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Species of *Peperomia* (Piperaceae) from the Saña River Valley, Peru

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Abstract

The Saña River Valley in Northern Peru is unusual for the western slopes of the Peruvian Andes because of its nearly year-round regime of precipitation instead of marked seasonal dry winters. This results in unexpected plant diversity. We surveyed the species of *Peperomia* (Piperaceae), occurring in this valley from 300 to 3000 m elevation, based on the study of specimens from ten herbaria and field collections, resulting in a total of 81 accessions, of which 48 were made by the authors. We found 16 different taxa: *Peperomia cacaophila*, from Ecuador, is reported for the first time in Peru; *P. cymbifolia*, *P. dolabriformis* and *P. emarginulata* are reported for the first time for the Saña River Valley; other widely distributed species like *P. fraseri*, *P. galioides*, *P. haematolepis*, *P. hispidula*, *P. inaequalifolia*, *P. microphylla*, and *P. rotundata* were also found. Five species new to science are described: *P. pilocarpa*, *P. riosaniensis*, close to *P. palmiformis* from Amazonas; *P. sagasteguii*, related to *P. trinervis*, *P. symmankii*, close to *P. ricardofernandezii* from Piura, and *P. vivipara*, related to *P. alata*. A key to the species of *Peperomia* from the Saña River Valley, based on vegetative characters, is provided.

Resumen

El valle del Río Saña en el norte de Perú es inusual para las vertientes occidentales de los Andes peruanos por su régimen de precipitación ininterrumpido en lugar de inviernos secos estacionales marcados. Esto resulta en una diversidad de plantas inesperada. Revisamos las especies de *Peperomia* (Piperaceae), del valle del Río Saña entre los 300 a 3000 m de altitud, basándonos en el estudio de especímenes de diez herbarios y colecciones de campo, resultando en un total de 81 accesiones, de las cuales 48 fueron realizadas por los autores. Encontramos 16 taxones diferentes: *Peperomia cacaophila*, de Ecuador, se reporta por primera vez en Perú; *P. cymbifolia*, *P. dolabriformis* y *P. emarginulata* se reportan por primera vez para el valle del

Río Saña; otras especies ampliamente distribuidas como *P. fraseri*, *P. galioides*, *P. haematolepis*, *P. hispidula*, *P. inaequalifolia*, *P. microphylla* y *P. rotundata* también se encontraron. Se describen cinco especies nuevas para la ciencia: *P. pilocarpa*, *P. riosaniensis*, cercana de *P. palmiformis* de Amazonas; *P. sagasteguii*, relacionada con *P. trinervis*, *P. symmankii*, cercana a *P. ricardofernandezii* de Piura, y *P. vivipara*, relacionada con *P. alata.* Se presenta una clave para las especies de *Peperomia* del Valle del Río Saña basada en caracteres vegetativos.

Keywords
Amotape-Huancabamba Zone, Andean cloud forest, Cajamarca, *Fenestratae*, Lambayeque, *Panicularia*, western slopes of the Andes

Palabras clave
Bosque montano andino, Cajamarca, *Fenestratae*, Lambayeque, *Panicularia*, Vertientes occidentales de los Andes, Zona Amotape-Huancabamba

Introduction

Peperomia (Ruiz & Pavón, 1794), was the name chosen to distinguish some species previously described by Linnaeus as *Piper*, and its first species were described in Peru (Ruiz and Pavón 1798). It is the second largest genus of the family Piperaceae after *Piper*, with a pantropical distribution of about 1,600 species (Samain et al. 2009; Mathieu et al. 2011; Samain et al. 2011). Most of them occur in the Neotropics, and approximately 400 species can be found in Peru (Trelease 1936). Due to its high species number, subgenera were proposed and used for classification, based only on morphology (Miquel 1843; Dahlstedt 1900) until this century, when their phylogeny was clarified using molecular studies (Wanke et al. 2006; Samain et al. 2007; Samain et al. 2009). Finally, Frenzke et al. (2015) published a new infrageneric classification as a reference for studies in the genus, based on fruit characters, macroscopic features, and molecular data, defining 14 monophyletic groups, and describing 5 new subgenera. Peru hosts representatives of all subgenera (Frenzke et al. 2015), and it also has the highest diversity of species in the world (Ulloa et al. 2017), many of which are still not described, whereas a considerable number of the currently accepted species are possible synonyms (unpublished results of the first author).

While some of the subgenera are highly diverse and widely distributed (e.g., *Micropiper* (Miq.) Miq., *Leptorhynchum* (Dahlst.) Trel. ex Samain, *Pseudocupula* Frenzke & Scheiris), others are small and restricted to the Neotropics, and even to some Andean countries (Colombia, Ecuador, Peru, and Bolivia) (e.g., *Perlucida* Scheiris & Frenzke, *Phyllobryon* (Miq.) Scheiris & Frenzke). Among these small groups, two of them were split from the former subgenus *Panicularia* sensu Dahlstedt, into two well-supported clades that are well characterized by morphological features. (*Panicularia* Miq. and *Fenestratae* Pino) with most of their species adapted to seasonal dry periods through succulence and circumscribed to Peru and Ecuador (Pino et al. 2020). Due to the lack of information, many species of these two groups need to be reviewed and new species are to be described. In the quest for these novelties, we explored the Saña River Valley, in the north of Peru, where we found many taxa together in a small area, that was not known to be diverse for *Peperomia*. Therefore, the objective of the present paper is to review the species of *Peperomia* present in the Saña River Valley, Peru, as a sample of the high diversity of this species existing in the country.

Materials and methods

Study area

The Saña (also spelled Zaña) River is a short course (ca. 125 km length) river on the western slopes of the northern Peruvian Andes, with two main tributaries: Udima River and Nanchoc River. Altogether they make up a total drainage area of 1754.7 m^2 (ANA 2010). The river rises in the district Calquis, province San Miguel, department Cajamarca, at approximately 3200 m elevation (ANA 1999), notoriously lower than similar rivers draining the Pacific Ocean basin.

After crossing the districts of Calquis and La Florida in the province of San Miguel and the district of Catache in the province of Santa Cruz (both provinces of the Cajamarca department), it enters the Oyotún district of the province of Chiclayo, Lambayeque department, after which it crosses the districts Nueva Arica, Cayaltí, Zaña, and Lagunas, as it flows to the sea across the coastal desert of the southernmost part of the Lambayeque department, close to the border with the department of La Libertad (Fig. 1).

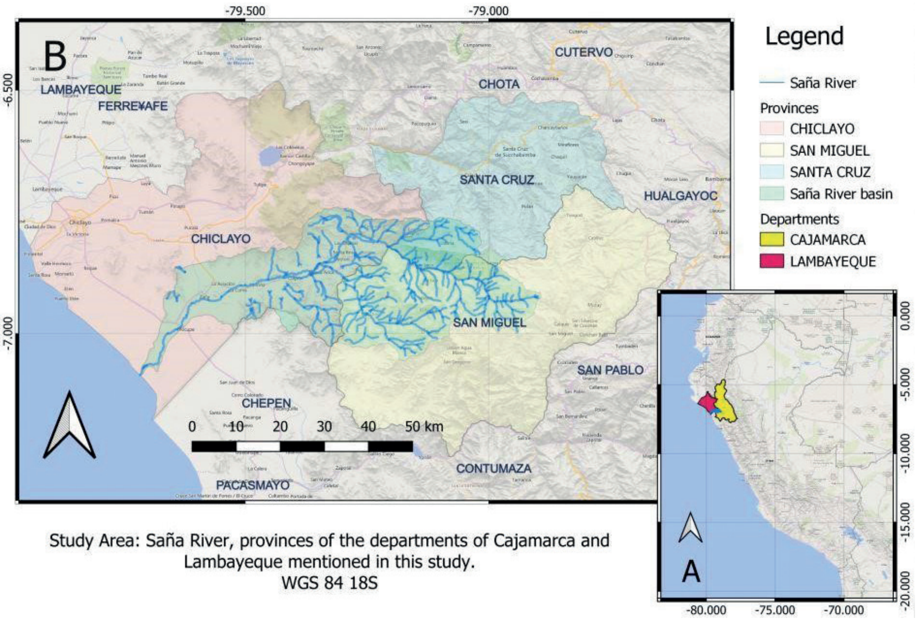

Figure 1. Study area **A** map of Peru and the localization of the departments Lambayeque and Cajamarca **B** close-up to show the Saña River and its basin (light green) shared by the provinces of Chiclayo (Lambayeque), San Miguel, and Santa Cruz (Cajamarca).

Unlike the Chancay-Reque River system located just north and the Jequetepeque River Valley South of it–both with typical coastal desertic valleys–the Saña River Valley is more humid on average, due to the influence of the Amotape-Huancabamba Zone (AHZ) (observation of the first author). This zone has been proposed as a biodiversity hotspot for its higher diversity levels more than adjacent zones (Weigend 2002). Its boundaries have been set from Río Jubones and Río Zamora systems in Ecuador to the Río Chicama system in Peru (La Libertad). Thus, its influence reaches the highlands of Lambayeque and particularly the Saña River Valley, where the humid forests on the western slopes of the Andes can only be explained by the relatively low elevation of the Andes in the AHZ, which allows the flow of moisture from the rainforests of the Amazon Basin on the east to the desert coasts of western Peru. Plants and animals typical of the Amazon Forest e.g. military macaws (*Ara militaris* L.) were reported here at the highest altitudes of the Saña River Valley (Taulis) before the anthropogenic deforestation of recent decades, (Koepcke 1961). Native forests of its middle elevations have been displaced by cultivated patches of the tropical bamboo *Guadua angustifolia* Kunth (Caña Guayaquil) which is extensively cultivated in northern Peru, but not in the adjacent valleys.

From the coast to the Andes, close to the riverbanks of the Saña River, from west to east, we find the localities of Lagunas, Mocupe, Zaña, Cayaltí, La Viña, Culpón, and Nueva Arica. After a detour of the road to the town of Nanchoc in the South, the river flows northwards to the town of Oyotún and Pan de Azúcar, turning later southeastward to El Espinal and La Florida, where a detour to the South moves the road away from the river to El Naranjo and Niepos. Beyond Nanchoc, there is a small relict forest called “La Oscurana” after the town of Bolívar, with four species of *Peperomia* reported, although only one was found in the Herbaria (Juárez et al. 2005). From La Florida, another small road continues east and then southwards along the Saña River leading to the former Taulis Estate, now a hamlet and no longer a cloud forest due to intense cultivation. From El Espinal on a short walk northwards, we find the Velo de Novia waterfall. Before reaching La Florida, after the bridge El Papayo over the Saña River, a detour to the northeast leads to the town of Monteseco, a former estate located south of a relict forest. From here, a trail leads to El Chorro Blanco waterfall and the former Udima Estate crossing the forest. River Udima, a northeastern affluent of Saña River, crosses the forest from east to west and flows into it at El Espinal.

The fauna and flora of the remaining forest North of Monteseco have been published by Cadle (1989), Cadle and McDiarmid (1990), and Sagástegui and Dillon (1991). The latter report 88 families, 200 genera, and over 326 species of ferns and flowering plants, among them nine species of *Peperomia*, in a cloud forest where native trees are covered with mosses, ferns, orchids and vines, and humidity is maintained by multiple streams and a waterfall. The forest has been partially destroyed by logging that occurred until the 1960s, and only patches of natural vegetation are left (Sagástegui and Dillon 1991). The Peruvian government has protected this area since 2010, declaring it as a reserved zone: “Zona Reservada Udima” (El Peruano 2010), and categorizing it as “Zona Reservada Udima en Refugio de Vida Silvestre, Bosques Nublados de Udima” (El Peruano 2011).

From 30 to 500 m elevations, the warm desertic climate with temperatures of up to 35 °C in summer (Clima.com) favors the abundance of cactus steppes intermingled with densely irrigated rice and sugar cane cultivation that almost dry up the river at this altitude. From 500 m upwards, the climate changes abruptly to temperate and humid with an annual average temperature of 18 °C. Most cacti grow below 500 m, but some species reach 1000 m of elevation. The unexpected diversity of species of cacti in such a coastal valley was described first by Mischler (1988) and more recently by Alomía (2020), who mentions 13 taxa: six are endemic to Peru but only the last one in the following list is endemic to the Saña River Valley; *Armatocereus oligogonus* Rauh & Backeb., *Espostoa melanostele* (Vaupel) Borg, *Haageocereus icosagonoides* Rauh & Backeb., *Haageocereus pseudoversicolor* Rauh & Backeb., *Neoraimondia arequipensis* (Backeb.) Buxb. and *Rauhocereus riosaniensis* Backeb. ssp. *riosaniensis*. Other plants adapted to this xerophytic environment are *Bursera graveolens* (Kunth) Triana & Planch, *Mimosa pellita* Kunth. ex Willd, *Rauvolfia tetraphylla* L., *Vachellia aroma* var. *huarango* (Ruiz ex J.F.Macbr.) Seigler & Ebinger and *Vallesia glabra* Link. (Sagástegui and Dillon 1991). From this altitude up to 2500 m, as precipitation increases, dense forests are seen, a combination of dry western Andean forests and eastern montane forests (observation by the first author). During the summer months (December to May), increased rain can cause downstream floods, that occasionally reach the lower basin, such as the one that wiped out the city of Zaña in 1720 (Angulo 2011).

Although the abovementioned studies have identified nine species of *Peperomia* in the relict humid forest north of the town of Monteseco and four species of *Peperomia* in the forest of La Oscurana, so far no research has been carried out for the rest of the valley, especially the drier areas where fewer species are supposed to occur. This study aims to assess the diversity of *Peperomia* species along the whole Saña River valley, adding new reports of already known species and describing new ones.

Plant material

This research was approved by the Bioethics Committee of the Facultad de Ciencias Biológicas de la Universidad Nacional Mayor de San Marcos, document 009-2021-CBE-FCB-UNMSM. Collections were enabled by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) permit numbers 009-2009-AG-DGFFS-DGEFFS, 0124-2011-AG-DGFFS-DGEFFS and authorization n° AUT-IFL-2018-064 issued by RDG N° 491-2018-MINAGRI-SERFOR-DGGSPFFS extended by RD N° D000170-2021-MIDAGRI-SERFOR-DGGSPFFS-DGSPF. Fieldwork was carried out by the teams of the Ghent University Botanical Garden (Belgium) and the Technische Universität Dresden (Germany) in 2009, and later by the Museo de Historia Natural – Universidad Nacional Mayor de San Marcos in the years 2020–2022, along the Saña River Valley starting from Zaña city up to Niepos, including the departments of Lambayeque (prov. Chiclayo) and Cajamarca (prov. San Miguel, La Florida, and Santa Cruz). No collections were made in the protected zone of Udima.

Field observations were complemented with the study of herbarium specimens of ten herbaria: F, GB, HAO, HLL, HUA, HUT, NY, UC, US, and USM, checking the types online. (acronyms following Thiers 2022). A total of 81 collections were included, of which 48 were made by the authors.

Photographs with either Sony DSC-HX400V or Olympus TG-6 cameras were taken of plants in habitat and plants *ex-situ* (vegetative, reproductive, and young plants). Flowers and seeds were photographed either with macro lenses, OPPO Reno-7, or stereomicroscopes. Measurements were taken from fresh plants, photographs, and dry herbarium specimens. Whenever possible, three or more measurements per structure. Floral organ measurements were based on photographs using ImageJ 1.53t. Colors were based on photographs of living plants and notes on herbarium labels.

All localities were georeferenced using GPS coordinates (https://www.gps-coordinates.net/) and Google Maps. For herbarium specimens without coordinates, approximate coordinates were calculated using Google Earth. Maps of distribution were drawn using the same set of coordinates using QGIS v.3.26 Buenos Aires (Official website QGIS: https://www.qgis.org/en/site/).

Finally, the subgenus to which each species belongs is mentioned according to the infrageneric classification of the genus *Peperomia* by Frenzke et al. (2015), who assigned all species described until then to their respective subgenus based on morphological and/or molecular data. The subgeneric placement of the new species described in this paper was defined based on morphological characters.

Results

Taxonomy

The present study found 81 accessions of 16 different taxa of *Peperomia* in the Saña River Valley (Fig. 2). We here present an identification key for these taxa. *Peperomia crystallina*, *P. hispiduliformis*, and *P. hartwegiana* are included in the key due to the high probability of occurrence in the region. Characteristics of the species were taken from the present study as well as Pino (2004), Scheiris (2013), Steyermark (1984), and Trelease and Yuncker (1950).

Key to the species of *Peperomia* from the Saña River Valley

1 Leaves papyraceous, stems friable, hispid, and transparent **2**

– Leaves succulent or semi-succulent, stems firm, opaque **4**

2 Stems erect, trichotomously branched, spadices in zigzag-shape, seemingly sessile on leaves, fruits verrucose.......... ***Peperomia crystallina* Ruiz & Pav.**

– Stems shortly erect, then subdecumbent, spadices straight, originating from upper leaf axils, hispid fruits **3**

3 Branches inserted at less than 45°, leaves ovate-orbicular, apex and base obtuse, venation pinnate........................ ***Peperomia hispidula* (Sw.) A. Dietr.**

– Branches inserted at 45–90°, leaves cordiform, apex round to obtuse, base cordate, venation palmate .... ***Peperomia hispiduliformis* Trel.**

4 Lower leaves in basal rosette, cordate, only reproductive stem growing upwards .... ***Peperomia fraseri* C. DC.**

– Lower leaves not in a basal rosette, leaves growing along a long stem **5**

5 Leaves alternate...**6**

– Leaves opposite or whorled **14**

6 Leaves vertically compressed, very succulent, adaxial size reduced, epidermis covering the internal hydrenchyma, and exposing the photosynthetic chlorenchymatous tissues to solar irradiance through the abaxial surface either directly or by reflection from the ground. (fenestra), inflorescence a panicle **7**

– Leaves not vertically compressed, adaxial size similar to abaxial side in size, succulent, semi-succulent or chartaceous **8**

7 Leaves oval elliptic, papillated surface, gray-glaucous to reddish dull green ... .***Peperomia cymbifolia* Pino.**

– Leaves dolabriform, smooth surface, light green to glaucous ....***Peperomia dolabriformis* Kunth.**

8 Leaves succulent, spirally crowded at the distal end, stem erect, succulent, inflorescence a panicle..***Peperomia riosaniensis* Hutchison ex Pino, Samain & L.E. Alomía, sp. nov.**

– Leaves semi-succulent or chartaceous, all along the stem, inflorescence simple, geminated or loosely flowered **9**

9 Stems many-branched distally and horizontally, plants densely pubescent............ ***Peperomia sagasteguii* Pino, Samain & L.E. Alomía, sp. nov.**

– Stems branching basally and at different angles, glabrous or puberulous.......**10**

10 Leaves distichous, stem winged ....***Peperomia vivipara* Pino, Samain & L.E. Alomía, sp. nov.**

– Leaves spirally attached **11**

– Leaves opposite or whorled **15**

11 Leaf base cordate, subpeltate, stem succulent, tortuous, inflorescence a panicle of clusters of spadices .... ***Peperomia symmankii* Pino & Samain, sp. nov.**

– Leaf base cuneate, lamina elliptical to ovate or obovate, seeds sticky **12**

12 Leaves with round, truncate, or emarginate apex... ....***Peperomia haematolepis* Trel.**

– Leaves with acute, obtuse to attenuate apex **13**

13 Stems erect, short, quadrangular in section, leaves elliptic-obovate, spadices white, terminal in umbels of 3, whitish, 8–12 cm long ....***Peperomia emarginulata* C. DC.**

– Stems trailing, long, terete, leaves elliptic ovate or obovate, spadix terminal simple, reddish or reddish green...**14**

14 Stems without wings, leaves ovate, acute to acuminate, succulent, canaliculated...***Peperomia cacaophila*** **Trel. & Yunck.**

– Stems with two small wings, leaves widely obovate,, apex obtuse, semisucculent, flat ....***Peperomia pilocarpa*** **Pino, Samain & L.E. Alomía, sp. nov.**

15 Leaves chartaceous, opposite or decussate, strongly pubescent leaves and stems ....***Peperomia rotundata*** **Kunth**

– Leaves succulent, verticillate, glabrous to puberulous...............................**16**

16 Leaves orbicular to oval, inflorescence terminal simple, red.......................... .... ***Peperomia hartwegiana*** **Miq.**

– Leaves narrow elliptical to obovate, inflorescences yellow or green **17**

17 Whorls of 4–5 leaves, small (usually less than 1 cm long), all homogeneous in size and thickness, inflorescence simple, terminal.. ....***Peperomia microphylla*** **Kunth**

– Whorls of 6–8 leaves, juvenile and mature leaves of different size and thickness, inflorescences in terminal umbellas and axillary from distal nodes...............**18**

18 Plants large (25–50 cm tall), stems 1.2–4.5 mm diam., basal leaves 6–12 mm long, terrestrial or lithophytic, above 2200 m.................................... ....***Peperomia galioides*** **Kunth**

– Plants small (10–24 cm tall), stems 3.5–8 mm diam., basal leaves 4–7 mm long, epiphytical, below 2000 m.............***Peperomia inaequalifolia*** **R. & P.**

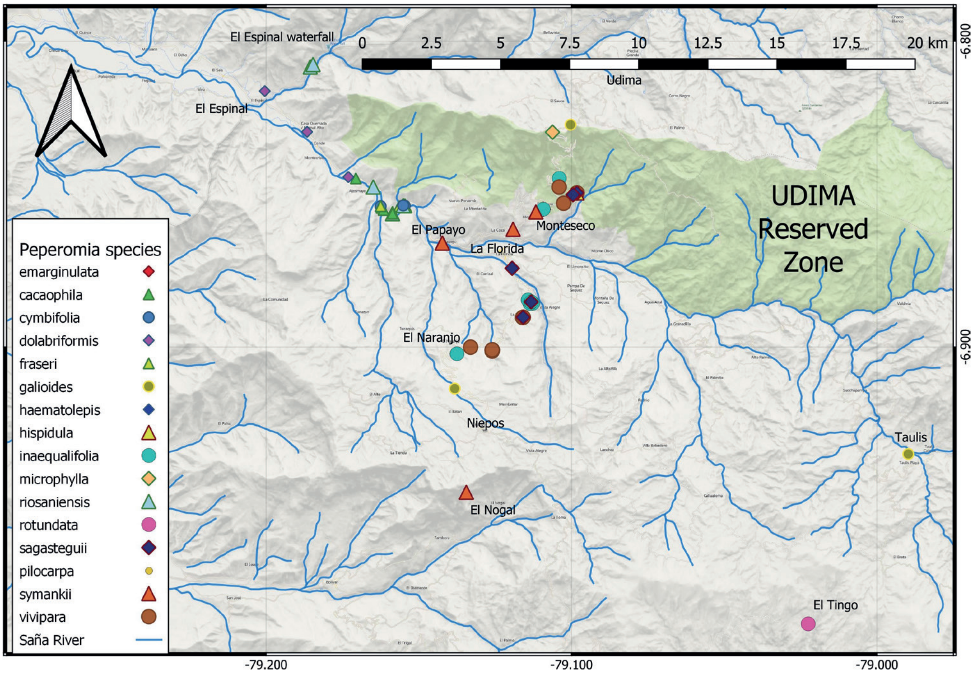

Figure 2. Distribution of the *Peperomia* species in the study area. Udima reserved zone in green shadow.

1. ***Peperomia cacaophila*** **Trel. & Yunck., Piperac. N. South Amer. 2(610). 1950.**
Fig. 3A–F

Type. Ecuador, prov. Los Ríos, cant. Quevedo, roadside at Quevedo, common at Cacao groves, *Haught 2966* (holotype: US 1707621!, isotype: ILL).

Distribution and habitat. Plants were known only from central Ecuador, prov. Los Ríos, Guayas, Esmeralda, and Pichincha, epiphyte on *Theobroma* or similar trees, in shaded warm forests from 200–1500 m. This is the first report for Peru.

Notes. The closest species we could compare to is *P. topoensis* Yunck., also from Ecuador, which is similar in its epiphytic, pendent, or assurgent habit with small, succulent, alternate ovate leaves, cordulate at the base and 7-plinerved, compared to the obtuse, subtruncate based and noticeable 3-nerved leaves of *P. cacaophila*. *Peperomia nitida* Dahlst. from Brazil, São Paulo (Campinas), a widely cultivated species, is similar but with larger, light green cordulate-based leaves, only stems slightly reddish. *Peperomia portobellensis* Beurl. from Panama is also similar in shape but with slightly larger leaves. No material other than the types of these species was available for further comparison.

This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

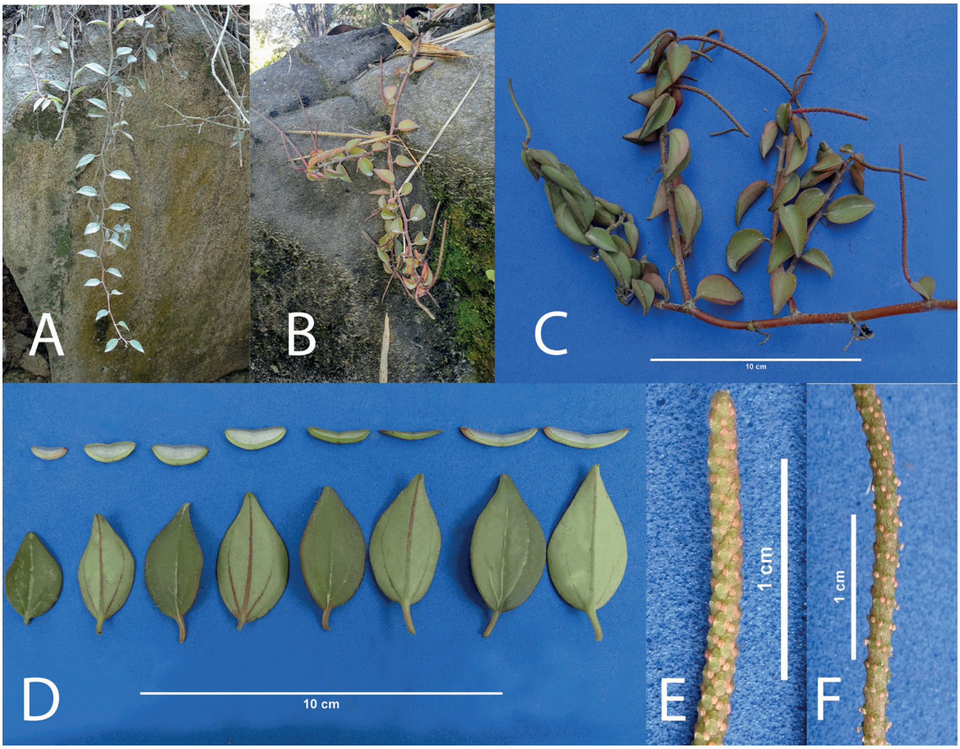

Figure 3. *Peperomia cacaophila* Trel. & Yunck **A** young plant hanging from a rock **B** long, trailing plant with distal inflorescence **C** plant *ex-situ* with several branches **D** detail of the leaves **E** spadix at the beginning of anthesis **F** mature spadix.

Specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Road to Hacienda Taulis, ca. 60 km east of Cayaltí on the Río Saña. 560 m, [06°50'41.5"S, 79°10'14.2"W], 28 Aug 1964, *P. C. Hutchison 6323* (UC, US, F 1642092, USM 16451); Road from El Espinal to La Florida, 550 m, 06°51'23.0"S, 79°09'31.0"W, Jul 26 2020, *G. Pino & L.E. Alomía 3234* (USM); Same road, 527 m, 06°51'16"S, 79°09'44"W, 28 Aug 2022, *G. Pino et al. 3625* (USM 330878); idem, 536 m, 06°51'18.6"S, 79°09'41.6"W, 28 Aug 2022, *G. Pino et al. 3630* (USM 330879).

2. *Peperomia cymbifolia* Pino, Pino, Peperomias de Cajamarca: 16–17, 50–51 f. 3 A–N. 2004.

Fig. 4A–F

Type. PERU, dept. Cajamarca, prov. San Pablo, dist. San Pablo, the road to Chilete, 2080 m, 14 May 1964, *P.C. Hutchison & J. K. Wright 5076* (holotype: UC 301913!, isotype: USM 16457!).

Distribution and habitat. Montane scrubs of the department of Cajamarca (Prov. San Pablo, Contumazá, Cajamarca, Chota, and San Marcos) between 1800 to 2800 m.

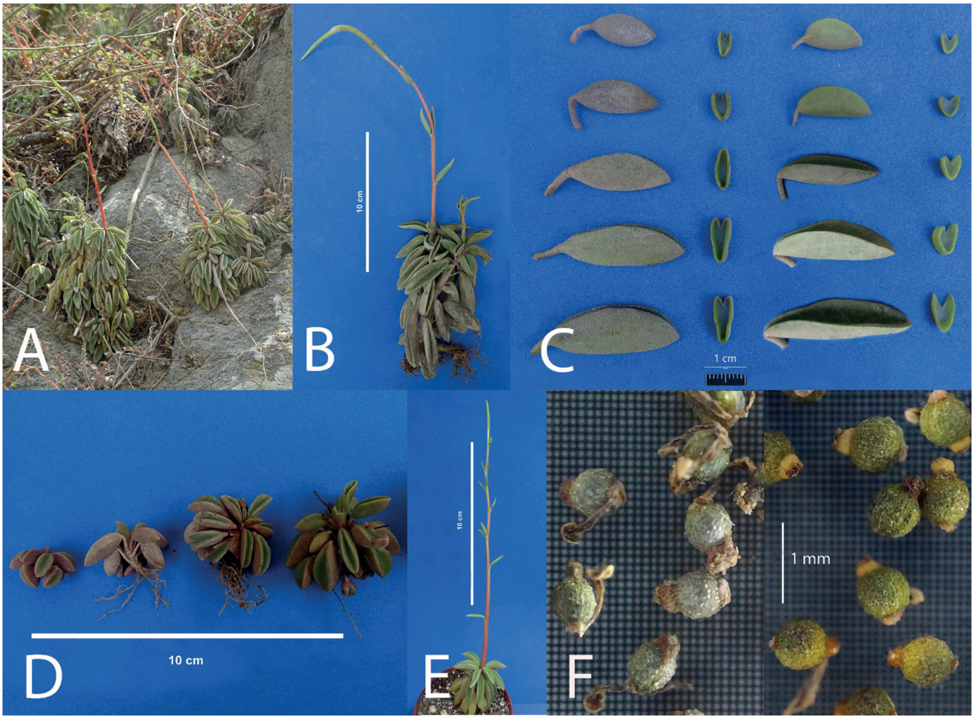

Figure 4. *Peperomia cymbifolia* Pino var. *occidentalis* Pino & L.E. Alomía var. nov. **A** plant in habitat **B** plant *ex situ* **C** comparison of the leaves of *P. cymbifolia* var. *cymbifolia* (left) and var. *occidentalis* (right) **D** young plants showing development **E** cultivated plant showing inflorescence **F** seeds of *P. cymbifolia* var. *cymbifolia* (right) and var. *occidentalis* (left).

Table 1. Comparison of the main differences between *P. cymbifolia* var. *cymbifolia* and var. *occidentalis* (Data from var. *cymbifolia* taken from Pino (2004), and from live plants).

Features	*P. cymbifolia* var. *cymbifolia*	*P. cymbifolia* var. *occidentalis*
Height (vegetative) in cm	10–20	5–15
Leaf (shape)	Adaxial side slightly canaliculate, Abaxial side convex.	Adaxial side strongly canaliculate, Abaxial side straight to slightly convex.
	Lateral faces flat to slightly convex or concave.	Lateral faces more constantly convex.
Leaf (length in cm)	(1.6–) 2.2–3.4	(1.4–) 1.9–4
Leaf (vertical height of lateral sides in mm)	9–13, flat to concave, nerves conspicuous	7–10, flat to convex, nerves obscure
Rachis of the spadix (length in cm)	(2–)3.8–6	7–15
Fruit (shape/color)	Globose, yellowish-green to brown	Ovoid to ellipsoid, light olive green
Fruit (length in mm)	0.7–0.8	0.6–0.8
Fruit (diam. in mm)	0.6–0.7	0.45–0.55
Fruit (stylopodium)	Broad conical, light brown,	Broad cylindrical, light brown – orangish,
	0.1–0.2 mm long,	0.2–0.25 mm long,
	0.2–0.3 mm diam.	0.2–0.35 mm diam.
Altitude range (m)	1800–2800	500–600

Notes. The samples collected were determined as *P. cymbifolia* (Pino 2004) However, comparing the plants of the Saña River Valley and the plants from the type locality we found some differences summarized in Table 1. These differences do not support the description of a new species but are sufficient to describe a new variety of this species. Moreover, while previous collections grow from 1800 to 2800 m in colder and moister places, this variety seems to be adapted to low altitudes of 500 to 600 m with higher temperatures and drier periods. It is easy to cultivate outdoors in the city of Lima, quite different from var. *cymbifolia*, which requires a cool greenhouse. This species belongs to *Peperomia* subg. *Fenestratae* Pino (Frenzke et al. 2015).

Peperomia cymbifolia Pino var. *occidentalis* Pino & L.E.Alomía, var. nov.

urn:lsid:ipni.org:names:77317651-1

Diagnosis. *Peperomia cymbifolia* var. *occidentalis* differs from the type variety mainly in size, plants are smaller and more compact; Leaves are slightly longer (4 cm maximum compared to 3.6 cm long), their lateral faces are not as high (7–10 mm compared to 9–13 mm), and they are more constantly convex than concave, its abaxial side is less convex, sometimes even straight; Its fruits are smaller and narrower, (0.6–0.8 × 0.45–0.55 mm compared to the 0.7–0.8 × 0.6–0.7 mm), light olive green instead of yellowish green, and with a relatively larger stylopodium. Populations of this variety are not only separated geographically from the type variety but mostly by altitude and climate: they grow 1200 m below the lowest occurrence of the type variety, at least 10 °Celsius warmer. The epithet reminds the localization of this variety, the most occidental of all three varieties of *P. cymbifolia*. (*P. cymbifolia* var. *cymbifolia*, var. *goodspeedii*, and var. *occidentalis*).

Type. **Peru**, dept. Cajamarca, prov. Santa Cruz, dist. Catache: road from Espinal to La Florida, 521 m, 06°51'14.2"S, 79°09'45"W, 28 Aug 2022, *G. Pino & L.E. Alomía 3634* (holotype: USM 330881!).

Distribution and habitat. Plants grow from 450 to 600 m, on exposed rock crevices facing southwards between the towns of El Espinal and La Florida in Department Cajamarca, province of Santa Cruz. A similar collection, very likely the same taxon, was found in Chota at 750 m, exactly 20 km to the North of the Saña River Valley in a straight line.

Phenology. Inflorescences appear from June to February; fruits ripen from October to March.

Additional specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Road from El Espinal to La Florida, 582 m, 06°51'13.7"S, 79°09'16.5"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3232* (USM 330872); Same road, 591 m, 06°51'13.4"S, 79°09'18.4"W, 28 Aug 2022, *G. Pino et al. 3638* (USM 330883). **Prov. Chota, dist. Chimbán**, Road from Cumbil to Llama, [between Potrerillo and Maychil], border of the road, on rocks, 750 m, [06°31'56"S, 79°11'51"W], 21 May 1965, *A. López & A. Sagástegui s/n* (HUT 5520). **Dept. Lambayeque, prov. Ferreñafe, dist. Incahuasi**: Before Laquipampa, 721 m, 06°20'31.5"S, 79°26'41"W, 08 Mar 2023, *G. Pino & J.E. Romero 3840* (USM).

3. *Peperomia dolabriformis* Kunth, Nov. Gen & Sp. [Humboldt] 1: 50, tab. 4. 1815.

Fig. 5A

Piper dolabriforme Poir., Lam. Encycl. Meth. Suppl. 4: 464. 1816. Type: Based on *Peperomia dolabriformis* Kunth.

Type. **Peru**, dept. Piura, prov. Huancabamba: "in Peruviae calidis, ad ripas flumini Guancabamba" [in the warmth of Peru, on the banks of the Huancabamba River], *Humboldt s/n* (holotype: B [lost?], isotype P!).

Distribution and habitat. Warm valleys of the Western slopes of the Andes of departments Lambayeque, La Libertad, and Cajamarca. Huancabamba, Marañón and Crisnejas Valleys in departments Piura, Cajamarca, Amazonas, La Libertad and Ancash (Sihuas) in Peru. In Ecuador, it occurs in the provinces of Loja and Zamora-Chinchipe.

Note. This species belongs to *Peperomia* subg. *Fenestratae* Pino (Frenzke et al. 2015).

Specimens examined. Peru, dept. Lambayeque, prov. Chiclayo, dist. Oyotún: Canyon above Chiclayo near Mocupa [Mocupe, 391 m, 06°48'58.7"S, 79°12'01.6"W], Johnson Cactus Garden, prepared at the BG of the University of California at Berkeley, accession 52.498, 24 Sep 1958, *Larrabie s/n* (F1567768, NY, UC088167, US2301205) **Dept. Cajamarca, prov. Santa Cruz, dist. Catache:** road from Oyotún to El Espinal, 397 m, 06°49'46.7"S, 79°11'11.7"W, 28 Aug 2022, *G. Pino & L.E. Alomía 3613* (USM 330874); same road, 440 m, 06°50'39.9"S, 79°10'23.1"W, 28 Aug 2022, *G. Pino & L.E. Alomía 3621* (USM 330875).

4. ***Peperomia emarginulata*** **C.DC. DC. Prodr. 185. 16(1): 433. 1869.**
Fig. 6A–F

Type. Peru, dept. [Huánuco], Casapí, In Peruvia, sylvis Andium occident. [In Perú, western Andes forests], *Mathews 1687* (lectotype: K, designated by Mathieu and Callejas (2006: 351; isolectotype: E, K!)).

Distribution and habitat. Plants are reported from Ecuador and Peru, in montane forests from 300 to 1500 m.

Notes. We compared the three species with features closer to our findings (Table 2) The plants we found are in the range of all three, but according to this table, it matches *P. emarginulata*. *Peperomia angularis* and *Peperomia caucana* from Colombia should be reviewed in the future to prove if they are conspecific with *P. emarginulata*. *Peperomia garcia-barrigana* Trel. & Yunck. and *P. gabinetensis* Trel. & Yunck. also show similarities that deserve further analysis, being mostly different in size. Some specimens in herbaria were also determined as *P. glabella* (Sw.) A. Dietr., a widely distributed species, very close to this group, that is relatively small.

This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimens examined. Peru. Dept. Cajamarca, prov. Santa Cruz, dist. Catache: El Papayo, El Espinal, Monteseco, 600 m, [06°51'31.7"S, 79°06'46.8"W], 18 Jul 1984, *A. Sagástegui*, *E. García & S. Leyva 12354* (HUT, F 1960604, MO 3226489); Monteseco, 3 km NE, 1800 m, [06°50'42.3"S, 79°06'17.1"W], 5 May 1987, *J. Santisteban C. & J. Guevara B. 013* (HUT, F 1994832). Same place: 13 May 1987, *J. Santisteban C. & J. Guevara B. 055* (HUT 24750, F 1995336). Path in Monteseco Forest, 1350 m. [06°51'17.8"S, 79°06'33.3"W], 10 Oct 1993, *S. Leiva et al. 911* (HAO, F 2142594); Road from Cayaltí to La Florida, 549 m, 06°51'23.2"S, 79°09'31.1"W, 1 Mar 2009, *G.Mathieu & L. Symmank 161* (USM 255771); Road from El Espinal to La Florida, 519 m, 06°51'13.5"S, 79°09'45"W, 28 Aug 2022, *G. Pino et al. 3623* (USM 330876); Same road, 527 m, 06°51'16"S, 79°09'44"W, 28 Aug 2022, *G. Pino et al.* 3627 (USM 330877); Idem, 536 m, 06°51'18.6"S, 79°09'41.6"W, 28 Aug 2022, *G. Pino et al. 3632* (USM 330880); **Prov. San Miguel, dist. Niepos:** Road from Naranjo to La Florida, 1316 m, 06°53'08.6"S, 79°06'45.8"W, Jul 26 2020, *G. Pino & L.E. Alomía 3218* (USM 330868); Same road, 1291, 06°53'08.7"S, 79°06'49.1"W, Jul 26 2020, *G. Pino & L.E. Alomía 3219*; Same road, 1265 m, 06°53'04.6"S, 79°06'51.2"W, Jul 26 2020, *G. Pino & L.E. Alomía 3220*; Idem, 1213 m, 06°52'54.2"S, 79°06'51.9"W, Jul 26 2020, *G. Pino & L.E. Alomía 3221*; Idem, 1210 m, 06°52'53.6"S, 79°06'51.0"W, Jul 26 2020, *G. Pino & L.E. Alomía 3222*; Idem, 1176 m, 06°52'49.2"S, 79°06'52.5"W, Jul 26 2020, *G. Pino & L.E. Alomía 3223*; Idem, 1130 m, 06°52'44.1"S, 79°07'00.0"W, Jul 26 2020, *G. Pino & L.E. Alomía 3224*; Idem, 1118 m, 06°52'42.0"S, 79°07'01.1"W, Jul 26 2020, *G. Pino & L.E. Alomía 3225*; Idem, 1067 m, 06°52'32.9"S, 79°07'10.4"W, Jul 26 2020, *G. Pino & L.E. Alomía 3226*; Road from La Florida to Niepos, 1297 m, 06°53'6.9"S, 79°06'47.6"W, 28 Aug 2022, *G. Pino et al. 3642* (USM 330885).

Table 2. Comparison of some features of the descriptions of *P. angularis*, *P. emarginulata*, and *P. caucana* with the specimens of *P. emarginulata* studied. All data according to Trelease and Yuncker (1950), complemented with Steyermark (1984) for *P. angularis* and Trelease (1936) for *P. emarginulata*.

Features	***P. emarginulata* of Saña River Valley**	***P. angularis***	***P. emarginulata***	***P. caucana***
Height in cm	15–45	25 or more	30 or more	15 or more
Stem (diam. in mm)	3–5	1–3	4–5	2
Internodes in cm	1.5–4	1–3	1–3	1–3
Petiole (length in mm)	5–15	5–10 (–22)	5–15	5–10
Leaf (shape)	Elliptic -obovate, lanceolate, subrhomboidal.	Elliptic, elliptic-oblanceolate or obovate.	Elliptic-lanceolate or obovate, somewhat rhomboidal.	Elliptic-obovate.
Leaf (apex)	Acute to shortly acuminate, emarginulate.	Protracted, blunt or acutish.	Shortly acute to attenuately acuminate, blunt and emarginulate.	Shortly attenuate, blunt or acutish.
Leaf (length in cm)	3.5–6	2–6 (–9)	3–6 (–11)	4–6.5
Leaf (width in cm)	2.5–4	1–2.5	2.5–4.5	2–3.5
Peduncle (length in cm)	1–2	1.4–2 (–4.5)	0.5–1	2–3
Spadix (length in cm)	8–12	5–7 (–10.5)	–12	5–7

Figure 5. *Peperomia* species that can be found in the Saña River Valley **A** *P. dolabriformis* **B** *P. fraseri* **C** *P. galioides* **D** *P. haematolepis* **E** *P.hispidula* **F** *P.inaequalifolia* **G** *P. microphylla* **H** *P. rotundata.*

5. ***Peperomia fraseri*** **C.DC., J. Bot. 4: 134. 1866.**

Fig. 5B

Peperomia rugosa Tafalla. Flora Huayaquilensis 1:12. 1989, nom. ined.

Peperomia resediflora Linden & André, Ill. Hort. 17: 135–137. fig. 26. 1870. [As resedaeflora] Type: (iconotype): Illustr. Hortic. 17: fig. 26.

Peperomia fraseri var. *resedaeflora* C.DC., Bull. Herb. Boissier 5: 703. 1897.Type: Based on *Peperomia resediflora* Linden & André.

Peperomia fraseri var. *peltata* Yunck., Piperac. N. South Amer. 2: 740. 1950. Type: Ecuador, Loja, Horta-Naque, *Espinosa 859* (holotype: ILL, isotype: NY).

Peperomia treleasei Standl. & Steyerm., Fieldiana, Bot. 24(3): 273. 1952. Type: Guatemala (cultivated), *Steyermark 46298* (holotype: F).

Peperomia fraseri var. *guayasana* Trel., nom. herb. [Mathieu (2007)]. Type: Ecuador, Guayas, *Haught 3022* (holotype: US).

Type. **ECUADOR**, sine loco: Fraser s/n, (lectotype, designated by Mathieu and Callejas (2006: 351–352: G-DC!, isotypes: BM, G-DC)).

Distribution and habitat. Ecuador (120–2100 m, prov. Loja, El Oro, Guayas, Chimborazo and Manabí). Peru, 500–1600 m in departments Tumbes, Piura, Lambayeque, and eastern Cajamarca along the Saña River valley, on rocky soil, shaded by trees and shrubs. This is the southernmost location of this species.

Specimens examined. PERU, dept. Lambayeque, prov. Chiclayo, dist. Oyotún: road from Oyotún to El Espinal, 515 m, 06°48'30.3"S, 79°11'08"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3236* (USM 325348); **Dept. Cajamarca, prov. Santa Cruz, dist. Catache:** road from Cayaltí to La Florida, 8.4 km from La Florida, 497 m, 06°50'51.6"S, 79°09'53.7"W, 1 Mar 2009, *G.Mathieu & L. Symmank 160* (USM 255770); road from Espinal to La Florida, 521 m, 06°51'14.2"S, 79°09'45"W, 28 Aug 2022, *G. Pino et al. 3636*; Same road, 527 m, 06°51'16"S, 79°09'44"W, 28 Aug 2022, *G. Pino et al. 3626*. Same road, 570 m, 06°51'14.1"S, 79°09'23.1"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3231* (USM 325349).

Note. This species belongs to *Peperomia* subg. *Panicularia* Miq. (Frenzke et al. 2015).

6. ***Peperomia galioides*** **Kunth, Nov. Gen & Sp. [Humboldt] 1: 58, tab. 17. 1815.**

Fig. 5C

Piper galioides Poir., Lam. Encycl. Meth. 4: Suppl. 4: 470. 1816. Type: Based on *Peperomia galioides* Kunth.

Peperomia suaveolens Hamilton, Prodr. Pl. Ind. Occ.:2. 1825. Type: Cuba, (holotype: P- Herbarium Desvaux?).

Piper mollugo Willd. [Miquel] 1843. Type: Based on *Peperomia galioides* Kunth.

Peperomia jamesoni Regel, Bull. Soc. Nat. Moscou 31: 544. 1858. Type: Ecuador, *Jameson 814* (holotype: G [not designated], isotypes: K, TCD).

Peperomia agapatensis C.DC., Prodromus 16: 455. 1869. Type: Perú, Junín, Agapata, *Lechler 1934* (holotype: G-DC; isotypes: G, GOET, K, MO, P, UPS, W).

Peperomia galioides Kunth var. *longifolia* C.DC., Prodromus 16 (1): 464. 1869. Type: Bolivia, *Mandon 1120* (syntypes: G-DC, B).

Peperomia galioides Kunth var. *menkeana* (Miq) C.DC., Prodromus 16 (1): 464. 1869. Type: Brazil, *Menke 125* (holotype: BR).

Peperomia galioides Kunth var. *nigro-punctulata* C.DC., Prodromus 16 (1): 464. 1869. Type: Brazil, Wawra 441, Ecuador, *Jameson s.n.* (syntype: K).

Peperomia galioides Kunth var. *aprica* Henschen. Nov. Act. Soc. Sci. Upsal. ser.3,8(2): 37. 1873. Type: Brazil, Minas Gerais, Caldas (Holotype: not designated).

Peperomia galioides Kunth var. *umbrosa* Henschen, Nov. Act. Soc. Sci. Upsal. ser.3,8(2):37. 1873. Type: Brazil, Minas Gerais, Caldas (Holotype: not designated).

Peperomia subcorymbosa Sodiro, Contrib. al Conoc. Fl. Ecuador. Monogr. 1 ed. 2:181. 1901. Type: Ecuador, Quito, El Alacatzo, *Sodiro s.n.* (holotype: Q, isotypes: G-DC, QPLS).

Peperomia galioides Kunth var. *saxicola* C.DC., Bull. Her. Boissier ser. 2,1: 360. 1901. Type: Brazil, *Schwacke 10279* (holotype: G).

Peperomia anisophylla C.DC., Bot. Jahrb. 40: 266. 1908. Type: Perú, Lima, Matucana, *Weberbauer 72* (holotype: B, isotype: G).

Peperomia galioides var. *aromatica* C.DC., Bot. Jahrb. Syst. 40: 266. 1908. Type: Peru. Ancash, Caraz. *Weberbauer 3227* (holotype: B [lost?]; isotype: G-DC).

Peperomia galioides Kunth var. *minutifolia* C.DC. Ann. Cons. Jard. Bot. Gen. 21: 262. 1920. Type: Ecuador, Quito, Nanegal, *Sodiro 2/52* (holotype: G-DC).

Peperomia granata Trel., Fedde Rep. Sp. Nov. 23: 24. 1926. Type: Cuba, Pico Turquino, *Ekman 14590* (lectotype: ILL [designated by Saralegui (2004)]; isolectotype: S).

Peperomia galiifolia Trel., Mem.N.Y. Bot.Gard. 7: 227. 1927. Type: Bolivia, La Paz, Pongo de Quime, *White 166* (holotype: NY).

Peperomia okarana Trel., Bull. Bot. Club. 55: 170. 1928. Type: Bolivia, La Paz, Larecaja, Okara, *Tate 970* (holotype: NY).

Peperomia artatiflora Trel., Flora of Peru [Macbride] 13(2): 23. 1936.Type: Perú, Palca, *Stevens 47* (holotype: ILL).

Peperomia brachyiula Trel., Flora of Peru [Macbride] 13(2): 26. 1936. Type: Perú, Lima, Matucana, *Macbride 129* (holotype: F, isotypes: G, ILL).

Peperomia ceapanana Trel., Flora of Peru [Macbride] 13(2): 28. 1936. Type: Perú, Cusco, Paucartambo, *Herrera 1468* (holotype:US).

Peperomia chillonensis Trel., Flora of Peru [Macbride]. 13(2): 30. 1936. Type: Perú, Lima, Canta, Obrajillo. *Pennell 14413* (holotype: F).

Peperomia dendroides Trel., Flora of Peru [Macbride]. 13(2): 38. 1936. Type: Perú, Junín, Chaglla, *Macbride 3640* (holotype: F, isotypes: G, ILL, US).

Peperomia distractiflora Trel., Flora of Peru [Macbride] 13(2): 40. 1936. Type: Perú, Junín, Challhuapuquio, *Stevens 214* (holotype: ILL).

Peperomia longispica Trel., Flora of Peru [Macbride] 13(2): 59. 1936. Type: Perú, Huánuco, Muña, *Macbride 3928* (isotype: BM).

Peperomia sanbuenaventurana Trel., Flora of Peru [Macbride] 13(2): 91. 1936. Type: Perú, Lima, Canta, San Buenaventura. *Pennell 14566* (holotype: PH).

Peperomia trullifolia Trel., Flora of Peru [Macbride] 13(2): 102. 1936. Type: Perú, Cusco, Ollantaytambo, *Cook 401* (holotype: US).

Peperomia inaequalifolia Ruiz & Pav. var. *galioides* (Kunth) Pino, Avonia 28(2): pages 45–49 (f.16–25). 2010. Type: Based on *Peperomia galioides* Kunth.

Type. **Colombia**, dept. Cundinamarca, prov. Tequendama: “Crescit in montanis Regni Novogranatensis, juxta cataractam Tequendamae, alt. 1300 hexap. Floret Augusto” [Grows in mountains of Colombia, close to the Tequendama Waterfall, 2400 m, Flowers in August], *Humboldt s/n*, (isolectotype, designated by Saralegui (2004: 341: B-W [00762])).

Distribution and habitat. Montane forests of Mexico, Central America, Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil, on rocks or terrestrial, always above 2200 m.

Note. This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Udima, herbácea, creciendo sobre piedra, [herb growing on rocks] 2500 m, [06°49'38.3"S, 79°06'01.1"W], 20 May 1987, *J.Santisteban C. & J. Guevara B. 087* (HUT, F1995293). **Prov. San Miguel, dist. Niepos:** Road from La Florida to Niepos, 2240 m, 06°54'49"S, 79°08'17.7"W, 28 Aug 2022, *G. Pino & L.E. Alomía 3647* (USM 330888); Dist. Calquis: Taulis Playa (Agua Blanca) 2650 m, [06°56'06"S, 78°59'23"W], 3 Jul 1986, *J. Mostacero et al. 1143* (HUT 22520, MO).

7. ***Peperomia haematolepis*** **Trel., Field. Mus. Pub. Bot. [Macbride] 13(2):52. 1936.** Fig. 5D

Type. **Peru**, dept. Junín, prov. Chanchamayo, dist. San Ramón: Hacienda Chalhuapuquio, *Stevens 212* (holotype: ILL).

Distribution and habitat. Plants are reported from Brazil, the Guyanas, Venezuela, Colombia, Ecuador, and Peru from 1000 to 2000 m, epiphytic in montane forests shaded by the canopy. Most of the collections in Peru are from the Amazon Basin; this is the first report for a Pacific Ocean draining Andean valley.

Notes. This species belongs to *Peperomia* subg. *Oxyrhynchum* (Dahlst.) Samain (Frenzke et al. 2015).

Specimen examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Upper Río Zaña Valley, ca. 5 km above Monteseco, on the path below the campsite, lower reaches of evergreen tropical montane forest, 1450 m, [06°51'10.8"S, 79°06'09.4"W], 19 Mar 1986, *M.O. Dillon & A. Sagástegui 4425* (US 3338748, F, GB 0167869, HUA 49003).

8. ***Peperomia hispidula*** **(Sw.) A. Dietr., Sp. Pl. 1: 165. 1831.**
Fig. 5E

Piper hispidulum Sw., Prodr. 15. 1788. Type: Jamaica, Swartz s.n. (holotype not designated: S) [Basionym for *Peperomia hispidula* (Sw.) A.Dietr.].

Acrocarpidium hispidulum Miq., Syst. Piperac. 54. 1843 Type: Based on *Piper hispidulum* Sw.

Acrocarpidium sellowianum Miq., Syst. Piperac. 55. 1843 [as 'sellovianum'] Type: Brazil, Brasilia, Sellow s.n. (holotype: B [lost?], lectotype: U [designated Zanotti et al. (2012: 133)], isolectotypes: G, K, W).

Peperomia tenera Miq., Fl. Bras. [Martius] 4(1): 19. 1852. Type: Based on *Acrocarpidium sellowianum* Miq.

Peperomia muscophila C.DC., Journ. Bot. 4: 133. 1866. [as 'muscophylla'] Type: Mexico, Tafalla s.n (holotype: G; isotypes: G-DC).

Peperomia hispidula C.DC., Prodr.16:1:397. 1869. Based on *Piper hispidulum* Sw.

Peperomia hispidula var. *sellowiana* (Miq.) Dahlst. Kongl. Svenska Vetenskapsakad. Handl. 33(2): 14 . 1900. Type: Based on *Acrocarpidium sellowianum* Miq.

Peperomia hispidula var. *swartziana* Dahlst., Kongl. Svenska Vetenskapsakad. Handl. 33(2): 13.1900. Type: Based on *Peperomia hispidula* C.DC.

Peperomia hispidula var. *swartziana* f. *barbensis* Dahlst., Kongl. Svenska Vetenskapsakad. Handl. 33(2): 14 .1900. Type: Costa Rica, Hoffmann 54 (holotype: B [lost?]).

Peperomia perhispidula C.DC., Bot. Jahrb. Syst. 40: 257. 1908). Type: Peru, Huacapistana, Weberbauer 2014 (holotype: B, F G-DC).

Peperomia hispidula var. *muscophila* (C.DC.) C.DC., Candollea 1: 335 .1923. Type: based on *Peperomia muscophila* C.DC.

Peperomia hispidula var. *perhispidula* Trelease & Yuncker, Candollea 1: 335. 1923. Type: Based on *Peperomia perhispidula* C.DC.

Peperomia hispidula var. *ellipticifolia* Trelease & Yuncker, Piper. North. S. Amer. 2: 705. Pl. 626. 1950. Type: Colombia, Suratá, Killip & Smith16580 (holotype: GH; isotypes: ILL, MA, NY, US).

Type. **Jamaica**, In nemorosis humidis montium altissimorum coeruleorum Jamaicae. [In shaded moist elevated forest on Blue Mountains Peak of Jamaica, 2200 m, 18°6'N, 76°40'W], *Swartz s.n.* (holotype not designated: S!)

Distribution and habitat. Terrestrial on humus near water courses, shaded, 1500–3000 m, in evergreen montane forests of West Indies, Mexico, Central America, and South America (except Chile). All the other collections in Peru are from the eastern slopes of the Andes; this is the only report for the western slopes.

Note. This species belongs to *Peperomia* subg. *Hispidula* Frenzke & Scheiris (Frenzke et al. 2015).

Specimen examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Al norte del Chorro Blanco (Monteseco), borde de acequia [North of Chorro Blanco

(Monteseco), border of stream] 1500 m, [06°50'58.6"S, 79°05'53.7"W], 20 Jan 1989, *S. Leyva G. 008* (F 2016256).

9. ***Peperomia inaequalifolia*** **Ruiz & Pav., Flora Peruviana & Chilensis 1: 30, plat. 46 fig.a. 1798.**

Fig. 5F

Piper inaequalifolium Vahl., Enum. Pl. 1: 355. 1804. Type: Based on *Peperomia inaequalifolia* Ruiz & Pav.

Piper aromaticum Willd., Enum. Pl. Hort. Berol. Suppl.: 3. 1813. Type: Not mentioned.

Peperomia chrysotricha Miq., Syst. Pip.:163. 1843. Type: Dombey 933 (holotype: P; isotype: U).

Peperomia parvula Sodiro, Piperac. Ecuator. 1: 139. 1900. Type: Sodiro s/n (Holotype not designated: G, P, Q).

Peperomia fasciculata Sodiro, Contrib. al Conoc. Fl. Ecuador Monog.1 ed. 3: 181. 1901. Type: Based on *Peperomia parvula* Sodiro.

Peperomia galioides Kunth var. *minutifolia* C.DC., Ann. Cons. Jard. Bot. Genève 21: 262. 1920. Type: Ecuador, Valle Nonegal. A. Sodiro 2/52 (holotype: G-DC).

Peperomia atocongona Trel., Publ. Field Mus. Nat. Hist., Bot. Ser. [Macbride J.F.] 13(2): 24. 1936. Type: Peru. Lima: Atocongo. F.W. Pennelll 14752 (holotype: PH).

Peperomia limaensis Trel., Publ. Field Mus. Nat. Hist., Bot. Ser. [Macbride J.F.] 13(2): 58. 1936. Type: Peru. Lima: San Gerónimo. J.F.Macbride 5920 (holotype: F).

Peperomia pseudogalapagensis Trel., Publ. Field Mus. Nat. Hist., Bot. Ser. [Macbride J.F.] 13(2): 79. 1936. Type: Peru. Lima: San Gerónimo. Wilkes Expl. Exped. 5920 (holotype: GH; isotype: K).

Type. **Peru**, dept. Lima, prov. Lima, dist. Rimac: “Habitat Limae in collibus altis in Amancaes copiosa, dicitur Congona Zimarrona” [Grows in Lima in high hills, abundant in Loma de Amancaes, it is called Congona Cimarrona], Ruiz & Pavón s/n: MA [29573]

Distribution and habitat. Coastal valleys of Peru and Galápagos (Ecuador) between 200 and 2000 m, in dry forests, almost always epiphytic on trunks, occasionally on rocks.

Note. This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Monteseco, 3 km NE, epífito, sobre tronco de árbol [epiphytic, on tree trunk] 1850 m, [06°50'41.4"S, 79°06'14.4"W], 5 May 1987, *J. Santisteban C. & J. Guevara B. 004* (HUT 24701, F1995288); Arriba de Monteseco, sobre árbol de *Erythrina* [Above Monteseco, on *Erythrina* tree] 1350 m, [06°51'17.8"S, 79°06'33.3"W], 10 Oct 1993, *S. Leyva et al. 904* (HAO, F 2165067) **Prov. San Miguel, dist. Niepos:** Road from La Florida to Monte Seco (Naranjo), 15.6 km from La Florida, 1700 m, 06°54'08"S, 79°08'15"W, 1 Mar 2009, *G. Mathieu & L. Symmank 166.* (USM 255775). Road from Naranjo to La Florida, 1316 m, 06°53'08.6"S, 79°06'45.8"W, 26 Jul 2020, *G. Pino*

& L.E. Alomía 3227 (observed). Same road, 1291 m, 06°53'08.7"S, 79°06'49.1"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3228* (observed). Idem. 1265 m, 06°53'04.6"S, 79°06'51.2"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3229* (observed). Road from La Florida to Niepos, 1297 m, 06°53'06.9"S, 79°06'47.6"W, 28 Aug 2022, *G. Pino & L.E. Alomía 3640*. (USM 330884).

10. *Peperomia microphylla* Kunth, Nov. Gen & Sp. [Humboldt] 1: 57, tab. 15, fig. 2. 1815.

Fig. 5G

Piper microphyllum (Kunth) Poir., Lam. Encycl. Meth. Suppl. 4: 469. 1816. Type: Based on *Peperomia microphylla* Kunth.

Peperomia aphylla C.DC., Prodr. 16(1): 456. 1869. Type: Colombia. Quindío, *Jameson 690* (holotype: G; isotypes: BM, K).

Peperomia gilbertii Trel., Publ. Field Mus. Nat. Hist., Bot. Ser. [Macbride J.F.] 13(2): 50.1936. Type: Peru. Cusco: Ollantaytambo, *Cook & Gilbert 740* (holotype: US).

Peperomia chachopoana Trel., Cat. Fl. Venez. 1:244. 1945, Nom. Nud. Type: Venezuela. Mérida. (2800 m) *Pittier 13165* (holotype: NY; isotypes: F, M, NY, US).

Type. Colombia, dept. Quindío: "Crescit in lapidosis frigidis Andium Quinduensis, juxta El Boquerón del Páramo, alt. 1650 hexap. Floret Octobri" [Grows in cold rocky

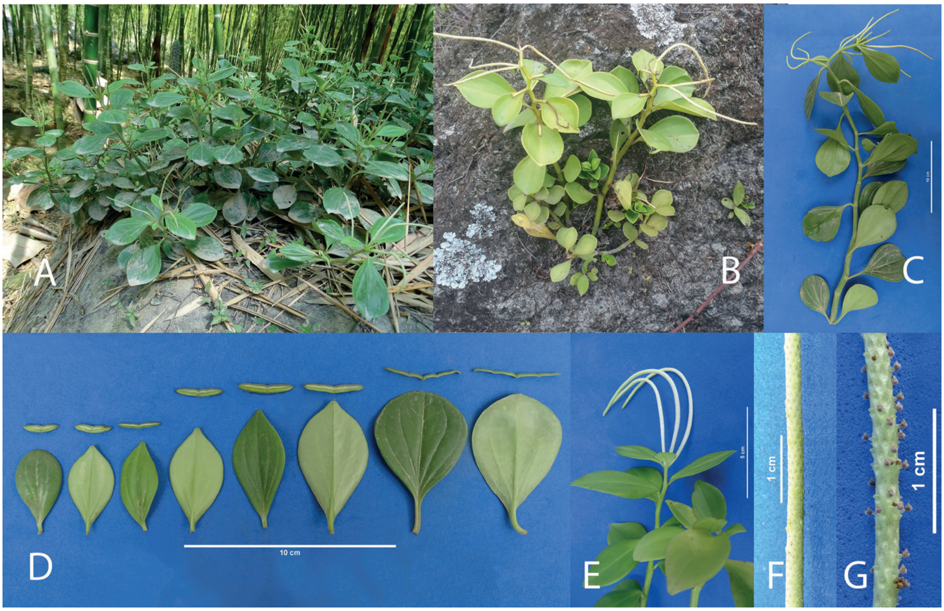

Figure 6. *Peperomia emarginulata* C.DC **A** colony growing on fallen *Guadua angustifolia* leaves **B** exposed plant growing on a rock **C** plant *ex-situ* showing 4-angled stems and inflorescences **D** detail of the leaves **E** terminal umbella with spadices **F** spadices at the beginning of anthesis **G** mature spadix with seeds.

places of the Andes of Quindiu, close to El Boquerón del Páramo, 3000 m, Flowers in October], Humboldt s/n, (lectotype, designated by Mathieu and Callejas (2006: 341: B!; isolectotype: P)).

Distribution and habitat. Montane forests of the Andes of Venezuela, Colombia, Ecuador, and Peru, on rocks or more frequently epiphyte.

Note. This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimen examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: ca. 4.2 Km (por aire) [in a straight line] NE Monteseco, 2500 m, [06°49'47.1"S, 79°06'22.4"W], 20 May 1987, *J. Santisteban C. & J. Guevara B 084* (HUT 24800, F1995295).

11. *Peperomia pilocarpa* Pino, Samain & L.E. Alomía, sp. nov.

urn:lsid:ipni.org:names:77317652-1
Fig. 7A–G

Type. Peru, Dept. Cajamarca, prov. San Miguel, dist. Niepos: road from La Florida to Niepos, 1613 m, 06°54'03.3"S, 79°07'33.5"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3217* (USM 333265!); Same collection, 28 Aug 2022, *G. Pino et al. 3646* (USM 333266!).

Diagnosis. Perennial, semi-succulent, prostate caespitose herb similar in habit to *P. cacaophila*, but differs mainly in leaf shape, which is widely obovate to elliptic or rotundate and sometimes slightly acuminate, compared to the ovate lamina and constantly acuminate apex of this species, leaves are flatter and less succulent, slightly puberulous compared to the canaliculate, glossy leaves of *P. cacaophila*. Stems are not terete as in this species but with two low prominent wings. Seeds are dimorphic, normal seeds are very similar in shape to the seeds of *P. sagasteguii*, modified seeds (probably galls) are conspicuous, large up to 2.5 mm long, bright green to brownish, densely covered with white trichomes.

Description. Perennial semi succulent terrestrial or semiepiphytic ***herb***, living in the shade and on abundant decayed vegetal matter, 10–15 cm tall, up to 25 cm when flowering. ***Roots*** basal and from basal nodes, very fibrous, light gray, 0.2–0.3 mm diam., 1–3 cm long. ***Stem*** mainly prostate, straight, procumbent when vegetative and decumbent sometimes at tips, up to 45 cm long or more, subterete, 2.5–3.5 mm diam. at the base, gradually tapering to 1.5–2 mm at the apex, dull olive green, reddish where exposed, with two not very prominent longitudinal wings decurrent with leaf petioles, internodes 1–5 cm, rarely with alternate branches from the base or every 10–15 cm. ***Leaves*** alternate, spirally attached one per internode, glabrous to slightly puberulous, present all along the stem; petiole circular in section, 0.8–1.5 cm long, 1–1.5 mm diam., with two lateral not prominent wings decurrent with stem, straight or slightly recurvate, lamina flat, widely obovate to oblong, (2–) 3–6 cm long, 1–3.5 mm thick, (1–)1.5–2.5 cm wide at distal third, (1.5–)2.8–3.8 cm wide at the middle, (1–)2–3 cm wide at proximal third, apex acute, obtuse in some leaves and slightly acuminate in larger leaves, subemarginate at tip, base rounded;

Figure 7. *Peperomia pilocarpa* **A** plant in habitat with assurgent stems **B** decumbent plant **C** young plants showing terminal inflorescence **D** plant *ex-situ* in anthesis showing normal inflorescence and inflorescence with galls **E** detail of leaves **F** spadix at the beginning of anthesis **G** mature spadix with galls and seeds. Details: (above, normal seed; below, gall with trichomes).

adaxially dull green, 3-palmatinerved, nerves slightly depressed; margin completely entire; abaxially light green, obscurely 3-palmatinerved, central nerve and proximal thirds of lateral nerves somewhat darker in color. ***Inflorescence*** a single terminal spadix appearing from November to December; peduncle terete or slightly funnel-shaped distally, sometimes reddish and obscurely furrowed, 7–12 mm long, 2–2.5 mm diam., with a small oval bract at the base, similar to leaves, ***rachis*** 6–10 cm long, 1.5–2.5 mm diam., light green. ***Floral bracts*** narrowly oval to subpentagonal, subacute, light green, 0.6–0.7 mm long, 0.5–0.6 mm wide. ***Stamens*:** filaments transparent, 0.2 mm diam., 0.4–0.5 mm long, anthers ovoid, 0.4–0.45 mm long, 0.25–0.3 mm wide, bright red at first, then white. Normal ***fruit*** globose, 0.7–0.8 mm long, 0.6–0.7 mm diam., brown, covered of white 0.05 mm long whitish papillae up to distal third of fruit, style conical, light brown. Modified ***fruit***, 2–2.5 mm long, 1.2–1.5 mm diam., bright green to brownish, minutely and densely covered with white 0.1–0.2 long trichomes, style prominent, bright green, 0.2–0.25 mm long, 0.3–0.4 mm diam., stigma dark, ripening from February to July.

Distribution and habitat. Plants grow from 1500 to 1600 m of the middle course of the Saña River valley, in the remnants of montane forest, mostly epiphytic.

Phenology. Inflorescences appear from October to March; fruits ripen from November to April.

Etymology. The epithet recalls the hairy surface of the modified fruits of this species, from the Latin *pilus* (hair) and Greek *καρπός* (fruit).

Notes. This specimen at first was considered a probable hybrid because it shows intermediate features between *P. emarginulata* and *P. cacaophila*. However, although those two species share their habitat to some extent they are found at lower altitudes and never close to *P. pilocarpa*. Instead, this species appears within the range of *P. vivipara*, but it seems not to be related to it. Another interesting fact is that most fruits are modified to form hairy galls. The etiology of these galls remains unknown.

This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Additional specimen examined. Peru, dept. Cajamarca, Prov. San Miguel, dist. La Florida: Road from Monteseco to Chorro Blanco, 1545 m, 6°50'51.3"S, 79°06'23.5"W, 10 Feb 2023, *G. Pino & L.E.Alomía 3830*, (USM 333267).

12. *Peperomia riosaniensis* Hutchison ex Pino, Samain & L.E. Alomía, sp. nov.

urn:lsid:ipni.org:names:77317653-1
Fig. 8A–H

Type material. Peru, [**dept. Lambayeque, prov. Chiclayo, dist. Oyotún**]: road to Hacienda Taulis, ca. 80 km up the Río Saña from the Pan American Highway, 500 m, [06°51'23"S, 79°09'31"W], 28 Aug 1964, *P. C. Hutchison 6308* (holotype: UC[1298471]!, isotypes US [2485139]!, USM [Not found]).

Diagnosis. Perennial, succulent terrestrial herb similar to *P. palmiformis* Pino & Samain, differs in inflorescences that have wider panicles, with more (30–60 compared to 16–40) and shorter spadices (1–5 cm long compared to 2–8 cm long), leaves attached all along the stem, slightly longer (6–9 cm compared to 5–7 cm), more succulent, canaliculate instead of flat, with longer petioles (2 cm compared to 0.7 cm), lamina wider at proximal third (1.2–1.8 cm compared to 0.5–1.2), margin entire distally instead of serrate, fruits larger (0.9 × 0.6 mm compared to 0.4 × 0.3 mm), widely ovoid instead of narrowly ovoid.

