PhytoKeys 242: 1–8 (2024)
DOI: 10.3897/phytokeys.242.119351

Research Article

Primula weiliei (Primulaceae), a new species from Hubei, Central China

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Abstract

In this study, we describe and illustrate a new species, *Primula weiliei* L.S.Yang, Z.K.Wu & G.W.Hu, from the Shennongjia Forestry District, Hubei Province in Central China. It is morphologically assigned to *Primula* sect. *Aleuritia* based on its dwarf and hairless habit, long petiole, fruits longer than calyx and covered by farina on the scape. This new species is similar to *P. gemmifera* and *P. munroi* subsp. *yargongensis* in the same section, but it can be distinguished by its smaller calyxes, homostylous flowers, corolla tube throat without annular appendage and only 1–2 flowers in each inflorescence. Based on the assessment conducted according to the IUCN Red List criteria, we propose that *P. weiliei* be classified as a Critically Endangered (CR) species.

Key words: China, conservation, *Primula*, Section *Aleuritia*, Shennongjia

Academic editor: Avelinah Julius
Received: 23 January 2024
Accepted: 19 April 2024
Published: 9 May 2024

Citation: Yang L-S, Wu Z-K, Liang H-W, Zhang M-H, Zhang X-C, Peng S, Hu G-W (2024) *Primula weiliei* (Primulaceae), a new species from Hubei, Central China. PhytoKeys 242: 1–8. https://doi.org/10.3897/phytokeys.242.119351

Introduction

Primula L. (1753: 142) comprises approximately 500 species worldwide (POWO 2024), making it one of the largest genera in the family Primulaceae-Primuloideae. Most *Primula* species are distributed in the north temperate zones and alpine areas (Hu 1990, 1994). China, particularly the Eastern Himalaya-Hengduan mountains, is the diversity center of the genus, with approximately 300 species spanning 24 sections of *Primula* (Hu 1990, 1994). Hubei province in central China has recorded around 23 species, most of which are distributed in the western Hubei (Hu and Kelso 1996; Yang et al. 2020). The Shennongjia area has been extensively explored since the first visit by Augustine Henry in 1888 and Ernest Henry Wilson's expedition from 1899 to 1911 (Wilson 1929). Recognized as one of the three centers of endemism for seed plants in China (Ying 1996), Shennongjia serves as the type locality for 659 vascular plant species (Xie and Xiong 2020), making it a significant area for biodiversity research and conservation.

In June 2019, during an investigation of a remote mountain peak in Shennongjia, we encountered an unknown plant belonging to the *Primula* sect. *Aleuritia*. We observed two distinct populations consisting of fewer than 50 individuals and collected flowering specimens. In August of the same year, we collected specimens at the fruiting stage, including seeds. In July 2020, we revisited the discovery site to collect additional specimens and capture further photographs of the flower.

According to the Flora of China, there are 49 species in *Primula* sect. *Aleuritia*, comprising 47 heterostylous, and 2 homostylous species viz. *Primula clutterbuckii* Kingdon-Ward and *Primula meiotera* (W. W. Sm. & H. R. Fletcher) C. M. Hu (Hu 1990; Hu and Kelso 1996; Wu et al. 2013; Xu et al. 2017; Ju et al. 2023). The heterostylous species is characterized by pin flowers (with longer styles) and thrum flowers (with shorter styles), while the homostylous type lacks such differentiation, featuring only longer styles (Hu 1990; Hu and Kelso 1996).

Through thorough morphological examination of the newly collected materials, literature review, and comparison with potentially similar species, we have confirmed that this collection is undescribed and distinct from all currently known *Primula* species. Therefore, we describe and illustrate this collection as a new taxon to science named *Primula weiliei* L.S.Yang, Z.K.Wu & G.W.Hu.

Materials and methods

Initial morphological observations, measurements and descriptions of the new taxa were based on living individuals from the wild. Detailed photographs were also taken using a NIKON D750 camera during collection. Some living plants were harvested from the field and cultivated in the Shennongjia National Park lab to study further their growth process, morphological characteristics, and measurements. The type specimens were collected directly from the field, then dried, labelled and databased before being deposited in the Herbarium of Wuhan Botanical Garden (HIB) and Herbarium of the Institute of Botany, Chinese Academy of Sciences (PE). To identify the morphological differences with related species, we consulted relevant literature in the Flora of China and relevant specimens, including some type specimens from the PE, A, E and K, acronym according to Thiers (2016).

Taxonomy

Primula weiliei **L.S.Yang, Z.K.Wu & G.W.Hu, sp. nov.**
urn:lsid:ipni.org:names:77341545-1
Figs 1, 2

Type. China. Hubei Province: Shennongjia Forestry District, Shennongjia National Park, in rock crevices of *Abies* forest, alt. 2700–2900 m, 11 June 2019 (fl.), *Lin-Sen Yang 103* (holotype HIB!; isotype PE!).

Diagnosis. This new species resembles *Primula gemmifera* and *P. munroi* subsp. *yargongensis* but differs significantly from the latter in several aspects: umbels are 1–2-flowered, scapes are 5–10 cm long, bracts measure 2–4 mm long, campanulate calyx is 3–4 mm long, flowers are homostylous, and the corolla throat lacks an annular appendage. Among the homostylous types in *Primula* sect. *Aleuritia*, *P. clutterbuckii*, *P. meiotera*, and *P. weiliei* share some similarities but are distinct from each other. *P. clutterbuckii* and *P. meiotera* feature multiple short stems with clustered leaves showing large and deep serrations along the leaf margin, along with a thick powder abaxially. In contrast, *P. weiliei* has a single rhizome, fewer leaves with fewer dentate or shallow teeth on the margin, and a slightly farinose abaxial surface.

Description. Perennial herbs, 3–5 cm tall, with a small rhizome and few fibrous roots. ***Leaves*** scale-like at the lower part, cauline on the upper part, 4–6; petiole 15–20 mm long, ca. 1/3–1× length of the blade, upper concave; blade spatulate, 13–23 × 8–18 mm, base attenuate, margin shallowly serrate to sharply incised-serrate, apex blunt, slightly farinose or none on both surfaces. Scape 5–10 cm long, obviously white farinose, 1–2(–3) flowered; bracts usually 2(when 1 flower)–3(when 2 flowers), linear-lanceolate, ca. 2–4 mm long, farinose on both surfaces, denser adaxially; pedicel 5–8 mm long, farinose. ***Flower*** homostylous; calyx campanulate, farinose on both surfaces, denser adaxially, tube *c*. 2 mm long, parted to middle, lobes 5, *c*. 2 mm long, lanceolate to triangular, apex mucronate or acuminate; corolla pink or purplish red, tube 7–9 mm long, tubular, narrowed in the middle, gradually widened apically, throat without annular appendage, mouth 2–3 mm wide, limb 10–14 mm wide, lobes obovate, 6–7 × 4 mm, slightly to deeply emarginate; stamen attached to near 3/4 of the tube, 1 × 0.2 mm, apex blunt, slightly lower of tube mouth; ovary nearly spherical, with a smooth surface, placentation free central, style 6 mm long, stigma spherical, *c*. 1 mm in diam., extending to tube apex. Capsule oblong, 4–7 × 3–4 mm, 1.5× to 2× as long as calyx; seeds 60–150, irregularly polygonal, light earthy yellow, black after exposure.

Phenology. Flowering occurs from June to July, and fruiting occurs from July to August.

Etymology. The specific epithet ‘weiliei’ honours Prof. Chen Weilie, a plant ecologist and geobotanist in China, and the first director of the Shennongjia Biodiversity Positioning Research Station, Chinese Academy of Sciences.

Vernacular name. Chinese Mandarin: wei lie bao chun (伟烈报春).

Distribution and habitat. *Primula weiliei* was found exclusively in Shennongjia National Park, located in Hubei, China (Fig. 3). It thrives in rock crevices near forests of *Abies fargesii* Franch., while coexisting with other herbs and bushes, such as *Rhododendon concinnum* Hemsl., *Juniperus squamata* Buch-Ham. ex D.Don, *Allium cyaneum* Regel, *Lonicera tangutica* Maxim and *Androsace henryi* Oliv.

Conservation status. *Primula weiliei* is an exceedingly rare species found in only two small, closely situated populations, with a total population size of approximately 50 individuals. According to the IUCN Red List Categories and Criteria (IUCN 2022), it meets the criteria for being classified as a Critically Endangered species (CR A2acde; B2ab; C2a(i)). Given the threats of climate change and animal damage contributing to population decline, it is imperative to monitor these populations closely to prevent further degradation or extinction.

Additional specimens examined. *Primula gemmifera*: China, Sichuan, 11500 ft, July 1904, *E. H. Wilson, 4031* (A barcode A00073544, image seen!); Yunnan, 14200 ft, Aug 1914, *George Forrest 13231* (K barcode K000750072, image seen!). *Primula meiotera*: China, Xizang, Kongbo, 11500 ft, 12 Jul 1938, *F. Ludlow, G. Sherriff, & G. Taylor 5218* (BM barcode BM000996905, E barcode E00024506, images seen!). *Primula clutterbuckii*: India, Bangladesh & Pakistan, [ca. 28°21'N, 96°37'E], 10000–11000 ft, 23 May 1928, *F. Kingdon-Ward 8235* (E barcode E00024452, K barcode K000750416, images seen!).

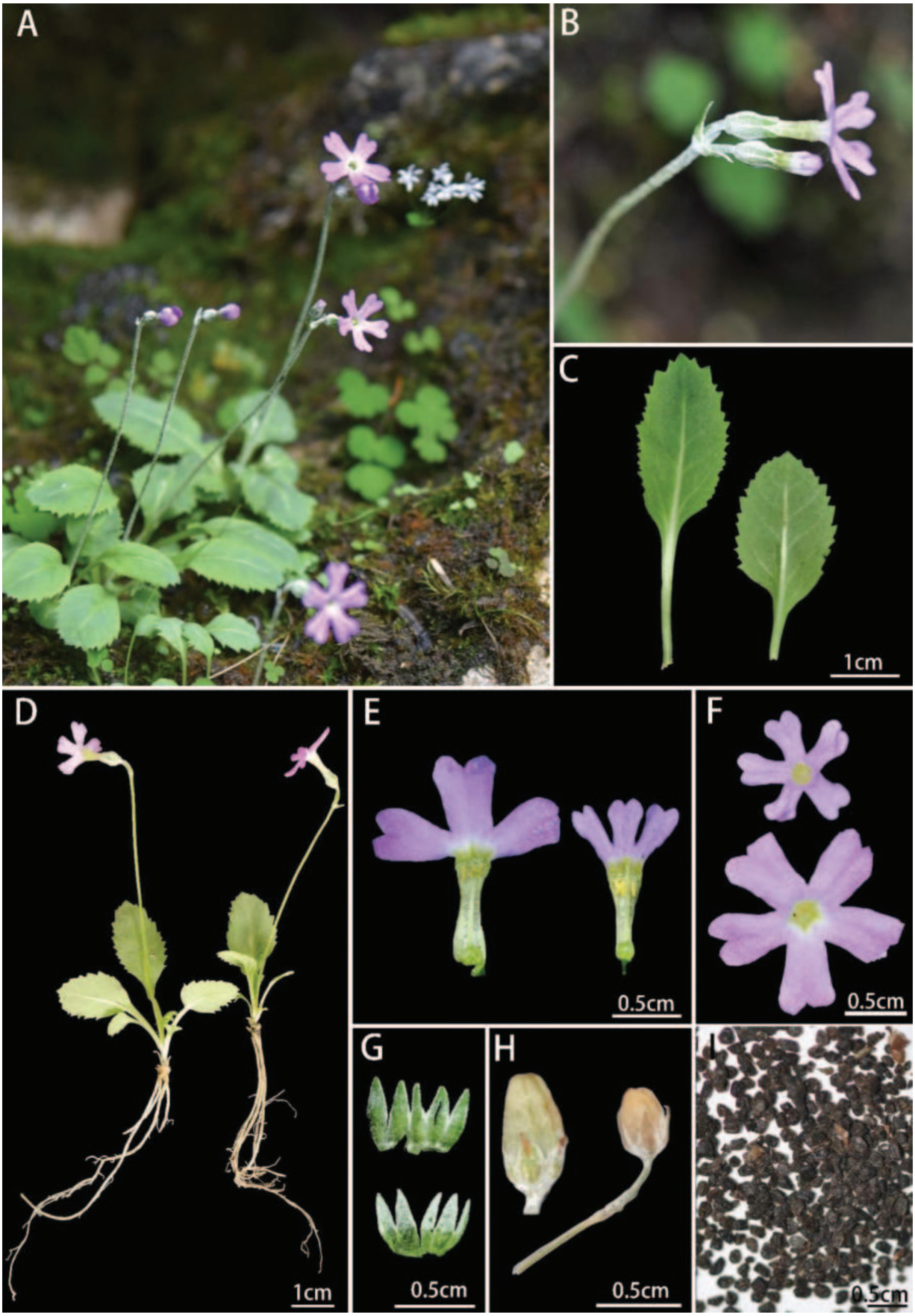

Figure 1. *Primula weiliei* L.S.Yang, Z.K.Wu & G.W.Hu **A** habitat **B** inflorescence **C** leaves **D** habits **E** corollas, long homostyly **F** corollas adaxial surface **G** calyxes, the upper abaxial, the lower adaxial **H** fruits **I** seeds.

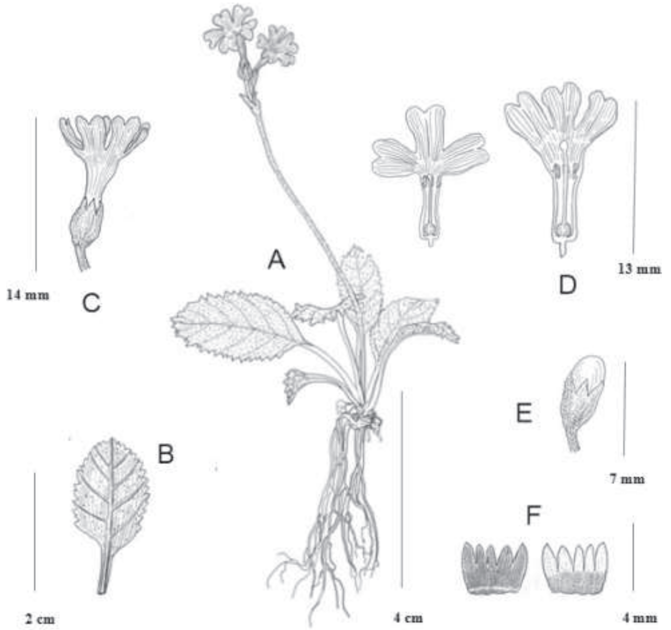

Figure 2. *Primula weiliei* **A** habit **B** leaf abaxial side **C** flower lateral view **D** corollas, long homostyly **E** ripe fruit **F** calyx, abaxial view (left), adaxial view (right). (Drawn by Ms Xiang-Li Wu).

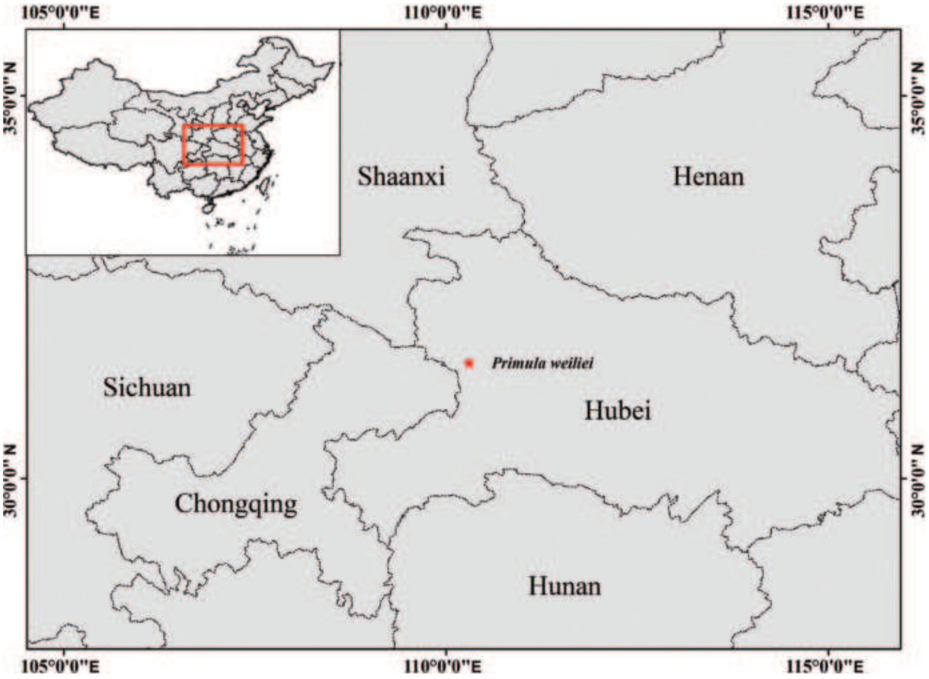

Figure 3. The distribution of *Primula weiliei* (star).

Taxonomic notes. We have thoroughly compared the new species and several closely related species, as detailed in Table 1. Notably, *Primula weiliei* and its closely related species exhibit similar characteristics, including irregularly denticulate leaf margins, winged leaf stalks, lanceolate bracts, campanulate calyx typically splitting to the middle or below, lanceolate sepals, and generally purple corollas. However, a few distinct characteristics can differentiate the new species from its closely related species. For instance, the calyx length of

Table 1. Morphological comparison between *Primula weiliei* and its related species.

Characters	*P. weiliei*	*P. munroi* subsp. *yargongensis*	*P. gemmifera*	*P. clutterbuckii*	*P. meiotera*
Plants farinose	Farinose	Efarinose	Farinose	Farinose	Farinose
Scape length	5–10 cm	10–30 cm	8–30 cm	0.8–2.5 cm	0.3–4 cm
Inflorescence	1–2(3)-flowered	2–6-flowered	3–10-flowered	1–2-flowered	1–2-flowered
Bracts bottom prolonged	Not	Bottom prolonged into auricles	Not	Not	Not
Calyx length	3–4 mm	5–10 mm	6–10 mm	8–10 mm	4 mm
Style	Homostylous	Heterostylous	Heterostylous	Homostylous	Homostylous
Corolla tube length	7–9 mm	10–12 mm	8–13 mm	15–16 mm	4 mm
Corolla throat appendage	Absent	Existing	Existing	Absent	Absent

P. gemmifera and *P. munroi* subsp. *yargongensis* exceeds that of the new species by double its length. Furthermore, while the latter species typically bear more than two flowers on one scape, the new species only bear 1–2 flowers. Additionally, both the latter species are heterostylous with throat appendages in the corolla tubes, making them easily distinguishable (Hu 1990; Hu and Kelso 1996). The scarcity of homostylous types in *Primula* sect. *Aleuritia* underscores the importance of their characteristics. Despite many similarities among the three known species with homostylous flowers, such as the presence of 1–2 flowers in the inflorescence, sepals splitting in half, and the stigma and anther tips located near the corolla tube mouth, notable differences exist among these species. For instance, *P. weiliei* has sparse leaf teeth, scarcely farinose leaves, and a 7–9 mm corolla tube length. In contrast, *P. clutterbuckii* and *P. meiotera* have corolla tubes that are 15–16 mm and 4 mm long, respectively, and their leaves have coarse marginal teeth and are densely farinose on the abaxial surface.

Shennongjia, located in central China, is recognised as a biodiversity hotspot that has garnered the attention of numerous botanists, increasing botanical surveys conducted in the area in recent years. The discovery of *Primula weiliei* further expands the known distribution of Primula species within this region, emphasising the significance of continual botanical exploration within biodiversity hotspots. Notably, the four species mentioned above, *P. munroi* subsp. *yargongensis*, *P. gemmifera*, *P. clutterbuckii*, and *P. meiotera*, closely related to *P. weiliei*, are distributed in southeastern Tibet and the Hengduan Mountains. This suggests a potential correlation between the plant floras of western Hubei and eastern Himalaya, necessitating further analysis involving a broader range of plant taxa to establish a confirmation. Given the limited number of known specimens originating from its type locality, it is imperative to expedite an investigation into the conservation status of this newly discovered species. Accordingly, the development and implementation of effective conservation strategies are pivotal to ensure the long-term survival of this species.

Acknowledgements

Thanks for their suggestions to Dr. Xin-Wei Li, David Boufford and Da-Yong Fan for improving this manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by Hubei Natural Science Foundation (2015CFA149), the National Natural Science Foundation of China (32270228, 31970211) and the Project of National Plant Specimen Resource Center (NPSRC) (E0117G1001).

Author contributions

Conceptualization: GWH. Data curation: MHZ. Formal analysis: LSY. Methodology: ZKW. Resources: HWL. Supervision: XCZ. Validation: SP. Visualization: ZKW. Writing – original draft: LSY. Writing – review and editing: ZKW, PS, YLS.

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Data availability

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

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PhytoKeys 242: 9–20 (2024)
DOI: 10.3897/phytokeys.242.121734

Research Article

Viola suavis var. *pannonica* (Violaceae), a new white-flowered violet from central Europe

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Abstract

Viola suavis var. *pannonica* (Violaceae) from central Europe is described here as a new variety to science. It is most similar to the blue-flowered *V. suavis* var. *suavis* and the white-flowered *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*, but exhibits differences in several characters, such as petal colour, spur shape, fimbriae length on the stipules, bracteoles position on the peduncle and lamina sinus shape. Although the new taxon is often considered a colour mutation of *V. suavis* var. *suavis*, previous genetic analyses revealed that these white-flowered plants do not arise recurrently at different locations (having multiple origins), but rather form a monophyletic evolutionary lineage. To date, the occurrence of *V. suavis* var. *pannonica* has been reported in the Slovak Republic, the Czech Republic and western Ukraine. In this paper, we report its occurrence in Austria and Hungary. Notes on its etymology, distribution, ecology, origin and hybridization, as well as photographs of the new variety (including the holotype) are also provided.

Key words: Pannonia, protologue, taxonomy, variety

Academic editor: Thomas Marcussen
Received: 26 February 2024
Accepted: 23 April 2024
Published: 9 May 2024

Citation: Hodálová I, Mereďa Jr P (2024) *Viola suavis* var. *pannonica* (Violaceae), a new white-flowered violet from central Europe. PhytoKeys 242: 9–20. https://doi.org/10.3897/phytokeys.242.121734

Introduction

Viola suavis M.Bieb. from *Viola* L. subsect. *Viola* (*Violaceae*) is a perennial herb, differing from related *Viola* species of the subsection in a number of characters: relatively short and stout stolons, long fimbriate stipules, bracteoles located below the middle of the peduncle, glabrous calycine appendages appressed to the peduncle, fragrant flowers (cf. Becker 1910; Gams 1925; Valentine et al. 1968; Kirschner and Skalický 1990; Marcussen and Nordal 1998; Hodálová et al. 2008; Mereďa et al. 2008a, 2008b), and 2n = 40 chromosomes (interpreted by different authors either as tetraploid- or (paleo)octoploid; cf. Schmidt 1961; Kirschner and Skalický 1990; Mereďa et al. 2008a, 2008b; Marcussen et al. 2022). The species has been described from northeastern Ukraine (town of Merefa near the city of Kharkiv; the type is deposited in the herbarium of the Komarov Botanical Institute of The Russian Academy of Sciences, Saint Petersburg, Russia; herbarium acronym LE; Marschall von Bieberstein 1819). The distribution range of *V. suavis* extends from the Caucasus and Ural Mountains through the European Mediterranean and sub-Mediterranean regions to the Iberian Peninsula and Morocco; secondarily, due to cultivation, its area also extends to some parts of western, central and northern Europe (Marcussen and Nordal 1998; Mereďa et al. 2011). An isolated occurrence of the species has been recently reported in Kashmir Himalaya (Ganie et al. 2023). *Viola suavis* prefers dry grasslands, shrublands and open deciduous forests; in addition, it frequently occurs in human-made or human-influenced habitats, such as gardens, parks and cemeteries (Kirschner and Skalický 1990; Marcussen and Nordal 1998; Hodálová et al. 2008; Mereďa et al. 2008b).

Viola suavis is a polymorphic species displaying geographically correlated morphological variation, which complicates its taxonomic treatment (Haesler 1975; Marcussen and Nordal 1998; Marcussen and Borgen 2000; Hodálová et al. 2008; van den Hof et al. 2008; Mereďa et al. 2008a, 2011; Ganie et al. 2023). The results of our previous molecular, morphological and chorological studies (Hodálová et al. 2008; Mereďa et al. 2008a, 2008b, 2011) provided strong support for the recognition of four major genetic-morphological lineages of *V. suavis* in Europe, three of which are currently treated in the majority of relevant studies at the subspecific level (e.g., Raab-Straube and Henning 2018+; Nikolić 2020; however, see Marcussen et al. 2022, according to which taxa within *V. suavis* do not merit formal taxonomic recognition): (1) *V. suavis* subsp. *suavis*, occurring in central and eastern Europe (e.g., Mereďa et al. 2008b; Danihelka 2019; Pyšek et al. 2022); (2) *V. suavis* subsp. *adriatica* (Freyn) Haesler (Haesler 1975: 111; bas. *V. adriatica* Freyn 1884: 679), occurring in northeastern Italy, southwestern Slovenia and northwestern Croatia (Mereďa et al. 2011; Nikolić 2020); and (3) *V. suavis* subsp. *austrodalmatica* Mereďa & Hodálová, occurring in southern Croatia, southern Bosnia and Herzegovina and southwestern Montenegro (Mereďa et al. 2011; Nikolić 2020). All three of these subspecies are morphologically clearly distinguishable by several characters, mainly the leaf indument (Mereďa et al. 2008a, 2011).

The detailed morphological pattern of the fourth European genetic lineage (provisionally named *V. suavis* 'Spain') has not yet been elucidated and requires a more thorough study (see Mereďa et al. 2008a, 2011). Populations of this lineage have been found in northeastern Spain and potentially in the adjacent part of France. In the relevant literature, the taxon is regarded as identical to *V. suavis* s. str. (e.g., Valentine et al. 1968; Muñoz Garmendia et al. 1993) or *V. suavis* subsp. *suavis* (e.g., Raab-Straube and Henning 2018+), depending on the taxonomic species concept.

While *V. suavis* subsp. *adriatica* and *V. suavis* subsp. *austrodalmatica* possess only blue to bluish violet petals, *V. suavis* subsp. *suavis* and *V. suavis* 'Spain' have two colour variants: one with typical blue to bluish violet petals (blue variant; Fig. 1C) and one with white petals (white variant; Fig. 1B). The blue and white variants within the given taxa are genetically distinct (Fig. 1A), and in addition to flower pigmentation, they differ in several other morphological characters (Mereďa et al. 2008a, 2008b, 2011; see also Diagnosis). Amplified fragment length polymorphism (AFLP) analyses revealed that white-flowered *V. suavis* subsp. *suavis* and white-flowered *V. suavis* 'Spain' do not arise recurrently at different locations (with multiple origins) but rather form two monophyletic, evolutionarily independent, parallel genetic entities descended from different blue-flowered progenitors in two distinct areas (central Europe and the Iberian Peninsula). Thus, the sympatric occurrence of two colour variants

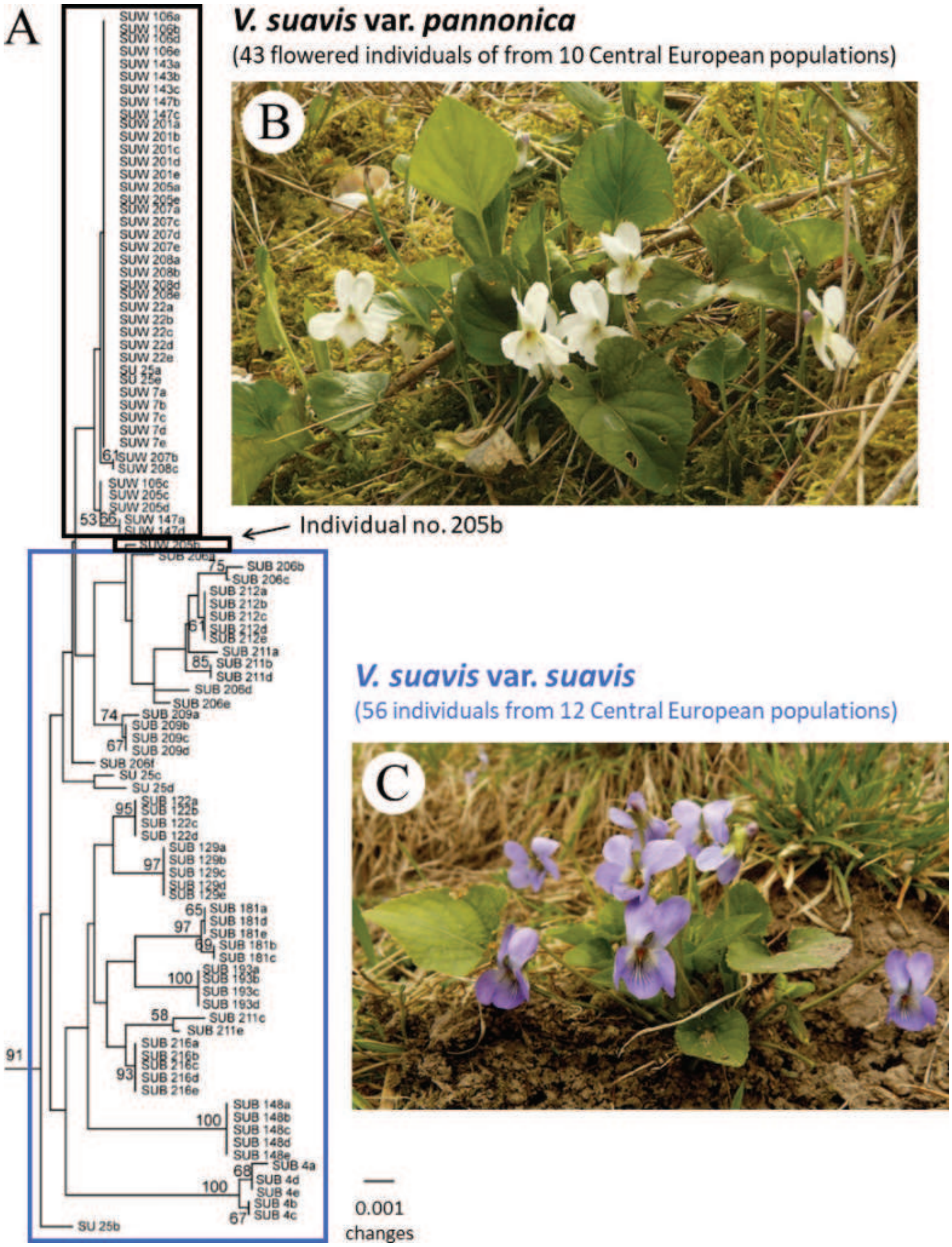

Figure 1. **A** Part of the neighbor-joining tree of AFLP data of 100 central European individuals of *Viola suavis* subsp. *suavis* using Nei and Li distance. Numbers above branches indicate bootstrap support above 50%. Accession labels include taxon abbreviation (SUB – blue-flowered variant (*V. suavis* var. *suavis*); SUW – white-flowered variant (*V. suavis* var. *pannonica*)) and population numbers. Taken from Mereďa et al. (2008a) **B** *V. suavis* var. *pannonica* (Slovakia, Zbrojníky village; photographed by P. Mereďa Jr., 17 April 2013) **C** *Viola suavis* var. *suavis* (Hungary, Visegrád village; photographed by P. Mereďa Jr., 26 March 2011).

within both *V. suavis* subsp. *suavis* and *V. suavis* 'Spain' is most likely the result of secondary contact (Mereďa et al. 2008a).

The white-flowered variant of *V. suavis* 'Spain' from the Iberian Peninsula (Fig. 2) was originally described as *V. catalonica* W.Becker (Becker 1929: 43) from the current public park Jardin del Turó del Putget in Barcelona (Spain)

Figure 2. *Viola suavis* var. *catalonica* (Spain, town of Manlleu; photographed by P. Mereďa Jr., 17 March 2006).

(the type is deposited in the Conservatoire et Jardin Botaniques de la Ville de Genève, Switzerland; herbarium acronym G); later, it was treated at the subspecific level [*V. suavis* subsp. *catalonica* (W.Becker) O.Bolòs & Vigo; Bolòs and Vigo 1974: 80] or as the variety *V. suavis* var. *catalonica* (W.Becker) Espeut (Espeut 1999: 16).

The central European white-flowered variant of *V. suavis* subsp. *suavis* (Fig. 1B) has not yet been formally described. In local databases, floras and keys, it is neglected (Farkas 2009), treated as "white-flowered violets of presumed hybrid origin" (Kirschner and Skalický 1990; Suda 2002) or a "white-flowered morphotype" of *V. suavis* subsp. *suavis* (Mereďa et al. 2008b), or considered a *V. suavis* variation (e.g., Michalcová 2011+; Danihelka 2019; FloraVeg.EU 2022+).

Recently, white-flowered individuals of *V. suavis* have been found in a third geographic area, the Kashmir Himalaya (India), and described as a new subspecies, *V. suavis* subsp. *naqshii* (Ganie et al. 2023). This taxon has not been studied morphometrically or genetically. However, it shares several common characters with *V. suavis* var. *catalonica*, such as a hooked spur (Fig. 3A, B) and bracteoles located on the peduncle at a relatively high position.

The aim of this study was to formally describe the central European white-flowered populations of *V. suavis* as a separate taxon at the variety level, based on the results of our previous genetic and morphological studies of the genus *Viola* (Mereďa et al. 2008a, 2011).

Material and methods

Living plant material was used for morphological studies, including 173 individuals from 16 populations of *Viola suavis* var. *suavis*, 108 individuals from 12 populations of *V. suavis* var. *pannonica* and 42 individuals from 5 populations of *V. suavis* var. *catalonica*. Whenever possible, three measurements were made for each vegetative character, and two measurements were made for each floral character. The value ranges represent the 10th and 90th percentiles, with the 1st and 99th percentiles in parentheses. All measurements were performed at the time of flowering; for character explanations, see Fig. 4. Details on the origin of the material used are given in Mereďa et al. (2008a). Character values for *V. suavis* subsp. *naqshii* have been taken from Ganie et al. (2023).

Taxonomy

***Viola suavis* var. *pannonica* Hodálová & Mereďa, var. nov.**
urn:lsid:ipni.org:names:77341546-1
Figs 1B, 3C, 5, 6

Diagnosis. *Viola suavis* var. *pannonica* can be unambiguously distinguished from *V. suavis* var. *suavis* by flower colour: *V. suavis* var. *pannonica* possesses white petals (and a pale to deep violet spur, very rarely whitish or slightly yellow-greenish; Figs 1B, 3C, 6A); *V. suavis* var. *suavis* possesses pale to deep blue or bluish violet petals with a large conspicuous white throat at the base, covering 1/3–1/2 of the length of the lateral and anterior petals (and a pale to deep violet spur; Fig. 1C). In addition to characters associated with pigmentation of the generative and vegetative parts, both varieties also differed in terms of the length of the fimbriae on the stipules ((0.8–)1.2–2.5(–3.1) mm long in *V. suavis* var. *pannonica* vs. (0.4–)0.7–2.0(–2.8) mm long in *V. suavis* var. *suavis*) and by the position of the bracteoles on the peduncle (at (4–)9–29(–40)% of the overall length of the peduncle in *V. suavis* var. *pannonica* vs. (7–)13–42(–52)% in *V. suavis* var. *suavis*).

In addition, *V. suavis* var. *pannonica* differs from the white-flowered *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*, having straight or only slightly upward-curved spur at the top (Fig. 3C) (vs. often distinctly hooked spur (curved up or backwards at the top) in *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*; Fig. 3A, B). Moreover, *V. suavis* var. *pannonica* differs from *V. suavis* var. *catalonica* in terms of the lamina sinus angle ((0–)35–105(–135)° in *V. suavis* var. *pannonica* vs. (-90–)-23–45(–85)° in *V. suavis* var. *catalonica*), lamina sinus depth ((0.1–)0.2–0.55(–1.4) cm vs. (0.3–)0.45–1.1(–1.4) cm), and bracteoles located near the base of the peduncle (at (4–)9–29(–40)% of the overall length of the peduncle vs. at (15–)25–52(–60)% of the overall length of the peduncle). *Viola suavis* var. *pannonica* differs from *V. suavis* subsp. *naqshii* in its longer petiole hairs (0.2–0.6(–0.8) mm in *V. suavis* var. *pannonica* vs. up to 0.1 mm in *V. suavis* subsp. *naqshii*).

Type. Slovak Republic. Devínska Kobyla Hills, Bratislava-Dúbravka borough, Brižite hill, Martina Granca street, 48°11'49"N, 17°01'29"E, elev. 240 m, 1 April 2003, I. Hodálová (Holotype: SAV (SAV0017750; Fig. 5)).

Phenology. Flowering from March to April.

Etymology. The epithet “pannonica” refers to the geographical region of Pannonia, which is the centre of the hitherto known distribution of the new variety (namely southeastern Moravia in the Czech Republic, northeastern Austria, southern Slovakia, the southern part of Zakarpattia Oblast in western Ukraine, and Hungary; see Distribution).

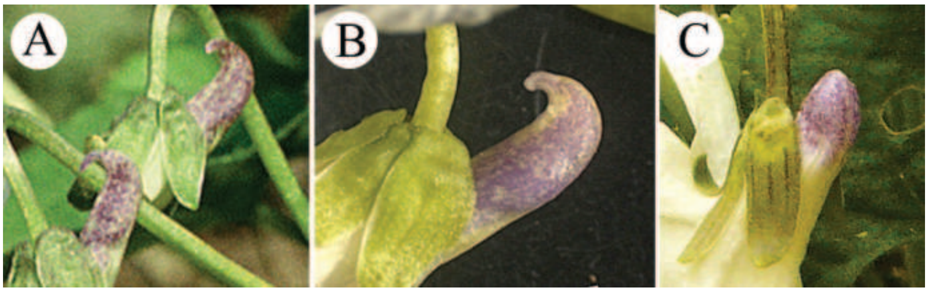

Figure 3. Shape of the spur **A** *Viola suavis* var. *catalonica* (Spain, town of Manlleu; photographed by P. Mereďa Jr., 17 March 2006) **B** *V. suavis* subsp. *naqshii* (India, town of Hazratbal; taken from Ganie et al. 2023) **C** *V. suavis* var. *pannonica* (Slovakia, Zbrojníky village; photographed by P. Mereďa Jr., 17 April 2013).

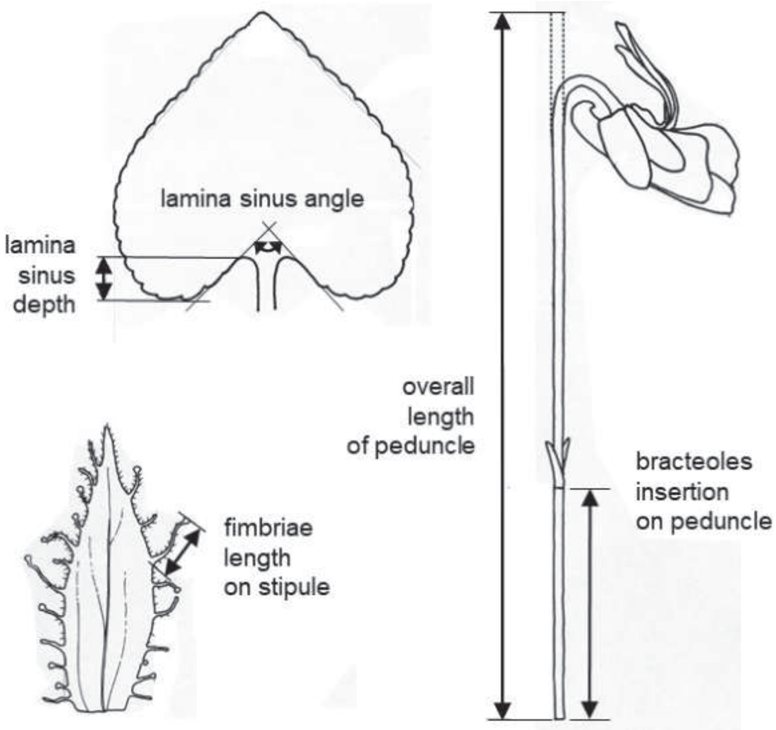

Figure 4. Selected morphological characters used in Diagnosis (after Hodálová et al. 2008).

Distribution. This variety has been reported in the Slovak Republic (Hodálová et al. 2008; Mereďa et al. 2008a; detailed distribution is given in Mereďa et al. 2008b; see also photographs of *V. suavis* at iNaturalist.org (Photo ID: 202520428, 201130424), nahuby.sk (Photo ID: 257298), http://flora.upol.cz/fotogalerie/info/9125-Viola-suavis/0-42.html, and www.botany.cz/cs/viola-suavis), the Czech Republic (Kirschner and Skalický 1990: 402; Suda 2002: 214 – both papers report the taxon in the note for *V. alba* as "white-flowered violets of presumed hybrid origin"; Hodálová et al. 2008; Mereďa et al. 2008a; Michalcová 2011+; Danihelka 2019; FloraVeg.EU 2022+; see also photographs of *V. suavis* at iNaturalist.org (Photo ID: 151489049, 151956929, 189937608, 201837659, 201843269, 201843461, 201905803, 201906388, 202177193, 202414626, 202716834, 202963367)), western Ukraine (Mereďa et al. 2008a), Austria, and Hungary (both this paper; Fig. 7).

Holotypus

HERBARIUM INSTITUTI BOTANICI
ACADEMIAE SCIENTIARUM SLOVACAE
Bratislava, Slovacia (SAV)

Flora Slovakiae

Viola suavis M. Bieb. var. pannonica
Hodálová & Mereďa Jr.

Loc.: SLOVAK REPUBLIC. Devinska Kobyla Hills, Bratislava-Dúbravka borough, Brižite hill, Martina Granca street; 49°36'24"N, 17°15'26" E

Alt. s. m.: 240 m
Leg.: Iva Hodálová
Die: 1 April 2003
Det.: Iva Hodálová & Pavol Mereďa, Jr.
Die: 1 April 2003

Figure 5. The holotype specimen of *Viola suavis* var. *pannonica* deposited in the herbarium of the Institute of Botany, Slovak Academy of Sciences (herbarium acronym SAV).

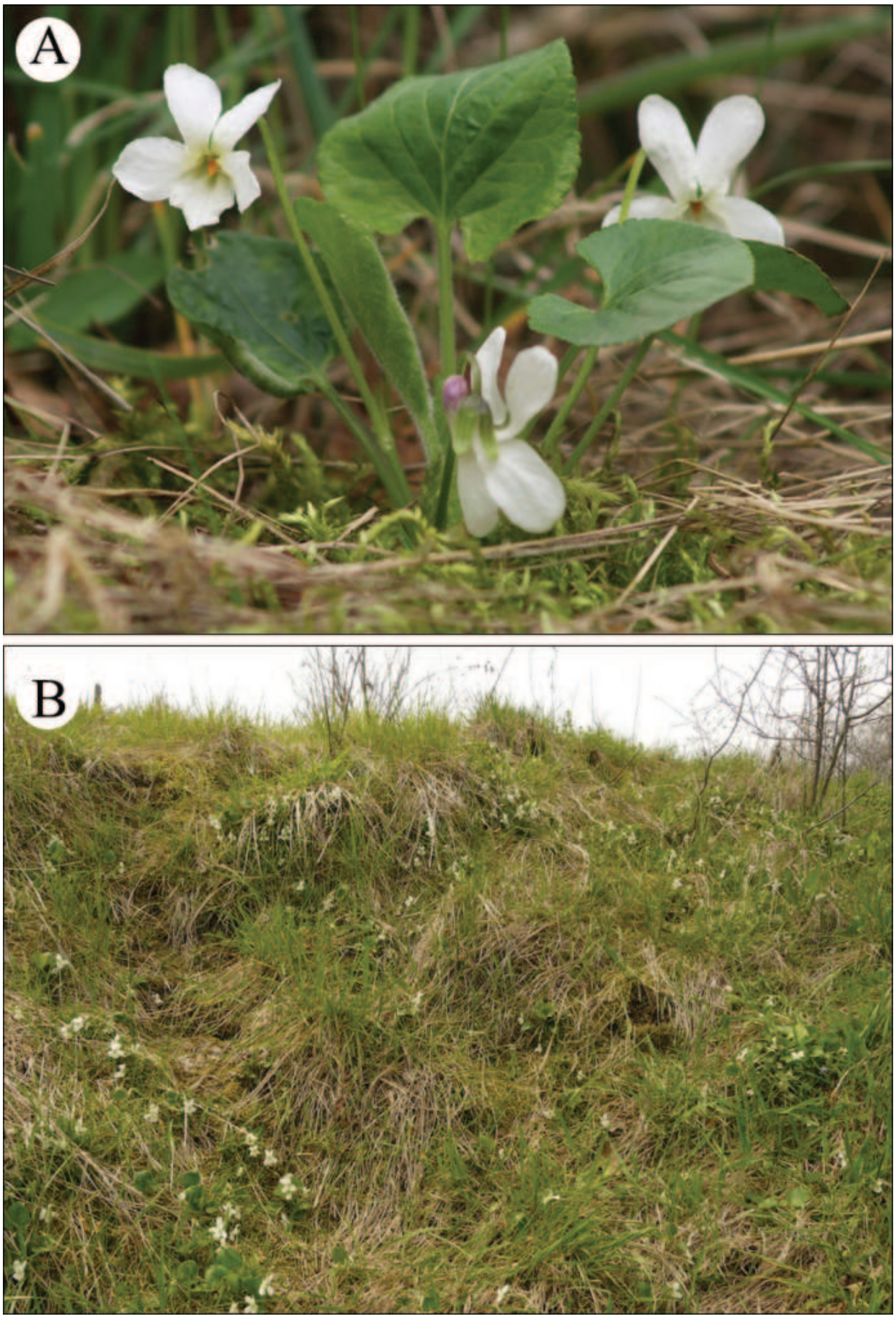

Figure 6. A *Viola suavis* var. *pannonica*, plant from the type population (Slovak Republic, Bratislava-Dúbravka borough; photographed by P. Mereďa Jr., 3 April 2008) **B** *V. suavis* var. *pannonica*, habitat (Slovak Republic, Zbrojníky village; photographed by P. Mereďa Jr., 17 April 2013).

This new variety has not yet been reported in the territories of Austria (cf. Fischer et al. 2008) and Hungary (cf. Farkas 2009). Its occurrence in Austria is documented by the photograph from Martin A. Prinz from the town of Traiskirchen, available from iNaturalist.org (Photo ID: 150078107, ut *V. suavis*). In Hungary we found *V. suavis* var. *pannonica* in one location in the northern part of the country: Visegrád village, at the end of Kálvária street, 47°47'09"N, 18°58'20"E,

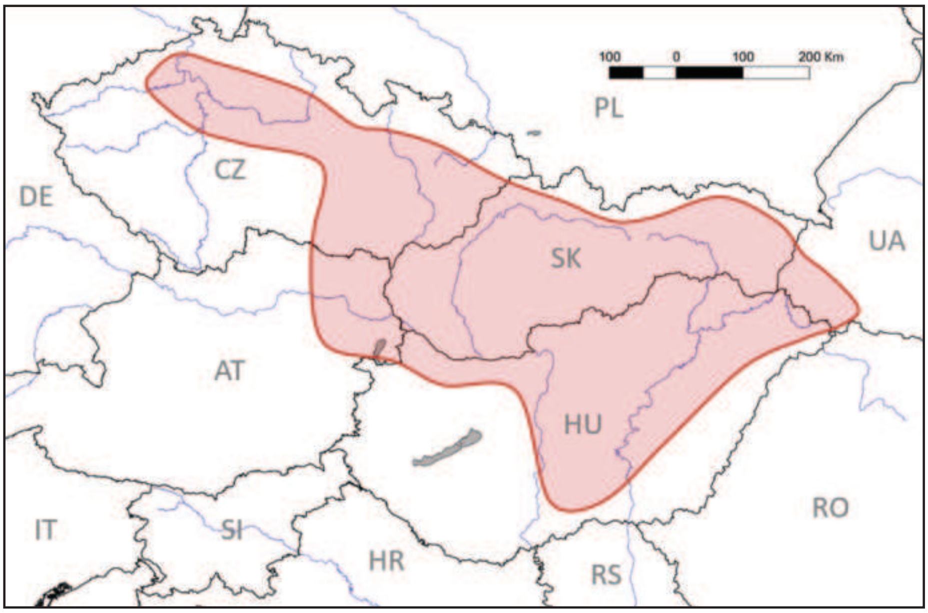

Figure 7. Distribution of *Viola suavis* var. *pannonica*.

126 m, 26 March 2011, P. Mereďa Jr. (photo). In addition, we examined seven other herbarium specimens of the taxon from Hungary (all deposited in the Hungarian Natural History Museum, Budapest, Hungary; herbarium acronym BP; localities are arranged from west to east): near the town of Győr, Csanak, 16 April 1917 and 21 April 1928, S. Polgár (BP), both ut *Viola alba*; Piliscsaba village, Disznófő hill, 6 April 1913, L. Vajda (BP), ut *V. alba*; Budapest city, district II, Hármashatárhegy hill, 12 March 2000, É. I. Bőhm (BP), ut *V. odorata*; Budapest city, district II, Szemlőhegy utca street, 2 April 1917, Á. Boros (BP), ut *V. odorata*; Sárospatak town, 10 April 1933, Á. Kiss (BP), ut *V. alba*; and near the town of Nyiregyháza, Nyiregyházai-erdő forest, 25 March 1927, Á. Boros (BP), ut *V. suavis*. In Hungary this variety has also been documented in two photographs available from iNaturalist.org (Photo ID: 201304283, 203637437). The precise locations of the new variety in the Czech Republic, Austria, Ukraine and Hungary are not yet known, and in these countries, this violet will certainly be more widespread than the data published thus far indicate. The occurrence of *V. suavis* var. *pannonica* is also expected in other central European countries.

Ecology. It grows (often in extensive patches; Fig. 6B) mainly in human-made or human-influenced habitats, such as lawns, parks, cemeteries and roadsides in human settlements. It is also commonly cultivated in gardens, from which it is escaping (due to efficient spreading by rooting procumbent stolons and a high seed set per capsule) into their vicinity. In contrast to the nominate variety, *V. suavis* var. *pannonica* only rarely extends into natural and semi-natural habitats outside settlements, where it grows in dry to mesophilous grasslands (Fig. 6B), shrublands, forest edges and open deciduous forests on various soil types (Mereďa et al. 2008a, 2008b).

Taxonomic notes and hybridisation. Although in some older studies the authors assumed a hybrid origin of *V. suavis* var. *pannonica* (based mainly on some shared morphological characters with other members of *V.* subsect. *Viola*, namely, *V. odorata* L., *V. collina* Besser, *V. hirta* L., *V. suavis*, and *V. alba*

Besser; cf. Kirschner and Skalický 1990; Suda 2002), molecular analyses clearly revealed that the variety is exclusively derived from the typical blue-flowered central European *V*. *suavis* subsp. *suavis* (similar to *V*. *suavis* var. *catalonica*, which is derived from the Iberian blue-flowered *V*. *suavis* 'Spain'; Mereďa et al. 2008a, 2011). Genetic analyses revealed that *V*. *suavis* var. *pannonica* has very low genetic variation (Fig. 1A), and most populations in central Europe likely represent the same strain, which was spread in the past by cultivation as ornamentals in gardens and parks and subsequently escaped into the surrounding natural environment. The highly reduced genetic diversity and absence of unique AFLP fragments in individuals of *V*. *suavis* var. *pannonica*, along with the patterns of fragment sharing and population clustering, clearly demonstrate that the origin of *V*. *suavis* var. *pannonica* has been recent, perhaps within the last few centuries (Mereďa et al. 2008a).

Although *V*. *suavis* var. *pannonica* is often sympatric with the blue-flowered *V*. *suavis* var. *suavis* as well as other species of *Viola* subsect. *Viola* (especially *V*. *odorata* and *V*. *hirta*), no morphologically or genetically intermediate individuals have been detected. The absence of hybrids with *V*. *odorata* and *V*. *hirta* is not surprising as both these species have a different number of chromosomes (2n = 20), and heteroploid hybrids are rare in *Viola* subsect. *Viola* (Mereďa et al. 2008b).

However, the absence of morphologically or genetically intermediate plants between *V*. *suavis* var. *suavis* and *V*. *suavis* var. *pannonica* is especially surprising. It is possible that the flower colour in violets may be encoded by a biallelic system where the blue allele is dominant; in that case, colour intermediates might not be possible. However, it is surprising that even in the AFLP analyses, we practically did not identify genetically intermediate individuals, even in locations where the blue- and white-flowered plants were found growing in close proximity or even partly intermingled (population nos 25 and 27, 205 and 206, 208 and 209; Mereďa et al. 2008a and Fig. 1A). An identical situation also occurred for the two colour variants of *V*. *suavis* in Spain (Mereďa et al. 2008a). The AFLP analyses indicated a possible hybrid origin in only one plant, white-flowered individual no. 205b, which grouped together (although with low bootstrap support) with the blue-flowered plants (Mereďa et al. 2008a and Fig. 1A).

Acknowledgements

This study was financially supported by the Grant Agency VEGA, Bratislava, Slovak Republic (grant no. 2/0161/21). We thank Jiří Danihelka (Masaryk University, Brno, Czech Republic), Marc Espeut (Prades, France) and Thoman Marcussen (University of Oslo, Norway) for valuable comments on the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was financially supported by the Grant Agency VEGA, Bratislava, Slovak Republic (grant no. 2/0161/21).

Author contributions

Conceptualisation, data curation, methodology, writing: IH, PM.

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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 242: 21–29 (2024)
DOI: 10.3897/phytokeys.242.115955

Research Article

Re-discovery and taxonomic clarification of *Oreocharis leveilleana* (Gesneriaceae) in Guizhou, China, over 100 years

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Abstract

Oreocharis leveilleana Fedde was collected in Ta-pin in 1910 and published in 1911. The collected location was verified within western Luodian County, Guizhou Province, China. However, there have been no records of the species' collection for more than 100 years since then. After extensive investigations by our research team on the type locality and its surrounding areas, we found that it is widely distributed in western Luodian County and eastern Wangmo County, Guizhou Province, China. During further research on the original literature, type specimens and type locality of *O. leveilleana*, the taxonomic position of *O. leveilleana*, which was once treated as a synonym of *O. auricula* (S.Moore) C.B.Clarke, was found to have a taxonomic problem. Through morphological research combined with geographical distribution analysis, it has been determined that it should belong to the genus *Petrocodon* Hance and it is the same species as *P. coccineus* (C.Y.Wu ex H.W.Li) Yin Z.Wang. According to the regulations and suggestions of the 2018 "International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)", we propose and confirm a new combination – *Petrocodon leveilleanus* (Fedde) X.X.Bai & F.Wen and treat *P. coccineus* as a synonym of the new combination. Due to its unique bright red flowers within *Petrocodon*, its original Chinese name has been retained.

Key words: *Oreocharis*, *Petrocodon*, *Petrocodon coccineus*, new combination, synonym

Academic editor: Laura Clavijo
Received: 19 November 2023
Accepted: 9 April 2024
Published: 10 May 2024

Citation: Xiong X-K, He S-T, Zhou Y-L, Wen F, Bai X-X (2024) Re-discovery and taxonomic clarification of *Oreocharis leveilleana* (Gesneriaceae) in Guizhou, China, over 100 years. PhytoKeys 242: 21–29. https://doi.org/10.3897/phytokeys.242.115955

Introduction

The genus *Oreocharis* Benth., established by G. Bentham (1876), belongs to the tribe Trichosporeae, subfam. Didymocarpoideae, Gesneriaceae (Weber et al. 2013). Currently, there are more than 150 recorded species (excluding infraspecific taxa), while China has about 158 taxa (including 15 varieties). These plants are predominantly distributed in the south-western region of China and most parts of southern China, with about ten species distributed in Vietnam, Myanmar, Japan and Thailand (GRC 2023). *Oreocharis* is a diverse group of plants with various morphologies. There have been significant discrepancies in taxonomic viewpoints amongst scholars in different periods, leading to substantial changes in its systematic position. It was not until Möller et al. (2011), based on molecular evidence and morphological analysis, merged nine genera including *Ancylostemon* Craib, *Opithandra* B.L.Burtt, *Isometrum* Craib, *Tremacron* Craib, *Bournea* Oliv., *Dayaoshania* W.T.Wang, *Thamnocharis* W.T.Wang, *Deinocheilos* W.T.Wang, *Paraisometrum* W.T.Wang and the rosulate taxa of *Briggsia* Craib into the enlarged concept of *Oreocharis*, that the systematic revision of this genus was essentially completed. Although the genus *Bournea* was considered an independent genus again (Chen et al. 2020), further research did not support this view (Lv et al. 2022). The frequent and extensive revisions in taxonomy have led to changes in the systematic positions and scientific names of numerous species, making the study of *Oreocharis* even more complex (Fu et al. 2019).

Additionally, some early published species were established, based on only one or two specimens, with limited or ambiguous information on their type localities. Furthermore, these species often lack important and valuable taxonomic characteristics and there have been no further collection records or literature after publication. The names and habitats of the type locality of some species have also changed over time, making it difficult to rediscover them. These issues have posed challenges for subsequent taxonomic research. For example, *Oreocharis rhytidophylla* C.Y.Wu ex H.W.Li was considered a doubtful species due to the lack of descriptive information regarding its floral characteristics. It was not until recently that Zhang et al. (2019) collected flowering specimens from its type locality, confirming it as a natural species rather than a doubtful one.

Oreocharis leveilleana Fedde, first collected in 1910 and described as a new species under the genus *Oreocharis* in 1911, had not been recorded again for over 100 years. Due to limited specimen and literature records, it was considered a doubtful species (Pan 1987; Wang et al. 1990). Subsequently, it was merged with *O. auricula* (S.Moore) C.B.Clarke due to the temporary unavailability of additional literature and collection records (Wang et al. 1998). Further, due to the unavailability of molecular data for this species, in the study by Möller et al. (2011), *O. leveilleana* was still treated as a synonym of *O. auricula*.

In recent years, our research team conducted a comprehensive survey of the Gesneriaceae in Guizhou Province. In April 2023, during the surveys in Luodian County and Wangmo County, we discovered an interesting species of Gesneriaceae. We observed the living plants and recorded their morphological characteristics. We were very certain that the vegetative organs of this species are morphologically almost identical to the type specimen of *O. leveilleana* (E00067459). To ensure that our judgement was not mistaken, we confirmed it was *O. leveilleana* after carefully comparing it with the descriptions in literature and the type specimen. Furthermore, while examining the literature on species in the genus *Oreocharis*, we found some issues with the current taxonomic position of *O. leveilleana*. We believe that *O. leveilleana* should be classified under *Petrocodon* Hance and that it is the same as *P. coccineus* (C.Y.Wu ex H.W.Li) Yin Z.Wang. *P. coccineus* was first published as a new species in 1982 as the type species of *Calcareoboea* C.Y.Wu ex H.W.Li, which was subsequently transferred to *Petrocodon*, based on molecular evidence and it has since become a species under *Petrocodon* (Wang et al. 2011).

Materials and methods

We reviewed the original literature and related records of *Oreocharis leveilleana* and *Petrocodon coccineus*, including the original literature description, information on type specimens and geographical distribution. In addition, we accessed the digital plant specimens of the E, K, P, IBK, PE, KUN and GXMI collections to check the type specimens and high-resolution images of both species, along with other specimens. The primary sources of original literature are from BHL (www.biodiversitylibrary.org), Tropicos (http://www.tropicos.org), and IPNI (http://www.ipni.org). Additionally, we made multiple visits to the type localities of both species to conduct extensive field surveys and document the growth and distribution of populations. The study was carried out using classical plant taxonomic methods.

Results and discussion

Comparison and discussion of morphological characteristics

Oreocharis leveilleana was originally published by French botanist, Augustin Abel Hector Léveillé (1911a). It was collected as a specimen with the number *2051* (Holotype E, E00067459) from Ta-pin (now located in the western Luodian County, Guizhou Province, China) by Joseph Henri Esquriol in 1910. The new species was described and published under the genus *Oreocharis*, named *O. esquirolii* H.Lév. as a tribute to the collector's name on the specimen. In the same year, another botanist Friedrich Karl Georg Fedde (1911) realised that this scientific name was identical to another species, *O. esquirolii* H.Lév., also published by H. Léveillé (1911b). To avoid confusion in taxonomy, a replacement name was proposed. The specific epithet was changed to "*leveilleana*", derived from the Latinised version of the original from Augustin Abel Hector Léveillé. According to the protologue, the morphological characteristics of *O. leveilleana* are simply described as follows: leaf blades oblong, 4–7 cm in length and 1.5–2 cm in width; margin sparsely serrulate, nerves parallel; petioles 3–6 cm long, dark brown tomentum; capsule ca. 5 cm long.

As is recorded in *Flora Reipublicae Popularis Sinicae* (Vol. 69) "based on the type specimen photos, this plant is glabrous; does this species belong to the genus *Oreocharis*? Whether this species belongs to the genus *Oreocharis* should be determined when complete specimens will be collected". Therefore, Wang et al. (1990) classified this species as a doubtful species. Later, *O. leveilleana* was treated as a synonym of *O. auricula* (Wang et al. 1998), although it was also treated as a synonym of *O. sericea* H.Lév. in related monographs (Li and Wang 2005; Wei et al. 2010). Ultimately, scholars followed the taxonomic viewpoint in *Flora of China* (Vol. 18) (Möller et al. 2011).

Careful observation of specimen *2051* (Holotype E, E00067459) (Fig. 1A) showed the following morphological characteristics of this specimen: rhizome robust, terete, ca. 6 mm in diameter; petiole densely puberulent; leaf blades densely pubescent, margin denticulate-serrulate; peduncle robust, densely puberulent, terete, 2–3 mm in diameter, unbranched; pedicel short, 2–6 mm long; inflorescence subumbellate, bracts more than 5, dense, densely pubescent;

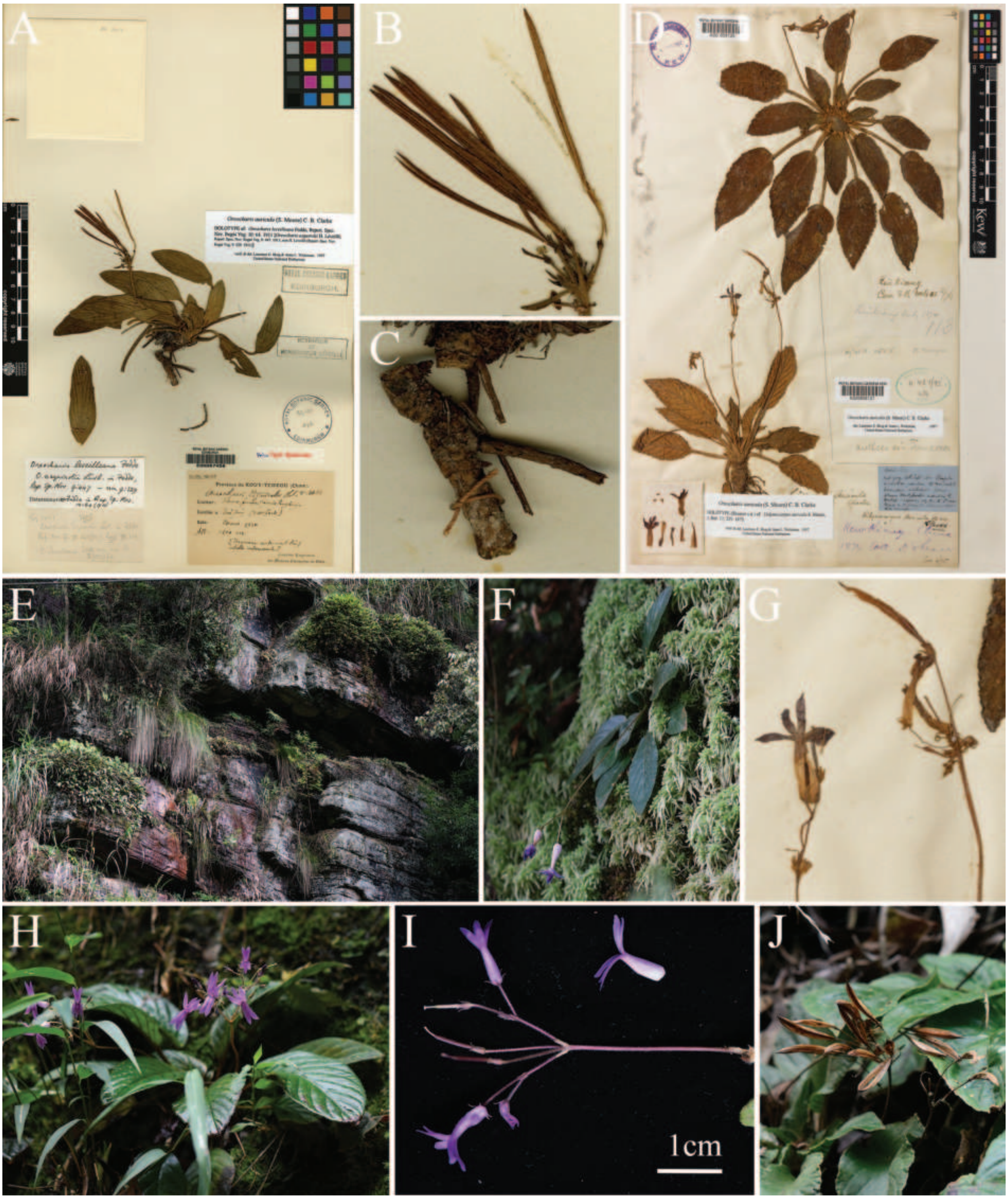

Figure 1. Morphological comparisons of *Oreocharis leveilleana* and *O. auricula* **A–C** *O. leveilleana* **D–J** *O. auricula* **A** holotype (E00067459) **B** capsules and bracts **C** rhizome **D** holotype (K000858120) **E** habitat **F, H** habit **G, I** inflorescence **J** capsules (Xin-Xiang Bai took the field survey photographs).

capsule linear, loculicidally dehiscent into two valves. Detailed morphological comparisons with *O. auricula* are provided in Fig. 1. Moreover, the morphological characteristics shown by specimen *2051* are clearly distinguished from those of other species within *Oreocharis*, such as inflorescence subumbellate

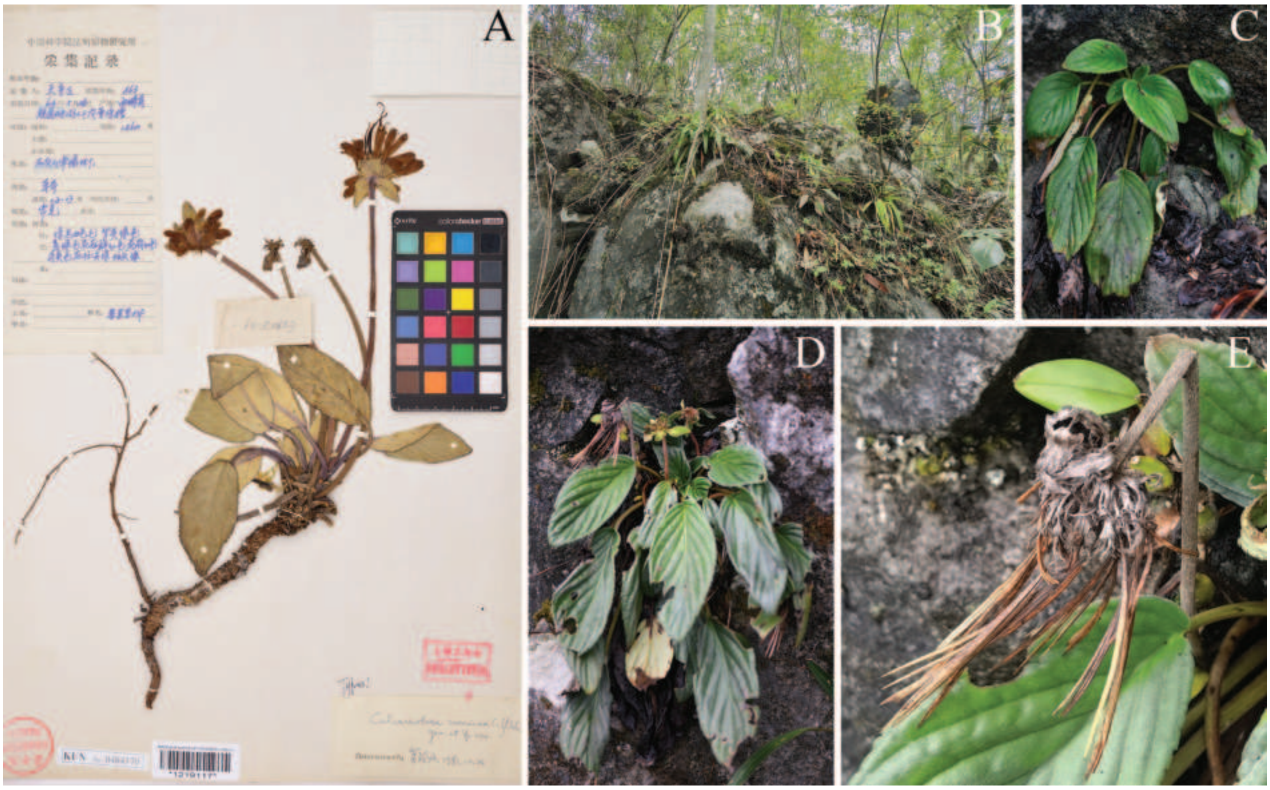

Figure 2. *Petrocodon coccineus* **A** holotype (KUN1219117) **B** habitat **C** habit **D** plant with infructescence **E** infructescence and peduncle (Xin-Xiang Bai took the field survey photographs).

(vs. cymes), bracts more than 5, dense (vs. bracts 2 or 3, opposite or whorled), capsule linear and loculicidally dehiscent into two valves (vs. capsule lanceolate-oblong or oblong). However, these morphological characteristics match well with *Petrocodon coccineus*.

Calcareoboea coccinea C.Y.Wu ex H.W.Li was published, based on the specimen of *S.C.Wang 463* (Holotype KUN, KUN1219117) (Fig. 2A) collected from Xichou County, Yunnan Province, China (Li 1982). The scientific name is derived from its bright red corolla and the genus *Calcareoboea* was established with *C. coccinea* as the type species. It was once a monotypic genus. Subsequently, Wang et al. (2011) provided molecular evidence to transfer the genus *Calcareoboea* into the genus *Petrocodon*. Consequently, the scientific name for the species was changed to *Petrocodon coccineus* (C.Y.Wu ex H.W.Li) Yin Z.Wang. The characteristics of the *P. coccineus* are as follows: inflorescence subumbellate and scapiform; peduncle elongated and robust, terete with numerous leafy involucres at the apex; bracts 6–10 or more, dense, small, linear; flowers with short pedicel, 2–4 mm long; capsule linear, ca. 6 cm long with stalk, loculicidally dehiscent into two valves. These morphological features are consistent with those of *Oreocharis leveilleana*.

Locality research

By consulting relevant historical records and referring to the Gazetteers of China History Collections (https://www.cvh.ac.cn/topics/counties.php), it has been found that the type locality of *Oreocharis leveilleana*, Ta-pin, is in western Luodian County, Guizhou Province. Further extensive investigations were conducted in the type locality and surrounding areas, revealing that *Petrocodon coccineus* is widely distributed in the western Luodian County and the eastern Wangmo County, Guizhou Province (Fig. 2).

In conclusion, based on the study of morphology, combined with geographical distribution analysis, according to the latest taxonomic viewpoint of the Gesneriaceae, *Oreocharis leveilleana* should belong to the genus *Petrocodon* and it is actually the same species as *P. coccineus*. Given that the publication of *Oreocharis leveilleana* predates the one of *Petrocodon coccineus* and, following the regulations and suggestions of the 2018 "International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)" (Turland et al. 2018), this study proposes a new combination – *Petrocodon leveilleanus* (Fedde) X.X.Bai & F.Wen and treats *P. coccineus* as the synonym of the new combination. The Chinese name of *P. leveilleanus* (= *P. coccineus*) is retained because it more accurately expresses the morphological characteristics of this species and is widely accepted.

Taxonomic treatment

***Petrocodon leveilleanus* (Fedde) X.X.Bai & F.Wen, comb. nov.**
urn:lsid:ipni.org:names:77341571-1
Fig. 3

Oreocharis leveilleana Fedde, Repert. Spec. Nov. Regni Veg. 10: 64. 1911. – *O. esquirolii* H.Lév., Repert. Spec. Nov. Regni Veg. Berlin. 9: 447. 1911 [non Léveillé (1911b: 329)]. Type: China, Guizhou: Ta-pin, March 1910, *Joseph Henri Esquriol 2051* (E: holotype, E00067459).

= *Petrocodon coccineus* (C.Y.Wu ex H.W.Li) Yin Z.Wang, J. Syst. Evol. 49(1): 60. 2011. syn. nov. – *Calcareoboea coccinea* C.Y.Wu ex H.W.Li, Acta Bot. Yunnan. 4(3): 243. 1982. Type: China, Yunnan: Xichou, Gankou, 26 May 1964, *C.S. Wang 463* (KUN: holotype, KUN1219117).

Chinese Vernacular name. 朱红苣苔 (Zhū Hóng Jù Tái).

Distribution and habitat. Luodian County, Wangmo County, Libo County and Zhenning County of Guizhou Province, as well as in the southeastern Yunnan Province and the southwestern and northern Guangxi Zhuang Autonomous Region of China and northern Vietnam. The species grow on wet rocks under the forest canopy at an elevation of 500–1500 m.

Specimens examined. China. Guangxi Zhuang Autonomous Region: Napo County, 1220 m elev., 2 Jun 2006, Haining Qin et al. 602018 (PE); Napo County, 1100 m elev., 8 Nov 1992, Yinzheng Wang 92038 (PE); Napo County, 1220 m elev., 24 Apr 1981, Ding Fang et al. 22421 (PE); Jingxi City, elevation unknown, 28 May 1990, Xiuxiang Chen et al. 14769 (GXMI); Du'an County, 274 m elev., 19 Jul 2019, Bo Pan et al. GXIBPB057B01 (KUN). **Yunnan Province:** Malipo County, 1000 m elev., 3 Jan 1940, Qiwu Wang 86147 (KUN); Malipo County, 1400–1500 m elev., 9 Dec 1992, Yinzheng Wang 92101 (PE); Malipo County, 1300–1500 m elev., 2 Nov 1947, Guomei Feng 13508 (KUN); Funing County, 1000 m elev., 8 May 1940, Qiwu Wang 87144 (KUN); Funing County, 1400 m elev., 18 Sep 2006, Lianming Gao GLM-06184 (KUN); Xichou County, elevation unknown, 7 May 1959, Quan'an Wu 7961 (KUN). **Vietnam. Son La Province:** Moc Chan District, 1400–1500 m elev., 6 Mar 2001, D.K.Harder et al. 7342 (E). **Hoa Binh Province:**

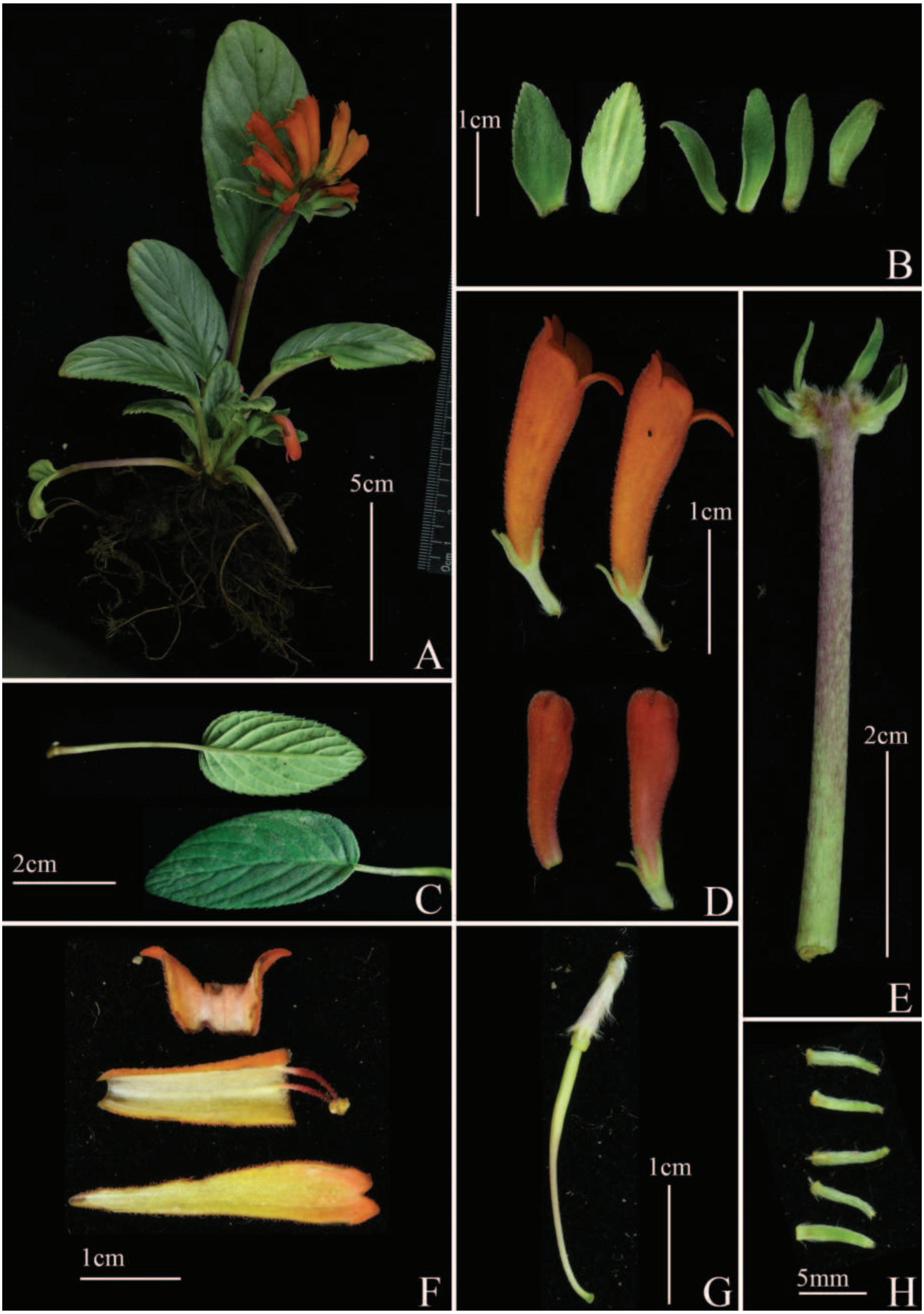

Figure 3. *Petrocodon leveilleanus* **A** plant **B** bracts **C** leaves **D** corolla **E** peduncle **F** dissected flower **G** Pistil **H** Sepals (photographs by Xin-Xiang Bai).

Mai Chau District, 1000 m elev., 20 Oct 2002, Northern Vietnam First Darwin Expedition 3 (E); Mai Chau District, 1066 m elev., 26 Sep 2018, S. Razafimandimbison et al. 2373 (P). **Ha Giang Province:** Vi Xuyen District, 300–1050 m elev., 16 Feb 2001, D.K.Harder 6449 (E); Quang Ba District, 1100 m elev., 3 Apr 2000, D.K.Harder et al. 4946 (E).

Acknowledgements

We want to thank Stephen Maciejewski, the Gesneriad Society and Michael LoFurno (Associate Professor, Temple University) from Philadelphia, the USA, for their editorial assistance. We are also grateful to the Herbaria mentioned above (E, K, P, IBK, PE, KUN, GXMI) for images/photos of specimens available.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was financially supported by the National Natural Science Foundation of China (grant 32260782), the Key Science & Technology Research and Development Project of Guangxi (Guike ZY21195050) and the capacity-building project of SBR of CAS (KFJ-BRP-017-68).

Author contributions

Data curation: STH. Investigation: XKX, STH. Writing – original draft: YLZ, XKX. Writing – review and editing: FW, XXB.

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Data availability

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

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PhytoKeys

PhytoKeys 242: 31–37 (2024)
DOI: 10.3897/phytokeys.242.121623

Research Article

Vaccinium dehongense (Ericaceae), a new species of *Vaccinium* sect. *Epigynium* from western Yunnan, China

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Abstract

Vaccinium dehongense (Ericaceae), a new species from Yingjiang County of Yunnan Province, China is described and illustrated. This new species belongs to *Vaccinium* sect. *Epigynium* and is most similar to *V. vacciniaceum*, but differs from the latter in the subsessile leaves, the inflorescence usually developing at leafless nodes, the shorter pedicels and the filaments being ca. 1/3 length of the stamens. Since the type locality of this new species is very near the border between China and Myanmar, it is probably also distributed in the adjacent area of Myanmar. As no population assessment of this species in its whole distribution area is made, it is best to assign a conservation status of 'Data Deficient' (DD) for this species.

Key words: Morphology, taxonomy, Vaccinieae, Yingjiang County

Introduction

China, with more than 41,000 species of higher plants, is one of the countries owning the highest plant diversity in the world (Xie et al. 2021). Even now, more than 280 new species were described from China each year from 2020 to 2022 (Du et al. 2023). Collaboration between experts and investigators is one of the factors that accelerates the findings of new species. As the taxonomic study of *Vaccinium* L. (Ericaceae) in China is continuously being undertaken, the number of specie of this genus from this country now reaches 103 (Guo et al. 2023; Qin et al. 2023; Tong et al. 2023).

During several field trips to Yingjiang County of Yunnan Province, China, we encountered an unknown *Vaccinium* species. Its pseudo-verticillate leaves indicate that it should belong to *V.* sect. *Epigynium* (Klotzsch) Hook. f. Only one formerly known species of this section, recorded from western Yunnan, is *V. scopulorum* W. W. Sm., which has an alternative phyllotaxis rather than a pseudo-verticillate one. After a careful comparison with similar species of the same section from China and adjacent countries (Rae 1991; Kress et al. 2003; Fang and Stevens 2005; Panda and Sanjappa 2014; Holt and Maden 2022), it was confirmed that this species is new to science, which is described and illustrated below.

Academic editor: Wendy A. Mustaqim
Received: 25 February 2024
Accepted: 8 April 2024
Published: 13 May 2024

Citation: Tong Y-H, Ye X-E, Ni J-B (2024) *Vaccinium dehongense* (Ericaceae), a new species of *Vaccinium* sect. *Epigynium* from western Yunnan, China. PhytoKeys 242: 31–37. https://doi.org/10.3897/phytokeys.242.121623

Materials and methods

Specimens were collected from Yingjiang County in two field trips in June 2015 and March 2023, respectively. Descriptions were based on dried collections, except the information of flower colour. Measurements were performed with a ruler and small plant parts were observed and measured under a stereomicroscope (Mshot-MZ101). General terminology follows Beentje (2016).

Taxonomic treatment

Vaccinium dehongense **Y.H.Tong, sp. nov.**
urn:lsid:ipni.org:names:77341761-1
Fig. 1

Type. China. Yunnan Province: Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Xima Township, Huoshigou Village, epiphytic on trees in evergreen broad-leaved forest, 24°47'5.4"N, 97°43'35.8"E, 1740 m a.s.l., 12 March 2023 (fl.), *Yi-Hua Tong et al. TYH-2651* (holotype: IBSC; isotypes: KUN, PE).

Diagnosis. This new species is morphologically similar to *V. vacciniaceum*, especially its subspecies, *V. vacciniaceum* subsp. *glabritubum* P. F. Stevens (with a glabrous internal corolla surface), in having pseudo-verticillate leaves with a serrate margin and a rounded leaf base, glandular-setulose twigs with scattered lenticels, elongate racemose inflorescences with many flowers, narrowly triangular bracts and bracteoles and a glabrous internal corolla surface, but can be distinguished by subsessile (vs. with 1–4 mm long petioles) leaves, the inflorescences usually developing at leafless nodes (vs. axils of leaves), shorter pedicels (6–7.5 mm vs. 7–13 mm) and filaments being ca. 1/3 length of the stamens (vs. ca. 1/2).

Description. Evergreen shrubs, 0.5–3 m tall, epiphytic on trees, with inflated root tubers. Young twigs yellowish-brown, angled, densely glandular-setulose, glabrescent; old branches purple brown, with sparse white lenticels. Bud scales subulate, margin glandular-ciliate. Leaves often 4–8-pseudoverticillate, subsessile, borne on a protuberance; blades firmly papery, oblong-lanceolate, 5.5–15 × 0.8–3 cm, apex acute to acuminate, base cuneate or slightly obtuse, margin plane, serrate, each serra tipped with a gland, glabrous on both surfaces, midvein slightly raised adaxially, strongly raised abaxially, lateral veins 11–14 on each side, together with fine veins raised on both surfaces. Inflorescences racemose usually at leafless nodes, rarely axillary, 2–8 cm long, with 7–21 flowers, rachis glabrous, with persistent bud scales at base; bracts narrowly triangular, 1.5–2.5 × 0.2–0.5 mm, glabrous on both sides, margin glandular-ciliate; pedicel 6–7.5 mm long, glabrous, thickened upwards; bracteoles 2, caducous, usually borne near the base of the pedicel, occasionally at the lower part, shape and indumentum similar to bracts, but smaller, ca. 1 × 0.2 mm. Hypanthium 0.8–1 × 1.2–1.5 mm, glabrous, smooth when fresh, rugose when dry; calyx limb 5–lobed to near base, lobes greenish-yellow, sometimes tinged with purplish, triangular to ovate-triangular, 1–1.5 × 1.2–1.5 mm, glabrous, apex acuminate. Corolla greenish-yellow, urceolate, 5-angled, 5–6 × 2–2.5 mm, glabrous on both surfaces, apex shallowly lobed, lobes recurved, triangular, ca. 1–1.2 × 1 mm, abaxially glabrous, adaxially papillose; stamens 10, 4.5–5 mm long, filaments

Figure 1. *Vaccinium dehongense* **A** habitat, the red arrow indicating this species **B** habit **C** flowering branchlets **D** inflorescences **E** infructescences with immature fruits **F** part of an inflorescence, showing bracts and bracteoles **G** flower with corolla removed **H** stamens, adaxial, lateral and abaxial view **I** ovary cross-section, showing pseudo-10-locular ovary. Scale bars: 5 mm (**F–G**); 3 mm (**H–I**). Photographs by Yi-Hua Tong.

flat, slightly expanded at base, 1.5–1.6 mm long, glabrous; anthers 3–4 mm long, thecae 1–1.2 mm long, more or less echinate on edges, with 2 small appendages at base, tubules 2–2.8 mm long, opened by a long slit more than half of the tubules, dorsal spurs absent; style 4.5–5.5 mm long, stigma slightly expanded, capitate; ovary pseudo-10-locular, each locule with several ovules, disc glabrous. Fruit unknown.

Etymology. The species epithet is derived from the type locality, Dehong Dai and Jingpo Autonomous Prefecture. Its Chinese name is given as 滇西越橘 (Pinyin: diān xī yuè jú).

Distribution and habitat. This species is currently known only from the type locality, i.e. Yingjiang County, Dehong Dai and Jingpo Autonomous Prefecture, Yunnan Province. It grows on trees in mountainous evergreen broad-leaved mixed forests at elevations of 1400–1750 m a.s.l.

Conservation status. Since the type locality of this new species is very near the border between China and Myanmar, it is probably also distributed in the adjacent area of Myanmar. As no population assessment of this species in its whole distribution area is made, 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 March.

Discussion. *Vaccinium dehongense* obviously belongs to *V.* sect. *Epigynium* due to its evergreen and pseudo-verticillate leaves with a serrate margin, urceolate corollas and stamens without spurs on the back of anthers (Sleumer 1941; Stevens 1969; Vander Kloet and Dickinson 2009). In the key to *Vaccinium* in the *Flora of China* (Fang and Stevens 2005), *V. dehongense* is keyed out to be close to *V. vacciniaceum*. The main differences between the two species are indicated in the diagnosis part. The most distinct character that distinguishes the two species is the position where inflorescences develop. A more detailed comparison between the two species is presented in Table 1. Besides, they have an allopatric distribution: *V. dehongense* is endemic to west Yunnan, China, while *V. vacciniaceum* is distributed in northwest Myanmar, northeast India, SE Xizang of China, Bhutan and Nepal. Panda and Sanjappa (2014) merged *V. vacciniaceum* subsp. *glabritubum* to the nominate subspecies without giving any reason. However, just as Stevens (1985) pointed out, *V. vacciniaceum* subsp. *glabritubum* has subsessile leaves with a round base and a glabrous corolla, while the nominate subspecies owns obviously petiolate leaves with a cuneate base and a hairy internal corolla surface. Besides, *V. vacciniaceum* subsp. *glabritubum* is distributed in Nepal, Sikkim, Bhutan and SE Xizang of China and the nominate subspecies has a further southeast distribution, viz. Meghalaya, Nagaland, Manipur, Mizoram of India and Chin State of Myanmar. Considering the morphological differences and allopatric distribution pattern of the two subspecies, it is better to treat them as two distinct subspecies for now, until new evidence (such as molecular evidence) is obtained.

In the type locality, there is another species from the same section, i.e. *V. scopulorum* W. W. Sm., which is much more common than *V. dehongense* and has a wider distribution including west China, Myanmar and Bhutan. *Vaccinium scopulorum* also has setose branchlets, but its alternate phyllotaxis, smaller leaf blades (2.5–4.5 × 0.6–1.7 cm) and yellowish-green corollas with a dark-purple apex are very different from those of *V. dehongense*.

Table 1. A comparison of *Vaccinium dehongense* and *V. vacciniaceum*. The data of the latter species are taken from Wight (1850), Stevens (1985), Fang and Stevens (2005) and the examined specimens listed in the text.

Comparison items	*V. dehongense*	*V. vacciniaceum*
Twigs	Angled	Round
Petiole length (mm)	Subsessile	1–4
Inflorescence position	Usually at leafless nodes, rarely axillary	Axillary
Pedicel length (mm)	6–7.5	7–13
Corolla colour	Greenish-yellow	Greenish-white or pinkish-yellow
Ratio of filament length to stamen length	Ca. 1/3	Ca. 1/2
Filament indumentum	Glabrous	Pubescent or subglabrous
Distribution	West Yunnan of China	Bhutan, northeast India, south Xizang of China and north Myanmar

Additional specimens examined. *Vaccinium dehongense* (paratypes): CHINA. Yunnan Province: Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Xima Xiang, 11 June 2015, *Yi-Hua Tong & Xing-Er Ye TYH-128* (IBSC), *TYH-129* (IBSC); ibid., No. 2 water power station of Mengnai River, 12 March 2023, *TYH-2659* (IBSC).

Vaccinium vacciniaceum subsp. *vacciniaceum*: INDIA. Meghalaya State: Garrow [Garo] hills, 1813, *W. Roxburgh s.n.* (holotype BM000802681, image); Silhit Mountains [Khasi hills], *W. Gomez 6299* (K000780682, image); ibid., 4000 ft [1219 m a.s.l.], *J. D. Hooker & T. Thomson s.n.* (K000780683, image); ibid., *W. Griffith s.n.* (K000780684, image; M-0164586, image); without precise locality, *J. O. Viogt 252* (IBSC0457574).

Vaccinium vacciniaceum subsp. *glabritubum*: BHUTAN. Chhukha State: 13 km SW of Gedu between Phuntsholing and Gedu, 1780 m a.s.l., *B. Bartholomew & D. E. Boufford 3940* (PE00197369). NEPAL. Arun Valley, Maghang Kola, E of Num, 9000 ft [2743 m a.s.l.], 30 April 1956, *Stainton 167* (holotype A00015998, image; isotype BM000802680, image). INDIA. Sikkim State: *J. D. Hooker s.n.* (E00438126, image).

Acknowledgements

We thank Bing-Mou Wang, Wei-Hao Pan, Emily, Zhen-Yu Shi, Mian Tang, Snowrainbow and Anita for their help during field trips. Our thanks also go to the curators of BM, E, IBSC and K for allowing us to examine their specimens or specimen photos.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was funded by Key-Area Research and Development Program of Guangdong Province (grant no. 2022B1111230001) and the National Natural Science Foundation of China (grant no. 31870180).

Author contributions

Conceptualization: YHT. Data curation: YHT. Funding acquisition: YHT. Investigation: XEY, YHT, JBN. Writing – original draft: YHT. Writing – review and editing: XEY.

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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 242: 39–50 (2024)
DOI: 10.3897/phytokeys.242.123316

Research Article

Cocconeis crisscrossis sp. nov., a new monoraphid diatom (Bacillariophyta) from southern China

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Abstract

A novel monoraphid diatom species, *Cocconeis crisscrossis* You, Yu, Kociolek & Wang, **sp. nov.** is examined and described from the Qingyi River and Maolan Nature Reserve of southern China. The morphological description is based on light microscopy and scanning electron microscopy observations and the new species is compared with similar taxa in this genus. The characteristics unique to *Cocconeis crisscrossis* **sp. nov.** include its central area extending irregularly to both sides, it having closed valvocopulae with heavily silicified fimbriate margins and poles of the valvocopulae have 'sword-shaped' siliceous extensions. These features differentiate this new species from others in the genus. This new species was found in alkaline waterbodies, including streams, waterfall and ponds. It was usually found as an epiphyte on the stones; however, it was present on other substrates such as mosses.

Key words: diatoms, monoraphid, morphology, new taxa, taxonomy

Academic editor: Kalina Manoylov
Received: 18 March 2024
Accepted: 23 April 2024
Published: 13 May 2024

Citation: Zhou H, Yu P, Guo L, Kociolek JP, Wang Q, You Q (2024) *Cocconeis crisscrossis* sp. nov., a new monoraphid diatom (Bacillariophyta) from southern China. PhytoKeys 242: 39–50. https://doi.org/10.3897/phytokeys.242.123316

Introduction

The first described genus of Cocconeidaceae Kützing was *Cocconeis* Ehrenberg (1838). In his early compendium book "*Infusionsthierchen*", Ehrenberg (1838) described the morphology, growth habit and ecology of the genus in French and Latin. The name of the genus is derived from its growth habit, adnate on filamentous algae. *Cocconeis* Ehrenberg is a monoraphid diatom genus widely distributed in marine and freshwater environments, with more than 200 described species, with the main taxa being marine species (Guiry 2023; Kociolek et al. 2023). The frustules of this genus are heterovalvar, with one raphe valve (RV) and one rapheless or sternum valve (SV), where the former is typically less convex than the latter (Jahn et al. 2009; Stancheva 2018; Mora et al. 2022). Solitary cells of *Cocconeis* are attached to filamentous algae or other substrates by their RV, while the SV is exposed to the environment. Valves of *Cocconeis* are elliptical or slightly linear-elliptical in shape and this genus has distinctly different areolae structures on both valves (Round et al. 1990). The areolae of the RV are fine and often have a semicircular hyaline area near the valve ends, while the areolae of the SV are relatively coarse extending to the valve edge and lacking a hyaline area. Striae are usually uniseriate in freshwater species and the poroids are closed by hymenes (Costa et al. 2020). The frustule structure of *Cocconeis* is diverse and complex, species delineation requires detailed observations of the RV morphology, the SV and their connecting elements including valvocopulae and the cingulum (Potapova and Spaulding 2013; Stancheva 2022).

In China, 18 freshwater *Cocconeis* taxa have been recorded, including ten species and eight varieties (Skvortsov 1935; Chin 1951; Zhu and Chen 1989, 1994, 2000; Lin and Wang 1992). China remains a poorly-researched area, with few studies of this genus having gained the attention of researchers. In recent years, we conducted an extensive biodiversity investigation of monoraphid diatoms in China and one new *Cocconeis* species was found, which is distributed in the Qingyi River and Maolan Nature Reserve. This paper describes the frustule morphological characteristics of *C. crisscrossis* sp. nov. using LM and SEM and compares this new species with similar species of the genus.

Materials and methods

Diatom samples were collected from two sites: Qingyi River (Yi County, Anhui Province) and Maolan Nature Reserve (Libo County, Guizhou Province). Samples were collected using tweezers or turkey baster. The samples were preserved using formalin solution before being stored in sealed plastic bottles. Sample information is listed in Table 1, including location of samples, longitude and latitude, habitat, pH, conductivity and collection date.

In the laboratory, the samples were processed with concentrated nitric acid using the Microwave Accelerated Reaction System (Model MARS, CEM Corporation, Charlotte, USA); the specific processing and observation steps are described in You et al. (2021). Images were compiled with Adobe Photoshop 2023. Morphological terminology follows Donadel et al. (2018) and Riaux-Gobin et al. (2021). The holotype image of the single specimen is a circled specimen on the type slide. The samples and permanent slides are preserved in Lab of Algae and Environment, College of Life Sciences, Shanghai Normal University.

Table 1. Locality data and habitat for samples studied.

No. of samples	Location	Coordinates	Habitat	K[μs/cm]	pH	Collection Date
QYJ201710Z12	Qingyi River	30°09'03"N, 117°53'28"E	Attached to stones in the stream	120	8.5	10.1.2017
GZ201510042	Maolan Nature Reserve	25°27'48"N, 107°69'19"E	Attached to stones in the pond	305	7.5	10.2.2015
GZ201510057	Maolan Nature Reserve	25°24'72"N, 107°70'19"E	Attached to floating material near the waterfall	297	7.5	10.2.2015
GZ201510064	Maolan Nature Reserve	25°25'08"N, 107°71'13"E	Attached to stones near the waterfall	297	8.0	10.4.2015
GZ201510088	Maolan Nature Reserve	25°15'71"N, 108°14'22"E	Attached to stones in the stream	296	8.2	10.4.2015
GZ201510096	Maolan Nature Reserve	25°15'74"N, 108°04'18"E	Attached to stones near the waterfall	271	8.2	10.4.2015
GZ201510103	Maolan Nature Reserve	25°17'23"N, 108°04'26"E	Attached to mosses in the stream	272	7.8	10.4.2015

Results

Cocconeis crisscrossis **Q.M. You, P. Yu, J.P. Kociolek & Q.X. Wang, sp. nov.**
Figs 1A–X, 2A–F, 3A–E, 4A–F, 5A–C, 6A–C

Holotype(designated here). SHTU! slide QYJ201710Z12, holotype illustrated in Fig. 1D, J. Diatom samples are housed in the Lab of Algae and Environment, College of Life Sciences, Shanghai Normal University, China.

Type locality. China. Qingyi River, Anhui Province, 30°9'3"N, 117°53'28"E, collected by Q.X. Wang & P. Yu, 1 October 2017.

Description. Light microscopy (LM) (Fig. 1A–X). Valve elliptical to slight round-elliptical, apices are obtusely rounded; 12.5–42.0 µm long, 9.5–25.0 µm wide. The number of striae on both valves is similar, with parallel orientation at the centre and radiate towards the apices. Both valves display striae with a density of 18–22 rows per 10 µm. Raphe valves (RV) have a thickened hyaline rim on the margin and striae composed of small, nearly round areolae. The raphe is straight, the axial area is narrow, the central area is irregularly narrow, cuniform and the axial area and central area form an irregular cross-like structure. Sternum valve (SV) areolae are rounded and form 7–9 undulating longitudinal lines per hemivalve (increasing in number with increased valve width). The sternum is narrow, linear. The valvocopula has irregularly-spaced digitate fimbriae.

Scanning electron microscopy (SEM) (Figs 2–6) shows RV face is flat with a weakly concave mantle and very narrow linear axial area; the central area extends irregularly to both sides (Figs 3A–C, E, 4A–D). Externally, the raphe is straight, filiform and proximal raphe endings are slightly drop-like and expanded (Fig. 3E). Internally, the proximal raphe fissures are bent to opposite sides (Fig. 4D); the distal raphe endings are straight and end in weakly-elevated helictoglossae on the hyaline rim (Fig. 4E). Striae are made up of round to slightly elliptical uniseriate areolae which are small and regularly spaced, increasing in size from the axial area towards the valve margin and the apices (Fig. 3A–C). Internally, the areolae are occluded by round lattice-structured hymens with short slits around the margin and tiny perforations in the middle (Fig. 4F). SV has a narrow and straight sternum (Fig. 5A, B). In the SEM, it can be seen that, on the SV, the areolae differ greatly between the internal and the external sides (Figs 5C, 6C). Externally, striae are composed of irregular, variably-sized and mostly round areolae, differentiated to the valve edge (Fig. 5A). Areolae are occluded by lattice-structured hymens of marginal slits (Fig. 5C). Internally, the areolae are like puncta. There is a linear and straight axial area (Fig. 6A). Valvocopulae with well-developed digitate fimbriae on both valves are characteristics typical of the *C. crisscrossis*, which are close and heavily silicified fimbriae which seem to be attached to the hyaline rim and are irregularly spaced (Fig. 2A–F). The poles of valvocopulae possess unique 'sword-shaped' siliceous extensions that extend towards the interior of the valve and may vary in length (see arrows in Fig. 2A–F).

Etymology. Species was named for its crisscross-shaped central area of the raphe valve.

Distribution and ecology. So far, the new species has been collected at Qingyi River and Maolan Nature Reserve. The Qingyi River population of the

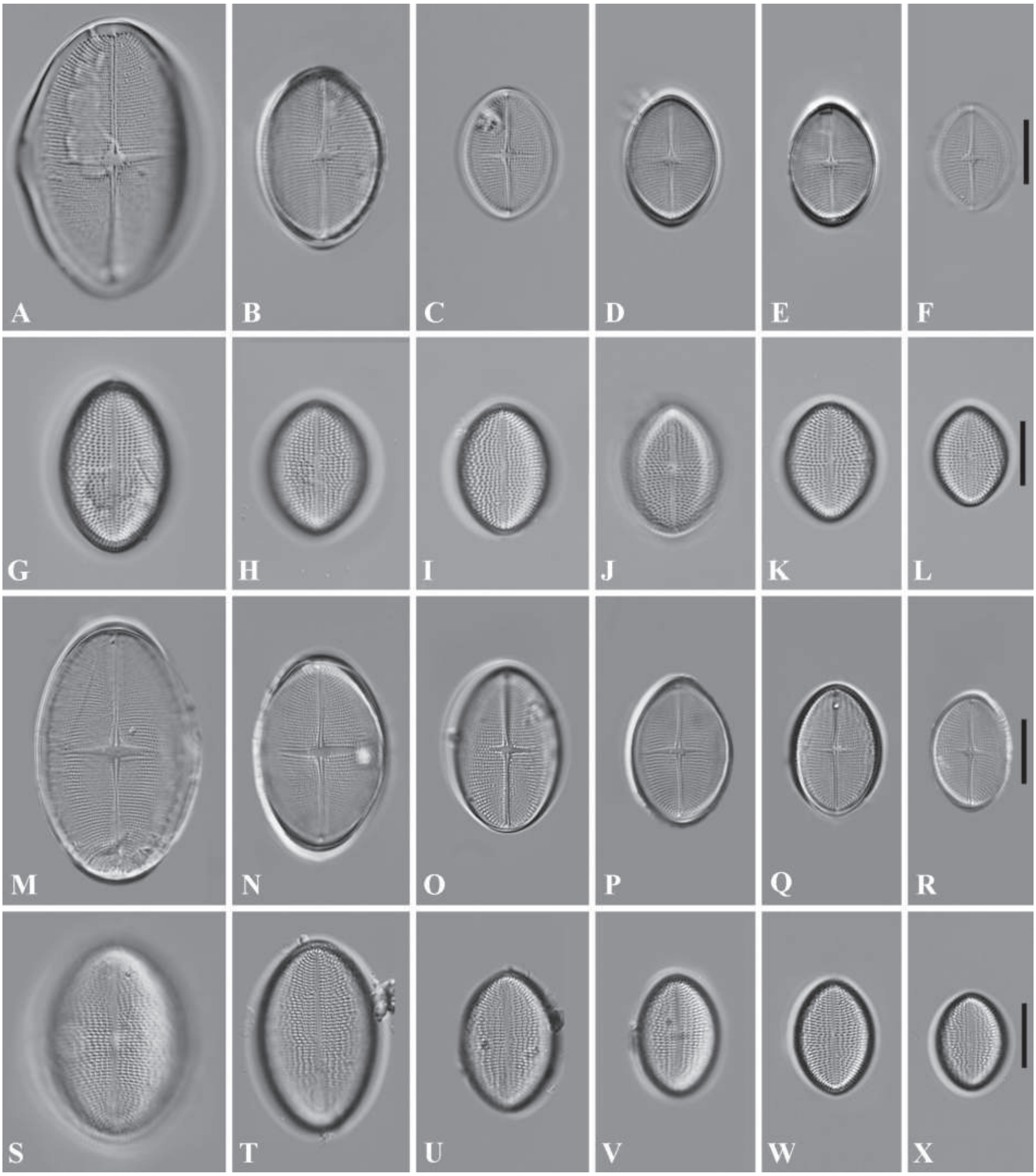

Figure 1. A–L Light micrographs of *Cocconeis crisscrossis* sp. nov. from Qingyi River **M–X** light micrographs of *C. crisscrossis* sp. nov. from Maolan Nature Reserve **A–F, M–R** raphe valves(RV) **G–L, S–X** sternum valves (SV). Scale bars: 10 µm (**A–X**).

new species appears to have a higher abundance in that location than populations from the Maolan Nature Reserve. The habitat of the new species is characterised by circumneutral to alkaline pH (7.5–8.5) and conductivity (120–305 µs/cm) and temperature range 18.0–24.0 °C.

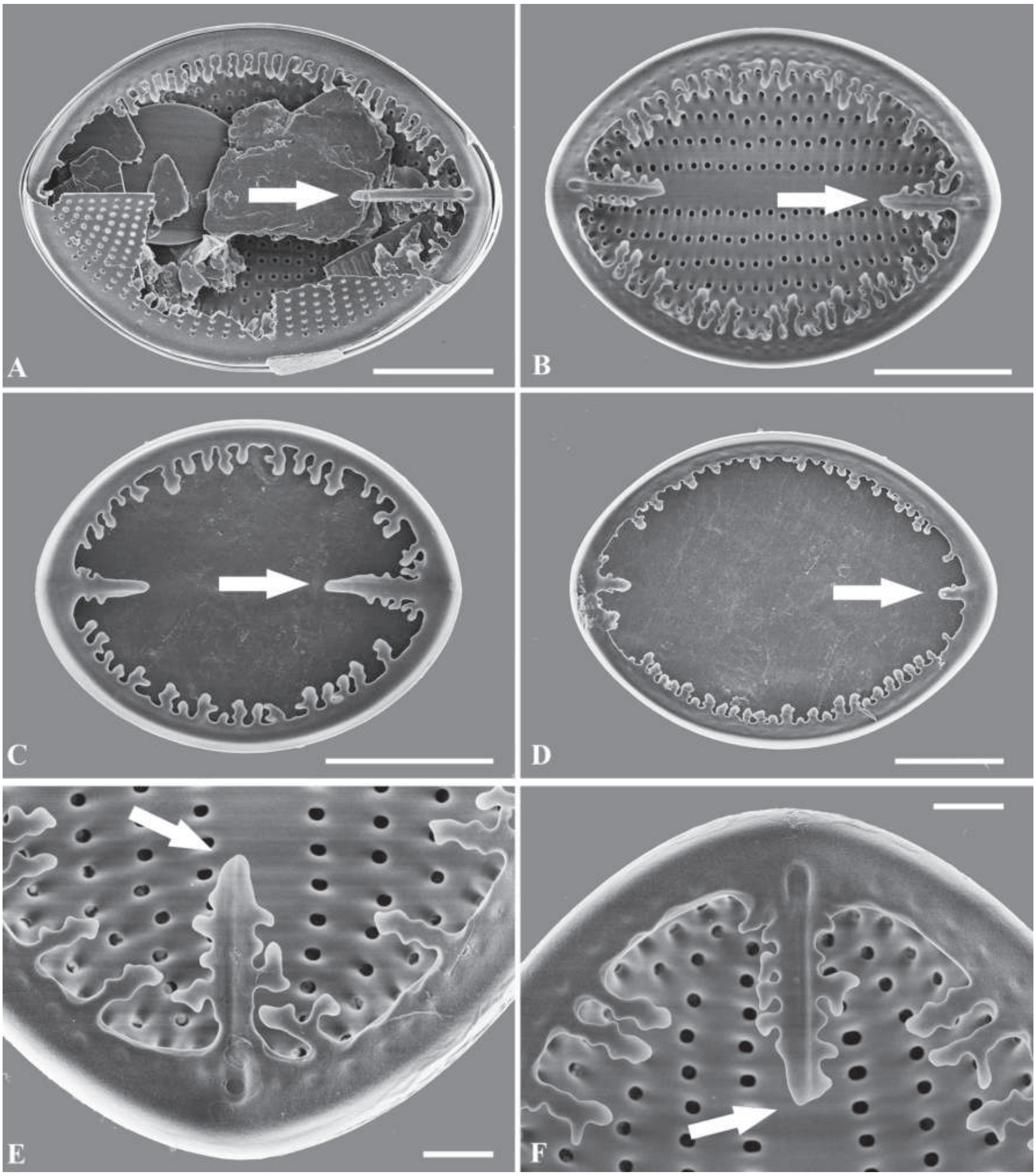

Figure 2. A–F SEM micrographs, the valvocopula of *C. crisscrossis* sp. nov. from Qingyi River with well-developed digitate fimbriae, which is close and heavily silicified clamp-like fimbriae seem to be attached to the hyaline rim and are irregularly spaced; the poles of valvocopulae possess unique 'sword-shaped' siliceous extensions (arrows in **A–F**) **A** valvocopula of the RV **B–F** valvocopula of the SV. Scale bars: 5 µm (**A–D**); 1 µm (**E, F**).

Discussion

The morphological differences between species of *Cocconeis* are limited (Stancheva 2022). *Cocconeis crisscrossis* sp. nov. was compared with other related species (e.g. *C. pediculus* Ehrenberg, *Cocconeis chernobyliensis* Genkal, Shcherbak & Semenyuk and *C. molesta* Kützing) which are structurally similar

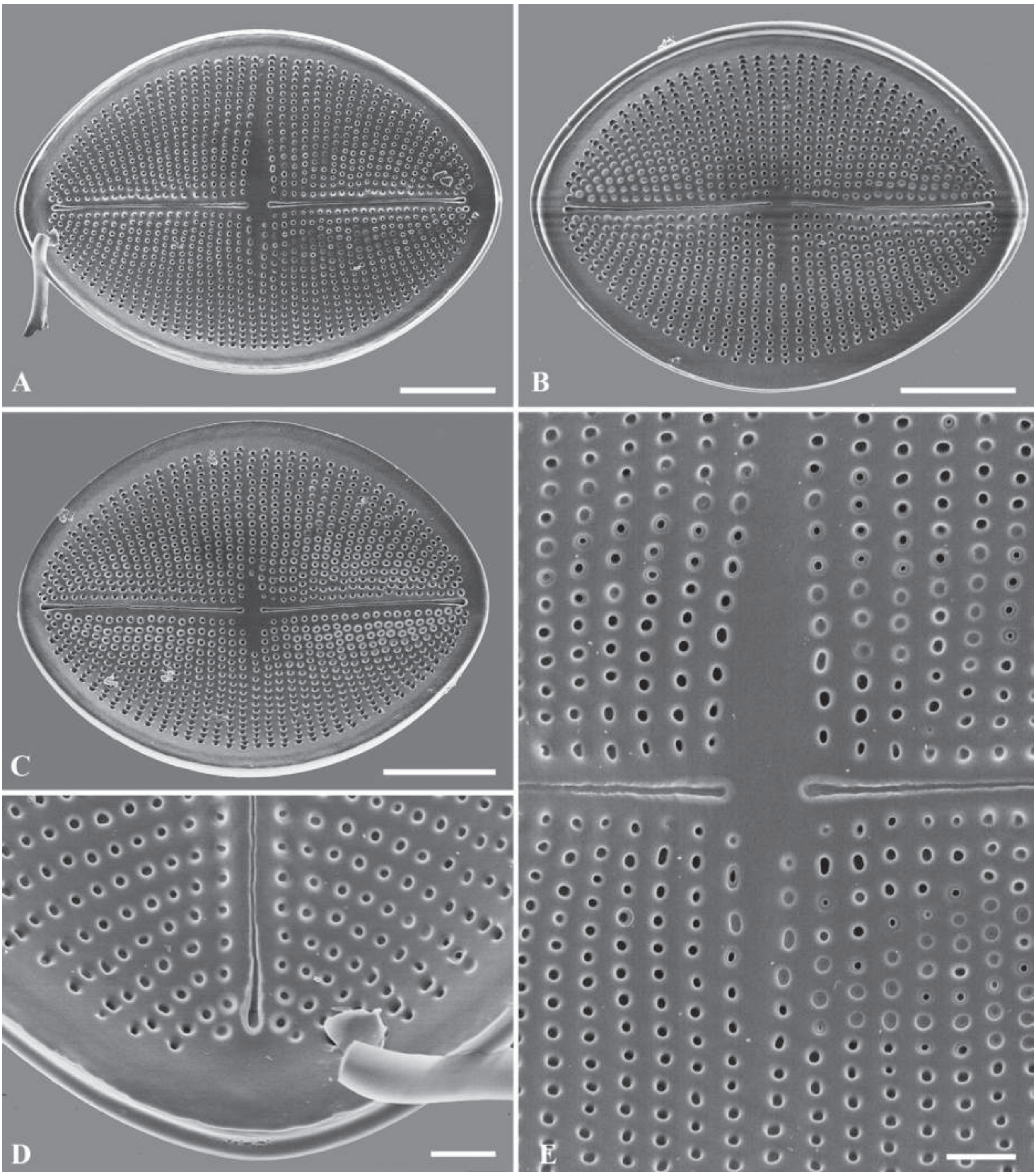

Figure 3. A–E SEM micrographs, RV external views of *C. crisscrossis* sp. nov. from Qingyi River **A–C** complete internal valve **D** proximal raphe endings are slightly drop-like expanded **E** irregular hyaline central area. Scale bars: 5 µm (**A–C**)**;** 1 µm (**D, E**).

under the light microscope: they all have an elliptical valve outline, concave valve curvature, as well as the size and the arrangement of the striae which are almost parallel in the centre, radiate and slightly curved towards the apices. While the most obvious differences are mainly with respect to the central area under the light microscope. The central area of *C. crisscrossis* sp. nov. extends irregularly to both sides. That feature is absent or not as distinct in morphologically similar taxa. it is one characteristic that distinguishes our new species from other similar species (Table 2).

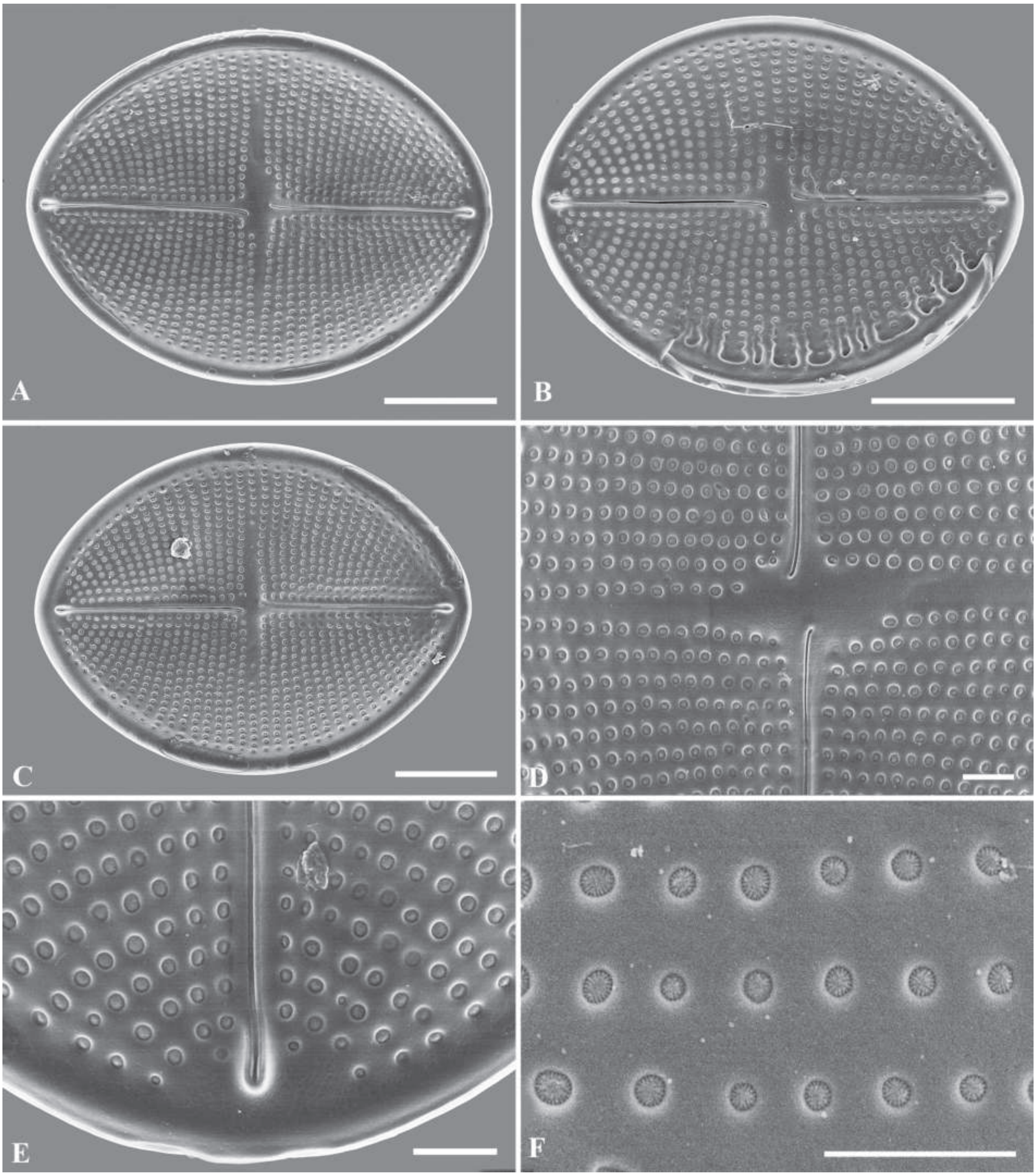

Figure 4. A–F SEM micrographs, RV internal views of *C. crisscrossis* sp. nov. from Qingyi River **A–C** complete internal valve **D** irregular hyaline central area and the proximal raphe fissures are bent to opposite sides **E** weakly elevated helictoglossae **F** the areolae are occluded by round lattice-structured hymens. Scale bars: 5 µm (**A–C**)**;** 1 µm (**D–F**).

The morphology of the RV, the SV and their connecting elements, such as the valvocopulae and the cingulum, are essential for delimiting species within the genus (Riaux-Gobin et al. 2013; Stancheva 2022). The valvocopula system and arrangement show significant variation amongst *Cocconeis* taxa, ranging from intricate fimbriae to no ornamentation; however, the morphology of the valvocopulae is thought to be diagnostic for each taxon (Holmes et al.

