

# A new species of *Sterculia* (Malvaceae) from Vietnam

Cam Nhung Kieu<sup>1</sup>, Duc Binh Tran<sup>1,2</sup>, Ngoc Han Le<sup>2</sup>, Thi Hoan Duong<sup>2</sup>,  
Thu Ha Bui<sup>3</sup>, Thu Thuy Nguyen<sup>1,2</sup>, Hong Quang Bui<sup>1,2</sup>, The Bach Tran<sup>1,2</sup>

<sup>1</sup> Graduate University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Ha Noi, Vietnam

<sup>2</sup> Department of Botany, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Ha Noi, Vietnam

<sup>3</sup> Faculty of Biology, Hanoi National University of Education, 136, Xuan Thuy, Cau Giay, Ha Noi, Vietnam

Corresponding author: The Bach Tran ([tranthebach.botany@gmail.com](mailto:tranthebach.botany@gmail.com))

## Abstract

A new species of *Sterculia* from Vietnam – *S. konchurangensis* – is described, illustrated, and compared with the similar *S. lanceolata*. *S. konchurangensis* differs from *S. lanceolata* by the length of the petiole (7.0–9.5 vs. 25–35 mm), shape of the leaf blade (obovate or elliptic vs. elliptic, lanceolate or elliptic-lanceolate), length of the leaf blade (6–8 vs. 9–20 cm), and length of the calyx lobe (11–12.5 vs. 4–6 mm). A diagnostic key of the 22 *Sterculia* species occurring in Vietnam is also provided.

**Key words:** Malvaceae, *Sterculia*, Tay Nguyen, Vietnam

## Introduction

The genus *Sterculia* L. (Malvaceae Juss.) comprises 100–200 species mainly distributed in tropics and subtropics of both hemispheres, most abundant in Asian tropics (see e.g., Ya et al. 2007; POWO 2023; WFO 2023). The genus is characterized by having leaves simple, flowers unisexual, androgynophore present, staminodes at top of androgynophore in whorl around base of carpels (Ya et al. 2007). In Vietnam, 22 species of *Sterculia* have been recorded so far (Gagnepain 1910; Nguyen et al. 1980; Pham 1999; Chamlong 2001; Nguyen 2003; Newman et al. 2007; Ya et al. 2007; POWO 2023).

During a botanical survey of the Gia Lai province (the Central Highlands of Vietnam) in 2022, plants referred to the genus *Sterculia* were observed in a primary evergreen forest in the Kon Chu Rang Nature Reserve. After comparing the collected specimens with others preserved in various herbaria, and by consulting relevant literature, we reached the conclusion that Vietnamese population represent a new species for science which is here described and illustrated. We also provide a key to the species of *Sterculia* that are now known to occur in Vietnam.

## Materials and methods

The morphology of the new species were observed on both living plants and herbarium specimens. Branches, leaves and (functionally female) flowers (lf. fl.) of type materials are stored at the Institute of Ecology and Biological



Academic editor: Duilio Iamónico

Received: 10 February 2023

Accepted: 13 May 2023

Published: 29 May 2023

Citation: Kieu CN, Tran DB, Le NH, Duong TH, Bui TH, Nguyen TT, Bui HQ, Tran TB (2023) A new species of *Sterculia* (Malvaceae) from Vietnam. *PhytoKeys* 227: 1–8, <https://doi.org/10.3897/phytokeys.227.101754>

Copyright: © Cam Nhung Kieu et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Resources (**HN**) and the Institute of Tropical Biology (**VNM**) (acronyms follow Thiers 2023[continuously updated]). The conservation status of the new species was assessed according to the guidelines of the International Union for Conservation of Nature (IUCN 2019).

## Taxonomy

***Sterculia konchurangensis*** C.N.Kieu, D.B.Tran & B.H.Quang, sp. nov.

urn:lsid:ipni.org:names:77320206-1

Figs 1–3

**Type.** VIETNAM. Tay Nguyen: Gia Lai province, Kon Chu Rang reserve, 1016 m a.s.l., 19 June 2022 (lf, f. fl.), *Bui Hong Quang et al. BHQ 576* (holotype HNI, isotypes: HNI, VNM!).

**Diagnosis.** *Sterculia konchurangensis* is most similar to *S. lanceolata* Cav. due to the number of veins on each side of midrib, length of inflorescence, deeply divided calyx, globose, hairy ovary and curved style. They are separated by morphology of leaf blades (obovate or elliptic in *S. konchurangensis* vs. elliptic, lanceolate or elliptic-lanceolate in *S. lanceolata*); petioles are shorter (7.0–9.5 mm vs. 25–35 mm in *S. lanceolata*), leaf blades are shorter (6–8 cm vs. 9–20 cm in *S. lanceolata*) and calyx lobes are longer (11–12.5 mm vs. 4–6 mm in *S. lanceolata*).

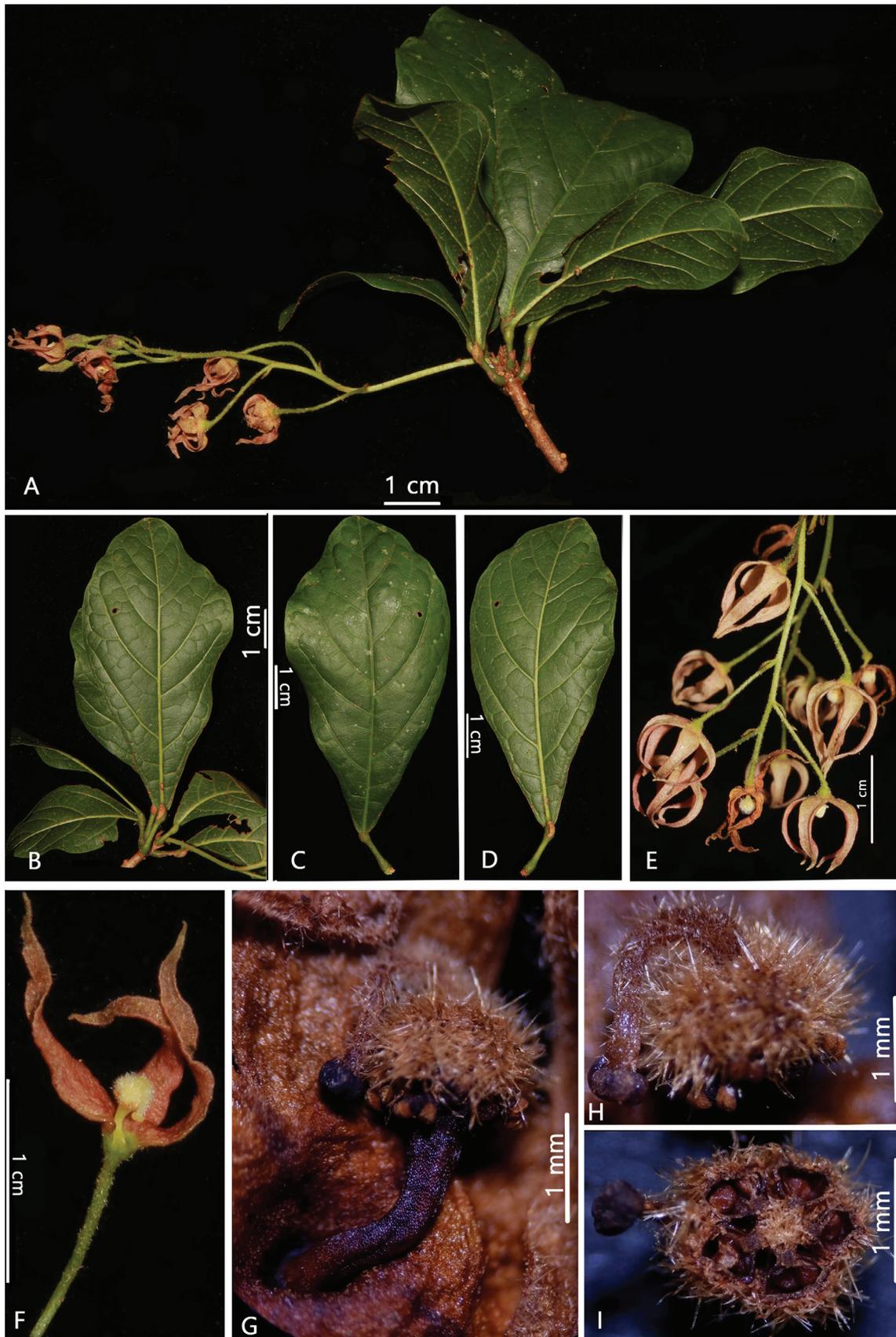
**Description.** *Shrubs*, ca. 3 m tall. **Branches** gray brown. **Leaves** alternate, apically clustered; **petiole** 7.0–9.5 mm long, glabrous, base and apex of petiole swollen; leaf blade simple, entire, glabrous, obovate, elliptic, base attenuate, apex shortly acuminate or obtuse, 6–8 × 3–4 cm, both surfaces glabrous; **lateral veins** 6–8 on each side of midrib. **Stipules** linear, ca. 1–2 mm long. **Inflorescence** slender, racemose, axillary, 8 cm long, few-12 flowered. **Pedicele** slender, 9.5–12.0 mm long, densely villous. **Flowers** 5-merous, functionally unisexual. Flowers: **Flower bud** lanceolate, 6.3 × 2.3 mm. **Calyx** divided almost to base, 5-lobed, pink, adaxial surface nearly glabrous to sparsely pubescent, abaxial surface pubescent; **tube** 1.3–1.7 mm long; **lobes** linear-lanceolate, 11–12.5 × 2.5–2.8 mm. **Petals** absent. **Androgynophore** slender, curved, ca. 2 mm long, glabrous. **Staminodes** at top of androgynophore in whorl around base of carpels; **anthers** of staminodes ovate, 0.22 × 0.18 mm. **Carpels** 5; **ovary** globose, densely pubescent, 1.3–1.8 mm in diameter; **style** curved, 2–3 mm long, sparsely pubescent; **stigma** glabrous, 0.3–0.6 mm in diameter. **Fruits and seeds** not observed.

**Etymology.** The specific epithet refers to the type locality, Kon Chu Rang reserve in Vietnam.

**Distribution and ecology.** *Sterculia konchurangensis* is only found in Vietnam, Gia Lai province, Tay Nguyen area, Kon Chu Rang reserve where it grows in primary evergreen forest at an altitude of 1016 m a.s.l. Flowering time is June; fruiting time is unknown.

**Conservation status.** Data Deficient (DD; IUCN 2019). *Sterculia konchurangensis* is known only from the type locality within Kon Chu Rang reserve. A comprehensive botanical survey of the *Sterculia* has not been carried out to date.

**Discussion.** *Sterculia konchurangensis* is morphologically similar to *S. lanceolata* Cav. due to the number of veins on each side of midrib, length



**Figure 1.** *Sterculia konchurangensis* C.N.Kieu, D.B.Tran & B.H.Quang **A** flowering branch **B, C, D** leaf blade **E** inflorescence **F** open flower showing androgynophore, ovary, style, stigma **G** androgynophore, staminodes, ovary, style, stigma **H** ovary, style, stigma **I** section ovary, style, stigma (Photos by D.B Tran).



**Figure 2.** *Sterculia konchurangensis* C.N.Kieu, D.B.Tran & B.H.Quang **A** flowering branch **B, C, D** leaf blade **E** apex branches and stipules **F** inflorescence **G** flower **H** flower **I** open flower showing androgynophore, ovary, style, stigma **J** androgynophore, ovary, style, stigma, staminodes **K** section ovary, style, stigma (Drawn by Le Kim Chi).

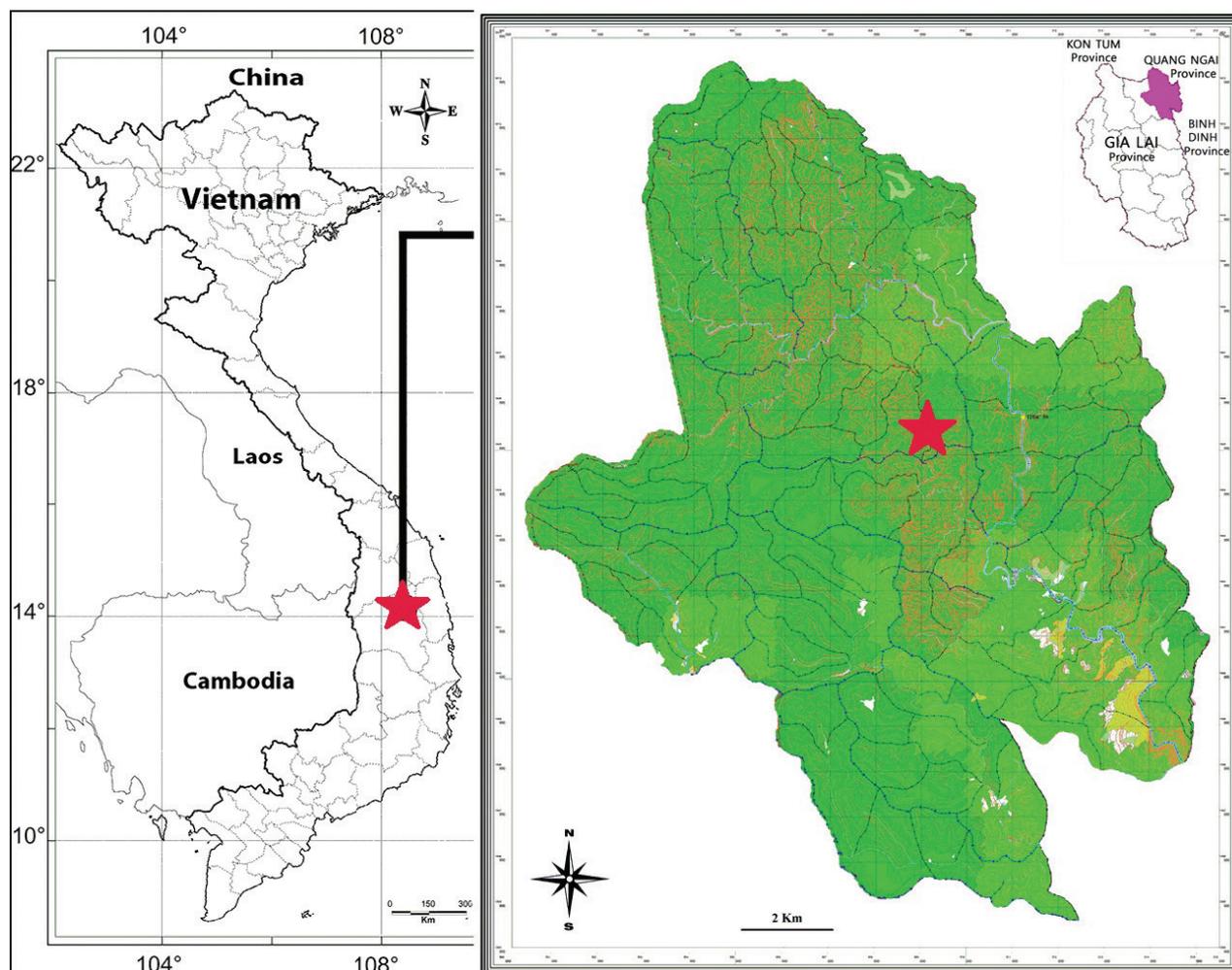


Figure 3. Map indicating the type locality of *Sterculia konchurangensis* C.N.Kieu, D.B.Tran & B.H.Quang (Made by D.B Tran & T.B. Tran).

of the inflorescence, deeply divided calyx, globose, hairy ovary, and curved style; furthermore, to be noted that both species have the same flowering time (June). However, *S. konchurangensis* differs from *S. lanceolata* by the morphology of length of petiole, shape of leaf blade, size of leaf blade and length of calyx lobe.

The identified key of 23 species of *Sterculia* in Vietnam was constructed. *Sterculia konchurangensis* differs from 22 species of *Sterculia* by having some characters such as simple, entire, glabrous leaves and length of petiole (less than 12 mm long). In addition, the comparison with the similar species (*S. lanceolata*) confirms that *S. konchurangensis* is a new species. Diagnostic characters separating the two species are listed in Table 1.

Table 1. Morphological differences between *S. lanceolata* and *S. konchurangensis*.

Characters	<i>S. lanceolata</i>	<i>S. konchurangensis</i>
Length of petiole (mm)	25–35	7.0–9.5
Shape of leaf blade	elliptic, lanceolate or elliptic-lanceolate	obovate or elliptic
Size of leaf blade (cm)	9–20 × 3.5–8.0	6–8 × 3–4
Length of calyx lobe (mm)	4–6	11–12.5

Key to the species of ***Sterculia*** in Vietnam

- 1 Leaves palmately compound.....2
- Leaves simple.....3
- 2 Calyx purple-red, ca. 12 mm long, divided nearly to base.....***S. foetida***
- Calyx white, ca. 6 mm long, divided to 1/2 of the total length .....***S. pexa***
- 3 Leaf blade lobed.....4
- Leaf blade not lobed .....5
- 4 Seeds 2 per follicle.....***S. hypochroa***
- Seeds 6–7 per follicle .....***S. thorelii***
- 5 Basal veins 3–7 .....6
- Basal veins absent .....9
- 6 Leave base shallow cordate ..... ***S. stigmatota***
- Leave base not shallow cordate.....7
- 7 Lateral veins 5–6 on each side of midrib.....8
- Lateral veins 7–10 on each side of midrib ..... ***S. principis***
- 8 Seeds 1–2 per follicle .....***S. lissophylla***
- Seeds 3–6 per follicle .....***S. chrysodasys***
- 9 Leave pubescent .....10
- Leaves glabrous .....14
- 10 Leaves obovate or oblanceolate .....11
- Leaves elliptic-oblong .....12
- 11 Lateral veins 16–24 on each side of midrib .....***S. hymenocalyx***
- Lateral veins less than 12 on each side of midrib.....***S. parviflora***
- 12 Petiole 5–7 cm long..... ***S. radicans***
- Petiole less than 4 cm long .....13
- 13 Leaves silver hairy beneath ..... ***S. pierrei***
- Leaves rufous hairy beneath ..... ***S. tonkinensis***
- 14 Petiole < 12 mm long ..... ***S. konchurangensis***
- Petiole > 15 mm long .....15
- 15 The upper parts of the lateral veins connected.....16
- The upper parts of the lateral veins not connected .....20
- 16 Lateral veins more than 6 pairs .....17
- Lateral veins 5–6-paired ..... ***S. cochinchinensis***
- 17 Lateral veins less than 12 pairs.....18
- Lateral veins 12–15 paired ..... ***S. henryi***
- 18 Petiole 2.5–8.0 cm long.....19
- Petiole 1–2 cm long..... ***S. hyposticta***
- 19 Calyx reddish, divided almost to base ..... ***S. lanceolata***
- Calyx dark brown, calyx united at the bottom 1/3.....***S. aberrans***
- 20 Calyx 3.5–4.5 mm long ..... ***S. gracilipes***
- Calyx longer than 5 mm .....21
- 21 Androgynophore longer than calyx tube.....***S. bracteata***
- Androgynophore shorter than calyx tube .....22
- 22 Petiole 2–5 cm long .....***S. monosperma***
- Petiole 7–10 cm long.....***S. scandens***

## Acknowledgements

We thank the directors and curators of the herbaria HN, HNU, HNPM, P and VNM for allowing access to and/or for providing high quality images of herbarium specimens and to Le Kim Chi for the drawing. Funding for this research was provided by the project ĐTDL.CN-72/22.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Cam Nhung Kieu: Identification, description, key establishing and manuscript writing. Duc Binh Tran: Collection and description of species during fieldwork. Ngoc Han Le: Study on specimens at VNM herbarium. Thi Hoan Duong: Study on specimens at HN herbarium. Thu Ha Bui: Study on specimens at the other herbaria and related references. Thu Thuy Nguyen: Study on specimens at the other herbaria and related references. Hong Quang Bui: Collection and description of species during fieldwork. The Bach Tran: Identification, description, key establishing and manuscript correction.

### Author ORCIDs

Cam Nhung Kieu  <https://orcid.org/0009-0002-7480-1030>

Duc Binh Tran  <https://orcid.org/0000-0001-6658-0739>

Ngoc Han Le  <https://orcid.org/0000-0003-2657-5091>

Thi Hoan Duong  <https://orcid.org/0000-0002-4298-5720>

Thu Ha Bui  <https://orcid.org/0000-0001-6971-0105>

Thu Thuy Nguyen  <https://orcid.org/0000-0002-0921-5652>

Hong Quang Bui  <https://orcid.org/0000-0001-6878-7514>

The Bach Tran  <https://orcid.org/0000-0003-3798-5969>

### Data availability

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

## References

- Chamlong P (2001) Sterculiaceae. Flora of Thailand (Vol. 7). The Forest Herbarium, Royal Forest Department, Bangkok, 351–654.
- Gagnepain F (1910) Sterculiacées. In: Lecomte PH (Ed.) Flore Générale de l'Indo-Chine (Fas. 1). Masson & Co., Paris, 454–481.

- IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Subcommittee. <http://cmsdocs.s3.amazonaws.com/RedListGuidelines.pdf>
- Newman M, Ketphanh S, Svengsuksa B, Thomas P, Sendala K, Lamxay V, Amstrong K (2007) A checklist of the vascular plants of Lao PDR. Royal Botanic Garden Edinburgh.
- Nguyen TB (2003) Sterculiaceae. In: Nguyen TB (Ed.) A Checklist of plant species in Vietnam (Vol. 2.). Agricultural Publishing House, 548–552.
- Nguyen BQ, Vu VD, Nguyen NC, Cao TC (1980) Vietnam Forest Trees (Vol. 3). Agricultural Publishing House, 152–153.
- Pham HH (1999) Sterculiaceae. An illustrated flora of Vietnam (Vol. 1). Youth Publishing House, Ho Chi Minh city, 491–513.
- POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. [Published on the Internet] <http://www.plantsoftheworldonline.org/> [Retrieved 09 February 2023]
- Thiers B (2023) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/> [Retrieved 11 May 2023]
- WFO (2023) World Flora Online. [Published on the Internet] <http://www.worldfloraonline.org/> [Retrieved 11 May 2023]
- Ya T, Michael GG, Laurence JD (2007) Flora of China (Vol. 12). Science Press, Beijing and Botanical Garden Press, Missouri, 303–310.

# A new species of *Piper* (Piperaceae) with peltate leaves from Serranía de las Quinchas, Colombia

M. Alejandra Jaramillo<sup>1</sup>, Dayro Rodríguez-Duque<sup>2</sup>, Magda Escobar-Alba<sup>2</sup>

<sup>1</sup> Grupo Diversitas, Facultad de Ciencias Básicas y Aplicadas, Universidad Militar Nueva Granada, km 2 Vía Cajicá-Zipacquirá, Cajicá, Colombia

<sup>2</sup> Grupo de Investigación Biodiversidad y Conservación, Museo de Historia Natural "Luis Gonzalo Andrade", Facultad de Ciencias, Universidad Pedagógica y Tecnológica de Colombia-Universidad Nacional de Colombia, Av. Central del Norte 39-115, Tunja-Boyacá, Tunja, Colombia

Corresponding author: M. Alejandra Jaramillo ([maria.jaramillo@unimilitar.edu.co](mailto:maria.jaramillo@unimilitar.edu.co))

## Abstract

*Piper quinchasense* is described and illustrated as a new species occurring in the understory of wet montane forest of the middle Magdalena Valley in Colombia, the easternmost portion of the Chocó Region. Its relationships are discussed with related taxa from the *Macrostachys* clade. An identification key for 35 Neotropical *Piper* species with peltate leaves is provided.

**Key words:** Boyacá, Chocó Region, *Macrostachys* clade, Piperales, tropical montane forests

## Resumen

*Piper quinchasense* se describe e ilustra como una nueva especie que ocurre en el sotobosque de bosques húmedos montaños del valle medio del Magdalena en Colombia, la porción más oriental del Chocó Biogeográfico. Se discuten sus relaciones con otras especies del clado *Macrostachys*. Se presenta una clave de identificación para 35 especies de *Piper* Neotropical con hojas peltadas.

**Palabras claves:** bosque montano tropical, Boyacá, Chocó Biogeográfico, clado *Macrostachys*, Piperales



Academic editor: Elton John de Lirio

Received: 3 February 2023

Accepted: 5 May 2023

Published: 29 May 2023

**Citation:** Jaramillo MA, Rodríguez-Duque D, Escobar-Alba M (2023) A new species of *Piper* (Piperaceae) with peltate leaves from Serranía de las Quinchas, Colombia. *PhytoKeys* 227: 9–24, <https://doi.org/10.3897/phytokeys.227.101405>

**Copyright:** © M. Alejandra Jaramillo et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

*Piper*, with more than 2000 species (Callejas-Posada 2020), is one of the most species-rich genera among flowering plants (Frodin 2004). *Piper* is also a common element in the understory of Neotropical forests (Gentry 1990; Draper et al. 2021). Species of *Piper* are a key resource for bats of the genus *Carollia* (Fleming 2004; Bohlender et al. 2018; Yohe et al. 2021), and they are a critical element that supports diverse trophic networks that involve moths and parasitoid wasps (Wilson et al. 2012; Slinn et al. 2018). *Piper's* enormous diversity of secondary metabolites is critical for their coexistence (Salazar et al. 2016a, 2016b) and diversification (Massad et al. 2022). And it is also of immense interest in the pharmaceutical industry (Perez Gutierrez et al. 2013; Salehi et al. 2019). This genus is, without doubt, an essential structural and trophic element

of the understory and lower strata of Neotropical forests (Salazar et al. 2016b; Draper et al. 2021).

Molecular phylogenetic studies have been instrumental in reviving the infrageneric classification of the genus, but also identifying convergence in morphological traits (Jaramillo and Callejas-Posada 2004; Trujillo et al. 2022). Molecular phylogenetics (Jaramillo and Manos 2001; Jaramillo et al. 2008) have validated the monophyly of groupings proposed in the mid-1800s (Kunth 1839; Miquel 1843). The infrageneric classification was not used during the 1900s, probably as the expeditions in the early 1900s produced too many species to classify. Today we know that *Piper* clades and subclades are easy to recognize with a combination of key morphological characters (Jaramillo et al. 2008). A formal infrageneric classification of *Piper* based on phylogeny is under preparation (Callejas pers. comm.). Molecular phylogenetics have been instrumental in clarifying the relationships of *Piper* species with “axillary” inflorescences, a polyphyletic set of taxa from the Chocó Region that were wrongly merged in the genus *Trianaeopiper* Trel. (Trelease 1928). Molecular phylogenetics demonstrated that *Trianaeopiper* is not monophyletic, revealing that the diagnostic character axillary inflorescence – which are shortened sympodial branches, is convergent (Jaramillo and Callejas-Posada 2004). Similarly, molecular phylogenetics have further supported that *Piper* species with peltate leaves are part of at least four Neotropical *Piper* clades (Trujillo et al. 2022). *Piper* classification, evolution and ecological studies have been greatly enriched with molecular phylogenetics.

Identifying *Piper* species continues to be difficult for the untrained eye, and many taxa are submerged in a few large, broadly distributed, but artificial taxa (Tebbs 1990, 1993). To the trained specialist, new *Piper* species are a common finding in the tropical forests, or even in the undetermined piles in the most important herbaria around the world. Additionally, molecular phylogenetics have confirmed the clade (subgeneric) affiliation of new species (Bornstein et al. 2014; Tepe et al. 2014; Trujillo et al. 2022). During our exploration to Serranía de las Quinchas we have identified a few undescribed species, one of the stands out because it has peltate leaves, a characteristic rarely observed in the genus.

“Serranía de las Quinchas” is a small mountain spur west of the Cordillera Oriental in the middle Magdalena Valley, in Colombia. The region’s flora is particularly interesting as it combines its own floristic elements, mixed with taxa from Mesoamerica, the Chocó Region, and Amazonia (Balcázar-Vargas et al. 2000). Additionally, various endemic species and genera occur in the area (Rodríguez-Duque et al. 2021). The middle Magdalena Valley deserves close examination and more fieldwork to uncover the history of its biological richness. For centuries, the forest has been preserved because of its scarp ridges and high rainfall. However, the construction of a pipeline and road in the 1990s opened the area to colonization (Stiles and Bohórquez 2000). Today the region is threatened by the extension of agriculture and mining activities. Fortunately, Serranía de las Quinchas Regional Park was created in 2008 by Corpoboyacá (the regional environmental protection agency) to protect the remaining forest (Bohorquez-Osorio et al. 2020). Despite the deforestation in the region, new species are still being encountered. Here we describe a new species of Neotropical *Piper* with peltate leaves that we detected during our expeditions in this interesting location.

## Materials and methods

Specimens were collected in Serranía de las Quinchas, located in the middle Magdalena Valley in Colombia, in the department of Boyacá. The sites visited range from 800–1200 m. a. s. l., the locality is dominated by humid montane forest (Fig. 1). Annual rainfall is 3333 mm on average; two dry seasons occur in January-February and June-August, and the average temperature is 26 °C (Instituto de Hidrología, Meteorología y Estudios Ambientales, IDEAM). Detailed observations in the field, combined with examination of available herbarium collections, allowed the description of growth habits and phenological stages. Voucher specimens were deposited in the following herbaria HUA, H-UPTC, and

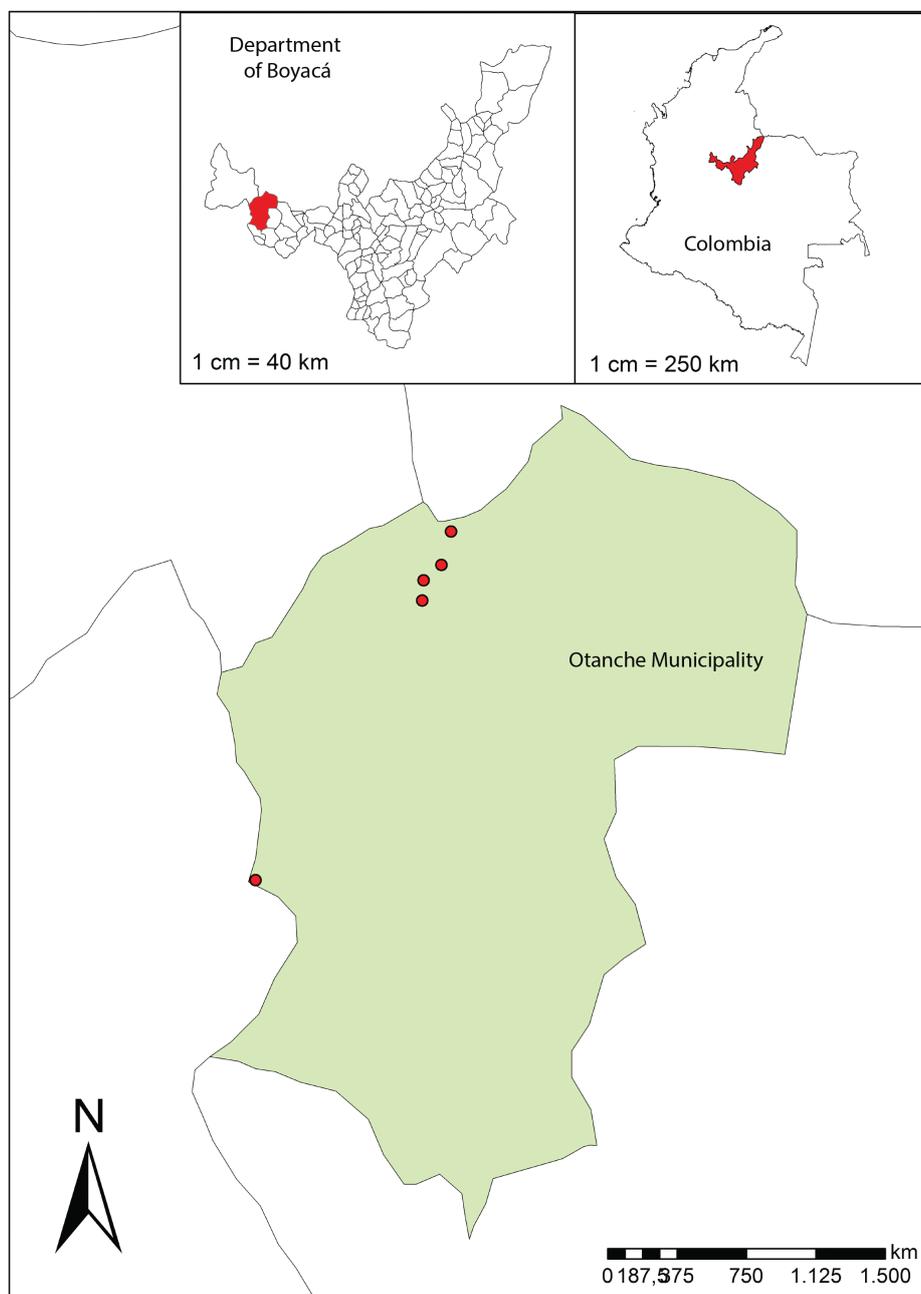


Figure 1. Geographic distribution map of *Piper quinchasense* M.A.Jaram.

**Table 1.** Genbank accessions for the new species of *Piper*.

Taxon	Voucher	Genbank Accession #
<i>Piper quinchasense</i> M. A. Jaram.	MAJ1807	OQ354973
	MAJ1939	OQ354974

UMNG-H (herbarium acronyms according to Index Herbariorum [Thiers continuously updated], and Instituto Humboldt – Red Nacional de Colecciones [http://rnc.humboldt.org.co/wp/]). In addition, taxonomic literature on *Piper* was examined (Trelease and Yuncker 1950, Steyermark 1984, Callejas-Posada 2020). The measurements included in the description below are based on herbarium specimens collected by the authors. Conservation status assessments employ the categories and criteria of the IUCN (2012, 2022). We calculated the extent of occurrence and area of occupancy using the R package *ConR* (Dauby et al. 2017).

For preparing the key of Neotropical *Piper* species with peltate leaves we used the literature (Trelease and Yuncker 1950, Steyermark 1984, Callejas-Posada 2020, Carvalho-Silva et al. 2022) and type specimens were examined using digitized plant specimens available on-line from JSTOR Global Plants (https://plants.jstor.org/).

We extracted DNA from silica gel dried tissue, using the DNAeasy plant mini kit (Qiagen, Valencia, California, USA). The ITS region was amplified using one of two pairs of primers ITS5-ITS4, or LEU1-ITS4 (Baldwin 1992). Sequencing was contracted with GenCore (Universidad de los Andes, Bogotá, Colombia). The resulting sequences (Table 1) were manually aligned against previously obtained alignments (Jaramillo et al. 2008). We selected 43 ITS sequences from the large alignment to portray here. Three sequences from *Piper* species from Asia and the South Pacific were used as outgroups. Forty sequences of Neotropical *Piper*, comprising representatives of all clades, and 14 species with peltate leaves were selected. Maximum Likelihood (ML) phylogenetic and bootstrap (100 replicates) analyses were conducted using RAxML (Stamatakis 2014).

## Taxonomic treatment

### *Piper quinchasense* M.A.Jaram., sp. nov.

urn:lsid:ipni.org:names:77320207-1

**Type.** COLOMBIA. Boyacá: Otanche, vereda Las Quinchas, Sector La Y, Finca Lote Terreno, 5°48'17"N, 75°15'24"W, 1210 m, 17 Mayo 2022 [fl], M. A. Jaramillo et al. 1807 (holotype: HUA; isotypes: UPTC, UMNG-H). Figs 1–3.

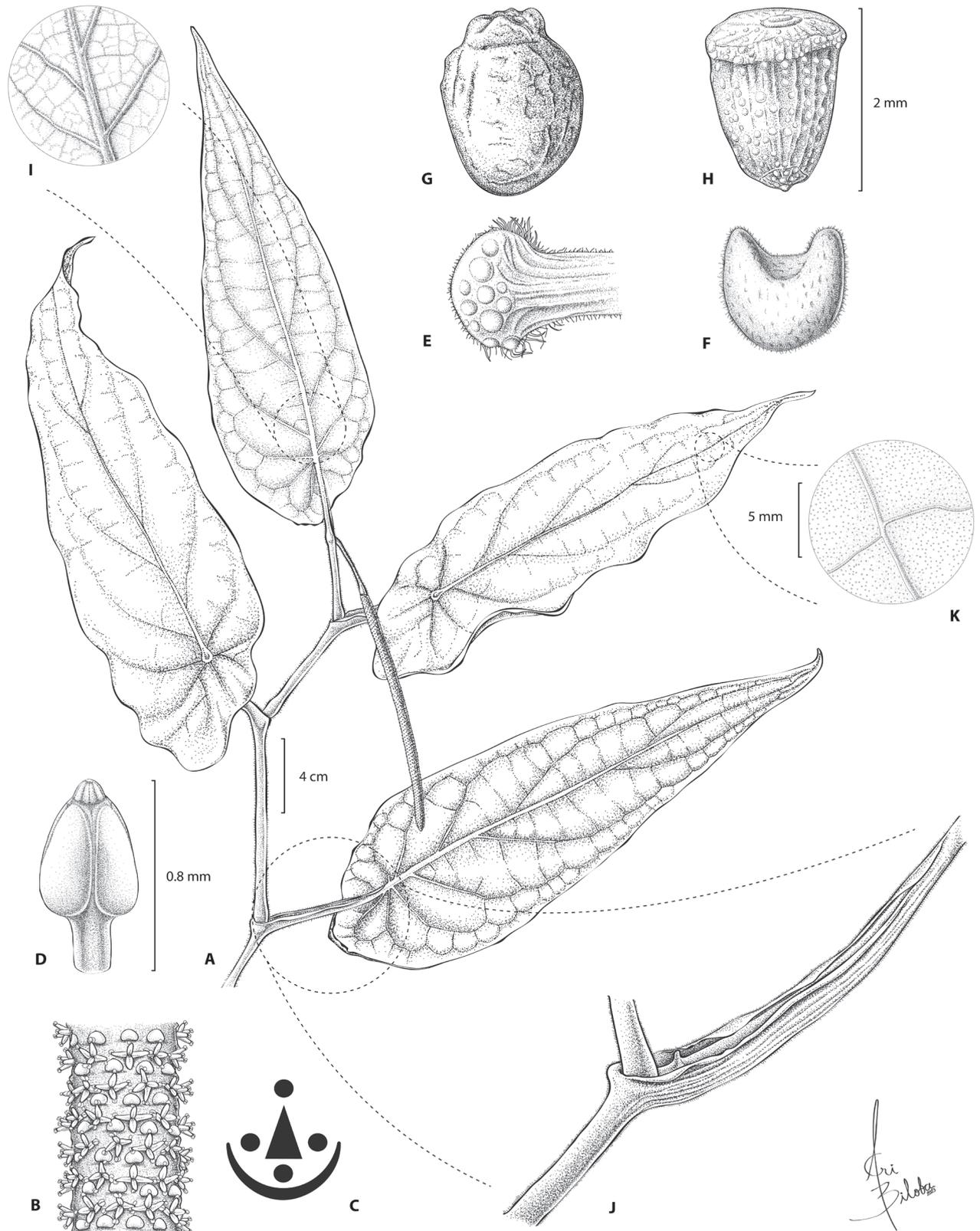
**Description.** *Piper quinchasense* is similar to *P. parianum*, it differs from the latter in having all leaf blades peltate (vs. leaves deeply lobed to peltate), and inflorescence peduncle 4–5 cm long, (vs. peduncle 1–2.7 cm long).

**Shrub**, 3 m tall, branched in the upper portion only, exhibiting stilt roots (Fig. 2C). **Internodes** 5–10 × 2.5–4.6 cm, green when young and becoming brown when maturing, tomentose, idioblasts not evident. **Prophylls** not seen. **Petioles** 4.5–8.5 cm long, vaginate the entire length (Figs 2D, 3J), tomentose, idioblasts evident. **Leaf** blades (28) 35–49 × 7.5–19 cm, oblong-lanceolate, base obliquely-peltate, asymmetric to truncate, peltate, petiole inserting 2.5–10.5 cm from the margin, on the adaxial surface leaf blade is depressed and umbonate above



**Figure 2.** *Piper quinchaense* M. A. Jaram. **A** habit **B** magnified view of inflorescence **C** stilt roots **D** sheathing petiole **E** adaxial surface of leaves **F** abaxial surface of leaves and inflorescence. Photographs by D. Rodríguez-Duque.

petiole insertion (Fig. 2E), blade medially asymmetric, apex long attenuate, green on the adaxial surface and green-silver on the abaxial surface when alive (Fig. 2E, F), coriaceous, chartaceous when dry, drying dark maroon on the adaxial surface and ochre on the abaxial surface, glabrous with visible idioblasts on the adaxial surface (Fig. 3K), sparsely tomentose on the blade and veins densely tomentose on the abaxial surface (Fig. 3I), eciliate, margin folds towards the abaxial surface appearing to form irregular spaced teeth; pinnately nerved to the distal third, 4–6 pairs of secondary veins, curved and ascending, diverging in angles that decrease towards the apex (from 80–30 degrees) and spacing slightly decreasing towards the base, tertiary veins forming areoles 1.2–1.8 × 0.5–1 cm, rectangular and not uniform in size, perpendicular to secondary nerves, nerves not impressed on the adaxial surface, elevated on the abaxial surface. **Inflorescences** a simple spike, terminal, pendulous; peduncle 4.5–5 cm long, tomentose, green, idioblasts not evident; rachis length in flower 12–19 cm × 3–4 mm, rachis length in fruit 25–27 cm. **Floral bracts** cucullate, sagitate from above (Fig. 3F), 1.8–2.3 × 0.9–1.0 mm, pellucid dotted, pedicel fimbriate on the distal portion (Fig. 3E), forming bands around the spike (Fig. 3B). **Flowers** sessile with 4 stamens (Fig. 3C), filaments 0.25–0.40 mm long, anthers 0.3–0.6 × 0.16–0.26 long, with connective glabrate, longitudinally dehiscent, ditheous (Fig. 3D), ovary four carpellate, four stigmas sessile, not persistent in fruit, 0.4–0.5 mm long



**Figure 3.** *Piper quinchaense* M. A. Jaram. **A** sympodial branch, showing both the abaxial and adaxial surface of the leaves **B** magnified view of inflorescence **C** floral diagram **D** anther **E** floral bract, abaxial view **F** floral bract view from above **G** fruit **H** seed **I** magnified view of leaf abaxial surface **J** sheathing petiole **K** magnified view of leaf adaxial surface. Illustration by Ariadna Valenzuela, based on M. Escobar-Alba 764, and photographs by D. Rodríguez-Duque.

(Figs 2B, 3G). **Fruits** obpyriform, 2.1–2.4 × 1.0–1.6 mm, glabrous, green when alive, brown when dry (Fig. 3G). **Seeds** smooth, pellucid dotted, obpyriform, 1.9–2.1 × 1.0–1.3 mm, glabrous, brown when dry (Fig. 3H).

**Phylogenetic relationships.** *Piper quinchasense* belongs to the *Macrostachys* clade (Fig. 4). A group of shrubs and treelets reaching 7–8 (15) m tall, petioles sheathing above the middle or throughout their length, pinnately nerved leaves, mostly larger than 30cm long, inflorescences mostly pendulous (erect in some species), and flowers forming bands around the spike (Jaramillo et al. 2008). Species with peltate leaves have evolved independently in clades *Macrostachys*, *Pothomorphe*, *Oxodium* (= *Schilleria*, Callejas 2020) and *Ottonia*. Peltate leaves are known to occur in the two large genera of Piperaceae: *Piper* and *Peperomia*. They are more common in plants that grow in the shade of humid tropical forests (Wunnenberg et al. 2021). There is still much to learn about the functional morphology and anatomy of *Piper* species with peltate leaves.

**Distribution and habitat.** The species is only known from the type locality Serranía de las Quinchas (Fig. 1). *Piper quinchasense* is a tall shrub in the understory of very humid forests; it often grows near streams. The occurrence of stilt roots (Fig. 2C), a character not commonly seen in *Piper*, suggests it is adapted for flooded areas near watercourses. It also is a very resilient plant that will produce adventitious roots if tumbled and it will continue growing, or even resprout, from a fallen leaf. Resprouting is common among shade-tolerant *Piper* (Lasso et al. 2009).

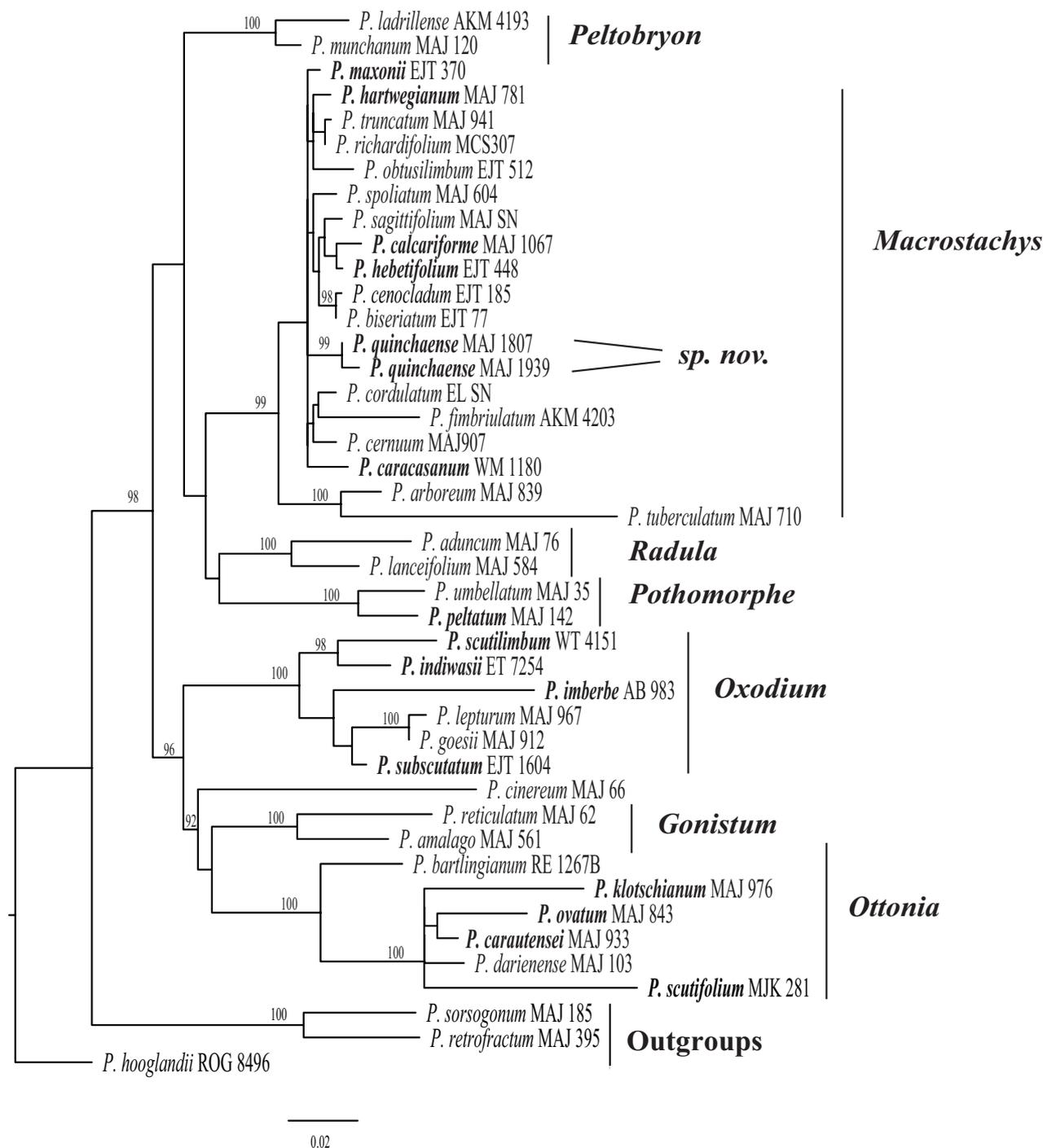
**Phenology.** Flowering specimens were collected in March, and May. Fruiting specimens were collected in October.

**Etymology.** The epithet *quinchasense*, refers to Serranía de las Quinchas, the type locality for this species. According to locals, Quinchas derives from the indigenous groups “Quinchos” that inhabited the region.

**Conservation status.** This species is known only from one population in the type locality (Fig. 1). The extent of occurrence (E00) of 8 km<sup>2</sup> and area of occupancy (AOO) of 8 km<sup>2</sup> are very small. The locality is under threat of disappearing for the extension of agricultural and mining activities (Rodríguez-Duque et al. 2021), which suggests it is Endangered [EN B1a]. Serranía de las Quinchas was declared a Regional Park in 2008; since its creation, the park extension has been reduced by 20% as the buffer zones were eliminated. Furthermore, the constant threat of coal mining makes the locality highly exposed to deforestation.

**Additional specimens examined.** COLOMBIA. —Boyacá: Otanche, vereda Las Quinchas, Sector La Y, Finca Lote Terreno, 5°48'17"N, 75°15'24"W, 26 October 2022, [fr] M. A. Jaramillo et al 1939 (HUA, UMNG-H); Boyacá: Otanche, Parque Regional Natural, Serranía de las Quinchas, 5°48'45.5"N, 75°15'22.2"W, [st] 14 June 2021, Magda Escobar-Alba et al. 489 (UPTC); Parque Regional Natural Serranía de las Quinchas, vereda las Quinchas, Finca Chorro Negro, 5°49'7.2"N, 75°14'57.3"W, [fl] 3 March 2022, Magda Escobar-Alba et al. 762 (UPTC).

**Notes.** *Piper quinchasense* is a handsome species that differs from related *Macrostachys* taxa in having long lanceolate-oblong leaves. It is morphologically similar to *P. parianum* from which it differs in having monomorphic leaves (all of them peltate) vs. leaves dimorphic, some peltate and others are deeply lobed. *P. parianum* is only known in the isolated cloud forests of “Peninsula de Paria”, a region located in the eastern portion



**Figure 4.** Phylogenetic relationships of *Piper quinchasense* M. A. Jaram. and 14 species of Neotropical *Piper* with peltate leaves (in bold). Topology based on Maximum likelihood analysis of nrITS sequences. Numbers on branches are maximum likelihood bootstrap support values (>90%).

of Coastal Cordillera in the extreme northeast of Venezuela. The flora of Paria Peninsula is characterized by the high occurrence of endemic species (Steyermark and Agostini 1966; Meier 2011) and several types of vegetation communities (Beard 1946). The flora of this region has many affinities to plants of Trinidad and Tobago (*Selaginella hartii* Hieron.; – Selaginellaceae; 5 Turrill – Acanthaceae: sensu Baksh-comeau et al. 2016), and the forests

of the Northeastern sector of Guayana Shield in Venezuela and the Guianas (e.g., *Besleria insolita* C.V. Morton – Gesneriaceae; Meier 2011). Serranía de las Quinchas, on the other hand, has the most floristic affinities with the Chocó region (e. g. *Dimerocostus cryptocalyx* N. R. Salinas & Betancur, Salinas and Betancur 2004). The regions have similar habitats driven by high precipitations despite their divergent biogeographical affinities.

A key to species of Neotropical *Piper* with peltate leaves is presented below.

### New status

While preparing the key for peltate Neotropical *Piper*, we realized some species deserve new status. New status and new names are proposed for two species.

#### ***Piper neovenezuelense* M.A.Jaram., stat. nov et nom. nov.**

urn:lsid:ipni.org:names:77320208-1

**Basionym.** *Piper veraguense* C. DC. var. *venezuelense* Steyermark. Fl. Venez. 2(2): 590 (1984). Type: Venezuela, Edo. Trujillo, 16 km de Boconó a lo largo de la carretera a Biscucuy, 1850 m, 11 aug 1964, F. Breteler 4082 (Holotype; VEN; Isotype: MER). Non *Piper venezuelense* C.DC., J. Bot. 4: 216 (1866).

**Note.** The epithet *P. neovenezuelense* is proposed here to replace *Piper veraguense* C. DC. var. *venezuelense* Steyermark. Because *Piper venezuelense* C. DC. (De Candolle 1866: 216) is already in use.

**Etymology.** The new epithet *neovenezuelense* honors the intention of J. Steyermark to highlight the occurrence of this species in Venezuela.

Steyermark (1984) synonymized under *P. veraguense* C. DC. various distinct species: *P. albert-smithii* Trel. & Yunck., and *P. mutisii* Trel. & Yunck., and proposed that *P. veraguense* C. DC. has three varieties: *P. veraguense* var. *veraguense*, *P. veraguense* var. *mutisii* (Trel. & Yunck.) Steyermark, and he added *P. veraguense* var. *venezuelense* Steyermark (Steyermark 1984). These species are similar in their overall morphology and potentially form a species complex. Unfortunately, we do not have sequence data to test the latter hypothesis. Here we consider them separate species. *P. veraguense* has glabrous leaves with nerves puberulent on the abaxial surface, not pellucid dotted (Callejas-Posada 2020); *P. albert-smithii* is distinct because it has fleshy warts below the nodes, and leaves are glabrous (Trelease and Yuncker 1950); and *P. mutisii* has fleshy warts below the nodes, nerves are dense velvety puberulent on abaxial surface; *P. neovenezuelense* has glabrous internodes without warty outgrowths, and nerves pilose on abaxial surface.

#### ***Piper andersii* M.A.Jaram., stat. nov. et nom. nov.**

urn:lsid:ipni.org:names:77320209-1

*Piper mikanianum* Steud. var. *peltatum* Yunck., Bol. Inst. Bot. (São Paulo) no. 3: 54 (1966). Type: Brazil, Minas Gerais, Caldas, A. F. Regnell II 256\*, 9 Jul 1864. Non *Piper peltatum* L.

**Note.** The epithet *P. andersii* is proposed here to replace *Piper mikanianum* Steud. var. *peltatum* Yunck. because *Piper peltatum* L., (Sp. Pl. 1: 30 1753) is already in use.

**Etymology.** The new epithet *andersii* honors Anders Fredrik Regnell (1807–1884), Swedish physician and botanist who established himself in Minas Gerais (Brazil) and collected the type specimen for this species.

T. Yuncker provided a key to four varieties of *Piper mikanianum* (Kunth) Steud: *P. mikanianum* (Kunth) Steud var. *mikanianum*; *P. mikanianum* f. *clausum* characterized by the closed sinus and overlapping lobes; *P. mikanianum* var. *pilosius* C. DC. with leaves and stems strongly pilose with hairs up to 1 mm long; and *P. mikanianum* var. *peltatum* Yunck with peltate leaves and nerves minutely hirtellous on the abaxial surface (Yuncker 1972). Yuncker had mentioned that this latter variety might deserve species rank, we propose to make the change suggested and propose the new name *P. andersii*. Furthermore, *P. mikanianum* occurs in the states of Minas Gerais, Paraná and Rio Grande do Sul in Brazil and in Argentina, *P. andersii*, with peltate leaves has only been registered from the state of Minas Gerais.

### Key to Neotropical *Piper* species with peltate leaves

- 1 Leaves subpeltate, petiole inserted slightly inside the leaf margin ..... **2**
- Leaves peltate, petiole inserted 0.5–11 cm from the leaf margin ..... **12**
- 2 Leaves ovate-lanceolate or elliptic, up to 18 cm long, petioles terete ..... **3**
- Leaves ovate, ovate –oblong or elliptic, more than 20 cm long, petioles sheathing ..... **5**
- 3 Inflorescence a raceme with glabrous to sparsely pubescent rachis ..... **4**
- Inflorescence a spike, with pubescent rachis .....  
..... ***P. klotzschianum* (Kunth) C. DC.**
- 4 Leaves elliptic and glabrous without hirtellous intramarginal nerve .....  
..... ***P. brumadinense* M. Carv.-Silva & E. Guim.**
- Leaves ovate, intramarginal nerve hirtellous on abaxial surface .....  
..... ***P. ovatum* Vahl**
- 5 Petioles sheathing only at the base, nerves puberulent on the abaxial surface ..... **6**
- Petioles sheathing over half their length, leaves and nerves glabrous or pubescent ..... **7**
- 6 Leaves 35–20 cm long, base lobate ..... ***P. omega* Trel.**
- Leaves 10–20 cm long, base barely cordate .....  
..... ***P. marginecontinuum* Callejas**
- 7 Leaf base rounded or cordate, inflorescences erect ..... **8**
- Leaf base lobate, inflorescences pendulous ..... **9**
- 8 Leaf ovate, leaf base rounded, peduncle up to 0.5 cm long .....  
..... ***P. palenquense* Callejas**
- Leaf broadly ovate, leaf base deeply cordate, sinus open, peduncle 0.7–1 cm long ..... ***P. vallicola* C. DC.**
- 9 Leaves more than 35 cm long, inflorescences 50–60 long ..... **10**
- Leaves up to 26 cm long, inflorescences up to 20 cm long ..... **11**

- 10 Leaves up to 50cm long, sinus closed, longer lobe overlapping the petiole, peduncle 1.5–2.7cm long ..... ***P. caracasenum* Bredem. ex Link**
- Leaves up to 35cm long, sinus open, peduncle 7 cm long ..... ***P. gualeanum* C. DC.**
- 11 Petioles shortly pubescent, inflorescences 10–20 cm long ..... ***P. calcariforme* Tebbs**
- Petioles with trichomes forming lines, inflorescences 6–9 cm long..... ***P. hebetifolium* W. C. Burger**
- 12 Plants herbaceous, inflorescences spikes, arranged in umbels ..... ***P. peltatum* L.**
- Shrubs, suffrutex, or climbers, inflorescences solitary racemes or spikes... **13**
- 13 Leaves 10–30 cm long, inflorescences erect..... **14**
- Leaves 35 cm long or longer, inflorescences erect or pendulous..... **31**
- 14 Lianescent vines..... **15**
- Shrubs or suffrutex..... **17**
- 15 Internodes, petioles and leaves glabrous, leaf blade ovate or oblong-elliptic, smooth ..... **16**
- Internodes, petioles and abaxial leaf surface pilose, leaf blade obovate, slightly bullate..... ***P. parmatum* Dressler**
- 16 Leaf blades with evident idioblasts on abaxial surface, spikes 1–2 cm long, with obtuse apices ..... ***P. foreroi* Gentry**
- Leaf blades without visible idioblasts, spikes 5–6 cm long with mucronate apices..... ***P. peltifolium* Callejas**
- 17 Leaf base lobed or cordate..... **18**
- Leaf base rounded, obtuse or scutellate ..... **24**
- 18 Leaves rounded –ovate, leaf base deeply cordate..... ***P. andersii* M.A.Jaram., stat nov. nom nov.**
- Leaves ovate, leaf base cordate or lobed ..... **19**
- 19 Shrubs densely crisp –villous..... ***P. copeyanum* (C.DC) Trel.**
- Shrubs glabrous ..... **20**
- 20 Idioblasts visible on both surfaces ..... ***P. subscutatum* (Miq.) C. DC.**
- Idioblasts not visible ..... **21**
- 21 Petioles vaginate at the base, flowers not forming bands on the spikes ... **22**
- Petioles vaginate half the length or more, flowers forming bands on the spikes ..... ***P. maxonii* C. DC.**
- 22 Leaves 5–10 cm wide, petiole inserted ca. 1 cm from the margin..... ***P. jacaleapaense* Callejas**
- Leaves 15 –20 cm wide, petiole inserted 5–6 cm from the margin ..... **23**
- 23 Leaves broadly ovate, glabrous on both surfaces..... ***P. veraguense* C. DC.**
- Leaves elliptic-oblong to ovate, nerves on the abaxial surface pilose..... ***P. neovenezuelense* M.A.Jaram., stat. nov. nom nov.**
- 24 Leaves glabrous ..... **25**
- Leaves pubescent at least abaxially on veins ..... **27**
- 25 Leaves oblong-lanceolate, leaf base rounded ..... ***P. imberbe* Trel.**
- Leaves ovate, leaf base obtuse or spatulate ..... **26**
- 26 Leaf base narrowly spatulate ..... ***P. indiwassii* W. Trujillo & M.A.Jaram.**
- Leaf base broadly obtuse ..... ***P. scutilimum* C. DC.**

- 27 Apex short acuminate, inflorescence obtuse .....28  
 – Apex long attenuate, inflorescences mucronate.....*P. tuerckheimii* C. DC.  
 28 Flowers forming bands around the spike ..... *P. hammelii* Callejas  
 – Flowers laxly arranged in a spike or raceme .....29  
 29 Plant glabrous, inflorescences a spike .....*P. scutifolium* Yunck.  
 – Villous shrub, inflorescence a raceme .....30  
 30 Petiole inserted ca. 1 cm from margin, with visible idioblasts on leaf lamina ..... *P. cariacicaense* M. Carv.-Silva & E.F.Guim.  
 – Petiole inserted 0.5 cm from margin, without visible idioblasts on leaf lamina..... *P. carautensei* E.F.Guim. & M. Carv.-Silva  
 31 Leaves broadly ovate, petiole vaginate to the middle.....32  
 – Leaves ovate, lanceolate or oblong, petiole vaginate above the middle...33  
 32 Leaf base rounded, inflorescence short-apiculate...*P. mutisii* Trel. & Yunck.  
 – Leaf base cordate, inflorescence obtuse.....*P. grandilimbus* C. DC.  
 33 Internodes warty above nodes, leaves glabrous .....  
 ..... *P. albert-smithii* Trel. & Yunck.  
 – Internodes smooth, leaves pubescent or tomentose, at least on the abaxial surface .....34  
 34 Leaf strongly bullate..... *P. hartwegianum* (Benth.) C. DC.  
 – Leaves not bullate, or occasionally softly bullate .....35  
 35 Leaves elliptic-ovate, apex acute or short acuminate.....36  
 – Leaves oblong-lanceolate, apex gradually acuminate or long attenuate...37  
 36 Heteromorphic trichomes of intermixed on the abaxial surface, inflorescence up to 43 cm long.....*P. peltilimbus* Yunck.  
 – Trichomes of uniform length on the abaxial surface, inflorescences 50–60 cm long ..... *P. candollei* Sodiro  
 37 Leaves 14–26 cm wide, leaf base deeply cordate sub-peltate to obliquely peltate ..... *P. parianum* Yunck.  
 – Leaves 7.5–19 cm wide, leaf base obliquely peltate .....  
 ..... *P. quinchasense* M.A.Jaram., sp. nov.

## Acknowledgements

We thank Juan E. Carvajal Cogollo for his assistance, Ariadna Valenzuela Zúñiga for preparing the illustration, A. F. Majin for field assistance, and Jenny Peña Varon for preparing the distribution map. We thank G. Aymard-Corredor, M. Carvalho-Silva, E. Tepe, E. J. Lirio and one anonymous reviewer for comments on previous versions of the manuscript. We thank K. Gandhi for his expert advice on nomenclatural issues regarding the new names proposed here. Special thanks to the Galvis Family: Don Lucindo, Doña Edilsa and Leidy for hosting our field expeditions in Serranía de las Quinchas. Don Lucindo's expert guidance in the forest was key to finding the plants. This work was supported by project "BPIN No. 2020000100003 – Investigación de la biodiversidad de Boyacá: complementación y síntesis a través de gradientes altitudinales e implicaciones de su incorporación en proyectos de apropiación social de conocimiento y de efectos de cambio climático." Funds for field expeditions were also provided by Universidad Militar Nueva Granada as part of the Plant Taxonomy and Systematics course. Gencore (Sequencing Center) at Los Andes University partially subsidized the sequencing analysis.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Conceptualization: MAJ. Investigation: DRD, MEA. Writing – original draft: MAJ.

### Author ORCIDs

M. Alejandra Jaramillo  <https://orcid.org/0000-0002-6539-4149>

Dayro Rodríguez-Duque  <https://orcid.org/0000-0002-3829-3377>

Magda Escobar-Alba  <https://orcid.org/0000-0002-3756-9132>

### Data availability

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

## References

- Baksh-Comeau YS, Maharaj SS, Adams CD, Hawthorne WD (2016) An annotated checklist of the vascular plants of Trinidad and Tobago with analysis of vegetation types and botanical “hotspots.” *Phytotaxa* 250: 1–431. <https://doi.org/10.11646/phytotaxa.250.1.1>
- Balcázar-Vargas M, Rangel-Ch JO, Linares E (2000) Diversidad florística de la Serranía de Las Quinchas, Magdalena Medio (Colombia). *Caldasia* 22: 191–224. <http://www.revistas.unal.edu.co/index.php/cal/article/viewFile/17571/18415>
- Baldwin BG (1992) Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: An example from the Compositae. *Molecular Phylogenetics and Evolution* 1(1): 3–16. [https://doi.org/10.1016/1055-7903\(92\)90030-K](https://doi.org/10.1016/1055-7903(92)90030-K)
- Beard JS (1946) Notes on the vegetation of the Paria Peninsula, Venezuela. *Caribbean Forester* 7: 37–46.
- Bohlender EE, Pérez-Torres J, Borray-Escalante NA, Stevens RD (2018) Dietary variation during reproduction in Seba’s short-tailed fruit bat. *Journal of Mammalogy* 99(2): 440–449. <https://doi.org/10.1093/jmammal/gyx189>
- Bohorquez-Osorio AF, Ulián T, Díazgranados M (2020) Guía de plantas útiles de la Serranía de las Quinchas. *Ecología, Economía y Ética, Rutas Turísticas por los Bosques y la Paz*. Royal Botanic Gardens, Kew, E3, UK.
- Bornstein AJ, Smith JF, Tepe EJ (2014) Two new species of *Piper* from the greater antilles. *Systematic Botany* 39(1): 10–16. <https://doi.org/10.1600/036364414X678206>
- Callejas-Posada R (2020) Piperaceae. In: Davidse G, Ulloa Ulloa C, Hernández Macías HM, Knapp S (Eds) *Flora Mesoamericana* 2. Missouri Botanical Garden Press, Saint Louis.
- Carvalho-Silva M, Eduardo P, Saraiva A, Guimarães EF (2022) Synopsis of the *Piper* subgenus *Ottonia* Spreng. (Piperaceae) from Brazil, 2: 1–25. <https://doi.org/10.1590/1677-941x-abb-2021-0360>

- Dauby G, Stévant T, Droissart V, Cosiaux A, Deblauwe V, Simo-Droissart M, Sosef M, Lowry P, Schatz GE, Gereau RE, Couvreur TL (2017) *ConR*: An R package to assist large-scale multispecies preliminary conservation assessments using distribution data. *Ecology and Evolution* 7(24): 11292–11303. <https://doi.org/10.1002/ece3.3704>
- De Candolle C (1866) Piperaceae Novae. *Journal of Botany, British and Foreign* 4: 210–219.
- Draper FC, Costa FRC, Arellano G, Phillips OL, Duque A, Macía MJ, ter Steege H, Asner GP, Berenguer E, Schiatti J, Socolar JB, de Souza FC, Dexter KG, Jørgensen PM, Tello JS, Magnusson WE, Baker TR, Castilho CV, Monteagudo-Mendoza A, Fine PVA, Ruokolainen K, Coronado ENH, Aymard G, Dávila N, Sáenz MS, Paredes MAR, Engel J, Fortunel C, Paine CET, Goret JY, Dourdain A, Petronelli P, Allie E, Andino JEG, Brienen RJW, Pérez LC, Manzatto ÂG, Zambrana NYP, Molino JF, Sabatier D, Chave J, Fauset S, Villacorta RG, Réjou-Méchain M, Berry PE, Melgaço K, Feldpausch TR, Sandoval EV, Martinez RV, Mesones I, Junqueira AB, Roucoux KH, de Toledo JJ, Andrade AC, Camargo JL, del Aguila Pasquel J, Santana FD, Laurance WF, Laurance SG, Lovejoy TE, Comiskey JA, Galbraith DR, Kalamandeen M, Aguilar GEN, Arenas JV, Guerra CAA, Flores M, Llampazo GF, Montenegro LAT, Gomez RZ, Pansonato MP, Moscoso VC, Vleminckx J, Barrantes OJV, Duivenvoorden JF, de Sousa SA, Arroyo L, Perdiz RO, Cravo JS, Marimon BS, Junior BHM, Carvalho FA, Damasco G, Disney M, Vital MS, Diaz PRS, Vicentini A, Nascimento H, Higuchi N, Van Andel T, Malhi Y, Ribeiro SC, Terborgh JW, Thomas RS, Dallmeier F, Prieto A, Hilário RR, Salomão RP, Silva RC, Casas LF, Vieira ICG, Araujo-Murakami A, Arevalo FR, Ramírez-Angulo H, Torre EV, Peñuela MC, Killeen TJ, Pardo G, Jimenez-Rojas E, Castro W, Cabrera DG, Pipoly J, de Sousa TR, Silvera M, Vos V, Neill D, Vargas PN, Vela DM, Aragão LEOC, Umetso RK, Sierra R, Wang O, Young KR, Prestes NCCS, Massi KG, Huaymacari JR, Gutierrez GAP, Aldana AM, Alexiades MN, Baccaro F, Céron C, Muelbert AE, Rios JMG, Lima AS, Lloyd JL, Pitman NCA, Gamarra LV, Oroche CJC, Fuentes AF, Palacios W, Patiño S, Torres-Lezama A, Baraloto C (2021) Amazon tree dominance across forest strata. *Nature Ecology & Evolution* 5(6): 757–767. <https://doi.org/10.1038/s41559-021-01418-y>
- Fleming TH (2004) Dispersal ecology of Neotropical *Piper* shrubs and treelets. In: Dyer L, Palmer AN (Eds) *Piper: A Model Genus for Studies of Phytochemistry, Ecology, and Evolution*. Kluwer Academic/Plenum Publishers, Boston, 58–77. [https://doi.org/10.1007/978-0-387-30599-8\\_4](https://doi.org/10.1007/978-0-387-30599-8_4)
- Frodin DG (2004) History and concepts of big plant genera. *Taxon* 53(3): 753–776. <https://doi.org/10.2307/4135449>
- Gentry AH (1990) Floristic similarities and differences between southern Central America and upper Central Amazonia. In: Gentry AH (Ed.) *Four Neotropical rainforests*. Yale University Press, New Haven, Connecticut, USA., 141–157.
- IUCN (2012) Guidelines for application of IUCN Red List criteria at regional and national levels: Version 4.0. IUCN, Gland, Switzerland, 41 pp.
- IUCN (2022) 1 Guidelines for Using the IUCN Red List Categories and Criteria.
- Jaramillo MA, Callejas-Posada R (2004) A reappraisal of *Trianaeopiper* Trelease: Convergence of dwarf habit in some *Piper* species of the Chocó. *Taxon* 53(2): 269–278. <https://doi.org/10.2307/4135607>
- Jaramillo MA, Manos PS (2001) Phylogeny and the patterns of floral diversity in the genus *Piper* (Piperaceae). *American Journal of Botany* 88(4): 706–716. <https://doi.org/10.2307/2657072>
- Jaramillo MA, Callejas-Posada R, Davidson C, Smith JF, Stevens AC, Tepe EJ (2008) A phylogeny of the tropical genus *Piper* using ITS and the chloroplast intron psbJ – petA. *Systematic Botany* 33(4): 647–660. <https://doi.org/10.1600/036364408786500244>

- Kunth K (1839) Bemerkungen über die Familie der Piperaceen. *Linnaea* 13: 562–726. <https://doi.org/10.5962/bhl.title.110118>
- Lasso E, Engelbrecht BMJ, Dalling JW (2009) When sex is not enough: Ecological correlates of asexual reproductive ability in eight co-occurring *Piper* species in Panama. *Oecologia* 161: 43–56. <https://doi.org/10.1007/s00442-009-1353-6>
- Massad TJ, Richards LA, Philbin C, Yamaguchi LF, Kato MJ, Jeffrey CS, Oliveira C, Ochsenrider K, de Moraes MM, Tepe EJ, Cebrian Torregón G, Sandivo M, Dyer LA (2022) The chemical ecology of tropical forest diversity: Environmental variation, chemical similarity, herbivory, and richness. *Ecology* 103(9): 1–12. <https://doi.org/10.1002/ecy.3762>
- Meier W (2011) Los bosques nublados de la Cordillera de La Costa de Venezuela. *Biollania* 10: 106–121.
- Miquel FAG (1843) *Systema Piperacearum*. Rotterdam, 304 pp. <https://doi.org/10.5962/bhl.title.151>
- Perez Gutierrez RM, Neira Gonzalez AM, Hoyo-Vadillo C (2013) Alkaloids from *Piper*: A Review of its Phytochemistry and Pharmacology. *Mini-Reviews in Medicinal Chemistry* 13(2): 163–193. <https://doi.org/10.2174/138955713804805148>
- Rodríguez-Duque DL, Allende JRG, García-González JD, Escobar-Alba M, Hernández-Avendaño P, Aymard-Corredor GA (2021) Rediscovering *Ternstroemia killipiana* (Pentapetalaceae, S.L.), a Colombian Andes species not collected since 1926: Its geographic distribution and current conservation status. *Harvard Papers in Botany* 26(2): 449–454. <https://doi.org/10.3100/hpib.v26iss2.2021.n11>
- Salazar D, Jaramillo MA, Marquis RJ (2016a) Chemical similarity and local community assembly in the species rich tropical genus *Piper*. *Ecology* 97(11): 3176–3183. <https://doi.org/10.1002/ecy.1536>
- Salazar D, Jaramillo MA, Marquis RJ (2016b) The impact of plant chemical diversity on plant-herbivore interactions at the community level. *Oecologia* 181(4): 1199–1208. <https://doi.org/10.1007/s00442-016-3629-y>
- Salehi B, Zakaria ZA, Gyawali R, Ibrahim SA, Rajkovic J, Shinwari ZK, Khan T, Sharifi-Rad J, Ozleyen A, Turkdonmez E, Valussi M, Tumer TB, Fidalgo LM, Martorell M, Setzer WN (2019) *Piper* species: A comprehensive review on their phytochemistry, biological activities and applications. *Molecules* 24(7): 1364 <https://doi.org/10.3390/molecules24071364>
- Salinas NR, Betancur J (2004) Una nueva especie de *Dimerocostus* (costaceae) de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas. Físicas y Naturales* 28: 465–470.
- Slinn HL, Richards LA, Dyer LA, Hurtado PJ, Smilanich AM (2018) Across multiple species, phytochemical diversity and herbivore diet breadth have cascading effects on herbivore immunity and parasitism in a tropical model system. *Frontiers in Plant Science* 9: 1–12. <https://doi.org/10.3389/fpls.2018.00656>
- Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Steyermark JA (1984) *Flora de Venezuela. Piperaceae. Vol. 2 Segunda Parte*. Ediciones Fundación Educación Ambiental, Caracas, Venezuela, 619 pp.
- Steyermark JA, Agostini G (1966) Exploración Botánica del Cerro Patao y zonas adyacentes a Puerto Hierro en la Península de Paria, Edo. Sucre. *Acta Botanica Venezuelica* 1: 7–80.
- Stiles F, Bohórquez CI (2000) Evaluando el estado de la biodiversidad: el caso de la avifauna de la Serranía de las Quinchas, Boyacá, Colombia. *Caldasia* 22: 61–92.

- Tebbs MC (1990) Revision of *Piper* (Piperaceae) in the New World. 1. Review of characters and taxonomy of *Piper* section *Macrostachys*. Bulletin of the Natural History Museum of London 19: 117–158.
- Tebbs MC (1993) Revision of *Piper* (Piperaceae) in the New World, 3. The taxonomy of *Piper* sections *Lepianthes* and *Radula*. Bulletin of the Natural History Museum of London 23: 1–50.
- Tepe EJ, Rodríguez-Castañeda G, Glassmire AE, Dyer LA (2014) *Piper kelleyi*, a hotspot of ecological interactions and a new species from Ecuador and Peru. PhytoKeys 2014: 19–32. <https://doi.org/10.3897/phytokeys.34.6376>
- Thiers B (2023) Index Herbariorum A global directory of public herbaria and associated staff. <http://sweetgum.nybg.org/ih/>
- Trelease W (1928) *Trianaeopiper*, a new genus of Piperaceae. Proceedings of the American Philosophical Society 67: 47–50.
- Trelease W, Yuncker TG (1950) The Piperaceae of Northern South America. University of Illinois Press, Indiana.
- Trujillo W, Trujillo ET, Ortiz-Morea FA, Toro DA, Jaramillo MA (2022) New *Piper* species from the eastern slopes of the Andes in northern South America. PhytoKeys 206: 25–48. <https://doi.org/10.3897/phytokeys.206.75971>
- Wilson JS, Forister ML, Dyer LA, Connor JMO, Burls K, Feldman CR, Jaramillo MA, Miller JS, Rodri G, Tepe EJ, Whitfield JB, Young B (2012) Host conservatism, host shifts and diversification across three trophic levels in two Neotropical forests. Journal of Evolutionary Biology 25(3): 1–15. <https://doi.org/10.1111/j.1420-9101.2011.02446.x>
- Wunnenberg J, Rjosk A, Neinhuis C, Lautenschläger T (2021) Strengthening structures in the petiole-lamina junction of peltate leaves. Biomimetics 6: 25. <https://doi.org/10.3390/biomimetics6020025>
- Yohe LR, Leiser-Miller LB, Kaliszewska ZA, Donat P, Santana SE, Dávalos LM (2021) Diversity in olfactory receptor repertoires is associated with dietary specialization in a genus of frugivorous bat. G3: Genes, Genomes. G3 (Bethesda, Md.) 11(10): jkab260. <https://doi.org/10.1093/g3journal/jkab260>
- Yuncker TG (1972) The Piperaceae of Brazil, I. *Piper*-group I, II, III and IV. Hoehnea 19: 336.

# *Primula jiaozishanensis* (Primulaceae), a new species in *Primula* sect. *Petiolares* subsect. *Davidii* from Yunnan, China

Yuan Wu<sup>1</sup>, Wu-Hai Yang<sup>1</sup>, Zhi-Kun Wu<sup>1</sup>

<sup>1</sup> Department of Pharmacy, Guizhou University of Traditional Chinese Medicine, Guiyang, 550025, Guizhou, China

Corresponding author: Zhi-Kun Wu (47390933@qq.com)

## Abstract

*Primula jiaozishanensis* Z.K.Wu, W.H.Yang & Yuan Wu, a new species of Primulaceae is described and illustrated from Jiaozi Snow Mountain of Dongchuan District, Yunnan, China. Morphological evidence supports *P. jiaozishanensis* as a member of *P.* sect. *Petiolares* subsect. *Davidii*, which is characterized by firmly papery or leathery leaves, with veins impressed adaxially, often prominently raised and alveolate abaxially. The new species is characterized by having long and stout rhizomes, smaller leaves with short petioles, short or almost obsolete scape, and larger flowers. The distribution, phenology and conservation status of the new species are also provided.

**Key words:** Jiao zi shan bao chun, new species, *Primula* sect. *Petiolares*, Yunnan

## Introduction

*Primula* L. is one of the largest genera in Primulaceae, comprising ca. 500 species worldwide (Hu 1990; POWO 2023). Most of the species occur in temperate and alpine regions of the Northern Hemisphere, e.g., ca. 75% of the total species are found in the Sino–Himalayan region (Hu 1994; Richards 2002). With more than 300 reported species, China has the highest diversity in *Primula*; most of these species are distributed mainly in the southwestern part (Yunnan, Sichuan and Tibet), and the range from the Himalaya–Hengduan mountain chains is the modern diversity center of the genus (Hu 1994; Hu and Kelso 1996; Richards 2002).

The *Primula* sect. *Petiolares* Pax is one of the largest sections in *Primula*; more than 60 species of this section are now recognized worldwide (Hu 1994; Hu and Kelso 1996; Richards 2002; Hu and Geng 2003; Li and Hu 2009; Rankin 2010; Hu and Hao 2011; Xu et al. 2014, 2016, 2022; Ju et al 2018; Yuan et al. 2018; Wei et al. 2022; Xu et al. 2022; Zhang et al. 2023), and are well represented in the Himalaya–Hengduan mountains, with only a few members extending into Kashmir, central China, and some other regions (Hu 1990; Hu and Kelso 1996). This section was further divided into seven subsections based on the presence or absence of the basal bud scales and farina, the shape of the leaf margin, and the type of hair (Smith and Fletcher 1944). Subsection *Davidii* is one of the subsections within *Primula* sect. *Petiolares*, with recently



Academic editor: Avelinah Julius

Received: 23 March 2023

Accepted: 9 May 2023

Published: 29 May 2023

Citation: Wu Y, Yang W-H, Wu Z-K (2023) *Primula jiaozishanensis* (Primulaceae), a new species in *Primula* sect. *Petiolares* subsect. *Davidii* from Yunnan, China. *PhytoKeys* 227: 25–33, <https://doi.org/10.3897/phytokeys.227.103985>

Copyright: © Yuan Wu et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

described species, *P. bergenioides* C.M.Hu & Y.Y.Geng, *P. tenuituba* C.M.Hu & Y.Y.Geng (Hu and Geng 2003), *P. dejuniana* G.Hao, C.M.Hu & Yuan Xu (Xu et al. 2014), *P. wawushanica* G.Hao, C.M.Hu & Yuan Xu (Xu et al. 2016), *P. luteoflora* X.F.Gao & W.B.Ju (Ju et al. 2018), and *P. pingbaensis* Na Zhang, X.Q.Jiang & Z.K.Wu (Zhang et al. 2023). *Primula* sect. *Petiolares* subsect. *Davidii* comprises 22 species in total, which is characterized by the leaves that are more or less coriaceous, often bullate above and strongly honeycombed–reticulate below, long septate hair more or less clothes the veins, and basal buds covered with paleaceous scales (Smith and Fletcher 1944), mainly distributed in Sichuan, Yunnan and Guizhou in China.

Yunnan is a particularly significant biodiversity hotspot in China, with a wide variety of ecological environments ranging from tropical to alpine subnival belt, possessing ca. 130 species of *Primula* distributed across its range (Fang 2003). With the increased exploration of the region, many new *Primula* species have been discovered and described over the past two decades (Gong and Fang 2003; Xue and Zhang 2004; Shui and Chen 2006; Li and Hu 2009; Hu and Hao 2011; Yang et al. 2017; Wu et al. 2019; Ma et al. 2021; Wang et al. 2022; Wu et al. 2023).

During a botanical expedition to the Jiaozi Snow Mountain in Dongchuan District, Yunnan, southwestern China in May 2017, we found a peculiar population of *Primula* with large flowers, coriaceous leaves persisting into the following spring, basal buds covering paleaceous scales, on a small patch of alpine meadow near the mountain top. For further clarification of the identity of the newly collected *Primula*, the Jiaozi Snow Mountain in Dongchuan District and adjacent areas were revisited in 2020 to observe and collect the plants in flowers. The collected *Primula* is a dwarf perennial herb with a long and stout rhizome, basal buds covered with paleaceous scales, leaves with short petioles and adaxially bullate, short or almost obsolete scape, and large flowers. These features indicate that it should be a member of *P.* sect. *Petiolares* subsect. *Davidii*. After a full observation of the morphological characteristics and comparing the relevant literature and specimens for related species, we confirmed that this plant represents an undescribed taxon of *Primula*. Therefore, we describe and illustrate the taxon as new to science here.

## Materials and methods

The morphological observation, measurements and description of the new species were based on living plants from Jiaozi Snow Mountain. Morphological comparison with closely related species was performed based on living plants collected from their type locality, specimens from the key herbaria of China (KUN, PE, WUK), type specimen images online from P, E, K, and relevant literature were also consulted (Smith and Fletcher 1944; Hu 1990; Hu and Kelso 1996). All morphological characters of *P. jiaozishanensis* and its morphologically similar species in the *P.* sect. *Petiolares* subsect. *Davidii*, including *Primula esquirolii* Petitm. and *Primula sinoexscapa* C.M.Hu, were measured using a Vernier caliper. The conservation assessment of the new species was evaluated using the IUCN categories of threat (see IUCN 2012 and IUCN Standards and Petitions Committee 2022).