Description. Perennial, succulent, terrestrial ***herb***, living in gorges or the shade of other plants, (4–) 9–18 cm tall, up to 50 cm tall when flowering. Roots fibrous, light gray, 0.7–0.4 mm diam., 2–4 cm long. Stem mainly erect or shortly decumbent at base, straight, terete, slightly puberulous, 0.7–1.2 cm diam. at the base, gradually tapering to 4–8 mm at the apex, bright green, brownish at the base, with reniform leaf scars spirally displayed every 3–8 mm, 1.5–2 mm × 3–4 mm, brownish; very rarely branching dichotomously from the distal 10 cm, but mostly with 4–6 branches from the base, resulting in a caespitose plant. ***Leaves*** alternate, glabrous, spirally inserted, present all along the stem or in the distal third of the main stem or branches under dry conditions, young leaves smaller, narrower, very succulent, induplicate or canaliculate, older leaves less succulent; petiole reniform in section, gradually continuing with leaf, 0.5–2 cm long, 2.5–3 mm wide, 1.5–2 mm thick, lamina convex to induplicate, narrowly obovate, (3–) 6–9 cm long, 1.2–2.4 mm thick, (1.4–)2–3 cm wide at distal third, (1.4–)1.8–3 cm wide at the middle, (1–)1.4–1.8 cm wide at proximal third, apex subacute, distal third slightly recurved, base cuneate; adaxially bright glossy green, convex to slightly induplicate, obscurely 3–5-palmatinerved, nerves lighter colored; canaliculate or markedly induplicate, only the central nerve is visible in young leaves; margin entire; abaxially pale green, obscurely 3–5-palmatinerved, central nerve subcarinate, the others rather depressed. ***Inflorescence*** is an open terminal panicle with 30–60 alternate spadices emerging solitary or from secondary axes with 2–7 spadices, each born from 10–20 nodes appearing 5–10 cm from the base of the central axis; each node with a basal lanceolate acute bract 0.4–2 cm long, 0.3–0.7 cm wide, bright green; central axis 30–40 cm long, 3–6 mm diam. at the base, gradually tapering to 1 mm, terete, longitudinally furrowed, very light green; ***peduncle*** terete or slightly funnel-shaped distally, 3–10 mm long, 0.7–1.2 mm diam., each with a 2 mm long, 0.5 mm wide oval bract at the base, deciduous; ***rachis*** 1–5 cm long, 1.2–1.6 mm diam., light green. ***Floral bracts*** broadly oval to round, subacute, light green, 0.5–0.6 mm diam. ***Stamens***, filaments 0.4 mm long, 0.2 mm diam., transparent, anthers white ovoid, 0.4–0.5 × 0.3 mm. ***Fruit*** an ovoid berry, 0.85–0.9 mm long, 0.55–0.6 mm diam., bright brown to olive green, minutely papillate, pedicel inconspicuous, dry anthers attached, style prominent, ovoid, bright brown, 0.15–0.2 mm long, 0.15–0.2 mm diam., stigma lighter colored.

Distribution and habitat. Plants grow from 450 to 600 m, the lowest and driest layer of the area studied, along the Saña valley between the towns of Oyotún and La Florida in the departments Lambayeque and Cajamarca, on rocky soil, in thickets shaded by shrubs and supplied with moisture from nearby water courses.

Phenology. Inflorescences appear from June to August; fruits ripen from July to September.

Etymology. The epithet was coined by Hutchison in 1967 after the Saña river, “Río Saña” in Spanish, which is Latinized to “riosaniensis” in the same way *Rauhocereus riosaniensis* was described by Backeberg. As Hutchison only labeled the herbarium sheets and never published this name it has been considered a *nomen herbariorum* (Mathieu 2007).

Notes. The closest species of *Peperomia riosaniensis* is *P. palmiformis* Pino & Samain (Pino et al. 2012) The web page “Peperomia.net” (http://www.peperomia.net/repertorysearch.asp) indicates that this taxon is merely a synonym of the latter. We compared both species in detail and the main differences between *P. riosaniensis* and *P. palmiformis* are resumed in Table 3.

While *P. palmiformis* grows from 800 to 900 m along the Utcubamba valley from Bagua to Pedro Ruiz in department Amazonas, Peru, *P. riosaniensis* grows 300 m lower. Nevertheless, the temperatures in the habitats of both species average 25–30 °C during the day and 18–22 °C at night, *P. riosaniensis* grows at 200 km distance from *P. palmiformis*, on the dry, xerophytic western slopes of the Andes, with 25 mm rain

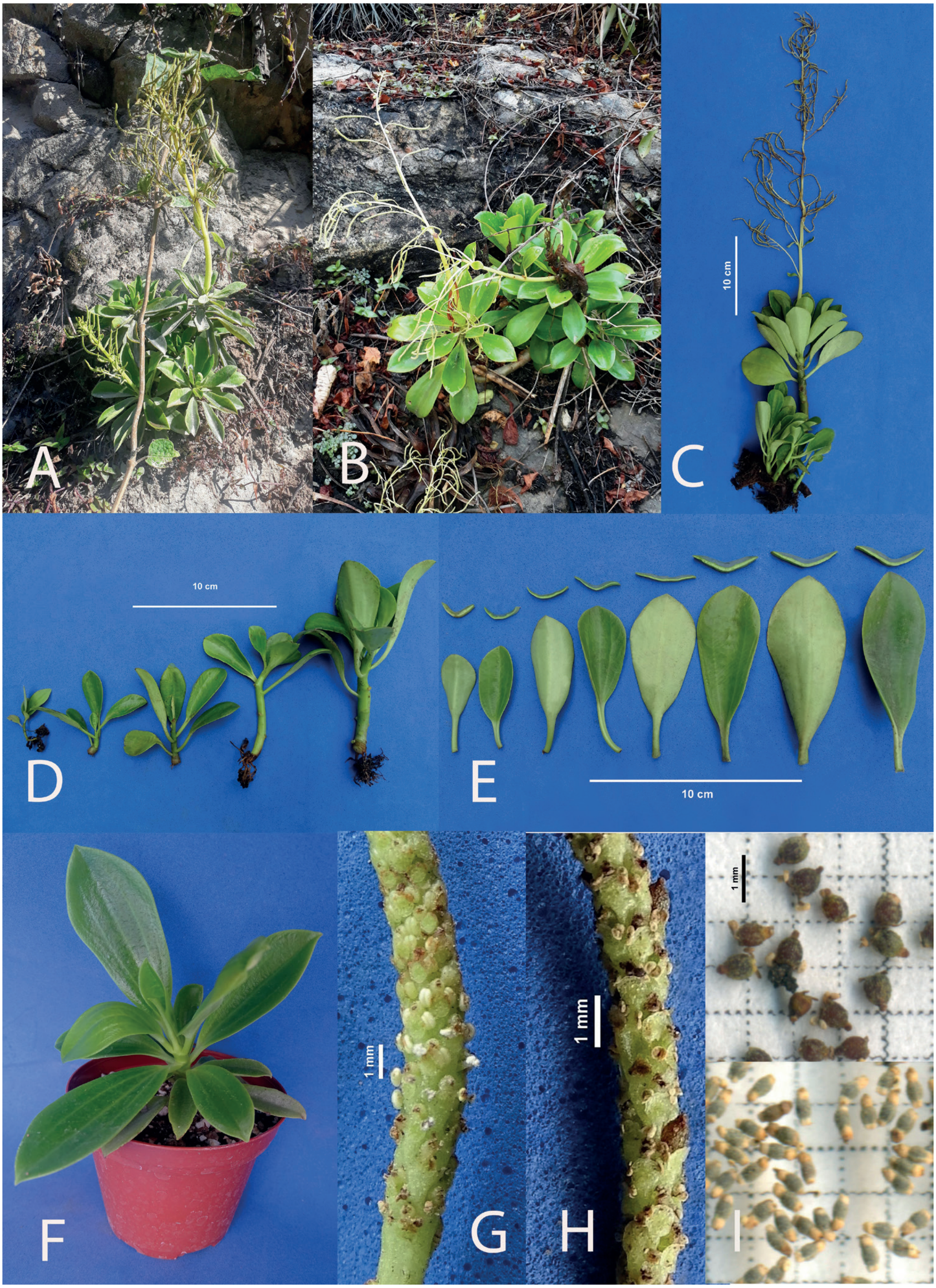

Figure 8. *Peperomia riosaniensis* Pino, Samain & L.E. Alomía, sp. nov. **A, B** plant in habitat **C** plant *ex situ* **D** early stages of development **E** detail of the leaves **F** young plant in cultivation **G** spadix in anthesis **H** mature spadix with fruits **I** comparison of the fruits of *P. riosaniensis* (above) and *P. palmiformis* (below).

Table 3. Comparison of the main differences between *P. riosaniensis* and *P. palmiformis*.

Features	*P. riosaniensis*	*P. palmiformis*
Height (vegetative in cm)	9–18	15–20
Distribution of leaves	All along the stem	Mainly on distal third.
Branches	Very common, basal, rarely dichotomous distally.	Rarely branched from the base, distal dichotomous branches.
Leaf (petiole)	0.5–2 cm long	3–7 mm long
	2.5–3 mm wide	1.2–1.8 mm wide
	1.5–2 mm thick	1–1.5 mm thick
Leaf (shape)	Canaliculate to induplicate, narrowly obovate. Distal third slightly recurved.	Mainly flat, occasionally slightly convex on both sides, very narrowly obovate.
Leaf (length in cm)	6–9	5–7
Leaf (thickness in mm)	1.2–2.4	0.5–3
Leaf (width)	2–3 cm wide at distal third	2–2.5 cm wide at distal third
	1.8–3 cm wide at the middle	1–2 cm wide at the middle
	1.4–1.8 cm wide at proximal third	0.5–1.2 cm wide at proximal third
Leaf (margin)	Completely entire.	Constantly serrate at distal third.
Inflorescence	Open panicle	Narrow panicle
	10–20 branches,	10–16 upright branches,
	30–60 spadices.	16–40 spadices.
Central axis	30–40 cm long	25–30 cm long
	3–6 mm diam. at base	3.5–5 mm diam. at base
Rachis of the spadix	1–5 cm long, 1.2–1.6 mm diam.	2–8 cm long, 1–1.4 mm diam.
Fruit (shape/color)	Ovoid, bright brown to olive green.	Narrowly ovoid, light olive green
Fruit (length in mm)	0.85–0.9	0.35–0.45
Fruit (diam. in mm)	0.55–0.6	0.25–0.35
Fruit (style)	Wide ovoid, bright brown,	Long ovoid to balaniform, bright orange,
	0.15–0.2 mm long,	0.25–0.30 mm long,
	0.15–0.2 mm diam.	0.22–0.28 mm diam.

per month average in summer and 0–4 mm in winter (Clima.com: https://www.clima.com/peru/cajamarca/florida). *Peperomia palmiformis* lives on the flatter eastern slopes of the Andes, along the lower basin of the Utcubamba river, in a dry valley but already under the influence of the Amazon Forest, with nearly 60 mm rain per month in summer and 5 mm monthly in winter (Clima.com). Both species look similar from far away, but *P. riosaniensis* is slightly shorter when vegetative; its inflorescences have relatively wider panicles, with more horizontal branches and more spadices that are relatively shorter. Although leaves look very much alike when pressed, the new species has longer and thicker petioles, longer leaves that are not as narrow and succulent, wider at the proximal third, making its margin convex, compared to the concave margin of *P. palmiformis* at this segment. The new species also has induplicate or canaliculate leaves, adaxially slightly darker and glossier, frequently carinate beneath and slightly recurved at the distal third, compared to the straight, flat, mostly biconvex succulent leaves of *P. palmiformis*, mainly due to its more developed fenestra. The serrate distal margin of the leaves observed in *P. palmiformis* similar to *P. erosa* Hutchison ex Pino (Pino et al. 2012) has never been observed in the new species. Fruits are entirely different, more globular, larger, thicker, and papillate in *P. riosaniensis*, frequently with dry anthers attached, and lacking the conspicuous bright orange persistent basal pedicel. *Peperomia palmiformis* fruits also have a larger, bright orange style, with a bulge that is sometimes even thicker than the fruit itself. These morphological differences are supported by the fact that in a recent phylogenetic study, *P. riosaniensis* is located in a different branch from *P. palmiformis* that is more related to *P. columella*, *P. ferreyrae*, *P. mathieui*, and *P. columnaris* from the Utcubamba valley (Frenzke et al. 2015). All these species mentioned belong to *Peperomia* subgenus *Fenestratae* Pino (Frenzke et al. 2015).

Additional specimens were examined. Peru, dept. Lambayeque, prov. Chiclayo, dist. Oyotún: road from Oyotún to El Espinal, on the trail to waterfall Velo de la Novia, 515 m, 06°48'30.3"S, 79°11'08"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3237* (USM 330870); same road, 520 m, 06°48'27.4"S, 79°11'04.7"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3238* (USM 330871); **Dept. Cajamarca, prov. Santa Cruz, dist. Catache:** Road from El Espinal to La Florida, 582 m, 06°51'13.7"S, 79°09'16.5"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3230* (USM 330869); Road from Cayaltí to La Florida, 8.4 km from La Florida, 492 m, 06°50'51,6"S, 79°09'53,7"W, 1 Mar 2009, *G. Mathieu & L. Symmank 2009-167* (BR, GENT, USM 258833!) Same road, 591 m, 06°51'13.4"S, 79°09'18.4"W, 28 Aug 2022, *G. Pino et al. 3637* (USM 330882) **prov. San Miguel, dist. La Florida,** Puente el Papayo, on slopes at the borders of the roadside, 18 Jul 1982, *S. Llatas Quiroz 861* (F 1931956, NY).

13. *Peperomia rotundata* Kunth. Nov. Gen & Sp. [Humboldt] 1: 67, tab.12. 1815.

Fig. 5H

Piper rotundatum (Kunth) Poir., Lam. Encycl. Meth. Suppl. 4: 468. 1816. Type: Based on *Peperomia rotundata* Kunth.

Piper villosum Rich. mss. in herb. Francov. in DC. Prodr. 16(1):442. 1869. Type: Based on *Peperomia rotundata* Kunth.

Type. Colombia, dept. Cauca: "Crescit in excelsis regni Novogranatensis, inter Pansitara et vallem Yacanocatu, alt. 980 hexap. Floret Novembri." [Grows in elevations of the Kingdom of New Granade, between Pacitará and the Yacanocatu valley, at 1800 m, Flowers in November], Humboldt s/n, (holotype: B [lost?]; isolectotype: P!)

Distribution and habitat. Montane forests of Venezuela, Colombia, Ecuador, Peru, and Bolivia: rare, but uniformly distributed, terrestrial in shaded places growing on humus.

Note. This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimen examined. Peru, dept. Cajamarca, prov. San Miguel, dist. Unión Agua Blanca: El Tingo, camino a Taulis, [on the way to Taulis] 3175 m, [06°59'26"S, 79°01'21"W], 18 Feb 2000, *E. Rodríguez et al. 2366* (HUT 37499, F, M, MO).

14. *Peperomia sagasteguii* Pino, Samain & L.E. Alomía, sp. nov.

urn:lsid:ipni.org:names:77317654-1

Fig. 9A–G

Type. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Monteseco, 1 Km above, on the path to Chorro Blanco, 1353 m, [06°51'17.8"S, 79°06'33.2"W], 16 Mar 1986, *M.O. Dillon & A. Sagástegui 4315a* (holotype: F [1978653]!).

Diagnosis. Perennial, semi-succulent, terrestrial, epiphytic, or saxicolous herb similar to *P. trinervis*, differs in stems more pubescent, dark red to olive green instead of bright red, leaves with a longer and wider petiole (7–17 long × 1.8–2 wide compared to 3–10 long × 1.2–1.5 wide), lamina more succulent, green adaxially and light green-pinkish abaxially instead of olive green with gray nerves adaxially and red-purple abaxially; spadices longer (4–20 cm compared to 10 cm long), but narrower.

Description. Perennial, semi-succulent, terrestrial, epiphytic, or saxicolous ***herb***, living in the shade of other plants, 10–30 cm tall, up to 45 cm tall when flowering. Roots fibrous, around 1 mm diam., transparent-reddish, 2–6 cm long, emerging from basal nodes and stolons. ***Stem*** stoloniferous at the base, then assurgent, thicker below, straight erect, terete, dark red to olive green, 0.4–0.6 cm diam. at the base, gradually tapering to 1.4–1.6 mm at the apex, readily branched alternately, internodes 2.5–3 cm at the base gradually descending to 0.8–1 cm towards the apex, surface crisp-pubescent, trichomes whitish, around 0.5 mm long at base, slightly shorter upwards. ***Branches*** 5–9, irregularly alternate, sometimes pseudo-opposite below, emerging almost horizontally mainly from the distal half, 7–15 cm long in the vegetative state. ***Leaves*** alternate, elliptic, elliptic obovate to subrotundate; petiole terete, same surface and color as stem, 0.7–1.7 cm long, 1.8–2 mm wide, slightly channeled above; lamina slightly convex to flat, 2.5–4 cm long, 1–2 mm thick, 1.6–2.8 cm wide, apex acute to attenuately subacuminate, base cuneate to sub truncate; adaxially bright glossy green, convex, 3-palmatinerved, nerves depressed; margin entire; abaxially pale green to pinkish, 3-palmatinerved, nerves elevated. Young leaves can be pinkish adaxially. Both sides are puberulous. ***Inflorescence*** terminal in an umbel of 1–3 spadices and sometimes 1–2 individual spadices from upper leaf nodes, umbel with 1–3 basal bracts at the base and lateral spadices with opposite bracts at base similar to leaves but much smaller; ***peduncle*** terete, light green, 4–6 mm long, 1.2–1.8 mm diam.; ***rachis*** 4–15 (–20) cm long, 1.5–1.7 mm diam., light green. ***Floral bracts*** broadly oval to round, light green, flat, almost inconspicuous, 0.35–0.45 × 0.30–0.40 mm. ***Stamens***, filaments short, anthers white ovoid, 0.3 × 0.4 mm. ***Fruita*** globose berry, borne on a 1–1.5 mm long, 0.25–0.3 mm diam. narrow-conical transparent pedicel; 0.7–0.8 mm long, 0.6–0.7 mm diam., brown, covered in white 0.05 mm long whitish papillae up to distal third of fruit, style conical, light brown, 0.15–0.2 mm long, 0.20–0.25 mm diam.

Distribution and habitat. Plants have only been found from 1200 to 1500 m of the middle course of the Saña River valley, in the remnants of montane forest, epiphytic or on rocks, always in shaded places. *Peperomia sagasteguii* is endemic to the Saña River valley.

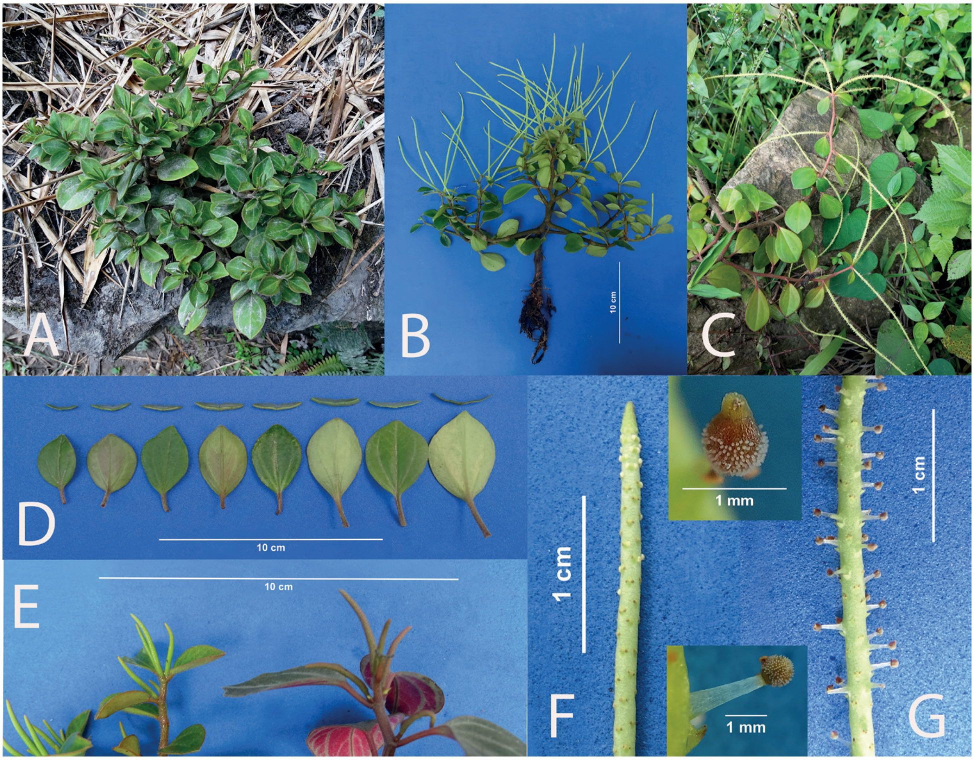

Figure 9. *Peperomia sagasteguii* Pino, Samain & L.E. Alomía, sp. nov. **A** plant in habitat in the dry period **B** plant *ex situ* in anthesis **C** plant in habitat with inflorescences **D** detail of the leaves **E** comparison of *P. sagasteguii and P. trinervis* at the beginning of anthesis **F** detail of immature spadix **G** mature spadix showing long pedicels and fruits. (Details: Above, mature fruit; Below, fruit standing on long pedicel).

Phenology. Inflorescences appear from October to November; fruits ripen from January to March.

Etymology. This species is dedicated to Abundio Sagástegui (1932–2012), collector of the type, a notable botanist, who worked at both Universidad Nacional de Trujillo and Universidad Privada Antonio Orrego, author of many books and articles, director of the journals "Bulletin of the Society of Botany of the UNT" and *Arnaldoa*, author of four genera and 97 species (Rodríguez and León 2012).

Notes. Most collections were determined initially as *P. trinervis* Ruiz & Pav., a species that seems to be very close, (see Table 4). The main differences are stem color, which is dull dark red and greenish in *P. sagasteguii* compared to the bright red of *P. trinervis*. The indumentum of *P. sagasteguii* seems to be denser and longer, like that of *P. rotundata*. Leaf petioles of *P. trinervis* are shorter and of similar color to its stems. The leaf color of *P. sagasteguii* is bright green adaxially with depressed nerves, while *P. trinervis* has a high color contrast between the dark olive green and the bright silver gray of the nerves. Abaxially leaf color of *P. sagasteguii* is light green, while *P. trinervis*

Table 4. Comparison of the main differences between *P. sagasteguii* and *P. trinervis*. Data of *P. trinervis* taken from Trelease and Yuncker (1950) and from live cultivated plants.

Features	*P. sagasteguii*	*P. trinervis*
Height (cm)	10–30 (–45)	20–25 or more
Internodes (in cm)	2.5–3 below, 0.8–1 above	2–3 below, 1 above
Stem (in mm)	4–6 diam. at the base, gradually tapering to 1.4–1.6	4–6 diam. at the base, gradually tapering to 1.5–2
Stem (color)	Dull dark red to olive green	Bright dark red
Leaf (petiole in mm)	7–17 long, 1.8–2 wide	3–10 long, 1.2–1.5 wide
Leaf (shape)	Elliptic, elliptic obovate to subrotundate.	Elliptic, elliptic obovate or elliptic obovate.
Leaf (measure)	2.5–4 cm long, 1–2 mm thick, 1.6–2.8 cm wide	2–3.5 cm long, less than 1 mm thick, 1.2–2.5 cm wide.
Leaf (color)	Adaxially bright glossy green, abaxially pale green to pinkish. Young leaves can be pinkish adaxially	Adaxially dark olive green with nerves in gray, abaxially bright dark red, nerves in light green. Young leaves can be purplish
Inflorescence	Terminal in an umbel of 1–3 spadices and sometimes 1–2 individual spadices from upper leaf nodes	Terminal and from the upper nodes.
Rachis of the spadix	4–15 (–20) cm long, 1.5–1.7 mm diam.	10 cm long, 1.8–2 mm diam.

is dark red with light green nerves. *Peperomia sagasteguii* has thicker, more succulent leaves. Finally, spadices of *P. sagasteguii* are much longer. The type collection was determined initially as *P. blanda* (Jacq.) Kunth, which bears no similarity and later it was determined as *P. rotundata* Kunth by R. Callejas, but this sample lacks the constant decussate leaves and inflorescences characteristic of that species. Some branches and leaves can be pseudo-opposite by shortening of the stem, leading to this confusion.

This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Additional specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Alrededor de campamento, Bosque Monteseco, borde de trocha sobre troncos secos [Around the campsite, Monteseco Forest, border of track, on dry logs] 1500 m, [06°50'58.6"S, 79°05'53.7"W], 20 Jan 1989, *S. Leyva G. 015* (F 2016269, USM 90066) **Prov. San Miguel, dist. La Florida:** Buenos Aires, La Florida, sobre troncos de Guaba [on trunks of *Inga* sp.] 1000 m, [06°52'27.3"S, 79°07'10"W], 22 Mar 1986, *S. Llatas Quiroz & R. Palacios 1822* (F 1963941). Road from La Florida to Monteseco, just before entering the reserved zone, 1531 m, 6°51'00.7"S, 79°05'58.2"W, 10 Feb 2023, *G. Pino & L.E. Alomía 3831* (USM 333270). **dist. Niepos:** Road from La Florida to Monte Seco (Naranjo), 5.8 km from La Florida, 1395 m, 06°53'25.5"S, 79°06'57.3"W, 1 Mar 2009, *G. Mathieu & L. Symmank 163* (USM); Road from La Florida to Niepos, 1297 m, 06°53'06.9"S, 79°06'47.6"W, 28 Aug 2022, *G. Pino et al. 3641* (USM 333268); Same road, 1393 m, 06°53'25"S, 79°06'57"W, 28 Aug 2022, *G. Pino et al. 3644* (USM 333269).

15. *Peperomia symmankii* Pino & Samain, sp. nov.

urn:lsid:ipni.org:names:77317655-1

Fig. 10A–F

Type. Peru, dept. Cajamarca, prov. San Miguel, dist. La Florida: road from Cayaltí to La Florida, 731 m, 06°51'57.6"S, 79°08'32.3"W, 1 Mar 2009, *G. Mathieu & L. Symmank 162* (holotype: USM[255772]!).

Diagnosis. Perennial, succulent, caulescent, terrestrial herb, similar to *P. ricardofernandezii* Pino & Samain, but shorter, less branched, and with more tortuous stems. Leaves are smaller (2.5–4.5 cm long compared to 4.5–8 cm long), more widely ovate, with an obtuse or rounded apex instead of acute-acuminate. Petioles are shorter (0.3–3.5 cm long compared to 2–4 cm), lighter in color, and attached closer to the cordate base, which is sometimes auriculate and overlapping compared to the truly peltate insertion of *P. ricardofernandezii*. The inflorescence is narrower and longer but otherwise very similar, with longer spadices (3–20 mm compared to 2–4 mm).

Description. Perennial, succulent, caulescent, terrestrial ***herb***, 12–20 cm when vegetative, up to 5 cm when flowering, growing on soil among rocks at slightly shaded places, near water courses. Vegetative ***stem***, 0.6–1.5 cm diam. At the base, light gray brownish, erect at first, then sometimes decumbent, rooting from the base, terete in the rainy period, slightly furrowed under dry conditions, with flat or projected spirally arranged round to reniform scars, 0.15–0.3 cm tall, 0.25–0.45 cm wide, distanced every 0.5–1 cm, corresponding to decurrent petioles. ***Leaves*** in young plants perennial, alternate, spirally attached, present at the distal 2–4 cm, glabrous; petiole reniform in cross-section, 0.5–3.5 cm long, 2–2.5 mm wide, erect or oblique upwards, light green or with a reddish blush, inserted almost at the base of the leaves, subpeltate at 1–2 mm from abaxial base; lamina widely ovate, 2–4.5 cm long, 2–4.5 cm wide at proximal third, 2.5–5 cm wide at the middle, 2.5–4 cm wide at distal third, apex obtuse, occasionally rounded, base cordate, sometimes auriculate and overlapping; adaxially dull green, flat to concave. 7-palmatinerved, nerves depressed; margin entire, undulated at distal half; abaxially very light green, sometimes reddish, nerves slightly carinate, darker green. A reproductive stem develops in the rainy season, from the apex the first time or from the next most distal node, with bracts similar to leaves, their lamina is first corrugate with undulate margins, and reddish abaxially, later they become larger, 4–7 cm long, 5–7 cm wide at proximal third, 3–6.5 cm wide at the middle, 4–5.5 cm wide at distal third, flat, adaxially bright green, abaxially very light green with nerves less conspicuous, apex acute to obtuse, base cordate, margins entire, petiole 4–7 cm long, light green. All bracts and inflorescences are deciduous after flowering. ***Inflorescence*** 2–5 (–10) panicles born alternately from the distal stem towards the apex, appearing from February to March. Each panicle is a raceme of 15–45 conferted, spirally arranged, horizontally inserted spadices around a vertical central axis, gradually opening from base to apex, longer and whiter at the base and shorter and greener distally. Central axis 10–30 cm long in total, 0.4–0.5 mm diam. at the base, gradually tapering to 0.9–1 mm, terete, light green to reddish, whitish towards the apex; ***peduncle*** terete or slightly funnel-shaped distally, 1–2 mm long, 0.3–0.4 mm diam., bright white; ***rachis*** 3–20 mm long, 0.4–0.5 mm diam., longitudinally furrowed, bright white. ***Floral bracts*** peltate, discoid, greenish white, 0.25–0.3 mm diam. ***Stamens*** white, pink when dry, filaments 0.2 mm long, transparent, anthers white ovoid, 0.15–0.20 mm. ***Ovary*** globose, white, 0.35–0.45 mm diam., stigma fimbriate. ***Fruit*** an ovoid berry, 0.75–0.85 mm long, 0.55–0.65 mm diam., olive green-brownish, minutely papillate, pedicel inconspicuous, style very broadly conical, white, stigma brown.

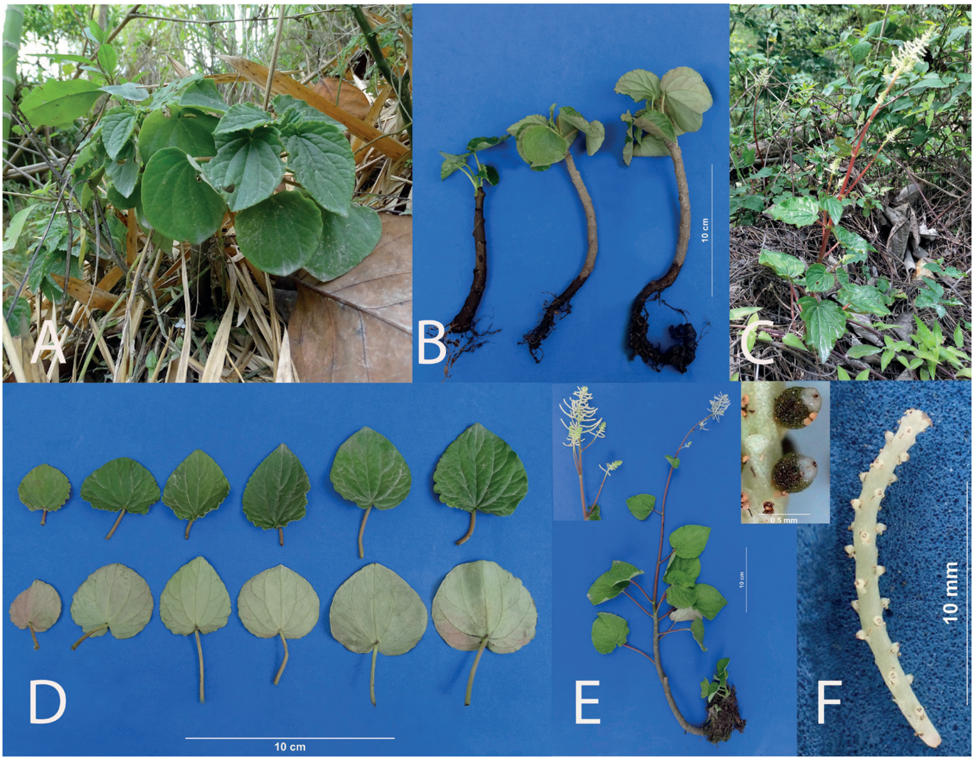

Figure 10. *Peperomia symmankii* Pino & Samain, sp. nov. **A** plant in habitat **B** plants *ex situ* in several stages of development **C** plant in habitat in blossom **D** detail of the leaves **E** plant ex situ in anthesis with bracts. (Detail: mature panicle) **F** young spadix (Detail: Mature spadix with fruits).

Distribution and habitat. Plants are rare and have been found only at four spots from 700 to 2400, semi-shaded on soil accumulated among huge rocks, on moist places near watercourses.

Phenology. Inflorescences appear from December to March; fruits ripen from February to April.

Etymology. The epithet is dedicated to Lars Symmank, a botanist from Dresden, Germany, who together with Guido Mathieu collected the specimen of this new species in the first expedition to Peru organized by Ghent University in 2009. He worked in several studies of subgenus *Tildenia* (Mathieu et al. 2011; Samain et al. 2011; Symmank et al. 2011).

Notes. The closest species to *P. symmankii* is *P. ricardofernandezii* from Piura. This species is mainly terrestrial, taller, and many branched with a bush-like appearance contrasted to the creeping habit of *P. symmankii*. The main difference is the leaf size and shape: *P. symmankii* has relatively smaller leaves, more widely ovate, with an obtuse to round apex, compared to the narrow ovate, acute-acuminate leaves of *P. ricardofernandezii*. Petioles of the new species are shorter, lighter in color, attached closer to the leaf base, which is truly cordate, even sometimes auriculate and overlapping, compared to

Table 5. Comparison of the main differences between *P. symmankii* and *P. ricardofernandezii*.

Features	*Peperomia symmankii*	*Peperomia ricardofernandezii*
Height (vegetative in cm)	12–20	10–50
Height (flowering, in cm)	25–45	15–60 or more
Petioles (surface and color)	Glabrous, light green or with reddish blush	Glabrous, burgundy red.
Petioles (length and insertion)	0.5–3.5 cm	2–4 cm
	Subpeltate 1–2 mm from abaxial base	Subpeltate 2–3 mm from abaxial base
Leaves (shape and color)	Widely ovate, apex acute, base cordate; adaxially dull green, abaxially very light green, sometimes with a slight blush.	Narrowly ovate, apex acute to subacuminate, base subcordate; adaxially light green, abaxially reddish to burgundy red.
Leaves (size)	2–4.5 cm long	4.5–8 cm long
	2.5–4 cm wide at distal third	1.5–3 cm wide at distal third
	2.5–5 cm wide at the middle	2.5–6 cm wide at the middle
	2–4.5 cm wide at proximal third	2.5–5.5 cm wide at proximal third
Vegetative stem	Perennial, usually one branch from subterminal bud.	Perennial, 1–3 branches from subterminal bud.
Bracts (petiole)	4–5 cm long, light green, inserted subpeltate at 1–3 mm from abaxial base	2–10 cm long, red, inserted subpeltate at 2–5 mm from abaxial base
Bracts (shape and size)	Widely ovate	Ovate
	4–7 cm long	4.5–8 cm long, 2.5–6 cm wide,
	3–7 cm wide,	apex acuminate and clearly acute distally
	apex acute to obtuse	
Central axis of panicle (length in cm)	10–30	3.5–7
Rachis of spadix (length in mm)	3–20	2–4

the more peltate insertion in *P. ricardofernandezii*. The inflorescence of *P. symmankii* is narrower and longer but otherwise very similar, with slightly longer spadices (Table 5).

This species belongs to *Peperomia* subg. *Panicularia* Miq. (Frenzke et al. 2015).

Additional specimens examined. Peru, dept. Cajamarca, prov. San Miguel, dist. La Florida: El Papayo bridge over Saña River, East bank, 10 m to North, under the shade of *Guadua angustifolia* plants, on rocks, 731 m, 06°51'57.6"S, 79°08'32.3"W, 28 Aug 2022, *G. Pino et al. 3639* (USM 333272). El Papayo, sobre materia orgánica de las rocas. [El Papayo, on rocks with the decayed organic matter] 850 m, [06°51'S, 79°08'W], 1 Feb 1986, *S. Llatas Q. 1770* (HUT 22496); Road from Florida to Monteseco, 1095 m, 6°51'41.3"S, 79°07'08.9"W, 10 Feb 2023, *G. Pino & L.E. Alomía 3832*; (USM 333273). **Dist. Bolívar:** Bosque Oscuraná, Caserío el Nogal, Bosque Húmedo [Oscuraná Wet Forest, El Nogal Hamlet], 2400 m, [6°56'51.0"S, 79°08'04.0"W], Sep 9 2003, *A. Juárez et al. s.n.* (HLL 435, HUT 42219). **Prov. Santa Cruz, dist. Catache:** Carretera al Bosque de Monteseco, borde de Carretera. [Road to Monteseco forest, border of road], 1200 m, [06°51'21"S, 79°06'42"W], 20 Jan 1996, *E. Rodríguez 750* (HUT 30979).

16. *Peperomia vivipara* Pino, Samain & L.E. Alomía, sp. nov.

urn:lsid:ipni.org:names:77317656-1
Fig. 11A–F

Type. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Monteseco Forest. 1500 m, [06°50'58.6"S, 79°05'53.7"W], 19 Dec 1984, *A. Sagástegui et al. 12396* (holotype: HUT [19867] !; isotype: F [2038843] !).

Diagnosis. Perennial, semi-succulent, caespitose herb similar to *P. alata*, but more succulent, with thicker and more stout branches, leaves are shorter, elliptic, acute based, instead of lanceolate and long acuminate. Leaf bases are obtuse or subtruncate instead of cuneate. After flowering, propagules are developed at the apex of old branches that readily wither to assure vegetative propagation.

Description. Perennial, semi-succulent, caespitose ***herb***, growing terrestrial, epiphytic, or saxicolous in the shade of other plants, 30–45 cm tall. Roots fibrous, emerging from the base of plants, 0.7–1 mm diam., light brown. ***Stem*** stoloniferous at the base, from which 3–10 deciduous ***branches*** emerge, straight erect, sometimes in zig-zag towards the apex, terete at the base, then prominently winged towards the apex with a triangular section, dark olive green, slightly puberulous at the base, then glabrescent towards the apex, 0.7–1 cm diam. At the base, gradually tapering to 0.3–0.5 mm at the apex, rarely branched close to the base, internodes 2.5–5 cm at the base gradually descending to 0.5–0.7 cm towards the apex, wings prominent at the distal half of the stems, from below the node towards the node after the next, semitransparent, 1–2 mm tall. ***Leaves*** alternate, distichous, glabrous, elliptic to elliptic ovate; petiole short, decurrent to next opposite node, reniform in section, channeled above, reddish green-pinkish, 0.2–0.4 (–1) cm long, 1.5–2 mm wide; lamina 3–6.5 cm long, 0.5–1.5 mm thick, 1.8–3.2 cm wide, apex acute to very slightly acuminate, slightly recurvate, base sub truncate; adaxially bright glossy green in young leaves, then very dark army green and even bluish, flat to slightly canaliculate, 3–5-palmatinerved, nerves depressed; margin entire; abaxially very light green with a pink blush, 3-palmatinerved, nerves elevated. ***Inflorescence*** simple terminal or up to 3 individually from upper leaf nodes opposite to the leaves; ***peduncle*** terete to infundibuliform, bright green, 2–9 mm long, 1.4–1.5 mm diam.; ***rachis*** 3–6 cm long, 2–3 mm diam., light green. ***Floral bracts*** rotundate, light green, flat, almost inconspicuous, only darker green than rachis, 0.4–0.5 mm diam. ***Stamens***, filaments transparent, 0.2 mm diam., 1.5–3 mm long, anthers white ovoid, 0.4–0.5 mm long, 0.3–0.4 mm wide. ***Fruit*** not seen. ***Propagule*** developing at the apex of the branch, 1–5 cm tall, persistent until the whole stem dries.

Distribution and habitat. Plants grow from 1500 to 1800 m of the middle course of the Saña River valley, in the remnants of montane forest, epiphytic or on rocks, always in shaded places.

Phenology. Inflorescences appear from December to March; fruits ripen from February to April.

Etymology. The epithet stands for the most striking feature of this plant, the production of offsets directly from the mother plant, bypassing germination, as a method of survival in extreme weather conditions, from the Latin *viviparus* (that brings forth its young alive).

Notes. The closest species to *P. vivipara* is *P. alata* Ruiz & Pav., a species of wide distribution in Mexico, Central America, and all countries of South America except Chile, Argentina, and Uruguay, in tropical forests at lower elevations. Plants

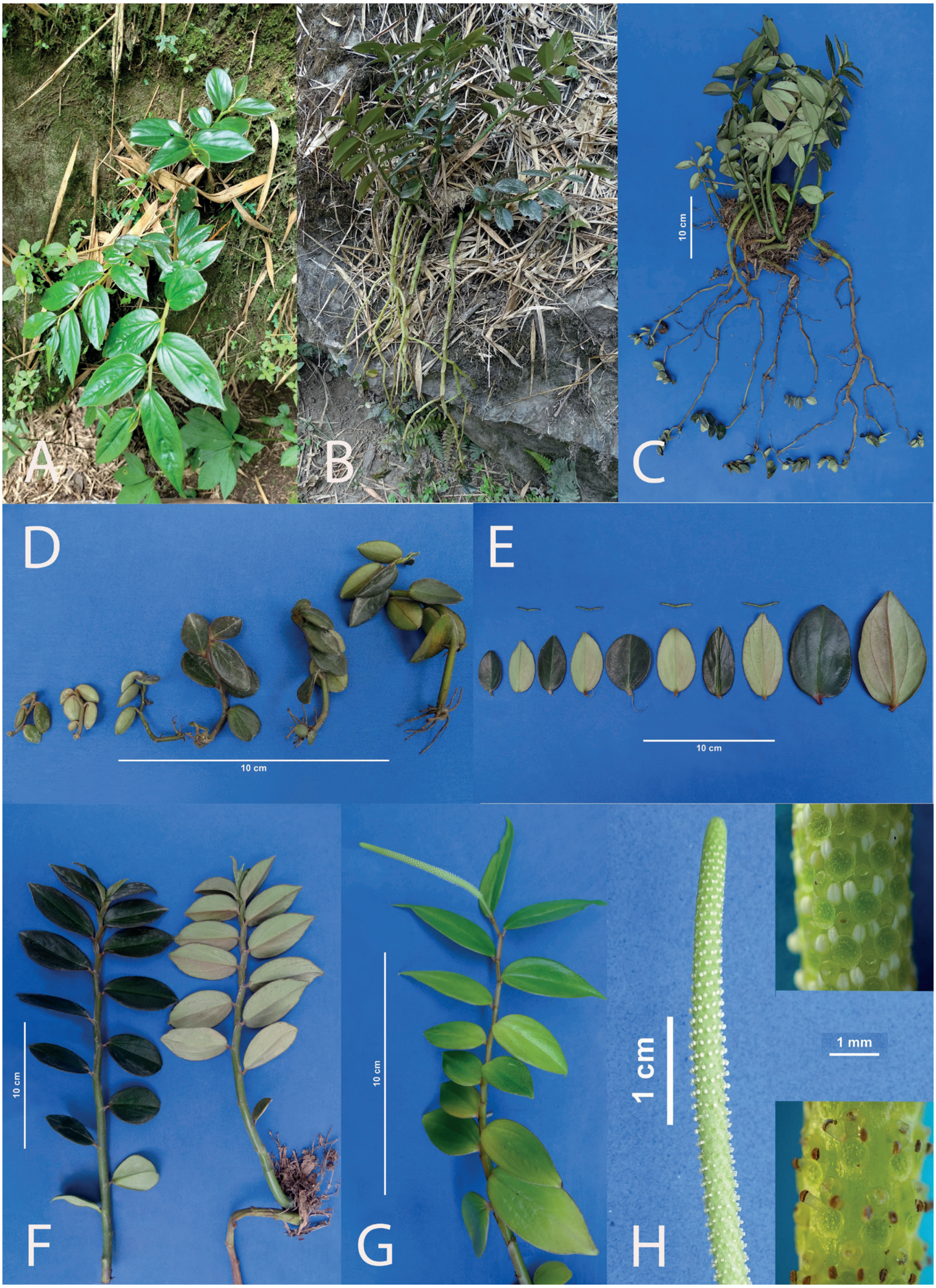

Figure 11. *Peperomia vivipara* Pino, Samain & L.E. Alomía, sp. nov. **A** young plant in habitat **B** mature plant in habitat showing offsets **C** plant *ex situ* showing offsets **D** propagules of different sizes just detached from mother plant **E** detail of leaves **F** detail of a branch: adaxial side (left), abaxial side (right) **G** branch with terminal spadix **H** spadix in anthesis.(Detail: Above, before; and below, after development of stamens).

Table 6. Comparison of the main differences between *P. vivipara* and *P. alata*.

Features	*Peperomia vivipara*	*Peperomia alata*
Height	30–45 cm	30 cm or more
Stem (diam. at base)	7–10 mm	3–8 mm
Internodes (distance)	2.5–5 cm	1–3 cm
Petioles (length and diam.)	2–10 mm long 1.5–2 mm diam.	3–20 mm long 0.8–2 mm diam.
Leaves (shape)	Elliptic to elliptic ovate, apex acute to slightly acuminate, base obtuse, subtruncate	Elliptic to elliptic-lanceolate, apex long acuminate, base acute, cuneate
Vegetative leaves (size)	3–6.5 cm long 1.8–3.2 cm wide	4.5–15 cm long 2–4.5 cm wide
Spadices (length)	3–6 cm	6–8 (–15) cm
Propagules at distal stem	Present	Absent

are similar in habit and size, they share the zig-zag winged internodes, although *P. vivipara* is stouter, with thicker and more erect branches with longer internodes. The main difference is in leaves, which are shorter, elliptic with an acute short apex and an obtuse or almost truncate base in *P. vivipara* compared to the lanceolate, long acuminate, and acute-based leaves of *P. alata*. A further difference is that *P. alata* does not produce propagules at the distal stems. (Table 6) These plantlets, that drop readily and root close to the mother plant propagating the plants vegetatively, have not been seen in any other species of *Peperomia* and give the name to the epithet of the species.

This species belongs to *Peperomia* subg. *Micropiper* (Miq.) Miq. (Frenzke et al. 2015).

Specimens examined. Peru, dept. Cajamarca, prov. Santa Cruz, dist. Catache: Monteseco, 5 km above, on the path to Chorro Blanco, 1500 m, [06°50'58.6"S, 79°05'53.7"W], 16 Mar 1986, *M.O. Dillon & A. Sagástegui 4366* (F 1993688); Same place, on the path below the campsite, 1450 m, [06°51'10.8"S, 79°06'09.4"W], 19 Mar 1986, *M.O. Dillon & A. Sagástegui 4432* (F 1993348); Monteseco, 3 km NE, 1750 m, 06°50'51.6"S, 79°06'14.7"W, 13 May 1987, *J. Santisteban C. & J. Guevara B. 044* (HUT 24730, F1995346). **Prov. San Miguel, dist. Niepos:** Road from La Florida to Monte Seco (Naranjo), 14.5 km from La Florida, 1643 m, 06°54'04.8"S, 79°07'33.5"W, 1 Mar 2009, *G . Mathieu & L. Symmank 165* (USM 258839); Road from Naranjo to La Florida, 1632 m, 06°54'00.2"S, 79°07'59.0"W, Jul 26 2020, *G. Pino & L.E. Alomía 3214*; Same road, 1613 m, 06°54'03.3"S, 79°07'33.5"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3215* (USM 330866); Idem, 1612 m, 06°54'03.3"S, 79°07'33.5"W, Feb 2 2023, *G. Pino & L.E. Alomía 3833* (USM 333271); Idem, 1393 m, 06°53'25.3"S, 79°06'57.7"W, 26 Jul 2020, *G. Pino & L.E. Alomía 3216* (USM 330867); Road from La Florida to Niepos, 1393 m, 06°53'25"S, 79°06'57"W, 28 Aug 2022, *G. Pino et al. 3643* (USM 330886); Same road, 1613 m, 06°54'03.3"S, 79°07'33.5"W, 28 Aug 2022, *G. Pino et al. 3645* (USM 330887).

Discussion

This research found 16 taxa of *Peperomia* in a radius of less than 25 km (Fig. 2). Previous studies had reported nine species of *Peperomia* in the protected area of Udima, north of the town of Monteseco (Sagástegui and Dillon 1991) and only four in the still unprotected forest La Oscurana in Bolívar (Juárez et al. 2005). It is noticeable that previous studies focus on "relict forests" that represent a sample of the former extension of the natural extents of these woodlands, but neglect to sample semi-arid environments that can also be rich in species, as we show in this article. This species richness could be explained by the influence of the AHZ, but the closest valleys to the north and south of Río Saña, also inside this zone have very scarce collections of this genus. Perhaps they deserve more research to verify if they share the same biodiversity.

We have observed that the highest diversity of *Peperomia* species occurs between 500 and 1600 m, although more rainfall and vegetation can be expected at higher altitudes. The species found in the upper layers (*P. hispidula*, *P. rotundata*. *P. microphylla*, *P. galioides*) have a broad distribution in the department of Cajamarca (Pino 2004) and even in the rest of the Americas. The fact that the endemic or rare species are concentrated in the middle range of mountain systems is an observation consistent with other floral studies (Vergara et al. 2017) but has no demonstrated explanation yet.

Another observation is that in the lower range, where more droughts threaten the diversity of species of *Peperomia*, we have found two species of subgenus *Fenestratae* and one of subgenus *Panicularia*. These subgenera are restricted to Ecuador and Peru, and they show an extreme adaptation to prolonged periods of drought through succulence. Other families adapted to this desertic environment, such as Cactaceae, – are also rich in diversity in this lower layer (Mischler 1988; Alomía 2020). Finally, our findings support the hypothesis that there are still many species of *Peperomia* in Peru awaiting their discovery.

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Supplementary material 1

Localities of *Peperomia* species from the Saña River Valley, Peru

Authors: Guillermo Eloy Pino Infante, Marie-Stéphanie Samain, Luis Enrique Aarón Alomía Collazos

Data type: COL (excel document)

Explanation note: Database of localities of *Peperomia* species found at the Saña River Valley Peru, data obtained from Herbarium sheets, personal collections, or calculations based on data from Herbarium labels.

Link: https://doi.org/10.3897/phytokeys.225.99277.suppl1

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RESEARCH ARTICLE

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Petrocodon wui (Gesneriaceae), a new species from Guizhou, China

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Abstract

Petrocodon wui F.Wen & R.B.Zhang (Gesneriaceae), a typically lithophyte occurring in the Danxia areas of north-western Guizhou, China, is described and illustrated as new to science. The new species shows overall similarity with *P. chishuiensis* Z.B.Xin, F.Wen & S.B.Zhou, which is also its sister species, based on molecular evidence. The new species can be distinguished from *P. chishuiensis* by the elongated rhizome, the relatively long indumentum on the peduncle, the shape, size and indumentum of calyx lobes, the location of the stamens in the corolla tube and the shape, size and indumentum of the stigma. We provide a diagnosis, detailed description, photographic images and a table with taxonomic notes to distinguish several other morphologically similar *Petrocodon* species.

Keywords

Didymocarpoideae, flora of Guizhou, lithophyte, new taxon, *Petrocodon chishuiensis*, taxonomy

Introduction

The genus, *Petrocodon* Hance (subfamily Didymocarpoideae, family Gesneriaceae), has 47 species, including the newly-published taxon *P. asterostriatus* F.Wen, Y.G.Wei & W.C.Chou (Möller 2019; GRC 2022; Yang et al. 2022). All known species of this genus are lithophytes (= rock dwelling), either growing in karst topographies or in Danxia landforms. This genus is mainly distributed in karst areas from eastern and south-western China to the northern Indo-China Peninsula, especially in Guangxi of China and North Vietnam (Wei 2018; Wei et al. 2022). Undoubtedly, China is the biodiversity centre of *Petrocodon* because there are at least 44 species (especially in Guangxi, with 25 species) (Wei 2018). Although many new taxa have been discovered and published in recent years, there were only two new taxa discovered and confirmed from Danxia landforms, namely *P. asterocalyx* F.Wen, Y.G.Wei & R.L.Zhang (Zhang et al. 2018) and *P. chishuiensis* Z.B.Xin, F.Wen & S.B.Zhou (Xin et al. 2020). It is well known that all species of *Petrocodon* are typically lithophilous and usually segregated into unique habitats, for example, karst caves and Danxia gorges, so that most of the species in this genus are narrow endemics (Fu et al. 2022a).

In early August 2021, we conducted a plant diversity survey in Xishui National Nature Reserve in Guizhou Province, China. We noticed an unknown species of Gesneriaceae growing on the surface of Danxia cliff in Niuqingshan, Dabaitang of the Xishui National Reserve. Based on its lithophytic habit and taxonomical characters, we considered it might belong to the genus *Petrocodon*. Upon closer examination of the flowering specimens in the lab and careful observation of living plants for comparison of vegetative and reproductive organs, we soon discovered several noticeable morphological differences that do not match any known *Petrocodon* species. Moreover, only two known species of *Petrocodon* endemic to Danxia landforms were confirmed before this species was discovered. Using morphology or molecular evidence, the new taxon of *Petrocodon* is recovered as sister to *P. chishuiensis*, but remarkably different from other species in surrounding cities and counties by some obvious characters. Thus, we concluded it corresponds to a species new to science.

Materials and methods

Taxonomic revision

The studied specimens were collected from the type locality and deposited in the Guangxi Institute of Botany Herbarium (IBK) and the Botany Herbarium of Zunyi Normal College (**ZY**). The macromorphological features were observed on the specimen sheets and taken from field notes and reports from the conservation nurseries at the National Gesneriaceae Germplasm Resources Bank (**NGGB**) of the Guangxi Institute of Botany (**GXIB**) and the Gesneriad Conservation Center of China (**GCCC**). Micromorphological observations were analysed and photographed using a stereomicroscope (Olympus Optical Microscope CX23). The morphological characters were compared with the protologue and type specimens of previously described *Petrocodon* species (Wang et al. 1990, 1998; Wei et al. 2010; Wei 2018), in particular those involving new taxa of *Petrocodon* from Guangxi and adjacent provinces (see notes) and herbarium specimens deposited at relevant herbaria (e.g. HITBC, IBK, IBSC, KUN, PE and VMNM).

The description of the new species follows the terminology used by Wang et al. (1998) and Harris and Harris (2001). Assessment of the conservation status of the new species was made according to the Categories and Criteria of the IUCN (IUCN Standards and Petitions Committee 2022).

Phylogenetic analysis

Leaf material of the undescribed species was collected from the type locality in Xishui County (Guizhou, China) and immediately dried in silica gel for DNA extraction (Chase and Hills 1991). The nuclear ribosomal internal transcribed spacer (ITS) region and plastid *trnL-F* intron spacer region (*trnL-F*) were used in the study. Primers, DNA extraction, PCR amplification and sequencing followed Yang et al. (2022). To elucidate the phylogenetic affinities of the undescribed species within the genus, we incorporated 39 samples representing 25 species (Table 1), following Yang et al. (2022). The ingroup contained 37 samples from 23 species of *Petrocodon*. *Primulina dryas* (Dunn) Mich. Möller & A.Weber and *P. pinnata* (W.T.Wang) Yin Z. Wang were chosen as outgroups, based on previous phylogenetic analyses (Möller et al. 2009; Weber et al. 2011; Zhang et al. 2018). We performed phylogenetic analyses of the included *Petrocodon* species, based on the combined dataset of *trnL-F* and ITS sequences using Maximum Likelihood (ML). We employed IQ-TREE v.2.0.6 (Nguyen et al. 2015) with 1000 bootstrap replicates (Hoang et al. 2018) and default ModelFinder (Kalyaanamoorthy et al. 2017) and found K3Pu+F+G4 as the best fit substitution model. Tree visualisation was carried out in FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/). Visual comparison of optimal tree topologies of *trnL-F* and ITS datasets was used to compare topological inconsistencies. Conflicts between tree topologies were considered significant when the inconsistent topologies received bootstrap values ≥ 80% (Fu et al. 2022b). As visual inspection showed no significant topological contradictions for bootstrap support consistency between the *trnL-F* and ITS datasets (results not shown), the two regions were combined in further analyses.

Taxonomic treatment

***Petrocodon wui* F.Wen & R.B.Zhang, sp. nov.**
urn:lsid:ipni.org:names:77317789-1
Figs 1, 2

Diagnosis. *Petrocodon wui* is distinguishable by the elongated rhizome, the shape, size and indumentum of calyx lobes, the two conspicuous rows of orange glands on throat and the abaxial surface of the corolla lip. It morphologically resembles *P. chishuiensis*, but can be distinguished by having an elongated rhizome up to 30 cm or longer after years of growth (vs. lacking obvious rhizome in *P. chishuiensis*, following same order); leaf blade oval-oblong (vs. oblong or oblanceolate) and margin conspicuously undulate

Table 1. The voucher and GenBank accession numbers used in this study.

Species name	Voucher number	*trnL-F*	ITS
Primulina dryas	C7a	FJ501524	FJ501348
Primulina pinnata	G26	FJ501526	FJ501349
Petrocodon retroflexus	–	KX579061	KX579060
Petrocodon nivelolanosus	–	JF697588	JF697576
Petrocodon lithophilus	CWH103	KF202303	KF202296
	CWH89	KF202302	KF202295
Petrocodon viridescens	Y .M.Shui et al 82661	HQ632939	HQ633036
	CWH41	KF202304	KF202297
Petrocodon integrifolius	M.Moeller MMO 06-865	HQ632940	HQ633037
Petrocodon lui	Y .G.Wei 8012	HQ632938	HQ633035
Petrocodon tiandengensis	09413	JX506850	JX506960
Petrocodon ainsliifolius	Y .M.Shui et al 44071	HQ632941	HQ633038
	CWH88	KF202298	KF202291
Petrocodon hispidus	CWH101	KF202301	KF202294
	CWH87	KF202300	KF202293
Petrocodon hunanensis	WF190107-02	MK941180	MK941179
Petrocodon tongziensis	Ren-Bo Zhang SBQ09383	MF872618	MF872617
Petrocodon chishuiensis	FW-2014	KF680503	KF680504
Petrocodon wui	WF065	OQ716553	OQ694978
Petrocodon coccineus	CWH14B	KF202299	KF202292
	G80E	FJ501516	FJ501341
Petrocodon hechiensis	–	KR476563	KR337018
	M.Moeller MMO 07-1077	HQ632942	HQ633039
Petrocodon hancei	M.Moeller MMO 08-1342	HQ632944	HQ633041
	–	KC904959	KC904956
	–	KC904958	KC904955
	GDLC05	KF498253	KF498051
Petrocodon asterocalyx	FW-2013	KC904957	KC904954
Petrocodon ferrugineus	M.Moeller MMO 06-784	HQ632946	HQ633043
Petrocodon multiflorus	HJ01-2	KM232660	KJ475411
Petrocodon coriaceifolius	M.Moeller MMO 06-913	HQ632943	HQ633040
Petrocodon scopulorus	W.Fang 2010-02	HQ632947	HQ633044
	–	GU350669	GU350637
	LJM06753	KR476567	KR337023
Petrocodon dealbatus	LJM1209291	KR476565	KR337020
	G12B	FJ501537	JF697578
	LJM-2003-104	GU350668	GU350636

Note. "–" indicates that the author did not provide the voucher number.

and densely ciliate (vs. serrate); cyme 4–10-flowered or more (vs. usually 1–3-flowered); anthers sparsely semi-transparent glands (vs. glabrous) and staminodes pale purple, club-like, glabrous (vs. absent or indistinctive).

Type. China, Guizhou Province, Zunyi City, Xishui County, Xishui National Nature Reserve, Dabaitang, Niuqingshan, elev. ca. 1100 m, growing on a shaded and moist rock surface on the Danxia cliff in the gorge, *Ren-Bo Zhang ZRB2401* (holotype: IBK!, isotypes: ZY!).

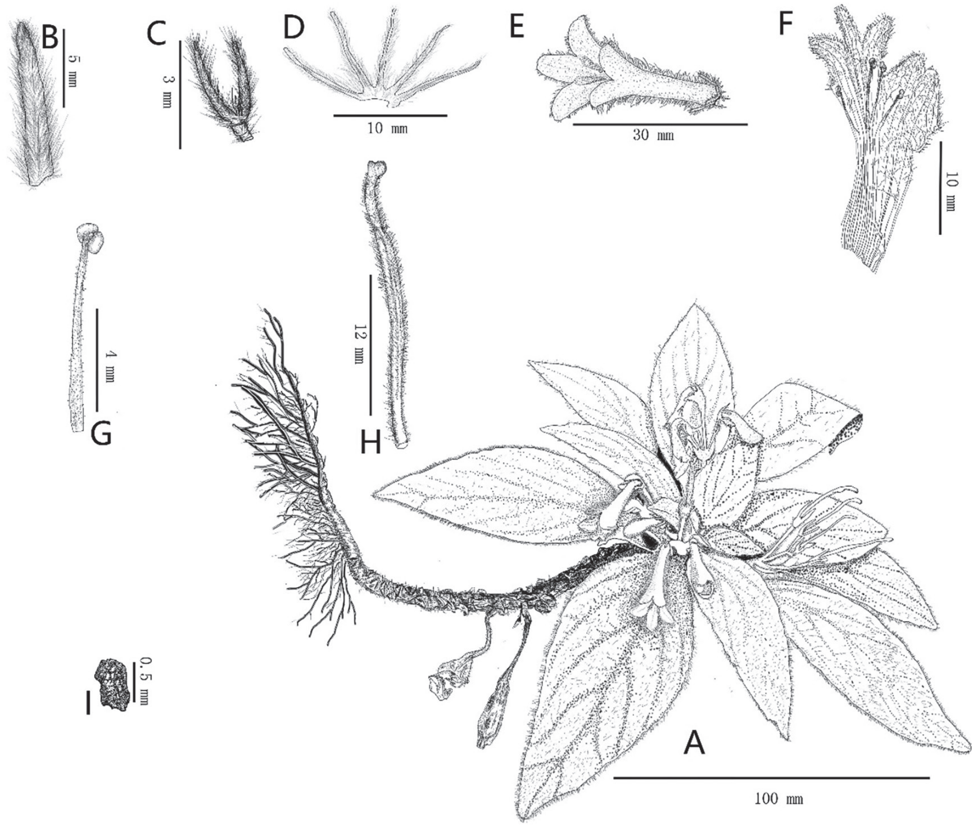

Figure 1. *Petrocodon wui* F.Wen & R.B.Zhang, sp. nov. **A** habit **B** bracts, showing the abaxial surface **C** bracteoles **D** abaxial surfaces of calyx lobe **E** top view of flower **F** opened corolla from the dried flower **G** one of stamens **H** pistil **I** seed. Drawings by Tan Deng from the type specimen.

Description. Perennial herb, strictly lithophytic. ***Rhizome*** brown, abundant fibrous roots, especially at the nodes, rhizome becoming very long and up to 30 cm or longer after years of growth, the lower half of long rhizome usually growing downwards along the surface of rock with lots of fibrous roots, apex of rhizome usually curved and forming a hooked shape, some persistent base of petioles spirally arranged on the surface of rhizome; upper rhizome densely covered with villous multicellular hairs ca. 2 mm long with 4–6 cells. ***Leaves*** in whorls of three, 6–15 crowded in a basal rosette or clustered at the top of elongated rhizome after years of growth, but usually some dried leaves persistent below foliage; petiole green, up to ca. 4 cm long, cylindrical, densely white pubescent; leaf blade chartaceous and thinly coriaceous when dried, oval-oblong, 6–10 × 1–3 cm, apex obtuse to acute or subacute, base cuneate, margin entire to inconspicuously or conspicuously undulate and densely ciliate, both surfaces densely white pubescent, lateral veins 4–5-paired; ***Inflorescences*** 1–4 or more, axillary, cymose, 4–10-flowered or more; peduncle pale green, 1–4 cm long, ca. 1.5 mm

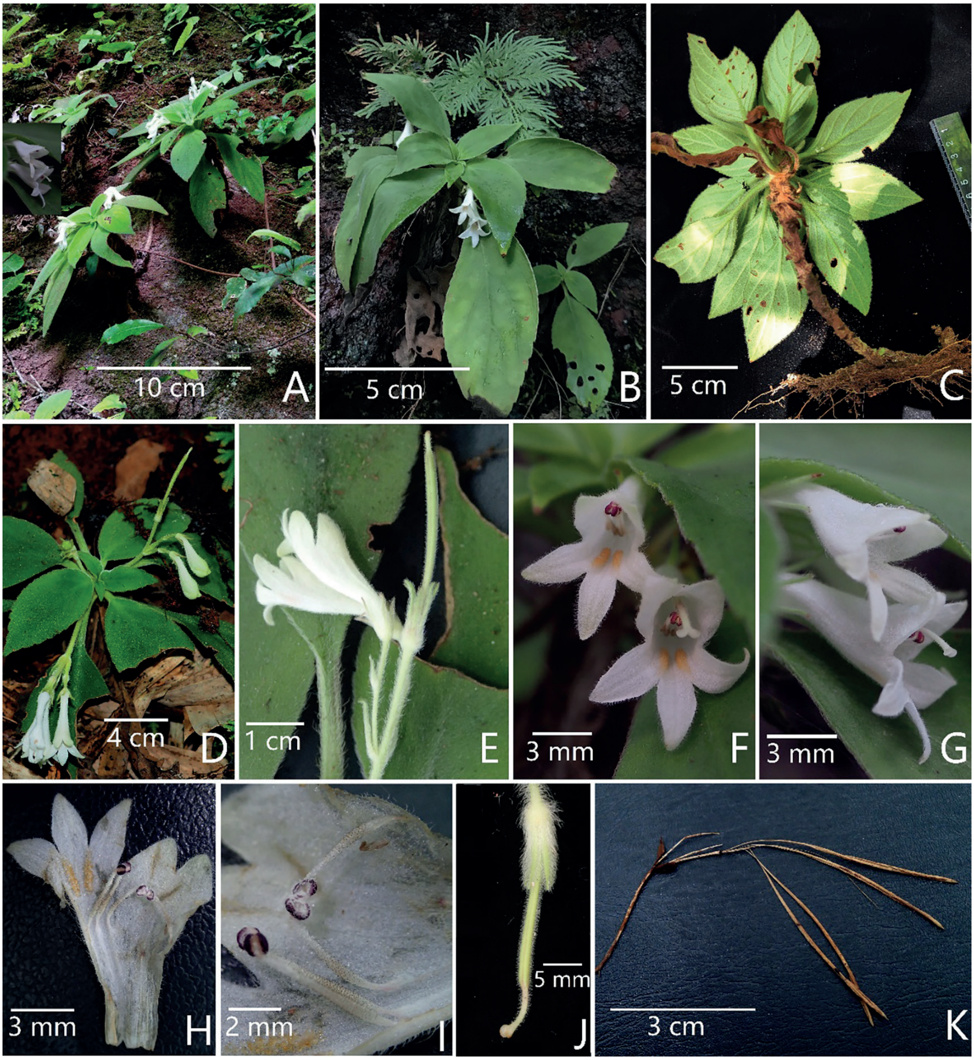

Figure 2. *Petrocodon wui* F.Wen & R.B.Zhang, sp. nov. **A** plants in bloom in natural habitat **B** plant in flower **C** upward view of plant showing the abaxial surfaces of leaf blade and petiole **D** flowering cyme **E** cymes, calyx and immature capsule **F** frontal view of corolla **G** lateral view of corolla and extended pistil **H** opened corolla **I** four fertile stamens **J** calyx and pistil **K** mature and dehiscent capsules (Photographed by F. Wen and R.B. Zhang).

in diameter, densely white villous; bracts 2, opposite, pale green, lanceolate, ca. 10 × 0.5 mm, apex acute, margin entire, both surfaces densely covered with villous multicellular hairs, ca. 1.5 mm long with ca. 3 cells; bracteoles 2, pale green, opposite, narrowly lanceolate, ca. 3 × 0.25 mm, indumentum same as bracts, but hairs on only ca. 2 cells; pedicels pale green, 0.8–2 cm long, indumentum same as peduncle. ***Calyx*** 5-sected to near the base, but base slightly united forming calyx tube ca. 1 mm long; lobes equal, pale green to whitish-green, nearly linear, 6–8 mm long, 5–6 mm wide at the base, apex obtuse to rounded, margin entire, outside densely covered with white villous hairs, inside sparsely covered with white villous hairs. ***Corolla*** tubular, white, zygomorphic, ca. 2.5 cm long, outside densely white pubescent, inside nearly glabrous, upper part of corolla close to mouth puberulent; corolla tube 1.7–2.2 cm long, ca. 2.5 mm wide at the base of corolla tube and ca. 4.5 mm at the widest part of corolla tube; limb 2-lipped, adaxial lip shorter, 2-lobed to the middle, lobes broadly triangular, ca. 1.5 mm long, ca. 2.5 mm at the bottom of lobe, abaxial lip longer, 3-lobed to the middle or slightly exceeding the middle, lobes ovate, central one longer than lateral ones, ca. 3.5 mm long, lateral ones ca. 2.8 mm long, with two conspicuous rows of orange glands on abaxial lip and corolla throat. ***Stamens*** 4, two longer ones adnate to corolla tube ca. 9.5 mm from the base, filaments ca. 4.5 mm long, two shorter ones adnate to corolla tube ca. 8.5 mm from the base, filaments ca. 4 mm long, all filaments linear, straight, but slightly arched at the base and turning into a sheet at the base, white to semi-transparent, densely with brownish-black glands, especially from the middle to the base and glandular-puberulent close to the upper of filament; anthers brownish-purple to dark purple, dorsi-fixed, elliptic to nearly rounded, ca. 1 mm long, ca. 0.9 mm wide, coherent in pairs, thecae confluent at middle, sparsely semi-transparent glands, dehiscing longitudinally. Staminode 1, pale purple, club-like, glabrous, adnate to corolla tube ca. 8 mm from the base. Disc annular, ca. 1 mm high, margin entire. ***Pistil*** ca. 2.5 cm long, densely erectly glandular-pubescent; ovary linear-cylindrical, ca. 2 cm long, ca. 1.5 mm wide, 1-loculed, placentas 2, parietal; style ca. 6 mm long, ca. 0.8 mm wide; stigma 2, lobes lamellar, rounded to shallowly spatulate, glabrous, ca. 1 mm long, 0.9−1 mm wide. ***Fruit*** a ***capsule*****,** ca. 5.5 cm long, linear-cylindrical, 4-valved, pubescent. ***Seeds*** appendaged, grain shortly cylindrical, rough, ca. 0.5 mm long, ca. 0.3 mm wide, covered densely verrucate.

Phenology. Flowering occurs in August in the wild; fruiting should occur in October, based on current flowering patterns.

Etymology. We dedicate this new species of *Petrocodon* to Wu Zheng-Yi (Wu Chengyih) (1916–2013), who devoted over 70 years to the flora of China. The scientific name, "*wui*", is the latinisation of Wu Zheng-Yi's family name. Coincidentally, a plant enthusiast, Lady Xiang-Hong Wu, took this species' flowering photos in 2017 and sent them to one of the authors (Fang Wen) and her surname is also Wu.