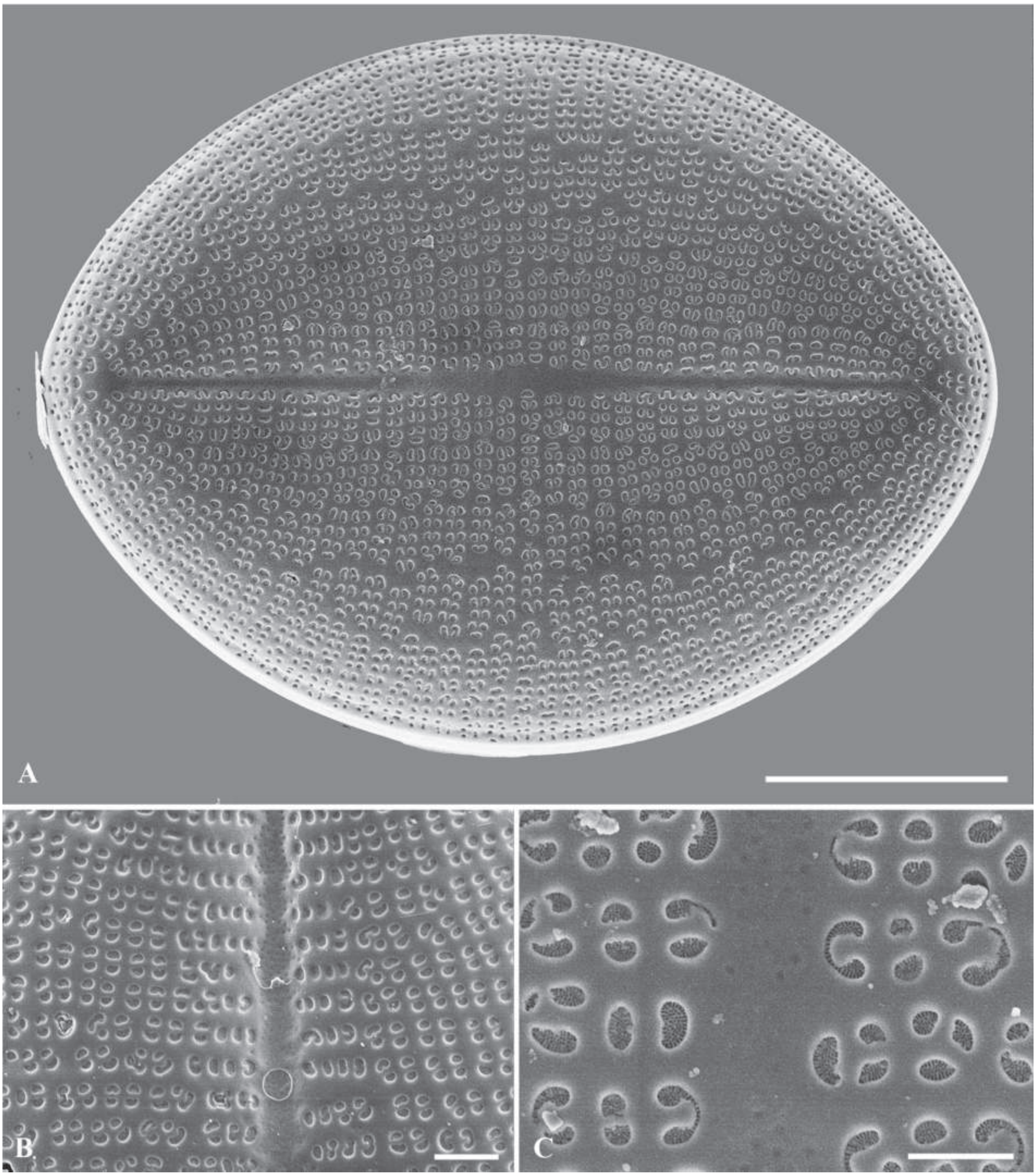

Figure 5. A–C SEM micrographs, SV external views of *C. crisscrossis* sp. nov. from Qingyi River **A** complete internal valve **B** narrow and straight sternum **C** Irregular areolae are occluded by lattice-structured hymens. Scale bars: 5 µm (**A**); 1 µm (**B**); 0.5 µm (**C**).

1982; Kobayasi and Nagumo 1985; Round et al. 1990; Riaux-Gobin et al. 2021; Stancheva 2022). As shown in Table 2, *C. crisscrossis* was compared with three similar taxa which are structurally different in ultrastructure, mainly in the valvocopulae. *Cocconeis crisscrossis* and *C. pediculus* possess close valvocopulae with fimbriate margins, while the fimbriae margins of *C. pediculus* are short and present only in the central part of the valve, never at the poles. In contrast

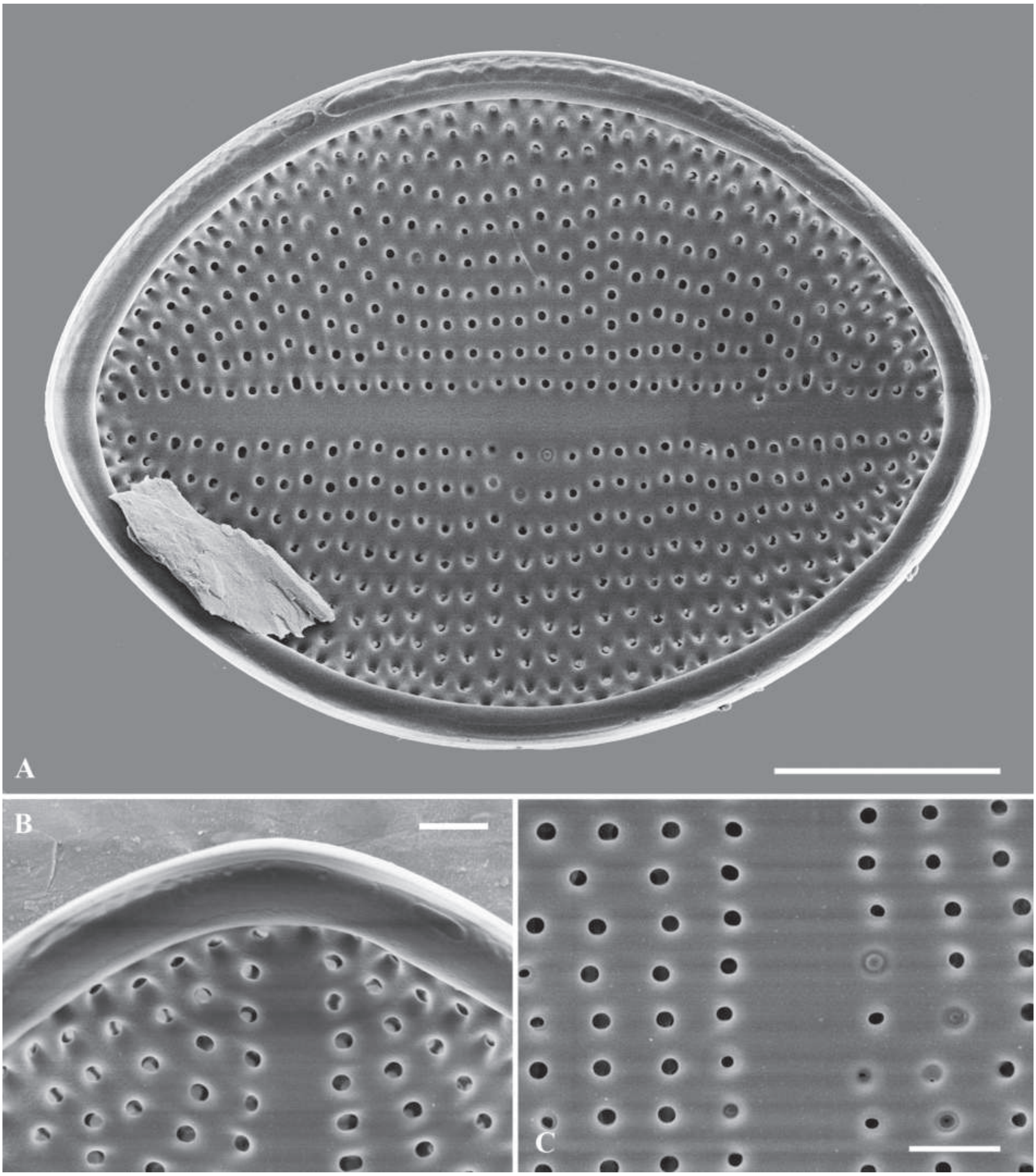

Figure 6. A–C SEM micrographs, SV internal views of *C. crisscrossis* sp. nov. from Qingyi River **A** complete internal valve **B, C** detail of the internal valves ends. Scale bars: 5 μm (**A**); 1 μm (**B, C**)).

to this, valvocopulae of *C. crisscrossis* surround the entire valve, which has longer fimbriae of uneven length and the poles of valvocopulae have distinct 'sword-shaped' siliceous extensions towards the interior of the valve, which vary in length, likely owing to different developmental stages. *C. crisscrossis* and *C. pediculus* exhibit remarkable morphological similarity, as both have closed valvocopulae and lack a submarginal hyaline area. These morphological similarities may indicate a close affinity between the two species.

Table 2. Comparison of morphological characteristics of *Cocconeis crisscrossis* sp. nov. and closely-related taxa.

	***Cocconeis crisscrossis* sp. nov.**	***Cocconeis pediculus***	***Cocconeis chernobyliensis***	***Cocconeis molesta***
Reference	This study	Jahn et al. (2009)	Genkal et al. (2022)	Riaux-Gobin et al. (2016)
Valve outline	Elliptical	Elliptical to somewhat rhombic-elliptical	Elliptical-lanceolate	Elliptical
Length (µm)	12.5–42.0	(11)13.5–40.0(56)	20–36.5	16.4
Width (µm)	9.5–25.0	(6)11.8–26.5(37)	16.5–28.9	9.1
Valvocopulae (RV and SV)	Close, with fimbriate margins, poles have extensions	Close, fimbriate margins in the central part of the valve	Nd	Nd
Central area (RV)	Irregular extends to submarginal to form a cross structure	Small, more or less oval	Narrow, well developed	Narrow, and half a valve in length
Raphe distal endings (RV)	Straight	Straight	Straight	Deflected
Striae (RV)	18–22/10 µm	14–22(24)/10 µm	11–18/10 µm	ca. 30/10 µm
Striae (SV)	18–22/10 µm	14–22(24)/10 µm	12–17/10 µm	40–42/10 µm

During our observation of this new species, we have discovered that the fimbriate margins of the valvocopula, which occur in the central part of the valve, display considerable morphological stability, while the size and length of the fimbriae exhibit variation. In addition, the size and length of the ‘sword-shaped’ siliceous extensions at the end of valvocopula also vary.

Acknowledgements

We are grateful for the comprehensive comments from reviewers and the editor in relation to scientific aspects, format and language.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was funded by the Natural Science Foundation of Shanghai (No.21ZR1447300).

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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 242: 51–67 (2024)
DOI: 10.3897/phytokeys.242.120717

Research Article

Orthotrichum camanchacanum, a remarkable new moss species from Chile (Bryopsida, Orthotrichaceae)

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Abstract

Orthotrichum camanchacanum is presented as a newly described species from Chile. The species is primarily distinguished by its emergent capsule with cryptoporous stomata, a double peristome, linear-lanceolate stem leaves with a long hyaline aristae in apex, conspicuously differentiated perichaetial leaves, and a densely hairy vaginula. The species was discovered in the mountain massif of the Andes in the Coquimbo region, notable for its unique climatic conditions. Molecular data and a brief discussion comparing the newly described species with the most closely related taxa are also provided.

Key words: Bryophytes, new taxa, Orthotrichaceae, South America, taxonomy

Academic editor: Matt von Konrat
Received: 11 February 2024
Accepted: 17 April 2024
Published: 20 May 2024

Citation: Plášek V, Sawicki J, Osorio F, Szczecińska M, Režnarová H (2024) *Orthotrichum camanchacanum*, a remarkable new moss species from Chile (Bryopsida, Orthotrichaceae). PhytoKeys 242: 51–67. https://doi.org/10.3897/phytokeys.242.120717

Introduction

Orthotrichum Hedw. is a cosmopolitan moss genus, mainly distributed in temperate regions of both northern and southern hemispheres. Similarly, as is the case with most of such moss genera, *Orthotrichum* has been recognized as a heterogeneous taxon (Sawicki et al. 2017). Extensive taxonomic and molecular investigations have confirmed its polyphyly, resulting in the separation of three distinct segregates from the genus: *Nyholmiella* Holmen & E. Warncke; *Pulvigera* Plášek, Sawicki & Ochyra and *Lewinskya* F. Lara, Garilleti & Goffinet (Sawicki et al. 2009, 2010, 2017; Plášek et al. 2015; Lara et al. 2016). In South America, the genus *Orthotrichum* s. str. displays a widespread presence, primarily inhabiting the forests or bushes of temperate regions. These mosses predominantly thrive as epiphytes on trees and shrubs, occasionally as epilithic species on boulders and rocks (Lewinsky 1984).

Orthotrichum in Chile was comprehensively treated by Lewinsky (1984). Subsequent taxonomic findings and new distribution data were further documented by Lewinsky and Deguchi (1989), Müller (2002, 2009), Buck (2005), Ireland et al. (2006, 2017), Goffinet et al. (2007), Medina et al. (2013), Larraín (2016), Larraín and Bahamonde (2017), Drapela and Larraín (2020), Lara et al. (2021), and Ellis et al. (2023). According to these studies, *Orthotrichum* s. str. is there represented by eight species and two varieties (see also Table 1): *Orthotrichum anomalum* Hedw., *O. assimile* Müll. Hal., *O. cupulatum* var. *austroamericanum* Lewinsky, *O. diaphanum* var. *podocarpi* (Müll. Hal.) Lewinsky, *O. freyanum* Goffinet, W.R. Buck & M.A. Wall, *O. gigantosporum* Lewinsky, *O. inclinatum* Müll. Hal., *O. perexiguum* Dusén ex Lewinsky, *O. tristriatum* Lewinsky, and *O. truncatum* Lewinsky & Deguchi. This paper describes a new species from Chile, bringing the total number of *Orthotrichum* taxa in the country to eleven.

Previously, *Orthotrichum aequatoreum* was also reported from the territory of Chile (Ireland et al. 2006). However, a subsequent review of the material revealed that this was a misidentification (Ireland et al. 2017).

Material and methods

Plant material

During a bryofloristic survey in the Andes Mountains in 2021, a remarkable epiphytic moss from the genus *Orthotrichum* was collected. Specimens were carefully gathered, air-dried, and sent to the University of Ostrava for identification and inclusion in the herbarium collections (herbarium OSTR). The material proved to be the first record of this taxon for Chile and, upon closer examination, also to represent a species new to science. Plants were subsequently documented using an Olympus SZ61 trinocular microscope for macrophotographs and Olympus BX53 and IPOS-810 microscopes for microphotographs. Detailed SEM photo-documentation of peristome structures and spores was carried out using a Jeol SEM microscope. All photographs were captured from the holotype (OSTR #8123).

Table 1. Occurrence of *Orthotrichum* taxa in Chile based on literature data summarizing taxonomic and floristic research.

Species / literature sources	**Lewinsky (1984)**	**Lewinsky and Deguchi (1989)**	**Müller (2002)**	**Buck (2005)**	**Goffinet et al. (2007)**	**Müller (2009)**	**Buck and Goffinet (2010)**	**Medina et al. (2013)**	**Ireland et al. (2017)**	**Larraín (2016)**	**Larraín and Bahamonde (2017)**	**Drapela and Larraín (2020)**	**Lara et al. (2021)**	**Ellis et al. (2023)**
Orthotrichum anomalum				♦		♦					♦			
O. assimile	♦					♦			♦	♦	♦			
O. cupulatum var. *austroamericanum*	♦					♦						♦		♦
O. diaphanum var. *podocarpi*			♦			♦								
O. freyanum					♦	♦			♦					
O. gigantosporum		♦				♦							♦	
O. inclinatum	♦					♦	♦							
O. perexiguum	♦					♦			♦					
O. tristriatum	♦					♦		♦	♦					
O. truncatum		♦				♦			♦					

Molecular analyses

Total genomic DNA from a single individual was extracted using the Qiagen Mini Spin Plant Kit (Qiagen, Germany). Details concerning DNA quantification and nanopore sequencing are identical to those in the previous studies (Plášek et al. 2023; Sawicki et al. 2023), but due to lower than required for native DNA sequencing amount of extracted DNA, the low input protocol for library preparation was used. The PCR amplification of total DNA was performed using EXP-PCA001 (Oxford Nanoporetech, UK, hereafter ONT) expansion module followed by SQK-LSK114 kit (ONT) protocol. The beads-based post PCR cleaning stage was replaced by column based method using Clean-Up kit (A&A Biotechnology, Poland) and remaining steps and reagents were as recommended in Lingation sequencing V14 - low input by PCR protocol (ONT). Prepared library was sequenced using FLO-MIN114 (ONT) flow cell and sequenced using Minion Mk1C device. Raw reads were basecalled using Dorado 0.5.1 (ONT) using SUP model with enabled duplex read calling. For downstream analyses, reads containing duplex flags were extracted using Samtools software (Danecek et al. 2021). Application duplex high quality reads (Q>30) allow assembling error-free plastomes using exclusively nanopore sequencing technology (Sawicki et al. 2024).

Obtained raw reads were trimmed using porechop 0.2.4 and assembled using Flye 2.91 assembler (Kolmogorov et al. 2019), which produced complete, circularized plastome contigs. The complete chloroplast genome was annotated using previously published *Orthotrichum* Hedw. sequences (Mizia et al. 2019; Frangedakis et al. 2021; Plášek et al. 2023) as references in Geneious Prime 2023.2.1 software (Biomatters, Auckland, New Zealand) and deposited in GenBank under PP274123 accession number. The newly sequenced genome was aligned with previously analyzed dataset of Orthotrichaceae plastomes (Plášek et al. 2023) using MAFFT 7.52 (Katoh and Standley 2013). The second copy of IR was removed from subsequent analyses and ambiguously aligned regions were trimmed by Gblocks 0.91 (Talavera and Castresana 2007). The plastome map was drawn using Chloe web server (https://chloe.plastid.org/).

Chloroplast sequences of 22 specimens of Orthotrichaceae, including seven from *Orthotrichum* were used for phylogenetic analysis. Phylogenetic analysis was carried out using the Bayesian inference (BI) according to model and parameters used in previous study (Plášek et al. 2023). The discrete molecular diagnostic characters (MDCs) for each species of *Orthotrichum*, were calculated according to the Jörger and Schrödl (2013) approach using FASTACHAR 0.2.4 (Merckelbach and Borges 2020).

Results

Taxonomic treatment

Orthotrichum camanchacanum **Plášek, Sawicki & Osorio, sp. nov.**

Diagnosis. *Plantae olivacea, obscure viridis, usque ad 1-cm altae. Folia erecta, lineari-lanceolata, carinata, apicibus longis acuminatis. Capsulae emergentes, cylindricae. Stomata cryptopora. Vaginula dense pilosa cum capilli longi.*

Peristomium duplex, exostoma 8 paribus dentium siccitate erectum, endostoma 16 segmentis. Calyptra dense pilosa. Sporae 19–24 μm, leniter papillosae.

Type. Chile, Región de Coquimbo (Region IV), Provincia del Elqui, Comuna de Coquimbo, 2 km southeast of Totoralillo town, GPS: 30°04'26"S, 71°21'13"W (-30.073972, -71.353583), on hills profoundly influenced by the humidity generated by camanchaca, vegetation formed mainly by shrubs (*Adesmia argyrophylla* Phil. and *Echinopsis chiloensis* subsp. *chiloensis* (Colla) H.Friedrich & G.D.Rowley), moss was found epiphytically on bark of shrubs, leg. F. Osorio *4378*, 10 Aug 2021, holotype (OSTR #8123); isotype (VALD *s.n.*).

Description. Plants in dense tufts to 1 cm tall, olive green above, dark green to brown below (Fig. 2). Stem moderately branched, branches up to 5 mm long. Rhizoids well developed, mainly at base of stems. Stem leaves erect to slightly recurved when dry, spreading to slightly recurved when moist; in upper third linear-lanceolate, long acuminate, 3.0–4.1 × 0.3–0.5 mm, carinate; costa ending just below apex or more often excurrent in hyaline long arista. Leaves in the middle and lower part of the stem wider and shorter, ovate-lanceolate, acuminate, 3.0–3.6 × 0.4–0.7 mm, carinate; costa ending just below apex or rarely excurrent in short aristae. Lamina of stem leaves unistratose, margins entire, recurved from the base to two-thirds of the leaf. Hyaline aristae rectangular, formed by (1–)2–3 gradually elongating cells, from 50–65 to 90–115 × 8–10 μm. Upper laminal cells isodiametric to short elongate, (9–)10–15 × 8–11 μm, fairly thick-walled, with one low papillae on both side; basal laminal cells elongate rectangular to rhomboidal, thick-walled, (18–)20–45 × 10–12 μm, smooth. Alar cells slightly differentiated. Sexual condition goniautoicous. Perichaetial leaves differentiated, ovate-lanceolate, acuminate, significantly shorter than stem leaves, only 1.7–2.2 × 0.5–0.8 mm; upper cells forming conspicuous hyaline (sometimes denticulate) apex (Fig. 3). Seta 1.1–1.5 mm long, ochrea up to 1/5 of the seta, vaginula densely hairy with 0.8–1.9 mm long, single-rowed or sometimes double-rowed, smooth hairs, which usually reach the base of the urn (Fig. 4). Capsule emergent; cylindric to oblong-ovoid, about 1.8–2.2 mm long, yellowish brown, slightly constricted below the mouth when dry. Exothecial cells differentiated mainly in the upper half of capsule, urn strongly furrowed when dry. Stomata cryptopore, scattered in the lower part of the urn, more than half covered by subsidiary cells. Peristome double (Figs 4, 5), preperistome absent. Exostome of 8 pairs of teeth, yellow to light brown, erect-spreading when dry. The outer peristome layer (OPL) ornamentation formed by dense papillae below and a mixture of papillae and distinct striae above. The primary peristome layer (PPL) finely and evenly ornamented by vermiculous lines, slightly also with low papillae. Endostome segments 16, almost as tall as exostome, reflexed when dry; 8 main segments double-rowed and 8 intermediate thinner, single-rowed, somewhat shorter or completely broken in matured capsules. The inner peristome layer (IPL) smooth or ornamented indistinctly by vermiculous lines in the lower part. Calyptra conic-oblong, more or less plicate, yellowish with longitudinal brown stripes, apex red-brown, densely hairy with long, yellowish, smooth hairs. Lid conic, apiculate. Spores light brown, 19–24 μm, densely papillose. Asexual reproduction not observed.

Figure 1. The map illustrates the geographical location where *Orthotrichum camanchacanum* was discovered.

Distribution and ecology. Moss *Orthotrichum camanchacanum* was discovered growing epiphytically on the bark of shrubs within vegetation predominantly composed of shrubs such as *Adesmia argyrophylla* and *Echinopsis chiloensis* subsp. *chiloensis*. This epiphytic growth pattern suggests a specific ecological niche for this moss within the ecosystem. See map (Fig. 1) for a visual representation of the study area. The territory under investigation lies within the Coquimbo region, characterized by numerous transverse valleys. Notably, the Elqui valley, where *Orthotrichum camanchacanum* was observed, is situated within this region. The environmental conditions in the study area are influenced by the Andes mountain range, contributing to a steppe-like climate. This climate is typified by sparse vegetation, consisting primarily of shrubs and scrubby vegetation. Precipitation, the heaviest of which occurs during the winter months, further shapes the ecological dynamics of the region.

Etymology. The authors are delighted to name the species (camanchacanum) after "camanchaca", a term derived from Aymara native language, signifying marine cloud (fog). Forming along the Chilean coast as a cloud, the camanchaca transforms into a dense fog as it moves inland towards the mountains. This fog provides the humidity essential for plant survival.

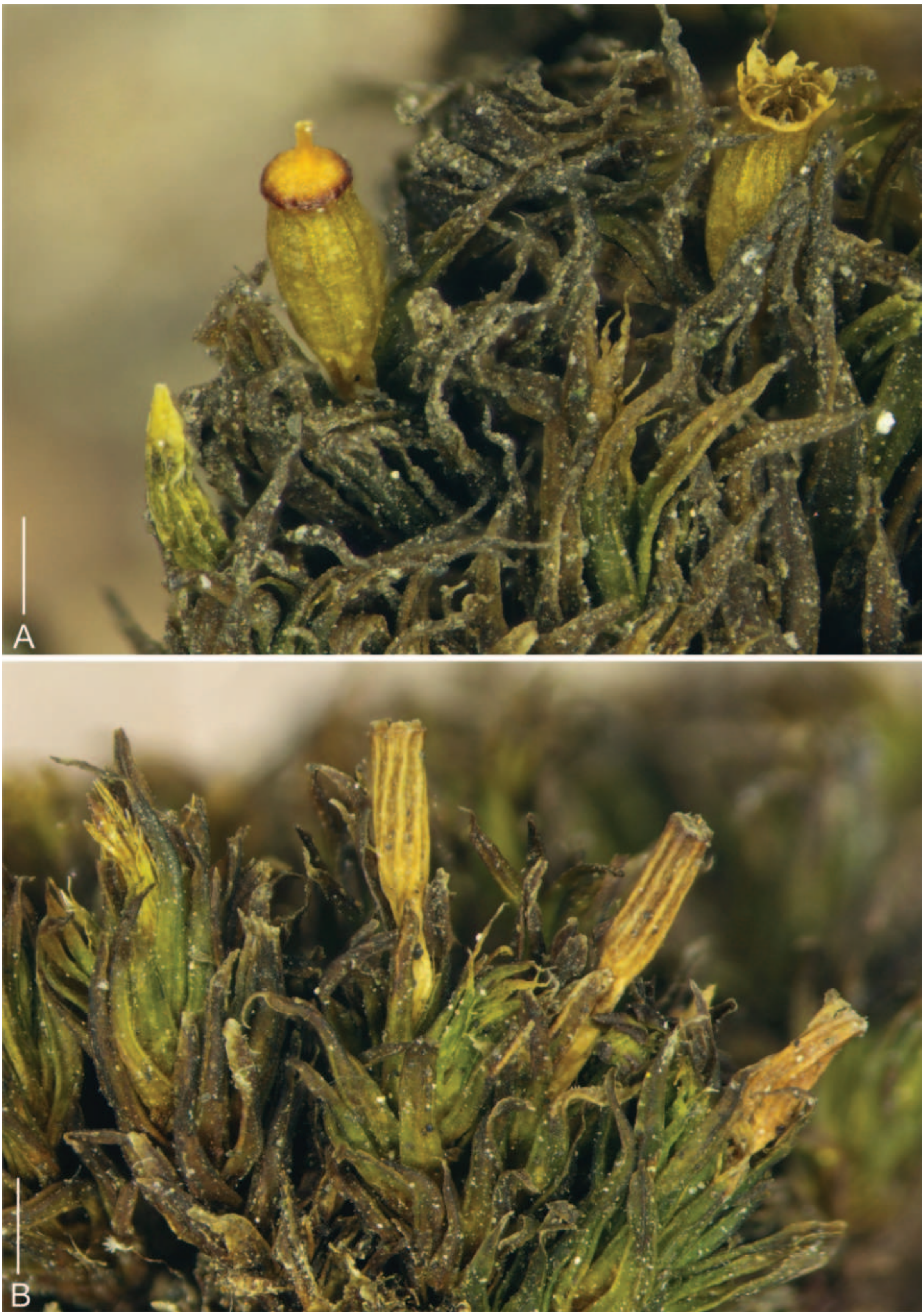

Figure 2. Macro photographs of *Orthotrichum camanchacanum*. View on fertile plants: **A** plants with capsules at various stages of development: young immature capsule (left), capsule closed by lid (middle), and mature capsule with open peristome (right) **B** dried furrowed capsules emergent from long leaves. Scale bars: 1 mm (**A, B**). Photographs were taken from the holotype (OSTR #8123).

Figure 3. Micro photographs of *Orthotrichum camanchacanum* leaves **A–G** leaves from upper part of a stem (linear-lanceolate with remarkable narrow hyaline apex) **H–N** leaves from middle and lower part of a stem (many of them are damaged and without apical part) **O–S** detail views of laminar cells, abaxial views (**O** apical part **P** upper part **Q** middle part **R** lower part and **S** base of leaf) **T–V** perichaetial leaves **W** leaf sections (from apical to basal part). Scale bars: 1 mm (**A–N**); 100 μm (**O–S**); 0.5 mm (**T–V**); 50 μm (**W**). Photographs were taken from the holotype (OSTR #8123).

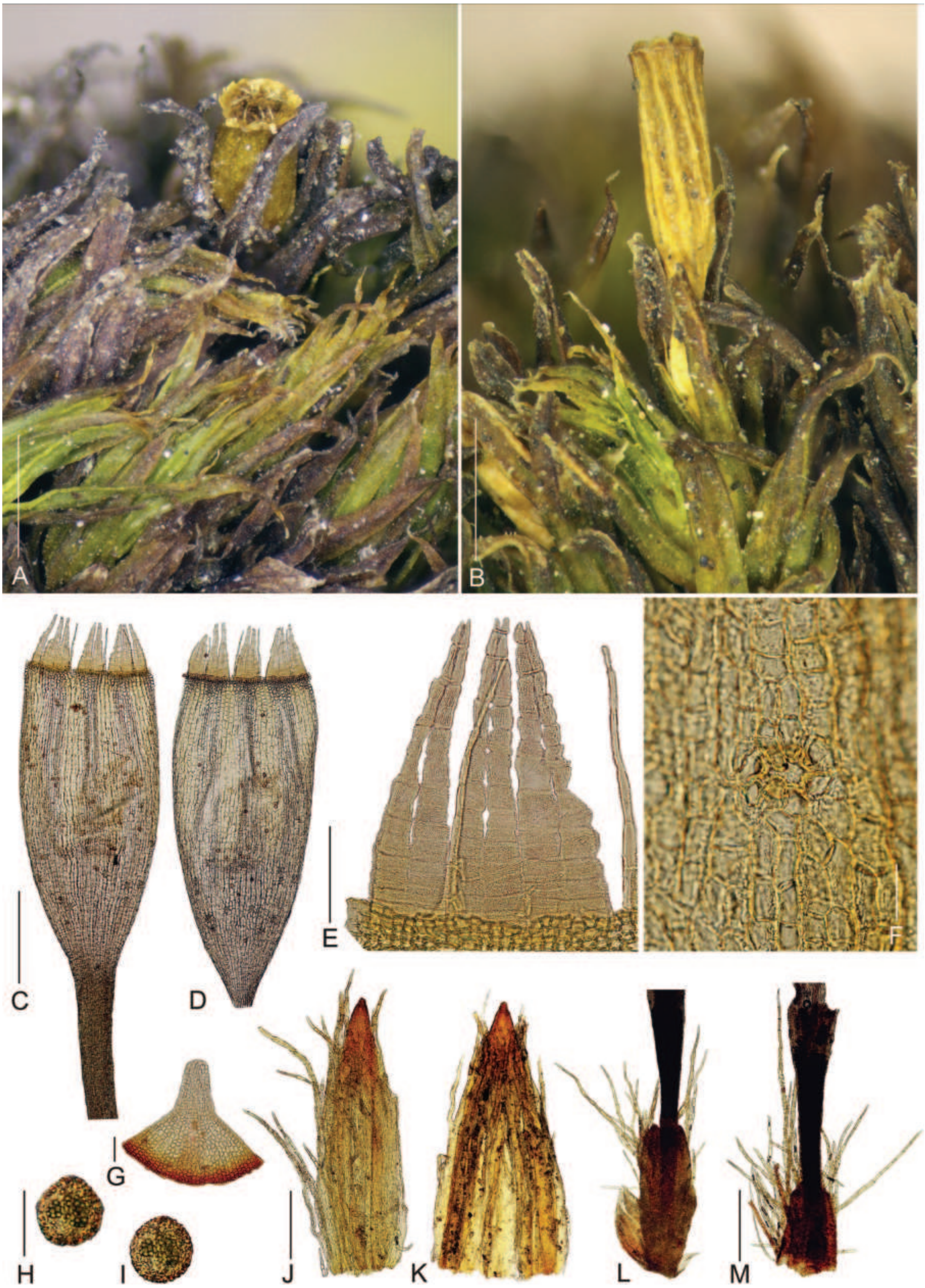

Figure 4. Macro and micro photographs of *Orthotrichum camanchacanum* sporophyte characters **A, B** view on mature capsules **C, D** mature capsule with peristome **E** detail of peristome **F** stoma (immersed) on capsule urn **G** lid **H, I** spores **J, K** calyptra covered by long hairs **L, M** hairy vaginula. Scale bars: 1 mm (**A, B**); 0.5 mm (**C, D**); 100 µm (**E**); 50 µm (**F**); 0.1 mm (**G**); 20 µm (**H, I**); 0.5 mm (**J–M**). Photographs were taken from the holotype (OSTR #8123).

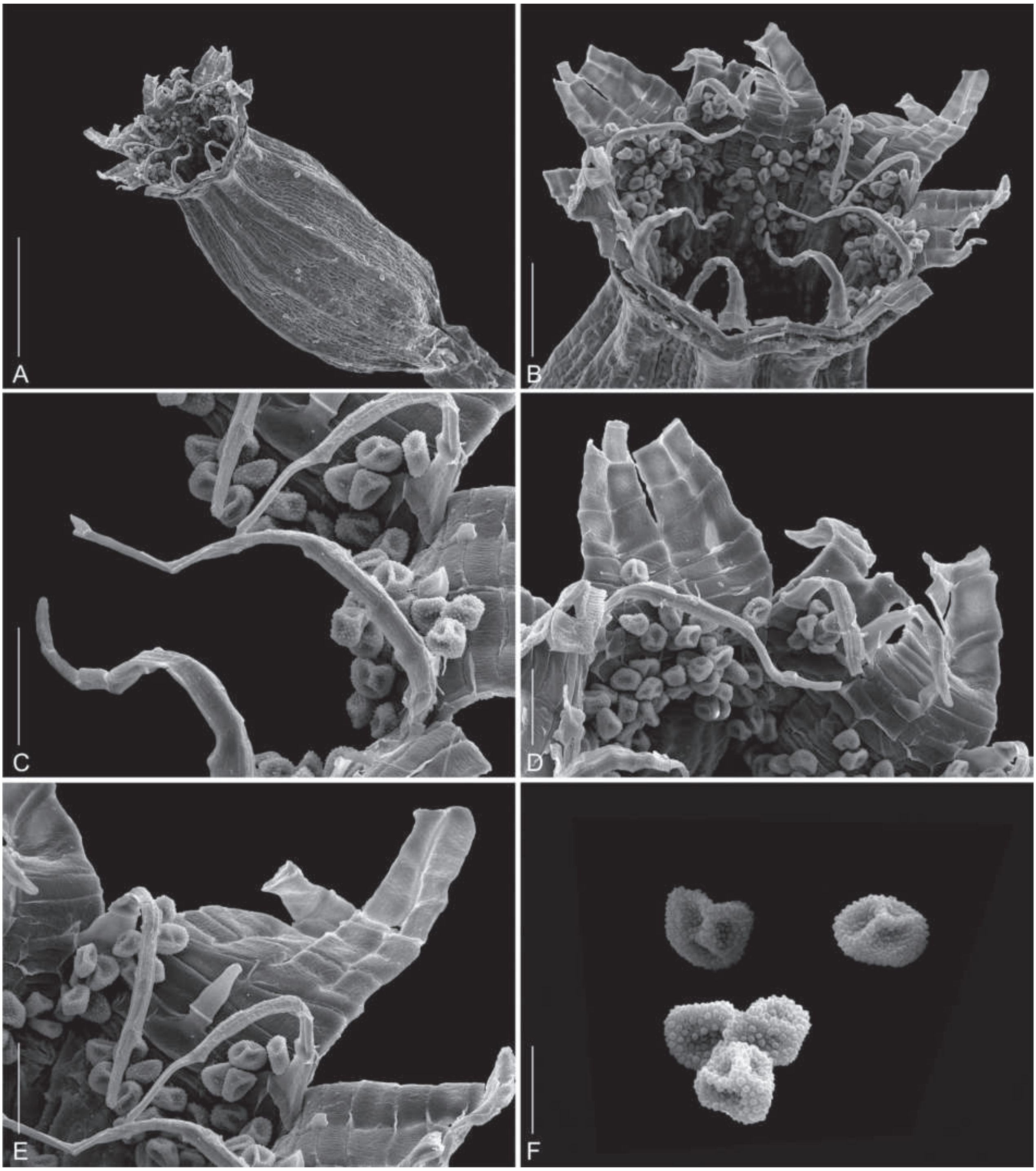

Figure 5. SEM photographs of *Orthotrichum camanchacanum* **A** capsule **B** double peristome **C–E** detailed view on exostome teeth and endostome segments **F** spores. Scale bars: 500 µm (**A**); 100 µm (**B**); 50 µm (**C–E**); 20 µm (**F**). Photographs were taken from the holotype (OSTR #8123).

Molecular survey

Chloroplast genome of *Orthotrichum camanchacanum* sp. nov. was 123,409 bp long and had a typical quadripartite structure with one small single-copy (SSC), one large single-copy (LSC), and two inverted repeats (IR). The use of third-generation sequencing did not identify any structural heteroplasmy associated with inversions in the SSC region. The newly sequenced plastome comprises 82 gene encoding proteins (including hypothetical chloroplast reading frames like ycf1, 2, 3, 4, 12, and 66), 32 transfer RNA (tRNA), and four ribosomal RNA (rRNA) genes. Notably, the rps12 gene is split into two separate transcription units, namely 5’-rps12 and 3’-rps12, and their transcripts undergo trans-splicing (Fig. 6).

Analysis of molecular diagnostics characters (MDCs) revealed 641 SNPs characteristic for *Orthotrichum camanchacanum* followed by 646 for *O. rogeri* and 890 in the case of *O. cupulatum*. Higher numbers of MDCs were detected for *O. crenulatum* and *O. stellatum*, 932 and 1304 respectively.

The phylogenetic relationships based on complete plastomes sequences results in a tree (Fig. 7) with all nodes maximally supported by Bayesian posterior probabilities (1.0).The Orthotrichaceae species were found to split into two separate groups, or clades. The first clade includes genera from the Lew-

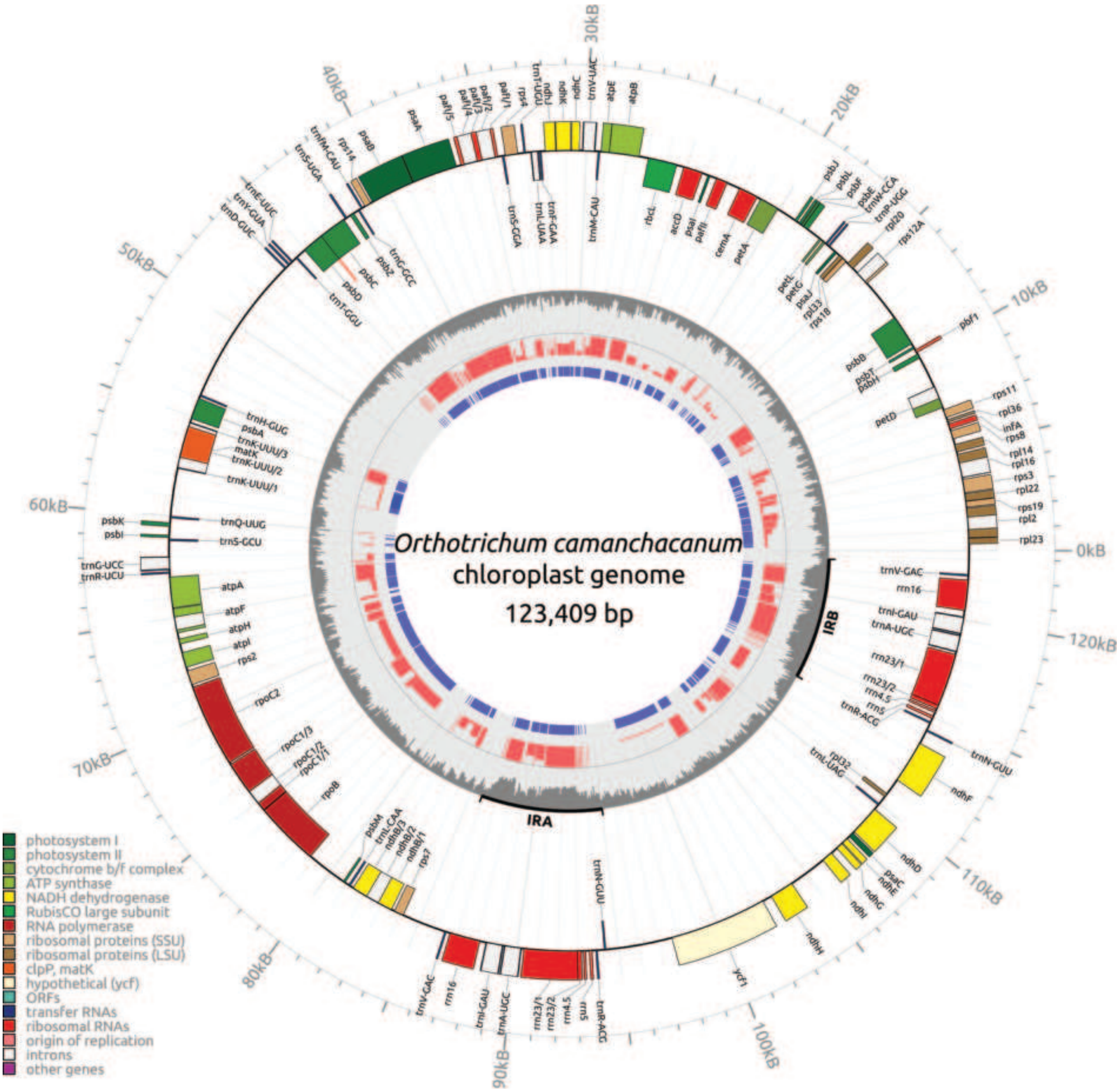

Figure 6. Chloroplast genome of newly described *Orthotrichum camanchacanum*. Gray inner circle indicates GC content. Red bars indicate normalized score form reference genome (*Orthotrichum rogeri*) while blue bars incidence percentage of reference genome features.

inskyinae subgroup, namely *Lewinskya*, *Pulvigera*, and *Ulota*. The second clade consists of genera from the Orthotrichinae subgroup, which are *Nyholmiella*, *Stoneobryum* D.H. Norris & H. Rob., and *Orthotrichum* s. str. Upon analysis, each of these genera was confirmed to be monophyletic. Within these groupings, *Ulota* was identified as the closest relative to the combined *Pulvigera*/*Lewinskya* clade. Similarly, *Nyholmiella* was found to be most closely related to *Orthotrichum*. The newly described *Orthotrichum camanchacanum* resolved as sister to *O. crenulatum*/*O. rogeri* clade.

Discussion

The combination of characters of the newly described species, *Orthotrichum camanchacanum*, is distinctive, making it easily recognizable. Upon initial observation, the most notable feature of the gametophyte is the shape of the stem leaves, particularly those in the upper third of the stem. They exhibit a linear-lanceolate form with a narrow apex that terminates in a long, hyaline arista (Fig. 3A–G, O). When comparing the shape of the stem leaves, the majority of the Chilean species within the *Orthotrichum* genus generally have ovate-lanceolate leaves (Table 2) with shorter apices. Only *O. inclinatum* (in Lewinsky 1984 as *O. compactum* Dusén) shares a similarly linear-lanceolate leaf shape, but it differs from *O. camanchacanum* in other gametophyte characters, such as the absence of a long aristate hyaline apex in the stem leaves, a naked vaginula, and the absence of differentiated perichaetial leaves. Adding sporophyte characters, then, *O. inclinatum* has long exserted capsule, naked vaginula and different combination of peristome (8+8).

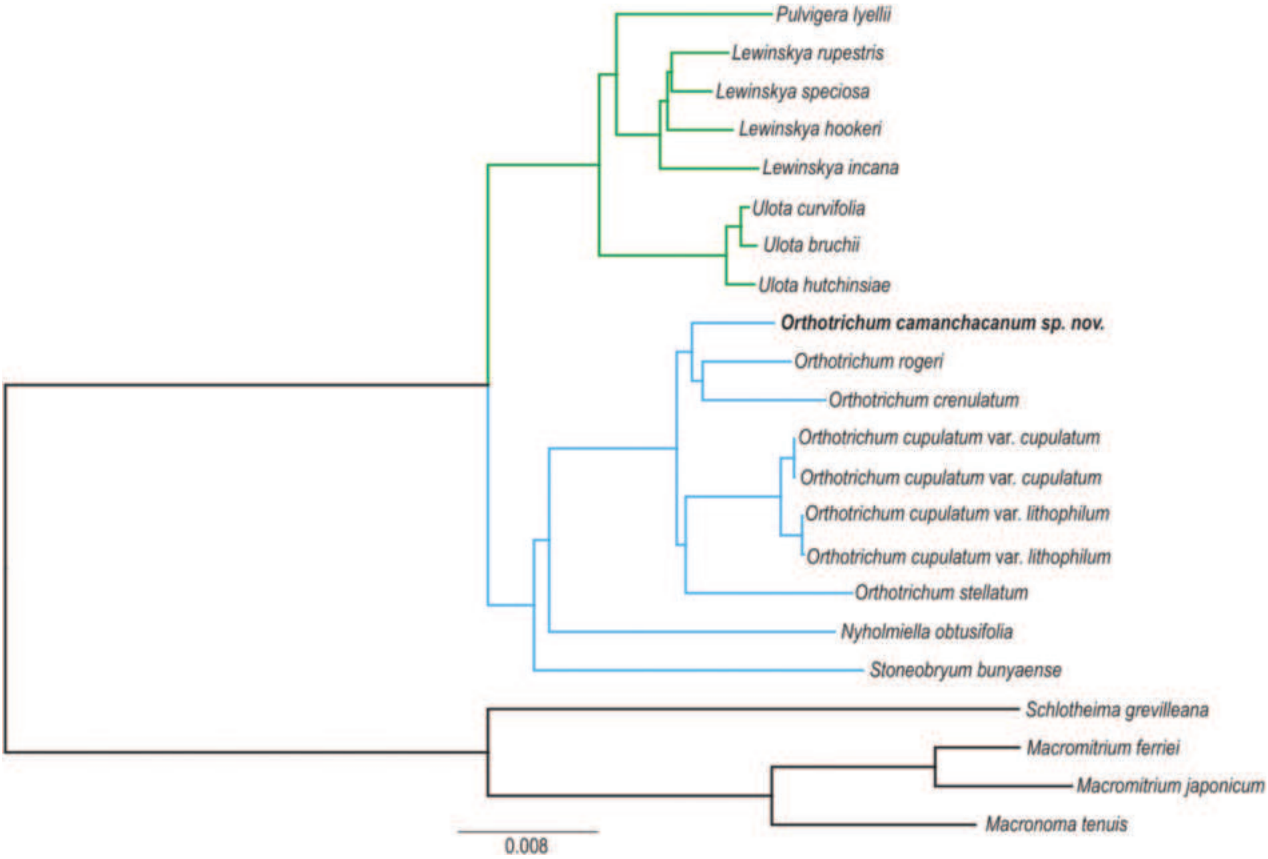

Figure 7. The Bayesian inference tree based on complete chloroplast genomes. All clades have maximum PP values (1.0).

Table 2. Comparison of diagnostic characters in Chilean species of the genus *Orthotrichum*. Data for the newly described species are presented in bold.

Species / Diagnostic characters	leaf shape	leaf margin	lamina	perichaetial leaves	vaginula	capsule position	exostome teeth	endostome segments	preperistome	spore size (µm)	calyptra	asexual repr.
Orthotrichum anomalum	lanceolate	revolute	unistratose	not differentiated	occasionally hairy	long exserted	8 pairs	absent	present	14–18	hairy	not observed
O. assimile	ovate-lanceolate	revolute	unistratose	not differentiated	naked	emergent	8 pairs	8 (or 16)	absent	15–20	naked or sparsely hairy	gemmae (uncommon)
O. camanchacanum	**linear-lanceolate**	**recurved**	**unistratose**	**differentiated**	**densely hairy**	**emergent**	**8 pairs**	**16 segments**	**absent**	**19–24**	**densely hairy**	**not observed**
O. cupulatum var. *austroamericanum*	ovate-lanceolate	recurved	unistratose	not differentiated	naked	shortly emergent	16 teeth	mostly absent	present	15.5–20	hairy	not observed
O. diaphanum var. *podocarpi*	ovate-lanceolate	revolute	unistratose	not differentiated	naked	immersed to emergent	8 pairs (splitting)	16 segments	absent	18–22	hairy	gemmae
O. freyanum	ovate-lanceolate	revolute	unistratose	not differentiated	naked	emergent to shortly exserted	8 pairs	8 segments	absent	12–15	hairy	gemmae
O. gigantosporum	ovate-lanceolate	plane or slightly recurved	unistratose	differentiated	hairly	long exserted	16 teeth	16 segments	absent	31–34 (–40)	naked	not observed
O. inclinatum	linear-lanceolate	plane or revolute	unistratose	not differentiated	naked	long exserted	8 pairs	8 segments	absent	13–19	with few scattered hairs	gemmae (occasionally)
O. perexiguum	narrow lanceolate	plane	bistratose	differentiated	naked	emergent to just exserted	8 pairs	8 segments	absent	14–16	naked	not observed
O. tristriatum	ovate-lanceolate	broadly revolute	unistratose	differentiated	naked	emergent to shortly exserted	8 pairs	8 segments	absent	14–18	with few scattered hairs	not observed
O. truncatum	ovate-lanceolate	reflexed	unistratose	not differentiated	hairly	shortly exserted	8 pairs	8 segments	mostly absent	20–23	with few scattered hairs	not observed

Although *Orthotrichum perexiguum* also exhibits a narrow and lanceolate leaf shape (Lewinsky 1984), this species is notably small, reaching only up to 0.5 cm. Moreover, it can be distinguished by a bistratose laminal in its marginal parts, a naked vaginula, and a different peristome combination (8+8).

The perichaetial leaves produced by *Orthotrichum camanchacanum* are distinctive and markedly different when compared with all South American species of this genus. Notably, they possess a unique apex formed by a group of conspicuous hyaline cells (Fig. 3T–V). In contrast, the perichaetial leaves of other Chilean *Orthotrichum* species that produce them (such as *O. gigantosporum*, *O. perexiguum*, and *O. tristriatum*), are similar in shape to the stem leaves, differing mostly in their smaller size (Lewinsky 1984).

The hairiness of the vaginula is considered a distinctive taxonomic character for identifying *Orthotrichum* species (Lewinsky 1993). However, in some European species, this character has not always proven suitable due to its considerable variability (Plášek and Sawicki 2010). Among the Chilean species, three exhibit a distinctly hairy vaginula (*O. camanchacanum*, *O. gigantosporum*, and *O. truncatum*), while in one other species (*O. anomalum*), its hairiness was only occasionally noted (Lewinsky 1984; Lewinsky and Deguchi 1989). In *O. camanchacanum*, the hairs in vaginula are dense and long, often reaching the base of the urn or clearly visible among upper stem leaves.

When comparing the sporophyte characters of the Chilean species within the genus *Orthotrichum*, most of them, including the newly described species, have emergent or shortly exserted capsules. However, three species (*O. anomalum*, *O. gigantosporum*, and *O. inclinatum*) produce significantly exserted capsules on a long seta (Lewinsky 1984; Lewinsky and Deguchi 1989). In *Orthotrichum* species, the peristome is of the arthrodontous type and primally diplolepidous. Typically, it consists of eight pairs of exostome teeth, occasionally splitting into 16, and eight or sixteen endostome segments. The combination of the number of teeth and segments, along with their surface ornamentation, is a crucial taxonomic feature for both the genus and the entire family Orthotrichaceae (Lewinsky 1993). In the case of *O. camanchacanum*, its peristome is formed by eight pairs of exostome teeth with the outer peristome layer densely papillose below and a mixture of papillae and striae in the upper part. A similar OPL surface is observed in *O. alpestre* Bruch & Schimp., a European species not found in South America (cf. Lara et al. 2009; Plášek and Ochyra 2020). Regarding the endostome of the newly described species, it consists of 16 thin segments, which are delicate and often partially broken. However, in well-developed capsules, all the segments are significantly long, almost reaching the length of the exostome teeth. Only two other Chilean species, *O. assimile* and *O. tristriatum*, have similarly long and thin endostome segments, but both of them generally have a total of eight segments.

It is widely acknowledged that species within the genus *Orthotrichum* have immersed stomata, distinguishing them from representatives of the related genus *Lewinskya*, whose urns possess superficial stomata (Lewinsky 1993). Despite this, some species across both genera exhibit macroscopic similarities. Paradoxically, in the case of *Orthotrichum camanchacanum*, certain South American *Lewinskya* species share a closer resemblance than *Orthotrichum* species, especially those with distinctly long and narrow leaves culminating in a markedly narrow apex, e.g. *L. elongata* (Taylor) F. Lara, Garilleti & Goffinet, *L. johnstonii* (E.B. Bartram) F. Lara, Garilleti & Goffinet or *L. mandonii* (Schimp. ex Hampe) F. Lara, Garilleti & Goffinet (cf. Lewinsky 1984). However, aside from the already mentioned distinct positions of the stomata, these *Lewinskya* species also differ in a clear combination of peristome parts. This marked difference in characters prevents any confusion between the newly described species and representatives of *Lewinskya* species.

The territory where the new species was collected possesses distinctive geographical and climatic conditions. The entire Coquimbo region features several transverse valleys that cut across perpendicular to the main Andes mountain chain, carving through the country horizontally (Alaniz and Carvajal 2019). Among these valleys is situated the Elqui interion region, where *Orthotrichum camanchacanum* was collected. The Andes contribute the Región de Coquimbo, providing a steppe-like climate characterized by bushy, scrubby vegetation and heaviest precipitation in the winter (Moreira-Muñoz 2011). On the coast, especially on the coastal mountain range influenced by the moderating effect of the ocean, an abundance of clouds and coastal fog, known as camanchaca, fosters the growth of Chile's northernmost forests (Moreira-Muñoz 2011). Inland, the climate becomes warm and typically dry (Alaniz and Carvajal 2019). This varied landscape relief combined with a unique climate may have significantly contributed to the speciation of this new species. The moss *O. camanchacanum* exhibits morphological characters that distinguish it from related species. The fact that it has not been found despite intensive research carried out in Chile since 2011 by the first author may be attributed to its geographical isolation and consequently a very limited area of occurrence. It seems to be endemic to this region of Chile. This situation is not unique; similar examples exist, such as the moss *Lewinskya johnstonii*, which also possesses unique morphological features and is limited to the National Park Fray Jorge and its close surroundings (Lewinsky 1984). This area similarly exhibits a specific and characteristic climate.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The project is co-financed by the European Union under the European Regional Development Fund RPO WO 2014–2020 Operation 1.2 R&D infrastructure. Agreement no. RPOP.01.02.00-16-0001/17-00 from 31.01.2018.; EU structural funding CZ.1.05/2.1.00/19.0388; Ministry of Education, Youth and Sports of the Czech Republic: LO1208; ANID PhD grant 21231650.

Author contributions

FO collected the original specimen and provided additional habitat information; VP identified the material, prepared macro, micro and SEM photographs, and completed the description of the new taxon; JS performed the molecular analyzes and prepared the molecular background for the verification of the new taxon, HR helped with preparation of the material; VP, JS, FO and HR prepared the draft version of the manuscript, which was reviewed, edited, and approved by all co-authors.

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Data availability

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

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PhytoKeys 242: 69–138 (2024)
DOI: 10.3897/phytokeys.242.117469

Research Article

A new classification system and taxonomic synopsis for Malpighiaceae (Malpighiales, Rosids) based on molecular phylogenetics, morphology, palynology, and chemistry

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OPEN ACCESS

Academic editor: Alexander Sennikov
Received: 16 December 2023
Accepted: 23 April 2024
Published: 22 May 2024

Citation: de Almeida RF, de Morais IL, Alves-Silva T, Antonio-Domingues H, Pellegrini MOO (2024) A new classification system and taxonomic synopsis for Malpighiaceae (Malpighiales, Rosids) based on molecular phylogenetics, morphology, palynology, and chemistry. PhytoKeys 242: 69–138. https://doi.org/10.3897/phytokeys.242.117469

Abstract

Malpighiaceae has undergone unprecedented changes in its traditional classification in the past two decades due to several phylogenetic studies shedding light on the non-monophyly of all subfamilies and most tribes and genera. Even though morphological characters were used to reconstruct the last molecular generic phylogeny of Malpighiaceae, a new classification system has never been proposed for this family. Based on a comprehensive review of the last twenty years of published studies for this family, we propose a new classification system and provide a taxonomic synopsis for Malpighiaceae based on molecular phylogenetics, morphology, palynology, and chemistry as a baseline for the systematics, conservation, and taxonomy of this family worldwide. Malpighiaceae currently comprises two subfamilies (Byrsonimoideae and Malpighioideae), 12 tribes (Acmanthereae, Acridocarpeae **trib. nov.**, Barnebyeae **trib. nov.**, Bunchosieae **trib. nov.**, Byrsonimeae, Galphimieae, Gaudichaudieae, Hiptageae, Hiraeeae, Malpighieae, Mcvaughieae **trib. nov.**, and Ptilochaeteae **trib. nov.**), 72 genera (incl. *Mamedea* **gen. nov.**), and 1,499 accepted species (715 of which are currently under some kind of extinction threat). We present identification keys for all subfamilies, tribes, and genera, a full morphological description for the proposed new genus, the re-circumscription of ten genera alongside the needed new combinations, the proposition of several new synonyms, the typification of several names, and notes on the taxonomy, distribution, conservation, and ecology up to the genus rank. Morphological plates are also provided to illustrate the immense diversity of morphological traits used in the new classification and synopsis.

Key words: Conservation, Elatinaceae, integrated monography, phylogeny, systematics, taxonomy

Introduction

Malpighiaceae (Malpighiales) is a family of flowering plants currently comprising 75 genera and ca. 1,350 species of trees, shrubs, subshrubs, and lianas distributed in tropical and subtropical regions of the world (Almeida et al. 2020, 2023a; POWO 2024). This family includes several economically important species in the Neotropics, such as the Barbados cherry (*Malpighia* ssp.), murici or nanche berry (*Byrsonima* ssp.), and the Ayahuasca hallucinogenic tea [*Banisteriopsis caapi* (Spruce ex Griseb.) C.V.Morton] (Almeida et al. 2020). Neotropical Malpighiaceae show a conspicuous floral conservatism characterised by monosymmetric (i.e., zygomorphic) and bisexual flowers with five sepals adnate at the base and abaxially (to the flower axis) bearing a pair of oil-secreting glands (i.e., elaiophores) near the base (sometimes absent from the anterior sepal or completely absent in few genera). This conspicuous floral conservatism of Neotropical Malpighiaceae was lost in the Old World genera due to a shift in their pollination system as an evolutionary adaptation to the absence of oil-collecting bees in the Paleotropics (Cameron et al. 2001; Davis et al. 2014; Almeida et al. 2023a). Consequently, Old World genera frequently show actinomorphic flowers with eglandular or nectariferous sepals and pantoporate pollen grains (Cameron et al. 2001; Davis et al. 2014).

In the past two decades, Malpighiaceae has gone through unparalleled changes in its traditional classification as a direct result of several molecular phylogenetic studies (Cameron et al. 2001; Davis et al. 2001; Davis and Anderson 2010; Almeida et al. 2017, 2018, 2023a, b; Almeida and van den Berg 2021, 2022). Key morphological characters of its traditional classification system (i.e., fruit types) were shown to be highly homoplastic (Cameron et al. 2001; Davis et al. 2001). The inevitable recognition of unforeseen relationships within Malpighiaceae brought to light deep taxonomic issues regarding the monophyly of several genera [e.g., *Banisteriopsis* C.R.Rob., *Mascagnia* (Bertero ex DC.) Bertero, *Stigmaphyllon* A.Juss., and *Tetrapterys* Cav.], tribes (i.e., only Gaudichaudieae was recovered as monophyletic), and all its subfamilies (i.e., Byrsonimoideae and Malpighioideae) (Cameron et al. 2001; Davis and Anderson 2010; Davis et al. 2001). Since then, different authors have gradually proposed new genera and combinations to accommodate these newly identified lineages (Anderson 2006; Anderson and Davis 2006; Anderson 2011; Davis et al. 2020; Almeida and van den Berg 2021; Almeida et al. 2023a, b). Even though morphological characters were used to reconstruct the last generic phylogeny of Malpighiaceae, no morphological characters were ever recovered and/or discussed for its major clades (Almeida et al. 2023a, b). As a result, its traditional classification was rejected, and several informal clades, without any morphological circumscription, were recognised in the most recent generic phylogeny for Malpighiaceae: 1. Byrsonimoids, 2. Acridocarpoids, 3. Mcvaughioids, 4. Barnebyoids, 5. Ptilochaetoids, 6. Bunchosioids, 7. Hiraeoids, 8. Tetrapteroids, 9. Malpighioids, and 10. Stigmaphylloids (Fig. 1; Davis and Anderson 2010; Almeida et al. 2023a).

As a result of over ten years of integrative studies worldwide, and based on a comprehensive review of the last twenty years of published studies for this family, we present a new classification system for Malpighiaceae based on molecular phylogenetics, morphology, palynology, and chemistry. We also present a taxonomic synopsis, including descriptions or diagnoses for the two subfamilies and 12 tribes currently recognised, besides identification keys for subfamilies, tribes, and genera. Some genera are re-circumscribed, while others are proposed, together with the necessary new combinations.

Several taxonomic changes are proposed for subfamilial, tribal, generic, and species ranks. A checklist of all currently accepted species of this family is also presented alongside their extinction threat risk (Suppl. material 1).

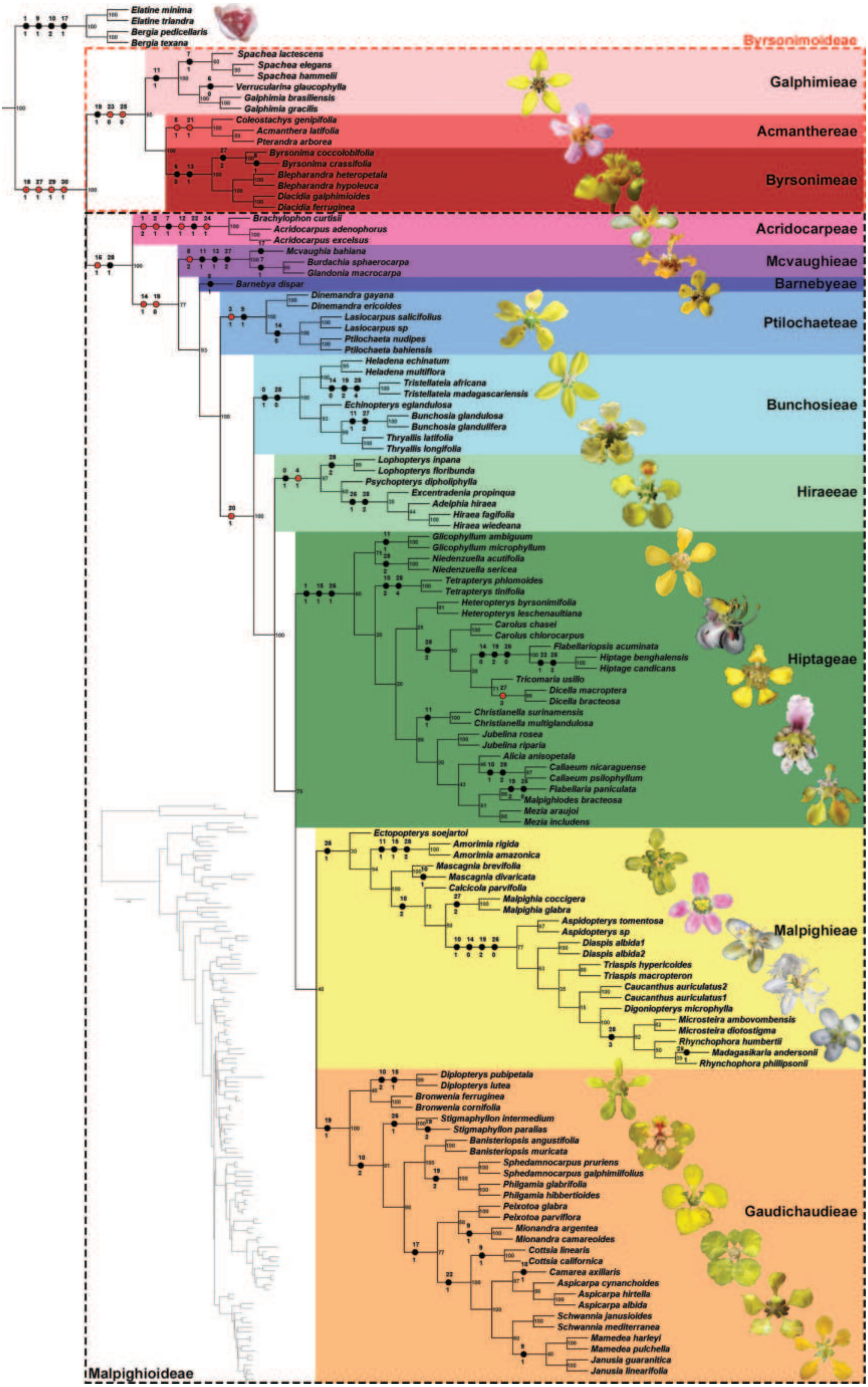
Materials and methods

Phylogenetics

We sampled one to three species and all 72 accepted Malpighiaceae genera recognised by us in the taxonomic treatment. The aligned matrix for *matK*, *ndhF*, *rbcL*, and PHYC from Davis and Anderson (2010) was retrieved from TreeBase (accession no. 10998) and reduced to our proposed sampling and edited using Geneious (Kearse et al. 2012) for gaps removal made manually by eye. All trees were rooted in Elatinaceae (*Bergia* + *Elatine*), the sister-group of Malpighiaceae, according to Davis and Anderson (2010). A combined analysis of plastid + nuclear regions was carried out using Maximum Likelihood (ML). We selected the model using hierarchical likelihood ratio tests (HLRT) on J Modeltest 2 (Darriba et al. 2012). The model-based method was conducted with a mixed model (GTR+G+I) and unlinked parameters using RAxML 8 (Stamatakis 2014) implemented on RAxMLGUI2 (Edler et al. 2021). ML analyses were performed with ten independent replicates, and default settings and support values were estimated using parametric bootstrapping with 500 replicates, with bootstrap support values presented on nodes. Character coding followed the recommendations for morphological analyses of Sereno (2007). Primary homology hypotheses (De Pinna 1991) were proposed for leaf, inflorescence architecture, floral, pollen, fruit, and chromosomic characters. A total of 31 characters were scored and coded (Suppl. material 2). All characters were optimised on the concatenated tree with the Maximum Likelihood function (mk1 model) using Mesquite 2.73 (Maddison and Maddison 2006) and visualised on Winclada (Nixon 1999).

Taxonomy

The analyses of morphological data were based on specimens from the following herbaria: ALCB, AMAZ, ASE, BAH, BM, BHCB, BOTU, CEN, CEPEC, CESJ, CGMS, COL, CPAP, CVRD, CTES, CUZ, EAC, ESA, F, FLOR, FUEL, FURB, FZB, G, GH, GUA, HAS, HB, HCF, HEPH, HISA, HRB, HRCB, HSJRP, HST, HUCP, HUCS, HUEFS, HUEM, HUESC, HUFG, HUFU, HUPG, HURB, HUT, HUVA, IAC, IAN, ICN, INPA, IPA, JPB, L, LIL, K, MAC, MBM, MBML, MG, MICH, MO, MOSS, MPU, NY, OUPR, P, PACA, PAMG, PEUFR, PMSP, R, RB, RBR, RFA, PRE, S, SI, SMF, SP, SPF, SPSF, TEPB, U, UB, UEC, UFP, UFMS, UFMT, UFRN, UPCB, US, USZ, W, VIC, and VIES (acronyms according to Thiers, continuously updated). Indumentum terminology and structure shapes follow Almeida and Morais (2022), inflorescence terminology and morphology follow Weberling (1965, 1989), and fruit terminology follows Spjut (1994). Chromosome numbers were retrieved from Anderson (1993) and Lombello and Forni-Martins (2002, 2003), and secondary metabolites were retrieved from Mannochio-Russo et al. (2022). Palynological data were retrieved from Lowri (1982), Silva et al. (2023), and Almeida et al. (2024) and complemented by the slide collections from the Instituto de Pesquisas Ambientais (São Paulo, Brazil) and the Royal Botanic Gardens, Kew.


Elatine minima
Elatine triandra
Bergia pedicellaris
Bergia texana
Byrsonimoideae
Spachea lactescens
Spachea elegans
Spachea hammelii
Verrucularina glaucophylla
Galphimia brasiliensis
Galphimia gracilis
Galphimieae
Coleostachys genipifolia
Acmanthera latifolia
Pterandra arborea
Acmanthereae
Byrsonima coccolobifolia
Byrsonima crassifolia
Blepharandra heteropetala
Blepharandra hypoleuca
Diacidia galphimioides
Diacidia ferruginea
Byrsonimeae
Brachylophon curtisii
Acridocarpus adenophorus
Acridocarpus excelsus
Acridocarpeae
Mcvaughia bahiana
Burdachia sphaerocarpa
Glandonia macrocarpa
Mcvaughieae
Barnebya dispar
Barnebyeae
Dinemandra gayana
Dinemandra ericoides
Lasiocarpus salicifolius
Lasiocarpus sp
Ptilochaeta nudipes
Ptilochaeta bahiensis
Ptilochaeteae
Heladena echinatum
Heladena multiflora
Tristellateia africana
Tristellateia madagascariensis
Echinopterys eglandulosa
Bunchosia glandulosa
Bunchosia glandulifera
Thryallis latifolia
Thryallis longifolia
Bunchosieae
Lophopterys inpana
Lophopterys floribunda
Psychopterys dipholiphylla
Excentradenia propinqua
Adelphia hiraea
Hiraea fagifolia
Hiraea wiedeana
Hiraeeae
Glicophyllum ambiguum
Glicophyllum microphyllum
Niedenzuella acutifolia
Niedenzuella sericea
Tetrapterys phlomoides
Tetrapterys tinifolia
Heteropterys byrsonimifolia
Heteropterys leschenaultiana
Carolus chasei
Carolus chlorocarpus
Flabellariopsis acuminata
Hiptage benghalensis
Hiptage candicans
Tricomaria usillo
Dicella macroptera
Dicella bracteosa
Christianella surinamensis
Christianella multiglandulosa
Jubelina rosea
Jubelina riparia
Alicia anisopetala
Callaeum nicaraguense
Callaeum psilophyllum
Flabellaria paniculata
Malpighiodes bracteosa
Mezia araujoi
Mezia includens
Hiptageae
Ectopopterys soejartoi
Amorimia rigida
Amorimia amazonica
Mascagnia brevifolia
Mascagnia divaricata
Calcicola parvifolia
Malpighia coccigera
Malpighia glabra
Aspidopterys tomentosa
Aspidopterys sp
Diaspis albida1
Diaspis albida2
Triaspis hypericoides
Triaspis macropteron
Caucanthus auriculatus2
Caucanthus auriculatus1
Digoniopterys microphylla
Microsteira ambovombensis
Microsteira diotostigma
Rhynchophora humbertii
Madagasikaria andersonii
Rhynchophora phillipsonii
Malpighieae
Diplopterys pubipetala
Diplopterys lutea
Bronwenia ferruginea
Bronwenia cornifolia
Stigmaphyllon intermedium
Stigmaphyllon paralias
Banisteriopsis angustifolia
Banisteriopsis muricata
Sphedamnocarpus pruriens
Sphedamnocarpus galphimiifolius
Philgamia glabrifolia
Philgamia hibbertioides
Peixotoa glabra
Peixotoa parviflora
Mionandra argentea
Mionandra camareoides
Cottsia linearis
Cottsia californica
Camarea axillaris
Aspicarpa cynanchoides
Aspicarpa hirtella
Aspicarpa albida
Schwannia janusioides
Schwannia mediterranea
Mamedea harleyi
Mamedea pulchella
Janusia guaranitica
Janusia linearifolia
Gaudichaudieae
Malpighioideae

Results

Phylogenetics

All ten major informal phylogenetic clades of Malpighiaceae recognised in the taxonomy section were well-supported by bootstrap values ranging from 60–100% (Fig. 1). *Rhynchophora* was the only genus recognised here recovered as paraphyletic due to the positioning of *Madagasikaria* nested within it (Fig. 1). *Ectopopterys* was the only genus not confidently placed within one of the ten major clades in Malpighiaceae, with it being positioned as the first lineage to diverge in Malpighioids or Stigmaphylloids depending on the number of species sampled within each genus (Fig. 1). Subfamily Byrsonimoideae was supported by one homoplasy (connective glands prominent) and two synapomorphies (styles subulate and stigmas punctiform; Fig. 1). Tribe Acmanthereae was supported by two synapomorphies (leaf venation camptodromous and carpels free), tribe Galphimieae by one homoplasy (bracteoles glandular), and tribe Byrsonimeae by two homoplasies (leaves eglandular and petals cucullate; Fig. 1). Subfamily Malpighioideae was supported by one homoplasy (androecium heteromorphic) and one synapomorphy (winged mericarps; Fig. 1). Tribe Acridocarpeae was supported by four synapomorphies (stipules absent, leaves alternate, bracts glandular, and styles reflexed in fruit) and two homoplasies (inflorescence main axis deflexed and styles two; Fig. 1). Tribe Mcvaughieae was supported by one synapomorphy (2–7-flowered cincinni) and three homoplasies (bracteoles glandular, petals cucullate, and drupes; Fig. 1). Tribe Barnebyeae was supported

Figure 1. Molecular phylogenetic tree recovered by the ML of the reduced alignment for *matK*, *ndhF*, *rbcL*, and PHYC presented by Davis and Anderson (2010) with the taxonomic sampling reduced to one or three terminals according to the accepted genera in the present study. Left tree shows branch lengths recovered. Right tree shows the names of families, subfamilies, and tribes coloured according to the current classification recognised in this study. Bootstrap support values from the ML presented on the nodes. Black circles represent homoplasies, and red circles represent synapomorphies/autapomorphies recovered for each lineage. Numbers above circles represent character numbers from Suppl. material 2, while the numbers below the circles represent character states from the same file. Galphimieae: flower of *Galphimia gracilis* Bartl. by M.O.O. Pellegrini. Acmanthereae: flower of *Pterandra pyroidea* L. by R.F. Almeida. Byrsonimeae: flower of *Byrsonima sericea* DC. by R.F. Almeida. Acridocarpeae: flower of *Acridocarpus longifolius* (G.Don) Hook.f. by E. Bidault. Mcvaughieae: flower of *Mcvaughia sergipana* Amorim & R.F.Almeida by R.F. Almeida. Barnebyeae: flower of *Barnebya harleyi* W.R.Anderson & B.Gates by F. Flores. Ptilochaeteae: flower of *Ptilochaeta bahiensis* Turcz. by R.F. Almeida. Bunchosieae: flowers of *Tristellateia madagascariensis* Poir. and *Bunchosia glandulifera* (Jacq.) Kunth by N. Rakotonirina and R.F. Almeida, respectively. Hiraeeae: flower of *Hiraea restingae* C.E.Anderson by R.F. Almeida. Hiptageae: flowers of *Niedenzuella multiglandulosa* (A.Juss.) W.R.Anderson, *Hiptage benghalensis* (L.) Kurz, *Christianella multiglandulosa* (Nied.) W.R.Anderson, *Alicia anisopetala* (A.Juss.) W.R.Anderson, and *Callaeum psilophyllum* (A.Juss.) D.M.Johnson all by R.F. Almeida. Malpighieae: flowers of *Amorimia andersonii* R.F.Almeida, *Mascagnia cordifolia* (A.Juss.) Griseb., *Aspidopterys wallichii* Hook.f., *Triaspis macropteron* Welw. ex Oliv., and *Madagasikaria andersonii* C.Davis by F. Michelangeli, M.O.O. Pellegrini, N. Singh, E. Bidault, and C.C. Davis, respectively. Gaudichaudieae: flowers of *Bronwenia megaptera* (B.Gates) W.R.Anderson & C.Davis, *Diplopterys lutea* (Ruiz ex Griseb.) W.R.Anderson & C.Davis, *Stigmaphyllon paralias* A.Juss., *Peixotoa hispidula* A.Juss., *Camarea axillaris* A.St.-Hil., and *Mamedea pulchella* (Griseb.) R.F.Almeida & M.Pell. by R.F. Almeida, M.O.O. Pellegrini, M.O.O. Pellegrini, R.F. Almeida, R.F. Almeida, and N. Taniguti, respectively.

by a single homoplasy (2-flowered cincinni), while tribe Ptilochaeteae by one synapomorphy (leaf blades revolute when young) and one homoplasy (only 4 1-flowered cincinni; Fig. 1). Tribe Bunchosieae was supported by two homoplasies (stipules epipetiolar and mericarps without wings; Fig. 1), while tribe Hiraeeae by one homoplasy (stipules epipetiolar) and one synapomorphy (leaf blades glandular at apex; Fig. 1). Tribe Hiptageae was supported by three homoplasies (stipules inconspicuous, petals pubescent, and stigmas lateral), while tribe Malpighieae by a single homoplasy (stigmas lateral; Fig. 1). Finally, tribe Gaudichaudieae was supported by a single homoplasy (connective glands prominent; Fig. 1).

Taxonomy

Despite *Madagasikaria* causing the non-monophyly of *Rhynchophora* (Fig. 1), the bootstrap support value for this clade is below 60%. Therefore, we have chosen to retain both genera as independent until further phylogenetic evidence sheds some light on the matter. Regarding the placement of *Ectopopterys*, which is either recovered as sister to the Malpighioids or the Stigmaphylloids, we have chosen what we believe to be the most parsimonious approach. Since the clade that includes the Malpighioids + *Ectopopterys* is supported by morphology, we have tentatively retained it as a member of that clade to prevent the unnecessary recognition of another monogeneric tribe. Finally, at this time, we refrain from recognising subtribes despite the large size of several tribes. This is due to the generally low statistical support for the relationships within the tribes or the lack of morphological characters circumscribing internal clades. Therefore, all previously proposed subtribes are temporarily treated under the synonymy of the tribe they are members of until future phylogenetic/omic studies shed some needed light on this matter.

Malpighiaceae Juss., Gen. Pl.: 252. 1789, nom. cons.

Figs 2–11

Type species. *Malpighia glabra* L.

Description. Trees, shrubs, subshrubs (erect, monopodial or scandent) or **lianas**, monoecious, rarely functionally dioecious or androdioecious, perennial; hairs unicellular, foot present, conspicuous or not, 2-branched (malpighiaceous), T-, Y- or V-shaped, rarely acicular or stellate, branches straight, undulate, or curled, surface smooth, rough or spiny (Fig. 2). ***Roots*** fibrous or tuberous, generally becoming woody with age. ***Xylopodium*** present or not. ***Branches*** woody, rarely herbaceous, lenticelate or not. ***Stipules*** present, rarely absent, inter- or epipetiolar, minute to expanded, free to connate, pair of stipules free or connate, deciduous or persistent (Fig. 3E–H). ***Leaves*** opposite, decussate, rarely verticillate, ternate, subopposite or alternate (Fig. 3A–D), petiolate; petioles short to very long (Fig. 3L–N), circular, plane-convex to canaliculate (Fig. 3I–K) in cross-section, usually glandular (Fig. 3O-S); blades simple, entire, rarely lobed (Fig. 4I–K), usually glandular, margin plane to revolute (Fig. 4O, P), entire, sometimes dentate, crenate or lobulate, glabrous, ciliate or pubescent (Fig. 4I–N). ***Inflorescences*** solitary or compound, terminal to axillary, pedunculate, rarely sessile (Fig. 5A);

flowers arranged in a 1–multi-flowered cincinnus (Fig. 5B), cincinni opposite to alternate, usually pedunculate (Fig. 5C), rarely sessile, solitary or arranged in 2–5-degrees of ramification into thyrses, corymbs, umbels, or dichasia (Fig. 6); leaves associated with the inflorescences similar to vegetative leaves but reduced in size (Fig. 6D); cincinni bract 1, minute to expanded, plane or concave, persistent, rarely deciduous, glandular or eglandular (Fig. 7A–I); bracteoles 2, opposite or alternate, usually inserted at the apex of peduncles, rarely subapical, medial or basal, minute to expanded, plane or concave, persistent, rarely deciduous, glandular or eglandular (Fig. 7A–I). ***Flowers*** chasmogamous, rarely cleistogamous, bisexual, rarely unisexual, zygomorphic, rarely actinomorphic, hypogynous, rarely perigynous (Fig. 7Q); pedicel well-developed, rarely absent or inconspicuous, straight, rarely circinate (Fig. 7D–F); sepals 5(–7), free to connate at base, imbricate in bud, rarely valvate, erect, rarely deflexed, apex erect to revolute, persistent in fruit, usually not accrescent in fruit, rarely accrescent, abaxially (0–)1–2(–many)-glandular, sometimes the anterior sepal eglandular, rarely all sepals eglandular (Fig. 7J–L), glands multicellular, usually sessile (Fig. 8C), rarely pedunculate (Fig. 8C), secreting oil (Fig. 8B), rarely nectar (Fig. 8A); petals 5(–7), free, imbricate in bud, rarely valvate, clawed, patent (Fig. 8O) or deflexed (Fig. 8J), usually yellow (Fig. 8F–J), sometimes white (Fig. 8C, E, K), pink (Fig. 8A, L, Y), orange (Fig. 8M) or red (Fig. 8T), rarely green, lilac (Fig. 8Z) or purple, usually changing colour after pollination, the posterior petal usually differing from the 4 lateral ones in size, colour, shape and/or presence of glands, limb generally crumpled in bud, plane, concave or cucullate at anthesis, margin entire (Fig. 8U), erose (Fig. 8V), denticulate (Fig. 8X), fimbriate (Fig. 8W), or glandular-fimbriate (Fig. 8Y); androecium with (3–5–6–)10 stamens (Fig. 9D–G), in two whorls, fertile stamens (2–6–)10 (Fig. 9E), staminodes 0(–2–5; Fig. 9F, G), filaments free (Fig. 9G) or connate (Fig. 9D, E) at base, rarely connate up to the middle, short to long, glabrous (Fig. 9E), rarely pubescent (Fig. 9F), homo- (Fig. 9E) or heteromorphic (Fig. 9D), anthers basifixed (Fig. 9A), connectives minute or expanded (Fig. 9A, B), usually glandular (secreting non-volatile oils, rarely essential oils; Fig. 9B), with or without an apical projection, glabrous (Fig. 9E) to pubescent (Fig. 9D), thecae 2, parallel, rarely divergent at base and connivant at apex, apex free, rarely confluent, rimose (Fig. 9A), rarely poricidal; gynoecium superior, (1–2–)3-carpelate (Fig. 9H), all fertile, rarely 1 abortive, carpels syncarpic, rarely basally syncarpic and apically apocarpic, locules 1-ovulate, ovules pendulous, anatropous, styles (1–2–)3 (Fig. 9L, M), free, rarely connate, basal, lateral, subapical or apical, straight (Fig. 9L), curved (Fig. 9O) or lyrate (Fig. 9N, P), apex subulate (Fig. 9K), cylindrical (Fig. 9L), laterally flattened, truncate (Fig. 9J) or uncinate (Fig. 9I), rarely expanded (Fig. 9N, P), stigmas terminal (Fig. 9L, M) or lateral (i.e., facing the centre of the flower or the posterior petal; Fig. 9I, N, P), subulate (Fig. 9K), punctiform (Fig. 9K), capitate (Fig. 9L) or crateriform (Fig. 9I). ***Fruits*** dry (Fig. 10O–W) or fleshy (Fig. 10A–N), schizocarps (Fig. 10O–W), nuts (Fig. 10B–D) or drupes (Fig. 10A, E–N), glabrous or pubescent, mericarps (1–2–)3, indehiscent or splitting at maturity, smooth (Fig. 10O–S), setose (Fig. 10T–W), or winged (Fig. 11A–M), when winged mericarps with 1 dorsal (Fig. 11A–E) and/or 1–several lateral (Fig. 11F–M) wings, free (Fig. 11F–H, J–M) or connate (Fig. 11I). ***Seeds*** 1 per locule (Fig. 10A), globose or ovoid (Fig. 10A), smooth (Fig. 10A) to rugose, without endosperm; embryo curved, bent or spiralled. Chromosome number *n* = 6–10.

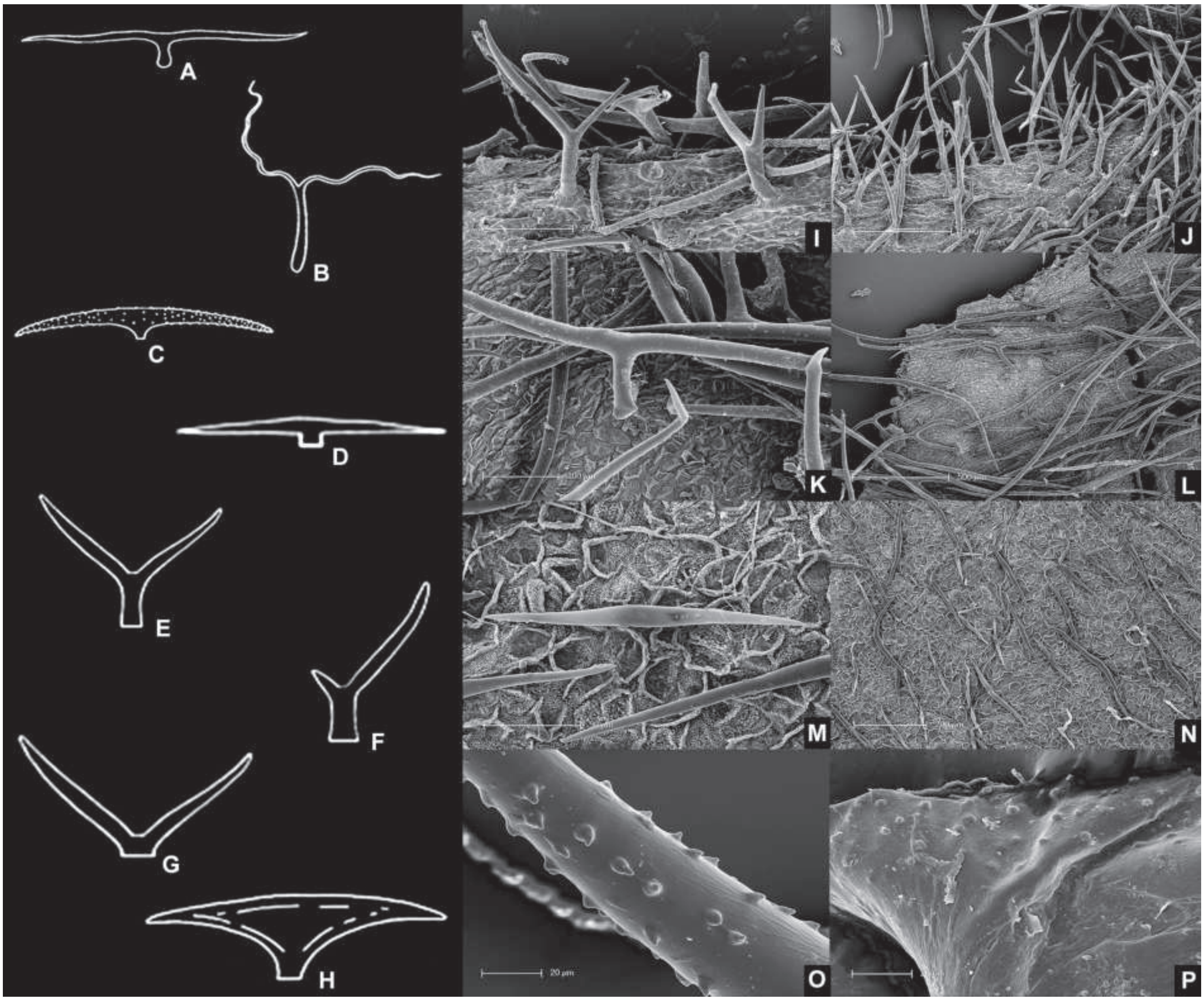


Figure 2. Line drawings and scanning electron micrographs of common types of malpighiaceous hairs **A** T-shaped with a short base (i.e., foot) **B** T-shaped with a long base **C** T-shaped with a very reduced base and branches with spiked cell wall **D** T-shaped with a very reduced base and branches with smooth cell wall **E** Y-shaped with a long base and two equally long branches **F** Y-shaped with a long base, one long and one very reduced branch **G** Y-shaped with a very reduced base **H** T-shaped with reduced base and laterally flattened (i.e., scaly) **I, J** detail of a velutine indumentum comprising Y-shaped hairs **K, L** detail of a tomentose indumentum comprising T-shaped hairs with long bases **M, N** detail of a sericeous indumentum comprising T-shaped hairs with very reduced bases **O** detail of the spikes on the cell wall of a hair branch **P** detail of the rugae on the cell wall of a hair branch (all line drawings and SEMs by R.F. Almeida).

Notes. Malpighiaceae is here circumscribed with two subfamilies, 12 tribes, 72 genera, and 1,499 species accepted (Table 1; Suppl. material 1). From this total, 60 genera and 715 species are currently under some kind of extinction threat (Bachman et al. 2024), representing 84.5% of the accepted genera and 47.82% of the species in our study (Suppl. material 1). Most of Malpighiaceae's diversity is confined to the American continent, with 55 genera (53 endemic) and 1,274 species (1,272 endemic), and just 15 genera (13 endemic) and 125 species (123 endemic) in Africa, seven genera (four endemic) and 84 species (77 endemic) in Asia, and four genera (all not endemic) and 21 species

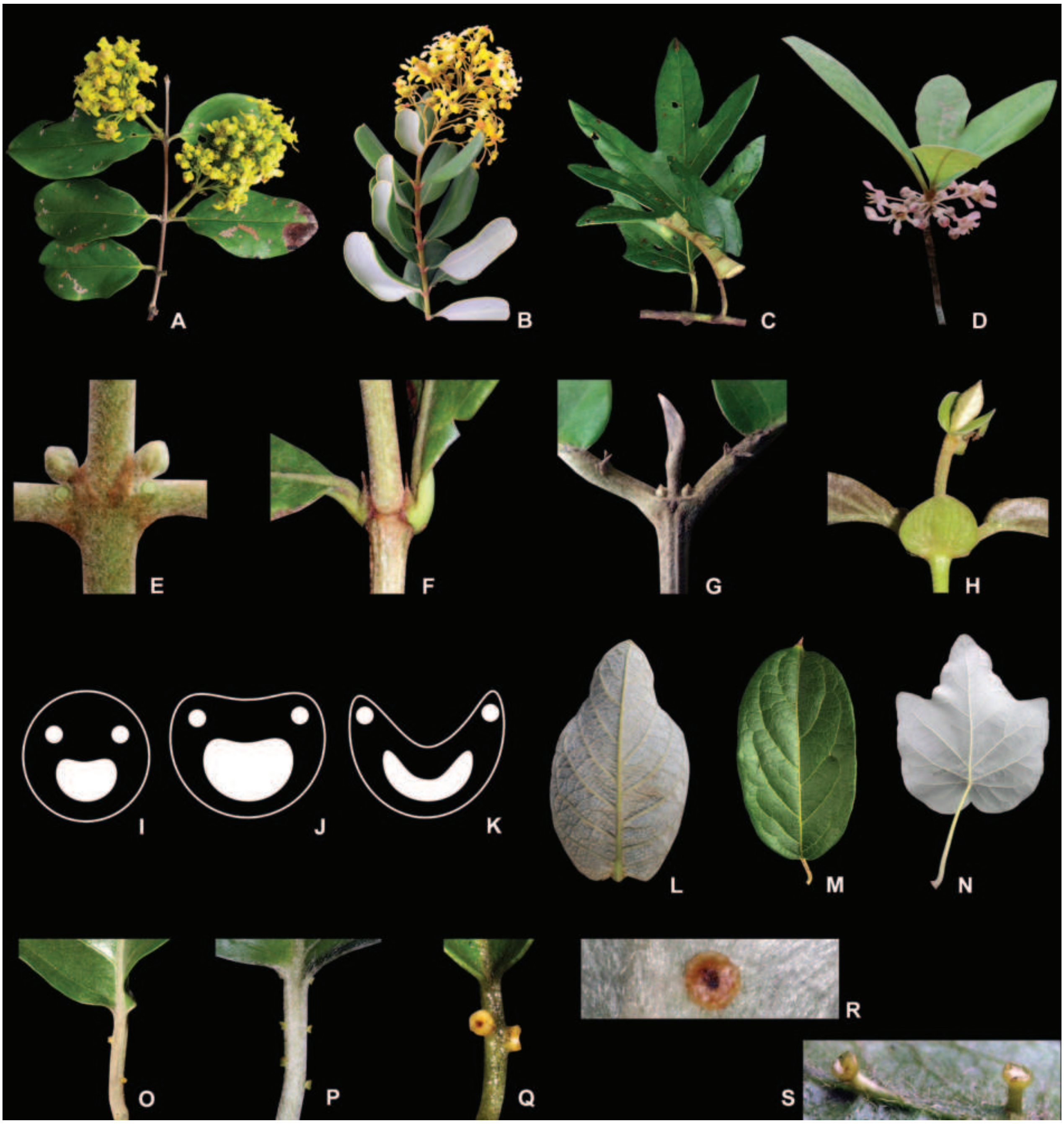


Figure 3. Phyllotaxis, stipules, and petioles of Malpighiaceae **A** branch with opposite leaves of *Bronwenia megaptera* **B** branch with decussate leaves of *Verrucularina glaucophylla* **C** branch with alternate leaves of *Stigmaphyllon angustilobum* **D** branch with verticillate leaves of *Pterandra pyroidea* **E** interpetiolar stipules of *Mascagnia cordifolia* **F** epipetiolar stipules of *Byrsonima intermedia* **G** free stipules of *Hiraea hatschbachii* **H** connate stipules of *Peixotoa catarinensis* **I** transverse section of a circular petiole **J** transverse section of a plane-convex petiole **K** transverse section of a canaliculate petiole **L** leaf with very reduced petiole of *Byrsonima basiloba* **M** leaf with short petiole of *Banisteriopsis adenopoda* **N** leaf with long petiole of *Stigmaphyllon caatingicola* **O** alternate glands on the petiole of *Banisteriopsis membranifolia* **P** opposite to alternate glands on the petiole of *Schwannia mediterranea* **Q** subopposite glands on the petiole of *Banisteriopsis membranifolia* **R** discoid and sessile gland of *Banisteriopsis laevifolia* **S** cupuliform and stalked glands of *Banisteriopsis adenopoda* (line drawings and photographs **A–C, G, I–K, L–O, Q–S** by R.F. Almeida; **D** by C. Silva, **E, F, H, P** by M.O.O. Pellegrini).

Table 1. Classification system proposed for Malpighiaceae in the present study.

Malpighiaceae Juss.	
Byrsonimoideae W.R.Anderson	**Malpighioideae** Burnett emend. R.F.Almeida
Acmanthereae W.R.Anderson	**Acridocarpeae** R.F.Almeida
3 genera, 23 species	2 genera, 38 species
Byrsonimeae W.R.Anderson	**Mcvaughieae** R.F.Almeida
3 genera, 181 species	3 genera, 12 species
Galphimieae Nied.	**Barnebyeae** R.F.Almeida
3 genera, 40 species	1 genus, 2 species
	Ptilochaeteae R.F.Almeida
	3 genera, 10 species
	Bunchosieae R.F.Almeida
	5 genera, 122 species
	Hiraeeae A.Juss. emend. R.F.Almeida
	5 genera, 105 species
	Hiptageae DC. emend. R.F.Almeida
	17 genera, 377 species
	Malpighieae DC. emend. R.F.Almeida
	13 genera, 253 species
	Gaudichaudieae Horan emend. R.F.Almeida
	14 genera, 337 species

(19 endemic) in Oceania (Suppl. material 1). Most threatened species are found in the Americas (564 species), with 86 threatened species in Africa, 57 in Asia, and 12 in Oceania (Suppl. material 1). Five African genera, more specifically endemic to Madagascar (i.e., *Digoniopterys*, *Madagasikaria*, *Microsteira*, *Philgamia*, and *Rhynchophora*) stand out, with all their current accepted species under some kind of extinction threat (Suppl. material 1). *Mcvaughia* was the only American genus to present all its species under some kind of extinction threat (Suppl. material 1). *Malpighia* was the American genus with most species under some kind of extinction threat (Suppl. material 1). *Hiptage* was the genus with highest number of threatened species in Asia, and *Stigmaphyllon* was the most threatened in Oceania (Suppl. material 1).

Identification keys for all subfamilies, tribes, and genera are presented, alongside a full morphological description for the proposed new genus, the recircumscription of ten genera accompanied by the needed new combinations, the proposition of several new synonyms, typification of miscellaneous names and notes on conservation, distribution, ecology, and taxonomy up to the genus rank.

Key to the subfamilies of Malpighiaceae

1 Posterior petal eglandular (Fig. 8O, P), androecium homomorphic (Fig. 9E), fertile stamens 10 (occasionally 6–10 in *Diacidia*), styles apex subulate (Fig. 9K), stigmas punctate (Fig. 9K); drupes or mericarps smooth (i.e., never winged or setose; Fig. 10A–S) .... **Byrsonimoideae**

– Posterior petal glandular (Fig. 8Y), androecium heteromorphic (Fig. 9D), fertile stamens 2–10, styles apex capitate, uncinate, truncate or expanded (Fig. 9L–Q), rarely subulate (Fig. 9K), stigmas capitate or crateriform (Fig. 9I, J, L), rarely punctate (Fig. 9K); nuts or mericarps, frequently winged (Fig. 11A–M) or setose (Fig. 10T–W), rarely smooth..........**Malpighioideae**

Figure 4. Leaf blades of Malpighiaceae **A** leaf with sagittate base of *Stigmaphyllon ciliatum* **B** leaf with rounded base of *Banisteriopsis adenopoda* **C** leaf with cordate base of *Stigmaphyllon blanchetii* **D** leaf with cuneate base of *Banisteriopsis vernoniifolia* **E** leaf with obtuse base of *Stigmaphyllon paralias* **F** leaf with truncate base of *Stigmaphyllon gayanum* **G** leaf with oblique base of *Stigmaphyllon lanceolatum* **H** leaf with attenuate base of *Acmanthera minima* **I** leaf with entire margin of *Stigmaphyllon caatingicola* **J** leaf with 3-lobed margin of *Stigmaphyllon caatingicola* **K** leaf with 5-lobed margin of *Stigmaphyllon angustilobum* **L** leaf with crenate margin of *Stigmaphyllon crenatum* **M** leaf with ciliate margin of *Stigmaphyllon ciliatum* **N** leaf with dentate margin of *Stigmaphyllon vitifolium* **O** leaf with plane blade margin of *Banisteriopsis membranifolia* **P** leaf with revolute blade margin of *Verrucularina glaucophylla* **Q** rounded leaf apex of *Tetrapterys phlomoides* **R** mucronate leaf apex of *Banisteriopsis magdalenensis* **S** emarginate leaf apex of *Hiraea cuiabensis* **T** cuspidate leaf apex of *Banisteriopsis adenopoda* **U** acuminate leaf apex of *Mamedea harleyi* **V** acute leaf apex of *Banisteriopsis membranifolia* (photographs **A–D, F, G, I, L, O, P, T–V** by R.F. Almeida; **E, M** by M.O.O. Pellegrini; **H** by F. Farronay, **Q** by G.A. Dettke, **N** by A.C. Dal Col, **R** by C. Baez, **S** by I.L. Morais).

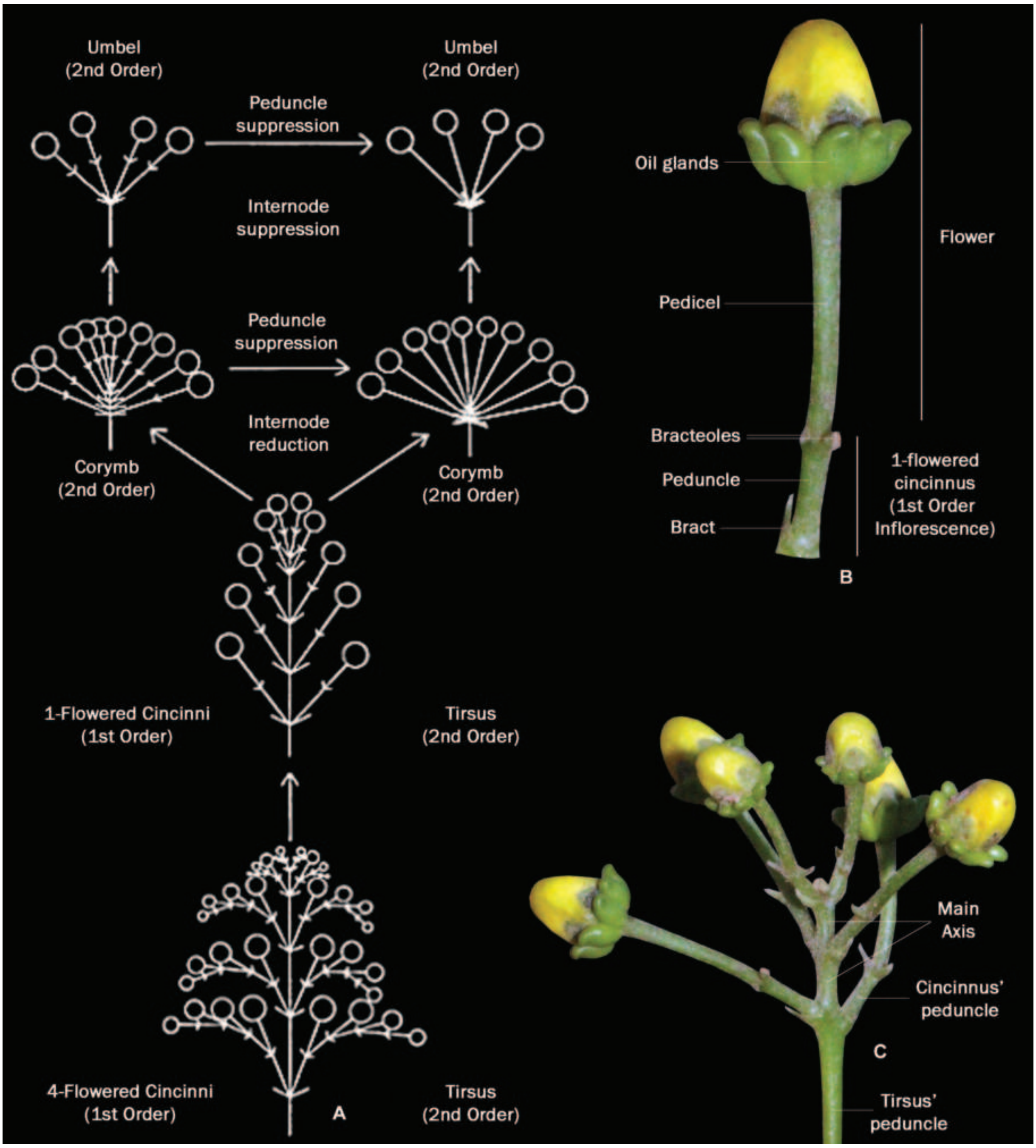


Figure 5. Inflorescence architecture of Malpighiaceae **A** inflorescence evolution in Malpighiaceae according to Anderson (1981) **B** 1-flowered cincinnus of *Niedenzuella lasiandra* **C** Thyrse of 1-flowered cincinni of *Niedenzuella lasiandra* (line drawings modified from Anderson 1981; photographs **A** modified from Anderson 1981; **B, C** by M.O.O. Pellegrini).

1. Byrsonimoideae W.R.Anderson, Leandra 7: 6. 1977.

Type genus. *Byrsonima* Rich. ex Kunth.

Diagnosis. Posterior petal eglandular, fertile stamens 10 (occasionally 6–10 in *Diacidia*), pollen 3-aperturate, zonoaperturate, colporate, styles apex subulate, mericarps smooth (i.e., never winged, or setose), chromosome number n = 6, presence of macrolactams and sulfenyl compounds.

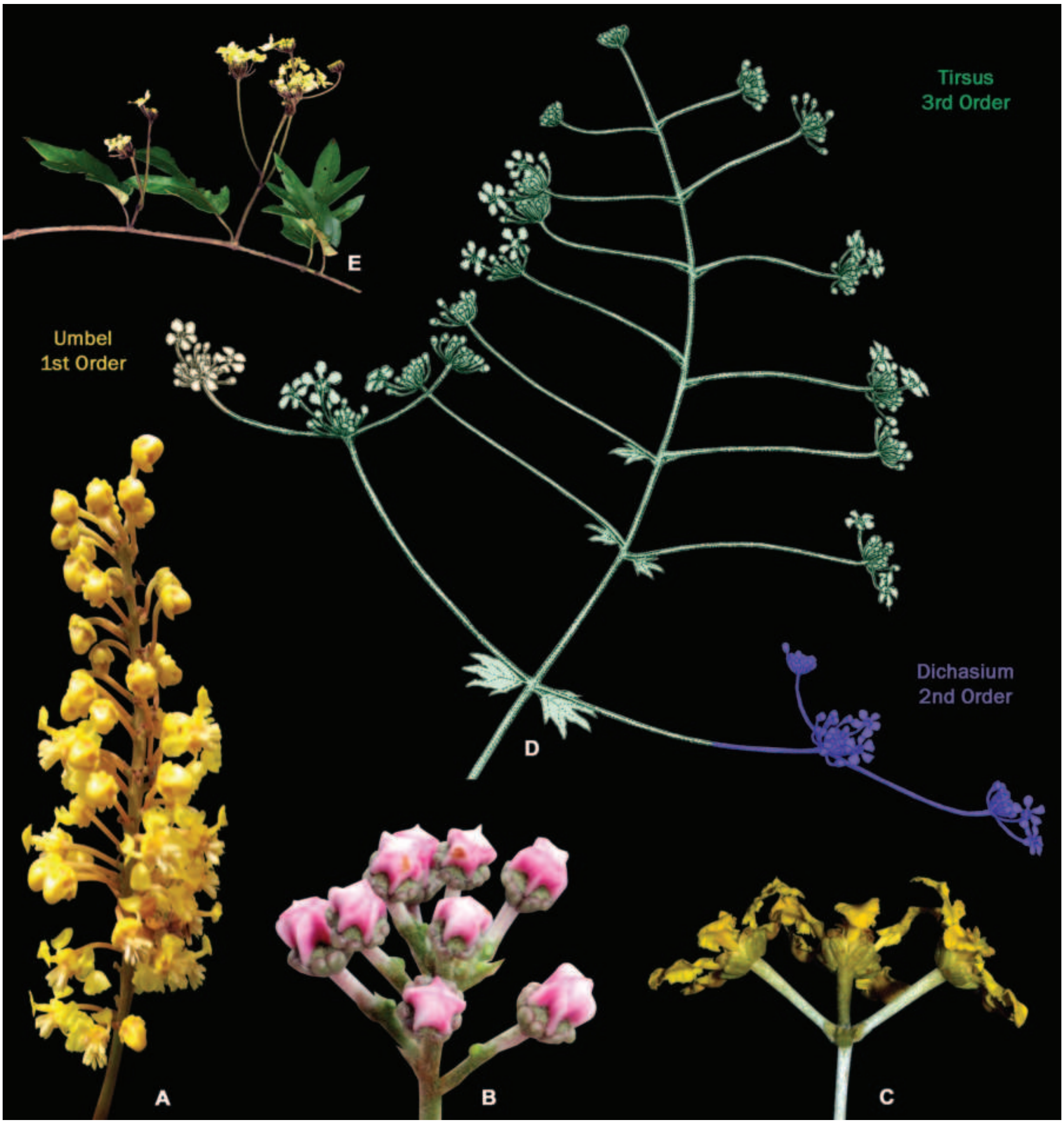


Figure 6. Compound inflorescences of Malpighiaceae **A** thyrse of 1-flowered cincinni of *Byrsonima sericea* **B** corymb of 1-flowered cincinni of *Mascagnia cordifolia* **C** umbel of 1-flowered cincinni of *Banisteriopsis argyrophylla* **D** line drawing of an inflorescence of *Stigmaphyllon angustilobum* showing 1-flowered cincinni arranged in umbels (1st order inflorescence), arranged in dichasia (2nd order inflorescence), arranged in a thyrse (3rd order inflorescence) **E** photograph of the inflorescence branch of *Stigmaphyllon angustilobum* (photographs **B, C** by M.O.O. Pellegrini; **A, E** by R.F. Almeida; line drawing **D** by K. Souza).

Notes. The subfamily Byrsonimoideae currently comprises the original three tribes published by Anderson (1977). However, tribe Byrsonimeae is re-circumscribed to exclude *Burdachia*, *Glandonia* and *Mcvaughia*, which made this tribe paraphyletic and are, thus, placed by us in their own tribe in Malpighioideae. In its new circumscription, Byrsonimoideae comprises nine genera and 243 species (91 threatened species; Suppl. material 1) of shrubs and trees endemic to the Americas.

Figure 7. Flowers of Malpighiaceae **A** side view of the flower of *Amorimia coriacea* showing the cincinnus peduncle with a bract at base and two bracteoles at apex **B** detail of the 2-glandular bracteoles of *Glicophyllum cardiophyllum* **C** details of the glandular margin of the bracteole of *Christianella multiglandulosa* **D** bracteoles of *Mezia araujoi* concealing the floral bud at pre-anthesis (floral pedicel is absent) **E** floral bud of *Niedenzuella multiglandulosa*, showing a very short peduncle with a bract at base and two bracteoles at apex **F** flower of *Banisteriopsis laevifolia* showing pedicel with bract and bracteoles at base (peduncle absent) **G** plane and patent bract and bracteoles of *Alicia anisopetala* **H** cucullate bract and bracteoles of *Dicella bracteosa* **I** deflexed bract and bracteoles of *Dicella nucifera* **J** eglandular sepals concealing petals at pre-anthesis in *Thryallis longifolia* **K** 1-glandular calyx of *Hiptage benghalensis* **L** 10-glandular calyx of *Camarea axillaris* **M** 8-glandular calyx of *Christianella multiglandulosa* showing the multi-glandular margin of sepals **N** erect sepals of *Galphimia australis* **O** revolute apex of sepals of *Byrsonima basiloba* **P** revolute and reflexed sepals of *Thryallis longifolia* **Q** floral diagram of a Malpighiaceae flower with sepals in green, sepal glands in red, lateral petals in yellow, posterior petal in brown, androecium in blue (connectives) and white (pollen sacs), and gynoecium in pink (diagram and photographs **B, E, F, H, K, L, N, O, Q** by R.F. Almeida; **A–D, G, M** by M.O.O. Pellegrini; **I** by Amaury Jr.; **J, P** by J.V. Santos).

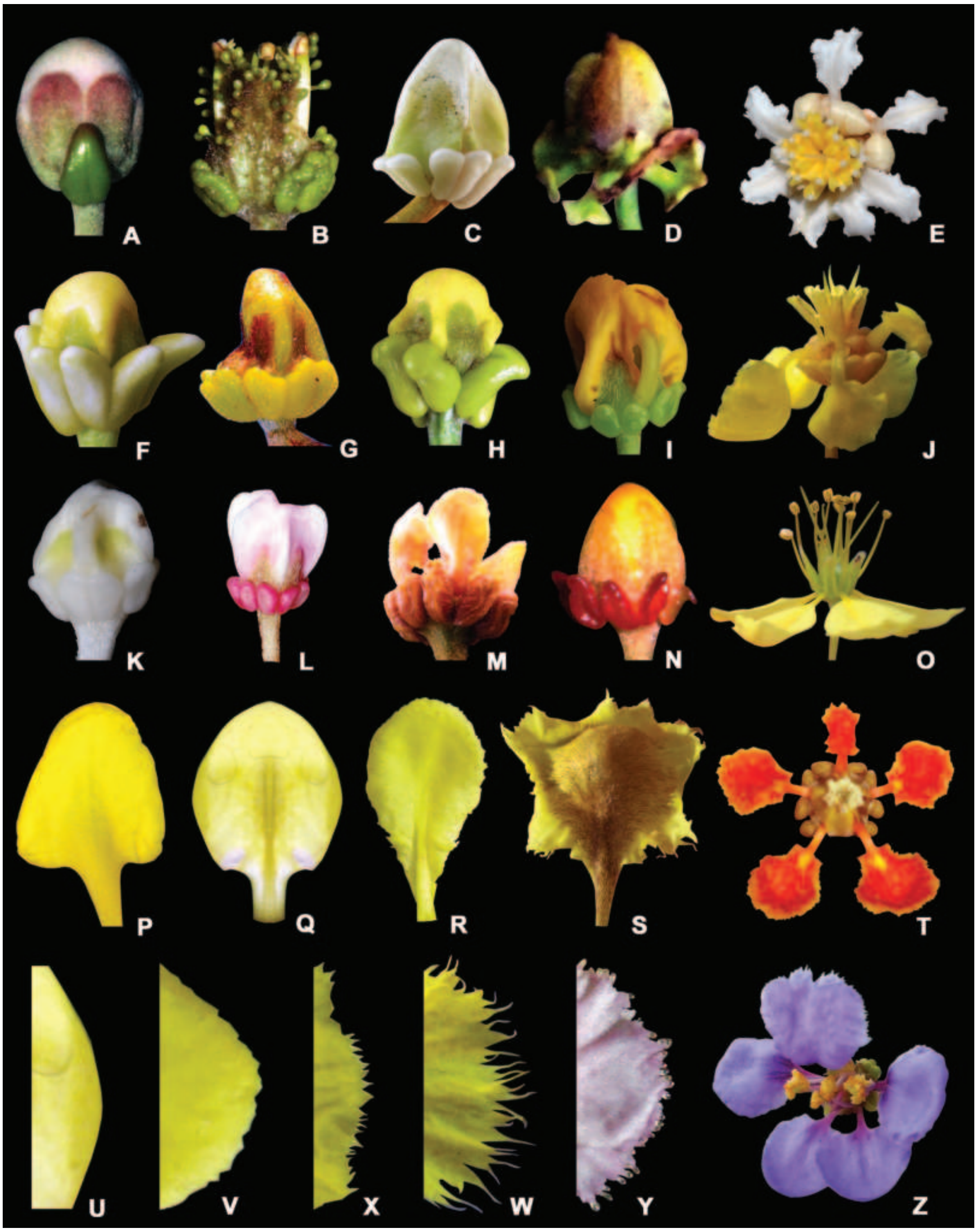


Figure 8. Sepals, glands, and petals of Malpighiaceae flowers **A** sepals with rounded apex of *Hiptage benghalensis* and sessile sepal gland **B** sepals with acute apex of *Christianella multiglandulosa* and sessile sepal glands **C** sepals with acute apex of *Byrsonima gardneriana* and sessile sepal glands **D** stalked sepal glands of *Heladena multiflora* **E** white petals of *Acmanthera latifolia* **F** pale yellow glands of *Bunchosia glandulifera* **G** yellow glands of *Mcvaughia sergipana* **H** pale green glands of *Bronwenia megaptera* **I** green glands of *Camarea axillaris* **J** yellow and deflexed petals of *Byrsonima sericea* **K** white glands of *Acmanthera parviflora* **L** pink glands of *Heteropterys rubiginosa* **M** brown glands of *Amorimia pellegrinii* **N** red glands of *Niedenzuella poeppigiana* **O** yellow and patent petals of *Ptilochaeta bahiensis* **P** oval petal limb of *Galphimia gracilis* **Q** elliptic petal limb of *Heteropterys oberdanii* **R** obovate petal limb of *Bronwenia megaptera* **S** pubescent petal surface of *Diplopterys bahiana* **T** orange-red petals of *Tetrapterys phlomoides* **U** entire margin of the petal of *Heteropterys oberdanii* **V** erose margin of the petal of *Bronwenia megaptera* **W** fimbriate margin of the petal of *Schwannia schwannioides* **X** dentate margin of the petal of *Peixotoa hispidula* **Y** glandular-fimbriate margin of the petal of *Alicia anisopetala* **Z** lilac petals of *Mascagnia lilacina* (**A, C, F–H, I, J, L–S, U–W** by R.F. Almeida; **B, N, T, Y** by M.O.O. Pellegrini; **D** by A. Francener; **E** by R. Goldenberg; **Z** by O.J.A. Ayala).

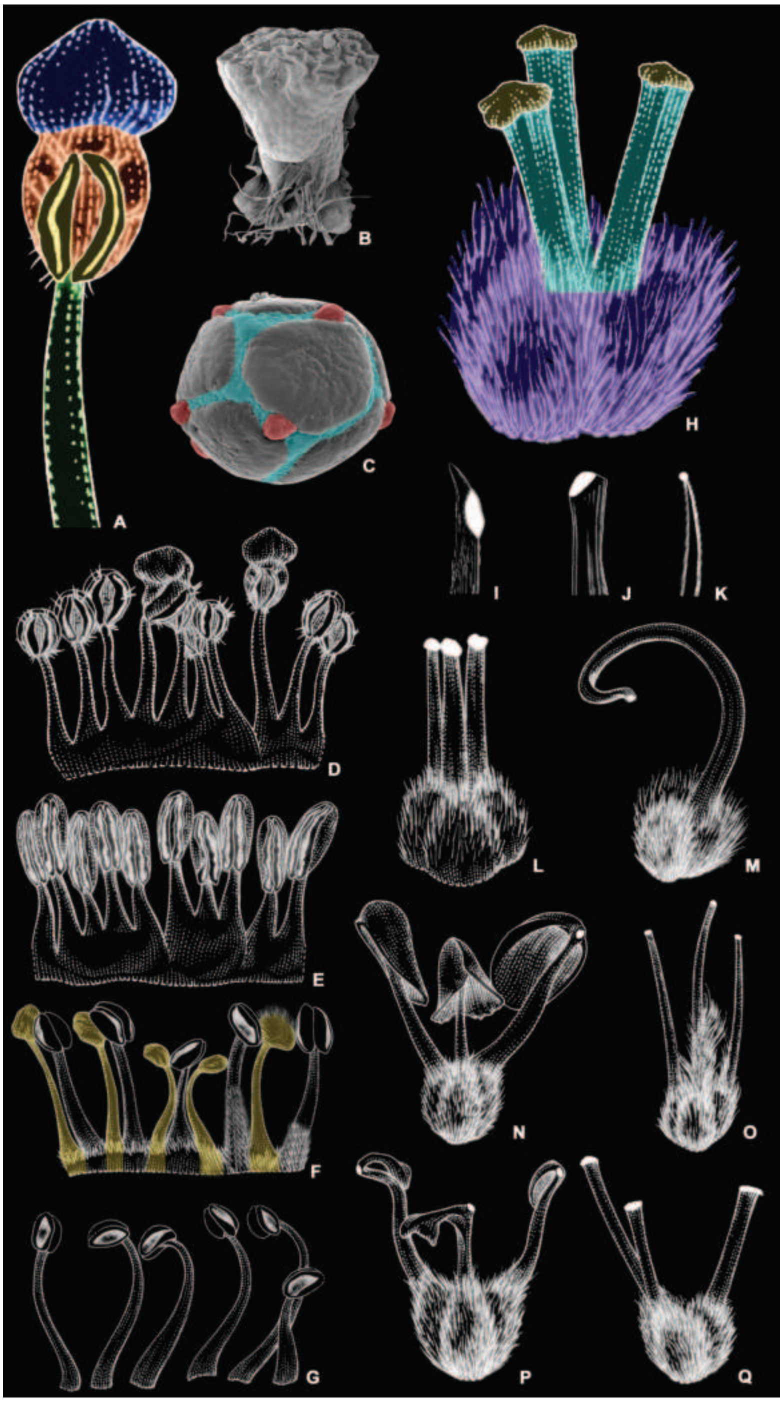


Figure 9. Androecium and gynoecium of Malpighiaceae **A** stamen of *Banisteriopsis multifoliolata* showing filament in green, anther in orange, glandular connective in blue, and pollen sacs in yellow **B** scanning electron micrograph of an anther of *Banisteriopsis multifoliolata* **C** SEM of a pollen grain of *Banisteriopsis multifoliolata* showing colpi in blue and endoaperture in red **D** heteromorphic stamen ring with 10 fertile stamens of *Banisteriopsis multifoliolata* **E** homomorphic stamen ring of *Bronwenia megaptera* with 10 fertile stamens **F** heteromorphic stamen ring of *Peixotoa hispidula* showing 5 fertile stamens and 5 staminodes in yellow **G** 6 fertile and free stamens of *Schwannia hexandra* **H** gynoecium of *Banisteriopsis multifoliolata* showing ovary in lilac, styles in blue and stigmas in yellow **I** uncinate apex of styles of *Amorimia septentrionalis* **J** truncate style apex of *Amorimia rigida* **K** subulate apex of style of *Byrsonima sericea* **L** 3 parallel and erect styles of *Bronwenia megaptera* **M** single curved style of *Schwannia hexandra* **N** 3 divergent styles of *Stigmaphyllon blanchetii* with foliate apices **O** 3 erect, slightly curved, and pubescent styles of *Diplopterys lutea* **P** 3 divergent styles of *Stigmaphyllon lalandianum* with reduced foliate apices **Q** 3 divergent styles of *Stigmaphyllon glabrum* without foliate apex (all line drawings by K. Souza; SEMs by R.F. Almeida; all scales: 1 mm, except for the pollen grain: 10 μm).