## Taxonomic treatment

*Primula jiaozishanensis* Z.K.Wu, W.H.Yang & Yuan Wu, sp. nov.

urn:lsid:ipni.org:names:77320210-1

Figs 1–3A, D

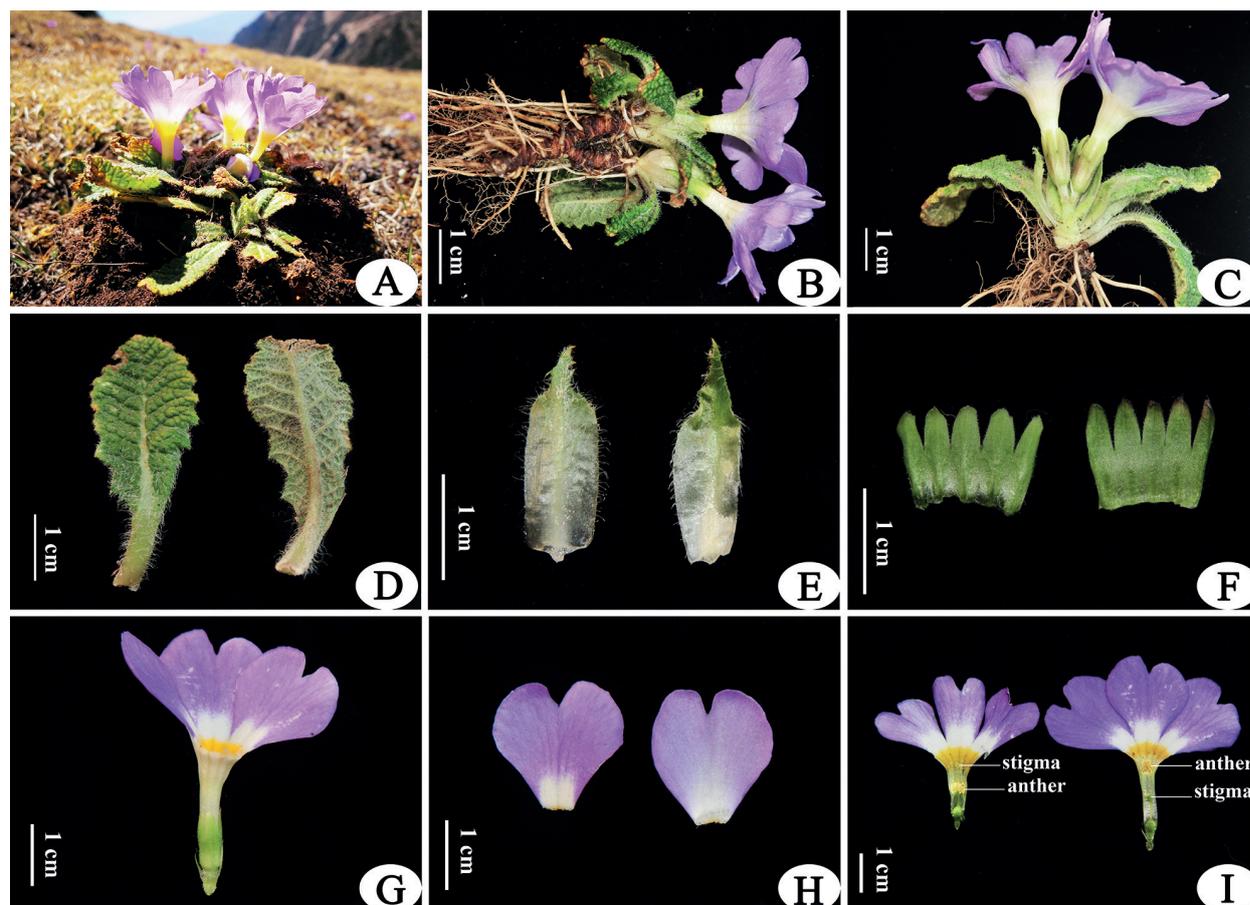
**Diagnosis.** The new species most resembles *P. esquirolii* and *P. sinoexscapa*, sharing similar leaves with a more or less rugose surface and short or almost obsolete scape at flowering time. However, the new species differs from the latter two mainly in its long and stout rhizome with 1–3 rosettes, smaller leaf blades with shorter petioles, shorter and stouter pedicels, and larger flowers (Figs 1–3). The main morphological distinctions between *P. jiaozishanensis*, *P. esquirolii* and *P. sinoexscapa* are summarized in Table 1.

**Type.** CHINA. Yunnan: Dongchuan District, Luoxue xiang, Jiaozi Snow Mountain. 26°9.77'N, 102°56.7'E, 3990 m alt., 1 May 2017 (fl.), *Zhikun WU ZKWu2017050* (holotype: KUN!; isotype: KUN!).

**Description.** A perennial hairy robust, dwarf herbaceous, efarinose, with a long stout rhizome and numerous fibrous roots, rhizome 3–4 cm long, ca. 0.5 cm in diameter; at flowering time girt at the base by ovate to oblong paleaceous bud scales, scales 1.5–1.8 cm long, 0.4–0.6 cm broad, acute at the apex, outer surface with a sparse covering of long multicellular hairs. **Leaves** forming 1–3 rosettes, leaves of current year not well-developed at anthesis, leaves of previous year at flowering time 2–4 cm long including the petiole, 1.5–2.5 cm broad, spatulate or elliptic–obovate, obtuse or rounded at the apex, gradually tapering into

**Table 1.** Morphological comparisons of *Primula jiaozishanensis* with *P. esquirolii* and *P. sinoexscapa*.

Characters	<i>P. jiaozishanensis</i>	<i>P. esquirolii</i>	<i>P. sinoexscapa</i>
Rhizome	long and stout, 3–4 cm long	short and stout, 1–2 cm long	short and stout, 1–2 cm long
Rosette	1–3	1	1
Scape	almost obsolete or to 1 cm in flowering time	almost obsolete or to 5 cm in flowering time	obsolete in flowering time
Leaf blade	2–4 × 1.5–2.5 cm, spatulate or elliptic–obovate, coriaceous, adaxially covered with sparse white long hairs, abaxially with multicellular hairs along veins.	5–13 × 1.5–5 cm, elliptic–obovate to obovate–oblanceolate, subcoriaceous, abaxially densely short glandular pubescent along veins	2.5–7 (12) × 1.5–3.5 (6) cm, oblong or oblong–obovate, firm papery, abaxially with multicellular hairs along veins, adaxially fulvous pilose along midvein
Petioles	0.5–1.0 cm, thick covering of long multicellular hairs.	short or almost obsolete to 1–2 cm, sparsely glandular.	2–5 cm, with long dense white pilose
Inflorescences	1 flowered or occasionally 2 flowered	2–8 flowered	1–4 flowered
Pedicels	1–3 mm, shorter than bracts	10–20 mm, longer than bracts	15–40 mm, longer than bracts
Calyx	6–8 mm long	5–7 mm long	7–9 mm long
Corolla	tube usually two times as the length of the calyx, limb 30–45 mm wide, lobes obcordate	tube usually 2–3 times as the length of calyx, limb 15–20 mm wide. lobes obovate	tube nearly two time as the length of the calyx, limb 15–20 mm wide, lobes narrowly obovate
Flower	heterostylous	homostylous	heterostylous
Habitat	open alpine meadow	moist limestone cliffs	moist limestone cliffs

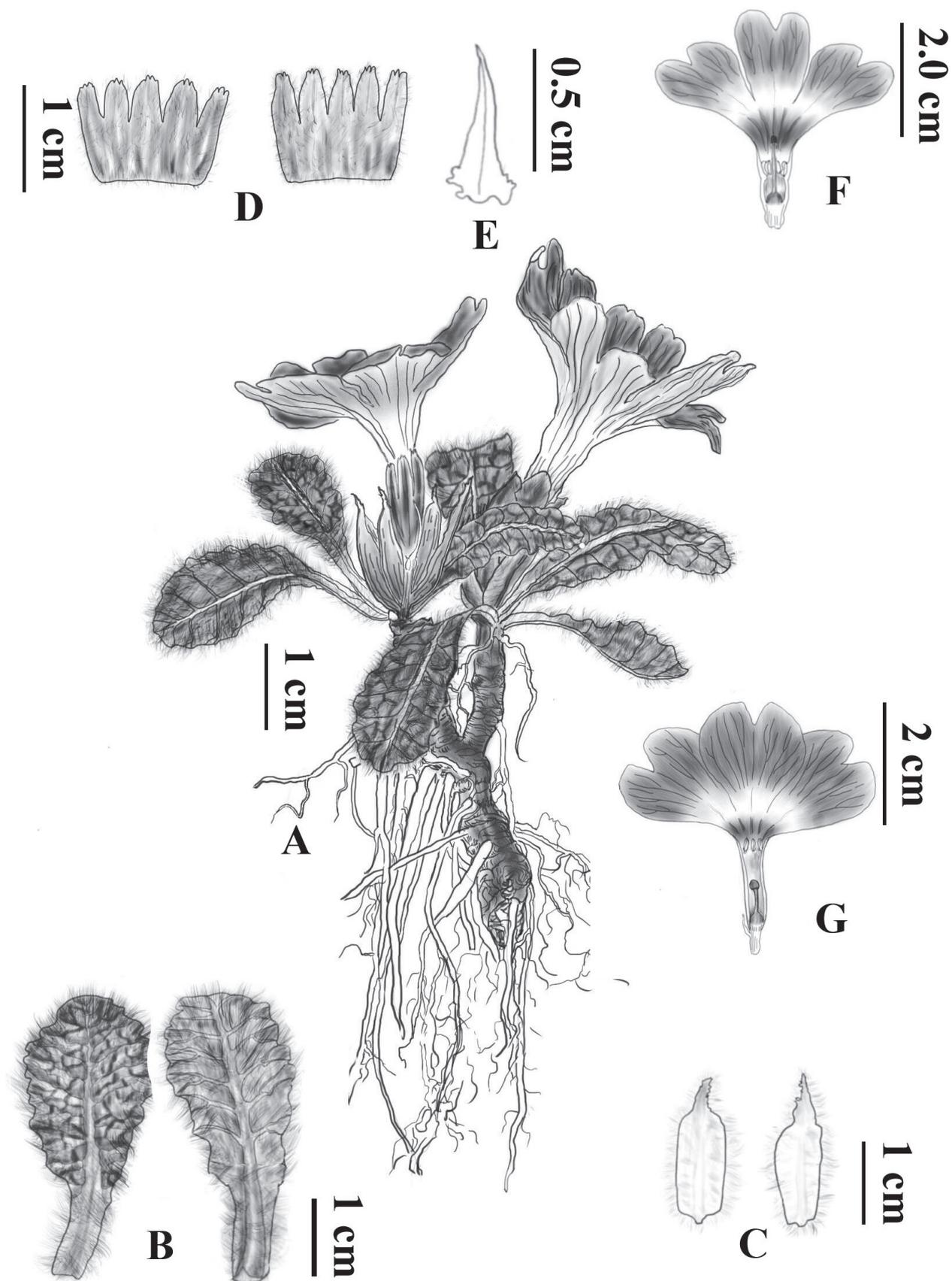


**Figure 1.** *Primula jiaozishanensis* sp. nov. **A–I** **A** habitat **B, C** habit in flowering **D** leaves, left: upper surface, right: lower surface **E** bud scales, left: outer surface, right: inner surface **F** calyx, left: outer surface, right: inner surface **G** flower shape **H** corolla lobes, left: upper surface, right: lower surface **I** dissected corolla showing anthers and stigmas, left: pin flower, right: thrum flower. Photographed by Z.K Wu.

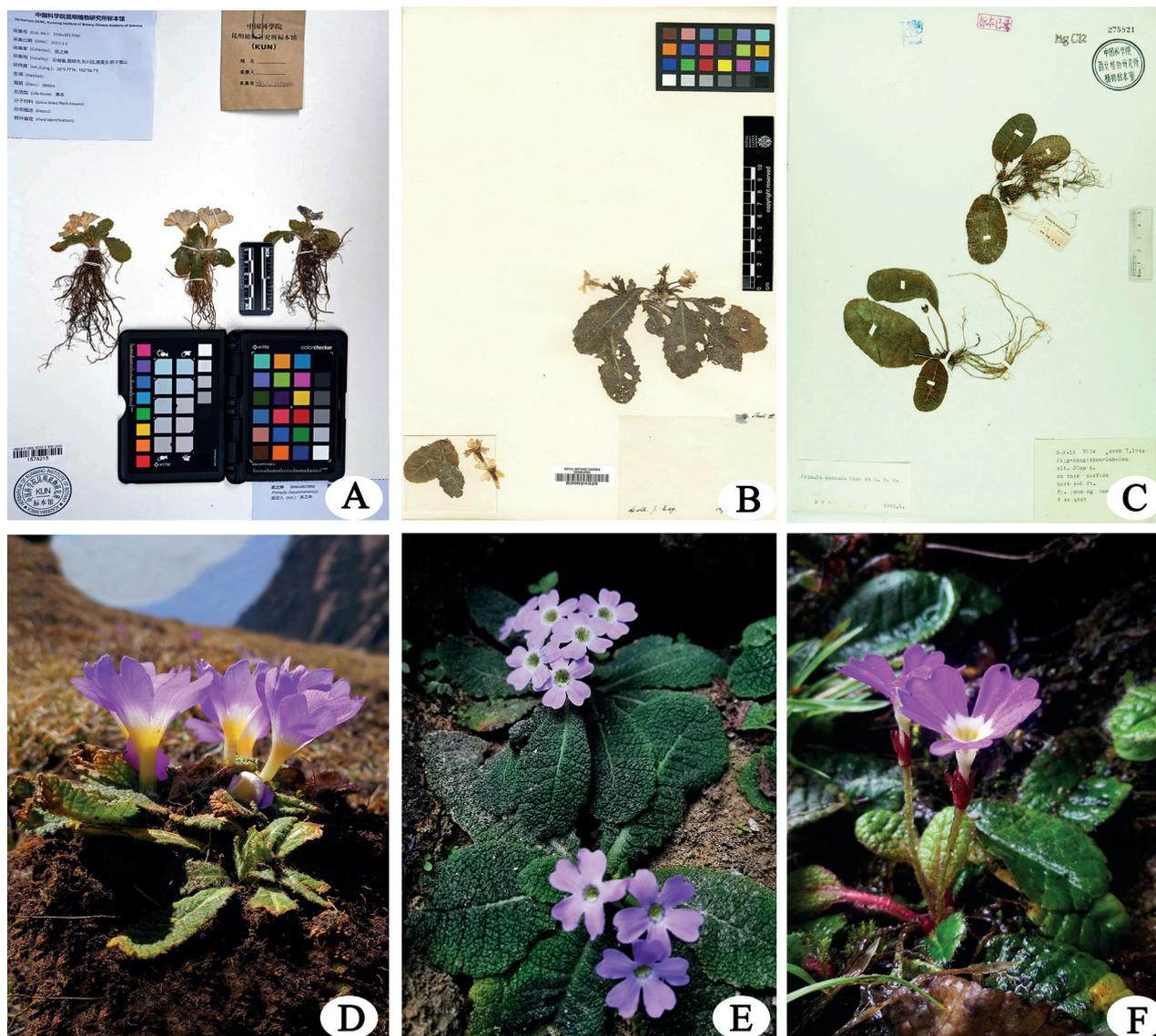
the winged petiole; petiole 0.5 to 1 cm, 1/4 as long as leaf blade, stout with a thick covering of long multicellular hairs; lamina coriaceous, adaxially bullate, covered with sparse white long hairs, abaxially with multicellular hairs along veins, margin with regular sparsely acute serrate. **Scap**e at flowering time almost obsolete or to 1 cm, usually solitary, covered by bud scales, with a thick covering of long multicellular hairs, usually 1 flowered or occasionally 2 flowered. **Bracts** linear-lanceolate, 3–6 mm long, glabrous; pedicel 1–3 mm, shorter than bract, with a thick covering of long multicellular hairs. **Flower** heterostylous; calyx campanulate, 6–8 mm long, puberulous, parted to 1/2 of its length, lobes ovate to ovate-lanceolate, apex obtuse or occasionally serrate; corolla funnel-shaped, purplish blue or violet, tube 15–20 mm long, usually twice the length of the calyx, limb 30–45 mm wide, lobes obcordate, 13–18 mm long, apex deeply emarginate. **Pin flowers**: corolla tube 14–16 mm long, stamens ca. 7 mm above the base of the corolla tube, style 14–16 mm long. **Thrum flowers**: corolla tube 16–20 mm; stamens 16–18 mm above base of corolla tube, style ca. 8 mm long. **Capsule** unknown.

**Distribution and ecology.** *Primula jiaozishanensis* is only known from the type locality on Jiaozhi Snow Mountain in Dongchuan District, Yunnan, China. The plant grows in the open alpine meadow (Fig. 1, Map 1).

**Phenology.** Flowering occurs from April to May.



**Figure 2.** *Primula jiaozishanensis* sp. nov. **A** habit **B** leaves, left: upper surface, right: lower surface **C** bud scales, left: outer surface, right: inner surface **D** calyx, left: outer surface, right: inner surface **E** bract **F** flower, long style (pin) **G** flower, short style (thrum). Drawn by Ms. Xiang–Li Wu.



**Figure 3.** *Primula jiaozishanensis* and two of its allies **A** holotype specimen of *P. jiaozishanensis* (ZKWU 2017050, KUN, specimen number KUN1576215) **B** the possible type of *P. esquirolii* (Martin, L. and Esquirol, J., E, specimen number E00024325) **C** paratype of *P. sinoexscapa* from its type locality (M.K. Li 3530, WUK, specimen number WUK0275821) **D** *P. jiaozishanensis* **E** *P. esquirolii* **F** *P. sinoexscapa*. **D–F** photographed by Z.K Wu from their type locality.

**Etymology.** The specific epithet of the new species is taken from the Chinese Pinyin, “Jiaozishan”, the name of the mountain in Northern Yunnan, China, where the type specimen was collected (Map 1).

**Vernacular name.** Chinese mandarin: *jiao zi shan bao chun* (轿子山报春).

**Provisional Conservation status.** Critically Endangered (CR B2ab(iii)). The authors have conducted field surveys several times in the type locality and adjacent districts (e.g., Luquan, Qiaojia and Huize) for this new species, and discovered only one population of *Primula jiaozishanensis*, with approximately 100 adult individuals, distributed over about 100 m<sup>2</sup> in the type locality. This site is in a dry alpine meadow; the new species grows very close to the path for visitors and faces a strong threat from grazing and human activities. Its status should therefore be of concern and addressed by further investigations.



Map 1. Location of the population of *Primula jiaozishanensis* in Dongchuan District, Yunnan.

We estimated the extent of occurrence of the species to be less than 10 km<sup>2</sup>. Over the last five years, we have observed a steady decline in the territory area of the habitat due to road construction and grazing. Considering the present field information and IUCN categories of threat (IUCN Standards and Petitions Committee 2022), this species should be included in the category Critically Endangered (CR B2ab(iii)).

**Additional specimens examined (paratypes).** The same locality as holotype, 8 May 2020 (fl.), Zhikun WU ZKWu 2020045 (KUN!).

## Discussion

The species in *Primula* sect. *Petiolares* subsect. *Davidii* usually tend to have larger leaves because the plants grow in small groups on shady and moist cliffs beside streams and waterfalls. The leaves of *P. davidii* we found in the field of Sichuan can even reach 30 cm in length, and they also have a short and stout rhizome. The new species *P. jiaozishanensis* grows in open alpine meadow, and its habitat differs from that of other members in the *P.* sect. *Petiolares* subsect. *Davidii*. Compared to other species in the same subsection, it is distinctive in its long and stout rhizome with 1–3 rosettes, smaller leaf blades, and very short and stout scape with one or occasionally two larger flowers. These features may be an adaptation to the harsh habit of the open alpine meadow, which is usually very windy and has insufficient water in late April and May when it starts anthesis.

## Acknowledgements

This study was supported by the Science and Technology Plan Project of Guizhou Province ([2022]–4016) and the National Wild Plant Germplasm Resource Center for Guizhou University of Traditional Chinese Medicine (ZWX–2015). We thank Ms. XiangLi Wu for the line drawings of the new species.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Y. Wu, W-H Yang and Z. K. Wu did the expedition, Y. Wu did the measurement, Y. Wu and Z. K. Wu wrote the manuscript.

### Author ORCIDs

Wu-Hai Yang  <https://orcid.org/0009-0007-6927-8309>

Zhi-Kun Wu  <https://orcid.org/0000-0002-4583-7782>

Yuan Wu  <https://orcid.org/0000-0003-2167-2351>

### Data availability

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

## References

- Fang RC (2003) *Primula*. In: Wu CY (Eds) *Flora Yunnanica* (Vol. 15). Science Press, Beijing, China, 400–509.
- Gong X, Fang RC (2003) *Primula calyptrata*, a new species in section *Carolinella* (Primulaceae) from Yunnan, China. *Novon* 13(2): 193–195. <https://doi.org/10.2307/3393517>
- Hu CM (1990) *Primula*. In: Chen FH, Hu CM (Eds) *Flora Republicae Popularis Sinicae* (Vol. 59). Science Press, Beijing, 288 pp.
- Hu CM (1994) On the geographical distribution of the Primulaceae. *Journal of Tropical and Subtropical Botany* 2(4): e114.
- Hu CM, Geng YY (2003) Two New Species of *Primula* (Primulaceae) from China. *Novon* 13(2): 196–199. <https://doi.org/10.2307/3393518>
- Hu CM, Hao G (2011) New and noteworthy species of *Primula* (Primulaceae) from China. *Edinburgh Journal of Botany* 68(2): 297–300. <https://doi.org/10.1017/S096042861100014X>
- Hu CM, Kelso S (1996) Primulaceae. In: Wu ZY, Raven PH (Eds) *Flora of China* (Vol. 15). Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 99–185.
- IUCN (2012) *IUCN Red List Categories and Criteria*. Version 3.1. (2<sup>nd</sup> edn.). IUCN Species Survival Commission, IUCN, Gland, Switzerland and Cambridge.

- IUCN Standards and Petitions Committee (2022) Guidelines for Using the IUCN Red List Categories and Criteria, Version 15.1. Prepared by the Standards and Petitions Committee. [Accessed 25. 04. 2023]
- Ju WB, Huang Q, Sun ZY, Huang WJ, Li HC, Gao XF (2018) *Primula luteoflora* (Primulaceae), a new species from Sichuan, China. *Phytotaxa* 367(3): 297–300. <https://doi.org/10.11646/phytotaxa.367.3.10>
- Li R, Hu CM (2009) *Primula lihengiana* (Primulaceae), a new Species from Yunnan, China. *Annales Botanici Fennici* 46(2): 130–132. <https://doi.org/10.5735/085.046.0208>
- Ma XD, Wang WG, Shi JP, Shen JY (2021) *Primula longistyla* (Primulaceae), a new species from Yunnan, China. *Nordic Journal of Botany* 39(10): 1–5. <https://doi.org/10.1111/njb.03341>
- POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. <http://www.plantsoftheworldonline.org/> [Retrieved 09 May 2023]
- Rankin DWH (2010) *Primula nghialoensis*. *Curtis's Botanical Magazine* 27(2): 132–139. <https://doi.org/10.1111/j.1467-8748.2010.01689.x>
- Richards J (2002) *Primula* (2<sup>nd</sup> Edn.). Batsford, 156–190.
- Shui YM, Chen WH (2006) Seed plants of the Karst region in China (Vol. 1) (Southeast Yunnan). Science Press, Beijing, 159 pp.
- Smith WW, Fletcher HR (1944) The genus *Primula*: Section *Petiolares*. *Transactions of the Royal Society of Edinburgh* 61(2): 271–314. <https://doi.org/10.1017/S0080456800004750>
- Wang ZH, Wang Y, Chen L, Peng H, Wu ZK, Guo G (2022) *Primula longipilosa* (Primulaceae), a new species from Yunnan, China. *PhytoKeys* 194: 15–22. <https://doi.org/10.3897/phytokeys.194.81335>
- Wei D, Wang W, Xu Y, Hao G (2022) *Primula tsaiana* (Primulaceae), a New Species from Yunnan, China, and a New Synonym of *P. wenshanensis*. *Annales Botanici Fennici* 59(1): 111–116. <https://doi.org/10.5735/085.059.0117>
- Wu ZK, Zhao FW, Chen JH, Huang Y (2019) *Primula dongchuanensis* (Primulaceae), a new species from northern Yunnan, China. *PhytoKeys* 130: 171–181. <https://doi.org/10.3897/phytokeys.130.35047>
- Wu ZK, Guo YJ, Zhang T, Burgess KS, Zhou W (2023) *Primula luquanensis* sp. nov. (Primulaceae), a new species from southwestern China, reveals a novel floral form in the heterostyly-prevaling genus. *Plants* 12(3): e534. <https://doi.org/10.3390/plants12030534>
- Xu Y, Yuan S, Hu CM, Hao G (2014) *Primula dejuniana* (Primulaceae), a New Species from Sichuan, China. *Annales Botanici Fennici* 51(6): 372–374. <https://doi.org/10.5735/085.051.0602>
- Xu Y, Li CH, Hu CM, Hao G (2016) *Primula wawushanica* sp. nov. (Primulaceae) from Sichuan, southwestern China. *Nordic Journal of Botany* 34(2): 156–158. <https://doi.org/10.1111/njb.00894>
- Xu Y, He DM, Yang LZ, Hao G (2022) *Primula surculosa* (Primulaceae), a new species from Yunnan, China. *PhytoKeys* 212: 29–35. <https://doi.org/10.3897/phytokeys.212.91133>
- Xue DW, Zhang CQ (2004) *Primula sinolisteri* var. *longicalyx*, a new variety of the Primulaceae from Yunnan, China. *Acta Phytotaxonomica Sinica* 42: 263–264.
- Yang B, Ding HB, Li ZH, Tan YH (2017) *Primula zhui* (Primulaceae) sp. nov. from south Yunnan, southwest China. *Nordic Journal of Botany* 35(6): 681–686. <https://doi.org/10.1111/njb.01656>
- Yuan S, Zhang DX, Hao G (2018) *Primula chimingiana* sp. nov. (Primulaceae) from Sichuan, China. *Nordic Journal of Botany* 36(1–2): 1–4. <https://doi.org/10.1111/njb.01390>
- Zhang N, Jiang XQ, Wu ZK (2023) *Primula pingbaensis* (Primulaceae), a new species from Guizhou, China. *PhytoKeys* 221: 85–93. <https://doi.org/10.3897/phytokeys.221.97948>



# Rediscovery of *Primula brachystoma* (Primulaceae), a rare species endemic to Gaoligong Mountain of Chinese-Burma frontier

Xiao-Qi Jiang<sup>1</sup>, Na Zhang<sup>1</sup>, Zhi-Kun Wu<sup>1</sup>

<sup>1</sup> Department of pharmacy, Guizhou University of Traditional Chinese Medicine, Guiyang, 550025, Guizhou, China  
Corresponding author: Zhi-Kun Wu (47390933@qq.com)

## Abstract

The rare *Primula brachystoma* W.W.Sm. is an endemic species confined to Gaoligong mountain of Chinese-Burma frontier, which has been rediscovered from the same region after nearly 100 years. In total, 11 specimens from Gaoligong Mountain have been found in the herbaria worldwide, since its first collection in 1920 by Farrer, Reginald John. Previously, this species was described as homostylous but our finding shows the species also exhibited heterostyly. A complete description of the species, the distribution, morphological comparison and identification key from closely related species are provided here. An assessment of its conservation status suggests that the species is 'Endangered' (EN).

**Key words:** Endangered species, Gaoligong Mountain, *Primula*, Primulaceae, rediscovery

## Introduction

*Primula brachystoma* W.W.Sm. was discovered by Farrer, Reginald John from Shing Hong of Burma in Gaoligong Mountain of Chinese-Burma frontier under the collection number Farrer 1635 in 1920, then was described as a new species in 1923 by Smith (Smith and Forrest 1923). A few of these type specimens were preserved as *P. brachystoma* in the Royal Botanic Gardens, Kew (K) and the Natural History Museum, London (BM). Others were preserved in the herbarium of Edinburgh. This species was considered closely related to *Primula prenantha* subsp. *prenantha* Balf.f. & W.W.Sm. and *Primula prenantha* subsp. *morsheadiana* (Kingdon-Ward) F.H.Chen & C.M.Hu, but the acute leaf apex makes it easily distinguishable from these two other species (Smith and Fletcher 1941). In the description of *P. prenantha* subsp. *prenantha* in the Flora Reipublicae Popularis Sinicae (Hu 1990), it was claimed that its closely related species *P. brachystoma* did not distribute to China. However, when we reviewed the specimens from key Herbaria (BM, E, IBSC, K, KUN, P, PE), we found one plant collected at Tsuga on the way from Gongshan downtown to Dulong River, Yunnan, east slope of Gaoligong mountain, which was identified as *Primula brachystoma* W.W.Sm. by Professor Chi-Ming Hu (Qinghai-Tibet team 8648, PE), and another specimen with a similar number collection was not identified (Qinghai-Tibet team 8648, PE). In contrast, two specimens with the same collection number at KUN were identified as



Academic editor: Avelinah Julius  
Received: 20 March 2023  
Accepted: 9 May 2023  
Published: 29 May 2023

Citation: Jiang X-Q, Zhang N, Wu Z-K (2023) Rediscovery of *Primula brachystoma* (Primulaceae), a rare species endemic to Gaoligong Mountain of Chinese-Burma frontier. *PhytoKeys* 227: 35–42, <https://doi.org/10.3897/phytokeys.227.103746>

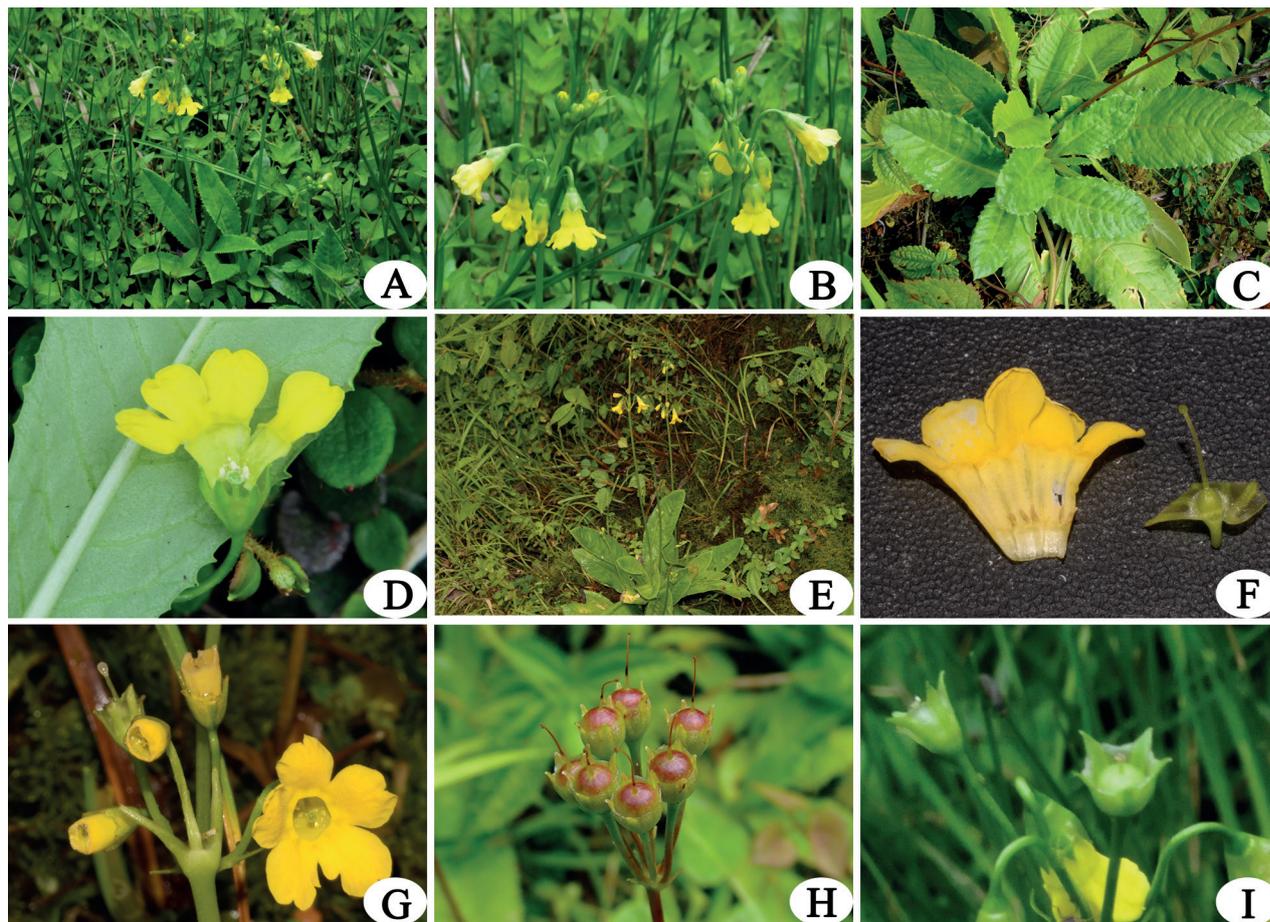
Copyright: © Xiao-Qi Jiang et al.  
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

*Primula elegans* Forrest var. *maculosa* H.Chuang. However, a comparison with the type specimen of *P. brachystoma* indicates that all these specimens belong to this species; therefore, our observation suggests that *P. brachystoma* is also distributed in China.

*Primula brachystoma* was originally described as homostylous by Smith (Smith and Forrest 1923). During a botanical expedition in the regions of Gaoligong Mountain in May 2015, we found a homostylous *Primula* with an acute leaf apex and regularly denticulate at margin, campanulate calyx and yellow corolla with annulus marked, on the western slopes of the Gaoligong Mountains near Dulong River. After a comparison with type specimens, the plant matched *P. brachystoma* (Fig. 1A–D). Another heterostylous *Primula* with an acute leaf apex and regularly denticulate at margin, campanulate calyx and yellow corolla with annulus marked, was found in Shibali and Yaping of Fugong county during a botanical expedition in Gaoligong Mountain of Fugong Xian, Yunnan, China in 2018. After comparing with the type specimens, excluding the heterostylous flowers, all its other characteristics match the description of *P. brachystoma*. Considering that some species in the genus *Primula* have both homostylous and heterostylous flowers such as *Primula chungensis* Balf.f. & Kingdon-Ward, *Primula oreodoxa* Franch., *Primula polonensis* Kingdon-Ward and *Primula sinensis* Sabine ex Lindl. etc (Hu 1990; Bawri et al. 2015), the plant from Shibali and Yaping could be *P. brachystoma* (Fig. 1E–I). Therefore, we believe that *P. brachystoma*, having both homostylous and heterostylous flowers, is similar to its closely allied species *P. polonensis* and *P. chungensis* in the same section. This paper provides a complete morphological description, distribution, morphological comparison and identification key from closely related species. The threat status of *P. brachystoma* through field surveys and review of type specimens, as well as color photographs, are also provided to facilitate proper identification of the species (Figs 1, 3).

## Materials and methods

We collected fresh material and specimens of *P. brachystoma* from Gongshan county, Yunnan on the way to the Dulong River in May 2015 while travelling from Yaping and Shibali of Fugong county in July 2018. The identity of our plant collection has been confirmed by consulting the original description and online images of the type specimens from key Herbaria (BM, E, K). Complete morphological characters of the species were measured using a vernier calliper. The voucher specimens are stored at KUN. For comparison purposes, specimens of closely related species, *P. polonensis*, *P. prenantha* subsp. *prenantha*, *P. prenantha* subsp. *morsheadiana*, *P. serratifolia* Franch., *Primula melanodonta* W.W.Sm. from the key herbaria of China (IBSC, KUN, PE), type specimens' images online of the closely related species from BM, E, K, P, and relevant literature (Smith et al. 1977; Hu 1990; Hu and Kelso 1996) were also consulted. The conservation status of *P. brachystoma* was assessed using the guidelines for IUCN Red List categories and criteria (IUCN 2022; IUCN Standards and Petitions Committee 2022).



**Figure 1.** *Primula brachystoma* **A–D** homostylous flower individuals: **A** habit **B** inflorescence **C** leaf blade **D** homostylous flower **E–I** heterostylous flower individuals: **E** habit **F–G** long style of heterostylous flower (pin) **H** fruits of pin flowers **I** fruits of thrum flowers. Photographed by Z. K. Wu.

## Taxonomic treatment

### *Primula brachystoma* W. W. Sm.

*Primula brachystoma* W. W. Sm. in Notes Roy. Bot. Gard. Edin., xiv, 35 (1923); W. W. Sm. et Forrest, *ibid.*, xvi, 17 (1928), and in Journ. Roy. Hort. Soc. London, liv, 43 (1929); W. W. Smith et Fletcher in Trans. Bot. Soc. Edinb. xxxiii: 166 (1941). Type: Burma, Shing Hong region, 20 June 1920, R. J. Farrer 1635 (holotype E! E00024386; isotypes BM, BM000996925, K, K000732874).

**Description.** A perennial herb, completely glabrous and efarinose, with numerous robust roots. **Leaves** forming a rosette; leaf blade oblanceolate to suboblanceolate, 6–12 cm long, 2–4 cm broad, acute and shortly apiculate at the apex, petiole very short or as long as 1/3 of the blade, base attenuate with broadly winged petiole, margin regularly fine dentate, teeth triangular, apex acute and subulate, leaf abaxially with prominent midrib and conspicuous lateral veins, and inconspicuous mesh vein. **Scapes** slightly slender, 15–25 cm long; umbels 1 (or rarely 2), 2–7 flowered. **Bracts** linear-lanceolate, 0.6–0.8 cm long. **Pedicel**

slightly recurved when flowering, erect when fruiting, 0.8–1 cm long in flowering, up to 1.5 cm long in fruiting. **Calyx** campanulate, green, 5–7 mm long, with 5 ribs, splitting slightly less than 1/3 of its full length, lobes triangular, apiculate at the apex. **Flowers** homostylous or heterostylous in different populations, corolla funnel-shaped, yellow, tube 8–10 mm long, with a marked annulus, limb 1–1.5 cm wide, lobes sub-quadrangular to obovate, 4–5 mm long, shallowly notched; homostylous flowers: the stamens are inserted in the middle of the corolla tube, filament ca. 0.5 mm long, anther ca. 0.8–1 mm long, yellowish white, the style reaches to the level of the stamens; heterostylous flowers: in long-styled flowers the style nearly reaches the annulus and the stamens are inserted towards the base of the corolla, in short-styled flowers the stamens are inserted slightly below the annulus and the style is shorter than the calyx, the filament and anther as those in homostylous flowers. **Capsule** globose, green in young fruiting time and pale purple in mature fruiting time, 5–6 mm long, as long as or slightly shorter than calyx, 4–5 mm in diameter.

**Distribution and habitat.** It is found on Gaoligong Mountain on the border between China and Burma. One homostylous population is at the type locality Shing Hong of Burma and two homostylous populations are at Sandui and Tsuga of Gongshan county, China; the other two heterostylous population are at Sibali and Luodigolu, Yaping of Fugong county, China. It grows along moist streams or on wet grassy slopes at forest margins, 2500–3000 m above sea level.

**Additional specimens examined.** CHINA, Gongshan Xian, Dulongjiang Xiang: Sandui [27°42'56.112"N, 98°25'24.048"E, 2580 m], May 2015, ZKWU 2015036 (KUN!); China, Fugong Xian, Lishadi Xiang: Yaduo Cun [27°10'36"N, 98°44'55.9"E, 2830 m], 6 August 2005, Gaoligong Shan Biodiversity Survey 26554 (KUN!); China, Fugong Xian, Lumadeng Xiang: Yaping Cun [27°10'3"N, 98°46'17.7"E, 2510 m], 16 August 2005, Gaoligong Shan Biodiversity Survey 28479 (KUN!); China, Fugong Xian, Lishadi Xiang: Yaduo Cun [27°10'1.8"N, 98°46'24.8"E, 2520 m], 16 August 2005, Gaoligong Shan Biodiversity Survey 28435 (KUN!); China, Gongshan Xian: Tsuga on the way from Gongshan Xian to Dulong River, east slope of Gaoligong mountain, 26 July 1982, Qinghai-Tibet team 8648 (PE, KUN!).

**Provisional conservation status.** *Primula brachystoma* is neither listed in the IUCN Red List (IUCN 2022), nor in the threatened Species List of China's Higher Plants (Qin et al. 2017). The authors have conducted field surveys in the regions of Gaoligong mountains many times and discovered only three populations of *Primula brachystoma* in Fugong county and Gongshan county. Surveys from other plant hunters also didn't find more populations in this area. We estimated the extent of occurrence of the species to be less than 1000 km<sup>2</sup>, and the adult individuals as fewer than 1000. The sites where the known populations grow are also places for grazing, so they face a strong threat from human activities. Accordingly, we evaluate the species as Endangered (EN B1ab(iii)), considering the IUCN standards (IUCN Standards and Petitions Committee 2022).

## Diagnosis

Morphologically, *P. brachystoma* is similar to *P. polonensis*, *P. prenantha* subsp. *prenantha*, *P. prenantha* subsp. *morsheadiana*, *P. serratifolia*, *P. melanodonta* in *P. sect. Proliferae* Pax. Among these species, *P. brachystoma* and *P. polonensis* have both homostyly and heterostyly flowers, longer leaves with inconspicu-

ous mesh vein on abaxial surface, and short corolla tube (8–10 mm) with a marked annulus; *P. brachystoma* differed from the latter by its leaf blade being acute and shortly apiculate, calyx splitting slightly less than 1/3 of its full length (Fig. 2A, B). *P. brachystoma* differed from the homostylous species *P. prenantha* subsp. *prenantha* and *P. prenantha* subsp. *morsheadiana* by the leaf blades of the latter two are both rounded at the apex, the abaxial surface of leaf blade with conspicuous mesh vein, corolla tube more elongated (Fig. 2A, C, D; Fig. 3A–E). *P. brachystoma* differed from the heterostylous species *P. serratifolia* and *P. melanodonta* by the leaf blades of *P. serratifolia* and *P. melanodonta* are both rounded to obtuse at the apex, the abaxial surface of leaf blade with conspicuous mesh vein (Figs 2A, E, F; 3A, F–I). The main morphological difference between *P. brachystoma* and its allies is summarized in Table 1, and the following Keys.

**Table 1.** Morphological comparisons among *P. brachystoma*, *P. polonensis*, *P. prenantha* subsp. *prenantha*, *P. prenantha* subsp. *morsheadiana*, *P. serratifolia* and *P. melanodonta*.

Characters	<i>P. brachystoma</i>	<i>P. polonensis</i>	<i>P. prenantha</i> subsp. <i>Prenantha</i>	<i>P. prenantha</i> subsp. <i>Morsheadiana</i>	<i>P. serratifolia</i>	<i>P. melanodonta</i>
<b>Leaf blade</b>	oblanceolate to suboblanceolate, 6–12×2–4 cm	narrowly ovate to obovate-oblong or oblanceolate, 3–20×1.2–5 cm	oblong-obovate to obovate-elliptic, 3.5–9×1.5–3 cm	elliptic to oblanceolate leaves up to 12 cm. long and 3 cm. broad	oblong to elliptic-obovate, 6–12×1.8–5 cm	oblanceolate or obovate leaves, 3–5×1.5–2 cm
<b>Leaf apex</b>	acute and shortly apiculate	rounded to obtuse	Rounded	obtuse or rounded	rounded	rounded or obtuse
<b>Leaf margin</b>	regularly fine dentate	regularly crenulate	erose-denticulate	Irregularly denticulate	erose-denticulate	deeply dentate
<b>Under surface of leaf blade</b>	prominent midrib and conspicuous lateral veins, and inconspicuous mesh vein	prominent midrib and conspicuous lateral veins, and inconspicuous mesh vein	midrib and lateral veins prominent, and conspicuous mesh vein	midrib and lateral veins prominent, and conspicuous mesh vein	midrib and lateral veins prominent, and conspicuous mesh vein	midrib and lateral veins prominent, and conspicuous mesh vein
<b>Calyx</b>	Campanulate	tubular-campanulate	campanulate	Campanulate	tubular-campanulate	campanulate
<b>Calyx lobes</b>	splitting slightly less than 1/3 of its full length, lobes triangular	parted to middle or below, lobes narrowly oblong	parted at most to 1/3, lobes triangular	parted 1/3, into broadly triangular	Parted 1/3–1/2, 5-ribbed, lobes triangular	cut almost to the middle into ovate
<b>Style</b>	homostylous and heterostylous	homostylous and heterostylous	homostylous	Homostylous	heterostylous	heterostylous
<b>Capsule</b>	globose, as long as or slightly shorter than calyx	globose, included in calyx	subglobose, slightly longer than calyx	subglobose, as long as calyx	ovoid, nearly as long as calyx	ovoid, included in calyx

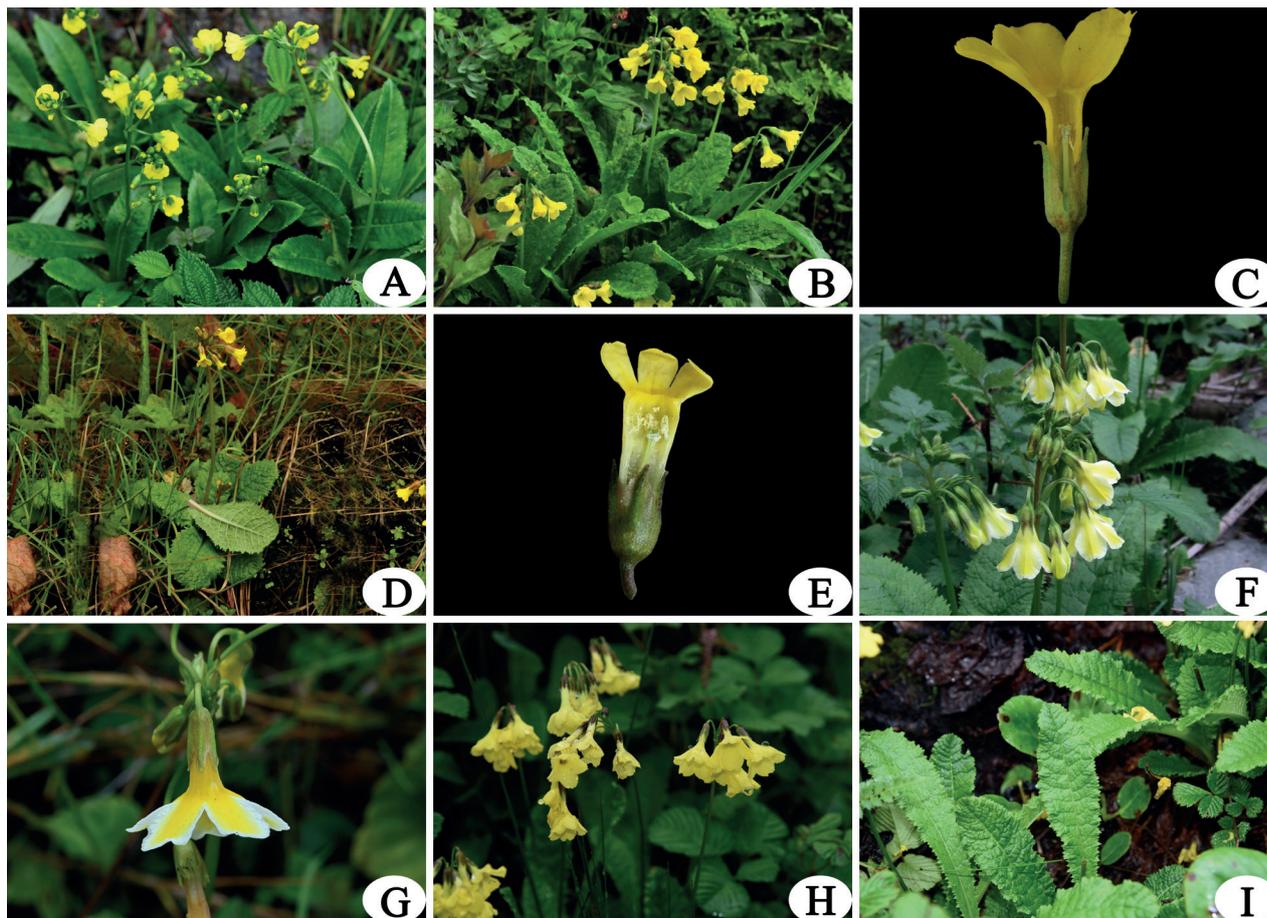
### Key for *Primula brachystoma* and its closely related species in the *P.* section *Proliferae*

- 1 Flowers homostylous or heterostylous in different populations.....**2**
- Flowers only heterostylous.....**5**
- 2 Flowers only homostylous, under surface of leaf blade with conspicuous mesh vein.....**3**
- Flowers homostylous and heterostylous in different populations, under surface of leaf blade with inconspicuous mesh vein.....**4**

- 3 Mature corolla limb 6–9 mm wide; lobes oblong-ovate, not spreading, capsule 5 mm long, longer than the calyx ..... ***P. prenantha* subsp. *prenantha***
- Mature corolla limb 9–12 mm wide; lobes obovate, ±spreading, capsule 7–8 mm, as long as the calyx..... ***P. prenantha* subsp. *morsheadiana***
- 4 Leaf blade apex acute and shortly apiculate; bract upper part not leafy.....  
..... ***P. brachystoma***
- Leaf blade apex rounded to obtuse; bract upper part leafy ..... ***P. polonensis***
- 5 Leaf blade 3–5 cm, margin densely fine denticulate; pin flower style or thrum flower stamens slightly exceeding middle of corolla tube, flower concolorous ..... ***P. melanodonta***
- Leaf blade 6–12 cm, margin denticulate; pin flower style or thrum flower stamens exerted from corolla tube, flower bicolorous ..... ***P. serratifolia***



**Figure 2.** Specimens of *P. brachystoma* and its related species **A** holotype of *P. brachystoma* (Farrer 1635, E, <https://data.rbge.org.uk/herb/E00024386>) **B** isotype of *P. polonensis* (Kingdon-Ward 8388, E, <https://data.rbge.org.uk/herb/E00024403>) **C** isosytype of *P. prenantha* subsp. *prenantha* (G. King's, E, <https://data.rbge.org.uk/herb/E00259794>) **D** type of *P. prenantha* subsp. *morsheadiana* (Ward, F. K. 5858, K, <http://apps.kew.org/herb/K000750095>) **E** holotype of *P. serratifolia* (Forrest 1816, E, <https://data.rbge.org.uk/herb/E00024076>) **F** syntype of *P. melanodonta* (Kingdon-Ward 7042, E, <https://data.rbge.org.uk/herb/E00531116>).



**Figure 3.** *Primula brachystoma* and four of its close taxa **A** *P. brachystoma* **B** *P. prenantha* subsp. *morsheadiana* (from its type locality: pass of Duoxiongla, Xizhang) **C** flower of *P. prenantha* subsp. *morsheadiana* (homostyly) **D** *P. prenantha* subsp. *prenantha* (from Gaoligong Mountain, Yunnan) **E** flower of *P. prenantha* subsp. *prenantha* (homostyly) **F** *P. serratifolia* (from its type locality: Cangshan Mountain, Yunnan) **G** flower of *P. serratifolia* (flower are biocolorous) **H** *P. melanodonta* (from Gaoligong Mountain, Yunnan, flowers are concolorous) **I** leaf blade of *P. melanodonta*. Photographed by Z. K. Wu.

## Acknowledgements

We thank Prof. Heng Li from Kunming Institute of Botany (CAS) for her kind assistance on reviewing the specimens from Gaoligong Mountain. This study was supported by the National Wild Plant Germplasm Resource Center for Guizhou University of Traditional Chinese Medicine (ZWX-2015), Science and Technology Basic Resources Investigation Program of China (Grant No. 2021FY100200) and the Science and Technology Plan Project of Guizhou Province ([2022]-4016).

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

## Funding

No funding was reported.

## Author contributions

Investigation: ZKW, NZ, XJ. Writing – original draft: XJ. Writing – review and editing: ZKW.

## Author ORCIDs

Xiao-Qi Jiang  <https://orcid.org/0000-0002-2101-6541>

Na Zhang  <https://orcid.org/0000-0002-7005-2848>

Zhi-Kun Wu  <https://orcid.org/0000-0002-4583-7782>

## Data availability

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

## References

- Bawri A, Gajurel PR, Khan ML (2015) Rediscovery of *Primula polonensis*. *Kew Bulletin* 70(4): 1–5. <https://doi.org/10.1007/s12225-015-9605-6>
- Hu CM (1990) *Primula*. In: Chen FH, Hu CM (Eds) *Flora Republicae Popularis Sinicae* (Vol. 59). Science Press, Beijing, 124 pp.
- Hu CM, Kelso S (1996) Primulaceae. In: Wu ZY, Raven PH (Eds) *Flora of China* (Vol. 15). Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 99–185.
- IUCN (2022) The IUCN Red List of Threatened Species. Version 2022-1. <https://www.iucnredlist.org> [Accessed 9. 11. 2022]
- IUCN Standards and Petitions Committee (2022) Guidelines for Using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. [Accessed 9. 11. 2022]
- Qin H, Yang Y, Dong S, He Q, Jia Y, Zhao L, Yu S, Liu H, Liu B, Yan Y, Xiang J, Xia N, Peng H, Li Z, Zhang Z, He X, Yin L, Lin Y, Liu Q, Hou Y, Liu Y, Liu Q, Cao W, Li J, Chen S, Jin X, Gao T, Chen W, Ma H, Geng Y, Jin X, Chang C, Jiang H, Cai L, Zang C, Wu J, Ye J, Lai Y, Liu B, Lin Q, Xue N (2017) Threatened species list of China's higher plants. *Shengwu Duoyangxing* 25(7): 696–744. <https://doi.org/10.17520/biods.2017144>
- Smith WW, Fletcher HR (1941) The Genus *Primula*: Section *Candelabra* Balf. *Transactions of the Botanical Society of Edinburgh* 33(2): 122–181. <https://doi.org/10.1080/13594864109441378>
- Smith WW, Forrest G (1923) New Primulaceae. *Notes from the Royal Botanic Garden Edinburgh* 203(14): 31–56.
- Smith WW, Forrest G, Fletcher HR (1977) The genus *Primula*. In: Cramer J (Ed.) *Plant Monograph Reprints*. Inder A. R. Gantner Vedag Konrmanditgesellschaft 11: 648–688.

# New and noteworthy species of the genus *Epidendrum* (Orchidaceae, Laeliinae) from the Área de Conservación Privada La Pampa del Burro, Amazonas, Peru

Jessy Patricia Arista<sup>1,2</sup>, Eric Hágsater<sup>3</sup>, Elizabeth Santiago<sup>3</sup>, José D. Edquén<sup>2</sup>, Elí Pariente<sup>2,4</sup>, Manuel Oliva<sup>4</sup>, Gerardo A. Salazar<sup>5</sup>

1 Instituto de Investigación, Innovación y Desarrollo del Sector Agrario y Agroindustrial (IIDAA), Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Chachapoyas, Amazonas, Peru

2 Escuela de Posgrado, Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Chachapoyas, Amazonas, Peru

3 Herbario AMO, Montañas Calizas 490, Lomas de Chapultepec. Miguel Hidalgo, Mexico City, 11000, Mexico

4 Instituto de Investigación para el Desarrollo Sustentable de Ceja de Selva (INDES-CES), Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Chachapoyas, Amazonas, Peru

5 Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico

Corresponding author: Gerardo A. Salazar ([gasc@ib.unam.mx](mailto:gasc@ib.unam.mx))

## Abstract

Fourteen species of the genus *Epidendrum*, recently collected in the Área de Conservación Privada La Pampa del Burro (ACPPB), five of them new to science (*Epidendrum echinatiantherum* sp. nov., *E. imazaense* sp. nov., *E. parvireflexilobum* sp. nov., *E. rosulatum* sp. nov., and *E. ochrostachyum* sp. nov.), are described and illustrated. The other species include a new record for Peru (*E. acrobatesii*) and four for the department of Amazonas (*E. brachyblastum*, *E. forcipatum*, *E. mavrodactylon*, and *E. tridens*). *Epidendrum enantilobum* is here considered a synonym of *Epidendrum brachyblastum*. The type locality of *Epidendrum cryptorhachis*, originally stated as Ecuador, Guayabamba, is corrected to indicate that it refers to the valley of Guayabamba, Rodríguez de Mendoza, Amazonas, Peru. Our results show the need to continue conducting botanical exploration in the ACPPB as a baseline for subsequent studies, including a full inventory of the orchid diversity.

**Key words:** Dwarf forest on white sand, eastern Andean ridge, Lankester Composite Dissection Plates, moist or wet montane forest, range extension

## Introduction

*Epidendrum* L. is the most species-rich Neotropical genus of Orchidaceae, with an estimated 2400 species, including undescribed species for which specimens or photographs have been recorded (e.g., Hágsater et al. 2016, 2019). Although earlier publications estimated the number of species at around 1500 (Hágsater and Soto Arenas 2005), the number of species presently monographed and confirmed is approximately 1900, with many added every year. The International Plant Names Index (IPNI, <https://ipni.org/>; accessed 12 March 2023) presently includes some 3425 names under *Epidendrum*, but many of these have



Academic editor: João Farminhão  
Received: 13 February 2023  
Accepted: 4 May 2023  
Published: 1 June 2023

Citation: Arista JP, Hágsater E, Santiago E, Edquén JD, Pariente E, Oliva M, Salazar GA (2023) New and noteworthy species of the genus *Epidendrum* (Orchidaceae, Laeliinae) from the Área de Conservación Privada La Pampa del Burro, Amazonas, Peru. *PhytoKeys* 227: 43–87, <https://doi.org/10.3897/phytokeys.227.101907>

Copyright: © Jessy Patricia Arista et al.  
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

been transferred to other genera, others are considered synonyms, and ten are subgeneric names. The genus is distributed from the southern United States to northern Argentina, and its species occupy nearly every habitat suitable for plant life, including mangroves and coastal dunes, tropical wet to seasonally dry forests, various types of montane forest and scrub, and Andean paramos, ranging from sea level to 4200 m elevation (Hágsater and Soto Arenas 2005; Hágsater and Krahl 2020). The plants are epiphytic, terrestrial, or lithophytic, displaying caespitose, repent, or pendulous growth forms. The stems often are slender and cane-like, but in some species the stems are thickened into pseudobulbs; and the leaves are usually distichously arranged along the stems. The flowers display a wide variety of sizes, colors, and fragrances, but the common theme among them is that the base of the labellum is united throughout the column length to form a narrow tunnel leading to a cuniculus that penetrates the pedicellate ovary to a varying extent. The small number of published observations indicate that pollination by diurnal and nocturnal lepidopterans is common, with some instances of hummingbird pollination (Dressler 1961, Hágsater and Soto Arenas 2005, Silveira et al. 2023).

According to a recent compilation, the orchid flora of Peru includes about 2900 species and 204 genera (Goicochea et al. 2019), in contrast with a conservative estimate given by Peru's Ministerio del Ambiente (MINAM), in which only 2206 species were recorded (MINAM 2015). Many species are considered endemic to the country and endemism seems to be concentrated in the departments of Amazonas, Apurímac, Ayacucho, Cajamarca, Cusco, Junín, Puno, and San Martín (Roque and León 2006). *Epidendrum* stands out as the largest genus of Orchidaceae in Peru, with about 480 species recorded (Quispe-Melgar et al. 2022).

In this study, we present initial results of our ongoing project aimed at documenting the orchid diversity present in the Área de Conservación Privada La Pampa del Burro. The information available on the floristic diversity of the area, and particularly that of the Orchidaceae, is very limited, with only 12 species of this family recorded to date (Shanee et al. 2012). Here, we focus on five undescribed and nine little-known species of the genus *Epidendrum* recorded in the ACPPB. Every species is described and illustrated with a detailed color plate, and information on their distribution and habitat, and a comparison with similar species, is provided. We aim to contribute to the knowledge of the genus *Epidendrum* in Peru and, particularly, to the orchid inventory of a highly diverse yet botanically unexplored protected area, as a baseline for subsequent studies. This contribution is not a complete inventory of the many species of *Epidendrum* in the ACPPB, but rather a first installment dealing with some of the new species found and new records for Peru or the region.

## Materials and methods

### Study area

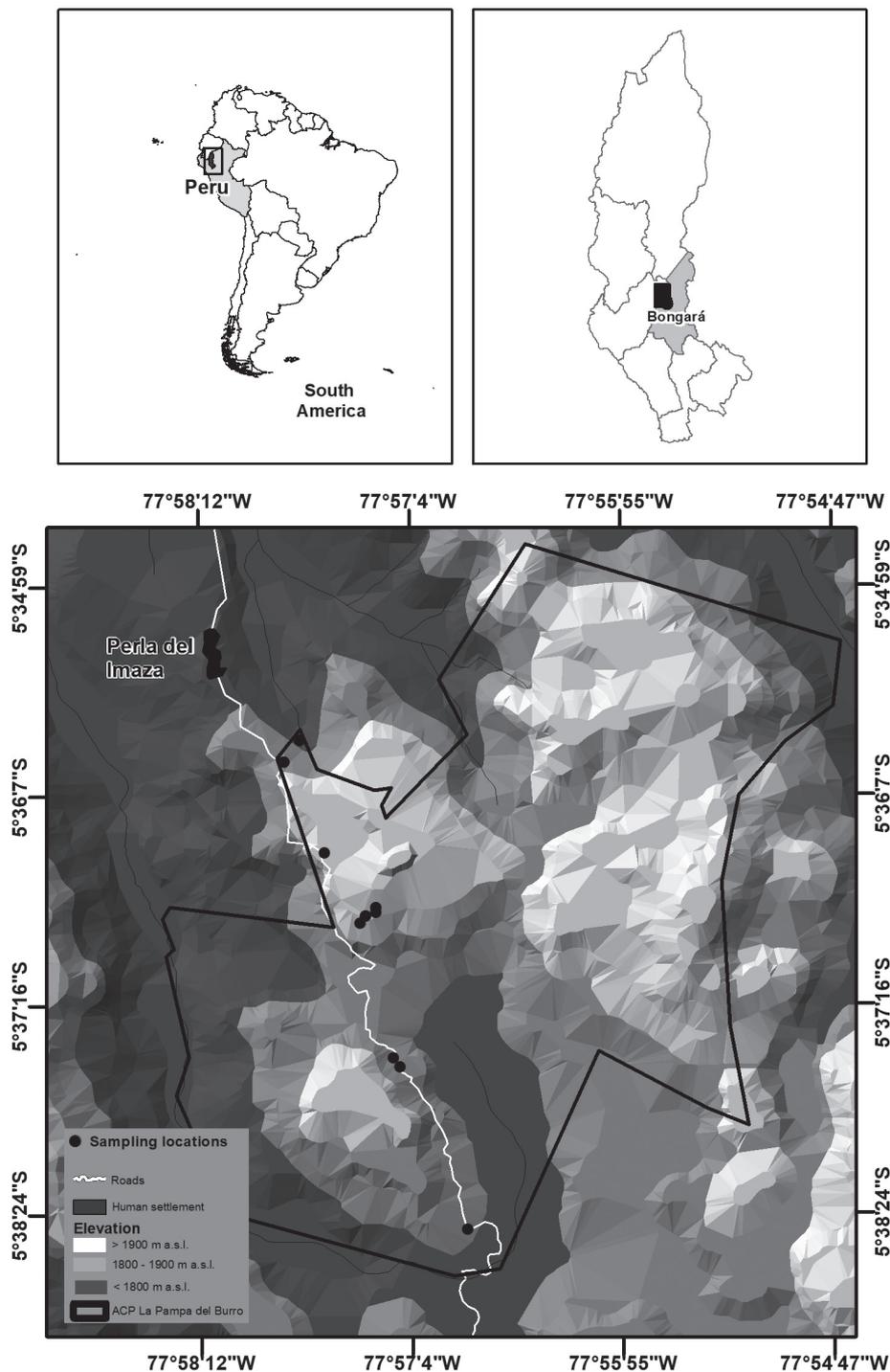
The Área de Conservación Privada La Pampa del Burro (ACPPB) belongs to the settlement of Perla del Imaza of the Comunidad Campesina de Yambrasbamba, province of Bongará, department of Amazonas, northeastern Peru, covering a surface of 2,776.96 ha on the eastern Andean range at 1750–1900 m

(ca. 5°34'59"–5°38'24"S, 77°54'47"–77°58'12"W; Fig. 1). The ACPBB forms a natural biological corridor between five other conservation units, namely the Bosque de Protección Alto Mayo, the Reserva Comunal Chayu Nain, the Área de Conservación Privada Abra Patricia, the Zona Reservada Río Nieva, and the Santuario Nacional Cordillera de Colán. Hence, the ACPBB is a key area to maintain the connectivity between various ecosystems and the continuity of natural cycles (Shanee et al. 2012). Two main ecosystems are present in the ACPBB, dwarf forest on white sand and moist or wet montane forest. The dwarf forest on white sand is a very particular type of vegetation characterized by high endemism (Ruokolainen and Tuomisto 1998) due to the nutrient deficiency and high acidity of the quartzite sand, which are highly restrictive for species not specialized to these conditions (Neill et al. 2014; Fig. 2). In contrast, the moist or wet montane forest is one of the most diverse ecosystems in the world as far as the number of species is concerned (e.g., Krömer et al. 2007). Moreover, the ACPBB was proposed as an important conservation area to preserve the habitat of the yellow-tailed woolly monkey, *Lagothrix flavicauda* Humboldt, 1812, the Peruvian night monkey, *Aotus miconax* Thomas, 1927, and the long-whiskered owlet, *Xenoglaux loweryi* O'Neill & Graves, 1977.

### Field collections and herbarium taxonomy

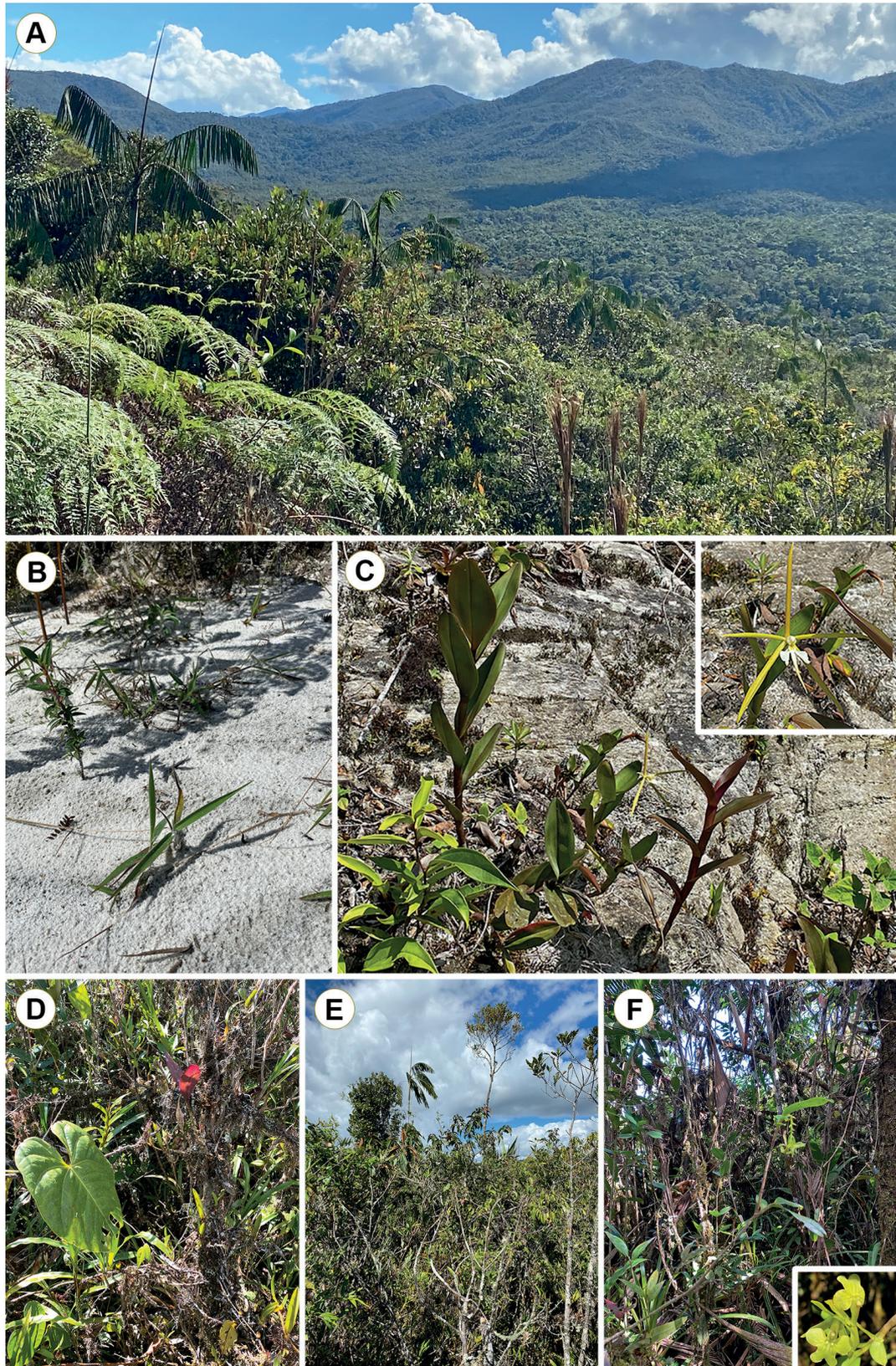
Material of the species reported here was collected during two field trips conducted in August 2021 and July 2022. A permit for scientific research was granted by Peru's Servicio Nacional Forestal y de Fauna Silvestre (SERFOR), with authorization code No. AUT-IFL-2021-033. Each species was photographed in the field and the laboratory using a digital camera (Nikon D850, Nikon Corporation, Tokyo, Japan) equipped with a Nikkor 60 mm, 2.8 lens and a Nikon Speedlight SB-70 (both from Nikon). Lankester Composite Dissection Plates (LCDP; Karremans 2020) were prepared with ADOBE PHOTOSHOP v. 24.1.0. Specimens of each species were pressed, dried, and deposited in the herbarium of the Universidad Nacional Toribio Rodríguez de Mendoza, Chachapoyas, Peru (KUELAP).

For the taxonomic identification of the various species, each specimen was first assigned to the appropriate group within the genus *Epidendrum* according to E. Hágsater and collaborators (Hágsater 1985), and subsequently it was tentatively identified to species level within the group. With a first tentative identification, a search was made for published illustrations, plates and descriptions in the various series of The Genus *Epidendrum* in Icones Orchidacearum (Hágsater and Salazar 1993; Hágsater et al. 1999; Hágsater and Sánchez Saldaña 2001, 2004, 2006, 2007, 2008, 2009, 2010, 2013, 2015, 2016a, b; Hágsater and Santiago 2018, 2019, 2020a, b, 2021, 2022a, b), Icones Orchidacearum Peruvianarum (Bennett and Christenson 1993, 1995a, b, 1998, 2001), and Icones Plantarum Tropicarum (Dodson and Dodson 1980a, b, c, 1982, 1984, 1989a, b; Vásquez and Dodson 1982; Dodson and Bennett 1989a, b). In addition, searches were carried out in AMODATA, the database of the AMO Herbarium (Hágsater and Sánchez Saldaña 2016b), which includes some 150000 digital color images taken in the field, as well as of herbarium specimens photographed since 1976 in herbaria in the United States, Europe and tropical America by the staff of AMO, in search of specimens under the preliminary name or from the relevant geographic region, to identify possible specimens of the same entity.



**Figure 1.** Location of the Área de Conservación Privada La Pampa del Burro in the province of Bongará, department of Amazonas, Peru.

The herbaria for which *Epidendrum* material was available for comparison include AAU, AMES, AMO, ANDES, B (photographs taken before its destruction), BM, BR, BRIT, C, CAS, CHAX, CM, COL, CPUN, CTES, CUVC, CUZ, E, ENCB, F, FI, G, GH, GOET, HAO, HB, HBG, HCEN, HNOP, HOXA, HURP, HUSA, HUT, INPA, ITA, JAUM, K, KUELAP, L, LE, LL, M, MA, MEXU, MICH, MO, MOL, NY, OXF, P, PR, PRC, PRG, QCA, QCNE, R, RENZ, S, SEL, TEX, TNS, U, UC, UFV, US, USF, USM, VEN, W, WIS, and WRSL. Most specimens were positively identified as a published spe-



**Figure 2.** Overview of the vegetation in the Área de Conservación Privada La Pampa del Burro **A** forested low hills and slopes, with dwarf forest on white sand in the forefront **B** exposed white sand in a cleared area **C** *Epidendrum tridens* on white sand on a roadside embankment; inset: close-up of a flower **D** dense tangle of epiphytes and climbers in the understory of the dwarf forest **E** canopy of the dwarf forest **F** *Epidendrum weigendii*, a climber orchid; inset: close-up of an inflorescence (Photographs by G. A. Salazar).

cies. The material found in the abovementioned sources was studied, in many instances allowing to widen previously known distribution ranges. In some cases, additional specimens were found to have been recorded earlier but filed without an identification or under the wrong name.

The information provided in the following for each species includes a full description, a LCDP color figure and, for narrowly distributed species with a small number of records, we cite all Peruvian material found. Additionally, in some instances specimens from neighboring Ecuador are also listed, not only when the type corresponds to that country, but in the few cases where the known range includes southern Ecuador, which shares the same biomes. In the case of common species widely distributed throughout the Andes, only Peruvian materials are cited. Specimens refer to herbarium sheets or in some cases flowers in spirit. Other Records refer to illustrations or color digital images where no herbarium specimens were prepared or found. Reference is made to where these materials are kept. Many have been gathered from Facebook, GBIF, or personal correspondence.

Finally, as this is not a floristic treatment, no key to the species of the genus for the area is given.

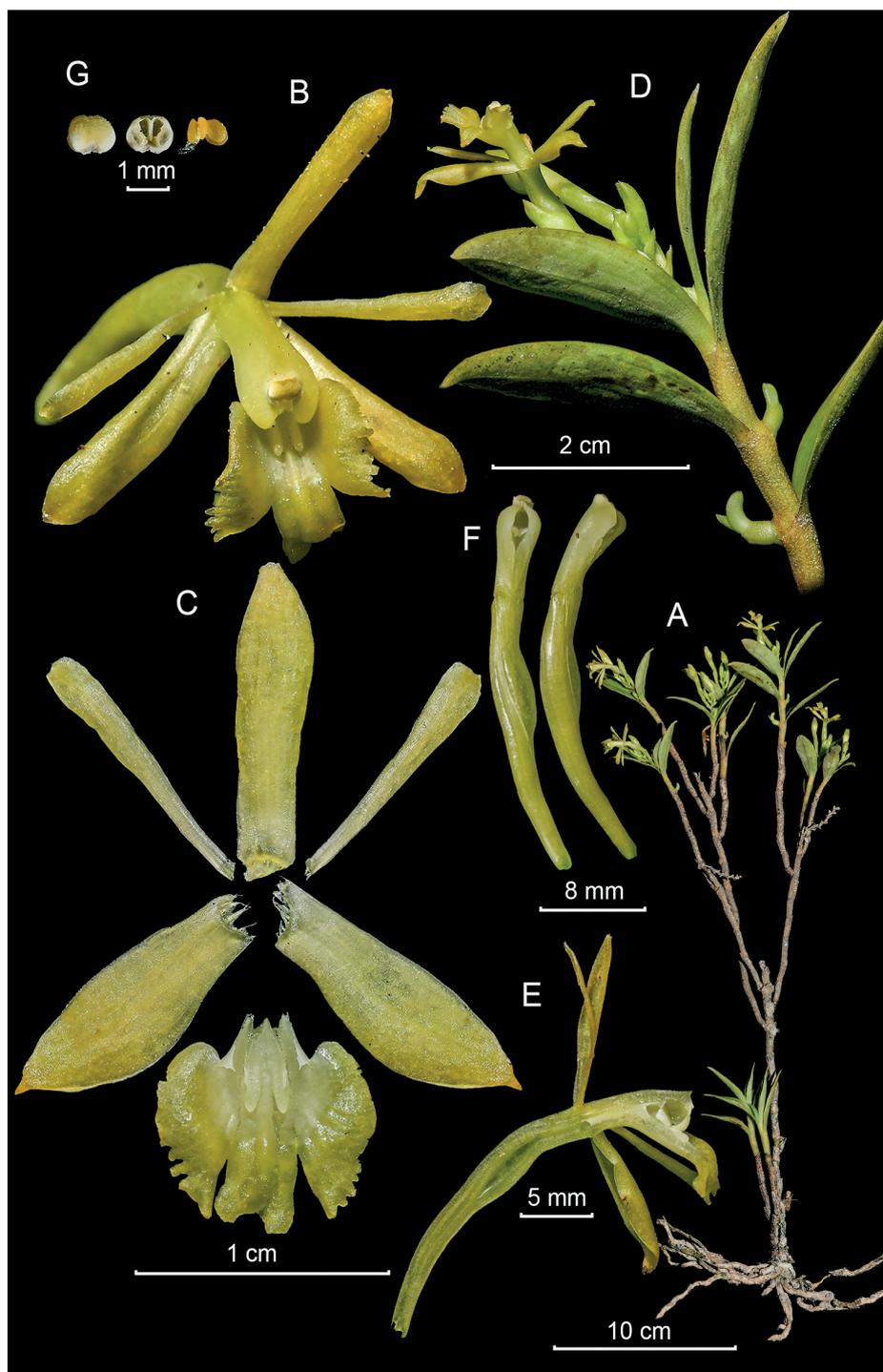
## Taxonomic treatment

*Epidendrum acrobatesii* Hågsater & Dodson, *Icon. Orchid.* 4: t. 402. 2001.

Fig. 3

**Type material.** ECUADOR. Loja: N slope of Nudo de Sabanilla S of Yangana on road to Valladolid, 4°28'S, 79°10'W, 2500 m, 24 Feb. 1988, U. Molau & B. Eriksen 3191 (holotype: GB!; isotypes: AAU! QCA!).

**Description.** Epiphytic or terrestrial, monopodial, branching, erect **herb**, 31–34 cm tall including inflorescence. **Roots** 1–3 mm in diameter, emerging only from base of primary stem, fleshy, thick. **Stems** cane-like, erect, somewhat sinuous, branching from sub-apical internodes; primary stem 16 × 0.5 cm; secondary stems 1.5–14.6 × 0.3–0.4 cm. **Leaves** ca. 19 on primary stem, 5–14 on secondary stems, distributed throughout stems, usually only apical 3–5 leaves remaining at flowering, alternate, articulate; sheath 0.7–1.4 × 0.3–0.5 cm, tubular, rugose, striated; blade 2.2–3.8 × 0.7–1.4 cm, length:width 3:1, apical leaf usually reduced, elliptic, mucronate, light green on both sides, apical margin minutely erose-dentate, spreading. **Spathes** lacking. **Inflorescence** up to 7.6 cm long including flowers, apical, flowering only once, racemose (sometimes with a short branch near base), erect in early stages, becoming arching-nutant as it develops; peduncle 5–7 mm long, terete, rachis 15–33 mm long, developing as new flowers are formed, flexuous, compact, ornamented with a short keel at base of each floral bract. **Floral bracts** 1–3 mm long, much shorter than ovary, ovate, conduplicate, acute to obtuse. **Flowers** 6–12, successive, 1–2 open at a time in different stages, with smaller buds present, erect, facing upwards, yellow to green; apparently not fragrant. **Sepals** 10–12 × 3.5–4.2 mm, free, spreading, narrowly elliptic to oblanceolate, acute, slightly aristate, especially the lateral sepals, 5-veined, margins entire, revolute. **Petals** 12 × 0.6–1.8 mm, free, spreading, linear or linear-obcuneate, obtuse to rounded, 1-veined, margins entire, spreading. **Lip** 5.0–7.7 × 7.0–9.0 mm, cordiform in general outline, deeply 3-lobed, somewhat concave basally in natural position with lateral margins and



**Figure 3.** *Epidendrum acrobatesii* from Arista et al. 21 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (left) and below (right), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

apex more or less revolute; bicallose, calli  $3.7 \times 0.6$  mm, elongate, parallel, with a mid-rib running to apical sinus, disc with multiple thickened veins, converging basally and radiating apically; lateral lobes  $3.2 \times 7.0$  mm, semi-sagittate, apex acute, margins progressively short-laciniate; mid-lobe  $3.1 \times 3.2$  mm, quadrate to obcuneate, apex truncate to emarginate, with a wide sinus, margins entire to erose. **Column** 7–8 mm long, thin, straight. **Clinandrium hood** truncate, margin

entire. **Anther** reniform. 4-celled. **Pollinia** 4, obovate, laterally compressed, inner face of each pair flat; caudicles short. **Rostellum** apical, slit; viscarium semi-liquid, transparent. **Cuniculus** penetrating half of pedicellate ovary and widened toward the middle of the ovary, forming a narrowly ellipsoid vesicle. **Ovary** 17–24 × 1.6–3.2 mm, slightly inflated ventrally beyond middle forming an elongate vesicle, but narrow near apex, furrowed. **Capsule** not seen.

**Additional specimens examined.** **PERU. Amazonas:** La Pampa del Burro, 22 Aug. 2021, *Arista et al.* 21 (KUELAP!); **Pasco:** Oxapampa, Parque Nacional Yanachaga–Chemillén, parte alta de la trocha Tunqui–Cajonpata, sector Tunqui, 1950 m, 31 Oct. 2007, *Monteagudo* 15793 (HOXA!).

**Other records.** **PERU. Amazonas:** Chachapoyas: Distr. Longuita, Fortaleza Kuelap, 14 Nov. 2019, *Harding s.n.*, digital images (AMO!); Bongará: Yambrasbamba; Progreso, 30 Dec. 2019, *Velásquez s.n.*, digital images (AMO!); **San Martín:** Prov. Rioja, Distr. Pardo Miguel Naranjos, 1962 m, 6 Nov. 2015, *Edquén* 2042, digital images (AMO!); *Ibid. loc.*, 1691 m, 22 Feb. 2017, *Edquén* 2043, digital images (AMO!); *Ibid. loc.*, 1790 m, 20 Feb. 2017, *Edquén* 2044, digital images (AMO!); hort. Moyobamba, 9 Jan. 2017, *Goicochea s.n.*, digital images (AMO!).

**Distribution.** Widespread from Ecuador (Napó and Zamora–Chinchipec) south to Oxapampa, Pasco, in central Peru. The range of the species along the upper eastern slope of the Andes in Ecuador and central Peru spans some 1150 km, with at least 7 known localities. Growing at 1691–2500 m.

**Habitat and ecology.** Epiphytic, found on very wet fallen logs with abundant moss, in primary montane humid forest or elfin forest, often with afternoon fog. Sometimes at the base of *Chusquea* Kunth. Also terrestrial on edge of roadside banks of white sand with abundant organic material in elfin forest.

**Phenology.** Flowering throughout the year.

**Taxonomic notes.** *Epidendrum acrobatesii* has leaves with a length:width proportion about 3:1, elliptic, with the margin minutely erose–dentate, the inflorescence 5 cm long, with 6–12 greenish yellow flowers, sepals 10–12 mm long, petals linear to linear–obcuneate, and the lateral lobes of the lip nearly as long as the mid-lobe, which is apically truncate to emarginate. *Epidendrum batesii* Dodson has proportionately narrower leaves, 2.5–3.4 × 0.6–0.8 cm, length:width 4:1, the mid-lobe of the lip shorter and entire, 2.3–2.5 mm long. *Epidendrum oxybatesii* Hágsater & Dodson from northern Ecuador is distinguished by the long, acicular mid-lobe of the lip.

This is an addition to the flora of Peru. The Batesii Group has a peculiar architecture in that the new stems produced from the apical half of the basal stem can be as long as the primary stem, and those closest to the apex are produced first, with shorter stems being later produced further down the primary stem.

***Epidendrum brachyblastum* Hágsater & Dodson, Icon. Orchid. 7: t. 713. 2004.**  
Fig. 4

**Type material.** **ECUADOR. Pastaza:** Mera, 11 km, cañada del Río Anzú, 1225 m, collected 10 Dec. 1986, flowered in cultivation 6 May 1987, *E. Hágsater & C. H. Dodson* 9093 (holotype: AMO, spirit! flower card and color slides, AMO!).