Vernacular name. The Chinese name proposed here is "吴氏石山苣苔." Phonetically, it is "Wú Shì Shí Shān Jù Tái".

Distribution and ecology. The new species is endemic to Guizhou Province and known only from the type locality, Xishui National Nature Reserve in Xishui County. It grows on the steep Danxia cliff in an evergreen, broad-leaved forest in a valley of the Danxia landform, at an altitude of 1100−1600 m. The cliff slope faces northwest at an angle of up to 60 to 80 degrees. The tree cover is up to 12 m tall, the canopy cover is 75%, the shrub layer cover is 85% and the herb layer cover is 35%.

Conservation status. *Petrocodon wui* is known only from the type locality, which is protected by national and local laws and regulations. However, it is clearly scarce, being known from only one very small area of occupancy, estimated at 20 m^2 on a rock surface in a valley of the Danxia landform. Obviously, this area of occupancy of *P. wui*

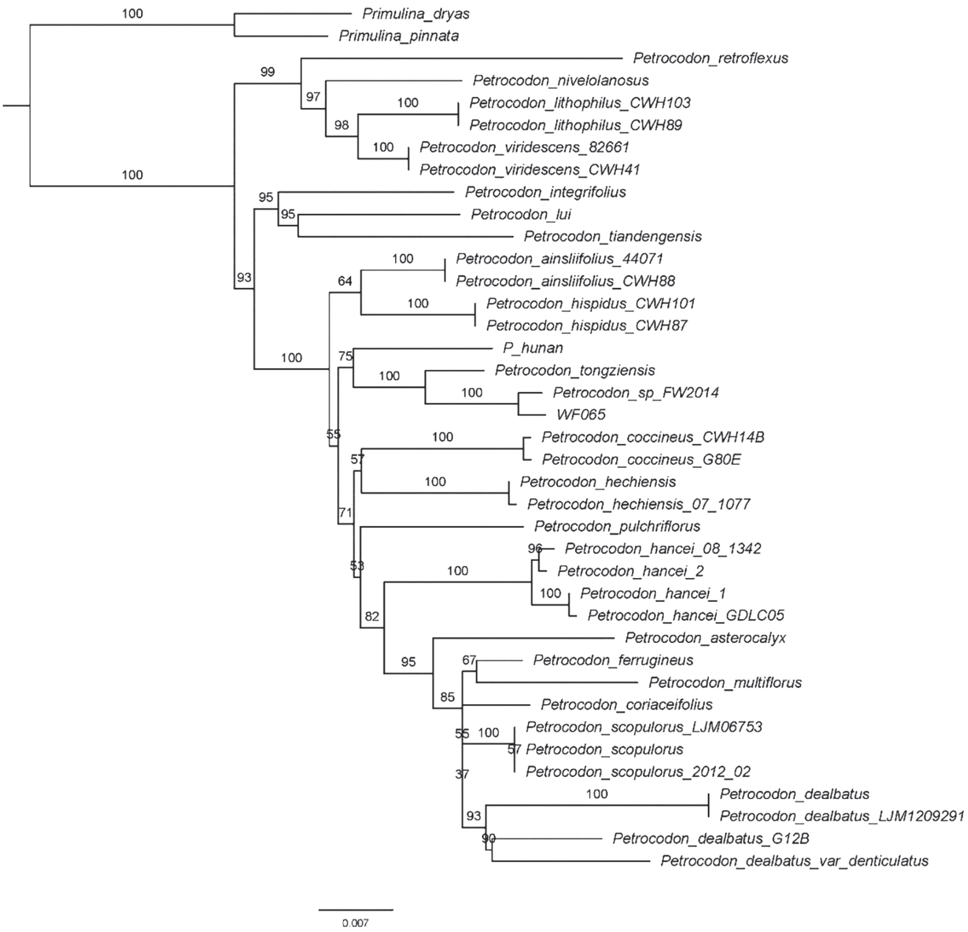

Figure 3. Phylogenetic tree of *Petrocodon* generated from Maximum Likelihood (ML) of *trnL-F* and ITS datasets. Numbers on the branches indicate ML bootstrap values (≥ 50%).

we found so far is significantly lower than the smallest AOO unit of IUCN which is 4 km^2 (2 × 2 km^2 grid) for Critically Endangered B2. According to the detailed information from our careful field observations on the surroundings of the type area, the known population has about 50 individuals, half of those being mature individuals and half being seedlings. According to the Guidelines for using the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022), *P. wui* is provisionally assessed as "Critically Endangered, CR B2ab(ii) + C2b" because of its limited distribution and vulnerable habitat.

Taxonomic and phylogenetic notes. The aligned matrix of *trnL-F* and ITS sequences comprised 1594 characters. Of the 370 (23.21%) variable characters, 222 (13.93%) were parsimony informative. The phylogenetic trees revealed that all sampled *Petrocodon* taxa clustered together as a monophyletic group (BP = 100%), which is consistent with previous studies (Yang et al. 2022). Three strongly-supported clades are attributed to *Petrocodon*. Of

Table 2. Morphological comparison of *Petrocodon wui* and *P. chishuiensis*.

Characters		***P. wui***	***P. chishuiensis***
Rhizome		present, becoming very long and up to 30 cm or longer after years of growth	lacking rhizome
Leaf blade			
	Shape	oval-oblong	oblong or oblanceolate
	Margin	entire to inconspicuously or conspicuously undulate and densely ciliate	serrate
	lateral veins	4–5-paired	5–6-paired
Flowers number per cyme		4–10-flowered or more	usually 1–3-flowered
Bracts			
	Shape	lanceolate	oblong
	Width	ca. 0.5 mm wide	ca. 3 mm wide
	Indumentum	both surfaces densely covered multicellular nodose villous and hairs ca. 1.5 mm long with ca. 3 cells	outside whitish pubescent, inside sparsely pubescent
Bracteoles	Size	ca. 3 × 0.25 mm	6–7 × ca. 1.5 mm
Calyx		5-sected to near the base, but base slightly united forming calyx tube and tube ca. 1 mm long	5-sected from base
Filaments			
	Length	two longer ones 4.5 mm long, two shorter ones ca. 4 mm long	two longer ones ca. 9 mm long, two shorter ones ca. 8 mm long
	Indumentum	densely with brownish-black glands especially from the middle to the base and glandular-puberulent close to the upper of filament	densely with glandular-puberulent hairs especially at the base
Anthers			
	Length	ca. 1 mm long	ca. 1.8 mm long
	Indumentum	sparsely semi-transparent glands	glabrous
Staminodes		pale purple, club-like, glabrous	absent or extremely indistinctive

these, the new species belonged in a moderately-supported subclade (BP = 75%) that also includes *P. hunanensis* X.L.Yu & Ming Li (Weber et al. 2011), *P. tongziensis* R.B.Zhang & F.Wen and *P. chishuiensis* (*Petrocodon_sp_FW2014*) (Fig. 3). This clade, denoted in Zhang et al. (2019), has four fertile stamens as a synapomorphy and our morphological observation of the new species supported this (Fig. 2). Within this clade, the new species is most closely related to *P. chishuiensis* (BP = 100%) (Fig. 3), whereas it can be easily distinguished from the latter by its rhizome, leaf blade, flowers number per cyme, bracts, bracteoles, calyx, filaments, anthers and staminodes, all of which are presented in Table 2.

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RESEARCH ARTICLE

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Palynological features and taxonomic significance for 16 species of *Gagea* (Liliaceae) from Xinjiang, China

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Abstract

Since pollen characters can be used to help distinguish species, our aim was to determine if palynological information has taxonomic significance for *Gagea* species from Xinjiang, China. *Gagea* is widely distributed in north temperate and the subtropical zones. The genus has limited taxonomic characteristics and large morphological variation, which results in difficulty of species classification. Pollen morphology of 16 species of this genus was examined comprehensively via light microscope (LM) and scanning electron microscope (SEM). One qualitative and nine quantitative traits of the pollen grains were surveyed, followed by hierarchical cluster analysis (HCA). The pollen grains were bilaterally symmetrical heteropolar monads with a mono-sulcus and they were oblate or peroblate (Polar diameter (P) / Equatorial diameter (E) = 0.36–0.73) in shape and medium to large (P = 17.17–34.64 µm, E = 27.63–81.65 µm) in size. Three types of exine ornamentation were observed: perforate, microreticulate and reticulate cristatum. The HCA divided the 16 species into two groups. This research provides new data on pollen morphology for *Gagea* (the pollen morphology of eight species was reported for the first time). Pollen morphology also can be used to identify species with similar external morphology, such as *G. nigra* and *G. filiformis*. Furthermore, the study of pollen morphology not only provides new data for palynology research on *Gagea*, but also provides a basis for future classification of this genus.

Keywords

HCA, pollen morphology, SEM, taxonomy

Introduction

Pollen morphology is scarcely affected by ecological conditions; thus, it is more stable than external macrographical morphology and has high genetic stability (Zarre and Zarrei 2005; Blackmore 2007; Kadluczka et al. 2022). Pollen size and morphology, such as shape, aperture type, mesocolpium diameter, exine ornamentation and perforation size, have great significance in plant taxonomy and pollen characteristics can be used to infer genetic relationships between ecological groups (Li et al. 2020) or interspecific taxonomic ranks (Heidarian et al. 2021).

Gagea Salisb. (Salisbury 1806) is a genus in tribe Tulipeae of Liliaceae and includes ca. 300 species (Patterson and Givnish 2002; Peruzzi 2016; Peterson et al. 2019). This genus has a wide distribution in regions of South Africa, Asia and Europe (Zarrei et al. 2007; Peterson et al. 2008; Peterson et al. 2019). In Asia, the western Pamir-Alai and western Tien-Shan Mountains are two centres of diversification of *Gagea*, and south-western Asia is the most probable ancestral area for *Gagea*. (Peterson et al. 2009; Peterson et al. 2019; Kurbaniyazova et al. 2022). Species circumscription in *Gagea* is difficult due to overlapping primitive and advanced morphological characters, particularly if only dried specimens are available for study (Zarrei et al. 2009; Tison et al. 2013). To add to the difficulty of identifying species of *Gagea*, there is enormous variation in vegetative and generative characters at various stages of ontogeny under variable ecological conditions (Levichev 1990, 1999) and polyploidy, hybridisation and convergent evolution make species boundaries unclear (Zarrei et al. 2011).

The initial phylogenetic analysis of *Gagea* was conducted in 2008 (Peterson et al. 2008), but the phylogenetic relationship between *Gagea* and *Lloydia* have been controversial. In accordance with the weight given to morphology and/or phylogeny and various molecular markers, various sections of *Gagea* have been suggested (Zarrei et al. 2011). Various molecular studies, based on ITS nrDNA and a distinct plastid dataset (*rbc*L, *ndh*F, *trn*L-*trn*F, *psb*A-*trn*H, *mat*K, *trn*K and *rpl*16 intron) have divided *Gagea* into seven sections (Zarrei et al. 2009), 13 sections (Levichev 2011), 14 sections (Peterson et al. 2008, 2016; Peruzzi 2012) or 15 sections (Levichev 2013; Tison et al. 2013). Molecular data reveal that *Lloydia* is phylogenetically nested within *Gagea*, forming a monophyletic group (Peterson et al. 2008; Zarrei et al. 2009). Therefore, a revision of *Gagea sensu lato* (including *Lloydia*) was proposed (Peruzzi et al. 2008; Zarrei et al. 2011) and recent data on pollen characteristics also supported the placement of *Lloydia* within *Gagea* (Hu et al. 2021).

The *Flora of China* includes 17 species of *Gagea* (Chen and Turland 2000); however, three new species from Inner Mongolia, three new species and two new records from Xinjiang recently have been described (Zhao and Zhao 2003, 2004; Zhao and Yang 2006; Peterson et al. 2011). Meanwhile, *G. nigra* was revised, based on morphological characters (Peterson et al. 2011). The Duocet Group (https://duocet.ibiodiversity.net/) moved eight species from *Lloydia* to *Gagea* according to APG IV and recognised that *Gagea sensu lato*. Xinjiang is located in northwest China which includes most of the Tien-Shan Mountains. According to statistics, there are 36 species of *Gagea* in China, 21 of which are naturally distributed in Xinjiang. These species are separated by morphological characters of the bulbs, leaves, flowers, fruits and seeds (Chen and Turland 2000; Peterson et al. 2011) and molecular data of cpDNA and nrDNA (Peterson et al. 2008, 2016).

At present, the pollen morphology of 46 species in *Gagea* has been described by various researchers from different regions in the world (Kosenko 1999; Zarre and Zarrei 2005; Wang et al. 2013; Hu et al. 2021; Sezer and Yildiz 2021). These studies demonstrated that shape and exine ornamentation have important information for taxonomic identification amongst species of *Gagea*. Eight species with reported pollen morphology were distributed in Xinjiang, China (Zarre and Zarrei 2005; Wang et al. 2013; Hu et al. 2021), but their taxonomic significance was not thoroughly investigated.

Through extensive field investigations in Xinjiang, we have found that *G. nigra* is similar to *G. filiformis*. The most salient resemblance characters were observed in *G. nigra* and *G. filiformis*, such as ovoid-globose bulb, brown or black tunic, leaf and flower number, umbellate or corymbose inflorescence, yellow tepals, capitate stigma, obovoid capsule and red-brown, ovoid-globose seeds. Furthermore, *G. jensii* shared morphological characters with *G. altaica* and *G. alberti*, including ovoid bulbs, taupe tunic, cauline leaves, corymbose or racemose inflorescence, yellow tepals, slightly 3-lobed stigma and brown flat seeds. Hence, the purpose of this research is to: (1) provide palynological information for 16 species of *Gagea* from Xinjiang, China, using a light microscope (LM) and scanning electron microscope (SEM); (2) distinguish species with similar morphology using palynological characters; and (3) explain the taxonomic significance of palynology in *Gagea*.

Materials and methods

Pollen materials

During April-July 2020–2022, a field investigation was carried out in Xinjiang, China, including the Altai Mountains, Tien-Shan Mountains, Kunlun Mountains and Junggar Basin to collect samples of pollen. Pollen collections were made from a total of 60 populations of the 16 *Gagea* species in Xinjiang. For widespread species (such as *G. bulbifera*, *G. fedtschenkoana* and *G. nigra*) at least five populations were included in this research. If there were no differences in pollen morphology amongst the populations of a species, one population was selected as a representative for SEM. If populations of a species varied, separate studies were conducted on all of the populations for the species.

The species were identified after collection by comparing their morphological characteristics to those listed in *Flora of China* (Chen and Turland 2000) and Peterson et al. (2011). Standardisation of the scientific names of species was according to Plants of the World Online (https://powo.science.kew.org). The voucher material of 16 species of *Gagea* used for SEM is given in Table 1. All voucher specimens were deposited in the Herbarium of Xinjiang Agricultural University (XJA).

Table 1. The list of materials for scanning electron microscope and vouchers of 16 species of *Gagea* from Xinjiang, China.

Species	Section (Peterson et al. 2016)	Locality	Coordinate	Altitude	Collection Date	Voucher
Gagea alberti Regel	*Plecostigm*a	Shihezi City, Xinjiang, China	44.188091°N, 86.088827°E	517 m	12 April 2022	J.Qiu & J.L.Li L-034 (XJA)
G. altaica Schischk. & Sumnev.	*Plecostigm*a	Fuyun County, Xinjiang, China	46.368831°N, 88.926181°E	777 m	15 April 2021	J.Qiu & M.S.Lin L-006 (XJA)
G. angelae Levichev & Schnittler	*Gagea*	Gongliu County, Xinjiang, China	43.110484°N, 82.751261°E	1660 m	4 May 2021	J.C.Chi Chijc4473 (XJA)
G. bulbifera (Pall.) Salisb.	*Bulbiferae*	Shawan County, Xinjiang, China	45.328851°N, 88.455975°E	561 m	7 April 2021	J.Qiu & M.S.Lin L-002 (XJA)
G. divaricata Regel	*Platyspermum*	Fukang City, Xinjiang, China	44.739223°N, 88.270266°E	616m	17 April 2021	J.Qiu & M.S.Lin L-011 (XJA)
G. fedtschenkoana Pascher	*Gagea*	Qinghe County, Xinjiang, China	46.746946°N, 90.873269°E	2761 m	6 June 2021	J.Qiu & M.S.Lin L-018 (XJA)
G. filiformis (Ledeb.) Kar. & Kir.	*Minimae*	Ürümqi City, Xinjiang, China	43.786772°N, 87.565508°E	1075 m	3 April 2021	J.Qiu & M.S.Lin L-004 (XJA)
G. fragifera (Vill.) E.Bayer & G.López	*Didymobolbos*	Burqin City, Xinjiang, China	48.429559°N, 87.207309°E	1988 m	9 June 2021	J.Qiu & M.S.Lin L-021 (XJA)
G. granulosa Turcz.	*Minimae*	Burqin City, Xinjiang, China	48.429694°N, 87.207108°E	1984 m	9 June 2021	J.Qiu & M.S.Lin L-023 (XJA)
G. jaeschkei Pascher	*Bulbiferae*	Qapqal County, Xinjiang, China	43.411647°N, 81.040648°E	2929 m	17 July 2021	J.Qiu & M.S.Lin L-30 (XJA)
G. jensii Levichev & Schnittler	*Plecostigm*a	Ürümqi City, Xinjiang, China	43.783443°N, 87.544818°E	1002 m	8 April 2021	J.Qiu & M.S.Lin L-005 (XJA)
G. nigra L.Z.Shue	*Minimae*	Ürümqi City, Xinjiang, China	43.783141°N, 87.544363°E	995 m	2 April 2021	J.Qiu & M.S.Lin L-003 (XJA)
G. neopopovii Golosk.	*Plecostigm*a	Huocheng County, Xinjiang, China	44.483283°N, 81.175174°E	2100 m	19 May 2021	X.J. Ge Gexj-21019 (XJA)
G. kunawurensis (Royle) Greuter	*Dschungaric*ae	Ürümqi City, Xinjiang, China	43.785813°N, 87.545323°E	997 m	20 April 2021	J.Qiu & M.S.Lin L-015 (XJA)
G. stepposa L.Z.Shue	*Bulbifera*e	Ürümqi County, Xinjiang, China	43.516102°N, 87.447984°E	1559 m	10 April 2022	J.Qiu & J.L.Li L-032 (XJA)
G. tenera Pascher	*Didymobolbos*	Nilka County, Xinjiang, China	43.724538°N, 82.070252°E	1033 m	22 April 2022	J.Qiu & J.L.Li L-041 (XJA)

Preparation and observation for pollen slides

All pollen grains were taken from fresh flowers, except for *G. angelae* and *G. neopopovii*, which were obtained from herbarium specimens. At peak flowering in each natural population, five individual plants were selected for pollen collection. Mature anthers were removed before dehiscence and placed in a clean glass bottle for natural drying.

Pollen slides were prepared following standard methods (Erdtman 1960) and observed under LM and investigated with the SEM following the methods of Halbritter et al. (2018). Mature pollen grains were mounted directly on dusted stubs with double-coated conductive glue and coated with gold-palladium, then examined under a Zeiss SUPRA 55VP (Carl Zeiss, Oberkochen, Germany). Terminology for the description of pollen follows Erdtman (1969), Punt et al. (2007) and Halbritter et al. (2018).

A label that referred to the number of the voucher specimen was attached to each slide. Pollen grains were photographed under LM (Nikon Eclipse 80i) at a magnification of 40× and SEM (Zeiss SUPRA 55VP) at an accelerating voltage of 2 kV. Each species/ population observed the polar diameter (P) and equatorial diameter (E) of 30 pollen grains under LM with an immersion objective lens (at 100× magnification). The microscopic morphological features of pollen [colpus width (Clt), colpus length (Clg), porus width (Plt), porus length (Plg), exine thickness (Ex), intine thickness (In) and ornamentation] were measured under SEM.

Data analysis

The results of palynological measurements were evaluated by statistical analysis and the contribution of each variable to the classification of each investigated was determined.

A one-way ANOVA was used to determine differences in pollen morphology of different populations of the same species. Prior to the analysis, the SPSS programme version 26 was used to test for normality and homogeneity of variance to satisfy the requirements of one-way analysis of variance (ANOVA). Differences amongst species were determined by the non-parametric Kruskal-Wallis test.

One qualitative (ornamentation) and nine quantitative palynological variables (polar diameter, equatorial diameter, P/ E, porus length, porus width, colpus length, colpus width, exine thickness and intine thickness) were evaluated in the comparative analysis for their value in distinguishing the studied *Gagea* species. Quantitative variables were represented by minimum (mean ± standard error) and maximum (for example: 20.34 (20.64 ± 0.24) 21.12 μm), whereas qualitative variables were recorded in the data matrix as 0, 1 or 2. Origin 2021 software was adopted for hierarchical cluster analysis (HCA) on *Gagea* pollen data. Euclidean distances of the stem were calculated after Z-score normalizing the original data and they were clustered using Ward's method (Ye et al. 2015).

Results

Within populations of each species, pollen shape and exine ornamentation were stable, but the size of pollen grains was not. One-way ANOVA showed that the means of equatorial diameter were not significantly different amongst populations of the same species ($p > 0.05$). Nevertheless, there was a significant difference in mean equatorial diameter amongst different species ($H = 378.016$, $df = 15$, $p < 0.001$). Therefore, a random population was selected as a representative material for each species for SEM and the micro-morphological characters of pollen grains were carefully observed.

In general, pollen grains of the *Gagea* species were similar in their morphological characters. The detailed pollen morphology data for the 16 species of *Gagea* are summarised in Table 2. Representative pollen grains of LM and SEM micrographs are shown in Figs 1–4.

Table 2. Pollen morphology of 16 species of *Gagea* from Xinjiang, China.

Species	P (μm) Min (Mean ± SE) Max	E (μm) Min (Mean ± SE) Max	P/E	Plg (μm) Min (Mean ± SE) Max	Plt (μm) Min (Mean ± SE) Max
Gagea alberti	20.34 (20.64±0.24) 21.12	42.77 (45.73±1.85) 49.14	0.45	0.28 (0.39±0.05) 0.72	0.24 (0.37±0.03) 0.57
G. altaica	27.93 (29.34±0.55) 30.61	57.32 (62.41±3.69) 73.36	0.47	0.24 (0.39±0.03) 0.58	0.21 (0.37±0.03) 0.49
G. angelae	26.38 (28.18±1.07) 30.07	71.97 (78.14±3.09) 81.65	0.36	0.46 (0.75±0.06) 1.04	0.42 (0.57±0.03) 0.71
G. bulbifera	26.28 (30.92±0.92) 34.64	36.73 (42.71±1.34) 51.34	0.73	0.16 (0.50±0.02) 0.49	0.14 (0.37±0.03) 0.43
G. divaricata	28.11 (28.56±0.40) 29.36	46.30 (56.86±5.30) 62.91	0.49	0.58 (0.72±0.08) 0.94	0.54 (0.68±0.11) 1.10
G. fedtschenkoana	22.37 (22.74±0.19) 23.02	49.12 (58.22±5.52) 68.18	0.41	0.13 (0.36±0.09) 0.62	0.13 (0.23±0.03) 0.33
G. filiformis	23.72 (24.58±0.41) 25.75	58.94 (62.60±2.21) 71.08	0.39	0.36 (0.45±0.05) 0.56	0.28 (0.40±0.06) 0.54
G. fragifera	20.98 (23.78±1.41) 25.50	62.22 (65.61±2.01) 69.16	0.36	0.44 (0.53±0.03) 0.63	0.29 (0.39±0.04) 0.50
G. granulosa	19.58 (25.50±2.96) 28.63	49.84 (51.89±1.04) 53.23	0.49	0.19 (0.30±0.02) 0.36	0.15 (0.22±0.02) 0.32
G. jaeschkei	15.07 (20.10±2.65) 29.43	33.36 (37.53±1.11) 39.43	0.54	0.12 (0.20±0.02) 0.26	0.06 (0.14±0.02) 0.26
G. jensii	22.86 (23.28±0.82) 25.80	46.89 (53.34±2.63) 62.16	0.44	0.13 (0.22±0.03) 0.44	0.10 (0.18±0.02) 0.33
G. neopopovii	17.17 (22.15±0.99) 26.13	27.63 (44.79±4.32) 66.88	0.54	0.30 (0.44±0.02) 0.69	0.15 (0.31±0.02) 0.62
G. nigra	20.26 (22.50±1.16) 24.14	41.77 (51.41±4.86) 57.35	0.45	0.27 (0.38±0.06) 0.55	0.13 (0.34±0.05) 0.42
G. kunawurensis	21.92 (23.58±0.88) 24.94	50.66 (56.82±3.20) 61.42	0.41	0.58 (0.78±0.05) 1.00	0.43 (0.64±0.03) 0.76
G. stepposa	25.31 (26.15±0.43) 26.68	58.51 (61.87±1.90) 65.10	0.42	0.28 (0.46±0.05) 0.73	0.17 (0.39±0.05) 0.63
G. tenera	18.34 (23.14±2.43) 29.17	42.89 (48.63±3.47) 58.31	0.47	0.28 (0.43±0.04) 0.63	0.18 (0.33±0.04) 0.52

Species	Clg (μm) Min (Mean ± SE) Max	Clt (μm) Min (Mean ± SE) Max	Ex (μm) Min (Mean ± SE) Max	In (μm) Min (Mean ± SE) Max	Ornamentation
Gagea alberti	41.35 (44.38±1.95) 48.02	1.67 (1.95±0.19) 2.32	0.93 (1.57±0.18) 2.93	0.50 (0.90±0.09) 1.45	Perforate (0)
G. altaica	56.01 (60.35±3.36) 70.38	3.25 (3.61±0.38) 4.01	0.81 (1.59±0.07) 2.08	0.58 (0.97±0.04) 1.39	Microreticulate (1)
G. angelae	69.65 (75.38±2.87) 78.32	0.87 (1.60±0.47) 2.48	0.88 (1.83±0.12) 2.42	0.61 (0.99±0.05) 1.29	Reticulate cristatum (2)
G. bulbifera	36.47 (42.05±2.02) 48.24	1.71 (2.14±0.23) 2.78	1.41 (1.90±0.08) 2.63	0.78 (1.16±0.07) 1.93	Microreticulate (1)
G. divaricata	43.60 (53.08±4.74) 57.84	3.74 (3.95±0.19) 4.33	1.11 (1.65±0.08) 2.26	0.51 (0.81±0.06) 1.42	Reticulate cristatum (2)
G. fedtschenkoana	47.10 (56.07±5.62) 66.42	1.51 (1.60±0.06) 1.71	1.32 (1.77±0.07) 2.17	0.72 (0.92±0.03) 1.14	Microreticulate (1)
G. filiformis	55.51 (59.02±2.45) 68.68	1.96 (2.17±0.13) 2.71	0.47 (1.41±0.12) 2.35	0.28 (0.75±0.06) 1.14	Microreticulate (1)
G. fragifera	57.64 (61.54±2.80) 66.98	1.85 (2.00±0.08) 2.12	0.76 (1.66±0.11) 2.16	0.39 (0.87±0.06) 1.38	Reticulate cristatum (2)
G. granulosa	46.19 (49.36±1.62) 51.54	2.04 (2.70±0.56) 3.81	1.72 (2.30±0.10) 2.73	0.94 (1.23±0.06) 1.57	Perforate (0)
G. jaeschkei	30.47 (34.31±1.01) 36.46	0.73 (1.54±0.27) 2.36	1.02 (1.94±0.13) 2.36	0.56 (1.04±0.08) 1.40	Perforate (0)
G. jensii	44.45 (51.18±2.70) 60.38	1.64 (2.59±0.29) 3.09	1.22 (1.49±0.18) 2.18	0.76 (1.06±0.14) 1.57	Perforate (0)
G. neopopovii	24.98 (41.03±4.53) 63.26	1.13 (1.30±0.06) 1.83	1.00 (1.79±0.20) 2.70	0.64 (1.04±0.14) 1.57	Reticulate cristatum (2)
G. nigra	39.05 (48.80±4.97) 55.39	0.92 (1.24±0.30) 1.85	1.12 (1.59±0.09) 2.24	0.53 (0.83±0.05) 1.12	Reticulate cristatum (2)
G. kunawurensis	48.20 (54.48±3.34) 59.61	1.18 (1.62±0.33) 2.26	1.34 (1.97±0.08) 2.51	0.78 (1.14±0.05) 1.46	Reticulate cristatum (2)
G. stepposa	57.46 (60.59±1.67) 63.19	2.30 (2.55±0.14) 2.78	0.66 (1.31±0.10) 1.85	0.27 (0.72±0.07) 1.32	Microreticulate (1)
G. tenera	38.48 (44.19±3.38) 53.58	0.54 (1.01±0.30) 1.87	1.08 (2.10±0.13) 2.89	0.44 (1.07±0.08) 1.48	Reticulate cristatum (2)

Abbreviations: P: Polar diameter; E: Equatorial diameter; Plg: Porus length; Plt: Porus width; Clg: Colpus length; Clt: Colpus width; Ex: Exine thickness; In: Intine thickness.

Figure 1. Light microscope micrographs of pollen grains of eight species of *Gagea* from Xinjiang, China **A, A1** *Gagea alberti* **B, B1** *G. altaica* **C, C1** *G. angelae* **D, D1** *G. bulbifera* **E, E1** *G. divaricata* **F, F1** *G. fedtschenkoana* **G, G1** *G. filiformis* **H, H1** *G. fragifera*. **A–H** Pollen grain in polar view **A1–H1** Pollen grain in equatorial view. Scale bars: 10 μm.

Shape and size

Pollen grains of all species were heteropolar monads and they were mono-sulcus, bilaterally symmetrical and ellipsoidal in polar view. Pollen shape was oblate (Figs 1D, 2J, L) or peroblate (Figs 1A–C, E–H, 2I, K, M, N–P), based on the P/E ranges (Table 2). Pollen size was medium (Figs 3A, D, 4J, L, P) to large (Figs 3B, C, E, F–H, 4I, K, M–O), based on measurements of the equatorial diameter (Table 2).

Exine, intine and ornamentation

Thickness of the pollen exine and intine of all species was similar, ranging from 1.31 ± 0.10 to 2.3 ± 0.1 μm and from 0.72 ± 0.07 to 1.23 ± 0.06 μm, respectively. Only *G. stepposa* had a thinner exine than the other species (Table 2).

Three types of pollen grain exine ornamentation were identified: type I, Perforate (Figs 3A1, 4I1, J1, K1), type II, Microreticulate (Figs 3B1, D1, F1, G1, 4O1) and type III, Reticulate cristatum (Figs 3C1, E1, H1, 4L1, M1, N1, P1).

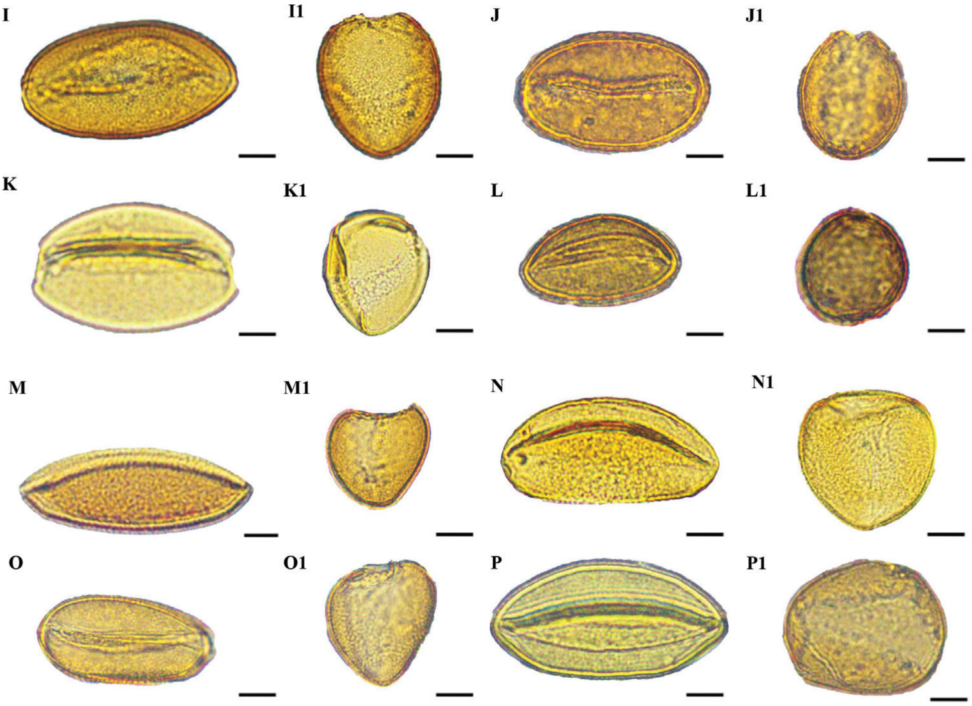

Figure 2. Light microscope micrographs of pollen grains of eight species of *Gagea* from Xinjiang, China. **I, I1** *Gagea granulosa* **J, J1** *G. jaeschkei* **K, K1** *G. jensii* **L, L1** *G. neopopovii* **M, M1** *G. nigra* **N, N1** *G. kunawurensis* **O, O1** *G. stepposa* **P, P1** *G. tenera*. **I–P** Pollen grain in polar view. **I1–P1** Pollen grain in equatorial view. Scale bars: 10 µm.

In type I, exine ornamentation had gemmate protuberances. Perforations were smaller than muri and observed throughout the pollen grains. This type was found in *G. alberti*, *G. granulosa*, *G. jaeschkei* and *G. jensii*. The smallest pollen grains were in *G. jaeschkei* with a size (i.e. polar diameter × equatorial diameter) of 20.10 ± 2.65 × 37.53 ± 1.11 µm and the largest pollen grains in *G. jensii* with a size of 23.28 ± 0.82 × 53.34 ± 2.63 µm.

In type II, lumina were not similar in diameter and they were as wide as the muri or smaller than the muri. Muri were complete or compound and the width was narrow from the proximal to distal surface. This type was found in *G. altaica*, *G. bulbifera*, *G. fedtschenkoana*, *G. filiformis* and *G. stepposa*. The smallest pollen grains were discovered in *G. bulbifera* with a size of 30.92 ± 0.92 × 42.71 ± 1.34 µm and the largest pollen grains in *G. filiformis* with a size of 24.58 ± 0.41 × 62.6 ± 2.21 µm.

In type III, lumina were similar in diameter, they were as wide as the muri or wider than the muri. Muri had regular prominent croton pattern or gemmate suprasculpture. Type III was found in *G. angelae*, *G. divaricata*, *G. fragifera*, *G. neopopovii*, *G. nigra*, *G. kunawurensis* and *G. tenera*. The smallest pollen grains were for *G. neopopovii* with a size of 22.15 ± 0.99 × 44.79 ± 4.32 µm and the largest pollen grains in *G. angelae* with a size of 28.18 ± 1.07 × 78.14 ± 3.09 µm.

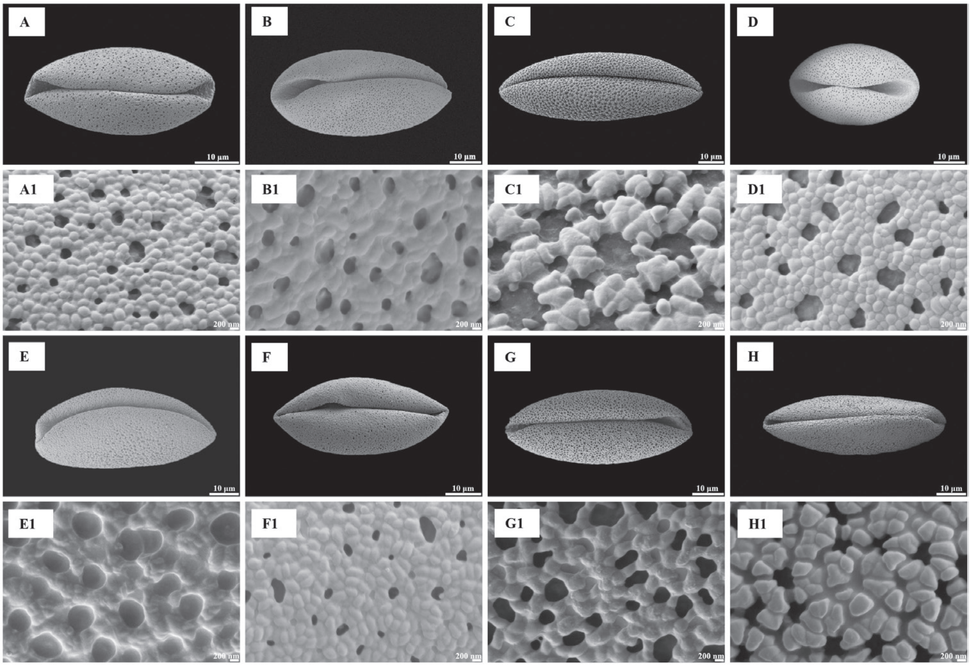

Figure 3. Pollen grains in polar view (**A–H**) and exine ornamentation (**A1–H1**) under scanning electron microscope for eight species of *Gagea* from Xinjiang, China **A, A1** *Gagea alberti* **B, B1** *G. altaica* **C, C1** *G. angelae* **D, D1** *G. bulbifera* **E, E1** *G. divaricata* **F, F1** *G. fedtschenkoana* **G, G1** *G. filiformis* **H, H1** *G. fragifera*.

Hierarchical cluster analysis (HCA)

The palynological groups of the species, based on their relevance, were evaluated by hierarchical cluster analysis. In this analysis, pollen morphology separated the *Gagea* species into two groups, based on Euclidean distance of 7.01. Group A included *G. alberti*, *G. bulbifera*, *G. granulosa*, *G. jaeschkei*, *G. jensii*, *G. neopopovii* and *G. tenera*. It was arranged into two subgroups (A1 and A2), based on Euclidean distance of 5.95. Whereas group B involved *G. altaica*, *G. angelae*, *G. divaricata*, *G. fedtschenkoana*, *G. filiformis*, *G. fragifera*, *G. kunawurensis*, *G. nigra* and *G. stepposa* (Fig. 5).

Discussion

Our results supported previous research showing that the pollen grains in *Gagea* were bilaterally symmetrical heteropolar monads with a mono-sulcus (Kosenko 1999; Su et al. 2004; Zarre and Zarrei 2005; Wang et al. 2013; Hu et al. 2021; Sezer and Yildiz 2021). Grain exine ornamentation was divergent amongst the species and often served as a diagnostic character (Chung et al. 2010). Additionally, exine ornamentation was one of the most variable characters in *Gagea* pollen, with three types observed in our

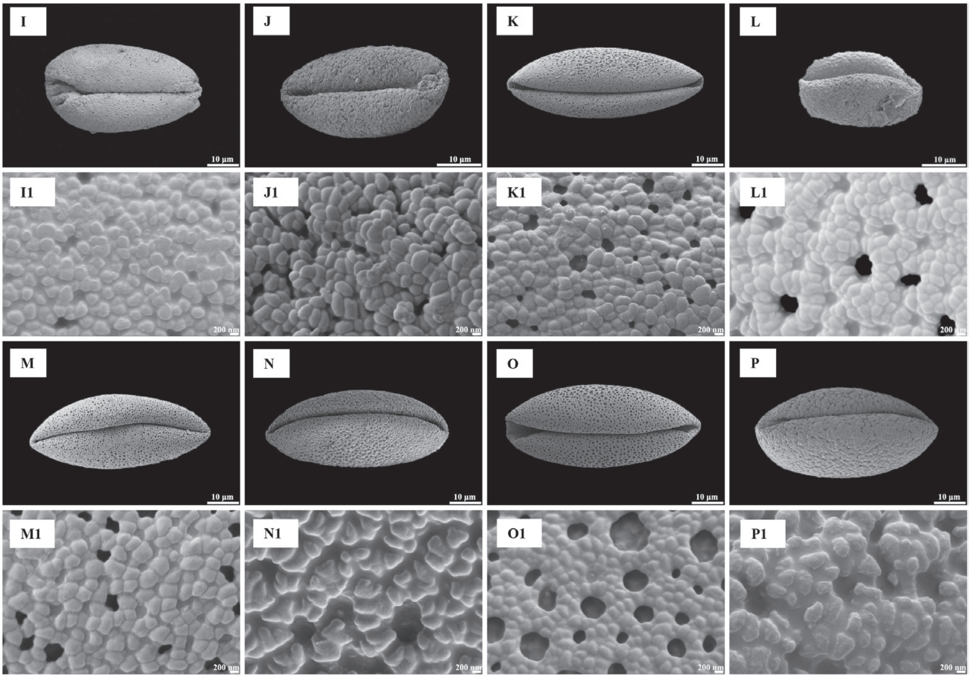

Figure 4. Pollen grains in polar view (**I–P**) and exine ornamentation (**I1–P1**) under scanning electron microscope for eight species of *Gagea* from Xinjiang, China **I, I1** *Gagea granulosa* **J, J1** *G. jaeschkei* **K, K1** *G. jensii* **L, L1** *G. neopopovii* **M, M1** *G. nigra* **N, N1** *G. kunawurensis* **O, O1** *G. stepposa* **P, P1** *G. tenera*.

research (Table 2). Zarre and Zarrei (2005) recognised four pollen exine ornamentation types within *Gagea* and *G. bulbifera* and *G. tenera* were described as microreticulate and reticulate, respectively and matched type II (microreticulate) and type III (reticulate cristatum) of our research, respectively (Table 2). Pollen exine ornamentation of *G. ova* (synonym of *G. kunawurensis*) was described as foveolate (Zarre and Zarrei 2005), differing from type III (reticulate cristatum) found in our research. This result remains to be further confirmed due to lack of photographs in literature.

Pollen morphology of five *Gagea* species (*G. alberti*, *G. bulbifera*, *G. fedtschenkoana*, *G. granulosa* and *G. nigra*) collected from Xinjiang have been described (Wang et al. 2013; Hu et al. 2021). Wang et al. (2013) and Hu et al. (2021) described the exine ornamentation of *G. fedtschenkoana* pollen as verrucate, whereas we described it as perforate (Table 2). Moreover, the exine ornamentation of *G. filiformis* and *G. granulosa* collected from other regions was described as rugulate-perforate and reticulate, respectively (Hu et al. 2021), whereas the exine ornamentation of *G. filiformis* and *G. granulosa* described in our research was microreticulate and perforate, respectively (Table 2). Our results are consistent with those in literature when we compare our results with the published figures and the divergence in descriptions might be due to variations in terminology. Overall, the available data provide compelling evidence that pollen morphology exhibits high genetic stability.

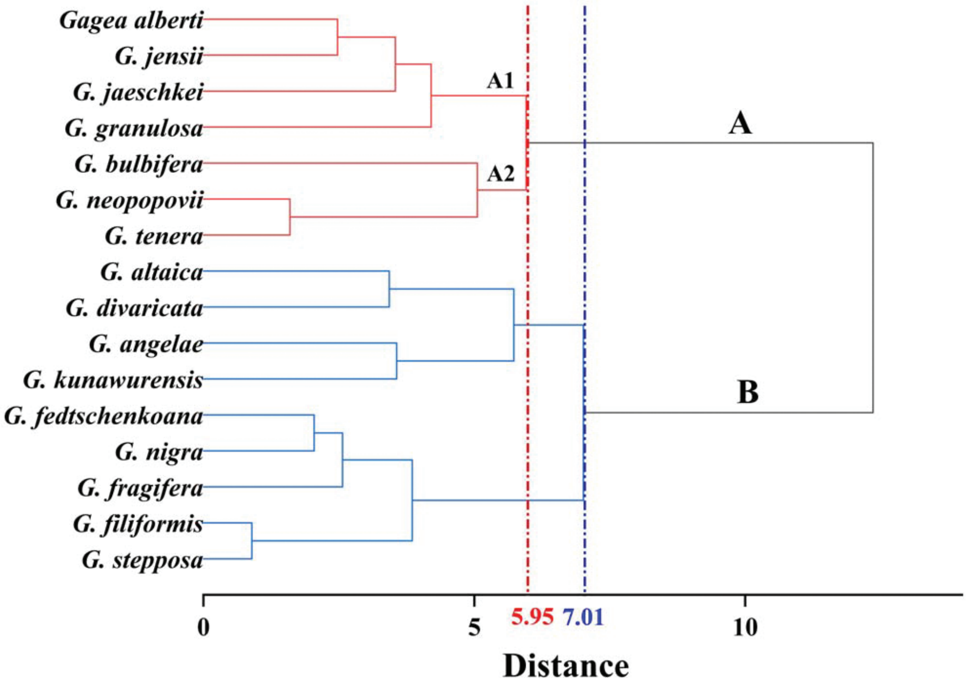

Figure 5. Cluster diagram (Ward's linkage) of 16 species in *Gagea* from Xinjiang, China, based on one qualitative and nine quantitative pollen characters.

Pollen characters have been employed as useful morphological features for the identification of species or genera and they have been applied widely to *Allium* (Nour et al. 2022), *Praxelis* (de Abreu et al. 2015), *Fritillaria* (Samaropoulou et al. 2022) and *Lythrum* (Vieira et al. 2022) to elucidate intricate taxonomic relationships. Moreover, pollen characters are effective and valuable in distinguishing species with similar morphological features (Ahmad et al. 2022). The pollen of *G. nigra* and *G. filiformis*; *G. jensii*, *G. altaica* and *G. alberti* displayed differences in morphological characters that could be used as identification tools, while the applicability of other morphological characters, such as shape of bulb, leaves, inflorescence, stigma and seeds, colour of tunic, tepals and seeds, number of leaves and flowers, for species identification is restricted. Pollen grains of the above five species were large and peroblate and only the pollen grains of *G. alberti* were medium in size (Table 2). In addition, the aperture type, porus size and pollen wall thickness of these species were similar between species. *Gagea nigra* pollen had reticulate cristatum exine ornamentation, whereas that of *G. filiformis* was microreticulate (Figs 3G1, 4M1). *G. jensii* and *G. alberti* pollen had perforate exine ornamentation, whereas that of *G. altaica* was microreticulate (Figs 3A1, B1, 4K1). Despite *G. jensii* and *G. alberti* pollen grains having similar exine ornamentation, they differed in size. (Table 2). Pollen size should be evaluated with circumspection, because it is known to be influenced by biological factors (Rahmawati et al. 2019).

Information on palynology should be used to provide new insight into the differences (or not) between species. For example, in the revision of *G. nigra* by Peterson et al. (2011) that also includes a description of three new species (including *G. jensii* and a comparison of the morphology of *G. jensii* and *G. alberti*), the morphology of *G. jensii* differs from that of *G. alberti*. However, we found that the pollen morphology of *G. jensii* and *G. alberti* is the same (Figs 3A1, 4K1), suggesting that they are possibly the same species. Thus, we suggest that verification of *G. jensii* and *G. alberti* as separate species must be further investigated using cytological, molecular phylogenetic or anatomical techniques. Our research provides a new way to diagnosis species with similar morphological characteristics, but they are not exhaustive.

According to recent infrageneric classification of *Gagea*, the species in this research belong to seven sections (Table 1) (Peterson et al. 2016). HCA was performed on the palynological data obtained from both LM and SEM. Group A included two subgroups (A1, A2) and contained three species of sect. *Plecostigma* (*G. alberti*, *G. jensii* and *G. neopopovii*), two species of sect. *Bulbiferae* (*G. bulbifera* and *G. jaeschkei*) and one species of sect. *Minimae* (*G. granulosa*), sect. *Didymobolbos* (*G. tenera*). The subgroup A1 enclosed four species with perforate exine ornamentation, while the subgroup A2 involved three species with medium size (Fig. 5, Table 2). Group B, which represents the large-sized and oblate-shaped pollen grains, encompassed the following sections: sect. *Plecostigma* (*G. altaica*), sect. *Bulbiferae* (*G. stepposa*), sect. *Didymobulbos* (*G. fragifera*), sect. *Dschungaricae* (*G. kunawurensis*), sect. *Gagea* (*G. angelae* and *G. fedtschenkoana*), sect. *Minimae* (*G. filiformis* and *G. nigra*) and sect. *Platyspermum* (*G. divaricata*) (Fig. 5, Table 2). Thus, the results of the HCA are equivocal as the subgroups contain species from both the same and different sections.

Gagea nigra and *G. filiformis* belong to the sect. *Minimae*, and morphology and molecular evidence suggest that *G. nigra* is an independent species separated from *G. filiformis* (Peterson et al. 2011). We have also confirmed this view through palynology results, based on two species clustered into one group (Fig. 5). In contrast, *G. altaica*, *G. jensii* and *G. alberti* belong to the sect. *Plecostigma*. However, *G. altaica* separated into a different group with *G. jensii* and *G. alberti*, based on palynology (Fig. 5). This may indicate that there are pollen synapomorphies related to the systematics in certain sections, but not necessarily in all sections.

Although the results are not able to offer a diagnostic key amongst groups of *Gagea* taxa in Xinjiang, China, they demonstrate that palynology may aid in the taxonomy of the genus by differentiating between taxa within their groups.

Conclusion

Pollen morphology of eight species of *Gagea* from Xinjiang, China was reported for the first time in our research. *Gagea* pollen grains were heterogenous in shape, size and exine ornamentation. Pollen characters have a certain taxonomic effect on the interspecies of *Gagea*, but the taxonomic relationship cannot be fully clarified only by pollen morphology. The results of the current research have provided palynological data for the classification of *Gagea* and also contribute to future classification of this genus.

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Supplementary material 1

Species collection table and a one-way ANOVA results of species with more than two populations

Authors: Musen Lin, Juan Qiu, Kaiqing Xie, Dunyan Tan

Data type: pdf file

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RESEARCH ARTICLE

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A new species of *Struthanthus* Mart. (Loranthaceae) from Oaxaca, Mexico

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Abstract

Struthanthus ibe-dzi **sp. nov.** is a new species described and illustrated from the cloud and pine-oak forests of the Sierra Madre del Sur in Oaxaca, Mexico. This species shares similarities of leaf shape and inflorescence type with *S. deppeanus*, *S. quercicola*, and *S. ramiro-cruzii*. However, *S. ibe-dzi* can be recognized by its glaucous branches, leaves and inflorescences; compressed nodes; convoluted distal half of styles in pistillate flowers; and staminate flowers with asymmetrical thecae and an extended connective forming an apiculate horn in both anther series. A distribution map and an identification key are provided to separate *S. ibe-dzi* from morphologically similar congeners present in the region.

Resumen

Struthanthus ibe-dzi **sp. nov.**, es una nueva especie descrita e ilustrada de los bosques de niebla y de pino-encino de la Sierra Madre del Sur en Oaxaca (México). La nueva especie se puede confundir con *S. deppeanus*, *S. quercicola*, y *S. ramiro-cruzii* por la forma de la hoja y el tipo de inflorescencia. Sin embargo, *S. ibe-dzi* se distingue por sus ramas, hojas e inflorescencias glaucas; sus nodos comprimidos; flores pistiladas con el estilo convoluto desde la mitad hacia la parte distal; y flores estaminadas con tecas asimétricas y un conectivo extendido apiculado en forma de cuerno en la serie baja de las anteras. Se incluye un mapa de distribución y una clave de identificación para separar *S. ibe-dzi* de sus congéneres regionales morfológicamente similares.

Keywords

Endemic, hemiparasitic, mistletoes, taxonomy

Introduction

Struthanthus Mart. is a neotropical genus in the Loranthaceae family with approximately 60–70 species (Caires and Dettke 2020) distributed from Northern Mexico to Argentina (Kuijt and Hansen 2015). The genus comprises hemiparasitic aerial shrubs or climbing plants which are dioecious (Kuijt 2009a; Kuijt and Hansen 2015; Nickrent et al. 2019). *Struthanthus* is commonly recognized by the presence of thick epicortical roots at the base of the plant and along stems. Additional important characters include stems teretes, sub-teretes or quadrangular (when young), with lenticels and a glabrous, striated, or sulcate texture (Kuijt 2009a; Kuijt and Hansen 2015; Caires and Dettke 2020); leaves opposite, subopposite, or rarely alternate, sometimes with stiffly recurved leaves and prehensile petioles (Caraballo-Ortiz and Acevedo-Rodríguez 2021; Maldonado 2021); axillar and indeterminate inflorescences in racemes, spikes, or head-like with pedunculate or sessile triads; flowers small (4–10 mm long), hexamerous, pedicellate or sessile; staminate flowers with dimorphic stamens, dorsifixed (Kuijt 2009b; Kuijt and Hansen 2015) but basifixed in at least some of the Mexican species (Maldonado 2021); and pistillate flowers with monomorphic staminodes and styles straight to strongly convolute in some Mexican species (Kuijt 1975a, 2003a; Maldonado 2021).

Despite the lack of a comprehensive taxonomic treatment for *Struthanthus*, new species have been described during the last 20 years (Kuijt 2003a, b, 2009a, 2014; González and Morales 2004; Martínez-Ambriz et al. 2017). Also, several generic transfers have occurred, including *Cladocolea* Tiegh. (Kuijt 1987, 1991b), *Panamanthus* Kuijt (Kuijt 1991a), *Passovia* H. Karst. (Kuijt 2011), *Peristhetium* Tiegh. (Kuijt 2012), *Phthirusa* Mart. (Kuijt 2009a) and *Pusillanthus* Kuijt (Caires et al. 2012).

Regarding generic affinities, *Struthanthus* has been found to be closely related to *Cladocolea*. This relationship has been supported by pollen morphology as described in Grímsson et al. (2018), where both genera were found to share type B pollen grains, showing an affinity to *Peristethium*. Molecular sequence data also support a relationship between *Struthanthus* and *Cladocolea* based on plastid DNA sequences (*matK*, *rbcL*, and *trnL-F*) and ribosomal nuclear cistron (SSU rDNA and LSU rDNA) (Vidal-Russell and Nickrent 2008). However, Kuijt and Lye (2005) analyzed foliar sclerenchyma across multiple species of *Struthanthus* and *Cladocolea* and found a wide morphological diversity in both genera, suggesting that they are polyphyletic as currently defined. This idea is supported by surveys of additional morphological characters from multiple species of *Struthanthus*, where taxa exhibit a wide variation typically observed in distantly related lineages (Kuijt 1975b, 1981, 2012; Kuijt and Hansen 2015).

About 14 species of *Struthanthus* have been reported from Mexico (Nickrent 2020; Maldonado 2021), with five of them endemic to the country. In the state of Oaxaca, seven species have been documented: *S. capitatus* Lundell, *S. crassipes* (Oliv.) Eichler, *S. deppeanus* (Schltdl. & Cham.) Blume, *S. hartwegii* (Benth.) Standl., *S. interruptus* (Kunth) G.Don, *S. matudae* Lundell, and *S. quercicola* (Schltdl. & Cham.) Blume. Here we describe a new species of *Struthanthus* from Oaxaca that shares morphological affinities with *S. deppeanus*, *S. quercicola*, and *S. ramiro-cruzii* Martínez-Ambr. & Sor.-Benítez. These affinities are based on both vegetative (stems and leaf shape) and reproductive (raceme inflorescence) characters.

Materials and methods

While preparing a floristic checklist for *Struthanthus* in Mexico, herbarium material and specimens collected during fieldwork were examined. The description provided below is based on our collections from Sierra Madre del Sur in the state of Oaxaca as well as herbarium specimens from ANSM, CHAPA, CIIDIR, ENCB, HUAA, HUAP, HUMO, IEB, MEXU, RSA, SLPM, UAMIZ, UAS, UAT, USON, XAL, and ZEA (acronyms follow Thiers (2021, continuously updated)).

Specimens were collected, pressed, and dried, with three to five duplicates per number. Vouchers were deposited at HUAP, HUMO, MEXU, and UAMIZ. All specimens gathered had reproductive structures (flowers and fruits) present. Morphological characters were measured from dried specimens and described using the terminology presented by Kuijt (1987, 2003a, b). Hosts and a distributional map are provided for *S. ibe-dzi*, as well as a taxonomic key and a comparative table to differentiate it from its three morphologically closest congeners in Mexico (*S. deppeanus*, *S. quercicola*, and *S. ramiro-cruzii*). The map was generated with QGIS (QGIS Development Team 2023) v 3.16. with points based on data from our field work and herbarium specimens from other collectors.

Taxonomic treatment

Struthanthus ibe-dzi Mald. & Cerros, sp. nov.

urn:lsid:ipni.org:names:77317963-1

Type. Mexico. Oaxaca: Tlaxiaco, Río Ocotepec, en el arroyo Yute kuini (San Juan del Río Cuquila), carretera Tlaxiaco-Putla, 17°10'26.48"N, 97°46'17.29"W [17.174022°N, -97.771469°W], 1962 m a.s.l., 30 Mar 2021, *M.G. Maldonado, L.G. Galván G. & R. Cerros T. 21* (♀ fl, fr) (holotype: HUMO-39855!, isotypes: MEXU!, UAMIZ!).

Diagnosis. *Struthanthus ibe-dzi* morphologically resembles *S. deppeanus* and *S. quercicola* in having epicortical roots on stems, similar leaf shapes, and inflorescences in racemes. However, the new taxon differs by its compressed nodes, stems, leaves, and inflorescence glaucous; leaf blade with base cuneate to oblique; staminate flowers 6–9 mm long with asymmetrical thecae and an extended horn-shaped apiculate connective in both anther series; and pistillate flowers with distally convoluted styles.

Description. Aerial hemiparasitic woody shrub, pendulous, perennial, with epicortical roots present at the base of main trunk; branches pendant. ***Stems*** green when young, brown with lenticels when mature; nodes glaucous, bicarinate and compressed, especially when young; internodes terete, with epicortical roots. ***Leaves*** opposite or subopposite; petioles 0.25–1.2 cm long, twisted, forming a shallow channel from the raised edge of leaf blade; blades ovate to lanceolate, rarely elliptical, 5.0–12.2 × 1.4–5.0 cm, papyraceous when dried; apex acute to acuminate, base cuneate to oblique, margin entire to repand, hyaline, venation pinnate. ***Inflorescences*** a solitary raceme of triads, indeterminate and axillar; bracts and bracteoles caducous at or after anthesis, cymbiform; rachis subterete to compressed, nodes compressed, triads opposite or subopposite, decussate, green, glabrous, glaucous. ***Staminate inflorescence*** 2.0–6.8 cm long, peduncle 0.2–0.8 cm with 6–16 (19) triads, triad peduncle 0.10–0.58 cm long. ***Pistillate inflorescence*** 2.0–5.0 cm long, peduncle 0.2–1.0 cm long with 6–12 (15) triads, triad peduncle 0.18–0.86 cm long. ***Staminate flowers*** hexamerous, rarely pentamerous, flower buds clavate with rounded apex; central flower of triad sessile, lateral pedicels 0.28–1.3 mm long; mature flowers 6.0–9.0 × 2.0–2.3 mm, petals linear, reflexed near the apex, 4.4–7.9 × 0.8–1.2 mm, anthers basifixed (not versatile) in two series, theca asymmetrical; prominent connectival apiculate horn in both the lower and upper series; calyculus irregularly dentate, whitish, vestigial ovary 1.5–2.2 mm; pistiloid straight to sigmoid 1/3 near the apex, 2.8–6.5 mm long, stigma undifferenced; nectary thick with six protuberances surrounding the pistiloid base. ***Pistillate flowers*** hexamerous, flower buds cylindrical, rounded at the apex; central flower of the triad sessile, pedicels of lateral flowers 0.18–0.8 cm long, slightly accrescent when bearing fruit; mature flowers 5.8–7.2 × 1.6–2.2 mm, linear petals 5.2–5.6 × 0.8–1.0 mm, staminodes in one series; calyculus whitish, irregularly dentate, inferior ovary 1.7–2.0 mm; style convolute 4.0–5.2 mm long (± 3 longitudinal folds) from the middle to the apex, stigma capitate; nectary thick with six protuberances surrounding the style. ***Fruit*** a one-seeded berry, ovoid, 3.85–6.0 × 6.52–8.60 mm. ***Seeds*** ovoid, 3.0–4.7 × 5.1–7.4 mm. Figs 1, 2.

Additional specimens examined (Paratypes). Mexico. Oaxaca: San Juan Mixtepec, Yucu Shúun (Monte de Tesoro) a 16 km S de San Juan Mixtepec, 17°13'37.46"N, 97°47'54.5"W [17.22707°N, -97.78484°W], 2,500 m a.s.l., 8 Nov 1988 (♀ fr), *J. Reyes S. 1064* (MEXU, UC/JEPS); Putla Villa de Guerrero, 2.1 km después de Santo Domingo Chicahuaxtla, hacia Putla, [17.142761°N, -97.848589°W], 2,050 m a.s.l., 5 Feb 1993 (♀ fr), *M. Cházaro B. 7088* (CHAPA, ENCB, MEXU, XAL); Santiago Juxtlahuaca, El Manzanal, senda para la parcela del Sr. Hemeterio, entrada por Santa Rosa-San Miguel Cuevas, Distrito Juxtlahuaca, 17°13'13.20"N, 98°3'38.30"W [17.22033°N, -98.06063°W], 2,060 m a.s.l., 13 Sep 1996 (♀ fl, fr), *J.I. Calzada 21381* (MEXU); San Juan Mixtepec, Camino a Santos Reyes Tepejillo, 1 km antes de la desviación al Capulín y Tinuama de Zaragoza, 17°19'23.4"N, 97°54'13.2"W [17.32317°N, -97.90367°W], 2,650 m a.s.l., 9 Apr 2019 (♂ fl), *L.G. Galván G. & R. Cerros T. 474* (HUMO); Putla Villa de Guerrero, orilla de la carretera, km 92, 2.8 km antes de San Andres Chicahuaxtla, 17°10'48.20"N, 97°49'32.48"W [17.18014°N, -97.82569°W], 2,363 m a.s.l., 13 Feb 2020 (♀ fr), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 13* (HUMO); ibid, 13 Feb 2020 (♀ fr), *M.G. Maldonado, R.*

UNIVERSIDAD AUTÓNOMA DEL ESTADO DE MORELOS
Struthanthus **de México**

LORANTHACEAE
Struthanthus ibe-dzi **sp.nov.**
Det.: Maldonado-Borja M. G., 2021
Edo.: Oaxaca, Mpio.: Tlaxiaco, Loc.: Río Ocotepec, en el arroyo Yute kuini (San Juan del Río Cuquila), carretera Tlaxiaco-Putla
17°10'26.48"N,-97°46'17.29"O 1962 m s.n.m.
Bosque de *Pinus-Quercus*, perturbada. Cerca de arroyo. Arbusto hemiparásito, escandente; flores femeninas, estilo convoluto; frutos inmaduros, verdes. Sobre *Salix* sp.
Col.: Maldonado-Borja M.G. **21**, Galván-González, L.G. y Cerros-Tlatilpa, R.
30/Abril/2021

Figure 1. *Struthanthus ibe-dzi* Mald. & Cerros, sp. nov. (Loranthaceae). Holotype: *M.G. Maldonado, L.G. Galván G. & R. Cerros T. 21* (♀ fl, fr), HUMO-39855.

Figure 2. *Struthanthus ibe-dzi* (Loranthaceae) **A** base of stem and disk of secondary haustoria (sh) **B** epicortical root (er) and swollen stem of host plant by the penetration of secondary haustoria (sh) **C** staminate inflorescences with caducous bracts (bra) and bracteoles (brc) **D** dissected petals of staminate flower showing two series of stamens (S1, S2), with anthers in the lower series (S1) displaying a prominent connectival horn (cn); receptacle showing an undifferentiated pistilloid and a nectary (ne) surrounded by the calyculus **E** pistillate inflorescences and compressed node (arrow) **F** dissected pistillate flower showing vestigial staminodes (st) opposite to petals, and an inferior ovary with convoluted style and calyculus (ca) **G** upper view of ovary in a pistillate flower showing its calyculus (ca) and nectary (ne) **H** immature fruits crowned by the calyculus.

Cerros T. & L.G. Galván G. 14 (HUMO); Tlaxiaco, Río Ocotepec, en el arroyo Yute kuini (San Juan del Río Cuquila), carretera Tlaxiaco-Putla, 17°10'26.48"N, 97°46'17.29"W [17.17402°N, -97.77146°W], 1,962 m a.s.l., 30 Apr. 2021 (♂ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 19* (HUMO); ibid, 30 Apr 2021(♀ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 20* (HUMO); ibid, 30 Apr 2021 (♀ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 22* (HUMO); ibid, 30 Apr 2021(♀ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 23* (HUMO); Putla Villa de Guerrero, km 92, carretera Tlaxiaco-Putla, 200 m antes de La Cañada Tejocote, 17°10'48.38"N, 97°46'31.94"W [17.18010°N, -97.82554°W], 2,374 m a.s.l., 30 Apr 2021(♂ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 24* (HUMO); ibid, 30 Apr 2021(♀ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 25* (HUMO); ibid, 30 Apr 2021(♂ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 26* (HUMO); Putla Villa de Guerrero, Orilla de carretera de Tlaxiaco-Putla, en San Andres Chicahuaxtla, 17°09'42.16"N, 97°50'11.85"W [17.16171°N, -97.83662°W], 2,473 m a.s.l., 30 Apr 2021(♂ fl), *M.G. Maldonado, R. Cerros T. & L.G. Galván G. 27* (HUMO).

Distribution, habitat, and hosts. *Struthanthus ibe-dzi* is endemic to Oaxaca, Mexico, where it is only known from cloud and oak-pine forests with secondary vegetation in the Sierra Madre del Sur (Morrone et al. 2017) in the municipalities of Putla Villa de Guerrero, San Juan Mixtepec, Santiago Juxtlahuaca, and Tlaxiaco (Fig. 3) at elevations between 1,962 to 2,650 m a.s.l. Recorded hosts to date include *Alnus* spp. (Betulaceae), *Quercus* spp. (Fagaceae), and *Salix* spp. (Salicaceae).

Phenology. Flowering from March to April and in September; fruiting in February to April and September to November. Individuals can be found bearing flowers and fruits on different branches.

Etymology. The epithet *ibe-dzi* refers to the common name given to any mistletoe in Zapotec language (*Ibë-dzí*) in the San Juan Mixtepec region, which means "hair(s) on top of", where "ibé" denotes "hair(s)" and "dzi" indicates "on top of".

Conservation status. *Struthanthus ibe-dzi* is only known from the western part of the state of Oaxaca, near the border with the state of Guerrero (Fig. 3). This species has an estimated area of occupancy of ca. 36 km^2 (criterion B1 < 500 km^2) and has been recorded in four localities (condition a: ≤5 locations). The specimen from *Reyes 1064* (MEXU, UC/JEPS) from 1988 was collected in a cloud forest. The areas within 1 km of this locality have been actively transformed into crop fields (personal observations from 2019–2021), leading us to consider that condition b(iii) is appropriate for this case, which refers to a projected decline in area, extent, and quality of habitat. Therefore, following the guidelines to the IUCN criteria (IUCN 2022), *S. ibe-dzi* should be classified as Endangered [EN B1ab(iii)].

Being a hemiparasitic plant with a complete dependence on hosts, mistletoe populations are vulnerable to the indirect effects of logging important host trees such as oaks (*Quercus* spp.), and habitat modification and fragmentation for livestock and agriculture (Ávalos and Nixon 2004). In addition, most of the *Quercus* species from Mexico have not been evaluated to determine their conservation status (Valencia-Ávalos and Morales-Saldaña 2016). Press and Phoenix (2005) indicated that the local extinction

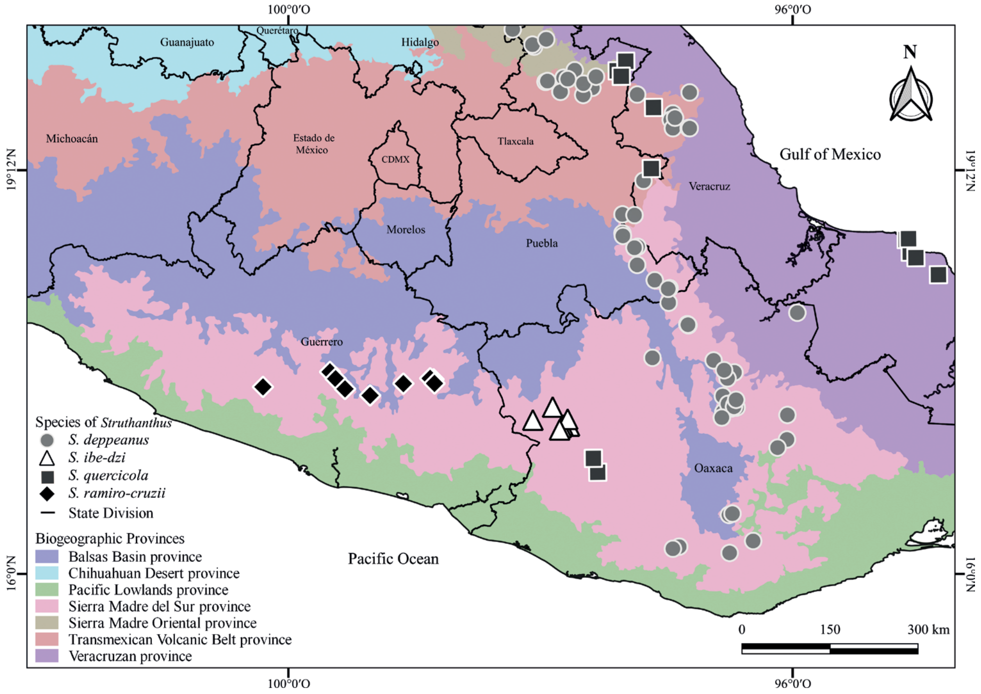

Figure 3. Distribution map of *Struthanthus deppeanus*, *S. ibe-dzi*, *S. quercicola*, and *S. ramiro-cruzii* in Oaxaca and surrounding states of central Mexico.

of a preferred host may lead to population declines and subsequent extinctions of associated parasites, highlighting the importance of hosts for the long-term survival of mistletoes such as *S. ibe-dzi*, and the perpetuation of populations. Furthermore, parasitic plants have been historically stigmatized and have not received full attention in terms of conservation priorities, even though mistletoes are particularly sensitive to environmental stress and considered keystone species in forests (Watson 2001; Fontúrbel et al. 2018; Crates et al. 2022; Watson et al. 2022).

Notes. Herbarium specimens of *S. ibe-dzi* have been previously identified as *S. deppeanus*, *S. quercicola*, or *Struthanthus* sp. However, the new taxon differs from *S. deppeanus* and *S. quercicola* by its compressed or bicarinate nodes and by having glaucous stems, leaves, and inflorescences which are covered by a whitish wax (observed in both fresh and dried specimens). In addition, *S. ibe-dzi* has one inflorescence raceme per axil, with peduncled triads with a sessile central flower and pedicellate lateral ones. The bracts and bracteoles are caducous, forming visible scars. Staminate flowers have asymmetrical thecae and an apiculate connectival horn in both series, while pistillate flowers have a convolute style with ± 3 longitudinal folds (Fig. 4C).

Struthanthus ibe-dzi, as other mistletoes in the San Juan Mixtepec region of Oaxaca, are locally known as birdlime vine, and known for the sticky substance (i.e., viscin) produced in the fruits, which is used to catch birds (Hunn 2008).

