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Research Article

Gomphonema vancampianum sp. nov. (Gomphonemataceae, Bacillariophyceae), a new large *Gomphonema* species from Europe

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Abstract

During a French biomonitoring survey of the lakes in the region Rhône-Méditerranée-Corse, a large, unknown *Gomphonema* taxon was observed in a lake in the vicinity of the City of Lyon (Département du Rhône, France), that could not be identified using the currently available literature. Detailed light and scanning electron microscopy investigations revealed the presence of two types of valves, one bearing a thick marginal crest and valves lacking the crest. Following comparison with similar, mostly tropical *Gomphonema* species, the unknown taxon is described as new: *Gomphonema vancampianum* **sp. nov.** Discriminating features of the new species include the peculiar valve shape resembling a Chinese spoon, the broad upper valve part with acuminate tip, the presence of shallow depressions in the axial area, distinctly punctate striae and the occasional presence of the marginal crest. The new species was observed in several samples collected in an oligo- to mesotrophic, calcium-carbonate rich lake with a high ecological quality.

Key words: Europe, France, *Gomphonema*, morphology, new species

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Introduction

The genus *Gomphonema* is one of the dominant freshwater genera in European rivers and lakes (Levkov et al. 2016; Abarca et al. 2020). During the past twenty-five years, there has been a steady increase in the number of taxa, not in the least due to intensive taxonomic work by Erwin Reichardt revising several groups within the genus, such as the *G. dichotomum* group (Reichardt and Lange-Bertalot 1991), the *G. pumilum* group (Reichardt 1997), the *G. coronatum/acuminatum* group (Reichardt 1999), the *G. truncatum* group (Reichardt 2001) and the *G. gracile* group (Reichardt 2015a). In 2016, Levkov et al. (2016) published a monograph on the genus *Gomphonema* in Northern Macedonia describing 30 new species, solely based on morphological features. Abarca et al. (2020) questioned the use of valve outline when analysing the core group within the genus *Gomphonema* and concluded that the "Gomphonema *core group has been overdescribed due to the use of outline as the main criterion for species delimitation*" (Abarca et al. 2020, p. 1) as they observed large outline variabilities without an underlying genetic differentiation. Nevertheless, unknown *Gomphonema* species, often with restricted ecological preferences, are still observed in lakes and rivers in Europe.

During a French biomonitoring survey of the lakes in the region Rhône-Méditerranée-Corse (southern France), several populations of a large, unusual *Gomphonema* taxon were observed in samples collected from the artificial Lac du Drapeau ("*Flag lake*") located in the vicinity of the French City of Lyon (Dépt. du Rhône, France). The largest populations seemed to be associated with submerged helophytes and aquatic plants. Despite a detailed morphological analysis, comparing the unknown taxon with all similar larger *Gomphonema* species worldwide, the taxon could not be identified. This contribution describes in detail the morphology of the new species highlighting its remarkable level of variability. Its morphology is compared with known species from the *Gomphonema apiculatum* Ehrenberg (1843: 416) group and the *G. augur* Ehrenberg (1841: 211) (including *G. apicatum* Ehrenberg 1854: pl. 9, fig. 41) group. As a result of the morphological comparison, the new species is described as new: *Gomphonema vancampianum* Van de Vijver, Pottiez & Chavaux, sp. nov. Details on its ecology are added not only based on measured physicochemical parameters, but also derived from the accompanying diatom flora, integrating longer periods of ecological conditions.

Materials and methods

Lac du Drapeau (elev. 170 m) is a 61 ha large lake of a calcium-carbonate sedimentary nature with a maximum depth of 3.2 m. The Lake was created following the extraction of materials in the Rhône plain and is fed by the aquifer of the Island of Miribel-Jonage and the Rizan Stream and finally flows into the Eaux Bleues gravel pit. Although the surrounding area experiences some anthropogenic (mainly recreational) pressure, the Lac du Drapeau is closed to the public as it is used for flood control and serves as a drinking water reservoir for the City of Lyon (Agence de l'Eau Rhône Méditerranée Corse 2021).

Six samples were collected from three different localities in the Lake. At each locality, one sample was gathered by scraping off five submerged stones, while a second sample was collected by squeezing five aquatic plants, keeping the water in small plastic vials. All samples were immediately fixed with ethanol on site.

All samples were prepared for LM and SEM observations following the method described in van der Werff (1955). Small amounts of each sample were cleaned by adding 37% hydrogen peroxide (H_2O_2) and heating to 80 °C for about 1 h, after which the reaction was completed by addition of saturated potassium permanganate ($KMnO_4$). Following digestion and centrifugation (three times for 10 minutes at 3700× rpm), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax (refraction index 1.73) and analysed using an Olympus BX53 microscope at 1000x magnification (N.A. 1.30), equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System, connected to the cellSense Standard programme. As middle striae are often more spaced, underestimating the actual stria density, the stria density was determined by counting striae between the central area and the apices. For SEM analysis, part of the suspension was filtered through 5-μm Isopore™ polycarbonate membrane filters (Merck Millipore), pieces of which were affixed with conductive double-sided adhesive carbon-tabs to aluminium stubs after air–drying. Stubs were subsequently coated with a platinum layer of 15 nm and studied using a JEOL-JSM-7100F field emission scanning electron microscope at 2 kV and a working distance of 4 mm. 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), Round et al. (1990, raphe structure) and Reichardt (1999, genus features for *Gomphonema*). The new species was compared with different *Gomphonema* taxa described from different locations worldwide (Reichardt 1995, 1999, 2001; Metzeltin and Lange-Bertalot 1998, 2007; Jahn and Kusber 2004; Kociolek 2011; Levkov et al. 2016).

For typification of the species, we chose to use the entire slide as the type, following article 8.2 of the International Code for Botanical Nomenclature (Turland et al. 2018). Diatoms show a broad variability during their cell cycle and choosing the entire population present on a slide as the type shows this variability. One valve was indicated to illustrate a typical valve of the new species (see Figs 1–3) to avoid confusion with other *Gomphonema* taxa. All novelties are registered proactively according to Art. 42.3 (Turland et al. 2018).

Results

Gomphonema vancampianum **Van de Vijver, Pottiez & Chavaux, sp. nov.**

Figs 1–3

Type materials. *Holotype*. BR-4839 (Meise Botanic Garden, Belgium). Fig. 1C represents the holotype. ***Isotype*.** Slide 441 (University of Antwerp, Belgium).

Registration. http://phycobank.org/104517.

Type locality. Lac du Drapeau (Lyon, Département du Rhône, France), sample Drapeau-U03-VEG, (coll. date 22.viii.2023, leg. R. Chavaux).

Etymology. This species is named in honour of Prof. Dr Karel Van Camp, former Physics professor of the first author at Antwerp University (Belgium) and life-long enthusiastic amateur diatomist and microscopist.

Description. ***LM*** (Fig. 1). Frustules in girdle view narrowly clavate with transapical striae continuing on to the valve mantle without interruption; adjacent to the striae, a line of isolated areolae (Fig. 1A, arrow). Headpole much broader than the footpole. Valves apiculate-clavate with elliptic-lanceolate upper valve part and largest width right above the valve middle. Lower valve part abruptly narrowing near the valve centre, then gradually tapering towards the acute footpole. Headpole acutely rounded with a narrow protracted, cuneate apex. Occasionally, valves surrounded by marginal crest, visible by changing focal depth (Fig. 1C, L, N, arrows). Valve dimensions (n = 25): length 30–60 μm, width 10–12 μm. Axial area moderately broad, linear with distinct, shallow markings, visible by changing focal depth. Central area asymmetrical: primary side with more distantly spaced single long stria and stigmoid, well separated near the valve middle. Isolated stria on the secondary side markedly shortened. Raphe

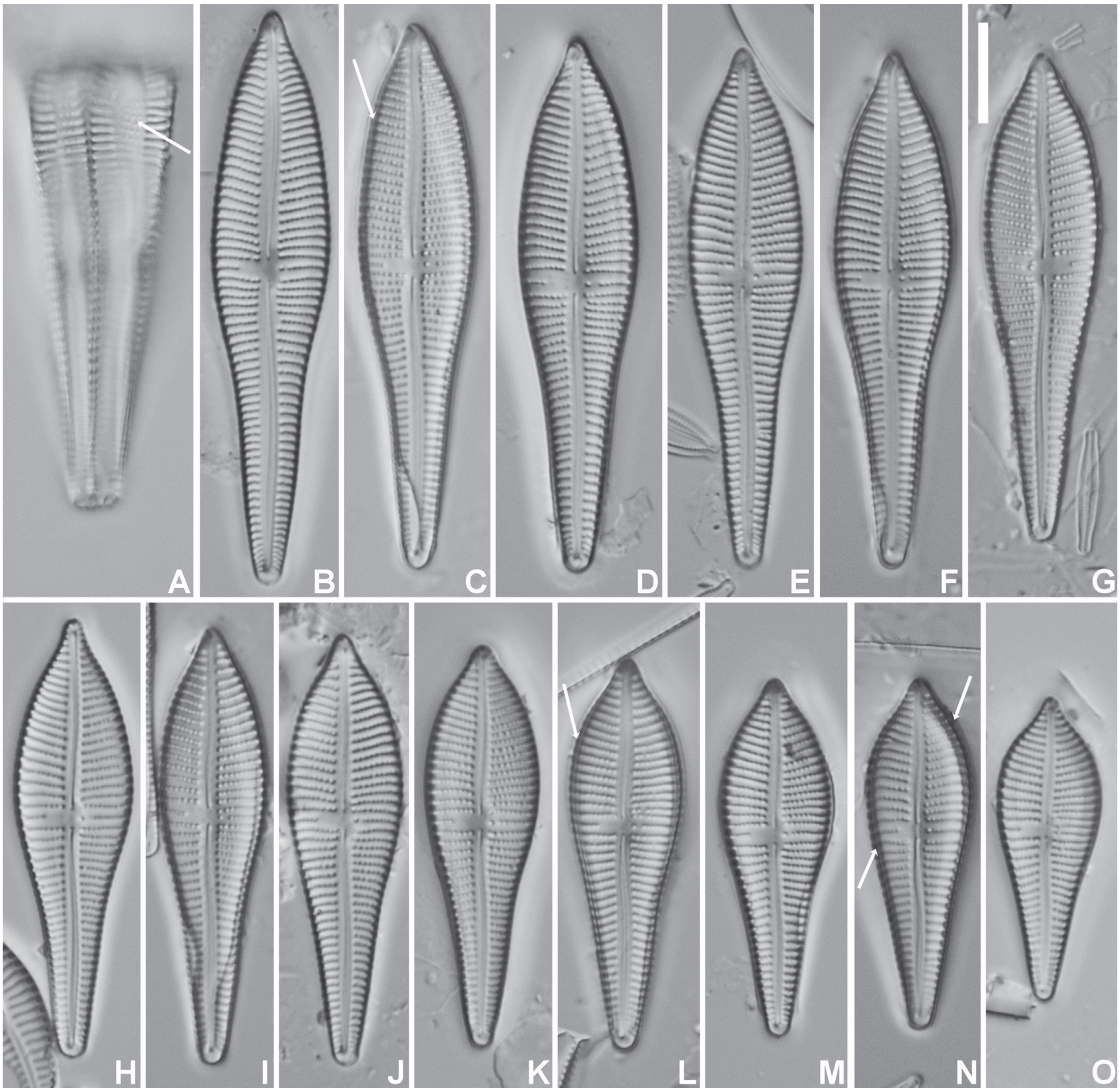

Figure 1. *Gomphonema vancampianum* sp. nov. LM micrographs taken from the holotype material (BR-4839, Lac du Drapeau, Sample DRAPEAU-U03VEG, France) **A** LM picture of a frustule in girdle view. The arrow indicates the smaller, more distantly spaced areolae on the mantle **B**–**O** LM pictures of valves in valve face view in decreasing length. The arrows indicate the possible presence of the marginal crest. Scale bar: 10 μm.

clearly lateral and weakly undulating. Central raphe endings indistinct, almost straight. Terminal raphe fissures not discernible in LM. Striae parallel in the middle, soon becoming radiate towards the headpole, but remaining almost parallel or slightly radiate towards the footpole, 10–11 in 10 μm, more closely spaced near the apices. Striae distinctly punctate, 18–24 areolae in 10 μm. ***SEM*** (Figs 2, 3). Two types of valves present: with marginal crest (Fig. 2A–C) and lacking marginal crest (Fig. 2D, F). Valve face and mantle striae in crested valves interrupted at the valve face/mantle junction by the thickened marginal crest. Marginal crest with undulating border near the headpole (Fig. 2A). Mantle striae in advalvar part composed of large, densely packed, c-shaped

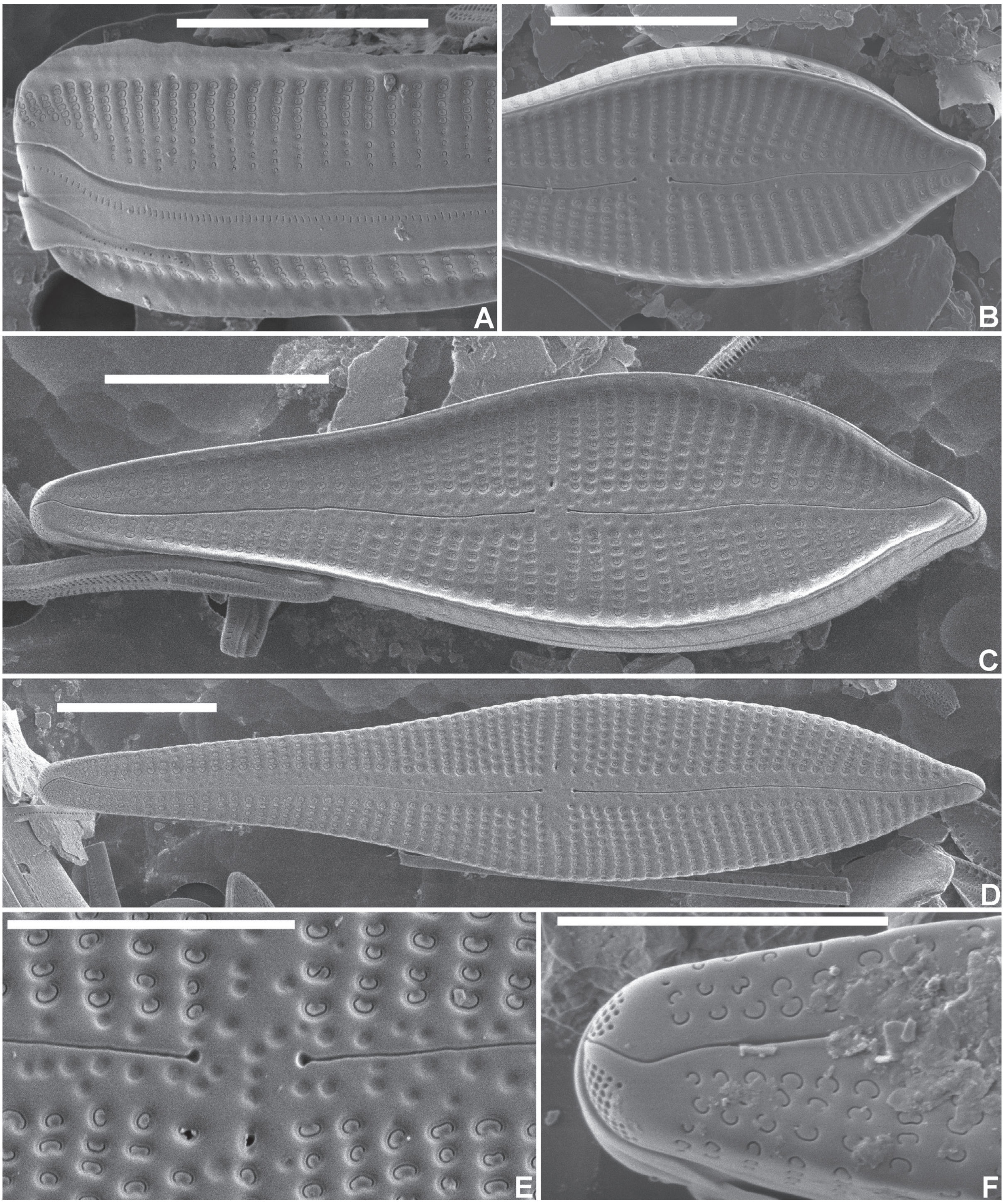

Figure 2. *Gomphonema vancampianum* sp. nov. SEM micrographs taken from the holotype material (BR-4839, Lac du Drapeau, Sample DRAPEAU-U03VEG, France) **A** SEM external view of the headpole in girdle view showing the marginal crest on both valves, the larger, reniformly occluded upper areolae and the smaller, more distant areolae towards the mantle edge. Note also the slit-like pores on the girdle band **B** SEM external detail of the upper valve part of a valve bearing a crest showing the lowering marginal crest at the apex **C** SEM external view of an entire crest-bearing valve. Note the shallow depressions in the axial area **D** SEM external view of valve without marginal crest. Note the shallow depressions in the axial area and the valve face striae continuing over the valve face/mantle junction **E** SEM external detail of the central area with the depressed large areolae and the stigmoid. The shallow pit-like depressions are well visible in the axial area **F** SEM external detail of the footpole with the distal raphe fissure bisecting the apical pore field. Scale bars: 10 µm (**A–D**), 5 µm (**E–F**).

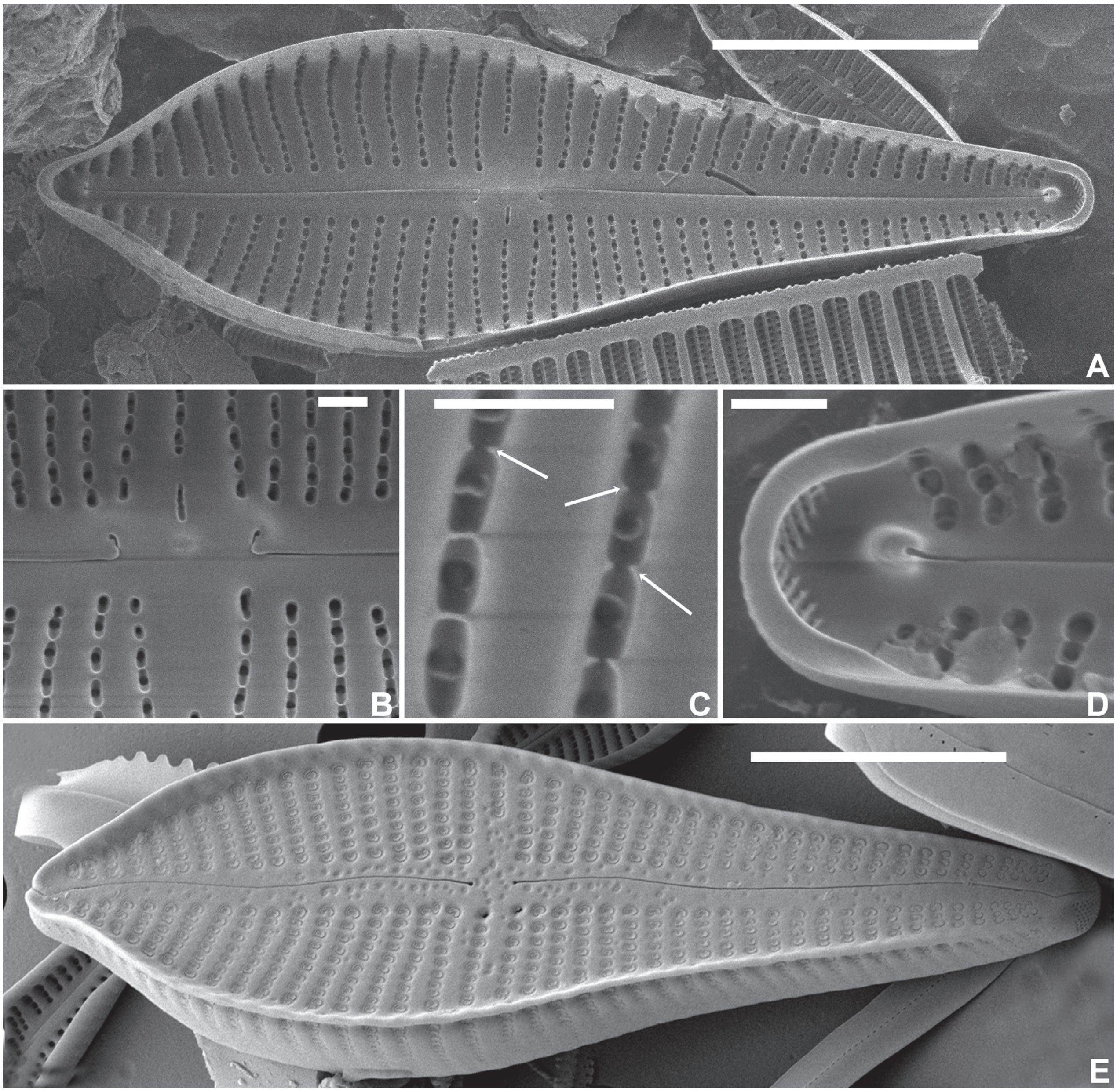

Figure 3. *Gomphonema vancampianum* sp. nov. SEM micrographs taken from the holotype material (BR-4839, Lac du Drapeau, Sample DRAPEAU-U03VEG, France) **A** SEM internal view of an entire valve **B** SEM internal detail of the central area with the stigmoid located in a long depression, the hooked central raphe endings and the long foramina with the areolae **C** SEM internal detail of the areolae with the small silica struts **D** SEM internal detail of the footpole with the small pseudoseptum, the helictoglossa and the apical pore field **E** SEM external view of an entire valve with marginal crest from Lac du Réaltor, Provence, France (photo courtesy of Dr Carlos E. Wetzel). Scale bars: 10 µm (**A, E**), 1 µm (**B–D**).

areolae, externally covered by small reniform siliceous flaps. Areolae in abvalvar part of the striae towards the mantle edge, smaller, c- to e-shaped (Fig. 2A). Girdle bands broad with continuous row of transapically elongated narrow pores. Marginal crest lowering towards the apices (Fig. 2B, C). Valves lacking crest with striae extending almost continuously across the valve face/mantle junction (Fig. 2F). Axial area covered with dense irregular pattern of shallow, pit-like depressions (Fig. 2B, D, E). Raphe branches clearly undulating (Fig. 2C, D). Central raphe endings almost straight, small drop-like (Fig. 2E). Distal raphe fissure at footpole bisecting apical pore field, continuing on to the mantle (Fig. 2F), at headpole splitting the marginal crest (when present) and continuing shortly on to the mantle (Fig. 2C). Apical pore field bisected, composed of several rows of densely packed, rounded pores (Fig. 2F), only present at footpole. Striae composed of c-shaped areolae, occluded by small reniform siliceous flaps, near the central area slightly sunken into valve surface (Fig. 2E), towards the apices on the same level as the virgae (Fig. 2F). Stigmoid external opening small, rounded, sunken into valve face (Fig. 2E). Internally valve face surface smooth (Fig. 3A). Small pseudoseptum visible at footpole (Fig. 3A, D). Striae located in shallow, narrow foraminal rows. Side walls of the areolae with continuous apical bars or small interrupted struts (Fig. 3C, arrows). Internal opening of the stigmoid short, transversely elongated, located in a long, shallow groove (Fig. 3B). Central raphe endings long, right-angled, hook-shaped (Fig. 3B). Terminal raphe endings terminating on to well-developed helictoglossae (Fig. 3D).

Distribution and ecology. *Gomphonema vancampianum* has so far only been found in several samples from the type locality in France. The largest population was found in a sample collected from submerged aquatic plants. The diatom flora is dominated by species typically found in calcium-carbonate rich, oligotrophic lakes with low nutrient concentrations and low saprobity. The sample is dominated by several cymbelloid taxa (e.g. *Encyonopsis subminuta* Krammer & E.Reichardt, *Cymbella affiniformis* Krammer, *C. lange-bertalotii* Krammer, *Cymbopleura amphicephala* (Nägeli) Krammer) together with a, so far, unidentified, long-celled *Fragilaria* species, *Brachysira neoexilis* Lange-Bertalot, *B.* cf. *chiaruccii* Cantonati et al. and *Nitzschia* cf. *subacicularis* Hustedt, all indicating the environmental conditions mentioned above (Lange-Bertalot et al. 2017). The species has also been found in several other French lakes, such as Lac du Réaltor (Provence, France) (Fig. 3E) by Luc Ector and Carlos E. Wetzel (LIST Luxemburg) who, despite an exhaustive review of existing *Gomphonema* literature, could not assign a name to this species (Wetzel, pers. comm.). It is likely that the species is more abundant than currently known due to confusion with similar taxa, such as *G. jadwigiae* Lange-Bertalot & E.Reichardt and *G. turris* Ehrenberg (see Discussion below).

Discussion

Despite its rather large valve dimensions, its conspicuous form and structure, *Gomphonema vancampianum* could not be identified using all currently available literature. In the editorial note to Levkov et al. (2016, p. 1), Horst Lange-Bertalot wrote that "*Macedonia hosts approximately 70%, i.e. 125 of about 180,* Gomphonema *taxa currently known from all over Europe*". A thorough comparison of all *Gomphonema* species illustrated in Levkov et al. (2016) did, however, not show any similar species. Cleve-Euler (1955), often a valuable resource for unusual diatom taxa, did not report any taxon showing the same peculiar valve outline, resembling a Chinese spoon with an acute headpole. Patrick and Reimer (1975, plate 15, fig. 1) illustrated one valve that most likely is conspecific with *G. vancampianum*. The valve was identified as *Gomphonema apicatum* Ehrenberg and the drawing was based on a Boyer sample from Birges Pond, Connecticut (USA). The American population had a valve length of

45–50 µm and width of 13–14 µm. On the Diatoms of North America website, Kociolek (2011) showed several valves he identified as *G. apicatum*, probably basing his identification on Patrick and Reimer (1975), but the depicted valves differ from *G. vancampianum*. The description of *G. apicatum* is based on only two illustrations Ehrenberg (1854) published in his Mikrogeologie and, in fact, replace a species, previously named *G. augur* Ehrenberg. One of the illustrations (Ehrenberg 1854, plate IX, I, fig. 41a, b) consists of two drawings made of specimens from Ceyssat, France. These drawings originally had been labelled *Gomphonema augur* on the drawing sheet 2311, kept in the Ehrenberg collection, an additional indication that *G. apicatum* is, in fact, a superfluous name for *G. augur*. Jahn and Kusber (2004) lectotypified *G. augur*, based on material from Ceyssat, as was already suggested by Metzeltin and Lange-Bertalot (1998, p. 112). Despite being illegitimate, the name *G. apicatum* appeared in several historic diatom monographs. Cleve (1891, pp 48–49, plate III, figs 20–21) discussed *G. apicatum* and illustrated two valves whose outline resembles more *G. vancampianum* than *G. augur*. However, the valve dimensions of the specimens illustrated by Cleve are much lower (approximately half the size of *G. vancampianum*) than what was measured in all populations of *G. vancampianum* [length 22–25 µm, width 6–7 µm in Cleve (1891) versus length 30–60 µm, width 10–12 µm in *G. vancampianum*]. Most likely Cleve (1891) had illustrated *G. jadwigiae*, a species that was described from the famous Julma Öllky Lake in Finland (length 24–46 µm, width 5–7.5 µm) by Metzeltin & Lange-Bertalot in 1996. Cleve (1891) also referred to a species described by Ralfs (1843) as *G. cristatum* Ralfs that Smith (1853, p. 79) considered to be possibly a synonym of *G. augur* Ehrenberg as illustrated by Kützing (1844, plate XXIX, fig. 74). The drawings in Ralfs (1843, fig. 6) and Smith (1853, fig. 239) are indeed very similar to the lectotype of *G. augur*, illustrated in Jahn and Kusber (2004, figs 25–26). The Finnish specimen (“*aus demselben finnischen Gewässer*”), illustrated and discussed in Hustedt (1930, p. 372, fig. 696) as *G. apicatum*, most likely also represents *G. jadwigiae*, as the reported valve dimensions fit the latter (length 20–35 µm, width 6–9 µm). The same applies to Mayer (1928, p. 19) who discussed *G. apicatum*, but the drawings (Mayer 1928, plate 2, figs 16–17) and the valve dimensions (length 21–32 µm, width 6–7 µm) indicate that he most likely also refers to *G. jadwigiae*. None of these reported specimens, however, are conspecific with the species identified and discussed in Patrick and Reimer (1975) as *G. apicatum*.

Although similar in some respect (valve length, stria density, areolae discernible in LM), the North-American population, (erroneously) identified by Kociolek (2011) as *G. apicatum*, differs from *G. vancampianum*. The largest valve width in *G. apicatum* sensu Kociolek (2011) is positioned more closely to the headpole than in *G. vancampianum*. Kociolek (2011) also reported a higher valve width (13–15 µm) than measured for *G. vancampianum* (10–12 µm). Moreover, the apices in *G. vancampianum* have less developed shoulders in comparison with *G. apicatum*. The final tip on the apices in *G. apicatum* is more acute and longer than in *G. vancampianum*. The valves in *G. apicatum* gradually narrow towards the footpole, but in a straighter line than in *G. vancampianum*. It is unfortunate that the North-American population was not studied in SEM to compare the ultrastructure, which would have enabled a more thorough comparison. Finally, the shortened stria opposite the stigmoid in the central area, is always longer in

G. vancampianum, compared to the illustrated valves of *G. apicatum*. Given the differences in valve outline and valve width and, despite the plea in Abarca et al. (2020) to use molecular evidence to support a possible differentiation of two species based on outline, we consider that there are sufficient morphological differences between both taxa to justify the description of *G. vancampianum* as a separate species.

Gomphonema vancampianum also shows some resemblance to a group of tropical species related to *G. apiculatum* Ehrenberg. De Toni (1891) considered this species as a synonym of *G. augur*, but the valves from the type material shown in Reichardt (1995) show clear differences from *G. augur* to exclude a possible conspecificity. *Gomphonema apiculatum* may be conspecific with *G. vancampianum*, but with only one complete and one half specimen known and the drawing in Ehrenberg's Mikrogeologie (Ehrenberg 1854, plate IV, II, fig. 39), it is almost impossible to come to a conclusion. The general valve outline in *G. apiculatum* is different showing more compact valves with only very gradually tapering margins towards the footpole, contrary to *G. vancampianum* that has a very narrow lower part of the valve. *Gomphonema neoapiculatum* Lange-Bertalot, E.Reichardt & Metzeltin, was described in 1988 from the Essequibo River in Guyana (Metzeltin and Lange-Bertalot 1998). Metzeltin and Lange-Bertalot (1998, p. 120) stated in their discussion that it is unclear if *G. apiculatum* was validly described by Ehrenberg (1843) since the name *G. apiculatum* was put between brackets and replaced by the name '*G. augur*'. As Reichardt had illustrated 1.5 valves, identified as *G. apiculatum* from Ehrenberg's Cayenne (Guyana) material, Metzeltin and Lange-Bertalot (1998) described these valves as *G. neoapiculatum*, a species widely distributed in the Neotropics. The valves illustrated in Metzeltin and Lange-Bertalot (1998, plate 157, figs 6–9) have a distinctly different valve outline with very gradually tapering margins and a less inflated upper part of the valve, excluding conspecificity with *G. vancampianum*. In 2007, Metzeltin and Lange-Bertalot described another species in this complex, *G. perapicatum* Metzeltin & Lange-Bertalot, but this species also lacks the concave lower part of the valve and the inflated upper part, making it sufficiently different from *G. vancampianum* to be the same species. Both *G. perapicatum* and *G. neoapiculatum* have a very elongated, acutely ending upper valve part, which has never been observed in *G. vancampianum*.

A final species showing some resemblance is *Gomphonema turris* Ehrenberg, described in 1843 from North America. The taxonomic history of the species had been analysed by Krammer and Lange-Bertalot (1985) who concluded that it should be considered only a variety of *G. augur* and subsequently made the new combination *G. augur* var. *turris* (Ehrenberg) Lange-Bertalot. They illustrated the species with several pictures from a population from Manaus (Brazil), unfortunately not the type population (Krammer and Lange-Bertalot 1985, plate 37, figs 1–7) and a population based on a historic slide from the Grunow collection from Rio de Janeiro (Krammer and Lange-Bertalot 1985, plate 37, figs 1–4). Reichardt (2015b) tried to locate the type specimens Ehrenberg (1843) used for his new species. Unfortunately, since the material from West Point (New York) and Smithfield, proved to be devoid of *G. turris* following the analysis by Regine Jahn (Reichardt 2015b, p. 147), Reichardt (2015b) illustrated one valve from a Japanese population, as Ehrenberg (1854) had referred in his Mikrogeologie to both the American and the Japanese population.

The latter, however, cannot be considered type material. The morphology of the type of *G. turris* is thus unclear. Based on the illustrations in Krammer and Lange-Bertalot (1985) and the Japanese specimen from the Ehrenberg sample in Reichardt (2015b), it is clear that *G. vancampianum* is not conspecific. *Gomphonema turris* has a complete different valve outline with a clearly undulating upper part, the presence of well-developed shoulders and a distinct apiculate headpole. The valves only gradually taper from the central area towards the footpole, contrary to *G. vancampianum* where there is an abrupt narrowing of the valve width below the central area before tapering to the footpole. Bahls (2023) illustrated a population he considered being *G. turris*, but these valves may represent *G. vancampianum* as they are in clear contrast with the generally accepted idea of *G. turris*, especially when considering the Japanese specimen in Reichardt (2015b). However, the valves in Bahls (2023) present an additional narrowing of the valve near the headpole contrary to the smooth, gradual margin in *G. vancampianum*, adding doubt to the possible conspecificity. It would be a good idea to analyse *G. turris* sensu Bahls (2023) in SEM to verify whether these valves also show the typical marginal crest. It is also likely that, in the illustrated valves in Bahls (2023, plate 52), several distinct species are included, but further analysis of these populations will be necessary to clarify this. An additional difference between the generally accepted idea of *G. turris* and *G. vancampianum* is the valve width: 12–20 μm in *G. turris* versus 10–12 μm in *G. vancampianum*, although the valve length overlaps. Therefore, conspecificity with *G. turris* should at present be excluded.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Bart Van de Vijver: specimen analysis, original draft, writing, editing, Margaux Pottiez: specimen analysis, editing, Rémy Chavaux: sampling, sample 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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Research Article

A recircumscription of *Geocharis* (Zingiberaceae) as a result of the discovery of a new species in Sumatra, Indonesia

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Abstract

Recent fieldwork conducted in Sumatra resulted in unusual collections of the conspicuous ginger genus *Geocharis*, a genus that harbours a total of six species distributed in Sumatra, the Malay Peninsula, Borneo and the Philippines. After carefully reviewing types and protologues of existing taxa, we conclude that the recent collections represent a new species described here as *Geocharis globosa*, which is similar to *G. aurantiaca*, *G. rubra* and *G. radicalis* by the flowers spreading evenly in all directions but differs from these by the less divided labellum and by the unstructured and smooth globose fruits. We provide a detailed description and a photographic plate as well as a preliminary Red List Assessment for the new species. With the new species added to *Geocharis macrostemon* and *G. radicalis*, the number of species in Sumatra hereby increases to three. A recircumscription of the genus is provided, taking into account the unusual fruit character of the new species.

Key words: *Geocharis globosa*, globose fruit, Mount Marapi, taxonomy, West Sumatra, wild gingers

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Introduction

The ginger genus *Geocharis* (K.Schum.) Ridl. (Ridley 1908) harbours only eight taxa: six species, two of which have two varieties each (World Flora Online Plant List 2023; Table 1) distributed in Sumatra, the Malay Peninsula, Borneo, and the Philippines (Newman et al. 2004; Fig. 1). Morphologically, this genus is characterized by having a radical inflorescence with flowers borne in cincinni of up to two flowers and it may easily be distinguished from other genera in the Zingiberaceae by the tessellate pattern (markings in squares and rectangles) on the leaf sheath, a linear and divided labellum and a broad, toothed filament formed by fusion with the lateral staminodes. Sampling three species of the genus (*Geocharis fusiformis* (Ridl.) R.M.Sm. var. *borneensis* R.M.Sm, *G. macrostemon* (K.Schum.) Holttum, *G. rubra* Ridl.) in a molecular-based study, Poulsen et al. (2018), demonstrated that the genus is monophyletic and sister to the genus *Sulettaria* A.D.Poulsen & Mathisen.

Table 1. Accepted taxa of *Geocharis* and their distribution.

Species	Distribution
G. aurantiaca Ridl.	Peninsula Malaysia
G. fusiformis (Ridl.) R.M.Sm. var. *fusiformis*	Philippines
G. fusiformis var. *borneensis* R.M.Sm.	Borneo
G. macrostemon (K.Schum.) Holttum	Sumatra
G. radicalis (Valeton) B.L.Burtt & R.M.Sm.	Sumatra
G. rubra Ridl. var *rubra*	Borneo
G. rubra var. *puberula* Meekiong	Borneo
G. secundiflora (Ridl.) Holttum	Peninsular Malaysia

Two species of *Geocharis* occur in Sumatra, *G. macrostemon* and *G. radicalis* (Valeton) B.L.Burtt & R.M.Sm., of which only a few collections have been made (Holttum 1950; Newman et al. 2004). *Geocharis macrostemon* was first collected in 1878 by the Italian naturalist, Odoardo Beccari, in West Sumatra, in the lowland forest at Ajer Mantjoer (Lembah Anai). Currently, this is a conservation area within the Anai Valley Nature Reserve. Despite several surveys of the reserve, we were unable to collect this species again.

Geocharis radicalis was collected by Lörzing (*Lörzing 5912*) in the forest at 1000 m elevation near Deli, North Sumatra. Valeton (1921) first placed this species in *Rhynchanthus* Hook.f. whereas Burtt and Smith combined it in *Geocharis* in 1972. New material of this species is lacking and desirable.

During our fieldwork conducted in Sumatra since 2020, collections of *Geocharis* were made at Mount Marapi, West Sumatra, which differed from the two known Sumatran species mentioned above. Comparisons made to all known species of the genus, also did not result in a match.

Materials and methods

We examined collections deposited at several herbaria (ANDA, BO, E, FI, K, L, KEP, SAN, SING), as well as and high-resolution photographs of specimens (herbarium abbreviations follow Thiers 2022). A literature review was conducted on other species of *Geocharis* (Holttum 1950; Smith 1986; POWO 2023).

Morphological descriptions were primarily obtained from living material collected in the field. Fertile material was preserved in spirit while other parts were dried and pressed for the herbaria. Detail characters were observed using a stereomicroscope. The measurements were made using a ruler and image-J software. The distribution map was based on existing records as a guideline. Terminology follows Stearn (1983), Harris and Harris (2001) and Beentje (2010).

Results

The recently collected material is clearly a species of *Geocharis* due to the distinct pattern of the leaf sheath, the narrow and incised labellum and the broad and toothed filament formed by fusion with the lateral staminodes. The smooth, glabrous and globose fruits are unlike any known species and below we update a circumscription of the genus as well as describe the new species.

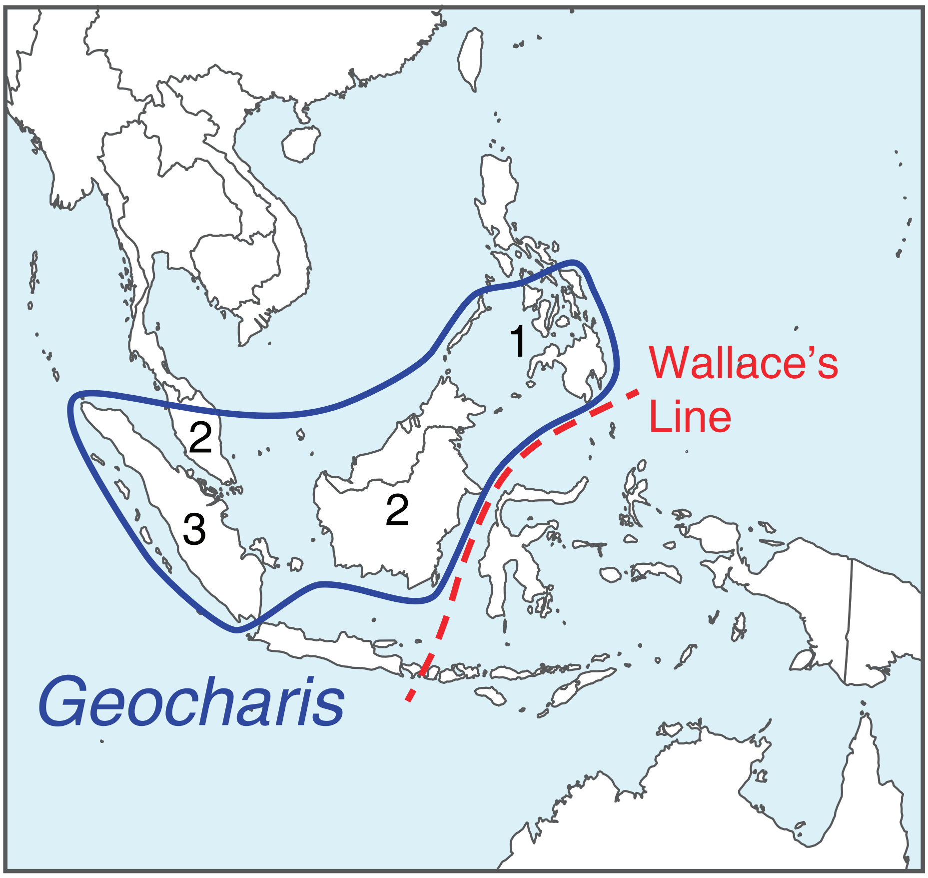

Figure 1. Distribution map of *Geocharis*. Number of species indicated for Sumatra including *G. globosa* described in the present paper. Map by A.D. Poulsen.

Taxonomic treatment

***Geocharis* (K.Schum.) Ridl.**

Alpinia Sect. *Geocharis* K.Schum., Pflanzenr. IV, 46 (1904) 363.

Type. *Geocharis macrostemon* (K.Schum.) Holttum (designated by De Boer et al. 2018: 31).

Description. Terrestrial herb with creeping rhizome, rhizome scales tessellate (with markings in squares) similar to the sheath. The leafy shoot of medium height. Sheath with remarkable white-felted cross-bars between the longitudinal ribs. Flowering shoots radical; peduncle long-prostrate, ascending or erect, with cross-barred sheaths, rachis ± curved with many flowers spreading evenly in all directions or secund. Inflorescence lax, bracts never imbricate, ± soon falling off, subtending at least two flowers in the lowermost bracts. Bracteole tubular at least at the very base. Flowers orange to red, shortly pedicellate. Calyx tubular, trilobed, apices toothed. Floral tube as long as calyx or longer. Dorsal corolla lobe larger than the laterals, enclosing the filament. Staminal tube (formed by fusion of labellum and filament) present above insertion of corolla lobes. Labellum narrow, deeply bilobed, incised in upper half or to base, lobes ± linear. Staminodes fused with filament forming a semi-tube broader than anther, apices tooth-like just below the anther. Anther oblong, crest entire, cucullate; thecae parallel, dehiscing through their entire length. Ovary globose to ellipsoid. Epigynous gland short. Stigma obcuneate. Fruit globose to elongate, smooth or ridged, often warty, glabrous or pubescent, base of calyx persistent. Seeds angular, arillate.

Etymology. The name means ground (geo) beauty (charis).

Distribution. The genus *Geocharis* occurs in Sumatra, Peninsular Malaysia, Sarawak, Sabah, and the Philippines (Fig. 1).

Note. Holttum (1950) and Smith (1986) made circumscriptions of *Geocharis*, which we have considered and expanded, taking into account the new material resulting in the new species described below.

Geocharis globosa **Zulaspita & Nurainas, sp. nov.**

urn:lsid:ipni.org:names:77344563-1
Fig. 2

Diagnosis. The new species is similar to *G. aurantiaca*, *G. rubra* and *G. radicalis* by the flowers spreading in all directions from an erect flowering shoot but differs from all of these by the labellum being incised only halfway from apex (not deeply or completely divided), and having a smooth and glabrous surface to the ovary and globose fruits (Table 2).

Type. Indonesia. West Sumatera province, Tanah Datar District, Andaleh village, 0°26'38.96"N, 100°27'20.41"E, 1149 m elevation, 26 March 2022, *Witri Zulaspita et al.* WZ29 (Holotype ANDA; isotype SING).

Description. Terrestrial, evergreen herb, forming clumps of 3–5 leafy shoots. Rhizome subterranean, 0.5–1.0 cm diam., aromatic; scales triangular, 4–6 × 2.5–3 cm, longitudinally ribbed, pale red with whitish green when fresh, pale brown when dry, lanate. Leafy shoots 2–2.5 m tall, 8–21 leaves per shoot, 13–15 cm apart; base 3.0–3.5 cm diam., bright pink; sheath dark green with irregular small horizontal white bars joining the longitudinal ribs, pubescent; ligule shortly bilobed, to 1.5 cm long, dark green, tomentose; petiole canaliculate, 1.0–1.5 cm long, green, glabrous; lamina narrowly ovate to oblong-elliptic, 48–58 × 9–10 cm, green adaxially and pale green abaxially, longitudinal ribbed, puberulent above, pubescent abaxially at margin, base attenuate, margin entire, apex caudate (1.5–2 cm long). Flowering shoot arising from rhizome, 10–14 cm distance from the base of the leafy shoot, ascending to erect, 10–25 cm long with 10–45 flowers distributed evenly in all directions, 5–15 flowers open at a time, rachis 7–15 long; peduncle 3–8 × 0.5 cm, red, glabrous; peduncular bract broadly ovate, 1.5–3 × 1–1.5 cm, pale red with irregular small horizontal white bars joining the longitudinal ribs, apex subapically mucronate; floral bract soon falling off, narrowly elliptic, 5–9.5 × 2.0–3.5 cm, reddish-brown, glabrous, subapically mucronate. Bracteole

Table 2. A comparison of species of *Geocharis* with an erect flowering shoot and flowers pointing in all directions (not secund).

Character	*G. aurantiaca*	*G. globosa*	*G. radicalis*	*G. rubra*
Labellum incision	Deeply bilobed	Halfway	Split to base	Deeply bilobed
Fruit shape	Ellipsoid	Globose (to ellipsoid)	–	Ellipsoid
Fruit macrostructure	–	Smooth	–	Ridged and grooved
Fruit surface	Verrucose	Smooth	Verrucose	Rugose

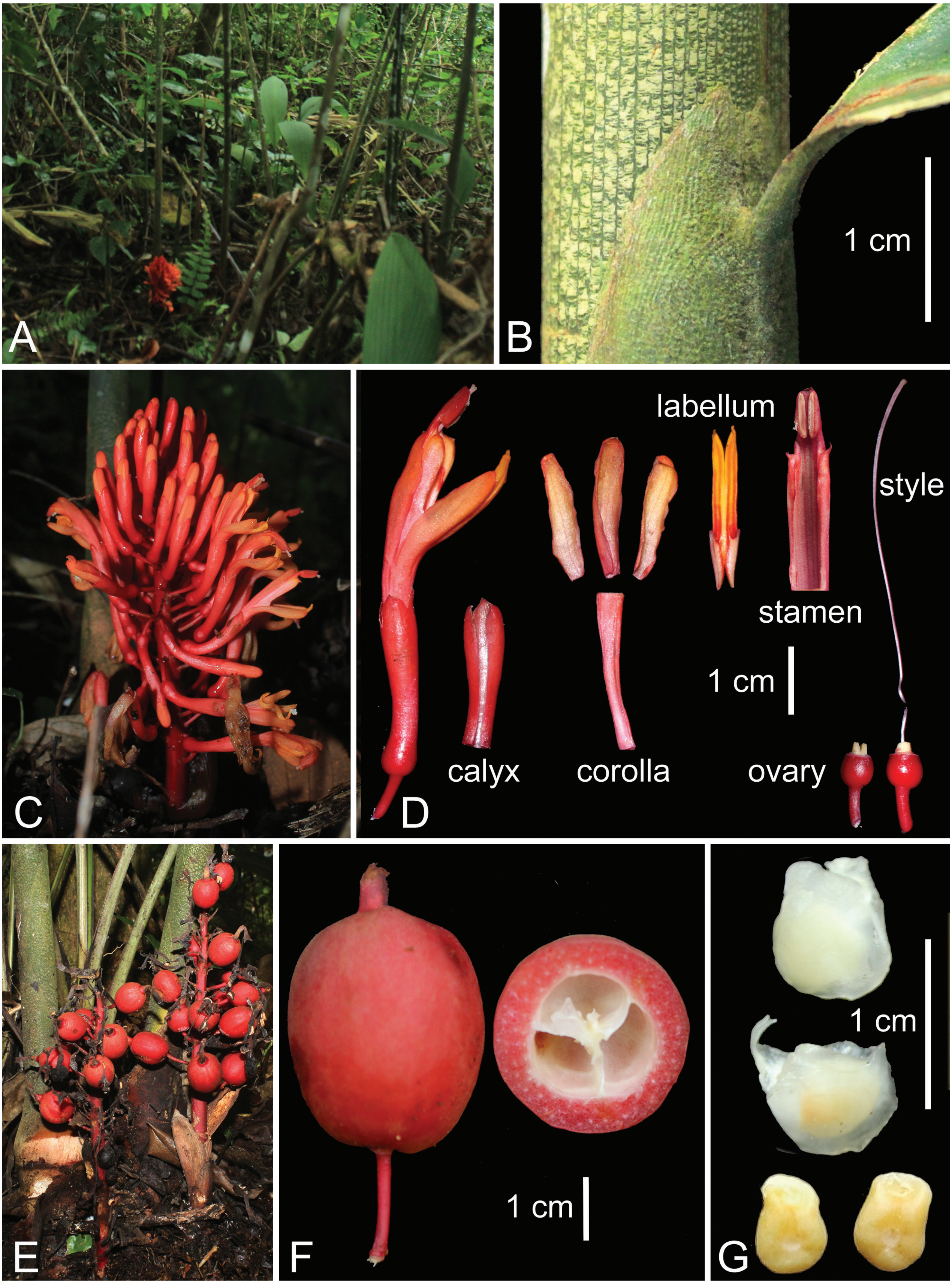

Figure 2. *Geocharis globosa* Zulaspita & Nurainas, sp. nov. **A** habit **B** sheath (with tessellate pattern), ligule and base of leaf blade **C** inflorescence **D** flower dissection **E** infructescence **F** fruit **G** seeds with and without aril. Photographs by T.A. Febriamansyah, edited by A.D. Poulsen.

narrowly elliptic, slit to base on one side, 5–7 mm long, transparent, caducous, apex irregularly bilobed, glabrous. Flower slender, 5–6 cm long; flowering pedicel 0.5–2 cm long, red, glabrous; calyx tubular, 2.0–2.5 × 0.5 cm, trilobed, puberulent, red; corolla tube 2.0–2.5 × 0.3 cm, bright pink, hirsute; dorsal corolla lobe oblong-elliptic, 1.5–2.0 × 0.5 cm, apex rounded, yellowish to red, glabrous, lateral corolla lobes oblong-elliptic, 1.5 cm × 0.3 cm, apex rounded, yellowish-red, glabrous; staminal tube ca. 5 mm long; labellum linear, bilobed, split half from apex, 10–15 × 4–5 mm, crimson with yellow edges, apex obtuse, glabrous; stamen 23–28 mm, reddish yellow, glabrous; filament 18–22 × 6–10 mm (incl. fusion with staminodes) free part 2–3 mm long, flattened, lateral staminodes tooth-like, ca. 2 mm long, pale violet, glabrous; anther 5–6 × 3–4 mm, white, puberulent, thecae, dehiscent through their entire length, pubescent; anther crest rounded, c. 1 mm long, slightly trilobed, dark-red, glabrous; ovary globose, 7 × 7 mm, smooth, red, puberulent; epigynous gland bipartite, rounded, 2 × 2 mm, yellowish, glabrous; style c. 5.5 cm long, pinkish white, setose; stigma clavate (with a lateral knob), pinkish white, ostiole apical, semi-circular, 0.5 mm across, margin ciliate. Fruit globose to slightly ellipsoid, 2–4 × 2–3 cm, reddish-orange, glabrous. Seeds irregular, ca. 6 × 5 mm (immature), aril white.

Distribution and habitat. Endemic to Sumatra and known only from the type locality (Mt. Marapi, West Sumatra). Montane forest, moist forest understorey.

Phenology. Flowering in March to June and fruiting in July to September.

Etymology. The epithet refers to the shape of the fruit.

Conservation status and preliminary IUCN Red List assessment. *G. globosa* is only known from the type locality of Mt Marapi, Andaleh, West Sumatra. The population of *G. globosa* has so far only been found at Andaleh in the border zone between Mount Merapi Nature Park and local agricultural areas. Following the IUCN Standards and Petitions Committee (2022), *G. globosa* we assess here preliminarily the status as Critically endangered (CR) based on EOO <100 km^2 (B1), limited geographic range (B1+ a, b) and a population of less than 20 individuals (D).

Additional specimens examined (paratypes). Indonesia. Sumatra. West Sumatra province, Tanah Datar District, Andaleh village, 0.442992756°S, 100.4552318°E, 1149 m elev., 2 July 2022. fruiting, *W. Zulaspita et al. WZ30* (ANDA); Tanah Datar District, Andaleh village, 0.442119833°S, 100.4542314°E, 1149 m elev, 2 July 2022, fruiting, *W. Zulaspita et al. WZ31* (ANDA); Tanah Datar District, Andaleh village, 0.440810449°S, 100.4549408°E, 1149 m elev., 30 July 2022, fruiting, *W. Zulaspita et al. WZ32* (ANDA); Tanah Datar District, Singgalang village, Trails to Mount Tandikek, 0.449753522°S, 100.3396321°E, 1195 m elev., 24 September 2023, flowering and fruiting.

Notes. *Geocharis globosa* is easily recognized by the completely smooth fruits, which are unlike any other known species of the genus. In Sumatra, it is most similar with *G. radicalis* that also has an erect flowering shoot with flowers pointing in all directions.

Further studies are needed to evaluate the usefulness of any vegetative characters, especially the ligule and petiole. The importance of pickled flowers and fruits must again be emphasized as previously pointed out by Khaw (2001) and Poulsen (2006). With only limited information about the detailed flower structure and generally lacking pickled flowers, there is yet much to learn about the floral morphology and its variation in *Geocharis*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

Ten lessons learned from the mass digitisation of a herbarium collection

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Abstract

Worldwide, herbaria maintain collections of reference specimens representing global plant diversity. These collections are a valuable resource for fundamental botanical research and applied scientific research across various disciplines, and play a significant role in addressing major societal challenges such as biodiversity conservation. The digitisation of herbarium specimens and their online dissemination is one of the most important recent developments in the curation of these collections. Digitisation significantly enhances access to the collections for the research community and facilitates large-scale analysis of biodiversity data. Digitisation also provides a means for preserving the physical specimens, as it reduces the need for handling and transportation. Rapid technological developments have greatly accelerated the rate of databasing and digital imaging of collections. Meise Botanic Garden recently completed a six-year project to mass digitise its herbarium collections of about 3 million specimens mounted on sheets and through this process we have learned valuable lessons. We have captured our experience in 10 recommendations for other collection-holding institutions to take inspiration from as they start planning their own digitisation efforts. We also present case studies where we delve deeper into certain topics as examples.

Key words: Biodiversity informatics, digitisation, herbarium specimens, natural history collections, taxonomy

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Introduction

As custodians of nomenclatural type specimens, herbaria are the foundation of plant taxonomy. They are also important as source material for new research as well as vouchers for past research. Data from herbaria have been used to assess biodiversity and monitor environmental changes (Vellend et al. 2013; Rawal et al. 2015); for phytogeography (Barney 2006; Lavoie 2013; Groom 2015; Vieira et al. 2021); in invasion biology (Fuentes et al. 2013); the history of science (Groom et al. 2014); building the plant tree of life (Bakker 2017) and many more subjects (Besnard et al. 2018; Carine et al. 2018; Heberling et al. 2019). Specifically, the Meise Botanic Garden herbarium's contribution to research can be illustrated through the GBIF resources search tool (https://www.gbif.org/resource/search?contentType=literature&gbifDatasetKey=b740eaa0-0679-41dc-acb7-990d562dfa37). These examples represent just the tip of the iceberg of what could be uncovered from the complete digitisation of specimens in herbaria and, in doing so, they fulfil target 21 of the Global Biodiversity Framework: to make data and knowledge on biodiversity globally available (https://www.cbd.int/gbf/targets/21). Furthermore, once specimens are digitised, the images are a target for machine learning to extract yet more data at increased speed and volume (Pearson et al. 2020; Nieva de la Hidalga et al. 2022). Finally, digitisation avoids unnecessary handling of the physical specimens, as this can cause damage or loss. Concurrently, it holds promise in augmenting the demand and utilisation of specimens (both digital and physical) by facilitating increased discovery.

The world's 3,522 active herbaria collectively house approximately 400 million specimens, providing comprehensive coverage of known plant life and a substantial representation of fungi (Thiers 2022). Together these herbaria are likely to possess at least one specimen of every known plant species. Yet, there is more to be done, the Global Biodiversity Information Facility (GBIF) now links to more than 118 million preserved specimens of Plantae and Fungi, meaning the majority of specimens are still to be imaged, transcribed and disseminated digitally.

Within Europe, the Distributed System of Scientific Collections (DiSSCo) is an emerging research infrastructure that aims to unify access to biodiversity and geodiversity specimens under common standards. Users of European collections will have access to, and be able to use, the full range of specimens and their data from across European institutions. Towards this vision considerable ground work has been done by creating a website with digitisation guides (https://dissco.github.io/) and the DiSSCo Knowledge Base (https://www.dissco.eu/services/knowledge-base/). Additionally, the iDigBio project (https://www.idigbio.org/) in the United States of America has extensive documentation on the digitisation of collections.

The herbarium of Meise Botanic Garden (BR) is, with its collection of around 4 million specimens, the 15th largest herbarium in the world, and is part of the DiSSCo infrastructure. In 2021 the Garden completed two 3-year projects to mass digitise (imaging the specimens and transcribing the label information) its herbarium collections of 2.8 million sheets. During the first project (2015-2018) 1.2 million herbarium sheets from the African and Belgian collection were digitised. During the second project (2018–2021), we have digitised 1.4 million specimens from the general herbarium. Through these two projects we have learned valuable lessons. Digitising a collection is a big undertaking for a herbarium, involving everyone from curators, technicians and scientists to management, human resources, ICT and accounting (Helminger et al. 2020; De Smedt and Bogaerts 2022a, 2022b; Thompson and Birch 2023). The rewards are numerous and it is well worth the effort, but it is important to know what you are letting yourselves in for and plan accordingly. Here we've tried to capture our experience in 10 recommendations for other institutions to take inspiration from as they start planning their own digitisation efforts. We also present case studies delving deeper into some of the issues we faced as examples.

10 lessons learnt from the mass digitisation of a herbarium collection

1. Knowing yourself is the beginning of all wisdom — Aristotle

Just as it is easy to assume you know yourself before life proves you wrong, it is easy to assume you know your collection. The process of digitisation delves into every dark corner and if there are skeletons hiding, they will be discovered. Most collections do have rough counts of their holdings, but few are really sure how many objects they actually have, because collections are compiled over hundreds of years and not always well documented. A detailed inventory of a representative tenth of your collection can be extrapolated to the entire collection (De Smedt and Bogaerts 2022b, https://dissco.github.io/Digitisation/PreDigCuration/PDCaseStudies.html#estimation-of-the-numbers-of-the-african-and-belgian-herbarium-collection-at-meise-botanic-garden). This will give you a good idea of how many objects you have, so that you can confidently budget for digitising that number (Table 1). While counting, you can also perform other checks: What is the curatorial state of the objects? Where do they come from? What size are they? What information is available on the covers, shelves and cupboards? Are the objects barcoded? How fragile are they? etc. (De Smedt and Bogaerts 2022b; Van Baelen et al. 2022).

Different types of objects require a different approach to digitisation and should be processed together. Some collections are more amenable to mass digitisation than others and require less expertise from digitisers. Flat herbarium sheets, for instance, are much easier to digitise using conveyor belts (Fig. 1) than blocks of wood or specimens in jars or envelopes.

Figure 1. Mass digitisation of herbarium specimens on a conveyor belt at Meise Botanic Garden, allowing the imaging of 3,000–5,000 specimens per day.

Table 1. Example of estimated numbers and actual counts of specimens in the African herbarium at Meise Botanic Garden. Estimated numbers are based on a 10% count of the collection.

	African herbarium	DR Congo, Rwanda and Burundi	Other African countries
Estimated number	904,003	515,784	399,218
Actual counts	953,748	520,106	432,642

The way specimens are stored can also provide information. If the specimens are arranged by scientific name or country of origin, then during digitisation the name or country only needs to be noted each time it changes in the sequence.

2. Prioritise (if lack of money forces you to do so)

Whether you're digitising your entire collection or just part of it, you have to prioritise the order. Every collection has its own priorities, but you should consider the size, collection type, origin, state of curation, scientific importance, historical importance and stakeholders like internal and external scientists, policy makers and funding bodies (Ahl et al. 2023).

Based on our experience, we recommend digitising the entire collection - in our case all specimens mounted on sheets. It is faster and more cost-effective than to select subcollections or, even worse, select individual specimens. Don't underestimate the logistics of retrieving and moving specimens around to be digitised. Partly digitising the collection can also create a significant management overhead and can imply different approaches to update the collection.

3. Learn from other people's successes - and mistakes

Do not reinvent the wheel. Learn from others' experiences and mistakes. Visit other institutes and talk to the project managers who have already gone through the process. Ask for tips and tricks, do's and don'ts. Use their experience to make your mass digitisation project run as smoothly as possible. If you think you have a better way of doing things, talk it over with someone with experience. Get to know where the pitfalls are, and things you need to take into account when setting up a project. One way to meet the community is through the Consortium of European Taxonomic Facilities (CETAF) who run a specific working group on digitisation. Use guidelines that are already available (https://www.dissco.eu/services/knowledge-base/; https://dissco.github.io/; https://osf.io/eaz38/wiki/home/; https://www.idigbio.org/wiki/index.php/Digitization_Resources) and adapt them to your needs.

Also, talk to digitisation companies that have worked with similar collections to see what is possible with your collection. They may see your collection and project from a different perspective and they can come up with solutions that you may not have thought of. This will also help you write the tender if you are planning to outsource any of the processes. Ensure you familiarise yourself with government and institutional procurement guidelines before you reach out to digitisation companies.

4. Decide whether you do it yourself or have it done for you

A mass digitisation project requires many resources, not only money to pay for equipment, supplies and outsourcing, but also personnel with the right skills. You will need people to maintain and prepare the collections, project managers, human resource managers, financial managers, technical and informatics personnel (De Smedt and Bogaerts 2022b; https://dissco.github.io/Digitisation/PreDigCuration/PDCaseStudies.html#staff-list-for-mass-digitisation-project-doe-at-meise-botanic-garden). Match the right profiles to the right tasks to have an overview on the resources that are needed to conduct each task in the process. Some people will have to wear more than one hat and it is important that those hats fit comfortably. An overall project manager dedicated to the digitisation project is an absolute must to make the project successful. Take into account that some daily tasks will move to the background, as more time is going to the digitisation project.

Do you have enough financial resources in your organisation? Or do you need to apply for funding? Explore opportunities regionally, governmentally, internationally, to a foundation or elsewhere. Consult other institutions to find out how they acquired funding for digitisation. Also, be aware that there are strings attached to funding. There may be restrictions on what the money can be used for, some funding agencies only supply money for subcontracting, while others pay for supplies or hiring personnel.

Based on the available funding, that needs to be in place prior to starting, and resources, you can decide which processes to outsource and which to do in house. Possible tasks to outsource may be the restoration, decontamination, mounting, barcoding, packing and transport of specimens, imaging, quality control of the images, long term preservation of the images, transcription of the label data, or website development. Remember that when you are outsourcing, you still need someone in your organisation who will coordinate the relationship with the external partners.

5. Make a plan

Now you can use your list of resources to prepare your plan. It should include the necessary workflows (Fig. 2; https://dissco.github.io/HerbariumSheets/MeiseBGHerbariumSheets.html), procedures and tracking systems for all the steps in the digitisation process, whether or not they are outsourced or done in house. Write down what you want and how you want to get it done in as much detail as possible. Don't forget quality control of the images and the data (see lesson 8), because it is easily underestimated what a huge and important task it is.

When writing tenders for the parts you want to outsource, be as specific as you can to clarify your needs, use examples and add additional information like internal quality control procedures, floor maps, images of your collections, descriptions of your collections, especially where hazardous materials are used. When outsourcing transcription, examples of labels, handwritings and signatures help frame discussions. Clarifying upfront how the tender applications will be evaluated will avoid misunderstandings. Include how well the applicants organise their answers to the tender proposition.

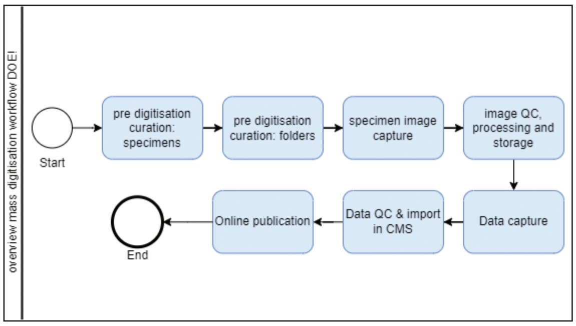


Figure 2. Overview of the mass digitisation workflow for outsourcing at Meise Botanic Garden (based on De Smedt and Bogaerts 2022a).

6. Go shopping

Once you have your plan ready, you can start listing the necessary supplies. You will definitely need barcodes for each specimen. If you want to replace old folders/jars/boxes, make sure you order enough. It is cheaper to buy in bulk. If you plan to restore specimens before starting the digitisation process, make sure you have adequate supplies and storage space before starting.

The IT infrastructure for image storage, software for image quality control and data transcription, and computers all need to be in place before you start digitising.

Find the necessary floor space for your imaging infrastructure and buy/rent the necessary parts for the installation like cameras, lighting, tables, computers, software, storage, logo of your institution, colour bars and scales.

7. Make your collection look its best for the photographer

In preparing your specimens for imaging, incorporate some pre-digitisation curation steps into your process like repairing and restoring specimens that may not be in optimal condition (Fig. 3; case study 1). This can be combined with adding a barcode to each sheet and marking specimens that don't need to be photographed, for example because an image already exists of the specimen.

When opportune you can rearrange the sheets and update taxonomy at the same time. If the specimens need to be transported before imaging, appropriate packaging is needed (Giraud et al. 2019). Also think about pest treatment in the whole process, especially when the specimens are leaving the collection building (Giraud et al. 2019).

Figure 3. Joint restoration session of the herbarium team at Meise Botanic Garden.

Remember to retrieve specimens loaned out to other institutes to make your collection as complete as possible before digitisation. Start this step well in advance because it may require considerable time to get your specimens back.

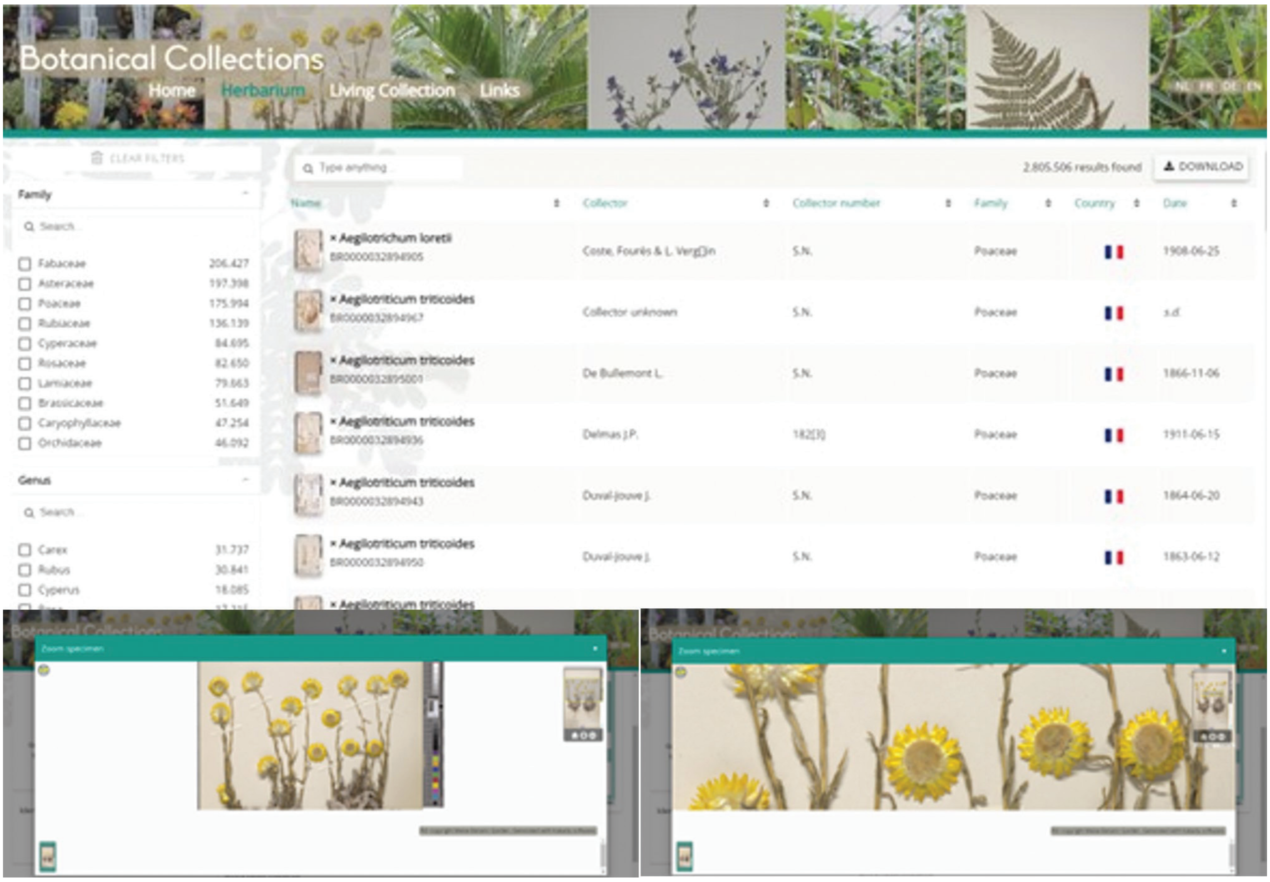
8. Expect problems, particularly ones that you don't expect

Equipment malfunctions and human mistakes are inevitable. You can do everything to avoid problems, but expect the unexpected. To avoid a problem turning into a disaster you will need a quality control process (Nieva de la Hidalga et al. 2020). This process should occur promptly after image capture, allowing for rephotographing of specimens before they are reshelved if issues arise. Some quality checks can be automated, including file size, embedded image metadata (i.e. Exif), barcode readability and conformity to standards, such as ISO 12234-2 for Tag Image File Format (TIFF). Other quality elements need human evaluation, such as focus, lighting and colour. All images cannot be inspected by a person, but a sub-sample can be inspected. If a problem is detected, then chances are high that the whole batch will have to be rejected, as quality issues tend to affect multiple images on production lines. Once the decision has been made to reject a batch there must be a mechanism to escalate the issue, correct the problem and clean the workflow of the rejected files.

Checking the quality of transcribed label data is another crucial step in the process. You will need a clear and detailed transcription protocol where your quality control process is set out (case study 2). Where possible, the use of lookup tables will greatly improve the quality of the transcribed data. Direct data quality control on a subset of the transcribed labels will help to reduce transcription errors (https://dissco.github.io/Digitisation/PreDigCuration/PDCaseStudies.html#quality-control-procedure-of-meise-botanic-garden-for-the-mass-digitisation-project-doe). This is particularly important at the beginning of the transcription process to weed out common errors and misunderstandings. Once the transcription process is complete, the data cleaning phase will start. Allow sufficient time for this task, as it often requires more time than initially anticipated. Tools like Open Refine (https://openrefine.org/) can be used for data cleaning. The process is often iterative, as corrected data in one field can often be used to fix data in another field.

9. Make your data visible - make a big deal of it

Digitisation of a herbarium is pointless if the data are not made publicly accessible. Don't be shy; make sure everyone knows what you have achieved. Your herbarium is coming of age and it should be celebrated. To ensure that everyone can find and use your digitised herbarium, images and their metadata need to conform to the FAIR principles (Wilkinson et al. 2016). Institutions generally opt to create an online portal to their collection where they can showcase their specimens (Fig. 4). Make sure you are aware of the state of the art for such portals and how your specimens can be cited (Güntsch et al. 2017, case study 3). There are also other outlets for your images that will extend the reach of your collection to different communities. JSTOR Global Plants specialises on nomenclatural type and historical specimens, but is behind a paywall, while publishing on Wikimedia Commons allows your specimens to illustrate species



Family

☐ Fabaceae	206.427
☐ Asteraceae	197.398
☐ Poaceae	175.994
☐ Rubiaceae	136.139
☐ Cyperaceae	84.695
☐ Rosaceae	82.650
☐ Lamiaceae	79.663
☐ Brassicaceae	51.649
☐ Caryophyllaceae	47.254
☐ Orchidaceae	46.092

Genus

☐ Carex	31.737
☐ Rubus	30.841
☐ Cyperus	18.085

Name	Collector	Collector number	Family	Country	Date
× Aegilotrichum loretii BR0000032894905	Coste, Fourès & L. Verg[]in	S.N.	Poaceae	🇫🇷	1908-06-25
× Aegilotriticum triticoides BR0000032894967	Collector unknown	S.N.	Poaceae	🇫🇷	s.d.
× Aegilotriticum triticoides BR0000032895001	De Bullemont L.	S.N.	Poaceae	🇫🇷	1866-11-06
× Aegilotriticum triticoides BR0000032894936	Delmas J.P.	182[3]	Poaceae	🇫🇷	1911-06-15
× Aegilotriticum triticoides BR0000032894943	Duval-Jouve J.	S.N.	Poaceae	🇫🇷	1864-06-20
× Aegilotriticum triticoides BR0000032894950	Duval-Jouve J.	S.N.	Poaceae	🇫🇷	1863-06-12

Figure 4. Screenshots of the virtual herbarium platform of Meise Botanic Garden (https://www.botanicalcollections.be), showing the start page and a detail of a specimen of *Helichrysum aureum*.

on Wikipedia. As long as you use suitable licences, like CC BY or CC0, for your images, Wikipedians can use them freely. Your data should also be published to the Global Biodiversity Information Facility (https://www.gbif.org/publishing-data). A great advantage of this is that your dataset will be citable with a Digital Object Identifier (DOI). GBIF keeps track of publications citing their DOIs so you too can see who is using your data and why (https://www.gbif.org/literature-tracking).

Develop a Data Management Plan that outlines a strategy for handling, storing, and sharing of data (Dillen et al. 2024). Such a Data Management Plan aids in establishing clear guidelines for both internal staff and external users, specifying the terms governing data usage (including licensing) and storage.

10. Save your data for the future

Backing up your data in a long-term offsite archive is an essential insurance against the loss of data and images. Depositing your images in that sort of cold storage should be part of the daily workflow of the digitisation pipeline. Think carefully about the formats of data too. Long-term storage formats, such as archive quality TIFF images, are not as suitable for day-to-day use as high quality jpg images. Storage will be an ongoing cost beyond the digitisation project and the institution will have to be able to sustain these costs (case study 4).

Conclusions

Now that you have read our ten lessons, you should be ready to start your own mass digitisation project. Be well prepared, divide the work into manageable small tasks. When creating workflows, protocols, specifications and tenders, be as specific and detailed as possible, it will save you a lot of worries in the future.

When the mass digitisation process is complete you will reap the benefits: your collections will be more visible and used, digitisation will lead to even more projects and new types of research.

The daily management of the collection will also change, becoming more labour intensive: all incoming material needs to be digitised before entering the collection, errors will be more noticeable and need to be fixed, and the rearrangement of the collection needs to match the data in the collection management system. You not only have a physical collection to maintain but a digital one too!

Case Study 1: Pre-digitisation curation

Our first and second mass digitisation projects employed different pre-digitisation approaches, because we had learned from the first project and adapted the workflow for some processes in the second project.

The first adjustment occurred in the preparation of herbarium sheets.

In the first project, 15 herbarium technicians worked 3 hours daily in the collection to make it ready for digitisation. Scattered throughout the collection, they meticulously checked every herbarium specimen, removed cellophane, plastic bags and paperclips, transferred loose material to envelopes, and added a barcode to each sheet. Sheets with multiple collections or specimens kept completely in envelopes were extracted from the collection to be digitised in-house. They also marked the specimens that were already digitised in the past, as well as sheets containing printed literature and pictures so the external digitisation company would recognise these as specimens not to digitise. A detailed workflow can be found on the following website: https://dissco.github.io/HerbariumSheets/MeiseBGHerbariumSheets.html#workflow.

It took us 1.5 years to finish the preparatory phase. This work came on top of the technicians' regular work so some tasks needed to be postponed, such as processing incoming material and issuing loans. The labour-intensive nature of this process led to waning enthusiasm among staff.

Consequently, the approach for the second mass digitisation project underwent considerable revision. We decided to outsource the barcoding to an external company, a task which could be done at the conveyor belt when the specimens were laid out for imaging. Restoration efforts were drastically reduced, limited only to new arrivals, which were prepared on a weekly basis. During these weekly sessions, staff gathered in a dedicated room to check and restore specimens, having a little teambuilding moment at the same time while enjoying refreshments. This revised approach proved more sustainable and enjoyable, with preparation sessions now continued bi-weekly.

In the herbarium, the only task undertaken was tagging previously digitised specimens from past projects. Specimens in envelopes were tagged during transcription of the labels by the external company.

Case Study 2: Label transcription

Numerous meetings were convened to determine the approach of label transcription and the specific fields to be transcribed. The outcome was to have multiple approaches depending on the collections. In general, we aimed to transcribe all key information fields essential for most scientific purposes, as agreed in de MIDS standards (Minimum Information about a Digital Specimen) (Hardisty et al. 2023). This resulted in a MIDS-2 level for most of the specimens.

At the start of our first project we opted to enter minimal data directly into our collection management system, BGBase. The fields that were transcribed in house by our technicians and volunteers included barcode, filing name, collector, collector number and country. For the central African specimens (specimens from DR Congo, Rwanda and Burundi) the phytoregion was also transcribed. This decision stemmed from budgetary constraints, as we were uncertain about funding for outsourcing transcription. For the remaining part of the African collection, we decided to outsource the transcription of the following fields: filing name, barcode, collector, collector number, country as given, country code, phytoregion, collection date, locality, altitude, altitude unit and coordinates as given. Label transcription was done based on the images by Alembo (https://alembo.nl/), a subcontractor of Picturae (https://picturae.com). A protocol was established by Picturae, Alembo and BR, and lookup lists were foreseen by BR for filing names, collectors, phytoregions (only for the first mass digitisation project) and countries. After multiple quality control steps (by Alembo, Picturae and Meise Botanic Garden), data was integrated in our collection management system.

For the Belgian herbarium, we created a multilingual crowdsourcing platform, DoeDat (www.DoeDat.be), where volunteers transcribed label information. We posted projects of around 2000 specimens per project so that citizens could help transcribe label information. We asked the public to transcribe all available label information on each specimen. We had foreseen a template with all possible fields and the necessary tutorials. DoeDat continues to assist with other collections. After finalisation of a DoeDat project, data is exported, cleaned and imported in our collection management system.

In the second mass digitisation project, the transcription of all specimens was outsourced to Alembo and Picturae. The same approach was used as in the first mass digitisation project, the same fields were requested in addition to collection name, curation notes with indications of multiple collections or envelope storage. These extra fields were added because of the different approach in pre-digitisation curation (see case study 1). The collection name field was added because the general herbarium contains much more different and older specimens, and thus handwritings that are more difficult to read than the African herbarium. This way we could easier group the specimens and facilitate the data cleaning afterwards.

The prospect of using Artificial Intelligence was not considered back in 2015, when we started the mass digitisation project. Although OCR was discussed, the high experimental cost at that time seemed to outweigh its potential benefits especially for handwritten labels. The use of AI for label transcription has since evolved considerably and should thus be considered in future digitisation projects.

All label information is made accessible on our virtual herbarium www.botanicalcollections.be.

Case study 3: Development of the virtual herbarium portal and licensing

Given that our collection management system, BG-Base, lacks direct website integration capability, we opted to develop our own virtual herbarium portal www.botanicalcollections.be with assistance from an external IT consultant. We continue to rely on external development for new features and maintenance, while an internal staff member is responsible for communication and coordination between the Garden and the developer, as well as for minor changes and fixes. This approach, though resource-intensive due to the rapid evolution of online software technology, proves more cost-effective than hiring and retaining an internal developer with all the required expertise and experience.

On our data portal, users can search for specimens using the following fields: barcode, family, genus, species name, imaging status, type specimen, country, collector, collector number, collection year, kind of specimen and collection. A general search box that searches through a combined set of indexed data elements is also available. The interface can be set in all official Belgian languages (Dutch, French and German) as well as English.

Specimens on our data portal all have a unique stable identifier, following the CETAF persistent identifier specification, and this way the data is also available in machine-readable RDF format (Güntsch et al. 2017). There are also links to IPNI, Tropicos and BHL. The portal holds data from other Belgian herbaria as well, such as sub-collections of Ghent University (GENT) and the Université Libre de Bruxelles (BRLU). The domain name and site description were kept generic so as to cover the scope of making data available for any Belgian botanical collection. As digitisation of collections in Belgium continues, we expect more data from other collections to flow in.

It is possible to download data from our website in bulk for free, but a valid e-mail address is required for notification as such downloads are produced asynchronically. Data exported this way makes use of the Darwin Core data standard. Images can be downloaded through the interface at high resolution, but we do not offer an easy method to acquire them in bulk. This is a necessary evil to make it more difficult for web-scraping bots to overload our servers.

The website is hosted using the App Engine of Google Cloud services, to facilitate deployment of new features and make use of flexible hardware resources. Images are served from lossless JPEG2000 files through the Internet Imaging Protocol (IIP), to make them available for scientists with no reduction in quality or resolution. Given the large storage requirements for these files (> 200TB) and the associated high costs of actively storing them in the cloud, they are made available from servers hosted locally in the garden. Images are also available through a IIIF server that is similarly hosted at the Garden.

We make regular exports from our CMS to keep the data of the website up to date. We also host our own local IPT (Integrated Publishing Toolkit) instance to serve our specimen data to the Global Biodiversity Information Facility (GBIF), an international biodiversity data aggregator. The Botanical Collections data portal serves as the primary method to make our digitised collections available to the public. For GBIF, we apply an additional layer of quality control to ensure the associated data of specimens is as scientifically accurate as possible.

Data of our specimens is licensed under a CC BY licence and our images under a CC BY-SA licence (Dillen et al. 2024). Open data remains a contentious topic among the different users and providers to a herbarium collection. Development of the Botanical Collections portal was preceded by a stakeholder analysis (Vissers et al. 2017), from which a compromise vision for the portal's access policies was distilled. Our data management plan has evolved over the years and all data is now available under a Creative Commons licence. Discussions on licenseless (Public Domain) publication of data continue and we have for instance published a minimal set of metadata this way to the Europeana platform.

Case study 4: Image storage

In today's digital age, the management of vast amounts of data, including images, is a crucial aspect. At Meise Botanic Garden, we employ a meticulous strategy for image storage, prioritising quality, security, and accessibility.

Our process for accepting and checking images is key to our storage system. Before archiving, each image goes through strict screening to meet our standards. Automated checks verify filename, file size, structure, resolution, and cropping, while visual inspections ensure quality and reliability (Nieva de la Hidalga et al. 2020).

After passing quality control, images are stored on two archive servers with capacities of 90TB and 112TB. Each server is backed up at a second location within the garden. We keep JPEG (jpg) and JPEG 2000 (jp2) versions locally for quick access, while the original TIFF files are stored with an external partner, Meemoo (https://meemoo.be). Meemoo employs cold storage on tape drives across three different locations, ensuring redundancy and long-term preservation. We use the TIFF format for long-term archiving due to its reliability and longevity. TIFF files provide a robust container for image data, safeguarding against format obsolescence and ensuring compatibility with future systems.

In our system, JPEG files serve as the go-to option for quick views on our portal, providing users with rapid access to image content. Conversely, JPEG 2000 files are instrumental in tiling via IIP MooViewer, enabling efficient and customizable image display across various platforms.

To facilitate access to archived images, we've implemented a reverse-proxy system coupled with an online webservice. This setup allows for quick queries, enabling our application to pinpoint the exact archiving server housing the required image. A Redis database in the background ensures rapid retrieval of image paths, enhancing efficiency.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

SDS: Conceptualization, Writing - Original draft, Visualization, Supervision, Project administration, Funding Acquisition. AB: Conceptualization, Writing - Original draft, Funding Acquisition. NDM, MD, HE, PVW: Data Curation, Writing - Review and Editing. FL, QG: Conceptualization, Writing - Original draft.

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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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Review Article

Redefining the megagenus *Erica* L. (Ericaceae): the contributions of E. G. H. Oliver and I. M. Oliver (née Nitzsche) to taxonomy and nomenclature

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Abstract

The megagenus *Erica* L. (Ericaceae), as it is recognised today, includes 851 species of evergreen shrubs or small trees, the majority of which are endemic to the Cape Floristic Region of South Africa. From the first descriptions in Linnaeus's *Genera plantarum*, a succession of authors ascribed the steadily accumulating numbers of known species to various of a total of 72 different genera. Until the latter half of the twentieth century, so called 'minor genera' such as *Philippia* Klotzsch and *Blaeria* L. were still recognised for many African species. The now uncontroversial inclusive circumscription of *Erica*, and a substantial proportion of its currently recognised species diversity, was conceptualised, described, and illustrated by the South African botanists E. G. H. ('Ted') Oliver and Inge M. Oliver in a succession of works published from 1964 to the present day. We review the historical development of generic delimitation in *Erica sens. lat.*, focusing on the contribution of the Olivers to the current state of systematic knowledge of the genus, and presenting an overview and complete lists of literature and of taxa that they authored.

Key words: Ericoideae, nomenclature, taxonomy

Introduction: historical conspectus

Erica L. (subfamily Ericoideae, family Ericaceae), as understood today, is one of the largest genera in the Angiospermae. World Flora Online (WFO; www.wfo.org) currently recognizes 851 included species (https://wfoplantlist.org/taxon/wfo-4000013772-2024-06; Oliver et al. 2024; Elliott et al. 2024). Within this concept of *Erica*, 72 genera that were designated and named at various times since 1753 have been subsumed – some of these were known informally as 'minor genera' following Phillips's use of that phrase (Phillips 1944), until the major revision by E. G. H. Oliver 'sank' all of them into *Erica* (Oliver 2000a; Oliver and Oliver 2000a).

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† Deceased.

The taxonomic and nomenclatural history of *Erica* is complicated. Carl Linnaeus's *Genera plantarum* (Linnaeus 1737: 110) and *Species plantarum* (Linnaeus 1753: 112, 352–356) are the starting points for modern classification and nomenclature (Oliver 2007; Jarvis 2007). In the first edition of *Genera plantarum*, Linnaeus (1737: 110 genus no. 312) defined *Erica* in just 51 Latin words, exclusively referring to the anatomy and morphology of the flowers, placing the genus in Class VIII 'Octandria Monogynia' based on the numbers of male (eight stamens) and female (one gynoecium) organs in each flower. (By way of contrast, the most recent definition of *Erica* (Oliver 2000a) exceeds 350 words (in English) (Suppl. material 1) (for a more succinct description, about 100 words, see Oliver 2004).)

In the first edition of *Species plantarum* Linnaeus described and named only 23 species of *Erica*. His artificial method of classification led him to nest the widespread, northern-hemisphere shrubby *Calluna vulgaris* L. within *Erica* (as *Erica vulgaris* L.: Linnaeus 1753: 352 no. 1). On the same artificial basis, another *Erica*-like African shrub with only four stamens and a solitary gynoecium ('Tetrandria Monogynia'), was placed by him in a separate genus named *Blaeria* L. (as *B. ericoides* L.: Linnaeus 1753: 112). Forty-eight of the binomial names published by Linnaeus in eight works produced during his lifetime – in *Species plantarum* (Linnaeus 1753) and its second edition (Linnaeus 1762), a dissertation defended by Jacob Printz entitled *Plantae rariores Africanae* (Linnaeus 1760), the tenth and twelfth editions of *Systema naturae* (Linnaeus 1759, 1767a), two editions of *Mantissa plantarum* (Linnaeus 1767b, 1771) and in a second dissertation *De Erica* (Linnaeus 1770) defended by Johan Adolph Dahlgren – are still in use in *Erica* (see entries in Jarvis 2007: 497–501). Since Linnaeus's time, the number of taxa recognized as belonging to *Erica* has multiplied vastly, presenting today's taxonomists with not a few difficulties in delimiting taxa at generic and subgeneric levels.

Vegetatively, *Erica* species (commonly called heaths or heathers) are relatively similar, being shrubs or less frequently small trees with small, evergreen, linear-oblong ('needle-like') leaves arranged in whorls. The leaves often have revolute margins that can touch on the underside – this general type of leaf morphology is termed 'ericoid'. As the individual taxa are so similar in foliage, taxonomists, since Linnaeus's time, have traditionally relied on floral characteristics to demarcate subgeneric taxa and distinguish between species, rather than foliage morphology (for example, see Linnaeus 1770) (Fig. 1). Linnaeus (1753: 352, 354) used the presence/absence of a pair of awns at the base of each anther to subdivide the species he knew – ten species with awned anthers ('Antheris bicornibus') were separated from thirteen species with muticous (without awns) anthers ('Anteris [*sic*] simplicibus obtusis emarginatis'). With additional species to accommodate, this scheme was modified to separate those species with included stamens – stamens that did not protrude beyond the mouth of the urn-shaped or tubular corolla – from others with exserted stamens (Linnaeus 1770) (Fig. 1). The number and morphology of the stamens in the flowers of shrubs that could be recognized as *Erica*-like continued to dominate *Erica* taxonomy until the end of the twentieth century. Additional characters linked with the morphology of the gynoecium, particularly the number of locules (ranging from one to eight) comprising the ovary and the number of ovules per locule, and whether the mature capsule was indehiscent or dehiscent, were employed in generic definitions.

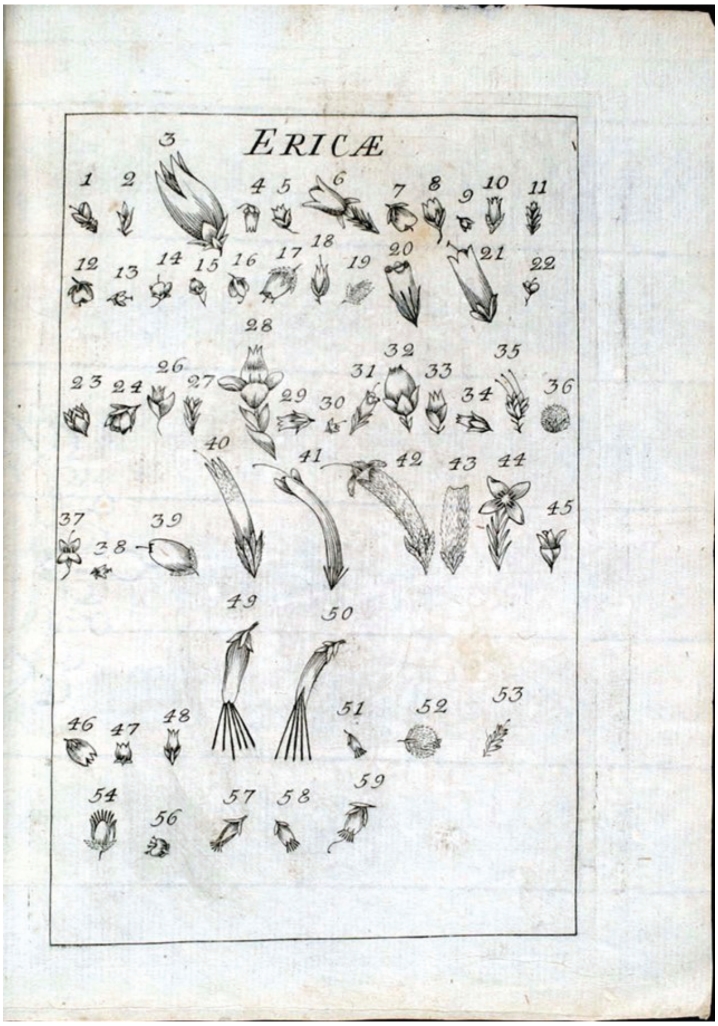


Figure 1. Flowers of *Erica* species known to Carl Linnaeus, from Linnaeus (1770).

The eighteenth-century and nineteenth-century botanists who worked to identify, name, and describe *Erica sens. lat.* species and who attempted to subdivide the numerous species into discrete genera were almost all based in Europe. A few had travelled and collected in Africa. Thus, most of their work entailed examining a relatively small number of pressed and dried specimens. Access to living material was largely limited to the species indigenous in the northern hemisphere, and to the relatively small number of cultivated plants maintained in European gardens. While there was a ‘mania’ for cultivating southern African *Erica* (the so-called ‘Cape heaths’) particularly during the first part of the nineteenth century (Nelson and Oliver 2004; Nelson and Pirie 2022), the plants grown were neither representative of the genus throughout its geographical range nor of its complex morphology. Small-flowered wind-pollinated heathers, for example, were not fashionable and did not attract gardeners. Besides, artificial and accidental cross-pollination in cultivation had produced a plethora of hybrids that tended to be preferred by horticulturists. The major attempts to produce monographs about *Erica* were thus both incomplete and compromised.

The only universal treatment available before 1900 was George Bentham’s contribution to the seventh volume of "Agustin Pyramus de Candolle’s Prodromus systematis naturalis regni vegetabilis" published in 1839 (Bentham 1839;

see also Nelson 2005). In late 1906, when the Ericaceae section (parts 1–3) of the fourth volume of "Flora Capensis" (Bolus et al. 1905 [–1906]), covering the plants of southern Africa, was completed, an integrated treatment of diverse *Erica* flora of the Cape Floristic Region became available. This treatment of *Erica* (in a restricted sense) had been produced by Francis Guthrie (1831–1899) and Harry Bolus (1834–1911) (with assistance latterly from his future daughter-in-law, Harriet Margaret Louisa Kensit (*olim* Bolus) (1877–1970)), botanists who lived in the Cape Province of South Africa where *Erica* species are indigenous and numerous. Regarding their concept of *Erica*, Guthrie and Bolus (1905: 5) commented that 'The genus is remarkable for an unusual degree of variability in the form of almost all its organs. It is therefore one difficult of definition as to its species and of arrangement into satisfactory natural groups.' They had subdivided the 469 southern African species of *Erica* that they recognized into five subgenera and 41 sections, as well as accepting that close to 160 other species should be placed outside *Erica* in 22 'minor genera' (Phillips 1944: 69; Oliver 2000b: 55). These 'minor genera', six being monotypic, were treated by Nicholas Edward Brown (1849–1934), a botanist based at the Royal Botanic Gardens, Kew (Brown 1906). However, many other species native elsewhere in tropical and subtropical Africa and on Atlantic and Indian Ocean islands were not integral in this treatment. Edwin Percy Phillips (1884–1967) was the next to tackle the complexities of the African *Erica sens. lat.* His treatments of Ericaceae (Phillips 1926, 1944, 1951) also include *Vaccinium* L. (Vaccinioideae), represented by a single species now treated as *V. exul* Bolus, which occurs on the Eastern Escarpment (Mpumalanga and Limpopo Provinces), in Swaziland and in Malawi, in habitats above 1,200m altitude (Bester 2015). All other Ericaceae in South Africa represent *Erica sens. lat.* In his paper 'Notes on the minor genera of Ericaceae', Phillips (1944) reduced the 22 'minor genera' retained in "Flora Capensis" to six, a scheme he maintained in the second edition of his "The genera of South African flowering plants" (Phillips 1951). Emphasising that he considered that the number of ovules per locule was 'a more important character than the number of ovary-chambers [locules]' in any attempt at a natural classification of the South African Ericoideae, Phillips (1944, 1951) retained only *Erica* L., *Blaeria* L., *Eremia* D.Don, *Sympezia* Licht., *Scyphogyne* Brongn., *Salaxis* Salisb. and *Lagenocarpus* Klotzsch.

