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Research Article

Yushania dezhui (Poaceae, Bambusoideae), a new bamboo species from Yunnan, China

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Abstract

A new bamboo species, *Yushania dezhui*, from Kunming, Yunnan, China is described and illustrated in this paper. The new species used to be misidentified as *Y. polytricha*. Based on careful comparison of morphological features and molecular phylogeny evidence, we confirmed its identity as a new member of the genus *Yushania*. *Yushania dezhui* resembles *Y. maculata*, *Y. polytricha* and *Y. weixiensis* in several aspects, such as culm height and branch complement structure. However, the glabrous culm leaf sheaths and internodes, the absence of auricles and oral setae on most foliage leaves, except the one-year-old foliage leaves, the pubescence on the adaxial surface of the one-year-old foliage leaves and its limestone habitat preference can readily distinguish this new species from its related taxa. Moreover, we emphasise that individuals from various populations and molecular markers with different inheritance patterns for phylogeny reconstruction should be included in new species discovery, especially in plant groups with complex evolutionary histories.

Key words: Limestone montane area, long-necked rhizome, new taxon, temperate woody bamboos

Introduction

Yushania P.C. Keng is a genus diversified within the Hengduan Mountains region and followed by subsequent spreading outside this region (Ye et al. 2019). It belongs to the subtribe Thamnocalaminae of the tribe Arundinarieae (Poaceae, Bambusoideae) (Zhang et al. 2020) and consists of more than 90 species (Vorontsova et al. 2017; Shi et al. 2022). Taxa of *Yushania* are usually distributed in mountainous areas above an elevation of 1000 m and most of them are narrowly endemic to a certain region (Li et al. 2006). Due to the special habitat and distribution pattern, new species of *Yushania* are continuously being described recently from different mountains, such as *Y. tongpeii* D.Z. Li, Y.X. Zhang & E.D. Liu (Zhang et al. 2019), *Y. longshanensis* D.Z. Li & X.Y. Ye (Ye et al. 2021b), *Y. stoloniforma* D.Z. Li & X.Y. Ye (Ye et al. 2021b), *Y. doupengshanensis* Y.Y. Zhang et N.H. Xia (Zhang and Xia 2021), *Y. tongziensis* N.H. Xia, Y.Y. Zhang & G. Xie (Zhang et al. 2023).

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There are two *Yushania* species recorded in Kunming, Yunnan, China, i.e. *Y. maculata* T.P. Yi and *Y. polytricha* T.P. Yi (Sun et al. 2003). The type specimen of *Y. polytricha* was collected at the Qiongzhu Temple in the west of Kunming (Yi 1986). During field investigations in recent years, we found a species of *Yushania* occurring in western and northern Kunming, sometimes sympatric with *Y. maculata* and *Y. polytricha*. This species has been misidentified as *Y. polytricha* for many years in floristic treatments and community ecology papers. The short and thin culms of this species resemble *Y. polytricha*, but the branches, auricles of culm leaves and foliage leaves and hairs on the culms, culm leaves and foliage leaves differ significantly from those of *Y. polytricha*. In order to clarify the identity of this species, we performed several field surveys at different times and localities during 2023. We finally confirm that it is new to science based on morphological and molecular evidence and describe it in this paper.

Materials and methods

Field investigation, morphological feature observation and comparison

Several field investigations were carried out during late June to late August 2023 in Kunming, including Changchong Hill and Xiaoshao Village of Ciba Town, Haikou Forest Farm of West Hill District and Xianfeng of Xundian County. Specimens were collected in the field and deposited at the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences. Young and healthy foliage leaves were sampled and dried in silica gel for the molecular experiment. Morphological features of the new species were observed and recorded in the field and the lab. Comparison of morphological characteristics amongst sympatric or morphologically similar taxa in *Yushania* (i.e. *Y. maculata*, *Y. polytricha*, *Y. weixiensis* T.P. Yi) was performed, based on field observation, specimens and literature (e.g. Li et al. (2006)).

DNA extraction, sequencing and assembly

Total genomic DNA was extracted from the silica gel-dried leaves using TIANGEN Magnetic Plant Genomic DNA Kit (TIANGEN, Beijing, China). All procedures were performed according to the manufacture's instruction. DNA concentration, integrity and purity were examined using the Agilent 5400 system (Agilent, USA). Subsequently, the DNA samples were fragmented by sonication to a size of 350 bp. Then DNA fragments were end-polished, A-tailed and ligated with the full-length adapter for Illumina sequencing, followed by further PCR amplification. PCR products were purified by AMPure XP system (Beverly, USA). Library quality was assessed on the Agilent 5400 system (Agilent, USA)and quantified by QPCR (1.5 nM). The qualified libraries were pooled and sequenced on Illumina NovaSeq 6000 platform (Illumina, San Diego, CA, USA) with PE150 strategy. Finally, a total of 2 GB data per sample was generated. All those experiments were carried out at Novogene Bioinformatics Technology Co., Ltd (Beijing, China).

After quality control of the raw data by Fastp 0.23.2 (Chen et al. 2018) with default parameters, all paired reads were extracted for plastid assembly using GetOrganelle 1.7.2 (Jin et al. 2020) and the plastome sequence of *Y. niitakayamensis*

(Hayata) P.C. Keng (MN310560.1) was used as a reference. Subsequently, the de novo assembled maps were conducted using Bandage 0.9.0 (Wick et al. 2015) to visualise the complete plastomes. The assembled plastome sequences were aligned and checked collinearly by Mauve 2.4.0 (Darling et al. 2004) with default settings in order to make sure the structure and direction were consistent with the reference plastome. The plastid genes were annotated using CPGAVAS2 online (Shi et al. 2019) based on the annotation of *Y. niitakayamensis* with manual adjustment in Geneious Prime 2022.0.1 (Kearse et al. 2012). In addition, the ribosomal DNA sequence of *Oryza sativa* cultivar TN1 (KM036285.1) (Guo et al. 2021) was used as a reference to assemble and annotate the entire nrDNA sequences in Geneious Prime 2022.0.1.

Phylogenetic analysis

To confirm the phylogenetic affinity of the new species, plastome and nrDNA sequences of representatives of the tribe Arundinarieae were used to reconstruct the phylogenetic trees, based on the results of Guo et al. (2021). A total of 30 sequences from 26 species were selected, including eight newly-sequenced plastome and nrDNA sequences, respectively (Table 1). The plastome and nrDNA sequences were aligned using MAFFT 7.520 (Katoh and Standley 2013). The TPM3+F+I+G4 model for plastomes and the TPM3+F+I+G4 model for nrDNA were selected using ModelFinder 2.2.5 (Kalyaanamoorthy et al. 2017), based on the Bayesian Information Criterion (BIC). Subsequently, Maximum Likelihood (ML) analyses were performed using IQ-TREE 2.2.5 (Nguyen et al. 2015) with 1000 ultrafast bootstrap replicates and SH-aLRT test (Hong et al. 2022). Bayesian Inference (BI) was conducted in MrBayes 3.2.7a (Ronquist et al. 2012) and the GTR+I+G model was selected by jModelTest 2.1.7 (Darriba et al. 2012) using BIC. Markov Chain Monte Carlo (MCMC) simulations were run for 1,000,000 generations, with a sampling every 1000 generations. The initial 25% of generations were discarded as burn-in. A 50% majority-rule consensus tree was constructed when the average standard deviation of split frequencies was below 0.01.

Results

The new species (*Yushania dezhui*), *Y. maculata* and *Y. polytricha* all have solid rhizome necks, while *Y. weixiensis* possesses hollow ones. The culm height of *Y. dezhui*, *Y. polytricha* and *Y. weixiensis* is usually less than 2 m, whereas *Y. maculata* is more than 2 m tall. The internode and sheath scar of *Y. dezhui* are glabrous, which is different from the other three related species, which have at least some hairs on the internode and sheath scar. Dark purple-brown spotted culm leaf sheaths and purple oral setae differentiate *Y. maculata* from *Y. dezhui*. Auricles and oral setae of culm leaves and foliage leaves of *Y. dezhui* are usually absent, while *Y. polytricha* has conspicuous auricles and oral setae. Moreover, a different branch number per node and setae on culm leaves and foliage leaves can also distinguish *Y. dezhui* from *Y. polytricha* (see Table 2 for details). Although *Y. dezhui* and *Y. weixiensis* both have relatively short culms, usually glabrous culm leaves without auricles and oral setae and similar branch numbers, characters of rhizome neck, internode and foliage leaf can differentiate these two species (see Table 2 for details).

Table 1. Voucher information and GenBank accession numbers for plant materials used in this study.

Taxon	Voucher information	GenBank accession No. / source	
		plastome	nrDNA
Ingroup			
Ampelocalamus actinotrichus (Merrill & Chun) S.L. Chen, T.H. Wen & G.Y. Sheng	ZXZ151102 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Chimonocalamus cibarius T.P. Yi & J.Y. Shi	YD04 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Chimonocalamus fimbriatus Hsueh & T.P. Yi	GC141-3 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Fargesia acuticontracta T.P. Yi	YXY266-1 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Fargesia frigidis T.P. Yi	ZXZ11023 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Fargesia melanostachys (Handel-Mazzetti) T.P. Yi	YXY145-3 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Fargesia nivalis T.P. Yi & J.Y. Shi	YXY125-2 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Gaoligongshania megalothyrsa (Handel-Mazzetti) D.Z. Li, Hsueh& N.H. Xia	GC120-5 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Hsuehochloa calcarean (C. D. Chu & C. S. Chao) D.Z. Li & Y.X. Zhang	GC82 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Indocalamus hirtivaginatus H.R. Zhao & Y.L. Yang	GC94-6 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Indocalamus latifolius (Keng) McClure	GC58-2 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Indocalamus tessellatus (Munro) P.C. Keng	GC88-8 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Indosasa crassiflora McClure	GY15039-B (KUN)	Guo et al. (2021)	Guo et al. (2021)
Phyllostachys incarnata T.H. Wen	ZLN-2011035 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Pleioblastus amarus (Keng) P.C. Keng	G14151-B (KUN)	Guo et al. (2021)	Guo et al. (2021)
Pleioblastus fortune (Van Houtte) Nakai	GC33-2 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Pseudosasa guanxianensis T.P. Yi	GC62-3 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Shibataea kumasaca (Zollinger ex Steudel) Makino ex Nakai	GC31-3 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Yushania brevipaniculata (Handel-Mazzetti) T.P. Yi	YXY043 (KUN)	Guo et al. (2021)	Guo et al. (2021)
Yushania dezhui Y.X.Zhang &R.L.Zhang	CCS03 (KUN)	OR750780	OR760053
Yushania dezhui Y.X.Zhang &R.L.Zhang	DSTQ02 (KUN)	OR750779	OR760052
Yushania dezhui Y.X.Zhang &R.L.Zhang	XS01 (KUN)	OR750778	OR760051
Yushania dezhui Y.X.Zhang &R.L.Zhang	ZSC03 (KUN)	OR750777	OR760050
*Yushania longiuscula*T.P. Yi	YXY154-1 (KUN)	Guo et al. (2021)	Guo et al. (2021)
*Yushania maculata*T.P. Yi	DSTQ01 (KUN)	OR750784	OR760057
Yushania niitakayamensis(Hayata) P.C. Keng	12321 (KUN)	Guo et al. (2021)	Guo et al. (2021)
*Yushania polytricha*T.P. Yi	QZS001 (KUN)	OR750783	OR760056
Yushania shuichengensis T.P. Yi & L. Yang	LPS15 (KUN)	OR750782	OR760055
Yushania shuichengensis T.P. Yi & L. Yang	LPS22 (KUN)	OR750781	OR760054
Outgroup			
Chusquea culeou E. Desvaux	GZH-089 (KUN)	Guo et al. (2021)	Guo et al. (2021)

The length of the eight newly-sequenced plastomes ranged from 139599 bp (*Y. shuichengensis* T.P. Yi & L. Yang LPS15) to 139653 bp (the new species *Y. dezhui* XS01), with a consistent GC content of 38.90%. They showed a typical quadripartite circular structure, which consisted of a pair of inverted repeat regions (IR), one large single copy region (LSC) and one small single copy region (SSC). The plastome length of the new species varied from 139616 bp (ZSC03) to 139653 bp (XS01). The newly-assembled eight nrDNA sequences had a length from 8337 bp in *Y. shuichengensis* (LPS22) to 9010 bp in *Y. polytricha* (QZS001) and comprised of 18S (1811 bp), ITS1 (215–216 bp), 5.8S (165

Table 2. Morphological comparison of *Yushania dezhui* and related species.

	Y. dezhui	***Y. maculata***	***Y. polytricha***	***Y. weixiensis***
Rhizome neck	5–12 mm in diameter, solid	5–10 mm in diameter, solid	3–8 mm in diameter, solid	7–10 mm in diameter, hollow
Culm	0.4–1.8 m tall, 1–5 mm in diameter	2–3.5m tall, 0.8–1.5 cm in diameter	1–2 m tall, 3–8 mm in diameter	1–2 m tall, 3–10 mm in diameter
Internode	Subsolid, purple-spotted initially, slightly white powdery below nodes	Hollow, initially densely white powdery, with grey or light yellow setae	Solid, initially densely purple spotted, thinly white powdery and yellow-brown setulose below nodes	Hollow, initially white powdery, white-grey setulose
Sheath scar	Corky, glabrous	Prominent, initially densely brown setose	Prominent, initially densely yellow-brown retrorse-setose	Prominent, initially yellow-brown setose
Branch complement	3–12	7–12	1–5	3–7
Culm leaf	Tardily deciduous, ca. 1/2 as long as the internode; sheaths glabrous abaxially, occasionally white pubescent at the base	Persistent, dark purple-brown spotted, ca. 1/3 as long as internodes, mainly glabrous, but sparsely brown setose at the base	Persistent, ca. 2/3 as long as internodes, yellow-brown setose	Persistent, glabrous or sparsely yellow-brown setose
Culm leaf auricle & oral setae	Auricles linear or absent, usually present on upper culm leaves; oral setae several when auricles present	Auricles absent; oral setae 3–5, erect, purple	Auricles purple, falcate; oral setae many, radiating, yellow-brown	Auricles and oral setae absent
Foliage leaf sheath	Glabrous, green, purple or purple-green, 2.5–5.2 cm long, margins glabrous	Glabrous, 4.5–6 cm long, margins glabrous	Densely brown setose, margins densely yellow ciliate	Glabrous, 1.2–2.7 cm long, margins glabrous
Foliage leaf auricle & oral setae	Auricles usually present on the one-year-old foliage leaves, linear, green or purple; oral setae several when auricles present	Auricles absent; oral setae 3–5, Erect, purple	Auricles purple, falcate or elliptic; oral setae several, erect or radiating, yellow-brown	Auricles absent; oral setae 3–5, yellow
Foliage leaf blade	2.5–12.5 × 0.5–1.3 cm, pubescent adaxially for the one-year-old blades, glabrous abaxially, secondary veins 2–4 paired	9–15 × 0.9–1.1 cm, glabrous, secondary veins 4-paired	9–21 × 1.2–2.5 cm, abaxially grey pubescent, secondary veins 4–6-paired	3.4–7 × 0.3–0.6 cm, glabrous, secondary veins 2- or 3-paired

bp), ITS2 (215–217bp), 26S (3392 bp) and an intergenic spacer (IGS, 2539–3212 bp). For the new species, individuals ZSC03 and CCS03 had the same length (8695 bp) of nrDNA sequences, while the length of the individual XS01 was four bp longer than the individual DSTQ02 (216 bp vs. 217 bp in the ITS2 region and 2898 bp vs. 2893 bp in the IGS region).

After alignment, the plastome sequences had a total length of 143257 bp, including 3994 variable sites and 783 parsimony informative sites. In the plastome tree, six lineages were recovered with high support, i.e. clades III-VI, clades IX and XI (Fig. 1). The four samples of the new species were nested within the clade V and formed two subclades. One subclade consisted of individuals ZSC03 and CCS03 (MLBP/BI = 98/1.00) and the other clade included individuals XS01 and DSTQ02 (MLBP/BI = 100/1.00). The new species had close relationships with *Fargesia nivalis* T.P. Yi & J.Y. Shi, *Yushania maculata*, *Y. niitakayamensis* (Hayata) P.C. Keng, *Y. polytricha* and *Y. shuichengensis* (LPS22).

The aligned length for nrDNA sequences was 13004 bp with 2571 variable sites and 1502 parsimony informative sites. In the nrDNA topologies, five subtribes were revealed, including subtribes Ampelocalaminae, Arundinariinae, Gaoligongshaniinae, Hsuehochloinae and Thamnocalaminae (Fig. 2). All the four individuals of the new species were grouped into a clade (MLBP/BI = 100/1.00) and nested in the subtribe Thamnocalaminae.

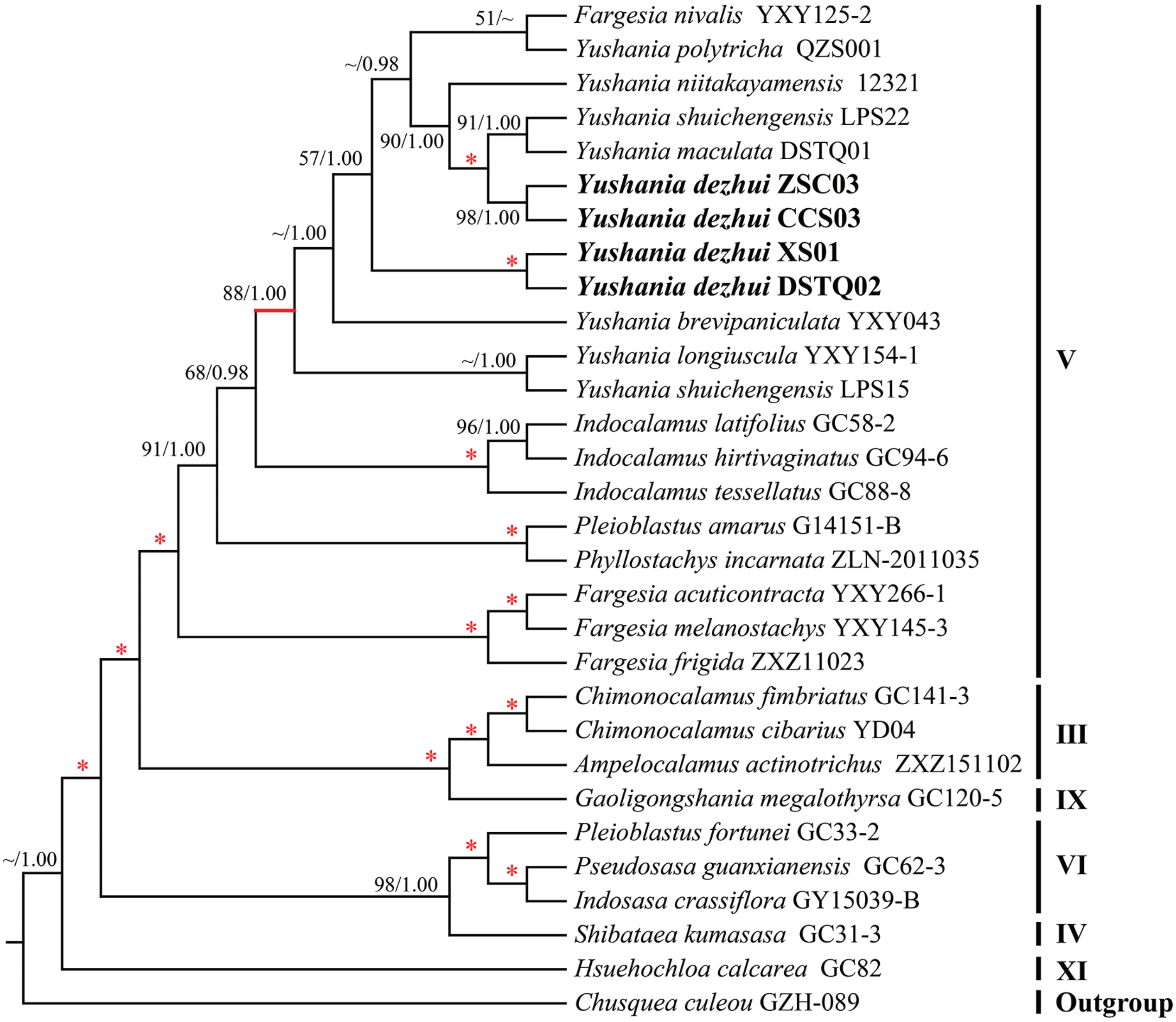

Figure 1. Maximum Likelihood phylogenetic tree reconstructed from plastome sequences of the tribe Arundinarieae. Numbers along branches indicate the Maximum Likelihood bootstrap values (MLBP) and Bayesian posterior probabilities (BI). * means MLBP/BI=100/1.00. The Roman numbers on the right of this tree correspond to those lineages recovered in previous studies (Yang et al. 2013). The branch in red (MLBP/BI = 88/1.00) denotes the clade containing *Yushania dezhui* and its relatives.

Taxonomic treatment

***Yushania dezhui* Y.X.Zhang & R.L.Zhang, sp. nov.**
urn:lsid:ipni.org:names:77346804-1
Figs 3–5

Diagnosis. *Yushania dezhui* resembles *Y. maculata* T.P. Yi, *Y. polytricha* Hsueh & T.P. Yi and *Y. weixiensis* T.P. Yi, but differs in having rhizome necks much thicker than culms, glabrous culm leaf sheaths, internodes and sheath scars, auricles and oral setae of most foliage leaves usually absent and the one-year-old foliage leaves with pubescence adaxially.

Type. CHINA • Yunnan: Kunming City, Panlong District, Ciba Town, Changchong Hill; 25°07'28.87"N, 102°42'17.41"E; 2226 m a.s.l.; 22 August 2023; *Y.X. Zhang et al. CCS03* (holotype, KUN!; isotype, IBSC!).

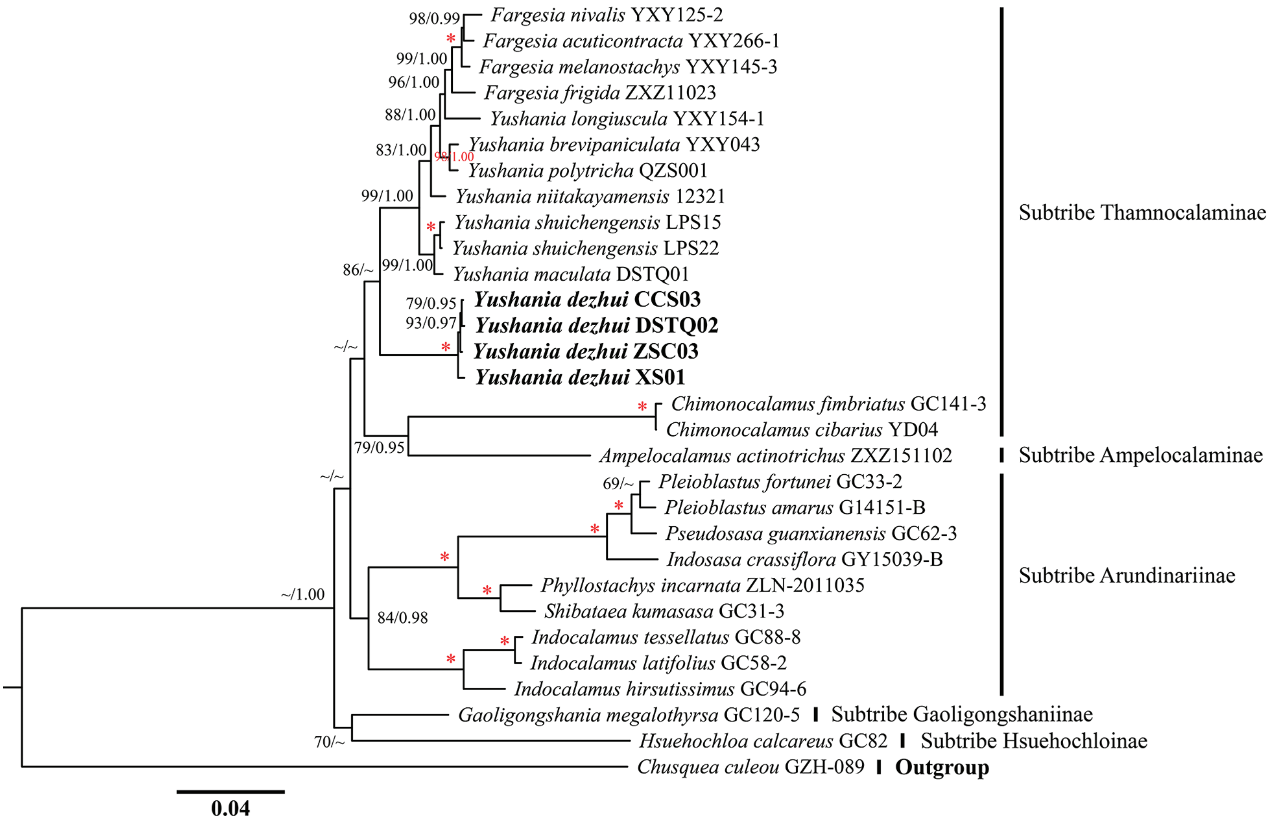

Figure 2. Phylogenetic tree reconstructed from nrDNA sequences of the tribe Arundinarieae by using the Maximum Likelihood method. Numbers along branches indicate the Maximum Likelihood bootstrap values (MLBP) and Bayesian posterior probabilities (BI). * means MLBP/BI = 100/1.00.

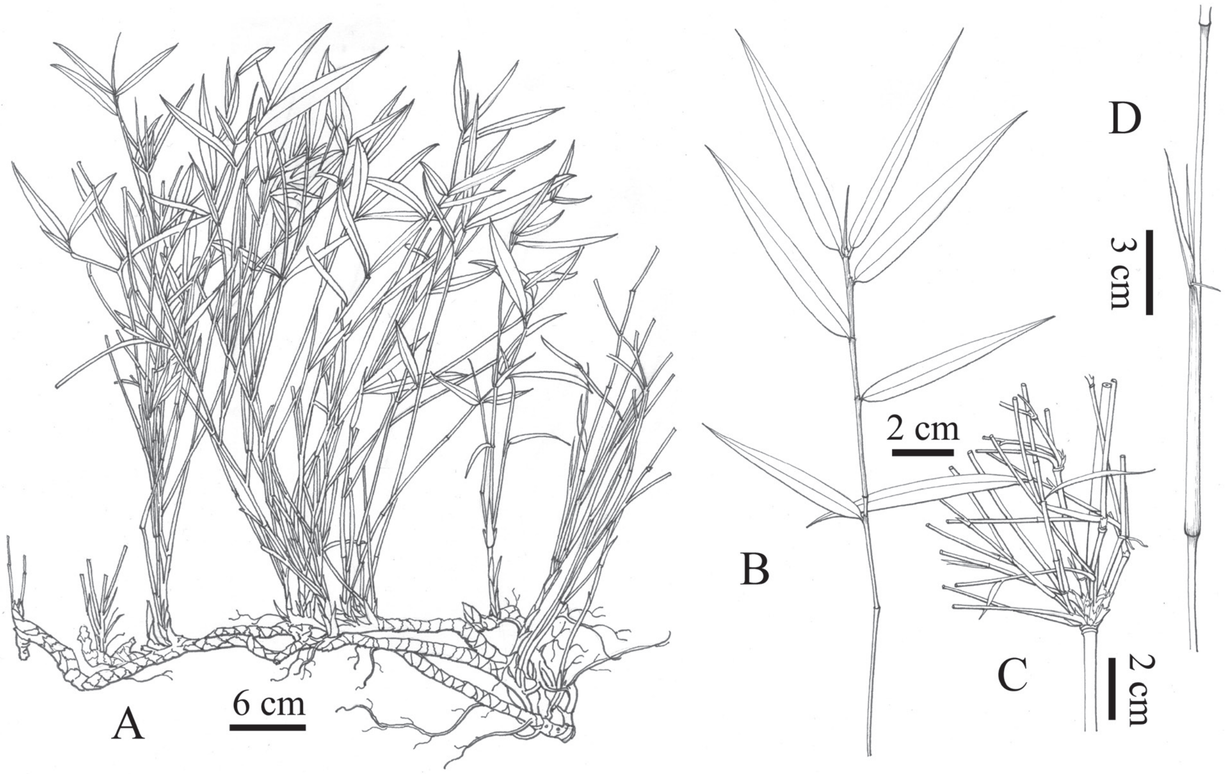

Figure 3. *Yushania dezhui* Y.X.Zhang & R.L.Zhang **A** clump **B** foliage leafy branch **C** branches **D** internode and culm leaf.

Figure 4. Habitats of *Yushania dezhui* Y.X.Zhang & R.L.Zhang **A** Changchong Hill, voucher No. CCS03 **B** Xiaoshao Village, voucher No. XS02 **C** Haikou, voucher No. ZSC03 **D** Xundian, voucher No. DSTQ02. Photos by Yu-Xiao Zhang.

Description. Rhizomes pachymorph, necks 2–30 cm long, 0.5–1.2 cm in diameter, internodes 0.2–1 cm long, solid. Culms diffuse, 0.4–1.8 m tall, 1–5 mm in diameter, subsolid; internodes 2.5–21.5 cm long, terete, purple-spotted initially, slightly white powdery below the nodes; nodes slightly prominent; sheath scars corky. Branches 3–12, slender and equal. Culm leaves tardily deciduous, ca. 1/2 as long as the internode; sheaths glabrous abaxially, green or purple apically,

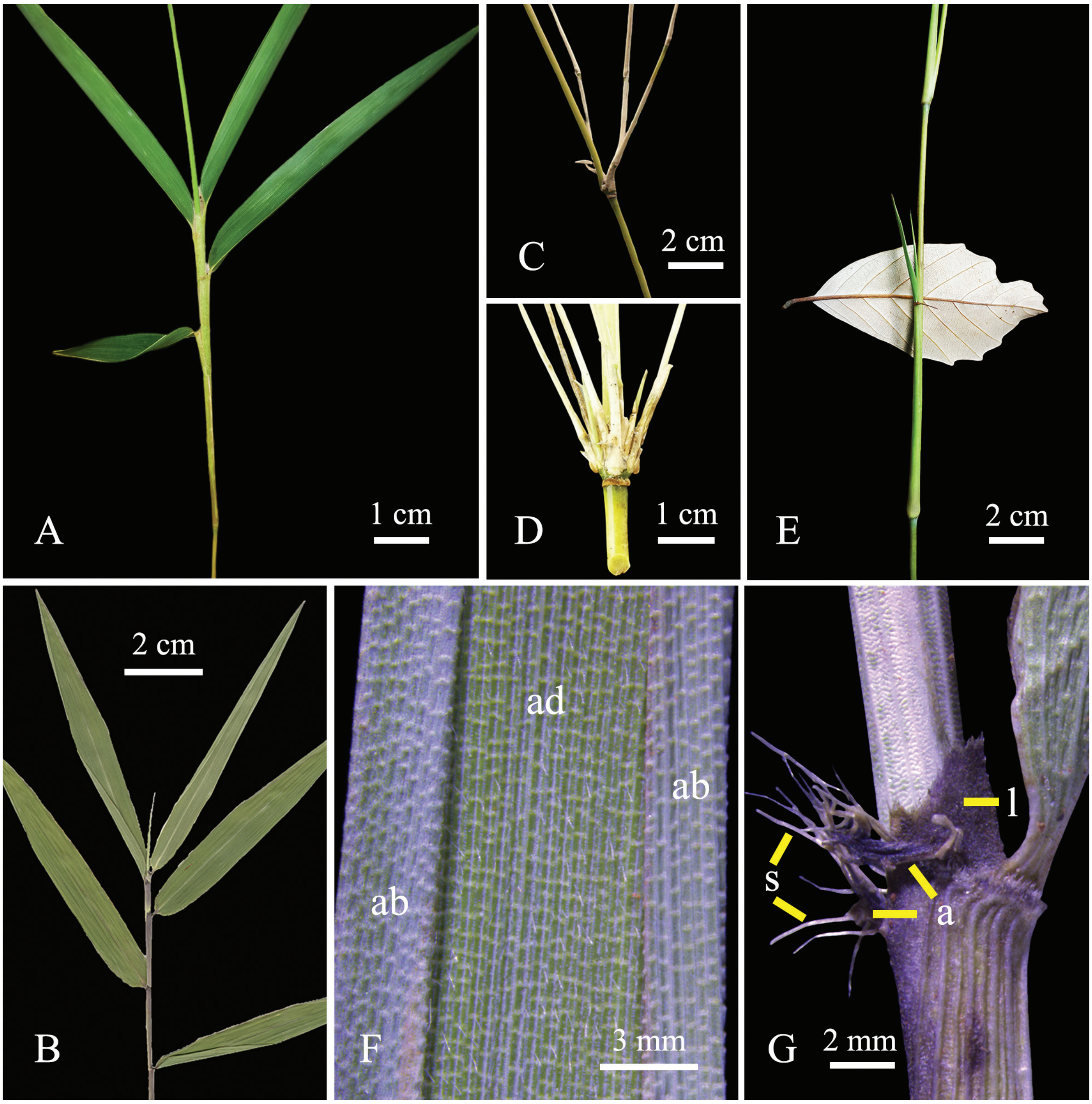

Figure 5. *Yushania dezhui* Y.X.Zhang & R.L.Zhang **A** foliage leaves with green sheath **B** foliage leaves with purple sheath **C, D** branches **E** internode with culm leaf **F** the one-year-old foliage leaf blade, showing the pubescent adaxial epidermis, ab = abaxial epidermis, ad = adaxial epidermis **G** auricles, oral setae and ligule of the one-year-old foliage leaf, a = auricles, l = ligule, s = oral setae. Photos **A–E** by Yu-Xiao Zhang **F**, **G** by Shun-Shun He.

margins ciliate, occasionally white pubescent at the base; auricles linear or absent, usually present on upper culm leaves; oral setae several when auricles present; ligules truncate, 1–2 mm tall, green or purple, margins ciliate or not; blades linear, recurved, glabrous, 0.3–2.3 cm long. Foliage leaves 3–5 per ultimate branch; sheaths glabrous, green, purple or purple-green, 2.5–5.2 cm long, margins glabrous; auricles and oral setae usually absent, except present on the one-year-old foliage leaves, auricles linear, green or purple; ligules truncate, 1–2 mm tall, green or purple; blades 2.5–12.5 × 0.5–1.3 cm, pubescent adaxially for the one-year-old blades, glabrescent later, glabrous abaxially, secondary veins 2–4-paired, transverse veins conspicuous, margins serrate on both sides. Inflorescence unknown.

Phenology. New shoots June to August.

Distribution and habitat. This new species is found in Kunming, Yunnan, China. It usually occurs in limestone montane areas at elevations of 2100–2400 m in the understorey of forests of *Quercus longispica* (Handel-Mazzetti) A. Camus, *Castanopsis delavayi* Franchet or *Cupressus* sp.

Etymology. The epithet honours Professor De-Zhu Li of Kunming Institute of Botany, Chinese Academy of Sciences, who has made great contributions to the taxonomy, molecular phylogeny, evolution and biogeography of bamboos and promoted the collaboration of bamboo research around the world.

Chinese name. Dé Zhū Yù Shān Zhú (Chinese pronunciation), 德铢玉山竹 (Chinese characters).

Additional specimens examined (paratypes). CHINA – Yunnan Province, Kunming City • Panlong District, Ciba Town, Changchong Hill; 25°7'31.85"N, 102°42'25.13"E; 2211 m a.s.l.; 26 June 2023; *Y.X. Zhang & C. ZhangCCS01* (KUN); • same collection data as for preceding; 25°6'55.28"N, 102°42'5.67"E; 2314 m a.s.l.; 27 August 2023; *R.L. Zhang et al. CCS04* (KUN); • same collection data as for preceding; 25°7'6.86"N, 102°42'9.98"E; 2310 m a.s.l.; 27 August 2023; *R.L. Zhang et al. CCS05* (KUN); • Panlong District, Ciba Town, Xiaoshao Village; 25˚11'12.22"N, 102˚44'41.14"E; 2243 m a.s.l.; 27 June 2023; *Y.X. Zhang & C. Zhang XS01* (KUN); • same collection data as for preceding; 25˚11'10.32"N, 102˚44'43.1"E; 2266 m a.s.l.; 27 June 2023; *Y.X. Zhang & C. Zhang* XS02 (KUN); • Xishan District, Haikou Forest Farm; 24°50'50.09"N, 102°36'19.75"E; 2147 m a.s.l.; 18 August 2023; *Y.X. Zhang & R.L. Zhang ZSC02*, *ZSC03* (KUN); • same collection data as for preceding; 2106 m a.s.l.; 25 July 2020; *H. Peng PHHK112* (KUN); • Xundian County, Xianfeng Town; 25°31'12.79"N, 103°04'28.80"E; 2429 m a.s.l.; 21 August 2023; *Y.X. Zhang et al. DSTQ02* (KUN).

Discussion

The branch number per node of the new species *Yushania dezhui* is 3–12, which is similar to *Y. maculata* and *Y. weixiensis*. In *Flora Reipublicae Popularis Sinicae* (Yi 1996), *Yushania* was divided into two sections, i.e. section *Brevipaniculatae* T. P. Yi and section *Yushania*. Taxa of the former section usually possess many branches per node, whereas species of the latter one have solitary branch or one branch on lower nodes and 3–5(-8) on middle and upper nodes. Therefore, we place *Y. dezhui* into section *Brevipaniculatae*. The most unique morphological character of *Y. dezhui* is the adaxial epidermis with pubescence for the one-year-old foliage blades. Up to now, there are no more than 20 bamboo species with hairy adaxial epidermis of foliage blades recorded in China, such as *Bambusa polymorpha* Munro, *Yushania qiaojiaensis* Hsueh & T. P. Yi (Li et al. 2006; Shi et al. 2022). Besides those morphological features (Table 2) that can differentiate *Y. dezhui* from sympatric species *Y. maculata* and *Y. polytricha* and morphologically similar species *Y. weixiensis*, the habitat preference is another diagnostic character. The new species *Y. dezhui* usually occurs in limestone montane areas from 2100 m to 2400 m a.s.l., while *Y. maculata* and *Y. weixiensis* are usually distributed on non-limestone shady slopes and at a slightly higher elevation than the new species (2200–3500 m) and *Y. polytricha* occurs at elevations from 1900 m to 1950 m (2000 m) (Li et al. 2006; Shi et al. 2022).

In the plastome phylogenetic analyses, the recovered six main lineages, i.e. clades III–VI, clades IX and XI, were consistent with previous studies (Guo et al.