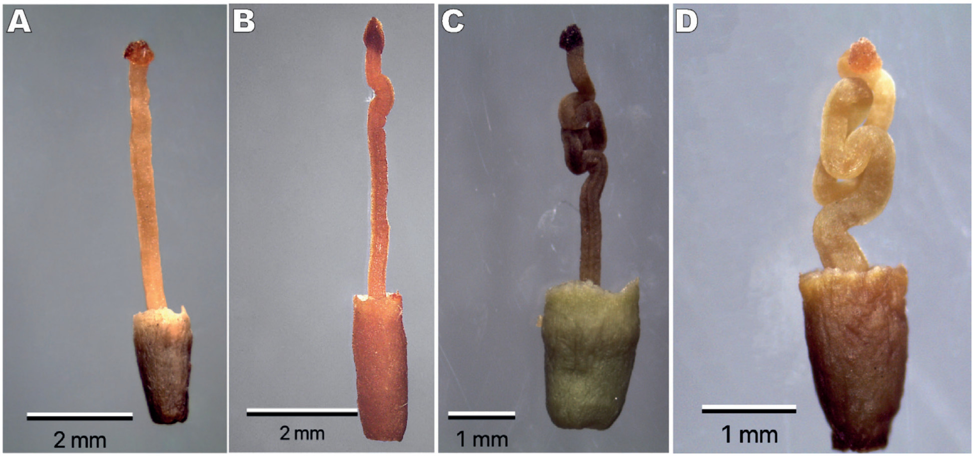

Figure 4. Style types in four species of *Struthanthus* (Loranthaceae) from Mexico **A** *S. quercicola* (straight to sigmoid) **B** *S. deppeanus* (sigmoid to slightly convoluted) **C** *S. ibe-dzi* (convolute) **D** *S. ramiro-cruzii* (strongly convolute).

Key to *Struthanthus ibe-dzi* and morphologically similar congeners

1 All floral triads pedicellate; pedicels accrescent when bearing fruit ..... ***S. deppeanus***

– Lateral floral triads pedicellate or subpedicellate, central one sessile; pedicels not accrescent when bearing fruit **2**

2 Bracts and bracteoles persistent, mainly in pistillate flowers; style straight to sigmoid in pistillate flowers ..... ***S. quercicola***

– Bracts and bracteoles caducous in both staminate and pistillate flowers; style convoluted to strongly convolute in pistillate flowers **3**

3 Leaf base subcordate to truncate; staminate flowers 6–7 mm long; pistillate flowers 5.0–5.8 mm long ..... ***S. ramiro-cruzii***

– Leaf base cuneate to oblique; staminate flowers 6–9 mm long; pistillate flowers 5.8–7.2 mm long ..... ***S. ibe-dzi***

Discussion

Among the currently accepted genera of Loranthaceae, *Struthanthus* is one of the most taxonomically challenging since no monographic treatment exists (Kuijt 2016; Robles et al. 2016). Numerous specimens in herbaria lack reproductive structures, have immature pistillate or staminate inflorescences, or contain only fruits, raising difficulties regarding their classification. Moreover, the shape of leaf blades may vary within the same individual from young to old branches (Heide-Jørgensen 2008), posing additional identification challenges when specimens are scant or sterile. In fact, many species of *Struthanthus* have been described from specimens presenting only pistillate or staminate individuals, resulting in numerous synonyms in the genus (Caires and Dettke 2020). Also, specimens only collected with fruits are not always possible to separate from the related genus *Passovia* (Kuijt 2014). Therefore, fertile specimens from the same locality with both pistillate and staminate mature flowers are essential to facilitate identification of *Struthanthus* at both generic and species levels.

Struthanthus ibe-dzi morphologically resembles *S. deppeanus*, *S. quercicola*, and *S. ramiro-cruzii*. All these four species have epicortical roots on stems and inflorescences in racemes. *Struthanthus deppeanus*, *S. ibe-dzi*, and *S. quercicola* have similar leaf shape ranging from ovate to lanceolate with a long acute apex (Table 1). Pistillate mature flowers in *S. quercicola* (Fig. 4A) have a straight to sigmoid style, whereas it is sigmoid to slightly convolute in *S. deppeanus* (Fig 4B), convolute in *S. ibe-dzi* (Fig. 4C), and strongly convolute in *S. ramiro-cruzii* (Fig. 4D). These stylar convolutions have been previously described for other Mexican species of *Struthanthus* and *Cladocolea* (Kuijt 1975a, b, 2003b, 2009a, 2014; Kuijt and Hansen 2015) as well as in three species of *Peristethium* and *Struthanthus* from Ecuador and Peru: *P. polystachyum* (Ruiz & Pav.) Kuijt, *P. tortistylum* (Kuijt) Kuijt, and *S. ophiostylus* Kuijt (Kuijt 2012, 2014). Besides the above-described characters, these four species of *Struthanthus* present geographical structure by being reported for the province of Sierra Madre del Sur. However, *S. deppeanus* and *S. quercicola* are also widely distributed across Mexico and Central America, while *S. ibe-dzi* and *S. ramiro-cruzii* are restricted to this province (Fig. 3). In terms of elevational ranges, *S. deppeanus* occurs at elevations from 950 to 2,900 m a.s.l., *S. ibe-dzi* from 1,960 to 2,650 m a.s.l., *S. quercicola* from 1,100 to 2,100 m a.s.l., and *S. ramiro-cruzii* is distributed from 1,600 to 2,200 m a.s.l.

Table 1. Comparison of morphological characters among four species of *Struthanthus* (Loranthaceae) from Mexico: *S. deppeanus*, *S. ibe-dzi*, *S. quercicola*, and *S. ramiro-cruzii*.

Character	*S. ibe-dzi*	*S. deppeanus*	*S. quercicola*	*S. ramiro-cruzii*
Stem nodes	compressed and bicarinate	terete	terete	terete
Leaf shape	ovate to lanceolate, rare elliptical	lanceolate to ovate-lanceolate	lanceolate to elliptic-lanceolate	ovate to lanceolate, cordate when mature
Leaf apex shape	acute to acuminate	acute to long acuminate	attenuate to acuminate	apiculate or acute
Leaf base shape	cuneate to oblique	acute	obtuse to round	subcordate to truncate
Petiole length (mm)	2.5–12	5–10	3–8	5–10
Inflorescences per axil	1	1–2	1–2	1 (2)
Triads per staminate inflorescence	6–16 (19)	8–10	8–16	10–12
Triads per pistillate inflorescence	6–12 (15)	8–10	6–12	8–14
Bracteoles persistence	caducous	caducous	persistent	caducous
Pistillate flower length from base of ovary (mm)	5.8–7.2	6.2–7.5	4.0–5.2	5.0–5.8
Style	convolute	sigmoid to slightly convoluted below the stigma	straight to sigmoid	strongly convolute
Staminate flower length from base of ovary (mm)	6–9	7.0–8.5	5.5–7	6–7

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All authors contributed to the preparation of the manuscript by providing data and reviewing and editing the text. MGMB, LGGG, and RCT conducted the fieldwork, RCT provided photos of living plants, and MGMB prepared stereoscopic photographs and the taxonomic key. MGMB and RCT made the descriptions (measurements and morphological data) of the new species.

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RESEARCH ARTICLE

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A note on the type of *Harpalyce* (Fabaceae, Brongniartieae), with description of two new local endemic species from Cuba

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Abstract

Two new species of *Harpalyce* are described from Cuba, *H. revoluta* **sp. nov.** from a serpentine area in the northern part of E. Cuba and *H. marianensis* **sp. nov.** from calcareous areas in the southern part of E. Cuba. Both have relatively small flowers, with an up to 6 mm long standard, and 2–3 mm long wings. *Harpalyce marianensis* is further characterized by strongly suberous (corky) young branches of a spongy consistence, deeply furrowed longitudinally, and by leaflets covered with a particular type of orange, apparently disk-shaped, sessile glands abaxially. *Harpalyce revoluta*, moreover, has suborbicular or broadly elliptic leaflets with a strongly recurved or sometimes revolute margin, secondary veins inconspicuous on either side; the foliar glands, by their morphology and anatomy, are of a different type. An epitype is designated for the name *Harpalyce* and its type, *H. formosa*; the distribution of both new species and their close relatives is mapped, and an updated identification key is offered, to cater for all 16 currently recognised Cuban species.

Resumen

Se describen dos nuevas especies de *Harpalyce* para Cuba oriental, *H. revoluta* **sp. nov.** de las áreas de serpentina del norte y *H. marianensis* **sp. nov.** de áreas de formaciones calcáreas del sur. Ambas se caracterizan por tener flores pequeñas, con estandarte de hasta 6 mm de largo y alas de hasta 3 mm de largo. *Harpalyce marianensis* se distingue además por sus ramas jóvenes fuertemente suberosas, de consistencia esponjosa, profundamente surcadas longitudinalmente, y los folíolos cubiertos abaxialmente por un tipo particular de glándulas sésiles anaranjadas. *Harpalyce revoluta*, por su parte, tiene folíolos suborbiculares o anchamente ovales, con margen fuertemente recurvado o hasta revoluto, con venas secundarias inconspicuas en ambas caras, y glándulas foliares, por su morphología y anatomía, son de un tipo distinto. Se designa un epitipo para el nombre *Harpalyce* y su tipo, *H. formosa*. Se presenta un mapa de distribución de las nuevas especies y las relacionadas con ellas y se ofrece una clave de identificación actualizada, que incluye las 16 especies cubanas actualmente reconocidas.

Keywords

Brongniartieae, Eastern Cuba, *Fabaceae*, *Harpalyce*, leaf gland morphology, limestone substrate, serpentine

Palabras clave

Brongniartieae, Cuba oriental, *Fabaceae*, *Harpalyce*, morfología de glándulas foliares, serpentinas, substratos calcáreos

Introduction

Harpalyce DC. is one of those genera that, so to say, sprouts new species on a regular basis, with apparently increasing frequency. The phenomenon is not limited to Cuba, but can also be observed in the two other, disjunct areas in which the genus occurs: Central Mexico to Nicaragua in Central America, and large parts of Brazil (São-Mateus 2018; São-Mateus et al. 2019; Rankin and González 2021). In Cuba, it is due to a variety of factors, among which are the occurrence in small populations of only a few individuals, long overlooked by collectors; and the fact that many collected specimens are incomplete, often lacking flowers and fruits, and unsuited for identification below the species group level, so that undescribed species often remain unrecognised in the herbaria.

In Cuba, from where 16 species (including the two present, new ones) are now known, *Harpalyce* was first collected by Charles Wright in the 1860s. The species described by Grisebach (1866) based on Wright's material remained the single Cuban one for well over half a century. In the 1920s, five more species were added, consequent to the intense collecting activities of the Swede E. L. Ekman and North American botanists based in New York. Cuban botanists recognised three more species, all described in 1950. Borhidi and Muñiz (1977) added no less than 5 species (not counting synonyms) based on the collections of local botanists kept in Cuban herbaria. Just recently, describing a new species of our own, we published an update of the genus for Cuba (Rankin and González 2021). Even then, we realised that our digest was by no means final, as several sterile specimens exist in Cuban herbaria, including the type material for species described by Borhidi and Muñiz (1977; see Rankin and González 2021) that cannot be placed reliably in the framework of the species so far described. Further field investigations are planned which, if successful, will yield complete, fertile material from the very same or nearby populations. Therefore, be warned: as soon as the so far incompletely known plants have been located and collected, further descriptions of new taxa will likely be forthcoming.

Materials and methods

The original and complementary literature dealing with *Harpalyce* (Fabaceae, Brongniartieae) was consulted. In addition to the ca. 170 materials studied earlier (Rankin and González 2021), about 80 specimens (including duplicates) of Cuban *Harpalyce* belonging to the herbaria B, HAJB, JE, and PAL-Gr were examined, not counting the digital images of other specimens (including types) available online and housed in relevant herbaria such as A, GH, GOET, HAC, HAJB, K, MO, NY, P, S, UC, and US (see also Rankin and González 2021 and its Appendix 1 [https://doi.org/10.3372/wi.51.51204]). Herbarium codes follow Thiers (2022+). Georeferenced specimen label data were incorporated into the Flora Database of the Republic of Cuba (Greuter 2003); geographical coordinates were used to generate a distribution map, using the mapping software QIGS for Windows, version 3.16.

Leaf glands were studied using the stereo-zoom microscope system Olympus SZX16; the photographs were taken using the microscope's camera Olympus DP72 and its CellSens Standard software. Cross cuts of the lamina were obtained by razor-cutting manually mature leaflets, previously soaked soap water at room temperature. Unstained cuts in aqueous solution were studied at 200× and 400× magnification by optical microscopy using a Carl Zeiss Axioscop instrument.

Notes on the type of and author citation for the name *Harpalyce*

While searching the literature for potentially relevant information, we came across McVaugh's (2000) book on the botany of Sessé and Mociño's expedition to New Spain (i.e., Mexico). McVaugh's excellent work includes a voluminous chapter on the scientific names of plants based on Sessé and Mociño's collection of paintings that had been used by Candolle and others in describing new species, and sometimes genera, as in the case of *Harpalyce* and its type, *H. formosa*. The corresponding entry, on p. 316 of the book, gives details on what is probably the holotype of the species name, or, failing this, the lectotype designated by Arroyo (1976). It is an original painting, numbered 227, kept in the library of the Conservatoire botanique de la Ville de Genève (G), a copy of which is present, as #0607, in the Torner Collection of the Hunt Institute for Botanical Documentation; drawings of analytical details based on that painting can be viewed online (as https://fm-digital-assets.fieldmuseum.org/369/473/30332.jpg), being kept in the type photograph collection of the Botany Department, Field Museum of Natural History. McVaugh (l.c.) wrote that the depicted material was probably found in 1789 in the state Guerrero in South Mexico; he also shared Standley's (1922) opinion that the type material is impossible to identify. No herbarium material of Sessé and Mociño corresponding to *H. formosa* is known to exist. Arroyo (1976) applied the name to a definite taxon, endemic to the south-eastern part of the state of Mexico and to the state of Puebla, but not known from Guerrero. We agree with her taxonomic assessment of the type illustration, but in view of the doubt expressed by Standley and McVaugh (ll. cc.), even with respect to generic placement, we believe it to be necessary to fix the application of the name by designating an epitype.

Harpalyce formosa DC., Prodr. 2: 523. 1825. Holotype [or, if lectotype, designated as such by Arroyo (1976: 40)]: Original painting (#227) of "*Astragalus Formosus*. Sp. N." in the Candolle collection "Icones florae mexicanae" of the Sessé and Mociño paintings, and copies thereof, in the library of the Conservatoire botanique in Geneva (G). **Epitype (designated here):** Tehuacán, Puebla, June 1905, *Purpus 1196* (UC 85301 [foto!]). This specimen was revised by Arroyo (1976) and considered by her as the holotype (more likely it is the lectotype) of *Harpalyce ferruginea* Brandegee, a taxonomic synonym of *H. formosa*; it can be viewed on the Internet (https://global.plants.jstor).

A further point of note clarified by McVaugh (2000: 14–17) is the appropriate author citation for the generic name, which had often (e.g. by Arroyo 1976) been cited as "*Harpalyce* Mociño and Sessé ex de Candolle" but should, along with all similar cases of Candolle's names based exclusively of the Icones Florae Mexicanae, be credited to DC. alone. This is abundantly clear in the case of *Harpalyce*, a genus that Mociño did not recognise, let alone propose a name for it, but that he included in *Astragalus*.

Description of two new Cuban species of *Harpalyce*

Harpalyce marianensis **R.Rankin, P.A.González & Greuter, sp. nov.**

urn:lsid:ipni.org:names:77318009-1

Type material. ***Holotype.*** **Cuba** – Guantánamo Prov. • San Antonio del Sur, Abra de Mariana en el barranco, 5 km al noroeste de San Antonio del Sur; [20.08828°N, 74.85846°W]; A. Álvarez de Zayas et al. HFC 43077; montes secos, caliza; 11 May 1980; JE 28983.

Isotypes. **Cuba** • Same collection data as for preceding; B 100364878 [http://herbarium.bgbm.org/object/B100364878]; HAJB 1289, 1290; JE 28984.

Other material examined. Cuba – Guantánamo Prov. • San Antonio del Sur, manigua costera cerca de Playa Baitiquirí; [20.02482°N, –74.85226°W]; May 1968, Bisse & Köhler HFC 9259; HAJB, JE; Baitiquirí, en el camino a la Mina del Yeso; [20.02482°N, 74.85226°W]; 11 Apr. 1972; Bisse & Berazaín HFC 21818; HAJB, JE; Abra de Mariana, loma al oeste del barranco; [20.08828°N, 74.85846°W]; 6 Feb. 1978; Bisse et al. HFC 36575; B 100362446, HAJB, JE; Abra de Mariana, loma al oeste del Abra; [20.08828°N, 74.85846°W]; 9 Feb. 1979; Berazaín et al. HFC 39129; B 100361112, HAJB, JE.

Shrubs or small trees; young branches very suberous (corky), with a spongy appearance, deeply longitudinally ridged (Fig. 1), ferruginous-pubescent, old branches also suberous, but glabrescent. Stipules not seen, probably early shed. Leaves imparipinnate, normally alternate, or frequently subopposite, 4–7.5 cm long; petiole 10–18 mm long, densely ferruginous-pubescent; rachis 2–5.5 cm long, ferruginous-pubescent; leaflets (5-)7–9(-11) per leaf, coriaceous; lamina elliptic to narrowly elliptic, with a rounded base, the tip rounded or slightly emarginate, sometimes shortly mucronulate; the margin entire, mostly flat; adaxially glabrous, shiny (when dry),

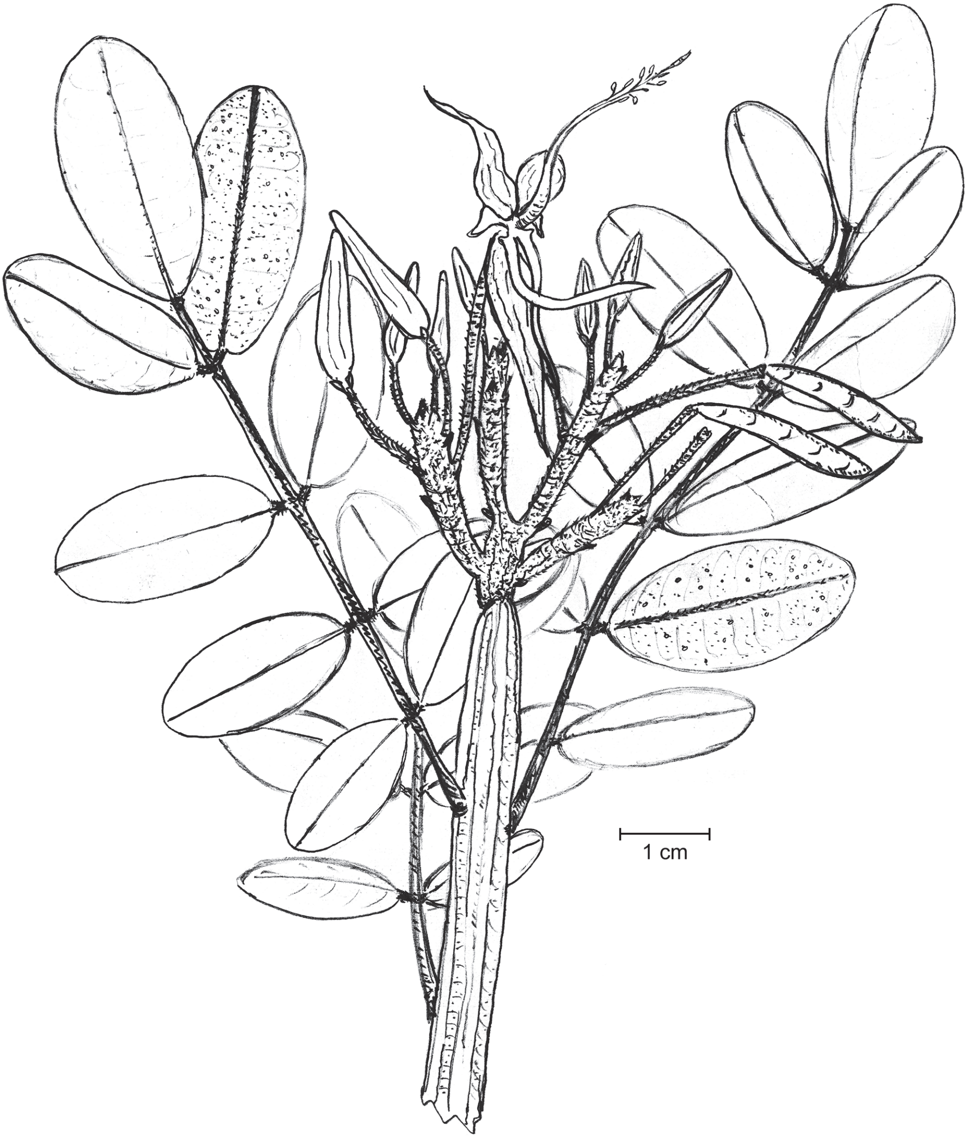

Figure 1. Flowering branch of *Harpalyce marianensis.* Drawing by PAGG from an isotype specimen (JE 28983).

abaxially subglabrous except on the midvein; the leaflets, abaxially, are densely covered with showy orange, apparently disk-shaped glands of "type A" (the plump, apically flattened gland body is sessile in a wide open depression of the mesophyll: Fig. 2A, B); leaflet midvein sunk adaxially, prominent and ferruginous-pubescent abaxially, glabrescent with age, secondary veins in 6–9 pairs, ± conspicuous abaxially; lateral leaflets in opposite pairs, with a 1–1.5 mm long, thick, ferruginous-pubescent petiolule, the lamina 1.2–2.5(-3) × 0.8–1(-1.3) cm; terminal leaflet with a 1.5–2.5 mm

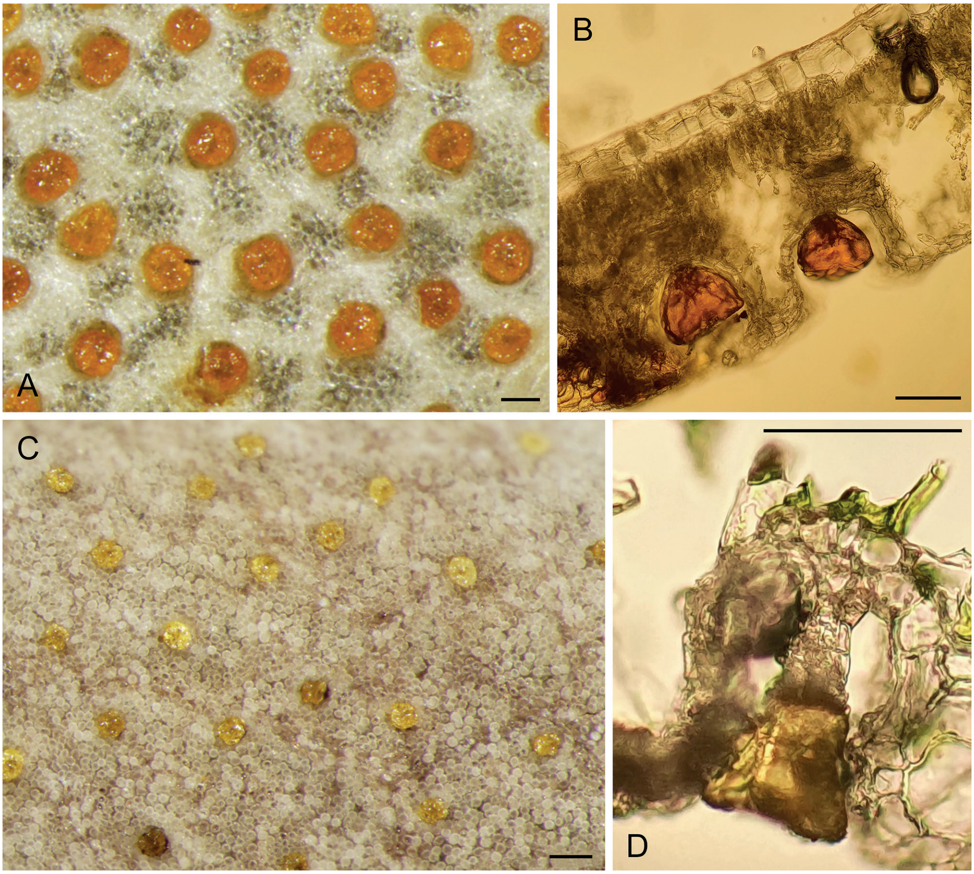

Figure 2. A–D leaf glands of *Harpalyce marianensis* (**A, B** from holotype specimen) and *H. revoluta* (**C, D** from specimen HFC 44956, B 100374694) **A, C** surface view **B, D** cross section. Preparations and photographs by Bibiana Moncada, Berlin. Scale bars: 100 µm.

long, thick and ferruginous-pubescent petiolule, the lamina 2–3.3 × 0.8–1.5 cm. Inflorescence terminal, many-flowered (with ≤ 50 flowers), 4–4.5 cm long, densely ferruginous-pubescent; bracts c. 1 mm long, densely ferruginous-pubescent; pedicels ≤ 2.5 cm long, ferruginous pubescent. Flowers zygomorphic. Calyx lips narrowly triangular, acute, outside densely covered with ferruginous hairs and sessile glands, inside glabrous or with scattered hairs; vexillary calyx lip (Fig. 3A) 3–3.2 × 0.5–0.6 cm, carinal calyx lip (Fig. 3B) 3.4–3.5 × 0.5–0.6 cm; petals membranaceous (when dry); standard (Fig. 3C) with a c. 2 mm long claw, the blade orbicular or broadly elliptic, apically rounded, 5–6 mm in diameter; wings (Fig. 3D) with a c. 2 mm long claw, the blade ± triangular, 2–3 × c. 2 mm, apparently lacking a basal auricle; keel petals (Fig. 3E) with a c. 2 mm long claw, the blades not connate, 2.3–2.5 × 0.2–0.3 cm, with a basal auricle on the vexillar side. Stamens 10; filaments 1.8–2.2 cm long, basally fused into a tube, distally free for 4–5 mm; anthers ± sagittate, c. 1.5 mm long (when

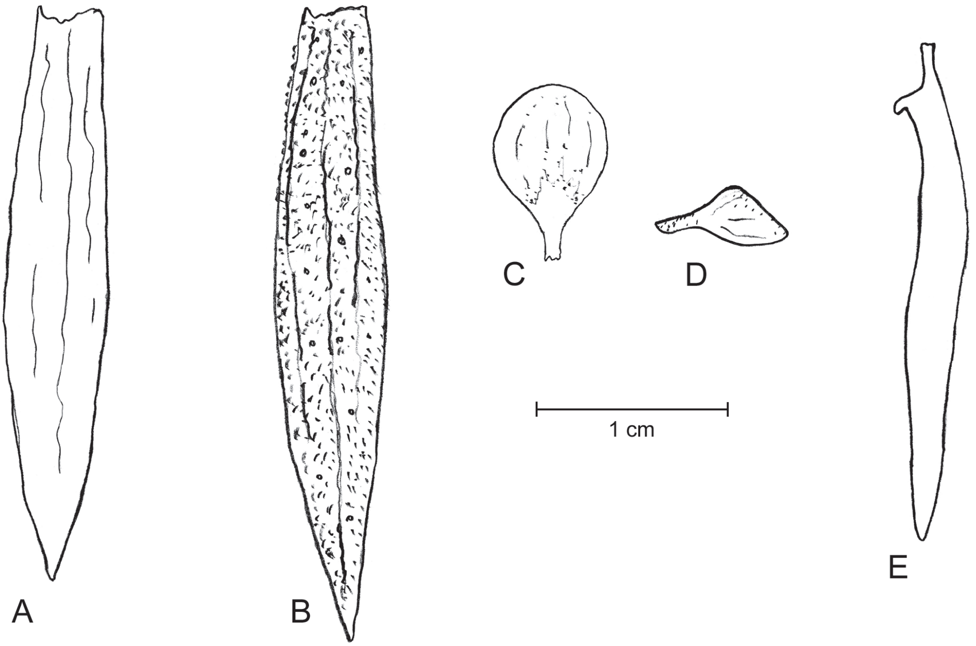

Figure 3. A–E analysis of the perianth of *Harpalyce marianensis* **A** vexillary calyx lip, from inside **B** carinal calyx lip, from outside **C** standard, frontal view **D** wing **E** keel, lateral view. Drawings by PAGG from a flower of an isotype specimen (JE 28983).

dry). Pistil 3–3.2 cm long; ovary fusiform, laterally compressed, 7–8 × 1.5–2 mm, glabrous, 6–7-ovulate; style filiform, curved, 2.3–2.5 cm long, glabrous. Legume linear, 3–3.3 × c. 1 cm, brown, tipped with a c. 2 mm long mucro. Seeds up to 6 per legume, 4 × 1.5 mm (when dry).

Phenology. Collected in flower and with fruits in April and May.

Etymology. Named after the type locality, Abra de Mariana.

Distribution. Southern part of E Cuba, province Guantánamo, municipality San Antonio del Sur: Abra de Mariana and Baitiquirí. Grows in dry scrub vegetation on limestone substrate. Fig. 4.

Affinities and diagnostic features. *Harpalyce marianensis* has morphological affinities with *H. revoluta* (see below) and other Cuban species that have a relatively small (≤ 8–9 mm in length or diameter), orbicular to broadly elliptic standard and free keel petals, such as: *Harpalyce ekmanii* Urb., *H. villosa* Britton & P. Wilson, and *H. baracoensis* Borhidi & O.Muñiz, particularly with *H. ekmanii*, with which it also shares glabrous or subglabrous leaflets; however, *H. ekmanii* has larger leaflets (2.5–7.5 × 1.5–3 cm vs 1.2–3.3 × 0.8–1.5 cm). *Harpalyce marianensis* has pronounced suberous young branches with a spongy consistence and deep longitudinal ridges, a feature that is not found in *H. ekmanii*. Also, *H. marianensis* grows in dry scrub on limestone in the southern part of E Cuba, whereas *H. ekmanii* grows in rainforest, pine woods or dry scrub on ultramaphic soils such as serpentines in the northern portion of E Cuba.

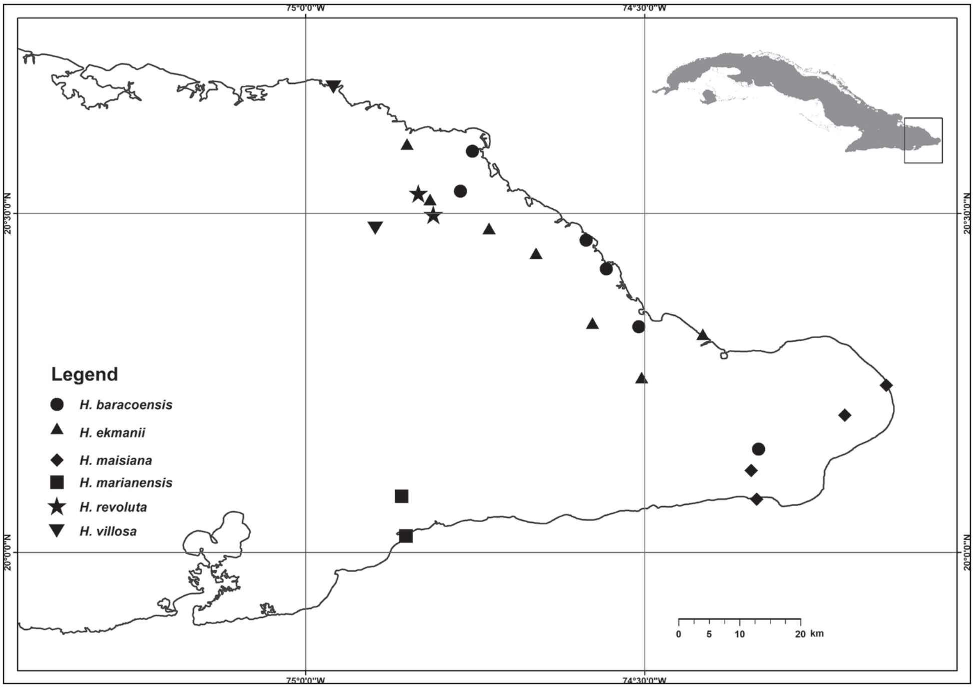

Figure 4. Distribution of the two new species and of related, small-flowered *Harpalyce* species with free keel petals endemic to E Cuba.

Sterile plants or specimens of *Harpalyce marianensis* might be confused with *H. maisiana* León & Alain, a species that also occurs in limestone areas of southern E. Cuba, but these two can be distinguished from each other through the colour of the glands on the adaxial face of the leaflets, yellow in *H. maisiana* vs orange in *H. marianensis*. When in flower, they can be easily told apart: the standard is oblanceolate, 1 × 0.2–0.3 cm and apically slightly emarginate in *H. maisiana* but orbicular or broadly elliptic, 5–6 mm in diameter or length and apically rounded in *H. marianensis*; the keel petals are partially connate in the apical third and 1.2–1.3 × 0.2–0.3 cm in *H. maisiana*, but totally free and 2.3–2.5 × 0.2–0.3 cm in *H. marianensis*.

Harpalyce revoluta **P.A.González, R.Rankin & Greuter, sp. nov.**

urn:lsid:ipni.org:names:77318010-1

Type material. ***Holotype*****.** **Cuba – Holguín Prov.** • Cuchillas de Moa; alrededores del aserrío La Melba; A. Álvarez de Zayas et al. HFC 42194; charrascales altos con *Bonnetia cubensis*; [20.51944°N, 74.81778°W]; alt.450–500 m; 28 Apr. 1980; B 100364586 [http://herbarium.bgbm.org/object/B100364586].

Isotypes**.** **Cuba** • Same collection data as for preceding; HAJB 1286-1288, JE 28985.

Other material examined. Cuba – Holguín Prov. • Moa; La Melba; charrascal cerca del aserrío; [20.51944°N, 74.81778°W]; Mar. 1968; Bisse & Köhler HFC 7066; HAJB, JE; La Melba, charrascal cerca del aserrío; [20.51944°N, 74.81778°W]; Mar. 1968; Bisse & Köhler HFC 7626; HAJB, JE; La Melba; charrascal cerca del aserrío; [20.51944°N, 74.81778°W]; 22 Dec. 1968; Bisse & Lippold HFC 11062, 11329; HAJB, JE; Cayo Probado; orillas de las cabezadas del río Jiguaní; [20.48864°N, 74.82188°W]; 3 Apr. 1972; Bisse & Berazaín HFC 21968; B 100462873, HAJB, JE; alrededores del aserrío La Melba; [20.51944°N, 74.81778°W]; 25 Apr. 1981; Bisse et al. HFC 44956; B 100374694, HAJB, JE.

Shrubs or small trees; young branches pubescent, old branches (Fig. 5) suberous and glabrescent. Stipules not seen, probably early shed. Leaves imparipinnate, normally alternate, sometimes subopposite, 3–7 cm long; petiole 0.5–10 mm long, very thick particularly at the basis, pubescent; rachis 2–6 cm long, pubescent, glabrescent with age; leaflets 7–11 per leaf, rigidly coriaceous, opposite or very rarely subopposite; lamina mostly suborbicular or ± broadly elliptic, with a rounded or obtuse base, the tip emarginate; margin entire, recurved to strongly revolute; the surface shiny (when dry), adaxially glabrous, abaxially glabrous except on the midvein and beset with well-spaced yellow to orange, somewhat funnel-shaped glands of “type B” (in which the obconical gland body is stalked in the bottom of a mesophyll cavity, barely protruding through its narrowed opening; Fig. 2C, D); leaflet midvein sunk adaxially, prominent and with some scattered hairs abaxially, secondary veins inconspicuous on both faces; lateral leaflets with a c. 1 mm long, thick and ferruginous-pubescent petiolule, the lamina 0.6–1.2 × 0.5–1 cm, terminal leaflets with petiolule 1–3 mm long, thick and ferruginous pubescent, lamina 1–2 × 0.8–1 cm. Inflorescence terminal, with ≤ ca. 20 flowers, 2–4 cm long, densely ferruginous-pubescent; peduncle 1–1.5 cm long, densely ferruginous-pubescent, bracts linear, 2.5–3 mm long, densely ferruginous-pubescent; pedicels 1–1.5 cm long, densely ferruginous-pubescent. Flowers (Fig. 5) zygomorphic. Calyx lips narrowly triangular, acute, outside densely covered with ferruginous hairs and sessile glands, inside glabrous and with scattered glands; vexillary calyx lip (Fig. 6A) 2.1 × 0.3 cm, carinal calyx lip (Fig. 6B) 2.3 × 0.4 cm; petals membranaceous (when dry); standard (Fig. 6C) with a 2–2.5 mm long claw, the blade broadly elliptic, apically rounded, c. 3.5 × 2.5 mm; wings (Fig. 6D) with a c. 2 mm long claw, the blade ± triangular, c. 2 × 2 mm, apparently lacking a basal auricle; keel petals (Fig. 6E) with a 2–3 mm long claw, the blades not connate, 1.2–1.3 × c. 0.2 cm, with an auricle on the vexillar side. Stamens 10; filaments 1.7–2 cm long, basally fused into a tube, distally free for 4–5 mm; anthers sagittate, c. 1.5 × 0.7 mm (when dry). Pistil c. 2.3 cm long; ovary fusiform, laterally compressed, 4 × 1–1.5 mm, glabrous; style filiform, 1.9–2 cm long, glabrous. Legume (immature) linear, 13–14 × 3–3.5 mm. Seeds not seen.

Phenology. When collected in late April, the type material was in flower and with immature fruits. Some other specimens seen, collected in April as well, similarly were in flower and with immature fruits.

Distribution. Northern part of E Cuba, province Holguín. Grows in rainforest, pine woods or xeromorphic scrub on ultramaphic substrate (serpentine). Fig. 4.

Figure 5. Branch with immature fruits of *Harpalyce marianensis.* Drawing by PAGG from the holotype specimen.

Etymology. The epithet refers to the characteristic, revolute leaflet margin.

Affinities and diagnostic features. *Harpalyce revoluta*, shows morphological affinities with *H. marianensis* (see above) and other Cuban species that have a relatively small (≤ 8–9 mm in length or diameter), orbicular to broadly elliptic standard and free keel petals, particularly with *H. ekmanii*, with which it shares glabrous or subglabrous leaflets; however, in *H. ekmanii* the leaflets are much larger (2.5–7.5 × 1.5–3 cm vs

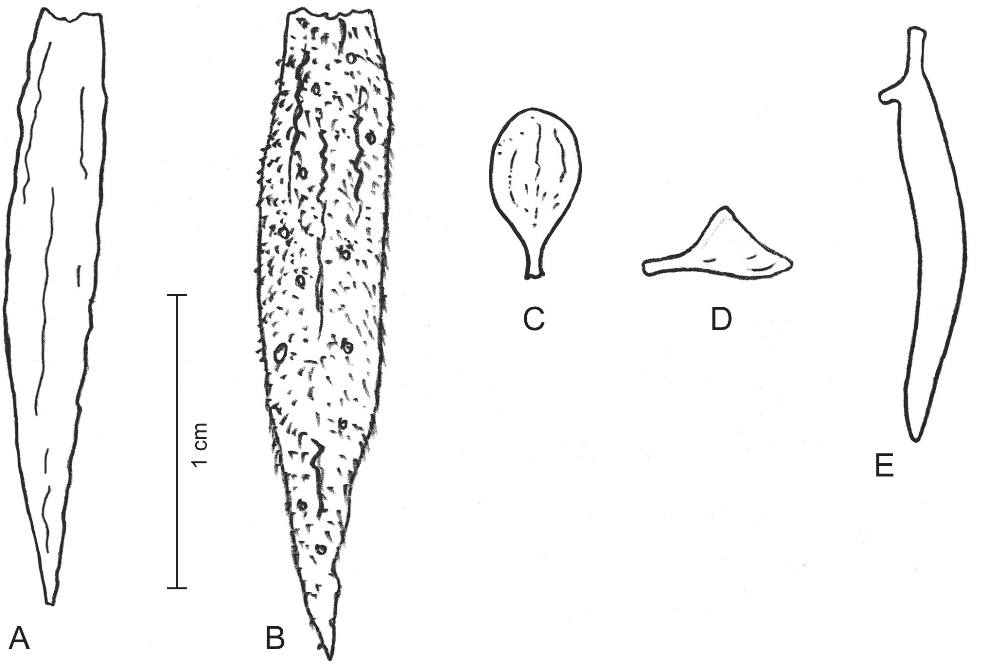

Figure 6. A–E analysis of the perianth of *Harpalyce revoluta* **A** vexillary calyx lip, from inside **B** carinal calyx lip, from outside **C** standard, frontal view **D** wing **E** keel, lateral view. Drawings by PAGG from a flower of specimen HFC 44956, B 100374694.

0.6–2 × 0.5–1 cm), with flat (vs recurved to revolute) margins, and the sessile glands on the abaxial leaf face are fairly dense, less spaced. The size and shape of the standard relates *H. revoluta* to *H. villosa*, but the latter has leaflets that, particularly when young, are densely hairy abaxially, not glabrous except on the loosely hairy midvein, as in *H. revoluta*.

An update of the identification key for Cuban *Harpalyce*

In their recent survey of Cuban *Harpalyce*, Rankin and González (2021) presented a key for identifying the species they recognise. To account for the present, additional species, that key needs some modification. That key is reproduced here, with its 8th dichotomy changed and expanded to account for the new species.

1 Leaflets (especially when young) densely hairy, tomentose or pubescent abaxially, indumentum obscuring glands until leaflets are older and hairs are less dense **2**
– Leaflets glabrous, subglabrous or with scattered hairs, these never obscuring glands **7**
2 Bracts leaf-like (foliose), 1–1.5 cm long .... ***Harpalyce toaensis***
– Bracts small, linear or triangular, < 3 mm long **3**

3 Leaflets (on dried specimens) green or greyish green adaxially, abaxially covered with a brownish yellow tomentum **4**

– Leaflets (on dried specimens) brown or dark grey adaxially, abaxially pubescent or puberulous, with brown or reddish brown hairs **5**

4 Leaflet margin recurved or flat, or in some leaflets revolute; inflorescence 1–6-flowered .... ***Harpalyce nipensis***

– Leaflet margin consistently revolute; inflorescence always 1-flowered .... ***Harpalyce acunae***

5 Petiolule of terminal leaflet 1–3 mm long .... ***Harpalyce villosa***

– Petiolule of terminal leaflet 4–10 mm long **6**

6 Leaflets 5–11 per leaf; secondary veins conspicuous abaxially .... ***Harpalyce alainii***

– Leaflets 11–17 per leaf; secondary veins inconspicuous abaxially .... ***Harpalyce baracoensis***

7 Keel petals completely free from each other **8**

– Keel petals connate for most of their length or at least in apical third **11**

8 Standard 1 cm in diameter; wings c. 1.5 cm long .... ***Harpalyce cristalensis***

– Standard 0.35–0.9 cm in diameter or length; wings 0.2–0.7 cm long **9**

9 Leaflets mostly suborbicular or ± broadly elliptic, their margin recurved to strongly revolute; secondary veins inconspicuous on both faces .... ***Harpalyce revoluta***

– Leaflets elliptic to narrowly elliptic, oblong or oblong-elliptic, their margin flat or almost so; secondary veins commonly conspicuous, at least abaxially **10**

10 Young branches very suberous, with a spongy consistence, deeply longitudinally ridged; leaflets 1.2–3.3 × 0.8–1.5 cm .... ***Harpalyce marianensis***

– Young branches without a spongy appearance, not longitudinally ridged; leaflets 2.5–7.5 × 1.5–3 cm .... ***Harpalyce ekmanii***

11 Standard ≤ 1.5 cm long **12**

– Standard ≥ 2 cm long **13**

12 Petioles 1.5–2 cm long; standard c.1.5 × 0.8–1 cm; wings c. 1.5 cm long, keel petals c. 1.7 cm long .... ***Harpalyce borhidii***

– Petioles 0.6–1.2 cm long; standard c. 1 × 0.2–0.3 cm; wings 1–1.1 cm long, keel petals 1.2–1.3 cm long .... ***Harpalyce maisiana***

13 Leaflets subopposite or alternate; wings black toward base, keel petals mostly black, with a yellow margin; legume 4–5 cm long .... ***Harpalyce greuteri***

– Leaflets opposite; wings and keel petals red, orange, yellow or white; legume either up to 2.3 cm or at least 5 cm long **14**

14 Legume 5–6.5 cm long .... ***Harpalyce macrocarpa***

– Legume 1–2.3 cm long **15**

15 Leaflets abaxially with well-spaced glands, these not touching each other .... ***Harpalyce cubensis***

– Leaflets abaxially with dense, partly contiguous or confluent glands .... ***Harpalyce suberosa***

Discussion

As we stated in the introduction, the two new species here described are likely not the last addition to the genus. There are incomplete specimens in the Cuban herbaria, HAC and HAJB in particular, that in all likelihood represent new, undescribed species, which we shall duly name as soon as we succeed in relocating them in the field and collect complete, fertile material; furthermore, in view of the species definition we here adopt, following the tradition established by other authors, any newly discovered *Harpalyce* population is likely to represent a new taxon.

The question may be asked legitimately: is such a narrow species definition practical and defendable? We ignore whether our species are valid under a biological species concept. For all we know, they might all, or at least some of them, be freely interbreeding when brought together. Without much experimental work involving artificial crossing, it is impossible to know whether and to which extent evolutionary divergence has succeeded in establishing genetic barriers and cross-incompatibility between morphologically distinct populations. We are similarly ignorant of the extent of genetic isolation, if any, for many and indeed most species currently recognised in polymorphic Cuban genera. It is therefore legitimate to recognise morphologically distinguishable populations as separate taxa, and currently, no workable alternative to this course is available.

The role of small, isolated populations in evolution and speciation in higher plants has been studied by Runemark in the Aegean archipelago of Greece. He has coined the expression "reproductive drift" (Runemark 1969, 1970) to describe and explain this phenomenon. His ideas have not received the attention that they deserve, and we would like to encourage others to apply them to understand and explain the polymorphism observed in Cuban species complexes with a comparable fragmented population structure which, in the case of Cuba, is usually associated with edaphic specialisation to small and scattered habitats which, for biological purposes, are comparable to archipelagos of small islands in a sea of generalistic environmental conditions.

Concerning the general evolutionary context in which the Cuban populations are to be seen, it is useful to be mindful of the results and conclusions of recent phylogenetic studies (São Mateus 2018). That work was based on sequence analyses of both nuclear ribosomal and plastid DNA of an impressive sampling of taxa from Brasil (*Harpalyce* sect. *Brasilienses* Arroyo) and Mexico (*H.* sect. *Harpalyce*) but only a single one from Cuba (two accessions of, allegedly, *H. cubensis* Griseb., which in fact, however, both belong to *H. suberosa* Urb.) representing *H.* sect. *cubenses* Rydb.). By São Mateus' (2018) results, the genus *Harpalyce* and, presumably, its three geographically vicariant sections are natural, monophyletic taxa, with *H.* sect. *Brasilienses* being the sister clade of the two remaining sections, which are in turn sisters to each other (a rather shaky assumption, as long as a single Cuban taxon has been studied). The genus is old, assumed to be of Oligocene origin (> 30 Ma b.p.). Divergence of the northern sections from the Brazilian clade is also old (> 20 Ma b.p.). Species diversification, however, is fairly young, basically post-Miocene, an assumption that obviously, for Cuba, remains to be verified by the study of a larger number of taxa.

A further promising field of additional studies that we propose to follow up in the near future has opened up through the preliminary study of leaf glands of the new species here described. We found that the slight but obvious difference of the gland pattern they presented was based on obvious structural differences, to be observed on leaf transects, which have led to the definition of two distinct gland types that we have named "type A" and "type B". Screening the remaining species of the genus for the presence in them of these gland types, and of possible further types yet to be defined, is a promising field of study. Preliminary results of leaf surface studies indicate that the "type A" glands of *Harpalyce marianensis* are also found in *H. ekmanii*, *H. maisiana* as well as *H. greuteri* R.Rankin & P.A.González (not discussed here); whereas "type B" glands of *H. revoluta* occur in *H. cristalensis* Borhidi & O.Muñiz. The scattered glands of the leaves of *H. villosa*, *H. baracoensis*, and *H. acunae* Borhidi & O.Muñiz, hidden by dense indumentum, might represent yet another type.

Acknowledgements

We express our gratitude to the herbaria B and HAJB, their technicians and curators for facilitating the study of specimens; to Alelí Morales and Wildee Alonso from HAJB, who provided information on, and photos of, some specimens; to Bibiana Moncada, Berlin, for providing preparations and micrographs of the leaf surface and leaf transects; to Michael Rodewald who edited the original illustrations; to H. Manitz for the loan of *Harpalyce* specimens housed in JE; and to Eddy Martínez Quesada and Isis Hernández from Camagüey, Cuba, for generating the distribution map based on our data. The revision of materials in the herbaria B and JE was possible thanks to scholarships awarded by the Verein der Freunde des Botanischen Gartens und des Botanischen Museums Berlin-Dahlem to Pedro A. González in 2022. This contribution to the taxonomic revision of *Harpalyce* for "Flora de la República de Cuba" is one of the results of the Cuban national project PN223LH010-018 "Estudios taxonómicos y fitogeográficos en familias de la flora cubana", which involves the National Botanical Garden of Cuba and other Cuban institutions. Thanks to the Stiftung Herbarium Greuter for bearing the publication cost.

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Silene ophioglossa (Caryophyllaceae, Sileneae), a new species from southwest China

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Abstract

Silene ophioglossa Huan C. Wang & Feng Yang, a new species of Caryophyllaceae, is here described and illustrated based on morphological and molecular evidence. The new species was found in Sichuan and Yunnan provinces, southwest China. Phylogenetic analysis based on ITS sequences showed this new species belongs to section *Cucubaloides*. Morphologically, it resembles *S. phoenicodonta* and *S. viscidula*, which were also found in the southwest China, but clearly differs from the latter two species by having 5–7 mm long calyces with sparsely hirtellous and short glandular hairs, white petals, linear limbs and lobes, and absent or oblong-linear coronal scales. A distribution map and a table with morphological diagnostic characters of new species and its closest relatives are provided, as well as a preliminary conservation assessment of *S. ophioglossa* under the IUCN criteria.

Keywords

Conservation assessment, endemism, ITS sequence, *Silene phoenicodonta*, *Silene* sect. *Cucubaloides*

Introduction

The genus *Silene* L. (Sileneae DC., Caryophyllaceae Juss.), with 700 to 870 species (Mabberley 2017; Jafari et al. 2020) is mainly distributed in temperate regions of the Northern Hemisphere (Greuter 1995; Oxelman and Lidén 1995; Zhou et al. 2001). The center of its diversity is considered to be in western Asia and the Mediterranean area, but areas of central Asia are also highly diverse (Jafari et al. 2020). There has been considerable controversy regarding delimitation of the genus *Silene*. Recent molecular studies have clearly demonstrated that *Silene* (in the traditional sense), is paraphyletic since *Lychnis* L., *Atocion* Adans. and *Viscaria* Bernh. are nested within it (Jafari et al. 2020). Some authors suggested lumping most members of Sileneae into the genus (e.g. Greuter 1995; Desfeux and Lejeune 1996; Jafari et al. 2020). Conversely, other authors (e.g. Oxelman and Lidén 1995; Oxelman et al. 1997, 2001; Popp and Oxelman 2004; Frajman et al. 2009a, b; Greenberg and Donoghue 2011) preferred to separate *Agrostemma* L., *Eudianthe* (Rchb.) Rchb., *Heliosperma* Rchb., *Petrocoptis* A. Braun, *Atocion* and *Viscaria*.

The first comprehensive revision of the genus *Silene* in China was made by Tang (1996) who recognized 112 species, 2 subspecies and 17 varieties. In the most recent treatment by Zhou et al. (2001), 110 species were accepted, 67 of which are endemic to China (endemism ratio of *Silene* in China is about 61%). More recently, three additional species of *Silene* were described or recorded from southwest China by Lin et al. (2019) and Yang et al. (2022 a, b); these findings highlight the need for continued field exploration and taxonomical research in the region.

During our field surveys and the herbarium studies for a taxonomic revision of *Silene* in the Sino-Himalayan region, an interesting plant was repeatedly encountered, but one that does not fit with any previously described species. Comparison with related species demonstrates that this plant actually represents a distinct species hitherto not described. Therefore, it is described as a new species herein and named as *Silene ophioglossa* Huan C. Wang & Feng Yang.

Material and methods

Morphological analyses

The study followed the normal practice of plant taxonomic survey and herbarium taxonomy. Morphological studies of the new species were based on observation of living plants and specimens from Yunnan and Sichuan, southwest China. Digital images available at the JSTOR Global Plants (http://plants.jstor.org/) and at the Chinese Virtual Herbarium (http://www.cvh.ac.cn/), as well the collections housed at CDBI, KUN, PE, PYU, XTBG and YUKU were examined and compared with the new species. Pertinent taxonomic literature (e.g. Wu 1993; Zhuang 1995; Tang 1996; Zhou et al. 2001) was consulted. Morphological studies were carried out on dried material under a stereomicroscope (Olympus SZX2, Tokyo, Japan) and measurements were made using a ruler and a metric vernier caliper.

Seed micromorphology

Mature seed samples were directly adhered to carbon adhesive tape. Then they were coated with gold palladium using a BAL-TEC SCD 005 cool sputter coater (BAL-TEC AG., Liechtenstein) at Yunnan University, Kunming, China. Observations were conducted using a QUANTA 200 scanning electron microscope (SEM) (FEI Co., U. S. A.) at 20.0 KV.

Phylogenetic study

To determine the phylogenetic position of the putative new species, the internal transcribed spacer region (ITS) of the nuclear ribosomal DNA was used as the molecular marker. Total genomic DNA of this new species and *S. phoenicodonta* were extracted from silica-gel dried leaves using the DNA secure plant kit (TIANGEN, Beijing, China). The PCR protocols followed Lin et al. (2019). The ITS primers used were ITS1 and ITS4, as described by White et al. (1990) and Urbatsch et al. (2000). The PCR products were bidirectionally sequenced with the same primers used for PCR amplifications in an ABI 3730xL DNA Analyzer (Applied Biosystems) at Kunming Branch of Beijing Qingke Biotechnology Co., Ltd. (Yunnan, China).

We used a total of 70 taxa of *Silene* as ingroups, being representatives of most sections of *Silene*, *Heliosperma oliverae* Niketić et Stevan., *Atocion armeria* (Fedor.) Fedor. and *Petrocoptis pyrenaica* A. Braun as outgroups following the previous phylogenetic analyses (Jafari et al. 2020). A total of 73-taxon data sets, including six newly published sequences, were obtained. Voucher specimen and GenBank accession information for taxa are listed in Appendix 1.

All sequences were aligned with MAFFT (Katoh and Standley 2013) using 'auto' strategy and normal alignment mode. Gap sites were removed with trimAl (Capella-Gutiérrez et al. 2009) using "-automated1" command. The best-fitting substitution models SYM+I+G model for Bayesian inference were selected using ModelFinder (Kalyaanamoorthy et al. 2017) in BIC criterion. MrBayes 3.2.6 (Ronquist et al. 2012) was used to conduct Bayesian phylogenetic analyses. Runs were performed for 5 million generations with sampling of trees every 500 generations. The initial 25% of sampled data were discarded as burn-in.

Results and taxonomic treatment

Silene ophioglossa Huan C. Wang & Feng Yang, sp. nov.

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Figs 1, 2

Type. China. Yunnan Province: Binchuan County, Pingchuan Town, Maojiaoshan Mountain, alt. 2198 m, 25°58'13.6"N, 100°42'8.28"E, under a walnut forest by a ravine stream, 17 June 2022, *F. Yang et al. BC17342* (holotype YUKU-02074705!; isotypes YUKU-02074706!, PE!, HITBC!).

Diagnosis. *Silene ophioglossa* is morphologically similar to *S. phoenicodonta* (Fig. 3), but clearly differs from the latter in having 5–7 mm (vs. 6–8 mm) long calyces sparsely hirtellous and short glandular hairs (vs. densely hirtellous and with short glandular hairs), white (vs. dark violet) petals, linear (vs. obovate) limbs and linear (vs. ovate or nearly band-shaped) lobes, absent or oblong-linear (vs. orbicular-linear) coronal scales.

Etymology. The specific epithet "*ophioglossa*" is derived from the Greek words "*ophis*" (meaning snake) and "*glossa*" (meaning tongue), which refer to the petal lobes of this new species which resemble the tongue of a snake.

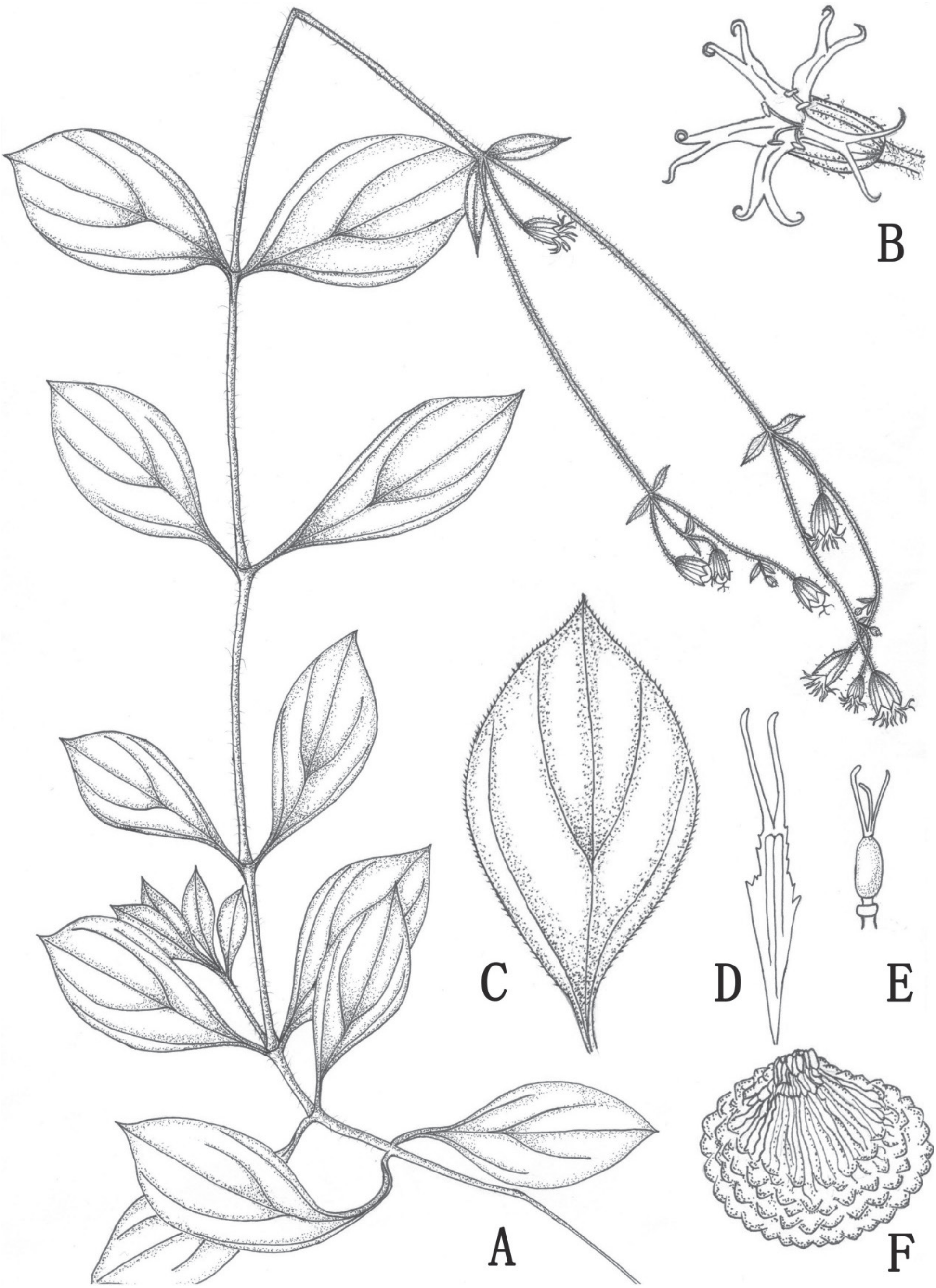

Figure 1. *Silene ophioglossa* sp. nov. (Drawn by Tingting Wang) **A** habit **B** flower (front view) **C** adaxial surface of leaf **D** petal **E** pistil and androgynophore **F** seed.

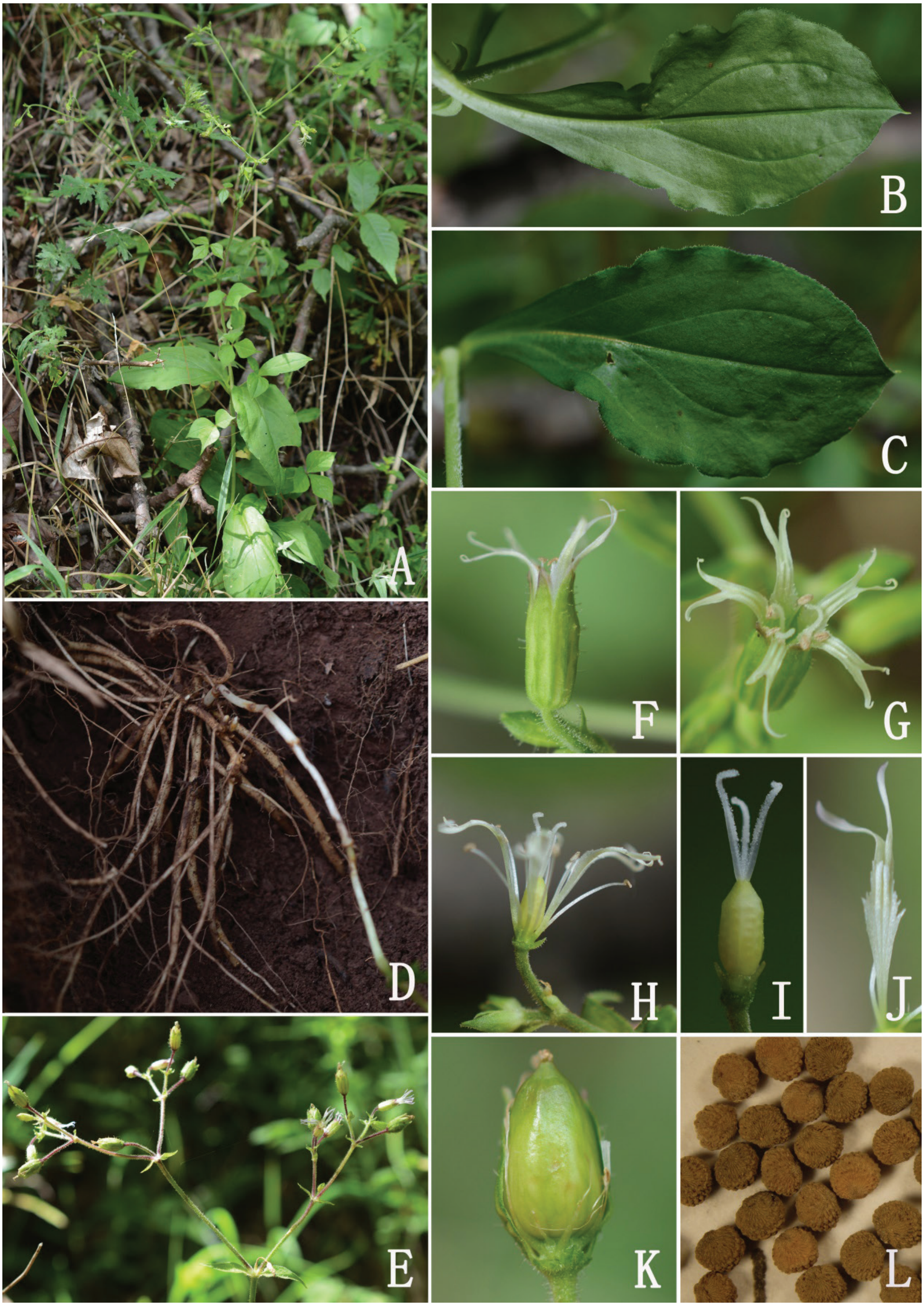

Figure 2. *Silene ophioglossa* sp. nov. (Photographed by F. Yang) **A** habit **B** abaxial surface of leaf **C** adaxial surface of leaf **D** roots **E** dichasial cymes **F** flower (side view, showing the calyx) **G** flower (front view) **H** dissected flower (showing the androgynophore and claws) **I** pistil and androgynophore **J** petal (showing the claw, auricles and coronal scales) **K** immature capsule **L** seeds.

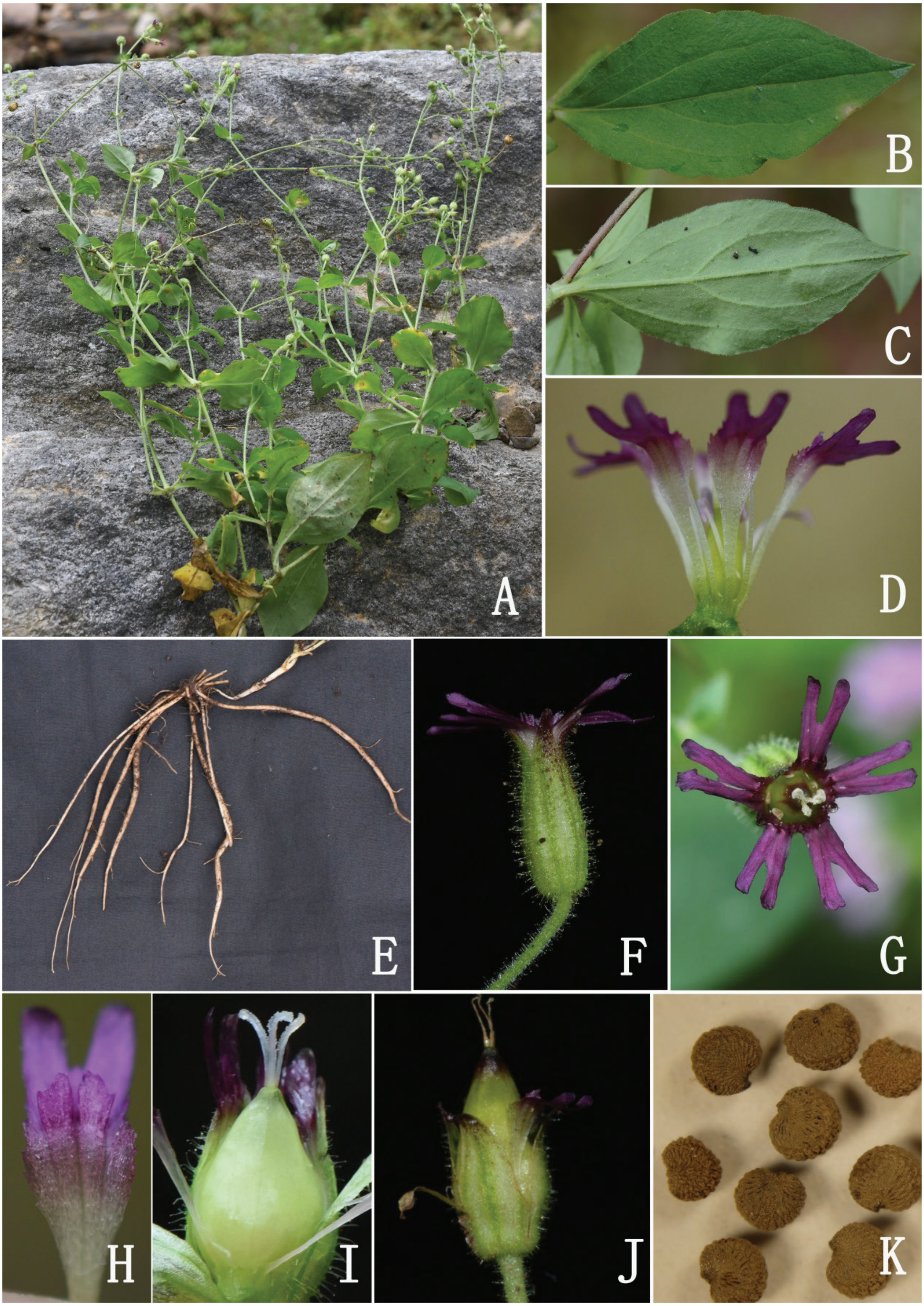

Figure 3. *Silene phoenicodonta* (Photographed by F. Yang and H. C. Wang) **A** habit **B** adaxial surface of leaf **C** abaxial surface of leaf **D** dissected flower (showing the androgynophore and claws) **E** roots **F** flower (side view, showing the calyx and pedicel) **G** flower (front view) **H** petal (showing the claw, auricles and coronal scales) **I** styles and immature capsule **J** calyx after anthesis **K** seeds.

Description. Herbs perennial. Roots numerous, clustered, cylindric, fleshy. Stems sparsely caespitose, ascending to sprawling, 30–80 cm long, slender, multibranched, with sparsely pubescent. Leaves ovate-elliptic or obovate-elliptic, 3–9 (–15) cm long, 1–4 cm wide, base cuneate or attenuate into petiole, apex acute, both surfaces puberulent to subglabrous, margin entire, minutely ciliate, lateral veins 2 pairs, midrib and lateral veins prominent abaxially. Dichasial cymes terminal, diffuse; peduncle 1–15 cm long, densely glandular-pilose. Pedicels densely glandular-pilose and sparsely eglandular villous, subequaling or longer than calyx; bracts ovate-lanceolate, apex acuminate. Calyx tubular-campanulate, 5–7 mm long, 2–3 mm in diameter, longitudinal veins green or violet, cohering at apex, sparsely hirtellous and with short glandular hairs, inflated after anthesis, 6–7 mm long, 4–5 mm in diameter in fruit stage; calyx teeth ovate-triangular, green or violet, ca. 1 mm long, apex acute, margin ciliate. Androgynophore ca. 1 mm long, glabrous. Petals white, 1.0–1.2 cm long; claws equaling to calyx, oblanceolate, glabrous, inflated above, margin erose; limbs linear, deeply bifid to middle, lobes linear, apex usually curly, without side lobe; coronal scales absent or oblong-linear, small, entire or emarginated at apex. Stamens 10, included in calyx tube; filaments glabrous, 5–7 mm long. Styles 3, included or slightly exserted beyond calyx. Capsule broadly ovoid, 7–9 mm long, 4–5 mm in diameter, slightly longer than calyx. Seeds dark brown, globose-reniform, ca. 1 mm long, tuberculate.

Molecular phylogenetics. The ITS sequence region of *Silene ophioglossa* comprises 687 and 821 base pairs with a GC content of 53.3% and 54.4%. The alignment of 73 ITS sequences resulted in a matrix of 582 total characters, 350 of which are constant, 58 of the variable characters are singleton sites and 174 characters are parsimony-informative sites.

Phylogenetic analyses using ITS sequences uncovered that the new species, *S. ophioglossa*, belongs to a clade A representing *S.* sect. *Cucubaloides* Edgeworth & Hook. f. which was recircumscribed by Jafari et al. (2020) in their recent studies (Fig. 4). This placement is also supported by its morphological characters, such as the ascending to sprawling, multibranched stems, ovate-elliptic or obovate-elliptic leaves, lax dichasial cymes and tubular-campanulate calyces. In the phylogenetic tree (Fig. 4), two sequences from *S. ophioglossa* constituted a monophyletic lineage with maximum support, and it is sister to a small subclade B that includes *S. phoenicodonta* and *S. viscidula*. This close relationship is also supported by their morphological similarity.

