.

Distribution. China – Hebei, Heilongjiang, Jilin, Liaoning, Nei Mongol; **Japan** – Hokkaido, north Honshu; **Mongolia**; **North Korea**; **Russia** – Amur, Buryatia, Irkutsk, Kamchatka, Khabarovsk, Krasnoyarsk, Kuril Islands, Primorye, Sakhalin, Yakutskiya, Zabaykalsky; **South Korea**.

Phenology. Flowering period is from June to July.

Lilium pensylvanicum var. *alpinum* (N.I.Kuznetsov) J.Compton & Sytin, comb. nov.

urn:lsid:ipni.org:names:77333277-1

Basionym. *Lilium dauricum* var. *alpinum* N.I.Kuznetsov, Trudy Bot. Muz. Rosiisk. Akad. Nauk 18: 80 (1920). *Lectotype* designated here from syntypes (Fig. 8): Russia Far East, Sakhalin Ostrov, Naibuchi Post, [near Dolinsk], 27 June 1899,

Herb, Acad, Se Petropo Mecmynobe. MUSEUM ECTANICUM ACADEMIAE SCIENTIARUM PETROPOLITANAE. 59. Lilium Tauricum ter О.Сахалинь. Посто Найбуше, И Улона 1899. Собр. Н. Шестуновъ.

Figure 8. Lectotype specimen *N.Shestunov* 59 of *Lilium dauricum* var. *alpinum* LE01075424 designated by Compton & Sytin, this paper.

N.Shestunov 59 (lecto. LE!) [LE01075424]; syntypes: Russia Far East, Amurskaya Oblast, Chamberlain N. L. Gondatti Expedition, railway construction line between Nevers and Urusha stations, loam deposits on river bank, 1 May 1910, *Kvashnin-Samarin* 204 (LE!) [LE01075428]; Russia Far East, Amur Oblast, upper reaches of the River Rakindi [Reka Pravaya Rakindi], no collector cited (n.v.); Russia Far East, Sakhalin Ostrov, among rocky mountains, near Due [Dui], 30 May 1872, [*Foma* or *Tomash, Matveyevich*] *Avgustinovich s.n.* (n.v.); Russia Far East, Primoriye Region [Primorsky Krai], Udskoi, [Udskoye, now Khabarovsk Krai] *P.Meyer s.n.* (n.v.).

Distribution. Russia - Amur, Khabarovsk, Primorye, Sakhalin.

This variety probably has a wider distribution than indicated from Herbarium material seen in LE. It is, for example, likely to include short plants known informally as "rebunense" from Rebun Island off the north-west corner of Hokkaido, Japan.

Phenology. Flowering period is from May to June.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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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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