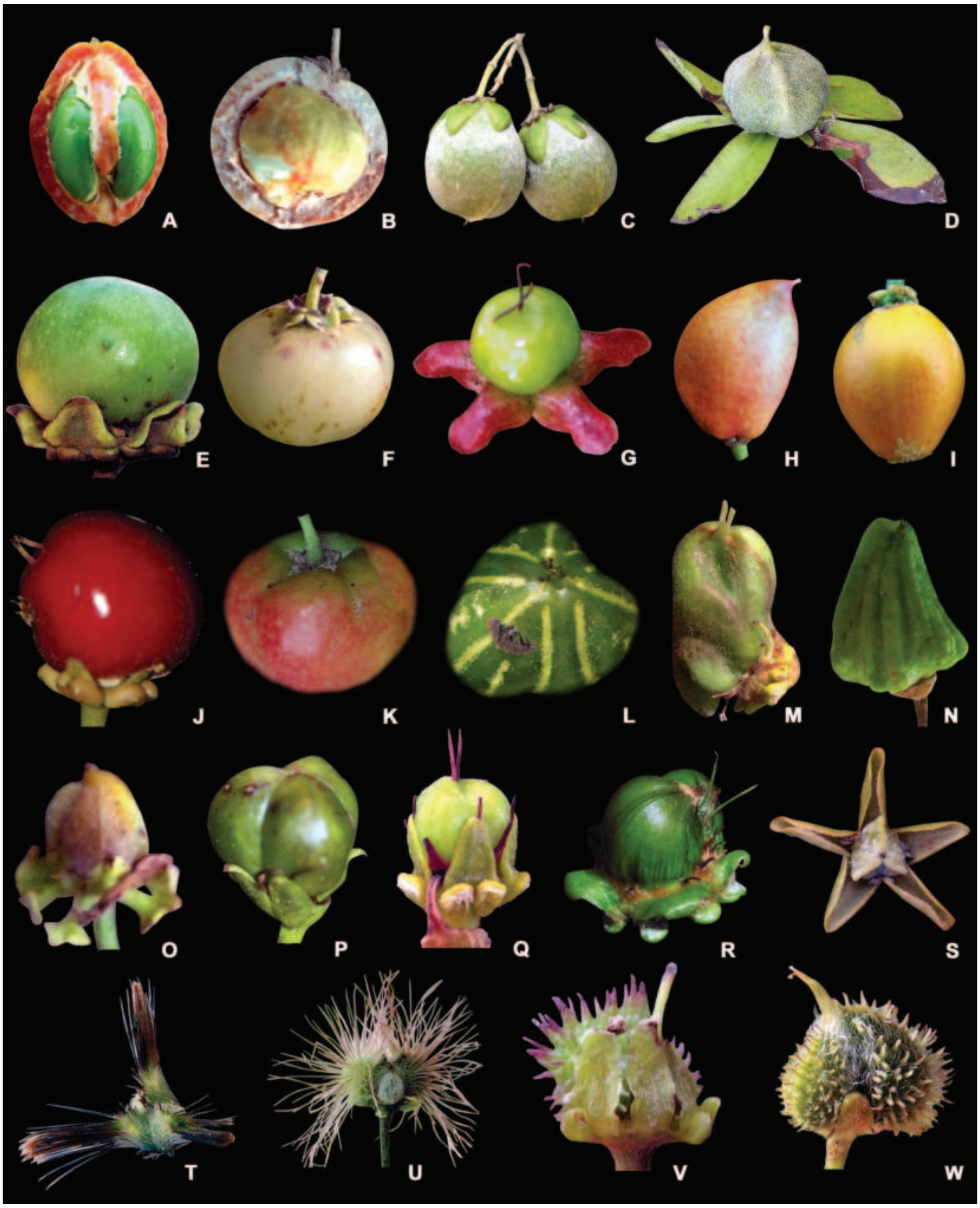


Figure 10. Types of fleshy fruits, nuts, and smooth to setose schizocarpic fruits in Malpighiaceae **A** transversely sliced drupe of *Bunchosia maritima* showing seeds **B** transversely sliced nut of *Dicella nucifera* showing the seed **C** nuts of *Dicella bracteosa* **D** nuts of *Dicella macroptera* **E** green drupe of *Byrsonima blanchetiana* **F** cream-coloured drupe of *Byrsonima ligustrifolia* **G** green drupe of *Byrsonima melanocarpa* with concrescent sepals **H** orange drupe of *Bunchosia glandulifera* **I** orange drupe of *Bunchosia maritima* **J** red drupe of *Malpighia glabra* **K** reddish-orange drupe of *Malpighia mexicana* **L** green drupe of *Malpighia fucata* **M** green and twisted drupe of *Mcvaughia sergipana* **N** striated drupe of *Burdachia prismatocarpa* **O** smooth mericarp of *Heladena multiflora* **P** smooth mericarp of *Galphimia gracilis* **Q** smooth and immature mericarp of *Verrucularina glaucophylla* **R** green and smooth mericarps of *Acmanthera latifolia* **S** smooth mericarps of *Thryallis longifolia* with concrescent sepals **T** setose mericarps of *Tricomaria usillo* **U** setose mericarps of *Lasiocarpus ferrugineus* **V** setose mericarp of *Camarea axillaris* **W** setose mericarp of *Echinopterys eglandulosa* (photographs **A, B** by Amaury Jr.; **C, D** by A. Assis; **E, H, I, M, Q, V** by R.F. Almeida; **F** by S.E. Martins; **G** by N. Bigio; **J** by P. Acevedo-Rodriguez; **K, L** by M.R. Pace; **N** by L.S.B. Calazans; **O** by A. Francener; **P** by M.O.O. Pellegrini; **R** by R. Goldenberg; **S** by J.V. Santos; **T** by I. Specogna; **U** by A. Nuno; **W** by S. Carnaham).

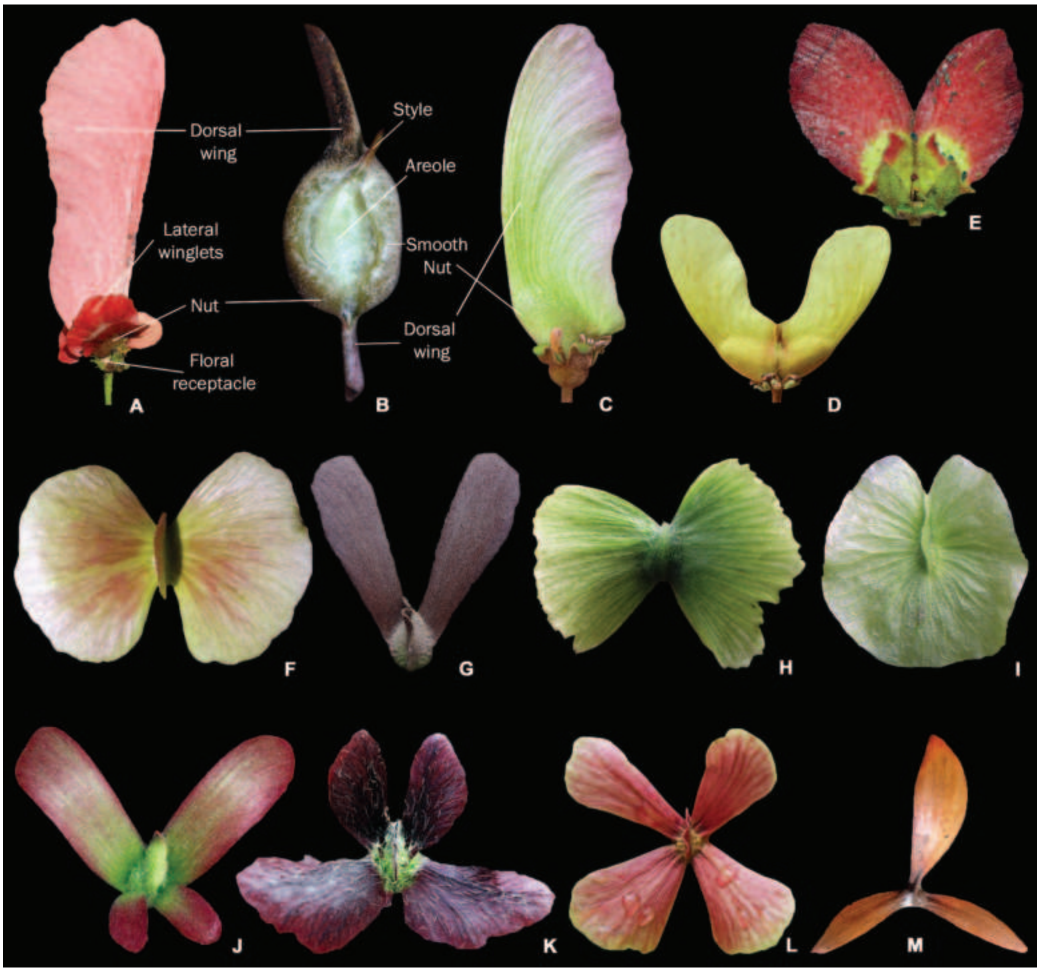


Figure 11. Types of winged schizocarpic fruits in Malpighiaceae **A** single dorsal winged mericarp of *Diplopterys pubipetala* showing lateral wings **B** detail of part of the winged mericarp of *Banisteriopsis argyrophylla* **C, D** 1 dorsal winged mericarp(s) of *Heteropterys byrsonimifolia* **E** winged mericarp of *Peixotoa catharinensis* showing lateral winglets **F** winged mericarp of *Amorimia candidae* with two lateral wings more developed than the reduced dorsal wing **G** winged mericarp of *Lophopterys floribunda* **H** winged mericarp of *Carolus chasei* with two lateral wings more developed (dorsal wing absent) **I** winged mericarp of *Mascagnia sepium* with 1 lateral orbicular wing **J** winged mericarp of *Tetrapterys phlomoides* with 4 free, lateral wings (superior ones longer, inferior ones shorter) **K** winged mericarp of *Glicophyllum cardiophyllum* with 4 free, lateral wings (superior ones shorter, inferior ones longer) **L** winged mericarp of *Niedenzuella acutifolia* with 4 free, equalling lateral wings **M** winged mericarp of *Hiptage benghalensis* with three free, lateral wings more developed (photographs **A** by A. Popovkin; **B, E, I, J** by M.O.O. Pellegrini; **C, D, F, H, K, L** by R.F. Almeida; **G** by G. Shimizu; **M** by G. Cahyadi).

Key to the tribes of Byrsonimoideae

1 Leaf veins camptodromous (Fig. 4H); sepals enclosing petals in bud (Fig. 8K), carpels free, styles basal, lateral or subapical (Fig. 9I, J) .... **Acmanthereae**

– Leaf veins brochidodromous (Fig. 4P); sepals not enclosing petals in bud (Fig. 8C), carpels connate, styles apical (Fig. 9K) **2**

2 Leaves eglandular; bracteoles eglandular (Fig. 7G–I); petals smooth in bud (Fig. 8C), cucullate at anthesis (Fig. 8J); fruits indehiscent (Fig. 10E–G) ... .**Byrsonimeae**

– Leaves glandular (except in *Verrucularina*); bracteoles glandular (Fig. 7B, C); petals keeled in bud, plane at anthesis (Fig. 8P), fruits dehiscent (Fig. 10P, Q)...**Galphimieae**

1.1. Acmanthereae W.R.Anderson, Leandra 7: 7. 1977.

Type genus. *Acmanthera* (A.Juss.) Griseb.

Diagnosis. Stipules absent, leaf veins camptodromous, sepals enclosing petals in buds, carpels free, styles ventrally to subapically inserted on ovaries, presence of diazanapaphthalenes, propargyl-type 1,3-dipolar organic compounds, absence of benzopyrans, lactams, lignam glycosides, pyrimidine nucleosides, pyrimidine nucleotides, saccharolipids, sulfenyl compounds.

Notes. Acmanthereae currently comprises only three accepted genera (*Acmanthera*, *Coleostachys*, and *Pterandra*) and 23 species (15 threatened species; Suppl. material 1) of trees, shrubs, or subshrubs endemic to the Americas (POWO 2024).

Key to the genera of Acmanthereae

1 Leaves lanceolate; flowers sessile, sepals eglandular, anthers poricidal.... .... ***Coleostachys***
– Leaves elliptic, ovate to obovate; flowers pedicellate, sepals glandular, anthers rimose..**2**
2 Flowers arranged in thyrses; sepals 2(–many)-glandular, petals 5(–7), glabrous, anthers with dorsal projections...***Acmanthera* (Figs 4H, 8E, K, 10R)**
– Flowers arranged in umbels; sepals 0–2-glandular, petals 5, pubescent, anthers with lateral projections......................................***Pterandra* (Fig. 3D)**

1.1.1. *Acmanthera* (A.Juss.) Griseb. in Martius, Fl. Bras. 12(1): 28. 1858.
Figs 4H, 8E, K, 10R

≡ *Pterandra* sect. *Acmanthera* A.Juss., Ann. Sci. Nat. Bot., ser. 2, 13: 328. 1840.

Type species. *Acmanthera latifolia* (A.Juss.) Griseb.

Notes. *Acmanthera* currently comprises seven accepted species (four threatened species; Suppl. material 1) of trees, shrubs or subshrubs endemic to flooded forests of the Amazon rainforest, South America, and just a single species occurring within the Cerrado biome (Almeida et al. 2020; POWO 2024). For an identification key for all species of *Acmanthera*, see Anderson (1980) or Almeida et al. (2020).

1.1.2. *Coleostachys* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 329. 1840.

Type species. *Coleostachys genipifolia* A.Juss.

Notes. *Coleostachys* is represented by a single species (not threatened; Suppl. material 1) of monopodial shrub endemic to non-flooded forests of the Amazon rainforest, South America (Almeida et al. 2020; POWO 2024). A comprehensive taxonomic revision was presented by Almeida and Hall (2016), but the information on type specimens presented by these authors was incomplete. Jussieu (1840) did not specify which specimen is the holotype nor in which herbarium it was deposited, therefore needing the lectotypification presented below.

1.1.2.a. *Coleostachys genipifolia* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 329. 1840.

Lectotype (designated here). French Guiana: Cayenne., s.d., *Martin s.n.* (P-JU barcode P00671745!; isolectotypes: BR barcode BR0000008577450!, F barcode V0062669F!, K barcode K000427026!, MICH barcode MICH1102137!, P barcodes P02428718!, P02428719!, P02428720!, P02428721!, RB barcode 540728!).

1.1.3. *Pterandra* A.Juss., Fl. Bras. Merid. (quarto ed.) 3(22): 72. 1832 [1833].

Fig. 3D

Type species. *Pterandra pyroidea* A.Juss.

Notes. *Pterandra* currently comprises 15 accepted species (11 threatened species; Suppl. material 1) of trees, shrubs or subshrubs endemic to non-flooded forests of the South American Amazon rainforest and Cerrado biomes, with just a single species occurring in non-flooded rainforests of Panama, Central America (Anderson 1997a; POWO 2024). For an identification key for all species of *Pterandra*, see Anderson (1997a).

1.2. Byrsonimeae W.R.Anderson, Leandra 7: 11. 1977.

≡ Byrsoniminae Nied. in Engler, Nat. Pflanzenr. 92: 17, 28. 1928.

Type genus. *Byrsonima* Rich. ex Kunth.

Diagnosis. Stipules epipetiolar, leaves smaller than inflorescences, at least one petal cucullate at anthesis, presence of hydroxy acids and derivatives, imidolactams, keto acids and derivatives, organic phosphoric acids and derivatives, organofluorides, absence of oxanes.

Notes. Byrsonimeae currently comprises only three accepted genera (*Blepharandra*, *Byrsonima*, and *Diacidia*) and 181 species (57 threatened species; Suppl. material 1) of trees, shrubs or subshrubs endemic to the Americas (POWO 2024).

Key to the genera of Byrsonimeae

1 Lateral petals deflexed at anthesis, anther connectives expanded, anthers without stiff hairs; mericarps drupaceous .... ***Byrsonima*** **(Figs 3F, L, 6A, 7O, 8C, J, 9K, 10E–G)**

– Lateral petals patent at anthesis, anther connectives inconspicuous, anthers glabrous or with soft hairs; mericarps dry **2**

2 Leaf base usually cordate, leaf apex rounded to emarginate; cincinni 2–3-flowered, sepals coriaceous, not accrescent in fruit, petals white, pink to red, anthers pubescent ....***Blepharandra***

– Leaf base rounded, leaf apex acute to acuminate; cincinni 1-flowered, sepals membranous, accrescent in fruit, petals yellow, anthers glabrous ....***Diacidia***

1.2.1. *Blepharandra* Griseb., Linnaea 22: 7. 1849.

= *Callyntranthele* Nied., Index Lect. Lyceo Braunsbergiensis 1897: 4. 1897. Type species: *Callyntranthele angustifolia* (Kunth) Nied. [≡ *Blepharandra angustifolia* (Kunth) W.R.Anderson].

Type species. *Blepharandra hypoleuca* (Benth.) Griseb.

Notes. *Blepharandra* currently comprises six accepted species (one threatened species; Suppl. material 1) of trees or shrubs endemic to islands of savanna (campinaranas) within the Amazon rainforest biome of South America (Almeida et al. 2020; POWO 2024). For an identification key for all species of *Blepharandra*, see Anderson (1981).

1.2.2. *Byrsonima* Rich. ex Kunth, Nov. Gen. Sp. (quarto ed.) 5: 147. 1821 [1822].

Figs 3F, L, 6A, 7O, 8C, J, 9K, 10E–G

= *Alcoceratothrix* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 1: 45. 1901. Type species: *Alcoceratothrix rugosa* (Benth.) Nied. (≡ *Byrsonima rugosa* Benth.).

Type species. *Byrsonima spicata* (Cav.) DC.

Notes. *Byrsonima* currently comprises 164 accepted species (49 threatened species; Suppl. material 1) of trees, shrubs, or subshrubs endemic to most biomes of the Neotropical region from swamps in the State of Florida (USA) to rainforests, savannas, dry forests, and grasslands of Southern Brazil (Almeida et al. 2020; POWO 2024). Two subgenera are currently recognised in *Byrsonima* (subg. *Byrsonima* and subg. *Macrozeugma* Nied.), but neither is monophyletic (Francener 2016). There is no updated identification key for all species of *Byrsonima*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, Pool (in prep.) for Mesoamerica, and Anderson (2016) for North America.

1.2.3. *Diacidia* Griseb. in Martius, Fl. Bras. 12(1): 119. 1858.

= *Sipapoa* Maguire, Mem. New York Bot. Gard. 8: 124. 1953. ≡ *Diacidia* subg. *Sipapoa* (Maguire) W.R.Anderson, Mem. New York Bot. Gard. 32: 63. 1981. Type species: *Sipapoa kunhardtii* Maguire [≡ *Diacidia kunhardtii* (Maguire) W.R.Anderson].

Type species. *Diacidia galphimioides* Griseb.

Notes. *Diacidia* currently comprises 11 accepted species (seven threatened species; Suppl. material 1) of trees, shrubs or subshrubs endemic to campos rupestres and tepuis within the Amazon rainforest biome of South America (Almeida et al. 2020; POWO 2024). For an identification key for all species of *Diacidia*, see Anderson (1981) for the Guyana Highland and Almeida et al. (2020) for Brazil.

1.3. Galphimieae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 53, 67. 1890.

≡ Galphimiinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 53, 69. 1890.

Type genus. *Galphimia* Cav.

Diagnosis. Peduncle of cincinni present, floral buds with petals keeled, anther projections laterally inserted on thecae, presence of naphthopyrans and oxazinanes.

Notes. Galphimieae currently comprises only three accepted genera (*Galphimia*, *Spachea*, and *Verrucularina*) and 40 species (20 threatened species; Suppl. material 1) of trees, shrubs or subshrubs endemic to the Americas (POWO 2024).

Key to the genera of Galphimieae

1 Trees; leaves as long as the inflorescences; inflorescences pendulous, bracteoles glandular, glands stalked; filaments not changing colour at post-anthesis .... ***Spachea***

– Shrubs to subshrubs; leaves shorter than the inflorescences; inflorescences erect, bracteoles eglandular; filaments changing colour at post-anthesis **3**

2 Leaves many-glandular; cincinni 1-flowered; calyx 0–5-glandular, when present secreting nectar, anthers smooth, unappendaged .... ***Galphimia* (Figs 7N, 8P, 10P)**

– Leaves eglandular; cincinni 1–3-flowered; calyx 10-glandular, glands secreting oil, anthers with 2 verrucose appendages at apex .... ***Verrucularina* (Figs 3B, 4P, 10Q)**

1.3.1. *Galphimia* Cav., Icon. 5: 61–62, pl. 489. 1799, nom. cons.

Figs 7N, 8P, 10P

= *Thryallis* L., Sp. Pl., ed. 2: 554. 1762, nom. rej. ≡ *Vorstia* Adans., Fam. Pl. 2: (23). 1763, nom. superfl. Type species: *Thryallis brasiliensis* L. [≡ *Galphimia brasiliensis* (L.) A.Juss.].

Type species. *Galphimia glauca* Cav.

Notes. *Galphimia* currently comprises 26 accepted species (13 threatened species; Suppl. material 1) of shrubs to subshrubs endemic to the seasonally dry tropical forest biome in the Neotropics from the U.S.A. to Brazil (Anderson 2007; POWO 2024). For an identification key for all species of *Galphimia*, see Anderson (2007).

1.3.2. *Spachea* A.Juss. in Deless., Icon. Sel. Pl. 3: 19. 1838 [1837].

= *Lophanthera* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 328. 1840, syn nov. Type species: *Lophanthera kunthiana* A.Juss., nom. superfl. [≡ *Spachea longifolia* (Kunth) R.F.Almeida & M.Pell.].

= *Spachea* sect. *Meckelia* Mart. ex A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 326. 1840 ≡ *Meckelia* (Mart. ex A.Juss.) Griseb. in Martius, Fl. Bras. 12(1): 25. 1858. Type species: *Spachea tricarpa* A.Juss.

= *Andersoniella* C.Davis & Amorim, Harvard Pap. Bot. 25(1): 51–56. 2020, nom. illeg., non *Andersoniella* K.J.F.Schmitz (1897) ≡ *Andersoniodoxa* C.Davis & Amorim, Phytotaxa 470(1): 121–122. 2020, syn. nov. Type: *Andersoniodoxa spruceana* (Nied.) C.Davis & Amorim [≡ *Lophanthera spruceana* (Nied.) R.F.Almeida & M.Pell.].

Type. *Spachea elegans* (G.Mey.) A.Juss.

Notes. *Spachea* was described by Jussieu (1837) to accommodate the species previously placed in *Byrsonima* with unisexual flowers. *Lophanthera* was initially described by Jussieu (1840) based on *L. kunthiana* A.Juss., an illegitimate renaming of *Galphimia longifolia* Kunth. Grisebach (1858) transferred *G. longifolia* to *Lophanthera* and placed *L. kunthiana* in synonymy. Niedenzu (1914) described the second species of *Lophanthera*, *L. spruceana* Nied., ca. 50 years after Grisebach. With the expansion of the Amazonian frontier in Brazil, Ducke described the third and fourth new species of the genus almost two decades later (1925, 1937). Finally, Davis et al. (2020a, b) proposed *Andersoniodoxa* for the three species of *Lophanthera* with white to pink flowers and winged anthers. This was, in theory, strongly supported by molecular data. Nonetheless, the authors never made the sequences used in their article available in public repositories, and the analysis produced by us includes the type species of the three genera and recovers them as a strongly supported clade. Thus, we propose the recognition of a broadly circumscribed but morphologically cohesive *Spachea*, including all species of *Lophanthera* and *Andersoniodoxa*.

In the expanded circumscription presented here, *Spachea* includes 12 species (five threatened species; Suppl. material 1) of large trees distributed in flooded to non-flooded rainforests from the Amazon basin and Central America (POWO 2024). The highly unusual structure of the fruits in *S. longifolia* and *S. spruceana* is worth mentioning, as it might be a water dispersal adaptation that enables buoyancy in the mericarp. For an identification key for *Spachea*, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica.

1.3.2.a. *Spachea hammelii* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342383-1

≡ *Lophanthera hammelii* W.R.Anderson, Brittonia 35: 37. 1983 ≡ *Andersoniella hammelii* (W.R.Anderson) C.Davis & Amorim, Harvard Pap. Bot. 25: 53. 2020 ≡ *Andersoniodoxa hammelii* (W.R.Anderson) C.Davis & Amorim, Phytotaxa 470: 121. 2020.

1.3.2.b. *Spachea lactescens* (Ducke) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342384-1

≡ *Lophanthera lactescens* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 103. 1925.

1.3.2.c. *Spachea longifolia* (Kunth) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342385-1

≡ *Galphimia longifolia* Kunth in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 5: 173. 1822 ≡ *Lophanthera longifolia* (Kunth) Griseb. in C.F.P.von Martius & auct. suc. (eds.), Fl. Bras. 12(1): 25. 1858.

1.3.2.d. *Spachea marcelae* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342386-1

≡ *Lophanthera marcelae* W.R.Anderson, Acta Bot. Mex. 109: 37 (2014) ≡ *Andersoniella marcelae* (W.R.Anderson) C.Davis & Amorim, Harvard Pap. Bot. 25: 53. 2020 ≡ *Andersoniodoxa marcelae* (W.R.Anderson) C.Davis & Amorim, Phytotaxa 470: 121. 2020.

1.3.2.e. *Spachea pendula* (Ducke) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342387-1

≡ *Lophanthera pendula* Ducke, Trop. Woods 50: 34. 1937.

1.3.2.f. *Spachea spruceana* (Nied.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342388-1

≡ *Lophanthera spruceana* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 5: 30. 1914 ≡ *Andersoniella spruceana* (Nied.) C.Davis & Amorim, Harvard Pap. Bot. 25: 55. 2020 ≡ *Andersoniodoxa spruceana* (Nied.) C.Davis & Amorim, Phytotaxa 470: 121. 2020.

1.3.3. *Verrucularina* Rauschert, Taxon 31(3): 560. 1982.

≡ *Verrucularia* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 327. 1840, nom. illeg., non *Verrucularia* Shur. Figs 3B, 4P, 10Q.

Type species. *Verrucularina glaucophylla* (A.Juss.) Rauschert (≡ *Verrucularia glaucophylla* A.Juss.).

Notes. *Verrucularina* is a replacement name for *Verrucularia* A.Juss. since the latter is a posterior homonym of *Verrucularia* Suhr, a genus previously assigned to algae but currently belonging to Bryozoa. The genus currently comprises two accepted species (one threatened species; Suppl. material 1) of shrubs endemic to campos rupestres of the Amazon rainforest and Caatinga biomes of Brazil, South America (Almeida et al. 2020; POWO 2024). For an identification key for all species of *Verrucularina*, see Anderson (1981) for the Guyana Highland or Almeida et al. (2020) for Brazil.

2. Malpighioideae Burnett, Outlines Bot.: 894, 1093, 1126. 1835, emend. nov. R.F.Almeida.

Type genus. *Malpighia* L.

Diagnosis. Posterior petal glandular, 2–10 fertile stamens, pollen 3–12-aperturate, zono- to pantoaperturate, porate or colporate, styles capitate, uncinate, truncate, expanded or rarely subulate, stigmas usually lateral, nuts or mericarps, frequently winged or setose, rarely smooth, chromosome number $n = 9–10$, presence of dithiols, furanoid lignans, organic phosphoric acids and derivatives, and propargyl-type 1,3-dipolar organic compounds.

Notes. Aside from subfamily Byrsonimoideae, all previously proposed subfamilies are recovered nested within Malpighioideae, making it non-monophyletic. Furthermore, most of these subfamilies are non-monophyletic on their own since they were traditionally circumscribed based on fruit morphology (especially dry vs. fleshy) and the presence or absence of mericarp wings. Therefore, in our current circumscription, subfamily Malpighioideae comprises nine main lineages of mostly Neotropical genera of Malpighiaceae (including *Burdachia*, *Glandonia*, and *Mcvaughia*, which were previously placed by Anderson 1977 in Byrsonimoideae). In its new circumscription, Malpighioideae comprises most of the family's diversity (i.e., 63 genera and 1,254 species, with 624 threatened species; Suppl. material 1), including lianas, subshrubs, shrubs and trees occurring in the Americas, Africa, Asia, and Oceania. We recognise nine tribes representing the main lineages within Malpighioideae, previously named by Davis and Anderson (2010) and Almeida et al. (2023a) as: 1. Acridocarpoid clade (Acridocarpeae), 2. Mcvaughioid clade (Mcvaughieae), 3. Barnebyoid clade (Barnebyeae), 4. Ptilochaetoid clade (Ptilochaeteae), 5. Bunchosioid clade (Bunchosieae), 6. Hiraeoid clade (Hiraeeae), 7. Tetrapteroid clade (Hiptageae), 8. Stigmaphylloid clade (Gaudichaudieae), and 9. Malpighioid clade (Malpighieae).

Key to the tribes of Malpighioideae

1 Stipules absent; leaves alternate (Fig. 3D) to subopposite; bracts usually 1–2-glandular; styles lyrate (Fig. 9P), deflexed in flower, reflexed in fruit ... . **Acridocarpeae**
– Stipules present; leaves opposite (Fig. 3A); bracts always eglandular (Fig. 7G–I), styles curved to straight (Fig. 9L, M), always erect.......................... **2**
2 Cincinni 2–7-flowered (Fig. 5A).. **3**
– Cincinni 1-flowered (Fig. 5A–C) **4**
3 Shrubs or subshrubs; leaves distributed along the branches (Fig. 3A, B); bracteoles glandular (Fig. 7B, C); posterior petal glandular; drupes (Fig. 10M, N) .... **Mcvaughieae**
– Trees; leaves congested at the apex of the branches (Fig. 3D); bracteoles eglandular (Fig. 7G–I); posterior petal eglandular; winged schizocarp (Fig. 11) .... **Barnebyeae**

4 Leaves margin revolute when young (Fig. 4P); thyrse main axis inconspicuous (Fig. 5A), usually with 4 cincinni .... **Ptilochaeteae**

– Leaves margin plane when young (Fig. 4O); thyrse main axis well-developed (Fig. 5A, C), with more than 4 cincinni **5**

5 Stipules inconspicuous (Fig. 3F); petals limb abaxially densely pubescent or claws pubescent .... **Hiptageae**

– Stipules conspicuous (Fig. 3H); petals limb abaxially usually glabrous or claws glabrescent **6**

6 Stipules epipetiolar (Fig. 3G) **7**

– Stipules interpetiolar (Fig. 3E, H) **8**

7 Leaf apex eglandular, tertiary veins reticulate; styles straight, parallel, apex capitate, stigma terminal (Fig. 9L); mericarps smooth (Fig. 10O, S), setose (Fig. 10W), drupaceous (Fig. 10H, I), or 4-winged (X-shaped), wings coriaceous, non-reticulate (Fig. 11J–L) .... **Bunchosieae**

– Leaf apex glandular, tertiary veins scalariform; styles curved, divergent, apex uncinate, stigma lateral (Fig. 9I); mericarps 2-winged, wings membranous, finely reticulate (Fig. 11G) .... **Hiraeeae**

8 Flowers arranged in umbels (thyrses in *Bronwenia*); fertile stamens 2–3–4–5–6–10; mericarps with a well-developed dorsal wing (larger than the lateral wings, when present), lateral wings reduced to absent (always smaller than the dorsal wing), free (Fig. 11A) .... **Gaudichaudieae**

– Flowers arranged in corymbs (thyrses in *Amorimia* and *Ectopopterys*); fertile stamens 10; drupes (*Malpighia*; Fig. 10J–L) or mericarps with a reduced dorsal wing (smaller than the lateral wings), lateral wings well-developed (larger than the dorsal wing), free (*Ectopopterys* and *Amorimia*; Fig. 11F) or fused into an orbicular wing (Fig. 11I)................. .... **Malpighieae**

2.1. Acridocarpeae R.F.Almeida, trib. nov.

urn:lsid:ipni.org:names:77342389-1

Type genus. *Acridocarpus* Guill. & Perr.

Diagnosis. Lianas, shrubs to treelets; thyrses, many-flowered, cincinni 1-flowered, bracts 1-glandular, peduncle absent, bracteoles eglandular; sepals glandular, nectariferous; posterior petals 2, margin crenate, eglandular; connectives eglandular, anthers poricidal, pollen 3-zonosyncolporate; styles reflexed in fruits; mericarps 1-winged, dorsal wing more developed, chromosome number $n = 9$, presence of diazanaphthalenes, isoflavonoids, oxacyclic compounds, absence of tetrahydrofurans.

Notes. Acridocarpeae currently comprises only two accepted genera (*Acridocarpus* and *Brachylophon*) and 38 species (20 threatened species; Suppl. material 1) of trees, shrubs or lianas endemic to Africa, Asia, and Oceania (POWO 2024).

Key to the genera of Acridocarpeae

1 Leaf apex rounded, acute or mucronate; corolla rotate, petals patent, margin not entire; dorsal wing well-developed; Africa to Western Asia .... ***Acridocarpus***

– Leaf apex caudate; corolla campanulate, petals erect, margin entire; dorsal wing very reduced; Southeastern Asia .... ***Brachylophon***

2.1.1. *Acridocarpus* Guill., Perr. & A.Rich., Fl. Seneg. Tent.: 123, t. 29. 1831.

= *Heteropterys* sect. *Anomalopterys* DC., Prodr. 1: 592. 1824 ≡ *Anomalopterys* (DC.) G.Don, Gen. Hist. 1: 647. 1831. Type species: *Anomalopterys spicata* G.Don [= *Acridocarpus smeathmanii* (DC.) Guill. & Perr.].

= *Rhinopteryx* Nied., Nat. Pflanzenfam. 3(4): 352. 1896. Type species: *Rhinopteryx spectabilis* Nied. [≡ *Acridocarpus spectabilis* (Nied.) Doorn-Hoekm.].

Type species. *Acridocarpus plagiopterus* Guill., Perr. & A.Rich.

Notes. *Acridocarpus* currently comprises 36 accepted species (19 threatened species; Suppl. material 1) of trees, shrubs, scandent shrubs, or lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Africa, Madagascar, the Arabic Peninsula, Iran, and Oceania (i.e., New Caledonia; POWO 2024). There is no updated identification key for all species of *Acridocarpus*, but Niedenzu's (1928) treatment covers 25 out of the 36 currently accepted species.

2.1.2. *Brachylophon* Oliv., Hooker's Icon. Pl. 16: 1566. 1887.

Type species. *Brachylophon curtisii* Oliv.

Notes. *Brachylophon* currently comprises two accepted species (one threatened species; Suppl. material 1) of shrubs endemic to the rainforest biome in Southeast Asia (Indonesia, Malaysia, and Thailand; POWO 2024). For a taxonomic treatment for *Brachylophon*, see Sirirugsa (1991) for Thailand.

2.2. Mcvaughieae R.F.Almeida, trib. nov.

urn:lsid:ipni.org:names:77342390-1

Type genus. *Mcvaughia* W.R.Anderson.

Diagnosis. Trees, shrubs to subshrubs; thyrses, cincinni 1–7-flowered, bracteoles 1-glandular; pollen 4-zonocolporate (3-zonocolporate in *Glandonia*); drupes, epicarp striated, presence of linear 1,3-diarylpropanoids, and the absence of dithiols, indoles and derivatives.

Notes. Mcvaughieae currently comprises three accepted genera, *Burdachia*, *Glandonia*, and *Mcvaughia*, and 12 species (five threatened species; Suppl. material 1) of trees, shrubs to subshrubs endemic to the Amazon rainforests and seasonally dry tropical forests of South America (POWO 2024).

Key to the genera of Mcvaughieae

1 Pedicel straight at pre-anthesis, lateral petals yellow, fertile stamens 7, staminodes 3, anthers horseshoe-shaped, ovary 1-locular, styles straight at apex, stigma lateral; fruit pubescent.............***Mcvaughia* (Figs 8G, 10M)**
– Pedicel circinate at pre-anthesis, lateral petals pink or white, fertile stamens 10, staminodes absent, anthers straight, ovary 3-locular, styles bent at apex, stigma terminal; fruit glabrous. **2**
2 Stipules connate in epipetiolar pairs, persistent; inflorescences deflexed; floral buds globose, lateral petals pink, filaments glabrous, connective expanded, locule apex rounded, shorter than the connective ....***Burdachia* (Fig. 10N)**
– Stipules connate in interpetiolar pairs, deciduous; inflorescences erect; floral buds pyramidal, lateral petals white, filaments pubescent, connective inconspicuous, locule apex acute, longer than the connective... ***Glandonia***

2.2.1. *Burdachia* A.Juss. ex Endl., Gen. Pl.: 1064. 1840.

Fig. 10N

= *Tetrapodenia* Gleason, Bull. Torrey Bot. Club 53: 289. 1926. Type species: *Tetrapodenia glandifera* Gleason (= *Burdachia sphaerocarpa* A.Juss.).

Type species. *Burdachia prismatocarpa* A.Juss.

Notes. *Burdachia* comprises only six currently accepted species (one threatened species; Suppl. material 1) of trees or shrubs endemic to flooded forests of the Amazon rainforests of Brazil, Colombia, Guyana, Peru, and Venezuela, South America (POWO 2024). For an identification key for all species of *Burdachia*, see Almeida et al. (2020) for Brazil or Anderson (1981) for the Guyana Highland.

2.2.1.a. *Burdachia glandifera* (Gleason) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342391-1

≡ *Tetrapodenia glandifera* Gleason, Bull. Torrey Bot. Club 53: 289. 1926 ≡ *Burdachia sphaerocarpa* var. *glandifera* (Gleason) W.R.Anderson, Mem. New York Bot. Gard. 32: 139. 1981.

2.2.1.b. *Burdachia loretoensis* (W.R.Anderson) R.F.Almeida & M.Pell., stat. nov.

urn:lsid:ipni.org:names:77342392-1

≡ *Burdachia prismatocarpa* var. *loretoensis* W.R.Anderson, Mem. New York Bot. Gard. 32: 143. 1981.

2.2.2. ***Glandonia*** Griseb. in Martius, Fl. Bras. 12(1): 23. 1858.

Type species. *Glandonia macrocarpa* Griseb.

Notes. *Glandonia* comprises only three currently accepted species (one threatened species; Suppl. material 1) of trees or shrubs endemic to flooded forests of the Amazon rainforests of Brazil, Colombia, and Venezuela, South America (POWO 2024). For an identification key for all species of *Glandonia*, see Almeida et al. (2020) for Brazil, Anderson (1981) for the Guyana Highland, or Guesdon et al. (2018) for the Brazilian Amazon.

2.2.3. ***Mcvaughia*** W.R.Anderson, Taxon 28: 157. 1979.

Figs 8G, 10M

Type species. *Mcvaughia bahiana* W.R.Anderson.

Notes. *Mcvaughia* comprises only three currently accepted species (all threatened species; Suppl. material 1) of shrubs endemic to the seasonally dry tropical forests of Northeastern Brazil, South America (i.e., Caatinga biome; POWO 2024). For an identification key for all species of *Mcvaughia*, see the taxonomic treatment of Almeida et al. (2019).

2.3. Barnebyeae R.F.Almeida, trib. nov.

urn:lsid:ipni.org:names:77342393-1

Type genus. *Barnebya* W.R.Anderson & B.Gates.

Diagnosis. Trees; thyrses, cincinni 2–3-flowered; pollen 4-zonoporate; mericarps 1-winged, dorsal wing more developed, presence of diarylheptanoids, keto acids and derivatives, oxazinanes, absence of benzopyrans, furanoid lignans, glycerophospholipids, lignan glycosides, naphthalenes, naphthopyrans, propargyl-type 1,3-dipolar organic compounds, pteridines and derivatives, tetrahydrofurans.

Notes. Barnebyeae currently comprises a single genus, *Barnebya*, and two accepted species (one threatened species; Suppl. material 1) of trees endemic to Brazil, South America (POWO 2024).

2.3.1. ***Barnebya*** W.R.Anderson & B.Gates, Brittonia 33(3): 275. 1981.

Type species. *Barnebya dispar* (Griseb.) W.R.Anderson & B.Gates.

Notes. *Barnebya* comprises two currently accepted species (one threatened species; Suppl. material 1) of large trees endemic to non-flooded forests of the Atlantic rainforest and Caatinga biomes in Brazil, South America (Almeida et al. 2020; POWO 2024). For an identification key for *Barnebya*, see Almeida et al. (2020).

2.4. Ptilochaeteae R.F.Almeida, trib. nov.

urn:lsid:ipni.org:names:77342394-1

Type genus. *Ptilochaeta* Turcz.

Diagnosis. Treelets to shrubs; thyrses reduced, 4-flowered; pollen 8-zonocolporate, styles apex geniculate to truncate; mericarp winged or setose, presence of 2-aryl-benzofuran flavonoids, dibenzyl-butane lignans, isoflavonoids, oxacyclic compounds, oxanes, pyrrolidines, thiocarbonyl compounds, absence of organothiophosphorus compounds, thiophenes.

Notes. Ptilochaeteae currently comprises three accepted genera, *Dinemandra*, *Lasiocarpus*, and *Ptilochaeta*, and ten currently accepted species (one threatened species; Suppl. material 1) of small trees or shrubs endemic to the Americas (POWO 2024).

Key to the genera of Ptilochaeteae

1 Sepals with stipitate glands, posterior petal glandular, fertile stamens 2 or 8; mericarps winged; arid and desert areas of Argentina and Chile .... ***Dinemandra***

– Sepals eglandular, posterior petal eglandular, fertile stamens 10; mericarps setose; seasonally dry forests of Argentina, Bolivia, Brazil, Paraguay, and Mexico **2**

2 Plants dioecious, sepal apex erect, petals narrowly elliptic, style apex expanded; Mexico .... ***Lasiocarpus* (Fig. 10U)**

– Plants monoecious; sepal apex convolute, petals widely elliptic to obovate, style apex truncate; Argentina, Bolivia, Brazil, Paraguay.. ***Ptilochaeta* (Fig. 8O)**

2.4.1. *Dinemandra* A.Juss. ex Endl., Ann. Sci. Nat., Bot., sér. 2, 13: 255. 1840.

= *Dinemagonum* A.Juss., Arch. Mus. Hist. Nat. 3: 585. 1843, syn. nov. Type species: *Dinemagonum bridgesianum* A.Juss. [= *Dinemandra gayana* (A.Juss.) R.F.Almeida & M.Pell.].

Type species. *Dinemandra ericoides* A.Juss. ex Endl.

Notes. *Dinemandra* and *Dinemagonum* were traditionally distinguished from each other based exclusively on their fruit morphology, with *Dinemandra* presenting dominant lateral wings and *Dinemagonum* presenting a dominant dorsal wing. Nonetheless, both genera are strongly supported as sister based on molecular data, being further morphologically supported by stalked sepal glands basally connate forming pairs (Simpson 1989) and 8-colporate and reticulate pollen (Lowrie 1982). Recognising them as distinct provides no phylogenetic information and unnecessarily inflates this already genus-rich family. Thus, we propose a broadly circumscribed *Dinemandra*, including *Dinemagonum*. In the current circumscription, *Dinemandra* comprises two currently accepted species (no threatened species; Suppl. material 1) of shrubs endemic to the semi-desert vegetation of Chile, South America (POWO 2024). For an identification key for all species of *Dinemandra*, see Simpson (2011).

2.4.1.a. *Dinemandra gayana* (A.Juss.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342395-1

≡ *Dinemagonum gayanum* A.Juss., Arch. Mus. Hist. Nat. 3: 585. 1843.

2.4.2. *Lasiocarpus* Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 90. 1854.

Fig. 10U

Type species. *Lasiocarpus salicifolius* Liebm.

Notes. *Lasiocarpus* comprises four currently accepted species (one threatened species; Suppl. material 1) of trees endemic to the seasonally dry tropical forests of Mexico, North America (POWO 2024). For an identification key for all species of *Lasiocarpus*, see Cardona-Cruz et al. (2021).

2.4.3. *Ptilochaeta* Turcz., Bull. Soc. Imp. Naturalistes Moscou 16: 52. 1843.

Fig. 8O

Type species. *Ptilochaeta bahiensis* Turcz.

Notes. *Ptilochaeta* comprises only three currently accepted species (no threatened species; Suppl. material 1) of trees endemic to the seasonally dry tropical forests of Argentina, Bolivia, Brazil, and Paraguay, South America (POWO 2024). After carefully analysing all type specimens of this genus, *Ptilochaeta densiflora* Nied. is proposed here as a new synonym of *Ptilochaeta nudipes* Griseb. An identification key for most species of *Ptilochaeta* can be found in Almeida et al. (2020) for Brazil.

2.5. Bunchosieae R.F.Almeida, trib. nov.

urn:lsid:ipni.org:names:77342396-1

= Thryallidinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 53, 67. 1890, syn. nov. Type genus: *Thryallis* Mart., nom. cons.

Type genus. *Bunchosia* Rich. ex Kunth.

Diagnosis. Trees, shrubs or lianas; thyrses, cincinni 1-flowered; pollen 4–12-pantoporate (colporate in *Echinopterys* and *Heladena*); styles free, rarely connate, parallel; stigma terminal, capitate; drupes or mericarps smooth or winged, presence of azolidines, benzodioxoles, organochlorides, quinolizines, absence of organic carbonic acids and derivatives, organic phosphoric acids and derivatives.

Notes. Bunchosieae currently comprises five accepted genera, *Bunchosia*, *Echinopterys*, *Heladena*, *Thryallis*, and *Tristellateia*, and 122 species (68 threatened species; Suppl. material 1) of mostly American taxa, except for the Paleotropical (i.e., tropics of Africa, Asia, and Oceania) *Tristellateia* (POWO 2024).

Key to the genera of Bunchosieae

1 Lianas; leaves glandular at or along margin **2**
– Trees, shrubs or scandent shrubs; leaves eglandular or glandular at base **3**
2 Floral buds smooth, sepals 2-glandular, glands pedunculate, petal margin fimbriate to denticulate, anthers rimose, styles 3; mericarps smooth or setose; Neotropics .... ***Heladena* (Figs 8D, 10O)**
– Floral buds keeled, sepals eglandular, petal margin entire, anthers poricidal, styles 1; mericarps winged; Paleotropics............................. ***Tristellateia***
3 Leaves eglandular; stamen filaments pubescent; mericarps setose.......... .... ***Echinopterys* (Fig. 10W)**
– Leaves glandular at base; stamen filaments glabrous; mericarps smooth or drupaceous.. **4**
4 Trees or erect shrubs; inflorescence, flowers and fruits with malpighiaceous hairs, bracteoles glandular, not surrounding floral buds; sepals 2-glandular, erect at anthesis, anthers connivant; mericarps drupaceous .. .. ***Bunchosia* (Figs 8F, 10H)**
– Scandent shrubs; inflorescence, flowers and fruits with stellate hairs, bracteoles eglandular, surrounding floral buds; sepals eglandular, deflexed at anthesis, anthers divergent; mericarps smooth....................................... .... ***Thryallis* (Figs 7J, P, 10S)**

2.5.1. *Bunchosia* Rich. ex Kunth, Nov. Gen. Sp. 5: 118. 1821.

Figs 8F, 10H

= *Malacmaea* Griseb., Linnaea 13: 248. 1839. Type species: *Malacmaea fluminensis* Griseb. [= *Bunchosia maritima* (Vell.) J.F.Macbr.].

Type species. *Bunchosia odorata* (Jacq.) DC.

Notes. *Bunchosia* comprises 93 currently accepted species (46 threatened species; Suppl. material 1) of trees or shrubs endemic to non-flooded rainforests and seasonally dry tropical forest biomes in the Neotropics from Mexico to Argentina (POWO 2024; Suppl. material 1). There is no updated identification key for all species of *Bunchosia*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, Pool (in prep.) for Mesoamerica, González-Gutiérrez and Meyer (2019) for the Antilles, and Anderson (2016) for North America.

2.5.2. *Echinopterys* A.Juss., Arch. Mus. Hist. Nat. 3: 342. 1843.

Fig. 10W

= *Bunchosia* sect. *Coelostylis* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 325. 1840 ≡ *Coelostylis* (A.Juss.) Kuntze, Revis. Gen. Pl. 1: 87. 1891, nom. illeg., non *Coelostylis* Torr. & A.Gray. Type species: *Coelostylis glandulosa* Kuntze [= *Echinopterys eglandulosa* (A.Juss.) Small].

Type species. *Echinopterys lappula* A.Juss. [= *Echinopterys eglandulosa* (A. Juss.) Small].

Notes. *Echinopterys* comprises only two currently accepted species of shrubs or lianas endemic to the seasonally dry tropical forests of Mexico (POWO 2024). For an identification key for all species of *Echinopterys*, see Pool (in prep.).

2.5.3. *Heladena* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 321. 1840.

Figs 8D, 10O

= *Henlea* Griseb., Abh. Königl. Ges. Wiss. Göttingen 9: 37. 1860, syn. nov., nom. illeg., non *Henlea* H.Karst. ≡ *Henleophytum* H.Karst., Fl. Columb. 1: 158. 1861. Type species: *Henleophytum echinatum* (Griseb.) Small [≡ *Heladena echinata* (Griseb.) R.F.Almeida & M.Pell.].
= *Malpigiantha* Rojas Acosta, Cat. Hist. Nat. Corrientes: 55. 1897. Type species: *Malpigiantha volubilis* Rojas Acosta [= *Heladena multiflora* (Hook. & Arn.) Nied.].

Type species. *Heladena multiflora* (Hook. & Arn.) Nied.

Notes. Similar to *Dinemandra* and *Dinemagonum*, *Heladena* and *Henleophytum* are strongly supported as sister by molecular data, being exclusively distinguished by their fruit morphology (*Heladena* having smooth mericarps and *Henleophytum* having setose mericarps). However, both genera share unique stalked peltate sepal glands, added to hairy petals, weakly coherent but soon separating styles, and stigmas elliptic and geniculate. Thus, we also propose the expansion of *Heladena* to include two currently accepted species (one threatened species; Suppl. material 1) of lianas endemic to the seasonally dry tropical forests of Cuba, Antilles, Central America, and South America (Argentina, Brazil, Paraguay and Uruguay) (POWO 2024).

2.5.3.a. *Heladena echinata* (Griseb.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342397-1

≡ *Henlea echinata* Griseb., Abh. Königl. Ges. Wiss. Göttingen 9: 37. 1860 ≡ *Henleophytum echinatum* (Griseb.) Small in Britton & al., N. Amer. Fl. 25: 149. 1910.

2.5.4. *Thryallis* Mart., Nov. Gen. Sp. Pl. 3: 77. 1829, nom. cons.

Figs 7J, P, 10S

≡ *Hemsleyna* Kuntze, Revis. Gen. Pl. 1: 88. 1891.

Type species. *Thryallis longifolia* Mart.

Notes. *Thryallis* comprises five currently accepted species (one threatened species; Suppl. material 1) of shrubs or lianas endemic to the rainforests, savannas, and seasonally dry tropical forests of Bolivia, Brazil, and Paraguay, South America (POWO 2024). For an identification key for all species of *Thryallis*, see Anderson (1995).

2.5.5. *Tristellateia* Thouars, Madagasc.: 14. 1806.

= *Zymum* Noronha ex Thouars, Hist. Vég. Îsles Austral. Afriq.: 69. 1808. Type species: *Zymum madagascariense* Spreng. (= *Tristellateia madagascariensis* Poir.).
= *Platynema* Wight & Arn., Edinburgh New Philos. J. 15: 179. 1833. Type species: *Platynema laurifolium* Wight & Arn. (= *Tristellateia australasiae* A.Rich.).

Type species. *Tristellateia madagascariensis* Poir.

Notes. *Tristellateia* comprises 21 species of lianas endemic to rainforests and seasonally dry tropical forests of Madagascar (19 threatened species; Suppl. material 1), with a single species occurring in continental Africa (Comoros, Kenya, Mozambique, Somalia, Tanzania) and another species endemic to Southeast Asia (Cambodia, Myanmar, Thailand, Malaysia, Philippines, Taiwan, and Vietnam), and Oceania (Australia, Bismarck Archipelago, Caroline Islands, Jawa, Lesser Sunda Islands, Maluku, Marianas, Nansei-shoto, New Caledonia, New Guinea, and Vanuatu; POWO 2024). For an identification key for all species of *Tristellateia*, see Arènes (1947).

2.6. Hiraeeae A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 255. 1840, as "Hireae", emend. nov. R.F.Almeida.

Type genus. *Hiraea* Jacq.

Diagnosis. Lianas; leaf blades with apex glandular; thyrses, many-flowered; pollen 4–12-pantocolporate (porate in *Psychopterys*); styles with apex uncinate, stigma lateral; mericarps winged, 2 lateral wings more developed than the dorsal, usually butterfly-shaped, presence of piperidines, absence of benzofurans, benzopyrans, dithiols, furanoid lignans, hydroxy acids and derivatives, naphthopyrans, pteridines and derivatives, pyrimidine nucleosides.

Notes. Hiraeeae currently comprises five accepted genera, *Adelphia*, *Excentradenia*, *Hiraea*, *Lophopterys* and *Psychopterys*, and 105 species (54 threatened species; Suppl. material 1) of lianas or shrubs endemic to the Americas (POWO 2024).

Key to the genera of Hiraeeae

1 Flowers arranged in thyrses **2**
– Flowers arranged in umbels **4**
2 Inflorescence branches longitudinally costate; sepals 1-glandular, posterior petal shorter than laterals; mericarps with 2 V-shaped lateral wings .... ***Lophopterys* (Fig. 11G)**
– Inflorescence branches smooth; sepals 2-glandular, posterior petal equalling or longer than laterals; mericarps with 2 butterfly-shaped lateral wings **3**
3 Leaves apex glandular; bracteoles glandular; petals yellow, deflexed, margin fimbriate, posterior petal longer than laterals, styles apex uncinate .... ***Adelphia***
– Leaves apex eglandular; bracteoles eglandular; petals white, patent, margin dentate to erose, posterior petal equalling laterals, styles apex capitate .... ***Psychopterys***

4 Stipules at base of petioles; posterior petal with fimbriae two times longer than those from the laterals; mericarps with lateral wings connate at base .... ***Excentradenia***

– Stipules at middle or apex of petioles; all petals with equally long fimbriae; mericarps with lateral wings free .... ***Hiraea* (Figs 3G, 4S)**

2.6.1. *Adelphia* W.R.Anderson, Novon 16(2): 170–171. 2006.

Type species. *Adelphia hiraea* (Gaertn.) W.R.Anderson.

Notes. *Adelphia* comprises four currently accepted species (two threatened species; Suppl. material 1) of lianas endemic to non-flooded rainforests of Central America and the Amazon basin, South America (POWO 2024). For an identification key for all species of *Adelphia*, see Anderson (2006).

2.6.2. *Excentradenia* W.R.Anderson, Contr. Univ. Michigan Herb. 21: 29. 1997.

Type species. *Excentradenia adenophora* (Sandw.) W.R.Anderson.

Notes. *Excentradenia* comprises four currently accepted species (two threatened species; Suppl. material 1) of lianas endemic to non-flooded forests of the Amazon rainforests of Bolivia, Brazil, Guyana, French Guyana, Suriname, and Venezuela, South America (POWO 2024). For an identification key for all species of *Excentradenia*, see Anderson (1997).

2.6.3. *Hiraea* Jacq., Enum. Syst. Pl. 4. 1760.

Figs 3G, 4S

Type species. *Hiraea reclinata* Jacq.

Notes. *Hiraea* comprises 81 currently accepted species (43 threatened species; Suppl. material 1) of scandent shrubs or lianas endemic to rainforests from Mexico (North America) to Argentina (South America) but absent in the Antilles (POWO 2024). There is no updated identification key for all species of *Hiraea*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica.

2.6.4. *Lophopterys* A.Juss. in Deless., Icon. Sel. Pl. 3: 18. 1838 [1837].

Fig. 11G

= *Dolichopterys* Kosterm., Recueil Trav. Bot. Néerl. 32: 279. 1935. Type species: *Dolichopterys surinamensis* Kosterm. [≡ *Lophopterys surinamensis* (Kosterm.) Sandwith].

Type species. *Lophopterys splendens* A.Juss.

Notes. *Lophopterys* currently comprises seven accepted species (two threatened species; Suppl. material 1) of lianas endemic to the non-flooded forests of the Amazon and Atlantic rainforests of Bolivia, Brazil, Guyana, French Guyana, Peru, Suriname, and Venezuela, South America (POWO 2024). For an identification key for all species of *Lophopterys*, see Anderson and Davis (2001).

2.6.5. ***Psychopterys*** **W.R.Anderson & S.Corso, Contr. Univ. Michigan Herb. 25: 116. 2007.**

Type species. *Psychopterys dipholiphylla* (Small) W.R.Anderson & S.Corso.

Notes. *Psychopterys* comprises nine currently accepted species (five threatened species; Suppl. material 1) of lianas endemic to seasonally dry tropical forests of Belize, Guatemala, Honduras, Mexico, and Nicaragua, Central and North America (Pool 2023; POWO 2024). For an identification key for all species of *Psychopterys*, see Anderson and Corso (2007) and Pool (2023).

2.7. Hiptageae DC., Prodr. 1: 583. 1824, emend. nov. R.F.Almeida.

= Banisterieae DC., Prodr. 1: 584. 1824, syn. nov. ≡ Banisteriinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 52, 60. 1890. Type genus: *Banisteria* L., nom. rej. (= *Heteropterys* Kunth).

= Tricomarieae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 52, 66. 1890, syn. nov. Type genus: *Tricomaria* Gillies ex Hook. & Arn.

Type genus. *Hiptage* Gaertn.

Diagnosis. Treelets, shrubs or lianas; thyrses, multi-flowered; pollen 4–12-pantocolporate (porate in *Hiptage* and some *Heteropterys*); nuts or mericarps winged, with 2–4-wings, butterfly, Y or X-shaped, rarely setose, absence of organic phosphonic acids and derivatives.

Notes. Hiptageae currently comprises 17 accepted genera, *Alicia*, *Callaeum*, *Carolus*, *Chlorohiptage*, *Christianella*, *Dicella*, *Flabellaria*, *Flabellariopsis*, *Glicophyllum*, *Heteropterys*, *Hiptage*, *Jubelina*, *Malpighiodes*, *Mezia*, *Niedenzuella*, *Tetrapterys*, *Tricomaria*, and 377 species (163 threatened species; Suppl. material 1) occurring in the Americas, Africa, Asia and Oceania (POWO 2024).

Key to the genera of Hiptageae (modified from Almeida and van den Berg 2021)

1 Styles 1–2; mericarps with 3 free lateral wings or setose **2**
– Styles 3; mericarps with 1–2–4 free lateral wings **3**
2 Style 1, apex truncate, stigma terminal; mericarps with 3 free lateral wings; Africa and Asia .... ***Hiptage*** **(Figs 7K, 8A, 11M)**
– Styles 2, apex uncinate, stigma lateral; mericarps setose; South America (Argentina) .... ***Tricomaria*** **(Fig. 10T)**
3 Petals green, styles shorter than the filaments; mericarps with 1 lateral wing; Asia (Vietnam) .... ***Chlorohiptage***
– Petals white, lilac, yellow, orange or red, styles longer than the filaments; mericarps with 2–4 free lateral wings; Africa or Americas **4**

4 Sepals deflexed, stigma terminal; Africa **5**

– Sepals erect, stigma lateral; Americas **6**

5 Leaves glandular at margin, petiole with 2–3 gland pairs; stigma capitate .... ***Flabellaria***

– Leaves glandular near or along margin, petiole eglandular; stigma truncate .... ***Flabellariopsis***

6 Petals glabrous to glabrescent **7**

– Petals densely pubescent **10**

7 Sepals not enclosing petals in bud, filaments usually glabrous **8**

– Sepals enclosing petals in bud, filaments usually pubescent **9**

8 Flowers arranged in thyrses, corymbs or umbels, inflorescences never arranged in dichasia; mericarps with 1 dominant dorsal wing .... ***Heteropterys* (Figs 8L, Q, U, 11C, D)**

– Flowers arranged in umbels, inflorescences arranged in dichasia; mericarps with 4 dominant lateral wings .... ***Tetrapterys* (Figs 4Q, 8T, 11J)**

9 Leaves glandular near or along margin, petioles eglandular; flowers arranged in umbels, 4-flowered, secondarily arranged in dichasia, bracteoles elliptic; mericarps with 2 dominant lateral wings, connate at base .... ***Malpighiodes***

– Leaves glandular at margin, petioles usually with 1 gland pair; flowers arranged in thyrses, many-flowered, solitary, bracteoles triangular; mericarps with 2–4 dominant lateral wings, free .... ***Niedenzuella* (Figs 5B, C, 7E, 8N, 11L)**

10 Bracteoles leaf-like; sepals enlarged in fruit; nuts .... ***Dicella* (Figs 7H, I, 10B–D)**

– Bracteoles minute; sepals not enlarged in fruit; schizocarps **11**

11 Flowers arranged in umbels, 4-flowered, secondarily arranged in dichasia **12**

– Flowers arranged in thyrses, many-flowered, solitary or grouped but never secondarily arranged in dichasia 14

12 Sepals deflexed at anthesis, anterior lateral petals deflexed at anthesis, posterior lateral petals patent at anthesis; mericarps with several lateral winglets, vertically inserted between lateral wings and the dorsal wing .... ***Jubelina***

– Sepals erect to patent at anthesis, lateral petals deflexed at anthesis; mericarps without lateral winglets, when present (in *Mezia*) horizontally inserted between the lateral wings and the dorsal wing **13**

13 Bracteoles not enclosing floral bud; connectives inconspicuous; lateral wings free .... ***Callaeum***

– Bracteoles enclosing floral bud; connectives expanded; lateral wings connate at base .... ***Mezia* (Fig. 7D)**

14 Bracts, bracteoles, sepals and petals glandular at margin; mericarps with acicular (unbranched) hairs .... ***Christianella* (Figs 7C, M, 8B)**

– Bracts, bracteoles, sepals and petals eglandular at margin; mericarps with 2-branched hairs **15**

15 Stipules interpetiolar; petioles eglandular; petal margin fimbriate, anthers pubescent .... ***Carolus* (Fig. 11H)**

– Stipules epipetiolar; petioles glandular; petal margin glandular, erose or dentate, anthers glabrous **16**

16 Petioles with 2–4 gland pairs; bracteoles eglandular; lateral petals erect; mericarps bearing 2 dominant lateral wings, usually connate at base ....***Alicia* (Figs 7G, 8Y)**

– Petioles eglandular or with 1 gland pair; bracteoles glandular; lateral petals patent; mericarps bearing 2–4 dominant lateral wings, free................. ....***Glicophyllum* (Figs 7B, 11K)**

2.7.1. *Alicia* W.R.Anderson, Novon 16: 174. 2006.

Figs 7G, 8Y

Type species. *Alicia anisopetala* (A.Juss.) W.R.Anderson.

Notes. *Alicia* comprises only two currently accepted species (no threatened species; Suppl. material 1) of lianas endemic to rainforests and seasonally dry tropical forests of Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Paraguay, Peru, Suriname, and Venezuela, South America (POWO 2024). For an updated identification key for all species of *Alicia*, see Anderson (2006) or Almeida et al. (2020).

2.7.2. *Callaeum* Small in Britton & al., N. Amer. Fl. 25: 128. 1910.

= *Cabi* Ducke, Arq. Serv. Florest. 2(1): 13. 1943. Type species: *Cabi paraensis* Ducke [= *Callaeum antifebrile* (Griseb.) D.M.Johnson].

Type species. *Callaeum nicaraguense* (Griseb.) Small.

Notes. *Callaeum* comprises 11 currently accepted species (five threatened species; Suppl. material 1) of scandent shrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests from the United States (North America) to Argentina (South America; POWO 2024). For an identification key for all species of *Callaeum*, see Johnson (1986).

2.7.3. *Carolus* W.R.Anderson, Novon 16: 186. 2006.

Fig. 11H

Type species. *Carolus chlorocarpus* (A.Juss.) W.R.Anderson.

Notes. *Carolus* comprises eight currently accepted species (five threatened species; Suppl. material 1) endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Brazil (South America; POWO 2024). For an identification key for all species of *Carolus*, see the synopsis of Anderson (2006) for the entire genus, Almeida et al. (2023c) for Brazil, and Pool (2023) for Mesoamerica.

2.7.4. *Chlorohiptage* T.V.Do, T.A.Le & R.F.Almeida, Plant Ecol. Evol. 157(2): 130. 2024.

Type species. *Chlorohiptage vietnamensis* T.V.Do, T.A.Le & R.F.Almeida.

Notes. *Chlorohiptage* comprises a single species (one threatened; Suppl. material 1) of lianas endemic to rainforests of Vietnam, Southeast Asia (Do et al. 2024). For a taxonomic treatment of the new genus, see Do et al. (2024).

2.7.5. *Christianella* W.R.Anderson, Novon 16: 190. 2006.

Figs 7C, M, 8B

Type species. *Christianella mesoamericana* (W.R.Anderson) W.R.Anderson.

Notes. *Christianella* comprises five currently accepted species (two threatened species; Suppl. material 1) of lianas endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Brazil (South America; POWO 2024). For an identification key for all species of *Christianella*, see Anderson (2006).

2.7.6. *Dicella* Griseb., Linnaea 13: 249. 1839.

Figs 7H, I, 10B–D

Type species. *Dicella bracteosa* (A.Juss.) Griseb.

Notes. *Dicella* comprises seven currently accepted species (one threatened species; Suppl. material 1) of lianas endemic to rainforests, savannas, and seasonally dry tropical forests from Costa Rica (Central America) to Argentina (South America; POWO 2024). For an identification key for all species of *Dicella*, see Chase (1981).

2.7.7. *Flabellaria* Cav., Diss. 9: 436. 1790.

Type species. *Flabellaria paniculata* Cav.

Notes. *Flabellaria* comprises a single currently accepted species of liana endemic to rainforests, savannas, and seasonally dry tropical forests of Africa (POWO 2024). For a taxonomic treatment for *Flabellaria*, see Wilczek (1958).

2.7.8. *Flabellariopsis* R.Wilczek, Bull. Jard. Bot. État 25: 303, pl. 8. 1955.

Type species. *Flabellariopsis acuminata* (Engl.) R.Wilczek.

Notes. *Flabellariopsis* comprises a single currently accepted species (not threatened; Suppl. material 1) of liana endemic to rainforests, savannas, and seasonally dry tropical forests of Cameroon, Congo, Gabon, Tanzania, Uganda, and Zaire, Africa (POWO 2024). For a taxonomic treatment for *Flabellariopsis*, see Wilczek (1958).

2.7.9. *Glicophyllum* R.F.Almeida, Nordic J. Bot. 39: 12. 2021.

Figs 7B, 11K

Type species. *Glicophyllum chamaecerasifolium* (A.Juss.) R.F.Almeida.

Notes. *Glicophyllum* comprises 28 currently accepted species (four threatened species; Suppl. material 1) of shrubs, subshrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Argentina (South America; POWO 2024). There is no updated identification key for all species of *Glicophyllum*, but for regional treatments, see Anderson (1981) for the Guyana Highland (under *Tetrapterys*), Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica.

2.7.9.a. *Glicophyllum argenteum* (A.Juss.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342398-1

≡ *Hiraea argentea* A.Juss., Fl. Bras. Merid. 3: 17. 1833 ≡ *Tetrapterys jussieuana* Nied. in Engler, Nat. Pflanzenr. 93: 169. 1928 ≡ *Glicophyllum jussieuanum* (Nied.) R.F.Almeida, Nordic J. Bot. 39(1)-e02876: 15. 2021.

2.7.10. *Heteropterys* Kunth, Nov. Gen. Sp. 5 [quarto]: 163. 1822 [1821], nom. cons.

Figs 8L, Q, U, 11C, D

= *Banisteria* L., Sp. Pl.: 427. 1753, nom. rej. Type species: *Banisteria brachiata* L. [≡ *Heteropterys brachiata* (L.) DC.].

= *Banisteria* sect. *Holopetalon* Griseb., Linnaea 13: 199. 1839 ≡ *Holopetalon* (Griseb.) Rchb., Deut. Bot. Herb.-Buch: 207. 1841. Type species: *Banisteria patens* Griseb. [≡ *Heteropterys patens* (Griseb.) A.Juss.]

= *Clonodia* Griseb. in Martius, Fl. Bras. 12(1): 26. 1858. Type species: *Clonodia verrucosa* Griseb. (= *Heteropterys racemosa* A.Juss.).

= *Atopocarpus* Cuatrec., Webbia 13: 454. 1958. Type species: *Atopocarpus papillosus* Cuatrec. (= *Heteropterys racemosa* A.Juss.).

= *Skoliopteris* Cuatrec., Webbia 13: 451. 1958. Type species: *Skoliopteris lehmanniana* (Nied.) Cuatrec. [= *Heteropterys complicata* (Kunth) W.R.Anderson & C.Davis].

Type species. *Heteropterys purpurea* (L.) Kunth.

Notes. *Heteropterys* comprises 166 currently accepted species (75 threatened species; Suppl. material 1) of treelets, shrubs, subshrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests from North America (Mexico) to South America (Argentina), and West Africa (Angola, Cameroon, Congo, Gabon, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Senegal, Sierra Leone, and Zaire; POWO 2024). There is no updated identification key for all species of *Heteropterys*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica. *Glicophyllum jussieuanum* (Nied.) R.F.Almeida is here placed in the synonymy of *G. argenteum* (A.Juss.) R.F.Almeida & M.Pell. *comb. nov.*, due to its basionym being a replacement name for *Hiraea argentea* A.Juss.

2.7.11. *Hiptage* Gaertn., Fruct. Sem. Pl. 2: 169. 1790, nom. cons.

Figs 7K, 8A, 11M

= *Gaertnera* Schreb., Gen. Pl., ed. 8[a]. 1: 290. 1789, nom. rej. Type species: *Gaertnera indica* J.F. Gmel. [= *Hiptage benghalensis* (L.) Kurz].
= *Molina* Cav., Diss. 9: 435. 1790. Type species: *Molina racemosa* Cav. [= *Hiptage benghalensis* (L.) Kurz].
= *Succowia* Dennst., Schlüssel Hortus Malab.: 32. 1818, nom. illeg., non *Succowia* Medik. Type species: *Succowia fimbriata* Dennst. [= *Hiptage benghalensis* (L.) Kurz].

Type species. *Hiptage madablota* Gaertn. [= *Hiptage benghalensis* (L.) Kurz].

Notes. *Hiptage* comprises 47 currently accepted species (39 threatened species; Suppl. material 1) of lianas endemic to rainforests and seasonally dry tropical forests of Southeast Asia (Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Sri Lanka, Taiwan, Thailand, and Vietnam) and Oceania (Fiji; POWO 2024). There is no updated identification key for all species of *Hiptage*, but for regional treatments, see Srivastava (1997) for India, Sirirugsa (1991) for Thailand, Chen and Funston (2008) for China, and Lim (2017) for Malaysia.

2.7.12. *Jubelina* A.Juss. in Deless., Icon. Sel. Pl. 3: 19, pl. 32. 1838 [1837].

= *Sprucina* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 3: 18. 1908. Type species (designated here): *J. grisebachiana* W.R.Anderson.

Type species. *Jubelina riparia* A.Juss.

Notes. No names have ever been published under the generic name *Sprucina*, but the collection cited in the protologue (Spruce 2853) refers to *J. grisebachiana* W.R.Anderson. Thus, *J. grisebachiana* is here designated as the type of *Sprucina* under Art. 10.2 Ex. 2 (Turland et al. 2018). *Jubelina* comprises six currently accepted species (one threatened species; Suppl. material 1) of lianas endemic to the rainforests of Brazil, Colombia, and Venezuela, South America (POWO 2024). For an identification key for all species of *Jubelina*, see Anderson (1990).

2.7.13. *Malpighiodes* Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1909–1910: 31. 1909.

Type species. *Malpighiodes spruceana* Nied. [=*Malpighiodes bracteosa* (Griseb.) W.R.Anderson].

Notes. *Malpighiodes* comprises four currently accepted species (one threatened species; Suppl. material 1) of lianas endemic to the rainforests of the Amazon basin of Brazil, French Guiana, Guyana, Suriname, and Venezuela, South America (POWO 2024). For an identification key for all species of *Malpighiodes*, see Anderson (2006).

2.7.14. *Mezia* Schwacke ex Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 58. 1890.

Fig. 7D

= *Stenocalyx* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 393. 1858, nom. illeg., non *Stenocalyx* O.Berg. (1856). Type species: *Stenocalyx involutus* Turcz. [= *Mezia includens* (Benth.) Cuatrec.].

Type species. *Mezia araujoi* Schwacke ex Nied.

Notes. *Mezia* comprises 15 currently accepted species (eight threatened species; Suppl. material 1) of lianas endemic to the rainforests of the Amazon and Atlantic rainforest biomes in South America (Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela) and Panama, Central America (POWO 2024). For a taxonomic treatment for all species of *Mezia*, see Anderson and Anderson (2018).

2.7.15. *Niedenzuella* W.R.Anderson, Novon 16(2): 194–198. 2006.

Figs 5B, C, 7E, 8N, 11L

= *Aenigmatanthera* W.R.Anderson, Novon 16: 173. 2006. Type species: *Aenigmatanthera lasiandra* (A.Juss.) W.R.Anderson [≡ *Niedenzuella lasiandra* (A. Juss.) R.F.Almeida].

Type species. *Niedenzuella poeppigiana* (A.Juss.) W.R.Anderson.

Notes. *Niedenzuella* currently comprises 18 accepted species (three threatened species; Suppl. material 1) of lianas endemic to rainforests, savannas, and seasonally dry tropical forests of South America (Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, and Venezuela) and Central America (Costa Rica and Panama; POWO 2024). For an identification key for all species of *Niedenzuella*, see Anderson (2006, also under *Aenigmatanthera*). *Aenigmatanthera* was reduced to a synonym of *Niedenzuella* by Almeida and van den Berg (2021) since its two species were recovered strongly supported as nested within the latter.

2.7.16. *Tetrapterys* Cav., Diss. 9: 433. 1790.

Figs 4Q, 8T, 11J

= *Adenoporces* Small in Britton & al., N. Amer. Fl. 25: 128. 1910. Type species: *Adenoporces buxifolius* (Cav.) Small (≡ *Tetrapterys buxifolia* Cav.).

Type species. *Tetrapterys inaequalis* Cav.

Notes. *Tetrapterys* comprises 56 currently accepted species (18 threatened species; Suppl. material 1) of shrubs and lianas endemic to rainforests, savannas, and seasonally dry tropical forests of the Neotropics from Mexico (North America to Argentina (South America; POWO 2024). There is no updated identification key for all species of *Tetrapterys*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica.

2.7.16.a. *Tetrapterys andina* (Nied.) R.F.Almeida & M.Pell., stat. nov.
urn:lsid:ipni.org:names:77342399-1

≡ *Tetrapterys discolor* var. *andina* Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1909–1910: 42. 1909.

2.7.17. *Tricomaria* Gillies ex Hook. & Arn., Bot. Misc. 3: 157. 1833.

Type species. *Tricomaria usillo* Gillies ex Hook. & Arn.

Notes. *Tricomaria* comprises a single currently accepted species (no threatened species; Suppl. material 1) of shrubs endemic to the seasonally dry tropical forests of Argentina, South America (POWO 2024). For a taxonomic treatment of *Tricomaria*, see Aliscioni and Torretta (2017).

2.8. Malpighieae DC., Prodr. 1: 577. 1824, emend. nov. R.F.Almeida

≡ Malpighiinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 53, 71. 1890.
= Aspidopteryinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 52, 53. 1890, as "Aspidopteridinae", syn. nov. Type genus: *Aspidopterys* A.Juss. ex Endl.
= Mascagniinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 52, 55. 1890, syn. nov**.** Type genus: *Mascagnia* (Bertero ex DC.) Bertero.
= Rhynchophoreae Arènes, Notul. Syst. (Paris) 12: 135. 1946, syn. nov. Type genus: *Rhynchophora* Arènes.

Type genus. *Malpighia* L.

Diagnosis. Treelets, shrubs or lianas; thyrses or corymbs; pollen 4–12-pantocolporate (porate in the Paleotropical species); styles with apex uncinate to truncate, stigma lateral; mericarps winged, 1–2-wings, butterfly-shaped to orbicular, rarely drupaceous or with dorsal wing more developed than lateral ones, presence of (3'–>5')-dinucleotides and analogues, piperidines, absence of benzofurans, furanoid lignans, imidolactams, lignan glycosides.

Notes. Malpighieae currently comprises 13 accepted genera: *Amorimia*, *Aspidopterys*, *Calcicola*, *Caucanthus*, *Diaspis*, *Digoniopterys*, *Ectopopterys*, *Madagasikaria*, *Malpighia*, *Mascagnia*, *Microsteira*, *Rhynchophora*, and *Triaspis*, and 253 species (157 threatened species; Suppl. material 1) occurring in the Americas, Africa, and Asia (POWO 2024).

Key to the genera of Malpighieae (modified from Almeida 2018)

1 Plants androdioecious; flowers actinomorphic, sepals eglandular, stigmas terminal **2**
– Plants dioecious (androdioecious in *Triaspis*); flowers zygomorphic, sepals glandular, stigmas lateral (terminal in *Triaspis*) **8**
2 Style apex truncate; continental Africa, Arabian Peninsula, and Asia **3**
– Style apex with projections (1–2-lobed); Madagascar **5**

3 Flowers arranged in umbels; flower buds obovoid, petal margin entire, reflexed, filaments slightly longer than sepals; Asia .... ***Aspidopterys***

– Flowers arranged in corymbs; flower buds ovoid to oblongoid, petal margin fimbriate to lobed, patent, filaments shorter or two times longer than sepals; Africa and Arabian Peninsula **4**

4 Leaves spirally-alternate, glabrous; petal margin fimbriate, limb base obtuse, 2-carpellate .... ***Diaspis***

– Leaves opposite, tomentose; petals margin undulate, limb base sagittate, 3-carpellate .... ***Caucanthus***

5 Leaves spirally-alternate, up to 5 mm wide; umbels 1-flowered; petals narrowly spatulate, abaxially completely densely sericeous, style apex long-lobed.. ***Digoniopterys***

– Leaves opposite, at least 1 cm wide (mostly much wider); umbels 4–many-flowered; petals elliptic to orbicular, glabrous or abaxially sparsely sericeous along the keel, style apex shortly-lobed... **6**

6 Stipules enlarged, leaf-like, persistent; flowers in thyrses; mericarps with wings fused into an orbicular wing .... ***Madagasikaria***

– Stipules reduced, triangular, persistent to deciduous; flowers in umbels; mericarps with lateral wings fused into a single apical geniculate wing or a Y-shaped wing **7**

7 Ovary bearing conspicuous initials for lateral wings and dorsal crest on each carpel, visible even in young flowers; mericarps dehiscent, lateral wings fused into a Y-shaped wing... ***Microsteira***

– Ovary lacking initials for wings or crests; mericarps indehiscent, lateral wings fused into a single apical geniculate wing.................. ***Rhynchophora***

8 Plants monoecious; stipules connate, leaf-like; bracteoles inserted at middle or below peduncle apex; floral buds keeled; sepals 1–2-glandular, glands very reduced, secreting nectar, petal margin long-fimbriate, limb base sagittate; Paleotropics .... ***Triaspis***

– Plants dioecious; stipules free, triangular; bracteoles inserted at peduncle apex (except in *Calcicola*); floral buds smooth (except in few *Mascagnia* spp.); sepals 2-glandular, glands large, secreting oil, petal margin entire, limb base obtuse, cuneate or rounded; Neotropics **9**

9 Sepals deflexed at anthesis, connectives bearing large glands, style apex lobed; mericarp with a dominant dorsal wing .... ***Ectopopterys***

– Sepals erect at anthesis, connectives bearing inconspicuous glandular tissue, style apex truncate; mericarp with dominant lateral wings or wings greatly reduced and fleshy at maturity.. **10**

10 Lianas; flowers arranged in thyrses or corymbs, bracteoles 1–6-glandular, rarely eglandular **11**

– Shrubs to treelets; flowers arranged in umbels, bracteoles eglandular... **12**

11 Flowers arranged in thyrses, bracteoles 2–6-glandular; floral buds smooth; petals yellow, turning orange to red at post-anthesis, pubescent; mericarp with lateral wings free, coriaceous .... ***Amorimia* (Figs 7A, 8M, 9I, J, 11F)**

– Flowers in thyrses or corymbs, bracteoles 0–1-glandular; floral buds keeled; petals white, pink or lilac, if yellow not turning orange to red at post-anthesis; glabrous; mericarp with lateral wings fused into an orbicular wing, membranous............................. ***Mascagnia* (Figs 3E, 6B, 8Z, 11I)**

12 Leaves with stiff, spine-like (generally urticating) hairs; bracteoles inserted at peduncle apex; ovary glabrous; mericarps indehiscent, fleshy, dorsal and lateral wings much reduced, free, fleshy at maturity ....***Malpighia*** **(Fig. 10J–L)**

– Leaves with soft hairs; bracteoles inserted at peduncle middle; ovary pubescent; mericarps dehiscent, dry, lateral wings conspicuous, fused......... ....***Calcicola***

2.8.1. *Amorimia* W.R.Anderson, Novon 16: 176. 2006.

Figs 7A, 8M, 9I, J, 11F

Type species. *Amorimia rigida* (A.Juss.) W.R.Anderson.

Notes. *Amorimia* comprises 15 currently accepted species (eight threatened species; Suppl. material 1) of lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay, and Peru, South America (POWO 2024). For a taxonomic treatment for all species of *Amorimia*, see Almeida (2018).

2.8.2. *Aspidopterys* A.Juss. ex Endl., Ann. Sci. Nat., Bot., sér. 2, 13: 266. 1840.

Type species. *Aspidopterys elliptica* (Blume) A.Juss. ex Endl.

Notes. *Aspidopterys* comprises 24 currently accepted species (ten threatened species; Suppl. material 1) of lianas endemic to rainforests of Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Thailand, Tibet, and Vietnam, Southeast Asia (POWO 2024). For an updated identification key for all species of *Aspidopterys*, see Hutchinson (1917) for a partial revision, Sirirugsa (1991) for Thailand, and Srivastava (1997) for India.

2.8.3. *Calcicola* W.R.Anderson & C.Davis, Contr. Univ. Michigan Herb. 25: 148. 2007.

Type species. *Calcicola parvifolia* (A.Juss.) W.R.Anderson & C.Davis.

Notes. *Calcicola* comprises only two currently accepted species (no threatened species; Suppl. material 1) of shrubs endemic to the seasonally dry tropical forests of Mexico, North America (POWO 2024). For an identification key for all species of *Calcicola*, see Anderson and Davis (2007).

2.8.4. *Caucanthus* Forssk., Fl. Aegypt.-Arab.: 91. 1775.

= *Caucanthus* sect. *Eriocaucanthus* Nied., Bull. Herb. Boissier, sér. 2, 4: 1010. 1904 ≡ *Eriocaucanthus* (Nied.) Chiov., Ann. Bot. (Rome) 10: 29. 1912. Type species: *Caucanthus argenteus* Nied.

Type species. *Caucanthus edulis* Forssk.

Notes. *Caucanthus* comprises only two currently accepted species (no threatened species; Suppl. material 1) of shrubs or lianas endemic to seasonally dry tropical forests of east Africa (Ethiopia, Kenya, Malawi, Mozambique, Somalia, Tanzania, Uganda, and Zimbabwe) and the Arabic Peninsula (Saudi Arabia and Yemen; POWO 2024). For an updated identification key for all species of *Caucanthus*, see Launert (1968).

2.8.5. *Diaspis* Nied., Bot. Jahrb. Syst. 14: 314. 1892.

Type species. *Diaspis albida* Nied.

Notes. *Diaspis* comprises a single currently accepted species (no threatened species; Suppl. material 1) of liana endemic to the seasonally dry tropical forests of Ethiopia, Kenya, and Somalia, Africa (POWO 2024). For a taxonomic treatment of *Diaspis*, see Niedenzu (1928).

2.8.6. *Digoniopterys* Arènes, Notul. Syst. (Paris) 12: 133. 1946.

Type species. *Digoniopterys microphylla* Arènes.

Notes. *Digoniopterys* comprises a single currently accepted species (one threatened species; Suppl. material 1) of shrub endemic to the seasonally dry tropical forests of Madagascar, Africa (POWO 2024). For a taxonomic treatment of *Digoniopterys*, see Arènes (1946).

2.8.7. *Ectopopterys* W.R.Anderson, Contr. Univ. Michigan Herb. 14: 11. 1980.

Type species. *Ectopopterys soejartoi* W.R.Anderson.

Notes. *Ectopopterys* comprises a single currently accepted species (no threatened species; Suppl. material 1) of liana endemic to rainforests and seasonally dry tropical forests of Colombia, Ecuador, and Peru, South America (POWO 2024). For a taxonomic treatment of *Ectopopterys*, see Anderson (1980).

2.8.8. *Madagasikaria* C.Davis, Amer. J. Bot. 89: 702. 2002.

Type species. *Madagasikaria andersonii* C.Davis.

Notes. *Madagasikaria* comprises a single currently accepted species (one threatened species; Suppl. material 1) of liana endemic to the seasonally dry tropical forests of Madagascar, Africa (POWO 2024). For a taxonomic treatment of *Madagasikaria*, see Davis (2002).

2.8.9. *Malpighia* Plum. ex L., Sp. Pl. 425. 1753.

Fig. 10J–L

= *Rudolphia* Medik., Malvenfam.: 111. 1787. Type species: *Rudolphia edulis* Medik. (= *Malpighia urens* L. subsp. *urens*).

Type species. *Malpighia glabra* Plum. ex L.

Notes. *Malpighia* comprises 110 currently accepted species (85 threatened species; Suppl. material 1) of treelets or shrubs endemic to rainforests and seasonally dry tropical forests from South America (Colombia, Ecuador, and Venezuela) to Central (Aruba, Bahamas, Belize, Cayman Islands, Costa Rica, Cuba, Dominican Republic, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Leeward Islands, Netherlands Antilles, Nicaragua, Panamá, Puerto Rico, Trinidad-Tobago, Turks-Caicos Islands, and Windward Islands) and North America (Mexico and United States of America; POWO 2024). For identification keys for all species of *Malpighia*, see the monographs by Vivaldi (1979) and Meyer (2000), the studies of González-Gutiérrez and Meyer (2019) for Cuba, and Pool (2023) for Mesoamerica.

2.8.10. ***Mascagnia*** **(Bertero ex DC.) Bertero, Hortus Ripul.: 85. 1824, nom. cons.**

Figs 3E, 6B, 8Z, 11I

≡ *Hiraea* [unranked] *Mascagnia* Bertero ex DC., Prodr. 1: 585. 1824.
= *Triopterys* L., Sp. Pl.: 428. 1753, nom. rej. Type species: *Triopterys jamaicensis* L. [= *Mascagnia lucida* (Kunth) W.R.Anderson & C.Davis].

Type species. *Mascagnia americana* Bertero [= *Mascagnia macradena* (DC.) Nied.].

Notes. *Mascagnia* comprises 48 currently accepted species (19 threatened species; Suppl. material 1) of shrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Argentina (South America; POWO 2024). There is no current updated identification key for all species of *Mascagnia*, but for regional treatments, see Anderson (1981) for the Guyana Highland, Almeida et al. (2020) for Brazil, and Pool (in prep.) for Mesoamerica.

2.8.11. ***Microsteira*** **Baker, J. Linn. Soc., Bot. 20: 111. 1883.**

Type species. *Microsteira curtisii* Baker.

Notes. *Microsteira* comprises 27 currently accepted species (all threatened species; Suppl. material 1) of lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Madagascar, Africa (POWO 2024). For an identification key for all species of *Microsteira*, see Arènes (1945).

2.8.12. ***Rhynchophora*** **Arènes, Notul. Syst. (Paris) 12: 127. 1946.**

= *Calyptostylis* Arènes, Notul. Syst. (Paris) 12: 131. 1946. Type species: *Calyptostylis humbertii* Arènes (= *Rhynchophora phillipsonii* W.R.Anderson).

Type species. *Rhynchophora humbertii* Arènes.

Notes. *Rhynchophora* comprises only two currently accepted species (all threatened species; Suppl. material 1) of lianas endemic to the seasonally dry tropical forests of Madagascar, Africa (POWO 2024). For an identification key for all species of *Rhynchophora*, see Anderson (2001a). Despite *Madagasikaria* causing the non-monophyly of *Rhynchophora* (Fig. 1), the bootstrap support value for this clade is below 60%. Therefore, we have chosen to retain both genera as independent until further phylogenetic evidence sheds some light on the matter.

2.8.13. *Triaspis* Burch., Trav. S. Africa 2: 280. 1824.

= *Umbellulanthus* S.Moore, J. Bot. 58: 220. 1920. Type species: *Umbellulanthus floribundus* S.Moore (≡ *Triaspis mooreana* Exell & Mendonça).

Type species. *Triaspis hypericoides* Burch.

Notes. *Triaspis* comprises 19 currently accepted species (five threatened species; Suppl. material 1) endemic to rainforests, savannas, and seasonally dry tropical forests of Angola, Benin, Botswana, Cameroon, Cape Green, Congo, Ethiopia, Gabon, Ghana, Guinea, Ivory Coast, Kenya, Liberia, Malawi, Mozambique, Namibia, Nigeria, Sierra Leone, Somalia, South Africa, Tanzania, Togo, Zambia, Zaire, and Zimbabwe, Africa (POWO 2024). There is no current identification key for all species of *Triaspis*, but for regional keys, see Niedenzu (1928), Launert (1968) for East Africa, Badré (1972) for Cameroon, Badré (1973) for Gabon, Hutchinson and Dalziel (1958) for West Tropical Africa, Wilczek (1958) for Democratic Republic of Congo, and Almeida et al. (2024) for Southern Africa.

2.9. Gaudichaudieae Horan., Char. Ess. Fam.: 182. 1847, emend. nov. R.F.Almeida

≡ Gaudichaudioideae A.Juss. ex C.V.Morton, Taxon 17: 318. 1968.
= Sphedamnocarpinae Nied. in Engler & Prantl, Nat. Pflanzenfam. III, 4: 52, 59. 1890, syn. nov. Type genus: *Sphedamnocarpus* Planch. ex Benth. & Hook.f.

Type genus. *Gaudichaudia* Kunth.

Diagnosis. Lianas, shrubs to subshrubs; umbels, rarely thyrses, usually 4-flowered; pollen 4–12-pantocolporate (porate in *Stigmaphyllon* subg. *Ryssopterys*, *Philgamia*, and *Sphedamnocarpus*); mericarps winged, 1-winged, dorsal wing more developed, rarely reduced, presence of macrolactams, absence of biotin and derivatives, sulfenyl compounds.

Notes. Gaudichaudieae currently comprises 14 accepted genera, *Aspicarpa*, *Banisteriopsis*, *Bronwenia*, *Camarea*, *Cottsia*, *Diplopterys*, *Janusia*, *Mamedea*, *Mionandra*, *Peixotoa*, *Philgamia*, *Schwannia*, *Sphedamnocarpus*, and *Stigmaphyllon*, and 336 species (154 threatened species; Suppl. material 1) occurring in the Americas, Africa, Asia and Oceania (POWO 2024).

Anderson (1993) proposed Gaudichaudieae (A.Juss.) W.R.Anderson with the aim to “validate” the name published by Jussieu (1840). Nonetheless, the name published by Jussieu (1840) was proposed as unranked and was not validly published until Morton (1968) provided a Latin diagnosis while also correcting its spelling and rank to be used as a subfamily. However, both authors overlooked that the name had already been validly published as a tribe, accompanied by a Latin diagnosis by Horaninow (1847). Therefore, Anderson's name is a superfluous, later homonym of Gaudichaudieae Horan.

Key to the genera of Gaudichaudieae

1 Petiole or leaf base glands ellipsoid, sunken; flowers arranged in thyrses, secondarily arranged in thyrses; sepal glands decurrent into the pedicel, stamens homomorphic........................***Bronwenia*** **(Figs 3A, 8H, R, V, 9E, L)**

– Petioles or leaf base glands discoid or cupuliform, not sunken; flowers arranged in corymbs or umbels, solitary or secondarily arranged in dichasia or thyrses, rarely solitary thyrses; sepals not decurrent, stamens heteromorphic 2

2 Leaves apex long-acuminate; petals abaxially pubescent, styles pubescent; mericarps with dominant lateral wings...........***Diplopterys*** **(Figs 8S, 9O, 11A)**

– Leaves apex emarginate, rounded, obtuse, acute, short-acuminate or acuminate; petals abaxially glabrous, styles glabrous; mericarps with a dominant dorsal wing, lateral wings reduced or absent.............................**3**

3 Branches with scale-like hairs; leaves long-petiolate, rarely short-petiolate; flowers arranged in corymbs or umbels, 5–many-flowered, peduncle curved; styles divergent and lyrate, apex expanded (foliaceous), rarely reduced............. ***Stigmaphyllon*** **(Figs 3C, N, 4A–C, E–G, I–N, 6D, E, 9N, P, Q)**

– Branches without scale-like hairs; leaves short-petiolate; flowers arranged in umbels or thyrses, 1–4-flowered, peduncle straight; styles parallel and straight, apex truncate or cylindrical..**4**

4 Cincinni sessile or short-pedunculate; styles 3...**5**

– Cincinni long-pedunculate; style 1(–2–3), if styles 2–3 then carpels slightly rotated so that no carpel aligns with the anterior sepals and posterior petal, and mericarps with dominant lateral wings **9**

5 Stipules minute, free; flowers chasmogamous, sepal apex straight, fertile stamens 10, staminodes absent..**6**

– Stipules expanded, fused or bifid; flowers chasmogamous or cleistogamous, sepal apex revolute or involute along margins, fertile stamens 5, staminodes 3–5 ....**8**

6 Flowers zygomorphic, sepals at anthesis bent towards the centre of the flower, connectives glandular; Neotropics..
.............***Banisteriopsis*** **(Figs 3M–S, 4B, D, O, R, T, V, 6C, 7F, 9A–D, H, 11B)**

– Flowers actinomorphic, sepals erect at anthesis, connectives eglandular; Africa..**7**

7 Petals yellow; mericarp dorsal wing well-developed; Africa and Madagascar..***Sphedamnocarpus***

– Petals white; mericarp dorsal wing absent or very reduced; Madagascar..
....***Philgamia***

8 Stipules connate at base or up to the middle (i.e., bifid); flowers arranged in umbels, 1-flowered, bract and bracteoles absent; sepals free, completely revolute or involute along margins, antherodes filiform, minute, styles apex truncate to slightly expanded ....***Mionandra***

– Stipules connate (i.e., entire); flowers arranged in umbels, 4-flowered, bract and bracteoles present; sepals connate at base, revolute only at apex, antherodes globose, conspicuous, styles apex capitate .... ***Peixotoa*** **(Figs 3H, 8X, 9F, 11E)**

9 Flowers chasmogamous, fertile stamens 2, staminodes 3, antherodes absent, carpels syncarpic...***Cottsia***

– Flowers chasmogamous or cleistogamous, fertile stamens 3–4–5–6, staminodes 0–2, antherodes present, carpels syncarpic at base and apically apocarpic...**10**

10 Flowers enantiostylous, petal margin long-fimbriate, fertile stamens 6, style curved...***Schwannia*** **(Figs 3P, 8W, 9G, M)**

– Flowers non-enantiostylous, petal margin entire, erose, denticulate or dentate, rarely short-fimbriate, fertile stamens 3–4–5, style straight............11

11 Fertile stamens 5, staminodes absent; mericarp dorsal wing developed ....***Janusia***

– Fertile stamens 3–4(–5), staminodes present; mericarp dorsal wing absent or reduced to a crest...**12**

12 Branches herbaceous, annual, with acicular hairs; leaf blades reduced and narrow, margin usually revolute; fertile stamens 4, homomorphic ....***Camarea*** **(Figs 7L, 8I, 10V)**

– Branches woody, perennial, with malpighiaceous hairs; leaf blades usually expanded and broad, margin plane; fertile stamens 3(–5), heteromorphic **13**

13 Leaf base never with filamentous or tooth-like projections; flowers arranged in 1–4-flowered umbels, peduncles absent to reduced, without associated reduced leaves; antherodes equalling or larger than anthers (reduced to an apical swelling in *M. harleyi* and *M. lanata*), pubescent (glabrous in *M. harleyi*), usually red to orange at post-anthesis, 2 posterior carpels rotated so that all face the posterior petal; mericarp wings reduced to crests to teeth; central to southern South America ......***Mamedea*** **(Fig. 4U)**

– Leaf base generally with a filamentous or tooth-like projection at each side of the blade; flowers arranged in 3–4-flowered umbels, peduncles long, with associated reduced leaves; antherodes smaller than anthers (few species with all anthers fertile), glabrous, yellow at post-anthesis, carpels slightly rotated so that no carpel aligns with the anterior sepals and posterior petal; mericarp lateral wings dominant (often fused), sometimes all wings equally developed into wings or reduced to crests; North and Central America ....***Aspicarpa***

2.9.1. *Aspicarpa* Rich., Mém. Mus. Hist. Nat. 2: 396–400, pl. 13. 1815.

= *Acosmus* Desv., J. Bot. Agric. 3: 229. 1816. Type species: *Acosmus pruriens* Desv. (=*Aspicarpa hirtella* Rich.).

= *Gaudichaudia* Kunth, Nov. Gen. Sp. (quarto ed.) 5: pl. 445. 1821, syn. nov. Type species: *Gaudichaudia cynanchoides* Kunth [≡ *Aspicarpa cynanchoides* (Kunth) Hassl.].

= *Gaudichaudia* [unranked] *Tritomopterys* A.Juss. ex Endl., Gen. Pl. 1058. 1840 ≡ *Tritomopterys* (A.Juss. ex Endl.) Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 4: 28. 1912. Type species (designated here): *Gaudichaudia confertiflora* A.Juss. [≡ *Aspicarpa confertiflora* (A.Juss.) R.F.Almeida & M.Pell.].

= *Rosanthus* Small in Britton & al., N. Amer. Fl. 25: 131. 1910. Type species: *Rosanthus subverticellatus* (Rose) Small [≡ *Aspicarpa subverticillata* (Rose) Hassl.].

Type species. *Aspicarpa hirtella* Rich.

Notes. In its current circumscription, *Aspicarpa* (now including *Gaudichaudia*) comprises 27 species (ten threatened species; Suppl. material 1) of shrubs, subshrubs or lianas with a long and tortuous taxonomic history. Most species have already been placed in the genera *Banisteria* (= *Heteropterys* Kunth), *Gaudichaudia*, *Hiraea*, *Triopterys* [= *Mascagnia* (Bertero ex DC.) Bertero], and *Tritomopterys*. However, *Aspicarpa sensu* W.R.Anderson is greatly non-monophyletic, with a South American clade recovered sister to *Janusia* s.str. and the mostly North and Central American species recovered mixed with *Gaudichaudia*. Thus, *Gaudichaudia* and the mostly North and Central American species of *Aspicarpa* are combined here, while the exclusively South American clade is proposed as a new genus, *Mamedea* (see below).

Most of the morphological diversity found in *Aspicarpa* s.lat. (especially the production of cleistogamous flowers and variation in the number of style number) might be attributed to polyploidy events (Jessup 2003). *Aspicarpa* species occur in seasonally dry tropical forests from North America (Mexico and the United States), Central America (Costa Rica, El Salvador, Guatemala, Honduras, and Nicaragua), to northern South America (Colombia and Venezuela; POWO 2024). No complete revision is available for the current circumscription of *Aspicarpa* or any of the previous circumscriptions of *Aspicarpa* and *Gaudichaudia*. A taxonomic revision of this genus is urgently needed, and species boundaries are especially fuzzy in the former *Gaudichaudia*.

2.9.1.a. *Aspicarpa andersonii* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342400-1

≡ *Gaudichaudia andersonii* S.L.Jessup, Madroño 49: 254. 2002.

2.9.1.b. *Aspicarpa arnottiana* (A.Juss.) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342401-1

≡ *Gaudichaudia arnottiana* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 252. 1840.

2.9.1.c. *Aspicarpa chasei* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342402-1

≡ *Gaudichaudia chasei* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 68. 1987.

2.9.1.d. *Aspicarpa confertiflora* (A.Juss.) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342403-1

≡ *Gaudichaudia confertiflora* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 252. 1840.

2.9.1.e. *Aspicarpa cycloptera* (DC.) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342404-1

≡ *Hiraea cycloptera* DC., Prodr. 1: 586. 1824.

2.9.1.f. *Aspicarpa filipendula* (A.Juss.) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342405-1

≡ *Gaudichaudia filipendula* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 252. 1840.

2.9.1.g. *Aspicarpa implexa* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342406-1

≡ *Gaudichaudia implexa* S.L.Jessup, Madroño 49: 247. 2002.

2.9.1.h. *Aspicarpa intermixteca* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342407-1

≡ *Gaudichaudia intermixteca* S.L.Jessup, Madroño 49: 251. 2002.

2.9.1.i. *Aspicarpa krusei* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342408-1

≡ *Gaudichaudia krusei* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 69. 1987.

2.9.1.j. *Aspicarpa mcvaughii* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342409-1

≡ *Gaudichaudia mcvaughii* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 72. 1987.

2.9.1.k. *Aspicarpa oxyota* (DC.) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342410-1

≡ *Hiraea oxyota* DC., Prodr. 1: 586. 1824.

2.9.1.l. *Aspicarpa palmeri* (S.Watson) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342411-1

≡ *Gaudichaudia palmeri* S.Watson, Proc. Amer. Acad. Arts 21: 421. 1886.

2.9.1.m. *Aspicarpa symplecta* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342412-1

≡ *Gaudichaudia symplecta* S.L.Jessup, Madroño 49(4): 253. 2002.

2.9.1.n. *Aspicarpa synoptera* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342413-1

≡ *Gaudichaudia synoptera* S.L.Jessup, Madroño 49(4): 251. 2002.

2.9.1.o. *Aspicarpa zygoptera* (S.L.Jessup) R.F.Almeida & M.Pell., comb. nov.
urn:lsid:ipni.org:names:77342414-1

≡ *Gaudichaudia zygoptera* S.L.Jessup, Madroño 49: 249. 2002.

2.9.2. *Banisteriopsis* C.R.Rob. in Britton & al., N. Amer. Fl. 25(2): 131. 1910.
Figs 3M–O, Q–S, 4B, D, O, R, T, V, 6C, 7F, 9A–D, H, 11B

Type species. *Banisteriopsis argentea* (Kunth) C.R.Rob. [= *Banisteriopsis muricata* (Cav.) Cuatrec.]

Notes. *Banisteriopsis* comprises 65 currently accepted species (24 threatened species; Suppl. material 1) of treelets, shrubs, subshrubs or lianas, endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Argentina (South America; POWO 2024). For an identification key for all species of *Banisteriopsis*, see Gates (1982) and Almeida et al. (2020).

2.9.2.a. *Banisteriopsis appressa* (B.Gates) R.F.Almeida & M.Pell., stat. nov.
urn:lsid:ipni.org:names:77342415-1

≡ *Banisteriopsis malifolia* var. *appressa* B.Gates, Fl. Neotrop. Monogr. 30: 79. 1982.

2.9.2.b. *Banisteriopsis subenervia* (B.Gates) R.F.Almeida & M.Pell., stat. nov.
urn:lsid:ipni.org:names:77342416-1

≡ *Banisteriopsis martiniana* var. *subenervia* Cuatrec., Webbia 13: 501. 1958.

2.9.2.c. *Banisteriopsis glabrata* (B.Gates) R.F.Almeida & M.Pell., stat. nov.
urn:lsid:ipni.org:names:77342417-1

≡ *Banisteriopsis pulchra* var. *glabrata* B.Gates, Fl. Neotrop. Monogr. 30: 109. 1982.

2.9.3. ***Bronwenia*** W.R.Anderson & C.Davis, Contr. Univ. Michigan Herb. 25: 138–140. 2007.

Figs 3A, 8H, R, V, 9E, L

Type species. *Bronwenia ferruginea* (Cav.) W.R.Anderson & C.Davis.

Notes. *Bronwenia* comprises 13 currently accepted species (four threatened species; Suppl. material 1) of shrubs or lianas endemic to rainforests and seasonally dry tropical forests from Mexico (North America) to Brazil (South America; POWO 2024). For an identification key for all species of *Bronwenia*, see Gates (1982) and Anderson and Davis (2007).

2.9.3.a. ***Bronwenia llanensis*** (B.Gates) R.F.Almeida & M.Pell., stat. nov.

urn:lsid:ipni.org:names:77342418-1

≡ *Banisteriopsis acapulcensis* var. *llanensis* B.Gates, Fl. Neotrop. Monogr. 30: 46. 1982 ≡ *Bronwenia acapulcensis* var. *llanensis* (B.Gates) W.R.Anderson & C.Davis, Contr. Univ. Michigan Herb. 25: 141. 2007.

2.9.3.b. ***Bronwenia maracaybensis*** (A.Juss.) R.F.Almeida & M.Pell., comb. et stat. nov.

urn:lsid:ipni.org:names:77342419-1

≡ *Banisteria maracaybensis* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 285. 1840 ≡ *Banisteriopsis cornifolia* var. *maracaybensis* (A.Juss.) W.R.Anderson, Contr. Univ. Michigan Herb. 20: 15. 1995 ≡ *Bronwenia cornifolia* var. *maracaybensis* (A.Juss.) W.R.Anderson & C.Davis, Contr. Univ. Michigan Herb. 25: 143. 2007.

2.9.3.c. ***Bronwenia standleyi*** (B.Gates) R.F.Almeida & M.Pell., comb. et stat.

urn:lsid:ipni.org:names:77342420-1

≡ *Banisteriopsis cornifolia* var. *standleyi* B.Gates, Fl. Neotrop. Monogr. 30: 44. 1982 ≡ *Bronwenia cornifolia* var. *standleyi* (B.Gates) W.R.Anderson & C.Davis, Contr. Univ. Michigan Herb. 25: 143. 2007.

2.9.4. ***Camarea*** A.St.-Hil., Bull. Philom.: 133. 1823.

Figs 7L, 8I, 10V

= *Camarea* sect. *Cryptolappa* A.Juss., Ann. Sci. Nat., Bot., sér. 2, 13: 254. 1840 ≡ *Cryptolappa* (A.Juss.) Kuntze, Revis. Gen. Pl. 1: 88. 1891. Type species: *Camarea affinis* A.St.-Hil.

Type species. *Camarea ericoides* A.St.-Hil.

Notes. *Camarea* comprises eight currently accepted species (three threatened species; Suppl. material 1) of subshrubs endemic to savannas and campos rupestres of Bolivia, Brazil, Guyana, Paraguay, and Suriname, South America (POWO 2024). *Camarea glazioviana* Nied. and *Camarea triphylla* Mart. ex A.Juss. are listed by POWO (2024) as accepted but represent synonyms of *Camarea sericea* A.St.-Hil. and *Camarea axillaris* A.St.-Hil., respectively. Alternatively, *Camarea linearifolia* A.St.-Hil. is listed by POWO (2024) as a synonym of *Camarea ericoides* A.St.-Hil., but actually represents a distinct species. For an identification key for all species of *Camarea*, see Mamede (1990) and Almeida et al. (2020).

2.9.5. ***Cottsia*** **Dubard & Dop, Rev. Gén. Bot. 20: 359. 1908.**

= *Janusia* sect. *Metajanusia* Nied., Verz. Vorles. Königl. Lyceum Hosianum Braunsberg 1912–1913: 50. 1912 ≡ *Gaudichaudia* sect. *Erostratae* Chodat, Bull. Soc. Bot. Genève, sér. 2, 9: 100. 1917, nom. superfl. ≡ *Aspicarpa* sect. *Metajanusia* (Nied.) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 212. 1918. Type species: *Janusia gracilis* A.Gray [≡ *Cottsia gracilis* (A.Gray) W.R.Anderson & C.Davis].

Type species. *Cottsia scandens* Dubard & Dop [= *Cottsia californica* (Benth.) W.R.Anderson & C.Davis].

Notes. *Cottsia* comprises four currently accepted species (one threatened species; Suppl. material 1) of lianas endemic to the seasonally dry tropical forests of Mexico and the United States, North America (POWO 2024). For an identification key for all species of *Cottsia*, see Anderson and Davis (2007).

2.9.6. ***Diplopterys*** **A.Juss. in Deless., Icon. Sel. Pl. 3: 20, pl. 33. 1837.**

Figs 8S, 9O, 11A

= *Jubistylis* Rusby, Mem. New York Bot. Gard. 7: 273. 1927. Type species: *Jubistylis mollis* Rusby [= *Diplopterys lutea* (Ruiz ex Griseb.) W.R.Anderson & C.Davis].

Type species. *Diplopterys paralias* A.Juss. [=*Diplopterys pauciflora* (G. Mey.) Nied.]

Notes. *Diplopterys* comprises 31 currently accepted species (11 threatened species; Suppl. material 1) of shrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests from Mexico (North America) to Argentina (South America; POWO 2024). For an identification key for all species of *Diplopterys*, see Gates (1982).

2.9.7. ***Janusia*** **A.Juss. ex Endl., Arch. Mus. Par. 3: 608. 1843.**

= *Peregrina* W.R.Anderson, Syst. Bot. 10(3): 303. 1985, **syn. nov.** Type species: *Peregrina linearifolia* (A.St.-Hil.) W.R.Anderson [≡ *Janusia linearifolia* (A.St.-Hil.) A.Juss.].

Type species. *Janusia guaranitica* (A.St.-Hil.) A.Juss. ex Endl.

Notes. With the reestablishment of *Schwannia*, the recognition of *Peregrina* as independent of *Janusia* based only on the subshrub habit (vs liana) and laterally flattened stigmas (vs rounded stigmas) unnecessarily inflates the number of genera in Malpighiaceae without providing any taxonomic or systematic benefits. Since *Janusia* and *Peregrina* share non-enantioustilous flowers and androecia with five fertile stamens, without staminodes, we choose to return *Peregrina* to *Janusia*. In its current sense, *Janusia* comprises only two currently accepted species (one threatened species; Suppl. material 1) of subshrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Argentina, Bolivia, Brazil, Paraguay, and Uruguay, South America (POWO 2024). For an identification key for all species of *Janusia*, see Sebastiani (2010).

2.9.8. *Mamedea* R.F.Almeida & M.Pell., gen. nov.

urn:lsid:ipni.org:names:77342421-1
Fig. 4U

Type species. *Mamedea pulchella* (Griseb.) R.F.Almeida & M.Pell.

Diagnosis. *Mamedea* can be recognised by its erect shrub to subshrub habit, present xylopodium, leaves entire at base, umbels, 1–4-flowered, peduncle usually absent or reduced, not bearing reduced leaves, sepals bent inwards between the petals at anthesis, petals fimbriate, androecium with 3 fertile stamens, anthers glabrous to pubescent, staminodes 2, antherodes present or not, when present larger than the fertile anthers, glabrous to pubescent, usually red to orange at post-anthesis, 2 posterior carpels rotated so that all face the posterior petal, mericarps with dorsal and lateral wings reduced to ribs or teeth, and with a rugose nut, chromosome number n = (20–)40.

Description. ***Shrubs to subshrubs***. ***Roots*** fibrous, woody near the xylopodium. ***Xylopodium*** present, small to large. ***Branches*** erect, slender, woody to herbaceous, sometimes brittle, sericeous to glabrescent; internodes inconspicuous to elongated. ***Stipules*** interpetiolar, minute, free to connate, sericeous or distally glabrous, deciduous or persistent. ***Leaves*** opposite or decussate; petioles short, sericeous, tomentose, lanate or glabrescent, eglandular; lamina entire, elliptical, lanceolate to ovate, velutinous, sericeous, lanate or tomentose, base cuneate or rounded, margin entire, apex acute, obtuse, rounded or mucronate; venation eucamptodromous or brochidodromous, secondary veins strongly ascending and subparallel. ***Umbels*** solitary, axillary, (1–)2–4-flowered, sessile to pedunculate; inflorescence leaves not reduced; bract alternate, minute, plane, persistent, sericeous to glabrous, eglandular, persistent; cincinni (1–)2–4, alternate, 1-flowered, pedunculate; bracteoles opposite, minute, plane, persistent, sericeous to glabrous, eglandular, persistent. ***Flowers*** chasmogamous or cleistogamous, bisexual, zygomorphic, hypogynous; pedicel elongated, longer or shorter than the peduncle, sparsely sericeous, tomentose, velutinous or glabrescent; sepals 5, free valvate in bud, erect in bud, bent inwards between the petals at anthesis, triangular to broadly ovate, sericeous or tomentose, apex acute, the anterior eglandular and narrower, the lateral 4 biglandular, the glands green, yellowish-green, dark red, or reddish-purple, secreting oil, in fruit persistent, somewhat accrescent, enclosing nutlets until maturity; petals 5, imbricate in bud, yellow to orange-yellow at anthesis, glabrous or abaxially sparsely tomentose, limb plane, margin short-fimbriate, basal fimbriae mostly tipped with tiny glands, posterior petal with claw slightly thicker, sometimes with a pair of glands near the limb, limb slightly broader than the 4 lateral ones; androecium with 5 stamens, filaments free or connate at base with adjacent filaments, fertile stamens 3, opposite anterior and posterior-lateral sepals, heteromorphic, filaments stout, glabrous, anthers rimose, glabrous or locules tomentose at apex, connective glandular; staminodes 2, opposite anterior-lateral sepals, homomorphic, filaments slender, antherode equalling or larger than anthers (reduced to an apical swelling in *M. harleyi* and *M. lanata*), glandular, pubescent (glabrous in *M. harleyi*); ovary superior, 3-carpellate, carpels syncarpic, the posterior 2 rotated so that all face the posterior petal, minutely puberulent, style 1, basal, straight, glabrous, borne low on inner face of anterior carpel, stigma terminal, truncate, held above anthers or at the same level at anthesis. ***Schizocarp*** with 3 mericarps, dorsal and lateral wings reduced to ribs or teeth, glabrous to velutine; carpophore absent. ***Chromosome number*** n = (20–)40.

Etymology. The genus name honours the Brazilian botanist Dra Maria Candida Henrique Mamede (b. 1956), friend, colleague, and long-time contributor to the Brazilian Malpighiaceae.

Notes. *Mamedea* currently comprises seven accepted species (one threatened species; Suppl. material 1) of shrubs or subshrubs endemic to altitudinal grasslands, savannas, campos rupestres, and seasonally dry tropical forests of Argentina, Bolivia, Brazil, Paraguay, and Uruguay, South America. For partial identification keys, see Almeida et al. (2020) for Brazil and Aliscioni and Torretta (2018, under *Aspicarpa*) for Argentina.

2.9.8.a. *Mamedea boliviense* (Nied.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342422-1

≡ *Aspicarpa boliviensis* Nied., Meded. Rijks-Herb. 19: 72. 1913.

2.9.8.b. *Mamedea harleyi* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342423-1

≡ *Aspicarpa harleyi* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 55. 1987.

2.9.8.c. *Mamedea pulchella* (Griseb.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342424-1

≡ *Camarea pulchella* Griseb. in Martius, Fl. Bras. 12(1): 105. 1858.

2.9.8.d. *Mamedea lanata* (Chodat) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342425-1

≡ *Camarea lanata* Chodat, Mém. Soc. Phys. Genève 31(2): 20. 1892 ≡ *Aspicarpa schininii* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 59. 1987.

2.9.8.e. ***Mamedea salicifolia*** (Chodat.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342426-1

≡ *Camarea salicifolia* Chodat, Arch. Sci. Phys. Nat., sér. 3, 24: 500. 1890.

2.9.8.f. ***Mamedea sericea*** (Griseb.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342427-1

≡ *Aspicarpa sericea* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 68. 1879.

2.9.8.g. ***Mamedea uruguariensis*** (Nied.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342428-1

≡ *Aspicarpa uruguariensis* Nied., Verzeichnis Vorles. Konigl. Akad. Braunsberg 1912/13: 62. 1912.

2.9.9. ***Mionandra*** Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 101. 1874.

= *Brittonella* Rusby, Bull. Torrey Bot. Club 20: 429. 1893. Type species: *Brittonella pilosa* Rusby [= *Mionandra camareoides* Griseb.].
= *Cordobia* Nied., Verzeichnis Vorles. Konigl. Akad. Braunsberg 1912–13: 41. 1912. Type species: *Cordobia argentea* (Griseb.) Nied. [≡ *Mionandra argentea* Griseb.].
= *Gallardoa* Hicken, Physis (Buenos Aires) 2: 101. 1916. Type species: *Gallardoa fischeri* Hicken [≡ *Mionandra fischeri* (Hicken) R.F.Almeida]

Type species. *Mionandra camareoides* Griseb.

Notes. *Mionandra* comprises four currently accepted species (one threatened species; Suppl. material 1) of shrubs endemic to savannas and seasonally dry tropical forests of Argentina, Bolivia, and Paraguay, South America (Almeida et al. 2023b). For an identification key for all species of *Mionandra*, see Almeida et al. (2023b).

2.9.10. ***Peixotoa*** A.Juss., Fl. Bras. Merid. (quarto ed.) 3(22): 59. 1832 [1833].

Figs 3H, 8X, 9F, 11E

Type species. *Peixotoa glabra* A.Juss.

Notes. *Peixotoa* comprises 29 currently accepted species (18 threatened species; Suppl. material 1) of shrubs, subshrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Bolivia, Brazil, and Paraguay, South America (POWO 2024). For an identification key for all species of *Peixotoa*, see Anderson (1982, 2001b).

2.9.11. *Philgamia* Baill., Hist. Phys. Madagascar 35, tome 5 (Atlas 3): pl. 265. 1894.

Type species. *Philgamia hibbertioides* Baill.

Notes. *Philgamia* comprises four currently accepted species (all threatened species; Suppl. material 1) of shrubs endemic to grasslands and savannas of Madagascar, Africa (POWO 2024). For an identification key for all species of *Philgamia*, see Arènes (1943a).

2.9.12. *Schwannia* Endl., Gen. Plan.: 1058. 1840

Figs 3P, 8W, 9G, M

≡ *Fimbriaria* A.Juss., Fl. Bras. Merid. (quarto ed.) 3(22): 63. 1833, nom. illeg., non Stackh. (1809), nec Nees ex Steud. (1824).

Type species. *Fimbriaria elegans* A.Juss. [= *Schwannia mediterranea* (Vell.) R.F.Almeida & M.Pell.].

Notes. Despite being the oldest available name for this genus, *Fimbriaria* A. Juss. is illegitimate for being a later homonym to *Fimbriaria* Stackh. (Rhodomelaceae, Rhodophyta). This is unaffected by the posterior rejection of *Fimbriaria* Stackh. against *Odonthalia* Lyngbye. Furthermore, even if this rejection made "*Fimbriaria*" available as a generic name, *Fimbriaria* Nees ex Steud. (Aytoniaceae, Marchantiophyta) still has priority over the Malpighiaceae name. Therefore, *Schwannia* is the earliest available name for this genus.

Schwannia comprises 14 currently accepted species (seven threatened species; Suppl. material 1) of shrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests of Bolivia, Brazil, and Paraguay, South America (POWO 2024). For an identification key for all species of *Schwannia*, see Sebastiani (2010) and Sebastiani and Mamede (2014), both under *Janusia*.

2.9.12.a. *Schwannia christianeae* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342430-1

≡ *Janusia christianeae* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 80. 1987.

2.9.12.b. *Schwannia diminuta* (R.Sebast. & Mamede) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342431-1

≡ *Janusia diminuta* R.Sebast. & Mamede, Hoehnea 41(1): 121. 2014.

2.9.12.c. *Schwannia hexandra* (Vell.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names: 77342435-1

≡ *Banisteria hexandra* Vell., Fl. Flum.: 188. 1825.

2.9.12.d. *Schwannia mediterranea* (Vell.) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342436-1

≡ *Banisteria mediterranea* Vell., Fl. Flumin.: 191. 1829.

2.9.12.e. *Schwannia occhionii* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342438-1

≡ *Janusia occhionii* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 84. 1987.

2.9.12.f. *Schwannia paraensis* (R.Sebast. & Mamede) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names: 77342437-1

≡ *Janusia paraënsis* R.Sebast. & Mamede, Hoehnea 41(1): 123. 2014.

2.9.12.g. *Schwannia prancei* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342439-1

≡ *Janusia prancei* W.R.Anderson, Contr. Univ. Michigan Herb. 16: 87. 1987.

2.9.12.h. *Schwannia schwannioides* (W.R.Anderson) R.F.Almeida & M.Pell., comb. nov.

urn:lsid:ipni.org:names:77342440-1

≡ *Janusia schwannioides* W.R.Anderson, Contr. Univ. Michigan Herb. 15: 133–135, f. 14. 1982.

2.8.13. *Sphedamnocarpus* Planch. ex Benth. & Hook.f., Gen. Pl. 1: 256. 1862.

= *Tricomariopsis* Dubard, Compt. Rend. Hebd. Séances Acad. Sci. 145: 1190. 1907. Type species: *Tricomariopsis madagascariensis* Dubard (= *Sphedamnocarpus dubardii* R.Vig. & Humbert ex Arènes).
= *Banisterioides* Dubard & Dop, Rev. Gén. Bot. 20: 356. 1908. Type species: *Banisterioides madagascariensis* (Baker) Dubard & Dop (= *Sphedamnocarpus multiflorus* Nied.).

Type species. *Sphedamnocarpus angolensis* (A.Juss.) Oliv.

Notes. *Sphedamnocarpus* comprises ten currently accepted species (nine threatened species; Suppl. material 1) of shrubs or lianas endemic to savannas of Angola, Madagascar, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe, Africa (POWO 2024). For an identification key for all species of *Sphedamnocarpus*, see Arènes (1943b).

2.9.14. *Stigmaphyllon* A.Juss., Fl. Bras. Merid. 3: 48. 1833 [1832].

Figs 3C, N, 4A–C, E–G, I–N, 6D, E, 9N, P, Q

= *Brachypterys* A.Juss. in Deless., Icon. Sel. Pl. 3: 20. 1838. Type species: *Brachypterys australis* A.Juss. (= *Stigmaphyllon paralias* A.Juss.).
= *Ryssopterys* Blume ex A.Juss. in Deless., Icon. Sel. Pl. 3: 21. 1838. Type species: *Ryssopterys timoriensis* (DC.) Blume ex A.Juss. [≡ *Stigmaphyllon timoriense* (DC.) C.E.Anderson].