2021). The relationships amongst the five subtribes in the nrDNA tree were not well resolved, which was also consistent with Guo et al. (2021). The four individuals of *Yushania dezhui* were grouped into two subclades in the plastome tree (Fig.1), whereas they formed a clade with high support (100%) in the nrDNA tree (Fig. 2). A similar situation applied to *Y. shuichengensis*. Discordance between plastome and nuclear gene trees has been recovered in the genus *Yushania* and other genera, even in the tribe Arundinarieae (e.g. Zhang et al. (2012); Yang et al. (2013); Guo et al. (2019); Guo et al. (2021); Ye et al. (2021a)). The cytonuclear incongruence was mostly caused by the complex evolutionary history of those taxa, including hybridisation, introgression, incomplete lineage sorting and so on. Ye et al. (2021a) revealed the reticulate evolutionary history of the genera *Fargesia* Franchet and *Yushania*, based on genome skimming and double digest restriction-site-associated DNA sequencing data. In their study, only several species with multiple individuals were clustered as monophyletic and most species with multiple individuals were resolved as polyphyletic in the plastome trees. Our results referring to *Y. dezhui* and *Y. shuichengensis* were consistent with Ye et al. (2021a). In the DNA barcoding study of *Fargesia*, the nrDNA sequences showed better discriminatory power than the plastomes and some species recovered as polyphyletic in the plastome trees were resolved as monophyletic in the nrDNA phylogenies (Lv et al. 2023). The cases of *Y. dezhui* and *Y. shuichengensis* were also congruent with that of *Fargesia*. However, the specific reasons for the cytonuclear incongruence of *Y. dezhui* and *Y. shuichengensis* need to be tested within a more comprehensive sampling background in the future. On the whole, all the aforementioned studies, including our own, have demonstrated that it was better to exploit molecular markers with different inheritance patterns in discovering new species, especially those with complicated evolutionary histories.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Yu-Xiao Zhang participated the field investigation, manuscript writing, and data analysis; Chao Zhang and Hu-Gang Zhao performed some field work; Ru-Li Zhang carried out some field work, data analysis, and paper writing.

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Data availability

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

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Research Article

A new species and a new record of *Phlomoides* (Lamiaceae) from Xizang, China

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Abstract

Phlomoides bomiensis, a new species in Bomi County, Xizang, China, was described and illustrated. In addition, *Phlomoides longidentata*, previously only known from Nepal and Bhutan, is newly recorded from Dingri County, Xizang, China. The phylogenetic placement of both species within the genus was analysed using nine plastid DNA markers (*atpB-rbcL*, *psbA-trnH*, *rpl16*, *rpl32-trnL*, *rps16*, *trnK*, *trnL-trnF*, *trnS-trnG*, *trnT-trnL*). Both species have brown-black trichomes inside the upper corolla lip and nested within the same subclade of Clade II. A diagnostic key to the *Phlomoides* species belonging to this subclade is provided.

Key words: Lamioideae, Phlomideae, *Phlomis*, taxonomy, Tibet

Introduction

As revealed by phylogenetic studies, the resurrected genus *Phlomoides* Moench includes traditionally defined *Phlomis* L. sect. *Phlomoides* (Moench) Briq., *Eremostachys* Ledeb., *Lamiophlomis* Kudô, *Metastachydium* Airy Shaw ex C.Y.Wu & H.W.Li, *Notochaete* Benth., *Pseudomarrubium* Popov, *Paraeremostachys* Adylov, Kamelin & Makhm. and *Pseuderemostachys* Popov (Scheen et al. 2010; Bendiksby et al. 2011; Mathiesen et al. 2011; Salmaki et al. 2012; Zhao et al. 2023a, b). With this updated circumscription, *Phlomoides* encompasses approximately 180 species. The genus is characterised by perennial habits, often tuberous roots, cordate to triangular-ovate, entire to bipinnatisect leaves, 5-toothed calyx, dome-shaped and apically hairy upper corolla lips. Notably, some species of *Phlomoides* have been used in traditional medicine, such as *P. rotata* (Benth. ex Hook.f.) Mathiesen, *P. betonicoides* (Diels) Kamelin & Makhm. and *P. medicinalis* (Diels) Kamelin & Makhm. (Peng and Xiang 2017).

China is one of the three diversity centres of *Phlomoides*, boasting 60 species and 17 varieties, of which 39 species are distributed in the Tibetan Plateau, Himalaya and Hengduan Mountains (Wu and Li 1977; Li and Hedge 1994; Zhao et al. 2021a, b, 2022, 2023a, 2024a, b, c). However, the diversity of *Phlomoides* in these areas remains understudied. Recent discoveries have shed light on this hidden species diversity, with the description of four species new to science within these

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regions. Amongst them, *Phlomoides liangwangshanensis* Y.Zhao, H.L.Zheng & C.L.Xiang and *P. henryi* Y.Zhao & C.L.Xiang are distributed in the Hengduan Mountains and *P. cuonaensis* Y.Zhao, C.L.Xiang & Sukhor. and *P. longidentata* Pendry are found in the Himalayas (Pendry 2021; Zhao et al. 2021a, 2024a, b).

During our field trip in Xizang, we found one new species of *Phlomoides* in Bomi County and one new record of the genus in Dingri County. Both species have brown-black trichomes inside the upper corolla lip. In this study, we provide detailed descriptions and illustrations of both the new and newly-recorded species. In addition, we make detailed morphological comparisons with other species which have brown-black trichomes in the upper corolla lip. This comparative analysis aims to facilitate accurate identification and classification within the genus *Phlomoides*.

Material and methods

Taxon sampling

Taxon sampling is primarily based on our previous molecular phylogenetic study (Zhao et al. 2024a). For this particular study, the putative new species (*Phlomoides bomiensis* C.L.Xiang & Y.Zhao), the newly-recorded species (*Phlomoides longidentata*), as well as three morphologically related species [three individuals of *Phlomoides tibetica* (C.Marquand & Airy Shaw) Kamelin & Makhm., one individual each of *Phlomoides rotata* (Benth. ex Hook.f.) Mathiesen and *Phlomoides nana* (C.Y.Wu) Y.Zhao & C.L.Xiang] were sequenced for the first time. In total, our molecular phylogenetic analyses comprised 59 individuals, representing 53 Chinese species of *Phlomoides*. In addition, three species of *Phlomis* were selected as outgroup.

DNA extraction, selection of markers and molecular phylogenetic analyses

The CTAB method was used to extract total genomic DNA from silica gel dried leaf materials (Doyle and Doyle 1987). Sequences of nine plastid DNA markers (*atpB-rbcL*, *psbA-trnH*, *rpl16*, *rpl32-trnL*, *rps16*, *trnK*, *trnL-trnF*, *trnS-trnG*, *trnT-trnL*) were chosen for the phylogenetic reconstruction. Primers, polymerase chain reaction (PCR), sequencing and alignment were carried out according to procedures used in Zhao et al. (2024a). The sequences, newly generated in this study together with their GenBank accession numbers, are listed in Suppl. material 1.

Bayesian Inference (BI) and Maximum Likelihood (ML) were used for phylogenetic reconstruction. Detailed settings for BI and ML analyses followed Zhao et al. (2024a). TreeGraph2 (Stöver and Müller 2010) was applied to visualise and edit all trees.

Morphological and taxonomy study

We thoroughly examined herbarium specimens or their digital images from the following Herbaria: B, BM, C, CDBI, E, FI, GH, HIB, IBSC, K, KUN, KYO, L, LE, M, MA, MAO, MO, MW, NAS, P, PE and TI. During our field investigations, we observed and documented important diagnostic characteristics of *Phlomoides* species. These observations were complemented by high-resolution photographs taken in their natural habitats. Trichome morphology was observed and measured under a Leica DM2500 optical microscope (Leica Microsystems GmbH, Wetzlar, Germany).

Results and discussion

Sequence characterisation

In total, 558 sequences were included for phylogenetic analyses, of which 63 sequences were newly sequenced in this study and they were submitted to GenBank (Suppl. material 1). The aligned cpDNA dataset was 9,222 nucleotides in length (2,382 bp for *atpB-rbcL*, 439 bp for *psbA-trnH*, 1,365 bp for *rpl16*, 677 bp for *rpl32-trnL*, 968 bp for *rps16*, 954 bp for *trnK*, 869 bp for *trnL-trnF*, 825 bp for *trnS-trnG* and 743 bp for *trnT-L*, respectively), of which 883 bp (9.57%) are variable. Characteristics for all datasets are listed in Table 1.

Phylogenetic reconstruction

The phylogenetic analyses using both Bayesian Inference (BI) and Maximum Likelihood (ML) methods yielded largely congruent tree topologies. Therefore, only the Bayesian 50% majority rule consensus tree is presented, with posterior probabilities (PP) and bootstrap values (BS) indicated near nodes (Fig. 1).

Consistent with our previous molecular phylogenetic analyses (Zhao et al. 2024a), six well-supported clades can be recognised (Fig. 1). Clade II includes the majority of species characterised by having linear-tuberous roots, without persistent basal leaves and glabrous nutlets (Zhao et al. 2024a). In the present study, we found that Clade II can be divided into two major subclades with strong support values. Subclade IIa (Fig. 1: PP = 1.00/BS = 100%) contains the putative new species (*P. bomiensis*), as well as *P. longidentata*. Most species in this subclade are characterised by brown-black trichomes inside the upper corolla lip, except for *P. rotata* and *P. henryi* (Zhao et al. 2024c). This subclade unites ten species [*P. rotata*, *P. longidentata*, *P. breviflora* (Benth.) Kamelin & Makhm., *P. bomiensis*, *P. tibetica*, *P. macrophylla* (Benth.) Kamelin & Makhm., *P. nyalamensis* (H.W.Li) Y.Zhao & C.L.Xiang, *P. nana*, *P. milingensis* (C.Y.Wu & H.W.Li) Kamelin & Makhm. and *P. henryi*]. All the species in subclade IIb (Fig. 1: 1.00/98%) have white and transparent trichomes inside the upper corolla lip.

Table 1. The statistics of all datasets for phylogenetic analysis.

Datasets	No. Taxa	Nucleotides (with ambiguous sites excluded) [bp]	GC content (%)	No. constant sites [bp]	No. variable sites [bp]	No. parsimony-informative sites [bp]
atpB-rbcL	62	2382	39.3	2244	138	88
psbA-trnH	62	439	32.7	384	55	29
rpl16	62	1365	36.2	1211	154	91
rpl32-trnL	62	677	31.7	576	101	66
rps16	62	968	35.6	891	77	45
trnK	62	954	34	844	110	65
trnL-trnF	62	869	36.1	794	75	42
trnS-trnG	62	825	33.5	738	87	50
trnT-trnL	62	743	29.4	657	86	56
combined	62	9222	35.5	8339	883	532

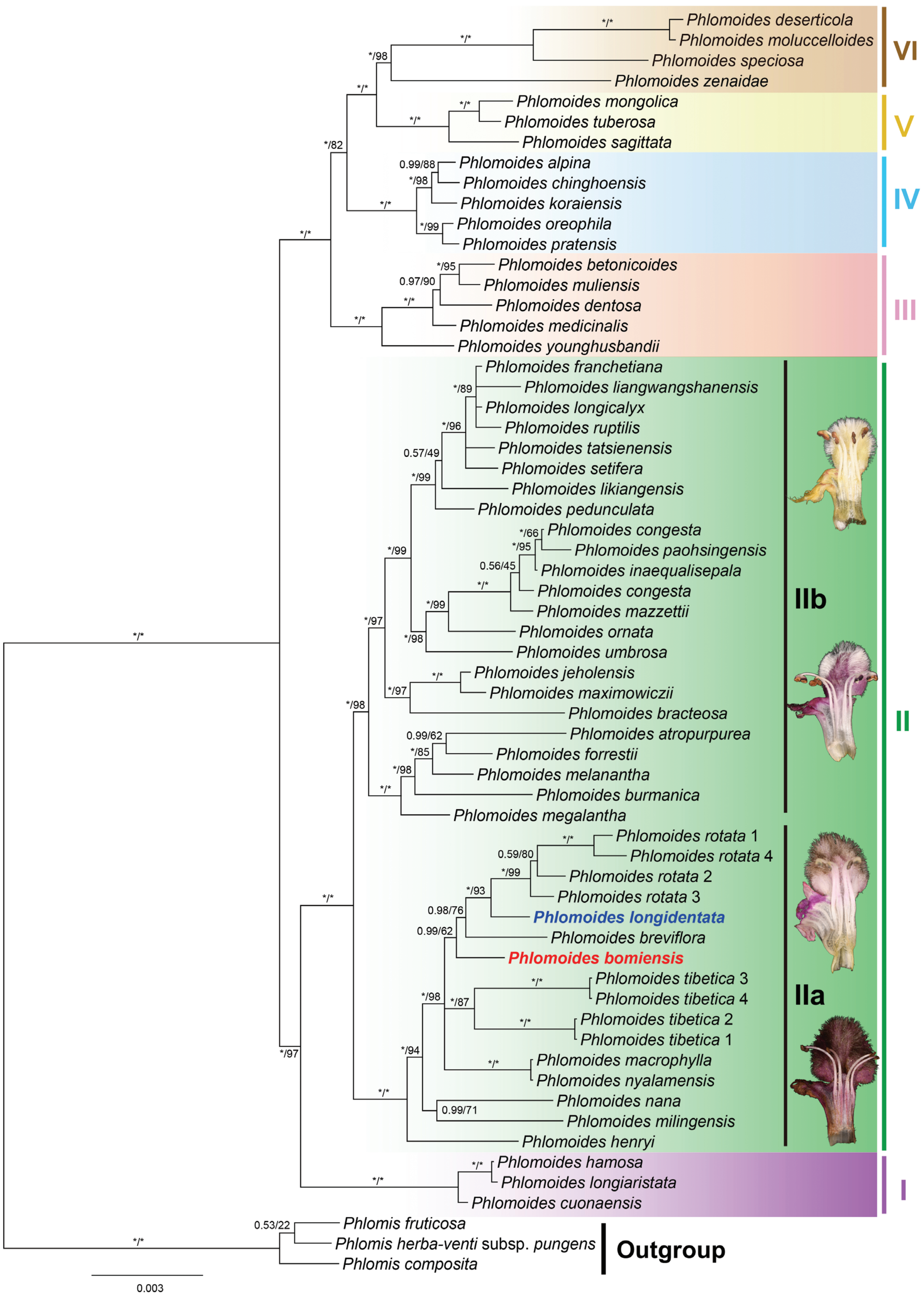

Figure 1. Phylogeny of *Phlomoides* inferred by Bayesian Inference (BI), based on the combined plastid dataset cpDNA. Support values displayed on the branches follow the order BI-PP/ML-BS (" * " indicates PP = 1.00 or BS = 100%).

Phlomoides longidentata is sister to *P. rotata* which is represented by four individuals (Fig. 1: 1.00/93%) and these species are sisters to *P. breviflora* (Fig. 1: 0.98/76%). *P. bomiensis* is sister to all three species (Fig. 1: 0.99/62%).

Morphological comparison

The species within subclade IIa are distributed in Tibetan Plateau, Himalaya and Hengduan Mountains. Here, we provide a morphological comparison of the ten species grouped in the subclade IIa (Table 2) to evaluate the most significant diagnostic traits. The trichome colour, floral leaves and calyx teeth were identified as having taxonomic significance within this subclade. A key is provided to differentiate these species.

Taxonomic treatment

***Phlomoides bomiensis* C.L.Xiang & Y.Zhao, sp. nov.**
urn:lsid:ipni.org:names:77347473-1
Fig. 2

Type. China, Xizang (Tibet), Linzhi City, Bomi County, on the road from Bomi to Motuo, near Galongla Tunnel, 29°48'22.4"N, 95°42'2.45"E, alt. 3454 m, 22 Aug 2023, *Y. Zhao, R.Z. Bai, Q. Tian & M.L. Qian XCL2584* (holotype: KUN 1614346!; isotypes: KUN 1614347!, KUN 1614348!, KUN 1614349!).

Diagnosis. *Phlomoides bomiensis* is morphologically most similar to *P. nyalamensis* and *P. breviflora*. These species are often taller than 1 m and have a purple corolla with brown to black trichomes inside the upper lip. It differs from *P. nyalamensis* by its subtruncate to slightly emarginate calyx teeth, posterior filaments with reflexed appendages at base and floral leaves with obvious petioles (vs. obviously emarginate calyx teeth, posterior filaments without appendages and sessile upper floral leaves). It differs from *P. breviflora* by its corolla that is longer than 2 cm and its oblong nutlets (vs. corolla often shorter than 1.5 cm and inflated globose nutlets). The differences between the ten species from subclade IIa are listed in Table 2.

Table 2. Comparative morphological characters amongst *Phlomoides bomiensis*, *P. longidentata* and their related species.

	Height	Basal leaves	Floral leaf petiole length	Flower colour	Trichome colour of upper corolla lip	Apical part of calyx tube
P. rotata	2.5–10 cm	+	Lack obvious petiole	Purple or white	White	Broadly triangular
P. longidentata	50–100 cm	–	5–100 mm	Light purple to pink	Black or brown	Emarginate
P. breviflora	60–150 cm	–	30–130 mm	Purple	Black or brown	Subtruncate or broadly triangular
P. bomiensis	50–180 cm	–	5–70 mm	Purple	Black or brown	Subtruncate or slightly emarginate
P. tibetica	10–30 (50) cm	+	0 (5) mm	Purple to light purple	Black or brown	Subtruncate or slightly emarginate
P. macrophylla	100–200 cm	–	1–10 (50) mm	White to light pink	Black or brown	Emarginate
P. nyalamensis	100–200 cm	–	1–10 (50) mm	Purple	Black or brown	Emarginate
P. nana	30–50 cm	+	2–5 (10) mm	White to light pink	Black or brown	Emarginate
P. milingensis	15–50 cm	+	2–10 mm	Purple	Black or brown	Subtruncate or slightly emarginate
P. henryi	100–150 cm	–	5–35 mm	Light purple to pink	White	Truncate

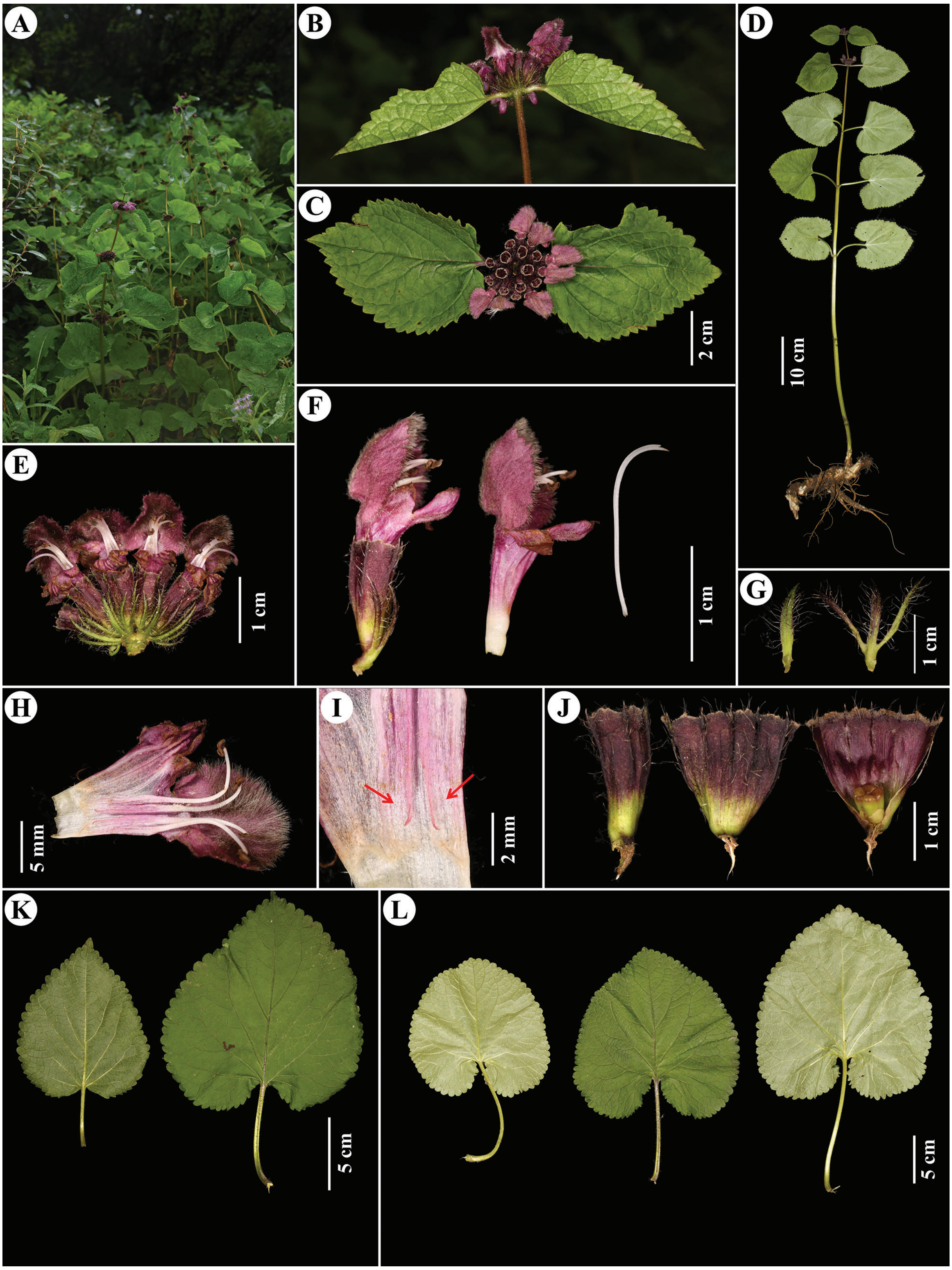

Figure 2. *Phlomoides bomiensis* C.L.Xiang & Y.Zhao **A** habitat **B, C** verticillaster with floral leaves **D** plant **E** verticillaster **F** flower **G** bracts **H** dissected flower **I** appendages at base of posterior filaments (arrow) **J** calyx and dissected calyx **K** floral leaves **L** Stem leaves (Photographed by Yue Zhao).

Description. Perennial herbs. ***Roots*** robust, linear-tuberous. ***Stems*** 0.5–1.8 m tall, subquadrangular, robust, lower stem part glabrous, upper part with simple trichomes. ***Basal leaves*** absent; ***stem leaves*** with petioles 5–14 cm long, with simple trichomes, blade cordate, papery, 8–21 × 8–18 cm, adaxially green with simple trichomes, denser on vein, abaxially light green, only with sparse simple trichomes on vein, margin crenate, apex acute. ***Verticillasters*** axillary, 8–18-flowered; ***floral leaves*** with petioles 0.5–7 cm long, blade cordate to truncate, 3–15 × 2–12 cm, gradually reduced upwards; ***bracts*** linear to lanceolate, 8–10 mm long, with sparse long (2–3 mm) simple trichomes. ***Calyx*** tubular, 12 × 5 mm, conspicuously 10-veined with sparse simple (2–3 mm long) trichomes on veins, tube subtruncate to slightly emarginate, teeth 5, ca. 1 mm long, apical spines 1 mm long. ***Corolla*** purple, 21–23 mm long, 2-lipped; posterior lip ca. 8–10 mm long, galeate, densely stellate tomentose outside, margin denticulate, brown to black bearded inside; anterior lip 3-lobed, ca. 7 × 8 mm, middle lobe largest, oblong, ca. 5 × 3 mm, lateral lobes ovate; tube glabrous outside, ca. 11 mm, annulate pilose inside. ***Stamens*** 4, included within posterior lip, with “cobweb-like” indumentum, posterior filaments with reflexed appendages at base. ***Style*** unequally 2-lobed. Nutlets oblong, apex truncate, glabrous.

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

Distribution and habitat. Based on our field collections and previously collected specimens, *P. bomiensis* is known to occur in Bomi County and Motuo County, Xizang (Tibet), China. It grows in forests and forest margins at altitudes between 3400 and 4200 m (Fig. 3).

Etymology. The specific epithet refers to the name of the Bomi County in Xizang Autonomous Region, where the new species was discovered.

Chinese name (assigned here). bō mì cǎo cāo sū (波密草糙苏)

Additional specimen examined (paratypes). China. Xizang (Tibet): • Linzhi City, Motuo County, Northern Galongla Pass, alt. 3500–3700 m, 20 Aug 1982, *S.Z. Cheng & B.S. Li 000315* (PE 00923558!, PE 00832483!, PE 00832484!) • Linzhi City, Bomi County, 30 km away from Zhamo Road, alt. 4200 m, 27 Jul 2010, *South Tibet Expedition Team STET1237* (PE 02328210!) • Linzhi City, Bomi County, Galongla Mountain, alt. 3879 m, 17 Jul 2022, *J.F. Xiao, H.Z. Feng & Er.F. Huang XJF114* (KUN 1614350!).

Phlomoides bomiensis was first collected more than 40 years ago (*S.Z. Cheng & B.S. Li 00315*; PE 00923558!, PE 00832483!, PE 00832484!), but the specimens were then identified as *Phlomoides umbrosa* (Turcz.) Kamelin & Makhm. var. *australis* (Hemsl.) C.L.Xiang & H.Peng. However, *Phlomoides umbrosa* var. *australis* was distinguished from *P. bomiensis* by having white or transparent trichomes on upper corolla and subsessile floral leaves (vs. brown-black trichomes on upper corolla and floral leaves with petioles 0.5–7 cm long). Another specimen of *P. bomiensis* was collected in 2010 (*South Tibet Expedition STET1237*; PE 02328210!), but it was misidentified as *Phlomoides tibetica*. The differences between *Phlomoides tibetica* and *P. bomiensis* are provided in Table 2.

Phlomoides longidentata **Pendry, Edinburgh J. Bot. 78: 4, 2021.**

Fig. 4

Type. Nepal, Solukhumbu District, Namche Bazar, above bridge over Dudh Kosi. 27°47'31"N, 86°42'57"E, alt. 3060 m, 12 Sep 2006, *DNEP3 BX36* (holotype: E!; isotypes: KATH!, TI!, TUCH!).

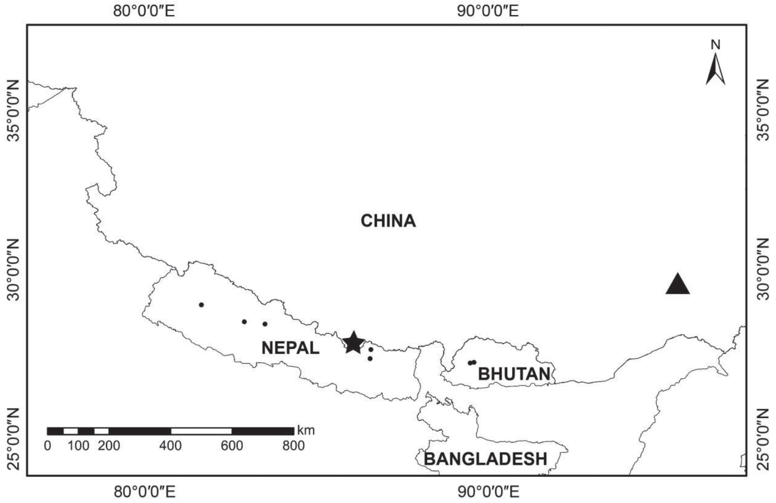

Figure 3. Distribution of *Phlomoides bomiensis* (black triangle), new location of *P. longidentata* (black star) and known localities of *P. longidentata* (black circle).

Diagnosis. *Phlomoides longidentata* is a recently described species from Bhutan and Nepal (Pendry 2021). Specimens of *P. longidentata* were collected by Chinese collectors as early as 1959 (*Anonymous 752*; PE 00832482!), when it was identified as *P. umbrosa* and *P. umbrosa* var. *australis*. During our field investigations in Rongxia Town, we rediscovered this species in the wild. It rather looks like a perennial herb, but not annual as described by Pendry (2021). Here we provide description of this species.

Description. Perennial herbs. ***Roots*** delicate, thin, linear-tuberous. ***Stems*** 30–60 cm tall, subquadrangular, unbranched, stellate pilose. ***Basal leaves*** absent; ***stem leaves*** with petioles 4–19 cm long, with stellate (with a long central ray) and simple trichomes, blade cordate, papery, 4–14 × 4–15 cm, adaxially green with sparse simple trichomes, denser and longer on the main vein, abaxially light green, with dense stellate trichomes with equal rays, (stellate trichomes denser and with longer central ray on the veins), base cordate, margin serrate or crenate, apex acute. ***Verticillasters*** axillary, 8–20-flowered; ***floral leaves*** with petioles 0.5–10 cm long, blade lanceolate, base cordate to truncate, 4.5–13 × 2–11 cm, gradually reduced upwards; ***bracts*** subulate, 7–8 mm long, with sparse long simple trichomes, ca. 2 mm long. ***Calyx*** tubular, 10–11 × 4–5 mm, pubescent outside with sparse stellate trichomes with equal rays outside (10 tubular veins have longer central rays); tube apically emarginate; teeth 5, unequal, two longer teeth 4 mm long, three shorter teeth 2–3 mm long. ***Corolla*** light purple to pink, 19–22 mm long, 2-lipped; posterior lip 7–8 mm long, galeate, densely stellate tomentose outside, margin denticulate, brown to black-bearded inside; anterior lip 3-lobed, ca. 6 × 8 mm, middle lobe largest, oblong, ca. 5 × 3 mm, lateral lobes ovate; tube glabrous outside, ca. 12 mm, annulate pilose inside. ***Stamens*** 4, included within posterior lip, with “cobweb-like” indumentum, posterior filaments with reflexed appendages at base. ***Style*** unequally 2-lobed. ***Nutlets*** oblong, apex truncate, glabrous.

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

Distribution and habitat. China, Bhutan and Nepal; new record for China found in Xizang (see below). It grows in forests and forest margins at altitudes between 2000 and 3800 m (Fig. 3).

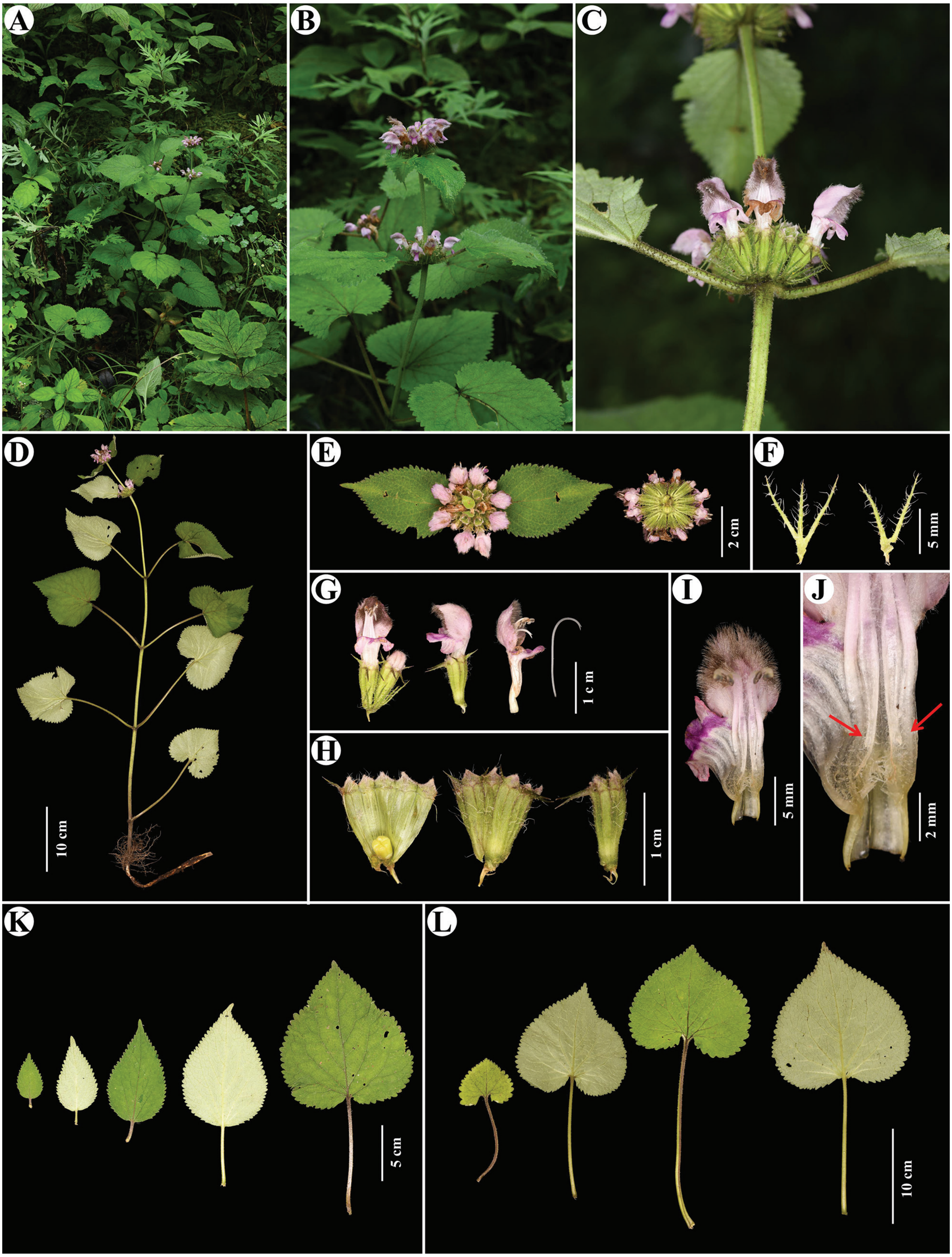

Figure 4. *Phlomoides longidentata* Pendry **A** habitat **B, D** plant **C, E** verticillaster **F** bracts **G** flower **H** dissected calyces **I** dissected flower **J** appendages at base of posterior filaments (arrow) **K** floral leaves **L** stem leaves (Photographed by Yue Zhao).

Chinese name (assigned here). cháng cì cǎo cāo sū (长刺草糙苏)

Additional specimens examined. CHINA. Xizang Province: • Rikaze City, Dingri County, Rongxia Town, 28°1'12.7"N, 86°15'52.1"E, alt. 2888 m, 29 Aug 2023, *Y. Zhao, R.Z. Bai, Q. Tian & M.L. Qian XCL2670* (KUN 1614352!, KUN 1614353!) • Rikaze City, Dingri County, Rongxia Town, 28°1'12.7"N, 86°15'52.1"E, alt. 2888 m, 11 Sep 2019, *Y.P. Chen, Y. Zhao & B.Y. Zhang EM1123* (KUN 1614351!) • Rikaze City, Dingri County, Rongxia Town, alt. 3200 m, 2 Aug 1959, *Anonymous 752* (PE 00832482!).

Key to species of *Phlomoides* from subclade IIa

1	Upper corolla lip with trichomes transparent to white	**2**
–	Upper corolla lip with trichomes brown to black	**3**
2	Stellate trichomes absent on leaves and bracts, plant often taller than 1 m	***P. henryi***
–	Stellate trichomes present on leaves and bracts, plant often shorter than 10 cm	***P. rotata***
3	Bracts and calyces with brown to black trichomes	**4**
–	Bracts and calyces with white trichomes	**5**
4	Bracts with black simple trichomes, stellate trichomes absent	***P. tibetica***
–	Bracts with brown simple and stellate trichomes	***P. milingensis***
5	Calyx teeth obviously emarginate	**6**
–	Calyx teeth subtruncate or slightly emarginate	**9**
6	Calyx with two longer and three shorter apical teeth	***P. longidentata***
–	Calyx with five equal teeth	**7**
7	Plant less than 0.5 m tall, basal leaves present; upper floral leaves with petiole ca. 2–5 mm long	***P. nana***
–	Plant often taller than 1 m, basal leaves absent; upper floral leaves lack petiole	**8**
8	Corolla purple	***P. nyalamensis***
–	Corolla white	***P. macrophylla***
9	Corolla less than l.5 cm long	***P. breviflora***
–	Corolla more than 2 cm long	***P. bomiensis***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

YZ and CLX conceived this research. YZ, YPC, RZB collected materials. YZ performed the experiments. YPC and XCL analyzed the data. All the authors wrote the manuscript. All authors read and approved the final version of manuscript.

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Data availability

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

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Supplementary material 1

List of *Phlomoides* taxa sampled with information related to taxonomy, voucher information, and GenBank accession numbers

Authors: Yue Zhao, Ya-Ping Chen, Rui-Zhu Bai, Colin A. Pendry, Alexander P. Sukhorukov, Chun-Lei Xiang

Data type: xlsx

Explanation note: GenBank accession numbers of the newly generated sequences are marked in bold, other sequences are taken from GenBank (– indicates missing information).

Link: https://doi.org/10.3897/phytokeys.246.129057.suppl1

PhytoKeys 246: 27–42 (2024)
DOI: 10.3897/phytokeys.246.131046

Research Article

Huperzia crassifolia (Lycopodiaceae), a new species from China based on morphological characters and molecular evidence

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Abstract

A new species of the firmoss from China, *Huperzia crassifolia* sp. nov., is described and illustrated based on morphological characters and molecular evidence. The new species resembles species associated with the *H. javanica* complex, in particular *H. javanica* based on leaf shape and serrations, but can be easily distinguished by elliptic lanceolate and thick coriaceous leaves, well differentiated seasonal constriction zones, and reflexed leaf margins when get dried. Phylogenomic reconstruction using whole chloroplast genome sequences recovered *H. crassifolia* as sister to *H. sutchueniana* and only distantly related to morphological similar species *H. javanica*, *H. nanlingensis*, and *H. serrata*. The genome size 2C = 17.2 pg indicated the new species to be a tetraploid, whereas diploid *H. javanica* had a genome size of 8.7 pg. Morphological characters, distribution, and conservation status of the new species are also presented.

Key words: Firmoss, integrative taxonomy, micromorphology, phylogenomics

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Introduction

Huperzia Bernh. is a genus of about 25 species (PPG I 2016) that occurs mainly in temperate and boreal climatic zones of the world (Zhang and Iwatsuki 2013; Field et al. 2016). Its taxonomic boundary with *Phlegmariurus* Holub has long been controversial (Holub 1964, 1985; Ching 1978, 1981; Wikström and Kenrick 1997; Zhang and Kung 2000; Zhang 2004; Christenhusz et al. 2011) and now an agreement was made about the segregation of these two genera (Zhang and Iwatsuki 2013; Field et al. 2016; PPG I 2016; Chen et al. 2021). Taxonomic uncertainty is not only restricted to the generic classification but affects the estimation of the species diversity that is expected still to be underestimated due to the difficulty in the taxonomy of this genus despite significant progress having been achieved (Zhang and Kung 2000; Zhang and Iwatsuki 2013; Shrestha et al. 2014; Lim and Sun 2015; Lim et al. 2015; Shrestha and Zhang 2015a, b; Testo et al. 2016).

Taxonomic treatments of the Southeast Asian species of *Huperzia* have mainly relied on morphology, including the shape of the trophophylls, serrations, leaf petiole, and ratio of width to length (Ching 1981; Yang 1989, 1990; Zhang and Kung 2000; Zhang and Iwatsuki 2013; Shrestha and Zhang 2015b; Shalimov et al. 2017), and still rarely combined with molecular evidence (Shrestha et al. 2014; Shrestha and Zhang 2015a). Recent taxonomical efforts have clarified the status of several local and confusing species, including the segregation of *H. asiatica* from *H. lucidula* (Lim et al. 2015; Shrestha and Zhang 2015a) and *H. continentalis* from *H. haleakalae* (Testo et al. 2016). Two new species *H. jejuensis* (Lim and Sun 2015) and *H. nanlingensis* (Shrestha et al. 2014) were discovered from Korea and China, respectively. However, species delimitation has been challenging because of the very subtle differences in the gross morphology among species. Besides the subtle differences among morphologically similar taxa in *Huperzia*, hybrids may also hinder the recognition of distinct species (Testo et al. 2016; Vejvodová et al. 2024).