Seed micromorphology. Seeds of *Silene ophioglossa* are dark brown when mature, globose-reniform in shape, 0.94–1.12 mm long, 0.79–0.94 mm wide. The lateral surface of seed is concave. The dorsal surface is flat, ca. 0.57 mm wide. Its seed coat is formed by elongate epidermis cells with S-undulate and V-undulate anticlinal walls. The periclinal walls are convex and have granulate-papillate ornamentation (Fig. 5A–C).

Phenology. Flowering and fruiting from June to September.

Distribution and habitat. *Silene ophioglossa* is endemic to southwest China, where it has been collected from western Sichuan and north Yunnan (Fig. 6). Currently, it seems to be restricted to the Jinsha River basin. *Silene ophioglossa* usually occurs at elevations

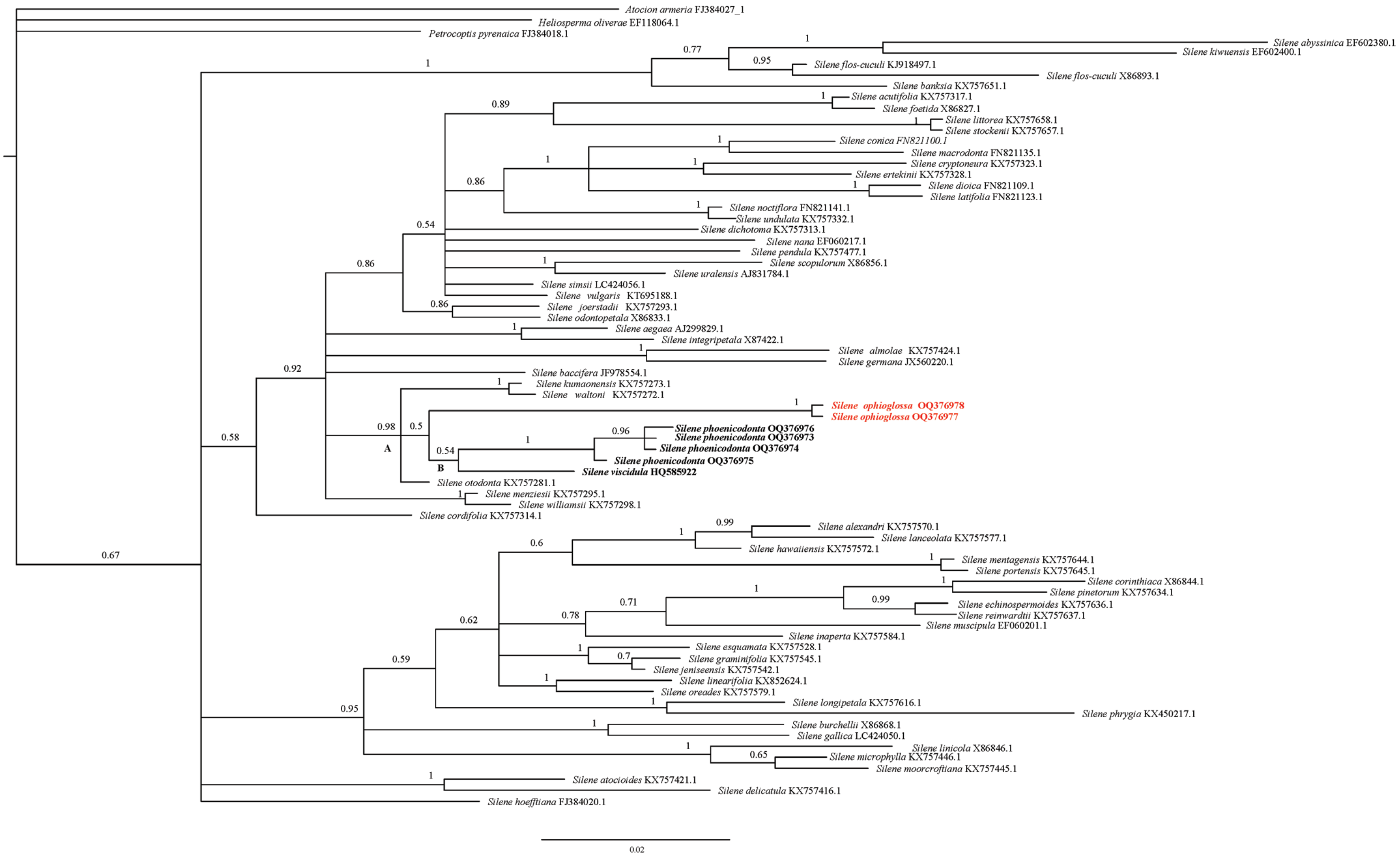

Figure 4. Bayesian inference tree of *Silene* based on ITS sequences showing phylogenetic placements of *S. ophioglossa*. Bayesian posterior probabilities are shown near the nodes. *Silene ophioglossa*, *S. viscidula* and *S. phoenicodonta* are marked in bold type, and *S. ophioglossa* is highlighted by using red colored text.

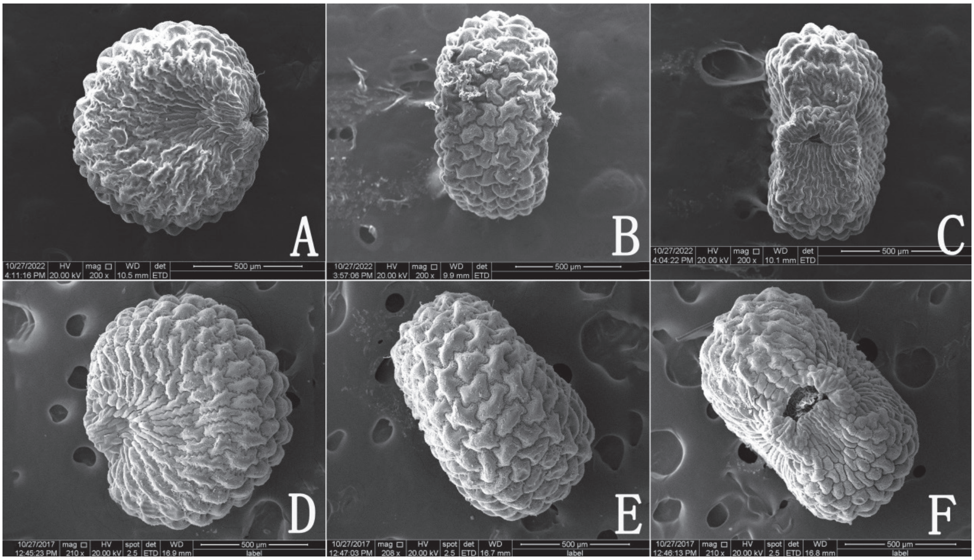

Figure 5. SEM micrographs of seed morphology in *Silene ophioglossa* (voucher specimen: Q. P. Wang et al. XY7908, **A–C**) and *S. phoenicodonta* (voucher specimen: D. Qiao DC2575, **D–F**). **A, D** lateral surface **B, E** dorsal surface **C, F** ventral surface.

ranging from 2000–3000 meters and grows in thickets or at forest margins, and its association includes *Lepisorus palmatopedatus* (Baker) C. F. Zhao, R. Wei et X. C. Zhang, *Lysimachia christiniae* Hance, *Corydalis triternatifolia* C. Y. Wu, *Indigofera pendula* Franch., *Lysimachia stenosepala* Hemsl. var. *flavescens* Chen et C. M. Hu, *Circaea cordata* Royle, *Quercus acutissima* Carr. and *Campylotropis teretiracemosa* P. C. Li et C. J. Chen.

Conservation status. *Silene ophioglossa* is known from five localities and has been found in thickets or at forest margins. However, we actually only investigated two points, and didn't have enough information about its distribution, abundance, or threats to this species. More information is needed for assignment of its conservation status. Therefore, we choose to assign this new species to the category data deficient (DD) following the IUCN guidelines (IUCN 2012, 2022).

Taxonomic notes. Morphologically and seed micromorphologically, *Silene ophioglossa* is most similar to *S. phoenicodonta* (Fig. 3), a species also distributed in southwest China (Fig. 6). They share ascending to sprawling, multibranched stems, ovate-elliptic or obovate-elliptic leaves, dichasial cymes, 3 styles and globose-reniform seeds (Fig. 5), but the new species is distinguishable from the latter by its calyces 5–7 mm (vs. 6–8 mm) long, sparsely (vs. densely) hirtellous and with short glandular hairs, petals white (vs. dark violet), limbs linear (vs. obovate), lobes linear (vs. ovate or nearly band-shaped) and coronal scales absent or oblong-linear (vs. orbicular-linear).

Silene ophioglossa is somewhat close to *S. viscidula*, an endemic species found from southwestern China. Nevertheless, *S. ophioglossa* differs from *S. viscidula* in having ovate-elliptic or obovate-elliptic (vs. elliptic or elliptic-oblanceolate) leaves, diffuse (vs.

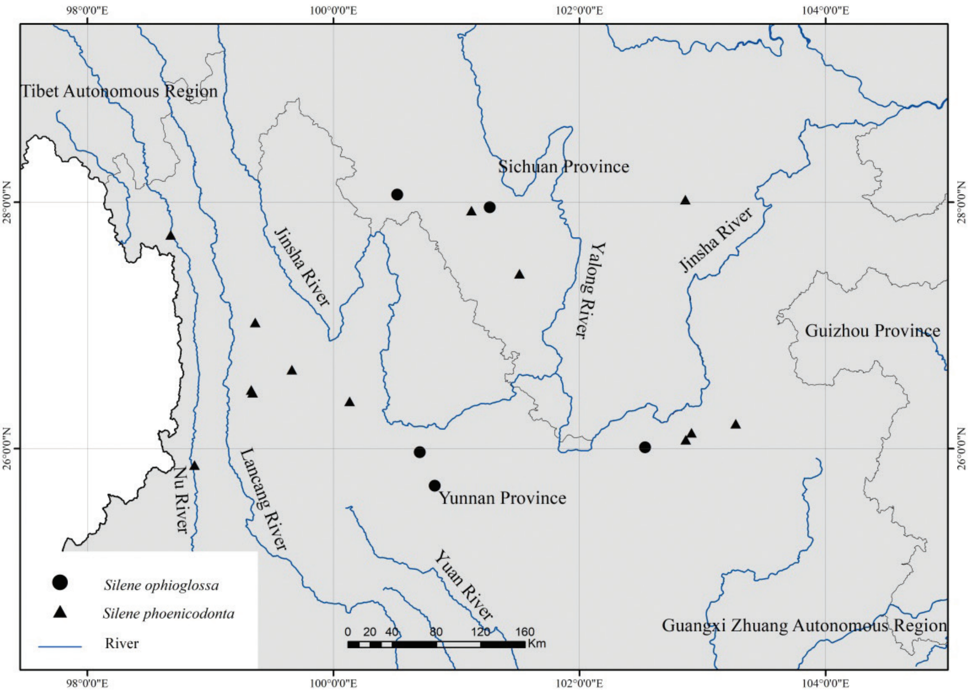

Figure 6. Distribution of *Silene ophioglossa* and *S. phoenicodonta* in southwest China.

compact, 3–7 (–15)-flowered) dichasia, 5–7 mm long (vs. 7–10 mm long) calyces, sparsely hirtellous and with short glandular hairs (vs. densely glandular hairs), white (vs. pale pink or white) petals, linear (vs. broadly obovate) limbs, linear (vs. ovate or square) lobes, absent or oblong-linear (vs. flabellate) coronal scales. A detailed morphological comparison between these three species is summarized in Table 1.

Additional specimens examined (Paratypes). China. Sichaun: Muli County, Qiaowa Town, Chutouwan village, under the shady and moist thickets by the river, alt. 2600 m, 28 June 1978, *Y. B. Yang 7097* (CDBI-0020627, CDBI-0020628); Muli County, Ninglang village, under *Tsuga* forest on the mountain slope, alt. 3000 m, 25 September 1983, *Qinghai-Tibet Expedition 14350* (KUN-0514408, KUN-0514409). **Yunnan:** Luquan County, Sayingpan Town, Sayongshan Mountain, at evergreen broad-leaved forest margins, alt. 2400 m, 21 June 1965, *W. M. Zhu & Y. M. Feng 00584* (YUKU-02006723); Xiangyun County, Midian Town, Yemaoshan Mountain, alt. 2300 m, 25°41'52.12"N, 100°49'26.69"E, 24 July 2018, *Xiangyun Medicinal Plant Investigation Team 5329230617* (YUKU-02074711, YUKU-02074712, YUKU-02074713) and *F. Yang et al. XY8075* (YUKU-02074710); same location, 26 August 2019, *Q. P. Wang et al. XY7908* (YUKU-02074714, YUKU-02074715).

Silene phoenicodonta. **China. Sichaun:** Zhaojue County, Sikai Town, thickets, alt. 2400 m, 30 June 1976, *Sichuan Vegetation Team 12763* (PE-00580695, CDBI-0020501). **Yunnan:** Huizhe County, Dahai village, Dahaicaoshan, ca. 2 km from

Table 1. Morphological comparison of *Silene ophioglossa*, *S. phoenicodonta* and *S. viscidula*.

Characters	Species		
	S. ophioglossa	***S. phoenicodonta***	***S. viscidula***
Roots	clustered, cylindric	clustered, cylindric	clustered, fusiform
Leaves	ovate-elliptic or obovate-elliptic	ovate-elliptic or obovate-elliptic	elliptic or elliptic-oblanceolate
Inflorescence	dichasial cymes, diffuse	dichasia diffuse, few flowered	dichasial cymes, 3–7 (–15)-flowered, compact
Calyces	5–7 mm long, outside sparsely hirtellous and with short glandular hairs	6–8 mm long, outside densely hirtellous and with short glandular hairs	7–10 mm long, outside with dense glandular hairs
Petals	white	dark violet	pale pink or white
Limbs	linear, deeply bifid to middle	obovate, deeply bifid to middle	broadly obovate, shallowly 2-lobed
Lobes of petals	linear, apex usually curly, without side lobe	ovate or nearly band-shaped, sometimes with one inconspicuous tooth on each lateral side	ovate or square, entire, sometimes with one inconspicuous tooth on each lateral side
Coronal scales	absent or oblong-linear, entire or emarginated at apex	Present, orbicular-linear, laciniate at apex	Present, flabellate, laciniate at apex

Xiaoxiniu, Dabaping, alpine meadows, 103°16'10.50"E, 26°12'6.19"N, alt. 3433 m, 24 July 2018, *H. Tang TH2018046* (KUN-1481546); Dongchuan District, Xueling Scenic Area, 29 August 2017, *D. Qiao DC2575* (YUKU-02074716); Heqing County, Songgui Town, Maershan Mountain, on the path from Chamujing to Zhulinkou, under forest, roadsides, 100°7'53.68"E, 26°23'2.58"N, alt. 2578 m, 5 August 2018, *H. Tang TH2018087* (KUN-1481543); Jianchuan County, Shizhongshan Mountain, July 1987, *S. Y. Bao 401* (KUN-0531671); Zhengkang County, Snow Range, in grassy slope, alt. 2600 m, 22 July 1938, *T. T. Yu 16881* (PE-00558309, KUN-0514405).

Silene viscidula. **China. Sichaun:** Yanbian County, Dapingzi District, Baoshishan, limestone mountainous region, at 2700 m, 29 June 1983, *Qinghai-Tibet Team 11677* (KUN-0514407). **Guizhou:** Weining County, Mazha Town, Gali village, Mabaidashan, 12 July 1959, *Bijie Team 191* (PE-00581476). **Yunnan:** Luquan County, Kedu Town, Dianwei village, grassy slope, at 2500 m, 25 October 1940, *Y. B Chang 347* (IBSC-0149532); Dongchuan District, November 1906, *E. E. Maire 87* (E-00109656); Mengzi, Yangliuhe village, sparse forest, at 1720 m, 30 July 1958, *Y. Y. Hu & S. K. Wen 580546* (KUN-0514415).

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Appendix 1

Table A1. Voucher information and GenBank accession of species used in our study.

GenBank	Species	Voucher information	Herbarium
AJ299829	*Silene aegaea* Oxelman	Christodoulakis 2826	UPA
AJ831784	*Silene uralensis* (Rupr.) Bocquet	Inger Skrede SUP02-38-08	UPS
EF060201	*Silene muscipula* L.	Bengt Oxelman 1780	GB
EF060217	*Silene nana* Kar. Et Kir.	Kereverzova and Mekeda 1976.V.5	LECB
EF118064	*Heliosperma oliverae* Niketić et Stevan.	LJU 137738	
EF602380	*Silene abyssinica* (Hochst.) H.Neumayer	P. Tuley 2091	K
EF602400	*Silene kiwuensis* (Fr.) F. Jafari, Oxelman et Rabeler	A. Gizaw AFR561	ETH
FJ384018	*Petrocoptis pyrenaica* A. Braun	Schneeweiss et al. 6549	WU
FJ384020	*Silene hoefftiana* Fisch. ex C. A. Mey.	Menitskiy and Portenier 1987.VIII4	LE
FJ384027	*Atocion armeria* (Fedor.) Fedor.	B. Frajman and M. Turjak 136972	LJU
FN821100	*Silene conica* L.	Erixon 70	UPS
FN821109	*Silene dioica* (L.) Clairv.	H. C. Prentice D130-2	GB
FN821123	*Silene latifolia* Poir.	H. C. Prentice L80-12	GB
FN821135	*Silene macrodonta* Boiss.	Bengt Oxelman 2441	GB
FN821141	*Silene noctiflora* L.	H. C. Prentice N2-2	
JF978554	*Silene baccifera* (L.) Roth	Z387	
JX560220	*Silene germana* J. Gay ex Coss.		
KJ918497	*Silene flos-cuculi* (L.) Clairv	S-99	
KT695188	*Silene vulgaris* (Moench) Garcke	BIOUG24049-D08	
KX450217	*Silene phrygia* Boiss.	MUFE12337	
KX757272	*Silene waltoni* F. N. Williams	G. and S. Miehe 03-048-12	Miehe
KX757273	*Silene kumaonensis* F. N. Williams	G. and S. Miehe 01-109-08	Miehe
KX757281	*Silene otodonta* Franch.	Miehe/Huang/Otsu/Tunsu 97-070-18	Miehe
KX757293	*Silene joerstadii* Wendelbo	Hedge and Wendelbo W 8992	GB
KX757295	*Silene menziesii* Hook.	A.R. Kruckeberg 2830	WTU
KX757298	*Silene williamsii* Britton	C. Brochmann and H. H Grundt	
KX757313	*Silene dichotoma* Ehrh.	Till s.n. 17.7.2004	WU
KX757314	*Silene cordifolia* All.	Lippert and Merxmueller 17265	
KX757317	*Silene acutifolia* All.	Rothmaler 13691	S
KX757323	*Silene cryptoneura* Stapf	Bengt Oxelman 2524	GB
KX757328	*Silene ertekinii* Aydin et Oxelman	Zeynep Aydin 31	
KX757332	*Silene undulata* Aiton	Bayliss, Roy Douglas Abbot BS7700	M
KX757416	*Silene delicatula* Boiss.	Bengt Oxelman 2456	GB
KX757421	*Silene atocioides* Boiss.	Bengt Oxelman 1627	GB
KX757424	*Silene almolae* J. Gay ex Coss.	Merxmueller, H. and Lippert, W. 25372	M
KX757445	*Silene moorcroftiana* Wall. ex Benth.	Ewald and Zetterllund 6278	GB
KX757446	*Silene microphylla* Boiss.	Abbas Gholipour 2	
KX757477	*Silene pendula* L.	Bengt Oxelman 2291	GB
KX757528	*Silene esquamata* W. W. Sm.	Podlech, D. 54568	M
KX757542	*Silene jeniseensis* Willd.	H. Solstad and R. Elven 04/1573	O
KX757545	*Silene graminifolia* Otth	Anja Rautenberg 241	UPS
KX757570	*Silene alexandri* Hillebr.	Wood 6036	US
KX757572	*Silene hawaiiensis* Sherff	MW Chase 2013	K
KX757577	*Silene lanceolata* A.Gray	S. Weller 4	
KX757579	*Silene oreades* Boiss. et Heldr.	Anja Rautenberg 167	UPS

GenBank	Species	Voucher information	Herbarium
KX757584	*Silene inaperta* L.	Silva 1688	LD
KX757616	*Silene longipetala* Vent.	Grey-Wilson and Hewer 899	GB
KX757634	*Silene pinetorum* Boiss. et Heldr.	Bengt Oxelman et al 2183	GB
KX757636	*Silene echinospermoides* Hub.-Mor.	Bengt Oxelman 2202	GB
KX757637	*Silene reinwardtii* Roth	T. Engel, Frey and H. Kuerschner 90-223	BSB
KX757644	*Silene mentagensis* Coss.	Jahandiez 329	LD
KX757645	*Silene portensis* L.	Podlech 46825	G
KX757651	*Silene banksia* (Meerb.) Mabb.	S.J. Enander	S
KX757657	*Silene stockenii* Chater	Holmdahl 1595	GB
KX757658	*Silene littorea* Brot.	Bengt Oxelman 2589	GB
KX852624	*Silene linearifolia* Otth	IB-13681	
LC424050	*Silene gallica* L.	27286	TUH
LC424056	*Silene simsii* F. Jafari, Rabeler et Oxelman	39821	TUH
X86827	*Silene foetida* Link ex Spreng.	Bengt Oxelman s.n	GB
X86833	*Silene odontopetala* Fenzl		
X86844	*Silene corinthiaca* Boiss. et Heldr.	Bengt Oxelman 1951	GB
X86846	*Silene linicola* C. C. Gmel.	Bengt Oxelman ITS-20605	GB
X86856	*Silene scopulorum* Franch.	KGB 810	GB
X86868	*Silene burchellii* Otth	Bengt Oxelman 2280	GB
HQ585922	*Silene viscidula* Franch.	SV6	
X87422	*Silene integripetala* Bory et Chaub.	Jagel 48	B
OQ376973	*Silene phoenicodonta* Franch.	H. C. Wang et al. LQ12915	YUKU
OQ376974	*Silene phoenicodonta* Franch.	F. Yang et al. LP4339	YUKU
OQ376975	*Silene phoenicodonta* Franch.	J. L. Liu et al. LQ14001	YUKU
OQ376976	*Silene phoenicodonta* Franch.	H. C. Wang et al. JC4486	YUKU
OQ376977	*Silene ophioglossa* Huan C. Wang et Feng Yang	Xiangyun Med. Pl. Exp. 5329230617	YUKU
OQ376978	*Silene ophioglossa* Huan C. Wang et Feng Yang	Q. P. Wang et al. XY7908	YUKU

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Nomenclature and typification in *Verbascum* (Scrophulariaceae) from North Africa

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Abstract

The progress of taxonomic work on native *Verbascum* L. taxa found in Morocco led to a search for reference specimens in various herbaria. This process was extended to the taxa found in the other four countries of North Africa (Algeria, Tunisia, Libya, and Egypt), which make up the southern shore of the Mediterranean basin. Numerous names were identified as needing typification or requiring corrections of their earlier lectotypifications in order to stabilize their nomenclature and provide a better definition of each taxon. As a result, lectotypes are now designated for 35 names, a neotype is proposed for *V. ballii* (Batt.) Hub.-Mor., and second-step lectotypes are proposed for *V. faurei* subsp. *acanthifolium* (Pau) Benedí & J.M.Monts. and *V. pinnatisectum* (Batt.) Benedí. Comments have been added for each typified name. Known isolectotypes are also mentioned whenever possible. Furthermore, some new combinations are proposed in this paper, namely *V. longirostre* var. *antiatlantica* (Emb.) Khamar, **comb. nov.**, *V. longirostre* var. *atlantica* (Maire) Khamar, **comb. nov.**, and *V. longirostre* var. *hoggarica* (Maire) Khamar, **comb. nov.**

Keywords

genus *Verbascum*, lectotypification, nomenclature, North Africa

Introduction

Verbascum L. (including *Celsia* L.) is a diverse genus of the figwort family Scrophulariaceae *sensu stricto*, tribe Scrophularieae (*sensu* Angiosperm Phylogeny Group (APG-IV)

2016), including 497 taxa (465 species and 32 subspecies) (Hassler 2022; Khamar 2022) broadly distributed throughout the Old World, particularly in the temperate northern hemisphere (Murbeck 1925, 1933; Huber-Morath 1978; Remal 2014; Sotoodeh et al. 2014, 2015; Zografidis 2016; Khamar et al. 2017). It reaches its highest species diversity in the Mediterranean region (Yılmaz and Dane 2012; Remal 2014; Sotoodeh 2015; Zografidis 2016) where 70% of all species can be found (Murbeck 1939; Sharifnia 2007; Benedí 2009; Catara et al. 2016). Outside its natural distribution area, the genus is naturalized in other regions around the world, *i.e.* the United States of America, Canada, South Africa, Hawaii, Mexico, Chile, Hispaniola, Argentina, Australia, New Zealand, the Indian Ocean island of La Reunion, and Japan (Parham and Healy 1976; Gross and Werner 1978; Gross 1980; Reinartz 1984; Juvik and Juvik 1993; Mito and Uesugi 2004; Baret et al. 2006; Durán-Espinosa 2006; Williams 2010; Alba 2011; Nesom 2019; Jaca 2017; Scaramuzzino et al. 2018). Further progress on the taxonomy of *Verbascum* has recently been made thanks to botanical studies, especially molecular studies in the north of the Mediterranean basin and in the Irano-Turanian biogeographic region (Al-Hadeethy et al. 2014; Ghahremaninejad et al. 2014; Remal 2014; Sotoodeh 2015). The results of these studies support the monophyly of the genus and its synonymy with *Celsia* L. However, the morphological infrageneric classifications proposed by Murbeck (1925, 1933) and Huber-Morath (1978) are not consistent with the molecular phylogeny.

In continental North Africa (Fig. 1), the genus is represented by 36 taxa belonging to 31 species (Dobignard and Chatelain 2013; Khamar et al. 2017, 2022). Endemism rate is estimated to be 48% of all taxa. *Verbascum* species of North Africa grow in various habitats, i.e. steppes, forests, scrublands, lowland and high mountain pastures, rocky places, dry stony ravines and wadis, and can be found from the seashore up to high mountains (Jahandiez and Maire 1934; Quézel and Santa 1963; Pottier-Alapetite 1981; Qaiser 1982; Boulos 2002; Ibn Tattou 2007).

In continental North Africa, the genus has been studied by different authors from the late 18th / early 19th centuries to the present, and various accounts have been made: Desfontaines (1798); Ball (1875, 1878); Ascherson and Schweinfurth (1887); Battandier and Trabut (1889, 1890, 1902); Battandier (1910, 1919); Bonnet and Barratte (1896); Murbeck (1905, 1921, 1923, 1925, 1927, 1933, 1936, 1939); Maire (1918, 1924, 1931, 1940); Pau (1922, 1928); Sennen (1936); Jahandiez and Maire (1934); Emberger and Maire (1941); Quézel (1957); Quézel and Santa (1963); Huber-Morath (1973); Pottier-Alapetite, (1981); Qaiser (1982); Fennane and Ibn Tattou (1998); Boulos (2002); Ibn Tattou (2007); Le Floc'h et al. (2010); Dobignard and Chatelain (2013); and Khamar et al. (2017). Nevertheless, few papers specifically deal with the typification of accepted *Verbascum* species names (Benedí and Montserrat 1985, 1997; Benedí 2003), so that significant numbers of binomials still lack unequivocal types. Moreover, the locations of the types are not fully resolved.

The present paper constitutes a preliminary step towards a taxonomic and nomenclatural revision of the taxa growing in North Africa. The purpose is to (1) contribute to nomenclatural stability of the species by clarifying the type citations, the designation of lectotypes, holotypes or neotypes when necessary, or the indication of previous typifications, and (2) provide an updated list of synonyms for each taxon.

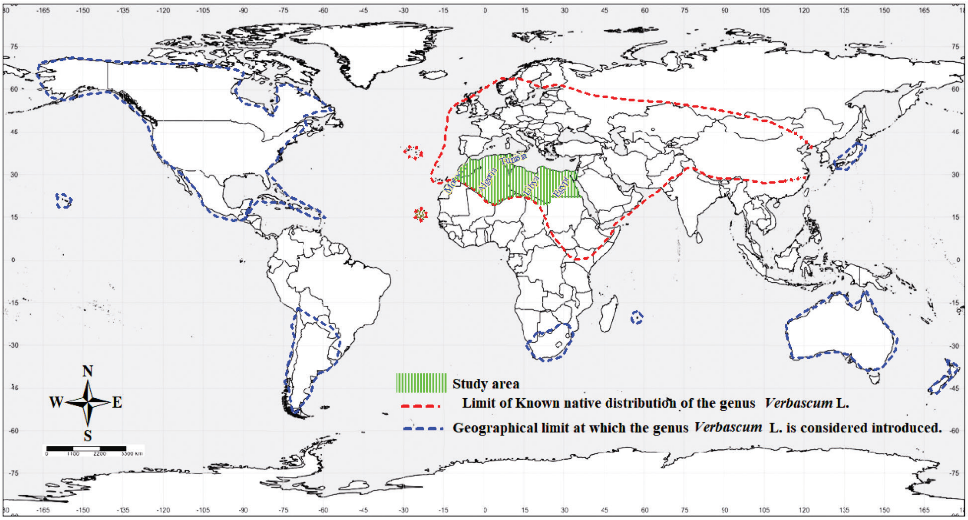

Figure 1. General distribution area of the Genus Verbascum L. modified from Murbeck (1925, 1933, 1939), Remal (2014), Sotoodeh et al. (2015) and Khamar (2022).

Materials and methods

All the protologues of each validly published name for *Verbascum* taxa occurring in continental North Africa, as well as their synonyms, were consulted and critically reviewed. The biogeographic area was considered to extend from the southern shore of the Mediterranean Sea to the southern phytogeographic limit of the genus *Verbascum*, which is marked in southwestern Morocco by the presence of *V. sinuatum* L., *V. tetrandrum* Barr and Murb, *V. maroccanum* (Ball.) Huber-Morath and *V. longirostre* (Murb.) Huber-Morath; by *V. dentifolium* Delile and *V. longirostre* (Murb.) Huber-Morath in the Algerian Sahara (Hoggar in southern Algeria), by *V. tibesticum* (Quézel) Hub.-Mor. in the northern part of the Tibesti mountain range in Chad near the Chadian-Libyan border (Fig. 1).

Three key elements were taken into account to verify the original type plants (Turland et al. 2018): (1) the specimen characteristics that matched those in the original description, (2) the date and locality of collection mentioned in the protologue, and (3) all handwritten annotations on the labels.

Type herbarium specimens and authentic collections were examined, from the corresponding herbaria or mainly from the material loaded on the Global Biodiversity Information Facility (GBIF; available online at http://www.gbif.org/occurence), JSTOR Global Plant Science (available online at http://plants.jstor.org), and also from online access to the permanent websites of herbaria (in bold are indicated herbarium codes according to Thiers 2021, continuously updated, and listed in alphabetic order): **AIX** (available online via the P website link), **B** (available online at: http://ww2.bgbm.org/herbarium/default.cfm), **BC** (via the GBIF and JSTOR Global Plants websites), **BCN** (available online via GBIF and JSTOR Globl Plants website links), **BM** (available online via GBIF and JSTOR Global Plants website links), **COI** (available online at https://www.uc.pt/en/herbario_digital/catalogues), **G** (available online at http://www.ville-ge.ch/musinfo/bd/cjb/chg/index.php?lang=en), **GDA** (available online via the GBIF website link), **JE** (available online at https://herbarium.univie.ac.at/database/search.php), **K (**available online at http://apps.kew.org/herbcat/gotoSearchPage.do), **LD** (available online at https://www.biomus.lu.se/en/botanical-collections), **LINN** (available online at http://linnean-online.org/linnaean_herbarium.html), **MA** (available online via the GBIF website link), **MAF** (available online via the GBIF website link), **MPU** (available online at https://collections.umontpellier.fr/collections/botanique/herbier-mpu/base-herbier-mpu), **P** (available online at https://science.mnhn.fr/institution/mnhn/search), **RAB** (available online via P website and JSTOR Global Plants website links), and **S** (available online at http://herbarium.nrm.se/search/specimens/). The herbaria where the personal collection of each author is kept were often verified using the Taxonomic Literature of Stafleu and Cowan (1976–1988).

Under the guidance of the International Code of Nomenclature for algae, fungi, and plants (ICN; Turland et al. 2018) and statements recently suggested by McNeill (2014), the lectotype was selected among others according to its quality and its accordance with the description and data provided in the protologue. When duplicates were traced in other herbaria, these were designated as isolectotypes. When no appropriate material for use as a lectotype was located, a neotype was designated and its duplicates – if available – were designated as isoneotypes.

The following websites were also checked to collect more data about types, bibliographical citations in the original publications, names, and synonymies: the Euro + Med PlantBase (http://ww2.bgbm.org/EuroPlusMed/query.asp), the International Plant Name Index (IPNI 2022; http://www.ipni.org), Plants of the World Online (POWO 2022; http://www.plantsoftheworldonline.org/), Tropicos (http://www.tropicos.prg/Home.aspx), and the African Plant Database (2022; APD; https://africanplantdatabase.ch/).

Lectotypifications

The taxa covered in this study are sorted in alphabetical order, according to their current accepted name (in bold), followed by the author citation, the bibliographic reference of the protologue or the nomenclatural recombination, the transcription of the original label of the specimen designated as type (lectotype, isolectotype, or neotype), and a barcode number following the herbarium acronym whenever available. Moreover, the homotypic and/or heterotypic synonyms for each name are quoted in chronological order. Comments have been added for each typified name.

Verbascum atlanticum **Batt., in Battandier & Trabut, Fl. Algèrie, Dicot.: 626. 1889.**

= *Verbascum repandum* Batt., in Suppl. aux Phanérog.: 69. 1910. Nonæ Willd. Enum. pl. hort. Berol.: 226, 1809.

= *Verbascum pseudoblattaria* auct., (sensu Batt) in Contrib. Fl. Atl.: 62. 1919., non. *pseudoblattaria* Schleicher, in Cat. Pl. Helv. ed. 4: 36. 1821. Type: [Algeria]. O. Djebel-M'zi, [without date], *J. A. Battandier s.n.* (Lectotype, designated here: MPU [MPU006498]!; isolectotype MPU [MPU006497]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu006498]

Type. [Algeria]. Djebel Aïssa, rocailles gréseuses près de l'Aïn-Aïssa, 1600 m, [without date], *J. A. Battandier s. n.* (Lectotype, designated here: P [P00083087]!; isolectotype MPU [MPU007787, MPU007788]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.p00083087]

Notes. *Verbascum atlanticum* was described by Battandier and Trabut (1889) based on material collected south of Oran, Algeria. In the protologue, the authors did not designate a holotype, nor did they provide data about the herbaria housing the original material. According to Stafleu and Cowan (1976–1988), the plants collected by Battandier and Trabut are kept at Herb. MPU, but a number of duplicates can be found at Herbs P and RAR. We traced three specimens stored at Herb. MPU (MPU007787, MPU007788) and Herb. P (P00083087). The morphology of all three specimens agreed with the original description, and their locality was also in agreement with the locality data given in the protologue. It should also be noted that the specimens housed at Herb. MPU were mounted as two preparations for the same collection – sheets MPU007788 and MPU007787. Cross-labeling indicated that they were a single specimen (see Art. 8.3. of the ICN, Turland et al. 2018). The herbarium sheet P00083087 and those kept at Herb. MPU bore original labels handwritten by Battandier "Université d'Alger / Herbier de l'Afrique du Nord / *Verbascum atlanticum* Batt.! / Type! / Djebel Aïssa, rocailles grèseuses près de l'Aïn-Aïssa, 1600 m, / Leg J. A. Battandier". Referring to Art. 9.6 of the ICN (Turland et al. 2018), all these specimens should be considered as syntypes. We selected sheet P00083087 as the lectotype, because it was in a better condition than the other Herb. MPU specimens, and part of its features closely agreed with the original description.

In his contributions for the Atlantic Flora, Battandier (1919) described another new species, *V. pseudoblattaria*, thirty years after the description of *V. atlanticum*. The original material of this new species, as referred to by Battandier (1919) in the protologue, was collected at Djebel-M'zi, south of Oran (Algeria). We traced two sheets at Herb. MPU (MPU006498, MPU006497), which are in complete agreement with the protologue and can be considered as original material. The sheet MPU006498 is selected here as the lectotype of the name *V. pseudoblattaria*, since it is in a better condition.

Verbascum ballii **(Batt.) Hub. -Mor., in Bauhinia 5(1): 10. 1973.**

≡ *Celsia ballii* Batt., in Battandier & Trabut, Fl. Algèrie, Dicot.: 628. 1889 [basionym]. Type: [Algeria]. Oued Biskra, April 1895, *J. A. Battandier, s.n.* (Neotype, designated here: MPU [MPU007789]!, isoneotype MPU [MP007790]!). [image of neotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu007789].

≡ *Celsia laciniata* var. *ballii* (Batt.) Batt., in Battand. & Trab. Fl. Anal. & Synopt. Alg.-Tun.: 243. 1902. ≡ *Verbascum ballii* (Batt.) Qaiser, in Fl. Libya 88: 26. 1982, comb. nov. superfl.

= *Celsia cretica* L. var. *cavanillesii* auct. Spicil. Fl. Maroc: 584. 1878, Non *Celsia cretica* var. *cavanillesii* Kunze ex Willk., in Willk. & Lange, Prodr. Fl. Hispan. 2: 545. 1870; nec *C. cavanillesii* Kunze in Flora 29: 698. 1846.

= *Celsia laciniata* Poir. var. *brvipes* Barratte, in Bonnet & Barratte Cat. Rais. Pl. Vasc. Tunisie: 311. 1896. Type: not designated.

Notes. When he described this species, Battandier (in Battandier and Trabut 1889) did not specify in which herbarium the type had been deposited. After an in-depth search, we found three sheets at Herb. MPU bearing labels handwritten by Battandier and rewritten by Dr. R. Maire, on which he noted "Type". The first sheet (MPU007789) bore a label reading "Oued Biskra, Avril 1895, [Battandier's signature]", the second one (MP007790) bore a label reading "*Celsia ballii* Batt. / El Kantara / Avril 1895 / *leg. J. A. Battandier* / [Battandier's signature]/" and the last one (MPU009629) bore a label reading "*Celsia ballii* Batt / C. Aïn-Oumach, montagne / *J. A. Battandier*". However, these sheets presented two inaccuracies when compared with the protologue: (1) specimens MPU007789 and MP007790 were collected after the protologue was published, and (2) the collection locality indicated on the label of sheet MPU009629 did not match with the one cited in the protologue. Therefore, the "type" notation by Maire on *Celsia ballii* sheets was mistaken. Since no specimen from the original gathering in any institution was traced, a neotype should be designated according to Arts 9.8 of the ICN (Turland et al. 2018). We selected sheet MPU007789 stored at Herb. MPU as a neotype since it was collected and identified by Battandier and display all the morphological features described in the protologue.

Verbascum battandieri (Murb.) Hub.-Mor., in Bauhinia 5(1): 10. 1973.

≡ *Celsia battandieri* Murb., in Lunds Univ. Arsskrift, 2 n.f., 22(1): 209.1925. Type: [Algeria]. Algérie occid. Oran, à Santa Cruz, rochers calcaires au-dessus du col, 15 May 1924, *A. Faure, s.n.* (Lectotype, designated here: JE [JE00013725]!; isolectotype: JE [JE00013700, JE00013701, JE00013702, JE00013703]!). [image available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.je00013725)].

= *Celsia laciniata* auct., in Battandier & Trabut, Fl. Alg. 1(4): 629. 1890, non *C. laciniata* Poir., Lam., in Encycl., Suppl. 2: 147. 1811, nec *C. laciniata* Coss. ex Ball, in J. Linn. Soc., Bot. 16: 585. 1878.

= *Celsia barnadesii* var. *mauritanica* Pau, in Mem. Mus. Ci. Nat. Barcelona, Ser. Bot. 1(1): 59. 1922 [basionym]. Type: [Morocco]. Riff oriental aux alentours de Zeluan, 2 May 1910, *C. Pau s.n.* (Lectotype designated by Nualart et al. 2018, p. 614): MA [MA108921]!; isolectotypes: BCN [BCN52463]!, G [G00414977]!,

LD [LD1967555]!, MA [MA108919]!, MA [MA108920]!, P [P03425530]!). ≡ *Celsia mauritanica* (Pau) Sennen & Mauricio, in Monde Pl. 3(66–181): 1. 1929.
= *Celsia rhiphaea* Murb., in Bot. Not. 1945: 109. 1945 [basionym]. Type: [Morocco]. In declivibus calc, littoris rhiphaei, ad pedem Yebel Malmusi (Bocoya), 100 m alt., 4 June 1927, *Font-Quer 565.* B: [n. v.] ([Type specimen is not traced; likely the sheet has been destroyed during the World War II (Hiepko, 1987)]). ≡ *Verbascum rhiphaeum* (Murb.) Hub.-Mor., in Bauhinia 5(1): 14. 1973.

Notes. In the protologue of this species, Murbeck (1925) cited more than 30 gatherings, and he indicated the herbaria (B, WU, JE) that housed the specimens he examined. In the absence of any indication of a single specimen as the type, all the specimens cited in the protologue can be considered as syntypes according to Art. 9.6 of the ICN (Turland et al. 2018). Following the indications of Murbeck (1925), we only traced five sheets (JE00013700, JE00013701, JE00013702, JE00013703, JE00013725) at Herb. JE. These specimens completely agree with the protologue and can be safely considered as original material. However, as the other sheets stored at Herb. B mentioned by Murbeck were not found, we can assume that they were all destroyed by the fire following bombing by the Allied forces during World War II (see Hiepko, 1987). A detailed examination of the specimen and photos of JE00013725, presumably examined by Murbeck, matched with all the criteria and the description provided in the protologue, so we select it here as the lectotype of the name *Verbascum battandieri*.

Verbascum blattaria L., Sp. Pl. 1: 178. 1753.

= *Blattaria alba* Mill., Fig. Pl. Gard. Dict. 1: 45. 1760.
= *Verbascum glabrum* Mill., Gard. Dict. ed. VIII: n. 8 1768.
= *Verbascum cordatum* Desf., in Fl. Atl. 1: 186. 1798.
= *Verbascum repandum* Willd., Enumeratio Plantarum: 226. 1809.
≡ *Thapsus blattaria* (L.) Raf., in Fl. Tellur. 4: 89. 1838.
= *Verbascum blattaria* var. *albiflorum* G.Don, in Gen. Hist. 4: 497 1838. ≡ *Verbascum blattaria* f. *albiflora* (G.Don) House, in Bull. New York State Mus. Nat. Hist. 243–244: 45. 1923.
= *Verbascum blattaria* var. *albiflorum* Kuntze, in Revis. Gen. Pl. 2: 468.1891, nom. illeg.
= *Blattaria vulgaris* Fourr., in Ann. Soc. Linn. Lyon, N. S. 17: 125. 1869.
= *Verbascum blattaria* L. var. *brevipedicellatum* Halácsy. in Ost. bot. Zeitschr. XLII: 419. 1892. Type: [Greece]. Insula Thasos. Limenas, in pratis arenosis in oliveto. 04 June 1891, *P. Sintenis & J. F. N Bornmüller 655* (Lectotype, designated here: LD [LD1393506 image!]; isolectotypes JE [JE00012328 image!], K [K000806399 image!], B [B100278360 image!, B100278359 image!]. [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ld1393506]. **(2)**
= *Verbascum blattaria* var. *crenatum* Rouy in Rouy & Foucaud, Fl. France 11: 10. 1909.

= *Verbascum rhinanthifolium* Davidov in Trav. Soc. Bulg. Sci. Nat. 8: 101. 1915.

= *Verbascum carduifolium* Murb. ex. Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30(2): 131. 1929. ≡ *Verbascum blattaria* var. *carduifolium* Murb., in Lunds Univ. Arsskrift, 2n.f., 29 (2): 567. 1933. Type: [Greece]. Malakasi; in vinetis, 17 June 1896, *P. Sintenis, 632.* (leolotype, designated here: B [B100278358 image!]; isolectotypes: WU [WU0126534 image!], LD [LD1364911 image!, LD1395023 image!, LD1392908 image!, LD1394623 image!]). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.b_10_0278358]. **(3)**

= *Verbascum blattaria* var. *gracilipes* Murb. in Lunds Univ. Arsskrift, 2n.f., 29 (2): 566. 1933. Type: [Greece]. Volo: Portaria, in vinetis, 02 September 1896, *P. Sintenis 1301* (Lectotype, designated here: B [B100278357 image!]; isolectotypes: JE [JE00012330 image!, JE00012331 image!]; WU [WU0126494 image!]). [Greece]. In valle Tempe: prope Papapuli 28–31 Jully 1913, *B. Tuntas, 1954* (Residual syntype: WU [WU0126493]!; In valle Tempe: prope Papapuli 28–31 July 1913, *B. Tuntas, 1955* (Residual syntype: WU [WU0126492 image!]). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.b_10_0278357]. **(4)**

= *Verbascum blattaria* var. *brachycalyx* Murb. in Lunds Univ. Arsskrift, 2n.f., 29 (2): 567. 1933. Type: [Greece]. Insula Zakynthos (Zante): in humidis montis Skopos; reg. infer, 4 May 1926, *J. F. N. Bornmüller 1177* (Lectotype, designated here: B [B100278364 image!]; isolectotypes: B [B100278363 image!]). [Greece]. Insula Kephalonia, in olivetis ad Argostoli, 23 May 1926, *J. F. N. Bornmüller 1174* (Residual syntype: JE [JE00012329 image!], S [S10-26942 image!, S12-12718 image!]). [Greece]. Insula Zakynthos (Zante), in herbidum montis Skopos, 04 May 1926, *J. F. N. Bornmüller 1177* (Residual syntype: S [S10-26943 image!]). [GREECE]. Insula Zakynthos (Zante); in olivetis 23 May 1926, *J. F. N. Bornmüller 1174* (Residual syntype: B [B100278367 image!]). [Greece]. Insula Zakynthos (Zante); in olivetis, 02 May 1926, *J. F. N. Bornmüller 1175* (Residual syntype: B [B100278366 image!]). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.b_10_0278364]. **(5)**

Type. (lectotype was designated by Huber-Morath 1971, pg. 143): LINN [Herb. Linn. No. 242.6.]).

Notes. Original material is kept in the Linnaean Herbarium at the Linnean Society of London; an image of the lectotype is available at http://linnean-online.org/1836/.

(2) No specimens were cited in the protologue (Halácsy 1892) of *Verbascum blattaria* L. var. *brevipedicellatum*. However, according to Murbeck (1933) the description of this taxon was based on material collected by Sintenis and Bornmüller from 1883 to1892 in Greece. We have located five sheets that have been lodged at the following four Herbs: LD (LD1393506), JE (JE00012328), K (K000806399), and B (B100278360, B100278359), the labels' data of which correspond to those reported by Murbeck (1933). Hence, these specimens are eligible and can be considered as original material. The sheet LD1393506 preserved at Herb. LD is here selected as the lectotype of the name *Verbascum blattaria* L. var. *brevipedicellatum*.

(3) The name of *Verbascum carduifolium* was first published by Murbeck (1925: 168), but without a description. Four years later, Hayek (1929) gave the description of *V. carduifolium* Murb. ex. Hayek and mentioned a locality "The." [as an abbreviation of Thessalía]. Four years later, the taxonomic status of this species has been assessed by Murbeck (1933: 567) and he regarded it as a variety under *Verbascum blattaria* L. In addition to the morphological description, Murbeck (1933) cited an element collected by P. Sintenis viz. "In monte pindo Malakasi, in pratis supra pagum. determ. Leg. P. Sintenis 17 /6/ 1896, n. 632" and he indicated the herbaria (B, WU, LD) that housed the specimens he surveyed. We located six sheets, all of them from the locality given in the protologue, belonging to the Sintenis collections: B (Barcode B100278358), WU (WU0126534) and LD (LD1364911, LD1395023, LD1392908, LD1394623) at Herb. The sheet B100278358 conserved at Herb. B is here designated as lectotype for the name *V. carduifolium.*

(4) In the protologue of *Verbascum blattaria* var. *gracilipes*, Murbeck (1933) cited 11 gatherings, but he does not provide the name of the herbarium where the original material has been deposited. Six sheets from three different Herbs (B, JE, WU) were traced only: B (Barcode B100278357), JE (JE00012330, JE00012331) and WU (WU0126492, WU0126493, WU0126494). All of these specimens are consistent with the location and diagnosis given in the protologue and can be considered as original material. Since no specimen-type has been designated, all of these specimens can be considered syntypes under Art. 9.6 of the ICN (Turland et al. 2018). The specimen B100278357 preserved at Herb. P is selected here as the lectotype for the name of this variety.

(5) In describing *Verbascum blattaria* var. *brachycalyx*, Murbeck (1933) referred to eight collections made in five different regions in Greece, but he did not designate a single type for the name. We traced eight specimens in Herbs. B (B100278364, B100278363, B100278367, B100278366), S (S10-26942, S10-26943, S12-12718) and JE (JE00012329) which can be considered original material. We here designate the specimen B100278364 preserved at Herb. B as the lectotype of the name *V. blattaria* var. *brachycalyx* since it is well preserved.

Verbascum boerhavii L. Sp. Pl. 1: 177. 1753, Syst. Nat. ed. 12, 2: 169. 1767, Mant. Pl.: 45. 1767.

= *Verbascum majale* DC., in Fl. Franç. 6: 415. 1815.
= *Verbascum bicolor* Badarò in Brugnat. Giorn. Fis. Dec. II. vii.: 365. 1824.
= *Lychnitis boerhavii* (L.) Fourr. in Ann. Soc. Linn. Lyon ser. 2 17: 125. 1869.
= *Celsia floccosa* Porta, in Nuovo Giorn. Bot. Ital. 19: 313. 1887, nom. illegit., non Benth.
= *Vrebascum portae* Willk. in Ill. Fl. Hispan. 2: 124. 1888.
= *Verbascum boerhavii* var. *knochei* Benedí, Orell & J.J.Orell in Butll. Inst. Catalana Hist. Nat. 57: 62. 1989.

= *Verbascum boerhavii* var. *longebracteatum* Willk., Suppl. Prodr. Fl. Hispan.: 170. 1893.

= *Verbascum majale* var. *bicolor* (Badarò) Rouy in Rouy & Foucaud, Fl. France 11: 9. 1909.

= *Verbascum majale* var. *lanceolatum* Rouy in Rouy & Foucaud, Fl. France 11: 9. 1909.

= *Verbascum boerhavii* var. *portae* (Willk.) Knoche, Fl. Balear. 2: 367. 1922.

= *Verbascum boerhavii* f. *bicolor* (Badarò) Murb., in Acta Univ. Lund. ser. 2 29(2): 159. 1933.

= *Verbascum hookerianum* var. *pseudocalycinum* Maire & Murb. in Bull. Sco. D'Hist. Nat. Afr. Du Nord 18: 84. 1927. Type: [Morocco]. Grand Atlas, Reraya: rocailles porphyriques au-dessous du Tizi-n-Tagherat, 2600–2800 m, 21 July 1922, *R. Maire s.n.* (lectotype, designated here: RAB [RAB030509!]!). [Morocco]. Grand Atlas, Reraya: rocailles porphyriques au-dessous du Tizi-n-Tagherat, 2500–2800 m, 23 July 1922, *R. Maire s.n.* (Residual syntype: MPU [MPU010269!; MPU010270!]). [Morocco]. Grand Atlas, Reraya: rocailles porphyriques au-dessous du Tizi-n-Tagherat, 3000 m, 23 July 1922, *R. Maire s.n.* (Residual syntype: MPU [MPU010268!]). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.rab030509] **(2)**

= *Verbascum boerhavii* subsp. *portae* (Willk.) Malag., Sin. Fl. Ibér. 92: 1465. 1978.

Type. (lectotype designated by Ferrer-Gallego 2014, pg. 253. 2014): LINN [Herb. Linn. No. 242.2]!). **(1)**

Notes. Original material is kept in the Linnaean Herbarium at the Linnean Society of London; an image of the lectotype is available at http://linneanonline.org/1832/.

(2) Maire and Murbeck (in Murbeck 1927) described *V. hookerianum* var. *pseudocalycinum* on the basis of specimens collected from Reraya region in the Great Atlas, Morocco. However, the protologue does not give the name of the herbarium where the original material was deposited. The search for type material brought us to four specimens housed at Herb. RAB (RAB030509) and at Herb. MPU (MPU010269; MPU010270, MPU010268). The sheet RAB030509 stored at herb RAB is here selected as the lectotype for the name *V. hookerianum* var. *pseudocalycinum*.

Verbascum calycinum Ball, in J. Bot. 13: 172. 1875.

Type. [Morocco]. High Atlas: rocks of the Ait Mesan valley 1300–1400 m, 13–16 May 1871, *J. Ball, s.n.* (Lectotype, designated here: K [K000410936]!; isolectotype: K [K000410937]!, P [P03420188]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000410936]

Notes. In the protologue of *Verbascum calycinum*, Ball (1875) cited one gathering and he mentioned the collection locality reading "Legimus in regione inferiori Atlantis Majoris, convalle Ait Mesanet prope Sketana". However, he did not quote any herbarium that houses the original material or accession numbers specified, nor the date of collection. According to Stafleu and Cowan (1976–1988), the main collections of Ball are preserved at Herbs E and K, and also some at Herbs OXF and GL. During searches of Ball's collections from Morocco, three specimens were traced. One of them is kept at Herb. P (P03420188) and another is stored at Herb. K (K000410937) and is mounted on the same sheet with K000410936. Both specimens K000410937 and P03420188 bear a label reading: "Iter Maroccanum. 1871 / *Verbascum calycinum*, Ball / *Ex regione* inferiori Atlantis Majoris, prope Sketana, alt. 1300–1400 met / Majo 18–19 / *J. A. ball* /". However, the specimen K000410936 bears a label reading "Ex rupibus arenaceis Atlantis Majoris in convalle Ait Mesan, alt. 1400–2000 met / Majo 13–16 / *J. A. ball* /". All of those sheets were collected by Ball in the High Atlas, Morocco. As the collection locality of both specimens K000410937 and P03420188 agree closely with the protologue, they can be safely considered as original material under Art. 9.4. of the ICN (Turland et al. 2018). In accordance with Art. 9.3 of ICN (Turland et al. 2018), the sheet K000410937 preserved at Herb. K is selected here as the lectotype, because it shows the best quality of preservation of the important diagnostic features.

Verbascum creticum **(L.) Cav., in Elench. Pl. Horti Matr. 39. 1803.**

≡ *Celsia cretica* L., in Syst. Veg. ed. 13: 470. 1774. Type: [Italy]. Ponae Ital. [Lectotype, designated here: Herb. Linn. No. 774.3 (LINN)! (image available at: http://linnean-online.org/7174/); isolectotype: Linn. No. 774.4 (LINN)! (image available at http://linnean-online.org/7175/)]. **(1)**
= *Verbascum lyratum* Lam., Encyclop. 4: 223. 1797, nom. illegit., non *V. lyratum* Pourret, Mém. Acad. Toulouse, ser. 1, 3: 332. 1788 (=*V. chaixii* Vill).
= *Ditoxia lyrata* Raf., in Précis Découv. Somiol.: 40. 1814, nom. illegit.
= *Celsia lyrata* (Lam.) G.Don, in Gen. Syst. 4: 499. 1837, nom. illegit.
= *Thapsandra cretica* (L.) Griseb., in Spic. Fl. Rumel. 2: 40. 1844.
= *Celsia cavanillesii* Kunze in Flora 29: 698. 1846.
= *Verbascum creticum* (L.) Kuntze, in Revis. Gen. Pl.: 468. 1891, comb. nov. superfl.
= *Celsia balearica* Gand. in Fl. Eur. 16: 112. 1889, nom. inval.
= *Celsia cretica* subsp. *balearica* Gand. ex Gand., in Nov. Consp. Fl. Eur.:345. 1910.
= *Lasiake lyratum* (Lam.) Raf., Fl. Tellur. 4: 89. 1838. nom. illegit.
= *Celsia verbascifolia* R.Hern. ex J.J.Rodr., Fl. Menorca: 94. 1901, nom. nud.
= *Celsia cretica* f. *pallenscens* Maire, in Bull. Soc. Hist. Nat. Afrique N. 22: 308. 1931. Type: [Algeria]. Bône, pentes de l'Edough, grès, 600 m., 30 April 1930, *R. Maire s.n* (lectotype, designated here: MPU [MPU002670]!; isolectotype: MPU [MPU002671]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu002670] **(2)**

Notes. (1) Linnaeus (1774: 470) described *Celsia cretica* in *Species Plantarum* as new nomen specificum legitimum. The diagnosis consists of "*Cretica, C. fol. Inferioribus lyratis, superiofibus ovati samplexi caulibus*" followed by a synonym, "*Blattaria perennis cretica incana,* *foliis binis conjugatis*" that was cited from Morison (1680: 488). The protologue also includes a morphological description "*Folia pinnato-lyrata alterna: Superiora simpilicis; cordato-amplexicolia. Calyces serrati. Filamenta 4: duobus superioribus pilofis; infeririobus, laevibus antheris que majoribis. Corolla flavae fundo superiore maculis 2. ferrugineis*". However, the collection locality is not indicated. Seven years later, in his *Supplementum Plantarum Systematis Vegetabilium*, Linnaeus [son] (1781: 281) gave a detailed morphological description of *Celsia cretica*, along with the statement "*Habitat in India, Creta*" followed by the symbol "♂" indicating the gender of the particular organs or individuals within a composite plate, according to Simpson (2010). Moreover, another polynomial "*Verbascum foliis radicalibus ovatis petiolatis, caulinis oblongis sessilimus serratis, subtus tomentosis*" from Miller (1758: 182, ic. t. 273) were cited in synonymy.

Among the original material of the genus *Celsia*, preserved in Linnaean herbaria, three sheets relevant to *Celsia cretica* were found: the first (Herb. Linn. No. 774.3, image available at: http://linnean-online.org/7174/) is annotated at the bottom "*celsia cretica*" and "774.3" at above the right hand of the sheet by Linnaeus. The second specimen (Herb. Linn. No. 774.4, image available at: http://linnean-online.org/7175/) is annotated "*cretica*" at the base and "774.4" at above the right corner of the sheet. Both specimens are clearly showing the characters mentioned in the Linnaeus [son] (1781) diagnosis. After careful examination of the available collections and consideration of all elements in the protologue, the sheet No. 774.3 is the most complete and well conserved, and it is designated here as the lectotype of the name *Verbascum creticum*. However, the sheet No. 774.4 is selected here as the isolectotype.

(2) In the protologue of *Celsia cretica* f. *pallenscens*, Maire (1931) provided the following locality "Bòne, pentes du Mont Edough, 300–700 m" but they did not specify the name of the herbarium where the type material has been stored. We traced three sheets (MPU002670, MPU002671), preserved at Her. MPU which is in complete accord with the protologue. The specimen MPU002670 is here chosen as the lectotype for the name *Celsia cretica* f. *pallenscens.*

Verbascum demnatensis (Maire & Murb.) Rankou, in Phytotaxa 78(1): 68. 2013.

≡ *Celsia sinuata var. demnatensis* Maire & Murb., in Murbeck, Contr. Fl. Maroc: 40. 1923. Type: [Morocco]: Rocailles calcaires au N. d'El-Arba près Demnat 3 Avril 1921, *R. Maire, s.n.* (Lectotype, designated here: MPU [MPU004004]!; isolectotype P [P00083083]!). [(image available at https://herbier.umontpellier.fr/zoomify/zoomify.php?fichier=MPU004004]

= *Celsia lyrata var. demnatensis* (Maire & Murb.) Murb., in Lund. Univ. Arssk., n. f. 2, 22(1): 199. 1925.

= *Celsia demnatensis* (Maire & Murb.) Maire in Bull. Soc. Hist. Nat. Afrique N. 29: 438. 1938.

= *Verbascum pseudocreticum* subsp. *demnatense* (Maire & Murb.) Ibn Tattou, in Index Syn. Fl. Afrique N. 5: 304. 2013.

Notes. This taxon was firstly published by Maire and Murberk (1923) as *Celsia sinuata* Cav. var. *demnatensis* Maire & Murb., and they referred to a plant collected by R. Maire in 1921 near Demnat, Morocco (Maire, 1938). In the protologue, the locality, collector, and collection date were indicated as follows: "Rocailles calcaires au N. d'El-Arba, près Demnat, Dr R. Maire, 3 avril 1921". As mentioned above, the main Réne Maire herbarium of plants from North Africa is now in Herb. MPU (Stafleu and Cowan 1976–1988). During our research, only two herbarium sheets kept at Herbs MPU (MPU004004) and P (P00083083) were traced, which were all collected by Maire. The sheet MPU004004 contains a plant fragment, with leaves, mature fruits, and some young flowers at the upper part of the inflorescence, and two original labels handwritten by Maire; the first one reads "Université d'Alger / Herbier de l'Afrique du Nord / *Celsia sinuata* Cavon. var. / M. Rocailles calcaires au N. d'El-Arba, près Demnat / 3-4-1921/ Dr R. Maire" and the second label states "*Celsia sinuata* Cavon. var. *a typo differt statura minore calyce ± glandulosa, radice perenni*". This sheet goes with a "letter" from Maire to Murbeck saying that he considered this new sample to be a new variety of *Celsia sinuata* Cav., and gave a diagnosis. The sheet P00083083 bears a fragment of root with basal leaves and a complete plant with flowers and an original label handwritten by Maire noting the same locality, collection date, and collector as those of the sheet at Herb. MPU. Anyway, these sheets agree with the protologue and are original material; in consequence the sheet MPU004004 preserved at Herb. MPU is selected here as lectotype.

Verbascum dentifolium Delile, in Sem. Hort. Bot. Monsp.: 28 1836, Ann. Sci. Nat., Bot., sér. 2, 7: 287 (1837)

= *Verbascum granatense* Boiss., in Voy. Bot. Espagne 2: 441. 1841. Type: [Spain]. Alhambra [*P. E. Boissier*] *s.n.* (lectotype, designated by Burdet et al. 1990, pg. 623: G [G00002293]!).

= *Verbascum cossonianum* Ball, in J. Linn. Soc., Bot. 16: 583. 1878. Locality citation in the Protologue of Type: [Morocco]. Mar. merid. In provincia Mtouga prope castellum gubernatoris, 29 May 1871, *Ball, J.* s.n. Type: Non vidi.

= *V. nevadense* sensu Batt., Fl. Algérie, Suppl. Phan.: 69. 1910. non Boiss.

Type. [France]. Hortus monspeliensis, Julio 1826, N:10 [*A. R. Delile*] *s.n.* (Lectotype designated here: MPU [MPU020145, MPU020144]!). [France]. Hortus Monspeliensis, July 1831, [*A. R. Delile*] *s.n.* (residual syntype: MPU [MPU020143]!). [images of lectotype available at (image available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu020144 and at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu020145]

Notes. *Verbascum dentifolium* was described by Delile (1836: 28; 1837: 287) based on material growing in the Montpellier botanical garden from collections made in Port-Juvenal at Montpellier. Port-Juvenal was a place where lots of wool bales were coming to France from the Middle East, introducing many species from seeds trapped in the wool. In his monograph of the genus *Verbascum*, Murbeck (1933) discussed in some detail the distribution and synonyms of a species to which this name has generally been applied, but he did not designate a lectotype for the name *V. dentifolium*. According to Murbeck (1933) the original material is kept at herbarium of Montpellier (MPU), in France. Research in Herb. MPU enabled us to locate two specimens bearing Delile's handwritten labels and agreeing closely with the protologue's description. The first one is mounted on two sheets. These two preparations, bearing the Herb. MPU barcodes MPU020144 and MPU020145, have a label reading "*Verbascum*, h. m. Julio 1826, N:10" that is accompanied by two other labels in which Delile gave a description of the species. According to Art. 8.3 of the ICN (Turland et al. 2018), the sheets (MPU020144 and MPU020145) must be considered as a single specimen. The second specimen (MPU020146) bears a label reading "*Verbascum dentifolium*, h. m. Julio 1831". Since the type is not specified, the two specimens are to be considered as syntypes according to Art. 9.6 of the ICN (Turland et al. 2018). The sheet corresponding to Herb. MPU barcodes MPU020144 and MPU020145 and with the collection date "Julio 1826" is selected here as the lectotype for the name *Verbascum dentifolium*.

***Verbascum erosum* Cav., Elench. Pl. Hort. Matrit.: 38. 1803.**

= *Celsia sinuata* Cav., in Anal. Cienc. Nat. 3: 68. 1801.
= *Celsia laciniata* Poir., Lam., in Encycl., Suppl. 2: 147. 1811.
= *Celsia barnadesii* (Vahl) G.Don fil. var. *baetica* Willk., in Ill. Fl. Hispan. 2(14): 55. 1888.
= *Celsia jeriaensis* Pérez Lara, in Willk. Ill. FI. Hispan. 2(14): 56. 1888, nom. nud.
= *Verbascum laciniatum* (Poir.) Kuntze, in Rev. Gen. 469. 1891.
= *Celsia baetica* (Willk.) Murb., in Lunds Univ. Arsskrift, n. s. 17 (9): 3. 1921.
= *Celsia baetica* (Willk.) Font Quer, in Butll. Inst. Catalana Hist. Nat . 26: 56. 1926. comb. nov. superfl.
= *Celsia lyrata* var. *sinuata* (Cav.) Maire, in Jahand. & Maire, Cat. Pl. Maroc: 668. 1934.

Type. [Morocco]: Tánger vicinii, [Without date], *Broussonet, s.n.* (lectotype, designated by Benedí and Montserrat 1985, pg.104): MA [MA108913]).

Notes. This species was originally described as *Celsia sinuata* by Cavanilles (1801: 68) based on material collected by Broussonet in Tangier, Morocco (Benedí and Montserrat 1998). When the genus *Celsia* was subsumed in the genus *Verbascum* the epithet *sinuata* could not be used for this species as it already exists in the combination *Verbascum sinuatum* L. for another species. We concur with the conclusion of Benedí and Montserrat (1985) that the correct name for this plant in question is *V. erosum* Cav.

Verbascum faurei (Murb.) Hub.-Mor., in Bauhinia 5: 12. 1973.

≡ *Celsia faurei* Murb., in Lunds Univ. Arsskrift, 2 n.f., 17(9): 7. 1921. Type: [Algeria]. Oued-Imbert (dépt d'Oran). Lieux rocailleux, 4 Juin 1911, *A. Faure, 304* [Superseded lectotype, selected by Benedí and Montserrat 1997, pg. 168 (Art. 9.19 of the ICN; Turland et al. 2018); lectotype, designated here: LD [LD1244709]!]. [Algeria]. Algérie. Oued-Imbert: Talus de la voie ferrée vers les Lauriers-Roses, 29 Mai 1921, *A. Faure, s.n.* (residual syntype: LD [LD1223485, LD1223785, LD1223665, LD1220485]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ld1244709]

Notes. Murbeck (1921) described *Celsia faurei* based on collections done by A. Faure in western Algeria. The author in the protologue includes an explicit reference to the locality (Algeria, Oran: Between Imbert River and the railway embankment), with several years for the collection (1911, 1916, 1918, and 1921) and the herbarium where the original material are kept (LD). Benedí and Montserrat (1997) designated the A. Faure material at Herb. MPU as lectotype and that preserved at Herb. LD as isolectotype. However, the material kept at Herb. MPU cannot be considered as original material since the herbarium that housed the type specimens is indicated in the protologue. The lectotype designation by Benedí and Montserrat (1997) is obviously flawed and cannot be considered here because it is in conflict with the protologue according to Art. 9.19 of the ICN (Turland et al. 2018). Pertaining to the original material specification provided in the protologue, five specimens at Herb. LD were traced (LD1223785, LD1220485, LD1223485, LD1223665, and LD1244709) on which are stamped "Type". In the absence of indicating a single specimen as the holotype, all of the specimens cited in the protologue are to be treated as syntypes (Art. 9.6 of ICN, Turland et al. 2018). The sheet LD1244709 is chosen here as the lectotype, because it shows the best quality of preservation of the important diagnostic features of the taxon. However, the other remaining specimens (LD1223485, LD1223785, LD1223665, LD1220485) traced are referred to as original material following the Art. 9.4 of ICN (Turland et al. 2018).

Verbascum faurei subsp. *acanthifolium* (Pau) Benedí & J.M.Monts., Lagascalia 20: 169. 1997.

≡ *Celsia acanthifolia* Pau in Font Quer. Iter Maroc. n° 566. 1927. Type: [Morocco]. pr. Badú (Atlante rhiphaeo); Hab. in saxosis, solo schistose, 6 July 1927, *P. Font Quer, 566* (lectotype, selected by Benedí and Montserrat 1997, pg. 169, first step "type", as "*Font Quer 566-1927*"; second step, designated here: BC [BC43694]!; isolectotypes: LD [LD1222710]!, GDA [GDA39155]!, G [G00015117]!, MPU [MPU009627, MPU009628]!, BCN [BCN18029]!, BM [BM000930561]!). [image available at http://psimg.jstor.org/fsi/img/pdf/i0/10.5555/al.ap.specimen.bc43694_normal.pdf]

≡ *Celsia acanthifolia* Pau, in Cavanillesia 1: 47. 1928, nom. nud.

≡ *Celsia faurei var. acanthifolia* (Pau) Maire in Jahand. & Maire. Cat. PI. Maroc.3: 669 (1934).

Notes. Font Quer (1927) based his species on a collection of plants from the Rif region that he has gathered during his 1927 campaign in Morocco. Font Quer gave the following diagnosis "Folia Acanthi mollis L., superiora oblonga, sinuato-dentata, floribus longe pedunculatis, pedicellis glanduliferis, racemosis; bractae lanceolatae brevissimae, calycis laciniae lanceolatae, margine integro, capsula globosa, obtusa calyce triplo longior" with the collection locality "hab. in saxosis, pr. Badù (Atlante rhiphaeo), 1500 m. alt., solo schistoso, 6 julii". This protologue has been validly published by Gonzâlez-Bueno (1988). According to Nualart (2017), Benedí and Montserrat (1997) wrongly cited the collection number of the lectotype as "BC436934" instead of "BC43694". So, in addition to the specimen kept at Herb. BC (BC43694), seven other specimens are in agreement with the description in the protologue. They are housed at Herbs LD (LD1222710), GDA (GDA39155), G (G00015117), MPU (MPU009627, MPU009628), BCN (BCN18029), and BM (BM000930561). According to Art. 9.6 of the ICN (Turland et al. 2018), all of these specimens and those persevered at Herb. BC must be treated as syntypes. The designation by Benedí and Montserrat (1997) can be considered here as a first-step typification (see Art. 9.17 of the ICN, Turland et al. 2018). As the herbarium specimen BC43694 [mounted on three sheets]) kept at Herb. BC is the one showing the best quality of preservation of morphological features described in the protologue, we select it here as second-step lectotype of the name.