Taxonomic studies of E. G. H. Oliver and I. M. Oliver

Edward ('Ted') George Hudson Oliver became fascinated by the diversity of Cape flora and especially fynbos vegetation after he enrolled as an undergraduate, to study zoology, at the University of Cape Town in the late 1950s. His attention was soon diverted from animals, and he became 'obsessed' by the Cape heaths because 'they were small and delicate with a seemingly infinite variety of shapes and colours' (Oliver 2000b). He was already collecting *Erica* in the field and making discoveries and, according to Colonel Hugh Arthur Baker (1896–1976) when he named *E. oliveri* (Fig. 2) in July 1962, 'Mr. E. G. H. Oliver … seems destined to add many more to the 600 or so [*Erica* species] already described' (Baker 1962: 198).

Following graduation, he undertook a study of *Acrostemon*, one of the 'minor' genera, presenting his Master's thesis in October 1964. In this (Oliver 1964)

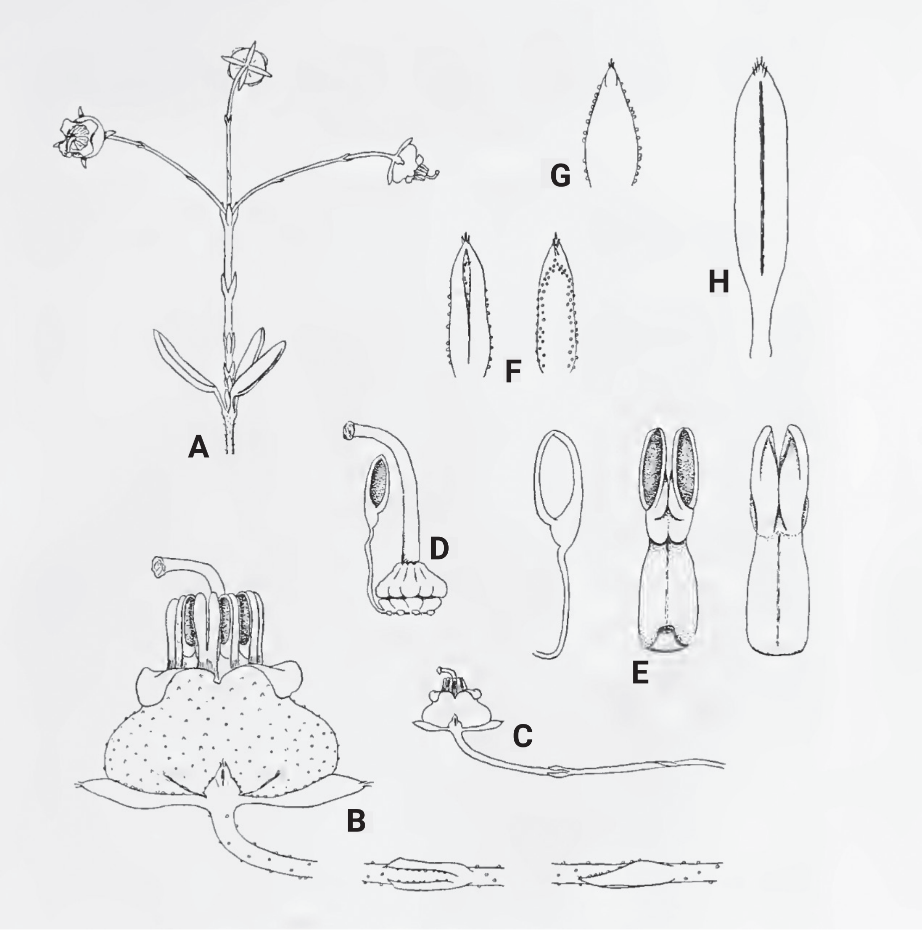


Figure 2. *Erica oliveri* H.A. Baker, drawn by E. G. H. Oliver (Baker 1962): "The species has been named after Mr. E. G. H. Oliver who is making a study of the genus and of the minor genera and has already collected a number of hitherto unknown species and seems destined to add many more to the 600 or so [*sic*] already described." **A** spring **B, C** flower **D** gynoecium **E** anther **F** sepals **G** bract **H** leaf.

he noted 'complete overlap between *Acrostemon* Klotzsch and *Hexastemon* Klotzsch allowing no character for the separation of the two genera' and therefore proposed to incorporate *Hexastemon* in *Acrostemon*. Likewise, comparing the monotypic genus *Arachnocalyx* Klotzsch, which had been designated by Robert Harold Compton (1886–1979) (Compton 1935), with the single species *Acrostemon viscidus* N.E.Br., Oliver found 'much closer similarity' between *Arachnocalyx eriocephalus* (Klotzsch) N.E.Br. and *Acrostemon viscidus* 'than had previously been suspected' (Oliver 1964: 105). To gain wider insights into the patterns of morphological similarities and differences, the species then assigned to *Syndesmanthus* Klotzsch and *Simochilus* Klotzsch were investigated too, and again Oliver (1964: 105) noted that 'a certain degree of intergrading occurs in the differentiating characters between the three genera to an extant where it becomes difficult to distinguish and place species into any one of the genera.' Discussing the six 'minor genera' that Phillips had retained, Oliver (1964: 115) concluded that Phillips's scheme was 'completely artificial' and did not 'reflect the correct relationships between the genera which [had] been reduced to synonymy. … With the addition of new and well collected material, a reconsideration of the generic boundaries will certainly be necessary in a future revision … [T]he problem of generic distinction will have to be worked out carefully and thoroughly.' At that time, some of the 'minor genera' were still regarded as monospecific, including the European endemic *Bruckenthalia* Rchb. and the last African 'minor' genus to be described, *Stokoeanthus* E.G.H. Oliv. (Oliver 1976a). Commenting on his decision to describe and name that new monotypic genus, he stated (Oliver 1976a):

The relationship of [*Stokoeanthus*] appears to me to be with *Erica* and *Blaeria* and to some extent with *Eremia*, but it does not fit into any of them as presently constituted. From *Erica* it differs in having 4 stamens and a 2-celled ovary, from *Blaeria* in having 2 cells to the ovary and from *Eremia* in having 4 stamens and more than 1 ovule per cell. To change the generic limits of any of these genera to force the inclusion of the new taxon would, in my opinion, be impracticable and would cause repercussions in the relationships of and differences between many other genera of the Ericoideae.

Thus, Ted laid down the basis for the work that consumed his time for the next 35 years, culminating in the elimination of all the 'minor genera' (Oliver 1987; 1988; 1992; 1993b; 1993a; 1993c; 1994; 1996; 2000a) and the subsuming of all their species into the megagenus *Erica* (Schumann et al. 1992: 244; Oliver 2000a; Oliver and Oliver 2000a). By examining many more plants than had been available to preceding botanists, he noticed clearly overlapping characters in the 'minor genera' and apparently discontinuous variation coalescing through various intermediate states, a good example being the capacity of the mature capsule to dehisce.

From about 1974, Oliver was assisted in his work on *Erica*, especially the 'minor genera', by Inge Magdalene Nitzsche (1947–2003), who had studied botany and zoology at the University of Cape Town (1967–1969) and also had a diploma in fine arts (1971–1972). They married in February 1974. Inge's remarkable pen-and-ink drawings of anatomical and morphological details of the species (often not signed) were to be an integral component of papers about *Erica* (and the 'minor genera') published from 1976 onwards: early (unsigned) examples of Inge Oliver's extraordinary illustrations were published in the paper 'revising' *Eremia* and *Eremiella* (Oliver 1976b: fig. 2, p. 34 *Eremia totta* (Thunb.) D.Don; fig. 9, p. 40 *E. curvistyla* (N.E.Br.) E.G.H. Oliv.; fig. 14, p. 44 *E. brevifolia* Benth.) (for the eponymous *Erica ingeana* E.G.H. Oliver, see Oliver and Oliver 1991: 140–142 (Fig. 3)).

In 1988, a grant enabled Inge to be employed as research assistant in the BRI Herbarium at the University of Stellenbosch 'to help with all the technical work – the numerous dissections, drawings and recording of all the details of variations in the plants. This … helped tremendously with the research and … Inge's work also helped with the finalisation of the analvses of the minor ericaceous genera …' (Oliver 2000b; Nelson 2004). Ted Oliver submitted his doctoral thesis to the University of Cape Town in 1999 (Oliver 1999) and published the monograph on the 'minor genera', integrating all of them into the redefined megagenus *Erica* in 2000. "Field guide to the Ericas of the Cape Peninsula" (Oliver and Oliver 2000b), a handy, pocketable manual, represents another aspect of these collaborative studies, making available an identification aid, illustrated with simple line drawings (Fig. 4), for naturalists in general.

Having come into contact with Colonel H. A. Baker by the early 1960s, Ted Oliver became co-author with Baker of "Ericas of South Africa" (Baker and Oliver 1967),

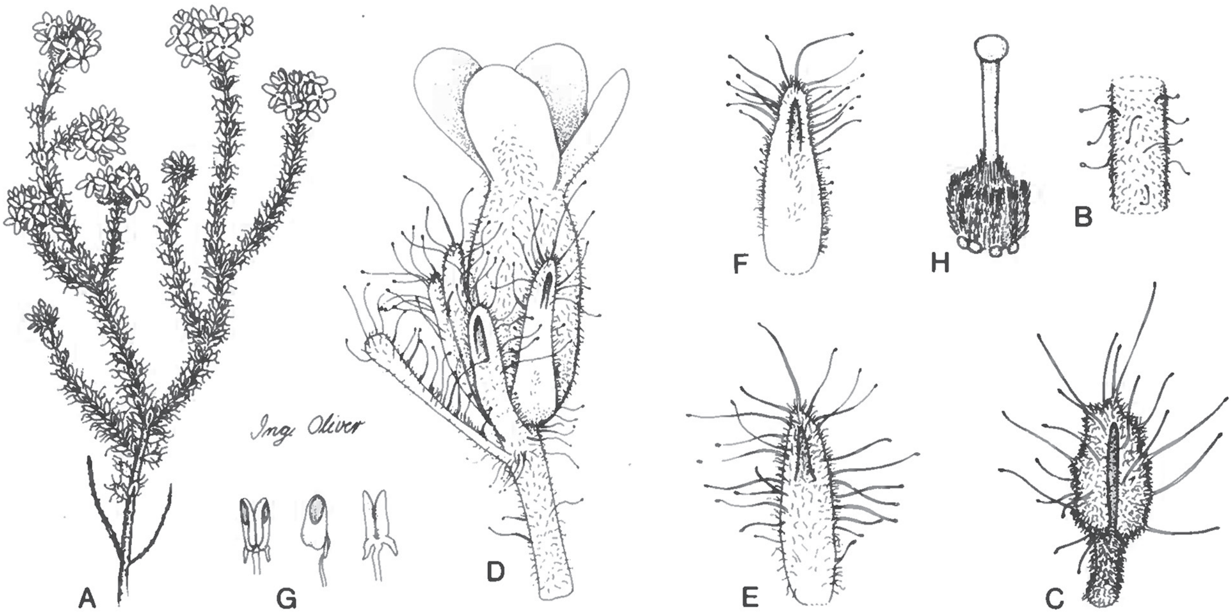
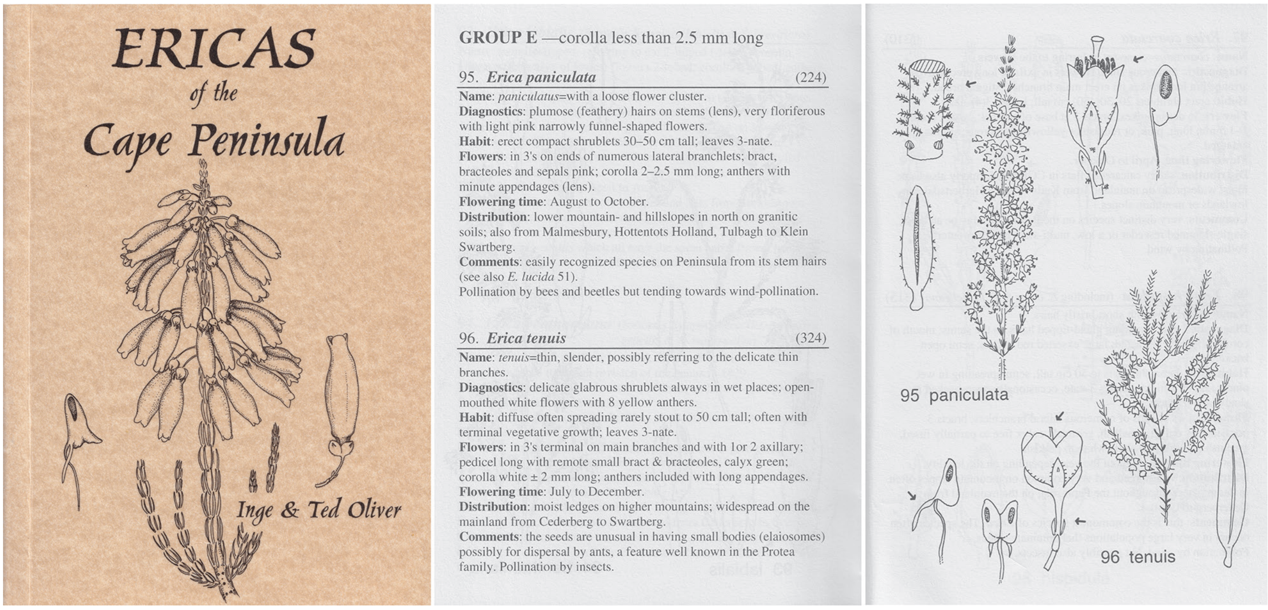


Figure 3. *Erica ingeana* E.G.H. Oliver, drawn by Inge M. Oliver (Oliver and Oliver 1991) **A** flowering branch **B** branch **C** leaf **D** flower **E** bract **F** sepal **G** anther, front, side and back views **H** gynoecium.


ERICAS
of the
Cape Peninsula

Inge & Ted Oliver

GROUP E —corolla less than 2.5 mm long

95. ***Erica paniculata*** (224)

Name: *paniculatus*=with a loose flower cluster.
Diagnostics: plumose (feathery) hairs on stems (lens), very floriferous with light pink narrowly funnel-shaped flowers.
Habit: erect compact shrublets 30–50 cm tall; leaves 3-nate.
Flowers: in 3's on ends of numerous lateral branchlets; bract, bracteoles and sepals pink; corolla 2–2.5 mm long; anthers with minute appendages (lens).
Flowering time: August to October.
Distribution: lower mountain- and hillslopes in north on granitic soils; also from Malmesbury, Hottentots Holland, Tulbagh to Klein Swartberg.
Comments: easily recognized species on Peninsula from its stem hairs (see also *E. lucida* 51).
Pollination by bees and beetles but tending towards wind-pollination.

96. ***Erica tenuis*** (324)

Name: *tenuis*=thin, slender, possibly referring to the delicate thin branches.
Diagnostics: delicate glabrous shrublets always in wet places; open-mouthed white flowers with 8 yellow anthers.
Habit: diffuse often spreading rarely stout to 50 cm tall; often with terminal vegetative growth; leaves 3-nate.
Flowers: in 3's terminal on main branches and with 1or 2 axillary; pedicel long with remote small bract & bracteoles, calyx green; corolla white ± 2 mm long; anthers included with long appendages.
Flowering time: July to December.
Distribution: moist ledges on higher mountains; widespread on the mainland from Cederberg to Swartberg.
Comments: the seeds are unusual in having small bodies (elaiosomes) possibly for dispersal by ants, a feature well known in the Protea family. Pollination by insects.

Figure 4. *Ericas of the Cape Peninsula* by Inge and Ted Oliver (2000, published by the Protea Atlas Project, National Botanical Institute, Cape Town); left (cover: 106 × 148mm): *E. mammosa*, pen-and-ink drawing by Inge Oliver: text page and accompanying illustrations by Inge Oliver, showing *E. paniculata* and "*E. tenuis*" (now *E. oliveranthus* E.C.Nelson & Pirie; Nelson et al. 2023). Reproduced with permission.

illustrated with botanical paintings by the South African botanical artist Irma von Below (1920–1984) and others. Two decades later he started to collaborate with 'Dolf' (Adolf Wilhelm Stander) Schumann (1918–2001) and Gerhard P. K. Kirsten (1932–2000) on a profusely illustrated photographic monograph "Ericas of South Africa" (Schumann et al. 1992) in which the amalgamation into the megagenus *Erica* of the last of the minor genera was announced, because they have 'so much in common … that their species should also be regarded as ericas [*sic*]' (Schumann et al. 1992: 244)

Writing for The Heather Society (of which he was an honorary member) in 2000, Ted noted that:

"Having begun work on the Ericaceae some 40 years ago as a student, I now find that I am getting to know the group properly, the more so recently because of the rapidly increased knowledge that Inge has also acquired. I am no longer a single person struggling in a "sea of ericas". There are now two of us to discuss the problems of species de-limitation, species evolution and the phylogeny, ecology or phytogeography of this fascinating genus. There are quite a number of new species to be described and surprisingly, other un-described species are still being brought in. The biggest problem ahead is that of sub-generic classification. The new techniques of DNA analysis will help to throw some light on this problem, which is now being tackled by a group of international experts with material that I am supplying for them."

In Table 1, we present an abridged timeline of the careers of Ted and Inge with selected publications, eponyms, and other noteworthy milestones.

Although big plant genera have expanded and contracted over time (Frodin 2004), it is relatively unusual for twentieth-century taxonomists working on morphology alone to change generic delimitations in favour of fewer, larger genera. More often, the emphasis has been placed on morphological differences in particular groups, without necessarily addressing the coherence of groups from which they are split (Humphreys and Linder 2009). Oliver's 'megagenus' concept for *Erica* (Oliver 2012; Oliver and Forshaw 2012) reflected a global understanding of the group that pre-empted subsequent molecular research in which he was instrumental. Phylogenetic trees including more than 40% (Pirie et al. 2011) and 60% (Pirie et al. 2016.) of the species diversity clearly showed that the 'minor genera' are nested within – and indeed scattered across – the redefined mega-genus *Erica*.

One example, *Philippia* Klotzsch, was characterised largely by reduced flowers without brightly coloured corollas or nectaries, but with greatly expanded stigmas (as illustrated in Oliver 1988: 4 & 5), together interpreted as a wind-pollination syndrome (Rebelo et al. 1985). Transition to wind pollination was shown to have occurred several times in *Erica* as then defined (Pirie et al. 2011), with similar characteristics shared by the wind-pollinated 'minor genera' such as *Salaxis* Salisb., *Coccosperma* Klotzsch and *Ericinella* Klotzsch (Oliver 1994, 2000a) and many individual species scattered within *Erica sens. str*.

Blaeria L., had been defined as including those species with four, rather than eight, stamens (Linnaeus 1753, Bentham 1839; Brown 1906; Phillips 1926, 1944; Oliver 1975, 1993b) but this definition was not subsequently applied consistently. Phillips (1944, 1951) included species with four, six or eight stamens in the 'minor genera' *Coccosperma* (4–8 stamens) and *Philippia* (6–8 stamens), but the numbers were also not consistent: four stamens can arise within an individual species usually characterised by having eight (for example, *Erica filiformis* Salisb., *E. blaerioides* E.G.H. Oliv., *E. arborea* L., *E. woodii* Bolus, *E. pleiotricha* S. Moore; Oliver 1993b). As anticipated by Oliver (1993b), neither the 'minor genus' *Blaeria*, nor species of *Erica sens. lat.* possessing only four stamens, proved to represent monophyletic groups, and former *Blaeria* species, such as *E. ericoides* (L.) E.G.H. Oliv., *E. barbigeroides* E.G.H. Oliv.

Table 1. Milestones in the careers of E. G. H. Oliver and I. M. Oliver, relating to their studies, separately and jointly, of the megagenus *Erica* (1937–2024).

	E. G. H. ("Ted") Oliver **1938–**	**Inge Magdalene Oliver (née Nitzsche)** **1947–2003**
1959	undergraduate, University of Cape Town (–1962)	
1962	commences Masters degree, in Bolus Herbarium; H. A. Baker describes and names *Erica oliveri*	
1964	submitted Masters thesis "Taxonomic studies in the genus *Acrostemon* Kl. and related genera"; M.Sc. awarded	
	Curator, Government Herbarium, University of Stellenbosch	
1967	*"Erica* of South Africa" published; co-author Colonel Hugh A. Baker	undergraduate, University of Cape Town (–1969)
1967	South African Botanical Liaison Officer, Royal Botanic Gardens, Kew, UK	
1970	returned to herbarium, University of Stellenbosch	
1971		commenced Fine Arts diploma
1972: December	elected honorary member of The Heather Society	
1974: February	marriage	
1975	Head of Herbarium Services and Curator National Herbarium, Pretoria	
1976		first illustrations (unsigned) of Erica published in E. G. H. Oliver, 'Studies in the Ericoideae. I. The genera *Eremia* and *Eremiella'*, Bothalia 12 (1).
1981	returns to Government Herbarium, University of Stellenbosch	
1988		research assistant at herbarium, University of Stellenbosch
1991	*Erica ingeana* named and described in earliest co-authored research paper ('Studies in the Ericoideae (Ericaceae). VIII. New species in *Erica*, section Pseuderemia, from southern Africa'. Bothalia 21 (2))	
1992	"Ericas of South Africa": published; co-authors Dolf Schumann and Gerhard Kirsten	
1999	submits doctoral thesis 'Systematic studies in the Tribe Ericeae (Ericaceae–Ericoideae)'	
2000	Ph.D. awarded; monograph (Systematics of Ericeae (Ericaceae: Ericoideae) species with indehiscent and partially dehiscent fruits. "Contributions from the Bolus Herbarium" no. 19) published; contained 84 full-page illustrations by Inge M. Oliver	"Field guide to the Ericas of the Cape Peninsula" published; 104 species illustrated
2003: July		deceased
2010	visited Madagascar (with group including DUB & MDP; Heathers 8: 47–54. 2011)	
2012	Genus *Erica* An identification aid version 3.00 published (Contributions from the Bolus Herbarium 22); co-author Nigel Forshaw [version 4.00 published 2024]	
2014	visited Mauritius (Heathers 11: 38–42. 2014)	

and *E. russakiana* (Klotsch ex Walp.) E.G.H. Oliv. from the Cape and the tropical East African species *E. filago* (Alm & T.C.E. Fr.) Beentje and *E. silvatica* (Welw. ex Engl.) Beentje (included in *Erica* by Beentje (2006), explicitly following Oliver's precedent; Fig. 5), proved to be distantly related.

With the megagenus concept already firmly embedded, the Olivers set out to revise systematically groups of species following the arrangement in "Flora Capensis" (Guthrie and Bolus 1905; Brown 1906). Two such works were accom-

Figure 5. Examples of the former genus *Blaeria*. Cape species included in *Erica* by Ted Oliver: **A** *E. ericoides* **B** *E. russakiana*; and **C** *E. barbigeroides*, and tropical East African species included in *Erica* by Beentje (2006): **D** *E. filago* and **E** *E. silvatica*. Photos **A** MDP **B–E** Berit Gehrke.

plished (Oliver and Oliver 2002, 2005), and many more might have been expected but for the early death of Inge in 2003 (Nelson 2004). Ted continued work on the *Erica* Identification Aid, which includes many of Inge's informal sketches

(Oliver and Forshaw 2012; Oliver et al. 2024) and provides a route towards species identifications that is also accessible to non-specialists. His support of molecular research from 2008 onwards has included analyses of European species (Mugrabi de Kuppler et al. 2015) and improvements to species delimitation in Cape groups (Pirie et al. 2017) as well as broad scale phylogenetic and biogeographic analyses (Pirie et al. 2016; 2019; 2024) reflecting his broader interests in patterns and origins of Cape plant diversity (Oliver et al. 1983).

Conclusion

By the end of the twentieth century, following almost 250 years of botanical exploration especially in the Cape Floristic Region of South Africa, the number of species of heaths and heathers known to botanists had exceeded eight hundred (Oliver and Oliver 2000a) – many hundreds more binomial names had been published (Nelson and Small 2004 [–2005]). By early 2024 the total number of accepted *Erica* species was 851 (Elliott et al. 2024). Not only is *Erica* confirmed as one of the largest genera of Angiospermae, it is one of the most widely distributed, its species ranging across more than 100 degrees of latitude from northern Norway to the Cape Floristic Province in South Africa, and, straddling the Equator, for almost 90 degrees of longitude from the Azores (31°W) in the Atlantic Ocean eastwards to islands in the Indian Ocean including Madagascar, the Mascarenes and Mauritius (57°E) (Oliver 1994, 2011, 2014). At this time, of the currently accepted species, 94 were described and named as new to science by Ted Oliver, and many of these were first collected by him too, while a further 206 are combinations and replacement binomials published under his name, as sole or joint author (Suppl. material 2). This includes not only Cape diversity, but also taxa from Tropical East Africa and Madagascar (Dorr and Oliver 1999a, 1999b), and the Mascarenes (Oliver 1993a). Ted and Inge Oliver (pictured in Fig. 6) jointly described and named 16 novel species of *Erica* (Table 2). Inga's illustrations occurred in many of the papers published since 1974 and (as noted) in the *Erica* Identification Aid (Oliver et al. 2024). A full list of their papers on *Erica* is presented in Suppl. material 3.

Table 2. New species named by E. G. H. Oliver & I. M. Oliver.

Erica amalophylla	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica annalis	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica cavartica	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica ceraria	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica croceovirens	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica gerhardii	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica hebdomadalis	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica jananthus	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica jugicola	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica lithophila	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica petrusiana	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica prolata	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica psittacina	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica schelpeorum	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica umbratica	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772
Erica viridimontana	E.G.H.Oliv. & I.M.Oliv.	wfo-4000013772

Figure 6. Inge M. Oliver (left) and E. G. H. (Ted) Oliver (photos provided by Tessa Oliver).

No single author has had greater impact on the taxonomy of *Erica*/Ericeae than Ted Oliver in numbers of new species (as predicted by his mentor, H. A. Baker, in 1962), but this contribution must be interpreted as part of a team effort of two enormously talented botanists. Their combined contribution both of improved knowledge of alpha taxonomy and of broad understanding of the structure of that diversity is fundamental to, and will have a lasting influence on, all future developments in the field.

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The authors have declared that no competing interests exist.

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Author contributions

ECN: Writing – Original draft, Writing – Review and Editing. MDP: Writing – Review and Editing. DUB: Writing – Review and Editing.

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Data availability

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

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Supplementary material 1

Generic description of *Erica* by E. G. H. Oliver (2000a; from Nelson 2011: 100)

Authors: E. Charles Nelson, Michael D. Pirie, D. U. Bellstedt

Data type: docx

Link: https://doi.org/10.3897/phytokeys.244.121705.suppl1

Supplementary material 2

A complete list of *Erica s.l.* taxa at all ranks authored by E.G.H. Oliver and I.M. Oliver

Authors: E. Charles Nelson, Michael D. Pirie, D. U. Bellstedt

Data type: xlsx

Explanation note: Including taxa new to science, replacement names, and new combinations, with synonymy and bibliographic data, derived from the World Flora Online (Elliott et al. 2024).

Link: https://doi.org/10.3897/phytokeys.244.121705.suppl2

Supplementary material 3

A complete list of *Erica* related publications authored by E.G.H. Oliver and I.M. Oliver

Authors: E. Charles Nelson, Michael D. Pirie, D. U. Bellstedt

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Research Article

Genetic and morphological evidence support the specific status of the endemic *Erica andevalensis* (Ericales, Ericaceae)

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Abstract

Assessing the taxonomic status of closely related taxa is crucial in plant systematics and can have important implications for conservation and human plant use. *Erica andevalensis* Cabezudo & Rivera is a metallophyte endemic species from highly metal-polluted soils of SW Iberian Peninsula, an area with a mining history going back more than 5,000 years. *Erica andevalensis* is closely related to *Erica mackayana* Bab., a northern Iberian species also present in western Ireland. The status of *E. andevalensis* as a species or subspecies subordinated to *E. mackayana* is subject to debate. Here, we assessed the genetic and phenotypic relationship between both species, including the population structure of *E. andevalensis*. We used high throughput sequencing to determine genome-wide Single Nucleotide Polymorphisms (SNPs), and morphometric analyses from 35 reproductive and vegetative traits. The morphological analysis showed at least eight characters that can discriminate the two species, from which ovary hairiness and the size of leaf glandular hairs were the most informative. Genetic analyses showed that each species formed a monophyletic cluster with full support, separated by an interspecific genetic distance >4-fold higher than intra-specific distance. Population genetic analyses of *E. andevalensis* shows that populations are highly structured, with the Portuguese one as the most isolated and less variable. These results support the recognition of *E. andevalensis* as a distinct species with a highly constrained ecological requirements and a narrow geographic distribution, but with a limited gene flow between populations. We discuss the implications of these outcomes in conservation policies and potential uses of *E. andevalensis* such as decontamination of polluted soils.

Key words: Endemic species, *Erica*, metallophyte, population structure, species delimitation, systematics

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Introduction

The species is the fundamental unit in taxonomy and systematics of living organisms (De Queiroz 2005). This perspective extends to all fields of biology, leading to considerable scientific effort being dedicated to this taxonomic category. Beyond a scientific perspective, species delimitation is relevant in conservation planning and biodiversity assessment of protected areas (Coates et al. 2018; Galtier 2019).

In plant taxonomy, morphological characters have historically been the primary source of evidence for delimitating species (Whittemore 1993; Soltis and Soltis 2012). However, the more recent application of DNA data to assess species diversity has significantly impacted the field of taxonomy. Ideally, species delimitation would be informed by a comprehensive understanding of variability and population structure, as well as knowledge of the connections among closely related lineages (Galtier 2019). Since most species exhibit geographic variation, it is important to obtain a good representation of the distribution area to distinguish true discontinuities, which could imply lineage separation, from within-lineage variation (De Queiroz 2007). In lineages with incipient separation, considering other lines of evidence (e. g. ecological, morphological, and/or phenological) in addition to molecular data provides the basis for a more robust integrative taxonomy (Pante et al. 2015).

High throughput sequencing (HTS) is the most significant recent advance in molecular techniques, as it greatly facilitates the generation of large amounts of DNA data. Restriction site-associated DNA (RAD-seq) and similar approaches involve enzymatic fragmentation of genomic DNA coupled with HTS to determine large numbers of molecular markers with genome-wide coverage (Andrews et al. 2016). The enhanced resolution provided by these techniques has been applied to disentangle complex relationships between closely related species as well as to study the genetic structure of populations (e.g. Pante et al. 2015; Feng et al. 2018).

Erica is among the largest genera of seed plants, with 851 accepted species (Elliott et al. 2024; Oliver et al. 2024; WFO 2024), most of them concentrated in the Cape Floristic Region (Manning and Goldblatt 2012). However, the genus most probably originated in the Palearctic region, where only 23 species live today (Mugrabi de Kuppler et al. 2015). Despite the relatively low number of *Erica* species in Europe, they hold a large phylogenetic diversity compared to the species-rich Cape floristic region (Pirie et al. 2024). *Erica* also plays an important ecological role as dominant species in different European habitats (Fagúndez 2013). European heathlands are facing many threats, and their habitats are decreasing, resulting in the isolation of populations and local extinctions (Fagúndez 2013). Understanding the genetic diversity and population structure of these species becomes essential to assess the conservation status of their populations and infer their future survival in a context of global change (Frankham 2010).

Erica andevalensis Cabezudo and Rivera, occurs in a restricted area in the south-west of the Iberian Peninsula, mainly in western Andalusia, Spain, and bordering Portugal (Cabezudo and Rivera 1980; Buira et al. 2017). It colonizes wet soils within the Iberian Pyrite Belt, characterized by high levels of sulfur and heavy metals. It frequently forms nearly monospecific communities along polluted riversides and in abandoned mines (Aparicio 1999; Fig. 1). As a restricted metallophyte endemic species, *E. andevalensis* is considered a threatened species (BOJA 2012; Carapeto et al. 2020).

Erica andevalensis is closely related to *E. mackayana* and both species are morphologically similar. However, they have disjunct distributions, as *E. mackayana* is restricted to the northern Iberian Peninsula (Mugrabi de Kuppler et al. 2015; Fagúndez and Díaz-Tapia 2023). Despite morphological similarities, both species can be distinguished by the pattern and size of glandular hairs and the presence/absence of other small non glandular hairs (Cabezudo and Rivera

Figure 1. A Flowering stems of *Erica andevalensis* **B** Tinto river shores in Huelva, SW Spain, the habitat of *E. andevalensis* **C** São Domingos, Portugal, abandoned mining area with *E. andevalensis* in front **D** *Erica andevalensis* in the shores of Odiel river **E** flowering stems of *Erica mackayana* **F** wet heathland dominated by *E. mackayana* in Galicia, NW Spain.

1980). However, some variability was found in these characters and both species can lack glandular hairs. As a result, *E. andevalensis* has been considered a subspecies under *E. mackayana* (McClintock and Nelson 1989), although Nelson (2012) subsequently treated *E. andevalensis* as a species in its own right. Additional research has revealed further characters that distinguish both taxa, as they differ in seed morphology (Fagúndez and Izco 2004). Seed characters have been proven useful in delimitating *Erica* species (e.g. Szkudlarz 2009; Fagúndez and Izco 2010). Also, Bayer (1993) described small hairs in the ovary of some individuals of *E. andevalensis* that were never observed in *E. mackayana*. The discussion on the taxonomic rank of *E. andevalensis* continues (see Nelson and Small 2000; BOJA 2012; Carapeto et al. 2020; GBIF 2023; WFO 2024).

In this study, we aim to reassess the taxonomic identity of *E. andevalensis* as a distinct species from *E. mackayana* combining molecular and morphological data. By studying the whole geographic range of both species, we aim to identify morphological traits that might reliably distinguish *E. andevalensis* from *E. mackayana*. In addition, we aim to study the population structure of *E. andevalensis*, to understand the level of isolation and gene flow among populations and provide better guidelines for conservation.

Material and methods

Plant material

We sampled 38 plants from four populations of *E. andevalensis* in August 2021. Seventy-one plants from ten populations of *E. mackayana* analysed in Fagúndez and Díaz-Tapia (2023) were also included in the analyses (Fig. 2, Suppl. material 1: table S1). Additionally, one *E. tetralix*, the closest species to the *E. mackayana-andevalensis* clade (Mugrabi de Kuppler et al. 2015), was included as outgroup in the phylogenetic analyses.

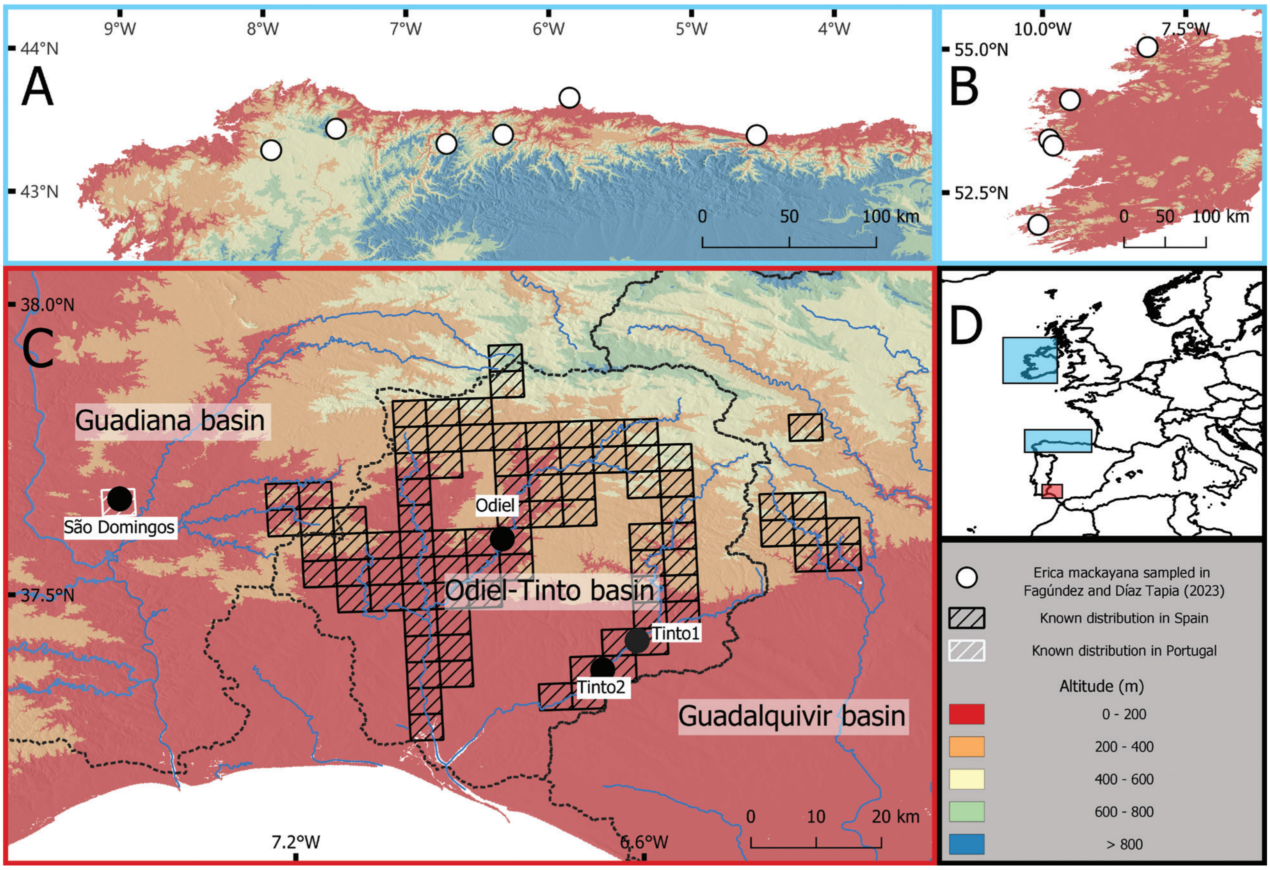

Figure 2. Distribution of the sampled populations of *E. andevalensis* and *E. mackayana* **A** *Erica mackayana* populations (as in Fagúndez and Díaz-Tapia 2023) sampled in NW Iberian Peninsula **B** *Erica mackayana* populations (as in Fagúndez and Díaz-Tapia 2023) sampled in Ireland **C** *Erica andevalensis* populations sampled. The distribution of *E. andevalensis* is represented in a 5×5 UTM grid from https://www.ideandalucia.es/catalogo/inspire/srv/api/records/625a6b54-bfc1-4589-8571-b4503bf262c2 (Spain) and Carapeto et al. (2020) (Portugal) **D** location of the three studied regions in Europe.

A subsample of each specimen was dried in silica gel, and the remaining material was prepared for morphological studies. All herbarium vouchers were deposited in SANT herbarium.

Morphometric data and analyses

Each sample was mounted in a herbarium sheet and scanned at a minimum resolution of 1000 dpi. In addition, a minimum of two fresh flowers per specimen were dissected to measure ovaries and anthers. Pictures of ovaries and anthers were taken using an OLYMPUS C3040-ADU for subsequent digital analysis. For leaf micro-characters, we used an optical microscope at 40–100 magnifications. All images were analyzed using ImageJ software (Schneider et al. 2012).

The final dataset for morphological analyses comprises 71 individuals of *E. mackayana* and 38 of *E. andevalensis*. In the dataset, each trait was represented by one value per specimen, thus the arithmetic mean was calculated for multiple measures (Suppl. material 1: table S2). We measured a total of 35 traits including 24 quantitative, 8 ordinal and 3 binary (Fig. 3, Suppl. material 1: table S2). Each trait was measured once or several times per sample. We tested for differences between the means in the two species for each variable using a non-transformed dataset. For quantitative variables, we applied t-tests or Wilcoxon rank-sum tests, depending on whether the variables met normality and homocedasticity assumptions. Ordinal variables were compared using Chi-squared tests. In the case of binary variables (LNR, L5 and LS2G), the Fisher's exact test was conducted (Suppl. material 1: table S3).

We performed a principal component analysis (PCA) with all samples and traits. Since each trait was on a different scale, the prep function from the PCAMETHODS package (Stacklies et al. 2007) was used to normalize and center all variables. Missing data in the final matrix represented 12.08%. To overcome this issue, we used a K-Nearest-Neighbor approach from DMWR2 package (Torgo 2016). Subsequently, the FACTOEXTRA package was used to perform the PCA (Kassambara and Mundt 2020). Next steps were carried out using the MORPHOTOOLS2 package (Šlenker et al. 2022). All statistical analysis were conducted in R (R Core Team 2020).

Molecular data

We used genomic data obtained from Fagúndez and Díaz-Tapia (2023) for *E. mackayana*, while genomic data of *E. andevalensis* was newly determined. One sample of *E. tetralix* from Fagúndez and Díaz-Tapia (2023) was included in the dataset to be used as the outgroup in phylogenetic analyses. DNA extraction, library preparation and sequencing followed Fagúndez and Díaz-Tapia (2023).

Nextera adaptors from sample reads were trimmed using BBDUK (BBMAP TOOLS v.38.79, http://sourceforge.net/projects/bbmap/) with the following parameters: ktrim = r, k = 17, hdist = 1, mink = 8, minlen = 100, ow = t, qtrim = r, trimq = 10. Quality of filter reads was checked using FastQC (v.0.11.9) (Andrews 2010). Denovo_map.pl pipeline from STACKS software v2.64 (https://catchenlab.life.illinois.edu/stacks/) was employed to denovo assembly and SNP calling.

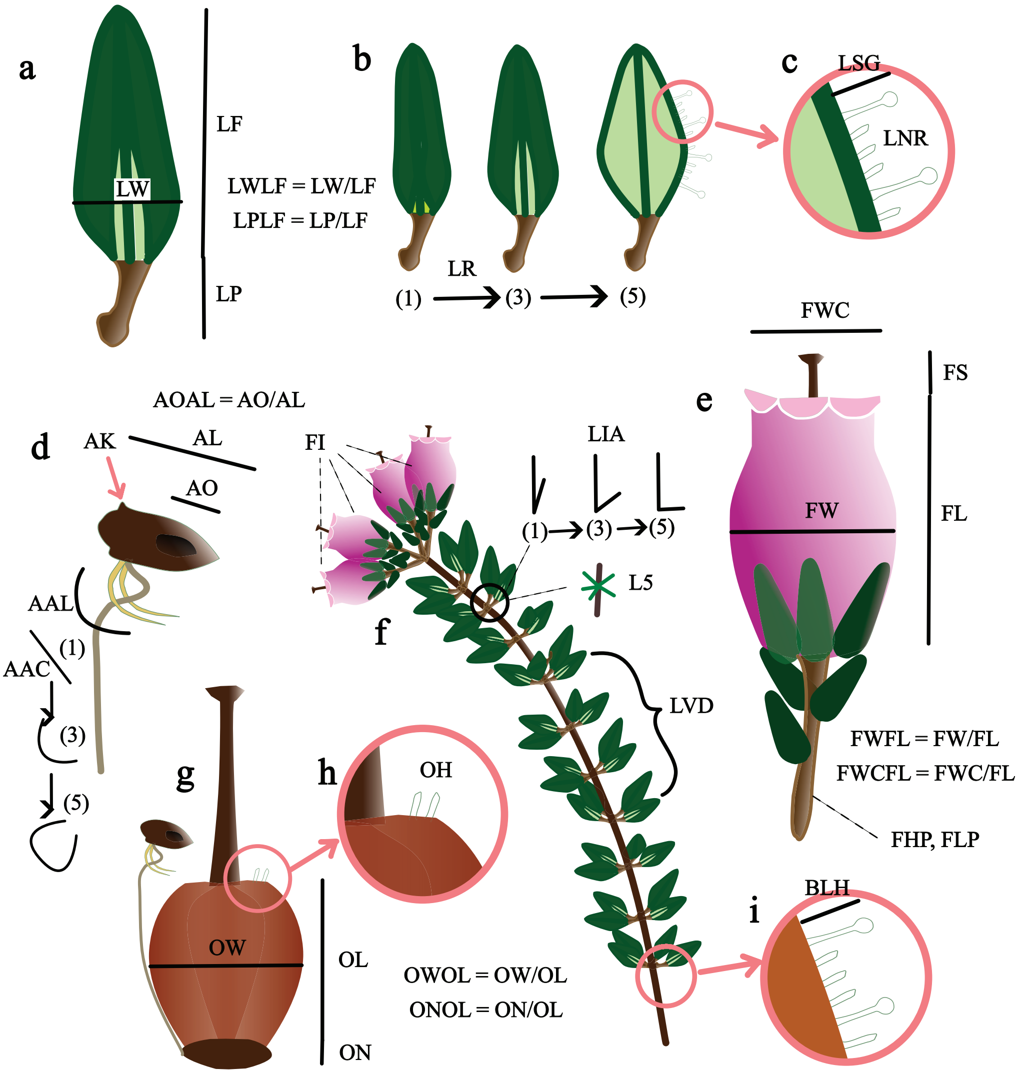

Figure 3. Schematic representation of the morphological traits measured in the samples of *Erica andevalensis* and *E. mackayana*. Leaf traits (**a**) (LF = Leaf length; LW = Leaf width; LP = Petiole length), variation on leaf morphology (**b**) (LR = Leaf rolling degree), and indumentum (**c**) (LSG = length of glandular hairs; LNR = presence of non-glandular hairs). Stamen traits (**d**) (AL = Anther length; AO = Anther pore; AAL = Anther appendix length; AAC = Anther appendix curvature; AK = Anther knob), flower morphology (**e**) (FL = Corolla length; FW = Corolla width; FWC = Corolla opening; FS = Style exertion; FHP = Pedicel hairiness, FLP = Pedicel length), and arrangement of a flowering branch (**f**) (FI = Flowers per inflorescence; LIA = Leaf insertion angle, L5 = 5nate leaves, LVD = Density of whorls). The ovary (**g**) (OL = Ovary length; OW = Ovary width; ON = Nectary size) and detail of ovary surface (**h**) (OH = Ovary hairiness) and stem (**i**) (BLH = Branch longest hair). Coding, measures, and additional information in Suppl. material 1: table S2.

To select the optimal parameters, a preliminary optimization step following the 80% rule (Paris et al. 2017) was conducted. Thirty percent of the samples with a minimum of two per population were selected. Reads with different lengths were allowed using –force-diff-len on ustacks module. We constructed 12 different catalogs, varying the -m (Minimum number of raw reads required to form a stack (a putative allele)), -M (Number of mismatches allowed between stacks (putative alleles) to merge them into a putative locus) and -n (Number of mismatches allowed between stacks (putative loci) during construction of the catalog) parameters. For all probes, -M = -n, but no -m, which ranged between 2 and 6. After optimization process, we created a new catalog choosing m = 4, M = 3, n = 3. Using a populations' module, the dataset was exported to variant call format (VCF).

Phylogenetic analysis

VCF file from STACKS was filtered with VCFTOOLS retaining the SNPs with less than 60% of missing data and those that were separated by at least 200 bp to avoid linkage disequilibrium issues. Furthermore, only variable SNPs present in a minimum of 4 samples were accepted. The VCF file was exported as interleaved phyllip using TASSEL (Bradbury et al. 2007). IQTREE v2.1-2 was used to filter invariant sites (Minh et al. 2020). Final dataset consisted of 6004 bp. MODELFINDER from WEB-IQTREE (Kalyaanamoorthy et al. 2017) was used to select the optimal model of the dataset based on Bayesian Inference Criterion (BIC). Using this approach, the best model was TVM+F+ASC+G4. Then, the final tree was calculated with this model in IQ-TREE v2.1-2 with 1000 non-parametric bootstrap replicates.

Genetic distance analysis

To assess genetic distance between *E. andevalensis* and *E. mackayana*, we used Tamura-Nei distance (Tamura and Nei 1993) in MEGA11 (Tamura et al. 2021). We compared only populations with >2 individuals. Then, we calculated mean pairwise distances for population of each species and compared them with mean pairwise distance between both species.

Population structure analysis

A new dataset per putative species was created. VCFTOOLS was used to remove indels, as well as filter SNPs retaining those that were present in at least 80% of samples and minor alleles were present in at least two samples. Also, to avoid linked loci, SNPs at a distance less than 500 base pairs (bp) were excluded. Both datasets were exported to plink format. The function filter_data() from SAMBAR package was used with default thresholds to detect and erase possible paralogous loci (De Jong et al. 2021). Final datasets consisted of 36 samples with 4,234 SNPs of *Erica andevalensis* and 62 samples with 5,178 SNPs of *E. mackayana*.

Observed heterozygosity (H_o) and expected heterozygosity (H_e) were calculated with function filter_data() in SAMBAR, and nucleotide diversity was calculated with calc_diversity() of the same package. F_{IS} was calculated as $1\text{-}H_o/H_e$ as in Weir and Cockerham (1984).

We further analysed the dataset of *E. andevalensis*, including a F_{ST} pairwise comparison among populations, using calc_diversity() function in SAMBAR and Bayesian population assignment (BPA). BPA probabilities were calculated using the function find_structure() in SAMBAR package. The optimal number of clusters (K) was determined using the elbow method on cross-entropy scores.

Results

Morphometric analyses

Twenty-eight out of 35 morphological characters measured showed statistically significant differences between *Erica mackayana* and *E. andevalensis* (Suppl. material 1: table S3).

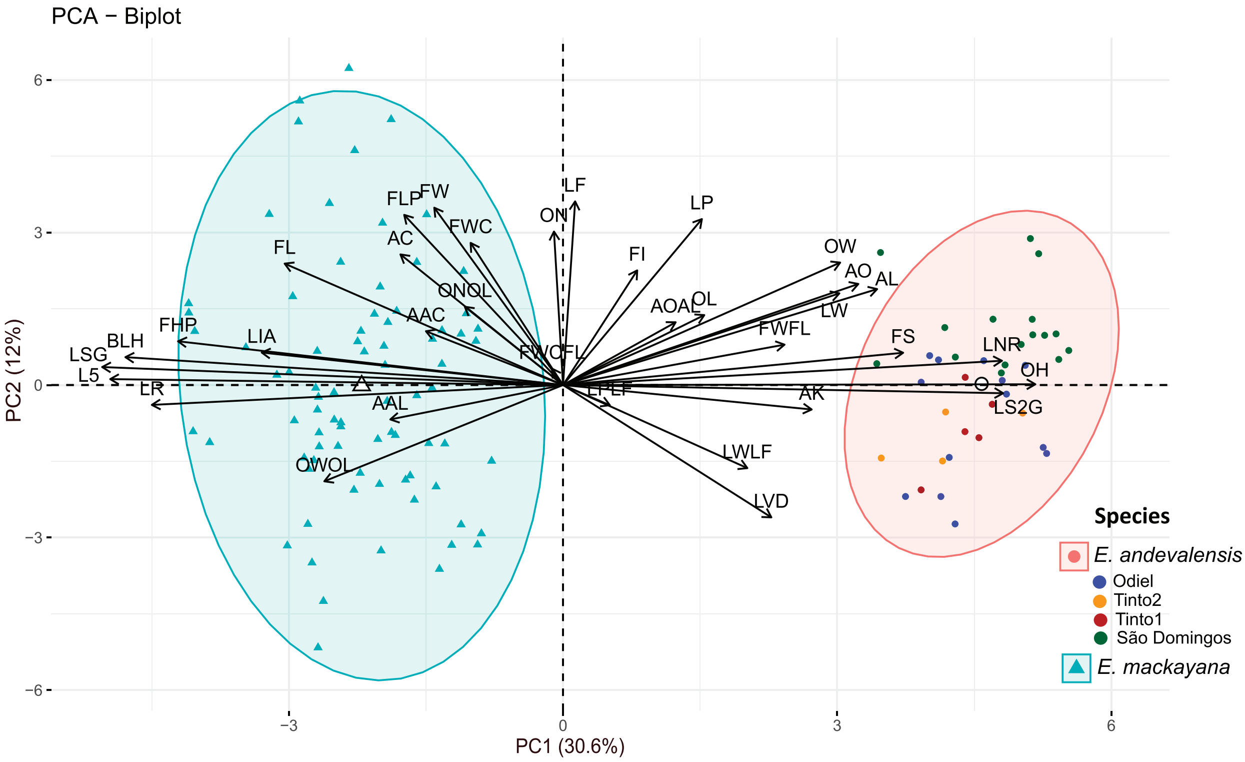

Figure 4. Biplot showing the first two principal components. Each ellipse represents the area that would encompass 95% of individuals assuming populations follow a normal distribution. White dots and triangles represent *E. andevalensis* and *E. mackayana* centroids respectively. *Erica andevalensis* populations are represented in different colors: Green (São Domingos), blue (Odiel), brown (Tinto1), yellow (Tinto2). Trait acronyms as in Fig. 3 and Suppl. material 1: table S2.

The first and second axes of the PCA explained 30.6% and 12% of the variance in the data, respectively. PC1 clearly delimitate the two species into two separated clusters (Fig. 4). PC2 depicts intra specific variation, with the species centroids close to 0 (-0.01 in *E. mackayana* and 0.02 in *E. andevalensis* respectively). PC2 can delimitate among *E. andevalensis* populations, particularly Spanish populations (Tinto1, Tinto2 and Odiel) populations vs São Domingos from Portugal. We identified the best diagnostic characters as those with a higher value on the first PC of the PCA, thus contributing to delimitate the two species, but lower values on the second PC, which represents variability within both taxa. Eight were selected as the best diagnostic characters including ovary hairiness, length and arrangement pattern of glandular hairs in leaves, length of glandular hairs on the stem, presence of non-glandular hairs in leaves, inflorescence hairiness, leaf rolling degree and number of leaves per whorl (Table 1, Fig. 5). The contribution of the remaining variables is provided in Suppl. material 1: table S4.

Phylogenetic analysis

The phylogenetic tree placed the samples of the two species in two distinct clades that received full support (Fig. 6). Within the *E. andevalensis* clade, the samples from Tinto 1 and São Domingos formed two fully supported clades. The samples from Tinto 2 were placed as sister to Tinto 1, but this relationship was unsupported. Most samples from Odiel were placed in a moderately supported clade, except two individuals of which one was sister to the clade formed plants from Tinto 1 and 2 and the other was sister to the clade formed by all the other samples.

Table 1. Selection of traits that most contribute to the two first PCA components. Percentage of variability within traits explained by the first two components. For each trait average values for each species are provided. Significance of correspondent mean differences tests is highlighted with *** if p-value <0.001. OH = Ovary hairiness; LSG = Length of glandular hairs; L5 = Presence of 5nate whorls; LS2G = Presence of more than two rows of glandular hairs; LNR = Presence of non-glandular hairs; BLH = Longest hair length in stem; LR = Leaf rolling degree; FHP = Pedicel hairiness.

Trait	Units/coding	Contribution to PC1	Contribution to PC2	*E. mackayana* mean	*E. andevalensis* mean	Significance
OH	0–5	8.584	0.000	0	1.083	***
LSG	μm	8.173	0.103	562.025	136.448	***
L5	0–1	7.890	0.011	0.958	0	***
LS2G	0–1	7.452	0.021	0	0.773	***
LNR	0–1	7.412	0.187	0	0.839	***
BLH	μm	7.369	0.246	0.986	0.333	***
LR	1–5	6.506	0.125	2.937	1	***
FHP	1–5	5.703	0.607	2.500	1.105	***

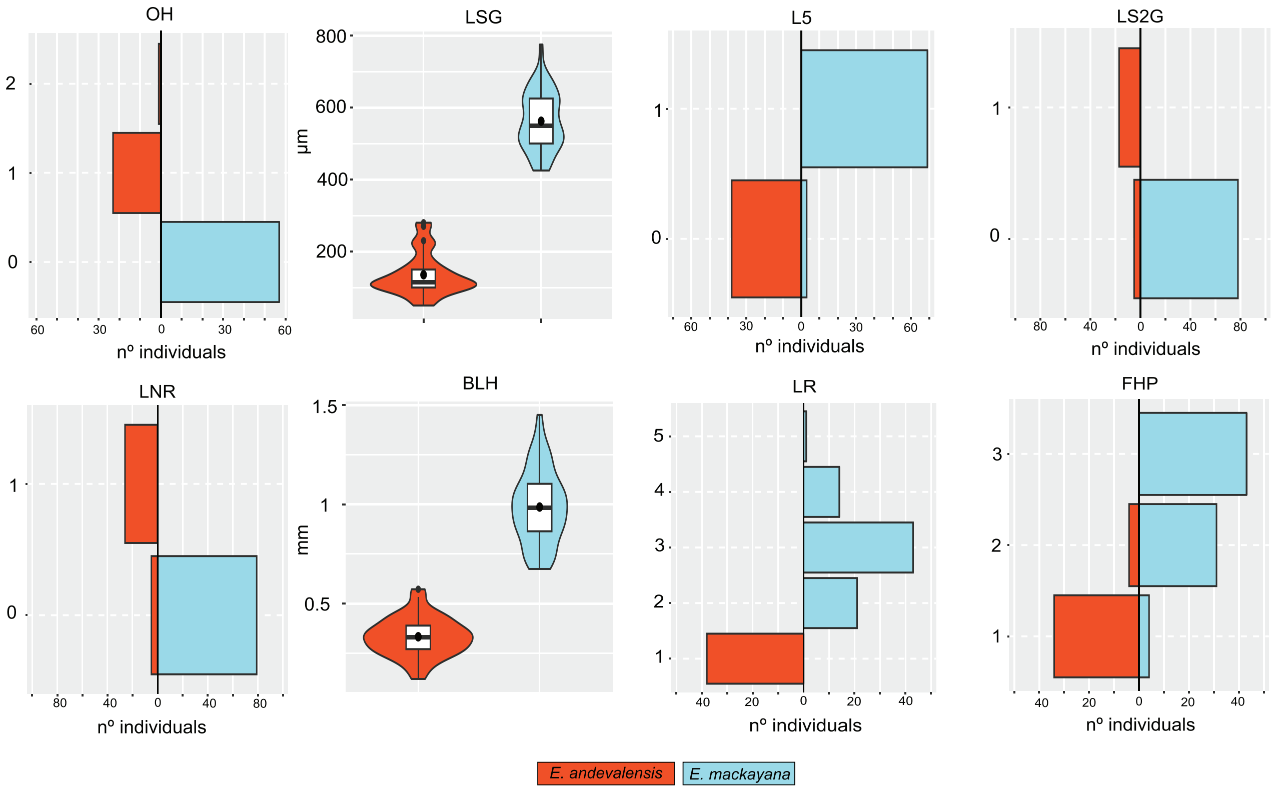

Figure 5. Boxplots and histograms of the traits with the highest contribution to PC1 of the PCA as in Table 1. Red corresponds to *E. andevalensis*, blue to *E. mackayana*. Black dots represent the mean. OH = Ovary hairiness; LSG = Length of glandular hairs; L5 = Presence of 5nate whorls; LS2G = Presence of more than 2 rows of glandular hairs; LNR = Presence of non-glandular hairs; BLH = Longest hair length in stem; LR = Leaf rolling degree; FHP = Pedicel hairiness.

Genetic distance

Nei's genetic distance among *E. mackayana* populations was 0.280 in average, while distance among *E. andevalensis* populations was 0.268 (Suppl. material 1: table S5). Mean Nei's genetic distance between both species was 1.146. Therefore, the inter-specific average distance between both species was >4 times greater than intra-specific.

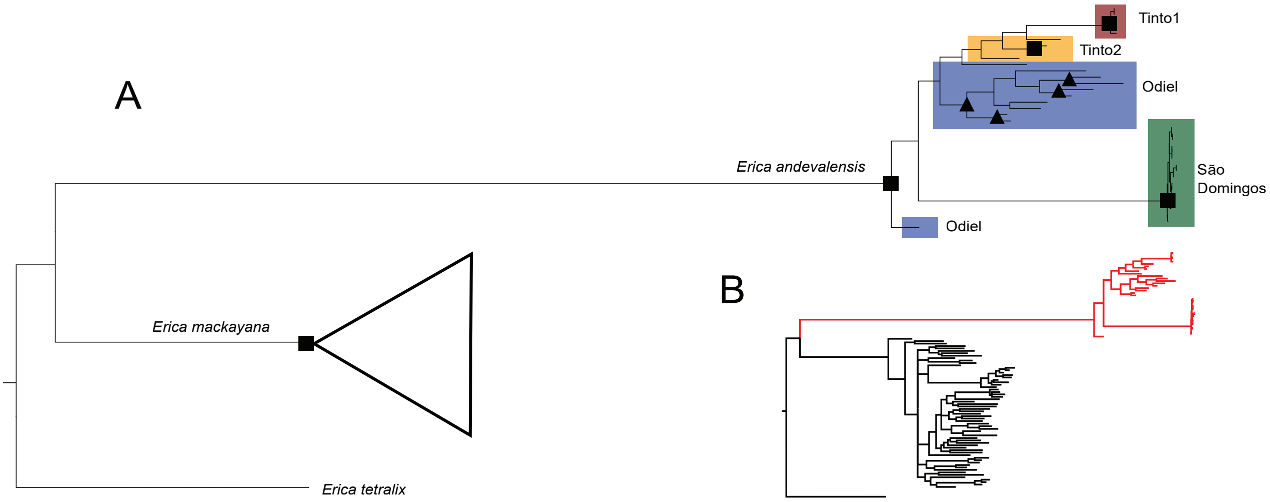

Figure 6. Phylogenetic tree of *E. andevalensis* and *E. mackayana* **A** tree showing the *E. mackayana* clade collapsed. Colors represent sites as in Fig. 4. Bootstrap support is indicated on nodes when >80: squares represent full support and triangles 80–99% **B** expanded tree.

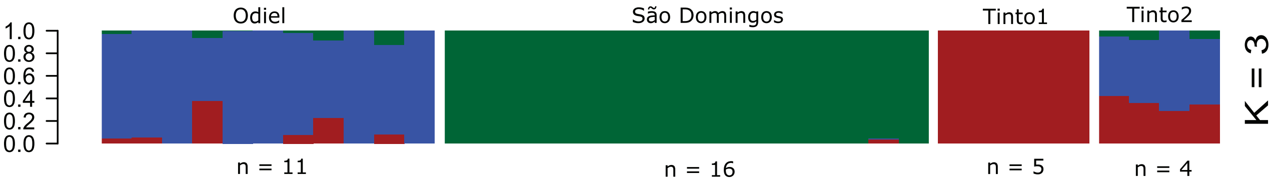

Figure 7. Bayesian individual assignment probabilities of all populations belonging to *E. andevalensis*. K = 3, was calculated by cross-entropy scores.

Populations structure of *E. andevalensis*

Bayesian population assignment probabilities revealed a highly structured assemblage into three clusters in *E. andevalensis*. This number of clusters was the optimal aggrupation within the dataset following cross-entropy scores. The assemblage is consistent with geographical distribution of populations from São Domingos and Tinto1, which were the most homogeneous, and admixture with other clusters is nearly absent. These two populations corresponded with two of the clusters (green and red, respectively in Fig. 7). The third cluster (blue) was dominant in the population from Odiel, in which the other two clusters were also represented. Finally, all plants from Tinto2 population showed high levels of admixture mainly from red and blue clusters.

We also assessed population structure through pairwise F_{ST} comparisons. The results align with clustering analyses, providing additional insights. Notably, São Domingos stood out as a genetically distinct population (F_{ST} = 0.906; 0.8; 0.652, from Tinto1, Tinto2 and Odiel populations respectively). Spanish populations (Odiel, Tinto1, and Tinto2) showed a lower genetic differentiation, although F_{ST} values among populations were relatively high (Odiel-Tinto1, F_{ST} = 0.392; Tinto2-Tinto1: 0.466). Only the genetic differentiation between Odiel and Tinto2 was moderate low (Fst = 0.122).

The nucleotide diversity (π_i) and heterozygosity (H_o and H_e) in *E. andevalensis* exhibited significant variation among populations, with Odiel and Tinto2 ranking as the most diverse, in that order. Additionally, these two populations showed a lower F_{IS} index (Table 2). In contrast, São Domingos displayed an

Table 2. Summary diversity statistics of *E. andevalensis* populations calculated across sampling locations in which more than two samples were collected.

Population	N	H_o	H_e	F_{IS}	π_i
Odiel	11	0.155	0.289	0.464	0.219
São Domingos	16	0.028	0.087	0.674	0.025
Tinto 1	5	0.049	0.106	0.537	0.044
Tinto 2	4	0.148	0.247	0.401	0.163
Total	**36**	**0.083**	**0.169**	**0.508**	**0.10**

exceptionally low level of diversity, being more than eight times less nucleotide diverse than the Odiel population. Furthermore, São Domingos emerged as the population with a higher excess of homozygotes than expected (F_{IS} = 0.674).

Nucleotide diversity (π_i) and heterozygosity (H_o and H_e) in *E. andevalensis* was in general similar to *E. mackayana* (Suppl. material 1: table S6). However, Odiel and Tinto2 populations were more diverse than those of *E. mackayana*, while Tinto1 and São Domingos are less. F_{IS} index was high in both species for the two species in all sampling areas, but higher in *E. andevalensis*.

Discussion

This study provides evidence supporting the status of *Erica andevalensis* as an accepted species, clearly distinct from its sister-group *E. mackayana*. Both morphological and genetic variability between species is much higher than among populations, and populations are highly structured in *E. andevalensis*, as previously found for *E. mackayana* (Fagúndez and Díaz-Tapia 2023). *Erica andevalensis* and *E. mackayana* share a number of traits that are rare or unique in the northern heathers such as broad leaves, umbel-like terminal inflorescences and the presence of pluricellular glandular hairs in leaves and stems. Together with *E. tetralix* and *E. ciliaris*, they belong to a robust clade that exhibits further unique features such as pluricellular glandular indumentum or unrolled leaf margins, compared to other paleartic species (Bayer 1993; Nelson 2012; Mugrabi de Kuppler et al. 2015).

Morphology and phenotypic analysis

The analysis of morphological traits provided reliable diagnostic characters for *E. mackayana* and *E. andevalensis* (Table 1, Figs 4, 5). These included the presence of some short hairs in the apex of the ovary near the insertion point of the style in *E. andevalensis*, which are absent in *E. mackayana*. This was previously stated by Bayer (1993), but not in the original description of *E. andevalensis*, in which it is described as having a glabrous ovary (Cabezudo and Rivera 1980). Variation in ovary hairiness is one of the most informative traits among species of the northern heathers, varying consistently between species even within closely related groups such as the *E. ciliaris-tetralix* clade (Nelson 2012). Hybridization among species of this group is recognized by the presence of hairs in the ovary, generally fewer and localized towards the apex as in *E.* × *stuartii* (*E. tetralix* × *E. mackayana*, Fagúndez 2006).

Other diagnostic characters related to leaf indumentum included the presence of short unicellular hairs in *E. andevalensis* which are nearly absent in *E. mackayana*, and long, pluricellular glandular trichomes in the two species but much longer in *E. mackayana*. Diagnostic differences in leaf hairiness are also reflected in the hairiness of other vegetative and non-vegetative organs, such as stems and flower pedicels (Cabezudo and Rivera 1980).

Leaf arrangement also contributed to species delimitation, as *E andevalensis* consistently shows 4-nate whorls of erect leaves. In *E. mackayana*, leaves are 4-6-nate and patent. Leaves of *E. andevalensis* are similar in size to those of *E. mackayana*, but narrower with more rolled-in margins. Remarkably, leaf length shows minimum contribution to PC1, but the highest weight in PC2, reflecting strong variation at the population level (Suppl. material 1: table S4). Leaf size is commonly described as a plant trait with high variation due to phenotypic plasticity (Stotz et al. 2022). This character may be informative to understand adaptation to stress factors or environmental constraints such as climate and soil condition in this group of heathers.

Other traits showed limited potential as diagnostic characters, particularly those related to reproductive biology. In *E. andevalensis*, flowers can be shorter and narrower, with a more pronounced style exertion. However, flower size and proportions can vary at different development stages. This variability is even more pronounced in ovary morphology and size (Suppl. material 1: table S3). *E. andevalensis* tends to have larger but flatter ovaries, but ovary size and shape depends on its development stage in transition towards fruit formation, which is difficult to assess. With regards to anther traits, *E. andevalensis* has darker and longer anthers, with a wider aperture, and a larger knob (a small protuberance in the anther) than *E. mackayana*, but these traits showed high overlapping values (Suppl. material 1: table S3).

Genetic identity of *Erica andevalensis*

Phylogenetic analyses show that both *Erica mackayana* and *E. andevalensis* are well supported monophyletic groups. Reciprocal monophyly is accepted as one of the most important lines of evidence on species delimitation (Moritz 1994; Mehta et al. 2019). Genetic distance has also been used extensively in species delimitation. We found that genetic distance was >4-fold higher between the species *E. andevalensis* and *E. mackayana* than among their populations. A much greater distance between species compared to populations supports their consideration as different species, in line with Birky et al. (2010) and Dellicour and Flot (2015). A combined framework for species delimitation, incorporating both phylogenetic tree-based approaches and genetic distance analysis, has been applied across various taxonomic groups (e. g. Bradley and Baker 2001; Meudt et al. 2009; Del Prado et al. 2011; Goicoechea et al. 2012).

The much greater branch lengths in *E. andevalensis* than in *E. mackayana* (Fig. 6), are consistent with results from phylogenetic analysis of plastid and nuclear ribosomal DNA sequences in Mugrabi de Kuppler et al. (2015) and could reflect a consistently faster rate of sequence divergence in *E. andevalensis*. Smaller population sizes resulting from edaphic specialization over time could contribute to this phenomenon. Small population size has been correlated with fast evolution empirically in many groups (Lanfear et al. 2014). There is potential for further exploration of the relation between genomic processes and enhanced ability of *E. andevalensis* to adapt to extreme environments. *Erica andevalensis*, has been extensively studied for its metal-tolerant characteristics, thriving in heavily polluted soils with high concentrations of Cu, Ni, or F (e.g. Márquez et al. 2005; Rossini-Oliva et al. 2018). Its close relative, *E. mackayana*, can grow in a wider range of soils, even in serpentine soils with high levels of heavy metals, (e.g. A Capelada mountain range in NW Spain) and can inhabit areas with pH as low as 3 (Webb 1955; Fagúndez and Pontevedra-Pombal 2022), so may also exhibit pyritic-soil tolerance.

Intraspecific variation in *Erica andevalensis*

Two of the studied populations of *E. andevalensis* showed low support for internal nodes in the phylogeny, but the population structure analysis showed low levels of admixture, meaning that *E. andevalensis* populations are highly structured. The genetic differentiation among populations separated by less than 85 km is higher than in the entire distribution area analyzed for the related species *E. mackayana* (Fagúndez and Díaz-Tapia 2023). A high differentiation among populations is typically found in taxa with a highly fragmented distribution, as in soil endemic plants (Leimu and Mutikainen 2005; Nistelberger et al. 2015). The large genetic divergence between Tinto1 and Tinto2, separated by only 7.5 km and initially considered as a single population, was a surprising finding. We found a lower proximity due to river section (medium *vs* low river course) than that of river identity (Odiel *vs* Tinto).

Soil endemic plants usually have low genetic diversity, but their F_{IS} index clearly diverge between different plants groups (e. g. Barbará et al. 2007; Wang et al. 2017; Nagasawa et al. 2019). It has been suggested that species traits such as self-compatibility or clonality might impact the F_{IS} index (Lavor et al. 2014), thus comparing soil endemic species F_{IS} values with related taxa with broader ranges can be interesting. Compared to its close relative *E. mackayana*, *E. andevalensis* had higher F_{IS} index values, and genetic diversity was highly variable among *E. andevalensis* populations. São Domingos population results show the highest F_{IS} value and lowest genetic diversity of all populations of both species, in line with results from the *E. andevalensis* microsatellites' analyses (Bandeira de Albuquerque et al. 2008), and probably reflecting a founder effect. This population is at the edge of the species distribution range, entirely located in an abandoned mining area (Figs 1C, 2).

The origin and migration history of different *Erica* species are a subject of debate, especially when there is a potential transportation linked to human activities (Fagúndez and Díaz-Tapia 2023; Skeffington and Scott 2023). Nelson et al. (1985) suggested that mining populations of *E. andevalensis* might not be native, originating with the commencement of mining activity in the area, estimated by Tornos et al. (2000) to be more than 5000 years ago. This hypothesis aligns with the low genetic diversity of São Domingos, but Bandeira de Albuquerque et al. (2008) found high genetic diversity in other populations in Huelva linked to mining activities. Nevertheless, the creation of new niches by humans (highly toxic damp mines), coupled with an increased concentration of heavy metals in rivers, could have facilitated the establishment of larger populations beyond their natural limits and possibly a recent migration between previously unconnected populations. This is consistent with the moderate connection between populations in the lower Odiel and Tinto basins and could explain higher genetic diversity in these populations and slightly lower F_{IS} index. The small size of the seeds which are produced in large numbers makes them easily dispersed by animals, wind and other vectors including humans (Aparicio and García-Martín 1996; Fagúndez and Izco 2004; Fagúndez and Izco 2010).

Implications for conservation

Clarifying cryptic or poorly understood taxa and species delimitation is needed for the design of conservation policies and actions, especially in large genera such as *Erica* (Pirie et al. 2022). Verification of specific status should give stronger support to the natural value of the Iberian Pyrite Belt, which is partly a protected area in Spain (BOJA 2005). *Erica andevalensis* is legally considered an endangered species, classified as vulnerable (VU), but only in Spain. The low genetic diversity and singularity of the Portuguese population, both phenotypical and genotypical, coupled with its presence in a very restricted area, should justify the consideration of *E. andevalensis* as an endangered species in Portugal as well, as proposed in Carapeto et al. (2020).

Conservation strategies for *E. andevalensis* should protect a variety of populations in different river basins and sections, and research evaluating its use for restoration should consider infraspecific variability and special issues of working with metallophyte species. For instance, habitat decontamination of heavy metal polluted river shores needs to be carefully considered, as it may have a negative effect in local populations of *E. andevalensis* (Márquez et al. 2005). Recommended conservation actions of metallophytes endemic species usually include prohibiting new mining activities in areas (Whiting et al. 2004). This recommendation was also made to conserve *Erica andevalensis* populations (Márquez et al. 2005). However, certain metallophytes may benefit from human perturbations in the long-term, potentially leading to an increase in their populations (Faucon et al. 2011), and this may be the case for *E. andevalensis*. Many conservation studies on metallophytes focus on areas where mining has been intensive but only during the last century. Our study, by contrast, shows the genetic and dispersal effects of long-term mining (>5000 years BP) in an endemic metallophyte species.

There is potential for use of *E. andevalensis* in bioremediation of polluted soils (Abreu et al. 2008; Monaci et al. 2010; Pérez-López et al. 2014). Differences with regards to soil preference between Spanish and Portuguese populations (Pérez-López et al. 2014), suggest a potential variability in bioremediation performance at the population level. These ecological differences, also reflected in genetics, should be considered in planning habitat restoration.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

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

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Supplementary material 1

Supplementary tables

Authors: Iván Rodríguez-Buján, Pilar Díaz-Tapia, Jaime Fagúndez

Data type: docx

Explanation note: **table S1:** Information on the populations of the studied species *Erica mackayana* and *E. andevalensis*, and one population of *E. tetralix* used as the outgroup. N_1: number of individuals used in the genetic analyses, based on having <50% of missing data in population structure analysis. N_2: number of individuals used in the morphological analyses. **table S2:** Morphological traits measured in plants of *Erica mackayana* and *E. andevalensis*, acronym names and methodology. QN = Quantitative trait, O = Ordinal trait, B = Binary trait. N = Number of measures per specimen. **table S3:** Results of univariant tests between *Erica mackayana* and *E. andevalensis*, including the arithmetic mean and range for each of the morphological traits named as in Fig. 1 and Suppl. material 1: table S2. *E. mack* = *E. mackayana*. *E. andev*. = *E. andevalensis*. * = p-value < 0.05, **= p-value < 0.01, *** = p-value < 0.001. **table S4:** Percentage of contribution of each morphological trait included in the PCA to the first two components (PC1 and PC2), named as in Fig. 1 and Suppl. material 1: table S2, ordered by their contribution to PC1. **table S5:** Distance matrix for the studied populations of *Erica mackayana* and *E. andevalensis*. Pairwise Tamura and Nei distance (1993) calculated upon MEGA 11. **table S6:** Summary of the genetic diversity statistics of *E. andevalensis* and *E. mackayana* populations. Statistics for populations with less than three individuals were not included.

Link: https://doi.org/10.3897/phytokeys.244.120914.suppl1

PhytoKeys 244: 77–87 (2024)
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Research Article

Polygala qii, a new species of Polygalaceae from limestone landform in Southern Hunan, China

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Abstract

Polygala qii, a new species, is described and illustrated from limestone landform in southern Hunan, China. The new species resembles *P. fallax* and *P. arillata* in flower structure of the plants, but readily differs from the latter two in having erect and shorter inflorescences (0.2–1cm VS 10–15cm VS 7–10cm), and fewer flowers (1–5 flowers VS 10–30 flowers VS 10–20 flowers), and the latter two have a later flowering period (late March to mid-April VS May to August VS May to October). And it is an extremely unique new species that will hibernate in the hot summer of July and August. Following the IUCN Red List Criteria, *P. qii* is assessed as 'Data Deficient (DD)'.

Key words: Hunan province, limestone landform, new species, *Polygala*, taxonomy

Introduction

There are approximately 500 species in the *Polygala* L. (1753:701) (Polygalaceae), which are almost globally distributed. The Flora of China includes 44 species, of which 21 are endemic to China (Chen et al. 1997; Chen et al. 2008; APG 2016). The roots of some plants in the genus *Polygala* can be used as medicinal materials, such as *P. fallax*.

In March 2020, during our investigation in the limestone area of southern Hunan, we discovered a unique species of *Polygala* plant which they grew in the crevices of dry limestone. The plant is different from all the plants of the Polygala genus recorded in Hunan Province; for example, it is a deciduous shrub, blooms very early (usually in late March), leaves have membranous transparent edges, and fewer but denser flowers on the inflorescence and so on. In August of the same year, when we visited the area again to investigate, we found that this plant had already fallen leaves.

In the following year, we collected more specimens of this species, and through phenological observation and morphological research, we finally confirmed that this is a new species.

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Material and methods

The specimens are mainly stored in the Herbarium of Forest Plants in Central South University of Forestry and Technology (CSFI). Morphological observations of the new species were derived from field observations, as well as study of specimens. The conservation status of this new species is based on field observations in accordance with IUCN Red List guidelines (IUCN 2022).

Taxonomic treatment

Polygala qii **X.L.Yu, J.J.Zhou & A.Liu, sp. nov.**
urn:lsid:ipni.org:names: 77344993-1
Figs 1, 2

Diagnosis. This new species is similar to *P. fallax* Hemsl. and *P. arillata* Buch.-Ham. & D. Don, but it differs from the latter two in having erect and shorter inflorescences (0.2–1cm VS 10–15cm VS 7–10cm) and fewer flowers (1–5 flowers VS 10–30 flowers VS 10–20 flowers). Its caruncle is foam, and the latter two are helmeted in shape. Please refer to Fig. 3 and Table 1.

Type. China. Hunan: Yongzhou City, Dao County, Yueyan Forest Farm, in the crevices of dry limestone, elevation ca. 290 m, 25 March 2021, *Ang Liu* DX01 (Holotype CSFI!, isotype CSFI!, HIB!). Please refer to Fig. 4.

Description. Shrubs, 0.5–1.5m high. ***Branchlets*** yellow, sparsely pilose, and the branch bark is cracked into irregular thin scales, especially on the specimens. ***Leaves*** alternate, clustered at the top of branchlets. ***Petiole*** ca. 1 cm, pubescent. ***Leaf blade*** papery, elliptic to oblong elliptic, 5–11 × 2–5cm, with membranous transparent edge, full margin, ciliate, both sides sparsely pubescent, dense along the veins, then gradually glabrous, midvein raised abaxially, depressed adaxially, lateral veins 5 or 6 pairs, apex acuminate or short tail tip, base cuneate or obtuse. ***Racemes*** opposite to leaves, with 1–5 flowers, erect or slightly drooping at the apex, densely pubescent, 0.2–1cm long, up to 5cm at fruiting. ***Pedicel*** glabrous, ca. 0.5cm long, to 1cm at fruiting. ***Flowers*** 1.6–2.3cm. ***Sepals*** 5, ciliate, fall off after flower, outer 3 small, unequal in size, upper 1 deep pocket shaped, 0.5cm long, lateral 2 oval, ca. 0.3cm long, inner sepals 2, petal shaped, yellowish white, obliquely obovate, edge rolled in a boat shape, 1.5–2cm, and at right angles to the petals. ***Petals*** 3, connate in lower 2/3, yellowish white, with light purplish red at the apex, slightly fleshy; keel longer than lateral petals, apex with multifid appendages, appendages with short stalks at the base, ca. 0.15cm. ***Stamens*** 8; filaments ca. 1.5cm, lower 2/3 united, forming an open staminal sheath, adnate with petals; anthers ovoid. Disk fleshy. ***Ovary*** round, flattened, ca. 0.4cm, glabrous, style ca. 1.5cm, bent to the top, with knee bending at 2 / 3, and obviously expanded to the apex in a trumpet shape. ***Capsules*** green, baccate, broadly reniform or slightly cordate, ca. 1 cm, margin winged, ciliate, apex emarginate, mucronate. ***Seeds*** globose, sparsely white pubescent, caruncle foam.

Phenology. Flowering from late March to mid-April; fruiting from late April to early May. What is very special is that this new species enters a dormant period with leaf withering in mid-July.

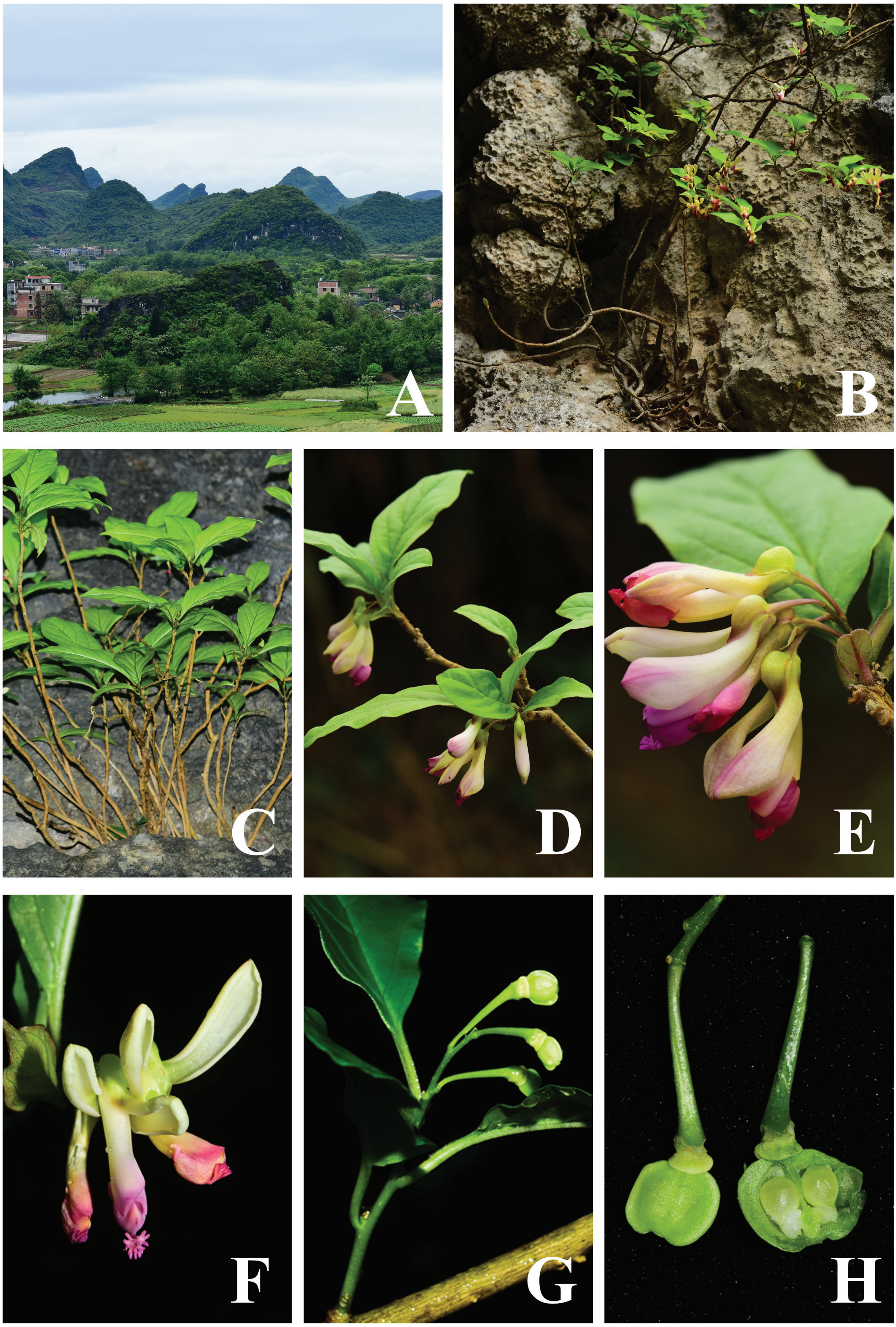


Figure 1. *Polygala qii* sp. nov. **A** habit **B** plant **C** plant **D** branch with flowers **E** inflorescence **F** front view of flowers **G** infructescence **H** capsules and Seeds. Photographed by Ang Liu.

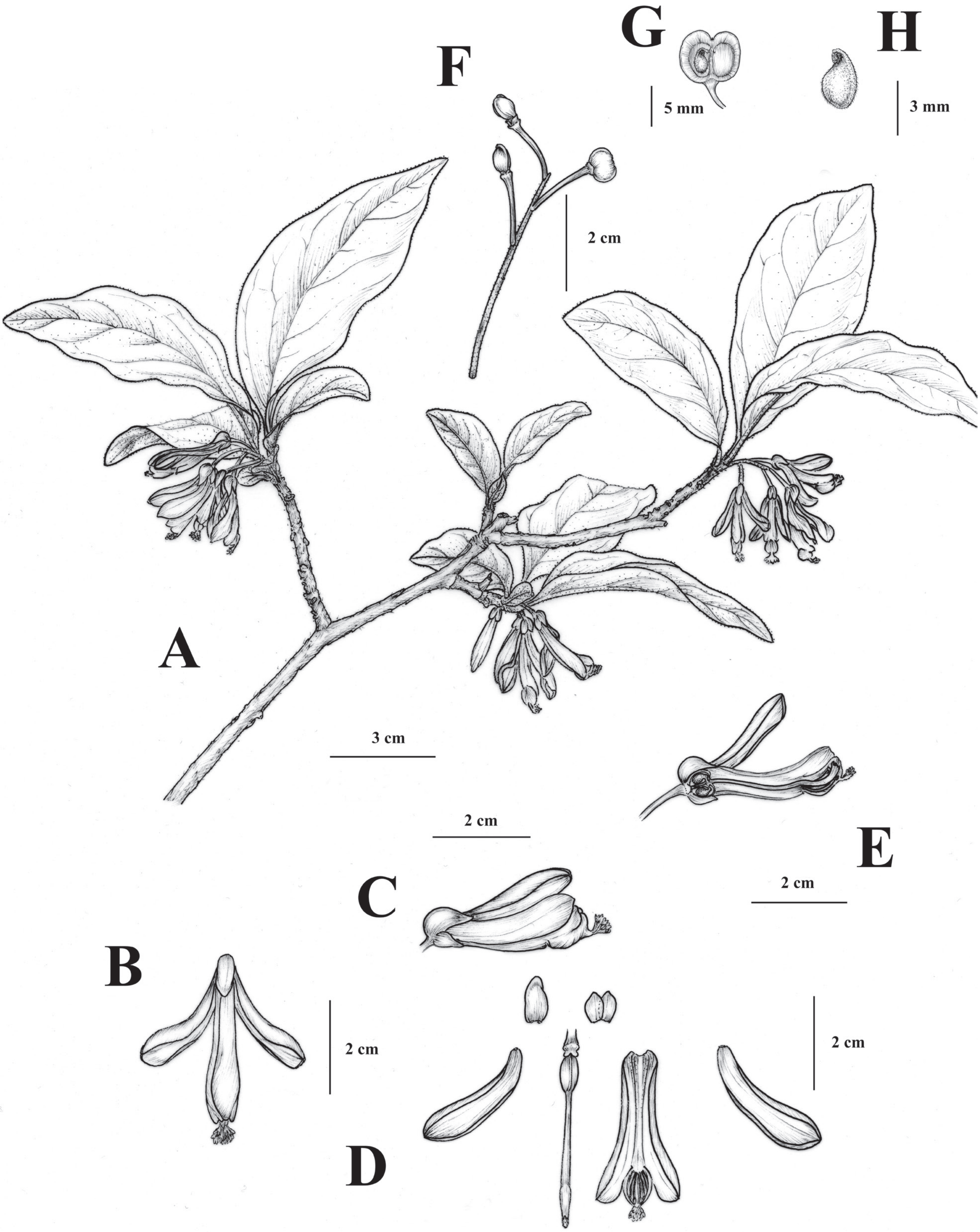


Figure 2. *Polygala qii* sp. nov. **A** branches with flowers **B** top view of flower **C** side view of flower **D** anatomical structure of flower, sepals, petals and pistil **E** longitudinal section of flower **F** infructescence **G** capsule **H** seed. Drawn by PhD Jing Tian.

Etymology. The new species is named after Professor Cheng-jing Qi (CSUFT&CSFI), who has made great contributions to the study of Hunan flora (Qi & Yu, 2002).

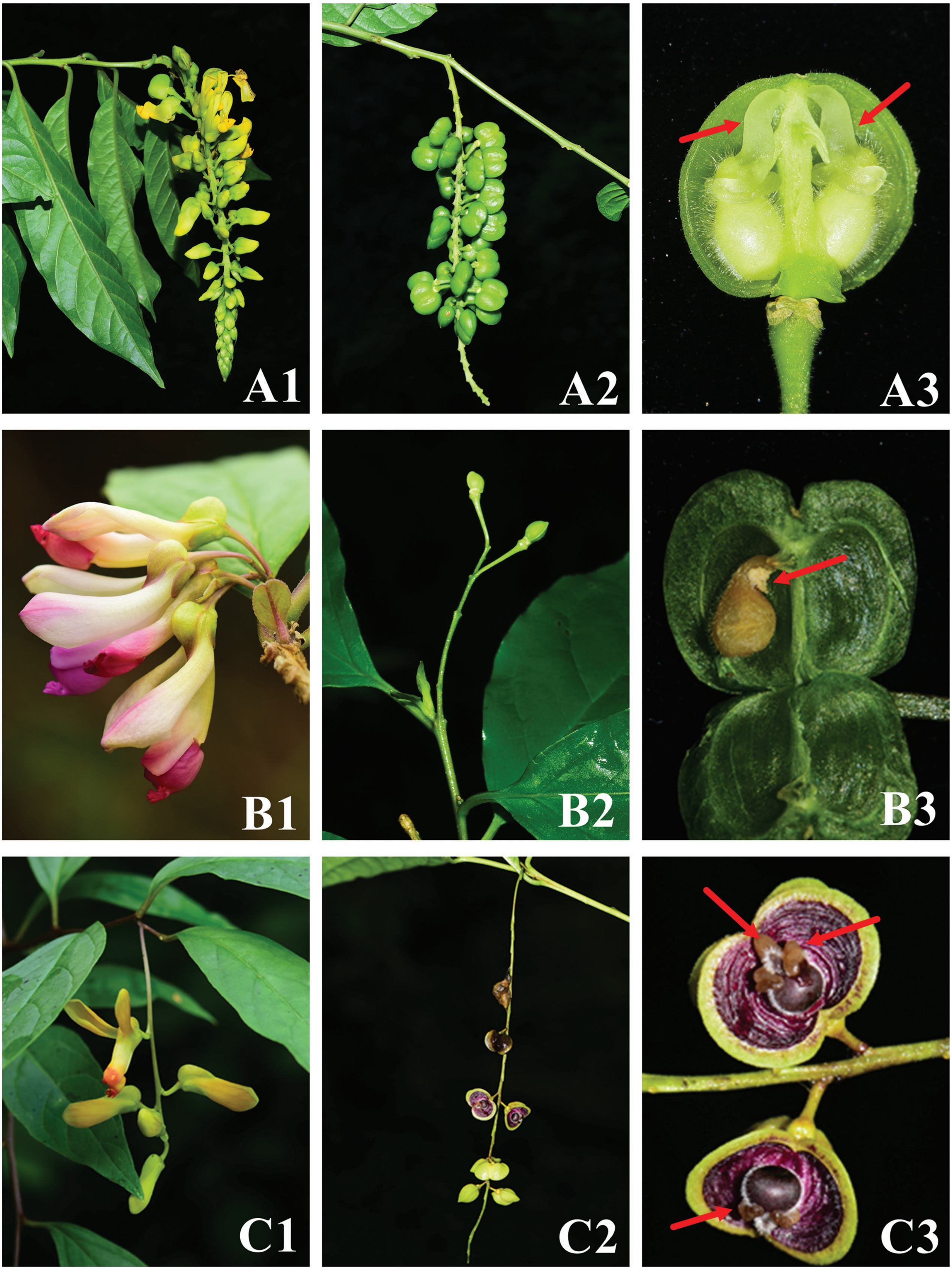


Figure 3. Morphological comparison between *Polygala fallax* (**A1–A3**), *Polygala qii* sp. nov. (**B1–B3**), *Polygala arillata* (**C1–C3**). **A1, B1, C1** inflorescence **A2, B2, C2** infructescence **A3, B3, C3** seeds, the red arrow represents caruncle. **C2, C3** photographed by Xin-xin Zhu, others photographed by Ang Liu.

中南林业科技大学森林植物标本室
采 集 记 录

标本号：
产地：湖南省道县月岩林场
海拔：290 m 生境：石灰岩石壁
习性：灌木 体高：0.8-1.5 胸径：
树皮：
叶：椭圆形
花：
果：
用途： 照片号：
采集人：刘昂 采集号：DX01
日期：2021年 3月25日 附记：
中名：远志属 当地名：
科名：远志科 Polygalaceae 科号：42
学名：Polygala

中南林业科技大学植物标本馆
CSFI076291

Holotype!
Polygala qii X.L.Yu, J.J.Zhu & A.Liu
石山远志 sp. nov
Det. 刘昂 2021.8.20

Figure 4. Holotype of *Polygala qii* sp. nov. (*Ang Liu* DX01, CSFI 076291).

Table 1. Comparison of morphological characters among *Polygala qii*, *P*. *fallax* and *P*. *arillata*.

Characters	***Polygala qii* sp. nov.**	***P. fallax***	***P. arillata***
Plants	0.5–1.5m	1–3m	1–5m
Leaves	5–11 × 2–5cm	8–20 × 4–6.5cm	6.5–14 × 2–2.5cm
Racemes	erect	drooping	drooping
	0.2–1cm, to 5cm at fruiting	10–15cm, to 30cm at fruiting	7–10cm, to 30cm at fruiting
	1–5 flowers	10–30 flowers (or more)	10–20 flowers (or more)
Flowers	yellowish white, apex with purplish red	yellow	yellow, or apex with orange red
Caruncle	foam	helmeted	helmeted
Flowering period	late March to mid-April	May to August	May to October

Vernacular name. The Chinese name of the new species is '石山远志',and the pronunciation of the Chinese Pinyin is 'shí shān yuǎn zhì'.

Distribution and habitat. This new species is currently only found in the limestone landform areas of Dao County and Ningyuan County, which usually grows in the crevices of dry limestone.