As has previously been recognized, *Huperzia serrata* is the most widely distributed and common *Huperzia* species in China (Ching 1981; Zhang and Kung 2000; Zhang 2004; Zhang and Iwatsuki 2013; Shrestha and Zhang 2015b). Species delimitation of *H. serrata* and its relatives was substantially improved by the efforts of several researchers who separated *H. crispata* and *H. javanica* from the broad species concept *H. serrata* (Ching 1981; Yang 1982; Lim et al. 2015; Shrestha and Zhang 2015b) as well as the recognition of the new species *H. nanlingensis* (Shrestha et al. 2014). Geographically, *H. javanica* occurs in areas along the Yangtze River and throughout southern China, while the distribution range of *H. serrata* is restricted to northeastern China (Shrestha and Zhang 2015b; Chen 2021). However, species delimitation of the *H. javanica* complex as well as other lineages of *Huperzia* remains unclear and awaits more efforts (Chen 2021; Vejvodová et al. 2024).

During medicinal plant inventories in Guizhou, we discovered two morphological distinct forms of *Huperzia javanica* which usually occur together. The gross morphology segregates one of these forms as typical *H. javanica*; the other form is considered as a distinct taxon. This proposal was studied by consulting *Huperzia* checklists of China, local floras, and careful comparison of morphological characters with previously described species by checking specimens and species protologue for all the known species of *Huperzia*. After all these taxonomical revisions, we accept this taxon to represent an undescribed new species. Genome size measurement and phylogenomic reconstruction using whole chloroplast genome sequence were employed to provide additional evidence to support this hypothesis and detect the phylogenetic relationship of this new taxon. Here, we describe this new species based on molecular, macro-, and micro-morphological evidence.

Materials and methods

Morphological observation

The specimens of the new taxon were collected from Duyun, Guizhou Province, Southwestern China, and field investigations were conducted in 2016. Careful comparison of morphological characters with previously described species was carried out at HITBC, KUN, PYU, and IMC (herbaria codes according to Thiers 2024) as well as on the digitalized specimens from online Chinese Virtual Herbarium (CVH). In order to identify the distinction of the new taxon in the genus *Huperzia*, we checked not only species with similar gross morphology, including *H. javanica* complex but also several congeneric taxa which co-occur in this area (Ching 1981; Zhang and Iwatsuki 2013; Shrestha and Zhang 2015b).

All studied accessions were checked and identified using the treatments provided in the Flora Reipublicae Popularis Sinicae (Zhang 2004) and the Flora of China (Zhang and Iwatsuki 2013) besides specific taxonomic treatments (Ching 1981; Yang 1989; Shrestha and Zhang 2015b). Gross morphology was compared among individuals of the new taxon and accessions of putative relatives such as *H. javanica* and *H. nanlingensis* by analyzing either freshly collected material or images of specimens including type specimens of both species. Several diagnostic characters were carefully checked and compared among all accessions. Several individuals of the new taxon from different localities and its similar species *H. javanica* were sampled to obtain a comprehensive coverage. The voucher specimens of the new species were deposited in the Herbarium of Qiannan Normal College for Nationalities (QNUN).

Spore morphology and ornamentation

Scanning electron microscopy (SEM) was used for spore ornamentation for the new taxon and its close relatives *Huperzia javanica*. In preparation, spores were taken from mature sporangia, fixed on carbon tape, and sputtered with gold. The morphology of spores was observed with a scanning electron microscope (Zeiss Evo LS10). The description of spore ornamentation followed Wang and Yu (2003) and Punt et al. (2007).

Assessing ploidy via genome size measurement

Living plants from the type locality were cultivated at Xishuangbanna Tropical Botanical Garden, CAS. Fresh leaves were removed from the cultivated plants and used to generate DNA C-value measurement using propidium iodide DNA staining and nuclei counting with a flow cytometer as described previously (Clark et al. 2016; Fujiwara et al. 2023). Leaf fragments were co-chopped together with an internal standard, *Vicia faba* 'Inovec' (2C = 26.90 pg) (Doležel et al. 1992) in General Purpose Buffer (GPB) as isolation buffer (Loureiro et al. 2006). The fluorescence intensities were analyzed on BD FACSVerseTM (BD Biosciences, San Jose, CA, USA). These reported measurements were obtained by estimating the average of measurements carried out for three leaf fragments obtained from three individuals (Table 1). These individuals were all collected from the type location. The interpretation of the obtained genome size values was carried out in the context of previously published estimates with special attention to recently published estimates of different cytotypes belonging to *Huperzia selago s.l.* (Vejvodová et al. 2024).

Table 1. Genome size measurement of *H. crassifolia* and its relatives. For newly generated genome size measurement, we provide besides the holoploid genome size (2C), the following information: CV (average of the repeatedly measured cytometric values), voucher, extraction buffer, internal calibration standard. For measurements obtained from the literature, we provide the reference instead. The ploidy interpretation assumes a conserved positive correlation between chromosome number and genome size (Clark et al. 2016; Fujiwara et al. 2023; Vejvodová et al. 2024). 2C-values between 8 to 12 pg are considered to be diploid, whereas 2C-values between 16 and 18 pg are considered to be tetraploid.

Taxon	2C (pg)	CV	Voucher or Publication	Buffer	Calibration	Ploidy interpretation
H. crassifolia	17.6	0.07	China, Guizhou/LHM2571A	GPB	*Vicia faba* 'Inovec'	4×
H. crassifolia	16.9	0.06	China, Guizhou/LHM2571B	GPB	*Vicia faba* 'Inovec'	4×
H. crassifolia	17.1	0.12	China, Guizhou/ LHM2571C	GPB	*Vicia faba* 'Inovec'	4×
H. javanica	8.6	0.13	China, Guizhou/LHM2569C	GPB	*Vicia faba* 'Inovec'	2×
H. javanica	8.6	0.05	China, Guizhou/LHM2569B	GPB	*Vicia faba* 'Inovec'	2×
H. javanica	8.5	0.04	China, Guizhou/LHM2569A	GPB	*Vicia faba* 'Inovec'	2×
H. javanica	9.2	0.03	China, Guizhou/LHM2572	GPB	*Vicia faba* 'Inovec'	2×
H. nanlingensis	8.7	0.06	China, Guizhou/LHM2568	GPB	*Vicia faba* 'Inovec'	2×
H. lucidula	11.4	NA	Wang et al. (2005)	NA	NA	2×
H. lucidula	9.6	NA	Bai et al. (2012)	NA	NA	2×
H. lucidula	11.3	NA	Bainard et al. (2011)	NA	NA	2×
H. selago	17.3	NA	Šmarda et al. (2019)	NA	NA	4×
H. selago	10.0	NA	Vejvodová et al. (2024)	OTTO	*Pisum sativum* 'Ctirad'	2×
H. selago	13.5	NA	Vejvodová et al. (2024)	OTTO	*Pisum sativum* 'Ctirad'	3×
H. selago	19.2	NA	Vejvodová et al. (2024)	OTTO	*Pisum sativum* 'Ctirad'	4×
H. selago	23.2	NA	Vejvodová et al. (2024)	OTTO	*Pisum sativum* 'Ctirad'	5×
H. selago	29.0	NA	Vejvodová et al. (2024)	OTTO	*Pisum sativum* 'Ctirad'	6×

Taxon sampling, DNA extraction, and sequencing

Multiple accessions were sampled for both the new species and its congeneric species. Complete chloroplast genomes were generated by extracting whole genomic DNA from silica gel dried leaf fragments using a modified CTAB approach (Yang et al. 2014). The DNA sample was indexed by tags and pooled together in one lane of a Genome Analyzer (Illumina HiSeq 2000) for sequencing at the Germplasm Bank of Wild Species, Kunming Institute of Botany, CAS (KIB) and Novogene Biotech (Beijing, China).

Plastome assemblage and annotation

GetOrganelle toolkit (Jin et al. 2020) and Geneious (https://www.geneious.com) were employed to assemble and annotate newly generated genomes. The previously published plastomes of *Huperzia lucidula* (NC_006861) and *H. serrata* (NC_033874) were utilized as reference genomes. The newly sequenced and annotated plastomes were submitted to the GenBank (Table 2). The circular genome plots were generated using Organellar Genome DRAW (Lohse et al. 2013). The boundary of the large-single copy (LSC), small-single copy (SSC), and inverted-repeat (IR) regions for each plastome was visually examined and manually adjusted using Geneious. Plastome characteristics, including genome length and GC content, length of LSC, SSC, and IR region, were compared among all chloroplast genomes from *Huperzia* (Table 2).

Table 2. Plastome sequences generated and/or utilized in this study and its characteristics.

Species	Voucher	Locality	GB accession	Genome (GC)	LSC	SSC	IR	Genes	Proteins	tRNA	rRNA
H. crassifolia	LHM2571B	China, Guizhou (Cult.)	OP223752*	153183 (36.3)	103419	19662	30102	131	88	35	8
H. crassifolia	ES946-1	China, Hubei, Enshi	OP223753*	153276 (36.3)	103324	19662	30290	131	88	35	8
H. crassifolia	YYH15893	China, Hunan, Sangzhi	unpublished[#]	163344 (36.1)	103324	19662	40358	131	88	35	8
H. javanica	LHM2743B	China, Yunnan, Lvchun	OP223759*	154275 (36.4)	103982	19669	30624	131	88	35	8
H. javanica	LHM2743A	China, Yunnan, Lvchun	OP223760*	154682 (36.4)	104048	19668	30966	131	88	35	8
H. javanica	LHM2569B	China, Guizhou (Cult.)	OP223761*	154247 (36.4)	103941	19668	30638	131	88	35	8
H. lucidula	Qiu 94173	USA, Wisconsin	MH549639[b]	154368 (36.3)	104083	19657	30628	131	87	36	8
H. lucidula	Renzaglia 3200	USA, North Carolina	NC_006861[c]	154373 (36.3)	104088	19657	30628	119	86	29	8
H. nanlingensis	GZY2021012001	China, Guizhou	OP223750*	154146 (36.4)	109852	19668	30626	131	88	35	8
H. nanlingensis	LHM2568	China: Guizhou	OP223754*	153806 (36.4)	104038	19668	30100	131	88	35	8
H. selago	LHM & HS s.n	Germany, Alps	OP223755*	153518 (36.3)	103901	19667	29950	131	88	35	8
H. selago	LHM & HS s.n.	Germany, Alps	OP223756*	153515 (36.3)	103898	19667	29950	131	88	35	8
H. serrata	LHM2121	Japan, Mie-ken	OP223757*	153495 (36.3)	104069	19668	29758	131	88	35	8
H. serrata	Zhang X.C. 6972	China, Jilin, Helongjiang	NC_033874[d]	154176 (36.3)	104080	19658	30438	130	87	35	8
H. serrata f. *longipetiolata*	R. Wei CBL011	China, Guangdong, Shaoguan	KY609860[a]	154415 (36.4)	104120	19667	30628	126	85	33	8
H. cf. *sutchueniana*	Guo Z.Y. s.n.	China, Guizhou (Cult.)	OP223758*	154697 (36.4)	104053	19678	30966	131	88	35	8
H. cf. *sutchueniana*	LHM2570	China, Guizhou (Cult.)	OP223751*	154318 (36.4)	104198	19678	30442	131	88	35	8
P. carinatus	Anonymous 5309270453	China, Yunnan, Cangyuan	MN566837[e]	150349 (34.0)	100582	19455	30312	120	79	33	8
P. phlegmaria	Jiang R.H./—	China, unknown	MT786212[f]	149711 (33.8)	99862	19465	30384	89	53	30	6

Notes: information given as: species name, voucher information, locality including Nation, Province or Prefecture, and location, and GenBank accession number. Dashes (—) indicate missing data, asterisks (*) indicate the sequences newly obtained in this study. Genomes available already in GenBank were cited with the GenBank accession number and its reference as [a] Zhang et al. (2017); [b] Mower et al. (2019); [c] Wolf et al. (2015); [d] Guo et al. (2016); [e] Luo et al. (2019); [f] Sequence from GenBank. The unpublished whole plastid sequence was kindly shared by Yue-Hong Yan. For the plastome, length of genome as well as the GC content, LSC, SSC and IR region in base pairs (bp) were given. Based on our annotation, the following numbers were reported: number of genes, number of proteins, number of tRNA, and number of rRNA.

Phylogenetic reconstruction

Phylogenetic trees were reconstructed using 17 complete chloroplast genome sequences. Among these, 13 plastomes were newly generated that were added by four genomes already available via GenBank. Both Maximum likelihood (ML) and Bayesian inference (BI) were employed in the phylogenetic relationship reconstruction. Models of molecular evolution were determined using jModeltest 2 (Darriba et al. 2012). ML analyses were performed as implemented in RAxML carried our using the web server RAxML-HPC 2 v.8.2.10 (Stamatakis 2014) with 1,000 non-parametric bootstrap replicates (MLBS). Posterior probabilities (PP) were obtained using MrBayes v.3.2.6 (Ronquist et al. 2012) with the model as identified in jModelTest without specifying parameter values.

Results

Plastome characteristics of *Huperzia*

The complete chloroplast genome of *Huperzia* possessed the typical quadripartite structure found in most land plants (Fig. 1), including the LSC, SSC, and a pair of IR regions. The assembled genomes contained 131 genes, comprising 88 protein-coding genes, 35 tRNAs, and eight rRNAs. Among the two *H. crassifolia* chloroplast genomes, variation was detected for total length as well as the length of the LSC and IR regions whereas the length of SSC was identical. The 17 *Huperzia* genomes showed some variations in gene order, gene content, and GC content (Table 2).

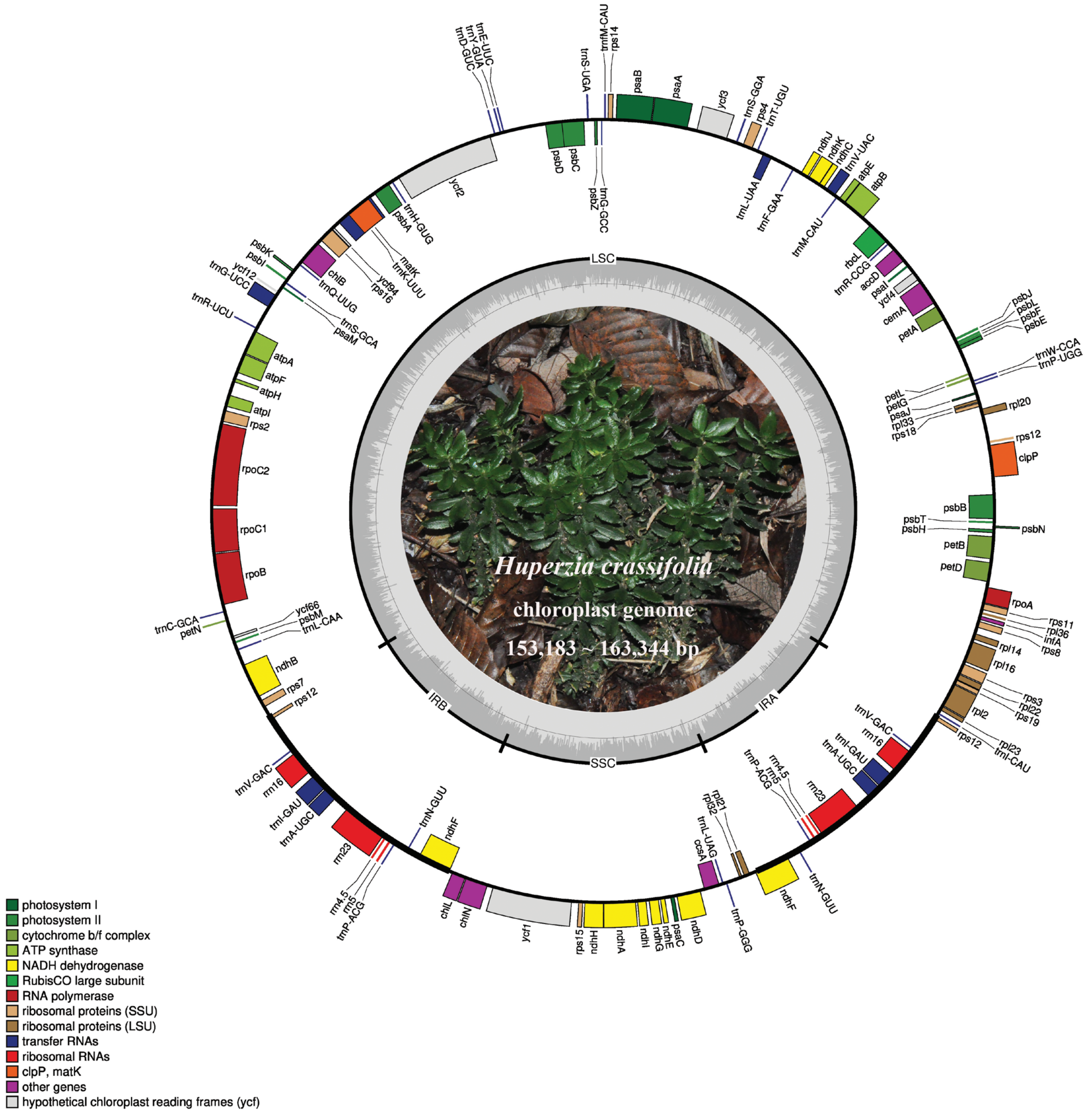

Figure 1. Plastome map of *Huperzia* represented by *H. crassifolia* sp. nov. Genes shown outside the circle were transcribed clockwise, and those inside were transcribed counterclockwise.

Phylogenetic relationships among *Huperzia* species

Alignment of the plastome sequences yielded a matrix of 72,403 positions, in which 4,188 variable sites (5.78%) were identified and 2,768 (3.82%) were parsimoniously informative. Both the complete chloroplast genome sequence and extracted 85 CDSs were used to reconstruct the phylogenetic relationships among the *Huperzia* species. ML and BI analyses of the complete genome sequences and CDSs dataset produced identical tree topologies (Fig. 2). Three accessions of *H. javanica*, the Japanese *H. serrata*, *H. nanlingensis* as well as *H. serrata* f. *longipetiolata* were grouped together as a monophyletic clade, whereas the three accessions of *H. crassifolia* were resolved as a well-supported monophyletic entity which formed a sister-taxon relationship to *H. sutchueniana* (Fig. 2).

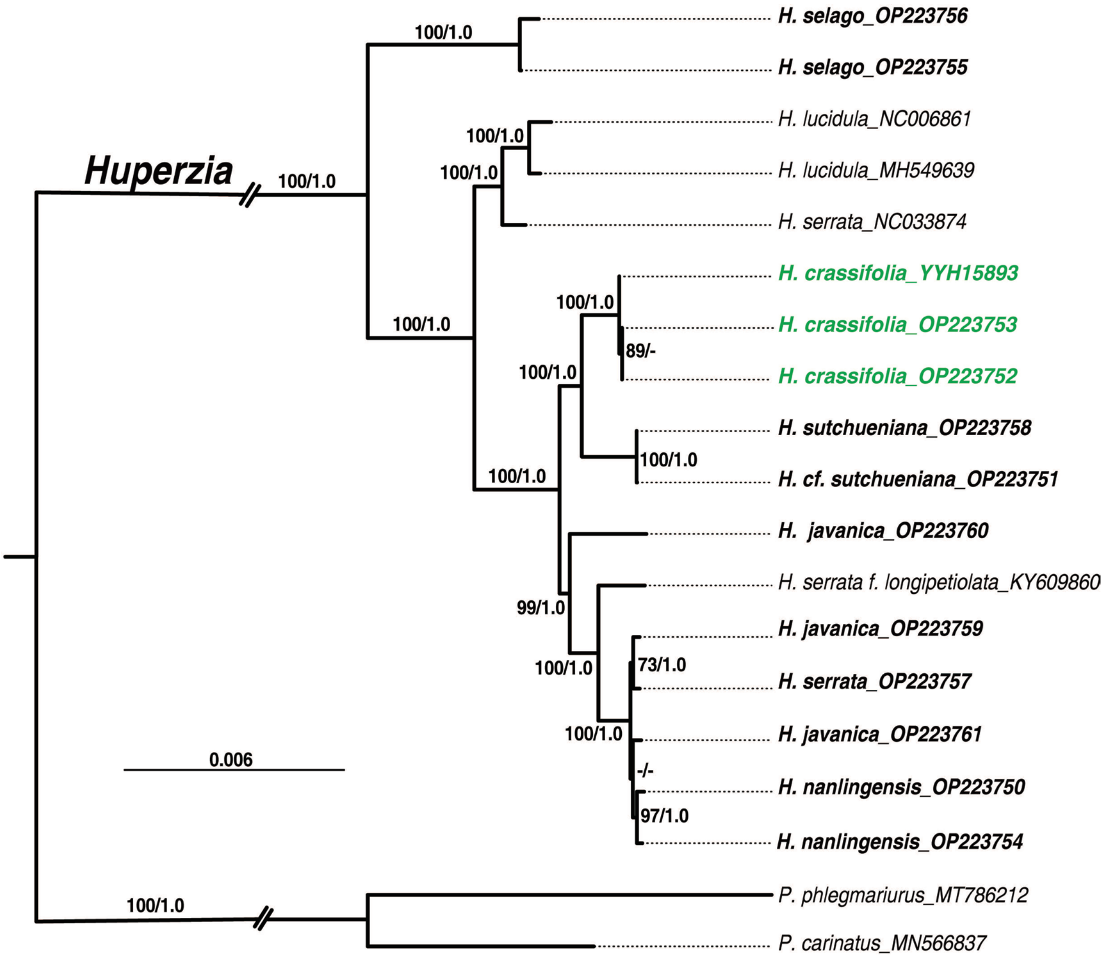

Figure 2. Phylogenetic relationships of *Huperzia* inferred by Bayesian inference (BI) and Maximum likelihood (ML) utilizing 85 CDSs. The consensus phylogram obtained from 1,000 trees sampled in the BI analyses. Branch lengths corresponded to the estimated number of substitution events. Maximum likelihood bootstrap values (MLBS) and posterior probability values (PP) were shown above and/or below the branches, dashes (-) indicate values below 50% (MLBS) and/or below 0.95 (PP). Two species of *Phlegmariurus* were assigned as outgroup taxa.

Macro- and micro-morphological comparison

The morphological comparison revealed that the new species was similar to the common species *Huperzia javanica* and *H. nanlingensis* in its macro-morphology including leaf shape and serrations on the leaf margin, but other morphological characters distinguished it unambiguously (Figs 3, 4; Table 3). The distinctive characters included round-lanceolate pinnae, thicker coriaceous texture, and slightly involute leaf margins when get dried (Table 3). Besides, plants of *H. crassifolia* have a character of well-differentiated seasonal constriction zones (Fig. 3). *Huperzia crassifolia* has trilete spores with the foveolate ornamentation but differed in the length of laesura besides slight differences in the density of the foveolae when compared with *H. javanica* (Fig. 5).

Accessions of *Huperzia crassifolia* were distinct in the holoploid genome size from accessions of *H. javanica* and *H. nanlingensis* by having a 2C value of 17.2 =/- SE 0.21 compared to 2C = 8.7 +/- 0.16 and 8.7, respectively (Table 1). Given the holoploid genome size values of the diploid *H. lucidula* and the tetraploid *H. selago*, *H. crassifolia* was interpreted to be a tetraploid.

Table 3. Morphological comparison of *Huperzia crassifolia* and its similar species.

Features	*H. crassifolia*	*H. javanica*	*H. nanlingensis*	*H. serrata*	*H. sutchueniana*
Leaf shape	Elliptic-lanceolate	Broadly elliptic-oblanceolate	Elliptic-lanceolate	Lanceolate	Lanceolate
Leaf texture	Thick coriaceous	Thin coriaceous	Coriaceous	Herbaceous	Coriaceous
Leaf margin	Serrate	Serrate	Serrate	Serrate	Sparsely toothed
Serration	Whole part	Whole part	Whole part	Whole part	Upper part
Abaxial vein	Strongly raised	Raised	Raised	Raised	Indistinct
Leaf margin when get dried	Reflexed	Flat	Flat	Flat	Slightly reflexed
Gemmae	Present	Present	Present	Present	Present
Annual constriction zones	Yes	Not prominent	Yes	No	No

Taxonomic treatment

***Huperzia crassifolia* W.M.Chu & B.Y.Zhang *ex* Z.Y.Guo, sp. nov.**
urn:lsid:ipni.org:names:77347495-1
Figs 3, 4

Type. China • Guizhou Province: Duyun City, Luosike Mountain, between Maozhuchong and Tuanshan, 26.2390, 107.2329, under the broad-leaf forests, alt. 1100–1500 m, 10 March 2016, *Zhi-You GUO 2016022* (Holotype, QNUN!).

Diagnosis. *Huperzia crassifolia* resembled species *H. javanica* in its gross morphology, but can be easily distinguished by the thicker texture and round-lanceolate pinnae. The well differentiated seasonal constriction zones, as well as the dark-green colour of the pinnae, provide further distinctions to species with similar morphology.

Description. Plants terrestrial. Stem erect or ascending, 2–4 times dichotomous branches, 5–25 cm tall, 0.2–0.4 cm in diam. Upper portion of the branches often with numerous gemmae. Leaves sparse, attached at right angles with stem, elliptic to slightly oblanceolate, conspicuously contracted towards base, 1.2–1.9 cm long, 0.4–0.6 cm wide, leathery, shiny, dark green above and light green below, glabrous, midrib conspicuous, base cuneate, decurrent, petiolate, margin straight, slightly reflexed when dry, irregularly serrated, apex acute to slightly cuspidate, teeth acute at apex, coarse; seasonal variation between sporophylls and trophophylls, sporophylls slightly dimorphic by reduced size compared to trophophylls; sporangia attached to the upper side of sporophylls, yellowish, reniform. Spores tetrahedral, with trilete aperture and foveolate ornamentation on distal pole.

Etymology. The specific epithet refers to its thick and coriaceous texture of the pinnae.

Vernacular name. 厚叶石杉 (Chinese pinyin: hou ye shi shan).

Distribution and habitat. *Huperzia crassifolia* is a terrestrial firmoss currently only known from Guizhou, Hubei, Hunan, and Chongqing, growing on humus rich soils in shady conditions formed in the undergrowth of broad leaf forests at elevations from 1100 to 1900 m a.s.l.

Additional specimens examined. China • Hubei Province, Shibing County, 5 September 2019, R. K. Li ES946 • Chongqing City, Nanchuan District, Jinfo Mountain, 1500 m, 16 April 1981, *Zhengyu Liu* 1327 (IMC0000082!) • Chongqing City, Nanchuan District, Jinfo Mountain, 1750 m, 15 June 1981,

Figure 3. *Huperzia crassifolia* sp. nov. **A, B** habit **C** adaxial view of trophophyll **D** abaxial view of trophophyll **E** fertile portion of the shoot **F** gemmae (Photographed by Zhi-You Guo).

Zhengyu Liu 1708 (IMC0000083!) • Chongqing City, Nanchuan District, Jinfo Mountain, 1900 m, 23 October 1978, *Zhengyu Liu* 784137 (IMC0000084!) • Chongqing City, Qianjiang District,1260 m, 23 May 1979, *Zhengyu Liu* 373 (IMC0000081!).

Figure 4. Illustration of *Huperzia crassifolia* sp. nov. **A** habit **B** adaxial view of trophophyll with prominently raised veins and serrate margin. Drawn by Mr. Ying-Bao Sun based on the type specimen Zhi-You Guo 2016022 (QNUN).

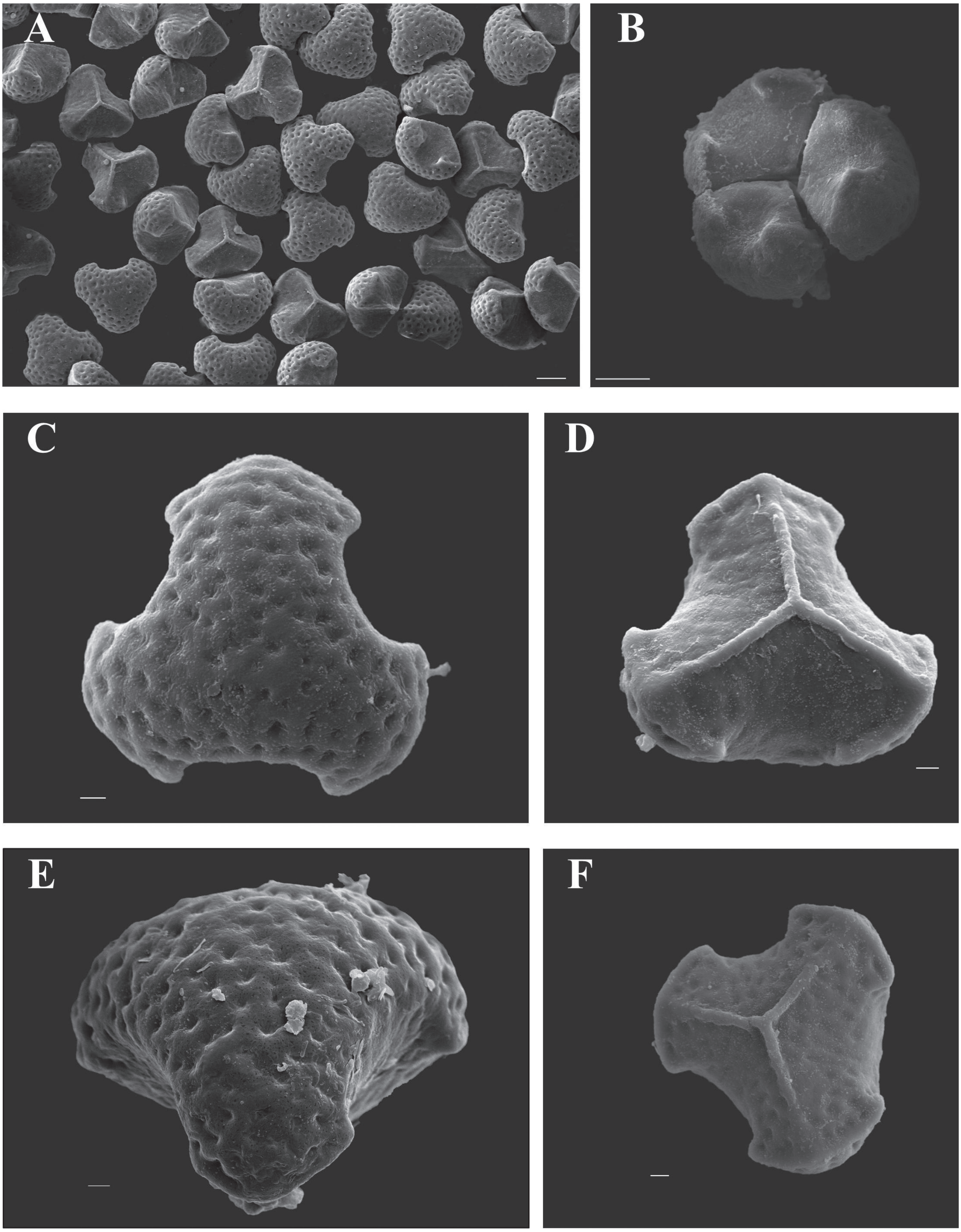

Figure 5. Spores of *Huperzia crassifolia* sp. nov. (**A–D**) and *H. javanica* (**E–F**) **A, B** well-developed trilete spore **C** distal view of the spore **D** proximal view of the spore **E** distal view of the spore **F** proximal view of the spore. Scales bars: 10 μm (**A, B**); 2 μm (**C–F**). Voucher specimen of **A–D**: Liu et al./LHM2571A, voucher specimen of **E, F** Liu ZY/Zhengyu Liu 1708.

Taxonomic notes. During our studies, the corresponding author had the opportunity to check the specimens collected by taxonomist Zheng-Yu Liu and found that he already noticed the distinctness of *Huperzia crassifolia*, but the taxon had not been properly published. The oldest specimen of *H. crassifolia* carries the species name plus W. M. Chu & B. Y. Zhang as the authorities. Thus, the name has been introduced by these two researchers. To honor their contribution, authorities of this new species are W. M. Chu & B. Y. Zhang *ex* Z. Y. Guo.

Conservation status. The new species *Huperzia crassifolia* is distributed in central and SW China; however the population size of each locality is very small. Especially when one considers the medicinal values of *Huperzia* species, it may reach the stage that it is over-collected. Thus, we tentatively propose *H. crassifolia* as Endangered (EN) according to the IUCN categories and criteria (IUCN 2022).

Discussion

Multiple evidence led us to the confirmation that *Huperzia crassifolia* differs from all previously recognized or proposed species. This species is morphologically distinct by its thick coriaceous texture and elliptic to slightly oblanceolate pinnae as well as the well-differentiated seasonal constriction zones. The new species shares with co-occurring members of the *H. javanica* complex the habitat preference to occur in the undergrowth of broad leaf forests.

The morphological variation of this new species has been considered as semi-cryptic with the consequence that this new species was reported as a form of *Huperzia javanica* in some studies (Wang and Pan 2018). The uncertainty caused by limited and somewhat hidden morphological differentiation has been a challenge to the taxonomy of *Huperzia*. One approach to overcome these challenges has been explored in the past by carrying out extensive morphological studies (Shrestha and Zhang 2015b), while this study explored another more powerful approach by integrating morphology and phylogenomics.

Whole chloroplast genomes are supported to be highly effective in providing reliable evidence for species identification in the genus *Huperzia*. Multiple standard chloroplast DNA sequences (our unpublished data as well as previous studies, e.g., Chen et al. 2021) showed that DNA mutation is very low in this old lycophyte lineage and therefore lacks resolution in the species identification. In the current study, we demonstrated that plastome is a powerful approach to investigate species boundaries in the genus *Huperzia*.

Cytological evidence enabling the detection of polyploid taxa has been arguably ignored in the taxonomy of *Huperzia* compared to other land plant groups. However, this is understandable given the reported difficulties in obtaining reliable chromosome counts (Manton 1950) that have been only recently resolved (Vejvodová et al. 2024). Employing genome size measurement may not completely replace the needs of chromosome counts but enables the detection of distinct ploidy levels in lineages of plants that show a highly conserved trend of a positive correlation between chromosome number and genome size such as ferns and lycophytes (Fujiwara et al. 2023; Vejvodová et al. 2024). Applying this approach to the species complex of *Huperzia* is highly promising given the results of the existing chromosome counts suggesting the existence of several ploidy levels (Wagner 1992). Thus, the high cytotype diversity reported for occurrence of the *H. selago* complex in the European Alps (Vejvodová et al. 2024) may be not the exception. This hypothesis is now testable using genome size measurements enabling the screening of many specimens without the need to overcome the technical difficulties of chromosome counting.

Finally, the phylogenetic placement of the new species as sister to *Huperzia sutchueniana* raises questions about its origin. The latter species is distinct by the sparsely toothed margin and lanceolate leaves (Table 3) from *H. crassifolia* and *H. javanica*. Together with the genome size indicating *H. crassifolia* as a tetraploid, the conflict between morphology and phylogenetic placement implies the hypothesis that *H. crassifolia* is an allotetraploid originating from hybridisation between *H. javanica* and *H. sutchueniana*. While reticulate evolution has been documented for the firmoss in North America (Wagner 1992), rather less attention has been given to reticulate evolution in the context of the taxonomy of firmoss occurring in China to date.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: HL. Data curation: HL, TF. Formal analysis: HL, KW. Funding acquisition: HL. Investigation: ZG, XZ, ZL. Methodology: HL. Project administration: HL. Supervision: HL. Visualization: HL. Writing - original draft: HL, HS. Writing - review and editing: HL, HS.

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Data availability

The newly generated plastomes have been submitted to the NCBI. All the other data that support findings of this study are available in the main text.

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Research Article

Evidence for moth pollination in a rhinomyiophilous *Erica* species from the Cape Floristic Region of South Africa

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Abstract

Contrasting pollination syndromes in closely related species suggest that floral trait divergence is associated with differences in pollination system, but empirical observations are required to confirm syndrome-based predictions. We present a comparative study of two closely related *Erica* species with contrasting pollination syndromes from the Cape Floristic Region of South Africa. *Erica cylindrica* has narrowly tubular pale and strongly scented flowers and is known to be hawkmoth-pollinated. The closely related *Erica infundibuliformis* has bright flower colours and appears to lack scent, traits that are suggestive of pollination by long-tongued nemestrinid flies (rhinomyiophily). Floral trait measurements revealed that both species exhibit predominantly upright flower orientation and elongated floral tubes, although tube length of *E. infundibuliformis* is consistently greater than that of *E. cylindrica*. For both species, petals are brighter than floral tube surfaces, but flowers of *E. cylindrica* lack the strong UV reflectance found in *E. infundibuliformis*. Nectar of *E. infundibuliformis* is more concentrated and produced in larger volumes. Scent composition, but not evening scent emission rates, differed between the species: scent of *E. cylindrica* is dominated by aromatic compounds, whereas scent of *E. infundibuliformis* is dominated by (E)-ocimene and other terpenoid compounds and is emitted at higher rates during the day than the evening. Pollinator observations contradicted trait-based predictions: although a single nemestrinid fly captured in the vicinity of *E. infundibuliformis* did carry *Erica* pollen, almost all other diurnal flower visitors were nectar-robbing Hymenoptera which did not carry *Erica* pollen. Contrary to predictions, at two sites and over two flowering seasons, flowers were consistently visited in the evenings by several species of settling moths and hawkmoths which carried pollen, almost exclusively of *Erica*, on their proboscides. Our findings thus suggest that, despite objective differences in key floral traits between the closely related hawkmoth-pollinated *E. cylindrica* and *E. infundibuliformis*, moths are also important pollinators of *E. infundibuliformis*. A bimodal pollination system involving predominant pollination by moths and occasional visits by long-proboscid flies could partially reconcile findings with predictions. Our study further suggests that hawkmoth pollination may be more widespread in both *Erica* and the broader Cape flora than has hitherto been assumed and emphasises the importance of nocturnal pollinator observations.

Key words: Colour, *Erica cylindrica*, *Erica infundibuliformis*, flower orientation, hawkmoth, long-proboscid fly, moth-pollination, scent

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Introduction

There is strong evidence that pollinators have been important drivers of the radiation of angiosperms, especially in lineages in which interspecific variation in suites of floral traits is associated with variation in functional pollinator groups (e.g. Grant and Grant (1965); Johnson et al. (1998); Goldblatt and Manning (2006); Whittall and Hodges (2007)). Such covariation often leads to recognition of particular suites of floral traits as 'pollination syndromes' (Faegri and van der Pijl 1979; Fenster et al. 2004). Pollination syndromes can be used in a predictive framework: based on a subset of species for which both floral traits and pollination systems have been documented, pollinators can be predicted for those species lacking pollinator observations. This approach has been utilised successfully for pollination systems characterised by high degrees of specialisation (Johnson and Steiner 2000; Rosas-Guerrero et al. 2014; Dellinger 2020), both for particular pollination guilds (Pauw 2006, 2022; Valverde-Espinoza et al. 2021;) and across an entire flora (Johnson and Wester 2017). Confirmation of syndrome-based predictions strengthens the evidence for associations between particular floral traits and specific pollinator groups. This information, in turn, provides better understanding of the ecology and sensory perception of functional pollinator groups (Schiestl and Johnson 2013). However, instances in which empirical evidence contradicts predictions also advance our understanding of evolutionary ecology. Firstly, falsification of syndrome-based predictions has revealed that pollination systems in some plant species may not be as specialised as suggested by pollination syndrome theory (Ollerton 1996; Waser et al. 1996). Secondly, observations that contradict syndrome-based predictions have generated useful insight into the ecological context in which specialised interactions implied by syndromes break down (e.g. de Merxem et al. (2009)). Finally, mismatches between observations and syndrome-based predictions shed light on differences between human and pollinator sensory perception (Cozien et al. 2019; Castañeda-Zárate et al. 2021), emphasising the importance of objective approaches for quantification and interpretation of floral traits, especially those such as floral scent and colour for which human perception is particularly biased (Leonardos et al. 1969; Kevan et al. 1996). Therefore, empirical tests of predictions derived from pollination syndromes can provide useful insights into plant-pollinator interactions and function of floral traits.