The taxonomic status of *Celsia acanthifolia* has been assessed by some authors. Maire (in Jahandiez and Maire 1934) regarded it as a variety under *Ceslia faurei* Murb. [*C. faurei var. acanthifolia* (Pau) Maire]. Later, Benedi and Montserrat (1997) raised it to the rank of subspecies and they published it as a new combination, *Verbascum faurei* (Murb.) Hub.-Morath subsp. *acanthifolium* (Pau) Benedí & J.M.Monts.

Verbascum fontanesii **Benedí, in Anales Jard. Bot. Madrid 60(2): 459. 2003.**

= *Celsia betonicifolia* Desf., in Flora Atlantica 2: 58. 1798. Type: [Algeria]. In arvis in cultis Algeriae, [without date], *R. L. Desfontaines, s.n.* (Lectotype, designated by Benedí 2003, pg. 459: P [P-DESF]!; isolectotype G [00439692]!).

= *Verbascum betonicifolium* (Desf.) Kunze, Revis. Gen. Pl.: 469. 1891, nom. illegit. non *V. betonicifolium* Desf. in Ann. Mus. Natl. Hist. Nat. 11: 54. 1808.

= *Ditoxia betonicifolia* (Desf.) Raf., Prec. Découv. Somiol.: 40. 1814.

Notes. Benedí (2003) indicated as a lectotype the Desfontaines collection kept at Herb. P [P-DESF] but he omitted to mention another sheet of this collection kept at Herb. G (image available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00439692). According to Lasègue (1845) and Stafleu and Cowan (1976–1988), around

600 Flora Atlantica plants was given by Desfontaines to Lemonnier and was acquired by Delessert with the Lemonnier herbarium at Herb. G. In Herb. G we have traced one sheet, with barcode G00439692, that is stamped (Typus). This sample matches the collection locality in the protologue and it is the one that morphologically agrees best with the original description. This specimen bears two labels. The first has "*Celsia betonicifolia* Desf., Fl. Atl. [Desfontaines' handwriting]"; the second is a printed label including, name, locality, reference, and a short historical French comment, and is annotated "R-L Desfontaines, Herbier de Barbarie / *Celsia betonicifolia* Desf. Loc: in arvis ìnculus Algeriae / Desf. Fl. Atl. II, P; 58, Tab. / Série de 600 n^{os} donnée par Desfontaines à L.-G. Lemnier; acquise en 1803 par B. Delessert: revue en 1928 et 1829 par Desfontaines pour servir à illustrer les types décrits dans Flora Atlantica, incorporé en 1916 dans la collection générale de l'Herbier Delessert.- Voyage Lasègue musée botanique de M. Benjamin Delessert. p 60".

Verbascum gaetulum (Maire) Murb., in Bull. Soc. Hist. Nat. Afrique N. 18: 82. 1927.

≡ *Verbascum thapsus* subsp. *gaetulum* Maire, in Bull. Soc. Hist. Nat. Afrique N. 9: 182. 1918. Type: Morocco]: Djebel Araïra, lits des oueds, 1400 m, 29 Mai 1918, *R. Maire, s.n.* (Lectotype, designated here: MPU [MPU000364]!; isolectotype: MPU[MPU000365]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu000364]

≡ *Verbascum simplex* var. *gaetulum* (Maire) Maire, in Cat. Pl. Maroc 3: 665. 1934.

Notes. Maire (1918) published the name *Verbascum thapsus* subsp. *gaetulum* based on a collection made by himself at the foothills of Araïra Mountain, Morocco. He also observed that this plant was very common in this locality. In the protologue, the author indicated that this plant has an intermediate morphology between *V. thapsus* L. and *V. simplex* Hoffmanns. and Link, but differed from both by its spatulate stigma and its tetrandrous or sub-tetrandrous flowers. Murbeck (1927) raised *V. thapsus* subsp. *gaetulum* to species rank. However, a few years later, Maire (in Jahandiez and Maire 1934) classified this taxon with the rank of variety in *V. simplex*, but without any justification for this new recombination. According to African Plant Database (APD) (2022), the accepted name should be *V. gaetulum* (Maire) Murb. despite Ibn Tattou (2007) also considering *V. thapsus* subsp. *gaetulum* an accepted taxon.

During our research, we have found two sheets (MPU000364, MPU000365) corresponding to the original material of this taxon preserved at Herb. MPU, where the main collection of Maire is kept. According to Stafleu and Cowan (1976–1988), if the original material of Dr. R. Maire are preserved at Herb. MPU, there are important sets of duplicates at Herbs Al, CAIM, P, and RAB. Since no holotype was specified, the cited specimens are all syntypes under the Art. 9.6 of the ICN (Turland et al. 2018). Therefore, the specimen MPU000364 is selected here as the lectotype, because it is the best original material, more complete and informative than the specimen MPU000365, even if this latter is accompanied by a handwritten detailed morphological description by Maire.

Verbascum hookerianum Ball, in J. Linn. Soc. Bot. 16: 584. 1878.

= *Verbascum tagadirtense* Murb., in Murbeck, Contr. Fl. Maroc 2(19): 39. 1923. ≡ *Verbascum hookerianum* var. *tagadirtense* (Murb.) Murb., in Bull. Soc. Hist. Nat. Afrique N. 18: 83. 1927. Type: [Morocco]. Région du Grand Atlas: Tagadirt N'Bourd, c. 1000 m, 09 May 1921, *Sv. Murbeck s.n.* (lectotype, designated here: LD [LD1216036]!; isolectotypes LD [LD1215976]!). **(2)**

= *Verbascum hookerianum* var. *ballii* Murb., in Bull. Soc. Hist. Nat. Afrique N. 18: 83. 1927, nom. nov. superfl.

Type. [Morocco]. South Morocco Greater Atlas, May 1871, *Hooker s. n.* (lectotype, designated here: K [K000410848]!). [image of the lectotype available at http://specimens.kew.org/herbarium/K000410848] **(1)**.

Notes. *Verbascum hookerianum*, was established by Ball (1878) based on a sample collected by Hooker in the district of Ourika at the foothills of the High Atlas Mountains in Morocco. Ball (1878) in his protologue did not use the term type or mention the herbarium that houses the type specimens. However, in his monograph of genus *Verbascum*, Murbeck (1933) indicated that the original material was kept at Herb. K. During our extensive research, we have traced only one sheet (K000410848) that is totally in agreement with the protologue. This sheet bears a label reading "*Verbascum hookerianum* Nob., South Morocco Greater Atlas, Coll. Dr. Hooker, May 1871" and includes a part of the inflorescence with basal leaf. Since the Herb. K has a single specimen of the Hooker collection, one may argue that the relevant specimen is the holotype. Nevertheless, Ball did not use the term type or mention the name of the herbarium housing the type. Therefore, we here designate the sheet K000410848 as lectotype of the name.

(2) The protologue of *V. tagadirtense* comprises a complete description in Latin, followed by the provenance "Région du Grand Atlas-. Pentes broussailleuses à Tagadirt N'Bourd, c. 900 m", but no indication about the name of the herbarium where the type is preserved (Murbeck 1923). Ten years later, Murbeck (1933), in his monograph of the genus *Verbascum*, indicated that the original material can be found at Herb. LD. During the course of the pursuit, two sheets were traced at Herb. LD which were in accordance with the protologue. The specimen LD1216036 is here selected as a lectotype of *V. tagadirtense*.

Verbascum letourneuxii Asch. ex Asch. & Schweinf., Ill. Fl. Egypt 2: 189 & 114. 1887.

= *Verbascum spinosum* Delile, Fl. AEg. Illustr.: 55. 1813; non L. Cent. II. plant.: 10. 1756. & Amoen. Acad. IV: 307. 1759.

= *Verbascum marniaricum* Letournex ap. Barbey Herboris, au Levant: 148. 1882, nom. nud.

= *Verbascum tourneuxii* Aschers., ap. Barbey 1. C: 182, nom. nud.. Aschers., ap. Aschers. & Schweinf. Illustr. l'I. d. Egypt. in Mém. Instit. Egypt., II: 114. 1887.

Type. [Egypt]. In apricis calcareo-argillosis prope Oum Rakoumi et Matrouka in Marmorica ad limites Cyrenaicae, April 1879, *A. Letourneux, s.n.* (lectotype, designated here: G [G00015113]!; isolectotype: W [W1889-0043225]!, G [G00015111, G00015112, G00015114]!, S [S10-27120]!, K [K000975868]!, P [P03417358, P03417357, P03417360, P03417361]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00015113].

Notes. Ascherson (in Ascherson and Schweinfurth 1887) described *Verbascum letourneuxii* on the basis of specimens separately collected by Ehrenberg and A. Letourneux from the Alexandria region in the north of Egypt. Within the protologue Ascherson and Schweinfurth (1887) confess that the specimen brought by Ehrenberg only constitutes a skeleton of a plant in fruit, while specimens collected by Letourneux, from a few kilometers from the collection locality of Ehrenberg, are well-developed specimens. However, the authors did not indicate the name of the herbarium housing the type specimen. According to Stafleu and Cowan (1976–1988), the original material of Ehrenberg, Letourneux, Ascherson and Schweinfurth were kept at Herbs B, C, G, K, L, LE, P, S, and W. Nevertheless, the Berlin (B) herbarium was bombed during World War II on the night of 1–2 March 1943 (Hiepko 1987); hence, a good part of the authors' collection has been lost (Stafleu and Cowan 1976–1988).

Based on the type specification given in the protologue (locality, collector, and collection date), eleven sheets were traced in different herbaria belonging to the Letourneux collections: W (W1889-0043225), G (G00015111, G00015112, G00015113, G00015114), S (S10-27120), K (K000975868), and P (P03417358, P03417357, P03417360, P03417361). Since the type has not been specified, all of the specimens are to be recognized as syntypes according to Art. 9.6 of the ICN (Turland et al. 2018). The sheet G00015113 preserved at Herb. G is here designated as lectotype for the name *V. letourneuxii*, since it is the specimen that shows the best quality of preservation of the important diagnostic features.

***Verbascum longirostre* (Murb.) Hub.-Mor. in Bauhinia 5(1): 13. 1973.**

≡ *Celsia longirostris* Murb., in Lunds Univ. Arsskrift, 2 n.f, 22(1): 190. 1925. Type: [Morocco]. Oudjan, Sud-Ouest du Maroc. 1875, *A. S. Mardochée, s.n.* (lectotype, designated here: P [P03425558]!, isolectotype: P [P03425557]!, K [K000410860, K000410861]!). [Morocco]. Chtouka, Sud-ouest du Maroc, 1875, *A. S. Mardochée, s.n.* (residual syntype: P [P03425553, P03425563]!). [Morocco]. Ida ouchemlal, Sud-ouest du Maroc, 1875, *A. S. Mardochée, s.n.* (residual syntype: P [P03425555, P03425559]!). [Morocco]. Districts de Tazeroualt et Issghivar jusqu'au Si Ahmed ou Moussa 1876, *A. S. Mardochée, s.n* (residual syntype: P [P03425560]!). [Morocco]. Tamelat, Sud-ouest du Maroc, 1875, *A. S. Mardochée,* *s.n* (residual syntype: P [P03425565]!). [image of lectotype available at https://science.mnhn.fr/institution/mnhn/collection/p/item/p0342555)] **(1)**

= *Celsia maroccana Coss.* (in sched) non Ball.

Notes. Murbeck (1925) described this species based on a collection made by A.S. Mardochée, a Moroccan plant specimen collector on account of French botanist Ernest Cosson. In the protologue, Murbeck (1925) cited several collections from south-west of Morocco as original material that are stored at Cosson's herbarium. The date and collection localities indicated in the protologue are: «Sud-Ouest du Maroc: Chtouka, Ida ouchemlal, Oudjan, Tamelat, 1875, Mardochée; Districts de Tazeroualt et Issghivar jusqu'au Si Ahmed ou Moussa, 1876, Mardochée; Ida Oubouzia, Takoust et Aït zelten, pays montagneux 1876, Mardochée». According to Stafleu and Cowan (1976–1988), the main collections of Cosson are preserved at Herb. P. During our searches we have traced ten specimens collected by Mardochée housed at Herb. P (P03425553, P03425555, P03425557, P03425558, P03425559, P03425560, P03425563, P03425565) and two at Herb. K (K000410860, K000410861). Detailed examination of all of them revealed that the plants and the information on the labels of the samples match well with the protologue description. Since no holotype is indicated in the protologue the ten specimens traced are all syntypes according to Art. 9.6 of the ICN (Turland et al. 2018). Therefore, we select here as the lectotype the sheet P03425558 because it is more complete and agrees best with the original description. This specimen bears two handwritten labels, one by Cosson: "*Celsia maroccana Coss. sp. nov.! Oudjan, Sud-Ouest du Maroc. Mardochée 1875*" and the other bears a 1924 annotation by Murbeck who correctly identified it as *C. longirostris* Murb.

Moreover, as mentioned by Murbeck (1925), Cosson (in sched.) have described this plant in question as a new species beneath the name "*Ceslia maroccana*" accompanied by a handwritten diagnosis written by him on 24 August 1876. However, rendering to Murbeck (1925), Cosson has misinterpreted the plant in question as a new species because at the time mentioned he did not seem to have known that a related species was published a year earlier by Ball (1875: 172) under the name of *Celsia maroccana*.

***Verbascum longirostre* var. *antiatlantica* (Emb.) Khamar, comb. nov.**

urn:lsid:ipni.org:names:77318320-1

≡ *Celsia longirostris* var. *antiatlantica* Emb., in Bull. Soc. Sci. Nat. Maroc 15: 185. 1936. Type: [Morocco]: Anti-Atlas occidental: Falaises gréseuses du Kest, 1400–1500m, 2 May 1936, *L. Emberger, s.n.* (lectotype, designated here: RAB [RAB030634]!; isolectotype: RAB [RAB030632, RAB030633!, RAB030635]!, MPU [MPU006100, MPU006101]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.rab030634]

Notes. Emberger (1936) cited a locality in the protologue of *Celsia longirostris* var. *antiatlantica*: "A A:in praeruptis siliceis montis Kest supra Imdrighis, 15oo m ubi maio floret", but he did not indicate in which herbarium the specimen(s) were deposited. We have traced six specimens which agree with the protologue and from which to select the lectotype: Four preserved at herb. RAB (RAB030634, RAB030632, RAB030633, RAB030635) and two from Herb; MPU (MPU006100, MPU006101). The sheet RAB030634 kept at Herb. RAB is chosen here as the lectotype of this variety.

***Verbascum longirostre* var. *atlantica* (Maire) Khamar, comb. nov.**

urn:lsid:ipni.org:names:77318321-1

≡ *Celsia longirostris* var. *atlantica* Maire, in Maire, Contrib. Étude Fl. Afrique Nord 31: 29. 1940. Type: [Morocco]. in faucibus amnis Dades Atlantis Majoris, solo lapidoso calcareo. 1500m, 21 June 1939, *R. Maire & M. Weiller, 355* (lectotype, designated here: MPU [MPU008974]!; isolectotype: RAB [RAB030628]!). [Morocco]. Grand Atlas: gorges de Tisgi au-dessus des sources du Todra, 11 Juin 1939, *G. Malençon s.n* (Residual syntype: MPU [MPU059325]!) [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu008974]

Notes. *Celsia longirostris* var. *atlantica* was described Maire (1940) based on collections made by Malençon from Tisgi gorges above the sources of Todra and by Maire and Weiller from Dades gorges between 1500–1600 m alt., both of which are situated in the Great Atlas Mountain. Since no holotype was designated in the protologue, these collections should be treated as syntypes in accordance with Art. 9.6 of the ICN (Turland et al. 2018). Three specimens of both collections were traced at Herbs. RAB and MPU. Maire and Weiller' collection, no. 355 consists of two sheets (RAB030628 and MPU008974), while Malençon' collection comprises one sheet housed at Herb. MPU (MPU059325). Of these, the specimen MPU008974 housed at Herb. MPU is here selected as the lectotype for the name *Celsia longirostris* var. *atlantica* due to its high degree of preservation and as it agrees well with the protologue.

***Verbascum longirostre* var. *hoggarica* (Maire) Khamar, comb. nov.**

urn:lsid:ipni.org:names:77318322-1

≡ *Celsia longirostris* var. *hoggarica* Maire, in Maire, Contrib. Étude Fl. Afrique Nord 31: 29. 1940. Type [Algeria]. In ditione Ahaggar: Tin-Ouzel, granit et roches volcaniques, 2070 m, 31 Mars 1928, *R. Maire, 880* (lectotype, designated here: MPU [MPU004308]!). [Algeria]. In montibus Tefedest, in alveo lapidoso granitico amnis Araghan, 1100 m, 10 Avril 1928, *R. Maire 881* (residual syntype: MPU [MPU004307]!). [Algeria]. Hoggar: Oued Tamanghasset, 28 Février 1933, *J. Lauriol, 363* (residual syntype: MPU [MPU004306]!). [Algeria]. Hoggar: ravins de l'Adrar Haggerane, 03 Mars

1933, *J. Lauriol, s.n.* (residual syntype: MPU [MPU059321]!). [Algeria]. In ditione Ahaggar: Tezzeït, in rupestribus basalticis, 1700–1800 m, 4 Avril 1928, *R. Maire 879* (residual syntype: MPU [MPU004304, MPU004305]!). In ditione [Algeria]. In ditione Ahaggar: in rupestribus graniticis secus amnem Tihaliouin, 2150 m, 22 Martii 1928, *R. Maire 876* (residual syntype: MPU [MPU059319]). [Algeria]. In ditione Ahaggar: Imerera in rupestribus basalticis, 1950–2000 m, 23 Martii 1928, R. *Maire 874* (residual syntype: MPU [MPU059318]!). [Algeria]. In montibus Atokor-n-Ahaggar: in rupestribus graniticis secus amnem Haman, 2000–2001 m, 14 Martii 1928, *R. Maire 875* (residual syntype: MPU [MPU059322]!). [Algeria]. In montibus Atokor-n-Ahaggar: in alvio amnis Temmes-Lezzemt, solo granitico, 2000 m, 15 Martii 1928, *R. Maire 878* (residual syntype: MPU [MPU059306]!). [Algeria]. In ditione Ahaggar: Issekkarassen in rupestribus basalticis, 2070 m 22 Martii 1928, *R. Maire 877* (residual syntype: MPU [MPU059320]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu004308]

Notes. When *Celsia longirostris* var. *hoggarica* was published (Maire 1940), the protologue listed nine collections, but no particular herbarium sheet was chosen as the holotype. We have traced eleven sheets (MPU004304, MPU004305, MPU004306, MPU004307, MPU004308, MPU059306, MPU059318, MPU059319, MPU059320, MPU059321, and MPU05932) preserved at Herb MPU that fit the protologue perfectly. The specimen MPU004308 appears to be the best preserved one and it shows more of the diagnostic features that are described in the protologue Therefore, it is the best candidate for typification and is chosen here as the lectotype for the name *C. longirostris* var. *hoggarica* according to Arts. 9.3 and 9.4 of the ICN (Turland et al. 2018).

Verbascum lychnitis **L., Sp. Pl. 1: 177. 1753.**

= *Verbascum album* Mill., in Gardeners Dictionary, Edition 8. London: 3. 1768.
= *Blattaria alba* Medik., in Vorles. Churpfälz. Phys.-Okon. Ges. 4(1): 230. 1789.
= *Verbascum biebersteinii* Besser, Index Seminum (Kalin) 1820: 8. 1820.
= *Verbascum micranthum* Moretti, Giornale di Fisica II, 5: 111. 1822.
= *Verbascum weldenii* F.Braun ex Moretti, Giornale di Fisica II, 5: 43. 1822.
= *Verbascum incanum* Gaudin, in Fl. Helv. 2: 121. 1828.
= *Verbascum orchideum* Host, in Fl. Austriaca 1: 288. 1827.
= *Verbascum leucanthemum* Dufour ex Gren. & Godr., in Grenier, Fl. France 2: 552. 1853.
≡ *Thapsus lychnitis* (L.) Raf., in Flora Telluriana 4: 89. 1838.
≡ *Lychnitis alba* Fourr., in Annales de la Société Linnéenne de Lyon., 17: 125. 1869.
≡ *Lychnitis lutea* Fourr., in Annales de la Société Linnéenne de Lyon., 17: 125. 1869.
= *Verbascum lychnitis* subvar. *albiflorum* Rouy in Rouy & Foucaud, Fl. France 11: 14. 1909.
= *Verbascum lychnitis* subvar. *aureiflorum* Rouy in Rouy & Foucaud, Fl. France 11: 14. 1909.
= *Verbascum lychnitis* var. *foliosum* Vayr. in Anales Soc. Esp. Hist. Nat. 30: 553. 1902.

= *Verbascum lychnitis* var. *longebracteatum* Rouy in Rouy & Foucaud, Fl. France 11: 14. 1909.

= *Verbascum pyrenaicum* Gand., in Dec. Pl. Nov. 2: 9. 1876.

= *Verbascum kanitzianum* Simonk. & L.Watlz, in Magyar Növényt. Lapok 2: 148. 1878.

= *Verbascum lychnitis* var. *kanitzianum* (Simonk. & L.Watz) Murb., in Lunds Univ. Arsskrift, 2 n.f 29(2): 344. 1933.

= *Verbascum lychnitis* f. *album* (Mill.) House in Bull. New York State Mus. Nat. Hist. 243–244: 45. 1923.

= *Verbascum lychnitis* var. *giganteum* Maire, in Mém. Soc. Sci. Nat. Maroc 7: 196. 1924. Type: [Morocco]. Moyen Atlas: Azrou, ravins des cédraies sur basalte et calcaire, 1700 m, 25 Juillet 1921, *R. Maire, s.n.* (Lectotype, designated here: RAB [RAB30546]!; isolectotype: MPU [MPU006911, MPU006912, MPU006913, MPU006910]!, P [P00083084]!). **(2)**

= *Verbascum nuriense* Sennen, in Diagn. Nouv. 44. 1936. [in shed]

Type. [Habitat in Europae ruderatis cultis.] (Lectotype, designated by Fischer 1997, pg.115: Herb. Clifford: 54, *Verbascum* 2, PM [BM000557980]!).

Notes. Original material is conserved in the Clifford Herbarium at the Natural History Museum of London and an image of the lectotype is available at http://data.nhm.ac.uk/dataset/clifford-herbarium.

(2) Maire (1924) described *Verbascum lychnitis* var. *giganteum* on the basis of plant material that he had collected himself in the Azrou cedar forest, Central Middle Atlas, Morocco. However, in the protologue, he did not identify any herbarium sheet as holotype, nor did he give the name of the herbarium where the original material was stored. Six specimens were located through our research at Herbrs RAB (RAB30546), MPU (MPU006910, MPU006911, MPU006912, MPU006913), and P (P00083084) which can be considered original material. The sheet RAB30546 preserved at Herb. RAB is selected here as the lectotype for the name *V. lychnitis* var. *giganteum* since it is in a better condition.

Verbascum mairei (Murb.) Hub.-Mor., in Bauhinia 5(1): 13. 1973.

≡ *Celsia mairei* Murb., Lunds Univ. Arsskrift, 2 n. f., 35(1): 59. 1939. Type: [Morocco]. Tafriat Banks by roadside, 3.000 ft, 10 July 1936, *E.K. Balls, B2792* (lectotype, designated here: S [S10-27049]!; isolectotype: RAB [RAB30643]!). [Morocco]. Moyen Atlas, Roches calcaires à Tizi-n-Ouria (supra Ksiba), 1600 m, 21 Juin 1936, *R. Maire s.n.* (residual syntype: MPU [MPU059317]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.s10-27049]

Notes. In the protologue of *Celsia mairei* [≡*Verbascum mairei* (Murb.) Hub.-Mor.], Murbeck (1939) cited two gatherings: “Imper. Maroccanum: In rupestribus calcareis Atlantis Medii ad Tizi-n-Ouria (supra Ksiba), 1600 m, R. Maire, 21/6/1936” and

"Tafriat, 3000 ft., some 50 or 60 km out of Marrakesh on the road to Ouarzazat across the Great Atlas by Tadert and the Tizi n' Tichka, E.K. Balls, 10 /7/ 1936, n. 2792". However, he did not give any information about herbaria housing the original samples, nor did he indicate which one is the holotype.

The search for the original material of *Celsia mairei* led us to discover three sheets kept at Herbs MPU, RAB, and S. The sheet kept at Herb. MPU was collected by R. Maire (Barcode MPU059317), but those found at Herb. S (Barcode S10-270499) and at Herb. RAB (RAB30643) were collected by E.K. Balls. All three specimens found are morphologically in agreement with the original description (Murbeck, 1939). Moreover, collection locations indicated on the labels match those indicated in the protologue. Following Art. 9.6 of the ICN (Turland et al. 2018), these specimens must be considered as syntypes. According to its quality of conservation, the sheet S10-27049 preserved at Herb. S is here selected as the lectotype, because it is well-conserved and shows more diagnostic features described in the protologue. The specimen housed at Herb. RAB is recognized here as an isolectotype.

Verbascum maroccanum **(Ball) Hub.-Mor., in Bauhinia 5: 13. 1973.**

≡ *Celsia maroccana* Ball, in Journal of Botany 13: 172. 1875. Type: [Morocco]. South Morocco. Greater Atlas, Seksaoua May 1871, *J. D. Hooker, s.n.* (lectotype, designated here: K [K000410855]!). [Morocco]. South Morocco. Greater Atlas, Milhain, May 1871, *J. D. Hooker, s.n.* (residual syntype: K [K000410856]!). [Morocco]. Near Mogadore. Djebel Hadid, April-May1871, *J. D. Hooker, s.n.* (residual syntype: K [K000410853]!). [Morocco]. South Marocco. Greater Atlas 17 May 1871, *G. Maw, s.n.* (residual syntype: K [K000410857]!). [Morocco]. South Marocco. Greater Atlas, Reraia, May 1871, *J. D. Hooker, s.n.* (residual syntype: K [K000410858]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000410855]

Notes. This species was described by Ball (1875: 172) from material gathered by himself, J.D. Hooker, and G. Maw during their botanical expedition in Morocco in 1871 (Hooker and Ball 1878; Stafleu and Cowan 1976–1988). Murbeck (1925) indicated that the original material is stored at Herbs K and B. During our research, we have traced five specimens kept at Herb. K and bearing K barcodes as follows: K000410853, K000410855, K000410856, K000410857, K000410858. However, no relevant specimens could be traced at Herb. B, so we have some reasons to think that this material was destroyed during the bombing raid at Berlin in 1943 (Hiepko, 1987). In all the specimens found the collecting localities on labels match those mentioned in the protologue and material morphologically agrees with the original description. Since no holotype was indicated, they are all syntypes according to Art. 9.6 of the ICN (Turland et al. 2018). Hence, among all the original material kept at Herb. K, the specimen bearing the K barcode K000410855 is selected here as the lectotype.

Verbascum masguindalii **(Pau) Benedí & J.M.Monts., in Collect. Bot. (Barcelona) 16: 108. 1985.**

= *Celsia ramosissima* Benth. in DC., Prodr. 10: 244. 1846. Type: [Morocco]. In Mauritania in silva Mamorae, *Durand, s.n.* (Lectotype, designated by Benedí and Montserrat 1985, pg.108: MPU [MAF4378]!).
= *Verbascum ramosissimum* Kuntze, Revisio Generum Plantarum 2: 469. 1891. non *Verbascum ramosissimum* Poir. in Lamarck & Poiret, Encycl. suppl. III: 718, 1813. nec *V. ramosissimum* DC. in Lam. & DC., Fl. Fr., VI: 416, 1815.
≡ *Celsia masguindalii* Pau, Monde des Plantes 66: 1. 1929.
= *Verbascum hamidoui* Rankou, in Phytotaxa 78(1): 68. 2013.

Type. [Morocco]. Rio Martin, June 1929, *Mas Guindal s.n.* (Lectotype, designated by Benedí and Montserrat 1985, pg. 108: MP [MA108916]!). Image of the lectotype is available at: http://colecciones.rjb.csic.es/#cardAdv.php?CatalogNumber=MA-01-00108916).

Notes. The name of this species was first published by Mas Guindal (1928: 102), but without a description. A year later, Pau (1929) gave the description of *Celsia masguindalii* Pau based on the specimens collected by Mas Guindal in Río Martín near Tetuán. In their 'Taxonomic and nomenclatural notes on some species of the genus *Verbascum* L. (incl. *Celsia* L.)', Benedí and Montserrat (1985) have wrongly cited the lectotype number (MA108989) for *Verbascum masguindalii* (Pau) Benedí & J.M.Monts. instead of the number MA108916 as shown by Nualart (2017). Besides, Nualart et al. (2021) have traced two other eligible sheets (BC89918, BC141503) in Herb. BC. Those two specimens were also collected by Mas Guindal in Río Martín, but without a collection date on the labels. According to Gonzâlez-Bueno and Gomis (2007) and Nualart (2017), Mas Guindal during his visit in Tetouan (Morocco) between 1926 and 1931, has collected many times at this site (Río Martín).

Verbascum maurum **Maire & Murb., in Lunds Univ. Arsskrift, 2 n.f., 19(1): 35. 1923.**

Type. [Morocco]. Region du Grand Atlas. Ourika: rocailles schisteuses le long du torrent, au-dessous de Tagentourt; 1400 m, 14 Juillet 1921, *R. Maire, s.n.* (Lectotype, designated here: MPU [MPU008183]!; isolectotype: MPU [MPU008015]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu008183].

Notes. Murbeck (1933), in his monograph of *Verbascum* L., indicated that original material of *Verbascum maurum* was kept at Maire's herbarium at Herb. MPU. We have only found two sheets of this taxon in Herb. MPU (MPU008015, MPU008183). Both have a handwritten label by Maire bearing the information about the gathering, collector, date, and locality that match the protologue. The specimen MPU008183 is designated here as the lectotype, because it shows more of the diagnostic features described in the protologue.

Verbascum pinnatisectum (Batt.) Benedí, in Anales Jard. Bot. Madrid 60(2): 460. 2003.

≡ *Celsia cretica* var. *pinnatisecta* Batt. in Bull. Soc. Brot. France 40: 263. 1893. Type: [Algeria]. A. Sersou: Aïn-Sfa, à 40 km de Teniet-el-Had sur la route de Tiaret. Juin 1893, *J.A. Battandier, s.n.* (Lectotype, selected by Benedí 2003, pg. 460, first step "type"; second step, designated here: MPU [MPU006805]!; isolectotype: MPU [MPU005282]! P[P03425758]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu006805]

≡ *Celsia pinnatisecta* (Batt.) Batt. in Batt. & Trab. Fl. Alger. Tunis.: 243. 1904.

Notes. Pursuant to the Art. 9.17 (Turland et al. 2018), the lectotypification of Benedí (2003) could be considered a first-step lectotypification, since he has cited wrongly the number of the lectotype and did not specify exactly which of the two sheets MPU005282 and MPU006805 kept at Herb. MPU as lectotype. In addition to these two sheets stored at Herb. MPU, we have traced another of this gathering kept at Herb. P (barcode P03425758). Hence, the sheet preserved at Herb. MPU that bears barcode "MPU006805" is here designated as the (second-step) lectotype.

Verbascum pseudocreticum Benedí & J.M. Monts., in Collect. Bot. (Barcelona) 16: 106. 1985.

= *Celsia sinuata* Colla, in Hortus Ripul. App. 2: 344. 1825., non Cav. 1801.

= *Celsia cavanillesii* Kunze in Flora 29: 698. 1846, nom. illegit., Type: [Spain]: In isthmo Gaditano, III-1846, *M. Willkomm, s.n.* (lectotype, designated by Benedí and Montserrat 1985, pg. 107: COI [COI00042221]!). ≡ *Celsia cretica* var. *cavanillesii* Kunze ex Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 545. 1870. Illegitimate name.

= *Celsia sinuata* sensu Willk., in III. Fl. Hisp. 2(14): 58. 1888, non *Celsia sinuata* Cav., in Anal. Cieñe. Nat. Madrid 111: 68. 1801.

= *Celsia lyrata* sensu Murb., in Lund. Univ. Arssk., n. f. 2, 22(1): 199. 1925, non *Celsia lyrata* (Lam.) G.Don, in Gen. Hist. 4: 499 1837.

Type. [Spain]. Hab. in regione calida maritima Baeticae: occidentali in arena mobili isthmi Gaditani Inter hortos prope ecclesiam Sancthi Josephi copiose, martii 1845, *M. Willkomm, 536* (lectotype, designated by Benedí and Montserrat 1985, pg. 107: COI [COI00042222]!).

Notes. Original material is conserved at the Herbarium Mediterraneum Pyrenaicum et Canariense of Moritz Willkomm, which is kept at the Herbarium of the Department of Life Sciences of the University of Coimbra (COI). An image of the lectotype is available at http://coicatalogue.uc.pt/specimen/42222.

Verbascum rotundifolium **Ten., Prod. Fl. Napol. 1: 92. 1815.**

Type. [Italy]: n.v.

Notes. According to Stafleu and Cowan (1976–1988), the original material of the Italian botanist, Michele Tenore are preserved at Herb. NAP, with further material in Herbs AWH, B-Willd., BASSA, BM, BR, C, CGE, DWG, E, FI, G, H, K, M, MPU, OXF, P, PH, REG, and UPS. However, we could not trace any specimen in any herbarium for this taxon.

Verbascum rotundifolium **subsp.** ***rotundifolium*****, in Lunds Univ. Arsskrift, 2n.f. 29 (2): 398. 1933.**

= *Verbascum numidicum* Pomel, in Nouv. Mat. Fl. Atlantique (1): 95. 1874. Type: [Algeria]. Rochers au sommet du Mécid à Constantine 23 Mai 1857, *S. Choulette 369* (Lectotype designated here: MPU [MPU004892]!, isolectotype JE [JE00013694]!). ≡ *Verbascum rotundifolium var. numidicum* (Pomel) Murb., in Bull. Soc. Hist. Nat. Afrique N. 18: 83. 1927. [image of lectotype available at https://herbier.umontpellier.fr/zoomify/zoomify.php?fichier=MPU004892] **(2)**

= *Verbascum kabylianum* Debeaux, in Rev. Bot. Bull. Mens. Soc. Franç. de Botan. 8: 265. 1890. Locality citation in the protologue of Type: [Algeria]. In sylyaticis montium kabylie surper. Prope fort-national, ad viam Taourirt-Amokran, 950 m, 6 Junio 1859, *O. Debeaux s.n.*: [n. v.] ≡ *Verbascum rotundifolium var. kabylianum* (Debeaux) Murb. in Bull. Soc. Hist. Nat. Afrique N. 18: 83. 1927.

= *Verbascum rotundifolium var. castellorum* Maire, in Bull. Soc. Hist. Nat. Afrique N. 29:, 438. 1938. Type: [Morocco]. In rupestribus calcareis Atlantis Medii infra Ksiba, 900 m, 22 Juinio 1936, *R. Maire, s.n.* (Lectotype designated here: P [P00083085]!; isolectotype: MPU [MPU004005, MPU004006]!, P [P01167373]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.mpu004006] **(3)**

Notes. This taxon was established by Murbeck (1933) under the recombination *V. rotundifolium* subsp. eu-*rotundifolium*. According to Ferguson (1972) and Benedí (2009), this subspecies is distributed in southern Italy, Sicily, Algeria, and Tunisia. However, for Fennane and Ibn Tattou (2005), Ibn Tattou (2007), and Dobignard and Chatelain (2013), this taxon is spontaneous in Morocco. Under its current recombination, *V. rotundifolium* subsp. *rotundifolium* it is accepted in the Partical flora of Morocco (Fennane and Ibn Tattou 2005, Ibn Tattou, 2007), in the index of synonyms for the flora of North Africa (Dobignard & Chatelain, 2013), and by the APD (African Plant Database 2022).

(2) Pomel (1874) described on *Verbascum numidicum* based on the collections of Choulette exs. [exsiccata] 369, but did not provide collection date nor the name of the herbarium where the original material were housed. After a thorough search, two specimens were found, one at Herb. MPU (MPU004892) and the other at Herb. JE (JE00013694), both of which matched the data provided in the protologue. Thus, the sheet MPU004892 is chosen here as the lectotype of the name *V. numidicum*, because it is better preserved and shows more diagnostic features described in the protologue.

(3) The protologue of *Verbascum rotundifolium* var. *castellorum* (Maire 1938) is composed of a Latin diagnosis, and the details of the collection locality on limestone rocks below Ksiba region at an altitude of about 900 m in the Middle Atlas, Morocco, but there is no mention of the name of the herbarium that houses the original material. Four herbarium sheets deposited in Herbs MPU (MPU004005, MPU004006) and P (P01167373, P00083085) were traced. These specimens can be considered as the original material according to the type details provided in the protologue. The specimen P00083085 persevered at Herb. P is better conserved and best represents the diagnostic features of the taxon given in the protologue; hence it is selected here as the lectotype for the name *V. rotundifolium* var. *castellorum*.

Verbascum rotundifolium **subsp.** ***haenseleri*** **(Boiss.) Murb., Bull. Soc. Hist. Nat. Afrique N. 18: 83. 1927.**

≡ *Verbascum haenseleri* Boiss., in Voy. Bot. Espagne 2: 442. 1841. Type: [Spain]. Sierra d'Estepona, 1837, [*Boissier*] *s.n.* (lectotype, designated by Burdet et al. 1990, pg. 624: G [G00025472]!). [Spain]. San Anton [*Boissier*] *s.n.* (residual syntype: G [G00025473]!). **(1)**

= *Verbascum aurantiacum* Coincy, in J. Bot. (Morot) 9: 332. 1895. Type: [Spain]. Espagne, Baza, 6 June 1895, *A. Coincy s.n.* (Lectotype designated here: P [P03808542]!). [image of lectotype available at http://coldb.mnhn.fr/catalognumber/mnhn/p/p03808542] **(2)**

= *Verbascum latesulcatifolium* Sennen & Mauricio, in Cat. Fl. Rif Orient.: 84. 1933, nom. nud.

= *Verbascum rotundifolium* subsp. *castellanum* Murb., in Lunds Univ. Arsskrift, 2n.f. 29 (2): 402. 1933. Type: [Spain]. Ávila; Navalmoral, cerros audossus, 2 June 1863, *E. Bourgeau, s.n.* (Lectotype designated here: MA [MA108794]!), [Spain]. San Agustín de los Reyes, June 1912, *C. Vicioso s.n.* (residual syntype: MA [MA108789]!), [Spain]. Escorial, 15 Juin 1852, *J. Lange, s.n.* (residual syntype: MA [MA108791]!), [Spain]. Prov. Albacete, in pascuis prope Alcaraz, sol. calcareo, 700–800 m, 21 June 1891, *P. Porta* and *G. Rigo, 337* (residual syntype: JE [JE00007506]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.ma108794] **(3)**

Notes. (1) When, Burdet et al. (1990) selected the lectotype of the name *Verbascum haenseleri*, they selected the sheet G00025472 as lectotype and sheet G00025473 as a syntype. An image of the lectotype is available at: https://www.ville-ge.ch/musinfo/bd/cjb/chg/result.php?type_search=advanced&lang=en&typecollection=&family=&

genus=&species=&infraspecificname=&collector=&nocoll_operateur=%3D&debut_nocoll=&fin_nocoll=&date_operateur=%3D&debut_recolte=&fin_recolte=&country=&locality=&barcode=G00025472.

(2) Coincy (1895) in the protologue of *Verbascum aurantiacum* mentioned the collection locality as "Les pentes de la Sierra de Aquila près Baza (prov. de Grenade) le 8 juin 1895, à une hauteur que j'évalue à 1,200 m. environ [The slopes of the Sierra de Aquila near Baza, in the province of Granada, on June 8, 1895, at an altitude that I estimate roughly 1200 m]". However, no specific herbarium specimen was identified as a holotype, nor was where the original material was housed indicated. According to Stafleu and Cowan (1976–1988), the plants collected by Coincy are preserved at Herb. P, and further material can be found at Herbs B and LY. After conducting exhaustive research in the three different Herbrs (P, B and LY), we located one sheet at Herb. P (P03808542) that is a perfect match with the protologue. Hence, we designate this specimen (P03808542) as the lectotype for the name *Verbascum aurantiacum*.

(3) When he described *Verbascum rotundifolium* subsp. *castellanum*, Murbeck (1933) included in the protologue 14 gatherings that were collected in Spain by diverse botanists, but he did not indicate any herbarium specimen as a holotype. Only four specimens related to the gatherings mentioned in the protologue have been traced. Three of these specimens were found at Herb. MA (MA108791, MA108794, MA108789), and the other specimen was found at Herb. JE (MA108792). (JE00007506). The specimen MA108794 preserved Herb. MA is here designated as lectotype for the name *V. rotundifolium* subsp. *castellanum* because it is complete and matches the information in the protologue.

***Verbascum sinuatum* L., in Sp. Pl.: 178. 1753.**

= *Celsia sinuata* (L.) Colla, in Hortus Ripul. App. 2: 344. 1826.
≡ *Thapsus sinuatum* (L.) Raf., in Fl. Tellur. 4: 89. 1838.
= *Lychnitis sinuata* (L.) Fourr., in Ann. Soc. Linn. Lyon ser. 2 17: 125. 1869.
= *Verbascum sinuatum* var. *pallidiflorum* Pau, Not. Bot. Fl. Españ. 3: 34. 1889, nom. nud.
= *Verbascum sinuatum* var. *subulatum* Rouy, in Rouy & Foucaud, Fl. France 11: 12. 1909.
= *Verbascum tetuanense* Pau, in Cavanillesia 1: 143. 1928.
= *Verbascum sinuatum* f. *subsinuatum* Pau, in Sched., nom. nud.
= *Verbascum arnaizii* Sennen, in Diagn. Nouv.: 238. 1936.
= *Verbascum sinuatum* f. *albiflorum* M. Silva, in Agron. Lusit. 14: 118. 1952.
= *Verbascum sinuatum* f. *albiflorum* Greuter, Matthäs & Risse, in Willdenowia 14: 291. 1984, nom. illegit.

Type. [Protologue locality: Habitat Monspelii, Florentiae] (lectotype, designated by Huber-Morath 1971, pg. 94.: Herb. Linn. No. 242.7 [LINN]!).

Notes. Original material is conserved in the Linnaean Herbarium at the Linnean Society of London and an image of the lectotype is available at http://linnean-online.org/1837/

Verbascum tetrandrum Barratte & Murb., in Contrib. Fl. Tunisie 2(14): 62. 1905.

Type. [Morocco]: Cult. Thurelles, [Cult. Thurelles e. sem. Maroc, 14 July 1877, [*E. Cosson*] *s.n.* (Lectotype, designated here: P [P03429051]!). [Morocco]. Tazeroualt, Sous independant (Maroc), [1874] *Robbin Mardochée* (residual syntype: P [P03429046]!). [image of the lectotype is available at: https://science.mnhn.fr/institution/mnhn/collection/p/item/p03429051?listIndex=288&listCount=7215]

Notes. Barratte and Murbeck's (in Murbeck 1905) description of *Verbascum tetrandrum* was based on specimens gathered by Rabbi Mardochée near Tazeroualt in the southwest of Morocco. Within the protologue, Barratte and Murbeck (in Murbeck 1905) did not designate any herbarium sheet as holotype, nor the name of the herbarium where the type material was housed. Moreover, the original description was accompanied by a photography of the type with a legend that reads "1-Specimen fructiferum ad Tazeroualt lectum / 2 & 3-Pars caulis foliumque basilare speciminis in Gallia anno 1877 a cl. Cosson culti / 4-Corollae; speciminis culti". Following this information mentioned in the legend, the type material is formed by the specimens bearing fruits collected by Mardochée and specimens from cultivated grains by Cosson. Murbeck (1933) indicates that the original material was preserved in the Cosson herbarium. During our extensive search, two sheets were found at Herb. P (P03429046, P03429051). All of these specimens agree with the protologue and the accompanied iconography.

The sheet P03429046 contains a fruiting part of an inflorescence and has three labels: an original label handwritten by Cosson "*Verbascum pycnostachyum* nov. sp. / Tazeroualt / Sous independant (Maroc) Robbin Mardochée"; the second is a revision label handwritten by R. Maire in 1921 who re-determined it as "*Verbascusm tetrandrum* Barr & Murb", and the last label is handwritten by Murbeck in 1926 who put just an exclamation mark (!) indicating that the sheet was verified by him. The sheet P03429051 has an apical part of stem and a basal leaf and two handwritten labels: the first one reads "*Verbascum* (*Celsia*) *pycnostachyum* / Cult. Thurelles / 1877", and the second is a revision label handwritten by Murbeck in 1924 who re-determined it as "*Verbascusm tetrandrum* Barr & Murb". All of these specimens should be considered as syntypes as stated by Art. 9.6 of the ICN (Turland et al. 2018). The specimen with barcode P03429051 is here chosen as the lectotype, because it is well preserved and it is the one that shows most of the morphological features in agreement with the original description.

Verbascum tibesticum (Quézel) Hub.-Mor., in Bauhinia 5(1): 15. 1973.

≡ *Celsia tibestica* Quézel, in Bull. Soc. Hist. Nat. Afrique N. 48: 95. 1957. Type: [Tchad]. Emi Koussi, Koudou. 2000 m, September-Novembre 1956, *P. Quézel, s n.* (Lectotype, designated here: AIX [AIX000033]!; isolectotype: AIX [AIX000034]!). [image of lectotype available at https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.aix000033]

Notes. The type material of this species was collected during Quézel's expedition to Borkou and to Tibesti in September–November 1956. In the protologue, Quézel (1957) did not designate a holotype nor did he mention the name of the herbarium where the original material was housed. We have traced three specimens at the herbarium of Muséum d'Histoire Naturelle d'Aix-en-Provence (AIX), France. The sheet AIX000033 contains a well conserved plant with mature fruit and rosette and an original label handwritten by P. Quèzel that reads "Mission Botanique de l'Institut de Recherches Sahariennes de l'Université d'Alger au Borkou et au Tibesti / *Celsia tibestica* nov; sp. / Emi Koussi, Koudou. 2000 m / Sept-November 1956, Dr. P. Quézel". The sheet AIX000034 bears only a rosette and an original label handwritten by P. Quèzel reading "Mission Botanique de l'Institut de Recherches Sahariennes de l'Université d'Alger au Borkou et au Tibesti / *Celsia tibestica* Qz. / Koudou / Sept-November 1956, Dr. P. Quézel". Both specimens are in accordance with the protologue, and based on Art. 9.6 of the ICN (Turland et al. 2018) both must be treated as syntypes. The sheet bearing the barcode AIX000033 is designated here as the lectotype, because it is in better condition than the other specimen and shows all relevant characters mentioned in the protologue.

Verbascum tripolitanum Boiss., in Diagn. Pl. Orient. 12: 9. 1853.

Type. [Syria]. Syria mar.: Tripoli, [Jul] 1846, *Ed. Boissier s.n.* (Lectotype, designated here: P [P03287124]!). [image of lectotype available at (Image available at: http://coldb.mnhn.../mnhn/p/p03287124].

Notes. This species was described by Boissier (1853) from material collected at the foot of Trobol mountain in Syria. In the protologue, Boissier (1853) gave information about the collection locality, but he does not provide the name of the herbarium where the original material has been deposited. Boissier (1853) notes that *V. tripolitanum* starts flowering at the beginning of June. According to Stafleu and Cowan (1976–1988) and Jacquemoud (2011), the Boissier herbarium related to the Flora Orientalis account is preserved at Herb. G. However, duplicates of Boissier's collections could be found in many other herbaria. During our research, we have traced one specimen (barcode P03287124) conserved in Herb. P that is in accordance with the protologue. The sheet P03287124 bears a part of an inflorescence, a basal leaf, and two handwritten labels, the left one reads "*Verbascum tripolitanum* Boiss /Syria Mar: / [Jul] 1846 / Tripoli / (donné par Mr. Boissier / Ed Boiss.)" and the second label on the right corner reads "Herbier Mus. Paris/ herbier tripolinatum / boiss / Syria /". So this sheet is designated here as the lectotype.

Verbascum zaianense (Murb.) Hub.-Mor., in Bauhinia 5(1): 16. 1973.

≡ *Celsia zaianensis* Murb., in Lunds Univ. Arsskrift, 2 n.f., 22(1): 218. 1925. Type: [Morocco]: Entre Aït Lias et Aïn Leuh, 5 Juin 1918, *P. Benoist, 525* (Lectotype, designated here: P [P03425567]!). [image of lectotype available at: http://coldb.mnhn.../mnhn/p/p03425567]

Notes. In the protologue of *Celsia zaianensis*, Murbeck (1923) cited an element collected by Benoist from Zaïan region, between Aït Lais and Ain-leuh, Morocco, and he indicated that type material is preserved at the Cosson Herbarium. The latter collection is housed at Herb. P according to Stafleu and Cowan (1976–1988). The protologue also includes citation of the locality "Entre Aït Lias et Aïn Leuh", collection date "5 Juin 1918", and name and number of collector "P. Benoist, 525". At Herb. P, we have found only one specimen with barcode P03425567 bearing a single plant, and determined by Murbeck as "*Celsia zaianensis* Murb.". This specimen is morphologically close to the original description. Furthermore, there is an indication on the label indicating a new species ("n. sp.") and the label has the collection date and collection locality, and collector number matching the information given in the protologue. Since only a single specimen is mentioned by Murbeck (1925), one may argue that the relevant specimen is the holotype. However, Murbeck (1925) did not use the term type. Therefore, we herein designate the sheet P03425567 as lectotype.

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Notes on *Carex* (Cyperaceae) from China (IX): three new species of section *Mitratae* s.l.

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Abstract

Carex sect. *Mitratae* s.l. was established by Kükenthal in 1909 and can be distinguished from the closely related sections in having nutlets frequently discoid-annulate at the apex and a persistent style base. Based on field surveys and specimen examination, three new species of sect. *Mitratae* are described and illustrated here. *Carex fatsuaniana* was collected from Yunnan and differs from *C. truncatigluma* in having the utricles nearly glabrous, the nutlets with a ca. 0.5 mm long beak at the apex, the staminate spikes cylindrical, 5–7.5 cm long, 4–5 mm wide, and the pistillate glumes acuminate at the apex. *Carex damingshanica* was collected from Guangxi and differs from *C. breviscapa* and *C. rhynchachaenium* in having 3 or 4 spikes, the lateral spikes cylindrical, the pistillate glumes, utricles and nutlets all shorter than in the other two species. *Carex radicalispicula* was collected from Sichuan and differs from *C. truncatirostris* in having the staminate spikes clavate, 1.5–2 mm wide, the pistillate glumes pale yellow-white, 3–3.2 mm long, acuminate or short-awned at the apex, and the nutlets with 3 angles shallowly constricted at the middle.

Keywords

Carex sect. *Mitratae*, China, new species, sect. *Lageniformes*

Introduction

Carex L. (Cyperaceae), a morphological diverse genus with about 2,000 species, is one of the largest genera of angiosperms and is distributed on all continents except Antarctica (Reznicek 1990; Govaerts et al. 2021; Pender et al. 2021). The main characters of this genus that distinguish it from the other genera in the Cyperaceae are flowers unisexual, the female ones contained within a prophyllar structure called a perigynium, which is referred to as a utricle when its margins are fused and closed (Dai et al. 2010; Jiménez-Mejías et al. 2016). Following an increasing number of samples and molecular markers, the systematic framework of *Carex* has become more robust, six strongly supported distinct main lineages were detected, viz. the *Siderostictae*, *Schoenoxiphium*, *Unispicate*, *Uncinia*, *Vignea* and core *Carex* clades (Villaverde et al. 2020; Roalson et al. 2021). A large number of new species of the core *Carex* clade were described during, or soon after, the preparation of the "Flora of China" (Dai et al. 2010; Lu and Jin 2022; Lu et al. 2022).

Carex sect. *Mitratae* Kük. s.l. (Kükenthal 1909), containing 80+ species, was traditionally divided into three sections: *Cryptostachyae* Franch., *Lageniformes* (Ohwi) Nelmes and *Mitratae* s.s. These are mainly distributed from E and SE Asia to Australia and New Zealand, with a few species reaching Europe, as well as into western and northern Asia (Akiyama 1955; Dai et al. 2010; Roalson et al. 2021). Recent phylogenetic studies revealed the sect. *Mitratae* s.l. is a polyphyletic group, and five clades which were named as Sect. *Cryptostachyae*, Tristachya Clade, Truncatigluma Clade, Mitrata Clade and Conica Clade in the core *Carex* clade are recognized (Roalson et al. 2021).

The group, sect. *Mitratae* s.l., is easily recognized on some morphological characters such as nutlet shape and utricle shape, as well as growth habits. During the field surveys and specimen examination of *Carex*, and during preparation of a taxonomic monograph of sect. *Mitratae* s.l., three new species were discovered, which are described below.

Taxonomic treatment

1. ***Carex fatsuaniana*** **X.F.Jin, Y.F.Lu & Z.C.Lu, sp. nov.**

urn:lsid:ipni.org:names:77318323-1
Fig. 1A–G

Diagnostic description. This new species is similar to *Carex truncatigluma* C.B.Clarke, but differs in having utricles nearly glabrous, nutlets with a ca. 0.5 mm long beak at apex, staminate spikes cylindrical, 5–7.5 cm long, 4–5 mm wide, and pistillate glumes acuminate at apex.

Type. China. Yunnan: Foo-ning [Funing County], Ban-loun [Banlun Township], under dense-thickets, alt. 700 m, 10 Apr 1940, *C. W. Wang 88293* (holotype: PE!; isotypes: IBK00181423!, PE!).

Description. Perennial herbs. Rhizomes woody, obliquely ascending. Culms lateral, 45–60 cm tall, trigonous, smooth, base with short leaves and brown fibrous sheaths. Leaves longer than culms, blades flat, leathery, 4.5–9 mm wide, scabrous on upper surfaces and margins. Bracts leaf-like or shortly leaf-like, base with

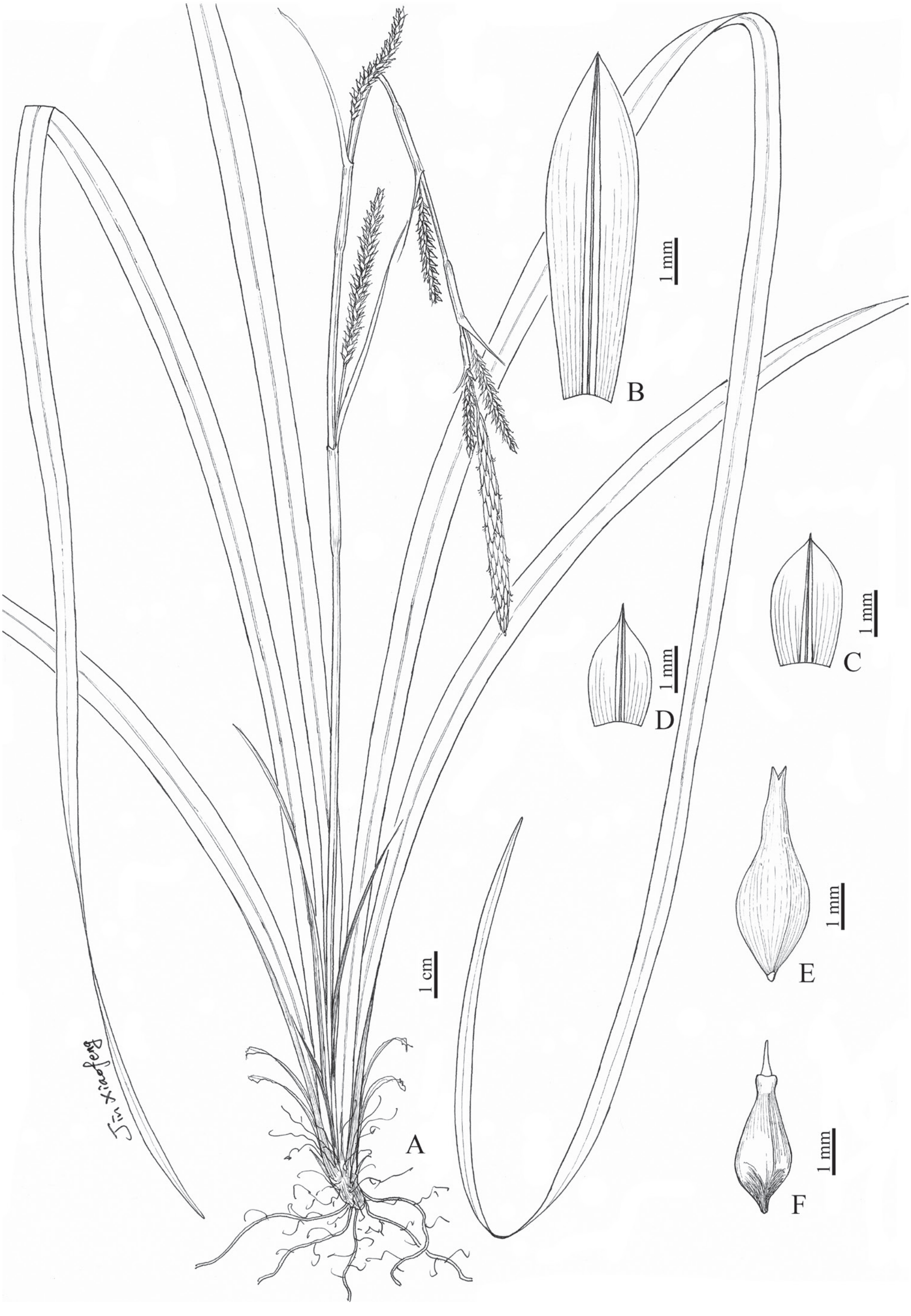

Figure 1. *Carex fatsuaniana* sp. nov. **A** habit **B** staminate glume **C, D** pistillate glume **E** utricle **F** nutlet. (Drawn by Xiao-Feng Jin; based on the holotype: *C. W. Wang 88293* in PE).

1–2.5 cm long sheath. Spikes 6; terminal spike staminate, cylindrical, 5–7.5 cm long, 4–5 mm wide, base with 8–20 mm long peduncles; lateral spikes pistillate, cylindrical, 2.5–4.5 cm long, 3–3.5 mm wide, densely flowered, with peduncles exserted from or enclosed in sheaths. Staminate glumes elliptic-lanceolate or oblanceolate, pale brown, 7–7.5 mm long, apex acuminate, with 3-veined yellow-brown costa. Pistillate glumes ovate-elliptic or obovate, pale yellow, 2.5–3 mm long, apex acuminate and mucronate, or acute, with 3-veined yellow-brown costa. Utricles yellow-green, narrowly ellipsoid-ovoid, obtusely trigonous, 4–4.5 mm long, longer than pistillate glumes, membranous, obliquely patent, distinctly thinly veined, nearly glabrous, base gradually cuneate, short-stipitate, apex gradually contracted into a ca. 1 mm long beak, orifice 2-lobed with short teeth. Nutlets tightly enveloped, brown, ovoid, trigonous, 2.5–3 mm long, with 3 sides slightly concave below, base short-stipitate, apex contracted into a ca. 0.5 mm long cylindrical beak; style base slightly thickened; stigmas 3.

Etymology. The specific epithet '*fatsuaniana*' is in honour of Prof. Fa-Tsuan Wang (Fa-Zuan Wang, 1899–1985), the taxonomic founder of Chinese monocots.

Phenology. Flowering and fruiting occur in early April.

Conservation status. Data Deficient (DD). Only four sheets (*C. W. Wang 88293*) of the new species were collected by Chi-Wu Wang in 1940 from the type locality. Adequate information is lacking on its distribution and population status to make a direct or indirect assessment of the risk of extinction (IUCN 2019).

Notes. *Carex fatsuaniana* has nutlets contracted distally into a ca. 0.5 mm long cylindrical beak at the apex, which morphologically belongs to sect. *Lageniformes* and is similar to *C. truncatigluma* (Dai et al. 2010). In sect. *Lageniformes*, the species has terminal staminate spikes thinly linear-clavate, whereas those of the new species are cylindrical, 5–7.5 cm long, 4–5 mm wide. The characters distinguishing the new species from *C. truncatigluma* are shown in Table 1.

Based on the phylogenetic scaffold for the *Carex* classification (Roalson et al. 2021), the sampled species in sect. *Lageniformes* were arranged in two clades: *Carex breviscapa* and *C. longicolla* in Tristachya clade, and *Carex truncatigluma* in Truncatigluma clade, but *C. densipilosa* was placed in the uncertain group. The new species, *Carex fatsuaniana*, is mostly closed to *C. truncatigluma* in morphology, so it's temporarily placed in the Truncatigluma clade.

Table 1. Morphological characters distinguishing *Carex fatsuaniana* from *C. truncatigluma*.

Characters	*C. fatsuaniana*	*C. truncatigluma*
1. Staminate spike	Cylindrical, 5–7.5 cm long, 4–5 mm wide	Thinly linear-clavate, 1–2 cm long, 1–2 mm wide
2. Staminate glume	Elliptic-lanceolate or oblanceolate, 7–7.5 mm long, acuminate at apex	Oblong-ovate or ovate, 3–3.5 mm long, obtuse at apex
3. Pistillate glume	Ovate-elliptic or obovate, acuminate and mucronate, or acute at apex	Broadly obovate, obtuse, truncate or emarginate at apex, sometimes short-awned or mucronate.
4. Utricle	Nearly glabrous	Pubescent
5. Nutlet	Beak ca. 0.5 mm long, cylindrical	Beak 0.5–1.5 mm long, thick-cylindrical

2. *Carex damingshanica* Z.C.Lu & X.F.Jin, sp. nov.

urn:lsid:ipni.org:names:77318324-1

Figs 2A–G, 3A–H

Diagnostic description. This new species is similar to *Carex breviscapa* C.B.Clarke and *C. rhynchachaenium* C.B.Clarke in having spikes in a short racemose and culms much shorter than leaves, but differs from these two relatives in having spikes 3 or 4, lateral spikes cylindrical, shorter, 4–11 mm long, pistillate glumes (1–1.2 mm long), utricles (2.5–3 mm long) and nutlets (1.5–1.9 mm long) all shorter than in related species.

Type. China. Guangxi: Nanning City, Shanglin County, Dafeng Town, Shuiyuan Village, Damingshan, 23°24'53.29"N, 108°31'45.16"E, under broad-leaved forest, alt. 423 m, 26 May 2020, *P. Yang et al. 450125200526074LY* (holotype: ZM!; isotypes: IBK00445399!, IBK00445400!, ZJFC!, ZM!).

Description. Perennial herbs. Rhizomes short, woody, stiff. Culms central, loosely turfed, 2.5–11 cm tall, trigonous, base with brown fibrous sheaths. Leaves much longer than culms, blades 1.5–3.5 mm wide, flat, leathery, scabrous on upper part and margins. Lowermost bract leaf-like, longer than inflorescence, base with 1–2 mm long sheath or sheathless, others setaceous, shorter than inflorescence, sheathless. Spikes 3 or 4, aggregated; terminal spike staminate, narrowly linear-cylindrical, 6–20 mm long, 1–1.5 mm wide, base with 1–3 mm long peduncles; lateral spikes pistillate, cylindrical, 4–13 mm long, 2.5–3 mm wide, loosely 9–14-flowered, with peduncles slightly exserted from sheaths. Staminate glumes broadly ovate, pale yellow-brown, ca. 1.5 mm long, apex obtuse, with 3-veined yellow costa. Pistillate glumes ovate, pale yellow, 1–1.2 mm long, apex acuminate, with 3-veined yellow costa. Utricles yellow-green, narrowly fusiform, obtusely trigonous, 2.5–3 mm long, longer than pistillate glumes, membranous, obliquely patent, distinctly thinly veined, sparsely pubescent, base gradually cuneate, short-stipitate, apex gradually contracted into a ca. 0.5 mm long beak, orifice 2-lobed with minute teeth. Nutlets tightly enveloped, brown, narrowly ovoid, trigonous, 1.5–1.9 mm long, with 3 sides slightly concave above and below, base with a ca. 0.2 mm long stipe, apex contracted into a 0.2–0.4 mm long cylindrical beak, truncate and shallowly concave at top; style base slightly thickened; stigmas 3.

Etymology. The specific epithet '*damingshanica*' refers to the type locality of this new species.

Phenology. Flowering and fruiting occur from late March to late May.

Additional specimens examined. China. Guangxi: Nanning City, Shanglin County, Xiyan Town, Jianglu Village, Damingshan, from Zuitun to Sanbao, 23°30'50.83"N, 108°28'22.42"E, under broad-leaved forest, alt. 473 m, 31 May 2020, *Y. L. Su et al. 450125200531038LY* (IBK00445401!, IBK00445402!, ZJFC!, ZM!); Nanning City, Shanglin County, Dalan River, Damingshan, alt. 460 m, 16 Oct 2011, *L. Wu & J. C. Yang D3254* (IBK00218552!); Nanning City, Shanglin County, Liangjiang Town, Chaoyang River, Damingshan, alt. 1030 m, 23 May 2011, *L. Wu D2120* (IBK00218553!).

Figure 2. *Carex damingshanica* sp. nov. **A** habit **B** upper part of inflorescence **C** staminate glume **D** pistillate glume **E** utricle **F** nutlet. (Drawn by Xiao-Feng Jin; based on the holotype: *P. Yang et al. 450125200526074LY* in ZM).

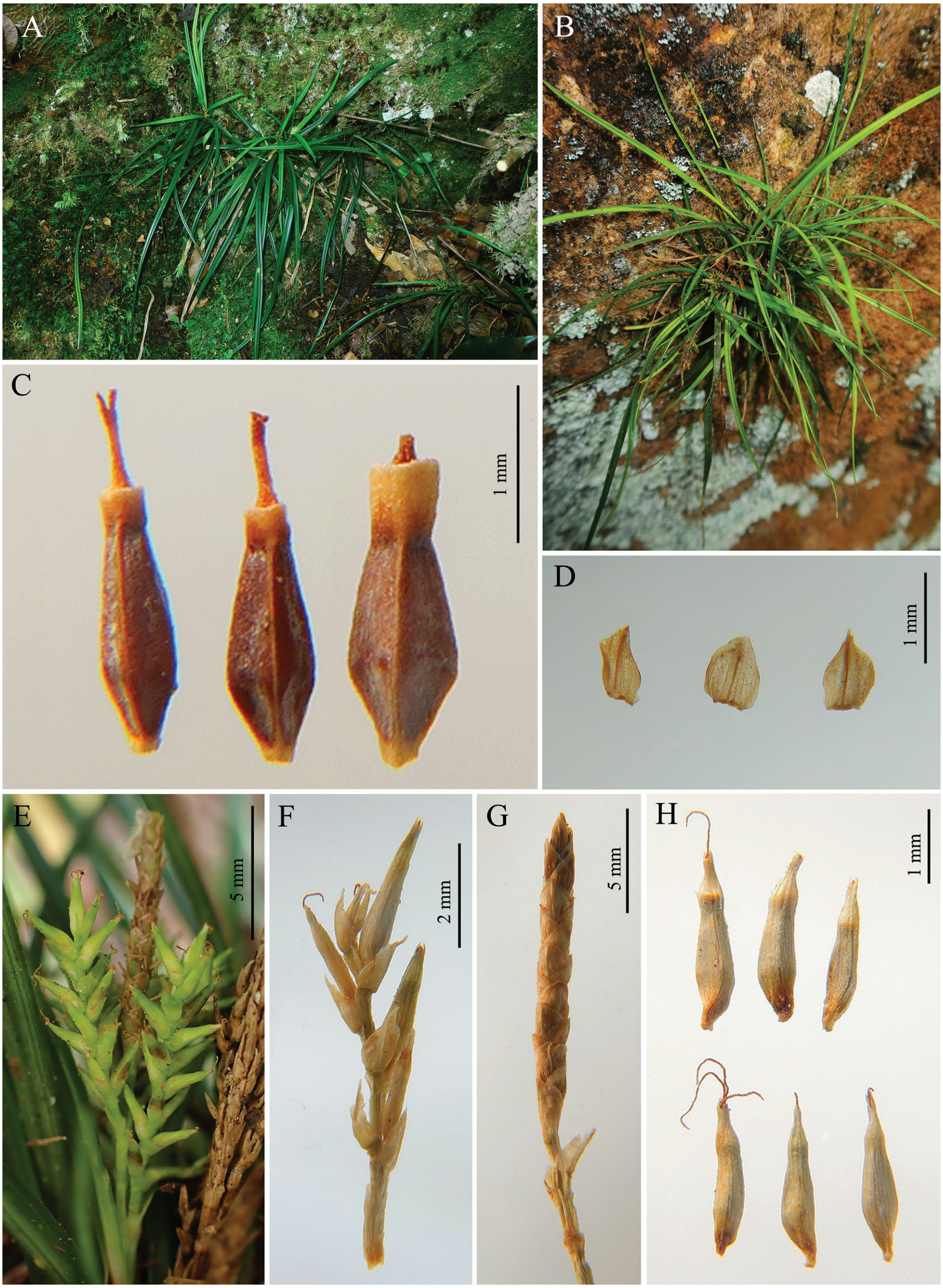

Figure 3. *Carex damingshanica* sp. nov. **A, B** habit **C** nutlets **D** pistillate glume **E** inflorescence **F** pistillate spike **G** staminate spike **H** utricle. (**C, D, F–H** from type material).

Conservation status. Least Concern (LC). The new species is known from four localities in Damingshan National Nature Reserve of Guangxi. These populations are in protected areas where they are not really threatened but need attention at ordinary times (IUCN 2019).

Notes. *Carex damingshanica* belongs to sect. *Lageniformes* in having terminal spikes staminate and nutlets apex contracted into a prominent long cylindrical beak (Dai et al. 2010). It is similar to *C. breviscapa* and *C. rhynchachaenium*, but differs from these two species in the characters of spikes, pistillate glumes, utricles and nutlets. The morphological differences of *C. damingshanica*, *C. breviscapa* and *C. rhynchachaenium* are shown in Table 2.

As above-mentioned, *Carex breviscapa* was placed in Tristachya clade, therefore its closed species, *C. damingshanica*, is temporarily placed in the Tristachya clade.

Table 2. Morphological characters distinguishing *Carex damingshanica* from *C. breviscapa* and *C. rhynchachaenium*.

Characters	*C. damingshanica*	*C. breviscapa*	*C. rhynchachaenium*
1. Spikes	3 or 4, aggregated	Many, 3–5 at each node	3–6
2. Lateral spikes	Pistillate, cylindrical, 4–13 mm long	Pistillate or mostly with male part at apex, narrowly cylindric, 3–4.5 cm long	Pistillate, shortly cylindric, 1–2 cm long
3. Pistillate glume	Ovate,1–1.2 mm long, apex acuminate	Ovate-oblong, 2.5–3 mm long, apex rounded	Oblong-elliptic, apex truncate-rounded, occasionally mucronate
4. Utricle	Narrowly fusiform, obtusely trigonous, 2.5–3 mm long	Rhombic-fusiform, trigonous, 3.5–5 mm long	Lageniform with weak constriction at middle, 5–6.5 mm long
5. Nutlet	Narrowly ovoid, 1.5–1.9 mm long	Rhombic-ovoid, 2.5–3 mm long	Rhombic-ovoid, ca. 4 mm long

3. *Carex radicalispicula* Tang & F.T.Wang ex Y.F.Lu & X.F.Jin, sp. nov.

urn:lsid:ipni.org:names:77318325-1

Fig. 4A–G

Diagnostic description. This new species is similar to *Carex truncatirostris* S.W.Su et S.M.Xu, but differs in having staminate spikes clavate, 1.5–2 mm wide, pistillate glumes pale yellow-white, 3–3.2 mm long, acuminate or short-awned at apex, nutlets with 3 angles shallowly constricted at middle.