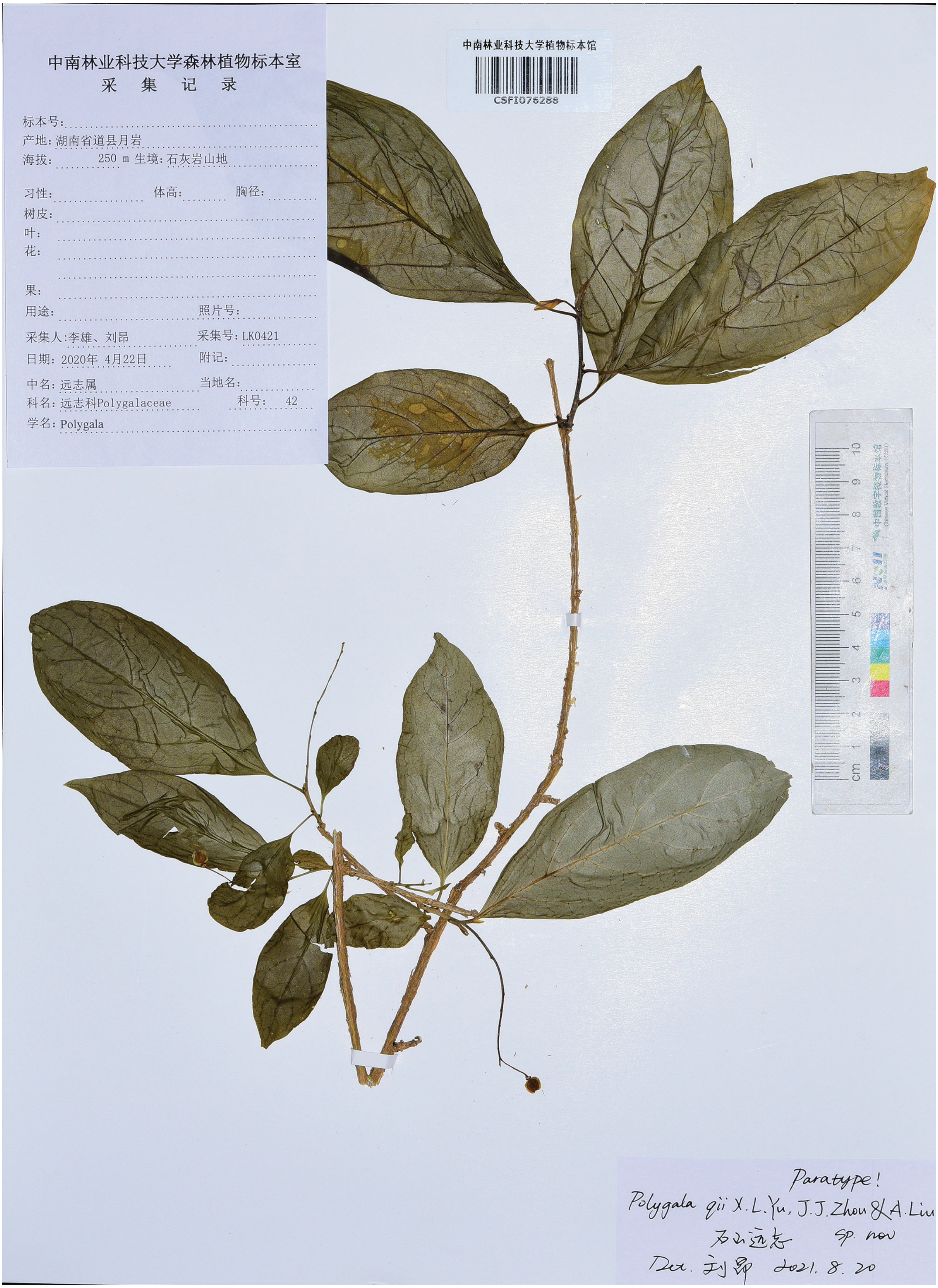
Additional specimens examined (Paratypes). China. Hunan: Yongzhou City, Dao County, Yueyan Forest Farm, in the crevices of dry limestone, elevation ca. 250 m, 22 April 2020, *Xiong Li &Ang Liu* LK0421(CSFI!, HIB!&CSH!); Yongzhou City, Ningyuan County, Jiuyi Mountain, in the crevices of dry limestone, elevation ca. 300 m, 29 April 2020, *Jian-jun Zhou* NY005(CSFI!). Please refer to Figs 5, 6.

Conservation status. At present, we have only found two populations with a total of about 30 individuals in the limestone areas of Dao County and Ningyuan County. However, there are vast limestone landforms in southern Hunan, and there may be distribution of this new species in these areas. Of course, we need a broader and deeper investigation to confirm that. According to the IUCN red list criteria (IUCN 2022), the conservation status of the new species should be better categorized as 'Data Deficient (DD)'.

Discussion

We have previously discovered some new species of *Primulina* in the limestone areas of southern Hunan, such as *P. jiangyongensis* X. L. Yu & Ming Li (Li et al. 2014), *P. porphyrea* X. L. Yu & Ming Li (Li and Yu 2015), *P. cataractarum* X. L. Yu & A. Liu (Ding et al. 2021) and *P. gracilipes* X. L. Yu & A. Liu (Gong et al. 2022) and so on. The discovery of the new species illustrates the rich plant diversity in limestone landforms of southern Hunan once again, most of which have inconvenient transportation and dangerous terrain, and explains that we still need to conduct more in-depth research in this area.

This unique new species withers its leaves in July and August (Please refer to Fig. 7), which may be to adapt to the high summer temperatures in the limestone areas of southern Hunan. This phenomenon has important reference significance for studying the adaptation of plants to the environment in limestone areas. Especially in areas with well-developed karst landforms, it's worth making a more profound study.



中南林业科技大学森林植物标本室
采　集　记　录

标本号：
产地：湖南省道县月岩
海拔：250 m 生境：石灰岩山地
习性：　体高：　胸径：
树皮：
叶：
花：
果：
用途：　照片号：
采集人：李雄、刘昂　采集号：LK0421
日期：2020年 4月22日　附记：
中名：远志属　当地名：
科名：远志科Polygalaceae　科号：42
学名：Polygala

Paratype!
Polygala qii X.L.Yu, J.J.Zhou & A.Liu
石山远志　sp. nov
Det. 刘昂 2021. 8. 20

Figure 5. Paratype of *Polygala qii* sp. nov. (*Xiong Li & Ang Liu* LK0421, CSFI 076288).

中南林业科技大学 林学院
森林植物标本室

采集人 周建军 采集号 NY00~~8~~5
采集时间 2020 年 4 月 29 日
产地 湖南省宁远县九嶷山
生境 山坡密林
地理坐标 ° ′ ″E ° ′ ″N
海拔 300m 性状 灌木
体高 体高
树皮/茎干
叶
花
果实
中文名 土名
科名 远志科
学名
附记

中南林业科技大学植物标本馆
CSFI080027

Paratype!
Polygala qii X.L. Yu, J.J. Zhou & A. Liu sp. nov.
石山远志
Det. 刘昂 2021. 8. 20

Figure 6. Paratype of *Polygala qii* sp. nov. (*Jian-jun Zhou* NY005, CSFI 080027).

Figure 7. The plants of *Polygala qii* sp. nov. had fallen leaves in July. Photographed by Jian-Jun Zhou, 21 July 2020.

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Thanks for PhD Jing Tian's exquisite preparation of the line drawing and PhD Xin-xin Zhu's beautiful Photos.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Investigation: XL, AL, JZ. Writing - original draft: AL. Writing - review and editing: XY, LW.

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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 244: 89–126 (2024)
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Research Article

Notes on *Strobilanthes* (Acanthaceae) with capitate inflorescences in Thailand

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Abstract

Twenty-three species of *Strobilanthes* Blume with capitate inflorescences are enumerated in Thailand. *Strobilanthes phengklaii* Kladwong & Chantar., a new species from North-eastern Thailand, is described and illustrated. *Strobilanthes paniculiformis* J.R.I.Wood, *S. phyllostachya* Kurz and *S. squalens* S.Moore are new records in Thailand. *Strobilanthes kerrii* Craib is reinstated, and *S. evrardii* var. *parviflora* J.B.Imlay, *S. bombycina* J.B.Imlay, *Hemigraphis hispidula* Craib and *Sericocalyx thailandicus* Bremek. are treated as new synonyms. 19 taxa are lectotypified. A key to species, taxonomic notes and photographs are provided as well as a preliminary conservation assessment and distribution maps.

Key words: Identification key, new record, new species, nomenclature

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Introduction

Strobilanthes Blume is a genus of Acanthaceae consisting of ca. 454 species mostly distributed in tropical and subtropical Asia (Mabberley 2008; Christenhusz et al. 2017; Tripp et al. 2021; POWO 2023; WFO 2024). *Strobilanthes* species are herbs, subshrubs, shrubs or small trees, rarely plants are creeping. Many species are gregarious, and some have a plietesial life cycle, living several years before flowering and then, once having flowered, dying (Beentje 2016). This genus is unique in having the rugula and trichomes retaining the style (Fig. 6F) on the inner surface of posterior corolla (Wood, 1994b; Carine and Scotland 2002; Moylan et al. 2004; Wood and Scotland 2009; Hu et al. 2011; Tripp et al. 2021; Kladwong and Chantaranothai 2022).

Furthermore, three inflorescence types, spicate, paniculate and capitate are found in *Strobilanthes* species. This informal grouping as used by Wood and Scotland (2003b), Hu et al. (2011) and Kladwong and Chantaranothai (2023) but is not used in other treatments, e.g., Bremekamp (1944), Wood (1994b). The informal grouping may not work throughout the range of *Strobilanthes*, but it does provide a robust way of identifying Thai species. In the capitate type the flowers are clustered towards the tips of the strongly abbreviated inflorescence axes, and the involucral bracts and flowers are densely arranged. The bracts are variable in size and shape with the outer bracts generally larger than the inner ones (Bremekamp 1944; Bennett and Scotland 2003; Wood and Scotland 2003b; Hu et al. 2011; Kladwong and Chantaranothai 2023). A species list of all three groups based on inflorescence types reported in Thailand is presented in Table 1.

Table 1. List of species in the three groups of inflorescence types present in Thailand.

Paniculate inflorescences [a, b]	Capitate inflorescences	Spicate inflorescences
1. *S. microcarpa* T.Anderson	1. *S. aprica*	1. *S. abbreviata* Y.F.Deng & J.R.I.Wood
2. *S. pedunculosa* Miq.	2. *S. articulata*	2. *S. alboviridis* J.B.Imlay
3. *S. peninsularis* Terao	3. *S. brandisii*	3. *S. alternata* (Burm.f.) Moylan ex J.R.I.Wood
4. *S. tenuiflora* J.R.I.Wood	4. *S. capitata*	4. *S. argentea* J.B.Imlay
5. *S. trichantha* J.R.I.Wood	5. *S. chiangdaoensis*	5. *S. auriculata* Nees
6. *S. violifolia* T.Anderson	6. *S. consors*	6. *S. bilabiata* J.R.I.Wood
	7. *S. cruciata*	7. *S. collina* Nees
	8. *S. dimorphotricha* subsp. *rex*	8. *S. corrugata* J.B.Imlay
	9. *S. echinata*	9. *S. cusia* (Nees) Kuntze
	10. *S. erecta*	10. *S. dalzielii* (W.W.Sm.) Benoist
	11. *S. esquirolii*	11. *S. decumbens* (Bremek.) J.R.I.Wood
	12. *S. falconeri*	12. *S. fluviatilis* (C.B.Clarke ex W.W.Sm.) Moylan & Y.F.Deng
	13. *S. graminea*	13. *S. fragrans* J.R.I.Wood
	14. *S. hypomalla*	14. *S. glaucescens* Wall. ex Nees
	15. *S. kerrii*	15. *S. heliophila* J.R.I.Wood
	16. *S. paniculata*	16. *S. hossei* C.B.Clarke
	17. *S. paniculiformis*	17. *S. imbricata* Nees
	18. *S. phengklaii*	18. *S. karensium* Kurz
	19. *S. phyllocephala*	19. *S. maxwellii* J.R.I.Wood
	20. *S. phyllostachya*	20. *S. moschifera* Blume
	21. *S. serpens*	21. *S. pateriformis* Lindau
	22. *S. speciosa*	22. *S. quadrifaria* (Wall. ex Nees) Y.F.Deng
	23. *S. squalens*	23. *S. ranongensis* Terao
		24. *S. repanda* (Blume) J.R.Benn.
		25. *S. reptans* (G.Forst.) Moylan ex Y.F.Deng & J.R.I.Wood
		26. *S. rivularis* J.R.I.Wood & J.R.Benn.
		27. *S. rufescens* subsp. *parishii* (C.B.Clarke) J.R.I.Wood subsp. *parvibracteata* (C.B.Clarke) J.R.I.Wood
		28. *S. schomburgkii* (Craib) J.R.I.Wood
		29. *S. serrata* J.B.Imlay
		30. *S. tonkinensis* Lindau
		31. *S. violascens* Ridl.
		32. *S. xanthosticta* C.B.Clarke

[a] Wood and Scotland (2003);
[b] Kladwong and Chantaranothai (2023).

During the preparation of the taxonomic account of *Strobilanthes* for the Flora of Thailand we recently reported six Thai *Strobilanthes* species with paniculate inflorescences (Kladwong and Chantaranothai 2023). Taxonomic work on the spicate species is ongoing and this paper enumerates the 23 native species and one subspecies of the capitate group in Thailand. Six species are endemic in Thailand. A new species of *Strobilanthes* is described and three species are newly recorded. The identification key and nomenclatural treatments are presented.

Material and methods

This taxonomic study is based on extensively field observations in Thailand and the investigation of herbarium specimens at AAU, BK, BKF, BM, CMU, CMUB, E, E-GL, K, K-W, KKU, KYO, L, PSU, QBG, TCD and U. Additionally, specimens from A, ABD, B, C, CAL, CORD, G, GH, GZU, M, NY, P and SING were studied from digital images since they are available on each herbarium website and the GBIF (https://gbif.org) website. Herbarium citations follow Thiers (2021). The nomenclature follows Turland et al. (2018), and binomial authorities follow IPNI (2023). Relevant literature including Hosseus (1907), Craib (1911, 1912, 1913, 1914), Benoist (1935), Imlay (1938, 1939), Bremekamp (1944, 1953, 1961, 1965, 1966, 1969), Terao (1980, 1981, 1983), Hansen (1985), Wood (1994b), Bennett and Scotland (2003), Wood and Scotland (2003b, 2009), Hu et al. (2011), Albertson and Wood (2012), Pooma and Suddee (2014), Newman et al. (2007, 2017), Wood et al. (2022) and Kladwong and Chantaranothai (2022, 2023) were consulted. Global conservation assessments were made using the categories and criteria of IUCN (2022); EOO and AOO were calculated using GeoCAT (Bachman et al. 2011).

Taxonomic treatment

Notes on taxonomic characters

The unequal leaf pairs are observed in many species of *Strobilanthes* (Wood 1994b; Hu et al. 2011). This character is variable in some species, but it can be used to group *S. articulata*, *S. phyllocephala* and *S. falconeri*. The bracts are commonly used to distinguish species, especially using shapes, sizes and indumentum types (Clarke 1884; Bremekamp 1944; Wood 1994b; Bennett and Scotland 2003; Hu et al. 2011). Moreover, the occurrence of leaf-like bracts or the bract having a petiolar base (Bremekamp 1944; Wood and Scotland 2009; Hu et al. 2011) are also used to recognize the species such as *S. brandisii*, *S. consors*, *S. cruciata*, *S. erecta*, *S. esquirolii*, *S. falconeri* and *S. phyllocephala*. The calyx is useful for taxonomic delimitation (Nees 1832; Bremekamp 1944; Wood and Scotland 2003a; Hu et al. 2011). The calyx lobes are subequal in almost all species whereas they have one lobe longer than others in *S. dimorphotricha* and *S. paniculiformis*. The colour of corolla is usually purple or pale purple or mauve or pale blue, but rarely white or yellow (Benoist 1935; Imlay 1938, 1939; Bennett and Scotland 2003). The white corolla is found only in *S. cruciata*. Purple and white can occur in species such as *S. kerrii* and *S. speciosa*. The yellow corolla is rare, and this character is observed in *S. phengklaii*, *S. squalens* and *S. phyllostachya*.

Conservation assessments

23 species of *Strobilanthes* with capitate inflorescences are enumerated in Thailand. Three species, *S. chiangdaoensis*, *S. paniculiformis* and *S. phyllostachya* are assessed as vulnerable. Two species, *S. graminea* and *S. hypomalla* are endangered. All localities of the threatened species are in protected areas such as the national park and wildlife sanctuary, but they have only a few records. Moreover, they also need specific habitats such as the rugged limestone ridge in mixed evergreen and deciduous forests or the open plateau of evergreen mountains and the sandy soil in dipterocarp forest. The changes of habitats are occurring through increasing droughts and fires caused by humans leading to the decline of the threatened species. *Strobilanthes chiangdaoensis* and *S. phyllostachya* are cultivated at Queen Sirikit Botanic Garden. *Strobilanthes articulata* and *S. phengklaii*, *S. phyllocephala* are Data Deficient with few collections; more field work is needed to assess these species. Further details on conservation assessments of the threatened species are provided under the species accounts below.

Key to the species of *Strobilanthes* with capitate inflorescences in Thailand

1 Flowers pedicellate, separately arranged into panicles .... **Paniculate inflorescence group**

– Flowers sessile or subsessile, lax or densely arranged **2**

2 Flowers arranged along inflorescence axes; bracts and flowers lax or densely arranged into spikes; bracts arranged into lower and upper ones, lower and upper bracts same size or the lower bracts generally larger than the upper ones .... **Spicate inflorescence group**

– Flowers clustered towards the tips of the inflorescence axes; bracts and flowers densely arranged into terminal heads; bracts arranged into outer and inner ones, outer bracts generally larger than the inner ones .... **Capitate inflorescence group 3**

3 Leaf margin entire or subentire except serrulate in *S. aprica*; stamens 2, exserted **4**

– Leaf margin serrate, crenate or dentate; stamens 4, included except *S. paniculata* **6**

4 Capsule 8-seeded .... **13.** ***S. graminea***

– Capsule 4-seeded **5**

5 Leaves lanceolate to oblong-lanceolate; leaf margin entire; corolla pubescent outside .... **14.** ***S. hypomalla***

– Leaves elliptic to oblong-elliptic; leaf margin serrulate; corolla glabrous or subglabrous outside .... **1.** ***S. aprica***

6 Corolla yellow **7**

– Corolla white or purple or whitish purple or pale purple or mauve or pale blue or whitish-cream or pale violet **9**

7 Leaves lanceolate to oblong-lanceolate; bracts densely sericeous .... **18.** ***S. phengklaii***

– Leaves obovate to obovate-oblong; bracts puberulous or hirsute **8**

8 Bracts lanceolate to linear-lanceolate, acute at apex; corolla sparsely hairy outside .... **23. *S. squalens***
– Bracts elliptic, ligulate at apex; corolla glabrous outside .... **20. *S. phyllostachya***
9 Stamens exserted .... **17. *S. paniculata***
– Stamens included **10**
10 Capsules 8-seeded .... **21. *S. serpens***
– Capsules 2-seeded or 4-seeded **11**
11 Capsules 2-seeded .... **5. *S. chiangdaoensis***
– Capsules 4-seeded **12**
12 Outer bracts leaf-like or with petiolar base **13**
– Outer bracts ovate to orbicular or ovate or obovate to spatulate or elliptic-lanceolate or lanceolate to linear-lanceolate or oblanceolate, sessile **19**
13 Corolla white; ovary glabrous .... **7. *S. cruciata***
– Corolla whitish-purple or blue; ovary hairy at apex **14**
14 Bracts, bracteoles and calyx densely white tomentose **15**
– Bracts, bracteoles and calyx hirsute or pilose or glabrous **17**
15 Stems sulcate, dark green; bracts oblong-lanceolate, dark green .... **11. *S. esquirolii***
– Stems not sulcate, yellowish-green; bracts obovate or oblanceolate or spathulate, yellowish-green or whitish-green **16**
16 Heads ellipsoid; bracts curved; bracteoles acute to acuminate at apex; calyx lobes acuminate at apex .... **6. *S. consors***
– Heads suborbicular; bracts flat; bracteoles obtuse at apex; calyx lobes acute at apex .... **3. *S. brandisii***
17 Plants isophyllous or subisophyllous .... **10. *S. erecta***
– Plants anisophyllous **18**
18 Stems villose or tomentose; leaves elliptic-lanceolate or lanceolate; bracteole acute at apex .... **12. *S. falconeri***
– Stems pubescent or glabrescent; leaves ovate or ovate-elliptic; bracteoles obtuse at apex .... **19. *S. phyllocephala***
19 Inflorescence axis very slender; bracteoles absent .... **2. *S. articulata***
– Inflorescence axis not as above; bracteoles present **20**
20 Bracteoles and calyx dentate or fimbriate or dentate-crenate at apex .... **9. *S. echinata***
– Bracteoles and calyx rounded or obtuse or acute to acuminate **21**
21 Calyx lobes with 1 lobe longer than others **22**
– Calyx lobes subequal **23**
22 Bracts ovate or elliptic-lanceolate; bracteoles lanceolate to ovate-lanceolate, acute at apex .... **8. *S. dimorphotricha* subsp. *rex***
– Bracts ovate-orbicular; bracteoles obovate to oblong-oblanceolate, rounded at apex .... **16. *S. paniculiformis***
23 Leaf pairs weakly unequal, similar in shape; bracts curved; corolla bluish to purplish blue .... **4. *S. capitata***
– Leaf pairs strongly unequal, differ in shape; bracts flat; corolla purplish or white **24**
24 Stems, petiole and peduncle with purplish hairs; smaller lamina elliptic or suborbicular-ovate .... **15. *S. kerrii***
– Stems, petiole and peduncle without purplish hairs; smaller lamina lanceolate to linear-lanceolate .... **22. *S. speciosa***

1. ***Strobilanthes aprica*** **(Hance) T.Anderson ex Benth., Fl. Hongk. 262. 1861.** Fig. 10A

Gutzlaffia aprica Hance, Hooker's J. Bot. Kew Gard. Misc. 1: 142. 1849. Type: China, Hong Kong, *Hance 536* (lectotype CAL [CAL0000019794 image!] designated by Albertson and Wood 2012, pg. 50; isolectotype GH [GH00387581 image!]).

Strobilanthes aprica var. *glabra* J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 116. 1939. Type: Thailand, Lamphun [Lampun]; Mae Kaw, 9 Sept 1924, *Winit 1231* (holotype ABD [ABDUH:2/885 image!]; isotypes BK [257642!], BKF [SN001358!]).

Gutzlaffia pedunculata Craib, Bull. Misc. Inform. Kew 1911(10): 436. 1911. Type: Thailand, Chiang Mai, Doi Suthep [Doi Sootep], 25 Sept 1910, *Kerr 1430* (lectotype K [K001514863!] designated here; isolectotypes BM [BM000796839!], C [C10005192 image!], K [K001514864!], L [L2832219!], P [P00719397 image!]).

Strobilanthes aprica var. *pedunculosa* (Craib) Benoist in Lecomte et al., Fl. Indo-Chine 4: 666. 1935. Type: Based on *Gutzlaffia pedunculata* Craib

Type. Based on *Gutzlaffia aprica* Hance

Distribution. Myanmar, China, Taiwan, Thailand, Laos, Vietnam, Cambodia.

Ecology. On open limestone hill or in open pine forest, open dipterocarp forest, open evergreen forest and open sandy grassland; 240–1,975 m alt, flowering and fruiting from August to April.

Selected specimens examined. THAILAND, Northern: **Mae Hong Son**, Khun Yuam, 650 m alt., 14 Jan 1988, *Santisuk 6671* (BKF); ibid., Mae La Noi, 430 m alt., 27 Dec 1965, *Hennipman 3494* (BKF); **Chiang Mai**, Doi Chiang Dao WS, 21 Dec 1931, *Put 4460* (BK, BM, K); ibid., Doi Pui, Huai Hee, 1,600 m alt., 22 Oct 2000, *Suksathan 2815* (QBG); ibid., 15 Oct 2019, Kiw Lom, *Kladwong 495* (KKU) & *496* (KKU); ibid., Doi Suthep NP, 25 Sept 1910, *Kerr 1430* (BM, K, L, P); ibid., 1,500 m alt., 11 Nov 1973, *Smitinand 11844* (BKF); ibid., 850 m alt., 1 Oct 1985, *Sørensen* et al. *5378* (BKF, E); ibid., 450 m alt., 12 Dec 1907, *Maxwell 87-1586* (AAU, BKF); **Lamphun**, Mae Kaw, 430 m alt., 9 Sept 1924, *Winit 1231* (ABD, BK, BKF); **Lampang**, Pa Tat, Pe Tra, 360 m alt., 13 Dec 1926, *Winit 1815* (AAU, BK, BKF); **Tak**, Tha Song Yang, Khao Hua Mot Noi, 5 km before Ban Tha Song Yang, 160 m alt., 23 Dec 2010, *Suksathan* et al. *5375* (L). North-eastern: **Phetchabun**, Nam Nao NP, Pha Daeng Cliff, 900–959 m alt., 26 Dec 1982, *Koyama* et al. *31730* (BKF, KYO); **Loei**, Phu Kradueng NP, 15 Aug 1946, *Din 189* (BKF); ibid., 1,300 m alt., 10 Nov 1976, *Smitinand 12221* (BKF). South-western: **Kanchanaburi**, Khao Meng, 14 Apr 1965, *Chantanamuck 1061* (BK).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 121,951.239 km^2 and an Area of Occupancy (AOO) of 56.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes aprica* is similar to *S. graminea* J.B.Imlay in having a gibbose and curved corolla, glabrous or subglabrous outside and 2 exserted stamens. It can be distinguished based on elliptic or oblong-elliptic to lanceolate leaf and hairy bract and bracteole vs. oblong-linear leaf and glabrous bracteole in *S. graminea*. Furthermore, the capsule of *S. aprica* has 4 seeds vs. 8 seeds in *S. graminea*.

Hance 536 from CAL [CAL0000019794] was designated as the lectotype of *Gutzlaffia aprica* by Albertson and Wood (2012). On examination, we found a duplicate of this collection deposited at GH [GH00387581]. The specimen has

Hance's handwriting as follows: *Gutzlaffia aprica* Hance. This specimen has branches, leaves and inflorescences, and it is the best preserved.

The original protologue of *Gutzlaffia pedunculata* was based on *Kerr 1430* (Craib 1911). We found that this collection has six duplicates. Two sheets are deposited at K [K001514863, K001514864] and one is housed at each of BM [BM000796839], C [C10005192], L [L2832219] and P [P00719397]. All duplicates are in good shape. We select K001514863 as the lectotype because it has more mature leaves, inflorescences and flowers.

2. ***Strobilanthes articulata*** **J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 121. 1939**

Fig. 10A

Type. THAILAND, **Chanthaburi**, Khao [Kao] Soi Dao, 12 Dec 1924, *Kerr 9630* (lectotype BM [BM001191001!] designated here; isolectotypes ABD [ABDUH:2/887 image!], BK [257638!], C [C10005193 image!], K [K001096856!, K001096857!], KYO!).

Distribution. Endemic to Thailand.

Ecology. In evergreen forest, often on rocks; 1,300 m alt, flowering and fruiting December.

Specimens examined. THAILAND, South-eastern: **Chanthaburi**, Khao Soi Dao, 1,300 m alt., 12 Dec1924, *Kerr 9630* (BK, BM, K-2 sheets, KYO).

Preliminary conservation status assessment. This species is only known from its type locality and is assessed as Data Deficient (DD) following IUCN (2022). More field work is needed to assess the conservation status of *S. articulata*.

Notes. *Strobilanthes articulata* superficially resembles *S. dimorphotricha* Hance in having zigzag stems in the upper parts, strongly unequal leaf pairs and glabrous and caducous bracts, but it differs in having no bracteoles vs. present in *S. dimorphotricha*.

Strobilanthes articulata was described by Imlay (1939) based on *Kerr 9630* which has seven duplicates. Two of which are at K [K001096856, K001096857] and one at each of ABD [ABDUH:2/887], BK [257638], BM [BM001191001], C [C10005193] and KYO. BM001191001 has *Imlay*'s handwriting as follows: "*Strobilanthes articulata* Imlay Type no.", and it also has the mature fruit and corolla which correspond with the protologue. Therefore, we select it as the lectotype.

3. ***Strobilanthes brandisii*** **T.Anderson, J. Linn. Soc., Bot. 9: 475. 1867.**

Figs 1, 10A

Strobilanthes evrardii var. *parviflora* J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 119. 1939. Type: Thailand, Ranong, Kraburi, Klong [Klawng] Wa, 50 m alt., 24 Dec 1928, *Kerr 16335* (lectotype BM [BM000906338!] designated here; isolectotypes ABD [ABDUH:2/906 image!], K [K001514907!]), syn. nov.

Type. MYANMAR, Hills of E. Tonghoo, without date, *Brandis 824* (lectotype CAL [CAL0000019781 image!] designated by Albertson and Wood 2012, pg. 54).

Distribution. Myanmar, Thailand, Laos.

Ecology. In partly shaded places of evergreen forest or mixed deciduous with bamboo; 10–1,531 m alt, flowering and fruiting from October to May.

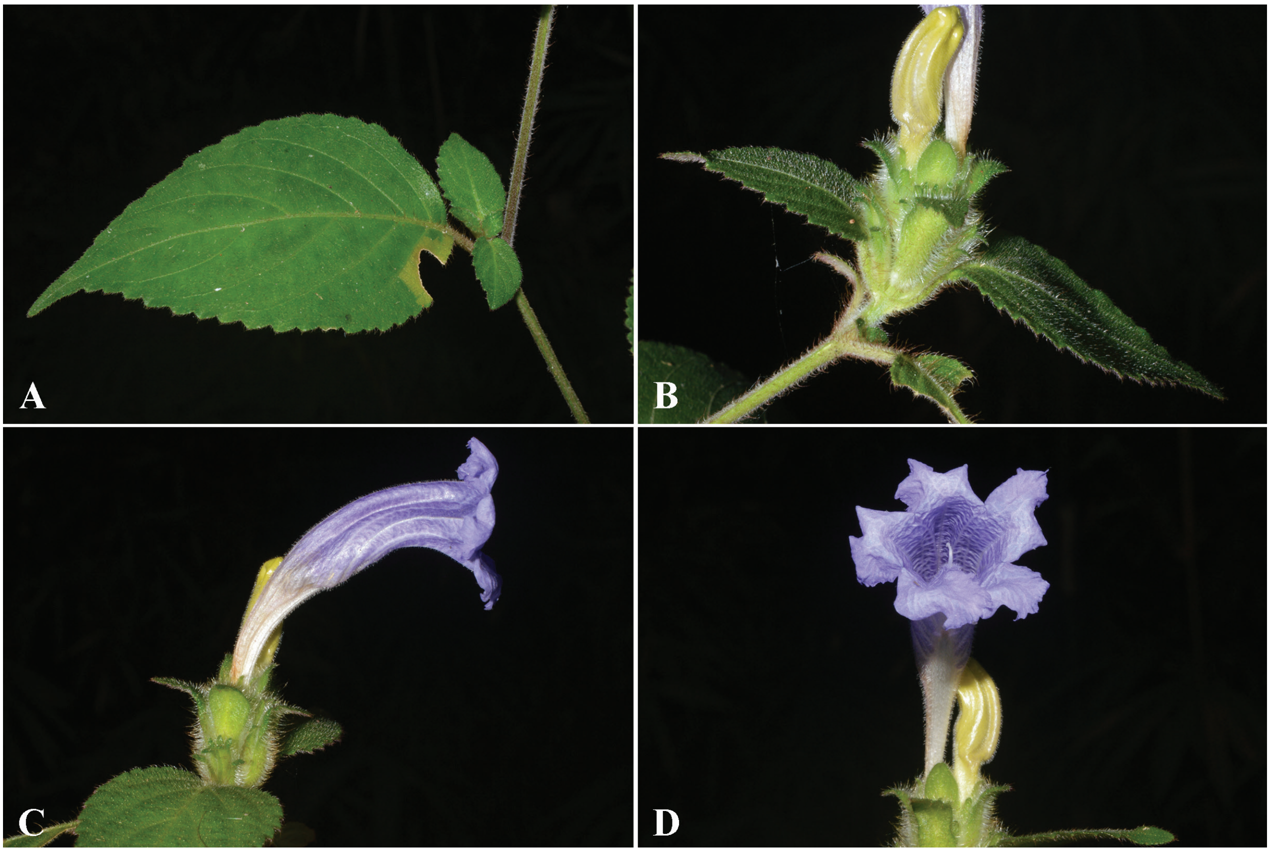

Figure 1. *Strobilanthes brandisii* T.Anderson **A** stem and leaves **B** inflorescences **C** corolla, side view **D** corolla and stigma.

Selected specimens examined. THAILAND, Northern: **Mae Hong Son**, Mae Tala, 1,376 m alt., 28 Apr 2014, *Norsaengsri 10909* (QBG); **Chiang Mai**, Doi Suthep-Pui NP, ca. 920 m alt., 19 May 1912, *Kerr 2604* (BM, E); ibid., Phrao, 1,050 m alt., 5 Dec 1990, *Hansen 44621* (CMU); **Tak**, Mae Sot, Khao Phra War, 695–800 m alt., 21 Jan 1983, *Koyama* et al. *32828* (BKF, K, KYO-2 sheets, L); **Phitsanulok**, Phu Hin Rong Kla NP, 1,300 m alt., 14 Oct 1998, *Suksathan 1306* (QBG); North-eastern: **Loei**, Phu Kradueng NP, 1,150–1,250 m alt., 1 Nov 1984, *Murata* et al. *42628* (BKF, L); ibid., Phu Luang WS, 980–1,531 m alt., 19 Feb 1983, *Koyama* et al. *33679* (BKF, L), *33686* (BKF, L); ibid., 19 Nov 2019, *Kladwong 503* (KKU); Eastern: **Nakhon Ratchasima**, Khao Yai NP, 1,170 m alt., 9 Oct 1979, *Shimizu* et al. *18097* (BKF, K, KYO, L); South-western: **Kanchanaburi**, Si Sawat, Tham Than Lod NP, Khao Kamphaeng, 1,100–1,370 m alt., 30 Nov 1982, *Koyama* et al. *30481* (BKF, KYO); South-eastern: **Chanthaburi**, Khao Soi Dao, 1,100–1,400 m alt., 12 Dec 1924, *Kerr 9629* (BK, BM, K); **Trat**, Khao [Kao] Kuap, 800 m alt., 24 Dec 1919, *Kerr 17792* (BK, BM, K); Peninsular: **Chumphon**, Ban Thung [Tung] Maha, 10 m alt., 10 Jan 1927, *Kerr 11363* (BK, BM); ibid., Lang Suan, 800 m alt., 22 Feb 1927, *Kerr 12074* (BK, K); **Ranong**, Kraburi, Klong [Klawng] Wa, 50 m alt., 24 Dec 1928, *Kerr 16335* (ABD, BM, K).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 303,322.469 km^2 and an Area of Occupancy (AOO) of 56.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes brandisii* is similar to *S. consors* C.B.Clarke in having decumbent habit, white sericeous obovate to oblanceolate or spathulate bracts and curved corolla. It differs in having an acute apex to the calyx lobes and linear bracts. Moreover, the bracts of *S. brandisii* are flat vs. curved in *S. consors*.

Kerr 16335 was mentioned as the type of *S. evrardii* var. *parviflora* (Imlay 1939). The type has three duplicates, one at each of ABD [ABDUH:2/906], BM [BM000906338] and K [K001514907]. BM000906338 has *Imlay*'s handwriting as follows "*Strobilanthes evrardii* R. Ben. var. *parviflorus* J.B.Imlay Type no. of var.". Additionally, this specimen has a flower and the corolla length that agrees with the protologue. Therefore, the sheet BM000906338 is selected as the lectotype.

We examined the type of *S. evrardii* var. *parviflora* and found it conspecific with *S. brandisii*.

4. ***Strobilanthes capitata*** **(Nees) T.Anderson, J. Linn. Soc., Bot. 9: 475. 1867.**

Fig. 10B

Goldfussia capitata Nees, Pl. Asiat. Rar. 3: 88. 1832. Type: Nepal, 1821, *Wall. Numer. List: 2351*, 1831–1832 (lectotype K-W [K001115708!] designated here; isolectotypes BM [BM000793162!], GZU [GZU000251594 image!, GZU000251595 image!], K [K000883084!]).

Ruellia capitata Wall., Numer. List [Wallich] n. 2351. 1830, nom. nud.

Type. Based on *Goldfussia capitata* Nees

Distribution. India, Bhutan, Nepal, Myanmar, China, Thailand.

Ecology. In mixed deciduous forest or evergreen forest near waterfall; 237–2,190 m alt., flowering and fruiting from September to March.

Selected specimens examined. THAILAND, Northern, **Mae Hong Son**, Khun Yuam, Huai Yuak village, 500 m alt., 13 Jan 1983, *Koyama* et al. *32434* (KYO, L); ibid., Mueang, Doi Mae Sakut, 800–1,000 m alt., 23 Sept 1995, *Nanakorn* et al. *4654* (QBG-2 sheets); ibid., Pang Mapha, Tham Lot, 850 m alt., 10 Nov 2004, *Maxwell 04-682* (BKF, CMUB, L-3 sheets); **Chiang Mai**, Mae Chaem, Huai Hom, Ban Wat Chan, 1,000 m alt., 2 Dec 2007, *Srisanga* et al. *3121* (KYO, QBG); **Lamphun**, Doi Khun Tan NP, 925 m alt., 29 Jan 1994, *Maxwell 94-135* (BKF, CMUB); **Phrae**, Song, Mae Tom NP, 400 m alt., 14 Dec 1993, *Maxwell 93-1499* (CMUB, L-2 sheets); **Tak**, Mae Sot, Khao Phra War, 700–850 m alt., 12 Oct 1979, *Shimizu* et al. *18428* (BKF, K, KYO, L); North-eastern: **Loei**, Phu Luang WS, 1,300–1,562 m alt., 5 Dec 1965, *Tagawa* et al. *1605* (BKF, KYO-2 sheets, L).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 63,122.391 km^2 and an Area of Occupancy (AOO) of 52.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes capitata* resembles *S. kerrii* Craib and *S. speciosa* Blume in having a straight corolla and nodding short stamens. The species differs from the former as it lacks purplish hairs on the stems, petioles and peduncles and from the latter by having ovate or oblong-elliptic and curved bracts and blue to purplish-blue flowers.

Nees (1832) described *Goldfussia capitata* based on *Wallich 2351* which has five duplicates, one at each of BM [BM000793162], K [K000883084] and K-W [K001115708] and two at GZU [GZU000251594, GZU000251595]. The sheet K001115708 is the best preserved and has completely mature leaves, inflorescences and flowers. Therefore, we select it as the lectotype.

5. ***Strobilanthes chiangdaoensis*** Terao, Acta Phytotax. Geobot. 32(1–4): 31. 1981.

Figs 2, 10B

Type. Thailand, Chiang Mai, Doi Chiang Dao, 4 Dec 1965, *Hennipman 3187* (holotype L [L0002847!]; isotypes C [C10005196 image!], BKF!, K [K001514861!], KYO!).

Distribution. Endemic to Thailand.

Ecology. On rugged limestone ridge, open areas in mixed evergreen and deciduous forests; 800–2,190 m alt., m alt., flowering and fruiting from September to March.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Pang Mapha, Tham Lot, 925 m alt., 11 Nov 2004, *Maxwell 04-698* (BKF, CMUB, L2 sheets); **Chiang Mai**, Doi Chiang Dao, 1050 m alt., 4 Dec 1965, *Hennipman 3187* (C, BKF, K, KYO, L); ibid., 500–1600 m alt., 3 Jan 1966, *Tagawa* et al. *4039* (AAU, BKF, K, KYO-3 sheets, P); ibid., 1,510–2,190 m alt. 8 Feb 1983, *Koyama* et al. *33225* (BKF, KYO); **Chiang Rai**, Mae Fa Luang, Doi Tung, 1,300 m alt., 22 Oct 1995, *Pooma 1176* (BKF, CMUB); ibid., 1,400 m alt., 5 Nov 2004, *Maxwell 04-573* (L); ibid., Huai Khrai, near Wat Phra That Doi Tung, 1,359 m alt., 15 Sept 2012, *Chamchumroon* et al. *VC 5434* (BKF-2 sheets, E); **Phayao**, Chiang Kham, Doi Pha Dam, Ban Pang Tham, 1,030 m alt., 14 Nov 2012, *La-ongsri* et al. *25886* (QBG); Wang Nuea, Ban Paak Bok, 1,100 m alt., 19 Jan 2006, *Suksathan 3659* (QBG); **Lampang**, Ngao, Ban Pha Daeng, 800 m alt., 16 Jan 2006, *Suksathan 3614* (KYO, QBG).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 19,556.802 km^2 and an Area of Occupancy (AOO) of 32.000 km^2 and is assessed as Vulnerable (VU), B1 a, b (i, ii, iii) following IUCN (2022). This species grows among rugged limestone rocks which occur at the top of limestone mountain. This habitat is subject to increasing droughts and fires leading to decline of *S. chiangdaoensis*.

Notes. *Strobilanthes chiangdaoensis* resembles *S. esquirolii* in having oblong-lanceolate bracts and bracteoles. However, the bracts and bracteoles of *S. chiangdaoensis* are glabrous or sparsely hairy on the adaxial surface and pubescent on the abaxial surface vs. sericeous on both surfaces in *S. esquirolii*. Moreover, the capsules of *S. chiangdaoensis* have two seeds with two lower rudimentary ovules vs. four seeds without rudimentary ovules in *S. esquirolii*.

6. ***Strobilanthes consors*** C.B.Clarke, Bot. Jahrb. Syst. 41(2): 66. 1907.

Fig. 10B

Type. Thailand, Chiang Mai, Doi Suthep, 13 Dec 1904, *Hosseus 256* (lectotype M [M0168698 image!] designated here; isolectotypes B [B101185735 image!], BM [BM000906339!], E [E00273462!], K [K001514905!], L [L2841550!], P [P00719278 image!]).

Distribution. Myanmar, Thailand.

Ecology. In evergreen forest, granite bedrock; 250–2,500 m alt., flowering and fruiting from September to May.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Mae Tala, 1,376 m alt., 28 Apr 2014, *Norsaengsri 10909* (QBG); **Chiang Mai**, Doi Inthanon NP, Doi Ang Ka, 1,600 malt., 26 Dec 1935, *Garrett 1026* (BKF, K-2 sheets, KYO);

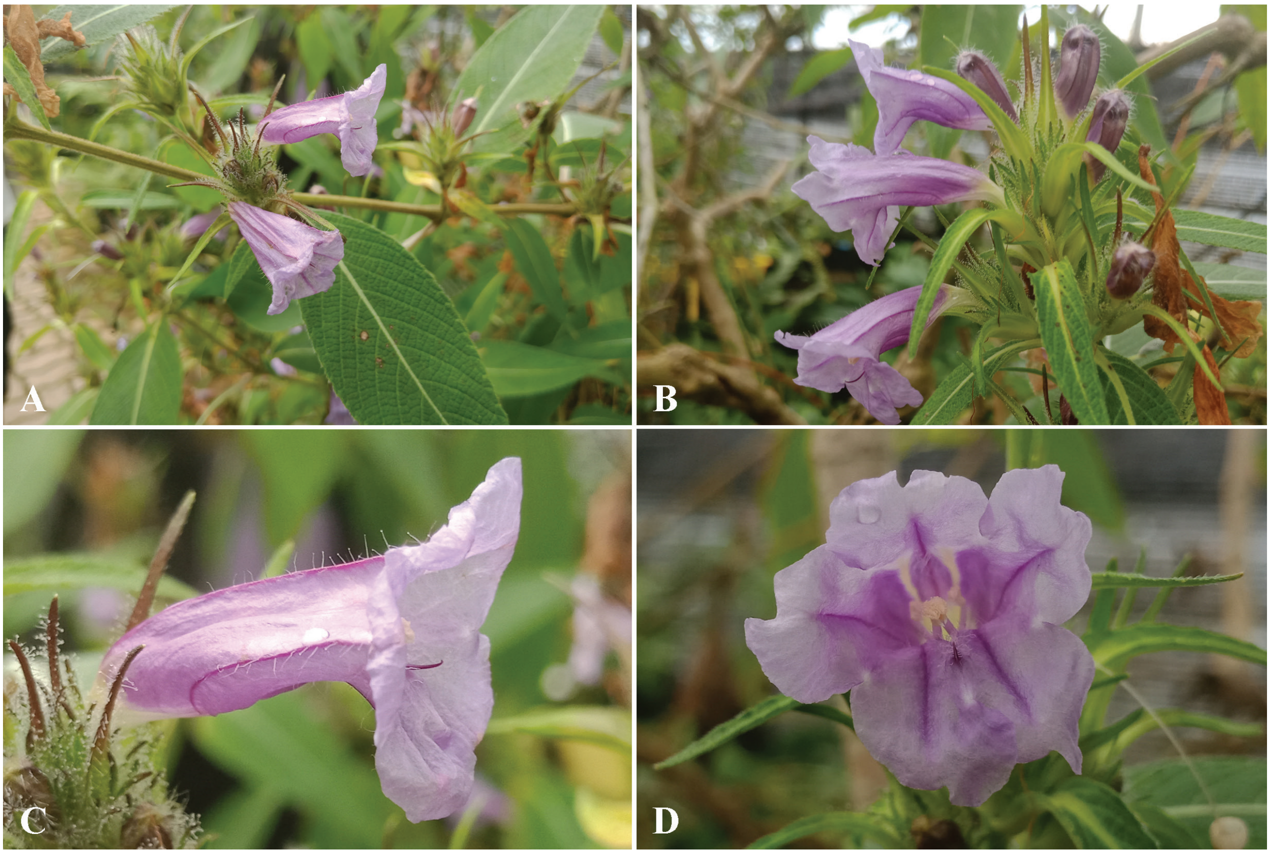

Figure 2. *Strobilanthes chiangdaoensis* Terao **A** stem and leaves **B** inflorescences **C** corolla, side view **D** corolla lobes, anthers and stigma. Photos taken from cultivated plant from QBG nursery.

ibid., Fang, Doi Pha Hom Pok NP, 1,900–2,000 m alt., 11 May 1905, *Hosseus 606* (M); ibid., Doi Suthep-Pui NP, 13 Dec 1904, *Hosseus 256* (B, BM, E, K, L, M, P); ibid., ca. 1,680 m alt., 10 Jan 1911, *Kerr 2279* (BM, K-2 sheets, L, TCD); ibid., ca. 1,520 m alt., 24 Dec 1911, *Kerr 2279A* (BM-2 sheets, E, L, TCD); ibid., ca. 1,580 m alt., 22 Sept 1912, *Kerr 2715* (AAU, BM-2 sheets, E, K); ibid., 1,510 m alt., 20 Dec 2009, *Balslev* et al. *10029* (AAU); **Nan**, Bo Kluea, Sapan Waterfall, 600 m alt., 17 Nov 1993, *Larsen* et al. *44464* (AAU); ibid., 780 m alt., 2 Sept 2000, *Srisanga 1587* (BKF, QBG, CMUB); **Chiang Rai**, Doi Chang, 1,260–1,765 m alt., 11 Jan 1922, *Rock 1771* (E, US); **Lamphun**, Mae Tha, Doi Khun Tan NP, 1,200 m alt., 20 Nov 1993, *Maxwell 93-1407* (BKF-2 sheets, CMUB, L); **Lampang**, Chae Son NP, 875 m alt., 24 Oct 1995, *Maxwell 95-991* (BKF, CMUB); ibid., Doi Luang NP, 1,125 m alt., 8 Nov 1998, *Petrmitr 335* (CMUB, L); North-eastern: **Loei**, Phu Kradueng NP, 1,250 m alt., 9 Sept 1988, *Takahashi & Tamura 63463* (BKF); ibid., Phu Luang WS, 1,150–1,530 m alt., 24 Dec 1982, *Koyama* et al. *31617* (KYO-2 sheets); ibid., Phu Ruea NP, 980–1,151 m alt., 23 Dec 1982, *Koyama* et al. *31543* (BKF, KYO).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 73,029.391 km^2 and an Area of Occupancy (AOO) of 76.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Hosseus 256* and *Hosseus 606* were cited in the original protologue of *S. consors* (Hosseus 1907). *Hosseus 256* has seven duplicates one in each of B [B101185735], BM [BM000906339], E [E00273462], K [K001514905], L [L2841550], M [M0168698] and P [P00719278] whereas *Hosseus 606* has only one duplicate deposited at M [M0168699]. M0168698 has the original label

"*Strobilanthes consors sp.nova.*" and the original description in *Clarke*'s handwriting. Moreover, this specimen has mature leaves, inflorescences and flowers. We, therefore, select the sheet M0168698 as the lectotype of *S. consors*.

7. ***Strobilanthes cruciata*** (Bremek.) Terao, Acta Phytotax. Geobot. 31(1–3): 59. 1980.

Fig. 10C

Tetragoga cruciata Bremk., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 300. 1944. Type: Indonesia, Sumatra, 1 May 1918, *Lörzing 5668* (holotype L [L0002848!]; isotypes BO [BO1352476 image!, BO1352477 image!], GH [GH00295522 image!], SING [SING0045507 image!]).

Tetragoga nagaensis Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 299. 1944. Type: India, Nagaland, Dec 1907, *Meebold 4891* (holotype B [B100002761 image!]).

Type. Based on *Tetragoga cruciata* Bremk.

Distribution. India, Myanmar, China, Thailand, Vietnam, Indonesia.

Ecology. In hilly evergreen forest; 150–1,700 m alt, flowering and fruiting from July to May.

Selected specimens examined. THAILAND, Northern: **Nan**, Doi Phu Kha NP, 1,700 m alt., 28 July 1992, *Larsen* et al. *43704* (AAU, P); ibid., 1,700 m alt., 26 May 2000, *Srisanga 1445* (QBG); ibid., 1,680 m alt., 11 Nov 2000, *Srisanga 1758* (BKF- 2 sheets, QBG); ibid., Pua, 1,650 m alt., 10 May 2006, *Srisanga 2762* (CMUB, KYO, QBG); Peninsular: **Chumphon**, Marine Nature Study Center, 9 Apr 2008, *Wessumritt 113* (QBG); ibid., Phato, Ban Racha Krude, 150–200 m alt., 6 July 1992, *Larsen 43165* (AAU, BKF, P).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 2,663,189.074 km^2 and an Area of Occupancy (AOO) of 44.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes cruciata* resembles *S. falconeri* T.Anderson in having leaf-like bracts with a petiolar base, but it is distinguishable from *S. falconeri* T.Anderson by its white corolla and glabrous ovary.

8. ***Strobilanthes dimorphotricha*** subsp. ***rex*** (C.B.Clarke) J.R.I.Wood, Kew Bull. 61(1): 2006.

Figs 3, 10C

Strobilanthes anfractuosa C.B.Clarke, Bot. Jahrb. Syst. 41(2): 66. 1907. Type: Thailand, Doi Inthanon [Doi Angka], 1150 m., 17 Jan 1905, *Hosseus 336* (holotype M [M0168700 image!]; isotypes BM!, K [K001514926!], P [P00719248 image!]).

Goldfussia anfractuosa (C.B.Clarke) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 269. 1944. Type: Based on *Strobilanthes anfractuosa* C.B.Clarke

Strobilanthes pentastemonoides (Nees) T.Anderson var. *anfractuosa* (C.B. Clarke) Benoist in Lecomte *et al*., Fl. Indo-Chine 4: 667. 1935. Type: Based on *Strobilanthes anfractuosa* C.B.Clarke

Strobilanthes rex C.B.Clarke, Bot. Jahrb. Syst. 41(2): 68. 1907. Type: Thailand, Doi Inthanon [Doi Anga], *Hosseus 352* (holotype M [M0168691]; isotypes BM [BM000793208!], C [C10005214 image!], CORD [CORD00005092 image!], E [E00749032!, E00749033!, E00749034!], K [K001514927!], P [P00719419 image!, P00719420 image!, P00719421 image!]).

Goldfussia rex (C.B.Clarke) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 283. 1944. Type: Based on *Strobilanthes rex* C.B.Clarke

Strobilanthes pentastemonoides (Nees) T.Anderson var. *rex* (C.B.Clarke) Benoist in Lecomte et al., Fl. Indo-Chine 4: 667. 1935. Type: Based on *Strobilanthes rex* C.B.Clarke

Type. Based on *Strobilanthes rex* C.B.Clarke

Distribution. Myanmar, China, Thailand, Laos.

Ecology. Common in evergreen forest; 375–2,540 m alt., flowering and fruiting from July to April.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Pai, Doi Kiew Lom, 1,490 m alt., 16 Jan 1983, *Koyama* et al. *32588* (BKF); **Chiang Mai**, Doi Chiang Dao WS, 13 Feb 1958, *Bunchuai 716* (BKF); ibid., 1,200 m alt., 17 Feb 1958, *Sørensen* et al. *1298* (E); ibid., 1,200–1,600 m alt., 6 Jan 1975, *Geesink* et al. *8117* (BKF, K, L); ibid., 14 Oct 2019, *Kladwong 489* (KKU); ibid., Doi Inthanon NP, ca. 2,500 m alt., 19 Jan 1905, *Hosseus 352* (BM, CORD, E-3 sheets, K, M, P-3 sheets); ibid., 17 Jan 1905, *Hosseus 334* (BM); ibid., 17 Jan 1905, *Hosseus 336* (BM, K, M, P); ibid., Doi Pha Hom Pok NP, 1,600–2,350 m alt., 12 Feb 1983, *Koyama* et al. *33423* (BKF); ibid., Doi Suthep-Pui NP, 14 Dec 1904, *Hosseus 244* (BM, E, K, L); ibid., 900 m alt., 16 Jan 1910, *Kerr 935* (AAU, BM, L); ibid., 1,676 m alt., 20 Nov 1910, *Kerr 1548* (BM); ibid., 900 m alt., 8 Jan 1911, *Kerr 1568A* (BM-2 sheets, K, TCD); ibid., 1,676 m alt., 10 Dec 1911, *Kerr 1568B* (AAU, BM, K, L); ibid., Doi Pui Campground trail, 1,510 m alt., 20 Dec 2019, *Balslev* et al. *10024* (AAU); ibid., 4 Oct 2019, *Kladwong 473* (KKU); **Chiang Rai**, Doi Luang NP, Pu Kaeng Waterfall, 592 m alt., 2 Mar 2015, *Norsaengsri 11746* (QBG); ibid., Mae Sai, 1,350 m alt., 4 Feb 2006, *Maxwell 06-129* (QBG, CMUB, L); ibid., Tham Luang-Khun Nam Nang Norn NP, 800 m alt., 22 Jan 2000, *Suksathan 2270* (QBG); **Phayao**, Chiang Kham, Phu Lang Ka, 1,500 m alt., 18 Jan 2006, *Suksathan 3641* (QBG, CMUB); Nan, Doi Phu Kha NP, 1,500–1,600 m alt., 13 Dec 1990, *Larsen* et al. *41910* (AAU); ibid., 1,700 m alt., 28 July 1992, *Larsen* et al. *43702* (AAU); **Lampang**, Chae Son NP, 1,150 m alt., 7 Jan 1996, *Maxwell 96-18* (BKF, CMUB); **Uttaradit**, Phu Soi Dao NP, Sai Thong Waterfall, 1,615 m alt., 17 Nov 2009, *Norsaengsri & Intamusik 6162* (QBG); **Tak**, Mae Sot, Pha Charoen Waterfall, 680 m alt., 10 Feb 2002, *Simpson* et al. *2078* (K, TCD); **Phitsanulok**, Chat Trakan, 22 Jan 2009, *Maknoi 3002* (QBG); ibid., Phu Hin Rong Kla NP, 1,400–1,600 m alt., 10–11 Dec 1990, *Larsen* et al. *41827* (AAU) & *41878* (AAU); North-eastern: **Phetchabun**, Nam Nao NP, 18 Jan 2003, *Chantaranothai* et al. *s.n.* (BKF); **Loei**, Phu Suan Sai NP, 19 Dec 2006, *Maknoi* et al. *1238* (QBG-2 sheets); ibid., Phu Kradueng NP, 1,100–1,200 m alt., 28 Nov 1965, *Tagawa 491* (BKF, KYO-2 sheets); ibid., Wang Kwang Waterfall, 1,190–1,250 m alt., 16 Nov 1979, *Shimizu* et al. *23219* (BKF, KYO, L); Eastern: **Chiyaphum**, Nam Phrom, 600 m alt., 10 Dec 1971, *van Beusekom* et al. *4097* (BKF, K, L); South-western: **Kanchanaburi**, Ta Kanun, 400 m alt., 19 Jan 1962, *Kerr 10267* (BK, BM, K); Peninsular: **Ranong**, Kaper, Khao Pawta Luang Kaeo, 940–1,300 m alt., 10 Dec 1979, *Shimizu* et al. *26724*

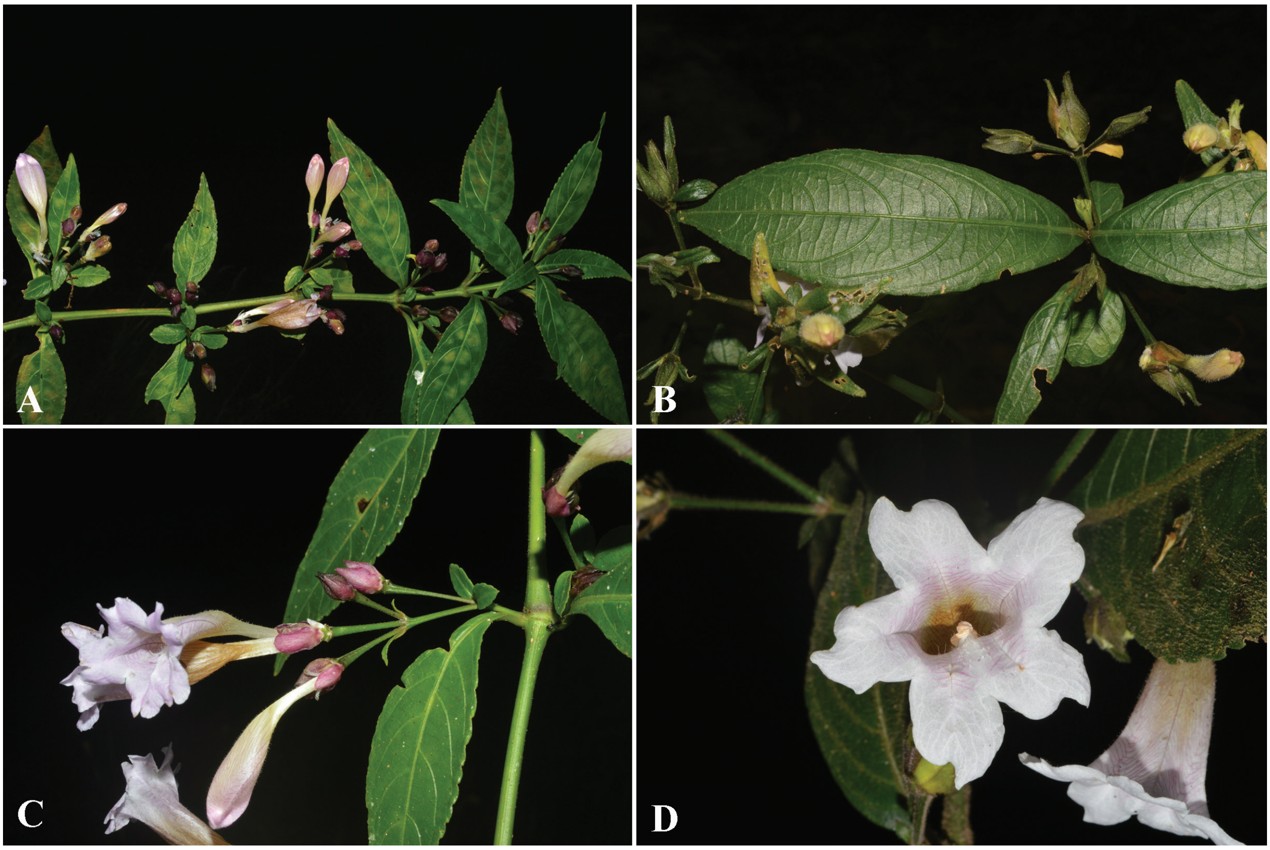

Figure 3. *Strobilanthes dimorphotricha* subsp. *rex* (C.B.Clarke) J.R.I.Wood **A, B** stem, leaves and inflorescences **C** inflorescence **D** corolla lobes and anthers.

(BKF, L), *26739* (BKF), *26841* (BKF) & *26887* (BKF, L); **Nakhon Si Thammarat**, Lan Saka, Khao Luang, 19 Nov 1955, *Snan 312* (BKF).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 295,960.413 km^2 and an Area of Occupancy (AOO) of 176.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes dimorphotricha* subsp. *rex* differs consistently from subsp. *dimorphotricha* Hance from China and Vietnam in the rigid and subequal or sometimes unequal leaves. Subsp. *rex* appears similar to *S. paniculiformis* J.R.I.Wood in which the calyx lobe has 1 lobe longer than others. However, it differs by having ovate or elliptic-lanceolate bracts vs. ovate-orbicular in *S. paniculiformis*.

9. *Strobilanthes echinata* Nees in Wall., Pl. Asiat. Rar. 3: 85. 1832.

Fig. 10C

Goldfussia echinata (Nees) N.P.Balakr., Fl. Jowai 2: 355. 1983. Type: Based on *Strobilanthes echinata* Nees

Dicliptera crenata Miq., Fl. Ned. Ind. 2: 844. 1858. Type: Indonesia, Sumatra, *Horsfield s.n.* (isotype BM [BM000884896!]).

Strobilanthes jugorum Benoist, Bull. Soc. Bot. France 81: 601. 1934. Type: Vietnam, Tonkin, Chapa, Sept 1929, *Pételot s.n.* (holotype P [P00204976 image!]).

Tetraglochidium jugorum (Benoist) Bremek., Dansk Bot. Ark. 23: 207. 1965. Type: Based on *Strobilanthes jugorum* Benoist

Strobilanthes latibracteata J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 122. 1939. Type: Thailand, Trang, Khao [Kao] Soi Dao, 28 Apr 1930, *Kerr 19190* (lectotype BM [BM000793157!] designated here; isolectotypes ABD [ABDUH:2/908 image!], BK [257645!]).

Strobilanthes maingayi C.B.Clarke in Hook.f., Fl. Brit. India 4(11): 448. 1884. Type: Malaya, *Maingay 1182* (lectotype K [K001514853!] first step designated by Bennett et al. (2008), second step designated here; isolectotypes BM [BM00088495!], K [K001514854!]).

Tetraglochidium maingayi (C.B.Clarke) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 221. 1944. Type: Based on *Strobilanthes maingayi* C.B.Clarke

Tetraglochidium maingayi var. *paucinervium* Bremek., Dansk Bot. Ark. 23: 206. 1965. Type: Thailand, Prachinburi, Khao Khieo, 20 June 1963, *Larsen 10159* (holotype U [U0000138 image!]; isotypes AAU!, BKF [BKF080038!], C [C10005203 image!]).

Strobilanthes maingayi var. *glabra* [glaber]J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 119. 1939. Type: Thailand, Prachuap Khiri Khan, Khao [Kao] Luang, 5 July 1926, *Kerr 10835* (lectotype BM [BM000793159!] designated here; isolectotypes ABD [ABDUH:2/909 image!], BK [257644!], K [K001514916!, K001514917!]).

Strobilanthes pectinata var. *acuminata* J.B.Imlay in Kew Bull. 1939: 119. 1939. Type: Thailand, Khao [Kao] Luang, 29 Apr 1928, *Kerr 15464* (lectotype BM [BM000793158!] designated here; isolectotypes ABD [ABDUH:2/912 image!], BK [231580!], K [K001514913!, K001514914!]).

Strobilanthes echinata var. *acuminata* (J.B.Imlay) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 274. 1944. Type: Based on *Strobilanthes pectinata* var. *acuminata* J.B.Imlay.

Strobilanthes pectinata var. *glandulosa* J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 119. 1939. Type: Thailand, Nan, Pua, Mt. Pu Huat, 3 Mar 1921, *Kerr 4993* (lectotype BM [BM000793160!] designated here; isolectotypes ABD [ABDUH:2/910 image!], BK [231583!], K [K001514918!]).

Strobilanthes echinata var. *glandulosa* (J.B.Imlay) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 274. 1944. Type: Based on *Strobilanthes pectinata* var. *glandulosa* J.B.Imlay

Strobilanthes pectinata var. *punctata* J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 119. 1939. Type: Thailand, Satun, Khao [Kao] Keo Range, 12 Mar 1928, *Kerr 14512* (lectotype BM [BM000793156!] designated here; isolectotypes ABD [ABDUH:2/911 image!], BK [231579!]).

Strobilanthes echinata var. *punctata* (J.B.Imlay) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 274. 1944. Type: Based on *Strobilanthes pectinata* var. *punctata* J.B.Imlay

Ruellia pectinata Wall., Numer. List [Wallich] n. 2356. 1830, nom. nud.

Type. India, Meghalaya, *de Silva* in *Wall. Numer. List: 2356*, 1831–1832 (lectotype K-W [K001115724!], designated by Bennett et al. 2008, pg. 133; isolectotype BM [BM000884989!]).

Distribution. India, Bhutan, Myanmar, China, Thailand, Laos, Vietnam Cambodia, Malaysia, Indonesia.

Ecology. In evergreen forest, granite bedrock; 310–2,580 m alt., flowering and fruiting from August to July.

Selected specimens examined. THAILAND, Northern: **Chiang Mai**, Doi Inthanon NP, 2,200–2,440 m alt., 2 May 1921, *Kerr 5308* (BK, BM, K); ibid., 2,170 m alt., 4 June 1930, *Garrett 564* (BKF, K-2 sheets, L); ibid., 1,200–2,580 m alt., 24 June 1978, *Phengklai* et al. *4066* (BKF, K, L, PSU); ibid., 2,565 m alt., 31 Dec 1989, *Maxwell 89-1629* (CMU, E, L); ibid., Fang, Doi Pha Hom Pok NP, 1,300 m alt., 12 Sept 1967, *Iwatsuki* et al. *9572* (BKF, K, KYO, L); **Nan**, Doi Phu Kha NP, 1,450 m alt., 25 June 1999, *Srisanga 735* (AAU, BKF, QBG, CMUB); ibid., Pua, Phu Huat, 1,500–1,600 m alt., 3 Mar 1921, *Kerr 4993* (ABD, BK, BM, K); **Uttaradit**, Phu Soi Dao NP, 1,960 m alt., 30 June 2009, *Intamusik* et al. *245* (QBG); North-eastern: **Loei**, Phu Luang WS, 1,200 m alt., 28 Aug 1996, *Phengklai & Fukuoka 10096* (BKF-3 sheets, QBG-2 sheets); Eastern: **Chaiyaphum**, Thung Kamang, 850 m alt., 1 June 1974, *Geesink* et al. *7129* (AAU, BKF, K, L); **Nakhon Ratchasima**, Khao Yai NP, 600–800 m alt., 7 July 1963, *Kasem 288* (BK); ibid., Khao Khieo, 1,300 m alt., 29 Aug 1963, *Smitinand & Sleumer s.n.* (BKF); South-western: **Prachuap Khiri Khan**, Khao Luang, 1,000 m alt., 5 July 1926, *Kerr 10835* (ABD, BK, BM, K-2 sheets); Central: **Saraburi**, Khao Khieo, 1,000 m alt., 8 June 1979, *Vidal* et al. *6360* (AAU, BKF, K, KYO, L, P); South-eastern: **Prachinburi**, Khao Khieo, 1,300 m alt., 20 June 1963, *Larsen 10159* (AAU, BKF, C, U); **Rayong**, Khao Cha Moa-Khao Wong NP, 650 m alt., 24 Nov 1979, *Shimizu* et al. *23465* (KYO); **Chanthaburi**, Khao Khitchakut NP, Krating Waterfall, 310 m alt., 29 Nov 1979, *Shimizu* et al. *23940* (BKF, KYO-2 sheets, L); **Trat**, Khao Kuap, 22 May 1930, *Put 2940* (BK, BM, K); Peninsular: **Ranong**, Kaper, Khao Pawta Luang Kaeo, 940–1200 m alt., 9 Dec 1979, *Shimizu* et al. *26595* (BKF, KYO); **Krabi**, Khao Phanom Bencha NP, 1,350 m alt., 8 Jan 2006, *Gardner ST2182* (BKF-2 sheets, K-2 sheets); **Nakhon Si Thammarat**, Khao Luang, 900 m alt., 29 Apr 1928, *Kerr 15464* (ABD, BK, BM, K-2 sheets); ibid., 3 May 1941, *Smitinand 827* (BKF, L); ibid., 1,200–1,300 m alt., 24 Feb 1995, *Larsen* et al. *45973* (AAU); **Trang**, Palian, Khao Soi Dao, 800 m alt., 28 Apr 1930, *Kerr 19190* (ABD, BK, BM); ibid., Yan Ta Khao, Khao Banthat, summit area of Phu Pha Mek, 1,240 m alt., 7 Apr 2003, *Middleton* et al. *1995* (BKF, E) & *2001* (BKF); **Satun**, Khao [Kao] Keo Range, 600 m alt., 12 Mar 1928, *Kerr 14512* (ABD, BK, BM); ibid., 700 m alt., 12 Mar 1928, *Kerr 14528* (BK, BM, K); **Songkhla**, Hat Yai, Ton Nga Chang Waterfall, 21 Aug 1992, *Niyomdham 3066* (BKF-2 sheets); **Pattani**, Khao [Kao] Kala Kiri, 800–900 m alt., 1 Apr 1928, *Kerr 14954* (BK, BM, K); **Yala**, Bannang Sata, Khao Pok Yok, 1,000 m alt., 10 Oct 1991, *Larsen* et al. *42276* (AAU, BKF).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 469,202.533 km^2 and an Area of Occupancy (AOO) of 88.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes echinata* differs from *S. cruciata* in its dentate or fimbriate or dentate-crenate vs. acuminate on the apex bracteoles and calyx. In addition, the bracts of *S. echinata* are sessile vs. bract with petiolar base in *S. cruciata*.

Strobilanthes maingayi was described based on *Maingay 1182* at K (Clarke 1884). Material at K was considered to be the holotype by Bennett et al. (2008). However, there is no indication in Clarke (1884) that only the material now in K was studied. We also found that there are three duplicates of *Maingay 1182*, two of which are deposited at K [K001514853, K001514854] and the other one at BM [BM00088495]. K001514853 has more leaves and inflorescences than the others. Bennett et al. (2008) can be considered as first step lectotypification (Turland 2019). We therefore, undertake the second step and select K001514853 as the lectotype.

Kerr 19190 was cited in the protologue of *S. latibracteata* (Imlay 1939). This number has three duplicates each one was deposited at ABD [ABDUH:2/908], BK [257645] and BM [BM000793157]. We found that the sheet BM000793157 has *Imlay*'s handwriting labelled as "*Strobilanthes latibracteata* Imlay Type no." and the specimen has well-preserved bracts as well as corolla. Furthermore, the size of the leaf, bract and corolla matches with the protologue. Therefore, the sheet BM000793157 is selected as the lectotype.

Kerr 10835 was mentioned as the type of *S. maingayi* var. *glabra* (Imlay 1939). [The varietal name was originally published as '*glaber*: but as *Strobilanthes* is feminine we follow Bennett et al. 2008 and use *glabra*]. *Kerr 10835* has five duplicates, two of which are at K [K001514916, K001514917] and one each at ABD [ABDUH:2/909], BK [257644] and BM [BM000793159]. The sheet BM000793159 agreed with the protologue based on leaf size and has *Imlay*'s handwriting as follows: "*Strobilanthes maingayi* C.B.Clarke var. *glabra* Imlay Type of var." Therefore, we designate the sheet BM000793159 as the lectotype.

Kerr 15464 was cited in the protologue of *S. pectinata* var. *acuminata* (Imlay 1939). This number has five duplicates, two of which were deposited at K [K001514913, K001514914] and each one was housed at ABD [ABDUH:2/912], BK [231580], BM [BM000793158]. The sheet BM000793158 has *Imlay*'s handwriting as follows: "*Strobilanthes pectinata* T. Anders. var. *acuminata* Imlay Type of var." and has well-preserved leaves. Therefore, the sheet BM000793158 is selected as the lectotype and the other duplicates are isolectotypes.

Imlay (1939) described a new taxon, *S. pectinata* var. *glandulosa* based on *Kerr 4993* which has four duplicates one each at ABD [ABDUH:2/910], BK [231583], BM [BM000793160] and K [K001514918]. We select the sheet BM000793160 as the lectotype because it has glandular hairs on the stem which correspond with the protologue. Additionally, it also has *Imlay*'s handwriting as follows: "*Strobilanthes pectinata* T. Anders. var. *glandulosa* Imlay".

Var. *pectainta* was described as a new taxon by Imlay (1939) based on *Kerr 14512* which has three duplicates, each one was deposited in ABD [ABDUH:2/911], BK [231579] and BM [BM000793156]. The sheet BM000793156 has the size of bracts, calyx and fruits corresponding with the protologue and it also has *Imlay*'s handwriting as follows: "*Strobilanthes pectinata* T. Anders. var. *punctata* Imlay Type no. of var.". Therefore, the sheet BM000793156 is selected as the lectotype.

10. *Strobilanthes erecta* C.B.Clarke, Bot. Jahrb. Syst. 41(2): 67. 1907.

Fig. 10D

Goldfussia laotica Bremek., Proc. Kon. Ned. Akad. Wetensch. C 60: 3. 1957. Type: Laos, Xieng Khouang, *Vidal 1685* (holotype U [U0000028!]; isotype P [P04366109 image!]).

Strobilanthes suborbicularis J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 118. 1939. Type: Thailand. Chiang Mai, Doi Inthanon [Doi Aang Ka], 2 Nov 1930, *Put 3302* (lectotype K n.v. designated by Son et al. (2018); isolectotypes ABD [ABDUH:2/914 image!], BK [257647!], BM [BM000906322!], C [C10005219 image!], KYO!).

Dossifluga suborbicularis (J.B.Imlay) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 235. 1944. Type based on *Strobilanthes suborbicularis* J.B.Imlay

Type. THAILAND, Doi Chiang Dao, 17 Feb 1905, *Hosseus 401a* (holotype M [M0168696 image!]; isotype P [P00719317 image!]).

Distribution. Myanmar, China, Thailand, Laos, Vietnam.

Ecology. In open hill evergreen scrub and pine forest on mountain top, sandy soil, limestone or granite bedrock; 980–2,200 m alt., flowering and fruiting from September to February.

Selected specimens examined. THAILAND, Northern: **Chiang Mai**, Doi Chiang Dao WS, 2,160 m alt., 17 Feb 1905, *Hosseus 401a* (M, P); ibid., 1,500–2,200 m alt., 3 Dec 1961, *Smitinand & Anderson 7305* (BKF-2 sheets); ibid., 2,000 m alt., 7 Dec 1965, *Hennipman 3273* (BKF, L); ibid., Chom Thong, Doi Inthanon NP, 2 Nov 1930, *Put 3302* (ABD, BM, C, K); ibid., 1,800 m alt., 18 Feb 1999, *Suksathan 1572* (QBG); ibid., 1,700 m alt., 22 Sept 2001, *Suksathan 3087* (QBG); ibid., 19 Nov 2020, *Kladwong 532 & 533* (KKU); **Nan**, Doi Phu Kha NP, Doi Phu Wae, 1,700 m alt., 10 Dec 1998, *Srisanga 412* (AAU, BKF, CMUB, KYO, QBG); North-eastern: **Loei**, Phu Luang WS, 1,300 m alt., 27 Nov 1959, *Bunpheng 955* (BKF); ibid., 1,500 m alt., 3 Jan 1983, *Niyomdham & Vidal 442* (AAU, BKF-2 sheets, P) & *501* (AAU, BKF-2 sheets, P); ibid., 1,400 m alt., 15 Apr 1968, *Chermsirivathana 872* (BK); ibid., 1,500 m alt., 26 Jan 1981, *Smitinand s.n.* (BKF); ibid., 19 Nov 2019, *Kladwong 501* (KKU).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 312,285.154 km^2 and an Area of Occupancy (AOO) of 44.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes erecta* resembles *S. phyllocephala* J.R.I.Wood & Scotland in the shape of its leaf base, but it differs in having ovate-elliptic or obovate and caducous bracts. Wood and Scotland (2006) treated *S. laotica* as a synonym of *S. dimorphotricha* subsp. *rex*, but after investigation of type specimens we found that this species is conspecific with *S. erecta*. This is corresponded with the report of Son et al. (2018).

Son et al. (2018) proposed the duplicate of *Put 3302* from K (without barcode) as the lectotype of *S. suborbicularis*. Unfortunately, we have not seen this duplicate. Moreover, they also provided a picture of the lectotype, but we found that this picture is the sheet BM000906322 at BM, not K: the citation of K may therefore be in error. We were able to locate five duplicates of *Put 3302* one deposited at each of ABD [ABDUH:2/914], BK [257647], BM [BM000906322], C [C10005219] and KYO.

11. *Strobilanthes esquirolii* H.Lév., Repert. Spec. Nov. Regni Veg. 12: 18. 1913.

Figs 4, 10D

Tetragoga esquirolii (H.Lév.) E.Hossain in Notes Roy. Bot. Gard. Edinburgh 32: 410. 1973.

Strobilanthes bombycina J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 124. 1939. Type: Thailand, Kanchanaburi; Si Sawat [Si Sawat], 14 Jan 1926, *Kerr 10211* (lectotype BM [BM000906285!] designated here; isolectotypes ABD [ABDUH:2/888 image!], BK [257639!], K [K001514899!]), syn. nov.

Strobilanthes leucocephala Craib, Bull. Misc. Inform. Kew 1914(3): 130. 1914. Type: Thailand, Lamphun, Mae Tha [Me Ta], Doi Din Deng, 3 Feb 1912, *Kerr 2317* (lectotype K [K001514901!] designated here; isolectotypes

BM [BM000906289!], E [E00133531!], K [K001514900!, K001514902!, K001514903!], TCD!).

Goldfussia leucocephala (Craib) C.Y.Wu ex H.P. Tsui & C.C.Hu in Fl. Reipubl. Popularis Sin. 70: 165. 2002. Type: Based on *Strobilanthes leucocephala* Craib.

Type. China, Kweichow, de Pa-Bonn a Ting-Chan, 16 Dec1904, *Esquirol 322* (holotype E [E00133561!]).

Distribution. Myanmar, China, Thailand, Laos, Vietnam.

Ecology. In hill evergreen forest or mixed deciduous forest with bamboo, limestone granite or sandstone bedrock; 107–2,190 m alt., flowering and fruiting from October to May.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Mueang, Tham Pla-Namtok Pha Suea NP, Doi Pha Daeng, 680 m alt., 26 Dec 2012, *Norsaengsri 10016* (BKF, QBG); ibid., Pai, Mae Yen Waterfall, 570 m alt., 15 Jan 1983, *Koyama 32503* (BKF, KYO, L); **Chiang Mai**, Doi Chiang Dao WS, 600–800 m alt., 4 Jan 1954, *Garrett 1427* (K, L2 sheets, P); ibid., 550 m alt., 8 Mar 1965, *Chermsirivathana 298* (BK, BKF); ibid., 1,250–1,425 m alt., 4 Dec 1965, *Hennipman 3216* (BKF, K, KYO, L, P); ibid., 6 Jan 1975, *Geesink 8111* (BKF, K, L); ibid., 1,625 m alt., 5 Nov 1995, *Maxwell 95-1077* (BKF, CMUB, L2 sheets); ibid., 14 Oct 2019, *Kladwong 482* (KKU) & *483* (KKU); ibid., Fang, 750 m alt., 27 Feb 1958, *Sørensen* et al. *1726* (E); ibid., 700–800 m alt., 11 Jan 1975, *Geesink 8217* (AAU, BKF, K, KYO, L, P) & *8220* (BKF, K, L); ibid., Mae Taeng, 1,300 m alt., 23 Nov 2001, *Maxwell 01-626* (BKF, CMUB, L); **Lamphun**, Mae Tha, Doi Din Deng, 3 Feb 1912, *Kerr 2317* (BM, E, K, TCD); **Lampang**, Doi Khun Than NP, 16 Dec 2019, *Balslev* et al. *9910* (AAU); ibid., 25 Oct 2019, *Kladwong 509* (KKU); **Tak**, Umphang, Ban Mae Lamung, 24 Dec 2010, *Suksathan* et al. *5429* (L); **Phitsanulok**, Chat Trakan, Phu Miang, 2 Oct 1968, *Phusomsaeng* et al. *11* (BKF, K, L); ibid., Phu Hin Rong Kla NP, 1,400–1,600 m alt., 10 Dec 1990, *Larsen* et al. *41828* (AAU); North-eastern: **Loei**, Na Haew, Phu Suan Sai NP, 15 May 2008, *Maknoi* & *Srisanga 2293* (QBG); ibid., Phu Kradueng NP, 900–1,300 m alt., 17 Dec 1982, *Koyama* et al. *31205* (BKF, KYO, L); ibid., Phu Luang WS, 1,300 m alt., 14 Mar 1980, *Smitinand s.n.* (BKF); **Bueng Kan**, Phu Wau WS, 197 m alt., 28 Dec 2011, *Norsaengsri* & *Tathana 8698* (BKF, QBG); South-western: **Uthaitani**, Ban Rai, Ban Poo Bon, 300 m alt., 2 Feb 1976, *Maxwell 76-56* (BK, L 2 sheets); **Kanchanaburi**, Si Sawat, Erawan NP, Huai Lam Tam Ton, 580–600 m alt., 26 Nov 1982, *Koyama* et al. *30306* (BKF, KYO, L); without locality, 14 Jan 1926, *Kerr 10211* (ABD, BK, BM, K).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 195,058.419 km^2 and an Area of Occupancy (AOO) of 68.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes esquirolii* resembles *S. brandisii* and *S. consors* in having a densely white tomentose indumentum on bracts, bracteoles and calyx, but it can be distinguished from both in having sulcate stems, oblong-lanceolate bracts. In addition, *S. esquirolii* is also different by dark green stems and bracts.

Craib (1914) described *S. leucocephala* based on *Kerr 2317* which has seven duplicates, four in K [K001514900, K001514901, K001514902, K001514903] and one in each of BM [BM000906289], E [E00133531] and TCD. K001514901 has more inflorescences and flowers than the others; therefore, we select this specimen as the lectotype.

Figure 4. *Strobilanthes esquirolii* H.Lév **A** stem and leaves **B, C** inflorescences **D** corolla, anthers and stigma.

We have examined the types of *S. bombycina* and *S. esquirolii* and found that they are conspecific because they are densely white tomentose on bracts, bracteoles and calyx and the bracts are oblong-lanceolate. The original protologue of *S. bombycina* was based on *Kerr 10211* (Imlay 1939), this number has four duplicates and one at each of ABD [ABDUH:2/888], BK [257639], BM [BM000906285] and K [K001514899]. The morphological characters of the specimen at BM correspond with the protologue, especially in leaf and fruit size and the sheet also has *Imlay*'s handwriting as follows: "*Strobilanthes bombycinus* Imlay Type no.". Therefore, we select the sheet BM000906285 as the lectotype.

12. *Strobilanthes falconeri* T.Anderson, J. Linn. Soc., Bot. 9: 484. 1867.

Fig. 10D

Type. Myanmar, Moulmain, 27 Feb 1849, *Falconer 423* (lectotype CAL [CAL0000019638 image!] designated here; isolectotypes CAL [CAL0000019639 image!], K [K000882995!]).

Distribution. Myanmar, Thailand.

Ecology. In evergreen forest; 250–1,300 m alt., flowering and fruiting from October to May.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Khun Yuam, Mae Yuam Noi, 800 m alt., 24 Mar 2009, *Pongamornkul 2579* (QBG); ibid., Mae Sariang, Mae Bow, 1,125 m alt., 2 Mar 1991, *Maxwell 91-212* (AAU-2 sheets, E, L); ibid., Sob Moei, 900 m alt., 29 Apr 2014, *Pongamornkul 4165* (QBG); **Chiang Mai**, Doi Inthanon NP, Doi Pha Tang, 1,300 m alt., 18 Jan 2009, *Niyomdham & Puudjaa 8356* (BKF); Tak, Umphang, Thung Yai Naresuan East WS, 22 Dec 2011, *Watthana & La-ongsri 4100* (QBG); South-western: **Kanchanaburi**, Sangklaburi, Khao Leam NP, 250 m alt., 16 Dec 2005, *Poopath 421* (BKF-2 sheets); ibid., Khao Yai, 800–900 m alt., 2 Apr 1968, *van Beusekom & Phengklai 302* (AAU, BKF, E, K, L); Central: **Nakhon Nayok**, Khao Yai NP, 1,170 m alt., 9 Oct 1979, *Shimizu* et al. *18097* (KYO-2 sheets); ibid., 800 m alt., 29 Jan 2008, *Maxwell 08-17* (QBG, CMUB, L).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 69,009.843 km^2 and an Area of Occupancy (AOO) of 36.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Falconer 423* was mentioned in the original protologue of *S. falconeri* (Anderson 1867). There are three duplicates two at CAL [CAL0000019638, CAL0000019639] and one at K [K000882995]. All the specimens were labelled as "*Strobilanthes falconeri* T.Anderson" in *Anderson*'s handwriting. The sheet CAL0000019638 has more leaves, inflorescences and fruits. Therefore, we select this specimen as the lectotype.

This species was formerly known only from Myanmar, but is now known from the Northern, South-Western and Central floristic regions of Thailand.

13. *Strobilanthes graminea* J.B.Imlay, Bull. Misc. Inform. Kew 1939(3): 116. 1939.

Fig. 11A

Gutzlaffia graminea (J.B.Imlay) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 155. 1944.

Type. Thailand, Tak, Khao [Kao] Hua Mod, 12 June 1922, *Kerr 6118* (holotype BM [BM001046226!]; isotype BK [257641!]).

Distribution. Endemic to Thailand.

Ecology. In open limestone hill; 300–933 m alt., flowering and fruiting from May to August.

Selected specimens examined. Thailand, Northern: **Tak**, Umphang, Doi Hua Mod [Kao Hua Mod], 12 June 1922, *Kerr 6118* (BK, BM); ibid., 800 m alt., 1 May 2006, *Watthana 1970* (CMUB); ibid., 900 m alt., 27 May 2008, *Pooma* et al. *6995* (BKF); ibid., 800 m alt., 2 May 20011, *Watthana 3805* (QBG); ibid., 933 m alt., 18 July 2015, *Phaosrichai 205* (QBG); **Kamphaeng Phet**, Mae Wong NP, 11 July 1999, *Chayamarit* et al. *1795* (BKF); South-western: **Kanchanaburi**, Sangkhla Buri, Nong Lu, Ban Dan Chedi, Khao Condo, 358 m alt., 25 Aug 2010, *Chamchumroon* et al. *4812* (BKF); ibid., Thong Pha Phum, along route 323, 4 km NW from Thong Pha Phum, 240 m alt., 29 Nov 1982, *Koyama* et al. *30473* (BKF, KYO); ibid., 25 Jan 1983, *Koyama* et al. *32887* (BKF, KYO-2 sheets).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 3,865.766 km^2 and an Area of Occupancy (AOO) of 16.000 km^2 and is assessed as Endangered (EN), B1 a, b (i, ii, iii) following IUCN (2022). This species grows on open limestone hills and is only recorded from a few records. The changes of the habitat through increasing droughts and fires are likely to lead to decline of *S. graminea*.

Notes. *Strobilanthes graminea* resembles *S. aprica* (Hance) T.Anderson and *S. hypomalla* Benoist in having two exserted stamens, but the fruit of *S. graminea* has 8 seeds whereas there are 4 seeds in *S. aprica* and *S. hypomalla*.

14. ***Strobilanthes hypomalla*** **Benoist, Bull. Mus. Natl. Hist. Nat. 27: 543. 1921.**
Fig. 11A

Type. Vietnam, Dalat, 27 Nov 1911, *Lecomte & Finet 1524* (lectotype P [P00218435 image!] designated by Kladwong and Chantaranothai 2022, pg. 182).

Distribution. Thailand, Laos, Vietnam.

Ecology. In dipterocarp forest, sandstone bedrock; 340–492 m alt., flowering and fruiting December.

Specimens examined. Thailand, North-eastern: **Bueng Kan**, Phu Lang Ka NP, 492 m alt., 26 Nov 2017, *Suddee* & *Puudjaa 5333* (BKF); ibid., Phu Wua WS, 340 m alt., 15 Oct 2016, *Suddee et al. 5561* (BKF); ibid., trails to Tham Noi Waterfall, 1 Dec 2020, *Kladwong* et al. *539* (KKU).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 10,177.798 km^2 and an Area of Occupancy (AOO) of 16.000 km^2 and is assessed as the Endangered (EN), B1 a, b (i, ii, iii) following IUCN (2022). This species grows on sandy soil in dipterocarp forest and is only recorded from a few records. The changes of the habitat through increasing droughts and fire are likely to lead to the decline of *S. hypomalla*.

Notes. *Strobilanthes hypomalla* resembles *S. aprica*, but differs in having greenish or yellowish green stems, linear-lanceolate leaf shape, and the outside of the corolla is pubescent. Moreover, the pollen of *S. hypomalla* is prolate or subprolate with a 3-colporate aperture and longitudinal spinose ribs on the exine sculpturing as opposed to 3-cryptoaperturate and with short conical spines over the exine in *S. aprica* (Kladwong and Chantaranothai 2022). According to the protologue of *S. hypomalla*, the corolla was described as glabrous outside but the specimens from Thailand show that it is pubescent. Further research based on more specimens is needed to comprehend this variation.

15. ***Strobilanthes kerrii*** **Craib, Bull. Misc. Inform. Kew 1912(6): 267. 1912.**
Figs 5, 11A

Goldfussia kerrii (Craib) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41: 231. 1944.

Goldfussia lanuginosa Bremek., Dansk Bot. Ark. 23: 276. 1966. Type: Thailand, Kawng San, 22 Jan 1964, *Hansen 10872* (holotype C n.v.; isotypes L [L0002856!], U [U0000027!]).

Type. Thailand, Phrae [Phrea], Huai [Hue] Kamin, 18 Feb 1910, *Kerr 988* (lectotype K [K001514920!] designated here; isolectotypes BM [BM000793163!], E [E00136697!], K [K001514921!, K001514922!], TCD!).

Distribution. Endemic to Thailand.

Ecology. By stream bank in dry evergreen forest and hill evergreen forest; 160–1,800 m alt., flowering and fruiting from September to March.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Pai, Mueang Sroi Waterfall, 800 m alt., 17 Jan 1983, *Koyama* et al. *32647* (K, KYO); **Chiang Mai**, Doi Chiang Dao WS, 1,500–1,800 m alt., 27 Oct 1979, *Shimizu* et al. *20918* (BKF, L) *& 20938* (BKF, KYO, L); ibid., Kawng San, 1,150 m alt., 22 Jan 1964, *Hansen 10872* (L, U); **Nan**, Doi Phu Kha NP, 1,510 m alt., 4 Dec 1999, *Srisanga*

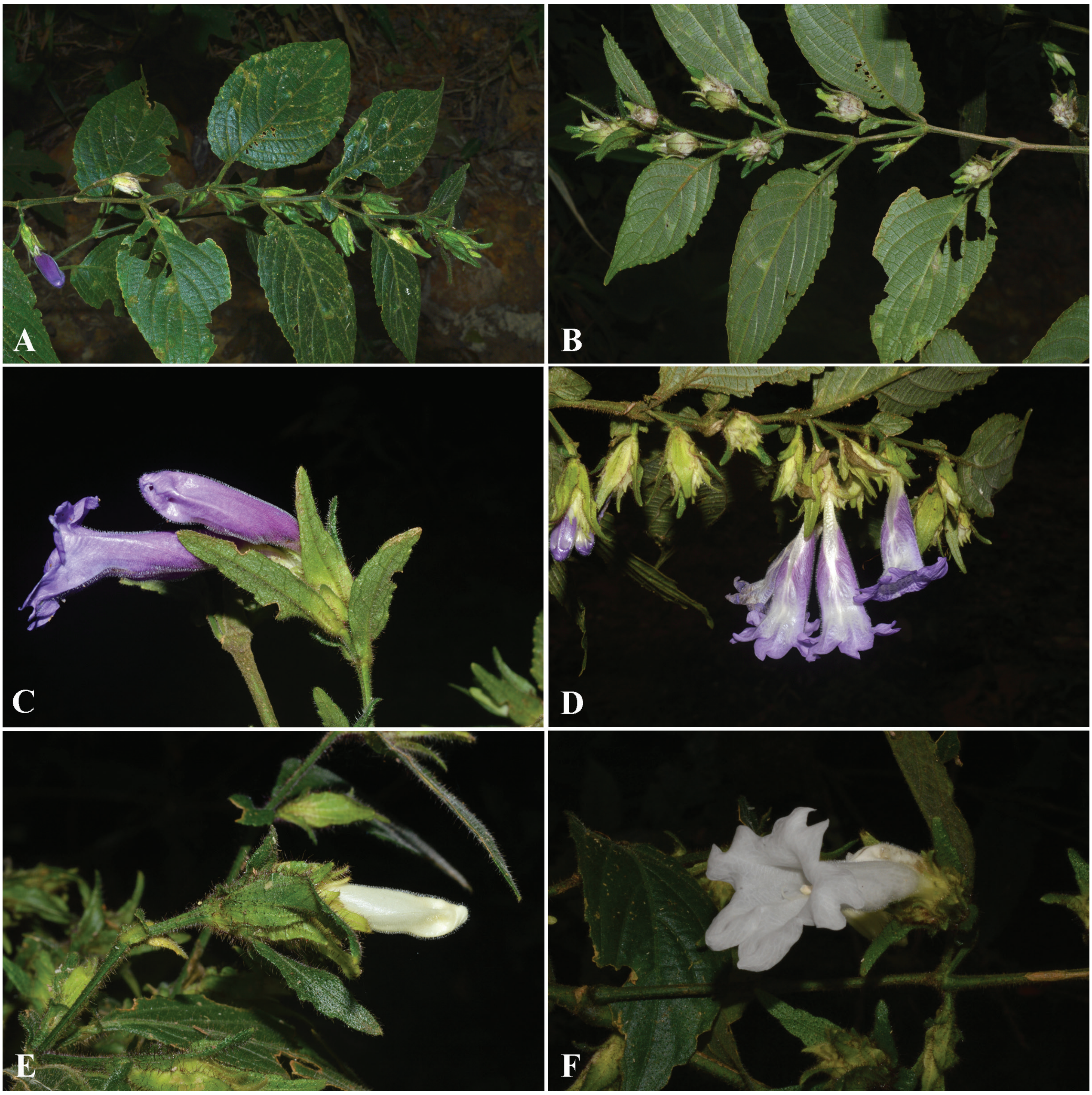

Figure 5. *Strobilanthes kerrii* Craib **A** adaxial surface of leaves **B** abaxial surface of leaves **C–F** inflorescences and corolla.

1233 (BKF, QBG); **Lamphun**, Li, Mae Ping NP, Ko Luang Waterfall, 500 m alt., 23 Jan 2017, *Pooma & Pattharahirantricin 7966* (BKF); **Phrae**, Huai Kamin, ca. 300 m alt., 18 Feb 1910, *Kerr 988* (BM, E, K-3 sheets, TCD); **Tak**, Mae Sot, Inthanin Cave Temple, 26 Dec 2010, *Suksathan* et al. *5447* (L); **Sukhothai**, Kirimat, Ramkhamhaeng NP, 275 m alt., 27 Jan 1995, *Maxwell 95-26* (BKF, CMUB, L); ibid., Srichatchanalai NP, Tham Thara Wasan, 160 m alt., 17 Nov 2014, *Norsaengsri 11509* (QBG). North-eastern: **Loei**, Na Haew, Phu Suan Sai NP, 3 Sept 2008, *Maknoi 2792* (BKF, QBG); ibid., Phu Luang WS, 19 Nov 2019, *Kladwong* et al. *505 & 506* (KKU).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 80,801.690 km^2 and an Area of Occupancy (AOO) of 52.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes kerrii* has many characteristics in common with *S. capitata* and *S. speciosa*, especially the leaf and bract shapes and inflorescence type. However, it can be distinguished due to the presence of rigid dark red trichomes on stems, petiole and peduncle that are absent in *S. capitata* and *S. speciosa*. *Strobilanthes kerrii* was treated as a synonym of *S. speciosa* (Bennett and Scotland 2003), but now we conclude that it should be regarded as species in its own right.

This species was described by Craib (1912) based on *Kerr 988* which has five duplicates, three of them were deposited at K [K001514920, K001514921, K001514922] and each one kept at BM [BM000793163], E [E00136697] and TCD. All are in good shape, but the sheet K001514920 has more mature leaves and flowers. Therefore, we select this specimen as the lectotype.