Type species. *Stigmaphyllon auriculatum* (Cav.) A.Juss.

Notes. *Stigmaphyllon* comprises 119 currently accepted species (60 threatened species; Suppl. material 1) of shrubs, subshrubs or lianas endemic to rainforests, savannas, and seasonally dry tropical forests of the Americas (from Mexico to Argentina), West Africa (Guinea, Guinea-Bissau, Liberia, Senegal, and Sierra Leone), Southeast Asia (Indonesia, Malaysia, Philippines, Timor-Leste), and Oceania (Australia, Papua New Guinea, Solomon Islands, Vanuatu, and New Caledonia; POWO 2024). For an identification key for all species of *Stigmaphyllon*, see Anderson (1997b, 2011) or Almeida et al. (2020) for Brazil.

Discussion

The phylogenetics of Malpighiaceae has been the subject of at least 17 different studies based on plastid and nuclear markers over the last two decades. Eight of these studies focused on the family as a whole, trying to sample its main morphological or phylogenetic groups (Cameron et al. 2001; Davis et al. 2001; Davis and Chase 2004; Davis and Anderson 2010; Davis et al. 2014; Willis et al. 2014; Cai et al. 2016; Almeida et al. 2023a, b, c; Do et al. 2024). Nine of these studies focused on phylogenetic clades (i.e., Tetrapteroid clade ≡ tribe Hiptageae) or specific genera (i.e., *Acridocarpus*, *Amorimia*, *Chlorohiptage*, *Hiptage*, *Lasiocarpus*, *Mionandra*, and *Stigmaphyllon*; Davis 2002; Almeida et al. 2018; 2023a, b, c; Tan et al. 2019; Almeida and van den Berg 2020, 2021, 2022; Cardona-Cruz et al. 2021; Do et al. 2024). All ten phylogenetic clades recognised by us here in the new classification system proposed for Malpighiaceae have consistently been recovered in almost all previous molecular phylogenetic studies (Cameron et al. 2001; Davis et al. 2001; Davis and Chase 2004; Davis and Anderson 2010; Davis et al. 2014; Willis et al. 2014; Almeida et al. 2023a, b, c; Do et al. 2024).

In fact, different lines of evidence, besides DNA, support our new classification system. Pollen grain morphology also recovered different pollen types in Malpighiaceae that characterise both subfamilies and most of the tribes recognized in our study (Lowrie 1982). Tribes Gaudichaudieae, Hiptageae, and Malpighieae were the only ones palynotaxonomically poorly characterised due to the incomplete taxonomic sampling for their currently accepted genera (Lowrie 1982). Secondary metabolites have also been recently evidenced as important characters supporting the classification system proposed here. Mannochio-Russo et al. (2022) studied over 300 samples of all phylogenetic clades of Malpighiaceae by GNPS + molecular networking methods, evidencing the presence of at least 78 different secondary metabolites produced by this family. The authors also evidenced that all subfamilies and tribes recognised here by us are supported by the presence/absence of one to twelve secondary metabolites.

Finally, the previously mentioned non-monophyly of *Rhynchophora* and *Madagasikaria* is a minor issue that will be easily solved by additional taxonomic and genomic sampling in future studies in the family. Additionally, the uncertain placement of *Ectopopterys* within tribe Malpighieae can only lead to its placement in another currently recognised tribe or to the proposition of a new tribe to accommodate this peculiar monospecific genus. Thus, the integrity and phylogenetic confidence of the new classification system proposed here for Malpighiaceae will remain strong, further advancing the taxonomic knowledge of this important family of flowering plants.

Conclusions

After over two decades of phylogenetic studies in Malpighiaceae and almost three centuries of taxonomic work, we finally have the proposition of the first classification system with a monophyletic recircumscription of all currently accepted genera and an updated species list for this family. A total of two subfamilies, 12 tribes, 72 genera, and 1,499 species are accepted in this study for Malpighiaceae worldwide as a solid basis for future systematic and taxonomic study in this family. Even though generic circumscriptions are now monophyletic and re-circumscribed, generic relationships within its most species-rich tribes (i.e., Gaudichaudieae, Hiptageae, Hiraeeae, and Malpighieae) still need further phylogenetic/omic studies for better statistical support and proposition of a subtribal system. Taxonomic revisions are urged for most genera of this family, especially the most species-rich ones [i.e., *Heteropterys* (166 spp.), *Byrsonima* (164), *Bunchosia* (93), *Hiraea* (81), *Tetrapterys* (56), *Mascagnia* (48), *Hiptage* (47), *Acridocarpus* (36), *Glicophyllum* (28), *Aspicarpa* (27), *Aspidopterys* (24), *Triaspis* (19), *Niedenzuella* (18), *Schwannia* (14), *Bronwenia* (13), *Spachea* (12), *Sphedamnocarpus* (10), *Psychopterys* (9), *Carolus* (8), *Mamedea* (7), *Jubelina* (6), *Christianella* (5), *Adelphia* (4), *Excentradenia* (4), *Malpighiodes* (4), *Ptilochaeta* (3), *Brachylophon* (2), *Calcicola* (2), *Caucanthus* (2), *Echinopterys* (2), *Heladena* (2), and *Janusia* (2)]. Finally, special attention is urgently needed to the taxonomy of the long-neglected and highly threatened African and Asian Malpighiaceae.

Acknowledgements

We would like to thank the staff of the visited herbaria for their support with herbarium specimens and images; Alexandre Sennikov, Jose Maria Cardiel and two anonymous reviewers for their constructive criticism on an earlier version of the manuscript; and Amaury Jr., A. Assis, A.C. Dal Col, A. Francener, A. Popovkin, C. Baez, C.C. Davis, C. Silva, E. Bidault, F. Farronay, F. Flores, F. Michelangeli, G. Cahyadi, G.A. Dettke, G. Shimizu, I. Specogna, Juvante's, K. Souza, L.S.B. Calazans, M.R. Pace, N. Bigio, N. Rakotonirina, N. Singh, N. Taniguti, O.J.A. Ayala, P. Acevedo-Rodriguez, R. Goldenberg, S. Carnaham, and S.E. Martins for allowing us to use their beautiful photographs and line drawings in our study.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

RFA was sponsored by Programa de Desenvolvimento Científico e Tecnológico Regional CNPq/FAPEG (grants #317720/2021-0 and #202110267000867) and UEG/PrP, Termo de Fomento do Recurso Pró-Programa UEG 2022 (grant #21/2022).

Author contributions

Conceptualization: RFA, MOOP. Data curation: ILM, TAS. Formal analysis: HAD, RFA, MOOP. Funding acquisition: ILM. Methodology: RFA, HAD, MOOP. Resources: ILM. Software: HAD. Validation: MOOP. Writing - original draft: RFA. Writing - review and editing: HAD, TAS, MOOP, ILM.

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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

Checklist of accepted species names of Malpighiaceae

Authors: Rafael F. de Almeida, Isa L. de Morais, Thais Alves-Silva, Higor Antonio-Domingues, Marco O. O. Pellegrini

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.242.117469.suppl1

Supplementary material 2

Morphological matrix including 31 scored and coded characters used in the phylogenetic optimization

Authors: Rafael F. de Almeida, Isa L. de Morais, Thais Alves-Silva, Higor Antonio-Domingues, Marco O. O. Pellegrini

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.242.117469.suppl2

PhytoKeys 242: 139–160 (2024)
DOI: 10.3897/phytokeys.242.122458

Research Article

Five new species in the genus *Staurosirella* (Bacillariophyta) from European freshwater habitats

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Abstract

Several populations belonging to the genus *Staurosirella* have been observed in European rivers that were previously identified as *Staurosirella pinnata*. In light of the recent taxonomic revisions of the genus *Staurosirella*, the morphology of the unknown *Staurosirella* populations has been critically investigated using light and scanning electron microscopy. Following the comparison with previously described *Staurosirella* species, five taxa could not be identified using the currently available literature on the genus. These five taxa are described as new based on differences in valve outline; shape, size and structure of the apical pore fields; structure of the striae; and the presence, position and structure of the marginal spines. Two new species were described using historic collection material: *Staurosirella binodiformis* **sp. nov.** and *Svanheurckiana* **sp. nov.** Two new species were observed in samples from rivers in Flanders: *S. marginostriata* **sp. nov.** and *S. stoksiana* **sp. nov.** whereas a fifth species was observed in rivers from Iceland: *S. jonssoniana* **sp. nov.** All new species are compared with similar *Staurosirella* species worldwide. Notes are added on their ecological preferences derived from both physicochemical data and the associated diatom flora.

Key words: Europe, morphology, new species, *Staurosirella*, taxonomy

OPEN ACCESS

Academic editor: Bing Liu
Received: 6 March 2024
Accepted: 11 April 2024
Published: 31 May 2024

Citation: Van de Vijver B, Peeters V, Hansen I, Ballings P, de Haan M (2024) Five new species in the genus *Staurosirella* (Bacillariophyta) from European freshwater habitats. PhytoKeys 242: 139–160. https://doi.org/10.3897/phytokeys.242.122458

Introduction

The genus *Staurosirella* D.M.Williams & Round was split in 1988 from the genus *Fragilaria* Lyngbye sensu lato (Williams and Round 1988) and is characterised by both isopolar or heteropolar valves with broad uniseriate striae composed of slit-like, linear, internally occluded areolae separated by narrow vimines. The original 1988 description was refined in 2006 (Morales and Manoylov 2006a). Since its erection, more than 50 *Staurosirella* species were either described as new species or transferred to it from other genera such as *Fragilaria*, *Odontidium* Kützing, *Staurosira* Ehrenberg or *Opephora* P.Petit (e.g. Morales and Manoylov 2006b; Van de Vijver et al. 2014; Almeida et al. 2015; Seeligmann et al. 2018; Guerrero et al. 2019; Morales et al. 2019, Osório et al. 2021; Van de Vijver 2022, 2023, Van de Vijver et al. 2022).

In the past 10 years, the number of *Staurosirella* species strongly increased, most likely due to a better understanding of several catch-all species such as *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round. An internet search for the name '*Staurosirella pinnata*' resulted in more than 12.000 hits with an extra 38.700 for the name '*Fragilaria pinnata*'. For comparison, the name '*Staurosirella neopinnata* E.Morales et al.' only resulted in 907 hits. Moreover, the name '*Staurosirella* (*Fragilaria*) *pinnata*' was reported worldwide from the tropics to the poles with more than 80 records from Asia, Africa, Antarctica, Australia, North, Central and South America, and Europe [see AlgaeBase] (Guiry and Guiry 2023). It is clear that this worldwide distribution is the result of taxonomic drift on one side (severely broadening the original description of the species) and force-fitting (Tyler 1996) populations from all over the world into *S. pinnata*. Most of the confusion was linked to a lack of knowledge of the type material of *S. pinnata* as can be seen in Krammer and Lange-Bertalot (1991, plate 133) that shows the complex of species related to *Fragilaria pinnata* and *F. leptostauron*. The former proved to belong to the genus *Denticula* (Morales et al. 2013) resulting in the description of a new species, *S. neopinnata* to accommodate some of the populations, formerly identified as *S. pinnata*. Since our knowledge of the morphology and taxonomic identity of this seemingly widespread species improved significantly, a lot of species, previously included within *S. pinnata*, have been described, several of them from Europe, such as *Staurosirella coutelasiana* Van de Vijver, *S. minutissima* Van de Vijver, *S. eruciformis* Van de Vijver and *S. lucectoriana* Beauger, C.E.Wetzel & Van de Vijver (Van de Vijver 2022, 2023; Beauger et al. 2023).

During a survey of *Staurosirella* populations in European rivers in the framework of a routine water quality biomonitoring exercise, a large number of unknown taxa has been recorded that formerly were identified as *S. pinnata* s.l. Detailed morphological analysis of the different populations indicated several morphological differences with the type population of *S. neopinnata* (as the species should be called since 2019). Comparison with all available (recent) literature, exposed that several of these populations showed sufficient morphological differences to justify their description as new species despite a growing number of described *Staurosirella* species from all continents (see Material and Methods for a complete overview of all used literature). The present contribution describes five new species based on detailed light (LM) and scanning electron (SEM) microscopy and comparisons with all known taxa worldwide: *Staurosirella binodiformis* Van de Vijver, sp. nov., *S. marginostriata* Van de Vijver & V.Peeters, sp. nov., *S. stoksiana* Van de Vijver, sp. nov., *S. jonssoniana* Van de Vijver & Iris Hansen, sp. nov., and *S. vanheurckiana* Van de Vijver, Ballings & M.de Haan, sp. nov. Information on their ecological preferences is derived from the associated diatom flora and, when available, measured physico-chemical parameters.

Material and methods

In the present paper, a mixture of historic (herbarium) materials and recently collected samples have been investigated to detail the morphological features of the new *Staurosirella* species. The following samples have been used in this investigation:

- Sample APM21-91, Bosbeek (Maaseik, Province of Limburg, Belgium), leg. Vlaamse Milieu maatschappij (VMM), 51°5.6348'N, 5°45.894'E, coll. date 25 Jun. 2021.
- Sample Foged 29/1954, outflow from a small lake near Þingvellir, Iceland, coll. date 15 Jul. 1954, leg. Niels Foged (original material kept in C!)
- Sample 81a, Voorste Nete (Dessel, Province of Antwerp, Belgium), 51°13.9482'N, 5°7.4497'E, coll. date 06 Jul. 1994, leg. B. Van de Vijver.
- Sampling site at Græntorfa, Grenlækur, southern, Iceland, 63°43.955'N, 17° 58.067'W, coll. date 03 Jul. 2017, leg. Iris Hansen.
- Types du Synopsis sample 315, Leuven, Belgium, Van Heurck exsiccata set, leg. (probably) Père Gautier

A sub-sample of each of the selected materials was prepared for LM and SEM observations following the method described in van der Werff (1955). Small parts of the sub-samples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about 1 h, after which the reaction was completed by addition of saturated $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700× rpm), the resulting cleaned diatom material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slide and mounted on permanent slide using Naphrax (refraction index 1.73). The resulting slides were analysed using an Olympus BX53 microscope at 1000× magnification (UPlan FL N 100× oil objective, N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System, connected to the Cell Sense Standard program. For each taxon, the number of specimens, measured at random on the type slide, is indicated (n=X). For each species, at least 15, but often many more, valves are illustrated using LM to determine its morphological variability. An ecological characterisation of the new species is added based on the accompanying diatom flora, assessed by counting at least 100 diatom valves along random transects. Relative abundances, when given, are expressed as percentage of counted valves.

For SEM, part of the suspension was filtered through 5-μm Isopore™ polycarbonate membrane filters (Merck Millipore), pieces of which were fixed on aluminum stubs after air–drying and coated with a platinum layer of 20 nm, and studied using a JEOL-JSM-7100F field emission scanning electron microscope at 2 kV. Slides, samples and stubs are stored at the BR-collection (Meise Botanic Garden, Belgium). Plates were prepared using Photoshop CS5.

Terminology used in the description of the various structures of the siliceous cell wall is based on Ross et al. (1979, areola structure), Cox and Ross (1981, stria structure), Morales (2005, girdle structure), Williams and Round (1988, *Staurosirella* genus features) and Morales and Manoylov (2006a,b, *Staurosirella* genus features). For taxonomic comparisons, the following papers were consulted: Lange-Bertalot (1993), Morales (2005), Morales and Manoylov (2006a, 2006b), Morales et al. (2010a, 2010b, 2015, 2019), Almeida et al. (2015), Guerrero et al. (2019), Osório et al. (2021), Seeligmann et al. (2018), Van de Vijver et al. (2014), Van de Vijver (2022, 2023), and Beauger et al. (2023).

For typification of the species, we chose to use the entire slide as the type, following article 8.2 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). Diatoms show a broad variability along their cell cycle making the choice for the entire population on the slide more obvious, but because of admixtures, one valve was indicated to best illustrate the taxon (see Figures). All novelties are registered proactively according to Art. 42.3 (Turland et al. 2018).

Results

Staurosirella marginostriata **Van de Vijver & V.Peeters, sp. nov.**
Fig. 1

Holotype. BR-4840 (Meise Botanic Garden, Belgium). Fig. 1C represents the holotype.

Isotype. Slide 442 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104533.

Type locality. Bosbeek (Maaseik, Province of Limburg, Belgium), sample APM21-91, 51°5.6348'N, 5°45.894'E, coll. date 25 Jun. 2021, leg. Vlaamse Milieu maatschappij (VMM).

Description. ***LM*** (Fig. 1A–R). Frustules in girdle view rectangular, singular. Chains linking several cells in colonies so far not observed. Valves isopolar, strictly lanceolate with convex margins and weakly protracted, rostrate apices. Smaller valves more rhombic-lanceolate with cuneate apices (Fig. 1R). Valve dimensions (n=20): length 10–20 µm, width 3.0–4.5 µm. Sternum broad, lanceolate, ghost striae present. Striae short, marginal, 14–15 in 10 µm. Areolae not discernible in LM. ***SEM*** (Fig. 1S–X). Valve face surface undulating with distinctly raised virgae extending almost up to the valve middle (Fig. 1T), occasionally almost flat (Fig. 1V). Virgae much broader that the striae. Striae very short, marginal, extending without interruption from the valve face onto the mantle (Fig. 1S–U, W). Large hyaline zone present at the abvalvar mantle edge (Fig. 1S–U), terminating at mantle edge by series of irregularly shaped mantle plaques (Fig. 1S–U). Striae uniseriate, composed of short, slit-like, linear areolae, running parallel to the apical axis (Fig. 1S–W). Vimines narrow, not raised. Marginal spines located on the virgae, irregular in number (1–3), shape and size (Fig. 1S–W). Large apical pore fields present at both apices, usually similar in size and shape (Fig. 1S, T, V), located at the valve face/mantle junction, extending more onto the valve mantle, isolated from neighboring striae. Pore fields composed of usually 4–5 rows of small, rimmed pores (Fig. 1W). Girdle composed of several probably open, plain copulae (Fig. 1S–U). Internally, striae distinctly sunken between the raised virgae and the sternum (Fig. 1X).

Etymology. The specific epithet *marginostriata* refers to the short, marginal striae.

Distribution. At present, only observed in Flanders (type locality) and the Morvan region in France. Confusion with the in LM similarly looking *Pseudostaurosira brevistriata* (Grunow) D.M.Williams & Round), may be at the base of the unclear distribution.

Ecology and associated diatom flora. The type locality has an almost circumneutral pH (6.9–7.3), moderate conductivity (160–200 µS/cm), higher nitrate levels (1.4–3.3 mg/l) and sulphate levels (12–30 mg/l). The sample is dominated by *Staurosirella stoksiana* Van de Vijver sp. nov. (15% of all counted valves), *Aulacoseira ambigua* (Grunow) Simonsen (12.5%), *Pseudostaurosira brevistriata* (9.5%), *A. granulata* (Grunow) Simonsen (9%), *Navicula cryptocephala* Kützing (5%), and *N. lanceolata* (C.Agardh) Ehrenberg (4%), pointing to more meso-eutrophic, alkaline conditions (Lange-Bertalot et al. 2017).

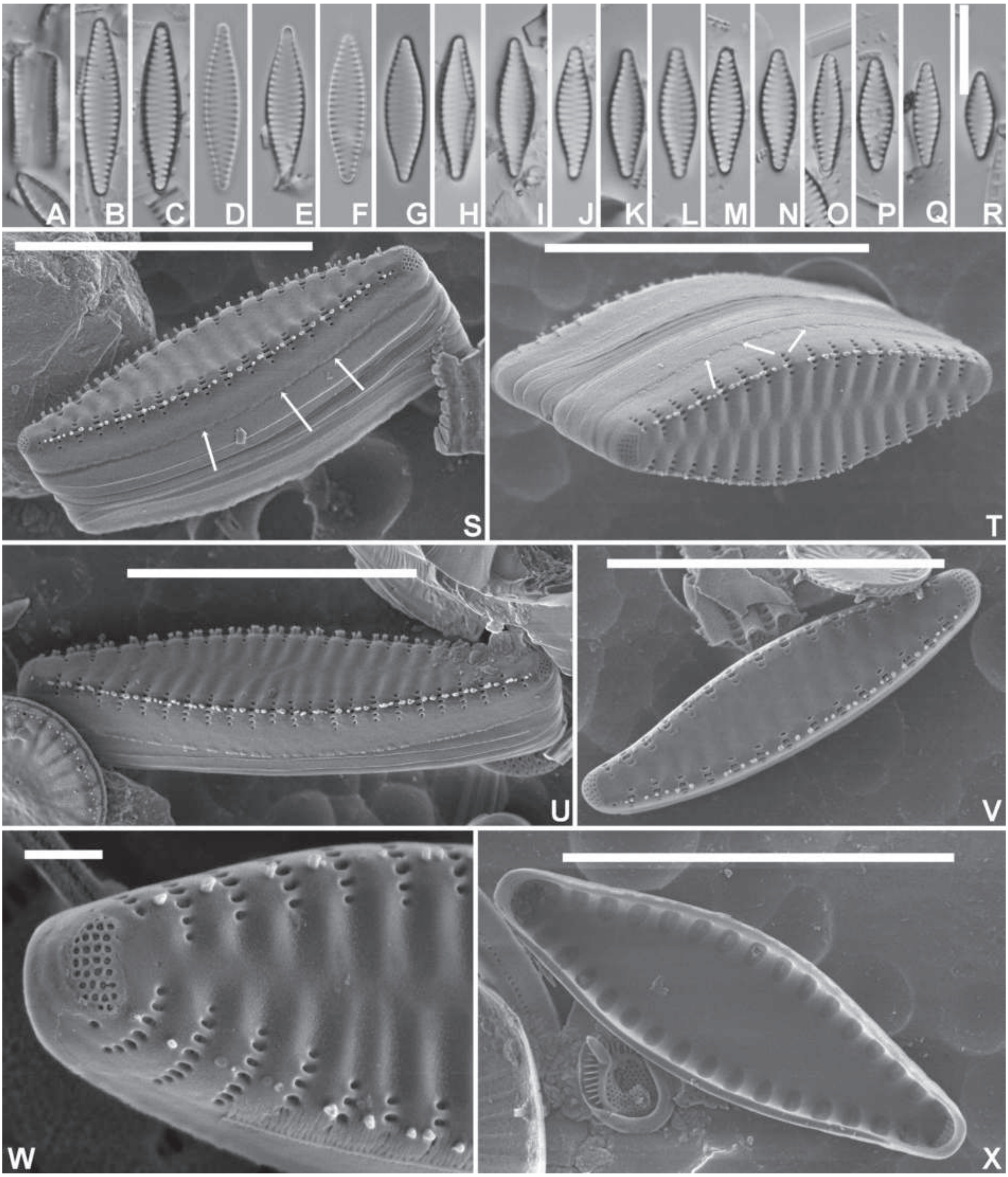

Figure 1. *Staurosirella marginostriata* Van de Vijver & V.Peeters, sp. nov., LM and SEM micrographs taken from the holotype material (BR-4840, Bosbeek, Maaseik, Belgium) **A** LM picture of a frustule in girdle view **B**–**R** LM pictures of valves in valve face view in decreasing length **S** SEM external view of a complete valve in oblique view showing the girdle structure and the mantle **T** SEM external view of a complete frustule with focus on the apical pore field and the transition between valve face and mantle **U** SEM external view of a complete valve. Note the undulating valve face surface and the small mantle plaques (see arrows) **V** SEM external view of a complete smaller valve with flattened valve face surface. The arrows indicate mantle plaques **W** SEM external detail of a valve apex showing the large apical pore field **X** SEM internal view of a complete valve. Scale bars: 10 μm (**A–V, X**); 1 μm (**W**).

Staurosirella binodiformis **Van de Vijver, sp. nov.**

Fig. 2

Holotype. BR-4841 (Meise Botanic Garden, Belgium). Fig. 2E represents the holotype.

Isotype. Slide 443 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104534.

Type locality. outflow from a small lake near Þingvellir, Iceland, sample 29, coll. date 15 Jul. 1954, leg. Niels Foged.

Description. ***LM*** (Fig. 2A–AP). Valves isopolar, linear, slightly constricted near the valve center in longer specimens (Fig. 2A–G), becoming linear, linear-lanceolate to even almost elliptical in smallest specimens (Fig. 2AM–AP). Apices in longer specimens protracted, rostrate to subcapitate, to not protracted, broadly rounded in smaller valves. Valve dimensions (n=50): length 6–21 µm, width 3.0–3.5 µm. Sternum narrow, linear. Striae almost parallel weakly radiate in the valve center, becoming more radiate towards the apices, long, almost reaching the sternum, 14–15 in 10 µm. Areolae not discernible in LM. ***SEM*** (Fig. 2AQ–AV). Valve face surface weakly undulating with raised virgae extending almost up to the valve middle (Fig. 2AR–AT). Virgae almost double as broad as the striae. Striae long, extending without interruption from the valve face onto the mantle (Fig. 2AQ). Very large hyaline zone present at the abvalvar mantle edge (Fig. 2AQ). Mantle plaques absent (Fig. 2AQ). Striae uniseriate, composed of slit-like, linear areolae, running parallel to the apical axis (Fig. 2AQ–AU). Areolae diminishing in size towards the sternum (Fig. 2AT), becoming almost rounded at the sternum. Mantle striae often very short, reduced to only one areola (Fig. 2AU), occasionally also longer (Fig. 2AS). Vimines very narrow, not raised. Irregular but dense series of short, marginal spines located on the virgae, usually bordering immediately the striae (Fig. 2AR–AS). Spines occasionally bifurcated (Fig. 2AQ, AS). Apical pore fields present at both apices, usually similar in size and shape (Fig. 2AR–AT), located at the valve face/mantle junction, extending more onto the valve mantle, isolated from neighbouring striae. Pore fields composed of usually 2–3 rows of small, rimmed pores (Fig. 2AU). Girdle composed of several open, plain copulae (Fig. 2AQ). Internally, striae distinctly sunken between the raised virgae and the sternum (Fig. 2AV).

Etymology. The specific epithet *binodiformis* refers to the outline resemblance with *Staurosira binodis* Ehrenberg.

Distribution. At present, only observed in Iceland on the type locality, probably due to confusion with *Staurosira binodis* and *Staurosirella oldenburgiana* (Hustedt) E.Morales.

Ecology and associated diatom flora. Niels Foged (1906–1988) collected the sample in 1954 from stones covered with moss and green algae in the outflow from a small lake near Þingvellir on the road between Reykjavik and Þingvellir, north of Mosfellsheidi (Iceland). The sample is dominated by a large number of small-celled araphid taxa belonging to the genera *Staurosira*, *Staurosirella* and *Pseudostaurosira* D.M.Williams & Round. As most of these taxa most likely belong to currently undescribed species, it is hard to derive the ecology from them. Several raphid taxa were observed, but in much lower frequencies such as *Placoneis explanata* (Hustedt) Mayama, *Planothidium joursacence* (Héribaud) Lange-Bertalot, *Skabitschewskia peragallii* (Brun & Héribaud) Kulikovskiy &

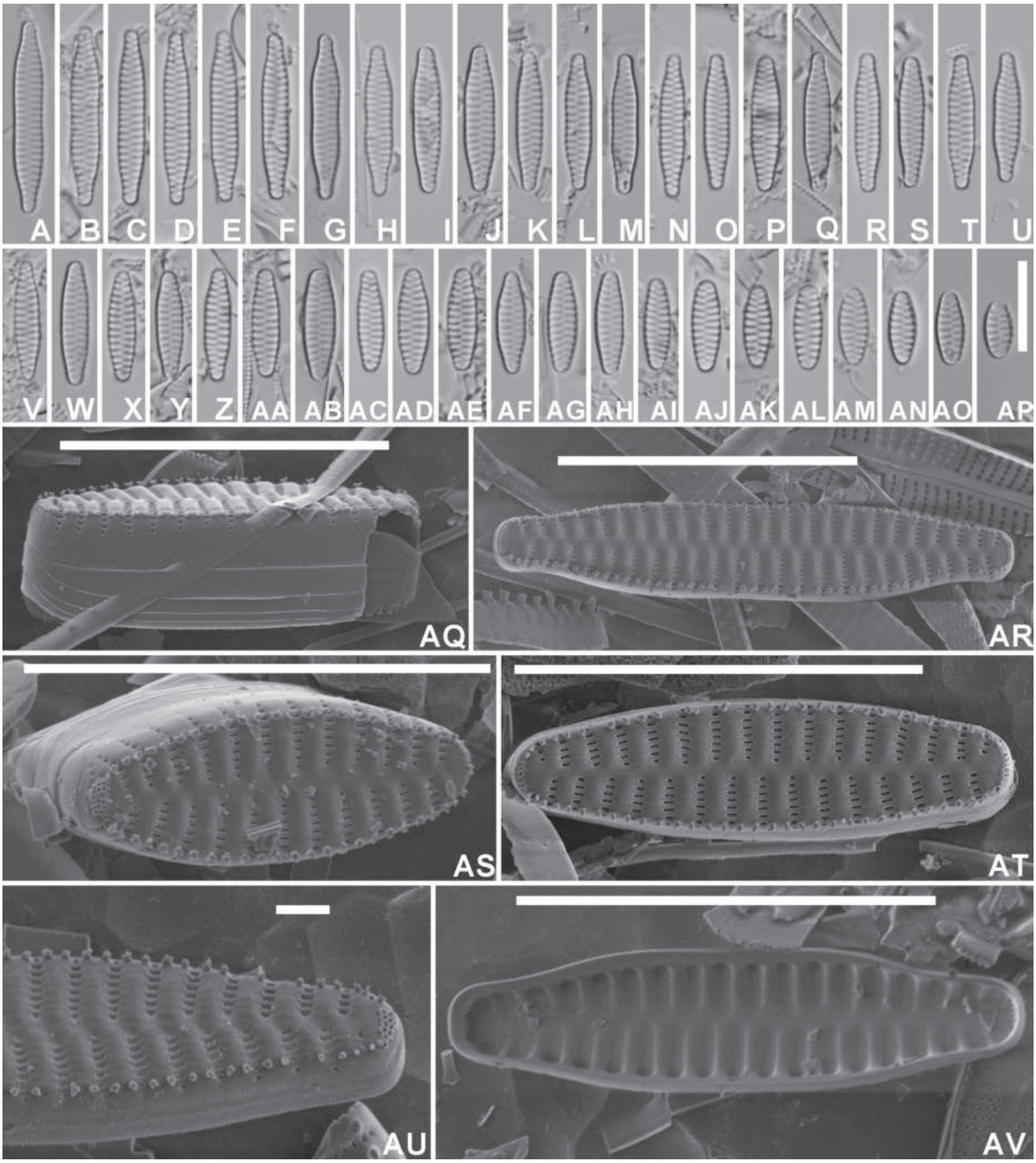

Figure 2. *Staurosirella binodiformis* Van de Vijver, sp. nov., LM and SEM micrographs taken from the holotype material (BR-4841, Foged sample 29) **A**–**AP** LM pictures of valves in valve face view in decreasing length **AQ** SEM external view of a complete valve in girdle view showing the girdle structure and the mantle **AR** SEM external view of a complete valve. Note the slight constriction at the valve middle, the undulating valve face surface and the series of spines **AS** SEM external view of a complete valve with focus on the apical pore field and the transition between valve face and mantle **AT** SEM external view of a complete valve **AU** SEM external detail of a valve apex showing the large apical pore field **AV** SEM internal view of a complete valve. Scale bars: 10 µm (**A–AS, AV**); 1 µm (**AU**).

Lange-Bertalot, *Cavinula jaernefeltii* (Hustedt) D.G.Mann & Stickle, and *C. pusio* (Cleve) Lange-Bertalot. Most likely, the diatom flora points to oligo- to mesotrophic, colder, pioneer conditions (Lange-Bertalot et al. 2017).

Staurosirella stoksiana **Van de Vijver, sp. nov.**

Figs 3, 4

Holotype. BR-4842 (Meise Botanic Garden, Belgium). Fig. 3H represents the holotype.

Isotype. Slide 444 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104535.

Type locality. Voorste Nete (Dessel, Province of Antwerp, Belgium), sample 81a, 51°13.9482'N, 5°7.4497'E, coll. date 06 Jul. 1994, leg. B. Van de Vijver.

Additional investigated population. Bosbeek (Maaseik, Province of Limburg, Belgium), sample APM21-91, 51°5.6348'N, 5°45.894'E, coll. date 25 Jun. 2021, leg. Vlaamse Milieu maatschappij (VMM).

Description. ***LM*** (Figs 3A–AD, 4A–P). Frustules rectangular, solitary. Chain-like colonies so far not observed. Valves weakly heteropolar, lanceolate to elliptic-lanceolate with convex margins, gradually narrowing towards the non-protracted, broadly rounded apices. Larger valves occasionally slightly ovoid (Fig. 3C) in outline with smallest valves almost elliptical (Fig. 3AD). Valve dimensions (n=40): length 6–21 μm, width 4.5–5.5 μm. Sternum narrow, linear. Striae alternating, almost parallel becoming very slightly radiate towards the apices, long, almost reaching the sternum, 8–9 in 10 μm. Areolae not discernible in LM. ***SEM*** (Figs 3AE–AK, 4Q–V). External valve face undulating with slightly raised, flattened virgae and striae sunken in 'punch hole-like' depressions (Figs 3AE, 4Q). Striae extending without interruption from valve face onto the mantle, gradually but distinctly narrowing at both ends (Figs 3AE, AI, 4S) giving the striae a lanceolate appearance. Abvalvar mantle edge forming a broad hyaline zone, almost half the entire mantle width (Figs 3AE, 4Q). Mantle plaques absent. Striae uniseriate, composed of long, slit-like, linear areolae, running parallel to the apical axis (Figs 3AE, AG, AJ, AK, 4R, S, U, V). Vimines very thin, not raised. Marginal spines usually present, one to two, located on the virgae, rudimentary, irregularly shaped (blunt, thick, papilla-like). Occasionally mixed populations with spineless and spine valves observed (Fig. 4R, S, U, V). Apical pore fields present at both apices. At the footpole, pore field rather large, composed of at least 7 long rows of very small, rounded pores, covering the entire foot pole (Figs 3AG, 4U–V). Pore field at the headpole smaller, located on the weakly depressed headpole (Fig. 3AG, AJ, AK).Valvocopula broad, with short but well developed fimbriae (Fig. 3AF). Internally, striae distinctly sunken between the flat, doubly flared virgae and sternum (Figs 3AH, 4T). Areolae occluded by irregularly shaped volae, extending from the longer inner side of each vimen (Fig. 3AH).

Etymology. The new species honours Prof. dr Robby Stoks (Catholic University of Leuven) study friend of the first author, in recognition of his important contributions to the Odonata research.

Distribution. *Staurosirella stoksiana* has been regularly observed in samples from Flanders (Belgium) and the United Kingdom. Most likely the new species has a broader distribution area but due to confusion with the presumably widespread *Staurosirella* (*neo*)*pinnata* and other similar species such as *Staurosirella ovata* and *S. coutelasiana*, its exact distribution is not clear. Peeters and Ector (2017, p. 262–263) illustrated several populations from Burgundy (eastern France) under the name *Staurosirella ovata*, that shows a very large similarity to *S. stoksiana*.

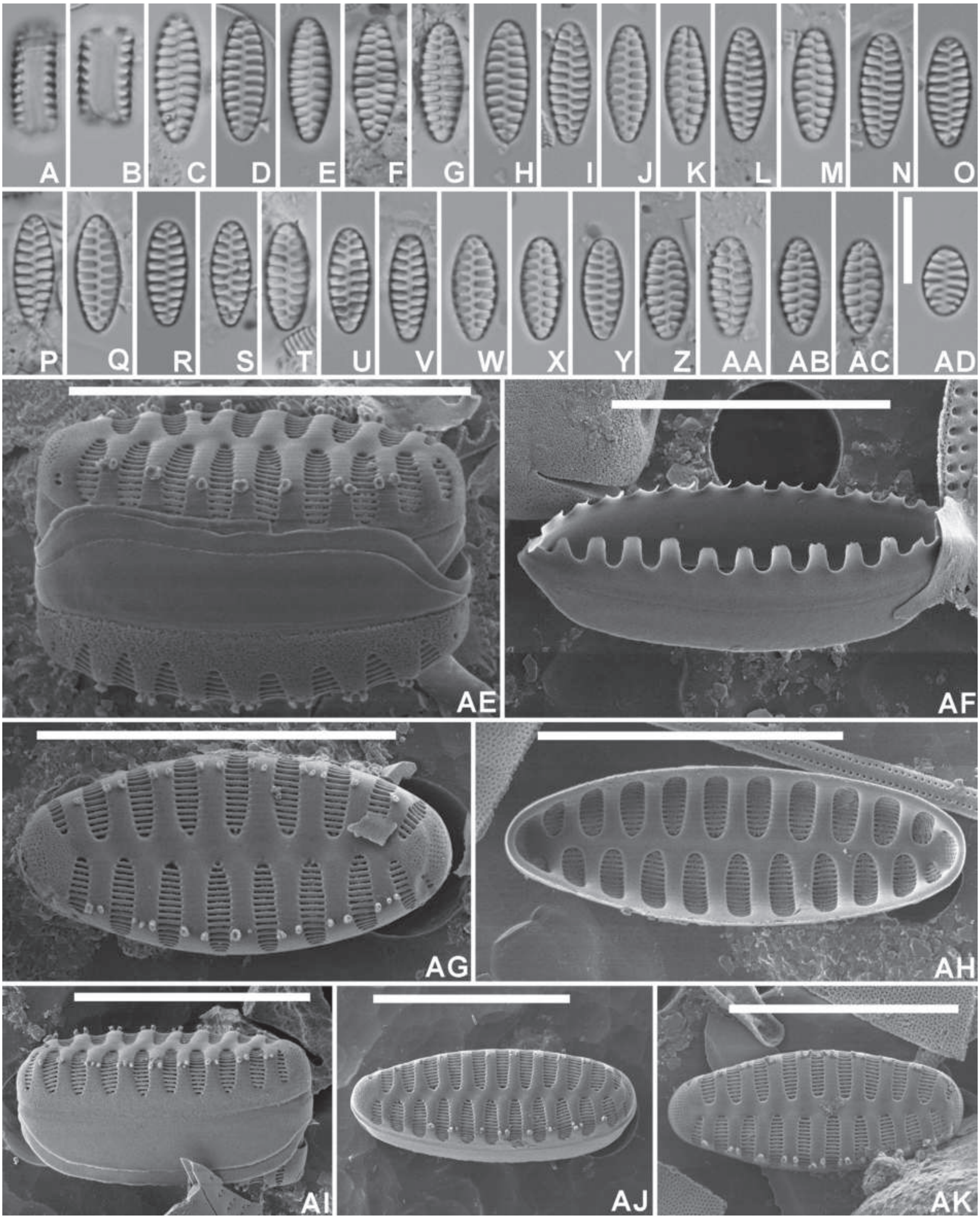

Figure 3. *Staurosirella stoksiana* Van de Vijver, sp. nov., LM and SEM micrographs taken from the holotype material (BR-4842, Voorste Nete, Dessel, Belgium) **A, B** LM pictures of a frustule in girdle view **C**–**AD** LM pictures of valves in valve face view in decreasing length **AE** SEM external view of a complete frustule in girdle view showing the girdle structure and the mantle **AF** Complete view of the valvocopula with the large fimbriae **AG** SEM external view of a complete valve with focus on the apical pore field and the depressed headpole **AH** SEM internal view of a complete valve **AI** SEM external view of a complete valve in girdle view **AJ–AK** Two SEM externals view of a complete, heteropolar valve. Scale bars: 10 µm.

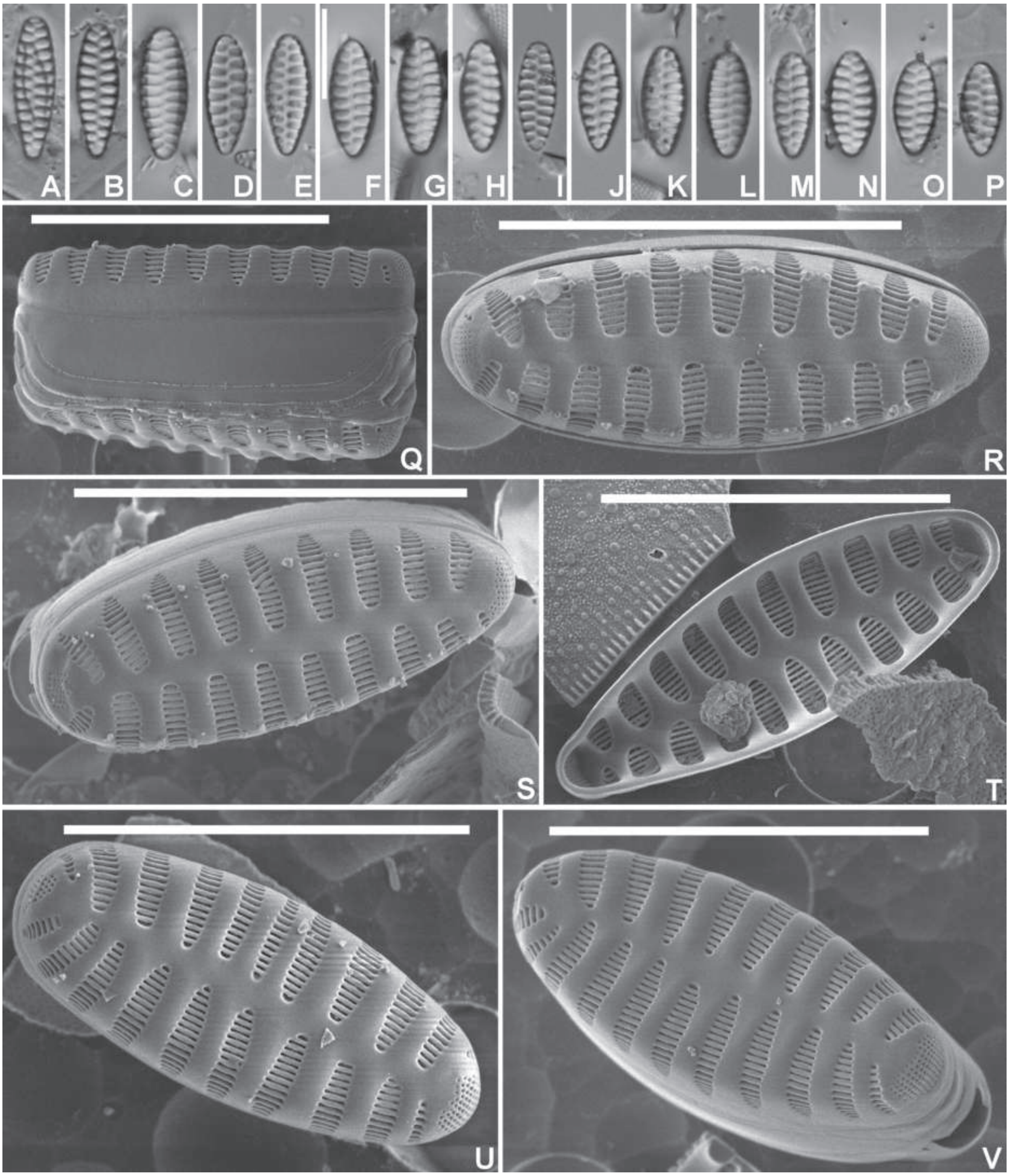

Figure 4. *Staurosirella stoksiana* Van de Vijver, sp. nov., LM and SEM micrographs taken from an additional population (BR-4840, Bosbeek, Maaseik, Belgium) **A–P** LM pictures of valves in valve face view in decreasing length **Q** SEM external view of a complete frustule in girdle view showing the girdle structure and the mantle **R, S** SEM external view of two complete valves with focus on the apical pore field and the depressed headpole. Both valves bear a series of marginal spines **T** SEM internal view of a complete valve **U, V** Two SEM externals view of a complete, heteropolar valve lacking marginal spines. Scale bars: 10 µm.

Ecology and associated diatom flora. The type population of *S. stoksiana* was observed in a small lowland river in the Netebekken (Flanders, Belgium). The sample was dominated, apart from *S. stoksiana* (16% of all counted valves) by *Nitzschia adamata* Hustedt (8.7%), *Geissleria decussis* (Østrup) Lange-Bertalot & Metzeltin (6.4%), *Navicula gregaria* Donkin (6%), *Craticula molestiformis* (Hustedt) Mayama (5.1%), *Melosira varians* C.Agardh (3.4%), *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot (3.2%), and *Cyclotella meneghiniana* Kützing (3.2%). According to the ecological preferences of the observed diatom flora, this indicates meso- to eutrophic, alkaline conditions with medium conductivities (Lange-Bertalot et al. 2017).

Staurosirella jonssoniana **Van de Vijver & Iris Hansen, sp. nov.**

Fig. 5

Holotype. BR-4843 (Meise Botanic Garden, Belgium). Fig. 5H represents the holotype.

Isotype. Slide 445 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104536.

Type locality. Grenlækur, southern Iceland, sampling site at Græntorfa, 63°43.96'N, 17° 58.07'W, coll. date 03 Jul. 2017, leg. Iris Hansen.

Description. ***LM*** (Fig. 5A–U). Valves isopolar to weakly heteropolar, lanceolate with convex margins, and narrowly protracted, rostrate apices. Smallest valves almost elliptical (Fig. 5T–U). Valve dimensions (n=25): length 6–15 µm, width 3.0–3.5 µm. Sternum narrow, linear. Striae alternating, almost parallel to very slightly radiate in the middle, more strongly radiate towards the apices, 12–13 in 10 µm. Areolae not discernible in LM. ***SEM*** (Fig. 5V–Y). External valve face weakly undulating with slightly raised virgae and striae sunken in 'punch hole-like' depressions (Fig. 5V–X). Striae extending without interruption from valve face onto the mantle (Fig. 5X), gradually narrowing towards the sternum (Fig. 5V–X) giving the striae a lanceolate appearance. Striae uniseriate, composed of long, slit-like, linear areolae, running parallel to the apical axis (Fig. 5V–X). Vimines very thin, not raised. Marginal spines very obvious, one per virga, each located in a shallow, pit-like depression (Fig. 5V–X). Apical pore fields absent, replaced by one or two spines. Internally, striae distinctly sunken between the flat, doubly flared virgae and sternum (Fig. 5Y). Areolae occluded by irregularly shaped volae, extending from the longer inner side of each vimen (Fig. 5Y).

Etymology. The new species honours our friend and colleague Gunnar Steinn Jónsson (Reykjavik, Iceland) in recognition of his important contributions to the diatom research in Iceland.

Distribution. *Staurosirella jonssoniana* has so far only been found in Iceland.

Ecology and associated diatom flora. The type locality, Grenlækur, is a small spring-fed stream in southern Iceland. The stream has a slightly alkaline pH (7.8), a rather low conductivity (156 µS/cm), low nitrate (0.02 mg/l) and phosphate (0.97 mg/l), and moderate sulphate (37.8 mg/l) levels. The diatom flora in the sample is quite diverse and dominated by a large number of species with *Staurosirella jonssoniana* only being relatively rare in the sample. The dominant species include *Fragilaria landnama* Van de Vijver & Iris Hansen, *F. sandellii* Van de Vijver & Jarlman, *Staurosira* cf. *sviridae* Kulikovskiy et al., *Planothidium lanceolatum* (Brébisson) Lange-Bertalot, different *Cocconeis* species (mainly *C. euglypta* Ehrenberg), *Surirella brebissonii* Krammer & Lange-Bertalot,

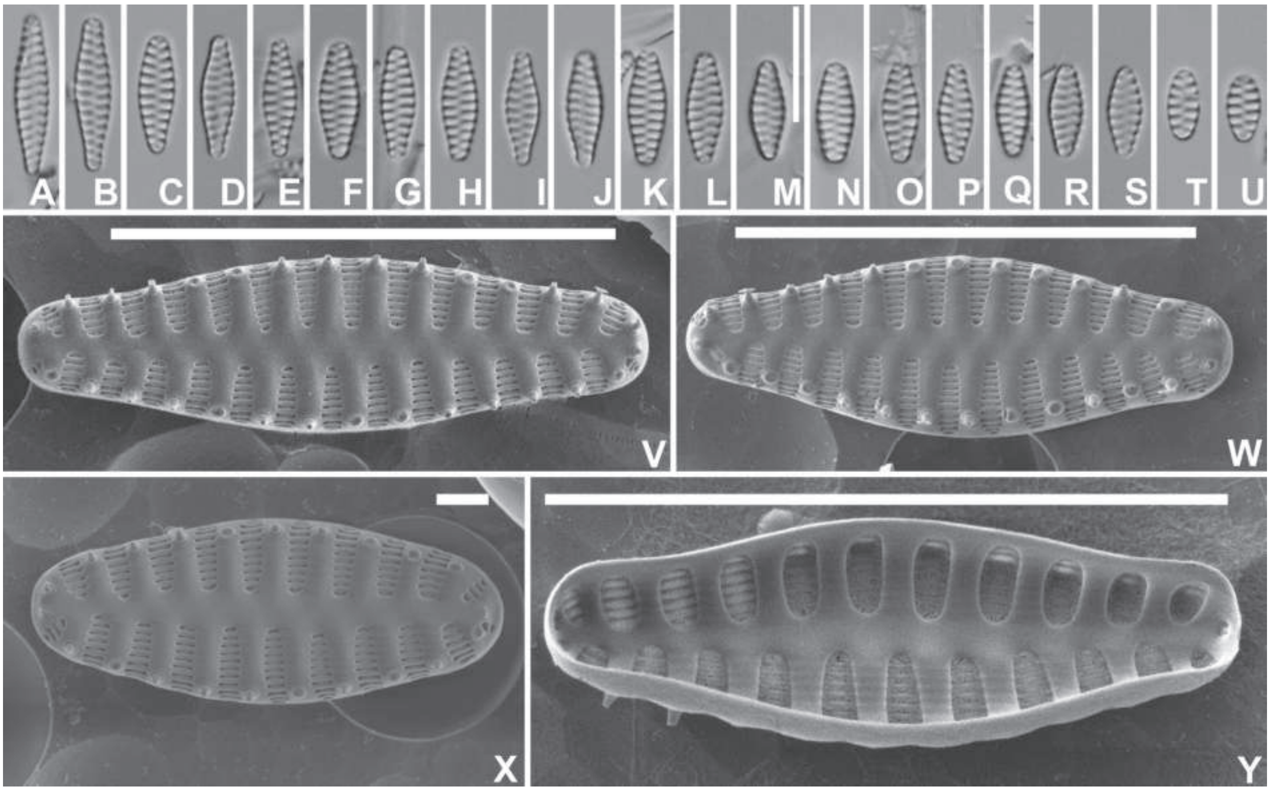

Figure 5. *Staurosirella jonssoniana* Van de Vijver & Iris Hansen, sp. nov., LM and SEM micrographs taken from the holotype material (BR-4843, Grenlækur, southern Iceland) **A**–**U** LM pictures of valves in valve face view in decreasing length **V–X** SEM external view of three complete valves with focus on the spines located in pit-like depressions. Note the absence of apical porefields **Y** SEM internal view of a complete valve. Scale bars: 10 µm (**A–W, Y**); 1 µm (**X**).

Gomphonema pumilum var. *rigidum* E.Reichardt & Lange-Bertalot, although none of them reaches more than 10% of all counted valves. Rarer species include *Odontidium mesodon* (Ehrenberg) Kützing, *Navicula radiosa* Kützing, *N. slesvicensis* Grunow and *Amphora ovalis* (Kützing) Kützing. The flora points to colder, fast-flowing, meso- to eutrophic, alkaline conditions (Lange-Bertalot et al. 2017; Van de Vijver et al. 2023).

Staurosirella vanheurckiana **Van de Vijver, Ballings & M.de Haan, sp. nov.**
Fig. 6

Holotype. BR-4844 (Meise Botanic Garden, Belgium). Fig. 6J represents the holotype.

Isotype. Slide 446 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104537.

Type locality. Leuven, Belgium, Van Heurck exsiccata set Types du Synopsis 315, leg. (probably) Père Gautier

Description. ***LM*** (Fig. 6A–AE). Frustules in girdle view rectangular, solitary or in pairs. Ribbon-like colonies so far not observed. Valves heteropolar, lanceolate to elliptic-lanceolate throughout the entire cell diminution series, with convex margins, gradually narrowing towards the acutely rounded foot pole. Head pole broadly rounded. Smaller specimens ovoid in shape (Fig. 6S–AE). Valve dimensions (n=40): length 8–22 µm, width 3.0–3.5 µm. Sternum moderately

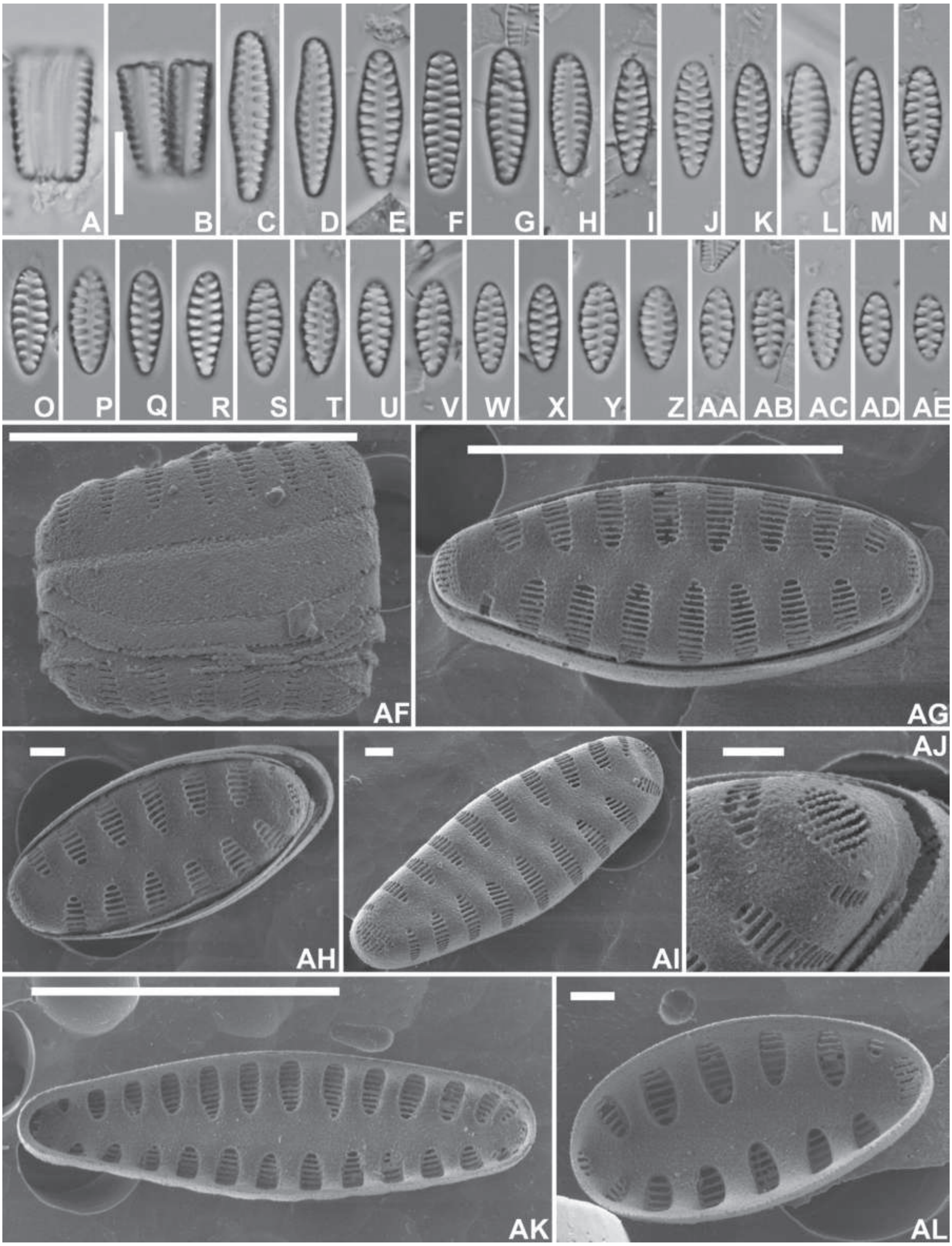

Figure 6. *Staurosirella vanheurckiana* Van de Vijver, Ballings & M.de Haan, sp. nov., LM and SEM micrographs taken from the holotype material (BR-4844, Van Heurck Types du Synopsis 315, Leuven, Belgium) **A, B** LM pictures of a frustule in girdle view **C–AE** LM pictures of valves in valve face view in decreasing length **AF** SEM external view of a complete (slightly eroded) frustule in oblique view showing the girdle structure and the mantle **AG–AI** SEM external view of a three complete heteropolar valves with focus on the apical pore field. Note the depressed headpole in AI **AJ** SEM external detail of a valve apex showing the large apical pore field **AK–AL** SEM internal view of two complete valve. Scale bars: 10 µm (**A–AG, AK**); 1 µm (**AH–AJ, AL**).

narrow, lanceolate. Striae alternating, almost parallel to very slightly radiate throughout, 8–10 in 10 µm. Areolae not discernible in LM. ***SEM*** (Fig. 6AF–AL). External valve face almost flat with very slightly raised virgae and striae sunken in 'punch hole-like' depressions (Fig. 6AI). Abvalvar mantle edge forming a broad hyaline zone, almost half the entire mantle width (Fig. 6AF). Virgae broader than the striae. Striae extending without interruption from valve face onto the mantle (Fig. 6AI–AJ), gradually narrowing towards the ends (Fig. 6AF–AI) giving the striae a lanceolate appearance. Striae uniseriate, composed of long, slit-like, linear areolae, running parallel to the apical axis (Fig. 6AG–AI). Vimines very thin, not raised. Spines absent. Apical pore fields present, different on both apices. Smallest pore field present at head pole, located on small depression (Fig. 6AG–AI). At footpole, apical pore field large, composed of a large number of parallel rows of very small rounded pores (Fig. 6AJ). Internally, striae distinctly sunken between the flat, doubly flared virgae and sternum (Fig. 6AK–AL). Due to erosion, areola occlusions no longer observed.

Etymology. The new species is named in honour of Henri Van Heurck (1838–1909), the most famous Belgian diatomist whose Types du Synopsis Atlas (Van Heurck 1880–1885) was one of the first comprehensive illustrated diatom monographs in the world.

Distribution. *Staurosirella vanheurckiana* has so far only been found in the type locality, most likely due to confusion with similar taxa such as *Staurosirella ovata*.

Ecology and associated diatom flora. The type sample is one of the samples in the Van Heurck exsiccata set Types du Synopsis des Diatomées de Belgique (Van Heurck 1882–1885). The sample was labelled "*Fragilaria mutabilis* (W.Sm.) Grun. *formae minores*" and was collected near Louvain (Leuven, prov. Vlaams Brabant, Belgium). The original vial of the sample also mentions the number "291" although it is unclear to what number this refers. Van Heurck (1885, p. 157) mentions that the Louvain sample was collected by P.G., which most likely stands for Père Vincent Gautier (1827–1903), who collected a large amount of samples that are now conserved in the Van Heurck collection in BR. The sample is dominated by *S. vanheurckiana* reaching more than 50% of all counted valves. Other, subdominant species include *Encyonema ventricosum* (C.Agardh) Grunow, *Melosira varians* C.Agardh, *Nitzschia linearis* (C.Agardh) W.Smith, *Ulnaria* cf. *verhaegeniana* Van de Vijver et al., *Gomphonema capitatum* Ehrenberg, *Planothidium lanceolatum* (Brébisson) Lange-Bertalot, *Amphora ovalis*, and *Meridion circulare* (Gréville) C.Agardh, but they never reached more than 2% of the total flora. This diatom flora most likely points to medium to higher trophic levels, and organic pollution up to the β-α- mesosaprobic levels (Lange-Bertalot et al. 2017).

Discussion

The combination of morphological features places all new species in the genus *Staurosirella*. The striae are composed of linear, apically aligned areolae, separated by thin vimines. Broad, often well-raised virgae separate the striae. Rimoportulae are absent. Apical pore field present, usually similar in shape and size on both apices. These features fit well with the description of the genus *Staurosirella* in Williams and Round (1988) and Morales and Manoylov (2006a).

Each of the new species can be distinguished from similar small-celled araphid taxa worldwide. Tables 1–4 highlight the different features of similar species.

Staurosirella marginostriata shows most resemblance to both *S. canariensis* (Lange-Bertalot) E.Morales et al. and *S. krammeri* E.Morales et al. (Table 1). There are hardly any *Staurosirella* species with short and only marginal striae (Morales et al. 2010b). *Staurosirella krammeri*, described from Oregon, USA, has an almost similar valve outline and comparable valve dimensions, but lacks apical pore fields often replaced by a marginal stria and has typically only one large, acute to spatulate spine per virga (Morales et al. 2010b, figs 33–35). Contrarily, *S. marginostriata* shows well-developed apical pore fields and irregular series of small marginal spines located on the virgae. *Staurosirella canariensis* is much smaller (length up to maximum 7 µm), has a more elliptical, broadly rounded valve outline, and possesses small apical pore fields composed of only a few pores (Lange-Bertalot 1993). In LM, probably most confusion can be caused by *Pseudostaurosira brevistriata*, despite the latter belonging to a completely different genus, which becomes clear when comparing the ultrastructure of both species. *Pseudostaurosira brevistriata* forms long, chain-like colonies using well-developed linking spines, and possesses striae composed of one, transapically elongated areola. In LM, however, the marginal striae and the similar valve outline may result in an incorrect identification. Careful observation of the striae shows that they are more vaguely elongated in *S. marginostriata*, continuing into well-developed ghost striae whereas in *P. brevistriata*, the striae appear to be composed of one large, rounded, well-delimited areola (Morales et al. 2015).

Staurosirella binodiformis shows some resemblance to *Staurosira binodis* Ehrenberg, *Staurosirella confusa* E.Morales, and *Staurosirella oldenburgiana* (Hustedt) E.Morales (Table 2). The type material of *S. binodis* from Santa Fiore, Italy has recently been investigated (Van de Vijver, unpublished results). *Staurosira binodis* presents the typical structure of the genus *Staurosira*: frustules forming long, ribbon-like colonies, each frustule connected to the next using large, spathulate linking spines; large apical pore fields composed of numerous rows of small, rounded pores, long striae composed of rounded, small areolae and numerous girdle bands. In LM, the valve outline, linear with a clear central constriction, may cause some confusion with *S. binodiformis*, but the lack of colonies and the more narrow valves (max. 3 µm vs 4–6 µm in *S. binodis*) of the latter, limit the confusion. The most similar species appears to be *S. oldenburgiana*, a species described by Hustedt in 1959 from the Oldenburg Canal (Lower Saxony, Germany), although the valves are a little bit broader (up to 4 µm), with more elongated, narrower apices. The most distinct difference is the number, shape and structure of the marginal spines (Hustedt 1959; Morales 2005). Whereas *S. binodiformis* has a continuous series of very small, blunt spines, usually located on each side of the striae, *S. oldenburgiana* possesses only one, long, acute marginal spine located in the middle of the virgae (Morales 2005, Van de Vijver unpubl. res.). Hustedt (1959, p. 29) most likely had observed this taxon already as he mentioned in the discussion of his new taxon *Fragilaria oldenburgiana*, "*Ähnliche Erscheinungsformen in Island [Similar forms in Iceland]*". Foged (1974, plate 3, fig. 3) illustrated one valve as *Fragilaria construens* var. *binodis* (Ehrenberg) Grunow, but the depicted valve clearly shows *S. binodis* and not the new *Staurosirella binodiformis*. *Staurosirella confusa*, finally, has a more lanceolate valve outline with usually convex margins and elongated, narrow rostrate apices, lacking in *S. binodiformis*. In Turkiye, a similar taxon was

Table 1. Comparison of valve features between *Staurosirella marginostriata* sp. nov. and similar species.

	***Staurosirella marginostriata* sp. nov.**	***Staurosirella canariensis***	***Staurosirella krammeri***	***Pseudostaurosira brevistriata***
reference	this study	Lange-Bertalot (1993)	Morales et al. (2010b)	Morales et al. (2015)
valve length (µm)	10–20	4–7	4–14	11–19
valve width (µm)	3.0–4.5	3–4	3–5	3.5–5.0
valve outline	lanceolate to rhombic-lanceolate	elliptic to elliptic-lanceolate	rhombical to elliptic	lanceolate to rhombic and elliptic in smaller valves
apices	weakly protracted, rostrate to not-protracted, cuneate in smaller specimens	not protracted, broadly rounded	not protracted, cuneate to broadly rounded	variable, ranging from narrowly or broadly rounded
apical pore field	large, present on both apices, 4–5 rows of large, rimmed pores	very small, present on both poles, 2 rows of a few small pores	absent	small, composed of a handful of areolae
spines	small, marginal, irregularly shaped, non-linking	small, marginal, irregularly shaped, non-linking	one per virga, large, spathulate, non-linking	spathulate linking spines
striae (in 10 µm)	14–15	12–15	12–14	13–14
stria structure	composed of a few, apically linear areolae	composed of a very few, apically linear areolae	composed of a few, apically linear areolae	composed of one large, transapical areola

Table 2. Comparison of valve features between *Staurosirella binodiformis* sp. nov. and similar species.

	***Staurosirella binodiformis* sp. nov.**	***Staurosirella oldenburgiana***	***Staurosirella confusa***	***Staurosira binodis***
reference	this study	Hustedt (1959) + unpublished results	Morales (2005)	Van de Vijver, unpublished results
valve length (µm)	6–21	10–20	11–20	15–21
valve width (µm)	3.0–3.5	3–4	3.5–4.5	4–6
valve outline	isopolar, linear with constricted valve middle in longer valves, lanceolate to elliptic lanceolate with convex margins in smaller specimens	isopolar, narrowly linear with weakly constricted margins	weakly heteropolar, lanceolate	linear with distinctly constricted central part
apices	protracted, rostrate to subcapitate (longer valves) to not protracted, broadly rounded in smaller specimens	protracted, very elongated, rostrate to subcapitate	protracted, elongated rostrate	protracted, rostrate to subcapitate
apical pore field	large, present on both apices, 2–3 rows of large, rimmed pores	large but compact, 4 short rows of large, rimmed pores	very large, at both apices, composed of up to 7 long rows of large pores	large, at both apices, composed of several rows of very small pores
spines	small, marginal, irregularly shaped, non-linking	small, marginal, acute, one per virga	large, spathulate, linking spines	spathulate linking spines
striae (in 10 µm)	14–15	ca. 13	ca. 11	15–16
stria structure	radiate to more strongly radiate at the apices, composed of linear, apically oriented areolae	almost parallel, composed of linear, apically oriented areolae	broad striae, composed of long, apically elongated areolae	long, parallel to weakly radiate, composed of small, rounded areolae

observed showing narrower valves (valve width max. 2.5 µm) giving that taxon a more slender, smaller outlook (C. Solak, pers. comm.). It is unclear whether those Turkish populations also belong to *S. binodiformis*. They were observed in a typical karstic environment, different from the Icelandic habitat.

Staurosirella stoksiana bears some similarity to a large number of European and North-American *Staurosirella* species (Table 3). The most similar species include *S. ovata* E.Morales and *S. martyi* (Héribaud) E.Morales & Manoylov, not in the least because of their heteropolar, often ovoid valve outline. Both, however, entirely lack spines, and have a more heteropolar valve outline with a clear difference between the very broadly rounded headpole and the more acutely rounded footpole (Morales and Manoylov 2006b, Van de Vijver et al. in press). *Staurosirella martyi* (syn. *Staurosirella dubia* (Grunow) E.Morales & Manoylov) usually has larger valves with a valve width up to 10 µm, whereas in *S. stoksiana*, the valve width rarely exceeds 5.5 µm. Larger valves of *S. martyi* also show a clear constriction just below the headpole, a feature lacking in *S. stoksiana*. *Staurosirella neopinnata* E.Morales et al. has typically parallel margins, isopolar valves, smaller apical pore fields and more regularly placed marginal spines (Morales et al. 2019) and *S. coutelasiana* Van de Vijver has longer, more slender valves, a less heteropolar valve outline, and a higher stria density (9–11 vs 8–9 in 10 µm (Van de Vijver 2022). The newly described *Staurosirella vanheurckiana* differs in a lower valve width (3.0–3.5 µm), a slightly wider sternum, a more clear heteropolar, ovoid valve outline with a broadly rounded head pole throughout its entire cell diminution series, the complete absence of marginal spines despite the analysis of a large population, and a different apical pore field structure with parallel rows of areolae along the apical axis (contrary to the transapical rows in *S. stoksiana*).

There are a few *Staurosirella* species that show some similarity to *S. jonssoniana*, based on the lanceolate valve outline with shortly protracted, rostrate apices (Table 4). The most similar is *S. acidophila* Almeida et al., described from southeastern Brazil. The species has a more elliptical-lanceolate central part with clearly convex margins and well protracted, elongated rostrate apices. The valves are always larger (width 4.5–7 µm vs 3.0–3.5 µm), have distinct apical pore fields (contrary to *S. jonssoniana* lacking apical pore fields), and with a different spine density (at least 2 per virga) and structure (lack of the pit-like depressions) (Almeida et al. 2015). *Staurosirella confusa* is also slightly larger (3.5–4.5 µm) with larger apical pore fields and at least 2 spines per virgae, each not located in a depression (Morales 2005). There are hardly any *Staurosirella* species lacking an apical pore field and most of these form long colonies such as *S. mutabilis* (W.Smith) E.Morales & Van de Vijver and *S. lapponica* (Grunow) D.M.Williams & Round (Van de Vijver et al. 2022). In LM, confusion may also arise with members of the genus *Punctastriata* D.M.Williams & Round, described in 1988 (Williams and Round 1988). Especially *P. linearis* D.M.Williams & Round has a more or less similar valve outline, although this species is always typically heteropolar with a more broadly rounded head pole and a more acute foot pole. The ultrastructure is entirely different with the typical *Punctastriata* feature of striae composed of several rows of small, rounded areolae. *Punctastriata linearis* also possesses one apical pore field on the foot pole and a clear depressed head pole, although these features are difficult to see in LM (Wetzel and Ector 2021). The larger *Staurosirella subcapitata* E.Morales differs in the presence of apical pore fields and a lower stria density (7–9 in 10 µm vs 12–13 in 10 µm) (Morales and Manoylov 2006b).

Table 3. Comparison of valve features between *Staurosirella stoksiana* sp. nov., *S. vanheurckiana* sp. nov. and similar species.

	***Staurosirella stoksiana* sp. nov.**	***Staurosirella vanheurckiana* sp. nov.**	***Staurosirella neopinnata***	***Staurosirella ovata***	***Staurosirella coutelasiana***	***Staurosirella martyi***
reference	this study	this study	Morales et al. (2019)	Morales and Manoylov (2006b)	Van de Vijver (2022)	Van de Vijver et al. (unpublished results)
valve length (µm)	6–21	8–22	4–25	6.5–38	15–35	9–38
valve width (µm)	4.5–5.5	3.0–3.5	4–5	3.5–7	5.0–5.5	5–10
valve outline	heteropolar, larger valves ovoid, smaller valves more elliptical, convex margins, gradually narrowing	heteropolar, lanceolate to elliptic-lanceolate, smaller specimens entirely ovoid	usually isopolar with parallel margins	typically heteropolar, ovoid	isopolar to occasionally very slightly heteropolar, linear-lanceolate in larger specimens to lanceolate, occasionally elliptic-lanceolate in smaller valves	heteropolar, larger valves with clear constriction between valve middle and headpole, smaller valves ovoid in shape
apices	not protracted, broadly rounded	not protracted, head pole broadly rounded, foot pole acutely rounded	not protracted, broadly rounded	headpole broadly rounded, footpole more acutely rounded	broadly rounded, not protracted	headpole broadly rounded, footpole more acute
apical pore field	present on both apices, larger pore field at footpole composed of up to 8 rows of very small pores, at headpole smaller and located on depression	pore field at head pole small, located on small depression, pore field at foot pole large, composed of a large number of parallel rows of very small rounded pores	very small, on both apices, composed of a handful of small pores	present at both apices, but more developed at the footpole.	present on both apices, similar in size and shape, composed of a handful of larger pores	at footpole very large, composed of more than 8 long rows of small pores, at headpole restricted to a compact group of a few small pores
spines	small, marginal, irregularly shaped, non-linking, occasionally valves without spines observed	Absent	small, irregularly shaped, 2–3 per virga, non linking	absent	marginal on the virgae, irregularly shaped (acute to spatulate), usually one or two per virga	absent
striae (in 10 µm)	8–9	8–10	8–9.5	6–9	9–11	6–7
stria structure	alternating, almost parallel becoming very slightly radiate towards the apices	alternating, almost parallel to very slightly radiate throughout	parallel almost throughout the entire valve	parallel to slightly radial toward the poles	alternating at both sides of the sternum, parallel to weakly radiate near the valve middle, becoming distinctly more radiate towards the apices	parallel in the middle becoming gradually weakly radiate towards the apices

Finally, *Staurosirella vanheurckii* shows some resemblance to *S. stoksiana* but as highlighted here above, both can be separated based on valve outline, valve width, absence/presence of marginal spines and the structure of the apical pore fields (see Table 3). *Staurosirella ovata*, also lacking spines, is much wider (3.5–7.0 µm, i.e. double the valve width of *S. vanheurckiana*) and has a different apical pore field structure (Morales and Manoylov 2006b). The same applies for *S. martyi* that has a different valve outline, especially in the longer valves and a higher valve width (5–10 µm). Both *S. ovata* (6–9 in 10 µm) and *S. martyi* (6–7 in 10 µm) have a lower stria density compared to *S. vanheurckiana* (8–10 in 10 µm).

Table 4. Comparison of valve features between *Staurosirella jonssonii* sp. nov. and similar species.

	***Staurosirella jonssonii* sp. nov.**	***Staurosirella confusa***	***Staurosirella acidophila***	***Staurosirella subcapitata***	***Punctastriata linearis***
reference	this study	Morales (2005)	Almeida et al. (2015)	Morales and Manoylov (2006b)	Wetzel and Ector (2021)
valve length (μm)	6–15	11–20	11–20	8–27	12–20
valve width (μm)	3.0–3.5	3.5–4.5	4.5–7	4.0–5.5	1.5–3
valve outline	isopolar to weakly heteropolar, lanceolate, with convex margins	weakly heteropolar, lanceolate	isopolar to slightly heteropolar, lanceolate to rhombic-lanceolate	isopolar, lanceolate	weakly heteropolar, lanceolate to elliptical in smaller valves
apices	narrowly protracted, rostrate	protracted, elongated rostrate	acuminate to rostrate rounded	acutely rounded, rostrate to subrostrate	shortly protracted, rostrate
apical pore field	absent	very large, at both apices, composed of up to 7 long rows of large pores	present at both apices, composed of small, rimmed pores	present on both apices, similar in size and shape, composed of several rows of small pores	one apical pore field present at foot pole, depression lacking pore field at head pole
spines	marginal, one per virga, each located in a shallow, pit-like depression	large, spathulate, linking spines	small, 2-3 located in costae valve, sometimes in double rows	present on the virgae, occasionally absent	irregular row of short, acute spines, placed on virgae and striae
striae (in 10 μm)	12–13	ca. 11	8–9	7–9	10–13
stria structure	alternating, almost parallel to very slightly radiate in the middle, more strongly radiate towards the apices	broad striae, composed of long, apically elongated areolae	alternating, slightly radiate	alternating, parallel, becoming radiate at the apices	parallel, composed of 4-6 rows of small, rounded areolae

Conclusions

The description of these five new European *Staurosirella* species is the result of the continuous revision of the genus *Staurosirella* following the careful analysis of the historic type material. Catch-all species such as *S. pinnata* (now *S. neopinnata*), *S. mutabilis* and *S. martyi* revealed a much higher diversity in the genus *Staurosirella* than previously understood. It is clear that more species will be discovered in the near future, when more populations, in the past identified as *S.* (*neo*)*pinnata* will be investigated. Morphological criteria such as valve outline and valve dimensions need to be completed with a better analysis of other structures such as the shape, size and structure of the apical pore fields, the structure and density of the marginal spines, the presence (or absence) of a head pole depression and the structure of the striae in combination with the virgae.

Acknowledgements

Dr Christian Lange and Prof. Dr Nina Lundholm are thanked for their help in the Foged collection for retrieving the original material for Foged sample 29 from Iceland. The Vlaamse Milieu Maatschappij is thanked for granting the permission to use one of their samples (APM21-91, Bosbeek, Belgium).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research received support (Bart Van de Vijver) from the SYNTHESYS project (www.synthesys.info), financed by the H2020 Research Infrastructures Programme, to visit C.

Author contributions

Bart Van de Vijver: sampling, specimen analysis, original draft, writing, editing, Valérie Peeters: sampling, specimen analysis, editing, Iris Hansen: sampling, sample analysis, editing, Myriam de Haan & Petra Balling: SEM analysis, editing.

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Data availability

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

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PhytoKeys 242: 161–227 (2024)
DOI: 10.3897/phytokeys.242.117481

Research Article

Refining the phylogeny and taxonomy of the apple tribe Maleae (Rosaceae): insights from phylogenomic analyses of 563 plastomes and a taxonomic synopsis of *Photinia* and its allies in the Old World

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Abstract

This study addresses the longstanding absence of a comprehensive phylogenetic backbone for the apple tribe Maleae, a deficiency attributed to limited taxon and marker sampling. We conducted an extensive taxon sampling, incorporating 563 plastomes from a diverse range of 370 species encompassing 26 presently recognized genera. Employing a range of phylogenetic inference methods, including RAxML and IQ-TREE2 for Maximum Likelihood (ML) analyses, we established a robust phylogenetic framework for the Maleae tribe. Our phylogenomic investigations provided compelling support for three major clades within Maleae. By integrating nuclear phylogenetic data with morphological and chromosomal evidence, we propose an updated infra-tribal taxonomic system, comprising subtribe Malinae Reveal, subtribe Lindleyinae Reveal, and subtribe Vauqueliniinae B.B.Liu (**subtr. nov.**). Plastid phylogenetic analysis also confirmed the monophyly of most genera, except for *Amelanchier*, *Malus*, *Sorbus* sensu lato, and *Stranvaesia*. In addition, we present a comprehensive taxonomic synopsis of *Photinia* and its morphological allies in the Old World, recognizing 27 species and ten varieties within *Photinia*, three species and two varieties within *Stranvaesia*, and two species and three varieties within *Weniomeles*. Furthermore, we also lectotypified 12 names and made two new combinations, *Photinia microphylla* (J.E.Vidal) B.B.Liu and *Weniomeles atropurpurea* (P.L.Chiu ex Z.H.Chen & X.F.Jin) B.B.Liu.

Academic editor: Hanno Schaefer
Received: 17 December 2023
Accepted: 21 April 2024
Published: 31 May 2024

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* These authors contributed equally to this work.

Citation: Wang H, Li X-Y, Jiang Y, Jin Z-T, Ma D-K, Liu B, Xu C, Ge B-J, Wang T, Fan Q, Jin S-H, Liu G-N, Liu B-B (2024) Refining the phylogeny and taxonomy of the apple tribe Maleae (Rosaceae): insights from phylogenomic analyses of 563 plastomes and a taxonomic synopsis of *Photinia* and its allies in the Old World. PhytoKeys 242: 161–227. https://doi.org/10.3897/phytokeys.242.117481

Key words: Classification, lectotype, nomenclature, *Pourthiaea*, *Stranvaesia*, typification, *Weniomeles*

Introduction

The apple tribe Maleae, one of the sixteen tribes within the Rosaceae family, comprises approximately 27 genera and 912 species, with a widespread distribution across the Northern Hemisphere (Robertson et al. 1991; Lu et al. 2003; Phipps 2014). This tribe includes diverse genera such as *Kageneckia* Ruiz & Pav., *Lindleya* Kunth, and *Vauquelinia* Corrêa ex Bonpl., noted for their follicles and capsules, alongside pome-bearing genera previously categorized under the subfamily Maloideae (Morgan et al. 1994). The monophyly of this lineage has been confirmed by a series of phylogenetic studies (Fig. 1; Potter et al. 2007; Xiang et al. 2017; Zhang et al. 2017; Liu et al. 2020a, 2022).

As a prominent member of the nine tribes within the subfamily Amygdaloideae, the apple tribe Maleae has been consistently supported as a monophyletic group and the sister relationship to the tribe Gillenieae (Fig. 1). Within Maleae, numerous prior studies have consistently confirmed the close phylogenetic relationship between the dry-fruited genera (*Kageneckia*, *Lindleya*, and *Vauquelinia*) and the pome-bearing genera. This phylogenetic hypothesis has been corroborated by a series of studies employing a range of methods, from the utilization of singular or multiple plastid and nuclear markers (Morgan et al. 1994; Evans et al. 2000; Evans and Campbell 2002; Evans and Dickinson 2005; Verbylaitė et al. 2006; Campbell et al. 2007; Potter et al. 2007; Li et al. 2012; Lo and Donoghue 2012; Sun et al. 2018) to the most recent phylogenomic approaches (Xiang et al. 2017; Zhang et al. 2017; Liu et al. 2019, 2020a, 2022; Jin et al. 2023; Zhang et al. 2023). However, despite these endeavors, earlier phylogenetic studies were unable to resolve the intergeneric relationships within Maleae due to the limited plastid and nuclear markers. For instance, early studies by Campbell et al. (2007) and Potter et al. (2007) grouped the dry-fruited and pome-bearing genera under the tribe Pyreae (also known as Maleae). They also reclassified the pome-bearing genera (formerly known as subfamily Maloideae) into the subtribe Pyrinae (or Malinae). Despite these developments, the precise phylogenetic relationships and taxonomic status of *Kageneckia*, *Lindleya*, and *Vauquelinia* remained unresolved. Recent advancements in phylogenomics have demonstrated that datasets encompassing plastomes and/or hundreds of nuclear genes can offer sufficient informative sites for elucidating phylogenetic relationships. However, the substantial costs for genome-level sequencing have led to limited taxon sampling in contemporary phylogenomic analyses, such as the studies by Liu et al. (2022), Jin et al. (2023), and Zhang et al. (2023).

Accurately resolving its genus-level phylogenetic relationships has also remained a significant challenge. This difficulty is primarily attributed to the lack of informative genetic markers and ample taxon sampling, as highlighted in studies by Lo and Donoghue (2012) and Liu et al. (2022). During the Sanger sequencing era, Lo and Donoghue (2012) made a substantial contribution by assembling a dataset comprising 486 individuals, representing 331 species

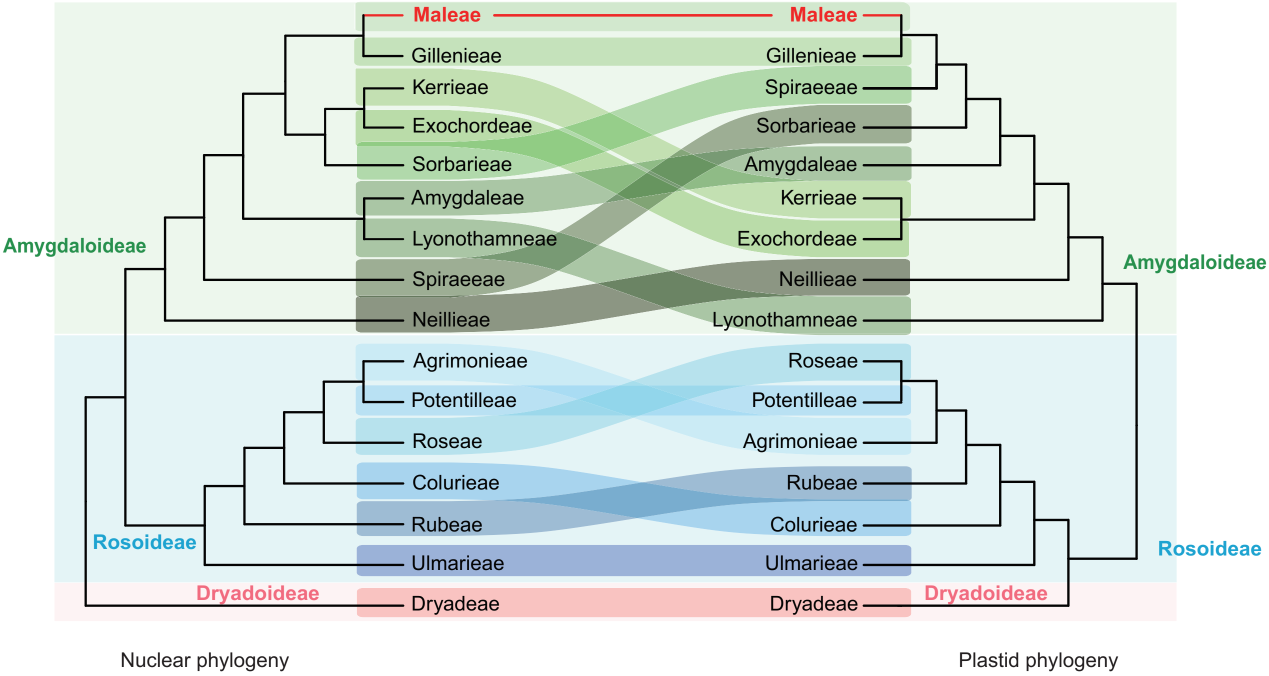


Figure 1. Infrafamilial- and tribe-level topological discordance within Rosaceae, highlighting the phylogenetic placement of the tribe Maleae **A** nuclear phylogeny based on transcriptome data (Xiang et al. 2017) **B** plastome-based phylogeny (Zhang et al. 2017).

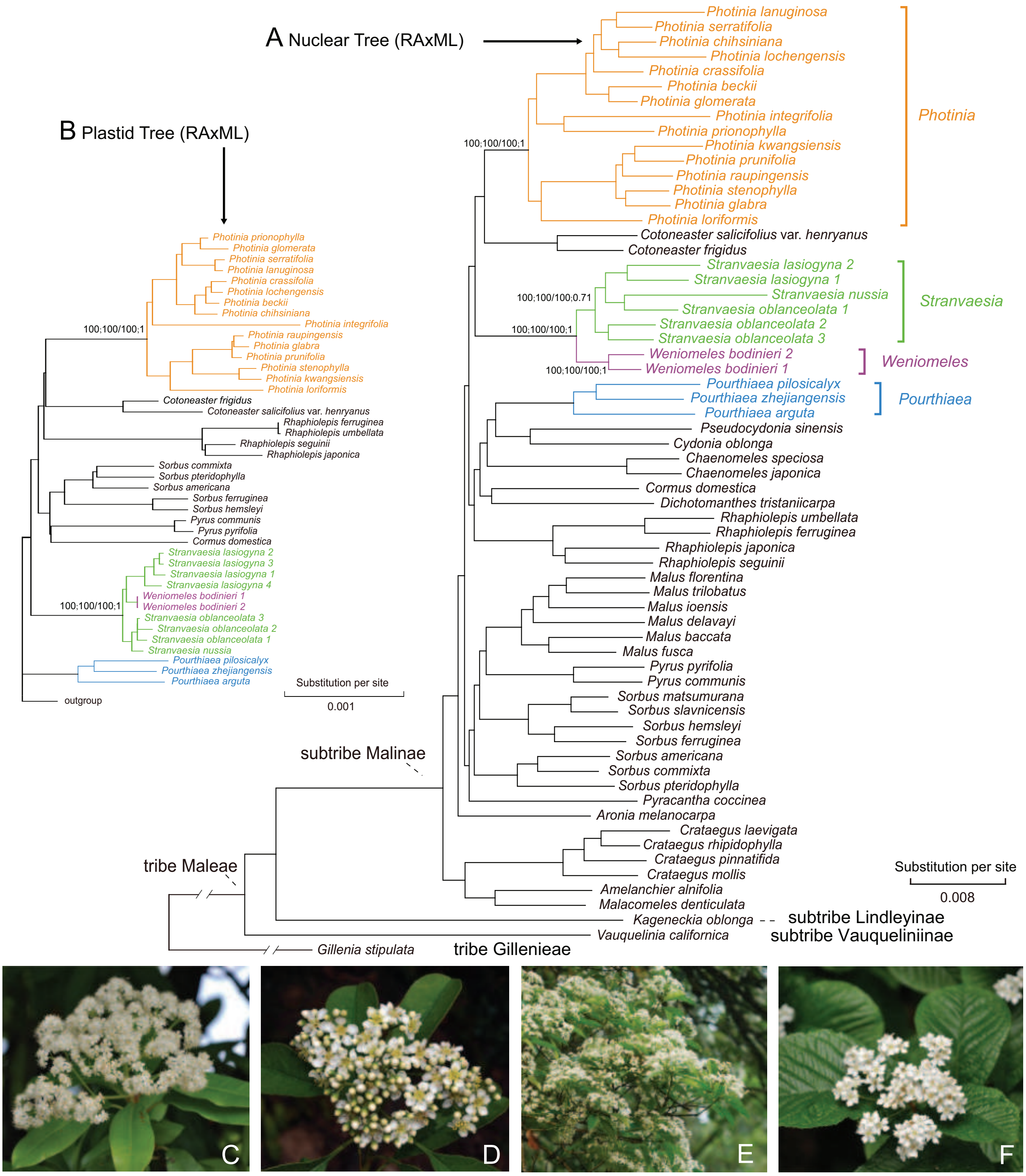
across 27 currently recognized genera. This dataset, one of the largest of its kind, utilized 11 plastid regions and one nuclear ribosomal internal transcribed spacer (nrITS) sequence. However, advancements in genetic research have revealed that such limited informative sites from several plastid and nuclear regions are insufficient for estimating a robust phylogenetic backbone. Next-generation sequencing (NGS) technologies, combined with decreasing sequencing costs and user-friendly bioinformatics tools, have revolutionized the approach to understanding phylogenetic relationships. The transition from Sanger sequencing to NGS has allowed for deeper phylogenetic analysis. A notable example of this progress is the study of Zhang et al. (2017), who estimated a plastid framework for the Rosaceae family using 122 plastomes, including 41 species from the Maleae tribe. This study marked a significant step in our evolutionary understanding of Maleae. Following this, there has been a surge of global research efforts to elucidate the phylogenetic relationships within Maleae using plastome-level datasets. Pioneering studies by Liu et al. (2019, 2020a, 2020b, 2022), Meng et al. (2021), Ulaszewski et al. (2021), Liu et al. (2023a, 2023b), Jin et al. (2023, 2024), and Ma et al. (2023) have significantly contributed to this field. These studies have employed extensive plastome datasets, vastly improving upon previous efforts in scale and depth. However, a common limitation of these studies has been the relatively narrow focus on a few species or a specific lineage within Maleae. This has resulted in an incomplete phylogenetic picture of Maleae. More comprehensive and inclusive research is needed, as it would provide a more thorough understanding of Maleae. Such an approach would involve extensive sampling across the tribe, incorporating a wide range of species to cover the full breadth of its genetic diversity.

The chloroplast genome, assembled from genome skimming data (Straub et al. 2012), has played a pivotal role in plant systematics and phylogenetics (Guo et al. 2023). Its highly conserved nature and areas of variable sequences make it widely used in phylogenetic analysis (Gitzendanner et al. 2018). Furthermore, this genetic stability, along with the non-recombinant of plastomes and often uniparental inheritance, offers a consistent and reliable framework for studying plant lineage and evolution, and the plastome-based phylogenetic inference has been successfully utilized in exploring the shallow (Zhang et al. 2017; Liu et al. 2019, 2020a, 2020b; Wang et al. 2020; Su et al. 2021) and deep phylogenies (Li et al. 2019, 2021). In this study, we assembled 563 plastomes from genome skimming data to reconstruct a comprehensive plastome-based phylogenetic framework for the tribe Maleae.

The taxonomic delimitation and phylogenetic relationship between *Photinia* Lindl. and its morphologically related genera in the Old World have been a subject of debate for centuries. In the Old World, the *Photinia*-affiliated genera comprised four groups: the deciduous genus *Pourthiaea* Decne., and the evergreen genera *Photinia*, *Stranvaesia* Lindl., and *Weniomeles* B.B.Liu. *Photinia* was initially described with a single evergreen species, *P. arbutifolia* Lindl., and later expanded to include four evergreen species (Lindley 1821). Subsequently, de Candolle (1825) incorporated two deciduous species into *Photinia*, thereby establishing the genus *Photinia*, encompassing both evergreen and deciduous species. *Photinia* has been recognized as comprising about 60 species, both evergreen and deciduous, distributed disjointedly across East and Southeast Asia, and Mexico (Rehder 1940; Vidal 1965; Yu 1974; Phipps et al. 1990; Robertson et al. 1991; Phipps 1992; Lu et al. 2003). Decaisne (1874) observed distinctive warty peduncles and pedicels on the fruits of deciduous species, setting them apart from their evergreen counterparts, leading to the establishment of these deciduous species under the newly formed genus *Pourthiaea*. This classification, recognizing *Pourthiaea* as a separate genus, gained widespread acceptance among botanists, including Nakai (1916), Ohashi (1989), Iketani and Ohashi (1991, 2001), Liu and Hong (2016a, 2016b, 2017), and Liu et al. (2023b). The separate generic status of *Pourthiaea* has also been further substantiated by recent molecular studies (Guo et al. 2011; Li et al. 2012; Zhang et al. 2017; Sun et al. 2018; Liu et al. 2019, 2022). Furthermore, Phipps (1992) revealed that the five species and three varieties of *Photinia* indigenous to Central America exhibit distinct morphological characteristics compared to the *Photinia* species from East Asia. This distinction was corroborated by phylogenomic evidence, which employed whole plastome and nuclear ribosomal DNA (nrDNA) datasets. Based on these findings, these Central American species were reclassified into a newly proposed genus, *Phippsiomeles* B.B.Liu & J.Wen, as elaborated in Liu et al. (2019).

First described by Lindley in 1837, the red-fruit genus *Stranvaesia* is a relatively small group, encompassing five species native to China, the Himalayas, and Southeast Asia (Lu et al. 2003). Morphologically similar to *Photinia*, *Stranvaesia* is distinguishable by its unique characteristics, including a four- or five-chambered ovary and dehiscent fruits. These distinct features have led to its classification as a separate genus in numerous taxonomic studies spanning from the mid-19th to early 21st centuries (Roemer 1847; Decaisne 1874; Wenzig 1883; Focke 1888; Koehne 1893; Rehder 1940, 1949; Yu 1974; Lu et al. 2003). However, this classification was challenged by Kalkman (1973), who observed negligible differences in the number of carpels between *Stranvaesia* and *Photinia*. He noted that the supposedly dehiscent fruits of *Stranvaesia davidiana* Decne. did not exhibit dehiscence in botanical garden observations, leading to the proposal of merging *Stranvaesia* into *Photinia* due to these morphological similarities. Despite this, the relationship between these two genera has been a long-standing taxonomic puzzle, with some botanists advocating for their distinct genus status (Yu 1974; Lu et al. 2003), while others supported merging them (Lu et al. 1991; Li et al. 1992; Zhang and Baas 1992). Recent phylogenetic and phylogenomic studies have shed light on this controversy. For instance, based on two chloroplast DNA regions and nrITS sequence, Guo et al. (2011) inferred that *Photinia davidsoniae* Rehder & E.H.Wilson (= *P. bodinieri* H.Lév.) and *P. nussia* (Buch.-Ham. ex D.Don) Kalkman (= *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne.) formed a clade with strong support; however, the phylogenetic relationship between this clade and *Photinia* has been uncertain due to the limited informative sites. Liu et al. (2019) expanded the taxon sampling in their phylogenomic study within the Maleae framework, providing strong support for a redefined *Stranvaesia* clade, including three species, *S. bodinieri* (H.Lév.) B.B.Liu & J.Wen, *S. oblanceolata* (Rehder & E.H.Wilson) Stapf, and *S. nussia* (type species). Additionally, Liu et al. (2019) identified a novel distinguishing character for *Stranvaesia* not previously used in differentiating it from *Photinia*: the presence of a cluster of sclereids forming an ellipsoid between carpels in the flesh of pomes. This discovery, alongside the robust phylogeny, led to a redefinition of the generic limits of *Stranvaesia* and several nomenclatural changes. Further molecular analysis by Guo et al. (2020) confirmed the distinct phylogenetic placement of *Stranvaesia* and introduced another distinguishing trait: the unarmed branches of young trees. Despite this progress, ongoing uncertainties in the generic delimitation of *Photinia* and *Stranvaesia* persist due to factors like insufficient sampling (Liu et al. 2019) and limited informative sites (Guo et al. 2011, 2020). The complexity is compounded by polyploidy and hybridization-driven lineages, which challenge traditional taxonomic treatments. Jin et al. (2023) provided further insights, suggesting that the origin of the redefined genus *Stranvaesia* may involve allopolyploidy and introgression, with the most recent common ancestor (MRCA) of *Stranvaesia bodinieri* likely acting as the maternal parent and an extinct lineage as the paternal parent. Consequently, *Stranvaesia bodinieri* was proposed as a new genus, *Weniomeles*, characterized by purple-black fruits, thorny trunks and/or branches, and a fruit core with multiloculars separated by a sclereid layer and a sclereid cluster at the top of the locules (Fig. 2A).

Our study focuses on three key goals: 1) to establish a robustly plastome-based phylogenetic backbone for the apple tribe Maleae, 2) to update and refine the infra-tribal taxonomic system within Maleae, and 3) to compile a detailed taxonomic synopsis of *Photinia* and its closely related groups in the Old World.



Photinia serratifolia *Stranvaesia lasiogyna* *Weniomeles bodinieri* *Pourthiaea magnoliifolia*

Figure 2. Phylogenetic tree of the apple tribe Maleae estimated by Maximum Likelihood (ML) algorithm using RAxML, based on a concatenated 426 single-copy nuclear genes (SCN genes) supermatrix **A** inset in the upper left corner **B** a segment of the RAxML tree focusing on *Photinia* and its allies, inferred from concatenated 78 plastid coding sequences (plastid CDSs). (Adapted from Jin et al. (2023)) **C** *Photinia serratifolia* (Zhejiang, China: Bin-Bin Liu) **D** *Stranvaesia lasiogyna* (Yunnan, China: Bin-Bin Liu) **E** *Weniomeles bodinieri* (Yunnan, China: Bin-Bin Liu) **F** *Pourthiaea magnoliifolia* (Zhejiang, China: Bin-Bin Liu).

Materials and methods

Taxon sampling, DNA extraction, and sequencing

In this study, we compiled 563 plastomes to estimate a plastid framework for the apple tribe Maleae. This collection encompasses 559 individuals within Maleae, representing almost all genera except for the Madeira endemic genus, *Chamaemeles* Lindl. We employed *Gillenia* Moench, comprising two species from four individuals, as the outgroup. Our dataset included 559 ingroup samples, covering a wide spectrum of species diversity across various genera: 14 out of 24 species in *Amelanchier* Medik. (14 individuals), all two species in *Aronia* Medik. (two individuals), all four species in *Chaenomeles* Lindl. (seven individuals), 63 taxa (53 species, eight varieties, one subspecies) out of 261 species in *Cotoneaster* Medik. (66 individuals), 20 out of 222 species in *Crataegus* L. (33 individuals), one species for the monotypic genus *Cydonia* Mill. (two individuals), one species for the monotypic genus *Dichotomanthes* Kurz (two individuals), six out of 11 species in *Hesperomeles* Lindl. (six individuals), one species for the monotypic genus *Heteromeles* M.Roem. (two individuals), all four species in *Kageneckia* Ruiz & Pav. (four individuals), one species for the monotypic genus *Lindleya* Kunth (one individual), one out of five species in *Malacomeles* (Decne.) Decne. (two individuals), three species in *Osteomeles* Lindl. (three individuals), one species for the monotypic genus *Peraphyllum* Nutt. (two individuals), three out of five species in *Phippsiomeles* (three individuals), 20 out of 27 species in *Photinia* (31 individuals), 14 species in *Pourthiaea* (53 individuals), one species for the monotypic genus *Pseudocydonia* (C.K.Schneid.) C.K.Schneid. (three individuals), three species in *Pyracantha* M.Roem. (five individuals), 17 out of 83 species in *Pyrus* L. (26 individuals), 30 out of 42 species in *Rhaphiolepis* Lindl. (40 individuals), all three species in *Stranvaesia* (three individuals), five species in *Vauquelinia* Corrêa ex Bonpl. (five individuals), and one species in *Weniomeles* (three individuals). Notably, we sampled 46 species and five cultivars in *Malus* Mill. (94 individuals) and 99 species out of 160 in *Sorbus* L. sensu lato (142 individuals), encompassing subgroups like *Aria* (Pers.) Host, *Chamaemespilus* Medik., *Cormus* Spach, *Micromeles* Decne., *Torminalis* Medik., and *Sorbus* sensu stricto. This comprehensive survey thus provides a significant insight into the plastid diversity of the Maleae tribe, covering a broad range of species and varieties across its numerous genera (Table 1).

Total genomic DNAs were extracted from silica-gel dried leaves and herbarium specimens using a modified cetyltrimethylammonium bromide (CTAB) method, as described by Li et al. (2013). This extraction was performed at the State Key Laboratory of Plant Diversity and Specialty Crops, Institute of Botany, Chinese Academy of Science (IBCAS) in China. The subsequent library preparation and sequencing processes were conducted at the Novogene laboratory in Beijing, utilizing the NEBNext® Ultra™ II DNA Library Prep Kit, designed specifically for the Illumina® platform. We generated paired-end reads of 150 bp using the Illumina HiSeq 2500 Instrument (Novogene Beijing). This approach ensured high-quality DNA sequencing, which is important for our research objectives.

Table 1. Accessions of the apple tribe Maleae utilized in this study. The rows highlighted in bold indicate that samples were sequenced by our PhyloAI team at the Institute of Botany, Chinese Academy of Sciences. Additionally, asterisks (*) appended to the accession numbers denote that these plastomes were sequenced for this study. Plastomes lacking locality and voucher information were retrieved from GenBank.

Species name	Accession number	Locality	Voucher
Amelanchier alnifolia (Nutt.) Nutt. ex M.Roem.	MN068255	-	-
Amelanchier arborea (F.Michx.) Fernald	MN068254	-	-
Amelanchier asiatica Endl.	MN068253	-	-
***Amelanchier bartramiana* (Tausch) M.Roem.**	**MN068256**	**Terrae-Novae, Canada**	***E. Rouleau 3959* (US2421653)**
***Amelanchier cusickii* Fernald**	**MN068257**	**Washington, USA**	***J. William & Thompson 14588* (US1889072)**
***Amelanchier fernaldii* Wiegand**	**MN068258**	**Quebec, Canada**	***F. Marie-Victorin & F. Rolland-Germain 27898* (US1435540)**
***Amelanchier humilis* Wiegand**	**MN068259**	**North Dakota, USA**	***O.A. Stevens 1424* (US2134929)**
***Amelanchier interior* E.L.Nielsen**	**MN068260**	**Iowa, USA**	***R.F. Thorne 12413* (US2230661)**
Amelanchier obovalis (Michx.) Ashe	MK920296	-	-
Amelanchier ovalis Medik.	MK920297	-	-
***Amelanchier pallida* Greene**	**MN068261**	**Baja California, Mexico**	***R.E. Broder 737* (US2412566)**
***Amelanchier sanguinea* (Pursh) DC.**	**MN068262**	**Quebec, Canada**	***J. Wen 10472* (US01176270)**
***Amelanchier sinica* Chun**	**MK920291**	**Beijing, China**	***B.B. Liu & G.N. Liu 220725* (PE)**
***Amelanchier spicata* (Lam.) K.Koch**	**MK920292**	**Washington DC, USA**	***J. Wen 12951* (US)**
***Aronia arbutifolia* (L.) Pers.**	**MN061996**	**Rhode Island, USA**	***J. Wen 13937* (US)**
Aronia melanocarpa (Michx.) Elliott	MT527725	-	-
Chaenomeles cathayensis C.K.Schneid. 1	MT561270	-	-
***Chaenomeles cathayensis* 2**	**MN061997**	**Beijing, China**	***B.B. Liu et al. 3909* (PE)**
***Chaenomeles japonica* (Thunb.) Lindl. ex Spach 1**	**MZ984211**	**Beijing, China**	***B.B. Liu & G.N. Liu 3926* (PE)**
Chaenomeles japonica 2	KT932966	-	-
***Chaenomeles speciosa* (Sweet) Nakai 1**	**MZ984212**	**Beijing, China**	***B.B. Liu 3985* (PE)**
Chaenomeles speciosa 2	MT937182	-	-
Chaenomeles thibetica T.T.Yu	MT561271	-	-
***Cotoneaster acuminatus* Lindl.**	**MN577874**	**Tibet, China**	***PE Tibet Team PE6623* (PE)**
Cotoneaster acutifolius var. *villosulus* Rehder & E.H.Wilson	MK650048	-	-
Cotoneaster adpressus Bois	OQ992642	-	-
Cotoneaster adpressus var. *praecox* Bois & P.Berthault	MK638986	-	-
Cotoneaster affinis Lindl.	MK650051	-	-
Cotoneaster argenteus G.Klotz	MK578683	-	-
Cotoneaster astrophoros J.Fryer & E.C.Nelson	MK650065	-	-
Cotoneaster bullatus Bois	MK614791	-	-
***Cotoneaster buxifolius* Wall. ex Lindl.**	**MN577892**	**Sichuan, China**	***B.B. Liu 2666* (PE)**
Cotoneaster buxifolius var. *vellaeus* (Franch.) G.Klotz	MK614795	-	-
Cotoneaster conspicuus C.Marquand	MK650062	-	-
Cotoneaster coriaceus Franch.	MK650049	-	-
Cotoneaster dammeri C.K.Schneid.	MK650059	-	-

Species name	Accession number	Locality	Voucher
Cotoneaster dammeri subsp. *songmingensis* C.Y.Wu & Li H.Zhou	MK605511	-	-
Cotoneaster delavayanus G.Klotz	MK605518	-	-
Cotoneaster dielsianus E.Pritz. ex Diels	MK614800	-	-
Cotoneaster foveolatus Rehder & E.H.Wilson	MK650046	-	-
Cotoneaster franchetii Bois 1	MK650050	-	-
Cotoneaster franchetii 2	KY419994	-	-
Cotoneaster franchetii var. *cinerascens* Rehder	MK638991	-	-
Cotoneaster frigidus Wall.	MN577875	-	-
Cotoneaster gamblei G.Klotz	MK650052	-	-
Cotoneaster glaucophyllus var. *serotinus* (Hutch.) L.T.Lu & Brach	MK578685	-	-
Cotoneaster hebephyllus Diels	MK638988	-	-
Cotoneaster hebephyllus var. *fulvidus* W.W.Sm.	MK614792	-	-
Cotoneaster horizontalis Decne.	MN577893	-	-
Cotoneaster huahongdongensis J.Fryer & B.Hylmö	MK614796	-	-
Cotoneaster insolitus G.Klotz	OP494721	-	-
Cotoneaster integerrimus Medik.	MK614799	-	-
Cotoneaster langei G.Klotz	MK605516	-	-
Cotoneaster leveillei J.Fryer & B.Hylmö	MK544857	-	-
Cotoneaster marginatus Hort. ex K.Koch	MK605510	-	-
Cotoneaster melanocarpus Fisch. ex Blytt	MK561977	-	-
***Cotoneaster microphyllus* Wall. ex Lindl.**	**MN577873**	**Tibet, China**	***PE Tibet Team PE5890* (PE)**
Cotoneaster microphyllus var. *cochleatus* (Franch.) Rehder & E.H.Wilson	MK524400	-	-
Cotoneaster microphyllus var. *microphyllus* Wall. ex Lindl.	MK544856	-	-
Cotoneaster mongolicus Pojark.	MZ475330	-	-
Cotoneaster moupinensis Franch.	MK614797	-	-
Cotoneaster multiflorus Bunge	OQ992643	-	-
Cotoneaster obscurus Rehder & E.H.Wilson	MK614798	-	-
Cotoneaster pannosus Franch.	MK605509	-	-
Cotoneaster perpusillus (C.K.Schneid.) Flinck & B.Hylmö	MK638994	-	-
Cotoneaster qungbixiensis J.Fryer & B.Hylmö	MK605513	-	-
Cotoneaster reticulatus Rehder & E.H.Wilson	MK650055	-	-
Cotoneaster rockii G.Klotz	MK605515	-	-
Cotoneaster rosiflorus Kun C.Chang & F.Y.Lu	OP800435	-	-
Cotoneaster rotundifolius Wall. ex Lindl.	MK650063	-	-
Cotoneaster rubens W.W.Sm.	MN577895	-	-
Cotoneaster salicifolius Franch. 1	KY419943	-	-
Cotoneaster salicifolius 2	MK638989	-	-
Cotoneaster salicifolius var. *henryanus* (C.K.Schneid.) T.T.Yu	MN577863	-	-
Cotoneaster schantungensis G.Klotz 1	MK650053	-	-
Cotoneaster schantungensis 2	MN457692	-	-

Species name	Accession number	Locality	Voucher
Cotoneaster shansiensis J.Fryer & B.Hylmö	MK650064	-	-
Cotoneaster sherriffii G.Klotz	MK614794	-	-
Cotoneaster silvestrii Pamp.	MN577894	-	-
Cotoneaster subadpressus T.T.Yu	MK650058	-	-
Cotoneaster submultiflorus Popov	**MK920286**	**Tibet, China**	**_PE Xizang Expedition 7046_ (PE)**
Cotoneaster taylorii T.T.Yu	MN577872	-	-
Cotoneaster tenuipes Rehder & E.H.Wilson	MK650047	-	-
Cotoneaster turbinatus Craib	MK650054	-	-
Cotoneaster vandelaarii J.Fryer & B.Hylmö	MK544858	-	-
Cotoneaster verruculosus Diels	MK605512	-	-
Cotoneaster wardii W.W.Sm.	OQ992644	-	-
Cotoneaster wilsonii Nakai	MN516695	-	-
Cotoneaster zabelii C.K.Schneid.	MK650056	-	-
Crataegus × *canescens* (J.B.Phipps) T.A.Dickinson & E.Y.Y.Lo	KY420022	-	-
Crataegus altaica (Loudon) Lange 1	**OR915923***	**Xinjiang, China**	**_Z.M. Zhang 263_ (PE01153350)**
Crataegus altaica 2	**OR915924***	**Xinjiang, China**	**_D.Y. Hong et al. 0136_ (PE01153341)**
Crataegus aurantia Pojark.	**OR897856***	**Gansu, China**	**_X.G. Sun et al. 2708_ (PE01841632)**
Crataegus bretschneideri C.K.Schneid.	MW963339	-	-
Crataegus chungtienensis W.W.Sm. 1	ON032469	-	-
Crataegus chungtienensis 2	KY419947	-	-
Crataegus cuneata Siebold & Zucc. 1	**OR915925***	**Hubei, China**	**_C.M. Zhao et al. EX2548_ (PE01857312)**
Crataegus cuneata 2	MZ504723	-	-
Crataegus germanica (L.) Kuntze	MK920295	-	-
Crataegus hupehensis Sarg. 1	**OR915900***	**Hubei, China**	**_B.B. Liu 2322_ (PE02070251)**
Crataegus hupehensis 2	MW201730	-	-
Crataegus kansuensis 1 E.H.Wilson	MF784433	-	-
Crataegus kansuensis 2	**OR915910***	**Shanxi, China**	**_D.M. Kong k0229_ (PE02039638)**
Crataegus laevigata (Poir.) DC.	OM232780	-	-
Crataegus marshallii Eggl.	MK920293	-	-
Crataegus maximowiczii C.K.Schneid. 1	MZ494512	-	-
Crataegus maximowiczii 2	**OR915918***	**Jilin, China**	**_B.B. Liu et al. 4499_ (PE)**
Crataegus mollis (Torr. & A.Gray) Scheele	OM232779	-	-
Crataegus monogyna Jacq.	ON641281	-	-
Crataegus oresbia W.W.Sm.	ON032470	-	-
Crataegus pinnatifida var. *major* N.E.Br. 1	KY419945	-	-
Crataegus pinnatifida var. *major* 2	MZ494513	-	-
Crataegus rhipidophylla Gand.	OM232778	-	-
Crataegus sanguinea Schrad.	**OR915926***	**Innermongolia, China**	**_Chifeng Collection Team 2-Z29_ (PE02044283)**
Crataegus scabrifolia (Franch.) Rehder 1	**OR915928***	**Yunnan, China**	**_Y.L. Shui et al. 64833_ (PE01438422)**
Crataegus scabrifolia 2	**OR915927***	**Yunnan, China**	**_G.P. Yang 333_ (PE01438424)**
Crataegus scabrifolia 3	OP021659	-	-
Crataegus songarica 1 K.Koch	**OR915930***	**Xinjiang, China**	**_Z.M. Zhang 222_ (PE01153664)**
Crataegus songarica 2	**OR915929***	**Xinjiang, China**	**_Y.R. Lin 74898_ (PE01153668)**

Species name	Accession number	Locality	Voucher
Crataegus marshallii **Eggl.**	**MK920294**	**Minnesota, USA**	***J. Wen 14051*** **(US)**
Crataegus wilsonii **Sarg. 1**	**OR915931***	**Sichuan, China**	***Bashan Collection Team 4974*** **(PE01872493)**
Crataegus wilsonii **2**	**OR915932***	**Sichuan, China**	***Bashan Collection Team 5683*** **(PE01872495)**
Cydonia oblonga Mill. 1	KX499857	-	-
Cydonia oblonga **2**	**MN061993**	**Beijing, China**	***B.B. Liu et al. 3873*** **(PE)**
Dichotomanthes tristaniicarpa **Kurz 1**	**MN577869**	**Yunnan, China**	***B.B. Liu P1921-7*** **(PE02070692)**
Dichotomanthes tristaniicarpa 2	KY420031	-	-
Gillenia stipulata **(Muhl. ex Willd.) Nutt. 1**	**MN068263**	**Kentucky, USA**	***J. Watson 205*** **(US03694390)**
Gillenia stipulata 2	KY419996	-	-
Gillenia trifoliata **(L.) Moench 1**	**MN068252**	**Washtington DC, USA**	***B.B. Liu 4677*** **(US)**
Gillenia trifoliata 2	MK905738	-	-
Hesperomeles cuneata **Lindl.**	**MN068270**	**La Paz, Bolivia**	***V.A. Funk & N. Bernal 11319*** **(US03695851)**
Hesperomeles ferruginea Lindl.	MN068272	-	-
Hesperomeles glabrata **M.Roem.**	**MK920298**	**Wisconsin, USA**	***P.E. Berry 4561*** **(US03695884)**
Hesperomeles goudotiana Killip	MN068271	-	-
Hesperomeles obovata (Pittier) Standl.	MK920299	-	-
Hesperomeles pernettyoides Wedd.	MN068273	-	-
Heteromeles arbutifolia **(Lindl.) M.Roem. 1**	**MK920281**	**California, USA**	***J. Wen 13512*** **(US)**
Heteromeles arbutifolia 2	KY419965	-	-
Kageneckia angustifolia D.Don	MN068264	-	-
Kageneckia crataegifolia Lindl.	KY420027	-	-
Kageneckia lanceolata **Ruiz & Pav.**	**MN068265**	**Loayza, Bolivia**	***P.M. Peterson et al. s.n.*** **(US03694560)**
Kageneckia oblonga **Ruiz & Pav.**	**MN068266**	**Maule, Chile**	***M. Mahu & C.H. Badilla 10358*** **(US03694604)**
Lindleya mespiloides **Kunth**	**MN068248**	**Nuevo León, Mexico**	***G.B. Hinton et al. 18696*** **(US00903453)**
Malacomeles denticulata (Kunth) G.N.Jones 1	KY419982	-	-
Malacomeles denticulata **2**	**MN068267**	**Mexico**	***A. Ventura 3359*** **(US03513083)**
Malus × atrosanguinea **(Späth) C.K.Schneid.**	**MN061983**	**Washington DC, USA**	***J. Wen 12947*** **(US)**
Malus × magdeburgensis **Schoch ex Rehder**	**OR897858***	**USA**	***Z.L. Yan 1039*** **(PE01656311)**
Malus angustifolia **(Aiton) Michx.**	**MN061984**	**Washington DC, USA**	***W.J. Kress 06-8218*** **(US00868046)**
Malus asiatica Nakai	MW115593	-	-
Malus baccata (L.) Borkh. 1	KX499859	-	-
Malus baccata **2**	**MK896774**	**Minnesota, USA**	***J. Wen 14050*** **(US)**
Malus baccata var. *gracilis* (Rehder) T.C.Ku	OQ737737	-	-
Malus baccata var. *xiaojinensis* (M.H.Cheng & N.G.Jiang) Ponomar. 1	MK434915	-	-
Malus baccata var. *xiaojinensis* 2	OM232782	-	-
Malus bhutanica **(W.W.Sm.) J.B.Phipps**	**OR897828***	**Shanxi, China**	***T.Y. Le 5728*** **(PE00927493)**
Malus coronaria **(L.) Mill. 1**	**OR915988***	**Ohio, USA**	***E.C. Leonard 17256*** **(US03696777)**
Malus coronaria **2**	**OR897841***	**USA**	***Z.L. Yan 1067*** **(PE01656272)**
Malus coronaria **3**	**OR897840***	**USA**	***D.E. Boufford et al. 22098*** **(PE01656271)**
Malus coronaria **4**	**OR915989***	**Virginia, USA**	***F.R. Fosberg 39620*** **(US03696787)**
Malus dawsoniana **Rehder**	**OR897842***	**USA**	***Z.L. Yan 1109*** **(PE01656287)**

Species name	Accession number	Locality	Voucher
***Malus delavayi* (Franch.) B.B.Liu**	**MN216025**	**Yunnan, China**	***B.B. Liu & F. Zhao 3959* (PE)**
***Malus domestica* (Suckow) Borkh. 1**	**OR897843***	**Hebei, China**	***T.T. Yu 145* (PE01461229)**
Malus domestica 2	MW115599	-	-
Malus domestica 3	MK434916	-	-
***Malus domestica* 4**	**OR885573***	**Maryland, USA**	***W.J. Kress et al. 06-8136* (US00868210)**
Malus domestica 5	MH595623	-	-
Malus domestica 6	LT996898	-	-
Malus doumeri A.Chev. 1	KX499861	-	-
Malus doumeri 2	MN577878	-	-
Malus florentina C.K.Schneid. 1	KX499856	-	-
Malus florentina 2	KX499862	-	-
Malus floribunda Siebold ex Van Houtte 1	MW115607	-	-
***Malus floribunda* 2**	**OR885571***	**Beijing, China**	***B.B. Liu et al. 3941* (PE)**
***Malus floribunda* 3**	**OR885577***	**England**	***T.T. Yu s.n.* (PE01656286)**
Malus fusca (Raf.) C.K.Schneid. 1	MW115592	-	-
***Malus fusca* 2**	**OR897844***	**USA**	***Z.L. Yan 1032* (PE01656291)**
Malus halliana Koehne 1	MT246302	-	-
***Malus halliana* 2**	**OR885572***	**Innermongolia, China**	***Y.S. Chen et al. 140606* (PE02036839)**
***Malus honanensis* Rehder 1**	**OR885580***	**Hebei, China**	***Wu 227* (PE01236726)**
Malus honanensis 2	MW115594	-	-
***Malus hupehensis* (Pamp.) Rehder 1**	**OR885568***	**Hubei, China**	***B.B. Liu 2076* (PE02071835)**
Malus hupehensis 2	MK020147	-	-
***Malus hupehensis* 3**	**OR897845***	**Guizhou, China**	***H. Mo 6117* (PE00952317)**
***Malus indica* (Wall.) B.B.Liu 1**	**OR897857***	**Chin State, Myanmar**	***P. Srisanga et al. 97079* (US03696266)**
Malus indica 2	MN088849	-	-
Malus ioensis (Alph.Wood) Britton 1	MN062004	-	-
***Malus ioensis* 2**	**OR915992***	**Wisconsin, USA**	***T.G. Hartley 1301* (US03696969)**
***Malus ioensis* 3**	**OR915993***	**Missouri, USA**	***E.J. Palmer 43794* (US03696964)**
***Malus kansuensis* (Batalin) C.K.Schneid. 1**	**MZ984209**	**Hubei, China**	***B.B. Liu 2278* (PE)**
Malus kansuensis 2	MW018863	-	-
***Malus leiocalyca* S.Z.Huang**	**OR897846***	**Fujian, China**	***236-6 Team 752* (PE00952788)**
Malus longiunguis (Q.Luo & J.L.Liu) B.B.Liu	MW367027	-	-
***Malus mandshurica* (Maxim.) Kom. ex Skvortsov 1**	**MZ984214**	**Tibet, China**	***FLPH Tibet Expedition 12-2086* (PE)**
***Malus mandshurica* 2**	**OR885579***	**Zhejiang, China**	***T. Wang hzbg0220* (PE)**
Malus mandshurica 3	MW115596	-	-
Malus melliana (Hand.-Mazz.) Rehder	MW115597	-	-
Malus micromalus Makino 1	MF062434	-	-
***Malus micromalus* 2**	**OR915902***	**Beijing, China**	***B.B. Liu et al. 3882* (PE)**
***Malus muliensis* T.C.Ku**	**OR897847***	**Sichuan, China**	***s.coll. s.n.* (PE)**
***Malus ombrophila* Hand.-Mazz. 1**	**MZ984213**	**Tibet, China**	***Y.S. Chen et al. 13-1130* (PE)**
Malus ombrophila 2	MW115598	-	-
Malus orientalis Uglitzk.	OM232788	-	-
***Malus orthocarpa* Lavalle**	**OR897848***	**Beijing, China**	***s.coll. s.n.* (PE)**