Type. China. Sichuan: Kangding County, Erdaoqiao, on roadside, alt. 2650 m, 26 May 1940, *K. L. Chü 6963* (holotype: PE!; isotypes: IBSC0654521!, PE!).

Description. Perennial herbs. Rhizomes short, woody. Culms central, loosely turfed, 8–30 cm tall, slender, trigonous, smooth, base with grey-brown sheaths. Leaves shorter than or rarely equal to culms, blades 1.5–2 mm wide, flat, leathery, scabrous on margins. Lowermost bract leaf-like, others setaceous, base with 4–6 mm long sheath. Spikes 3 or 4; terminal spike staminate, clavate, (5–)9–12 mm long, 1.5–2 mm wide; lateral spikes pistillate, with the lowermost arising from the base of culms, shortly cylindrical or cylindrical, 7–15 mm long, 3.5–4 mm wide, 4–12-flowered, with the lowermost peduncle slightly exserted from the sheath. Staminate glumes elliptic-lanceolate, yellow-brown, 4.5–5.5 mm long, apex obtuse, with 1-veined yellow costa. Pistillate glumes broadly ovate, pale yellow-white, 3–3.2 mm long, apex acuminate or with a ca. 0.5 mm long scabrous awn, with 3-veined green costa. Utricles yellow-green, rhombic-ovoid, obtusely trigonous, ca. 3.8 mm long, ca. 1.3 mm wide, longer than pistillate glumes, membranous, obliquely patent, distinctly thinly veined, sparsely pubescent, base gradually cuneate, short-stipitate, apex gradually contracted into a 0.8–1 mm long beak, orifice 2-lobed with short teeth. Nutlets tightly enveloped, pale yellow, rhombic-ovoid, trigonous, ca. 2.5 mm long, with 3 angles shallowly constricted at middle, lateral sides slightly concave above and below, base shortly curved-stipitate, apex abruptly contracted into a discoid-annulate style-base; style base thickened; stigmas 3.

Etymology. The specific epithet '*radicalispicula*' refers to the lowermost spike arising from the base of culm.

Phenology. Flowering and fruiting occur in late May.

Conservation status. Least Concern (LC). The new species was collected by Kuei-Ling Chü (*K. L. Chü 6963*) from the type locality, including two sheets deposited in PE and one in IBSC. The authors carried out a field trip to the type locality in 2019, but failed to locate and collect any similar specimens. The type locality has been disturbed and the quality of the habitat appears to be continuously declining now (IUCN 2019).

Notes. With rhombic-ovoid nutlets abruptly contracted into a discoid-annulate style-base at the apex, 3 angles constricted at the middle, and the lowermost spike arising from a culm base, *Carex radicalispicula* is similar to *C. truncatirostris*. A taxonomic revision of *C. chungii* Z.P.Wang and the allied species has been conducted (Jin 2017), and these very closely related species can be distinguished from each other using the following key.

1a Lowermost spikes exserted from the basal sheaths of culms; lowermost bract sheaths < 6 mm long **2a**
2a Terminal staminate spikes 1.5–2 mm wide; nutlets shallowly constricted at middle angles; pistillate glumes pale yellow-white, 3–3.2 mm long, acuminate or short-awned at apex .... ***Carex radicalispicula***
2b Terminal staminate spikes 0.6–1 mm wide; nutlets constricted at middle angles; pistillate glumes pale brown or yellow-brown, 2–2.5 mm long, emarginate or obtuse at apex .... ***Carex truncatirostris***
1b Lowermost spikes exserted from the middle sheaths of culms; lowermost bract sheaths > 1 cm long **3a**
3a Terminal spikes 1–3 cm long; pistillate glumes long-awned at apex; staminate glumes short-awned or mucronate at apex .... ***Carex chungii***
3b Terminal spikes 3.5–6 cm long; pistillate glumes mucronate at apex; staminate glumes acute at apex .... ***Carex nanpingensis***

Figure 4. *Carex radicalispicula* sp. nov. **A** habit **B** lowermost spike **C** staminate glume **D, E** pistillate glume **F** utricle **G** nutlet. (Drawn by Xiao-Feng Jin; based on the holotype: *K. L. Chü 6963* in PE).

The new species is closed to *Carex truncatirostris*, and the species have nutlets apex abruptly contracted into a discoid-annulate style-base which were divided into two clades in the recent phylogenetic scaffold for the *Carex* classification (Roalson et al. 2021). The species in the Mitrata Clade have shorter lateral spikes and smaller plants, and the new species is temporarily placed in the Mitrata clade.

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RESEARCH ARTICLE

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Parallel developments in floral adaptations to obligate moth pollination mutualism in tribe Phyllantheae (Phyllanthaceae)

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Abstract

Several groups within tribe Phyllantheae (Phyllanthaceae) formed, independently, an (obligate) pollination mutualism with *Epicephala* moths, which originally had been parasitic. In this pollination system, female moths actively collect pollen from staminate flowers and deposit it on the stigma of pistillate flowers, after which they place at least one egg in or against the ovary. The high pollination rate makes the system beneficial for the plants, whereas the larvae are provided with food (part of the developing seeds) and some protection against predation. Qualitative comparisons are made between non-moth-pollinated lineages, used as outgroups and various, independently moth-pollinated Phyllantheae clades, used as ingroups, thereby looking for parallel developments. The flowers of both sexes of various groups display similar, convergent morphological adaptations to the pollination system, likely to secure the obligate relationship and to improve efficiency. Sepals in both sexes, free or partly to highly connate, are commonly upright and form a narrow tube. The staminate flowers often have united, vertical stamens with the anthers along the androphore or on top of the androphore. Pistillate flowers generally reduce the stigmatic surface, either by making the stigmas shorter or by uniting them into a cone with a small opening at the top for pollen deposition. Less obvious is the reduction of the stigmatic papillae; these are often present in non-moth-pollinated taxa, but absent in the moth-pollinated species. The most diverging, parallel adaptations to moth pollination are currently found in the Palaeotropics, whereas in the Neotropics, some groups continue to also be pollinated by other insect groups and are morphologically less changed.

Keywords
Breynia, *Cicca*, *Dendrophyllanthus*, *Epicephala* moths, *Glochidion*, *Kirganelia*, morphological adaptation, *Phyllanthus*

Introduction

Obligate pollination mutualisms between insects and plants have developed in several plant families and they provide interesting study systems for reciprocal morphological evolution and adaptation between the partners. Kato and Kawakita (2017, chapter 13) provide a nice overview of the various plant groups and their pollinators. Three examples where the relationship between both parties is obligate and where a proliferation of co-speciation occurred, are famous: figs and fig-wasps, *Yucca* L. and *Yucca* moths and leafflower and leafflower moths (Kato and Kawakita 2017). The latter group forms the main topic of this paper, particularly tribe Phyllantheae Dumort. (Hoffmann et al. 2006). The tribe mainly consists of the large (paraphyletic) *Phyllanthus* L. (Wurdack et al. 2004; Samuel et al. 2005; Kathriarachchi et al. 2005, 2006), a clade that also includes *Breynia* J.R.Forst. & G.Forst., *Glochidion* J.R.Forst. & G.Forst. and *Synostemon* F.Muell.

Kato et al. (2003) were the first to report the obligate pollination mutualism between the Phyllanthaceae plants (genus *Glochidion*) and the *Epicephala* moths. Most active research on this relationship was done by Kawakita and Kato and their results are summarised in their book (Kato and Kawakita 2017). It is now obvious that the relationship between Phyllantheae and moths originated at least six times independently (Kawakita and Kato 2009), which is confirmed by the phylogeny of Bouman et al. (2021), see the (partly) red-boxed groups in Fig. 1A, likely also several times in the genus *Phyllanthus* (Fig. 1B, see also Discussion). The morphology of staminate and pistillate flowers changed and adapted accordingly (for example, see Zhang et al. (2012); Yang and Li (2018)). The female moths of mutualistic species actively collect pollen from staminate flowers, whereby the sensilla or setae (hairs) on the proboscis sweep up the pollen (these hairs are absent in male moths and in (cheating) moths with no mutualistic relationship; Kato and Kawakita (2017); Yang and Li (2018); Wang et al. (2020)). The female moths then place the pollen on the stigmas of the pistillate flowers and finally place an egg either between the calyx and the ovary, or in the ovary by drilling through the stigma or through the ovary wall (Kato et al. 2003). This system provides the plants with a (usually) specific pollinator and, in return, the moths gain shelter and food for the developing larvae, which feed on some of the developing seeds. Seed consumption is variable and indicative of variations in the relationship between plant and pollinator; in some cases, only some of the seeds are consumed, while in others all can be eaten (Zhang et al. 2012).

Epicephala belongs to the family Gracillariidae, a family of micro-lepidoptera with ca. 100 genera and 2000 species (see Kato and Kawakita (2017): chapter 5, for a good overview and references). Most of them are leaf miners, which sometimes create galls. A few are plant-borers that attack seeds or other parts of the plant. *Epicephala* is part

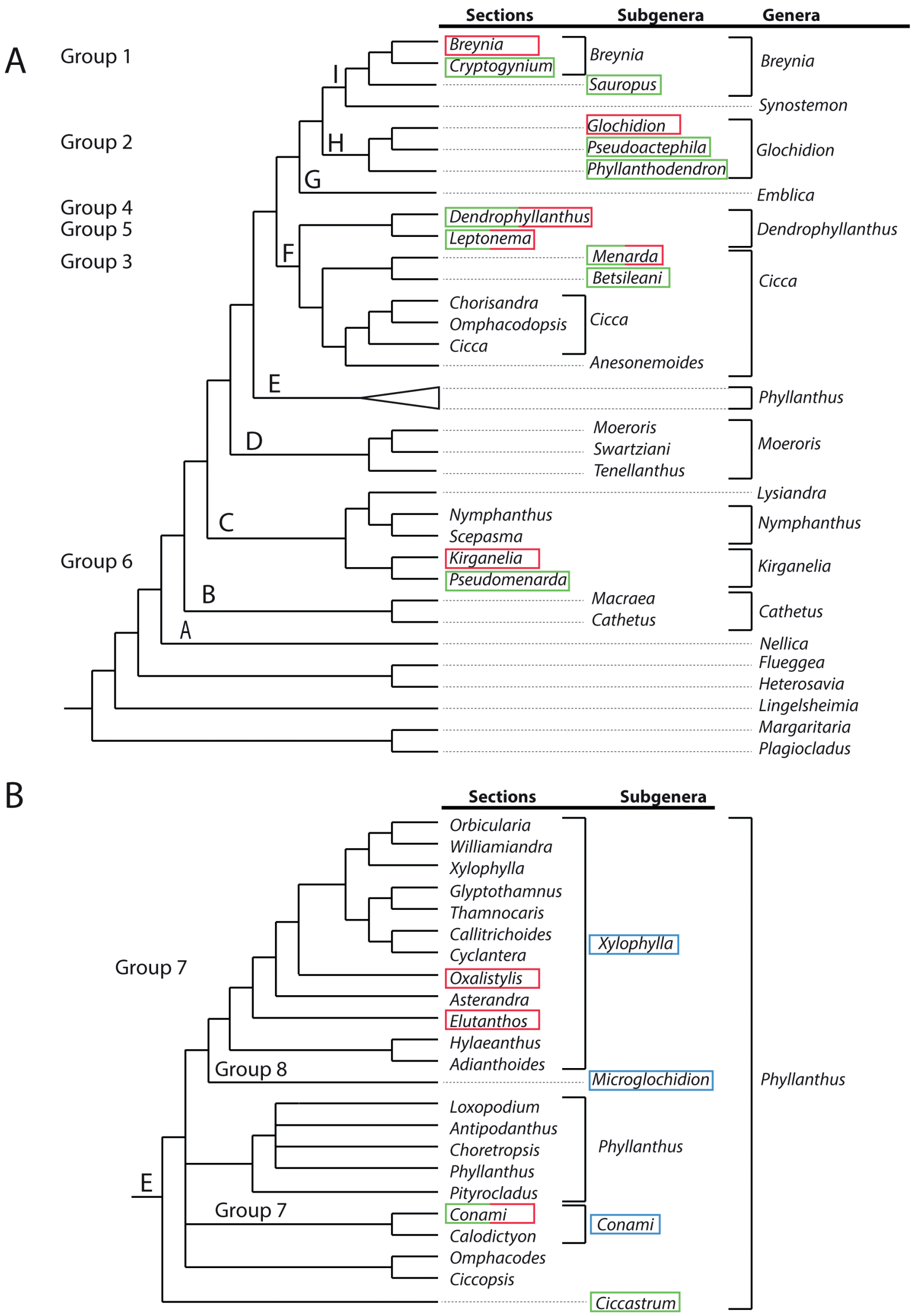

Figure 1. Summary of the Bayesian phylogeny and new classification of tribe Phyllantheae, based on the markers ITS, PHYC, *accd*, *trnSG* and matK; Bouman et al. (2022)) **A** the new classification runs from right to left **B** shows the detail of the classification and phylogeny of *Phyllanthus* L. Red boxes in **A** indicate the six groups with moth pollination; in green are the clades used as outgroups with which they are morphologically compared. Boxes with green and red represent clades with first splitting off the non-moth-pollinated species and in the top part of the clade the moth-pollinated ones. In blue boxes (**B**), two South American groups in *Phyllanthus* are highlighted, which, based on morphology, might also have moth pollination.

of the generally parasitic leaf-borer group, which has been found to occur also in tribe Phyllantheae (Luo et al. 2011). The phylogeny of *Epicephala* (Kato and Kawakita 2017: fig. 5.3) shows (disputably) *Conopomorpha flueggella* Li, 2011, as outgroup to the *Epicephala* clade. The first group to split off is the New Caledonian group (Kato and Kawakita 2017: fig. 5.3: clade 7). The species in this group are still seed parasites (like *C. fluegella*) (Hu et al. 2011) and lack the sensilla and ovipositor. The species in the remaining six clades have sensilla and an ovipositor and developed the mutualistic pollination syndrome. The exception is clade 2 (Kato and Kawakita 2017: fig. 5.3), where the moths returned to parasitism in the herbaceous *Phyllanthus* species. *Conopomorpha* and clade 7 (Kato and Kawakita 2017: fig. 5.3) are still seed predators, whereby seeds possibly survive due to a high mortality rate amongst the larvae. *Conopomorpha flueggella* feeds on the seeds of *Flueggea* Willd. *Flueggea* is sister to *Phyllanthus* sensu lato (Wurdack et al. 2004; Bouman et al. 2021) and did not develop pollination mutualism. *Flueggea* has very open flowers, whereas the moth-pollinated species generally show more closed flowers. Similarly, seed predation has only been found in developing fruits in species of *Phyllanthus* subgenus *Macraea* (Wight) Jean F.Brunel and not in flowers that were yet to be pollinated, which suggests a solely parasitic relationship (Kato and Kawakita 2017). With *Breynia* and (former) *Sauropus* Blume (now subsumed in *Breynia*), it was obvious that both genera were distinguished because of morphological differences in the flowers, seemingly caused by moth pollination (van Welzen 2003). A similar difference seems to be present between *Glochidion* and *Phyllanthus* subgen. *Phyllanthodendron* (Hemsl.) G.L.Webster.

The aims of this paper are: 1. to show the qualitative morphological changes in the various flowers of the different plant groups associated with the pollination mutualism by *Epicephala* moths in comparison with their non-mutualistic relatives and 2. to see if there are parallel developments in the morphological adaptations of the (confirmed) six different groups of plants that are now pollinated by the moths, with also a consideration of possibilities in the New World.

Materials and methods

Kawakita and Kato (2009: fig. 3) listed six independent origins of obligate moth pollination and these groups will be treated here (sequence as in Kawakita and Kato (2009)). For each group, simple qualitative descriptions or comparisons are provided of the general type of staminate and pistillate flowers. The species selected are those mentioned either by Kawakita and Kato (2009) or by Bouman et al. (2021) in the new phylogeny of the Phyllantheae. Qualitative descriptions of staminate and/or pistillate flowers were made if specimens were available in the herbarium material of Naturalis Biodiversity Center (L, U and WAG in Index Herbariorum, http://sweetgum.nybg.org/science/ih/), but for many species, specimens were lacking or they were too poor to be used or they only showed one sex. The flowers in the moth-pollinated taxa (red-boxed in Fig. 1) are compared with taxa in their sister group (green-boxed in Fig. 1) to observe possible morphological changes in flowers, likely induced by the moth pollination. The groups treated here are all Old World taxa. In a more recent paper, Kawakita et al. (2019) also demonstrated moth pollination in the New World (Fig. 1B), so these taxa, blue-boxed in Fig. 1, are discussed as well.

The genus *Phyllanthus* in its present circumscription is paraphyletic because *Breynia* (including *Sauropus*), *Glochidion* and *Synostemon* are part of it. Two views exist, either to include the four genera into one large genus (e.g. Hoffmann et al. (2006)) or to subdivide *Phyllanthus* in smaller, recognisable genera (e.g. van Welzen et al. (2014)). The latter option has now become feasible with a phylogeny based on a much larger sampling (Bouman et al. 2021). In the rest of the text, we will present the current names and the new classification of Bouman et al. (2022) with the newly-proposed names. Fig. 1 shows the new classification and simplified phylogeny of tribe *Phyllantheae* (Bouman et al. 2022). Table 1 shows the names in *Phyllanthus* as used by Kawakita and Kato (2009) and the new names according to Bouman et al. (2022).

The terms style and stigma need some explanation as these are sometimes used differently. The style is the united part (of the stigmas) on top of the ovary, it can be present (Fig. 2b) or absent (Fig. 3c). The stigmas are the split part. There are usually three stigmas, which, at the end, usually split into two short lobes. The stigmatic tissue, the part receiving the pollen, is often the papillate part on the adaxial side of the stigmas (Figs 3c, 12b). However, in various species, these are absent (e.g. Fig. 14b) and, therefore, the three arms are considered as stigmas. This is concordant with the use of the terms in the Flora Malesiana revisions of the Euphorbiaceae s.l. (including Phyllanthaceae): www.nationaalherbarium.nl/euphorbs/.

Results

The general flower type in the Phyllantheae shows usually six sepals (in two whorls of three), a nectar disc (annular or consisting of three or six separate glands) and then either three or more stamens in the staminate flowers (free or variously connate; Fig. 2a) or an ovary with usually three locules with two ovules per locule and on top a short style branching into the stigmas (Fig. 2b). The latter are often split at the top (Fig. 5c). For each group, the possible changes in these organs are discussed and Table 2 shows short descriptions of both sexes of flowers for the species mentioned in the text and an indication whether or not they are (likely) moth-pollinated.

Breynia versus former *Sauropus* (Group 1 in Fig. 1A; Table 2)

Formerly, *Sauropus* (van Welzen, 2003) was a separate genus of which the species are not pollinated by moths. Based on phylogenetic analyses (Pruesapan et al. 2008, 2012) both genera had to be united under the oldest name *Breynia* (van Welzen et al. 2014). Former *Sauropus* is now divided over *Breynia* subgen. *Breynia* sect. *Cryptogynium* Welzen & Pruesapan and *Breynia* subgen. *Sauropus* Welzen & Pruespan (Fig. 1A).

Table 1. Groups and species with obligate pollination mutualism and parasitic pollination in Kawakita and Kato (2009) and Bouman et al. (2022).

Kawakita and Kato (2009)	Bouman et al. (2022)
Obligate Pollination Mutualism	
Goup 1: *Breynia* J.R.Forst. & G.Forst.	***Breynia* subgen. *Breynia* sect. *Breynia***
B. disticha J.R.Forst. & G.Forst.	idem
B. fruticosa (L.) Müll.Arg.	idem
B. olongifolia (Müll.Arg.) Müll.Arg.	idem
B. retusa (Dennst.) Alston	idem
B. vitis-idaea (Burm.f.) C.E.C.Fisch.	idem
Group 2: *Glochidion* J.R.Forst. & G.Forst.	***Glochidion* subgen. *Glochidion***
G. acuminatum Müll.Arg.	idem
G. lanceolatum Hayata	idem
G. obovatum Siebold & Zucc.	idem
G. rubrum Blume	idem
G. zeylanicum (Gaertn.) A.Juss.	idem
Group 3: *Phyllanthus* L. (no subgen., Madagascar)	***Cicca* L. subgen. *Menarda* (Comm. ex A.Juss.) R.W.Bouman**
P. humbertii (Leandri) Petra Hoffm. & McPherson	*C. humbertii* (Leandri) R.W.Bouman
P. marojejiensis (Leandri) Petra Hoffm. & McPherson	*C. marojejiensis* (Leandri) R.W.Bouman
Group 4: *Phyllanthus* L. subgen. *Gomphidium* (Baill.) G.L.Webster	***Dendrophyllanthus* S.Moore sect. *Dendrophyllanthus***
P. bourgeoisii Baill.	*D. bourgeoisii* (Baill.) R.W.Bouman
P. chamaecerasus Baill.	*D. chamaecerasus* (Baill.) R.W.Bouman
P. caudatus Müll.Arg.	*D. caudatus* (Müll.Arg.) R.W.Bouman
P. mangenotii M.Schmid	*D. mangenotii* (M.Schmid) R.W.Bouman
Group 5: *Phyllanthus* L. subgen. *Gomphidium* (Baill.) G.L.Webster	***Dendrophyllanthus* S.Moore sect. *Leptonema* (Baill.) R.W.Bouman**
P. aeneus Baill.	*D. aeneus* (Baill.) R.W.Bouman
P. gneissicus S.Moore	*D. gneissicus* (S.Moore) R.W.Bouman
P. guillauminii Däniker	*D. guillauminii* (Däniker) R.W.Bouman
P. vulcani Guillaumin	*D. vulani* (Guillaumin) R.W.Bouman
Group 6: *Phyllanthus* L. subgen. *Kirganelia* (A.Juss.) Kurz	***Kirganelia* A.Juss. sect. *Kirganilia***
P. reticulatus Poir.	*K. reticulata* (Poir.) Baill.
P. sp.	*K.* sp.
Parasitic pollination	
***Phyllanthus* L. subgen. *Swartziani* (G.L.Webster) Ralim. & Petra Hoffm.**	***Moeroris* Raf. subgen. *Swartziani* (G.L.Webster) R.W.Bouman**
P. amarus Schumach. & Thonn.	*M. amara* (Schumach. & Thonn.) R.W.Bouman
	***Emblica* Gaertn.**
P. lepidocarpus Siebold & Zucc. (= *P. urinaria* L.)	*E. urinaria* (L.) R.W.Bouman
***Phylanthus* L. subgen. *Isocladus* G.L.Webster** **(must be subgen. *Macraea* (Wight) Jean F.Brunel)**	***Cathetus* Lour. subgen. *Macraea* (Wight) R.W.Bouman**
P. ussuriensis Rupr. & Maxim.	*C. ussuriensis* (Rupr. & Maxim.) R.W.Bouman

Both genera were formerly separated because of the strong differences in floral morphology in both sexes. The flowers of both sexes in former *Sauropus* are usually flat, open and disc-like. The staminate flowers (Fig. 3a) have six sepals, basally to almost completely united; they lack nectar glands, but (usually) have scales inside, which are

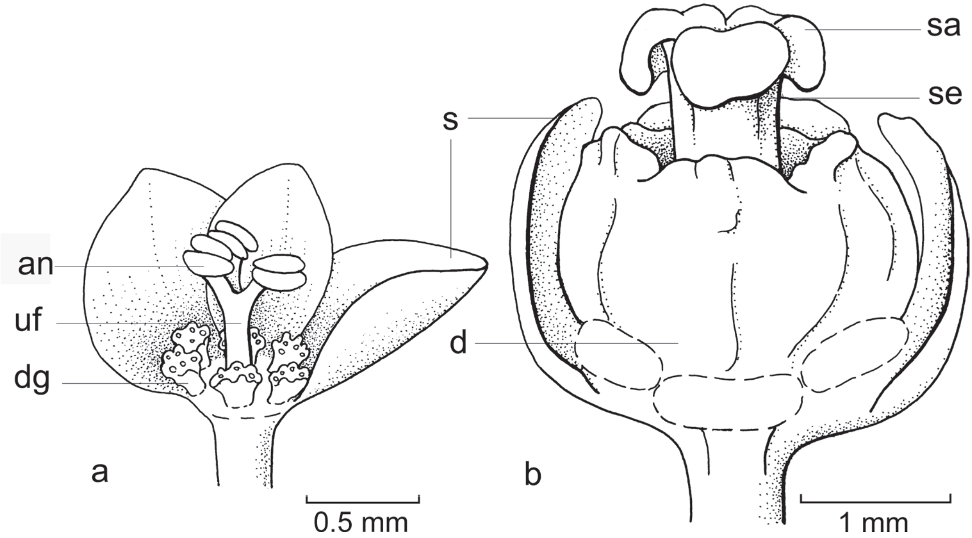

Figure 2. General flower characters of Phyllantheae **a** staminate flower of *Moeroris debilis* (Klein ex Willd.) R.W.Bouman (formerly *Phyllanthus debilis* Klein ex Willd.) (re-used with permission, Flora of Thailand 8, 2: fig. 54B2. 2007) **b** pistillate flower of *Cathetus gracilis* (Hassk.) R.W.Bouman (formerly *P. albidiscus* (Ridl.) Airy Shaw); part of sepals of both flowers removed (re-used with permission, Flora of Thailand 8, 2: fig. 55A2. 2007); an = anther; d = disc; dg = disc glands; s = sepals, sa = stigma; se = style; uf = united filaments (**a** *Maxwell 97-915* **b** *Shimizu et al. T-26280*; both in L). Illustrations by Anita Walsmit Sachs, 2007.

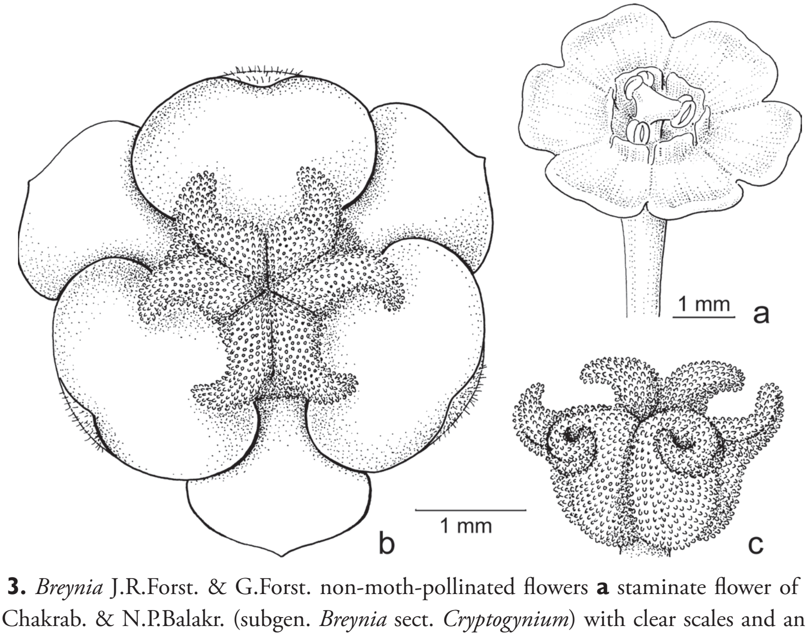

Figure 3. *Breynia* J.R.Forst. & G.Forst. non-moth-pollinated flowers **a** staminate flower of *B. bicolor* (Craib) Chakrab. & N.P.Balakr. (subgen. *Breynia* sect. *Cryptogynium*) with clear scales and androecium (re-used with permission, Flora of Thailand 8, 2: fig. 72F. 2007). – *B. lithophila* Welzen & Pruesapan (subgen. *Sauropus*) **b** pistillate flower **c** gynoecium with papillae (re-used with permission: Thai Forest Bulletin (Botany) 38: 116, fig. 3. 2010) (**a** *Maxwell 96-712* **b** *Phonsena*, *Chusithong*, *de Wilde & Duyfjes 5594*; both in L). Illustrations by: **a** Jan van Os, 2002 **b, c** Anita Walsmit Sachs, 2009.

probably transformed disc glands. The scales keep the flower closed when the stamens are still immature. The filaments of the three stamens are basally united into a column, but at the top they form three, ± horizontal, free arms with the anthers underneath. The ovary of the pistillate flowers (Fig. 3b) has a flat top, on which there are three, well-developed stigmas that are usually flat and split at the apex and resemble a crescent-moon with papillae to catch pollen (Fig. 3c). Exceptions are that, in some species, the stigmas are erect and, in some, the staminate flowers lack the scales, but instead they have three sepals that are folded inwards and the stamens are enlarged and point diagonally upwards. The potential pollinators of these '*Sauropus*-flower' species have not yet been elucidated by any study.

Breynia subgen. *Breynia* sect. *Breynia* (Fig. 1A) is pollinated by moths (Kawakita and Kato 2004b, 2009). The staminate flowers are narrow and campanulate, with united sepals forming a tube, with the disc scales on the top inside (sometimes the sepal lobes are reduced to a thickened ring and the scales resemble the calyx lobes; Fig. 4a). Within the tube, three stamens are united into a massive stalk (androphore) with the anthers orientated vertically along it (Fig. 4b). The pistillate flowers are less open than in former *Sauropus*, but the main difference is in the stigmas. The style is lacking and the stigmas are greatly reduced in size, sometimes completely split (Fig. 4c). In some species, there are six short vertical stalks on top of the ovary without any stigmatic papillae. Only two species in this section, *B. fruticosa* (L.) Müll.Arg. and *B. glauca* Craib (Fig. 4), still have larger stigmas, but these are not united in a style.

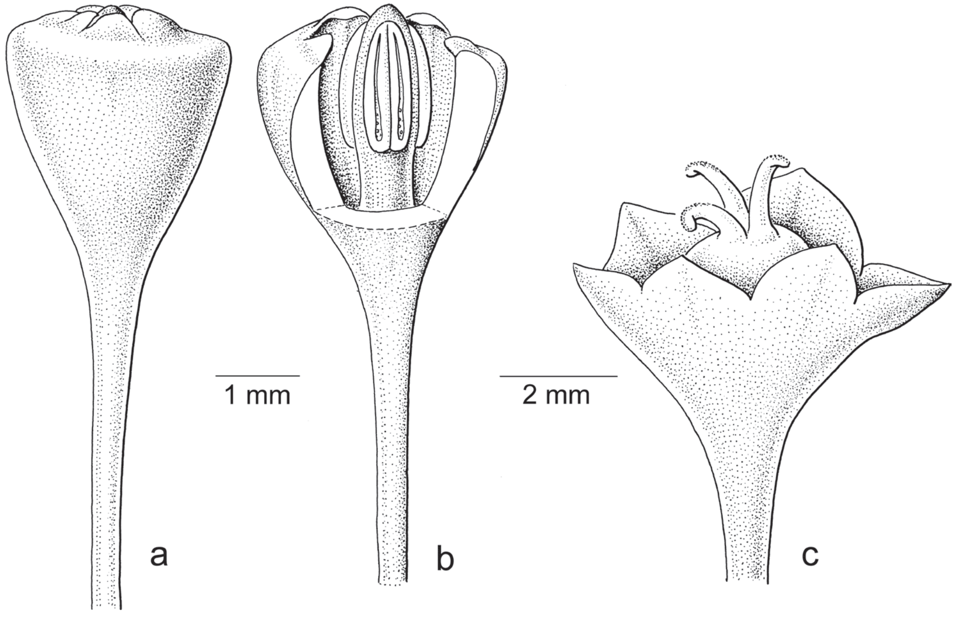

Figure 4. *Breynia glauca* Craib **a** staminate flower with scales slightly upright, calyx lobes reduced to thickened ring **b** idem with part of calyx removed, showing androecium **c** pistillate flower with three entire stigmas, style absent. Illustrations by Jan van Os, 2002. Re-used with permission of the Flora of Thailand (Flora of Thailand 8, 1: fig. 30B–D. 2005).

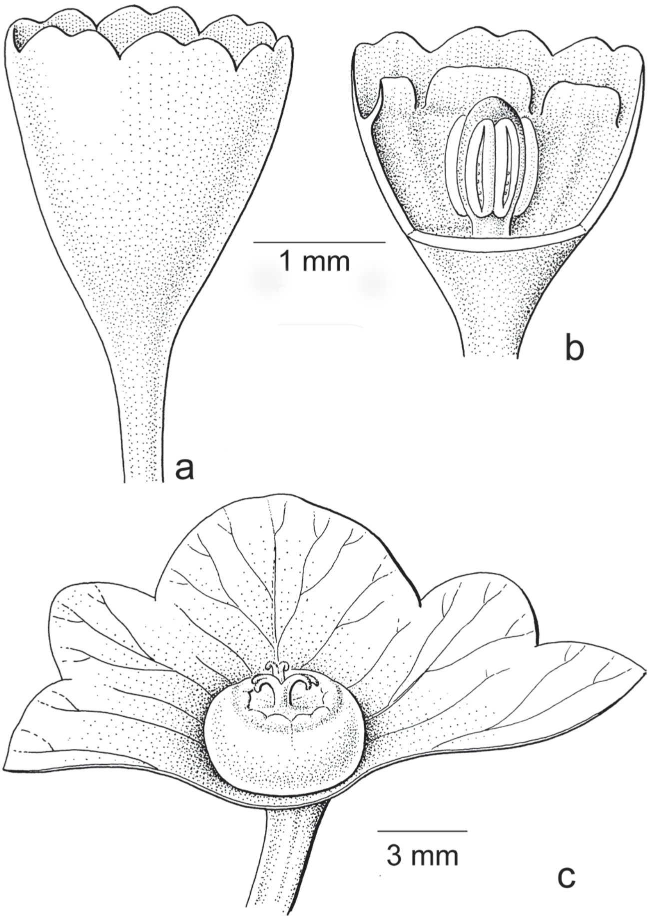

Figure 5. *Breynia retusa* (Dennst.) Alston **a** staminate flower **b** idem, part of calyx removed, androecium and scales visible **c** pistillate flower with part of calyx removed, distinct style and branching stigmas visible. Illustrations by Jan van Os, 2002. Re-used with permission of the Flora of Thailand (Flora of Thailand 8, 1: fig. 29A, B, D. 2005).

Furukawa and Kawakita (2017) showed that a gynophore (of variable length) often develops after fruit set in *B. officinalis* Hemsl. on Amami-Oshima Island (Ryukyu Islands, Japan), also mentioned by Zhang et al. (2012), which likely precludes overconsumption by *Epicephala vitisidaea* Li, Wang & Zhang, 2012, as the larvae have to eat their way up through the gynophore (unfortunately, they used the name *B. vitis-idaea* (Burm.f.) C.E.C.Fisch., a species not present in the Ryukyu Islands and southern China and which definitely lacks a gynophore; see van Welzen and Esser (2005)).

Seemingly, in comparison to the outgroup, the flowers in the ancestral species of sect. *Breynia* evolved in response to moth pollination: the staminate flowers became closed, campanulate and, inside, the anthers became vertical with united stamens (Fig. 4a, b); in the pistillate flowers, the stigmas are strongly reduced (Fig. 4c). *Breynia retusa* shows a reversal towards a normal style and stigma (Fig. 5c), thus likely this species underwent a host switch. Kato and Kawakita (2017: table 6.1) recorded that *B. retusa* is not pollinated by *Epicephala* moths, but the (new) pollinators are unknown. The staminate flowers of *B. retusa* are rather narrow (Figs. 5a, b), but more open than other flowers of the moth-pollinated species.

Stigmatic papillae are often present in *Breynia* subgen. *Breynia* sect. *Cryptogynium* and *Breynia* subgen. *Sauropus* (Fig. 2c), but absent or strongly reduced in *Breynia* subgen. *Breynia* sect. *Breynia* (Fig. 4). The disappearance of the papillae may be another adaptation to moth pollination.

Glochidion versus former *Phyllanthus* subgenus *Phyllanthodendron* (Group 2 in Fig. 1A; Table 2)

A similar situation as with *Breynia* occurred in these two groups. Former *Phyllanthodendron* Hemsl. (or *Phyllanthus* subgenus *Phyllanthodendron* (Hemsl.) G.L.Webster) is presently split into *Glochidion* subgen. *Phyllanthodendron* (Hemsl.) R.W.Bouman and *G.* subgen. *Pseudoactephila* (Croizat) R.W.Bouman. These two taxa are not moth-pollinated (Fig. 1A; Kato and Kawakita (2017)). The staminate flowers of former *Phyllanthodendron* are rather open, with five or six basally connate sepals with an attenuate apex (Fig. 6a, b), the disc glands are often large and somewhat petal-like, the generally three stamens have connate filaments and diverging upper parts and the connectives

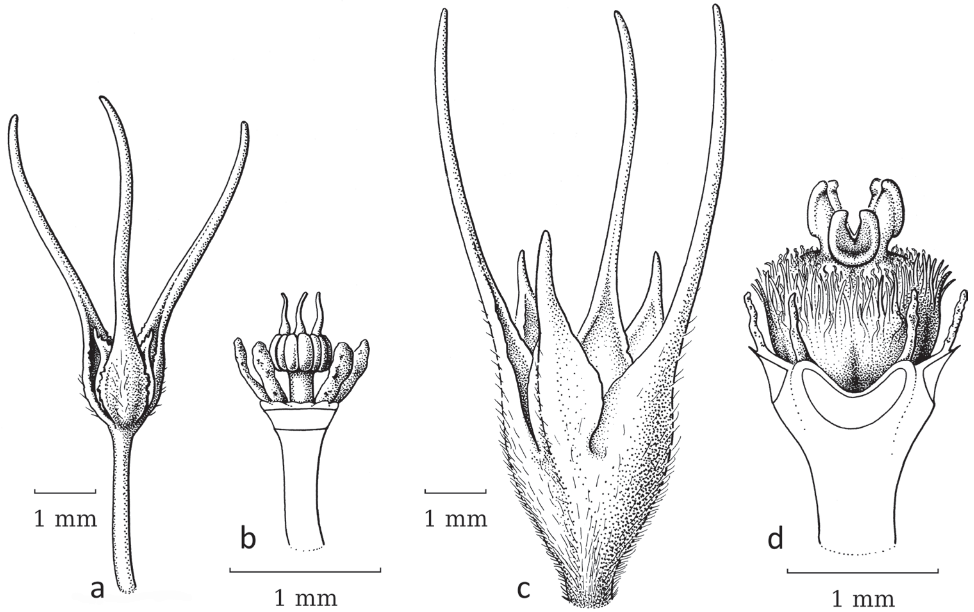

Figure 6. *Glochidion minutiflorum* (Ridl.) R.W.Bouman (formerly *Phyllanthus* (subg. *Phyllanthodendron*) *ridleyanus* Airy Shaw **a** staminate flower which has three outer sepals with elongated apices **b** idem, part of sepals removed, petaloid disc glands visible and stamens with appendices on the connectives **c** pistillate flower **d** pistillate flower with part of sepals removed, petaloid disc glands visible and hairy ovary with the stigmas on top (**a, b** *Kiew & Anthonysamy 2977* **c, d** *Stone 9494*; both L). Illustrations by Esmée Winkel, 2021.

have an apical appendage. The pistillate flowers (Fig. 6c, d) have similar sepals and disc glands as the staminate flowers and on top of the ovary are well-developed stigmas (often with a short style) that are apically entire or shortly bifid.

In subgenus *Glochidion*, which is moth-pollinated, flowers of both sexes lack a disc. The staminate flowers (Fig. 7a) are campanulate and the androecium resembles that of *Breynia* (Fig. 5b) as the filaments are vertical and tightly together with the anthers along them and the connectives have apical appendages that form a pyramidal cone. When wilting, the stamens start to detach from each other and bend outwards and then resemble the stamens of the staminate flowers in *Glochidion* subgenera *Phyllanthodendron* and *Pseudoactephila*. In the pistillate flowers (Fig. 7b, c), the stigmas are upright and united into a cone terminating in the often slightly split apices of the stigmas that form a cavity in the middle where the female moth deposits the pollen (Fig. 7b, c).

As with the first group (*Breynia*, including former *Sauropus*), the differences in flower morphology led to this group being separated into two genera. Based on the phylogeny (Bouman et al. 2021) and the resulting new classification (Bouman et al. 202), both former genera are now united under *Glochidion* (*Phyllanthodendron* was paraphyletic and *Glochidion* is the older name). The staminate flowers in subgenus *Glochidion* (Fig. 1A) are narrower than in the other two subgenera with more strongly united stamens and the connective appendages touching, while in the pistillate flowers, the stigmatic surface is reduced by uniting the stigmas into an erect pyramidal structure. In both sexes, the disc/disc glands are gone, as seemingly the moths do not need a nectar stimulus. As in *Breynia*, there is one *Glochidion* species, *G. sericeum* (Blume) Zoll. & Moritzi, showing a reversal, not in the staminate flowers (Fig. 8a, b) but in the pistillate flowers, where a well-developed style (covered by the sepals) with free, spreading stigmas is present (Fig. 8c, d); Kato and Kawakita (2017: fig. 10.2) did not record any *Epicephala* moth on this species.

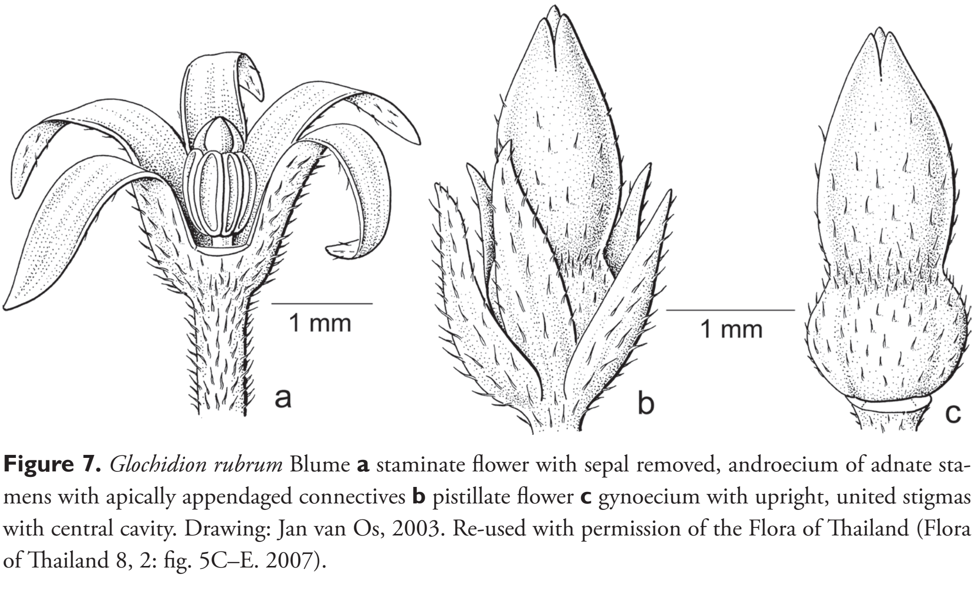

Figure 7. *Glochidion rubrum* Blume **a** staminate flower with sepal removed, androecium of adnate stamens with apically appendaged connectives **b** pistillate flower **c** gynoecium with upright, united stigmas with central cavity. Drawing: Jan van Os, 2003. Re-used with permission of the Flora of Thailand (Flora of Thailand 8, 2: fig. 5C–E. 2007).

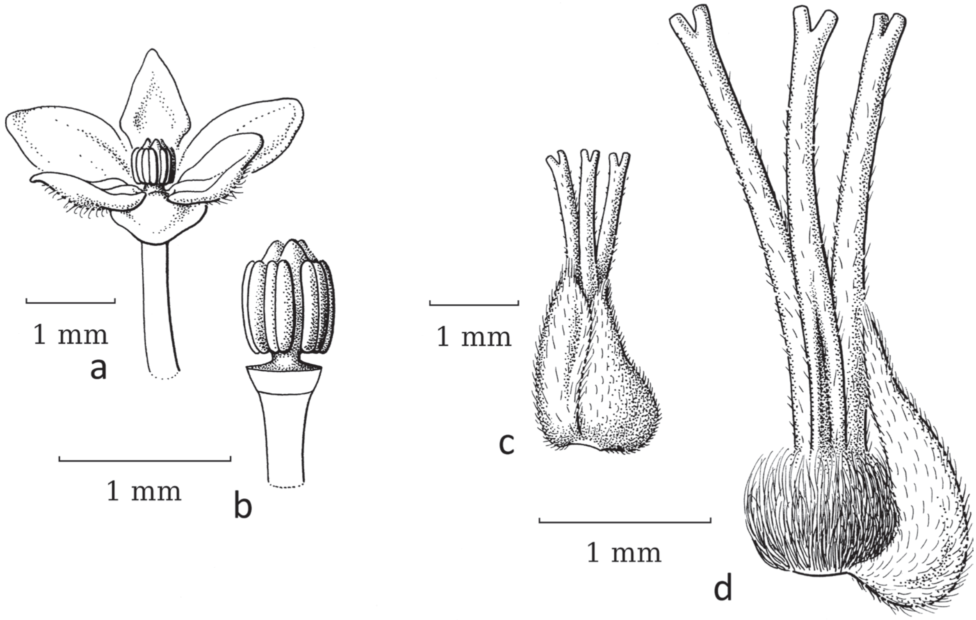

Figure 8. *Glochidion sericeum* (Blume) Zoll. & Moritzi **a** staminate flower **b** staminate flower with part of sepals removed, showing adnate stamens **c** pistillate flower with a reduced number (2) of sepals **d** pistillate flower with sepal removed showing well-developed style and stigmas (*Sinclair 10680*, L). Illustration by Esmée Winkel, 2021.

Cicca subgenus *Menarda* versus *Cicca* subgenus *Betsileani* (Group 3 in Fig. 1; Table 2)

Cicca L. is separated from *Phyllanthus* (Bouman et al. 2022) and restricted to a few subgenera, most of which are only found in Madagascar. Of the local outgroup, *Cicca* subgenus *Betsileani* (Jean F.Brunel) R.W.Bouman, only *C. betsileani* (Leandri) R.W.Bouman could be studied, a non-moth-pollinated species. Its flowers are open with six thin sepals; the staminate flowers have six disc glands and three free stamens; the pistillate flowers have a 3-locular ovary bearing terminal, well-developed, spreading stigmas that are split in the upper 2/3.

Cicca subgenus *Menarda* (Comm. ex A.Juss.) R.W.Bouman has staminate and pistillate flowers with 5(6) sepals; the staminate flowers have separate disc glands and three or five stamens; the pistillate flowers show a circular disc or separate disc glands and a 3-locular ovary (a revision and drawings can be found in Ralimanana and Cable (2020)). In Kato and Kawakita (2017), subgenus *Menarda* is represented by *Cicca humbertii* (Leandri) R.W.Bouman and *C. marojejiensis* (Leandri) R.W.Bouman (latter not included in this study) as being moth-pollinated. Various species of subgenus *Menarda* were investigated. Morphologically, *Cicca humbertii* (Leandri) R.W.Bouman, *C. perrieri* (Leandri) R.W.Bouman (Fig. 9) and *C. sambiranensis* (Leandri) R.W.Bouman have staminate flowers with (rather) stiff, upright sepals, making the flowers narrow and three united filaments with anthers vertically along the androphore in *C. humbertii*,

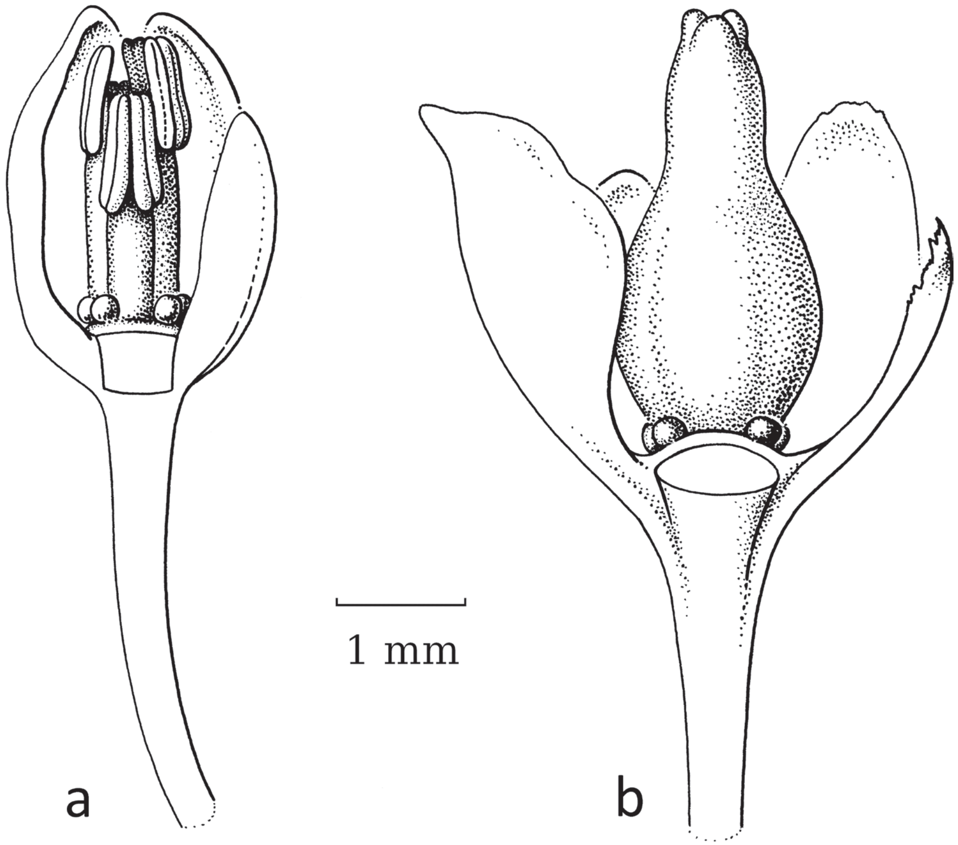

Figure 9. *Cicca perrieri* (Leandri) R.W.Bouman **a** staminate flower with part of sepals removed showing free, upright stamens **b** pistillate flower with part of sepals removed showing upright, united stigmas (*Gautier LG 3009*, WAG). Illustration by Esmée Winkel, 2021.

but five free stamens (Fig. 9a) in the other two species (at least close together in young flowers of *C. sambiranenensis*); the pistillate flowers have the stigmas united into an upright cone with a narrow opening between them (Fig. 9b).

Cicca coodei (Ralim. & Petra Hoffm.) R.W.Bouman and *C. cryptophila* (Comm. ex A.Juss.) R.W.Bouman, also in subgenus *Menarda*, have rather open staminate flowers with free stamens and the stigmas in the pistillate flowers are on a short style, but well-developed and spreading and clearly split halfway.

Unlike in the previous two groups, the switch to moth pollination resulted in less distinct differences in the flowers; therefore, the moth- and non-moth-pollinated species had not been divided into separate genera. In comparison to the former two groups, *C. betsileani*, *C. coodei* and *C. cryptophila* conform in their morphology to non-moth-pollinated with open flowers with either well-developed stigmas or free, spreading stamens. *Cicca cryptophila* is in the basal clade of subgenus *Menarda* (Bouman et al. 2022: suppl. fig. 1). The other three species, *C. humbertii*, *C. perrieri* and *C. sambiranensis*,

Table 2. Possible adaptations or lack of adaptations to moth pollination in staminate and pistillate flowers. Group refers to the groups as discussed in the text and in Fig. 1, I means Ingroup, O = local outgroup (related clade/taxon with which the ingroup is compared). The classification follows Bouman et al. (2022). Adapted: – = primitively not adapted to moth pollination; + = adapted to moth pollination, obs.+ = moth adaptation observed (Kawakita et al. 2019), but morphologically not adapted (morph.-); R = reversal to non-moth pollination.

Genus/Species	Infrageneric taxon	Group	Staminate flowers	Pistillate flowers	Adapted
Breynia	section *Breynia*	1-I	Tight, upright united sepals, with subapically scales closing flower when young; filaments upright, united, glands along androphore.	Sepals rather small or accrescent; disc and scales absent; stigmas reduced in length.	+
B. retusa	section *Breynia*	1-I	Idem, but flowers more open.	Idem; sepals not accrescent, stigmas well-developed, recurved.	R
Breynia	section *Cryptogynium*	1-O	Sepals partly to complete united, disc-like, scales present (idem); filaments united, splitting apically with anthers underneath (exceptions exist)	Sepals partly united, disc-like; scales absent; stigmas well-developed, separate, flat to ovary, apically split and recurved (exceptions exist)	–
	+ subgen. *Sauropus*	1-O			
Glochidion	subgen. *Glochidion*	2-I	Tight, upright sepals; no disc; stamens tightly upright, anthers along filament.	Sepals more or less upright; disc absent; stigmas united in cone.	+
		-			
G. sericeum	subgen. *Glochidion*	2I	idem.	2 small sepals; disc absent; stigmas well-developed, reflexed.	R
Glochidion	subgen. *Phyllanthodendron*	2-O	Sepals upright, more loose, long apex; large petal-like	Sepals more loose; disc glands present;	–
	+ subgen. *Pseudoactephila*	2-O	disc glands; filaments basally united, apically diverging, anthers separate.	stigmas well developed, free, reflecting.	
***Cicca** humbertii*	subgen. *Menarda*	3-I	Sepals upright, narrow inside, small disc glands, stamens vertically united, androphore sturdy, anthers vertically along it.	Sepals tight, no disc observed; stigmas forming cone with small opening.	+
C. perrieri		3-I	Sepals stiff, upright, disc glands small; stamens free.	Sepals tight, disc glands; stigmas forming cone with small opening.	+
C. sambiranensis		3-I	Sepals upright, not so stiff; disc glands; stamens tight when young, older free	Sepals stiff, thick, upright; disc glands; stigmas forming short cone	+
C. coodei		3-O	Open flowers; disc glands present, stamens free, diverging	Disc present; ovary with upright short style and three well-developed stigmas, split till halfway	–
C. cryptophila		3-O	Open flowers, disc glands present, stamens free	Disc present, ovary on short gynophore, upright short style, three well-developed spreading stigmas, split	–
C. betsilaeana	subgen. *Betsileani*	3-O	Sepals thin; disc glands; stamens free.	Sepals thin; disc circular; stigmas well-developed, spreading, largely apically split.	–
Dendrophyllanthus* sect. *Dendrophyllanthus					
D. aphanostyla	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas very short, cone-like, split, in circle	+
D. bourgeoisii	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas short, free, apically slightly split, in circle around opening	+
D. castus	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas upright, free, forming circle around opening	+
D. clamboides	sect. *Dendrophyllanthus*	4-I	sepals 6, ± equal, disc lobes 6, thick; stamens 3, united.	Sepals 6, large, inner broader; disc lobes 6, ovary 3-locular, on top style and three, upright, split stigmas in tight circle.	+
D. cuscutiflorus	sect. *Dendrophyllanthus*	4-I	Not seen	stigmas upright in small cone, apices split.	+
D. dzumacensis	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas short, free, forming cone, tips slightly bifid.	+

Genus/Species	Infrageneric taxon	Group	Staminate flowers	Pistillate flowers	Adapted
D. effusus	sect. *Dendrophyllanthus*	4-I	Sepals 6, big 2-lobed disc glands, three united stamens, stout androphore, 3 anthers upright, united.	Sepals 6, outer three smaller, disc ring-like, margin erose, ovary 3-locular, style long, stigmas, upright, in circle with opening in middle.	+
D. glochidioides	sect. *Dendrophyllanthus*	4-I	(bud) sepals 6, inner much larger, six disc glands, stamens 3, filaments united, apically split and diagonally upwards, stamens underneath.	Sepals 6, inner larger, six disc glands; ovary 3-locular, style long with on top united stigmas, upright, forming tight circle.	+
D. kostermansii	sect. *Dendrophyllanthus*	4-I	Three outer small sepals, three inner large, closing flower. Six disc glands, stamens erect, free, filaments with anther 3-locular, stigmas erect, forming circle, slightly along at abaxial side, connective appendiculate.	(young) Sepals 6 in two whorls, disc circular, ovary bilobed at apex.	+
D. mangenotii	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas free, narrow, upright, apically not split.	+
D. poumensis var. *poumensis*	sect. *Dendrophyllanthus*	4-I	Not seen	Stigmas forming connected high dome	+
D. rosselensis	sect. *Dendrophyllanthus*	4-I	(bud) sepals 6, outer narrower, Three large disc glands; stamens 3, filaments likely united.	Sepals 6, inner larger, disc ring-like; ovary 3-locular, apically with ring of erect stigmas, apically split.	+
D. buxoides	sect. *Dendrophyllanthus*	4-O	Not seen	Style sturdy, three well-developed, broad stigmas upright but slightly diverging	+/–?
D. caudatus	sect. *Dendrophyllanthus*	4-?	Not seen	Style stout, stigmas 3, long, free, very slender, apically not split, slightly curled inwards	+/–?
D. finschii	sect. *Dendrophyllanthus*	4-O	Not seen	Stigmas free, well-developed, apically split.	–
D. poumensis var. *longistylis*	sect. *Dendrophyllanthus*	4-O	Not seen	Stigmas separate	–
D. pancherianus	sect. *Dendrophyllanthus*	4-O	Not seen	Stigmas well-developed, bent backwards.	–
D. tabularis	sect. *Dendrophyllanthus*	4-O	Sepals 6, inner larger, three large disc glands, stamens 3, large, filaments united, anthers apiculate and large.	Sepals 6, inner larger, disc?, ovary 3-locular, stigmas well-developed, recurved, apically split	–
D. tenuirhachis	sect. *Dendrophyllanthus*	4-O	Not seen	Stigmas upright, well-developed, apically split	–
D. wilkesianus	sect. *Dendrophyllanthus*	4-O	Sepals 6, inner broader; disc gland 3, large; stamens 3, free, anthers short.	(young fruit) sepals 6, inner broader, disc glands 6, small, ovary 3-locular, stigmas well-developed	–
Dendrophyllanthus* sect. *Leptonema					
D. aeneus	sect. *Leptonema*	5-I	Not seen	Sepals 5, circular disc, ovary 3-locular, on top columnar stigma of which some spreading	+
D. ligustrifolius	sect. *Leptonema*	5-I	sepals 5, disc glands 5, stamens 3, free.	(young fruit): 3-locular, on top columnar style and stigma, apex not split; in fruit completely splitting.	+
D. favieri	sect. *Leptonema*	5-?	Sepals fleshy, 5, inner larger; disc ring-like, stamens 5, two free outer, three partly united inner.	Not seen	?
D. bupleuroides	sect. *Leptonema*	5-O	Not seen	Stigmas well-developed, spreading, not apically split	–
D. hypospodius	sect. *Leptonema*	5-O	Sepals 5, disc glands 5, free stamens, three inner longer than two outer.	Style short, stigmas well-formed, spreading, apically very slightly split/erose.	–
D. kanalensis	sect. *Leptonema*	5-O	Sepals 5, outer two smaller, bilobed disc glands; stamens five, filaments united, two outer, three inner.	Sepals 5, outer two smaller, disc narrow ring; ovary 3-locular, apically short spreading stigmas.	–

Genus/Species	Infrageneric taxon	Group	Staminate flowers	Pistillate flowers	Adapted
D. lacunarius	sect. *Leptonema*	5-O	Sepals 6, disc glands, 3 stamens, mainly free, upright.	Style short, stigmas well-developed, spreading, apically split, completely splitting in fruit.	–
D. loranthoides	sect. *Leptonema*	5-O	Not seen	Sepals 5/6, small, inner larger; disc glands large, 2-lobed; ovary 3-locular, spreading, sessile, well-developed stigmas, apically not split.	–
D. sauropodoides	sect. *Leptonema*	5-O	Sepals 5, disc glands five with kind of honey-comb structure on top, stamens 5, free, three central, all upright.	Style present; stigmas 3, well-developed, spreading, apically bifid.	–
D. serpentinus	sect. *Leptonema*	5-O	Disc ring-like; stamens 5, free, two outer, three inner.	Style short, stigmas well-developed, spreading, apically (seemingly) not split.	–
D. vulcani	sect. *Leptonema*	5-O	Sepals 5, outer two smaller, many disc glands, also inside stamen ring; stamens 5 in one whorl.	Sepals small, thick; disc inconspicuous; ovary 3-locular, stigmas 3, widely spreading, sessile, very slightly splitting apically.	–
***Kirganelia** reticulata*	section *Kirganelia*	6-I	Small, sepals thin, small disc glands, stamens in two whorls, outer free, inner filaments basally united	Small, sepals thin, small disc glands, ovary on top four or five short, apically slightly split stigmas, bent towards each other and forming a cone.	+
K. somalensis	section *Pseudomenarda*	6-O	Larger than former, five sepals, five disc lobes, five stamensin two whorls, outer two free, inner basally united.	Sepals 5, relatively large, open, ring disc, 5-locular ovary with short style and five horizontal well-developed stigmas apically split to 1/3	–
New World Herbaceous species					
Moeroris amara	subgenus *Swartziani*	-	Small, hanging down, open	Small, hanging down; stigmas short, well-developed, spreading.	–
Moeroris stipulata	subgenus *Moeroris*	-	Small, hanging down, open	Small, hanging down; stigmas short, well-developed, spreading.	–
Phyllanthus orbiculatus	sbg. *Conami* sct. *Apolepis*	-	Small, hanging down, open	Small, hanging down; stigmas short, well-developed, spreading.	–
Phyllanthus* subgenus *Ciccastrum					
P. purpusii	subgenus *Ciccastrum*	O	six sepals, outer three smaller, inner stiff and upright, forming narrow cylinder, disc glands, three united stamens with apically anthers along it.	Sepals 6, like staminate, ring-like disc; 3-locular ovary, short style, 3 spreading stigmas, recurved, apically split.	♂+ ♀–
P. riedelianus	subgenus *Ciccasrum*	O	Sepals 6, disc glands 6, stamens 3, upright, partly united, anthers free, slightly spreading.	Young fruit: sepals and disc glands caducous; ovary 3-locular, with three sessile free stigmas, bent upwards and towards each other (only fruit?)	–
Phyllanhus* subgenus *Conami* & *Xylophylla					
	subgenus *Conami*				
P. acuminatus	section *Conami*	7-O	Open, anthers pointing downward from filaments.	Open, stigmas well-developed, spreading over ovary, tips broadened and slightly split.	–
P. graveolens	section *Conami*	7-I	Open, stamens free, obliquely upright.	Open, stigmas short, well-developed and spreading over ovary	obs.+ morph.±
	subgenus *Xylophylla*				
P. huallagensis	section *Elutanthos*	7-I	In bud, sepals soft, stamens united, apically splitting anthers underneath.	sepals soft, stigmas well-developed, radiating horizontally.	obs.+ morp.–
P. salviifolius	section *Oxalistylis*	7-I	Open, soft sepals, stamens with horizontally bent anthers (opening downward)	Open, soft sepals, three stigmas spreading apices fan-like.	obs.+ morph.–
Phyllanthus* subgenus *Microglochidion					
P. duidae		8-I	Sepals 6, disc glands 6; stamens 3, free, large, erect.	Sepals 6; disc ring; gynophore short; ovary 3-locular, stigmas 3, united, at top 3-lobed	+

Genus/Species	Infrageneric taxon	Group	Staminate flowers	Pistillate flowers	Adapted
P. majus		8-I	not seen	Young: sepals 6; disc ring; ovary 3-locular, stigmas united (as thick as ovary), upright, cone-like, top-3 lobe, bent inside, each lobe bifid	+
P. pycnophyllus		8-I	Sepals 6, three large disc glands, three free large stamens.	Young: six sepals, disc likely present; ovary 3-locular, stigmas upright, grown together, small teeth around opening apically.	+
P. vacciniifolius		8-I	Sepals 6, inner larger; disc glands 3; stamens 3, basally united and attached to inner sepals, upright, most part free, connectives extended.	Pedicel strongly thickened apically and invaginated under sepals; sepals 6, small disc; ovary 3-locular, stigmas united, upright, 3-lobed at top, not split.	+
P. lediformis		8-O	Young; sepals 6; disc glands 3; stamens 3, free, erect, anthers long, seems that connective appendage is developing	Sepals 6; disc not seen, too poor material; ovary 3-locular, apically style splitting into three flat stigmas, broadened at apex.	–
P. maguirei		8-O	Sepals 6, spreading, top inrolled; disc glands 6; stamens 3, free, anthers on top bent downwards.	Not seen	–
P. myrsinites ssp. *myrsinites*			Sepals 6, weak, spreading; disc glands 6, stamens 3, free, on slightly higher receptacle.	Sepals 6, disc ring-like; ovary 3-locular, stigmas 3, well-developed, free, recurved over ovary, tips split.	–
P. neblinae			not seen	Older fruit: stigmas 3, well-developed, spreading, flat, apically split and divergent (like crescent-moon)	–
Phyllanthus* subgenus *Xylophylla* section *Epistylium					
P. axillaris	section *Epistylium*	n.a.-I	Buds too young	In bud: stigmas forming closed cone	+

are in higher clades. Their pistillate flowers are similar to those of the moth-pollinated subgenus *Glochidion* in the cone-like united stigmas. Their staminate flowers have narrow, stiff sepals, but differ in the degree of connation of the stamens.

As few species could be observed, it is not possible to show where in the *Cicca* group moth pollination started, but likely between the basal group (with *C. cryptophila*) and the upper clades (which partly form a trichotomy).

Due to the high similarity with the pistillate flowers of *Glochidion*, several of the species in *Cicca* were formerly described or transferred to *Glochidion* (see Leandri (1937); Hoffmann and McPherson (2003)), but generally differ in the presence of disc glands, which are absent in *Glochidion* (Table 2).

Dendrophyllanthus section *Dendrophyllanthus* (Group 4 in Fig. 1A, Table 2)

With this group, *Cicca betsileani* can serve as a non-moth-pollinated outgroup; see the previous group for a short description.

Dendrophyllanthus S.Moore sect. *Dendrophyllanthus* is a New Caledonian group that comprises moth- and non-moth-pollinated species (Table 2) based on the comparison with the outgroup. However, the staminate flowers were often not seen or were young and in bud. They do not present a clear picture of morphological adaptations. The stamens are generally erect and free to completely united (Table 2). The pistillate

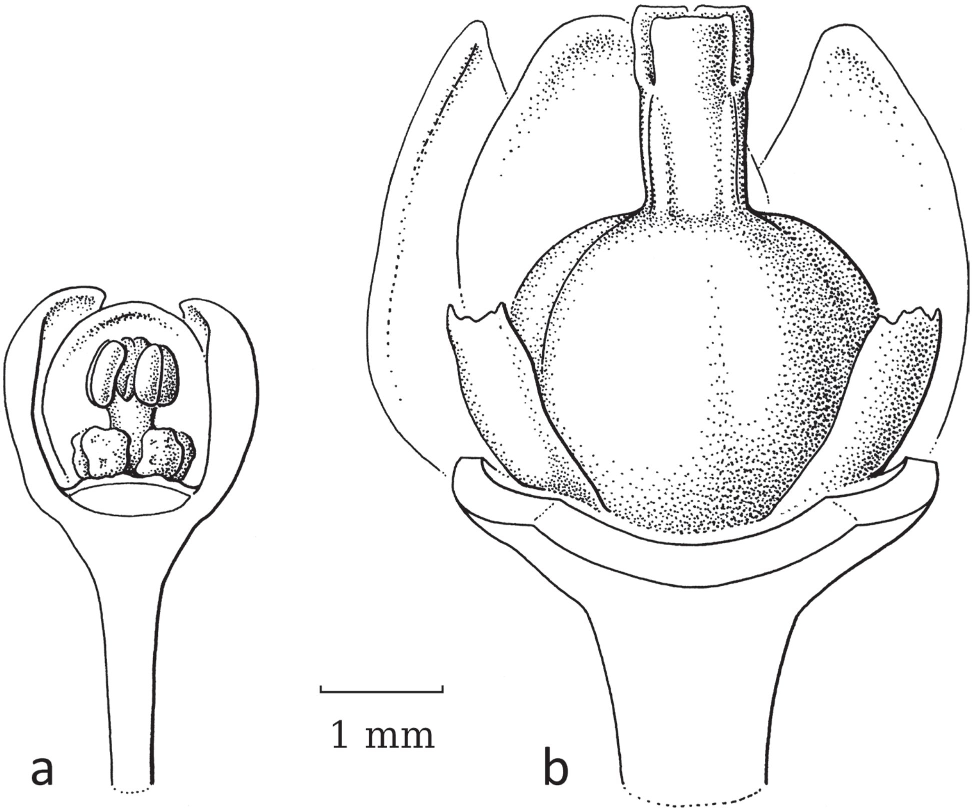

Figure 10. *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman **a** staminate flower with part of sepals removed showing disc glands and united stamens **b** pistillate flower with part of sepals removed showing disc glands and united stigmas (**a** *Carr 15875* **b** *NGF* (*Vandenberg*, *Womersley & Galore*) *42044*; both L). Illustration by Esmée Winkel, 2021.

flowers show either large, well-developed stigmas, generally free and sometimes recurved, or the stigmas are erect, free or united, sometimes small, in a tight upright circle with the stigmatic tissue on the inside (Table 2). *Dendrophyllanthus clamboides* (F.Muell.) R.W.Bouman (Fig. 10) shows united stamens and stigmas and is likely moth-pollinated like *D. glochidioides* (Elmer) R.W.Bouman with partly free stamens (Fig. 11). The interpretation that united stamens and stigmas are indicative of moth pollination is not necessarily always correct. *Dendrophyllanthus buxoides* (Guillaumin) R.W.Bouman and *D. caudatus* (Müll.Arg.) R.W.Bouman are recorded by Kawakita and Kato (2004a) to be moth-pollinated, but their sturdy stigmas point at the opposite conclusion, though the stigmas are more or less upright (slightly spreading) and, in case of *D. caudatus*, bent inwards towards each other (only seen in young fruit). *Dendrophyllanthus wilkesianus* (Müll.Arg.) R.W.Bouman (Fig. 12) shows more or less united stamens (but small anthers with horizontal slits), but free, recurved, papillate stigmas and likely is not moth-pollinated.

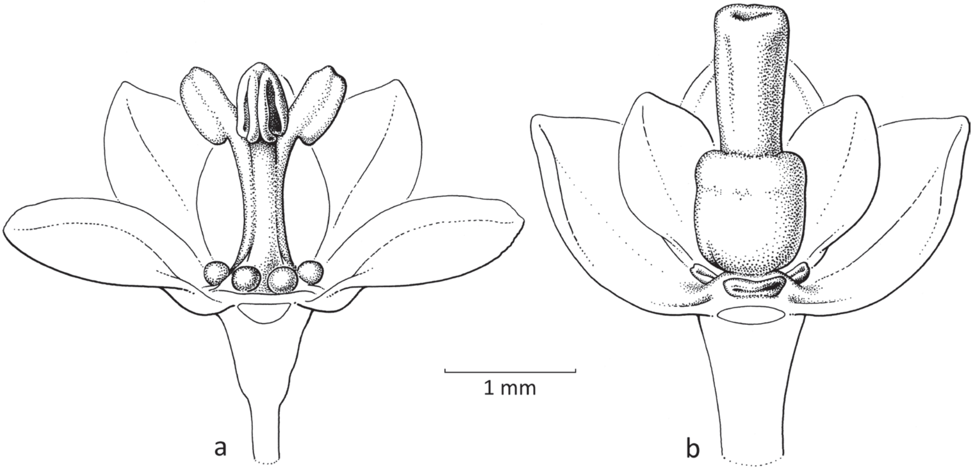

Figure 11. *Dendrophyllanthus glochidioides* (Elmer) R.W.Bouman **a** staminate flower with part of sepals removed showing disc glands and partly united stamens **b** pistillate flower with part of sepals removed showing disc glands and united stigmas (**a** *PNH* (*Edaño*) *40177* **b** *PPI* (*Stone* et al.) *24*; both L). Illustration by Esmée Winkel, 2021.