16. ***Strobilanthes paniculata*** (Nees) Miq., Fl. Ned. Ind. 2: 802. 1858.

Fig. 11B

Goldfussia paniculata Nees in Compan. Bot. Mag. 2: 313. 1837. Type: Indonesia, Java, *Hooker s.n.* (lectotype E-GL [E00749036!] designated by Wood 1994a, pg. 112).

Microstrobilus paniculatus (Nees) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 250. 1944. Type: Based on *Goldfussia paniculata* Nees.

Strobilanthes deminuta S.Moore in J. Bot. 63: 78. 1925. Type: Indonesia, South Sumatra, Krui, 1880, *Forbes 1929* (lectotype BM [BM0007933206!] designated by Bennett and Scotland 2003, pg. 46; isolectotype L [L0614259!]).

Strobilanthes subcapitata C.B.Clarke in J.D.Hooker, Fl. Brit. India 4: 455. 1884. Type: Myanmar, Tenasserim, *Helfer 6111* (lectotype K [K000883112!] designated here; isolectotypes K [K000883113!], P [P00719448 image!]).

Strobilanthes microcephala Benoist, Bull. Soc. Bot. France 80: 730. 1934. Type: Laos, Bolaven [Boloven], *Poilane 15853* (lectotype P [P00719373 image!] designated here; isolectotypes A [A00286779 image], K [K001514870!, K001514871!], P [P00719376 image!]).

Type. Based on *Goldfussia paniculata* Nees

Distribution. Myanmar, Thailand, Laos, Indonesia.

Ecology. Near stream in evergreen forest or bamboo forest; 10–1,000 m alt., flowering and fruiting from November to March.

Selected specimens examined. Thailand, Peninsular: **Chumphon**, Lang Suan, 14 Feb 1927, *Kerr 11939* (BK, BM, K, KYO); ibid., 100 m alt., 1 Mar 1927, *Kerr 12172* (BK, BM, K); ibid., Siep Yuan, 10 m alt., 20 Dec 1928, *Kerr 16236* (BK, BM, K); **Ranong**, Kaper, 10 m alt., 17 Feb 1929, *Kerr 16707* (BK, BM, K); ibid., Khao Pawta Luang Kaeo, 400–1,000 m alt., 27 Feb 1983, *Koyama* et al. *33815* (BKF, K, KYO-3 sheets, L); ibid., Klong Naka WS, 80 m alt., 17 Nov 1973, *Santisuk 593* (BKF-3 sheets); ibid., 23 Nov 1974, *Indrapong 39* (BKF); ibid., 30–50 m alt., 8 Dec 1979, *Shimizu* et al. *26398* (BKF, KYO-2); ibid., 30–230 m alt., 6–7 Jan 1990, *Hoover 5072* (E) *& 5429* (E); ibid., Kra Buri, 29 Feb 1968, *Vacharapong 186* (BK) *& 190* (BK); **Surat Thani**, Klong Sok, 14 Feb 1975, *Damrongsak 159* (BKF).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 1,739,203.963 km^2 and an Area of Occupancy (AOO) of 28.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes paniculata* resembles *S. paniculiformis* J.R.I.Wood in having a panicle of capitate inflorescences and glabrous bracts. It differs in having the obovate bracts and linear-obovate bracteoles vs. the ovate-orbicular bracts and obovate to narrowly obovate bracteoles in *S. paniculiformis*.

Helfer's collection was cited in the protologue of *S. subcapitata* (Clarke 1884). This collection has three duplicates. Two of which were deposited at K [K000883112, K000883113] and one housed at P [P00719448]. Both the duplicates at K have *Clarke*'s handwriting as follows: "*Strobilanthes subcapitata* Clarke": but K000883112 has more mature leaves. Therefore, we select this specimen as the lectotype.

The original protologue of *S. microcephala* was based on *Poilane 15853* (Benoist 1934). This collection has five duplicates one at A [A00286779], two at K [K001514870, K001514871] and two at P [P00719373, P00719376]. P00719373 has more mature leaves and inflorescences; therefore, it is selected as the lectotype. The others are isolectotypes.

17. *Strobilanthes paniculiformis* J.R.I.Wood, Kew Bull. 61: 10. 2006.

Figs 9A, 11C

Type. India, Naga Hills, 1887, *Clarke 40945* (holotype K [K000545689!]; isotype K [K000545690!]).

Distribution. India, Myanmar, Thailand.

Ecology. In hill evergreen forest or open plateau; 1,200–2,285 m alt., flowering and fruiting from October to December.

Selected specimens examined. Thailand, Northern: **Chiang Mai**, Fang, Doi Pha Hom Pok NP, 2,285 m alt., 10 Nov 2012, *Chamchumroon 5541* (BKF); **Phitsanulok**, Phu Hin Rong Kla NP, 1,400–1,600 m alt., 10 Dec 1990, *Larsen* et al. *41827* (AAU, P); ibid., 1,200 m alt., 11 Dec 1990, *Larsen* et al. *41870* (AAU); ibid., 1,300 m alt., 14 Oct 1998, *Suksathan 1302* (QBG-2 sheets); North-eastern: **Loei**, Phu Kradueng NP, 1,150–1,250 m alt., 1 Nov 1984, *Murata* et al. *42539* (BKF, L).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 12,195.648 km^2 and an Area of Occupancy (AOO) of 12.000 km^2 and is assessed as Vulnerable (VU), B1 a, b (i, ii, iii) following IUCN (2022). This species grows on the open plateau of evergreen mountains and is recorded from only a few collections. The changes of the habitat through increasing droughts and fire might lead to causing decline of *S. paniculiformis*.

Notes. *Strobilanthes paniculiformis* was formerly known from the Naga Hills of Eastern India was also recently recorded in the Kachin State and Sagaing Region of Myanmar (Wood et al. 2022) but is now seen to have a wider distribution stretching into the Northern and North-Eastern floristic regions of Thailand.

18. *Strobilanthes phengklaii* Kladwong & Chantar., sp. nov.

urn:lsid:ipni.org:names:77344994-1

Figs 6, 7, 11B

Type. Thailand, Chaiyaphum, Phu Khieo WS, Oct 1999, *Phengklai et al. 12261* (holotype BKF [SN127785!]; isotypes BKF [SN143321!, SN127784!]).

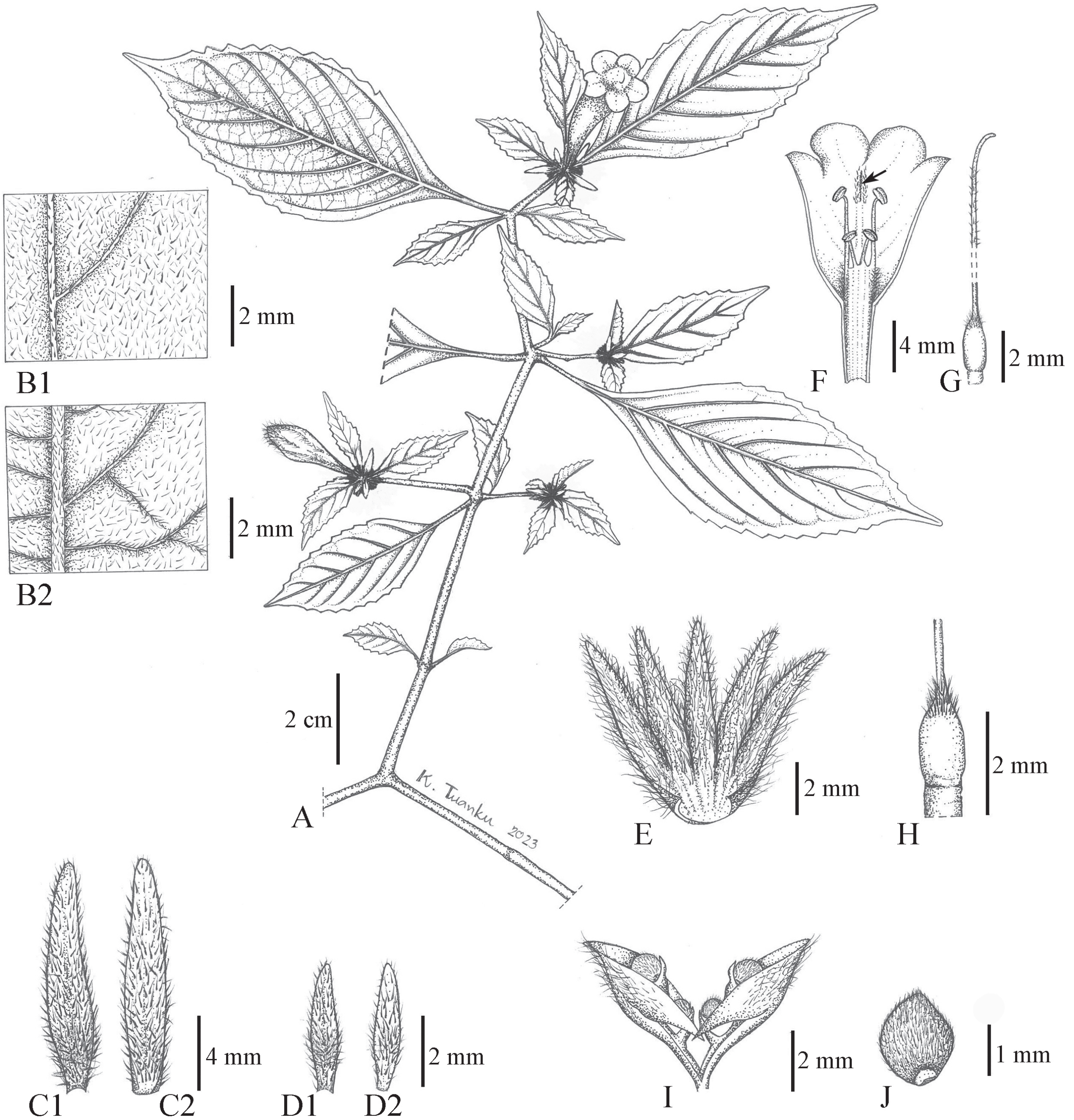

Figure 6. *Strobilanthes phengklaii* Kladwong & Chantar. **A** stem, leaves and inflorescences **B** adaxial surface of leaf (**B1**) and abaxial surface of leaf (**B2**) **C** outer surface of bract (**C1**) and inner surface of bract (**C2**) **D** outer surface of bracteole (**D1**) and inner surface of bracteole (**D2**) **E** calyx **F** corolla, stamens and rugula and trichomes retaining the style (arrow) **G** pistil, style and stigma **H** ovary **I** fruit **J** seed. **A**–**H** drawn from *Phengklai* et al. *12261* (BKF: holotype), **I**–**J** drawn from *Tagawa* et al. *1076* (BKF). Drawn by K. Tuanku.

Diagnosis. Similar to *S. brandisii* T.Anderson and *S. esquirolii* H.Lév. in having single capitate inflorescences, sessile or subsessile and densely white sericeous bracts but differs in having lanceolate or linear-lanceolate bracts and yellow corolla vs. spathulate bracts and purple corolla in *S. brandisii* and oblong-lanceolate bracts and violet corolla in *S. esquirolii*. The morphological difference among *S. brandisii*, *S. esquirolii* and *S. phengklaii* are presented in Table 2.

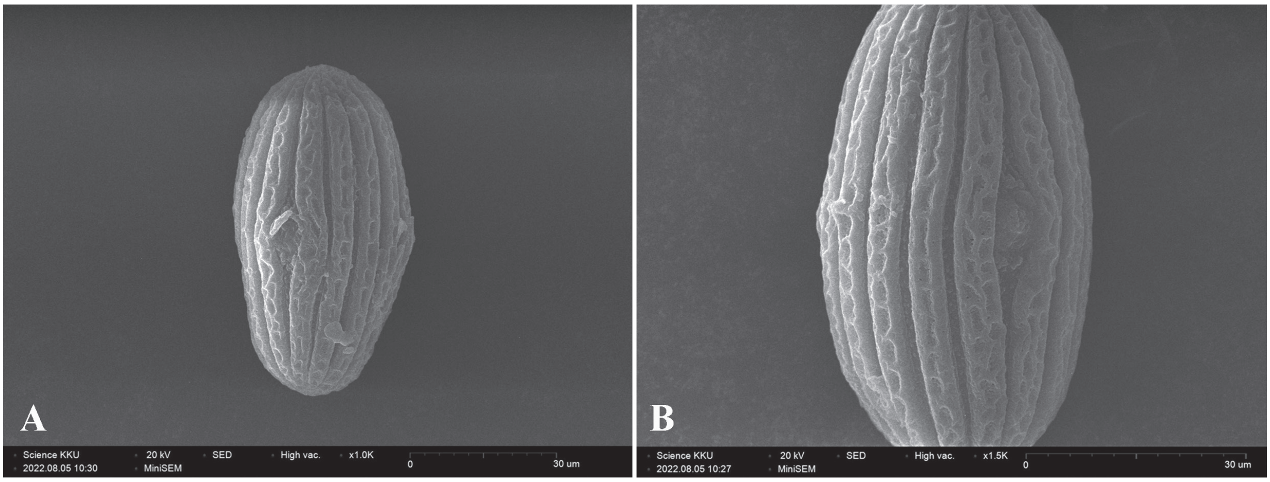

Figure 7. Scanning electron microscope micrographs of pollen of *S. phengklaii* Kladwong & Chantar., equatorial view **A** shape **B** exine sculpturing, from *Phengklai* et al. *12261* (BKF).

Table 2. Morphological differences between *Strobilanthes phengklaii* and similar species.

Characters	*S. brandisii*	*S. esquirolii*	*S. phengklaii*
Leaf blade	lanceolate or ovate-lanceolate	ovate-elliptic to ovate-elliptic	lanceolate to oblong-lanceolate
Bract shape	spathulate	oblong-lanceolate	lanceolate or linear-lanceolate
Bracteoles	linear	oblanceolate	linear
Corolla	purple	violet	yellow
Long filaments	hairy	hairy	glabrous
Capsule	ovoid	oblongoid	fusiform

Description. ***Herbs*** up to 40 cm tall, perennial, erect or decumbent, anisophyllous. ***Stems*** 4-angled, sulcate or subterete when mature, pubescent or glabrescent. ***Leaves*** petiolate; blades lanceolate to oblong-lanceolate, 1.8–10 × 0.6–3.5 cm, hairy on adaxial surface, pubescent on abaxial surface, lateral veins 3–7 pairs, prominent on both surfaces, apex attenuate to caudate, base attenuate, and decurrent onto petiole, margin serrate or crenate, ciliate; petiole 0.3–2.5 cm long, pubescent. ***Inflorescences*** terminal capitate, 3–5-flowered; peduncle absent; bracts lanceolate or linear-lanceolate, 5–13 × 2–4 mm, persistent, the outer one longer than the inner, white sericeous on both surfaces, the upper part sparsely hispid, apex obtuse, margin entire or obscurely serrate, base sessile, ciliate; bracteoles linear, 3–5 × ca. 0.8 mm, white sericeous on both surfaces. ***Calyx*** 5-lobed; lobes linear, 4–5 × 0.5 mm, subequal, apex acute, white sericeous on both surfaces. ***Corolla*** yellow, funnel shaped, 2–4 cm long, densely white sericeous on top at bud, sparsely pubescent at anthesis, glabrous inside except hairs retaining style; tube yellow, cylindric for 4–6 mm long; mouth 1–1.5 cm wide; lobes 5, ovate, 3–4.5 × 3.5–5 mm, apex obtuse. ***Stamens*** 4, included, didynamous; short filaments 2 mm long, long filament 3–5 mm long, all filament straight and glabrous; anther thecae ca. 1.5 mm long, white, without spur; pollen 3-colporate, prolate or subprolate in equatorial view, circular in polar view, polar range 51–67 μm, equatorial range 31–41 μm; ectoapertures fusiform; exine divided into longitudinal ribs, each rib with a coarse ladder-like reticulum. ***Ovary*** ellipsoid, 2 mm long, densely white sericeous at apex; style 2.5–3 cm long, puberulous. ***Capsule*** fusiform, 5–7 × 3–4 mm, white sericeous, 4-seeded. ***Seeds*** ovate in outline, ca. 1.8× ca. 1.5 mm, hairy.

Distribution. Endemic to Thailand.

Ecology. Common in shaded areas in dry evergreen forest; ca. 600 m alt., flowering and fruiting from October to December.

Etymology. Named in honour of Dr Chamlong Phengklai, a senior botanist at the Forest Herbarium (BKF) who collected the type specimens of *S. phengklaii*.

Additional specimens examined (*paratypes*): THAILAND, North-eastern: **Loei**, Phu Luang WS, from Ban Na Luang to north ride ca. 600 m alt., 3 Dec 1965, *Tagawa* et al. *1076* (BKF, KYO, L [L2842098]).

Preliminary conservation status assessment. This species is only known from two populations suggesting that this species is endemic to the north-eastern floristic region of Thailand. It is assessed as Data Deficient (DD) following IUCN (2022). However, *S. phengklaii* was legally collected from a protected area and it is recorded as common in the locality. *Strobilanthes phengklaii* has a few records. The changes of the habitat through increasing droughts and fire is likely to lead to the decline of this species. More field work is needed to assess the conservation status of *S. phengklaii*.

19. *Strobilanthes phyllocephala* J.R.I.Wood & Scotland, Nat. Hist. Bull. Siam Soc. 62(1): 31. 2017.

Fig. 11C

Type. THAILAND: Phetchaburi, Kaeng Krachan NP, 6 Aug 1995, *Larsen* et al. *45466* (holotype K [K000224872!]; isotype AAU!).

Distribution. Endemic to Thailand.

Ecology. Near stream in evergreen forest or bamboo forest; 10–1,000 m alt., flowering and fruiting from November to March.

Selected specimens examined. THAILAND, South-western: **Phetchaburi**, Kaeng Krachan NP, 400–600 m alt., 6 Aug 1995, *Larsen* et al. *45466* (AAU, K); ibid., 840 m alt., 24 Oct 2013, *Tagane* et al. *2132* (BKF).

Preliminary conservation status assessment. This species is only known from its type locality and is assessed as Data Deficient (DD) following IUCN (2022). More field work needed to assess the conservation status of *S. phyllocephala*.

Notes. *Strobilanthes phyllocephala* resembles *S. falconeri*. It differs in having the ovate or ovate-elliptic leaves vs. elliptic-lanceolate or lanceolate leaves in *S. falconeri*. The apex of bracteoles of *S. phyllocephala* is obtuse vs. acute in *S. falconeri*.

20. *Strobilanthes phyllostachya* Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(1): 75. 1871.

Figs 8, 11C

Sericocalyx phyllostachyus (Kurz) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 163. 1944.

Type. MYANMAR, Bago Region [Beeliz], *Brandis s.n.* (syntype K! [without barcode]).

Distribution. Myanmar, Thailand.

Ecology. Near stream in evergreen forest or bamboo forest; 10–1,000 m alt., flowering and fruiting from November to March.

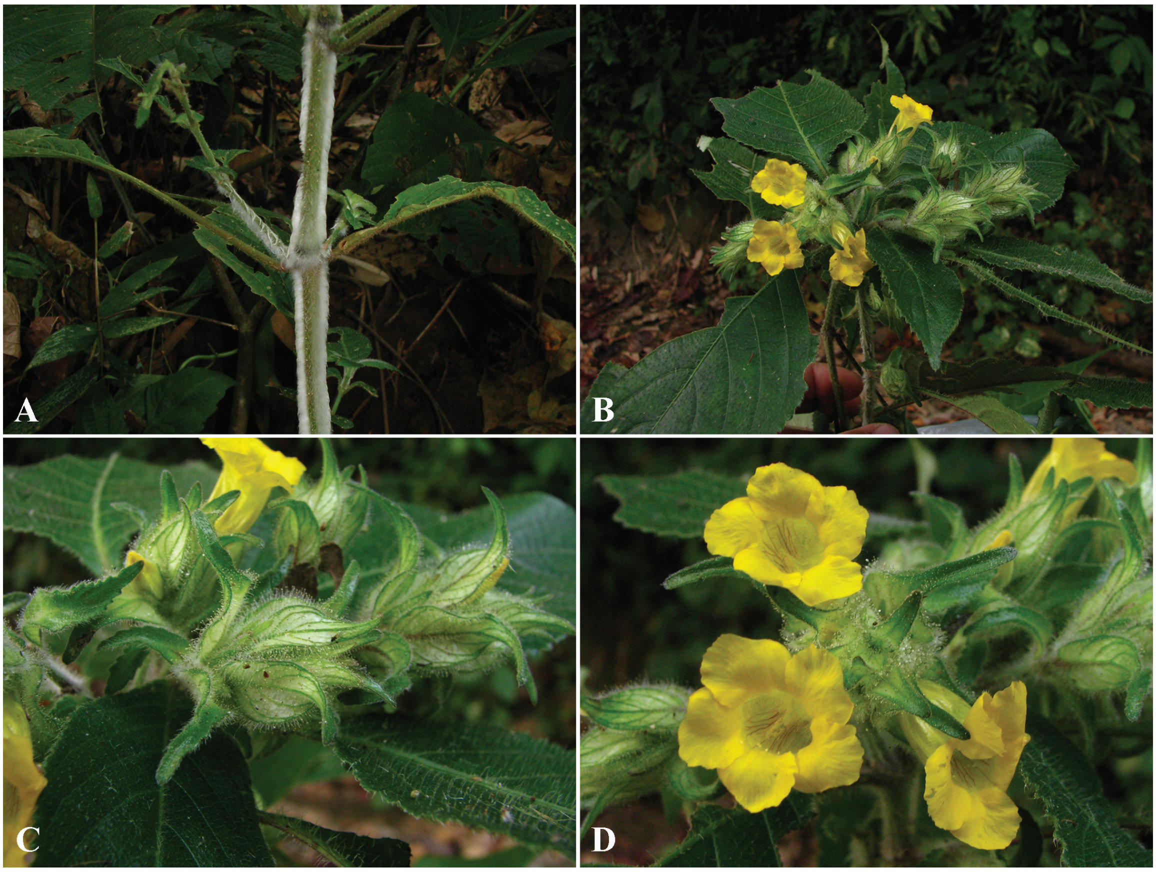

Figure 8. *Strobilanthes phyllostachya* Kurz **A** stem **B** leaves and inflorescences **C** bracts **D** corolla. Photo by P. Suksathan.

Figure 9. Photographs of dried specimens **A** *S. paniculiformis* J.R.I.Wood from *Larsen* et al. *41870* (AAU) **B** *S. squalens* S.Moore from *Maxwell 74-164* (BK).

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Mae Sariang, 400 m alt., 21 Feb 1982, *Wongprasert 6* (BKF-2 sheets, K, L, P); ibid., Huai Ngae, 350 m alt., 14 Feb 1971, *Smitinand & Boonkird 11422* (BKF); 450 m alt., 13 Jan 1988, *Santisuk 6668* (BKF-2 sheets); ibid., Salawin WS, Huai Ka Han, 500 m alt., 23 Mar 2006, *Watthana & Wongnak 1860* (QBG); ibid., Sob Moei, 950 m alt., 24 Jan 2015, *Pongamornkul 4782* (QBG); ibid., Mae Ngao NP, 13 Jan 2015, *Tanming 757* (QBG); **Tak**, Mae Ngo NP, 395 m alt., 23 Dec 2010, *Suksathan* et al. *5336* (L); ibid., Tha Song Yang, 22 Mar 2006, *Pooma* et al. *6226* (AAU, BKF-2 sheets, QBG); South-western: **Kanchanaburi**, Thong Pha Phum, 14 Dec 1993, *Parinya* et al. *364* (BK); ibid., Wangka, Kwae Noi River Basin, 150 m alt., 13 May 1949, *Kostermans 412* (K).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 10,101.500 km^2 and an Area of Occupancy (AOO) of 28.000 km^2 and is assessed as Vulnerable (VU), B1 a, b (i, ii, iii) following IUCN (2022). This species grows near streams in evergreen forest or bamboo forest with a few records. The changes of the habitat through increasing droughts and fire are likely to lead to the decline of *S. phyllostachya*.

Notes. *Strobilanthes phyllostachya* is distinguishable from *S. squalens* S. Moore by its elliptic bract and hairlessness on the outside of the corolla. This species was formerly only known from Myanmar (Kurz 1871; Wood et al. 2022), but is now newly recorded from the Northern and Southwestern floristic regions of Thailand.

21. *Strobilanthes serpens* (Nees) J.R.I.Wood & Scotland, Kew Bull. 77: 834. 2021.

Fig. 11C

Ruellia serpens Nees, Prodr. [A. P. de Candolle] 11: 145. 1847. Type: Indonesia [insular Java], Tjiserae, 1826, *Blume s.n.* (holotype GZU [GZU000250312 image!]; isolectotypes B [B101182406 image!], L [L0065807!]).

Hemigraphis serpens (Nees) Boerl., Handl. Fl. Ned. Ind. 2(2): 658. 1899. Type: Based on *Ruellia serpens* Nees.

Hemigraphis hispidula Craib, Bull. Misc. Inform. Kew 1913(6): 203. 1913. Type: Thailand, Nan, 21 Feb 1912, *Kerr 2383a* (lectotype K [K000882585!] designated here; isolectotype E [E00273431!]), syn. nov.

Sericocalyx hispidulus (Craib) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41(1): 163. 1944. Type: Based on *Hemigraphis hispidula* Craib.

Hemigraphis ridleyi C.B.Clarke, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74(3): 652. 1908. Type: Malaysia, Pahang, Jerantut, Kuala Tembeling, Aug 1891, *Ridley 2180* (holotype SING [SING0027181 image!]).

Type. Based on *Ruellia serpens* Nees

Distribution. Thailand, Malaysia, Singapore, Indonesia.

Ecology. In grass thickets and meadows or by streams under the shade of mixed deciduous and evergreen forests; 10–1,250 m alt., flowering and fruiting from June to May.

Selected specimens examined. Thailand, Northern: **Chiang Rai**, Doi Luang NP, 580 m alt., 3 Nov 2015, *Muangyen 217* (QBG); **Chiang Mai**, Mae Taeng, Pong Dueat, 825 m alt., 19 Nov 1992, *Maxwell 92-742* (CMUB, L); **Nan**, Tha Wang Pha,

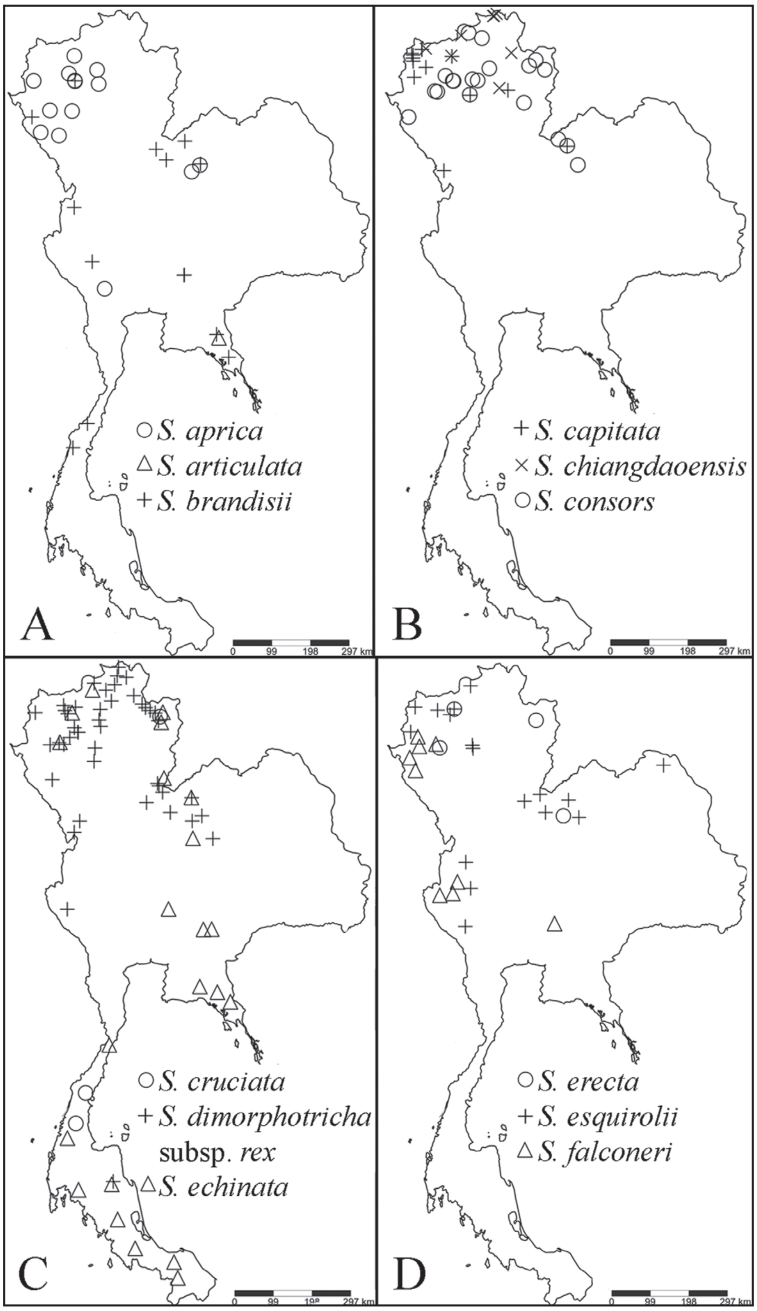

Figure 10. Distribution maps of *Strobilanthes* with capitate inflorescence in Thailand **A** *S. aprica* (Hance) T.Anderson, *S. articulata* J.B.Imlay and *S. brandisii* T.Anderson **B** *S. capitata* (Nees) T.Anderson, *S. chiangdaoensis* Terao and *S. consors* C.B.Clarke **C** *S. cruciata* (Bremek.) Terao, *S. dimorphotricha* subsp. *rex* (C.B.Clarke) J.R.I.Wood and *S. echinata* Nees **D** *S. erecta* C.B.Clarke, *S. esquirolii* H.Lév. and *S. falconeri* T.Anderson.

500 m alt., 14 Nov 1993, *Larsen* et al. *44347* (AAU); ibid., Huai Mae Sakawn, between Phrae and Nan, ca. 427 m alt, 15 Feb 1912, *Kerr 2383* (E, K); ibid., common in Jungle, 21 Feb 1912, *Kerr 2383a* (E); **Phitsanulok**, Thung Salang Luang NP, 600 m alt., 25 July 1996, *Larsen* et al. *885* (AAU, BKF); Kamphaeng Phet, Klong Klung, 200 m alt., 1 June 1922, *Kerr 6044* (BK, K); North-eastern: **Phetchabun**, Nam Nao NP, 11 June 1964, *Chantanamuck 751* (BK), **Loei**, Na Haew, 1,000 m alt., 26 Apr 1994, *Nanakorn* et al. *3168* (QBG); ibid., Phu Kradueng NP, Phen Phop Mai Waterfall, 1,230 m alt., 4 Sept 1988, *Tsuchiya & Tamura*

60534 (BKF); **Khon Kaen**, Chum Phae, Pha Nok Khao, 400 m alt., 26 Nov 1965, *Tagawa 294* (BKF, K, L); ibid., Phu Pha Man NP, Nakarat Cave, 483 m alt., 25 July 2010, *Norsaengsri & Thangson 6950* (QBG); South-western: **Kanchanaburi**, Huai Bankao, 800 m alt., 13 Nov 1971, *van Beusekom* et al. *3758* (BKF, K, L); ibid., Sai Yok, Thung Kang Yang, 5 July 1963, *Larsen 10516* (BKF, L); ibid., Sangkhla Buri, Mueang Cha area, 800 m alt., 8 July 1973, *Maxwell 73-218* (AAU, BK); **Ratchaburi**, Chom Bueng, Ban Baw, 100 m alt., 26 Mar 1975, *Maxwell 75-332* (AAU, BK); ibid., Thung Kang Yang, 350 m alt., July 1963, *Larsen* et al. *10517* (AAU); South-eastern: **Chon Buri**, Si Racha, 15 Nov 1926, *Put 458* (BK, K); **Chanthaburi**, Pong Nam Ron, Khao Soi Dao, 250 m alt., 5 May 1975, *Maxwell 75-485* (AAU); Peninsular: **Chumphon**, Sawi, 9 Sept 1927, *Put 1023* (BK, K); **Ranong**, Kra Buri, Nam Chut, 29 Jan 1927, *Kerr 11704* (BK, K); La-un, 10 m alt., 2 Jan 1929, *Kerr 16493* (BK, K); **Krabi**, Khao Panom Bencha, 24 Oct 1991, *Larsen* et al. *42533* (AAU); **Nakhon Si Thammarat**, Lan Saka, 50 m alt., 25 Apr 1928, *Kerr 15384* (BK); **Trang**, Khao Chong, 200 m alt., 12 Aug 1975, *Maxwell 75-767* (AAU); **Songkhla**, Rattaphum, Boriphat Waterfall, 100–200 m alt., 19 Oct 1991, *Larsen* et al. *42390* (AAU, BKF); ibid., 250 m alt., 16 Aug1984, *Maxwell 84-67* (BKF, L).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 399,832.702 km^2 and an Area of Occupancy (AOO) of 100.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes serpens* differs from *S. hirta* Blume in having petioles which are 2–3.5 cm long, obovate bracts and white anthers. *Strobilanthes hirta* has very short or sessile petioles, ovate-elliptic bracts and purplish-red anthers.

Hemigraphis hispidula was described by Craib (1913). However, after investigation of type and non-type specimens from Thailand, we find that this species has many characteristics in common with *S. serpens*. Therefore, *H. hispidula* is placed as a synonym of *S. serpens*. The original protologue of *H. hispidula* was based on *Kerr 2383* and *Kerr 2383a* (Craib 1913). There are two duplicates of *Kerr 2383* one at E [E00273430] and the other at K [K000882584] and there are two duplicates of *Kerr 2383a* one at E [E00273431] and the other at K [K000882585]. All are in good shape: we designate the sheet K000882585 as the lectotype because it has more mature stems and leaves.

22. *Strobilanthes speciosa* Blume, Bijdr. Fl. Ned. Ind. 14: 799. 1826.

Fig. 11D

Goldfussia speciosa (Blume) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41: 227. 1944. Type: Based on *Strobilanthes speciosa* Blume.

Strobilanthes apoesensis Hochr., Candollea 5: 228. 1934. Type: Indonesia, Mt. Salak, 7 Mar 1904, *Hochreutiner 101* (syntype G [G00236511 image!]).

Strobilanthes kinabaluensis Stapf, Trans. Linn. Soc. London, Bot. 4: 214. 1894. Type: Malaysia, Sabah, Kadamaian River, *Haviland 1362* (syntype K *fide* Bennett and Scotland 2003, pg. 40).

Goldfussia kinabaluensis (Stapf) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. 41: 229. 1944. Type: Based on *Strobilanthes kinabaluensis* Stapf.

Strobilanthes pierrei Benoist, Bull. Soc. Bot. France 80: 730. 1934. Type: Thailand, Khao [Kow] Luang, Aug 1868, *Pierre s.n.* (lectotype P [P00218442 image!] designated here; isolectotypes A [A00286777 image!], P [P00719405 image!, P00204977 image!], NY [00278319 image!]).

Type. Indonesia, Megamendung, *Blume 1802* (lectotype L [L0537293!] designated by Bennett and Scotland 2003, pg. 39).

Distribution. China, Thailand, Laos, Cambodia, Malaysia, Indonesia.

Ecology. Common in evergreen forest or on rugged limestone area, 100–2,150 m alt. Flowering and fruiting from August to March.

Selected specimens examined. Thailand, Northern: **Mae Hong Son**, Khun Yuam, 1,000 m alt., 20 Nov 2014, *Prommanut & Rattanathip 618* (BK-4 sheets); **Chinag Mai**, Doi Chiang Dao WS, 1,500 m alt., 15 Sept 1967, *Shimizu & Hutoh 10152* (BKF, KYO-2 sheets, L); ibid., Fang, Doi Ang Khang, 1,600 m alt., 17 Nov 1973, *Sadakorn 289* (BK); **Chiang Rai**, Doi Chang, 868 m alt., 28 Nov 2010, *Norsaengsri & Tathana 7365* (QBG); ibid., Mae Sai, 1,350 m alt., 4 Oct 1992, *Banziger 1055* (CMUB, L); **Nan**, Song Khwae, Bo Pra Kang, 657 m alt., 2 Feb 2011, *La-ongsri* et al. *2067* (QBG, PSU); **Lampang**, Wang Nuea, Chae Son NP, 525 m alt., 25 Oct 1995, *Maxwell 95-1006* (BKF, CMUB, L); **Tak**, Doi Muser, 700 m alt., 27 Feb 1987, *Paisooksantivatana 2029-87* (BK); ibid., Phummipol Dam, Dec 1959, *S.N. 675* (BK); **Sukhothai**, Mueang Kao, 4 Nov 1971, *Maxwell 71-677* (AAU, BK); South-western: **Phetchaburi**, Kaeng Krachan NP, 210 m alt., 12 Dec 2002, *Middleton 1588* (BKF, CMUB, E); **Prachuap Kiri Khan**, Kaeng Krachan NP, 260 m alt., 15 Aug 2002, *Middleton 1078* (AAU, BKF, CMUB, E, L); ibid., Huai Yang, 6 Oct 1980, *Put 3229* (BK, K, KYO); Peninsular: **Surat Thani**, Phanom, Chong Lom, Khao Sok NP, 100–150 m alt., 12 Dec 1979, *Shimizu* et al. *27115* (BKF, KYO-2 sheets, L); **Nakhon Si Thammarat**, Kiriwong, 100 m alt., 28 Apr 1928, *Kerr 15420* (BK, BM, K); ibid., 100–700 m alt., 17 Jan 1966, *Tagawa* et al. *4545* (BKF, KYO-2 sheets, L); ibid., Khao [Kow] Luang, Aug 1868, *Pierre s.n.* (A, NY, P-4 sheets).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 250,984.816 km^2 and an Area of Occupancy (AOO) of 64.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Pierre*'s collection was cited in the protologue of *S. pierrei* (Benoist 1934). This collection has five duplicates, there are three at P [P00218442, P00719405, P00204977], one at A [A00286777] and one at NY [00278319]. All specimens bear *Benoist*'s handwriting as follows: "*Strobilanthes pierrei* R. Benn.". However, P00218442 has more leaves and inflorescences; therefore, it is selected as the lectotype. The others are isolectotypes.

23. *Strobilanthes squalens* S.Moore, J. Nat. Hist. Soc. Siam 4: 151. 1921.
Figs 9B, 11D

Sericocalyx thailandicus Bremek., Dansk Bot. Ark. Dansk Bot. Ark. 20: 68. 1961. Type: Thailand, Chanthaburi, between Makham and Soi Dao, 100–200 m alt., 14 Jan 1958, *Sørensen* et al. *241* (holotype L [U0000114!]: isotype C [C10005215 image!]), syn. nov.

Type. Vietnam, South Annam, Langbian, Dran, Mar 1918, *Kloss s.n.* (holotype BM [BM000810180!]).

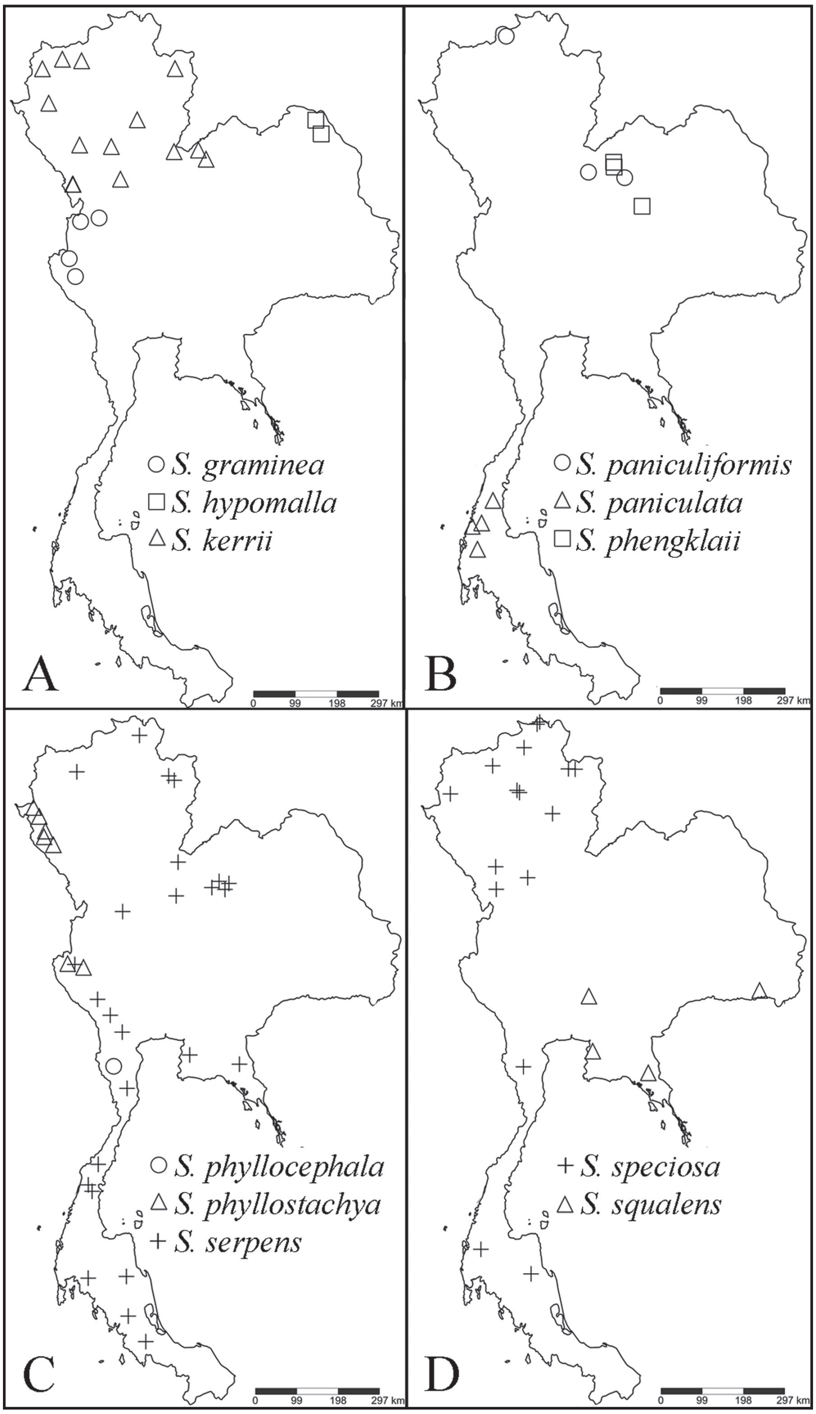

Figure 11. Distribution maps of *Strobilanthes* with capitate inflorescence in Thailand **A** *S. graminea* J.B.Imlay, *S. hypomalla* Benoist and *S. kerrii* Craib **B** *S. paniculiformis* J.R.I.Wood, *S. paniculata* (Nees) Miq. and *S. phengklaii* Kladwong & Chantar. **C** *S. phyllocephala* J.R.I.Wood & Scotland, *S. phyllostachya* Kurz and *S. serpens* (Nees) J.R.I.Wood & Scotland **D** *S. speciosa* Blume and *S. squalens* S.Moore.

Distribution. Thailand, Vietnam.

Ecology. Near stream in evergreen forest or bamboo forest; 10–1,000 m alt., flowering and fruiting from November to March.

Specimens examined. Thailand, Eastern: **Si Sa Ket**, Kantharalak, Khao Phra Wihan NP, 400 m alt., 21 Dec 2005, *Pooma* et al. *6036* (BKF); ibid., 200 m alt., 22 Dec 2005, *Pooma* et al. *6091* (BKF, E, L); Central: **Saraburi**, Mueang, Sam Lan

Forest, 125 m alt., 18 Feb 1974, *Maxwell 74-164* (AAU, BK); ibid., 100 m alt., 26 Jan 1975, *Geesink & Maxwell 8377* (BKF, L); South-eastern: **Chon Buri**, Sriracha, Nong Kam Kheo, ca. 122 m alt., 1 Dec 1927, *Collins 1832* (BK, BM, K); **Chanthaburi**, between Makham and Soi Dao, 100–200 m alt., 14 Jan 1958, *Sørensen et al. 241* (C, L); ibid., Tap Sai, 200 m alt., 17 Dec 1924, *Kerr 9693* (BK, BM, K); ibid., 200 m alt., 19 Dec 1924, *Kerr 9693A* (BK, BM).

Preliminary conservation status assessment. This species has an Extent of Occurrence (EOO) of 46,083.781 km^2 and an Area of Occupancy (AOO) of 16.000 km^2 and is assessed as Least Concern (LC) following IUCN (2022).

Notes. *Strobilanthes squalens* was formerly thought to be an endemic to Southern Vietnam (Baker et al. 1921), but it is now found to occur in the Eastern and Central floristic regions of Thailand.

Sericocalyx thailandicus was described by Bremekamp (1961). After investigation of type specimens from Thailand, we find that this species is conspecific with *S. squalens*. Therefore, *S. thailandicus* is placed as a synonym of *S. squalens*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

Spatial decoupling of taxon richness, phylogenetic diversity and threat status in the megagenus *Erica* (Ericaceae)

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Abstract

Estimates of the number of vascular plant species currently under threat of extinction are shockingly high, with the highest extinction rates reported for narrow-range, woody plants, especially in biodiversity hotspots with Mediterranean and tropical climates. The large genus *Erica* is a prime example, as a large proportion of its 851 species, all shrubs or small trees, are endemic to the Cape Floristic Region (CFR) of South Africa. Almost two hundred are known to be threatened and a further hundred are 'Data Deficient'. We need to target conservation efforts and research to fill the most problematic knowledge gaps. This can be especially challenging in large genera, such as *Erica*, with numerous threatened species that are closely related. One approach involves combining knowledge of phylogenetic diversity with that of IUCN threat status to identify the most Evolutionarily Distinct and Globally Endangered (EDGE) species. We present an expanded and improved phylogenetic hypothesis for *Erica* (representing 65% of described species diversity) and combine this with available threat and distribution data to identify species and geographic areas that could be targeted for conservation effort to maximise preservation of phylogenetic diversity (PD). The resulting 39 EDGE taxa include 35 from the CFR. A further 32 high PD, data deficient taxa are mostly from outside the CFR, reflecting the low proportion of assessed taxa outside South Africa. The most taxon-rich areas

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are found in the south-western CFR. They are not the most phylogenetically diverse, but do include the most threatened PD. These results can be cross-referenced to existing living and seed-banked *ex situ* collections and used to target new and updated threat assessments and conservation action.

Key words: Conservation prioritisation, heathers, large genera, phylogeny, threatened species

Introduction

The world's biosphere is currently experiencing a human-mediated mass extinction (Lughadha et al. 2020), with habitat destruction and degradation, pollution, invasive alien species and climate change extirpating species (IPBES 2019). These processes are dramatically reducing numbers and genetic diversity of populations and impacting the viability of their complex interdependencies with other organisms (Pollock et al. 2020). Over a third of vascular plant species are estimated to be under threat of extinction (e.g. 39%, Lughadha et al. (2020); 45%, Bachman et al. (2023)). The highest extinction rates are reported for narrow-range, woody plants, particularly those in Mediterranean climate and tropical biodiversity hotspots (Humphreys et al. 2019).

The genus *Erica* (of the heather family, Ericaceae) is a prime example of such a group of plants. One of the largest flowering plant genera (Frodin 2004), its 851 species (Elliot et al. 2024) are all woody. They are distributed from Europe to southern Africa, with significant diversity at higher elevations across tropical Africa and Madagascar, but concentrated in the Mediterranean-type climate of the Cape Floristic Region (CFR) of South Africa, a world biodiversity hotspot (Myers et al. 2000). Within a modest geographical extent (ca. 90,000 km^2), the CFR is home to a disproportionately high number of plant species (> 9,000), most of which are found nowhere else (70% species endemism) (Linder 2003). Of this spectacular and unique flora, around 7% of the species richness is represented by over 700 species of *Erica*. These are abundant in many CFR communities, mostly found in fynbos habitats which are subject to regular fires after which they are adapted either to re-seed or to resprout (Ojeda 1998; Segarra-Moragues and Ojeda 2010). Individually, the species often exhibit patterns of narrow local endemism (Oliver et al. 1983).

Habitat destruction and degradation have already resulted in species extinctions in *Erica* and, due to their restricted ranges, many are endangered. The South African National Biodiversity Institute (SANBI)'s Red List includes 944 taxa of *Erica* for South Africa (species, subspecies and varieties) of which 108 are classified as rare, a further 84 as vulnerable (VU), 60 endangered (EN) and 46 critically endangered (CR). Three are already extinct in the wild (EW) (Raimondo et al. 2009). Furthermore, over a hundred species are classified as 'Data Deficient', their populations insufficiently known to allow us to estimate the degree of threat they face. Such taxa are more likely to be rare and threatened too (Bachman et al. 2023).

Resources for conservation are limited and efforts need to focus on meaningful priorities. For example, the most critically-endangered species might be prioritised as an immediate response to prevent extinction and those not already protected in *ex situ* collections might be targeted for seed banking or cultivation in botanic gardens (Westwood et al. 2021). In *Erica*, two species have been saved from the brink of extinction by a combination of the fortuitous preservation of living collections and concerted action to re-introduce them into the wild: *Erica verticillata* P.J.Bergius (Hitchcock & Rebelo, 2017) and *E. turgida* Salisb. Substantial efforts have been made to preserve material in seed banks of other threatened species before their last wild populations are lost (Liu et al. 2020). Ideally, species would be conserved in their native habitats, i.e. *in situ*, as parts of species assemblages that may include further threatened taxa. With numerous threatened taxa distributed across a complex mosaic of habitats, we need formal criteria to decide which species and which areas should have priority.

Potential criteria for conservation prioritisation include threat status of individual species and numbers of such species in given areas. However, species are not equal in evolutionary terms. Extinction destroys unique lines of evolutionary innovation by removing branches from the tree of life. The long branch of an isolated species on the tree of life represents more unique evolutionary history, or ‘phylogenetic diversity’ (PD) (Faith 1992), than the short branch of a recently-evolved species with several extant close relatives. PD, a metric compiled from the sum of all the branches linking a set of species on a phylogenetic tree, can be used in combination with threat status to derive phylogenetically informed conservation priorities, such as through the Evolutionarily Distinct and Globally Endangered (EDGE) approach (Isaac et al. 2007). A prioritisation approach that takes PD into account could deliver very different results in a group such as *Erica*. South Africa is the most species rich area for *Erica* species, with a well-established centre of diversity within the Western Cape (Oliver et al. 1983) including many of the known threatened taxa (Raimondo et al. 2008). However, CFR diversity appears to be represented exclusively by a single Cape clade that shares a relatively recent common ancestor (Pirie et al. 2016). The geographic distribution of threatened phylogenetic diversity may not reflect that of threatened species or of species richness overall.

To estimate the evolutionary distinctiveness of each *Erica* species in a geographical framework, we need a robust phylogenetic hypothesis representing as many species of the genus as possible. The most comprehensive molecular phylogenetic tree of *Erica* currently available is that of Pirie et al. (2016) who included ca. 60% of species from across the distribution of the genus and based on DNA sequence data from the plastid genome (cpDNA) and nuclear ribosomal gene region (nrDNA). An exemplar sampling approach of multiple plastid markers delivered increased support particularly for deeper nodes (Pirie et al. 2016) and within the limits of phylogenetic resolution, the trees based on plastid and nrDNA data were largely congruent. Going forward, we need: a) to reduce the current 40% shortfall of species, b) improved resolution of the nrDNA tree to better test the degree to which cpDNA might track the *Erica* species tree and c) to reduce the substantial remaining phylogenetic uncertainty, particularly within the large Cape clade.

In this paper, we develop an expanded and improved phylogenetic hypothesis for *Erica*. Using the phylogeny, we analyse extensive openly available threat and distribution data to summarise both the taxa and areas that harbour most phylogenetic diversity, and whether that diversity is known to be, or could be threatened with extinction. These results can be cross-referenced to existing living and seed-banked ex situ collections and used to help target new and updated threat assessments and to prioritise conservation action.

Materials and methods

Taxon and molecular sampling

We generated new data from 81 new field-collected, silica-dried leaf samples and additional data from 79 previously analysed samples, expanding existing datasets to include a total of 730 accessions representing 551 *Erica* species (587 specific and subspecific taxa) and six outgroup taxa (four species). This represents 65% of 851 currently recognised (non-hybrid) species (Elliot et al. 2024) following the taxonomic concepts of E.G.H. Oliver (Oliver et al. 2024). In summarising known threat status and taxonomic data for use in the EDGE analyses (see below), we compiled an extended list of 1048 species, subspecies and varieties (Suppl. material 1). This number included a proportion of subspecific taxa which are validly described and for which threat status may have been formally assessed, but which may be of questionable taxonomic status. Of this more inclusive list, 55% were represented in the phylogenetic analyses. Accession details are presented in Suppl. material 2 (table; https://doi.org/10.15468/tae99n) and Suppl. material 3 (a Google Earth map). The existing body of published sequence data comprises broad taxon sampling of the plastid (cpDNA) *trnT-trnL-trnF-ndhJ* region (including genes and intervening introns and spacers) and of the nuclear ribosomal (nrDNA) internal transcribed spacer (ITS) region (including partial flanking 18S and 26S genes) and sparser sampling of cpDNA *atpI-atpH* spacer, *trnK-matK* intron and *matK* gene, *psbM-trnH* spacer, *rbcL* gene, *rpl16* intron, *trnL-rpl32* spacer and part of the nrDNA external transcribed spacer (ETS). To incorporate our new samples, we sequenced the two best represented cpDNA and nrDNA markers for *Erica*, i.e. parts of *trnT-trnL-trnF-ndhJ* and ITS and, to improve support for relationships in the nrDNA tree, we extended our sampling approach to include ETS for a subset of taxa (including some of the same samples used in Pirie et al. (2016)).

Lab protocols

We used two different lab protocols for Sanger sequencing: 1) Direct amplification (without DNA isolation) using the method of Bellstedt et al. (2010); and 2) DNA isolation, (followed by separate PCR) using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). In both cases, leaf material was ground using a Qiagen Tissuelyser (Retsch GmbH & Co., Haan, Germany).

PCR primers and protocols followed Mugrabi de Kuppler et al. (2015) and Pirie et al. (2017) (for ETS). We included per 25 µl reaction 2.5 µl 10× buffer, 2.0 µl 25 mM $MgCl_2$, 1.0 µl 5 mM dNTPs, 0.25 µl 4 µg/µl BSA, 1 µl DMSO (ITS only), 0.1 µl Taq polymerase, 0.25 µl each of 20 µM solutions of the two primers and 1 µl DNA template. For PCR clean-up before sequencing, PCR products were treated in the original PCR reaction tube by addition of a 10 µl solution including 0.025 of 20 units/µl exonuclease I (Fermentas Life Sciences), 0.25 µl of 1 unit/µl shrimp alkaline phosphatase (Promega) and incubation (in a thermocycler) at 37 °C for 30 min and at 95 °C for 5 min. One µl of the resulting product was used for cycle-sequencing with the primers reported by Mugrabi de Kuppler et al. (2015) and Pirie et al. (2017) using Applied Biosystems (Foster City, CA, USA) Big Dye terminator kits according to the manufacturer's instructions. Cycle-sequencing products were analysed using an automatic sequencer 3130XL Genetic Analyzer (Applied Biosystems).

Alignment, data assessment and phylogenetic inference

We aligned new sequences to alignments of Pirie et al. (2016) by eye in Mesquite (Maddison and Maddison 2021), adopting those of the *atpI-atpH* spacer, *trnK-matK* intron and *matK* gene, *psbM-trnH* spacer, *rbcL* gene, *rpl16* intron and *trnL-rpl32* spacer without change. We performed preliminary phylogenetic analyses of markers separately under Maximum Likelihood (ML) as implemented in RAxML (as below), to identify any topological differences within plastid and nrDNA datasets that would indicate experimental error or paralogy. Individual markers were imported into SequenceMatrix (Vaidya et al. 2011) which was used to export concatenated matrices (nrDNA, cpDNA and all markers) for further analyses.

To infer topologies and clade support for cpDNA and nrDNA gene trees, we analysed matrices under ML. Analyses were performed in RAxML v. 8.1.22 (Stamatakis 2014) under the GTR-CAT model and including 1000 rapid bootstrap analysis with bootstrap support (BS) presented on the best scoring ML tree. We assessed conflict between nrDNA and cpDNA gene trees by visual inspection, comparing nodes subject to 70% or higher bootstrap support. Where we identified gene tree conflict, prior to combined analysis, the taxa with conflicting phylogenetic signals were divided into separate cpDNA and nrDNA taxa, each to be represented by one gene tree partition only. The latter allowed us to include taxa showing evidence for reticulate processes or incomplete lineage sorting in downstream analyses without violating the assumption of a strictly bifurcating tree (Pirie et al. 2009). To obtain ultrametric phylogenetic trees reflecting phylogenetic uncertainty, we performed rate smoothing on the best ML tree and 100 randomly-selected trees from the bootstrap analysis using the Penalized Likelihood (PL) approach as implemented in the function chronos in the R package ape v.5.7 (Paradis and Schliep 2019; R Core Team 2022). Before analysis, we removed outgroup taxa and tested different assumptions for among-branch-substitution-rate variation in transforming branch lengths on the ML tree in order to approximate the divergence time estimates in Pirie et al. (2016). In the final analysis on the ML and the 100 bootstrap trees, one rate category reflecting a strict clock model was optimised for 200 iterations per tree using a rate smoothing parameter of 1 and calibrated using a secondary calibration point derived from a wider fossil-calibrated analysis of Ericaceae (Schwery et al. 2015), also following Pirie et al. (2016); (crown node of Ericeae - *Erica*, *Calluna* and *Daboecia* - constrained at 62 Ma).

Species distributions

We used geo-referenced distribution data obtained by a GBIF-query searching for “*Erica*” (11.05.2023, GBIF.org 2023) which delivered 801,625 records. We removed occurrences outside the native range of the genus and then processed the data using the “CoordinateCleaner v. 2.0-20” R package (for details see: “GBIF_occurence_cleaning_Erica_2023-05-16.R”), filtering by CoordinateCleaner::clean_coordinates with tests = c(“capitals”, “centroids”, “equal”, “gbif”, “institutions”, “seas”, “zeros”). We retained many records from South Africa represented by centroids of quarter degree squares (QDS, equivalent to a grid of ca. 25 km × 27 km) which matched the precision of additional distribution data available from the Genus *Erica* Interactive Identification Key (Oliver et al. 2024). We renamed records as necessary, based on accepted names and synonymy derived from WFO (Elliot et al. 2024) as of May 2023 (Suppl. material 4). Combination resulted in a global dataset of *Erica* with 659,696 occurrence records. A summary of numbers of records per taxon and a presence/absence matrix for taxa per QDS across the total distribution of the genus is presented in Suppl. material 5.

EDGE priority list

We used the Evolutionarily Distinct and Globally Endangered (EDGE) approach as described in Gumbs et al. (2023). Though EDGE is typically calculated across large clades of species related at the class-level, it can be applied to smaller monophyletic groups where there is interest in maintaining a group's phylogenetic diversity. We therefore used the approach with the set of 100 dated phylogenetic trees (see above) and the most recent conservation assessments for *Erica* species (Raimondo et al. 2009) to produce an *Erica*-specific EDGE species priority list. Given that the approach requires a complete species level tree, species for which DNA sequence data were not available and, thus, were missing in the tree, were added to the tree using the function addTaxa from the R package addTaxa (Mast et al. 2015; https://github.com/eliotmiller/addTaxa), which binds the missing species to a randomly-selected close relative. Here, we assigned the European species to one of five lineages, based on current and previous results (Mugrabi de Kuppler et al. 2015), while, within the single African clade comprising the rest of the diversity of the genus, we assigned species to clades following the strong geographic patterns uncovered by Pirie et al. (2019). All Cape species sampled to date in phylogenetic analyses are found within a single clade comprising exclusively Cape species. We assumed that all unsampled Cape species will be assigned to this Cape clade. The other African and Madagascan species belong to an "Afrotemperate" clade, with the exceptions of *E. arborea* L. (widespread, but grouped with the European *E. lusitanica* Rudolph in the "ARB" clade), the subspecies of *E. trimera* (Engl.) Beentje ("TRIM" clade) and the subspecies of *E. kingaensis* Engl. ("KIN" clade). The imputation step was replicated on all 100 ultrametric trees to take into account the phylogenetic uncertainty associated with both the reconstruction process and the imputation of missing species.

We computed EDGE scores for all species of *Erica* using the EDGE2 protocol (Gumbs et al. 2023), once for each of the 100 dated complete species-level trees (i.e. including imputed missing species). We took into account uncertainty in the probability of extinction by sampling a distribution of extinction probability, based on the Red List category of a species (see Gumbs et al. (2023) for details). Extinct species are assigned a probability of extinction of 1.0 and extinction probabilities are sampled across the distribution for DD and NE species. Of the 1,048 taxa recognised here (combining assessments from Raimondo et al. (2009) and IUCN (2023)), 51 are Critically Endangered (CR), 62 are Endangered (EN), 86 are Vulnerable (VU), nine are Near Threatened (NT), 562 are Least Concerned (LC), four are Extinct (EX) and 274 are either Data Deficient (DD) or Not Evaluated (NE). These analyses result in 100 EDGE scores for each species, obtained from the 100 trees. A species is considered an EDGE species if it is both threatened and has an EDGE score above the median EDGE score for all species in at least 95% of the iterations (i.e. trees; Gumbs et al. (2023)).

We also produced a list of species that have an EDGE score above the median in 95% of the iterations, but which are either DD or NE; this list is referred to as the EDGE Research list by Gumbs et al. (2023).

We also explored spatial phylogenetic patterns of species richness and phylogenetic diversity. We compiled taxon richness and EDGE taxon richness values for each quarter degree square (QDS) where *Erica* species are found. In addition, we also calculated the phylogenetic diversity (Faith 1992) and the expected PD loss for each QDS. Phylogenetic diversity is the sum of all branches linking a set of terminals on a phylogenetic tree, while expected PD loss is the amount of evolutionary diversity that is at risk of extinction given the probability of extinction associated with each terminal. Phylogenetic diversity was calculated for each QDS by pruning the dated trees (i.e. set of 100 dated trees used for species prioritisation; see above) so that they were reduced to only the terminals found within a given QDS. PD was then compiled by summing the branch length of the pruned trees. The same approach was used to compile expected PD loss, but this time using the extinction-risk weighted trees produced by the EDGE score compilation (Gumbs et al. 2023). Median values from the 100 trees were compiled and mapped.

Results

DNA sequencing and alignment

Alignment of DNA sequences was generally unambiguous, except for patterns of length variation in the *trnT-L* spacer for which several positions of the alignment were problematic and excluded from analyses (1–27, 111–150, 212–224, 342–665, 672–877, 984–1012, 1097–1107, 1150–1182, 1279–1360, 1462–1491, 2031–2049, 2139–2155, 2399–2437); three shorter regions in ETS (1–15, 784–811, 1023–1178) were also excluded.

For four taxa (*E. banksii* var. *banksii* EO12873, *E. caffra* MP655, *E. filago* BG68 and *E. insignis* [= *E. adelopetala*] MP1290), we failed to obtain plastid data, but chose to include them in the analyses, based on nrDNA only. nrDNA sequences of a small number of taxa consistently showed polymorphism indicating multiple copies were present and the resulting consensus would incorporate paralogy (*Erica articularis* L., *E. glabella* Thunb. ssp. *glabella*, *E. longipedunculata* G.Lodd., *E. macowanii* ssp. *lanceolata* (Bolus) E.G.H.Oliv. & I.M.Oliv., *E. paucifolia* ssp. *squarrosa* (Benth.) E.G.H.Oliv., *E. petraea* Benth., *E. schlechteri* Bolus, *E. seriphiifolia* Salisb., *E. syngenesia* Compton, *E. tenuifolia* L., *E. venustiflora* E.G.H.Oliv. ssp. *venustiflora* and *E. viscosissima* E.G.H.Oliv.). These were excluded. Matrices of concatenated cpDNA and nrDNA represented 726 and 730 accessions, respectively. Sequence matrices are presented in Suppl. material 6.

Phylogenetic tree inference

Analyses of individual cpDNA markers showed no supported topological conflicts, so we concatenated the data in a single cpDNA supermatrix. The two nrDNA markers also showed consistent results. The resulting cpDNA and nrDNA phylogenetic trees are presented in Suppl. material 7 and all data are archived at TreeBase (study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S30617). By comparing cpDNA and nrDNA gene trees, we identified 22 taxa with conflicting positions with bootstrap support ≥ 70%, including four that represented common patterns of conflict shared by different accessions of the same taxon (3.4% of the taxa analysed). One involved the European species *E. lusitanica* (both accessions f_ANA and PJ) that is sister to European clades EUR4/EUR5 (cpDNA) and to *E. arborea* (ARB; nrDNA). One accession of *E. woodii* Bolus (RC513) and one of *E. flanaganii* Bolus (MP631) represented conflicts within the Afrotemperate clade. The remaining 17 phylogenetic conflicts were located within the Cape clade: *E. collina* Guthrie & Bolus (EO12613), *E. conferta* Andrews (MP887), *E. cruenta* Aiton (MP745 and MP999), *E. elimensis* L.Bolus (EO12843), *E. equisetifolia* Salisb. (ANA), *E. eugenea* Dulfer (EO12485), *E. fairii* Bolus (CM12), *E. grisbrookii* Guthrie & Bolus (EO12716), *E. intervallaris* Salisb. (MP556), *E. mollis* Andrews (CM5), *E. monadelphia* Andrews (FO2), *E. peziza* G.Lodd. [= *E. nivalis* Andrews] (MP719), *E. phillipsii* L.Bolus (MP1357), *E. recurvata* Andrews (EO12467), *E. rhopalantha* Dulfer (MP909), *E. stokoei* L.Bolus (MP825) and *E. turgida* Salisb. (S1962). After dividing these into separate cpDNA and nrDNA taxa, the combined supermatrix included 752 taxa. The resulting (multil-abelled) phylogenetic tree shows the same major geographically defined clades discovered in previous analyses, with newly-added accessions of Cape and Afrotemperate species consistently placed in Cape and TEA clades, respectively. The ML tree with summarised bootstrap support is presented in Suppl. material 7, along with both the single ML tree rate-smoothed under PL (represented in Fig. 1) and a sample of 100 rate-smoothed trees derived from bootstrap resampled data.

EDGE analyses

Within *Erica*, 149 Ma of evolutionary history is at risk, of a total of 804 Ma (18%) represented by the genus. Thirty-nine species were identified as EDGE species (Table 1, Fig. 1) and 34 species are found on the EDGE Research list (Table 2).

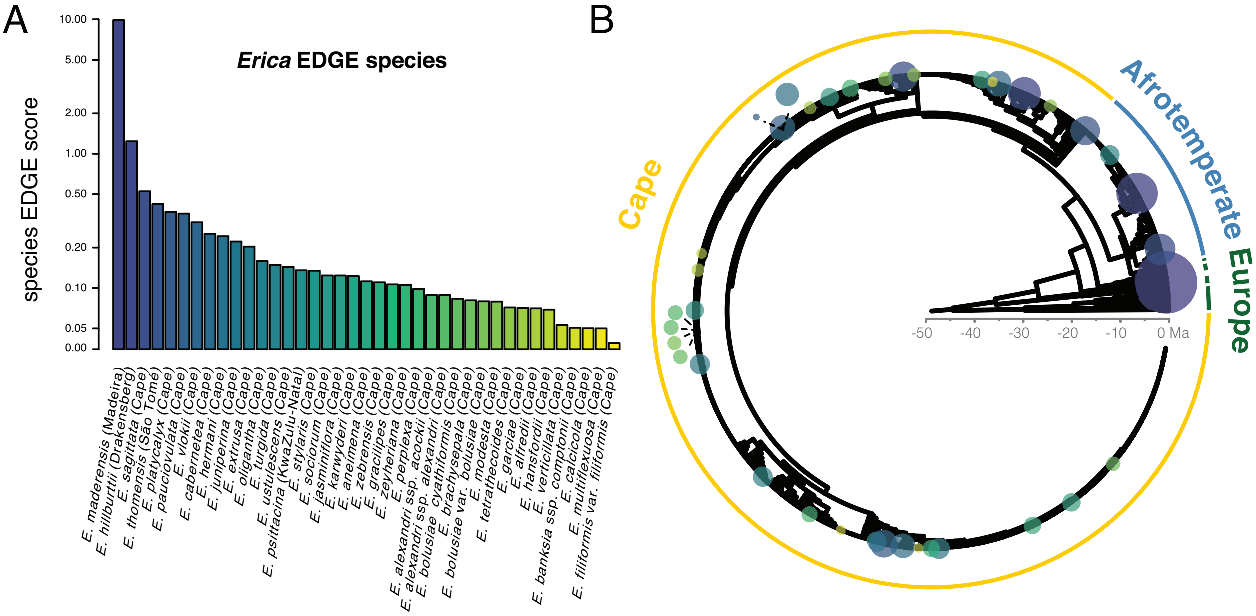

Figure 1. *Erica* EDGE species ranked by EDGE score (**A**) and indicated on the *Erica* phylogenetic tree (**B**; tree 69 of the 100 complete species level trees with missing taxa imputed) by circles coloured and size-scaled according to species EDGE scores. Scores are given in natural logarithmic scale..

Table 1. *Erica* EDGE Species: the list of 39 EDGE Species of *Erica* (ranked by median EDGE score). These are species which have an EDGE score above the median in at least 95% of the iterations (trees) and that are threatened. Note that DD/NE are excluded from this list. This follows the definition of EDGE Species in Gumbs et al. (2023). Clade: *Erica* clade to which a species is assigned (see text); Rank: overall EDGE rank; above.med: number of iterations in which the EDGE score of this species is above the median EDGE scores of all species; ED.med: median ED score from 100 trees; EDGE.med: median EDGE score from 100 trees; TBL.med: median terminal branch length from 100 trees; TBL%: percentage of ED attributed to the terminal branch length (rounded to the nearest decimal); RL.cat: IUCN Red List category.

Clade	Species	Overall EDGE rank	above. median_total	ED.med	EDGE.med	TBL.med	TBL%	RL.cat
EUR4	*E. maderensis* (Benth.) Bornm.	1	100	10.5439	9.8898	10.0860	95.7%	CR
TEA	*E. hillburttii* (E.G.H.Oliv.) E.G.H.Oliv.	14	99	1.4121	1.2389	1.1702	82.9%	CR
CAPE	*E. sagittata* Klotzsch ex Benth.	31	100	1.0621	0.5252	0.9217	86.8%	EN
TEA	*E. thomensis* (Henriq.) Dorr & E.G.H.Oliv.	36	98	0.4975	0.4214	0.3944	79.3%	CR
CAPE	*E. platycalyx* E.G.H.Oliv.	38	100	0.7239	0.3693	0.7209	99.6%	EN
CAPE	*E. pauciovulata* H.A.Baker	39	100	1.5021	0.3584	1.3918	92.7%	VU
CAPE	*E. vlokii* E.G.H.Oliv.	41	100	1.3418	0.3085	1.2818	95.5%	VU
CAPE	*E. cabernetea* E.G.H.Oliv.	45	99	0.2715	0.2536	0.1320	48.6%	CR
CAPE	*E. hermani* E.G.H.Oliv.	47	100	0.5207	0.2429	0.5088	97.7%	EN
CAPE	*E. juniperina* E.G.H.Oliv.	49	97	0.4950	0.2220	0.4901	99.0%	EN
CAPE	*E. extrusa* Compton	52	100	0.2396	0.2034	0.1284	53.6%	CR
CAPE	*E. oligantha* Guthrie & Bolus	56	100	0.3145	0.1584	0.2872	91.3%	EN
CAPE	*E. turgida* Salisb.	58	97	0.1680	0.1488	0.1640	97.6%	CR
CAPE	*E. ustulescens* Guthrie & Bolus	60	99	0.1621	0.1437	0.1504	92.8%	CR
TEA	*E. psittacina* E.G.H.Oliv. & I.M.Oliv.	61	95	0.2651	0.1354	0.2091	78.9%	EN
CAPE	*E. stylaris* Spreng.	62	99	0.5635	0.1346	0.5507	97.7%	VU
CAPE	*E. sociorum* L.Bolus	64	98	0.1417	0.1240	0.1339	94.5%	CR
CAPE	*E. jasminiflora* Salisb.	65	100	0.1349	0.1240	0.1349	100.0%	CR
CAPE	*E. karwyderi* E.G.H.Oliv.	66	97	0.1244	0.1226	0.1172	94.2%	CR
CAPE	*E. aneimena* Dulfer	69	98	0.4616	0.1121	0.4415	95.7%	VU
CAPE	*E. zebrensis* Compton	70	99	0.2545	0.1102	0.2360	92.7%	EN
CAPE	*E. gracilipes* Guthrie & Bolus	71	98	0.1185	0.1064	0.1182	99.7%	CR
CAPE	*E. zeyheriana* (Klotzsch) E.G.H.Oliv.	72	98	0.4618	0.1056	0.4579	99.2%	VU
CAPE	*E. perplexa* E.G.H.Oliv.	78	98	0.1079	0.0984	0.1079	100.0%	CR
CAPE	*E. alexandri* ssp. *acockii* (Compton) E.G.H.Oliv. & I.M.Oliv.	82	99	0.0885	0.0885	0.0336	37.9%	EX
CAPE	*E. alexandri* Guthrie & Bolus ssp. *alexandri*	83	99	0.0952	0.0885	0.0336	35.3%	CR
CAPE	*E. bolusiae* var. *cyathiformis* H.A.Baker	86	97	0.0858	0.0832	0.0325	37.9%	CR
CAPE	*E. brachysepala* Guthrie & Bolus	87	97	0.1683	0.0809	0.1641	97.5%	EN
CAPE	*E. bolusiae* T.M.Salter var. *bolusiae*	89	96	0.0888	0.0795	0.0325	36.6%	CR
CAPE	*E. modesta* Salisb.	90	95	0.1446	0.0792	0.1366	94.5%	EN
CAPE	*E. tetrathecoides* Benth.	95	98	0.3047	0.0716	0.2899	95.1%	VU
CAPE	*E. garciae* E.G.H.Oliv.	97	98	0.2728	0.0711	0.2587	94.9%	VU
CAPE	*E. alfredii* Guthrie & Bolus	99	99	0.2807	0.0705	0.2712	96.6%	VU
CAPE	*E. hansfordii* E.G.H.Oliv.	101	96	0.0781	0.0690	0.0767	98.2%	CR
CAPE	*E. verticillata* P.J.Bergius	120	95	0.0591	0.0530	0.0504	85.2%	CR
CAPE	*E. banksia* ssp. *comptonii* (T.M.Salter) E.G.H.Oliv. & I.M.Oliv.	125	97	0.1017	0.0506	0.0911	89.5%	EN
CAPE	*E. calcicola* (E.G.H.Oliv.) E.G.H.Oliv.	126	96	0.0981	0.0501	0.0979	99.8%	EN
CAPE	*E. multiflexuosa* E.G.H.Oliv.	127	95	0.2133	0.0500	0.1925	90.3%	VU
CAPE	*E. filiformis* Salisb. var. *filiformis*	163	97	0.1723	0.0388	0.1215	70.5%	VU

Table 2. EDGE Research List: the list of 34 species (ranked by median EDGE score) which have an EDGE score above the median, but which are of status data deficient or not evaluated (DD/NE). Gumbs et al. (2023) identify such species as part of the EDGE Research List. Column names as in Table 1.

Clade	Species	Overall EDGE rank	above. median_total	ED.med	EDGE. med	TBL. med	TBL%
EUR1	*E. spiculifolia* Salisb.	2	100	24.0947	5.2325	23.8520	99.0%
EUR2	*E. sicula* ssp. *bocquetii* (Peșmen) E.C.Nelson	3	100	21.3982	5.1615	17.1120	80.0%
EUR5	*E. australis* L.	4	100	17.6798	4.8616	17.6798	100.0%
EUR2	*E. sicula* Guss. ssp. *sicula*	5	100	21.7980	4.4735	17.1120	78.5%
EUR3	*E. umbellata* L.	6	100	15.8209	3.4070	15.4362	97.6%
EUR1	*E. carnea* L.	7	100	11.7892	2.7542	9.8654	83.7%
EUR1	*E. ciliaris* L.	8	100	14.7178	2.6840	14.6815	99.8%
EUR1	*E. erigena* R.Ross	9	100	10.8225	2.6388	9.8462	91.0%
EUR1	*E. terminalis* Salisb.	10	100	9.9058	2.5128	8.6242	87.1%
EUR1	*E. multiflora* L.	11	100	8.1951	2.1022	7.6223	93.0%
EUR1	*E. tetralix* L.	12	100	9.9433	1.7605	9.9058	99.6%
EUR1	*E. numidica* (Maire) Romo & Borat.	13	100	6.1181	1.3575	4.6816	76.5%
EUR1	*E. manipuliflora* Salisb.	16	100	3.9974	0.9240	3.9458	98.7%
KIN	*E. kingaensis* ssp. *bequaertii* (De Wild.) R.Ross	17	97	2.7247	0.7081	1.8967	69.6%
TEA	*E. caffrorum* var. *luxurians* Bolus	19	98	2.4957	0.6172	1.8676	74.8%
EUR1	*E. platycodon* (Webb & Berthel.) Rivas Mart., Capelo, J.C.Costa, Lousã, Fontinha, R.Jardim & M.Seq. ssp. *platycodon*	20	98	2.3410	0.6104	1.5741	67.2%
TRIM	*E. trimera* ssp. *meruensis* (R.Ross) Dorr	21	99	2.3811	0.6100	1.9316	81.1%
KIN	*E. kingaensis* Engl. ssp. *kingaensis*	22	95	2.7433	0.6032	2.0653	75.3%
TRIM	*E. trimera* ssp. *keniensis* (S.Moore) Beentje	23	100	2.6154	0.5944	2.2616	86.5%
TRIM	*E. trimera* ssp. *kilimanjarica* (Hedberg) Beentje	25	99	2.3724	0.5911	1.6678	70.3%
TRIM	*E. trimera* ssp. *abyssinica* (Pic.Serm. & Heiniger) Dorr	26	98	2.4190	0.5707	1.7166	71.0%
TRIM	*E. trimera* (Engl.) Beentje ssp. *trimera*	27	100	2.3415	0.5696	2.0926	89.4%
EUR1	*E. scoparia* L.	28	100	2.0276	0.5475	1.6054	79.2%
EUR1	*E. platycodon* ssp. *maderincola* (D.C.McClint.) Rivas Mart., Capelo, J.C.Costa, Lousã, Fontinha, R.Jardim & M.Seq.	29	98	2.5841	0.5337	1.9248	74.5%
TEA	*E. drakensbergensis* Guthrie & Bolus	30	96	1.8822	0.5262	1.3220	70.2%
TEA	**E. caffrorum* Bolus var. *caffrorum*	32	97	2.7462	0.4863	1.8676	68.0%
EUR1	*E. azorica* Hochst. ex Seub.	33	98	2.0295	0.4502	1.5852	78.1%
TEA	*E. mauritiensis* E.G.H.Oliv.	34	98	1.9370	0.4382	1.8783	97.0%
TRIM	*E. trimera* ssp. *elgonensis* (Mildbr.) Beentje	35	96	2.1595	0.4377	1.8427	85.3%
TEA	*E. whyteana* Britten	37	95	1.9573	0.3727	1.7905	91.5%
TEA	*E. microdonta* (C.H.Wright) E.G.H.Oliv.	48	95	1.3526	0.2370	1.2561	92.9%
TEA	*E. galioides* Lam.	50	95	1.0123	0.2097	0.7480	73.9%
CAPE	*E. orientalis* R.A.Dyer	74	96	0.2856	0.1024	0.2723	95.3%
CAPE	*E. gibbosa* Klotzsch ex Benth.	79	95	0.4205	0.0981	0.4139	98.4%

*Threat status for *Erica caffrorum* ssp. *caffrorum* was mistakenly omitted: it has been assigned the LC category and, therefore, can be disregarded as a member of the Research list.

Priority areas

Mapping of taxon richness per QDS illustrates the disparity between the Cape Floristic Region and all other areas of the distribution (Fig. 2c), with taxon richness of 100 or more in 13 QDS between 33–34°S and 18–19°E in the Western Cape (Table 3). Geographical patterns of phylogenetic diversity (PD) and expected PD loss (i.e. the amount of evolutionary history expected to be lost give ex-

Table 3. Southern Hemisphere QDS that scored highest for taxon richness (≥ 100), PD (≥ 90), EDGE taxon richness (≥ 3) and expected PD loss, sorted by taxon richness. All are in the Western Cape; they are indicated by numbers in Fig. 3e. The QDS that scored highest overall for PD, in Galicia, northern Spain, is included for comparison. Numbers in bold indicate the highest value for each metric.

Fig. 3e	Name	QDS	X	Y	PD.med	ePDloss.med	Taxon richness	Edge richness
1	Somerset West	3418BB	18.875	-34.125	117.45	5.23	**188**	5
2	Stanford	3419AD	19.375	-34.375	111.80	4.96	162	4
3	Grabouw	3419AA	19.125	-34.125	105.29	4.27	150	**7**
4	Hermanus	3419AC	19.125	-34.375	105.35	4.46	139	5
5	Greyton	3419BA	19.625	-34.125	101.18	3.24	130	2
6	Franschhoek	3319CC	19.125	-33.875	102.44	2.69	127	3
7	Hangklip	3418BD	18.875	-34.375	100.17	2.92	126	3
8	Cape Peninsula	3418AB	18.375	-34.125	96.69	2.72	113	3
9	Ceres	3319AD	19.375	-33.375	96.31	1.39	111	0
10	Jongensklip	3419BC	19.625	-34.375	96.37	3.50	110	3
11	Caledon	3419AB	19.375	-34.125	95.17	2.59	103	5
12	Bain’s Kloof	3319CA	19.125	-33.625	86.06	1.78	100	2
13	Elim	3419DB	19.875	-34.625	84.92	2.26	100	3
14	Riviersonderend	3419BB	19.875	-34.125	90.90	2.44	97	2
15	Langvlei	3319DC	19.625	-33.875	90.05	1.62	96	1
16	Villiersdorp	3319CD	19.375	-33.875	96.33	2.19	95	1
17	Baardskeerdersbos	3419DA	19.625	-34.625	75.88	2.05	86	4
18	Stellenbosch	3318DD	18.875	-33.875	**143.43**	5.36	82	1
19	George	3322CD	22.375	-33.875	96.87	2.32	80	4
20	Jonkersberg	3322CC	22.125	-33.875	94.99	2.43	77	5
21	Napier	3419BD	19.875	-34.375	66.13	1.92	62	3
-	Galicia, Spain	-	-7.875	43.125	**219.96**	**29.19**	11	0

tinction of taxa) are similar to each other and highest overall around the Atlantic coast of the Iberian Peninsula, whilst, in the Southern Hemisphere, they are highest in the Cape within the region of top taxon diversity. Cape PD peaks in the ‘Stellenbosch’ QDS, followed by ‘Somerset West’ and ‘Stanford’ (Table 3; Fig. 3a). Within the Cape Region, there is overlap between area PD and EDGE taxon richness (both high in "Somerset West"; Fig. 3), but no obvious link: the QDS with high EDGE taxon richness correspond to different QDS within the Overberg region ("Grabouw", followed by "Hermanus" and "Caledon") with a more distant regional peak ("Jonkersberg") in the eastern Langeberg. "Stellenbosch", with highest PD and taxon richness, scores lowest in terms of EDGE taxon richness (Table 3).

Discussion

Inverted patterns of taxon richness and phylogenetic diversity in *Erica*

Summarising taxon richness, phylogenetic diversity and EDGE taxon richness reveals stark contrasts across the distribution of *Erica*. Whilst Cape *Erica* species greatly outnumber those from other regions, the Cape clade is no older than the other African *Erica* clades and considerably younger than the European ones (Pirie et al. 2016): the species are, on average, much more closely related, individually representing less unique phylogenetic diversity. In plants, in general, local species radiations contribute to regional disparities in species richness

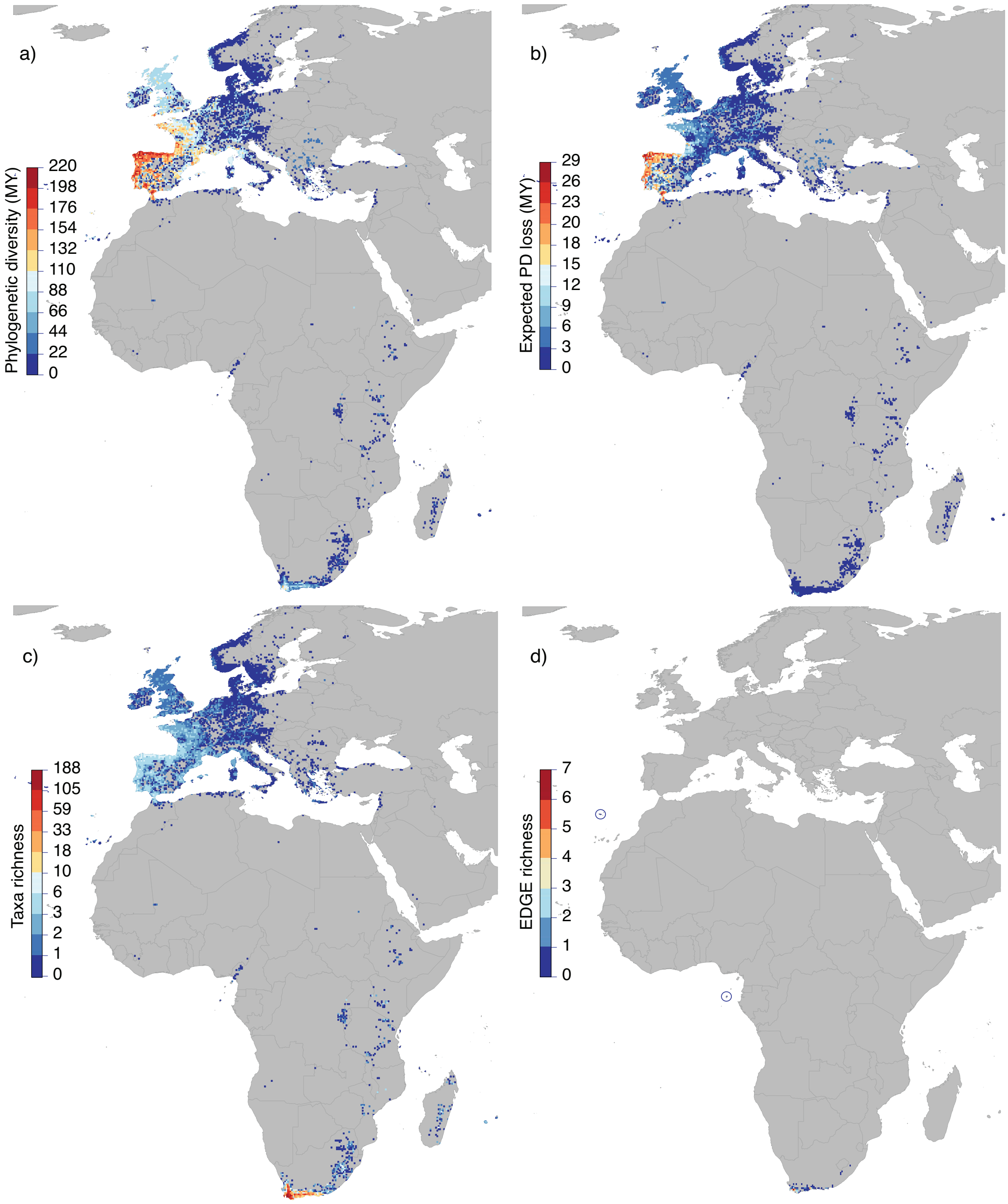

Figure 2. Global distribution of *Erica*: **a** phylogenetic diversity (PD; in millions of year, MY) **b** expected PD loss (in millions of year, MY) **c** taxon richness; and **d** EDGE species richness. Note: the only EDGE species found outside of South Africa are *E. maderensis* from Madeira and *E. thomensis* from São Tomé and Príncipe; these islands are circled in map **d**) (upper left and centre, respectively).

that tend to be greater than the corresponding differences in PD (Tietje et al. 2023). The rapid radiation in Cape *Erica* (Pirie et al. 2016) results in an inversion of the disparity at the QDS level: taxon richness is lowest and PD highest in Europe, whilst the by far highest taxon richness found in the Cape (Oliver et al. 1983) is only reflected in moderate to low PD (Fig. 2).

Oliver et al. (1983) analysed patterns of taxon richness across the whole Cape flora. As the largest genus in the CFR, *Erica* data contributed significantly to the results of the Oliver et al. (1983) analysis. It is, therefore, perhaps unsurprising

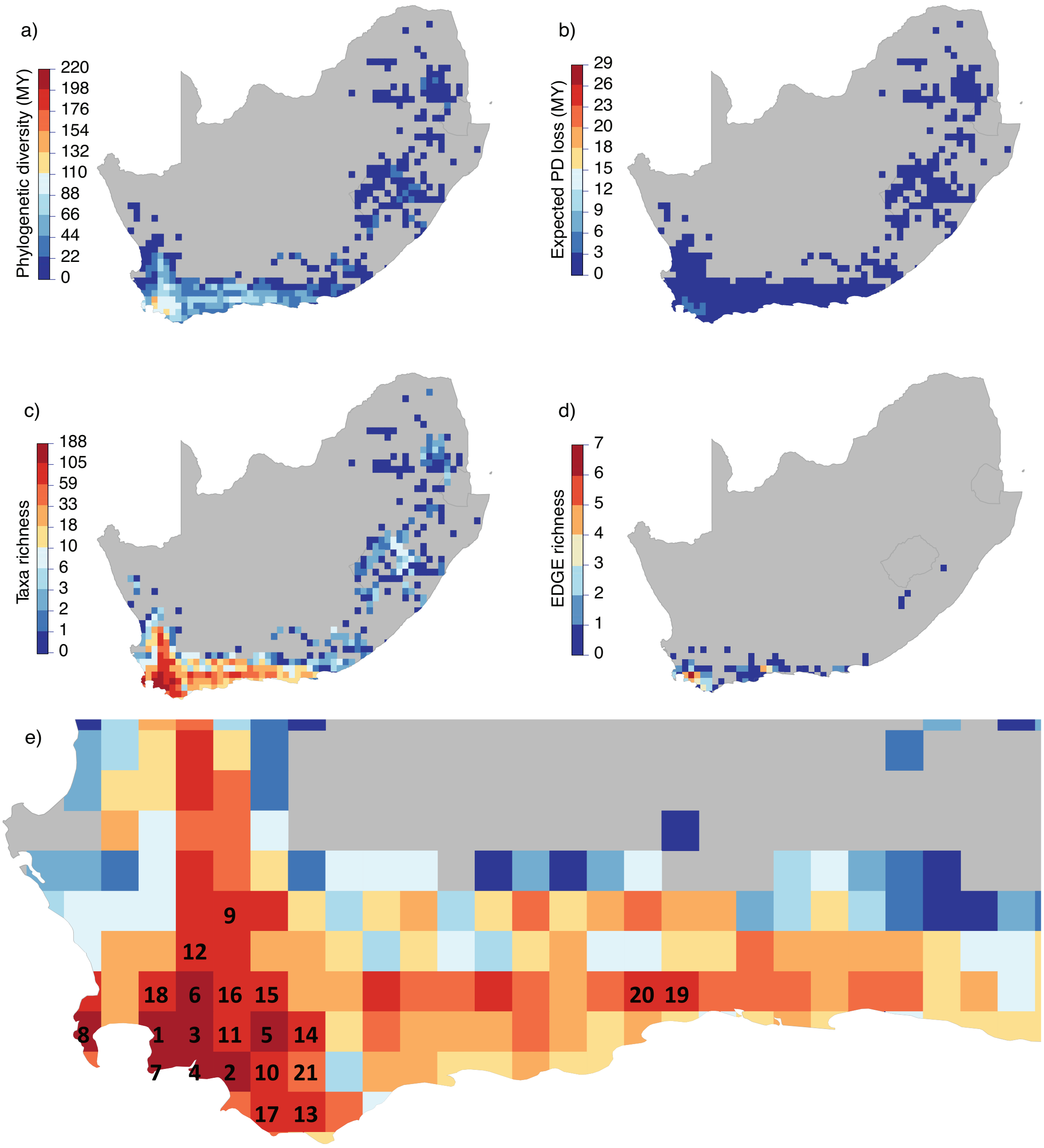

Figure 3. South African distribution of *Erica* **a** phylogenetic Diversity (PD) **b** expected PD loss **c** taxon richness; and **d** EDGE species richness. The scales follow those presented in Fig. 2 at the global level (i.e. from zero to the global maximum). In **e** the highest scoring Quarter Degree Squares (QDS) for taxon richness in the region are numbered following Table 3 (colour coding as per c).

that the QDS that they identified as having the highest taxon richness, 'Somerset West' (3418BB; which includes a fynbos-rich mountainous region straddling both the northern part of the Kogelberg Biosphere Reserve and southern end of the Hottentots Holland Nature Reserve), also harbours the highest taxon richness of *Erica* in data analysed here. Taxon richness decreases towards the east and north from this peak in the south-western corner of the Western Cape, both for *Erica* and for plants in general (Levyns 1964; Goldblatt 1978; Linder 2003; Forest et al. 2007; Colville et al. 2020), a pattern that was referred to as "Levyns' Law" by Cowling et al. (2017). Explanations for the causes of high species richness in the SW Cape include lower extinction rates of seeder lineages concentrated in this area of winter rainfall (Cowling et al. 2018). The highest *Erica* PD in the Cape is found in 'Stellenbosch' (3318DD), adjacent to 'Somerset West' and PD roughly tracks taxon richness regionally. The epicentre of *Erica* PD in the Cape is, therefore, found within a much smaller total area than European peak PD around the Atlantic coast of the Iberian Peninsula, where it is represented by a relatively homogenous suite of distantly related, mostly widespread taxa. For comparisons of PD and associated metrics within regions such as the Cape, it may be important to take into account the impact of such disparities between regions. For example, a similar analysis within the Cape clade only would most likely reveal EDGE species from this region that are not identified in the global analysis.

The relationship between taxon richness, PD and EDGE taxon richness is not direct: the richest areas do not necessarily include much threatened PD. This is abundantly clear when comparing Europe to other areas, but also the case when comparing within the Cape. Although the highest EDGE score in the Cape, in 'Grabouw' (3419AA), is also in the hyper-diverse south-west, we identified one area further east that also shows amongst the highest values for EDGE taxon richness ('Jonkersberg', 3322CC). Individual *Erica* taxa are often narrowly endemic within the Cape, resulting in a rapid geographic turnover of species assemblages. Since threat status of taxa is in part dependent on the conservation status of habitats (threatened taxa tend to be local endemics that are not in protected areas), high regional EDGE scores may reflect a local shortfall in coverage of endemic taxa by protected areas and, hence, point to a need for conservation action outside the most obviously diverse regions.

Threat assessments and alpha taxonomy needed to identify more EDGE species

Despite its lower overall PD, South Africa's Cape clade still comprises most of the *Erica* taxa identified as EDGE species. Of 1048 *Erica* taxa, we identified 39 EDGE species, i.e. taxa known to be threatened and scoring above median EDGE values for the genus in 95% or more of the iterations (i.e. trees). All but four are members of the Cape clade. The only EDGE species found outside of the Cape Region are the critically endangered *E. maderensis* (Benth.) Bornm. found only on Madeira, *E. thomensis* (Henriq.) Dorr & E.G.H.Oliv. endemic to São Tomé and Príncipe and *E. hillburttii* (E.G.H.Oliv.) E.G.H.Oliv. from the north-eastern Eastern Cape and *E. psittacina* E.G.H.Oliv. & I.M.Oliv. found in adjacent KwaZulu-Natal.

Several gaps in fundamental knowledge can be assumed to have depressed both the number of *Erica* EDGE species and regional EDGE taxon richness values, particularly with regard to wider African and Madagascan species diversity. A particular challenge is the lack of threat assessments for 274 taxa within *Erica*.