**New taxonomic synonym.** *Epidendrum enantilobum* Hágsater, Icon. Orchid. 16(1): pl. 1616 (2018) syn. nov. Type: Peru. San Martín: Rioja–Pomacochas road,

below Venceremos, ca 20 km NW of Rioja, near Restaurante El Amigo, 1600 m, 8 Feb. 1984, A. H. Gentry & D. N. Smith 45148 (holotype: NY!; isotype: MO-349072!)

**Description.** Epiphytic, sympodial, caespitose, erect **herb**, 30–55 cm tall including inflorescence. **Roots** 2 mm in diameter, basal, fleshy. **Stems** 6–53 × 0.3–0.5 cm, simple, cane-like, terete, thin, straight. **Leaves** 5–12 distributed along apical 2/3 of stem, sub-erect, alternate, sub-coriaceous; sheath 10–14 mm long, tubular, minutely striated; blade 3.3–11.5 × 1.0–2.5 cm, narrowly elliptic to oblong-elliptic, acuminate, minutely apiculate; margin entire, spreading. **Spathe** lacking. **Inflorescence** 5–12.5 cm long, apical, racemose to paniculate, compact, arched; peduncle 4 cm long, short, terete, thin, nearly totally covered by 1–3 basal bracts, 1.5–2.2 cm long, terete, triangular-lanceolate, acuminate, embracing; rachis 2–3.5 cm long, short, terete, thin, straight to arching. **Floral bracts** 4–14 mm long, progressively shorter, triangular-lanceolate, acuminate. **Flowers** 9–25 per raceme, simultaneous, resupinate, lip always oriented toward rachis, medium to dark green, lip and apical half of column white; fragrance not registered. **Sepals** 6.0–7.0 × 3.2–3.8 mm, free, fleshy, spreading, slightly concave, obovate, obtuse, minutely apiculate, margins entire, spreading; dorsal sepal 3-veined; lateral sepals 3-veined, with lateral veins bifurcate from base and appearing 5-veined. **Petals** 5.0–6.1 × 1.0–1.6 mm, free, spreading, narrowly spatulate, obtuse, 1-veined, apical margin slightly erose, spreading. **Lip** 4.5–6.4 × 5.0–7.0 mm, united to column, 3-lobed, base cordate; bicallose, calli thin, short, disc provided with a low, rounded mid-rib reaching apical sinus; lateral lobes 2.4–2.8 × 1.3–3.0 mm, falcate, narrow, sub-acute, posterior margin somewhat erose; mid-lobe 2.0–3.7 × 1.5–4.5 mm, isthmus sub-rectangular, gradually narrower then deeply bifid toward the apex, lobes long, narrowly triangular, cirrhose, acuminate, divaricate, apices revolute. **Column** 5–8 mm long, slightly arched, base thin, abruptly thickened ventrally, with a pair of truncate lateral wings. **Rostellum** sub-apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** half as long as stigmatic cavity. **Anther** ovoid, 4-celled. **Pollinia** 4, bird-wing-type, unequal, inner pair about  $\frac{3}{4}$  size of outer pair. **Cuniculus** without penetrating pedicellate ovary, narrow at base and widening toward entrance, unornamented. **Ovary** 7–15 mm long including pedicel, terete, thin, not inflated, unornamented, furrowed. **Capsule** not seen.

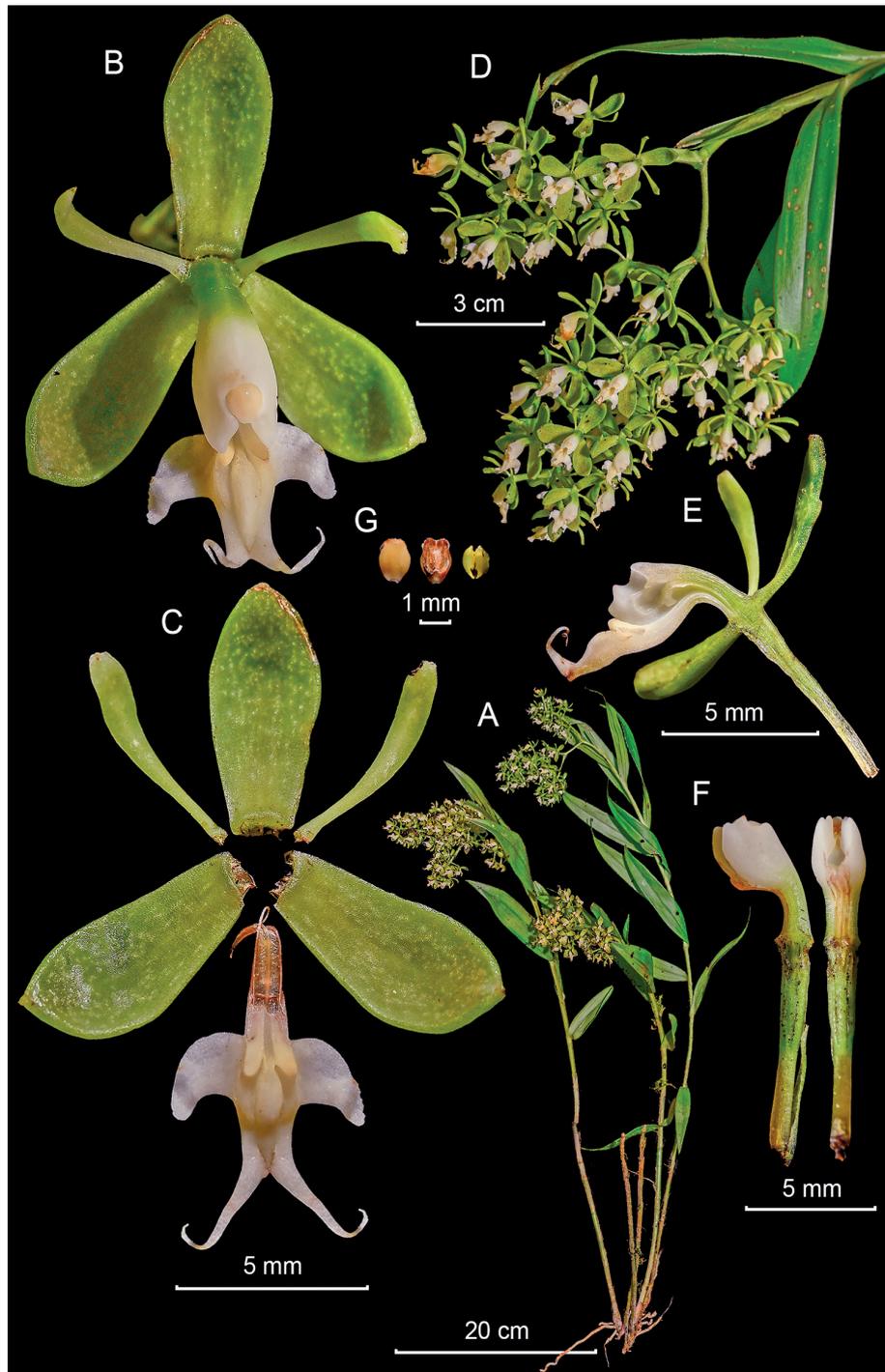
**Additional specimens examined. PERU. Amazonas:** Bongará, Florida, Laguna Pomacocha, km 335 on the road to Rioja, 2360 m, 26 Jan. 1964, *Hutchinson 3809* (UC! USM!); Yambrasbamba, Perla del Imaza, Área de Conservación privada La Pampa del Burro, 1682 m, 28 Aug. 2021, *Arista et al. 148* (KUELAP!); **San Martín:** Carretera Rioja–Pedro Ruiz, 1450 m, 24 Mar. 1998, *van der Werff 15568* (MO!).

**Other records. PERU. Amazonas:** alrededores de Chachapoyas, 2400 m, *Morón s.n.*, digital images (AMO!); **San Martín:** Moyobamba, Soritor, San José El Doncel, 3 Feb. 2021, *Bazan 1*, digital images (AMO!).

**Distribution.** Presently known from Ecuador, near Mera in Pastaza, to north-eastern Peru, in the border between Amazonas and San Martín, on the eastern Andean range near Moyobamba. The species has only been collected along two well-paved roads: the Troncal Amazónica, in Ecuador, and the Carretera Marginal de la Selva Fernando Belaunde Terry, in Peru. Growing at 1100–2360 m.

**Habitat and ecology.** Epiphytic in wet forest.

**Phenology.** Flowering from January to August.



**Figure 4.** *Epidendrum brachyblastum* from Arista et al. 148 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicle from side (left) and below (right) **G** anther from above (left) and below (right), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

**Taxonomic notes.** *Epidendrum brachyblastum* belongs to the Bicirrhatum Group, which is characterized by the caespitose habit, simple, cane-like stems, short, arching, pluriracemose, sub-capitate inflorescence, narrowly spatulate petals, 3-lobed lip, generally with cirrate apical lobes and unequal, laterally compressed pollinia, with the inner pair smaller. *Epidendrum brachyblastum* medium to deep green flowers with the lip and apical half of the column snow white,

the lateral lobes of the lip are narrow and falcate, the mid-lobe is split into two apical cirrhose lobes. It closely resembles *Epidendrum tiwinzaense* Hágsater & Dodson, which has pale green (vs. deep green) flowers, with the column and lip cream-colored, the lip with very wide dolabriform lateral lobes. It also closely resembles *E. bicirrhatum* D.E.Benn. & Christenson, which has opaque, pale cream-orange flowers, the sepals and petals green at the base, the tips of the calli keels lavender, and the column white at the base, cream-yellow above.

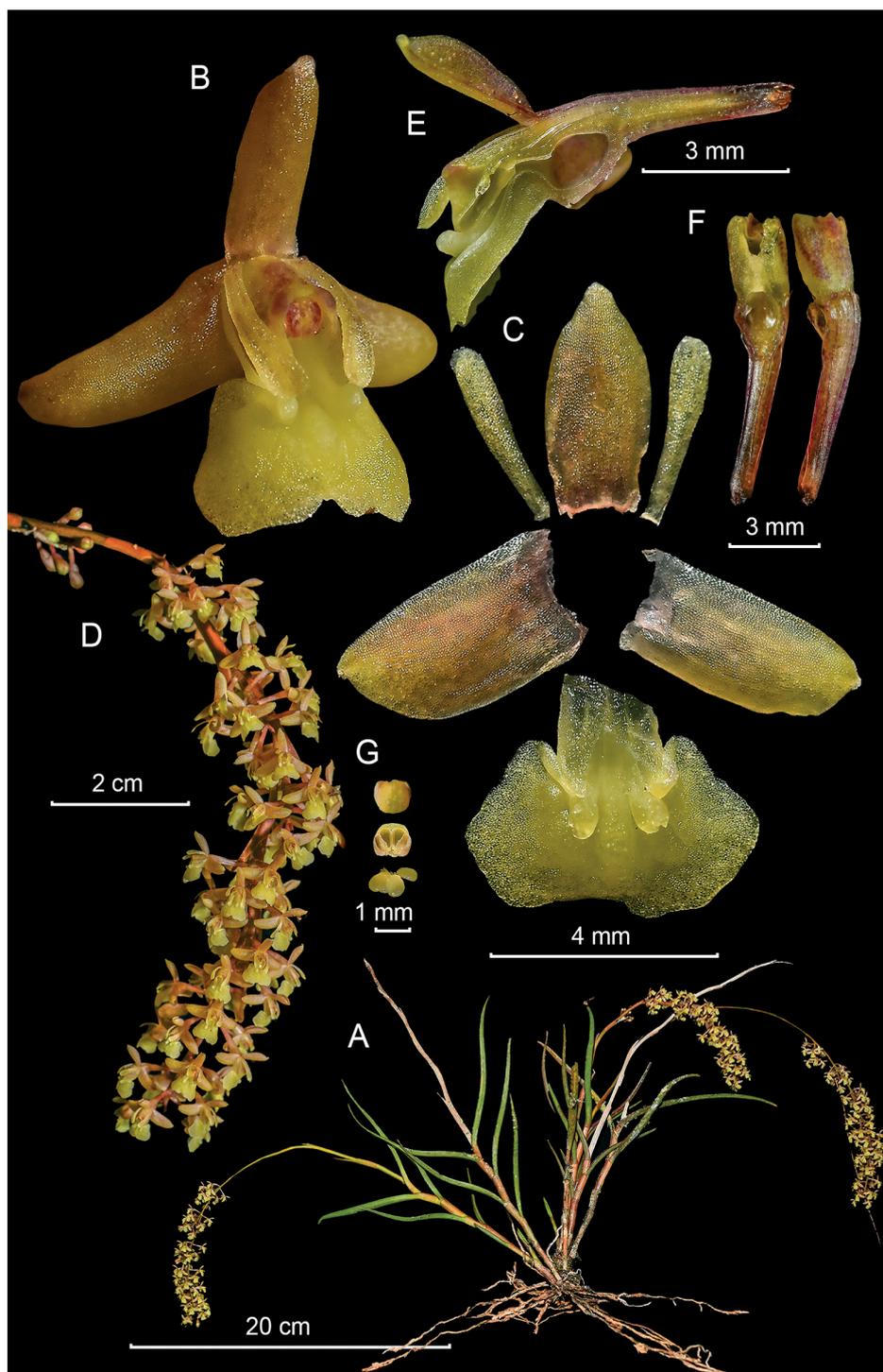
The type specimen of *E. brachyblastum* was prepared from a cultivated plant not in the best cultural conditions, with few, large flowers, and shorter apical lobes of the lip, thus not being a good representative of the species, which was later described as *E. enantilabium* Hágsater, here included in the synonymy of *E. brachyblastum*. *Hutchison 3809* was collected in 1964, but only recently identified as *E. enantilabium*, ergo the species was known earlier from Peru.

***Epidendrum cryptorhachis* Hágsater, Icon. Orchid. 8: t. 823. 2006.**

Fig. 5

**Type material.** PERU. [Amazonas: Rodríguez de Mendoza: Valle de] Guayabamba, 8 Mar. 1877, M. Vidal-Sénège s.n. (holotype: P!; isotype: P!). [Locality corrected, see note under Distribution.]

**Description.** Lithophytic or epiphytic, sympodial, caespitose, erect and arching **herb**, 17–43 cm tall including inflorescence. **Roots** ca. 2–3 mm in diameter, basal, scarce, thin. **Stems** 6–11 × 0.2–0.6 cm, simple, short, cane-like, terete at base, laterally compressed toward apex, thin, flexuous. **Leaves** 3–6, distributed throughout stems, alternate, sub-erect; sheath 0.8–2.0 × 0.2–0.6 cm, infundibuliform when dry, minutely striated; blade 2.8–10 × 0.4–0.8 cm, linear-lanceolate, acuminate, succulent and coriaceous, canaliculate, margin entire. **Inflorescence** 16–32 cm long, apical, paniculate, arching–nutant, densely, many-flowered; peduncle 6–16 × 0.07–0.4 cm, elongate, longer than leaves, thin, ancipitose, two-winged, slightly sinuous, provided with 1–5 bracts 1.7–3.2 × 0.1–0.4 cm, each subtending a raceme, tubular and ancipitose at base, conduplicate above, long, acuminate; panicle with 6–9 short, straight, short racemes 1.4–2.7 cm long, densely 8–10-flowered, sub-parallel to axis of inflorescence, enveloped at base by large conduplicate bracts 1.0–2.5 × 0.1–0.3 mm, similar to those of peduncle but progressively shorter toward apex. **Floral bracts** 1–2 mm long, small, shorter than ovary, triangular, acute. **Flowers** ca. 90, 4–14 per raceme, small, membranaceous, simultaneous, resupinate, sepals ochre to pale green, petals and lip yellow, column yellow tinged brown, anther brown red; fragrance not registered. **Sepals** spreading, free, 3-veined, margin entire, revolute; dorsal sepal 3.3–3.7 × 1.6–2.0 mm, ovate-elliptic, sub-acute, lateral sepals 3.5–4.2 × 1.0–2.2 mm, oblong, apex obtuse, slightly oblique, short apiculate. **Petals** 3.0–3.7 × 0.6–0.7 mm, free, parallel to column and embracing it, narrowly obovate, apex rounded, 1-veined, margin entire, revolute. **Lip** 3 × 5.3 mm, united to column, bilobed, widely hexagonal, base cordate, apex emarginate, margin entire, sides revolute in natural position, somewhat apron shaped; lobes 2.0–2.8 × 3.3–4.3 mm, from semi-orbicular to obliquely triangular-quadrate; bicallose, calli prominent, finger-like, short, sub-erect at apex, disc with a low-wide, mid-rib reaching apical sinus, and 3 low rounded thickenings on each side. **Column** 2.8 × 0.9 mm,



**Figure 5.** *Epidendrum cryptorhachis* from Arista et al. 128 **A** habit **B** flower **C** dissected perianth **D** inflorescence **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (up) and below (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

short, slightly arching, apex oblique, with short, obliquely truncate fleshy column wings. **Clinandrium hood** short, concave, margin entire. **Anther** spherical, with a very low rounded keel in front, 4-celled. **Pollinia** 4, nearly lentil-shaped, laterally compressed, translucent; caudicles very short. **Rostellum** apical, slit; viscarium semi-liquid, transparent. **Lateral lobes of stigma** 1.7 mm long, very

short,  $\frac{1}{4}$  length of stigmatic cavity, very slender. **Cuniculus** penetrating  $\frac{1}{3}$  of ovary, much inflated behind perianth, smooth. **Ovary**  $5.3 \times 2$  mm at apex (including vesicle), terete, glabrous, furrowed, thin along basal  $\frac{2}{3}$ , ventrally inflated toward apical  $\frac{1}{3}$ , forming a prominent globose vesicle. **Capsule** not seen.

**Additional specimens examined.** **ECUADOR. Zamora-Chinchipe:** km 44 Loja-Zamora, *Dodson s.n. ex Missouri Bot. Garden "61-150-57 SEL! (illustration AMO!);"* **Peru. Amazonas:** Bongará: Yambrasbamba, Perla del Imaza, Área de conservación privada La Pampa del Burro, 1763 m, 28 Aug. 2021, *Arista et al. 128 (KUELAP!);* **Cajamarca:** San Ignacio, San José de Lourdes, Buenos Aires, 1880 m, 3 Nov. 2000, *Calatayud 804 (CUZ!);* **Huánuco:** Between Huánuco and Pampayacu, 28 Jan. 1927, *Kanehira 26 (AMES!)*.

**Other records.** **PERU. Amazonas:** Chachapoyas: Molinopampa, 2400–2700 m, 13 Nov. 2010, *Dalström 3240*, digital images (AMO!).

**Distribution.** The species is presently known from the Amazon slope of the Andes in northern Peru and southern Ecuador, spanning some 720 km, at about 1750–2700 m elevation. Six localities have been identified, but the species is probably more widespread and common, and the terrain in between has not been thoroughly botanized. When first published, this species was thought to have come from Guayabamba in Ecuador, but recently we have learned that the Valley of Guayabamba is the valley of Rodríguez de Mendoza, south of Chachapoyas, in the department of Amazonas, Peru. Thus, this is the first confirmed record for Peru, though it had been collected earlier.

**Habitat and ecology.** Lithophytic in cliffs and trunk epiphyte on *Inga* Mill. in humid premontane forest, "Ceja de Selva", with *Cinchona* L. (Rubiaceae) and *Cedrela* P.Browne (Meliaceae).

**Phenology.** Flowering from August to March.

**Taxonomic notes.** *Epidendrum cryptorhachis* belongs to the Epidendropsis Group, Gracillimum Subgroup, characterized by the sympodial, caespitose, relatively small plants with non-thickened stems, long, paniculate inflorescences, delicate small flowers, and long, narrow, sub-coriaceous leaves. The species is recognized by long, many-raceme inflorescence, about twice as long as the apical leaf or more, appearing at first sight racemose, with the racemes parallel to the peduncle, each raceme subtended by a bract, petals narrowly spatulate, with a wide reniform, sub-hexagonal bilobed lip, deeply cordate, the sides revolute and thus appearing apron-shaped. It is similar to *Epidendrum gracillimum* Rchb.f. & Warsz. but that species has narrower leaves, fewer flowers, a long narrow cuniculus penetrating about half the ovary, linear petals, and an entire, reniform lip. *Epidendrum physophorum* Schltr. from Bolivia has a much shorter inflorescence, the branches spreading, the flowers smaller, the inflated cuniculus at the apex of the ovary, the comparatively slender column, the petals linear, and the reniform, entire lip with a dentate-erose margin.

***Epidendrum echinatiantherum* Hágsater, E.Santiago, J.P.Arista & Edquén, sp. nov.**  
urn:lsid:ipni.org:names:77320357-1

Fig. 6

**Type material.** **PERU. Amazonas:** Prov. Bongará: Distr. Yambrasbamba: Perla del Imaza, Área de Conservación Privada La Pampa del Burro, Bosque de Pie-

dra, 1682 m, 28 Aug. 2021, J. P. Arista, J. D. Edquén, E. Yrigoín & L. Iliquin 151 (holotype: KUELAP!).

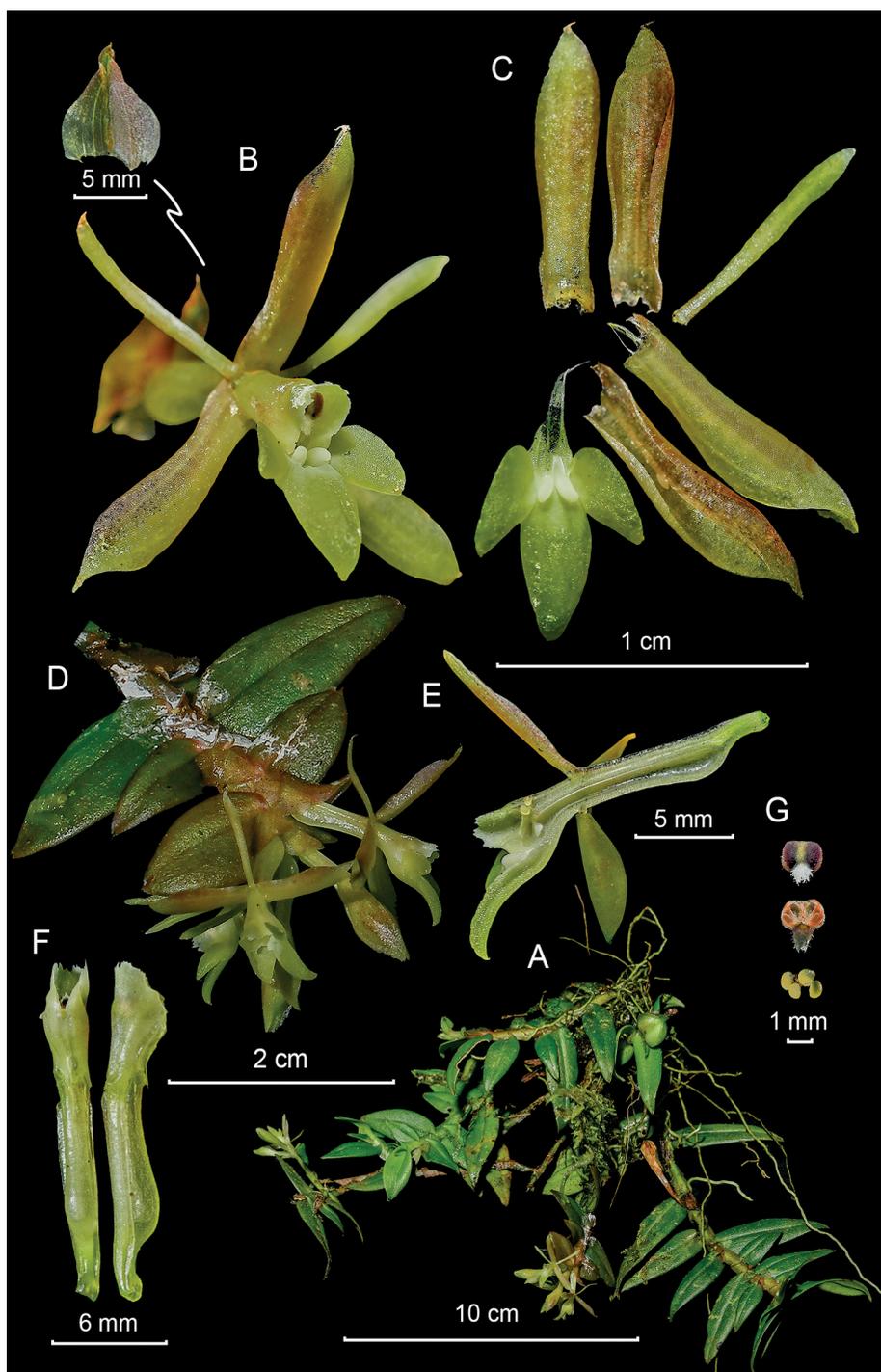
**Diagnosis.** Similar to *Epidendrum madsenii* Hágsater & Dodson, both vegetatively and florally, but the main distinguishing feature is the dark vinaceous anther with the central green vertical rib with a heavily echinate apical, elongate, pyramidal, truncate process, covered by numerous disorganized white bristles (vs. dark brown-black anther without a green vertical rib, and an unornamented apical process, which is laminar, forming an erect, semi-tubular laminar flap, the margins dentate).

**Description.** Epiphytic, sympodial, branching, pendulous, **herb**, 8–13 cm long. **Roots** ca. 0.7 mm in diameter very thin, basal on primary stems. **Stems** 4.5–13 × 2–3 cm, laterally compressed, new stems produced from sub-apical node of previous stem, sometimes from base of primary stem. **Leaves** 10–25 per stem, distributed throughout the length of the stems, articulate, twisted at base so as to be on same plane of stem as in *Dichaea*; sheaths 0.4–0.6 × 0.35–0.45 cm, tubular, laterally compressed, ancipitose, minutely rugose, green; leaves 1.1–4.3 × 0.6–1.2 cm, ovate to lanceolate, acute, fleshy, succulent, margins entire, spreading, medium green. **Spathe** lacking. **Inflorescence** apical, racemose, sub-corymbose, pendulous, from mature stem, sessile, 3-flowered. **Floral bracts** 6–8 × 6–7 mm, conduplicate, widely cordiform when spread, dorsally carinate, especially toward apex, embracing. **Flowers** 3, more or less simultaneous, pendulous, pale green, sepals tinged pale brown, calli white; fragrance not recorded. **Sepals** 9.5 × 3 mm, nearly spreading, free, narrowly lanceolate, acute, 3-veined, lateral sepals dorsally carinate, apex aristate, margins entire, somewhat revolute. **Petals** 9 × 1 mm, free, nearly spreading, linear-lanceolate, acute, 1-veined, margins entire, slightly revolute. **Lip** 7.5 × 6.0 mm, united to basal half of column, deeply 3-lobed, fleshy, thick, calli 1.1 mm long, basal, digitiform, divergent, disc unornamented, lateral lobes 4.0 × 2.2 mm, transversely ovate, apex narrowly rounded, nearly spreading flat in natural position, at a 45° angle to midline of lip; mid-lobe 4.5 × 2.6 mm, semi-elliptic, apex rounded. **Column** 5.5–6.2 mm long dorsally including clinandrium hood, straight, body of column (to rostellum) about half as long as hood. **Clinandrium hood** prominent, semi-tubular, somewhat funnel-shaped, margin erose-dentate, anther deep within. **Anther** reniform, dark vinaceous with central green vertical rib, with an elongate pyramidal, truncate flap at apex, covered by numerous disorganized white bristles, heavily echinate. **Pollinia** 4, lentil-shaped, caudicles soft and granulate. **Rostellum** apical, nearly at an 80° angle with axis of column, slit; viscarium semi-liquid. **Lateral lobes of stigma** large, transverse, triangular with stigmatic cavity vertical, transverse. **Cuniculus** penetrating nearly to base of pedicellate ovary, somewhat wide, forming an elongate ventral vesicle in pedicel. **Ovary** 7.5–10 × 2–3 mm including pedicel, terete, straight, inflated nearly to base by elongate vesicle, slightly more inflated basally. **Capsule** not seen.

**Distribution.** Known only from the type collection, in Amazonas, Peru, on the eastern slope of the Andes at 1682 m altitude.

**Habitat and ecology.** Epiphytic in wet montane forest on white sand, covered by accumulated organic material, dominated by palms, with *Cinchona* sp. and *Cedrela* sp. Presence of many Bromeliaceae, mosses. Growing on dry hanging thin branch covered by moss.

**Phenology.** Flowering in August.



**Figure 6.** *Epidendrum echinatiantherum* from Arista et al. 151 **A** habit **B** flower and floral bract **C** dissected perianth with dorsal and one lateral sepal shown from above and below, not spread **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (up) and below (down), and pollinarium **H** floral bract (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

**Taxonomic notes.** *Epidendrum echinatiantherum* belongs to the Nanum Group, which is characterized by the *Dichaea*-like horizontal or pendulous stems and the inflorescence produced by pairs of opposite flowers without spathes, but with prominent floral bracts. The new species is characterized by the few flowers, the cuniculus forming a long ventral swollen vesicle nearly reaching

the base of the pedicellate ovary, relatively large, the sepals 9.5 mm long, the deeply 3-lobed lip with prominent ovate lateral lobes on the lip, the semi-elliptic mid-lobe and the prominent clinandrium hood, somewhat funnel-shaped and especially the reniform anther, dark wine-red with central green vertical rib, with an elongate pyramidal, truncate flap at apex, covered by numerous disorganized white bristles, heavily echinate. It is most similar to *Epidendrum madsenii*, which also has a prominent, very long swollen vesicle at the base of the ovary, nearly as long as the ovary itself, the pale green flowers, the prominent 3-lobed, erose clinandrium hood, the triangular, acute mid-lobe of the lip, and the ornamentation of the anther consisting of a transverse, dentate process in front. It closely resembles *Epidendrum lueri* Dodson & Hágsater, which has pinkish yellow flowers with a bright yellow lip, a denticulate clinandrium-hood, but it is neither 3-lobed nor fimbriate.

**Etymology.** From Latin *echinatus*, bristly, furnished with numerous rigid hairs, or straight prickles, and *anthera*, the cover of the pollinarium at the apex of the column, which has an appendage heavily covered with white bristles, a rare and prominent feature of this species.

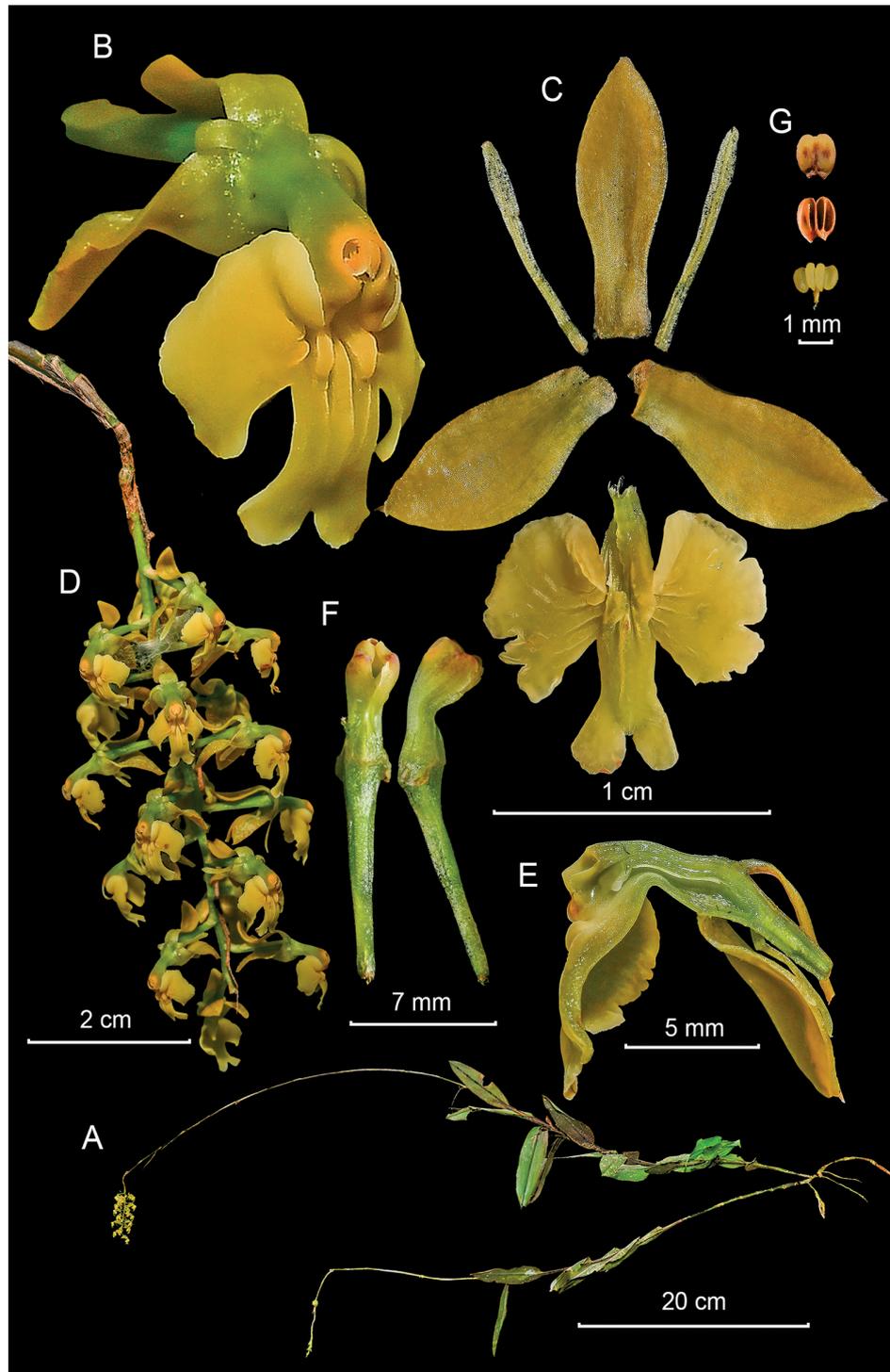
***Epidendrum forcipatum* C.Schweinf., Fieldiana (Bot.) 33: 36. 1970.**

Fig. 7

**Type material.** PERU. *Sine loc.*, pressed 24 Jul. 1959, F. Woytkowski s.n., cultivated at University of California Botanical Garden at Berkeley 52.1853-1 (holotype: AMES 69508 HUH00070356!; isotypes: AMES 90057 HUH00070357! MO 1785100!); "clonotypes": pressed 11 Jul. 1962, UC 229015! pressed 15 Mar. 1963, US 2949871 US00093812! Pressed 1 Jul. 1965, UC 1350745!). Pressed by Paul C. Hutchison, 11 Jan. 1961, at University of California Botanical Garden at Berkeley 52.1853, MO 1785407! Pressed 1 Oct. 1963, UC 1350837!

**Taxonomic synonym.** *Epidendrum pseudoanceps* D.E.Benn. & Christenson, Lindleyana 13(1): 46. (1998). Type: Peru. Huánuco: Leoncio Prado, below El Mirador, 1800 m, 10 Aug. 1966, D. E. Bennett Jr. 2333 (holotype: AMES!).

**Description.** Epiphytic, sympodial, caespitose, erect **herb** 47–100[215] cm tall. **Roots** basal, fleshy. **Stem** 25–45[65] × 0.47–0.57 cm, cane-like, ancipitose, erect. **Leaves** 6–8, distributed throughout apical half of stem, sub-erect; sheath 1.1–3.0 × 0.47–0.57 cm, tubular, ancipitose, smooth; blade 6–10 × 2.0–2.4[6.4] cm, oblong to elliptic, apex obtuse, coriaceous, dorsally carinate, erect, alternate, margin entire, spreading, somewhat undulate. **Inflorescence** 24–65[150] cm long, apical, racemose, flowering repeatedly over several years and producing new racemes from the apical internodes; peduncle 16[34.5] cm long, thin, elongate, ancipitose, totally covered by tubular, acute, bracts, 2–4 cm long; rachis 3.5–4.3[16] cm long, terete, smooth. **Floral bracts** 3–5 mm long, much shorter than the ovary, triangular, acuminate. **Flowers** 10–17[30] per raceme, simultaneous, resupinate, yellow-ochre, not fragrant. **Sepals** 10–12 × 3.3–4.2 mm, free, oblanceolate, slightly concave, subacute, somewhat papillose dorsally toward the apex, 5-veined, fleshy, the **dorsal** reflexed, the **laterals** spreading to reflexed, somewhat oblique. **Petals** [8]10–11 × 0.7–0.8 mm, hanging, free, reflexed, linear, rounded, 1-veined, margin entire, spreading. **Lip** [7.5]9.0–9.7 × 10.0–11.4 mm, united to column, 3-lobed, base cordate, mar-



**Figure 7.** *Epidendrum forcipatum* from Arista et al. 134 **A** habit **B** flower **C** dissected perianth **D** inflorescence **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (up) and below (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

gin entire, convex; bicallose, calli laminar, smooth, prolonged into rounded keels, with a central keel running down most of mid-lobe; lateral lobes 4.2–4.7 × 5.5–7.6 mm, dolabriform, with 3 short, thickened keels; mid-lobe 4.2–5.0 × 2.8–3.8 mm, sub-rectangular, emarginate. **Column** 6–8.6 mm long, short, thin, straight, dilated toward apex. **Clinandrium hood** reduced, entire. **Anther** ovoid,

with a rounded keel in front, 4-celled. **Pollinia** 4, obovoid, laterally flattened; inner pair somewhat smaller; caudicles granulose, longer than pollinia. **Rostellum** apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** less than  $\frac{1}{4}$  length of stigmatic cavity. **Cuniculus** short, slightly penetrating ovary, somewhat inflated behind stigmatic cavity. **Ovary** 9.5–10[14] mm long including pedicel, terete, thin, smooth. **Capsule** not seen.

**Additional specimens examined. ECUADOR. Zamora-Chinchipe:** Los Encuentros, Cordillera del “Cóndor”, Mirador, hort, Ecuagenera, 8 Mar. 2003, *H. Medina* sub *E. Hágsater* 13834 (AMO!). **Peru: Amazonas:** Prov. Bongará, Yambrasbamba, Perla de Imaza, Bosque de Piedras, 1682 m, 28 Aug. 2021, *Arista et al.* 134 (KUELAP!); **Huánuco:** Leoncio Prado, along road above Cueva de Pavas, 1400 m, 10 Nov. 1991, *Bennett* 5354 (MOL! USM, n.v.); **Junín:** Tarma, 6 III 1967, 1500 m, *Bennett* 2333 (SEL!) [this specimen has the same collecting number of the type, but a different locality and date; the non-flowering specimen conforms to the species; *E. Hágsater*, pers. obs.].

**Other records. PERU. Sine loc.**, received 01 May 2012, *Morón s.n.*, digital image (AMO!); **Junín:** Selva Central, received 03 June 2015, *Torres Paucar s.n.*, digital image (AMO!). **Pasco:** Oxapampa, Huancabamba, P.N. Yanachaga-Chemillén, sector Tunqui-Naciente de la quebrada Muchumayo, 2153 m, 14 Feb. 1009, *R. Vásquez et al.* “35300 (USM!)”. **San Martín:** Moyobamba: Quebrada Doncel, 3 Feb. 2021, *Bazan 01*, digital images (AMO!)

**Distribution.** Known only from the Amazon side of the Andes from southern Ecuador (Cordillera del Cóndor, Zamora-Chinchipe) and northern and central Peru, at 1500–1800 m.

**Habitat and ecology.** Epiphytic, growing on tree trunk in 20–30 m tall lower montane forest, primary sclerophyllous forest, and montane humid forest with *Cinchona* sp. and *Cedrela* sp.

**Phenology.** Flowering from March to November

**Taxonomic notes.** The square brackets in the description indicate the unusually large specimens prepared from cultivated material in the greenhouses of the University of California Botanical Garden at Berkeley, and not seen in wild-collected material. Therefore, they are indicated separately. The original description is based on these measurements.

*Epidendrum forcipatum* belongs to the Anceps Group and Polyanthum Subgroup, recognized by the caespitose habit, the simple stems, the pluriracemose inflorescence, flowering over several years, the elongate racemes and the fleshy flowers and linear petals. The species is recognized by the generally crisped-undulate leaves, about 10–17[30] flowers, green-ochre in color, and filiform petals. *Epidendrum forcipatoides* Hágsater from Bahia and Minas Gerais, Brazil attains a smaller size and bears leaves with non-undulate margins and smaller flowers, the obovate sepals being about 6.0–6.5 mm long.

***Epidendrum imazaense* Hágsater, E.Santiago, J.P.Arista & Edquén, sp. nov.**

urn:lsid:ipni.org:names:77320358-1

Fig. 8

**Type material. PERU. Amazonas:** Prov. Bongara, Distr. Yambrasbamba, camino a la Perla del Imaza, 1886 m, 17 Jul. 2022, *J. P. Arista, J. D. Edquén, E.*

Hágsater, E. Santiago, G. A. Salazar, E. Yrigoín, L. I. Cabrera & K. Edquen 272 (holotype: KUELAP!).

**Diagnosis.** Similar to *Epidendrum freireanum* Hágsater & E. Santiago, but the plants are smaller, 3.6–10 cm tall (vs. plants 10–40 cm tall), the leaves 1.1–3.6 cm long (vs. leaves 3.7–7.0 cm long), the ovary 10 mm long, sigmoid, with a prominent ventral vesicle, inflated in the middle (vs. ovary 6 mm, straight, not inflated), the sepals 5.5 mm long (vs. sepals 10 mm long), and the flowers pale green with a red-brown tinge on the tepals (vs. flowers purple brown with lip and apex of column ivory white).

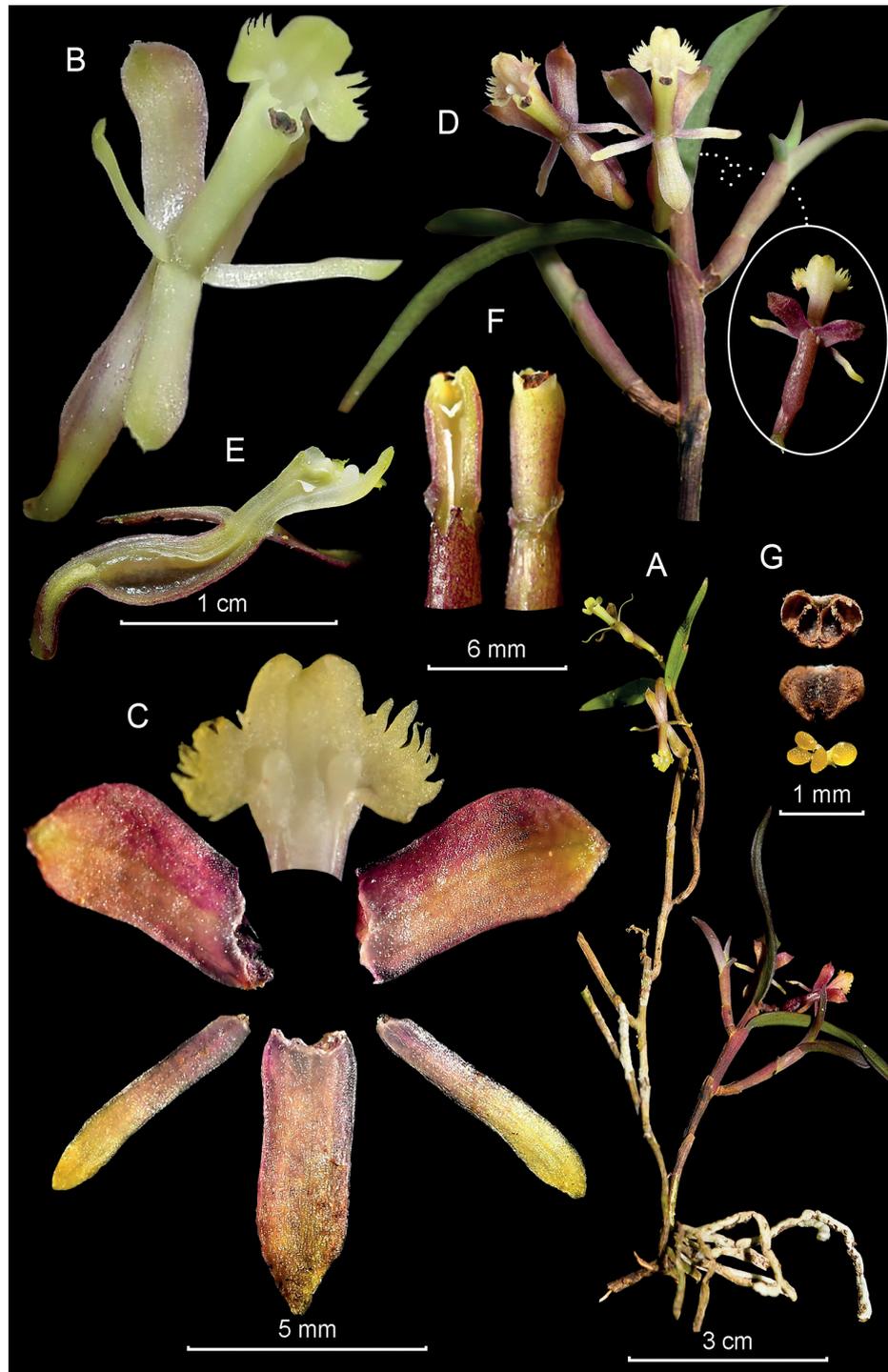
**Description.** Epiphytic, monopodial, branching, erect **herb**, ca. 10 cm tall, with new stems produced from upper internodes of previous stem. **Roots** ca. 2 mm in diameter, from base of primary stem only, fleshy, thick. **Stems** 2–4 × 0.1–0.25 cm, simple, cane-like, produced from sub-apical internodes of previous stem, sometimes two from same stem, thin, laterally compressed, erect, straight or slightly arched upward, base covered by sheaths 1–10 mm long, tubular, non-foliar. **Leaves** 2–3, aggregate toward apex of stem, alternate, articulate, coriaceous, slightly conduplicate; sheaths 7–8 × 1.2–2.5 mm, tubular, minutely striated, red; blade 1.1–3.6 × 0.25–0.5 cm, lanceolate, acute, minutely apiculate, margin entire, spreading. **Spathe** lacking. **Inflorescence** ca. 2 cm long, apical, racemose, few-flowered; peduncle 1 cm long, sub-terete, rachis 0.3 cm long. **Floral bracts** 1.5–2.8 mm long, much shorter than ovary, triangular, long acuminate, embracing. **Flowers** 3, simultaneous, non-resupinate, tepals pale green turning yellow tinged red brown ventrally, dorsally red brown, lip and column pale green to yellow, concolor; fragrance not registered. **Ovary** 10 mm long, sigmoid, with a prominent ventral vesicle inflated toward middle and involving 2/3 of ovary length, verrucose. **Sepals** free, 3-veined, dorsally verrucose, margins entire, spreading; dorsal sepal 5.5 × 2.0 mm, reflexed, oblong, obtuse; lateral sepals 5.5 × 2.5 mm, partly spreading, narrowly obovate, oblique, obtuse, minutely apiculate. **Petals** 5 × 1 mm free, spreading, oblong, obtuse, 1-veined, margins entire, spreading. **Lip** 3.0–3.3 × 5.5 mm, totally united to column, 3-lobed, cordate at base; bicallous, calli spherical, widely spaced, disc with a single mid-rib, thickened and reaching apical sinus; lateral lobes 1.3–1.7 × 2.2–2.4 mm, dolabriform with apical margin fimbriate; mid-lobe 1.5 × 2.3 mm, rectangular apex slightly emarginate. **Column** 4.5–5.0 mm long, thin, straight. **Clinandrium hood** short, margin entire. **Cuniculus** penetrating 2/3 of ovary, inflated in middle of ovary, forming an elongate prominent vesicle, unornamented. **Anther** reniform, 4-celled. **Pollinia** 4, obovoid, laterally compressed. **Rostellum** apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** prominent, half as long as stigmatic cavity. **Ovary** 10 mm long including pedicel, sigmoid, with a prominent ventral vesicle inflated toward middle and involving 2/3 of ovary length, verrucose, furrowed. **Capsule** not seen.

**Distribution.** Presently known only from the type from northern Peru, department of Amazonas, eastern range of the Andes around the ACPBB, at 1886 m.

**Habitat and ecology.** Epiphytic in relict wet montane forest.

**Phenology.** Flowering in July.

**Taxonomic notes.** *Epidendrum imazaense* belongs to the Fruticetorum Group, which is characterized by the monopodial, branching habit, the few-leaved stems, flattened above, the erect to arching racemose to pluri-racemose inflorescence producing new racemes from the same peduncle in successive



**Figure 8.** *Epidendrum imazaense* from Arista et al. 272 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary apex from below (left) and above (right) **G** anther from below (up) and above (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by X. Alcántara).

years, the flowers generally non-resupinate, and the 3-lobed lip with the distal margins of the lateral lobes dentate to shortly fimbriate. The new species is recognized by the short inflorescences, nearly sessile, with 3 non-resupinate flowers, yellow tepals, ventrally tinged red-brown, dorsally red-brown; lip and column pale green, concolor, the sepals 5.5 mm long, dorsally verrucose and the ovary sigmoid with a prominent, elongate vesicle in the middle of the ovary.

*Epidendrum freireanum* has purple leaves and stems, smaller flowers, the sepals being 10 mm long, the sepals, petals and basal half of column vinaceous to purple-brown, apical half of column and the lip ivory white, immaculate, and the lip with a single wide mid-rib. *Epidendrum fruticetorum* Schltr. (see Cisneros and Hágsater in Hágsater and Santiago 2019: t. 1721) is similar but larger in habit and flowers, the sepals are 14 mm long, the flowers are green, the lip with 3 narrow parallel ribs is pale green and the column green. Bennett and Christenson (1995a: t. 247) misidentified their plate of *Epidendrum fruticetorum* as *E. odontospathum* Schltr.

**Etymology.** In reference to the Imaza river, whose basin includes the Pampa del Burro. This river is a tributary of the Chiriaco river, an affluent of the Marañón river.

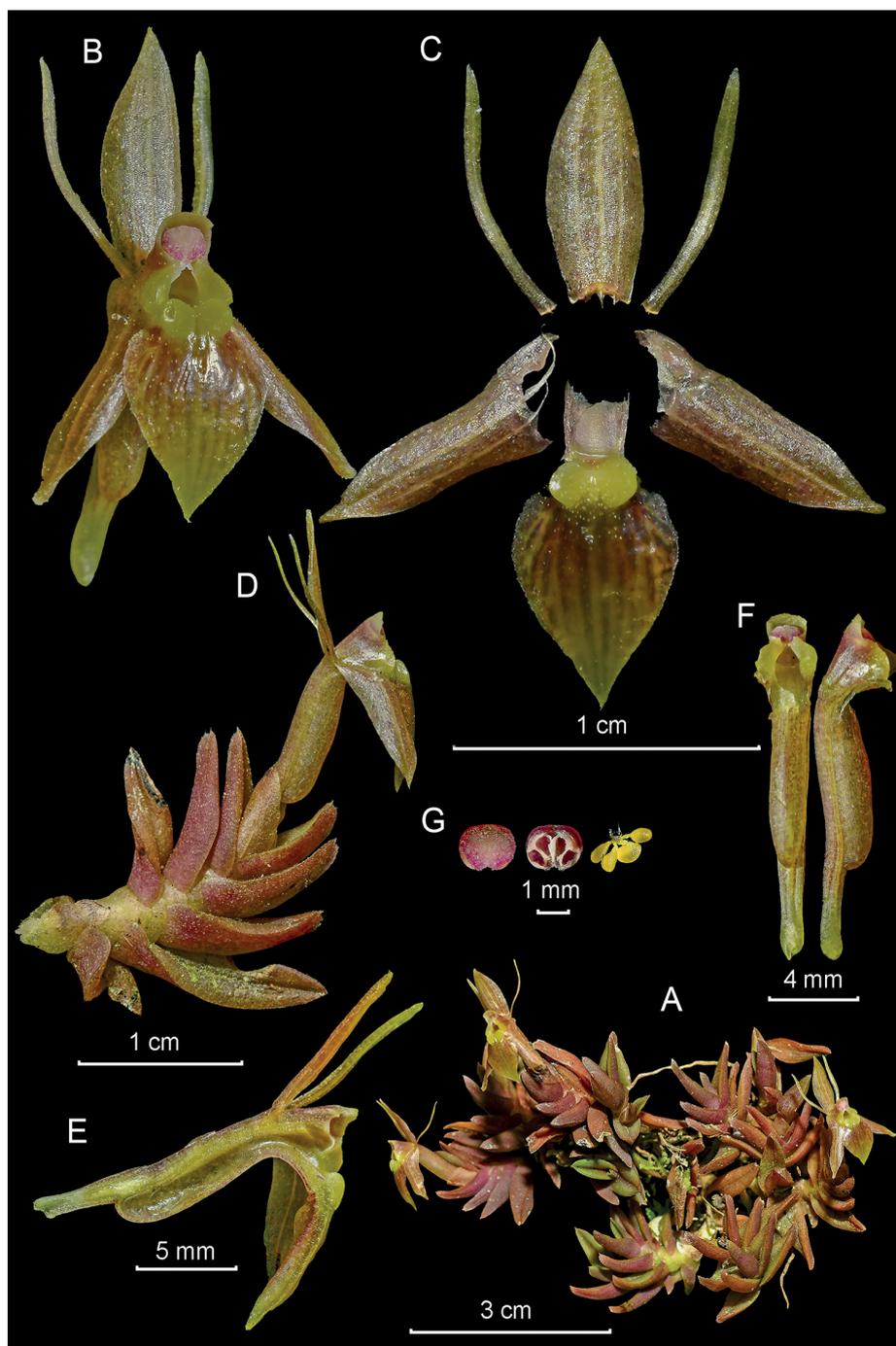
***Epidendrum mavrodactylon* Hágsater, Edquén & E.Santiago, Icon. Orchid. 16(2): t. 1682. 2018.**

Fig. 9

**Type material. PERU. San Martín:** Prov. Rioja, correspondiente al área natural protegida Bosque de Protección Alto Mayo-BPAM, Sector Venceremos, Zona 18, 1807 m, 30 Jan. 2018, *J. D. Edquén 401* (holotype: HURP!).

**Description.** Epiphytic, caespitose, sympodial, compact, small, reclining **herb**, 3 cm tall. **Roots** 1 mm in diameter, basal along rhizome, thin, white. **Stems** 1.3–2 × 0.3–0.4 cm, cane-like, simple, laterally compressed, somewhat reclining. **Leaves** 4–7, fleshy, distichous, erect, semi-terete, concave, arching and partially imbricated, somewhat conduplicate, dark green, concolor; sheath 1–3 mm long, tubular, narrow at base gradually widened toward apex; blade 0.5–1.4 × 0.2–0.4 cm, narrowly lanceolate obtuse to sub-acute, minutely apiculate, margin entire, dentate at apex. **Spathe** 1, 5–9 × 5–7 mm when spread, elliptic, obtuse, minutely apiculate, conduplicate. **Inflorescence** apical, sessile, single-flowered. **Floral bract** not seen (hidden within spathe). **Flower** 1, resupinate yellowish green, sepals and petals with a bronze tinge; fragrance not registered. **Sepals** 8–10 × 3.0–4.0 mm, apex acuminate, minutely apiculate, 3-veined; dorsal sepal free, partly spreading, nearly parallel to column, narrowly lanceolate, margin minutely papillose toward apex, spreading; lateral sepals obliquely untied to base of column, spreading, narrowly ovate-triangular, oblique, margin entire, revolute. **Petals** 8–8.5 × 0.5 mm, free, partly spreading, parallel to dorsal sepal, linear, falcate, acute, 1-veined, margin entire, spreading. **Lip** 7.0–7.2 × 4–5 mm, united to column, entire, elliptic, base cuneate, apex acute, minutely apiculate, margin slightly erose; bicallose, calli globose, prominent; disc with a very low midrib. **Column** 4 mm long, thin at base, gradually wider toward apex, triangular in lateral view. **Rostellum** apical, slit; viscarium semi-liquid, white. **Clinandrium hood** prominent, slightly longer than body of column, totally covering anther, margin erose. **Anther** reniform, 4-celled. **Pollinia** 4, obovate, complanate, convex-flat, caudicles as long as pollinia. **Lateral lobes of stigma** not seen. **Cuniculus** inflated ventrally along apical half of ovary. **Ovary** 11–15 mm long, ventrally inflated, forming a prominent, elongate vesicle along apical, ventral half of ovary. **Capsule** not seen.

**Additional specimens examined. PERU. Amazonas:** Prov. Bongará, Distr. Yambrasbamba, Perla del Imaza, 1763 m, 28 Aug. 2021, *Arista & Edquén 156* (KUELAP!).



**Figure 9.** *Epidendrum mavrodactylon* from Arista et al. 156 **A** habit **B** flower **C** dissected perianth **D** flower at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (left) and below (right), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

**Other records. PERU.** Cultivated in Moyobamba in the private collection of José Altamirano, 16 May 2009, digital images, *Jenny s.n.* (AMO!).

**Distribution.** Known presently only from northern Peru, from the limits between the departments of San Martín and Amazonas. On both sides of the ridge that forms the border of the two departments. In montane wet forest at 1763–1800 m elevation.

**Habitat and ecology.** Epiphytic on *Erythrina* L. Ground with abundant moss, and accumulation of organic matter.

**Phenology.** Flowering in January to August.

**Taxonomic notes.** *Epidendrum mavrodactylon* represents an addition to the orchids of the department of Amazonas. It belongs to the Porpax Group, which is characterized by the sympodial, somewhat repent habit, usually forming large mats; the short, cane-like stems with very fleshy, succulent, articulate, distichous leaves, the apical margin minutely ciliate; the single-flowered inflorescence with sessile flowers; and the lip generally reddish purple. *Epidendrum mavrodactylon* is recognized by the very small plants, up to 3 cm tall, with leaves 0.5–1.4 cm long, semi-terete, concave and arching, flowers yellowish green, sepals and petals tinged bronze; dorsal sepal and petals nearly parallel to the column, lip 7.0–7.2 × 4–5 mm, elliptic, acute, and the ovary with a prominent ventral, elongate vesicle, half as long as the ovary. *Epidendrum althianorum* Hágsater & Collantes from Cusco has larger plants, 4.5–10 cm tall, leaves 1.3–5 cm long, straight, flowers lime-yellow, lip orbicular, rounded with a heart-shaped red blotch in the middle, and the ovary not inflated, not forming a vesicle. *Epidendrum neolehmannia* Schltr. of the same group has an equally inflated vesicle ventrally along the ovary caused by the inflated cuniculus, but the flowers have a cordiform lip 12–15 × 12–17 mm, with two parallel calli at the base, no obvious mid-rib, and the leaves are semi-terete, 1.0–2.5 × 0.4–0.7 cm.

***Epidendrum ochrostachyum* Hágsater, E.Santiago, J.P.Arista & Edquén, sp. nov.**

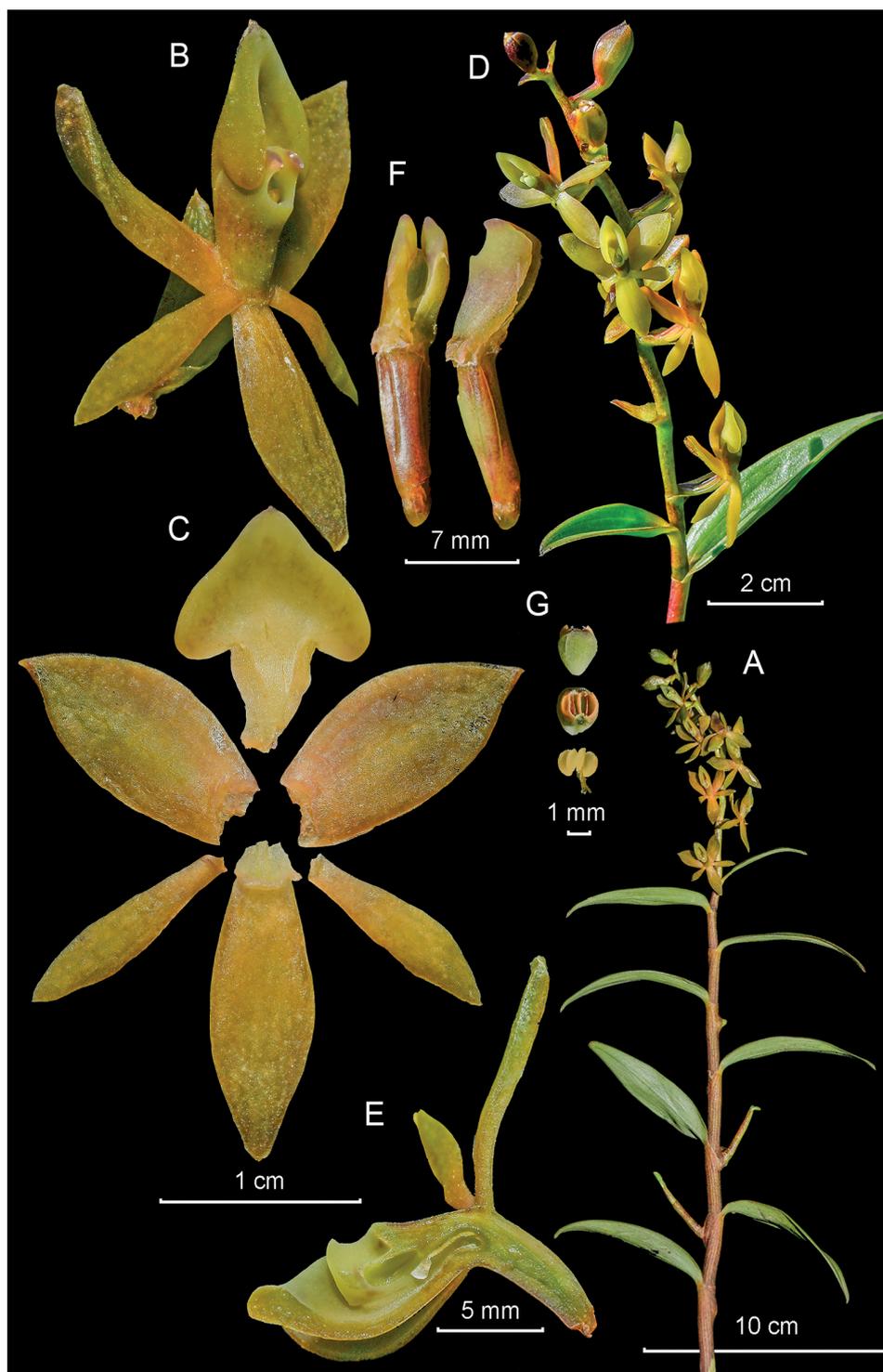
urn:lsid:ipni.org:names:77320359-1

Fig. 10

**Type material. PERU. Amazonas:** Prov. Bongará, Distr. Yambrasbamba, Perla del Imaza, Río Rojo, Pampa del Burro, 1839 m, 25 Aug. 2021, *J. P. Arista, J. D. Edquén, E. Yrigoín & L. Iliquin* 79 (holotype: KUELAP!).

**Diagnosis.** Similar to *Epidendrum bangii* Rolfe but differs by the shorter lateral sepals, 13 mm long, spreading, ovate-elliptic, the apex obtuse (vs. lateral sepals 16–18 mm long, slightly reflexed, obliquely ovate, with the apex acuminate), the shorter petals, 10 mm long, oblanceolate, apex obtuse (vs. petals 13–15 mm long, linear, apex acuminate), the floral bracts 8–13 mm long, nearly as long as the ovary (vs. floral bracts 11–22 mm long, longer than the ovary), and the column with a pair of truncate wings (vs. column with a pair of rounded wings).

**Description.** Terrestrial, monopodial, branching, erect **herb**, ca. 66 cm tall including inflorescence. **Roots** 1.0–2.5 mm in diameter, basal, scarce, fleshy. **Stems** cane-like, erect, straight, scarcely branching sub-apically, primary stem 54 × 0.6 cm, branches 7 × 0.3 cm; base covered by sheaths 6–30 mm long, tubular, non-foliar, scarious. **Leaves** 9 on primary stem, 3–5 on branches, distributed throughout the stems, articulate, slightly conduplicate, spreading, coriaceous, rigid, medium green on both sides, margins red-brown; sheaths 0.5–5.0 × 0.3–0.6 cm, tubular, minutely striated, rugose, red; blade 2.5–12 × 0.6–2 cm, lanceolate, acute, margin entire, spreading. **Spathe** lacking. **Inflorescence** 12 cm long on primary stem, ca. 6 cm long from branches, apical, racemose, erect, laxly few-flowered; peduncle 1.2 cm long, terete, without bracts, red-



**Figure 10.** *Epidendrum ochrostachyum* from Arista et al. 79 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (up) and below (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

brown; rachis 5–11 cm long. **Floral bracts** 8–13 × 5–7 mm, nearly as long as ovary, widely ovate, sub-acuminate, oblique, embracing. **Flowers** up to 15, successive, non-resupinate, fleshy, ochre-yellow to olive green, sometimes tinged orange, dorsal surface of sepals red-brown to wine-brown, lip yellow; fragrance not registered. **Sepals** free, spreading, ovate to ovate-elliptic, obtuse, minutely

apiculate, 3-veined, margins entire, spreading; dorsal sepals 12 × 5 mm, lateral sepals 13 × 7 mm. **Petals** 10 × 3 mm, free, spreading, oblanceolate, obtuse, 1-veined, margin entire, spreading. **Lip** 8 × 10 mm, united to column, entire, widely cordiform, base deeply cordate, apex acute, embracing apex of column in natural position; ecallose, strongly pubescent in front of stigmatic cavity. **Column** 8 mm long, thick, apex bidentate, with a pair of truncate wings. **Clinandrium hood** reduced, margin entire. **Anther** ovoid, apex acute, 4-celled. **Pollinia** 4, obovoid, laterally compressed; caudicles soft and granulose. **Rostellum** apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** small, ¼ length of stigmatic cavity. **Cuniculus** shallow, without penetrating pedicellate ovary, strongly pubescent in front of stigmatic cavity. **Ovary** 8–9 mm long, terete, thick, furrowed. **Capsule** not seen.

**Additional specimens examined. PERU. Amazonas:** Prov. Bongará, Distr. Yambasbamba, La Perla Vieja, Pampa del Burro, 1880 m, 22 Aug. 2021, *Arista et al.* 12 (KUELAP!); *ibid. loc.*, 1850 m, 22 Aug. 2021, *Arista et al.* 61 (KUELAP!); Jumbilla–Molinopampa, 2500–2900 m, 6 Nov. 2012, *van der Werff 25206* (HOXA! USM!).

**Other records. PERU. Amazonas:** Prov. Bongará, Distr. Florida, Pomachapanda, 2300–2500 m, 8 Nov. 2010, *Dalström 3178*, digital image (AMO!); Bosque Protector Alto Nieva, 2184 m, 17 Mar. 2019, *Hágsater 16077*, digital image (AMO!); **San Martín:** Prov. Rioja, Distr. Pardo Miguel Naranjos, Sector Venceremos, 1959 m, 23 Feb. 2017, *Edquén 2019*, digital images (AMO!); *ibid. loc.*, 1715 m, 21 Feb. 2017, *Edquén 2020*, digital images (AMO!); *ibid. loc.*, 1730 m, 22 Feb. 2017, *Edquén 2021*, digital images (AMO!); *ibid. loc.*, 1975 m, 20 Feb. 2017, *Edquén 2022*, digital images (AMO!); *ibid. loc.*, 1918 m, 6 Nov. 2015, *Edquén 2023*, digital images (AMO!).

**Distribution.** Known only from northern Peru, on the border between the departments of Amazonas and San Martín, growing at 1715–2500 m.

**Habitat and ecology.** Terrestrial, on road bank, in white sand with abundant organic matter 10 cm deep, in low forest.

**Phenology.** Flowering in August to March.

**Taxonomic notes.** *Epidendrum ochrostachyum* belongs to the Macro-stachyum Group, which is characterized by the monopodial plants with sub-apical branching, the rugose leaf sheaths, the large leaves, generally spreading, the erect racemose inflorescence, the fleshy flowers generally green to black (ripe olive colored), as well as yellow to pink to purple, with an entire, conduplicate, generally ecallose lip embracing the column, and the cuniculus pubescent to papillose in front of the stigmatic cavity and at least at the base of the lip. The species is recognized by the small plant (up to 66 cm tall), leaves 2.5–12 × 0.6–2 cm, lanceolate, acute, the inflorescence of primary stem with up to 15 flowers, the floral bracts nearly as long as the ovary, the flowers ochre-yellow to olive green, sometimes tinged orange, dorsal surface of sepals red-brown to wine-brown, lip yellow, the lateral sepals 13 mm long, spreading, petals oblanceolate, obtuse, the lip deeply cordiform, acute, and the column with a pair of truncate wings. *Epidendrum bangii* is vegetatively similar, but the floral bracts are longer than the ovary, the flowers are purple, the lateral sepals 16–18 mm long, the petals are linear, acuminate, the lip is cordiform, and the column has a pair of rounded apical wings. *Epidendrum odontostachyum* Hágsater & E.Santiago has larger plants, ca 1 m tall, leaves 6–8 × 0.6–1.6 cm, linear-lanceolate, the inflorescence up to 20 cm long, the flowers dark green with the lip pur-

ple-green, the petals  $12 \times 1.5$  mm, slightly reflexed, and the floral bracts triangular and acuminate.

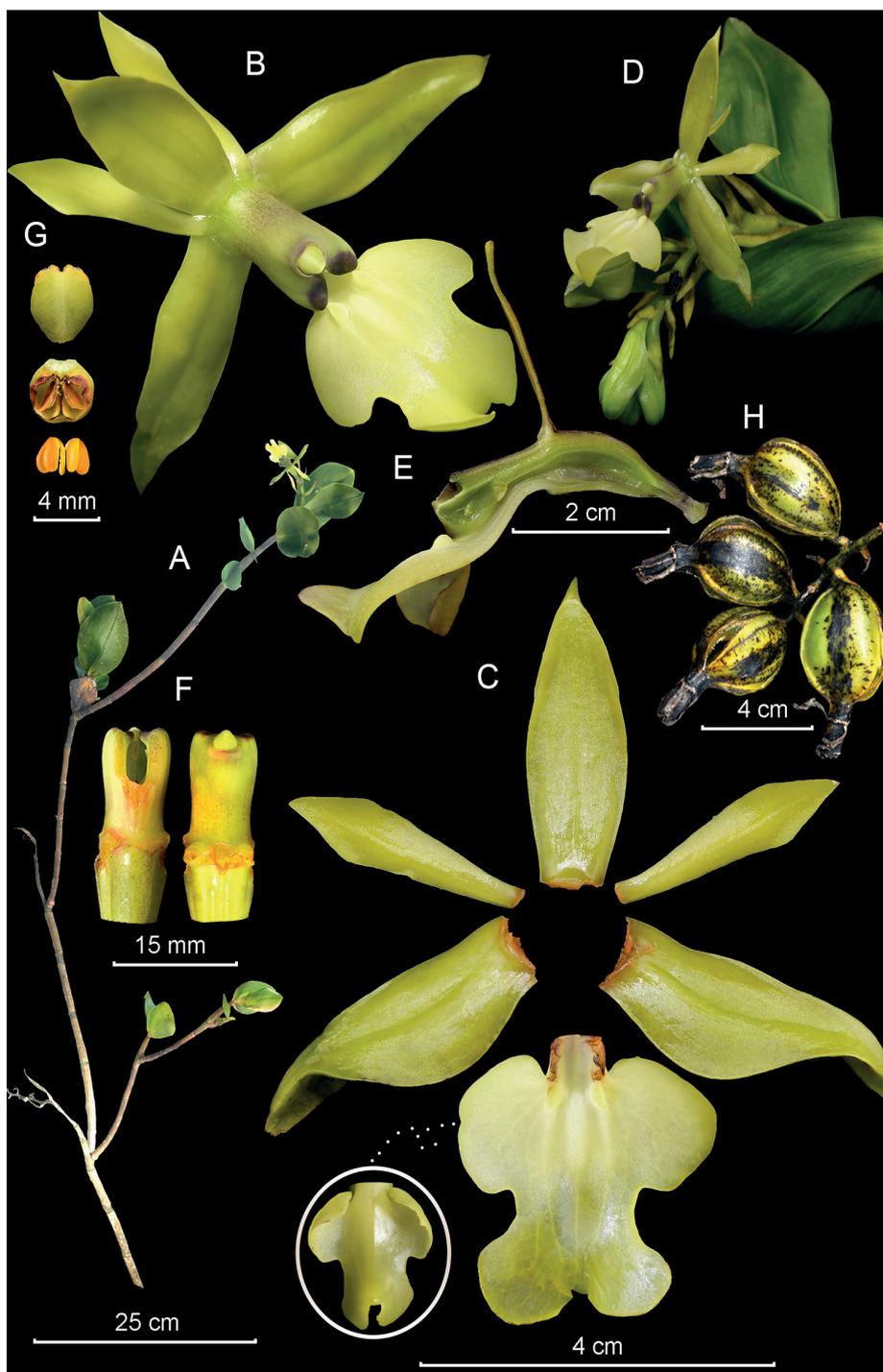
**Etymology.** From the ochre color of the flowers, from the Greek ὄχρος, and σταχυς, from the Greek spike, in reference to the *Macrostachyum* Group to which the species belongs.

***Epidendrum olortegui* Damián, Hágsater & Mitidieri, Phytotaxa 552(1): 100. 2022.**

Fig. 11

**Type material. PERU. Amazonas:** Prov. Bongará: Distr. Yambrasbamba: Centro Poblado El Progreso, 2200–2300 m, Nov. 2020, S. *Olortegui* & A. *Damián* 5050 (holotype: USM!; isotype: UFV!).

**Description.** Epiphytic, sympodial, scandent, erect **herb**, up to 120–140 cm tall, new stems produced from middle of previous stem. **Roots** 5–6 mm in diameter, thick, scarce, from base of primary stems. **Stems** 14–45  $\times$  0.9–1.3 cm, simple, cane-like, terete, new stem produced from sub-apical internode of previous stem, lower part covered by 3–5 tubular, imbricate, chartaceous, gray non-foliar sheaths. **Leaves** 2–5 aggregate toward apex apical half of stem, distichous, articulate, spreading, base embracing; sheaths 1.4–3.5  $\times$  0.9–1.3 cm, tubular, infundibuliform in dry specimens; blade 6.0–14.5  $\times$  2.2–6.0 cm, elliptic to elliptic-lanceolate in mature specimens, acute, thin, margin entire. **Spathe** lacking. **Inflorescence** 16–20 cm long, apical, racemose, arching nutant, few-flowered; peduncle 3–5 cm long, laterally compressed, slightly ancipitose, rachis 12–15 cm long, sub-terete. **Floral bracts** 1.0–2.3  $\times$  0.6–0.8 cm, slightly shorter than ovary, progressively shorter toward apex of rachis, triangular, acuminate, margins microscopically denticulate. **Flowers** 4–13, flowers successive, 2–5 open at a time, resupinate, green to yellow or rarely ivory white (*Léon Martínez s.n.*), column darker green or dirty white, tinged purple toward apex, lip when green pale toward disc and calli; fragrance not detected. **Sepals** spreading, fleshy, slightly convex, free, 5-veined, margins entire, spreading; dorsal sepal 30–38  $\times$  9–12 mm, lanceolate to oblong-lanceolate, acute, basal margins revolute, slightly carinate dorsally; lateral sepals 32–40  $\times$  8–13 mm, lanceolate to oblong-lanceolate, oblique, acuminate, with a prominent dorsal keel. **Petals** 27–35  $\times$  5–7 mm, strongly reflexed, parallel to ovary, fleshy, narrowly oblanceolate, acuminate, 3-veined, margins entire, spreading. **Lip** 22–32  $\times$  28–30 mm, fleshy, trilobed, fused to column, base obliquely cordate; bicallose, calli divergent, elongate, rounded, disc 3-ribbed, lateral ribs in front of calli inconspicuous, low, parallel, with a low, wide mid-rib reaching apex of labellum; lateral lobes 10–15  $\times$  10–14 mm, prominent, convex, transversely sub-rectangular, basal corners narrowly rounded to obtuse, distal corner widely rounded, multi-veined, margins entire, slightly revolute; mid-lobe 8–13  $\times$  20–22 mm, curved in natural position, flabellate with two obliquely triangular lobes and a narrow, cuneate isthmus in basal half, apical half truncate, with a short, thickened, narrowly triangular, reflexed, apiculus at apex, lobes divergent, obliquely triangular, obtuse, slightly revolute at apex, margins entire. **Column** 14–16 mm long, short, thick, straight, slightly widening apically, constricted near base. **Clinandrium hood** very short, margin entire. **Anther** ovoid, glandular-papillose, 4-celled. **Pollinia** 4, dark yellow,



**Figure 11.** *Epidendrum olorteguii* from Arista et al. 271 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary apex from below (left) and above (right) **G** anther from above (up) and below (down), and pollinarium **H** capsules (Photographs by J. D. Edquén; plate prepared by X. Alcántara).

obovate, laterally compressed, subequal, caudicles granulose, as long as pollinia. **Rostellum** apical, slit; viscarium semi-liquid, translucent. **Lateral lobes of stigma** small, 1/5 length of stigmatic cavity. **Cuniculus** deep, penetrating two thirds of ovary, widened behind perianth, unornamented. **Ovary** 16–28 mm long, slightly arching, terete, furrowed, ventrally thickened apical third. **Capsule** ellipsoid, 6.3 cm long, pedicel 3 mm long, body 4 × 3 cm, apical neck 2 cm long.

**Additional specimens examined. PERU. Amazonas;** Prov. Bongará, Distr. Yambrasbamba, centro poblado El Progreso, 2300 m, Nov. 2017, *Olórtegui s.n.* (USM!); Distr. Buenos Aires, centro poblado Santa Rosa, 2079 m, 15 Jul. 2022, *Arista et al. 271* (KUELAP!).

**Other records. PERU. Amazonas:** Prov. Bongará: Distr. Yambrasbamba: El Progreso, Vivero “Mi Angelito,” colectada en el área de Nicolasa Velásquez, white form, *Martínez s.n.*, digital image (AMO!); km 5.5, camino a la Perla del Imaza, 2083 m, 15 Jul. 2022, *Hágsater 16418*, digital images (AMO!); La Esperanza, hort. vivero alto, Orquídeas Amazónicas, 16 Jul. 2022, *Hágsater 16490*, digital images (AMO!); **San Martín:** Prov. Rioja, Distr. Pardo Miguel Naranjos, Chisquilla, 2100 m, 22 June 2019, *Edquén 2092*, digital images (AMO!).

**Distribution.** *Epidendrum olorteguii* is presently known from two localities 50 km distant from each other, on the eastern slopes of the Andes in northern Peru, at 2100–2300 m.

**Habitat and ecology.** Epiphytic in humid montane forests.

**Phenology.** Flowering from July through November.

**Taxonomic notes.** *Epidendrum olorteguii* belongs to the Incomptum Group which is characterized by having erect successive lateral growths produced from the middle of the previous growth, few leaves aggregated toward the apex of the stems, the short apical inflorescence with fleshy green to violet-green flowers with short ovaries, and the lip entire to 3-lobed. *Epidendrum olorteguii* is recognized by its large habit, the large leaves, 6.0–14.5 × 2.2–6.0 cm, the large green flowers to yellow or rarely ivory white, column darker green or dirty white, tinged purple toward apex, the lip cream suffused with light green at the mid-lobe, the lanceolate to oblong-lanceolate sepals 30–40 mm long, the petals narrowly elliptic, and the lip 22–32 × 28–30 mm, 3-lobed, the lateral lobes 10–15 × 10–14 mm, prominent, transversely sub-rectangular, basal corners narrowly rounded, distal corner widely rounded and the mid-lobe 8–13 × 20–22 mm, constricted at base, then transversely elliptic, sides involute; apex with a short, thickened, narrowly triangular, reflexed apiculus. It is somewhat similar to *Epidendrum tamaense* Foldvats found from Ecuador to Venezuela, which has smaller plants, leaves 3–14 × 2.0–4.3 cm, green to olive-green flowers, lip marked with purple veins; sepals 15–21 mm long; petals narrowly obtrullate, obtuse to acute, and the 3-lobed lip has lateral lobes sub-orbicular, mid-lobe obcuneate, deeply emarginate, with two sub-orbicular lobes.

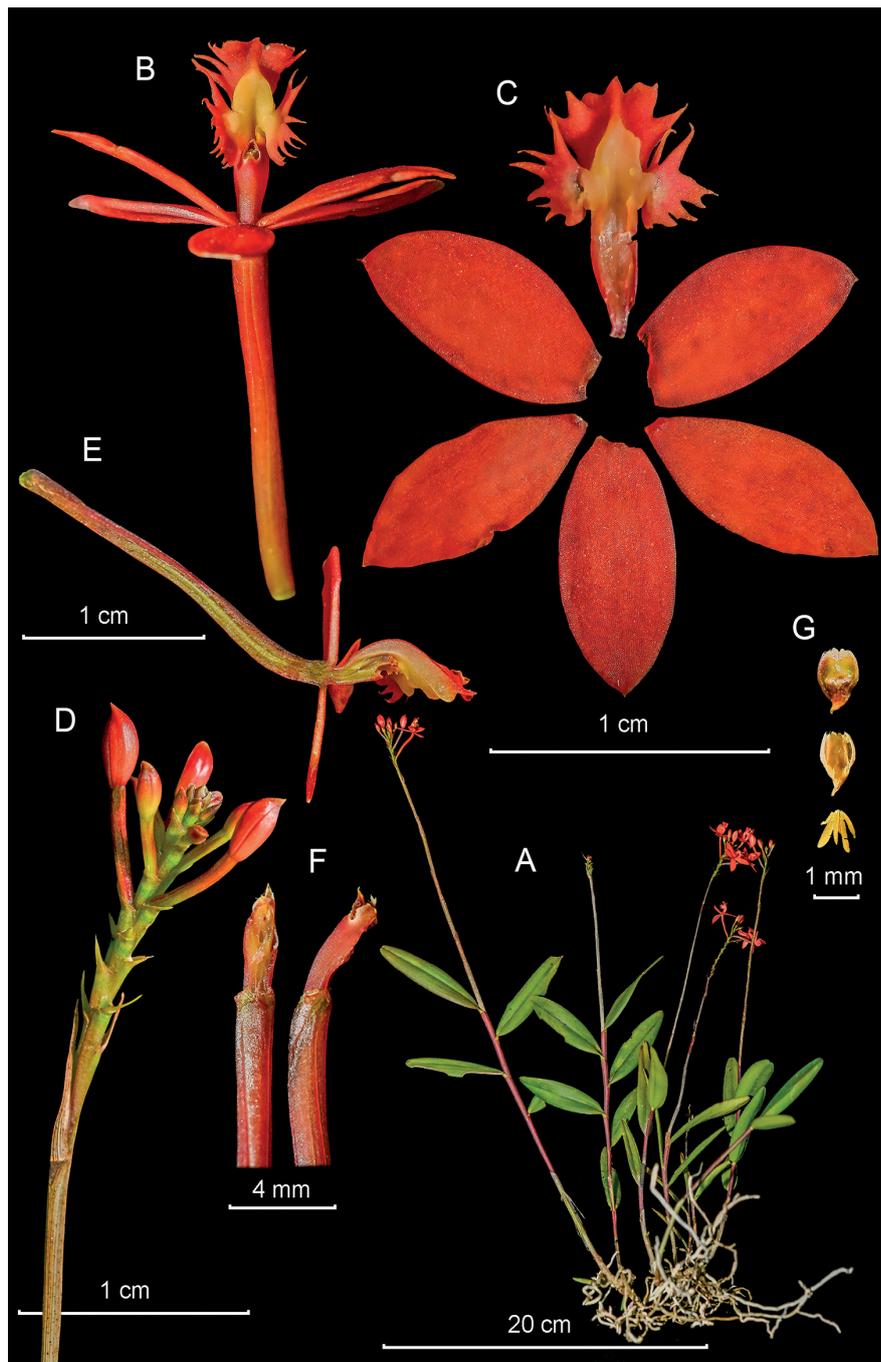
***Epidendrum parvireflexilobum* Hágsater, J.P.Arista & Edquén, sp. nov.**

urn:lsid:ipni.org:names:77320360-1

Fig. 12

**Type material. PERU. Amazonas:** Prov. Bongará: Yambrasbamba: Perla del Imaza, La Perla Vieja, Pampa del Burro, 1871 m, 22 Aug. 2021, *J. P. Arista, J. D. Edquén, E. Yrigoín, L. Iliquin 49* (holotype: KUELAP! [LCDP voucher]).