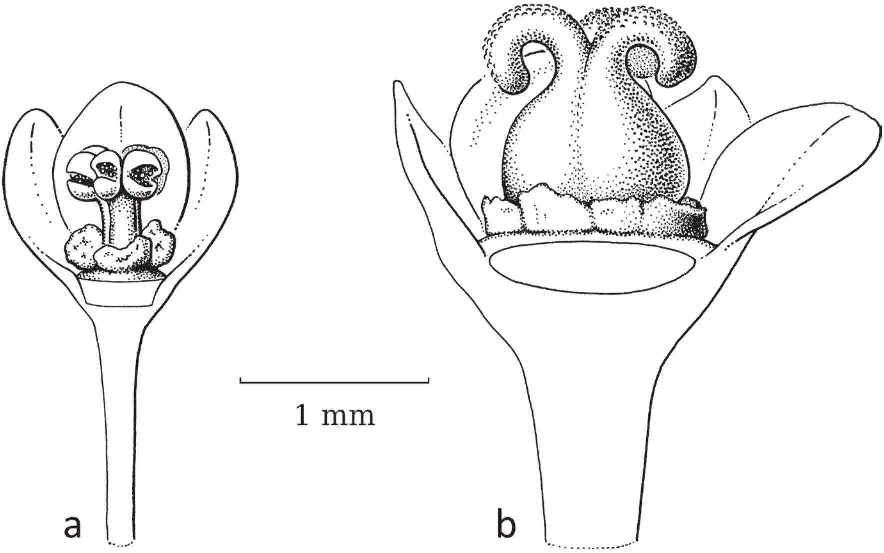

Figure 12. *Dendrophyllanthus wilkesianus* (Müll.Arg.) R.W.Bouman **a** staminate flower with partly removed sepals showing disc glands and the united stamens with small anthers with horizontal slits **b** pistillate flower with part of sepals removed, showing disc glands and well-developed, free, recurved, papillate stigmas (**a** *A.C. Smith 6294* **b** *A.C. Smith 9630*; both L). Illustration by Esmée Winkel, 2021.

Unfortunately, the published phylogenies for this group either only contain moth-pollinated species (Kawakita and Kato (2009), as *Phyllanthus* subgen. *Gomphidium* sect. *Adenoglochidion*) or show a basal polytomy (Bouman et al. 2021). This means that it is uncertain where moth pollination started in the phylogeny and if there are species reversing to non-moth pollination. Additionally, due to lack of material, not all species mentioned by Kawakita and Kato (2004a, 2009) could be analysed.

Dendrophyllanthus section *Leptonema* (Group 5 in Fig. 1A; Table 2)

Dendrophyllanthus S.Moore sect. *Leptonema* (Baill.) R.W.Bouman is an Australian–New Caledonian group that shows the same developments as the previous group. Again, *C. betsileani*, which has free stigmas, can serve as the outgroup. The staminate flowers do not show any obvious morphological adaptations to moth-pollination and the pistillate flowers show either well-developed spreading stigmas or cone-like, united or free, upright stigmas (Table 2). Thus, some of the species in this group may already have adapted to moth pollination, some not. Kawakita and Kato (2004a, as *Phyllanthus* subgen. *Gomphidium* sect. *Gomphidium*) listed a number of moth-pollinated species and three non-moth-pollinated species. The overlap with the species investigated here is very small with only two moth-pollinated species, of which *D. aeneus* (Baill.) R.W.Bouman has pistillate flowers that are adapted to moth pollination, but *D. vulcani* (Guillaumin.) R.W.Bouman seemingly has not (yet) adapted morphologically as it has well-developed, spreading stigmas.

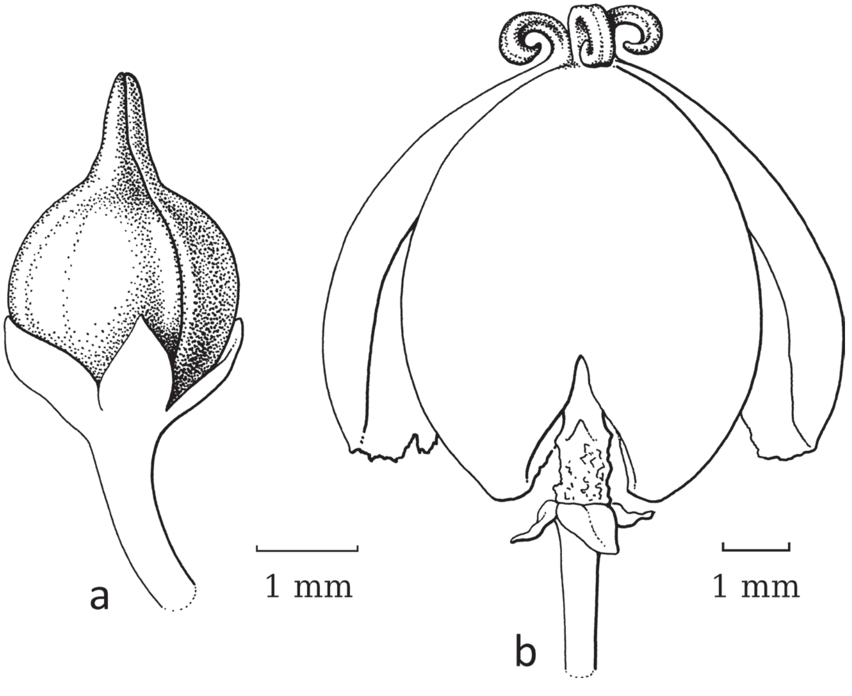

Figure 13. *Dendrophyllanthus ligustrifolius* (S.Moore) R.W.Bouman **a** developing fruit with stigmas erect and closed **b** dehiscing fruit with non-papillate stigmas recurved (**a** *MacKee 19634* **b** *McPherson 5025*; both L). Illustration by Esmée Winkel, 2021.

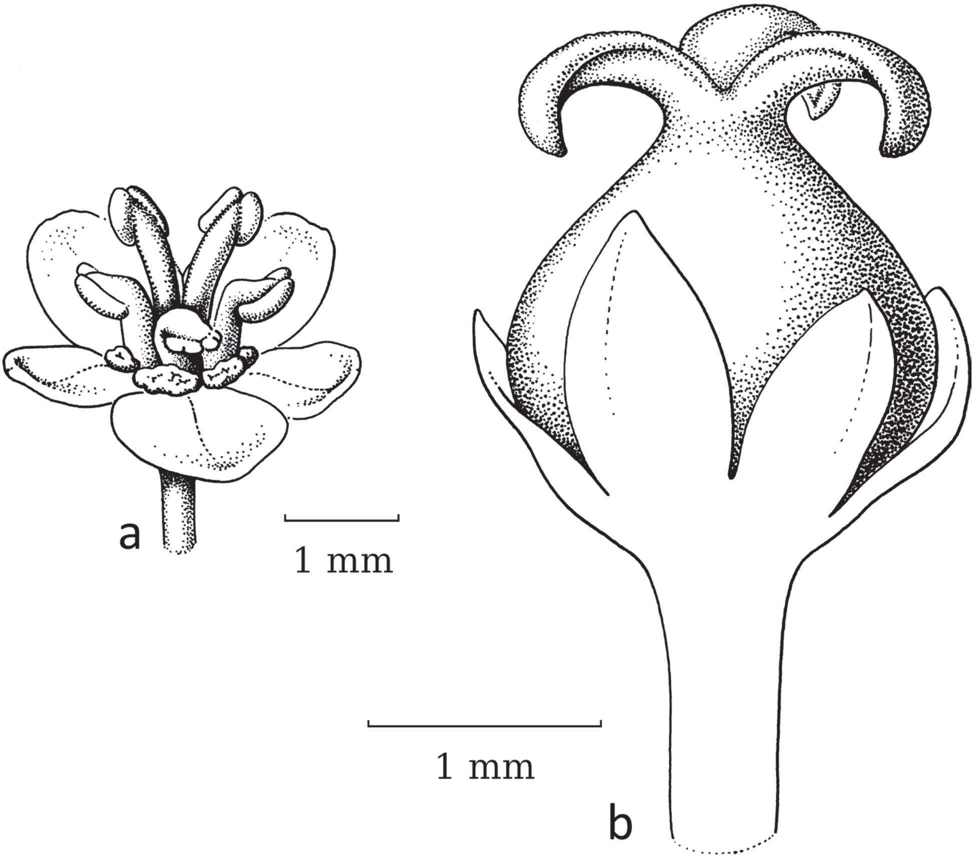

Figure 14. *Dendrophyllanthus hypospodius* (F.Muell.) R.W.Bouman **a** staminate flower with free stamens **b** pistillate flower with free, recurved stigmas (*Bruhl et al. 1123*, L). Illustration by Esmée Winkel, 2021.

The phylogeny of Kawakita and Kato (2009) included only moth-pollinated species, whereas the phylogeny of Bouman et al. (2021) showed that, perhaps in part of the clade, with *D. ligustrifolius* (S.Moore) R.W.Bouman at the base, a switch to moth pollination occurred, because *D. ligustrifolius* likely is moth-pollinated (Fig. 13) and *D. hypospodius* (F.Muell.) R.W.Bouman (Fig. 14) and *D. serpentinus* (S.Moore) R.W.Bouman likely are not moth-pollinated. Unfortunately, the upper part of the clade comprises a few polytomies and weakly-supported branches, thus this may change in the future when more species and/or markers are added. In this group, *D. bupleuroides* (Baill.) R.W.Bouman, *D. kanalensis* (Baill.) R.W.Bouman and *D. loranthoides* (Baill.) R.W.Bouman are probably not moth-pollinated; *D. vulcani* is disputable (it seems to have moth pollination (Kawakita and Kato 2004a, 2009), but is morphologically not adapted); *D. aeneus*, *D. guillauminii* (Däniker) R.W.Bouman and *D. ligustrifolius* have moth-pollination; and the pollination of *D. favieri* (M.Schmid) R.W.Bouman and *D. unifoliatus* (M.Schmid) R.W.Bouman is unknown.

Kirganelia A.Juss. subgenus *Kirganelia* section *Kirganelia* versus section *Pseudomenarda* (Group 6 in Fig. 1A; Table 2)

In *Kirganelia*, section *Pseudomenarda* (Müll.Arg.) R.W.Bouman is the non-moth-pollinated outgroup to section *Kirganelia*, where moth pollination is recorded. Section *Pseudomenarda* is a small taxon with two species, of which *K. somalensis* (Hutch.) R.W.Bouman (Fig. 16) was seen. It shows staminate flowers of 2.5–3 mm in diameter with five sepals, five disc lobes, two outer free and three inner united stamens. The pistillate flowers are very open, ca. 3.5 mm in diameter, with five relatively large sepals, a broad, ring-like disc and a 5-locular (can be 3-locular; see Hutchinson (1912)) ovary with a terminal, ca. 0.3 mm long style and then five horizontally spreading stigmas ca. 1 mm long, split in the upper third.

Section *Kirganelia*, *Kirganelia reticulata* (Poir.) Baill. was reported to be moth-pollinated (Kawakita et al. 2015; Fig. 15). The staminate flowers are very small and inconspicuous (ca. 2 mm in diameter) with five or six sepals in two whorls, five or six small disc glands and five or six stamens in two very tight whorls, outer two or three free, inner three with filaments basally connate; these staminate flowers are usually

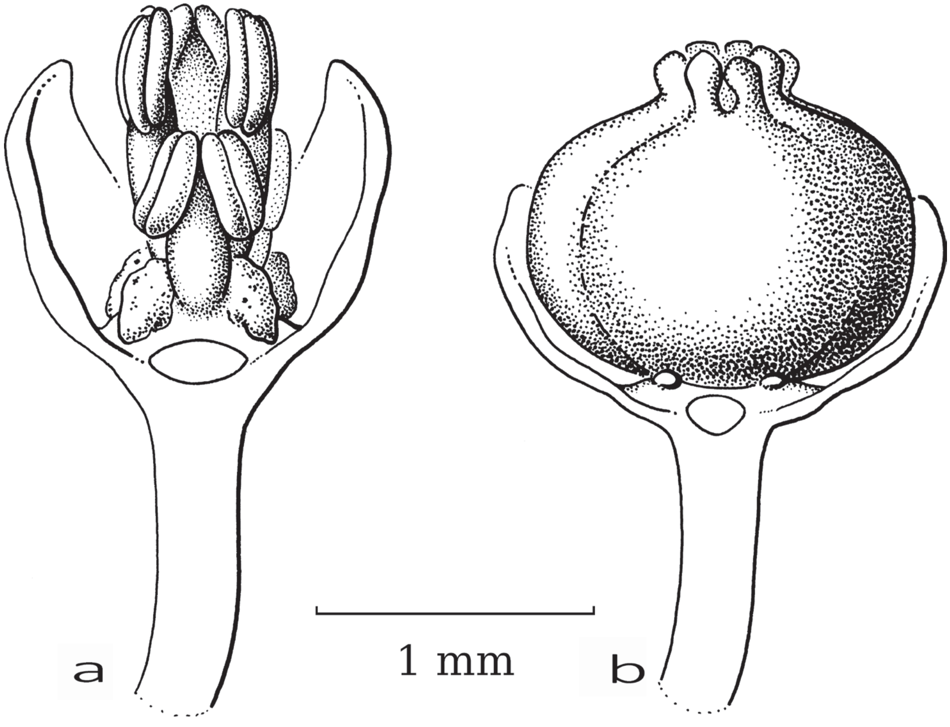

Figure 15. *Kirganelia reticulata* (Poir.) Baill. **a** staminate flower with part of sepals removed, showing disc glands and two layers of united stamens **b** pistillate flower with part of sepals removed showing small disc glands and small, upright, split free stigmas bent towards each other (**a** *Maxwell 91-1025* **b** *Put 2297*; all L). Illustration by Esmée Winkel, 2021.

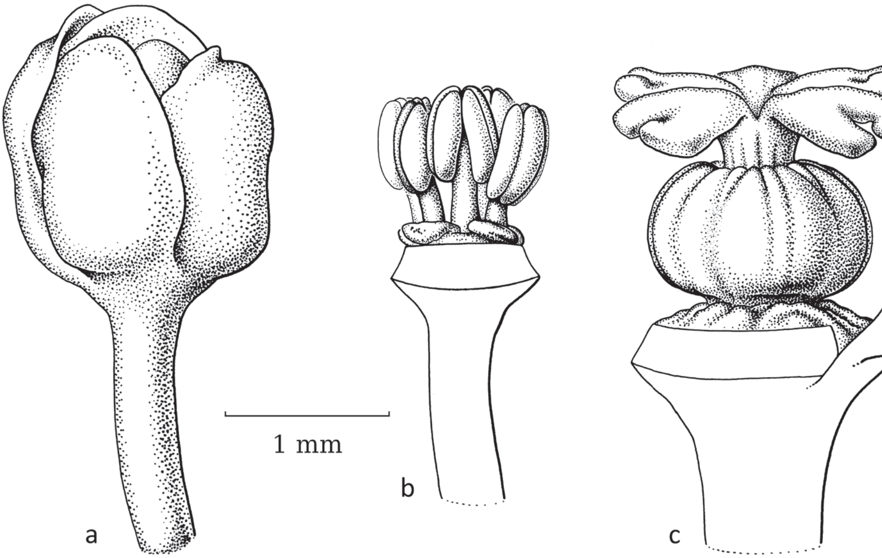

Figure 16. *Kirganelia somalensis* (Hutch.) R.W.Bouman **a** staminate flower, closed **b** staminate flower with part of sepals removed showing disc glands and free stamens **c** pistillate flower with part of sepals removed showing flat, circular and indistinct disc and well-developed, horizontal free stigmas (*Kilian 1718 & Lobin 6572*, WAG). Illustration by Esmée Winkel, 2021.

found unopened in dried specimens. The pistillate flowers have the same number of sepals and disc lobes as the staminate flowers, the ovary is small with four or five short stigmas, slightly split apically, bent towards each other and forming a circular cone that is open on the inside. Kawakita et al. (2015) reported that six moth species visit the flowers of *K. reticulata*, of which three have become parasitic again, causing the ovules/fruits to gall and one species also induces the fruit to become inflated. A possible reason for the reversal to parasitism is protection against predation by specialised braconid wasps (Kawakita et al. 2015). Predation by the wasps is likely as *K. reticulata* has relatively small fruits (ca. 4.5 mm in diameter), thus long ovipositors are not needed.

Adaptation in flower morphology of *K. reticulata* for moth pollination is seemingly only visible in the pistillate flowers; the staminate flowers with tightly, vertically grouped stamens are, at most, smaller than those in other species and then less accessible for various groups of insects. As in *Breynia* section *Breynia*, the stigmas in the pistillate flowers are shorter and, as in *Glochidion*, the stigmas are united, upright and short, forming an erect ring on top of the ovary and forming a depression inside. In contrast, in section *Pseudomenarda,* the stigmas are still well-developed and spreading. Additionally, some species within the genus, belonging to the now-subsumed group *Phyllanthus* section *Hemicicca* (Baill.) Müll.Arg., possess different flower features; especially *K. flexuosa* (Siebold & Zucc.) R.W.Bouman, which has staminate flowers with reddish, spreading sepals and two free stamens (see Kato and Kawakita (2017)). Their pollinators are unknown.

Discussion

Palaeotropics

As a result of obligate leafflower moth pollination, adaptations in the morphology of staminate and pistillate flowers were expected because they can improve pollination efficiency and the fit with the moths, while also optimising pollen uptake, pollen deposition and oviposition for the pollinators. However, because the mutualistic relationship has evolved several times in tribe Phyllantheae, there could be differences in morphological adaptations or similar morphological patterns in the different groups could have arisen through convergent evolution. Recent studies have shown that the mutualism between leafflowers and leafflower moths is more complex than first described (Kato et al. 2003) as there are differences in the level of species specificity (Kawakita and Kato 2004a, 2006; Zhang et al. 2012; Li et al. 2015; Yang and Li 2018), cheaters of the mutualism (Kawakita et al. 2015; Wang et al. 2020) and defences against this antagonistic relationship (Goto et al. 2010; Furukawa and Kawakita 2017). Furthermore, possible reversals in flowers are indicated here.

Flowers associated with the obligate moth pollination mutualism show, as a visual stimulus to attract the nocturnally active *Epicephala* moths, a contrast between the light (green to yellowish) sepals and the dark night sky, but this is also observed in non-moth-pollinated flowers. Olfactory cues were detected in a number of studies, differences that likely promoted speciation as they differed either in strength or composition between the sexes (Svensson et al. 2010; Okamoto et al. 2013; Okamoto 2017; Huang et al. 2015; Zhang et al. 2016). Okamoto et al. (2007; see also Okamoto (2017)) showed that *Glochidion* subgenus *Glochidion* produces floral odours, often typical of each species, but different between flower sexes, that attract the female moths. Additionally, *Breynia vitis-idaea* (Burm.f.) C.E.C.Fisch. produces two floral odours. Attractants are likely crucial, especially during the nocturnal pollination and differences in smell between the sexes can help guide the moth first to the staminate and later the pistillate flowers. Therefore, nectar glands like the disc or disc glands may still be as important as the tissue to emit the odours; the moths themselves do not seek nectar and the plants likely do not attract other insects. The glands/discs are present in most Phyllantheae, except in *Glochidion* subgenus *Glochidion* and *Breynia*; in these taxa, perhaps the receptacle produces the odour. The two other subgenera of *Glochidion* (*Pseudoactephila* and *Phyllanthodendron*) have disc glands in the flowers, but these have become almost petal-like and likely are not producing nectar any longer.

The majority of the moth-pollinated flowers are small with no bright colours, while the narrow shape of many is geared more towards a mechanical fit to the pollinator. The adaptations in staminate flowers that seem most common are a tight, cylindrical ring of sepals, with united, or at least upright, stamens with the anthers vertically along the androphore (opening towards the sepals) or with the anthers at the top of the androphore. This is especially demonstrated in *Breynia* section *Breynia* and *Glochidion* subgenus *Glochidion* (groups 1 and 2, respectively). With herbarium material, it is difficult to access the tightness of the sepals; therefore, this is often not noted, except when the sepals are thick and upright like several species in *Cicca* subgenus *Menarda* (group 3), *Pyllanthus graveolens* (*Phyllanthus* subgenus *Conami*; group 7) and several species in *Phyllanthus* subgenus *Microglochidion* (Group 8). If the staminate flowers produce a tight calyx cylinder, then as soon as the moth probes with its proboscis, covered with sensilla, the sensilla become dusted with pollen. This seemingly is a very effective mechanism.

Female moths have to transfer the pollen to the pistillate flowers, which is generally facilitated by the plant as most Phyllantheae species are monoecious and may have fascicles with both sexes (often many-flowered in *Glochidion*), whereby the sexes can be receptive at different moments, or the sexes are separated in space on one branch with the staminate flowers proximally and the pistillate flowers distally (often in *Breynia* and *Phyllanthus* s.l.). A few species are reported as dioecious, but this is not easy to judge from herbarium specimens; it can also be the result of dichogamy (an extended separation in time as the staminate flowers usually develop later than the pistillate flowers). For the placements of the different sexes along branches in the various species in Thailand, see for *Breynia*: van Welzen and Esser in van Welzen (2007), for *Glochidion*: van Welzen (2007) and for *Phyllanthus* s.l.: Chantaranothai (2007).

In the pistillate flowers, the upright, closely set sepals and the reduced stigmatic surface may serve two functions, to facilitate the pollen transfer and to preclude visits by insects other than leafflower moths. Two reversals (*Breynia retusa* and *Glochidion sericeum*) show that well accessible, completely developed and spreading stigmas no longer attract moths. A reduction in the style length and stigmas spreading was shown as an indicator of *Epicephala* pollination by Kawakita and Kato (2009: fig. 2). The reduction of the stigmatic tissue is achieved in two ways, either by shortening the stigmas or by folding the stigmas into a vertical (pyramidal) cone with a small, apical opening where the female moth can deposit the pollen. A reduction of the stigmas is seen in *Breynia* section *Breynia*. *Kirganelia reticulata* seems to follow both strategies: the stigmas are short and folded together. All other groups show cone-like united stigmas as in *Glochidion*. Several moth-pollinated South American species of *Phyllanthus* may still have well-developed, spreading stigmas (Kawakita et al. 2019; see below). Additionally, the stigmatic papillae seem to disappear in the moth-pollinated species; compare Fig. 3 (*Breynia lithophila* Welzen & Pruesapan, not moth-pollinated) with Fig. 4 (*Breynia glauca* Craib, moth-pollinated).

The taxa included here have been shown by other authors to be pollinated and/or parasitised by *Epicehala*. However, several taxa display similar morphological adaptations to those treated here and future studies might uncover new instances of plants in tribe Phyllantheae in a mutualistic relationship with *Epicephala* moths. The main pollination system in *Nymphanthus* Lour. has not yet been uncovered. Kawakita and Kato (2009) reported miscellaneous observations of dipterans visiting the typical cross-shaped flowers, but this has not been confirmed. However, species of *N.* section *Scepasma* (Blume) R.W.Bouman have very different flowers with erect sepals and *N. lamprophyllus* (Müll.Arg.) R.W.Bouman, for example, has a long style with small stigma lobes at the top. Similarly, pistillate flowers of *Emblica rufuschaneyi* (Welzen, R.W.Bouman & Ent) R.W.Bouman also have a long stylar column and a reduced disc (Bouman et al. 2018). Other species of *Emblica* usually have well-developed spreading stigmas, but whether they are associated with *Epicephala* is not well known.

Adaptation to moth pollination seems to be comparatively more pronounced in the Palaeotropics (and Pacific islands) in what was formerly known as *Breynia* (*B.* subgen. *Breynia* section *Breynia*) and *Glochidion* (*G.* subgenus *Glochidion*) (Kawakita et al. 2019). It is often speculated that the obligate moth pollination contributed to a proliferation in species (Kato et al. 2003; Kawakita and Kato 2004a), especially in *Glochidion* (> 300 spp.) and New Caledonian *Dendrophyllanthus* (~ 160 spp.), which are speciose groups that have radiated relatively recently (see Kawakita and Kato (2009)). *Breynia* is somewhat less species rich, thus other factors than moth pollination likely contributed to the high speciation rate seen in these groups. The olfactory attractants may play a role (see above), but also the greater variation in flower shapes in *Glochidion* and *Dendrophyllanthus*.

In conclusion, these Palaeotropical groups show some general trends in morphological adaptation in flowers resulting from obligate moth pollination:

– Sepals are usually stiff and upright and in a tight group around either the stamens or the ovary.
– Disc and disc glands are reduced.
– Stamens are united with the anthers upright along the androphore.
– Stigmatic surface is reduced, either by reducing the length of the stigmas to short stigmas or by uniting them into a cone with an apical round opening.
– Likely stigma papillae disappear.

However, these trends are not always completely present, for example, mutualistic relationships were found in species with well-developed stigmas (see some discussions above and Table 2).

Neotropics

Based on the morphological trends found in the Palaeotropics, the situation in the Americas is evaluated here. Moth pollination in the Neotropics was recently reported by Kawakita et al. (2019). The moth *Epicephala chancapiedra* Kawakita & Kato, 2019, was found on three herbaceous species: *Moeroris amara* (Schumach. & Thonn.) R.W.Bouman, *M. stipulata* Raf. and *Phyllanthus orbiculatus* Rich. (Fig. 17). These three herbaceous species are pollinated by ants and as female *E. chancapiedra* does not have sensilla on the proboscis, the moths are (secondary) parasites, only laying eggs in the pistillate flowers without active pollination (Kawakita et al. 2019). The flowers of both sexes in these three species are small, hanging, quite open and the stigmas are generally short, but well-developed and spreading. Only the short stigmas might be an adaptation to moths, but it is more likely an adaptation to the ants or no pollination is needed as all pistillate flowers develop fruits (also in a hothouse without pollinators, but with limited seed production, pers. observ.).

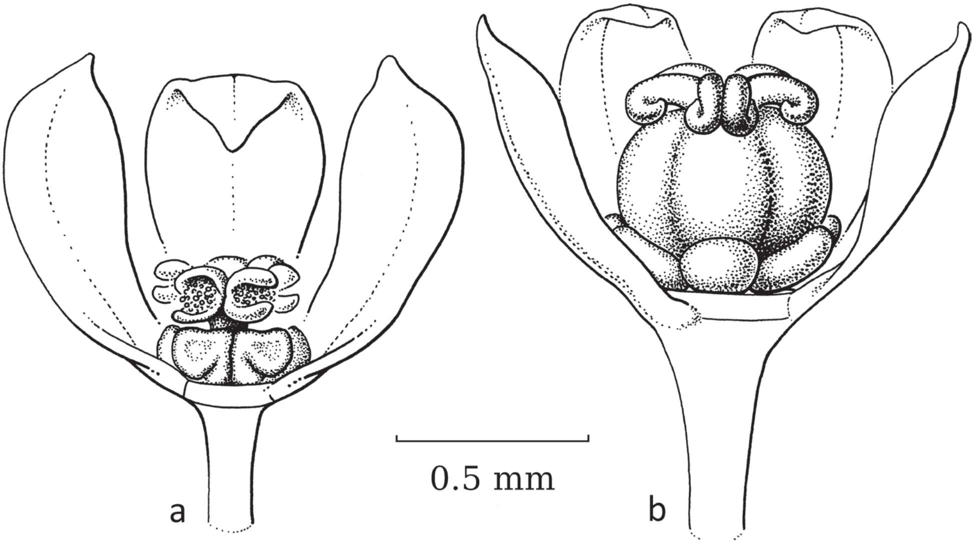

Figure 17. *Phyllanthus orbiculatus* Rich **a** staminate flower with part of sepals removed, showing large disc gland and united stamens with small anthers with horizontal slits **b** pistillate flower with part of sepals removed showing large disc glands and well-developed free, horizontal to recurved stigmas (*Herzog 1314*, L). Illustration by Esmée Winkel, 2021.

In the genus *Phyllanthus* L. subgenus *Ciccastrum* (Müll.Arg.) R.W.Bouman (Fig. 1B) can act as a local outgroup for comparisons. This group consists of two species, *P. purpusii* Brandegee (Fig. 19) and *P. riedelianus* Müll.Arg. Both species have free stigmas that recurve over the ovary (*P. purpusii*) or that are bent towards each other in fruit (*P. riedelianus*). Only the staminate flowers of *P. purpusii*, each consisting of a narrow and tight cylinder of stiff upright sepals and three united stamens with the anthers apically along the androphore (like *Breynia* sect. *Breynia*), may point at moth pollination. The staminate flowers of *P. riedelianus* show no distinct adaptations to moth pollination (more like *Breynia* subg. *Sauropus*). However, *P. riedelianus* (not in the phylogeny of Bouman et al. (2021)) is doubtfully placed in this group and is strongly divergent from *P. purpusii* (Webster, 2002); see Torres et al. (2020).

Kawakita et al. (2019) also looked for moth pollination in four woody species in the subgenera *Conami* (Aubl.) G.L.Webster and *Xylophylla* (L.) Pers. of *Phyllanthus*: *P. acuminatus* Vahl, *P. graveolens* Kunth, *P. huallagensis* Standl. ex Croizat and *P. salviifolius* Kunth (Fig. 18). In all cases, the stigmas do not show reduced surfaces and the stamens are often not upright (except more or less in *P. graveolens*) and are, thus, usually not readily accessible to moths. The pollination relationship does not appear to be obligate as other pollinators are present (gall midges and thrips; Kawakita et al. (2019)), which may mean that the relationship with the moths is rather recent and perhaps still developing and morphological adaptations are still lacking.

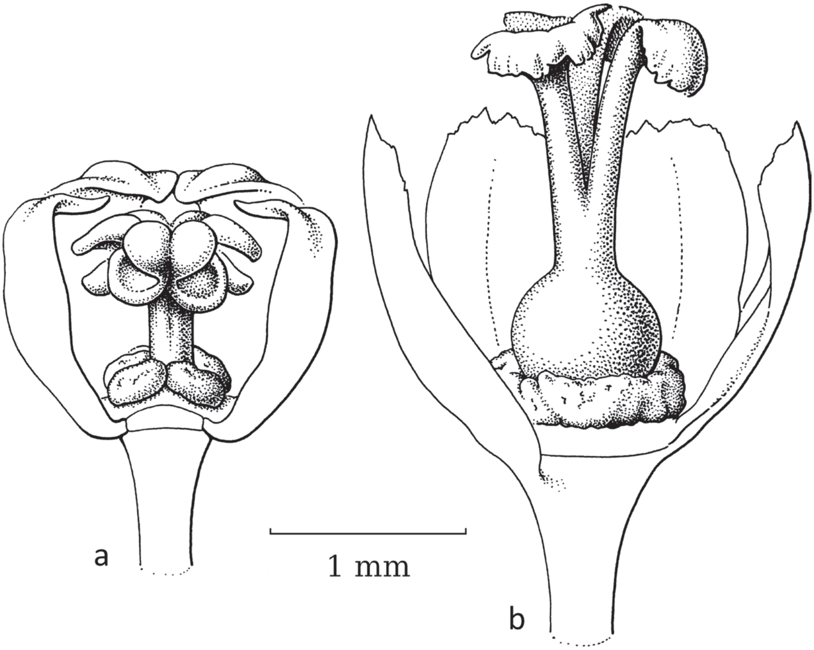

Figure 18. *Phyllanthus salviifolius* Kunth **a** staminate flower with part of sepals removed showing disc glands and three united stamens with free small anthers with horizontal slits **b** pistillate flower with part of sepals removed showing disc glands and upright stigmas recurved at the apex (*Breteler 3312*, L). Illustration by Esmée Winkel, 2021.

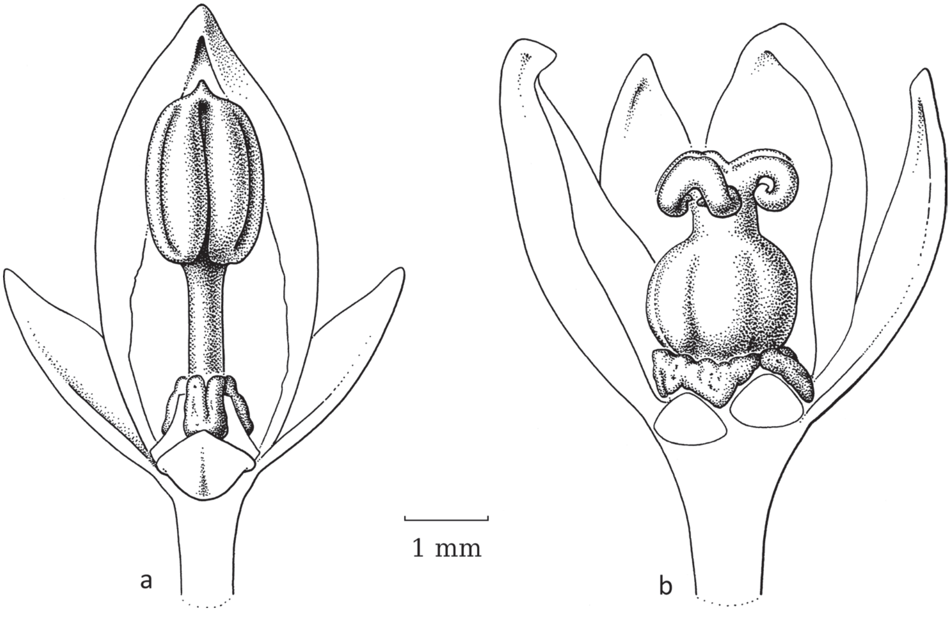

Figure 19. *Phyllanthus purpusii* Brandegee **a** staminate flower with sepal removed showing disc glands and three united erect stamens with the anthers along the androphore **b** pistillate flower with sepal removed showing circular disc and spreading stigmas (*Quarles van Ufford 266*, U). Illustration by Esmée Winkel, 2021.

Kawakita et al. (2019) mentioned *Phyllanthus* L. subgenus *Microglochidion* (Müll. Arg.) Jean F.Brunel as a group with likely mutualistic pollination as there is some floral resemblance with *Glochidion*. Typical in the group is that the leaves often have a subapical extrafloral nectary abaxially, generally subapical above the mid-rib. In this group, as defined by Bouman et al. (2022), there are generally six sepals in two whorls; staminate flowers with six disc glands and three free, upright stamens; and pistillate flowers generally with a circular disc and a 3-locular ovary with the stigmas variously arranged. The situation is not completely clear as a large number of taxa could not be sampled. Not all taxa show visible morphological adaptations to moth pollination. *Phyllanthus lediformis* Jablonski, *P. majus* Steyerm., *P. myrsinites* Kunth (Fig. 20) and *P. neblinae* Jablonski have pistillate flowers with well-developed stigmas and thin sepals that generally are spreading and also have relatively large anthers and upright stamens. *Phyllanthus duidae* Gleason, *P. pycnophyllus* Müll.Arg. and *P. vacciniifolius* (Müll.Arg.) Müll.Arg. (Fig. 21) show an apical cone of united stigmas with three small lobes apically around a narrow opening, the typical situation as in *Glochidion* subgenus *Glochidion*; their staminate flowers have upright stamens and high stiff, upright sepals. Very likely, the species with united stigmas are moth-pollinated as the staminate and pistillate flowers show adaptations like those in other groups: limited stigma surface and narrow staminate flowers. The phylogeny of Bouman et al. (2021) only shows one representative for this group (*P. vacciniifolius*); thus, it is not clear if a single adaptation to moth pollination occurred in an ancestral species or multiple adaptations.

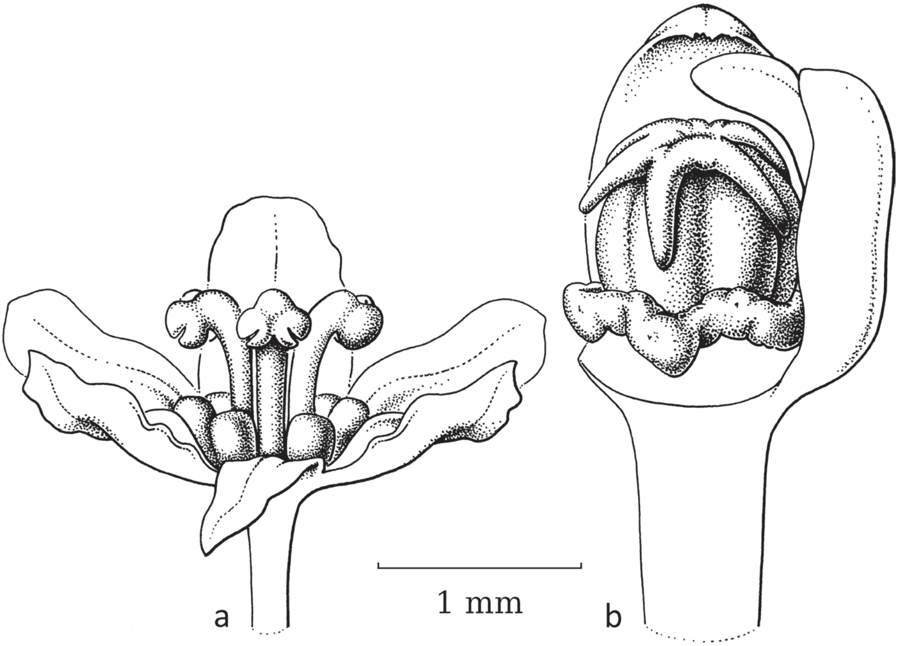

Figure 20. *Phyllanthus myrsinites* Kunth **a** Staminate flower with part of sepals removed showing disc glands and free stamens **b** pistillate flower with part of sepals removed showing ring-like disc and well-developed free and recurved stigmas (*Wade Davis 14*, U). Illustration by Esmée Winkel, 2021.

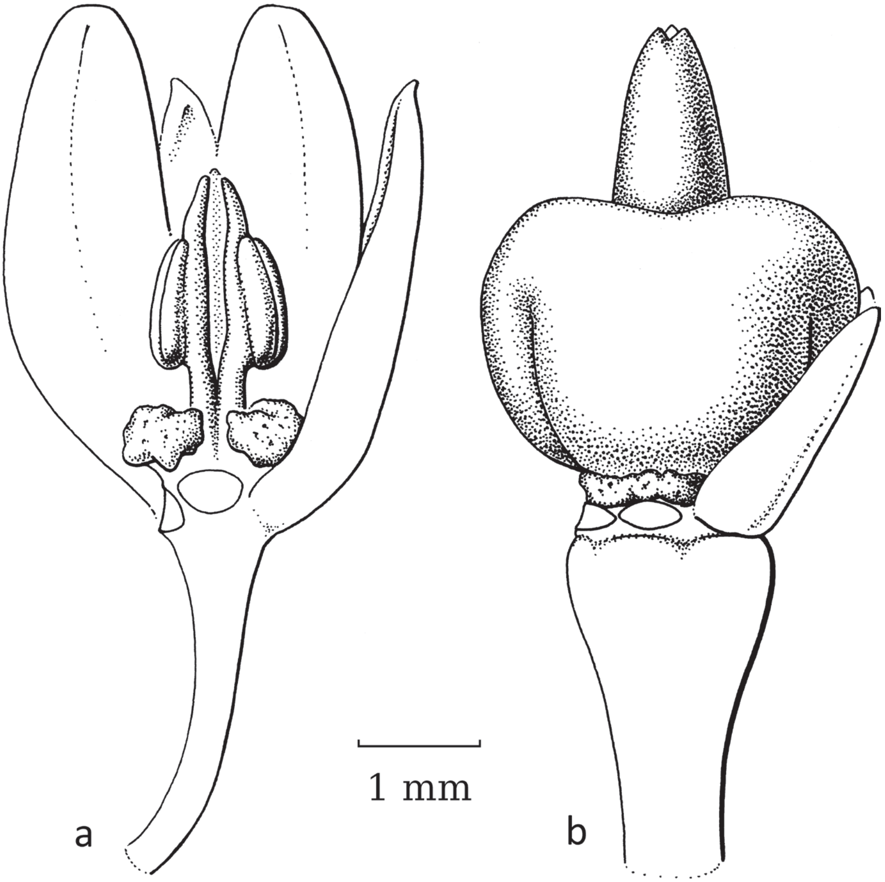

Figure 21. *Phyllanthus vacciniifolius* Müll.Arg. **a** staminate flower with part of sepals removed showing disc glands and three erect, free stamens with appendaged connectives **b** pistillate flower with part of sepals removed showing indistinct circular disc and upright, connate stigmas (*Prance 28343*, U). Illustration by Esmée Winkel, 2021.

Phyllanthus L. subgenus *Xylophylla* (L.) Pers. section *Epistylium* (Sw.) Griseb. was another taxon mentioned by Kawakita et al. (2019) as a Central American (West Indies) group that might have mutualistic relationships with *Epicephala* moths. Herbarium material was largely lacking; we saw only a single sheet of *P. axillaris* with young pistillate buds (*Proctor 18349*, Jamaica, U), which seem to have a closed stigma cone as in *Glochidion* subgen. *Glochidion*, which may be indicative of mutualistic pollination.

Thus, it appears that, in the Neotropics, the relationship with *Epicephala* moths probably is evolutionarily younger than in the Palaeotropics, because many plant species do not show strong adaptations to moth pollination and, as shown by Kawakita et al. (2019), several groups are likely not obligately moth-pollinated as other insect groups also pollinate the flowers. However, the pollination systems in the Neotropics are very understudied in comparison to those in the Palaeotropics.

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RESEARCH ARTICLE

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A new species of *Argyreia* (Convolvulaceae) from Yunnan, China

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Abstract

Argyreia subrotunda, a new species from Yunnan Province, China, is described and illustrated. The new species resembles *A. fulvocymosa* and *A. wallichii*, but differs from these in the flowers with an entire or shallowly lobed corolla, as well as smaller elliptic bracts, lax flat-topped cymes and shorter corolla tubes. An updated key to the species of *Argyreia* from Yunnan province is also provided.

Keywords

Argyreia subrotunda, flora of Yunnan, morphology, new taxon, taxonomy

Introduction

Argyreia Lour., a genus comprising scandent shrubs or lianas, is mainly distributed throughout tropical Asia (Staples and Traiperm 2017). *Argyreia* species mainly inhabit open and sunny places such as roadsides, thickets, and edges of mingled forest (Fang and Huang 1979; Fang and Staples 1995). The number of *Argyreia* species has been increasing and is now up to 143 species following the discovery of new species (Traiperm et al. 2019; Traiperm and Suddee 2020) and the establishment of new combinations (Shalini et al. 2017; Staples and Traiperm 2017; Rattanakrajang et al. 2022). There are about 25 species in China (14 of which are endemic) and 92% of the species found in

China in Yunnan Province (23 recorded species). The province of Yunnan is, therefore, the main center of diversity in China (Fang and Huang 1979; Fang and Staples 1995; Yang et al. 2015).

Loureiro (1790) published *Argyreia* as a genus within Convolvulaceae. The genus is mainly characterized by indehiscent fleshy or mealy berries (Staples and Traiperm 2017). The various types of indumentum, inflorescence architecture, depth of corolla lobes, and number of seeds in individual berries are the main taxonomically informative characters for the delimitation of species in *Argyreia*.

Argyreia seems to be non-monophyletic in recent works, because it includes at least one of the moth-pollinated species of *Rivea* Choisy (Manos et al. 2001; Stefanovic et al. 2003). Furthermore, there is evidence that *Blinkworthia* Choisy should be subsumed under *Argyreia* (Rattanakrajang et al. 2022). We support this conclusion and although the *Argyreia* alliance clade as recovered is paraphyletic, only one *Rivea* species was used and the inclusion of other species might lead to different conclusions in the future (Rattanakrajang et al. 2022). Therefore, we think that *Rivea* and *Argyreia* are two independent genera and both supposedly monophyletic, but their limits should be revised under a phylogenetic perspective with a comprehensive sampling.

Although recent studies have shown that *Argyreia* should be treated as part of *Ipomoea* L. (Muñoz-Rodríguez et al. 2019) and *Argyreia* is merged into *Ipomoea* by Wood et al. (2020), we chose not to follow the proposed classification in the present work, as further study of Old World taxa is still required (Traiperm and Suddee 2020). As it concerns *Ipomoea*, the possibility to keep the several established smaller genera has the potential to maintain nomenclatural stability (Eserman et al. 2020). So we do not subsume *Argyreia* into *Ipomoea* at this time and accordingly maintain the well-established generic concepts (Rattanakrajang et al. 2022).

During recent field surveys in Yunnan Province, an interesting population of *Argyreia* with an entire or shallowly lobed corolla was found. After reviewing literature and comparing specimens, especially native species in Yunnan Province and adjacent countries (Vietnam, Laos, Myanmar, Cambodia and Thailand), we found that the taxon was not completely similar to any species known worldwide. Therefore, a new *Argyreia* species from China is described and illustrated here.

Material and method

Plant material was collected during field surveys in Yunnan Province from 2020 to 2021. The type specimens have been stored in the herbarium of Beijing Normal University (**BNU**). Morphological measurements were made from dried specimens of herbarium by Nikon digital camera, Stereoscope (ZEISS V8) and software ImageJ (Abràmoff et al. 2004). Materials for observation of pollen morphology were obtained from herbarium, picking mature pollen from the dried specimens, sticking it on the sample stages with conductive adhesive, spraying gold and photographing by Scanning Electron Microscope. The collected specimens were compared with the type specimens of morphologically similar species at main herbariums in China (BNU, HITBC, IBSC, KUN, PE, WUK, YUKU), as well as digital images available online provided by JSTOR and herbaria abroad that are relevant for the group (A, BM, E, G, K, P). Fresh plant materials of the similar species (*A. wallichii*) were also collected for further careful comparison. All type specimens (or photos of type specimens) of accepted names and their synonyms in *Argyreia* known around the world were examined, which refer to the voucher information provided by Staples and Traiperm (2017).

Taxonomic treatment

Argyreia subrotunda **Q.R.Liu & M.L.Zhang, sp. nov.**
urn:lsid:ipni.org:names:77318528-1
Figs 1, 2

Type. China. Yunnan Province: Malipo County, Xinzhai Village, 22°57'48.01"N, 104°46'31.11"E, along roadside, 1300 m elev., 27 Aug 2021, fl. *M. L. Zhang BNU2021YN074* (holotype: BNU0053319!; isotypes: BNU!).

Diagnosis. *A. subrotunda* is unique, a small-flowered type with an entire or shallowly lobed corolla as well as exserted stamens and pistils (included in dry specimens), smaller elliptic bracts, and outer sepals ovate-circular. It is similar to *A. wallichii* in indumentum features (whitish tomentose) and fruit types (red globose berry), but differs by its smaller elliptic bracts (vs. ovate-oblong), lax flat-topped cymes (vs. compact capitate) and shorter corolla tubes (2–2.5 cm vs. 4–5 cm). Additionally, *A. subrotunda* is similar to *A. fulvocymosa* in leaf shape (broadly ovate-circular to nearly circular) and inflorescence (flat-topped cymes), but the latter is covered with densely yellowish villus and has a distinctly 5-lobed corolla, which is very easy to distinguish (Table 1).

Description. Climbing lianas; stem woody at base, herbaceous above, the former puberulent, the latter covered with whitish trichomes. Leaves simple, alternate; petiole 6–10 cm long, tomentose; leaf blades broadly ovate to rounded, 13–16 × 12–15 cm; base truncate or slightly cordate, occasionally oblique, margins entire, apex acute or obtuse, sometimes slightly emarginate; adaxially green, sparsely whitish velutinous only along leaf veins, abaxially paler, densely shining tomentose; secondary veins 13–15 on either side, curved to edge, veins slightly raised adaxially, more prominently raised abaxially. Inflorescences flat-topped cymes, axillary or terminal; peduncle 2–5 cm long, tomentose, angulate, secondary and tertiary peduncle 6–12 mm long; bracts small, elliptic, 8–10 × 4–8 mm, obtuse, hairy outside, veined; pedicels 5–7 mm long, up to 10 mm in fruit. Flowers diurnal; sepals unequal, 2 outer ovate-circular, 8–9 × 6–7mm, 3 inner elliptic, 6–7 × 3–5 mm, apex obtuse, abaxially whitish tomentose, adaxially glabrous, veined, enlarged in fruit, rose-red, shiny. Corolla tubular-funnelform, 2–2.5 cm long, pink, densely whitish villous outside on mid-petaline bands, otherwise glabrous, limb entire or shallowly lobed. Stamens exserted; filaments filiform, 14–15 mm long, attaching to the site of ca. 5 mm from stamens base, expanded at attachment points

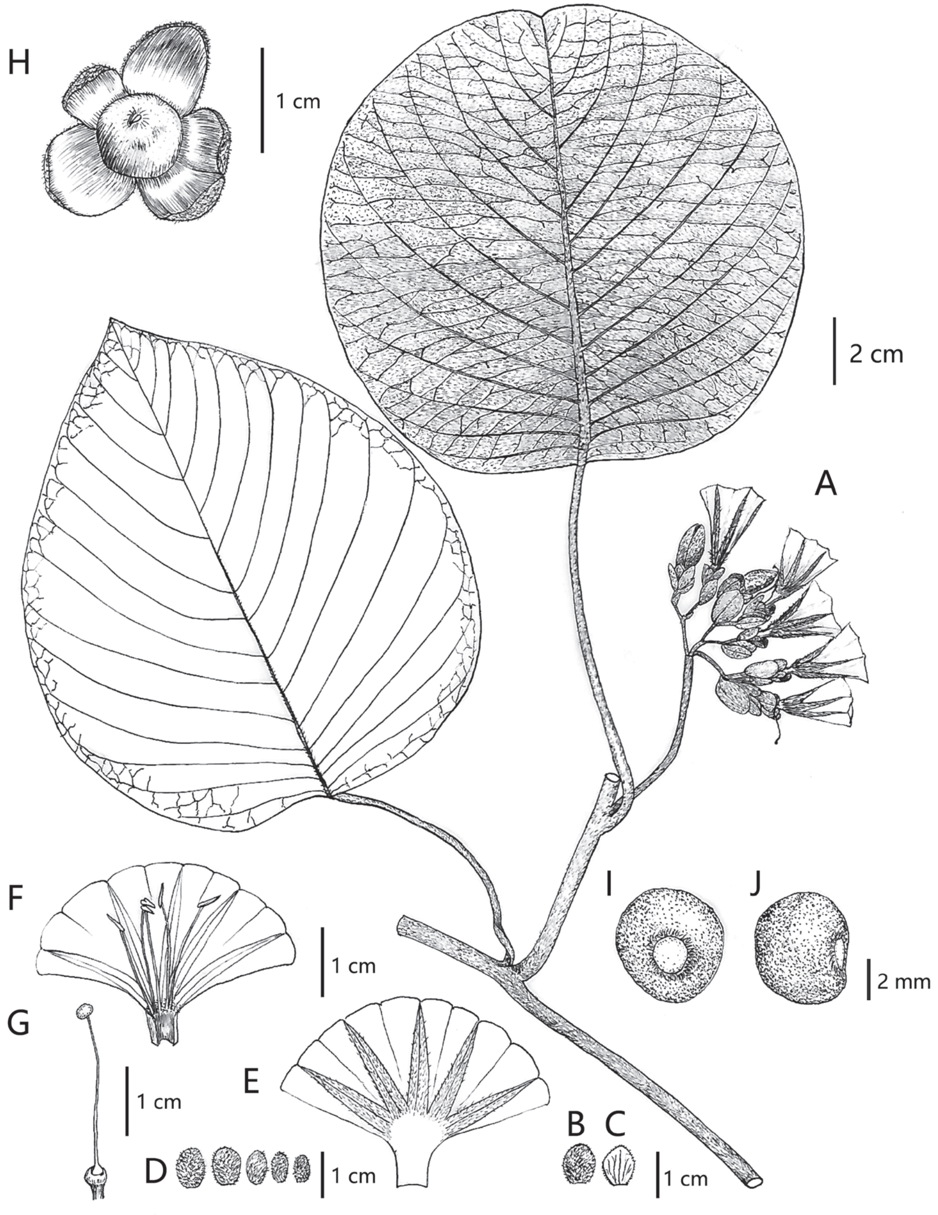

Figure 1. *Argyreia subrotunda* Q.R.Liu & M.L.Zhang, sp. nov. **A** stem with leaves and inflorescences **B** bract (outside) **C** bract (inside) **D** sepals from outer (left) to innermost (right) **E** opened corolla showing mid-petaline bands **F** opened corolla with stamens **G** pistil **H** fruit with persistent sepals **I** seed (adaxial surface) **J** seed (lateral surface). All drawn by Quan-Ru Liu from voucher specimens *M. L. Zhang BNU2021YN074* (BNU!) (**A–G**), *X. B. Guo BNU2021YN081* (BNU!) (**H–J**).

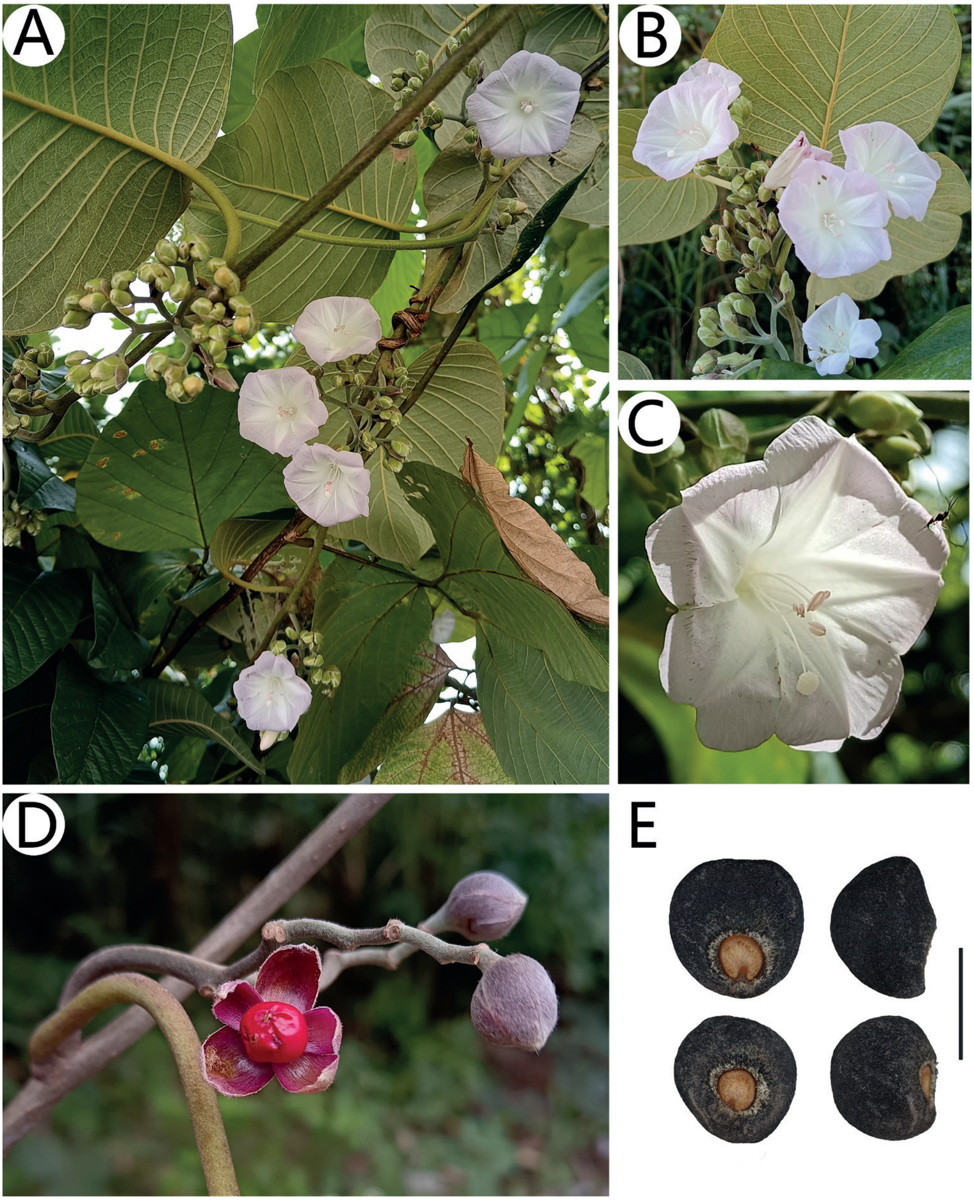

Figure 2. *Argyreia subrotunda* Q.R.Liu & M.L.Zhang, sp. nov. **A** plant habit **B** inflorescence **C** flower in frontal view **D** fruit with persistent sepals **E** seeds: adaxial surface (left); lateral surface (right). Scale bar: 5 mm. Photographs **A–C, E** by Mao-Lin Zhang, **D** by Xi-Bing Guo.

and densely whitish hairy there; anthers oblong, 3–4 mm long; pollen globose, pantoporate, with spines, 90–101 µm in diameter. Pistil exserted; disc ringlike, glabrous, ca. 1 mm high; ovary glabrous, ovoid, 2–3 mm high; style filiform, glabrous, 20–22 mm long; stigmas capitate, 2-lobed. Fruit enclosed in persistent, accrescent calyx, 2 outer fruiting sepals enlarging to 10–11 × 7–8 mm, 3 inner sepals 8–10 × 5–6 mm; berry subglobose, 7–10 mm in diam., purple-red, glabrous, exocarp leathery shiny, with obvious stomata under a magnifier, wrinkled when dry. Seeds 1–2, subglobose or hemispherical, 3.5–4 × 4–4.5 × 2.5–3 mm, black, glabrous, surface not smooth; hilum subcordate, brown, basal, margin with sparsely whitish hairy.

Phenology. Flowering from August to November; fruiting in November to February.

Distribution and habitat. Distributed in Yunnan and Gaungxi Province (Fig. 3), occurring at elevations of ca. 650–1300 m, distributed at open and sunny places such as roadsides, thickets, edges of mingled forest.

Preliminary conservation status. Least Concern (LC). At present, five populations have been collected in Malipo County, Maguan County and Napo County. Each population is large with high flowering rates, and the number of mature individuals in the population is more than 50. According to the IUCN (2019) red list categories and criteria, *A. subrotunda* should be categorized as a 'Least Concern (LC)' species, which needs further investigation and research to more fully assess the conservation status.

Etymology. The specific epithet refers to the leaf shape, which is near-round.

Chinese name. 近圆叶银背藤 (Jìn Yuán Yè Yín Bèi Téng).

Additional specimens examined. China, Guangxi Province: Napo County, Baisheng Township, Naen Reservoir, 26 Nov. 2013, fr. *B. Y. Huang et al. 451026131126017LY* (GXMG!); Yunnan Province: Malipo County, Bar-bu,

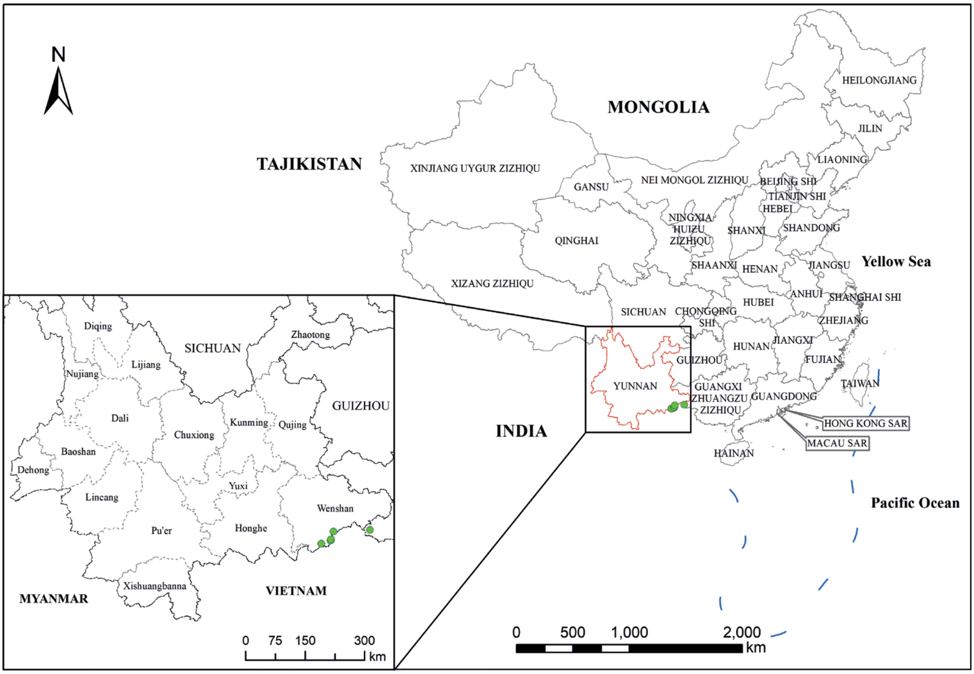

Figure 3. Distribution of *Argyreia subrotunda* in China. Drawn by Yi He.

1000 m elev., 2 Feb. 1940, fr. *C. W. Wang et al. 86509* (PE!); Malipo County, Wentian Road beside National Highway G246, 650 m elev., 23 Nov. 2021, fr. *X. B. Guo BNU2021YN081* (BNU!); Malipo County, Xinzhai Village, 1300 m elev., 23 Nov. 2021, fl. *X. B. Guo BNU2021YN082* (BNU!).

Pollen morphology

The observed pollen grains of *A. subrotunda* were monad, spheroidal to subspheroidal and radially symmetrical, with polypantoporate and echinate ornamentation (Fig. 4). It was possible to divide into two types based on the pollen morphology as follows: the diameter of the pollen grain was less than 100 μm with shorter bottle-like spines (5–7 μm), such as *A. wallichii* and the new species *A. subrotunda*; the diameter of pollen grains was over 100 μm with longer cone-shaped spines (≥ 10 μm), such as *A. marlipoensis*, which is endemic to Yunnan province, and the flower of which is first seen in this study.

Discussion

Morphologically, this species is most similar to *A. wallichii* and *A. fulvocymosa*, and it can be easily distinguished by the characters summarized in Table 1. The new species was similar to *A. wallichii*, both having similar indumentum features and fruit types as well as being almost sympatric. However, based on 17 specimens from two populations of *A. subrotunda*, we found the length of corolla was a very stable feature, about 2–2.5 cm, which was significantly shorter than *A. wallichii* (4–5 cm). The latter could also be easily distinguished from the new species by its compact capitate cymes and ovate-oblong bracts instead of flat-topped cymes and elliptic bracts. Additionally, *A. subrotunda* was similar to *A. fulvocymosa* in leaf shape and inflorescence, but the latter had a distinctly 5-lobed corolla instead of an entire or shallowly lobed corolla. Morphological comparisons of fresh plants between *A. subrotunda* and *A. wallichii* were provided in Figure 5. Furthermore, detailed comparisons of *A. fulvocymosa*, *A. subrotunda* and *A. wallichii* were provided in Table 1.

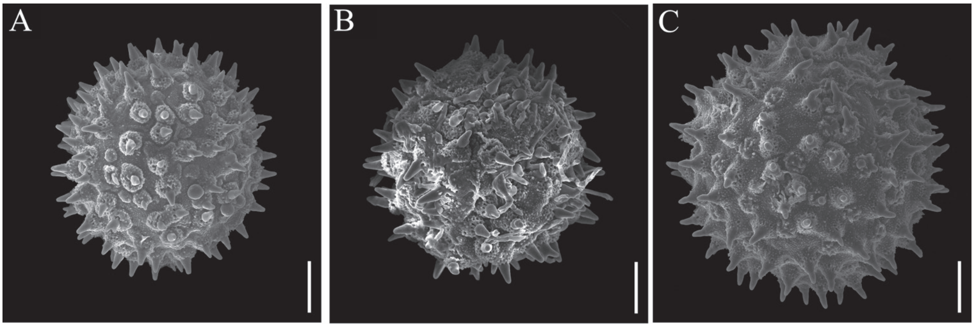

Figure 4. Comparison of pollen morphology **A** *Argyreia subrotunda* **B** *A. wallichii* **C** *A. marlipoensis*. Scale bars: 20 μm.

Table 1. Comparisons of *A. fulvocymosa*, *A. subrotunda* and *A. wallichii*.

Character		*A. fulvocymosa*	*A. subrotunda*	*A. wallichii*
Inflorescence		flat-topped cymes	**flat-topped cymes**	**capitate cymes**
Bract	Shape	unknown	**elliptic**	**ovate-oblong**
	Size	unknown	**0.8–1** cm × **0.4–0.8** cm	**2.5–3.5** cm × **1.5–2.5** cm
Outer sepal	Shape	broadly ovate-circular	ovate-circular	elliptic-oblong
Corolla	Length	ca. 2 cm	**2–2.5** cm	**4–5** cm
	Mid-petaline bands indumentum	yellowish hirsute	whitish villous	whitish villous
	Limb	**distinctly 5-lobed**	**entire or shallowly lobed**	entire or shallowly lobed
Stamen and pistil		exserted	exserted	included

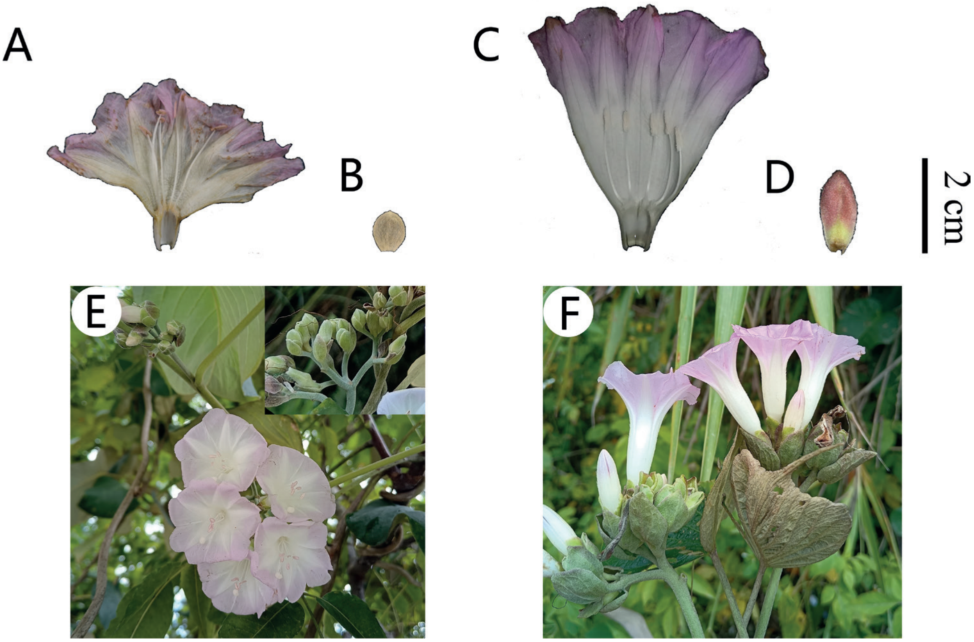

Figure 5. *Argyreia subrotunda* **A** opened corolla with 5 stamens **B** bract **E** inflorescence. *A. wallichii* **C** opened corolla with 5 stamens **D** bract **F** inflorescence.

The discovery of the new species has important value for further understanding of the morphological patterns of *Argyreia* in China. The new species is endemic to southwest China and compared to other species with an entire or shallowly lobed corolla in China, it seems to have comparative smaller corollas, which reinforces its recognition as a new taxa.

Key to the species of *Argyreia* from Yunnan, China

1 Corolla entire or shallowly lobed.. **2**
– Corolla deeply 5-lobed.. **17**

2 Climbing herb, stems slender, roots thick **3**

– Climbing shrubs or lianas, stem woody at base **4**

3 Leaf blade linear; sepals ovate; corolla pale purple, 4–4.5 cm long .... ***A. leariloba***

– Leaf blade ovate to ovate-deltate; sepals linear-lanceolate; corolla red, ca. 7 cm long .... ***A. baoshanensis***

4 Bracts soon deciduous **5**

– Bracts persistent **7**

5 Leaf blade densely yellowish sericeous-velutinous abaxially .... ***A. velutina***

– Leaf blade sparsely strigose or hispid abaxially **6**

6 Leaf blade lanceolate or ovate to ovate-elliptic .... ***A. henryi***

– Leaf blade broadly ovate to nearly circular, truncate or slightly cordate .... ***A. strigillosa***

7 Bracts with more than 15 mm in length **8**

– Bracts 2–13 mm in length **13**

8 Inflorescence paniculate-umbelliform, lax **9**

– Inflorescence capitate, condensed **10**

9 Leaf blade sparsely hispid abaxially, somewhat reddish purple colored; bracts narrowly lanceolate; corolla campanulate-funnelform, 5–7 cm long .... ***A. marlipoensis***

– Leaf blade densely silvery sericeous; bracts ovate-circular; corolla urceolate-funnelform, 2.5–3.5 cm long .... ***A. monosperma***

10 Indumentum brown or dull yellow, hirsute .... ***A. capitiformis***

– Indumentum whitish or pale yellow, villous or pubescent **11**

11 Bracts ligulate, petiolate, apex acuminate .... ***A. roxburghii* var. *ampla***

– Bracts ovate-circular or broadly ovate, apex acute or obtuse **12**

12 Bracts densely curly sericeous villous abaxially, ovate-circular; sepals brown, narrow-oblong .... ***A. eriocephala***

– Bracts densely pubescent abaxially, broadly ovate; sepals rose purplish, ovate-oblong .... ***A. wallichii***

13 Leaf blade broadly ovate-circular, base truncate or slightly cordate, densely yellowish villous or whitish tomentose abaxially **14**

– Leaf blade narrowly oblong or ovate-oblong, to elliptic, base rounded or broadly cuneate, densely silvery sericeous-pilose abaxially **15**

14 Leaf blade densely dull yellowish sericeous villous abaxially; corolla broadly funnelform, ca. 4.5 cm long, purple .... ***A. fulvovillosa***

– Leaf blade densely whitish tomentose abaxially; corolla tubular-funnelform, 2–2.5 cm long, pink .... ***A. subrotunda***

15 Peduncle 10.5–13.5 cm long .... ***A. splendens***

– Peduncle less than 10 cm long **16**

16 Sepals subequal, ovate-oblong; corolla white .... ***A. cheliensis***

– Sepals unequal, elliptic or oblong; corolla purple .... ***A. monglaensis***

17 Inflorescence capitate; bracts persistent; peduncle short to none, 0–0.3 cm long .... ***A. osyrensis***

– Inflorescence paniculate-umbelliform; bracts tiny or caducous; peduncle elongated, ca. 0.5 cm long **18**

18 Young stems, leaves abaxially, inflorescence all densely silvery sericeous-pilose; cymes axillary or terminal, 3–10-flowered .... ***A. obtusifolia***

– Young stems, leaves abaxially, inflorescence all densely yellowish tomentose; cymes axillary, 9–40-flowered .... ***A. fulvocymosa***

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