In plant groups for which phylogenetic relationships have been reconstructed, syndrome-based predictions of pollination systems are particularly useful for investigating potential pollinator-driven divergence between closely-related species with contrasting pollination syndromes. Differences in floral syndromes suggest that divergence is potentially driven by adaptation to different pollinators (Johnson 2006; Van der Niet et al. 2014a). Such pollinator shifts often occur along 'lines of least resistance' (Stebbins 1970; Johnson et al. 1998), potentially involving only minor divergence in few key traits. Investigation of phenotypic differences between closely-related taxa that differ in pollination system can thus be used to identify which key traits underpin pollinator shifts (Goldblatt et al. 2004; Shuttleworth and Johnson 2009; Castañeda-Zárate et al. 2021). However, floral divergence may not necessarily be accompanied by pollinator shifts (e.g. Ellis and Johnson (2009)) and empirical pollination studies are, therefore, required to evaluate predictions.

The flora of the Cape Floristic Region is characterised by a high incidence of specialised pollination systems (Johnson and Steiner 2003; Johnson 2010) and strong predictability of pollination systems based on floral syndromes (Vogel 2012; Johnson and Wester 2017). The monophyletic “Cape clade” of the genus *Erica* is characterised by tremendous floral diversity (Baker and Oliver 1967; Schumann and Kirsten 1992; Vogel 2012). Rebelo et al. (1985) used floral traits to categorise flowers of 426 *Erica* species as consistent with four broadly defined pollination syndromes, distinguishing anemophilous, ornithophilous and entomophilous syndromes and coining the term “rhinomyiophily” to identify the suite of traits indicative of pollination by long-proboscid flies (Rebelo et al. 1985). Although some empirical studies have shown that the syndrome-based categorisations by Rebelo et al. (1985) are not consistently reliable (summarised in Van der Niet (2021)), predictions of pollination by long-proboscid flies (LPF) have been confirmed for several *Erica* species with a characteristic suite of traits including unscented, brightly coloured tubular flowers with a narrow orifice (Lombardi et al. 2021; Newman and Johnson 2021; Pauw 2022; McCarren et al. 2023).

The LPF syndrome of *Erica* flowers is consistent with that of LPF-pollinated species from other plant families (Goldblatt and Manning 2000). Further, narrowly tubular rhinomyiophilous *Erica* flowers restrict access to floral nectar for most other potential pollinators. It is, therefore, likely that predictions based on the LPF syndrome are reliable in *Erica* and that LPF syndrome traits in species which are closely related to species with different floral traits indicate a pollinator shift. *Erica cylindrica*, with narrow floral tubes and upward-facing, pale-coloured and strongly scented flowers, was recently discovered to be pollinated by hawkmoths, a pollination system that is hitherto unique in *Erica* and rare in the CFR (Van der Niet and Cozien 2022). The hawkmoth-pollinated *E. cylindrica* is part of a small clade of species that are all characterised by tubular, upward-facing flowers (Baker and Oliver 1967; Schumann and Kirsten 1992; Pirie et al. 2016); within this clade, *Erica infundibuliformis* is closely related to *E. cylindrica* (Pirie et al. 2016). Floral traits of the two species show strong similarities, with two key exceptions in colour and scent: flowers of *E. infundibuliformis* are bright pink and not reported to be scented. The combination of apparently unscented, brightly coloured upward-facing flowers and a narrow flower opening conforms to the rhinomyiophilous pollination syndrome and is considered indicative of pollination by LPF in *Erica* (Rebelo et al. 1985). Within LPF-pollinated ericas, flower orientation may also be an important trait for distinguishing pollination by two main groups of LPF pollinators, tabanid and nemestrinid flies. Since tabanid flies are unlikely to feed on upward-facing flowers, plants with such flower orientation are likely pollinated by nemestrinid flies (McCarren et al. 2022; McCarren et al. 2023). Thus, based on differences in floral syndromes, *E. infundibuliformis* was predicted to be pollinated by long-proboscid nemestrinid flies in contrast to pollination by hawkmoths in *E. cylindrica*.

The aim of this study was threefold: firstly, to quantify floral traits to objectively characterise differences between *E. cylindrica* and *E. infundibuliformis*; secondly, to verify predictions of LPF pollination in *E. infundibuliformis* with empirical observations and, finally, to use these combined data to test whether a shift in colour and scent mediates a shift between hawkmoth and nemestrinid fly pollination between the two species.

Methods

Study species and field sites

Erica infundibuliformis Andr. is distributed along the mountains of the south-western part of the Cape Floristic Region of South Africa (Baker and Oliver 1967). The species grows in fynbos vegetation in damp sandy areas, often in highly localised patches where it may be the dominant plant in the community (Fig. 1A). Fieldwork for this study was carried out at two sites in the Stettynsberg (33.866146°S, 19.325076°E; Stettynsberg hereafter) and Agtertafelberg Mountains (33.800156°S, 19.171326°E; Agtertafelberg hereafter), respectively. Both these sites are in relatively inaccessible parts of the Cape Fold Mountains, which limited opportunities for extensive fieldwork. Plants at the Stettynsberg site had just passed peak flowering on 28–29 November 2023, during which fieldwork was carried out in a patch of several hundreds of plants in a ca. 100 m × 50 m area. Fieldwork at Agtertafelberg was carried out over two consecutive summer seasons: 30 December 2022-1 January 2023, 27–29 December 2023 and 20 January 2024, when the Agtertafelberg population, consisting of many thousands of plants that dominate the vegetation in an area of ca. 500 m × 250 m (Fig. 1A), was in peak flower. All measurements and observations described below mirrored those done for *E. cylindrica* (Van der Niet and Cozien 2022) and were, with the exception of the nectar measurements that were only done at Agtertafelberg, repeated at both study sites.

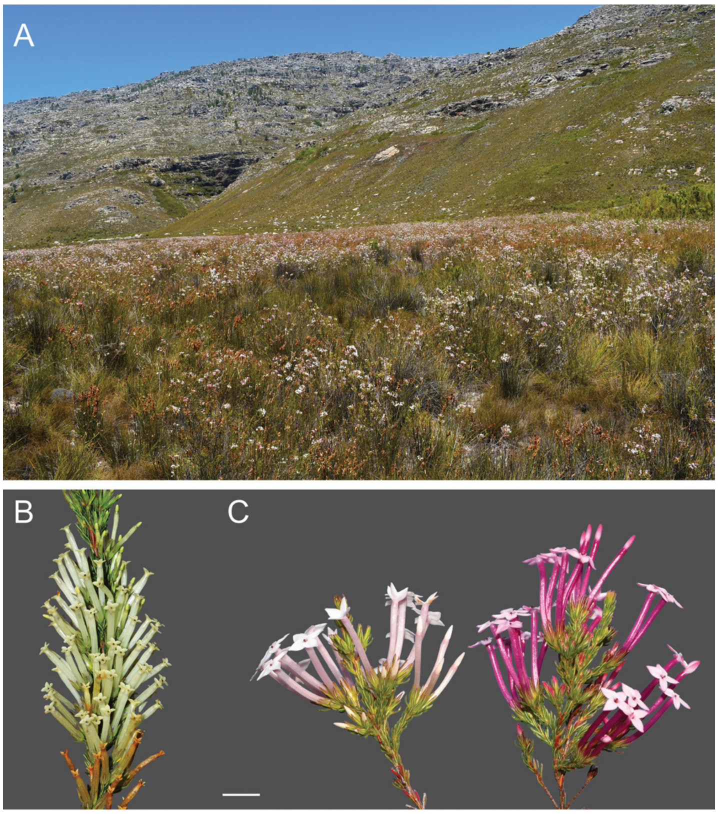

Figure 1. Habitat and flower morphology of the study species. Habitat of *Erica infundibuliformis* at Agtertafelberg; the white flowers of thousands of *E. infundibuliformis* plants dominate the fynbos of the sandy flats in the foreground (**A**). Inflorescence of *E. cylindrica* from the Voëlvleiberge (**B**). Inflorescences of *E. infundibuliformis* from Agtertafelberg, showing intraspecific flower colour variation (**C**). Scale bar: 10 mm (**B, C**).

Flower measurements

The length of the corolla tube and angle of flower orientation were measured at both sites. Corolla tube length, the distance from the base of the sepals to the corolla aperture, was measured to the nearest 0.1 mm using digital calipers for three randomly selected flowers per plant on 20 plants per site. Tube length was compared between the populations and with published data for *E. cylindrica* (Van der Niet and Cozien 2022).

The orientation of flowers can be distinguished as upward-facing (ranging from an angle of 30° to vertically upward-facing), horizontally-facing (ranging from an angle of -30° to 30°) and downward-facing (ranging from vertically downward-facing to -30°) (cf. Van der Niet and Cozien 2022). For 30 plants at Stettynsberg and 34 plants at Agtertafelberg, flowers of a randomly selected inflorescence were categorised according to these three classes, based on the methods described in Van der Niet and Cozien (2022) and measurements were compared with those of *E. cylindrica* (Van der Niet and Cozien 2022). Measurements found that almost no flowers face downwards in either of the study species; consequently, there were only two orientation categories and comparisons were, thus, based on the proportion of upward-facing flowers out of the total number of flowers.

Spectrophotometry

To quantify flower colour, spectral reflectance was recorded using an Ocean Optics S2000 spectrophotometer, coupled with a DT-mini deuterium-tungsten halogen light source and a fibre optic reflectance probe (QR-400 UVVIS, 400 lm) (Ocean Optics, Inc., Dunedin, Fla.). Reflectance was measured for one flower from each of twenty and twelve different plants at Agtertafelberg and Stettynsberg, respectively. Following the methods used for *E. cylindrica* (Van der Niet and Cozien 2022), two measurements were taken from each *E. infundibuliformis* flower: firstly, from the upper surface of the petal lobe, which is the surface that faces a visitor as it approaches a flower from above or feeds legitimately on nectar and secondly, reflectance of the external surface of the corolla tube was also measured as this may form part of the floral display when flowers are viewed by a visitor approaching from any other angle or by visitors feeding by robbing through punctures in the side of the floral tube. Spectra were imported into R (R Core Team 2021), averaged at 1 nm intervals between 300 and 700 nm and smoothed with a smoothing span of 0.3 nm using the package *pavo* (Maia et al. 2019) to reduce noise for visualisation and for plotting.

To compare spectra from the perspective of LPF, including those of *E. cylindrica* as presented in Van der Niet and Cozien (2022), spectra were also plotted in the categorical colour space developed by Troje (1993). In this colour space, spectra that fall within the same quadrant are considered indistinguishable to flies, whereas spectra located in different quadrants are considered discriminable (Troje 1993). This model is based on spectral sensitivities and experimentally determined discrimination capabilities of *Lucilia* blowflies (Troje 1993), but has also been utilised in studies of pollinator perception of flower colours involving nemestrinid flies (e.g. Whitehead et al. (2018)).

Scent sampling

To quantify floral scent emission and characterise the scent bouquet of *E. infundibuliformis*, the headspace of flowering branches was sampled and analysed using gas chromatography coupled with mass spectrometry (GC-MS). Headspace sampling in the field was done according to the protocol described in Van der Niet and Cozien (2022). To quantify differences in per-flower emission rates during day and evening, sampling was repeated twice using the same plants. At Stettynsberg, three plants were sampled from 15:15 h until 16:00 h (daytime) and again from 19:30 h until 20:30 h (evening) on 28 November 2023. These samples were also analysed for scent composition. At Agtertafelberg, four plants were sampled in the evening of 31 December 2022. These samples could not be used to calculate emission rates because the number of flowers was not recorded. For quantifying emission rates at Agtertafelberg, an additional four plants were sampled from 10:50 h until 11:35 h (daytime) and again from 19:55 h until 20:45 h (evening) on 28 December 2023. As these samples contained a large number of minor compounds (n = 62) that could not be identified (making up on average less than 1.5% of the entire blend), composition of these samples is not reported because it was deemed that presenting such a large number of unknown minor compounds would not add any information that can be used for downstream analyses. In all sampling sessions, air from an empty bag was also sampled to control for any compounds present in the ambient air. Samples were stored at -20 °C until further analysis.

Samples were run on the same Varian CP-3800 gas chromatograph with a 30 mm × 0.25 mm internal diameter (film thickness 0.25 μm) Alltech EC-WAX column, coupled to a Bruker 300-MS quadrupole mass spectrometer as was used to analyse the evening samples of *E. cylindrica* (Van der Niet and Cozien 2022), under an identical temperature programme. Compound identification followed the same procedure as described in Van der Niet and Cozien (2022), although a more recent version of the NIST Mass Spectral Search Program (version 2.4, 2020) was used. Mass spectra of compounds that could not be identified and that were found across all samples in a batch or across multiple samples in multiple batches, are presented in Suppl. material 1, arranged by ascending Kovats Retention Index.

Nectar

Standing crop nectar volume and sugar concentration were measured from flowers from Agtertafelberg in 2024. Twenty-four inflorescences, each one sampled from a different plant, were collected at 10:00 h in the morning, kept cool with stems in water and measured in the laboratory at 18:00 h on the same day. Nectar volume was measured from one randomly selected flower per inflorescence by cutting the base of the flower and gently squeezing the liquid into graduated 5 μl glass micro-capillary tubes. Sugar concentration from flowers that produced more than 0.1 μl of nectar was measured as % Brix by spotting the nectar on to a hand-held Bellingham & Stanley pocket sugar refractometer. Nectar volume and sugar concentration of *E. cylindrica* as reported in Van der Niet and Cozien (2022) are presented for comparison.

Pollinator observations

Pollinator observations were carried out over six days and three nights, for a total of 31 observer hours, of which one third were during the evening, over the 2021–2022 and 2022–2023 flowering seasons at Agtertafelberg. Observations at Stettynsberg were limited to a single day and evening (total five and a half hours, all with two observers) in the 2023 flowering season. At both sites, observations included morning, afternoon and evening hours from 07:30 h until 21:00 h, to increase the likelihood of observing both diurnal and nocturnal visitors.

Visitor behaviour was observed and photographed, to distinguish legitimate visits involving insertion of insects' proboscides into the floral tube, facilitating contact with reproductive parts, from illegitimate robbing visits in which visitors fed on nectar though a hole in the base of the floral tube, without potential for contacting anthers or stigma. Visitors were identified according to their functional pollinator group at the level of insect genera, families or superfamilies. No flower visits by vertebrates were observed. For identification, and to assess potential of different visitors as pollen vectors, 1–10 (median n = 3) representatives of each functional pollinator group were captured with a hand-held sweep net, immediately transferred to Eppendorf tubes and then kept in a freezer until processing. Insect bodies were sampled in the laboratory for pollen grains using a 1 mm^3 cube of fuschin gel (Beattie 1971), which was subsequently melted on to a microscope slide for pollen counts using a Zeiss Lab.A1 light microscope. *Erica infundibuliformis* produces pollen in tetrads (unpublished data). Pollen counts distinguished between *Erica* tetrad pollen and other pollen grains. Although several other *Erica* species flowered simultaneously, *E. infundibuliformis* was by far the most common *Erica* species in the community where visitors were caught and, with the exception of a single fly (see Results), all insects were caught while visiting *E. infundibuliformis*. We, therefore, assume that the majority of *Erica* tetrads on caught insects were from *E. infundibuliformis*. Proboscis length of the caught visitors was measured to the nearest 0.1 mm using a pair of digital calipers. Voucher specimens of representative insects were submitted to the KwaZulu-Natal Museum or University of KwaZulu-Natal collections.

Nectar robbing and anther ring disruption

Rates of both legitimate visitation and illegitimate (nectar robbing) visitation in an *Erica* population can be quantified indirectly, without the need for direct observations, from physical evidence. Damage to the tissue of floral tubes is indicative of nectar robbing, whereas legitimate visits by pollinators results in disruption of the anthers that are fused in a ring surrounding the style (Baker and Oliver 1967; Geerts and Pauw 2011). For the same flowers as for which corolla tube length was measured, signs of nectar robbing in the form of a pierced corolla tube and pollination in the form of anther ring disruption were evaluated and compared between the two populations.

Statistical analyses

Floral phenotypic traits were compared using Generalised Linear Models (GLM). The continuous morphometric traits ‘floral tube length’ and ‘floral scent emission rate’ were both modelled with a gamma distribution and log link function. Comparisons of evening scent emission rates amongst the single *E. cylindrica* population and the two *E. infundibuliformis* populations were analysed with GLM, whereas variation in diurnal and evening scent emission rates between *E. infundibuliformis* plants from Stettynsberg and Agtertafelberg was analysed using Generalised Estimating Equations (GEE) with “plant” as subject variable and “time period” as within-subject variable and an exchangeable correlation matrix, to account for repeated measures of the same plant. We tested for an effect of time period, population and the interaction between these factors. Variation in corolla tube length amongst *E. cylindrica* and the two *E. infundibuliformis* populations was analysed using GEE to account for correlations amongst flowers measured on the same plant individual, with “plant” as the subject variable and “flowers” as within-subject variables and an exchangeable correlation matrix. Flower orientation, as the number of upward-facing flowers out of the number assessed on each inflorescence, was modelled using a binary logistic distribution and logit link function. Variation in scent composition was visualised using non-metric multi-dimensional scaling, based on Bray-Curtis similarity of square-root transformed proportions of compounds amongst samples, including the samples of *E. cylindrica* that were reported in Van der Niet and Cozien (2022). Similarity in scent composition between *E. cylindrica* and *E. infundibuliformis* was statistically compared between species using an ANalysis Of SIMilarity (ANOSIM), whereas the compounds that contribute most to dissimilarity between the species were identified using a Similarity Percentage (SIMPER) analysis. These analyses were conducted as described in Van der Niet and Cozien (2022), using PAST 4.03 (Hammer et al. 2001). Nectar volume and sugar concentration of *E. infundibuliformis* flowers were compared to those of *E. cylindrica* (Van der Niet and Cozien 2022) using a Mann-Whitney U-test singular in PAST 4.03 (Hammer et al. 2001), due to the small and highly unequal sample sizes and nature of the data. Nectar robbing and anther ring disturbance were compared between populations using a GLM with number of affected flowers out the number assessed (almost always three) modelled with a binary logistic distribution and logit link function. In case a log or logit link function was used, means and standard errors were back-transformed to the original scale for graphing purposes, resulting in asymmetrical error bars. All statistical analyses were carried out in in SPSS v. 29 (IBM, Corp.), unless mentioned otherwise.

Results

Corolla length differed significantly amongst all three populations (Figs 1, 2) and was shortest in *E. cylindrica* and longest in *E. infundibuliformis* from Agtertafelberg. In both species, more than 75% of flowers of an inflorescence faced upright and this proportion did not differ amongst the populations (Fig. 2).

Floral spectral reflectance patterns were largely similar for flowers of both populations of *E. infundibuliformis*, despite some variation in brightness (Fig. 3). Petals of flowers from both populations of *E. infundibuliformis* had great-

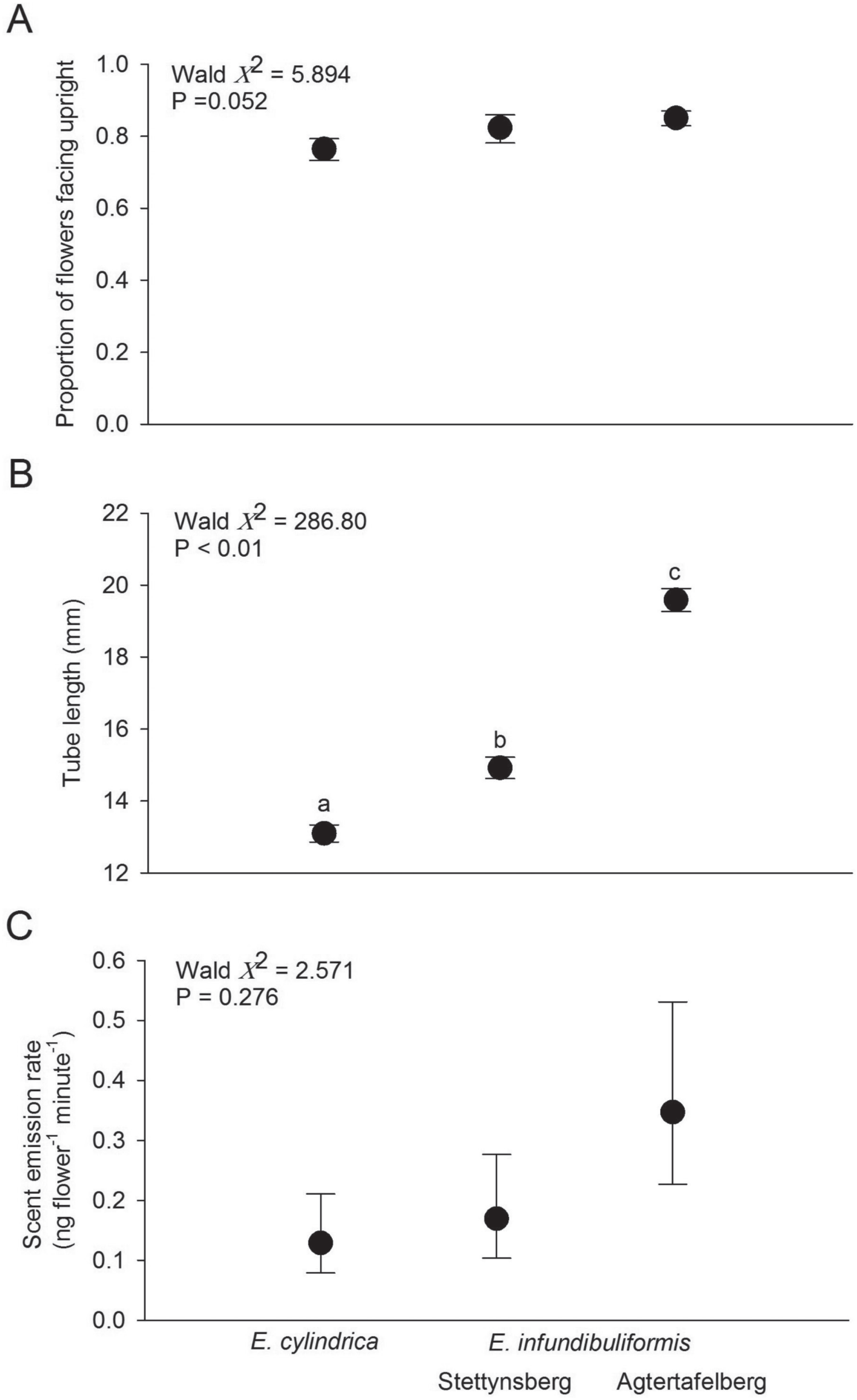

Figure 2. Comparisons of floral and inflorescence characteristics between *Erica cylindrica* and populations of *E. infundibuliformis*: flower orientation (**A**), corolla tube length (**B**) and evening scent emission rates (**C**). Letters indicate significant pairwise comparisons at $P < 0.05$ (**B**).

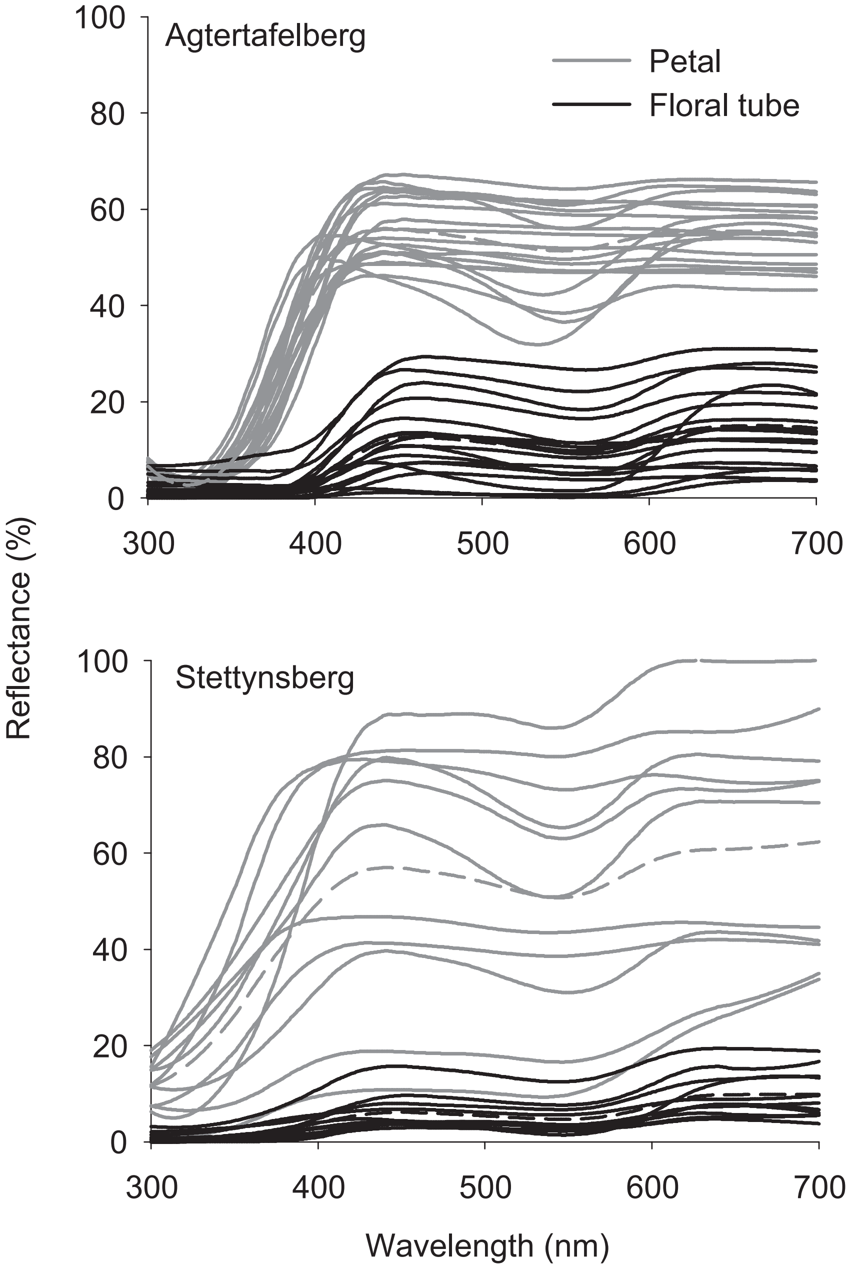

Figure 3. Reflectance of floral petal surfaces (grey) and outer surfaces of corolla tubes (black) of *Erica infundibuliformis* from Agtertafelberg and Stettynsberg. Solid lines represent reflectance measurements recorded from individual flowers, dashed lines show means for all spectra recorded for the respective floral parts in each population.

er overall brightness than flowers of *E. cylindrica* and also were consistently characterised by a steep increase to maximum reflectance in the UV region, around 350 nm (Fig. 3), which was almost absent in flowers of *E. cylindrica*. Overall brightness varied somewhat amongst flowers within both *E. infundibuliformis* populations, but was usually consistently close to maximum between 350 and 700 nm, with an average of approximately 50% for petals and 10% for floral tube surfaces (Fig. 3), which is approximately double that observed for flowers of *E. cylindrica*. The variation in flower colour within *E. infundibuliformis* populations was mostly in the degree of reflectance between 500 and 600 nm (Figs 1, 3).

A total of 82 compounds were detected in the scent samples of *E. infundibuliformis* (Table 1). Just over half of these (n = 42) could not be identified, but these unknown compounds on average only made up between 0.49% and 2.87% of the entire blend. The largest number of identified compounds were monoterpenes and these were also the most dominant in terms of scent emission, with (E)-ocimene being the most important compound at both sites and during both day and evening (Table 1). Of the 48 compounds produced by *E. cylindrica*, only ten were in common with *E. infundibuliformis* and the bouquets of these two species were consequently significantly different in composition (Fig. 4). The main difference between the species involved the unique presence of a large number of dominant aromatic compounds in *E. cylindrica*, contrasting with the large number of dominant monoterpenes in *E. infundibuliformis* (Table 2). Evening emission rates did not differ significantly amongst the populations (Fig. 2), whereas there was an effect of both population and period (but no significant interaction) in the comparison of daytime and evening scent emission rates of the two *E. infundibuliformis* populations: emission rates were higher at Agtertafelberg and during daytime (Fig. 5).

Flowers of *E. infundibuliformis* produced a mean ± SD of 0.49 ± 0.42 μl of nectar (n = 24 flowers), with a sugar concentration of 35.8 ± 10.9% (n = 19 flowers), whereas flowers of *E. cylindrica* produced a mean ± SD of 0.19 ± 0.17 μl of nectar (n = 10 flowers), with a sugar concentration of 24.1 ± 5.3% (n = 6 flowers). Both nectar volume and sugar concentration were higher for *E. infundibuliformis* compared to *E. cylindrica* (nectar volume: $z = 2.052$, $P < 0.05$; sugar concentration: $z = 2.39$, $P < 0.05$).

At both study sites, moths were the most frequently observed visitors that fed legitimately from *E. infundibuliformis* flowers (Table 3, Fig. 6). At Agtertafelberg, a total of 12 hawkmoths were observed feeding on flowers of *E. infundibuliformis* over all three evenings of observations. At Stettynsberg, five hawkmoths were observed on a single evening, in addition to 15 settling moths which were observed feeding during daytime and evening hours (Table 3). Both hawkmoths and settling moths carried up to 1000 pollen grains per individual (overall mean ± SD 540.7 ± 362.9 grains, n = 11), of which on average 97% constituted *Erica* tetrads (SD = 7.4%, n = 11); 90% of *Erica* pollen carried by moths was located on moths' proboscides (mean ± SD 90.1 ± 18.6%, n = 11) (Table 3).

No dipteran visitors to flowers of *E. infundibuliformis* were observed at Stettynsberg, despite the presence of several individuals of *Philoliche* (Tabanidae) which visited Iridaceae (*Tritoniopsis cooperi*, *Geissorhiza confusa*) and Proteaceae (*Serruria*) species in close proximity to *Erica* at this study site. Pollen on captured individuals of *Philoliche* also did not include *Erica* pollen (Table 3). At Agtertafelberg, one Bombyliid (*Exoprosopa* sp.) was observed foraging on flowers of *E. infundibuliformis* and one nemestrinid, *Moegistorhynchus* sp. nov., was captured in the population and carried approximately 250 grains of exclusively *Erica* pollen.

Floral larceny was observed almost constantly during diurnal observations at Agtertafelberg, but was not observed at Stettynsberg. At Agtertafelberg, 136 incidences of insects feeding through slits in the side of floral tubes, without potential for contact with reproductive parts, were observed, of which 90% were by carpenter bees and the balance by other hymenopterans including wasps and honeybees (Table 3). Monkey beetles were present on flowers, but did not

Table 1. Percentage (mean ± SD) of each compound as part of the headspace of *Erica infundibuliformis*. Compounds are grouped by major compound class (cf. Knudsen and Tollsten 1993) and sorted within class according to the Kovats Retention Index (KRI). CAS number is provided for compounds that could be identified. In case a compound could be identified without information of which the particular stereoisomer was present, no CAS number is provided. Compound names in cells with light grey shading were also found in *E. cylindrica*. Sample sizes of percentages are only given in case a compound was not found in all samples within a particular batch. Mass spectra of compounds for which the KRI is marked with an asterisk are provided in Suppl. material 1.

Compound name	KRI	CAS number	Stetteynsberg day (n = 3)	Stetteynsberg evening (n = 3)	Agtertafelberg evening (n = 4)
Aliphatics					
Aliphatic alcohols					
(E)-Hex-3-en-1-ol	1364	928-97-2	1.57 ± 2.50	0.02 ± 0.02 (2)	1.46 ± 0.63
Oct-1-en-3-ol	1426	3391-86-4	0.02 ± 0.02	0.02 ± 0.02 (2)	0.67 ± 0.30
4-Hexen-3-ol	1754	4798-58-7	0.03 ± 0.02 (2)	0.04 ± 0.03 (2)	0.18 ± 0.13
Aliphatic aldehydes					
(E)-Hex-2-enal	1213	6728-26-3			0.09 ± 0.10
(E)-4-Oxohex-2-enal	1568	20697-55-6	0.51 ± 0.83		0.65 ± 0.50
Aliphatic alkanes					
Tetradecane	1400	629-59-4			0.06 ± 0.13 (1)
Pentadecane	1500	629-62-9			0.12 ± 0.24 (1)
Hexadecane	1600	544-76-3			0.14 ± 0.29 (1)
Heptadecane	1700	629-78-7			0.05 ± 0.11 (1)
Octadecane	1800	593-45-3			0.03 ± 0.05 (2)
Aliphatic esters					
(E)-Hex-4-en-1-yl acetate	1302	72237-36-6	1.05 ± 0.77		0.95 ± 0.69
(E)-3-Hexen-1-yl butyrate	1445	53398-84-8	0.40 ± 0.58		0.39 ± 0.23
(Z)-3-hexenyl 2-methylbutyrate	1460	53398-85-9	0.03 ± 0.04		0.03 ± 0.01
(Z)-3-Hexenyl hexanoate	1638	31501-11-8	0.03 ± 0.02		
Benzenoids					
Benzaldehyde	1503	100-52-7	0.11 ± 0.04	3.20 ± 5.47	0.18 ± 0.09
Phenylethyl alcohol	1881	60-12-8	0.02 ± 0.00	0.19 ± 0.31	0.03 ± 0.01
Isoprenoids					
Irregular terpene					
6-Methyl-5-hepten-2-one	1322	110-93-0	0.10 ± 0.05	0.04 ± 0.07 (1)	0.96 ± 0.67
Monoterpenes					
β-Myrcene	1163	123-35-3	1.13 ± 0.44	0.65 ± 0.57 (2)	0.95 ± 0.36
(Z)-Ocimene	1231	3338-55-4	5.36 ± 1.59	1.20 ± 1.05 (2)	3.79 ± 0.40
(E)-Ocimene	1251	3779-61-1	80.0 ± 5.02	89.1 ± 3.15	82.9 ± 2.06
2,6-Dimethylocta-2,4,6-triene stereoisomer 1	1367		0.39 ± 0.40		0.15 ± 0.07
2,6-Dimethylocta-2,4,6-triene stereoisomer 2	1384		0.47 ± 0.81 (1)		
2,6-Dimethyl-1,3,5,7-octatetraene stereoisomer 1	1423		0.05 ± 0.06	0.09 ± 0.10 (2)	0.28 ± 0.18
2,6-Dimethyl-1,3,5,7-octatetraene stereoisomer 2	1435		0.35 ± 0.28	0.34 ± 0.38 (2)	1.58 ± 0.48
(Z)-Furan linalool oxide stereoisomer	1453		0.03 ± 0.01	0.01 ± 0.02 (1)	
Myroxide stereoisomer	1469		0.06 ± 0.05 (2)	0.04 ± 0.03 (2)	0.10 ± 0.04
Linalool	1520	78-70-6	6.49 ± 5.66	4.01 ± 2.81	
Cinerone stereoisomer	1542*		0.04 ± 0.03 (2)	tr (1)	0.12 ± 0.09
Pinocarvone	1561	30460-92-5	0.03 ± 0.03 (2)	0.07 ± 0.10 (2)	
α-Terpineol	1672	98-55-5	0.02 ± 0.01		
Pinocarveol	1685	5947-36-4	0.06 ± 0.01	0.01 ± 0.01 (1)	0.07 ± 0.04
p-Mentha-1,5-dien-8-ol	1695	1686-20-0	tr (2)	0.01 ± 0.01 (2)	0.02 ± 0.02 (3)
2,6-dimethylocta-3,5,7-trien-2-ol stereoisomer 1	1770		tr (2)	0.03 ± 0.02 (2)	0.08 ± 0.07 (3)
2,6-dimethylocta-3,5,7-trien-2-ol stereoisomer 2	1787		0.11 ± 0.10 (2)	0.22 ± 0.19 (2)	0.59 ± 0.28
2,6-Dimethyl-3,7-octadiene-2,6-diol	1900*	13741-21-4	0.02 ± 0.01 (2)		
Miscellaneous compounds					
3-Methyl-2-(2-methyl-2-butenyl)-furan	1389	15186-51-3	0.10 ± 0.06	0.03 ± 0.03 (2)	0.11 ± 0.04
5,5-dimethyl-2(rH)-furanone	1583	20019-64-1	0.03 ± 0.02 (2)	0.02 ± 0.02 (2)	0.01 ± 0.03 (1)
5-Methyl-5-vinyldihydrofuran-2(3H)-one	1648	1073-11-6	0.01 ± 0.01 (2)	0.01 ± 0.01 (1)	