**Diagnosis.** Similar to *Epidendrum reflexilobum* C.Schweinf., but overall smaller, with plants 22–46 cm tall including the inflorescence (vs. 40–120 cm tall), sepals 9.5–10.8 mm long, elliptic (vs. sepals 12.5–13.5 mm long, obovate-elliptic), the lateral lobes of the lip semi-ovate, erect (vs. lateral lobes spreading, twisted 90° in natural position, narrowly obovate), the callus 3-ribbed, forming a



**Figure 12.** *Epidendrum parvireflexilobum* from Arista et al. 49 **A** habit **B** flower **C** dissected perianth **D** inflorescence **E** longitudinal section of flower **F** column and ovary apex from below (left) and side (right) **G** anther from above (up) and below (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

cuneate platform only reaching middle of mid-lobe (vs. callus 3-ribbed, ribs not forming a platform, with the mid-rib longer and reaching apical sinus).

**Description.** Epiphytic, sympodial, caespitose, erect **herb**, 22–46 cm tall including inflorescence. **Roots** 2 mm in diameter, basal, terete, fleshy, white. **Stems** 8–22 × 0.3 cm, simple, cane-like, terete to slightly compressed toward apex, thin, basal half covered by non-foliar sheaths. **Leaves** 7–12, distichous, distributed along upper 1/4 of stem; sheaths 4.4–6.0 × 0.4 cm, tubular, smooth, vinaceous, papyraceous when dry; blade 4.0–7.8 × 0.8–2.8 cm, oblong, apex

unequally bilobed, articulate, coriaceous, smooth, medium green on both sides, margins entire. **Spathes** lacking. **Inflorescence** 12–33 cm long, racemose to pluri-racemose, laxly flowered, cylindrical; peduncle 10–28 cm long, elongate, covered by numerous tubular, imbricate bracts 4.5 × 0.4 cm, acute, scarious when dry, striated, papyraceous; rachis ca. 4.8 cm long. **Floral bracts** 1–3 × 0.7–3.0 mm, much shorter than ovary, decreasing in size toward apex, triangular, acuminate to acute, embracing. **Flowers** ca. 6–12, per raceme, successive, 3–6 open at a time, non-resupinate, pale to bright red, callus yellow; fragrance none. **Sepals** spreading, apex obliquely rounded, short apiculate, 7-veined, margin entire, spreading; dorsal sepal 9.5–10.2 × 4.5–4.9 mm, elliptic; lateral sepals 9.9–10.8 × 5.0–5.5 mm, elliptic, oblique, sub-obtuse. **Petals** 10.6–13.5 × 4.0–5.0 mm, extended, oblanceolate or cuneate-spathulate, apex acute, 3–5-veined, margin entire, spreading. **Lip** 5.7–7.8 × 8.2–9.0 mm, united to column, deeply 3-lobed, in natural position mid-lobe flat, extended, lateral lobes sub-erect, base cordate, distal margins irregularly lacinate; callus low, rectangular, truncate to rounded, with mid-rib formed by 3 straight, parallel ribs on mid-lobe, mid-rib longer, with two divergent bifid calli at base of lateral lobes; lateral lobes 3.0–3.5 × 4.2–5.9 mm, semi-obovate, erect in natural position; mid-lobe 4.6 × 8.2 mm, obtuse, bifid, slightly divergent, deeply and narrowly emarginate. **Column** 4.0 mm long, straight, wider at apex, with a pair of long, apical recurved fleshy wings with distal margin erose. **Clinandrium hood** very short, margin entire, leaving anther totally exposed. **Anther** ovoid, apiculate, surface rugose, 4-celled. **Pollinia** 4, narrowly obovoid, laterally compressed, caudicles formed by a pile of elongate pollen tetrads like a pile of tiles. **Rostellum** apical, split; viscarium semi-liquid. **Lateral lobes of stigma** short, occupying  $\frac{1}{4}$  length of stigmatic cavity. **Cuniculus** penetrating half pedicellate ovary, minutely papillose. **Ovary** 20 mm long, terete, thin, not inflated, green to red, furrowed. **Capsule** not seen.

**Additional specimens examined.** **PERU. Amazonas:** Prov. Bongará: Yambrasbamba: Perla del Imaza, La Perla Vieja, Pampa del Burro, 1871 m, 22 Aug. 2021, *Arista et al.* 25 (KUELAP!); **Piura:** Huancabamba, 1 Oct. 1990, *Castillo* 5 (AMO!); **San Martín:** Rioja: Pardo Miguel Naranjos, Mirador Venceremos, 1867 m, 6 Dec. 2015, *Edquén* 1979 (HURP!; color plate published in Hágater and Santiago 2020b: t. 1835, as *E. reflexilobum*).

**Other records.** **PERU. Amazonas:** Chachapoyas: Balsas–Leimebamba, Cordillera Calla Calla, ca. 2400 m, 4 Feb. 2022, *Deza s.n.*, digital images (AMO!); *ibid. loc.* 2363 m, *Harding s.n.*, digital images (AMO!); **San Martín:** Rioja: Nuevo Cajamarca, Sector Yuracyacu, Río Yuracyacu, 1905 m, 15 Jul. 2018, *Edquén* 1815, digital images (AMO!).

**Distribution.** Known presently from northern Peru in the Regions of Amazonas and San Martín. Growing at 1850–1905 m elevation.

**Habitat and ecology.** Epiphytic and terrestrial in humid montane forest, secondary forest and abandoned coffee plantations, on *Coffea arabica* L. and *Citrus × aurantium* L.

**Phenology.** Flowering from July to December.

**Taxonomic notes.** *Epidendrum parvireflexilobum* belongs to the Schistochilum Group, Secundum Subgroup, which is characterized by the caespitose habit, the erect, simple, cane-like stems, the normally elongate peduncle of the inflorescence, the erect raceme of generally non-resupinate, yellow, orange, red or purple flowers, and the lip adorned by a complex callus. The novelty is rec-

ognized by the shorter plants, up to 22–46 cm including the inflorescence, thus being one of the “dwarf species” in the *Secundum* Subgroup, as most species can be over 150 cm tall; the floral segments are short and proportionately wide, the lateral lobes of the lip are flat and not twisted and the callus is formed by a single platform with 3 short ribs, that only reaches the middle of the mid-lobe. *Epidendrum reflexilobum* occurs in the regions of Huánuco and Junín, and is overall larger, has the same red flowers with a yellow callus, and the lateral lobes of the lip spreading, twisted 90° in natural position, narrowly obovate. The novelty is also similar to *Epidendrum macrocyphum* Kraenzl. which has pink-purple flowers with a white callus formed by 3–5 straight parallel ribs on the mid-lobe, has the mid-rib longer nearly reaching the apical sinus, with two divergent bifid calli at the base of the lateral lobes, the longer segment projecting on the junction of the mid-lobe with the lateral lobes, and the lip in natural position has the mid-lobe flat, extended, the lateral lobes erect, embracing the entire column with outer margin strongly revolute. In a previous publication of *Epidendrum reflexilobum* (Hágsater and Santiago 2020a: t. 1835), the description is a mixture of the new species and *Epidendrum reflexilobum*; the latter species corresponds to the photograph on the text page, but the color plate corresponds to the new entity here described.

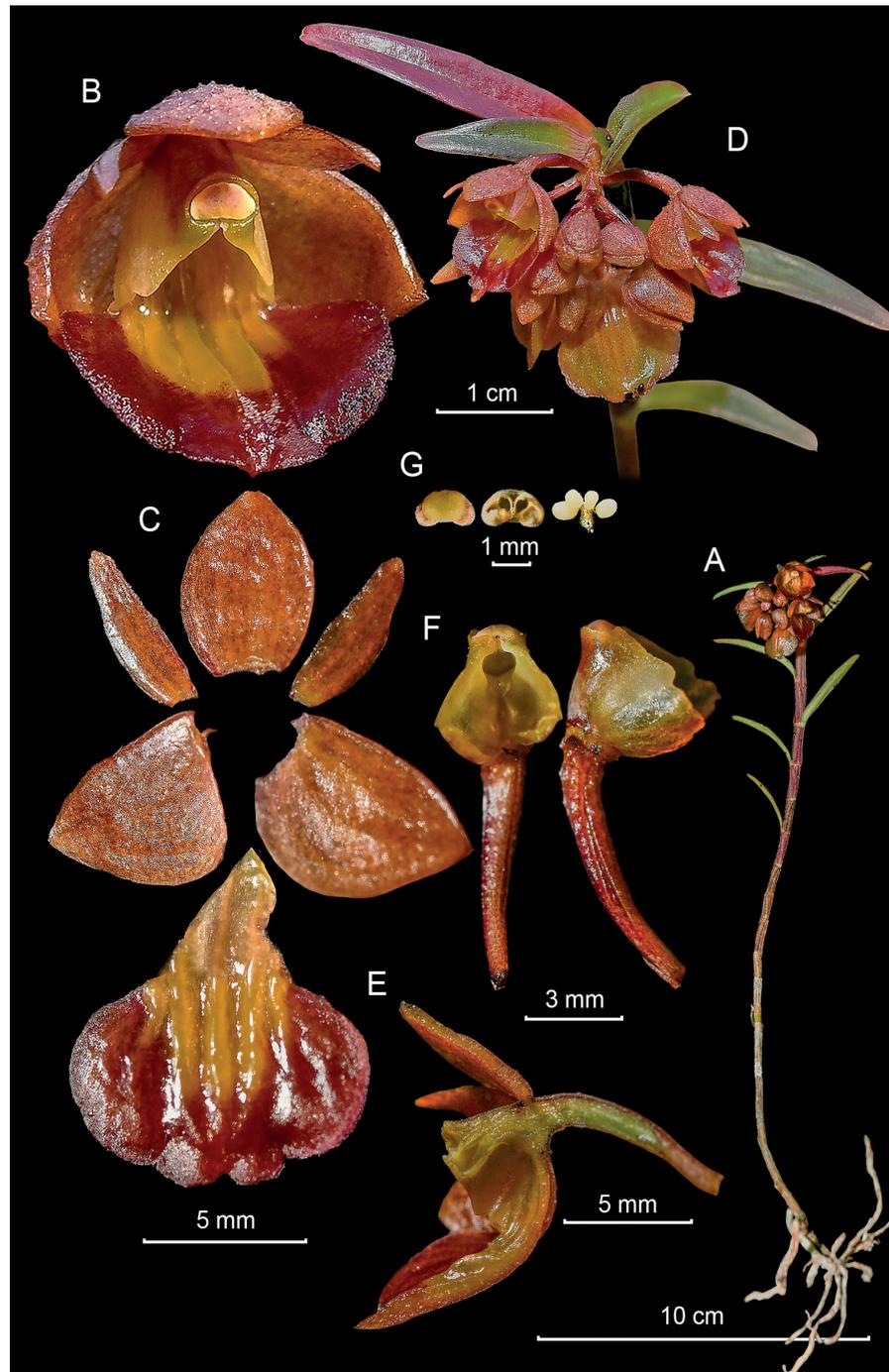
**Etymology.** From the Latin *parvi-*, small, and *reflexilobum*, reflexed lobes, in reference to the smaller flowers and lobes of the lip relative to those of closely allied *E. reflexilobum*.

***Epidendrum pomacochense* Hágsater, Icon. Orchid. 3: t. 374. 1999.**

Fig. 13

**Type material. PERU. San Martín:** Mirador, between Moyobamba and Pomacochas, just before Pomacochas, 1700 m, pressed 23 Nov. 1993, *hort. J. & L. Orchids sub E. Hágsater 11391* (holotype: AMO!).

**Description.** Epiphytic or lithophytic, monopodial, branching, erect **herb**, 15–20 cm tall. **Roots** 1–2 mm in diameter, basal from primary stem, fleshy, thin. **Stems** 12–18 × 0.15–0.4 cm, cane-like, terete, branching, branches produced from sub-apical internodes of previous stems, progressively shorter. **Leaves** 3–13 per stem, distributed along apical half of primary stem, and aggregate toward apex in shorter branches, distichous, articulate, sub-coriaceous, green, concolor; sheathes 0.6–1.2 cm long, tubular, striated, red; blade 1.2–4 × 0.3–0.4 cm, linear-lanceolate, apex unequally bilobed, margin entire, spreading. **Spathe** lacking. **Inflorescence** to 3 cm long including flowers, apical, racemose, arching-nutant, densely few-flowered; peduncle 6–8 mm long, terete, thin, scarcely verrucose. **Floral bracts** 2.0–2.5 mm long, much shorter than ovary, narrowly triangular, embracing. **Flowers** up to 9, resupinate, successive, 2–3 open simultaneously, sepals and petals copper-red, lip dark brick-red, with disc and column yellow, anther yellow slightly tinged brick-red on sides; fragrance none registered. **Sepals** partly spreading, free, membranaceous, dorsally scarcely verrucose, not carinate, 3-veined, somewhat concave, margins entire, spreading; dorsal sepal 4.6–5.5 × 3.1–4.3 mm, widely elliptic, apex rounded-obtuse; lateral sepals 5.5–7.0 × 3.8–5.5 mm, obliquely ovate, apex obtuse. **Petals** 4.2–6 × 1–1.5 mm, partly spreading, free, membranaceous, linear-lanceolate,



**Figure 13.** *Epidendrum pomacochense* from Arista et al. 38 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** longitudinal section of flower **F** column and ovary-pedicel from below (left) and side (right) **G** anther from above (left) and below (right), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

obtuse, 3-veined, margin entire, spreading. **Lip** 7–8.4 × 6.7–9 mm, united to column, shallowly 3-lobed, transversely elliptic in outline, concave, base cuneate; ecallose, disc 5-ribbed, smooth, parallel, 3 mid-ribs reaching middle of lip, lateral pair shorter; lateral lobes semi-orbicular, mid-lobe smaller, formed by two small semi-orbicular lobes, emarginate. **Column** 4 mm long, slightly arched with apex recurved upward, thick, apical aperture wide, triangular. **Clinandrium hood** short, margin entire. **Anther** 4-celled, obreniform, papillose. **Pollinia** 4, obovoid, later-

ally compressed, subequal, cream-colored; caudicles soft and granulose, as long as pollinia. **Rostellum** subapical, slit; viscarium semi-liquid. **Lateral lobes of stigma** small. **Cuniculus** a very wide cavity formed by column and lip, triangular, reaching perianth, unornamented, with a longitudinal widened slit ventrally at base of column. **Ovary** 6–9 mm long, terete, thin, not inflated, furrowed and scarcely verrucose. **Capsule** not seen.

**Additional specimens examined. PERU. Amazonas:** Perla del Imaza, La Perla Vieja, 1863 m, 22 Aug. 2021, *Arista et al.* 38 (KUELAP!); Perla de Imaza, Rio Rojo, 1875 m, 25 Aug. 2021, *Arista et al.* 108 (KUELAP!); road Chachapoyas–Mendoza, a little past Molinopampa, 2400 m, 15 Mar. 1998, *van der Werff 15019* (SEL!); **San Martín:** Bosque de protección Alto Mayo. Sector Venceremos, 1955 m, 21 Feb. 2017, *Edquén 195* (UNACH!) Prov. Rioja, Distrito Pardo Miguel, Chisquilla, 3278 m, 11 Apr. 2019, *Edquén 1810* (UNACH!).

**Other records. PERU. Sine loc., Jenny s.n.,** digital image (AMO!); **Amazonas:** Rodríguez de Mendoza, 30 Jan. 2017, *Arbilo s.n.,* digital image (AMO!); Huamantapa, R[odríguez]. de Mendoza, 9 Apr. 2015, *Fernández s.n.,* digital image (AMO!); Área de Conservación Pampa del Burro, camino a Perla del Imaza, km 14.5, 1823 m, 14 Jul. 2022, *Hágsater 16407,* digital image (AMO!); *ibid. loc.,* km 16, 1837 m, 15 Aug. 2022, *Hágsater 16428,* digital image (AMO!); **Cajamarca:** Prov. Cajabamba, Parubamba, 2600 m, 10 Dec. 2005, *Trujillo 243,* illustrated by *M. Alcántara 1558,* copy of illustration (AMO!); **San Martín:** Prov. Rioja, Distr. Pardo Miguel Naranjos, Venceremos, 1699 m, 21 Feb. 2017, *Edquén 2025,* digital images (AMO!); *ibid. loc., Edquén 2026,* digital images (AMO!); *ibid. loc., Edquén 2027,* digital images (AMO!); *ibid. loc., Edquén 2028,* digital images (AMO!).

**Distribution.** Known only from northeastern Peru, in Amazonas, San Martín and Cajamarca where it is common in protected areas with wet Andean forests, at 1700–2000 m.

**Habitat and ecology.** Epiphytic in humid montane forest, sclerophyllous shrubs, and very wet dwarf forest, and lithophytic on road-side banks of white sand and sandstone.

**Phenology.** Flowering from January to August.

**Taxonomic notes.** *Epidendrum pomacochense* belongs to the Diothonea Group and Subgroup, which is characterized by the monopodial, branching plants, the linear lanceolate to oblong, bilobed leaves, the racemose, arching-nutant inflorescence, the membranaceous flowers (rarely fleshy), the entire to 3-lobed, ecallose lip with the margin erose without or with 1–10 thin, smooth to erose keels, the column completely to obliquely united to the lip, and the anther reniform. *Epidendrum pomacochense* is recognized by the small plants, 15–20 cm tall, the copper-red flowers with the disc of the lip and column yellow, the sepals 4.6–7 mm long, dorsally sparsely verrucose, the column short and forming a large triangular aperture with the lip, the lip 3-lobed, transversely elliptic, the disc of the lip 5-ribbed, the ribs low, rounded, the 3 central ribs reaching the middle of the lip, the lateral lobes semi-orbicular, the mid-lobe smaller, formed by two small semi-orbicular lobes, emarginate. *Epidendrum cochabambanum* Dodson & Vásquez has larger plants up to 30 cm tall, linear leaves to 4.5 cm long, the inflorescence up to 4 cm long with flowers white tinged pink, and the lip 5-ribbed, the ribs high and apically truncate. *Epidendrum stenophyllum* Hágsater & Dodson is florally similar but the plants are up to 55 cm tall, with linear leaves, nearly acicular, 2–5.5 × 0.2–0.3 cm, the sepals up to 10 mm long.

***Epidendrum rosulatum* Hágsater, E. Santiago, J.P. Arista & Edquén, sp. nov.**

urn:lsid:ipni.org:names:77320361-1

Fig. 14.

**Type material. PERU. Amazonas:** Prov. Bongará, Distr. Yambrasbamba, camino a la Perla del Imaza, 1842 m, 15 Jul. 2022, *J. P. Arista, J. D. Edquén, E. Hágsater, E. Santiago, G. A. Salazar, E. Yrigoín, L. I. Cabrera & K. Edquen 278* (holotype: KUELAP!).

**Diagnosis.** Similar to *Epidendrum croceoserpens* Hágsater & Salas-Guerr. but the plants much smaller, up to 2.5 cm tall (vs. plants 9 cm tall), the leaves 0.8–1.2 cm long, orbicular, 4–7 forming a rosette (vs. leaves 3.5–5.6 cm long, 1–3, lanceolate), the flowers 7, ochre–yellow, with sparse red dots (vs. flowers 3–6, orange, turning pink with age), and the lip ovate-triangular, acute (vs. lip widely cordiform, base sub-cordate, apex short apiculate, margin erose-crenulate).

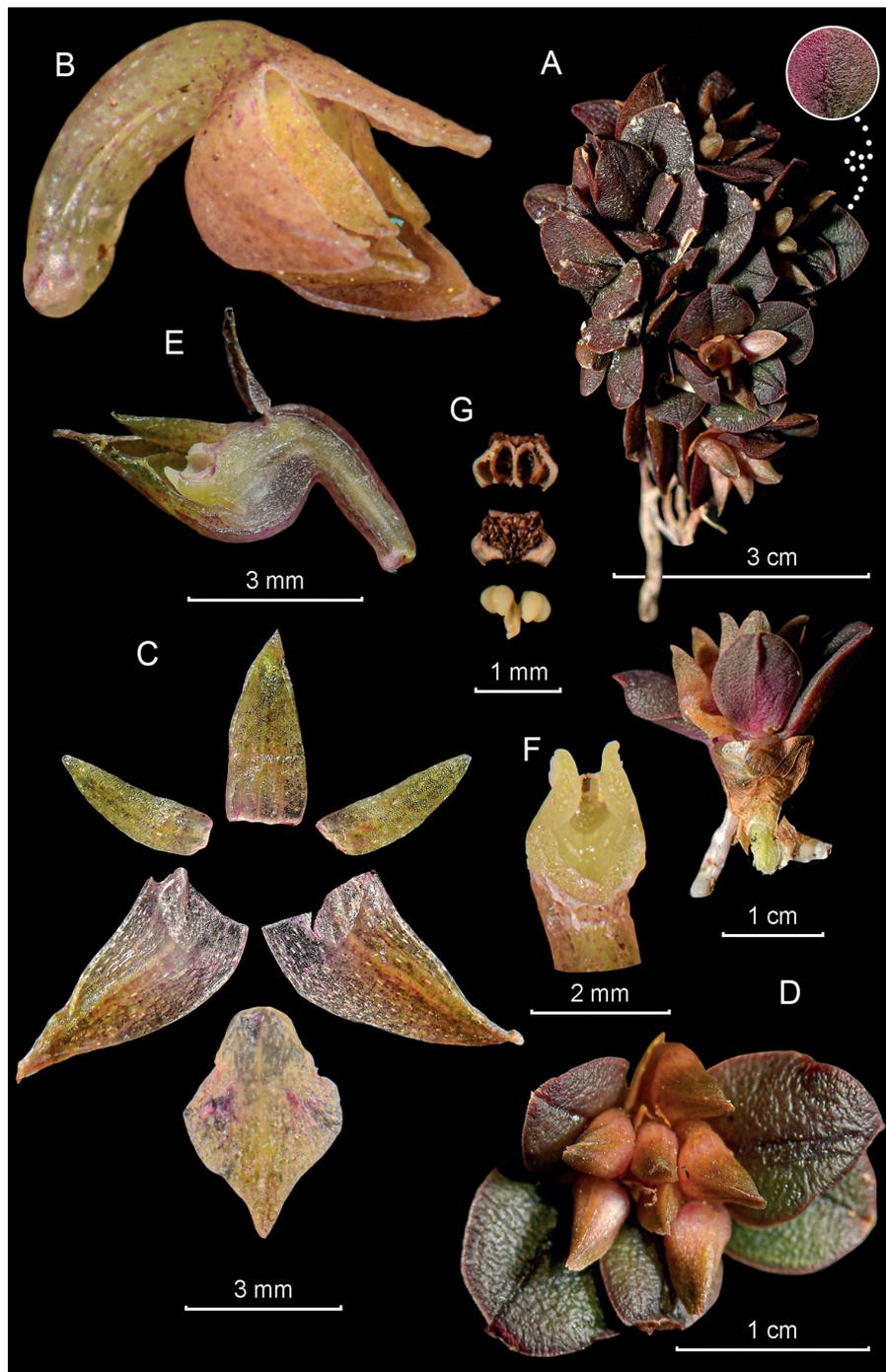
**Description.** Epiphytic, sympodial, caespitose **herb** 1.8–2.5 cm tall, forming a small mat. **Roots** 2 mm in diameter, basal, fleshy, thin, white. **Stems** 0.6–1.0 × 0.8 cm, thickened, forming a pseudobulb, globose, compact, homoblastic, medium green, somewhat coppery, completely covered by several sheaths 5–6 mm long, non-foliar, somewhat striated when dry, light brown. **Leaves** 4–6, forming a rosette at apex of pseudobulb, sessile; leaves 0.8–1.2 × 0.65–0.9 cm, orbicular, apex rounded, minutely apiculate, apical margin denticulate, spreading, fleshy thickened, succulent, surface strongly rugose, adaxially dark green, margin red-brown, abaxially red-purple, margins brownish black. **Spathe** lacking. **Inflorescence** apical, sessile, racemose, densely few-flowered, not surpassing leaves. **Floral bracts** 4 mm long, prominent, somewhat longer than ovary, widely triangular, acute, embracing. **Flowers** up to 7, simultaneous, upright, ochre-yellow with sparse red dots; fragrance not detected. **Sepals** partly spreading, free, 3-veined, acute, margins entire, spreading; dorsal sepal 3.5–4 × 1.6–1.7 mm, narrowly triangular; lateral sepals 5.0–5.8 × 2.4–2.5 mm, ovate triangular, oblique, apiculate. **Petals** 3.0–3.2 × 1 mm, free, partly spreading, oblong-lanceolate, 1-veined, obtuse, margin entire, spreading. **Lip** 3.0–3.2 × 3.0–3.1 mm, totally united to column, entire, ovate-triangular, acute, base truncate, margins entire, spreading; ecallose and without ribs on disc. **Column** 2.2 mm long, thick, slightly arched, forming a 120° angle with apex of ovary. **Clinandrium hood** short, margin erose. **Anther** sub-reniform, base and apex truncate, 4-celled, cream colored with center brown and rugose. **Pollinia** 4, lenticular; caudicles soft and granulose, longer than pollinia. **Rostellum** apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** large, about half length of stigmatic cavity. **Cuniculus** shallow, without penetrating ovary, very wide in column, unornamented. **Ovary** 3.0–3.5 mm long including pedicel, terete, not inflated, furrowed. **Capsule** not seen.

**Distribution.** Presently known only from the type. Peru, Amazonas: Prov. Bongará, Distr. Yambrasbamba, camino a la Perla del Imaza, at 1842 m.

**Habitat and ecology.** Epiphytic in an isolated *Inga* sp. tree amidst a pasture for cattle grazing, near remnants of wet montane forest. In the crown of the tree with several individuals on branches below the leaves of the tree.

**Phenology.** Flowering in July–August.

**Taxonomic notes.** *Epidendrum rosulatum* belongs to the Kaloptenix Group, Serpens Subgroup, characterized by the aggregate, globose pseudobulbs with fleshy-coriaceous leaves, and a sessile inflorescence, and one or few fleshy,



**Figure 14.** *Epidendrum rosulatum* from Arista et al. 278 **A** habit; the inset shows a slightly enlarged portion of the leaf underside **B** flower **C** dissected perianth **D** top view of inflorescence and leaves **E** longitudinal section of flower **F** column and ovary apex from below **G** anther from below (up) and above (down), and pollinarium (Photographs by J. D. Edquén; plate prepared by X. Alcántara).

compact, stellate flowers, often burgundy red in color, and the lip entire, more or less cordiform. The new species is recognized for having very small plants, up to 2.5 cm tall, globose pseudobulbs, 4–6 apical, leaves forming a rosette around the inflorescence, the leaves orbicular tinged purple red with the margins brown black, the inflorescence of up to 7 flowers, ochre with some red dots, lateral sepals 5.0–5.8 mm long and the lip 3.0–3.2 × 3.0–3.1 mm, ovate-triangular,

acute. *Epidendrum croceoserpens* has 1–3 leaves per pseudobulb, the leaves lanceolate, to 5.1 cm long, green above, underside vinaceous, margin minutely erose; flowers 3–6, facing upwards, orange, turning somewhat pink with age, petals 4.2 mm long, ovate, and lip with a low wide mid-rib. *Epidendrum citroserpens* Hágsater, Cisneros & J. Duarte has 2 leaves per pseudobulb, a 2–3 flowered inflorescence, the flowers yellowish green, a cordiform lip, short apiculate, the disc with a thick mid-rib, and a column about 5 mm long. *Epidendrum brevivyacuriense* Hágsater, H. Medina & J. Duarte has a single apical leaf, ovate, 4 simultaneous, reddish violet flowers, petals 5.0 × 1.5 mm, margin somewhat erose, the lip widely cordiform, margin irregularly dentate-erose, and disc with a thin mid-rib from the base to the middle of the disc.

**Etymology.** From the Botanical Latin *rosulatus*, rosette (a circular cluster of leaves) shaped, in reference to the distinctive rosette formed by the leaves, which is a rare trait in the genus.

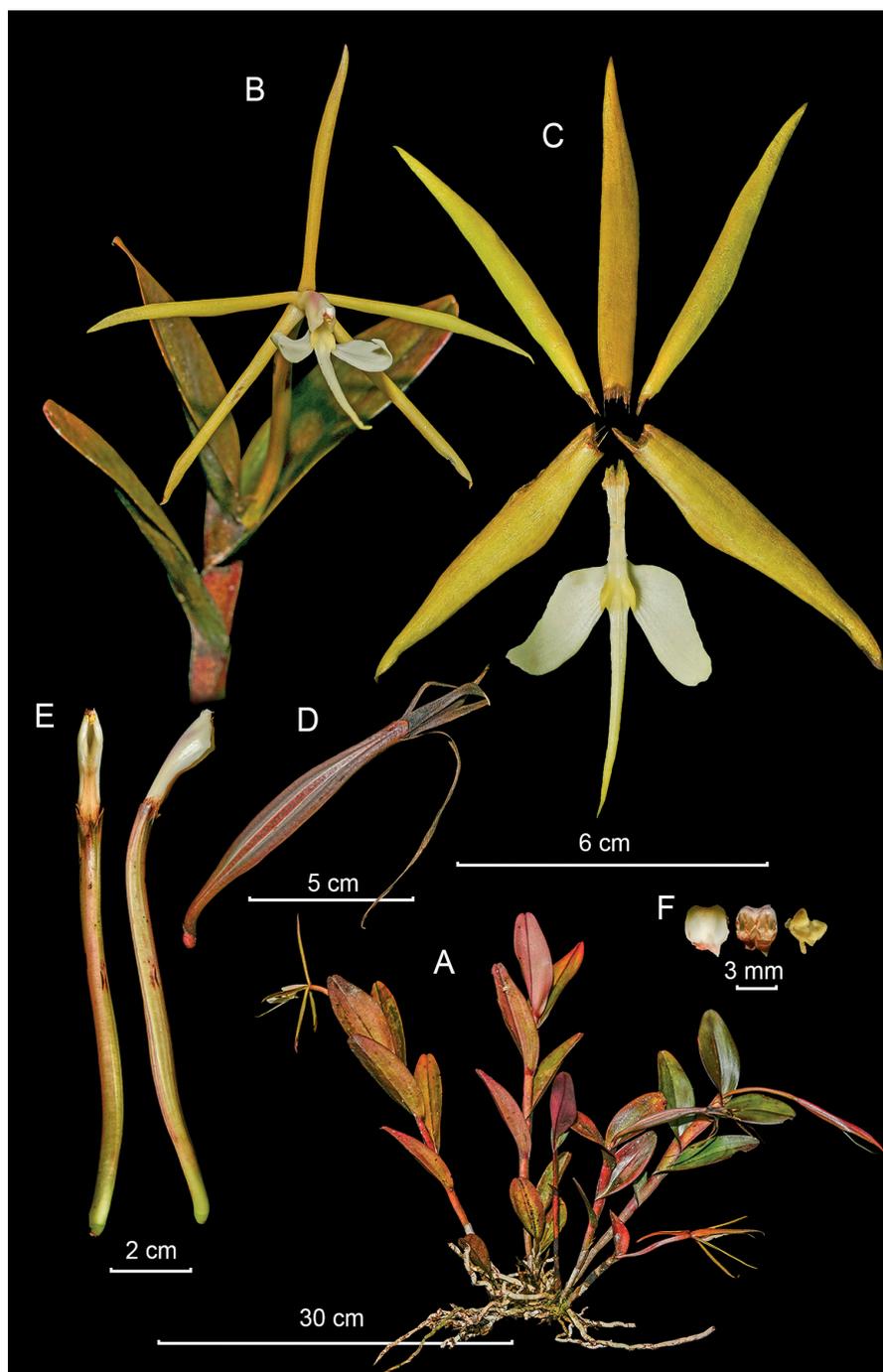
***Epidendrum tridens* Poepp. & Endl., Nov. Gen. & Sp. Pl. (Poeppig & Endlicher) 2: 2. t. 103. 1838.**

Fig. 15

**Type material.** PERU. [Huánuco:] Subandin. supra arbores, Cuchero, *E. F. Poeppig s.n.* (holotype: W-R!; isotype: W-R 42400!).

**Taxonomic synonym.** *Epidendrum tunguraguae* Schltr. Repert. Spec. Nov. Regni Veg. Beih. 8: 87 (1921). Type: Ecuador. Tunguragua: In rupibus in convalle subandina montis Tunguragua, c. 1800 m, Jun. 1886, L. A. Sodiro 69a (holotype: B, destroyed; illustration AMES36134!; neotype, designated by Sánchez Saldaña and Hágsater in Hágsater and Sánchez Saldaña 2015, t. 1565: Wulkan Tunguragua, 1500–2000 m, blooms in June and July, *F. C. Lehmann 6719*, K! (pencil illustration of live plant in flower, *Lehm. Ic. Pl. Tabul. 438*, K!; isoneotype AMES!).

**Description.** Epiphytic, lithophytic or terrestrial, sympodial, caespitose, erect **herb** 26–100 cm tall, including inflorescence. **Roots** 3–4 mm in diameter, basal, fleshy. **Stems** 18–56 × 0.6–1.5 cm, simple, cane-like, laterally compressed toward apex, straight, green, sometimes tinged purple. **Leaves** 4–8, distributed along apical  $\frac{3}{4}$  of stems, erect, coriaceous; plants deep green sometimes tinged purple, especially sheaths and underside of leaves; sheath 2–6 cm long, foliaceous, laterally compressed, ancipitose; blade 8.0–15 × 2–5 cm, unequal, progressively larger toward apex of stem, narrowly elliptic, 3–5 times longer than wide, apically unequally bilobed, minutely mucronate, venation and dorsal keel evident, dark green, occasionally tinged purple. **Spathe** lacking. **Inflorescence** apical, racemose, becoming pluri-racemose, producing one flower at a time, over several years from same stem; peduncle 3–4 mm long, reduced, rachis 5–7[10] mm long. **Floral bracts** 7–11 × 5–6 mm, much shorter than ovary, triangular, acuminate, amplexicaul. **Flowers** successive, one at a time from each raceme, resupinate, sepals and petals green to yellow, occasionally tinged purple, lip and column white; scented at night. **Sepals** 42–73 × 5–8 mm, spreading, linear-lanceolate, acuminate, 10-veined, with numerous secondary veins, margin entire, revolute. **Petals** 40–70 × 2.5–3.0 mm, partly spreading, linear-lanceolate, acuminate, 5-veined, with numerous secondary veins, margins entire, spreading. **Lip** 27–53 × 24–30 mm, united to column, 3-lobed, margin entire,



**Figure 15.** *Epidendrum tridens* from Arista et al. 9 **A** habit **B** flower **C** dissected perianth **D** developing capsule **E** column and ovary-pedicel from below (left) and side (right) **F** anther from above (left) and below (right), and pollinarium (Photographs by J. D. Edquén; plate prepared by A. Cisneros).

spreading; bicallose, calli laminar, prominent; lateral lobes 14–26 × 6–9 mm, semi-ovate, rounded; mid-lobe 20–37 × 2–3 mm, ensiform, acute, margin entire. **Column** 21–25 mm long, straight to slightly arched, strongly dilated toward apex. **Clinandrium hood** slightly surpassing body of column, generally somewhat dentate, occasionally deeply dentate. **Anther** obovoid, 4-celled. **Pollinia** 4, semi-obovoid, laterally compressed; caudicles soft and granulose, about as long as pollinia. **Rostellum** apical, slit; viscarium semi-liquid, transparent. **Lat-**

**eral lobes of stigma** reduced. **Cuniculus** penetrating nearly half length of ovary, unornamented. **Ovary** 60–100[120] × 2.0–3.5 [5] mm long including pedicel, shorter to slightly longer than apical leaf, terete, inflated, unornamented. **Capsule** ellipsoid, slender; pedicel 25–35 × 2.0–2.5 mm, body 45–60 × 17–21 mm, at center of capsule; apical neck 13–16 × 2.3–3.5 mm.

**Additional specimens examined. PERU.** *Sine loc.*, Bennett 57 (MOL!); *Ibid. loc.* Bennett 3669 (MOL!); *ibid. loc.*, 1803, Ruiz & Pavón s.n. (MA!); *Sine loc.*, 1876–1877, Vidal-Sénègne 68 (P!); **Amazonas:** Prov. Bongará, Dist. Yambrasbamba, Perla del Imaza, La Perla Vieja, Arista et al. 9 (KUELAP!); **Cajamarca** Bongará near Pedro Ruiz, 2200 m, Aug. 1979, Königler 24/1 (SEL!); Bongará, 1 Sep. 1985, Moore s.n. (SEL!); Bongará, Dist., Yambrasbamba, viaje al puente Vilcaniza, 1840–2020 m, 9 Jul. 1999, Sánchez-Vega 10028 (AMO! F!); **Ayacucho:** Aina, between Huanta and Río Apurímac, 750–1000 m, 7 May 1929, Killip 23169 (US!); **Cajamarca:** San Ignacio Huarango, Nuevo Mundo, 1140 m, 11 Mar. 2000, Calatayud 425 (CUZ!); San José de la Alianza, Rinconada, 2200 m, 18 Mar. 2009, Vásquez 242 (MOL!) **Cusco:** Paucartambo, Mirador, Unión-Cosñipata, 1750 m, Feb. 1994, Moscoso 760 (CUZ!) Paucartambo, San Pedro–Cosñipata, 1480 m, Mar. 1994, Moscoso 1112 (CUZ!); *ibid. loc.*, Mar. 1994, Moscoso 1113 (CUZ!); Quispicanchis, Río Arazá, between Pan de Azúcar and Quince Mil Airport. 292 km from Cusco, 643 m, 10 Aug. 1991, Nuñez 14065 (MO!); Marcapata, Murayaca, Quispicanchis, 1685 m, 6 Nov. 2006, Villafuerte 620 (CUZ!); **Huánuco:** Leoncio Prado, La Alcantarilla, Tingo María, 650 m, 6 Jul. 1984, Fernández 385 (USM!); Carpish, entre Huánuco y Tingo María, 2800–2900 m, 6 Feb. 1950, Ferreyra 6713 (AMES! UC! USM!); Carpish pass, Tingo María side, 2000 m, 18 Jul. 1964, Hutchison 5977 (UC! US!); Carpish Hill, between Huánuco and Tingo María, 2100 m, 10 Aug. 1980, Luer 5351 (SEL!); Carpish, km 453, 2500 m, 7 May 1976, Plowman 6070 (AMES!); San Pedro de Carpish, Mirador, *Ridoutt s.n.* (USM!); Chinchao–Carpish, 2400 m, Woytkowski 5024 (MO! AMES!); **Junín:** Chanchamayo, La Merced, Quebrada del Carmen, 850 m, 6 May 1984, Fernández 305 (USM!); Chanchamayo, El Refugio, San Ramón, 800 m, 16 May 1984, Fernández 318 (USM!); Tarma, Agua Dulce, 1900 m, 16 Mar. 1948, Woytkowski 35478 (MO!); **Loreto:** Coronel Portillo, Divisoria, entre Tingo María y Pucallpa, 1500–1600 m, 28 Feb. 1947, Ferreyra 1677 (USM!); **Pasco:** Chontabamba, La Suiza Nueva, 2190–2200 m, 7 Jan. 2005, Arias 70 (HOXA! MO!); Oxapampa, Sector San Alberto, P[arque]. N[acional]. Yanachaga–Chemillén, 2100 m, 18 Mar. 2005, Ortiz 507 (HOXA! MO!); Oxapampa, Huancabamba, localidad Grapanazu, Sector San Daniel, P[arque]. N[acional]. Yanachaga–Chemillén, 2236 m, 10 Jul. 2004, Perea 1476 (HOXA! MO!); Oxapampa, Chontabamba valley, 23 km W of Oxapampa 1900 m, 26 Jan. 1984, Smith 5881 (MO! USM!); Huancabamba, Parque Nacional Yanachaga–Chemillén, Sector Quebrada Yanachaga. 1700–2265 m, 17 Feb. 2004, Vásquez 29534 (HOXA! USM!); **Puno:** Carabaya, San Gaban, alrededores de San Gaban, 1810 m, 9 Mar. 2017, Trinidad 4134 (USM!); alrededores Sandia, 2250 m, 5 Feb. 1964, Vargas 15149 (AMES! CUZ!); **San Martín:** Cordillera Azul, Coronel Portillo, Tingo María on highway to Pucallpa, near Divisoria, ca. 1600 m, 17 Nov. 1949, Allard 21786 (AMES! US!); **Ucayali:** Padre Abad, Parque Nacional Cordillera Azul, Divisoria, entre Tingo María y Pucallpa, 1500 m, 28 Feb. 1947, Ferreyra 1677 (USM!).

**Other records. PERU.** *Sine loc.*, illustration by I. Pulgar, Ruiz and Pavón 1282 (MA!); **Jaén:** *Ocupa-Horna s.n.*, color plate (AMO!); **San Martín:** Moyobamba

above Naranjo at km 468 along Olmos–Moyobamba road, 1020 m, 9 Dec. 1990, *Bennett 4800*, illustration in *Icon. Orchid. Peruvianum* t. 51 (Bennett and Christenson 1993); Bosque de Protección Alto Mayo, Jan. 2015, *Collantes s.n.*, digital images (AMO!); Rioja: Pardo Miguel Naranjos, Venceremos, 1887 m, 6 Feb. 2017, *Edquén 1088*, digital images (AMO!); *ibid. loc.*, 1750 m, 26 May 2022, *Edquén 6038*, digital images (AMO!).

**Distribution.** Widespread on the Amazonian slope of the eastern Andean range in Colombia, Ecuador, and Peru, and further northeastern into the Guiana Shield in Venezuela, at 640–2900 m.

**Habitat and ecology.** Usually growing as a terrestrial or lithophytic on roadside embankments and sometimes epiphytic in montane wet forest and dwarf forest on white sand.

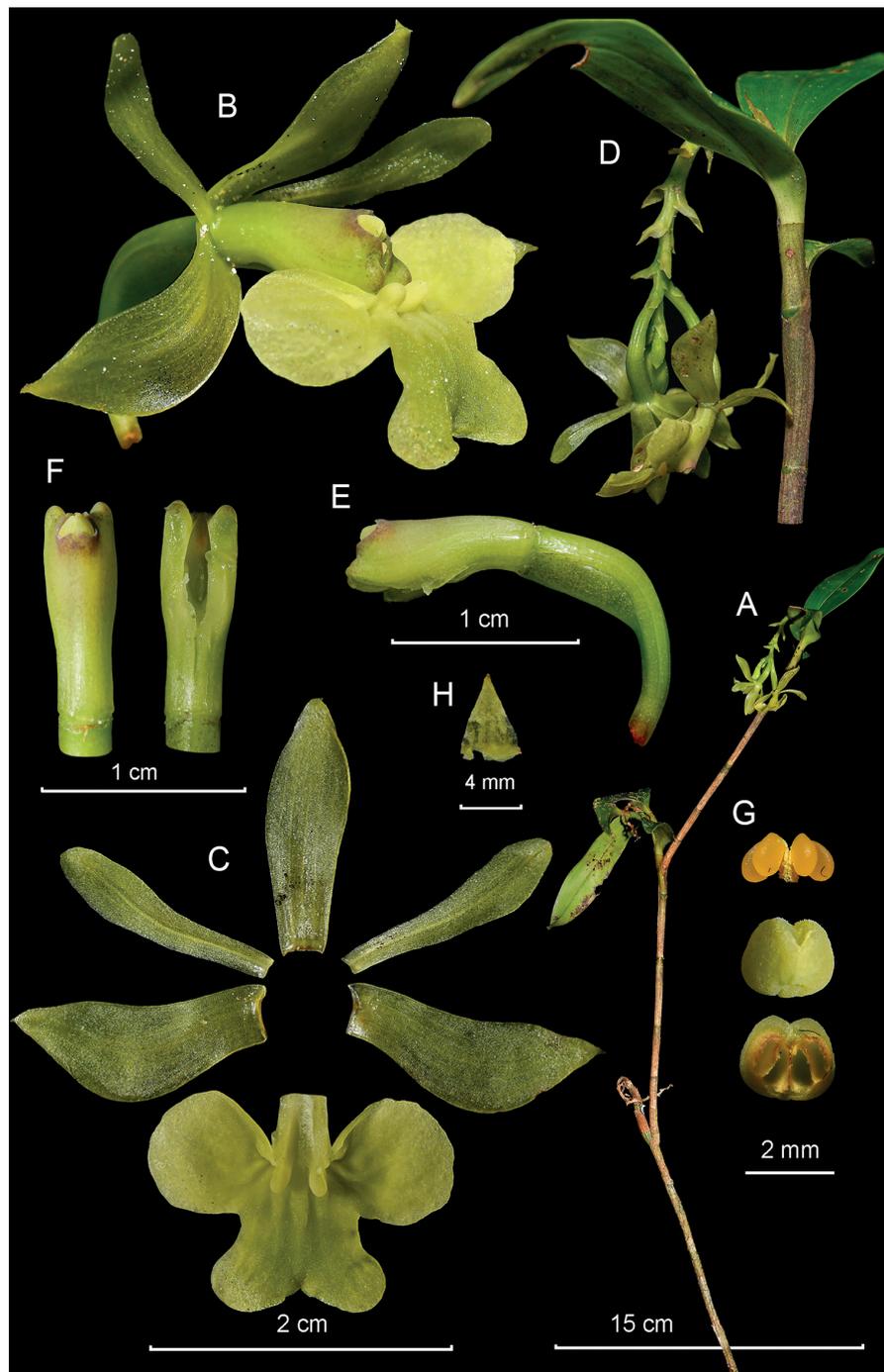
**Phenology.** Flowering throughout the year, fruiting mainly from June to September.

**Taxonomic notes.** *Epidendrum tridens* belongs to the Nocturnum Group which is characterized by the sympodial, caespitose plants, cane-like, non-fusiform stems, successive flowers on a short, racemose or pluri-racemose inflorescence, without spathaceous bracts, and large, star-shaped flowers, with similar sepals and petals; the flowers are mostly indistinguishable in shape. The species is recognized by the dark green plants, the underside of the leaves and sheaths tinged with purple, laterally compressed stems, 4–8 erect leaves, generally longer toward the apex of the stem, length/width 3:1–5:1 (8.5–15 × 2–5 cm), distributed along the apical  $\frac{3}{4}$  of the stems, green often tinged with purple; the ovary 60–100 [120] mm long, equal or occasionally longer than apical leaf, the sepals 42–73 mm long, the lateral lobes of lip semi-ovate, rounded to acute, acuminate, 14–26 mm long; the mid-lobe 20–37 mm long, the column 21–25 mm long; body of the capsule centered. *Epidendrum nocturnum* Jacq. is widely distributed from Florida to Bolivia, has green plants, terete stems, smaller leaves distributed along the apical  $\frac{2}{3}$  of the stems, a short ovary, 50–70 mm long, and the body of the capsule occupying nearly its whole length. *Epidendrum tumuc-humaciense* (Veyret) Carnevali & G.A.Romero is found along the Guiana Shield, and at lower altitudes in the Amazon basin in Colombia, Venezuela, Guyana, Surinam, French Guiana and the northern border of Brazil. Plants are frequently vinaceous, or yellow-green, it has numerous, shorter, narrower, erect leaves (3–9.2 × 1.2–2.8 cm), distributed throughout the stems, the basal ones generally longer; sepals and petals 48–81 mm long; body of the capsule occupying the apical half of the fruit.

***Epidendrum weigendii* Hágsater & Cisneros, *Icon. Orchid.* 18(2): t. 1899. 2021.**  
Fig. 16

**Type material.** PERU. Amazonas: Chachapoyas: Molinopampa: Road Chachapoyas to Mendoza, km 36, cloud forest, on sandstone, 2800 m, 5 June 1998, *M. Weigend, T. Franke, J. Skrabal & M. A. González 98/429* (holotype: F-2211499!; isotype: USM!).

**Description.** Epiphytic, sympodial, scandent, erect **herb** up to 58 cm tall, new stems produced from a middle internode of previous stem. **Roots** fleshy, from base of primary stem or occasionally from base of upper stems. **Stems** 8–15



**Figure 16.** *Epidendrum weigendii* from Arista et al. 253 **A** habit **B** flower **C** dissected perianth **D** inflorescence at apex of stem **E** column with ovary-pedicel from side **F** column and ovary apex from above (left) and below (right) **G** pollinarium and anther from above (up) and below (down) **H** floral bract (Photographs by J. D. Edquén; plate prepared by X. Alcántara).

× 0.3–0.5 cm, erect, simple, cane-like, terete, basal 3/4 of stem covered with non-foliar sheaths. **Leaves** 2–3, aggregate toward apex of stem, spreading, alternate; sheaths 0.6–2.5 × 0.3–0.5 cm, tubular, striated; blades 2.1–9.6 × 0.9–2.1 cm, unequal in size, elliptic-oblong, acute, sub-coriaceous, medium green. **Spathe** lacking. **Inflorescence** 4–6 cm long, apical, from mature stem, racemose, arcuate; peduncle 1.4–2.3 × 0.3 cm, somewhat laterally compressed, sometimes with a single bract near base, 8 mm long, acute, embracing; rachis 2.3–5 cm

long, arching-nutant. **Floral bracts** 3–6 mm long, much shorter than ovary, decreasing in size, triangular, acute, embracing. **Flowers** 7–11, opening in succession, until most open at same time, resupinate, facing downward, medium green, lip pale green, apex of column around anther slightly tinged purple, anther green; fragrance none. **Sepals** free, spreading, fleshy, 5-veined, margins entire, spreading; dorsal sepal 13–16 × 5.4–6.0 mm, narrowly obovate, obtuse; lateral sepals 14.5–15.0 × 5.4–6.0 mm, obliquely oblong oblanceolate, somewhat falcate, acute. **Petals** 13.5–16 × 3.5–6.0 mm, free, spreading, oblanceolate, apex sub-acute to rounded, 3-veined, margin entire, spreading. **Lip** 14.8 × 17.7 mm, united to column, deeply 3-lobed, fleshy, wider than long, base strongly cordate, apex emarginate, margin entire, spreading; bicallose, calli globose, slightly separate, conspicuous, disc with three parallel, thick, low ribs running down middle, lateral ribs arching closer to mid-rib at apex, reaching apical sinus of lip; lateral lobes 7.0 × 8.0–9.0 mm, semi-orbicular; mid-lobe 6.7 × 10.9–12.5 mm, formed by two small, semi-orbicular lobes, with a short, narrow isthmus 1.6 mm long. **Column** 10 mm long, somewhat thick toward apex, truncate, straight. **Clinandrium hood** reduced, margin entire. **Anther** globose, apex emarginate, apical surface minutely echinate, 4-celled. **Pollinia** obovoid, laterally compressed, subequal; caudicles granulate, shorter than pollinia. **Rostellum** apical, slit; viscarium semi-liquid. **Lateral lobes of stigma** not seen. **Cuniculus** penetrating the apical one third to one half of the pedicellate ovary. **Ovary** 16–20 × 3 mm, slightly inflated ventrally along apical half, thin, terete, somewhat arcuate, furrowed. **Capsule** [immature] 45 × 0.6 mm long, narrowly ellipsoid; pedicel 0.7 × 0.2 mm, body 25–30 × 0.6 mm.

**Additional specimens examined.** **PERU. Amazonas:** Prov. Bongará: Distr. Yambrasbamba: Pampa del Burro, Perla del Imaza, a 100 m de la carretera, en bosque chaparro esclerófilo, 1886 m, 14 Aug. 2022, *Arista et al.* 253 (KUELAP!); Chachapoyas: Molinopampa: along Río Ventilla, 1–2 km W of Molinopampa, 2350–2400 m, 23 Aug. 1962, *Wurdack 1485* (US!).

**Distribution.** Known presently from three collections from the ACPPB and from near Molinopampa, Amazonas, on the border with San Martín, northeastern Peru, 1800–2800 m.

**Habitat and ecology.** Epiphytic in dwarf forest on white sand of Andean tepui, dwarf sclerophyllous forest and cloud forest.

**Phenology.** Flowering from June to August.

**Taxonomic notes.** *Epidendrum weigendii* belongs to the Incomptum Group. It is recognized by the very thin stems, 2–3 elliptic-oblong leaves aggregate at the apex, the successive flowers, until most open at same time, the flower green, the lateral lobes of the lip orbicular, as are the two lobes of the mid-lobe, the disc of the lip with 3 short parallel ribs, and the short radiating ribs at base of lateral lobes. *Epidendrum tamaense* has the floral segments strongly reflexed and a strongly arcuate ovary, sepals 15–21 mm long, lateral sepals acute to acuminate, with a conspicuous dorsal keel, petals obtrullate, and the lip larger, 22–24 × 33 mm, bicallose, with a single mid-rib.

## Acknowledgements

We thank Peru's Programa Nacional de Investigación Científica y Estudios Avanzados (PROCIENCIA) of the Consejo Nacional de Ciencia, Tecnología e Innovación Tecnológica (CONCYTEC) for financing our project Diversidad Táxi-

ca y Filogenética del Género *Epidendrum* L. (Orchidaceae) en dos Ecosistemas del Área de Conservación Privada La Pampa del Burro, Amazonas–Perú, under contract N°058-2021-CONCYTEC; Peru's Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) for issuing the authorization for scientific collecting (AUT-IFL-2021-033); the community of the Anexo Perla del Imaza for their permission to explore the ACPPB; Kely Edquen, Lucy Iliquín, Katherin Inga, Yhomara Maslucá, and Elmer Yrigoín for their help during fieldwork; Norma Castillo for her support in the administration of the project; and Jaime González for transportation to the field. Our sincere gratitude to Shirlay Rafael, Elvira Goicochea, Heber Cabanillas, and Edilberto Vásquez for their hospitality, and Benjamín López, Wilson Delgado, Isidoro Lozano, and Félix Díaz for their enthusiastic guidance in the field; Anaís Cisneros and Ximena Alcántara of Herbario AMO for the preparation of the color plates; and Patricia Harding for revising the manuscript and proof-reading the English language. We also thank the following herbaria for permitting us to study and photograph the collections in their charge over the past 40 years: AAU, AMES, AMO, ANDES, B, BM, BR, BRIT, C, CAS, CHAX, CM, COL, CPUN, CTES, CUVU, CUZ, E, ECUAMZ, ENCB, F, FI, G, GH, GOET, HAO, HB, HBG, HCEN, HNOP, HOXA, HURP, HUSA, HUT, INPA, ITA, JAUM, K, KUELAP, L, LE, LL, M, MA, MEXU, MICH, MO, MOL, NY, OXF, P, PR, PRC, PRG, QCA, QCNE, R, RENZ, S, SEL, TEX, TNS, U, UC, UFV, EE, UU., USF, USM, VEN, W, WIS, and WRSL.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Conceptualization and funding acquisition: EH, EPM, GAS, JPA, MO. Investigation: EH, ES, JDE, JPA, GAS. Project administration: EPM, JPA, MO. Writing and proofreading of the manuscript: EH, EPM, ES, GAS, JDE, JPA, MO.

### Author ORCIDs

Jessy Patricia Arista  <https://orcid.org/0000-0001-8334-5538>

Eric Hágsater  <https://orcid.org/0000-0002-2371-9427>

Elizabeth Santiago  <https://orcid.org/0000-0002-1368-9025>

José D. Edquén  <https://orcid.org/0000-0002-7289-3974>

Elí Pariente  <https://orcid.org/0000-0002-9197-0218>

Manuel Oliva  <https://orcid.org/0000-0002-9670-0970>

Gerardo A. Salazar  <https://orcid.org/0000-0002-5203-5374>

### Data availability

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

## References

- Bennett DE, Christenson EA (1993) *Icones Orchidacearum Peruvianum* t. Privately published, Sarasota, 200 pp.
- Bennett DE, Christenson EA (1995a) *Icones Orchidacearum Peruvianum* t. Privately published, Sarasota, 201–300.
- Bennett DE, Christenson EA (1995b) *Icones Orchidacearum Peruvianum* t. Privately published, Sarasota, 301–400.
- Bennett DE, Christenson EA (1998) *Icones Orchidacearum Peruvianum* t. Privately published, Sarasota, 401–600.
- Bennett DE, Christenson EA (2001) *Icones Orchidacearum Peruvianum* t. Privately published, Sarasota, 601–800.
- Dodson CH, Bennett DE (1989a) *Orchids of Peru, Icones Plantarum Tropicarum* ser 2, 1: t. 001–100. St. Louis, Missouri.
- Dodson CH, Bennett DE (1989b) *Orchids of Peru, Icones Plantarum Tropicarum* ser 2, 2: t. 101–200. St. Louis, Missouri.
- Dodson CH, Dodson PM (1980a) *Orchids of Ecuador, Icones Plantarum Tropicarum* 1: t. 001–100. Sarasota.
- Dodson CH, Dodson PM (1980b) *Orchids of Ecuador, Icones Plantarum Tropicarum* 3: t. 201–300. Sarasota.
- Dodson CH, Dodson PM (1980c) *Orchids of Ecuador, Icones Plantarum Tropicarum* 4: t. 301–400. Sarasota.
- Dodson CH, Dodson PM (1982) *Orchids of Ecuador, Icones Plantarum Tropicarum* 5: t. 401–500. Sarasota.
- Dodson CH, Dodson PM (1984) *Orchids of Ecuador, Icones Plantarum Tropicarum* 10: t. 901–1000. Sarasota.
- Dodson CH, Dodson PM (1989a) *Orchids of Ecuador, Icones Plantarum Tropicarum* ser 2, 5: t. 401–500. St. Louis, Missouri.
- Dodson CH, Dodson PM (1989b) *Orchids of Ecuador, Icones Plantarum Tropicarum* ser 2, 6: t. 501–600. St. Louis, Missouri.
- Dressler RL (1961) *Phylogeny and Classification of the Orchid Family*. Cambridge University Press, 31 pp. [26–79.]
- Goicochea A, Gutiérrez A, Ruiz A, Salas M (2019) *Orquídeas de Perú: Relación de especies y sus sinónimos*. Corporación G y G E.I.R.L, Moyobamba, San Martín, 285 pp.
- Hágsater E (1985) *Toward the Understanding of the Genus Epidendrum*, Proceedings of the Eleventh World Orchid Conference, Miami, 195–201.
- Hágsater E, Krahl A (2020) *Epidendrum deditae*, a new species of Orchidaceae (Laeliinae) from northern Brazil. *Phytotaxa* 440(3): 225–231. <https://doi.org/10.11646/phytotaxa.440.3.4>
- Hágsater E, Salazar GA [Eds] (1993) *The Genus Epidendrum, Part 1, Icones Orchidacearum* 2: t. 201–300. [https://herbarioamo.org/index\\_archivos/Fascicle2.pdf](https://herbarioamo.org/index_archivos/Fascicle2.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2001) *The Genus Epidendrum, Part 3, Icones Orchidacearum* 4: t. 401–500. [https://herbarioamo.org/index\\_archivos/Fascicle4.pdf](https://herbarioamo.org/index_archivos/Fascicle4.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2004) *The Genus Epidendrum, Part 4, Icones Orchidacearum* 7: t. 701–800. [https://herbarioamo.org/index\\_archivos/Fascicle7.pdf](https://herbarioamo.org/index_archivos/Fascicle7.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2006) *The Genus Epidendrum, Part 5, Icones Orchidacearum* 8: t. 801–900. [https://herbarioamo.org/index\\_archivos/Fascicle8.pdf](https://herbarioamo.org/index_archivos/Fascicle8.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2007) *The Genus Epidendrum, Part 6, Icones Orchidacearum* 9: t. 901–1000. [https://herbarioamo.org/index\\_archivos/Fascicle9.pdf](https://herbarioamo.org/index_archivos/Fascicle9.pdf)

- Hágsater E, Sánchez Saldaña L [Eds] (2008) The Genus *Epidendrum*, Part 7, Icones Orchidacearum 11: t. 1101–1200. [https://herbarioamo.org/index\\_archivos/Fascicle11.pdf](https://herbarioamo.org/index_archivos/Fascicle11.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2009) The Genus *Epidendrum*, Part 8, Icones Orchidacearum 12: t. 1201–1300. [https://herbarioamo.org/index\\_archivos/Fascicle12.pdf](https://herbarioamo.org/index_archivos/Fascicle12.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2010) The Genus *Epidendrum*, Part 9, Icones Orchidacearum 13: t. 1301–1400. [https://herbarioamo.org/index\\_archivos/Fascicle13.pdf](https://herbarioamo.org/index_archivos/Fascicle13.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2013) The Genus *Epidendrum*, Part 10, Icones Orchidacearum 14: t. 1401–1550. [https://herbarioamo.org/index\\_archivos/Fascicle14.pdf](https://herbarioamo.org/index_archivos/Fascicle14.pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2015) The Genus *Epidendrum*, Part 11, Icones Orchidacearum 15(1): t. 1501–1558. [https://herbarioamo.org/index\\_archivos/Fascicle15\(1\).pdf](https://herbarioamo.org/index_archivos/Fascicle15(1).pdf)
- Hágsater E, Sánchez Saldaña L [Eds] (2016a) The Genus *Epidendrum*, Part 11, Icones Orchidacearum 15(2): t. 1559–1600. [https://herbarioamo.org/index\\_archivos/Fascicle15\(2\).pdf](https://herbarioamo.org/index_archivos/Fascicle15(2).pdf)
- Hágsater E, Sánchez Saldaña L (2016b) AMO–DATA en la taxonomía y en el manejo de colecciones. *Lankesteriana*. *Lankesteriana* 3(2). <https://doi.org/10.15517/lank.v3i2.22999>
- Hágsater E, Santiago E [Eds] (2018) The Genus *Epidendrum*, Part 12, Icones Orchidacearum 16(1): t. 1601–16. [https://herbarioamo.org/index\\_archivos/Fascicle16\(1\).pdf](https://herbarioamo.org/index_archivos/Fascicle16(1).pdf)
- Hágsater E, Santiago E [Eds] (2019) The Genus *Epidendrum*, Part 13, Icones Orchidacearum 17(1): t. 1701–1756. [https://herbarioamo.org/index\\_archivos/Fascicle17\(1\).pdf](https://herbarioamo.org/index_archivos/Fascicle17(1).pdf)
- Hágsater E, Santiago E [Eds] (2020a) The Genus *Epidendrum*, Part 13, Icones Orchidacearum 17(2): t. 1757–1800. [https://herbarioamo.org/index\\_archivos/Fascicle17\(2\).pdf](https://herbarioamo.org/index_archivos/Fascicle17(2).pdf)
- Hágsater E, Santiago E [Eds] (2020b) The Genus *Epidendrum*, Part 14, Icones Orchidacearum 18(1): t. 1801–1848. [https://herbarioamo.org/index\\_archivos/Fascicle18\(1\).pdf](https://herbarioamo.org/index_archivos/Fascicle18(1).pdf)
- Hágsater E, Santiago E [Eds] (2021) The Genus *Epidendrum*, Part 14, Icones Orchidacearum 18(2): t. 1849–1900. [https://herbarioamo.org/index\\_archivos/Fascicle18\(2\).pdf](https://herbarioamo.org/index_archivos/Fascicle18(2).pdf)
- Hágsater E, Santiago E [Eds] (2022a) The Genus *Epidendrum*, Part 15, Icones Orchidacearum 19(1): t. 1901–1949. [https://herbarioamo.org/index\\_archivos/Fascicle19\(1\).pdf](https://herbarioamo.org/index_archivos/Fascicle19(1).pdf)
- Hágsater E, Santiago E [Eds] (2022b) The Genus *Epidendrum*, Part 15, Icones Orchidacearum 19(2): t. 1950–1962. [https://herbarioamo.org/index\\_archivos/Fascicle19\(2\).pdf](https://herbarioamo.org/index_archivos/Fascicle19(2).pdf)
- Hágsater E, Soto Arenas MA (2005) *Epidendrum*. In: Pridgeon AM, Cribb PJ, Chase MW, Rasmussen FN (Eds) *Genera Orchidacearum, Epidendroideae* 4. Oxford University, Oxford, 236–251.
- Hágsater E, Sánchez Saldaña L, García-Cruz J [Eds] (1999) The Genus *Epidendrum*, Part 2, Icones Orchidacearum 3: t. 301–400. [https://herbarioamo.org/index\\_archivos/Fascicle3.pdf](https://herbarioamo.org/index_archivos/Fascicle3.pdf)
- Hágsater E, Santiago E, Rodríguez L (2016) *Epidendrum lasiostachyum* (Orchidaceae): A new Colombian species of the *Epidendrum macrostachyum* group. *Lankesteriana* 16(1): 25–35. <https://doi.org/10.15517/lank.v16i1.23621>
- Hágsater E, Granados Mendoza C, Salazar GA, Quiroga-González S, Magallón S, van den Berg C, Moriarty Lemmon E, Lemmon AR (2019) Phylogenomics of *Epidendrum*: untangling a Neotropical mega-diversification. In: Pridgeon AM, Arosamena AR (Eds) *Proceedings of the 22<sup>nd</sup> World Orchid Conference 2017* (Vol. 1). Asociación Ecuatoriana de Orquideología, Guayaquil, 249–254.
- Karremans AP (2020) LCDP – 2019, How to prepare Lankester Composite Dissection Plates (LCDP). [www.researchgate.net/publication/346141908\\_LCDP\\_-\\_2019](http://www.researchgate.net/publication/346141908_LCDP_-_2019)
- Krömer T, Gradstein SR, Acebey A (2007) Diversidad y ecología de epífitas vasculares en bosques montanos primarios y secundarios de Bolivia. *Ecología en Bolivia* 42(1): 23–33.

- MINAM (2015) Guía de identificación de orquídeas con mayor demanda comercial. Editora Image Print, Peru.
- Neill DA, Ríos Paredes M, Torres Montenegro LA, Mori Vargas TJ, Vriesdorp C (2014) Vegetación y flora/Vegetation and flora. In: Pitman N, Vriesdorp C, Alvira D, Markel JA, Johnston M, Ruelas Inzunza E, Lancha Pizango A, Sarmiento Valenzuela G, Álvarez-Loayza P, Homan J, Wachter T, del Campo Á, Stotz DF, Heilpern S (Eds) Perú Cordillera Escalera–Loreto. Rapid Biological and Social Inventories Report 26. The Field Museum, Chicago, 98–119. [292–311, 408–465.]
- Quispe-Melgar HR, Llacua-Tineo YS, Ames-Martínez FN, Huayta D, Lagones Poma KL, Hágsater E (2022) *Epidendrum alejandrinae* (Orchidaceae: Laeliinae), a new species from the high Andean forests of central Peru. *Phytotaxa* 541(3): 217–224. <https://doi.org/10.11646/phytotaxa.541.3.1>
- Roque J, León B (2006) Orchidaceae endémicas del Perú. *Revista Peruana de Biología* 13(2): 759–878. <https://doi.org/10.15381/rpb.v13i2.1953>
- Ruokolainen K, Tuomisto H (1998) Vegetación natural de la zona de Iquitos. In: Kalliola R, Flores Paitán S (Eds) *Geoecología y desarrollo amazónico: estudio integrado en la zona de Iquitos, Perú*. *Annales Universitatis Turkuensis* 114: 253–365.
- Shanee N, Shanee S, Allgas N (2012) Expediente técnico que sustenta el reconocimiento área de conservación privada “Pampa del Burro – Yambrasbamba”. Neotropical Primate Conservation (NPC) y Sociedad Peruana de Derecho Ambiental (SPDA). <https://docplayer.es/227697568-Expediente-tecnico-que-sustenta-el-reconocimiento-area-de-conservacion-privada-pampa-del-burro-yambrasbamba.html>
- Silveira RS, Singer RB, Ferro VG (2023) Pollination in *Epidendrum densiflorum* Hook. (Orchidaceae: Laeliinae): Fraudulent trap-flowers, self-incompatibility, and a possible new type of mimicry. *Plants* 2023(12): e679. <https://doi.org/10.3390/plants12030679>
- Vásquez R, Dodson CH (1982) Orchids of Bolivia, *Icones Plantarum Tropicarum* 6: t. 501–600. Sarasota.



# *Amanoa condorensis* (Phyllanthaceae), a new shrubby species from the Cordillera del Condor in southern Ecuador

John L. Clark<sup>1</sup>, David A. Neill<sup>2</sup><sup>1</sup> Marie Selby Botanical Gardens, 1534 Mound St., Sarasota, FL 34236, USA<sup>2</sup> Universidad Estatal Amazónica, Puyo, Pastaza, EcuadorCorresponding author: John L. Clark ([jclark@selby.org](mailto:jclark@selby.org))

## Abstract

A new species of *Amanoa* (Phyllanthaceae) is described from the sandstone Nangaritza Plateau in the Cordillera del Cóndor Region in southern Ecuador. *Amanoa condorensis* J.L.Clark & D.A.Neill is a small tree, 4 m tall that is only known from the type collection. The new species is distinct by a shrub habit, presence of coriaceous leaves with an acuminate apex, and congested inflorescences. The relatively high elevation of the type locality, presence of an androphore, and the habit as shrub or low tree are an unusual combination for *Amanoa*. The conservation status of *A. condorensis* is assessed as Critically Endangered (CR), based on IUCN Criteria.

## Resumen

Se describe una nueva especie de *Amanoa* (Phyllanthaceae) de la meseta de arenisca de Nangaritza en la región de la Cordillera del Cóndor en el sur de Ecuador. *Amanoa condorensis* J.L.Clark & D.A.Neill es un pequeño árbol de 4 metros de altura que sólo se conoce de la colección tipo. La nueva especie se distingue por la presencia de inflorescencias congestionadas, hojas coriáceas con ápice acuminado, y porte arbustivo. La elevación relativamente más alta de la localidad tipo, la presencia de un andróforo, y el hábito de arbusto o árbol pequeño son una combinación inusual para *Amanoa*. El estado de conservación de *A. condorensis* se evalúa como En Peligro Crítico (CR) según los Criterios de la UICN.

**Key words:** Andean tepui, Andes, androphore, Ecuador, Nangaritza Plateau, Phyllanthaceae, taxonomy



Academic editor: Alexander Sennikov

Received: 12 April 2023

Accepted: 12 May 2023

Published: 2 June 2023

Citation: Clark JL, Neill DA (2023) *Amanoa condorensis* (Phyllanthaceae), a new shrubby species from the Cordillera del Condor in southern Ecuador. *PhytoKeys* 227: 89–97, <https://doi.org/10.3897/phytokeys.227.104703>

Copyright: © John L. Clark & David A. Neill. This is an open access article distributed under terms of the CC0 Public Domain Dedication.

## Introduction

*Amanoa* Aublet is a genus with a trans-Atlantic disjunct distribution. Most species of *Amanoa* are endemic to the Neotropics (14 species presently known: Ulloa Ulloa et al. (2018)) and two species are endemic to Africa. The most recent monograph is by Pax and Hoffman (1922) and, at that time, *Amanoa* comprised nine species. An overview of the Neotropical members of *Amanoa* was provided by Hayden (1990), who summarized and evaluated all currently-recognized taxa from the Neotropics. Hayden (1990) designated taxonomic typifications, updated circumscriptions with synonyms, and described four new

species. An additional endemic species to Pará State of Brazil was discovered and described by Secco (2014) and an update to the Brazilian species of *Amanoa*, with detailed descriptions and illustrations, was provided by Secco et al. (2014). This included the resurrection of *A. pubescens* Steyerm. which was later placed in synonymy with *A. almerindae* Leal (Secco and Rosário 2016). The description of *Amanoa condorensis* brings the number of *Amanoa* to 17 species, of which 15 are Neotropical in distribution.

Phylogenetic studies (Wurdack et al. 2004; Hoffmann et al. 2006) support the placement of *Amanoa* in Phyllanthaceae Martynov subfamily Phyllanthoideae, tribe Brideliae Müll. Arg., subtribe Amanoinae Pax & K. Hoffm. *Amanoa* is the only genus currently recognized in subtribe Amanoinae. A detailed overview of the morphological characters that define *Amanoa* was summarized by Hayden (1999). Several field-based vegetative and reproductive features help identify *Amanoa*, such as the presence of two-ranked leaves and intrapetalous stipules. Other vegetative characters that *Amanoa* species share include coriaceous leaves that are evergreen, glabrous and with entire margins. The flower morphology for the Neotropical members of *Amanoa* is remarkable for the presence of an extra-staminal nectary and sessile stigmas (Hayden 1990). The presence of a short androphore is sometimes present. The flowers usually consist of showy sepals and highly-reduced petals that are difficult to see without a 10× hand lens.

## Materials and methods

Plants were vouchered and photographed during a 2017 field expedition to Ecuador. Specimens were deposited at the Universidad Estatal Amazónica (**ECUAMZ**), Marie Selby Botanical Gardens (**SEL**) and the Smithsonian Institution's National Museum of Natural History (**US**). Digital images were taken of live specimens in the field using a Nikon D100 DSLR with a Nikon 105 mm lens and a Nikon SB-29s ring flash. Morphological observations and measurements were made from live collections and herbarium specimens.

We assessed the extinction risk of *Amanoa condorensis* following the IUCN (2012) and guidelines of the IUCN Standards and Petitions Committee (2022). We considered observations, collection localities, and population estimates from fieldwork. Species extent of occurrence (EOO) and area of occupancy (AOO) were calculated using GeoCAT (Bachman et al. 2011; <http://geocat.kew.org/>) with the default setting of 2 km<sup>2</sup> grid.

## Taxonomic treatment

***Amanoa condorensis* J.L.Clark & D.A.Neill, sp. nov.**

urn:lsid:ipni.org:names:77320398-1

Figs 1, 2

**Diagnosis.** Amongst the Neotropical species of *Amanoa*, *A. condorensis* shares with *A. almerindae* Leal. and *A. caribaea* Krug & Urb. the presence of an androphore, formed from the fusion of the basal filaments. Differs from *Amanoa almerindae* by the densely pubescent and more widely-spaced flowers along an inflorescence axis 5.5–11 cm long in *A. almerindae* vs. nearly glabrous inflo-

rescence axis to 4.5 cm long in *A. condorensis*. Differs from *A. caribaea* by the presence of inflorescences in an elongate erect raceme appearing congested throughout vs. inflorescences in elongate erect spikes with evenly-spaced fascicles (i.e. not congested throughout) in *A. caribaea*.

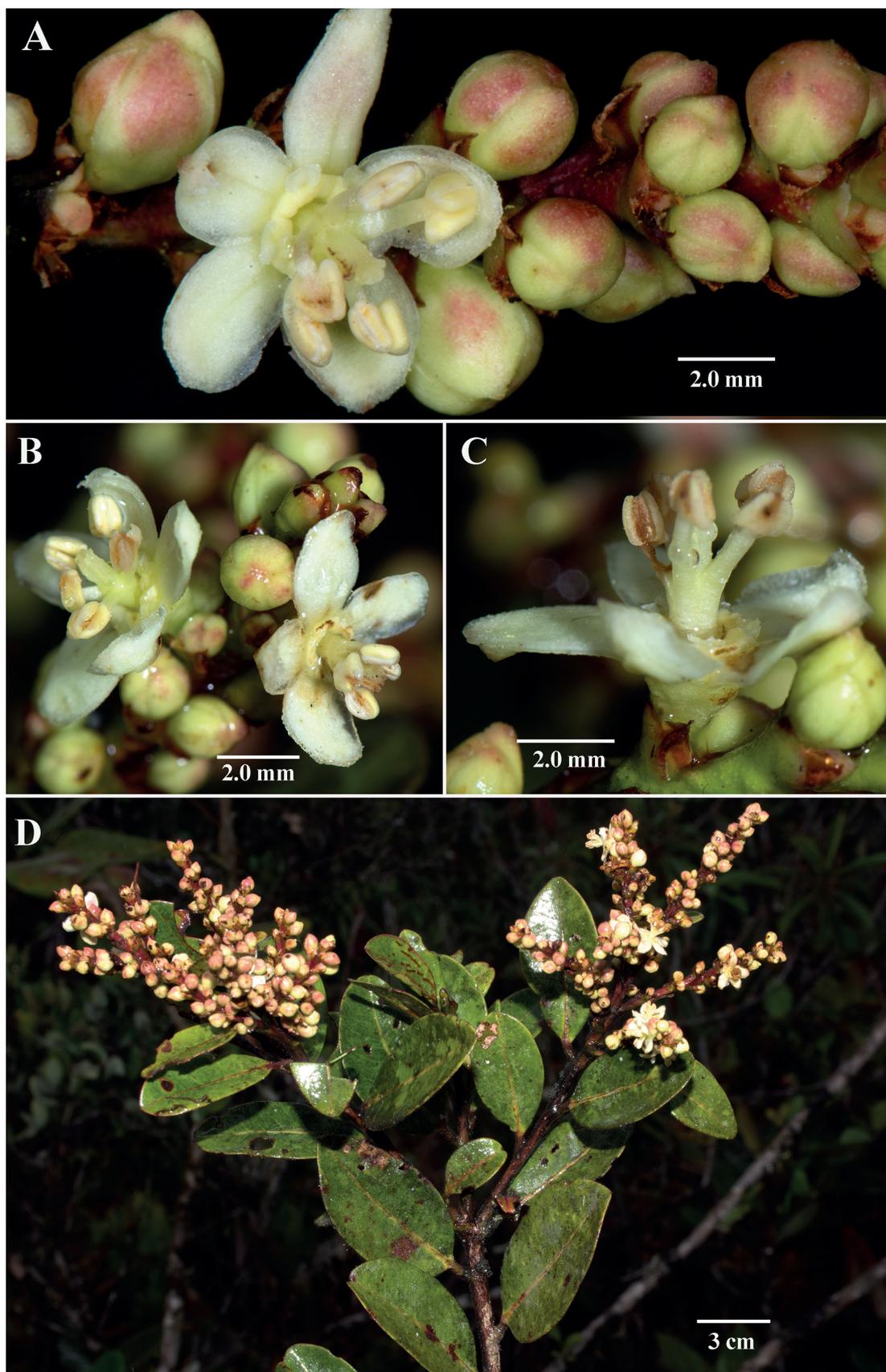
**Type. ECUADOR. Zamora-Chinchipe:** Nangaritza Cantón, Cordillera del Cóndor, trail west of Cabañas Yankuam in conservation area that is owned/operated by ATASMO (Asociación de Trabajadores Autónomos San Miguel de las Orquídeas). Forested tepui (sandstone plateau). Summit ridge and sandstone cliff face. Low scrub and elfin forest, canopy mostly 2–3 m tall, occasional emergent trees to 5 m, 4°15'47.5"S, 78°41'28.1"W, 1840 m elev., 10 Mar 2017, J.L. Clark, J.A. Mayr & D.A. Neill 15257 (holotype: ECUAMZ [08582]; isotypes: SEL [120063], US).

**Description.** Tree, 4 m tall. **Leaves** 1.2–2.5 × 3–4.5 cm, oblong to ovate, coriaceous, glabrous, secondary venation suppressed adaxially when live and becoming prominent when dry, abaxial secondary venation prominent when live and dry, sparsely pubescent on abaxial and adaxial surface, blade flat, base narrowly cuneate to acute, apex acute; petiole 4–8 mm long, slender, black, rugose, sparsely pilose, sometimes appearing sessile from the intrapetiolar stipule; stipules conspicuous, to 0.5 mm long, triangular and glabrous. **Inflorescence** terminal or lateral, to 4.5 cm long, in congested erect elongate raceme-like inflorescences derived from reduced cymules, the primary inflorescence branch dark black, nearly glabrous to sparsely pubescent with short curved trichomes of 3–5 cells, each flower or pair of flowers subtended by a prominent brown triangular bracteole, 2–3 mm long and glabrous. **Staminate flowers** actinomorphic, 5-merous, 6.5–7.5 mm in diam. during anthesis, on short pedicels and appearing sessile; sepals 3.0–3.5 × 1.5–2.0 mm, broadly ovate, glabrous, white; petals ca. 1 × 1.5 mm, reniform, margins entire, glabrous; androecium surrounded by a prominent hypogynous extra-staminal disc, stamens fused at base, forming a short androphore, filaments 1.5–2 mm long, anthers 1–2 mm long, dehiscing longitudinally; pistillode ca. 2.5 mm long with trilobed apex, mature gynoecium or pistillate flowers not observed. Fruits not observed.

**Phenology.** Mature male flowers were observed in March.

**Etymology.** The specific epithet is derived from the Cordillera del Cóndor mountain range in southern Ecuador where this species is presumably endemic.

**Distribution and associated vegetation.** *Amanoa condorensis* is only known from the type collection. It is presumed endemic to the Cordillera del Condór from where it was collected during a collaborative field course in 2017 with the Lawrenceville School (Lawrenceville, NJ, USA) and the Universidad Estatal Amazónica (Puyo, Ecuador). The type locality is situated at the summit ridge of a sloping plateau (1840 m elevation) west of the upper Nangaritza River, with nutrient-poor soil derived from the Cretaceous Hollín sandstone formation. The vegetation at the site is a low, dense scrub, dominated by shrubs and low trees 3–5 m high. These environments in the Cordillera del Cóndor and other mountain ranges east of the main Andean chain in Ecuador and Peru have been referred to as “Andean tepuis” in recognition of the similarity in vegetation and some phytogeographic connections with the low-nutrient sandstone tepuis of the Guiana Shield Region (Neill et al. 2014; Neill 2018). Associated plants at the collection site include the local endemic *Blakea nangaritzana* D.Fernández, C.Ulloa & Penneys (Melastomataceae) as well as other species that are



**Figure 1.** *Amanoa condorensis* J.L.Clark & D.A.Neill **A–C** mature staminate flower featuring prominent sepals, reduced petals, extra-staminal disc and androphore **D** shoot featuring two-ranked foliage and congested inflorescences. (**A–D** J.L. Clark, D.A. Neill & J. Mayr 15257). Photos by John L. Clark.

common in Andean tepui elfin forest vegetation at 1500–2000 m elevation, including *Godoya obovata* Ruiz & Pav. (Ochnaceae), *Ternstroemia circumscissilis* Kobuski (Pentaphragmaceae), *Macroparpea innarrabilis* J.R. Grant (Gentianaceae), *M. ericii* J.R. Grant (Gentianaceae), *Cybianthus magnus* (Mez) Pipoly (Primulaceae), *Podocarpus tepuiensis* J. Buchholz & N.E. Gray (Podocarpaceae), *Ladenbergia franciscana* C.M. Taylor (Rubiaceae), *Pterozonium brevifrons* (A.C. Sm.) Lellinger (Pteridaceae) and *Everardia montana* Ridl. (Cyperaceae).

**Preliminary assessment of conservation status.** The type locality is located within a community-based protected forest managed by the Asociación de Trabajadores Autónomos San Miguel de las Orquídeas (ATASMO) on the remote summit ridge of a sloping Andean tepui at 1840 m elevation, accessible via a 6 km trail from the Cabañas Yankuam (= Yankuam Lodge) located at 890 m elevation on the banks of the Río Nangaritzá. Yankuam is a family-owned lodge specializing in bird tours and ecotourism. The Río Nangaritzá is at risk from ongoing illegal mining. Many of the areas visited in 2017 (especially along the Río Nangaritzá) have been invaded by illegal mining operations. The forest that corresponds to the only known population of *Amanoa condorensis* is protected by the local community, which was granted this jurisdiction by the Ministry of Environment of Ecuador. Between 2017 and 2019 (three years), annual field courses were run with Cabañas Yankuam and the local community to different sandstone tepuis. *Amanoa condorensis* was only observed once throughout three consecutive years of field courses. Following the IUCN (2012) and guidelines of the IUCN Standards and Petitions Committee (2022), *Amanoa condorensis* is categorized as Critically Endangered (CR), based on the following criteria: B1, B2 ab (all criteria), area of occupancy (AOO) is calculated at 4 km<sup>2</sup> (criterion B2 < 10 km<sup>2</sup>). The species is known only from the type collection; it is hoped that this publication will stimulate more intensive search for additional material near the type locality and on other Andean tepuis in the region, including specimens with pistillate flowers.