Species name	Accession number	Locality	Voucher
Malus platycarpa Rehder	**OR897849***	**USA**	**_Z.L. Yan 1051_ (PE01656326)**
Malus prattii (Hemsl.) C.K.Schneid.	MH929090	-	-
Malus prunifolia (Willd.) Borkh. 1	KU851961	-	-
Malus prunifolia 2	**OR915903***	**Beijing, China**	**_B.B. Liu 3968_ (PE)**
Malus × purpurea (Eug.Barbier) Rehder	**OR897850***	**Beijing, China**	**_s.coll. s.n._ (PE)**
Malus robusta Rehder 1	**OR885575***	**Liaoniing, China**	**_J.H. Sun s.n._ (PE)**
Malus robusta 2	MW115602	-	-
Malus rockii Rehder 1	**OR897851***	**Yunnan, China**	**_C. Xu et al. 44_ (PE)**
Malus rockii 2	MW115600	-	-
Malus sargentii Rehder 1	**OR885576***	**Beijing, China**	**_B.B. Liu 3920_ (PE)**
Malus sargentii 2	MW115605	-	-
Malus sieboldii Rehder 1	**MZ984210**	**Shandong, China**	**_B.B. Liu P1995-4_ (PE)**
Malus sieboldii 2	MT268884	-	-
Malus sieboldii 3	MT593044	-	-
Malus sieversii M.Roem. 1	**MN061985**	**Xinjiang, China**	**_X.X. Zhou s.n._ (PE)**
Malus sieversii 2	MH890570	-	-
Malus sieversii var. *turkmenorum* (Juz. & Popov) Ponomar.	MW018864	-	-
Malus sikkimensis (Wenz.) Koehne 1	**MZ984215**	**Tibet, China**	**_PE Tibet Team PE6293_ (PE)**
Malus sikkimensis 2	MW115603	-	-
Malus sikkimensis 3	**OR885578***	**Beijing, China**	**_Y.L. Liu 29_ (PE)**
Malus spectabilis Borkh. 1	**OR885570***	**Beijing, China**	**_B.B. Liu et al. 3900_ (PE)**
Malus spectabilis 2	MT501657	-	-
Malus sylvestris (L.) Mill. 1	MK434921	-	-
Malus sylvestris 2	LS398109	-	-
Malus sylvestris 3	**OR885569***	**Silesia: Breslau, Germany**	**_C. Baenitz s.n._ (US03697121)**
Malus sylvestris 4	MK434924	-	-
Malus toringo K.Koch	**OR885574***	**Surisan, South Korea**	**_H.J. Jung s.n._ (PE01656258)**
Malus toringoides (Rehder) Hughes 1	MT483999	-	-
Malus toringoides 2	MT442040	-	-
Malus transitoria C.K.Schneid.	MK098838	-	-
Malus trilobata C.K.Schneid.	KX499858	-	-
Malus tschonoskii (Maxim.) C.K.Schneid. 1	KX499864	-	-
Malus tschonoskii 2	KX499863	-	-
Malus yunnanensis C.K.Schneid. 1	MH394388	-	-
Malus yunnanensis 2	MH394387	-	-
Malus zhaojiaoensis N.G.Jiang	OM793283	-	-
Osteomeles anthyllidifolia Lindl.	KY419940	-	-
Osteomeles schwerinae C.K.Schneid.	**MN062000**	**Gansu, China**	**_D.Y. Hong et al. 3429_ (PE)**
Osteomeles subrotunda K.Koch	MK977586	-	-
Peraphyllum ramosissimum Nutt. 1	**KY420011**	**Nevada, USA**	**_B. Maguire & A.H. Holmbren 25288_ (US03513221)**
Peraphyllum ramosissimum 2	**MN068268**	**Mexico**	**_J.B. Phipps & P.G. Smith 5865_ (US00909013)**

Species name	Accession number	Locality	Voucher
Phippsiomeles matudae **(Lundell) B.B.Liu & J.Wen**	**MN062002**	**Jalisco, Mexico**	***R. Mevaugh 13607*** **(US00909015)**
Phippsiomeles mexicana **(Baill.) B.B.Liu & J.Wen**	**MN062003**	**Michoacán, Mexico**	***T.R. Soderstron 4693*** **(US00909034)**
Phippsiomeles microcarpa subsp. *hintonii* (J.B.Phipps) B.B.Liu & J.Wen	MN062001	-	-
Photinia × *fraseri* Dress	MZ128520	-	-
Photinia beckii **C.K.Schneid. 1**	**OP021702**	**Yunnan, China**	***L.Y. Wang et al. 1625*** **(SYS)**
Photinia beckii 2	MN577889	-	-
Photinia chihsiniana **K.C.Kuan**	**OP021703**	**Guangxi, China**	***L.Y. Wang et al. 1540*** **(SYS)**
Photinia crassifolia H.Lév.	MZ984217	-	-
Photinia davidiana Cardot	KY420003	-	-
Photinia glabra **(Thunb.) Poit. 1**	**MK920277**	**Guangxi, China**	***B.B. Liu P1901-2*** **(PE02071209)**
Photinia glabra 2	MZ984218	-	-
Photinia glomerata **Rehder & E.H.Wilson 1**	**OP021704**	**Yunnan, China**	***L.Y. Wang 1666*** **(SYS)**
Photinia glomerata **2**	**OR915979***	**China**	***J. Wen 14605*** **(US)**
Photinia glomerata 3	OM772659	-	-
Photinia integrifolia **Lindl. 1**	**OP021705**	**Yunnan, China**	***L.Y. Wang et al. 1598*** **(SYS)**
Photinia integrifolia 2	MN577879	-	-
Photinia kwangsiensis **H.L.Li**	**OP021706**	**Guangxi, China**	***L.Y. Wang et al. 1719*** **(SYS)**
Photinia lanuginosa **T.T.Yu 1**	**OR915933***	**Hunan, China**	***L.B. Luo 720*** **(PE01498455)**
Photinia lanuginosa 2	MN577890	-	-
Photinia lochengensis **T.T.Yu**	**MN577888**	**Guangxi, China**	***G.R. Long 89009*** **(PE01498456)**
Photinia loriformis **W.W.Sm**	**OP021707**	**Yunnan, China**	***L.Y. Wang 1671*** **(SYS)**
Photinia prionophylla C.K.Schneid. 1	KY419946	-	-
Photinia prionophylla **2**	**MN577891**	**Yunnan, China**	***Z.D. Fang 20-427*** **(PE01498397)**
Photinia prunifolia **(Hook. & Arn.) Lindl. 1**	**OP021708**	**Zhejiang, China**	***B.B. Liu et al. 3233*** **(PE02108424)**
Photinia prunifolia **2**	**OR915934***	**Hainan, China**	***X.X. Zhou 376*** **(PE)**
Photinia pustulata **Lindl.**	**OR149024**	**Lam Dong, Vietnam**	***J. Wen 11063*** **(US00863110)**
Photinia raupingensis **K.C.Kuan 1**	**OP021709**	**Guangdong, China**	***L.Y. Wang 1788*** **(SYS)**
Photinia raupingensis **2**	**MK920279**	**Guangdong, China**	***X.X. Zhou BOP217164*** **(PE)**
Photinia serratifolia **(Desf.) Kalkman 1**	**OP021710**	**Zhejiang, China**	***B.B. Liu et al. 2887*** **(PE02108425)**
Photinia serratifolia **2**	**MN577865**	**Fujian, China**	***B.B. Liu 2408*** **(PE)**
Photinia sp.	MT230547	-	-
Photinia stenophylla **Hand.-Mazz.**	**OP021711**	**Guizhou, China**	***L.Y. Wang 1648*** **(SYS)**
Photinia taishunensis **G.H.Xia, L.H.Lou & S.H.Jin**	**MK920278**	**Zhejiang, China**	***B.B. Liu P1950-5*** **(PE)**
Photinia undulata Cardot	MZ562937	-	-
Pourthiaea amphidoxa **(C.K.Schneid.) Stapf 1**	**MT249042**	**Hubei, China**	***B.B. Liu 2072*** **(PE)**
Pourthiaea amphidoxa **2**	**MN061992**	**Sichuan, China**	***L. Xie SC2014013*** **(PE02050150)**
Pourthiaea amphidoxa **3**	**MT249049**	**Sichuan, China**	***W.B. Ju et al. HGX12711*** **(CDBI0227127)**
Pourthiaea amphidoxa **4**	**MT249053**	**Guangxi, China**	***S.Q. Chen 16816*** **(PE00738651)**
Pourthiaea amphidoxa **5**	**MT249052**	**Hunan, China**	***Y.F. Deng et al. 11700*** **(PE01598124)**
Pourthiaea amphidoxa **6**	**MT249059**	**Guizhou, China**	***B.B. Liu 2530*** **(PE)**
Pourthiaea amphidoxa **7**	**MT249061**	**Guizhou, China**	***M.T. An 0086*** **(PE00738553)**
Pourthiaea amphidoxa **8**	**MT249055**	**Chongqing, China**	***B.B. Liu P1918-4*** **(PE02090670)**
Pourthiaea amphidoxa **9**	**MT249062**	**Guangxi, China**	***Flora Survey Team of Hua Ping Nature Reserve H0528*** **(PE02108460)**

Species name	Accession number	Locality	Voucher
Pourthiaea arguta Decne. 1	MT249051	-	-
Pourthiaea arguta 2	MT249027	-	-
Pourthiaea arguta 3	MT249038	-	-
Pourthiaea arguta 4	MT249039	-	-
Pourthiaea arguta 5	MT249067	-	-
***Pourthiaea arguta* 6**	**MT249028**	**Guangdong, China**	***B.B. Liu 2124* (PE02080624)**
Pourthiaea arguta 7	MT249044	-	-
Pourthiaea arguta 8	MT249046	-	-
Pourthiaea arguta 9	MT249037	-	-
Pourthiaea arguta 10	MT249048	-	-
***Pourthiaea arguta* 11**	**MN061991**	**Sichuan, China**	***B.B. Liu 2208* (PE02080332)**
Pourthiaea arguta 12	MT249035	-	-
Pourthiaea blinii subsp. *blinii* (Lévl.) Iketani & H.Ohashi 1	MN061990	-	-
***Pourthiaea blinii* subsp. *blinii* 2**	**MT249060**	**Yunnan, China**	***S.S. Zhou 1907* (PE01498581)**
***Pourthiaea blinii* subsp. *blinii* 3**	**MT249034**	**Guizhou, China**	***B.B. Liu 2171* (PE02070183)**
***Pourthiaea hirsuta* (Hand.-Mazz.) Iketani & H.Ohashi 1**	**MT249031**	**Zhejiang, China**	***B.B. Liu 2385* (PE)**
Pourthiaea hirsuta 2	MT249032	-	-
***Pourthiaea hirsuta* 3**	**MN061986**	**Fujian, China**	***B.B. Liu 2595* (PE)**
Pourthiaea impressivena (Hayata) Iketani & H.Ohashi	MT249047	-	-
Pourthiaea parvifolia E.Pritz. ex Diels	OR149023	-	-
***Pourthiaea pilosicalyx* (T.T.Yu) Iketani & H.Ohashi 1**	**MN216024**	**Guizhou, China**	***G.F. Wang 29437* (PE01498390)**
Pourthiaea pilosicalyx 2	MT249045	-	-
Pourthiaea pustulata (Lindl.) B.B.Liu & D.Y.Hong 1	MT249033	-	-
Pourthiaea pustulata 2	MT249054	-	-
Pourthiaea salicifolia Decne.	KY419919	-	-
Pourthiaea sorbifolia (W.B.Liao & W.Guo) B.B.Liu & D.Y.Hong 1	MN061994	-	-
Pourthiaea sorbifolia 2	MT249065	-	-
***Pourthiaea tomentosa* (T.T.Yu & T.C.Ku) B.B.Liu & J.Wen 1**	**MT249066**	**Chongqing, China**	***G.F. Li 60885* (PE00739363)**
Pourthiaea tomentosa 2	MN061995	-	-
***Pourthiaea tsaii* (Rehder) Iketani & H.Ohashi**	**MN061987**	**Yunnan, China**	***B.B. Liu 2186* (PE02080401)**
***Pourthiaea villosa* Decne. 1**	**MT249063**	**Hondo, Japan**	***M. Furuse 50324* (PE01656471)**
Pourthiaea villosa 2	MT249058	-	-
Pourthiaea villosa 3	MN061989	-	-
Pourthiaea villosa 4	MT249029	-	-
***Pourthiaea villosa* 5**	**MT249041**	**Guangxi, China**	***B.B. Liu P1906-1* (PE02070280)**
***Pourthiaea villosa* 6**	**MT249050**	**Honshu, Japan**	***K. Yonekura 1907* (PE01523677)**
***Pourthiaea villosa* 7**	**MT249064**	**Japan**	***M. Furuse 29437* (PE01156868)**
***Pourthiaea villosa* 8**	**MT249057**	**Shandong, China**	***B.B. Liu P1993-1* (PE02070879)**
***Pourthiaea villosa* 9**	**MT249040**	**Jiangxi, China**	***B.B. Liu P1978-1* (PE02070057)**
***Pourthiaea villosa* 10**	**MT249056**	**Hubei, China**	***B.B. Liu P2085-2* (PE02071412)**

Species name	Accession number	Locality	Voucher
Pourthiaea villosa 11	MT249030	-	-
Pourthiaea villosa 12	MT249043	-	-
Pourthiaea villosa 13	MT249036	-	-
***Pourthiaea zhejiangensis* (P.L.Chiu) Iketani & H.Ohashi**	**MN061988**	**Zhejiang, China**	***L.Y. Wang 29509* (SYS)**
Pseudocydonia sinensis (Thouin) C.K.Schneid. 1	MN577871	-	-
Pseudocydonia sinensis 2	KT932967	-	-
Pseudocydonia sinensis 3	KX499860	-	-
***Pyracantha angustifolia* C.K.Schneid. 1**	**OR915905***	**Sichuan, China**	***FLPH Sichuan Expedition 151081* (PE)**
Pyracantha angustifolia 2	KY419957	-	-
Pyracantha coccinea M.Roem.	OM232776	-	-
***Pyracantha fortuneana* (Maxim.) H.L.Li 1**	**MK920290**	**Shaanxi, China**	***D.Y. Hong et al. 3443* (PE)**
Pyracantha fortuneana 2	KY419954	-	-
***Pyrus bretschneideri* Rehder 1**	**OR897831***	**Beijing, China**	***B.B. Liu 3977* (PE02234013)**
Pyrus bretschneideri 2	KX450881	-	-
Pyrus calleryana Decne. 1	OK545538	-	-
***Pyrus calleryana* 2**	**OR897832***	**Guangdong, China**	***B.B. Liu P1896-2* (PE02071584)**
***Pyrus communis* L. 1**	**MN577870**	**Beijing, China**	***B.B. Liu 3978* (PE)**
Pyrus communis 2	KX450879	-	-
Pyrus demetrii Kuth.	MT028510	-	-
Pyrus elata (G.Klotz) M.F.Fay & Christenh.	MN594522	-	-
Pyrus fauriei C.K.Schneid.	OK545529	-	-
Pyrus georgica Kuthath.	MN594523	-	-
Pyrus hopeiensis T.T.Yu	MF521826	-	-
Pyrus pashia Buch.-Ham. ex D.Don 1	KY626169	-	-
Pyrus pashia 2	KY419974	-	-
***Pyrus pashia* 3**	**OR897833***	**Sichuan, China**	***FLPH Sichuan Expedition 151625* (PE)**
***Pyrus phaeocarpa* Rehder 1**	**OR897834***	**Beijing, China**	***B.B. Liu et al. 3881* (PE)**
Pyrus phaeocarpa 2	MK488091	-	-
Pyrus pyraster (L.) Burgsd.	MT028511	-	-
Pyrus pyrifolia (Burm.f.) Nakai	KX450877	-	-
Pyrus salicifolia Pall.	MT028513	-	-
Pyrus spinosa Forssk.	HG737342	-	-
Pyrus trilocularis D.K.Zang & P.C.Huang	ON660523	-	-
Pyrus turcomanica Maleev	MN594524	-	-
Pyrus ussuriensis Maxim. 1	KX450883	-	-
***Pyrus ussuriensis* 2**	**OR897835***	**Liaoning, China**	***Y.N. Xiong & B.B. Liu 201812* (PE02234050)**
Pyrus ussuriensis 3	MK507863	-	-
Pyrus ussuriensis 4	MK172841	-	-
Rhaphiolepis angustissima (Hook.f.) B.B.Liu & J.Wen	MT890259	-	-
Rhaphiolepis bengalensis (Roxb.) B.B.Liu & J.Wen	MT876406	-	-
Rhaphiolepis bengalensis f. *angustifolia* (Cardot) B.B.Liu & J.Wen	KY419922	-	-

Species name	Accession number	Locality	Voucher
Rhaphiolepis bibas (Lour.) Galasso & Banfi 1	KT633951	-	-
Rhaphiolepis bibas 2	MK787302	-	-
Rhaphiolepis bibas 3	MN577877	-	-
Rhaphiolepis brevipetiolata J.E.Vidal	OK638182	-	-
***Rhaphiolepis cavaleriei* (H.Lév.) B.B.Liu & J.Wen 1**	**MK920283**	**Hunan, China**	***B.B. Liu 2585* (PE02070509)**
Rhaphiolepis cavaleriei 2	MT473722	-	-
Rhaphiolepis deflexa (Hemsl.) B.B.Liu & J.Wen 1	MT473724	-	-
***Rhaphiolepis deflexa* 2**	**MK920282**	**Guangdong, China**	***H.M. Li & B.B. Liu 201818* (PE)**
Rhaphiolepis dubia (Lindl.) B.B.Liu & J.Wen	MT890261	-	-
Rhaphiolepis elliptica (Lindl.) B.B.Liu & J.Wen	MT890256	-	-
Rhaphiolepis ferruginea F.P.Metcalf	MN577866	-	-
Rhaphiolepis fulvicoma (Chun ex W.B.Liao, F.F.Li & D.F.Cui) B.B.Liu & J.Wen	MT890255	-	-
Rhaphiolepis glabrescens (J.E.Vidal) B.B.Liu & J.Wen	MT890258	-	-
***Rhaphiolepis henryi* (Nakai) B.B.Liu & J.Wen**	**MN577880**	**Yunnan, China**	***J.S. Yang 91-002* (PE00799430)**
***Rhaphiolepis impressivena* Masam.**	**MN577886**	**Taiwan, China**	***T.C. Chen 11873* (PE01438973)**
Rhaphiolepis indica (L.) Lindl. 1	KY419927	-	-
Rhaphiolepis indica 2	MN577864	-	-
***Rhaphiolepis lanceolata* Hu**	**MN577867**	**Guangxi, China**	***B.B. Liu 2153* (PE)**
Rhaphiolepis laoshanica (W.B.Liao, Q.Fan & S.F.Chen) B.B.Liu & J.Wen 1	MT130714	-	-
Rhaphiolepis laoshanica 2	MT130715	-	-
Rhaphiolepis major Cardot	MN577887	-	-
Rhaphiolepis malipoensis (K.C.Kuan) B.B.Liu & J.Wen 1	MN577881	-	-
Rhaphiolepis malipoensis 2	LAU10002	-	-
***Rhaphiolepis obovata* (W.W.Sm.) B.B.Liu & J.Wen**	**MN577882**	**Yunnan, China**	***W.Q. Yin 580* (PE00799660)**
Rhaphiolepis philippinensis (S.Vidal) Kalkman	MT890262	-	-
Rhaphiolepis prinoides (Rehder & E.H.Wilson) B.B.Liu & J.Wen	MT876398	-	-
***Rhaphiolepis salicifolia* Lindl.**	**MN577876**	**Guangdong, China**	***H.M. Li et al. 201815* (PE)**
***Rhaphiolepis salwinensis* (Hand.-Mazz.) B.B.Liu & J.Wen**	**MN577883**	**Guizhou, China**	***Qingzang Team 7390* (PE01147725)**
Rhaphiolepis seguinii (H.Lév.) B.B.Liu & J.Wen 1	MN577885	-	-
Rhaphiolepis seguinii 2	MN577884	-	-
Rhaphiolepis serrata (J.E.Vidal) B.B.Liu & J.Wen	MT876401	-	-
Rhaphiolepis stipularis (Craib) B.B.Liu & J.Wen	MT890260	-	-
Rhaphiolepis tengyuehensis (W.W.Sm.) B.B.Liu & J.Wen	MT876397	-	-
Rhaphiolepis umbellata Makino 1	MN577868	-	-
Rhaphiolepis umbellata 2	KY419931	-	-
Rhaphiolepis williamtelliana (Champ. ex Benth.) B.B.Liu & J.Wen 1	MT473725	-	-
Rhaphiolepis williamtelliana 2	LAU10001	-	-

Species name	Accession number	Locality	Voucher
Sorbus aestivalis Koehne	ON049656	-	-
***Sorbus albopilosa* T.T.Yu & L.T.Lu 1**	**OR915913***	**Tibet, China**	***PE Xizang Expedition PE6822* (PE02330063)**
Sorbus albopilosa 2	ON049662	-	-
Sorbus alnifolia (Siebold & Zucc.) K.Koch 1	KY420010	-	-
Sorbus alnifolia2	MZ145061	-	-
***Sorbus alnifolia* 3**	**OR885566***	**Shandong, China**	***B.B. Liu 1998* (PE02071140)**
Sorbus amabilis Cheng ex T.T.Yu	MT357029	-	-
***Sorbus americana* Marshall 1**	**MZ984219**	**USA**	***L.R. Philippe et al. 42803* (PE02002820)**
***Sorbus americana* 2**	**OR915946***	**Gander, Canada**	***E. Rouleau 5564* (US03697424)**
***Sorbus aria* Wimm. ex Nyman**	**OR897837***	**Russian**	***s.coll. (4)82* (US03698455)**
***Sorbus aronioides* Rehder**	**OR915950***	**Shanxi, China**	***W.S. Gong et al. 3287* (PE01863128)**
***Sorbus arranensis* Hedl.**	**OR915935***	**Norway**	***s.coll. s.n.* (US03697966)**
***Sorbus astateria* (Cardot) Hand.-Mazz.**	**OR915952***	**Tibet, China**	***Eco Shi Plateau Formation 14121* (PE02093614)**
Sorbus aucuparia L. 1	MT610101	-	-
***Sorbus aucuparia* 2**	**OR915953***	**Poland**	***J. Zelazny s.n.* (PE01863032)**
***Sorbus bakonyensis* (Jáv.) Kárpáti**	**OR897827***	**Hungary**	***D. Zsolt et al. 64808* (PE01498819)**
***Sorbus borbasii* Jáv.**	**OR897859***	**Hungary**	***D. Zsolt et al. 64814* (PE01498820)**
***Sorbus buschiana* Zinserl.**	**OR915954***	**Russian**	***T. Zaikonnikova 5921a* (PE01683210)**
***Sorbus californica* Greene**	**OR915947***	**California, USA**	***A.A. Heller 14706* (US03697546)**
***Sorbus caloneura* Rehder 1**	**OR897830***	**Hunan, China**	***B.B. Liu 2583* (PE02071916)**
***Sorbus caloneura* 2**	**OR915955***	**Guangxi, China**	***B.B. Liu P1910-1* (PE02071948)**
***Sorbus cashmiriana* Hedl.**	**OR915991***	**India**	***W. Koelz 5195* (US03698176)**
Sorbus chamaemespilus Crantz	MN061999	-	-
Sorbus cibagouensis H.Peng & Z.J.Yin	ON049660	-	-
Sorbus commixta Hedl.	MK920288	-	-
Sorbus coronaria MacMill.	MN068247	-	-
***Sorbus coronata* (Cardot) T.T.Yu & Tsai 1**	**OR915907***	**Sichuan, China**	***FLPH Sichuan Expedition 151726* (PE)**
***Sorbus coronata* 2**	**OR915957***	**Sichuan, China**	***FLPH Sichuan Expedition 151374* (PE)**
***Sorbus corymbifera* (Miq.) T.H.Nguyên & Yakovlev**	**OR915958***	**Hainan, China**	***X.X. Zhou s.n.* (PE)**
***Sorbus cretica* (Lindl.) Fritsch & Rech.**	**OR897852***	**Bohemia, Czech Republic**	***M. Deyl s.n.* (US03697898)**
***Sorbus cuspidata* Hedl.**	**OR915922***	**Tibet, China**	***PE Xizang Expedition 7936* (PE)**
***Sorbus decora* (Sarg.) C.K.Schneid.**	**OR915948***	**Quebec, Canada**	***J.A. Calder 2680* (US03697599)**
***Sorbus discolor* (Maxim.) Maxim. 1**	**OR915986***	**Beijing, China**	***B. Liu 6746***
Sorbus discolor 2	OP613260	-	-
Sorbus domestica L. 1	MZ984208	-	-
Sorbus domestica 2	KY419956	-	-
***Sorbus domestica* 3**	**OR915994***	**Griechenland, Greece**	***J. Mattfeld 2839* (US03698004)**
***Sorbus dumosa* Greene**	**OR915949***	**New York, USA**	***E.D. Mcdonald s.n.* (US03697559)**
Sorbus dunnii Rehder	OK054488	-	-
Sorbus edulis K.Koch ex G.Kirchn.	MN061998	-	-
***Sorbus epidendron* Hand.-Mazz.**	**OR915990***	**Yunnan, China**	***B. Bartholomew et al. 237* (US03698096)**

Species name	Accession number	Locality	Voucher
Sorbus ferruginea Rehder	MZ984220	-	-
Sorbus filipes Hand.-Mazz. 1	ON049661	-	-
***Sorbus filipes* 2**	**OR915908***	**Sichuan, China**	***FLPH Sichuan Expedition 152814* (PE)**
***Sorbus folgneri* Rehder 1**	**OR915901***	**Chongqing, China**	***B.B. Liu P1921-7* (PE02070692)**
Sorbus folgneri 2	MK161058	-	-
Sorbus foliolosa Spach 1	ON049652	-	-
***Sorbus foliolosa* 2**	**OR915909***	**Tibet, China**	***Y.S. Chen et al. 13-1493* (PE01992580)**
***Sorbus globosa* T.T.Yu & H.T.Tsai**	**OR915985***	**Yunnan, China**	***B. Liu 2470***
***Sorbus graeca* (Spach) Lodd. ex S.Schauer**	**OR915960***	**Croatia**	***V. Mikolas et al. s.n.* (PE02022194)**
Sorbus helenae Koehne 1	KY419924	-	-
Sorbus helenae 2	ON049667	-	-
Sorbus hemsleyi Rehder 1	ON262427	-	-
***Sorbus hemsleyi* 2**	**MZ984221**	**Sichuan, China**	***J.I. Jeon et al. SI1557* (PE01993957)**
***Sorbus himalaica* Gabrieljan**	**OR897829***	**Nepal**	***C.S. Chang et al. NE020422* (PE01597503)**
***Sorbus hupehensis* C.K.Schneid.**	**OR915961***	**Sichuan, China**	***C.S. Chang et al. SI0955* (PE02007902)**
Sorbus hupehensis var. *paucijuga* (D.K.Zang & P.C.Huang) L.T.Lu	MT916771	-	-
***Sorbus hybrida* L.**	**OR915937***	**Helsinki, Finland**	***A. Haakana s.n.* (US03697979)**
Sorbus hypoglauca (Cardot) Hand.-Mazz.	ON049664	-	-
Sorbus insignis Hedl. 1	MT677871	-	-
***Sorbus insignis* 2**	**OR915962***	**Yunnan, China**	***Qingzang Team 6939* (PE01596471)**
***Sorbus intermedia* (Ehrh.) Pers.**	**OR915938***	**Uppland, Sweden**	***C.G. Alm & H. Smith 435* (US03697970)**
***Sorbus istriaca* Kárpáti**	**OR915939***	**Slovenia**	***V. Mikolas et al. s.n.* (US03697968)**
***Sorbus keissleri* Rehder**	**OR915963***	**Chongqing, China**	***PE Sanxia Expedition 0463* (PE01710431)**
***Sorbus kiukiangensis* T.T.Yu**	**OR915919***	**Yunnan, China**	***X.H. Jin et al. ST1263* (PE01969766)**
***Sorbus koehneana* C.K.Schneid. 1**	**OR915899***	**Hubei, China**	***B.B. Liu 2279* (PE02069831)**
Sorbus koehneana 2	OQ992656	-	-
***Sorbus macrantha* Merr.**	**OR915904***	**Sichuan, China**	***FLPH Sichuan Expedition 150829* (PE)**
***Sorbus matsumurana* Koehne 1**	**OR915980***	**Kokkaido, Japan**	***E.H. Wilson 7281* (US03698324)**
Sorbus matsumurana 2	MZ984222	-	-
***Sorbus mayeri* (Kárpáti) Mikoláš**	**OR897853***	**Croatia**	***V. Mikolas et al. s.n.* (PE02012130)**
***Sorbus megalocarpa* Rehder 1**	**OR915911***	**Tibet, China**	***FLPH Tibet Expedition 12-1867* (PE01960095)**
Sorbus megalocarpa 2	ON259046	-	-
***Sorbus meliosmifolia* Rehder**	**OR915964***	**Gansu, China**	***Baishuijiang Expedition 0409* (PE01857052)**
***Sorbus microphylla* Wenz.**	**OR915906***	**Sichuan, China**	***FLPH Sichuan Expedition 151286* (PE)**
***Sorbus mougeotii* Soy.-Will. & Godr. 1**	**OR915940***	**Gallia, France**	***H. Burdet et al. 134* (US03697969)**
***Sorbus mougeotii* 2**	**OR915965***	**USA**	***Kim & Altvatter 7023V95* (PE01598121)**
Sorbus multijuga Koehne 1	OP613261	-	-
***Sorbus multijuga* 2**	**OR915966***	**Sichuan, China**	***D.E. Boufford et al. 27546* (PE01640135)**
Sorbus munda Koehne	MT683851	-	-
***Sorbus ochracea* (Hand.-Mazz.) J.E.Vidal**	**OR915967***	**Yunnan, China**	***E.D. Liu et al. 3639* (PE01921218)**

Species name	Accession number	Locality	Voucher
Sorbus oligodonta (Cardot) Hand.-Mazz.	**OR915912***	**Tibet, China**	**_PE Xizang Expedition PE5687_ (PE02330070)**
Sorbus pallescens Rehder	**OR915968***	**Sichuan, China**	**_D.E. Boufford et al. 33170_ (PE01579585)**
Sorbus pannonica Kárpáti	**OR915969***	**Croatia**	**_V. Mikolas et al. s.n._ (PE02022195)**
Sorbus persica Hedl. 1	**OR915987***	**Uzbekistan**	**_F.R. Fosberg & S.S. Ikonnikow 55873_ (US03698332)**
Sorbus persica 2	**OR915970***	**Russian**	**_V. Goloskokov 4461_ (PE01683284)**
Sorbus pohuashanensis Hedl. 1	OP613257	-	-
Sorbus pohuashanensis 2	**OR915971***	**China**	**_S.M. Zhang s.n._ (PE)**
Sorbus pohuashanensis 3	**OR915917***	**Jilin, China**	**_Y.N. Xiong & B.B. Liu 201803_ (PE)**
Sorbus poteriifolia Hand.-Mazz.	**OR915972***	**Yunnan, China**	**_Qingzang Team 8804_ (PE01159949)**
Sorbus prattii Koehne 1	MK814479	-	-
Sorbus prattii 2	**OR915915***	**Tibet, China**	**_PE Xizang Expedition PE6854_ (PE02330094)**
Sorbus pseudovilmorinii McAll.	**OR915973***	**Sichuan, China**	**_D.E. Boufford et al. 37204_ (PE01902219)**
Sorbus pteridophylla Hand.-Mazz. 1	ON049651	-	-
Sorbus pteridophylla 2	MZ984223	-	-
Sorbus pteridophylla 3	**OR915916***	**Tibet, China**	**_PE Xizang Expedition 3354_ (PE)**
Sorbus randaiensis Koidz.	**OR915974***	**Taiwan, China**	**_W.H. Hu et al. 2814_ (PE01821897)**
Sorbus reducta Diels	OP613259	-	-
Sorbus rehderiana Koehne 1	**OR915914***	**Tibet, China**	**_PE Xizang Expedition PE6297_ (PE)**
Sorbus rehderiana 2	OK012001	-	-
Sorbus rehderiana var. _cupreonitens_ Hand.-Mazz.	ON049663	-	-
Sorbus rehderiana var. _grosseserrata_ Koehne	**OR897860***	**Tibet, China**	**_Y.S. Chen 13-1489_ (PE01992578)**
Sorbus rhamnoides Rehder	KY419962	-	-
Sorbus rufopilosa C.K.Schneid. 1	KY419990	-	-
Sorbus rufopilosa 2	**OR915921***	**Tibet, China**	**_PE Xizang Expedition 7895_ (PE02333234)**
Sorbus rutilans McAll.	ON049654	-	-
Sorbus salwinensis T.T.Yu & L.T.Lu	**OR915975***	**Yunnan, China**	**_Qingzang Team 9784_ (PE01172077)**
Sorbus sambucifolia (Cham. & Schltdl.) M.Roem. 1	**OR915976***	**Japan**	**_Fusako & Yamazaki 6628_ (PE01638241)**
Sorbus sambucifolia 2	**OR915956***	**Montana, USA**	**_J.L. McMullen 2984_ (US03697621)**
Sorbus sambucifolia 3	**OR915951***	**Alaska, USA**	**_A. Nelson & R.A .Nelson 4149_ (US03697557)**
Sorbus sargentiana Koehne 1	**OR915977***	**Sichuan, China**	**_H.G. Xu 1532_ (PE01640045)**
Sorbus sargentiana 2	ON049655	-	-
Sorbus scalaris Koehne	**OR915920***	**Yunnan, China**	**_X.H. Jin et al. ST2145_ (PE01978718)**
Sorbus scopulina Greene 1	**OR915959***	**Colorado, USA**	**_J. Barrell & S. Spongberg 66-73_ (US03697703)**
Sorbus scopulina 2	**OR915978***	**USA**	**_B. Barhtolomew 6000_ (PE01638246)**
Sorbus semi-incisa Borbás	**OR915941***	**Budapest, Hongary**	**_J.B .Kümmerle s.n._ (US03698033)**
Sorbus setschwanensis Koehne	MK914535	-	-
Sorbus sibirica Hedl.	**OR897838***	**Russia**	**_S. Kharkevich & T. Buch 526_ (PE01638237)**
Sorbus sitchensis var. _grayi_ (Wenz.) C.L.Hitchc. 1	**OR897862***	**USA**	**_Richard & R. Halse 8075_ (PE01921537)**

Species name	Accession number	Locality	Voucher
Sorbus sitchensis var. _grayi_ 2	**OR897861***	**Vancouver, Canada**	**_J.A. Calder & K.T. Mackay 32269_ (US03697841)**
Sorbus slavnicensis Kárpáti 1	**MZ984224**	**Croatia**	**_V. Mikolas et al. s.n._ (PE02012131)**
Sorbus slavnicensis 2	**OR915942***	**Slovenia**	**_V. Mikolas & W. Starmuhler s.n._ (US03698030)**
Sorbus sp. 1	**OR897839***	**Tibet, China**	**_W.B. Ju et al. YLZB0591_**
Sorbus sp. 2	**OR915936***	**Montsalvens, Switzerland**	**_Jaquel 15_ (US03697991)**
Sorbus sp. 3	KY419964	-	-
Sorbus suecica Briq	**OR897854***	**Oland Island, Sweden**	**_F.R. Fosberg 32735_ (US03698026)**
Sorbus tapashana C.K.Schneid.	**OR897863***	**Gansu, China**	**_Y.M. Yuan 1104_ (PE01596429)**
Sorbus tauricola Zaik. ex Sennikov	**OR897836***	**Russia**	**_T. Zaikonnikova 7011_ (PE01499098)**
Sorbus thibetica (Cardot) Hand.-Mazz. 1	**OR915981***	**Tibet, China**	**_PE Xizang Expedition 3240_ (PE)**
Sorbus thibetica 2	MK920287	-	-
Sorbus thomsonii (King ex Hook.f.) Rehder	**OR915982***	**Sichuan, China**	**_PE Gulin Expedition 0159_ (PE01864938)**
Sorbus tianschanica Rupr.	MK920289	-	-
Sorbus torminalis (L.) Crantz 1	**OR915945***	**Hongary**	**_J.B. Kummerle 754_ (US03698129)**
Sorbus torminalis 2	MN062005	-	-
Sorbus torminalis 3	KY457242	-	-
Sorbus torminalis 4	**OR915944***	**Madrid, Spain**	**_A. Rodriguez s.n._ (US03698124)**
Sorbus ulleungensis Chin S.Chang	MG011706	-	-
Sorbus umbellata (Desf.) Fritsch	**OR915943***	**Bohemia, Czech**	**_R. Missbach s.n._ (US03698121)**
Sorbus wilsoniana C.K.Schneid. 1	**OR915983***	**Sichuan, China**	**_PE Gulin Expedition 1059_ (PE01864943)**
Sorbus wilsoniana 2	ON049657	-	-
Sorbus xanthoneura Rehder	**OR897855***	**Hubei, China**	**_B. Bartholomew et al. 1317_ (PE00997146)**
Sorbus zahlbruckneri C.K.Schneid.	**OR915984***	**Hunan, China**	**_Y.B. Luo 3104_ (PE01499118)**
Stranvaesia lasiogyna (Franch.) B.B.Liu 1	**OP021694**	**Yunnan, China**	**_H. Wang 3666_ (PE01439780)**
Stranvaesia lasiogyna 2	**OP021696**	**Sichuan, China**	**_Qingzang Team 11412_ (PE01158556)**
Stranvaesia lasiogyna 3	**OP021697**	**Sichuan, China**	**_Qingzang Team 13564_ (PE00336586)**
Stranvaesia nussia Decne. 1	MK920285	-	-
Stranvaesia nussia 2	MK920284	-	-
Stranvaesia oblanceolata Stapf 1	MK920280	-	-
Stranvaesia oblanceolata 2	**OP021701**	**Yunnan, China**	**_P.Y. Mao 06729_ (PE00739347)**
Stranvaesia oblanceolata 3	**OP021700**	**Yunnan, China**	**_G. Forrest 11855_ (PE00739340)**
Vauquelinia australis Standl.	**MN068250**	**Oaxaca, Mexico**	**_W. Hess & G. Wilhelm 4382_ (US00908940)**
Vauquelinia californica (Torr.) Sarg.	KY419925	-	
Vauquelinia californica subsp. _sonorensis_ W.J.Hess & Henrickson	**MN068269**	**Baja California, Mexico**	**_J. Henrickson 20281_ (US00903444)**
Vauquelinia corymbosa subsp. _heterodon_ (I.M.Johnst.) W.J.Hess & Henrickson	**MN068249**	**California, USA**	**_J. Henrickson 189230_ (US00903439)**
Vauquelinia pauciflora Standl.	**MN068251**	**Arizona, USA**	**_F. Reichenbacher 872_ (US03694614)**
Weniomeles bodinieri (H.Lév.) B.B.Liu 1	MK920276	-	-
Weniomeles bodinieri 2	**OP021698**	**Jiangxi, China**	**_B.B. Liu P1941-3_ (PE02070677)**
Weniomeles bodinieri 3	**OP021695**	**Guangxi, China**	**_Y.M. Wang 322_ (PE01439811)**

Plastome assembly and annotation

In our study, we adopted the Successive Approach combining Reference-based and De novo assembly (SARD approach: Liu et al. 2021, 2023b; Jin et al. 2024), a method offering the possibility of obtaining nearly all plastome-related reads, thus facilitating the production of high-quality chloroplast genomes even from datasets with low coverage. For initial data preparation, we used Trimmomatic v. 0.33 (Bolger et al. 2014) for quality trimming and adapter removal, complemented by FastQC v. 0.11.8 (Andrews 2018) for quality assessment. We then employed NOVOPlasty v. 4.3.3 (Dierckxsens et al. 2016), a *de novo* assembly program known for its accuracy and efficiency. The seed sequence chosen was the ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbc*L), a 600 bp plastome-specific sequence with absence in the mitochondrial genome, to initiate the assembly process. While NOVOPlasty performs well for the deeply sequenced data, the SARD approach is notably effective even with lower-quality raw data. For the assembly process with SARD approach, all plastome-related reads were aligned to a reference genome using Bowtie2 (Langmead and Salzberg 2012), followed by generating a consensus sequence through Geneious Prime (Kearse et al. 2012). Concurrently, a *de novo* assembly was conducted using SPAdes v. 3.13.1 (Bankevich et al. 2012), which included error correction and employed a range of K-mer lengths (21, 33, 55, 77). The final step involved aligning scaffolds from the de novo assembly and contigs from NOVOPlasty to the draft plastome, and this step will effectively correct errors and ambiguities introduced from the first step, yielding a high-quality complete plastome.

We annotated the assembled plastid genomes using the PGA tool (Qu et al. 2019) with a closely related plastome as a reference. This process was followed by a thorough manual review of the coding sequences. We then translated these sequences into proteins using Geneious Prime to confirm the accuracy of the start and stop codons. To precisely delineate the boundaries of the large-single copy (LSC), small-single copy (SSC), and inverted repeats (IRs) regions, we employed the Find Repeats function in Geneious Prime based on the characteristic presence of two reverse complementary repeats in the plastomes of Rosaceae species. After this detailed annotation process, we converted our custom annotations into the format required for NCBI submissions. This involved creating both FASTA files and five-column feature tables, a task we accomplished using the GB2sequin tool (Lehwark and Greiner 2019).

Data matrix generation and sequence cleaning

Our previous studies have consistently shown that phylogenetic trees derived from entire plastome datasets and the 79 concatenated plastid protein-coding sequences (plastid CDSs) yield almost identical topologies within the apple tribe framework (Liu et al. 2020a, 2020b, 2022). This similarity underscores the minimal influence of potential misalignments in the intron regions. Consequently, we opted to utilize the whole plastome for phylogenetic inference in this study. To mitigate systematic errors stemming from alignment inaccuracies, we applied trimAL v. 1.2 (Capella-Gutiérrez et al. 2009) to fine-tune the alignment of the plastome. Additionally, we incorporated Spruceup (Borowiec

2019) to identify, visualize, and eliminate outlier sequences. In this process, we set a window size of 50 and an overlap of 25, ensuring a rigorous and precise approach to enhance the quality and reliability of our phylogenetic analysis.

Phylogenomic analyses based on various inference methods

In our comprehensive study, we implemented a variety of robust inference methodologies to achieve precise and reliable phylogenetic results. Initially, we employed PartitionFinder2 (Stamatakis 2006; Lanfear et al. 2016) to identify the most appropriate partitioning schemes and molecular evolution models, utilizing its default settings. This critical step ensured that the chosen models and schemes were best suited for our dataset, enhancing the accuracy of our subsequent analyses.

For estimating Maximum Likelihood (ML) trees, we utilized the advanced capabilities of IQ-TREE2 v. 2.2.0.3 (Minh et al. 2020), conducting analyses with 1000 SH-aLRT and ultrafast bootstrap replicates. This method provided us with a robust statistical framework to evaluate the reliability of the phylogenetic tree branches. In parallel, we used RAxML v. 8.2.12 (Stamatakis 2014), adopting the GTRGAMMA model for each partition. This process included running 200 rapid bootstrap replicates to support the clade structures in our phylogenetic tree, thus ensuring a comprehensive and reliable assessment of clade support.

Nomenclatural synopsis and typification

Over 11 years, from 2013 to 2023, we conducted an in-depth taxonomic study to examine all names published under the genus *Photinia* and its related genera. This comprehensive review was not a trivial undertaking; it involved a thorough exploration of multiple renowned online botanical databases. These included Tropicos (accessible at https://www.tropicos.org), the International Plant Names Index (IPNI) at https://www.ipni.org/, and The Plant List, available at http://www.theplantlist.org/. Our investigation extended beyond these databases to encompass a wide range of literature pertinent to the genus *Photinia*, ensuring no relevant information was overlooked.

Results

A plastid phylogenetic backbone of *Photinia* and allies

We newly generated 147 complete plastomes for this study, and we collected 563 plastomes representing 370 species to create a detailed phylogenetic framework for the apple tribe. Our efforts resulted in a comprehensive aligned plastome matrix that was used for ML analyses. This matrix, spanning a significant length of 158,752 base pairs, was curated with poorly aligned regions being carefully trimmed to ensure the accuracy of our phylogenetic inferences.

We successfully generated two phylogenetic trees using the ML method, i.e., RAxML and IQ-TREE trees. All these phylogenetic trees consistently corroborated the monophyly of three major clades within the apple tribe (Fig. 3, Suppl. materials 1, 2). Clade I, identified as the most basal of the three, comprises two genera: *Lindleya* and *Kageneckia*. This clade lays the foundation of our phylogenetic understanding of the tribe. Clades II and III, on the other hand, demonstrate a sister relationship to each other and, collectively, they are sister to Clade I. Clade II is uniquely composed of a single genus, *Vauquelinia*, highlighting its distinct evolutionary path within the tribe. Clade III is particularly noteworthy as it corresponds to what was previously known as the subfamily Maloideae, encompassing approximately 24 genera. This finding solidifies the genetic distinctiveness of these genera within the apple tribe. However, there were notable exceptions, including *Amelanchier*, *Malus*, *Sorbus* s.l., and *Stranvaesia*.

Discussion

Refining the phylogenetic backbone with plastome data: towards an updated infra-tribal classification of Maleae

In our study, we integrated representative species from three dry-fruited genera—*Kageneckia*, *Lindleya*, and *Vauquelinia*—alongside a comprehensive sampling of pome-bearing genera to estimate their maternally phylogenetic relationships. The inferred plastid phylogeny (Fig. 3, Suppl. materials 1, 2) corroborated the monophyly of these groups, each representing distinct subtribes within Maleae. Furthermore, this topology indicates a clear successive sister relationship between a combined clade (*Kageneckia* + *Lindleya*) and *Vauquelinia*, relative to the pome-bearing genera. Morphologically, these three clades can be easily distinguished, a distinction further elaborated in the identification key provided later.

However, the phylogenetic relationships among these subtribes have been subject to variability across different studies leveraging diverse genomic datasets (Fig. 4). Phylogenies inferred from transcriptomic data (Xiang et al. 2017; Zhang et al. 2023) reveal a topology similar to the plastome-based topology analyses among these three subtribes, i.e., combined clades of Vauqueliniinae and Malinae together sister to Lindleyinae (Fig. 4A). Conversely, recent phylogenomic studies employing ML inference method with hundreds of single-copy nuclear genes (SCN genes) datasets–785 genes in Liu et al. (2022) and 426 genes in Jin et al. (2023)—have elucidated an alternative phylogenetic hypothesis, (Malinae, Lindleyinae) Vauqueliniinae (Fig. 4B). In contrast, a species tree inferred through a coalescent-based method (Jin et al. 2023) presents a unique topology, i.e., the sister relationship between Lindleyinae and Vauqueliniinae, and then together sister to Malinae (Fig. 4C). Despite the emergence of three divergent topologies, the monophyly of these three clades has been consistently supported across multiple previous studies. This convergence underscores the robustness of this newly proposed infra-tribal taxonomic classification within tribe Maleae, despite the methodological diversity and inherent complexities of phylogenomic analysis.

While the maternally inherited characteristics of plastomes in the Maleae tribe obviate the need for orthology inference, their utility is somewhat limited in identifying hybridization and polyploidization events (McKain et al. 2018; Guo et al. 2023). The complex evolutionary processes within Maleae, such as hybridization, polyploidization, and incomplete lineage sorting, have profoundly influenced its origin and diversification. This is evident from a series of phylogenomic studies that highlight cytonuclear discordance within the tribe (refer to Fig. 2A, B and studies by Liu et al. 2022; Hodel et al. 2023; Jin et al. 2023; Zhang et al. 2023).

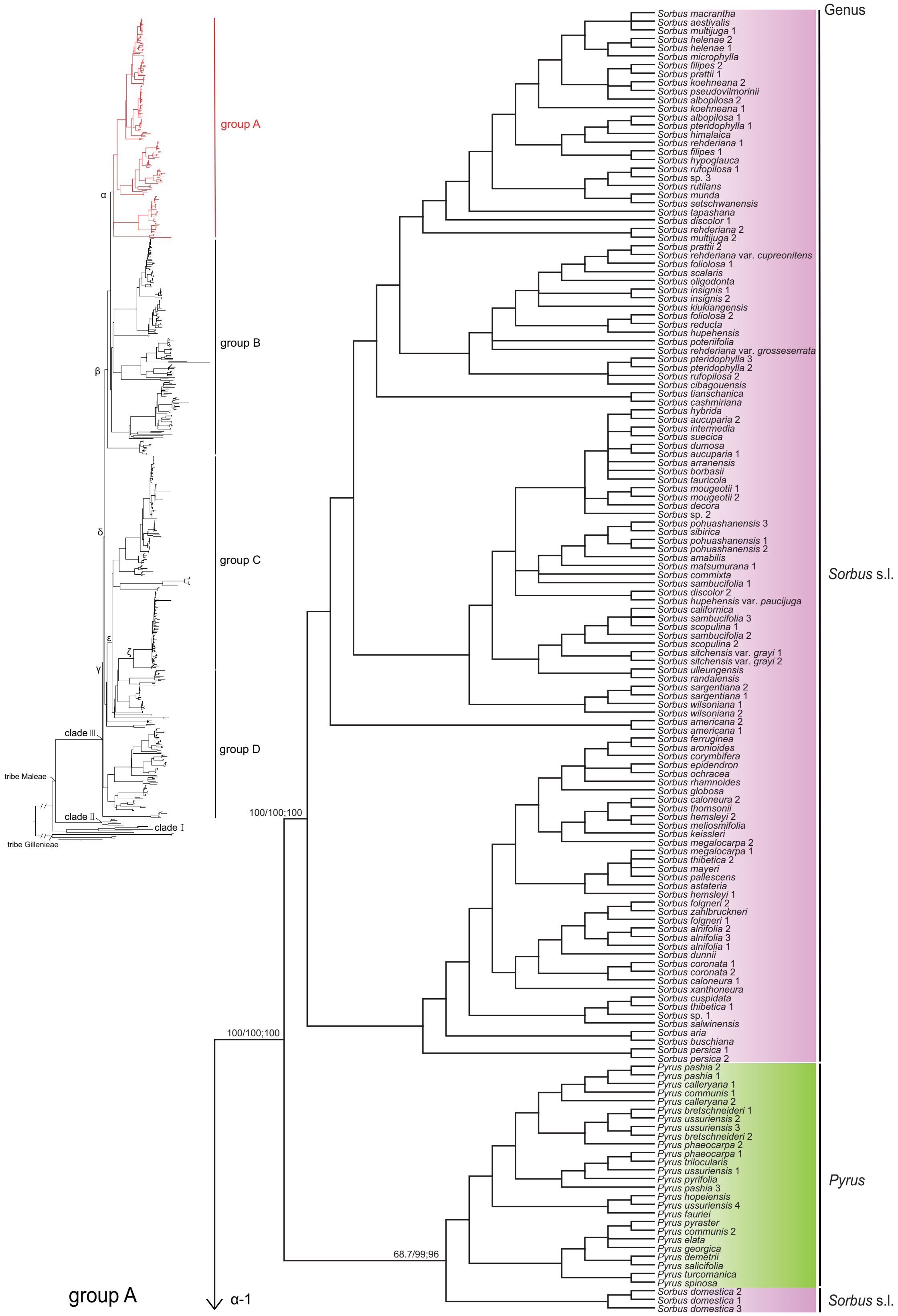


Figure 3. A comprehensive phylogenetic backbone of the apple tribe Maleae, including 563 plastomes across 370 species and 26 genera, estimated by IQ-TREE2 based on the whole plastome dataset. Each of the 26 genera is represented by a unique color for clear distinction. Owing to the extensive scope of the tree, it is segmented into four distinct groups (labeled Group A, B, C, and D), each depicted in separate images. The interconnections among these subgroups are denoted by branch connectors labeled α, β, γ, δ, ε, and ζ.

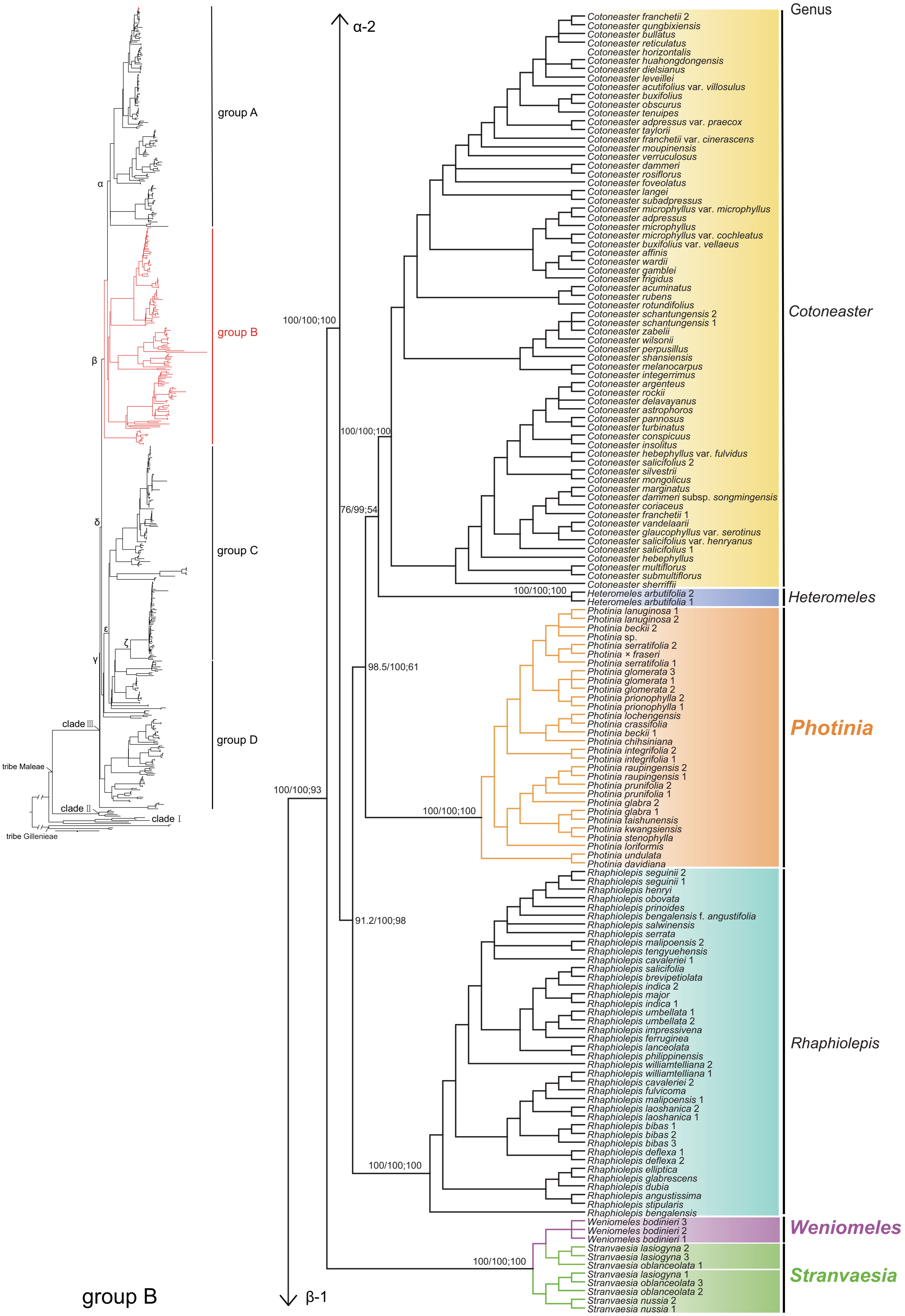


Figure 3. Continued.

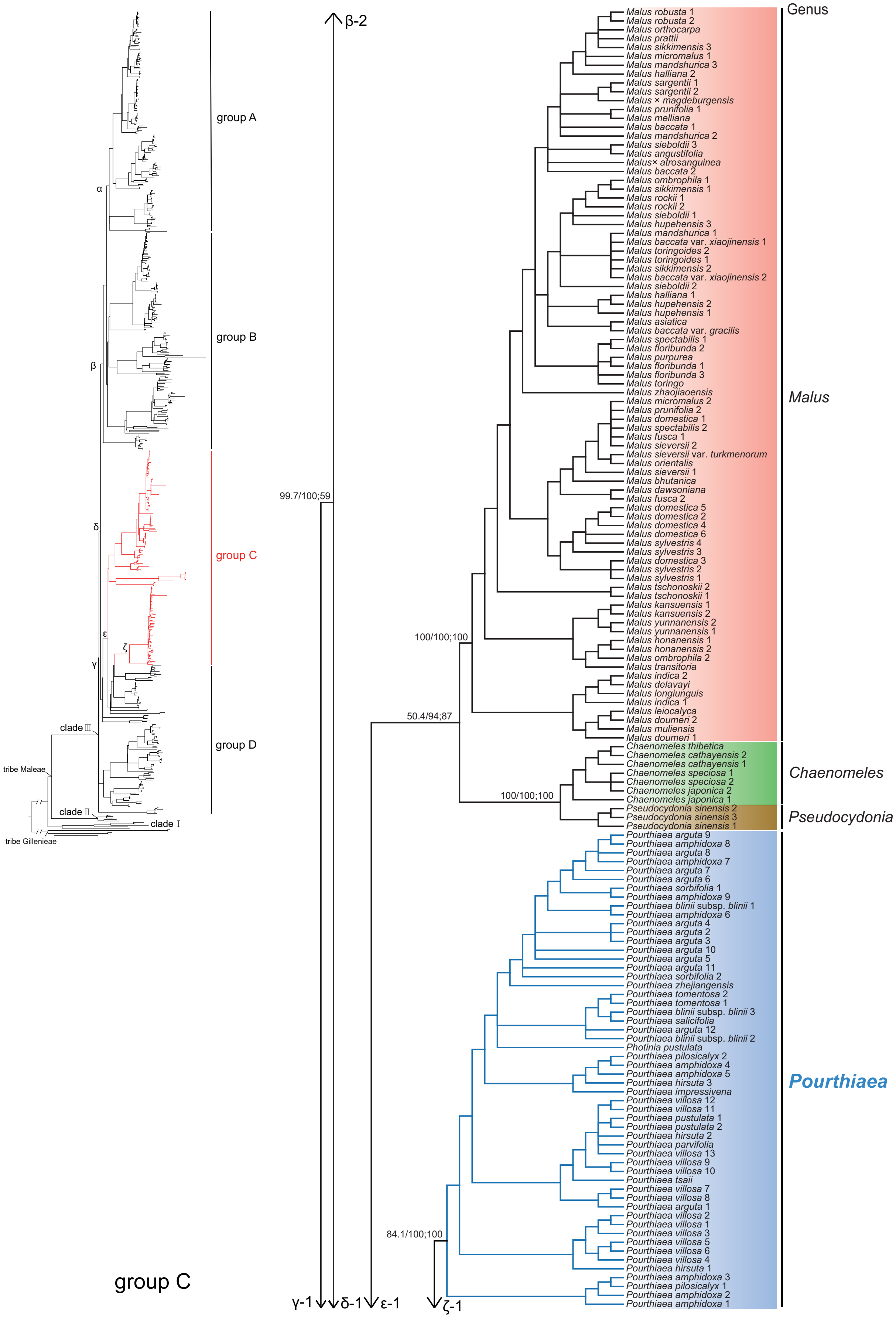


Figure 3. Continued.

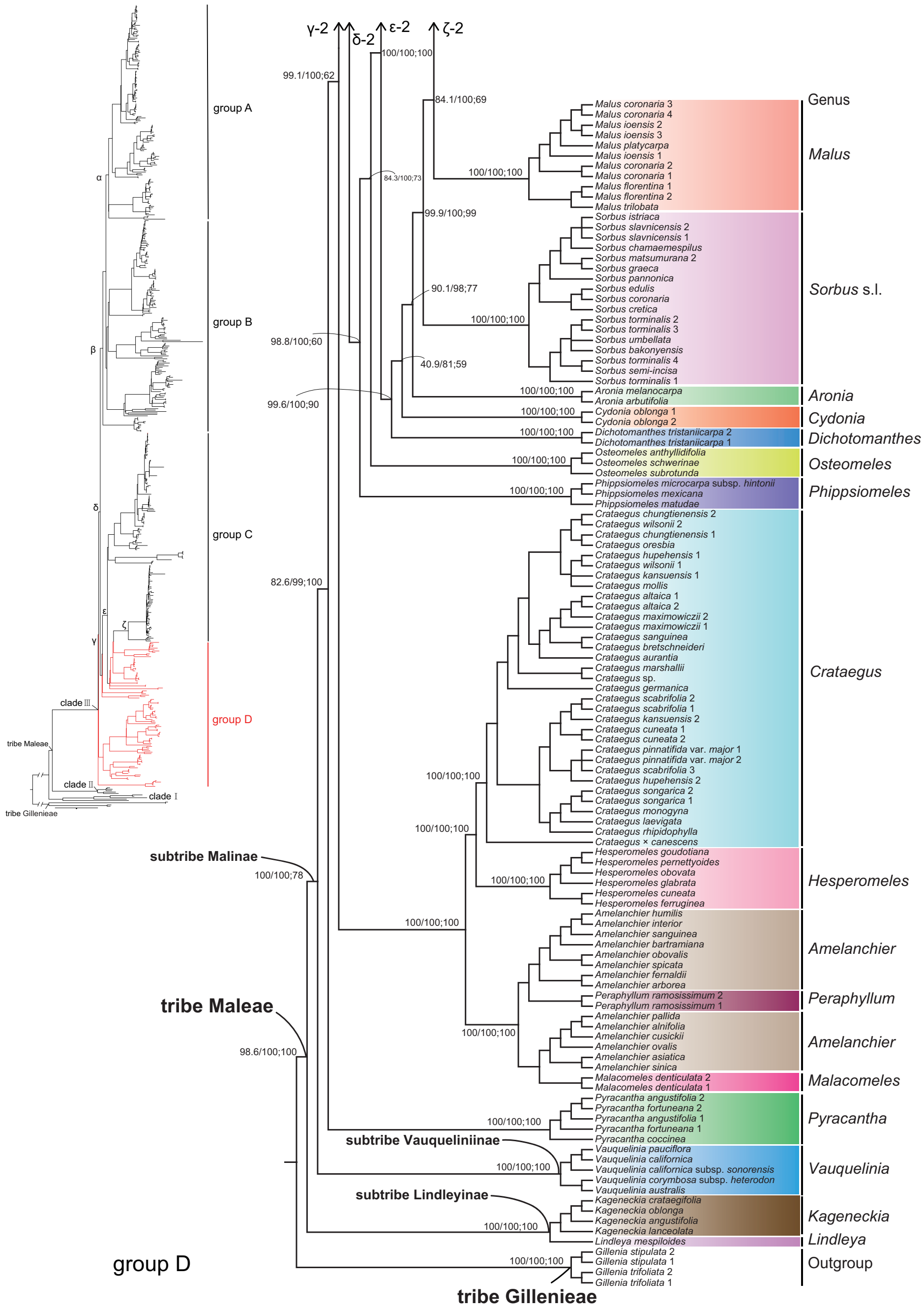


Figure 3. Continued.

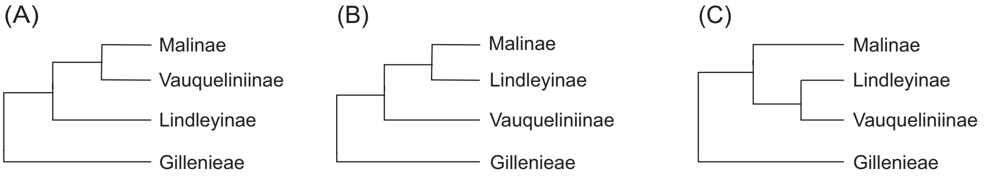


Figure 4. Phylogenetic hypotheses among subtribes within the apple tribe Maleae. **A** plastome-based topology (current study; Liu et al. 2020a); 11 plastid regions- and nuclear ribosomal internal transcribed spacer (nrITS)-based topology (*atp*B-*rbc*L, *psb*A-*trn*H, *rbc*L, *rpl*16 intron, *rpl*20-*rps*12, *rps*16 intron, *trn*C-*ycf*6, *trn*G-*trn*S, *trn*H-*rpl*2, *trn*L-*trn*F, and *trn*K + *mat*K; Lo and Donoghue 2012); transcriptome-based topology (Xiang et al. 2017; Zhang et al. 2023) **B** single-copy nuclear genes (SCN genes)-based topology (inferred from Maximum Likelihood (ML) methods: Liu et al. 2022; Jin et al. 2023) **C** SCN genes-based topology (ASTRAL-III species tree: Liu et al. 2022; Jin et al. 2023).

However, the phylogenetic topologies inferred from hundreds of SCN genes, as illustrated in our previous studies (Liu et al. 2022; Jin et al. 2023), lend strong support to the three major clades identified in our plastid tree (Fig. 3, Suppl. materials 1, 2). These findings have led us to formally propose a taxonomic system for the tribe Maleae, delineating it into three subtribes, i.e., subtribe Lindleyinae, subtribe Malinae, and subtribe Vauqueliniinae. Consequently, this study not only elucidates the phylogenetic placement of these dry-fruited genera within the tribe but also significantly contributes to refining their taxonomy.

Tribe Maleae Small, Man. S.E. Fl. 632. 1933. Type: *Malus* Mill.

= Pyreae Baill., Hist. Pl. 1: 442, 475. 1869. Type: *Pyrus* L.

Key to subtribes of Maleae

1a Leaf margins not horny; carpels ± adnate to hypanthium; flowers: perianth and androecium epigynous; fruit pome; seed not winged or pyrenes; Northern Hemisphere, rarely extending to Central America; 2n = 34 ... **subtribe Malinae**
1b Leaf margins usually horny; carpels free; flowers: perianth and androecium perigynous; Fruit woody capsule or follicle; seed winged; Central & South America; 2n = 30 or 34 .... **2**
2a Fruit capsule or follicle; seed 2 or many; 2n = 34 .... **subtribe Lindleyinae**
2b Fruit capsule; seed 2; 2n = 30 .... **subtribe Vauqueliniinae**

1. Subtribe Malinae Reveal, Phytoneuron 2012-33: 2. 2012.

≡ Malaceae Small, Fl. S.E. U.S. [Small]. 529. 1903, nom. cons. Type: *Malus* Mill.

Remark. This tribe contains ca. 24 genera (ca. 905 species), *Amelanchier* (24 species), *Aronia* (two species), *Chaenomeles* (four species), *Chamaemeles* (one species), *Cotoneaster* (261 species), *Crataegus* (222 species), *Cydonia* (one species), *Dichotomanthes* (one species), *Hesperomeles* (11 species), *Heteromeles* (one species), *Malacomeles* (five species), *Malus* (33 species), *Osteomeles* (two species), *Peraphyllum* (one species), *Phippsiomeles* (five species), *Photinia* (27 species), *Pourthiaea* (seven species), *Pseudocydonia* (one species), *Pyracantha* (six species), *Pyrus* (83 species), *Rhaphiolepis* (42 species), *Sorbus* s.l. (*Chamaemespilus*, *Aria*, *Torminalis*, *Cormus*, *Micromeles*, and *Sorbus* s.s.; ca. 160 species), *Stranvaesia* (three species), and *Weniomeles* (two species). 2n = 34.

2. Subtribe Lindleyinae Reveal, Phytoneuron 2012-37: 217. 2012.

≡ Lindleyaceae J.Agardh, Theoria Syst. Pl. 166. 1858. Type: *Lindleya* Kunth., nom. cons.

Remark. This subtribe contains two genera, *Lindleya* (one species) and *Kageneckia* (ca. three species), distributed in Central and South America. 2n = 34.

3. Subtribe Vauqueliniinae B.B.Liu, subtr. nov.

urn:lsid:ipni.org:names:77342732-1

Type. ***Vauquelinia*** Corrêa ex Bonpl.

Description. Large shrubs or small trees, evergreen. Leaves simple, coriaceous, with serrate margins. Inflorescences terminal, 15–25+-flowered, compound corymbs. Flowers bisexual, 5-merous. Hypanthium hemispherical. Sepals 5, erect, broadly ovate, valvate. Petals 5, white, oblong-ovate to oblong-obovate. Stamens 18-20. Carpels 5, free from hypanthium, ventrally connate; ovules 2 per cell, ascending, apotropous. Fruits capsules, broadly ovoid, sericeous, ventrally (fully) and dorsally (in distal 1/2) dehiscent, splitting into 5 follicles; hypanthium persistent; sepals persistent, erect; styles persistent. Seeds 2 per follicle. 2n = 30.

Remark. This subtribe comprises only one genus, *Vauquelinia*, with about three species distributed in Mexico and the Southwestern United States.

A taxonomic synopsis of *Photinia* and its morphological allies in the Old World

Within the Old World, the genus *Photinia* and its morphologically allied genera can be classified into four distinct clades. These include the deciduous genus *Pourthiaea* and three evergreen genera: *Photinia*, *Stranvaesia*, and *Weniomeles*, as redefined in recent studies (Liu et al. 2019; Jin et al. 2023). This study undertook the most extensive taxonomic sampling to date and inferred a well-supported phylogenetic backbone of these four genera in the framework of the tribe Maleae based on the whole plastome. This finding suggests that the evergreen genus *Photinia* is closely related to a clade combining *Heteromeles* and *Cotoneaster*, the deciduous genus *Pourthiaea* is sister to the transatlantic group of *Malus*, and *Weniomeles* is phylogenetically nested within *Stranvaesia*. Contrarily, the recent transcriptome-based nuclear phylogeny (Zhang et al. 2023) suggested an alternative phylogenetic relationship, positioning *Photinia* alongside *Heteromeles*, and *Pourthiaea* sister to a group of genera characterized by multiple ovules, including *Chaenomeles*, *Cydonia*, and *Pseudocydonia*. It is noteworthy that Zhang et al. (2023) did not include any species of *Stranvaesia* and *Weniomeles* in their sampling. Addressing this sampling gap, the phylogenomic investigation by Jin et al. (2023) elucidated the close phylogenetic relationship between *Stranvaesia* and *Weniomeles*, which, in turn, collectively form a sister clade to a group comprising *Photinia* and *Cotoneaster*. The significant cytonuclear discordance revealed the potential reticulation events in the origin of these genera.

Nomenclaturally, the genus *Pourthiaea* has been thoroughly evaluated, including 213 names in a comprehensive checklist (Lou et al. 2022). In this study, we focus on the remaining three evergreen genera: *Photinia*, *Stranvaesia*, and *Weniomeles*. We aim to conduct an in-depth nomenclature assessment and typification for these genera. This entails a critical review of the existing names, verification of their validity according to botanical nomenclature rules, and clarification of type specimens for each taxon. Our analysis aims to provide clarity and precision in the taxonomic classification of these genera, contributing to a better understanding of their evolutionary relationships and aiding in their accurate identification and study in botanical and ecological research.

***Photinia* Lindl., Bot. Reg. 6: t. 491. 1820., nom. cons.**
Common name: 石楠属 (Chinese name); pinyin (spelled as sounds in Chinese): shi nan shu

Type. *Photinia serrulata* Lindl., nom. illeg. ≡ *Crataegus glabra* Thunb. ≡ *Photinia glabra* (Thunb.) Franch. & Sav., type conserved by Nesom and Gandhi (2009).

Remark. Approximately 27 species and 10 varieties are found across East, South, and Southeast Asia.

1. *Photinia anlungensis* T.T.Yu, Acta Phytotax. Sin. 8: 228. 1963.
Common name: 安龙石楠 (Chinese name); pinyin (spelled as sounds in Chinese): an long shi nan

≡ *Pyrus anlungensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 95. 2018.

Type. China. Guizhou: Anlong, 15 June 1960, *C.S. Chang & Y.T. Chang 5359* (holotype: PE [barcode 00061327!]; isotype: HGAS [barcode 021155!]).

Distribution. China (Guizhou).

2. *Photinia beckii* C.K.Schneid., Ill. Handb. Laubholzk. [C.K.Schneider] 1: 707. 1906.
Common name: 椭圆叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tuo yuan ye shi nan

≡ *Pyrus beckii* (C.K.Schneid.) M.F.Fay & Christenh., Global Fl. 4: 98. 2018.

Type. China. Yunnan: Mengtze, woods, 5500 feet, *A. Henry 9795A* (lectotype, designated by Pathak et al. (2021: 39): E [barcode E00010996!]; isolectotypes: A [barcode 00045594!], US [barcode 00097493!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00010996.

Distribution. China (Yunnan).

3. *Photinia berberidifolia* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1(2): 191. 1912.
Common name: 小檗叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): xiao bo ye shi nan

≡ *Pyrus berberidifolia* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 98. 2018.

Type. China. Sichuan, Tung Valley, May 1904, *E.H. Wilson 3508* (holotype: A [barcode 00038561!]; isotypes: A [barcode 000385610!], K [barcode K000758250!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038561.

Distribution. China (Sichuan).

4. *Photinia chihsiniana* K.C.Kuan, Acta Phytotax. Sin. 8(3): 227. 1963.
Common name: 临桂石楠 (Chinese name); pinyin (spelled as sounds in Chinese): lin gui shi nan

≡ *Pyrus chihsiniana* (K.C.Kuan) M.F.Fay & Christenh., Global Fl. 4: 100. 2018.

Type. CHINA. Guangxi: Lingui, 8 May 1950, *C.S. Chung 808097* (holotype: IBK [barcode IBK00062054!]; isotypes: GAC [barcode GAC0010558], IBSC [barcode 0004364!], PE [barcode 00299791!]). ibidem, 22 November 1953, *C.F. Liang 31096* (paratypes: GAC [barcode GAC0010567!], IBSC [barcode 0004332!], KUN [barcode 607115!], PE [barcode 00299793!], SYS [barcode sys00075317!]). Lingui, Yanshan, 20 April 1951, *C.S. Chung 808829* (paratypes: GAC [barcode GAC0010559!], IBSC [barcode 0318308!], PE [barcode 00299794!]). ibidem, *C.S. Chung 808871* (paratypes: GAC [barcode GAC0010557!], IBK [barcode IBK00062057!, IBK00062205!], IBSC [barcode 0318305!, 0318306!]). ibidem, 23 July 1950, *C.S. Chung 808679* (paratypes: GAC [barcode GAC0010573!], IBK [barcode IBK00062224!], IBSC [barcode 0318307!]). Pinglou, 23 April 1958, *Z.Z. Chen 52327* (paratypes: IBK [barcode IBK00062052!, IBK00190808!], IBSC [barcode 0335042!], KUN [barcode 607345!]). Guilin, 8 July 1937, *W.T. Tsang 27773* (paratypes: IBSC [barcode 0318304!], SYS [barcode SYS00074928!]). ibidem, August 1937, *W.T. Tsang 27992* (paratypes: IBSC [barcode 0318303!], SYS [barcode sys00095740!]). ibidem, 29 March 1948, *C.N. Tang 13423* (paratype: IBK [barcode IBK00062056!]).

Distribution. China (Guangxi and Hunan).

5. *Photinia chingiana* Hand.-Mazz., Sinensia 2: 125. 1932.
Common name: 宜山石楠 (Chinese name); pinyin (spelled as sounds in Chinese): yi shan shi nan

≡ *Pyrus chingiana* (Hand.-Mazz.) M.F.Fay & Christenh., Global Fl. 4: 100. 2018.

Type. CHINA. Kwangsi (Guangxi, Yishan): Bui-tung, Nibai ad conf. prov. Kweichou, 1000 m, in silvis apertis vel ripis rivorum, raro, 27 June 1928, *R.C. Ching 6244* (lectotype, designated by Pathak et al. (2021: 39): NY [barcode NY00436112!; isolectotypes: IBSC [barcode 0004365!], NAS [barcode NAS00071252!, NAS00071253!], PE [barcode 00026318!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00436112.

Distribution. China (Guangxi and Guizhou).

5a. *Photinia chingiana* var. *chingiana*
Common name: 宜山石楠 (原变种) (Chinese name)

= *Photinia austroguizhouensis* Y.K.Li, Bull. Bot. Res., Harbin 6(4): 107. 1986. Type: CHINA. Guizhou: Libo, *M.Z. Yang et al. 810333* (holotype: HGAS; isotype: PE [barcode 01432751!]).

= *Photinia simplex* Y.K.Li & X.M.Wang, Bull. Bot. Res., Harbin 8(3): 133. 1988. Type: CHINA. Guizhou: Sandu County, Yaorenshan, *Y.K. Li 10173* (holotype: HGAS; isotype: PE [barcode 01432750!]).

Distribution. China (Guangxi and Guizhou).

5b. *Photinia chingiana* var. *lipingensis* (Y.K.Li & M.Z.Yang) L.T.Lu & C.L.Li, Acta Phytotax. Sin. 38(3): 277. 2000.

Common name: 黎平石楠 (Chinese name); pinyin (spelled as sounds in Chinese): li ping shi nan

≡ *Photinia lipingensis* Y.K.Li & M.Z.Yang, Bull. Bot. Res., Harbin 8(3): 134. 1988.

Type. China. Guizhou: Liping, Zhongchao, October 1987, *D.F. Huang 714* (holotype: HGAS; isotype: PE [barcode 01432752!]).

Distribution. China (Guizhou).

6. *Photinia chiuana* Z.H.Chen, Feng Chen & X.F.Jin, J. Hangzhou Univ., Nat. Sci. Ed. 20(1): 32. 2021.

Common name: 裘氏石楠 (Chinese name); pinyin (spelled as sounds in Chinese): qiu shi shi nan

Type. China. Zhejiang: Qujiang, Hunan Town, Poshi Village, Bijiashanzhuang, alt. 140 m, 20 May 2019, *Z.H. Chen, L. Chen, & Q.S. Lin QJ19052001* (holotype: ZM; isotype: ZM).

Distribution. China (Zhejiang).

7. *Photinia crassifolia* H.Lév., Flore du Kouy-Tchéou 349. 1915.

Common name: 厚叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): hou ye shi nan

≡ *Pyrus crassifolia* (H.Lév.) M.F.Fay & Christenh., Global Fl. 4: 101. 2018.

= *Photinia cavaleriei* H.Lév., Repert. Spec. Nov. Regni Veg. 11: 66. 1912. later homonym. non H.Lév., Repert. Spec. Nov. Regni Veg. 4: 334. 1907. Type: CHINA. Guizhou: Tin-fan (= Huishui), June 1909, *J. Cavalerie 3571* (holotype: E [barcode E00011309!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011309.

= *Photinia crassifolia* var. *denticulata* Cardot, Notul. Syst. (Paris) 3: 372. 1918. Type: CHINA. Guizhou, San-chouen (= Anshun), 1910, *J. Cavalerie 3571-pp* (lectotype, designated by Pathak et al. (2021: 39): P [barcode P02143157!]; isotype: P [barcode P02143156!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143157.

Type. China. Guizhou: Gan-chouen (= Anshun), April 1912, *J. Cavalerie 3571* (lectotype, designated by Pathak et al. (2021: 39): E [barcode E00284677!];

isolectotype: P [barcode P02143158!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143158.

Distribution. China (Guangxi, Guizhou, and Yunnan).

8. *Photinia cucphuongensis* T.H.Nguyên & Yakovlev, Bot. Zhurn. (Moscow & Leningrad) 65(9): 1351 (in error as 1251). 1980.

Common name: 菊芳石楠 (Chinese name); pinyin (spelled as sounds in Chinese): ju fang shi nan

≡ *Pyrus cucphuongensis* (T.H.Nguyên & Yakovlev) M.F.Fay & Christenh., Global Fl. 4: 101. 2018.

Type. Vietnam. Ninh Binh: Cuc Phuong, 29 January 1975, *A.L. Takhtadjan & N.T. Hiep 8565* (holotype: LE; isotype: HN).

Distribution. Vietnam.

9. *Photinia davidiana* (Decne.) Cardot, Bull. Mus. Natl. Hist. Nat. 25(5): 399. 1919.

Common name: 红豆果树 (Chinese name); pinyin (spelled as sounds in Chinese): hong dou guo shu

≡ *Stranvaesia davidiana* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 179. 1874.

Type. China. Tibet: Baoxing, Mou-Pin "now belongs to Sichuan", 1870, *A. David s.n.* (holotype: P [barcode P02143103!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143103.

9a. *Photinia davidiana* var. *davidiana*

Fig. 5

Common name: 红豆果树(原变种)(Chinese name)

= *Stranvaesia integrifolia* Stapf, Hooker's Icon. Pl. 23: t. 2295. 1894. ≡ *Photinia havilandii* Stapf, Bot. Mag. 149: sub t. 9008. 1924, replacement name. Type: MALESIA. Borneo: Kinabalu, *G.D. Haviland 1071* (holotype: K [barcode K000758362!]; isotypes: K [barcode K000758363!], BM [barcode BM000602185!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758362.

= *Stranvaesia henryi* Diels, Bot. Jahrb. Syst. 36(5, Beibl. 82): 52. 1905. Type: CHINA. Sichuan, February 1890, *A. Henry 8953* (lectotype, designated by Vidal (1965: 232): K [barcode K000758304!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758304.

= *Photinia niitakayamensis* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 103. 1911. ≡ *Stranvaesia niitakayamensis* (Hayata) Hayata, Icon. Pl. Formosan. 8: 33. 1919. Type: CHINA. Taiwan: Chiayi, Yushan, Mt. Niitaka, *S. Nagasawa 551* (**lectotype, designated here**: KYO [barcode KYO00022357!]; isolectotype: KYO [barcode KYO00022358!]).

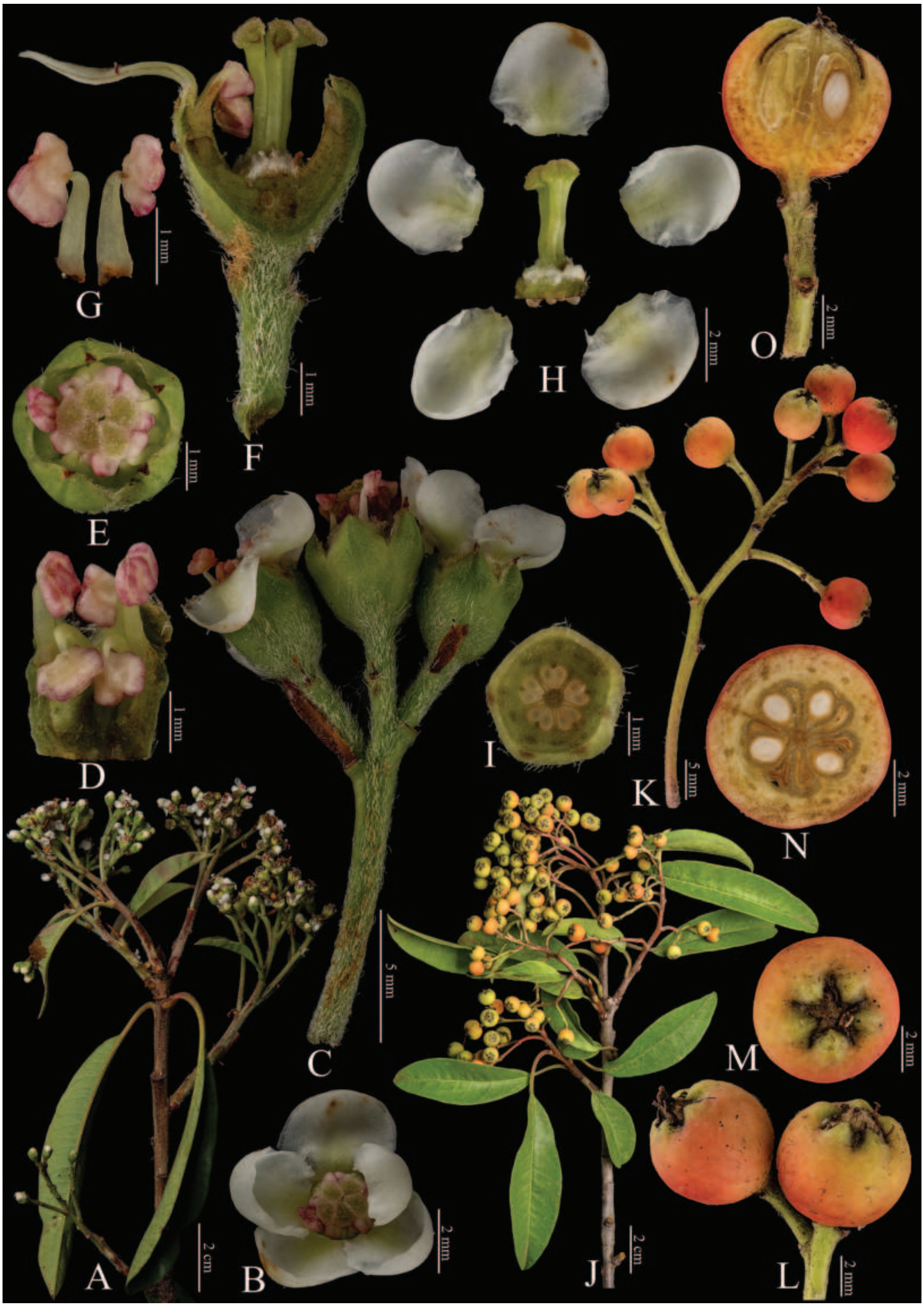


Figure 5. Fine structure of *Photinia davidiana*, encompassing various developmental stages and perspectives. **A** inflorescence branch **B** top view of a single flower **C** inflorescence branchlet **D, G** stamens **E** top view of an unopened flower **F** longitudinal section through the ovary **H** dissected flower showing internal structures **I** cross-section of the immature ovary **J** infructescence branch **K** infructescence branchlet **L** mature fruit **M** fruit, viewed from above **N** cross-sections of fruit **O** longitudinal section of fruit. The inflorescence branches (**A–I**) were collected on April 15, 2024, while the infructescence branches (**J–O**) were gathered on October 7, 2023. Yan-Li Wen was responsible for the collection of all fresh specimens at the Kunming Institute of Botany, Chinese Academy of Sciences (Yunnan, China). Furthermore, Bin-Jie Ge (Chenshan Botanical Garden, Shanghai, China) dissected and photographed all the samples.

= *Pyrus cavaleriei* H.Lév., Repert. Spec. Nov. Regni Veg. 11: 67. 1912. Type: CHINA. Guizhou: Pin-Fa, *J. Cavalerie 3569* (holotype: P [barcode P02143101!]; isotypes: A [barcode 00045576!], E [barcode E00011338!, E00284670!], P [barcode P02143100!, P02143102!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143101.

= *Photinia undulata* var. *formosana* Cardot, Notul. Syst. (Paris) 3: 372. 1914. ≡ *Photinia davidiana* var. *formosana* (Cardot) H.Ohashi & Iketani, J. Jap. Bot. 69(1): 22. 1994. Type: CHINA. Formose (Taiwan): Arisan (Alishan), *L.U. Faurie 77* (lectotype, designated by Wang et al. (2018: 90): P [barcode P02143109!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143109.

= *Photinia davidiana* f. *latifolia* Cardot, Bull. Mus. Natl. Hist. Nat. 25(5): 399. 1919. Type: CHINA. Yunnan: bois de Kou-toui, au-dessus de Mo-so-yn, *J.M. Delavay 3978* (holotype: L [barcode 1901178!]).

= *Stranvaesia salicifolia* Hutch., Bot. Mag. 146: t. 8862. 1920. ≡ *Stranvaesia davidiana* var. *salicifolia* (Hutch.) Rehder, J. Arnold Arbor.7(1): 29. 1926. Type: CHINA. Hupeh (Hubei): north and south of Ichang, alt. 1300–2000 m, October 1907, *E.H. Wilson 382a* (**lectotype, designated here**: A [barcode 00045607!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00045607.

Distribution. China (Gansu, Guangxi, Guizhou, Hubei, Jiangxi, Shaanxi, Sichuan, Taiwan, Yunnan) and Malaysia (Kinabalu).

9b. *Photinia davidiana* var. *undulata* (Decne.) LongY.Wang, W.Guo & W.B.Liao, Phytotaxa 361(1): 91. 2018.

Common name: 波叶红豆果树 (Chinese name); pinyin (spelled as sounds in Chinese): bo ye hong dou guo shu

≡ *Stranvaesia undulata* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 179. 1874. ≡ *Eriobotrya undulata* (Decne.) Franch., Pl. Delavay. 226. 1890. ≡ *Photinia undulata* Cardot, Bull. Mus. Natl. Hist. Nat. 25: 399. 1919. ≡ *Stranvaesia davidiana* var. *undulata* (Decne.) Rehder & E.H.Wilson, Pl. Wilson. 1(2): 192. 1912.

= *Stranvaesia davidiana* var. *suoxiyuensis* C.J.Qi & C.L.Peng, J. Wuhan Bot. Res. 7(3): 239. 1989. Type: CHINA. Hunan: Cili, *C.L. Peng & C.L. Long 120358* (holotype: CSFC).

Type. China. Kouy-Tcheou (= Guizhou): *Perny s.n.* (holotype: P [barcode P02143104!]; isotype: P [barcode P02143105!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143104.

Distribution. China (Fujian, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Shaanxi, Sichuan, Yunnan, and Zhejiang) and Vietnam (Tonkin).

10. *Photinia glabra* (Thunb.) Franch. & Sav., Enum. Pl. Jap. 1(1): 141. 1873.

Common name: 光叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): guang ye shi nan

≡ *Crataegus glabra* Thunb., Syst. Veg., ed. 14 (J. A. Murray). 465. 1784. ≡ *Mespilus glabra* Poir., Encycl. [J. Lamarck & al.] 4(2): 446. 1798. ≡ *Photinia serrulata* Lindl., Trans. Linn. Soc. London 13: 103, t. 10 (1821), nom. illeg. ≡ *Photinia glabra* (Thunb.) Poit., Rev. Hort. (Paris) 11: 228. 1849. ≡ *Photinia glabra* (Thunb.) Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 19(2): 178. 1873, isonym. ≡ *Photinia glabra* (Thunb.) Decne., Nouv. Arch. Mus. Hist. Nat. 10: 140. 1874, isonym. ≡ *Pyrus thunbergii* M.F.Fay & Christenh., Global Fl. 4: 123. 2018.

= *Photinia glabra* var. *typica* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 19(2): 179. 1873.

Type. Japan. Kanname, *Thunberg 11860* (syntype). ibidem, *Thunberg 11861* (syntype).

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Yunnan, and Zhejiang), Japan, Myanmar, Thailand, and Vietnam.

11. *Photinia griffithii* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 142. 1874.

Fig. 6

Common name: 球花石楠 (Chinese name); pinyin (spelled as sounds in Chinese): qiu hua shi nan

≡ *Eriobotrya griffithii* (Decne.) Franch., Pl. Delavay. 1: 224. 1890. ≡ *Photinia serrulata* var. *congestiflora* Cardot, Notul. Syst. (Paris) 3: 373. 1918. nom. superfl. ≡ *Pyrus griffithiana* M.F.Fay & Christenh.; Global Fl. 4: 105. 2018.

= *Photinia glomerata* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1(2): 190. 1912. ≡ *Pyrus glomerata* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 105. 2018. Type: CHINA. Yunnan, Szemao, *A. Henry 11716* (lectotype, selected by Vidal (1965: 226), first step; second step, designated by Wang et al. (2019: 599): E [barcode E00011310!]; isolectotypes: A [barcode 00038560!], K [barcode K000758251!], MO [barcode MO-255089!], US [barcode 00097496!]). *A. Henry 11716A* (syntypes: US [barcode 00097497!], A [barcode 00045567!, 00045568!], E [barcode E00284676!], K [barcode K000758252!], MO [barcode MO-255088!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011310.

= *Photinia franchetiana* Diels, Notes Roy. Bot. Gard. Edinburgh 5: 272. 1912. Type: CHINA. Yunnan, *G. Forrest 487* (holotype: E [barcode E00011311!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011311

= *Photinia glomerata* Rehder & E.H.Wilson var. *cuneata* T.T.Yu, Acta Phytotax. Sin. 8(3): 227. 1963. Type: CHINA. Yunnan, Yung-jen, *H.T. Tsai 52879* (holotype: PE [barcode 00336359!]; isotypes: IBSC [barcode 0318765!], PE [barcode 00336360!], A [barcode 00137699!], NAS [barcode NAS00071255!], KUN [barcode 608247!]).

= *Photinia glomerata* Rehder & E.H.Wilson var. *microphylla* T.T.Yu, Acta Phytotax. Sin. 8(3): 227. 1963. Type: CHINA. Yunnan, Teng-chuan, Mt. Chih-shan, *R.C. Ching 24894* (holotype: PE [barcode 00336361!]; isotypes: PE [barcode 00336291!], KUN [barcode 607608!]).

= *Photinia semiserrata* H.Li, Fl. Dulongjian Reg. 131. 1993, nom. nud.

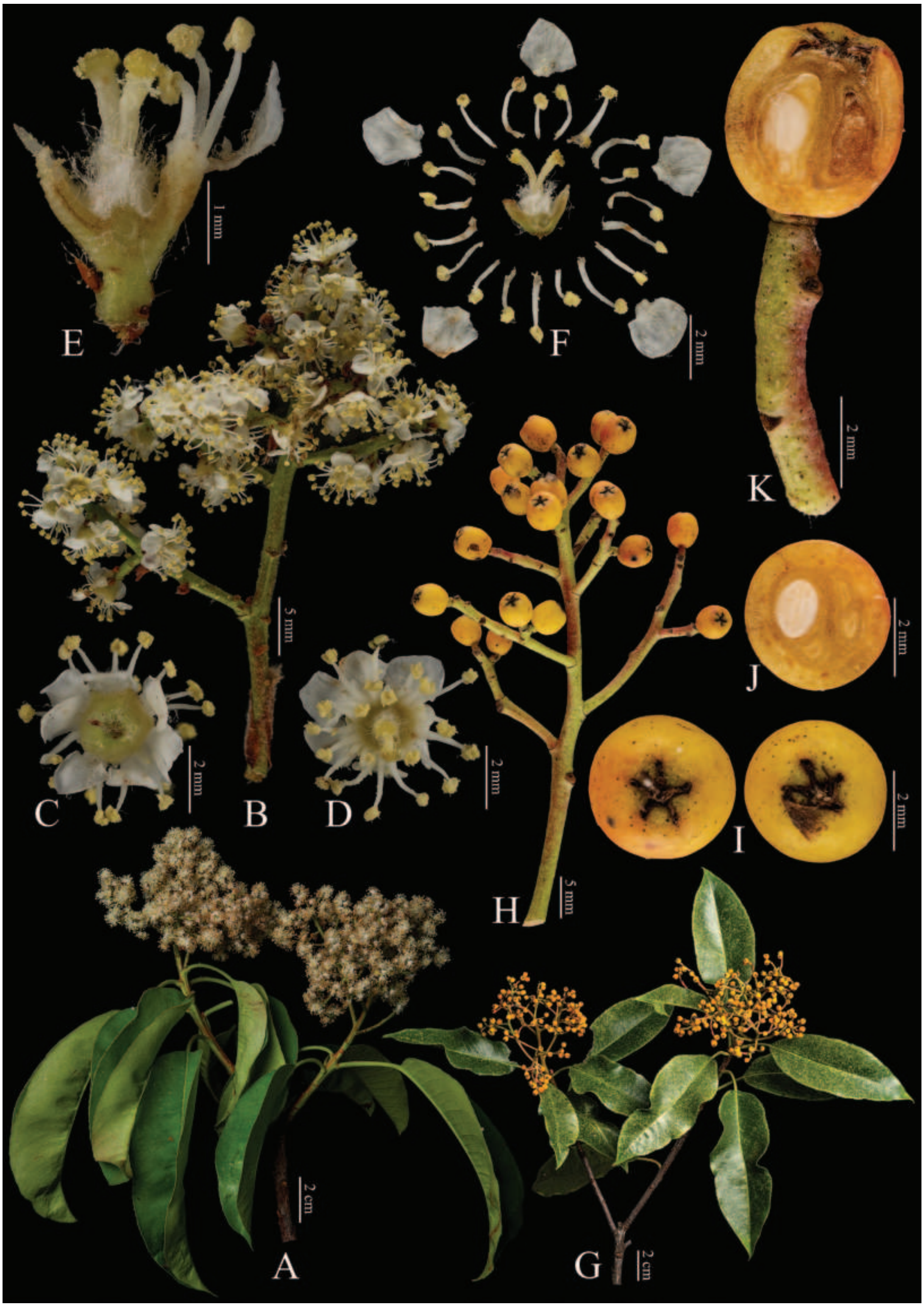


Figure 6. Fine structure of *Photinia griffithii*, encompassing various developmental stages and perspectives. **A** inflorescence branch **B** inflorescence branchlet **C** bottom perspective of an individual flower **D** top view of a single flower **E** longitudinal section through the ovary **F** dissected flower showing internal structures **G** an infructescence branch **H** infructescence branchlet **I** fruit, viewed from above **J** cross-sections of fruit **K** longitudinal section of fruit. The inflorescence branches (**A–F**) were collected on April 15, 2024, while the infructescence branches (**G–K**) were gathered on October 7, 2023. Yan-Li Wen was responsible for the collection of all fresh specimens at the Kunming Institute of Botany, Chinese Academy of Sciences (Yunnan, China). Furthermore, Bin-Jie Ge (Chenshan Botanical Garden, Shanghai, China) dissected and photographed all the samples.

Type. Bhutan. Himalaya orientalis, 1837–1838, *Griffith 2087* (lectotype, designated by Wang et al. (2019: 599): P [barcode P02143170!]; isotypes: K [barcode K000758185!], L [barcode L0019505!], M [barcode M-0213887!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143170.

Distribution. Bhdan and China (Hubei, Sichuan, and Yunnan).

12. *Photinia integrifolia* Lindl., Trans. Linn. Soc. London 13(1): 103, t. 10. 1821.

Common name: 全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): quan yuan shi nan

≡ *Eriobotrya integrifolia* (Lindl.) Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 45(4): 304. 1877. ≡ *Pyrus integrifolia* (Lindl.) M.F.Fay & Christenh., Global Fl. 4: 108. 2018.

Type. Nepal. 7 November 1821, *Wallich 669* (lectotype, selected by Kalkman (1973: 419) 'holotype', first step; second step, designated by Pathak et al. (2019: 184): K [barcode K001111555!]; isolectotypes: E [barcode E00011312!], GH [barcode 00045579!], GZU [barcode 000283019!], K [barcode K000758314!, K001111556!], L [barcode L0019506!, L0019507!], P [barcode P02143206!], NY [barcode 00436120!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k001111555.

Distribution. Bangladesh, Bhutan, China (Guangxi, Guizhou, Tibet, Yunnan), India (Arunachal Pradesh, Assam, Manipur, Meghalaya, Sikkim, Tamil Nadu, Uttar Pradesh, West Bengal), Indonesia (Gunung Ulu Kali, Pahan, Java, Lesser Sunda Isl.), Laos, Myanmar (Chin, Kachin, Mandalay, Sagaing), Nepal, Thailand, and Vietnam.

12a. *Photinia integrifolia* var. *integrifolia*

Fig. 7

Common name: 全缘石楠(原变种)(Chinese name)

= *Pyrus integerrima* Wall. ex D.Don, Prodr. Fl. Nepal. 237. 1825, nom. illeg. superfl. ≡ *Photinia integerrima* (Wall. ex D.Don) N.P.Balakr., Fl. Jowai 1: 191. 1981.

= *Photinia scandens* Stapf, Bot. Mag. 149: sub t. 9008. 1924. ≡ *Stranvaesia scandens* (Stapf) Hand.-Mazz., Symb. Sin. 7(3): 483. 1933. Type: CHINA. Yunnan: Shweli-Salwin divide, *G. Forrest 9329* (holotype: E [barcode E00011339!]; isotypes: K [barcode K000758309!], IBSC [barcode 0318894!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011339.

= *Photinia myriantha* Merr., Brittonia 4: 82. 1941. Type: MYANMAR. Adung Valley, *F.K.Ward 9276* (holotype: A [barcode 00026802!]); Ngawchang Valley, near Black Rock, *F.K. Ward 359* (paratype: NY [barcode 00436121!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00026802.

= *Photinia integrifolia* var. *yunnanensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 229. 1963. Type: CHINA. Yunnan: Wei-si, alt. 2500 m, *K.M. Feng 4167* (holotype:

Figure 7. Fine structure of *Photinia integrifolia*, encompassing various developmental stages and perspectives. **A** inflorescence branch **B1** top view of an unopened flower **B2** top view of an opening flower **C** inflorescence branchlet **D** bottom perspective of an individual flower **E** top view of a single flower with the absence of petals **F** longitudinal section through the ovary **G** dissected flower showing internal structures **H** petals **I** stamens **J** an infructescence branch **K** fruit, viewed from above **L** infructescence branchlet **M** longitudinal section of fruit **N** cross-sections of fruit. The inflorescence branches (**A–I**) were collected on April 15, 2024, while the infructescence branches (**J–N**) were gathered on October 7, 2023. Yan-Li Wen was responsible for the collection of all fresh specimens at the Kunming Institute of Botany, Chinese Academy of Sciences (Yunnan, China). Furthermore, Bin-Jie Ge (Chenshan Botanical Garden, Shanghai, China) dissected and photographed all the samples.

PE [barcode 00004602!]; isotypes: PE [barcode 00336524!, 00336554!], KUN [barcode 607497!]). Kung-shan (Champutung) alt. 1600–1800 m, *K.M. Feng 8153* (paratypes: PE [barcode 00336477!, 00336552!]).

Distribution. Bangladesh, Bhutan, China (Guangxi, Guizhou, Tibet, Yunnan), India, Indonesia, Myanmar, Nepal, Thailand, and Vietnam.

12b. *Photinia integrifolia* var. *flavidiflora* (W.W.Sm.) J.E.Vidal, Adansonia, n.s. 5: 227. 1965.

Common name: 黄花全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): huang hua quan yuan shi nan

≡ *Photinia flavidiflora* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 59. 1917.

Type. China. Yunnan: Mingkwong Vally, November 1912, *G. Forrest 9221* (lectotype, designated by Vidal (1965: 227): E [barcode E00011313!]; isolectotype: A [barcode 00026742!]). Hills to the N. W. Tengyueh, *G. Forrest 9294* (syntypes: BM [barcode BM000602131!], E [barcode E00072939!], K [barcode K000758267!], A [barcode 00026743!]). Divide between the Tengyueh and Shweli Valleys, *G. Forrest 7901* (syntype). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011313.

Distribution. China (Yunnan) and Myanmar (Kachin).

12c. *Photinia integrifolia* var. *notoniana* (Wight & Arn.) J.E.Vidal, Addisonia 5: 227. 1965.

Common name 长柄全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chang bing quan yuan shi nan

≡ *Photinia notoniana* Wall. ex Wight & Arn., Prodr. Fl. Ind. Orient. 1: 302. 1834. ≡ *Eriobotrya notoniana* (Wall. ex Wight & Arn.) Kurz, Prelim. Rep. Forest Pegu App. B. 48. 1875.

= *Photinia eugenifolia* Lindl., Edwards's Bot. Reg. 23: t. 1956. 1837. ≡ *Photinia notoniana* var. *eugenifolia* Hooker, Fl. Brit. India 2: 381. 1878. Type: INDIA. Pundua, 1832, *Wallich 670B* (lectotype, designated by Vidal (1965: 226): K [barcode K001111558!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k001111558.

= *Photinia micrantha* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 143. 1874. ≡ *Photinia notoniana* f. *micrantha* (Decne.) Koord. & Valeton, Bijdr. Boomsoort. Java 5: 364. 1900. Type: INDIA / BABGLADESH. Bengalia orientalis, *Griffith 2098* (lectotype, selected by Vidal (1965: 227), first step; second step, designated by Kalkman (1973: 420): K [barcode K000758325!]; isolectotype: P [barcode P02143138!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758325.

= *Photinia notoniana* var. *ceylanica* Hook.f., Fl. Brit. India 2: 381. 1878. Type: INDIA. *G. Walker s.n.* (lectotype, designated by Pathak et al. (2019: 185): K [barcode K000758326!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758326.

= *Photinia notoniana* var. *macrophylla* Hook.f., Fl. Brit. India 2: 381. 1878. Type: INDIA. Khasia Hills, *J.D. Hooker & T. Thomoson s.n.* (lectotype, designated by Pathak et al. (2019: 185): K [barcode K000758321!]; isolectotypes: K [barcode K000758319!, K000758322!, K000758323!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758321.

= *Photinia sambuciflora* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 60. 1917. Type: CHINA. Yunnan: Hills to the north of Tengyueh, *G. Forrest 9722* (**lectotype**, selected by Vidal (1965: 227), first step; **second step, designated here**: E [barcode E00011314!]; isolectotypes: HBG [barcode HBG-511070!], BM [barcode BM000602132!]); Shweli-Salween divide, *G. Forrest 12293* (syntypes: BM [barcode BM000602133!], E [barcode E00072952!], K [barcode K000758268!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011314.

Type. INDIA. Nilghiris, *Wight 1014* (lectotype, selected by Vidal (1965: 226) 'holotype': K [barcode K000758317!]; isolectotypes: E [barcode E00011315!], P [barcode P02143139!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758317.

Distribution. China (Yunnan), India, and Laos.

12d. *Photinia integrifolia* var. *sublanceolata* Miq., Fl. Ned. Ind.1(1): 387. 1855.

Common name: 狭叶全缘石楠 (Chinese name); pinyin (spelled as sounds in Chinese): xia ye quan yuan shi nan

= *Photinia integrifolia* var. *subdenticulata* Miq., Fl. Ned. Ind.1(1): 387. 1855. Type: INDONESIA. Java: Mount Prahu, *T. Horsfield 1135* (lectotype, designated by Kalkman (1973: 420) 'holotype': K [barcode K000758360!]; isolectotype: BM [barcode BM000602182!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758360.

= *Photinia dasythrysa* Miq., Fl. Ned. Ind. 1(1): 387. 1855. ≡ *Photinia integrifolia* var. *dasythrysa* (Miq.) J.E.Vidal, Adansonia 5: 227. 1965. Type: INDONESIA. Sumatra: Sunda-eilanden, *Miquel s.n.* (holotype: U [barcode U0123984!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.u0123984.

= *Photinia notoniana* var. *angustata* Blume ex K.Koch, Ann. Mus. Bot. Lugduno-Batavi 1: 250. 1864, nom. nud.

= *Photinia blumei* Decne., Nouv. Arch. Mus. Hist. Nat. 11: 142. 1874. Type: INDONESIA. Java, mons Malabar, 19 October 1861, *Anderson 83* (lectotype, designated by Vidal (1965: 227): P [barcode P02143205!]; isolectotype: K [barcode K000758361!]); *Wight 923* (syntype: P [barcode P02143136!]); *Wight 924* (syntype: P [barcode P02143137!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143205.

= *Photinia notoniana* f. *grandiflora* Koord. & Valeton, Bijdr. Boomsoort. Java 5: 364. 1900. Type: not designated.

= *Photinia notoniana* f. *vulgaris* Koord. & Valeton, Bijdr. Boomsoort. Java 5: 364. 1900. Type: not designated.

Type. INDONESIA. Java: Surakarta, *T. Horsfield 432* (lectotype, designated by Kalkman (1973: 420) 'holotype': K [barcode K000758357!]; isolectotype: BM [barcode BM000602183!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758357.

Distribution. Indonesia (Java and Sumatra).

13. *Photinia lanuginosa* T.T.Yu, Acta Phytotax. Sin. 8(3): 227. 1963.

Fig. 8

Common name: 绵毛石楠 (Chinese name); pinyin (spelled as sounds in Chinese): mian mao shi nan

≡ *Pyrus atalantae* M.F.Fay & Christenh., Global Fl. 4: 96. 2018.

Type. CHINA. Hunan, Mt. Xuefengshan, *C.T. Li 1882* (holotype: PE [barcode 00026329!]; isotype: IBSC [barcode 0344338!], PE [barcode 00004601!]).

Distribution. China (Hunan).

14. *Photinia lindleyana* Wight & Arn., Prodr. Fl. Ind. Orient. 1: 302. 1834.

Common name: 川滇石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chuan dian shi nan

≡ *Photinia serrulata* var. *lindleyana* (Wight & Arn.) Wenz., Linnaea 38: 94. 1873. ≡ *Pyrus lindleyana* (Wight & Arn.) M.F.Fay & Christenh., Global Fl. 4: 110. 2018.

= *Photinia lindleyana* var. *tomentosa* Gamble, Fl. Madras 1(3): 445. 1919. ≡ *Photinia serratifolia* var. *tomentosa* (Gamble) Vivek. & B.V.Shetty, Bull. Bot. Surv. India 23(3–4): 256. 1983. ≡ *Pyrus lindleyana* var. *tomentosa* (Gamble) K.S. Kumar & Arum., Indian Forester 148(1): 115. 2022. Type: INDIA. Tamil Nadu, Nilgiris District, between Bangi Tappal and Sispara, alt. 7500 ft. ASL, May 1889, *J.S. Gamble 20638* (lectotype, designated by Kumar and Arumugam (2022: 115): MH [barcode MH00234090!]).

Type. INDIA. Peninsula Ind. orientalis, *Wight 1012* (lectotype, selected by Kalkman (1973: 424), first step; second step, designated by Kumar and Arumugam (2022: 117): K [barcode K000758313!]; isolectotypes: BM [barcode BM000602140!], E [barcode E00011327!]). *Wight 1013* (syntypes: BM [barcode BM000602139!], E [barcode E00174590!, E00174591!], GZU [barcode GZU000283017!], K [barcode K000758312!], P [barcode P02143117!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758313.

Distribution. China (Sichuan and Yunnan) and India (Kerala and Tamil Nadu).

14a. *Photinia lindleyana* var. *lindleyana*

Common name: 川滇石楠 (原变种) (Chinese name)

Distribution. China (Sichuan and Yunnan) and India (Kerala and Tamil Nadu).

Figure 8. Fine structure of *Photinia lanuginosa*, encompassing various developmental stages and perspectives. The inflorescence branches, depicted in **A–I**, include **A** whole branch **B** branchlet **C** top view of an unopened flower **D** bottom perspective of an individual flower **E** top view of a single flower **F** dissected flower showing internal structures **G** longitudinal section through the ovary **H** stamens **I** cross-section of the immature ovary. These were collected on April 3, 2024. The infructescence branches, shown in **J–O**, comprise: **J** whole branch **K** branchlet **L** top view of a developing fruit **M** longitudinal section of the fruit **N** cross-sections of the fruit **O** seed. These were collected on November 29, 2023. All fresh specimens were collected by Ting Wang at the Hangzhou Botanical Garden, Zhejiang, China. Additionally, Bin-Jie Ge from the Chenshan Botanical Garden in Shanghai, China, dissected and photographed all samples.

14b. *Photinia lindleyana* var. *yunnanensis* Cardot, Notul. Syst. (Paris) 3: 374. 1918.

Common name: 滇石楠 (Chinese name); pinyin (spelled as sounds in Chinese): dian shi nan

Type. China. Yunnan: ao Kouy Chan près My Li, 1906, *F. Ducloux & P. Ngeou 4242-pp* (**lectotype, designated here**: P [barcode 02143143!]; isolectotype: P [barcode 02143144!]). Yunnan: Lan argy tsin, près Lou lan, 17 April 1908, *F. Ducloux & J.B. Lo 5936* (syntype: P [barcode P02143144!]).

Distribution. China (Yunnan).

15. *Photinia lochengensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 226. 1963.

Common name: 罗城石楠 (Chinese name); pinyin (spelled as sounds in Chinese): luo cheng shi nan

≡ *Pyrus lochengensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 110. 2018.

Type. China. Guangxi: Lo-cheng (=Luocheng), *W. Chen 84410* (holotype: IBSC; isotypes: PE [barcode 00004611!, 01790013!]). Note A.

Distribution. China (Guangxi).

Note A. In the protologue, Yu and Kuan (1963) designated the type specimen as being deposited in the herbarium “HC”, which they referenced as “Herb. Inst. Austro-Sin. Acad. Sin. Canton”. The correct standard name for this institute is the South China Botanical Garden (IBSC). However, we could not locate any specimens from this collection in IBSC. Instead, we found two isotype sheets at the PE herbarium.

16. *Photinia loriformis* W.W.Sm., Notes Roy. Bot. Gard. Edinburgh 10: 60. 1917.

Common name: 带叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): dai ye shi nan

≡ *Pyrus loriformis* (W.W.Sm.) M.F.Fay & Christenh., Global Fl. 4: 111. 2018.

Type. China. Yunnan, Yunnanfu (=Kunming), *E.E. Maire 1118* (**lectotype, designated here**: E [barcode E00011317!]; isolectotypes: A [barcode A00045580!], K [barcode K000758253!]). *E.E. Maire 1117* (syntype: E [barcode E00285982!]), *E.E. Maire 1755* (syntype: E [barcode E00285984!]), *E.E. Maire 2099* (syntype: E [barcode E00285985!]). Note B. Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011317.

Distribution. China (Sichuan and Yunnan).

Note B. In the protologue, the author referenced four collections collected by *E.E. Maire: 1118, 1117, 1755, and 2099*, all housed in the herbarium E. However, Smith did not designate a specific type, meaning all four collections are syntypes. A lectotypification is required (Turland et al. 2018). Upon examination of each specimen from the herbarium E, it was observed that *E.E. Maire 1117* (barcode E00285982) and *1755* (barcode E00285984) lack flowers and fruits. *E.E. Maire 2099* (barcode E00285985) has fruits, but they are damaged by worms. As a result, *E.E. Maire 1118* (barcode E00011317), which is in good condition and has flowers, has been selected as the lectotype.

17. *Photinia maximowiczii* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 143. 1874.
Common name: 琉球石楠 (Chinese name); pinyin (spelled as sounds in Chinese): liu qiu shi nan

= *Photinia wrightiana* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 32: 486. 1888. Type: JAPAN. Bonin-sima, *Wright s.n.* (syntype). Liukiu, *A. Tashiro s.n.* (syntype).

Type. Japan. Bonin Islands, *Wright 80* (holotype: P [barcode P02143127!]; isotype: K [barcode K000758301!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143127.

Distribution. Japan (Bonin Islands and Liukiu).

18. *Photinia megaphylla* T.T.Yu & L.T.Lu, Acta Phytotax. Sin. 18(4): 493. 1980.
Common name: 大叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): da ye shi nan

= *Pyrus megaphylla* (T.T.Yu & L.T.Lu) M.F.Fay & Christenh., Global Fl. 4: 111. 2018.

Type. China. Tibet: Motuo, *Qingzang Exped. 74-4158* (holotype: PE [barcode 00026327!]).

Distribution. China (Tibet).

19. *Photinia microphylla* (J.E.Vidal) B.B.Liu, comb. nov.
urn:lsid:ipni.org:names:77342733-1
Common name: 少花石楠 (Chinese name); pinyin (spelled as sounds in Chinese): shao hua shi nan

= *Stranvaesia microphylla* J.E.Vidal, Notul. Syst. (Paris) 13: 300. 1949. ≡ *Pyrus pluto* M.F.Fay & Christenh., Global Fl. 4: 116. 2018.

Type. Vietnam. Tonkin: massif du Lo Sui Tong, Près Chapa (Cha-pa and Cho-bo), 2200 m, 29 July 1926, *E. Poilane 12674* (holotype: P [barcode P02143106!]; isotypes: P [barcode P02143107!, P02143108!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143106.

Distribution. Vietnam.

20. *Photinia prionophylla* (Franch.) C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 153. 1906.
Common name: 刺叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): ci ye shi nan

≡ *Eriobotrya prionophylla* Franch. Pl. Delavay. 225, pl. 46. 1890. ≡ *Pyrus prionophylla* (Franch.) M.F.Fay & Christenh., Global Fl. 4: 116. 2018.

Type. China. Yunnan: les taillis à Kiao che tong au dessus de Kiang yn, 30 May 1888, *J.M. Delavay 3545* (lectotype, designated by Idrees et al. (2021: 167): P [barcode P03342590!]; isolectotypes: K [barcode K000758254!], LE [barcode LE01015176!]). ibidem, 28 October 1888, *J.M. Delavay 3545* (syntypes: K [barcode K000758255!]). Mo-so-yn, Lau Kong, 1 June 1884, *J.M. Delavay 1077* (syntypes: A [barcode 00026479!, 00026749!, 00026750!], P [barcode P02143153!, P02143154!, P02143155!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758254.

Distribution. China (Sichuan and Yunnan).

20a. *Photinia prionophylla* var. *prionophylla*
Common name: 刺叶石楠 (原变种) (Chinese name)

Distribution. China (Sichuan and Yunnan).

20b. *Photinia prionophylla* var. *nudifolia* Hand.-Mazz., Symb. Sin. 7(3): 480. 1933.
Common name: 无毛刺叶石楠 (变种) (Chinese name); pinyin (spelled as sounds in Chinese): wu mao ci ye shi nan

Type. China. Yunnan: Yunnanfu (= Kunming), Prope vicum Hsiao-Magai ad septentr. urbis Yünnanfu, 25°26’ lat., in regionis calide temperatae inte Döge et Hsiaodjiadsum. 1800 m. 8 March 1914, *H. Handel-Mazzetti 404* (holotype: WU [barcode 0059448!]).

Distribution. China (Yunnan).

21. *Photinia prunifolia* (Hook. & Arn.) Lindl., Edwards’s Bot. Reg. 23: sub t. 1956. 1837.
Fig. 9
Common name: 桃叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tao ye shi nan

≡ *Photinia serrulata* var. *prunifolia* Hook. & Arn., Bot. Beechey Voy. 4: 185. 1833. ≡ *Pyrus uranus* M.F.Fay & Christenh., Global Fl. 4: 124. 2018.
= *Photinia melanostigma* Hance, J. Bot. 20: 5. 1882. Type: CHINA. Guangdong, North River, March 1881, *B.C. Henry 21691* (holotype: BM [barcode

Figure 9. Fine structure of *Photinia prunifolia*, encompassing various developmental stages and perspectives. **A** inflorescence branch **B, C** inflorescence branchlet **D** bottom perspective of an individual flower **E** top view of a single flower **F, G** longitudinal section through the ovary **H** stamens **I** petals **J** dissected flower showing internal structures **K** cross-section of the immature ovary **L** an infructescence branch **M, N** comparative fruit in both inmature and mature states **O** fruit, viewed from above **P** longitudinal section of fruit **Q** cross-sections of fruit **R** fully matured seed. The inflorescence branches (**A–K**) were collected on April 13, 2024. The infructescence branches in the immature state (**L, M**) were collected on October 7, 2023, while the remaining samples (**N–R**) were gathered on November 29, 2023. Ting Wang was responsible for the collection of all fresh specimens at the Hangzhou Botanical Garden (Zhejiang, China). Furthermore, Bin-Jie Ge (Chenshan Botanical Garden, Shanghai, China) dissected and photographed all the samples.

BM000602202!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000602202.

= *Photinia consimilis* Hand.-Mazz., Anz. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 59: 103. 1922. Type: CHINA. Hunan: Dschaoschan (=Shaoshan), 27 October 1917, *Handel-Mazzetti 11382* (**lectotype, designated here**: WU [barcode 0059452!]). Hunan: Shaoshan, 27 October 1917, *Handel-Mazzetti 11382* (syntype: WU [barcode 0059467!]). ibidem, 16 February 1918, *Handel-Mazzetti 11472* (syntype: WU [barcode 0059453!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.wu0059467.

= *Photinia prunifolia* var. *denticulata* T.T.Yu, Acta Phytotax. Sin. 8(3): 228. 1963. Type: CHINA. Zhejiang, Pingyang, 28 June 1959, *S.R. Zhang 5867* (holotype: PE [barcode 00026328!]; isotypes: KUN [barcode 607582!], HTC [barcode 0003151!]).

= *Photinia stapfii* Chun, nom. nud.

Type. CHINA. Macao and adjacent islands, *Beechey s.n.* (lectotype, designated by Wang et al. (2019: 68): K [barcode K000758258!]; isolectotypes: E [barcode E00369054!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758258.

Distribution. Cambodia, China (Fujian, Guangdong, Guangxi, Hainan, Hongkong, Hunan, Jiangxi, Zhejiang), and Vietnam.

22. *Photinia raupingensis* K.C.Kuan, Acta Phytotax. Sin. 8(3): 228. 1963.

Common name: 饶平石楠 (Chinese name); pinyin (spelled as sounds in Chinese): rao ping shi nan

≡ *Pyrus raupingensis* (K.C.Kuan) M.F.Fay & Christenh., Global Fl. 4: 118. 2018.