Compound name	KRI	CAS number	Stetteynsberg day (n = 3)	Stetteynsberg evening (n = 3)	Agtertafelberg evening (n = 4)
Nitrogen-containing compounds					
3-Methylpyrazole	1654	1453-58-3	tr (2)	0.02 ± 0.01 (2)	0.16 ± 0.08
Benzyl isocyanide	1657	10340-91-7	0.08 ± 0.03	0.02 ± 0.02 (2)	0.01 ± 0.00
Unknown compounds					
m/z: 53,81,82,54,50,55	1121*		0.46 ± 0.17	0.18 ± 0.31 (1)	0.32 ± 0.16
m/z: 91,96,119,67,95,41	1358*		0.07 ± 0.02	0.06 ± 0.05 (2)	0.36 ± 0.20
m/z: 73,56,59,86,72,55	1464*		0.05 ± 0.04	0.03 ± 0.04 (2)	
m/z: 91,107,43,92,65,79	1490*		0.03 ± 0.03 (2)	0.01 ± 0.01 (2)	0.13 ± 0.11
m/z: 55,43,32,83,41,42	1501				0.02 ± 0.02 (3)
m/z: 95,93,123,67,91,81	1511*		0.03 ± 0.02 (2)	0.01 ± 0.01 (1)	0.06 ± 0.01
m/z: 57,85,86,43,55,72	1524*				0.28 ± 0.22
m/z: 95,93,79,41,55,69	1525				0.06 ± 0.00
m/z: 82,83,55,41,53,39	1546				0.01 ± 0.01 (2)
m/z: 43,71,57,70,41,55	1551				0.01 ± 0.02 (1)
m/z: 108,82,79,42,80,81	1650*				0.03 ± 0.01
m/z: 57,71,43,41,55,85	1666				0.01 ± 0.03 (1)
m/z: 60,91,73,107,79,150	1700*		0.03 ± 0.00	0.01 ± 0.01 (2)	0.09 ± 0.05
m/z: 83,55,84,57,82,112	1730		0.05 ± 0.10 (1)		
m/z: 57,43,71,55,84,41	1742				0.01 ± 0.03 (1)
m/z: 82,67,71,43,81,79	1771*		0.04 ± 0.01	tr (1)	0.02 ± 0.05 (1)
m/z: 95,54,43,59,81,67	1844*		0.01 ± 0.02 (1)	tr (2)	0.04 ± 0.02
m/z: 95,43,55,59,81,67	1848*		tr (1)	tr (2)	0.02 ± 0.00
m/z: 43,95,110,59,81,71	1890*				0.04 ± 0.01
m/z: 57, 85, 43, 41, 55, 39	1925*		0.18 ± 0.20	0.01 ± 0.02 (2)	0.51 ± 0.46 (3)
m/z: 153,109,83,69,43,32	1940*				tr (2)
m/z: 71,43,41,39,53,69	1941*		tr (2)	tr (2)	0.01 ± 0.01 (3)
m/z: 59,71,43,53,55,113	1946*			0.01 ± 0.00 (2)	0.03 ± 0.02
m/z: 59,42,71,55,41,113	1951*		tr (1)		0.06 ± 0.05 (3)
m/z: 97,72,43,68,95,79	1964*		0.07 ± 0.07 (2)	0.02 ± 0.02 (2)	0.11 ± 0.04
m/z: 43,125,83,107,81,55	1971*				0.01 ± 0.02 (3)
m/z: 43,57,69,41,55,91	1972				tr (1)
m/z: 97,67,41,72,68,43	1987*		0.01 ± 0.01 (2)	0.01 ± 0.01 (2)	0.06 ± 0.03
m/z: 59,43,71,113,73,83	1993*				0.04 ± 0.02
m/z: 71,59,43,85,113,73	2004*				0.02 ± 0.01
m/z: 79,91,150,39,107,32	2030*		0.02 ± 0.00	0.01 ± 0.01 (2)	0.04 ± 0.01
m/z: 58,43,71,59,55,445	2104				tr (1)
m/z: 43,111,32,41,91,93	2124*		tr (1)	0.01 ± 0.00 (2)	0.16 ± 0.13
m/z: 79,108,77,39,80,82	2127*		tr (1)	tr (2)	0.02 ± 0.00
m/z: 43,95,59,41,55,79	2134*		tr (1)	tr (2)	tr (1)
m/z: 121,149,138,194,93,65	2137				tr (1)
m/z: 43,95,32,55,97,59	2141*		tr (1)	0.01 ± 0.01 (2)	
m/z: 95,43,97,41,83,59	2150*		tr (1)	0.02 ± 0.02 (2)	0.02 ± 0.01
m/z: 109,79,81,152,67,121	2154*		tr (1)	0.01 ± 0.01 (2)	0.03 ± 0.02
m/z: 74,87,43,41,55,75	2196				tr (1)
m/z: 88,43,100,41,54,30	2236				tr (1)
m/z: 69,93,41,81,79,91	2257				0.01 ± 0.01 (2)
Aliphatic alcohols			**1.63 ± 2.50**	**0.09 ± 0.08**	**2.32 ± 0.96**
Aliphatic aldehydes			**0.51 ± 0.83**	**0**	**0.75 ± 0.59**
Aliphatic alkanes			**0**	**0**	**0.42 ± 0.83**
Aliphatic esters			**1.53 ± 1.41**	**0**	**1.39 ± 0.91**
Benzenoid compounds			**0.14 ± 0.04**	**3.40 ± 5.79**	**0.22 ± 0.10**
Irregular terpene			**0.10 ± 0.05**	**0.04 ± 0.07**	**0.96 ± 0.67**
Monoterpenes			**93.55 ± 5.46**	**95.19 ± 4.57**	**89.77 ± 1.97**
Miscellaneous compounds			**0.15 ± 0.03**	**0.06 ± 0.06**	**0.13 ± 0.05**
nitrogen-containing compounds			**0.08 ± 0.04**	**0.04 ± 0.03**	**0.17 ± 0.07**
Unknown compounds			**1.13 ± 0.33**	**0.49 ± 0.50**	**2.87 ± 0.75**

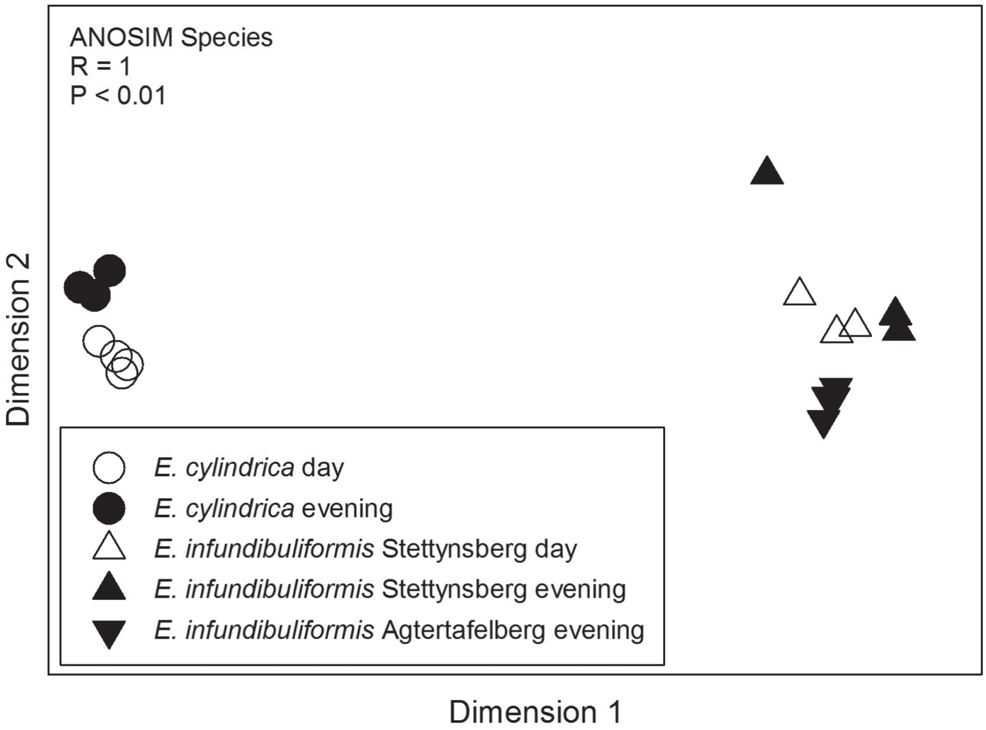

Figure 4. Non-metric multidimensional scaling of daytime and evening scent bouquets of *Erica cylindrica* and *E. infundibuliformis* populations.

Table 2. Results from the Similarity Percentage (SIMPER) analysis comparing the scent bouquets of *Erica cylindrica* and *E. infundibuliformis*. Listed are the 20 compounds that contribute the most to dissimilarity, which together contribute almost 70% of the entire dissimilarity, arranged in descending order of contribution.

Compound name	Compound class	Cumulative contribution to dissimilarity (%)	Mean proportion *E. cylindrica*	Mean proportion *E. infundibuliformis*
(E)-Ocimene	Monoterpene	15.40	0.041	0.916
Benzyl alcohol	Benzenoid compound	24.99	0.534	0
Benzyl acetate	Benzenoid compound	34.16	0.517	0
Benzaldehyde	Benzenoid compound	39.09	0.347	0.062
Eugenol	Benzenoid compound	42.26	0.181	0
(Z)-Hex-3-en-1-ol	Aliphatic alcohol	45.42	0.192	0
(Z)-Ocimene	Monoterpene	48.37	0	0.174
(E)-Hex-4-en-1-yl acetate	Aliphatic ester	50.85	0.181	0.067
Hexyl acetate	Aliphatic ester	53.23	0.141	0
Linalool	Monoterpene	55.59	0	0.128
Methyleugenol	Benzenoid compound	57.28	0.097	0
β-Myrcene	Monoterpene	58.82	0	0.09
Hexan-1-ol	Aliphatic alcohol	60.27	0.087	0
Octyl acetate	Aliphatic ester	61.67	0.081	0
(E)-5-Decen-1-ol, acetate,	Aliphatic ester	63.06	0.086	0
2,6-Dimethyl-1,3,5,7-octatetraene	Monoterpene	64.42	0	0.081
(Z)-Methyl isoeugenol	Benzenoid compound	65.65	0.071	0
Pentyl acetate	Aliphatic ester	66.85	0.074	0
(E)-Hex-3-en-1-ol	Aliphatic alcohol	68.02	0.021	0.080
(E)-4-Oxohex-2-enal	Aliphatic aldehyde	68.95	0.035	0.046

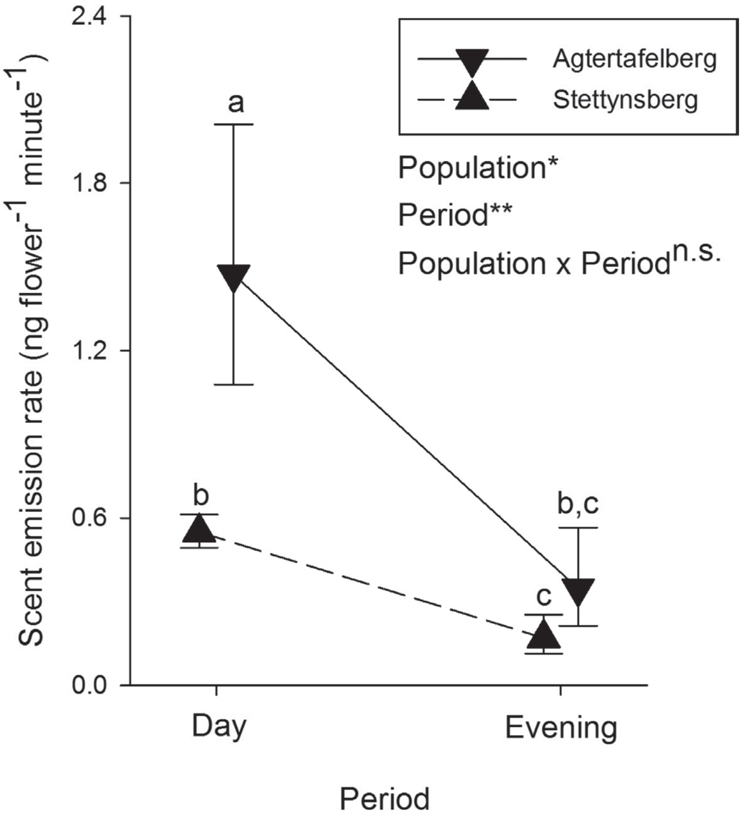

Figure 5. Comparison of daytime and evening scent emission rates in the two *Erica infundibuliformis* study populations. Different letters indicate significant pairwise differences in emission rates at P < 0.05. Asterisks refer to levels of significance: ** P < 0.01, * P < 0.05.

Table 3. Flower visitors of *Erica infundibuliformis* at both study sites, including tongue lengths and pollen loads. Numbers represent mean ± SD (sample size), apart from visitors observed, which are counts.

	Number observed	Tongue length (mm)	Pollen load	Percent *Erica* tetrads in pollen
Agtertafelberg				
Legitimate feeding				
Hawkmoth spp.	12	20.7 ± 0.92 (3)	259.3 ± 33.9 (3)	88.2 ± 10.2 (3)
In population				
Moegistorhynchus sp.	1	19.0 (1)	245 (1)	100
Robbing				
Xylocopa sp.	121	5.94 ± 1.33 (8)	187.9 ± 392.3 (11)	0.44 ± 1.3 (9)
Other bee sp.	3	3.24 (2)	2768.0 ± 3805.7 (3)	1.6 ± 1.2 (3)
Wasp sp.	12	2.01 ± 0.37 (4)	66.5 ± 111.7 (4)	25.0 ± 43.3 (4)
On plant				
Monkey beetles	10	0.9 (1)	0	0
Stettynsberg				
Legitimate feeding				
Hawkmoth spp.	5	19.6 (2)	851.0 ± 67.2 (3)	99.5 ± 0.44 (3)
Settling moth spp.	15	12.3 ± 3.27 (4)	523.4 ± 425.2 (5)	100 ± 0.0 (5)
In vicinity				
Philoliche sp.	5	25.5 ± 0.41 (3)	1020.3 ± 484.3 (3)	0 (3)

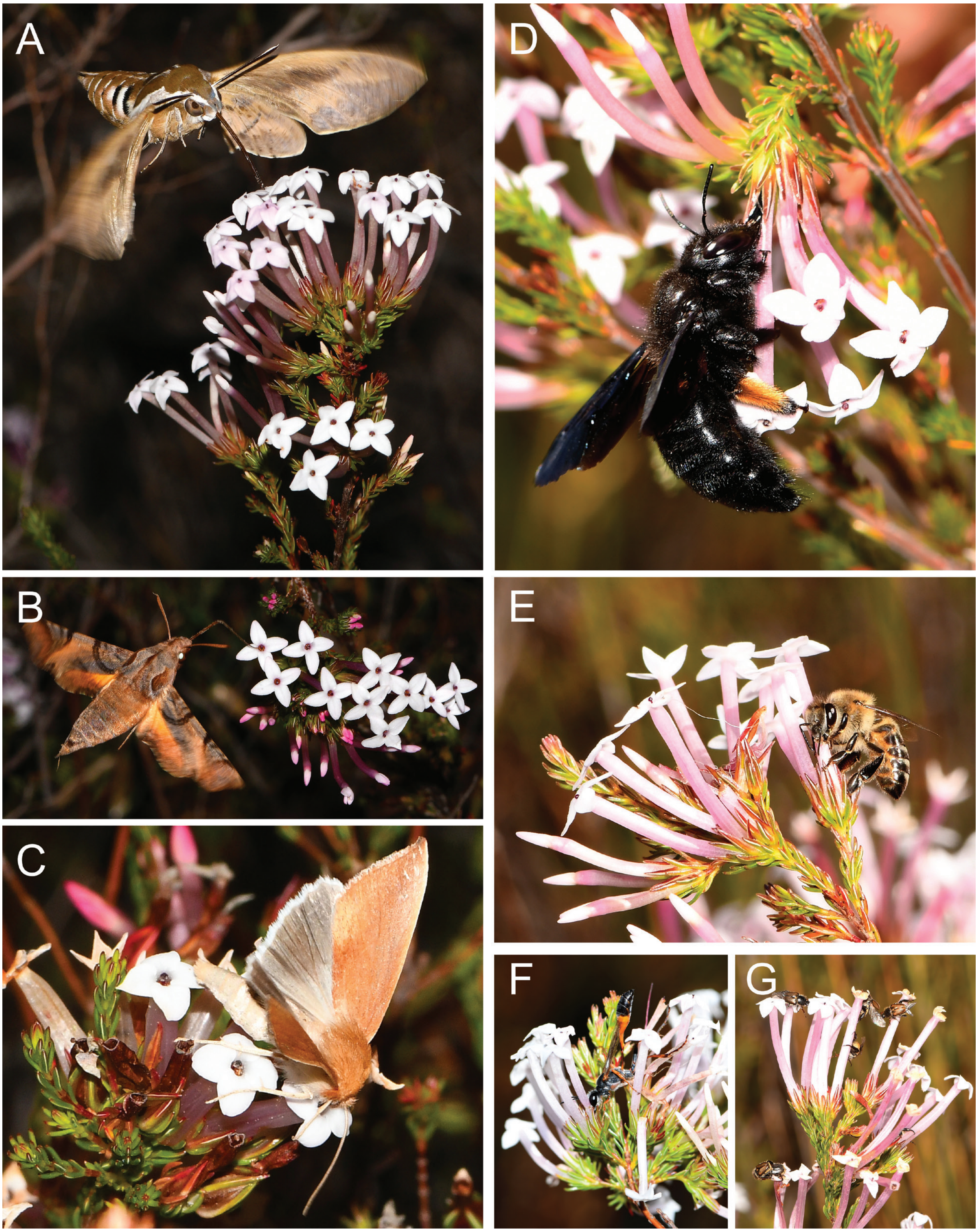

Figure 6. Interactions between *Erica infundibuliformis* and flower visitors. Legitimate visits with potential for effective pollen transfer are shown on the left: *Hippotion osiris* with white pollen grains visible along the proboscis (**A**), *Temnora* sp. (**B**), both at Agtertafelberg; and Geometrid moth (possibly *Acrasia* sp.) visiting a flower at Stettynsberg (**C**). Illegitimate robbing visits, all photographed at Agtertafelberg, are shown on the right: *Xylocopa* sp. (D), *Apis mellifera capensis* (**E**) and a Sphecidae wasp sp. (**F**) feed on nectar through a puncture in the base of the floral tube without contacting reproductive parts of flowers. *Hopliini* sp. visiting flowers, possibly feeding on floral tissue (**G**).

feed on any flower parts (Table 3). Of 18 captured representatives of insects considered to exhibit robbing behaviour, only one individual carried more than ten grains of *Erica* pollen (Table 3). Carpenter bees captured on *E. infundibuliformis* flowers carried an average of 188 pollen grains (SD = 392.38, n = 10), of which less than 1% were *Erica* tetrads (mean ± SD 0.44 ± 1.26%, n = 9).

Rates of nectar robbing (as assessed from the proportion of flowers with evidence of puncturing in the tissue of the floral tube) varied between 30% (Stettynsberg) and 35% (Agtertafelberg), whereas anther ring disruption varied between 41% (Agtertafelberg) and 58% (Stettynsberg) of assessed flowers, but neither differed significantly between sites (Fig. 7).

Discussion

Results from this study revealed divergence in several floral traits, including scent, colour, corolla tube length and nectar, between *E. cylindrica* and *E. infundibuliformis*. Despite these floral differences, pollinator observations revealed that both species are pollinated by moths, contrary to the idea that the differences in floral traits indicate a difference in pollination system.

Although *E. infundibuliformis* was visited by a large number of insect species during both daytime and the evening, legitimate visits were almost exclusively limited to settling moths and hawkmoths, which carried large amounts of *Erica* tetrads. These observations strongly contradict the expectation that the pollination system of *E. infundibuliformis* differs from that of the hawkmoth-pollinated *E. cylindrica*. Moth visits were observed consistently on all evenings, over multiple years and at two different sites with somewhat different flowering phenology; the two study sites have non-overlapping flowering periods, such that by the time of peak flowering in December-January at Agtertafelberg, flowering at Stettynsberg – which peaks in November – is completely over. Consistent observations of moth pollination, in combination with the fact that pollen loads on moths consisted largely of *Erica* pollen, therefore suggests an established plant-pollinator interaction, rather than opportunistic foraging by (hawk)moths from plants that are adapted for pollination by other insects (see Haber and Frankie 1989; Martins and Johnson 2013). This study, hence, adds another record of moth pollination in *Erica*. The observed visits were associated with disrupted anther rings (a proxy for pollination in *Erica*) in roughly half the flowers examined, suggesting that moth visitation results in reasonably high pollination rates. Similar to the mechanism of pollen transfer in *E. cylindrica* (Van der Niet and Cozien 2022), pollen was found on the moths' proboscises. Visits by *Helicoverpa armigera* at Stettynsberg were somewhat unexpected, as the proboscis of this moth species is much shorter than the corolla tube of *E. infundibuliformis*. It is possible that this moth species, which is also the main pollinator of the moth-pollinated *E. plukenetii* subsp. *breviflora* (Van der Niet et al. 2014b), is nevertheless able to access nectar that accumulates as droplets along most of the length of the corolla tube. A single bombyliid fly briefly visited *E. infundibuliformis* flowers during extensive daytime observation hours. Additionally, one individual of a *Moegistorhynchus* sp. was captured in the *E. infundibuliformis* population at Agtertafelberg. This fly not only carried *Erica* tetrads, but also had a tongue that closely matched the corolla tube of the local *E. infundibuliformis* plants in length. The pollen load and close morphological match with flower

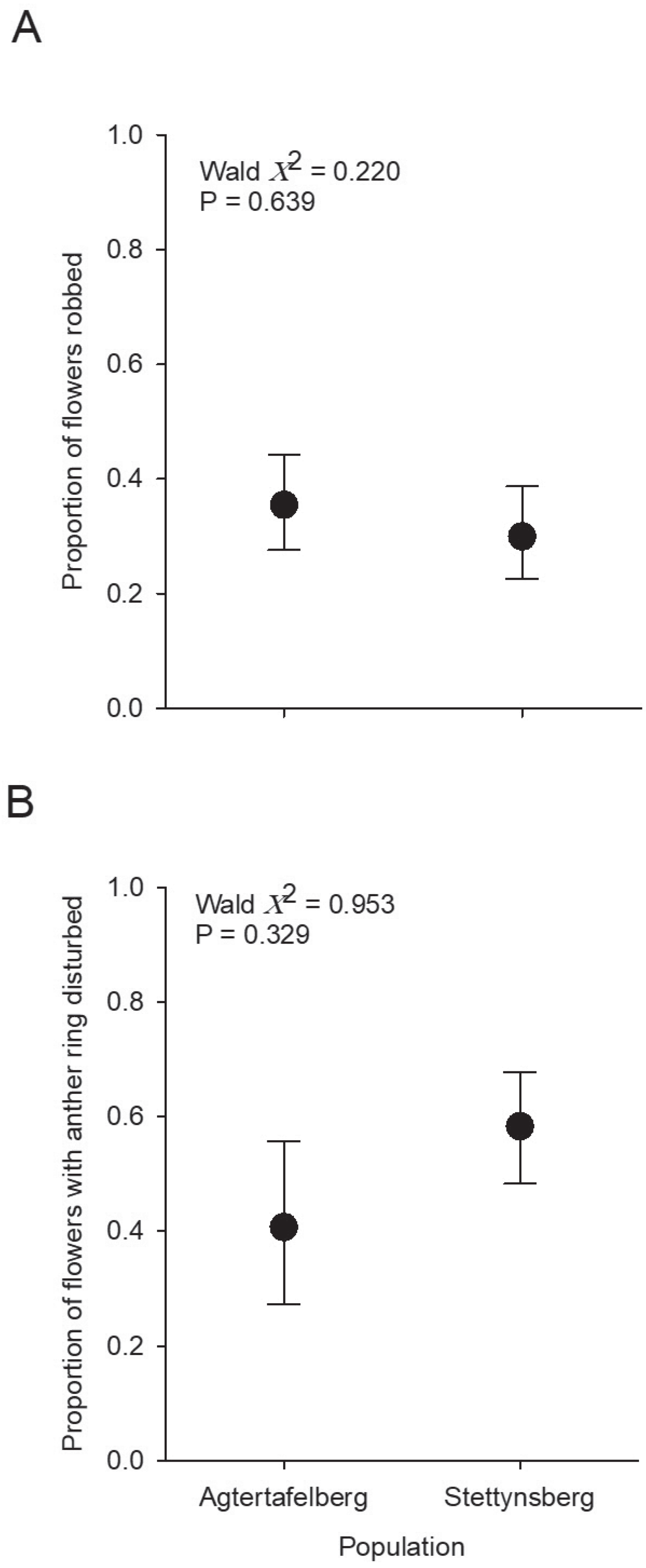

Figure 7. Frequencies of nectar robbing and anther ring disruption (as a proxy for pollination rate) in the two *Erica infundibuliformis* study populations.

dimensions together suggest that *Moegistorhynchus* flies do occasionally visit the species, albeit at a lower rate than moths during the time that we observed plants. Low visitation rates of LPF to *Erica* species that are specialised for this pollinator group, with complete absence in some years, appears to be the norm (e.g. Newman and Johnson 2021; McCarren et al. 2023), raising the possibility that, in some years, flies may be more common visitors than observed during our study. However, regardless of whether and to what extent LPF contribute to pollination of *E. infundibuliformis*, evidence from this study shows that moths unambiguously contribute to pollination in this *Erica* species.

Moth visitation to *E. infundibuliformis* flowers is surprising because strong nocturnal floral scent is considered a key characteristic of moth-pollinated flowers (Faegri and van der Pijl 1979; Knudsen and Tollsten 1993; but see Martins and Johnson (2013)), whereas *E. infundibuliformis* flowers have not been described as scented to the human nose. Nevertheless, a weak scent was detectable when flowers were assessed in the field at the Stettynsberg study site, possibly owing to the elevated presence of linalool at this site in particular, and GC-MS analysis of *E. infundibuliformis* scent confirmed the presence of a scent bouquet that is richer in compounds than that of the closely related *E. cylindrica*, which is perceived as strongly scented by humans (Rebelo et al. 1985). Further, comparison of rates of scent emission showed that, at the time when moth pollinators are most active, during the evening hours, rates of scent emission are similar for both *E. infundibuliformis* and *E. cylindrica*. The main difference between the scent of the two *Erica* species is that *E. cylindrica* flowers emit aromatic compounds, whereas the scent of *E. infundibuliformis* flowers is dominated by monoterpenes, such as ocimene. In analyses of human perception of volatiles, based on gas chromatography coupled with olfactometry, (E)-ocimene is often reported as an active compound (Lee et al. 2011; Zhao et al. 2022), but it is sometimes described by humans as grass-like and perhaps, therefore, not considered a typical floral volatile. Together, these results reinforce the need to objectively quantify floral traits when assigning pollination syndromes to plant species.

Although the function of scent for moth attraction in *E. infundibuliformis* was not established experimentally, some evidence supports the idea. Despite the scent of *E. infundibuliformis* not conforming to a typical bouquet associated with moth pollination, hawkmoth (including the species visiting *E. infundibuliformis*) antennae respond to (E)-ocimene (Shuttleworth and Johnson 2022) and high emission rates of the two stereoisomers of ocimene in an orchid were found to coincide with the peak activity of hawkmoths (Steen et al. 2019), suggesting a functional role for monoterpenes in moth attraction. Additionally, the objective absence of scent recorded by GC-MS analysis of flowers of two *Erica* species pollinated exclusively during the day by LPF (McCarren et al. 2023) further supports a functional role of scent emission for pollinator attraction in *E. infundibuliformis*. Although lower scent emission during the evening than during daylight hours contradicts a typical moth syndrome (Jürgens et al. 2014; Balducci et al. 2020; Powers et al. 2020), this pattern has also been found in other moth-pollinated plant species (Van der Niet et al. 2015). An interesting analogous case of interspecific variation in floral scent composition, as found in this study between *E. infundibuliformis* and *E. cylindrica*, occurs in two closely-related *Zaluzianskya* species, although these species do differ in the pollination system: *Z. natalensis*, with a bouquet dominated by aromatics, is pollinated by hawkmoths, whereas *Z. microsiphon*, dominated by monoterpenes, is pollinated by long-proboscid nemestrinid flies (Campbell et al. 2016). However, unlike in *Erica*, in this *Zaluzianskya* species pair, the flowers of the fly-pollinated species close during the evening and experimental manipulations and bioassays showed that flower visitation by hawkmoths was determined by flower orientation rather than by scent composition.

Flowers of both moth-pollinated *Erica* species studied here were found to be predominantly facing upwards, which is highly unusual in the genus (Van der Niet and Cozien 2022). In other systems, the upward-facing orientation of flowers has been shown to be important for pollination by hawkmoths (Fulton and Hodges 1999; Campbell et al. 2016). Upward-facing flowers should, therefore, not be considered exclusively associated with nemestrinid fly pollination in *Erica* (see McCarren et al. 2022; McCarren et al. 2023), as this study further confirms its association with pollination by moths (and hawkmoths in particular) in *Erica* (see also Van der Niet and Cozien (2022)).

Variation in corolla tube length is often associated with covariation with pollinator morphology as the match may be important for effective pollen transfer (e.g. Van der Niet et al. 2014b; Newman and Johnson 2021). In this study, corolla tube length was found to differ amongst the three *Erica* populations, with the longest corolla tubes found for *E. infundibuliformis* at Agtertafelberg and the shortest in *E. cylindrica*, albeit only marginally shorter than *E. infundibuliformis* at Stettynsberg. However, there was no consistent covariation or trait matching between pollinator proboscis length and floral tube length amongst populations or species; many legitimate flower visitors had proboscides that exceeded the floral tube in length (Fig. 6). This general absence of covariation is not unexpected for interactions in which pollination precision is low, as is the case for both the study species of *Erica*, when anthers of the flowers do not protrude beyond the floral tube and pollen is mostly placed quite imprecisely along the moth proboscis (also see Johnson 2024). It is possible that shorter floral tubes at Stettynsberg might reflect higher rates of visitation by relatively short-tongued settling moths versus predominant visitation by longer-tongued hawkmoths at Agtertafelberg, but more pollinator observations are required to firmly establish any difference in moth species composition between the two sites.

The two studied *Erica* species differ in colour as perceived by humans and differences were confirmed by objectively measured reflectance spectra of the two species. In both species, brightness of the corolla tube is lower than for the petals, but in both Agtertafelberg and Stettynsberg, reflectance of petal lobes of *E. infundibuliformis* is approximately twice that recorded for *E. cylindrica* (see Van der Niet and Cozien (2022)). Flowers of *E. cylindrica* have maximum reflectance between the 500 and 700 nm region, mainly in the human-visible part of the spectrum, whereas flowers of *E. infundibuliformis* also strongly reflect light in the UV range of the spectrum, with a steep increase in the UV region around 350 nm and consistently high maximum reflectance from 400 to 700 nm. The flower colour is perhaps the most puzzling trait in association with moth-pollination, as moth-pollinated flowers usually do not exhibit this steep increase in reflectance in the UV range (e.g. Johnson and Raguso (2005)), which is, instead, strongly characteristic for other fly-pollinated *Erica* species (Lombardi et al. 2021; Newman and Johnson 2021; Pauw 2022; McCarren et al. 2023). The colour of the floral tube, which does not reflect light in the UV region may be particularly visible to many Hymenoptera and, therefore, explain their attraction to this flower part for nectar consumption (Chittka et al. 1994). However, they may also be attracted by the scent or their presence may be driven by local distribution, since they were not observed at Stettynsberg.

The apparent contradiction between observed pollinators and floral traits of *E. infundibuliformis* raises the question for what kind of pollinator the species is adapted. Although the possibility that LPF pollination was underestimated cannot be excluded, effective pollination by moths is unambiguous. Some of the quantified traits, such as the presence of floral scent, suggest a functional role in moth pollination, but not fly pollination. Flower colour, on the other hand, was more typical for LPF-pollinated ericas (McCarren et al. 2021). One possibility is that, for these two traits (scent and colour) in this system, there are not strong trade-offs associated with attraction of moths versus flies, as has been suggested for other specialised pollination systems (Aigner 2001) and shown for particular floral traits in other plant species (Muchhala 2007; Peakall et al. 2010). Cases where trade-offs have been demonstrated involved roles of highly specific sex pheromones for pollinator attraction or morphological mismatches. It is possible that the presence of certain scent compounds may not compromise fly pollination (Campbell et al. 2016), whereas flower colour may be less critical for nocturnal moth pollination. The pollination system of *E. infundibuliformis* may, thus, represent a combination of traits in which an absence of trade-offs facilitates a bimodal pollination system, which has been observed in several species of *Tritoniopsis* (Manning and Goldblatt 2005) and in *Protea punctata* (Johnson et al. 2012). Indeed, visitation by hawkmoths and LPF has been demonstrated in other long-tubed plants in South Africa that are seemingly unscented to the human nose, such as *Satyrium hallackii* (Johnson 1997). Such bimodal pollination systems may be particularly important if visitation by one of the pollinator groups is unpredictable, as in this case may apply to LPF. Interpretation of traits of *E. infundibuliformis* in the context of bimodal pollination rather than as exclusive adaptations for moth pollination is also consistent with the observed trait divergence relative to *E. cylindrica*. If both species were specialised for moth pollination, the observed differences in floral traits, most strikingly flower colour, which has shifted between quadrants in a model of fly vision (Fig. 8), would be particularly puzzling. Further studies, including temporal selective pollinator exclusion experiments to assess the potential role of diurnal versus nocturnal pollinators (e.g. Wenzell et al. 2024) and phylogenetic analyses that can be used to determine the evolutionary direction of floral trait divergence, are needed to obtain a better understanding of the evolution of pollination systems (Van der Niet et al. 2014b).

This study adds to a number of cases in which syndrome-based hypotheses were contradicted by empirical observations (e.g. de Merxem et al. 2009; Cozien et al. 2019; Castañeda-Zárate et al. 2021). In the study system examined here, the combination of rarity of hawkmoth pollination in the CFR, in general and in *Erica*, in particular, in combination with the inadequacy of human perception for identification of floral scent, were probably the main reasons why moth pollination was not correctly predicted. It is also possible that the trait combination in *E. infundibuliformis* represents a syndrome indicative of bimod-

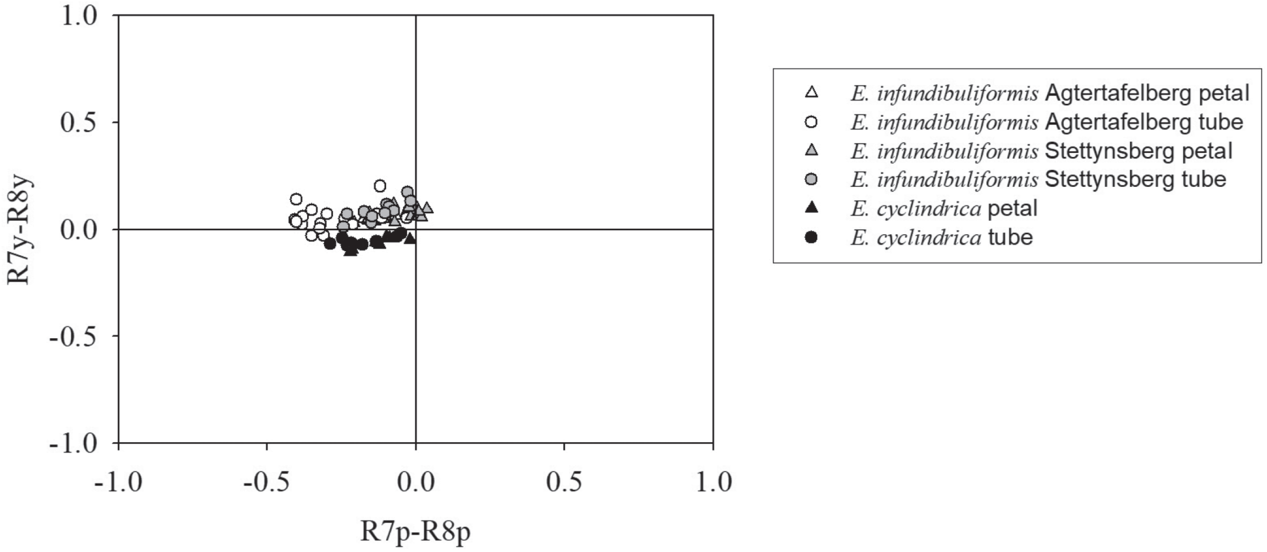

Figure 8. Loci of colours of petals and corolla tubes for flowers of *Erica infundibuliformis* from Aftertafelberg and Stettynsberg and for *E. cylindrica*, plotted in the fly vision colour space of Troje (1993). Loci of most, but not all spectra of both petals and floral tubes of flowers from both populations of *E. infundibuliformis* fell within a single quadrant in the fly vision colour space; spectra of both petals and floral tube surfaces of *E. cylindrica* fell into a different quadrant, suggesting that neither species has within-flower contrast for flies, but that flies may perceive flowers of the two species differently.

al pollination by flies and moths, but data are currently inadequate to confirm or refute this idea. Our findings again underline the importance of verifying pollination systems predicted by syndromes with empirical pollinator observations (Van der Niet 2021). Results also indicate that hawkmoth pollination, which has now been documented at multiple sites and years and during different seasons, may be more common in the CFR than previously suggested (Johnson 1997) and emphasise that, despite the associated challenges, pollinator observations during evening hours should be considered a critical component in any pollination study of plant species with long-tubed flowers and to characterise the pollination systems of any region (cf. Cai et al. 2024).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: TN, RJC. Data curation: RJC, TN. Formal analysis: TN, RJC. Investigation: RJC, TN. Methodology: RJC, TN. Writing - original draft: TN. Writing - review and editing: RJC.

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Data availability

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

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Supplementary material 1

Mass spectra of unknown compounds

Authors: Timotheüs van der Niet, Ruth Cozien

Data type: pdf

Explanation note: Mass spectra of unknown compounds that were found across an entire batch or in samples across multiple batches in the scent of *Erica infundibuliformis*. Two compounds for which identification was somewhat ambiguous are also included.

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Research Article

The genus *Coleus* (Lamiaceae) in Central Africa (Democratic Republic of the Congo, Rwanda, Burundi), with the description of 15 new species

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Abstract

The genus *Coleus* is revised for DR. Congo, Rwanda, Burundi, based on herbarium taxonomy. Ninety-five taxa are reported (89 species, 1 subspecies, 5 varieties). Fifteen new species and one new variety are described (*Coleus duvigneaudii*, *C. esculentus* var. *kolweziensis*, *C. hildei*, *C. kaminaensis*, *C. kundelunguensis*, *C. linarioides*, *C. lisowskii*, *C. marunguensis*, *C. minusculus*, *C. mitwabaensis*, *C. mystax*, *C. pengbelensis*, *C. piscatorum*, *C. pseudoschizophyllus*, *C. ruziziensis* and *C. zigzag*). Fourteen species are newly recorded in DR. Congo and two species are newly recorded in Burundi. Four new combinations are made (*Coleus betonicifolius* var. *kasomenensis*, *C. esculentus* var. *densus*, *C. esculentus* var. *primulinus* and *C. parvifolius*). Ten names are lectotypified. One name is neotypified. Thirteen new synonyms are reported. Particular attention is paid to the *Coleus bojeri* complex. Three names are resurrected to accommodate the extensive variation patterns in Central Africa (*C. chevalieri*, *C. collinus* and *C. heterotrichus*); their distribution in Africa is outlined and the circumscription of *C. bojeri* is amended accordingly. Fifteen taxa are endemic to the study region. A determination key is provided.

Key words: Distribution, endemic, flora, identification key, Katanga, new records, taxonomy

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Introduction

The circumscription of the genus *Coleus* Lour. (Lamiaceae) has changed considerably in the last decades, producing a copious amount of synonymy. *Coleus* was transferred to *Plectranthus* L'Hér. by Morton (1962). That concept was followed by Flora of West Tropical Africa (Morton 1963), the Flore du Rwanda (Troupin and Ayobangira 1985) and Lebrun and Stork (1997). Harley et al. (2004) further merged *Solenostemon* Thonn., *Englerastrum* Briq. and *Holostylon* Robyns & Lebrun in *Plectranthus*, whereas *Pycnostachys* Hook. was kept distinct; this concept was followed by Flora of Tropical East Africa (Paton et al. 2009) and Flora Zambesiaca (Paton et al. 2013). However, recent phylogenetic analyses, based on molecular markers, have shown that this expanded *Plectranthus* is polyphyletic and that *Coleus* and *Plectranthus* should be kept distinct (Paton et al. 2018). The genus *Coleus* thus resuscitated now comprises 294 species, i.e. all the species formerly included in *Pycnostachys*, *Solenostemon*, *Holostylon* and *Englerastrum*, in addition to part of *Plectranthus* sensu Morton (1962) (Paton et al. 2019). Part of the remaining species of *Plectranthus* are now accommodated in a new genus, i.e. *Equilabium* Mwany., A.J.Paton & Culham (Paton et al. 2018). The necessary nomenclatural combinations have been published by Paton et al. (2019). This concept is also followed in the Flore du Gabon (Paton 2022).