Worldwide, both Madagascar and South Africa have amongst the highest numbers of species that are unassessed, but predicted to be threatened (Bachman et al. 2023). In South Africa, the proportion of taxa that have been assessed is high (87%) compared with other regions of high endemism such as Mexico or Brazil (24% and 28%, respectively; Gallagher (2023)). In total, 190 of 944 South African *Erica* taxa are known to be threatened (VU, EN or CR; Raimondo et al. (2009)). This is lower than the global figure of 39% cited by Nic Lughadha et al. (2020), but the *Erica* numbers do not include the over 100 taxa classified as 'rare' by SANBI, nor, importantly, the further 100 plus assessed as Data Deficient (DD) or Not Evaluated (NE). Many of these are also likely to be rare. Bachman et al. (2023) estimated that 69% of DD species are likely to be threatened, of which 86% with high certainty.

This important knowledge gap is reflected in the EDGE research list, comprising taxa that have an EDGE score above the median in more than 95% of trees, but that are either DD or NE. This list includes a very different suite of taxa, predominantly representatives of the minority, non-Cape clades. Not all of these are of immediate concern: the widespread European species of *Erica*, while not formally assessed, are unlikely to be threatened. However, there are narrowly distributed species, such as the endemic Iberian *E. andevalensis* Cabezudo & J.Rivera and *E. mackayana* Bab. (Rodríguez-Buján et al. 2024), which, as close sister species, are mutually excluded from either EDGE or research lists, but may nevertheless be of concern. Those with restricted island and coastal Mediterranean distributions, such as taxa of the wind pollinated *E. scoparia* L. / *E. platycodon* (Webb & Berthel.) Rivas Mart., Capelo, J.C.Costa, Lousã, Fontinha, R.Jardim & M.Seq. complex and *E. sicula* complex, require assessment (Pasta et al. 2024). There is also regional variation, such as represented by *Erica numidica* (Maire) Romo & Borat. (Romo & Boratynski, 2010) which is currently included within the widespread *Erica cinerea* L. (Nelson, 2011), but would otherwise be considered threatened in its restricted range in Algeria (Hamel et al. 2021).

Formal assessments – even of common species – would be useful to confirm their status. Although the threat status of a substantial proportion of South African species has been assessed (including over 80% of Cape clade taxa), current figures were not updated within the last decade (Raimondo et al. 2009). In other regions across Africa and Madagascar with lower species richness, but generally higher phylogenetic diversity per species, there have been far fewer threat assessments (less than 25% of taxa outside the Cape clade).

Clearly, neither the EDGE List nor the EDGE research list can include undescribed species diversity. For Africa, Ondo et al. (2023) estimated that the greatest shortfall in plant species remaining to be described and geolocated were in Madagascar and Cape Provinces - i.e. centres of *Erica* diversity - and that species with small geographic ranges were more likely to remain undescribed. The shortfall for the poorly-understood Madagascan taxa is known (Dorr, in prep.) and even the better-known South African flora includes numerous putative undescribed species, often local endemics (Hoekstra et al., in prep.), as well as diversity within species complexes potentially under-represented by formal taxa (Pirie et al. 2017; Musker et al. 2023). These also lack formal threat status and are not taken into account in our overviews of diversity and endemism. Such undescribed and range-restricted species are more likely to be threatened (Brown et al. 2023).

Improving the phylogenetic hypothesis for *Erica*

The phylogenetic hypothesis presented here represents a further improvement on previous work (McGuire and Kron 2005; Pirie et al. 2011, 2016; Mugrabi de Kuppler et al. 2015), including more species, improved resolution and one further nrDNA sequence marker to validate results based on ITS. The phylogenetic tree has already been used for the inference of ancestral wood anatomy within *Erica* (Akinlabi et al. 2023) and as a means to control for phylogenetic signal in analyses of the impact of flower colour on nectar robbing (Coetzee et al., in prep.). It will also be an important tool for identifying and testing the closest relatives of undescribed species diversity (Hoekstra et al., in prep.). However, there is still a substantial shortfall in representation of species and their genomes and in phylogenetic resolution.

Despite our clade-based inclusion of taxa not being represented in the phylogenetic tree, in almost all cases, these will fail to feature on EDGE lists until their precise relationships are known. The subspecies of *E. trimera* and of *E. kingaensis* are exceptions, featuring on the EDGE research list due to the isolated positions of these species in the African *Erica* clade. The *E. trimera* subspecies are closely related according to the results of Gizaw et al. (2013), but we are unable to confirm this for the subspecies of *E. kingaensis* due to the lack of equivalent data. All the subspecific taxa of a species were grouped together by the imputation approach if they were not already included in the phylogenetic tree. Even where we have DNA sequence data, the remaining (and considerable) phylogenetic uncertainty within the Cape clade will serve to average out the diversity of individual taxa where they are not placed with confidence and will, therefore, also likely depress the number of EDGE species.

Given these factors, the current EDGE list for *Erica* must be viewed as a conservative underestimate, to aid focusing research and conservation priorities, but not to the exclusion of action where data are incomplete.

Future research

Successful targeting and implementation of conservation efforts, both in-situ and ex-situ, require improved understanding of taxonomy, species boundaries, distributions, genetic diversity, morphology, ecology and threat levels. By providing the current phylogenetic resources (e.g. data, protocols, Musker et al., in prep.) and tools to aid effective identification of species (Oliver et al. 2024), we can improve both phylogenetic and alpha taxonomic knowledge. Gathering sequence data for putative undescribed or cryptic diversity (of species or subspecific taxa) may help identify closest relatives and focus diagnoses (Hoekstra et al., in prep.) or even assist in complex species delimitation challenges, particularly with high-throughput DNA sequencing approaches (Musker et al. 2023).

Updated and new threat assessments are needed and these results may help in prioritising work given limited resources. A potential route forward could be to use automated preliminary assessments to target DD and NE species that are likely to be threatened, whilst deprioritising those that can be assumed with confidence to be of least concern (Bachman et al. 2023). Such assessments are dependent on the available distribution data, which, given the concentration of PD in regions close to the City of Cape Town, would be important to audit for potential sampling bias and to target fieldwork.

Trends in habitat and population persistence are an important aspect of threat assessments. Areas subject to formal protection may be spared direct human-mediated habitat destruction, but will not necessarily be resilient to impact of invasive species, changes to the fire regime or climate change. Predictions for the Cape indicate both warming and decline in winter rainfall, with Lötter & Le Maitre (2014) predicting long term species extinctions of 23% in the fynbos biome. The likely impact, for example on high mountain versus lowland species of *Erica*, is still largely unclear. Analysing the genus *Thesium* in the CFR, Zhigila et al. (2023) used niche modelling to project past, current and future distributions and tested for phylogenetic signal in range size, niche specialisation and threat status. They concluded that species at greatest risk were not more closely related than might be expected by chance and that the range of some species would decrease whilst others increased under projected climatic conditions. This would seem to support conservation prioritisation based on EDGE in addition to a case-by-case assessment of the future prospects for individual species. Equivalent work would be highly valuable, despite the greater scale of the task, with the numerous species of *Erica*.

Conclusions

With an improved phylogenetic hypothesis and existing threat status assessments, we have identified 39 evolutionarily distinct and globally endangered (EDGE) taxa out of the over 1,000 currently recognised in the megagenus *Erica*. All but two EDGE taxa are from South Africa and all but four are endemic to the Cape Floristic Region. Using openly accessible distribution data, we were able to map taxon and phylogenetic diversity as well as EDGE taxon richness to regions of the *Erica* distribution. The results serve to highlight both particular threatened taxa and areas beyond the known centres of diversity and endemism as priorities for further research and conservation action. As widely recognised, such analyses are qualified by the grave limitations of our basic knowledge (Pollock et al. 2020). Ours represents a conservative underestimate of threatened *Erica* PD: an additional EDGE research list includes 34 evolutionarily distinct taxa for which threat status is unknown and substantial numbers of yet unsampled (and undescribed) taxa do not feature at all. This work will aid prioritisation of future research and conservation action, feeding directly into action through the Global Conservation Consortium for *Erica* (Pirie et al. 2022).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Fieldwork, collection of samples: MDP, EGHO, NMN, MK, JF, RB, DUB, BG, NCLM, EN, TvdN. Lab work: NCLM, RWB, MDP. Data analysis: FF, NMN, SP, MDP. Obtained funding: MDP, DUB. Drafted the ms: MDP. Edited the ms: all authors (except EGHO).

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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

Extended list of 1048 *Erica* species, subspecies and varieties used in the EDGE analyses

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl1

Supplementary material 2

Accessions table

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl2

Supplementary material 3

Google map of accessions

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: kmz

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl3

Supplementary material 4

Synonymy table used for parsing GBIF data

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: xlsx

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl4

Supplementary material 5

Presence/absence of taxa per QDS and numbers of QDS per taxon

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: zip

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl5

Supplementary material 6

DNA sequence alignments

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: zip

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl6

Supplementary material 7

Phylogenetic trees (cpDNA, nrDNA, combined)

Authors: Michael D. Pirie, Dirk U. Bellstedt, Roderick W. Bouman, Jaime Fagúndez, Berit Gehrke, Martha Kandziora, Nicholas C. Le Maitre, Seth Musker, Ethan Newman, Nicolai M. Nürk, E. G. H. Oliver, Sebastian Pipins, Timotheus van der Niet, Félix Forest

Data type: zip

Link: https://doi.org/10.3897/phytokeys.244.124565.suppl7

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Research Article

Notes on the genus *Syzygium* (Myrtaceae) from Cambodia, Thailand, Vietnam, China and Taiwan

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Abstract

Syzygium kampotense is a new species from Cambodia. *Syzygium cerasiforme*, *S. foxworthianum*, and *S. angkae* and *S. thorelii* are new records from Cambodia, Vietnam and China, respectively. *Syzygium prainianum* subsp. *minor* and *S. densinervium* var. *insulare* are placed under *S. prainianum* and *S. densinervium*, respectively. *Eugenia cochinchinensis*, *E. eburnea* and *E. ripicola*, are reduced to synonymy under *S. pellucidum*. Lectotypes for *Eugenia densiflora* var. *angustifolia*, *E. pellucida* and *E. pellucida* var. *contracta* are designated.

Key words: Lectotype, Myrtales, new record, new species, synonym, taxonomy

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Introduction

Syzygium Gaertn. is the largest genus in the family Myrtaceae and many species from allied genera, namely *Acmena* DC. and *Cleistocalyx* Blume, are now included in *Syzygium* based on molecular studies. Thus *Syzygium* currently comprises ca. 1,200–1,500 species (Biffin et al. 2006; Craven and Biffin 2010), the majority of which occur in the Old World tropics and subtropics (Biffin et al. 2006). A comprehensive revision of the genus in Thailand was published by Parnell and Chantaranothai (2002). Since then, the number of taxa recorded in Thailand has increased through the discovery of new species and new country records (Chantaranothai 2014; Soh and Parnell 2015; Chantaranothai et al. 2016; Tagane et al. 2018). Similar discoveries have been made in China (Chen and Craven 2007) and Indochina (Soh and Parnell 2015).

During my visits to herbaria in Asia and Europe between 2017 and 2023, many unidentified specimens of *Syzygium* from Thailand and neighbouring countries were examined. Material of an unidentified taxon from Cambodia was found to represent a species new to science, which is described below. Previously unidentified specimens of *S. cerasiforme* (Blume) Merr. & L.M.Perry from Cambodia, *S. foxworthianum* (Ridl.) Merr. & L.M.Perry from Vietnam, *S. angkae* (Craib) Chantar. & J.Parn. and *S. thorelii* (Gagnep.) Merr. & L.M.Perry from China are newly recorded. *Syzygium prainianum* (King) Chantar. & J.Parn. subsp. *mi-*

nor Chantar. & J.Parn. and *S. densinervium* (Merr.) Merr. var. *insulare* C.E.Chang are placed under *S. prainianum* and *S. densinervium*, respectively. *Eugenia cochinchinensis* Gagnep., *E. eburnea* Gagnep. and *E. ripicola* Craib (*S. ripicola* (Craib) Merr. & L.M.Perry) are reduced to synonymy under *S. pellucidum* (Duthie) N.P.Balakr. Lectotypes are designated for *E. densiflora* (Blume) Duthie var. *angustifolia* Ridl., *E. pellucida* Duthie and *E. pellucida* var. *contracta* Wall. ex Duthie.

Material and methods

This study is based on both herbarium and field collections in Thailand. Herbarium material was also consulted in the following herbaria: AAU, BK, BKF, BM, K, KKU, KYO, P and QBG (herbarium acronyms following Thiers, updated continuously). Specimens were examined with a binocular microscope and via digital images on the JSTOR website (https://plants.jstor.org/). An illustration of the new species was prepared.

Taxonomic treatment

Syzygium kampotense **Chantar., sp. nov.**

urn:lsid:ipni.org:names:77345020-1
Figs 1–3

Diagnosis. *Syzygium kampotense* resembles *S. championii* (Benth.) Merr. & L.M.Perry and *S. claviflorum* (Roxb.) Wall. ex Steud., in the clavate hypanthium shape, cuneate leaf base, small leaves and short petioles. The new species differs from both species in having thickly coriaceous leaves with strongly revolute leaf margins, an acute or obtuse leaf apex and fewer secondary veins (Fig. 1, Table 1).

Type. Cambodia: Kampot Province, Kampot District, southern summit of Phnom Bokor, vicinity of Bokor, 1–2 km NE of artificial on near Church toward Prek Kaoh Toch, 13 May 1997, *McDonal et al. 5676* (holotype AAU, isotype QBG).

Description. Shrub ca. 1 m tall; branching sparingly, bark corky, whitish grey or reddish. ***Leaves*** with petiole 2–3 mm long, wrinkled; lamina thickly coriaceous, 4–6.5 × 1.7– 3 cm, elliptic or elliptic-oblong, base broadly cuneate, apex acute or obtuse, margin strongly revolute; midrib impressed on the upper surface, rounded with sparse pustules on the lower surface; secondary veins in ca. 12 pairs, indistinct on upper surface and distinct on lower surface; intramarginal vein 1. ***Inflorescence*** not seen. ***Hypanthial cup*** 13–15 mm long, clavate. ***Pseudostipe*** absent. ***Sepals*** red 4, ca. 1 × 1.5 mm, triangular. ***Petals*** not seen. ***Stamens*** numerous, white. ***Ovary*** 2-locular, ca. 9 ovules per locule. ***Fruit*** purple, 8–10 mm in diameter, globose or ellipsoid, crowned with remnant of calyx lobes.

Distribution. Endemic to Cambodia.

Ecology. Dense sclerophyllous, short-tree forest, canopy 2–4 m tall, some emergent to 7 m tall; associates include *Ardisia*, *Lithocarpus*, *Elaeocarpus*, *Melastoma*, *Schima*, *Syzygium* and *Vaccinum*.

Conservation status. The species is only known from the type locality. It should be categorised as Critically endangered [CR, B1ab (iii)] according to the IUCN Red List Criteria and Categories version 3.1 (IUCN 2012). The Extent of Occurrence is estimated to be less than 20 km^2 and this species is found in a restricted area on open limestone hills which is a threatened ecosystem.

FLORA OF CAMBODIA

(Myrtaceae)

Syzygium

Kampot Province, Kampot District, southern summit of Phnom Bokor, vicinity of Bokor Village, 1-2 km NE of artificial pond near Church toward Prek Kaoh Toch.

Dense sclerophyllous, short-tree forest, canopy 2-4 m high, some emergents to 7 m; associates include *Ardisia*, *Lithocarpus*, *Elaeaocarpus*, *Melastoma*, *Schima*, *Syzygium* and *Vaccinium*.

Shrot shrub 1 m tall, branching sparingly, brak corky; calyx red, stamens numerous, white; fruit purple.

McDonald et al. 5676 13 May 1997

Figure 1. *Syzygium kampotense* Chantar.: holotype, *McDonal et al. 5676* (AAU). In set leaf, hypanthial cups and fruit. Photographed by B. Boonsuk.

Figure 2. *Syzygium kampotense* Chantar., showing leaf, hypanthial cups and fruit. Photographed by B. Boonsuk.

Table 1. Morphological comparison of *S. kampotense* and similar species.

Characters	*S. championii*	*S. claviflorum*	*S. kampotense*
Petiole (mm)	1.5–2	3–6	2–3
Leaf texture	coriaceous	chartaceous to coriaceous	thickly coriaceous
Leaf shape	elliptic to oblong	elliptic, ovate, sometimes obovate	elliptic or elliptic-oblong
Leaf size (cm)	4–8.5 × 1–4	6–10 (–22) × 1.5–3.5(–7.5)	4–6.5 × 1.7–3
Leaf base	cuneate, slightly attenuate	cuneate, slightly attenuate	broadly cuneate
Leaf apex	acuminate with acumen	mostly acute without acumen, sometimes acuminate with distinct acumen	acute or obtuse
Leaf margin	flat	flat	strongly revolute
Secondary veins (pairs)	25–30	15–30	ca 12
Hypanthium cup (mm)	10–13	5–10	13–15
Sepal (mm)	0.5 × 2	0.5–1 × 0.8–2.5	ca. 1 × 1.5
Fruit (mm)	oblongoid, clavate, 12.5 × 5	ellipsoid to obovoid, 1–15 × 5–9	globose or ellipsoid, 8–10 × 8–10

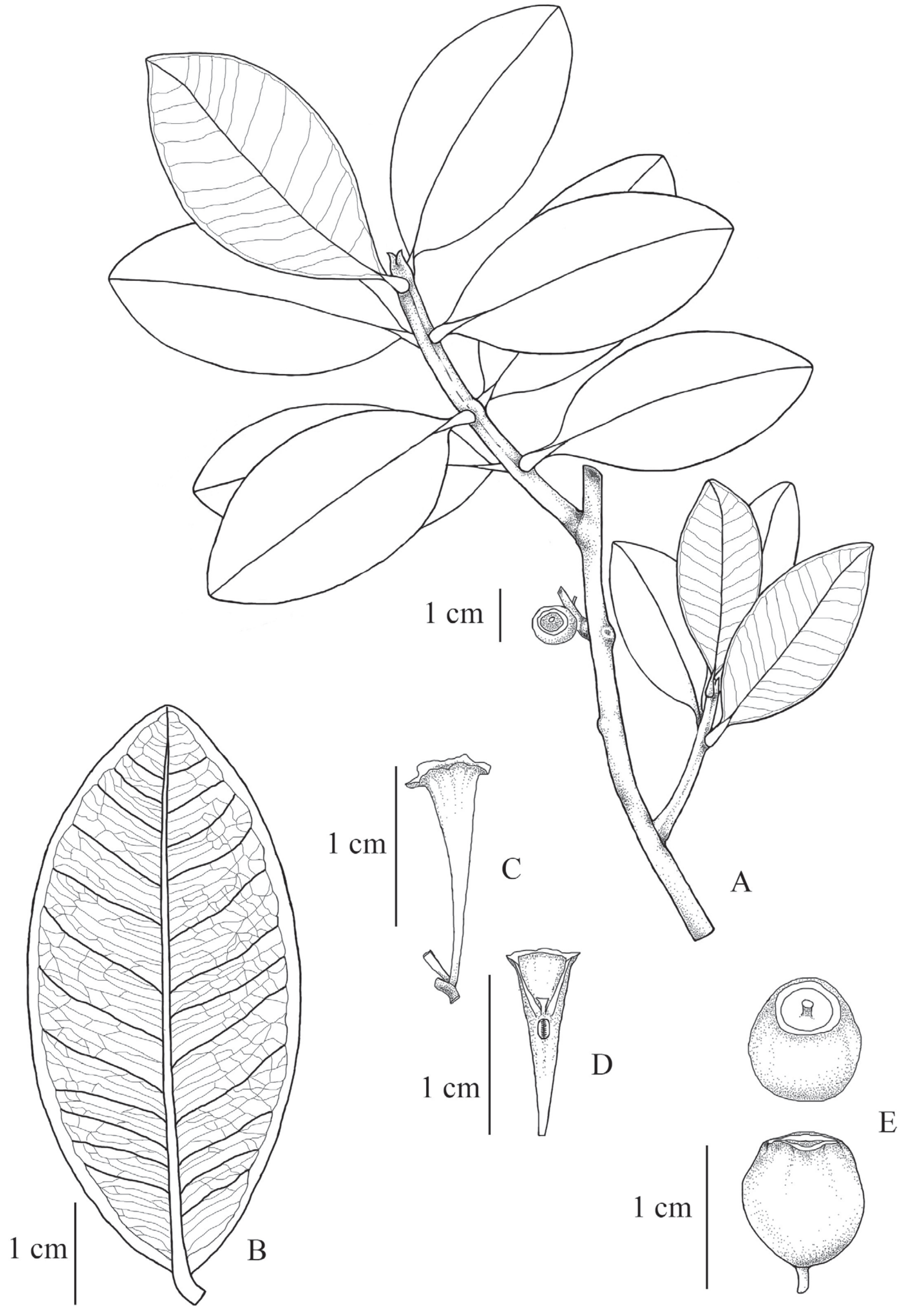

Figure 3. *Syzygium kampotense* **A** habit **B** lower surface of leaf **C** calyx tube (side view) **D** longitudinal section of calyx tube and ovary, showing two locules **E** fruit (from *McDonald et al. 5676*; drawn by N. Triyutthachai).

Etymology. The name of this species is given based on the location where the plant was collected.

Notes. The new species most likely belongs to *Syzygium* subgenus *Perikion* Craven & Biffin (Craven and Biffin 2010; Hatt et al. 2023, because of its clavate hypanthium shape and ellipsoid, obovoid or globose fruit. These characteristics resemble *S. claviflorum*, the type of this subgenus.

Additional specimens examined. Cambodia, Kampot Province, Bokor National Park, near field station, near top of plateau, 10°20.38'N, 104°01.4'E, alt. 1,045 m, 10 Mar. 2001, *Midlleton & Monyrak 660* (P [P00589160]); Bokor, *Dy Phon 1130* (P [P04658853]).

New Records

Syzygium cerasiforme **(Blume) Merr. & L.M.Perry, Mem. Amer. Cad. Arts. 18: 187. 1939.**

Myrtus cerasiformis Blume, Bijdr. Fl. Ind. Ned.: 1087. 1826. Type: Indonesia, Java, *Blume s.n.* (Isotype NY [NY00405548]).

Type. Based on *Myrtus cerasiformis* Blume.

Distribution. Thailand, Cambodia, Malaysia, Java, Borneo.

Ecology. In evergreen swamp forest and a drainage along river.

Notes. POWO (2023) accepts *Syzygium lineatum* as a synonym of *S. cerasiforme* and also shows the distribution of *S. cerasiforme* in Cambodia, Laos, Vietnam and China. I agree with Merrill and Perry (1939) that both species are not conspecific. Moreover, Parnell and Chantaranothai (2002), Chen and Craven (2007), and especially Soh and Parnell (2015) and Tagane et al. (2015, 2018) working on Cambodian taxa, indicated that *Syzygium cerasiforme* had never been recorded in Cambodia. *Syzygium cerasiforme* is similar to *S. lineatum* in having terminal and axillary inflorescences, leaf shape and 14 or more pairs of secondary veins. It differs by smaller leaves, sepals and petals and the outer stamens and style are shorter (4.3–6.7 mm vs 10–15 mm and 5.2–7.7 mm vs 11–13 mm, respectively). However, the Cambodian specimens were collected from Kampong Thom and Stung Treng provinces in Cambodia and I identified them as *S. cerasiforme*. Therefore, these two specimens are the first new record for Cambodia.

Specimens examined. Cambodia, Kampong Thom Province, Sandan District, Rey Long, ca. 13 km south-eastern of Spong, 'Cheum Takong' (Takong swam; 3 × 4 km), a drainage of O Long River, Base camp 13°20.27'N, 105°36.077'E, 7 Apr. 2008, *McDonald et al. 7901* (AAU) & Stung Treng Province, Prey Long Forest, Cheum Takong and O Long River, 13°20.359'N, 105°36.32'E, 7–10 April 2009, *McDonald et al. PL8* (AAU).

Syzygium foxworthianum **(Ridl.) Merr. & L.M.Perry, Mem. Mer. Acad. Arts 18: 168. 1939.**

Eugenia foxworthyi Ridl., Fl. Mal. Penins. 1: 728. 1922, non Elmer, 1912.

Eugenia foxworthiana Ridl., Fl. Mal. Penins. 5: 308. 1925. Type: Peninsular Malaysia, Pahang, Bukit Goh Reserve, 12 Jan. 1920, *Foxworthy Field No. 3624* (lectotype, designated by Chantaranothai and Parnell 1994, p. 63: K [K001005521]).

Syzygium foxworthianum (Ridl.) Masam., Enum. Phan. Born.: 528. 1942.

Eugenia densiflora Miq. var. *angustifolia* Ridl., Fl. Mal. Penins. 1: 729. 1922. Type: Peninsular Malaysia, Perak, Ulu Temengoh, *Ridley s.n.* (lectotype, designated here: K [without barcode]).

Syzygium pycnanthum Merr. & L.M.Perry var. *angustifolium* (Ridl.) P.S.Ashton, Tree Fl Sabah & Sarawak 7: 270. 2011.

Type. Based on *Eugena foxworthiana* Ridl.

Distribution. Thailand, Peninsular Malaysia, Sumatra, Borneo, Vietnam (Lao Cai (Laokhay), Pakha, 10 Dec. 1935, *Poilane 25052* (K).

Ecology. In evergreen forest, 50–200 m alt.

Notes. Ashton (2011) placed *S. foxworthianum* under *S. pycnanthum* (*Eugenia densiflora* Miq.) but I do not agree with this placement because the former differs from the latter by having a long and lax inflorescence (vs short and dense), slightly smaller and narrower leaves, 16–18.5 × 4–6.5 cm (vs larger and broader, 17.5–26 × 4.5–8.5 cm), two intramarginal veins, sometimes without the intramarginal vein and secondary veins ascending to a shallow loop (vs 2–3 intramarginal veins). Although the Vietnamese specimen *Poilane 25052* (K), has young fruits, I found that it belongs to *S. foxworthianum*. Therefore, it is a new record of this species for Vietnam.

Eugenia densiflora var. *angustifolia* Ridl. was described based on two specimens from Peninsular Malaysia, Peak (*Ridley s.n.*) and Kelantan (*Yapp s.n.*). *Ridley s.n.* (K) is available and is designated here as the lectotype.

Syzygium angkae (Craib) Chantar. & J.Parn., Kew Bull. 48(3): 592. 1993.

Eugenia angkae Craib, Bull. Misc. Inform. Kew 1929: 115. 1929.

Type. Thailand, Doi Inthanon (Doi Angka), 30 April 1921, *Kerr 5287* (lectotype, designated by Chantaranothai and Parnell 1994, p. 35: BK; isolectotypes: BM, K, TCD).

Distribution. Myanmar, Thailand, Laos, Cambodia, Vietnam and China (Yunnan province, Menghai county, Xiding country, Mt. Dahei, Hesong, 2 May 2011, *Li-Jianwu 625* (HITBC no. 136852, QBG no. 64320, fruiting specimen).

Ecology. In evergreen broad-leaf forest, ca. 1,960 m alt.

Notes. *Syzygium angkae* is characterized by having axillary or terminal inflorescences ca. 2 cm long and numerous secondary veins. It is found on mountains at an altitude of at least 1,500 m or more. The unidentified fruiting specimen at QBG belongs to *S. angkae*. The distribution of the species was mainly in Myanmar, Thailand, Laos, and Vietnam; it is now extended to China.

Syzygium thorelii (Gagnep.) Merr. & L.M.Perry, J. Arnold Arbor. 19: 107. 1938.

Eugenia thorelii Gagnep. in Lecomte., Notul. Syst. (Paris) 3: 333. 1918.

Type. Thailand, Ubon Ratchathani, Kemmarat, *Thorel 3010* (lectotype, designated by Soh and Parnell 2015, p. 261: P [P00589178]; isolectotypes: A [A00069448], P [P00589179], K [K000276196]).

Distribution. Thailand, Laos, Cambodia, Vietnam, China (Yunnan Province, Mengla County, Mt. Gongbeng, Luosuo River Estuary, 500 m alt., 3 Jan. 2011, *Li-Jianwu 239* (HITBG, no. 135842, QBG).

Ecology. Open rock crevices in the Mekong River, partly submerged at high water or in sandy soils along the side of the river.

Notes. *Syzygium thorelii* is distinctive in having an obtuse or acute leaf apex and alternate leaves in the lower parts of the plant. A previously unidentified specimen seen at QBG undoubtedly belongs to *S. thorelii* and is a new record for China. The Chinese specimen extends the range of the species from Thailand, Laos, Cambodia and Vietnam to Yunnan.

New synonymy

Syzygium densinervium (Merr.) Merr., Phillip. J. Sci. 79: 387. 1951.

Eugenia densinevia Merr., Philipp. J. Sci. 1(Suppl.): 105. 1905. Type: Philippines, Luzon, Laguna province, Los Banos, Mt. Maquiling, Jun. 1917, *Elmer 18011*, (holotype K [K000800201]).

Eugenia silvestrei Elm, Leafl. Philipp. Bot. 8: 3095. 1919. Type: Philippines, Luzon Island, Los Baños, Mount Maquiling, July 1917, *Elmer 18011* (holotype A [A00069784]).

Syzygium densinervium var. *insulare* C.E.Chang, Bull. Taiwan Prov. Pingtung Inst. Agri. 5: 52. 1964. Type: Taiwan, Botel Tobago, 17 Apr. 1962, *Chang 2846*, (isotype L [L0009615]), syn. nov.

Type. Based on *Eugenia densinevia* Merr.

Distribution. Philippines (Luzon) and Taiwan (South Cape).

Ecology. In evergreen forest, mountain slope.

Notes. *Syzygium densinervium* resembles *S. fastigiatum* (Blume) Merr. & L.M.Perry in having paniculate inflorescence, funnel-shaped hypanthium and persistent bracts and bracteoles. It differs by its rugulose hypanthial cup. I have examined an unidentified specimen, *Henry 1998* at K [K001003761] and found that it belongs to *S. densinervium*. I have also examined the isotype type of *S. densinervium* var. *insulare* from Taiwan and then placed it under *S. densinervium*. This species is distributed in the Philippines and Taiwan.

Specimens examined. Taiwan, Botel Tobago, 7 Feb. 1980, *Chang 14691* (KYO); ibid., 6 Sept. 1980, *Chang 14694* (KYO).

Syzygium pellucidum (Duthie) N.P.Balakr., Bull. Bot. Surv. India 22(1–4): 14. 1982.

Eugenia pellucida Duthie, Fl. Brit. India 25(4): 485. 1878. Type: Tenasserim & Andamans, *Helfer 2406* (lectotype, designated here: K [K000821333]; isolectotype A [GH00069438].

Eugenia pellucida var. *contracta* Wall. ex Duthie, Fl. Brit. India 25(4): 485. 1878. —*Syzygium contractum* Wall., *nom.nud*., non *Eugenia contracta* Poir., 1828. Type: Myanmar, Ataran [Attran] river, 1827, *Wallich 3602* (lectotype, designated here: K-W [K001119797]; isolectotypes: K [K000821331, K000821332], A [A01143296]).

Eugenia ripicola Craib, Bull. Misc. Inform. Kew 1915(10): 428. 1915.— *Syzygium ripicola* (Craib) Merr. & L.M.Perry, Britt. 4: 127. 1941. Type: Thailand, Mae [Mê] Ping Rapids, Keng Soi, 16 Mar. 1913, *Kerr 2944* (lectotype, designated by Chantaranothai and Parnell 1994, p. 104: ABD; isolectotypes: BM [BM000944095], E [E00284095], K [K000800078]), syn. nov.

Eugenia cochinchinensis Gagnep. in Lecomte, Notul. Syst. (Paris) 3: 324. 1918.— *Syzygium cochinchinense* (Gagnep.) Merr. & L.M.Perry, J. Arnold Arb. 19:107. 1938. Type: Cambodia, Kompong Speu, Samroang Tong, April 1870, *Pierre 527* (lectotype, designated by Soh and Parnell 2015, p. 254: P [P00589286]; isolectotypes: P [P00589287, P00589288, P00589350], syn. nov.

Eugenia eburnea Gagnep. in Lecomte, Notul. Syst. (Paris) 3: 324. 1918.— *Syzygium eburneum* (Gagnep.) Merr. & L.M.Perry, J. Arnold Arb. 19:107. 1938. Type: Cambodia, plain of Pen-lovier, May 1870, *Pierre 991* (lectotype, designated by Soh and Parnell 2015, p. 255: P [P00589209]; isolectotypes: P [P00589210, P00589211], K [K000276209], E [E00284602], syn. nov.

Type. Based on *Eugenia pellucida* Duthie

Distribution. India, Myanmar, Thailand, Vietnam.

Ecology. Along rivers or streams.

Notes. Based on three collections, *Helfer 2406* (K000821333, GH00069438), *Helfer 2407* and *Kurz s.n.*, the last two have not been seen. Therefore, K000821333 is designated here as the lectotype of *E. pellucida.* The original description of *E. pellucida* var. *contracta* is based on *Wallich 3602* which has four sheets. The specimen, K001119797 is designated here to be the lectotype because it has more leaves and inflorescences. *Syzygium pellucidum* was considered to be endemic to Myanmar (POWO 2023) but its distribution is now extended to Thailand, Laos and Vietnam.

***Syzygium prainianum* (King) Chantar. & J.Parn., Kew Bull. 48: 608. 1993.**

Eugenia prainiana King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 70(1): 116. 1901. Type: Peninsular Malaysia, Perak, Blanta Mabok, Apr. 1890, *Wray 3990* (lectotype, designated by Chantaranothai and Parnell 1994, p. 97: K).

Syzygium prainianum subsp. *minor* Chantar. & J.Parn., Kew Bull. 48: 608. 1993. Type: Thailand, Phangnga, Khao (Kao) Kata Kwam, 9 Mar. 1930, *Kerr 18481* (holotype BM, isotypes BKF, K [K001007999]), syn. nov.

Type. Based on *Eugenia prainiana* King.

Distribution. Thailand, Peninsular Malaysia, Borneo.

Ecology. In evergreen forest, 900 m alt.

Notes. Chantaranothai and Parnell (1993) proposed subsp. *minor* for Thai material with a slightly shorter hypanthial cup (3–4 mm long vs 5 mm long for the typical variety), stamens and style. After examination of *Gardner & Chamchumroon ST2467* K [001007729], a second new specimen collected from Trang, Thailand, I found that these characteristics are variable. Therefore, subsp. *minor* is here placed into synonymy of *S. prainianum*. This species is uncommon in Thailand but widespread in Peninsular Malaysia and Borneo.

Specimens examined. Trang, Yanta Khao, Khao Banthat Wildlife Sanctuary, valley above Sai Rung Waterfall, Camp 2, 800 m alt., 14 Mar. 2006, *Gardner & Chamchumroon ST2467* (K).

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

The author solely contributed to this work.

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Data availability

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

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Research Article

Ixeridium nujiangense (Crepidinae, Cichorieae, Asteraceae), a new species from southwest Yunnan, China

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Abstract

In this paper, we describe *Ixeridium nujiangense*, a novel species identified in southwestern Yunnan, China. Two populations have been found along the riverbanks of the Nujiang River in Yongde and Zhenkang Counties. Morphologically, *I. nujiangense* is most similar to the recently described *I. malingheense*, but it can be readily distinguished by its mostly divided basal leaves, narrower non-clasping cauline leaves, notably shorter corolla tube, pale brown anthers, and considerably longer beak of achenes.

Key words: *Ixeridium malingheense*, morphology, new species, Nujiang River, taxonomy

Introduction

The Asteraceae, recognized as the most species-rich plant family, continues to draw scholarly attention with reports of new genera and species discovered within its ranks. Over the past five years, five new genera have been identified in China: *Sinoseris* N.Kilian, Ze H.Wang & H.Peng (Wang et al. 2020), *Lipschitzia* Zaika, Sukhor. & N.Kilian (Zaika et al. 2020), *Lihengia* Y.S.Chen & R.Ke (Chen et al. 2021), *Mojiangia* Ze H.Wang, N.Kilian et H.Peng (Yin et al. 2022), and *Qineryangia* Y.S.Chen et L.S.Xu (Xu LS et al. 2024). In addition, numerous new species from various genera have been reported (Wang et al. 2020; Liu et al. 2021; Lu et al. 2021; Xiao et al. 2022; Yin et al. 2022; Jin et al. 2023; Zhong et al. 2023; Xu JJ et al. 2024; Xu LS et al. 2024; Xu Q et al. 2024), highlighting that the exploration and documentation of the Asteraceae species are far from complete.

Ixeridium (A.Gray) Tzvelev is a moderately-sized genus in the Crepidinae subtribe of the Asteraceae family. The significant morphological variations, along with overlapping distributions, create challenging groups that are hard to differentiate. The most typical example is the *I. dentatum* complex. Tanaka and Takahara (2013) conducted a comprehensive and detailed study on this complex, redefined the taxonomic ranks of various groups, and resolved the long-standing classification issues of this complex. The taxonomy of *Ixeridium* species in China has also undergone significant changes in recent years.

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First, during the compilation of the Flora of China, Shih and Kilian (2011) discovered that *I. beauverdianum* (H.Lév.) Springate had been misidentified as *I. gracile* (DC.) Pak & Kawano in China and revised the classification accordingly. Secondly, research by Zhang et al. (2023) revealed that *I. sagittarioides* (C.B.Clarke) Pak & Kawano should belong to the genus *Lactuca* L., hence requiring its removal from *Ixeridium*. Additionally, the newly described species *I. calcicola* C.-I.Peng, S.W.Chung & T.C.Hsu (Nakamura et al. 2014), *I. dimorphifolium* Y.L.Xu, Y.F.Lu & X.Cai (Lu et al. 2021), and *I. malingheense* Z.Li & Q.Xu (Xu Q et al. 2024) have expanded our understanding of the morphological diversity within this genus.

Through the continuous efforts of taxonomists, the species range and systematic relationships within *Ixeridium* are becoming increasingly clear. Recent studies have established that the genus *Ixeridium* comprises 17 species, predominantly distributed across East and Southeast Asia. Of these, ten species are native to China, with six being endemic (Shih and Kilian 2011; Nakamura et al. 2014; Lu et al. 2021; Zhang et al. 2023; Xu Q et al. 2024). The plants of this genus are characterized by yellow ligulate florets, somewhat compressed achenes with a slender beak, and a typically yellowish to straw-colored pappus (Shih and Kilian 2011). Although *Ixeridium* is morphologically similar to *Ixeris* (Cass.) Cass., it can be distinguished by its achenes, which have 9–12 prominent, non-wing-like ribs, vs. the wing-like, 10-ribbed achenes of *Ixeris* (Shih 1997).

In December 2023, while collecting plant seeds in Banlao Village, Xiaomengtong Town, Yongde County, the authors discovered a plant with slender leaf petioles on the exposed riverbank of the Nujiang River. Upon returning to the site in February 2024, further observations were made regarding the plant's floral and fruit morphology. On the same day, another population was found along the Nujiang River in Yakou Village, Mengpeng Town, Zhenkang County, adjacent to Yongde County. Detailed examination of these specimens confirmed that they belong to a previously undescribed species, which we present and describe herein.

Materials and methods

Morphological analysis

To characterize the morphology of the newly discovered species, we conducted on-site observations and captured photographs of the plants in their natural surroundings. Additionally, we analyzed herbarium specimens sourced from these locations (KUN, GTZM). To facilitate a comparative morphological study, we referred to the taxonomic keys provided in the Flora Reipublicae Popularis Sinicae (Shih 1997) and the Flora of China (Shih and Kilian 2011), in conjunction with examining the original descriptions and types of *I. yunnanense* C.Shih and the three new Chinese species of *Ixeridium* (Nakamura et al. 2014; Lu et al. 2021; Xu Q et al. 2024). Our examination of the achenes and pappus involved the use of an anatomical microscope (SDPTOP OD500H), while the lengths of ligules, anther tubes, and achenes were measured using a light microscope (Olympus DP72) on both fresh and preserved specimens.

Taxon sampling and outgroup selection

A phylogenetic analysis was conducted to determine the systematic position of the new species within the genus *Ixeridium*. Sequencing of the new species was carried out along with *I. yunnanense* and *I. malingheense*. The analysis was primarily based on the established framework of *Ixeridium* outlined in Nakamura et al. (2014) and Xu Q et al. (2024). When multiple sequences were available for species of *Ixeridium*, two sequences were randomly selected to represent their systematic positions. A total of 24 sequences representing 15 species (including 6 subspecies) of *Ixeridium* were included in the phylogenetic analysis. Additionally, 6 sequences from 6 species of the sister genera *Ixeris* were included to assess their relationships. To maintain consistency, *Youngia japonica* (L.) DC., *Crepidiastrum lanceolatum* (Houtt.) Nakai, and *Paraixeris denticulata* (Houtt.) Nakai were used as outgroups. The species names in all sequences are followed by GenBank accession numbers for easy identification of their sources. Information on the newly sampled taxa, along with their voucher details and GenBank accessions, is provided in Table 1.

DNA extraction and PCR amplification

We selected the nuclear ribosomal internal transcribed spacer (nrITS), a commonly used barcoding fragment, to explore the phylogenetic relationship between the new species and other *Ixeridium* species. The modified CTAB method was employed to extract DNA from the samples. Universal primers ITS4 and ITS5 (White et al. 1990) were used for PCR amplification. The PCR mixture employed in the study was procured from Sangon Biotech Company (China), and the recommended PCR cycling conditions for this mixture (95 °C for 3 min, 30 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 30 s, with a final extension at 72 °C for 5 min) were applied for amplification. Subsequently, gel electrophoresis was conducted, and the eligible samples were forwarded to Sangon Biotech Company, China, for sequencing.

Phylogenetic reconstruction

The sequencing quality and chromatograms of the newly acquired five sequences were assessed with Bioedit v.7.0 (Hall 1999). These sequences were aligned with others from GenBank via Muscle (Edgar 2004), followed by manual adjustment and trimming in PhyDE v.0.9971 (Müller et al. 2010).

Table 1. Information on the newly sampled taxa, along with their voucher details, and GenBank accessions.

Sample name	Locality	Collector & Collection no.	Genbank accession
Ixeridium nujiangense	China, Yunnan, Yongde, Xiaomengtong, Banlao, along the bank of Nujiang River, alt. 541 m	Wang Zehuan & Li Yongliang wzh20240201	PP892766
	China, Yunnan, Zhenkang, Mengpeng, Yakou, along the bank of Nujiang River, alt. 537 m	Wang Zehuan & Li Yongliang wzh20240202	PP892767
Ixeridium malingheense	China, Guizhou, Xingyi, Zhaojiadu, along the bank of Malinghe Canyon, alt. 833 m	Wang Zehuan et al. wzh20240301	PP906177
Ixeridium yunnanense	China, Yunnan, Yongde, Wumulong, on the slope of Yanglang River, alt. 1860 m	Li Yongliang 20240601	PP906175
			PP906176

The resulting .fas file was then transferred to Phylosuite v.1.2.3 (Xiang et al. 2023) for analysis. Phylogenetic relationships were reconstructed through Maximum Likelihood (ML) and Bayesian Inference (BI) methods. Models were selected by ModelFinder in Phylosuite with default parameters based on the Akaike Information Criterion (AIC). The ML tree was constructed with IQ-TREE in Phylosuite, applying the selected IQ-TREE model and 1,000 bootstrap replicates for branch support. The BI tree was generated through MrBayes in Phylosuite, using the selected MrBayes model and running for 5,000,000 generations with default parameters. Finally, both trees were visualized and edited with FigTree v.1.4.4 (Rambaut 2018).

We defined branches with posterior probabilities (PP) < 0.70 and bootstrap values (BS) < 60 as weakly supported, 0.70 ≤ PP < 0.95 and 60 ≤ BS < 80 as moderately supported, and PP ≥ 0.95 and BS ≥ 80 as strongly supported.

Results

Morphological studies

After detailed morphological studies, we found that among all currently published and accepted species of the genus *Ixeridium*, *I. nujiangense* is morphologically most similar to the recently described *I. malingheense*. Although the two species have different distribution locations (Fig. 1), they both grow along river banks and have an early flowering period, usually in winter and spring. Morphologically, they both possess 5 inner phyllaries and relatively few ligulate florets (typically 5–6), with similar corolla and achene lengths. However, the two species exhibit significant differences in the morphology of their basal and cauline leaves, anther color, and the length of the achene beak (Fig. 2). The main morphological differences between the two species are detailed in Table 2.

Phylogenetic analysis

The matrix used for the final phylogenetic analysis includes a total of 33 sequences, their final aligned matrix is 643bp long, with 126 informative sites. Using the Akaike Information Criterion (AIC), ModelFinder selected the SYM+G4

Table 2. Comparison of the morphological characteristics between *Ixeridium nujiangense* and *I. malingheense*.

Characteristics	*I. nujiangense*	*I. malingheense*
Basal leaves	usually pinnatisect or pinnately divided, with only a few entire leaves	all entire
Cauline leaves	lanceolate to linear-lanceolate, 0.1–0.3 cm wide, with upper leaf base attenuate, not clasping the stem	oblong or narrowly elliptical, 0.2–0.9 cm wide, with upper leaf base auriculately clasping the stem
Phyllary	apex purplish-brown, inner phyllaries 4.8–5.9 mm in length	apex green, inner phyllaries 4.1–5.3 mm in length
Corolla	5.9–8.1 mm in length	5.1–6.2 mm in length
Corolla tube	ca. 1/5 of the corolla length, pale yellow	ca. 1/3 of the corolla length, white
Anther	pale brown	yellow
Style	apex ca. 2/3 of the ligule	apex equals the ligule
Achene	2.9–3.1 mm in length	2.5–2.6 mm in length
Beak	0.9–1.1 mm long, ca. 1/3 of the achene length	0.5–0.8 mm long, ca. 1/6 of the achene length

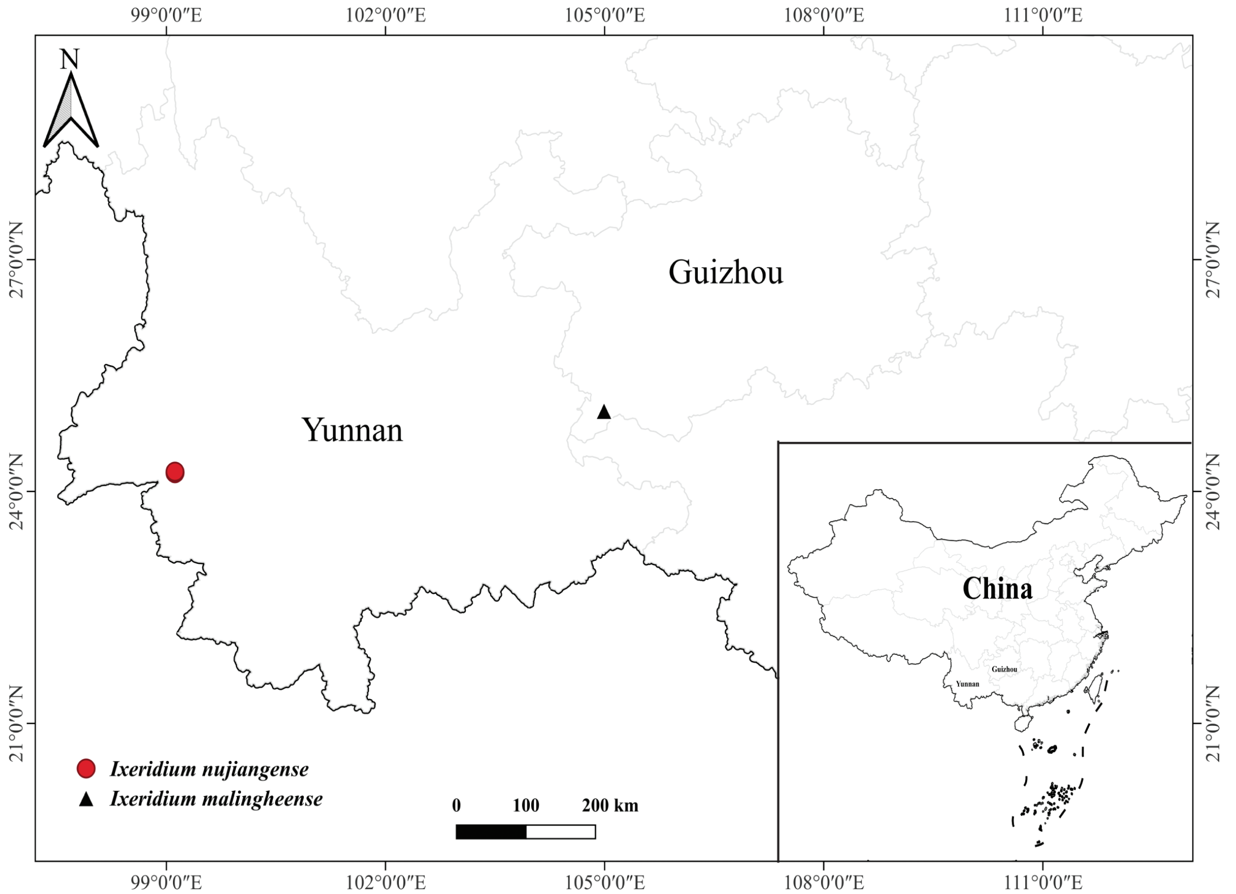

Figure 1. Distribution map of *Ixeridium nujiangense* and *I. malingheense*.

model for both IQ-Tree and MrBayes. The Maximum Likelihood (ML) and Bayesian Inference (BI) phylogenetic tree constructed based on this model exhibit almost the same topology. The BI consensus tree, including both bootstrap support (BS) and posterior probabilities (PP) values, is shown in Fig. 3.

The phylogenetic tree shows that all sequences of *Ixeridium* cluster into a single clade with strong support (BS=100, PP=1). Within this clade, there are three subclades with moderate or strong support: clade A (BS=83, PP=0.94), clade B (BS=71, PP=0.85), and clade C (BS=99, PP=1). The two sequences of the new species *I. nujiangense* from two distribution points cluster into a strongly supported small subclade (BS=99, PP=1), forming the basal branch of clade C, and sister to a subclade (BS=88, PP=0.96) formed by *I. malingheense*, *I. yunnanense*, *I. gracile*, and *I. beauverdianum*.

Taxonomy

***Ixeridium nujiangense* Ze H.Wang, sp. nov.**
urn:lsid:ipni.org:names:77345032-1
Figs 2, 4

Type. China, Yunnan Province, Lincang City, Yongde County, Xiaomengtong Town, Banlao Village, along the bank of Nujiang River, 24°15'19.70"N, 99°07'03.02"E, alt. 541 m, 25 Feb 2024, *Wang Zehuan & Li Yongliang wzh20240201* (holotype: KUN!, isotypes: KUN!, GTZM!).

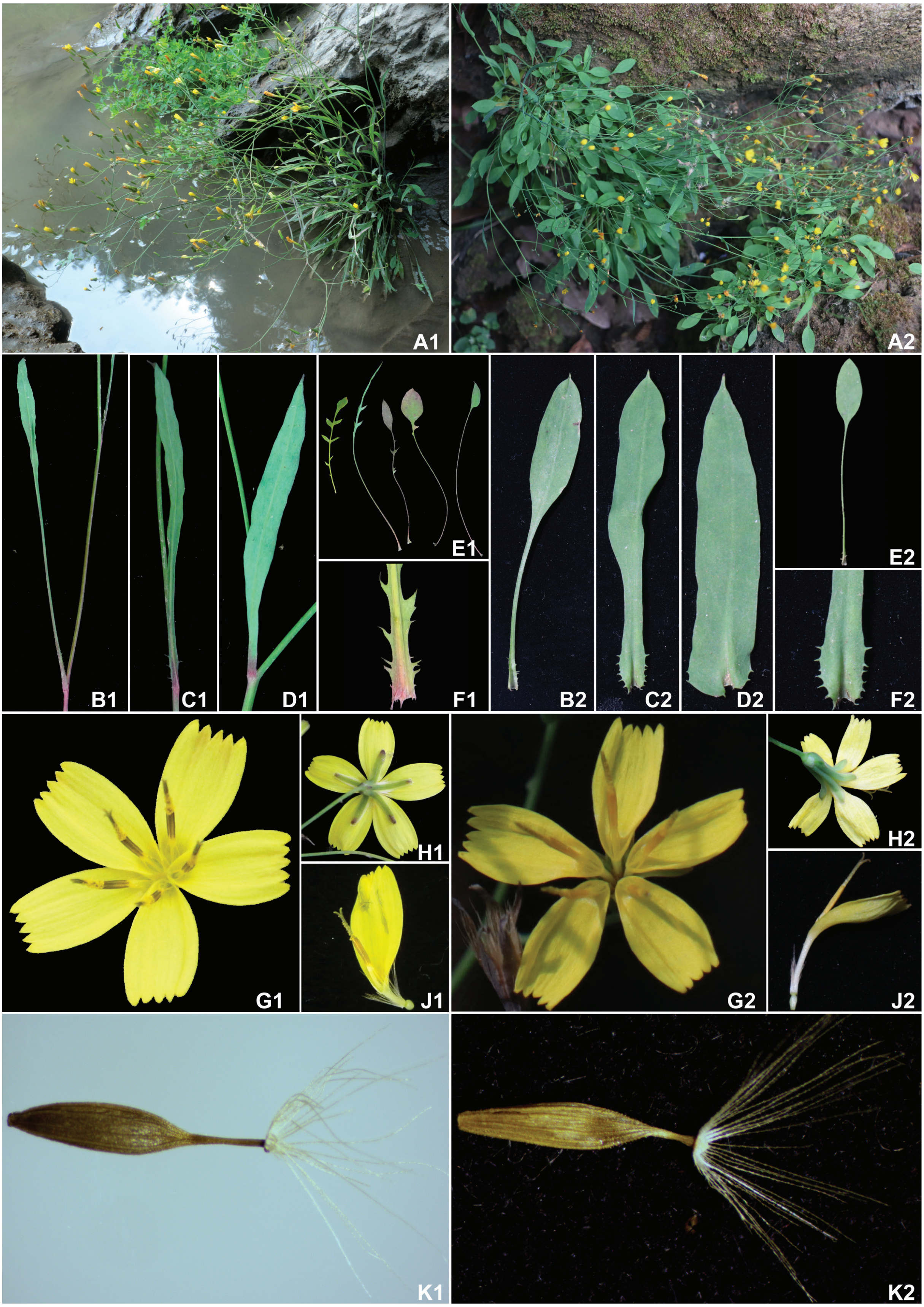

Figure 2. Comparison of the morphological characteristics between *Ixeridium nujiangense* (A1–K1) and *I. malingheense* (A2-K2). **A** plants **B** lower cauline leaves **C** middle cauline leaves **D** upper cauline leaves **E** basal leaves **F** base of middle cauline leaves **G** capitula in front view **H** capitula in back view **J** florets **K** achenes.

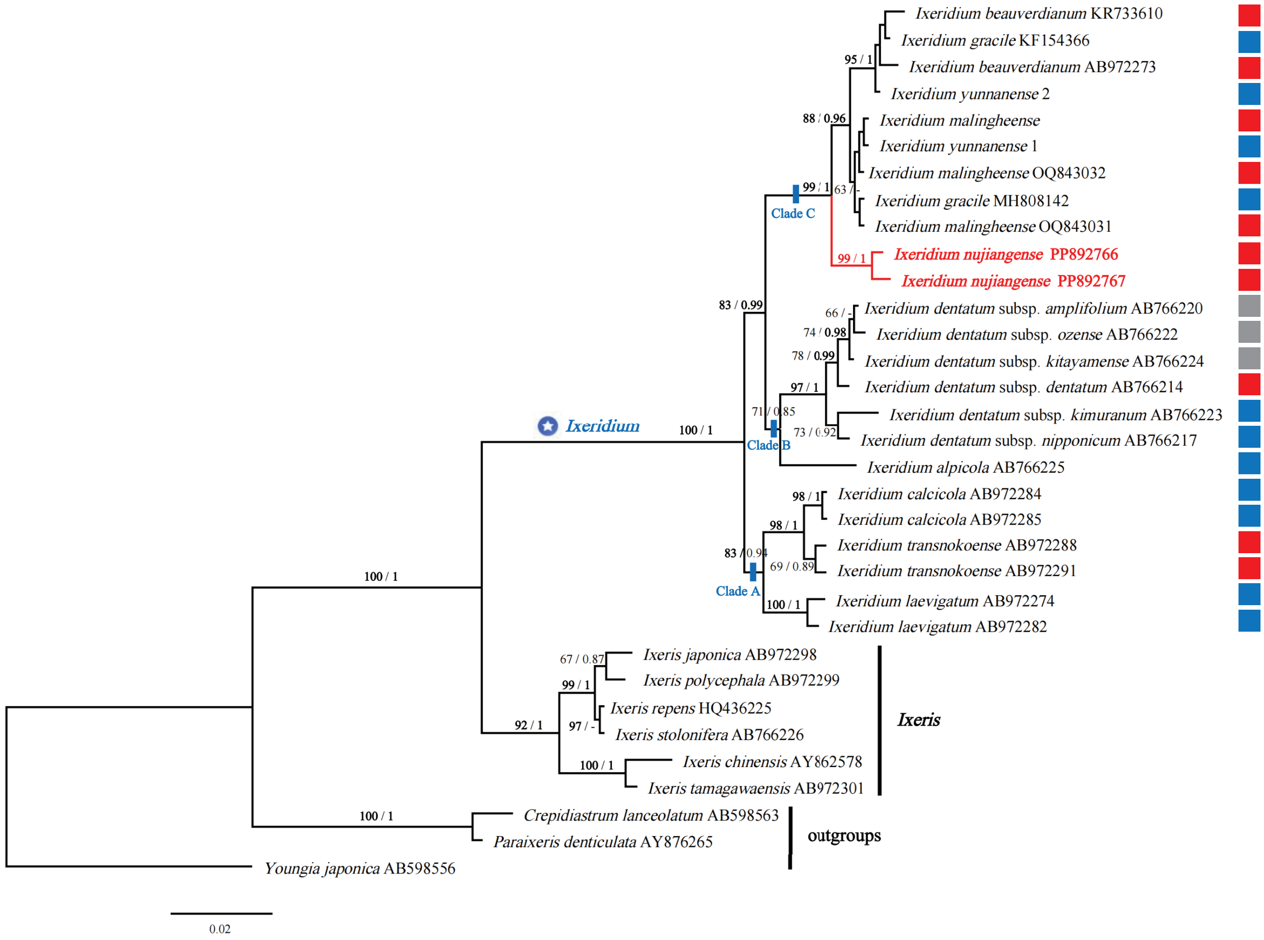

Figure 3. The consensus phylogenetic tree derived from Bayesian Inference (BI) analysis based on nrITS sequence data. Bootstrap support values from Maximum Likelihood (ML) analysis (ML > 60, left) and Bayesian posterior probabilities (PP > 0.70, right) are indicated above the branches. Strongly supported values (BS > 80, PP > 0.95) are shown in bold. Small boxes represent capitulum morphology: red indicates inner phyllaries ca. 5 and ligulate florets usually 5–6, blue indicates inner phyllaries ca. 8 and ligulate florets 8–12, and gray indicates uncertain characteristics.

Diagnosis. *Ixeridium nujiangense* is morphologically most similar to *I. malingheense* but can be distinguished by the following traits: basal leaves usually pinnatisect or pinnately divided, with only a few entire leaves (vs. basal leaves all entire), cauline leaves lanceolate to linear-lanceolate, with upper leaf base attenuated, not clasping (vs. cauline leaves oblong or narrowly elliptical, with upper leaf base auriculately clasping), corolla tube ca. 1/5 of the corolla length (vs. corolla tube ca. 1/3 of the corolla length), anthers pale brown (vs. anthers yellow), achenes 2.9–3.1 mm in length (vs. achenes 2.5–2.6 mm in length), beak ca. 1/3 of the achene length (vs. beak ca. 1/6 of the achene length).

Description. Perennial herbs, 17–37 cm tall, glabrous totally, with white latex. Roots fibrous and densely shoot-bearing, fleshy, up to 0.6 cm in diameter. Stems erect, slender, often branched near the base or below the middle. Leaves glabrous, green on the upper surface and pale green on the lower surface, margin entire or with sparsely slender teeth. Basal leaves rosulate, persistent at anthesis, blades 1.5–5.5 × 0.5–1 cm, entire, pinnatisect or pinnately divided, petioles 6.2–7.5 cm long. Terminal lobes of divided leaves 1.1–3 × 0.3–0.6 cm, ovate, elliptic to narrowly lanceolate, apex obtuse, acute to acuminate, base slightly

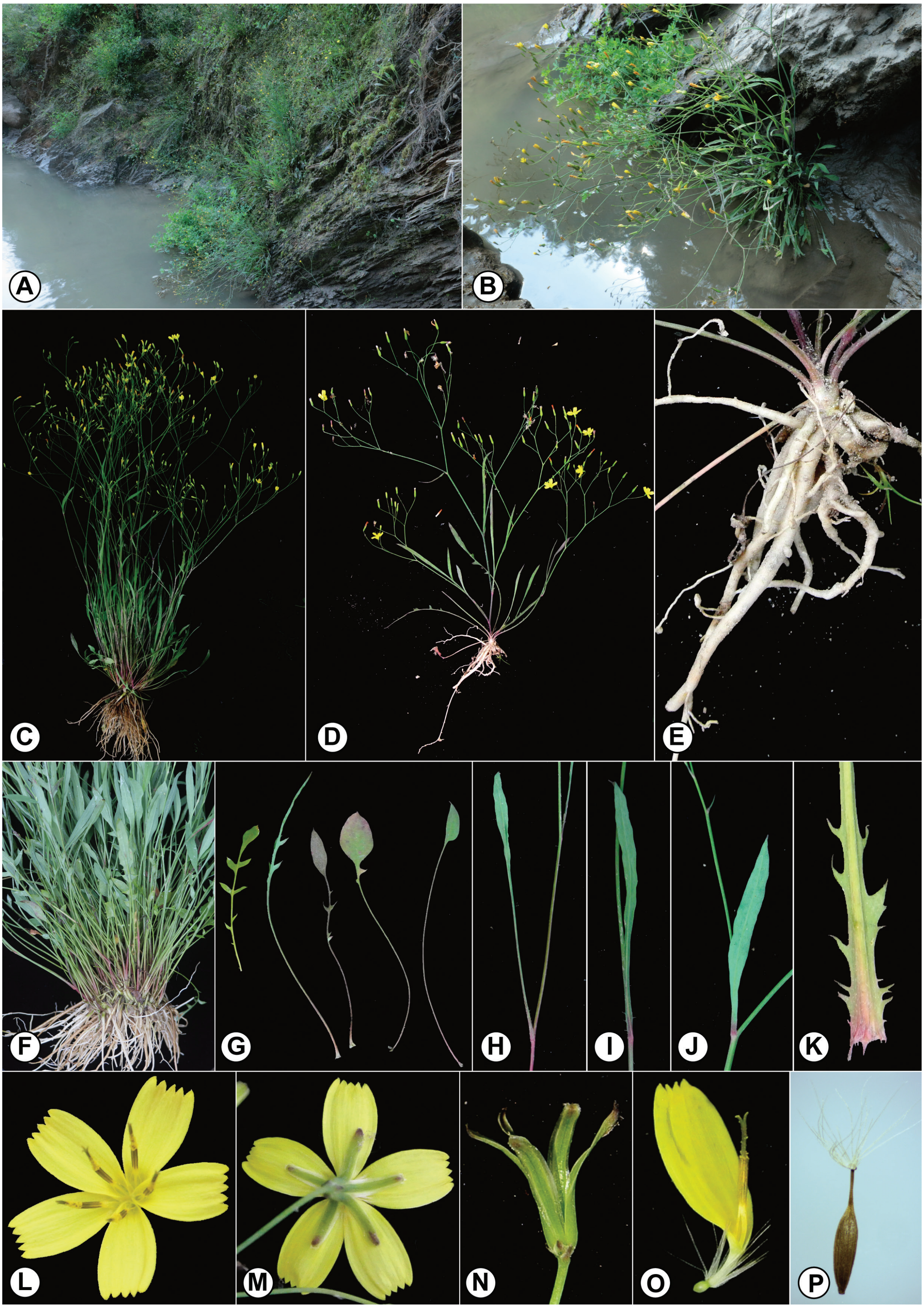

Figure 4. *Ixeridium nujiangense* sp. nov. **A**–**B** habitat **C**–**D** plants **E** fleshy root **F** intertwined roots and basal leaves **G** basal leaves **H** lower cauline leaf **I** middle cauline leaf **J** upper cauline leaf **K** lower part of middle cauline leaf **L** capitulum in front view **M** capitulum in back view **N** involucre **O** floret **P** achene with pappus.

attenuate; lateral lobes 1–4, concentrated at the lower and middle portions of the leaf, the lower lobes smaller and serrate, the middle lobes larger, elongated or obliquely triangular, gradually tapering towards the acuminate apex. Cauline leaves 3–4, blades lanceolate to linear-lanceolate, 1.3–9.4 × 0.1–0.3 cm, apex acute to acuminate, base attenuate, margin entire and with/without sparsely slender ciliate teeth or serrate lobes at the base. Synflorescence corymbiform, with numerous capitula; capitula with 5(–6) florets, base with slender, long peduncle. Bracts linear-lanceolate, up to 7 mm long. Involucre narrowly cylindrical, ca. 5–6 mm long. Phyllaries in two series, glabrous; outer phyllaries broadly ovate, 0.3–0.5 × 0.5 mm, apex obtuse and purplish-brown; inner phyllaries 5, linear-lanceolate, 4.8–5.9 × 0.5–0.9 mm, green on both sides, with transparent membranous margins, apex obtuse and purplish-brown. Receptacle flattened, glabrous, alveolate. Florets 5(–6), ligulate, yellow, corolla 5.9–8.1 mm long, tube 1.0–1.9 mm long, pale yellow, ligules ca. 4.9–6.2 × 1.5–2.1 mm; anthers brown, anther tube 1.8–1.9 mm long; ovary ellipsoid, style ca. 5 mm long. All achenes uniform in shape, pale brown, narrowly fusiform, slightly compressed, 2.9–3.1 mm long, with 3 fine ribs on each side, apex attenuate to a slender beak approximately 0.9–1.1 mm in length. Pappus straw-colored, ca. 3 mm long, 1-seriate, scabrid.

Distribution and habitat. *Ixeridium nujiangense* is currently known from two locations in Yongde and Zhenkang Counties, Yunnan, China. This species thrives on the banks of the Nujiang River, which are exposed during the dry season, at an elevation of ca. 540 m. *Lotus corniculatus* L. (Fabaceae) is the primary associated species, sharing the barely vegetated riverbank terrain with *I. nujiangense*.

Phenology. Flowering and fruiting occur from December to March.

Etymology. The specific epithet ‘*nujiangense*’ is derived from the name of the Nujang River along whose banks the type locality is situated.

Vernacular name. Simplified Chinese:怒江小苦荬; Chinese Pinyin: Nùjiang Xiǎokǔmǎi.

Additional specimens examined. China, Yunnan Province, Lincang City, Zhenkang County, Mengpeng Town, Yakou Village, along the bank of Nujiang River, 24°14'08.11"N, 99°07'03.02"E, alt. 537 m, 25 Feb 2024, Wang Zehuan & Li Yongliang wzh20240202 (KUN!, GTZM!).

Discussion

In this study, we sampled all Chinese *Ixeridium* species, except for the doubtful species *I. aculeolatum* C.Shih and the newly described species *I. dimorphifolium* (Lu et al. 2021), to explore their phylogenetic relationships. From the ML and BI phylogenetic trees, it can be seen that the genus *Ixeridium* is monophyletic and can be divided into three clades. The new species *I. nujiangense* is located in Clade C and forms a sister group with a subclade that includes the recently described *I. malingheense*, as well as *I. beauverdianum*, *I. gracile*, and *I. yunnanense*.

Two types of capitula can generally be classified based on the morphology of Chinese *Ixeridium* species: Type One, usually has 5 inner phyllaries and often 5–6 ligulate florets, and Type Two, commonly has 8 inner phyllaries and 8–12 ligulate florets. However, all three evolutionary lineages within the genus *Ixeridium* contain species exhibiting both types of capitula (Fig. 3). This indicates that the easily discernible morphological characteristics of the capitula do not correspond to the evolutionary relationships among species within the genus *Ixeridium*.

Additionally, within Clade C, the two sequences of the new species *I. nujiangense* cluster closely together (BS=99, PP=1). Notably, one sequence each from *I. gracile* and *I. yunnanense* clusters with *I. beauverdianum*, while their other sequences cluster with *I. malingheense*. Upon careful examination of the sequence mutations, researchers observed that the sequences of *I. gracile* and *I. yunnanense*, which are grouped with *I. beauverdianum*, do indeed exclusively share two informative mutational sites with it. These shared mutations likely play a key role in forming a well-supported branch for these four sequences (BS=95, PP=1). To better differentiate these five species, an identification key is provided as follows.

Key to the five species of Clade C

1a Inner phyllaries 7–8; florets 8–12; achene ca. 5–6 mm in length............**2a**
2a Involucre 5–6 mm; basal leaves elliptic or obovate, sometimes lanceolate or oblanceolate, 2–5 × 0.5–1.2 cm ....***Ixeridium yunnanense***
2b Involucre 7–8 mm; basal leaves narrowly spatulate, narrowly elliptic, or almost linear, 4–15 × 0.4–1 cm...***Ixeridium gracile***
1b Inner phyllaries 5; florets 5–6(–7); achene less than 4 mm in length **3a**
3a Basal leaves usually pinnatisect or pinnately divided, with only a few entire leaves; beak ca. 1/3 of the achene length ....***Ixeridium nujiangense***
3b Basal leaves entire or with a few very slender linear teeth; beak ca. 1/6 of the achene length...**4a**
4a Basal leaves long-spatulate or spatulate; anthers yellow; achenes 2.5–2.6 mm in length..***Ixeridium malingheense***
4b Basal leaves narrowly elliptic to linear; anthers brown; achenes 3.2–3.5 mm in length.. ***Ixeridium beauverdianum***

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: QWS, ZHW. Data curation: QQZ, JJX. Formal analysis: JJX, ZHW, QQZ. Funding acquisition: QWS. Investigation: ZHW, YLL. Project administration: ZHW. Resources: YLL. Software: QQZ, JJX. Supervision: QWS. Visualization: QQZ. Writing - original draft: QQZ. Writing - review and editing: QWS, ZHW.

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Data availability

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

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Research Article

A taxonomic revision of *Garcinia* section *Garcinia* (Clusiaceae) in Thailand

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Abstract

Garcinia section *Garcinia* (Clusiaceae) is revised for Thailand with three species and one variety, i.e., two native species: *G. celebica* and *G. exigua*, and one cultivated species: *G. mangostana* var. *mangostana*. Detailed morphological descriptions, illustrations, and an identification key to the species are presented, along with notes on distributions, habitats and ecology, phenology, conservation assessments, etymology, vernacular names, uses, and specimens examined. The section is recognized by its terminal inflorescences of simple cymes, or sometimes a solitary flower; flowers with 4 sepals and 4 petals; male flowers often with a pistillode, and stamens united into a single 4-lobed or 4-angled bundle, and with 2-thecous anthers; usually multilocular ovaries and stigmas with distinct or weak lobes and smooth or rough; and fruits with a smooth surface. Three associated synonyms of *G. celebica*: *G. ferrea*, *G. basacensis*, and *G. hombroniana*, are lectotypified here in a second-step. In Thailand, *Garcinia celebica* is found in a very wide variety of habitats, at elevations of 0–1,500 m amsl., and is known to be naturally distributed in all floristic regions. *G. exigua* is found in dry evergreen forest on limestone hills and in littoral dry evergreen forest on limestone hills, at elevations of 50–100 m amsl. in Krabi Province, the peninsular region. *G. mangostana* var. *mangostana* is found only in cultivation. *Garcinia exigua* has a conservation status of Vulnerable [VU B2ab(iii)] and the other two species have a conservation status of Least Concern [LC]. The fleshy pulp surrounding the seeds of two species, *G. celebica* and *G. mangostana* var. *mangostana* is edible and has a sweet-sour taste.

Key words: Agamospermy, dioecy, edible fruits, Guttiferae, Malpighiales, second-step lectotypification, taxonomy

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Introduction

Garcinia L. is the largest genus in the Clusiaceae Lindl. (Guttiferae Juss.). The genus contains at least 250 species (Stevens 2007) and maybe as many as c. 400 species (POWO 2024). It is a pantropically distributed genus and has centers of diversity located in Africa (Madagascar), Australasia, and Southeast Asia (Sweeney and Rogers 2008; Gaudeul et al. 2024). In Asia, *Garcinia* is most diverse in the Malesian region but also spreads north into southern China, west to India, and east to the Micronesian islands (Nazre et al. 2018). The genus is a group of evergreen small to large trees, or occasionally shrubs, which are usually dioecious, but sometimes polygamo-dioecious (also called trioecious). It also has obligately and facultatively agamospermous species (e.g., *G. mangostana* L.). Several species are well known because they have edible fruits or leaves (e.g., *G. atroviridis* Griff. ex T. Anderson, *G. cowa* Roxb. ex DC., *G. dulcis* (Roxb.) Kurz, *G. lanceifolia* Roxb., *G. mangostana*, *G. pedunculata* Roxb. ex Buch.-Ham., *G. schomburgkiana* Pierre) and used for medicinal purposes.

Garcinia honours Laurentius Garcin (1683–1752) who was a Dutch army doctor and naturalist in the Dutch Indies (Indonesia) in the years 1720–1729. During his voyage to the Maluku Islands (also called the Moluccas), Indonesia, he examined the fruit-bearing tree which the locals called ‘mangoustan’ (mangosteen) and gave a description of the fruiting female specimen (Garcin 1733). The species was named *Garcinia mangostana* by Linnaeus (1753) and is the type species of the genus. The genus is characterized by a dioecious habit (sometimes apparently polygamo-dioecious); yellow, pale yellow, white, cream, or clear latex secreted from cut boles, twigs, leaves, and fruits; terminal buds concealed between the bases of the uppermost pair of petioles; decussate leaves with scattered black or brown gland dots, or interrupted wavy lines of differing lengths; male flowers with many to numerous stamens untied into a column in the center of the flower, or into a variously lobed or angled, or into 4 or 5 separate bundles; berry fruits and seeds usually with thick or thin fleshy pulp (Ngernsaengsaruay et al. 2022a).

Engler’s (1893) monograph of the genus *Garcinia* recognized 34 sections. Engler’s work was an elaboration of Pierre (1882, 1883), who established the first monograph of *Garcinia* and used mainly flower and inflorescence characters to classify the species into 37 sections. The other monograph of the genus *Garcinia* is that of Vesque (1893), who used floral morphology and leaf anatomy to classify the species into three subgenera and nine sections. A worldwide sectional treatment of *Garcinia* was presented by Jones (1980), in an unpublished Ph.D. thesis in which the genus was classified into 14 sections based mainly on floral morphology, especially male flowers and pollen morphology. Jones’s (1980) treatment recognized 46 species in the section *Garcinia*. This section was recently monographed by Nazre et al. (2018), who based on molecular and morphological data, recognized 13 species, two of which have three varieties each. Several species are excluded from *Garcinia* section *Garcinia*, reported as insufficiently known, or reduced to synonymy (Nazre et al. 2018). The latest infrageneric classification of *Garcinia* was presented by Gaudeul et al. (2024), who recovered nine major clades falling within two major lineages, and recognized 11 sections, and recognized 15 species in section *Garcinia*. The section is distinguished by its flowers with 4 sepals and 4 petals; male flowers often with a pistillode, and stamens united into a single 4-lobed or 4-angled bundle, and with 2-thecous anthers; multilocular ovaries and stigmas with or without lobes and smooth or corrugated; fruits with a smooth surface; and terminal inflorescences and comprised of simple cymes (Nazre et al. 2018). Species of *Garcinia* section *Garcinia* are typically understorey trees in tropical rain forests and are distributed in Southeast Asia from eastern India to Malesia (Nazre et al. 2018).

A taxonomic revision of the genus *Garcinia* in Thailand has recently been undertaken by the first author as part of the Flora of Thailand. Ngernsaengsaruay and Suddee (2016, 2022) described additional new species: *G. nuntasaenii* Ngerns. & Suddee from north-eastern and *G. santisukiana* Ngerns. & Suddee from eastern Thailand, respectively. Ngernsaengsaruay (2022) recognized three species in *Garcinia* section *Brindonia* (Thouars) Choisy in Thailand: *G. atroviridis*, *G. lanceifolia*, and *G. pedunculata*. Ngernsaengsaruay et al. (2022a, 2023a) published additional new species records from peninsular Thailand: *G. dumosa* King and *G. exigua* Nazre, respectively. Ngernsaengsaruay et al. (2022b) published *Garcinia siripatanadilokii* Ngerns., Meeprom, Boonthasak, Chamch. & Sinbumr. as a new species from Peninsular Thailand. Finally, *Garcinia* section *Xanthochymus* (Roxb.) Pierre (Clusiaceae) was revised for Thailand with four native species: *G. dulcis* (Roxb.) Kurz, *G. nervosa* (Miq.) Miq., *G. prainiana* King, and *G. xanthochymus* Hook. f. ex T. Anderson (Ngernsaengsaruay et al. 2023b).

From these publications, the genus has a total of c. 30 accepted species in Thailand. However, identifications mostly rely on the literature, and this is the case for *Garcinia* section *Garcinia*, which has never been revised for Thailand. Therefore, in this paper, we provide here an updated account for section *Garcinia* in Thailand in order to present a taxonomic treatment that includes lectotypifications, detailed morphological descriptions, illustrations, and an identification key to the species, together with notes on distributions, habitats and ecology, phenology, conservation assessments, etymology, vernacular names, uses, and specimens examined.

Materials and methods

Specimens collected for the Flora of Thailand were examined by consulting taxonomic literature (e.g., Anderson 1874; Kurz 1874, 1877; Pierre 1882, 1883; King 1890; Vesque 1893; Pitard 1910; Gagnepain 1943; Corner 1952; Maheshwari 1964; Ridley 1922; Backer and Bakhuizen van den Brink 1963; Whitmore 1973; Singh 1993; Nazre 2010; Nazre et al. 2018), and by comparing with herbarium specimens housed in the following herbaria: AAU, BK, BKF, BM, C, CMUB, K, P, PSU, QBG, SING, and those included in the virtual herbarium databases of A (https://kiki.huh.harvard.edu/databases/specimen_index.html), AAU (https://www.aubot.dk/search_form.php), BR (http://www.botanicalcollections.be), CAL (https://ivh.bsi.gov.in/phanerogams), E (https://data.rbge.org.uk/search/herbarium/), G (http://www.ville-ge.ch/cjb/), K (including K-W) (http://www.kew.org/herbcat), KUN (Kunming Institute of Botany, Chinese Academy of Sciences, http://nsii.org.cn/2017/), L (including U) (https://bioportal.naturalis.nl/), MPU (https://explore.recolnat.org), P (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form), The Wallich Catalogue Online (https://wallich.rbge.org.uk/), US (https://collections.nmnh.si.edu/search/botany/), and W (https://www.nhm-wien.ac.at/en/research/botany). All herbaria acronyms follow Thiers (2024, continuously updated). All specimens cited have been seen by the authors unless stated otherwise. The taxonomic history of the species was compiled using the taxonomic literature and online databases (IPNI 2024; POWO 2024). The morphological characters, distributions, habitats and ecology, phenology, and uses were described from historic and newly collected herbarium specimens and the author's observations during field work. The vernacular names were compiled from the specimens examined and the literature (e.g., Ridley 1922; Corner 1952; Maheshwari 1964; Whitmore 1973; Verheij and Coronel 1992; Pooma and Suddee 2014). Thailand floristic regions follow Flora of Thailand. Vol. 4(3.3) (The Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation 2023). The assessment of conservation status was performed following the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022) for a preliminary assessment of the conservation category in combination with GeoCAT analysis (Bachman et al. 2011) and field information. The calculation of Extent of Occurrence (EOO) and Area of Occupancy (AOO) are based on GeoCAT (https://www.kew.org/science/our-science/projects/geocat-geospatial-conservation-assessment tool).

Results and discussion

Taxonomic treatment

Garcinia L. section Garcinia L., Sp. Pl. 1: 443. 1753; S. W. Jones, Morphology and Major Taxonomy of *Garcinia* (Guttiferae), Ph.D. Thesis (unpublished): 284. 1980; Nazre et al., Phytotaxa 373(1): 14. 2018; M. Gaudeul et al., PhytoKeys 239: 93. 2024.

Type. *Garcinia mangostana* L., Sp. Pl. 1: 443. 1753.

Description. ***Habit*** evergreen trees, sometimes with buttresses near the base of the main stem of large trees; latex yellow (i.e., *G. exigua* and *G. mangostana* var. *mangostana*) or white, turning yellow (i.e., *G. celebica*), sticky; branches decussate, horizontal or nearly horizontal; branchlets 4-ridged, glabrous. ***Terminal bud*** concealed between the bases of the uppermost pair of petioles. ***Leaves*** decussate, small (i.e., *G. exigua*) or big (i.e., *G. celebica* and *G. mangostana* var. *mangostana*); lamina coriaceous or thickly coriaceous, glabrous; secondary veins curving towards the margin and connected in distinct loops and united into one (i.e., *G. celebica* and *G. exigua*) or two intramarginal veins (i.e., *G. mangostana* var. *mangostana*), with interrupted long wavy lines (glandular wavy lines, also called exudate containing canals) of differing lengths, running across the secondary veins to the apex or the margin; petiole grooved or not grooved above, transversely rugose, usually with a basal appendage clasping the branchlets. ***Inflorescences*** terminal, simple cymes, in a cluster of two to several flowers, or sometimes a solitary flower (in the female flowers). ***Flowers*** unisexual, plants dioecious, 4-merous; bracteoles caducous; sepals and petals decussate. ***Male flowers***: stamens numerous, united into a single 4-lobed (i.e., *G. celebica* and *G. exigua*) or 4-angled bundle (i.e., *G. mangostana* var. *mangostana* from Nazre et al. 2018), antepetalous (opposite the petals); anthers small, 2-thecous; pistillode present or absent. ***Female flowers***: staminodes absent or present; pistil fungiform (mushroom-shaped); ovary unlobed, usually multilocular; stigma sessile, distinctly or weakly lobed and smooth or rough. ***Fruits*** berries, subglobose, globose, depressed globose or broadly ellipsoid, small (i.e., *G. exigua*) or big (i.e., *G. celebica* and *G. mangostana* var. *mangostana*), without or with a short beak at the apex, with thick or thin pericarp, turning woody when dry; persistent stigma flattened or slightly convex, distinctly or weakly lobed; persistent sepals usually larger than in flowering materials. ***Seeds*** (1–)4–9, usually with a fleshy pulp.

Garcinia section *Garcinia* is characterized by its terminal inflorescences of simple cymes (in a cluster of two to several flowers), or sometimes a solitary flower (in the female flowers); flowers with 4 sepals and 4 petals; male flowers often with a pistillode, stamens united into a single 4-lobed or 4-angled bundle, and with 2-thecous anthers; usually multilocular ovaries, and stigmas with distinctly or weakly lobed and smooth or rough; and fruits with a smooth surface.

A section of 15 species worldwide (Gaudeul et al. 2024); three species in Thailand (i.e., two native species: *Garcinia celebica* L. and *G. exigua* Nazre, and one cultivated species and variety: *G. mangostana* L. var. *mangostana*). Numbers of species in *Garcinia* section *Garcinia* recognized by Jones (1980), Nazre et al. (2018), and Gaudeul et al. (2024) is shown in Table 1.

Table 1. Numbers of species in *Garcinia* section *Garcinia* recognized by Jones (1980), Nazre et al. (2018), and Gaudeul et al. (2024).

Jones (1980)	Nazre et al. (2018)	Gaudeul et al. (2024)
–	1. *Garcinia acuticosta* Nazre	1. *Garcinia acuticosta* Nazre
1. *Garcinia affinis* Wall.	*Garcinia affinis* Wall. ex Pierre, *nom. illeg.* = *Garcinia celebica* L. (Nazre 2010)	–
2. *Garcinia anomala* Planch. & Triana	Excluded species	Unplaced species
3. *Garcinia baillonii* Pierre	–	–
4. *Garcinia basacensis* Pierre	= *Garcinia celebica* L.	–
5. *Garcinia benthamii* Pierre	= *Garcinia celebica* L.	–
6. *Garcinia blancoi* Pierre	With unknown status	Unplaced species
7. *Garcinia calleryi* Pierre	–	–
8. *Garcinia celebica* L.	2. *Garcinia celebica* L.	2. *Garcinia celebica* L.
9. *Garcinia chapelieri* (Planch. & Triana) H. Perrier	Excluded species	*Garcinia* section *Brindonia* (Thoars) Choisy
10. *Garcinia cornea* L.	= *Garcinia celebica* L.	–
11. *Garcinia costata* Hemsl. ex King	Excluded species	*Garcinia* section *Brindonia* (Thoars) Choisy
12. *Garcinia cumingiana* Pierre	–	–
13. *Garcinia diospyrifolia* Pierre	3a. *Garcinia diospyrifolia* Pierre var. *Diospyrifolia*	3. *Garcinia diospyrifolia* Pierre
–	3b. *Garcinia diospyrifolia* Pierre var. *cataractalis* (Whitmore) Nazre	–
–	3c. *Garcinia diospyrifolia* Pierre var. *minor* Ng ex Nazre	–
–	4. *Garcinia discoidea* Nazre	4. *Garcinia discoidea* Nazre
14. *Garcinia erythrosperma* Lauterb.	With unknown status	Unplaced species
–	5. *Garcinia exigua* Nazre	5. *Garcinia exigua* Nazre
15. *Garcinia fabrilis* Miq.	= *Garcinia celebica* L.	–
16. *Garcinia fascicularis* Wall.	–	–
17. *Garcinia ferrea* Pierre	= *Garcinia celebica* L.	–
18. *Garcinia harmandii* Pierre	6. *Garcinia harmandii* Pierre	6. *Garcinia harmandii* Pierre
19. *Garcinia hombroniana* Pierre	= *Garcinia celebica* L.	–
20. *Garcinia jawoera* Pierre	= *Garcinia celebica* L.	–
21. *Garcinia kingii* Pierre ex Vesque	= *Garcinia celebica* L.	–
22. *Garcinia krawang* Pierre	= *Garcinia celebica* L.	–
23. *Garcinia kurzii* Pierre	= *Garcinia celebica* L.	–
24. *Garcinia lucens* Pierre	With unknown status	Unplaced species
25. *Garcinia macrophylla* (Miq.) Miq.	–	–
26. *Garcinia maingayi* Hook. f.	Excluded species	*Garcinia* section *Brindonia* (Thoars) Choisy
27. *Garcinia malaccensis* Hook. f.	= *Garcinia mangostana* L. *malaccensis* (Hook. f.) Nazre	–
28. *Garcinia mangostana* L.	7a. *Garcinia mangostana* L. var. *Mangostana*	7. *Garcinia mangostana* L.

Jones (1980)	Nazre et al. (2018)	Gaudeul et al. (2024)
–	7b. *Garcinia mangostana* L. var. *malaccensis* (Hook. f.) Nazre	–
–	7c. *Garcinia mangostana* L. var. *borneensis* Nazre	–
–	–	8. *Garcinia mangostifera* Kaneh. & Hatus.
29. *Garcinia moselleyana* Pierre	Excluded species	*Garcinia* section *Macrostigma* Pierre
30. *Garcinia moulmeinensis* Pierre ex Vesque	With unknown status	Unplaced species
31. *Garcinia nitida* Pierre	8. *Garcinia nitida* Pierre	9. *Garcinia nitida* Pierre
–	9. *Garcinia ochracea* Nazre	10. *Garcinia ochracea* Nazre
32. *Garcinia opaca* King	= *Garcinia diospyrifolia* Pierre	–
33. *Garcinia penangiana* Pierre	10. *Garcinia penangiana* Pierre	11. *Garcinia penangiana* Pierre
34. *Garcinia porrecta* Wall.	*Garcinia porrecta* Wall. ex Vesque = *Garcinia celebica* L. (Nazre 2010)	–
35. *Garcinia propinqua* Craib	Excluded species	Unplaced species
36. *Garcinia pseudoguttifera* Seem.	Excluded species	–
37. *Garcinia riedeliana* Pierre	= *Garcinia celebica* L.	–
38. *Garcinia rigida* Miq.	11. *Garcinia rigida* Miq.	12. *Garcinia rigida* Miq.
39. *Garcinia rumphii* Pierre	= *Garcinia celebica* L.	–
–	12. *Garcinia sangudsangud* Nazre	13. *Garcinia sangudsangud* Nazre
40. *Garcinia schefferi* Pierre	–	–
–	–	14. *Garcinia sibeswarii* Shameer, J. Sarma, N. Mohanan & A. Begum
41. *Garcinia speciosa* Wall.	= *Garcinia celebica* L.	–
42. *Garcinia squamata* Lauterb.	With unknown status	Unplaced species
43. *Garcinia tonkinensis* Vesque	Excluded species	–
44. *Garcinia trianii* Pierre	Excluded species	–
45. *Garcinia venulosa* (Blanco) Choisy	13. *Garcinia venulosa* (Blanco) Choisy	15. *Garcinia venulosa* (Blanco) Choisy
46. *Garcinia vidua* Ridl.	Excluded species	–
46 species	13 species, two of which have three varieties	15 species

A key to the species of *Garcinia* section *Garcinia* in Thailand

1 Leaves more than 6.3 × 3.2 cm, tough when crushed (in fresh leaves); petiole more than 10 × 1.5 mm; fruits more than 1.3 × 1.1 cm; bark scaly or fissured **2**

– Leaves up to 6.3 × 3.2 cm, brittle when crushed (in fresh leaves); petiole up to 10 × 1.5 mm in diam.; fruits up to 1.3 × 1.1 cm; bark mottled, flaking and leaving roundish or irregularly shaped scars .... **2. *Garcinia exigua***

2 Leaves with one intramarginal vein; petiole 2–4 mm in diam., grooved; mature flower buds up to 1 cm in diam.; female flowers 2–2.8 cm in diam.; petals creamish white or pale yellow; stigma shallowly lobed (also seen in fruiting materials); fruits yellow, orange, reddish orange to red when ripe, broadly ellipsoid, subglobose, globose or depressed globose, without or with a short, thick beak at the apex; persistent sepals usually up to 1.5 × 1.4 cm (in fruiting materials); latex white, turning yellow; found in the wild.... **1. *Garcinia celebica***

– Leaves with two intramarginal veins; petiole 4–7 mm in diam., not grooved; mature flower buds more than 1 cm in diam.; female flowers 3.2–5 cm in diam.; petals yellowish red or yellowish pink; stigma deeply lobed (also seen in fruiting materials); fruits pinkish pale yellow, pink, reddish purple to blackish purple when ripe, subglobose or globose, without a beak at the apex; persistent sepals usually up to 2.5 × 2.8 cm (in fruiting materials); latex yellow; found only in cultivation .... **3. *Garcinia mangostana* var. *mangostana***

1. *Garcinia celebica* L., Herb. Amboin.: 7. 1754; DC., Prodr. 1: 561. 1824; Miq. Fl. Ned. Ind. 1(2): 507. 1859; Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 328. 1860; Pierre, Fl. Forest. Cochinch. 1(5): 13. 1883; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 404. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Koord. & Valeton, Bijdr. Boomsoort. Java 9: 367. 1903; Backer & Bakh. f., Fl. Java (Spermatoph.) 1: 387. 1963; Nazre, Genet. Resour. Crop. Evol. 57: 1256. 2010; Nazre et al., Phytotaxa 373(1): 17. 2018. Figs 1, 2, 3

≡ *Brindonia celebica* (L.) Thouars in F. Cuvier, Dict. Sci. Nat. 5: 341. 1806.
≡ *Oxycarpus celebica* (L.) Poir., Encyc. Suppl. 4: 258. 1816.
≡ *Stalagmitis celebica* (L.) G. Don, Gen. Hist. 1: 621. 1831. Type. Rumphius's illustration, *Mangostana celebica* Rumph., Herb. Amboin. 1: 134. t. 44 (Rumphius 1741) (lectotype, designated by Merrill 1917: 373).
= *Garcinia cornea* L., Syst. Veg., ed. 13. 368. 1774; Blume, Bijdr. Fl. Ned. Ind.: 214. 1825; G. Don, Gen. Hist. 1: 620. 1831; Roxb. in Carey, Fl. Ind. 2: 629. 1832; Wight, Icon. Pl. Ind. Orient. 1(10): 6. t. 105. 1839; Miq., Fl. Ned. Ind. 1(2): 506. 1859; Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 325. 1860; Laness., Mém. Gen. Garc.: 20. 1872; Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43(2): 86. 1874 et Forest Fl. Burma 1: 88. 1877; Pierre, Fl. Forest. Cochinch. 1(5): 12. t. 78B. 1883; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 397. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Merr., Interpr. Herb. Amboin.: 374. 1917; Maheshw., Bull. Bot. Surv. India 6: 122. t. 2. fig. 16. 1964; Nazre, Genet. Resour. Crop. Evol. 57: 1256. 2010. Type. Rumphius's illustration, *Lignum corneum* Rumph., Herb. Amboin. 3: 55. t. 30 (Rumphius 1743) (lectotype, designated by Merrill 1917: 374).
= *Garcinia affinis* Wall. [Numer. List: 171. Wallich Cat. 4854. 1831, *nom. nud.*] ex Pierre, Fl. Forest. Cochinch. 1(5): 16. t. 78C, 79G. 1883, *nom. illeg.*
= *Garcinia speciosa* Wall., Pl. Asiat. Rar. 3: 37. 1832; Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 326. 1860; T. Anderson in Hook. f., Fl. Brit. India 1(2): 260. 1874; Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43(2): 86. 1874 et Forest Fl. Burma 1: 88. 1877; Pierre, Fl. Forest. Cochinch. 1(5): 14. t. 79H, I. 1883; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 59(2): 154. 1890; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 402. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Brandis, Indian Trees: 50. 1906; C. E. Parkinson, Forest Fl. Andaman Isl.: 90. 1923; Craib, Fl. Siam. 1(1): 117. 1925; Gagnep. in Gagnep., Fl. Indo-Chine Suppl.: 267. 1943; Maheshw., Bull. Bot. Surv. India 6: 123. t. 2. fig. 18. 1964; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 125. 1993; S. Gardner, P. Sidisunthorn & V. Anusarnsunthorn, Field Guide Forest Trees of N. Thailand: 50. fig. 53. 2000; Nazre, Genet. Resour. Crop. Evol. 57: 1256. 2010; S. Gardner, P. Sidisunthorn & Chayam., Forest Trees S. Thailand 1: 355. fig. 545. 2015. Type. Myanmar, Amherst, 1827, *Wallich Cat. 4855* (lectotype, designated by Maheshwari 1964: 123), CAL [CAL0000065160, photo seen]; isolectotype K-W [K001104074!]).
= *Garcinia fabrilis* Miq., Fl. Ned. Ind., Eerste Bijv. 3: 496. 1861 [as *Discostigma febrile*]; Pierre, Fl. Forest. Cochinch. 1(5): 15. t. 80A. 1883; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 401. 1893. Type. Indonesia, Sumatra, Priaman, s.d., *Diepenhorst HB2152* (lectotype, designated by Nazre 2010: 1256), L [U1572338, photo seen]).

= *Garcinia benthamii* Pierre, Fl. Forest. Cochinch. 1(4): t. 55, 56. 1882 [as *Garcinia benthami*]; Vesque, Epharmosis 2: 18. t. 109, 110. 1889 et in A. DC. & C. DC., Monogr. Phan. 8: 392. 1893 [as *G. benthami*]; Merr., Philipp. J. Sci. 3: 364. 1908 [as *G. benthami*]; Pit. in Lecomte et al., Fl. Indo-Chine 1(4): 305. 1910 [as *G. benthami*]; Merr., Enum. Philipp. Fl. Pl. 3: 83. 1923 [as *G. benthami*]; Gagnep. in Gagnep., Fl. Indo-Chine Suppl.: 261. 1943 [as *G. benthami*]; P. H. Hô, Câyco Vietnam 1: 561. fig. 1550. 1991 [as *G. benthami*]. Type. Vietnam, ad Bung in prov. Saïgon, Jan 1875, *Pierre 700* (lectotype, designated by Nazre 2010: 1256), P [P00329872, photo seen]; isolectotypes A [without barcode, reported by Nazre 2010 and Nazre et al. 2018, not seen], K [without barcode, reported by Nazre 2010 and Nazre et al. 2018, not seen], L [U1208099, U1208248, photos seen], P [P04701491, photo seen].