Type. CHINA. Guangdong, Raoping, Fenghuangshan, in silvis, 16 April 1931, *N.K. Chun 42691* (holotype: IBSC [barcode 0318920!]; isotypes: AU [barcode 039768!], IBK [barcode IBK00062558!, IBK00062559!], NAS [barcode NAS00374075!], PE [barcode 00020609!, 00004599!]).

Distribution. China (Guangdong and Guangxi).

23. *Photinia serratifolia* (Desf.) Kalkman, Blumea 21(2): 424. 1973.

Common name: 石楠 (Chinese name); pinyin (spelled as sounds in Chinese): shi nan

≡ *Crataegus serratifolia* Desf., Tabl. École Bot., ed. 3 (Cat. Pl. Horti Paris.) 408. 1829. ≡ *Pyrus serratifolia* (Desf.) M.F.Fay & Christenh., Global Fl. 4: 121. 2018.

Type. not designated.

23a. *Photinia serratifolia* var. *serratifolia*

Fig. 2C
Common name: 石楠 (原变种) (Chinese name)

= *Photinia glabra* var. *chinensis* Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg, sér. 3 19(2): 179. 1873. Type: CHINA. *R. Fortune A-30* (**lectotype, designated here**: P [barcode P00781062!]; isolectotypes: P [barcode P00781061!, P00781063!, P00781064!]). Note C. Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p00781062.

= *Stranvaesia argyi* H.Lév., Mem. Acad. Sci. Art. Barcelona ser. 3 12: 560. 1916. Type: CHINA. *Argy s.n.* (holotype: E [barcode E00011323!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011323.

= *Photinia serrulata* var. *aculeata* G.H.M.Lawr., Gentes Herbarum 8: 80. 1949. Type: CHINA. Taiwan: Seisiu, *E.H. Wilson 11061* (**lectotype, designated here**: US [barcode 00097504!]; isolectotype: A [barcode 00045608!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.us00097504.

Distribution. China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hebei, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Taiwan, Yunnan, and Zhejiang), Indonesia, India, Japan, and Philippines.

Note C. In the protologue, the author cited only one collection of specimen, *R. Fortune A-30*, four sheets of this collection have been observed in P, one preserved well (barcode P [barcode P00781062]) was designated as lectotype here.

23b. *Photinia serratifolia* var. *ardisiifolia* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988.

Common name: 紫金牛叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): zi jin niu ye shi nan

≡ *Photinia ardisiifolia* Hayata, Icon. Pl. Formosan. 5: 65. 1915. ≡ *Photinia serrulata* f. *ardisiifolia* (Hayata) H.L.Li, Lloydia 14(4): 234. 1951. ≡ *Photinia serrulata* var. *ardisiifolia* (Hayata) K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 224. 1974.

Type. China. Taiwan: Taidong, Taito, Manchosha, 1 October 1906, *G. Nakahara s.n.* (**lectotype, designated here**: TAIF [accession no. 22366!]; isolectotype: IBSC [barcode 0285883!]).

Distribution. China (Taiwan).

23c. *Photinia serratifolia* var. *daphniphylloides* (Hayata) L.T.Lu, Acta Phytotax. Sin. 38(3): 277. 2000.

Common name: 宽叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): kuan ye shi nan

≡ *Photinia daphniphylloides* Hayata, Icon. Pl. Formosan. 7: 30. 1918. ≡ *Photinia serrulata* f. *daphniphylloides* (Hayata) H.L.Li, Lloydia 14(4): 234. 1951. ≡ *Pho-*

tinia serrulata var. *daphniphylloides* (Hayata) K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 222. 1974.

Type. China. Taiwan: Hualian, Tarako, Batagan-sya, 27 April 1917, *S. Sasaki s.n.* (**lectotype, designated here**: TAIF [accession no. 11810!]; isolectotype: TAIF [accession no. 11811!]).

Distribution. China (Taiwan).

23d. *Photinia serratifolia* var. *lasiopetala* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988.

Common name: 毛瓣石楠 (Chinese name); pinyin (spelled as sounds in Chinese): mao ban shi nan

≡ *Photinia lasiopetala* Hayata, Icon. Pl. Formosan. 6: 17. 1916. ≡ *Photinia serrulata* var. *lasiopetala* (Hayata) K.C.Kuan, Fl. Reipubl. Popularis Sin. 36: 222. 1974. ≡ *Photinia serratifolia* var. *lasiopetala* (Hayata) H.Ohashi, J. Jap. Bot. 63(7): 234. 1988. ≡ *Pyrus lasiopetala* (Hayata) M.F.Fay & Christenh., Global Fl. 4: 110. 2018.

Type. China. Taiwan: Nantou, 1 April 1916, *B. Hayata s.n.* (holotype: TAIF [accession no. 11814!]; isotype: PH [barcode PH00067378!]).

Distribution. China (Taiwan).

24. *Photinia stenophylla* Hand.-Mazz., Symb. Sin. Pt. 7(3): 480, pl. 15, f.3. 1933.

Common name: 窄叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): zhai ye shi nan

≡ *Pyrus stenophylla* (Hand.-Mazz.) M.F.Fay & Christenh., Global Fl. 4: 122. 2018.

Type. China. Guizhou, Sandjio, *H. Handel-Mazzetti 10827* (lectotype, designated by Pathak et al. (2021: 41): WU [barcode 0059446!]). Sanhoa (= Sandu), Yao-ren-shan, *Y. Tsiang 6374* (syntypes: A [barcode 00026800!], NY [barcode 00436117!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.wu0059446.

Distribution. China (Guangxi and Guizhou).

25. *Photinia taishunensis* G.H.Xia, L.H.Lou & S.H.Jin, Nordic J. Bot. 30(4): 439. 2012.

Common name: 泰顺石楠 (Chinese name); pinyin (spelled as sounds in Chinese): tai shun shi nan

Type. China. Zhejiang: Taishun County, Yangxi Village, *C.S. Ding 4116* (holotype: ZJFC [barcode 00030313!]; isotype: ZJFC [barcode 00030312!]).

Distribution. China (Zhejiang).

26. *Photinia tushanensis* T.T.Yu, Acta Phytotax. Sin. 8(3): 229. 1963.
Common name: 独山石楠 (Chinese name); pinyin (spelled as sounds in Chinese): du shan shi nan

≡ *Pyrus tushanensis* (T.T.Yu) M.F.Fay & Christenh., Global Fl. 4: 124. 2018.

Type. China. Guizhou, Dushan, *Libo Exped. 1296* (holotype: PE [barcode 00020611!]; isotype: PE [barcode 01498407!]).

Distribution. China (Guangxi and Guizhou).

27. *Photinia wardii* C.E.C.Fisch., Bull. Misc. Inform. Kew 1936(4): 281. 1936.
Common name: 长叶石楠 (Chinese name); pinyin (spelled as sounds in Chinese): chang ye shi nan

Type. India. Assam, Chibaon, Delei Valley, *F.K. Ward 8042* (holotype: K [barcode K000758348!]; isotypes: K [barcode K000758349!, K000758350!]). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758348.

Distribution. India (Assam).

***Stranvaesia* Lindl., Edwards's Botanical Register 23: t. 1956. 1837.**
Common name: 红果树属 (Chinese name); pinyin (spelled as sounds in Chinese): hong guo shu shu

Type. Lectotype, designated by Liu et al. (2019: 686): *Crataegus glauca* Wall. ex G.Don (= *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne.).

1. *Stranvaesia nussia* (Buch.-Ham. ex D.Don) Decne., Nouv. Arch. Mus. Hist. Nat. 10: 178. 1874.
Common name: 红果树 (Chinese name); pinyin (spelled as sounds in Chinese): hong guo shu

≡ *Pyrus nussia* Buch.-Ham. ex D.Don, Prodr. Fl. Nepal. 237. 1825. ≡ *Photinia nussia* (Buch.-Ham. ex D.Don) Kalkman, Blumea 21(2): 429. 1973.

= *Crataegus glauca* Wall. ex G.Don, Gen. Hist. 2: 598, descr. 1832. Type: Nepalia & Kumaon. 1829, *Wallich 673* (**lectotype, designated here**: K [barcode K000758343!, excluding the infructescence]; isolectotypes: G [barcode G00437202!, excluding the infructescence, G00437203!], GZU [barcode GZU000283039!], K [barcode K000758344!, K001111566!], L [barcode L0019509!], LE [barcode LE00013505!], M [barcode M-0213867!, M-0213868!, M-0213872!], P [barcode P02143111!], PH [barcode PH00028193!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758343.

= *Stranvaesia glaucescens* Lindl., Edwards's Bot. Reg. 23: t. 1956. 1837. nom. superfl.

= *Eriobotrya ambigua* Merr., Publ. Bur. Sci. Gov. Lab. 35: 19. 1906. ≡ *Stranvaesia ambigua* (Merr.) Nakai, J. Arnold Arbor. 5: 72. 1924. Type: PHILIPPINES.

Lamao River, Mt. Mariveles, Province of Bataan, Luzon, March 1905, *R. Meyer 2796* (lectotype, designated by Kalkman (1973: 429) 'holotype': K [barcode K000758366!]; isolectotypes: NY [barcode 00436214!], US [barcode 00097488!]). ibidem, March 1905, *H.N. Whitford 1155* (syntype: K [barcode K000758368!]). ibidem, March 1905, *H.N. Whitford 1168* (syntype: K [barcode K000758367!]). ibidem, June 1905, *H.N. Whitford 1307* (syntype: K [barcode K000758365!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000758366.

= *Eriobotrya oblongifolia* Merr. & Rolfe, Philipp. J. Sci., C 3: 102. 1908. ≡ *Rhaphiolepis oblongifolia* (Merr. & Rolfe) B.B.Liu & J.Wen, Frontiers Pl. Sci. (Online journal) 10-1731: 11. 2020. Type: PHILIPPINES. Mindanao. Misamis: Mount Malindang, May 1906, *E.A. Mearns & W.J. Hutchinson 4680* (lectotype, designated by Liu et al. (2020b: 108): NY [barcode 00436215!]; isolectotype: US [barcode 00097490!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00436215.

= *Photinia harmandii* Cardot, Notul. Syst. (Paris) 3: 375. 1918. ≡ *Stranvaesia harmandii* (Cardot) Vidal, Notul. Syst. (Paris) 13: 301. 1948. Type: LAOS. Attopeu, 1877, *Harmand 1366* (**lectotype, designated here**: P [barcode P02143112!]; isolectotype: P [barcode P02143113!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143112.

Type. NEPAL. Nilcunt [Nilkantha, Shading District, Bagmati Zone, Madhyamanchal, Nepal; coordinates 27.91/84.94]. *Francis Buchanan-Hamilton s.n.* (lectotype, selected by Vidal (1965: 231), first step; second step, designated by Guo et al. (2020: 110): BM [barcode BM000522002!]). *Wallich 658* (syntype: L [barcode L0062739!, L0062740!], M [barcode M-0213869!]). *Wallich 658a* (syntype: M [barcode M-0210542!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.bm000522002.

Distribution. China (Tibet and Yunnan), India, Laos, Myanmar, Nepal, Philippines, and Thailand.

1a. *Stranvaesia nussia* var. *nussia*

Common name: 红果树(原变种)(Chinese name)

Distribution. China (Tibet and Yunnan), India, Laos, Myanmar, Nepal, Philippines, and Thailand.

1b. *Stranvaesia nussia* var. *angustifolia* (Decne.) C.K.Schneid., Ill. Handb. Laubholzk. 1: 713. 1906.

Common name: 狭叶红果树(变种)(Chinese name); pinyin (spelled as sounds in Chinese): xia ye hong guo shu

≡ *Stranvaesia glaucescens* var. *angustifolia* Decne., Nouv. Arch. Mus. Hist. Nat. 10: 178. 1874.

Distribution. India (Mt. Khasia).

2. *Stranvaesia oblanceolata* (Rehder & E.H.Wilson) Stapf, Bot. Mag. 149: sub t. 9008. 1924.
Common name: 滇南红果树 (Chinese name); pinyin (spelled as sounds in Chinese): dian nan hong guo shu

≡ *Stranvaesia nussia* var. *oblanceolata* Rehder & E.H.Wilson, Pl. Wilson. (Sargent) 1: 193. 1913. ≡ *Pyrus oblanceolata* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4: 114. 2018.

Type. China. Yunnan: forests around Szemao (Simao), alt. 1500–1600 m, *A. Henry 11615* (lectotype, selected by Vidal (1965: 232), first step; second step, designated by Guo et al. (2020: 110): US [barcode 00097547!]; isolectotype: A [barcode 00038562!]). ibidem, *A. Henry 11615a* (syntype: A [barcode 00038566!], K [barcode K000758307!], PE [barcode 01432740!]). ibidem, *A. Henry 11615b* (syntype: A [barcode 00038563!], K [barcode K000758306!], PE [barcode 01432741!], US [barcode 00429887!]). ibidem, *A. Henry 11615e* (syntype: A [barcode 00038564!], K [barcode K000758308!], PE [barcode 01432742!], US [barcode 00429888!]). ibidem, *A. Henry 11615f* (syntype: A [barcode 00038565!], K [barcode K000758306!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038562

Distribution. China (Yunnan), Laos, Myanmar, and Thailand.

3. *Stranvaesia lasiogyna* (Franch.) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 11. 2023.
Common name: 倒卵叶红果树 (Chinese name); pinyin (spelled as sounds in Chinese): dao luan ye hong guo shu

≡ *Eriobotrya lasiogyna* Franch., Pl. Delavay. 225. 1890. ≡ *Photinia lasiogyna* (Franch.) C.K.Schneid., Repert. Spec. Nov. Regni Veg. 3: 153. 1906. ≡ *Pyrus avalon* M.F.Fay & Christenh., Global Fl. 4: 96. 2018. replacement name.
= *Stranvaesia glaucescens* var. *yunnanensis* Franch., Pl. Delavay. 226. 1890. Type: CHINA. Yunnan, in silvis supra Che-tong, prope Tapin-tze, May 18, 1885, *J.M. Delavay 1992* (lectotype, designated by Idrees and Shaw (2022: 31): P barcode P02143161!; isolectotype: P barcode P02143140!). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143161.
= *Photinia mairei* H.Lév., Bull. Acad. Int. Géogr. Bot. 17: 28. 1916. Type: CHINA. rochers-brousse des mont a Kiao-me-ti, May 1911–1913, *E.E. Maire s.n.* (lectotype, designated by Pathak et al. (2021: 41): E [barcode E00011316!]; isotype: A [barcode 00038571!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011316.

Type. China. Yunnan, in silvis montanis ad fauces San-tchang-kiou supra Hokin, alt. 2300 m., 22 May 1884, *J.M. Delavay 732* (lectotype, designated by Pathak et al. (2021: 40): P [barcode P02143141!]; isolectotypes: P [barcode P02143142!], US [barcode 00097489!], image A [barcode 00026747! with plant material sampled from P02143141!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143141.

Distribution. China (Fujian, Guangdong, Guangxi, Hunan, Jiangxi, Sichuan, Yunnan, and Zhejiang).

3a. ***Stranvaesia lasiogyna*** var. ***lasiogyna***

Fig. 2D
Common name: 倒卵叶红果树(原变种)(Chinese name)

Distribution. China (Sichuan and Yunnan).

3b. ***Stranvaesia lasiogyna*** var. ***glabrescens*** (L.T.Lu & C.L.Li) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 11. 2023.

Common name: 无毛倒卵叶红果树(变种)(Chinese name); pinyin (spelled as sounds in Chinese): wu mao dao luan ye hong guo shu

≡ *Photinia lasiogyna* var. *glabrescens* L.T.Lu & C.L.Li, Acta Phytotax. Sin. 38(3): 278. 2000.

Type. China. Jiangxi, Shangrao, 4 May 1972, *Jiangxi Exped. 1071* (holotype: PE [barcode 00336583!]; isotype: PE [barcode 00336582!]).

Distribution. China (Fujian, Guangdong, Guangxi, Hunan, Jiangxi, Sichuan, Yunnan, and Zhejiang).

Weniomeles B.B.Liu, Molec. Phylogen. Evol. 189-107914: 11. 2023.

Common name: 椤木属 (Chinese name); pinyin (spelled as sounds in Chinese): luo mu shu

Type. *Weniomeles bodinieri* (H.Lév.) B.B.Liu ≡ *Photinia bodinieri* H.Lév.

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi, Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.

1. ***Weniomeles bodinieri*** (H.Lév.) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 12. 2023.

Common name: 椤木 (Chinese name); pinyin (spelled as sounds in Chinese): luo mu

≡ *Photinia bodinieri* H.Lév., Repert. Spec. Nov. Regni Veg. 4: 334. 1907. ≡ *Pyrus eureka* M.F.Fay & Christenh., Global Fl. 4:103. 2018. replacement name. ≡ *Stranvaesia bodinieri* (H.Lév.) B.B.Liu & J.Wen, J. Syst. Evol. 57(6): 686. 2019. ≡ *Stranvaesia bodinieri* (H.Lév.) Long Y.Wang, W.B.Liao & W.Guo, Phytotaxa 447(2): 110. 2020. later homonym.

= *Photinia davidsoniae* Rehder & E.H.Wilson, Pl. Wilson. 1: 185. 1912. ≡ *Pyrus davidsoniae* (Rehder & E.H.Wilson) M.F.Fay & Christenh., Global Fl. 4:101. 2018. Type:

CHINA, Western Hupeh (Hubei): near Ichang (Yichang), alt. 300–600 m., April 1907, *E.H. Wilson 685* (lectotype, selected by Vidal (1968), first step "type"; second step, designated by Liu et al. (2019: 687): A [barcode 00038567!] excluding the fruits and seeds in the packet; isolectotypes: BM [barcode BM000602130!], E [barcode E00011306! excluding the fruiting branch), GH [barcode 00045598! excluding the fruiting branch], HBG [barcode HBG511078! excluding the fruiting branch], US [barcode 00097494! excluding the fruiting branch]). ibidem, *E.H. Wilson 685* (paratype: A [barcode 00038567, only the fruits and seeds in the packet, 00045599!], E [barcode E00011306, excl. the flowering branch!], GH [barcode 00045598, excl. the flowering branch!], HBG [barcode HBG511078, excl. the flowering branch!], US [barcode 00097494, excl. the flowering branch!]). CHINA, Hubei: south-west of Ichang, alt. 300 m, November 1907, *E.H. Wilson 484* (paratypes: BM [barcode BM000946991!], HBG [barcode HBG511080!]). mountains south of Ichang, May 1900, *E.H. Wilson 462* (paratypes: HBG [barcode HBG511079!], P [barcode P02143162!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.a00038567.

= *Hiptage esquirolii* H.Lév., Repert. Spec. Nov. Regni Veg. 10:372. 1912. Type: CHINA, Kouy-Tchéou (now as Guizhou): Choui-Teou, route de Tin-Pan-Lo-Fou, alt. 900 m, 4 May 1900, *J Esquirol 2097* (lectotype, designated by Liu et al. (2019: 687): E [barcode E00011307!]; isolectotypes: A [barcode 00015103!, 00045102!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.e00011307.

Type. CHINA, Kouy-Tchéou (now Guizhou): environs de Kouy-Yang, mont. du Collège, ca et là autour des villages, 18 May 1898, *E. Bodinier 2256* (lectotype, designated by Liu et al. (2019: 686): P [barcode P02143207!]; isolectotypes: A [barcode 00045584!], E [barcode E00010998!], P [barcode P02143208!, P02143209!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143207.

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi, Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.

1a. *Weniomeles bodinieri* var. *bodinieri*

Fig. 2E, 10

Common name: 椤木(原变种)(Chinese name)

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Shaanxi, Sichuan, Yunnan, and Zhejiang), Indonesia, and Vietnam.

1b. *Weniomeles bodinieri* var. *longifolia* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

Common name: 长叶椤木 (Chinese name); pinyin (spelled as sounds in Chinese): chang ye luo mu

≡ *Photinia bodinieri* H.Lév. var. *longifolia* Cardot, Notul. Syst. (Paris) 3: 374. 1918. ≡ *Stranvaesia bodinieri* var. *longifolia* (Cardot) B.B.Liu & J.Wen, J. Syst. Evol. 57(6): 687. 2019.

Figure 10. Comprehensive structural anatomy of *Weniomeles bodinieri*. **A** branch of the inflorescence **B** flowers **C, D** comparative top view of a single flower in both unopened and opened states **E** bottom perspective of an individual flower **F** longitudinal section through the ovary **G** stamens **H** cross-section through the ovary **I** detailed view of the pistil **J** dissected flower, illustrating internal structure **K** branch of the infructescence **L** cross-section of a young fruit **M** top view of a developing fruit **N** mature fruits **O** longitudinal-section through a mature fruit **P** cross-section through a mature fruit **Q** cross-section through a mature seed **R** a fully matured seed. The inflorescence branches were collected on June 14, 2022, and the infructescence branches were gathered on December 15, 2023, by Bin-Jie Ge at the Chenshan Botanical Garden, Shanghai. Additionally, Bin-Jie Ge dissected and photographed all the samples.

Type. China, Kouei Tchéou (now as Guizhou Province): grande route Kouei Tchéou au Kuangsi (Guangxi Province), Kout'ong (now as Gudong Xiang, Pingtang County), 22 May 1899, *Beauvais J. 175* (lectotype, designated by Liu et al. (2019: 687): P [barcode P02143211!]; isolectotype: P [barcode P02143210!]). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143211.

Distribution. China (Guizhou).

1c. *Weniomeles bodinieri* var. *ambigua* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

Common name: 尖瓣椤木 (Chinese name); pinyin (spelled as sounds in Chinese): jian ban luo mu

≡ *Photinia davidsoniae* var. *ambigua* Cardot, Notul. Syst. (Paris) 3: 374. 1918.

Type. China, Su-Tchuen (Sichuan): Eul Se Yug, vallée du Yalory, alt. 2000 m, 5 May 1911, *Legendre 834* (lectotype, designated by Jin et al. (2023: 13): P [barcode P02143164!]; isolectotype: P [barcode P02143165!). Image of lectotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143164.

Distribution. China (Sichuan).

1d. *Weniomeles bodinieri* var. *pungens* (Cardot) B.B.Liu, Molec. Phylogen. Evol. 189-107914: 13. 2023.

Common name: 尖叶椤木 (Chinese name); pinyin (spelled as sounds in Chinese): jian ye luo mu

≡ *Photinia davidsoniae* Rehder & E.H.Wilson var. *pungens* Cardot, Notul. Syst. (Paris) 3: 374. 1918.

Type. China, Hubei: Ichang, *A. Henry 7174* (holotype: P [barcode P02143163!). Image of holotype available from https://plants.jstor.org/stable/10.5555/al.ap.specimen.p02143163.

Distribution. China (Hubei).

2. *Weniomeles atropurpurea* (P.L.Chiu ex Z.H.Chen & X.F.Jin) B.B.Liu, comb. nov.

urn:lsid:ipni.org:names:77342734-1

Common name: 黑果椤木 (Chinese name); pinyin (spelled as sounds in Chinese): hei guo luo mu

≡ *Photinia atropurpurea* P.L.Chiu ex Z.H.Chen & X.F.Jin, J. Hangzhou Univ., Nat. Sci. Ed. 20(4): 393. 2021.

Type. China, Zhejiang: Taishun, Zuoxi, Lishuqiu, alt. 400 m, 3 May 2020, *Z.H. Chen, Z.P. Lei & W.Y. Xie TS20050316* (holotype: ZM; isotype: ZM).

Distribution. China (Zhejiang).

Conclusion

In summary, our study addresses the long-standing deficiency of the comprehensive phylogenetic backbone in the apple tribe Maleae, primarily stemming from limited taxon and marker sampling in prior research efforts. Our phylogenomic investigations conclusively identified three major clades within the tribe. Integrating evidence from nuclear phylogeny, morphology, and ploidy estimation, we present an updated infra-tribal taxonomic system, introducing subtribe Malinae Reveal, subtribe Lindleyinae Reveal, and subtribe Vauqueliniinae B.B.Liu (subtr. nov.). Notably, our plastid phylogenetic analysis underscored the monophyly of most genera, albeit with exceptions such as *Amelanchier*, *Malus*, *Sorbus* s.l., and *Stranvaesia*. Furthermore, we contribute a comprehensive taxonomic synopsis of *Photinia* and its morphological counterparts in the Old World, recognizing and delineating 27 species along with ten varieties within *Photinia*, three species and two varieties within *Stranvaesia*, and two species paired with three varieties within *Weniomeles*. Additionally, our study makes a valuable contribution by lectotypifying 12 names and making two new combinations, thereby aiding in clarifying nomenclatural ambiguities.

Acknowledgements

The computational analyses in this study were performed on the PhyloAI supercomputer (https://doi.org/10.12282/PhyloAIHPC), under the ownership of Bin-Bin Liu at the Institute of Botany, Chinese Academy of Sciences (IBCAS). All the molecular experiments were performed on the Plant DNA and Molecular Identification Platform (PDMIP) of IBCAS. We thank Xin-Tang Ma (China National Herbarium), Wen-Bin Ju (Chengdu Institute of Biology, Chinese Academy of Sciences), Yu-Ning Xiong (Institute of Botany, Jiangsu Province and Chinese Academy of Sciences), You-Sheng Chen (South China National Botanical Garden), and Meng Li (Nanjing Forestry University) for their valuable contributions to sample collections.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Financial support for this work was provided by the National Natural Science Foundation of China (grant number 32270216 to BBL and 32000163 to BBL), the Youth Innovation Promotion Association CAS (grant number 2023086 to BBL), and Shanghai Municipal Administration of Forestation and City Appearances (grant number G212416 to BJG).

Author contributions

B.B.L conceptualized and led the project, with collaborative supervision from G.N.L and S.H.J. The data assembly and phylogenomic analysis were carried out by H.W, X.Y.L, and Y.J. C.X was responsible for conducting the experimental work. The initial draft of the

manuscript was skillfully prepared by H.W, X.Y.L, Y.J, D.K.M, and Z.T.J. B.J.G examined and detailed the fine structure of the species represented in the study. T.W contributed by providing fresh samples essential for analyzing the fine structure. B.L offered valuable insights and feedback on the Chinese names proposed in the research. All the authors 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 or Supplementary Information.

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Supplementary material 1

Phylogenetic tree of the apple tribe Maleae extimated through maximum likelihood analysis using IQ-TREE2

Authors: Hui Wang, Xiao-Ya Li, Yan Jiang, Ze-Tao Jin, Dai-Kun Ma, Bing Liu, Chao Xu, Bin-Jie Ge, Ting Wang, Qiang Fan, Shui-Hu Jin, Guang-Ning Liu, Bin-Bin Liu

Data type: pdf

Explanation note: Phylogenetic tree of the apple tribe Maleae extimated through maximum likelihood analysis using IQ-TREE2, based on the whole plastome dataset. The numbers displayed above each branch represent the SH-aLRT support values and Ultrafast Bootstrap support percentages, respectively.

Link: https://doi.org/10.3897/phytokeys.242.117481.suppl1

Supplementary material 2

Phylogenetic tree of the apple tribe Maleae extimated through maximum likelihood analysis using RAxML

Authors: Hui Wang, Xiao-Ya Li, Yan Jiang, Ze-Tao Jin, Dai-Kun Ma, Bing Liu, Chao Xu, Bin-Jie Ge, Ting Wang, Qiang Fan, Shui-Hu Jin, Guang-Ning Liu, Bin-Bin Liu

Data type: pdf

Explanation note: Phylogenetic tree of the apple tribe Maleae extimated through maximum likelihood analysis using RAxML, based on the whole plastome dataset. The numbers displayed above each branch represent the Bootstrap support value.

Link: https://doi.org/10.3897/phytokeys.242.117481.suppl2

PhytoKeys

PhytoKeys 242: 229–239 (2024)
DOI: 10.3897/phytokeys.242.120967

Research Article

Thismia malayana (Thismiaceae), a new mycoheterotrophic species from Peninsular Malaysia

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Abstract

A new species of the mycoheterotrophic genus *Thismia* from Malaysia is described and illustrated. *Thismia malayana* introduced here was found in two localities: in the lowlands of Gunung Angsi Forest Reserve, Negeri Sembilan, and in the hilly dipterocarp forests of Gunung Benom in Tengku Hassanal Wildlife Reserve, Pahang. *Thismia malayana* falls into the section *Thismia* subsect. *Odoardoa*, as it has creeping vermiform roots and free equal tepals. It is characterised by the following taxonomically important features: a sepia-brown, urceolate-curved floral tube, free equal tepals with terminal appendages, prominent bright yellow annulus and bright violet-blue stamens each bearing five appendages (one pair of club-shaped inwards-pointing, one pair of acute outwards-pointing, and one central appendage). According to the categories and criteria of the IUCN Red List, *T. malayana* is provisionally classified as Vulnerable.

Key words: Negeri Sembilan, new species, Pahang, *Thismia* subsect. *Odoardoa*, vulnerable

Academic editor: Michal Hroneš
Received: 15 February 2024
Accepted: 4 May 2024
Published: 31 May 2024

Citation: Siti-Munirah MY, Hardy-Adrian C, Mohamad-Shafiq S, Irwan-Syah Z, Hamidi AH (2024) *Thismia malayana* (Thismiaceae), a new mycoheterotrophic species from Peninsular Malaysia. PhytoKeys 242: 229–239. https://doi.org/10.3897/phytokeys.242.120967

Introduction

The tropical rainforests of Southeast Asia together form the second largest area of tropical rainforests in the world. Also, the tropical lowland evergreen rainforest is the most species-rich forest formation in the region and structurally the most complex one, with species composition varying according to local soil and drainage conditions (Davis et al. 1995). Native plants of this type of forest include *Thismia* Griff., a genus of non-photosynthetic, mycoheterotrophic plants belonging to the family Thismiaceae. The genus *Thismia* comprises around 100 currently recognised species, and its range extends across various regions of the world, including tropical and subtropical Asia, northern and eastern Australia to New Zealand, the north-central USA, Costa Rica and southern tropical America (POWO 2024).

One of the most remarkable characteristics of *Thismia* is its mycoheterotrophic way of life. Unlike most plants, its species do not produce chlorophyll and are not capable of photosynthesis. A mycoheterotrophic plant is in fact a parasite of the mycorrhizal symbiosis, cheating it of the carbon resources that are shared in the mycorrhizal symbiosis, and this adaptation allows it to survive in the undergrowth of forests where the light availability is low (Merckx 2013; Watkinson 2016). *Thismia* species are known for their small size, which is usually only a few centimeters (Leake 1994). They are typically hidden in leaf litter and grow near tree roots or old rotten logs. Despite their small size, they are very sensitive to environmental changes, e.g. they decay easily when pulled out of its original habitat. *Thismia* species exhibit a number of unusual morphological features that continue to fascinate due to their amazing diversity of flower shapes and colours (Feller et al. 2022). The flower structure of *Thismia* is highly specialised to pollination by fungus gnats or other small insects (Thorogood and Siti-Munirah 2021). The flowers often have a complex shape with cup-like or spherical structures and intricate patterns that presumably attract pollinators. Due to their cryptic appearance, many *Thismia* species are still poorly known in terms of taxonomy and other biological aspects.

Another *Thismia* species is described here that is new to science. It was first discovered in 2020 in the Tengku Hassanal Wildlife Reserve (WR) (formerly known as Krau Wildlife Reserve) in the state of Pahang in Malaysia. It was later found also in a forested area in Ulu Bendul Recreation Park (RP), a popular nature and recreation area in Negeri Sembilan, Malaysia. It is located near the town of Kuala Pilah, about 25 kilometres from Seremban. The Ulu Bendul RP is also part of the Gunung Angsi Forest Reserve (FR) and offers nature lovers, hikers and explorers the opportunity to immerse themselves in the beauty of the tropical rainforest and discover its rich flora and fauna as well as its contribution to wildlife conservation. The type material of the new species was collected in February 2023 at the edge of the Gunung Angsi main trail in the forest area of Ulu Bendul RP.

Materials and methods

The specimens of the new species were collected from both localities (Map 1), preserved in 70% ethanol and deposited in the Kepong Herbarium (KEP). Morphological characters were examined, and measurements were made using an Olympus SZ61 stereomicroscope and high-resolution macrophotography of fresh and preserved material. The morphology of the new species was carefully compared with all related species of the genus *Thismia*. Assessment of the conservation status according to the categories and criteria of the IUCN Red List (IUCN Standards and Petitions Committee 2022).

Taxonomic account

***Thismia malayana* Siti-Munirah, Hardy-Adrian, Mohamad-Shafiq & Irwan-Syah, sp. nov.**
urn:lsid:ipni.org:names:77342735-1
Figs 1–3

Diagnosis. *Thismia malayana* resembles *T. chrysops* but differs by the brown-whitish colour of the floral tube (vs. very dark sepia brown), glabrous surface of the tepal appendages (vs. finely ciliate), presence of transverse bars at inner surface of floral tube (vs. bars absent), supraconnective apex of each stamen with 5 appendages: one pair of club-shaped inwards-pointing, one pair

Map 1. Distribution of *Thismia malayana* (black circle) in Peninsular Malaysia: the type locality in Ulu Bendul RP, Gunung Angsi FR in the state of Negeri Sembilan and the Tengku Hassanal WR, Temerloh in the state of Pahang.

of acute outwards-pointing, and one central appendage (vs. 7 appendages: one pair of club-shaped, one pair of acute and 3 central appendages).

Type. Malaysia. Peninsular Malaysia: Negeri Sembilan, Kuala Pilah Distr., Gunung Angsi FR, Ulu Bendul RP, a trail to Gunung Angsi., elevation ca. 206–208 m a.s.l., 9 February 2023. *Siti-Munirah* FRI 101705 (holotype KEP!, spirit collection, barcode no. SC12021]).

Description. Achlorophyllous herb, up to 10 cm tall, predominantly glabrous. ***Roots*** vermiform, unbranched, ca. 1 mm in diameter, light brown. ***Stem*** erect, up to ca. 6 cm long, 0.2 cm in diameter, pale brownish, bearing 1–4 flowers. ***Leaves*** 2–4, alternate, distant, triangular to narrowly triangular, scale-like, apex acute, margin slightly irregularly serrate (almost entire), 6 mm long, ca. 1 mm wide at base, pale brown. ***Involucral bracts*** 3, spirally/alternately arranged, similar to leaves but slightly larger, triangular to narrowly triangular, scale-like, apex acute, margin entire, 8 mm long, ca. 1.5–2.5 mm wide at base, pale brown or pale orange. ***Pedicel*** ca. 2 mm long at anthesis, elongating to ca. 5 cm long after anthesis, pale brown. ***Flowers*** terminal, asymmetrical, slightly zygomorphic, ca. 13 mm long (including ovary).

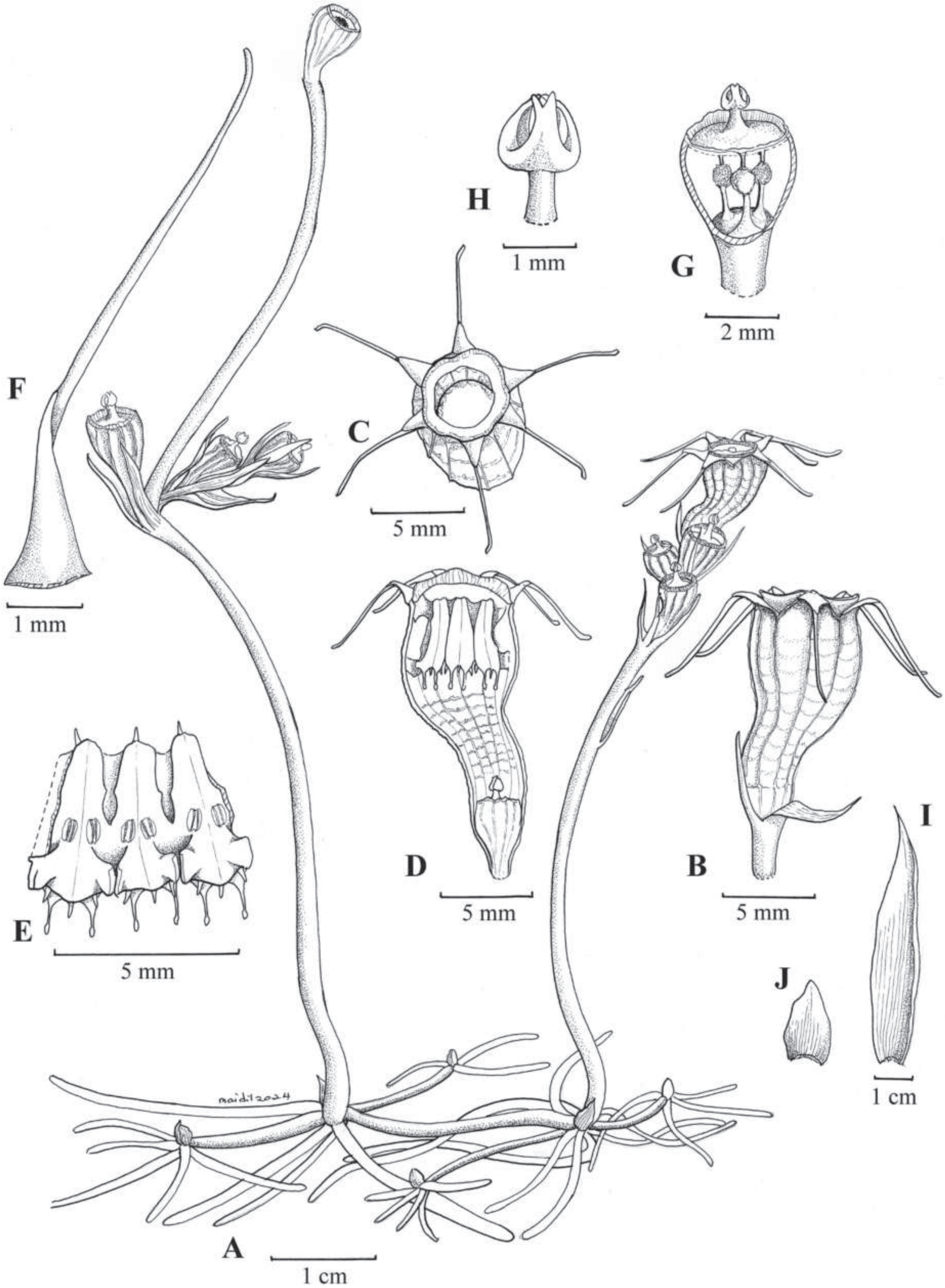

Figure 1. *Thismia malayana* **A** flowering plant **B** flower, side view **C** flower, view from above **D** flower, longitudinal section **E** three stamens, outer view **F** tepal with terminal appendage, adaxial view **G** ovary, longitudinal section **H** style and stigma **I** involucral bract, adaxial view **J** leaf, adaxial view. All drawn by Mohamad Aidil Noordin from spirit material, *Siti-Munirah FRI 101705* (**A–C**); *FRI 101701* (**D–J**).

Figure 2. *Thismia malayana* **A** flowering plant **A1** floral tube, inner surface **A2** annulus and stamen filaments, view from inside **B** inflorescence with anthetic flower and several young fruits **B1** style and stigma **B2** annulus, top view **C** flower, side view **D, E** stamens, view from inside and from outside, **E1** stamen supraconnectives: one pair of club-shaped inwards-pointing, one pair of acute outwards-pointing, and one central appendage **F** stamen supraconnectives, apical view **G** stamen tube, view from below **H, H1** fruit after dehiscence, top view, **H2** seeds **I** shoot base with roots. Photos by Siti-Munirah (**A1–I**) and Hardy-Adrian (**A**) from *FRI 101701* (**A**), *FRI 101702* (**F, G, I**), *FRI 101703* (**E1**), *FRI 101705* (**B, B2, H, H1, H2**) & *FRI 101710* (**A1, A2, B1, C, D, E**). Images not to scale (see dimensions in description and Figs 1, 3).

Figure 3. *Thismia malayana* with scales (the finest grade is 0.5 mm) **A** side view **B** top view **C** the size compared to the 20-sen coin (23.59 mm in diameter). Photos by Hardy-Adrian from uncollected plants.

Floral tube urceolate-curved, ca. 7 mm long, ca. 5 mm wide at middle, ca. 4 mm wide at base, sigmoidally bent in lower part; ***outer surface*** brown to whitish-sepia (whitish proximally & brown distally), with 12 longitudinal ribs orangish proximally & dark brown distally; ***inner surface*** reticulate, with whitish transverse bars, of similar color as outer surface. ***Tepals*** 6, free, triangular to ovate, apex acute, up to ca. 2.5 mm long, ca. 1.5–2.6 mm wide at base, dark brown, apically bearing a tentacle-like appendage; appendage narrowing towards apex, each equal in length up to ca. 6 mm long, 0.5 mm wide, whitish towards apex, becoming brownish with age. ***Annulus*** moderately raised, ring-shaped, ca. 5.4 mm in diameter, with ring width ca. 1.2 mm, orange, becoming bright yellow with age, aperture ca. 3.2 mm in diameter. ***Stamens*** 6, pendent from annulus; ***filaments*** free, ca. 1 mm long, curved downwards, yellowish to whitish; anther ca. 0.7 mm long; ***connectives and supraconnectives*** narrow at base (ca. 1.5 mm wide) and broad at apex (ca. 2 mm wide), with outer side bluish to violet; inner side bluish, violet, whitish to yellowish, flattened at inner surface, laterally connate to form a tube, ca. 4.5 mm long, supraconnective apex with one pair of club-shaped inwards-pointing, ca. 0.8–1 mm long and one pair of acute outwards-pointing ca. 0.3 mm long appendages, and one central appendage ca. 0.5–0.6 mm long; supraconnective bearing a skirt-like lateral appendage at outer side protruding towards inner side of floral tube, bearing trichomes at both sides; lateral appendage not exceeding the tip of the supraconnective appendages, margin lobed with translucent trichomes; ***interstaminal glands*** inserted on the line of fusion between supraconnectives at the level of attachment of lateral appendages, bluish (concolorous with supraconnectives). ***Ovary*** inferior, unilocular; ***placentas*** 3, free, column-like, arising from the bottom of the ovary; ovules numerous. ***Style*** ca. 0.74 mm long, dark blackish; ***stigma*** ca. 0.85 mm long, papillose, 3-lobed, with lobes ± rectangular and bifurcate at apex, dark blackish. ***Fruit*** dehiscent, cup-shaped, 6 mm in height, 6–8 mm in diameter, pale white to creamy. ***Seeds*** long oval, ca. 0.38–0.41 mm long, ca. 0.15–0.17 mm wide.

Additional specimens examined. MALAYSIA. Peninsular Malaysia: Negeri Sembilan, Kuala Pilah District, Gunung Angsi FR, Ulu Bendul RP, elev. ca. 206–208 m, February 2023, *Siti-Munirah, FRI 101701* (KEP), *FRI 101702* (KEP), *FRI 101703* (KEP), *FRI 101704* (KEP) *FRI 101709* (KEP), *FRI 101710* (KEP), *FRI 101711* (KEP); Pahang, Temerloh District, Tengku Hassanal WR, elev. ca. 200 m, 31 December 2020, *Mohamad-Shafiq & Irwan-Syah, FRI 91126* (KEP).

Distribution. Endemic to Peninsular Malaysia. Recorded in two localities: one in Gunung Angsi FR in Negeri Sembilan state and another in Tengku Hassanal WR in Pahang state (Fig. 4).

Ecology. In medium-moist or mesic, shady areas of lowland dipterocarp forests at elevations of 200–450 m a.s.l. Flowering and fruiting usually from December to February but flowering also observed in June. According to the third and fourth author's observations, *T. malayana* was only sighted and observed a few times a year, especially during the rainy season.

Etymology. The specific epithet *malayana* is derived from Malaya, a name formerly used for Peninsular Malaysia. The epithet refers to the known region of the species distribution.

Conservation status. According to the IUCN standards (IUCN 2022), we propose to classify the preliminary conservation status of *Thismia malayana* as VU (Vulnerable). This particular species has only been found in two locations. One of the sites is located in a protected area (Tengku Hassanal WR), the other in a water catch-

Figure 4. Habitat (in situ) of *Thismia malayana* in Ulu Bendul RP in Gunung Angsi FR (**A, B**) and the Tengku Hassanal WR (**C–E**) **A** *Thismia malayana* at its habitat, which is located right next to the main trail to Gunung Angsi **B** Siti-Munirah showing the habitat of *T. malayana* **C** path to Lata Bujang and Gunung Benom **D** the plants growing on rotten wood **E** Mohamad-Shafiq observed a *Thismia malayana* in its habitat. Photos by Siti-Munirah (**A, B**) and Mohamad-Shafiq (**C–E**).

ment forest under the PRF class protection forest (Gunung Angsi FR), which also includes Ulu Bendul RP. Both habitats are therefore considered stable. However, the population of this species was detected near a hiking trail at both sites, which exposes this species to the risk of trampling due to its small size. During the survey conducted between 2022 and 2023, only less than 10 individuals were found. However, due to the limited time and area of the survey and also mycoheterotrophic nature of the species which remains hidden in the soil for most of its life, it was not possible to determine the estimated number of mature individuals in the population. Therefore, this species is classified as Vulnerable based on criterion D2.

Notes. According to the classifications of Jonker (1938) and Kumar et al. (2017), *T. malayana* is placed in subgenus *Thismia* section *Thismia* subsection *Odoardoa* Schltr. (Schlechter 1921), as it has six free, equal tepals and vermiform roots. Among the *Thismia* subsection *Odoardoa*, the following species share the curved or bent floral tube characteristic of *T. malayana*: *T. chrysops* from Johor (Gunung Ledang, Peninsular Malaysia) (Ridley 1895), *T. cornuta* from Sarawak (Malaysia) (Hroneš et al. 2018), *T. inconspicua* from Brunei (Sochor et al. 2017) and *T. kinabaluensis* from Sabah (Malaysia) (Nishioka et al. 2018). A detailed morphological comparison of *T. malayana* and these morphologically most similar four species is presented in Table 1.

Table 1. Morphological comparison of *T. malayana* with *T. chrysops* (Ridley 1895), *T. cornuta* (Hroneš et al. 2018), *T. kinabaluensis* (Nishioka et al. 2018) and *T. inconspicua* (Sochor et al. 2017).

Characteristics	*T. malayana*	*T. chrysops*	*T. cornuta*	*T. inconspicua*	*T. kinabaluensis*
Floral tube					
Outer					
colour	brown to whitish-sepia	very dark sepia brown	translucent-white	(light) brownish	brown or beige
colour of longitudinal ribs					
upper part	dark brown in	rose pink	pale pinkish	sepia-brown	light brown or beige streaks
lower part	orangish	chocolate-brown	pale pinkish	both ribs and background gradually darkening toward the apex	of the same colour as the floral tube
Inner					
transverse bars	present	absent	absent	absent	present
Annulus					
colour	bright yellow	bright yellow	pinkish	sepia-brown on the outer margin, brownish-orange to light orange on the inner margin and grayish in between	with blue circle on the outer margin, orange to yellow on the inner margin
Tepal					
colour	dark brown	bright sienna, brown/ chocolate brown	white	sepia-brown	pale blue
Appendages					
colour	brown to whitish	bright sienna brown	white	sepia-brown	pale blue
surface	glabrous	finely ciliate	glabrous	glabrous	glabrous
Stamens					
colour	bluish, violet, whitish, yellowish	unknown	translucent-white	translucent-white	translucent-white
appendages of supraconnectives	5 (2 club-shaped pointing centripetally, 2 acute pointing centrifugally and 1 central appendage)	several, (2 club-shaped and few shorter ones)	2 club-shaped	4 (2 club and 2 tooth-shaped)	3 (1 filiform between 2 club-shaped)

Acknowledgements

We thank the Jabatan Perhutanan Negeri Sembilan (JPNNS) and Jabatan Perhutanan Semenanjung Malaysia (JPSM) for permission to conduct a botanical collection, Jabatan Perlindungan Hidupan Liar dan Taman Negara (PERHILITAN) and Persatuan Pemandu Pelancong Mukim Ulu Cheka (PAMUC) for deposited specimen from Tengku Hassanal WR to Kepong Herbarium (KEP). We would like to thank the staff of Ulu Bendul RP for their assistance and Angan Atan for his help during the fieldwork. We would like to thank all reviewers, Michal Hroneš, Michal Sochor, Martin Dančák and Maxim Nuraliev for constructive comments on our manuscript. We thank Mohamad Aidil Noordin for the botanical drawings, Wendy SY Yong for the assistance in conservation status assessment and Mohd Faizal MT for the encouragement and great help in many ways to the first author in the preparation of the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was conducted under the Flora of Peninsular Malaysia Project (FPM) at the Forest Research Institute Malaysia (FRIM), Kepong, funded by the Ministry of Natural Resources and Environmental Sustainability (NRES), under the 12th Malaysian Plan (SPPII No. P23085100018003). Special thanks to the Nagao Research Grant (NEF) for partially funding the *Thismia* research.

Author contributions

All authors contributed equally to this study and made a significant contribution to the overall result.

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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 242: 241–271 (2024)
DOI: 10.3897/phytokeys.242.110474

Research Article

Seven new species of *Rinorea* (Violaceae) from the Neotropics

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Abstract

Over the course of revising the genus *Rinorea* (Violaceae) from Colombia, field observations and herbarium studies revealed seven new species. Several of the new species described here belong to species complexes that required examination of herbarium material from across the Neotropics. Each of the new species described here have oppositely arranged leaves and belong to *Rinorea* sect. *Pubiflorae*, a section restricted to the Neotropics. Two new species are segregated from the *R. ovalifolia* species complex: *Rinorea chiribiquetensis* from Chiribiquete National Park in the Colombian Amazon and *Rinorea stevensii* from the Orinoco River near the border of Colombia and Venezuela. Two new species are segregated from the *Rinorea hirsuta* species complex: *Rinorea galeanoae-bernalii* and *Rinorea cogolloi*, both from the eastern slopes of the Andean Central Cordillera along the mid-Magdalena River Valley in Colombia. From the widely distributed *R. pubiflora* species complex, we segregated one new species, *Rinorea callejasii*, from southeast Panama and the Chocó in Colombia. In addition to these five new taxa segregated from widely distributed species complexes, we discovered two previously unknown species with affinities to other Neotropical *Rinorea*. *Rinorea aymardii* is described from the Alto Orinoco-Casiquiare Biosphere Reserve in Venezuela and most closely resembles *R. melanodonta* from Colombia. *Rinorea betancurii* is segregated from *R. macrocarpa* and occurs in the Amazonian Regions of Colombia, Brazil, Peru and Venezuela. In this study, we provide descriptions, illustrations and distribution maps of the new species and make preliminary assessments of the risk of extinction using the IUCN Red List Categories and Criteria. We also furnish an identification key to the species of *Rinorea* sect. *Pubiflorae* in Colombia.

Key words: Conservation, Malpighiales, morphology, Neotropics, new species, taxonomy, Violaceae

Academic editor: Alexander Sennikov
Received: 3 August 2023
Accepted: 15 March 2024
Published: 3 June 2024

Citation: Hoyos-Gómez SE, Callejas Posada R, Wahlert GA (2024) Seven new species of *Rinorea* (Violaceae) from the Neotropics. PhytoKeys 242: 241–271. https://doi.org/10.3897/phytokeys.242.110474

Introduction

The genus *Rinorea* Aubl. has a pantropical distribution and is the second largest genus in the Violaceae after *Viola* (Ballard et al. 2014). It is composed of 225–275 species of shrubs and trees with ca. 30 species in Asia, 115–155 species in Africa, 24 species in Madagascar and, in the Neotropics, where species of *Rinorea* typically occur in lowland rainforests, 47 species and two infraspecific taxa are currently recognised (Hekking 1988; Wahlert and Ballard 2009; Wahlert 2010; Marquete Ferreira da Silva and Medeiros 2012; Oliveira and de Queiroz

2020). They are often locally common shrubs and treelets of the forest understorey and frequently co-occur with other species of *Rinorea* (ter Stegee 2013).

In his taxonomic treatment of Neotropical *Rinorea*, Hekking (1988) classified the species into one of two groups: Super Group I 'Apiculata' and Super Group II 'Rinorea.' The three species in Super Group I 'Apiculata' were segregated into the genus *Bribria* Wahlert & H.E. Ballard, based on morphological, anatomical and molecular phylogenetic evidence (Wahlert et al. 2017; Wahlert and Ballard 2012; van Velzen et al. 2015). Hekking divided Super Group II 'Rinorea' into three groups: Group IIa 'Rinorea,' Group IIb, 'Uxpanapana,' and Group IIc 'Pubiflora' Hekking (1988). Wahlert et al. (2017) established these groups as taxa: Group IIa was recognised as *Rinorea* sect. *Rinorea* and includes all Neotropical *Rinorea* with alternately arranged leaves, Group IIb was segregated into the genus *Ixchelia* H.E. Ballard & Wahlert, with two species from Mexico and Mesoamerica and Group IIc was recognised as *Rinorea* sect. *Pubiflorae* Wahlert & H.E. Ballard and includes all Neotropical *Rinorea* with oppositely arranged leaves. The seven new species described in this study all belong to *R*. section *Pubiflorae*, which is endemic to the Neotropics.

The present study was undertaken as part of a revision of *Rinorea* for Colombia. However, because several taxa are allied to widely distributed complexes, we examined specimens from across the Neotropics, from Mexico to Brazil and the Caribbean. We employed many of the same traits used by Hekking (1988) to circumscribe taxa and we found that previously overlooked characters of lamina venation are also useful in delimiting some species of *Rinorea*. The venation characters used in this study include details of the patterning of primary and tertiary veins and the spacing and angle of attachment of the secondary veins to the mid-vein, amongst others. In addition to three species discovered since Hekking's (1988) monograph, the seven new species described here bring the total number of taxa in *Rinorea* sect. *Pubiflorae* to 44 (41 species and three infraspecific taxa). The 13 remaining Neotropical species, all with alternate leaves, belong to *R*. sect. *Rinorea*.

Materials and methods

Field collections were made in lowland tropical rainforests in Bolivia, Colombia, Costa Rica and Peru, from 0–500 m elevation. All available herbarium material was examined from BHO, COAH, COL, F, FAUC, GH, HUA, JAUM, MEDEL, MO, NY, TOLI, UBDC and US (herbarium acronyms according to Thiers (2023)). Several digitised herbarium collections and records from the Global Biodiversity Information Facility (GBIF) were consulted to locate duplicate specimens for the following Herbaria: AAH, CM, FMB, G, INPA, K, MA, MBM, MG, MICH, RB, P, U and VEN. All cited collections have been seen by the first author. Species descriptions are based primarily on field observations and herbarium specimens. When available, flowers from herbarium specimens were rehydrated before dissection and measurement. A digital caliper and dissecting stereoscope were used to measure indument, flowers, fruits and seeds.

Leaf laminae were cleared to study venation architecture. Leaves were placed in a glass container and submerged in 1–5% sodium hydroxide (NaOH). The NaOH solution was changed every 1–2 days during the clearing process, which took 8–10 days. Leaves were then washed in a 50% Clorox® solution followed by a final wash in water to stop the bleaching process. Staining was made with safranin for 5–8 minutes and then the leaves were put through a dehydration series in 50%, 95% and 100% ethanol (Ellis et al. 2009). The cleared leaves were photographed with a digital camera using a scale bar.

Post-factum georeferences for specimens lacking coordinates were assigned using either Google Earth or Tropicos specimen records with the same collecting localities. Collections lacking unambiguous locality information were omitted from the conservation assessment calculations. The online GeoCat facility (Bachman et al. 2011) was used to calculate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) of each species to preliminarily estimate the risk of extinction using IUCN Red List Categories and Criteria (IUCN 2012); a 2 × 2 km cell was used for calculating AOO.

Taxonomic treatment

1. *Rinorea callejasii* Hoyos-Gómez, sp. nov.

urn:lsid:ipni.org:names:77342886-1

Type. Panamá. Prov. Colón: forested slopes of Cerro El Jefe, near large coffee finca, 9°14'02"N, 79°22'30"W, 700–1000 m elev., 24 Jan 1970, *R. L. Wilbur et al. 11327* (holotype: MO [acc. 2027894; barcode MO-554811]!; isotypes: F [cat. 1694605]!, GH!, NY [barcode 04112199]!, US [cat. 2640360; barcode 03009254]!).

Description. *Rinorea callejasii* is most similar to *R. pubiflora* var. *pubiflora* s.s. by the lamina with symmetrical bases and bearing domatia, filaments free and fruit symmetrical, but it differs by the branchlets densely pubescent with ferruginous trichomes (vs. branchlets glabrescent in *R. pubiflora* var. *pubiflora* s.s.), primary and secondary veins on the abaxial lamina surface densely villous with ferruginous trichomes (vs. primary and secondary veins on the abaxial lamina surface glabrescent), fruit 1.5–2 cm long with 2 ovules per carpel (vs. fruit 2–3.5 cm long with 3 ovules per carpel) and the seeds glabrous (vs. seeds pubescent).

Shrubs or trees 2–12 m tall, terminal branchlets pubescent with erect ferruginous trichomes 0.4–0.5 mm long. Leaves opposite, petiolate; petioles 2–10 mm long, pubescent with erect ferruginous trichomes 0.2–0.3 mm long; stipules deciduous, free, elliptic, 1.6–4.8 × 0.8–1.3 mm, pubescent with appressed ferruginous trichomes 0.5 mm long; lamina elliptic, 4.6–15 × 2–6.5 cm, adaxial surface pilose on the mid-vein and secondary veins with erect ferruginous trichomes 0.4–0.5 mm long, abaxially pubescent on the mid-vein, trichomes on the secondary and tertiary veins, trichomes 0.3–0.5 mm long, erect, ferruginous, base cuneate, symmetrical, margin subserrate, apex acuminate, acumen 0.7–1.2 cm long, mucronate; with 8–10 major secondary vein pairs, major secondary veins eucamptodromous becoming brochidodromous distally, with regular spacing and uniform angle of the major secondary vein; major secondary attachment to mid-vein decurrent, leaf domatia present. Inflorescence axillary, terminal or subterminal, racemose, 3–5 cm long, 0.7–1.5 cm diam., axis pubescent with erect ferruginous trichomes 0.3–0.5 mm long; pedicels 1.8–3.6 mm long, pubescent with erect golden trichomes 0.3–0.5 mm long, articulated near the base; peduncle bracts deciduous, narrowly triangular, 1.5–1.8 × 1.5–1.8 mm, herbaceous, pubescent along the costa with appressed golden trichomes 0.3–0.5 mm long, margin ciliolate; bractlets persistent below articulation, subopposite, 1 × 1 mm. Flowers 3–3.6 × 3–3.4 mm; sepals subequal, triangular, 1.3–2 × 1.4–1.6 mm, 5- to 9-veined, pubescent along the costa with appressed golden trichomes 0.3 mm long, margin ciliolate, apex apiculate; petals lanceolate, 3.4–3.8 × 0.7–1.4 mm, pubescent along the costa with appressed golden trichomes 0.3–0.4 mm long, margin entire, apex acute, white; stamens 2.9–3.3 mm long, all filaments free, dorsal gland pilose with spreading golden trichomes 0.2–0.3 mm long covering lower half of the filament, anthers elliptic, 1.1–1.4 × 0.3–0.5 mm, apex rounded, connective 0.7–0.8 mm long, dorsal connective scale conspicuous, lateral as well as apical, lanceolate, 2.2–2.5 × 0.8–1 mm, margin entire, orange-brown; ovary globose, 0.8–1 × 0.9–1 mm, pubescent with erect, golden trichomes 0.4–0.5 mm long; style erect, filiform, 2–2.3 × ca. 0.1 mm, pubescent proximally with appressed golden trichomes 0.2–0.3 mm long, stigma undifferentiated. Fruit a symmetrical, subligneous capsule dehiscent along three sutures, ellipsoid, 1.5–2 × 0.5–0.6 cm, apex acuminate, pubescent with erect golden trichomes 0.2–0.3 mm long, green in vivo, brown when dry. Seeds two per valve, globose, 4–5 mm diam., glabrous, with maculae, brown when dry. (Fig. 1)

Distribution and habitat. *Rinorea callejasii* is restricted to the Caribbean coast of Colón and San Blas Provinces, Panama and the Pacific coast of Chocó Department, Colombia, a region belonging to the biogeographic Province of Chocó-Darien in the Pacific Dominion (*sensu* Morrone (2014)). It occurs in lowland humid rainforests at elevations of 30–500 m. (Fig. 2)

Etymology. *Rinorea callejasii* honours Dr. Ricardo Callejas Posada, Professor of Biology at Universidad de Antioquia, Medellín, Colombia. Prof. Callejas has made many contributions to the taxonomic knowledge of the Piperaceae and expanded the understanding of the diverse flora of Colombia, especially in the Department of Antioquia. He was the major advisor of SEHG.

Phenology. The species flowers January through March; specimens in fruit were collected in March and May.

Conservation status. *Rinorea callejasii* has a geographic range in the form of an EOO of 40,729 km^2 and AOO of 52 km^2. In Panama, it is represented by two locations within Chagres National Park and one location in Soberanía National Park. Outside of the protected areas, where the species exists at nine locations, it is threatened by the exploitation of natural resources, mineral extraction and energy development. In Colombia, it is represented by two locations, both outside protected areas. The species does not meet the criteria necessary to assign a threatened status. However, given ongoing habitat disturbance, it is likely that the species will qualify in the near future for a threatened status and, thus, it is preliminarily assessed with a status of “Near Threatened” (NT).

Notes. *Rinorea pubiflora*, as circumscribed by Hekking (1988), was morphologically variable across its large distribution in the Neotropics. He recognised a variety of *R. pubiflora*: var. *grandifolia* (Eichler) Hekking, which was further divided into two forms: f. *grandifolia* and f. *andersonii* (Sandwith ex Hekking) Hekking. *Rinorea callejasii* is a segregate of *R. pubiflora* var. *pubiflora* s.s. In attempting to explain the morphologically divergent specimens of var. *pubiflora* from Panama (e.g. *G. C. de Nevers et al. 5075*), Hekking (1988) invoked a scenario of hybridisation between *R. squamata* S.F.Blake and var. *pubiflora*. However, our analysis of morphological divergence and biogeographic distribution

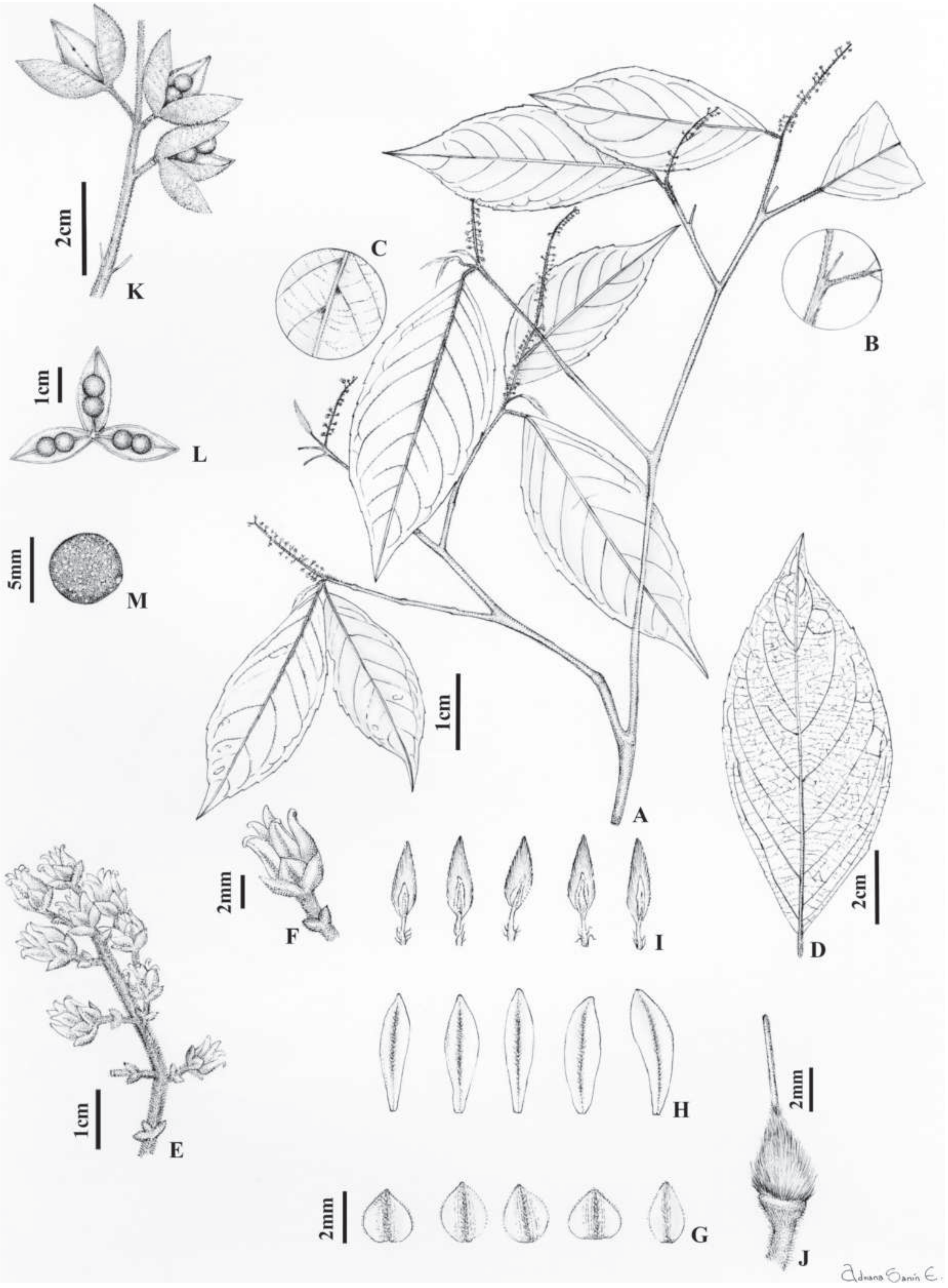

Figure 1. *Rinorea callejasii* Hoyos-Gómez **A** habit **B** detail of young twig with pubescence **C** detail leaf showing domatia, abaxial surface **D** leaf architecture **E** inflorescence **F** flower **G** sepals, abaxial surface **H** petals, abaxial surface **I** stamens, adaxial surface **J** gynoecium **K** infructescence **L** fruit, showing two seeds per valve **M** seed. (**A–J**: *M. D. Correa 765* [MO]; **K–M**: *G. D. McPherson 6851* [MO]).

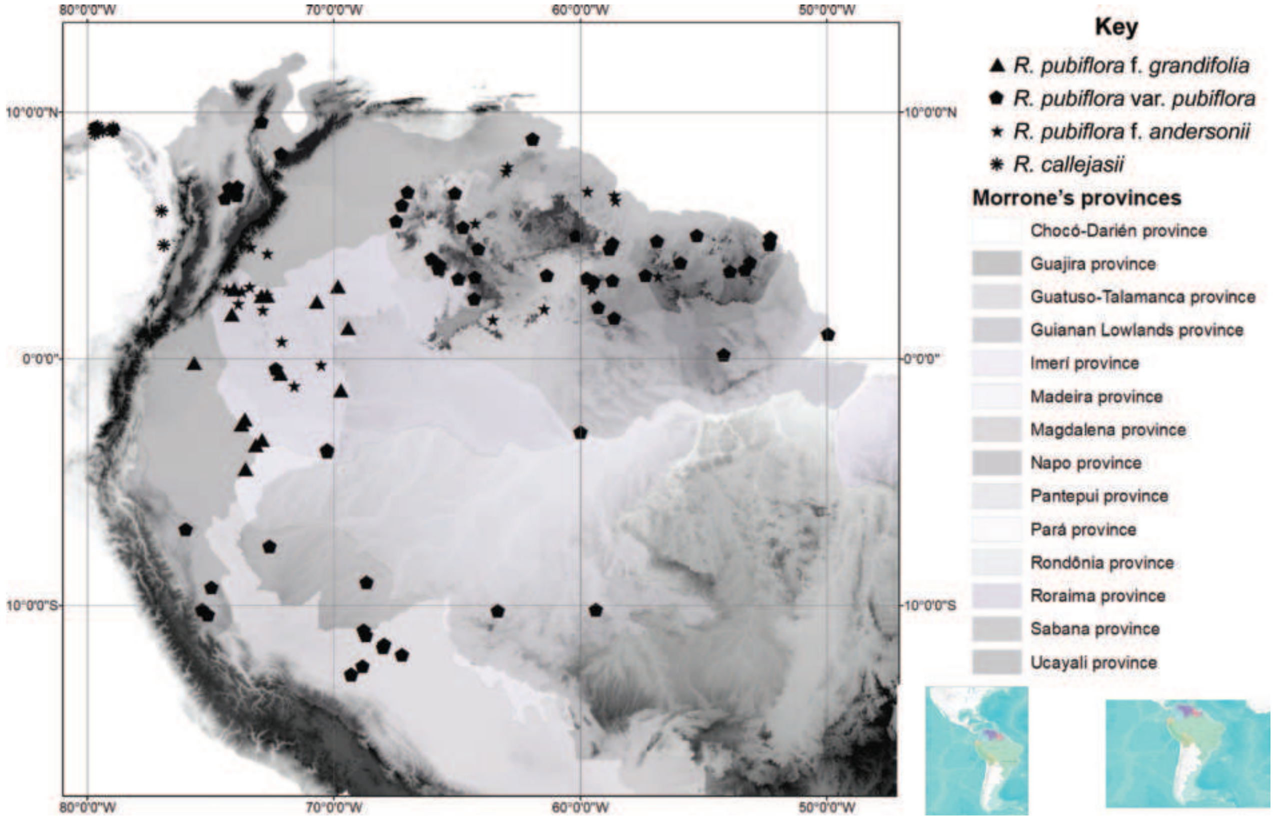

Figure 2. Distribution of *R. pubiflora* f. *grandifolia* (triangles), *R. pubiflora* var. *pubiflora* (pentagons), *R. pubiflora* f. *andersonii* (stars), *Rinorea callejasii* (asterisks).

suggest that *R. callejasii* is a separately evolving lineage from the nominate species (*sensu* De Queiroz (2008)) and deserving of recognition as a new taxon at the rank of species.

Rinorea callejasii is sympatric with four other taxa of *Rinorea*. *Rinorea squamata* and *R. hirsuta* Hekking can be differentiated by their single glabrous seed per valve (vs. two glabrous seeds per valve in *R. callejasii*). *Rinorea dasyadena* is distinguished by its two pubescent seeds per valve and asymmetrical lamina base (vs. two glabrous seeds and symmetrical lamina base). *Rinorea lindeniana* var. *fernandeziana* can be separated by its one pubescent seed per valve (vs. two glabrous seeds per valve).

Additional specimens examined. Colombia. Dept. Chocó. Mpio. de San José del Palmar: Hoya del río San Juan, 04°36'N, 76°54'W, 7 Apr 1979 (fr), *E. Forero et al. 4780* (COL, MO, US); Mpio. Bahía Solano: hills behind Bahía Solano, 6°13'14"N, 77°24'27"W, 0–250 m elev., 5 Jan 1973 (fl), *A. H. Gentry & E. Forero 7245* (COL, F, MO, U). **Panamá. Prov. Colón:** Santa Rita Ridge lumber road, 23 Feb 1968 (fl), *M. D. Correa-A. & R. L. Dressler 765* (MO, NY, US); Santa Rita Ridge, 9°19'N, 79°39'W–9°24'N, 79°48'W, 1 Mar 1971 (fl), *T. B. Croat 13831* (MO); El Llano-Cartí Road, 10 miles from Inter-American Highway near El Llano, 9°17'45"N, 78°56'15"W, 330 m elev., 28 Mar 1976 (fl, fr), *T. B. Croat 33754* (COL, MO); El Llano-Cartí Road, 5–6 miles N of Inter-American Highway at El Llano, 09°15'30"N, 78°55'50"W, 350–375 m elev., 7 May 1976 (fl), *T. B. Croat 34788* (COL, MO); El Llano-Cartí Road, km 26.5, trail NE from road, [coordinates on original label: 9°19'N, 78°55'W; corrected to 9°22'N, 78°58'W], 175 m elev., 9 Mar 1985 (fl), *G. C. de Nevers et al. 5075* (MBM, MO); Santa Rita Ridge road, 4 miles from Transisthmian Highway to Agua Clara weather station, 9°21'N, 79°42'W, 11 Dec 1973 (fl), *R. L. Dressler et al. 8846* (MO); Santa Rita Ridge road, 4 miles from Transisthmian Highway to Agua Clara weather station, 9°21'N, 79°42'W, 500 m elev., 11 Dec 1973 (fl), *A. H. Gentry et al. 8846* (MO, COL); along road into Santa Rita, E of Agua Clara, 9°07'10"N, 79°42'02"W, 4 Mar 1973 (fl), *H. Kennedy 2741* (MO); Santa Rita Ridge, 9°20'N, 79°45'W, 13 May 1986 (fl), *G. D. McPherson 9168* (MG, MO); 12.7 km from Inter-American Highway, 350 m elev., 15 Feb 1975 (fr), *S. A. Mori 4694* (COL); Santa Rita Ridge Road, 17 km from Boyd-Roosevelt Hwy, 9°22'N, 79°40'W, 450 m elev., 14 Mar 1975 (fl), *S. A. Mori et al. 5041* (COL, MO); El Llano-Cartí Road, 20.7 km north from Inter-American Hwy, 9°17'58"N, 78°55'58"W, 20 Mar 1975, *S. A. Mori & J. A. Kallunki 5115* (COL, MO); 9 km from Inter-American Highway, 9°15'50"N, 78°55'51"W, 350 m eelv, 22 Mar 1975 (fr), *S. A. Mori 5154* (COL, MO); upper Río Piedras headwaters, along trail from end to Santa Rita Ridge road, ca. 11 km SW of Cerro Braja, 9°25'N, 79°35'W, 4 May 1981 (fr), *K. J. Sytsma et al. 4311* (MO). **Prov. San Blas:** El Llano-Cartí Road, 7 miles on Interamerican Highway, 9°15'N, 79°00'W, 550 m elev., 14 Mar 1985 (fr), *G. D. McPherson 6851* (MO).

2. *Rinorea aymardii* Hoyos-Gómez, sp. nov.

urn:lsid:ipni.org:names:77342872-1

Type. Venezuela. Dept. Amazonas de Atabapo: “Caño Iguapo” Alto Orinoco, 15 km al SE de la Esmeralda, 3°8'N, 65°27'W, 100–180 m elev., 20 Feb 1990, *G. Aymard et al. 8050* (holotype: MO [acc. 5983541; barcode MO-1980109]!; isotype: MA [cat. 543845]!).

Description. *Rinorea aymardii* is similar to *R. melanodonta* S.F.Blake by the lamina with domatia and symmetrical bases, filaments free and style erect, but it differs by the smaller, herbaceous, lanceolate lamina, 4–11 × 1–2.7 cm (vs. larger, coriaceous, elliptic lamina, 6.5–17 × 1.7–5.2 cm in *R. melanodonta*), 7–8 major secondary vein pairs (vs. 9–12 major secondary vein pairs), abaxial tertiary venation percurrent, pubescent (vs. abaxial tertiary veins reticulate, glabrescent), petals 2.8–3 × 1–1.2 mm, with entire margin and pubescent at the apex (vs. petals 5–5.7 × 1.5–2.2 mm, with margin ciliolate and glabrous at the apex), shorter stamens, 2.8–3 mm long (vs. longer stamens, 4–4.5 mm long), dorsal gland glabrous (vs. dorsal gland pilosulous) and smaller anther connective scales, 2–2.1 × 0.7–0.8 mm (vs. larger anther connective scales, 3.2–3.5 × ca. 1.5 mm).

Treelets to 3 m tall, young branchlets strigose with erect golden trichomes 0.1–0.2 mm long, glabrescent. Leaves opposite, petiolate; petiole 1.8–3.8 mm long, pubescent with erect golden trichomes 0.1–0.2 mm long; stipules deciduous, free, lanceolate 2–2.4 × 0.9–1 mm, herbaceous, pubescent with appressed golden trichomes 0.1–0.2 mm long, apex mucronate; lamina elliptic-lanceolate, 4–11 × 1–2.7 cm long, adaxially glabrous, abaxially pubescent on the mid-vein and veins with appressed golden trichomes 0.2–0.4 mm long, with 7–8 major secondary vein pairs, secondary veins with irregular spacing, vein angles smoothly decreasing proximally, mixed epimedial tertiary veins, symmetrical and rounded base, margin crenate, apex acuminate, acumen 0.5–1 cm, mucronate, leaf domatia absent. Inflorescence axillary, terminal or subterminal, racemose, 1.7–4 cm long, 0.8–1 cm diam., axis pubescent with erect golden trichomes 0.2 mm long; pedicels 1.7–2 mm, pubescent with erect golden trichomes 0.2 mm long, articulated near the middle; bractlets persistent below articulation, opposite, ca. 1 × 1 mm, herbaceous, the costa pubescent with appressed golden trichomes 0.2 mm long, peduncle bracts triangular, ca. 1 × 1.2 mm, herbaceous, pubescent with appressed ferruginous trichomes 0.2 mm long, margin ciliolate. Flowers 3–3.5 × 3–3.5 mm, sepals subequal in size and shape, triangular, 1.4–2.4 × 1–1.3 mm, 3–5-veined, costa pubescent with appressed golden trichomes, 0.2 mm long, margin ciliolate, apex apiculate; petals lanceolate, 2.8–3 × 1–1.2 mm, pubescent with erect golden trichomes 0.1–0.2 mm long near the apex, margin entire, apex acute, cream-coloured in vivo, brown when dry; stamens 2.8–3 mm long, filaments free, glabrous, 0.4–0.6 mm long, dorsal glands glabrous, completely covering the filaments; anthers lanceolate, 1–1.2 × 0.4–0.5 mm, glabrous, apex rounded, connective 1–1.2 mm long, dorsal connective scale lanceolate, 2–2.1 × 0.7–0.8 mm, scarious, brown–orange, margin subentire; ovary globose, 0.8–1 × 0.8–0.9 mm, pubescent with erect golden trichomes 0.2–0.3 mm long; style erect, filiform, glabrous, 1.7–1.9 × ca. 0.1 mm, stigma acute. Fruit unknown. (Fig. 3)

Distribution and habitat. *Rinorea aymardii*, which is only known from the type specimen, occurs the Alto Orinoco–Casiquiare Biosphere Reserve in Amazonas State, Venezuela, a biogeographic area classified as the Province of Imerí in the Boreal Brazilian Dominion (*sensu* Morrone (2014)). It grows in terra firma humid forest at elevations of 100–180 m. The landscape of the type locality is characterised by gently sloping (10–20%) hills composed of granitic and quarzitic rocks (Aymard 2000). (Fig. 4)

Etymology. *Rinorea aymardii* honors the Venezuelan botanist Gerardo Aymard, who has made significant contributions to the taxonomic knowledge of the flora of Venezuela, especially the south-western part of the country in the Río Negro and Orinoco River Basins.

Phenology. The species is only known from one flowering specimen collected in February.

Conservation status. *Rinorea aymardii* has a geographic range in the form of an EOO of 4 km^2 and AOO of 4 km^2. It is currently known only from the type collection, which represents one location within the terra firma forests of the Alto Orinoco–Casiquiare Biosphere Reserve in Venezuela where it is threatened by illegal logging and mining. Based on its limited AOO, the single location and the projected continuing decline in the quality of habitat due to uncontrolled deforestation and resource extraction, the species might be preliminarily assigned to the "Critically Endangered." However, given the difficulty accessing this inadequately explored area, it is likely there are additional occurrences that would allow a more accurate assessment of the risk of extinction than is possible at this time. The species is therefore preliminarily assigned to the IUCN (2012) Category of "Data Deficient" [DD].

Notes. *Rinorea aymardii* is sympatric with *R. macrocarpa* from which it can be differentiated by the smaller lamina 4–11 × 1–2.7 cm with crenate margins (vs. larger lamina 5.5–21.5 × 2–9.2 cm with subentire to subcrenate margins in *R. macrocarpa*), filaments free (vs. filament fused into a tube) and style filiform (vs. style conical).

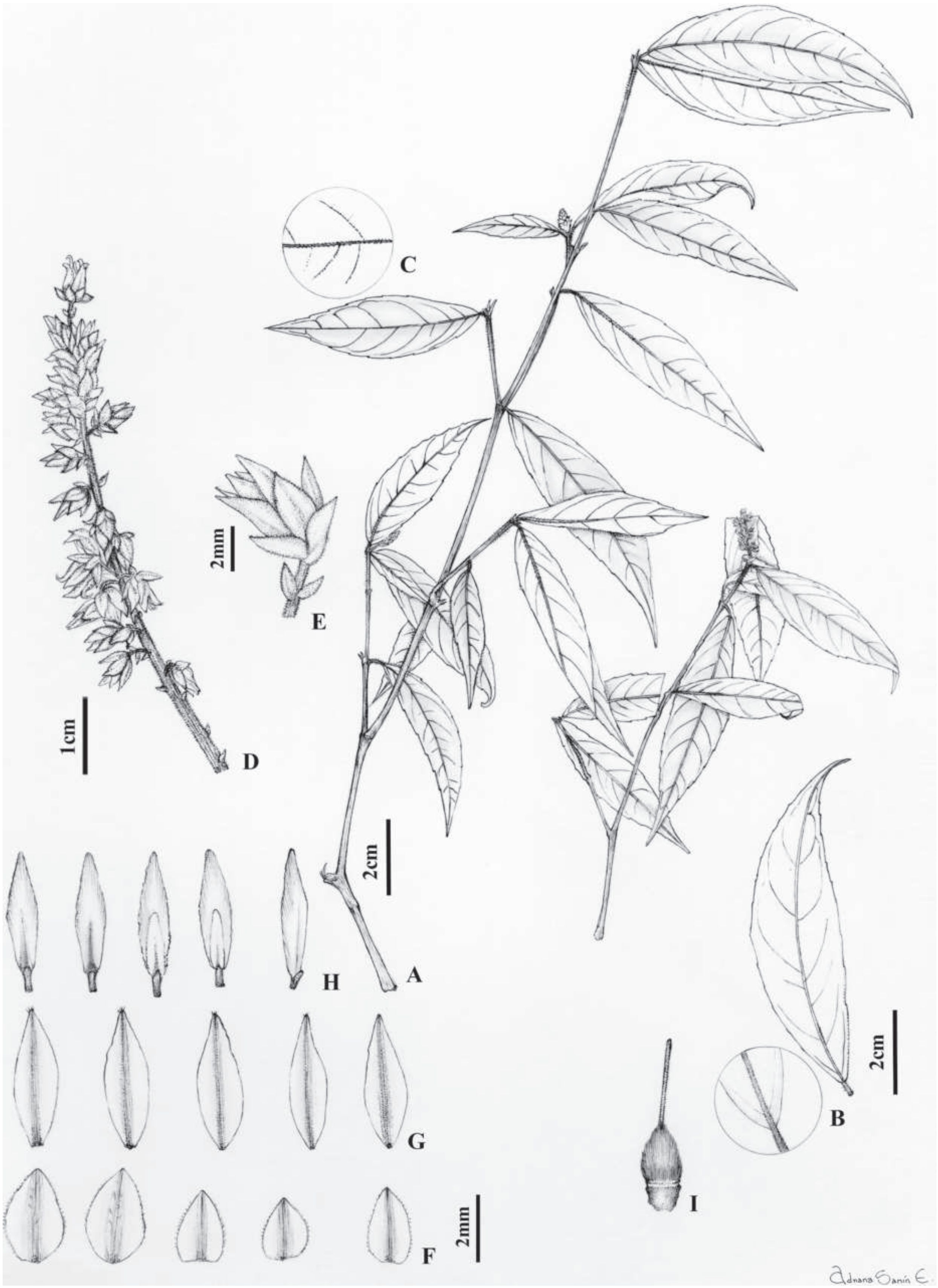

Figure 3. *Rinorea aymardii* Hoyos-Gómez **A** habit **B** leaf architecture **C** detail of leaf, abaxial surface **D** infructescence **E** flower **F** sepals, abaxial surface **G** petals, abaxial surface **H** stamens, showing both surfaces **I** gynoecium. (**A–I**: *G. Aymard 8050* [MO]).

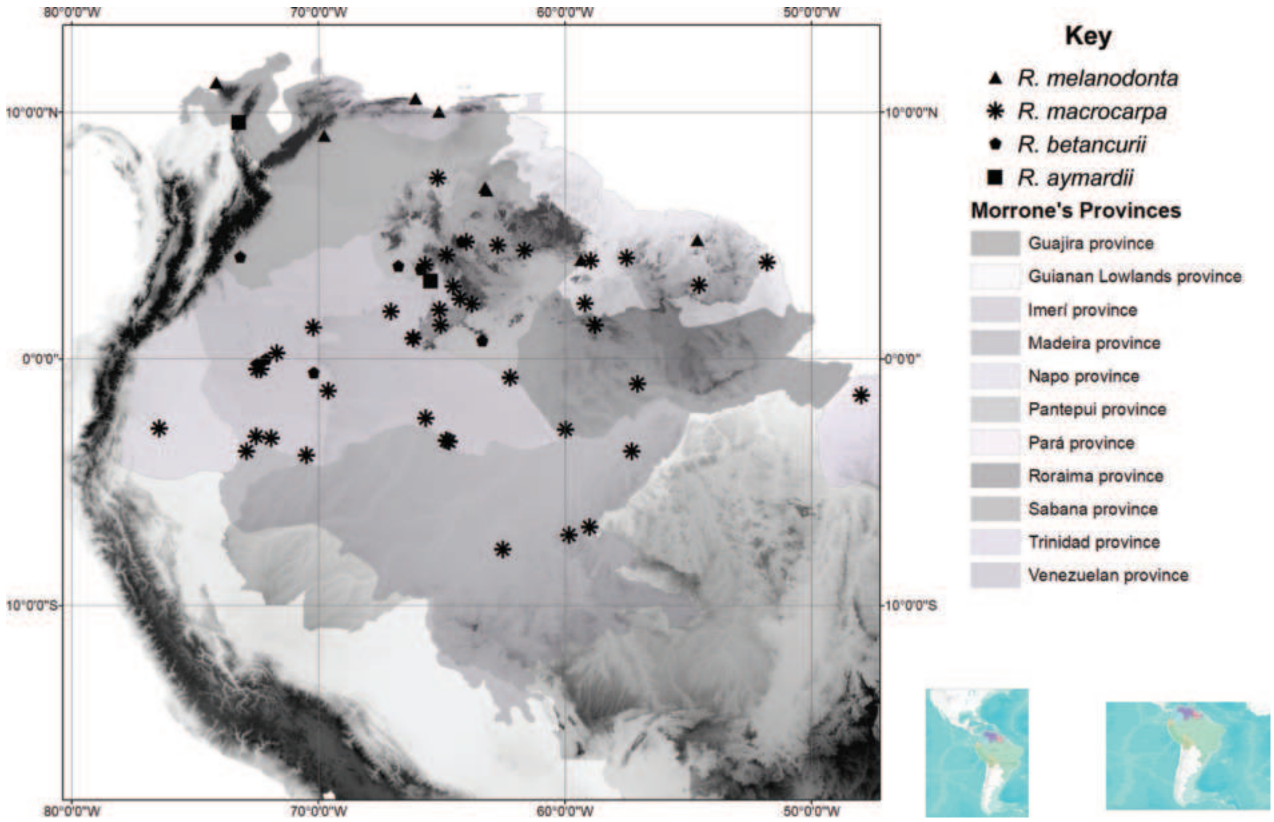

Figure 4. Distribution of *R. melanodonta* (triangles), *R. macrocarpa* (asterisks), *R. betancurii* (pentagons), *Rinorea aymardii* (squares).

3. *Rinorea chiribiquetensis* Hoyos-Gómez, sp. nov.

urn:lsid:ipni.org:names:77342873-1

Type. Colombia. Dept. Caquetá: alrededores del refugio la Selva, 1°4'0.23"N, 72°44'24.6"W, 630 m elev., 1 Dec 1992, *M. Velayos et al. 6509* (holotype: MO [acc. 4644279; barcode MO-1590549]!; isotypes: COL!, MA [cat. 543845]!).

Description. *Rinorea chiribiquetensis* is similar to *R. ovalifolia* (Britton) S.F.Blake by the lamina base symmetrical, margin subserrate, ovary globose and style filiform, but it differs by the smaller lamina, 3.2–7.2 × 1.6–3.6 cm, with appressed pubescence on the abaxial surface and domatia present (vs. the larger lamina, 3–16 × 2–7.5 cm, glabrescent and lacking domatia in *R. ovalifolia*), shorter inflorescence, 1.5–5 cm long (vs. longer inflorescence, 4–12 cm long), shorter pedicels, 1.7–3.3 mm long (vs. longer pedicels, 4–6 mm long) and stamens with filaments free (vs. stamens with filaments fused).

Shrubs to 1.5 m tall, terminal branchlets pubescent with appressed golden trichomes 0.3 mm long, lenticels 0.5–0.6 mm. Leaves opposite, petiolate; petiole 3–6 mm long, pubescent with erect golden trichomes 0.2–0.3 mm long; stipules deciduous, free, lanceolate 1.9–2.1 × 0.9–1 mm, pubescent with appressed golden trichomes 0.2 mm long, margin entire; lamina elliptic, 3.2–7.2 × 1.6–3.6 cm, adaxially pubescent on mid-vein with appressed golden trichomes 0.2–0.3 mm long, abaxially pubescence on mid-vein, secondary and tertiary veins with appressed golden trichomes 0.2–0.3 mm long; with 5–6 major secondary vein pairs, semi-craspedodromous; secondary veins with irregular spacing, and veins angle smoothly decreasing proximally between them; symmetrical base, cuneate, margin subserrate, apex acuminate, acumen 5–6 mm long, mucronate, leaf domatia present. Inflorescence axillary, lateral or terminal, racemose, 1.5–5 cm long, 0.5–1 cm diam., axis pubescent with erect golden trichomes 0.2 mm long; pedicels 1.7–3.3 mm long, articulated near the middle, pubescent with erect golden trichomes 0.2 mm long,; bractlets persistent below articulation, subopposite, ca. 1 × 1 mm, herbaceous, costa pubescent with appressed golden trichomes 0.2 mm long, 3–5 veins; peduncle bracts deciduous, narrowly triangular 1–1.4 × 1–1.5 mm, herbaceous, pubescent with appressed golden trichomes 0.2 mm long, 3–5 veins, margin ciliolate. Flowers 3.2–3.5 × 3–3.3 mm; sepals subequal in size and shape, triangular, 1.5–1.7 × 1.7–1.9 mm, 5–7 veined, costa pubescent with appressed golden trichomes 0.2 mm long, margin ciliolate, apex apiculate; petals lanceolate, 3–3.3 × 1.4–1.6 mm, pubescent with erect golden trichomes 0.2 mm long near the apex, margin entire, apex acute; stamens 2.6–3 mm long, filaments free, 0.7–0.9 mm, dorsal gland glabrous, completely covering the filament; anthers elliptic, 1–1.1 × 0.3–0.5 mm, glabrous, apex rounded, connective 0.6–0.7 mm long, dorsal connective scale lanceolate, 2.2–2.4 × 0.8–1 mm, scarious, margin subentire, brown-orange; ovary globose, 0.7–0.8 × 0.8–0.9 mm, pubescent with appressed golden trichomes 0.4 mm long; style erect, filiform, 1.7–2 × ca. 0.1 mm, glabrous, stigma acute. Fruit unknown. (Fig. 5)

Distribution and habitat. *Rinorea chiribiquetensis* is endemic to Caquetá Department, Colombia, an area belonging to the Biogeographical Province of Imerí in the Boreal Brazilian Dominion (sensu Morrone (2014)). It occurs in lowland tropical rainforest from rocky substrates at an elevation of 630 m. (Fig. 6)

Etymology. *Rinorea chiribiquetensis* is named for the Chiribiquete National Park in Colombia.

Phenology. The species is only known from one flowering specimen collected in December.

Conservation status. The region encompassing the vast and remote Chiribiquete National Park is relatively little explored as evidenced by the scarcity of collections in the Tropicos database (https://www.tropicos.org; accessed 25 February 2023), GBIF (https://www.gbif.org; accessed 25 February 2023) and other Colombian Herbaria (e.g. COAH, COL, HUA). There are insufficient data to assess the risk of extinction of *Rinorea chiribiquetensis* and, therefore, the species is preliminarily assigned to the IUCN (2012) category of "Data Deficient" [DD].

Notes. *Rinorea chiribiquetensis* is sympatric with *R. macrocarpa*, but it can be differentiated by the presence of domatia (vs. domatia absent in *R. macrocarpa*), smaller lamina, 3.2–4.2 × 1.6–3.6 cm (vs. larger lamina, 5.5–21.5 × 2–9.2 cm), filaments free (vs. filaments fused into a tube) and style filiform (vs. style conical). *Rinorea chiribiquetensis* can be differentiated from *R. stevensii* by the smaller lamina, 3.2–4.2 × 1.6–3.6 cm (vs. larger lamina, 4–12.5 × 2.5–7 cm in *R. stevensii*) and less dense pubescence on the abaxial lamina surface, with trichomes 0.2–0.3 mm long (vs. denser pubescence on the lamina, with trichomes 0.4–0.5 mm long).

Figure 5. *Rinorea chiribiquetensis* Hoyos-Gómez **A** habit **B** detail of young twig with pubescence **C** detail of young twig showing lenticels **D** detail of leaf showing pubescence, adaxial surface **E** detail of leaf showing domatia, abaxial surface **F** leaf architecture **G** infructescence **H** flower **I** sepals, abaxial surface **J** petals, abaxial surface **K** gynoecium **L** stamens, showing adaxial and abaxial surfaces, with a detail of the dorsal gland (left). (**A–L**: *M. Velayos 6509* [MO)].

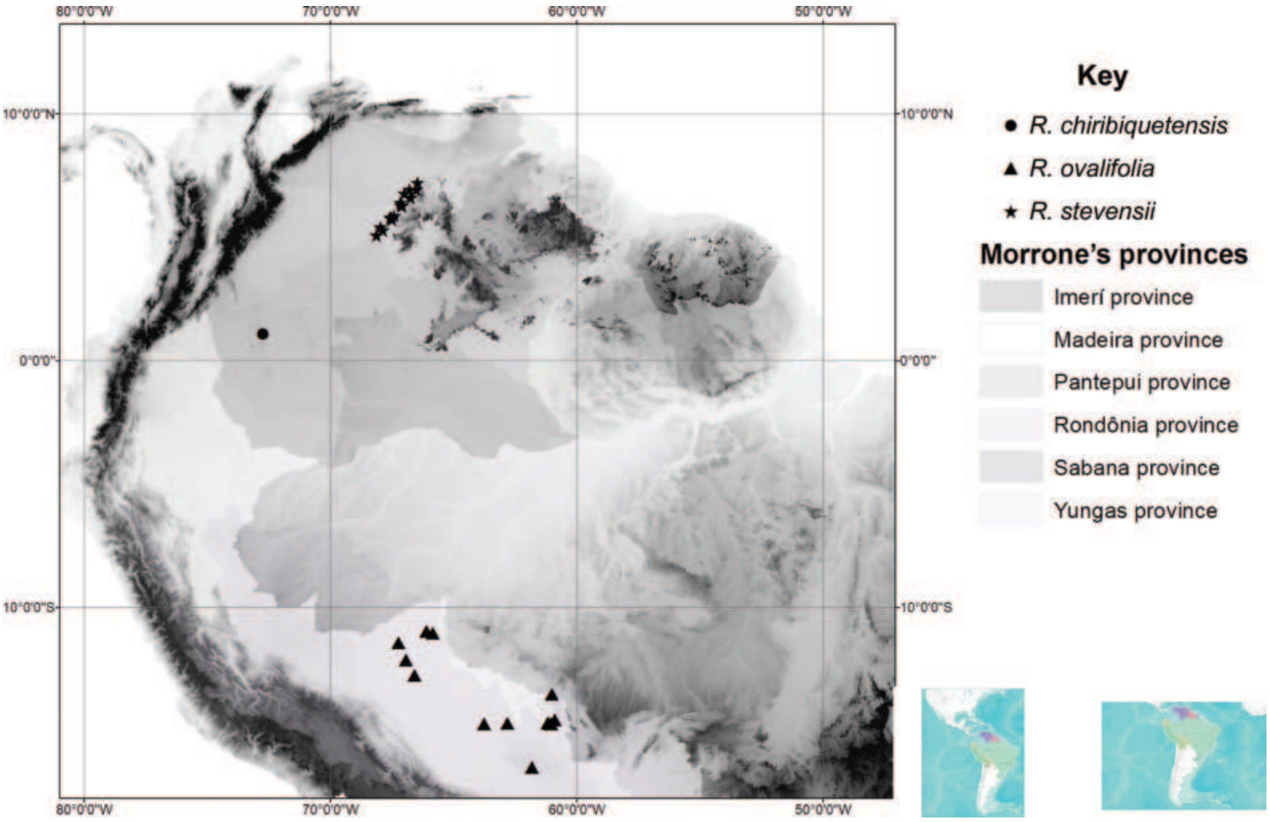

Figure 6. Distribution of *Rinorea chiribiquetensis* (circle), *R. ovalifolia* (triangles), *R. stevensii* (stars).

4. ***Rinorea stevensii*** **Hoyos-Gómez, sp. nov.**

urn:lsid:ipni.org:names:77342874-1

Type. Colombia. Dept. Vichada: Parque Nacional "El Tuparro," piedra canal near the south end of airstrip at Centro Administrativo, 5°17'N, 67°52'W, ca. 100 m elev., 5 Mar 1985, *J. L. Zarucchi et al. 3577* (holotype: NY [barcode 04205808]!; isotypes: COAH [cat. 24597]!, COAH [cat. 55474]!, FMB [cat. 4307]!, FMB [cat. 21506]!, MO [acc. 3499269; barcode MO-1592746]!, U [barcode U1766360]!).

Description. *Rinorea stevensii* is similar to *R. ovalifolia* by the lamina base symmetrical, style erect and two glabrous seeds per valve, but it differs by the lamina abaxial surface with golden pubescence (vs. the lamina abaxial surface glabrescent in *R. ovalifolia*), domatia present (vs. domatia absent), inflorescences cylindrical, 2–5 cm long (vs. inflorescence conical, 4–12 cm long), costa of petals and sepals pubescent (vs. costa of petals and sepals glabrescent), filaments free (vs. filaments fused), and capsule pubescent (vs. capsule glabrescent).

Trees 1.5–4 m tall, terminal branchlets pubescent with erect golden trichomes 0.4–0.5 mm long. Leaves opposite, petiolate; petiole 2–6 mm, pubescent with long golden trichomes 0.3–0.4 mm long; stipules deciduous, free, lanceolate, herbaceous, 2.5–5 × 1–1.5 mm, pubescent with appressed golden trichomes 0.4–0.5 mm long; margin entire; lamina elliptic, 4–12.5 × 2.5–7 cm, adaxially pubescent on mid-vein and abaxially pubescent on mid-vein and secondary veins with erect golden trichomes 0.4–0.5 mm long; semi-craspedodromous, with 6–9 major secondary vein pairs, secondary veins with irregular spacing and vein angles smoothly decreasing proximally between them, base rounded, symmetrical, margin crenate, ciliate, apex acuminate, acumen 0.5–1 cm long, mucronate, domatia present. Inflorescence axillary, lateral or terminal, racemose, 2–5 cm long, 1–1.5 cm diam., axis pubescent with erect golden trichomes 0.4–0.5 mm long; pedicels 2.5–6.5 mm, pubescent with erect golden trichomes 0.4–0.5 mm long, articulated near the middle; bractlets persistent below articulation, subopposite, ca. 1 × 1 mm, herbaceous, costa pubescent with appressed golden trichomes 0.4–0.5 mm long; peduncle bracts persisting, broadly triangular, 1–1.5 × 1–1.5 mm, herbaceous, pubescent with appressed golden trichomes 0.4–0.5 mm long, margin ciliolate. Flowers 2.8–3.8 × 3–3.4 mm long, sepals subequal, triangular, 2–2.5 × 1–1.6 mm, 7–11-veined, pubescent with appressed golden trichomes 0.5 mm long, margin ciliolate; petals lanceolate, 2.8–4.3 × 1.2–1.9 mm, costa pubescent with appressed golden trichomes 0.3–0.4 mm long, margin entire, cream to yellow in vivo, pale brown when dry; stamens 2.5–3 mm long, all filaments free, 0.4–0.6 mm, dorsal gland covering completely the filament, glabrous; anthers elliptic, 1.4–1.7 × 0.3–0.8 mm, apex obtuse, connective 0.8–0.9 mm, dorsal connective scale lanceolate, 2.4–2.5 × 0.9–1.0 mm long, margin subentire, scarious, orange-brown; ovary globose, 0.8–1.5 × 0.7–1.3 mm, pubescent with appressed golden trichomes 0.5 mm long; style erect, filiform, 1.8–2.4 × ca. 0.1 mm long, pubescent proximally with appressed trichomes 0.5 mm long, stigma acute. Fruit a symmetrical, subligneous capsule dehiscent along three sutures, ellipsoid, 1.5–2.3 × 0.5–0.6 cm, acuminate at the apex, veined, pubescent with erect golden trichomes 0.5 mm long, green when fresh, brown when dry. Seeds two per valve, globose, 4–5 mm diam., glabrous, without maculae, brown when dry. (Fig. 7)

Distribution and habitat. *Rinorea stevensii* occurs in Colombia in the border region with Venezuela near the Orinoco River and in El Tuparro National Park. It also occurs in Venezuela in the vicinity of Puerto Ayacucho. This distribution corresponds to the Biogeographical Provinces of Pantepui and Sabana, in the Boreal Brazilian and Pacific Dominions, respectively (*sensu* Morrone (2014)). The species grows on granitic hills and slopes in lowland semi-deciduous tropical rainforests and savannahs, at elevations of 85–520 m. (Fig. 6)

Etymology. *Rinorea stevensii* is named in honour of Dr. Peter Stevens, Professor of Biology at the University of Missouri Saint-Louis and curator of the Missouri Botanical Garden. Prof. Stevens was the major advisor for SEHG's master's degree.

Vernacular names. *Aruni yó* (*B. M. Boom et al. 6564*).

Conservation status. *Rinorea stevensii* has a geographic range in the form of an EOO of 5,070 km^2 and AOO of 56 km^2. It is represented by two locations within the El Tuparro National Park in Colombia and eight locations outside of protected areas in Venezuela where it is threatened by deforestation, illegal resource extraction and uncontrolled fires. Based on its limited AOO, the number of locations and the projected continuing decline in the quality of habitat, the species is preliminarily assigned to the "Vulnerable" category [VU B2ab(iii)].

Notes. Based on several morphological differences and an allopatric distribution, *Rinorea stevensii* is segregated from *R. ovalifolia* (as circumscribed by Hekking (1988)). Hekking noted the variable morphology of some specimens now representing *R. stevensii*, but he was unsure of their placement: "The leaves of *Rinorea ovalifolia* are variable in character, e.g. the underside of the leaves varies from densely hispidulous to glabrescent and domatia may be present or not". Hekking invoked introgressive hybridisation between *R. ovalifolia* and

Figure 7. *Rinorea stevensii* Hoyos-Gómez **A** habit **B** detail of young twig showing lenticels and pubescence **C** detail of leaf showing domatia, abaxial surface **D** detail of leaf showing margin ciliate, adaxial surface **E** branchlet with inflorescences **F** leaf architecture **G** infructescence **H** flower **I** sepals, abaxial surface **J** petals, abaxial surface **K** stamens, showing adaxial and abaxial surfaces **L** gynoecium **M** fruit **N** detail of fruit showing two seeds per valve **O** seed. (**A–D**: *B. M. Boom 6564* [MO]; **E–O**: *J. L. Zarucchi 3577* [MO]).

R. pubiflora var. *pubiflora* to explain the morphological variability, but we disagree with his opinion. We hypothesise that the distinctive morphological characteristics and the discrete biogeographic distribution suggest that *R. stevensii* is a separately evolving lineage (*sensu* De Queiroz (2007)) making it worthy of recognition at the rank of species. Key morphological differences amongst *R. stevensii*, *R. ovalifolia* and *R. pubiflora* var. *pubiflora* are presented in Table 1.

In addition to an allopatric distribution, *Rinorea stevensii* can be differentiated from *R. chiribiquetensis* (the other species segregated from *R. ovalifolia*) by several morphological characters. It has longer and more abundant pubescence on the lamina, with trichomes 0.4–0.5 mm long (vs. shorter and less abundant pubescence on the lamina, with trichomes 0.2–0.3 mm long in *R. chiribiquetensis*), larger lamina, 4–12.5 × 2.5–7 cm (vs. smaller lamina, 3.2–4.2 × 1.6–3.6 cm) and larger petals 2.8–4.3 × 1.2–1.9 mm (vs. 3–3.3 × 1.4–1.6 mm). *Rinorea pubiflora* var. *pubiflora* co-occurs with *R. stevensii*, but it is differentiated by having three pubescent seeds per valve, whereas *R. stevensii* has two glabrous seeds per valve.

Additional specimens examined. Colombia. Dept. Vichada. Mpio. de Puerto Carreño: Cerro al N del Centro Adm. Inderena, 5°21'17.0"N, 67°51'40.6"W, 4 Apr 1995 (fr), *M. P. Córdoba et al. 1266* (COAH, COL, FMB); base del cerro Rocoso, 100 m elev., 8 Oct 1979 (fl), *P. Vincelli 1047* (COAH, COL, FMB). **Venezuela. Estado Amazonas.** Mpio. De Puerto Ayacucho: 35 km. south of Puerto Ayacucho, at the "Tobagón". Large igneous outcrop bordering forest on slope, 85 m elev., 4 May 1977 (fr), *J. Steyermark & O. Huber 113844* (COL, MO). Mpio. de Atures: 23 km NE of Puerto Ayacucho and 10 km E of the highway, hills and base of hills, near Cachama, 90 m elev., 5°51'N, 67°24'W, 90 m elev., 19 Apr 1978 (fr), *G. Davidse et al. 15300* (MO, NY, U, US); 14–15 km NE of Puerto Ayacucho, along road to "El Burro," 5°47'N, 67°32'W, 85 m elev., 15 Apr 1978 (fr), *G. Davidse et al. 15070* (MO, NY, US); alrededores de Puerto Ayacucho +/- 11 km N, 5°44'N, 67°30'W, 15 Apr 1978 (fl), *O. Huber et al. 1450* (U, US); *ibid*., 5°43'N, 67°30'W, 29 Jan 1978 (fl), *O. Huber et al. 1502* (K, NY, U, US); Piedra el Berraco, laja granítica que conduce a Provincial, 10 km al NE de Puerto Ayacucho, 5°47'N, 67°34'W, Apr 1997 (fl, fr), *Á. Fernández-Pérez et al. 10800* (US); E of río Parguaza, 125 km N of Puerto Ayacucho, 6°17'N, 67°5'W, 11 Sep 1985 (st), *J. A. Steyermark et al. 131751* (MO, U); Parguaza, 22 Apr 1946 (fr), *I. Velez 2448* (US). **Estado Bolivar.** Mpio. Cedeño: vicinity of Panare village of Corozal, 6 km from Manipure towards Caicara, 6°55'N, 66°30'W, 24 Sep 1985 (st), *B. M. Boom et al. 6083* (NY); *ibid*., 6°55'N, 66°30'W, 90 m elev., 19 Apr 1986 (fr), *B. M. Boom & M. Grillo*

Table 1. Key morphological differences among *R. stevensii*, *R. ovalifolia*, and *R. pubiflora*.

Character	*R. stevensii*	*R. ovalifolia*	*R. pubiflora* var. *pubiflora*
Lamina base	Rounded	Decurrent	Decurrent
Lamina pubescence	Pubescent	Glabrescent	Glabrous on both surfaces
Domatia	Present	Absent	Present
Inflorescence length	2–5 cm	4–12 cm	3–7 cm
Petal pubescence	Glabrous with costa pubescent	Glabrescent	Glabrous with costa pubescent
Setal pubescence	Glabrous with costa pubescent	Glabrescent	Densely pubescent
Filament fusion	Not fused	Fused to form a staminal tube	Not fused
Seeds per valve	2	2	3

6564 (MO, F, U, US); carretera Caicara–El Burro, 16 Apr 1984 (fl), *B. Stergios et al. 8494* (MO); Caicara 100 m elev., 10 Jun 1940 (st), *L. W. Williams 13255* (F). Mpio. Foráneo La Urbana: cerca a la desembocadura del río Orinoco, 6°46'N, 67°00'W, 31 Jan 1989 (fl), *N. Cuello 718* (MO, U, US); Los Pijiguaos, afloramiento granítico 1.5 km al N del campamento Bauxiven, 6°35'N, 66°47'W, 7 Aug 1993 (st), *A. Gröger et al. 1077-B* (MO); E slopes of cerro Pijiguao (N end of serrania Suapure) above Pijiguao, ca. 70 km from mouth of Río Suapure, 110–520 m eelv., 19 Jan 1956 (fl), *J. J. Wurdack et al. 41295* (F, K, MG, MO, NY, U, US).

5. *Rinorea cogolloi* Hoyos-Gómez, sp. nov.

urn:lsid:ipni.org:names:77342875-1

Type. Colombia. Dept. Antioquia: Mpio. de San Luis, Cañón del Río Claro, sector norte, margen izquierda, 5°53'N, 74°39'W, 340–500 m elev., 24 Dec 1983, *A. Cogollo 1075* (holotype: HUA [032011]!; isotypes: COL [299700]!, MO [acc. 3737288; barcode MO-1590440]!).

Description. *Rinorea cogolloi* is similar to *R. hirsuta* by the elliptic lamina with ferruginous trichomes and lacking domatia, but it differs by the asymmetrical lamina base (vs. lamina base symmetrical in *R. hirsuta*), inflorescence thyrsoid (vs. inflorescence racemose), petals 2–3 × 0.7–1.3 mm (vs. 4–4.3 × 1.5–1.8 mm), stamens 1.7–2 mm long (vs. 3–3.3 mm long), dorsal gland pubescent (vs. dorsal gland glabrous), seeds pubescent (vs. glabrous) and capsule asymmetrical and pilose (vs. capsule symmetrical and velutinous).

Shrubs or trees 2–6 m tall, terminal branchlets pubescent with erect ferruginous trichomes 0.4–0.6 mm long. Leaves opposite, petiolate; petiole 1.9–5 mm, pubescent with erect ferruginous trichomes 0.3–0.4 mm long; stipules deciduous, free, lanceolate, membranous, 1.9–2.5 × 0.7–1 mm, pubescent with appressed ferruginous trichomes 0.2–0.3 mm long, margin ciliolate; lamina elliptic, 7–17 × 2.5–7 cm long, herbaceous, adaxially pubescent on mid-vein with erect ferruginous trichomes 0.2–0.3 mm long, abaxially pubescent with erect ferruginous trichomes 0.4–0.5 mm long, with 5–8 major secondary vein pairs, semi-craspedodromous, secondary veins with regular spacing and angled to the mid-vein, base rounded, asymmetrical, margin crenate, apex acuminate, acumen 0.5–1 cm long, mucronate, leaf domatia absent. Inflorescence axillary, lateral or terminal, thyrsoid, 4–8 cm long, 0.5–1 cm diam., axis pubescent with erect ferruginous trichomes 0.2–0.3 mm long; cymules 3–5 flowered; common peduncule 1–1.5 mm, pubescent with erect ferruginous trichomes 0.2 mm long; pedicels 0.5–1 mm, articulated at the base, pubescent with erect ferruginous trichomes 0.2 mm long; bractlets alternate, persistent below articulation, ca. 0.5 × 0.5 mm, herbaceous, costa pubescent with appressed ferruginous trichomes 0.2 mm long, margin ciliolate; peduncle bracts persistent, broadly triangular, 1–1.5 × 1–1.5 mm, herbaceous, costa pubescent with appressed ferruginous trichomes 0.3–0.4 mm long; margin ciliolate. Flowers 2.5–2.8 × 2.5–2.8 mm, sepals subequal in size and shape, triangular, 1–1.5 × 0.5–0.7 mm, pubescent with appressed ferruginous trichomes 0.2 mm long, margin ciliolate; petals elliptic, 2–3 × 0.7–1.3 mm long, pubescent with appressed ferruginous trichomes 0.2 mm long, margin ciliolate, cream to yellow in vivo, brown when dry; stamens 1.7–2 mm long, filaments free, glabrous, 0.9–1 mm, dorsal gland covering the filament, pubescent with spreading ferruginous trichomes 0.2 mm long; anthers elliptic, 0.6–1 × 0.4–0.6 mm, pubescent with spreading ferruginous trichomes 0.2 mm long, apex obtuse, connective 0.6–0.7 mm, pubescent with appressed ferruginous trichomes 0.2 mm long, dorsal connective scale lanceolate, 1.2–1.6 × 0.7–0.9 mm, scarious, margin subentire, orange-brown; ovary globose, 1–1.5 mm diam., pubescent with erect ferruginous trichomes 0.3–0.5 mm long; style erect subclavate, filiform, 1.5–1.8 × 0.1 mm, stigma acute. Fruit an asymmetrical, subligneous capsule dehiscent along three sutures, ellipsoid, 0.8–1.5 × 0.5–0.6 cm, apex acuminate, veined, pubescent with erect ferruginous trichomes 0.2–0.3 mm long, green when fresh, brown when dry. Seeds one per valve, globose, 5–7 mm diam., with maculae, pubescent with erect ferruginous trichomes 0.3 mm long, brown when dry. (Fig. 8)

Distribution and habitat. *Rinorea cogolloi* is narrowly distributed in Antioquia Department, Colombia, an area that coincides with the Biogeographical Province of Magdalena in the Pacific Dominion (sensu Morrone 2014). The species grows in lowland tropical rainforests in a region characterised by a karstic topography, occurring at elevations of 30–500 m. (Fig. 9)

Etymology. *Rinorea cogolloi* is named in honour of Professor Alvaro Cogollo who has made contributions to the knowledge of Magnoliaceae taxonomy and the flora of Colombia, especially the middle Magdalena River Valley, where the species is endemic.

Phenology. The species flowers between August and December; fruiting specimens were collected in February and August through October.

Conservation status. *Rinorea cogolloi* has a geographic range in the form of an EOO of 1,641 km^2 and AOO of 32 km^2. It is currently known from eight locations outside of protected areas. The region, underlain by karstic rocks, is heavily impacted by limestone extraction for concrete production and uncontrolled deforestation for grazing, agriculture and logging. Another location in north-eastern Antioquia Department is threatened with gold mining and deforestation. Given the high demand for cement products, the generally poor management of forest resources in the area and the number of locations, we project a continuing decline in the extent and quality of habitat for the species. *Rinorea cogolloi* is preliminarily assigned to the “Vulnerable” category [VU B1+B2ab(iii)] in accordance with the IUCN Red List Categories and Criteria (IUCN 2012).

Notes. Hekking (1988) noted the aberrant lamina pubescence of several specimens of *Rinorea lindeniana* (e.g. *A. Cogollo 786*, *1075*, *1483*). *Rinorea cogolloi* and *R. lindeniana* share several characteristics, such as leaf venation architecture and asymmetrical lamina bases, but *R. cogolloi* is readily separated from *R. lindeniana* by the densely pubescent indument on the abaxial lamina surface (vs. the abaxial lamina surface pilose to glabrescent in *R. lindeniana*). *Rinorea cogolloi* occurs sympatrically with *R. galeanoae-bernalii* (see below), but *R. cogolloi* has densely pubescent indument on the abaxial lamina surface (vs. abaxial lamina surface glabrescent in *R. galeanoae-bernalii*), pubescent fruit with spreading, erect ferruginous trichomes 0.3–0.4 mm long (vs. densely tomentose fruit) and the seeds pubescent with erect ferruginous trichomes 0.3 mm long (vs. seeds glabrous). *Rinorea cogolloi* and *R. hirsuta* have been confused by the similarity of the leaves and indumenta, but they can be differentiated by the asymmetrical lamina base, thyrsoid inflorescence, dorsal gland pubescent, pubescent seeds and capsule asymmetrical and pilose. In addition,

Figure 8. *Rinorea cogolloi* Hoyos-Gómez **A** habit **B** detail of leaf pubescent, abaxial surface **C** leaf architecture **D** infructescence **E** cymule with flowers **F** sepals, abaxial surface **G** petals, abaxial surface **H** stamens, showing adaxial and abaxial surfaces **I** gynoecium **J** infructescence **K** detail of fruit showing one seed per valve **L** seed. (**A–L**: *A. Cogollo 786* [MO]).

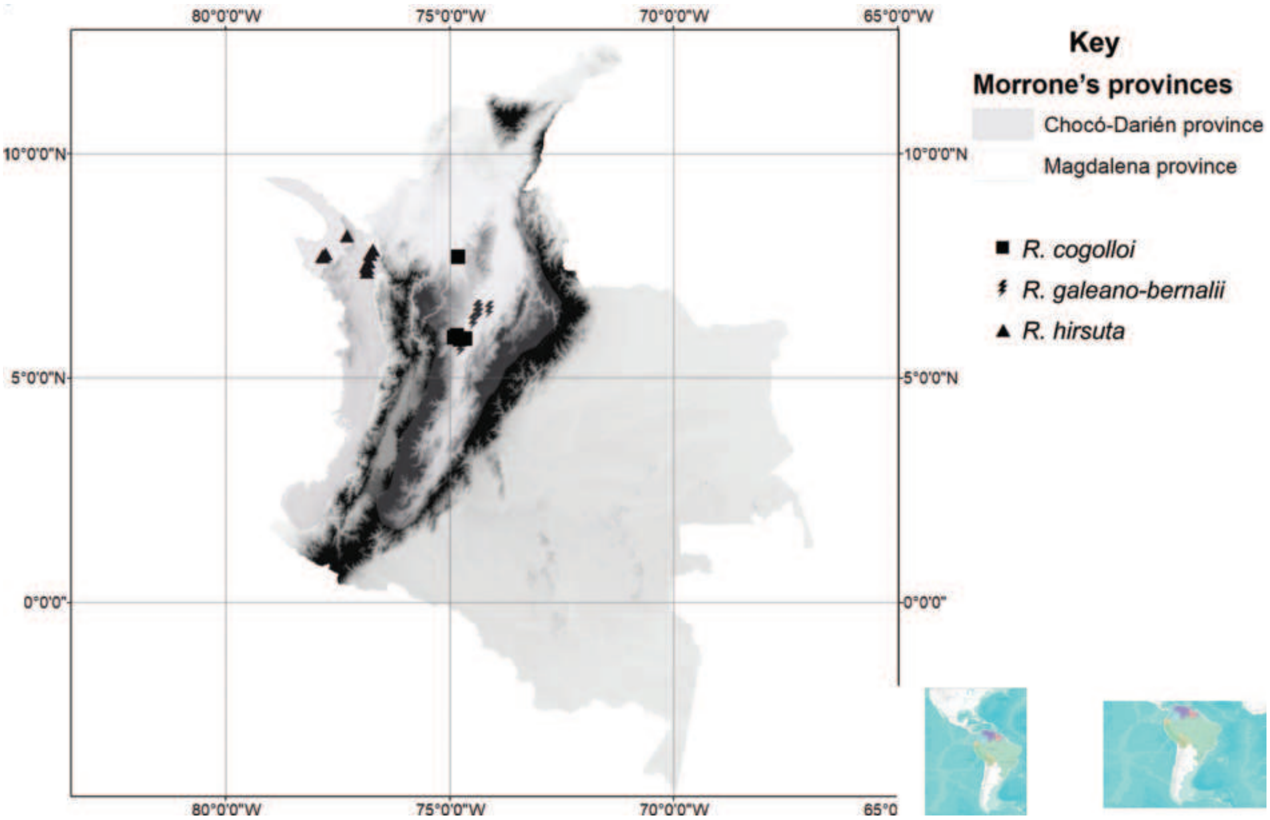

Figure 9. Distribution of *Rinorea cogolloi* (squares), *R. galeano-bernalii* (bolts), *R. hirsuta* (triangles).

these two species have different distributions, with *R. cogolloi* occurring in the Magdalena Province and *R. hirsuta* restricted to the Chocó-Darien Province (sensu Morrone (2014)). *Rinorea cogolloi* is also similar to *R. pubiflora* var. *pubiflora*, but it can be differentiated by its valves containing one seed (vs. valves containing three seeds in *R. pubiflora*) and the thyrsoid inflorescence (vs. racemose inflorescence). Table 2 highlights the key morphological differences amongst these five species.