For Central Africa (defined here as DR. Congo, Rwanda, Burundi), only local accounts of *Coleus* are available, including Troupin and Ayobangira (1985) for the Flore du Rwanda and Robyns (1947) for the Virunga National Park. Other important references for DR. Congo include De Wildeman (1920), Robyns and Lebrun (1929), Bruce (1940) and Robyns (1943). In order to prepare the treatment of *Coleus* for the Flore d'Afrique Centrale, we have critically revised all the relevant materials from the Democratic Republic of the Congo (DR. Congo), Rwanda and Burundi. During the preparation of this revision, particular attention was paid to the complex of *C. bojeri*, a particularly difficult group which was left incompletely resolved by Paton et al. (2009, 2013). We here present a key to the species, a check-list with a revised synonymy and original descriptions for the species not included in recent floras.

Materials and methods

Herbarium specimens of *Coleus* collected in DR. Congo, Rwanda and Burundi were studied in BR which hosts the largest collection for that region (available online [https://www.botanicalcollections.be]), BRLU, K and POZG (available online [https://amunatcoll.pl/]). Additional specimens, in particular from B, BM, COI, HBG, K, LISC, LWI, P, WAG and YBI were investigated using the JSTOR Global Plants facility (https://plants.jstor.org/) and GBIF (https://www.gbif.org) and online databases of the respective herbaria. All cited specimens have been seen (except otherwise indicated).

Plants of the World Online (POWO, http://www.plantsoftheworldonline.org/, consulted 25 June 2023) was used to build up a first checklist. Fifty-seven species of *Coleus* were hitherto accepted for DR. Congo, Rwanda and Burundi.

For the *Coleus bojeri* complex, all the names based on type materials from DR. Congo, Rwanda and Burundi (i.e. *Coleus claessensii* De Wild., *C. collinus* Robyns & Lebrun, *C. dewevrei* Briq., *C. heterotrichus* Briq., *C. homblei* De Wild., *C. ringoetii* De Wild., *C. platostomoides* Robyns & Lebrun, *C. quarrei* De Wild. and *C. termetophilus* De Wild.), were synonymised by Paton et al. (2009, 2013) as *Plectranthus bojeri* and by Paton et al. (2019) as *Coleus bojeri*. *Coleus delpierrei* De Wild., synonymised with *C. welwitschii* by Paton et al. (2019) was also included, on account of its close resemblance with *C. bojeri*. The original materials of all these names have been critically revised.

Taxonomic treatment

Our revision shows that 95 taxa of *Coleus* (89 species, 1 subspecies, 5 varieties) occur in Central Africa; all taxa occur in DR. Congo, 34 species and 29 species occur in Burundi and Rwanda, respectively. Fifteen species and one variety new to science are described (*Coleus duvigneaudii*, *C. esculentus* var. *kolweziensis*, *C. hildei*, *C. kaminaensis*, *C. kundelunguensis*, *C. linarioides*, *C. lisowskii*, *C. marunguensis*, *C. minusculus*, *C. mitwabaensis*, *C. mystax*, *C. piscatorum*, *C. pengbelensis*, *C. pseudoschizophyllus*, *C. ruziziensis* and *C. zigzag*). Four new combination are made (*Coleus betonicifolius* var. *kasomenensis*, *C. esculentus* var. *densus*, *C. esculentus* var. *primulinus* and *C. parvifolius*). Thirteen new synonyms are reported.

In addition to the new species, 14 species are newly recorded in DR. Congo and two species are newly recorded in Burundi. A total of fifteen taxa are endemic to the study area, i.e. all new taxa, except *C. pengbelensis* (also present in Central African Republic) and *C. zigzag* (also present in Uganda), in addition to the previously described *C. globosus*.

Ten names are lectotypified (*C. celsus* A.J.Paton, *C. claessensii* De Wild., *C. delpierrei* De Wild., *C. homblei* De Wild., *C. kasomenensis* De Wild., *C. kisanfuensis* De Wild., *C. seretii* De Wild., *C. termetophilus* De Wild., *Plectranthus hockii* De Wild. and *Pycnostachys congensis* Gürke). One name is neotypified (*Pycnostachys goetzenii* Gürke).

The *Coleus bojeri* complex

Paton et al. (2009, 2013) adopted a very broad circumscription of *Coleus bojeri*, comprising virtually all the annual taxa formerly referred to the genus *Solenostemon* while admitting that variation in DR. Congo was more complex compared to neighbouring regions and in need of revision. Nine names, based on type materials from DR. Congo, were synonymised with *C. bojeri* by Paton et al. (2009, 2013) (*C. claessensii* De Wild., *C. collinus* Lebrun & L. Touss., *C. dewevrei* Briq., *C. heterotrichus* Briq., *C. homblei* De Wild., *C. platostomoides* Robyns & Lebrun, *C. quarrei* De Wild., *C. ringoetii* De Wild. and *C. termetophilus* De Wild.).

Our revision shows that flower morphology is relatively uniform, but with little information value in this group. However, traits of taxonomic value include bract persistence, pubescence pattern of the stem, especially in the inflorescence, verticil spacing, cincinni length and leaf blade size and shape (Table 1). Variation in DR. Congo can be accommodated in four different species. Three binomials are resurrected i.e. *C. chevalieri* Briq., *C. collinus* Lebrun & L.Touss. and *C. heterotrichus* Briq. Accordingly, the circumscription of the binomial *Coleus bojeri* is amended. It is restricted here to plants with early deciduous bracts, stem indumentum (especially in the inflorescence) homotrichous, consisting only of retrorse, more or less appressed hairs, without glandular hairs and long patent hairs and cincinni rachis not exceeding 7 mm long in fruit. See Table 1 for a comparison of the four species. Finally, *C. homblei* De Wild. is resurrected as an earlier synonym of *C. sigmoideus* A.J.Paton.

Table 1. Comparison of four taxa in the *Coleus bojeri* species complex. Cincinni length refers to the length of the rachis of the cyme, excluding pedicels and flowers.

	C. bojeri	***C. chevalieri***	***C. collinus***	***C. heterotrichus***
Bracts	caducous	persistent	persistent	caducous
Indumentum of stem	Short, retrorse, appressed eglandular hairs	Short, retrorse, appressed eglandular hairs	Long, retrorse and patent eglandular hairs	Very short, often papilliform, patent eglandular hairs, microglandular hairs, and sparse long hairs
Cincinni length at fruiting	1–7(–12) mm	2–3(–6) mm	0–4 mm	5–50 mm
Leaf blade size	1.5–4.5(–7.5) × 1.0–4.0(–6.2) cm	3–10(–11) × 1–5.5 cm	0.9–2.2 × 0.7–2.0 cm	1.0–7.0(–8.5) × 1.0–5.0(–8.5) cm
Verticil spacing	(5–)10–25(–30) mm	5–10 mm	7–15 mm	10–25(–40) mm

Key to the species of *Coleus* in DR. Congo, Rwanda, Burundi

Notes: 1. *C. tetragonus*, found in Zambia very close to the border of DR. Congo, is included in the key; 2. All measurements of calyx refer to the fruiting state unless otherwise stated.

Key to the groups

1 Corolla yellow or orange .... **Group 1**

– Corolla white, pink, mauve, purple or blue **2**

2 Flowers sessile on inflorescence axis, forming a compact spike-like inflorescence; calyx lobes all similar in size and shape, subulate, becoming spinescent after anthesis .... **Group 2**

– Flowers mostly pedicellate; inflorescence mostly lax, more rarely congested; calyx lobes more or less unequal, never all subulate, not spinescent...**3**

3 Inflorescence cylindrical, congested, with axis not visible between the cymes; pedicel 0–3 mm long .... **Group 3**

– Inflorescence lax, with the axis conspicuous between most of the cymes; pedicel (1–)2–12 mm long...**4**

4 Flower solitary in the axil of a bract; 1 or 2 flowers to each inflorescence node.. **Group 4**

– Flowers 2–20 in the axil of each bract..**5**

5 Median lobes of lower lip of calyx fused over most of their length into a bidentate lip, much exceeding the lateral lobes .... **Group 5**

– Median lobes of lower lip of calyx free, not fused into a lip .... **Group 6**

Group 1. Corolla yellow or orange

1 Flowers solitary or in pairs at each inflorescence node **2**

– Flowers > 2 at each inflorescence node **5**

2 Stem with stiff lignified bristles...**3**

– Stem without stiff lignified bristles **4**

3 Annual with unbranched shoots < 0.5 m; fruiting calyx 6–10 mm long ....(***C. tetragonus***)

– Shrub with branched perennial shoots, up to 2 m; fruiting calyx ca. 4.5 mm long... ***C. conglomeratus***

4 Shoot slender, < 40 cm high; leaves (1.0–)1.5–2.7 × (0.1–)0.3–1.0 cm; inflorescence terminal; rootstock a globose tuber ca. 1 cm .... ***C. mitwabaensis***

– Shoot robust, 60–200 cm high; leaves 3.0–8.0(–20) × 1.0–3.0(–8) cm; inflorescence of lateral thyrses; rootstock a rhizome sometimes with elongated tubers... ***C. esculentus***

5 Geofrutex of burnt savannah, leafless at flowering, < 25 cm high; corolla pale yellow with purple spots .... ***C. buchananii***

– Shrub of moist forest, leafy at flowering, > 25 cm high; corolla deep orange yellow **6**

6 Stem with fusiform propagules in the upper axils; hooked hairs present on propagules and, sometimes, near shoot apices; leaf blade 5–14 × 2–5 cm,

not decurrent into the petiole; pedicel 4–10 mm long .... ***C. melleri***
– Stem without propagules; hooked hairs lacking; leaf blade 15–30 × 6–10 cm, long attenuate into the narrowly winged petiole; pedicel ca. 4 mm long .... ***C. decurrens***

Group 2. Inflorescence compact, spike-like; flowers sessile; calyx lobes subulate, spinescent

1 Leaves sessile or petiole < 0.5 cm, blade occasionally attenuate into a pseudopetiole **2**
– Leaves conspicuously contracted into a distinct petiole > (0.5–)1.0 cm... **14**
2 Corolla 4–7 mm long **3**
– Corolla ≥ 8 mm long **6**
3 Floral bracts densely ciliate, with cilia length exceeding bract width .... ***C. deflexifolius***
– Floral bracts with cilia shorter than bract width or only sparsely ciliate or not ciliate **4**
4 Dorsal side of calyx tube curving over to form a hood over the mouth; calyx lobes slightly curving upwards .... ***C. ruandensis***
– Calyx tube not as above; calyx lobes straight 5
5 Leaves opposite, without fascicles of young leaves in the axils; inflorescence 5–7 mm broad at anthesis (corolla excluded), 8–12 mm broad in fruit; calyx tube funnel-shaped .... ***C. stenostachys***
– Leaves with fascicles of small leaves in the axils; inflorescence > 7 mm broad at anthesis (corolla excluded), 14–23 mm broad in fruit; calyx tube ventrally gibbose .... ***C. dewildemanianus***
6 Fascicles of small leaves or short branches in the axils of leaves **7**
– No fascicles of leaves or short branches in the axils of leaves **8**
7 Inflorescence 20–45 mm long in fruit; leaf blade 0.5–1.5(–3.0) cm long .... ***C. parvifolius***
– Inflorescence 55–140 mm long in fruit; leaf blade 1.5–6.0 cm long .... ***C. descampsii***
8 Secondary veins diverging at a very open angle (60–90°), fusing into a submarginal vein; mid-vein thickened .... ***C. stuhlmannii***
– Secondary veins diverging at a narrow angle (<60°), not joining into a marginal vein; mid-vein not thickened **9**
9 Leaves heteromorphic, the median and upper ones with blade almost linear, 0.2–0.6 cm wide, the lowermost ones abruptly broader, ovate-elliptic, obovate-elliptic, to broadly elliptic, (0.5–)1.0–1.5 cm wide .... ***C. lisowskii***
– Leaves homomorphic, the lowermost ones not abruptly broader **10**
10 Leaves amplexicaulous, strongly recurving, much longer than the internodes; calyx throat and base of lobes tomentose .... ***C. pseudospeciosus***
– Leaves attenuate at base, ascending to spreading, not exceeding internode length by much; calyx throat glabrous to pubescent **11**

11 Secondary veins almost parallel to mid-vein, prominent on both surfaces; leaf blade narrowly obovate; bracts forming a conspicuous coma; calyx compressed dorsally .... ***C. prittwitzii***

– Secondary veins divergent, not prominent; leaf blade narrowly elliptic to linear; bracts not forming a conspicuous coma; calyx not compressed dorsally **12**

12 Inflorescence 75–115 mm long in fruit; calyx tube ventrally compressed at throat, then gibbous, the dorsal side curving outwards and almost forming a hood over the throat; calyx lobes (7–)10–13 mm long at fruiting, with long eglandular hairs near base .... ***C. affinis***

– Inflorescence 30–55 mm long in fruit; calyx tube not compressed at throat; calyx lobes 3–7(–10) mm, with short glandular hairs **13**

13 Leaves 0.4–2.0 cm broad, > 7× as long as broad, somewhat pubescent beneath; calyx tube somewhat ventrally gibbous, with short glandular hairs; calyx lobes not winged; bracts ca. 3 mm long .... ***C. scruposus***

– Leaves 1.4–4.0 cm broad, < 7× as long as broad, densely pubescent beneath; calyx tube funnel-shaped, with eglandular hairs; calyx lobes narrowly winged; bracts 4–8 mm long .... ***C. sphaerocephalus***

14 Dorsal side of calyx tube curving outwardly to form a hood over calyx mouth; corolla 4–5 mm long; calyx lobes ± 2.5 mm, somewhat upwardly curving .... ***C. ruandensis***

– Dorsal side of calyx straight, not forming a hood over the mouth; corolla 6–19 mm long; calyx lobes 3–9 mm, straight **15**

15 Secondary veins diverging at a very open angle (60–90°), fusing into a marginal vein; leaf blade 0.4–2.2 cm broad, at least 5× as long as broad... .... ***C. stuhlmannii***

– Secondary veins diverging at a narrower angle (< 60°), not fusing into a submarginal vein; leaf blade 1.5–7.0 cm broad, 2–3× as long as broad **16**

16 Leaf blade broadly ovate, length/width ratio < 2, almost truncate at base; marginal lobes < 8 on either side .... ***C. batesii***

– Leaf blade ovate to elliptic, length/width ratio > 2, base cuneate to attenuate; marginal lobes > 10 on either side **17**

17 Leaf undersurface mostly with stellate hairs; corolla 15–20 mm long; stamens exserted > 5 mm; calyx lobes 8–13 mm long .... ***C. elliotii***

– Leaf undersurface with simple hairs; corolla 6–15(–20) mm long; stamens included in the corolla or exserted over 1–4 mm; calyx lobes 2.5–9 mm long **18**

18 Calyx lobes 2.5–3.5(–4) mm long **19**

– Calyx lobes 4–9 mm long **20**

19 Calyx throat and base of lobes tomentose; bract cilia somewhat undulate... .... ***C. eminii***

– Calyx throat and base of lobes not tomentose; calyx lobes very shortly pubescent; bract cilia straight .... ***C. erici-rosenii***

20 Corolla 6–8(–9) mm long, generally pale-coloured .... ***C. meyeri***

– Corolla 12–15(–20) mm long, generally with vivid colours **21**

21 Calyx lobes narrowly winged; petiole 0–1 cm; leaf blade oblong-elliptic, widest near the middle; leaf blade coriaceous............***C. sphaerocephalus***

– Calyx lobes not winged; petiole 1–3.5 cm; leaf blade ovate, widest under the middle; leaf blade membranous...**22**

22 Inflorescence 45–80 mm long, distinctly tapering and less dense apically; calyx tube with sessile glands rare; calyx lobes 6–9 mm long, eglandular ... . ***C. goetzenii***

– Inflorescence 25–45 mm long, not tapering and remaining dense near the apex; calyx tube with many red sessile glands; calyx lobes 4.5–6 mm long, thinly glandular .... ***C. schliebenii***

Group 3. Inflorescence dense, spiciform, cylindrical; corolla violet, purplish or blue

1 Calyx hairy inside throat; verticils 6-flowered; annual.................................. ....***C. caninus* subsp. *flavovirens***

– Calyx glabrous inside throat; verticils 6–40-flowered; perennial **2**

2 Corolla 3–9 mm long; calyx 2–3.5 mm long **3**

– Corolla 8–22 mm long; calyx 5–9 mm long **5**

3 Inflorescences on short lateral shoots; pedicel 0–1 mm long; verticils 6–10-flowered; stamens with filaments fused; leaf blade 1–2 cm long ....***C. guerkei***

– Inflorescence terminal; pedicel 1–3 mm long; verticils 10–40-flowered; stamens free; leaf blade 1.2–6.0 cm long...**4**

4 Leaf petiolate; corolla 5–9 mm long, with tube 3–4.5 mm long .... ***C. succulentus***

– Leaf sessile; corolla 3–5 mm long, with tube 2–2.5 mm long .... ***C. cylindraceus***

5 Calyx upright; calyx lobes arranged in two groups, 3 upper lobes and 2 lower lobes; plant almost leafless at flowering.......................***C. lactiflorus***

– Calyx patent; calyx lobes in a 1+4 pattern; plant leafy at flowering **6**

6 Upper lobe of calyx forming a hood over the throat, the other four lobes much smaller..***C. engleri***

– Upper lobe of calyx not forming a hood over the throat, the other four lobes less different...**7**

7 Calyx with pale sessile glands; inflorescence terminal, often subtended by subsessile lateral inflorescences, greenish, villose, with bracts much exceeding flowers; verticils 12–20-flowered....................... ***C. stachyoides***

– Calyx with red sessile glands; inflorescence terminal not subtended by lateral inflorescences, purplish, not villose, with bracts inconspicuous; verticils 6–12-flowered ....***C. betonicifolius***

Group 4. Inflorescence lax with the axis conspicuous between most of the single flowered cymes; flowers solitary; corolla violet, purplish or blue

1 Petiole 2–7 cm; leaf blade 4–10 cm broad; calyx bearded inside throat; plant leafy at flowering, in evergreen forest .... ***C. longipetiolatus***

– Petiole shorter, leaf blade narrower; calyx throat glabrous inside; plant with or without leaves at flowering, in dry woodland and savannah..........**2**

2 Leaves linear, 1.5–3.5 × 0.1–0.4 cm, margin strongly revolute, upper surface glabrous; internodes ca. 1 cm .... ***C. linarioides***
– Leaves different or absent at flowering; margin not strongly revolute, upper surface usually with hairs; internodes much longer **3**
3 Annual, with weak roots; calyx not caducous at fruiting **4**
– Perennial, with thickened rootstock; calyx caducous or persistent **8**
4 Pedicel 6–20 mm long, much exceeding calyx .... ***C. gracillimus***
– Pedicel 1–6 mm long, shorter or equalling calyx **5**
5 Upper calyx lobe ovate, very different in shape from the other four lobes, these narrowly triangular, acute to acuminate; calyx 5–10 mm long in fruit .... ***C. efoliatus***
– Upper calyx lobe triangular, similar in shape to the others; calyx 2.5–4 mm long in fruit **6**
6 Pedicel and calyx with patent 2–5 mm long smooth cilia .... ***C. mystax***
– Pedicel shortly pubescent or glabrous **7**
7 Plant leafless at flowering; stem with 3 to 5 pairs of opposite branches, diverging at a very open angle, almost horizontal, each with 1 or 2 dichotomous ramifications; corolla ca. 10 mm long; inflorescence 3–7 mm long .... ***C. piscatorum***
– Plant leafy at flowering; branching pattern different; corolla 4–5 mm long; inflorescence 3–12 cm long .... ***C. rhodesianus***
8 Dwarf plant < 10 cm, leafless at flowering, glutinous; rootstock a globose to elliptic tuber .... ***C. minusculus***
– Plant > 10 cm high, leafy or not at flowering, not glutinous; rootstock a rhizome **9**
9 Pedicel jointed near the middle **10**
– Pedicel jointed near tip or without a joint **11**
10 Plant robust, 100–150 cm high; leaves petiolate; leaf blade broadly ovate; thyrses ca. 1.5 cm long, with flowers solitary, arranged helicoidally .... ***C. celsus***
– Plant more slender, 30–50 cm high; leaves sessile; leaf blade narrowly ovate-elliptical; thyrses 4–20 cm long, with flowers mostly opposite .... ***C. kundelunguensis***
11 Pedicel 5–25 mm long, filiform; rachis slightly zigzagging near apex; inflorescence a large diffuse panicle **12**
– Pedicel 3–14 mm long, not filiform; rachis straight near apex; inflorescence different **13**
12 Leaves subsessile; leaf blade elliptic to ovate-elliptic, at least 4× as long as broad; anthers not forming a pouch; style not divided or shallowly lobed; calyx lobes subulate .... ***C. kaminaensis***
– Leaves petiolate; leaf blade broadly ovate, ca. 2 × as long as broad; anther forming a pouch, opening near apex; style with two branches; calyx lobes deltate .... ***C. gracilipedicellatus***
13 Main shoot ending in a sterile leafy twig; inflorescence lateral, often exceeding main shoot; calyx in fruit 5–7 mm long; pedicel 4–6 mm long, attached almost centrally on calyx; leaf blade rounded at apex .... ***C. modestus***
– Main shoot ending in flowering axis; inflorescence terminal; calyx in fruit 9–12 mm long; pedicel 3–14 mm long, attached asymmetrically in front of upper calyx lobe; leaf blade acute to rounded at apex **14**

14 Plant leafless at flowering; pedicel jointed, with the distal part more pubescent than the proximal part, with eglandular hairs............***C. articulatus***

– Plant leafy at flowering; pedicel without a joint, uniformly pubescent, with glandular and eglandular hairs **15**

15 Leaves 3-whorled; mid-leaves with blade narrowly elliptic, oblong-elliptic to almost linear, 6–9 × 0.5–1.3 cm, cuneate at base, acute at apex ....***C. duvigneaudii***

– Leaves almost always opposite; mid-leaves with blade ovate-elliptic, 2–7 × 0.5–2 cm, base rounded to almost clasping stem, mostly obtuse at apex... ....***C. foliatus***

Group 5. Calyx with two lower lobes fused

1 Leaf blade pinnatifid to deeply toothed .... ***C. pseudoschizophyllus***

– Leaf blade crenate or serrate..**2**

2 Plant prostrate, rooting at nodes, forming carpets; leaf blade almost round, 1–2.5 × 1–2.5 cm; inflorescence of one or two verticils ....***C. repens***

– Plant ascending to erect, not forming carpets; leaf blade ovate, acute to obtuse at apex; inflorescence with more than 2 verticils **3**

3 Upper lip of calyx at least 3× longer than the other lobes, lanceolate and acuminate; nutlets verrucose .... ***C. pengbelensis***

– Upper lip of calyx not much longer than the other lobes, ovate, rounded, obtuse to subacute, never acuminate; nutlets smooth...............................**4**

4 Lower lip of calyx broadly ovate-elliptic, strongly curving upwards and almost closing the throat; lateral lobes of calyx much longer than broad, acute, convergent, inconspicuous...**5**

– Lower lip of calyx linear to oblong, not curving upwards except near tip; lateral lobes of calyx as long as broad, truncate to rounded, not convergent, conspicuous **8**

5 Corolla 4–15 mm long; pedicel 2–4 mm long; verticils in fruit 12–15 mm broad **6**

– Corolla 10–22 mm long; pedicel 4–10 mm long; verticils in fruit 20–45 mm broad **7**

6 Perennial with lower part of shoot lignified; stem prostrate to ascending or erect; corolla (8–)10–15 mm long, with lower lip 5–8 mm long; leaf blade subentire to shallowly crenate...***C. calaminthoides***

– Annual; stem mostly erect; corolla 4–7 mm long, with lower lip 2–4 mm long; leaf blade crenate to serrate ....***C. monostachyus* subsp. *monostachyus***

7 Lower lip of calyx curving upwards at a right angle to the tube, tightly appressed on the upper lip and closing the throat; calyx tube without long hairs...***C. mannii***

– Lower lip of calyx curving upwards at an obtuse angle, not touching the upper lip and not closing the throat; calyx tube with long patent hairs.... ***C. shirensis***

8 Pedicel (4–)5–10 mm long at fruiting **9**

– Pedicel 1–5 mm long at fruiting..**11**

9 Shrub with persistent lignified, branching shoots; rootstock without tubers..***C. autranii***

– Herb, mostly with a single short-lived shoot; rootstock with tubers (but these rarely collected)..**10**

10 Cymes pedunculate, 7–11(–19)-flowered, with two divergent cincinni with rachis elongating to 20 mm in fruit; leaf blade 6–8.5 cm long, margin crenate... ***C. hildei***

– Cymes sessile, ca. 5-flowered; rachis ca. 2 mm long, not divided in two cincinni; leaf blade 1.5–4.0 cm long, margin sharply serrate..... ***C. homblei***

11 Cymes with a 5–15 mm peduncle; cincinni diverging at a right angle, with rachis zigzagging in fruit; inflorescence axis subglabrous; leaf blade almost rounded, reniform, obtuse to rounded at apex..................... ***C. zigzag***

– Cymes sessile or with peduncle 1–2 mm; cincinni less strongly diverging, straight to slightly undulate; inflorescence axis pubescent to puberulent; leaf blade variable in shape, but neither rounded nor reniform................**12**

12 Perennial, with a rhizome (this sometimes thin) or tubers; lower part of stem lignified **13**

– Annual, stem not lignified, with fibrous root, lacking a rhizome or tubers **16**

13 Flower bud and calyx beige tomentose; leaf blade truncate at base; stem hairs antrorse..***C. marunguensis***

– Flower bud and calyx pubescent, not tomentose; leaf blade attenuate at base; stem hairs retrorse or spreading **14**

14 Plant often not forming an inflorescence or this ill-developed; tubers plentiful; cultivated or escaped... ***C. rotundifolius***

– Inflorescence normally developed; tubers lacking or scarce; native species of natural vegetation **15**

15 Rhizome thin, not lignified; stem slender, < 2 mm thick at base, often rooting at nodes near base, mostly unbranched; lower part of stem and petiole villose, with patent hairs > 2 mm long; leaf blade membranous, ovate, shortly decurrent on petiole; cincinni rachis up to 6 mm long in fruit; on moist soil in W DR. Congo ....***C. brazzavillensis***

– Rhizome thick, lignified; stem > (2–)3 mm thick at base, not rooting at nodes, often branching from base; lower part of stem base and petiole with hairs retrorse to spreading < 2 mm long; leaf blade thick, trullate, decurrent over most of petiole length; cincinni rachis up to 20 mm long in fruit; on dry soil, widespread..***C. welwitschii***

16 Bracts persisting at all inflorescence nodes **17**

– Bracts caducous or, rarely, persisting at lower nodes...............................**18**

17 Leaf blade 3–10 cm long, mostly obtuse at apex; inflorescence with 15–30 verticils; bracts longer than broad, 2–3 mm broad............. ***C. chevalieri***

– Leaf blade 0.9–2.2 cm long, acute at apex; inflorescence with 4–11 verticils; bracts as long as broad, 3–5 mm broad .... ***C. collinus***

18 Inflorescence axis with indumentum of appressed retrorse hairs only, without glandular hairs or long patent hairs; cincinni rachis elongating to 1–12 mm in fruit..***C. bojeri***

– Inflorescence axis with indumentum comprising short papilliform hairs, short microglandular hairs and sparse long multicellular patent hairs; cincinni rachis elongating to 5–50 mm in fruit .... ***C. heterotrichus***

Group 6. Corolla blue, purple, mauve, pink or white, not yellow; inflorescence lax at least in lower half, the axis conspicuous between most of the cymes; if condensed, then only in upper half or globose, not a dense conical spike; flowers pedicellate; calyx with upper lobe narrowly triangular, ovate to obovate, often broader and differing in shape and size from lower four lobes, lobes not all subulate and spinescent; lower calyx lobes free, not fused into a lip; cymes of two flowers or more

1 Inflorescence of 1–2 globose very congested verticils; leaf blade 0.6–0.9 cm broad .... ***C. globosus***

– Inflorescence verticils more numerous, less congested; leaf blade (0.3–) 0.9–12 cm broad **2**

2 Upper lobe of calyx not very different in size and shape from the other lobes, all narrowly triangular-lanceolate, often curving upwards **3**

– Calyx upper lobe ovate, elliptic, obovate, oblong, very different in size and/or shape from the other four lobes **7**

3 Calyx with yellow sessile glands; sinus between lower calyx lobes deeper than sinus between the other lobes; corolla 3–9 mm long **4**

– Calyx with red sessile glands; sinus between the lower calyx lobes no deeper than the other sinuses; corolla 8–25 mm long **5**

4 Leaf petiolate; corolla 5–9 mm long .... ***C. succulentus***

– Leaf sessile; corolla 3–5 mm long .... ***C. cylindraceus***

5 Leaf blade broadly ovate to almost round, rounded at apex, succulent; calyx tube markedly curving upwards, with all lobes pointing upwards .... ***C. tetradenifolius***

– Leaf blade ovate-elliptic, acute at apex, not succulent; calyx tube almost straight or slightly curving, with lobes not all pointing upwards **6**

6 Calyx 8–11 mm long, at least 2× longer than the pedicel, with red glands; plant leafy at flowering; inflorescence with adjacent verticils almost touching .... ***C. mirabilis***

– Calyx 4–6 mm long, slightly exceeding pedicel, with pale glands; plant mostly leafless at flowering; inflorescence with adjacent verticils widely spaced .... ***C. defoliatus***

7 Fruiting calyx bearded inside throat, with nutlets obscured; calyx pointing downwards after anthesis; pedicel 3–7 mm long **8**

– Fruiting calyx glabrous to slightly pubescent inside throat, not bearded; calyx patent or downwardly pointing at fruiting; pedicel length variable... **9**

8 Corolla 5–7 mm long; calyx contracted at throat and gibbose ventrally; annual .... ***C. kivuensis***

– Corolla 8–22 mm long; calyx neither contracted nor gibbose; perennial .... ***C. barbatus***

9 Fruiting pedicel (5–)7–15 mm long, as long as or longer than calyx (consider the longest pedicels) **10**

– Fruiting pedicel 1–5(–6) mm long, shorter than or equalling calyx **16**

10 Plant with at least a few leaves at flowering **11**

– Plant wholly leafless at flowering **14**

11 Leaf blade 0.7–2.5 cm broad; petiole 0–0.6 cm long **12**
– Leaf blade 1–7 cm broad; petiole (0.3–)0.7–7 cm long **13**
12 Leaf axils with globose propagules; leaf blade narrowly elliptic, acute at apex; verticils 2–6-flowered .... ***C. kapatensis***
– Leaf axils lacking propagules; leaf blade elliptic to obovate, obtuse at apex; verticils 8–16-flowered .... ***C. decimus***
13 Calyx 4–5(–6) mm long, with red sessile glands; verticils (4)12–20-flowered .... ***C. alpinus***
– Calyx 6–7(–10) mm long, with yellow sessile glands; verticils 4–6(12)-flowered .... ***C. sylvestris***
14 Calyx tube strongly curving, with lobes pointing upwards; shrub > 1.2 m high .... ***C. penicillatus***
– Calyx tube straight to slightly curving, with lobes not all pointing upwards; herbaceous perennial < 1.2 m high **15**
15 Verticils 2–6-flowered; pedicel 6–10 mm long .... ***C. kapatensis***
– Verticils 10–16-flowered; pedicel 10–15 mm long .... ***C. buchananii***
16 Cymes pedunculate (at least lowermost ones); pedicel not inserted on inflorescence axis **17**
– Cymes sessile; pedicels generally inserted on nodes of main inflorescence axis or on a very short cyme rachis **21**
17 Calyx 8–11 mm long, with lobes subequal, all acute; leaves markedly discolorous .... ***C. mirabilis***
– Calyx 4–8.5 mm long, with upper lobe different in shape from the other four lobes, rounded to obtuse; leaf blade not discolorous **18**
18 Stem with stiff spinescent bristles; corolla 7–9 mm long .... ***C. seretii***
– Stem lacking stiff spinescent bristles; corolla 8–18 mm long **19**
19 Lower calyx lobes oblong, obtuse-rounded at tip; leaf margin irregularly sharply serrate .... ***C. thyrsoideus***
– Lower calyx lobes acute; leaf margin regularly serrate **20**
20 Corolla ca. 18 mm long; verticils ca. 10-flowered; leaf blade cordate at base .... ***C. frederici***
– Corolla 8–14 mm long; verticils 10–25-flowered; leaf blade obtuse to rounded at base .... ***C. tenuicaulis***
21 Upper half of inflorescence spike-like, with verticils touching; corolla 3–5 mm long; sinus between the lower middle calyx lobes markedly deeper than the other sinuses .... ***C. cylindraceus***
– Upper half of inflorescence not spike-like, with verticils not touching (except uppermost ones); corolla > 5 mm long; sinus between the lower middle calyx lobes no deeper than the other sinuses **22**
22 Pedicel 1–2 mm long; upper calyx lobe horizontal, cucullate, not decurrent, oblong, rounded to apiculate at apex; corolla 4–9 mm long; calyx with pale sessile glands .... ***C. amboinicus***
– Pedicel (1–)3–6(–9) mm long; upper lobe of calyx variable in shape, but never horizontal and cucullate; corolla 6–22 mm long; calyx with red sessile glands **23**

23 Plant almost leafless at flowering; calyx upright, with all lobes narrowly triangular, acute, the lateral lobes closer to the upper lobe, forming a 3+2 pattern; bracts strikingly large (5–25 mm long) and conspicuous near inflorescence apex at anthesis .... ***C. lactiflorus***

– Plant leafy at flowering; calyx patent to deflexed, with lateral lobes closer to the lower lobes, forming a 1+4 pattern; upper calyx lobe elliptic, generally curving upwards; bracts < 12 mm long **24**

24 Leaves in 2–4 pairs, grouped in lower third of shoot, almost forming a rosette; leaf blade rounded at apex.. ***C. ruziziensis***

– Leaves more numerous, more regularly spread along the shoot, not forming a rosette; leaf blade acute to rounded at apex **25**

25 Petiole 0–1(–2) cm long, < 20% of leaf blade length; stem often purple-spotted; fruiting calyx downwards pointing .... ***C. maculosus***

– Petiole 1–5 cm long, > 25% of leaf blade length; stem not spotted; fruiting calyx patent to deflexed **26**

26 Calyx (3–)6–7 mm long, often downwards pointing, villose, with hairs more or less purplish tinged; upper lobe of calyx 2–3 mm wide .... ***C. lanuginosus***

– Calyx 3–6 mm long, patent, pubescent, not villose, with white hairs; upper lobe of calyx 1–2 mm wide **27**

27 Leaf blade membranous; base of leaf blade broadly obtuse to rounded and then shortly decurrent on the petiole; apex of leaf blade generally acute; bracts 3–12 mm long; in dense forest and savannah on moist soil .... ***C. alpinus***

– Leaf blade succulent; base of leaf blade truncate to subcordate, not decurrent on petiole; apex of leaf blade obtuse to rounded; bracts 1–3 mm long; in savannah on dry soil .... ***C. hadiensis***

Annotated checklist and descriptions

In the following checklist, synonym citation is limited to: i) the names used in the Flore du Rwanda (Troupin and Ayobangira 1985) and the Flore du Parc national Albert (Robyns 1947), ii) names based on type materials collected in DR. Congo, Rwanda, Burundi, iii) new synonyms and iv) newly-lectotypified names; for a full account of synonymy in the genus *Coleus*, see Paton et al. (2019). For each taxon, specimens are cited according to the phytogeographic regions of Central Africa, as used in the Flore d'Afrique centrale. For the species of the *Coleus bojeri* complex, which were sunk into *C. bojeri* in earlier floras, the overall distribution in Africa has been explored and, when necessary, new country records are testified by one voucher specimen per country. When our taxonomic treatment departs from recent floras, a concise justification is provided.

Extensive descriptions are included only for: i) the new taxa, ii) the taxa not included in recent floras (Paton et al. 2009, 2013; Paton 2022) (*C. brazzavillensis*, *C. celsus*, *C. conglomeratus*, *C. frederici, C. globosus* and *C. tenuicaulis*), iii) the taxa in the *C. bojeri* complex, the circumscription of which is amended here. In the descriptions, the length of cincinni refers to the rachis of the cyme, excluding pedicels and flowers.

Coleus affinis **(Gürke) A.J.Paton, Phytokeys 129: 14. 2019.**

= *Pycnostachys speciosa* Gürke, in H.G.A.Engler, Pflanzenw. Ost-Afrikas, C: 345. 1895., non *Coleus speciosus* Baker f. Type: Kenya/Tanzania, east shore of Lake Victoria, *A.Fischer 499* (lectotype B designated by Bruce (1940), destroyed).

Type. Tanzania, Muansa [Mwanza], May 1892, *F.Stuhlmann 4693* (holotype B destroyed; isotype K [K000405978] fragment).

Description. Paton et al. (2009: 397), as *Pycnostachys speciosa* Gürke.

Distribution. Rwanda to E Tropical Africa.

Habitat and ecology. Savannah, ca. 1350 m elev. in Rwanda (1150 -1750 m elev. elsewhere).

Additional specimen. Rwanda, Akagera, environs du lac Ihema, Jun. 1960, *G.Bouxin & M.Radoux 1959* (BR).

Note. This species was not recorded in Rwanda by Troupin and Ayobangira (1985).

Coleus alpinus **Vatke, Linnaea 37: 322. 1872.**

≡ *Plectranthus alpinus* (Vatke) Ryding, Bot. Jahrb. Syst. 121: 147. 1999. Type: Ethiopia, Amara, Edda Jesus near Dawra Tabor [Debra Tabor], 25 Sep 1863, *G.W.Schimper s.n*. (lectotype BM [BM000513299], designated by Ryding (1999b); isolectotype JE, US, W).

= *Coleus assurgens* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 428. 1900.

≡ *Plectranthus assurgens* (Baker) J.K.Morton, J. Linn. Soc., Bot. 58: 267. 1962. Type: Ethiopia, Begemder, Aug 1863. *G.W.Schimper s.n*. (holotype K [K000431867]).

= *Coleus lebrunii* Robyns, Bull. Jard. Bot. État Bruxelles 17: 73. 1943. Type: DR. Congo, Ruwenzori, Butagu Valley, Nov 1931. *J.Lebrun 4579* (holotype BR [BR0000008910035], [BR0000006262631]; isotype K [K000431884]).

= *Coleus wittei* Robyns Bull. Jard. Bot. État Bruxelles 17: 74. 1943. Type: DR. Congo, Kamatembe, R. Bishkishaki, 16 Apr 1934. *G.F.de Witte 1551* (holotype BR [BR0000006262914], [BR0000006262631]).

Description. Paton et al. (2009: 296), Paton et al. (2013: 245), as *Plectranthus alpinus* (Vatke) Ryding.

Distribution. Nigeria to Ethiopia and south to Malawi.

Habitat and ecology. Savannah, river banks, marshland, mountain forest, *Erica* shrubland, fallow fields, 1300–2700 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Ruwenzori, Lamia, 14 May 1914, *J.Bequaert 4262* (BR); Ruwenzori, 20 Dec 1949, *de Wilde 439* (BR); Masisi, Bohenda, 7 May 1957, *R.Gutzwiller 904* (BR); Kabare, Birava, 20 Aug 1959, *Meurillon 791*; Lwiro, marais Lushala, 14 Jun 1958, *G.Troupin 7495* (BR); Nyamuragira, N-hang, 21 Aug 1954, *H.U.Stauffer 106* (BR).