= *Garcinia ferrea* Pierre, Fl. Forest. Cochinch. 1(4): t. 57. 1882; Vesque, Epharmosis 2: 18. t. 110, 111. 1889; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Pit. in Lecomte et al., Fl. Indo-Chine 1(4): 303. 1910; Gagnep. in Gagnep., Fl. Indo-Chine Suppl.: 261. 1943; Pételot, Arch. Rech. Agron. Cambodge Laos Vietnam 1: 60. 1952; P. H. Hô, Câyco Vietnam 1: 562. fig. 1553. 1991. Type. Vietnam, Phu Quoc, Jan 1877, *Herb. Pierre 3634* (lectotype, first-step designated by Nazre 2010: 1256), P [without barcode], second-step designated here P [P00379823!]; isolectotype P [P00379824!]).

= *Garcinia basacensis* Pierre, Fl. Forest. Cochinch. 1(4): t. 58. 1882 [as *G. bassacensis*]; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 398. 1893 [as *G. bassacensis*]; Pit. in Lecomte et al., Fl. Indo-Chine 1(4): 306. 1910 [as *G. bassacensis*]; P. H. Hô, Câyco Vietnam 1: 561. fig. 1549. 1991 [as *G. bassacensis*]. Type. Laos, Bassin d'Attopeu, Mont de Bassac, Feb 1877, *Harmand 1074* (lectotype, first-step designated by Nazre 2010: 1256), P [without barcode], second-step designated here P [P00329871!]; isolectotypes K [K000380454!], P [P00329870!, P05062473!]).

= *Garcinia riedeliana* Pierre, Fl. Forest. Cochinch. 1(5): 12. t. 79A. 1883; Vesque, Epharmosis 2: 18. t. 156. 1889 et in A. DC. & C. DC., Monogr. Phan. 8: 388. 1893. Type. Indonesia, Sulawesi, Gorontalo, 1875, *Riedel s.n.* (lectotype, designated by Nazre et al. 2018: 17), K [K000380456, photo seen]; isolectotypes P [P04700635!, P04700640!, P04700639, photo seen]).

= *Garcinia hombroniana* Pierre, Fl. Forest. Cochinch. 1(5): 12. t. 79D–F, J. 1883; Vesque, Epharmosis 2: 18. t. 113. 1889; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 59(2): 155. 1890; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 395. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Ridl., Fl. Malay Penins. 1: 171. 1922; Craib, Fl. Siam. 1(1): 115. 1925; Corner, Wayside Trees Mal. 1: 318. fig. 109. ed. 2. 1952; Maheshw., Bull. Bot. Surv. India 6: 121. t. 2. fig. 15. 1964; Corner & Watan., Ill. Guide Trop. Pl.: t. 190. 1969; Whitmore in Whitmore, Tree Fl. Malaya 2: 212. fig. 7. 1973; S. W. Jones, Morphology and Major Taxonomy of *Garcinia* (Guttiferae), Ph.D. Thesis (unpublished): 290. 1980; H. Keng, Concise Fl. Singapore: 49. 1990; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 111. 1993; M. Turner, Gard. Bull. Singapore 47(1): 262. 1995; S. Gardner, P. Sidisunthorn & Chayam., Forest Trees S. Thailand 1: 354. fig. 544. 2015. Type. Peninsular Malaysia, Malacca, 1841, *J. B. Hombron s.n.* (lectotype, first-step designated by Nazre 2010: 1256), P [without barcode], second-step designated here P [P00329889!]; isolectotypes P [P00329878, P04700177, P04700178, P04700180, P04700181, P04700182, photos seen]).

= *Garcinia rumphii* Pierre, Fl. Forest. Cochinch. 1(5): 13. t. 77A. 1883; Vesque, Epharmosis 2: 18. t. 114. 1889 et in A. DC. & C. DC., Monogr. Phan. 8: 400. 1893. Type. Indonesia, Bangka Island, Nov 1881, *Treub 4169* (lectotype, first-step designated by Nazre 2010: 1256–1257), P [without barcode], second-step designated by Nazre et al. 2018: 17, P [P04700302!]; isolectotypes K [K000380451, photo seen], P [P04700298!, P04700299!]).

= *Garcinia kurzii* Pierre, Fl. Forest. Cochinch. 1(5): 14. t. 78A. 1883; Vesque, Epharmosis 2: 18. t. 114. 1889; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 59(2): 155. 1890; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 403. 1893; Maheshw., Bull. Bot. Surv. India 6: 123. 1964; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 115. 1993. Type. India, South Andaman, 1867, *Kurz 24* (lectotype, designated by Maheshwari 1964: 123), CAL [without barcode, not seen]; isolectotypes P [P00329891!, P00329890, photos seen]).

= *Garcinia jawoera* Pierre, Fl. Forest. Cochinch. 1(5): 37. 1883; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 399. 1893. Type. Indonesia, Java, Tandjoor, cultivated in Hort. Bog., 1877, *Pierre 4607* (lectotype, first-step designated by Nazre 2010: 1257), P [without barcode], second-step designated by Nazre et al. 2018: 17), P [P00379817!]; isolectotypes L [without barcode, reported by Nazre 2010 and Nazre et al. 2018, not seen], P [P00379816!, P00379818!]).

= *Garcinia krawang* Pierre, Fl. Forest. Cochinch. 1(5): 37. 1883; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 398. 1893. Type: Indonesia, Borneo, South Kalimantan, Pulau Lampei (Lampei Island), s.d., *Korthals 1313a* (*Herb. Pierre 4601*) (lectotype, first-step designated by Nazre 2010: 1257), P [without barcode], second-step designated by Nazre et al. 2018: 17), P [P00379812, photo seen]; isolectotype P [P00379813, photos seen]).

= *Garcinia kingii* Pierre ex Vesque in A. DC. & C. DC., Monogr. Phan. 8: 407. 1893; Maheshw., Bull. Bot. Surv. India 6: 124. 1964; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 114. 1993. Type: Andaman Island, 1884, *King's Collector s.n.* (lectotype, designated by Nazre 2010: 1257), K [K000380453, photo seen]).

Description. ***Habit*** trees, 5–25-(–30) m tall, 30–150(–200) cm GBH, sometimes with buttresses near the base of the main stem of large trees; latex white, turning yellow, sticky; branchlets green, 4-ridged, glabrous. ***Bark*** greyish brown, brown, dark brown or blackish brown, scaly or fissured; inner bark reddish pink or red. ***Leaves***: lamina variable in shape and size, elliptic, oblong-elliptic, ovate, elliptic-ovate or lanceolate-ovate, 10–24 × 4–9.5 cm, apex acute, base cuneate or oblique, margin repand or undulate, thickly coriaceous, smooth, shiny dark green above, paler below, glabrous on both surfaces, midrib raised on both surfaces, secondary veins 12–25 each side, curving towards the margin and connected in distinct loops and united into an intramarginal vein, flattened on both surfaces, intramarginal veins not grooved above, with intersecondary veins, veinlets reticulate, visible below, interrupted long wavy lines of differing lengths, running across the secondary veins to the apex, conspicuous below; petiole green, stout, 1–2 cm long, 2–4 mm in diam., grooved above, distinctly transversely rugose, glabrous, with a basal appendage clasping the branchlet; young leaves brownish green, turning pale green, glossy; fresh leaves tough when crushed; mature leaves turning greenish yellow to pale yellow before falling off; dry leaves pale brown or reddish brown. ***Inflorescences*** terminal; bracts 2, caducous, narrowly triangular or triangular, 0.8–1.3 × 0.1–0.4 cm, apex acute (in female inflorescences). ***Flowers***: sepals and petals glabrous; sepals concave; petals creamish white or pale yellow, somewhat fleshy, concave or not concave, apex rounded, margin entire or irregularly lobed and undulated. ***Flower buds*** subglobose to globose, 0.5–1 cm in diam. ***Male flowers*** lightly fragrant, in a cluster of 2–7 flowers, 1.8–2.5 cm in diam.; bracteoles caducous; pedicel pale yellow, reddish pale yellow or yellowish red, slender, terete (circular in cross-section) or slightly 4-angled, 0.4–1 cm long, 1.5–3 mm in diam., glabrous; sepals 4, pale yellow, reddish pale yellow or yellowish red, thinly coriaceous, broadly elliptic, elliptic, suborbicular or orbicular, 0.5–1 × 0.4–1 cm, the outer pair slightly smaller than the inner pair, apex rounded; petals 4, suborbicular, orbicular, broadly elliptic or elliptic, 0.7–1.2 × 0.5–1.1 cm, subequal; stamens 144–198, united into a single 4-lobed bundle (35–53 each lobe), surrounding a pistillode, lobes 5–9 × 5–8.5 mm; filaments very short; anthers 1–2 × 0.5–1 mm; pistillode fungiform, 5–7.5 mm long; sterile stigma pale yellow or yellow, sessile, convex, radiate, shallowly 4–9-lobed, 3.5–5 mm in diam., smooth. ***Female flowers*** solitary or in a cluster of 2–3 flowers, 2–2.8 cm in diam.; bracteoles caducous, triangular, 1.5–5 × 1–4 mm; pedicel (of a flower in an inflorescence) or peduncle (of a solitary flower) green, stout, terete or slightly 4-angled, 0.4–1.5 cm long, 2–4 mm in diam., glabrous; sepals 4, pale green, thickly coriaceous, suborbicular, orbicular or broadly elliptic, 0.4–1.2 × 0.4–1.2 cm, the outer pair slightly smaller than the inner pair, apex rounded; petals 4, suborbicular, orbicular, broadly elliptic or elliptic, 0.7–1.5 × 0.7–1.3 cm, subequal; staminodes absent or present, united into 9–15 bundles, surrounding the ovary, each bundle 1–2 mm long; pistil fungiform, 0.5–1 cm long; ovary pale green, subglobose or globose, 4–6.5 × 4–7.5 mm, glabrous, 4–9-locular; stigma pale yellow or yellow, convex, radiate, shallowly 4–9-lobed, 2–4 mm long, 5.5–8 mm in diam., smooth. ***Fruits*** pale green, turning yellow, orange, reddish orange to red when ripe, smooth, glabrous, with a sticky white latex, turning yellow, broadly ellipsoid, subglobose, globose or depressed globose, 1.8–5.5 × 2–5.6 cm (length including a beak), without or with a short, thick beak at the apex, 2.5–6.5 × 5–11.5 mm, pericarp 2–7 mm thick, fleshy, becoming woody when dry; persistent stigma dark brown or blackish brown, flattened, radiate, shallowly 4–9-lobed, 0.4–1.1 cm in diam.; persistent sepals green or green tinged with red, turning yellowish green to yellow or yellow tinged with red, thickly coriaceous, 0.5–1.5 × 0.5–1.4 cm, usually larger than in flowering materials; fruiting stalk green, strong and thick, 0.5–1.7 cm long, 2.5–6.5 mm in diam., glabrous. ***Seeds*** 4–9, sometimes aborted, brown mottled with irregular lines, ellipsoid or broadly ellipsoid, 0.7–2.4 × 0.4–1.6 cm, compressed, rounded at both ends, with a white fleshy pulp.

Distribution. India [North-Eastern India (Assam, Meghalaya, West Bengal), Andaman and Nicobar Islands], Bangladesh, Myanmar (Martaban, Tenasserim), Vietnam, Laos, Cambodia, Thailand, Peninsular Malaysia (Perlis, Kedah, Penang, Perak, Terengganu, Pahang, Selangor, Malacca), Singapore, Indonesia (Sumatra, Java, Lesser Sunda Islands, Sulawesi, Maluku), Borneo [Malaysia (Sarawak, Sabah), Brunei, Indonesia (Kalimantan)], Philippines (Luzon, Palawan, Mindanao), New Guinea [Indonesia (Western New Guinea), Papua New Guinea].

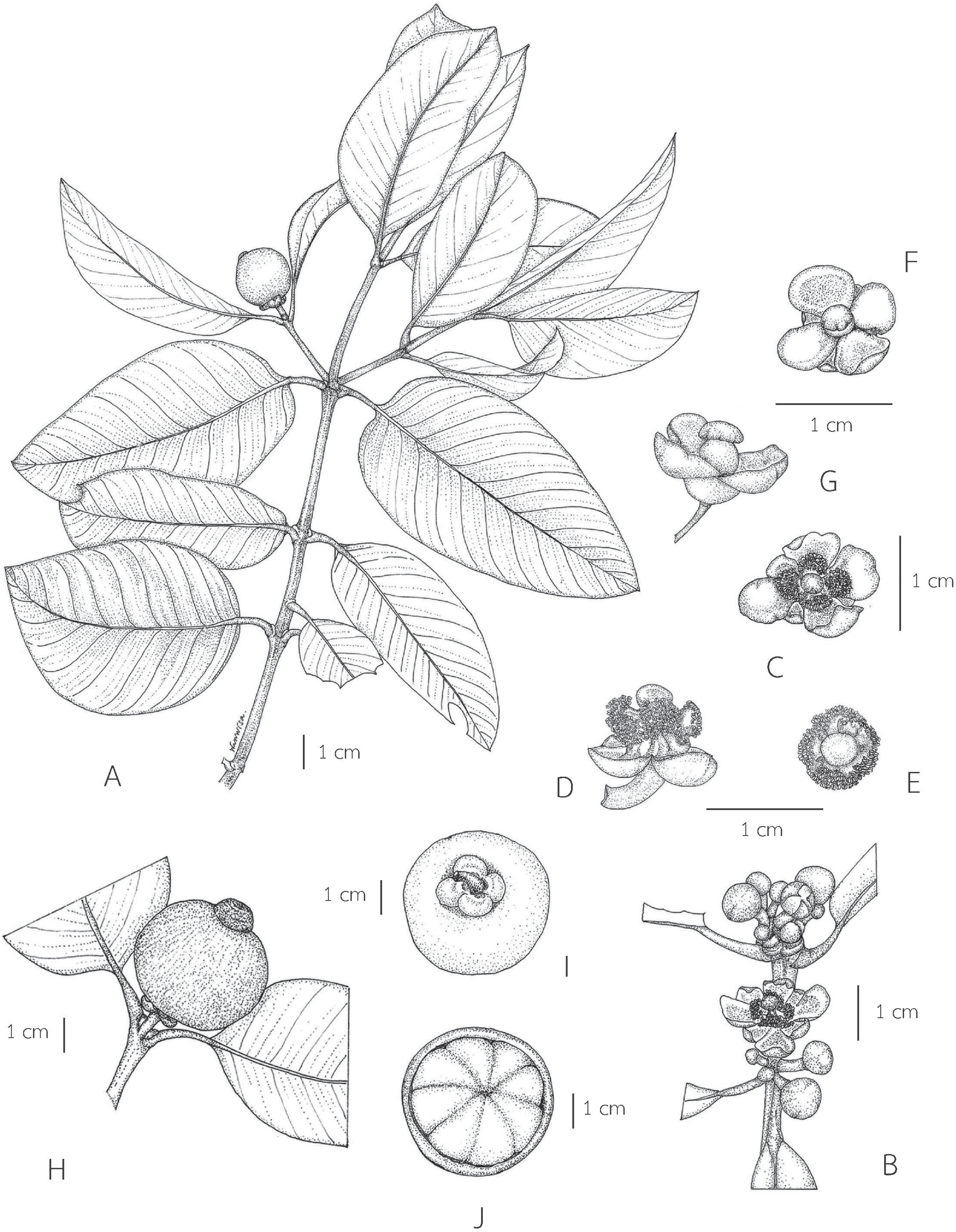

Figure 1. *Garcinia celebica* **A** branchlets, leaves, and fruit **B** branchlets and male inflorescences with male flower buds and male flower **C** male flower (top view) **D** male flower (side view) **E** male flower showing 4-lobed stamen bundle and a pistillode (sepals and petals removed) **F** female flower (top view) **G** female flower (side view) **H** branchlet and fruit **I** fruit showing persistent sepals **J** fruit (transverse section) and seeds with a fleshy pulp. Photo: Drawn by Wanwisa Bhuchaisri.

Distribution in Thailand. Northern: Chiang Mai, Chiang Rai, Phayao, Phrae, Phitsanulok; **North-Eastern:** Loei, Nong Khai, Bueng Kan, Sakon Nakhon, Khon Kaen; **Eastern:** Chaiyaphum, Ubon Ratchathani; **South-Western:** Uthai Thani, Kanchanaburi, Phetchaburi, Prachuap Khiri Khan; **Central:** Saraburi; **South-Eastern:** Sa Kaeo, Prachin Buri, Chon Buri, Chanthaburi, Trat; **Peninsular:** Chumphon, Ranong, Surat Thani, Phangnga, Krabi, Nakhon Si Thammarat, Trang, Satun, Songkhla, Pattani, Yala, Narathiwat.

Habitat and ecology. This species is found in a very wide variety of habitats, including coastal strand vegetations, littoral dry evergreen forests, dry evergreen forests, tropical evergreen rain forests, freshwater swamp forests, lower montane rain forests, lower montane coniferous forests, pine-deciduous dipterocarp forests, mixed deciduous forests, secondary forests, on limestones, on sandstone plateaus, sometimes along streams, 0–1,500 m amsl.

Phenology. Flowering and fruiting more than once, nearly throughout the year; flowering usually in November to February; fruiting usually in February to May.

Conservation status. *Garcinia celebica* is widely distributed from Eastern India to the Malesian region. It is known from many localities and has a large Extent of Occurrence (EOO) of 21,968,911.92 km^2 and a relatively large Area of Occupancy (AOO) of 700 km^2. In Thailand, this species is known to be naturally distributed throughout the seven floristic regions, and has an EOO of 427,003.87 km^2 and an AOO of 96 km^2. Because of this wide distribution and the number of localities, therefore, we consider the conservation assessment here as Least Concern (LC).

Etymology. The specific epithet of *Garcinia celebica* indicates the type locality, Sulawesi (formerly known as Celebes), Indonesia (Nazre 2010), as described by Rumphius (1741). The specific epithet of *G. speciosa* is a Latin word meaning showy or splendid (Stearn 1992; Gledhill, 2002) and refers to the ripe fruits are orangish red to red. The specific epithet of *G. hombroniana* is named after J. B. Hombron, a French physician and explorer who collected the type specimen during his journey from Singapore to Malacca (Peninsular Malaysia) (Corner 1952; Whitmore 1973; Nazre 2010).

Vernacular names. Kwak mai (กวกไหม) (Bueng Kan, Nongkhai, Laos); Kawa (กะวา) (Surat Thani); Khwat (ขวาด) (Chiang Rai, Laos); Chamuang (ชะม่วง) (Phichit); **Phawa** (พะวา) (Surat Thani); Mada khinok (มะดะขีนก) (Chiang Mai, Laos); Mapong (มะปอง) (Northern); Mangkhut pa (มังคุดปา) (Narathiwat); Wa (วา) (Phangnga, Songkhla, Surat Thani, Yala); Wa nam (วาน้ำ) (Trang); Sommong Pa (ส้มโมงปา) (Nongkhai); Saraphi pa (สารภีปา) (Central, Chiang Mai); Mak kwak (หมากกวก) (Bueng Kan, Nongkhai, Laos); Beruas, Bruas, Mangis hutan (Peninsular Malaysia); Parawa (Myanmar); Jungle mangosteen, Seashore mangosteen (English).

Uses. The fleshy pulp surrounding the seeds can be consumed and has a sweet-sour taste. The wood is used for house construction, making oars (Maheshwari 1964; Burkill et al. 1966), the handles of the tools, and bridge posts (Maheshwari 1964). In Andaman Islands, the wood is used for making bows (Maheshwari 1964). In Malaysia, *Garcinia celebica* have been recorded at more than 50 cm dbh and may be logged for timber (Nazre et al. 2018). The fruits are reported to cause constipation (Sastri 1956). In Peninsular Malaysia, the roots and leaves are used to relieve itching (Sastri 1956; Maheshwari 1964). A decoction of the root may be administered after childbirth as a preventive medicine (Burkill et al. 1966).

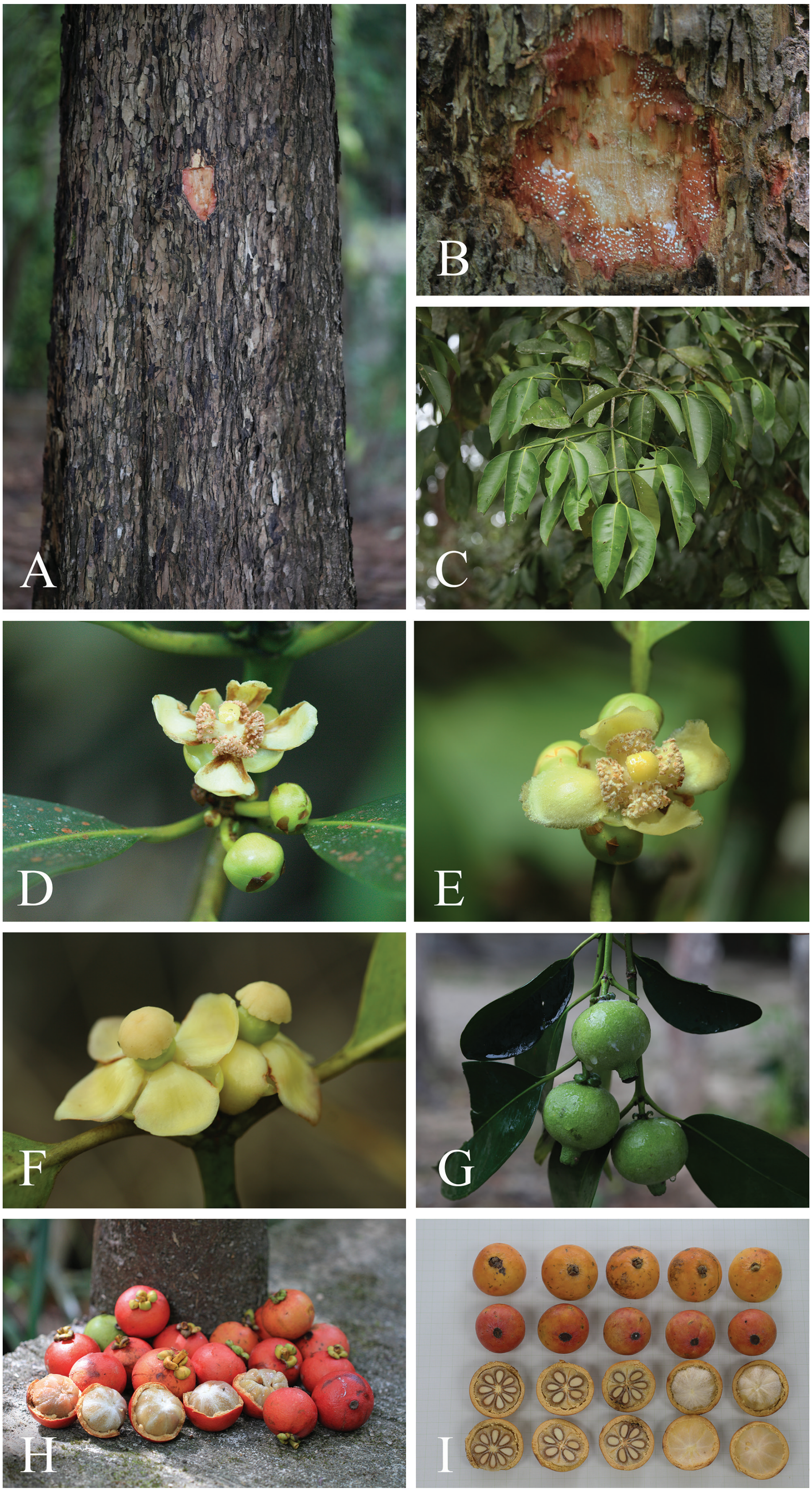

Figure 2. *Garcinia celebica* **A** stem and bark **B** slashed bark with white latex **C** branchlets and leaves **D, E** branchlets and male inflorescences with male flower buds and male flowers **F** branchlet and female inflorescence with female flowers **G** branchlets, leaves, and mature fruits **H, I** mature and ripe fruits and seeds with a white fleshy pulp. Photos: Chatchai Ngernsaengsaruay.

Lectotypifications. *Garcinia ferrea* was named by Pierre (1882: t. 57), who cited three gatherings: *Herb. Pierre 3634*, *3635*, and *3695* but he did not mention the name of the herbarium where the materials were kept, and following Art. 9.6 of the ICN (Turland et al. 2018), they constitute syntypes. The name *G. ferrea* has been lectotypified twice, first by Nazre (2010: 1256), who selected a specimen *Herb. Pierre 3634* in Cambodia, and deposited at P [without barcode], while Nazre et al. (2018: 17) chose a Cambodian specimen of Pierre (*Herb. Pierre 3635*) housed at P [P00329882]. Hence, the first lectotypification has priority (as the first-step). We located two sheets of the specimen *Herb. Pierre 3634* at P [P00379823, P00379824]; therefore, the P [P00379823] specimen is selected here in a second-step lectotypification (following Art. 9.17 and Ex. 14 of the Shenzhen Code). Incidentally, from our examination of specimens at P Herbarium, *Herb. Pierre 3634* (Phu Quoc) and *Herb. Pierre 3635* (in montibus Dinh ad Baria Gallicae Austro-Cochinchinae) were not collected from Cambodia as mentioned by Nazre (2010) and Nazre et al. (2018), but were collected in Vietnam.

In the original publication of *Garcinia basacensis* by Pierre (1882: t. 58), only one gathering is mentioned, *Hermand 1074* (*Herb. Pierre 3637*). The name *G. basacensis* has been lectotypified twice, firstly, Nazre (2010: 1256) lectotypified this name using the material at P [without barcode], with an isolectotype at K [without barcode] collected from Laos, and secondly, Nazre et al. (2018: 17) lectotypified this name using the same material. Therefore, the first lectotypification has priority (as the first-step). However, there are three sheets of this gathering at P [P00329870, P00329871, P05062473] and the P [P00329871] material is selected here in a second-step lectotypification. We located one sheet of isolectotype at K [K000380454].

Garcinia hombroniana was named by Pierre (1883: 12. t. 79D–F, J) based on the specimens collected from Ile de Singapoor-Détroit de Malacca. He did not designate a holotype nor did he mention the name of the herbarium where the specimens were housed. The name *G. hombroniana* has been lectotypified twice, first by Nazre (2010: 1256), who designated the specimen collected by J. B. Hombron (*Hombron s.n.*) from Malacca housed in P [without barcode], and second by Nazre et al. (2018: 17), who selected the same specimen. Therefore, the first lectotypification has priority (as the first-step). We traced seven specimens of *J. B. Hombron s.n.* at P [P00329878, P00329889, P04700177, P04700178, P04700180, P04700181, P04700182]. The P [P00329889] specimen is better preserved and more complete than the others, and hence is chosen here as the second-step lectotype.

Notes. According to Nazre et al. (2018), the shape and size of leaves of *Garcinia celebica* are elliptic, broadly elliptic, lanceolate, sub-orbiculate or round and 3.3–17.5 × 1.7–11 cm; the male inflorescences in clusters of 2–14(–18) flowers; the staminodes are absent; the ovaries have 4–6 locules; and the shape and size of fruits are ovoid, ellipsoid or globose and up to 5 cm across. Furthermore, from our examinations, we found the shape and size of leaves of this species can be elliptic, oblong-elliptic, ovate, elliptic-ovate or lanceolate-ovate and sometimes larger, 10–24 × 4–9.5 cm; the male inflorescences in clusters of 2–7 flowers; the staminodes are absent or present; the ovaries have 4–9 locules; and the shape and size of fruits can be broadly ellipsoid, subglobose, globose or depressed globose and sometimes larger, 1.8–5.5 × 2–5.6 cm, without or with a short, thick beak at the apex.

Figure 3. Lectotype of *Garcinia hombroniana*, a synonym of *Garcinia celebica*, *J. B. Hombron s.n.* (P [P00329889]) from Malacca, Peninsular Malaysia, second-step lectotype designated here. Photo: Muséum National d'Histoire Naturelle, Paris, France, http://coldb.mnhn.fr/catalognumber/mnhn/p/p00329889.

Nazre (2010: 1256) notes that no type specimen was mentioned by Wallich (Wallich, 1832) in his description of *Garcinia speciosa* but appeared earlier in *Wallich Catalogue 4855* (Wallich, 1828–1849) collected from Amherst, Myanmar which Maheshwari (1964: 123) considered the specimen at CAL [without barcode] as the lectotype, and Nazre et al. (2018: 17) mentioned with an isolectotype at K-W [without barcode]. However, we located the lectotype at CAL [CAL0000065160] and isolectotype at K-W [K001104074].

In the original description of *Garcinia benthamii* by Pierre (1882: t. 55, 56.), only one specimen is cited, "*Herb. Pierre n° 70*" collected from Cambodia but he did not select a holotype nor did he mention the name of the herbarium where the specimen was housed, and following Art. 9.6 of the ICN (Turland et al. 2018), it constitutes a syntype. The name *G. benthamii* has been lectotypified by Nazre (2010: 1256), who designated the specimen *Pierre 700* collected from Cambodia, and deposited at P [P00329872], with isolectotypes at A [without barcode] and K [without barcode]. However, this specimen has a different collector number than that reported in the original publication of this name. According to Nazre (2010), type specimens of *G. benthamii* have multiple sheets taken from different localities in Cambodia and Vietnam where some were cultivated. However, based on the *Pierre 700* sheets that we examined from P [P00329872, P04701491] and L [U1208099, U1208248], they were all collected in Vietnam (ad Bung in prov. Saïgon). We have not seen isolectotypes at A and K. The collector number *Pierre 70* cited in Pierre (1882) appears to have been an error and should have been *700*.

Garcinia riedeliana was named by Pierre (1883: 12. t. 79A), who stated only one specimen, *Riedel s.n.* collected from Gorontalo, Sulawesi (also known as Celebes). Nazre et al. (2018: 17) designated this material at K [without barcode] as the lectotype, with an isolectotype at P [without barcode]. However, we could locate the lectotype at K [K000380456] and we located three sheets of isolectotypes at P [P04700635, P04700639, P04700640].

Garcinia rumphii was named by Pierre (1883: 13. t. 77A), who cited two specimens: *Treub 4168* and *Treub 4169* collected from Bangka Island, Indonesia. He did not mention the name of the herbarium where the materials were kept, and following Art. 9.6 of the ICN (Turland et al. 2018), they constitute syntypes. The name *G. rumphii* has been lectotypified in a first-step by Nazre (2010: 1256–1257) using the material *Treub 4169* at P [without barcode], and in a second-step by Nazre et al. (2018: 17) using the material *Treub 4169* at P [P04700302], with isolectotypes at P [P04700298, P04700299, P04700301]. However, from our examination of specimens, we found that the P [P04700301] sheet is labeled with *Treub 4168*. We also located one sheet of isolectotype at K [K000380451].

In the original publication of *Garcinia kurzii* by Pierre (1883: 14. t. 78A.), only one gathering is stated, *Kurz 24* collected from Andamans. He did not mention the name of the herbarium in which it was present, and following Art. 9.6 of the ICN (Turland et al. 2018), it constitutes a syntype. Maheshwari (1964: 123) selected a specimen at CAL [without barcode] as the lectotype, without isolectotype. However, we could not locate the lectotype at CAL, and we could trace two sheets of isolectotypes at P [P00329890, P00329891].

Pierre (1883: 37) established *Garcinia jawoera* based on the materials collected from Tandjoor, Java but he did not choose a holotype nor did he mention the name of the herbarium where the specimens were housed. This name has been lectotypified twice, first by Nazre (2010: 1257), who designated the material *Pierre 4607* at P [without barcode] collected from Tandjoor, Java, with isolectotypes at P [without barcode] and L [without barcode], and second time by Nazre et al. (2018: 17), who selected the same collection at P [P00379817], with isolectotypes L [without barcode] and P [P00379816, P00379818]. We have not seen the isolectotype at L.

Pierre (1883: 37) erected *Garcinia krawang* based on the specimen *Korthals 1313a* collected from Pulau Lampei (Lampei Island), South Kalimantan, Borneo. The name *G. krawang* has been lectotypified in a first-step by Nazre (2010: 1257) using the specimen *Korthals 1313a* at P [without barcode], and in a second-step by Nazre et al. (2018: 17) using the specimen *Korthals 1313a* (*Herb. Pierre 4601*) at P [P00379812], without isolectotype. However, we located an isolectotype at P [P00379813].

Garcinia kingii was named by Pierre but unpublished, and then this name was described by Vesque (1893: 407) based on the specimen collected from Andaman Island. This name has been lectotypified twice, first by Nazre (2010: 1257), who selected the specimen collected by King (*King's Collector s.n.*) from Andaman Island housed in K [without barcode], and then again by Nazre et al. (2018: 17), who designated the same specimen. The first lectotypification has priority. We viewed the lectotype at K [K000380453].

Additional specimens examined. Thailand. Northern. Chiang Mai [Mae Kuang, near Doi Saket, female fl., 1 Mar 1910 (as *G. cornea*), *A. F. G. Kerr 1020* (BM, K); Doi Suthep, male fl., 27 Mar 1910 (as *G. cornea*), *A. F. G. Kerr 1073* (BM, K, L [L2408860]); Doi Suthep, fl., 11 Feb 1923 (as *G. cornea*), *Winit s.n.* (BK, BM); Suthep Subdistrict, male fl., 5 Mar 1937 (as *G. speciosa*), *J. Samutnavee 13/2481* (BKF); Doi Suthep, fr., 28 Apr 1958 (as *G. speciosa*), *T. SØrensen* et al. *3103* (BKF, C); Doi Suthep, 12 Jul 1958 (as *Garcinia* sp.), *T. SØrensen* et al. *4025* (C); Doi Suthep, 5 Oct 1958 (as *Garcinia* sp.), *T. SØrensen* et al. *5460* (C); Doi Suthep, 19 Feb 1959 (as *G. speciosa*), *T. SØrensen* et al. *6958* (BKF, C); Montha Than Waterfall, Doi Suthep, sterile, 5 Feb 1983 (as *G. thorelii*), *W. Wattanadechseri 25205368* (QBG); Doi Suthep, male fl., 16 Feb 1988 (as *G. speciosa*), *J. F. Maxwell 88-190* (AAU, BKF, L [L2408855]); Doi Suthep-Pui National Park, sterile, 23 Apr 2003 (as *G. speciosa*), *J. F. Maxwell* et al. *4* (CMUB); Mae Khan, male fl., Mar 1913 (as *G. cornea*), *Winit 70* (BM, K); Doi Inthanon, fr., 9 May 1958 (as *G. speciosa*), *T. SØrensen* et al. *3334* (BKF, C); Wachirathan Waterfall, Doi Inthanon, male fl., 27 Feb 1979 (as *G. speciosa*), *H. Koyama* et al. *15566* (AAU, BKF); Doi Inthanon National Park, sterile, 21 Jul 1988 (as *G.* cf. *vilersiana*), *C. Phengklai* et al. *6708* (BKF); Ban Mae Bon, Phrao District, fr., 12 Jul 1996 (as *G.* cf. *speciosa*), *BGO Staff 6823* (QBG); Ban Kio Lom, Bo Luang Subdistrict, Hot District, male fl., 18 Mar 2003 (as *Garcinia* sp.), *T. Wongprasert 033-53* (BKF); Forest Fire Control Station, Doi Inthanon National Park, fr., 18 May 2003 (as *Garcinia* sp.), *T. Wongprasert & S. Khaoiam 035-25* (BKF)]; Chiang Rai [Doi Duan, male fl., 19 Mar 1921 (as *G. speciosa*), *A. F. G. Kerr 5107* (BM, K, P [P04899657]); Mae Fang, fl., 3 Mar 1928 (as *Garcinia* sp.), *Winit 1876* (BK, K)]; Phayao [Doi Luang National Park, Mueang Phayao District, fl., 10 Feb 2016 [as *G. propinqua*], *N. Muangyen 717* (QBG)]; Phrae [Mae Yuak, male fl., 3 Mar 1911 (as *G. speciosa*), *Luang Vanpruk 237* (BKF)]; Phitsanulok [Thung Salaeng Luang National Park, fr., 20 Jun1967 (as *Garcinia* sp.), *S. Phusomsaeng 243* (BKF); Lan Hin Taek, Phu Hin Rong Kla National Park, Nakhon Thai District, female fl., 24 Feb 2007, *C. Ngernsaengsaruay G52-24022007* (BKF, spirit material)]; **North-Eastern.** Loei [Phu Kradueng, Wang Saphung District, male fl., 6 Mar

1942 (as *G. speciosa*), *Amporn 128* (BKF); Phu Kradueng, male fl., 6 Mar 1942 (as *G. speciosa*), *Warison 128* (BKF 2834); Phu Kradueng, male fl., 6 Mar 1946 (as *Garcinia* sp.), *Nat 214* (P [P05062030]); Phu Kradueng, fl., 13 Mar 1948 (as *G. speciosa*), *K. Suvatabundhu 83*, *84* (BK); Phu Kradueng, fr., 20 Apr 1955 (as *G. speciosa*), *T. Smitinand 2483* (BKF); near Huai Phai Waterfall, Phu Ruea National Park, male fl., 4 Mar 1993 (as *Garcinia* sp.), *P. Chantaranothai* et al. *1034* (BKF); Na Haeo, young fr., 26 Apr 1994 (as *G. cowa*), *W. Nanakorn* et al. (*BGO. Staff*) *3186* (AAU, QBG); en route from Khok Nok Kraba to Lon Tae, Phu Luang Wildlife Sanctuary, very young fr., 14 May 1998 (as *Garcinia* sp.), *T. Wongprasert* et al. *s.n.* (BKF 123962); Phu Luang Wildlife Sanctuary, very young fr., 14 May 1998 (as *Garcinia* sp.), *K. Chayamarit* et al. *1398* (BKF); Huai Baeng Forest Protection Station, Phu Luang Wildlife Sanctuary, fr., 22 Jun 2003 (as *Garcinia* sp.), *T. Wongprasert 036-46* (BKF); Phu Luang Wildlife Sanctuary, fr., 11 Jun 2023, *C. Ngernsaengsaruay G53-11062023* (BKF); Phu Ruea National Park, fr., 23 Mar 2004 (as *Garcinia* sp.), *S. Bunwong* et al. *267* (AAU); Phu Ruea District, fr., 23 Jul 2007 (as *Garcinia* sp.), *T. Wongprasert 077-31* (BKF)]; Nong Khai [Phon Phisai District, male fl., 25 Feb 1924 (as *G. speciosa*), *A. F. G. Kerr 8572*, *8572A* (BK, BM, K)]; Bueng Kan [Mueang Bueng Kan District (formerly Chaiyaburi), fl., 20 Feb 1924 (as *G. speciosa*), *A. F. G. Kerr 8513* (BM, K); Chet Si Waterfall, Seka District, male fl., 25 Feb 2003 (as *Garcinia* sp.), *T. Wongprasert 032-30* (BKF)]; Sakon Nakhon [Phu Phan National Park, male fl., 9 Mar 1996 (as *G. hombroniana*), *P. Puudjaa* 194 (BKF)]; Khon Kaen [Locality not specified, female fl. and young fr., 20 Mar 1942 (as *G. speciosa*), *Jirapha 36* (BKF 8457)]; **Eastern.** Chaiyaphum [Phu Khiao, male fl., 25 Feb 1931 (as *G. speciosa*), *A. F. G. Kerr 20261* (BK, BM, K); Phu Khiao, fr., 3 Aug 1972 (as *Garcnia* sp.), *K. Larsen* et al. *31355* (AAU); Ban Nam Phrom, young fr., 24 May 1974 (as *G. speciosa*), *R. Geesink* et al. *6922* (AAU, BKF, C, K, L [L 0089486], P [P05061691]); Tat Ton Waterfall, Tat Ton National Park, fr., 19 Jun 2003 (as *Garcnia* sp.), *T. Wongprasert 036-3* (BKF)]; Ubon Ratchathani [Huai Phok Waterfall, Dong Na Tham Forest, Pha Taem National Park, Khong Chiam District, fr., 1 Mar 2007 (as *G. cowa*), *S. Suddee* et al. *3082* (BKF)]; **South-Western.** Uthai Thani [Ban Rai District, fr., 17 Nov 1961 (as *Garcnia* sp.), *B. Sangkhachand 250* (AAU, C, K); Huai Kha Khaeng Wildlife Sanctuary, Ban Rai District, male fl., 20 Feb 1970 (as *G.* cf. *hombroniana*), *C. F. van Beusekom & T. Santisuk 2866* (AAU, BKF, C, E [E00839762], P [P05062059]); ibid., female fl., 20 Feb 1970 (as *G.* cf. *hombroniana*), *C. F. van Beusekom & T. Santisuk 2879* (AAU, BKF, C, E [E00839761], P [P05062010]); ibid., male fl., 22 Feb 1970 (as *G.* cf. *hombroniana*), *C. F. van Beusekom & T. Santisuk 2916* (AAU, BKF); Huai Kha Khaeng Wildlife Sanctuary, fr., 10 Apr 1996 (as *Garcnia* sp.), *T. Wongprasert* et al. *s.n.* (BKF 109898)]; Kanchanaburi [Ban Cha Kae Yai, male fl., 28 Feb 1973 (as *Garcnia* sp.), *C. Phengklai* et al. *3069* (BKF, C, K, L [L2409478], P [P05062048]); Than Thong Waterfall trail, Chaloem Rattanakosin National Park, Si Sawat District, sterile, 28 Mar 2018 (as *G. mangostana*), *W. La-ongsri* et al. *5577* (QBG)]; Phetchaburi [Kaeng Krachan National Park, sterile, 8 Mar 1994 (as *G. hombroniana*), *T. Santisuk* et al. *s.n.* (BKF); Kaeng Krachan National Park, male fl., 29 Jan 2005 (as *Garcnia* sp.), *K. Williams* et al. *1189* (BKF)]; Prachuap Khiri Khan [Bang Saphan Yai, Bang Saphan District. male fl., 13 Nov 1944 (as *G. hombroniana*), *Taew 117* (BKF); Huai Yang National Park, Thap Sakae District, male fl., 26 Jan 2004 (as *Garcnia* sp.), *D. J. Middleton* et al. *2509* (A [00466332], BKF)]; **Central.** Saraburi [Phu Khae Botanical Garden, 23 Apr 2017, *C. Ngernsaengsaruay* own observation] **South-Eastern.** Sa Kaeo [Nong I Lom, sterile, 15 Mar 1932 (as *G. speciosa*), *Unkonwn 82* (BKF 209)]; Prachin Buri [Yan Ri Subdistrict, Kabin Buri District, sterile, 13 Jun 1936 (as *G. speciosa*), *S. Arirop s.n.* (BKF)]; Chon Buri [Si Racha District, fr., 14 Apr 1922 (as *G. speciosa*), *D. J. Collins 788* (BK, K); Si Racha District, fl. buds, 23 Apr 1923 (as *G. speciosa*), *D. J. Collins 898* (BK, K, L [L0535229, L2408870]); Nong Nok Takrum, near Si Racha District, male fl., 3 Nov 1927 (as *G.* cf. *cornea*), *D. J. Collins 1693* (BK, K, L [L2408856]); Si Racha District, young fr., 19 Dec1927 (as *G.* cf. *speciosa*), *D. J. Collins 1823* (BK, BM, K); Si Racha District, male fl., Nov 1934 (as *G. speciosa*), *D. J. Collins s.n.* (K, P [P04701267]); Ko Khram, Sattahip District, male fl., 22 Oct 1999 (as *G. speciosa*), *C. Phengklai* et al. *12064* (BKF); Khao Khiao Open Zoo, very young fr., 10 Dec 2000 (as *G. speciosa*), *C. Phengklai* et al. *12847* (BKF)]; Chanthaburi [Khlung District, young fr., 3 Dec 1924 (as *G.* cf. *speciosa*), *A. F. G. Kerr 9526* (BK, BM, K); Khao Khitchakut National Park, fr., 14 Apr 1925 (as *G. speciosa*), *Nai Noe 71* (BK, BM, K); Ban Phluang, fl., 24 Nov 1930 (as *G.* cf. *speciosa*), *M. C. Lakshnakara 522* (BK, C, K, L [L2408869], P [P04701266]); Pong Nam Ron District, male fl., 19 Feb 1956 (as *Garcnia* sp.), *B. Sangkhachand 600* (C, P [P05062028]); Makham District, fr., 12 Jan 1958 (as *Garcnia* sp.), *T. SØrensen* et al. *162*, *163* (C); Khao Khitchakut National Park, fr., 8 Feb 1987 (as *G. hombroniana*), *C. Niyomdham* et al. *1319* (AAU, BKF, C, K); Trat [Bo Rai District, male fl., 27 Nov 1924 (as *G. speciosa*), *A. F. G. Kerr 9451* (BM, K); Dan Chumphon, fr., 19 Dec 1929 (as *G.* cf. *speciosa*), *A. F. G. Kerr 17613* (BK, BM, K); Khao Kuap, fl., 26 Dec 1929 (*Garcinia* sp.), *A. F. G. Kerr 17784* (BK); Ko Chang, fr., 22 Feb 1955 (as *G. hombroniana*), *T. Smitinand 2274* (BKF); Than Mayom Waterfall, Ko Chang, fr., 12 Mar 1970 (as *Garcinia* sp.), *C. F. van Beusekom & T. Santisuk 3195* (AAU, BKF, C, L [L0089540, L2409572, L2409573], P [P04700768]); Ao Salat, Ko Kut, fr., 5 Apr 1959 (as *G. hombroniana*), *T. Smitinand 5678* (BKF); Ko Kut, fr., 5 Apr 1959 (as *Garcinia* sp.), *T. SØrensen* et al. *7177* (BKF, C); Ko Kut, female fl. and young fr., 20 Oct 2000 (as *G. speciosa*), *C. Phengklai* et al. *13092* (BKF); Khlong Chao, Ao Phrao, Ko Kut [Leaves belong to *G. celebica* but fruits belong to *G. cowa*], 7 Apr 2002 (as *G. speciosa*), *C. Phengklai* et al. *13468* (BKF); Khao Lan, Khlong Yai District, fr., 24 Feb 2018, *C. Ngernsaengsaruay G53-24022018* (BKF); Ko Kut, 15 Oct 2022, *C. Ngernsaengsaruay* own observation]; **Peninsular.** Chumphon [Ban Thung Kha, young fr., 13 Jan 1927 (as *G.* cf. *speciosa*), *A. F. G. Kerr 11412* (BK, BM, K); Sand dune, Pathio District, 24 Apr 2022, *C. Ngernsaengsaruay* own observation]; Ranong [Ko Boi Noi, fr., 22 Feb 1966 (as *G. hombroniana*), *Sakol Sutheesorn 902* (BK)]; Surat Thani [Ko Tao, fr., 30 Dec 1926 (as *G. speciosa*), *A. F. G. Kerr 11179* (BM, C, K, L [L2408868], P [P04701273]); Ko Tao, male fl., 15 Apr 1927 (as *G.* cf. *cornea*), *A. F. G. Kerr 12752* (BM, K, L [L2408857]); Tha Khanon Subdistict, fl., 28 Aug 1931 (as *G. speciosa*), *Luang Saman 45* (BKF); Tha Chang District, fl., 15 Jan 1935 (as *G. hombroniana*), *Luang Saman 2585* (C, SING); Khao Tok Nong, Thung Thong Non-hunting Area, Khiansa District, fl., 23 Apr 2005 (as *Garcnia* sp.), *R. Pooma* et al. *5172* (AAU, BKF); Ko Pha Luai, male fl., 21 Apr 2009 (as *G. cowa*), *C. Phengklai* et al. *15862* (BKF); Khao Ra, Than Sadet-Ko Pha-Ngan National Park, 17 Sep 2017, *C. Ngernsaengsaruay* own observation]; Phangnga [Ko Yao Yai, fr., 4 Mar 1929 (as *G.* cf. *speciosa*), *A. F. G. Kerr 17338* (BK, BM, K); Ko Boi Noi, fr., 22 Feb 1966 (as *G. hombroniana*), *B. Hansen & T. Smitinand 12429* (BKF, E [E00839760]); Ko Miang, Mu Ko Similan National Park, fl., 15 Jan 1992 (as *Garcnia* sp.), *C. Niyomdham 2904* (AAU, BKF); Ko Yao, fr., 2 Apr 1998 (as *Garcnia* sp.), *P. Triboun & M. Triboun 922* (BK); Ko Yao Yai, sterile, 30 Apr 2007 (as *G. mangostana*), *C. Phengklai* et al. *15518* (BKF)]; Krabi

[Khao Pra Bang Khram, fr., 4 Apr 1988 (as *G. hombroniana*), *C. Niyomdham & W. Ueachirakan 1762* (AAU, BKF, K); Khao Pra Bang Khram Wildlife Sanctuary, Khlong Thom Nuea Subdistrict, Khlong Thom District, fr., 26 Mar 2006 (as *G. hombroniana*), *J. F. Maxwell 06-205* (CMUB, QBG); ibid. fr., 15 Feb 2022, *C. Ngernsaengsaruay* et al. *G54-15022022* (BKF, spirit material); Ao Nang, fr., s.d. (as *Garcnia* sp.), *K. Larsen* et al. *43371* (AAU); Ko Lanta, female fl., 5 May 2013 (as *Garcnia* sp.), *B. Sonsupab L-50* (BK)]; Nakhon Si Thammarat [Khiriwong, sterile, 1 Sep 1952 (as *G. hombroniana*), *P. Suvarnakoses 423* (BKF); Karome Waterfall, Khao Luang National Park, Lansaka District, fr., 17 Mar 1985 (as *G. hombroniana*), *J. F. Maxwell 85-300* (A [00466348], AAU, BKF, PSU); Krung Ching Waterfall, Khao Luang National Park, Tha Sala District, fr., 14 Mar 2005 (as *Garcinia* sp.), *S. Gardner* et al. *ST1671* (BKF, K); ibid., female fl., 27 Feb 2006 (as *Garcinia* sp.), *S. Gardner & P. Sidisunthorn ST1671a* (K)]; Trang [Kachong, sterile, 9 Jun 1933 (as *G. speciosa*), *Put 271* (BKF); Khao Chong, male fl., 15 Jun 1966 (as *G. speciosa*), *C. Boonnab & L. Phuphathanaphong 293* (BKF); Ton Te Waterfall, Palian District, fr., 2003 (as *G. speciosa*), *A. Sinbumroong & S. Davies AS405* (BKF); Locality not specified, male fl., 14 Jan 1916 (as *G. cornea*), *Luang Vanpruk 816* (K)]; Satun [Ko Adang, Tarutao National Park, fl., 14 Jan 1928 (as *G. cornea*), *A. F. G. Kerr 14078* (BK, BM, K, L [L2408859]); Ko Tarutao, fl., 20 Jan 1928 (as *G. cornea*), *A. F. G. Kerr 14225* (BK, K); Ko Tarutao, male fl., 11 Nov 1979 (as *G. hombroniana*), *G. Congdon 148* (AAU, PSU); Ko Tarutao, fl., 14 Nov 1979 (as *G. hombroniana*), *G. Congdon 165* (AAU, PSU); Ao Phante, Ko Tarutao, sterile, 30 Jul 1980 (as *G.* cf. *hombroniana*), *G. Congdon 801* (A [00466349], AAU, PSU); Ao Son, Tarutao National Park, La Ngu District, fr., 10 Feb 2005 (as *Garcinia* sp.), *P. Sidisunthorn & P. Tippayasri ST1488* (K); road to Ao Son, Tarutao National Park, La Ngu District, fl., 11 Feb 2005 (as *Garcinia* sp.), *S. Gardner ST1501* (K); Ao Russi, Tarutao National Park, La Ngu District, sterile, 21 May 2005 (as *Garcinia* sp.), *S. Gardner* et al. *ST1859* (K); ibid., fr., 21 May 2005 (as *Garcinia* sp.), *Gardner* et al. *ST1860* (K); Tarutao National Park, La Ngu District, fl., 1 Apr 2006 (as *Garcinia* sp.), *P. Sidisunthorn ST2535* (K); Ko Tarutao, young fr., 8 Apr 2008 (as *G. mangostana*), *C. Phengklai* et al. *15703* (BKF); Ko Tarutao, fr., 8 Apr 2008 (as *G. mangostana*), *C. Phengklai* et al. *15806* (BKF); Ko Tarutao, 8 Apr 2008 (as *Garcinia* sp.), *B. Sonsupab 3981* (BK)]; Songkhla [Sadao District, fl., 22 Feb 1941 (as *G. hombroniana*), *T. Premrasami s.n.* (BKF); Khlong Huai Phlu, Prik Subdistrict, Sadao District, sterile, 12 Mar 1954 (as *G. speciosa*), *Snguan s.n.* (BKF); Khao Noi, fl., Feb 1950 (as *Garcnia* sp.), *L. Williams 17272* (K); Khao Noi, female fl., s.d. (as *G. hombroniana*), *T. Smitinand & Williams 17272* (BKF); Ton Nga Chang Wildlife Sanctuary, fr., 10 May 1979 (as *G. hombroniana*), *H & C 444* (PSU); Ton Nga Chang Waterfall level 5, Hat Yai District, fl., 14 May 2004 (as *Garcinia* sp.), *S. Gardner ST0524* (K); Ton Nga Chang Waterfall level 3, Hat Yai District, fl., 30 Jan 2006 (as *Garcinia* sp.), *S. Gardner ST2278* (K); Boriphat Waterfall Park, Rattaphum District, male fl., 8 Feb 1985 (as *G. hombroniana*), *J. F. Maxwell 85-167* (BKF, PSU); Boriphat Waterfall, fl., 17 Dec 2003 (as *Garcnia* sp.), *A. S. Barfod* et al. *583* (AAU); Prince of Songkhla University, Hat Yai District, fr., 29 Apr 1985 (as *G. hombroniana*), *P. Sirirugsa 1013* (BKF, PSU); Khao Kho Hong, Prince of Songkhla University, Hat Yai District, fr., 24 Mar 2008 (as *G. hombroniana*), *N. Boonnak 006*, *007* (PSU); Khlong Rhang Hill, Na Mom District, fr., 15 May 1985 (as *G. hombroniana*), *J. F. Maxwell 85-474* (AAU, BKF, PSU); Khlong Rhang Hill, Na Mom District, male fl., 15 Feb 1986 (as *G. hombroniana*), *J. F. Maxwell 86-68* (AAU, BKF, PSU); Khao Tang Kuan, fl., 30 Aug 1997 (as *G. hombroniana*), *N. Yutaworawit*

2E (PSU); Ban Taling Chan, Chana District, fr., 17 May 1999 (as *G. maingayi*), *S. Petchsri 1* (PSU)]; Pattani [Nong Chik District, fr., 21 Jul 1990 (as *G. hombroniana*), *T. Santisuk s.n.* (BKF)]; Yala [Betong District, fl., 24 Feb 1941 (as *G. hombroniana*), *T. Premrasami 129* (BKF)]; Narathiwat [Waeng District, fr., 6 Sep 1966 (as *G. robusta*), *B. Sangkhachand & B. Nimanong 1320* (BKF); Waeng District, fr., 8 Sep 1966 (as *Garcinia* sp.), *Prayad 373* (BK); Khao Tan Yong, sterile, 5 Jun 1973 (as *Garcinia* sp.), *C. Chai-anan 451* (BKF); Forest behind Wat To Mo, Sukhirin District, fr., 9 Aug 1996 (as *Garcinia* sp.), *P. Puudjaa 264* (BKF)].

2. *Garcinia exigua* Nazre, Phytotaxa 373(1): 28. figs 2g, 3i & 10. 2018.; Ngerns. et al., Thai Forest Bull., Bot. 51(1): 36–44. figs 1–3. 2023.

Fig. 4

Type. Malaysia, Borneo, Sarawak, Bintulu, Buan Forest Reserve, 18 Sep 1972, *P. Chai S31750* (holotype SAR, reported by Nazre et al. 2018, not seen; isotype L [L2403372, photo seen]).

Description. ***Habit*** trees, 2.5–20 m tall, 20–100 cm GBH, sometimes with buttresses near the base of the main stem of large trees; latex yellow, sticky; branchlets green, 4-angular, glabrous. ***Bark*** brown or dark brown, after the peel pale yellow or pale brown, mottled, flaking and leaving roundish or irregularly shaped scars; inner bark red. ***Leaves***: lamina narrowly elliptic, elliptic, broadly elliptic, sometimes obovate, 3–6.3 × 1–3.2 cm, apex narrowly obtuse or obtuse, base cuneate, margin entire and finely revolute, coriaceous, smooth, shiny dark green above, paler below, glabrous on both surfaces, midrib raised on both surfaces, secondary veins 10–18 each side, curving towards the margin and connected in distinct loops and united into an intramarginal vein, faint above, inconspicuous below, with intersecondary veins, veinlets reticulate, faint on both surfaces, with a few scattered black gland dots on both surfaces, interrupted long wavy lines of differing lengths, nearly parallel to the midrib, running across the secondary veins to the apex or the margin, visible on both surfaces especially on the lower surface of dry leaves; petiole green, 0.3–1 cm long, 1–1.5 mm in diam., grooved above, finely transversely rugose, glabrous, with a basal appendage clasping the branchlet; young leaves pale green, glossy; fresh leaves brittle when crushed; dry leaves pale brown or reddish brown. ***Inflorescences*** terminal, in fascicles of 3 male flowers and usually solitary in female flowers (observations based on infructescence); bracts 2, caducous, green or brownish green, conduplicate with a central keel, ovate, 8–10 × 4–5.5 mm, apex acuminate, thinly coriaceous (of male inflorescences). ***Flowers***: sepals and petals glabrous. ***Male flower buds*** subglobose to globose, 3.5–5.5 mm in diam. ***Male flowers*** lightly fragrant, 1.5–2 cm in diam., the middle flowers always largest; bracteoles caducous; pedicel pale green, turning pale yellow, 3–4.5 mm long, 1.3–1.7 mm in diam., glabrous; sepals 4, pale yellow, concave, thinly coriaceous, with wavy lines outside, the outer pair broadly ovate, 4.2–5 × 3.5–5 mm, apex acute, the inner pair elliptic or broadly elliptic, 4.2–6 × 3–4.5 mm, apex obtuse; petals 4, pale yellow, elliptic, 6.5–9 × 3.5–8 mm, subequal, apex obtuse, margin revolute, thinly coriaceous, with wavy lines outside; stamens numerous, united into a single 4-lobed bundle, surrounding a pistillode, lobes 3–3.5 × 3–4 mm; filaments 0.5–0.7 mm; anthers 0.9–1.2 × 0.8–1 mm; pistillode fungiform, 3–3.5 mm long; sterile stigma yellow, sessile, convex, weakly 4-lobed, 2.5–3 mm in diam., smooth. ***Female flowers*** not seen. ***Fruits*** green, smooth with fine longitudinal striate, glabrous, with a sticky yellow latex, subglobose, globose or broadly ellipsoid, 1–1.3 × 0.8–1.1 cm, pericarp coriaceous; persistent stigma dark brown or blackish brown, flattened or slightly convex, 2–3 mm in diam., weakly 4-lobed; persistent sepals green, concave, coriaceous, lanceolate-ovate or ovate, 3.5–5.5 × 3–5 mm, the outer pair slightly smaller than the inner pair, apex acute; fruiting stalk green, 1–2 mm long, 1–1.8 mm in diam., glabrous. ***Seeds*** 1, brown (dark brown when dry) mottled with irregular lines, ellipsoid, c. 6 × c. 3.5 mm, c. 1.8 mm thick, compressed, rounded at both ends, with a thin fleshy pulp. The morphological characters and data reported here for this species were mostly taken from Ngernsaengsaruay et al. (2023a).

Distribution. Thailand, Malaysia [Borneo, Sarawak (Bintulu, Buan Forest Reserve; Mulu National Park: Matong Ubong, Ulu Matong, Sungai Ubong)]; Brunei [Temburong (Ulu Belalong)].

Distribution in Thailand. Peninsular: Krabi.

Habitat and ecology. It is found in dry evergreen forest on limestone hills and littoral dry evergreen forest on limestone hills, 50–100 m amsl.

Phenology. Flowering January to March; fruiting April to June.

Conservation status. *Garcinia exigua* is a rare species in Borneo, and is represented only from three localities in lowland and hill forest in Sarawak and Brunei (Nazre et al. 2018). In Thailand, the species is known only from two localities in Krabi Province, but to be expected in other limestone hills. Globally, it is known only from Borneo to Thailand, and has an Extent of Occurrence (EOO of 51,767.17 km^2) and a relatively small Area of Occupancy (AOO of 16 km^2) which lies within protected and non-protected areas. It is inferred to be experiencing a continuing decline in habitat area, extent, and quality. We therefore consider the conservation assessment as Vulnerable [VU B2ab(iii)].

Etymology. The specific epithet of *Garcinia exigua* is a Latin word, referring to the small size of all parts in the specimens (Nazre et al. 2018).

Vernacular names. Phawa bai lek krabi (พะวาใบเล็กกระบี่) (Ngernsaengsaruay et al. 2023a); Kandis (Sarawak) from the material *Runi S. Pungga & P. C. Yii S61132* (K, L [L3811193], as *Garcinia sarawhensis* Pierre).

Uses. Not known.

Notes. *Garcinia exigua* is recognized by the following characters: (1) The leaves and fruits are small. (2) The fresh leaves are brittle when crushed. (3) The stamens of the male flowers are united into a single 4-lobed bundle, surrounding a pistillode, and (4) The bark is mottled, flaking and leaving roundish or irregularly shaped scars similar to the bark of some species of *Lagerstroemia* L. in the Lythraceae, e.g., *L. duperreana* Pierre ex Gagnep., *L. floribunda* Jack and some species of *Terminalia* L. in the Combretaceae, e.g., *T. corticosa* Pierre ex Laness.

According to Nazre et al. (2018), the shape and size of leaves of *Garcinia exigua* are elliptic and 0.8–2.1 × 0.3–1 cm; however, from our observations, we found the leaves can be narrowly elliptic to broadly elliptic, sometimes obovate, and larger, 3–6.3 × 1–3.2 cm.

As mentioned by Nazre et al. (2018), the shape, size, and color of fruits of *Garcinia exigua* are globose or ellipsoid, 9.5–10.5 × 8.5–11 mm, and shiny green turning yellow when ripe; however, in this study, we found the fruits can be subglobose, globose or broadly ellipsoid, sometimes slightly longer, 1–1.3 × 0.8–1.1 cm, and green. However, we did not observe ripe fruits.

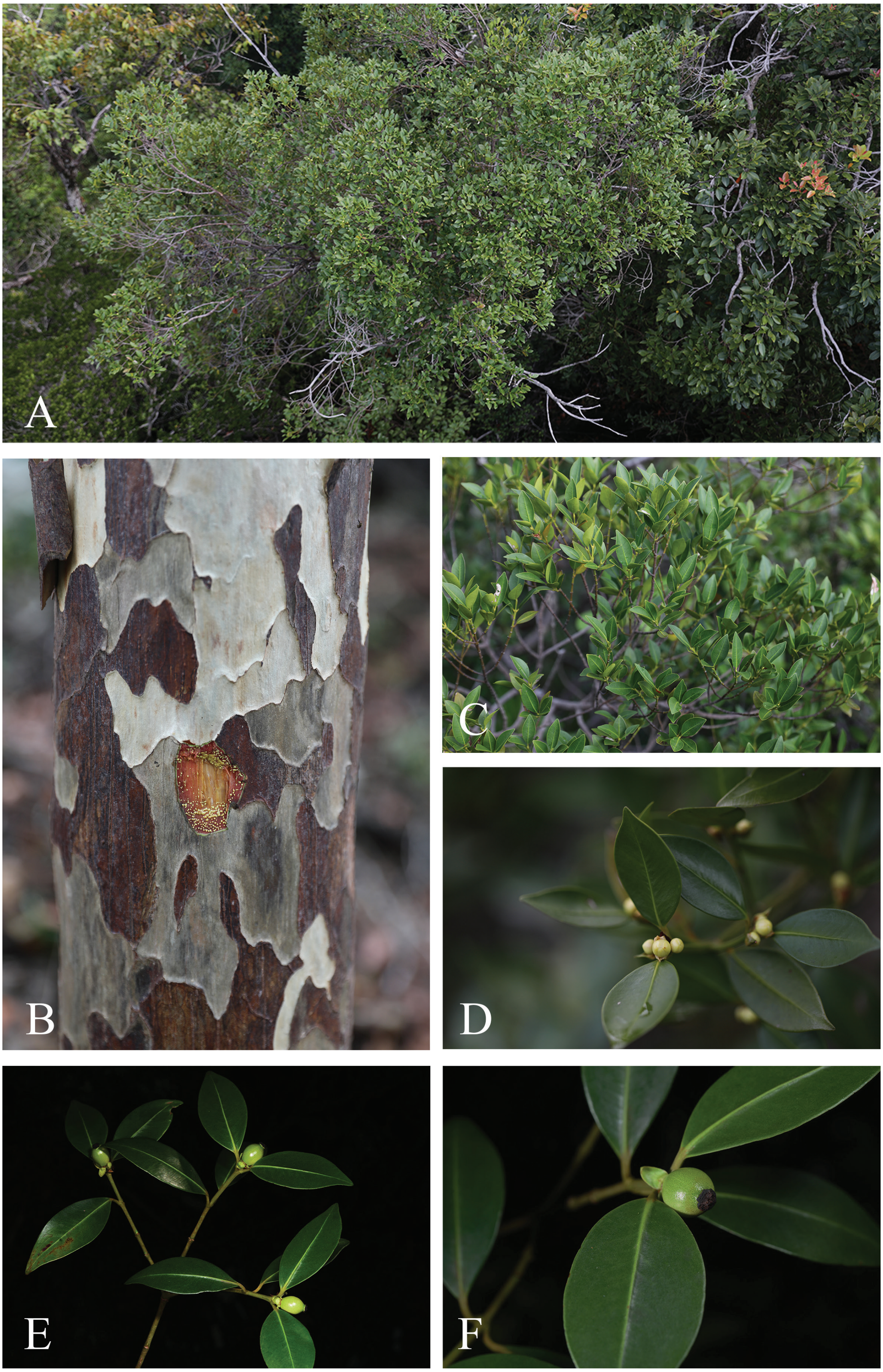

Figure 4. *Garcinia exigua* **A** habitat and canopy (top view) **B** stem, bark, and slashed bark with yellow latex **C** branchlets and leaves **D** branchlets and male inflorescences with male flower buds **E, F** branchlets, leaves, and young fruits. Photos: Chatchai Ngernsaengsaruay (**A–D**), Naiyana Tetsana (**E, F**).

Additional specimens examined. Thailand. Peninsular: Krabi [Wat Tham Suea (originally “Tham Sue” on the label), Mueang Krabi District, fr., 8 May 2002 (as *Garcinia* sp.), *P. Pooma* et al. *3612* (BKF, QBG); Ko Hong, trail up to view point, Than Bok Khorani National Park, Mueang Krabi District, male fl., 13 Feb 2022, *C. Ngernsaengsaruay* et al. *G27-13022022* (BKF, K, QBG); ibid., male fl., 13 Feb 2022, *C. Ngernsaengsaruay* et al. *G28-13022022* (BKF, K, QBG)].

Malaysia. Borneo: Sarawak [Mulu National Park, Sg. Matong Ubong, fr., 11 Nov 1990, *P. C. Yii & Runi S. Pungga S57293* (L [L3810871], SAR [reported by Nazre et al. 2018], as *Garcinia sarawhensis*); Mulu National Park, Ulu Matong, fr., 13 Nov 1990, *P. C. Yii & Runi S. Pungga S60529* (BKF, L [L3811190], as *G. sarawhensis*); Mulu National Park, Sungai Ubong, fr., 19 Nov 1990, *Runi S. Pungga & P. C. Yii S61132* (K, L [L3811193], SAR [reported by Nazre et al. 2018], *as G. sarawhensis*). **Brunei.** Temburong [Ulu Belalong, 22 Jan 1994, *Coode* et al. *7886* (A [reported by Nazre et al. 2018]).

3. *Garcinia mangostana* L., Sp. Pl. 1: 443. 1753; Roxb. in Carey, Fl. Ind. 2: 619. 1832; Miq. Fl. Ned. Ind. 1(2): 506. 1859; Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 325. 1860; Laness., Mém. Gen. Garc.: 15. 1872; T. Anderson in Hook. f., Fl. Brit. India 1(2): 260. 1874; Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43(2): 86. 1874 et Forest Fl. Burma 1: 87. 1877; Pierre, Fl. Forest. Cochinch. 1(4): t. 54. 1882; Vesque, Epharmosis 2: 17. t. 160, 161. 1889; King, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 59(2): 156. 1890; Vesque in A. DC. & C. DC., Monogr. Phan. 8: 386. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 235. fig. 114 A, B. 1893; Brandis, Indian Trees: 49. 1906; Merr., Philipp. J. Sci. 3: 364. 1908; Gamble, Fl. Madras 1: 73. 1915; Pit. in Lecomte et al., Fl. Indo-Chine 1(4): 307. 1910; Ridl., Fl. Malay Penins. 1: 172. 1922; Merr., Enum. Philipp. Fl. Pl. 3: 85. 1923; C. E. Parkinson, Forest Fl. Andaman Isl.: 88. 1923; Corner, Wayside Trees Mal. 1: 318. ed. 2. 1952; Pételot, Arch. Rech. Agron. Cambodge Laos Vietnam 1: 62. 1952; Backer & Bakh. f., Fl. Java (Spermatoph.) 1: 387. 1963; Maheshw., Bull. Bot. Surv. India 6: 120. t. 2. fig. 14. 1964; Corner & Watan., Ill. Guide Trop. Pl.: t. 191. fig. 8. 1969; Whitmore in Whitmore, Tree Fl. Malaya 2: 215. 1973; D’Arcy, Ann. Missouri Bot. Gard. 67: 998. fig. 4B. 1980; S. W. Jones, Morphology and Major Taxonomy of *Garcinia* (Guttiferae), Ph.D. Thesis (unpublished): 288. 1980; Kosterm. in Dassan. & F. R. Forsberg, Revis. Handb. Fl. Ceylon 1: 88. 1980; H. Keng, Concise Fl. Singapore: 49. 1990; P. H. Hô, Câyco Vietnam 1: 559. fig. 1544. 1991; E. W. M. Verheij & R. E. Coronel (eds), PROSEA 2: 177, t. 178. 1992; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 143. 1993; X. W. Li, J. Li, N. Robson & P. F. Stevens in C. Y. Wu, P. H. Raven & D. Y. Hong, Fl. China 13: 43. 2007; W. E. Cooper, Austrobaileya 9(1): 17. 2013; S. Gardner, P. Sidisunthorn & Chayam., Forest Trees S. Thailand 1: 355. fig. 546. 2015. var. *mangostana*, Nazre et al., Phytotaxa 373(1): 31. fig. 12. 2018.
Fig. 5.

≡ *Mangostana garcinia* Gaertn., Fruct. Sem. Pl. 2: 105. t. 105a–g. 1790.

Type. illustration, “Mangoustan”, Garcin (1733: Philosop. Transact. 431. figs 1–9.) (lectotype, designated by Hammel in Jarvis et al. 1993: 28).

Description. ***Habit*** trees, 7–20(–25) m tall, 40–150 cm GBH; latex yellow, sticky; branchlets green, 4-ridged, glabrous. ***Bark*** dark brown, scaly; inner bark brownish orange. ***Leaves***: lamina elliptic, oblong-elliptic, oblong or ovate, 15.5–36 × 6.5–13 cm, apex acute or acuminate, base obtuse or oblique, sometimes cuneate, margin entire or repand, thickly coriaceous, smooth or slightly bullate, shiny dark green above, paler below, glabrous on both surfaces, midrib slightly raised above, raised as a prominent ridge below, secondary veins 10–18 each side, curving towards the margin and connected in distinct loops and united into 2 intramarginal veins, flattened above, raised and conspicuous below, intramarginal veins shallowly grooved above, with intersecondary veins, veinlets reticulate, visible below, interrupted long wavy lines of differing lengths, running across the secondary veins to the apex or the margin, conspicuous below; petiole green, stout, 1.5–2.7 cm long, 4–7 mm in diam., not grooved, distinctly transversely rugose, glabrous, with a basal appendage clasping the branchlets; young leaves brownish red or reddish brown, turning pale green, glossy; fresh leaves tough when crushed; mature leaves turning greenish yellow to pale yellow before falling off; dry leaves pale brown or reddish brown. ***Inflorescences*** terminal. ***Flowers***: sepals and petals glabrous. ***Male flowers*** not seen. ***Female flower buds*** subglobose to globose, 1–2 cm in diam. ***Female flowers*** solitary or in a cluster of 2–5(–7) flowers, 3.2–5 cm in diam.; bracteoles caducous; pedicel (of a flower in an inflorescence) or peduncle (of a solitary flower) green, stout, terete or slightly 4-angled, 1–2.4 cm long, 5.5–8 mm in diam., glabrous; sepals 4, pale green outside, bright red or yellowish red inside, concave, thickly coriaceous, suborbicular, orbicular or broadly elliptic, 1–2 × 1–2.2 cm, the outer pair slightly smaller than the inner pair, apex rounded; petals 4, yellowish red or yellowish pink, somewhat thick and fleshy, suborbicular, broadly elliptic, broadly obovate or broadly ovate, 1.1–2.1 × 1.4–2.6 cm, unequal, apex rounded, margin entire or irregularly lobed and undulated; staminodes 10–18, free, surrounding the ovary; filaments filiform, 2–5 × 0.5–1.2 mm, unequal; anthers pale yellow or brownish yellow, 1.2–1.7 × 1–1.4 mm; pistil fungiform, 0.6–1.2 cm long; ovary pale green, depressed globose or subglobose, 0.4–0.7 × 0.6–1.3 cm, glabrous, 4–8-locular; stigma pale yellow, convex, radiate, deeply 4–8-lobed, 1.5–3 mm long, 0.7–1.2 cm in diam., smooth. ***Fruits*** pale green or greenish pale yellow, turning pinkish pale yellow, pink, reddish purple to blackish purple when ripe, smooth, glabrous, with a sticky yellow latex, subglobose or globose, 3.4–6.2 × 3.8–7 cm, pericarp 0.4–1.2 cm thick, reddish purple, fleshy, becoming woody when dry; persistent stigma dark brown or blackish brown, flattened, radiate, deeply 4–8-lobed, 1.4–2.5 cm in diam., lobes wedge-shaped; persistent sepals green or green tinged with reddish purple, thickly coriaceous, 1.2–2.5 × 1.2–2.8 cm, usually larger than in flowering materials; fruiting stalk green, strong and thick, 1.2–2.6 cm long, 0.6–1.2 cm in diam., glabrous. ***Seeds*** 4–8, sometimes aborted, brown mottled with irregular lines, broadly ellipsoid, ellipsoid or semi-ellipsoid, 1.5–2.5 × 0.8–2 cm, compressed, rounded at both ends, with a white fleshy pulp.

Distribution. The native range of this variety is Peninsular Malaysia. Cultivated throughout the tropics, mainly in Southeast Asia.

Distribution in Thailand. It is cultivated throughout the country, especially in the peninsular and the south-eastern regions.

Habitat and ecology. It is known only in cultivation. This species prefers humid climate.

Figure 5. *Garcinia mangostana* **A** habit and habitat **B** stem, bark, and slashed bark with yellow latex **C** branchlets, young and mature leaves **D** branchlet and female flower **E** branchlet and female inflorescence with female flowers **F** ripe fruits **G** ripe fruits and seeds with a white fleshy pulp **H** seeds with a white fleshy pulp. Photos: Chatchai Ngernsaengsaruay.

Phenology. In the south-eastern region: flowering December to February (March); fruiting February to June; harvesting April to May (June). In the peninsular region: flowering February to April; fruiting April to August; harvesting July to August [out-of-season: flowering August to October; fruiting October to February; harvesting December to February].

Conservation status. *Garcinia mangostana* var. *mangostana* is widely cultivated throughout the tropics, especially in Southeast Asia. Because of its wide distribution, the number of localities, and because it is not facing any threat of extinction, we consider the conservation assessment as LC.

Etymology. The specific epithet of *Garcinia mangostana* is a Latin word, and is derived from the French "Mangoustan", which translated to the English "Mangostan", refers to mangosteen.

Vernacular names. Mangkhut (มังคุด) (General); Măng cụt (Vietnam); Manggis (Malaysia, Indonesia, and Philippines); Manggustan (Philippines); Mangoustan, Mangoustanier (France); Mingut (Myanmar); Mongkhut (Cambodia); Mangosteen, Purple mangosteen (English).

Uses. Mangosteen is widely cultivated as a fruit tree, especially in Southeast Asia. The juicy fleshy pulp surrounding the seeds is edible and has a sweet and sour taste. It is commonly known as the "queen of tropical fruits". The juicy fleshy seed pulp can be used for making jams, beverages, ice creams, preserves ("Mang khut kuan" in Thai), and used fresh in syrup. In Nakhon Si Thammarat Province, the seeds with white fleshy pulp can be eaten raw ("Mang khut khat") (Fig. 5H) or cooked, e.g., used for consumption in the southern Thai spicy sour yellow curries with fish or shrimp: "Kaeng Som" (sour curry) or "Kaeng Lueang" (yellow sour curry).

The fruit rind (pericarp) is used to tan leather and to produce black dye (Maheshwari 1964; Verheij and Coronel 1992). The wood is used for cabinetry, building purposes, rice pounders, and spear handles (Maheshwari 1964). It has been used in Thai traditional medicine for treatment of diarrhea and skin infections (Gritsanapan 1994). It contains tannins and xanthones, i.e., alpha-, beta- and gamma-mangostins (Govindachari et al. 1971; Jinsart et al. 1992; Nakatani et al. 2002). Alpha-mangostin is a major component which possesses anti-inflammatory (Chen et al. 2008) and antibacterial activities against methicillin-resistant *Staphylococcus aureus*, *S. epidermidis*, and *Propionibacterium acnes* (Iinuma et al. 1996; Chomnawang et al. 2005). The fruit rind extract and mangostin have been known to possess antibacterial activity against bacteria causing acne. In Thailand, mangosteen fruit extract is popularly used as a food supplement while the fruit rind extract has been used in herbal cosmetics and pharmaceutical products. (Pothitirat and Gritsanapan 2008). The bark, young leaves, and fruit rind are used as a gargle for a sore mouth (Maheshwari 1964). In Thailand, the extract is popularly used in herbal cosmetics for anti-acne effect (Pothitirat and Gritsanapan 2008).

Notes. *Garcinia mangostana* was named by Linnaeus 1753: 443. It is the most important cultivated species in the genus of *Garcinia*. However, the latest taxonomic revision by Nazre et al. (2018) revealed that the species can be classified into three varieties: the cultivated variety *G. mangostana* var. *mangostana* and two wild varieties *G. mangostana* var. *malaccensis* (Hook. f.) Nazre and *G. mangostana* var. *borneensis* Nazre. The varieties can only be distinguished with fertile and mature materials although male trees are rarely found.

Garcinia mangostana var. *mangostana* is very similar to *G. mangostana* var. *malaccensis* and *G. mangostana* var. *borneensis* and is distinguished by its male flowers with dwarf-fungiform (broadly fungiform) pistillodes, c. 5 mm long; fruits ovoid or globose; smooth stigma surface; and it is found only in cultivation. In contrast, the other two varieties have male flowers with small pistillodes c. 2 mm long or without pistillodes; globose, ellipsoid or ovoid fruits; rugose stigma surfaces; and they are found in the wild or in cultivation. *G. mangostana* var. *malaccensis* differs from G. *mangostana* var. *borneensis* in its stamens in a conical mass or slightly 4-angled, up to 1 cm long (vs in 4-angled, square-shaped, up to 6 mm long); fruits globose, ellipsoid or ovoid (vs globose); and stigma weakly to strongly raised (vs sessile). *G. mangostana* var.

malaccensis is found in lowland forests in Peninsular Malaysia, Singapore, Sumatra, and Borneo (Brunei and Sarawak), while *G. mangostana* var. *borneensis* is found only in lowland forest of Borneo (East Coast of Sabah and Kalimantan) (Nazre et al. 2018).

As mentioned by Nazre et al. (2018), the shape and size of leaves of *Garcinia mangostana* var. *mangostana* are elliptic to broadly elliptic, ovate or oblanceolate and 9.2–25.5 × 7–9 cm; base of petiole without ligule-like appendage; however, from our observations, we found the leaves can be elliptic, oblong-elliptic, oblong or ovate, and sometimes larger, 15.5–36 × 6.5–13 cm; petiole with a basal appendage clasping the branchlets.

According to Nazre et al. (2018), the male flowers of *Garcinia mangostana* var. *mangostana* have a single square (4-angled) mass of stamens surrounding the base of the pistillode and up to 8 mm long. Based on our observations, the male plants have never been found in Thailand. Therefore, in Thailand mangosteen appear to be an obligately agamospermous species (apomictic species) with the production of seeds without fertilization.

As stated in Nazre et al. (2018), the shape and size of fruits of *Garcinia mangostana* var. *mangostana* are ovoid or globose and up to 6 cm across; however, from our examination of specimens, we found the fruits can be subglobose or globose, and sometimes larger, 3.4–6.2 × 3.8–7 cm.

Additional specimens examined. Thailand. Northern: Chiang Mai [Doi Chiang Dao, fl., 28 Oct 1979 [as *Garcinia* sp.], cultivated, *T. Shimizu* et al. *T-20980* (AAU, BKF)]; **Central:** Suphan Buri [Si Samran Subdistrict, Song Phi Nong District, sterile, 9 Mar 2016, cultivated, *W. Sueksakit M10-1* (BK)]; Nakhon Pathom [Silpakorn University, sterile, 20 Apr 2017, cultivated, *W. Sueksakit M10-3* (BK)]; Bangkok [locality no specified, fl., Feb 1869, [as *Garcinia* sp.], cultivated, *C. A. Feilberg s.n.* (C); locality no specified, fl., 14 Mar 1920, cultivated, *A. F. G. Kerr s.n.* (BM); locality no specified, fl., 14 Mar 1920, cultivated, *A. Marcan 102A* (BM); Khong San District, young fr., 20 Feb 1970, cultivated, *J. F. Maxwell 70-23* (BK, L [L2416561])]; **South-Eastern:** Rayong [locality not specified, fr., 16 Jul 2013, cultivated, *Naiyana 01* (BKF)]; Chanthaburi [Khitchakut District, fr., 12 Jul 2003, cultivated, *P. Palee s.n.* (CMUB)]; Trat [Salak Phet Waterfall, Mu Ko Chang National Park, young fr., 29 Mar 2000, cultivated, *T. Wongprasert s.n.* (BKF128511); Wang Saem Subdistrict, Makham District, female fl., 20 Jan 2024, cultivated, *C. Ngernsaengsaruay* et al. *G55-20012024* (BKF)]; **Peninsular:** Surat Thani [Ko Samui, fr., 31 May 1960, cultivated, *Chirayupin 111* (BK); Ban Song Subdistrict, fr., 12 Aug 1979, cultivated, *Supatra 27* (PSU)]; Phangnga [Si Phang Nga National Park, sterile, 17 Dec 2003, cultivated, *A. Sloth 561* (AAU); Ko Phra Thong, fl., 8 Feb 2005, cultivated, *C. Phengklai* et al. *13945* (BKF); Bang Nai Si Subdistrict, Takua Pa District, sterile, 1 Sep 2016, cultivated, *W. Sueksakit M10-1* (BK)]; Nakhon Si Thammarat [locality no specified, sterile, 24 Aug 1980, cultivated, *Students s.n.* (PSU); locality no specified, fr., 20 Aug 1981, cultivated, *Mai 4* (PSU); Khao Luang, fl., 25 Apr 1990, cultivated, *R. Pooma P37* (BKF)]; Phatthalung [Khao Pu-Khao Ya National Park, Si Banphot District, fr., 26 Jul 1986, cultivated, *J. F. Maxwell 86-499* (AAU, BKF, L [L2416615], P [P05061446], PSU)]; Narathiwat [Chat Warin Waterfall, fr., 15 Aug 1995, cultivated, *K. Larsen* et al. *45615* (AAU, BKF)].

Excluded and unplaced species

Garcinia anomala **Planch. & Triana, Ann. Sci. Nat., Bot., sér. 4, 14: 329. 1860; Laness., Mém. Gen. Garc.: 30. 1872; T. Anderson in Hook. f., Fl. Brit. India 1(2): 266. 1874; Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 43(2): 87. 1874 et Forest Fl. Burma 1: 89. 1877; Vesque, Epharmosis 2: 17. t. 105. 1889 et in A. DC. & C. DC., Monogr. Phan. 8: 369. 1893; Engl. in Engl. & Prantl, Die Naturlichen Pflanzenfamilien 3(6): 236. 1893; Brandis, Indian Trees: 51. 1906; Kanjilal, P. C. Kanjilal & A. Das, Fl. Assam 1(1): 109. 1934; Maheshw., Bull. Bot. Surv. India 6: 117. t. 1. fig. 7. 1964; S. W. Jones, Morphology and Major Taxonomy of *Garcinia* (Guttiferae), Ph.D. Thesis (unpublished): 291. 1980; D. G. Long in Grierson & D. G. Long, Fl. Bhutan 1(2): 368. 1984; N. P. Singh in B. D. Sharma & Sanjappa, Fl. Ind. 3: 104. 1993; Wang et al., Phytotaxa 327(2): 167–174. figs 1, 3. 2017.**
Fig. 6

= *Garcinia propinqua* Craib, Bull. Misc. Inform. Kew 1924(3): 85. 1924; Craib, Fl. Siam. 1(1): 117. 1925; Gagnep. in Gagnep., Fl. Indo-Chine Suppl.: 267. 1943. Type. Thailand, Chiang Mai, Doi Chiang Dao, c. 1500 m alt., fl., 5 Jun 1921, *A. F. G. Kerr 5611* (lectotype, designated by Nazre et al. (2018: 48), K [K000380474!]; isolectotype BM [BM000611616, photo seen].

= *Garcinia bracteata* C. Y. Wu ex Y. H. Li, Acta Phytotax. Sin. 19(4): 490. fig. 1. 1981; H. W. Li et al., Fl. China 13: 44. fig. 31(1–5). 2007. Type. China, Yunnan, Mengla, Mengyuan, 600–700 m alt., male fl., 19 May 1962, *Y. H. Li 4103* (holotype, KUN [KUN0406601, photo seen]).

Type. India, Khasia, 3000–5000 ft alt., female fl., fr., s.d., *J. D. Hooker & T. Thomson 14* (lectotype, designated by Wang et al. (2017: 168), K [K000380443!]; isolectotypes A [reported by Nazre et al. (2018), not seen], BR [BR0000005107803, photo seen], E [E00438018, photo seen], G [G00418238, G00458403, photos seen], L [L0489482, L2409535, U1208227, photos seen], MPU [MPU014371, MPU014372, photos seen], P [P04022020, P04022021, P05062484, P05062485, P05062488, photos seen], W [W0073366, W1889-0318023, W1889-0318024, W1889-0318030, photos seen].

Description. ***Habit*** trees, 5–13 m tall, 15–70 cm GBH; latex pale yellow; branches decussate, horizontal or nearly horizontal; branchlets green or yellowish pale green, terete, glabrous. ***Bark*** mottled with dark brown and brown, thin, rather smooth or flaking; inner bark reddish brown. ***Leaves*** decussate; lamina elliptic, oblong-elliptic, ovate or lanceolate-ovate, 6–21.5 × 2.5–9 cm, apex acute, bluntly acute or shortly acuminate, base cuneate or obtuse, sometimes rounded or oblique, margin entire or repand, slightly revolute, coriaceous, shiny dark green above, pale green below, glabrous on both surfaces, midrib flattened above, raised below, secondary veins 11–21 each side, curving towards the margin and connected in distinct loops and united into an intramarginal vein, flattened above, slightly raised below, visible on both surfaces, with intersecondary veins, veinlets reticulate, visible on both surfaces, interrupted long wavy lines of differing lengths, running across the secondary veins to the apex, obscure or visible below; petiole green, 0.4–2 cm long, 1.5–3 mm in diam., grooved above, transversely rugose, glabrous, with a basal appendage clasping the branchlets;

young leaves brownish red or reddish brown, turning pale green, glossy. ***Inflorescences*** axillary, cymose, often in a cluster of 3 flowers or 2–7 flowers; leafy bracts 2, opposite, ovate, broadly ovate or lanceolate-ovate, 0.7–4.3 × 0.4–2 cm, apex acute, base obtuse, margin entire, coriaceous; petiole 1–4.5 mm long, 0.5–1.5 mm in diam.; peduncle green, short to slender, 0.2–4 cm long, 1–2.5 mm in diam., glabrous. ***Flowers*** unisexual, plants dioecious, 4-merous, 1–1.5 cm in diam.; bracteoles 2, opposite, caducous, triangular, 1.5–2.5 × 1.3–2 mm; pedicel 3–6 mm long, 0.8–1.5 mm in diam., glabrous; sepals and petals decussate, concave, gradually reflexed after anthesis, glabrous; sepals 4, pale green, orbicular, suborbicular, broadly ovate or lanceolate-ovate, 2–6 × 1.5–4 mm, the outer pair slightly smaller than the inner pair; petals 4, pale yellow or yellowish white, elliptic, oblong-elliptic or broadly elliptic, 4.5–6 × 2.5–4 mm, subequal. ***Flower buds*** subglobose to globose, 4–5 mm in diam. ***Male flowers***: stamens white or creamish white, numerous, united in a central depressed globose bundle surrounding the pistillode; filaments very short; anthers 2-thecous, small, longitudinally dehiscent; pistillode small. ***Female flowers***: staminodes many; filaments short, basally connate into a cup surrounding the base of the ovary but distally free; anthers yellow, small; pistil fungiform, 4–5.5 mm long; ovary pale green, broadly ovoid, 2.5–3.5 × 3–4 mm, unlobed, glabrous, 1–2-locular; stigma yellow, sessile, slightly convex, weakly lobed, 4–5 mm in diam., smooth. ***Fruits*** berries, dark green, turning purple when ripe, smooth with fine longitudinal striate, glabrous, ellipsoid or broadly ellipsoid, 1.8–2.5 × 1.2–2.2 cm, without or with a short, thick beak; persistent stigma dark brown or blackish brown, flattened, weakly lobed, 4.5–6 mm in diam. smooth; persistent sepals green, slightly larger than in flowering materials; fruiting stalk green, 0.6–1 cm long, 1.2–2.5 mm in diam., glabrous. ***Seeds*** 1–2, c. 8 × c. 6 mm. The size of seeds was taken from Vesque (1893).

Distribution. India [Eastern India (Sikkim, Assam, Meghalaya), Bangladesh, Myanmar (Martaban), China (South Guangxi, South and South-East Yunnan), Vietnam, Thailand.

Distribution in Thailand. NORTHERN: Chiang Mai, Chiang Rai, Tak.

Habitat and ecology. It is found in lower montane rain forests or on limestones in lower montane rain forests, at elevations of 1,300–1,750 m amsl.

Phenology. Flowering February to October; fruiting September to November.

Conservation status. *Garcinia anomala* is widely distributed from Eastern India to North Indo-China and Thailand. It is known from many localities and has a large Extent of Occurrence (EOO) of 1,980,330.45 km^2 and a relatively large Area of Occupancy (AOO) of 156 km^2. In Thailand, this species is known to be naturally distributed in three provinces of the northern region, and has an EOO of 26,685.60 km^2 and an AOO of 48 km^2. Because of this wide distribution and the number of localities, it is considered LC.

Etymology. The specific epithet of *Garcinia anomala* is a Latin word meaning abnormal (Stearn 1992), unlike its allies, out of the ordinary (Gledhill 2002) and refers to inflorescences subtended by 2 small leaf-like bracts which can be used as a spot character for distinguishing the species. The specific epithet of *G. propinqua* is a Latin word meaning closely allied, of near relationship, related (Stearn 1992; Gledhill 2002), in reference to *G. propinqua* being closely related to *G. anomala*. The specific epithet *Garcinia bracteata* is a Latin word meaning with bracts, bracteate (Stearn 1992; Gledhill 2002) and refers to bracteate cymes (inflorescences with 2 opposite leafy bracts).

Figure 6. *Garcinia anomala* **A** lectotype of *Garcinia anomala*, *J. D. Hooker & T. Thomson 14* (K [K000380443]) from Khasia, India, designated by Wang et al. (2017) **B** lectotype of *Garcinia propinqua*, a synonym of *Garcinia anomala*, *A. F. G. Kerr 5611* (K [K000380474]) from Doi Chiang Dao, Chiang Mai Province, Thailand, designated by Nazre et al. (2018). Photos: Royal Botanic Gardens, Kew, England. https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:427802-1.

Vernacular names. Phawa thiam bai pradap (พะวาเทียมใบประดับ) (suggested here); Dieng-sa-slung, Dieng-soh-lang-sain (Jain, India), Dieng-soh-kwang, Soh-lain-khlaw (Khasi, India); Haibung (Manipur, India); Thechu (Garo, India).

Uses. The ripe fruits have a sour taste (from the specimen *B. Hansen & T. Smitinand 12915*).

Notes. Based on morphological characters and molecular data Nazre et al. (2018) excluded several species that were included in *Garcinia* section *Garcinia* by Jones (1980). *Garcinia anomala* is treated by Jones (1980) as belonging to *Garcinia* section *Garcinia* but Nazre et al. (2018) exclude it from the section. Molecular results of Gaudeul et al. (2024) fully support the decision of Nazre et al. (2018); they recovered two major lineages, nine major clades, and 11 sections. *G. anomala* is unplaced species within these11 sections (Gaudeul et al. 2024). It differs from *Garcinia* section *Garcinia* by having axillary cymose inflorescences often in clusters of 3 flowers or 2–7 flowers on the short to slender peduncles, each subtended by 2 small leaf-like bracts and the male flowers having glomerate, depressed globose bundles of stamens surrounding the pistillode. From our examination of specimens, we agree with the results of Nazre et al. (2018).

Wang et al. (2017) treated *Garcinia bracteata* and *G. propinqua* as synonyms of *G. anomala*. *G. anomala* is the earliest named species and thus has nomenclatural priority. The three purported species of *Garcinia* have similar morphological characters (overlapping variation in leaf shape and size, petiole length, foliar bract shape and peduncle length). There were no significant differences between these traits. They asserted that the traits previously used for distinguishing between *G. bracteata*, *G. anomala*, and *G. propinqua* are unreliable for distinguishing these species.

According to Singh (1993) the shape, size, and color of fruits are ellipsoid, c. 4.2 × c. 3.5 cm, and dark olive green, turning orange-yellow when ripe; however, from our examinations, we found the fruits are ellipsoid or broadly ellipsoid, 1.8–2.5 × 1.2–2.2 cm, without or with a short, thick beak, dark green, and turning purple when ripe (color of ripe fruits from the specimen *B. Hansen & T. Smitinand 12915*).

Garcinia anomala was described by Planchon and Triana (1860: 329), who cited the specimens collected by *W. Griffith* (without collector number) and *J. D. Hooker & T. Thomson 14* in Khasia, India. The name *G. anomala* has been lectotypified thrice, firstly, Wang et al. (2017: 168) lectotypified this name using the specimen *J. D. Hooker & T. Thomson 14* at K [K000380443], secondly, Nazre et al. (2018: 47) lectotypified this name using the same collector number at MPU [without barcode] with isolectotypes at A, E, K, and L [without barcodes], and thirdly, Shameer and Mohanan (2019: 181) selected the specimen *W. Griffith 848* at G [G00458432] as the lectotype, with isolectotypes at CAL [CAL0000046566], and W [W0073367]. Therefore, the first lectotypification has priority. We located the lectotype at K [K000380443] with isolectotypes at BR [BR0000005107803], E [E00438018], G [G00418238, G00458403], L [L0489482, L2409535, U1208227], MPU [MPU014371, MPU014372], P [P04022020, P04022021, P05062484, P05062485, P05062488], US [US02961086], and W [W0073366, W1889-0318023, W1889-0318024, W1889-0318030], but we could not find an isolectotype at A.

Garcinia propinqua was described by Craib (1924: 85), who cited the specimen *A. F. G. Kerr 5611* collected from Doi Chiang Dao, Chiang Mai Province, Thailand but he did not mention the name of the herbaria where the materials were housed, and following Art. 9.6 of the ICN (Turland et al. 2018), they constitute syntypes. Nazre et al. (2018) selected this specimen at K [K000380474] as the lectotype, with an isolectotype at BM [BM000611616].