**Comments.** Most species of *Amanoa* are canopy to sub-canopy trees in the lowland tropics. The only other species that is known to occur above 1000 m is *Amanoa steyermarkii* Jabl. in the riparian and tepui forests of the Venezuelan Guayana Region at 1500–2100 m elevation (Hayden 1999). *Amanoa condorensis* was collected above 1800 m. *Amanoa condorensis* differs from *A. steyermarkii* by its sessile staminate flowers (vs. pedicellate flowers in *A. steyermarkii*) and its congested inflorescence (vs. the relatively lax inflorescence in *A. steyermarkii*). It also differs in its shrubby habit (vs. trees in *A. steyermarkii*).

*Amanoa condorensis* differs from most other congeners in its relatively small height of 4 m. Most other *Amanoa* species are understory to emergent canopy trees above 12 m tall (e.g. *A. guianensis* Aubl. reaches 35 m tall). It is also distinguished by the relatively small, thick and sclerophyllous leaves, characters that are shared by many plants in different genera that occur in the dense scrub vegetation of the Andean tepuis (Neill et al. 2014) and that may be an adaptation to the nutrient-poor sandy soils of these habitats. The two other *Amanoa* species that are recorded as shrubs or small trees include *A. cupatensis* Huber and *A. almerindae*; both species are endemic to the white-sand areas of the Rio Orinoco-Casiquiare lowlands and the adjacent Río Negro lowlands in Amazonas State of Venezuela and Amazonas State of Brazil. *Amanoa cupatensis* is a low shrub less than 2 m tall. *Amanoa condorensis* differs from *A. cupatensis*



Figure 2. Holotype (ECUAMZ) of *Amanoa condorensis* J.L.Clark & D.A.Neill.

by the presence of an acute leaf apex (vs. rounded to emarginate leaf apex in *A. cupatensis*).

*Amanoa condorensis* shares the following characters with other congeners: an extra-staminal disc (Fig. 1), intrapetiolar stipules, and a showy perianth represented by conspicuous sepals and inconspicuous petals (Fig. 1). The petals are only apparent with a 10× hand lens or higher magnification (Fig. 1A). The intrapetiolar stipules in *A. condorensis* are conspicuous on herbarium specimens and in the field.

*Amanoa condorensis* has an androphore, a structure formed by the basal fusion of the filaments (Fig. 1C), a character that is only reported for two additional species: *A. almerindae* and *A. caribaea* Krug & Urb. The inflorescence of *A. caribaea* is an elongate spike-like inflorescence with broadly spaced fascicles of numerous flowers. In contrast, *A. condorensis* has congested inflorescences, but never more than two flowers per bracteole. *Amanoa caribaea* is endemic to the Caribbean (Dominica and Guadeloupe), where it is reported as a common co-dominant important timber tree in native forests of Dominica (Nicolson 1991).

*Amanoa pubescens* was previously considered a synonym of *A. almerindae*, but was separated and resurrected by Secco et al. (2014), based on the presence of an androphore in *A. pubescens* and its absence in *A. almerindae*. However, Secco and Rosário (2016) re-examined the type material of both taxa and determined that *A. almerindae* does possess an androphore that is evident in open staminate flowers, but not in bud. As a result, Secco and Rosário (2016), once again, reduced *A. pubescens* to synonymy with *A. almerindae*. *Amanoa almerindae* differs from *A. condorensis* in its thinner, larger more widely-spaced leaves, and more elongate inflorescences with more broadly spaced fascicles (vs. thick, sclerophyllous, smaller leaves and short, congested inflorescence in *A. condorensis*).

Hayden (1990) reported that most flowers in *Amanoa* are protandrous and species can be either monoecious or dioecious. Only two Neotropical species are known to be dioecious: *A. glaucophylla* Müll.Arg of Amazonian and coastal Brazil, as well as Amazonian Colombia and Venezuela and *A. anomala* Little, endemic to the Pacific coast of Ecuador. The remaining species are presumed to be monoecious, but this has not been confirmed for most species. The flowers featured here (Fig. 1) have mature androecia with vestigial gynoecia. Therefore, if the species is monoecious, we expect the pistillate flowers would appear at a later stage. If dioecious, then separate staminate and pistillate individuals would be expected.

## Acknowledgements

We are grateful to Steve Ginzburg from The University of Alabama Herbarium (UNA) for processing our plant specimens. The participants from the 2017 Lawrenceville School in Ecuador program are acknowledged for their engagement in learning field biology and the science of biodiversity. Special thanks to the Asociación de Trabajadores Autónomos San Miguel de las Orquídeas (ATASMO) for providing access to their reserve. We are especially grateful for logistical support from our local guides, Segundo Velez, Iván Merino, Laura Merino, María Tillaguango and Luis Jiménez. We are also grateful to Clara

Guillermina León García and Carlos Humberto Gálvez Guamán from Cabañas Yankuam (Yankuam Lodge) for hosting us throughout three consecutive years of field courses. We thank Yeison Londoño-Echeverri and Ana María Trujillo López (Herbario Nacional Colombiano) for facilitating the initial determination of our field collection. We thank Paul Berry and Ricardo de Secco for their constructive comments on an earlier version of the manuscript.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

JLC and DN wrote the manuscript and conducted the field work.

### Author ORCIDs

John L. Clark  <https://orcid.org/0000-0002-1414-6380>

David A. Neill  <https://orcid.org/0000-0002-5143-9430>

### Data availability

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

## References

- Bachman S, Moat J, Hill A, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Hayden WJ (1990) Notes on Neotropical *Amanoa* (Euphorbiaceae). *Brittonia* 42(4): 260–270. <https://doi.org/10.2307/2806814>
- Hayden WJ (1999) *Amanoa*. In: Berry PE, Yatskievych K, Holst BK (Eds) *Flora of the Venezuela Guyana* (Vol. 5) Eriocaulaceae–Lentibulariaceae. Missouri Botanical Garden Press. St. Louis, Missouri, 95–99.
- Hoffmann P, Kathriarachchi H, Wurdack KJ (2006) A Phylogenetic Classification of Phyllanthaceae (Malpighiales; Euphorbiaceae *sensu lato*). *Kew Bulletin* 61: 37–53.
- IUCN (2012) *IUCN Red List Categories and Criteria: Version 3.1*. (2<sup>nd</sup> edn.). Gland, Switzerland and Cambridge.
- IUCN Standards and Petitions Committee (2022) *Guidelines for using the IUCN Red List Categories and Criteria. Version 15.1*. <https://www.iucnredlist.org/resources/redlist-guidelines>
- Neill DA (2018) Flora y vegetación de los “Tepuyes Andinos”: Endemismo, diversidad y conexiones fitogeográficas con el Escudo Guayanés. *Memorias del XII Congreso Latinoamericano de Botánica*, Quito, Ecuador, 17–18.

- Neill DA, Rios Paredes M, Torres Montenengro LA, Mori Vargas TJ, Vriesendorp C (2014) Vegetación y Flora/Vegetation and flora. In: Pitman N, Vriesendorp C, Alvira D, Markel JA, Johnston M, Ruelas Inzunza E, Lancha Pizango A, Sarmiento Valenzuela G, Álvarez-Loayza P, Homan J, Wachter T, del Campo Á, Stotz DF, Heilpern S (Eds) Peru: Cordillera Escalera-Loreto. Rapid Biological and Social Inventories Report 26. The Field Museum, Chicago, 98–119. [292–311, 408–465.]
- Nicolson DH (1991) Flora of Dominica, Part 2: Dicotyledoneae. *Smithsonian Contributions to Botany* 77: 1–274. <https://doi.org/10.5479/si.0081024X.77>
- Pax F, Hoffman K (1922) Euphorbiaceae-Phyllanthoideae-Phyllanthaceae. *Amanoa*. In: Engler A (Ed.) *Das Pflanzenreich* IV. 147. XV (Heft 81): 195–199.
- Secco R de S (2014) A New Species of *Amanoa* (Phyllanthaceae) from Para State, Amazonian Brazil. *Systematic Botany* 39(1): 235–238. <https://doi.org/10.1600/036364414X678242>
- Secco R de S, Campos J de M, Hiura A de L (2014) Taxonomia atualizada de *Amanoa* (Phyllanthaceae) no Brasil. *Acta Amazonica* 44(1): 25–44. <https://doi.org/10.1590/S0044-59672014000100004>
- Secco R de S, Rosário AS (2016) Notes on the identity of *Amanoa pubescens* Steyerem. (Phyllanthaceae). *Brazilian Journal of Biosciences* 14: 45–48.
- Ulloa Ulloa C, Acevedo-Rodríguez P, Beck SG, Belgrano MJ, Bernal R, Berry PE, Brako L, Celis M, Davidse G, Forzza RC, Gradstein SR, Hokche O, León B, León-Yáñez S, Magill RE, Neill DA, Nee MH, Raven PH, Stimmel H, Strong MT, Villaseñor JL, Zarucchi JL, Zuloaga FO, Jørgensen PM (2017) [Onwards]. An integrated assessment of vascular plant species of the Americas. *Science* 358(6370): 1614–1617. <https://doi.org/10.1126/science.aao0398>
- Wurdack KJ, Hoffmann P, Samuel R, de Bruijn A (2004) Molecular phylogenetic analysis of Phyllanthaceae (Phyllanthoideae pro parte, Euphorbiaceae *sensu lato*) using plastid *RBCL* DNA sequences. *American Journal of Botany* 91(11): 1882–1900. <https://doi.org/10.3732/ajb.91.11.1882>



# Morphology and molecular phylogeny of *Pleurosigma pacificum* sp. nov. (Pleurosigmataceae), a new tropical pelagic species from the Western Pacific Ocean

Fei-Chao Du<sup>1,2\*</sup>, Yu-Hang Li<sup>1\*</sup>, Kui-Dong Xu<sup>1,2,3</sup>

1 Laboratory of Marine Organism Taxonomy and Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Shandong Province Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

2 University of Chinese Academy of Sciences, Beijing 100049, China

3 Laboratory for Marine Biology and Biotechnology, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266237, China

Corresponding author: Kui-Dong Xu ([kxu@qdio.ac.cn](mailto:kxu@qdio.ac.cn))

## Abstract

A new species of pelagic diatom, *Pleurosigma pacificum* sp. nov., is described from the tropical Western Pacific Ocean. It has the typical features of *Pleurosigma*, including a slightly sigmoid raphe, intersected transverse and oblique striae, and loculate areolae with external opening slits and internal poroids. Morphologically, *P. pacificum* belongs to a species group of *Pleurosigma* with lanceolate valves, including *P. atlanticum* Heiden & Kolbe, *P. nubecula* W. Smith, *P. indicum* Simonsen, and *P. simonsenii* Hasle. However, *P. pacificum* differs by its smaller lanceolate valve and smaller intersection angle as well as elliptical areolae without a silica bar. The SSU rDNA and *rbcL* sequence data place *P. pacificum* in a basal position relative to other species of *Pleurosigma*. Our molecular phylogenetic analyses did not support the monophyly of lanceolate and slightly sigmoid species. Thus, the sigmoidality of valve outline cannot be considered as a criterion to define the species group.

**Key words:** Marine diatoms, morphology, new species, phylogeny, *Pleurosigma*, Western Pacific Ocean



Academic editor: Bing Liu

Received: 22 March 2023

Accepted: 18 May 2023

Published: 2 June 2023

**Citation:** Du F-C, Li Y-H, Xu K-D (2023) Morphology and molecular phylogeny of *Pleurosigma pacificum* sp. nov. (Pleurosigmataceae), a new tropical pelagic species from the Western Pacific Ocean. *PhytoKeys* 227: 99–108, <https://doi.org/10.3897/phytokeys.227.103890>

**Copyright:** © Fei-Chao Du et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

Smith (1852) established the genus *Pleurosigma* W. Smith for some sigmoid naviculoid diatoms. Peragallo (1891) clarified the infrageneric delimitation by combining the orientation of the striae and their angle of the intersection. Species with transverse and oblique striae were separated from those with transverse and longitudinal striae as well as species with centrally interrupted striae. Subsequently, Cleve (1894) transferred all those species with transverse and longitudinal striae into the genus *Gyrosigma* and retained species with transverse and oblique striae in the genus *Pleurosigma*. Hendey (1964) gave a clearer delimitation of *Pleurosigma* and provided chloroplast characters. Round et al. (1990) and Reid (2012) used ultrastructural features for their description of *Pleurosigma*. Currently, *Pleurosigma* is characterized by having two or four ribbon-like plastids, (slightly) sigmoid valves, transverse and two obliquely intersecting

\* These authors contributed equally to this work.

striae and loculate areolae with external opening slits and internal poroids (Round et al. 1990; Reid and Williams 2003; Sterrenburg et al. 2005; Reid 2012). To date, this genus contains more than 700 named taxa (Kocielek et al. 2021).

*Pleurosigma* is a group of diatoms that is widely distributed in brackish to marine environments (Round et al. 1990; Sterrenburg et al. 2003). It is predominantly found as a large population on sediments (Reid 2012) with a sigmoid valve or raphe, but some *Pleurosigma* species have lanceolate or nearly straight valves and are commonly found in planktonic samples. Metabarcoding data have revealed that *Pleurosigma* species are highly diverse in pelagic ocean (Malviya et al. 2016). However, only five species are known to be pelagic, namely *P. antarcticum* Grunow, *P. atlanticum* Heiden & Kolbe, *P. indicum* Simonsen, *P. simonsenii* Hasle and *P. directum* Grunow (Cleve and Möller 1877–1882; Heiden 1928; Simonsen 1974; Sar et al. 2012).

In this paper, we describe a new species of *Pleurosigma* isolated from the tropical Western Pacific Ocean by using light microscopy (LM) and scanning electron microscopy (SEM). Its phylogenetic position is determined by DNA sequence.

## Materials and methods

### Sampling, cultivation and morphological observation

Phytoplankton samples were collected from upper 200 m water column by using a phytoplankton net (64 µm mesh), on the Western Pacific Ocean (7°0.26'N, 141°59.63'E). Single cells of diatoms were isolated using capillary pipettes and cultivated in F/2 medium. Cultures were maintained at 24–26 °C under a light intensity of 120–150 µmol photon/m<sup>2</sup>/s, with a light/dark cycle of 12:12 h. Five milliliters of vegetative cells were fixed with 2.5% glutaraldehyde and then cleaned with hydrogen peroxide (Trobajo and Mann 2019). For LM observation, cleaned samples were mounted on glass slides with Mountmedia (Wako Pure Chemical Industries, Ltd., Osaka, Japan). A Zeiss Imager Z2 microscope (Carl Zeiss Microimaging GmbH, Jena, Germany) with differential interference contrast (DIC) was used for LM observation. The measurement methods of the raphe angle and the intersection angle of the oblique striae followed Sterrenburg (1991). For SEM observations, specimens were placed on coverslips, air-dried and coated with osmium. A Hitachi S-4800 (Hitachi, Ltd., Tokyo, Japan) was used for SEM observation.

### DNA extraction and sequencing

The DNA was extracted and sequenced according to the method described in Li et al. (2022). Algal cell pellets were obtained by centrifuged 10 mL diatom cultures at 5,000 g for 5 min. Total DNA was extracted by using the Plant Genomic DNA Kit (Tiangen Biotech Co., Beijing, China). The small-subunit ribosomal DNA (SSU rDNA), large-subunit ribosomal DNA (LSU rDNA), chloroplast-encoded genes *rbcL* and *psbC* were amplified by polymerase chain reaction (PCR). Forward and reverse strands were amplified using the follow primers (Table 1). The PCR cycles of the four markers follow Alverson et al. (2007). The PCR products were purified using TIANGel Midi Purification Kit (Tiangen Biotech Co., China) and sequenced by Tsingke Biotechnology Co.,Ltd. (Beijing, China).

**Table 1.** Primers used to amplify SSU rDNA, LSU rDNA, *rbcL* and *psbC* fragments for *P. pacificum*.

Name	Marker	Sequence (5' to 3')	Reference
SSU1	SSU	AACCTGGTTGATCCTGCCAGT	(Medlin et al. 1988)
ITS1DR	SSU	CCTTGTTACGACTTCACCTTCC	(Edgar and Theriot 2004)
D1R	LSU	ACCCGCTGAATTTAAGCATA	(Scholin et al. 1994)
D3Ca	LSU	ACGAACGATTTGCACGTCAG	(Lenaers et al. 1989)
<i>rbcL</i> 66+	<i>rbcL</i>	TTAAGGAGAAATAAATGTCTCAATCTG	(Alverson et al. 2007)
<i>rbcL</i> 1444-	<i>rbcL</i>	GCGAAATCAGCTGTATCTGTW G	(Ruck and Theriot 2011)
<i>psbC</i> +	<i>psbC</i>	CACGACCWGAATGCCACCAAT	(Alverson et al. 2007)
<i>psbC</i> -	<i>psbC</i>	ACAGGTTYGCTTGGTGGAGTGG	(Alverson et al. 2007)

### Molecular phylogenetic analyses

To examine the phylogenetic position of *P. pacificum*, a two-gene dataset (SSU rDNA–*rbcL*) including 30 recognized species and 12 unnamed strains, was used to construct the phylogenetic trees (Suppl. material 1). Due to the lack of LSU rDNA and *psbC* data of most *Pleurosigma* species in GenBank, the two genes were not used for the phylogenetic analysis. Since a previous molecular phylogenetic study indicates that Pleurosigmataceae is closely related to *Haslea* and *Navicula* (Li et al. 2017), we selected all the available sequence of Pleurosigmataceae and *Haslea* species in GenBank for analysis. For *Navicula* species, we selected sequences of species with voucher slides or reliable morphological data.

The SSU rDNA and *rbcL* sequences were aligned using MAFFT v.7.313 (Katoh and Standley 2013) with normal mode and Q-INS-I strategy which considered the secondary structure of RNA, respectively. The trimAl was used to trim the alignment with parameter automated1 (Capella-Gutiérrez et al. 2009). The final concatenated alignment included 2,224 positions, of which 1,535 columns were SSU rDNA and 689 were *rbcL*. PartitionFinder 2 was used to select best-fit models for ML and BI analysis (Lanfear et al. 2017), according to the Bayesian information criterion (BIC). The *rbcL* gene was partitioned by codon position. IQ-TREE v.1.6.8 (Nguyen et al. 2015), MrBayes v.3.2.7 (Huelsenbeck and Ronquist 2001) and TNT v.1.6 (Goloboff and Morales 2023) were used to perform maximum likelihood (ML), Bayesian inference (BI) and maximum parsimony (MP) analysis, respectively. The ML analysis with 1,000 bootstrap was executed with the default settings. The BI program was run for 10<sup>7</sup> generations with samples every 1,000 generations and the first 25% of trees were discarded as burn-in. Convergence was judged based on the average standard deviation of split frequencies (all less than 0.01) and the ESS values (more than 3,000) were analyzed in the R package RWTY (Warren et al. 2017). The consensus topology and posterior probabilities of all branches were derived from the remaining trees using a majority-rule consensus approach. In the MP analysis, we used a traditional search with TBR branch swapping on 1,000 replicates and holding 10 trees per replication. The resulting 31 most parsimonious trees (MPTs) were used to calculate a strict consensus tree; Standard bootstrap and Jackknife (with 35 removal probability) analyses were performed using a traditional search and 1,000 replicates, with outputs saved as frequency differences. FigTree v.1.4.4 and Adobe Illustrator were used to view and edit trees.

## Results

### *Pleurosigma pacificum* sp. nov.

Fig. 1, Table 2

**Description.** Valves lanceolate, gradually tapering towards the subacute ends, 45.0–51.5  $\mu\text{m}$  long and 13.0–15.6  $\mu\text{m}$  wide (Fig. 1A–D). Raphe filiform, straight, slightly curved near poles (Fig. 1A–D). Raphe angle  $+2^\circ$  to  $+4^\circ$ . Valve center roundish (Fig. 1E, arrowhead). Terminal area funnel-shaped (Fig. 1F). Transverse striae straight, parallel throughout, 21–22 in 10  $\mu\text{m}$ , oblique striae 21–23 in 10  $\mu\text{m}$ , intersecting at an angle between  $32^\circ$  to  $35^\circ$ .

In SEM, internally, raphe fissures terminate in helictoglossae at apices, orientated in opposite direction to one another (Fig. 1G, I, arrowhead). Internal central fissures straight, slightly expanded (Fig. 1H, arrowhead). Central nodule is raised and flanked by two central bars (Fig. 1H). External central raphe fissures straight, simple (Fig. 1K, arrowhead). Terminal fissures bent to opposite side of valve, not extending onto valve mantle (Fig. 1L, arrowhead). Areolae loculate with external opening slits and internal poroids (Fig. 1G, J).

**Holotype.** MBMCAS286904, an example is illustrated in Fig. 1A, E, F. This slide was deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China.

**Isotype.** MBMCAS286905, an example is illustrated in Fig. 1C. This slide was deposited in the Marine Biological Museum, Chinese Academy of Sciences, Qingdao, China.

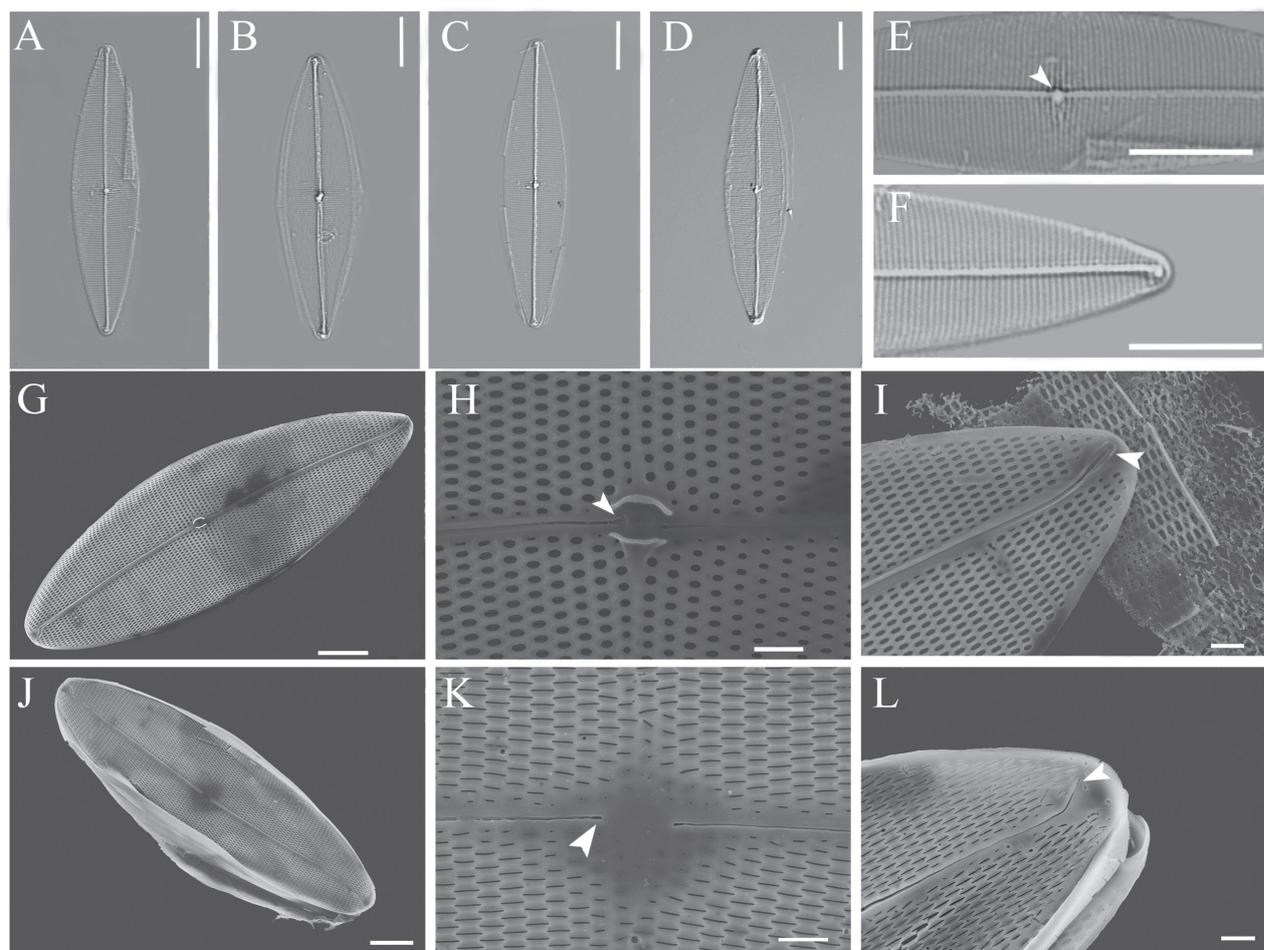
**Type locality.**  $7^\circ 0.26'N$ ,  $141^\circ 59.63'E$ , the upper 200 m water column in the tropical Western Pacific Ocean.

**Etymology.** Named after the Pacific Ocean where the species was discovered.

**Table 2.** Comparison of morphological features of *Pleurosigma pacificum* sp. nov. with similar species.

Characteristics	<i>P. pacificum</i> sp. nov.	<i>P. simonsenii</i> <sup>#</sup>	<i>P. indicum</i>	<i>P. atlanticum</i>	<i>P. nubecula</i>
Length ( $\mu\text{m}$ )	45.0–51.5	300–600	70–90	69–76	82–85
Width ( $\mu\text{m}$ )	13.0–15.6	40–75	8–11	13.0–16.5	16
Raphe angle	$2-3^\circ$	ND	$2.5-2.6^\circ$	$1.2^\circ$	$1.2-1.9^\circ$
Transverse striae in 10 $\mu\text{m}$	21–22	28–30	23–28	20	25–26
Oblique striae in 10 $\mu\text{m}$	21–23	30	20–24	20	23–25
Stria angle	$32-35^\circ$	$60^\circ$	$44-48^\circ$	$60^\circ$	$60-61^\circ$
Valve outline	lanceolate	Lanceolate, slightly sigmoid	Lanceolate, slightly sigmoid	Lanceolate	Narrowly lanceolate
Raphe	Straight, slightly deflected near the apices	Straight, sigmoid before the ends	Straight, eccentric towards the ends	Straight, slightly deflected at poles	Very slightly deflected
Apices	Subacute	very acute	Subacute	Blunt rounded obtuse	Subacute
Internal view areolae	elliptical without bars	ND	elliptical, bisected by a narrow silica bar	ND	elliptical, bisected by a narrow silica bar
Sources	This study (n = 20)	Simonsen (1974)	Simonsen (1974); Sar et al. (2012)	Heiden and Kolbe (1928)	Sar et al. (2012)

ND = not documented. <sup>#</sup>Identified as *P. planctonicum* in original description.



**Figure 1.** A–F LM photographs of *P. pacificum* A–D cleaned frustules showing parallel transverse striae under LM E valve center showing a roundish central area (arrowhead) F funnel-shaped terminal area in apical position G–L SEM photographs of *P. pacificum* G internal view of the whole valve H internal valve central area showing straight, slight expanded raphe fissures (arrowhead) and nodule bordered by two arched bars I internal raphe fissures terminate in helictoglossae at the apices (arrowhead) J external view of the whole valve showing the terminal fissures curving into opposite directions K external central area of valve showing straight, simple raphe fissures (arrowhead) L terminal fissures (arrowhead). Scale bars: 10  $\mu\text{m}$  (A–F); 5  $\mu\text{m}$  (G, J); 1  $\mu\text{m}$  (H, I, K, L).

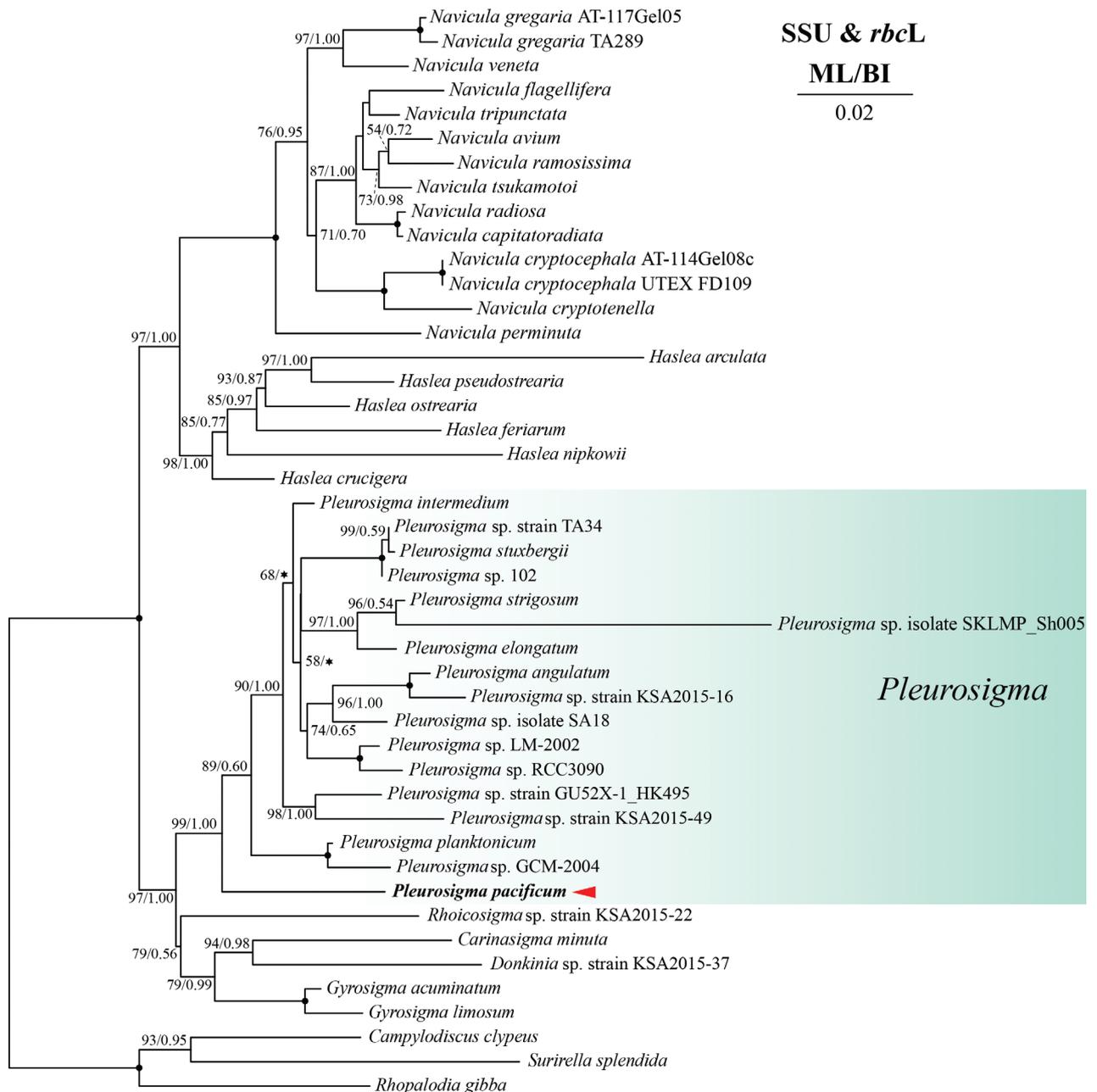
**Distribution and ecology.** *Pleurosigma pacificum* is a planktonic species known only from the type locality. The water temperature was 28.5 °C and salinity about 33.4 during sampling.

**Gene sequences.** These sequences were deposited in the GenBank (SSU rDNA OQ437519, LSU rDNA OQ549922, *rbcL* OQ473490 and *psbC* OQ437519).

**Phycobank registration.** <http://phycobank.org/103761>.

### Molecular phylogenetic analyses

The BLASTn search showed that the SSU rDNA sequence of *P. pacificum* shares 97.65% identity with an uncultured marine eukaryote (KC771201). The *rbcL* gene sequence of *P. pacificum* shares 92.54% identity with *P. intermedium* (NC\_066077). The ML, BI and MP phylogenetic tree based on the concatenated SSU rDNA and *rbcL* gene showed that *P. pacificum* belongs to the clade of the genus *Pleurosigma* with high support (IQ-TREE ultrafast bootstrap value = 99,



**Figure 2.** Maximum likelihood (ML) and Bayesian inference (BI) phylogenetic trees based on the concatenated SSU rDNA and *rbcL* sequences. The values on each node indicate ML bootstrap and Bayesian posterior probabilities (%), respectively. Only bootstrap values over 50% are shown on the tree. Black dot indicate ML/BI = 100/1.00. The asterisk indicates the topological incongruence between ML and BI trees.

Mrbayes posterior probability = 1.00, MP standard bootstrap value = 77 and MP jackknife value = 85). The *P. pacificum* is basal to all other species of *Pleurosigma*, and branched earlier than the two slightly sigmoid species, *P. planktonicum* and *P. intermedium* (Fig. 2, Suppl. material 2).

## Discussion

The valves of *Pleurosigma pacificum* sp. nov. possess intersected transverse and oblique striae, opposite curved raphe distal endings, two internal central

bars, and loculate areolae with an internal poroids and an external slit opening. These are considered to be the main characters of the genus *Pleurosigma* (Hendey 1964; Reid 2002; Sterrenburg et al. 2005). Molecular data place *P. pacificum* in a basal position relative to other species of *Pleurosigma*.

The morphological data place *P. pacificum* in a group of species, which includes *P. nubecula* W. Smith, *P. indicum* Simonsen, *P. simonsenii* Hasle, and *P. atlanticum* Heiden & Kolbe, with lanceolate valves and a straight raphe (Table 2). Among them, *P. pacificum* can be easily distinguished from *P. simonsenii* by its much smaller valves (45.0–51.5  $\mu\text{m}$  vs. 300–600  $\mu\text{m}$  long). *P. pacificum* differs from *P. indicum* as its internal poroids of areolae are not bisected by a central bar (Fig. 1G in this study vs. figs 41 and 42 in Sar et al. 2012), and from *P. atlanticum* and *P. nubecula* by the smaller stria angle (32–35° in *P. pacificum*, 60° in *P. atlanticum* and 60–61° in *P. nubecula*).

The definition of the genus *Pleurosigma* has undergone constant debate and modifications (Cleve 1894; Hendey 1964; Round et al. 1990; Reid 2012). *Pleurosigma* is characterized by its (slightly) sigmoid valve and raphe, two or four ribbon-like chloroplasts, areolae opening to outside by elongate slits and inside by a poroid, areolae arranged in decussate rows, and central internal raphe ending in a central nodule. Reid (2012) indicates that the equal thickening of the raphe sternum on both sides of raphe is a synapomorphic feature of *Pleurosigma* and further revised the generic definition based on morphological phylogenetic analyses. Although Reid (2012) did not include any slightly sigmoid *Pleurosigma* species, recent studies and the present work showed that all these lanceolate and slightly sigmoid *Pleurosigma* species share this synapomorphic feature as well as the other features mentioned above (Sar et al. 2012; Sterrenburg et al. 2015). However, our molecular phylogenetic analyses did not support the monophyly of these lanceolate and slightly sigmoid species (Fig. 2, Suppl. material 2). Therefore, the sigmoidality of valve outline cannot be considered as a criterion to define the species group.

## Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant numbers 42276099 and 31800171). This work was also supported by Oceanographic Data Center, Institute of Oceanology, Chinese Academy of Sciences. We are very grateful to two reviewers and the editors for their careful revisions and constructive comments. We are also grateful to staff of the Research Vessel *KEXUE* for sample collection.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

## Author contributions

Conceptualization: KDX. Funding acquisition: YHL. Investigation: FCD. Methodology: YHL. Supervision: KDX. Writing - original draft: FCD. Writing - review and editing: YHL, KDX.

## Author ORCIDs

Fei-Chao Du  <https://orcid.org/0009-0005-0674-5761>

Yu-Hang Li  <https://orcid.org/0000-0002-5546-1774>

Kui-Dong Xu  <https://orcid.org/0000-0002-5186-519X>

## Data availability

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

## References

- Alverson AJ, Jansen RK, Theriot EC (2007) Bridging the Rubicon: Phylogenetic analysis reveals repeated colonizations of marine and fresh waters by thalassiosiroid diatoms. *Molecular Phylogenetics and Evolution* 45(1): 193–210. <https://doi.org/10.1016/j.ympev.2007.03.024>
- Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 25(15): 1972–1973. <https://doi.org/10.1093/bioinformatics/btp348>
- Cleve PT (1894) Synopsis of the naviculoid diatoms. *Kongliga Svenska Vetenskaps Akademiens Handlingar* 26(2): 1–194.
- Cleve PT, Möller JD (1877–1882) *Diatoms (Exsiccata)* edited by Cleve PT and Möller JD. Esaias Edquists Boktryckeri, Upsala, 1–38.
- Edgar SM, Theriot EC (2004) Phylogeny of *Aulacoseira* (Bacillariophyta) based on molecules and morphology. *Journal of Phycology* 40(4): 772–788. <https://doi.org/10.1111/j.1529-8817.2004.03126.x>
- Goloboff PA, Morales ME (2023) TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics* 39(2): 144–153. <https://doi.org/10.1111/cla.12524>
- Heiden H (1928) Die marinen diatomeen der Deutschen Sudpolar expedition 1901–3. *Deutsche Sudpolar-Expedition* 8: 447–715.
- Hendey NI (1964) An introductory account of the smaller algae of British coastal waters. Part 5 (Eds) Bacillariophyceae (Diatoms). Her Majesty Stationery Office, London, 1–317.
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17(8): 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kocielek JP, Blanco S, Coste M, Ector L, Liu Y, Karthick B, Kulikovskiy M, Lundholm N, Ludwig T, Potapova M, Rimet F, Sabbe K, Sala S, Sar E, Taylor J, Van de Vijver B, Wetzel CE, Williams DM, Witkowski A, Witkowski J (2021) DiatomBase. *Pleurosigma* W. Smith, 1852. <http://diatombase.org/aphia.php?p=taxdetails&id=149181> [Accessed on 15.12.2022]
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34(3): 772–773. <https://doi.org/10.1093/molbev/msw260>

- Lenaers G, Maroteaux L, Michot B, Herzog M (1989) Dinoflagellates in evolution. A molecular phylogenetic analysis of large subunit ribosomal RNA. *Journal of Molecular Evolution* 29(1): 40–51. <https://doi.org/10.1007/BF02106180>
- Li Y, Chen X, Sun Z, Xu K (2017) Taxonomy and molecular phylogeny of three marine benthic species of *Haslea* (Bacillariophyceae), with transfer of two species to *Navicula*. *Diatom Research* 32(4): 451–463. <https://doi.org/10.1080/0269249X.2017.1401008>
- Li Y, Nagumo T, Xu K (2022) Morphology and molecular phylogeny of *Amphora baotunensis* sp. nov., a new freshwater benthic diatom from a karst spring in China. *Diatom Research* 37(2): 145–153. <https://doi.org/10.1080/0269249X.2022.2063390>
- Malviya S, Scalco E, Audic S, Vincent F, Veluchamy A, Poulain J, Wincker P, Iudicone D, De Vargas C, Bittner L, Zingone A, Bowler C (2016) Insights into global diatom distribution and diversity in the world's ocean. *Proceedings of the National Academy of Sciences of the United States of America* 113(11): E1516–E1525. <https://doi.org/10.1073/pnas.1509523113>
- Medlin L, Elwood HJ, Stickel S, Sogin ML (1988) The characterization of enzymatically amplified eukaryotic 16S-like rRNA-coding regions. *Gene* 71(2): 491–499. [https://doi.org/10.1016/0378-1119\(88\)90066-2](https://doi.org/10.1016/0378-1119(88)90066-2)
- Nguyen L-T, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. <https://doi.org/10.1093/molbev/msu300>
- Peragallo H (1891) Monographie du genre *Pleurosigma* et des genres alliés. *Le Diatomiste* 1(4): 1–35.
- Reid G (2002) Four new species of *Pleurosigma* (Bacillariophyta) from Alexandria, Egypt. *Botanical Journal of the Linnean Society* 140(1): 77–92. <https://doi.org/10.1046/j.1095-8339.2002.00084.x>
- Reid G (2012) A revision of the family Pleurosigmataceae (Bacillariophyta). A. R. G. Gantner, Ruggell, Liechtenstein, 1–115.
- Reid G, Williams DM (2003) Systematics of the *Gyrosigma balticum* complex (Bacillariophyta), including three new species. *Phycological Research* 51(2): 126–142. <https://doi.org/10.1111/j.1440-1835.2003.tb00179.x>
- Round FE, Crawford RM, Mann DG (1990) The diatoms: biology and morphology of the genera. Cambridge university press, Cambridge, 1–774.
- Ruck EC, Theriot EC (2011) Origin and evolution of the canal raphe system in diatoms. *Protist* 162(5): 723–737. <https://doi.org/10.1016/j.protis.2011.02.003>
- Sar EA, Hinz F, Sterrenburg FA, Lavigne AS, Lofeudo S, Sunesen I (2012) Species of *Pleurosigma* (Pleurosigmataceae) with lanceolate or slightly sigmoid valve outlines: Analysis of type material. *Diatom Research* 27(4): 237–253. <https://doi.org/10.1080/0269249X.2012.720611>
- Scholin C, Villac M, Buck K, Krupp J, Powers D, Fryxell G, Chavez F (1994) Ribosomal DNA sequences discriminate among toxic and non-toxic *Pseudonitzschia* species. *Natural Toxins* 2(4): 152–165. <https://doi.org/10.1002/nt.2620020403>
- Simonsen R (1974) The diatom plankton of the Indian Ocean Expedition of R/V "Meteor" 1964–1965. *Meteor Forschungsergebnisse: Reihe D. Biologie* 19: 1–107.
- Smith W (1852) Notes on the Diatomaceae with descriptions of the British species included in the genus *Pleurosigma*. *Annals & Magazine of Natural History* 29: 1–12.
- Sterrenburg F (1991) Studies on the genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae) light microscopical criteria for taxonomy. *Diatom Research* 6(2): 367–389. <https://doi.org/10.1080/0269249X.1991.9705182>

- Sterrenburg FA, Meave Del Castillo ME, Tiffany MA (2003) Studies on the Genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae): *Pleurosigma* species in the plankton from the Pacific coast of Mexico, with the description of *P. gracilitatis* sp. nov. *Cryptogamie. Algologie* 24(4): 291–306.
- Sterrenburg F, Tiffany MA, Del Castillo MEM (2005) Valve morphogenesis in the diatom genus *Pleurosigma* W. Smith (Bacillariophyceae): Nature's alternative sandwich. *Journal of Nanoscience and Nanotechnology* 5(1): 140–145. <https://doi.org/10.1166/jnn.2005.012>
- Sterrenburg FAS, Stidolph SR, Sar EA, Sunesen I (2015) A comparative study of *Pleurosigma subrectum* and *P. acus* (Bacillariophyta). *Phytotaxa* 207(3): 273–280. <https://doi.org/10.11646/phytotaxa.207.3.5>
- Trobajo R, Mann DG (2019) A rapid cleaning method for diatoms. *Diatom Research* 34(2): 115–124. <https://doi.org/10.1080/0269249X.2019.1637785>
- Warren DL, Geneva AJ, Lanfear R (2017) RWTY (R We There Yet): An R package for examining convergence of Bayesian phylogenetic analyses. *Molecular Biology and Evolution* 34(4): 1016–1020. <https://doi.org/10.1093/molbev/msw279>

## Supplementary material 1

### GenBank accession of SSU rDNA and *rbcL* gene sequences

Authors: Fei-Chao Du, Yu-Hang Li, Kui-Dong Xu

Data type: tables (pdf file)

Explanation note: GenBank accession of SSU rDNA and *rbcL* gene sequences derived from the species used in the phylogenetic analysis.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.103890.suppl1>

## Supplementary material 2

### Maximum parsimony (MP) phylogenetic trees based on the concatenated SSU rDNA and *rbcL* gene sequences

Authors: Fei-Chao Du, Yu-Hang Li, Kui-Dong Xu

Data type: figure (pdf file)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.103890.suppl2>

# Rediscovery of *Rubus pendulus* Rusby (Rosaceae) and a new record for the flora of Ecuador and Peru

David A. Espinel-Ortiz<sup>1,2</sup>, Carla J. Rodríguez<sup>1</sup>, Katya Romoleroux<sup>1</sup>

<sup>1</sup> Laboratorio de Botánica Sistemática, Herbario QCA, Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076 y Vicente Ramón Roca, 170525 Quito, Ecuador

<sup>2</sup> Herbario Padre Luis Sodiro (QPLS), Centro Cultural Biblioteca Ecuatoriana Aurelio Espinosa Pólit, José Nogales 69-22 y Francisco Arcos, 170301 Quito, Ecuador  
Corresponding author: Katya Romoleroux ([kromoleroux@puce.edu.ec](mailto:kromoleroux@puce.edu.ec))

## Abstract

We report the rediscovery of *Rubus pendulus* Rusby, “Mora India”, described in 1933 from Colombia and not mentioned again until the present study. We also update its distribution with eight new localities in Colombia, seven in Ecuador and one in Peru, being a new record for the flora of the latter two countries. This is the first time that *R. pendulus*’ stipules and flowers are found and detailed through a botanical description, illustrations and photographs. *Rubus pendulus* is morphologically differentiated from *R. bogotensis* Benth., *R. mollifrons* Focke, *R. porphyromallos* Focke and *R. urticifolius* Poir., with whom it was previously confused and we give a brief explanation on the type specimen status of *R. mollifrons* and *R. porphyromallos*.

**Key words:** Andes, Ecuadorian, Rubeae, taxonomy

## Introduction

*Rubus* L. presents ca 836 species classified in 10 subgenera; thus, being one of the most diverse genera of the Rosaceae family (Huang et al. 2023). Despite the cosmopolitan distribution of the genus, it is more abundant in Asia, where at least 208 species (139 endemic) were reported in China alone (Lingdi and Boufford 2003). South America contains a low *Rubus* diversity with fewer than 60 species classified in the native subgenus *Rubus* L., and the introduced subgenera *Batothamnus* (Focke) E.H.L.Krause and *Idaeobatus* Focke (Macbride 1938; Romoleroux 1996; Forzza et al. 2010; Romoleroux et al. 2014; Bernal et al. 2020; Espinel-Ortiz and Romoleroux 2020, 2021; Moreno-Medina et al. 2020; Huang et al. 2023). Thus, more focalized taxonomic studies will help to uncover more species of *Rubus* in the Neotropics.

The “Mora India”, *Rubus pendulus* Rusby (subgenus *Rubus*), is among the few *Rubus*’ vine species in South America. Its holotype is the only collection, and thus, the only locality known for this species, and its flowers’ description



Academic editor: Ali Dönmez

Received: 21 January 2023

Accepted: 24 April 2023

Published: 2 June 2023

**Citation:** Espinel-Ortiz DA, Rodríguez CJ, Romoleroux K (2023) Rediscovery of *Rubus pendulus* Rusby (Rosaceae) and a new record for the flora of Ecuador and Peru. *PhytoKeys* 227: 109–122, <https://doi.org/10.3897/phytokeys.227.100859>

**Copyright:** © David A. Espinel-Ortiz et al. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

is non-existent (Rusby 1933). Despite the type locality in Colombia, this name was excluded from the Colombian Plant Catalogue (Bernal et al. 2020), and has not been mentioned for over 90 years. Curiously, this species is not the only one that should be revised for the Colombian flora. *Rubus mollifrons* Focke and *R. porphyromallos* Focke also should be reviewed, as both do not have any type collection. In fact, during their original description Focke (1911b) did not cite any sample, but affirmed that *R. mollifrons* is found in Colombia and *R. porphyromallos* could inhabit the South American Andes.

After careful examination of more than 3000 *Rubus* samples from different herbaria, specimens representing this species showed only a few samples and were often annotated as *R. bogotensis* Benth. *R. mollifrons*, *R. porphyromallos*, *R. urticifolius* Poir. or were unidentified. However, *R. pendulus* vegetative and reproductive characters differ greatly from those of the species reported for Colombia, Ecuador and Peru (Macbride 1938; Romoleroux 1996; Bernal et al. 2020; Moreno-Medina et al. 2020; Espinel-Ortiz and Romoleroux 2020, 2021). Here, we provide information to support *Rubus pendulus* as a valid species, its differences from other *Rubus* species and a brief explanation of the type status of *R. mollifrons* and *R. porphyromallos*. We also updated the key for the Ecuadorian *Rubus* species.

## Methodology

The *Rubus* collections of the Herbaria HA, HUTI, LOJA, NY, Q, QAP, QCA, QCNE, QPLS and QUSF were revised, and samples not fitting with the species reported for Ecuador were studied. Additional samples from AAU, COL, F, MO and US were revised from online images to cover the original distribution of this species in Colombia and see if it reached Peru. In total, ca 2500 samples of Ecuador, ca 700 samples of Colombia and one of Peru were revised. During 2021, we recollected more material near Quito (Ecuador) in several field trips in order to complete the species descriptions of its flowers and update the ecological data. A taxonomic key for the Ecuadorian *Rubus*' species is provided as supplementary material (See Suppl. material 1).

To categorize *R. pendulus* as a valid species, we used the *Rubus* species definition proposed by Weber (1977) and Haveman and Ronde (2013). These proposals suggest that a widely-distributed biotype, whose diameter of distribution area goes from 500 km to more than 1000 km, can be considered a species.

The botanical terms used in the descriptions followed those used by Stearn (1986), and the pubescence types were based on the terminology of Hickey and King (2000), and Wilhelm and Rericha (2020). Some specimens examined for the description (e.g. D. Espinel-Ortiz & H.G. Abad 300) were mounted in more than one herbarium sheet, and/or have additional dry or alcohol material; therefore, each part had its own herbarium barcode (QAP and QCA). For these samples, we wrote all the herbarium barcodes for each part in examined specimens when available. We used QGIS (QGIS.org 2022) for the distribution map, using the geographic coordinates from the samples. Additionally, geographic reference coordinates based on locality description were selected for the samples from Colombia that lacked this information.

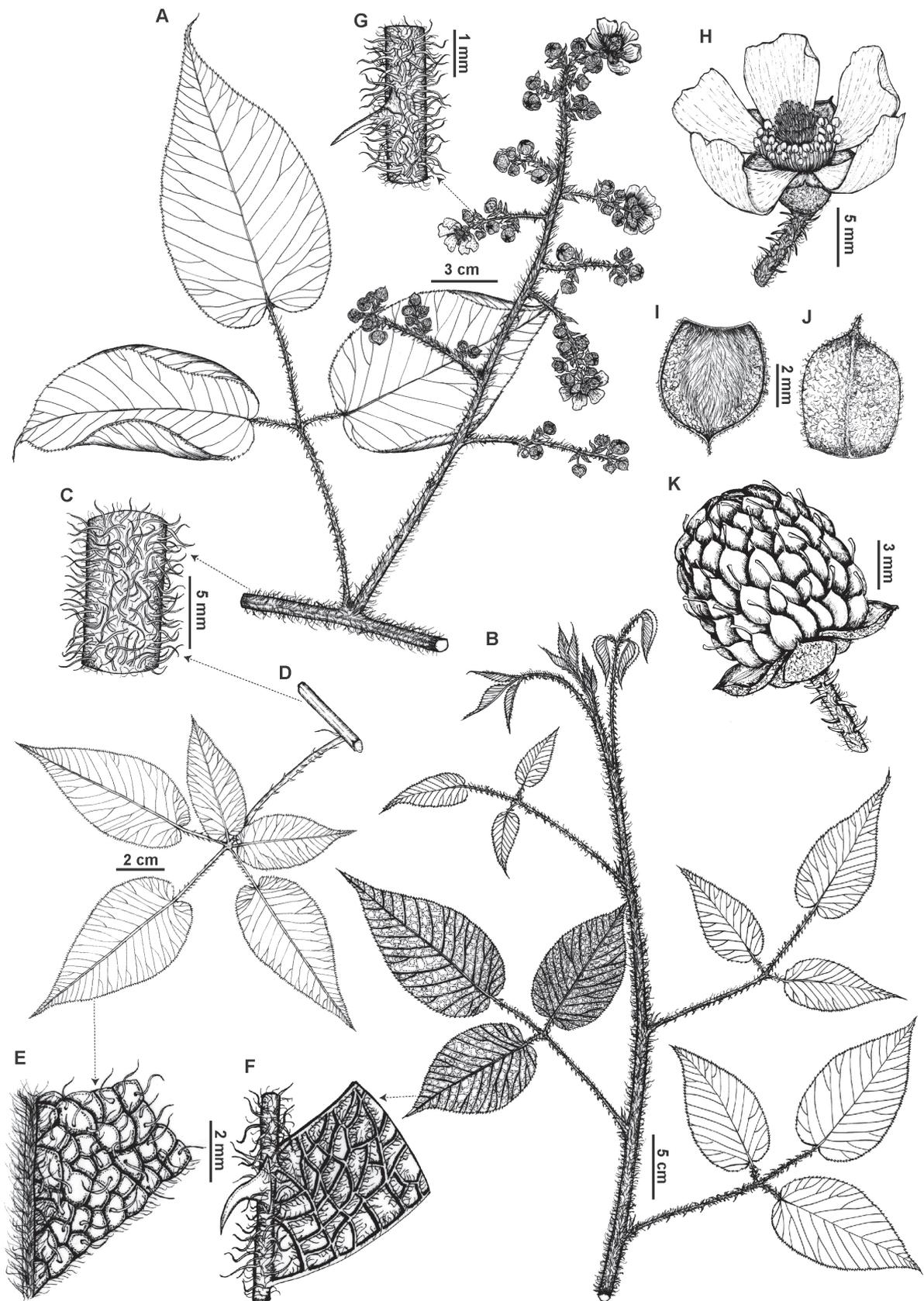
## Taxonomic treatment

***Rubus pendulus* Rusby, *Torreyia* 33:41. 1933.**

Figs 1–3

**Type. COLOMBIA. Huila:** Balsillas, at Balsillas river, edge of forest, 2000–2100 m, 03–05 Aug 1917, *H.H. Rusby & F.W. Pennell* 719 (holotype: NY (NY-424649)).

**Description.** **Woody vine** growing up to 10 m long, **or scandent or climbing shrub**, with all prickles from the base 1/3–2/3 sparsely villous-hirsute with red setose hairs, glabrous towards the apex, eglandular or with sessile glands. **Branches** obtuse-angled, red to slightly brownish, with red setose hairs, and hirsute, 3.4–9.4 mm diam., eglandular or with some setose hairs ending in a gland, unarmed or with up to 5 prickles (per total area of 5 cm long of the branch), gradually narrowed from a broad base, curved at the apex, 1.1–4.1 × 1.2–7.4 mm. **Stipules** asymmetrically narrow, subulate, 4.7–9.7 × 0.4–1.8 mm, margin entire, chartaceous; adaxial surface sparsely hirsute on veins, with red sessile glands on margin; abaxial surface with red setose hairs on veins and towards the margin, and hirsute, with red sessile and sessile glands. **Petioles** 4.8–10.6 (–15.2) cm long, with red setose hairs, and hirsute, with 17–35 prickles, gradually narrowed from a broad base, curved at the apex, 0.9–2.8 × 0.6–2.8 mm; basal petiolules 3.0–6.5 mm long, unarmed or with up to 5 prickles, gradually narrowed from a broad base, curved at the apex, 0.7–1.1 × 0.3–1.1 mm; lateral petiolules 7.0–29.7 (–45.5) mm long, with 3–17 (–34) prickles, gradually narrowed from a broad base, curved at the apex, 0.6–2.0 × 0.4–1.6 mm; terminal petiolules 2.8–5.1 (–9.0) cm long, with 8–27 (–42) prickles, gradually narrowed from a broad base, curved at the apex, 0.6–2.8 × 0.4–3.1 mm. **Leaves** trifoliate to 5-foliate; leaflets ovate to elliptic, base subcordate or asymmetrically subcordate, apex acuminate, margin serrate or bidentate towards the apex, basal leaflets (2.6–) 5.3–7.7 × (1.1–) 2.5–4.0 cm, lateral leaflets 7.1–14.3 × 3.7–7.0 cm, terminal leaflet (6.7–) 10.4–15.1 × (3.8–) 4.8–7.3 cm, chartaceous, with 10–19 secondary veins, adaxial surface bullate, sparsely villous-hirsute on each bubble, and densely villous hirsute on the midvein and secondary veins, with red sessile glands, unarmed, abaxial surface glabrous with red setose hairs, and villous only on the veins, with red sessile glands on the veins, rarely unarmed or with 8–18 (32) prickles on the primary vein, gradually narrowed from a broad base, curved at the apex, 0.2–1.8 × 0.3–2.1 mm. **Inflorescences** compact, compound, terminal and axillary cymes, 6–53-flowered, 8.2–15.3 cm long, with simple or trifoliate leaves below; peduncles terete, red to slightly brownish, (5.7–) 8.1–20.3 (–48.7) mm long, villous with abundant red setose hairs, eglandular, unarmed or with up to 14 prickles, gradually narrowed from a broad base, curved at the apex, 1.4–2.2 × 0.4–1.6 mm; pedicels terete, red to slightly brownish, 2.4–7.5 (–9.1) mm long, villous with abundant red setose hairs, eglandular, with 6–20 prickles, gradually narrowed from a broad base or triangular, curved at the apex, 0.8–2.4 × 0.1–1.4 mm. **Flowers** 8.21–15.25 mm diam.; sepals 5, obovate to elliptic or slightly lanceolate, apex mucronulate, margin entire, 5.1–7.9 × 2.5–4.6 mm, greenish-red to red, adaxial surface concave, villous-sericeous, and tomentose towards the apex and the margin, with sessile and sessile glands, unarmed, abaxial surface convex, tomentose, with sub-



**Figure 1.** *Rubus pendulus* Rusby **A** inflorescence **B** habit and leaves **C** branch **D** 5-foliolate leaf **E** leaf adaxial surface **F** leaf abaxial surface **G** pedicel **H** flower **I** sepal adaxial surface **J** sepal abaxial surface **K** fruit (**K** based on Fernández et al. 606 (QCNE) **B** based on Espinel-Ortiz et al. 301 (QCA) **C–F** based on Espinel-Ortiz et al. 304 (QCA), **A**, **G–J** based on Espinel-Ortiz et al. 382 (QCA)). Illustrations by Carla Rodríguez.



**Figure 2.** *Rubus pendulus* Rusby **A** habit **B** trifoliate leaf adaxial surface **C** bullate leaf adaxial surface **D** flowers. Photos by David A. Espinel-Ortiz.

sessile glandular, unarmed; petals 5, narrowly obovate to elliptic, margin entire, 9.0–13.9 × 6.1–7.8 mm, fuchsia to pink, glabrous, eglandular, adaxial surface deeply concave, abaxial surface deeply convex, stamens with anthers glabrous, filaments pale pink, glabrous; pistils, stigmas glabrous, styles slightly hirtellous, ovaries densely villous. **Fruits** green to red when immature, and black at maturity, ovoid to globose, 7.8–15.4 × 6.6–11.0 mm (when dry); drupelets 66–115 per receptacle, 2.1–4.3 × 1.1–2.8 mm (when dry), sparsely villous.

**Specimens examined. COLOMBIA.** — **Huila:** Neiva, Vereda La Plata, Finca La Colonia (Antigua Carolina), 2000 m, 31 Oct 1996 (fl), *F. Llanos & W.F. Gerardino* 2797 (COL). — **Magdalena:** Sierra Nevada de Santa Marta, Finca Cecilia, Quebrada Indiana, ca 10°59.000'N, 73°58.000'W, ca 1750 m, 03 Sep 1972 (fl), *J.H. Kirkbride* 2082 (COL); Sierra Nevada de Santa Marta, Finca Los Arroyitos, ca 10°56.000'N, 73°58.000'W, ca 1800 m, 07 Oct 1972 (fl, fr), *J.H. Kirkbride* 2436



Figure 3. *Rubus pendulus* Rusby. Collection Fernández et al. 606 (QCNE) with flowers and fruits.

(COL, US (US-3733777)). — **Santander:** Between Piedecuesta and Las Vegas, 2000–2500 m, 19–24 Dec 1926 (fr), *E.P. Killip & A.C. Smith 15567* (NY); Municipio Onzaga, Vereda Chaguacá, 2640 m, 30 Mar 1976 (fr), *J.H. Torres, G. Lozano & S. Díaz 539* (COL). — **Cundinamarca:** Facatativá, Alto de Peña Negra, 2810–2820 m, 29 May 1941 (fl, fr), *H. García-Barriga & R. Jaramillo 104033* (US (US-3733540)). — **Bogotá-DC:** 25 miles SW of Bogotá, 18 Mar 1952 (fr), *G.M. Darrow s.n.* (US (US-3733541)). — **Cesar:** Municipio Valledupar, Corregimiento de Puerto Bello, 1200–2000 m, 13 Jul 1983 (fl), *Cuadros H.V. 1685* (COL). **ECUADOR.** — **Pichincha:** San José de Mindo, Nono-Tandayapa road, route of the OCP Heavy Crude Oil Pipeline, Cerro Castillo and La Bola, 00°01.750'S, 78°40.984'W, 2600 m, 05 Oct 2001 (fl, fr), *D. Fernández, E. Toapanta, M. Mites & C. Morales 606* (MO, QCNE (QCNE-159936)); Quito, Nanegalito, vía a San Tadeo, Área Protegida Privada Bellavista, 00°02.170'S, 78°42.067'W, 2297 m, 03 Dec 2021, *D.A Espinel-Ortiz & H.G. Abad 300* (QCA (QCA-244065, QCA-7010819 to QCA-7010822 and QCA-7010828)); same locality as for preceding, 00°02.178'N, 78°42.227'W, 2297 m, 03 Dec 2021, *D.A Espinel-Ortiz & H.G. Abad 301* (QCA (QCA-244068 and QCA-7010829 to QCA-7010831)); Quito, Nanegalito, vía al Área Protegida Privada Bellavista desde carretera E26, 00°00.077'N, 78°41.356'W, 2281 m, 07 Dec 2021, *D.A Espinel-Ortiz & H.G. Abad 303* (QCA (QCA-244067 and QCA-7010825 to QCA-7010827)); same locality as for preceding, 00°02.178'S, 78°42.227'W, 2315 m, 20 Apr 2022, *D.A Espinel-Ortiz & H.G. Abad 327* (QCA); same locality as for preceding, 00°02.274'S, 78°42.275'W, 2303 m, 20 Apr 2022, *D.A Espinel-Ortiz & H.G. Abad 328* (QCA); same locality as for preceding, 00°02.281'S, 78°42.316'W, 2 m, 16 May 2022 (fl), *D.A Espinel-Ortiz & H.G. Abad 382* (QCA); Quito, Nanegalito, El Golán, between El Alí and El Porvenir, 00°06.570'N, 78°35.150'W, 2444 m, 25 May 2021 (fl), *C.E. Cerón & C.I. Reyes-Tello 88459* (QAP (QAP-106468 and QAP-106757)); Quito, Nanegalito, El Golán, between Edén Mágico and El Porvenir, 00°05.270'N, 78°33.230'W, 2402 m, 10 Jul 2021, *C.E. Cerón, C.I. Reyes-Tello, D. Bacuilima & A. Acosta 88667* (QAP (QAP-106886)); Quito, Yunguilla, pasando la entrada a la comunidad El Golán, 00°06.485'N, 78°33.207'W, 2641 m, 08 Dec 2021, *D. Espinel-Ortiz & H.G. Abad 304* (QCA (QCA-244066 and QCA-7010824)). — **Napo:** National Park Los Llanganates, Salcedo-Tena road, km 60, “La Poderosa” ranch, descending to Mulas river, 4 km, 00°57.000'S, 78°14.000'W, 2500–2870 m, 16 Mar 1995 (fl, fr), *H. Vargas & D. Sandoval 451* (MO (MO-1610744), NY). — **Loja:** Ca. 5 km of Paso de Sabanilla, on road Yangana-Valladolid, 04°27.00'S, 79°10.000'W, 2500 m, 03 Sep 1985, *S. Lægaard 55178* (AAU). — **Morona Santiago:** Sangay National Park, Guamote-Macas road, near Purshi-Zuñá, 02°11.000'S, 78°20.000'W, 2400–2700 m, 07 Jun 1998, *C.E. Cerón 36281* (QAP (QAP-91)). — **Zamora Chinchipe:** Nanguipa Cordillera, Cerro Colorado, about 8 km by air SSE of Nambija, 20 km ESE of Zamora, montane cloud forest, 04°07.483'S, 78°46.417'W, 2500 m, 18 Feb 2002 (fr), *D. Neill, W. Quizhpe, J. Manzanares, A. Hirtz, T. DeLinks & C. Cole 13778* (MO, QCNE (QCNE-162651)); Parque Nacional Yacuri, San Andrés, colecciones en la vía Jimbura-Zumba, ca 500 m del río Isimanchi, 04°47.100'S, 79°22.668'W, 2653 m, 29 Apr 2015, *Á.J. Pérez, N. Zapata, W. Santillán & R. Jiménez 8997* (QCA (QCA-233885)). **PERU.** — **Cajamarca:** Cutervo, San Andrés de Cutervo, Parque Nacional Cutervo, arriba de Sucedal pasando por Chorro Blanco, 6°11.353'S, 78°41.578'W, 2250 m, 03 Aug 1988 (fr), *C. Díaz & H. Osoreo 2942* (F, MO).

**Distribution.** *Rubus pendulus* is distributed in the Northern and Central Andes (Fig. 4). In Colombia, it is known from seven collections in Bogotá DC and

the Departments of Cesar, Cundinamarca, Huila, Magdalena and Santander. In Ecuador it was found in the provinces of Loja, Morona Santiago, Napo, Pichincha and Zamora Chinchipe. Lastly, from Peru it is known from one collection in Cajamarca. This species inhabits the Andean cordillera from 2000 to 2900 m a.s.l.; however, there were two specimens from Magdalena which showed a lower distribution from ca 1700 to 1800 m.

**Ecology.** This species occurs in montane cloud forests dominated by trees and shrubs and in nearby disturbed areas. *Rubus pendulus* can be found living in sympatry with *Rubus adenotrichos* Schldl., *R. boliviensis* Focke, *R. longistipularis*, *R. porphyromallos* and *R. urticifolius*. Flowering and fruiting collections dated from February, March, May and October.

**Conservation status.** *Rubus pendulus* is known from at least 18 localities, impacted by human activities, including regression to agriculture and road openings. Following the IUCN (2022) guidelines, based on the geographic distribution and altered land use at the localities, this species should be categorized as least concern (LC).

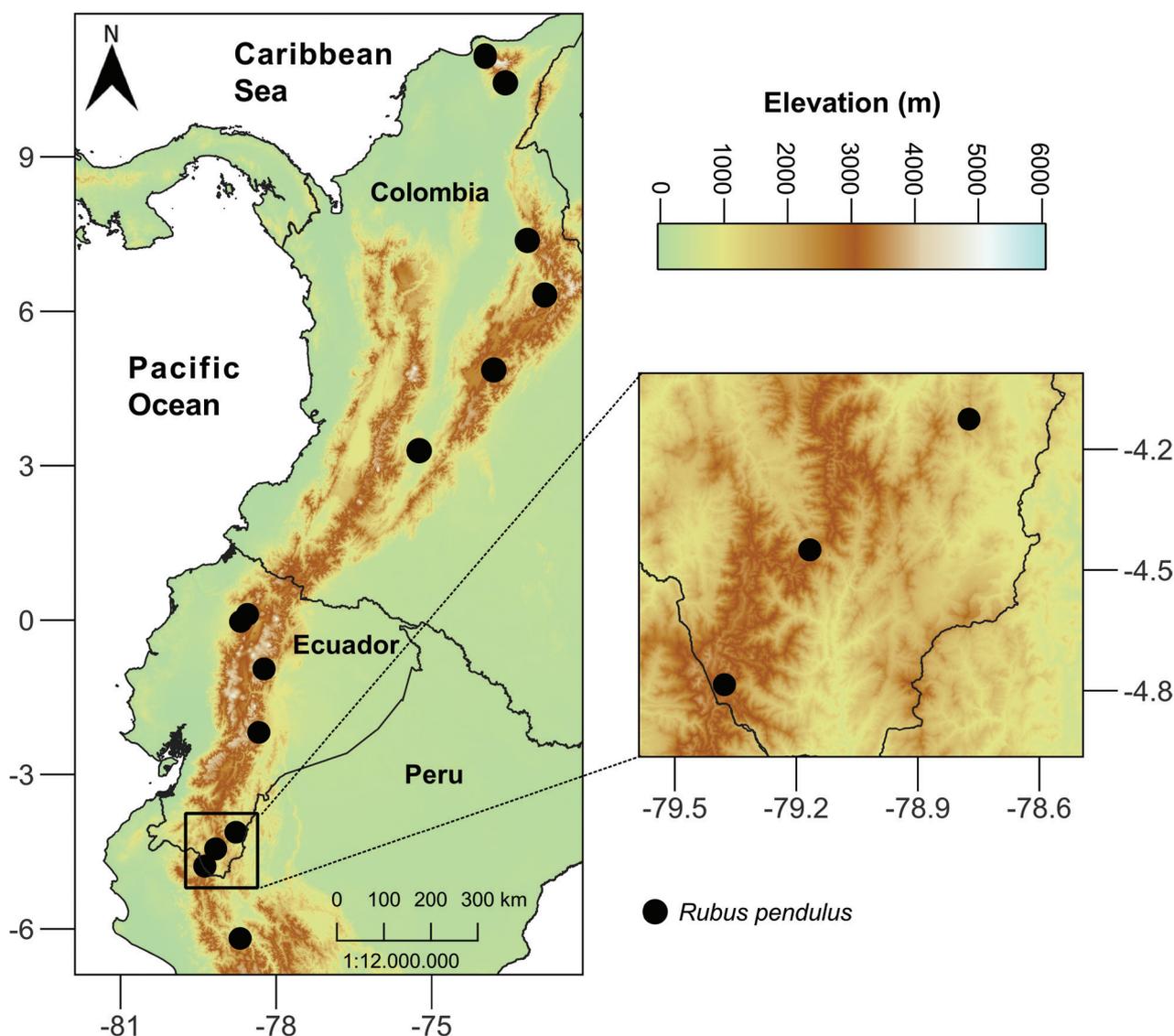


Figure 4. Distribution map of *Rubus pendulus* (black circle) in Colombia, Ecuador and Peru.

## Discussion

*Rubus pendulus* was described by Rusby (1933) with a sample collected at Balsilla's river, Balsillas, Huila Department in Colombia. All the revised material agrees with the original description and resembles the holotype collection. The most conspicuous characteristics from both, the holotype and the material examined here, are the setose hairs and hirsute pubescence referred in by Rusby as ferrugineous-tomentose, long petioles (4.8–10.6 cm long), bullate leaves, long and slightly thin leaflets (5.3–15.1 × 2.5–7.3 cm) with subcordate base, the secondary veins pattern (at an angle of about 45 degrees with the main vein), concave sepals with a mucronulate apex referred by Rusby as apiculate, and compact (crowded) and nearly sessile fruits with small drupelets (2.1–4.3 × 1.1–2.8 mm).

Since its description (Rusby 1933), no other records of *R. pendulus* were reported until Romoleroux (1996) suggested that sample Lægaard 55178 (AAU) may belong to this species. However, the available material could not be properly identified as it lacked flowers and fruits. During this revision, several samples annotate here as *R. pendulus*, were previously identified as *R. bogotensis*, *R. mollifrons*, *R. porphyromallos* or *R. urticifolius*. From these, only the latter two show similar characteristics to *R. pendulus*, whereas *R. bogotensis* and *R. mollifrons* have almost nothing in common with it.

*Rubus bogotensis* is characterized for is abundant shortly stipitate glands covering all the plant, absence of setose hairs, long pedicels (5–20 mm long) and big fruits (15–20 × 10–20 mm) with only a few drupelets (10–35) per fruit (Romoleroux, 1996). On the other hand, *R. pendulus* has red setose hairs covering all the plant, glands only in some of the setose hairs, shorter pedicels (2.4–7.5 mm long) and smaller fruits (7.8–15.4 × 6.6–11 mm) with more drupelets (66–115) per fruit. In addition, *R. pendulus*' bullate leaves differentiate it from *R. bogotensis* and the other species, as this is only a characteristic previously found in *R. azuayensis* Romol. and *R. betonicifolius* Focke, both simple-leaf species (See Suppl. material 2).

*Rubus pendulus* may resemble *R. urticifolius* by its red setose hairs, mostly eglandular trifoliate to 5-foliate leaves, and ovate to elliptic leaflets, but it differs from the latter by its bullate leaves, few flowered inflorescences (up to 60 flowers), and mucronulate sepals in contrast with the non-bullate leaves, many flowered inflorescences (60–150 flowers), and apiculate or acuminate sepals of *R. urticifolius*. Furthermore, *R. pendulus* has bigger fruits (7.8–15.4 × 6.6–11 mm) with more (66–115) and bigger drupelets (2.1–4.3 × 1.1–2.8 mm), whereas *R. urticifolius* has smaller fruits (7–10 × 6–9 mm) with fewer (30–50) and smaller drupelets (1.5–3 × 1–2 mm) (See Suppl. material 2).

The two species mentioned before were registered in Colombia, Ecuador, Peru and Bolivia (Romoleroux 1996). However, *R. mollifrons* was recorded only from Colombia and *R. porphyromallos* was said to inhabit the South American Andes (Focke 1911a, 1911b). These two species lack a holotype as Focke did not mention any sample during their original description (Focke 1911b). Even in his monograph (Focke 1911a), no sample was cited for either species. Following the Shenzhen Code's art. 9, as no sample or illustration was presented in the protologue, neotypes should be selected for both species (Turland et al. 2018). Luckily, Focke (1911a) included a photograph of *Rubus mollifrons* collection

in his monograph; should this sample be found, it could be designated as the neotype for this species. On the other hand, no illustration of *R. porphyromallos* was included; therefore, a neotype following the species description should be selected. However, for both cases, before the designation of any neotype, an extensive revision of historic Colombian *Rubus* samples is necessary. For this reason, here, we proceed to differentiate *R. pendulus* from both species based on their descriptions (Focke 1911a, 1911b). Also, we give a brief explanation of the identity of the samples identified as *R. porphyromallos* in COL and NY.

*Rubus mollifrons* is described as a climbing shrub with tomentose stems; short, tomentose petioles, lateral petioles ca 1 cm long, and terminal petiolule ca 2 cm long; linear-lanceolate stipules; trifoliolate leaves, with leaflets oblong-ovate, base subcordate, apex acuminate, 6–8 × 4–5 cm and 10–12 secondary veins; leaf adaxial surface densely pubescent and abaxially grayish-pannose (“canescent-velutina”); the inflorescences are grayish-tomentose, subarmed, pauciflora or uniflora; the flowers are short-peduncled, ca 5 cm; sepals ovate and grayish-tomentose; petals elliptic, white or slightly pink on the outside, and the petals are shorter than the sepals; no fruits observed (Focke 1911a, 1911b).

Focke (1911a, 1911b) described *R. porphyromallos* as a shrub covered in two kinds of pubescences: the first one is said to be “rufous-villous” or reddish-villous, and the other one tomentose. The stems are eglandular, with prickles; long petioles with prickles, basal petiolules 2–2.5 cm long, lateral petiolules ca 4 cm long, terminal petiolules 5–6 cm long; palmate-compound 5-foliolate leaves, leaflets oblong-ovate or ovate, base emarginate or subcordate, apex pointed, margin unevenly serrated, 15 × 10 cm, leathery, with 12–15 secondary veins; adaxial surface strigose; abaxial surface softly grayish-pannose (“canescenti-velutina”), young leaflets white; broad compound inflorescences, tomentose-villous, with prickles and trifoliolate leaves; flowers shortly pedicellate, ca 1.5 cm diam.; sepals ovate, apex acute or minute, greyish-tomentose, not villous; petals obovate; stamens shorter than sepals; no fruits observed.

In Focke’s original description, the latin word “velutina” is literally translated to velvet; the equivalent pubescence is pannose, as he used the same word to describe the pubescence of *R. boliviensis* holotype which is pannose (Romero, 1996). It is also worth mentioning that Focke already used the term bullate in *R. betonicifolius*, and red-setose pubescence as “rufo-setosi” in *R. urticifolius* (annotated as “*R. urticaefolius*”) (Focke 1911a), as both are among the most conspicuous characteristics of *R. pendulus* and were not mentioned for either *R. mollifrons* or *R. porphyromallos* (Focke 1911a, 1911b). *Rubus pendulus* differs from *R. mollifrons* by having red setose hairs all over the plant, longer lateral (0.7–2.97 cm long) and terminal (2.8–5.1 cm long) petiolules, bullate leaves, ovate to elliptic and bigger (5.3–15.1 × 2.5–7.3 cm) leaflets, with more secondary veins (10–19), leaf abaxial surface glabrous with red setose hairs, and villous only on the veins, more flowers (6–56) per inflorescence, shorter peduncles (0.8–2.0 mm long), sericeous-villous and tomentose sepals (See Suppl. material 2).

In the case of *R. porphyromallos*, its description has similar characteristics to that of *R. pendulus*, but it presents some differences such as eglandular stems, longer basal petiolules (2–2.5 cm long), non-bullate leaves, broader leaflets (15 × 10 cm), leaf abaxial surface pannose, ovate and greyish-tomentose, not villous sepals. Whereas *Rubus pendulus* has some red setose hairs ending in glands, shorter basal petiolules (0.3–0.7 cm long), bullate leaves, thinner

leaflets (5.3–15.1 × 2.5–7.3 cm), leaf abaxial surface glabrous with red setose hairs, and villous only on the veins, obovate to elliptic or slightly lanceolate, sericeous-villous and tomentose sepals (See Suppl. material 2). Another difference could be the absence of setose hairs in *R. porphyromallos* as this term was not mentioned in its original description (Focke 1911b).

### **Why has the name *Rubus porphyromallos* been widely used in Colombia?**

Most of the Colombian collections identified here as *R. pendulus* were collected between the 1970s and the 2000s. However, sample Killip & Smith 15567 was collected in 1926 and identified by Killip as *R. porphyromallos* in 1932. Interestingly, Rusby described *R. pendulus* the next year, but he never saw the collection from Killip. The same way, Killip never saw Rusby's collection as both worked in different herbaria, with most of Killip's samples deposited in US, and Rusby's in NY. Taking into account that Focke (1910, 1911a, 1914) did not cite many samples of Colombia, it is possible that because of Killip's ongoing field trips and extensive work and influence in the Colombian flora, his *Rubus* identifications were used as a reference to identify this genus. So it is that the name *R. porphyromallos* has been conserved for samples that were highly similar until recent years (COL, NY).

### **Conclusions**

*Rubus pendulus* is a widely spread species from the north of South America that has been poorly collected before and thus confused with different species. However, morphologically it is different from other similar species. More collection efforts are necessary to have an assessment of this species' complete distribution. Additionally, as *R. porphyromallos* showed the closest resemblance to *R. pendulus*, it is fundamental to designate a neotype for *R. porphyromallos* and study both of them genetically to understand their evolutive history.

### **Acknowledgements**

We would like to thank Pontificia Universidad Católica del Ecuador (PUCE) for funding this research under the investigation projects: "Caracterización de la diversidad genética y fenología de *Rubus ellipticus* Sm. (Rosaceae), especie introducida en Ecuador", "Morfometría de las especies del género *Rubus* L. de Ecuador (PUCE)" and "Evaluación de la distribución de las especies introducidas en Ecuador del género *Rubus* L. en base a información de colecciones botánicas de los herbarios ecuatorianos (PUCE)". Ministerio de Ambiente, Agua y Transición Ecológica (MAATE) for research permit MAAE-DBI-CM-2021-0171. Gonzalo Abad and Martín Morocho for their assistance during field trips. We would also like to thank Carlos Cerón, and Carmita Reyes for collecting additional material of *R. pendulus* in Yunguilla and Jorge A. Pérez for the suggestions to improve this work.

### **Additional information**

#### **Conflict of interest**

No conflict of interest was declared.

## Ethical statement

No ethical statement was reported.

## Funding

Pontificia Universidad Católica del Ecuador (PUCE) funded this research under the investigation projects: “Caracterización de la diversidad genética y fenología de *Rubus ellipticus* Sm. (Rosaceae), especie introducida en Ecuador”, “Morfometría de las especies del género *Rubus* L. de Ecuador (PUCE)” and “Evaluación de la distribución de las especies introducidas en Ecuador del género *Rubus* L. en base a información de colecciones botánicas de los herbarios ecuatorianos (PUCE)”.

## Author contributions

DAEO did the field trips, the writing and herbaria collection reviewing, CR did the scientific illustrations and the writing, KR help in the writing and editing of the manuscript.