Rwanda, Entre Mutura et Kanama, 14 Jun 1984, *J.Lejoly 84/353* (BRLU); Préfecture Gisenyi, route Muramba-Rutsiro, Ramba, 14 Jun 1974, *C.Nuyt 292*

(BR); Gisovu, 15 Jun 1978, *J.Raynal 20580* (BR); Rangiro, Kirambo, 4 Jun 1981, *G.Troupin 16268* (BR); R. Mukungwa, waterfalls near Rwaza, 23 Feb 1972, *P.Van der Veken 9510* (BR).

Burundi, Nkaka, 1 Mar 2003, *E.Bizuru 728* (BRLU).

Note. New species record for Burundi.

Coleus amboinicus Lour., Fl. Cochinch.: 372. 1790.

≡ *Plectranthus amboinicus* (Lour.) Spreng., Syst. Veg. 2: 690. 1825. Type: Rumphius plate in Herb. Amb. 5, t. 102/2. 1750 (lectotype designated by Cramer [1978]); Thailand, Pai District, Mae Hong Son, 25 May 1921. *F.Kerr s.n*. (epitype BM, designated by Suddee et al. [2004]).

= *Coleus amboinicus* var. *violaceus* Gürke, Bot. Jahrb. Syst. 19: 210. 1894. Type: Tanzania, Moshi District, Dschallasee [Lake Chala], Jun 1893, *G.Volkens 321* (syntype B destroyed; isosyntype BM, K [K000431981]), & Pangani River, Jul 1893, *G.Volkens 487* (syntype B destroyed; isosyntype BM, K).

Description. Paton et al. (2009: 320), Paton et al. (2013: 262), as *Plectranthus amboinicus* (Lour.) Spreng.

Distribution. Kenya to South Africa, Arabian Peninsula, India.

Habitat and ecology. Steppe, ca. 925 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Kabare, bords du Lac Kivu, Sep 1914, *J.Bequaert 5522* (BR).

Note. Apparently, a rare species in Central Africa, known from a single collection. Other collections previously reported to this species were errors.

Coleus articulatus (I.M.Johnst.) A.J.Paton, Phytokeys 129: 21. 2019.

≡ *Symphostemon articulatus* I.M.Johnst., Contr. Gray Herb., n.s., 73: 38. 1924. Type: Angola, east of Cuanza [Coanza] R., 23 Sep 1923, *A.G.Curtis* 309 (holotype GH [GH00002146]).

= *Plectranthus hockii* De Wild., Repert. Spec. Nov. Regni Veg. 11: 542. 1913. Type: DR. Congo, Plateau de Shinkwari (Manika), 1911, *A.Hock s.n.* (lectotype BR [BR0000006263287], designated here).

Description. Paton et al. (2009: 285), Paton et al. (2013: 233), as *Plectranthus hockii* De Wild.

Distribution. SW Tanzania, DR. Congo, Malawi, Zambia, Angola.

Habitat and ecology. Savannah and steppic savannah, often in highlands and in frequently burnt places, miombo woodlands, occasionally on copper rich soil, 1480–1810 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kansenia, 13 Aug 1933, *H.Lynes s.n*. (BR); Upemba, entre Mabwe et Mukana, 1 Oct 1948, *G.F.de Witte 4402* (BR); Upemba, env. Mukana, 1949, *G.F.de Witte 7025* (BR); Env. Lubudi, 1937, *D.Cabu 49* (BR, WAG); Upemba, entre Masombwe et Lusinga, 20 Sep 1948, *W.Robyns 3638* (BR); Env. Fungurume, Kwatebala, 22 Oct 2006, *E.Kisimba*, *L.Saad & F.Malaisse 50* (BR); Entre Nzilo et Kansenia, 6 Sep 1956, *P.Duvigneaud & J.Timperman 2626* (BRLU).

Note. Lectotypification of *Plectranthus hockii* De Wild. De Wildeman (1913b) cited two syntypes, i.e. *A.Hock s.n.* (syntype BR [BR0000008109453]; isosyntype K), DR. Congo, Haut-Katanga, bords de la Dilemba, 1911 & *A.Hock s.n.* (syntype BR [BR0000006263287]), Plateau de Shinkwari (Manika), 1911. The specimen [BR0000008109453] departs somewhat from the protologue in having the pedicel glabrous under the joint (protologue: “breviter tomentoso”), while [BR0000006263287] is slightly puberulous below the joint; moreover, [BR0000006263287] has a thick woody rootstock, quite typical of the species; it is selected as the lectotype.

Coleus autranii **Briq., Bull. Herb. Boissier 2: 129. 1894.**

≡ *Calchas autranii* (Briq.) P.V.Heath, Calyx 5: 160. 1996.
≡ *Solenostemon autranii* (Briq.) J.K.Morton, Novon 8: 266. 1998.
≡ *Plectranthus autranii* (Briq.) Erhardt, Götz & Seybold, Grosse Zander 2: 1825. 2008. Type: Ethiopia, 6 Sep 1952, *G.W.Schimper 693* (holotype G [G00435189]; isotype K, P [P00450781], [P00450782], [P00450783]).
= *Coleus silvaticus* Gürke, Bot. Jahrb. Syst. 19: 219. 1894.
≡ *Solenostemon silvaticus* (Gürke) Agnew, Upland Kenya Wild Fl.: 640. 1974. Type: Tanzania, W Usambara Mts, Shagai Forest, near Sunga, *R.B.Drummond & J.H.Hemsley 2593* (neotype K, designated by Paton et al. [2009]).

Description. Paton et al. (2009: 326), Paton et al. (2013: 265), as *Plectranthus autranii* (Briq.) A.J.Paton.

Distribution. Ethiopia, Central Africa, East Africa to South Africa.

Habitat and ecology. Mountain forests, clearings with *Hagenia*, scrub, *Senecio-Philippia* vegetation, riparian forest, 1000–3200 m elev.

Additional specimens. DR. Congo, ***Forestier central***: Route Baudouinville [Moba] à Katele (?), Sep 1922, *S.de Giorgi 67* (BR). ***Lacs Edouard et Kivu***, Karisimbi, versant sud, riv. Bikuri, 27 Feb 1935, *G.F.de Witte 2265* (BR); Entre Kasindi et Lubango, W du Lac Edouard, Jan 1932, *J.Lebrun 4737* (BR); Wimbi, 26 km S Lubero, 22 Jul 1937, *J.Louis 4658* (BR). ***Haut-Katanga***, Upemba, 16 Apr 1949, *G.F.de Witte 6141* (BR); Marungu, Mashini, 28 Jun 1957, *P.Duvigneaud 3750Co* (BRLU).

Rwanda, Kareba, versant sud du Karisimbi, 10 Oct 1974, *P.Auquier 4513* (BR); Dorwa, Dec 1932, *A.Becquet 194*; Route Pindura-Ibigugu, km 88, 9 Jan 1980, *D.Bridson 158* (BR, K, WAG); Route Astrida [Butare]-Shangugu, km 71, crête Congo-Nil, 9 Sep 1959, *M.Reynders 403* (BR); Forêt de Nyungwe, env. Uwinka, 26 May 1981, *G.Troupin 16256* (BR, WAG).

Burundi, Bukeye, Mt Teza, 19 Jun 1971, *J.Lewalle 6007* (BR); Bubanza, Mugomero, 12 Jun 1981, *M.Reekmans* 10601 (BR, WAG).

Coleus barbatus (Andrews) Benth. ex G.Don in J.C.Loudon, Hort. Brit.: 483. 1830.

≡ *Plectranthus barbatus* Andrews, Bot. Repos. 10: t. 594. 1810. Type: Illustration of cultivated material in Bot. Rep. 9, t. 594. 1809 (lectotype); ERITREA, Dekemehare, 5 Sep 1954, *J.W.Colville 47* (epitype K [K000431890], designated by Ryding [1999a]).

Key to the varieties of *Coleus barbatus*

1 Trailing, ascending or erect perennial, < 0.6(–1.5) m high; leaf blade elliptic, 0.9–7 × 0.3–3 cm, cuneate at base................ **_C. barbatus_ var. _barbatus_**

– Shrub up to 4.5 m high; leaf blade ovate, 1.5–20 × 0.8–11 cm, base rounded to subcordate .... **_C. barbatus_ var. _grandis_**

Coleus barbatus var. *barbatus*

Description. Paton et al. (2009: 338), as *Plectranthus barbatus* Andrews var. *barbatus*.

Distribution. Eritrea to N Tanzania and E DR. Congo, Arabian Peninsula, Indian Subcontinent to SC China.

Habitat and ecology. Savannah, 1000–1400 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Rutshuru, haute vallée de la Fuku, Dec 1937, *J.Lebrun 9133* (BR).

Rwanda, Mohasi-See [Lac Mohazi], Aug 1907, *J.Mildbraed 671* (B destroyed); territ. Miumba, Mutara, near Mimuli, *G.Troupin 2781* (BR).

Notes. 1. New record to DR. Congo.

2. The type variety is apparently rare in Central Africa.

Coleus barbatus var. *grandis* (L.H.Cramer) A.J.Paton, Phytokeys 129: 24. 2019.

≡ *Coleus grandis* L.H.Cramer, Kew Bull. 32: 556. 1978.

≡ *Plectranthus barbatus* var. *grandis* (L.H.Cramer) Lukhoba & A.J.Paton, Kew Bull. 58: 915. 2003. publ. 2004. Type: Sri Lanka, Sita Eleiya. 3 Oct 1972, *L.H.Cramer 3869* (holotype PDA; isotype K [K000820136], US).

= *Coleus kilimandschari* Gürke, Abh. Königl. Akad. Wiss. Berlin 1891: 359. 1892.

≡ *Plectranthus kilimandschari* (Gürke) H.I.Maass in R.Mansfeld, Verz. Landwirtsch. Gärtn. Kulturpfl. 3: 1136. 1986. Type: Tanzania, Kilimanjaro, Marangu, Jun 1893, *G.Volkens 427* (neotype K [K000975992] designated by Paton et al. [2009]; isoneotype G [G00435190]).

= *Plectranthus neochilus* sensu Troupin & Ayobangira, Fl. Rwanda 3: 339. 1985. non (Schltr.) Codd.

Description. Paton et al. (2009: 339), Paton et al. (2013: 273), as *Plectranthus barbatus* var. *grandis* (L.H.Cramer) Lukhoba & A.J.Paton.

Distribution. NE & E Tropical Africa to DR. Congo.

Habitat and ecology. Savannah, rock outcrops, fallow fields, often planted in villages for hedgerows, 800–2250 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Mont Aboro (Djugu), 26 Feb 1958, *D.Froment 348* (BR); Mt Ota, NE of Gote (Mahagi), 12 Jul 1945, *R.Germain 3975* (BR); ***Lacs Edouard et Kivu***, Beni, 7 Apr 1914, *J.Bequaert 3447* (BR); Masisi, Bugobe, 18 Jan 1957, *R.Gutzwiller 702* (BR, WAG); Mulungu, 20 Sep 1940, *F.L.Hendrickx 1393* (BR); Entre Walikale et Kalihe, May 1932, *J.Lebrun 5349* (BR).

Rwanda, Kigali, Buliza, Nov 1932, *A.Becquet 222* (BR); Butare, Muhura, 17 May 1972, *L.Van Puyvelde & A.Kayonga 4* (BR); Rubona, 17 Apr 1958, *G.Michel 5283* (BR); Route Usa-Astrida [Butare], km 72.5, 11 Feb 1960, *F.L.Hendrickx 7776* (BR, BRLU, LSHI). BURUNDI, Bukeye, Mt Teza, 26 Jun 1969, *J.Lewalle 3839* (BR); *M.Reekmans 3060* (BR); Ngozi, Remera, 26 Feb 1976, *M.Reekmans 4808* (BR); Irubura, 31 May 1926, *W.Robyns 2394* (BR).

Coleus batesii (Baker) A.J.Paton, Phytokeys 129: 25. 2019.

≡ *Pycnostachys batesii* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 386. 1900. Type: Cameroon, Efulen, 11 Sep 1885, *G.L.Bates 372* (holotype K [K000405951]; isotype BM [BM000884040]).

Description. Paton et al. (2009: 406), as *Pycnostachys batesii* Baker.

Distribution. Cameroon to SW Uganda and DR. Congo.

Habitat and ecology. Rainforest, riparian forest, 750–1300 m elev.

Additional specimens. DR. Congo, ***Forestier Central***, Riv. Mangbana, afffl. Djuma-Semliki, 14 Mar 1955, *G.F.de Witte 12002* (BR); Confluent Mamudjoma-Djuma, 7 Mar 1955, *G.F.de Witte 12042* (BR, K); Urega (Maniema), Jun 1932, *J.Lebrun 5604* (BR, K); Ituri, between Lodjo and Ituri River crossing, 27 Jan 2011, *B.Bytebier et al. 3403* (BR, EA, EPU, K); ***Lac Albert***, Ituri, Mont Hoyo, route forestière vers le poste de Hoyo, 2 Aug 1975, *S.Lisowski 40875* (POZG).

Coleus betonicifolius (Baker) A.J.Paton, Phytokeys 129: 26. 2019.

≡ *Plectranthus betonicifolius* Baker, Bull. Misc. Inform. Kew 1895: 72. 1895. Type: Zambia, Fwambo, *A.Carson 79* (lectotype K [K000431993], designated by Pollard and Paton [2009]).

Description. Paton et al. (2009: 307) as *Plectranthus betonicifolius* Baker.

Note. *C. betonicifolius* is variable in leaf shape; variation is clearly bimodal; varietal rank is proposed here.

Key to the varieties of *Coleus betonicifolius*

1 Leaf blade ovate, abruptly contracted at base .... ***C. betonicifolius* var. *betonicifolius***

– Leaf blade narrowly elliptic to almost linear, progressively attenuated at base... ***C. betonicifolius* var. *kasomenensis***

Coleus betonicifolius **(Baker) A.J.Paton var.** ***betonicifolius***

Description. Paton et al. (2009: 307), Paton et al. (2013: 252), as *Plectranthus betonicifolius* Baker, restricted to specimens with leaf blade ovate, 1–3 cm wide, abruptly contracted into the petiole.

Distribution. Tanzania, DR. Congo, Zambia, Malawi and Angola.

Habitat and ecology. Steppic savannah, on seasonally flooded soil (dilungu and dambo), often on highlands, from 1100 to 1880 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Upemba, vallée de la Musibari (?), 25 Apr 1959, *J.de Wilde 738* (BR); Upemba, Mukana, 14 Apr 1947, *G.F.de Witte 2494* (BR, WAG); Upemba, tête de source de la Mubale, 16 Jan 1948, *G.F.de Witte 3247* (BR); Muhila, riv. Mutungulu, 16 May 1971, *F.Malaisse 1355* (BR); N'konda, piste Nasondoye-Kasofu, 4 Jan 1983, *M.Schaijes 1774* (BR).

Burundi, Mosso Urundi, Butetsi (?), 9 May 1952, *G.Michel & J.Reed 1905* (BR).

Coleus betonicifolius **(Baker) A.J.Paton var.** ***kasomenensis*** **(De Wild.) Meerts & A.J.Paton, comb. et stat. nov.**

urn:lsid:ipni.org:names:77347688-1

Coleus kasomenensis (in protologue as *"kasonememsis"*) De Wild., in Rep. Spec. Nov. Reg. Veg. 11: 515. 1913. Type: DR. Congo, Elisabethville [Lubumbashi], Mar. 1912, *H.Homblé 246* (in protologue "*206*") (lectotype BR [BR0000006258283], designated here). (Basionym)

= *Coleus hockii* De Wild., Repert. Spec. Nov. Regni Veg. 11: 514. 1913. Type: DR. Congo, Haut-Katanga, vallée de la petite Luembe, lieux humides, Feb1910, *A.Hock s.n.* (holotype BR [BR0000008907790]), syn. nov.

= *Coleus baumii* Gürke, in O. Warburg (ed.), Kunene-Sambesi Exped.: 357. 1903. Type: Angola, Cuito, 14 Dec 1899, *H.Baum 544* (holotype B destroyed; isotype BM [BM000910139], E, G [G00435191], HBG [HBG518672], K [K000431990], M [M0104724], S [S-G-1537], W [W1901-0006713]), syn. nov.

= *?Leocus lyratus* A.Chev., J. Bot. (Morot) 22: 126. 1909. Type: Guinea, Fouta-Djalon, Mt. Tinka, near Dalaba. Sep-Oct 1907, *A.Chevalier 18824* (holotype P [P00541249], syn. nov.

Description. Differs from the type variety by the leaf blade narrowly elliptic to almost linear (< 1 cm wide), progressively attenuate at base (vs. ovate, abruptly contracted at base).

Distribution. DR. Congo, Angola, Zambia.

Habitat and ecology. Savannah, on seasonally flooded soil, marshland, often on sand, ca. 1050–1300 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kapanga, 1933, *F.Overlaet 915* (BR); ***Bas-Katanga***, Route Kaniama-Kamina, 85 km from Kamina, 21 Dec 1957, *J.Brynaert 670* (BR); Kelambwe, 8 Dec 1948, *G.Kevers 228* (BR); ***Haut-Katanga***, Dilolo, dilungu de la Mangoa, 1 May 1959, *S.Risopoulos 1032* (BR); Kasumbalesa, 26 Mar 1951, *A.Schmitz 3509* (BR); Kipopo, 13 Mar 1960, *A.Schmitz 6890* (BR).

Angola, **Lunda Norte**, S of River Luovwa [Lovua?], 18 Jan 1938, *E.Milne-Redhead 4205* (BR, K); **Bié**, Serpa Pinto, 26 Apr 1906, *J.Gossweiler 2679* (COI).

Zambia, District Chingola, 19 Apr 1954, *D.B.Fanshawe 1128* (K); Kawambwa District, Kalungweshi River, 26 Apr 1957, *H.M.Richards 9446* (K).

Notes. 1. *Coleus hockii* De Wild. was wrongly interpreted as a synonym of *Coleus buchananii* (Baker) Brenan by Paton et al. (2019), due to confusion with *A.Hock s.n.* (BR [BR0000008109613]), which is the type specimen of *C. kisanfuensis* De Wild. (= *Coleus buchananii* (Baker) Brenan). The protologue and the original materials of *Coleus hockii* De Wild. clearly refer to *C. betonicifolius*. See also note under *C. buchananii*.

2. The spelling of the epithet in the protologue is "*kasonememsis*", obviously a typo; the locality cited in the protologue is "Kasomenia" and on the specimen label "Kasonema". The current name of the locality is Kasomeno (10°45'S, 28°16'E); therefore, we correct the epithet to "*kasomenensis*" following Art. 60.1. and Rec. 60D.1. of the ICN.

3. Lectotypification of *Coleus kasomenensis*. De Wildeman (1913a) cited four syntypes: *T.Kassner 2555* (syntype BR; isosyntype E, K), DR. Congo, Haut-Katanga, Kasomenia (in protologue; Kasonema on specimen label) [Kasomeno], 10 Mar 1908, & *H.Homblé 246* (in protologue "*206*") (syntype BR [BR0000006258283] & [BR0000006258917]), Elisabethville [Lubumbashi], Mar 1912, & *J.Bequaert 382* (syntype BR [BR0000009824553] with a collecting label, [BR0000009824577] without a collecting label), Welgelegen, 2 May 1912 and *J.Bequaert 564* (syntype BR [BR0000009824553]), Welgelegen, dembo, 2 May 1912. All these specimens match the protologue; *H.Homblé 246* [BR0000006258283] is selected as the lectotype because it is the only specimen with De Wildeman's handwriting on the label.

4. Material of *C. betonicifolius* from Guinea and Sierra Leone is similar to the type of *Leocus lyratus* A.Chev. and resembles var. *kasomenensis*, but the leaves are much larger than material from the remainder of the distribution (Pollard and Paton 2009); further work is needed.

Coleus bojeri Benth., Labiat. Gen. Spec.: 52. 1832.

Figs 1A, B, 2B

= ?*Coleus dewevrei* Briq., Bull. Soc. Roy. Bot. Belgique 37: 71. 1899. Type: DR. Congo, s.l., s.d. (see note), *A.Dewèvre 1092A* (holotype BR [BR0000006262211], [BR0000006262525]).

Type. Madagascar, Emirna, Betani-Mena, *W.Bojer s.n.* (lectotype P [P00541359], designated by Hedge et al. (1998); isolectotype W [W0002279]).

Description. Annual herb, 0.3–0.9(–1.2) m high, more or less aromatic; rootstock fibrose, without tubers. Stem erect or, rarely, ascending, quadrangular, branched, indumentum mostly of retrorse and patent eglandular hairs, in the inflorescence only of retrorse, appressed hairs, without glandular hairs or long patent hairs. Leaves opposite, spreading, petiolate, occasionally with small leaves in the axils; petiole (0.5–)1.0–4.0 cm long, ciliate, more or less flat and narrowly winged in the upper half; blade ovate-triangular to narrowly ovate, 1.5–4.5(–7.5) × 1.0–4.0(–6.2) cm, base broadly cuneate, then shortly attenuate into the petiole, rarely subcordate, apex rounded to obtuse or subacute, ca. 4–5 pairs of secondary veins, occasionally impressed on upper surface, sparsely

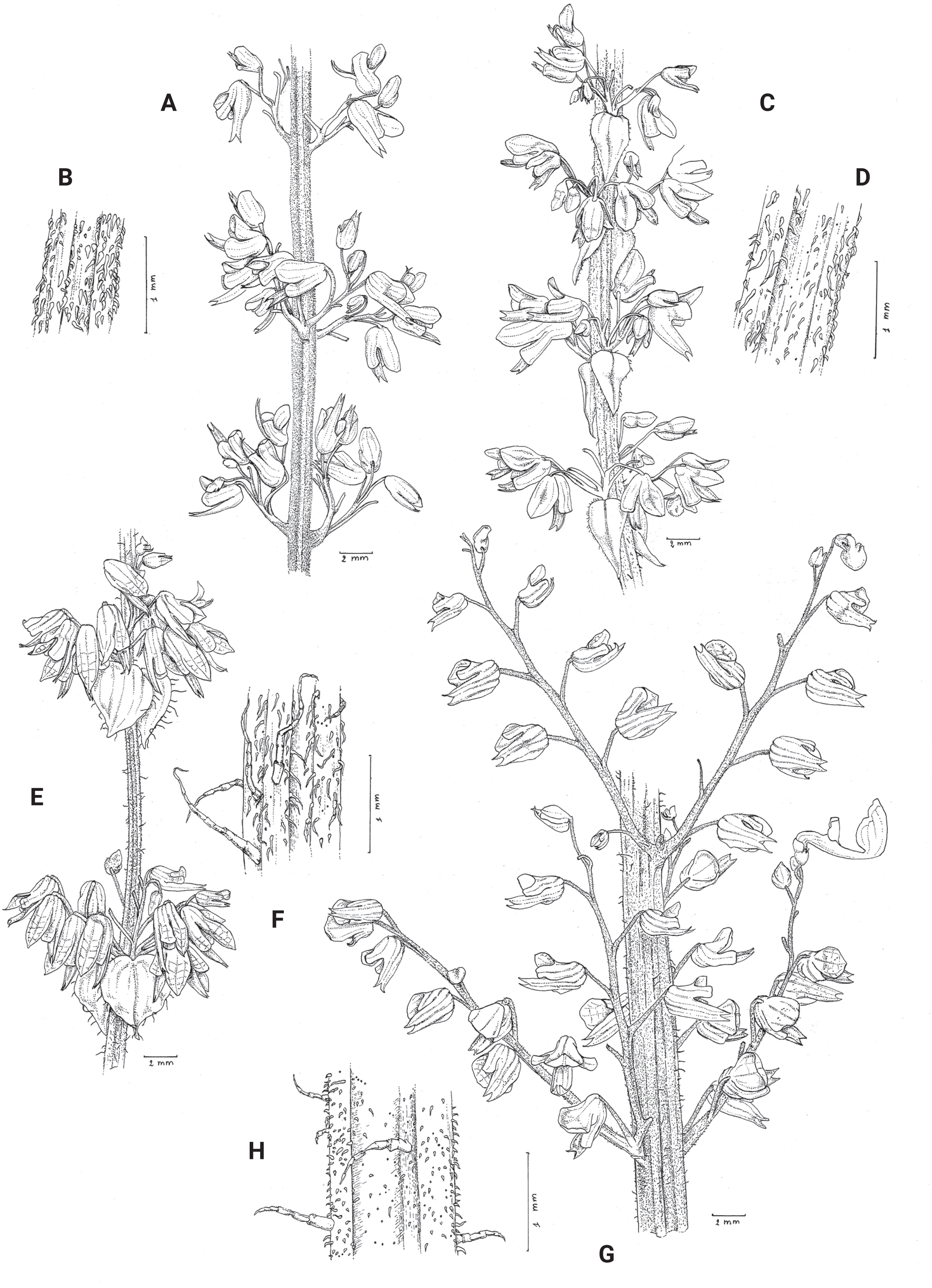

Figure 1. *Coleus bojeri* complex, details of inflorescence architecture and stem pubescence in four species **A, B** *Coleus bojeri* Benth. (*T.Sperry 179*) **C, D** *Coleus chevalieri* Briq. (*P.Gérard 4297*) **E, F** *Coleus collinus* Robyns & Lebrun (*J.Lebrun 9041*) **G, H** *Coleus heterotrichus* Briq. (*M.Micha 300*). Drawn by Hilde Orye.Scale bars: 1 mm (**B, D, F, H**); 2 mm (**A, C, E, G**).

pilose to shortly pubescent on the upper surface, pubescent on veins on the lower surface (either spreading pilose or with antrorse appressed hairs), margin crenate or rarely undulate and subentire. Inflorescence terminal, lax, (4–)12–42 × 1.2–2.5 cm in fruit, with 9–30 verticils spaced 5–25(–30) mm, cymes sessile, ascending, ca. (7–)9–25-flowered, cincinni ca. 1–2 mm long at anthesis, elongating in fruit to 1–7(–12) mm, pedicels 1–3(–4) mm long, inserted eccentrically in front of calyx upper lobe, curved at tip, bracts ovate, 2–4 mm long, acute to acuminate, cucullate, forming an inconspicuous coma, early caducous. Flower: calyx shortly pubescent, with red sessile glands, 1.5 mm long at anthesis, 3–5 mm long in fruit, tube shortly cylindrical, truncate, slightly constricted at throat, upper lip often purplish tinged, ovate to obovate, curved upwards, obtuse to rounded, occasionally subacute, apiculate, 1.5–2 mm long, lateral lobes of lower lip truncate, ca. 1 mm, middle lobes of lower lip fused in a linear bidentate lobe 2–3 mm long. Corolla blue or violet, rarely white, with red sessile glands, 8–9 mm long, tube 3–4 mm, sigmoid, lower lip 4–6 mm long, 1.5–2.5 mm deep, enclosing stamens and style, stamens fused, style bifid. Nutlets globose, brown, red speckled, 0.8–1 mm.

Distribution. Senegal, Mali, Sierra Leone, Ivory Coast, Ghana, Togo, Benin, Nigeria, Cameroon, Congo, Gabon, Sudan, South Sudan, Ethiopia, Uganda, Kenya, Tanzania, Mozambique, Malawi, Zambia, Zimbabwe, Angola, Madagascar.

Habitat and ecology. Rainforest, dry woodland, savannah, fallow fields, rock outcrops, occasionally an epiphyte, 370–1900 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, 15 km N Kisantu, 5 Apr 1944, *R.Germain 2043* (BR); **Kasaï**, Bilala, 22 Feb 1937, *J.Gillardin 210* (BR); Route Kindu-Katako Kombe (km 64), 14 Apr 1959, *P.Bamps 475* (BR); ***Bas-Katanga***, Lofu, 26 Mar 1947, *L.Van Meel 1283* (BR); ***Forestier Central***, Namoya, near Shapandi, 15 Apr 2008, *B.Bytebier & W.R.Q.Luke 2965* (BR); Secteur Bangengele, Lomami, 3.9 km NNE Katopa, 6 Apr 2015, *R.Gereau et al. 7407* (BR, MO); ***Ubangi-Uele***, Dendu, Sep 1921, *J.Claessens 1708* (BR); Bambesa, 31 Oct 1956, *P.Gérard 2392* (BR); ***Lac Albert***, Nioka, 1934, *F.Jurion in J.Claessens 215* (BR); Kasengi, Oct 1931, *J.Lebrun 4100* (BR); ***Lacs Edouard et Kivu***, Riv. Kahekavitiri, affl. de rive droite de la Mukandwe, près de Mutsora, 12 Jun 1954, *G.F.de Witte 10529* (BR); Ruwenzori, entre Mutwanga et le gîte Kalonge, 28 Dec 1977, *J.Lejoly 2233* (BR); ***Haut-Katanga***, Env. Elisabethville [Lubumbashi], 1923, *S.de Giorgi s.n.* (BR); Kumanua, 4 Feb 1976, *F.Malaisse 8963* (BR); Marungu, ravin de Kafwampa, May 1945, *P.J.J.Vanden Brande 279* (BR).

Rwanda, Lac Kivu, route Nyamasheke-Kibuye, km 19, 29 Mar 1972, *G.Bouxin & M.Radoux 1526* (BR).

Burundi, Mosso, 7 Jun 1952, *G.Michel 2584* (BR); Bururi, Resha, 26 May 1981, *M.Reekmans 10379* (BR, MO, US).

Senegal, Massif de Kita, 7 Oct 1943, *P.Jaeger 32* (K).

Mali, Kayes Region, Kenieba Cercle, Falea Rockgate Mine, 24 Oct 2012, *W.R.Q. Luke & Sanogo 15850* (EA, K, IER).

Sierra Leone, West of Kambia N.P. 3 Nov 1963, *J.K.Morton SL74* (SL, GC, FHI, K, WAG).

Ivory Coast, Northern part of Bouna Reserve, Téhini, about 40 km E of Ouangofétini, 24 Aug 1963, *W.J.J.O.de Wilde 752a* (K, WAG).

Ghana, Gambaga Scarp, grown from seed at Legon, 3 Apr 1961, *J.K.Morton s.n.* (GC, K).

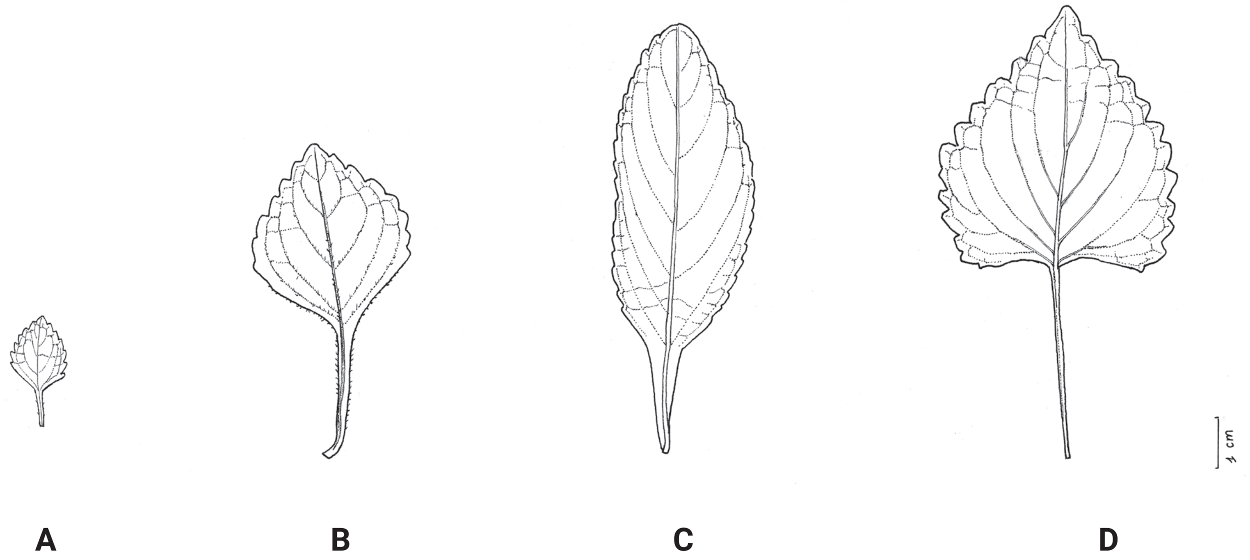

Figure 2. *Coleus bojeri* complex, leaf shape in four species **A** *Coleus collinus (J.Lewalle 1936)* **B** *Coleus bojeri (T.Sperry 179)* **C** *Coleus chevalieri (P.Gérard 4297)* **D** *Coleus heterotrichus* (*P.Quarré 3159*). Drawn by Hilde Orye. Scale bar: 1 cm.

Togo, 15 km S of Dapaon, 10°44'N, 0°12'E, 11 Oct 1977, *Ern et al. 1546* (B, K). Benin, Borgou, Tchaourou, Ouari-Maro, 9°00'N, 2°15'E, 24 Aug 1999, *B.Sinsin 2900* (K, WAG). Nigeria, NE State, Mambilla Plateau, 27 May 1972, *J.D.Chapman* 2835 (FHI, K). Cameroon, Balowa, Balikambat, 13 Sep 1960, *S.Gillett 2* (K).

Congo (Brazzaville), Lekoumou Préfecture, Zanaga Project, near Yakatopema/MPD Congo SA camp. 2°46'40"S, 13°35'52"E, 4 Oct 2009, *M.Cheek 15095* (IEC, K).

Gabon, Haut-Ogooué, Plateaux Batéké National Park, Mpassa River Drainage, Harunga forest, 2°12'36"S,14°01'56"E, 2 Mar 2003, *G.Walters & R.Niangadouma 1194* (K, MO).

Sudan, Jebel Marra, Colol, 23 May, 1968, *A.A.Kamil 1088* (K).

South Sudan [Bongo Land], Oct 1877, *G.Schweinfurth 2490* (K; type of *Plectranthus bongensis* Baker). Ethiopia, Joje, 10 km S of middle Abay Bridge, 10°12.70'N, 36°59.29'E, 11 Oct 2010, *I.Friis, W. Abebe, E.Getachew 13412* (AAU, K).

Uganda, Ajai Wildlife Reserve, 10 Dec 2001, *J. Kalema JK 1094*, (K).

Kenya, 4 km from Webuye on road to Kitale, 0°38'N, 34°46'E, 10 Oct 1981, *M.G.Gilbert & M.Tadessa 6583* (EA, K).

Tanzania, Kagera, Bukoba Rural District, Minziro Forest Reserve, Nyokabanga, kaiyamba Hill, 01°02'20"S, 31°32'04"E, 18 May 2001, *L.Festo, W, Bayona, & W.Wibard 1485* (K, MO).

Mozambique, Sussundenga Distr., E slopes of Chimanimani Mts, West of Dombe, Mevumosi River Valley, streamside, 27 Apr 1974, *G.Pope & T.Müller 1330* (K).

Malawi, Rumphi Distr., Rukuru Bridge, junction to Rumphi to Livingstonia, 29 Apr 1971, *Pawek 4756* (K, MAL).

Zambia, Chingola, 5 Aug 1955, *D.B.Fanshawe 2411* (K, NDO).

Zimbabwe, Mrewa, Shawanae River, 23 Apr 1956, *H.Wild 4806* (K, SRGH).

Angola, Lunda Norte, near Kasamba Village ca.59 km NNW of Capaia on road to Carumbo, 7°50'15"S, 20°01'46"E, 4 Apr 2013 *D.J.Goyder & I.Darbyshire 7209* (K).

Madagascar, N of Ankazobe, Mar 1930, *M.R.Decary 7364* (K, P).

Notes. 1. *C. bojeri* is defined here in a narrower sense compared to recent floras (Paton et al. 2009, 2013, 2022), excluding *C. chevalieri*, *C. collinus* and *C. heterotrichus*. It is restricted to specimens without persistent bracts (or rarely persistent at the two lowermost nodes), with short cincinni and stem indumentum mostly of retrorse hairs, without long patent hairs in the inflorescence.

2. *C. bojeri* is a polymorphic taxon possibly still in need of further splitting. One of the most distinctive morphs was named *Coleus platostomoides* Robyns and Lebrun (1928) 362. (Type: *W.Robyns 2482* (holotype BR; isotype P), DR. Congo, Lac Kivu, baie de Sake, plaine de lave de Kateruzi, 10 Jun 1926). It differs in the shoot much branched from base, the longer cincinni (rachis up to 12 mm long in fruit) with closely spaced pedicels (ca. 15 flowers/cincinni) distichously arranged in a fish-bone pattern at fruiting; it has a distinctive ecogeographic distribution, restricted to volcanic lava in Kivu (e.g. Parc National Albert [Rumoka], 21 Apr 1945, *R.Germain 3785* & 3786 (BR, L); Territ. Beni, Kusolu, Oct 1938, *P.Gille 129* (BR); Beni, 31 Jul 1914, *J.Bequaert 5140* (BR); Parc National Albert [Virunga], Kahodju, Aug 1937, *J.Lebrun 6925* (BR, P); Entre le volcan Rumoka et la baie de Sake, Aug 1937, *J.Louis 4861* (BR, P); Plaine de lave près de Ngoma [Goma], Apr-May 1929, *H.Humbert 7901* (P). However, specimens showing one or several of these traits are occasionally found elsewhere (e.g. Kasaï, Territ. Dibaya, riv. Mwanzangoma, 9 Jan 1957, *L.Liben 2220* (BR); Uganda, *A.D.Poulsen, G.Eilu & D. Hafashimana 1260* [C, K, MHU]) and intermediates with typical *C. bojeri* are not rare in Kivu. Evidence from molecular markers is needed to further resolve the taxonomy of this difficult group.

3. The specimen *A.Léonard 2040* (Mikwati, territ. Walikale, 16 Dec 1958 [BR]), a subglabrous plant with very small (ca. 10 × 5 mm), acute leaves and a long calyx (6 mm in fruit), is probably a different taxon, but more materials are needed.

4. The specimen *Yona Mleci 19* (BRLU), collected on termite mounds in miombo woodland near Lubumbashi, has roots with numerous clavate tubers; it approaches *Coleus botryosus*, differing in the caducous bracts; it could be a different taxon, but more materials are needed.

5. In Burundi, a few specimens are more or less intermediate between *C. bojeri* and *C. homblei* (e.g. Bururi, Lac Nyanza, route de Makamba, 19 Mar 1967, *J.Lewalle 1698* [BR]) and between *C. bojeri* and *C. collinus* (e.g. Munvugo, 3 km N Nyanza, 16 Apr 1978, *M.Reekmans 6920* (BR, LG).

6. The type specimen of *Coleus dewevrei* De Wild. is possibly a perennial plant, more or less intermediate between *C. bojeri* and *C. welwitschii* or *C. brazzavillensis*.

7. See observations under *C. homblei*.

Coleus brazzavillensis **A.Chev., Veg. Ut. Afr. Trop. Franç. 1: 124. 1905.**

Type. Republic Of Congo (Brazzaville), 1904, *A.Chevalier 11154* (holotype P [P00450785]).