Garcinia bracteata was named by C. Y. Wu but unpublished, and then this name was described by Li (1981: 490), who cited the specimen *Y. H. Li 4103* collected from Mengyuan, Mengla, Yunnan, China, and housed in KUN as the holotype.

Additional specimens examined. Thailand. Northern. Chiang Mai [Doi Chiang Dao, fl., 28 Oct 1979 [as *Garcinia* sp.], *T. Shimizu* et al. *T-20980* (AAU, BKF); Doi Chiang Dao Wildlife Sanctuary, Chiang Dao District, fr., 9 Nov 1995 [as *G. propinqua*], *J. F. Maxwell 95-1129* (CMUB); Doi Ang Khang, Fang District, fl., 27 May 1998 (as *G. bracteata*), *T. Wongprasert* et al. *s.n.* (BKF124408); Doi Ang Khang, fl., s.d. [as *Garcinia* sp.], *P. Triboun s.n.* (BK265941)]; Chiang Rai [Summit of Doi Tung near temple, Mae Sai District (originally “Mae Fa Luang District” on the label), fr., 11 Oct 1997 [as *Garcinia* sp.], *R. Pooma & M. Tamura RP-MT10* (BKF, K); Doi Tung, near Wat Phra That Doi Tung, Huai Khrai Subdistrict, Mae Sai District, male fl., 23 May 2006 [as *G. propinqua*], *J. F. Maxwell 06-312* (CMUB, L

[L3878616], QBG); ibid., fr., 6 Sep 2006 [as *G. propinqua*], *J. F. Maxwell 06-637* (CMUB, L [L3812984], QBG); along trail near summit of Pha Hung, above Wat Phra That Doi Tung, fr., 22 Oct 2012 [as *G. propinqua*], *M. van de Bult 1275* (BKF, CMUB, L [L4311877]); near Wat Phra That Doi Tung, Mae Sai District (originally "Mae Fa Luang District" on the label), fl., 27 Feb 2003 [as *Garcinia* sp.], *R. Pooma & V. Chaemchumroon 3742* (BKF, SING [SING0095616]); near Wat Phra That Doi Tung, Mae Sai District, male fl., 19 May 2020 [as *G. propinqua*], *M. van de Bult 1732* (BKF); Phu Chi Fa, male fl., 20 Mar 2000 [as *Garcinia* sp.], *BKF Sc404* (BKF180336)]; Tak [Doi Pae Poe, about 90 km NW of Tak, female fl., 14 Mar 1968 [as *G.* cf. *anomala*], *B. Hansen & T. Smitinand 12915* (BKF, AAU, C, K, L [L2408816], P [P00329869])].

India. Khasia, fl., s.d., *J. D. Hooker & T. Thomson s.n.* (P [P05062486]); Indes Orientales, locality not specified, female fl., fr., 1859, *J. D. Hooker & T. Thomson s.n.* (P [P05062491]); East Bengal, Khasya, male fl., s.d., distributed at the Royal Botanic Gardens, Kew (1861–1862), *W. Griffith 848* (CAL [CAL0000046566], G [G00458432], K [K000677605, K000677606], L [L0489483], P [P00329868]), US [US02961086], W [W0073367]); Khasia, fl. s.d., *W. Griffith 654* (K [K000677607]); locality not specified, fl., 1843, *W. Griffith s.n.* (P [P05062487]); Khasia, fr., 1864, *Unreadable s.n.* (P [P05062482]); India, Jaintia (originally "Jaintea" on the label), 14 Dec 1885, *C. B. Clarke 42547H* (G [G00458506]), *C. B. Clarke 42547J* (US [US02961087]); Assam, male fl., 1893, *G. King's Collector s.n.* (L [L2408817], P [P05062492], US [US02961088]); Assam, Laitlynkot, Khasi Hills, young fr., 13 Jul 1949, *T. R. Chand 1786* (L [L2409534]); Assam, Cherrapunjee, Khasi Hills, 4000 ft alt., fl., 21 Jul 1952, *W. N. Koelz 30721* (L [L2409592]); ibid., fl., 29 Apr 1952, *W. N. Koelz 29534a* (L [L2409594]; ibid., fl. 9 May 1952, *W. N. Koelz 29795* (L [L2409595]).

China. Yunnan, Mengyuan, Mengla, Xishuangbanna, 850 m alt., fl., 4 Sep 2004 [as *G. bracteata*], *Zhou Shi-shun 2056* (QBG); Guangxi, Na Po County, Nong Hua, fl., 5 Jun 1989 [as *G. bracteata*], *H. Q. Wen W014* ([US02961079]).

Vietnam. Ha Giang, Dong Van District, Municipality Ho Quang Phin, Vicinity of Ta Xa Village, male fl., 28 Apr 1999 [as *Garcinia* sp.], *P. K. Loc* et al. *CBL1740* ([P05061735]); Ha Giang, Meo Vac District, Municipality Sung Chang, Vicinity of Lu Lu Phin Village, Cao Bang Limestone, male fl., 29 Apr 1999 [as *Garcinia* sp.], *P. K. Loc* et al. *CBL1851* (P [P05061727]); Cao Bang, Nguyen Binh District, Municipality Ca Thanh, Cao Bang Limestone, male fl., 13 Apr 1999 [as *Garcinia* sp.], *P. K. Loc* et al. *CBL1317* (P [P05061730]); Hoa Binh Province, Mai Chau District, Hang Kla, fr., 22 Sep 2005 [as *Garcinia* sp.], *Vu Xuan Phong* et al. *HNK750* (K [K000576423]).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CN. Data curation: CN, PC. Formal analysis: CN. Funding acquisition: CN. Investigation: CN, PC, NL, MC, RT. Methodology: CN, PC, NL, MC, RT. Project administration: CN. Resources: CN, PC. Writing – original draft: CN, PC. Writing – review and editing: CN, PC, NL, MC, RT.

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Data availability

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

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Research Article

Didymocarpus pingyuanensis (Gesneriaceae), a new species endemic to Danxia landscape from Guangdong Province, China, and two new combinations in *Didymocarpus*

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Abstract

Didymocarpus pingyuanensis, endemic to the Danxia landscape in Pingyuan County, Guangdong, China, is described and illustrated here. This species can be distinguished from other members of *Didymocarpus* sect. *Heteroboea* by its calyx deeply 5-lobed to about three quarters of its length. The phylogenetic position of the new species within *Didymocarpus* was examined using nuclear ribosomal internal transcribed spacer (ITS) sequences. Based on phylogenetics analysis and morphological evidence, we propose two new combinations, elevating the two varieties to species level, namely *D. yinzhengii* and *D. gamosepalus*.

Key words: *Didymocarpus heucherifolius* var. *gamosepalus*, *Didymocarpus heucherifolius* var. *yinzhengii*, flora of Danxia, taxonomy

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Introduction

Didymocarpus Wall. was once a large genus with approximately 200 species (Weber and Brutt 1998). Recent molecular phylogenetic studies and morphological revisions of *Didymocarpus* have led to a reduction in the estimated number of species from 200 down to 60–80, with some species being transferred to *Henckelia* Spreng., *Hovanella* A.Weber & B.L.Burtt, *Petrocodon* Hance (Weber and Brutt 1998; Weber et al. 2000, 2011; Möller and Clark 2013).

For species of this genus in China, Wang et al. (1990) classified them into two sections: sect. *Didymocarpus* (herbs with stems) and sect. *Heteroboea* W.T.Wang auct. non Benth (herbs without stems). Sect. *Heteroboea* were initially defined by morphological characters, but on the basis of recent systematic results and morphological comparison, four species have been assigned to the genus *Petrocodon*, these species are *P. bonii* (Pellegr.) A.Weber & Mich.

Möller, *P. mollifolius* (W.T.Wang) A.Weber & Mich.Möller, *P. niveolanosus* (D. Fang & W.T.Wang) A.Weber & Mich.Möller, *P. hancei* (Hemsl.) Mich.Möller & A.Weber (Weber et al. 2011). Recently, four new taxa within this section were discovered and published: *Didymocarpus dissectus* F.Wen, Y.L.Qiu, Jie Huang & Y.G.Wei (Wen et al. 2013) from Fujian Province, *D. heucherifolius* Hand.-Mazz var. *yinzhengii* J.M.Li & S.J.Li (Li and Li 2014) from Hunan Province, *D. heucherifolius* Hand.-Mazz var. *gamosepalus* Xin Hong & F.Wen (Xu et al. 2019) from Guangdong, China, and *D. lobulatus* F.Wen, Xin Hong & W.Y.Xie (Xie et al. 2020) from Zhejiang, China. In addition, *D. subpalmatinervis* W.T.Wang, which was placed in sect. *Heteroboea* has been transferred to *Petrocodon* as a new combination with *P. subpalmatinervis* (W.T.Wang) F.Wen & Z.L.Li after a thorough study (Li et al. 2023). Thus, before the completion of the revision work for this article, there were eight species and two varieties in sect. *Heteroboea*, all of which are endemic to China.

During a field investigation of Danxia landscapes in Pingyuan County, Guangdong, in April 2023, we encountered a *Didymocarpus* species in bloom and confirmed its classification within sect. *Heteroboea* of this genus as it was stemless herb (Wang et al. 1990). However, it differs from all known species in this section by having a calyx that is deeply 5-lobed to about three quarters of its length. After thorough morphological comparisons using herbarium specimens, digital images, and relevant literature on other similar species, we concluded that this plant represents an undescribed species. Here, the putative species is described and illustrated based on morphological observations and compared with closely related species. Additionally, we used nuclear DNA internal transcribed spacer (ITS) to reconstruct the phylogeny to evaluate the phylogenetic position of *Didymocarpus pingyuanensis*.

Material and methods

Morphological study

We used a micrometer and a stereomicroscope to observe and measure the morphological traits of the putative species. Morphological comparisons between *Didymocarpus pingyuanensis* and its related species were based on dry specimens we collected, relevant literature (Wen et al. 2013; Li and Li 2014; Xu et al. 2019; Xie et al. 2020), as well as digital images on the Chinese Virtual Herbarium (https://www.cvh.ac.cn/) and the China Field Herbarium (https://www.cfh.ac.cn/). Morphological observation was conducted in the Herbarium of Sun Yat-sen University (SYS).

Taxon sampling and molecular analysis

The ITS region was used for examining the phylogenetic position of the putative species. During May 2023, we collected 6 taxa belonging to sect. *Heteroboea* for this study. These taxa included *Didymocarpus cortusifolius* (Hance) H.Lév., *D. salviiflorus* Chun, *D. lobulatus*, *D. heucherifolius* var. *heucherifolius* Hand.-Mazz, *D. heucherifolius* var. *yinzhengii*, *D. heucherifolius* var. *gamosepalus*. Except for *D. heucherifolius* var. *gamosepalus*, all species were collected from their type localities. The population of *D. heucherifolius* var. *gamosepalus* at its type locality has gone extinct due to human disturbance caused by nearby village activities. Consequently, we were unable to find it at its type locality in Pingyuan County, Guangdong. Instead, we collected specimens from Zijin County, Guangdong. Voucher specimens were deposited in SYS. We sequenced their ITS gene sequences to verify the molecular differences; the sequences have been uploaded to GenBank. Thirty-eight species of *Didymocarpus* and related genera with ITS gene sequences in NCBI GenBank were downloaded for analysis. In total, we got 45 ITS gene sequences of 45 taxa, GenBank accession numbers were followed after their Latin name in the phylogenetic tree. These taxa encompass three *Gyrocheilos* W.T.Wang species, one *Allocheilos* W.T.Wang species, one *Raphiocarpus* Chun species, six *Primulina* species, three *Petrocodon* species, nineteen species from *Didymocarpus* sect. *Didymocarpus* and nine from *Didymocarpus* sect. *Heteroboea*. *Sinningia incarnata* (Aubl.) D.L.Denham and *S. tubiflora* Fritsch were selected as outgroups. All but one species of *Didymocarpus* sect. *Heteroboea* were included in this study. The excluded species was *Didymocarpus reniformis* W.T.Wang, which was not located during multiple expeditions, and only imprecise locality data were available.

Total DNA was extracted from silica-gel-dried leaves using the modified cetyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle 1987). Polymerase chain reaction was carried out based on the program setting as proposed by Lee et al. (2022) using the universal primers, ITS1 and ITS4 (White et al. 1990). The ITS sequence was aligned with Clustal W which is embedded in MEGA-11 (Tamura et al. 2021). The sequences in the alignment were manually adjusted. Phylogenetic trees were reconstructed using the maximum likelihood (ML) methods and Bayesian inference (BI) methods via MEGA-11 (Tamura et al. 2021) and MrBayes v3.2.1 (Ronquist et al. 2012). The optimum DNA substitution model calculated using the “Find best DNA/Protein Models (ML) function embedded in MEGA-11 was Kimura 2-parameter model (K2) with Gamma Distributed With Invariant Sites (G+I) (=K2+G+I). All branch nodes were calculated with 1000 bootstrap (BS) replicates. BI analysis employed random starting trees and four Markov chain Monte Carlo (MCMC) simulations were run simultaneously and sampled every 1000 generations for 1 million generations. Bayesian posterior probabilities (PP) were calculated as the majority consensus of all sampled trees with the first 25% discarded as burn-in.

Results and discussion

Molecular analysis

The aligned length of the ITS sequences was 730 bps. The topologies of the Bayesian and ML trees are incongruent. The BI tree is displayed below (Fig. 1), ML tree is displayed in Appendix 1: Fig. A1. The topology indicates that *Didymocarpus* sect *Heteroboea* is paraphyletic, and eight taxa of *Didymocarpus* sect *Heteroboea* belong to clade I (Fig. 1. PP = 1, BS = 100%). In this clade, the putative new species forms a sister group with *Didymocarpus dissectus*, *D. heucherifolius* var. *gamosepalus* and *D. heucherifolius* var. *yinzhengii* (Fig. 1. PP = 1, BS = 81%), while *D. heucherifolius* var. *heucherifolius* belongs to another group (Fig. 1, PP = 1, BS = 81%).

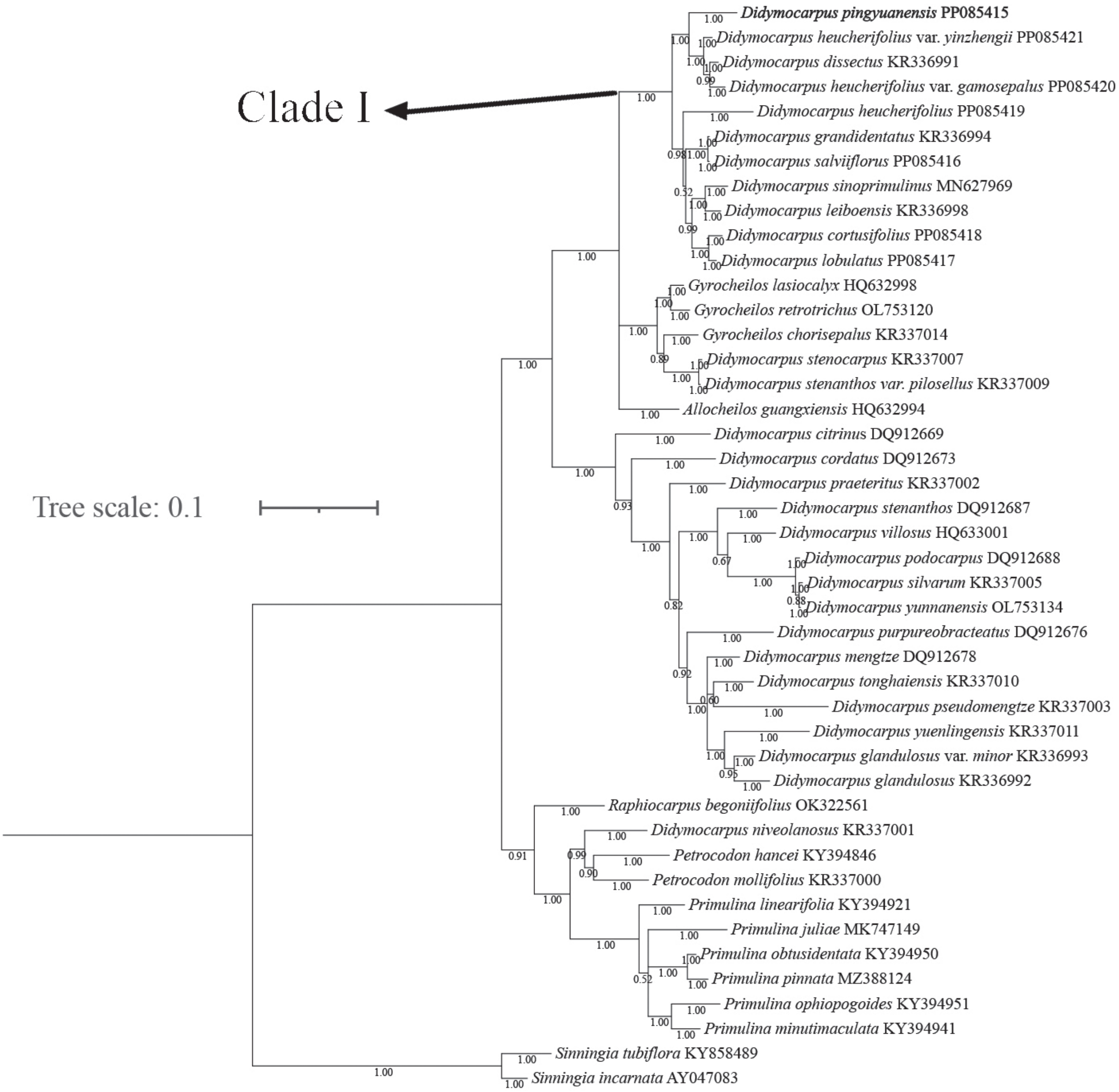

Figure 1. Bayesian inference (BI) tree based on ITS sequences of the new species *Didymocarpus pingyuanensis* and related species. Bayesian posterior probabilities are shown along the branches. The new species described in this study is shown in bold.

Morphological comparison

In *Didymocarpus* sect. *Heteroboea*, most species exhibit similar vegetative characteristics, except for *D. dissectus*, whose leaf margin is irregularly and distinctly 3- or 4-lobed in the distal 1/3–1/2. There are two varieties, *D. heucherifolius* var. *gamosepalus* and *D. heucherifolius* var. *heucherifolius* distributed in Guangdong Province, China. Both *D. pingyuanensis* and *D. heucherifolius* var. *gamosepalus* share the same distribution area, namely Pingyuan County in Guangdong, and both are distributed within the Danxia landscape. During the field investigation, we also found *D. heucherifolius* var. *heucherifolius* in Wuzhishi scenic spot, which is about 50 km from the locality of *D. pingyuanensis*. However, *D. pingyuanensis* can be distinguished from *D. heucherifolius* var. *heucherifolius* by its glabrous corolla.

Furthermore, it can be distinguished from *D. heucherifolius* var. *gamosepalus* by its shorter corolla, and calyx deeply 5-lobed to about three quarters of the calyx length, lobes equal, obovate, apex rounded, rarely cuspidate, overlapping at margin.

Although *Didymocarpus pingyuanensis* and *D. salviiflorus* share calyx lobed and overlapping at margin, however, the former is deeply 5-lobed to about three quarters of the calyx length, contrasting with the latter 5-lobed to about half of the calyx length from the base. Additionally, *D. pingyuanensis* can also be distinguished from *D. salviiflorus* by bracts free, elliptic, and corolla glabrous outside.

Differences between the putative species and its morphologically related species, *Didymocarpus heucherifolius* var. *heucherifolius*, *D. heucherifolius* var. *gamosepalus*, and *D. salviiflorus* are shown in the following identification table (Table 1) and Fig. 2.

Table 1. Morphological differences between the species *Didymocarpus pingyuanensis*, *D. heucherifolius* var. *heucherifolius*, *D. heucherifolius* var. *gamosepalus*, *D. salviiflorus*.

Character	***Didymocarpus pingyuanensis***	***D. heucherifolius* var. *heucherifolius***	***D. heucherifolius* var. *gamosepalus***	***D. salviiflorus***
Shape of calyx	deeply 5-lobed to about three quarters of the calyx length, obovate, overlapping at margin	5-lobed to the base, broadly lanceolate to oblanceolate-linear or triangular	5-lobed from middle to above middle	5-lobed to about half of the calyx length from the base, depressed oblong, overlapping at margin
Bracts	bracts free, elliptic, 5–12 mm, serrate, long ciliate	bracts free, elliptic, 5–10 mm, serrate, long ciliate	bracts free, 4–8 mm, serrate, long ciliate	bracts free to connate, semiorbicular, ca. 5 mm, margin sparsely crenate
Size of corolla	1.8–3.8 cm long	2.5–3.2 cm long	3.6–4.3 cm long	2.5–3 cm long
Indumentum of corolla	glabrous	puberulent	glabrous	puberulent
Staminodes	1.5–4 mm from the base	1–2 mm from the base	1–1.6 cm from the base	3–5 mm from the base

Figure 2. Morphological differences between *Didymocarpus pingyuanensis*, *D. heucherifolius* var. *heucherifolius*, *D. heucherifolius* var. *gamosepalus*, and *D. salviiflorus* **A** *D. pingyuanensis* **B** *D. heucherifolius* var. *heucherifolius* **C** *D. heucherifolius* var. *gamosepalus* **D** *D. salviiflorus*; **1**. front view of corolla; **2**. lateral view of corolla, showing calyx and bracts (Photographers: **A–C** by Qiang Fan **D** by Ling-Han Yang).

Taxonomic treatment

Didymocarpus pingyuanensis **Ling H.Yang, Q.Fan & F.Wen, sp. nov.**
urn:lsid:ipni.org:names:77345325-1
Figs 3, 4

Diagnosis. *Didymocarpus pingyuanensis* is similar to *D. heucherifolius var. gamosepalus* and *D. salviiflorus* in having a similar zygomorphic corolla and pink to pinkish-purple funnel-shaped to tubular corolla tube, but can be distinguished from *D. heucherifolius* var. *gamosepalus* by its corolla size 1.8–3.8 cm long (*vs.* 3.6–4.3 cm long), calyx deeply 5-lobed to about three quarters of the calyx length, apex rounded, rarely cuspidate, overlapping at margin (*vs.* 5–lobed from middle to above middle); from D. salviiflorus, it differs by having calyx 5-lobed to about three quarters of the calyx length (*vs.* 5-lobed to about half of the calyx length from the base), bracts free, elliptic (*vs.* bracts free to connate, semiorbicular), and corolla glabrous outside (*vs.* puberulent outside).

Type. China. Guangdong Province: Meizhou City, Pingyuan Town, 24°32'N, 115°50'E, 491 m a.s.l., 1 April 2023 (fl.), *Qiang Fa, Xing-yue Zhang, Li-juan Liao, Jie-hao Jin, Ling-han Yang DNPC 3352* (holotype: SYS!; isotypes: IBK! IBSC! SYS!)

Description. Acaulescent perennial herb. ***Rhizome*** horizontal, 2–4 cm long, ca. 1 cm in diameter. ***Leaves*** 4–9 basal, clustered at the apex of the rhizome, whorled; leaf blades chartaceous, orbicular-ovate to triangular, 4–11 cm long, 4.5–12 cm wide, apex slightly acute, base cordate, margin lobed (lobes 18–21, irregularly triangular, with irregular teeth), upper surface densely cover with white pilose hairs, green, lower surface with sparsely short hairs and pilose brown hairs confined to the veins, pale green, basal veins 5, palmate; petiole terete, pale green, 2.5–9 cm long, densely covered with pilose brown hairs, ***Cymes*** axillary, usually 3–6 on a stem, pseudodichotomous, scapiform, each 2- to numerous flowered; Peduncle 10–18 cm long, covered with white dense short hairs and sparsely pilose brown hairs; ***Bracts*** free, elliptic, 5–12 mm long, serrate, long ciliate; Pedicel up to ca. 2.5 cm long, with short hairs; ***Calyx*** deeply 5-lobed to about three quarters of the calyx length, lobes equal, obovate, apex rounded, rarely cuspidate, overlapping at margin, 6–9 mm long, 4.5–6 mm wide at the widest part and 2–3 mm wide at the base, lobes margin denticulate, puberulent outside, glabrous inside. ***Corolla*** zygomorphic, pink to magenta, up to ca. 3.8 cm long; glabrous outside, inside with glandular puberulent hairs from the throat to the corolla base and two wide bright yellow strips at the throat; tube funnel-shaped to tubular, 1.2–2.3 cm long, ca. 6.5 mm in diameter at base, ca. 1.1 cm in diameter at throat; limb distinctly 2–lipped, adaxial lip 2-lobed to near middle, 0.6–1 × ca. 1.3 cm, obliquely triangular, abaxial lip 3-lobed to base, lobes rounded or oblong, ca. 0.9 × 1.6 cm, more or less equal. ***Stamens*** 2, adnate to corolla ca. 2 cm above the base of the corolla tube; filaments white, 8–13 mm long, slightly geniculate above base, swollen at middle, glabrous with glandules on the surface; anthers pale yellow, ca. 3 mm long, cohering face to face, white woolly. ***Staminodes*** 3, adnate to 1.5–4 mm above the base of the corolla tube, 0.4–0.8 mm long, white, glabrous. ***Pistil*** 2.2–3 cm long, puberulent; ovary

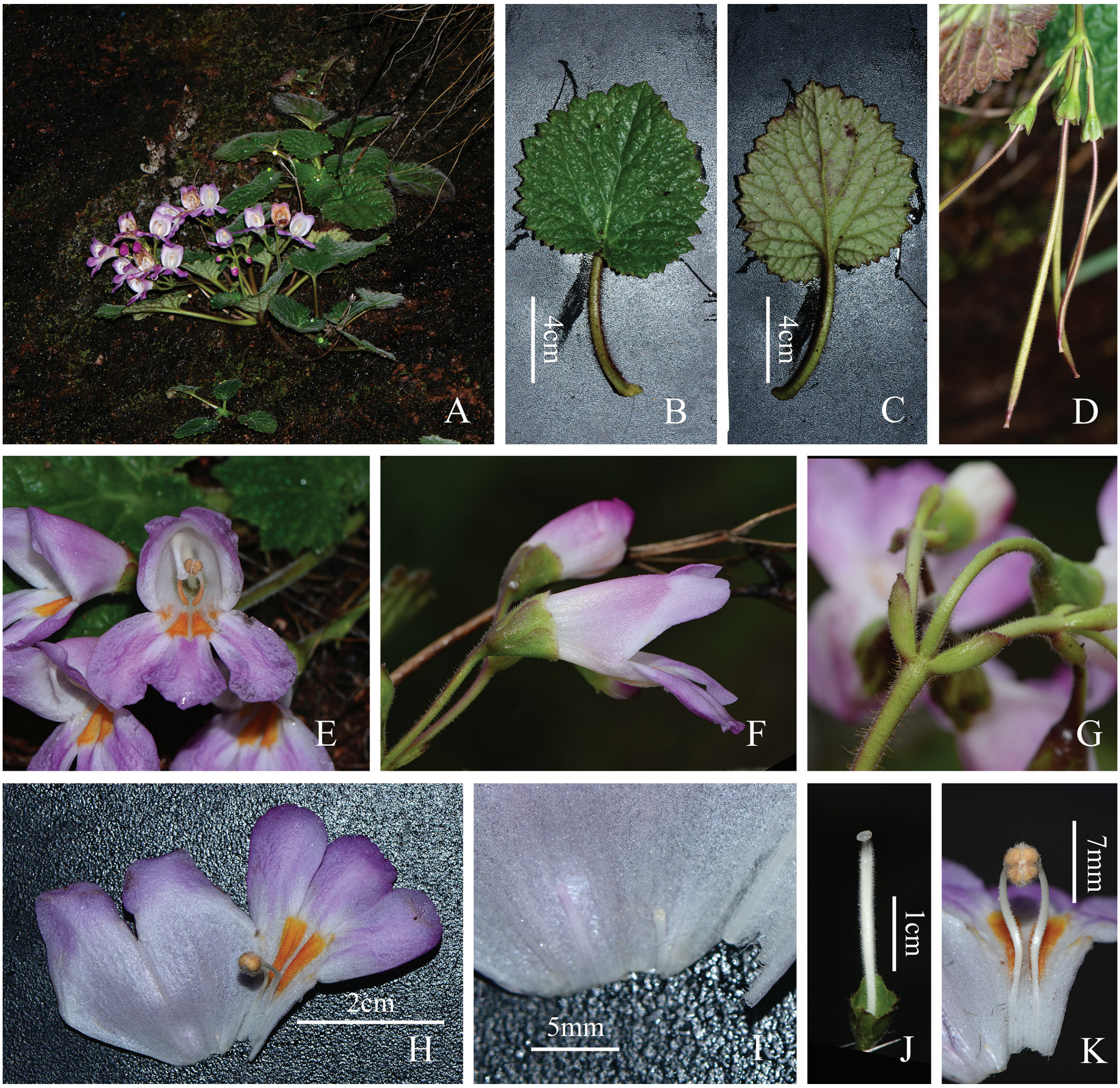

Figure 3. *Didymocarpus pingyuanensis* **A** habitat in flowering **B** adaxial surface view of leaf blade **C** abaxial surface view of leaf blade **D** capsule **E** front view of corolla **F** lateral view of corolla, showing calyx deeply 5-lobed to about a quarter of the calyx length from the base **G** bracts **H** opened corolla **I** staminodes **J** pistil **K** stamens (Photographers: **A–K** by Qiang Fan).

white, cylindrical, puberulent; style ca. 2.3 mm long; stigma 1, cephaloid, centrally sunken, undivided, translucent. ***Capsule*** purplish-red when young, linear-cylindrical, glandular puberulent, up to ca. 9 cm long.

Phenology. The flowering of *Didymocarpus pingyuanensis* is from April to May; and the fruiting is in June.

Distribution and habitat. *Didymocarpus pingyuanensis* so far has only been found on three Danxia landscapes within Pingyuan County. It is locally abundant and endemic to a narrow area near the type locality. This species prefers moist, but sunny cliffs, at an elevation of 100–500 m a.s.l. In Pingyuan, the average temperature is 21.7 °C, and the average annual precipitation is 1637 mm.

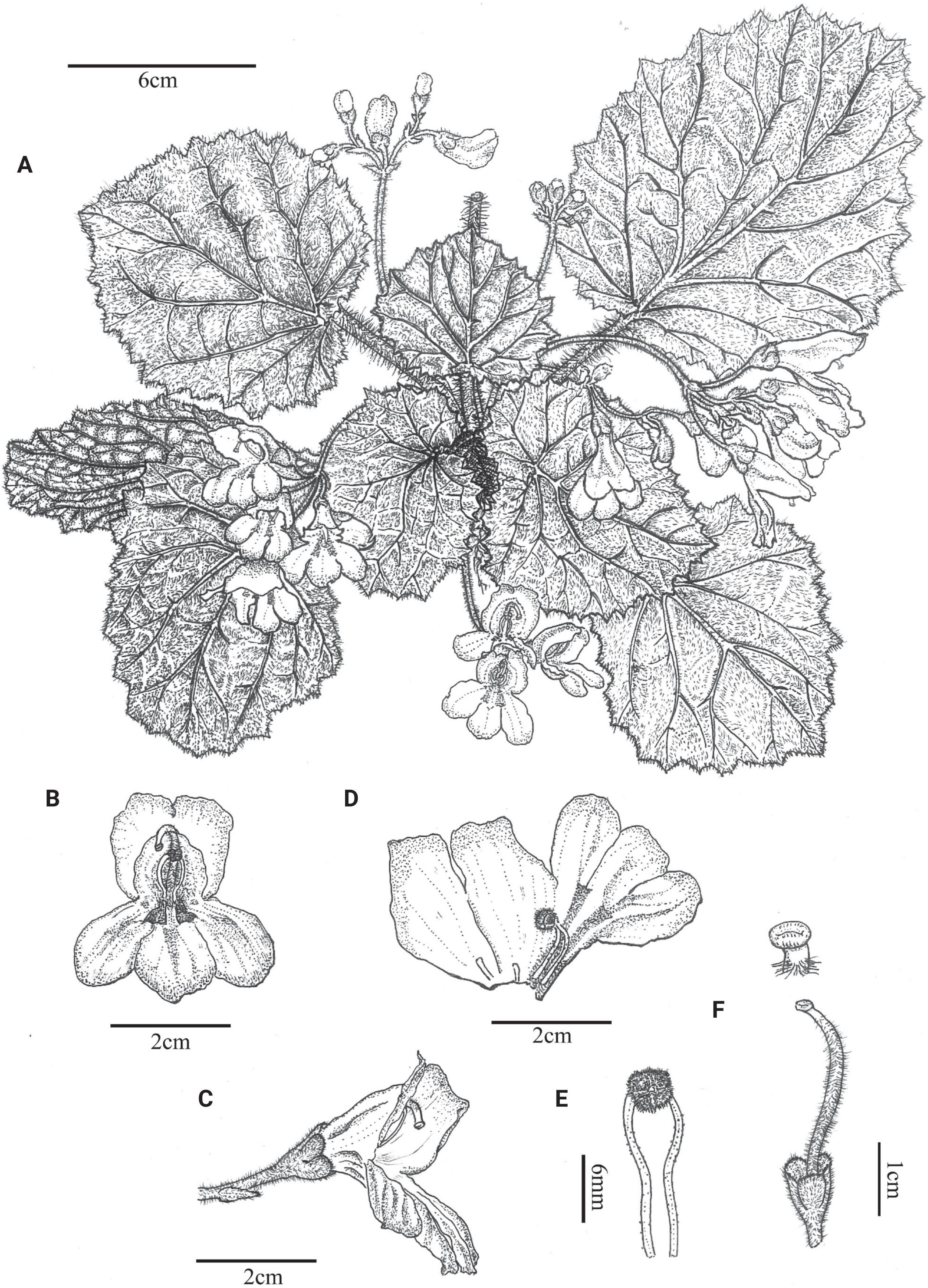

Figure 4. *Didymocarpus pingyuanensis* Ling H. Yang, Q. Fan & F. Wen **A** habit **B** flower in front view **C** flower in lateral view **D** opened corolla, showing stamens and staminodes **E** stamens **F** pistil and stigma (Drawn by Rong-En Wu).

Etymology. The specific epithet refers to the type locality, Pingyuan County, Guangdong Province, China. The Chinese name of the new species is here given as 平远长蒴苣苔 (Píng Yuǎn Cháng Shuò Jù Tái).

Additional specimens examined. *Didymocarpus pingyuanensis* (paratypes): China, Guangdong, Pingyuan: Nantai Mountain, 24°33'N, 115°53'E, 168 m a.s.l., 6 May 2023, *Qiang Fan, Zheng-Fei Li, Ling-Han Yang 20212* (SYS); Nantai Mountain, 24°32'N, 115°50'E, 491 m a.s.l., 7 May 2023, *Qiang Fan, Zheng-Fei Li, Ling-Han Yang 20219* (SYS); Dahebei scenic spot, 24°36'N, 115°49'E, 300 m a.s.l., 7 May 2023, *Qiang Fan, Zheng-Fei Li, Ling-Han Yang 20221* (SYS).

Didymocarpus heucherifolius: China, mountains between Shicheng in southeastern Jiangxi and Ninghua in western Fujian, 1200 m a.s.l., 7 May 1921, *Te-Hui Wang* (IBSC0005130, isotype).

Didymocarpus salviiflorus: China, Zhejiang, Lishui, 19 April 1930, *Guan-Guang Zhong* (00030758, isotype).

Didymocarpus heucherifolius var. *yinzhengii*: China, Hunan, Yongxing, 26°2'28"N, 113°9'8"E, 140 m a.s.l., 13 May 2023, *Qiang Fan, Zheng-Fei Li, Ling-Han Yang 20265* (SYS).

Discussion

Morphologically, *Didymocarpus pingyuanensis* can be distinguished from other species within this genus belonging to *Didymocarpus* sect. *Heteroboea* by calyx deeply 5-lobed to about a quarter of the calyx length from the base, lobes equal, obovate, apex rounded, rarely cuspidate, overlapping at margin. Initially, *Didymocarpus pingyuanensis* seems morphologically like a new variety of *D. heucheifolius* var. *heucheifolius*, because only *D. heucheifolius* var. *heucheifolius* and *D. heucherifolius* var. *gamosepalus* distributed in Guangdong in *Didymocarpus* sect. *Heteroboea*. In addition, *Didymocarpus pingyuanensis* shares corolla glabrous outside with *D. heucherifolius* var. *gamosepalus* and *D. heucherifolius* var. *yinzhengii*, both of them were varieties of *D. heucherifolius*. However, according to the phylogenetic trees, *D. pingyuanensis*, two varieties of *D. heucherifolius* and *D. dissectus* form a sister group, while *D. heucherifolius* var. *heucherifolius* forms a sister group with *D. cortusifolius*, *D. salviiflorus*, *D. lobulatus*, *D. grandidentatus*, *D. leiboensis* and *D. sinoprimulinus*. Thus, we suppose *D. pingyuanensis* is a distinct species (Fig. 1), and elevate the two varieties of *D.heucherifolius* to species level, namely *D. yinzhengii* and *D. gamosepalus*.

New combination

***Didymocarpus yinzhengii* (J.M.Li & S.J.Li.) Ling H.Yang, Q.Fan & F.Wen, comb. nov.**
urn:lsid:ipni.org:names:77345326-1

≡ *Didymocarpus heucherifolius* var. *yinzhengii* J.M.Li & S.J.Li. Phytotaxa 156 (3): 187. 2014.

Type. China. Hunan: near Yongxing County. alt. 300 m, 26°17'10"N, 113°11'25"E, 6 May 2011, *Jia-Mei Li 1105062* (holotype: HEAC!); ibid. *Jia-Mei Li 11501* (paratype: IBK!).

Didymocarpus gamosepalus **(Xin Hong & F.Wen) Ling H.Yang, Q.Fan & F.Wen, comb. nov**
urn:lsid:ipni.org:names:77345327-1

≡ *Didymocarpus heucherifolius* var. *gamosepalus* Xin Hong & F.Wen. PhytoKeys 128: 34. 2019.

Type. China. Guangxi Province, cultivated in the nursery of Gesneriad Conservation Center of China (GCCC), introduced from north of Guangdong Province: Pingyuan County, Meizhou City, growing in rocky crevices at the foot of a calcareous sedimentary rocky hill. 22 February 2019, flowering, *WF20190222-05* (holotype: IBK!; isotype: AHU!)

Acknowledgments

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Ling-Han Yang participated in field investigation, and taxonomic confirmation and wrote the original draft. Jing-Min Dai assists in the molecular analysis. Jian-Hui Liu, Xue-Zheng Lan participated in field investigation and collected the plants. Qiang Fan and Fang Wen are project leaders and contributed to paper writing.

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Data availability

The newly obtained sequences of *Didymocarpus cortusifolius*, *D. salviiflorus*, *D. lobulatus*, *D. heucherifolius* var. *heucherifoliu*, *D. heucherifolius* var. *yinzhengii*, *D. heucherifolius* var. *gamosepalus* have been submitted to the NCBI website. The ITS sequence data supporting the findings of this study are available in Fig. 1.

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Appendix 1

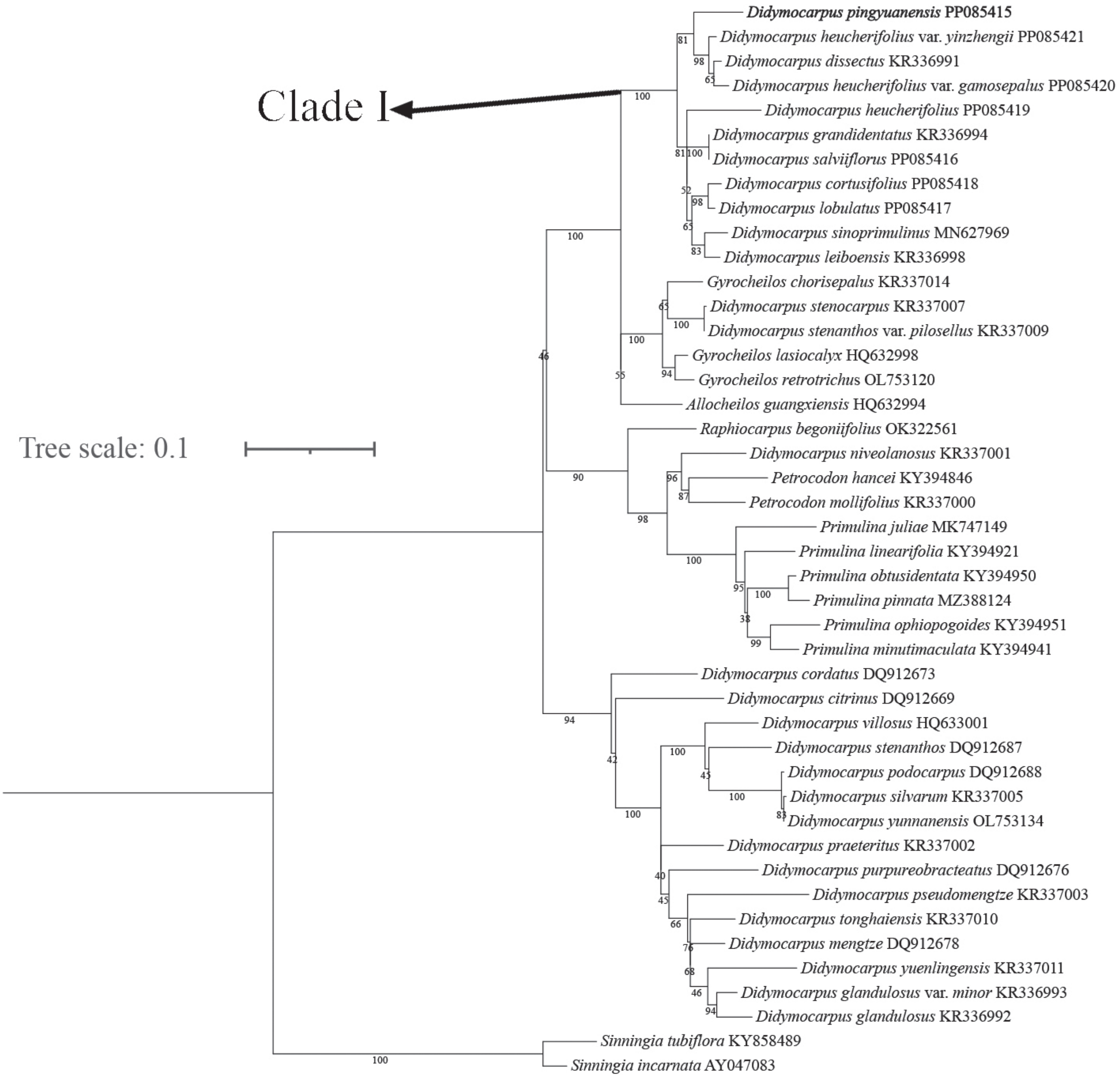

Figure A1. Maximum Likelihood (ML) tree based on ITS sequences of the new species *Didydmocarpus pingyuanensis* and related species. Values of bootstrap support are shown along the branches. The new species described in this study is shown in bold.

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Research Article

Coptis austrogaoligongensis (Ranunculaceae), a new species from West Yunnan, China

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Abstract

Based on morphological and plastid data, we have described and confirmed that *Coptis austrogaoligongensis* distributed in Tongbiguan Provincial Nature Reserve, Yingjiang County, Yunnan Province, is a new species of *Coptis*. It is distinctly different from *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis* with differences mainly reflected in the following features: former leaf segment lobes contiguous to each other, and lateral segments equal to central one; plants without developed stolons; inflorescences with only 1–3 flowers; petals have short claws. Phylogenetic analysis indicated that *C. austrogaoligongensis* is a sister to *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis*.

Key words: *Coptis*, *Coptis austrogaoligongensis*, taxonomy, Yunnan Province

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Introduction

Coptis Salisb. is a small genus of Ranunculaceae, consisting of perennial herbs with yellowish rhizomes and numerous fibrous roots (Wang 1979, 2001). The taxonomy of *Coptis* has traditionally been based on vegetative (leaf type and shape) and reproductive (flower number, color and shape of sepals and petals, and beak length) characters (Xiang et al. 2016, 2018). The genus *Coptis* comprises 17 species worldwide, which is mainly distributed in the warm temperate to the cold coniferous forests of eastern Asia and North America (Xiang et al. 2016, 2018; Wang et al. 2020). Representatives of the genus *Coptis* are considered essential medicinal plants in Eastern Asia. They are rich in isoquinoline type alkaloids, such as berberine, epiberberine, coptisine, palmatine, jatrorrhizine, and columbamine, and their dried rhizomes are used in traditional Chinese medicine as *Rhizoma Coptidis*, which is famous for clearing heat, removing dampness, and reducing fire (Wang et al. 2019; Yang et al. 2021).

According to the morphology, especially flower and leaf, genus representatives distributed in China had been classified into seven species, one variant and one subspecies, i. e., *C. chinensis* Franch. (endemic to SW China), *C. chinensis* var. *brevisepala*

W. T. Wang & P. K. Hsiao (endemic to SE China), *C. deltoidea* C. Y. Cheng & P. K. Hsiao (endemic to Sichuan, China), *C. omeiensis* (Chen) C. Y. Cheng (endemic to Sichuan, China), *C. quinquefolia* Miq. (distributed in Taiwan Province and Japan), *C. quinquesecta* W. T. Wang (endemic to Yunnan, China), *C. teeta* Wall. (distributed in East Himalaya), *C. teeta* subsp. *lohitensis* Pandit & Babu (distributed in East Himalaya), and *C. huanjiangensis* L.Q. Huang, Q.J. Yuan & Y.H. Wang. *C. huanjiangensis* as a new species was described during the survey of traditional Chinese medicine resources in Huanjiang, Guangxi in 2022 (Wang et al. 2022).

Coptis teeta complex is an important local medicinal plant in China. The *C. teeta* complex is divided into two subspecies, *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis*, based on the presence of stolons and reproduction methods (Pandit and Babu 1993, 2000, 2003). *Coptis teeta* subsp. *teeta* is mainly distributed in Changdu and Linzhi of Xizang, China. It used as a medicinal plant by the Monba and Lhoba ethnic groups in southeastern Xizang. *C. teeta* subsp. *lohitensis* is mainly distributed in the Gaoligong Mountains in the northwest of Yunnan Province. It was used as a currency equivalent exchange in the past. *C. teeta* subsp. *lohitensis* is used in the treatment of diarrhea, dysentery and eye diseases by the Lisu, Dulong and Nu ethnic minorities in Gaoligong Mountain of Yunnan Province (Cheng et al. 2022, 2024).

In March 2023, during the investigation of *C. teeta* resources in southeast Tibet and northwest Yunnan, we found one population in Yingjiang County of Dehong Dai and Jinpo Autonomous Prefecture, which was different from the previously observed materials of *C. teeta* complex. The difference was mainly reflected in the fact that leaf segment lobes were contiguous to each other, and lateral segments equal to central one. Plants had no developed stolons. But there was no option to evaluate the morphological features of flowers at that time. In March 2024, we obtained flowers material. It was found that inflorescence consists of 1–3 flowers. The petals have short claws. This was obviously different from *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis* characteristics. At the same time, we also collected materials for the molecular studies, and the results of consequent phylogenetic analysis proved that this population is the sister group of *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis*.

Methods

Material sampling and DNA extraction

Samples of the new species were collected from Yingjiang County, Dehong Dai and Jinpo Autonomous Prefecture. The plastome sequences of 8 related *Coptis* species (a total of sixteen accessions) and an outgroup species were obtained from GenBank (http://www.ncbi.nlm.nih.gov). The total genomic DNA was extracted from the fresh leaves using the modified CTAB method (Doyle and Doyle 1987), and libraries were prepared using the TruePrep DNA Library Prep Kit (Vazyme Biotech Co., Ltd, Nanjing, CN). All the DNA and molecular materials were deposited in the herbarium of Minzu University of China (MUC). Sample information is listed in Suppl. material 1: table S1. For principal component analysis (PCA), we measured more than 20 individuals with complete traits. In our examination, we focused on 19 morphological characters, which also encompassed both vegetative and reproductive characteristics (Suppl. material 1: table S2). These characters were chosen based on their relevance in species identification and establishment, as described by Sun and Zhang (1995).

Plastome sequencing and assembly

Genomic paired-end sequencing was conducted using the Illumina Novaseq 6000 platform. The chloroplast genome was assembled and analyzed using the program NOVOPlasty v. 4.3.1 (Dierckxsens et al. 2017). Annotation was performed with CPGView to determine the initial location of the chloroplast genome and the IR region (Liu et al. 2023), with the chloroplast genome of *C. teeta* (NC 054331) serving as a reference. The annotations were manually checked for errors using Zhou et al. (2021) as reference. The final chloroplast genome of new species was deposited in the NCBI GenBank under accession numbers: PP786562 and PP786563.

Phylogenetic reconstruction

Fifty-six single copy protein-coding genes (PCGs) were extracted from 19 chloroplast sequences using the PhyloSuite v. 1.2.3 software (Zhang et al. 2020; Xiang et al. 2023). They were aligned using the MAFFT v. 7.149b algorithm (Katoh et al. 2019). All these single gene alignments were concatenated to create a document for phylogenetic analyses. The best-fit model was determined using the Akaike information criterion (AIC) in ModelFinder program (Kalyaanamoorthy et al. 2017). To determine its phylogenetic position, a maximum likelihood (ML) tree was constructed by IQ-TREE v. 1.6.10. Bayesian inference (BI) analysis was performed with MrBayes based on 56 PCGs of 8 other *Coptis* species through PhyloSuite v. 1.2.3 software. Phylogenetic trees were visualized, rooted with *Asteropyrum peltatum*, and edited using the iTOL v. 5 (Ivica and Peer 2021). R v.4.3.2 was employed for data analysis, the ggplot2 package was used for statistical chart visualization, and the factoextra package was used for presenting the PCA plot charts.

Results

Phylogenetic and morphological analysis

Consensus phylogenetic tree reconstructed by ML and BI analyze based on 56 PCGs of 10 species, with *Asteropyrum peltatum* as outgroups is represented in the Fig. 1. The topologies of the ML and BI trees were identical with all the branches strongly-supported (ML BS≥90% and BI PP = 1). All the accessions of *Coptis* formed a monophyletic group with high support. The two samples of the new species (*C. austrogaoligongensis* C. L. Long & Z. Cheng, sp. nov.) were clustered into one clade and sister to the *C. teeta* subsp. *teeta* and *C. teeta* subsp. *lohitensis* clade (Fig. 1). Morphological PCA results show that the three species are obviously divided into three clusters, with an interpretation of 39.9% for PCA1 and 23.6% for PCA2. The long distance between the three species indicates obvious differences between them (Fig. 2).

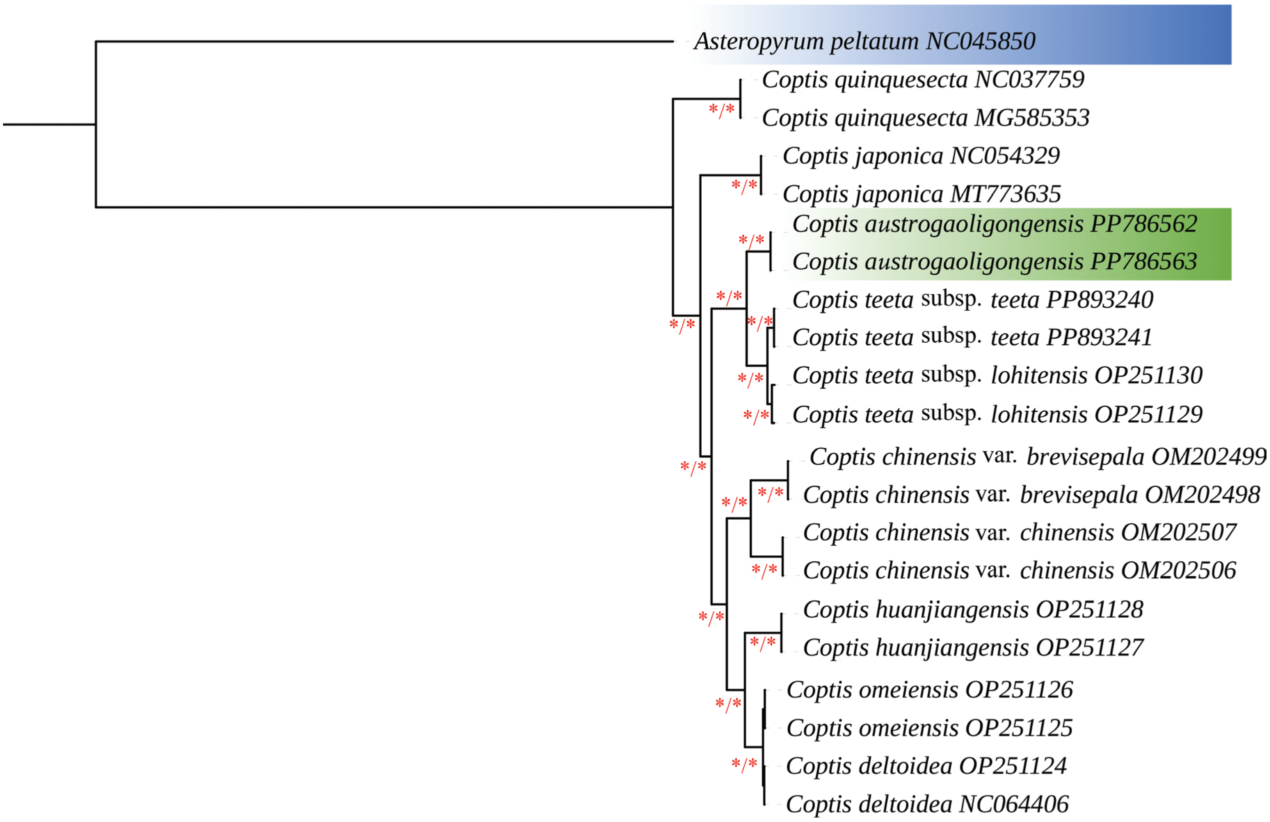

Figure 1. Consensus phylogenetic tree reconstructed by ML and BI analysis based on 56 protein-coding sequences (CDS) of 10 species, with *Asteropyrum peltatum* as outgroups. Asterisks near the branches indicate bootstrap support (BS) percentages obtained from maximum likelihood inference and posterior probabilities (PP) obtained from Bayesian analysis (BS/PP). Those nodes with BS≥90%, PP =1.00 were shown with asterisks.

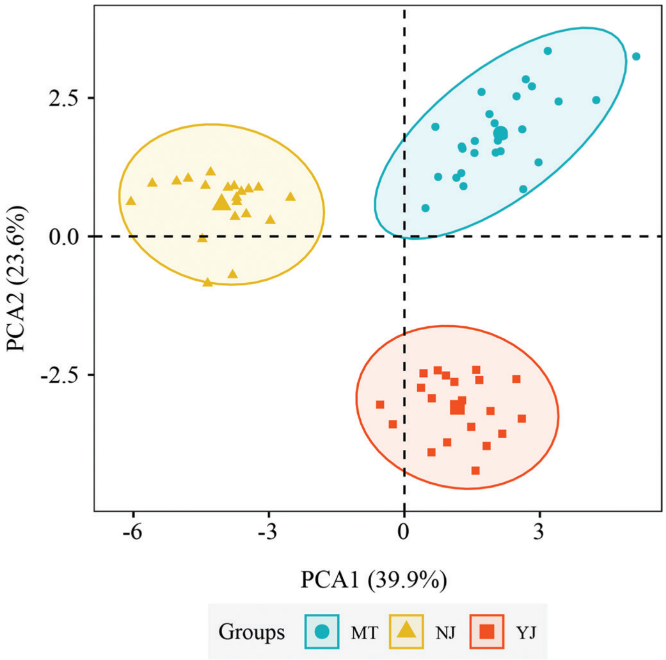

Figure 2. Morphological principal component analysis (PCA) of three species based on some individuals (20 NJ individuals, 20 YJ individuals, and 27 MT individuals) and 19 morphological traits. MT: *C. teeta* subsp. *teeta*, NJ: *C. teeta* subsp. *lohitensis*, YJ: *C. austrogaoligongensis*.

Taxonomic treatment

Coptis austrogaoligongensis C. L. Long & Z. Cheng, sp. nov.

urn:lsid:ipni.org:names:77345372-1
Figs 3–4
"南高黎贡黄连"(Nan Gao Li Gong Huang Lian)

Type. China, Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Zhina Township, 2444 m a.s.l., 25°15'55"N, 98°4'11"E, 20 March 2023, *Zhuo Cheng YNHL021* (holotype: KUN!; isotype: KUN!).

Description. Herbs perennial, rhizomes branched, without stolons. Leaves basal, petioles 24–35 cm, glabrous. Leaf blade ovate, 7–12 × 6–12 cm, three-segmented, margin with sparsely upturned spiny hairs; central segment petiolulate (petiole 0.5–1 cm), ovate-rhombic, 6–12 × 3.5–6 cm, four-ten-lobed, lobes remote, ultimate lobes margin acute serrate, apex acute or obtuse. Scapes one to several, erect, longer or shorter than the leaves, 25–40 cm wide, glabrous, sulcate. Inflorescences terminal, often monochasial, three-five-flowered; flowers small, actinomorphic, bisexual; bracts lanceolate, palmately divided. Sepals five, greenish, long ellipsoid or lanceolate, 0.5–0.6 × 0.15–0.2 cm, sparsely puberulous. Petals spatulate, 0.15–0.25 cm long, glabrous, apex rounded to obtuse, 1/4–1/3 as long as sepals. Stamens numerous, glabrous, 2–4 mm long, outer ones slightly shorter than petals. Pistils 8–14, 3–5 mm long; follicles 4.5–9.0 mm long, stipitate; seeds ellipsoid, ca. 2–3 mm long, brown.

Distribution and habitat. The only known locality of this taxon is in Zhidong Village, Zhina Township, Yingjiang County, Dehong Dai and Jingpo Autonomous Prefecture, Yunnan Province. The site is located in an open area in a primeval forest dominated by Fagaceae and Magnoliaceae. The observed population is very small, with about 100 plants growing in the bamboo forest along the roadside, accompanied by some pteridophytes. The elevation is 2400–2500 m above sea level.

Etymology. The specific epithet is derived from the type locality, Gaoligongshan, Yunnan.

Phenology. The species was observed flowering in February – March and fruiting in April–June.

Conservation status. This species has not been recorded or described so far, and there is only one known site in Yingjiang County, which is relatively unknown to botanists. In addition, *C. austrogaoligongensis* is very small and has a short flowering period, making it easily overlooked. At the moment, without further biogeographical investigations, we can suggest that this species satisfies the IUCN 3.1 Red List CR (Critically Endangered) Criteria B1ab(ii,iii)+2ab(i,ii,iii) (IUCN 2012), which has an EOO (Extent of occurrence) < 100 km^2 and AOO (Area of occupancy) < 10 km^2, it may be classified as "critically endangered" (CR). The distribution site of *C. austrogaoligongensis* is next to the road, which causes a great risk of human disturbance and extreme weather, such as tourist activities, road building, grazing and landslides. Additionally, regional management in pursuit of economic development is likely to pose a threat through trampling and pollution of soil and water, probably causing negative impacts to the small and fragile habitat.

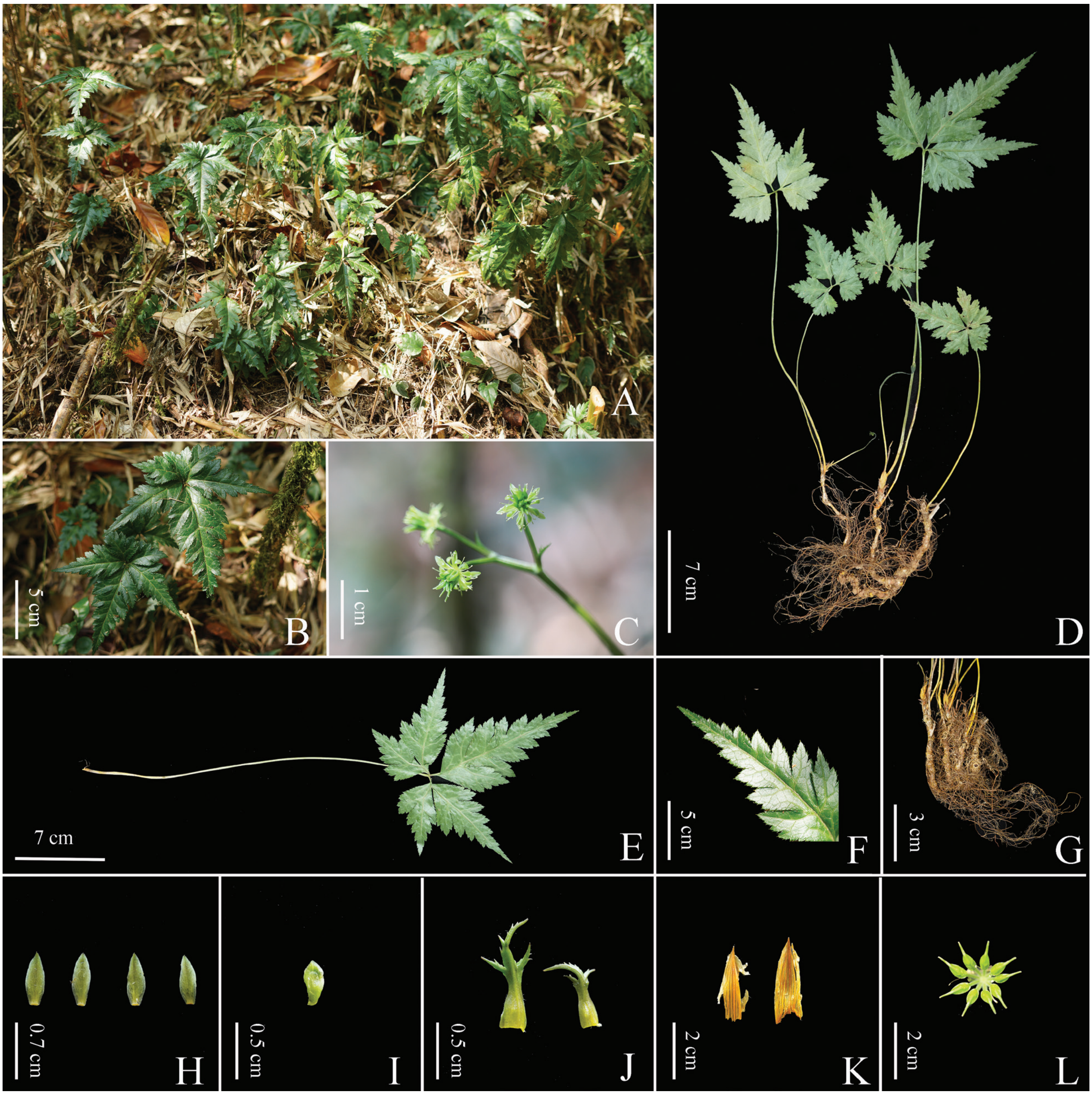

Figure 3. *Coptis austrogaoligongensis* C. L. Long & Z. Cheng, sp. nov. **A** species habitat **B** leaf **C** plant in florescence stage **D** whole plant **E** petiole **F** margin with sparsely upturned spiny hairs **G** rhizome and fibrous roots **H** calyx **I** petal **J, K** bract **L** fruit. Photos by Zhuo Cheng & Jiahua Li.

Taxonomic notes. The new species belongs to *Coptis* section *Chrysocoptis* based on the following characters: leaves tri-lobed, leaflets sessile or short petiolate (Cheng et al. 1965; Wang 2001; Wang et al. 2022). There were seven species, one variant and one subspecies belonging to *Coptis* Section *Chrysocoptis* in China prior to the discovery of *C. austrogaoligongensis*. From the perspective of geographical distribution, *C. teeta* subsp. *lohitensis* and *C. quinquesecta* are both distributed in Yunnan, *C. teeta* subsp. *lohitensis* is mainly distributed in north Gaoligong Mountains and *C. quinquesecta* is mainly found in Jinping County, whereas *C. austrogaoligongensis* is mainly distributed in south Gaoligong Mountains. According to the key to the species of *Coptis* occurring in China (Wang 2001), the morphology of *C. austrogaoligongensis* is similar to

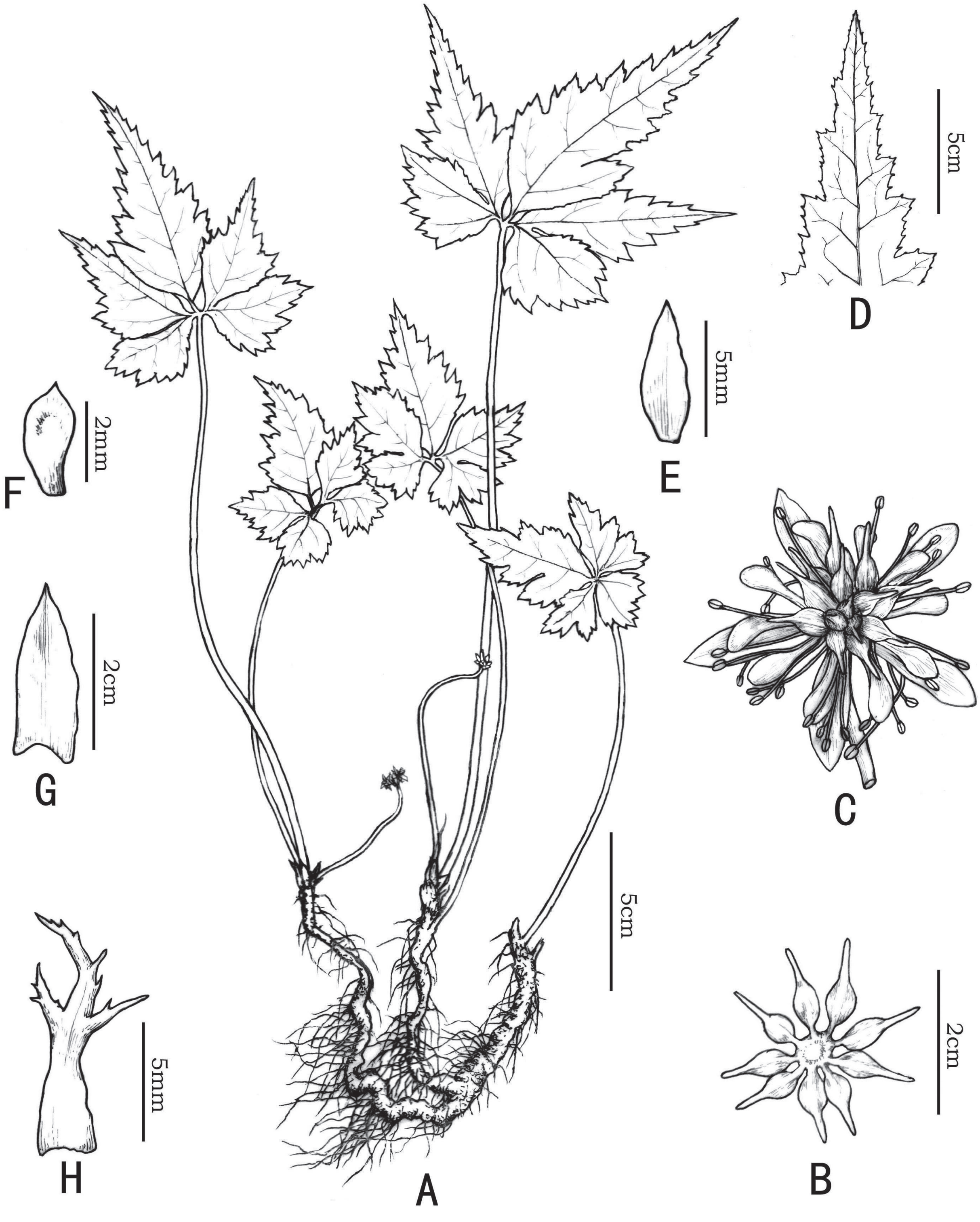

Figure 4. *Coptis austrogaoligongensis* C. L. Long & Z. Cheng, sp. nov. **A** species habitat **B** Fruit **C** Flower **D** margin with sparsely upturned spiny hairs **E** calyx **F** petal **G** bract **H** bract. Drawn by Xinchen Qu.

C. teeta subsp. *teeta* and *C. teeta* subsp. *lohitensis*. However, *C. austrogaoligongensis* can be clearly distinguished by the following features: leaves with deep pinnate cleavages on whole lobes adjacent to each other, lateral segments equal to central one; plants without developed stolons; inflorescences with only 1–3 flowers; petals have short claws. A comparative summary of the characters that differentiate these three taxa is presented in Table 1.

Table 1. Distinguishing features of *C. austrogaoligongensis* in comparison with *C. teeta* subsp. *lohitensis* and *C. teeta* subsp. *teeta*.

Characters	*C. austrogaoligongensis*	*C. teeta* subsp. *lohitensis*	*C. teeta* subsp. *teeta*
Leaf blade	Ovate, 7–12 × 6–12 cm	Ovate-triangular, 6–12 × 5–9 cm	Ovate-triangular, 12–17.5 ×7.7–14.5cm
Leaves shape	lateral segments equal to central one, the petiole length of the middle lobe is 0.3–0.8 cm; leaves with deep pinnate cleavages on whole lobes adjacent to each other	lateral segments subsessile, shorter than central one, the petiole length of the middle lobe is 1–2.1 cm; obliquely ovate, unequally parted	lateral segments equal to central one, the petiole length of the middle lobe is 1.5–2.4 cm; obliquely ovate, unequally parted
Inflorescences	1–3 flowers	3–5 flowers	3–5 flowers
Petiole length	24–35 cm	8–19 cm	19–31 cm
Scape length	25–40 cm	15–25 cm	20–30 cm
Sepal number	5 or 6	5	5
Sepal shape	long ellipsoid or lanceolate, 0.5–0.6 × 0.15–0.2 cm, sparsely puberulous	elliptic, 0.75–0.8 × 0.25–0.3 cm, glabrous.	long ellipsoid or lanceolate, 0.5–0.6 × 0.2–0.25 cm, sparsely puberulous
Petal length	spatulate, 0.2–0.3 cm, glabrous, apex rounded to obtuse	spatulate, 0.54–0.59 cm, glabrous, apex rounded to obtuse	0.3–0.35 cm, glabrous, apex rounded to obtuse
Petal shape	petal with short claws	petals have long claws	petals have long claws
The length ratio of sepal vs petal	ca. 3 times	ca. 2 times	ca. 2 times
Are there any stolons	No	Yes	No

Additional *C. austrogaoligongensis* specimens examined. CHINA. Yunnan: Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Zhina Township, 2444 m a.s.l., 25°15'55"N, 98°4'11"E, 20 March 2023, Zhuo Cheng YNHL021, Zhuo Cheng YNHL022, Zhuo Cheng YNHL023, Zhuo Cheng YNHL024, Zhuo Cheng YNHL025, Zhuo Cheng YNHL026 (KUN!).

Specimens of *C. teeta* subsp. *lohitensis* examined. CHINA. Yunnan: Lushui County, 29 September 2009, L. Xie 83-0381(KUN); Lushui County, 20 November 2007, H. Li 24283 (PE); Longyang District, 23 April 2014, H.J. Dong et al. 935 (KUN); Fugong County, 15 March 2008, X.H. Jin & T. Zhang 071 (PE); Fugong County, 12 November 2007, H. Li 20256 (PE); Gongshan County, 27 September 1984, Qingzang team 9763 (PE).

Key to the species of *Coptis* in China

There are eight species and one variant of *Coptis* distributed in China. An identification key is presented below.

1 Leaves five-sectioned..**2**
– Leaves three-sectioned..**3**
2 Rhizome robust; leaf blade 5.5–14 cm wide, central segment pinnately divided, apex Attenuate..***C. quinquesecta***
– Rhizome slender; leaf blade 2–6 cm wide, central segment three-lobed, apex acute ....***C. quinquefolia***
3 Leaf blade lanceolate to narrowly ovate; lateral segments 3–3.5× shorter than central segment; sepals linear-lanceolate....................... ***C. omeiensis***
– Leaf blade ovate to ovate-triangular; lateral segments slightly shorter than central segment; sepals lanceolate, elliptic, or narrowly ovate..................**4**
4 Petals spatulate..**5**
– Petals lanceolate to linear-lanceolate..**8**

5 Inflorescences three–five-flowered **6**
– Inflorescences more than five-flowered .... ***C. huanjiangensis***
6 Sparse lobes of leaf, long petals clawed **7**
– Close lobes of leaf; without stolons; short claws in petals .... ***C. austrogaoligongensis***
7 stolons developed .... ***C. teeta* subsp. *lohitensis***
– stolons absent .... ***C. teeta* subsp. *teeta***
8 Leaf segment lobes ± contiguous to each other; stamens ca. 1/2 as long as petals .... ***C. deltoidea***
– Leaf segment lobes remote; outer stamens slightly shorter than petals **9**
9 Sepals 9–13 mm, ca. 2× as long as petals .... ***C. chinensis* var. *chinensis***
– Sepals ca. 6.5 mm, slightly longer than petals .... ***C. chinensis* var. *brevisepala***

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We are very grateful to the local people of Yingjiang County, Yunnan, who guided us to the habitats of *Coptis* species and continued to send us information in different seasons. Many thanks to Xinlei Zhao, a respected taxonomist and expert of *Coptis* from the Institute of Medicinal Plant Development, Chinese Academy of Medical Sciences and Peking Union Medical College, for his confirmation of this new species. We also thank Jun Yang from the Kunming Institute of Botany, Chinese Academy of Sciences for their helpful suggestions.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CL, ZC. Data curation: LZ, ZC. Formal analysis: ZC. Funding acquisition: CL. Investigation: CX, ZC, QG, JL, LZ. Resources: JL. Supervision: CX. Writing - original draft: ZC. Writing - review and editing: CL.

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Data availability

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

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Supplementary material 1

Supplementary information

Authors: Zhuo Cheng, Jiahua Li, Congli Xu, Lixiang Zhang, Qiangbang Gong, Chunlin Long

Data type: xlsx

Explanation note: **table S1.** Accession numbers of 21 sequenced or downloaded chloroplast genomes in this study. **table S2.** List of analyzed morphological traits. Data type: table (excel file).

Link: https://doi.org/10.3897/phytokeys.244.127978.suppl1

PhytoKeys 244: 237–248 (2024)
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Research Article

Pollen transfer efficiency in *Erica* depends on type of pollinator

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Abstract

Pollen transfer efficiency (PTE; the proportion of pollen removed from flowers that reaches conspecific stigmas) is expected to vary with the type of pollinator and flower morphology, and to influence male siring success. Many species in the genus *Erica* are pollinated by bees (which consume pollen and should thus lower PTE) but during its radiation in the Cape, several independent shifts to both sunbird and long-proboscid fly (LP fly) pollinators, which do not consume pollen have taken place. Improvements in PTE could be one of the factors driving these pollinator shifts. PTE data for 15 *Erica* species (five for each of the three pollinator types) were collected and compared in relation to type of pollinator and anther exsertion. LP fly- and bird-pollinated species had higher PTE in comparison with bee-pollinated species. Species with inserted anthers had higher PTE than those with exserted anthers. This suggests that sunbirds and LP flies are more efficient pollinators than bees. Additionally, the study suggests that insertion of anthers within the corolla tube can reduce pollen losses.

Key words: bee, bird, exserted anthers, long-proboscid fly

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Introduction

The reproductive success and number of seeds produced in flowering plants strongly depends on the efficiency of pollen removal and its subsequent deposition on conspecific stigmas (Johnson and Harder 2023). This can be quantified through the index of pollen transfer efficiency (PTE), which reflects the proportion of pollen removed from flowers that reaches stigmas (Johnson et al. 2005), and is expected to vary with type of pollinator (Laverty and Plowright 1988; Shuttleworth and Johnson 2008; Willmer et al. 2017). For example, it was shown that PTE was higher in a hummingbird-adapted *Penstemon* than in a bee-adapted congener (Castellanos et al. 2003). While it has been suggested that bees often act as pollen thieves by collecting pollen without effectively pollinating flowers (Hargreaves et al. 2009), e.g., to consume it or due to their grooming behaviour which cleans pollen off them, there have not been direct comparisons of the pollen transfer efficiencies of bees, nectarivorous birds and long-proboscid flies (LP flies), which are all important pollinator groups in southern Africa (Goldblatt and Manning 2000). In general, increased PTE could explain why shifts to non-grooming pollinators such as birds and LP flies have occurred, even though these shifts require investment in larger flowers (Castellanos et al. 2003).

The genus *Erica* is highly suitable for studying differences in PTE between pollinator groups because of its species diversity (ca. 700 in South Africa) and diversity of pollinators (van der Niet 2021). Most *Erica* species are pollinated by short-tongued insects, such as bees, but during its radiation in the Cape of South Africa, several independent shifts to both sunbird and LP fly pollination syndrome have taken place in the genus (Pirie et al. 2011). Nevertheless, it is not understood what factors precipitated these shifts and, if there are any differences in PTE, then those could be one of the selective factors driving the morphological changes associated with pollinator shifts (Kobayashi et al. 1997).

Erica species pollinated by bees or other short-tongued insects are the largest group in the genus (Rebelo et al. 1985). They typically produce many small flowers with low volumes of nectar (Bouman et al. 2017). Bees as pollinators tend to effect lower pollen carryover among plants compared to other pollinators, which is most likely due to their pollen grooming behaviour (Castellanos et al. 2003; Holmquist et al. 2012). Since grooming pollen lowers the fraction of removed pollen that can land on conspecific stigmas, bee-pollinated species are likely to have lower PTE than *Erica* species with other pollinators.

Adaptations to non-bee pollinators such as sunbirds and LP flies in the genus *Erica* might incur greater flower production costs but could also increase pollination success as a trade-off. For sunbird-pollinated *Erica* species, their long corollas in a variety of colours (Rebelo and Siegfried 1985), a higher volume of nectar (Rebelo et al. 1984) and the provision of a perch (Siegfried et al. 1985) might be costly. Similarly, LP fly-pollinated *Erica* species also tend to have long sticky corollas (McCarren et al. 2021a) and produce nectar high in volume and concentration (Goldblatt and Manning 2000; McCarren et al. 2023). Further, they reflect light in the ultraviolet range (McCarren et al. 2021b) which might make them more vulnerable to damage by UV-B radiation due to the lack of protection by ultraviolet-absorbing compounds (Llorens et al. 2015). Additionally, LP flies visit *Erica* flowers infrequently, resulting in relatively low pollination rates (McCarren et al. 2023). The adaptations mentioned above are likely to make both bird and LP fly pollination more energetically expensive for the plants and thus it is expected that these pollinators must confer other fitness benefits to compensate for the associated costs (Stiles 1978). These benefits could include the pollinators moving greater distances between plants while foraging, higher pollen carryover, limited pollen grooming (Krauss et al. 2017) and increased pollination accuracy (Armbruster et al. 2009). Therefore, *Erica* species pollinated by non-bees are expected to have relatively high PTE.

Many *Erica* species have exserted anthers, which appears to be a trait that evolved independently in multiple lineages (Pirie et al. 2011). Having exserted anthers can cause more pollen to be removed during the first pollinator visit (Harder and Barrett 1993), which could be beneficial when pollinator visits are rare or unpredictable. The function of exserted anthers in bird-pollinated species is likely to place pollen on their head feathers once the bill is fully inserted in the tube (Ojeda et al. 2016). Because pollen is less likely to be lost during transport on feathers than on the smooth bill of birds, *Erica* species with exserted anthers are expected to have higher PTE compared to species with included anthers. However, exserted anthers are also found in some bee-pollinated species and this may be associated with pollen being offered as a reward, which may decrease PTE. Therefore, it is unclear what the effect of anther exsertion is on PTE overall.

The aims of this study were to (a) compare PTE between bee-, bird- and LP fly-pollinated *Erica* species, and (b) compare PTE between *Erica* species with exserted and included anthers. This was addressed by collecting PTE data for 15 *Erica* species in total, with five species per type of pollinator, six species with exserted anthers and nine with included anthers.

Methods

Sample collection and analysis

A total of 15 *Erica* species were sampled in the Cape Floristic Region of South Africa with five species for each of three pollination syndromes: bird, LP fly and bee (Table 1). Syndrome classification was based on flower morphology (Rebelo et al. 1985) and confirmed by literature (Rebelo et al. 1984; Lombardi 2014; van der Niet et al. 2014; Bouman et al. 2017; Lombardi et al. 2021; Pauw 2022; McCarren et al. 2023), iNaturalist records and pollinator observations. Six of these species have exserted anthers, with three of them bee-pollinated and three bird-pollinated. Per species, 30 flowers were sampled, including ten unvisited flowers, which can be recognised by their intact anther ring (Geerts and Pauw 2011) and 20 flowers in late anthesis from different plants, whose corollas had begun to wilt (and therefore had no further opportunity to be pollinated). Flowers were randomly collected from different individuals. The anthers from undisturbed flowers, and the anthers and stigma from flowers in late anthesis were separated and kept individually in Eppendorf tubes. In the laboratory, the anthers were suspended in 1 ml ethanol and stained with fuchsin. The pollen suspension was homogenised with a vortex and then immediately four 20 µl drops from the sample were placed on a slide to count the pollen grains under a Leica DM500 compound microscope at 100× magnification.

The stigmas were mounted in molten fuchsin gel on a microscope slide using a cover slip. Pollen was counted under a Leica DM500 compound microscope at 100× magnification. There was no noticeable altitudinal or spatial clustering of species sharing types of pollinators, and at most of the sites no other *Erica* species from the same pollination syndrome were in flower at the time, except for some bee-pollinated species which co-flowered with one other bee-pollinated *Erica*. However, even when sharing pollinators, the high levels of flower constancy exhibited by bees cause high pollen purity (i.e., pollen from only one species) on the stigmas of co-occurring *Erica* species (van der Niet et al. 2020), and the difference in pollen aggregation for the co-flowering species (monads and tetrads) would have indicated heterospecific pollen transfer. Thus, it was assumed that the pollen counted on the stigmas was monospecific.

Table 1. Mean number of pollen grains deposited and removed ± standard deviation in 15 *Erica* species, the calculated PTE, their type of pollinator (long-proboscid fly = LP fly), anther exsertion, sample location and time.

Species	Pollen deposition	Pollen removal	Pollen production	PTE (%)	pollinator	Anther exsertion	Sample location	Month
E. aristata aristata Andrews	199 ± 136	45130 ± 12752	46495 ± 15151	0.4	LP fly (Rebelo et al. 1985; Lombardi et al. 2021)	included	Vogelgat	September
E. cristata Dulfer	91 ± 56	3541 ± 1681	3748 ± 1969	2.6	LP fly (Rebelo et al. 1985, iNaturalist record 39626162)	included	Vogelgat	March
E. retorta Montin	362 ± 236	18873 ± 17444	19125 ± 17740	1.9	LP fly (Rebelo et al. 1985)	included	Kogelberg	November
E. ampullacea ampullacea Curtis	830 ± 296	38800 ± 29292	46020 ± 35044	2.1	LP fly (Rebelo et al. 1985; McCarren et al. 2023, observations)	included	Boskloof	August
E. fastigiata coventryi Bolus	222 ± 149	2969 ± 2084	3461 ± 2483	7.5	LP fly (Rebelo et al. 1985; Pauw 2022, iNaturalist record 11115439)	included	Vogelgat	September
E. sessiliflora L.f.	224 ± 208	15549 ± 9200	16060 ± 9845	1.4	bird (Rebelo et al. 1985; Lombardi 2014, observations)	included	Vogelgat	September
E. viscaria pustulata L.	790 ± 272	14205 ± 8768	14400 ± 8939	5.6	bird (observations)	included	Vogelgat	March
E. plukenetii plukenetii L.	206 ± 72	35935 ± 12152	37695 ± 14016	0.6	bird (Rebelo et al. 1984, 1985, van der Niet et al. 2014, observations)	exserted	Vogelgat	September
E. monadelpha Andrews	246 ± 188	14003 ± 8972	15185 ± 10414	1.8	bird (Rebelo et al. 1985, observations)	exserted	Fernkloof	June
E. melastoma melastoma Andrews	548 ± 248	36023 ± 15724	39405 ± 23879	1.5	bird (observations)	exserted	Vogelgat	September
E. imbricata L.	49 ± 36	5480 ± 3132	5635 ± 3497	0.9	bee (Rebelo et al. 1985; Bouman et al. 2017, observations)	exserted	Vogelgat	June
E. laeta Bartl.	168 ± 120	3488 ± 1596	3550 ± 1766	4.8	bee (Rebelo et al. 1985, observations)	included	Vogelgat	March
E. labialis Salisb.	8 ± 4	7453 ± 1873	7465 ± 1899	0.1	bee (Bouman et al. 2017, observations)	exserted	Vogelgat	March
E. ericoides L.	44 ± 21	9880 ± 3008	5130 ± 5130	0.4	bee (observations)	exserted	Table Mountain National Park	December
E. quadrangularis Salisb.	198 ± 108	4785 ± 4868	9928 ± 3068	4.1	bee (Rebelo et al. 1985, observations)	included	Hottentot Hollands	December

Statistical analysis

Since most *Erica* species produce pollen in tetrads (Wrońska-Pilarek et al. 2018), the number of pollen tetrads in the anthers and on the stigmas was further multiplied by four to calculate the total number of pollen grains, except for *E. cristata*, *E. ericoide*s, *E. fastigiata* and *E. labialis* since those species produce pollen monads. Pollen removal was calculated as mean pollen removal per species by subtracting the mean pollen remaining in all disturbed anthers from the mean pollen produced in all unvisited anthers. Pollen transfer efficiency (PTE) was calculated for each species following the formula PTE= mean pollen deposition/mean pollen removal (Johnson et al. 2005). Statistical analyses were carried out in R (R Core Team 2022) by fitting generalised linear models with negative binomial error structure and using the log link function from the package 'MASS' (Ripley et al. 2019). Due to the many problems with analysing ratios (Johnson and Harder 2023), the variation in PTE was not tested directly. Instead pollen deposition (the response variable) was explored in relation to type of pollinator as explanatory variable with pollen removal as a covariate. Pollen removal was log transformed prior to the analysis so that it had the same scale of measurement as the response variable. The same model was repeated with anther exsertion as the explanatory variable and both pollen removal and type of pollinator as additional predictors. Since no LP fly-pollinated flowers had exserted anthers, those species were excluded from the analysis testing for an effect of anther exsertion. Due to the small sample size and consequently low statistical power, the interaction of type of pollinator and anther exsertion was not included in the model. Additionally, pollen production in relation to PTE, as well as pollen production and deposition in relation to type of pollinator, were modelled. The proportion of pollen removed was also modelled in response to type of pollinator using a beta GLM from the package 'betareg' (Cribari-Neto and Zeileis 2010). A beta distribution was used here since the model had a proportion as its response variable. The models comparing pollen production, pollen deposition and proportion of pollen deposited in relation to type of pollinator were repeated for bird- and bee-pollinated species only with anther exsertion as an additional predictor. Tukey's post hoc tests from the package 'emmeans' (Lenth and Lenth 2018) were used to identify the differences for models with significant terms.

Results

Almost all sampled flowers (98.3%) had at least some pollen deposited on their stigma and 85% had some pollen remaining in their anthers in late anthesis, so that on average 5.1% of the total pollen produced remained in the anthers. The recorded PTE values (Table 1) ranged from 0.1% to 7.5%. There was a significant effect of type of pollinator on pollen deposition after adjusting for pollen removal (χ^2 = 6.64, df = 2, p= 0.036, Fig. 1). Pollen deposition (adjusted for pollen removal) was about four-fold greater in bird- and LP fly-pollinated species than it was in bee-pollinated species (Fig. 1). The partial regression coefficient associated with removal did not differ significantly from zero (b= 0.070, Z= 0.346, p= 0.729), indicating that pollen deposition did not vary with removal. The post-hoc test showed that mean adjusted pollen deposition in bee-pollinated species was significantly less than that for both bird- (Z= 2.86, p= 0.012) and LP fly-pollinated species (Z= 2.69, p= 0.020), while there was no difference in pollen deposition between bird- and LP fly-pollinated species (Z= 0.40, p= 0.917). In the model with pollen deposition in response to anther exsertion, adjusted for both pollen removal and type of pollinator, pollen deposition was lower for species with exserted anthers than for species with included anthers (χ^2 = 5.04, df= 1, p= 0.025, Fig. 2). In this model, the partial regression coefficient associated with removal also did not differ significantly from zero (b= - 0.140, Z= 0.456, p= 0.648) further supporting that pollen deposition did not vary with removal. Pollen deposition in response to anther exsertion still differed between bird- and bee-pollinated species after accounting for the differences in anther position (χ^2 = 13.18, df= 1, p< 0.001). There was a negative relationship between pollen production and PTE (χ^2 = 5.57, df= 2, p= 0.018), i.e. PTE was lower for species producing large quantities of pollen and higher for species producing fewer grains. Pollen production (χ^2 = 11.30, df= 2, p= 0.004) and deposition differed (χ^2 = 9.55, df= 2, p= 0.008) significantly between types of pollinators. This was due to both bird- and LP fly-pollinated species producing (bird-pollinated: Z= 3.25, p= 0.003; LP fly-pollinated: Z= 3.17, p= 0.004) and receiving (bird-pollinated: Z= 3.11, p= 0.005; LP fly-pollinated: Z= 1.30, p= 0.016) more pollen than bee-pollinated species. The proportion of pollen removed did not vary among types of pollinators (χ^2 = 4.61, df= 2, p= 0.099). Pollen production was higher in species with exserted anthers (χ^2 = 12.31, df= 1, p< 0.001) and in this model bird-pollinated species had higher pollen production than bee-pollinated species (χ^2 = 55.81, df= 1, p< 0.001).

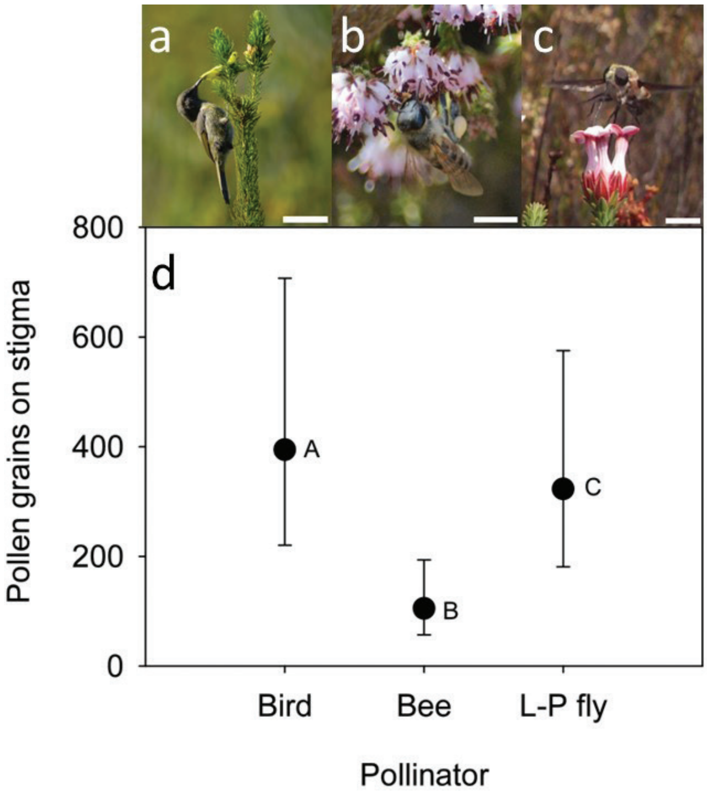

Figure 1. a Orange-breasted sunbird (*Anthobaphes violacea*) visiting the bird-pollinated *Erica viscaria* **b** honeybee (*Apis mellifera*) visiting the bee-pollinated *Erica ericoides* **c** long-proboscid fly (*Prosoeca westermanni*) visiting the LP fly-pollinated *Erica ampullacea* **d** mean (±95% confidence interval) pollen deposition for *Erica* species in relation to their type of pollinator after adjusting for pollen removal. Means that share letters are not significantly different. Scale bars: 40 mm (**a**); 5 mm (**b**); 15 mm (**c**).

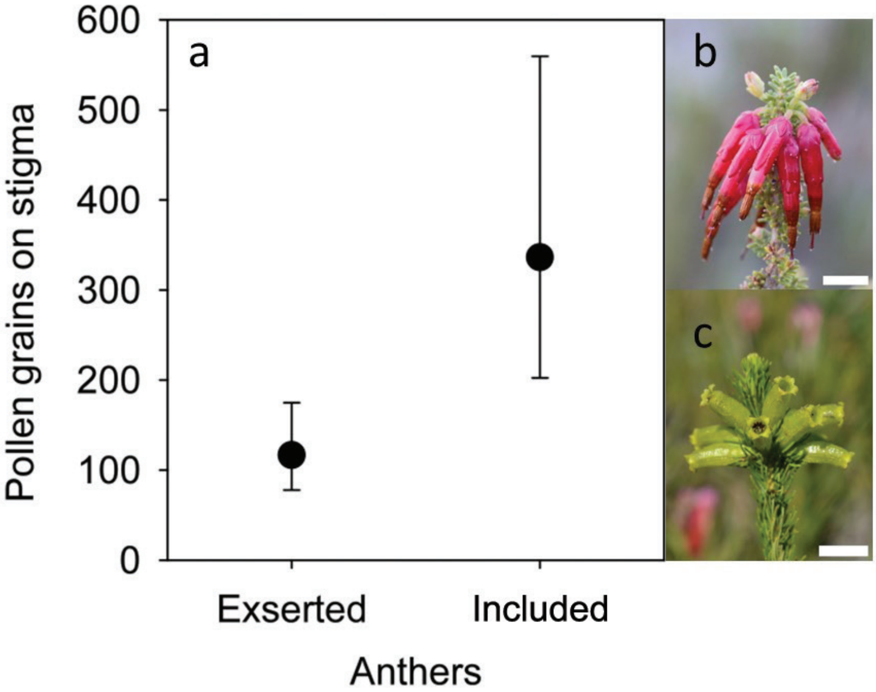

Figure 2. a Mean (±95% confidence interval) pollen deposition for *Erica* species in relation to their anther exsertion after adjusting for pollen removal and type of pollinator **b** exserted anthers in *E. monadelpha* **c** included anthers in *E. viscaria.* Scale bars: 10 mm (**b**); 15 mm (**c**).

Pollen deposition, on the other hand, was lower in species with exserted anthers ($\chi^2 = 7.65$, df= 1, p= 0.006) while bird-pollinated species still received more pollen than bee-pollinated species ($\chi^2 = 19.16$, df= 1, p< 0.001). The proportion of pollen removed did not differ between different anther positions ($\chi^2 = 0.50$, df= 1, p< 0.482) but it remained higher for bee-pollinated species compared to bird-pollinated species, as in the model above ($\chi^2 = 5.34$, df= 1, p= 0.021).

Discussion

PTE in the sampled *Erica* species averaged 2.4%, which is mostly higher than in other plants with granular pollen, for which PTE is typically <1% (Harder and Johnson 2008). This might be related to the relatively specialized pollination systems of the sampled *Erica* species. However, even though relatively high for plants with granular pollen, PTE in the sampled *Erica* species is still relatively low compared to values of up to 40% recorded for some orchids (Johnson et al. 2005; Hobbhahn and Harder 2016) and asclepiads (Shuttleworth and Johnson 2008) that produce aggregated pollen in the form of pollinia. There is generally a negative relationship between PTE and pollen production (Gong and Huang 2014; Harder and Johnson 2023), which suggests that production of pollen may evolve in relation to the risk of it being lost in transit between flowers (Harder and Johnson 2023). Relatively low pollen-ovule ratios in *Erica* may reflect the aggregation of pollen in tetrads and high PTE in this genus (Harder and Johnson 2008; Arendse et al. 2021). However, the expected association between pollen-ovule ratios and type of pollinator has not been confirmed in *Erica* (Arendse et al. 2021)

As expected, we found relatively low PTE in bee-pollinated *Erica* species and higher PTE in both bird- and LP fly-pollinated species. This supports the idea that nectarivorous birds are more efficient pollinators than bees (Castellanos et al. 2003). This study is one of the first to compare PTE between LP flies and other pollinators (see also Johnson and Harder 2023), and our observation that PTE of LP fly-pollinated species is higher than in bee-pollinated species, but does not differ from bird-pollinated species, is consistent with the idea that non-grooming pollinators confer greater PTE to the plants that they pollinate (Johnson and Harder 2023). However, the distinguishing feature of *Erica* species pollinated by LP flies could be that their anthers are always included, rather than the characteristics of their pollinator. Since the type of pollinator and anther exsertion are confounded for LP fly-pollinated species, experiments that specifically tease apart these factors are necessary to make unequivocal statements.