Additional specimens examined. Colombia. Dept. Antioquia. Mpio. de Caucasia: Vda. la Arenosa, km 45 vía al Bagre, Finca la Natalia, 7°47'46"N, 74°53'9"W, 70–100 m elev., 26 Aug 2022 (st), *S. E. Hoyos-Gómez et al. 5184* (HUA, UBDC); *ibid*., 7°47'59"N, 74°52'45"W, 80 m elev., 10 Nov 2022 (fr), *M. Montoya M9004* (HUA); Mpio. de Nechí: Vda. El Catorce, entre la mina el 14 y la roca del camino, 8°94'60"N, 74°46'14"W, 30–40 m elev., 6 Mar 2010 (fl), *W. Rodríguez 6599* (COL, MEDEL); Mpio. de Puerto Triunfo: alrededores de la Gruta "El Condor," 5°56'N, 74°50'W, 12 Oct 1983 (fl, fr), *A. Cogollo 786* (COL, HUA, MO); *ibid*., 22 Oct 1989 (fr), *J. G. Ramírez 4263* (JAUM); Río Claro carretera al Cairo, 17 Sep 1982 (fl, fr), *E. Rentería 2722* (JAUM, MO). Mpio. de Sonsón: vereda Jerusalén, 5°55'00"N, 74°51'00"W, 200 m elev., 24 Dec 2010 (st), *S. E. Hoyos-Gómez et al. 1145* (HUA, JAUM, MO); *ibid*., 5°55'00"N, 74°51'00"W, 200 m elev., 24 Dec 2010 (fl), *S. E. Hoyos-Gómez et al. 1152* (HUA, JAUM); *ibid*., 5°55'00"N, 74°51'00"W, 200 m elev., 24 Dec 2019 (fl), *S. E. Hoyos-Gómez & G. A. Wahlert 3780* (HUA, JAUM); *ibid*., 5°53'30"N, 74°50'58"W, 200 m elev., 23 Sep 2018 (fl, fr), *J. P. Tobón et al. 2798* (HUA, JAUM); vereda Jerusalén, 5°53'30"N, 74°50'58"W, 380 m elev., 23 Sep 2018 (fr), *J. P. Tobón et al. 2799* (HUA, JAUM); *ibid*., 5°53'39"N, 74°51'08"W, 380 m elev., 24 Sep 2018 (fl, fr), *J. P. Tobón et al. 2803* (HUA, JAUM);

Table 2. Key morphological differences among *R. cogolloi*, *R. lindeniana*, *R. galeano-bernalii*, *R. hirsuta*, and *R. pubiflora*.

Character	*R. cogolloi*	*R. lindeniana*	*R. galeano-bernalii*	*R. hirsuta*	*R. pubiflora* var. *pubiflora*
Lamina base	Rounded	Rounded	Decurrent		Decurrent
Lamina pubescence	Adaxial surface glabrous, pubescent midvein; abaxial surface densely pubescent	Both surfaces glabrescent	Adaxial surface glabrous, pubescent midvein; abaxial surface pubescent to glabrescent	Adaxial surface glabrous, pubescent midvein; abaxial surface densely pubescent	Glabrous on both surfaces
Inflorescence	Thrysoid	Pseudo-racemose (basal portions of inflorescence with lateral cymules)	Racemose	Racemose	Racemose
Inflorescence length	4–8 cm	5–15 cm	3–10 cm	5–10 cm	3–7 cm
Petal pubescence	Pubescent	Pubescent	Glabrous with costa pubescent	Glabrous with apex pubescent	Glabrous with costa pubescent
Setal pubescence	Pubescent	Pubescent	Glabrous with costa pubescent distally	Glabrous with costa and apex pubescent	Pubescent
Filament fusion	Not fused	Not fused	Fused to form a staminal tube	Not fused	Not fused
Seeds per valve	1	1	1	1	3
Seed pubescence	Pubescent	Pubescent	Glabrous	Glabrous	Pubescent

ibid., 5°53'25"N, 74°50'50"W, 24 Sep 2018 (fl, fr), *J. P. Tobón et al. 2806* (HUA, JAUM); *ibid*., 5°53'44.1"N, 74°51'18"W, 1 Feb 2019 (fr), *J. P. Tobón et al. 2897* (JAUM); vereda Jerusalén, Reserva Natural Cañón del Río Claro, "El Refugio", margen derecha, 5°53.759'N, 74°51.219'W, Apr 2013 (fr), *L. Cano et al. 43* (HUA); corregimiento Jerusalén, vía Medellín-Bogotá, predios de Sumicol, cuenca del Río Claro, en cercanías de la torre de energía T 66, 5.915756°N, 74.849186°W, 4 Aug 2020 (fl, fr). *J. M. Velez et al. 7388* (MEDEL, COL); *ibid*., 5.916104°N, 74.849473°W, 17 Sep 2020 (fl), *J. M. Velez et al. 7511* (JAUM); *ibid*., 5.916182°N, 74.850481°W, 16 Feb 2021 (fr). *J. M. Velez et al. 7604* (JAUM).

6. *Rinorea galeanoae-bernalii* Hoyos-Gómez, sp. nov.

urn:lsid:ipni.org:names:77342876-1

Type. Colombia. Dept. Caldas: La Dorada, vereda la Atarraya, finca los Achiles, relictos de bosque al margen trasera de la finca, 5°40'20.3"N, 74°44'26.4"W, 214 m elev., 3 Aug 2021 (fl), *D. Sanín et al. 7966* (holotype: HUA [acc. 225716]!; isotype: FAUC!).

Description. *Rinorea galeanoae-bernalii* is similar to *R. hirsuta* by the elliptic lamina with symmetrical base and lacking domatia, inflorescence racemose, capsule symmetrical and pubescent with velutinous trichomes and one glabrous seed per valve, but it differs by the abaxial surface of the lamina glabrescent (vs. abaxial surface of the lamina pubescent with ferruginous trichomes in *R. hirsuta*), filaments fused at the base forming a staminal tube (vs. filaments free not forming a staminal tube), anthers with pubescence between the thecae (vs. anthers glabrous between the thecae) and style proximally pubescent (vs. style proximally glabrous).

Treelets 1.5–4 m tall, terminal branchlets pubescent with erect golden trichomes 0.2–0.4 mm long. Leaves opposite, petiolate; petiole 4–13 mm, pubescent with erect golden trichomes 0.2 mm long, glabrescent; stipules deciduous, free, elliptic, 2.5–4 × 1–1.5 mm, pubescent with appressed golden trichomes, 0.3–0.5 mm long; lamina elliptic, 7–19 × 2.5–8 cm, adaxially pubescent on the mid-vein with appressed golden trichomes 0.1 mm long, glabrescent, abaxially pubescent with appressed golden trichomes 0.3–0.5 mm long, glabrescent, semi-craspedodromous, with 6–8 major secondary vein pairs, secondary vein spacing decreasing proximally between them, base symmetrical, cuneate, margin subcrenate, apex acuminate, acumen 0.5–1 cm, mucronate, leaf domatia absent. Inflorescence axillary or terminal, racemose, 3–10 cm, 1.5–3 cm diam., axis pubescent with erect golden trichomes 0.2 mm long; pedicels 3–6 mm, pubescent with erect golden trichomes 0.1–0.2 mm long, articulated at the base, peduncle bracts deciduous, triangular, 1.5–1.8 × 1.5–1.8 mm, herbaceous, pubescent with appressed golden trichomes 0.3–0.5 mm long, margin ciliolate, bractlets persistent, 1 × 1 mm, herbaceous, pubescent with appressed golden trichomes 0.1 mm long, margin ciliolate. Flowers 3–4 × 3–4 mm, sepals subequal in size and shape, triangular, 1.6–2 × 1–1.5 mm, 1–5-veined, pubescent on the distal part of the costa with appressed golden trichomes 0.1–0.2 mm long, margin ciliolate, apex apiculate; petals elliptic, 3–4 × 1.4–2 mm, costa pubescent with spreading golden trichomes 0.1 mm long, margin ciliolate, apex acute, white; stamens 2.5–3 mm long, all filaments united at the base forming a staminal tube, tube glabrous, filaments 0.4–0.5 mm, anthers elliptic, 1.1–1.4 × 0.4–0.6 mm, pubescent between the thecae adaxially with spreading golden trichomes 0.1–0.2 mm long, apex rounded, connective 0.7–0.8 mm, dorsal connective scale conspicuous, lanceolate, 2.3–2.5 × 0.8–1 mm, margin entire, orange-brown; ovary globose, 0.8–1 × 0.9–1 mm, pubescent with appressed golden trichomes 0.1–0.2 mm long; style filiform, curved, 1.5–2 × 0.1 mm, pubescent proximally with appressed trichomes 0.1 mm long, stigma acute. Fruit a symmetrical, subligneous capsule dehiscent along three sutures, ellipsoid, 1–2 × 0.5–0.8 cm, apex acuminate, tomentose with golden trichomes 0.1 mm long. Seeds one per valve, globose, 5–7 mm diam., glabrous, with maculae, brown when dry. (Fig. 10)

Distribution and habitat. *Rinorea galeanoae-bernalii* is apparently endemic to Colombia, where it occurs in the Departments of Antioquia, Caldas and Santander. Its distribution corresponds to the Biogeographical Province of Magdalena in the Pacific Dominion (*sensu* Morrone (2014)). It grows in lowland tropical rainforest at elevations of 192–500 m. (Fig. 9)

Etymology. *Rinorea galeanoae-bernalii* is named in honour of the late Dr. Gloria Galeano Garcés (1958–2016) and Dr. Rodrigo Bernal, a husband-wife botanical team who contributed greatly to the knowledge of the Colombian flora and the taxonomy of Neotropical palms, Cyclanthaceae and Marantaceae. As professors and mentors, they inspired many of their students to pursue a botanical career studying the flora of Colombia.

Phenology. The species flowers between July and October; fruiting specimens were collected in January, April, July and September through November.

Conservation status. *Rinorea galeanoae-bernalii* has a geographic range in the form of an EOO of 9,409 km^2 and AOO of 48 km^2. It is known from 11 locations that are not included in any protected area. The locations in the middle Magdalena River Valley are heavily impacted by deforestation for grazing and agriculture, especially for cultivation of *Elaeis guineensis* (oil palm), while

Figure 10. *Rinorea galeano-bernalii* Hoyos-Gómez **A** habit **B** detail of leaf, abaxial surface **C** leaf architecture **D** infructescence **E** flower **F** detail of filaments fused at the base forming a staminal tube **G** sepals, abaxial surface **H** petals, abaxial surface **I** stamens, adaxial and abaxial surfaces **J** detail of anthers showing pubescence between the thecae **K** gynoecium **L** fruit **M** detail of fruit showing one seed per valve **N** seed. (**A–E, N**: *D. Sanin 7704* [HUA]; *D. Sanin 7966* [HUA]).

some known locations in Antioquia Department are threatened with limestone extraction for concrete production. Given ongoing habitat disturbance and projected continuing decline in the quality and extent of habitat, it is likely that the species will qualify in the near future for a threatened status and, thus, it is preliminarily assessed with a status of "Near Threatened" (NT).

Notes. Hekking noted the unusual glabrous lamina in at least one specimen which he had identified as *Rinorea hirsuta* (e.g. *E. Rentería et al. 1779*). Based on the discrete biogeographic distributions of *R. galeanoae-bernalii* and *R. hirsuta* (Magdalena Valley vs. Chocó-Darien, respectively) and the morphological characters that differentiate the two (e.g. the presence of a staminal tube and the patterns of pubescence on the anther connectives and style), we hypothesise that *R. galeanoae-bernalii* is a separately evolving lineage worthy of recognition at the rank of species.

Rinorea galeanoae-bernalii is sympatric with *R. cogolloi*, but it can be differentiated by the racemose inflorescence and glabrous seeds (vs. thyrsoid inflorescence and pilose seeds in *R. cogolloi*). *Rinorea galeanoae-bernalii* is also sympatric with *R. pubiflora* var. *pubiflora*, but it can be differentiated by the valves that each contain one glabrous seed (vs. valves that each contain three pubescent seeds in *R. pubiflora* var. *pubiflora*); see Table 2 for a comparison of key diagnostic characters differentiating *R. galeanoae-bernalii*, *R. cogolloi* and *R. pubiflora* var. *pubiflora*.

Additional specimens examined. Colombia. Dept. Antioquia. Mpio. Puerto Triunfo: corregimiento Puerto Perales, hacienda Cerritos, 7.65833, -74.81861, 192 m elev., Nov 2009 (fr), *L. Londoño et al. 938* (HUA). Mpio de Sonsón: Corregimiento de Jerusalén, Vía Medellín-Bogotá, predios de Sumicol, cuenca del Río Claro, 5.915969. -74.850459, 370 m elev., 16 Mar 2021 (fl), *J. M. Vélez et al. 7621* (MEDEL, HUA). Mpio de Yondó: ciénaga de Barbacoas, Hacienda Java, bosque Catanga, 6°43'N, 74°19'W, 100–130 m elev., 18 Apr 2011 (fr), *J. Betancur 15261 et al.* (COL, HUA, NYBG, US). **Dept. Caldas.** Mpio. La Dorada: vereda la Atarraya, finca los Achiles, relictos de bosque de la finca, 5°41'03.9"N, 74°44'16.4"W, 30 Jan 2021 (fr), *D. Sanín et al. 7704* (HUA, FAUC). Mpio. La Dorada: Vda. La Habana, 250 m elev., 16 Jan 2000 (fr), *M. V. Bustos Giraldo 62* (COL); predio el palmar, 5°18.551'N, 74°47.839'W, 305 m elev., 4 Nov 2012 (fl, fr), *J. M. Vélez 4303* (MEDEL). **Dept. Santander.** Mpio. Cimitarra: Potrero Quito, 6°28.285'N, 74°21.116'W, 3 Mar 1999 (st), *Á. Idárraga et al. 902* (HUA); corregimiento Puerto Olaya, Hacienda el Bosque, Puerto Arturo, 6°27.576'N, 74°21.034'W, 4 Aug 1999 (fl), *Á. Idárraga et al. 1491* (JAUM); corregimiento Puerto Olaya, Hacienda Piamonte, 6°26'17.8"N, 74°22'07.6"W, 29 May 2015 (fr), *Á. Idárraga et al. 6034* (HUA); *ibid*., 6°26'25.3"N, 74°22'22"W, 123 m elev., 22 Jul 2015 (fl), *Á. Idárraga et al. 6116* (HUA); *ibid*., 23 Jul 2015 (fl, fr) *Á. Idárraga et al. 6138* (HUA); Puerto Araujo, 500 m elev., 18 Sep 1979 (fr), *E. Rentería et al. 1779* (COL, HUA, JAUM, US); *ibid*., 700 m elev., 20 Sep 1979 (fr), *E. Rentería et al. 1809* (COL); corregimiento Puerto Olaya, Hacienda el Bosque, fragmento Monte Cristo, 6°28'N, 74°21'W, 19 Sep 2001 (fl), *A. Rivas et al. 152* (HUA, JAUM); vereda los Ranchos, Hacienda Monterrey, 6°15'42"N, 74°27'51"W, 123 m elev., 1 Oct 1998 (fl, fr), *W. Rodríguez et al. 1070* (JAUM); *ibid*. (fl, fr), *W. Rodríguez et al. 1505* (JAUM). Mpio. Girón: vereda Sogamoso, hacienda Trigueros, 7°05'27.1"N, 73°21'41.4"W, 332 m elev., 25 Feb 2011 (fl, fr), *E. Y. Rodríguez-Ch. 1989* (COL).

7. ***Rinorea betancurii*** **Hoyos-Gómez, sp. nov.**

urn:lsid:ipni.org:names:77342877-1

Type. Colombia. Dept. Caquetá: Mpio. de Solano, región de Araracuara, sector Chiribiquete, camino a Tepuí, 0°12'16"S, 72°29'14"W, 170 m elev., 10 Dec 2010, *F. Castro 10919* (holotype: COAH [acc. 78339]!; isotype: NY [barcode 02691382]!).

Description. *Rinorea betancurii* is similar to *R. macrocarpa* by the elliptic lamina lacking domatia, lamina base symmetrical and capsule symmetrical with apex acuminate, but it differs by the abaxial lamina surface pubescent (vs. abaxial lamina surface glabrous in *R. macrocarpa*), lamina base obtuse (vs. lamina base cuneate), fruit smaller 2.5–3 cm long (vs. fruit larger, 3–5.7 cm) and valves containing two pubescent seeds (vs. valves containing three glabrous seeds).

Treelets 1.5–5 m tall, branchlets with puberulent erect ferruginous trichomes 0.1–0.2 mm long, glabrescent. Leaves opposite, petiolate; petiole 2–4 mm long, pubescent with erect ferruginous trichomes 0.2 mm long; stipules deciduous, free, lanceolate, 2.3–3 × 1–1.1 mm, herbaceous, pubescent with appressed ferruginous trichomes 0.2 mm long, lamina elliptic, 6.3–14.4 × 2.6–7 cm, adaxially glabrous, abaxially pubescent with erect ferruginous trichomes 0.2–0.4 mm long, semi-craspedodromous, with 5–7 major secondary vein pairs, secondary veins with spacing between them decreasing proximally, symmetrical, base obtuse, margin entire to subcrenate, apex acute, acumen 8–14 mm long, mucronate, domatia absent. Flowers unknown. Fruit a symmetrical, subligneous capsule dehiscent along three sutures, ellipsoid, 2.5–3 × 0.5–0.6 cm, apex acuminate, pubescent with curved golden trichomes 0.3–0.4 mm long, green in vivo, brown when dry. Seeds two per valve, globose, 7–8 mm diam., pubescent with spreading trichomes 0.1–0.2 mm long, with maculae, seeds brown when dry. (Fig. 11)

Distribution and habitat. *Rinorea betancurii* occurs in Brazil, Colombia and Venezuela, an area that corresponds to the Biogeographic Provinces of Imerí and Pantepui in the Boreal Brazilian Dominion (*sensu* Morrone (2014)). The species grows in lowland tropical rainforest at elevations of 60–170 m. *Rinorea betancurii* has been recorded as growing in sandy soils near rivers and on slopes and hills. (Fig. 4)

Etymology. *Rinorea betancurii* honours Julio Betancur, Colombian botanist and curator at the National Herbarium in Bogotá. Dr. Betancur has inspired a new generation of students to pursue a career in botany and has made many contributions to the taxonomic knowledge of the Bromeliaceae, Heliconiaceae and the flora of Colombia.

Phenology. Fruiting specimens were collected in February through May and in September, November and December.

Conservation status. *Rinorea betancurii* has a geographic range in the form of an estimated EOO of 511,480 km^2 and an AOO of 36 km^2. The species is known from eight localities, none of which appear to be in protected areas. Based on satellite imagery from Google Earth, the locations in Colombia and Brazil appear to be heavily impacted by deforestation, while the four Venezuelan locations are in remote and vast primary forests with large buffers from disturbed areas. Even though we project continuing decline in the extent and

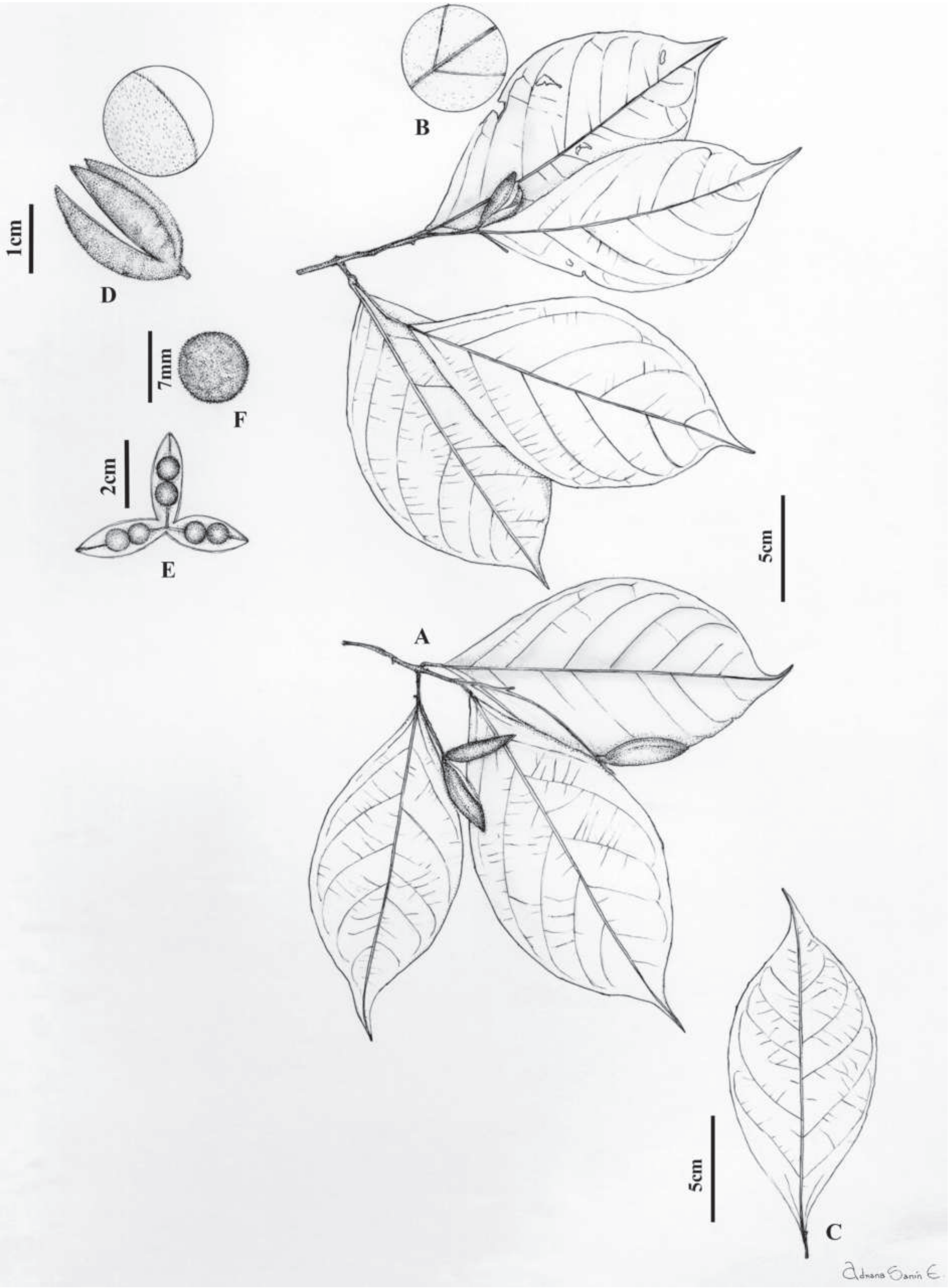

Figure 11. *Rinorea betancurii* Hoyos-Gómez **A** habit **B** detail of leaf, abaxial surface **C** leaf architecture **D** fruit and detail of pubescence **E** detail of fruit showing two seeds per valve **F** seed. (**A–F**: *R. L. Liesner 15689* [MO]).

quality of habitat for the Colombian and Brazilian locations, the undisturbed forests in southern Venezuela appear to be safe from large-scale disturbance for the foreseeable future. Nevertheless, it appears unlikely that the species will qualify for a threatened status in the near future and is assigned a preliminary status of Least Concern (LC).

Notes. *Rinorea betancurii* occurs with *R. pubiflora* var. *pubiflora*, but it can be separated by the valves that contain two seeds (vs. valves that contain three seeds in *R. pubiflora* var. *pubiflora*).

Additional specimens examined. Colombia. Dept. Caquetá: cabeceras del río Masay, desembocadura del río San Jorge al río Cuñaré, 1–6 Mar 1980 (fr), *M. Pabón 946* (COL). **Dept. Meta:** Mpio. Puerto López, vereda el Tigre, finca Pista, orilla del canal, 8 Feb 2008 (fr), *F. Castro 4760* (UBDC). **Dept. Vaupés:** Mpio Taraira, comunidad Jotabeyá, 0°35'S, 70°11'W, 150–250 m elev., 27 Mar 2009 (fr), *J. Betancur et al. 13854* (COAH, COL, HUA). **Venezuela. Bolivar State:** Mpio. Foráneo Aripao, margen derecha del caño Minchaquene (Hormiga), tributario del Alto Caura, entre Araguaña y Campamento, 4°45'N, 64°12'W, 2 May 1988–5 May 1988 (fr), *G. Aymard 6810* (MO, NY, U). **Amazonas State:** Mpio. Atabapo, río Cunucunuma, raudal Mapaco, 3°37'N, 65°51'W, Apr 1990 (fr), *W. R. Anderson 13343* (F, MICH); close to cerro Neblina base camp on río Mawarinuma, 0°50'N, 66°10'W, 6 Feb 1984 (fr), *R. L. Liesner 15689* (BHO, MO, U, VEN); Cerro Yapacana, 3°45'N, 66°45'W, 125–400 m elev., 3 May 1970 (fr), *J. Steyermark et al. 113015* (COL). **Brazil. Amazonas State:** Mpio. Barcelos, base cerro Aracá, 0°42'N, 63°22'W, 14 Jul 1985 (fr), *I. Cordeiro 193* (INPA, NY).

Key to species of *Rinorea* sect. *Pubiflorae* in Colombia

1 Inflorescence racemose **2**

– Inflorescence thyrsoid **22**

2 Lamina papery, base slightly asymmetric and oblique **3**

– Lamina membranous, papery or coriaceous, base symmetric and equilateral **4**

3 Inflorescence 4–23 cm long; sepals ca. half as long as the petals; seeds two per valve, with maculae .... ***Rinorea dasyadena* A.Robyns**

– Inflorescence 1–4 cm long; sepals nearly as long as the petals; seeds three per valve, without maculae .... ***Rinorea sylvatica* (Seem.) Kuntze**

4 Lamina coriaceous **5**

– Lamina papery or membranous **7**

5 Lamina margin entire; style pilosulous at the base; seeds three per valve .... ***Rinorea marginata* (Triana & Planch.) Rusby ex Johnston**

– Lamina margin subcrenate to serrate; style strigose at the base, seeds two per valve **6**

6 Lamina elliptic, 6.5–17 × 2.7–6 cm, margin subcrenate to subserrate .... ***Rinorea melanodonta* S.F.Blake**

– Lamina narrowly ovate, 11.5–21 × 4–7.5 cm, margin serrate .... ***Rinorea brachythrix* S.F.Blake**

7 Indument composed of one type of trichome **8**

– Indument composed of two types of trichomes **17**

8 Lamina lanceolate .... ***Rinorea aymardii* Hoyos-Gómez**

– Lamina elliptic or obovate to ovate **9**

9 Lamina obovate to ovate, domatia absent .... ***Rinorea ovalifolia*** **(Britton) S.F.Blake**

– Lamina elliptic, domatia present or absent **10**

10 Domatia present **11**

– Domatia absent **13**

11 Lamina margin ciliate .... ***Rinorea stevensii*** **Hoyos-Gómez**

– Lamina margin not ciliate **12**

12 Lamina pubescent on both surfaces; inflorescence 1.5–5 cm long; dorsal gland completely covering the filament .... ***Rinorea chiribiquetensis*** **Hoyos-Gómez**

– Lamina glabrous on both surfaces; inflorescence 8–12.5 cm long; dorsal gland free, adnate to the filaments .... ***Rinorea falcata*** **(Mart. ex Eichler) Kuntze**

13 Lamina abaxially pubescent, with trichomes on the entire surface **14**

– Lamina abaxially glabrous or glabrescent, if glabrescent, then trichomes only on the veins **15**

14 Lamina with 9–14 lateral veins; seeds one per valve; glabrous; NW Colombia and Darién (Panama) .... ***Rinorea hirsuta*** **Hekking**

– Lamina with 5–7 lateral veins; seeds two per valve, pubescent; Amazon Basin (Brazil, Colombia and Venezuela) ***Rinorea betancurii*** **Hoyos-Gómez**

15 Filaments free, not forming a glandular tube; seeds two per valve, glabrous .... ***Rinorea flavescens*** **(Aubl.) Kuntze**

– Filaments fused forming a glandular tube; seeds one or three per valve **16**

16 Pedicels 3–6 mm long; connective scales with entire margins; capsule pubescent, seeds one per valve; endemic to the Magdalena Valley, Colombia .... ***Rinorea galeanoae-bernalii*** **Hoyos-Gómez**

– Pedicels 0.5–1 mm long; connective scale with the margin proximally fringed; capsule sparsely ferruginous hispidulous; seeds three per valve .. .. ***Rinorea macrocarpa*** **(Mart. ex Eichler) Kuntze**

17 Fruits with one seed per valve, seed glabrous **18**

– Fruits with two or three seeds per valve, seeds glabrous or pubescent **19**

18 Lamina with 11–14 pairs of lateral veins; style golden pilosulous to strigillose proximally; Central America and Magdalena River Valley and Chocó Region in Colombia .... ***Rinorea squamata*** **S.F.Blake**

– Lamina with 7–10 pairs of lateral veins; style pilose proximally; Magdalena Valley and Amazon Basin (Bolivia, Brazil, Ecuador, Colombia, Peru) ...... ***Rinorea viridifolia*** **Rusby**

19 Fruits with three seeds per valve .... ***Rinorea pubiflora*** **var.** ***pubiflora***

– Fruits with two seeds per valve **20**

20 Seeds pilosulous, with maculae .... ***Rinorea pubiflora*** **f.** ***andersonii*** **(Sandwith ex Hekking) Hekking**

– Seeds glabrous, without maculae **21**

21 Lamina with 8–10 pairs of lateral veins, margin subserrate; pedicels articulated near the base; dorsal gland pilose, seeds with maculae; Panamá and Chocó Region in Colombia .... ***Rinorea callejasii*** **Hoyos-Gómez**

– Lamina with 6–8 pairs of lateral veins, margin crenate; pedicels articulated near the middle; dorsal gland pubescent, seeds without maculae; Amazon Basin (Brazil, Colombia, Peru, Ecuador) .... ***Rinorea pubiflora*** **var.** ***grandifolia*** **(Eichler) Hekking**

22 Lamina glabrous on upper surface, base symmetric, cuspidate at the apex, domatia absent; seeds one per valve, glabrous .... ***Rinorea villosiflora* Hekking**

– Lamina glabrous or pubescent on upper surface, base symmetric or asymmetric, apex always acuminate, domatia present or absent, seeds one or two per valve, glabrous or pubescent **23**

23 Lamina base asymmetric, domatia absent; seeds one per valve **24**

– Lamina base symmetric, domatia present or absent; seeds one or two per valve **26**

24 Seeds obovoid, glabrous, without maculae .... ***Rinorea ulmifolia* Kuntze**

– Seeds globose, pubescent, with maculae.. **25**

25 Lamina glabrous on upper surface; dorsal gland adnate to the filament, glabrous; capsule symmetric .... ***Rinorea lindeniana* (Tul.) Kuntze**

– Lamina pubescent on upper surface along the mid-vein; dorsal gland covering the filament, pubescent-pilose; capsule asymmetric .... ***Rinorea cogolloi* Hoyos-Gómez**

26 Domatia absent; capsule asymmetric or symmetric; seeds one or two per valve, glabrous or pubescent **27**

– Domatia present; capsule asymmetric; seeds two per valve, glabrous...... **28**

27 Inflorescence 8–18 cm long; capsule asymmetric; seeds one per valve, glabrous .... ***Rinorea vaupesana* L.B.Sm. & Á.Fernández**

– Inflorescences 1–8 cm long, capsule symmetric; seeds two per valve, pubescent .... ***Rinorea hummelii* Sprague**

28 Petals elliptic to ovate, 1.7–2.2 mm long, pilose along the costa; stamens 1.2–1.7 mm long, glandular tube glabrous; seeds one per valve................ .... ***Rinorea racemosa* (Mart.) Kuntze**

– Petals narrowly ovate, 3–3.5 mm long, pubescent along the costa; stamens 2.2–3 mm long, glandular tube ciliate; seeds two per valve .... ***Rinorea sprucei* (Eichler) Kuntze**

Acknowledgements

We are grateful to the herbaria and curators of different institutions that helped during the revision of their collection (BHO, COAH, F, GH, HUA, JAUM, MO, NYBG, UBDC, US). Financial support was provided by Fulbright-Colombia and Universidad de Antioquia to SEHG to visit herbaria in the United States. We greatly appreciate Juliana Paula-Souza (Federal University of Santa Catarina, Brazil) and Harvey Ballard (Ohio University) who reviewed our manuscript and provided valuable feedback that helped to improve it. We thank Adriana Sanín for her excellent illustrations of the new species and Mateo Sánchez for assistance with making the distribution maps.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Financial support was provided by Fulbright-Colombia and Universidad de Antioquia to SEHG to visit herbaria in the United States.

Author contributions

Conceptualization: SEHG, RCP. Data curation: GAAW, SEHG. Investigation: SEHG. Supervision: RCP. Writing - original draft: SEHG. Writing - review and editing: RCP, GAAW.

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Data availability

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

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PhytoKeys

PhytoKeys 242: 273–280 (2024)
DOI: 10.3897/phytokeys.242.122869

Research Article

Gymnostachyum calcicola (Acanthaceae), a new species from limestone karst of Peninsular Malaysia

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Abstract

A new species, *Gymnostachyum calcicola* Rafidah, **sp. nov.** (Acanthaceae) is described from limestone karst in Peninsular Malaysia. Characters distinguishing it from related species, colour photographs, botanical illustration and provisional conservation status are provided.

Key words: Andrographidae, endemic, flora, Kelantan, taxonomy

Introduction

Gymnostachyum Nees (Acanthaceae) is a genus consisting of about 30–50 species distributed mainly in tropical Asia (Hu et al. 2011; Deng 2014; Mabberley 2017; Deng et al. 2020; Manzitto-Tripp et al. 2022). The genus is characterized by a combination of two stamens and many seeds (Hansen 1985), absence of staminodes, ovary with 3-several ovules per locule, capsule cylindrical, and seeds compressed, covered with hygroscopic hairs (Lindau 1895). It belongs to tribe Andrographideae (Lindau 1895; Scotland 1992; Scotland and Vollesen 2000; McDade et al. 2008), however Somprasong et al. (2015) placed *Gymnostachyum* under subtribe Andrographinae. In Peninsular Malaysia, Clarke (1908) recognized eleven species of *Gymnostachyum*, including ten new species, while Ridley (1923) recorded *Gymnostachyum* with 13 species (including four doubtful species) and described a new species *Gymnostachyum hirtum* Ridl. from Perak (Ridley 1926). Tan et al. (2014) described *Gymnostachyum kanthanense* Kiew from a limestone hill, Gunung Kanthan, Perak.

The discovery of this distinctive new species is part of the comprehensive survey of the Peninsular Malaysia limestone flora in 2017. The species was found on the limestone hills in Federal Land and Development Authority (FELDA) Chiku and Perasu in Kelantan, and is endemic in Kelantan. The species inhabits partially shaded areas, and roots in cracks with thin soil layer on rocks at the base to the summit of karst limestone. After carefully examining the herbarium specimens and living material and reviewing the relevant literature, here we concluded that the newly discovered plants represented an undescribed species. Herewith, the new species is described and illustrated in detail.

Academic editor: Bo Li
Received: 15 March 2024
Accepted: 27 April 2024
Published: 3 June 2024

Citation: Rafidah AR, Ummul Nazrah AR, Ong PT (2024) *Gymnostachyum calcicola* (Acanthaceae), a new species from limestone karst of Peninsular Malaysia. PhytoKeys 242: 273–280. https://doi.org/10.3897/phytokeys.242.122869

Materials and methods

Measurements and morphological character assessments of the new species were undertaken and described using specimens collected from their natural habitat and living materials grown in the Forest Research Institute Malaysia (FRIM) Biodiversity Nursery. Photographs of the habit and all parts of the plants were made and botanical line drawings of floral and fruiting parts were prepared. Materials collected were deposited at the herbarium of Forest Research Institute Malaysia (KEP) and the flowers were preserved into the spirit collection in Copenhagen mixture. The available *Gymnostachyum* specimens from other herbaria such as BK, BKF, CAL, KLU, SING, UKMB and PSU were examined (herbarium acronyms follow Thiers 2024, continuously updated). In addition, images of the type specimens of *Gymnostachyum* were obtained from JSTOR Global Plants (http://plants.jstor.org) and Tropicos (http://www.tropicos.org). The provisional conservation assessment is based on the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2012) and guidelines of the IUCN (2022).

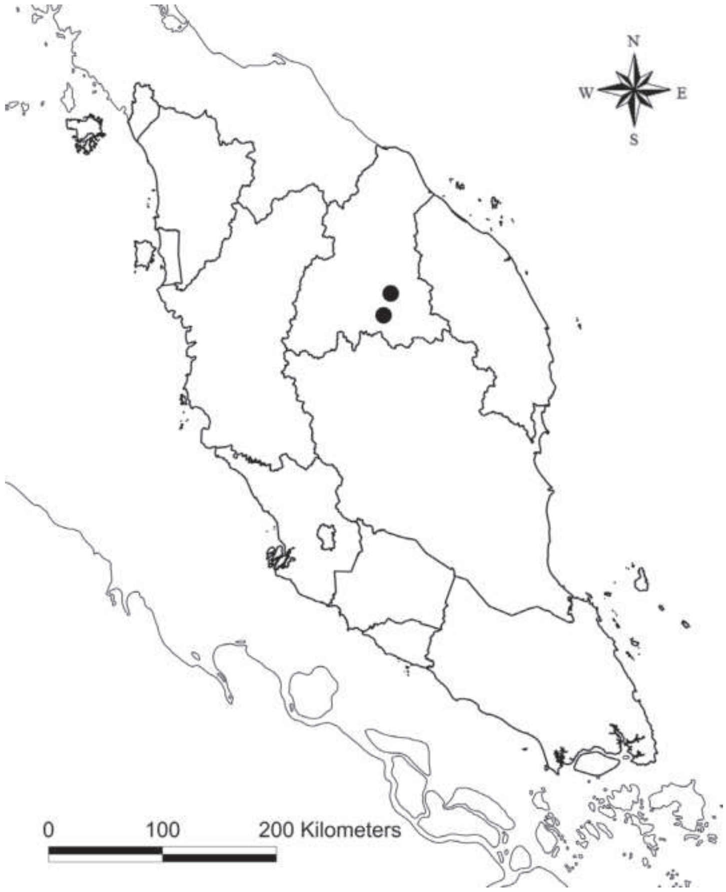
Taxonomic treatment

Gymnostachyum calcicola **Rafidah, sp. nov.**
urn:lsid:ipni.org:names:77342878-1
Figs 1–3

Diagnosis. Unique among Peninsular Malaysian species of *Gymnostachyum* by having a racemose inflorescences occasionally lower axils with pairs of flowers and dichasium inflorescence with opposite branches. *Gymnostachyum calcicola* shows affinity with *Gymnostachyum decurrens* var. *decurrens* and var. *robinsonii* by its crowded rosette leaves at the base, however it is different in the inflorescences type.

Type. Peninsular Malaysia. Kelantan: Chiku, FELDA Chiku, 11 October 2017, *Aliaa-Athirah et al. FRI 90707* (holotype KEP, isotype SING).

Description. Rosette herbs. Leaves opposite; petiole pale green, to 7 cm long, not winged; lamina membranous to subcoriaceous, dark green above, sometimes with grey blotches, white-green beneath, narrowly oblong to elliptic, ca. 11 × 4–5 cm, base abruptly truncate, decurrent for 2 cm, margin entire, slightly wavy, apex unequal, slightly acute to blunt; midrib and veins slightly sunken above, glabrous beneath; lateral veins ca. 9–10 pairs. Inflorescences green, erect, terminal, racemose occasionally lower axils with pairs of flowers, dichasium with opposite branches, rachis up to 30 cm long or more, minutely hairy, branches ca. 14 cm long with up to 5 flowers; bracts green, ca. 1 mm long; pedicels very short, ca. 0.5 mm long; bracteoles minute, 0.5 mm long. Flowers suberect. Calyx divided near the base, lobes 5, equal, narrowly linear, 2–3 × 0.5–1 mm long, green, hairy outside, clasping the corolla tube. Corolla white outside, inside white with scattered minute purple spots except for the deep purple lower lip, deep purple at the median lobe, minutely glandular hairy outside, ca. 12–14 mm long, narrowly cylindric at base, tube 10 × 1 mm, expanding distally to funnel-shaped throat, upper lip erect, ca. 3 mm long, apex slightly bilobed, flat, lower lip unequal, the middle lobe much shorter. Stamens 2, filaments white, 6–7 mm long, inserted at the base of the throat, glabrous, anthers purple-white, inserted, positioned below



Map 1. Map of the Peninsular Malaysia indicating the location of *Gymnostachyum calcicola* in Peninsular Malaysia.

the apex of upper lip, narrowly oblong, ca. 2 mm long, thecae 2, equal, both with minute mucronate appendages at base, densely covered with short stalked glandular hairs with dense white hairs along longitudinal line of dehiscence; staminodes absent. Nectary annular, cream-coloured, ca. 1 mm high, upper margin entire. Ovary green, cylindric, 1–1.5 mm long, densely covered in short glandular hairs, ovules many per locule; style white, up to 8 mm long, sparsely hairy, stigma hooked, less than 1 mm long, positioned between the anthers. Capsule narrowly cylindric, 10–12 × 1–2 mm, retinacula 6–7 per locule, calyx persisting after the fruit has fallen. Seeds up to 12 (probably more), obliquely ovoid, strongly compressed, ca. 1 mm longitudinal, surface minutely pitted, hairy.

Distribution and habitat. Endemic to Kelantan, Peninsular Malaysia; known only from limestone hills. Species grows in small populations, always observed in shaded areas, rooting in cracks on thin soil on limestone rocks, almost to the summit of the hill.

Etymology. The specific epithet refers to the limestone habitat of this species.

Provisional IUCN regional conservation status. Endangered B2 ab(i,ii,iii). Most Chiku limestone hills were visited, but only two to three hills were home to this new species. A part of Chiku limestone hills is scheduled for quarries. The survival of the species remains uncertain. The species also has been recorded in Perasu limestone hills, about 40 km away from Chiku hills. Parts of FELDA Perasu limestone have been quarried, and surrounding areas are currently disturbed by the road constructions. All hills lie outside the network of Protected Areas.

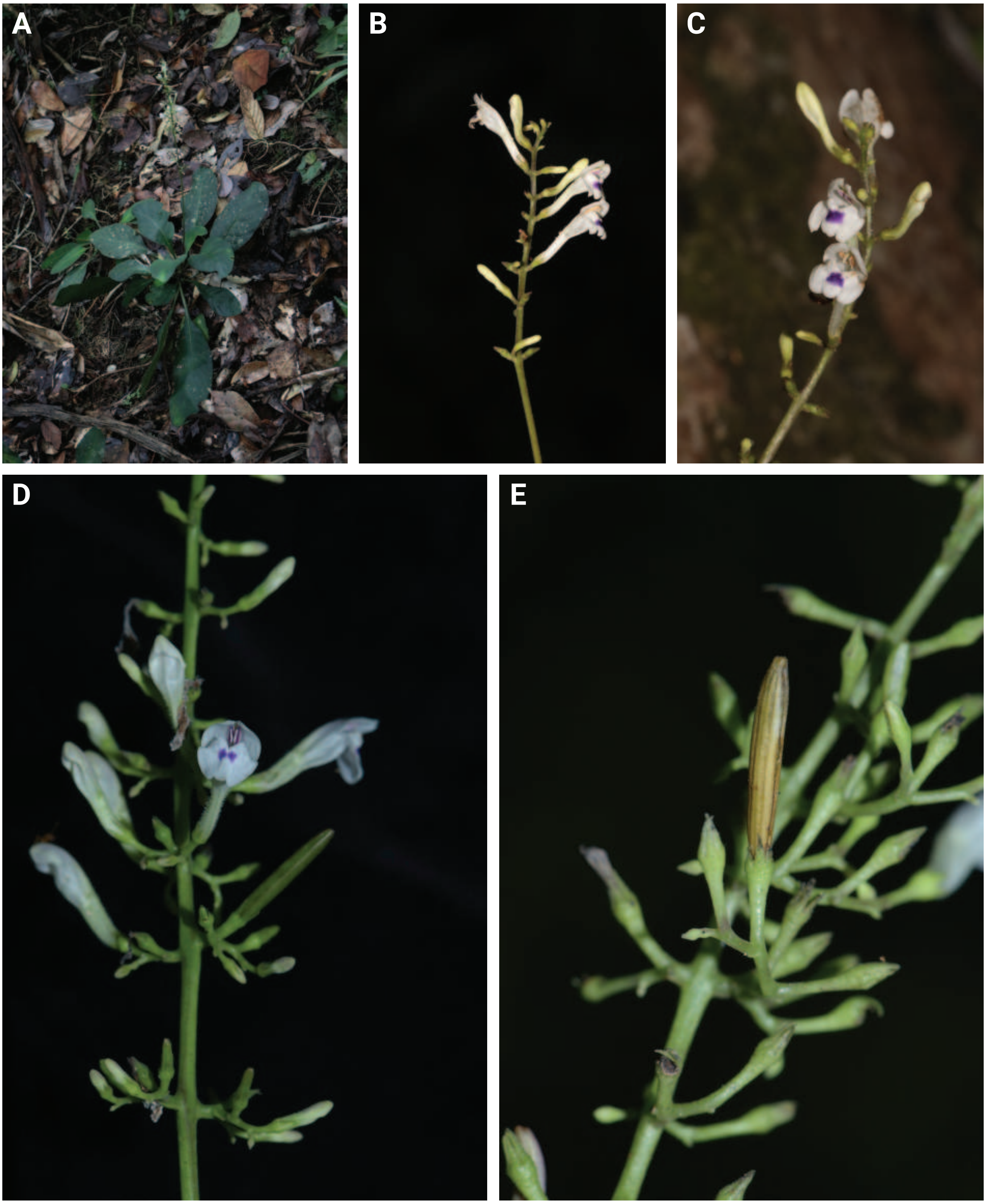


Figure 1. *Gymnostachyum calcicola* Rafidah **A** habit **B** flower (side view) **C** flower (front view) **D** portion of inflorescence showing dichasial cymose branches **E** portion of infructescence.

Additional specimens examined. Peninsular Malaysia, Kelantan: FELDA Chiku, 11 October 2017, Aliaa-Athirah *et al*. 90712 (KEP), 10 October 2017, Wan Syafiq *et al*. FRI 90123 (KEP); FELDA Perasu, 24 April 2019, Rafidah FRI 93064 (KEP).

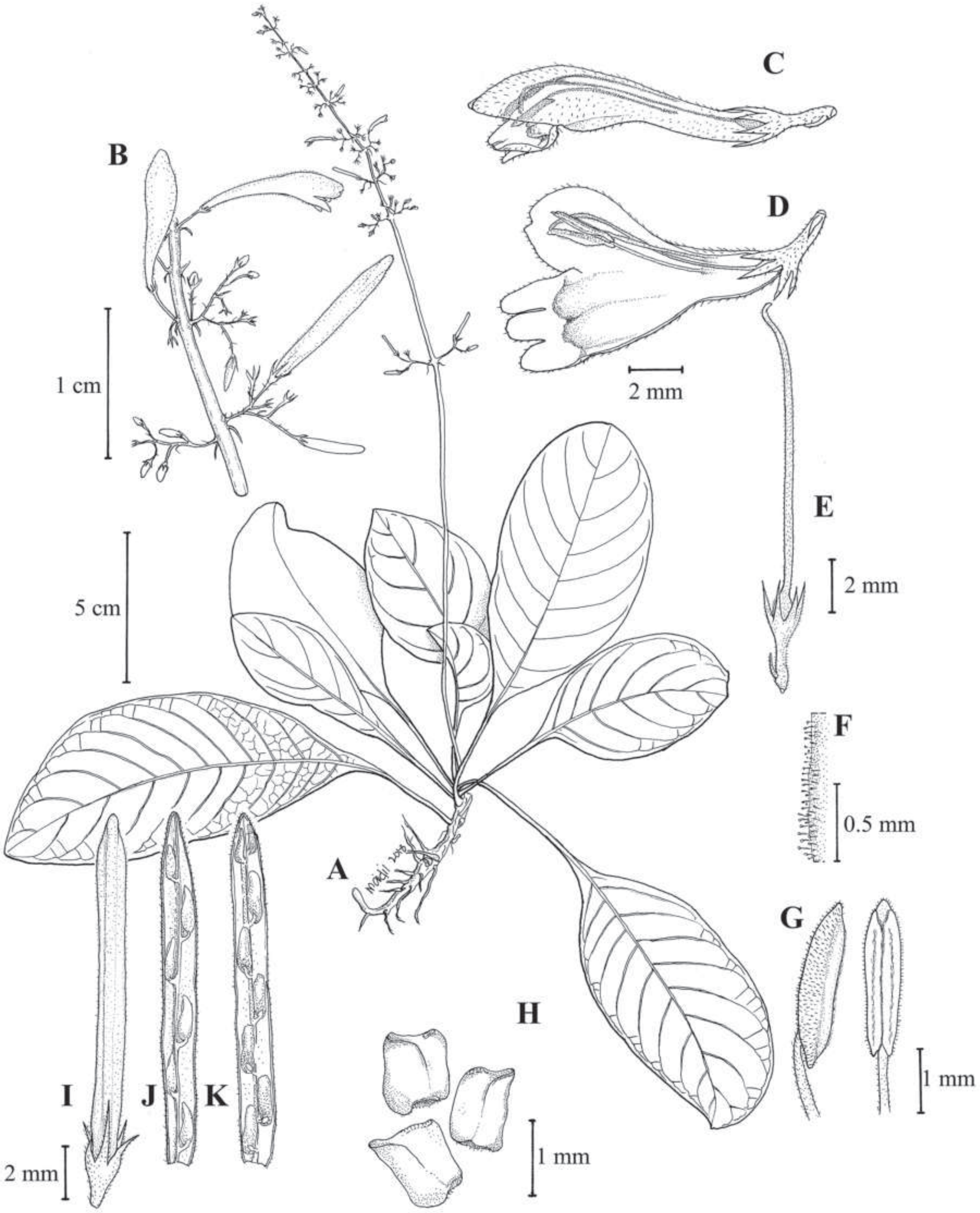


Figure 2. *Gymnostachyum calcicola* Rafidah **A** flowering plant **B** portion of inflorescence with flowers **C** flower **D** flower with opened corolla **E** bract, calyx and carpel with corolla and stamens removed **F** indumentum of anther along longitudinal line of dehiscence **G** anthers (dorsal and ventral views) **H** seeds **I** fruit **J-K** attachment of seeds (all drawn by Mohd Aidil Nordin).

Notes. Ridley (1923) divided the Peninsular Malaysian species into two groups: (i) dwarf plants with single flower of long inflorescences and; (ii) shrubby plants with elongate stem. This new species falls into the first group (Table 1) together with *Gymnostachyum decurrens* Stapf var. *decurrens*

Figure 3. Home of *Gymnostachyum calcicola*.

Table 1. Comparison of Peninsular Malaysia species in *Gymnostachyum* in Group 1.

Characters / Species	***G. calcicola***	***G. decurrens* var. *decurrens***	***G. decurrens* var. *robinsonii***	***G. diversifolium***	***G. ceylanicum****	***G. kanthanense***	***G. pallens***
Petiole	not winged	broadly-winged	winged	winged	winged	not winged	winged
Lamina							
Base	abruptly truncate	broad	abruptly truncate	broad	unknown	abruptly rounded or truncate	abruptly truncate
	decurrent for 2 cm	undulate margin, decurrent	decurrent	decurrent	undulate margin, decurrent	decurrent for 2–8 mm	shortly decurrent
Indumentum surface (both)	Glabrous	pubescent	scabrid	pubescent	pubescent	pubescent	densely punctate
Inflorescence							
Type	racemose	spikes	racemes	spikes	spikes	spikes	spike
	dichasium inflorescence with opposite branches	several	branched	1 to 3	several	3	slightly branched
Flower	occasionally lower axils with pairs of flowers	single	single	single	single opposite or in long spikes in short cymes	on one side of the rachis	single
Calyx							
Colour	green	purple	green	pale green	dark green	purplish green	green
Corolla							
colour	white	white	unknown	pale blue	pinkish / pale purple	white tinged purple	white
length (mm)	12–14	12–15	10	25	12	18	12
lower lip (median)	deep purple	violet	unknown	purplish (all)	yellow	deep purple	white
indumentum	minutely glandular hairy	glandular pubescent	glandular pubescent	glandular and e-glandular hairs	unknown	stalked glandular hairs	unknown
Capsule							
length (mm)	10–12	18	12	unknown	unknown	12	> 12

**Gymnostachyum ceylanicum* absolutely indistinguishable from Sri Lanka specimen from the corolla colour.

and var. *robinsonii* (Ridl.) J.B. Imlay, *G. diversifolium* C.B.Clarke, *G. pallens* C.B.Clarke, *G. kanthanense*, and doubtful species recorded for Peninsular Malaysia, *G. ceylanicum* Arn. & Nees. The new species shows affinity with *Gymnostachyum decurrens* var. *decurrens* and var. *robinsonii* by its crowded rosette leaves at the base and its racemose and spicate inflorescences and *G. pallens* from its branched peduncle. It differs from the other species by not having a winged petiole and in having racemose inflorescences, occasionally lower axils with pairs of flowers and dichasium inflorescence with opposite branches.

Acknowledgements

We would like to thank the staff of the Flora Biodiversity Programme, FRIM who helped in botanical collections, to all the Merapoh and FELDA Chiku guides for assistance in the field, to Mohamad Aidil Noordin and Wendy Yong for preparing the botanical drawing and distribution map, and also to Dr Ruth for her fruitful comments in this manuscript. Special thanks to our former and current FRIM Director General and former Forest Biodiversity Director, Dr Richard Chung for his strong support of this project. We also thank Kelantan Forestry Department for permission to make botanical collections in Kelantan State. We thank the curators of the following herbaria for access to examine herbarium specimens and providing the specimens on loan: BK, BKF, CAL, KEP, KLU, SING, UKMB and PSU.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research is financially supported by National Conservation Trust Fund (NCTF) Grant, under the Project “Towards conservation strategy/policy for limestone hills in Peninsular Malaysia: Understanding and documenting plant biodiversity with focus on Kelantan and Perlis limestone hills (Phase 2)” and under the Twelfth Malaysia Plan 2021-2025.

Author contributions

All authors have contributed equally.

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Data availability

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

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PhytoKeys

PhytoKeys 242: 281–291 (2024)
DOI: 10.3897/phytokeys.242.115679

Research Article

Alseodaphnopsis maguanensis is conspecific with *A. hokouensis* (Lauraceae) based on morphological and molecular evidence

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Abstract

Based on both morphological and molecular evidence, it is confirmed that *Alseodaphnopsis maguanensis* is conspecific with *A. hokouensis*. Hence, *Alseodaphnopsis maguanensis* is treated as a synonym of *A. hokouensis* here. The conservation status of *Alseodaphnopsis hokouensis* is also re-evaluated according to the IUCN Red List Categories and Criteria in this study.

Key words: *Alseodaphnopsis*, Lauraceae, morphology, phylogeny, synonym, taxonomy

Academic editor:
Andrés E. Ortiz-Rodriguez
Received: 13 November 2023
Accepted: 8 May 2024
Published: 3 June 2024

Citation: Li L, Zou D-y, Mao Y-m, Li J (2024) *Alseodaphnopsis maguanensis* is conspecific with *A. hokouensis* (Lauraceae) based on morphological and molecular evidence. PhytoKeys 242: 281–291. https://doi.org/10.3897/phytokeys.242.115679

Introduction

As one of the largest basal angiosperm families, Lauraceae includes more than 50 genera and 2500 ~ 3000 species distributed in tropical and subtropical regions worldwide (Chanderbali et al. 2001). The delimitation, delineation and identification of Lauraceae species, especially for tropical species, are always complicated due to limited variation in floral and other morphological characters and insufficient specimen collection (van der Werff and Richter 1996; Rohwer 2000; Li and Li 2004; Yang and Liu 2015).

Alseodaphnopsis hokouensis (H. W. Li) H. W. Li & J. Li was first published as an *Alseodaphne* Nees species (Lee et al. 1979) and then it was transferred to *Alseodaphnopsis* H. W. Li & J. Li, a recently described genus of the Lauraceae (Mo et al. 2017). Since it was first collected in 1953, only three herbarium records (including two type specimens) of *Alseodaphnopsis hokouensis* can be found and no fruiting specimen has been collected.

During recent field surveys in SE Yunnan (SW China), some flowering and fruiting individuals of *Alseodaphnopsis hokouensis* were found and they resembled a recently-published *Alseodaphnopsis* species, *A. maguanensis* L. Li & J. Li (Li et al. 2020). Based on both morphological and molecular evidence, we confirm that *Alseodaphnopsis maguanensis* is conspecific with *A. hokouensis*. Therefore, we treat *Alseodaphnopsis maguanensis* as a synonym of *A. hokouensis* here. Based on the field survey data, we also re-evaluate the conservation status of *Alseodaphnopsis hokouensis* in this study.

Materials and methods

Field surveys

We conducted field surveys in both Hekou (Hokou) County and Maguan County (Yunnan Province, China) from 2020 to 2022. Flowering specimens of *Alseodaphnopsis hokouensis* and *A. maguanensis* were collected from May to June and fruiting specimens were collected from July to September.

Morphological studies

Morphological characters of *Alseodaphnopsis hokouensis* and *A. maguanensis* were examined and compared in detail, based on fresh and preserved materials as well as dried specimens collected in the field. Herbarium specimens of these two species from the Herbaria HITBC, KUN and PE were also examined.

Molecular studies and phylogenetic analyses

Based on the work of Li et al. (2020), three individuals of *Alseodaphnopsis hokouensis* and two additional individuals of *A. maguanensis* were sampled in the present study. DNA extraction, fragment amplification and sequencing, as well as DNA sequence alignment, followed the work of Li et al. (2020). The newly-obtained DNA sequences were integrated into the ITS + *LEAFY* intron II combined dataset of the work by Li et al. (2020). Species examined in this study, voucher information, collection locality and GenBank accessions for ITS and *LEAFY* intron II sequences are given in Table 1.

The combined dataset including ITS and *LEAFY* intron II sequences was used for phylogenetic analysis according to the works of Li et al. (2011), Mo et al. (2017) and Li et al. (2020). Phylogenetic analyses were performed using the Maximum Parsimony (MP) and Bayesian Inference (BI) methods. The MP analysis was performed using PAUP* 4.0b10 (Swofford 2003). The BI analysis was performed using MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003). Different DNA sequences were defined as separate data partitions. The evolutionary model for each partition (ITS: GTR+I+G; *LEAFY* intron II: HKY+G) was estimated using jModelTest v.2.1.10 (Darriba et al. 2012) with the Akaike Information Criterion (AIC) (Akaike 1974; Posada and Buckley 2004). The parameters used in both MP and BI analysis followed the work of Li et al. (2020).

Results and discussion

During our field surveys in SE Yunnan, two populations of *Alseodaphnopsis hokouensis* were found in Huayudong and Qincaitang, Nanxi Town, Hekou County (Fig. 1), each with about 10 mature individuals. No individual was found at the type locality of *Alseodaphnopsis hokouensis*, Masike, Nanxi Town, Hekou County. Two populations of *Alseodaphnopsis maguanensis*, each with about 20 mature individuals, were also investigated in Gulinqing Provincial Natural Reserve (Maguan County) according to the work of Li et al. (2020).

Table 1. Species examined in this study, voucher information, collection localities and GenBank accession numbers for ITS and *LEAFY* sequences.

Taxon	**Voucher**	**Locality**	**ITS**	***LEAFY***
Ingroups				
***Alseodaphne* (4)**				
A. gigaphylla Kosterm.	Arifiani DA657 (BO)	Indonesia, Java	HQ697181	HQ697004
A. gracilis Kosterm.	Li L. 20070187 (HITBC)	China, Yunnan	HQ697187	HQ697036
A. huanglianshanensis H. W. Li & Y. M. Shui	Li L. 20080006 (HITBC)	China, Yunnan	HQ6971812	HQ697007
A. semecarpifolia Nees	Arifiani DA658 (BO)	Indonesia, Java	HQ6971814	HQ697015
***Alseodaphnopsis* (8)**				
A. andersonii (King ex Hook. f.) H. W. Li & J. Li,	Li J. & Li L. 20070074 (HITBC)	China, Yunnan	FM957793	HQ697002
A. hainanensis (Merr.) H. W. Li & J. Li	Li L. & Wang Z. H. JFL07 (HITBC)	China, Hainan	MG188587	MG188634
	Li L. & Wang Z. H. LMS10 (HITBC)	China, Hainan	MG188586	MG188633
A. hokouensis (H. W. Li) H. W. Li & J. Li	Li L. et al. 2020064 (HITBC)	China, Yunnan	PP736795	PP737831
	Li L. et al. 2020071 (HITBC)	China, Yunnan	PP736796	PP737832
	Li L. et al. 2020072 (HITBC)	China, Yunnan	PP736797	PP737833
A. maguanensis L. Li & J. Li	Li L. et al. GLQ45 (HITBC)	China, Yunnan	MN906900	MN906896
	Li L. et al. GLQ46 (HITBC)	China, Yunnan	MN906901	MN906897
	Li L. et al. 2020086 (HITBC)	China, Yunnan	PP736798	PP737834
	Li L. et al. 2020091 (HITBC)	China, Yunnan	PP7367999	PP737835
A. petiolaris (Meisn.) H. W. Li & J. Li	Chen J. Q. 07003 (HITBC)	China, Yunnan	FM957796	HQ697008
A. putaoensis L. Li, Y. H. Tan & J. Li	Li L. & Ma H. MM254 (HITBC)	Myanmar, Kachin	MN906902	MN906898
	Li L. & Ma H. MM266 (HITBC)	Myanmar, Kachin	MN906903	MN906899
A. rugosa (Merr. & Chun) H. W. Li & J. Li,	Li L. & Wang Z. H. MYH02 (HITBC)	China, Hainan	MG188585	MG188635
	Li L. & Wang Z. H. MYH08 (HITBC)	China, Hainan	MG188584	MG188640
A. sichourensis (H. W. Li) H. W. Li & J. Li	Song Y. 33225 (HITBC)	China, Yunnan	MG188597	MG188626
A. ximengensis H.W. Li & J. Li	Li J. W. 1235 (HITBC)	China, Yunnan	MG188591	MG188599
***Dehaasia* (1)**				
D. hainanensis Kosterm.	Li L. & Wang Z. H. 20070373 (HITBC)	China, Hainan	FJ719308	HQ697026
***Machilus* (8)**				
M. duthiei King ex Hook. f.	Zhong J. S. 2006094 (HITBC)	China, Yunnan	FJ755425	HQ697055
M. gongshanensis H. W. Li	Chen J. Q. 07002 (HITBC)	China, Yunnan	FJ755416	HQ697047
M. grijsii Hance	Chen J. Q. et al. 2006028 (HITBC)	China, Guangdong	FJ755420	HQ697049
M. kwangtungensis Yang	Chen J. Q. et al. 2006027 (HITBC)	China, Guangdong	FJ755424	HQ697051
M. monticola S. Lee	Li L. & Wang Z. H. 20070323 (HITBC)	China, Hainan	FJ755418	HQ697057
M. platycarpa Chun	Chen J. Q. et al. 2006073 (HITBC)	China, Guangdong	FJ755421	HQ697067
M. robusta W. W. Sm.	Li J. 2002116 (HITBC)	China, Guangxi	FJ755426	HQ697071
M. yunnanensis Lec.	Zhong J. S. 2006093 (HITBC)	China, Yunnan	FJ755415	HQ697084
***Nothaphoebe* (1)**				
N. umbelliflora (Blume) Blume	Arifiani DA495 (BO)	Indonesia, Java	HQ697191	HQ697088
***Phoebe* (6)**				
P. chekiangensis C. B. Shang	Li J. & Li L. 20070188 (HITBC)	China, Zhejiang	FJ755407	HQ697128
P. cuneata (Blume) Blume	Arifiani 40 (MO)	Indonesia, Java	HQ697202	HQ697130

Taxon	Voucher	Locality	ITS	*LEAFY*
P. formosana (Hayata) Hayata	Rohwer 156 (MJG)	Germany, Bonn	HQ697205	HQ697136
P. lanceolata (Wall. ex Nees) Nees	Chen J. Q. et al. 2006093 (HITBC)	China, Guangdong	FJ755410	HQ697141
P. glaucifolia S. K. Lee & F. N. Wei	Chen J. Q. et al. 2005002 (HITBC)	China, Yunnan	FJ755409	HQ697150
P. neurantha (Hemsl.) Gamble	Li J. & Li L. 20070214 (HITBC)	China, Zhejiang	HQ697209	HQ697151
Outgroups				
***Actinodaphne* (1)**				
A. trichocarpa C. K. Allen	Li L. 20070282 (HITBC)	China, Sichuan	HQ697214	HQ697166
***Lindera* (1)**				
L. erythrocarpa Makino	Li J. & Li L. 20070203 (HITBC)	China, Zhejiang	HQ697215	HQ697167
***Litsea* (1)**				
L. auriculata Chien & Cheng	Li J. & Li L. 20070195 (HITBC)	China, Zhejiang	HQ697217	HQ697174
***Neolitsea* (1)**				
N. howii C. K. Allen	Li L. & Wang Z. H. 20070379 (HITBC)	China, Hainan	HQ697220	HQ697178

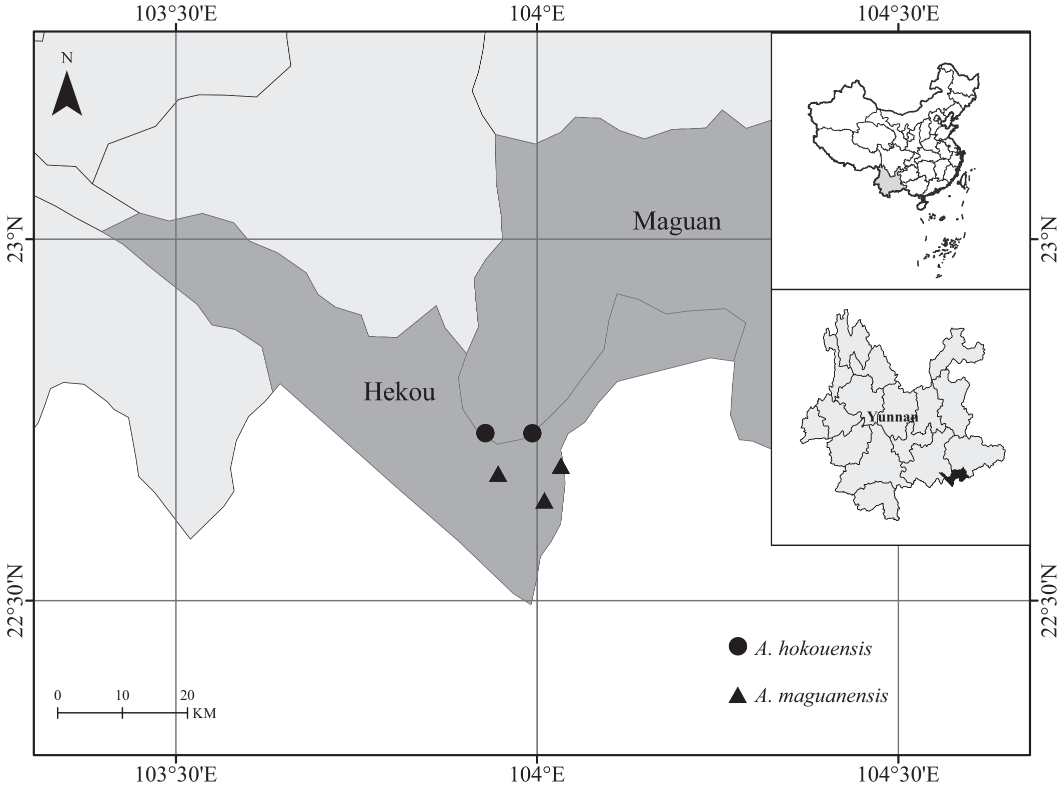

Figure 1. The recorded localities of *Alseodaphnopsis hokouensis* and *A. maguanensis* in SE Yunnan, SW China.

The MP and BI analyses of the ITS + *LEAFY* intron II combined dataset generated congruent topologies. The Bayesian consensus tree with MP bootstrap (BS) and Bayesian posterior probability (PP) values is shown in Fig. 2. As in the work of Li et al. (2020), all *Alseodaphnopsis* specimens sampled in the present study formed a well-defined clade (BS 88%, PP 1.00). Within the *Alseodaphnopsis* clade, there are two well-supported subclades which consist of four and five species, respectively. All individuals of *Alseodaphnopsis hokouensis* and *A. maguanensis* formed a strongly-supported clade (BS 100%, PP 1.00), closely

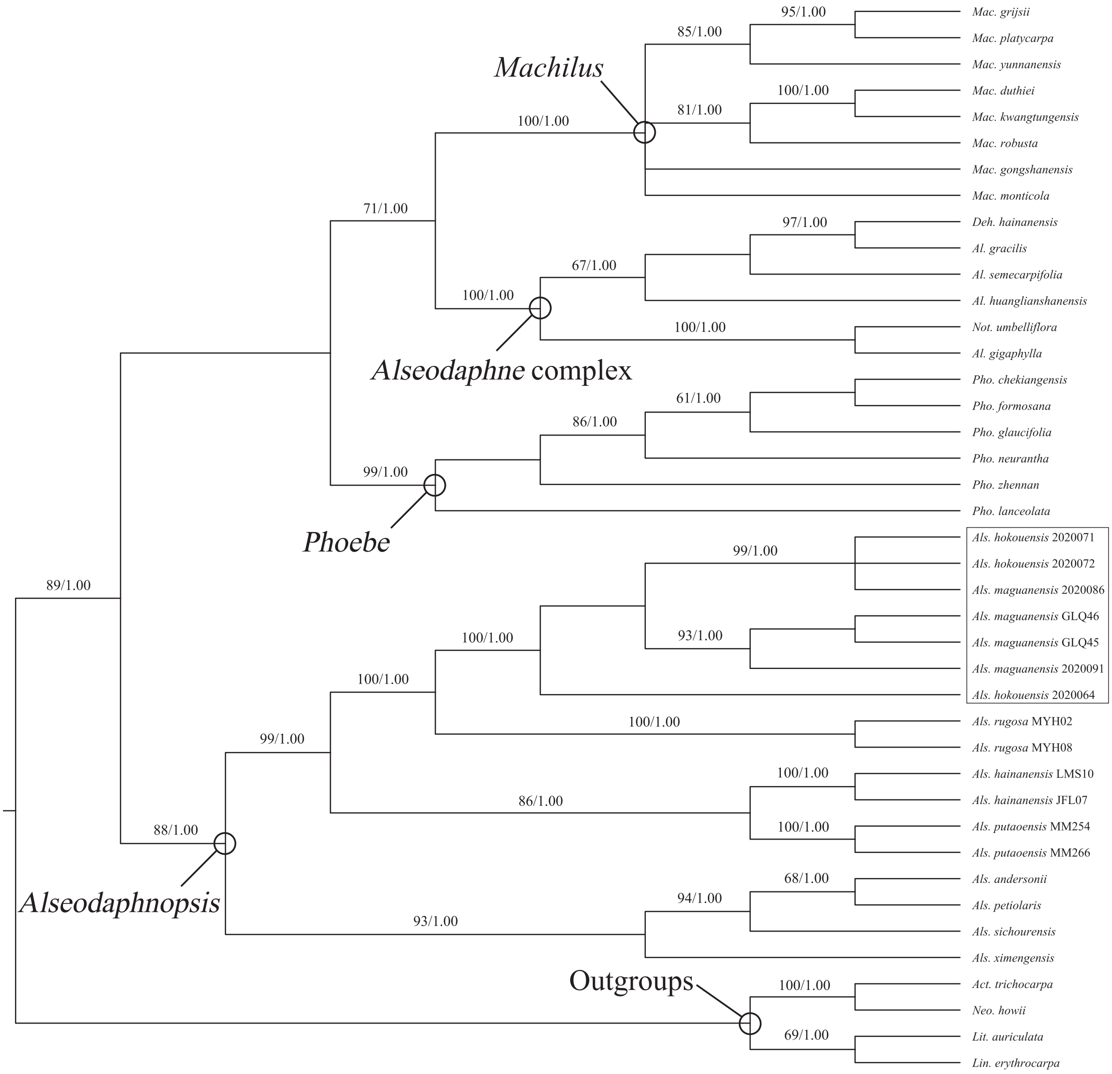

Figure 2. Bayesian consensus tree of ITS + *LEAFY* intron II combined dataset. MP bootstrap (BS ≥ 50%) and Bayesian posterior probability (PP ≥ 0.95) values are shown above branches. *Act. = Actinodaphne*, *Al. = Alseodaphne*, *Als.= Alseodaphnopsis*, *Deh. = Dehaasia*, *Lin. = Lindera*, *Lit. = Litsea*, *Mac. = Machilus*, *Neo. = Neolitsea*, *Not. = Nothaphoebe*, *Pho. = Phoebe.*

related to *A. rugosa*. Within this clade, the individuals of these two species are mixed with each other and their relationships are poorly resolved.

The morphological characters of *Alseodaphnopsis hokouensis*, *A. maguanensis* and closely related *A. rugosa* were compared in detail, based on the data from type specimens and protologues (Li et al. 2008; Li et al. 2020). Morphological comparisons showed that *Alseodaphnopsis maguanensis* is almost the same as *A. hokouensis*, except that the leaves of the former are oblong-obovate or oblong-oblanceolate and those of the latter are elliptic to oblong (Table 2). After carefully checking the specimens collected from field surveys, we found that the leaves of both species can vary from elliptic, oblong to oblong-obovate or oblong-oblanceolate (Fig. 3). They are usually oblong-obovate or oblong-oblanceolate and occasionally elliptic to oblong. According to the newly-obtained fruiting specimens of *Alseodaphnopsis hokouensis*, the fruit characters of *Alseodaphnopsis hokouensis* are also consistent with those of *A. maguanensis* (Fig. 3). Additionally, the phenologies and habitats of these two species are quite similar and their distribution areas are adjacent as well (Fig. 1).

Table 2. Comparison of morphological characters, phenologies, habitats and distributions of *Alseodaphnopsis hokouensis*, *A. maguanensis* and *A. rugosa*.

	A. hokouensis	***A. maguanensis***	***A. rugosa***
Morphological characters			
Branchlet	terete, brownish when dry, striate, glabrous	terete, greyish, wrinkled, glabrous, with lenticels and leaf scars	terete, robust, wrinkled, with dense leaf scars near top
Terminal bud	subglobose, bud scales broadly ovate, acute at apex, glabrous	subglobose, bud scales broadly ovate, acute at apex, glabrous	
Leaf arrangement	leaves alternate	leaves clustered at apex of branchlet, alternate or subverticillate	leaves inserted at apex of branchlet, dense and nearly verticillate
Petiole	1.5–3 cm, concave-convex, glabrous	1.5–2.5 cm, concave-convex, glabrous	robust, 1.5–2.5 cm, glabrous
Leaf blade	elliptic to oblong, 10.5–17 × 4–6.5 cm, subleathery, glabrous on both surfaces, base broadly cuneate to subrounded, apex abruptly shortly acuminate	oblong-obovate or oblong-oblanceolate, 12–32 × 3.5–9 cm, leathery, glabrous on both surfaces, base cuneate, apex shortly acuminate	oblong-obovate or oblong-oblanceolate, 15–36 × 4–10 cm, leathery, glabrous on both surfaces, base cuneate, apex shortly acuminate.
Leaf veins	mid-rib elevated abaxially, impressed adaxially, lateral veins 9–13 pairs, transverse veins and veinlets densely reticulate, conspicuous on both surfaces when dry	mid-rib elevated abaxially, impressed adaxially, lateral veins 8–12 pairs, veins and veinlets conspicuous, reticulate, elevated on both surfaces when dry	mid-rib conspicuously elevated abaxially, impressed adaxially, veins and veinlets conspicuous, reticulate
Inflorescence	panicles subterminal or inserted on lower part of young branchlet, 10.5–15 cm, peduncle and rachis glabrous, pedicels 3–4 mm, glabrous	panicles subterminal, 15–20 cm, peduncle glabrous, pedicels 5–8 mm, glabrous	not seen
Perianth lobes	perianth lobes 6, ovate, slightly acute, subequal, ca. 2 × 1.5 mm, glabrous outside, grey pubescent inside, deciduous	perianth lobes 6, broadly ovate, acute, subequal, outer ones ca. 2 × 1.5 mm, inner ones ca. 2.5 × 2 mm, glabrous outside, white pubescent inside, deciduous	not seen
Fertile stamens	fertile stamens 9, minute, ca. 1.5 mm in 1st and 2nd whorls, ca. 1.7 mm in 3rd whorl; filaments villous, ca. 0.7 mm in 1st and 2nd whorls, ca. 1 mm in 3rd whorl, those of 3rd whorl each with 2 stalked orbicular-reniform glands at base, others glandless; anthers of 1st and 2nd whorls oblong, almost as long as filament, with introrse cells, those of 3rd whorl rectangular, with extrorse cells	fertile stamens 9, ca. 2 mm in 1st and 2nd whorls, ca. 2.2 mm in 3rd whorl; filaments villous, those of 3rd whorl each with 2 shortly-stalked orbicular-cordate glands at base, others glandless; anthers of 1st and 2nd whorls ovate, almost as long as filament, cells all introrse, those of 3rd whorl elliptic, with extrorse cells	not seen
Staminodes	not seen	ca. 1.5 mm, sagittate, stalked	not seen
Pistil	ovary ovoid, ca. 1.5 mm, glabrous, attenuate into a ca. 0.5 mm long style; stigma discoid, slightly lobed	ovary ovoid, ca. 1.2 mm, glabrous, attenuate into a ca. 0.8 mm long style; stigma discoid, inconspicuous	not seen
Infructescence	not seen	subterminal, 10–18 cm, robust, glabrous, with only one or two well-developed fruits	subterminal, ca. 12.5 cm, robust, glabrous
Fruit	not seen	oblate, 4–5 × 5–6 cm, brown when mature; fruit stalk robust, 3–4 mm in diameter, apex dilated, 5–10 mm in diameter, sometimes nearly cylindrical, fleshy and warty when fresh	oblate, ca. 2.5 × 3 cm deep purple or black when mature; fruit stalk robust, 5–8 mm in diameter on top, fleshy, red and warty when fresh
Phenology	flowering in May; fruit unknown	flowering in May–Jun; fruiting in Jul–Sep	flower unknown; fruiting in Jul–Dec (fruits mostly found in Oct–Dec)
Habitat	evergreen broad-leaved forests; ca. 700 m alt.	tropical montane forests in valleys; ca. 800 m alt.	mixed forests in valleys; 1200–1300 m alt.
Distribution	SE Yunnan, China	SE Yunnan, China	Hainan, China

Figure 3. *Alseodaphnopsis hokouensis* **A** flowering branchlet **B** fruiting branchlet **C** different shapes of leaf blades. Photographed by Lang Li.

To sum up, the results of both morphological comparison and phylogenetic analysis showed that *Alseodaphnopsis maguanensis* is conspecific with *A. hokouensis*. Therefore, we propose that *Alseodaphnopsis maguanensis* should be treated as a synonym of *A. hokouensis*. The insufficient specimen collection of *Alseodaphnopsis hokouensis*, especially the lack of fruiting specimens, hinders a comprehensive understanding of the species. The same situation is found in many other rare and endemic Lauraceae species in SE Yunnan, such as species of *Alseodaphne*, *Beilschmiedia* Nees, *Caryodaphnopsis* Airy Shaw, *Cryptocarya* R. Br., *Endiandra* R. Br., *Machilus* Rumph. ex Nees, *Phoebe* Nees and *Syndiclis* Hook. f., etc. (Li et al. 2008). Thus, more field surveys and specimen collections are suggested in SE Yunnan in order to improve the understanding of these rare and endemic Lauraceae species.

Taxonomic treatment

Alseodaphnopsis hokouensis (H. W. Li) H. W. Li & J. Li

Alseodaphne hokouensis H. W. Li, Act Phytotax. Sin. 17 (2): 71. 1979. Basionym. Type: CHINA. Yunnan Province: Hekou County, 10 May 1953, K. H. Tsai *1039* (holotype: KUN [KUN0047456!]; isotype: KUN [KUN0108581!]).

= *Alseodaphnopsis maguanensis* L. Li & J. Li, PhytoKeys 138: 27–39. 2020. **syn. nov.** Type: CHINA. Yunnan Province: Maguan County, 14 May 2016, Lang Li et al. *GLQ26* (holotype: HITBC!).

Revised description. Trees evergreen, up to 20 m tall. Branchlets terete, 3–6 mm in diameter, greyish, striate, glabrous, with lenticels and leaf scars. Terminal buds subglobose, ca. 2 mm in diameter; bud scales broadly ovate, acute at apex, glabrous. Leaves clustered at apex of branchlet, alternate or subverticillate; petiole robust, 2–3 mm thick, 1.5–3 cm long, concave-convex; leaf blade green adaxially, glaucous abaxially when young, but green or pale green when mature, oblong-obovate or oblong-oblanceolate, sometimes elliptic to oblong, 10.5–32 × 3.5–9 cm, subleathery to leathery, glabrous on both surfaces, mid-rib elevated abaxially, impressed adaxially, lateral veins 8–13 pairs, slightly elevated on both surfaces, oblique, evanescent and interconnected near leaf margin, transverse veins and veinlets densely reticulate, conspicuous on both surfaces when dry, base cuneate to broadly cuneate, apex shortly acuminate, sometimes abruptly shortly acuminate. Panicles subterminal, clustered at apex of branchlet, 10.5–20 cm, many-flowered; peduncle branched at middle or above, peduncle and rachis glabrous; bracts and bracteoles linear, ca. 1.5 mm, acute, ciliate, caducous. Pedicels slender, 3–8 mm, slightly dilated on top, glabrous. Flowers small, ca. 2.5 mm. Perianth tube short; perianth lobes 6, broadly ovate, slightly acute, glabrous outside, pubescent inside, subequal, outer ones ca. 2 × 1.5 mm, inner ones ca. 2.5 × 2 mm, deciduous. Fertile stamens 9, minute, 1.5–2 mm in 1st and 2nd whorls, 1.7–2.2 mm in 3rd whorl; filaments villous, 0.7–1 mm in 1st and 2nd whorls, 1–1.2 mm in 3rd whorl, those of 3rd whorl each with 2 shortly stalked orbicular-cordate glands at base, others glandless; anthers of 1st and 2nd whorls ovate, almost as long as filaments, with introrse cells, those of 3rd whorl elliptic, slightly shorter than filaments, with extrorse cells. Staminodes conspicuous, ca. 1.5 mm, sagittate, stalked. Ovary ovoid, 1.2–1.5 mm, glabrous, attenuate into a 0.5–0.8 mm long style; stigma discoid, inconspicuous. Infructescence subterminal, 10–18 cm, robust, glabrous, with one or two well-developed fruits. Fruit oblate, 4–5 × 5–6 cm, immature fruit green, brown when mature, fruit stalk robust, 3–4 mm in diameter, apex dilated, 5–10 mm in diameter, sometimes nearly cylindrical, fleshy and warty when fresh.

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

Distribution and habitat. Hekou County and Maguan County, Yunnan Province, China. Tropical limestone forests in valleys, usually near streams, at an elevation of 150–850 m.

Conservation status. Currently, *Alseodaphnopsis hokouensis* is known from Hekou Country and Maguan Country (Yunnan Province, China) with four populations (Fig. 1). Two populations found in Maguan Country are all located in Gulinqing Provincial Nature Reserve, each with about 20 mature individuals

Figure 4. Different habitats of *Alseodaphnopsis hokouensis* **A** in the forest of the Nature Reserve **B** on the roadside **C** in the strongly disturbed forest near the village.

(Fig. 4). The other two populations found in Hekou Country, each with about 10 mature individuals, are not located in any nature reserve and those individuals mostly occur on the roadsides or in strongly-disturbed forests near the villages (Fig. 4). No individual was found at the type locality, Masike, Nanxi Town, Hekou County. According to the IUCN Red List Categories and Criteria version 15.1 (July 2022), the conservation status of *Alseodaphnopsis hokouensis* is re-evaluated as Critically Endangered (CR, C2a(i)).

Additional specimens examined. China. Yunnan Province: **Hekou County**, 17 June 2020, Lang Li et al. *2020064* (HITBC); 18 June 2020, Lang Li et al. *2020071* & *2020072* (HITBC); 25 August 2020, Lang Li and Guan-long Cao, *2020135*, *2020136*, 2020137 & *2020138* (HITBC). 13 May 2022, Lang Li and Dian-yang Zou, *2022027* (HITBC). **Maguan County**, 19 June 2020, Lang Li et al. *2020082*, *2020083* & *2020086* (HITBC); 20 June 2020, Lang Li et al. *2020091*, *2020092*, *2020093*, *2020094*, *2020095 & 2020096* (HITBC); 24 August 2020, Lang Li and Guan-long Cao, *2020127* & *2020128* (HITBC); 2 August 2022, Lang Li et al. *2022034*, *2022035* & *2022036* (HITBC).

Acknowledgements

The authors are grateful to Xi-bing Guo and Jin-guo Zhang for their kind help during the field surveys and to Jens G. Rohwer for his valuable comments on the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was financially supported by grants from the National Natural Science Foundation of China (No. 31970222), the Yunnan Fundamental Research Projects (No. 202101AT070067, No. 202201AS070055) and the 14th Five-Year Plan of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG-1450101).

Author contributions

Conceptualization: JL, LL. Data curation: LL, DZ. Formal analysis: DZ, LL. Funding acquisition: JL, LL. Investigation: LL, DZ, YM. Methodology: LL. Project administration: JL, LL. Supervision: JL, LL. Visualization: YM, LL. Writing - original draft: LL. Writing - review and editing: JL, DZ, YM, LL.

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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 242: 293–306 (2024)
DOI: 10.3897/phytokeys.242.119702

Research Article

Impatiens yingjingensis (Balsaminaceae), a new species from Sichuan, China

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Abstract

This study describes *Impatiens yingjingensis* X.Q. Song, B.N. Song & Biao Yang, **sp. nov.**, a new species collected from the Yingjing area of the Giant Panda National Park. This new species is distributed at an altitude of 1400–2100 m, with a plant height of 30–130 cm. The flowers are purple-red or light purple red, with 3–9 flowers on each inflorescence and the dorsal auricle of the lateral united petals is thread-like and about 2 cm long, differing significantly from other species of *Impatiens*. Furthermore, molecular data, as well as micro-morphological evidence under SEM (of pollens), also support the establishment of the new species.

Key words: Balsaminaceae, Giant Panda National Park, *Impatiens*, new species, Yingjing County

Academic editor: Bing Liu
Received: 27 January 2024
Accepted: 20 May 2024
Published: 6 June 2024

Citation: Song X, Song B, Fu M, Wang J, Liu J, Qin W, Jiang Y, Fan L, Yang B (2024) *Impatiens yingjingensis* (Balsaminaceae), a new species from Sichuan, China. PhytoKeys 242: 293–306. https://doi.org/10.3897/phytokeys.242.119702

Introduction

The genus *Impatiens* L. is the largest genus in the family Balsaminaceae, with more than 1,000 species (Grey-Wilson 1980; Yu et al. 2016; Song et al. 2021; Yuan et al. 2022). It predominantly inhabits the tropical and subtropical mountainous regions of the Eurasian continent and tropical Africa, with a minor presence in temperate zones of Eurasia and North America (Ren 2022). China is one of the five global hotspots for *Impatiens* diversity (tropical Africa, Madagascar, southern India and Sri Lanka, the eastern Himalayas and southeast Asia), accounting for more than 360 species (Chen et al. 2023). Most species are concentrated in southwest China, specifically in Yunnan, Sichuan, Guangxi, Guizhou and Xizang, showcasing narrow distributions and unique characteristics (Chen 2001; Yuan et al. 2022; Xiang et al. 2023).

In recent years, several new species and new records of this genus, including *I. longiaristata*, *I. tripetala*, *I. wawuensis*, *I. longlinensis*, *I. wutaishanensis*, *I. longshanensis*, *I. lihengiana* and *I. cavaleriei* have been discovered in southwest

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[*] The authors contributed equally to this work.

China (Ding et al. 2016; Xue et al. 2020; Liao et al. 2021; Peng et al. 2021; Song et al. 2021; Huang et al. 2023). These findings underscore the presence of numerous potential new species awaiting discovery within this diverse genus.

The Yingjing area of the Giant Panda National Park (GPNP) is located in Yingjing County, Sichuan Province, spanning a total area of 836 km^2. It is situated in the mountainous area transitioning from the Sichuan Basin to the Qinghai-Tibet Plateau. The unique geographical position, varying altitudes and distinct climate conditions have given rise to a diverse array of flora and fauna, fostering complex ecological communities within the vicinity (Shao et al. 2022). During a survey in the Yingjing area of the GPNP from August to October of 2021, an intriguing *Impatiens* species was discovered thriving at the forest edge and in valleys at altitudes ranging from 1400 to 2100 m. It was similar to *I. lateristachys* in overall morphology, but after consulting a large number of specimens and investigating the morphological and micromorphological characteristics, significant differences were observed in flower, inflorescences, dorsal petal, lower petal, lateral united petals and lower sepal. Based on the combination of detailed field observation, morphological, micromorphological and molecular data, we confirmed that it represents a previously undescribed species. The primary objective of this research is to present a detailed description of this newly-discovered species.

Materials and methods

Plant sampling and morphological observation

Fresh plant material of the unidentified *Impatiens* species was collected from the Mount Yunwu area of Yingjing County, within the GPNP. The location was at Shaidianping (29°33.98'N, 102°45.00'E, 1624 m alt.). The collected specimens were deposited at the Herbarium of Sichuan University (Chengdu, China). Following the guidelines of Flora Reipublicae Popularis Sinica, Balsaminaceae, Tomus 47 (part 2) (Chen 2001) and Balsaminaceae of China (Yu 2012), various morphological characteristics of this species, such as plant height, leaf size and shape, inflorescence type, flower colour, pedicel length, petal width and stamen length, were meticulously observed and measured in the field. A comparative analysis with other *Impatiens* species was conducted. Additionally, colour photographs of the plants were taken and the inflorescences were dissected indoors. Furthermore, scanning electron microscopy was employed to observe the pollen of the plant.

DNA extraction and sequencing

The fresh adult basal leaves of this species were collected in the field and then dried immediately with silica gel for the next step. Voucher specimens were stored at the Herbarium of Sichuan University (Chengdu, China) under deposition number 202108001. Firstly, we extracted the total genomic DNA from silica-dried leaves with a plant genomic DNA kit (Cwbio Biosciences, Beijing, China) referring to the manufacturer's protocols. Then, the quality and quantity of extracted DNA were tested using 1% agarose gel electrophoresis and high-quality DNA was sequenced on Illumina NovaSeq platform at Personalbio

(Shanghai, China) according to the standard Illumina sequencing protocols (Shendure and Ji 2008), with the sequence depth 6G. Paired-end 150 reads were obtained from libraries with an insert size of 300 bp. Finally, the software fastP v.0.15.0 (-n 10 and -q 15) (Chen et al. 2018) was used to filter the low-quality reads and gain high-quality reads.

In addition, total genomic DNA was also employed to amplify the Internal Transcribed Spacer (ITS) regions and the 30 μl amplification system was performed, which included 2 μl extracted total DNA, 10 μl ddH_2O, 15 μl Taq MasterMix (CWBio, Beijing, China), 1.5 μl of 10 pmol $μl^{-1}$ forward primers ITS4 (5’-TCC TCCGCT TAT TGATAT GC- 3’) and 1.5 μl of 10 pmol $μl^{-1}$ reverse primers ITS5 (5’-GGA AGTAAA AGTCGT AAC AAG G-3’ (White et al. 1990). By executing the following programme: initial denaturation for 3 min at 94 °C, followed by 30 cycles of 45 s at 94 °C, 70 s at 54 °C and 90 s at 72 °C and then a final extension of 10 min at 72 °C, we obtained the amplified PCR products. Finally, we used a 1.5% (w/v) agarose TAE gel to examine all PCR products which were sent to Sangon (Shanghai, China) for sequencing. The software Geneious v.9.0.2 (Kearse et al. 2012) was used to edit the newly-sequenced ITS sequence and consensus sequences were gained.

Plastome assembly and annotation

The plastome of this species was de novo assembled by NOVOPlasty v.2.6.2 (Dierckxsens et al. 2017) with the default parameters and *rbc*L sequence extracted from the plastome of *I. balsamina* (MZ902354) as the seed. The Plastid Genome Annotator (PGA) (Qu et al. 2019) was applied to annotate the plastome of this new species, setting the plastome of *I. balsamina* (MZ902354) as reference. Then, we manually corrected the start and stop codons and intron positions in Geneious v.9.0.2 (Kearse et al. 2012) based on the plastomes of congeneric species. The circular plastome map of this new species was drawn by the online Organellar Genome DRAW tool (OGDRAW) (Lohse et al. 2007). Finally, the newly-generated ITS sequence and plastome of this *Impatiens* species were submitted to the NCBI under accession numbers OR982404-OR982405 and OR978441, respectively.

Phylogenetic analysis

To investigate the phylogenetic position of this species, 62 complete plastome data and 62 ITS sequences were employed to reconstruct the phylogenetic trees, and *Hydrocera triflora* was selected as outgroup (Suppl material 1). The plastome data and ITS sequences were straightway aligned with MAFFT v.7.221 (Katoh and Standley 2013) to generate the matrix, respectively. The matrixes were subjected to Maximum Likelihood (ML) and Bayesian Inference (BI) analyses. The ML analyses were inferred by adopting RAxML version 8.2.11 (Stamatakis 2014) with the GTRGAMMA model and 1000 replicates as suggested by the RAxML manual. The BI analyses were performed by using MrBayes v.3.2.7 (Ronquist et al. 2012) with the best-fit substitution model (GTR+I+G) for plastome data and (GTR+G) for ITS sequence determined by ModelTest v.3.7 (Posada and Crandall 1998) based on the Akaike Information Criterion (AIC). The Markov Chain Monte Carlo (MCMC) algorithm was run for

1,000,000 generations, sampling every 500 generations. The run finished when the average standard deviation of split frequencies was below 0.01. The first 25% of samples were discarded as burn-in and the remaining trees were maintained to yield the consensus tree. The phylogenetic trees of two analyses were visualised and edited by Interactive Tree of Life (iTOL) (Letunic and Bork 2019) and the nodes under 50% bootstrap support were collapsed.

Results

Morphological characteristics

We investigated carefully the morphology of this new species and observed that its distinctive morphological features are its flower, inflorescences, dorsal petal, lower petal, lateral united petals and lower sepal, such as it has purple-red or light purple-red flowers with 7–12 pairs of lateral veins. The inflorescences are axillary, slightly shorter than the leaf length or approximately equal to the leaf blade in length, 3–9 flowered arranged in a one-sided raceme on the inflorescence axis. The dorsal petal is orbicular approximately 15 mm in diameter, with a concave apex and obtuse tip, the mid-vein on the back thickening with narrow wings, wings 2-angled. The lower petal is gradually narrowing at the base into a sickle-shaped spur approximately 2 cm long; lateral united petals 2-lobed, auricle linear approximately 2 cm, elongate, inserted into spur (Fig. 1, Table 1).

Micromorphological observations of pollen

In further investigation of this species, we also observed its micromorphology of pollen grains under the scanning electron microscope. The results showed that the pollen grains of this species had a unique micromorphology, characterised by single-grain pollen with a flattened spherical shape. Its polar view was capsule-like, irregular and reticulated (Fig. 2).

The structure and features of plastome

This species exhibited a typical quadripartite structure (Fig. 3), with a length of 151,642 bp, including a large single copy region (LSC: 82,588 bp), a small single copy region (SSC: 17,628 bp) and a pair of inverted repeat regions (IRs: 25,713 bp). The total GC content was 36.80%, with the GC content of the IRs regions being 43.1%, significantly higher than that of the LSC region (34.6%) and the SSC region (29.3%). The genome encoded 114 unique genes, including 80 protein-coding genes, 30 tRNA genes and four ribosomal RNA genes (Table 1). In addition, these unique genes had four categories: Self-replication, Genes for photosynthesis, other genes and Genes of unknown function (Table 2).

Phylogenetic analysis

We employed 62 complete plastomes and 62 ITS sequences to reconstruct the phylogeny of this new species. Although the plastome data and ITS sequence yielded incongruent tree topologies, both strongly supported the fact that this new species clustered with other *Impatiens* members, belonging

Table 1. Comparative morphological characters of *I. yingjingensis* and related species.

Characters	*I. yingjingensis*	*I. siculifer*	*I. drepanophora*	*I.lateristachys*	*I. imbecilla*	*I. faberi*
Plant height (cm)	30–130	30–60	100	40–100	40–60	60–70
Leaf shape	ovate or elliptic	ovate-lanceolate or elliptic-lanceolate	ovate-lanceolate	obovate-lanceolate	ovate or ovate-oblong	ovate-lanceolate or elliptic
Leaf length (cm)	5–22	5–13	6–13	0.5–15	5–11	5–15
Leaf width (cm)	3.5–7	2.5–5	2–4	6	2.5–4	2.5–4.5
Length of petiole (cm)	0.5–4	1.5–3	5		2–4	2–4
Lateral veins	7–12	5–11	7–9	6–8		5–8
Inflorescence	unilateral cyme	cyme	cyme	unilateral cyme		
Pedicel length	12–29		15–20			10–20
Flower	3–9	5–8		3–6	2	2
Bracts	base, lanceolate	base, lanceolate	base, ovate-lanceolate	base, 2mm	ovate-lanceolate, 3–5mm	lanceolate, 2–3 mm
Flower colour	purple-red or light purplish-red	yellow	yellow	red, light red or white	light red	purple-red
Dorsal petal	orbicular, 15 mm, with a concave apex, the mid-vein on the back thickening with narrow wings, 2-angled	nearly circular, with the mid-rib on the back thickening into narrow wings	orange-yellow, slightly stalked	1.5–1.8 cm, top concave, with a blunt pointed head, deeply bifid at the base, the mid-vein on the back thickening with narrow wings, 2-angled	7–8 mm, with 2 shallow clefts at the top, the mid-rib on the back thickened, with a cockscomb-like projection	orbicular, 13–17 mm, concave or 2-cleft at the top, blunt, deeply bifid at the base, with thickened mid-rib on the back, with wings
Lateral united petals	2-lobed, auricle linear, 2 cm long, inserted into spur	2-lobed	2-lobed	auticula dorsalis in filum 1–1.5 mm latum, 1–1.3 cm long	2-lobed, auticula dorsalis in filum	2-lobed, auticula dorsalis in filum
Lower sepal	sickle-shaped, the eaves are boat-shaped, and the mouth is flat	narrowly funnel-shaped, with a beak-like short point at the apex	upper edge of the lip petal has a green elongated lobe	angular, 2.5–3 cm long, with an oblique blunt mouth	12–15 mm long; the mouth is oblique and tapering towards the tip, narrowing downwards	angular, 3–4cm, mouth is oblique, with a small point, bending inwards or straight from the middle
Spur	sickle-shaped spur, 2cm	introrse or extrorse stamens	long spirally inwardly curved	straight	straight or sickle-shaped	
Lateral sepals	ovate, 2–4 × 2 mm, with a pointed apex	narrowly elliptic, with an acute apex	sickle-shaped, 2 mm long, light green	diamond-shaped, about 2 mm long, with a truncated base and three veins	oval-shaped, 4 × 1.5–2 mm, with a long tapering tip at the top	green, egg-shaped, 6–8 × 3–5mm, with 3–5 veins and a thickened mid-rib
Flowering period	July to October	May to October	August		August to September	August to September
Capsule	clavate	clavate	clavate		clavate, 2.5–3 cm	Narrow linear , 2.5–3 cm

to the genus *Impatiens*. In the plastome-based and ITS-based phylogenetic tree, the results of the Maximum Likelihood (ML) and Bayesian Inference (BI) analyses generated well-resolved topologies and the topologies were highly identical as expected (Fig. 4). It was clearly observed that this new species formed a clade with *I. piufanensis* in the plastome-based tree (BS = 100, PP = 1.00) (Fig. 4A). However, in the ITS-based phylogenetic tree, this new species was clustered with *I. lateristachys* (BS = 100, PP = 1.00) (Fig. 4B). In addition, both phylogenetic trees also indicated that this new species was clearly distant from other related *Impatiens* members that were morphologically similar to it, including *I. faberi*, *I. drepanophora*, *I. siculifer* and *I. imbecilla* (Fig. 4).

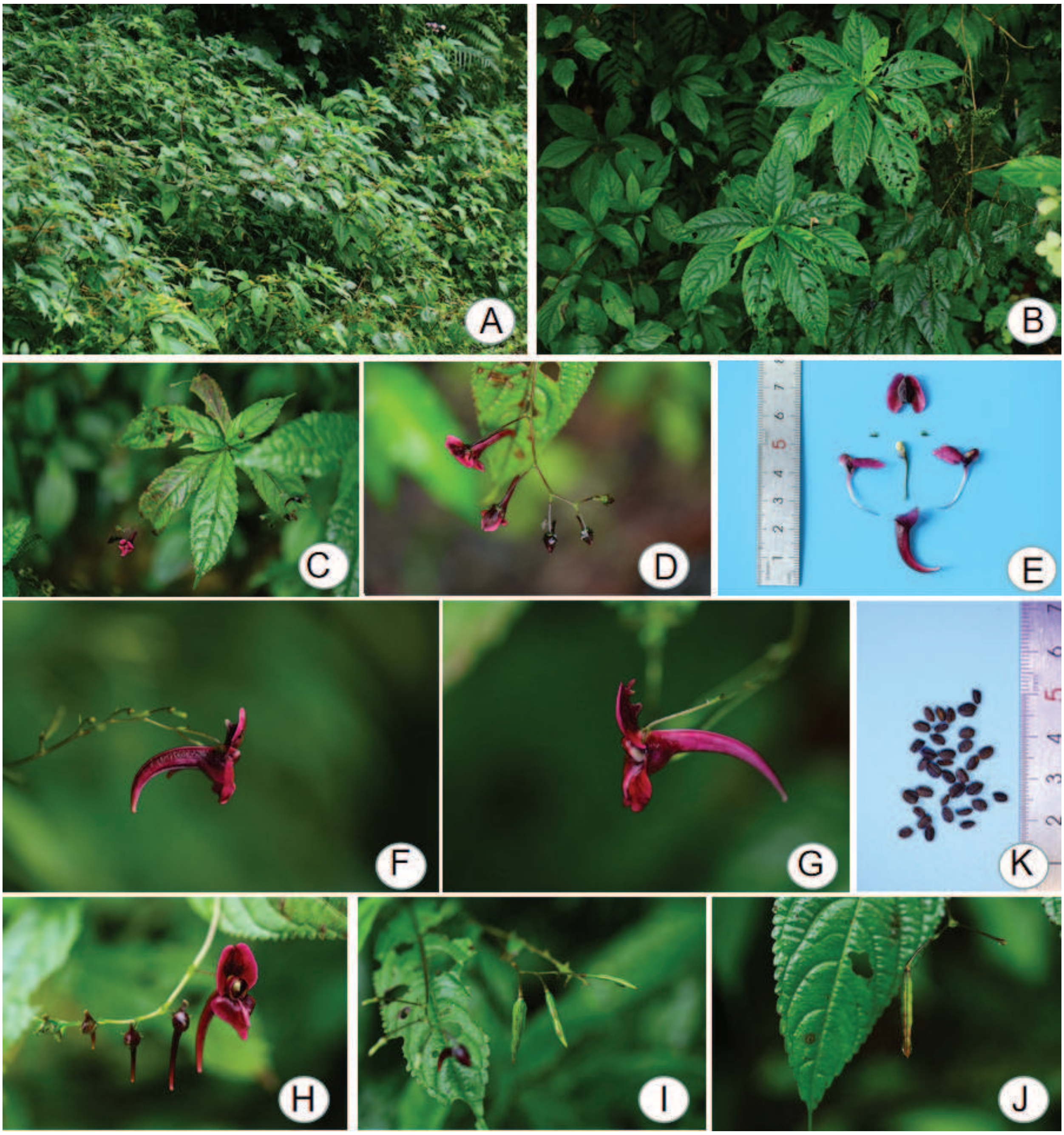

Figure 1. Habitat and morphology of *I. yingjingensis* **A** habitat **B** plants **C** leaf **D** flower branch **E** the floral anatomy of *I. yingjingensis* **F, G** flower, lateral view **H** flower, front view **I, J** capsule **K** seed.

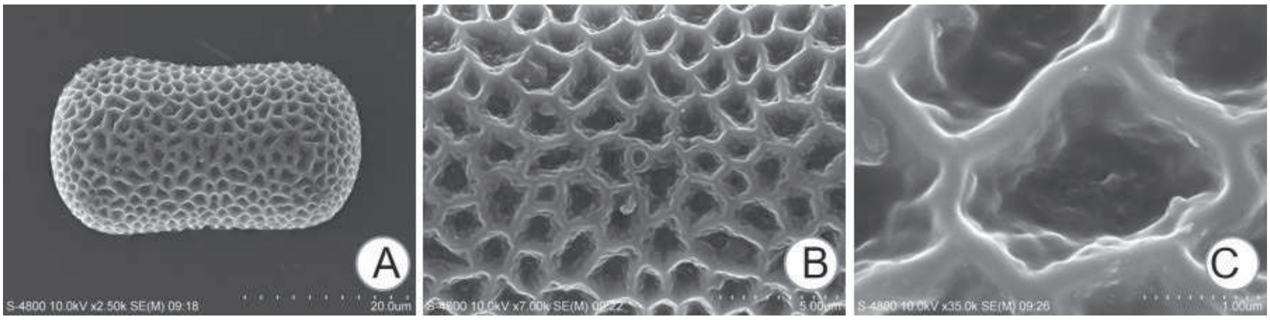

Figure 2. SEM images of pollen grains **A** polar view **B, C** partial view.

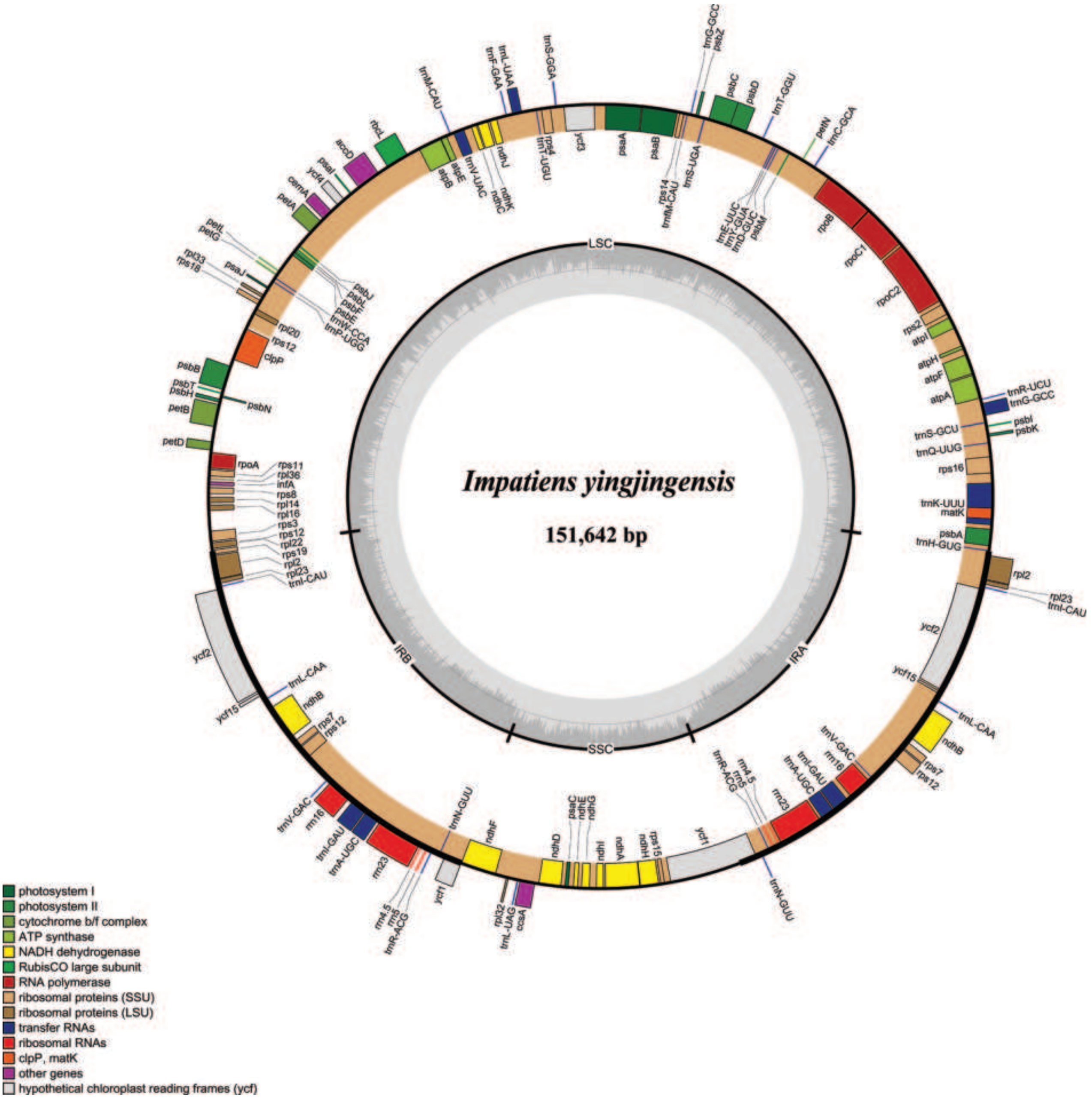

Figure 3. Plastome map of this new species. Genes shown in outside and insides of the circle are transcribed counter-clockwise and clockwise, respectively. The dark grey area of the inner circle denotes the GC content of plastome.

Discussion

China is recognized as a significant hotspot for the distribution of *Impatiens*. It offers a variety of habitat conditions for the genus *Impatiens* and breeds a variety of *Impatiens* resources, including regional endemics and Chinese-specific varieties. Due to the complexities associated with collection and identification, there is a lack of comprehensive and in-depth floristic surveys for the genus *Impatiens* in China. As a result, the resource status and phylogenetic relationships of the genus *Impatiens* in China, especially in key and vulnerable areas, are still unclear. Therefore, strengthening the floristic surveys and specimen collection of the *Impatiens* genus, especially in these critical and vulnerable regions, is an important task for the current research in taxonomy and floristics.

Table 2. Annotated unique genes information of _I. yingjingensis_.

Category of Genes	Group of gene	Name of gene
Self-replication	Ribosomal RNA genes	_rrn_4.5, _rrn_5, _rrn_16, _rrn_23
	Transfer RNA genes	_trn_C-GCA, _trn_D-GUC, _trn_E-UUC, _trn_F-GAA, _trn_G-GCC, _trn_G-UCC*, _trn_H-GUG, _trn_I-CAU, _trn_K-UUU*, _trn_L-CAA, _trn_L-UAA*, _trn_L-UAG, _trn_M-CAU, _trn_P-UGG, _trn_Q-UUG, _trn_R-UCU, _trn_S-GCU, _trn_S-GGA, _trn_S-UGA, _trn_T-UGU, _trn_T-GGU, _trn_V-GAC, _trn_V-UAC*, _trn_Y-GUA, _trn_W-CCA, _trnf_M-CAU, _trn_A-UGC*, _trn_I-GAU*, _trn_N-GUU, _trn_R-ACG
	Ribosomal protein (small subunit)	_rps_2, _rps_3, _rps_4, _rps_7, _rps_8, _rps_11, _rps_12**, _rps_14, _rps_15, _rps_16*, _rps_18, _rps_19
	Ribosomal protein (large subunit)	_rpl_2*, _rpl_14, _rpl_16*, _rpl_20, _rpl_22, _rpl_23, _rpl_32, _rpl_33, _rpl_36
	RNA polymerase	_rpo_A, _rpo_B, _rpo_C1*, _rpo_C2
	Translational initiation factor	_inf_A
Genes for photosynthesis	Subunits of photosystem I	_psa_A, _psa_B, _psa_C, _psa_I,_psa_J, _ycf_3**, _ycf_4
	Subunits of photosystem II	_psb_A, _psb_B, _psb_C, _psb_D, _psb_E, _psb_F, _psb_H, _psb_I, _psb_J, _psb_K, _psb_L, _psb_M, _psb_N, _psb_T, _psb_Z
	Subunits of cytochrome	_pet_A, _pet_B*, _pet_D*, _pet_G, _pet_L, _pet_N
	Subunits of ATP synthase	_atp_A, _atp_B, _atp_E, _atp_F*, _atp_H, _atp_I
	Large subunit of Rubisco	_rbc_L
	Subunits of NADH dehydrogenase	_ndh_A*, _ndh_B*, , _ndh_C, _ndh_D, _ndh_E, _ndh_F, _ndh_G, _ndh_H, _ndh_I, _ndh_J, _ndh_K
Other genes	Maturase	_mat_K
	Envelope membrane protein	_cem_A
	Subunit of acetyl-CoA	_acc_D
	Synthesis gene	_ccs_A
	ATP-dependent protease	_clp_P**
	Component of TIC complex	_ycf_1
Genes of unknown function	Conserved open reading frames	_ycf_2, _ycf_15

*: Gene with one intron.
**: Gene with two introns.

Through the investigation and research of the genus _Impatiens_ in the Yingjing area, it has been found that the distribution points and population numbers of _I. yingjingensis_ are relatively small, mainly being found in the valley, forest edge and roadsides at altitudes of 1400–2100 m in the areas of Mount Yunwu. Surveys and protection have not received adequate attention and it is essential to strengthen the investigation of the local resources of _I. yingjingensis_ and conduct systematic research on the species diversity of the genus _Impatiens_ in Yingjing County.

Through field observation and literature review, _I. yingjingensis_ was found to bear the closest morphological resemblance to _I. lateristachys_, _I. drepanophora_, _I. siculifer_, _I. imbecilla_ and _I. faberi_. However, their distinct differences were noted. The key features that distinguish _I. yingjingensis_ and _I. lateristachys_ are lower sepal and lateral sepals. Lower sepal in _I. yingjingensis_ is sickle-shaped, the leaves are boat-shaped and the mouth is flat, while the lower sepal in _I. lateristachys_ is angular with an oblique blunt mouth. The lateral sepals in _I. yingjingensis_ are ovate with a pointed apex, while the ones in _I. lateristachys_ are diamond-shaped with a truncated base and three veins, about 2 mm long. The most notable feature that distinguishes _I. yingjingensis_ from _I. drepanophora_ and _I. siculifer_ is flower colour. _I. yingjingensis_ has purple-red or light purplish-red flowers, whereas the flowers in _I. drepanophora_ and _I. siculifer_ are yellow. In addition, _I. yingjingensis_ can be easily distinguished from _I. imbecilla_ by the bracts. Bracts in _I. yingjingensis_ are lanceolate, while _I. imbecilla_ has ovate-lanceolate bracts. Additionally, the dorsal petal between _I. yingjingensis_ and _I. imbecilla_ is also different., The dorsal petal of _I. yingjingensis_ is 2-angled, orbicular with a concave apex and the mid-vein on the back thickening with narrow wings, whereas two shallow clefts at the top, the mid-rib on the back thickened and a cockscomb-like projection of dorsal

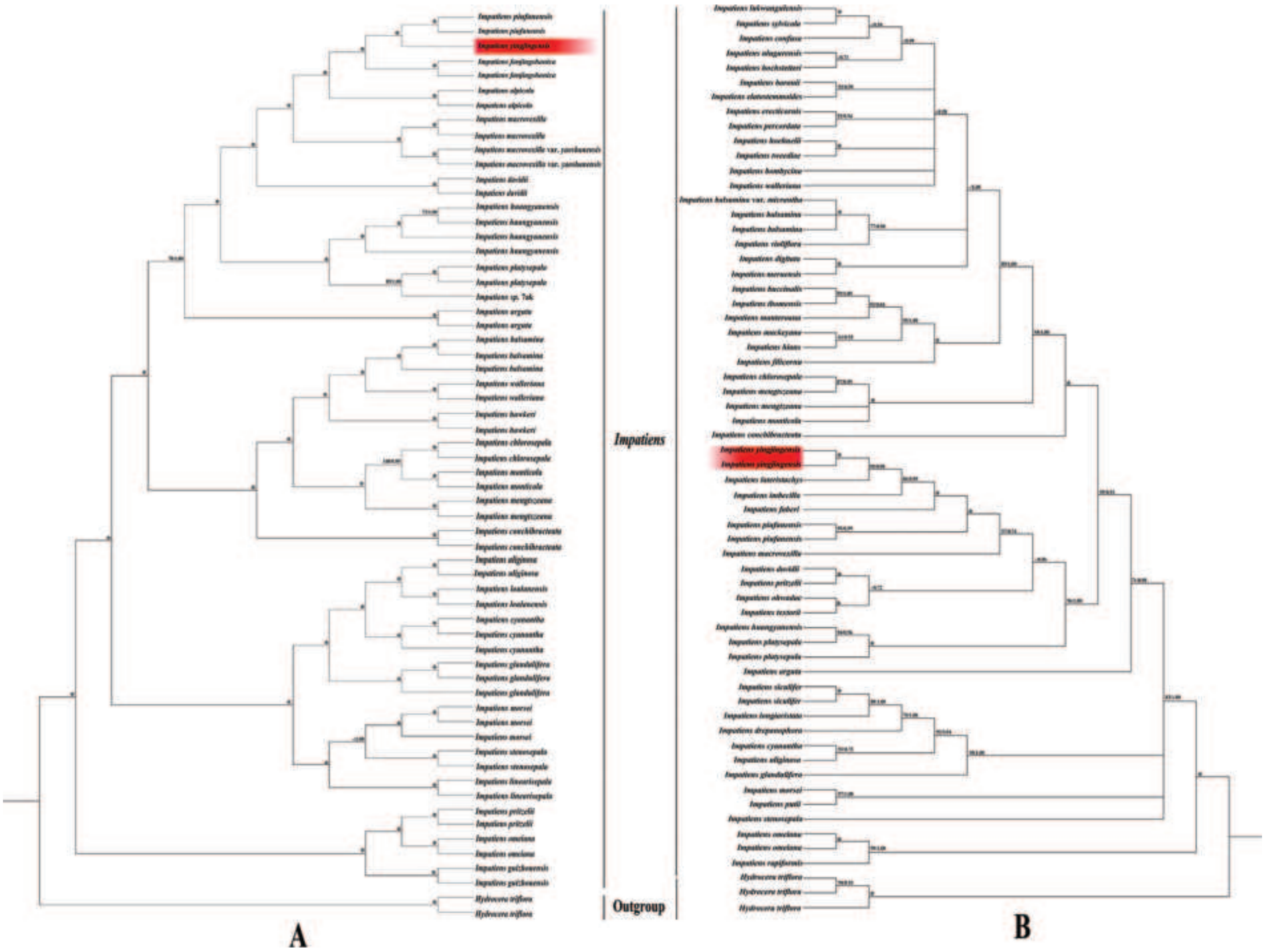

Figure 4. Phylogenetic trees constructed by Maximum Likelihood (ML) and Bayesian Inference (BI). The bootstrap values (BS) of ML and posterior probabilities (PP) of BI are listed at each node. (*) represents the node with PP = 1.00/BS = 100. "–" means the values < 0.50/50. Red background indicates the newly-sequenced unknown *Impatiens* species **A** plastomes-based tree **B** ITS-based tree.

petal are observed in *I. imbecilla*. *I. yingjingensis* can be clearly distinguished from *I. faberi* by their lateral sepals. The ovate lateral sepals with a pointed apex are detected in *I. yingjingensis*, but green, egg-shaped and a thickened mid-rib of lateral sepals with 3–5 veins are found in *I. faberi* (Table 1). Furthermore, we also observed the pollen grains of *I. yingjingensis* and found they have unique micromorphology (single-grain pollen with a flattened spherical shape, polar view capsule-like, irregular and reticulated) (Fig. 2). Previous studies have illustrated that the pollen grains of different species of *Impatiens* show significant differences in size, equatorial view, polar view and exine thickness and these morphological characteristics serve as natural evidence for the systematic classification of the genus *Impatiens* (Zhang et al. 2014; Zeng et al. 2016; Zhang et al. 2023). Therefore, both the morphological and micromorphological features strongly support that *I. yingjingensis* is very different from other members of *Impatiens* and should be treated a new member of the genus *Impatiens*.

Although the explicit systematic position of *I. yingjingensis* remains undefined, both phylogenetic trees based on plastome data and ITS sequences, strongly supported that *I. yingjingensis* is nested within the genus *Impatiens*, indicating its affiliation with the genus. Consistent with Yu et al. (2016), *Impatiens* can be divided into *I.* subgen. *Clavicarpa* and *I.* subgen. *Impatiens*. The molecular phylogenetic analysis of *Impatiens* species, based on complete plastomes and ITS sequences, supported our proposed new species, to cluster into a clade which belongs to *I.* subgen. *Impatiens*. To confirm the phylogenetic position of *I. yingjingensis* within *Impatiens*, further molecular sequences, such as additional nuclear DNA fragments, are required in future studies. Thus, the molecular evidence further bolsters the argument that *I. yingjingensis* should be classified as a novel member of *Impatiens*. In conclusion, considering the evidence obtained from morphology, micromorphology and molecular evidence, the designation of *I. yingjingensis* as a new species of *Impatiens* is both logical and compelling.