## Author ORCIDs

David A. Espinel-Ortiz  <https://orcid.org/0000-0003-3405-0375>

Carla J. Rodríguez  <https://orcid.org/0000-0002-4204-1316>

Katya Romoleroux  <https://orcid.org/0000-0002-0679-9218>

## Data availability

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

## References

- Bernal R, Gradstein SR, Celis M [Eds] (2020) Catálogo de Plantas y Líquenes de Colombia. v1.1. Universidad Nacional de Colombia. Dataset/Checklist. <https://doi.org/10.15472/7avdhn>
- Espinel-Ortiz DA, Romoleroux K (2020) *Rubus rosifolius* Smith: A new record of an alien species in the flora of Ecuador. *BioInvasions Records* 9(4): 712–722. [https://www.reabic.net/journals/bir/2020/4/BIR\\_2020\\_Espinel-Ortiz\\_Romoleroux.pdf](https://www.reabic.net/journals/bir/2020/4/BIR_2020_Espinel-Ortiz_Romoleroux.pdf)
- Espinel-Ortiz DA, Romoleroux K (2021) Two new species of *Rubus* L. (Rosaceae) from the western Andes of Ecuador. *PhytoKeys* 187: 141–159. <https://doi.org/10.3897/phytokeys.187.76963>
- Focke WO (1910) *Species Ruborum*, Monographiae generis *Rubi* prodromus part I. Stuttgart, E. Schweizerbart, New York (NY), USA, 1–120. <https://doi.org/10.5962/bhl.title.15533>
- Focke WO (1911a) *Species Ruborum*, Monographiae generis *Rubi* prodromus part II. Stuttgart, E. Schweizerbart, New York (NY), USA, 120–223. <https://doi.org/10.5962/bhl.title.15533>
- Focke WO (1911b) *Rubi novi Americae australis et centralis*. I. Feddes Repertorium Specierum Novarum Regni Vegetabilis 9(13–15): 235–237. <https://doi.org/10.1002/fedr.19110091311>
- Focke WO (1914) *Species Ruborum*, Monographiae generis *Rubi* prodromus part III. Stuttgart, E. Schweizerbart, New York (NY), USA, 224–498.
- Forzza RC, Leitman PM, Costa A, de Carvalho AA, Peixoto AL, Walter BMT, Bicudo C, Zappi D, da Costa DP, Lleras E, Martinelli G, de Lima HC, Prado J, Stehmann JR, Baumgratz JFA, Pirani JR, Sylvestre L da S, Maia LC, Lohmann LG, Paganucci L,

- Silveira M, Nadruz M, Mamede MCH, Bastos MNC, Morim MP, Barbosa MR, Menezes M, Hopkins M, Secco R, Cavalcanti T, Souza VC (2010) Catálogo de Plantas e Fungos do Brasil, volume 2. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brasil 1544. <https://doi.org/10.7476/9788560035090>
- Haveman R, Ronde ID (2013) The role of the Weberian Reform in European *Rubus* research and the taxonomy of locally distributed species—which species should we describe? *Nordic Journal of Botany* 31(2): 145–150. <https://doi.org/10.1111/j.1756-1051.2012.01558.x>
- Hickey M, King C (2000) *The Cambridge Illustrated Glossary of Botanical Terms*. Cambridge University Press, United Kingdom, 1–208.
- Huang TR, Chen JH, Hummer KE, Alice LA, Wang WH, He Y, Yu S-X, Yang M-F, Chai T-Y, Zhu X-Y, Ma L-Q, Wang H (2023) Phylogeny of *Rubus* (Rosaceae): Integrating molecular and morphological evidence into an infrageneric revision. *Taxon* 72(2): 278–306. <https://doi.org/10.1002/tax.12885>
- IUCN (2022) *Guidelines for Using the IUCN Red List Categories and Criteria, Version 15.1* Prepared by the Standards and Petitions Committee. [https://nc.iucnredlist.org/redlist/content/attachment\\_files/RedListGuidelines.pdf](https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf) [Accessed 17.03.2023]
- Lingdi L, Boufford D (2003) 28. *Rubus* Linnaeus, Sp. P1. 1:492. 1753. In: Wu Z, Raven P, Hong D (Eds) *Flora of China*, vol. 9. Science Press, Beijing, China; Missouri Botanical Garden Press, St. Louis, USA, 195–285.
- Macbride JF (1938) Rosaceae. In: *Flora of Peru*. Field Mus. Nat. Hist. Botanica Serbica 13(2,3): 1063–1119.
- Moreno-Medina BL, Casierra-Posada F, Albesiano S (2020) *Rubus alutaceus* (Rosaceae), a new species for Colombia with agronomic potential. *Revista Brasileira de Fruticultura* 42(2): e-542. <https://doi.org/10.1590/0100-29452020542>
- QGIS.org (2022) QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>
- Romoleroux K (1996) Rosaceae. In: Harling G, Andersson L (Eds) *Flora of Ecuador*, vol. 56. University of Gothenburg, Göteborg, Sweden; Riksmuseum, Stockholm, Sweden; Pontificia Universidad Católica del Ecuador, Quito, Ecuador, 1–151.
- Romoleroux K, Meneses RI, Achá S (2014) Rosaceae. In: Jørgensen PM, Nee MH, Beck SG, Arrázola S, Saldías M (Eds) *Catálogo de las Plantas Vasculares de Bolivia*, vol. 2. Missouri Botanical Garden Press, St. Louis, USA, 1131–1140.
- Rusby HH (1933) A new blackberry from Colombia. *Torreyia* 33(2): 41–43.
- Stearn WT (1986) *Botanical Latin: History, Grammar, Syntax, Terminology and Vocabulary*, third Edition. David & Charles Publishers plc, Great Britain, 1–555.
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF [Eds] (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)* adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- Weber HE (1977) *Die ehemalige und jetzige Brombeerflora von Mennighüffen, Kreis Herford, Ausgangsbiet der europäischen Rubus-Forschung durch KEA Weihe (1779–1834)*.
- Wilhelm G, Rericha L (2020) *Illustrated Glossary of Botanical Terms. Flora of the Chicago Region, A Floristic and Ecological Synthesis*, fourth Edition. Indiana Academy of Sciences and Conservation Research Institute, USA, 1–43. <http://conservationresearchinstitute.org/forms/CRI-FLORA-Glossary.pdf> [Accessed 02.08.2021]

## Supplementary material 1

### Taxonomic identification key for Ecuadorian *Rubus*' species

Authors: David A. Espinel-Ortiz, Carla J. Rodríguez, Katya Romoleroux

Data type: Taxonomic identification key (table)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.100859.suppl1>

## Supplementary material 2

### Comparison of main morphological characters between *Rubus pendulus*, *R. urticifolius*, *R. porphyromallos*, *R. bogotensis* and *R. mollifrons*

Authors: David A. Espinel-Ortiz, Carla J. Rodríguez, Katya Romoleroux

Data type: Morphological differences between five *Rubus* species (table)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.100859.suppl2>

# *Silene isabellae* (Caryophyllaceae), a new campion species from serpentine soils of Albania

Federico Selvi<sup>1,2</sup>, Cristina Gonnelli<sup>2,3</sup>, Elisabetta Bianchi<sup>1,2</sup>

<sup>1</sup> Department of Agriculture, Food, Environment and Forestry, Laboratories of Botany, University of Florence, Piazzale delle Cascine 28, I-50144, Florence, Italy

<sup>2</sup> NBFC, National Biodiversity Future Center, I-90133, Palermo, Italy

<sup>3</sup> Department of Biology, University of Florence, via Micheli 1, I-50121, Italy

Corresponding author: Elisabetta Bianchi (e.bianchi@unifi.it)

## Abstract

The new species *Silene isabellae* is described and illustrated from the Skënderbëut mountain range of central Albania. It grows on the ultramafic mountain slopes around Qafë Shtamë, in the understorey of open *Pinus nigra* forests and in the rocky grasslands above the forest belt, at 1000–1600 m a.s.l. *Silene isabellae* is a serpentine endemic likely belonging to section *Elisanthe* (Fenzl ex Endl.) Ledeb. and shows affinities with the widespread European species *S. noctiflora* L. It is sharply distinct from the latter species in habit, stem and leaf pubescence, morphology, and biology of the flowers and length of the carpophore. Moreover, the ecology of the two taxa is also contrasting, being *S. noctiflora* a synanthropic-ruderal, mostly in lowlands. Weaker similarities were also observed with the south European subalpine taxa of the group of *S. vallesia* L. of section *Auriculatae* (Boiss.) Schischk., though these are not likely to reflect a real systematic affinity.

**Key words:** Albanian flora, morphology, new species, serpentine endemism, *Silene*, taxonomy



Academic editor: Duilio Iamónico

Received: 20 January 2023

Accepted: 14 May 2023

Published: 5 June 2023

**Citation:** Selvi F, Gonnelli C, Bianchi E (2023) *Silene isabellae* (Caryophyllaceae), a new campion species from serpentine soils of Albania. PhytoKeys 227: 123–134. <https://doi.org/10.3897/phytokeys.227.100850>

**Copyright:** © Federico Selvi et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

*Silene* L. is a large genus of family Caryophyllaceae Juss. including ca. 870 species of annual or perennial herbs, more rarely shrubs, that are mainly distributed in the Northern Hemisphere, south America and South Africa (Eggens et al. 2020; Jafari et al. 2020). Based on recent molecular phylogenetic evidence, the genus is subdivided into three subgenera and 44 sections (Jafari et al. 2020). About 200 native species are currently known from Europe (Mabberley 2017), which grow in temperate to Arctic regions and a wide range of environmental conditions, including forests and open habitats. A large part of the European species is found in the Mediterranean area and a high proportion of these are endemic (40% according to Greuter (1997)). In particular, the south-western countries of the Balkan Peninsula are major centres of species richness. According to Dimopoulos et al. (2018); ([http://portal.cybertaxonomy.org/flora-greece/cdm\\_dataportal](http://portal.cybertaxonomy.org/flora-greece/cdm_dataportal)), a total of 140 taxa of *Silene* taxa (species and subspecies) is quoted for Greece, while the most recent checklist of the Albanian flora (Barina

et al. 2018) lists as many as 52 native taxa (excluding erroneously reported and doubtful taxa). Several of these are stenocious endemic to restricted areas, mountain ranges or particular geo-pedological conditions.

During field trips between 2006 and 2022, we had the opportunity to collect a large amount of plant material especially in the vast serpentine areas of internal Albania, which was the basis for floristic, systematic and taxonomic contributions to the Albanian flora (Cecchi et al. 2007; Cecchi and Selvi 2009; Coppi et al. 2014; Cecchi et al. 2018).

Amongst these collections, the specimens of a perennial *Silene* found on serpentine soils of the Skënderbëut Mountains (central Albania) were quite morphologically distinct. Concerning floral and seed characters, these plants approached *S. noctiflora* L. [*Silene* sect. *Elisanthe* (Fenzl ex Endl.) Ledeb.], an annual species of lowland and mostly ruderal habitats, which is widely distributed in central Europe, but unknown from Albania. Weak similarities were observed also with the subalpine taxa of the *S. vallesia* group [*Silene* sect. *Auriculatae* (Boiss.) Schischk.] of some mountain regions of southern Europe, including the Balkans (Ferrarini and Cecchi 2001). However, even stronger differences existed between the Albanian plant and these taxa. Based on the geographical isolation and ecological specialisation of the plant, we concluded that these specimens belong to a new species endemic to Albania, that is described here.

## Materials and methods

Identification of the specimens was first attempted using “Flora Europea” (Chater et al. 1993) as well as floras of Albania (Vangjeli 2015; Pils 2016) and Greece (Melzheimer 1986; Greuter 1997). We then went through whole lists of taxa of *Silene* reported in comprehensive checklists of the Albanian and Greek floras, especially Meyer (2011), Barina et al. (2018) and Flora of Greece web. Next, we examined material of *S. noctiflora* and the *S. vallesia* group kept in FI, FIAF and PAD, as well as scanned images of specimens from several virtual herbaria (BP, K, W, G). The herbarium acronyms follow Thiers (2023 [continuously updated]).

Specimens were morphologically examined with a Nikon stereomicroscope and a Dino-Lite & Dino-Eye digital microscope connected to DinoCapture 2.0 software vs. 1.5.38B, which was also used to take exact measurements of even small morphological structures, such as seeds and hairs.

Despite various attempts, seeds did not germinate and this prevented us from analysing chromosome features.

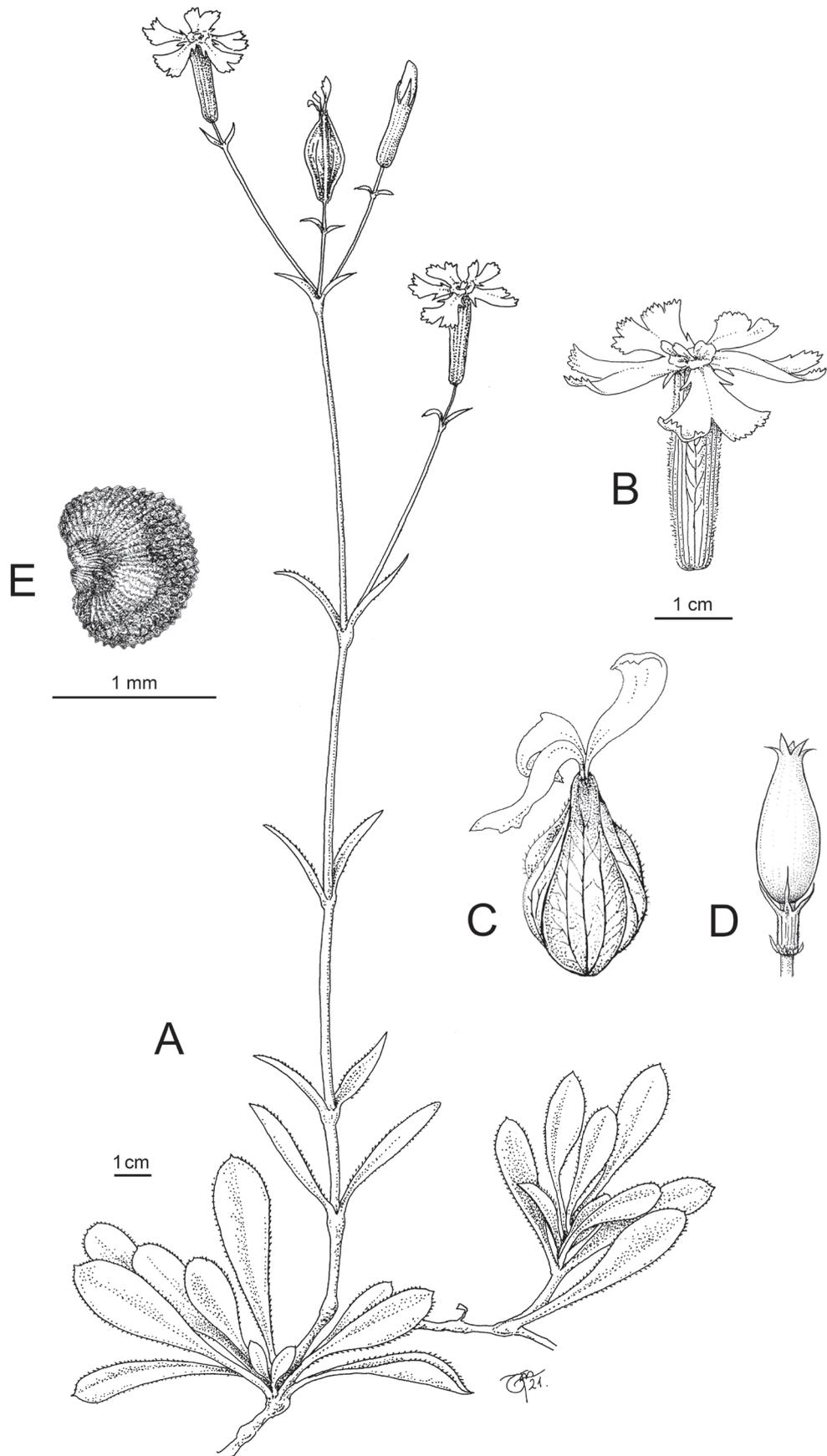
## Taxonomic treatment

### *Silene isabellae* Selvi & Bianchi, sp. nov.

urn:lsid:ipni.org:names:77320611-1

Figs 1, 2, 3A–C

**Type.** ALBANIA, Krujë, verso Qafë Shtamë, pendice ripida del monte sopra la fonte lungo la strada prima del passo, sottobosco della foresta rada di *P. nigra*, suolo roccioso ultramafico (serpentino), 1100 m elev., 41°31.33'N, 19°53.27'E; *F. Selvi*, *E. Bianchi*, *I. Colzi* & *A. Coppi*, 12 Jul 2022 (holotype: FI068201; isotypes: K, G, TIR).



**Figure 1.** *Silene isabellae* **A** whole plant **B** flower with calyx and corolla **C** fruiting calyx **D** capsule and carpophore **E** seed. Original drawing by Laura Vivona.

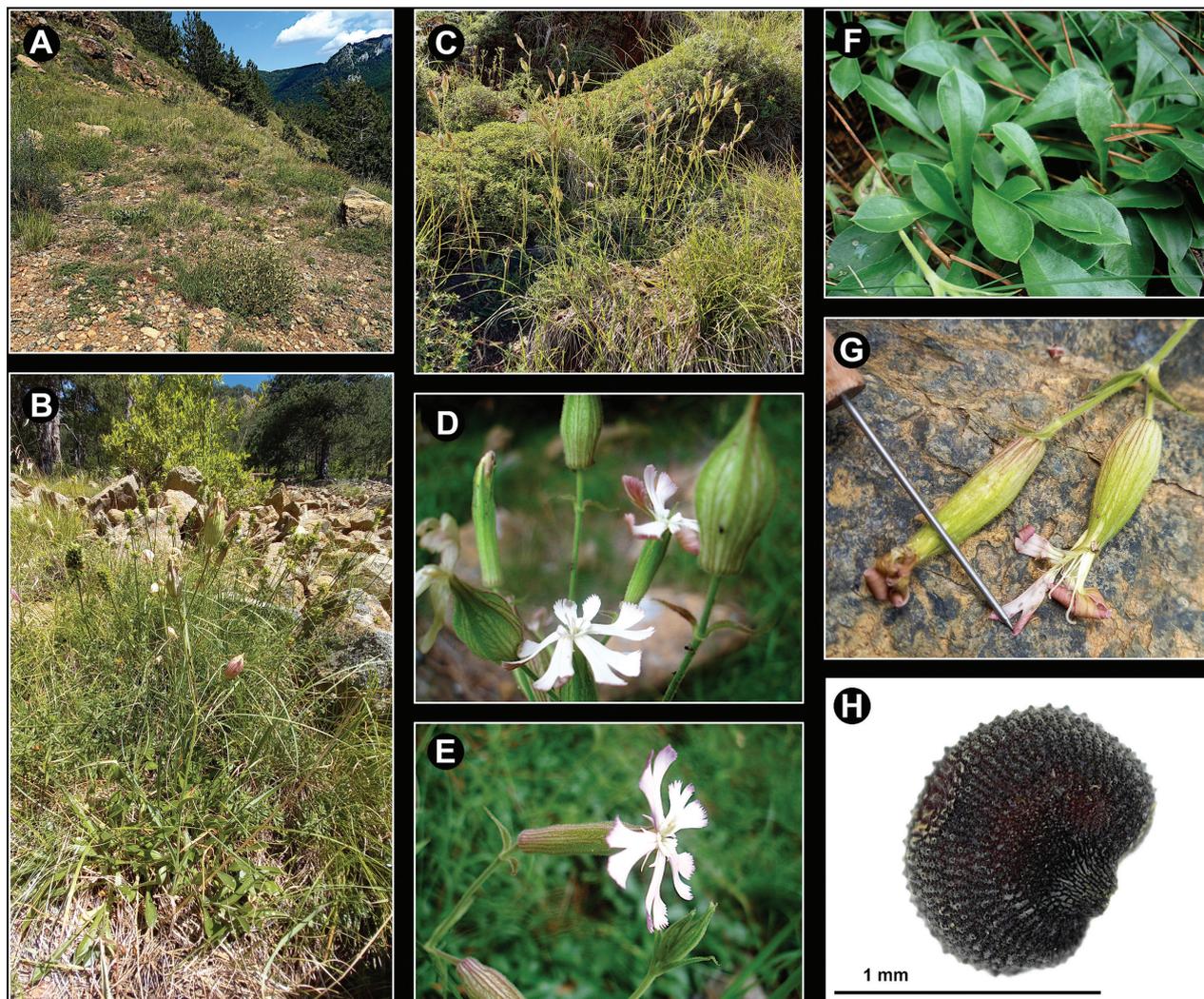
**Diagnosis.** *Silene isabellae* differs from *S. noctiflora* by the perennial habit with stoloniferous stems forming thick mats (instead of annual), the sparsely and shortly glandular-pubescent stem (vs. densely hairy), the basal leaves of the sterile stems present and widely obovate-spathulate (vs. absent), the cauline leaves linear-lanceolate (3–5 mm vs. ovate-lanceolate 25–35 mm wide), with shortly ciliate margins (vs. densely pubescent on both surfaces), the longer calyx teeth (ca. 8.5 vs. 7.0 mm), the corolla unscented and open during daytime (instead of scented and opening at evening), the petal lobes dentate (vs. entire), the fruiting calyx with prominent longitudinal ribs and the longer carpophore (6–7 vs. 2–3 mm).

**Description.** Perennial herb forming thick mats, with branched stoloniferous stems thickened at the nodes. Flowering stems up to 40 cm, rigid, usually 1–4 branched in the upper half, rarely simple, shortly glandular-pubescent. Basal leaves mostly appressed to the ground, 30–80 × 8–18 mm, tapering into the petiole, widely obovate-spathulate, apiculate at tip; leaf blade thick, glabrous and finely papillose on both surfaces, shortly ciliate at the margins (hairs ca. 0.15 mm). Cauline leaves in pairs of 4–5, the uppermost narrowly lanceolate to almost linear, 30–50 × 3–5 mm, acuminate, the mid- and upper ones much shorter than the internodes, finely ciliate along margins with glandular and simple hairs on both surfaces. Inflorescence with 1–4 branches each bearing a single flower, rarely simple; branches finely glandular-pubescent, with two linear-lanceolate leaf-like bracts 6–8 mm long. Flowering calyx narrowly cylindrical, 25–30 mm, including teeth 8.2–8.6 mm, linear-lanceolate, surface glandular-pubescent, veins tinged with purplish, reticulate especially in the upper half; fruiting calyx obconical, truncate at the base and swollen at the middle, up to 13 mm wide, with 5–6 prominent longitudinal ribs. Corolla spreading 19–21 mm wide, petals 25–30 mm long (claw 15–20 mm long and slightly exerted), divided to ca. 1/3 in two lobes dentate at the outer margin, pale pink above, tinged with mauve red beneath; coronal scales exerted, truncate, nearly white; styles 3. Capsule smooth and glossy, ovoid-conical, 13–15 × 4–5 mm, dehiscent with 6 teeth curved outwards, carpophore 6–7 mm. Seeds ca. 1.1 × 0.83 mm, reniform, with surface finely papillose-tuberculate in concentric crests around the hilum, dark brown to blackish.

**Etymology.** This species is dedicated to the first author's wife, for her continuous support and advice during many botanical trips across the Mediterranean and the Middle East.

**Phenology.** Flowering is from June to early July; fruiting is from end of June to end of July, depending on slope aspect and altitude.

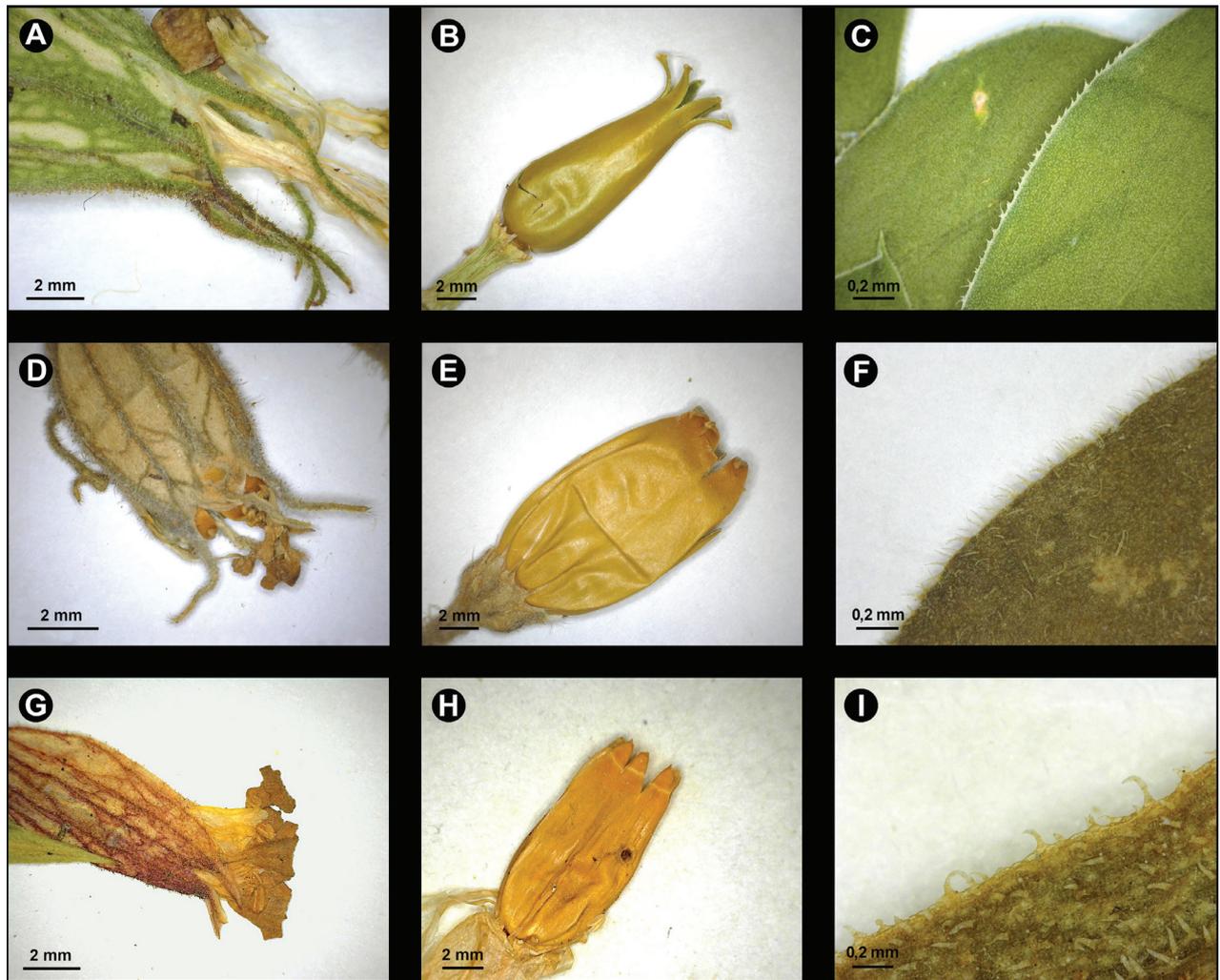
**Distribution and ecology.** *Silene isabellae* is likely endemic to central Albania, precisely to the ultramafic sectors of the Skënderbëut mountain range running along the border between the districts of Krujë and Mat (Fig. 4). We could not observe it in other parts of this mountain range with calcareous soil. Additionally, we could not find it during our botanical trips across other ultramafic mountain areas of the country (amongst which were Tropojë, Pashtrik, Lurë, Bulqizë, Shebenik, Shpat, Moravë and Vallamarë), suggesting a restricted range and, possibly, the reason why this species has remained unknown until present. The plant is found in patches in the understorey of the open *Pinus nigra* forests and in the rocky grasslands on the mountain slopes around the pass Qafë Shtamë, between 1100 and 1600 m a.s.l., but possibly even higher (Fig. 2A, B). Slope



**Figure 2.** Field photos of *Silene isabellae* **A** habitat **B**, **C** whole plants in natural habitat **D** inflorescence with flowers and fruiting calyces **E** flower **F** basal leaves **G** flowers at late stage **H** seed.

aspect was prevalently south and south-west. This area is geologically characterised by vast outcrops of ultramafic rocks hosting a rich serpentine flora including remarkable Balkan endemics, such as *Forsythia europaea* Degen & Bald., *Festucopsis serpentini* (C.E. Hubb.) Melderis and the Ni-hyperaccumulator *Odontarrhena smolikana* (Bald.) Španiel, Al-Shehbaz, D.A. German & Marhold, subsp. *glabra* (Nyár. ex Markgr.) L. Cecchi & Selvi. We assume that *S. isabellae* is an obligate serpentine endemic.

**Conservation status.** *Silene isabellae* grows in a mountain area which has been subjected for a long time to grazing mainly by sheep and goats. This ancient land use form has implied the creation and conservation of large grassland areas at the expenses of the forest. Fire is also a recurrent disturbance especially to the pine forest on the mountain slopes. Over the area that we could visit (ca. 5 km<sup>2</sup>), the species was relatively frequent, though discontinuously distributed. Based on the present state of knowledge, its range and extent of occurrence seem quite restricted, suggesting categorising it as “nearly threatened” (NT), mainly according to IUCN criterion B (IUCN 2012). However, more field studies are needed to define the correct conservation category of this species.



**Figure 3.** Calyx teeth, capsule, and margin of basal leaves of *Silene isabellae* (respectively **A–C**), *S. noctiflora* (respectively **D–F**) and *S. vallesia* subsp. *graminea* (respectively **G–I**).

**Discussion.** *Silene isabellae* shows morphological affinities with taxa of *Silene* subg. *Behenantha* (Otth) Torr. & A. Gray sect. *Elisanthe* (Fenzl ex Endl.) Ledeb. and is assumed to belong here. This is a well-defined group supported by molecular evidence (Jafari et al. 2020) that includes annual, biennial and perennial species with large flowers, solitary or in dichasia, often dioecious, with bifid petal limb, prominent coronal scales, often five styles, capsule without basal septa dehiscent with 6 or 10 teeth and a very short carpophore (Chater et al. 1993). In Europe, the section includes widespread species, such as *S. latifolia* Poir., *S. dioica* (L.) Clairv. and *S. noctiflora* L. (Prentice 1978). The latter species, described by Linnaeus (1753) from Sweden and Germany (“Habitat in Suecia, Germania”; see Jonsell and Jarvis (1994)), is apparently the more closely related one to *S. isabellae*, with which it shares the thick stem, the few-flowered inflorescence, the texture and shape of the calyx, the usually hermaphrodite flowers with three styles and the reniform seeds with a nearly identical ornamentation pattern. On the other hand, *S. isabellae* differs from *S. noctiflora* in several striking characters (see Table 1). Most importantly, it is a perennial plant forming thick mats with sterile stoloniferous stems and basal leaves (Fig. 1A), while *S. noctiflora* is annual with usually a single stem and lacking basal leaves.

**Table 1.** Main diagnostic morphological characters of *S. isabellae*, *S. noctiflora* and *S. vallesia* subsp. *graminea*.

	<i>Silene isabellae</i>	<i>Silene noctiflora</i>	<i>Silene vallesia</i> subsp. <i>graminea</i>
<b>Habit and life cycle</b>	perennial, mat-forming	annual, not mat-forming	perennial, mat-forming
<b>Flowering stems and branches</b>	sparsely and shortly glandular pubescent, 15–40 cm, usually branched, rarely simple, with 1–4 flowers	densely glandular pubescent, 12–50 cm, usually simple with a single flower, rarely branched with more flowers	sparsely pubescent, 5–15 cm, usually simple with a single flower
<b>Basal leaves of sterile stems</b>	widely obovate-spathulate, 8–18 mm wide, blade glabrous, but finely and densely ciliate along margins (Fig. 3C)	absent	linear 1.5–2 mm wide, blade with few simple hairs (Fig. 3I)
<b>Cauline leaves of flowering stems</b>	linear-lanceolate, 3–5 mm wide, shorter than internodes, shortly ciliate along the margins, blade with short glandular and simple hairs	ovate-lanceolate, up to 30 mm wide, blade and margins densely pubescent (Fig. 3F)	linear-lanceolate, 1.5–2 mm wide, subequal or longer than internodes, marginally ciliate at the base, with simple and few glandular hairs
<b>Flowers</b>	calyx 25–30 mm, teeth 8 mm, narrowly cylindrical in flower, truncate-obconical in fruit and prominently ribbed (Fig. 3A); corolla unscented, open during daytime; petals not enrolled during daytime pale pink above, tinged with mauve red beneath, lobes dentate	calyx 20–30 mm, teeth ca. 7 mm (Fig. 3D); attenuate at the base in fruit, not ribbed; corolla opening in evening with petals enrolled during daytime, pink above and yellowish beneath, lobes entire	calyx 12–16 mm, teeth ca. 1.8 mm, narrowly obconical and not ribbed in fruit (Fig. 3G); corolla unscented, open during daytime, petals usually white, lobes entire
<b>Fruits</b>	capsule conic-ovoid, 13–15 × 5 mm, surface smooth, glossy (Fig. 3B); carpophore 6–7 mm	capsule ovoid 13–15 × 8–10 mm, glossy (Fig. 3E); carpophore 2–3 mm	capsule conic-ovoid 12–13 × ca. 4 mm, glabrous, but finely rugose (Fig. 3H); carpophore 9 mm

The latter is also different in the dense and long pubescence of the lower leaves and stems which are lacking in *S. isabellae*, where the lower leaves are nearly glabrous and the lower stem is very shortly glandular-pubescent. The flowers of *S. isabellae* are open during daytime and unscented, while *S. noctiflora* is characterised by scented flowers with petals enrolled during daytime, opening in evening and night. Moreover, the petal lobes of the latter are entire or nearly so, while these are distinctly dentate in the Albanian plant (Figs 1B, 2D, E). The fruiting calyx is more distinctly truncate at the base and obconical, provided with prominent veins forming longitudinal ribs (Figs 1C, 2D). The capsule is borne by a longer carpophore (Fig. 1D). Additional evidence comes from the comparison of the chorological and ecological traits of the two taxa. In fact, *S. noctiflora* is widespread in Central and Eastern Europe (Jalas and Suominen 1988), including Serbia, Kosovo and Methojia, where it occurs south of Priština, on the eastern rim of the Kosovo Basin (Prodanović et al. 2016; Fig. 4). The plant is not known from Albania (according to Vangjeli (2015), Pils (2016); Barina et al. (2018)) and there is, thus, no range overlap with *S. isabellae*. Moreover, *S. noctiflora* is a weed usually growing in ruderal places, arable fields, cultivated ground and other synanthropic habitats, usually in lowland areas (Chater et al. 1993).

*Silene isabellae* shows a weak morphological affinity also with the taxa of the *S. vallesia* group [sect. *Auriculatae* (Boiss.) Schischk.]. This group includes taxa endemic to some mountain regions of southern Europe (Fig. 4), in France (*S. petrarcae* Ferrarini & Cecchi), the western Alps (*S. vallesia* L. subsp. *vallesia*), the Apuan Alps in Italy (*S. pichiana* Ferrarini & Cecchi), the central Apennines

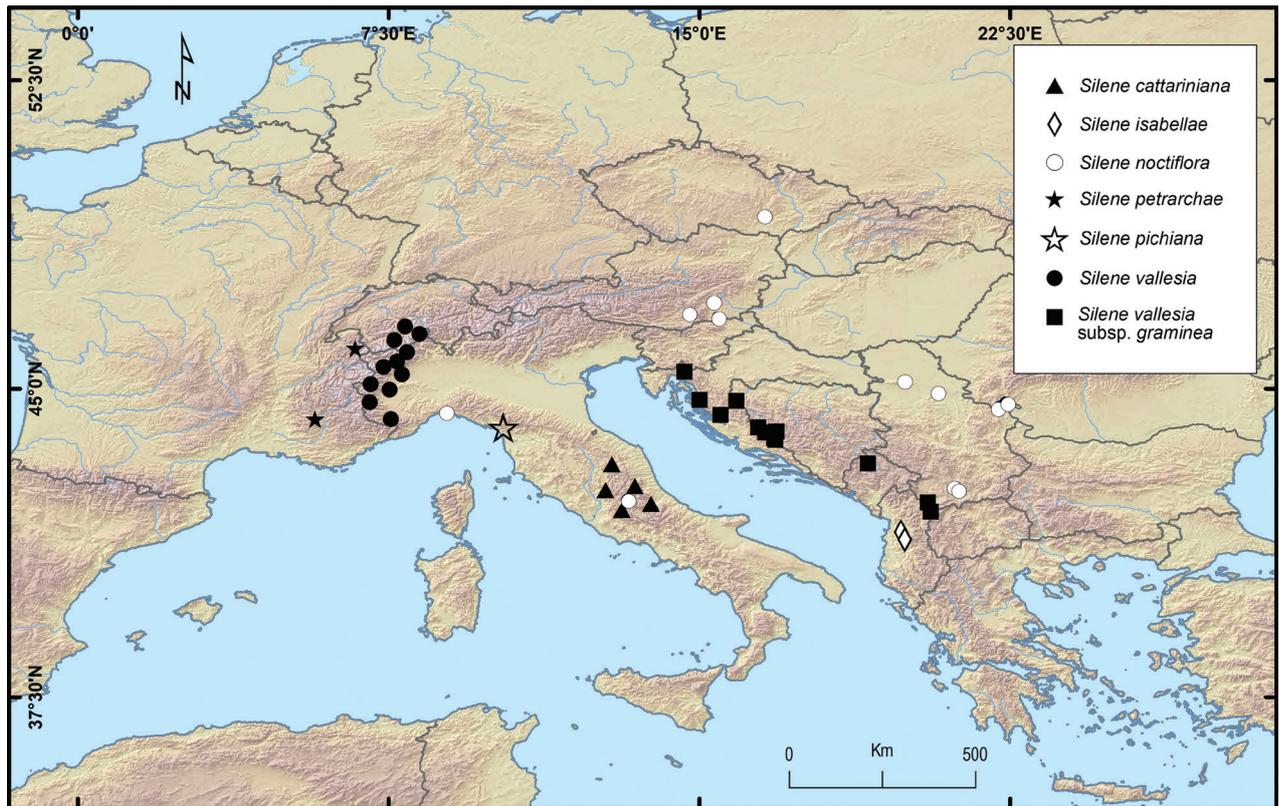


Figure 4. Distribution of *Silene isabellae*, *S. noctiflora* (partial) and the taxa of the *S. vallesia* L. group.

(*S. cattariniana* Ferrarini & Cecchi) and the Balkan massifs [*S. vallesia* subsp. *graminifolia* (Vis ex. Rchb.) Nyman, Ferrarini and Cecchi 2001]. Similarities are in the perennial habit with stoloniferous stems forming mats, the glandular-pubescent stems and leaves, the few-flowered inflorescence, the large flowers with narrowly cylindrical and reticulate-veined calyx, truncate at base, the corolla with bifid petals, the conical-ovoid capsule and the reniform seeds with a similar surface ornamentation. However, the only taxon of this group occurring in the Balkans and Albania, *S. vallesia* subsp. *graminea*, is strongly differentiated from *S. isabellae* in the much smaller size of the plant, the shape of the leaves (narrowly linear-lanceolate), the usually single flower per stem and other features of the calyx teeth and capsule (Table 1, Fig. 3G). Moreover, this taxon is only found in the Alpine massifs of the north-east of the country in the district of Kükes and close to the border with Kosovo and Macedonia, such as Mt. Pashtrik, Mt. Gjallica and Mt. Koritnik, where it reaches the southern limit of its distribution. This taxon is, thus, likely to be allopatric and geographically isolated with respect to *S. isabellae*, which is found over 80 km to the southwest (Fig. 4). Based on Vangjeli (2015), *S. vallesia* subsp. *graminea* is found in the alpine belt at 1700–2000 m a.s.l., thus, at higher elevation than *S. isabellae* and is typical of calcareous substrates especially limestone (Ferrarini and Cecchi 2001; Pils 2016).

*Silene isabellae* is apparently found only on serpentine soils. Thanks to this specialisation, the plant can be categorised as a “metalphyte”, being able to cope with the typical chemical and physical anomalies of the serpentine soils and especially the poverty in nutrients, the high levels of Mg and in trace metals like Ni, Zn and Cr (Wójcik et al. 2017). We plan further studies to assess the

concentration of these metals within the plant and, consequently, the strategies that it adopts to thrive on such hostile soils. Adaptation to serpentine soils is not uncommon in the genus *Silene*, being found in several other taxa of especially the Balkan flora. According to Stefanović et al. (2003), the Balkan countries host seven taxa of this genus that can be classified as obligate serpentine endemics, while others are found on serpentine as well as non-serpentine soils (the so-called “facultative serpentinophytes”). The distant phylogenetic position of these species suggests that ecological speciation driven by the “serpentine factor” has occurred through multiple and independent events, as in other plant groups of the Mediterranean and Balkan flora (Cecchi and Selvi 2009; Cecchi et al. 2011, 2013). Remarkably, some of the serpentine-tolerant species were also found at the same locality of *S. isabellae*, such as *S. paradoxa* L., *S. italica* L., *S. saxifraga* L., *S. vulgaris* L. subsp. *prostrata* (Gaud.) Schinz & Thell. and *S. damboldtiana* Greuter.

*Silene isabellae* shows some variation in quantitative characters associated with site conditions. Plants from the coniferous forest at lower altitude (1000–1200 m a.s.l.) were characterised by taller flowering stems and larger leaves, in particular those of the sterile stems. In plants from open and rocky sites, we observed a general reduction in the size of the plants, also associated with altitude (above 1400 m a.s.l.), while qualitative characters remained constant.

**Additional specimens examined. *Silene isabellae*: ALBANIA.** District of Krujë, Qafë Shtamë, rocce di serpentino nella foresta di *Pinus nigra*, ca. 800 prima del passo, 41°31.35'N, 19°53.32'E, 1100 m elev., 30 Jun 2018, *F. Selvi & I. Bettarini* (FI053966); District of Krujë, Qafe Shtamë, pascoli rupestri e margini di bosaglia rocciosa lungo la pista che sale dal passo verso Nord, suolo ultramafico (serpentino), 41.5251°N, 19.5251°E, 1150–1450 m elev., 12 July 2022, *F. Selvi, E. Bianchi, I. Colzi & A. Coppi* (FI068202).

***Silene noctiflora*: AUSTRIA.** Kärnten. Lavanttal: auf dem Autobahn-Rastplatz in St. Andrä, Bezirk Wolfsberg, Gemeinde Sankt Andrä, Katastralgemeinde Kollegg, 46°47'08"N, 14°48'46"E, 450 m elev., 27 May 2008, *Helmut M.* s.n. (GJO 0041410); Österreich, Steiermark; Steirisches Randgebirge, Westliches Grazer Bergland; Bezirk Graz (Stadt); Gösting, Ruine Gösting, 47°06'13.44"N, 15°22'48.28"E, 541 m elev., 6 September 2010, *Leonhartsberger S.*, (GJO 0062960); Windische Bühel, Kreuzberg bei Leutschach, Oberfahrenbach - Gamlitz - Karnerberg, Gasthof Eichbergho, 46.725°N, 15.45833°E, 07 November 1989, *Maurer W.* s.n., (GZU 000239138); **BELGIUM.** Moissons, Hackerinver, July 1863, *Thieleus Armand*; cultivè de cinq pieds sauvages trouvés en 1865 entre Haekendover (Brabant) et Overhespen (Liège), July 1866, (FI). **CZECH REPUBLIC.** Bohemia, distr. Český Krumlov. VÚ Boletice: Nová Víska, okraj cesty přes louky 6 km JV od kostela v Křišťanově, 48.86556°N, 14.07°E, 14 July 2017, *Grulich V.* (BRNU 636522); Moravia centr., distr Brno: inter segtes ad pedem collis Zlobica dicti situ septentr-orientali ad oppido Kuřim, 280 m elev., 23 July 1974, *Dvořák F.* (FI). **FRANCE.** Environs de Strasbourg, 1805, *Nestler C. G.* sn, (G00215384); Douai (Nord), abondant dans un jardin où il a peut-être été introduit accidentellement, 26 July 1882, *Maugin* (FI); Versailles, 17 August 1853, *Caruel L.* (FI). **GERMANY.** Thuring, 1822, *Wallroth K.F.W.* sn, (G00215386). **ITALY.** Luoghi erbosi presso Cretone di Tornimparte (L'Aquila), 1200 m elev., 10 September 1971, *Pelliccione G.* (FI), Valle del Lagaccio, Liguria, June, *Baglietto* (FI); Cult. nell'Orto Botanico Sperimentale di Vallombrosa, 29 August 1894, *Solla n.* 1413 (FI); Giardino dei Semplici, 1830, *Ricasoli* (FI).

***Silene vallesia* subsp. *graminea*: ALBANIA.** Velika Golia, 1700 m elev., 17 July 1904 (FI); Hais Patrik An Felsen in der Gipfelregion, 1800 m elev., 24 July 1877, *I. Dolfler* (W); Aufdem Berge Patrik bei Prizzen, 1900 m elev., 20–21 July 1936, *O.V.E. Behr* (FI); Prizren: Mt. Pastrik in graminosis alpinis, 21 July 1936, *Skrivanek* (BP591483); Distrikt Hasi, Pastrik, An Felsen in der Gipfelregion, 24 July 1918, *Dörfler & Ignaz* (BP455289, BP455288). **BOSNIA AND HERZEGOVINA.** Gipfelregion der Golia: Sudskamn (?) der Velica Golja, 1700 m elev., 18 July, *J. Stdlmann & F. Faltis* (FI); KameKnica bai Livno, 1800 m elev., 27 July 1897, *E. Brandis* (PAD). **CROAZIA.** Ex rupibus Dinaricis ad ...Dalmaticae, Herb Levier (FI); In saxosis apricis, Dinara, Ghnjat, Prologh, *Visiani* (PD); Mont Ghnjat (PAD); In dorso apricot et saxoso Mts. Dinara, July, 51K (Jos. Kargl) (PAD); Am Chemeschniza am Prolog, 18 July 1868, *Th Pichler* (PAD); Dalmatien M. Prolog, 18 July 1868, *Th. Pichler* (TSB); Croatia. Velebit in lapidosis herbosis m. Risioica supra Allau, alt. ca. 1400 m, 1908, *G. Lengyel* (PI042104); In montib. Dalmatia, s.d., *R. Visiani* (HAL0012278). **MONTENEGRO.** In saxosis excelsioribus M. Durmitor, 870, *J. Panic* (PAD).

### Key to distinguish *Silene isabellae* from *S. noctiflora*

- 1 Perennial, with stoloniferous stems forming mats; basal leaves of the sterile stems widely obovate-spathulate, cauline leaves linear-lanceolate 3–5 mm wide, with sparse and short hairs; fruiting calyx longitudinally ribbed in fruit with teeth ca. 8.5 mm long; corolla unscented, open during daytime, petals not enrolled during daytime, with lobes dentate; carpophore 6–7 mm.....***S. isabellae***
- Annual without sterile stoloniferous stems; basal leaves absent, cauline leaves ovate-lanceolate, up to 30 mm wide, densely pubescent; fruiting calyx not ribbed in fruit, with teeth ca. 7 mm; corolla scented, opening in evening with petals enrolled during daytime, petal lobes not dentate, carpophore 2–3 mm.....***S. noctiflora***

### Acknowledgements

Authors wish to acknowledge Andrea Coppi and Ilaria Colzi (Firenze) for their support during fieldwork, Lorenzo Cecchi for his assistance in the study of herbarium material and Laura Vivona (Firenze) for preparing the original iconography. Reviewers provided helpful comments on the first version of the manuscript, Aida Bani (Tirana) and Zoltán Barina (Budapest) provided useful information on *Silene* in Albania. The authors acknowledge the support of NBFC to University of Florence, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, “Dalla ricerca all’impresa”, Investimento 1.4, Project CN00000033.

### Additional information

#### Conflict of interest

No conflict of interest was declared.

#### Ethical statement

No ethical statement was reported.

## Funding

No funding was reported.

## Author contributions

Conceptualization: FS. Funding acquisition: CG. Investigation: FS, EB. Methodology: FS, EB. Project administration: FS. Writing - original draft: EB, FS. Writing - review and editing: EB, FS, CG.

## Author ORCIDs

Federico Selvi  <https://orcid.org/0000-0002-3820-125X>

Cristina Gonnelli  <https://orcid.org/0000-0001-5201-586X>

Elisabetta Bianchi  <https://orcid.org/0000-0003-1197-4081>

## Data availability

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

## References

- Barina Z, Somogyi G, Pifkó D, Rakaj M (2018) Checklist of vascular plants of Albania. *Phytotaxa* 378(1): 1–339. <https://doi.org/10.11646/phytotaxa.378.1.1>
- Cecchi L, Selvi F (2009) Phylogenetic relationships of the monotypic genera *Halacsya* and *Paramoltkia* and the origins of serpentine adaptation in circum-mediterranean Lithospermeae (Boraginaceae): Insights from ITS and matK DNA sequences. *Taxon* 58(3): 700–714. <https://doi.org/10.1002/tax.583002>
- Cecchi L, Coppi A, Selvi F (2007) Erborizzazioni nell'Albania settentrionale, con particolare riferimento alla flora serpentinicola del bacino del Drin. *Informatore Botanico Italiano* 39: 313–323.
- Cecchi L, Coppi A, Selvi F (2011) Evolutionary dynamics of serpentine adaptation in *Onosma* (Boraginaceae) as revealed by ITS sequence data. *Plant Systematics and Evolution* 297(3–4): 185–199. <https://doi.org/10.1007/s00606-011-0506-3>
- Cecchi L, Colzi I, Coppi A, Gonnelli C, Selvi F (2013) Diversity and biogeography of Ni-hyperaccumulators of *Alyssum* section *Odontarrhena* (Brassicaceae) in the central western Mediterranean: Evidence from karyology, morphology and DNA sequence data. *Botanical Journal of the Linnean Society* 173(2): 269–289. <https://doi.org/10.1111/boj.12084>
- Cecchi L, Bettarini I, Colzi I, Coppi A, Echevarria G, Pazzagli L, Bani A, Gonnelli C, Selvi F (2018) The genus *Odontarrhena* (Brassicaceae) in Albania: Taxonomy and Nickel accumulation in a critical group of metallophytes from a major serpentine hot-spot. *Phytotaxa* 35(1): 1–28. <https://doi.org/10.11646/phytotaxa.351.1.1>
- Chater AO, Walters SM, Akeroyd JR, Wrigley F (1993) *Silene* L. in *Flora Europaea* 2°edn., vol. 1 Cambridge.
- Coppi A, Cecchi L, Mengoni A, Pustahija F, Tomović G, Selvi F (2014) Low genetic diversity and contrasting patterns of differentiation in the two monotypic genera *Halacsya* and *Paramoltkia* (Boraginaceae) endemic to the Balkan serpentines. *Flora* 209(1): 5–14. <https://doi.org/10.1016/j.flora.2013.11.002>
- Dimopoulos P, Raus T, Strid A (2018) "Flora of Greece" Web, version 2. [http://portal.cybertaxonomy.org/fora-greece/cdm\\_dataportal/taxon/8b89251c-a8ca-4ac7-a055-bd97fd023201](http://portal.cybertaxonomy.org/fora-greece/cdm_dataportal/taxon/8b89251c-a8ca-4ac7-a055-bd97fd023201) [Accessed 16 Jan 2023]

- Eggens F, Jafari F, Tholleson M, Crameri S, Zarre S, Oxelman B (2020) Phylogeny and species delimitation in *Silene* sect. *Arenosae* (Caryophyllaceae): A new section. *PhytoKeys* 159: 1–34. <https://doi.org/10.3897/phytokeys.159.51500>
- Ferrarini E, Cecchi O (2001) Nuove specie del genere “*Silene*” (Caryophyllaceae) delle Alpi Apuane, dell’Appennino centrale (Italia) e della Francia meridionale. *Webbia* 56(2): 241–263. <https://doi.org/10.1080/00837792.2001.10670717>
- Greuter W (1997) *Silene* L. In: Strid A, Tan K (Eds) *Flora Hellenica* 1. Lubrecht & Cramer, 239–323.
- IUCN [International Union for Conservation of Nature] (2012) IUCN red list categories and criteria. version 3.1, 2<sup>nd</sup> edn. IUCN, Gland and Cambridge.
- Jafari F, Zarre S, Gholipour A, Eggens F, Rabeler RK, Oxelman B (2020) A new taxonomic backbone for the infrageneric classification of the species-rich genus *Silene* (Caryophyllaceae). *Taxon* 69(2): 337–368. <https://doi.org/10.1002/tax.12230>
- Jalas J, Suominen J (1988) *Atlas Florae Europaeae*, volume 3: distribution of vascular plants in Europe (Vol. 3), Caryophyllaceae. Cambridge.
- Jonsell B, Jarvis CE (1994) Lectotypifications of Linnaean names for *Flora Nordica* Vol. 1 (Lycopodiaceae-Papaveraceae). *Nordic Journal of Botany* 14(2): 145–164. <https://doi.org/10.1111/j.1756-1051.1994.tb00581.x>
- Linnaeus C (1753) *Species Plantarum* 1. Holmiae.
- Mabberley D (2017) *The Plant Book*, 4<sup>th</sup> edn. Oxford. <https://doi.org/10.1017/9781316335581>
- Melzheimer V (1986) *Silene* L. In: Strid A (Ed.) *Mountain Flora of Greece* vol. 1. Cambridge, 135–170.
- Meyer FK (2011) Beiträge zur Flora von Albanien. *Thüringische Botanische Ges. Haussknechtia* (suppl. 15): 1–220.
- Pils G (2016) *Illustrated Flora of Albania*. Eigenverlag, St. Stefan, 576 pp.
- Prentice HC (1978) Experimental taxonomy of *Silene* section *Elisanthe* (Caryophyllaceae): Crossing experiment. *Botanical Journal of the Linnean Society* 77(3): 203–216. <https://doi.org/10.1111/j.1095-8339.1978.tb01399.x>
- Prodanović D, Stanojević M, Krivošej Z (2016) *Silene noctiflora* L., present in the flora of Kosovo and Metohija (Serbia). *Biologica Nyssana* 7: 83–86. <https://doi.org/10.5281/zenodo.200403>
- Stefanović V, Tan K, Iatrou G (2003) Distribution of the endemic Balkan fora on serpentine I.—Obligate serpentine endemics. *Plant Systematics and Evolution* 242(1–4): 149–170. <https://doi.org/10.1007/s00606-003-0044-8>
- Thiers B (2023) [continuously updated] *Index Herbariorum*: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. <http://sweetgum.nybg.org/ih/> [Accessed 14 May 2023]
- Vangjeli J (2015) *Excursion Flora of Albania*. Koeltz Botanical Books, Oberreifenberg, 661 pp.
- Wójcik M, Gonnelli C, Selvi F, Dresler S, Rostánski A, Vangronsveld J (2017) Metallophytes of Serpentine and Calamine Soils – Their Unique Ecophysiology and Potential for Phytoremediation. *Advances in Botanical Research* 83: 1–42. <https://doi.org/10.1016/bs.abr.2016.12.002>

# *Selaginella densiciliata* (subg. *Heterostachys*, Selaginellaceae), a new spikemoss species from China based on morphological and molecular data

Shao-Li Fang<sup>1</sup>, Bo Xu<sup>2</sup>, Liang Zhang<sup>3</sup>, Zhao-Rong He<sup>1</sup>, Xin-Mao Zhou<sup>1</sup>

<sup>1</sup> School of Ecology and Environmental Science & School of Life Sciences, Yunnan University, Kunming, 650500, Yunnan, China

<sup>2</sup> CAS Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization and Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China

<sup>3</sup> CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences (CAS), Kunming 650201, Yunnan, China

Corresponding authors: Zhao-Rong He ([zhrhe@ynu.edu.cn](mailto:zhrhe@ynu.edu.cn)); Xin-Mao Zhou ([xinmao.zhou@ynu.edu.cn](mailto:xinmao.zhou@ynu.edu.cn))

## Abstract

A new species of spikemoss, *Selaginella densiciliata* in *S.* subg. *Heterostachys* sect. *Tetragonostachyae*, China, is described from southeastern Xizang, based on morphological and molecular phylogenetic data. Morphologically, *S. densiciliata* is similar to *S. repanda*, *S. subvaginata* and *S. vaginata*, but the new species can be easily distinguished from them by having sterile leaves margins densely ciliate, symmetrical axillary leaves oblong ovate to ovate-triangular, and ovate dorsal leaves obviously carinate. Molecular phylogenetic analysis resolves *S. densiciliata* as sister to the clade comprised with *S. vaginata* and *S. xipholepis*, which confirms the recognition of the new species.

**Key words:** Medog, *Selaginella vaginata*, submonomorphic sporophylls, *S.* subg. *Heterostachys*



Academic editor: Angelo Troia

Received: 30 January 2023

Accepted: 29 April 2023

Published: 7 June 2023

**Citation:** Fang S-L, Xu B, Zhang L, He Z-R, Zhou X-M (2023) *Selaginella densiciliata* (subg. *Heterostachys*, Selaginellaceae), a new spikemoss species from China based on morphological and molecular data. *PhytoKeys* 227: 135–149. <https://doi.org/10.3897/phytokeys.227.101222>

**Copyright:** © Shao-Li Fang et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

Located in southeastern Xizang, Medog county and adjacent regions are one of the biodiversity hotspots in the world (Myers et al. 2000; Mittermeier et al. 2005), even harboring the highest species diversity of plants in China (Sun and Zhou 1996). According to Du et al. (2021), the most number of new species of plants have been discovered in Medog, among all the counties in China in 2020. From 2015 to 2022, most of the authors (Bo Xu, Liang Zhang, Xin-Mao Zhou and Zhao-Rong He) carried out several field investigations and collected a large number of specimens in Medog. Based on those collections, three fern species, *Athyrium aberrans* Liang Zhang & Li Bing Zhang, *Hymenasplenium tholiformis* Liang Zhang, W.B. Ju & K.W. Xu, and *Selliguea wusugongii* Liang Zhang, X.P.Fan & Li Bing Zhang have been discovered (Fan et al. 2021; Qiu et al. 2022a, b). When we studied the lycophytes from these collections, we found some materials of *Selaginella* belonging to the *S. vaginata* group, but differing from all recognized species in this group.

The *Selaginella vaginata* group, including at least three species, i.e., *S. subvaginata* X.C.Zhang & Shalimov, *S. repanda* (Desv. & Poir.) Spring, and *S. vaginata* Spring, represents a taxonomically difficult group in *S.* sect. *Tetragonostachyae* of *S.* subg. *Heterostachys* sensu Zhou and Zhang (2015). Another classification with seven subgenera in *Selaginella* was also proposed by Weststrand and Korall (2016a). However, a subsequent study has evidenced that *Stachygynandrum* Weststrand & Korall (2016a) (~600 species) was not monophyletic (Zhou et al. 2022). In this study, Zhou and Zhang (2015)'s classification was followed. The *Selaginella vaginata* group is characterized by generally small plants, nearly monomorphic sporophylls, and more or less ciliate margins of leaves (Zhang et al. 2013).

Our previous phylogenetic study of *Selaginella* firstly found that the *S. vaginata* (= *S. compta* Hand.-Mazz. in Zhou et al. 2016) group was not monophyletic and it clustered with those species with distinctly dimorphic sporophylls (e.g., *S. albociliata* P.S.Wang, *S. ciliaris* (Retz.) Spring, *S. lutchuensis* Koidz, *S. xipholepis* Baker) in the *S. ciliaris* clade (= "Asia" clade in Zhou et al. 2016) of *S.* sect. *Tetragonostachyae* (Zhou and Zhang 2015; Zhou et al. 2016). Also, *S. vaginata* (= *S. compta*) was paraphyletic in relation to *S. xipholepis* (Zhou et al. 2016). Subsequently, Zhang et al. (2020) confirmed the non-monophyly of the *S. vaginata* group and described a new species, *S. subvaginata* X.C. Zhang & Shalimovin. *Selaginella vaginata* is widely distributed in East, Southeast and South Asia, and its elevations range from 500 to 3,600 m according to Zhang et al. (2013) and our own field investigation.

Our further studies of the morphology, phylogeny, and spore morphology of those species related to the *S. vaginata* group confirm that materials from Medog represent a new species. We describe it here as *Selaginella densiciliata*.

## Materials and methods

### Morphological study

Field observations were conducted in June (in 2015) and October (in 2017) respectively. The photos of plants, leaves, and strobili were taken in the field. All research materials were deposited at KUN and PYU (Index Herbarium: Thiers 2018). More details of morphology were observed and photographs were taken using SMZ1270 stereo microscope (Nikon, Japan). Megaspores and microspores were selected and attached to Carbon Adhesive Tape (CAT) using anatomical lens, then samples were coated with gold using the BAL-TEC SCD 005 Cool Sputter Coater (BAL-TEC AG., Liechtenstein) and visualized via QUANTA 200 Scanning Electron Microscope (SEM) (FEI Co., USA) at 25 kV at Yunnan University, Kunming, China. The morphological terminology of spore follows Tryon and Lugardon (1991) and Zhou et al. (2015).

### DNA extraction, amplification and sequencing

Total genomic DNA of seven samples (one from *Selaginella dianzhongensis* X.C.Zhang, two from *S. wuyishanensis* K.W.Xu, X.M.Zhou & Y.F.Duan, and four from the new species) was extracted from silica-dried material using the TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China) following the manufacturers' protocols. One nuclear locus (ITS) and one plastid

gene (*rbcl*) were selected for amplification and sequencing. Primers and the PCR conditions followed Zhou et al. (2016). Amplified fragments were purified with TIANquick Mini Purification Kits (Tiangen Biotech, Beijing, China) and purified polymerase chain reaction (PCR) products were sequenced by Tsingke (Kunming, China). Fourteen sequences were newly generated in this study (7 5.8S+ITS2 and 7 *rbcl*) (Appendix 1). Newly generated sequences were edited and assembled using Sequencher v. 4.1.2 (Gene Codes Corporation, Ann Arbor, Michigan).

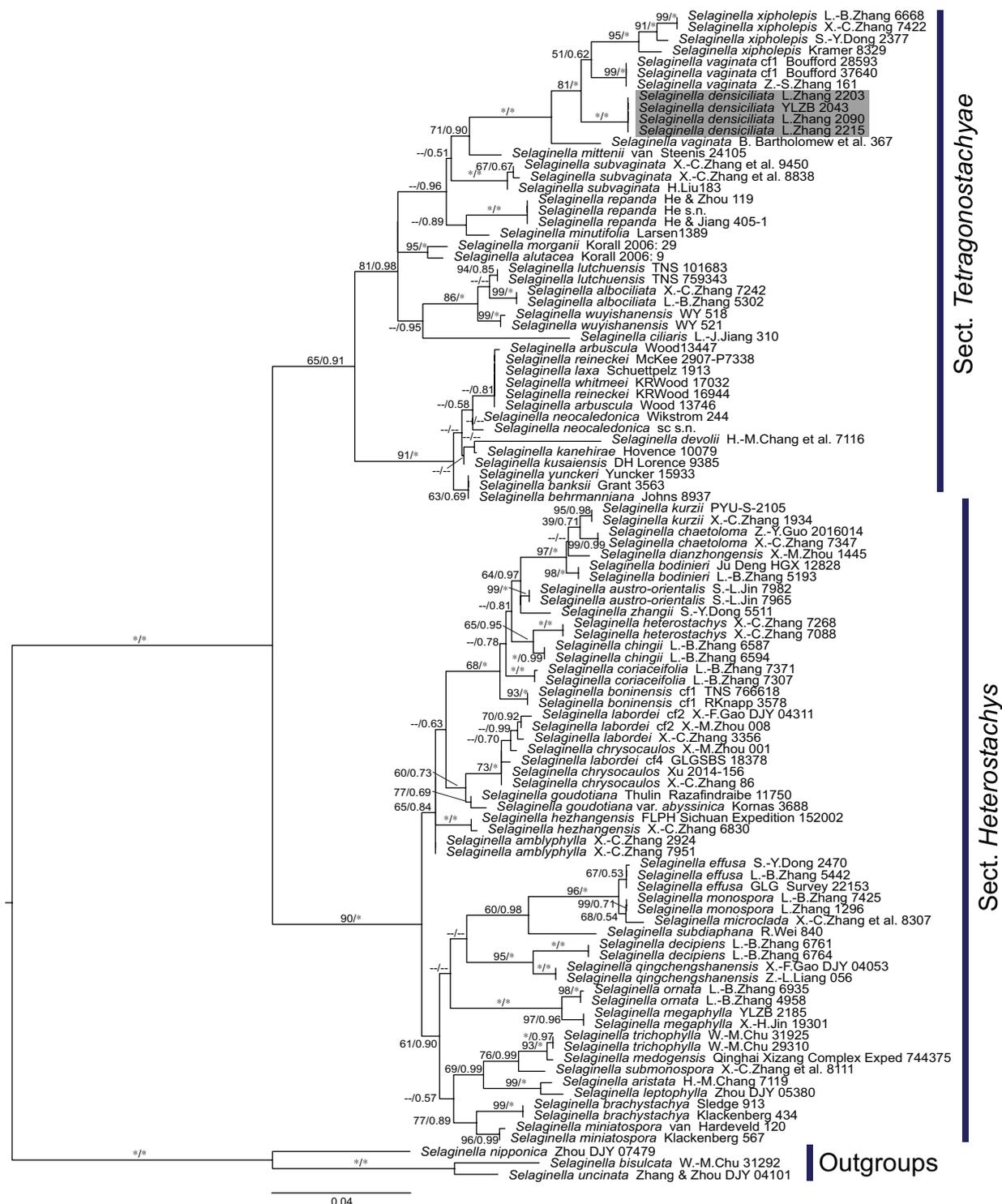
### Phylogenetic analysis

Based on a previous phylogenetic study of *Selaginella* (Zhou et al. 2016; Weststrand and Korall 2016b), three species, *S. bisulcata* Spring, *S. nipponica* Franch. & Sav., and *S. uncinata* (Desv. ex Poiret) Spring from subg. *Heterostachys* sensu Zhou and Zhang (2015) were selected as outgroups. A total 102 accessions representing 58 species of *Selaginella* were sampled (Appendix 1). All sequences were aligned using MAFFT ver. 7 (Katoh and Standley 2013), followed by manual adjustment in BioEdit (Hall 1999). A matrix with 1702 characters (5.8S + ITS2: 425 and *rbcl*: 1277) was used for phylogeny study. The jModeltest2 (Darriba et al. 2012) was used to choose the best-fitting likelihood model. The AIC (Akaike information criterion) was used to select the best model (Akaike 1974), GTR+I+G, was chosen for the Maximum likelihood (ML) and Bayesian inference (BI) analysis for combined dataset. Maximum likelihood (ML) bootstrapping was performed with 1000 rapid bootstrap replicates (BS) analyses followed by a search for the best-scoring tree in a single run in RAxML v. 8 (Stamatakis et al. 2008). Bayesian inference (BI) was conducted using MrBayes ver. 3.2.7a (Ronquist and Huelsenbeck 2003) with two runs of four Markov chain Monte Carlo (MCMC) chains, each beginning with a random tree and sampling every 1000 generations for 10,000,000 generations. Convergence among runs and stationarity was assessed using Tracer ver. 1.4 (Rambaut and Drummond 2007), and the first 25% was discarded as burnin. The remaining trees were used to calculate a 50% majority-rule consensus topology and posterior probabilities (PP). ML and BI analyses were executed on Cipres (Miller et al. 2010).

### Results and discussion

The aligned length of combined plastid gene (*rbcl*: 1277 bp) and nuclear loci (ITS: 425 bp) was 1702 bp, of which 1242 sites were identical, 389 characters were parsimony informative, and 71 variable characters were parsimony-uninformative.

As our previous phylogenetic studies for *Selaginella* (Zhou et al. 2016, 2022), phylogeny showed that *S. sect. Heterostachys* (Baker) Li Bing Zhang & X.M.Zhou is sister to *S. sect. Tetragonostachyae* (Fig. 1). The trees from the ML and BI analyses revealed identical topologies, and four samples of the new species form a highly supported clade (MLBS=100; BIPP=1.00, Fig. 1). *Selaginella densiciliata* is sister to a clade containing some samples of *S. vaginata* and all samples of *S. xipholepis*. *Selaginella densiciliata* is a distant relative of its morphologically similar species (*S. repanda*, *S. subvaginata* and *S. vaginata*). As previous studies (e.g., Zhou et al. 2016; Zhang et al. 2020) have suggested, both the *S. vaginata* group (including *S. repanda*, *S. subvaginata* and *S. vaginata*)



**Figure 1.** Maximum likelihood phylogeny of *Selaginella densiciliata* and its allies in subg. *Heterostachys*. based on molecular data. The numbers associated with branches are maximum likelihood bootstrap support (MLBS)  $\geq 50\%$  and Bayesian posterior probability (BIPP)  $\geq 0.50$ ; the dash (–) indicates MLBS < 50% or BIPP < 0.50; the asterisk indicates MLBS = 100 or BIPP = 1.00; omitted support values indicate both MLBS < 50% and BIPP < 0.50. Sections followed Zhou and Zhang (2015)'s classification.

and *S. vaginata* itself are not monophyletic (Fig. 1) and two lineages were found. With extensive sampling, potentially, more new taxa will be detected and evidenced in the *S. vaginata* group.

Comparison of morphological characters between *Selaginella densiciliata* and its morphologically similar species is shown in Table 1. *Selaginella densiciliata* is easily distinguished from other species in the *S. vaginata* morphological group by sterile leaves with margins densely ciliate at the lower parts (or at least at base) (Fig. 2H–J), ventral leaves falcate (Fig. 2C, E, J), dorsal leaves obvious carinate (Fig. 2D, I), axillary leaves symmetrical (Fig. 2C, E, H), and fine reticulation of megaspore surfaces (Fig. 2M, N).

Submonomorphic sporophylls are similar dorsal and ventral sporophylls in morphology, but dorsal sporophylls are slightly larger than ventral ones. Submonomorphic sporophylls are only present in some species of *S.* sect. *Heterostachys* (e.g., *S. monospora* Spring) and *S.* sect. *Tetragonostachyae* (Hook. & Grev.) Hieron. & Sadeb. in *S.* subg. *Heterostachys* sensu Zhou and Zhang (2015). Submonomorphic sporophylls are derived from distinctly dimorphic sporophylls in *S.* subg. *Heterostachys* Baker sensu Zhou and Zhang (2015) (Fig. 1, Zhou et al. 2016).

### Taxonomic treatment

#### ***Selaginella densiciliata* X.M.Zhou, Liang Zhang & Bo Xu, sp. nov.**

urn:lsid:ipni.org:names:77320720-1

**Type.** CHINA. Xizang: Medog County, Beibeng Township, on the way from A'niqiao to #3 bridge, in broad-leaved evergreen forest, 29°20'41.56"N, 95°9'56.99"E, elev. 1600 m, 15 Oct. 2017, *Liang Zhang, Wen-Bin Ju & Heng-Ning Deng*2215 (holotype: KUN-1572683!, isotypes: KUN-1572684!, PYU-02074721!, PYU-02074722!).

**Diagnosis.** *Selaginella densiciliata* is similar to *S. repanda*, *S. subvaginata*, and *S. vaginata* in having relatively small plants (Fig. 3E), base of stem with ventral leaves strongly curly and surrounding stem when dry (Fig. 3E), submonomorphic sporophylls (Fig. 2B, F, G), but the new species has sterile leaves margins densely ciliate at base (Fig. 2H–J), dorsal leaves obviously carinate (Fig. 2D, I), symmetrical axillary leaves oblong-ovate ovate-triangular (Fig. 2H), and megaspore surfaces fine reticulate (Fig. 2M, N).

**Description.** **Plants** terrestrial, evergreen, ascending to suberect, 7.0–15.0 cm tall, without creeping rhizomes or stolons, without elongate tuber at base of stem (Fig. 3E). **Rhizophores** grow from the base to the middle of stem, borne on ventral side in axils of branches (Figs 2C, 3E), 0.2–0.3 mm in diam. **Main stem** branched upwards from near the base, pinnately branched (Figs 2A, 3), unbranched main stem is 0.5–3.5 cm tall, terete, glabrous, 0.4–0.6 mm in diam (Fig. 3). **Branches** 6–14 pairs, 2 or 3 times pinnately branched; adjacent main branches on main stem 3.1–5.0 mm apart, the terminal branches 2.6–5.2 mm wide (Fig. 3C–E). **Sterile leaves** four rows, leathery, margins densely ciliate on the lower parts or at least at base (Fig. 2H–J). **Axillary leaves** on main stems not larger than those on branches, symmetrical, oblong-ovate to ovate-triangular ovate-triangular, base not peltate, truncate; axillary leaves on branches symmetrical, oblong-ovate to ovate-triangular, base cordate, 1.6–2.1×0.8–1.2 mm, slightly carinate, margins densely ciliate in basal half to denticulate at apex, apex acute (Fig. 2C, E, H). **Dorsal leaves** asymmetrical, those on main stems strongly larger than those on branches; ovate, 1.2–1.9 × 0.5–1.0 mm, strongly carinate, base truncate, oblique, peltate,

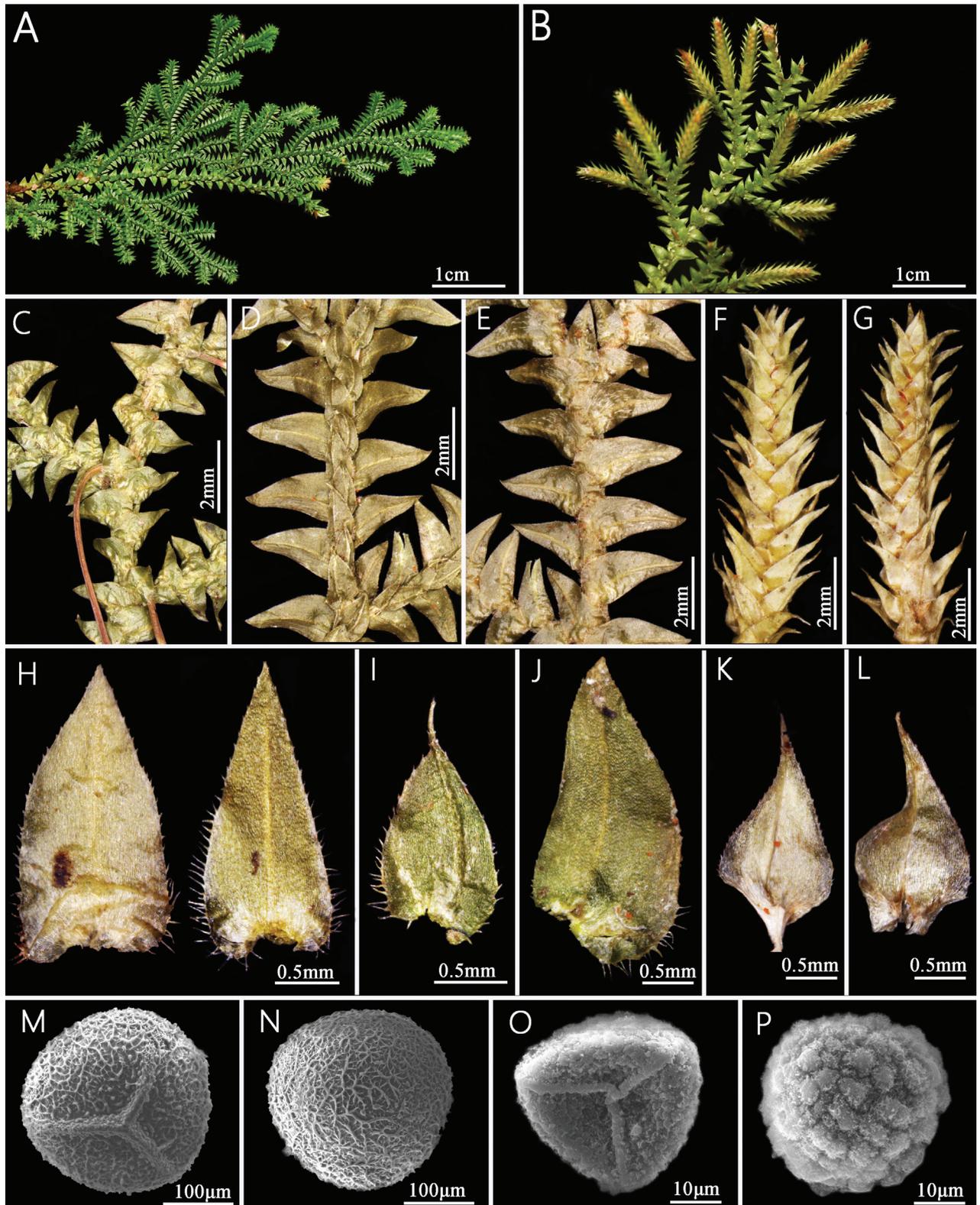
margins slightly densely ciliate at basal half, upward denticulate, apex shortly aristate (Fig. 2C, E, J). **Ventral leaves** asymmetrical, overlapping stem and branches, those on main stem strongly larger than those on branches, oblong-falcate, 2.0–2.7×1.0–1.5 mm, carinate, base round, peltate, apex acute; basispic margins slightly denticulate at base, upward subentire; acrosopic base margins densely ciliate at lower part, upward subentire (Fig. 2D, I). **Strobili** solitary, terminal, compact, quadrangular, 4.3–7.9 mm (Figs 2B, F, G, 3A, B). **Sporophylls** slightly dimorphic, dorsal sporophylls slightly longer than ventral sporophylls (Fig. 2B, F, G); dorsal sporophylls ovate, carinate, 1.4–1.5×0.7–0.9 mm, margins denticulate, base cuneate, not peltate, apex acuminate, without sporophyll-ptyx (Fig. 2K); ventral sporophylls broadly ovate, carinate, 1.23–1.47×0.69–0.81 mm, base truncate, not peltate, apex acuminate, margin denticulate (Fig. 2G). Megasporophylls in basal portion on lower side of strobilus. **Megaspore** white-yellow, oblate spheroid to subglobose, 225.6–280.2 µm in diam., prominent laesurae extend 2/3 of the distance to the equator; surface finely reticulate ornamentation (Fig. 2M, N). **Microspore** orange, hemispherical, 27.4–37.7 µm, surfaces with dense and large verrucate ornamentation covered with densely irregular granular microstructure (Fig. 2O, P).

**Geographical distribution and habitat.** *Selaginella densiciliata* is only known from Beibeng Township, Medog County, Xizang Province, China. It grows in humid places in evergreen broadleaved forests, at elevations of 1000–1600 m.

**Additional specimens examined (paratypes).** **CHINA. Xizang: Nyingchi City, Medog county, Beibeng township.** on the way from A'niqiao to Hanmi village, elev. ca. 1000 m, 29°20'14.40"N, 95°10'19.19"E, 4 Jun. 2015, *Bo Xu & Xin-Mao Zhou YLZB2043* (CDBI, PYU); on the way from A'niqiao to Hanmi village, elev. 1530 m, 29°20'29.51"N, 95°10'12.74"E, 15 Oct. 2017, *Liang Zhang, Wen-Bin Ju & Heng-Ning Deng 2090* (KUN, PYU); on the way from A'niqiao to Hanmi village, alt. 1120 m, 29°19'42.75"N, 95°10'36.47"E, 17 Oct. 2017, *Liang Zhang, Wen-Bin Ju & Heng-Ning Deng 2203* (KUN, PYU).

**Table 1.** Morphological comparison among *Selaginella densiciliata*, *S. repanda*, *S. subvaginata*, and *S. vaginata*.

	<i>Selaginella densiciliata</i>	<i>S. repanda</i>	<i>S. subvaginata</i>	<i>S. vaginata</i>
Habit	Ascending to suberect	Suberect or ascending	Suberect	Creeping
Leaves margin	Not white-margined	White-margined	Not white-margined	White-margined
Axillary leave	Symmetrical, oblong-ovate to ovate-triangular	Symmetrical, ovate-lanceolate	Asymmetrical, ovate to ovate-triangular	Asymmetrical, ovate-triangular
Dorsal leave	Ovate, margins ciliate, apex aristate; carinate	Obliquely ovate, margins denticulate; slightly carinate	Ovate-lanceolate, inner margins ciliate; slightly carinate	Ovate-lanceolate or ovate-triangular, base margins ciliate; slightly carinate
Ventral leave	Oblong-falcate, basispic base margins denticulate	Ovate or obliquely ovate, basispic base margins ciliate	Oblong-falcate, basispic base margins denticulate	Ovate-lanceolate or ovate, basispic base margins denticulate
Dorsal sporophyll	Ovate, margins denticulate	Ovate-lanceolate, margins denticulate	Ovate, base margins ciliate	Ovate-lanceolate, base margins ciliate
Ventral sporophyll	Broadly ovate, margins denticulate	Broadly ovate, margins denticulate	Ovate, base margins ciliate	Ovate-lanceolate, margins denticulate
Megaspore	Fine reticulate	Verrucate	Fine reticulate	Verrucate
Microspore	Verruetae and rugulate with spiny microstructure	Verruetae and rugulate	Smooth	Verruetae and rugulate



**Figure 2.** *Selaginella densiciliata* **A** dorsal view of branches **B** ventral view of branches with strobili **C** ventral view of branches, showing rhizophores, axillary leaves, and ventral leaves **D** dorsal view of branches, showing dorsal leaves **E** ventral view of branches, showing axillary leaves, and ventral leaves **F** dorsal view of strobilus **G** ventral view of strobilus **H** axillary leaf on stems (left) and branches (right) **I** dorsal leaf **J** ventral leaf **K** dorsal sporophyll **L** ventral sporophyll **M** proximal surface of megaspore **N** distal surface of megaspore **O** proximal surface of microspore **P** distal surface of microspore (from the holotype: *L. Zhang et al. 2215*).



Figure 3. Type of *Selaginella densiciliata* A dorsal view of branches with strobili B ventral view of branches with strobili C dorsal view of branches D ventral view of branches E holotype of *Selaginella densiciliata* (L. Zhang et al. 2215).

**Etymology.** The specific epithet “*densiciliata*” is a compound word derived from the Latin word “*dense*” which means dense and suffix “*ciliata*” which means ciliate. The specific epithet “*densiciliata*” refers to sterile leaf (axillary leaves, dorsal leaves, and ventral leaves, Fig. 2H–J) margins with dense cilia at base.

### Key to *Selaginella densiciliata* and its relative species of the *S. vaginata* group

- 1 Stem nearly creeping, only fertile parts (strobili) ascending ..... ***S. vaginata***
- Stem more or less suberect or ascending ..... **2**
- 2 Leaves distinctly white-margined ..... ***S. repanda***
- Leaves not obviously white-margined ..... **3**
- 3 Base of sterile leaf margins sparsely ciliate or denticulate; axillary leaves asymmetrical; dorsal leaves ovate-lanceolate, slightly carinate; microspore surface smooth ..... ***S. subvaginata***
- Base of sterile leaf margins densely ciliate; axillary leaves symmetrical; dorsal leaves ovate, obvious carinate; microspore surface verrucate .....  
..... ***S. densiciliata***

### Acknowledgements

The research was supported by the National Natural Science Foundation of China (NSFC) to X.M. Zhou (#31900186, #32260050). We thank the two anonymous reviewers for their valuable comments and suggestions.

### Additional information

#### Conflict of interest

No conflict of interest was declared.

#### Ethical statement

No ethical statement was reported.

#### Funding

No funding was reported.

#### Author contributions

Conceptualization: BX. Formal analysis: SLF. Funding acquisition: XMZ. Methodology: SLF. Project administration: XMZ. Resources: BX. Software: SLF. Supervision: XMZ. Writing - original draft: XMZ, SLF. Writing - review and editing: ZRH, BX, LZ.