Seed production of *Erica* species pollinated by LP flies is often pollen-limited (McCarren et al. 2023). This is seemingly in contradiction to the results of this study which showed that they receive more pollen than bee-pollinated species and have high PTE with most stigmas appearing to be saturated with pollen grains. It is possible that geitonogamous pollen transfer, as a result of LP flies visiting several flowers per plant, could play a role in clogging stigmas with self-pollen reducing the number of seeds produced (Coetzee et al. 2020), and this effect would be exacerbated in the case of LP fly-pollinated *Erica* species that have late-acting self-incompatibility as commonly found in the genus (Arendse et al. 2021). While PTE methodology cannot discriminate between cross- and self-pollen, the risk of geitonogamous selfing is a general disadvantage of producing many flowers per plant (de Jong et al. 1992). However, because LP fly- and bird-pollinated *Erica* species tend to have fewer flowers per plant than those pollinated by bees, it seems unlikely that their higher levels of PTE would be caused by geitonogamous pollen transfer. It is more likely that the link between PTE and seed production is weak, since PTE is a measure of male fitness, while seed production is a measure of female fitness and might be impacted by additional traits, such as differences in style length and number of ovules.

This study shows that in most cases pollen still can be found in *Erica* anthers in late anthesis. The first visit to a flower causes the anther ring to break and release an explosive puff of pollen (Geerts and Pauw 2011), which might cause a large amount of pollen to be removed, but successive visits could still place some pollen on the pollinator. It has been predicted that increased pollen removal by one pollinator causes diminishing returns in pollen deposition (Harder and Thomson 1989; Harder and Wilson 1994) which would likely make it inefficient to place all or most pollen on the first visitor unless there are very few pollinator visits. Thus, in *Erica* the exploding anther ring might be an advantage when visitation rates are low like it has been reported e.g. for LP fly-pollinated species (McCarren et al. 2023), or it could increase pollen placement in hard-to-reach sites on the pollinator bodies where it is less likely to be groomed off.

We found that *Erica* species with exserted anthers have lower PTE than species with included anthers. Pollen removal typically increases with anther exsertion (Conner et al. 1995), but we found no difference in the proportion of pollen removed in relation to anther exsertion. *Erica* species with exserted anthers do, however, produce higher amounts of pollen but this increase in production does not coincide with an increase in deposition, which indicates that more of the removed pollen is lost to the environment. It is not clear how the pollen is lost, but once the anther ring has been broken, it could more easily be blown away by wind and washed away by rain, while in species with included anthers the pollen would likely remain inside the floral tube where it is still available to pollinators. Further, it might be easier for bees and other pollen thieves to collect and rob pollen from exserted anthers. Having exserted anthers thus imposes a cost since the plants produce more pollen while less of it ends up on conspecific stigmas. This could be a trade-off against other benefits like a different pollen placement site, which can reduce the risk of the stigma receiving heterospecific pollen (Manning and Goldblatt 1997; Muchhala and Thomson 2012).

With increasing pollen production, PTE decreases for *Erica* species, which is consistent with findings from other studies (Harder and Johnson 2023). This could be caused by plant species with less efficient pollinators compensating for low PTE with increased pollen production as a strategy that ensures reproductive success.

This study has shown that PTE differs among *Erica* species with different types of pollinators, as well as in relation to anther exsertion. These differences in PTE are likely the result of costs and benefits associated with different reproductive strategies, which in turn might have driven pollinator shifts and consequently speciation in the genus *Erica*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

The idea for this study originally came from Steve Johnson. Data collection was carried out by Sam McCarren. Statistical analyses were performed by Sam McCarren guided by Steve Johnson and Anina Coetzee. The manuscript was prepared by Sam McCarren, Jeremy Midgley, Anina Coetzee and Steven Johnson.

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Data availability

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

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Research Article

Nomenclature and typification of plant names related to *Centaurea aplolepa* and *C. leucophaea* (Asteraceae) from Italy and France

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Abstract

Centaurea aplolepa Moretti and *C. leucophaea* Jord. (Asteraceae) are endemic to the central-western Mediterranean and include, respectively, ten and six subspecies, mostly occurring in north-western Italy and south-eastern France. As part of an ongoing systematic study on *Centaurea* L. sect. *Centaurea* from the central Mediterranean, 17 nomenclatural types (13 lectotypes, three neotypes and one epitype) are designated to fix the application of all names of the taxa described for France and Italy and related to *C. aplolepa* and *C. leucophaea*. In addition, previous typifications are critically revised and discussed. *Centaurea aplolepa* subsp. *maremmana* (Fiori) Dostál and *C. litigiosa* (Fiori) Arrigoni, two currently accepted taxa endemic to Tuscany (central Italy), are respectively considered here as heterotypic synonyms of *C. aplolepa* subsp. *carueliana* (Micheletti) Dostál and *C. aplolepa* subsp. *cosana* (Fiori) Dostál. Finally, *C. aplolepa* subsp. *gallinariae* (Briq. & Cavill.) Dostál, a currently accepted subspecies narrowly endemic to the Gallinara island (Liguria, northern Italy), is considered here as a heterotypic synonym of *C. leucophaea* subsp. *brunnescens* (Briq.) Dostál.

Key words: Endemism, epitype, ICN, lectotype, Mediterranean, neotype, taxonomy

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Introduction

Centaurea L. (Asteraceae), with approximately 600 currently accepted species, is one of the most species-rich genera of the Mediterranean area (Greuter 2008). Due to several biological phenomena, such as hybridization, introgression, and polyploidy, it is considered as a taxonomically critical genus. Previous phylogenetic studies, carried out by using both a nuclear (ITS) and a plastid marker (*rpl32-trnL* intergenic spacer), were able to shed light on the systematic relations among wide groups of species (Hilpold et al. 2014). However, within these groups, the relations among taxa were not resolved due to large polytomies.

Other authors, using more informative molecular approaches at finer geographic scales, were able to better clarify the taxonomy of critical species groups such as the *C. cineraria* L. group in the central Mediterranean (Hilpold et al. 2011), the *C. calocephala* Willd. group in the Balkans (Novaković et al. 2022), and the *C. tenorei* Guss. ex Lacaita group in southern Italy (De Luca et al. 2023). A great gap of taxonomic knowledge still remains for several taxa endemic to the central Mediterranean included in *C.* sect. *Centaurea*. Within this section, along with the lack of systematic studies, several accepted names (Greuter 2008), related to the two phylogenetically close species *C. aplolepa* Moretti and *C. leucophaea* Jord. (Hilpold et al. 2014), are still not typified (Peruzzi et al. 2015).

Centaurea aplolepa is endemic to central and north-western Italy, and its wide morphological variability is currently organized in ten subspecies (Bartolucci et al. 2024). Under the binomial *Centaurea aplolepa*, diploid (Viegi et al. 1972; Giacò et al. 2024) biennial or perennial plants growing in arid environments (limestone, sand, and ophiolites, depending on the subspecies) are included. They show glabrous to rarely tomentose pinnatisect leaves, and capitula disposed in a cymose sub-corymb; the involucral bracts show a decurrent appendage with cilia that, depending on the subspecies, can be long to very short (Arrigoni 2003). Conversely, under the binomial *C. leucophaea*, six subspecies, five of which are endemic to south-eastern France and a little portion of north-western Italy, are included. From a morphological perspective, *C. leucophaea* is similar to *C. aplolepa*, but more tomentose (Pignatti 2018).

The aim of this work is to critically revise the typifications available in literature and to typify all the remaining names (either currently accepted or synonyms) with type localities in Italy and France, which were referred in taxonomic literature to *C. aplolepa* or *C. leucophaea*. This paper is part of an ongoing integrative taxonomic study of taxa included in the section *Centaurea* endemic to the central Mediterranean.

Materials and methods

Accepted names and synonyms related to *C. aplolepa* or *C. leucophaea* were searched in Greuter (2008), IPNI (2024), and WFO (2024). Protologues were investigated and original material was searched in the following herbaria: BR, CGE, G, GE, FI, LY, MPU, MW, P, PAL, PAD, PI, RO, SE, TL, and W. Some Briquet's specimens were searched in Clarence Bicknell's herbarium, preserved in the "Museo e Biblioteca Clarence Bicknell", Bordighera, Imperia, Italy. Types were designated and previous typifications were critically revised following the Shenzhen Code (Turland et al. 2018, ICN hereafter). Names are listed in alphabetical order of their basionyms.

Typifications

1. *Centaurea aeolica* Guss. ex Lojac., Fl. Sicul. 2(1): 136. 1903 ≡ *Centaurea cineraria* var. *aeolica* (Guss. ex Lojac.) Fiori in Fiori & Paoletti, Fl. Italia 3: 334. 1904 ≡ *Centaurea paniculata* subsp. *aplolepa* var. *aeolica* (Guss. ex Lojac.) Arènes in Mém. Mus. Natl. Hist. Nat., Ser. B, Bot. 1(2): 223. 1951 ≡ *Acosta aeolica* (Lojac.) Holub in Preslia 46: 226. 1974 ≡ *Centaurea aplolepa* subsp. *aeolica* (Lojac.) Dostál in Bot. J. Linn. Soc. 71: 202. 1976. Type: ITALY. Sicily: "in insula Lipari, rara et localis", June s.d., *M. Lojacono s.n.* (lectotype, designated by Cela Renzoni and Viegi (1983: 136): PAL [barcode PAL10639] photo!, https://herbarium.unipa.it/zoomify/view_img.asp?ic=10639)

Centaurea aeolica is an accepted name and applies to a species endemic to the Aeolian Islands, Sicily (Bartolucci et al. 2024).

2. *Centaurea aplolepa* Moretti in Giorn. Fis., ser. 2, 9: 154–155. 1826 ≡ *Centaurea bertolonii* var. *aplolepa* (Moretti) Hausskn. in Mitt. Thüring. Bot. Vereins 6: 35. 1894, as "*haplolepis*" ≡ *Centaurea paniculata* var. *aplolepa* (Moretti) Fiori in Fiori & Paoletti, Fl. Italia 3: 336. 1904 ≡ *Centaurea paniculata* subsp. *aplolepa* (Moretti) Briq. & Cavill. in Burnat, Fl. Alpes Marit. 7: 172. 1931 ≡ *Acosta aplolepa* (Moretti) Holub in Preslia 45: 142. 1973. Type: ITALY. Liguria: "Caprazoppa e Promontorio di Noli", 20 August 1824, *Moretti s.n.* (lectotype, designated here: PAD 9476! [individual and label on the right of the sheet])

We detected a specimen (Fig. 1) at PAD collected in 1824 at "Promontorio di Noli", in Liguria, the same date and place mentioned in the protologue (Moretti 1826). This specimen, designated as the lectotype, shows basal pedunculate pinnatisect leaves, while the cauline leaves are also pinnatisect but become progressively shorter along the branch. Capitula are globose and the involucral bracts are pointed at the apex, with few, and very short, lateral teeth. This morphology is congruent with the protologue and with the application of the name *C. aplolepa* s.str. to a taxon endemic to western Liguria (Arrigoni 2003). The name *C. aplolepa* var. *genuina* Briq. (Briquet 1902) is invalid under Art. 24.3 of the ICN.

3. *Centaurea aplolepa* var. *integrans* Fedde, Repert. Spec. Nov. Regni Veg. 1(9): 144. 1905 ≡? *Centaurea paniculata* f. *integrans* Fiori in Fiori & Paoletti, Fl. Italia 4(1): 188. 1907 ≡? *Centaurea integrans* Naggi ex Prain, Index Kew., Suppl. 3: 38. 1908. Type: not designated

Naggi (1905) failed to validly publish the name *Centaurea integrans*, since this binomial appears only in the title. Elsewhere in the protologue, in place of *C. integrans*, the author doubtfully refers the morphological description to another putative rank and epithet ("*genuensis*"), tentatively placed as a variety of *C. aplolepa*. Accordingly, the name *C. integrans* is a nomen nudum, invalid under Art. 38.1 of the ICN, and *C. aplolepa* var. *genuensis* is invalid under Art. 36.1 of the ICN. Later, Fedde (1905), Fiori (1907), and Prain (1908) independently and validly published, respectively, the names at different ranks: *C. aplolepa* var. *integrans* Fedde, *C. paniculata* var. *aplolepa* f. *integrans* Fiori, and *C. integrans* Prain, in all cases referring explicitly to Naggi as the author. Accordingly, the original material for these names can be searched among those specimens belonging to Naggi, or among the specimens of each respective author (i.e., Fedde, Fiori and Prain) matching with the diagnosis provided by Naggi (1905). In the former case, the names provided by Fedde (1905), Fiori (1907), and Prain (1908) would be homotypic. Naggi (1905) described plants similar to *C. aplolepa*, but with totally entire leaves, and indicated Genoa (Liguria) as the only locality of occurrence. We searched in GE and FI, but we did not locate any pertinent *Centaurea* specimen labelled with the epithet "*integrans*" or "*genuensis*". Similarly, we were not able to locate any pertinent specimen by Fedde, Fiori, or Prain. In the absence of original material, a neotype can be selected for each of the three validly published names. Nevertheless, based on the morphological description provided by Naggi (1905), even the designation of a neotype is not straightforward. Indeed, based on the current knowledge (Arrigoni 2003; Hilpold et al. 2011), the plants described by Naggi (1905) cannot be readily related

Figure 1. Lectotype of *Centaurea aplolepa* Moretti (individual and label on the right of the sheet). Reproduced with the permission of the herbarium of the University of Padua (PAD).

either to *C. aplolepa* or to other similar species as *C. cineraria* L., *C. leucophaea*, or *C. paniculata* L., since they all show pinnatisect leaves. Moreover, the absence of information in Naggi (1905) concerning the morphology of involucral bracts does not allow to safely fit this description to any *Centaurea* species with entire leaves. Accordingly, we prefer to abstain from designating neotypes.

4. *Centaurea aplolepa* var. *ligustica* Briq., Monogr. Centaurées Alpes Marit.: 142. 1902 ≡ *Centaurea paniculata* var. *aplolepa* f. *ligustica* (Briq.) Fiori in Fiori & Paoletti, Fl. Italia 3: 339. 1904 ≡ *Acosta ligustica* (Briq.) Holub in Preslia 46: 226. 1974 ≡ *Centaurea aplolepa* subsp. *ligustica* (Briq.) Dostál in Bot. J. Linn. Soc. 71: 202. 1976 ≡ *Centaurea paniculata* subsp. *ligustica* (Briq.) Arrigoni in Parlatorea 6: 73. 2003. Type: ITALY. Liguria: "entre Pieve di Teco et Rezzo", 28 July 1890, *E. Burnat and F.G. Cavillier s.n.* (lectotype, designated here: G [barcode G00848137], photo!, https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=716970&base=img&lang=en)

In the protologue, Briquet (1902) cited two specimens, one collected between Pieve di Teco and Rezzo (Liguria) in 1890 and another collected between Pieve di Teco and Nava (Liguria) in 1886. We located the former specimen at G, which is designated here as the lectotype. It is a tomentose plant with thin branches and small oblong capitula; the bracts at the lower portion of the involucre are dentate, whereas the ones at the upper portion show longer cilia. According to Greuter (2008), *C. aplolepa* var. *ligustica* is a heterotypic synonym of *C. aplolepa* var. *parvula* Ces. However, based on the higher degree of tomentosity and the geographical provenance of the type here designated, we deem more reliable considering it as a heterotypic synonym of *C. leucophaea* subsp. *brunnescens* (Briq.) Dostál., a taxon endemic to northern-western Italy (Arrigoni 2003; Tison and de Foucault 2014; Pignatti 2018).

5. *Centaurea aplolepa* var. *parvula* Ces. in Cesati & al., Comp. Fl. Ital.: 495. 1878 ≡ *Centaurea aplolepa* subsp. *parvula* (Ces.) Arcang., Comp. Fl. Ital.: 391. 1882. Type: ITALY. Piedmont: Acqui, August 1867, *V. Cesati s.n.* (lectotype, designated here: RO-HC-FAN_768, photo! [the three individuals on the left of the sheet])

We detected a specimen at RO (Fig. 2), where Cesati's material is conserved, including four individuals. They were all collected near Acqui (Piedmont, northern Italy), the same locality mentioned in the protologue. In the label mounted at the bottom, it is reported that the individuals belong partly to *C. aplolepa* var. *parvula* Ces. and partly to *C. aplolepa* var. *subciliata* DC. Based on the label, it is not possible to attribute these plants to a single name. However, in the protologue, Cesati et al. (1878) stated that *C. aplolepa* var. *parvula* shows capitula that are two or three times smaller than those in *C. aplolepa* var. *subciliata*. With this information, it is possible to safely attribute the individual located on the right, showing larger capitula, to *C. aplolepa* var. *subciliata* sensu Cesati et al. (1878), whereas the remaining three, showing smaller capitula, can be attributed to *C. aplolepa* var. *parvula*. These three specimens are designated as the lectotype for *C. aplolepa* var. *parvula*. They are tomentose erect plants showing pinnatisect leaves; capitula are small and show involucral bracts with

Figure 2. Lectotype of *Centaurea aplolepa* var. *parvula* Ces. (the three individuals on the left of the sheet). Reproduced with the permission of the herbarium RO.

short teeth. This morphology is congruent with the protologue and with the application of the name *C. aplolepa* subsp. *parvula* (Ces.) Arcang. to a taxon endemic to north-western Italy (Piedmont and Liguria) (Bartolucci et al. 2024).

6. *Centaurea aplolepa* var. *subciliata* DC., Prodr. 6: 584. 1838 ≡ *Centaurea aplolepa* subsp. *subciliata* (DC.) Arcang., Comp. Fl. Ital.: 391. 1882 ≡ *Centaurea paniculata* var. *aplolepa* f. *subciliata* (DC.) Fiori in Fiori & Paoletti, Fl. Italia 3: 339. 1904 ≡ *Centaurea paniculata* subsp. *subciliata* (DC.) Arrigoni in Parlatorea 6: 67. 2003. Type: ITALY. Tuscany: Livorno, 1832, *J.F. Schow s.n.* (lectotype, designated [as holotype] by Arrigoni (2003: 67): G [barcode G00473209], photo!, https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=339879&base=img&lang=en)

The name *C. aplolepa* subsp. *subciliata* (DC.) Arcang. is accepted and applies to a taxon endemic to central Italy (Tuscany) (Bartolucci et al. 2024).

7. *Centaurea bertolonii* Hausskn. in Mitt. Thüring. Bot. Vereins 6: 34. 1894, nom. illeg. (Art. 52.1) ≡ *Centaurea paniculata* subsp. *bertolonii* Arrigoni in Parlatorea 6: 60. 2003 ≡ *Centaurea aplolepa* subsp. *bertolonii* (Arrigoni) Greuter in Willdenowia 33: 249. 2003. Type: ITALY. Liguria: Genova, in glareos vallis Bisagno, 26 August 1892, *C. Haussknecht s.n.* (lectotype, designated by Greuter (2003: 249): JE [barcode JE00010556], photo!, http://131.130.131.10/herbaria/jacq-viewer/viewer.html?rft_id=je_00010556&identifiers=je_00010556)

The nomenclature of *Centaurea bertolonii* Hausskn. was clarified by Greuter (2003). Despite the illegitimacy of this species name under Art. 52.1, due to the taxonomic inclusion of *C. aplolepa*, its typification is not automatic under Art. 7.6. The name *C. aplolepa* subsp. *bertolonii* (Arrigoni) Greuter is currently accepted and applies to plants endemic to eastern Liguria (Arrigoni 2003; Bartolucci et al. 2024).

8. *Centaurea biformis* Timb.-Lagr. in Rev. Bot. Bull. Mens. 10: 262. 1892 ≡ *Centaurea paniculata* subsp. *biformis* (Timb.-Lagr.) Rouy in Rev. Bot. Syst. Géogr. Bot. 2: 159. 1904 ≡ *Centaurea paniculata* var. *biformis* (Timb.-Lagr.) Briq. & Cavill. in Burnat, Fl. Alpes Marit. 7: 191. 1931 ≡ *Centaurea leucophaea* subsp. *biformis* (Timb.-Lagr.) Dostál in Bot. J. Linn. Soc. 71: 200. 1976. Type: FRANCE. Occitanie: "entre le Château de Caladroer et le village de Cassagnes", 28 Juin 1881, *G. Gautier s.n.* (neotype, designated here: LY [barcode LY0000848], photo!, https://explore.recolnat.org/search/botanique/simplequery=LY0000848)

In the protologue, Timbal-Lagrave (1892) provided a detailed morphological description and listed several localities of occurrence in Occitanie (southern France). We searched for the original material at TL, BR, CGE, FI, MPU, MW, and P, where Timbal-Lagrave's material is known to be conserved (Stafleu and Cowan 1986), but we did not locate any specimen suitable for lectotypification. In this case, a neotype can be selected. We found several specimens (e.g. P04309069, LY0365918, LY0365919, and LY0719809) that were collected at Roquevert, near Sournia (Occitanie), one of the localities mentioned in the protologue. However, all these specimens show involucral bracts with light yellow cilia, whereas in the protologue it is stated that both forms of *C. biformis* show reddish or dark brown cilia. The specimen LY0000848 was collected between Cassagnes and Caladroer (Occitanie), at just approximately 12 km from Trevillach, one of the localities mentioned in the protologue. This specimen shows dark brown cilia and its overall morphology matches with the first of the two forms of *C. biformis* described in the protologue (Timbal-Lagrave 1892). Indeed, the plant shows a long taproot with a single stem that is branched in the upper portion. It is designated here as the neotype for *C. biformis*. *Centaurea leucophaea* subsp. *biformis* (Timb.-Lagr.) Dostál is a name accepted by Greuter (2008), albeit Tison and de Foucault (2014) considered *C. biformis* as a heterotypic synonym of *C. leucophaea* s.str. Timbal-Lagrave (1892) suggested that *C. biformis* is included in the group of *C. maculosa* Lam. (= *C. stoebe* L.). Based on the morphology of the neotype here designated, we confirm the observations made by the latter author, so that *C. biformis* has to be considered a heterotypic synonym of *C. stoebe*, a species widespread in central-eastern Europe (Greuter 2008).

9. *Centaurea cineraria* var. *pandataria* Fiori & Bég. in Fiori & Paoletti, Fl. Italia 3: 334. 1904 ≡ *Centaurea pandataria* (Fiori & Bég.) Bég. in Ann. Bot. (Rome) 3: 443. 1905 ≡ *Centaurea aplolepa* subsp. *pandataria* (Fiori & Bég.) Dostál in Bot. J. Linn. Soc. 71: 202. 1976 ≡ *Centaurea aeolica* subsp. *pandataria* (Fiori & Bég.) Anzal. in Boll. Soc. Sarda Sci. Nat. 30: 512. 1995. Type: ITALY. Lazio: sulle rupi maritime a Ventotene, 20 September 1901, *A. Béguinot s.n.* (lectotype designated by Brullo et al. (2021: 17): FI [barcode FI051939!])

This taxon was considered as a subspecies of *C. aeolica* by Greuter (2008). After Brullo et al. (2021) and Del Guacchio et al. (2022), it is considered as a distinct species, endemic to Ventotene island (Lazio).

10. *Centaurea leucophaea* Jord., Observ. Pl. Nouv. 5: 64. 1847 ≡ *Centaurea paniculata* subsp. *leucophaea* (Jord.) Arcang., Comp. Fl. Ital.: 392. 1882 ≡ *Centaurea paniculata* var. *leucophaea* (Jord.) Briq., Monogr. Centaurées Alpes Marit.: 147. 1902 ≡ *Acosta leucophaea* (Jord.) Holub in Folia Geobot. Phytotax. 7: 314. 1972. Type: [Illustration] "F. *C. leucophæa*" in Jordan, Observ. Pl. Nouv. 5: Pl 4. 1847 (lectotype, designated here). FRANCE. Provence-Alpes-Côte d'Azur: De Brumebou, près Serres, H. Alpes, 3 July 1847, *A. Jordan s.n.* (epitype, designated here: LY [barcode LY0799389], photo!, https://explore.recolnat.org/occurrence/D6453FD94C5A46BBBC365B9DBC1D970F; isoepitype: LY [barcode LY0799390], photo!)

In the protologue, Jordan (1847) reported a detailed description and several diagnoses; he also mentioned several localities in Provence-Alpes-Côte d'Azur (southern France): Briançon, Guillestre, Gap, Serres, Sisteron, and Castellane. We found two specimens at LY (LY0799389 and LY0799390) that were collected near Serres in July 1847 (interpretation of the calligraphy confirmed by the LY curator M. Thiébaut, pers. comm.). However, these two specimens are not original material since the name was published six months earlier (Stafleu and Cowan 1979). Along with the protologue, Jordan (1847) provided an illustration in which a capitulum, an involucral bract, and a cypsela of *C. leucophaea* are depicted. The illustration is the only available original material and is designated as the lectotype. However, such a minimalistic illustration does not provide an exhaustive interpretation of the overall plant morphology. Indeed, several characters, mostly related to the leaf morphology, mentioned in the protologue as discriminant with respect to other species, are missing in the illustration. For this reason, since the lectotype is ambiguous and does not allow a clear identification of the taxon, following Art. 9.9 of the ICN, we designate the above mentioned specimen LY0799389 as the epitype for *C. leucophaea*. The specimen shows capitula and involucral bracts as in the lectotype illustration, and pinnatisect tomentose leaves with oblong lobes. This morphology is congruent with the protologue and with the application of the name *Centaurea leucophaea* to a species native to Spain, France, and Italy (Greuter 2008). According to the latter author, this species includes six subspecies, and our typification confirms the application of *C. lecuophaea* s.str. to plants endemic to southern France and north-western Italy, as also circumscribed by Arrigoni (2003). The name *C. paniculata* var. *euleucophaea* Briq. (Monogr. Centaurées Alpes Marit.: 149. 1902) is invalid under Art. 24.3 of the ICN.

11. *Centaurea mierghii* Jord., Cat. Graines Jard. Bot. Grenoble: 15. 1850 ≡ *Acrolophus mierghii* (Jord.) Fourr. in Ann. Soc. Linn. Lyon, sér. 2, 17: 97. 1869 ≡ *Centaurea paniculata* subsp. *leucophaea* var. *mierghii* (Jord.) Rouy in Rev. Bot. Syst. Geogr. Bot. 2: 148. 1904. Type: FRANCE. Provence-Alpes-Côte d'Azur: Lyon [plants cultivated from seeds collected in Occitanie, Anduze], 24 June 1851, *A. Jordan s.n.* (neotype, designated here: LY [barcode LY0368554], photo!, https://explore.recolnat.org/occurrence/E92AB6A-81F9147258A3B77D327171727)

In the protologue, Jordan (1850) stated that he had grown plants in his garden from *Centaurea* seeds sampled by Miergue in Occitanie. At LY, we found two specimens (LY0368554 and LY0368558) that were collected in Jordan's garden ("mj" = mon jardin [my garden]) in 1851 and 1852, respectively. On the same labels, it is reported "Anduze, Gard 1849", so it is plausible to assume that 1849 is the date of collection of seeds in Anduze (Occitanie), one of the localities mentioned in the protologue. It is plausible, that the protologue was based on living plants grown in Jordan's garden from seeds collected in Anduze, later herborized in 1851 and 1852 (M. Thiébaut, pers. comm.). However, following Art. 9.4 of the ICN, since both specimens were collected after the publication of the name, they cannot be considered as original material. No illustration is provided in the protologue, so that following Art. 9.8 of the ICN a neotype can be selected. Both specimens show ovoid-oblong involucres with brown appendages and lateral upper cilia that exceed in height the central mucro. Cauline leaves are pinnatisect and are composed by several linear segments. This morphology is in accordance with the protologue, and the above-mentioned specimen LY0368554 is designated as the neotype for *C. mierghii*. Based on the neotype morphology, we agree with Greuter (2008) in considering *C. mierghii* as a heterotypic synonym of *C. stoebe*, a species widespread in central and eastern Europe.

12. *Centaurea paniculata* var. *aetaliae* Sommier in Nuovo Giorn. Bot. Ital. 9: 329. 1902 ≡ *Centaurea aetaliae* (Sommier) Bég. in Arch. Bot. (Forlì) 7: 93. 1931 ≡ *Centaurea aplolepa* subsp. *aetaliae* (Sommier) Dostál in Bot. J. Linn. Soc. 71: 203. 1976. Type: ITALY. Tuscany: Insula Elba, valle di Monserrato in rupibus, 17 June 1900, *S. Sommier s.n.* (lectotype, designated by Arrigoni (2020: 372): FI [barcode FI002032!])

Centaurea aetaliae is an accepted name and applies to a species endemic to the eastern portion of Elba island, Tuscany (Arrigoni 2003, Bartolucci et al. 2024).

13. *Centaurea paniculata* var. *aetaliae* f. *maremmana* Fiori in Fiori & Paoletti, Fl. Italia 3: 339. 1904 ≡ *Centaurea paniculata* var. *maremmana* (Fiori) Fiori, Nuov. Fl. Italia 2: 732. 1927 ≡ *Centaurea aplolepa* subsp. *maremmana* (Fiori) Dostál in Bot. J. Linn. Soc. 71: 202. 1976 ≡ *Centaurea paniculata* subsp. *maremmana* (Fiori) Arrigoni in Parlatorea 6: 71. 2003. Type: ITALY. Tuscany: presso M. Cerboli, s.d., *Amidei s.n.* (lectotype, designated by Arrigoni (2003: 71): FI!)

Fiori (1904) provided a short diagnosis for *C. paniculata* f. *maremmana* and cited two collections from Tuscany ("*M. Cerboli*, Amidei in hb. flor.!" and "*Castiglioncello*, Campana in hb. flor.!") conserved at FI. The specimen from Montecerboli was designated as the lectotype by Arrigoni (2003). Later, the same author (Arrigoni 2012) revised his previous typification by stating that the lectotype is in conflict with the original description for showing shortly ciliate, and not dentate, involucral bracts. Accordingly, the other specimen from Castiglioncello, showing dentate involucral bracts, was designated as a new lectotype for *C. paniculata* f. *maremmana*. Indeed, the Melbourne Code (McNeill et al. 2012) allowed to resolve these cases through Art. 9.19(b), albeit this article was not mentioned by Arrigoni (2012). However, the current Code (Turland et al. 2018), due to Note 7, does not allow to apply Art. 9.19(c) when gatherings are explicitly cited in the protologue (i.e. syntypes), as in this case. Thus, the second typification provided by Arrigoni (2012) is not effective and the first lectotypification made, despite being perhaps less accurate, is final. The lectotype is glabrous and shows pinnatisect leaves with linear lobes; its capitula are small (diameter 4–5 mm, and the involucral bracts are shortly ciliate. Based on this lectotype, as also stated by Arrigoni (2012), *C. paniculata* f. *maremmana* has to be considered a heterotypic synonym of *C. aplolepa* subsp. *carueliana* (Micheletti) Dostál, a taxon endemic to Tuscany, central Italy. More studies are needed to understand if the populations growing in the areas surrounding Castiglioncello, showing dentate involucral bracts, deserve a distinct taxonomic treatment with respect to the typical population, showing shortly dentate involucral bracts.

14. *Centaurea paniculata* var. *aplolepa* f. *virescens* Fiori in Fiori & Paoletti, Fl. Italia 3: 339. 1904. Type: ITALY. Tuscany: "pineta di Viareggio", 10 September 1903, *A. Fiori s.n.* (lectotype, designated here: FI! [the individual on the upper portion of the sheet])

Fiori (1904) described *C. paniculata* var. *aplolepa* f. *virescens* as "quasi glabra e verde" [almost glabrous and green] comparing it to the white tomentose

C. paniculata var. *aplolepa* f. *subciliata* (DC.) Fiori. Contrary to the usual procedure, the author did not provide a Latin letter for *C. paniculata* f. *virescens*, or mention localities of occurrence or herbarium specimens. We searched in FI, where Fiori's herbarium is conserved, but we did not locate any specimen signed by him as "*virescens*". Since the intention of the author was to describe individuals of *C. aplolepa* subsp. *subciliata* showing less tomentosity, we deem that the original material of *C. aplolepa* f. *virescens* has to be searched among those specimens identified by Fiori as *C. aplolepa* subsp. *subciliata* and showing less tomentum. We located a single specimen matching these features that was collected before of the publication of the name. This herbarium sheet is composed by a complete individual showing just sparse tomentum, and by two further distinct tomentose basal rosettes. The former is designated as the lectotype for *C. aplolepa* f. *virescens*. Since the variability of *C. aplolepa* subsp. *subciliata* includes white tomentose to almost glabrous plants (Arrigoni 2003), *C. aplolepa* f. *virescens* is just a heterotypic synonym of *C. aplolepa* subsp. *subciliata*.

15. *Centaurea paniculata* var. *brunnescens* Briq., Monogr. Centaurées Alpes Marit.: 152. 1902 ≡ *Centaurea paniculata* var. *leucophaea* f. *brunnescens* (Briq.) Fiori in Fiori & Paoletti, Fl. Italia 3: 337. 1904 ≡ *Centaurea leucophaea* subsp. *brunnescens* (Briq.) Dostál in Bot. J. Linn. Soc. 71: 200. 1976 ≡ *Centaurea paniculata* subsp. *brunnescens* (Briq.) Arrigoni in Parlatorea 6: 55. 2003. Type: ITALY. Liguria: "lungo la strada fra Pigna e Monte Cavanelli", 13 October 1893, *C. Bicknell s.n.* (lectotype, designated here: Herbarium Bicknell, 23b-30-1 photo!, conserved in the herbarium of the Museo e Biblioteca Clarence Bicknell, Bordighera, Imperia, Italy)

In the protologue, Briquet (1902) mentioned eight specimens from the following localities: Albenga (Savona, Liguria), Gallinara island (Savona, Liguria), Oneglia valley (Imperia, Liguria), between San Bartolomeo and San Bernardo (Imperia, Liguria), Porto Maurizio (Imperia, Liguria), between Pigna and Monte Cavanelle (Imperia, Liguria), Roquebrune (Alpes Maritimes, Provence-Alpes-Côte d'Azur), and Peïra Cava (Alpes Maritimes, Provence-Alpes-Côte d'Azur). Peruzzi et al. (2015) suggested that the lectotype has to be selected among the specimens collected "between San Bartolomeo and San Bernardo" or "between Pigna and Monte Cavanelle", since the six remaining localities fall in the circumscription of other currently accepted taxa as *C. paniculata* subsp. *paniculata*, *C. leucophaea* subsp. *leucophaea*, and *C. aplolepa* subsp. *gallinariae*. In the Herbarium Bicknell, we located a specimen revised by Briquet that was collected between Pigna and Monte Cavanelle, that is designated here as the lectotype (Fig. 3). It is composed of two tomentose flowering branches showing capitula with ovoid involucres (1–1.2 × 0.8–1 mm) and large involucral bracts; the appendages are fawn and cilia are around 1 mm long. This morphology is congruent with the protologue and with the application of the name *C. leucophaea* subsp. *brunnescens* to plants endemic to western Liguria (Arrigoni 2003; Tison and de Foucault 2014; Bartolucci et al. 2024).

Figure 3. Lectotype of *Centaurea paniculata* var. *brunnescens* Briq. Reproduced with the permission of the herbarium of the Museo e Biblioteca Clarence Bicknell, Bordighera, Liguria, Italy.

16. *Centaurea paniculata* f. *carueliana* Micheletti in Nuovo Giorn. Bot. Ital. 23: 316. 1891 ≡ *Centaurea paniculata* var. *carueliana* (Micheletti) Fiori in Fiori & Paoletti, Fl. Italia 3: 335. 1904 ≡ *Centaurea aplolepa* subsp. *carueliana* (Micheletti) Dostál in Bot. J. Linn. Soc. 71: 202. 1976 ≡ *Centaurea paniculata* subsp. *carueliana* (Micheletti) Arrigoni in Parlatorea 6: 69. 2003. Type: ITALY. Tuscany: Monte Ferrato (Agro fiorentino), 27 July 1857, *Pirotta s.n.* (lectotype designated by Arrigoni (2003: 69): FI!)

Centaurea aplolepa subsp. *carueliana* (Micheletti) Dostál is an accepted name that applies to plants endemic to Tuscany, central Italy (Arrigoni 2003; Bartolucci et al. 2024).

17. *Centaurea paniculata* subsp. *controversa* Briq. & Cavill. in Burnat, Fl. Alpes Marit. 7: 182. 1931 ≡ *Centaurea leucophaea* subsp. *controversa* (Briq. & Cavill.) Kerguélen in Lejeunia, ser. 2, 120: 65. 1987. Type: FRANCE. Provence-Alpes-Côte d'Azur: Baus-Rous, près Villefranche, 20 June 1872, *C. Sarato s.n.* (lectotype, designated here: G [barcode G00848147], photo!, https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=728535&lang=en)

In the protologue, Briquet and Cavillier (1931) cited several specimens collected at Baus Rous, Provence-Alpes-Côte d'Azur, southern France. We located at G the specimen collected by C. Sarato in 1872 near Villefranche, at Baus Rous. It is a white tomentose plant with capitula 8–12 mm large showing dark appendages and long cilia. As stated in the protologue, the main diagnostic character with respect to *C. leucophaea* subsp. *leucophaea* lie in the involucral bracts, which show prominent veins. According to Greuter (2008), *C. leucophaea* subsp. *controversa* (Briq. & Cavill.) Kerguélen is an accepted name that applies to plants endemic to southern France. However, based on the lectotype, we agree with Tison and de Foucault (2014) in considering this name as a heterotypic synonym of *C. pseudocineraria* (Fiori) Rouy, a species endemic to Provence-Alpes-Côte d'Azur.

18. *Centaurea paniculata* var. *cosana* Fiori in Fiori & Paoletti, Fl. Italia 3: 338. 1904 ≡ *Centaurea aplolepa* subsp. *cosana* (Fiori) Dostál in Bot. J. Linn. Soc. 71: 203. 1976 ≡ *Centaurea paniculata* subsp. *cosana* (Fiori) Arrigoni in Parlatorea 6: 73. 2003. Type: ITALY. Tuscany: Monte Argentario verso Porto Ercole, 8 July 1886, *A. Fiori s.n.* (lectotype, designated by Baldini (1995: 147): FI [barcode FI002013]!)

Centaurea aplolepa subsp. *cosana* (Fiori) Dostál is an accepted name that applies to plants endemic to southern Tuscany, central Italy (Arrigoni 2003; Bartolucci et al. 2024).

19. *Centaurea paniculata* var. *cosana* f. *litigiosa* Fiori in Fiori & Paoletti, Fl. Italia 3: 338. 1904 ≡ *Centaurea paniculata* var. *litigiosa* (Fiori) Sommier in Nuovo Giorn. Bot. Ital. n.s. 19: 121. 1912 ≡ *Centaurea paniculata* subsp. *aplolepa* var. *cosana* subvar. *litigiosa* (Fiori) Arènes in Mém. Mus. Natl. Hist. Nat., Ser. B, Bot. 1: 226. 1951 ≡ *Centaurea litigiosa* (Fiori) Arrigoni in Parlatorea 6: 77. 2003. Type: ITALY. Tuscany: sopra Port'Ercole, Monte Argentario,

5 July 1873, *H. Groves s.n.* (lectotype, designated by Baldini (1995: 147): FI [barcode FI002008!]; isolectotypes: FI [barcode FI002062!], FI [barcode FI002063!])

In the protologue of *C. paniculata* var. *cosana*, Fiori (1904) described also *C. paniculata* var. *cosana* f. *litigiosa* providing the following diagnosis: "a rami brevi, in pianta ricordante la *C. dissecta* v. *ilvensis* (cioè a capolini un po' più grandi, meno strozzati all'apice ed a ciglia delle squame più lunghe)" [branches short, plants reminding *C. dissecta* var. *ilvensis* (i.e. with capitula slightly larger, less tight at the apex, and involucral bracts with longer cilia)]. Both *C. paniculata* var. *cosana* and *C. paniculata* var. *cosana* f. *litigiosa* were described based on material from Porto Ercole, on the promontory of Monte Argentario (Tuscany, central Italy). The original material of *C. paniculata* f. *litigiosa*, conserved at FI, consists of four individuals of the same gathering mounted on two distinct herbarium sheets. On the first sheet, the individual under barcode FI002062 is mounted, whereas on the second sheet, the three remaining individuals (one under barcode FI002008 and two under barcode FI002063) can be found. Baldini (1995) designated the individual under barcode FI002008 as the lectotype. It is a small but fully developed plant showing branches shorter than the lectotype of *C. paniculata* var. *cosana*. This morphology is in accordance with the protologue and the choice made by Baldini (1995) is accurate, since the individual under the barcode FI002062 shows branches that are even longer than the lectotype of *C. paniculata* var. *cosana*. Sommier (1912), based on morphological observations conducted on further material collected by himself on the promontory of Monte Argentario, proposed the combination *C. paniculata* var. *litigiosa*. According to this author, *C. paniculata* var. *litigiosa*, if compared to *C. paniculata* var. *cosana*, shows short, entirely prostrate, and densely foliose branches, ovate capitula, and involucral bracts with dark appendages. In the same publication, Sommier (1912) pointed out the presence of individuals with a suberect habitus and a general morphology that is intermediate between *C. paniculata* var. *cosana* and *C. paniculata* var. *litigiosa*. These intermediates were interpreted as a new taxon, namely *C. paniculata* var. *litigiosa* f. *suberecta* Sommier. Later, Arrigoni (2003), possibly based on the observations made by Sommier (1912), raised *C. paniculata* f. *litigiosa* at species rank, then followed by Greuter (2008) and Bartolucci et al. (2024). Arrigoni (2020) interpreted the individuals showing an intermediate morphology as hybrids between *C. paniculata* var. *cosana* and *C. litigiosa*. However, some of the characters used by Sommier (1912) and Arrigoni (2003, 2020) to circumscribe *C. paniculata* f. *litigiosa*, such as the entirely prostrate branches and the dark appendages, are neither shown by the lectotype of *C. paniculata* f. *litigiosa*, nor by the isolectotypes. These features can be observed only in some of the specimens from Monte Argentario collected later by Sommier. Accordingly, the current taxonomic position of *C. litigiosa* (Fiori) Arrigoni as a species distinct from *C. aplolepa* subsp. *cosana* is based on a misinterpretation of the former taxon. After critically checking and comparing the original material and types of both taxa, our conclusion is that *C. paniculata* f. *litigiosa* can be considered just as a heterotypic synonym of *C. paniculata* var. *cosana*. In this perspective, the latter taxon, currently accepted as *C. aplolepa* subsp. *cosana*, includes individuals with both short and long erect and suberect branches, capitula with involucres 6–8 mm large, and light yellow to brown appendages with cilia at most 0.8 mm long. More studies are needed to understand whether the individuals showing only prostrate branches, larger involucres with dark brown to black appendages and longer cilia, ascribed by Sommier (1912) to *C. paniculata* f. *litigiosa*, are actually a distinct taxon or are part of the variability of *C. aplolepa* subsp. *cosana*. The occurrence of individuals showing an intermediate morphology seemingly supports the latter option. This latter interpretation is supported also by Baldini (1995), who observed that *C. paniculata* var. *cosana* occurs in ruderal and disturbed areas, whereas *C. paniculata* f. *litigiosa* sensu Sommier (1912) grows on cliffs. Then, the distinct morphology could be just a consequence of local adaptations or morphological plasticity induced by the environment.

20. *Centaurea paniculata* var. *gallinariae* Briq. & Cavill. in Burnat, Fl. Alpes Marit. 7: 175. 1931 ≡ *Centaurea aplolepa* subsp. *gallinariae* (Briq. & Cavill.) Dostál in Bot. J. Linn. Soc. 71: 203. 1976 ≡ *Centaurea paniculata* subsp. *gallinariae* (Briq. & Cavill.) Arrigoni in Parlatorea 6: 55. 2003. Type: ITALY. Liguria: "Ile de Gallinara", 2 July 1880, *E. Burnat s.n.* (lectotype, designated here: G [barcode G00848144], photo!, https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=716981&base=img&lang=en)

Briquet and Cavillier (1931) described this taxon based on material from the Gallinara island, western Liguria, northern Italy. We located a specimen at G, identified by Briquet as *C. paniculata* var. *gallinariae*, that was collected by E. Burnat in 1880 at Gallinara island. This specimen is a tomentose plant with pinnatisect leaves composed of several linear lobes. Capitula are isolated or grouped by two or three and are shortly pedunculate; the involucre is ovoid and is composed by ciliate bracts. This morphology is congruent with the protologue and the specimen is designated here as the lectotype. Briquet (1902) formerly included this taxon within the variability of *C. paniculata* var. *brunnescens*. When describing *C. paniculata* var. *gallinariae*, Briquet and Cavillier (1931) stated that the only discriminant character between these two taxa lies in the morphology of the lower involucral bracts, which show entire to sub-entire, and just rarely scarcely dentate, margin in *C. paniculata* var. *gallinariae*. Currently, this taxon is accepted as *C. aplolepa* subsp. *gallinariae* and applies to plants narrowly endemic to the Gallinara island, Liguria, northern Italy (Greuter 2008, Bartolucci et al. 2024). However, the only discriminant character mentioned by Briquet and Cavillier (1931) has no taxonomic value, since also the type of *C. paniculata* var. *brunnescens* shows lower bracts with sub-entire to rarely dentate margins. Thus, *C. paniculata* var. *gallinariae* should be considered as a heterotypic synonym of *C. leucophaea* subsp. *brunnescens*.

21. *Centaurea paniculata* subsp. *levantina* Arrigoni in Parlatorea 6: 62. 2003 ≡ *Centaurea aplolepa* subsp. *levantina* (Arrigoni) Greuter in Willdenowia 33: 249. 2003. Type: ITALY. Liguria: "Rupi marittime tra Sestri Levante e Lavagna", 4 July 1977, *P.V. Arrigoni & al. s.n.* (holotype: FI [barcode FI002314]!)

The name *C. aplolepa* subsp. *levantina* (Arrigoni) Greuter is accepted and applies to plants endemic to eastern Liguria (Arrigoni 2003; Bartolucci et al. 2024).

22. *Centaurea paniculata* var. *lunensis* Fiori in Fiori & Paoletti, Fl. Italia 3: 338. 1904 ≡ *Centaurea aplolepa* f. *lunensis* (Fiori) Gugler, Centaur. Ungar. (Ann. Mus. Nat. Hungar. VI.): 162. 1907 ≡ *Centaurea aplolepa* subsp. *lunensis* (Fiori) Dostál in Bot. J. Linn. Soc. 71: 203. 1976 ≡ *Centaurea paniculata* subsp. *lunensis* (Fiori) Arrigoni in Parlatorea 6: 64. 2003. Type: ITALY. Liguria: "Bocca di Magra", July 1873, *H. Groves s.n.* (lectotype, designated by Arrigoni (2003: 64): FI [barcode FI002012!])

The name *C. aplolepa* subsp. *lunensis* (Fiori) Dostál is accepted and applies to plants endemic to eastern Liguria and small portions of Emilia-Romagna and Tuscany, central and northern Italy (Arrigoni 2003; Bartolucci et al. 2024).

23. *Centaurea paniculata* subsp. *pallidula* Rouy in Rev. Bot. Syst. Geogr. Bot. 2: 147. 1904 ≡ *Centaurea paniculata* subsp. *leucophaea* subvar. *pallidula* (Rouy) Arènes in Mém. Mus. Natl. Hist. Nat., Ser. B, Bot. 1(2): 203. 1951. Type: FRANCE. Occitanie: Cerdagne, 1 or 5 August 1902, *F. Sennen s.n.* (lectotype, designated here: LY [barcode LY0000818], photo! (the individual at the upper portion of the sheet, on the left), https://explore.recolnat.org/occurrence/DF9CA0CBBEAB4A8C9A4CE4407420D52D)

In the protologue (Rouy 1904) mentioned a gathering collected by himself and F. Sennen at Cerdagne (Pyrénées-Orientales, Occitanie). The specimen LY0000818, conserved in Rouy's herbarium, matches with the information provided in the protologue. On the herbarium sheet, five individuals, collected on the 1st and 5th August 1902, are mounted. The morphology of all the individuals agrees with the protologue, since they show the general morphology of *C. leucophaea* but with light green leaves and involucral bracts with pale fawn appendices and whitish cilia. In addition, we remark the presence, not mentioned in the protologue, of involucral bracts with a peculiar membranous appendices connecting the lower cilia. The best preserved and most developed individual, mounted at the upper portion of the sheet on the left, is designated as the lectotype. Since it is not possible to know the precise date of collection, the remaining four individuals cannot be safely considered as isolectotypes, since they can possibly belong to a distinct gathering.

Greuter (2008) considered this taxon as a heterotypic synonym of *C. paniculata* subsp. *paniculata*. However, based on the peculiar lectotype morphology, we agree with Tison and de Foucault (2014) considering *C. paniculata* subsp. *pallidula* as a distinct taxon endemic to Pyrénées-Orientales, southern France.

24. *Centaurea paniculata* var. *pseudocineraria* Fiori in Fiori & Paoletti, Fl. Italia 3: 338. 1904 ≡ *Centaurea pseudocineraria* (Fiori) Rouy in Rev. Bot. Syst. Géogr. Bot. 2: 141. 1904 ≡ *Centaurea paniculata* subsp. *pseudocineraria* (Fiori) Arènes in Mém. Mus. Natl. Hist. Nat., Ser. B, Bot. 1(2): 206. 1951. Type: FRANCE. Provence-Alpes-Côte d'Azur: Baus-Rous, between Beaulieu and Èze, 21 May 1889, *H. Groves s.n.* (lectotype, designated here: FI!)

In the protologue, Fiori (1904) provided a short diagnosis and reported Villafranca (Baus Rous, Provence-Alpes-Côte d'Azur, France) as locality of occurrence. We located two specimens in FI that were identified by Fiori as

C. paniculata var. *pseudocineraria*. They were both collected before the publication of the name near Villafranca, the place mentioned in the protologue. We selected the best preserved specimen, collected by Groves in 1889, as the lectotype. It is a white tomentose plant, 30 cm tall, with capitula 12 mm large showing a dark appendage and long cilia. This morphology is congruent with the protologue and with the application of the name *C. pseudocineraria* (Fiori) Rouy to a species endemic to Provence-Alpes-Côte d'Azur (Tison and de Foucault 2014).

25. *Centaurea paniculata* var. *pseudocoerulescens* Briq., Cent. Alp. Marit.: 148. 1902 ≡ *Centaurea paniculata* var. *leucophaea* f. *pseudocoerulescens* (Briq.) Fiori in Fiori & Paoletti, Fl. Italia 3: 337. 1904 ≡ *Centaurea leucophaea* subsp. *pseudocoerulescens* (Briq.) Dostál in Bot. J. Linn. Soc. 71: 200. 1976. Type: FRANCE. Provence-Alpes-Côte d'Azur: "près d'Aurent (environs d'Annot)", 21 July 1885, *E. Burnat s.n.* (lectotype, designated here: G [barcode G00628035], photo!; isolectotype: G [barcode G00628034], photo!)

In the protologue, Briquet (1902) provided a short diagnosis and cited several herbarium specimens. We located five of them at G and the best preserved and complete specimen (G00628035) is designated as the lectotype. It is a white tomentose plant, with large ovoid involucres, and involucral bracts with dark brown appendages and long cilia. Based on this morphology, we agree with Greuter (2008) and Tison and de Foucault (2014) considering *C. paniculata* var. *pseudocoerulescens* as a heterotypic synonym of *C. pseudocineraria* (Fiori) Rouy, a species endemic to Provence-Alpes-Côte d'Azur, southern France.

26. *Centaurea paniculata* var. *valesiaca* DC., Prodr. 6: 584. 1838 ≡ *Centaurea valesiaca* (DC.) Jord. in Mém. Acad. Roy. Sci. Lyon, Sect. Lett., ser. 2 1: 322. 1851 ≡ *Centaurea paniculata* subsp. *valesiaca* (DC.) Nyman, Consp. Fl. Eur.: 426. 1879 ≡ *Centaurea maculosa* var. *valesiaca* (DC.) Gugler in Centaur. Ungar. (Ann. Mus. Nat. Hungar. VI.): 167. 1907 ≡ *Acosta valesiaca* (DC.) Holub in Preslia 46: 227. 1974. Type: SWITZERLAND. Valais: Simplon, 1824, *M.N. Puerari s.n.* (lectotype, designated here: G [barcode G00473215] photo!, https://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=339867&base=img&lang=en)

In the protologue, Candolle (1838) provided a short diagnosis and indicated the canton of Valais (Switzerland) as region of occurrence. We located a specimen (G00473215) in Candolle's herbarium that is original material. It was collected in 1824 in Simplon (Valais, Switzerland), in the geographic circumscription mentioned by Candolle (1838). The specimen is in accordance with the short morphological description reported in the protologue (almost hairless leaves, pinnatisect with acute segments), and is designated as the lectotype. This taxon was formally placed under *C. leucophaea* by Rouy (1904: 148) as *C. paniculata* subsp. *leucophaea* var. *valesiaca*. According to Greuter (2008), *C. valesiaca* (DC.) Jord. is accepted and applies to a species native to Switzerland, France and western-northern Italy. Later, Tison and de Foucault (2014) excluded France from the range of this species, while Bartolucci et al. (2024) confirmed its occurrence in Italy.

27. *Centaurea reuteri* Rchb.f. in Reichenbach, Icon. Fl. Germ. Helv. 15: 33. 1852 ≡ *Centaurea paniculata* subsp. *reuteri* (Rchb.f.) Nyman, Consp. Fl. Eur.: 426. 1879 ≡ *Centaurea paniculata* var. *reuteri* (Rchb.f.) Briq., Cent. Alp. Marit.: 151. 1902 ≡ *Centaurea paniculata* f. *reuteri* (Rchb.f.) Fiori in Fiori & Paoletti, Fl. Italia 3: 337. 1904 ≡ *Centaurea leucophaea* var. *reuteri* (Rchb.f.) Gugler, Centaur. Ungar. (Ann. Mus. Nat. Hungar. VI.): 177. 1907 ≡ *Centaurea leucophaea* subsp. *reuteri* (Rchb.f.) Dostál in Bot. J. Linn. Soc. 71: 200. 1976. Type: [Illustration] t. 49 I (1–9), in Reichenbach, Icon. Fl. Germ. Helv. 15. 1852 (lectotype, designated here)

In the protologue, Reichenbach (1852) cited two specimens: one collected by himself and G.F. Reuter at Col de Braus (Provence-Alpes-Côte d'Azur), close to the current Italian border, and another specimen collected by J.P. Barla at Cimiez (Nice, Provence-Alpes-Côte d'Azur). We searched for original material at W, where H.G. Reichenbach's herbarium is conserved (Stafleu and Cowan 1983), but we did not locate any specimen. Along with the protologue, the illustration (t. 49 I, 1–9) of a green plant with pinnatisect leaves and ovoid capitula with involucral bracts showing fawn and long cilia is mounted. In the absence of herbarium specimens, this illustration is the only original material and is designated as the lectotype for *C. reuteri*. According to Greuter (2008), *C. leucophaea* subsp. *reuteri* (Rchb.f.) Dostál is an accepted name and applies to plants endemic to France and Italy. However, based on the lectotype, we agree with Tison and de Foucault (2014) in considering *C. reuteri* as a heterotypic synonym of *C. leucophaea* subsp. *leucophaea*, a taxon endemic to southern France and northern Italy.

28. *Centaurea subalbida* Jord. in Mém. Acad. Roy. Sci. Lyon, Sect. Lett. 1: 320. 1851 ≡ *Centaurea paniculata* subsp. *leucophaea* var. *subalbida* (Jord.) Rouy in Rev. Bot. Syst. Geogr. Bot. 2: 149. 1904. Type: FRANCE. Provence-Alpes-Côte d'Azur: Lyon [plants cultivated from seeds collected in Les Vans, Auvergne-Rhône-Alpes], 22 July 1869, *A. Jordan s.n.* (neotype, designated here: LY [barcode LY0375186], photo!; isolectotype: LY [barcode LY0825495], photo!, https://explore.recolnat.org/occurrence/FE21B1BB9A494C92B5E33BD5446CEEEE)

In the protologue, Jordan (1851) provided a detailed description and reported Les Vans and Banne (Auvergne-Rhône-Alpes) as localities of occurrence. We searched in Jordan's herbarium but, as for *C. mierghii*, we located just specimens collected from Jordan's garden after the publication of the name. In the absence of original material, a neotype can be designated. The specimen LY0375186, in Jordan's herbarium, was grown from seeds mature plants collected at Les Vans, one of the two localities mentioned in the protologue. This specimen shows pubescent leaves composed of several linear-oblong segments. The involucres are oblong-ovoid and the involucral bracts show yellow to brown appendages, with lateral upper cilia that exceed in length the central mucro. Since this morphology agrees with the protologue, the specimen LY0375186 is designated as the neotype for *C. subalbida*. Based on the neotype morphology, we agree with Greuter (2008) and Tison and de Foucault (2014) in considering *C. subalbida* as a heterotypic synonym of *C. stoebe*, a species widespread in central-eastern Europe.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

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

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Review Article

Phaeoceros perpusillus var. *scabrellus* (Notothyladaceae, Anthocerotophyta), a new taxon from northern Thailand

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Abstract

A new variety of hornwort from northern Thailand, *Phaeoceros perpusillus* var. *scabrellus* is described based on morphological characters and molecular phylogenetic analyses. In this study, phylogenetic analyses supported that the new variety is closely related to *P. perpusillus* var. *perpusillus*. Morphologically, it is distinguished from the autonimic variety in nearly smooth spores under light microscope. A taxonomic description, illustrations, and light and scanning electron micrographs are provided. In addition, the new variety is assessed as Endangered (EN), demonstrating its rarity by being currently known from only three subpopulations.

Key words: Endangered, hornwort, low-copy nuclear markers, new variety, spore ornamentation

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Introduction

Phaeoceros Prosk. (Notothyladaceae) is the third largest genus of hornwort with about 34 currently accepted species worldwide (Söderström et al. 2016) and widely distributed in both the Northern and Southern Hemispheres (Cargill and Fuhrer 2008). The genus is defined by a smooth solid thallus, single chloroplast per cell, presence of a pyrenoid, antheridial chambers with usually (1–)2–6(–8) antheridia, irregularly arranged jacket cells of the antheridia, and yellow spores (Duff et al. 2007; Cargill and Fuhrer 2008; Chantanaorrapint 2009; Villarreal et al. 2010). In Thailand three species have been reported: *P. carolinianus* (Michx.) Prosk., *P. himalayensis* (Kashyap) Prosk. ex Bapna & G.G.Vyas, and *P. perpusillus* Chantanaorr. (Lai et al. 2008; Chantanaorrapint 2009; Chantanaorrapint et al. 2015).

During the bryological surveys in Chiang Mai Province, northern Thailand, some interesting specimens of the hornwort genus *Phaeoceros* were collected. These specimens resemble *P. perpusillus*, an endemic species of northern Thailand, in having small gametophytes, short sporophytes (usually less than 1 cm long), yellow spores, and subquadrate pseudoelater cells. Following a detailed comparison with closely related taxa, we here describe and illustrate these specimens as a new variety of *P. perpusillus*. We also used for the first time three hornwort specific low-copy nuclear markers. In theory, low-copy nuclear genes tend to have higher mutation rates than organellar genes, resulting in more variable sites that can be used for phylogenetic reconstruction, especially at species-level (Sang 2002; Feliner and Rosselló 2007). However, despite the advantages of biparental inheritance, which provides a more comprehensive view of the genetic history and evolution, low-copy nuclear genes have not been widely used (Zhang et al. 2012). In this study, we combined selected low-copy nuclear sequences with chloroplast sequences to enhance the resolution of our phylogenetic analyses. By using both chloroplast and nuclear markers, our study aims to explore alternative genetic regions for species-level phylogenies, thus providing a greater understanding of hornwort evolution.

Materials and methods

Morphological study

This study is based on recent collections from Thailand. Voucher specimens of the new species are deposited in BKF, NICH, and PSU herbaria. Morphological and anatomical characters were studied using stereo- and compound microscopes. The distinctive characters of the species were photographed using an Olympus BX51 microscope equipped with a DP74 digital camera and illustrated with the aid of an Olympus drawing tube. Mature spores were coated with a thin layer of gold and examined under a FEI Quanta 400 scanning electron microscope operating at 20 kV. The preliminary conservation status was assessed following the International Union for Conservation of Nature (**IUCN**) Red List criteria (IUCN 2022) and using GeoCAT (Bachman et al. 2011) to calculate the area of occupancy (**AOO**) and extent of occurrence (**EOO**). In addition, distribution and ecological data were compiled; descriptions and illustrations are provided.

Taxon sampling

Twenty-seven samples of *Phaeoceros* spp. were included in our molecular dataset. Additionally, *Notothylas levieri* Schiffn. ex Steph. and *Paraphymatoceros* sp. were employed as the outgroup. List of newly generated sequence used in the phylogeny with voucher information and GenBank accession numbers are provided in Table 1.

DNA extraction, amplification, and sequencing

Total genomic DNA from silica gel-dried sporophytes was extracted using E.Z.N.A. Plant DNA kit (Omega Bio-Tek, USA) following manufacturer's protocols. An alignment of more than 400 loci from a probe developed and explained by Breinholt et al. (2021) was used to reconstruct the phylogeny of all hornworts (Peñaloza-Bojacá et al. submitted). From the alignment we selected three loci found in *Phaeoceros* species (L138, L178, and L315) and designed internal primers using Geneious 2021.1.1. Amplification was accomplished using four primers listed in Table 2, one for the *rbc*L gene as described in Duff et al. (2004) and three primers newly designed for *Phaeoceros* nuclear loci (L138, L178 and

Table 1. List of newly generated sequence used in the phylogeny with voucher information and GenBank accession numbers.

Taxa	Collector	***rbc*L**	**L138**	**L178**	**L315**
Paraphymatoceros sp. Mexico	*Morales 22*	**OR943578**	**PP481902**	**PP471573**	**PP471590**
Phaeoceros carolinianus Thailand1	*Chantanaorrapint & Suwanmala 3955*	**OR943588**	**PP481909**	**PP471580**	**PP471598**
P. carolinianus Thailand2	*Chantanaorrapint & Suwanmala 3909*	**OR943586**	**PP481911**	**PP471581**	**PP471600**
P. carolinianus Thailand3	*Chantanaorrapint & Suwanmala 4057*	**OR943585**	**PP481913**	**PP471583**	**PP471602**
P. carolinianus India1	*Villarreal & Uniyal1314*	**OR943596**	**PP481901**	**PP471572**	**PP471589**
P. carolinianus India3	*Villarreal 1233*	**OR943593**	**PP481904**	**PP471575**	**PP471593**
P. carolinianus India2	*Duckett IE45*	**OR943592**	**PP481905**	**PP471576**	**PP471594**
P. carolinianus Czech Republic	*Kopal* s.n.	**OR943591**	**PP481906**	**PP471577**	**PP471595**
P. carolinianus Indonesia	*Gradstein 12362*	**OR943595**	**-**	**-**	**PP471591**
P. carolinianus Vietnam	*Suwanmala 849*	**OR943582**	**PP481916**	**PP471585**	**PP471604**
P. exiguus Thailand2	*Chantanaorrapint & Suwanmala 4129*	**OR943580**	**PP481918**	**PP471587**	**PP471606**
P. himalayensis India	*Duckett IW15*	**OR943594**	**PP481903**	**PP471574**	**PP471592**
P. kashyapii Thailand	*Chantanaorrapint & Suwanmala 3901*	**OR943589**	**PP481908**	**PP471579**	**PP471597**
P. mohrii USA	*Doyle 11341*	**OR943590**	**PP481907**	**PP471578**	**PP471596**
P. perpusillus var. *perpusillus* Thailand2	*Chantanaorrapint & Suwanmala 3883*	**OR943587**	**PP481910**	**-**	**PP471599**
P. perpusillus var. *perpusillus* Thailand3	*Chantanaorrapint & Suwanmala 4076*	**OR943584**	**PP481914**	**PP471584**	**PP471603**
P. perpusillus var. *scabrellus* Thailand1	*Chantanaorrapint & Suwanmala 4077*	**OR943583**	**PP481915**	-	-
P. perpusillus var. *scabrellus* Thailand2	*Chantanaorrapint & Suwanmala 4116*	**OR943581**	**PP481917**	**PP471586**	**PP471605**
Phaeoceros sp. Thailand	*Chantanaorrapint & Suwanmala 4488*	**OR943579**	**PP481919**	**PP471588**	**PP471607**

Table 2. Primer sequence used for PCR amplification and sequencing.

Region	Sequence 5’-3’	Reference
L138		
Phaeoceros_L138_58F	TTG TCC TGA ATT CAC GTG GT	This study
Phaeoceros_L138_607R	GCT TTG CTA GGG TCT GGT AAG A	This study
L178		
Phaeoceros_L178_232F	CTC GGG GAT GAG CGG GAC	This study
Phaeoceros_L178_1088R	GCT TCA AGA GAT GGC TCC TT	This study
L315		
Phaeoceros_L315_676F	GGA TTT TGG GGA CTT GCA CA	This study
Phaeoceros_L315_1325R	CTT CTG CCC AAC AAC AGG AG	This study
***rbc*L**		
rbcL2_16F	GAG ACT AAA GCA GGT GTT GGA	Duff et al. (2004)
rbcL_976R	ACA CGA AAG TGA ATA CCA TG	Duff et al. (2004)

L315). The conditions for PCR were as follows: (1) for *rbc*L, L138 and L315: initial denaturation for 3 min at 94 °C, followed by 35 cycles of 1 min at 94 °C, 30 s at 55 °C, 1 min at 72 °C, and final extension for 10 min at 72 °C, (2) for L178: initial denaturation for 3 min at 94 °C, followed by 35 cycles of 1 min at 94 °C, 30 s at 58 °C, 1 min at 72 °C, and final extension for 10 min at 72 °C. The final products were incubated at 10 °C to complete the reaction. The PCR products were purified and sequenced by Plate-forme d’analyses génomiques (Quebec, Canada), except for *O. Suwanmala 849*, *S. Chantanaorrapint & O. Suwanmala 4116, 4129, 4488* which were performed by the Macrogen sequencing service (Macrogen, Korea).

Forward and reverse sequences were edited initially and assembled using Geneious 2021.1.1. We gathered published data from six samples generated by Breinholt et al. (2021), UFG_393201_P02_WH01, UFG_393201_P02_WA02, UFG_393201_P02_WB02, UFG_393201_P02_WH02, UFG_393201_P02_WG02, UFG_393201_P02_WD01, one sample of UFG_393202_P054_WD04 generated by Bechteler et al. (2023), and three samples, UFG_393202_P033_WD01, UFG_393202_P054_WE04, UFG_393202_P033_WC01, generated by Peñaloza-Bojacá et al. (submitted). Nineteen newly generated sequences (Table 1) and ten published sequences were aligned using the Geneious alignment algorithm with default settings. Uncertain alignment positions and columns displaying a large number of gaps were excluded from the phylogenetic assessments. Any incomplete sequence segments and nucleotide gaps were treated as missing data.

Phylogenetic analysis

A maximum likelihood (ML) analysis was performed in RAxML HPC BlackBox v.8.2 (Stamatakis 2014) using GTR+I+GAMMA substitution model following default setting with 1000 bootstrap replications. The best model scheme of each partition was carried out in Partitionfinder 2 (Lanfear et al. 2016). Bayesian analysis was performed in MrBayes 3.2 (Ronquist et al. 2012) using Markov chain Monte Carlo (MCMC) searches with two runs and four chains of 3,500,000 generations. Trees were sampled every 1000th generation and the first 10% of sampled trees were discarded as a burn-in to ensure a convergence of the analyses. We used Tracer 1.5 (Rambaut et al. 2018) to evaluate the burn-in and convergence. Figtree was used to graph and edit trees (Rambaut 2017). Both maximum likelihood and Bayesian analyses were performed on CIPRES Science Gateway (Miller et al. 2010).

Results

A concatenated dataset of the coding region of one plastid and three nuclear markers (*rbc*L, L138, L178 and L315) contained 2856 characters (892, 549, 781, and 634 characters respectively). Tree topologies generated by Bayesian inference (**BI**) and maximum likelihood exhibited congruent patterns shown in Fig. 1, with posterior probabilities (**PP**) and maximum likelihood bootstrap values (**MLBS**) plotted on the branches. The monophyly of the genus *Phaeoceros* is well supported by posterior possibility (PP = 1) but weakly supported by maximum likelihood analysis (MLBS = 53). In the tree topology (Fig. 1), *Phaeoceros* was divided into two major lineages with strong support, clade A including twenty-three terminals, containing the new taxon and other papillate spore *Phaeoceros* (PP = 1, MLBS = 94), and clade B comprising four terminals of non-papillate spore *Phaeoceros* including *P. himalayensis* and *P. kashyapii* A.K. Asthana & S.C. Srivast. (PP = 1, MLBS = 100).

The inclusion of *P. perpusillus* var. *scabrellus* and its autonimic variety in the data matrix resolves this species lineage as monophyletic with good support (PP = 1, MLBS = 90). The new variety is recovered as sister to the autonimic variety with less posterior probability and bootstrap support (PP = 0.56, MLBS = 80).

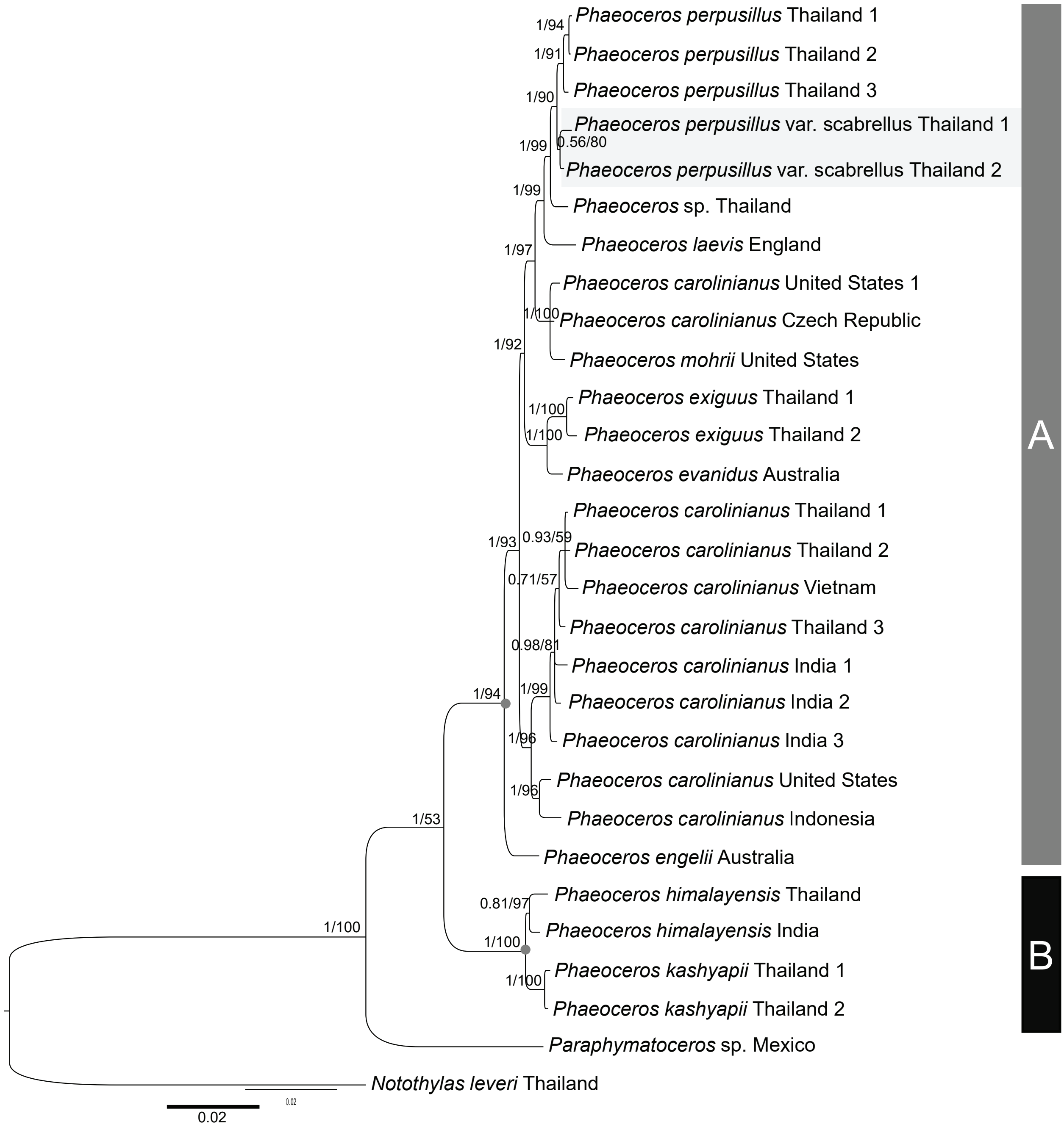

Figure 1. Majority rule consensus tree of phylogenetic relationships of *Phaeoceros* derived from Bayesian analyses of the combined dataset of *rbc*L, L138, L178, and L315 genes. Bayesian posterior probability values (PP) and bootstrap percentages values (MLBS) are shown on branches respectively. Nucleotide substitution rates indicated below the tree. Clade A include papillate spore *Phaeoceros* and the new variety (highlighted), and Clade B include non-papillate spore *Phaeoceros*.

Taxonomic treatment

Phaeoceros perpusillus **Chantanaorr. var.** ***scabrellus*** **Suwanmala & Chantanaorr., var. nov.**
Figs 2–4

Type. Thailand. Chiang Mai Province: Doi Suthep-Pui, Bhu Bing Palace, 1400 m, 18 October 2020, *S. Chantanaorrapint & O. Suwanmala 4077* (holotype: PSU!; isotype: BKF!, NICH!).

Diagnostic. *Phaeoceros perpusillus* var. *scabrellus* is similar to the autonimic variety but differs in nearly smooth spores under light microscope (or vermiculate under SEM), whereas the autonimic variety have pluripapillae on the distal surface and vermiculate on the proximal.

Description. ***Thallus*** yellowish-green to dark green in fresh material, dull green to blackish- brown in dry material, prostrate or moderately adhering to the substratum, solid, ecostate, orbicular to sub-orbicular, dichotomously branched into several lobes, with a smooth dorsal surface; lobes ensiform or sometimes fan-shaped, up to 0.8 mm long, 1–3 mm wide; margins wavy, nearly entire to shallowly crenulate; apex flat, rarely ascending, occasionally tapering into apical tubers; tubers sometimes present on ventral surface. Thallus in cross section plano-convex to concave-convex, 4–10 cells thick in the middle region, without mucilage cavities. Dorsal epidermal cells rectangular to heptagonal, 28–75 × 25–50 μm, thin-walled, smooth. Chloroplast one per cell, large, occupying almost entire cell, variable in shape; pyrenoid present. ***Nostoc colonies*** scattered through the ventral side of thallus, appearing as dark dots. ***Rhizoids*** hyaline or pale brown along ventral surface, inner wall smooth or tuberculate. ***Sexuality*** monoicous. Androecia scattered and slightly raised over the dorsal surface of thallus, 2–3 antheridia per chamber; antheridia subglobose to globose, exposed at maturity, irregularly arranged jacket cells, shortly stalked, stalk with quadriseriate cells. Archegonia embedded in thallus, connected to the upper surface, scattered near the lobe of thallus. ***Involucre*** solitary, conical-cylindrical, up to 2 mm long, 2–4 cells thick, mouth smooth to crenulate. ***Sporophytes*** capsule somewhat inclined, stout to narrowly cylindrical, 0.5–1(–1.2) cm long, yellow at apex, dehiscing from top toward base, bivalves rarely twisted when dry; epidermal cells of capsule elongate-rectangular, 68–200 × 12–30 μm, thick-walled, stomata present with two reniform guard cells, surrounded by 5–8 epidermal cells; assimilative layers 3–6 cells thick in cross section; the innermost capsule cells dark brown, subquadrate to rectangular; 27–67 × 22–53 μm; columella well-developed, red-brown, consisting of 16 cells (4 × 4 lines of cells) in cross section. ***Spores*** unicellular, yellow, rounded-triangular in polar view, equatorial diameter 32–50 μm in diameter, nearly smooth under light microscope (LM), proximal surface with a distinct trilete mark, bordered by vermiculate strip on each side of trilete mark, each facet covered with fine vermiculate pattern; distal surface with a slightly dome-like region at the center, more densely vermiculate than proximal surface, sometimes with minute granules. ***Pseudoelaters*** light brown or yellowish-brown at maturity, thin-walled, occasionally branched; pseudoelater cells subquadrate to short rectangular, 30–45 × 25–30 μm, without helicoidal band.

Etymology. The epithet of the variety refers to scabrate ornamentation observed under light microscope.

Habitat and distribution. *Phaeoceros perpusillus* var. *scabrellus* is currently known only from northern Thailand. It grows on disturbed soil and sandstone in open site in grassland, pine-oak mixed montane deciduous forests at elevation of 1390–2100 m. It may grow associated with other bryophytes such as *Anthoceros subtilis* Steph., *Notothylas levieri*, *N. orbicularis* (Schwein.) Sull. ex A.Gray, and *P. carolinianus*.

Conservation status. This variety is currently known from three subpopulations, which are in protected areas (Chiang Dao Wildlife Sanctuary and Doi Suthep-Pui National Park). One of the subpopulations is located in a camping

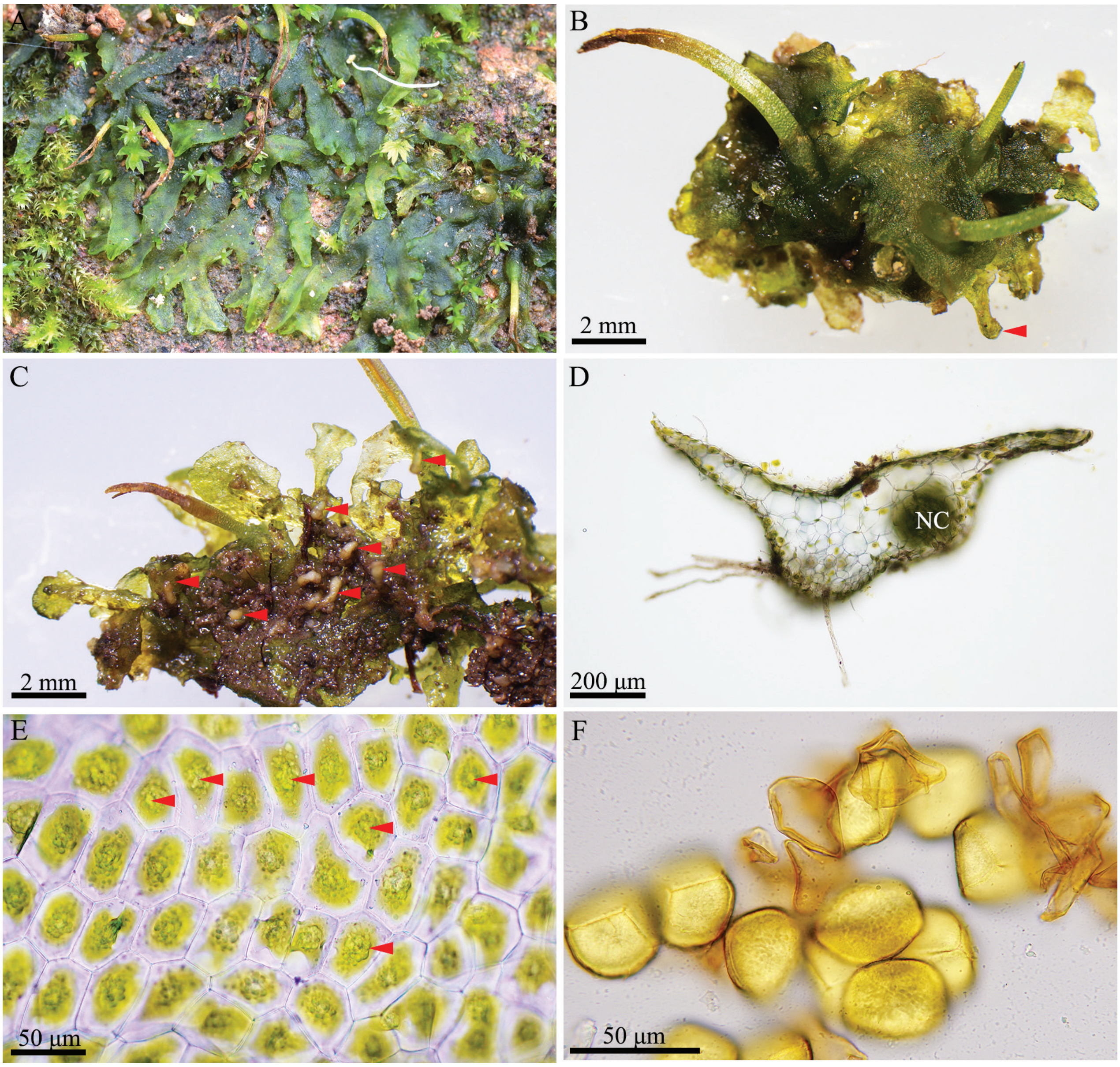

Figure 2. *Phaeoceros perpusillus* var. *scabrellus* **A** plants in natural habitat **B** dorsal view of thallus showing marginal tubers (arrow) **C** ventral view of thallus showing ventral tubers (arrows) **D** cross-section of thallus showing the large dark lump of Nostoc colony (NC = Nostoc colony) **E** dorsal epidermal cells of thallus showing a single chloroplast with pyrenoid (arrows) per cell **F** spores and pseudoelaters. Photos by O. Suwanmala (**A** from *S. Chantanaorrapint & O. Suwanmala 4116* **B–F** from *S. Chantanaorrapint & O. Suwanmala 4077*).

area, which is a common visiting site for tourists and dominated by *Ageratina adenophora* (Spreng.) R.M.King & H.Rob. (invasive species). Therefore, habitat quality is threatened by trampling and other destructive activities potentially caused by regular visits by tourists to the area, and invasive plant species. Together, these have the potential to cause a population reduction. The other subpopulation is also somewhat disturbed by human activities such as shifting cultivation. The extent of occurrence (EOO) of *P. perpusillus* var. *scabrellus* is estimated to be 262.925 km^2 and its area of occupancy (AOO) is estimated to be 12 km^2, which falls within the limits for Endangered status under criterion B1 and B2 of IUCN Red List Categories and Criteria. Conservation efforts should focus on implementing strict regulations to reduce the impact of human

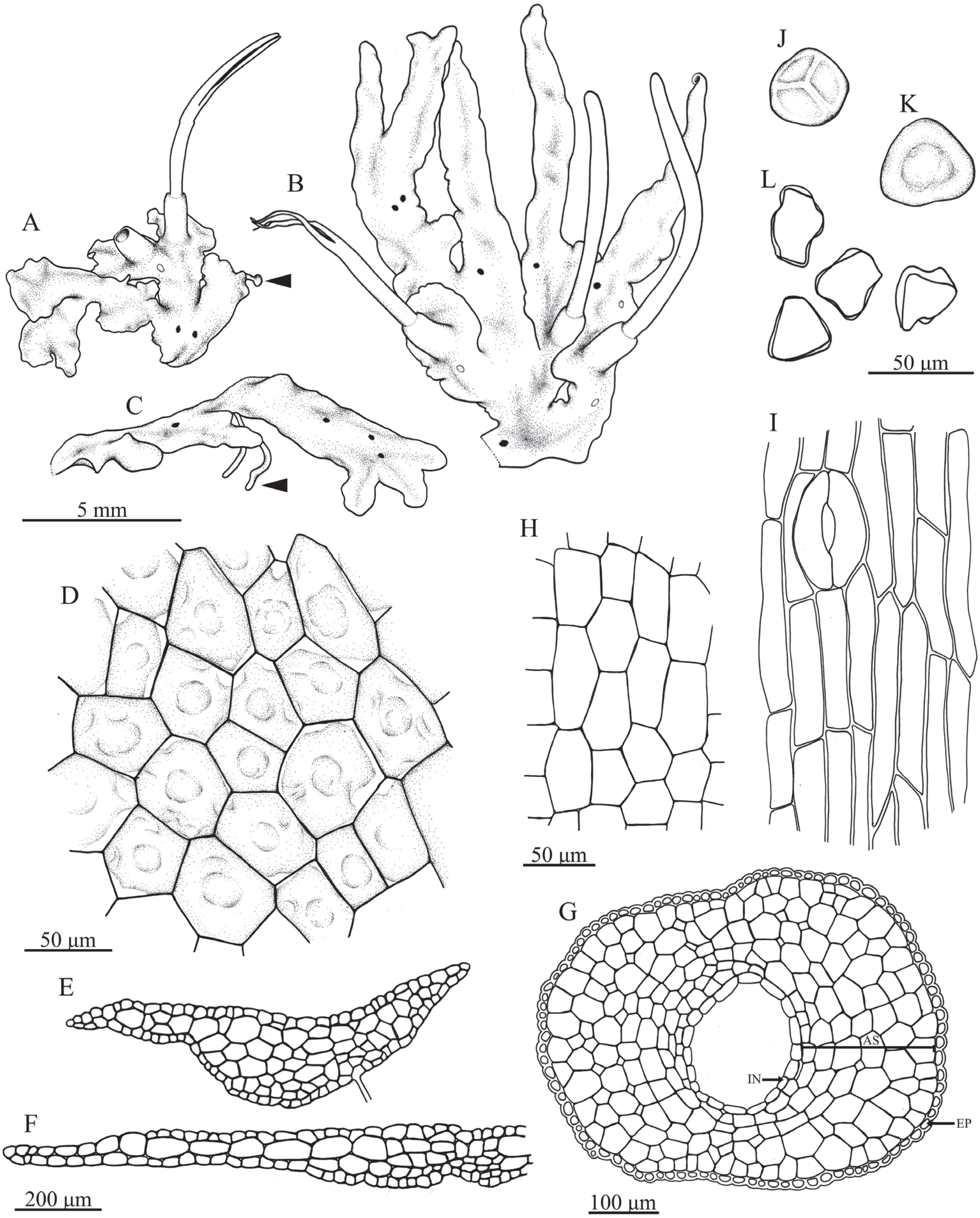

Figure 3. *Phaeoceros perpusillus* var. *scabrellus* **A** gametophyte forming half-rosettes with sporophyte (arrow indicate tuber) **B** ensiform thalli and sporophytes **C** gametophyte showing ventral tuber (arrow) **D** dorsal epidermal cells of thallus **E, F** cross sections of thalli **G** cross section of sporangium (AS = assimilative tissue, EP = epidermal cell of capsule, IN = inner most sporangium wall) **H** inner most cells of sporangium wall **I** epidermal cells of capsule with stoma **J** proximal view of spore **K** distal view of spore **L** pseudoelaters. All from holotype and drawings by O. Suwanmala. (All drawing from *S. Chantanaorrapint & O. Suwanmala 4116*).

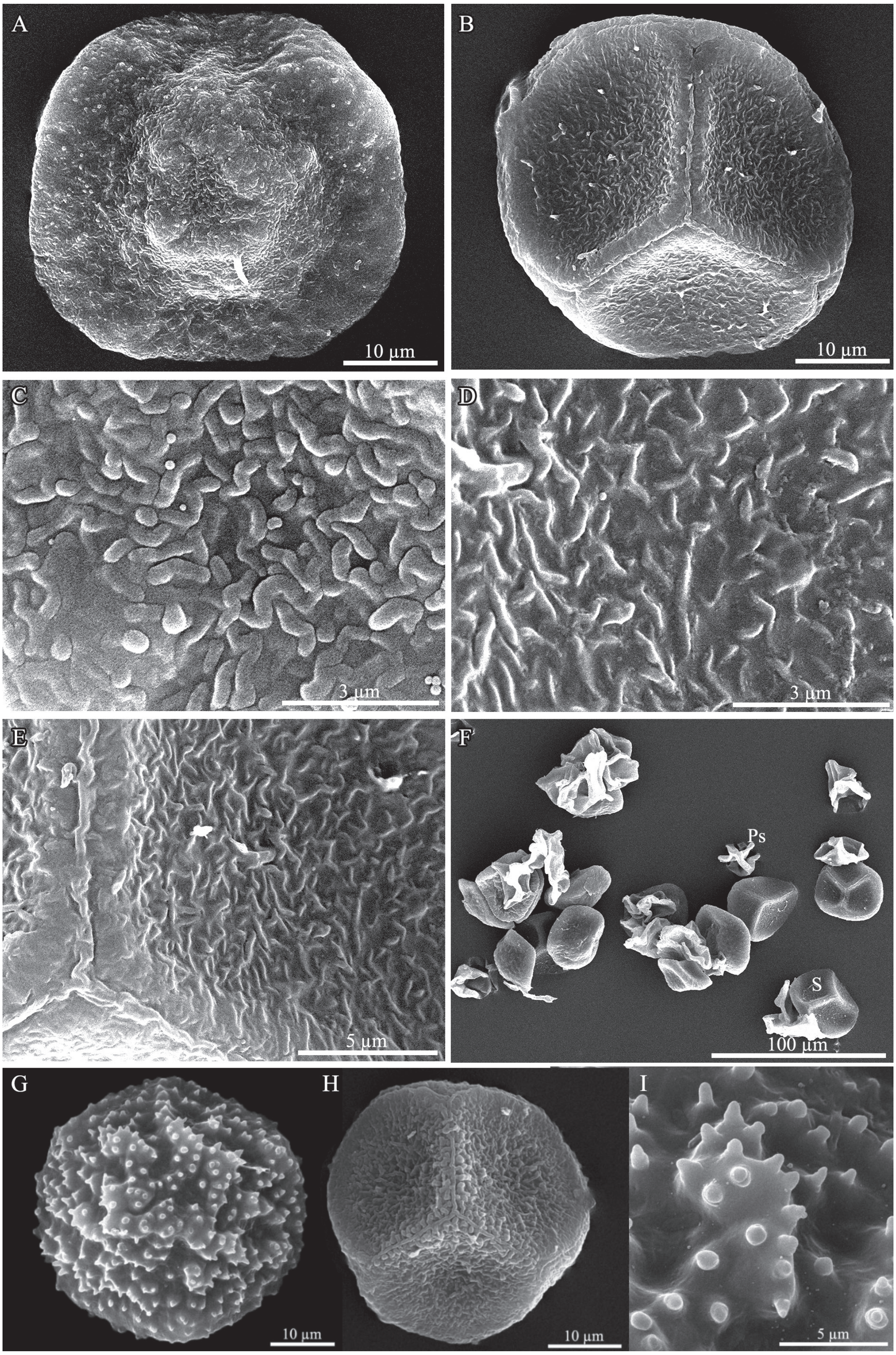

Figure 4. Scanning electron micrographs of spores **A–F** *Phaeoceros perpusillus* var. *scabrellus* **A** distal view of spore showing a central hump-like projection **B** proximal view of spore with a distinct triradiate mark **C** close-up of distal surface showing packed vermiculae **D** close-up of proximal surface showing loosely arranged vermiculae **E** proximal surface showing trilete mark and loosely arranged vermiculae **F** spores and pseudoelaters **G–I** *P. perpusillus* var. *perpusillus* **G** distal view of spore **H** proximal view of spore **I** close-up of distal surface showing pluripapillae. Photos by O. Suwanmala. (**A–F** images from *S. Chantanaorrapint & C. Promma 3129* **G–I** images from *S. Chantanaorrapint & O. Suwanmala 3883*).

activity and controlling invasive species, while also raising awareness among local communities about the importance of protecting the habitat.

Additional specimens examined. Thailand. Chiang Mai Province: Chiang Dao Wildlife Sanctuary, 1700–2000 m, 1 November 2013, *S. Chantanaorrapint & C. Promma 3125B, 3129, 3216* (PSU); Doi Suthep-Pui National Park, Doi Mon Long Viewpoint, 1390 m, 4 November 2015, *S. Chantanaorrapint & W. Juengprayoon 143B* (PSU); 15 November 2020, *S. Chantanaorrapint & O. Suwanmala 4089, 4090* (PSU); Bhu Ping Palace, 1400 m, 8 September 2013, *S. Rattanamanee 3* (PSU); 18 October 2020, *S. Chantanaorrapint & O. Suwanmala 4077* (PSU); 5 October 2021, *S. Chantanaorrapint & O. Suwanmala 4116* (PSU).

Discussions

Phaeoceros perpusillus var. *scabrellus* is morphologically similar to the autonimic variety which is endemic to northern Thailand (Chantanaorrapint 2009). These two varieties share some common features, viz. small orbicular gametophytes (Fig. 2A, B), monoicous sexual condition, very short capsules (usually less than 1 cm long) (Figs 2B, 3A, B), yellow spores, and pseudoelater cells being subquadrate to short rectangular (Figs 2F, 3L). The new variety also resembles *P. exiguus* (Steph.) J. Haseg., a species found in Indonesia, New Caledonia and Taiwan (Hasegawa 1986, 1993; Siagian et al. 2021). They are monoicous, and have a small thallus, very short capsules, and small pseudoelaters. However, they can be distinguished by the spore ornamentation. *Phaeoceros perpusillus* var. *scabrellus* is distinct from the autonimic variety and *P. exiguus* in nearly smooth spores under light microscope or vermiculate spores under SEM (Fig. 4A–F). In contrast, spores of *P. perpusillus* var. *perpusillus* are pluripapillose on distal face and finely vermiculate on proximal face (Fig. 4G–I), while *P. exiguus* have button-like papillae on distal face and minutely papillae on proximal face.

In addition, the small plants of *P. carolinianus*, a common species, can be confused with *P. perpusillus* or *P. exiguus* in general appearance. The comparisons of morphological characters between these three monoicous species are summarized in Table 3.

Table 3. The comparisons of characters between *P. perpusillus* var. *scabrellus*, *P. perpusillus* var. *perpusillus*, *P. exiguus* and *P. carolinianus*.

Characters	*P. perpusillus* var. *scabrellus*	*P. perpusillus* var. *perpusillus*	*P. exiguus*	*P. carolinianus*
Thallus	4–10 cells thick in the middle	6–9 cells thick in the middle	6–7 cells thick in the middle	8–13 cells thick in the middle
Capsule placement	oblique	oblique	usually erect	Erect
Capsule length	usually less than 1 cm	less than 1 cm	up to 1.5 cm	usually more than 1.5 cm
Involucre	up to 2 mm high	1–2 mm high	1–2 mm high	2–4 mm high
Spore diameter	32–50 μm	40–47 μm	40–42 μm	30–37 μm
Distal surface of spore	densely vermiculate, with minute granules	pluripapillose	dense clusters of button-like papillae	densely spinose
Proximal surface of spore	loosely vermiculate in each facet	finely vermiculate in each facet	minutely papillate throughout each facet	minutely papillate in central part of each facet
Pseudoelaters (length/width ratio)	1–1.5 ×	1.5–2.5 ×	1.2–2 ×	≥4 ×

Although both varieties of *P. perpusillus* have been reported only from the northern part of Thailand, *P. perpusillus* var. *perpusillus* seems to have a wider range of distribution and is more abundant than the new variety. The new variety has been found in only three subpopulations, overlapping with the autonimic variety, which is assessed as Endangered (EN) according to IUCN Red List.

The placement of the new variety falls into the papillate spore *Phaeoceros* lineage (Fig. 1, clade A), despite the absence of spines or papillae on its spore surface which sets the new variety apart from other taxa. Within an assemblage of autonimic variety *P. perpusillus* and the new variety clade, the two taxa share a sister relationship with low support, and they show only one morphological difference in spore morphology. The vermiculate spore ornamentation observed in *P. perpusillus* var. *scabrellus* seems to be an unusual form of the autonimic variety. However, based on careful investigation, it becomes evident that the absence of papillae on the spore surface is consistently observed throughout the entire capsule and reveals a uniform pattern in each population. Spore morphology serves as a key trait to differentiate hornwort species, allowing two distinct spore ornamentations to be considered as separate taxa.

This proposal for the new variety's classification was made due to its gametophyte and sporophyte morphological similarity to the autonimic variety with the exception of the spore ornamentation, and was also supported by phylogenetic inference, and the shared distribution area.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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