Taxonomic treatment

***Impatiens yingjingensis* X.Q. Song, B.N. Song & Biao Yang, sp.nov.**
urn:lsid:ipni.org:names:77343115-1

Diagnosis. *Impatiens yingjingensi* can be distinguished by the following morphological features from related species of *Impatiens*: purple-red or light purple-red flowers; inflorescence with 3–9 flowers; lower petal gradually narrowing at the base into a sickle-shaped spur approximately 2 cm long; lateral united petals 2-lobed, auricle linear approximately 2 cm, elongate and inserted into spur.

Type. CHINA. Sichuan: Yingjing County, at the forest edge and in valleys, 29°33.98'N, 102°45.00'E, 1624 m alt., 26 August 2021, P. Liang & L.J. Zhang 202108001 (holotype: SZ;isotypes: SZ). (Fig. 5).

Etymology. The species is named after Yingjing County, Sichuan Province, China, which is the type locality. The Chinese name is given as "荥经凤仙花".

Description. Herbs annual, 30–130 cm tall, glabrous, stems fleshy, erect or ascendant, branched, basal nodes swollen adventitious roots. Leaves alternate,

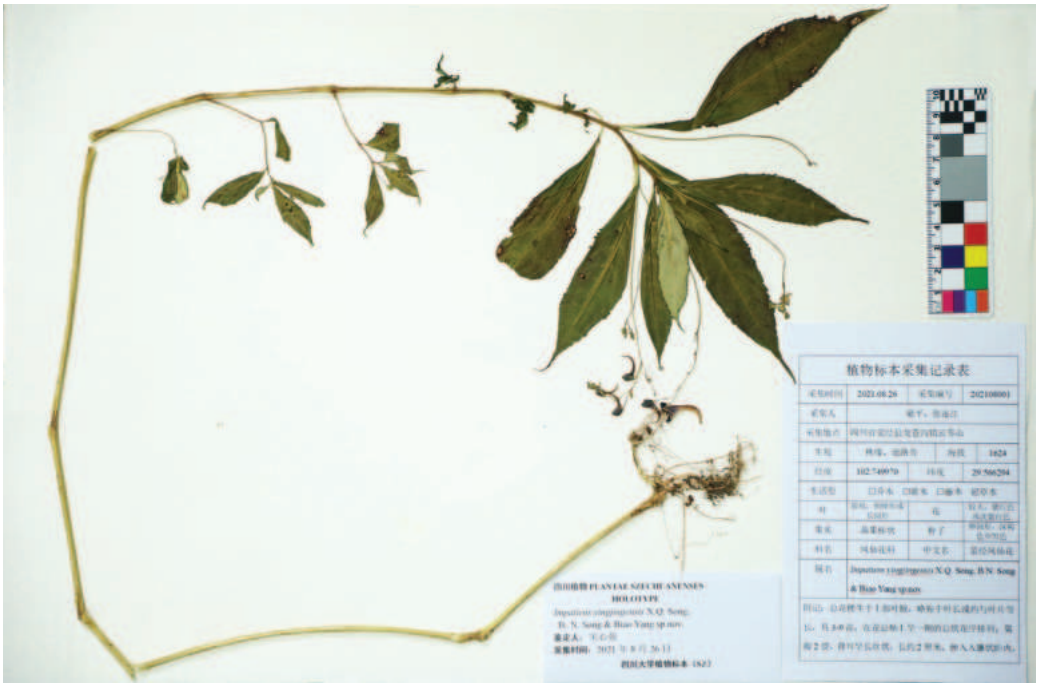

Figure 5. Holotype of *Impatiens yingjingensis* X.Q. Song, B.N. Song & Biao Yang, sp. nov.

petiolate or subsessile on upper stem; leaf blades ovate-oblong, 5–22 × 3.5–7 cm, membranaceous, abaxially puberulent, with 2 stipitate glands at base, base cuneate, margin crenate, apex acuminate; lateral veins 7–12 pairs, petioles 0.5–4 cm long. Inflorescences axillary, slightly shorter than the leaf length or approximately equal to the leaf blade in length, unilateral cyme, 3–9 flowers; pedicels 12–29 mm long, with bracts above base; flowers relatively large, purple-red or light purple-red, 2–3.5 cm long; lateral sepals ovate, ca. 3 × 2 mm, entire, apex acuminate, mucronulate; dorsal petal orbicular, approximately 15 mm in diameter, with a concave apex and obtuse tip, the mid-vein on the back thickening with narrow wings, wings 2-angled; lower petal sickle-shaped, 2.5 cm long and the mouth is flat, gradually narrowing at the base into a sickle-shaped spur, approximately 2 cm long; lateral united petals 2-lobed, the lower lobe approximately 0.5 cm long, the upper lobe oblong and approximately 1 cm long, auricle linear and approximately 2 cm, elongate, inserted into spur. Capsule clavate, 2–5 cm long, hairless. Seed ellipsoid, dark brown to black (Figs 1, 6).

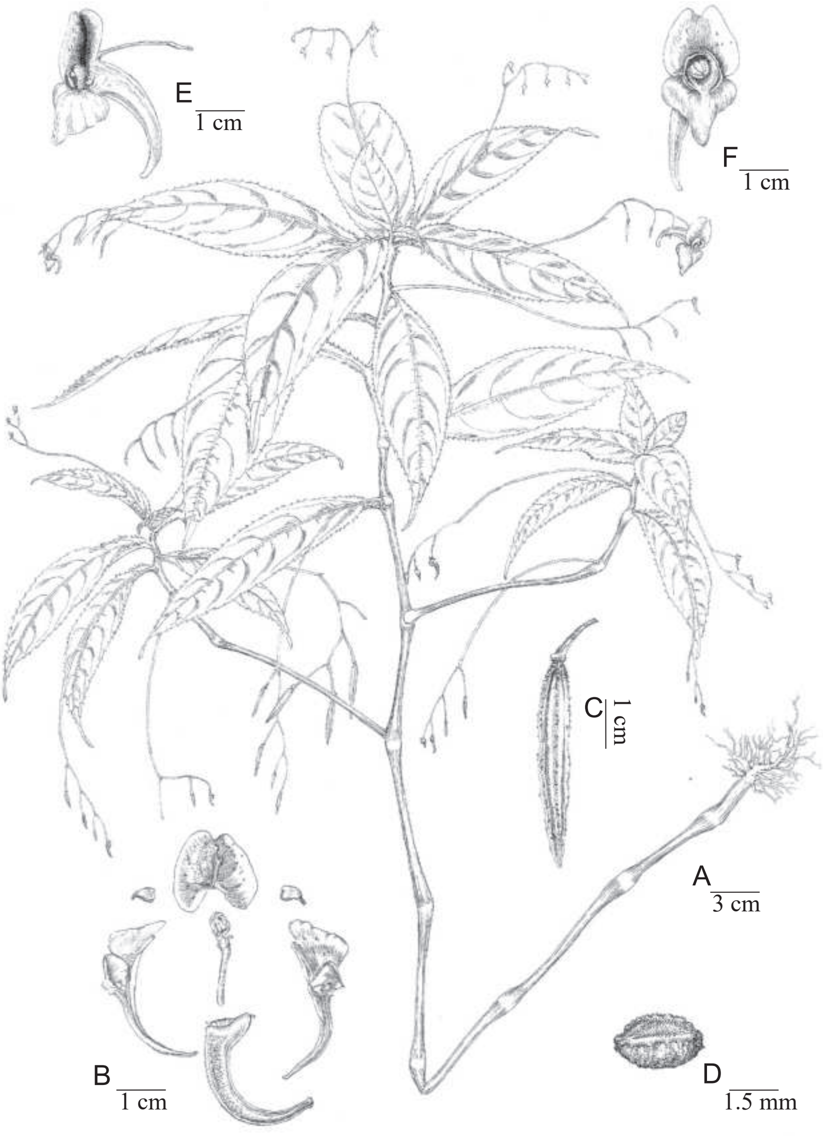

Figure 6. *Impatiens yingjingensis* **A** plants **B** the floral anatomy of *Impatiens yingjingensis* **C** capsule **D** seed **E** flower, lateral view **F** flower, front view. (Drawn by Liuqing Zhu)

Phenology. The flowering period is from July to October and the fruiting period is from August to November.

Distribution and habitat. *I. yingjingensis* is distributed in Yingjing County, Sichuan Province, China, at altitudes of 1400–2100 m.

Additional specimens examined (paratypes). China. Sichuan: Yingjing County, at the forest edge and in valleys, 29°36.76'N, 102°44.23'E, 1534 m alt., 24 August 2022, P. Liang & L.J. Zhang 202208001, P. Liang & L.J. Zhang 202208002, P. Liang & L.J. Zhang 202208003, P. Liang & L.J. Zhang 202208004, P. Liang & L.J. Zhang 202208005, P. Liang & L.J. Zhang 202208006 (SZ).

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

Investigating: XS, MF, JW, JL, WQ, YJ, LF. Writing-original draft: XS, BS, BY. Writing-review and editing: XS, BS, BY.

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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

Plastomes data and ITS sequence included in phylogenetic analyses with GenBank accession

Authors: Xinqiang Song, Boni Song, Mingxia Fu, Jiacai Wang, Jingyi Liu, Weirui Qin, Yuzhou Jiang, Leni Fan, Biao Yang

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.242.119702.suppl1

PhytoKeys 242: 307–316 (2024)
DOI: 10.3897/phytokeys.242.118069

Research Article

Amalophyllon miraculum (Gesneriaceae), an exceptionally small lithophilous new species from the western Andean slopes of Ecuador

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Abstract

Recent exploratory field expeditions to the western slopes of the Ecuadorian Andes resulted in the discovery of a new species of *Amalophyllon* (Gesneriaceae). *Amalophyllon miraculum* J.L.Clark, **sp. nov.** is described from two localities in the Centinela region in the Santo Domingo de los Tsáchilas province. The new species is differentiated from congeners by the pendent habit, basal rosette of leaves, leaf blades with deeply serrate margins, and miniature size. Based on IUCN guidelines, a preliminary conservation status is assigned as Critically Endangered (CR).

Resumen

Recientes expediciones exploratorias de campo a las laderas occidentales de los Andes ecuatorianos dieron como resultado el descubrimiento de una nueva especie de *Amalophyllon* (Gesneriaceae). *Amalophyllon miraculum* J.L.Clark, **sp. nov.** se describe de dos localidades de la región de Centinela en la provincia de Santo Domingo de los Tsáchilas. La nueva especie se diferencia de otros congéneres por el hábito colgante, la roseta basal de las hojas, las láminas foliares con márgenes profundamente aserrados y su tamaño en miniatura. Según las directrices de la UICN, se le asigna el estado de conservación preliminar de En Peligro Crítico (CR).

Key words: Andes, *Amalophyllon*, Centinela, Chocó, Conservation, Ecuador, endemic, lithophyte, Montañas de Ila

Academic editor: Laura Clavijo
Received: 1 January 2024
Accepted: 3 May 2024
Published: 11 June 2024

Citation: Clark JL, Fernández A, Zapata JN, Restrepo-Villarroel C, White DM, Pitman NCA (2024) *Amalophyllon miraculum* (Gesneriaceae), an exceptionally small lithophilous new species from the western Andean slopes of Ecuador. PhytoKeys 242: 307–316. https://doi.org/10.3897/phytokeys.242.118069

Introduction

The flowering plant family Gesneriaceae is in the order Lamiales and comprises 3400+ species in 150+ genera (Weber 2004; Weber et al. 2013). The family is divided into three strongly supported monophyletic subfamilies (Ogutcen et al. 2021) and seven tribes (Weber et al. 2013, 2020). The majority of New World members are in the subfamily Gesnerioideae and are represented by 1200+ species and 77 genera (Clark et al. 2020; GRC 2024). *Amalophyllon* Brandegee is classified in the tribe Gesnerieae and subtribe Gloxiniinae (Weber et al. 2013, 2020).

Amalophyllon is a genus of terrestrial or lithophytic herbs distributed from Mexico (Chiapas) through Central America to Venezuela, Colombia, Ecuador, and northern Peru. The presence of subrotate to rotate white corollas defines the following three currently recognized genera from the subtribe Gloxiniinae G.Don: *Amalophyllon*, *Niphaea*, and *Phinaea*. Phylogenetic studies based on molecular sequence data (Smith et al. 2004; Roalson et al. 2005; Roalson et al. 2008; Clark et al. 2011) strongly support the independent origins of subrotate to rotate corollas from recent ancestors with corollas that are bilaterally symmetrical and tubular. The similarity of floral structures in these three clades is likely a convergence that is correlated with vibrational or a “buzz” pollination syndrome (Wiehler 2002).

Amalophyllon was initially recognized as a monotypic genus in the Scrophulariaceae (Brandegee 1914). More recently, the name was applied to Gesneriaceae by Boggan et al. (2008) based on phylogenetic studies that strongly supported a clade that included several previously recognized species of *Phinaea*. Thus, *Amalophyllon* was expanded by Boggan et al. (2008) to include 13 species. The description of *Amalophyllon miraculum* increases the total to 14 species of *Amalophyllon*. There are currently two species of *Amalophyllon* in Ecuador and the addition of *A. miraculum* increases the total to three species (Fig. 1). *Amalophyllon divaricatum* is known from two populations in southern Ecuador (El Oro and Loja) and at least four populations in Peru (Huánuco, Junín, San Martín, Ucayali). *Amalophyllon clarkii* Boggan & L.E.Skog is endemic to western Ecuador. The type locality of *A. clarkii* is in Azuay, near the provincial border of Guayas in the Bosque Protector Molleturo Mullopungo (Fig. 1). Additional populations of *A. clarkii* are in the Ecuadorian provinces of Guayas and Los Ríos (Fig. 1).

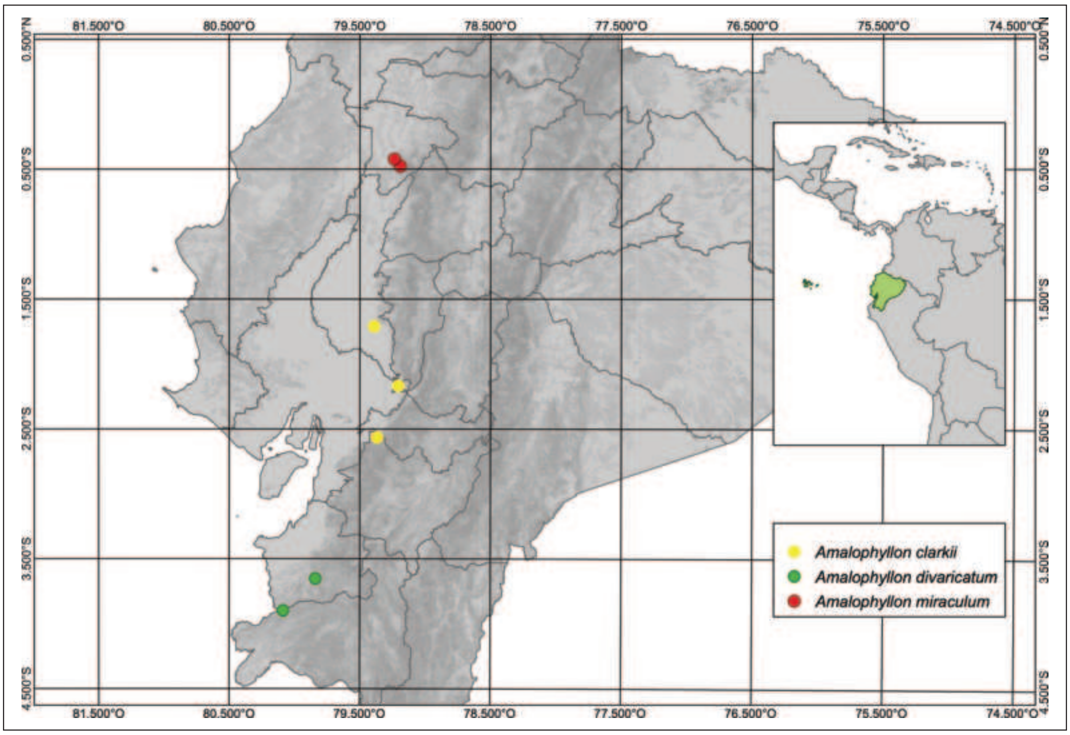

Figure 1. Distribution map of *Amalophyllon* in Ecuador. Localities with yellow circles =*Amalophyllon clarkii* Boggan & L.E.Skog, green circles =*A. divaricatum* (Poepp.) Boggan, L.E.Skog & Roalson, and red circles =*A. miraculum* J.L.Clark.

The genera *Amalophyllon*, *Niphaea*, and *Phinaea* were recently circumscribed based on phylogenetic studies (Smith et al. 2004; Roalson et al. 2005; Roalson et al. 2008; Clark et al. 2011). A summary of morphological differences between *Amalophyllon*, *Niphaea*, and *Phinaea* is provided in Boggan et al. (2008). There are floral characters that differentiate *Niphaea*, but there are only fruit characters that separate *Phinaea* from *Amalophyllon*. In addition, a fourth clade of rotate flowers is represented by *"Phinaea" pulchella* (Griseb.) C.V.Morton from Cuba (Clark et al. 2011). *Amalophyllon* differs from *Phinaea* by fruit characters outlined in Boggan et al. (2008). The capsules of *Phinaea* are subtended by erect pedicels. In contrast, the pedicel posture in *Amalophyllon* is usually curved. The seeds in *Phinaea* are typically sticky and adhere to the fruit valves, whereas the seeds fall freely from the capsules of *Amalophyllon*.

Materials and methods

Plants were vouchered and photographed during two field expeditions to the western Andes of Ecuador in 2022 (Clark 2022). Specimens were deposited in the following herbaria: Pontificia Universidad Católica del Ecuador (QCA), Marie Selby Botanical Gardens (SEL), United States National Herbarium (US), New York Botanical Garden (NY), and Missouri Botanical Garden (MO). Digital images of live specimens were taken in the field using a Nikon D100 DSLR with a Nikon 105 mm lens and a Nikon SB-29s ring flash. Morphological observations and measurements were made from live collections, alcohol-preserved material, and digital images using the software program *ImageJ* (Schneider et al. 2012).

We assessed the extinction risk of *Amalophyllon miraculum* following the IUCN Red List Categories and Criteria and guidelines of the IUCN (2022). We considered observations, collection localities and population estimates from fieldwork. We refrained from calculating extent of occurrence (EOO) because of the limited number of known populations. The area of occupancy (AOO) was calculated using the software program *GeoCAT* (Bachman et al. 2011) with the default setting of a 4 km^2 grid.

Taxonomic treatment

Amalophyllon miraculum **J.L.Clark, sp. nov.**
urn:lsid:ipni.org:names:77343140-1
Fig. 2

Type. Ecuador. Santo Domingo de los Tsáchilas: cantón Santo Domingo, parroquia El Esfuerzo, El Respaldo, 3.5 km east of Segundo Respaldo, finca de Paul Henry, 0°25'25.8"S, 79°14'7.4"W, 672 m alt., 19 Mar 2022, *J.L. Clark, X. Cornejo, P. Henry & C. Restrepo-Villarroel 16634* (holotype: QCA; isotypes: G, MO, NY, SEL, US).

Diagnosis. Similar to *Amalophyllon clarkii*, differing in larger and broadly ovate leaves in *A. clarkii* (>8 cm long) vs. smaller elongate to lanceolate leaf blades in *A. miraculum* (< 6 cm long); calyx lobes elongate in *A. clarkii* vs. broadly oblong in *A. miraculum*; and abaxial leaf surface green with purple venation in *A. clarkii* vs. uniformly dark purple in *A. miraculum*.

Description. Lithophytic herb with scaly rhizomes; stem short; pendent to horizontal with leaves in a basal rosette. ***Leaves*** opposite, subequal; petiole glabrous

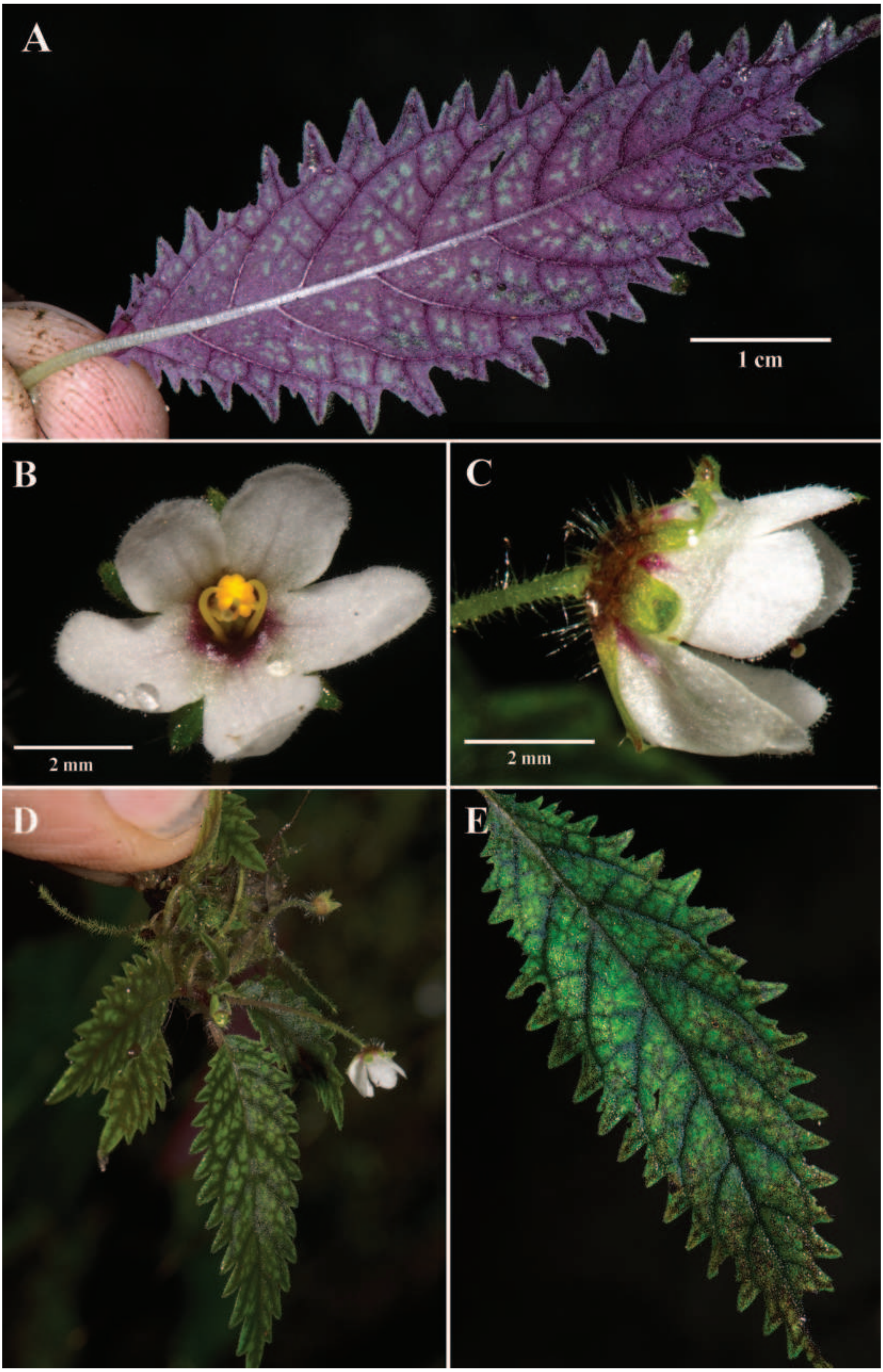

Figure 2. *Amalophyllon miraculum* J.L.Clark **A** abaxial view of leaf **B** front view of flower **C** lateral view of flower **D** pendent habit featuring rosette of leaves **E** adaxial view of leaf. (**A, E** from *J.L. Clark et al. 16805*; **B, C, D** from *J.L. Clark et al. 16634*). Photos by J.L. Clark.

to sparsely pubescent, 2–5 mm long; blade membranous, fragile when dried, oblong to lanceolate, 1.5–5.0 cm long, 1–2 cm wide, with 6–9 pairs of lateral veins, margins deeply serrate, bright green with dark green venation on adaxial surface, dark purple on abaxial surface, apex acute. ***Inflorescence*** reduced to a single axillary flower (without peduncles), usually produced at the apex of leaves or axis of clustered leaves, with 1–3 flowers per axil, inflorescence bracts absent; pedicels slender, curved, 1.5–2.0 cm long; calyx lobes 5, uniformly green, subequal, broadly oblong, nearly free, entire, rounded at apex, ca. 2.0 mm long × 1.0 mm wide; corolla lobes 5, fused at base for 1–2 mm forming a shallow tube, tube light red, lobes uniformly white, lobes entire, subequal, spreading broadly during anthesis, apices rounded, corolla lobes broadly ovate, ca. 2.5 mm long × 2.5 mm wide, glabrous inside and outside; stamens 4, adnate to the base of the corolla tube, filaments yellow, ca. 0.5 mm long, glabrous; nectary absent; ovary nearly superior, subglobose, glabrous, ca. 1 mm long and wide, style ca. 2 mm long, curved, glabrous, stigma capitate. ***Fruits*** not observed.

Phenology. Flowering in March and July. Fruits not observed.

Etymology. The specific epithet reflects the extraordinary and unexpected persistence of remnant forest patches of an area broadly defined as “Centinela” (see next section). Dodson and Gentry (1991) popularized this legendary biodiversity hotspot and brought it to prominence when they reported a mass extinction of plant species from this region. Many of the presumed “extinct” species were recently documented, including *Gasteranthus extinctus* L.E.Skog & L.P.Kvist (Gesneriaceae) (Pitman et al. 2022). *Amalophyllon miraculum* is sympatric with *Gasteranthus extinctus*. The presence of several critically endangered species and the recent discovery and description of new species from Centinela represent a miraculous discovery that has shattered a prevailing assumption that the once-thought-lost biodiversity of Centinela had vanished entirely. The heroic efforts of local landowners who maintained small patches of forests (usually surrounding waterfalls) were instrumental in conserving remnant forest fragments. Also crucial are current conservation initiatives by foundations and academic institutions such as the Ecuadorian conservation NGO Fundación de Conservación Jocotoco and the Jardín Botánico Padre Julio Marrero (JBJM) of the Pontificia Universidad Católica del Ecuador in the nearby city of Santo Domingo.

Distribution and preliminary assessment of conservation status. *Amalophyllon miraculum* has been collected in Ecuador’s western Andean slopes in the Santo Domingo de los Tsáchilas province. The only two known subpopulations are in small patches of forest surrounded by large swaths of deforested agricultural landscapes. The forest patch at the Paul Henry farm is approximately 10 hectares and is located in the northernmost part of the Montañas de Ila range in Recinto Milton Murillo. The southern forest patch in the Bosques y Cascadas Las Rocas private reserve is approximately 50 hectares and lies in the intermontane area between the Andean Cordillera and the northern Montañas de Ila (Fig. 1). These patches are approximately 8 km from each other. The current landowners (Paul Henry and Eduardo Díaz C.) are committed to preserving the forest fragments on their property, but broader efforts are urgently needed by governmental and non-governmental agencies to protect these and other nearby forest fragments. The GeoCAT calculated AOO is 8 km^2. *Amalophyllon miraculum* is preliminarily assessed as Critically Endangered (CR) based on a limited area of occupancy (IUCN criterion B1 where AOO <10 km^2) and the severely fragmented forests (B2a) and ongoing decline of the Centinela forests in western Ecuador (B2bi, ii, iii, iv). Intact forests in the Centinela region are mostly reduced to small (<10 hectares) fragments. Extensive deforestation in western Ecuador, especially Centinela, has resulted in an alarming habitat loss. The area was popularized by E.O. Wilson's (1992) term as the 'Centinelan extinction' because of initial reports of wide-scale plant extinctions by Dodson and Gentry (1991). One of the presumed extinctions was *Gasteranthus extinctus* L.E.Skog & L.P. Kvist (Gesneriaceae), which was recently documented in more than five forest fragments (Pitman et al. 2022). The rediscovery resulted in a re-evaluation of its IUCN assessment from Critically Endangered (CR) to Endangered (EN). We conducted five field expeditions between 2021 and 2023 and located the only two currently known populations of *Amalophyllon miraculum*, which is sympatric with the more widespread *Gasteranthus extinctus*. The only documented populations of *Amalophyllon miraculum* are inside privately protected areas surrounded by agriculture in unprotected parts of the Santo Domingo de los Tsáchilas province. Effective conservation of this and the other endemic species of the Centinela region will require constant vigilance.

Locating current and future populations of *Amalophyllon miraculum* is a major challenge because of their small size, ephemeral flowers, and camouflaged foliage on wet moss-covered rock faces. For example, authors Fernández and Zapata recently (April 2024) searched forests in the type locality in Paul Henry's farm but did not locate extant populations. Likewise, it will require targeted and careful searching to document and locate this elusive species.

Comments. Most *Amalophyllon* have leaf margins that are serrate to crenate. *Amalophyllon miraculum* and *A. clarkii* (Fig. 2A) are differentiated from other congeners by the presence of deeply serrate to biserrate leaf margins (Figs 2A, 3A). The leaf blades of *A. clarkii* are broadly ovate and nearly 8 cm long (Fig. 2A). In contrast, the leaves of *A. miraculum* are never more than 6 cm long (Fig. 2A). The calyx lobes in *A. clarkii* are elongate and narrow (Fig. 3C) vs. broadly oblong in *A. miraculum* (Fig. 2C). Both *Amalophyllon clarkii* and *A. miraculum* share a lithophytic habit but differ in their habitat and posture. Populations of *A. clarkii* were observed growing erect on a rock in the understory of a shaded forest without direct moisture. Populations of *A. miraculum* are pendent and have only been observed on wet rocks in streams or where mist is persistent. It was common to locate populations of 10–20 individuals of *A. miraculum* on wet areas of rock faces and no populations on adjacent dry areas, even when mosses and ferns were shared between the two microhabitats. The rosette-forming individuals of *A. miraculum* were often pendent. In contrast, populations of *A. clarkii* are either rosette-forming or with elongate erect shoots, but usually erect. There are always five corolla lobes in *Amalophyllon miraculum*. In contrast, the number of corolla lobes in *A. clarkii* is usually five, but occasionally six (Fig. 3B).

Amalophyllon miraculum and *A. clarkii* are geographically isolated. *Amalophyllon miraculum* is a narrow endemic from the northern lowlands of the western Andes of Ecuador in the province of Santo Domingo de los Tsáchilas (Fig. 1). Populations of *A. clarkii* are mainly from the southern lowlands of western Ecuador (Azuay, Guayas, and Los Ríos). One disjunct population of *A. clarkii* was reported in Boggan et al. (2008) from a unicate collection by Alexander Hirtz from the northern province of Esmeraldas. The collection by Hirtz (*A. Hirtz 3629* - SEL) could not be located or verified and is therefore not included in the distribution map (Fig. 1).

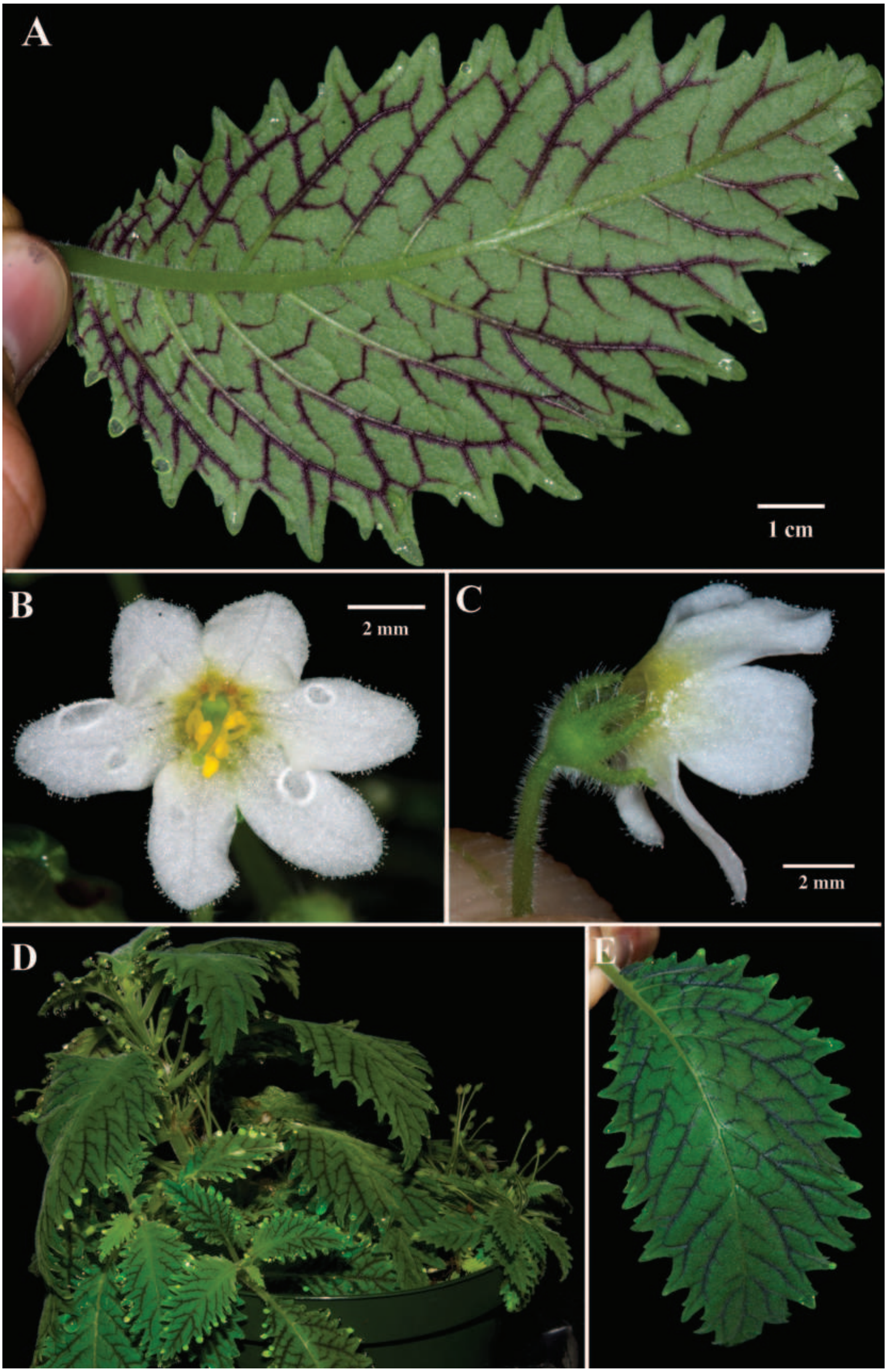

Figure 3. *Amalophyllon clarkii* Boggan & L.E.Skog **A** abaxial view of leaf **B** front view of flower **C** lateral view of flower **D** erect habit featuring evenly spaced and rosette-forming leaves **E** adaxial view of leaf. (**A–E** from *J.L. Clark 13101*). Photos by J.L. Clark.

Additional specimen examined. Ecuador. Santo Domingo de los Tsáchilas: cantón Santo Domingo, parroquia Polanco, sector Bolo Alto, Bosques y Cascadas Las Rocas, propiedad de Eduardo Díaz, near waterfall of the Bolo watershed, 0°28'38.1"S, 79°11'22.4"W, 560–600 m alt., 19 Mar 2022, *J.L. Clark, L. Hooge, C. Restrepo-Villarroel, R. Clark & E. Muñoz 16805* (MO, NY, QCA, SEL, US).

Acknowledgments

We thank the Ministry of the Environment of Ecuador for providing specimen collection and transportation permits (Research permit Aves y Conservación N° 007-2018-IC-FLO-FAU and mobilization permit Aves y Conservación 005-FLO-2019-DPAP-MA). We are grateful to Alejandro Tobos for generating the distribution map (Fig. 1). We thank Jeanne Katzenstein, Laurence E. Skog, Álvaro J. Pérez, and an anonymous reviewer for providing valuable feedback on an earlier version of the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

We are indebted to the following institutions for their valuable support of this work: Fundación de Conservación Jocotoco, the Jardín Botánico Padre Julio Marrero at the Pontificia Universidad Católica del Ecuador-Santo Domingo, QCA Herbarium at the Pontificia Universidad Católica del Ecuador-Quito, and Ecuador's National Biodiversity Institute and National Herbarium (QCNE). We thank Eduardo Díaz and Paul Henry for their generous hospitality in the field. We thank the Field Museum's Keller Science Action Center for providing financial support for this publication. Additional funding for research on the flora of Centinela was supplied by the Field Museum's Grainger Bioinformatics Center and Women's Board, the Harvard University Herbaria, the Mohammed Bin Zayed Species Conservation Fund, the Universidad de Las Américas, The Walder Foundation, Lawrenceville School's Hutchins Scholars in Science Research Program, Marie Selby Botanical Gardens, and The Winnetka Garden Club.

Author contributions

All authors participated in field expeditions in western Ecuador and wrote the manuscript.

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Data availability

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

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PhytoKeys 242: 317–332 (2024)
DOI: 10.3897/phytokeys.242.122824

Research Article

A missing piece is found: a new species of *Paepalanthus* (Poales, Eriocaulaceae) and the puzzling relations of the campos rupestres mountaintop floras of eastern Minas Gerais, Brazil

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Abstract

Paepalanthus is a diverse genus characteristic of the campos rupestres, a megadiverse vegetation found on mountaintops of mainly quartzitic mountain ranges of central-eastern Brazil. Recent efforts on prospecting the biodiversity of Serra do Padre Ângelo, a small mountain complex in eastern Minas Gerais, yielded several new plant and animal species, highlighting the urgency of conservation actions towards this still unprotected area. Here, we describe yet another new species found in the campos rupestres of these mountains, *Paepalanthus magnus*, a mountaintop microendemic species morphologically similar to taxa found in the Espinhaço Range, over 200 km distant, a biogeographic pattern shared by several other species. The affinities of the new species are discussed, and we provide illustrations, photographs, and SEM photomicrographs of the seed. We also discuss the conservation status of the species, which is preliminarily assessed as Critically Endangered, reinforcing the urgent need to address the conservation of the unique biodiversity of Serra do Padre Ângelo.

Resumo

Paepalanthus é um gênero característico dos campos rupestres, uma vegetação megadiversa encontrada no topo de montanhas de cadeias montanhosas, principalmente quartzíticas, do centro-leste do Brasil. Esforços recentes de inventariar a biodiversidade da Serra do Padre Ângelo, um pequeno complexo montanhoso no leste de Minas Gerais, resultaram na descoberta de várias novas espécies de plantas e animais, destacando a urgência de ações de conservação para esta área ainda não protegida. Aqui, descrevemos mais uma nova espécie encontrada nos campos rupestres dessas montanhas, *Paepalanthus magnus*, uma espécie microendêmica, morfologicamente semelhante a táxons encontrados na Serra do Espinhaço, a mais de 200 km de distância, um padrão biogeográfico repetido por várias outras espécies. As afinidades da nova espécie são discutidas e fornecemos ilustrações, fotografias da planta e de microscopia eletrônica de varredura (MEV) da semente. Também discutimos o status de conservação da espécie, que é preliminarmente avaliada como Criticamente Em Perigo, reforçando a necessidade urgente de abordar a conservação da biodiversidade única da Serra do Padre Ângelo.

Academic editor: Leonardo Versieux
Received: 13 March 2024
Accepted: 8 May 2024
Published: 11 June 2024

Citation: Rocha LH, Gonella PM, Oliveira Andrino C (2024) A missing piece is found: a new species of *Paepalanthus* (Poales, Eriocaulaceae) and the puzzling relations of the campos rupestres mountaintop floras of eastern Minas Gerais, Brazil. PhytoKeys 242: 317–332. https://doi.org/10.3897/phytokeys.242.122824

Key words: Atlantic Forest, endemism, João Pinto Formation, Serra do Padre Ângelo, threatened species

Palavras-chave: Espécie ameaçada, endemismo, Formação João Pinto, Mata Atlântica, Serra do Padre Ângelo

Introduction

Eriocaulaceae Martinov is a monocotyledon family belonging to the Poales (APG IV 2016), which comprises around 1400 species divided into 18 genera (Giulietti et al. 2012; Andrino et al. 2023; Sano et al. 2024) and two subfamilies: Eriocauloideae Ruhland and Paepalanthoideae Ruhland (Ruhland 1903). It has a pantropical distribution, but an important center of diversity is found in the campos rupestres of east Brazil, especially in the Espinhaço Range (ER), where the family represents around 10% of the diversity of vascular plants, with an endemism rate of 85% (Costa et al. 2008, 2018). *Paepalanthus* Mart. is the most representative genus of the family in the campos rupestres (Giulietti et al 1997), however, its traditional circumscription, which once included more than 400 species (Ruhland 1903), no longer adequately represents the diversity of the genus. It was found to be polyphyletic and lacked diagnostic characters, prompting a recent proposal for a new classification by Andrino et al. (2023). In this new classification, *Paepalanthus* is delimited as a monophyletic genus comprising 256 species, and the remaining species were segregated into eight new genera, in addition to *Actinocephalus* (Körn.) Sano, *Tonina* Aubl., and *Lachnocaulon* Kunth, previously nested within *Paepalanthus* (Andrino et al. 2023). According to the new circumscription, *Paepalanthus* is characterized by having trimerous and isostemonous flowers, the pistillate flowers with free petals and free stigmatic branches, and the seed coat presenting rectangular or narrow hexagonal cells with appendices with truncate apex or with a “T” form along the periclinal walls, and lacking micropapillae (Andrino et al. 2023).

Although re-circumscribed, *Paepalanthus* remains one of the most speciose genera of Eriocaulaceae, with an elevated rate of microendemic species exclusive to a single mountaintop, with around 82% of the ca. 200 species that occur in the Espinhaço Range being endemic to its campos rupestres (Costa et al. 2008). Such endemism is a combination of various factors, including the fragmented landscapes of the Espinhaço Range (ER) and other quartzitic massifs, isolating plant populations among areas of complex topography characterized by dystrophic soils. Moreover, past climate fluctuations and the reduced dispersal capacity of species have also played crucial roles in this process contributing to speciation, resulting in the emergence of new species that are isolated on mountaintops (Vasconcelos et al. 2020).

Recently, species of Eriocaulaceae were identified in small quartzitic mountains in the Doce River basin, located around 200 km east of the Espinhaço Range. First, it was a new species of *Paepalanthus*, *P. oreodoxus* Andrino & Gonella, belonging to *P.* subgen. *Xeractis* (Körn.) Hensold, a lineage considered restricted to the ER and surrounding areas, but which “escaped” to these mountains further east (Andrino and Gonella 2021). More recently, a species known only from the holotype collected in the ER, *Paepalanthus minimus* Silveira, was rediscovered in these mountains and was combined into the genus *Giuliettia* due to its morphological characteristics (Andrino et al. 2024). These discoveries add to many other taxonomic novelties that have been described for the mountains of the medium Doce River basin in the last decade, many of them reflecting similar patterns of disjunction with the ER (Gonella et al. 2015, 2021; Siniscalchi et al. 2016; Mello-Silva 2018; Loeuille et al. 2019; Antar et al. 2021; Kollmann and Gonella 2021).

These mountains of the medium Doce River basin make up the João Pinto Geological Formation (Oliveira 2000), a set of outcrops of quartzitic rocks that form small mountains immersed in a matrix of seasonal forests of the Atlantic Forest domain, now severely transformed into pastures and plantations (Gonella et al. 2015). The quartzitic outcrops, particularly those above 800 meters, prominently feature campos rupestres, a vegetation that remains inadequately researched and protected in the region. Among these areas, Serra do Padre Ângelo deserves special attention, as most of the discoveries made in the region come from this complex of mountains south of the municipality of Conselheiro Pena. During the development of the project "Flora da Serra do Padre Ângelo", an unidentified species of *Paepalanthus* was collected at one of the highest points of this mountain range, the Pico do Pinhão. After detailed studies, this species is described here as new and its affinities are discussed, along with data on its conservation status, reinforcing the urgency of taking action to protect the Serra do Padre Ângelo.

Material and methods

The authors undertook fieldwork and collection efforts during an expedition in April 2022, during which the species was studied in its natural habitat and collected following traditional herborization techniques (Mori et al. 1985). Specimens were deposited at UB, MBML (paratype), and SPF (acronym according to Thiers 2024, continuously updated). Additional expeditions were conducted to locate the species on other isolated peaks within the type locality in October 2022 and February 2023, albeit without success. Subsequent investigations and consultations of materials deposited in herbaria (Reflora 2024; SpeciesLink 2024) yielded no previous collections of this species. The collected material underwent analysis using a stereomicroscope, considering both reproductive and vegetative characters according to specific terminology for describing Eriocaulaceae (Andrino et al. 2015; Andrino et al. 2023).

Conservation risk assessment was conducted following the criteria outlined by the International Union for Conservation of Nature (IUCN 2012). The distribution and occurrence map of the species and its related taxa were generated using QGIS software (QGIS Software Team 2024), employing layers provided by the Brazilian Institute of Geography and Statistics (IBGE 2024) and MapBiomas (2024). The coordinates of the new species, collected via GPS at the type locality, were used alongside the coordinates of related species obtained from data available in herbaria and virtual databases (JSTOR 2024; Reflora 2024; SpeciesLink 2024).

For the Scanning Electron Microscopy (SEM) analysis, seeds were retrieved from the selected holotype (*P.M. Gonella et al. 3402*). Seeds were immersed in water to facilitate the removal of fruit remnants, dried, and affixed onto stubs.

They underwent gold coating using a Leica SCD 500 sputter coater. Subsequently, the specimens were examined and photographed using a scanning electron microscope JEOL-JSM-7001F.

Results

Taxonomic treatment

Paepalanthus magnus **L.H.Rocha, Gonella & Andrino, sp. nov.**
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Fig. 1–5

Type. Brazil. Minas Gerais: Conselheiro Pena, Serra do Padre Ângelo, Serra do Pinhão, Pico do Pinhão, 19°15'21"S, 41°34'57.24"W, 1500 m elev., fl. & fr., 18 Apr 2022, *P.M. Gonella, L.H. Rocha, D.R. Couto, D.P. Cordeiro & E.C. Ribeiro 3402* (holotype: UB; isotype: SPF).

Diagnosis. The new species is most similar to *Paepalanthus regelianus* Körn., with which it shares the pilose abaxial surface of the leaves. However, *P. regelianus* presents scapes that are about twice as long as the leaves and tomentose (*vs*. scapes at least 3 times longer than the leaves, and glabrous in *P. magnus*) and involucral bracts with a glabrous abaxial surface and ciliated margin (*vs*. pilose in *P. magnus*). Furthermore, the spathes of *P. regelianus* are shorter than its leaves, approximately half as long as the leaves (*vs*. spathes about as long as the leaves), present uniformly distributed trichomes (*vs*. along longitudinal nerves), and possess a short opening, no longer than 1 cm long (*vs*. opening distinctly longer, 2.5–6.0 cm long).

Description. Terricolous or rupicolous perennial ***herb***, 55.0–94.5 cm high. *Roots* fibrous. ***Caudex*** present. ***Stem*** aerial, elongate, erect, thick, surrounded by marcescent leaves, 6.5–35.0 cm long. ***Leaves*** rosulate, 14.3–27.0 × 0.4–1.6 cm, linear-lanceolate, green, abaxial surface with trichomes ca. 4 mm long along the marked nerves, adaxial surface smooth and glabrous, margins ciliate, apex acute, mucronate. ***Inflorescences*** solitary per subtending leaf, axillary. ***Spathes*** 13.0–24.0 cm long, chartaceous, cylindrical, closed, abaxial surface pilose along the marked nerves (striate), adaxial (internal) surface glabrous, obliquely opened, opening 2.5–6.0 cm long, margin ciliate, apex acuminate. ***Scapes*** 50.0–89.0 cm long, 1–21 per plant (rosette), 5-costate, erect, glabrous, green to golden, free. ***Capitula*** 5.0–15.0 mm diam., white. ***Involucral bracts*** in 7–9 series, ca. 1.7–3.8 × 1.3–2.1 mm, ovate, castaneous, margin ciliate, abaxially pubescent, shorter than the flowers. ***Floral bracts*** ca. 3.5 mm long, linear-lanceolate, pigmented, densely pilose in the apical half with uniseriate trichomes ca. 2 mm long, margin ciliate. ***Flowers*** 3-merous, diclinous, arranged in concentric circles without clear organization. ***Staminate flowers*** ca. 3.5 mm long; pedicels ca. 1 mm long, pilose, with trichomes 2–2.5 mm long; sepals ca. 2.5–3 × 1 mm, oblanceolate, united in the base to up to 1/3 of length, castaneous with pigmentation concentrated in the center and becoming more translucent towards the margins, abaxial surface densely pilose in the apical 2/3, trichomes reducing in size towards the apex, adaxial surface glabrous, margin ciliate, apex acuminate; corolla tubular, ca. 2.5 mm long, free lobes ca. 0.3 mm long, entirely glabrous, hyaline; stamens epipetalous, filament ca. 1.5 mm long, anther dorsi-

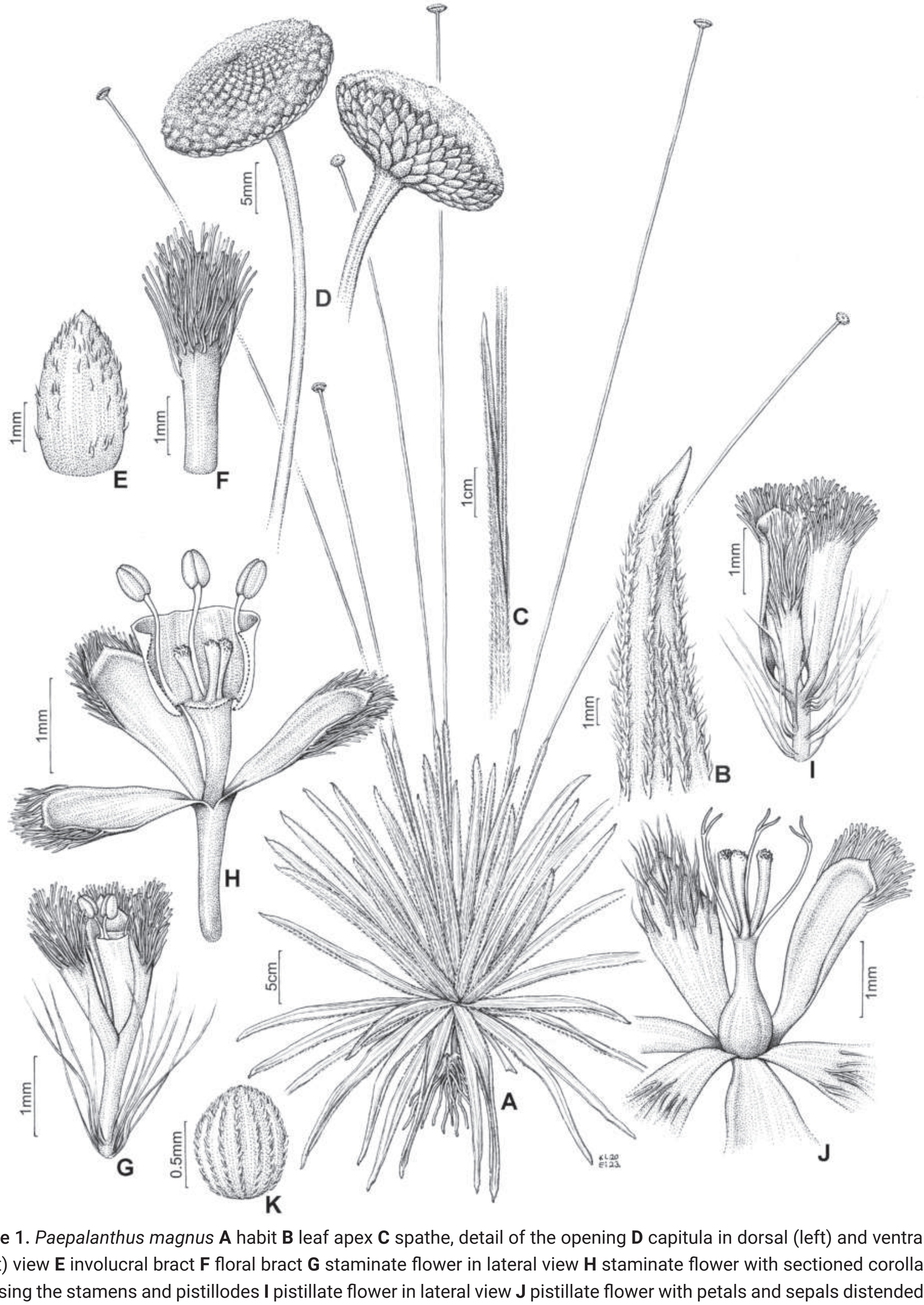

Figure 1. *Paepalanthus magnus* **A** habit **B** leaf apex **C** spathe, detail of the opening **D** capitula in dorsal (left) and ventral (right) view **E** involucral bract **F** floral bract **G** staminate flower in lateral view **H** staminate flower with sectioned corolla, exposing the stamens and pistillodes **I** pistillate flower in lateral view **J** pistillate flower with petals and sepals distended, exposing the gynoecium **K** seed with numerous appendices along the periclinal walls. Illustration by Klei Souza based on the holotype (*P.M. Gonella et al. 3402*).

Figure 2. *Paepalanthus magnus* **A** habitat at Pico do Pinhão, with the Pico da Bela Adormecida (Pico do Padre Ângelo) in the background **B** habit among grasses and quartzitic rocks **C** rosette in detail **D** leaves, showing ciliate margin and striate abaxial surface **E** the base of the leaves, showing the adaxial surface and a scape enclosed by a spathe emerging from a leaf axil **F** spathe opening **G** capitulum in posterior view evidencing the involucral bracts **H** capitulum, lateral view **I** capitulum, frontal view. **A** by Lucian Medeiros **B–I** by PMG.

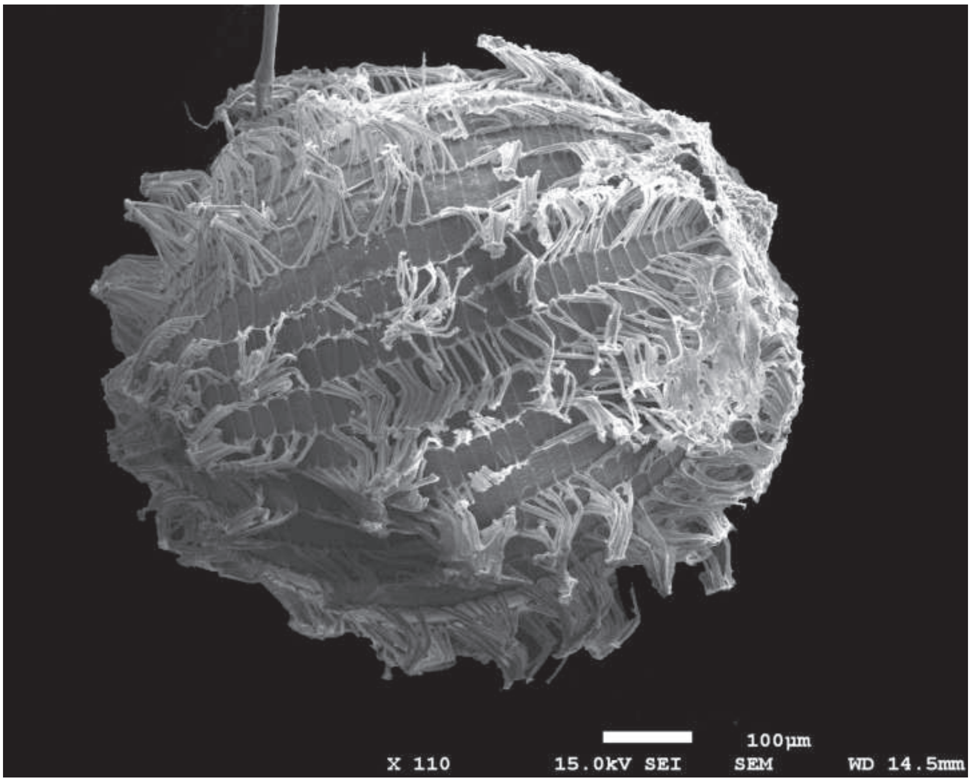

Figure 3. *Paepalanthus magnus*. SEM micrograph of the seed coat (from the holotype, *P.M. Gonella et al. 3402*).

fixed, ca. 0.3 mm long; pistillodes papillose, ca. 1 mm long. ***Pistillate flowers*** ca. 4.5 mm long; pedicel ca. 0.5 mm long, densely pilose with long trichomes; sepals ca. 3.5 mm long, oblong, united only at the very base, castaneous with apex more strongly pigmented, adaxial surface glabrous, abaxial surface with apex slightly pilose, margin ciliate, apex acuminate-truncate; petals ca. 3 mm long, hyaline, base slightly pigmented, narrow obovate, free, adaxial surface pilose, abaxial surface glabrous, margin ciliate, apex acute; gynoecium with stigmatic and nectariferous branches emerging at the same height in the column, stigmatic branches ca. 1 mm long, apex bifid, nectariferous branches ca. 0.7 mm long, apex papillose, ovary ca. 1 mm diam, ovoid; *Seed* ca. 0.76 × 0.60 mm ovoid to ellipsoid, reddish, hilum acute, micropile obtuse, with numerous appendices with truncate apex along the periclinal walls.

Etymology. The epithet “magnus” derives from the Latin “great”, “large”. This epithet was selected to denote the characteristic of the species being large in size, contrasting with the majority of Eriocaulaceae species found in the region where it occurs but also a reference to its larger size compared to its putative closest taxa.

Distribution and habitat. *Paepalanthus magnus* is a microendemic species, found only at the top plateau of Pico do Pinhão (1540 m a.s.l.), one of the highest peaks of Serra do Padre Ângelo, a mountain complex located in the municipality of Conselheiro Pena, eastern Minas Gerais, southeastern Brazil (Fig. 4). The species was found at elevations above 1500 m a.s.l., forming a population of no more than 100 individuals growing directly on sandy soil among grasses or between large blocks of quartzitic rock, exposed to direct sunlight, in campos rupestres vegetation (Fig. 2A, B).

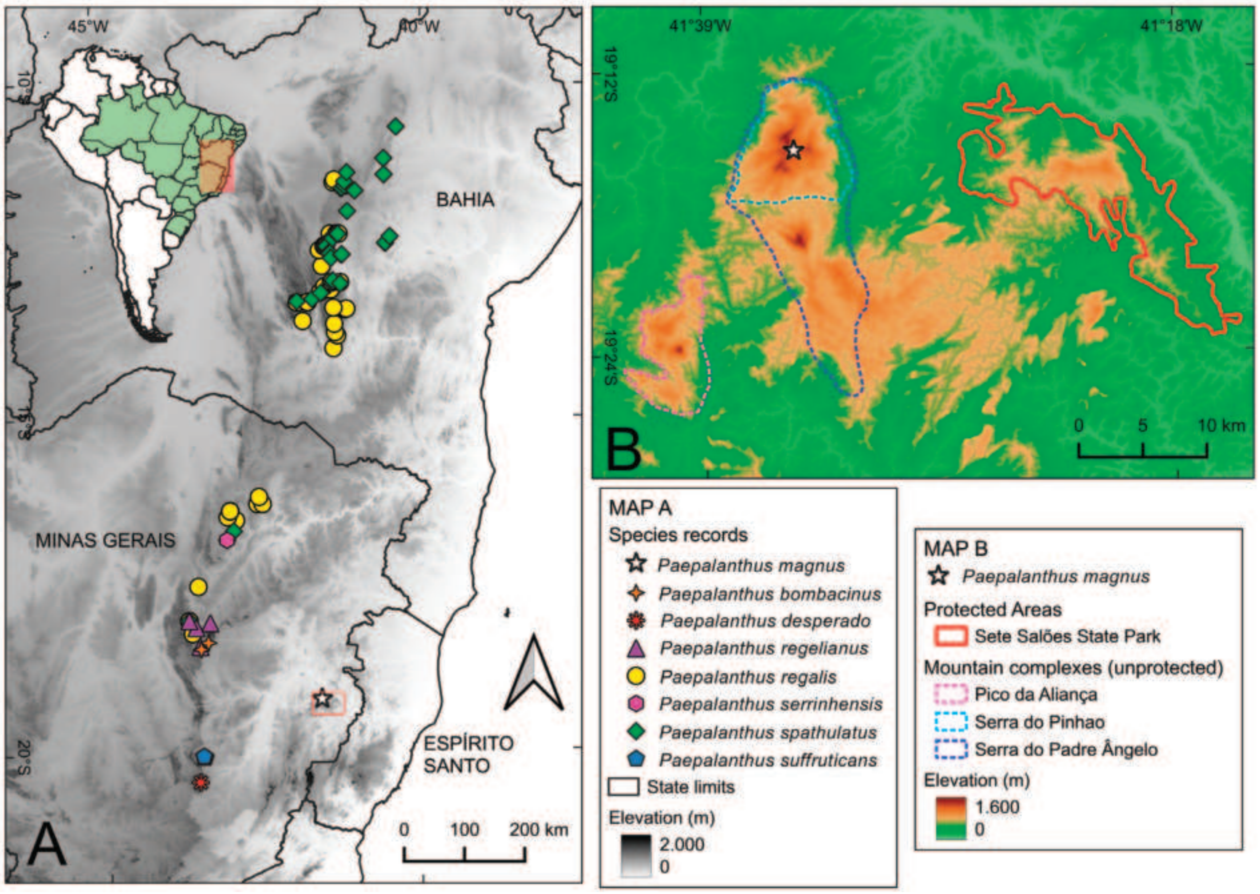

Figure 4. Distribution maps **A** distribution map of the new species and compared taxa cited in the text **B** distribution map of *P. magnus* at Serra do Padre Ângelo region, with other landmarks of the region indicated.

Pico do Pinhão is part of the northern massif of SPA, the Serra do Pinhão, whose culminating point is Pico do Sossego (1605 m), to the northwest of Pico do Pinhão. Expeditions to the former failed to find new populations of the species, which were also not found in the other higher peaks of the region, such as Pico da Bela Adormecida (also known as Padre Ângelo; 1550 m) and Pico da Aliança (1430 m), reinforcing the microendemic character of the species. At Pico do Pinhão, the campos rupestres are found at elevations above 1300 m. They are surrounded by a matrix of the Montane Seasonal Forest, which harbors the last individuals of the northernmost population of the endangered gymnosperm *Araucaria angustifolia* (Bertol.) Kuntze (Moura 1975), locally known as "pinhão" hence the name of the Serra. Such forest matrix, however, is severely degraded and is still subject to fires for land clearing and pasture formation (Fig. 5), as well as by the presence of cattle. The surrounding area is also severely invaded by alien species, especially the fern *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae) and molasses grass *Melinis minutiflora* P. Beauv. (Poaceae).

Phenology. Specimens were collected with flowers and fruits in April, which is by the end of the rainy season. The presence of old inflorescences with viable fruits, however, suggests that the flowering may occur since the beginning of the rainy season, which in the region starts in October/November.

Conservation status. Preliminarily assessed as Critically Endangered – CR B1ab(iii) + B2ab(iii). The species is known from a single location in an area that

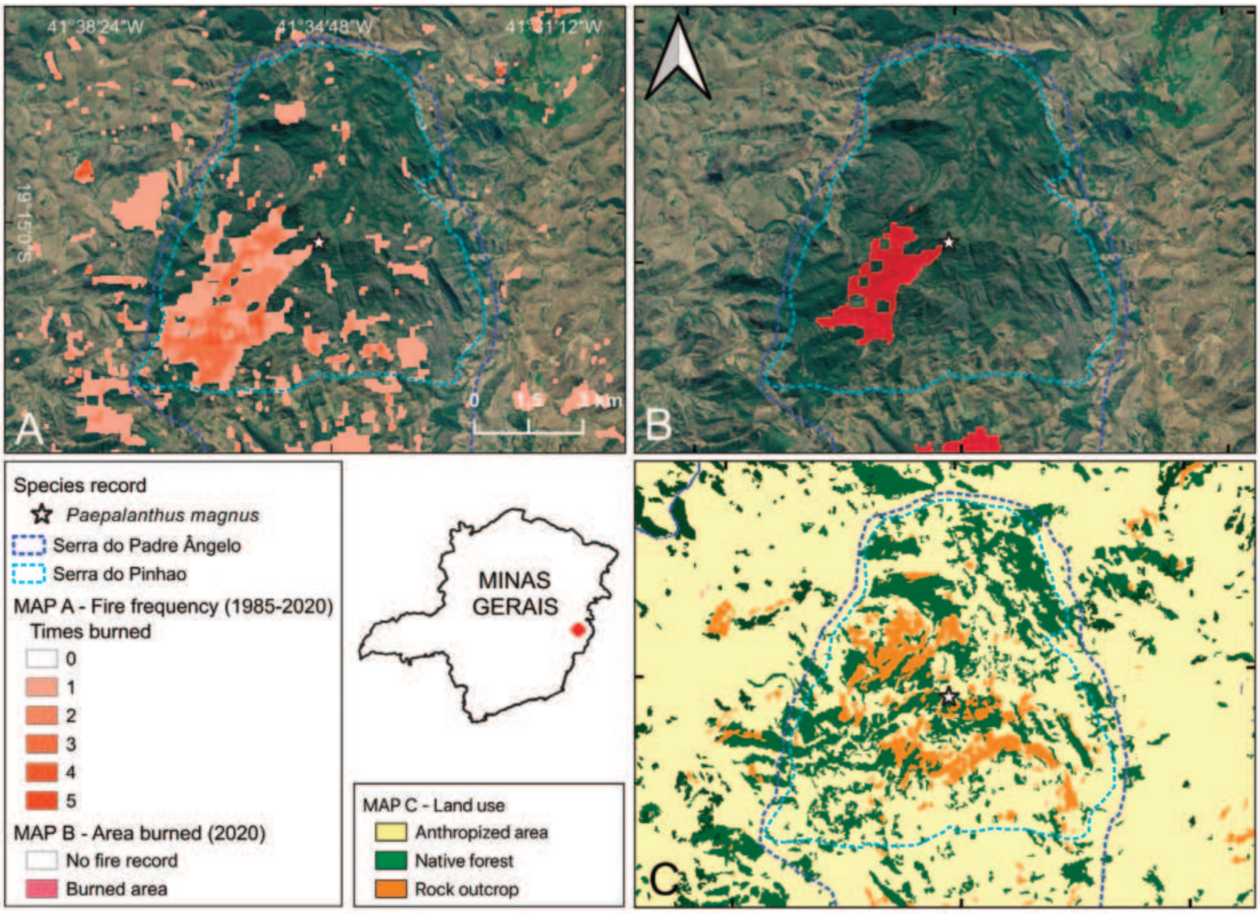

Figure 5. Conservation threats to *Paepalanthus magnus* **A** 35-year fire record (1985–2020) in the region of Serra do Pinhão, part of Serra do Padre Ângelo **B** fire record in the year 2020 **C** land use of the region. Data on fire and land use from MapBiomas (2024). **A**, **B** Map data ©2024 Google.

is not protected, and which is subject to several ongoing threats to the quality of the habitat, such as deforestation, the presence of cattle, recurrent use of fires, and the presence of invasive species. Furthermore, species restricted to mountaintop habitats are especially vulnerable to the effects of climate change, especially intense droughts that may cause increased mortality (already observed in other taxa in the region) or intense rainfalls, which may cause landslides (already reported in the SPA following intense rainfall in the 2021/2022 rainy season). Arson fires are especially recurrent in the southwest of Serra do Pinhão (Fig. 5A) and are used by local farmers to renovate pastures and clear land for coffee and *Eucalyptus* plantations. These fires, however, often escape to native vegetation, causing the observed reduction of forest remnants and the intensification of invasion by the aforementioned alien species. The last of these intense fire events was in 2020 (Fig. 5B), also the year of another intense fire affecting the Pico da Bela Adormecida and its species (Andrino and Gonella 2021; Gonella et al. 2022; Andrino et al. 2024).

Since the species is known from a single location, it has an estimated AOO of 4 km^2, and it does not have an associated EOO polygon, which, combined with the small population size and the listed ongoing threats, allow us to project a continuing decline in the quality of the habitat. Therefore, we suggest that the species should be declared Critically Endangered under the IUCN (2012) criteria. This preliminary assessment will be submitted to the Brazilian Flora authority of the IUCN Red List, coordinated by Centro Nacional de Conservação da Flora (CNCFlora), for validation.

Additional specimen examined (paratype). Brazil. Minas Gerais: Conselheiro Pena, Serra do Padre Ângelo, complexo Serra do Pinhão, Pico do Pinhão, 18 Apr 2022, *D.R. Couto, P.M. Gonella, D.P. Cordeiro & L.H. Rocha-Pinto 6286* (MBML).

Discussion

Paepalanthus magnus unquestionably falls under the classification of *Paepalanthus* sensu Andrino et al. (2023). Its distinct seed coat morphology is characterized by rectangular or narrow hexagonal cells adorned with appendices exhibiting either a truncate apex or a “T” shape, devoid of micropapillae along the periclinal walls (Fig. 3). This unique feature set offers a robust foundation for the unequivocal placement of the species. Other distinctive characteristics include a habit featuring basal rosettes devoid of any reproductive or elongated axis (Fig. 1A, 2C), trimerous flowers with gamopetalous staminate flowers, and dialipetalous pistillate flowers. Additionally, its gynoecium exhibits free appendices, all releasing at the same level within the gynoecium (Fig. 1J). Its placement is also supported by the characteristic geographic distribution of the genus, centered in the campos rupestres of NE and SE Brazil (Andrino et al. 2023).

Based on the morphological features presented here, we suggest that *P. magnus* likely belongs to a lineage of species primarily distributed in the Chapada Diamantina, Bahia state (referred to as clade Q in Andrino et al. 2021). This lineage spans along the ER from the Chapada Diamantina to the northern region of the adjacent state of Minas Gerais (Fig. 4A), where some species are found in the biogeographic district of Grão Mogol and also on the Diamantina Plateau district (districts according to Colli-Silva et al. 2019). This lineage comprises species with a robust habit, often presenting a caudex, basal rosettes, and numerous long scapes emerging from leaf axils. The newly described species from Serra do Padre Ângelo likely aligns with this lineage based on morphological resemblance, although its placement needs to be properly tested.

Other species belonging to this lineage and likely closely related to *P. magnus* are *P. bombacinus* Silveira, *P. regelianus*, *P. regalis* Mart. ex Körn., *P. spathulatus* Körn., and *P. serrinhensis* Silveira. The comparison of *P. magnus* with these taxa, however, reveals unique morphological characteristics that make it a distinct addition to the diversity of the *Paepalanthus* genus in the region. The leaves and spathes with pilosity restricted to the veins (striate), the spathe as long as the leaves with long oblique opening, combined with glabrous green to golden scapes, and the capitula with bracts in more than seven series, are characteristics not shared by other species in this group, thus being important diagnostic features (Table 1). Furthermore, the observation of tufts of golden trichomes at the base of the leaves and on the sepals of staminate and pistillate flowers are characteristics that provide additional diagnostic information, a striking feature of the species that is also present in putative closely related species, such as *P. regelianus*.

Besides the aforementioned unique features of *P. magnus* in comparison with the putative closely related species, these taxa can be distinguished by their unique features: *P. bombacinus* can be recognized by its involucral bracts

Table 1. Diagnostic characters of the new species and the most similar taxa. Measurements of similar species were taken from herbarium specimens and literature (Andrino et al. 2015; Sano et al. 2010; Echternacht et al. 2021).

Character/Species	*P. magnus*	*P. bombacinus*	*P. regalis*	*P. regelianus*	*P. serrinhensis*	*P. spathulatus*
Stem	Elongate, 6.5–35.0 cm long	Restricted to the rosette	Restricted to the rosette	Restricted to the rosette	Restricted to the rosette to elongate, 12.0–17.0 cm long	Elongate, 4–10 cm
Leaf length	14.3–27.0 cm	14–24 cm	24.0–41.5 cm	15–26 cm	10.4–19.1 cm	9–32 cm
Leaf indumentum	Adaxial surface glabrous, abaxial surface pilose along conspicuous longitudinal nerves (striate)	Both surfaces glabrescent to pubescent	Glabrous on both surfaces	Adaxial surface glabrous to glabrescent, abaxial surface uniformly pilose	Glabrous to glabrescent on both surfaces	Glabrous
Spathe length	13–18 cm	11–15 cm	7.4–30.0 cm	8–13 cm	5.5–6.7 cm	4.5–6.5 cm
Spathe indumentum	Pilose along longitudinal nerves (striate)	Pilose along longitudinal nerves (striate)	Glabrous	Uniformly pilose	Glabrous	Glabrous
Spathe opening	25–60 mm long	15 mm long	40 mm long	10 mm long	15 mm long	4.5–8.0 mm long
Scape length	50–89 cm	45–50 cm	18–62 cm	36–45 cm	17–32 cm	18–29 cm
Scape indumentum	Glabrous	Tomentose	Glabrous	Tomentose	Glabrous to sparsely pilose	Glabrous
Involucral bracts number of series and shape	7–9 series, ovate, shorter than the flowers	4–6 series, narrowly ovate to deltoid, shorter than the flowers	7 series, deltoid, shorter than the flowers	4–5 series, triangular, shorter than the flowers	Up to 4 series, ovate, shorter than the flowers	3–4 series, lanceolate, surpassing the height of the flowers
Involucral bracts abaxial indumentum	Pubescent	Lanuginose	Glabrous	Pubescent	Pubescent to glabrescent	Glabrous

that are densely tomentose (lanuginose) abaxially; *P. regelianus* (including the synonym *P. coronarius* Silveira; Andrino et al. 2022) is distinctive in having densely pilose scapes; *P. regalis* is not to be confused by its glabrous leaves, spathes, and scapes, as well as by its unique laterally flattened capitula; *P. serrinhensis* presents a slender habit, glabrous leaves and small capitula with ovate involucral bracts; and *P. spathulatus* presents spatulate glabrous leaves and distinctive lanceolate bracts with an acute apex that surpass the length of the flowers (see Table 1 for further distinctive characters).

Among the specimens of *P. regelianus* studied for this work, there was a specimen (*Irwin 27519*) with many duplicates spread in different herbaria with different identifications, including *P. regalis* (at K), *P. bombacinus* (F), and *P. desperado* Ruhland (NY, US). *Paepalanthus desperado* is a remarkable species known only from the type and a few recent collections, all from around Lavras Novas (district of Ouro Preto, in the Iron Quadrangle; Fig. 4A). This species bears similar spathes with the new species, which are as long as the leaves, present trichomes disposed on longitudinal ridges, and a large oblique opening. *Paepalanthus desperado*, however, is a slenderer species, with a more delicate elongate stem, narrower and more delicate leaves, and less robust capitula with fewer series of involucral bracts. Such species appears to be closely related to another more delicate species, *P. suffruticans* Ruhland, microendemic to the Serra do Caraça, also in the Iron Quadrangle (Fig. 4A). Based on general morphology, we hypothesize that these species might not be closely related to the new species or the group to which it belongs, but molecular phylogenetic studies could better test this hypothesis.

The discovery of *Paepalanthus magnus* in the Serra do Padre Ângelo reinforces a pattern observed in other mountainous regions, such as the Espinhaço Range. In these high-altitude environments, many species of Eriocaulaceae are microendemic, often exclusive to a single mountaintop (Costa et al. 2023). This distribution pattern can be explained by the fragmentation of landscapes, which isolate lineages in areas of high topography with dystrophic soils, fostering speciation (Vasconcelos et al. 2020). Analyzing the pattern of microendemism on mountaintops in the Serra do Padre Ângelo may provide additional insights into the evolution of plants in the region, as this pattern is repeated in other campo rupestre lineages from different angiosperm families, such as Asteraceae, Begoniaceae, Bromeliaceae, and Droseraceae, among others.

While species closely related to *P. magnus* are restricted to the northern ER (Fig. 4A; Andrino et al. 2021), other Eriocaulaceae species from SPA have a closer connection with the southern ER, such as the Iron Quadrangle (Andrino and Gonella 2021) or the Diamantina Plateau (Andrino et al. 2024). This pattern of geographic disjunction is intriguing and suggests the possibility of a myriad of historical events and environmental factors influencing the distribution of these species. This discovery contributes a piece to the intricate puzzle of the flora in the easternmost campos rupestres of Minas Gerais, where a diverse assembly of species with distinct biogeographic histories converge. While this finding enriches our understanding, it's important to note that it is just one part of the larger puzzle. Future research, such as genetic and biogeographic studies, may properly test this hypothesis and provide a deeper understanding of the phylogenetic relationships within clade Q of *Paepalanthus* and the evolution of Eriocaulaceae in the northern Espinhaço and disjunct campos rupestres areas, such as the João Pinto Formation.

The discovery of yet another new and potentially threatened species in the quartzitic mountains of the João Pinto Formation reinforces the recognition of this area as an endemism center of the campos rupestres flora, as more than 30 new species have been described in the last decade (see Leme et al. 2023 and references therein). However, the situation of these species must be viewed with concern, particularly regarding their conservation. These mountains are only protected by a single State Park (Parque Estadual de Sete Salões), which does not encompass any of the highest peaks of the region (Fig. 4B). Instead, these peaks are situated in unprotected public lands surrounded by small farmlands, and criminal and uncontrolled arson fires continue to threaten native species and exacerbate the invasion by alien species. Urgent action is needed to establish a conservation strategy for these higher areas, with a proposition for the creation of a protected area in the Serra do Padre Ângelo currently under discussion through the Territorial Action Plan "Capixaba-Gerais" ("PAT Capixaba-Gerais"). The success of any conservation effort, however, relies on the active involvement of local and regional administrations and the engagement of local communities to ensure the long-term preservation of this region and its unique biodiversity.

Acknowledgments

The authors are grateful to Ednilson Caetano Ribeiro, resident of the SPA, who guided us to the Pico do Pinhão; to Júlio César Ribeiro and Lucian Medeiros for additional information about the species and for allowing us to use a photo in this work (Lucian); to Dayvid Couto and Danilo Cordeiro for the company and support during fieldwork; to Ingrid Gracielle Martins da Silva and the Microscopy and Microanalysis Laboratory of the Institute of Biological Sciences of the University of Brasilia (LMM-UnB) for the electron microscopy photos; to Rafael Gomes Barbosa-Silva for photo plates; to Klei Souza for the line drawings; to Instituto Nacional da Mata Atlântica (INMA) for the logistic support pre- and post-expedition; and to the editor, Leonardo Versieux, and to Fabiane Nepomuceno Costa and an anonymous reviewer for their contributions to improve the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

Fieldwork was undertaken with the support of The Mohamed bin Zayed Species Conservation Fund (project 212527281) and GEF Pró-Espécies; we also thank the financial support of WWF-Brasil for publications related to the territory of the PAT Capixaba-Gerais. LHR received research fellowships from FAPEMIG (grant APQ-00653-21) and Universidade Federal de São João del-Rei/Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). PMG offers thanks to Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG—grant APQ-00653-21), and IDEA WILD for research equipment.

Author contributions

Writing – Original draft: LHR; Writing – Review and Editing, Investigation: all authors; Visualization: PMG; Supervision, Funding Acquisition: PMG and COA.

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Data availability

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

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PhytoKeys

PhytoKeys 242: 333–348 (2024)
DOI: 10.3897/phytokeys.242.122407

Research Article

Molecular, morphological, and morphometric evidence reveal a new, critically endangered rattlepod (*Crotalaria*, Fabaceae/Leguminosae, Papilionoideae) from tropical China

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Abstract

Here, we describe a new species of *Crotalaria* L. discovered in Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan, China. The new species, *Crotalaria menglaensis* S.A.Rather, was confirmed by identifying diagnostic morphological characteristics, performing principal component analyses of phenotypic traits, and phylogenetic analyses based on nuclear ITS and plastid *mat*K sequences. Phylogenetic analyses recovered the two accessions of the new species to be sister to *C. bracteata* Roxb. ex DC. In turn, these two species formed the sister clade to the two accessions of *C. incana* L. The morphometric analyses revealed that all three species were distinct, while the analyses of distinctive characters enabled unambiguous distinction of the new species by its growth habit, leaflets, flower structure and pod morphology. In contrast to the two related species, the new species is currently known only from *ca*. 100 mature individuals. Thus, this species is considered to be critically endangered.

Key words: Biodiversity, conservation, *Crotalaria*, endemism, Leguminosae, Xishuangbanna

OPEN ACCESS

Academic editor: Stephen Boatwright
Received: 6 March 2024
Accepted: 30 April 2024
Published: 11 June 2024

Citation: Rather SA, Radbouchoom S, Wang K, Xiao Y, Liu H, Schneider H (2024) Molecular, morphological, and morphometric evidence reveal a new, critically endangered rattlepod (*Crotalaria*, Fabaceae/Leguminosae, Papilionoideae) from tropical China. PhytoKeys 242: 333–348. https://doi.org/10.3897/phytokeys.242.122407

Introduction

Xishuangbanna, located in the most southwestern part of Yunnan Province and sharing borders with Myanmar and Laos, is well recognized for its rich biodiversity. Its tropical forests play a vital role in global terrestrial biodiversity conservation efforts (Feng et al. 2018). Unfortunately, many plants in Xishuangbanna have recently faced significant threats from deforestation and the establishment of artificial plantations, especially rubber plantations (Brinck et al. 2017; Liu et al. 2017; Yang et al. 2021; Yang et al. 2023). To enable effective protection of the unique and rich diversity of Xishuangbanna, efforts are needed to record species diversity, including that of many species still unknown to science (Chang et al. 2018; Chang et al. 2022; Chen et al. 2022).

Here, we focus on accessions belonging to the legume genus *Crotalaria* L., which comprises approximately 702 species worldwide (Rockinger et al. 2017; Rather et al. 2018). Its highest species diversity is found in Africa and Madagascar, with an estimated 540 species. It has also expanded to South America and North America, with 64 and 34 species, respectively (Flores et al. 2006; Pandey et al. 2010; Le Roux et al. 2013; Rather et al. 2018). India hosts the largest number of species in Asia (ca. 80 species), followed by Southeast Asian countries, which collectively host 105 species (Lock and Simpson 1991; Rather et al. 2018). Approximately 45 species have been recorded to occur in China, predominantly in Southwest China, including nine endemics and six introduced species (Li et al. 2010). The genus exhibits both annual and perennial life forms and various growth forms (prostrate to erect herbs, undershrubs, robust shrubs, and occasionally small trees) and occupies various habitats, such as open grasslands, roadsides, and forest edges (Polhill 1982; Rather et al. 2018). *Crotalaria* is characterized by papilionoid flowers, the presence of paired callosities on the standard petal, a rostrate keel, 5 + 5 dimorphic anthers, a hairy style, inflated pods and the presence of pyrrolizidine alkaloids (Le Roux et al. 2013; Rather et al. 2018).

In the present study, several interesting specimens of *Crotalaria* were collected during field trips to Mengla County in Yunnan Province, China. Initially, some plants observed in the Mengpengzhen area of the Xishuangbanna Dai Autonomous Prefecture could not be assigned to any known taxa. Thus, we considered three priority explanations. The first explanation considered interpreted that these accessions are natural hybrids formed between two sympatrically occurring *Crotalaria* species, namely, *C. bracteata* Roxb. ex DC. and *C. incana* L. However, upon closer examination, the newly discovered species did not match either of these taxa. The plants exhibited differences in numerous characteristics, including plant height, leaflet shape, inflorescence, flower, pod shape, indumentum, and number of seeds per pod, among others. The subsequent discovery of numerous plants during further surveys, which included nearly 50 mature individuals and several immature plants spread over an area of 0.1 km^2, eliminated the possibility that these plants were hybrids. The second explanation interpreted these accessions as a new distributional record of a known species within the genus *Crotalaria* L. However, there have been no documented new records for the genus *Crotalaria* L. This possibility was ruled out after unsuccessful attempts to identify the plants using existing identification keys (Brach and Song 2006; Li et al. 2010). Additionally, we consulted taxonomists at various institutes in China who were unable to recognize the taxa collected. Furthermore, comparisons with verified images of other *Crotalaria* L. taxa available in the Plant Image Library of China (PPBC; https://ppbc.iplant.cn/) also failed to yield any proper matches. The final explanation considered these plants to represent a new, previously undescribed taxon. This study was designed to confirm this hypothesis by focusing on three lines of evidence, namely, traditional diagnostic morphological character identification, morphometric studies using principal component analyses, and phylogenetic analyses using both plastid *mat*K and nrITS DNA sequences. Finally, we present a comprehensive taxonomic description of this newly discovered *Crotalaria* L. species, supplemented with taxonomic comments and accompanying photographs.

Materials and methods

Ethics statement

The geographic sites where the newly identified species was found do not coincide with any designated natural conservation areas. Therefore, specific permission for access to these locations was not needed.

Morphological observations

The morphological analysis and description of the newly discovered species were prepared using freshly collected samples. The flowers were preserved in FAA solution (formaldehyde–glacial acetic acid–alcohol) for further studies. They were rehydrated using a mixture of water and detergent to observe the corolla in detail, followed by dissection. Minute corolla features were examined using a Stemi 305 binocular microscope. Morphological terminology adhered to the standards set by Harris and Harris (2001), Hickey and King (2007) for vegetative characters, Hewson (1990) for indumentum description, and Endress (2010) for inflorescence morphology. A comparison of the significant morphological features of the new species with those of its allied species *C. incana* L. and *C. bracteata* Roxb. ex DC. was performed (Table 1).

The identification of the allied species *C. incana* L and *C. bracteata* Roxb. ex DC. was established through previous revisionary and systematic studies (Brach and Song 2006; Ansari 2008; Le Roux et al. 2013) and examinations of their types and other authentic specimens housed in large herbaria, such as PE, KIB, WUK, HITBC, CAL, DUH, FRLH, M, MH, SJC, and SKU. Additionally, virtual images of these species sourced from repositories such as the JSTOR Global Plants (JSTOR 2024), China Virtual Herbarium (Chinese Virtual Herbarium 2024), Flora of Pakistan (Eflora of Pakistan 2024), and several other prominent online herbaria (B, BM, BR, E, FI, FOB, G-DC, K, L, LINN, NYBG, P, TUB) were also analysed.

A distribution map was constructed to visualize the geographical distribution of the newly identified species. This map was developed with a foundational base map constructed from Natural Earth (www.naturalearthdata.com) and generated using QGIS version 3.28.2 (QGIS 2021) (Fig. 1).

Taxa sampling for molecular study

Fresh and disease-free leaves were collected from specimens in the field and promptly dried using silica gel to facilitate subsequent DNA extraction. The voucher specimens were preserved at the Herbarium of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (HITBC), and detailed information about each sample is provided in Suppl. material 1. The analysis included a total of 81 accessions, covering both the ITS region and the plastid marker *mat*K. Additionally, this dataset included two outgroup sequences from *Bolusia amboensis* and *Euchlora hirsuta*, as well as nine publicly available sequences of African *Crotalaria* sourced from the NCBI databases (https://www.ncbi.nlm.nih.gov). Overall, our dataset comprised 81 individuals, representing 56 distinct *Crotalaria* species (Suppl. material 1).

Table 1. Comparisons among *Crotalaria menglaensis* S.A.Rather, *C. incana* L. and *C. bracteata* Roxb. ex DC. The bold font represents the main distinguishing features of the new species.

Morphological characters	***Crotalaria menglaensis* S. A. Rather**	***Crotalaria incana* L.**	***Crotalaria bracteata* Roxb. ex DC**
Habit	**Stiff, erect herbs**	**Shrublets**	**Shrublets**
Height	**0.5 m**	**1 m**	**0.6–1.2 m**
Stem surface	**Pubescent with white hairs**	**Pubescent brownish**	**Densely pubescent, brownish-yellow hairs**
Petiole	23–39 mm	30–50 mm	30–50 mm
Petiole surface	**Pubescent with white hairs**	**Glabrous**	**Glabrous**
Stipule	Acicular	Acicular	Acicular
Leaflet size	**30–80 × 21–31 mm**	**20–40 × 10–20 mm**	**50–70(–90) × 25–40 mm**
Leaflet shape	**Ovate to oblanceolate**	**Elliptic obovate, obovate, or suborbicular**	**Narrowly elliptic**
Leaflet apex	Acute	Obtuse and mucronate	Acuminate
Leaflet base	Attenuate	Rounded to broadly cuneate	Attenuate
Leaflet surface (abaxial)	**Pubescent**	**Glabrous**	**Sparsely pilose**
Leaflet margin	**Puberulent entire margin**	**Simple and ciliate**	**Slightly involute and non ciliate**
Bract shape	**Lanceolate**	**Caducous**	**Acicular**
Bract surface	**Pilose**	**Glabrous**	**Glabrous**
Bract size	1.2–2.0 × 0.6–0.7 mm	1.5–2.2 × 0.4–0.7 mm	1–1.5 × 0.1–1 mm
Bract position	**Attached to the base of the pedicel**	**None**	**None**
Bract number	**One**	**None**	**None**
Bracteole size	2.7–3.1 × 1.6–1.8 mm	2–3 mm	1–2 mm
Bracteole surface	Hirsute	Pubescent	Pubescent
Bracteole margin	Entire	Slightly involute	Slightly involute
Bracteole shape	**Ovate to obovate with an asymmetrical base**	**Linear**	**Linear**
Inflorescence	Terminal or axillary raceme	Terminal or axillary raceme	Axillary raceme or rarely terminal
Inflorescence length	**80–120 mm terminal raceme; 110–170 mm axillary raceme**	**100–200 mm**	**100–150 mm**
Number of flowers per inflorescence	**Up to 12 terminal racemes; up to 47 axillary racemes**	**5–15**	**10–30**
Flower colour	Primrose or Strong pale yellow	Yellow	Yellow
Flower size	10–11.9 × 3.3–4 mm	10 × 5 mm	7–10 × 9 mm
Pedicel length	0.47 mm	0.3–0.4 mm	0.3–0.7 mm
Calyx length	5 mm	6–8 mm	5–6 mm
Calyx tube	2.4 mm	8.1 mm	7.6 mm
Standard shape	**Obovate-orbicular**	**Elliptic**	**Oblong**
Standard dorsal surface	Hispid at the middle and tomentose at the base	Pubescent	Pilose on the back at the apex
Standard size	88 × 74 mm	8–1 mm	9 mm
Standard apex	**Notched**	**Rounded**	**Rounded**
Standard Claw size	1.4 mm	6 mm	2.4 mm
Callosity	**Planar**	**Ridge**	**Ridge**
Wing size	7.1–7.3 × 2.3–2.9 mm	Staminal sheath ca. 1.5 mm long	8 mm
Wing claw size	1.52–1.84 × 6.3–0.77 mm	6–7.5 × 1–2.2 mm	2–2.7 × 1.1–0.9 mm
Keel size	10.1–15.1 × 4.8 mm	5.5–6.5 × 2.5–6 mm	8 mm
Keel shape	**Angled**	**Subangled**	**Subangled**
Keel alae	Present	Absent	Absent
Keel curvature	**Below middle**	**Lower third**	**Lower third**
Keel vestiture	**Glabrous**	**Lanate**	**Lanate**

Morphological characters	*Crotalaria menglaensis* S. A. Rather	*Crotalaria incana* L.	*Crotalaria bracteata* Roxb. ex DC
Keel beak	**Straight**	**Spirally twisted up to 90°**	**Slightly incurved**
Keel claw	3.4–3.6 × 1.2–1.4 mm	4.5–4.7 × 1.5–1.7 mm	3.6–3.9 × 1.1–1.5 mm
Androecium size			
	Staminal sheath, 7.78 mm	Staminal sheath ca. 4.5 mm	Staminal sheath ca. 3.2–3.7 mm
	Filaments 1–1.3 mm long	Filaments 1.7–2.7 mm long	Filaments 5–2.9 mm long
	Longer anther, 1.2–1.5 mm	Longer anther, 1–1.4 mm	Longer anther, 1.2–1.7 mm
	Shorter anther, 0.5–0.6 mm	Shorter anther, 0.7–0.9 mm	Shorter anther, 0.8–0.9 mm
Gynoecium	Sub sessile	Sessile	Sessile
Gynoecium size	3.3 × 1.5 mm	2.1 × 1.5 mm	4.2 × 1.1–6 mm
Style hairs	**One row**	**All round**	**All round**
Style bent from ovary/ curved	**Geniculate**	**Subgeniculate**	**Subgeniculate**
Pod stalk	4.63 mm	2 mm	7 mm
Pod shape	**Elliptic to oblong**	**Fusiform**	**Ellipsoid-fusiform**
Pod size	14.2–15 × 6–7.7 mm	20–30 × 6–7.7 mm	20 × 5–10 mm
Pod indumentum	**Tomentose**	**Rusty pilose**	**Densely rusty pubescent**
Number of seeds per pod	**12**	**20–30**	**7–8**
Seed size	2.2–2.5 × 0.9–1.2 mm	1.2–5 × 0.32–2 mm	1.8 × 5 mm
Seed colour	Bright citrine	Brown	Brownish black

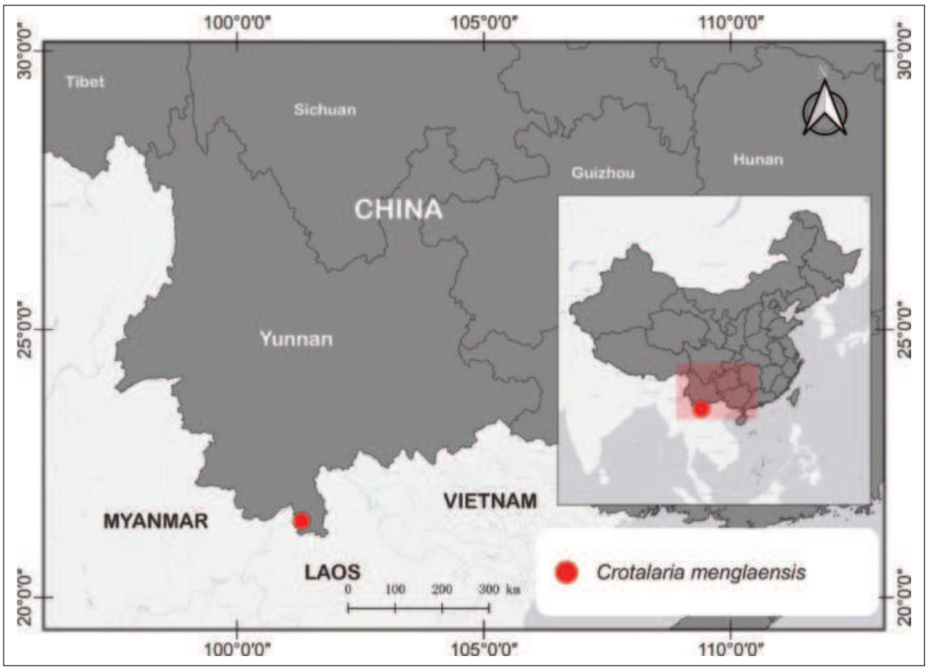

Figure 1. Map visualizing the only known occurrences of *Crotalaria menglaensis* S.A.Rather in Mengpeng village of Xishuangbanna Dai Autonomous Prefecture, Yunnan, China (red dot).

DNA Extraction, PCR Amplification and Sequencing

Genomic DNA was isolated using a DNeasy Plant Mini Kit (Qiagen, Amsterdam, The Netherlands) following the manufacturer's protocol. The DNA quantity was confirmed via 0.8% agarose gel electrophoresis, and its concentration was determined using a SmartSpec^{TM} Plus Spectrophotometer (Bio-Rad, Hercules, CA, United States). Before amplification, the DNA samples were stored at -20 °C. Polymerase chain reactions (PCR) were performed in a 25 μL reaction volume comprising 2.5 μL of 10× buffer with 2 mM MgCl2, 1 U of Taq DNA polymerase, 1 μL of dNTPs (0.125 mM), 1 μL of each primer (5 pM), and 30–50 ng of total DNA. Nuclease-free water was added to reach the final volume. The optimal PCR conditions and detailed primer information are listed in Suppl. material 2. PCR products were visualized by electrophoresis on 0.8% agarose gels, followed by purification using BioMed multifunctional DNA fragment purification recovery kits (Beijing, China). The purified products were sequenced using the same primers used for PCR amplification. Sequencing was conducted on an ABI 3730 automated sequencer at Sangon Biotech, Shanghai, China.

Sequence alignment and data analysis

To ensure the accuracy and authenticity of the sequences, the original trace files were subjected to rigorous validation through web-based BLASTn searches on the NCBI platform. We conducted sequence alignment in Geneious version 8.1.7, which included trimming, visual inspection, and manual adjustments (Kearse et al. 2012). The trimming parameters were set to an error probability of 0.1 per base and a quality threshold of 20, allowing the removal of any low-quality base calls at the 5’ and 3’ ends of the sequenced PCR products. Each gene was aligned separately using MUSCLE (Edgar 2004) within Geneious. To improve alignment quality and accuracy, ambiguous regions were trimmed using Gblocks v0.91b (Castresana 2000). Individual alignments were then concatenated to create a two-gene alignment for all 81 samples. Microsatellite repeats were excluded, and gaps were considered as missing data. Phylogenetic analyses were performed using the standard-maximum-likelihood (ML) method with IQ-TREE (Nguyen et al. 2015), Bayesian analysis with MrBayes (Ronquist et al. 2012), and the optimal nucleotide substitution model was determined with ModelFinder (Kalyaanamoorthy et al. 2017). Branch support in the ML tree was assessed through 10,000 ultrafast bootstrap replicates (Minh et al. 2013). All procedures were executed using PhyloSuite v1.2.2 (Zhang et al. 2020). The nrITS region of the newly discovered species yielded a 715 bp sequence, while the *mat*K region produced a 775 bp sequence. Concatenating these sequences generated a 1490 bp sequence-aligned matrix, with a total of 1690 characters across 81 accessions. The new species, *C. menglaensis*, differed from *C. incana* and *C. bracteata* by 12 nucleotide substitutions and one inversion at site 601 in both the ITS and *mat*K regions. Additionally, it showed three insertions, with lengths of 3 and 12 at sites 420–422 and 795–806, respectively, compared to its closest relatives. The multiple sequence alignment was submitted to TreeBASE with ID 31180.

Morphometric analyses

To assess potential differences between the new species and their closest relatives and to determine which traits were most relevant for their identification, we conducted a principal component analysis (PCA) using the “factoextra” package in R version 4.3.0 (Kassambara and Mundt 2020; R Core Team 2023) with a significance level set at 5%. We examined three to five specimens of *C. menglaensis* S.A.Rather, *C. incana* L., and *C. bracteata* Roxb. ex DC. The length and width of leaflets, flowers, standards, wings, keels, seeds and pods were measured (Suppl. material 3). Correlation analysis was performed to eliminate highly correlated traits ($r > 0.71$) using the "corrplot" package in R version 4.3.0 (Wei and Simko 2021; R Core Team 2023). In total, four traits were retained for the PCA biplot analysis: keel length (KL), standard width (SW), seed width (SEW), and seed length (SEL) (Suppl. material 3).

Results and discussion

The proposed new species, *Crotalaria menglaensis* S.A.Rather, resembles *C. incana* L. and *C. bracteata* Roxb. Ex DC. However, it differs from the former in several aspects. It has an ovate to oblanceolate leaflet shape with a pubescent leaf surface, an obovate-orbicular standard shape, a straight keel beak, and an elliptical to oblong pod shape. It differs from the latter in having a stem surface covered with white hairs, a pilose bract surface, a notched standard apex, planar callosity, an angled keel shape, and a tomentose pod indumentum. A comprehensive morphological comparison is presented in Table 1 to elucidate the distinctions between the new taxon and its closest relatives.

The maximum likelihood (ML) and Bayesian tree phylogenies showed congruent topologies (Fig. 2). The phylogenetic tree identified seven major clades, corresponding to seven of the 11 sections proposed by Le Roux et al. (2013). These seven major clades (i.e., Calycinae, Crotalaria, Incanae, Stipulosae, Grandiflorae, Geniculatae and Glaucae) had bootstrap values greater than 80%. These clades are consistent with previous phylogenetic analyses (Subramaniam et al. 2013; Rather et al. 2018). Furthermore, phylogenetic analysis strongly supported the monophyletic status of the genus (100% BS). The phylogeny places the newly discovered species *C. menglaensis* S.A.Rather within a separate clade, supporting its distinction from other allied species included (Fig. 2). *C. menglaensis* S.A.Rather forms a distinct clade with *C. bracteata* Roxb. Ex DC. And *C. incana* L. (100% BS). Additionally, *C. menglaensis* S.A.Rather and *C. bracteata* Roxb. ex DC. form a sister clade with strong support (100% BS), and in turn, they are sisters of *C. incana* L. (100% BS) (Fig. 2).

Morphometric analyses based on principal component analysis using Pearson's coefficient were employed to identify significant morphological characteristics that facilitated differentiation between the new species and its closest relatives based on gross morphology (Fig. 3, Suppl. material 4, Table 2). These morphometric analyses have proven highly valuable for elucidating correlations among variables or distances among groups and assessing the significance of each character. Fig. 3 illustrates the significant characteristic ratios that contribute to the uniqueness of the new species. Following Pearson's correlation analysis, highly correlated traits were excluded, and four traits were used for statistical analysis (Fig. 3, Suppl. material 4, Table 2). The results showed significant differences in morphological characters, including keel length (KL), standard width (SW), seed width (SEW), and seed length (SEL), compared to those of allied species (Fig. 3). Dimension 1 of the PCA explained the greatest variance, followed by dimensions 2, 3, and 4, which collectively accounted for 84.48% of the variation, a substantial proportion (Fig. 3, Suppl. material 4, Table 2).

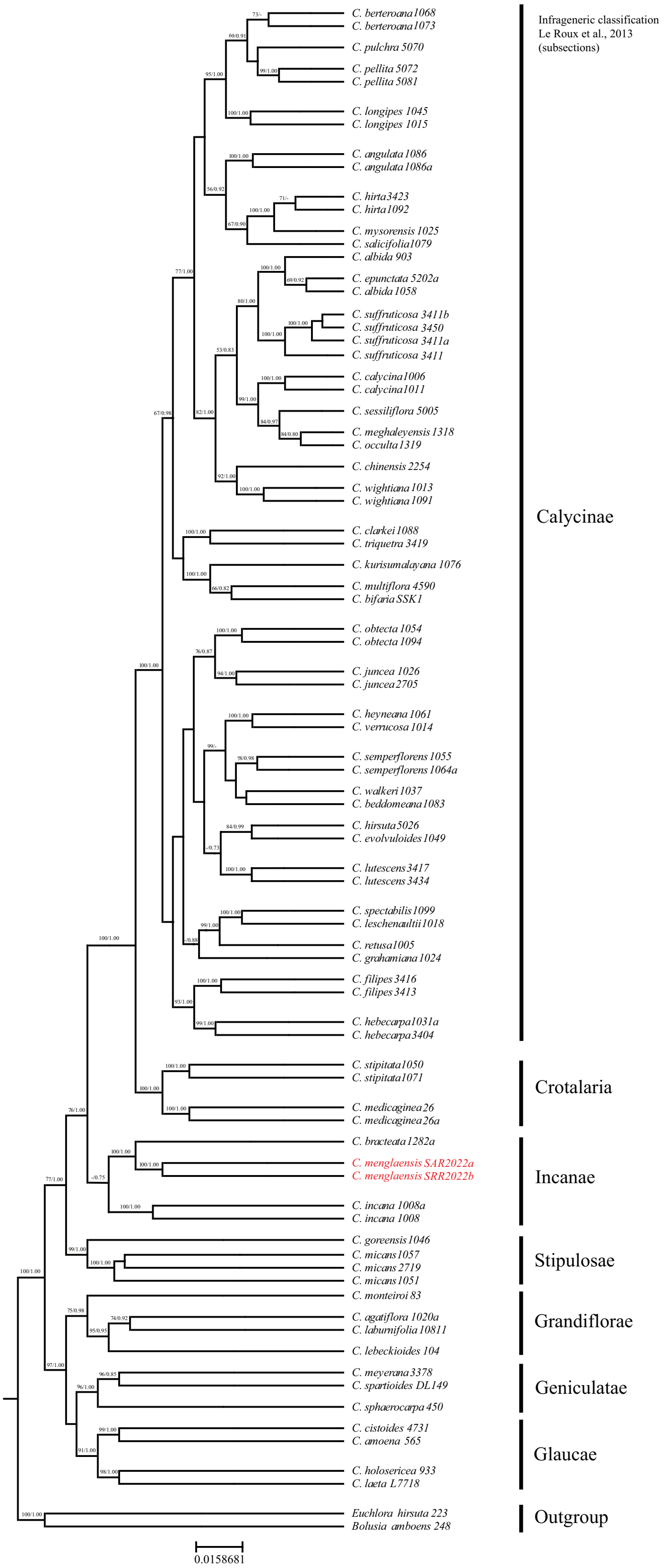

Figure 2. Phylogenetic hypothesis of the genus *Crotalaria* based on the concatenated matrix including *mat*K and nrITS sequences constructed via maximum likelihood as implemented in IQ Tree. Bootstrap values are printed above the branches. Since Bayesian analyses resulted in almost the same topology, only the ML tree made is presented here. The new species *Crotalaria menglaensis* S.A.Rather was marked in red. The names on the right side of the phylogeny correspond to the infrageneric classification of the genus *Crotalaria* by Le Roux et al. (2013).

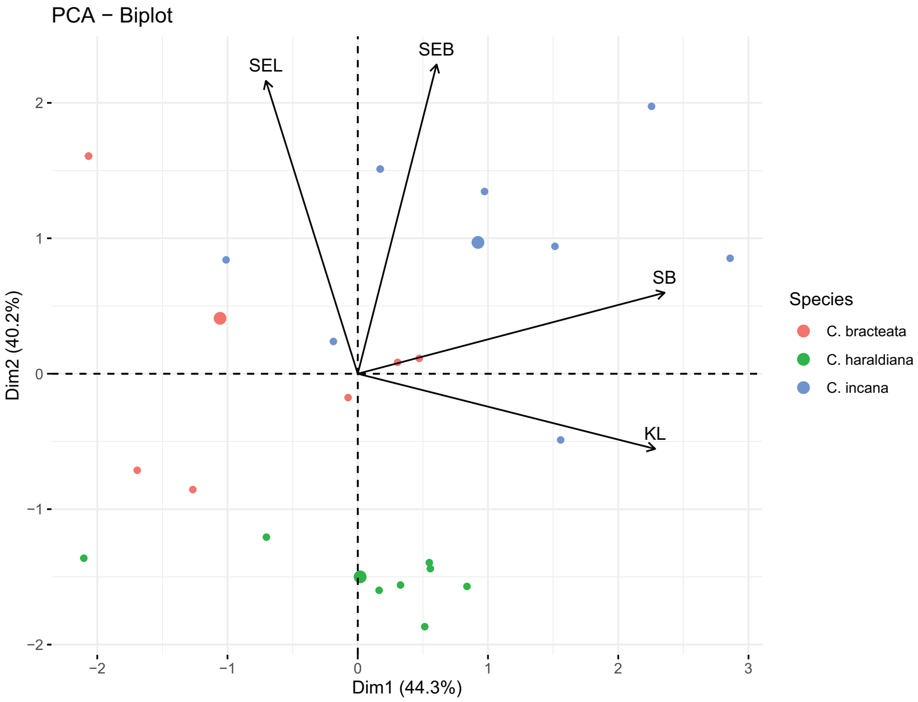

Figure 3. Scatter plot visualizing Dim1 and Dim2 from the principal component analyses based on the assembled morphological trait variables and accessions of the three species nested in the Incanae clade (see Fig. 2), namely, *C. incana* L., *C. bracteata* Roxb. ex DC. and the new species *Crotalaria menglaensis* S.A.Rather. Dim1 explained 44.3% of the variation, whereas DIM2 explained 40.2%. The vectors corresponded to KL = keel length, SW - standard width, SEW - seed width, and SEL - seed length.

Table 2. Variance in the contributions of morphological trait variables as determined by principal component analysis.

Dimensions	Eigenvalue	Variance	Cumulative Variance Percent (%)
1	1.77	44.28	44.28
2	1.61	40.20	84.48
3	0.43	10.66	95.14
4	0.19	4.86	100.00

Taxonomic treatment

***Crotalaria menglaensis* S.A. Rather, sp. nov.**
urn:lsid:ipni.org:names:77343398-1
Fig. 4

Type. CHINA. Yunnan: Xishuangbanna Dai Autonomous Prefecture, Mengla County, Mengpengzhen., 21°26'57.42"N, 101°18' 31.49"E, alt. 577 m, 23 November 2022, SAR 202305 (holotype HITBC! isotypes KIB! PE! DUH! CAL!).

Diagnosis. The new species is similar to two sympatrically occurring species, *C. incana* L. and *C. bracteata* Roxb. ex DC. However, *C. menglaensis* S.A.Rather differs from the former and latter in its height, 0.5 m (*vs* 1 *vs* 60–1.20); stem surface, pubescent with white hairs (*vs* pubescent brownish *vs* densely brownish yellow); bract surface, pilose (*vs* glabrous *vs* glabrous); leaflet shape, ovate to oblanceolate (*vs* elliptic obovate, or suborbicular *vs* narrowly elliptic); leaflet surface, pubescent (*vs* glabrous *vs* sparsely pilose); standard shape, obovate-orbicular (*vs* elliptic *vs* oblong); planar callosities (*vs* ridge *vs* ridge); keel shape, angled (*vs* subangled *vs* subangled); keel beak, straight (*vs* spirally twisted up to 90° *vs* slightly incurved); pod shape, elliptic to oblong (*vs* fusiform *vs* ellipsoid-fusiform); and pod indumentum tomentose (*vs* rusty pilose *vs* densely rusty pubescent).

Description. Stiff and erect herbs, ca. 0.5 m tall. Stems terete and densely pubescent. Stipules acicular. Leaves trifoliolate, alternate, petiole up to 30 mm long, lamina ovate to oblanceolate, 30–80 × 21–31 mm, terminal leaflet larger than the lateral ones, attenuated at the base, acute at apex, margin entire with puberulent indumentum, adaxial surface glabrescent, abaxial surface pubescent. Inflorescence a terminal or axillary raceme, a terminal raceme 80–120 mm bearing up to 12 flowers, and an axillary raceme 110–170 mm bearing up to 47 florets. Flower 10–11.9 × 3.3–4 mm. Bract lanceolate, 1.2–2 × 0. 6–0.7 mm covered with white pilose hairs inserted at the base of a pedicel. Pedicel ca. 4.7 mm, pubescent, reflexed downwards; bracteole ovate to obovate with an asymmetric base, 2.7–3.1 × 1.6–1.8 mm, hirsute, margin entire. Calyx 5-lobed, calyx tube ca. 2.4 × 2.9 mm, oblong-lanceolate, 2.2–2.9 × 0.4–0.71 mm, apex attenuate, densely ciliate along margins. Corolla primrose or strongly pale yellow, exserted beyond calyx, obovate-orbicular, ca. 8.8 × 7.4 mm, claw ca. 1.4 mm, with paired planar callosites at the base, ca. 0.6–0. 7 × 0. 7–0.8 mm; wing petals 7.1–7.3 × 2.3–2.9 mm, claw 1.52–1.84 × 6.3–0.77 mm, cavae 4.2–4.4 mm; keel angled, curvature below the middle, claw 3.4–3.6 × 1.2–1.4 mm, glabrous, beak straight. Staminal sheath 7.8 mm; filaments free, glabrous, shorter filament 3.7–6.7 mm, longer filament 7.7–8.0 mm; anthers dimorphic, basifixed ones longer, ensiform, ca. 1.2–1.5 mm, dorsifixed ones shorter, orbicular ca. 0.5–0.6 mm. Ovary sessile, linear, ca. 3.3 × 1.5 mm, inflated, style 8.2 mm long, geniculate, trichomes in a single row; stigma brush-like and contracted, ca. 0. 21 mm long, hairy. Pods elliptic to oblong, 14.2–15 × 6–7.7 mm, tomentose, with persistent style. Seeds 2.2–2.5 × 0.9–1.2 mm, bright citrine, smooth and glossy.

Phenology. The plants were observed to bear flowers and fruits from October to January.

Etymology. The specific epithet of the new species “*menglaensis*” is derived from the type locality of this species.

Distribution and habitat. *Crotalaria menglaensis* S.A. Rather is found in grasslands and exposed areas of Mengpeng, Mengla County, within the Xishuangbanna Dai Autonomous Prefecture, Yunnan, China.

Uses. Locals use the pods of this species as a food source. Additionally, its roots and seeds are utilized in traditional medicine to treat various digestive disorders.

IUCN Red List Category. This species is exclusively documented in a single location where clustered populations of fewer than 100 mature individuals have been observed. Its habitat is adjacent to roads and agricultural land and is consistently affected by anthropogenic activities such as grazing, deforestation, cultivation, and landscape management. The potential degradation of its natural habitat and restricted geographical range significantly threatens its survival. Therefore, according to the IUCN Standards and Petitions Committee (2019), this species should be considered critically endangered under criteria A4, B2a, C2a, and D1. These criteria denote species facing a very high risk of extinction in the wild.

Additional specimens examined (paratypes). China, Yunnan. Mengla, in forest, alt. 1600 m, 12 June 2012, *Y.M. Shi & W.S. Chen 254655* (KUN).

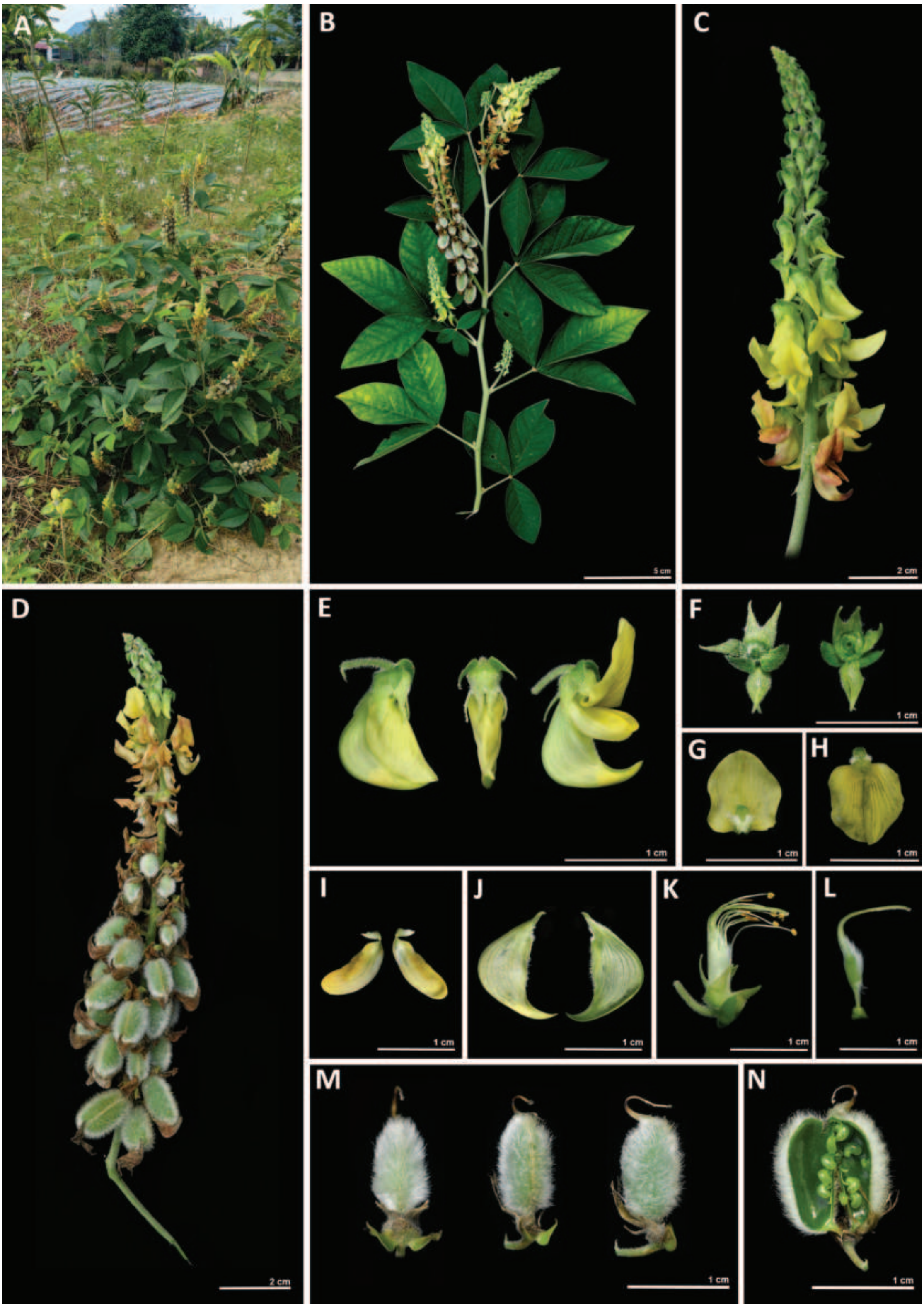

Figure 4. *Crotalaria menglaensis* S.A.Rather **A** habit **B** plant twigs with leaves and flowers **C** inflorescence with flowers **D** inflorescences with flowers and fruits **E** flower in dorsal, lateral, and ventral views **F** calyx showing the dorsal and ventral surfaces **G** standard adaxial surface **H** standard abaxial surface with paired planar callosity pairs at the base with white silky pubescence **I** wing petals with prominent cavae and a distinct claw **J** adaxial and abaxial surfaces of keel petals, beak not twisted, pubescence along the margins from the middle to the base of the keel petal **K** anthers monodelphous, 10 dimorphic anthers (common to all the species within the genus) **L** gynoecium showing the ovary, style, and stigma **M** pod in ventral, dorsal, and lateral views **N** pod splitted longitudinally with young seeds.

Xishuangbanna, Mengla, in the forest, 1650 m, 16 July 2014, *Y.M. Shui & W.S. Chen 245266* (KUN). Xishuangbanna, Mengla, in the forest, 1450 m, 14 August 2016, *Z.Y Wen & Z.A Wang 524694* (KUN). Hekou, on forest edges, 1459 m, 25 November 2005, *Z.Y. Chang et al. 162458* (KUN). Xishuangbanna, Mengla, in grasslands, 1200 m, 3 August 2007, *Z. Y. Chang 445123* (KUN). Xishuangbanna, Mengla, 1180 m, 25 August 2010, *Z.Y. Chiang 2005387* (HITBC).

Acknowledgements

This work would not have been possible without the invaluable resources provided by the International Plant Names Index (https://www.ipni.org/), JSTOR Global Plants (https://plants.jstor.org/), Biodiversity Heritage Library website (http://www.biodiversitylibrary.org/), The World Checklist of Vascular Plants (WCVP, http://wcvp.science.kew.org/), the online botany collections of the Smithsonian Museum of Natural History (https://naturalhistory.si.edu/re-search/botany), Plant Photo Bank of China (https://ppbc.iplant.cn/), and Tropicos (http://legacy.tropicos.org/Home.aspx) databases. Additionally, we acknowledge the financial support provided by the Chinese Government Scholarship (CSC) for the second author (SR). Thanks to Marjorie Angeles for her help with the early description of the species. We would also like to express our gratitude to the two anonymous reviewers for their valuable comments, which significantly enhanced the quality of the manuscript. Additionally, we extend our thanks to the subject editor, Dr. Stephen Boatwright, for his comments and handling of the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This work was supported by the National Natural Science Foundation of China (Grant No. 32250410305) and the Yunnan Science and Technology Department (Grant Nos. Y8BSH11008 and 202401AT070238) awarded to Shabir A. Rather.

Author contributions

SAR and YX collected this species. SAR, SR and KKW performed the data analysis. SAR wrote the manuscript. SAR, HL and HS revised the manuscript. All authors have read and agreed to the final version of the manuscript for publication.

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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

Plant accessions used for the molecular analysis of *Crotalaria* along with their GenBank accession numbers

Authors: Shabir A. Rather, Sirilak Radbouchoom, Kaikai Wang, Yunxue Xiao, Hongmei Liu, Harald Schneider

Data type: doc

Link: https://doi.org/10.3897/phytokeys.242.122407.supp1

Supplementary material 2

Details of primers used for amplification and subsequent sequencing in the present study

Authors: Shabir A. Rather, Sirilak Radbouchoom, Kaikai Wang, Yunxue Xiao, Hongmei Liu, Harald Schneider

Data type: doc

Link: https://doi.org/10.3897/phytokeys.242.122407.suppl2

Supplementary material 3

The morphological traits of *Crotalaria menglaensis* S.A.Rather. and its close relatives *C. bracteata* Roxb. ex DC. and *C. incana* L.

Authors: Shabir A. Rather, Sirilak Radbouchoom, Kaikai Wang, Yunxue Xiao, Hongmei Liu, Harald Schneider

Data type: docx

Link: https://doi.org/10.3897/phytokeys.242.122407.suppl3

Supplementary material 4

Pearson correlation analysis of 14 morphological traits of *Crotalaria menglaensis* S.A.Rather.

Authors: Shabir A. Rather, Sirilak Radbouchoom, Kaikai Wang, Yunxue Xiao, Hongmei Liu, Harald Schneider

Data type: tif

Link: https://doi.org/10.3897/phytokeys.242.122407.suppl4