#### Data availability

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

### References

- Akaike H (1974) A new look at the statistical model identification. Institute of Electrical and Electronics Engineers Transactions on Automatic Control 19(6): 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9(8): 772–772. <https://doi.org/10.1038/nmeth.2109>

- Du C, Liu J, Ye W, Liao S, Ge BJ, Liu B, Ma JS (2021) New taxa of plants of China, new name 2020 Annual Report. *Biodiversity (Nepean)* 29(8): 1011–1020. <https://doi.org/10.17520/biods.2021122>
- Ebihara A, Nitta JH, Ito M (2010) Molecular species identification with rich floristic sampling: DNA barcoding the pteridophyte flora of Japan. *PLoS ONE* 5(12): e15136. <https://doi.org/10.1371/journal.pone.0015136>
- Fan XP, Zhang L, Zhang LB, Zhang L (2021) *Selliguea wusugongii* (Polypodiaceae), a new fern species from southeastern Xizang, China based on morphological and molecular evidence. *Phytotaxa* 480(1): 57–68. <https://doi.org/10.11646/phytotaxa.480.1.5>
- Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- He M, He ZR, Zhang LB, Zhou XM (2021) *Selaginella qingchengshanensis* (sect. *Heterostachys*; Selaginellaceae), a new species from Sichuan, China. *Phytotaxa* 522(4): 285–293. <https://doi.org/10.11646/phytotaxa.522.4.2>
- Huang L, Li SH, Dong SY (2022) Two new species of the lycophyte genus *Selaginella* (Selaginellaceae) from China, with Notes on the phylogenetic positions of related species. *Systematic Botany* 47(1): 85–96. <https://doi.org/10.1600/036364422X16442668423400>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Klaus KV, Schulz C, Bauer DS, Stützel T (2017) Historical biogeography of the ancient lycophyte genus *Selaginella*: Early adaptation to xeric habitats on Pangea. *Cladistics* 33(5): 469–480. <https://doi.org/10.1111/cla.12184>
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. 14 November 2010. New Orleans, LA, 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Mittermeier RA, Hawkins F, Rajaobelina S, Langrand O (2005) Wilderness conservation in a biodiversity hotspot. *International Journal of Wilderness* 11(3): 42–45.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858. <https://doi.org/10.1038/35002501>
- Nitta J, Steier J, Schuettpelz E (2020) Biogeography of Pacific pteridophytes in a global context. [Unpublished]
- Qiu YL, Xu KW, Ju WB, Zhao WL, Zhang L (2022a) *Hymenasplenium tholiformis* (Aspleniaceae), a new fern species from southeastern Xizang, China based on morphological and molecular evidence. *PhytoKeys* 204: 43–56. <https://doi.org/10.3897/phytokeys.204.85746>
- Qiu YL, Zhang L, Zhang LB, Zhou XM, Zhang L (2022b) *Athyrium aberrans* (Athyriaceae), a new species of the lady ferns from southeastern Xizang, China, based on morphological and molecular evidence. *Phytotaxa* 533(3): 165–172. <https://doi.org/10.11646/phytotaxa.533.3.2>
- Rambaut A, Drummond AJ (2007) Tracer 1.4. <http://beast.bio.ed.ac.uk/Tracer> [Accessed 15 Jan. 2022]
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12): 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>

- Shalimov AP, Zhang XC (2021) A taxonomic revision of *Selaginella monospora* Spring (Selaginellaceae). *Turczaninowia* 24(3): 175–193. <https://doi.org/10.14258/turczaninowia.24.3.14>
- Shalimov AP, Zhang XC (2022) *Selaginella submonospora* (Selaginellaceae), a new species from Yunnan. *Turczaninowia* 25(1): 153–165. <https://doi.org/10.14258/turczaninowia.25.1.15>
- Shalimov AP, Zhu YM, Zhang MH, Zhang XC (2019) *Selaginella dianzhongensis* (Selaginellaceae), a new spikemoss from China. *PhytoKeys* 118: 75–87. <https://doi.org/10.3897/phytokeys.118.30375>
- Sheue CR, Chesson P, Li SF, Liu JW, Chang HM, Valdespino I, Salazar N, Chesson C, Oppenheimer H, Bakutis A, Saenger P, Yong JWH, Das S, Adjie B, Kiew R, Nadkarni N, Dong SY, Kao MF, Huang CL (2017) Recent chloroplast diversification in the ancient genus *Selaginella*. [Unpublished]
- Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology* 57(5): 758–771. <https://doi.org/10.1080/10635150802429642>
- Sun H, Zhou ZK (1996) The characters and origin of the flora from the big bend gorge of Yalutsangpu (Brahmabutra) river, eastern Himalyas. *Acta Botanica Yunnanica* 18(2): 185–204.
- Thiers B (2018) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/> [Accessed 26 November 2018]
- Tryon AF, Lugardon B (1991) Spores of the Pteridophyta. Springer-Verlag, New York, 156 pp. <https://doi.org/10.1007/978-1-4613-8991-0>
- Wei HJ, Chen B, Fang SL, Zhou XM (2023) *Selaginella austro-orientalis* (Selaginellaceae), a new species from Southeast China. *Phytotaxa* 579(2): 87–97. <https://doi.org/10.11646/phytotaxa.579.2.2>
- Weststrand S, Korall P (2016a) A subgeneric classification of *Selaginella* (Selaginellaceae). *American Journal of Botany* 103(12): 2160–2169. <https://doi.org/10.3732/ajb.1600288>
- Weststrand S, Korall P (2016b) Phylogeny of Selaginellaceae: There is value in morphology after all! *American Journal of Botany* 103(12): 2136–2159. <https://doi.org/10.3732/ajb.1600156>
- Xu KW, Chen SF, Song Q, Zheng X, Li M, Fang YM, Wei HJ, Ding H, Zhou XM, Duan YF (2022) *Selaginella wuyishanensis* (sect. *Tetragonostachyae*, Selaginellaceae), a new species from East China and its phylogenetic position based on molecular data. *PhytoKeys* 202(3): 107–119. <https://doi.org/10.3897/phytokeys.202.85410>
- Ye ZY, Lu NT, Zhang L, Zhou XM, Zhang LB (2020) *Selaginella coriaceifolia* (sect. *Heterostachys*; Selaginellaceae), a new lycophyte species from central Vietnam. *Phytotaxa* 453(2): 121–129. <https://doi.org/10.11646/phytotaxa.453.2.3>
- Zhang XC, Nooteboom HP, Kato M (2013) Selaginellaceae. In: Wu Z-Y, Raven PH, Hong D-Y (Eds) *Flora of China* (Vol. 2–3). Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, 37–66.
- Zhang XC, Shalimov AP, Kang JS, Zhang MH (2020) *Selaginella subvaginata* (Selaginellaceae), a new spikemoss from China. *Journal of Species Research* 9(3): 221–232. <https://doi.org/10.12651/JSR.2020.9.3.221>
- Zhou XM, Zhang LB (2015) A classification of *Selaginella* (Selaginellaceae) based on molecular (chloroplast and nuclear), macromorphological, and spore features. *Taxon* 64(6): 1117–1140. <https://doi.org/10.12705/646.2>

- Zhou XM, Jiang LJ, Zhang L, Gao XF, He ZR, Zhang LB (2015) Spore morphology of *Selaginella* (Selaginellaceae) from China and its systematic significance. *Phytotaxa* 237: 001–067. <https://doi.org/10.11646/phytotaxa.237.1.1>
- Zhou XM, Rothfels CJ, Zhang L, He ZR, Le Péchon T, He H, Lu NT, Knapp R, Lorence D, He XJ, Gao XF, Zhang LB (2016) A large-scale phylogeny of the lycophyte genus *Selaginella* (Selaginellaceae: Lycopodiopsida) based on plastid and nuclear loci. *Cladistics* 32(4): 360–389. <https://doi.org/10.1111/cla.12136>
- Zhou XM, Zhao J, Yang JJ, Le Péchon T, Zhang L, He ZR, Zhang LB (2022) Plastome structure, evolution, and phylogeny of *Selaginella*. *Molecular Phylogenetics and Evolution* 169: 107410. <https://doi.org/10.1016/j.ympev.2022.107410>

## Appendix 1

List of taxa sampled with information related to taxonomy, GenBank accession numbers (*rbcL*, ITS), references, and vouchers information. Herbarium codes follow Index Herbariorum (Thiers 2018).

***S. albociliata* P. S. Wang** (1) L.-B. Zhang et al. et al. 5302 (CDBI), China (Guangxi), KT161379 (Zhou et al. 2016), KT161648 (Zhou et al. 2016); (2) X.-C. Zhang 7242 (PE), China (Guizhou), MH814882 (Shalimov et al. 2019), –.

***S. alutacea* Spring** Korall 2006-9 (S), Malaysia, KY022958 (Weststrand and Korall 2016b), –.

***S. amblyphylla* Alston** (1) X.-C. Zhang 2924 (PE), China (Yunnan), MH814883 (Shalimov et al. 2019), –; (2) X.-C. Zhang 7951 (PE), China (Yunnan), MH814884 (Shalimov et al. 2019), –.

***S. arbuscula* Spring** (1) Wood 13447 (PTBG), Hawaii (Kauai, Wainiha), KT161387 (Zhou et al. 2016), KT161656 (Zhou et al. 2016); (2) Wood 13746 (PTBG), Hawaii (Maui, Kipahulu), KT161388 (Zhou et al. 2016), KT161657 (Zhou et al. 2016).

***S. aristata* Spring** H.-M. Chang et al. 7119 (TAIE), MF313959 (Sheue et al. Unpublished), –.

***S. austro-orientalis* H. J. Wei & X. M. Zhou** (1) S.-L. Jin et al. 7965 (CSH, IBK, PYU), China (Jiangxi), OP690605 (Wei et al. 2023), OP683200 (Wei et al. 2023); (2) S.-L. Jin et al. 7982 (CSH), China (Jiangxi), OP690606 (Wei et al. 2023), OP683199 (Wei et al. 2023).

***S. banksii* Alston** Grant 3563 (L), French Polynesia, KY022972 (Weststrand and Korall 2016b), –.

***S. behrmanniana* Hieron** Johns 8937 (L), Indonesia, KY022973 (Weststrand and Korall 2016b), –.

***S. bisulcata* Spring** Chu et al. 31292 (PYU), China (Yunnan), KT161404 (Zhou et al. 2016), KT161673 (Zhou et al. 2016).

***S. bodinieri* Hieron.** (1) Ju & Deng HGX12828 (CDBI), China (Sichuan), KT161414 (Zhou et al. 2016), KT161677 (Zhou et al. 2016); (2) L.-B. Zhang et al. 5193 (CDBI), China (Guangxi), KT161409 (Zhou et al. 2016), KT161680 (Zhou et al. 2016).

***S. boninensis* Baker.** (1) Knapp 3578 (P), China (Taiwan), MZ571146 (He et al. 2021), –; (2) TNS766618 (TNS), Japan (Tokyo), AB574642 (Ebihara et al. 2010), –.

***S. brachystachya* (Hook. & Grev.) Spring** (1) J. Klackenberg 434 (S), Sri Lanka, KY022980 (Weststrand and Korall 2016b), –; (2) W.A. Sledge 913 (L), Sri Lanka, KY022979 (Weststrand and Korall 2016b), –.

***S. chaetoloma* Alston** (1) Z.-Y. Guo 2016014 (PE), China (Guizhou), MH814888 (Shalimov et al. 2019), –; (2) X.-C. Zhang 7347 (PE), China (Guizhou), MH814889 (Shalimov et al. 2019), –.

***S. chingii* Alston** (1) L.-B. Zhang et al. 6587 (CDBI, MO, VNMN, PYU), Vietnam (Lang Son), KT161417 (Zhou et al. 2016), KT161683 (Zhou et al. 2016); (2) L.-B. Zhang et al. 6594 (CDBI, MO, VNMN, PYU), Vietnam (Lang Son), KT161416 (Zhou et al. 2016), KT161868 (Zhou et al. 2016).

***S. chrysocaulos* (Hook. &**

**Grev.) Spring** (1) *Xu et al. 2014-156* (CDBI), China (Sichuan), KT161427 (Zhou et al. 2016), KT161690 (Zhou et al. 2016); (2) *X.-M. Zhou 001* (CDBI), China (Yunnan), MZ532020 (He et al. 2021), –; (3) *X.-C. Zhang 86* (PE), China (Sichuan), MH814891 (Shalimov et al. 2019), –. ***S. ciliaris* (Retz.) Spring** *Jiang 310* (PYU, CDBI), China (Hainan), KT161428 (Zhou et al. 2016), KT161691 (Zhou et al. 2016). ***S. coriaceifolia* X. M. Zhou, N. T. Lu & Li Bing Zhang** (1) *L.-B. Zhang et al. 7307* (CDBI, MO, VNMN), Vietnam (Quang Binh), MT386596 (He et al. 2021), MZ570596 (He et al. 2021); (2) *L.-B. Zhang et al. 7371* (CDBI, MO, VNMN), Vietnam (Quang Binh), MT386598 (Ye et al. 2020), MT386595 (Ye et al. 2020). ***S. decipiens* Warb.** (1) *L.-B. Zhang et al. 6761* (CDBI, MO, VNMN, PYU), Vietnam (Bac Kan), KT161439 (Zhou et al. 2016), KT161697 (Zhou et al. 2016); (2) *L.-B. Zhang et al. 6764* (CDBI, MO, VNMN, PYU), Vietnam (Bac Kan), KT161438 (Zhou et al. 2016), KT161698 (Zhou et al. 2016). ***S. densiciliata* Xin-Mao Zhou & Liang Zhang** (1) *L. Zhang et al. 2090* (KUN, PYU), China (Xizang), OQ723681 (this study), OQ728789 (this study); (2) *L. Zhang et al. 2203* (KUN, PYU), China (Xizang), OQ723684 (this study), OQ728792 (this study); (3) *L. Zhang et al. 2215* (KUN, PYU), China (Xizang), OQ723682 (this study), OQ728790 (this study); (4) *B. Xu & X.-M. Zhou 2043* (CDBI, PYU), China (Xizang), OQ723683 (this study), OQ728791 (this study). ***S. devolii* H. M. Chang** *H.-M. Chang et al. 7116* (TAIE), Unknown, MF313957 (Sheue et al. 2017), –. ***S. dianzhongensis* X. C. Zhang X.-M. Zhou 1445** (PYU), China (Yunnan), OQ723685 (this study), OQ728793 (this study). ***S. effusa* Alston** (1) *Dong 2470* (PYU), China (Guangdong), (Zhou et al. 2016), KT161705 (Zhou et al. 2016); (2) *GLG Survey 22153* (GH), China, KY023020 (Weststrand and Korall 2016b), –; (3) *L.-B. Zhang et al. 5442* (CDBI), China (Guangxi), KT161451 (Zhou et al. 2016), KT161707 (Zhou et al. 2016). ***S. goudotiana* Spring** *M. Thulin and H. Razafindraibe 11750* (UPS), Madagascar, KY023039 (Weststrand and Korall 2016b), –. ***S. goudotiana* Spring var. *abyssinica* (Spring) Bizzarri** *J. Kornaś and A. MedweckaKornaś 3688* (BR), Zamb, KY023036 (Weststrand and Korall 2016b), –. ***S. heterostachys* Baker** (1) *X.-C. Zhang 7088* (PE), China (Guizhou), MH814896 (Shalimov et al. 2019), –; (2) *X.-C. Zhang 7268* (PE), China (Guizhou), MH814897 (Shalimov et al. 2019), –. ***S. hezhangensis* P. S. Wang et X. Y. Wang** (1) *FLPH Sichuan Expedition 152002*, China (Sichuan), OM864654 (Shalimov and Zhang 2022), –; (2) *X.-C. Zhang 6830* (PE), China (Guizhou), OM864656 (Shalimov and Zhang 2022), –. ***S. kanehirae* Alston** (1) *Hovence 10079* (PTBG), Hawaii, MZ571148 (He et al. 2021), –. ***S. kurzii* Baker** (1) *X.-M. Zhou et al. PYU-S-2105* (PYU), China (Yunnan), MZ532022 (He et al. 2021), MZ570598 (He et al. 2021); (2) *X.-C. Zhang 1934* (PE), Unknown, MH814898 (Shalimov et al. 2019), –. ***S. kusaiensis* Hosok. D.H. Lorence** *9385* (PTBG), Unknown, MT657911 (Nitta et al. 2020), –. ***S. labordei* Hieron. ex Christ** (1) *Gao et al. DJY04311* (CDBI), China (Sichuan), KT161503 (Zhou et al. 2016), KT161751 (Zhou et al. 2016); (2) *X.-M. Zhou 008* (CDBI), China (Sichuan), KT161505 (Zhou et al. 2016), –; (3) *Gaoligong Shan Biodiversity Survey 18378* (GH), China (Yunnan), KY023061 (Weststrand and Korall 2016b), –; (4) *X.-C. Zhang 3356* (PE), China (Hubei), MH814899 (Shalimov et al. 2019), –. ***S. laxa* Spring** (1) *Schuettpelz 1913* (US), French Polynesia (Marquesas Islands), MT216111 (He et al. 2021), –. ***S. leptophylla* Baker** *X.-M. Zhou et al. DJY05380* (CDBI), China (Sichuan), KT161513 (Zhou et al. 2016), KT161756 (Zhou et al. 2016). ***S. lutchuensis* Koidz.** (1) *TNS101683* (TNS), Japan, MT680176 (Zhang et al. 2020), –; (2) *TNS759343* (TNS), Japan (Okinawa), AB574648

(Ebihara et al. 2010), –. ***S. medogensis* Ching et S. K. Wu** Qinghai-Xizang Complex Exped 74-4375 (PE), China (Xizang), OK247696 (Shalimov and Zhang 2021), –. ***S. megaphylla* Baker** (1) X.-H. Jin 19301 (PE), Unknown, MH814901 (Shalimov et al. 2019), –; (2) X.-M. Zhou YLZB2185 (CDBI, PYU), China (Xizang), ON994456 (Xu et al. 2022), ON994203 (Xu et al. 2022). ***S. microclada* Baker** X.-C. Zhang et al. 8307 (PE), China (Yunnan), OK247702 (Shalimov and Zhang 2021), –. ***S. miniatospora* (Dalzell) Baker** (1) J. Klackenberg and R. Lundin 567 (S), India (Kerala), KY023081 (Weststrand and Korall 2016b), –; (2) C. van Hardeveld and H. H. van der Werff 120 (U), India (Tamil Nadu), KY023080 (Weststrand and Korall 2016b), –. ***S. minutifolia* Spring** Larsen et al. 1389 (S), Thailand, KY023082 (Weststrand and Korall 2016b), –. ***S. mittenii* Baker** van Steenis 24105 (L), South Africa, KY023083 (Weststrand and Korall 2016b), –. ***S. monospora* Spring** (1) L.-B. Zhang et al. 7425 (CDBI), Vietnam (Quang Binh), MZ571145 (He et al. 2021), –; (2) L. Zhang 1296, China (Yunnan), MZ532023 (Xu et al. 2022), –. ***S. morganii* Zeiller** P. Korall 2006-29 (S), Peninsular Malaysia, KY023088 (Weststrand and Korall 2016b), –. ***S. neocaledonica* Baker** (1) sc s.n. Unknown, KY985453 (Klaus et al. 2017), –; (2) Wikstrom 244 (S), New Caledonia, KY023095 (Weststrand and Korall 2016b), –. ***S. nipponica* Franch. & Sav.** (1) Zhou et al. DJY07479 (CDBI), China (Sichuan), KT161542 (Zhou et al. 2016), KT161784 (Zhou et al. 2016). ***S. ornata* Spring** (1) Zhang 4958 (CDBI), China (Guizhou), KT161522 (Zhou et al. 2016), KT161768 (Zhou et al. 2016); (2) Zhang et al. 6935 (CDBI, MO, VNMN, PYU), Vietnam (Ha Giang), KT161526 (Zhou et al. 2016), KT161772 (Zhou et al. 2016). ***S. qingchengshanensis* Li Bing Zhang & X. M. Zhou** (1) Gao et al. DJY04053 (CDBI), China (Sichuan), KT161381 (Zhou et al. 2016), KT161649 (Zhou et al. 2016); (2) Z.-L. Liang & X. Pu 056 (CDBI, PYU), China (Sichuan), MZ532027 (He et al. 2021), MZ570603 (He et al. 2021). ***S. reineckeii* Hieron.** (1) K.R. Wood 16944 (PTBG), Samoa (Savaii), MT657902 (Nitta et al. 2020), –; (2) McKee 2907-P7338 (L), Samoa, KY023129 (Weststrand and Korall 2016b), –. ***S. repanda* (Desv. ex Poir.) Spring** (1) He & Jiang 405-1 (CDBI), China (Yunnan), KT161584 (Zhou et al. 2016), –; (2) Z.-R. He & X.-M. Zhou 119 (PYU, CDBI), China (Yunnan), KT161583 (Zhou et al. 2016), KT161816 (Zhou et al. 2016); (3) He s.n. China (Yunnan), KT161817 (Zhou et al. 2016). ***S. subdiaphana* (Wall. ex Hook. et Grev.) Spring** (1) Y.-D. Wu 840 (PE), China (Yunnan), OM864659 (Shalimov and Zhang 2022), –. ***S. submonospora* Shalimov et X.-C. Zhang** X.-C. Zhang et al. 8111 (PE), China (Yunnan), OM864660 (Shalimov and Zhang 2022), –. ***S. subvaginata* Shalimov et X. C. Zhang** (1) H. Liu 183 (PE), China (Sichuan), MT680178 (Zhang et al. 2020), –; (2) X.-C. Zhang et al. 8838 (PE), China (Sichuan), MT680179 (Zhang et al. 2020), –; (3) X.-C. Zhang et al. 9450 (PE), China (Sichuan), MT680181 (Zhang et al. 2020), –. ***S. trichophylla* K. H. Shing** (1) W.-M. Chu et al. 29310 (PYU), China (Yunnan), KT161622 (Zhou et al. 2016), KT161846 (Zhou et al. 2016); (2) Chu et al. 31925 (PYU), China (Yunnan), KT161621 (Zhou et al. 2016), KT161847 (Zhou et al. 2016). ***S. uncinata* (Desv. ex Poir.) Spring** Zhang & Zhou DJY04101 (CDBI), China (Sichuan), KT161626 (Zhou et al. 2016), KT161852 (Zhou et al. 2016). ***S. vaginata* Spring** (1) D.E. Boufford et al. 28593 (A), China (Sichuan), KY023167 (Weststrand and Korall 2016b), –; (2) D.E. Boufford 37640 (A), China (Gansu), KY023168, (Weststrand and Korall 2016b), –; (3) B. Bartholomew et al. 367 (PE), China (Guizhou), MT680182 (Zhang et al. 2020), –; (4) Z.-S. Zhang 161 (PE), China (Shanxi), MH814907 (Shalimov et al. 2019), –. ***S. whitmeei* Baker** K.R. Wood

17032 (PTBG), Samoa (Savaii), MT657910 (Nitta et al. 2020), –. **S. wuyishanensis** **K. W. Xu, X. M. Zhou & Y. F. Duan** (1) *K.-W. Xu* WY518 (NF), China (Fujian), OQ723687 (this study), OQ728795 (this study); (2) *K.-W. Xu* WY521 (NF), China (Fujian), OQ723686 (this study), OQ728794 (this study). **S. xipholepis** **Baker** (1) *S.-Y. Dong* 2377 (PYU), China (Guangdong), KT161645 (Zhou et al. 2016), –; (2) *K.U. Kramer* et al. 8329 (U), China (Hong Kong), KY023179 (Weststrand and Korall 2016b), –; (3) *L.-B. Zhang* et al. 6668 (CDBI, MO, VNMN, PYU), Vietnam (Bac Kan), KT161646 (Zhou et al. 2016), KT161867 (Zhou et al. 2016); (4) *X.-C. Zhang* 7422 (PE), China (Guizhou), MH814908 (Shalimov et al. 2019), –. **S. yunckeri** **Alston** *Yuncker* 15933 (U), Tonga, KY023182 (Weststrand and Korall 2016b), –. **S. zhangii** **S. Y. Dong** *Dong* 5511, China (Yunnan), MW316869 (Huang et al. 2022), –.



# A new remarkable *Vanilla* Mill. (Orchidaceae) species endemic to the Espinhaço Range, Brazil: its phylogenetic position and evolutionary relationships among Neotropical congeners

Emerson Ricardo Pansarin<sup>1</sup>, Euler da Luz Fernandes Menezes<sup>2</sup>

<sup>1</sup> Department of Biology, Faculty of Philosophy, Sciences and Literature of Ribeirão Preto, University of São Paulo, Av. Bandeirantes 3900, Ribeirão Preto, SP, 14040-901, Brazil

<sup>2</sup> Postgraduate Program of Graduation in Forest Science, Federal University of Vales do Jequitinhonha e Mucuri (UFVJM), Highway MGT 367-km 583, n° 5.000, Alto da Jacuba, Diamantina, MG, 39.100-000, Brazil

Corresponding author: Emerson Ricardo Pansarin (epansarin@ffclrp.usp.br)

## Abstract

During surveys conducted on Neotropical *Vanilla*, a new endemic species was found in the Brazilian campos rupestres of the Espinhaço Range. Here, this new remarkable *Vanilla* species, namely *V. rupicola* Pansarin & E.L.F. Menezes, is described and illustrated. A phylogeny for *Vanilla* is presented and the relationships between Neotropical species are discussed. The position of *V. rupicola* among Neotropical *Vanilla* is discussed within an evolutionary context. *Vanilla rupicola* is recognized by its rupicolous habit, its reptant stems, and its sessile and rounded leaves. This remarkable new taxon emerges in a clade that includes *V. appendiculata* Rolfe and *V. hartii* Rolfe. Vegetative and floral features support a close relationship between *V. rupicola* and sister taxa, mainly regarding the apical inflorescence (*V. appendiculata*), the type of appendages of the central crest of the labellum, and the labellar color pattern. Phylogenetic inference suggests that the circumscription of Neotropical *Vanilla* groups needs revision.

**Key words:** Atlantic forest, Brazilian campos rupestres, Cerrado vegetation, evolution, molecular phylogeny, Neotropics, orchids, Vanilleae, Vanilloideae



Academic editor: Timothée Le Péchon

Received: 14 February 2023

Accepted: 26 May 2023

Published: 8 June 2023

**Citation:** Pansarin ER, Menezes ELF (2023) A new remarkable *Vanilla* Mill. (Orchidaceae) species endemic to the Espinhaço Range, Brazil: its phylogenetic position and evolutionary relationships among Neotropical congeners. *PhytoKeys* 227: 151–165. <https://doi.org/10.3897/phytokeys.227.101963>

**Copyright:** © E. R. Pansarin & E. da L. F. Menezes. This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

An endemism area is defined as a geographic region that contains species that do not occur anywhere else (e.g. Platnick 1991). Among the Brazilian biodiversity hotspots, the Espinhaço Range of Minas Gerais (ERMG), situated between the Atlantic Forest and Cerrado Biomes, shows one of the richest floras in Brazil (Myers et al. 2000), with a high frequency of endemisms (Hensold 1988; Rapini et al. 2002; Versieux and Wendt 2007). Orchidaceae Juss. is one of the most diverse and important plant families in ERMG, with many endemic taxa having been described (Barros 1987; Barros and Pinheiro 2004; Azevedo and Van Den Berg 2007; Batista et al. 2016; Salazar et al. 2019), including members of the Vanilloideae Szlach. (Pansarin 2004).

Vanilloideae is divided into two tribes: Pogonieae Pfitzer ex Garay & Dunst. and Vanilleae Blume. With more than 100 species distributed throughout tropical

regions of Asia, Africa and Americas, *Vanilla* Mill. is the most species-rich genus among Vanilleae (e.g. Cameron 2003). *Vanilla* is monophyletic (*Dictyophyllaria* Garay included; Pansarin 2010; Pansarin et al. 2012) with three well-supported clades, two of which occur throughout the Neotropics (Bouetard et al. 2010; Pansarin and Ferreira 2022). Among *Vanilla*, a Neotropical clade with thin and reticulate-veined leaves emerges as a sister to a clade that includes two sub-clades, an African/Asian/Caribbean group and a second, strictly Neotropical one. In the latter, the epiphyte and bird-pollinated *V. palmarum* (Salzm. ex Lindl.) Lindl. is positioned as a sister to a hemi-epiphytic clade whose species are almost completely pollinated by euglossine bees (Pansarin and Ferreira 2022).

Besides showing high diversity and ecological importance (Pansarin and Pansarin 2014; Pansarin et al. 2014), *Vanilla* is also the most economically important genus among the orchids since the fruits of the Neotropical *V. planifolia* Andrews and their relatives are a source of vanillin flavor. Efforts are currently underway to determine the diversity and the natural history of Neotropical *Vanilla* (Pansarin 2019, 2022; Pansarin and Ferreira 2022; Pansarin and Suetsugu 2022), and its potential use for gastronomy and industry (e.g. Oliveira et al. 2022). However, there is still much to know since new species have been found and described, notably in the Brazilian flora (e.g. Pansarin and Miranda 2016; Fraga et al. 2017).

In the course of the developing studies on Neotropical *Vanilla*, a new species has been found in Brazilian campos rupestres. A taxonomic description of this new remarkable *Vanilla* is presented here and a morphological comparison with other Neotropical taxa is provided. The phylogenetic position of *V. rupicola* within *Vanilla* and the relationships among Neotropical groups are discussed based on a molecular phylogeny for the genus.

## Materials and methods

The fieldwork was performed in the municipality of Diamantina (approx. 18°14'17"S, 43°36'40"W; 1,288 m elevation) in the state of Minas Gerais, Southeastern Brazil. The Diamantina Plateau is situated in the southern region of the Espinhaço Range, at the boundaries of Serra do Cipó and Grão Mogol (Gonçalves et al. 2017). It is included in the Espinhaço Range Biosphere Reserve (UNESCO 2005), located between the Atlantic Forest and the Cerrado domains, two of the main global biodiversity hotspots in the world (Myers et al. 2000). The climate of the region is classified as "Cwb", namely subtropical highland climate with dry winters (Köppen 1948).

Fresh and herbarium material of flowering and fruiting plants was used for the study. Photographs were based on specimens collected in the field. Measurements were made directly on floral structures using a Vernier Caliper. The vegetative structures, inflorescence and flowers were photographed with a Nikon D-SLR D800 camera and a Micro Nikkor 105 mm f2.8 lens. Floral details were analyzed with a Stereozoom Leica S8 APO stereomicroscope with an integrated photo output. Digitized images were used for diagramming a template over a black background, following the model presented by Hoehne (1945), using a Microsoft PowerPoint software. The final template was exported as a 600 dpi .TIFF file.

The terminology for describing shapes followed Radford et al. (1974). Features specific to Orchidaceae were based on Dressler (1993) and Pridgeon et al. (1999). The infrageneric classification of Neotropical *Vanilla* groups followed Soto-Arenas and Cribb (2010). The original description and digital images from holotypes of related species of *Vanilla* were consulted. Plant specimens were vouchered according to usual techniques (Fidalgo and Bononi 1989) and then deposited in the BHCB, DIAM, HDJF, LBMBP, SPFR, SPF and UEC herbaria, which were also examined in order to study the Brazilian diversity of *Vanilla*. Additional living specimens were collected in the field and are under cultivation at the *Vanilla* germplasm bank from the LBMBP Orchid House (Orchidarium of the Laboratory of Molecular Biology and Systematics of Plants), University of São Paulo (FFCLRP-USP), municipality of Ribeirão Preto (approx. 21°10'S, 47°48'W; 546 m a.s.l.), state of São Paulo, Brazil, available at <https://www.lbmbplab.net/vanillacollection>.

The conservation status of the new taxon was defined according to the IUCN red list categories and criteria and guidelines (IUCN 2012, 2016).

### **Taxon sampling for phylogenetic analysis**

A total of 42 *Vanilla* accessions (37 species) were analyzed and are referred to here as the ingroup, which represents an increase of 10 *Vanilla* species (16 new accessions) over previous investigations (Pansarin and Ferreira 2022). *Lecanorchis multiflora* J.J. Sm. was selected as an outgroup according to previous phylogenetic studies on Vanilloideae (e.g. Pansarin and Ferreira 2022). A data matrix was built based on sequences available in the genbank database and obtained during the development of this study (Suppl. material 1). A list of ingroup and outgroup species, vouchers and GenBank accession numbers is given in Suppl. material 1.

### **DNA extraction, amplification and sequencing**

DNA of *Vanilla* species was extracted from fresh material according to a modified CTAB method (Doyle and Doyle 1987). The amplifications were carried out using 50 µL PCR volumes. Relaxation of the DNA strands was achieved by the addition of a 5M betaine solution to the PCR preparations. Primers of the nuclear ribosomal transcribed spacer region (ITS), including the 5.8S gene (Sun et al. 1994) were used for amplification and sequencing. *Taq* DNA polymerase was added to the PCR mixture at 80 °C following a 10 min period of denaturation at 99 °C in the thermocycler. Thirty-five cycles were run according to the following program: denaturation, 1 min, 94 °C; annealing, 45 sec, 64 °C; extension, 1 min, 72 °C; final extension, 5 min, 72 °C. Amplified PCR products were purified using GFX PCR columns (GE Health Care). Sequencing reactions were prepared using Big Dye 3.1 (ABI), purified PCR products and the same aforementioned primers. Samples were dehydrated and re-suspended with loading dye. Sequences were obtained using an Applied Biosystems automated sequencer model 3100. Sequence Navigator and Autoassembler (Applied Biosystems) software was used for sequence editing and assembly of complementary and overlapping sequences. DNA sequences were aligned using the BioEdit version 5.0.9 software (Hall 1999). The sequence alignment is available upon request from the first author.

## Phylogenetic analyses

A data matrix of ITS containing 43 taxa was used for phylogenetic analyses.

Maximum parsimony analysis (MP) was run with PAUP\* version 4.0b5 (Swofford 2001) software. A heuristic search was conducted with 1000 replicates of random taxon entry additions, MULTREES option, and the tree bisection-reconnection (TBR) swapping algorithm, holding 10 trees per replicate and saving all the shortest trees. Support for clades was assessed using 1,000 bootstrap replicates (Felsenstein 1985). Bootstrap support (BS) values above 50% were calculated and mapped above the branches of the consensus tree. For bootstrap support levels, we considered bootstrap percentages of 50–70% as weak, 71–85% as moderate, and >85% as strong (Kress et al. 2002).

Maximum Likelihood (ML) analysis was run using the MEGA X tool (Kumar et al. 2018) with bootstrapping for 3,000 replicates. The analysis was based on the Kimura 2-parameter model (Kimura 1980). Initial trees for the heuristic search were obtained automatically by applying Neighbour-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with the superior log likelihood value.

Bayesian Inference (BI) was conducted using the MrBayes program, version 3.1 (Ronquist and Huelsenbeck 2003). The optimal model of sequence evolution for each partition was selected using MEGA X (Kumar et al. 2018) and Bayesian Information Criterion (BIC). The software selected the HKY+G as the best evolution model for the ITS region. Four Markov chains were run simultaneously for three million generations, with parameters sampled every 100 generations. The consensus tree was calculated after removal of the first 3,000 trees, which were considered to be “burn-in”. Posterior probability (PP) values above 0.5 were calculated and mapped below the branches of the consensus tree.

## Results

### Taxonomic treatment

#### *Vanilla rupicola* Pansarin & E.L.F.Menezes, sp. nov.

urn:lsid:ipni.org:names:77320774-1

Figs 1, 2

**Type.** BRAZIL. Minas Gerais: Mun. Diamantina, Distrito de Sopa, Afloramento rochoso ca. 2 km de Morrinhos, 18°11'43"S, 43°43'18"W, 817 m, 29 November 2022, E.R. Pansarin & E.L.F. Menezes 1561 (holotype: SPFR18105!).

*Vanilla rupicola* differs from all Neotropical *Vanilla* species by its rupicolous habit, its reptant stem and its rounded leaves. The overall characteristics of *V. rupicola* resemble those of *V. appendiculata* Rolfe and *V. hartii* Rolfe. However, the remarkable new taxon (*V. rupicola*) is easily distinguishable from both related species by its leaves and flowers, which are smaller than those of *V. appendiculata* and larger than those of *V. hartii* (Table 1), its sessile leaves (vs. petiolate in *V. appendiculata* and *V. hartii*), and its papillose labellar protrusions (vs. finger-like in *V. appendiculata* and verrucose in *V. hartii*).



**Figure 1.** Habit of *Vanilla rupicola* Pansarin & E.L.F. Menezes on the rock outcrops of the Espinhaço Range, Minas Gerais, Brazil. Note the creeping stem on the rock.

**Table 1.** Comparison of the morphological features of *Vanilla rupicola* and of closely related species. Morphological data from *V. hartii* were obtained from Ferreira et al. (2020), while characteristics of *V. appendiculata* were obtained from Engels and Ferneda Rocha (2016)<sup>a</sup> and Barona-Colmenares (2018)<sup>b</sup>.

Species characteristic	<i>Vanilla rupicola</i>	<i>Vanilla appendiculata</i>	<i>Vanilla hartii</i>
Habit	rupicolous	hemiepiphytic <sup>a, b</sup>	hemiepiphytic
Stem	reptant	scandent <sup>a, b</sup>	scandent
Leaves	3.2–9 × 2.8–5.2 cm	13–19 × 3.9–5.7 cm <sup>a</sup> 14–17.7 × 4.2–49 cm <sup>b</sup>	6.5–8 × 2.5–3.5 cm
Leaves	sessile	petiolate <sup>a, b</sup>	petiolate
Leaf blade	ovate to rounded	obovoid <sup>a</sup> spatulate <sup>b</sup>	elliptic
Inflorescence	apical/lateral	apical <sup>a, b</sup>	lateral
Sepals	5.8–6.3 × 1–1.3 cm	6.6 × 0.7 cm <sup>a</sup> 7.5–7.8 × 0.8–1.1 cm <sup>b</sup>	4.9–5.3 × 0.8–1.1 cm
Petals	5.7–6.2 × 0.7–1.2 cm	6.5 × 0.6 cm <sup>a</sup> 7.6–7.7 × 0.7–0.8 cm <sup>b</sup>	4.9–5.1 × 0.7–0.9 cm
Labellum	5.6–6.3 × 3.2–3.5 cm	6.8 × 1.6 cm <sup>a</sup> 3.8 × 2.9 cm <sup>b</sup>	4.4–4.7 × 2.3–2.4 cm
Labellar protrusions	papillous	finger-like <sup>b</sup>	verrucose
Column	4.2–4.8 × 0.3–0.4 cm	5.4 × 0.2 cm <sup>a</sup> 6.1 × 0.3 cm <sup>b</sup>	3.8–4 × 0.2–0.3 cm

**Description.** Rupicolous herbs up to 12 m in length. Roots axillary, 1.8–2.2 mm diam., yellowish-green, one per node. Stem reptant, flexuous, cylindrical, fleshy, glabrous, green to yellowish-green; internodes 40–130 × 3–13 mm. Leaves 3.2–9 × 2.8–5.2 cm, alternate, ovate to rounded, fleshy, glabrous, green to yellow-



**Figure 2.** *Vanilla rupicola* Pansarin & E.L.F. Menezes **A** part of a flowering plant showing the stem and a lateral inflorescence with a typical-colored flower **B** detail of an apical inflorescence of an albino plant. Note the white flower **C** leaf and inflorescence **D** detail of a raceme. Note the addressed floral bracts **E** dissected perianth. The detail shows the penicillate callus and the central labellar crest **F** detail of the adaxial surface of a petal showing the longitudinal keel **G** detail of a flower with a typical color showing the apex of the labellum, the penicillate callus and anther **H** detail of an albino flower showing the apex of the labellum, the penicillate callus and anther. Note that the labellum apex is more projected than in the typically-colored flower **I** detail of the apex of the labellum of a typically-colored flower showing the yellowish longitudinal lines and the yellow projections **J** detail of the apex of the labellum of an albino flower showing the whitish projections **K** labellum in lateral view **L** column in lateral view **M** apex of the column: in lateral view with an articulated anther (above), in lateral view with a disarticulated anther (mid), and in abaxial view (below) **N** immature fruit.

ish-green, apex acute to acuminate, sessile. Inflorescence 4.5–6 cm long, apical or axillary, racemose, with up to 10 flowers opening in succession; one flower opening each morning; bracts 5–9 × 3.5–7 mm progressively smaller toward the apex, alternate, triangular to ovate, coriaceous, adpressed to patent, concave, apex acute to acuminate. Flowers resupinate, whitish-green, pedicellate, abscission layer between perianth and ovary present; pedicel with ovary 2.8–3.2 × 0.40–0.52 cm, green, incurved, dilated to the apex, triangular in transverse section. Sepals 5.8–6.3 × 1–1.3 cm, free, oblanceolate, fleshy, slightly concave, pale green, margin entire, slightly incurved, apex acute to obtuse; dorsal sepal symmetric; lateral sepals asymmetric. Petals 5.7–6.2 × 0.7–1.2 cm, free, linear to slightly spatulate, asymmetric, membranous, pale green, apex acute to acuminate, adaxial surface with a longitudinal rib. Labellum 3-lobed, 5.6–6.3 × 3.2–3.5 cm, white, inner surface with longitudinal brown stripes, with a prominent central crest near the apex, and with a penicillate callus just below the anther; central crest ca. 4–5 mm wide, with yellow or white papillose protrusions arranged in five longitudinal lines near the apex; penicillate callus 5–6 × 5.2 mm, white; margins fused from the base to ca.  $\frac{3}{4}$  of the column length forming a tubular nectar chamber; nectary chamber 2.2–2.6 cm in length; lateral lobes rounded, overlapping above the column, undulate margins; apical lobe rounded to emarginated, reflexed, undulate to slightly fimbriate. Column 4.2–4.8 × 0.3–0.4 cm, semi-cylindrical, slender, sinuous, white, attenuate base, dilated to the apex, with white-hyaline hairs close to the stigma, apex ending in a membranous ochrea; anther 4.9–5.1 × 3.9–4.2 mm, white, versatile; rostellum 3.8–4.1 × 3.9–4.0 mm, rectangular to trapezoidal, white. Fruits 9–13 × 1–1.8 cm, linear, tapering towards the apex, triangular in transverse section, green when immature. Seeds ovate, black.

**Distribution and ecology.** The species has been reported for the campos ruprestres vegetation of the Espinhaço Range of Minas Gerais (ERMG), municipality of Diamantina, Southeastern Brazil. In this locality, *Vanilla rupicola* shows a repent habit on rock outcrops and rooting in rock clefts. The elevation is from 800 to 1300 m a.s.l. The flowers produce a sweet fragrance perceptible during the hottest hours of the day. Each flower lasts ca. 12 hours.

**Phenology.** *Vanilla rupicola* has been collected with flowers from late September to early November. The fruits ripen from May to June.

**Etymology.** The specific epithet (*rupicola*) refers to the rupicolous habit, uncommon among Neotropical *Vanilla*.

**Conservation status.** *Vanilla rupicola* is a rare species currently known to grow in a mountain-chain of Diamantina, in the ERMG. The populations found are composed of few specimens. According to the IUCN red list categories and criteria and guidelines, the species can tentatively be considered as Endangered (EN) due to its geographic range which is estimated to consist of 30 km<sup>2</sup>, and fewer than 250 individuals were recorded in the occurrence area.

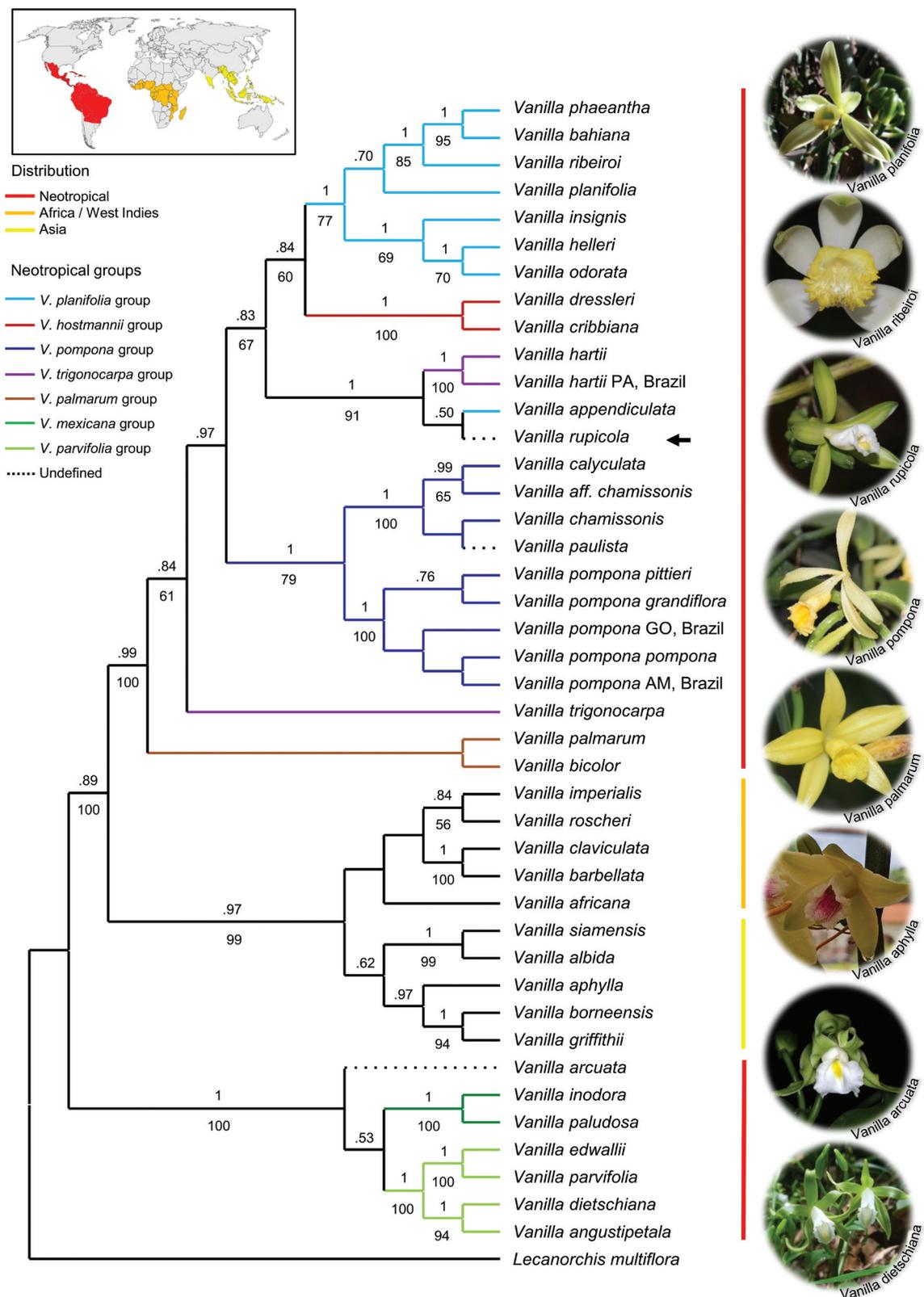
**Additional specimens examined (paratypes).** BRAZIL. Minas Gerais: Mun. Diamantina, Parque Nacional das Sempre Vivas, Próximo a Serra do Landim, 17°53'27,6"S, 43°45'51.3"W, 1293 m elev., 22 October 2019, *E.L.F. Menezes 133* (DIAM!). Município de Sopa. Estrada vicinal, 18°11'33.2"S, 43°47'07.5"W, 1210 m alt., 19 November 2022, *E.L.F. Menezes 752* (HDJF!); Distrito de Sopa, Afloramento rochoso ca. 2 km de Morrinhos, 18°11'43"S, 43°43'18"W, 817 m, 29 November 2022, *E.R. Pansarin & E.L.F. Menezes 1562* (BHCB!); Distrito de Sopa, Afloramento rochoso ca. 2 km de Morrinhos, 18°11'43"S, 43°43'18"W,

817 m, 29 November 2022, *E.R. Pansarin & E.L.F. Menezes 1563* (UEC!); Distrito de Sopa, Afloramento rochoso ca. 2 km de Morrinhos, 18°11'43"S, 43°43'18"W, 817 m, 29 November 2022, *E.R. Pansarin & E.L.F. Menezes 1564* (SP!); Distrito de Sopa, Afloramento rochoso ca. 2 km de Morrinhos, 18°11'43"S, 43°43'18"W, 817 m, 29 November 2022, *E.R. Pansarin & E.L.F. Menezes 1565* (LBMBP!).

**Morphological affinities.** *Vanilla rupicola* is easily recognized by its uncommon rupicolous habit, by its reptant stems, and by its sessile and rounded leaves. These characteristics differ significantly from those of the remaining non-membraceous *Vanilla* species, which are characterized by their hemiepiphytic or more rarely epiphytic habit and by their elliptic to lanceolate leaves. Floral features suggest a close relationship between *V. rupicola* and some species currently recognized in the *V. planifolia* group and *V. trigonocarpa* group mainly regarding the type of appendages of the central crest of the labellum, and labellar color pattern, with longitudinal brown lines over a white background that converge at the entrance of the nectary. In addition, species of the *V. planifolia* group show a white penicillate callus just below the gynostemium apex. Among the members currently recognized in the *V. planifolia* group, our data suggest taxonomic affinities between *V. rupicola* and the Amazonian *V. appendiculata*. In fact, both species share characteristics that are uncommon among Neotropical *Vanilla*, such as the production of apical inflorescences and ovate to obovoid leaf blades. The inflorescences of members of the *V. planifolia* group are lateral, and their leaves are elliptical to lanceolate. In addition, *V. rupicola* also shares some floral features with the Amazonian *V. hartii* (currently included in the *V. trigonocarpa* group), such as the lip lobes with undulate margins, labellar protrusions arranged on five longitudinal lines near the apex, and brown lines converging at the nectar chamber. The main differences between *V. rupicola* and related species (*V. appendiculata* and *V. hartii*) are summarized in Table 1.

### Phylogenetic relationships

Phylogenies obtained by analysis of the ITS1-5.8S-ITS2 region using distinct methods (BI, ML and MP) yielded trees with congruent topologies (ML (Fig. 3) is shown). In all analyses, the Neotropical *Vanilla* with reticulate-veined leaves (PP 1, BS 100%; Fig. 3) was recovered as sister to a large clade (PP .89, BS 100%) with two subclades: an Old-World/Caribbean clade (PP .97, BS 99%), and a well-supported clade including the remaining Neotropical *Vanilla* (PP .99, BS 100%; Fig. 3). Among the Neotropical reticulate-veined *Vanilla*, *V. arcuata* Pansarin & Miranda emerged as sister -without support- to a clade containing two sister groups, the *Vanilla mexicana* group, (*V. inodora* Schiede/*V. paludosa* Pansarin, J.M. Aguiar & A.C. Ferreira; PP 1, BS 100%) and the *V. parvifolia* group (*V. diestschiana* Edwall, *V. angustipetala* Schltr., *V. edwallii* Hoehne and *V. parvifolia* Barb. Rodr.; PP 1, BS 100%). Two well-supported clades were recovered within the latter group: *V. diestschiana*/*V. angustipetala* (PP 1, BS 94%), and *V. edwallii*/*V. parvifolia* (PP 1, BS 100%; Fig. 3). Within the Old-World/Caribbean *Vanilla*, the phylogenetic analyses (BI, ML and MP) recovered two poorly supported subclades: an Asian clade, and an African/Caribbean clade (Fig. 3). In the Asian *Vanilla*, the clade including *V. siamensis* Rolfe ex Downie and *V. albida* Blume (PP 1, BS 99%) emerged as sister to a clade comprising *V. aphylla* Blume/(*V. borneensis* Rolfe/*V. griffithii* Rchb. f.). In the African/Caribbean clade, *V. africana*



**Figure 3.** Maximum Likelihood analysis of *Vanilla* (Orchidaceae) based on ITS (nrDNA). Bootstrap values (%) >50 obtained by maximum parsimony analysis (MP) are given below the branches, while posterior probabilities values > 0.5 (BI) are given above branches. Vertical colored bars refer to the geographic distribution of *Vanilla*. The black arrow indicates the position of *V. rupicola* among the Neotropical thick-leaved *Vanilla*. The colored branches in the cladogram refer to Neotropical *Vanilla* groups according to the infrageneric classification presented in Soto-Arenas and Cribb (2010). AM = Amazonas, GO = Goiás, PA = Pará.

Lindl. was nested as sister to two subclades: a West Indies clade that included *V. claviculata* Sw. and *V. barbellata* Rchb. f. (PP 1, BS 100%), and an African clade containing *V. imperialis* Kraenzl. /*V. roscheri* Rchb. f. (PP .84, BS 56%; Fig. 3). Within the thick-leaved Neotropical *Vanilla* (PP .99, BS 100%), species currently recognized among the *V. palmarum* group, i.e. the epiphytes *V. palmarum* and *V. bicolor* Lindl., emerged as sisters to a large clade whose species are mostly hemiepiphytes or nomadic vines (PP .84, BS 61%). Within the hemiepiphytic clade, the Amazonian *V. trigonocarpa* Hoehne emerged as sister to a clade including the remaining Neotropical taxa. The latter showed two subclades: one including the members of the *V. pompona* group (*V. pompona* Schiede, *V. calyculata* Schltr., and *V. chamissonis* Klotzsch, besides *V. paulista* Fraga & Pansarin (PP 1, BS 79%)), and the other a large and predominantly Amazonian clade that contained the remaining Neotropical taxa (Fig. 3). In the latter, a strongly supported clade (PP 1, BS 91%) including *V. hartii* (*V. rupicola*/*V. appendiculata*) emerged as sister to a large clade in which the members of the *V. hostmanii* group, *V. dressleri* Soto Arenas/*V. cribbiana* Soto Arenas (PP 1, BS 100%) were recovered as sister to a large clade that included two subclades: *V. insignis* Ames/(*V. odorata* C. Presl/*V. helleri* A.D. Hawkes) plus *V. planifolia*/(*V. ribeiroi* Hoehne/(*V. phaeantha* Rchb. f./*V. bahiana* Hoehne)) with moderate support (PP 1, BS 77%; Fig. 3).

## Discussion

Neotropical *Vanilla* species are represented by two distinct lineages, one including representatives with membranous leaves and the other including species with non-membranous, usually fleshy, leaves. Our results strongly agree with previous phylogenetic inferences based on the sequencing of the cpDNA (Boutard et al. 2010) and nrDNA (Pansarin and Ferreira 2022) regions. The membranous reticulate-veined *Vanilla* (i.e. subgenus *Vanilla*; Soto-Arenas and Cribb 2010) includes members of two groups, i.e.: *V. mexicana* group and *V. parvifolia* (non *V. parviflora*) group. In fact, our data matrix including rare and endemic species from Brazil recovered both groups proposed for the subgenus *Vanilla*. However, although *V. arcuata* is a member of the membranaceous-leaved *Vanilla* (Pansarin and Miranda 2016), our data suggest further studies are needed in order to better determine the circumscription of infrageneric groups proposed by Soto-Arenas and Cribb (2010), as this Brazilian species emerges in a basal position within this Neotropical subgenus (Fig. 3).

Among the non-membranaceous *Vanilla* taxa, the basal taxa *V. palmarum* and *V. bicolor*, both occurring as epiphytes on palms (e.g. Soto-Arenas and Cribb 2010; Van Dam et al. 2010, E.R. Pansarin, pers. obs.), emerge as sisters to the hemiepiphytic and thick-leaved groups. Among the groups proposed by Soto-Arenas and Cribb (2010), the *V. pompona* group is recovered as monophyletic (*V. paulista* included). Within this clade, *V. aff. chamissonis*, which is found in semideciduous forests and Cerrado areas of Brazil, is more related to *Vanilla calyculata* (= *V. columbiana* Rolfe, Karremans et al. 2020) than to *Vanilla chamissonis*, which occurs along the Atlantic coast. Further studies involving members of this *Vanilla* group are needed in order to better understand their species boundaries. According to the classification of Soto-Arenas and Cribb (2010), *V. appendiculata* is a member of the *V. planifolia* group, while *V. hartii* has been placed in the *V. trigonocarpa*

group. Our data suggest that realignment is necessary because *V. trigonocarpa* emerges in a basal position within the non-membranous hemiepiphyte *Vanilla*, while *V. hartii* emerges among the most derived clades in the genus. Indeed, the clade containing *V. hartii*, *V. rupicola* and *V. appendiculata* emerges as sister to the *V. hostmanii* group. Consequently, both the *V. trigonocarpa* group and *V. planifolia* group are polyphyletic (Soto-Arenas and Cribb 2010). According to the current *Vanilla* classification, *V. rupicola* emerges in an unrecognized group. As detailed in the results section (see Morphological Affinities and Table 1), *V. rupicola* shares a number of characteristics with *V. hartii* and *V. appendiculata*, mainly with regard to leaf shape, inflorescence position (i.e. apical, as in *V. appendiculata*), the type of appendages of the central crest of the labellum, and labellar color pattern (Ferreira et al. 2020; Engels and Ferneda Rocha 2016; Barona-Colmenares 2018).

The rupicolous habit of *V. rupicola* is unique among the members of the non-membranaceous Neotropical *Vanilla*. The emergence of a rupicolous species within an entirely hemiepiphytic clade appears to be a result of evolutionary convergence (reversion), as some leafless Old-World species grow on rocks (e.g. Andriamihaja et al. 2020). Despite its rarity in Neotropical *Vanilla*, the rupicolous habit is widespread among Angiosperms distributed in the Espinhaço Range (e.g. Barros 1987; Azevedo and Van Den Berg 2007). Indeed, Neotropical *Vanilla* species are diverse and widespread throughout the Atlantic Forest and the Amazon Biome (Hoehne 1945). Based on the evidence that *V. rupicola* emerges in an essentially Amazonian clade, it seems plausible that the ancestor of this new taxon derived from an Amazonian ancestor adapted to the environmental conditions of the Espinhaço Range and evolved in this particular environment. Nowadays, there is consensus about the evolution of the Neotropical Biomes. During the Paleogene, the ancient Amazon Forest and Atlantic Forest were spatially interconnected and continuous (Morley 2000). The Espinhaço refuges evolved between the two Biomes as a consequence of extreme environmental conditions and climatic fluctuations during the Tertiary and Quaternary periods (Zappi 2008). Their unique geomorphological and climatic conditions resulted in a huge number of endemisms (Rapini et al. 2008; Zappi 2008), whose exclusive diversity is the consequence of a long process of evolution in this singular environment (Silva et al. 2008). Many orchids occur exclusively in the Espinhaço Range of Minas Gerais (e.g. Barros 1987; Azevedo and Van Den Berg 2007; Batista et al. 2016; Salazar et al. 2019). Here, an endemic *Vanilla* from the ERMG is reported for the first time. This is not surprising because Brazil, with more than 38 species, is the center of diversification for Neotropical *Vanilla* (Pansarin 2019). Furthermore, five species are endemic to the Brazilian Biomes (Hoehne 1945; Pansarin 2010; Pansarin and Miranda 2016; Fraga et al. 2017). Therefore, knowledge about the taxonomy and phylogeny of Brazilian *Vanilla* is fundamental in order to understand the evolution and natural history of this Pantropical orchid genus (Pansarin et al. 2012).

## Acknowledgements

The first author thanks ICMBIO for permission to collect (Protocol SISBIO number 35178-1), and Elettra Greene for English correction. E.L.F.M. Thanks are due to Fabiane Nepomuceno da Costa (DIAM) and Evandro Luiz Mendonça Machado (HDJF) for logistical support and to FAPEMIG for granting a scholarship.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

Research supported by the São Paulo Research Foundation – FAPESP (Grant 2018/07357-5) and by CNPq (Productivity Research Grant 301773/2019-0).

### Author contributions

Both authors have read and approved the manuscript: E.R.P. - concept of the study, field work, phylogenetic analysis, preparation of draft version of manuscript, and contribution to final version; E.L.F.M. - field work, and contribution to final version.

### Author ORCIDs

Emerson Ricardo Pansarin  <https://orcid.org/0000-0002-0355-8363>

Euler da Luz Fernandes Menezes  <https://orcid.org/0000-0002-1861-9552>

### Data availability

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

## References

- Andriamihaja CF, Ramarosandratana AV, Grisoni M, Jeannoda V, Besse P (2020) The leafless *Vanilla* species-complex from the South-West Indian Ocean region: A taxonomic puzzle and a model for orchid evolution and conservation. *Research. Diversity (Basel)* 12(12): 443. <https://doi.org/10.3390/d12120443>
- Azevedo CO, Van Den Berg C (2007) Análise comparativa de áreas de campos rupes-tres da Cadeia do Espinhaço (Bahia e Minas Gerais, Brasil) baseada em espécies de Orchidaceae. *Sitientibus. Série Ciências Biológicas* 7: 199–210.
- Barona-Colmenares AA (2018) Two new records in Orchidaceae (Vanillinae) from southernmost Colombian Amazonia: *Vanilla javieri*, a new species, and *Vanilla appendiculata*. *Phytotaxa* 375(4): 261–273. <https://doi.org/10.11646/phytotaxa.375.4.2>
- Barros F (1987) Orchidaceae. In: Giuliatti AM, Menezes NL, Pirani JR, Meguro M, Wanderley MGL, Flora da Serra do Cipó, Minas Gerais: caracterização e lista de espécies. *Boletim de Botânica da Universidade de São Paulo* 9(0): 1–151. <https://doi.org/10.11606/issn.2316-9052.v9i0p1-151>
- Barros F, Pinheiro F (2004) Flora de Grão-Mogol, Minas Gerais: Orchidaceae. *Boletim de Botânica da Universidade de São Paulo* 22(2): 361–383. <https://doi.org/10.11606/issn.2316-9052.v22i2p361-383>
- Batista JAN, Vale AA, Carvalho BM, Proite K, Ramalho AJ, Munhoz ACD, vandenBerg C, Bianchetti LB (2016) Four new species in *Habenaria* (Orchidaceae) from the Espinhaço Range, Brazil. *Systematic Botany* 41(2): 275–292. <https://doi.org/10.1600/036364416X691858>
- Bouetard A, Lefeuvre P, Gigant RL, Bory S, Pignal M, Besse P, Grisoni M (2010) Evidence of transoceanic dispersion of the genus *Vanilla* based on plastid DNA phylogenetic

- analysis. *Molecular Phylogenetics and Evolution* 55(2): 621–630. <https://doi.org/10.1016/j.ympev.2010.01.021>
- Cameron KM (2003) Vanilloideae. In: Pridgeon A, Cribb P, Chase MW, Rasmussen F (Eds) *Genera Orchidacearum*. Oxford University Press, Oxford, 281–334.
- Doyle JJ, Doyle JS (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
- Dressler RL (1993) *Phylogeny and classification of the orchid family*. Dioscorides Press, Portland, 1–314.
- Engels ME, Ferneda Rocha LC (2016) *Vanilla appendiculata* (Orchidaceae): Primeiro registro para o estado do Mato Grosso, Brasil. *Rodriguésia* 67(3): 855–858. <https://doi.org/10.1590/2175-7860201667323>
- Felsenstein J (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution; International Journal of Organic Evolution* 39(4): 783–791. <https://doi.org/10.2307/2408678>
- Ferreira AWC, Pansarin ER, Franken EP (2020) Confirmation of the presence of *Vanilla hartii* Rolfe (Orchidaceae, Vanilloideae) in Brazil. *Check List* 16(4): 951–956. <https://doi.org/10.15560/16.4.951>
- Fidalgo O, Bononi VLR (1989) Técnicas de coleta, preservação e herborização de material botânico. Instituto de Botânica, São Paulo, 1–62.
- Fraga CN, Couto DR, Pansarin ER (2017) Two new species of *Vanilla* (Orchidaceae) in the Brazilian Atlantic Forest. *Phytotaxa* 296(1): 63–72. <https://doi.org/10.11646/phytotaxa.296.1.4>
- Gonçalves DJP, Shimizu GH, Yamamoto K, Semir J (2017) Vochysiaceae na região do Planalto de Diamantina, Minas Gerais, Brasil. *Rodriguésia* 68(1): 159–193. <https://doi.org/10.1590/2175-7860201768124>
- Hall TA (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis. Program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hensold N (1988) Morphology and Systematics of *Paepalanthus* Subgenus *Xeractis* (Eriocaulaceae). In: Anderson C (Ed.) *Systematic Botany Monographs*, vol. 23. The American Society of Plant Taxonomists, Michigan, 1–150. <https://doi.org/10.2307/25027709>
- Hoehne FC (1945) Orchidáceas. In: Hoehne FC (Ed.) *Flora Brasílica*, Fasc. 8 (Vol. XII, II; 13–43). Secretaria da Agricultura, Indústria e Comércio de São Paulo, São Paulo, 1–389. [+ 209 Tabs]
- IUCN (2012) IUCN red list categories and criteria. Version 3.1. Second edition. Gland and Cambridge: International Union for Conservation of Nature and Natural Resources. <http://www.iucnredlist.org/technical-documents/categories-and-criteria>
- IUCN (2016) Guidelines for using the IUCN red list categories and criteria. Version 12. IUCN, Gland, Switzerland and Cambridge, UK. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Karremans AP, Chinchilla IF, Rojas-Alvarado G, Cedeño-Fonseca M, Damián A, Léotard G (2020) A reappraisal of Neotropical *Vanilla*. With a note on taxonomic inflation and the importance of alpha taxonomy in biological studies. *Lankesteriana* 20: 395–497. <https://doi.org/10.15517/lank.v20i3.45203>
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16(2): 111–120. <https://doi.org/10.1007/BF01731581>
- Köppen W (1948) *Climatologia: con un estudio de los climas de la tierra*. Fondo de Cultura Económica, México, 478 pp.

- Kress WJ, Prince LM, Williams KJ (2002) The phylogeny and a new classification of the ginger (Zingiberaceae): Evidence from molecular data. *American Journal of Botany* 89(10): 1682–1696. <https://doi.org/10.3732/ajb.89.10.1682>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35(6): 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Morley RL (2000) *Origin and evolution of tropical Rainforests*. Wiley, New York, 384 pp.
- Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858. <https://doi.org/10.1038/35002501>
- Oliveira JPS, Garrett R, Koblitz MGB, Macedo AF (2022) *Vanilla* flavor: Species from the Atlantic forest as natural alternatives. *Food Chemistry* 375: 131891. <https://doi.org/10.1016/j.foodchem.2021.131891>
- Pansarin ER (2004) *Cleisthes pusilla* (Orchidaceae): A new species from Central Brazil. *Kew Bulletin* 59(4): 555–558. <https://doi.org/10.2307/4110910>
- Pansarin ER (2010) Taxonomic notes on Vanilloideae (Orchidaceae: Vanilloideae): *Vanilla dietschiana*, a rare south American taxon transferred from *Dictyophyllaria*. *Selbyana* 30: 198–202.
- Pansarin ER (2019) The use of multiple data sources to elucidate the identity of Brazilian vanillas (Vanilloideae, Orchidaceae). *Proceedings, 22<sup>nd</sup> World Orchid Conference*. Asociación Ecuatoriana de Orquideología, Guayaquil, Ecuador, 162–167.
- Pansarin ER (2022) *Vanilla* flowers: Much more than food-deception. *Botanical Journal of the Linnean Society* 198(1): 57–73. <https://doi.org/10.1093/botlinnean/boab046>
- Pansarin ER, Ferreira AWC (2022) Evolutionary disruption in the pollination system of *Vanilla* (Orchidaceae). *Plant Biology* 24(1): 157–167. <https://doi.org/10.1111/plb.13356>
- Pansarin ER, Miranda MR (2016) A new species of *Vanilla* (Orchidaceae: Vanilloideae) from Brazil. *Phytotaxa* 267(1): 84–88. <https://doi.org/10.11646/phytotaxa.267.1.9>
- Pansarin ER, Pansarin LM (2014) Floral biology of two Vanilloideae (Orchidaceae) primarily adapted to pollination by euglossine bees. *Plant Biology* 16: 1104–1113. <https://doi.org/10.1111/plb.12160>
- Pansarin ER, Suetsugu K (2022) Mammal-mediated seed dispersal in *Vanilla*: Its rewards and clues to the evolution of fleshy fruits in orchids. *ESA Ecology* e3701. <https://doi.org/10.1002/ecy.3701>
- Pansarin ER, Salatino A, Pansarin LM, Sazima M (2012) Pollination systems in Pogonieae (Orchidaceae: Vanilloideae): A hypothesis of evolution among reward and rewardless flowers. *Flora (Jena)* 207(12): 849–861. <https://doi.org/10.1016/j.flora.2012.09.011>
- Pansarin ER, Aguiar JMRBV, Pansarin LM (2014) Floral biology and histochemical analysis of *Vanilla edwallii* Hoehne (Orchidaceae: Vanilloideae): an orchid pollinated by *Epicharis* (Apidae: Centridini). *Plant Species Biology* 29(3): 242–252. <https://doi.org/10.1111/1442-1984.12014>
- Platnick NI (1991) On areas of endemism. *Australian Systematic Botany* 4: 11–12.
- Pridgeon AM, Chase MW, Cribb PJ, Rasmussen FN (1999) *Genera Orchidacearum*, Vol. 1. General Introduction, Apostasioideae, Cyripedioideae. Oxford University, Oxford, 1–197.
- Radford AE, Dickson WC, Massey JR, Bell CR (1974) *Vascular Plant Systematics*. Harper & Row Publishers, New York, 891 pp.
- Rapini A, Mello-Silva RD, Kawasaki ML (2002) Richness and endemism in Asclepiadoideae (Apocynaceae) from the Espinhaço Range of Minas Gerais Brazil – a conservationist view. *Biodiversity and Conservation* 11(10): 1733–1746. <https://doi.org/10.1023/A:1020346616185>

- Rapini A, Ribeiro PL, Lambert S, Pirani Jr (2008) A flora dos campos rupestres da Cadeia do Espinhaço. *Megadiversidade* 4: 16–24.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* (Oxford, England) 19(12): 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Salazar GA, Batista JAN, Meneguzzo TEC, Cabrera LI, Figueroa C, Calvillo-Canadell L, do Vale AA, Jiménez-Machorro R (2019) Polyphyly of *Mesadenus* (Orchidaceae, Spiranthinae) and a New Genus from the Espinhaço Range, Southeastern Brazil. *Systematic Botany* 44(2): 282–296. <https://doi.org/10.1600/036364419X15562054132974>
- Silva JA, Machado RB, Azevedo AA, Drumond GM, Fonseca RL, Goulard MF, Moraes Júnior EA, Martins CS, Ramos Neto MB (2008) Identificação de áreas insubstituíveis para conservação da Cadeia do Espinhaço, estados de Minas Gerais e Bahia, Brasil. *Megadiversidade* 4: 273–309.
- Soto Arenas MA, Cribb P (2010) A new infrageneric classification and synopsis of the genus *Vanilla* Plum. ex Mill. (Orchidaceae Vanillinae). *Lankesteriana* 9: 355–398.
- Sun Y, Skinner DZ, Liang GH, Hulbert SH (1994) Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. *Theoretical and Applied Genetics* 89(1): 26–32. <https://doi.org/10.1007/BF00226978>
- Swofford DL (2001) PAUP: Phylogenetic analysis using parsimony (and Other Methods), version 4.b.8. Sinauer Associates, Sunderland.
- UNESCO [United Nations Educational, Scientific and Cultural Organization] (2005) Espinhaço Range Biosphere Reserve, Brazil. <https://en.unesco.org/biosphere/lac/espinhaco> [Accessed 30 Oct. 2022]
- Van Dam AR, Householder JE, Lubinsky P (2010) *Vanilla bicolor* Lindl. (Orchidaceae) from the Peruvian Amazon: Auto-fertilization in *Vanilla* and notes on floral phenology. *Genetic Resources and Crop Evolution* 57(4): 473–480. <https://doi.org/10.1007/s10722-010-9540-1>
- Versieux LM, Wendt T (2007) Bromeliaceae diversity and conservation in Minas Gerais state, Brazil. *Biodiversity and Conservation* 16(11): 2989–3009. <https://doi.org/10.1007/s10531-007-9157-7>
- Zappi DC (2008) Fitofisionomia da Caatinga associada à Cadeia do Espinhaço. *Megadiversidade* 4: 34–38.

## Supplementary material 1

### Species of *Vanilla* included in the molecular study, their locations, vouchers and GenBank accession numbers

Authors: Emerson Ricardo Pansarin, Euler da Luz Fernandes Menezes

Data type: docx. file

Explanation note: VAN = Vanilla germplasm bank, LBMBP Orchid House, Department of Biology, FFCLRP-USP, University of São Paulo, Brazil available at <https://www.lbmb-plab.net/vanillacollection>.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.101963.suppl1>



# *Clermontia hanaulaensis* (Campanulaceae, Lobelioideae), a new, critically endangered species from Maui, Hawaiian Islands

Hank Oppenheimer<sup>1</sup>, David H. Lorence<sup>2</sup>, Warren L. Wagner<sup>3</sup>

<sup>1</sup> Plant Extinction Prevention Program, Pacific Cooperative Studies Unit, University of Hawaii, PO Box 909, Makawao, HI 96768, USA

<sup>2</sup> National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741, USA

<sup>3</sup> Department of Botany, Smithsonian Institution, P.O. Box 37012, Washington, DC, 20013-7012, USA

Corresponding author: David H. Lorence ([lorence@ntbg.org](mailto:lorence@ntbg.org))

## Abstract

*Clermontia hanaulaensis* H. Oppenheimer, Lorence & W.L. Wagner, **sp. nov.**, a newly discovered, narrowly distributed endemic species, is herein described based on its morphological characteristics and illustrated with field photos and a line drawing. It is currently known only from the slopes of Hana'ula, in Pōhākea Gulch, Mauna Kahālāwai, west Maui, Hawaiian Islands. It differs from all other species of *Clermontia* Gaudich. by the combination of its (2)3–4(–5) flowered inflorescence, violet colored perianth often suffused with creamy white streaks or sometimes creamy white with violet-purple irregular veins, (30)35–45(–50) mm long, perianth tube 15–25(–27) mm long, 9–10 mm wide, the lobes 20–26 mm long, (2–)3–3.5 mm wide, with petaloid calyx lobes  $1/2$ – $4/5$  as long as the petals. A key to the *Clermontia* species and subspecies occurring on Maui is provided. Its habitat is described. Its conservation status is proposed as critically endangered (CR), and conservation efforts are discussed.

**Key words:** Campanulaceae, *Clermontia*, conservation, endemism, Hawaiian Islands



Academic editor: Clifford Morden

Received: 18 January 2023

Accepted: 13 May 2023

Published: 19 June 2023

Citation: Oppenheimer H, Lorence DH, Wagner WL (2023) *Clermontia hanaulaensis* (Campanulaceae, Lobelioideae), a new, critically endangered species from Maui, Hawaiian Islands. *PhytoKeys* 227: 167–179. <https://doi.org/10.3897/phytokeys.227.100725>

Copyright: © Hank Oppenheimer et al.

This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

## Introduction

The Hawaiian lobeliads (Campanulaceae, Lobelioideae) are the largest plant clade restricted to any archipelago, and originated from a single introduction ca. 13 mya (Givnish et al. 2009). In the most recent monograph of the genus *Clermontia* Gaudich., 22 species and nine non-autonymic subspecies were recognized (Lammers 1999). *Clermontia* occurs as terrestrial or epiphytic shrubs or small trees on the six largest Hawaiian Islands from 150 m to 2100 m elevation in mesophytic to wet forests, cloud forests, bogs, and shrublands. Lammers (1995) argued, based on a morphological analysis of relationships within *Clermontia*, that the genus arose on Maui rather than Kaua'i or older islands. However, Givnish et al. (2013) used plastid and nuclear DNA sequence data to show that *Clermontia* did arise on Kaua'i or an older island and largely obeyed the progression rule, with inferred inter-island dispersal events largely down the Hawaiian chain, from older to younger islands. Kaua'i, the oldest current high island is estimated to be 5.1 mya, and has just a single species of *Clermontia*. Hawai'i Island on the other hand is <1 mya and is home to 11 species (Lammers 1995, 1999). Maui has 14 taxa (not including

*C. hanaulaensis*). One is presumed extinct (*C. multiflora* Hillebr.), while *C. peleana* Rock subsp. *singuliflora* (Rock) Lammers is apparently extirpated on east Maui, but is still extant on Hawai'i Island. *Clermontia lindseyana* Rock is included in this tally based on two specimens at the Bernice P. Bishop Museum Herbarium [BISH], although populations on the leeward slope of Haleakalā are probably not this taxon, but may instead be *C. kakeana* Meyen (R. Pender, pers. comm.). Therefore, additional studies are needed to determine if *C. lindseyana* occurs on Maui.

During the course of rare plant field work in the mountains of west Maui, plants belonging to the genus *Clermontia* were found across several small ridges and gullies on the slopes below Hana'ula, in the Pōhākea Gulch drainage basin (Fig. 1). Initially only eight mature individuals and several immature plants were observed. These plants were not assignable to any taxa known from Mauna Kahālāwai, or elsewhere on Maui. Three possibilities were considered.

The first possibility considered was that these plants represented natural hybrids. Three congeners occur sympatrically in the study area: the at-risk, but locally common *C. arborescens* (H. Mann) Hillebr. subsp. *arborescens*, endemic to Mauna Kahālāwai; *C. grandiflora* Gaudich. subsp. *grandiflora*, also endemic to Mauna Kahālāwai, but not considered to be rare; *C. grandiflora* subsp. *munroi* (H. St. John) Lammers, which is less common locally, but one of the most widespread of all taxa in the genus, occurring on east and west Maui, Lana'i, and Moloka'i. However, the newly discovered plants do not resemble any of these three taxa as might be expected if they are hybrids, as they differ in the height of the plants, size and texture of the flowers, the length of the peduncles, the number of flowers per inflorescence, and the relative length of the calyx lobes compared to the corolla, among other features. The discovery of many more plants during subsequent surveys tends to negate the possibility that these plants could be hybrids as there are nearly 100 mature individuals and several dozen immature plants and seedlings occurring over an area of 0.1 km<sup>2</sup>.

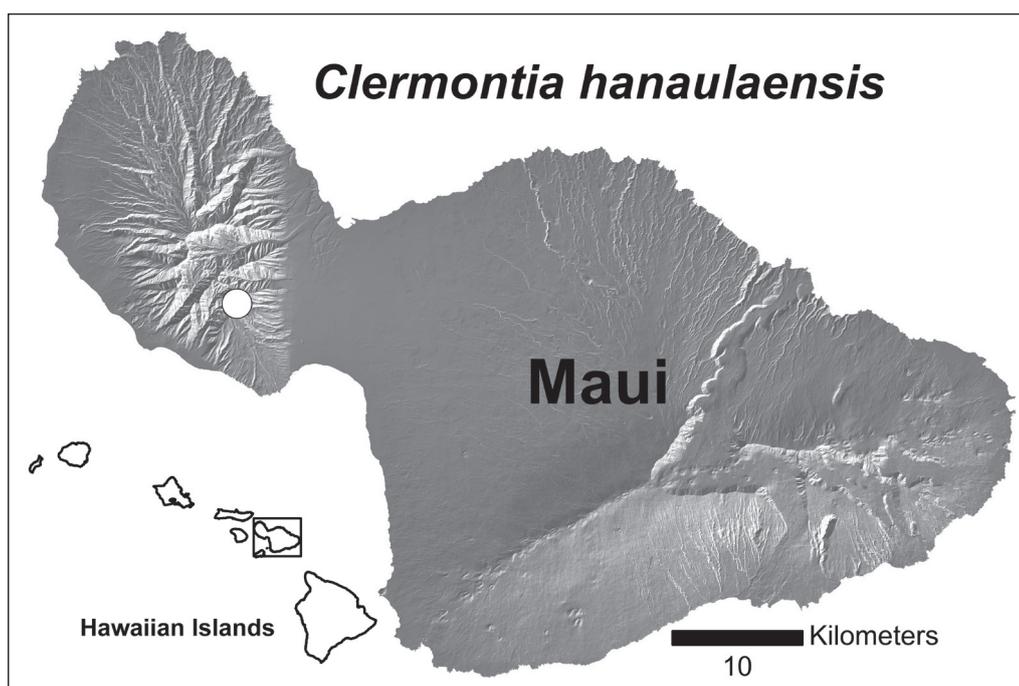


Figure 1. Distribution map of *Clermontia hanaulaensis* on Maui (white dot).

The second possibility considered these plants to potentially represent a new distributional record for a species previously known from another island. However, there have been no new records documented for the genus *Clermontia*, and only a single new distributional record exists for Hawaiian Campanulaceae, namely *Lobelia hillebrandii* Rock (Lorence et al. 1995; Wagner et al. 1999, 2005). This possibility was discarded after unsuccessful attempts to key it out using the keys in Wagner et al. (1999) and Lammers (1991). Furthermore, images were sent to botanists at the Hawai'i Branch of the Division of Forestry and Wildlife (DOFAW) who did not recognize the new plants (Josh VanDeMark and Lyman Perry pers. comm.). Finally, flowers of *C. hanaulaensis* were compared to verified images of other *Clermontia* taxa on Richard Pender's Flickr website (<https://flickr.com/photos/123604592@N07/>) which also did not result in a match.

The final possibility remaining was that these plants represent a new, undescribed taxon. Although new species of *Cyanea* Gaudich. continue to be discovered and described (Oppenheimer and Lorence 2012; Spork-Koehler et al. 2015; Oppenheimer 2020), only one new subspecies of *Clermontia* has been described in the past 30 years (e.g., *C. grandiflora* subsp. *maxima* Lammers). No new taxon at full specific rank has been described and accepted since *C. lindseyana* Rock was published in 1962 (Rock 1962). Study of the material collected, herbarium vouchers, literature, field observations, and photographs revealed these plants are morphologically distinct from all other known taxa and represent a new species, herein described.

## Methods

All measurements given herein are taken from dried herbarium specimens unless otherwise noted. Certain features, such as shapes and colors, were supplemented with information from field notes and photos. Measurements are presented in the description as follows: dimensions followed by units of measurement (mm, cm, m). All specimens cited have been seen by the authors and are deposited at the herbaria cited herein. The area of occupancy (AOO) was calculated based on field observations and herbarium collection data, and the conservation status is proposed following the IUCN Red List Category criteria Version 14 (IUCN Standards and Petitions Committee 2019; <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>).

## Taxonomic treatment

***Clermontia hanaulaensis* H. Oppenheimer, Lorence, & W.L. Wagner, sp. nov.**

urn:lsid:ipni.org:names:77321536-1

**Type. USA. Hawaiian Islands: Maui:** west Maui, Wailuku District, slopes of Hana'ula, Pōhākea Gulch, ca. 1183 m, 4 Aug 2021, *H. Oppenheimer & K. Severson H82102* (Holotype: PTBG [PTBG1000093350]; Isotypes BISH, US). Figs 2, 3.

**Description.** Shrubs or small trees up to 3 m tall, flowering at 1.5–3 m tall, terrestrial, branched from near base, with repeated candelabra-like branching, bark rugose-fissured, light brown, leafy branches green, latex white. Leaves clustered at the distal ends of the branches, alternate, with short internodes, simple, petiolate; lamina 10–12(–18) cm long, 2.0–3.5(–4) cm wide, narrowly elliptic to



**Figure 2.** *Clermontia hanaulaensis* H.Oppenheimer, Lorence & W.L.Wagner **A** habit of flowering stem **B** detail of flower at anthesis **C** fruit. (**A, B**, drawn from type collection and field images of type plant (Oppenheimer & Severson H82102; isotype US) **C** drawn from field image of non-type plant in Pōhākea Gulch). Illustration by Alice Tangerini.

oblanceolate, chartaceous; adaxial surface green, glossy when fresh, drying dull, glabrous; abaxial surface paler than adaxial surface, glabrous, secondary veins 15–16 on each side; margins entire in basal  $\frac{1}{4}$ , otherwise callose-crenulate; apex acute to short-acuminate, occasionally with a short mucro 1 mm long; base cuneate to attenuate; petiole 3–4(–6) cm long, glabrous; seedling leaves pubescent.



**Figure 3.** *Clermontia* from Pöhākea Gulch area, west Maui **A–C** *Clermontia hanaulaensis* H. Oppenheimer, Lorence & W.L. Wagner **A, B** habit, from field images of type collection with purple and white perianth (from Oppenheimer & Severson H82102) **C** mature fruit, taken in Sep. 2020 **D–F** from other *Clermontia* plants in Pöhākea Gulch showing variations that could represent hybridization between *C. hanaulaensis* and other sympatric species or between other species in the area **D** habit, form with shorter, wider calyx showing slight separation of calyx tube from corolla tube, taken in Sep. 2020 (unvouchered) **E** habit, form with shorter, wider calyx, taken in Aug. 2020 (unvouchered) **F** habit, form with white perianth, taken in Aug. 2020 (H. Oppenheimer & K. Severson H82101, BISH, PTBG, US). All photos by H. Oppenheimer.

Inflorescence (2)3–4(–5)-flowered, glabrous; flowers 5-merous; peduncle 15–30(–42) mm long; bracts triangular, ca. 1 mm long, deciduous; pedicels 8–18 mm long; bracteoles basal, 1.0–1.2 mm long, narrowly lanceolate, acute to acuminate, sometimes short mucronate, ciliate; hypanthium obconic or hemispheric, green, ca. 7–10 mm long, 8–10 mm wide; corolla weakly zygomorphic to nearly rotate when fresh, slightly to moderately curved, perianth (30–)35–45(–50) mm long, perianth tube 15–25(–27) mm long, 9–10 mm wide, the lobes 20–26 mm long, (2.0–)3.0–3.5 mm wide, the dorsal and ventral lobes spreading in distal half, pale violet-purple, often suffused with creamy white streaks, occasionally creamy white, glabrous; calyx  $1\frac{1}{2}$ – $4\frac{1}{5}$  as long as petals, lobes petaloid, similar in color to corolla, often pale greenish tinged toward base, sometimes creamy white with violet-purple irregular veins, lobes connate for  $\frac{1}{3}$ – $\frac{1}{2}$  their length, not appressed to petals, erect to spreading; staminal column violet, 2.0–2.5 mm wide, filaments 30–40 mm long, anthers darker violet, anther tube 9–12 mm long, 2.3–3.0 mm wide. Fruit dull orange, obconic to turbinate, 15–20 mm long, 10–15 mm wide, smooth, sepals and petals caducous. Seeds obovoid, slightly compressed, 0.5–0.6 mm long, 0.5 mm wide, testa dark brown, glossy, smooth.

**Distribution.** *Clermontia hanaulaensis* is known only from a single population on west Maui in several small ridges and gullies on the slopes below Hana'ula, in the Pōhākea Gulch.

**Habitat and ecology.** *Clermontia hanaulaensis* occurs in *Metrosideros* Banks ex Gaertn. Montane Wet Forest (Wagner et al. 1999) at ca. 1158–1213 m elevation with an annual rainfall of ca. 2600–2900 mm. The common associated woody elements are species of *Cheirodendron* Nutt. ex Seem., *Clermontia* Gaud., *Coprosma* J.R. Forst. & G. Forst., *Cyrtandra* J.R. Forst. & G. Forst., *Hydrangea* L., *Ilex* L., *Kadua* Cham. & Schldl., *Myrsine* L., *Perrottetia* Kunth, *Pipturus* Wedd., and *Psychotria* L. Pteridophyte genera include *Athyrium* Roth, *Cibotium* Kaulf., *Dicranopteris* Bernh., *Diplazium* Sw., *Dryopteris* Adans., and *Sadleria* Kaulf. that are prevalent and form a dense ground cover. *Freycinetia arborea* Gaudich. is a widespread liana. Common epiphytes include species of *Adenophorus* Gaudich., *Asplenium* L., *Elaphoglossum* Schott ex J. Sm., and several herbaceous species of *Peperomia* Ruiz & Pav. The terrestrial sedge *Carex alligata* Boott is occasional. The herbaceous *Ranunculus mauensis* A. Gray is a distinctive, but extremely rare element of this plant community.

Soil is of typical basaltic origin derived from the original shield-building Wailuku Volcanic Series (Stearns and MacDonald 1942). The average annual rainfall is approximately 2700 mm. (Giambelluca et al. 1986).

*Clermontia arborescens* subsp. *arborescens* occurs sympatrically throughout the range of *C. hanaulaensis*, whereas *C. grandiflora* subsp. *munroi* is scattered although locally common, and *C. grandiflora* subsp. *grandiflora* occurs at the upper perimeter of the population. Even further away in much wetter habitat with annual rainfall above ca. 2900 mm are populations of *C. micrantha* (Hillebrand) Rock, while *C. kakeana* occurs in lower, drier areas with annual rainfall below ca. 2600 mm. These taxa are readily distinguished morphologically from *C. hanaulaensis* by the characters given in the key to the Maui species below.

**Phenology.** *Clermontia hanaulaensis* has been observed to be flowering from July through September, with fruit maturing from August through October.

**Etymology.** The specific name honors Hana'ula, a peak on southern Mauna Kahālāwai (aka west Maui Mountains). *Lit.* red bay (Pukui et al. 1966); + Latin suffix *-ensis*, indicating a place of origin or growth. The Hawaiian vernacular names

'ōhā wai, 'ōhā, hāhā, 'ōhāhā, 'ōhā wai nui, and 'ōhāhā wai nui apply to other species of *Clermontia* (Pukui and Elbert 1986; Lammers 1991; Wagner et al. 1999).

**Specimens examined (paratypes).** USA, Hawaiian Islands. Maui, Wailuku District, slopes of Hana'ula, Pōhākea Gulch, 30 Jul. 2020, H. Oppenheimer H72005 (BISH, PTBG, US); H. Oppenheimer H72006 (BISH, PTBG); H. Oppenheimer H72007 (BISH, PTBG, US); H. Oppenheimer H72008 (BISH); H. Oppenheimer H72009 (BISH); 21 Aug. 2020, H. Oppenheimer & K. Bustamente H82005 (BISH, PTBG); H. Oppenheimer & K. Bustamente H82006 (BISH); 28 Sep. 2020, H. Oppenheimer & K. Severson H92014 (BISH, PTBG, flowers and mature fruit in alcohol); H. Oppenheimer & K. Severson H92015 (PTBG); 2 Oct. 2020, H. Oppenheimer H102002 (BISH), H. Oppenheimer H102003 (BISH); 10 Sep. 2021, H. Oppenheimer & Z. Pezzillo H92101 (BISH, PTBG, US).

## Discussion

### Affinities

Hillebrand (1888) recognized 11 *Clermontia* species with six varieties, divided into two sections: Section *Genuinae* with calyx lobes as long as the corolla or a little shorter, and Section *Clermontioideae*, with the calyx lobes shorter and persistent. Rock (1919), in his monograph of the Hawaiian species of Tribe Lobelioideae, maintained both of Hillebrand's Sections and recognized 23 species with four infraspecies. These two divisions are consistent with later treatments, but Section *Genuinae* was nomenclaturally corrected to Section *Clermontia* by Lammers (1991). In the most recent monograph of the genus, Lammers (1991) divided the genus into two sections, each with three series for a total of six taxonomic subdivisions.

A re-analysis of Lammer's morphological data by Givnish et al. (2013) shows that the two sections are not supported even by morphology when properly analyzed, with almost all resolution disappearing in the unweighted strict consensus tree. Furthermore, their analysis of plastid and nuclear sequence data demonstrates that petaloid sepals – almost certainly the product of a single homeotic mutation (Hofer et al. 2012; Givnish et al. 2013) – do not define a clade in *Clermontia*, with maximum-parsimony and Bayesian inference both showing multiple origins and losses of the trait. Similarly, Pender (2013) concluded that these entities were not fully supported by cpDNA. Givnish et al. (2013) demonstrated that the molecular data place *Clermontia fauriei* H. Lév. from Kaua'i, and then *C. persicifolia* from West O'ahu sister to all other *Clermontia* species (mostly from Maui Nui and Hawaii), pointing to an initial adherence to the progression rule. Finally, they show that *C. pyricularia* Hillebr. is actually a species of *Cyanea*. Hunter (2018) used large amounts of cpDNA and nuclear sequence data to show that *Clermontia* s.s. is sister to the purple-fruited clade of *Cyanea*, and that the orange-fruited clade of *Cyanea* is sister to them both.

The corolla of *C. hanaulaensis* is weakly zygomorphic to almost rotate at anthesis with the lobes connate only in the basal half. Although Lammers (1991: 8–9) discussed perianth shape and uses this character throughout his key, these states are often not clear-cut or apparent in herbarium specimens and may depend on the stage at which the flowers were pressed. Photos of mature fresh flowers shows they are at least somewhat zygomorphic in virtually all *Clermontia* species [<https://flickr.com/photos/123604592@N07/>], even those described by Lammers as being

rotate. Field photos of *C. hanaulaensis* flowers show a transition from somewhat zygomorphic to almost rotate as the perianth lobes mature and spread (Fig. 3).

Because gene regions of this new species have not yet been sequenced or included in molecular-phylogenetic studies of *Clermontia* and additional work needs to be done regarding relationships within the genus, our inferences about putative interspecific relationships are based on morphological characters. *Clermontia hanaulaensis* resembles *C. samuelii* C.N. Forbes with two subspecies on east Maui (subsp. *hanaensis* (H. St. John) Lammers and subsp. *samuelii*). However, the latter species differs by its smaller leaves with the blade 5–11 cm long and sparsely to densely pubescent beneath, relatively larger flowers with a more strongly curved or arcuate perianth tube 20–38 mm long, shorter less spreading perianth lobes 10–20 mm long, and larger fruits 28–35 mm long and 15–18 mm wide. We have adapted the following key from Lammers (1999) to include *C. hanaulaensis*, which keys out in couplet 10. *Clermontia lindseyana* has been considered to occur on Maui based on two poor and hard to identify collections and is included in the key. It is likely that they represent *C. kakeana*, and if so, *C. lindseyana* would be endemic to Hawai'i Island and does not occur on Maui; nevertheless we have left it in the key.

Several atypical individuals were encountered among the population of *Clermontia hanaulaensis*. One individual has pure white outer and inner perianths that are also shorter and wider than typical for *C. hanaulaensis* (Fig. 3 F, H. Oppenheimer & K. Severson H82101 BISH, PTBG, US). Two others have purple-pink and white perianth lobes that are shorter and wider than typical for *C. hanaulaensis* (Fig. 3D, E), and in one the calyx tube is slightly separated from the corolla tube (Fig. 3D). These variants were excluded from the circumscription of *C. hanaulaensis* on the basis of their morphology, although we mention them as they may represent hybridization between *C. hanaulaensis* and other sympatric species or between other species in this area. Further study is needed, but is beyond the scope of this paper.

### Key to the species of *Clermontia* on Maui, adapted from Lammers (1999)

- 1 Calyx lobes less than 1/2 as long as corolla, persistent in fruit, distinct or rarely connate at the base, triangular or deltate, rarely oblong or ovate, green ..... **2**
- Calyx lobes 1/2 as long to as long as corolla lobes, deciduous in fruit, connate for 1/5–4/5 their length, mimicking corolla in shape, color and texture ..... **3**
- 2 Corolla unilabiate, the tube arcuate, 40–60 mm long, the lobes deflexed, 10–20 mm long, 1/5–1/4 the length of the tube ..... ***Clermontia peleana* subsp. *singuliflora***
- Corolla bilabiate, the tube suberect or curved, 10–36 mm long, the lobes erect or spreading (17–)20–61 mm long, equaling or exceeding tube in length ..... **4**
- 3 Corolla, hypanthium, pedicels, peduncle, and petiole muricate; corolla dark rose or occasionally green, the ventral lobes 20–30 mm long ..... ***Clermontia tuberculata* C. Forbes**
- Corolla, hypanthium, pedicels, peduncle, and petiole smooth; corolla green, the ventral lobes 5–15 mm long ..... ***Clermontia arborescens* [two subspecies on Maui]**

- 4 Perianth tubular, the tube curved or arcuate, the lobes 1/5–1/2 as long as tube ..... **5**
- Perianth bilabiate or rotate, the tube erect, suberect, or curved, the lobes equaling or exceeding tube in length ..... **7**
- 5 Lamina coriaceous, the upper surface glossy; hypanthium hemispheric or obconic, anther tube 13–18 mm long, 3–5 mm in diameter .....  
..... ***Clermontia oblongifolia* Gaudich. subsp. *mauiensis* (Rock) Lammers**
- Lamina chartaceous, the upper surface dull; hypanthium turbinate or obovoid; anther tube 10–14 mm long, 2.5–3.5 mm in diameter ..... **6**
- 6 Inflorescences pendent, the peduncle (1–) 3–11 mm long; hypanthium 9–19 mm in diameter; perianth 51–85 mm long .....  
..... ***Clermontia grandiflora*** [three subspecies on Maui]
- Inflorescences spreading, the peduncle 4–18 mm long; hypanthium 5–10 mm in diameter; perianth 36–55 mm long .....  
..... ***Clermontia samuelii*** [two subspecies on Maui]
- 7 Perianth bilabiate ..... **8**
- Perianth rotate or at most weakly zygomorphic ..... **9**
- 8 Perianth 45–55 mm long, glabrous or sparsely pubescent, the lobes 19–28 mm long; hypanthium 8–14 mm long; anther tube purple or rarely white, 11–14 mm long; lamina chartaceous ..... ***Clermontia kakeana***
- Perianth 55–65 mm long, pubescent, the lobes 26–38 mm long; hypanthium 12–20 mm long; anther tube white, 17–20 mm long; lamina coriaceous ..... ***Clermontia lindseyana***
- 9 Inflorescence 7–10-flowered ..... ***Clermontia multiflora***
- Inflorescence 2–5 (–10)-flowered ..... **10**
- 10 Perianth lobes 10–16 mm long, perianth tube 3–5 mm wide .....  
..... ***Clermontia micrantha***
- Perianth lobes 20–26 mm long, perianth tube 9–10 mm wide .....  
..... ***Clermontia hanaulaensis***

### Conservation status

*Clermontia hanaulaensis* should be considered Critically Endangered (CR) due to its limited range and low population numbers (ca. 120–130 individuals), assumed loss and/or decline of most or all of its avian pollinators and dispersal agents, threats such as landslides and treefall, herbivory by alien slugs (*Limax maximus*, *Derocerus* spp.) and rats (*Rattus* spp.), and competition with habitat-modifying invasive alien plants including *Ageratina adenophora* (Spreng.) R.M. King & H. Rob., *Buddleia asiatica* Loureiro, *Erigeron karvinskianus* DC, *Melinis minutiflora* P. Beauv., *Psidium cattleianum* Sabine, *Rubus rosifolius* Sm., and *Tibouchina herbacea* (DC) Cogn. *Fraxinus uhdei* (Wenz.) Lingelsh. and *Sphaeropteris cooperi* (Hook. ex F. Muell.) R.M. Tryon are incipient invasive species and are being controlled as encountered. The area was previously impacted by domestic cattle (*Bos taurus*) and feral pigs (*Sus scrofa*) which has led in large part to the subsequent alien plant invasion. The progressive upslope spread of axis deer (*Axis axis*) from areas below the population of *C. hanaulaensis* is of growing concern. Stochastic events such as a hurricane, as well as landslides and treefalls, have the potential to gravely impact this species. Fire is also a threat, although the cumulative effects from climate change are presently unknown.

When evaluated using the World Conservation Union (IUCN) criteria for endangerment (IUCN 2019), *Clermontia hanaulaensis* falls into the Critically Endangered (CR) category, which designates species facing a very high risk of extinction in the wild. The CR designation is indicated when any of the criteria A to E are met. Both Criterion B1 (Extent of Occurrence or EOO) and B2 (Area of Occupancy or AOO) are met with an EOO of less than 100 km<sup>2</sup> and an AOO of less than 10 km<sup>2</sup>, occurring in a single population of less than the minimum, single 2 km<sup>2</sup> grid. Criteria A & C address an anticipated decline in population for which there is no data. However, decline is inferred by the lack of robust demographics, with many fewer immature and seedling stages observed compared to mature, reproductive individuals. Criterion D reflects a very limited distribution, currently calculated as a single population of 0.1 km<sup>2</sup>. No quantitative analysis predicting the likelihood of extinction (Criterion E) was conducted. The alphanumeric formula CR B1a, b(v)+B2a,b(iii,v)+C1 represents the current status under IUCN guidelines.

Furthermore, *Clermontia hanaulaensis* should be considered by the US Fish and Wildlife Service as a Candidate for listing as Endangered under the Endangered Species Act of 1973, and a Recovery Plan written, funded, and implemented.

### Conservation efforts

It is remarkable that this species occurs in a relatively accessible area (no helicopter support is necessary) that has been botanized reasonably well over the past 150 years. Mann & Brigham first collected *Phlegmariurus mannii* (Hillebr.) W.H. Wagner “on the mountains above Ma’alaea bay” (Hillebrand 1888). Degener collected the type of *Clermontia furcata* F.E. Wimmer (now a synonym of *C. arborescens* subsp. *arborescens*) “mauka of McGregor” in 1952 (Degener 1956). Field work was carried out in this area for at least three decades to varying degrees by Robert Hobdy, Steven Perlman, Kenneth Wood, as well as the first author. Botanical survey work has taken place on adjacent ridges, and further search effort is warranted and planned. This species may have the most restricted range of any taxon in the genus, occupying an area of only 0.1 km<sup>2</sup>.

The Maui Invasive Species Committee (MISC) has been working to control the incipient *Cortaderia jubata* (Lemoine ex Carrière) Stapf infestation in adjacent areas. The region formerly had feral pigs (*Sus scrofa*) that the previous landowner, Wailuku Water Co., along with the Mauna Kahālāwai Watershed Partnership (MKWP), formerly West Maui Mountains Watershed Partnership, has successfully controlled through strategic fencing, at least for the time being. Domestic and escaped cattle grazing on adjacent lands have occasionally entered the study area; this threat has also been mitigated, and cattle are no longer on adjacent lands. Axis deer (*Axis axis*) range is pushing uphill, and the Division of Forestry and Wildlife (DOFAW) of the Hawai’i Department of Land and Natural Resources (DLNR) and MKWP have begun to renovate an existing pig fence to exclude deer as well as implementing other strategies to limit the size of the herd (Lance DeSilva, DOFAW, pers. comm.).

While this new species exceeds the threshold of 50 wild individuals required to be a target of the Plant Extinction Prevention Program (PEPP), the population will continue to be monitored in case it undergoes a decline. More than 80 mature individual plants have been mapped with GPS, flagged and tagged to assist monitoring and ensure genetic representation *ex situ*. Almost 26,000

seeds from 20 individual plants have already been collected and are in storage at the Lyon Arboretum Seed Storage Laboratory in Honolulu. The PEP Program (<http://www.pepphi.org/>) strives to collect seeds or cuttings from every individual plant on the USFWS endangered species list, with *ex situ* seed storage, propagation of nursery stock, restoration outplantings into appropriate habitat, and living collections being the main conservation goals.

## Acknowledgements

The authors extend their deepest gratitude to Duane Ting and Mike “Coach” Atherton of Hana’ula Ranch, and to Lance DeSilva at the Hawai’i Department of Land & Natural Resources, DOFAW for permission to access the study area; Anna Sugiyama and Nathaniel Kingsley at Lyon Arboretum Seed Conservation Laboratory for processing of fruit and seed storage; Keahi Bustamente of the Hawai’i Snail Extinction Prevention Program; Kanoa Severson of the DOFAW Native Ecosystems Protection and Management Program, and Zach Pezzillo of the PEP Program for field assistance. The authors are indebted to Barbara Kennedy, the collections manager at the Bernice P. Bishop Museum *Herbarium Pacificum* (BISH), Tim Flynn, collections manager at the National Tropical Botanical Garden Herbarium (PTBG), and to the collections manager at the U.S. National Herbarium (US) for the handling, curation, accession and repository of specimens. Alice Tangerini provided the outstanding botanical illustration and assistance with the color plate. Our thanks to Kenneth Wood for helpful discussions and suggestions on the manuscript. We are grateful for support from the Plant Extinction Prevention Program, funded by the U.S. Fish and Wildlife Service, the State of Hawai’i Department of Land and Natural Resources, DOFAW, and private donations. Finally, we thank the reviewers for their helpful comments on an earlier version of this manuscript.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

Hank Oppenheimer: conceptualization, investigation, writing original draft

David H. Lorence: Writing–review and editing

Warren L. Wagner: Writing–review and editing.

### Author ORCIDs

Hank Oppenheimer  <https://orcid.org/0000-0002-9416-1889>

David H. Lorence  <https://orcid.org/0000-0002-6735-9531>

Warren L. Wagner  <https://orcid.org/0000-0001-5012-8422>

## Data availability

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

## References

- Degener O (1956) Flora Hawaiiensis. The New Illustrated Flora of the Hawaiian Islands. Book 5. Privately published, Honolulu.
- Giambelluca TW, Nuller D, Schroeder TA (1986) Rainfall Atlas of Hawai'i. Department of Land and Natural Resources, Honolulu.
- Givnish TJ, Millam KC, Theim TT, Mast AR, Patterson TB, Hipp AL, Henss JM, Smith JF, Wood KR, Sytsma KJ (2009) Origin, adaptive radiation, and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings. Biological Sciences* 276(1656): 407–416. <https://doi.org/10.1098/rspb.2008.1204>
- Givnish TJ, Bean GJ, Ames M, Lyon SP, Sytsma KJ (2013) Phylogeny, Floral Evolution, and Inter-Island Dispersal in Hawaiian *Clermontia* (Campanulaceae) Based on ISSR Variation and Plastid Spacer Sequences. *PLoS ONE* 8(5): e62566. <https://doi.org/10.1371/journal.pone.0062566>
- Hillebrand W (1888) Flora of the Hawaiian Islands. 1965 reprint, Hafner Publishing Co., New York and London.
- Hofer KA, Ruonala R, Albert VA (2012) The double corolla phenotype in the Hawaiian lobelioid genus *Clermontia* involves ectopic expression of PISTILLATA B-function MADS box gene homologs. *EvoDevo* 3(1): 1–26. <https://doi.org/10.1186/2041-9139-3-26>
- Hunter SJ (2018) Phylogeny and Historical Biogeography of the Native Hawaiian Lobeliads (Campanulaceae: Lobelioideae). PhD thesis, The University of Wisconsin, Madison. 2018, 13418838.
- IUCN Standards and Petitions Committee (2019) SJ Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Lammers TG (1991) Systematics of *Clermontia* (Campanulaceae-Lobelioideae). *Systematic Botany Monographs* 32: 1–97. <https://doi.org/10.2307/25027798>
- Lammers TG (1995) Patterns of speciation and biogeography in the endemic Hawaiian genus *Clermontia* (Campanulaceae: Lobelioideae). In: Wagner WL, Funk VA (Eds) *Hawaiian biogeography: Evolution on a hot spot archipelago*. Washington DC. Smithsonian Institution Press, 338–362.
- Lammers TG (1999) Campanulaceae. In: Wagner WL, Herbst DR, Sohmer SH (Eds) *Manual of the Flowering Plants of Hawai'i*. University of Hawai'i Press and Bishop Museum Press, Honolulu, 420–489.
- Lorence DH, Flynn TW, Wagner WL (1995) Contributions to the Flora of Hawai'i. III. New additions, range extensions, and rediscoveries of flowering plants. *Records of the Hawai'i Biological Survey for 1994. Part 1: Articles. Bishop Museum Occasional Papers* 41: 19–58.
- Oppenheimer H (2020) A new species of *Cyanea* Gaud. (Lobelioideae, Campanulaceae) from Maui, Hawai'i. *PhytoKeys* 167: 1–11. <https://doi.org/10.3897/phytokeys.167.55107.figure3> [20 Nov 2020]
- Oppenheimer H, Lorence DH (2012) A new species of *Cyanea* (Campanulaceae: Lobelioideae) from Maui, Hawaiian Islands. *PhytoKeys* 13: 15–23. <https://doi.org/10.3897/phytokeys.13.3447> [20 Jun 2012]

- Pender RJ (2013) Floral Trait Evolution and Pollination Ecology in the Hawaiian Lobeliad Genus, *Clermontia* (Campanulaceae). PhD thesis, University of Hawai'i, Manoa, 3577263.
- Pukui MK, Elbert SH (1986) Hawaiian Dictionary. Revised Edition. University of Hawai'i Press, Honolulu. <https://doi.org/10.1515/9780824842260>
- Pukui MK, Elbert SH, Mookini ET (1966) Place names of Hawai'i. University of Hawai'i Press, Honolulu. <https://doi.org/10.1515/9780824885625>
- Rock JF (1919) A monographic study of the Hawaiian species of the tribe Lobelioideae, Family Campanulaceae. Bishop Museum Press, Honolulu, 1977 Krauss Reprint Co., Millwood, New York.
- Rock JF (1962) Hawaiian Lobelioids. Bishop Museum Occasional Papers 23(5): 66–75.
- Spork-Koehler MJ, Koehler TB, Marquez SN, Waite M, Williams AM (2015) A new species of *Cyanea* (Campanulaceae, Lobelioideae), from the Ko'olau Mountains of O'ahu, Hawaiian Islands. *PhytoKeys* 46: 45–60. <https://doi.org/10.3897/phytokeys.46.8694>
- Stearns HT, MacDonald GA (1942) Geology and ground-water resources of the island of Maui, Hawaii. U.S. Geological Survey Bulletin 7, Advertiser Publishing Co. Ltd., Honolulu.
- Wagner WL, Herbst DR, Sohmer SH (1999) Manual of the Flowering Plants of Hawai'i, revised edition with supplement by Wagner WL and Herbst DR. University of Hawai'i Press, Vol. 2, 1919 pp. Bishop Museum Special Publication 97.
- Wagner WL, Herbst DR, Lorence DH (2005) Flora of the Hawaiian Islands website. <https://naturalhistory2.si.edu/botany/hawaiianflora/> [Accessed 01-10-2023]



# *Desmopsis terriflora*, an extraordinary new species of Annonaceae with flagelliflory

María Fernanda Martínez-Velarde<sup>1,2</sup>, Carlos Rodrigues-Vaz<sup>3,4</sup>, Vincent Soulé<sup>4</sup>, Francis J. Nge<sup>4</sup>, George E. Schatz<sup>5</sup>, Thomas L. P. Couvreur<sup>4</sup>, Andrés Ernesto Ortiz-Rodríguez<sup>2</sup>

1 Posgrado en Ciencias biológicas, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, Mexico

2 Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, Mexico

3 Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National d'Histoire Naturelle-CNRS-SU-EPHE-UA, Paris, France

4 DIADE, Université de Montpellier, CIRAD, IRD, Montpellier, France

5 Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, USA

Corresponding author: Andrés Ernesto Ortiz-Rodríguez ([andres.ortiz@ib.unam.mx](mailto:andres.ortiz@ib.unam.mx))

## Abstract

Flagelliflory refers to the production of inflorescences exclusively on long, whip-like branches which emerge from the main trunk and extend along the ground or below it. It is the rarest type of cauliflory and only a few cases have been reported in the world. Here, a new species of Annonaceae with flagelliflory is described and illustrated. The phylogenetic relationships of the new species were inferred using a hybrid-capture phylogenomic approach and we present some notes on its reproductive ecology and pollen characteristics. The new species, namely *Desmopsis terriflora* **sp. nov.**, is part of a clade composed of Mexican species of *Stenanona* with long, awned petals. *Desmopsis terriflora* is distinguished by its flagelliflorous inflorescences, basely fused sepals, thick red petals, reduced number of ovules per carpel, pollen grains with a weakly rugulate to fossulate exine ornamentation, and its globose, apiculate fruits with a woody testa. The morphological characteristics of the flagella suggest that these are specialized branches rather than inflorescences, and the absence of ramiflory implies an exclusively reproductive function. The flowers are infrequently visited by insects, their potential pollinators being flies and ants.

**Key words:** Anatomy, Cauliflory, Mexico, phylogeny, tropical rain forest



## Academic editor:

M. Alejandra Jaramillo

Received: 17 February 2023

Accepted: 3 May 2023

Published: 23 June 2023

**Citation:** Martínez-Velarde MF, Rodrigues-Vaz C, Soulé V, Nge FJ, Schatz GE, Couvreur TLP, Ortiz-Rodríguez AE (2023) *Desmopsis terriflora*, an extraordinary new species of Annonaceae with flagelliflory. *PhytoKeys* 227: 181–198. <https://doi.org/10.3897/phytokeys.227.102279>

## Copyright: ©

María Fernanda Martínez-Velarde et al.

This is an open access article distributed under terms of the Creative Commons Attribution

License (Attribution 4.0 International – CC BY 4.0).

## Introduction

Cauliflory is the general term used to refer to the production of inflorescences along the main trunk and on leafless branches of woody plants (Richards 1996). It is a common phenomenon in tropical forests and rarely seen in temperate ecosystems. In very dense forests, cauliflory facilitates the visit of plant pollinators and seed dispersers, since its flowers and fruits are more visible and easily accessible (Richards 1996). Flagelliflory can be seen as an extreme and spectacular case of cauliflory, referring to the production of inflorescences exclusively on long, whip-like branches (flagella), sometimes with scale leaves and long internodes. The flagella arise from the main trunk and then extend along the surface of the ground or slightly below it and most of the flowers

appear to rise directly from the soil (Milbraed 1922, Fig. 1). Thus, flagelliflory has a strictly reproductive function since the flowers only grow on the flagella and not on branches.

Flagelliflory is a very rare phenomenon in nature and has been documented in ca. 20 tree species, most belonging to the Annonaceae and Moraceae families and restricted to the tropical forests of Asia, Africa, Mexico and South America (Schatz and Wendt 2004; Couvreur 2009; Harrison et al. 2012; Maas et al. 2015; Lobão 2017). Maas et al. (1993, 2003) distinguish two, non-homologous, types of flagelliform structures in Annonaceae: type 1: Flagella are specialized sympodial *branches* arising from the main trunk and characterized by the presence of poorly developed leaves, often reduced to bracts and by the successive lateral shoots ending in inflorescences; type 2: Flagella composed of internodal elongations of a single *inflorescence*, the extreme development of a sympodial rachis with all flowers growing towards the tips of the flagella. Very little is known about the origin and evolution of flagelliflory and about the ecological-evolutionary advantages that this condition provides to the species (Couvreur 2009). Some studies have shown that in species with flagelliflory, the flowers have a very low diversity of floral visitors and that pollinators and dispersers are specific species (Harrison et al. 2012; Teichert et al. 2012; Xicohténcatl-Lara et al. 2016).

In Mesoamerica (southern Mexico and Central America), flagelliflory has been documented in just one species of Annonaceae restricted to the karst forests of southern Mexico: *Stenanona flagelliflora* T.Wendt & G.E.Schatz (Schatz and Wendt 2004). This species, which belongs to a clade of Central American genera within the larger south east Asian tribe Miliuseae (subfamily Malmeoideae Chatrou et al. 2012) is known from two allopatric localities in Veracruz, Mexico, one in the Uxpanapa-Chimalapas region and the other in the Los Tuxtlas region (Schatz and Wendt 2004; Xicohténcatl-Lara et al. 2016). *Stenanona flagelliflora* is a small tree up to 2 m tall, with all its inflorescences borne on woody and branched flagella up to 3 m long, which often have small leaves or leaves reduced to bracts (Schatz and Wendt 2004). Its red flowers, with a reduced number of carpels, all with a single ovule, and its vegetative characteristics, clearly relate it to three clonal species of *Stenanona*, *S. humilis*, *S. monticola* and *S. wendtii*. The close relationship of these species was also corroborated by phylogenetic analyses of plastid data (Ortiz-Rodriguez et al. 2016).

Schatz (1987) mentions that a second species of Annonaceae with flagelliflory is present in Mexico. The species (a tree up to 8 meters tall) has a combination of characters such as distichous phyllotaxy, upper side of leaves with impressed to flat midrib, simple hairs indument, three or four sepals, pedicels basally articulated, a tiny bract at the base of the pedicels, bisexual flowers with red petals and fertile stamens, and a fruit consisting of indehiscent, two-seeded monocarps, that relate it to the Neotropical genera *Desmopsis*, *Stenanona* and *Sapranthus*. However, Schatz (1987) did not place the new species in either of those three genera (as they were delimited at that time), as the species showed a unique combination of characters that did not conform to any of the genera (Table 1). Schatz (1987) tentatively named it *Uxpanapanona flagellaris*, but this name was never formally described. This undescribed species is only known from two specimens collected more than 30 years ago in Veracruz, Mexico (collection number: *T. Wendt et al.* 3125 and, *Schatz & Wendt* 985), so its

**Table 1.** Comparison of diagnostic morphological characters of the unpublished name "*Uxpanapanona flagellaris*" (Schatz 1987) and the genera of subtribe Sapranthinae.

Characters	" <i>Uxpanapanona</i> "	<i>Desmopsis</i>	<i>Sapranthus</i>	<i>Stenanona</i>
Number of petals	6, rarely 8	6	6	6, rarely 8
Number of sepals	3, rarely 4	3	3	3, rarely 4
Petals texture	Stiff and thick	Stiff and thick	Thin and fleshy	Thin and fleshy
Colour of petals	Red	Yellow, greenish or rarely white	Red to purple, rarely yellow or green	Red to purple, rarely yellow or white
Fused petals	No	No	No	No, rarely yes
Fused sepals	Yes, basely	Yes, basely	No	No, rarely yes
Food bodies	Present	Absent, rarely present	Present	Absent
Number of ovules per carpel	1 or 2	1 or 2, rarely several	Several	several, rarely 1 or 2
Leafy bracts	Absent	Present, rarely absent	Present, rarely absent	Absent
Monocarps shape	Globose	Globose	Cylindrical	Cylindrical
Wall of monocarps	Thick	Thin	Thick	Thick
Seeds ruminations	Spiniform	Peg-shaped	Lamelate	Spiniform
Pollen grains aperture	?	Disulcate	Disulcate	Inaperturate

taxonomic status at the genus level, its phylogenetic relationships and its conservation status remain unresolved.

Here, we carried out botanical explorations in Uxpanapa, Veracruz Mexico with the aim of finding individuals of this new species, documenting some aspects of its reproductive ecology, phylogenetic position and to describe it formally.

## Materials and methods

### Study area

Field explorations to find the new flagelliflorous species were carried out in the region of Uxpanapa, Veracruz, Mexico (Fig. 2). The Uxpanapa region in southern Mexico between the states of Chiapas, Oaxaca and Veracruz, comprises species-rich, warm-humid forests that develop mainly on limestone karst soils (Wendt 1987, Fig. 2). These forests harbour a high number of endemic species and species that in Mexico are known only from the Uxpanapa region. The Uxpanapa region is considered one of the wettest areas in Mexico with mean annual precipitation greater than 4,000 mm (Wendt 1987). Unfortunately, the change in land use, forest exploitation, fragmentation and fires have had an impact on the connectivity and extension of the Uxpanapa forests and today they persist only in the form of isolated patches that are harder to access.

Based on the field notes of only one of the two collections, the species should occur around "El Poblado 11" (currently named Helio Garcia Alfaro) where it was collected in 1981 by Thom Wendt. Our first explorations around Poblado 11 were unsuccessful; the vegetation surrounding the town is very fragmented and consists of secondary vegetation. A community-led protected forest area in front of Poblado 11 offered a better chance of finding the species (Fig. 2). This protected area is part of the Ejido Progreso Chapultepec and is one of the few areas near

Poblado 11 that still preserves original and fire-free vegetation. New explorations within this protected area of forest gave results and in 2014 we found a population of a large tree species with long flagelliflorous inflorescences, which we have been studying in detail since 2022. This species appeared to represent the undescribed taxon of Schatz (1987) relocated 30 years after its last collection.

### Phylogenetic position of the new species

The phylogenetic relationships of the new species were inferred using a hybrid-capture phylogenomic approach. Representatives of the genera *Desmopsis*, *Sapranthus*, *Stenanona* and *Tridimeris*, as well as some representatives of the Miliuseae tribe were included to assess the taxonomic status of this flagelliflorous species at the genus level (Suppl. material 2). As the phylogenetic hypotheses proposed so far suggest that *Stenanona* and *Desmopsis* are not monophyletic groups and their species appear intermingled in a strongly supported clade (Ortiz-Rodriguez et al. 2016), it is expected that if the new species is a separate genus as speculated by Schatz (1987), it will not cluster within the *Desmopsis-Stenanona* clade nor within the *Sapranthus* clade.

The Annonaceae baiting kit (Couvreur et al. 2019) was used for DNA sequencing. This kit targets a total of 469 Annonaceae wide exons. DNA extraction, DNA sequencing protocols, and the bioinformatic procedure are presented in Couvreur et al. (2019) and Breé et al. (2020). Thus, after filtering our data for the genes covering 75% of each exon for 75% of the individuals, and eliminating suspected paralogues following HybPier approach (see Couvreur et al. 2019; Breé et al. 2020), we ended up with a total of 323 genes used for the phylogenetic analyses.

Phylogenetic relationships among taxa were estimated using maximum likelihood (ML) methods performed with RAxML (Stamatakis 2014). We also ran an ASTRAL-III (v5.5.11) analysis (Zhang et al. 2017) as performed by Couvreur et al. (2019). The paired fastq sequences for individuals included in this study are available in Genbank SRA under Bioproject number PRJNA508895 (<http://www.ncbi.nlm.nih.gov/bioproject/508895>).

### Pollen characteristics

We analysed the pollen of the new species using scanning electron microscopy (SEM) at the Photography and Microscopy of the Biodiversity Laboratory 1, Universidad Nacional Autónoma de México (UNAM). The flowering material for SEM was collected and preserved in alcohol 70%. The material was dehydrated with gradual alcohol (ethanol) solutions at 70%, 80%, 96%, and 100%, 24 hours each. Then, the material was dried to the critical point using CO<sub>2</sub>, placed on aluminium sample holders, and covered with a layer of gold. Finally, specimens were observed under a scanning electron microscope (Hitachi- SU1510, Tokyo, Japan) at a voltage of 10 or 15 kw.

### Notes on reproductive ecology

Flower phenology was documented to determine the timing of the onset of stigmatic receptivity, its duration and the start and duration of the staminal

phase (see Ratnayake et al. 2007). Also, extensive observations on mature flowers of different individuals were made. Observations were made every hour from 8:00 a.m. to 6:00 p.m. on 10 different individuals. The identity of the visitor, visitor behavior and stage of sexual maturity of the flower (pistillate: colour change and stigma exudate; staminate: dehiscence in anthers or stigmas fall) were recorded. External visitors and visitors inside the flower were captured when possible. To determine potential pollinators, we used a poisson regression modelling approach for handling the visit frequency data (Cameron and Trivedi 1998). We used generalized linear models (glm) using the frequency of visits per hour as response variables and each visitor as a factor [glm (variable ~species, family = "poisson")]. For each analysis, we performed an Analysis of Deviance to determine differences within species (chi-square test, Fox and Weisberg 2019). Then, we carried out a Least-squares means test to assess differences between pairs of species (tukey p-adjust), using the "emmeans" function (Lenth 2022). A higher frequency of visits and presence of pollen grains of the new species on the visitors' bodies was considered as evidence of potential flower pollinators.

## Results

### Phylogenetic relationships of the new species

The ASTRAL and the ML (Fig. 3) analyses resulted in similar tree topologies. Our phylogenetic analysis recovered two strongly supported clades of Central American genera: the *Desmopsis-Stenanona* clade (bootstrap support, BS 100; Posterior Probabilities, PP 1.0) and the *Sapranthus-Tridimeris* clade (BS 100, PP 1.0). The genera *Desmopsis-Stenanona* are in fact recovered here as non-monophyletic. In the *Sapranthus-Tridimeris* clade, both genera were recovered as reciprocally monophyletic with maximum support (*Sapranthus*, BS = 100, PP 1.0; *Tridimeris*, BS = 100, PP 1.0). The phylogenetic hypothesis showed that the new species is not a new genus but clustered within the *Desmopsis-Stenanona* clade (Fig. 3). It is placed within a sub-clade of Mexican trees that includes species of *Stenanona* with long, awned petals (BS = 100, PP 1.0).

### Pollen characteristics

Pollen grains of the new species are solitary, symmetrical, and ellipsoid, with two depressed germinative zones and are inaperturate. The grains are 40–45 µm long, 30–40 µm wide, with a weakly rugulate to fossulate (-perforate) exine ornamentation (Fig. 4).

### Notes on reproductive ecology

The individuals of the new species were in full bloom during the observation period (April). All the individuals with flagella had inflorescences at different stages of development ( $36 \pm 12.69$  inflorescences per flagellum in 10 measured individuals). The number of flagella ( $7.7 \pm 4.9$  flagella per trunk) is positively correlated with the diameter of the main trunk ( $r^2 = 51$ ,  $p < 0.05$ ). The length of the flagella ( $8 \pm 4.0$  m) is not directly associated with the diameter of the main trunk ( $r^2 = 33$ ,

not significant), while the number of inflorescences is positively correlated to the length of the flagellum ( $r^2 = 49$ ,  $p < 0.05$ ). The flowers were markedly protogynous, with the entire extent of reproductive activity restricted to a 27 hour-period. The pistillate phase lasted for 4–5 h. from ca. 1400 hours to 1800–1900 hours of a first day (Fig. 5). During this phase, the red inner petals closed so they formed a pollination chamber over the reproductive organs, while outer petals are extended or slightly reflexed (Fig. 1E), the stigmas seem enlarged, although they are not observed wet, nor with exudate; this phase was clearly correlated with the emission of a strong banana-like odour and with a further increase in floral visitors. The pistillate phase was succeeded by a long interim period of 11–12 h, during which the flowers were not sexually functional, neither floral scent dissipated, nor floral visitors observed (Fig. 5). The inner petals are more distant in this phase. The interim period was followed by a staminate phase (from the 0700 hours to the 1200–1300 hours of the second day) during which the petals closed once again to form a pollination chamber, the anthers dehisced, and there was an obvious increase in floral scent (Fig. 1G). The staminate phase ends with the detachment of the petals and the fall of all the stamens.

Throughout flower anthesis, low diversity and abundance of floral visitors were observed (9 insects' observations in 27 hrs, 1 to 4 insects per observation). Floral visitors were insects from three main groups, flies, beetles, and ants. Flies were observed most often (7/9), followed by ants (5/9) and beetles (4/9) (Suppl. material 1). However, non-significant differences (tukey pairwise comparisons,  $P > 0.05$ ) in number of visits were found between the three groups of insects. Both ants and beetles had pollen grains of the new species on their bodies (Fig. 6), but only the flies and ants were observed during the two flower phases (Fig. 5). Accordingly, flies and ants can be considered here as the most effective potential pollinator of the new species.

## Discussion

### Neither *Sapranthus* nor *Stenanona* – a new species of *Desmopsis*

The new species described here was suggested more than 35 years ago (Schatz 1987) to be part of a new genus. The combination of basely fused sepals, rigid petals with food bodies (abrupt thickening) at the base of the inner ones and its globose fruits with woody testa, prevented its inclusion in *Desmopsis*, *Sapranthus* or *Stenanona*, to which it is morphologically related (Schatz 1987, Table 1). After 35 years, knowledge about diversity, phylogenetic relationships and morphology of the genera involved has advanced considerably (Schatz and Maas 2010; Ortiz-Rodriguez et al. 2016; Schatz et al. 2018a, b; Ortiz-Rodriguez 2022). This currently allows the enigma of its phylogenetic position and taxonomic status to be resolved. The phylogenomic results presented here showed that the species is placed within the *Desmopsis-Stenanona* clade (Fig. 3), a lineage composed of *Desmopsis* and *Stenanona* species in which neither genera are monophyletic. Our phylogenetic results suggest that *Desmopsis* is the correct name for all species within this lineage (Schatz et al. in prep) and therefore we named the new species, *Desmopsis terriflora*. This decision is further supported by the pollen characteristics and floral morphology of *Desmopsis terriflora* (Fig. 4). The inaperturate pollen grains of the new

species are a feature shared with all species of *Desmopsis* with red flowers (= *Stenanona*). However, in most of them, the exine sculpturing ornamentation is strongly rugulate-verrucate (Fig. 4). Thus, exine sculpturing ornamentation in the pollen grains of the new species is similar to that present in all species of *Desmopsis* with yellow-green flowers (most with aperturate grains) and in some species of *Stenanona* with pink or yellow flowers (*S. migueliana* and *S. zoque*) to which the new species is related (Fig. 4). Moreover, its flowers with stiff and thick (rigid) petals and the reduced number of ovules per carpel, are features also shared with most species of *Desmopsis* (Schatz et al. 2018a). Finally, some characteristics that prevented its inclusion in *Desmopsis*, such as the presence of an abrupt thickening in the base of the inner petals (food bodies) and the partial fusion of the sepals (Table 1), are present in the flowers of two species of *Desmopsis* endemic to Mexico (Ortiz-Rodriguez 2022).

### Flagelliflory in Mexico

Flagelliflory is rare phenomenon in nature and its presence in different lineages of angiosperms suggests an independent origin (Schatz and Wendt 2004). Even within the same genus or family, flagelliflory can occur due to convergence (Saunders 2010). Within the *Desmopsis-Stenanona* clade flagelliflory is now documented to occur in two species, *Stenanona flagelliflora* and *Desmopsis terriflora* (Fig. 3). As suggested by the morphological characteristics, both species have the same type of flagellum (type 1, *sensu* Maas et al. 2003), specialized whip-like branches that trail along the ground or below it. Also both species share the red colour of the petals, and the reduction in the number of carpels and ovules (Table 2), features also present in other Annonaceae species with flagelliflory like *Duguetia flagellaris* Huber, *D. sessilis* (Vell.) Maas (Maas et al. 2003) or *Isolona cauliflora* Verdc. (Couvreur 2009). Based on our phylogenetic results, the origin of flagelliflory within the *Desmopsis-Stenanona* clade is an independent phenomenon since *Stenanona flagelliflora* and *Desmopsis terriflora*, are not sister species (Fig. 3). However, flagelliflory in both species could be linked to similar ecological constraints, Specifically, related to vegetative reproduction. It has been observed in the field that *Desmopsis/*

**Table 2.** Morphological features of *Desmopsis terriflora* G.E.Schatz, T.Wendt, Ortiz-Rodr. & Martínez-Velarde compared to those of *Stenanona flagelliflora* T.Wendt & G.E.Schatz.

Features	<i>Stenanona flagelliflora</i>	<i>Desmopsis terriflora</i>
Size	Up to 2 m tall	up to 10 m tall
Leaves length	Up to 18 cm	up to 31 cm
Sepals	Free	Fused
Outer petals size	13–14 mm long	13–16 mm long
Pedicels	4–7 mm long	8–30 mm long
Food bodies	Absent	Present
Number of carpels	Up to 6	6–9
Ovules per carpel	1	1–2
Flagella length	Up to 3 m long	Up to 15 m long
Monocarps	Ellipsoid, thin wall	Globose, thick wall

*Stenanona* species can reproduce vegetatively when branches or secondary trunks detach from the main individual (observed in *S. migueliana* and *S. zoque*, species closely related to *Desmopsis terriflora*). Other species such as *Stenanona monticola* (sister species of *S. flagelliflora*) usually clone by stolons. Thus, this is a line that deserves further investigation and could shed light on the origin and evolution of the flagelliflory.

### Does the flagelliflory mean pollinator specialization?

Our results on the reproductive ecology of *Desmopsis terriflora* suggest that flowers on flagella present a depressed visitation rate (low frequency and diversity of floral visitor), probably linked to the fact that the species has a very narrow distribution and is rare in the locality studied (Benadi and Pauw 2018). In addition, its flowers are mainly visited by flies, which could represent a certain degree of specialization considering that most Annonaceae species are visited only by beetles (Gottsberger 2012). Also, Xicohténcatl-Lara et al. (2016) reported flies as the main floral visitors of *Stenanona flagelliflora*. Interestingly, an ecological study focused on *Duguetia cadaverica* (Annonaceae), another species with flagelliflory, supports a specialization hypothesis (Teichert et al. 2012). In that study, flowers of *D. cadaverica* are visited only by one species of small beetles. However, our results should be used with caution, flies as floral pollinators have been hypothesized for all the species of *Desmopsis* with red flowers (= *Stenanona*) (Schatz 1987) so that the higher frequency of flies in *Desmopsis terriflora* and *Stenanona flagelliflora* flowers is not necessarily associated with the flagelliflory but an evolutionary convergence. Moreover, non-significant differences (tukey pairwise comparisons,  $P > 0.05$ ) in number of visits were found between floral visitor of *Desmopsis terriflora*. Therefore, more studies are necessary to investigate this further.

### Taxonomic treatment

***Desmopsis terriflora* G.E.Schatz, T.Wendt, Ortiz-Rodr. & Martínez-Velarde, sp. nov.**

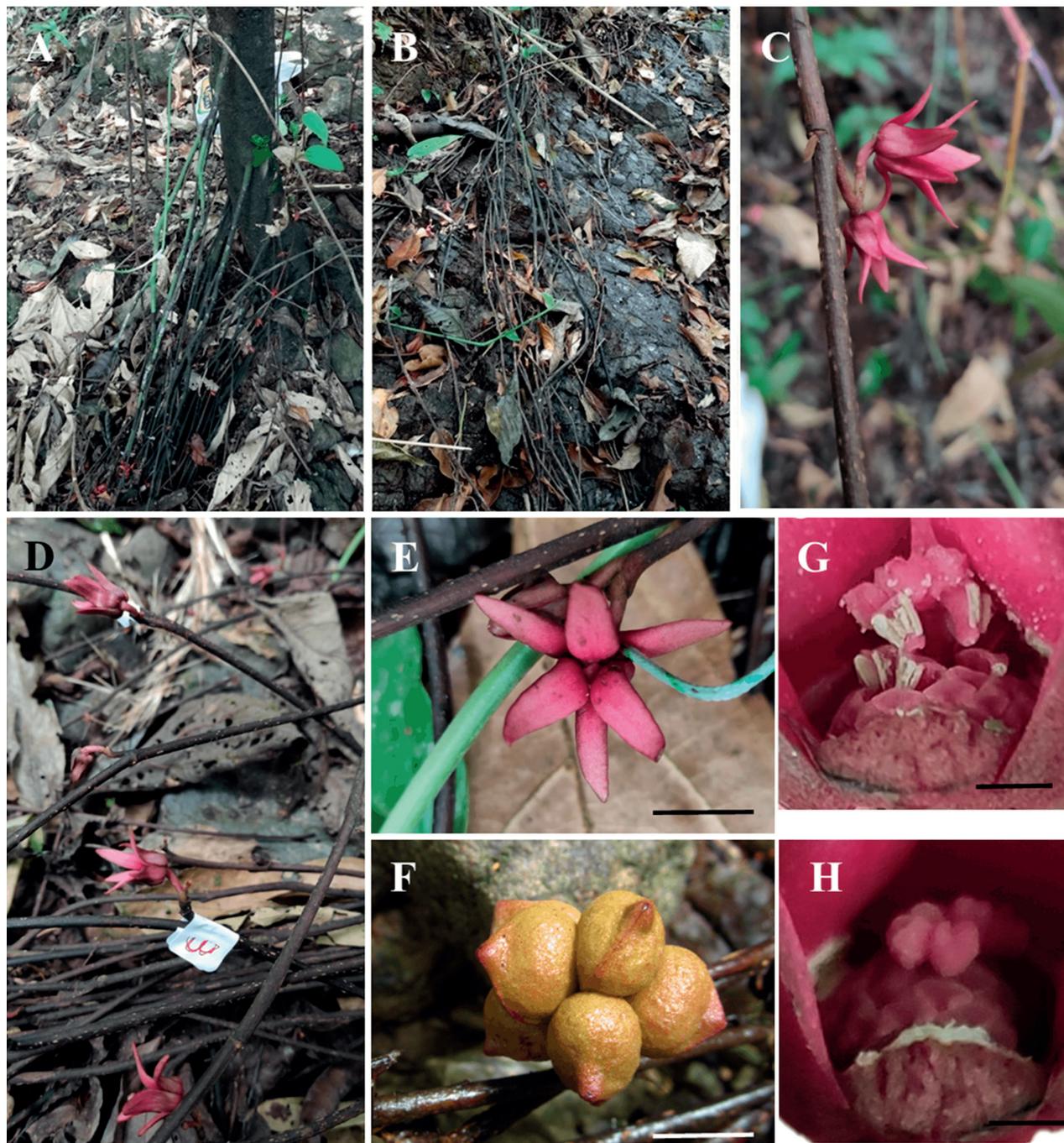
urn:lsid:ipni.org:names:77321861-1

Figs 1–6

**Type.** MEXICO. Veracruz, Municipio Uxpanapa, Ejido Progreso Chapultepec, 17°13'58.9"N, 94°18'20.5"W, 105 m, 26 April, 2022 (fl,yfr), Ma. F. M. Velarde 72 (holotype MEXU; isotypes: MO, P).

**Diagnosis.** *Desmopsis terriflora* is similar to *Stenanona flagelliflora* since both species have flowers and inflorescences growing exclusively on flagella. *Desmopsis terriflora* differs from it by the combination of larger-sized individuals, flowers with rigid petals, food bodies at the base of the inner petals, fused sepals, a greater number of carpels and ovules per carpel, by its monocarps with a hard and woody testa, and its flagella up to 15 meters in length (Table 2).

**Trees,** 7–10 m tall, 12–45 cm DBH, bark dark green, verrucose *in vivo*, dark brown when dry, young branches and terminal shoots golden sericeous. **Leaves** membranaceous, alternate, distichous, broadly elliptic to oblong-elliptic, 17–31 cm long, 4–10 cm wide, base obtuse to rounded, apex acute to acuminate,



**Figure 1.** *Desmopsis terriflora* G.E.Schatz, T.Wendt, Ortiz-Rodr. & Martínez-Velarde **A** multiple flagella emerging from the base of the main trunk **B** flagella lying on the rocky ground **C, D** lateral inflorescences on the flagellum **E** flower in anthesis **F** monocarps **G** male flower releasing pollen **H** female flower.

young leaves golden sericeous on both sides, mature leaves glabrous above and below, venation brochidodromous, 13–18 secondary veins per side, barely elevated to impressed above, raised below, the midrib impressed above but slightly canaliculate toward the base (sometimes with erect to appressed pale brown hairs), raised below and sparsely covered by golden brown hairs, petiole swollen, canaliculate, 5–8 mm long, sparsely covered by golden brown hairs. **Inflorescences** flagelliflorous, 5–20 woody flagella per trunk, glabrous, shoots emerging from the main trunk from near the base to 2 to 3 m high, then buried

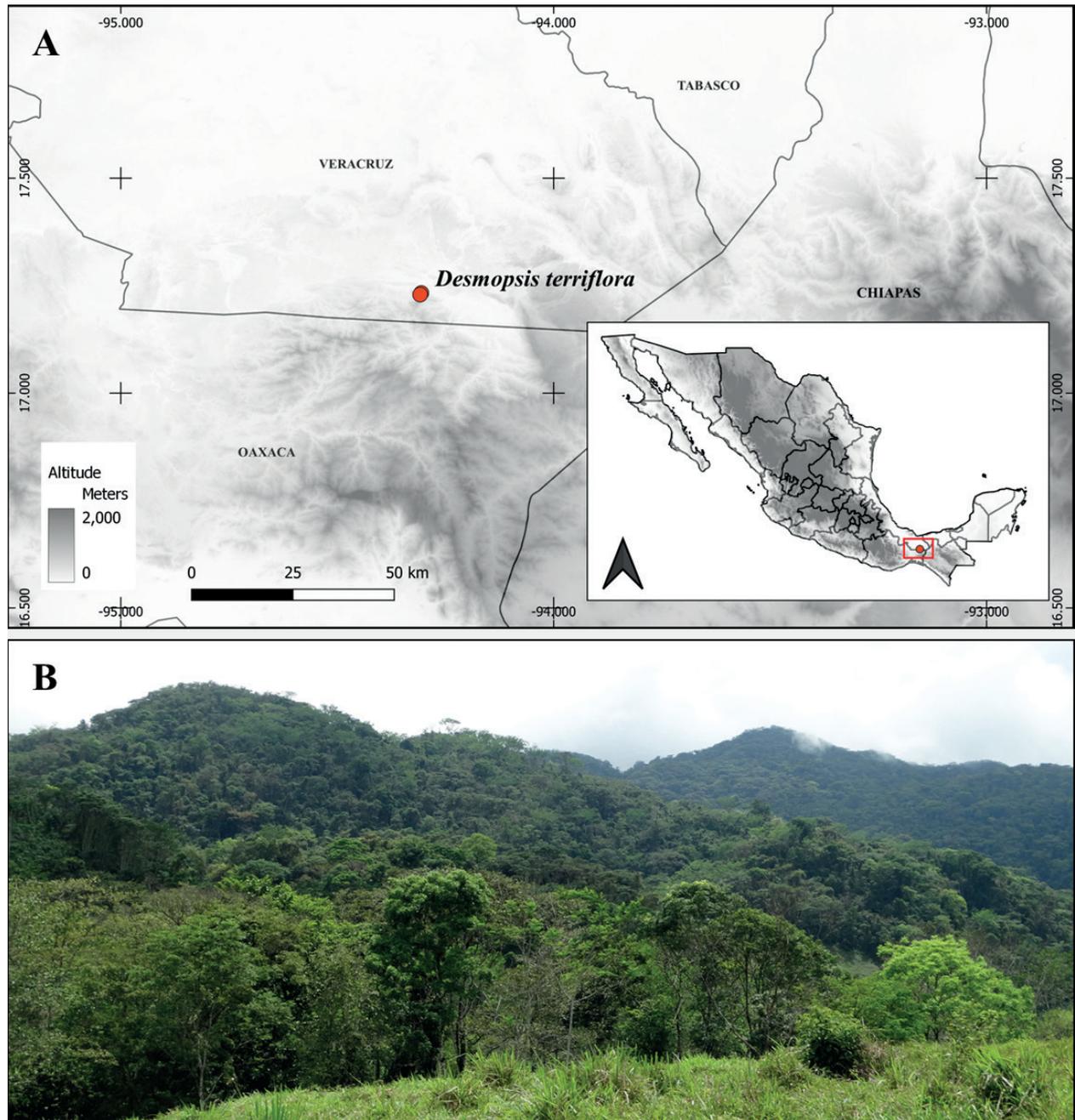
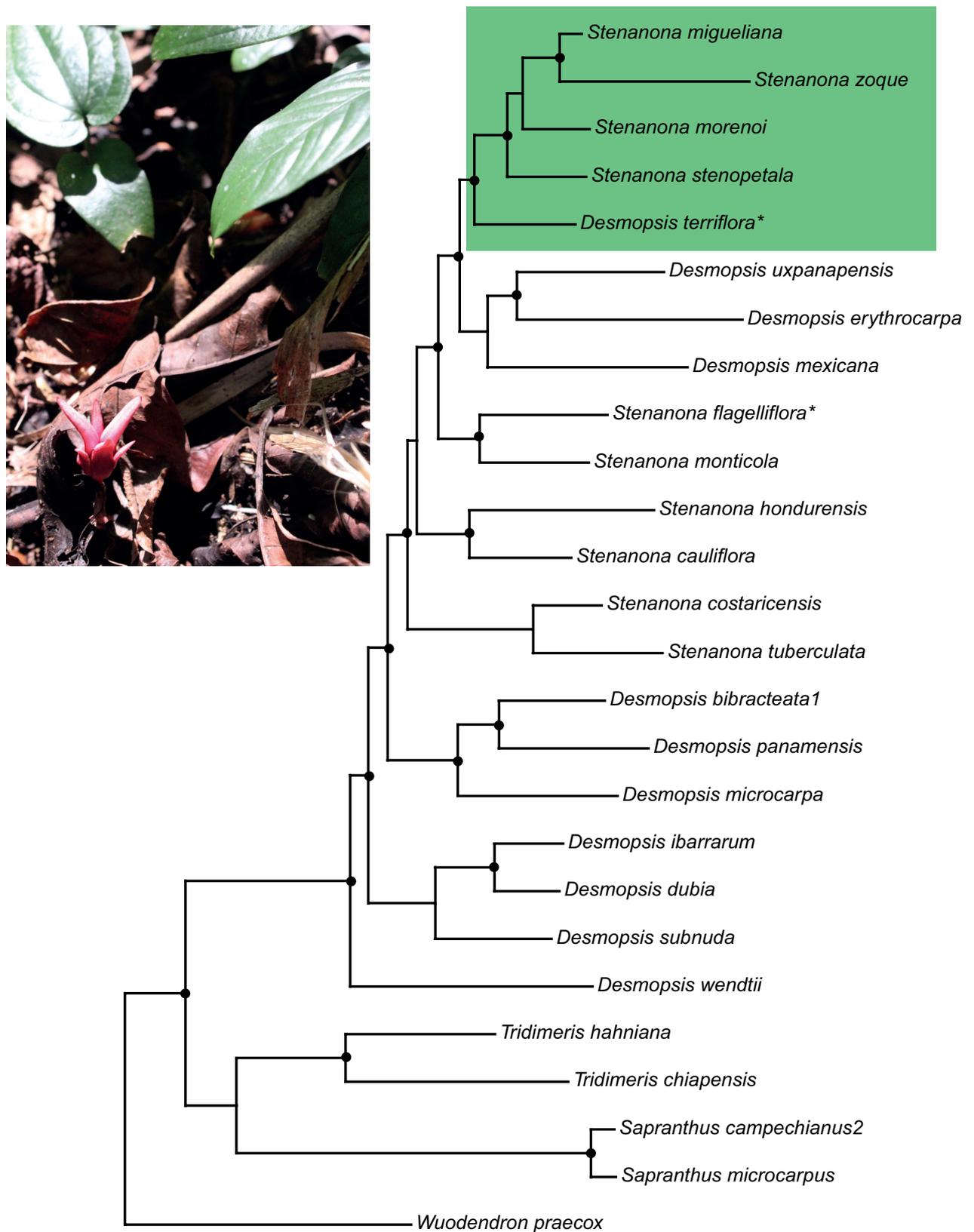
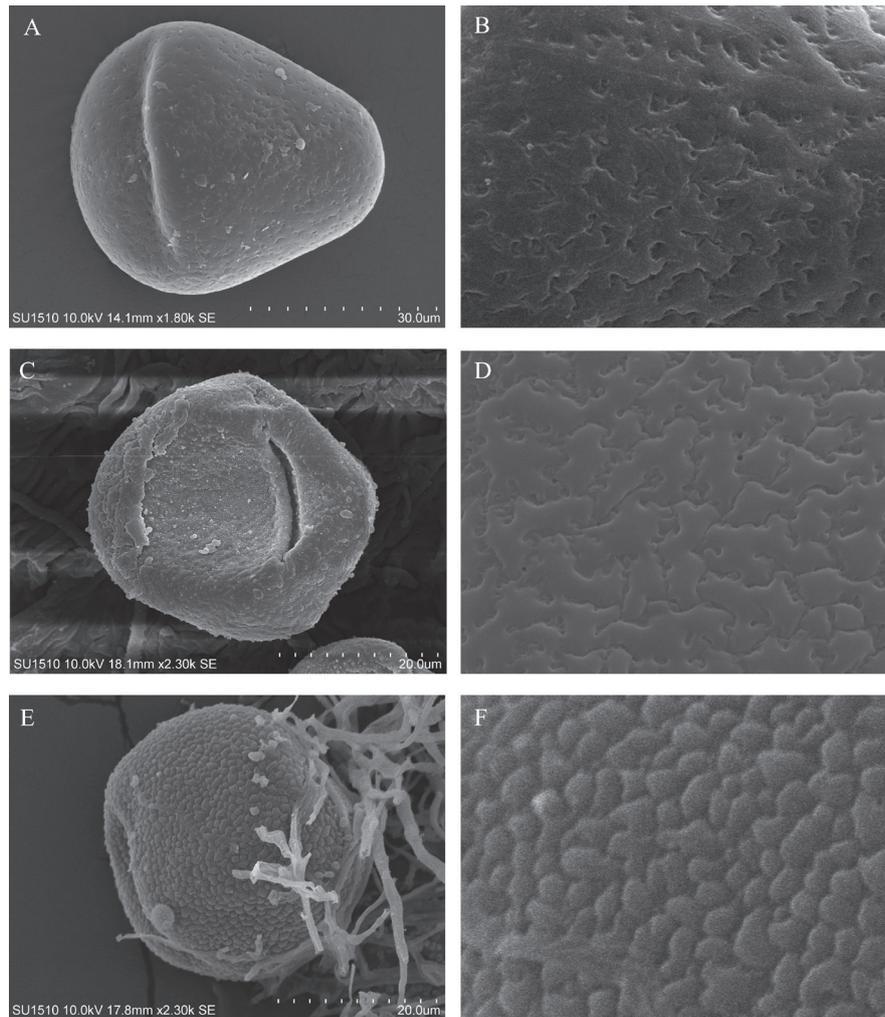


Figure 2. Geographic distribution of *Desmopsis terriflora* Schatz, T.Wendt, Ortiz-Rodr. & Martínez-Velarde **A** currently known localities for the species **B** tropical rainforest at Poblado 11 in Uxpanapa, Veracruz, México.

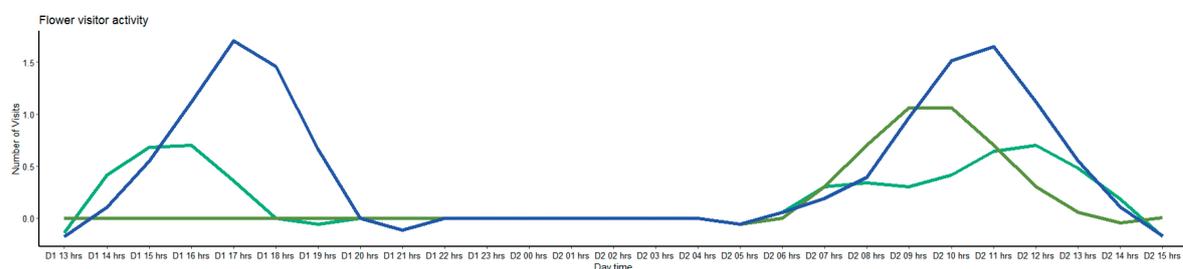
in the leaf litter just below the surface (subterranean), to 15 m long, branching; leaves and roots absent, apical parts of flagella greenish and thin, becoming progressively dark and woody toward the base, bearing perennial rhipidia at leafless nodes: the rhipidia terminal but lateral at each node because the flagellum keeps growing by a renewal shoot. Flower bearing part of the generally inflorescence erect, protruding above the leaf litter; **Flowers** 1 or 2 per inflorescence, flowering pedicels 8–30 mm long, densely covered by golden brown hairs, borne in the axil of a minute, clasping, ovate bract, and bearing a second minute, clasping ovate bract ca. midway, each bract 2 mm long, 2 mm wide, apex acute, outer surface densely covered by golden brown hairs, sepals 3



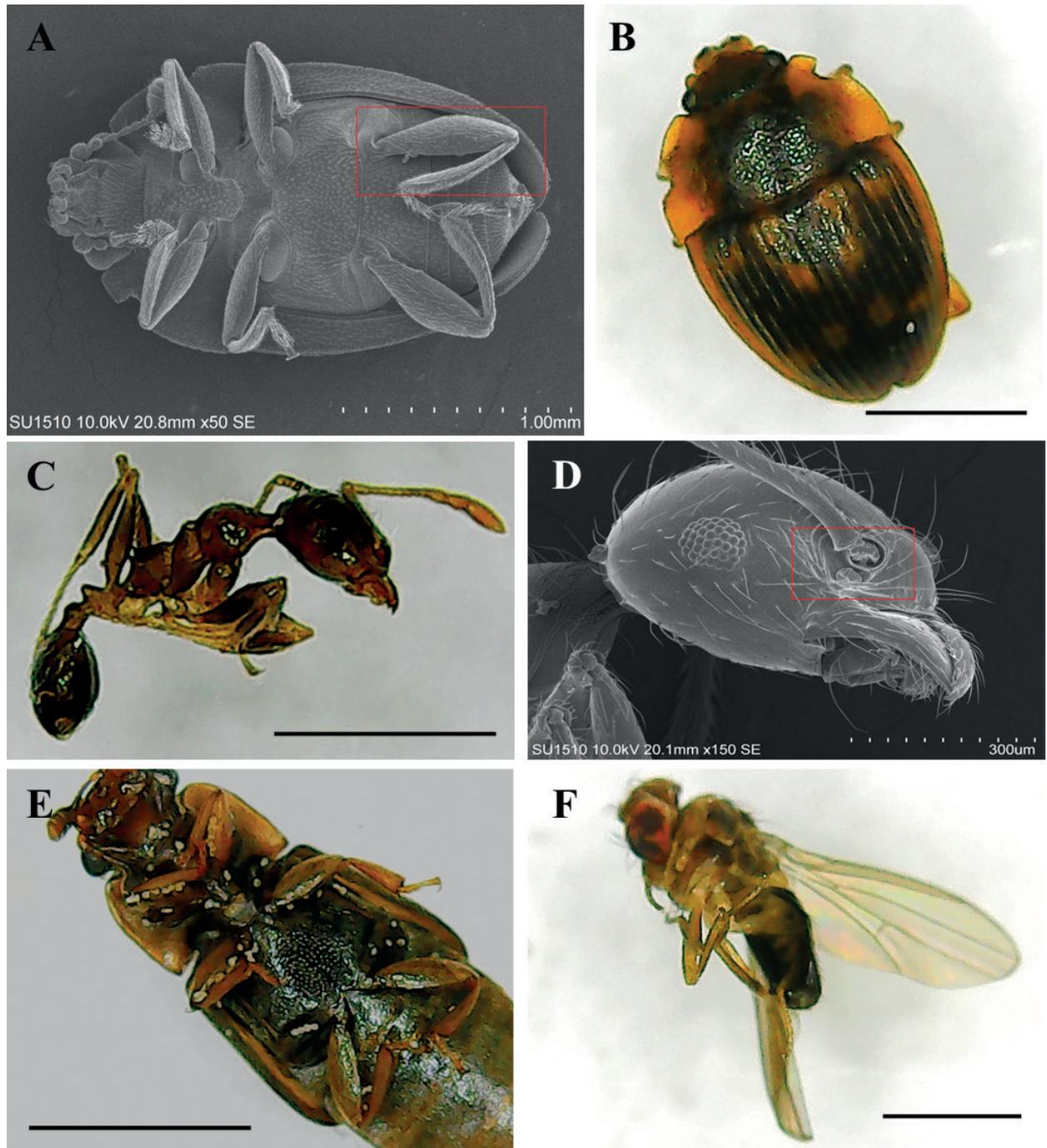
**Figure 3.** Maximum likelihood tree (RaxML) of the Neotropical clade of Miliuseae (subtribe Sapranthinae) based on 323 Annonaceae wide exons and with emphasis on the species of *Stenanona* Standl. and *Desmopsis* Saff. Darker circles indicate strongly supported clades (bootstrap values greater than 90 and Posterior Probabilities greater than 9.0). The shaded clade includes the new species.\*= flagelliflorous species. In the photo, a flower of *Desmopsis terriflora* emerging from the ground is shown.



**Figure 4.** Scanning electron microscopy (SEM) images of pollen grains **A** *Desmopsis terriflora* G.E.Schatz, T.Wendt, Ortiz-Rodr. & Martínez-Velarde, pollen grain without externally visible aperture(s) **B** exine sculpturing weakly rugulate to fossulate (-perforate) ornamentation **C** *Desmopsis trunciflora* (Schltld. & Cham.) G.E.Schatz, pollen grain showing one (another one at the opposite side likely to be also present) aperture exine area **D** exine sculpturing weakly rugulate to fossulate (-perforate) ornamentation **E** *Stenanona tuberculata* G.E. Schatz & Maas, pollen grain without externally visible aperture(s) **F** exine sculpturing verrucate ornamentation.



**Figure 5.** Timing of phenological events and visitor activity during sexually functional phases of *Desmopsis terriflora* flowers. The pistillate phase occurs between 1400 hours and 1800–1900 hours of the day, during this phase the floral visitors (light green: flies, blue: ants) are attracted by the strong banana-like odor in the flowers. The pistillate phase is succeeded by a long interim period of 11–12 h, during which the flowers were not sexually functional, neither floral scent dissipated, nor floral visitors observed. The staminate phase occurs between 1200–1300 hours of the second day, during which there is an obvious increase in floral scent and visitors are again attracted. Note that the beetles (dark green) are only present in the staminate phase.



**Figure 6.** Scanning electron microscopy (SEM) pictures and stereoscopic images of the potential pollinators of *Desmopsis terriflora* flowers **A, B** unidentified beetles **C, D** unidentified ants **E** unidentified beetle **F** unidentified fly.

(rarely 4), valvate, connate at the base, triangular, 3–10 mm long, 3–4 mm wide, apex obtuse, outer surface sparsely covered by minute golden brown hairs, glabrous on the inner surface, petals 6 (rarely 8), free, subequal, in two whorls, thick and stiff, pinkish-red, outer petals oblong-lanceolate 13–16 mm long, 4–5 mm wide, apex obtuse to acute, outer surface sparsely covered by minute golden brown hairs, essentially glabrous on inner surface, margin ciliate, inner petals oblong-lanceolate, 17–20 mm long, 4–6 mm wide, apex acute, outer surface sparsely covered by minute golden brown hairs, essentially glabrous on inner

surface, food bodies (an abrupt thickening) in the basal adaxial side, often with white striations below the food bodies, stamens ca. 30, 1.5–1.7 mm long, the filament 0.3 mm long, thecae 1–1.3 mm long, the anther connective 0.1 mm thick, either expanded discoid or prolonged into a deltoid ligulate appendage bent toward the gynoecium, carpels 6–9, stigmata globose, capitate to napiiform, ca. 1 mm in diameter, covered by minute golden brown hairs, ovaries 1.2–1.6 mm long, densely covered by minute golden brown hairs, 1–2 ovules per carpel, lateral. **Fruits** apocarpous, consisting of 4–8, subsessile, globose monocarps, 1–2 cm in diameter, apex apiculate, base rounded, the longitudinal suture visible (ribbed), stipe up to 1 mm long, exocarp dark reddish to brown, ligneous when mature, endocarp yellow, coconut-scented at maturity. **Seeds** 1–(2) per monocarp, ellipsoid or rarely discoid, surface slightly rugose, endosperm ruminant (spiniform) 1–1.5 cm long, 1–1.7 cm wide.

**Distribution.** *Desmopsis terriflora* is only known to date from the Uxpanapa region (Veracruz state) in southern Mexico (Fig. 2).

**Habitat and ecology.** The species occurs in lowland tropical rainforests (100–200 m elevation) on karstic rock formations and on shallow soils, mainly occurring along ravines and river banks, protected from the wind and sun. It forms part of the middle stratum along with species of *Amphitecna* (Bignoniaceae), *Dialium* (Fabaceae), *Mortoniendron* (Malvaceae) and *Terminalia* (Combretaceae). At the type locality, most individuals were found along a shallow river, and the flagella were all directed downstream and the woody fruits usually float on the water.

**Phenology.** Flowering from April to May; fruiting between May and September.

**Etymology.** The specific epithet “*terriflora*” refers to its flowers emerging from the ground.

**Phylogenetic relationships.** *Desmopsis terriflora* is phylogenetically related to *Stenanona migueliana*, *S. morenoi*, *S. stenopetala*, and *S. zoque* (Fig. 3), from which the new species is distinguished by its glabrous leaves (*versus* sparsely to densely pubescent), flagelliflorous habit (*versus* trunciflorous), the red color of its flowers (*versus* pink, yellow and white), the basal fusion of its sepals (*versus* totally free sepals), and by the reduced number of ovules (1 to 2) per carpel (*versus* several (5 to 10) ovules per carpel) (Ortiz-Rodríguez et al. 2018; Moreno-Méndez and Ortiz-Rodríguez 2020).

**Additional specimens examined.** MEXICO, Veracruz, Municipio Minatitlán, Lomas al S. de Poblado 11, ca. 27 km al E de La Laguna, 17°13'45"N, 94°18'30"W, 370 m, 1 April 1981 (fl), T. Wendt, A. Villalobos C. and I. Navarrete 3125 (CHAPA). loc. cit., 14 April 1984 (fl, yng fr), Schatz & Wendt 985 (MO); type locality, abril 2014 (fl, fr), Andres E. Ortiz-Rodríguez 783, 784 (MEXU).

## Acknowledgements

We extend our sincere gratitude to Héctor Gómez Dominguez, for his valuable support during the field trip and to Paul J.M. Maas, Adriana Lobão and Michael Pirie for their encouraging and constructive comments on the manuscript. Thanks to Christopher Davidson and Sharon Christoph for financing visits to the type locality through the project “KarstBio”. Also we thank Leopoldo Hurtado for his support during the preparation of Fig. 2, and Berenit Mendoza-Garfias at the Laboratory of Electron Microscopy and Photography, Instituto de

Biología of Universidad Nacional Autónoma de México (IBUNAM) for the SEM pictures. Finally, we are in debt to Don Urbano Altamirano from Poblado 11 who guided us to the locality of this species back in 2014, and has helped us ever since. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No. 865787) to TLPC. The first author is supported by a doctoral scholarship from CONACyT (CVU 777312). This paper is part of the requirements for obtaining a Doctoral degree at the Posgrado en Ciencias Biológicas, UNAM of MFM-V.

## Additional information

### Conflict of interest

No conflict of interest was declared.

### Ethical statement

No ethical statement was reported.

### Funding

No funding was reported.

### Author contributions

MFMV, TLPC and AEOR conceived the ideas, CR, VS conduct the species sampling and laboratory work, FN, MFMV and AEOR analysed the data, MFMV and AEOR wrote the main manuscript text, GES reviewed the manuscript. All authors read and approved the final version.

### Author ORCIDs

María Fernanda Martínez-Velarde  <https://orcid.org/0000-0001-9022-9658>

Carlos Rodrigues-Vaz  <https://orcid.org/0000-0002-4263-3573>

Vincent Soulé  <https://orcid.org/0009-0001-3910-2317>

Francis J. Nge  <https://orcid.org/0000-0002-0361-8709>

Thomas L. P. Couvreur  <https://orcid.org/0000-0002-8509-6587>

Andrés Ernesto Ortiz-Rodriguez  <https://orcid.org/0000-0003-4583-6701>

### Data availability

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

## References

- Benadi G, Pauw A (2018) Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *Journal of Ecology* 106(5): 1892–1901. <https://doi.org/10.1111/1365-2745.13025>
- Breé B, Helmstetter J, Bethune K, Ghogue JP, Sonké B, Couvreur TLP (2020) Diversification of African Rainforest restricted clades: Piptostigmateae and Annickieae (Annonaceae). *Diversity* 12(227): 1–28. <https://doi.org/10.3390/d12060227>
- Cameron C, Trivedi PK (1998) *Regression Analysis of Count Data*. *Econometric Society Monograph No.30*, Cambridge University Press, 432 pp. <https://doi.org/10.1017/CBO9780511814365>

- Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott JR, Mols JB, Maas JW, Saunders RMK, Chase MW (2012) A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. *Botanical Journal of the Linnean Society* 169(1): 5–40. <https://doi.org/10.1111/j.1095-8339.2012.01235.x>
- Couvreur TLP (2009) Monograph of the syncarpous African genera *Isolona* and *Mondora* (Annonaceae). *Systematic Botany Monographs* 87: 1–150. [A.]
- Couvreur TLP, Helmstetter AJ, Koenen EJM, Bethune K, Brandão RD, Little SA, Sauquet H, Erkens RHJ (2019) Phylogenomics of the Major Tropical Plant Family Annonaceae Using Targeted Enrichment of Nuclear Genes. *Frontiers in Plant Science* 9: e1941. <https://doi.org/10.3389/fpls.2018.01941>
- Fox J, Weisberg S (2019) *An R Companion to Applied Regression* (3<sup>rd</sup> Edn.), Sage.
- Gottsberger G (2012) How diverse are Annonaceae with regard to pollination? *Botanical Journal of the Linnean Society* 169(1): 245–261. <https://doi.org/10.1111/j.1095-8339.2011.01209.x>
- Harrison RD, Rønsted N, Xu L, Rasplus J-Y, Cruaud A (2012) Evolution of fruit traits in *Ficus* subgenus *Sycomorus* (Moraceae): to what extent do frugivores determine seed dispersal mode? *PLoS ONE* 7(6): e38432. <https://doi.org/10.1371/journal.pone.0038432>
- Lenth RV (2022) *Emmeans: Estimated Marginal Means, Aka Least-Squares Means*. <https://github.com/rvlenth/emmeans>
- Lobão AQ (2017) A new species of *Trigynaea* (Annonaceae) endemic to the Atlantic Forest of Brazil. *Phytotaxa* 309(2): 193–196. <https://doi.org/10.11646/phytotaxa.309.2.13>
- Maas PJM, Westra LYTh, Merijdam NAJ, van Tol IAV (1993) Studies in Annonaceae XV. A taxonomic revision of *Duguetia* A. F. C. P. de Saint-Hilaire Sect. *Geanthemum* (R.E. Fries) R. E. Fries (Annonaceae). *Boletim do Museu Paraense Emilio Goeldi. Serie botanica* 9: 31–58.
- Maas PJM, Westra LYTh, Chatrou LW (2003) *Duguetia* (Annonaceae). *Flora Neotropica* 88: 1–274.
- Maas PJM, Westra LYT, Arias S, Lobão AQ, Scharf U, Zamora NA, Erkens RHJ (2015) Confronting a morphological nightmare: Revision of the Neotropical genus *Guatteria* (Annonaceae). *Blumea* 60(1): 1–219. <https://doi.org/10.3767/000651915X690341>
- Milbraed J (1922) *Wissenschaftliche Ergebnisse der zweiten deutschen Zentral-Afrika-Expedition, 1910–1911, unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg*. Verlag von Klinkhardt & Biermann, Leipzig.
- Moreno-Méndez G, Ortiz-Rodríguez AE (2020) A new species of Annonaceae endemic to the limestone karst forests of Chiapas, Mexico. *Acta Botánica Mexicana* 127(127): e1625. <https://doi.org/10.21829/abm127.2020.1625>
- Ortiz-Rodríguez AE (2022) Naming the long-known: A new species of *Desmopsis* (Annonaceae) endemic to Mexico. *Acta Botánica Mexicana* 129: e2110.
- Ortiz-Rodríguez AE, Escobar-Castellanos MA, Pérez-Farrera MA (2016) Phylogenetic analyses and morphological characteristics support the description of a second species of *Tridimeris* (Annonaceae). *PhytoKeys* 74: 79–85. <https://doi.org/10.3897/phytokeys.74.10371>
- Ortiz-Rodríguez AE, Gómez-Domínguez H, Espinosa Jiménez JA, Ruiz-Sanchez E, Ornelas JF, Brewer S (2018) Living on the rocks: A new species of *Stenanona* (Annonaceae) from karst limestone forests of southern Mexico. *Phytotaxa* 383(3): 293–300. <https://doi.org/10.11646/phytotaxa.383.3.6>

- Ratnayake RMCS, Gunatilleke IAUN, Wijesundara DSA, Saunders RMK (2007) Pollination ecology and breeding system of *Xylopia championii* (Annonaceae): Curculionid Beetle pollination, promoted by floral scents and elevated floral temperatures. *International Journal of Plant Sciences* 168(9): 1255–1268. <https://doi.org/10.1086/521689>
- Richards PW (1996) *The tropical rain forest: an ecological study* (2<sup>nd</sup> edn.). Cambridge Univ. Press, Cambridge.
- Saunders RM (2010) Floral evolution in the Annonaceae: Hypotheses of homeotic mutations and functional convergence. *Biological Reviews of the Cambridge Philosophical Society* 85: 571–591. <https://doi.org/10.1111/j.1469-185X.2009.00116.x>
- Schatz GE (1987) *Systematic and Ecological studies of Central American Annonaceae*. PhD Thesis. University of Wisconsin, Madison.
- Schatz GE, Maas PJM (2010) Synoptic revision of *Stenanona* (Annonaceae). *Blumea* 55(3): 205–223. <https://doi.org/10.3767/000651910X535618>
- Schatz GE, Wendt T (2004) A new flagelliflorous species of *Stenanona* (Annonaceae) from Mexico, with a review of the phenomenon of flagelliflory. *Lundellia* 7(1): 28–38. <https://doi.org/10.25224/1097-993X-7.1.28>
- Schatz GE, Maas PJM, Maas-van de Kamer H, Westra LYT, Wieringa JJ (2018a) Revision of the Neotropical genus *Sapranthus* (Annonaceae). *Blumea* 63(1): 54–66. <https://doi.org/10.3767/blumea.2018.63.01.06>
- Schatz GE, Maas PJM, Maas-van de Kamer H, Westra LYT, Wieringa JJ (2018b) Revision of the Neotropical genus *Desmopsis* (Annonaceae). *Blumea* 63(1): 67–86. <https://doi.org/10.3767/blumea.2018.63.01.07>
- Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Teichert H, Dötterl S, Frame D, Kirejtshuk A, Gottsberger G (2012) A novel pollination mode, saprocanthrophily, in *Duguetia cadaverica* (Annonaceae): A stinkhorn (Phallales) flower mimic. *Flora* 207(7): 522–529. <https://doi.org/10.1016/j.flora.2012.06.013>
- Wendt T (1987) The forest of Uxpanapa Veracruz Oaxaca Mexico, evidence of Cenozoic florostic refugia. *Anales del Instituto de Biología Universidad Nacional Autónoma de México* 58: 29–54.
- Xicohténcatl-Lara L, Figueroa-Castro D, Andrés-Hernández A, Campos-Villanueva A (2016) Aspects of the reproductive biology of *Stenanona flagelliflora* (Annonaceae). *Pakistan Journal of Botany* 48: 211–221.
- Zhang C, Sayyari E, Mirarab S (2017) ASTRAL-III: increased scalability and impacts of contracting low support branches. In: McLysaght A, Huson DH (Eds) *Comparative Genomics, Lecture Notes in Computer Science* (Vol. 10562). Springer, Cham, 53–75. [https://doi.org/10.1007/978-3-319-67979-2\\_4](https://doi.org/10.1007/978-3-319-67979-2_4)

## Supplementary material 1

### Total number of flower visits per hour

Authors: María Fernanda Martínez-Velarde, Carlos Rodrigues-Vaz, Vincent Soulé, Francis J. Nge, George E. Schatz, Thomas L. P. Couvreur, Andrés Ernesto Ortiz-Rodriguez

Data type: image (PDF file)

Explanation note: The fitted number of visits (in original scale) according to the results of the GLM analysis.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.102279.suppl1>

## Supplementary material 2

### Country of origin and voucher information of the species used in the phylogenetic analyses

Authors: María Fernanda Martínez-Velarde, Carlos Rodrigues-Vaz, Vincent Soulé, Francis J. Nge, George E. Schatz, Thomas L. P. Couvreur, Andrés Ernesto Ortiz-Rodriguez

Data type: table (word document)

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/phytokeys.227.102279.suppl2>