Description. Perennial herb 0.30–0.75 m high, not reported to be aromatic, with a thin creeping rhizome, tubers not collected in DR. Congo (present in Rep. Congo). Stem ascending, rooting at lower nodes, simple or more rarely sparingly branched, quadrangular, more or less villous, with long patent flexuous hairs up to 2 mm long, these occasionally sparse or restricted to nodes and short retrorse hairs, in the inflorescence with shorter patent or antrorse hairs (0.5 mm), intermingled with sparse much longer hairs and also with red sessile glands. Leaves opposite, petiolate, ascending to spreading, occasionally with smaller leaves in the axils; petiole 0.5–2.5 cm long, with flexuous patent hairs 2–3 mm long, these sometimes sparse, and short retrorse hairs, narrowly winged in upper half, blade ovate to ovate-elliptic, 1.5–8 × 1–3 cm, apex obtuse to acute, base cuneate and shortly attenuate, ca. 5 pairs of secondary veins, margin crenate, narrowly recurved, both surfaces pubescent with long erect to appressed hairs, especially on veins beneath and with red sessile glands beneath. Inflorescence lax, (4–)9–18 cm long, with 7–15 verticils spaced (5–)10–25(–45) mm, bracts ovate, ca. 5 × 3 mm, acuminate, forming an apical coma, deciduous, except often at 1–2 lowermost nodes where they are somewhat foliaceous and crenate; cymes sessile to very shortly pedunculate (1 mm), ascending, ca. 13-flowered, cincinni up to 6 mm long in fruit, pedicels 1–4 mm, inserted eccentrically behind calyx upper lobe. Flower: calyx shortly pubescent and with red sessile glands, ca. 1.5 mm long in flower, up to 4.5 mm long in fruit, tube shortly cylindrical, constricted at throat, truncate, upper lobe ovate, recurved, subacute, purplish tinged, ciliolate, lateral lobes truncate, middle lobes of lower lip fused in a linear lip ca. 3 mm long, with two subulate points; corolla ca. 9–14 mm long, tube ca. 4 mm long, strongly sigmoid, lower lip ca. 5–7 mm long, 2.5–3 mm deep, cucullate, upper lip 2 mm long, with a broad gap between the two lips. Nutlets pale brown, globose, ca. 0.9 mm diam., smooth.

Distribution. Republic of Congo (Brazzaville), DR. Congo.

Habitat and ecology. Marshland, wet savannah, grassy clearings, *Sphagnum* bogs, dry woodlands; 300–750 m elev.

Additional specimens. DR. CONGO, ***Bas-Congo***, Léopoldville [Kinshasa], 15 Apr 1915, *J.Bequaert 7341* (BR); Boko Mfumu Disu, 15 Nov 1948, *H.Callens 1911* (BR); Madimba, 2 Apr 1948, *P.Duvigneaud 609Ca* (BRLU); Entre Ngidinga et Kimvula, 12 Apr 1948, *P.Duvigneaud 703C* (BRLU); Boko sur chemin de fer, Apr 1932, *H.Vanderyst 29736, 29747, 29751* (BR); ***Kasaï***, Kwango, Mela, *H.Callens 1677* (BR); Panzi, 8 Feb 1950, *H.Callens 2185* (BR); Region of Luebo, s.d., *L.Achten 415a&b*; ***Forestier Central***, Entre Bokatola et Bikoro, Lac Léopold II [Lac Mai Ndombe], Sep 1930, *J.Lebrun 1445* (BR).

Notes. 1. New species record for DR. Congo.

2. *C. brazzavillensis* was hitherto a poorly-known species. It is superficially similar to *C. bojeri*, differing in being perennial. *C. brazzavillensis* is closely related to and, arguably, only a variety of *C. welwitschii*, differing in the much more slender rhizome, longer hairs on shoot and petiole, shorter cincinni, persistent bracts at lowermost verticils and its occurring in moist habitats; blade length/width ratio also tends to be greater than in *C. welwitschii*. Its range is restricted to W DR. Congo and Congo (Brazzaville).

3. *H.Callens 2185* (BR) has the indumentum of the stem much sparser than usual. *J.Lebrun 1445* (BR) is unusual in having persistent bracts at all verticils.

Coleus buchananii **(Baker) Brenan, Mem. New York Bot. Gard. 9: 43. 1954.**

≡ *Plectranthus buchananii* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 402. 1900. Type: MALAWI, Shire Highlands, Nakajumbu, 15 Oct 1881, *J.Buchanan 365* (holotype K [K000431996]; isotype E [E00193487]).

= *Coleus kisanfuensis* De Wild., Contr. Fl. Katanga: 174. & Ann. Soc. Sci. Bruxelles 41(2): 48. 1921. Type: DR. Congo, Elisabethville [Lubumbashi], Sep 1911, *A.Hock s.n.* (lectotype BR [BR0000008730572], designated here), syn. nov.

Description. Paton et al. (2009: 324), Paton et al. (2013: 263), as *Plectranthus buchananii* Baker.

Distribution. Tanzania to S Tropical Africa.

Habitat and ecology. Dry woodlands, wooded savannah, steppic savannah, often on rocky soil, occasionally on copper-rich soil; 950–1550 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Upemba, près de la Lufira, 30 Aug 1948, *G.F.de Witte 4222* (BR); Vallée de la Lofoi, près du village Nkonko, 3 Oct 1970, *S.Lisowski 23358* (POZG); Luiswishi, 21 Sep 1984, *F.Malaisse 13191* (BR); Région de Fungurume, colline “monde arabe”, 24 Jul 2007; *B.Senterre 4676* (BR); Tantara, autour de la mine, 3 Sep 1977, *R.Wechuysen 865, 866, 867* (BR).

Burundi, Bururi, 1951, *A.Becquet 2149* (BR); Bururi, route Makamba-Dunga, km 20, 21 Sep 1977, *M.Reekmans 6378* (BR).

Notes. 1. *Coleus kisanfuensis* De Wild. was unplaced in Paton et al. (2019), because the original materials had not been found. The materials were misfiled in BR as “*Coleus hockii* De Wild.” (which is *Coleus betonicifolius* var. *kasomenensis* (De Wild.) Meerts & A.J.Paton). The specimen [BR0000008109613] indeed bears a label handwritten by De Wildeman as “*Coleus hockii* De Wild.”, but this is obviously a mistake, because the protologue of *C. kisanfuensis* clearly refers to *C. buchananii*, not to *C. betonicifolius*.

2. Lectotypification of *Coleus kisanfuensis* De Wild. De Wildeman (1921b) cited two syntypes, i.e. *A.Hock s.n.* (syntype BR [BR0000008109613]), DR. Congo, Kisanfu, Sep 1911 and *A.Hock s.n.* (syntype BR [BR0000008732835] and [BR0000008730572]), Elisabethville [Lubumbashi], Sep 1911. The three sheets match the protologue. We designate [BR0000008730572] as the lectotype because it does not bear the erroneous name *Coleus hockii* De Wild.

Coleus calaminthoides **(Baker) A.J.Paton, Phytokeys 129: 30. 2019.**

≡ *Solenostemon calaminthoides* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 421. 1900. Type: Gabon, Gabon River, *G.Mann s.n*. (holotype K [K001615425]).

Description. Paton (2022: 44). The materials from DR. Congo differ from the materials in the rest of the range in having the hairs on the stem either retrorse or antrorse (always antrorse out of DR. Congo).

Distribution. Cameroon, Equatorial Guinea, Gabon, DR. Congo.

Habitat and ecology. Coastal scrub on sandy soil; 0–100 m elev.

Additional specimens. DR. Congo, ***Côtier***, Plateau de Tshikai, route Boma-Banana, 13 Apr 1960, *Compère 1863* (BR); Route Boma-Banana, entre Malemba et Matamba ma Kanzi, 13 Mar 1959, *J.Wagemans 2230* (BR); ***Mayumbe***, Luki, 5°34'50.73"S, 13°9'34.16"E, 6 Apr 2010, *S.Dessein 3222* (BR); Forêt de Moba [entre Luki et Boma], route de Boma, 5 Dec 1948, *C.Donis 2233* (BR); without locality, Aug-Sep 1899, *Tilman* in *Cabra 67* (BR).

Notes. 1. The species was identified in DR. Congo for the first time by A.J.Paton in 2021; it had been hitherto misidentified as *C. monostachyus*. The Congolese localities represent the southernmost limit of the species' distribution range.

2. Paton et al. (2022) consider that *C. calaminthoides* differs from *C. monostachyus* in having antrorse hairs on the stem. However, this character is variable in DR. Congo, with *C. Donis 2233* having antrorse hairs, while the other specimens have retrorse hairs.

3. The specimen *Tilman* in *Cabra 67* (BR) is close to *C. calaminthoides*, except for the yellow corolla; it could be a different taxon.

Coleus caninus subsp. *flavovirens* (Gürke) A.J.Paton, Phytokeys 129: 32. 2019.

≡ *Coleus flavovirens* Gürke in H.G.A.Engler, Pflanzenw. Ost-Afrikas, C: 347. 1895.

≡ *Plectranthus caninus* subsp. *flavovirens* (Gürke) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 345. 2009. Type: Tanzania, Dschallasee [Lake Chala], 1893, *G.Volkens 1771* (holotype B destroyed; isotype BR [BR0000021453960]).

Description. Paton et al. (2009: 345), Paton et al. (2013: 274), as *Plectranthus caninus* Roth subsp. *flavovirens* (Gürke) A.J.Paton.

Distribution. Ethiopia to South Africa.

Habitat and ecology. Savannah, often on dry or rocky soil; 780–1590 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Kabare, Lac Kivu, 21 Aug 1914, *J.Bequaert 5384* (BR); May ya Moto, 14 Nov 1934, *G.F.de Witte 2037* (BR); Plaine de la Ruzizi, Apr 1950, *R.Germain 6851* (BR); Ruindi, Sep 1937, *J.Lebrun 7750* (BR). Rwanda, Akagera, Rwisirabo, 21 Jan 1980, *D.Bridson 255* (BR, K, WAG); Kabare, Gabiro, May 1933, *A.Becquet 607* (BR); Rwabiega, Jan 1938, *J.Lebrun 9824* (BR); Akagera, Rwisirabo, 2 Jul 1978, *J.Raynal 20794* (BR, P); Utara, env. Nyagatare, 1 May 1958, *G.Troupin 7240* (BR).

Burundi, Rugombo, plaine de la Ruzizi, 20 May 1969, *J.Lewalle 3590* (BR); Plaine de la Ruzizi, 13 May 1978, *M.Reekmans 6988* (BR, WAG).

Coleus celsus A.J.Paton, Phytokeys 129: 34. 2019.

≡ *Solenostemon robustus* Hiern, Cat. Afr. Pl. 1: 864. 1900., non *Coleus robustus* (Hook.f.) A.J.Paton.

≡ *Plectranthus robustus* (Hiern) A.J.Paton in Fl. Zambesiaca 8,8: 234. 2013. Type: Angola, Pungo Andongo, from Lombe to Condo, Mar 1857, *F.Welwitsch 5538* (lectotype BM [BM00564035] designated here; isolectotypes [BM 00564268], LISU [LISU220992], [LISU220993]).

Description. Woody perennial herb, ca. 1.0–1.5 m high, more or less leafless at flowering; rootstock with tubers up to 10 × 5 cm. Stem erect, up to 1 cm thick, woody and cylindrical in lower half, striate, lenticellate, puberulous with short eglandular hairs, obtusely quadrangular in upper half, densely white pubescent with short antrorse hairs, branching only in the inflorescence. Leaves opposite, petiolate, ascending, beginning to fall off at time of flowering; blade yellowish-green, coriaceous to somewhat crassulescent, broadly ovate, 4.5–8.5(–14.0) × 3.5–6.0(–9.0) cm long, base broadly cuneate, obtuse to rounded and then shortly attenuate into the blade, apex rounded to acute or shortly acuminate, margin crenate, not recurved, upper surface subglabrous to puberulous, lower surface shortly pubescent on veins, ca. 6–8 pairs of secondary veins; petiole 0.5–2.0(–3.0) cm long. Inflorescence 20–30 cm long, pyramidal-paniculiform, with 5–7 pairs of opposite ascending branches ca. 1.5–7 cm long, spaced ca. 5 cm, each terminating in 1–4 condensed ca. 1.5 cm long racemes, with tomentose to villous rachis; flowers solitary in the axil of each bract, arranged helicoidally around axis, bract ovate, ca. 2 mm long, villous on back, pedicel in fruit (8–)18 mm long, jointed ca. 2–5 mm above base and breaking at joint at maturity, leaving persistent base on rachis, pubescent, adnate eccentrically to calyx; calyx campanulate, beige to fulvous villous at first, ca. 5 mm long at anthesis, fruiting calyx (9–)13–14 mm long, coriaceous, tube campanulate, pubescent, with pale sessile glands, throat slightly oblique, lobes ciliate, upper lobe ovate-triangular, slightly curved, not decurrent, acute, ca. 2 mm long, lateral lobes of lower lip triangular, ca. 3 mm long, middle lobes of lower lip narrowly triangular ca. 4 mm long. Corolla purplish-pale blue with pale sessile glands, tube strongly sigmoid 7–8 mm long, upper lip ca. 3 mm long separated from lower one by a 3 mm gap, lower lip 9–11 mm long, 4–5 mm deep, cucullate, with two small auricles near base, anther pouch-like, style entire. Nutlets light brown, red speckled, smooth, broadly ovoid, ca. 2 mm.

Distribution. Angola, DR. Congo.

Habitat and ecology. Wooded savannah, steppe; 1000–1670 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kwango, Village Shamafuka (15 km S de Bwana Mutombo), 1 Apr 1948, *P.Duvigneaud 970E* (BRLU).

Notes. 1. New species record for DR. Congo. The Congolese locality represents the northernmost limit of the species' distribution range.

2. Lectotypification. *Solenostemon robustus* Hiern was described most likely based on Welwitsch's materials at BM. BM holds two sheets of *F.Welwitsch 5538*. We designate the sheet with complete collecting data on the label as the lectotype.

Coleus chevalieri **Briq., Mém. Soc. Bot. France 8: 287. 1917.**

Figs 1C, D, 2C

= *Coleus delpierrei* De Wild., Bol. Soc. Ibér. Ci. Nat. 19: 119. 1920. Type: DR. Congo, Ubangi-Uele, Van Kerkhovenville [Watsa], 1904, *A.Delpierre s.n*. (lectotype BR [BR0000006261559], designated here), syn. nov.

Type. Central African Republic, Haut-Oubangui, Krébédjé (Fort Sibut), vallée de la moyenne Tomi, bord d'un sentier sur un plateau ferrugineux, 8 Nov 1902, *A.Chevalier 5662* (holotype P [P00450788], [P00450786]; isotype BR [BR0000006245498], G [G00437733]).

Description. Annual herb, 0.15–0.70 m high, rootstock fibrose, without tubers. Stem erect, quadrangular, generally much branched from base, with short appressed retrorse hairs and red sessile glands, often purplish. Leaves opposite, ascending to spreading, petiole (0.2–)0.8–3.5(–4.5) cm long, narrowly winged in upper half, blade occasionally red spotted in the middle, ovate, narrowly ovate, 3–10(–11) × 1–4(–5.5) cm, mostly 2–3 times as long as broad, apex generally obtuse, rarely acute, base cuneate, shortly attenuate in the petiole, 4–8 pairs of secondary veins, occasionally impressed, margin crenate to obtusely serrate (teeth obtuse to rounded), subglabrous to very shortly pubescent above, shortly pubescent on veins beneath (antrorse or retrorse hairs). Inflorescence spiciform, (3–)5–12 cm long, 8 mm wide at anthesis (corolla excluded), congested, occasionally more lax, moderately dense at fruiting, up to 32 cm long, 10–15(–20) mm wide at fruiting, with (5–)15–30 verticils typically spaced 5–10 mm, the lowermost ones occasionally up 25 mm, bracts persistent, at first erect and cucullate, soon reflexed, ca. (1.5–)4–6 × (0.5–)2–3 mm long, ovate-triangular, sessile, acute to acuminate, occasionally almost caudate, ciliate, upper surface glabrous, lower surface sparsely pubescent and with red glands, forming a short apical coma; cymes sessile, ca. 11(–17)-flowered, cincinni ascending, elongating to 2–3(–6) mm, pedicels ca. 2–3 mm long. Flower: calyx shortly pubescent, with red sessile glands, ca. 2 mm long at anthesis, fruiting calyx subglabrous to shortly pubescent, 3.5–4 mm long, narrowly tubular, slightly constricted a throat, upper lip often purplish tinged, ovate-elliptic to obovate-elliptic, ca. 2.5 mm long, acute to more rarely rounded, recurving, not decurrent, lateral lobes truncate, ca. 1 mm long, median lobes of lower lip fused, linear, ca. 2 mm long, with two acute points, slightly curving upwards; corolla blue to pale mauve, with or without red sessile glands, ca. 8–12 mm long, tube 2.5–3 mm long, sigmoid, lower lip 3–7 mm long. Fruit: nutlets yellowish-brown with red speckles, globose ca. 0.8 mm diam., smooth.

Distribution. Cameroon, Central African Republic, DR. Congo.

Habitat and ecology. Savannah, dry woodland, fallow fields, often on lateritic crust, 300–1000 m elev.

Additional specimens. DR. Congo, ***Bas-Katanga***, Haut-Lomami, Kaniama, 20 Apr 1947, *W.Mullenders 295* (BR); ***Forestier Central***, Eala, 28 Sep 1937, *G.Couteaux 338* (BR); Ikulu, 14 Feb 1940, *Freyne 4* (BR); Bambesa, 1936, *Pittery 424* (BR); Route Niangara-Kisangani, 55 km d'Isiro, vers Wamba, 20 Apr 1936, *J.Louis 1738* (BR); Asaka, 30 Oct 1923, *Nannan 623* (BR); ***Ubangi-Uele***, Doruma, 10 Sep 1933, *A.M.De Graer 101* (BR); Garamba, 10 Sep 1951, *H.De Saeger 1396* (BR, K); Uele-Nipoko, entre Niangara et Wamba, Jun 1931, *J.Lebrun 3199* (BR); Yakuluku, 29 Sep 1953, *P.Gérard 790* (BR).

Central African Republic, ***Haut-Oubangui***, Yalinga, 18 Sep 1921, *G.Le Testu 3256* (P); 60 km N of Bambari, 26 Nov 1928, *Ch.Tisserant 2296* (P); Oubangui-Chari, Koukourou, Sep. 1957, *J.Trochain 10648* (P).

Cameroun, Sabal Maba, 60 km NNE Tibati, 23 Sep 1963, *R.Letouzey 5920* (P).

Notes. 1. Within the *C. bojeri* complex, this species is easily recognised on account of the persistent bracts, long spiciform inflorescence with congested, closely-spaced verticils; the leaves tend to be obtuse, with blade more than 2× as long as broad, with numerous secondary veins, but these traits are more variable.

2. Robyns and Lebrun (1928) had already synonymised *C. delpierrei* De Wild. and *C. chevalieri* Briq.

3. Near the southern margins of the species' distribution range, specimens intermediate between *C. chevalieri* and other species occur: e.g. *L.Pynaert 1702* (intermediate with *C. bojeri*); *H.Vanderyst 34394* (intermediate with *C. welwitschii*); *S.Risopoulos 146* (intermediate with *C. botryosus*); *L.Pynaert 1092, G.Couteaux 338* (BR) (intermediate with *C. brazzavillensis*).

4. Lectotypification of *Coleus delpierrei* De Wild. De Wildeman (1920) cited two syntypes: *A.Delpierre s.n*. (BR [BR0000006261559]), DR. Congo, Vankerkhovenville [Watsa], 1904 & *A.Delpierre s.n*. (BR [BR0000006261887]), Niangara, 1904. Both match the protologue; [BR0000006261559] is selected because its inflorescence is better developed.

5. The most typical specimens of *C. chevalieri* occur in the Sudanian part of DR. Congo, in the region of Ubangi-Uele, where they grow on lateritic crust. In other regions of DR. Congo, *C. chevalieri* is often less typical and intermediates with other species of the *C. bojeri* complex occur.

***Coleus collinus* Lebrun & L.Touss., Bull. Jard. Bot. État Bruxelles 17: 81. 1943.**
Figs 1E, F, 2A

≡ *Solenostemon collinum* (Lebrun & L.Touss.) Troupin, Bull. Jard. Bot. Natl. Belg. 55: 299. 1985. Type: DR. Congo, Kivu, Rutshuru, Nov 1937, *J.Lebrun 8232* (holotype BR [BR0000006262990], [BR0000006262983]; isotype P).

Description. Annual herb, aromatic, 0.15–0.40(–0.60) m, often in groups, rootstock fibrose, without tubers. Stem prostrate or ascending, more rarely erect, slender, occasionally rooting at lower nodes, quadrangular, with long patent multicellular eglandular hairs (ca. 1.5 mm long) and short appressed retrorse hairs, with red sessile glands, simple or much branched. Leaves opposite, spreading to ascending, petiole 0.2–1.1(–1.5) cm long, ciliate; blade ovate to trullate, 0.9–2.2 × 0.7–2.0 cm, base obtuse and then shortly attenuate into the petiole, apex acute, margin crenate, 4–6 teeth on either side, with sparse long hairs on both surfaces, dense red sessile glands on the lower surface, ca. 3 pairs of secondary veins. Inflorescence dense at anthesis, then lax at fruiting, simple, 2–5 cm long, ca. 6 mm wide (corollas excluded) at anthesis, elongating to 5–8 cm long, ca. 1 cm wide in fruit, with 4–11 verticils spaced 7–15 mm in fruit, cymes ca. 9-flowered, peduncle lacking, cincinni 0–4 mm long, ascending, pedicels 2–4 mm long, ascending, with short papilliform hairs, bracts broadly ovate, subsessile, 3–6 × 3–5 mm, foliaceous, the lowermost ones often serrate, persistent, reflexed, margin long ciliate, upper surface glabrous to papillate, lower surface pubescent, with red sessile glands. Flower: calyx shortly pubescent, with red sessile glands, 1–1.5 mm long at anthesis, fruiting calyx ca. 4 mm long, tube shortly campanulate, throat truncate, upper lobe obovate-elliptic, ca. 2 mm long, more or less acute, margin shortly ciliate, recurving, not decurrent, lateral lobes rectangular, truncate to rounded, median lobes of lower lip fused in a linear lip, straight, ca. 3 mm long, with two acute points. Corolla pale blue (rarely white), lower lip deep blue, ca. 2–4.5 mm long, tube 1–1.5 mm long, slightly curved, lower lip ca. 2 mm long, stamens included or occasionally exserted, anthers ca. 0.3 mm long. Fruit: nutlets yellowish to pale brown speckled with red, globose, ca. 0.8 mm diam., smooth.

Distribution. Cameroon, DR. Congo, Rwanda, Burundi, Uganda, Kenya, Tanzania, Malawi, Zambia.

Habitat and ecology. Savannah, fallow fields, rocky steppe, pastures, gravel, river banks; 1200–1800 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Luberizi, 1953, *A.Gilon 346* (BR); Rutshuru, Mt. Katale, Dec 1937, *J.Lebrun 9154* (BR, P); Rutshuru, 15 Apr 1937, *J.Ghesquière 4291* (BR); Mumosho, 8 May 1951, *J.F.Laurent 223* (BR).

Rwanda, Kibungo, Gahororo, environs de Zaza, 27 May 1970, *G.Bouxin & M.Radoux 2211* (BR, WAG); Rubona, Inéac, 28 Apr 1958, *G.Michel 5332* (BR, WAG).

Burundi, Bururi, Mosso, Bugiga, 21 May 1980, *M.Reekmans 9219* (BR, WAG); Ruyigi, Kitaba, 15 May 1981, *M.Reekmans 10333* (BR, MO, US, WAG); Gitega, Karuzi, 31 May 1981, *M.Reekmans 10517* (BR, WAG); Kitega Chefferie: Bweru, Environs Karuzi, colline Nyarusange, 16 May 1958, *van der Ben 2091* (BR).

Cameroon, Bamenda, Bambili, Bafut-Ngema, 19 Aug 1951, *E.Ujor FHI 29985* (FHI, K). Uganda, Serere Teso, Dec 1931, *Chandler 211* (K).

Kenya, Trans-Nzoia Distr., Kitale, 19 Sep 1961, *Verdcourt 3211* (EA, K).

Tanzania, Ngara distr., Nyakiziba, 26 Apr 1960, *R.E.S.Tanner 4890* (BR, K).

Malawi. Kondowe to Karonga, Jul. 1896, *A.Whyte s.n.* (K).

Zambia, By Katete River, where Great East Road crosses it, 16 Jan 1957, *J.M.Wright 124* (K).

Notes. 1. This species differs from *C. bojeri* in having persistent bracts, smaller corolla, narrower inflorescence. It often has ascending, somewhat flexuose shoots and smaller leaves, but these traits are more variable.

2. *C. collinus* is most likely a self-pollinating species, with corollas often not exceeding 1.5 mm long, often cleistogamous and anthers much smaller than in most *Coleus* species in Central Africa.

3. New species record for Cameroon, Uganda, Kenya, Tanzania, Zambia and Malawi.

Coleus conglomeratus (T.C.E.Fr.) Robyns & Lebrun, Ann. Soc. Sci. Bruxelles, Sér. B 49: 105. 1929.

≡ *Englerastrum conglomeratum* T.C.E.Fr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 72. 1924.

≡ *Plectranthus conglomeratus* (T.C.E.Fr.) Hutch. & Dandy, Bull. Misc. Inform. Kew 1926:481. 1926. Type: Togo, Sokode, Dec 1904, *H.Kersting 93* (holotype B destroyed; isotype K [K000431858] fragment).

Description. Shrub or perennial woody herb, up to 2 m high, almost leafless at flowering, rootstock with tubers. Stem erect, sparingly branching, rounded in the lower part, quadrangular upwards, striate, lenticellate, purplish, densely covered with ca. 4 mm-long patent stiff bristles and with very short appressed hairs, young growth beige tomentellose, with dense retrorse hairs and more sparse patent hairs, these turning into bristles in older growth. Leaves opposite, patent, petiole 0.5–1.0 cm (up to 5.0 cm outside Central Africa), blade ovate to ovate-elliptic, 1–3 × 1–2 cm (up to 16 × 8 cm outside Central Africa), apex acute to subobtuse, base cuneate and shortly attenuate into the petiole, margin crenate, upper surface puberulous and with pale sessile glands, lower surface shortly pubescent on veins and with pale sessile glands. Inflorescence in short lateral and terminal subsessile panicles, each comprising 3 to 5 branches 2–5 cm long; rachis densely covered with short glandular hairs, flowers solitary in the axil of a bract, helicoidally arranged on the rachis, distally often subopposite; bracts narrowly elliptic, ca. 1 mm long, pedicels ascending, with thin patent eglandular hairs, ca. 3 mm long, eccentrically inserted on calyx; calyx tubular, with dense short glandular hairs and pale sessile glands, 2 mm long at anthesis, ca. 4.5 mm in fruit, tube slightly curved, upper lobe broadly ovate to obovate, subobtuse, somewhat curving upwards, slightly decurrent, lobes of the lower lip narrowly triangular, 1–1.5 mm long, the median ones slightly longer; corolla ca. 6 mm long (up to 10 mm outside Central Africa), yellow inside, suffused with purple outside, with pale sessile glands, tube ca. 4 mm long, funnel-shaped, lower lip equalling the tube, upper lip shorter, with a broad emarginate median lobe and two smaller rounded lateral lobes, stamens with filaments free for most of their length, anthers golden; style golden, stigma bifid. Nutlets somewhat compressed, brown, shiny, red speckled, ca. 1 mm.

Distribution. Togo, Benin, Sierra Leone, DR. Congo.

Habitat and ecology. Savannah on lateritic crust; 100–500 m elev.

Additional specimens. DR. Congo, ***Ubangi-Uele***, Entre Businga et Banzyville [Mobayi-Mbongo], Jan 1931, *J.Lebrun 2061* (BR).

Notes. 1. New species record for DR. Congo.

2. The record in NW DR. Congo is remarkably disjunct, ca. 2000 km east of the nearest previously known locations in Togo. It had been misidentified in collections as *C. tetragonus*, on account of the bristles on the stem. It differs from the latter in the shorter pedicel (ca. 3 mm vs. 5–8 mm), shorter calyx (4.5 mm vs. 6–10 mm) and corolla suffused with purple.

Coleus cylindraceus (Hochst. ex Benth.) A.J.Paton, Phytokeys 129: 37. 2019.

≡ *Plectranthus cylindraceus* Hochst. ex Benth. in A.P.de Candolle, Prodr. 12: 60. 1848. Type: Ethiopia, near Gapdia, ad rupes, 29 Nov1838, *G.W.Schimper II. 1113* (holotype K [K000431901], [K000431904], [K000431900]; isotype BM [BM000564023], E, FI [FI011097], [FI000844], G [G00435204], [G00435206], [G00435205], HAL [HAL0114463], M [M0104743], [M0104744], MPU [MPU015435], P [P00450713], [P00450711], [P00450712], PRE [PRE0235122-0], TUB [TUB009112], UPS, W).

= *Plectranthus montanus* Benth. in N.Wallich, Pl. Asiat. Rar. 2: 17. 1830., non *Coleus montanus* Hochst. ex Ces. Type: India, Deccan Peninsula, exact locality unknown (“Peninsula India Orientalis”), Herb. Wight in Wall. Cat. 2747B (lectotype K [K000820120]), designated by Suddee et al. (2004); isolectotype K-W [K001117007]).

Description. Paton et al. (2009: 318), Paton et al. (2013: 260), as *Plectranthus montanus* Benth.

Distribution. Tropical and S Africa, Arabian Peninsula, S India.

Habitat and ecology. Wooded savannah, rock outcrops, marshland, fallow fields; 1000–1400 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, May ya Moto, 14 Nov 1954, *G.F.de Witte 2042* (BR).

Rwanda, Ngoma, Rukoma Nganza, Jun 1933, *A.Becquet 685* (BR); Préfecture Kibungo, Concession minière de Géorwanda-Rwinkwavu-colline dominant la plaine de Matinza, 21 May 1969, *G.Bouxin & M.Radoux 455* (BR); Préfecture

Kigali, entre Karama et frontière du Burundi, à 14 km de Karama (Bugesera), 18 May 1978, *G.Troupin 15922* (BR); Biumba. marais Kibondo, 26 May 1955, *A.R.Christiaensen 895* (BR).

Burundi, Muyinga, Murehe, 30 May 1981, *M.Reekmans 10495* (BR, MO, WAG).

Note. *G.F.de Witte 6449* (BR), from Haut-Katanga, Upemba National Park, is intermediate between *C. cylindraceus* and *C. succulentus*. See also note under the latter species.

Coleus decimus **(A.J.Paton) A.J.Paton, Phytokeys 129: 38. 2019.**

≡ *Plectranthus decimus* A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 324. 2009. Type: Zambia, Mbala (Abercorn) District, Kawimbe, 15 Dec 1956, *H.M.Richards 7288* (holotype K [K000431998]).

Description. Paton et al. (2009: 324), Paton et al. (2013: 264), as *Plectranthus decimus* A.J.Paton.

Distribution. W Tanzania, Zambia to Angola.

Habitat and ecology. Pionneer vegetation on rocky soil, often near rivers, ca. 1300 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Tilwizembe, 8 May 1957, *P.Duvigneaud 3084L* (BRLU), Env. Kolwezi, rive gauche Musonoye, 13 Jan 2005, *F.Malaisse 16065* (BR); Près des chutes de la rivière Musonoi, 12 Mar. 1989, *M.Schaijes 4317* (BR).

Note. New species record for DR. Congo.

Coleus decurrens **Gürke, Bot. Jahrb. Syst. 19: 215. 1894.**

= *Coleus variifolius* De Wild., Bol. Soc. Ibér. Ci. Nat. 19: 124. 1920. Type: DR. Congo, between Buta and Bima, 15 Oct 1905, *F.Seret 96* (lectotype BR [BR0000021453991], designated by Paton et al. 2009).

Type. Cameroon, Buea, 1891, *P.Preuss 948* (holotype B destroyed; isotype COI [COI00005778], HBG).

Description. Paton et al. (2009: 294) as *Plectranthus decurrens* (Gürke) J.K.Morton, Paton (2022: 46) as *Coleus decurrens* Gürke.

Distribution. Nigeria to Uganda, Gabon, Republic of Congo, DR. Congo, Angola.

Habitat and ecology. Rainforest, often seasonally flooded, riparian forest, river banks; 470–2000 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Without locality, 1904, *J.Gillet s.n.*, & *J.Gillet 3783* (BR); ***Kasaï***, Panzi, galerie de la Makita, 18 Feb 1952, *H.Callens 3438* (BR); ***Forestier central***, Avakubi, 9 Jan 1914, *J.Bequaert 1853* (BR); Bongo, 26 Jul 1955, *C.Evrard 1512* (BR); Parc national de la Maïko, 45 km N of Lubutu, 2 Jun 1977, *J.Lejoly 1905C* (BR, BRLU); Yangambi, 7 km NW, 8 May 1936, *J.Louis 1834* (BR); Bolanda, 29 Oct 1913, *Nannan 85* (BR); Entre Buta et Banalia, Ambelati, 11 Jan 1926, *W.Robyns 1333* (BR); ***Ubangi-Uele***, entre Libenge et Géména, Dec 1930, *J.Lebrun 1866* (BR); ***Lac Albert***, Kilo, 28 Jun 1914, *J.Bequaert 4866* (BR); ***Lacs Edouard et Kivu***, Route Kibabi-Kikoma, km 50, 29 Apr 1958, *R.Pierlot 1943* (BR); Route Kavumu-Walikale, km 107, Irangi, 24 Oct 1959, *G.Troupin 10926* (BR); Kidedeya, près riv. Lusilube, 13 Sep 1955, *Vanschuytbroeck* in *de Witte 12687* (BR).

Note. Two specimens (*J.Bequaert 6460; A.Leonard 3939*) are dwarf plants (< 20 cm), with small leaves and blade not long attenuated at base; they are either a juvenile form or a different taxon; more materials are needed.

Coleus deflexifolius **(Baker) A.J.Paton, Phytokeys 129: 39. 2019.**

≡ *Pycnostachys deflexifolia* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 381. 1900. Type: Kenya, Naivasha District, near Lake Elmenteita, 1893, *G.F.Scott Elliot 6756* (holotype K [K000405969]).

Description. Paton et al. (2009: 394), as *Pycnostachys deflexifolia* Baker.

Distribution. E Tropical Africa.

Habitat and ecology. Savannah on wet soil; 1300–2300 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kapemba, 1957, *P.Duvigneaud 3648Pyc* (BRLU).

Note. New species record for DR. Congo.

Coleus defoliatus **(Hochst. ex Benth.) A.J.Paton, Phytokeys 129: 39. 2019.**

≡ *Plectranthus defoliatus* Hochst. ex Benth. in in A.P.de Candolle, Prodr. 12: 60. 1848. Type: Ethiopia, Jomara [Dschomara], 26 Dec 1839, *G.W.Schimper II.847* (holotype K; isotype BR [BR0000006250720], FI [FI000843], G [G00435210], [G00435211], HAL HAL0114469], LG, M [M0104742], MPU [MPU015434], P [P00450715], [P00450716], TUB [TUB009113], W).

Description. Paton et al. (2009: 297), Paton et al. (2013: 246), as *Plectranthus defoliatus* Hochst. ex Benth.

Distribution. Eritrea to S Tropical Africa.

Habitat and ecology. Savannah, steppe, riparian forest; 1600–2300 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Nioka, Mont-Ri, 23 Nov 1957, *P.Bamps 66* (BR, POZG).

Burundi, Mugonga Manga, 14 Sep 1974, *P.Auquier 4087* (BR); Niambikiwe, Oct 1932, *A.Becquet 154* (BR); Route Bujumbura-Kitega, 19 Aug 1958, *A.Christiaensen 2477* (BR); Murambi, km 80 route Bujumbura-Butare, 20 May 1960, *F.L.Hendrickx 7962* (BR); Mubimbi, 24 May 1966, *J.Lewalle 827* (MO); Teza, 19 Jun 1971, *J.Lewalle 6028* (BR, WAG); Honga, 14 Oct 1971, *M.Reekmans 1055* (BR).

Coleus descampsii **(Briq.) A.J.Paton, Phytokeys 129: 40. 2019.**

≡ *Pycnostachys descampsii* Briq., Bull. Soc. Roy. Bot. Belgique 37: 63. 1899. Type: DR. Congo, Katanga, Lufonzo [Lufogo] R., Mar. 1896, *G.Descamps s.n.* (holotype BR [BR0000008910042]).

Description. Paton et al. (2009: 388), as *Pycnostachys descampsii* Briq.

Distribution. Cameroon to W Tanzania.

Habitat and ecology. Savannah, most often on moist, organic soil; 1000–1720 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Marungu, 1940, *F.Jurion 343* (BR); Kasanga, 23 Mar 1908, *T.Kassner 2660* (BR); Territ. des Baanza, sur la Luvua, 18 May 1931, *F.Luxen 35* (BR); Environs de Lubumbashi, May 1945, *P.Quarré 8012* (BR); Kasambi, 20 Apr 1926, *W.Robyns 2037* (BR); Marungu, Kasiki, 12 Jun 1939, *P.J.J.Vanden Brande 247* (BR).

Note. As already mentioned by Paton et al. (2009) in Tanzania, intermediates exist between *C. descampsii* and *C. parvifolius* (e.g. *S.Lisowski, F.Malaisse & J.-J.Symoens 11228* (POZG), Kundelungu, 25 Apr 1970).

Coleus dewildemanianus **(Robyns & Lebrun) A.J.Paton, Phytokeys 129: 40. 2019.**

≡ *Pycnostachys dewildemaniana* Robyns & Lebrun, Rev. Zool. Bot. Africaines 16: 352. 1928. Type: DR. Congo, Katanga, Munama, 1 Apr 1928 *P.Quarré 1143* (holotype BR [BR0000008910370], [BR0000008909732], [BR0000008910066]; isotype K, YBI).

Description. Paton et al. (2009: 387), Paton et al. (2013: 315), as *Pycnostachys dewildemaniana* Robyns & Lebrun.

Distribution. Tanzania to S Tropical Africa.

Habitat and ecology. Shrub savannah, road verges, rocky steppe, miombo woodland, disturbed soil; 1100–1900 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kundelungu, 10 km NNE du Mont Kibwe wa Sanga, 26 Apr 1970, *S.Lisowski, F.Malaisse, J.-J.Symoens 11317* (POZG); Mont Mukuen, 1 Apr 1948, *A.Schmitz 1495* (BR).

Rwanda, Gahororo, env. Zaza, 27 May 1970, *G.Bouxin et M.Radoux 2223* (BR); Mahumna, commune Birenga, 4 Jul 1978, *B.Runyinya 864* (BR).

Burundi, Route Gitega-Karuzi, 27 May 1971, *J.Lewalle 5801* (BR, WAG); Kininya Mosso, 4 Jun 1952, *G.Michel et J.Reed 2384* (BR); Ruyigi, Gitwenge, 17 May 1978, *M.Reekmans 7056* (BR).

Coleus duvigneaudii **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347689-1

Fig. 3A–F

Type. DR. Congo. Haut-Katanga, 15 km N de Mitwaba, steppe frais de plaine, 16 Jan 1960, *P.Duvigneaud 5082L* (holotype BRLU [BRLU0037795], isotype K).

Diagnosis. Closely related to *Coleus foliatus* (A.J.Paton) A.J.Paton, differing in the leaves ternate at all nodes, blade longer and narrower, mostly cuneate at base and acute at apex.

Description. Perennial herb ca. 0.60 m high, with several shoots from a thick woody rootstock. Stem erect, branching only in the inflorescence, rounded near base, rounded to quadrangular in upper part, pubescent to hispidulous, with

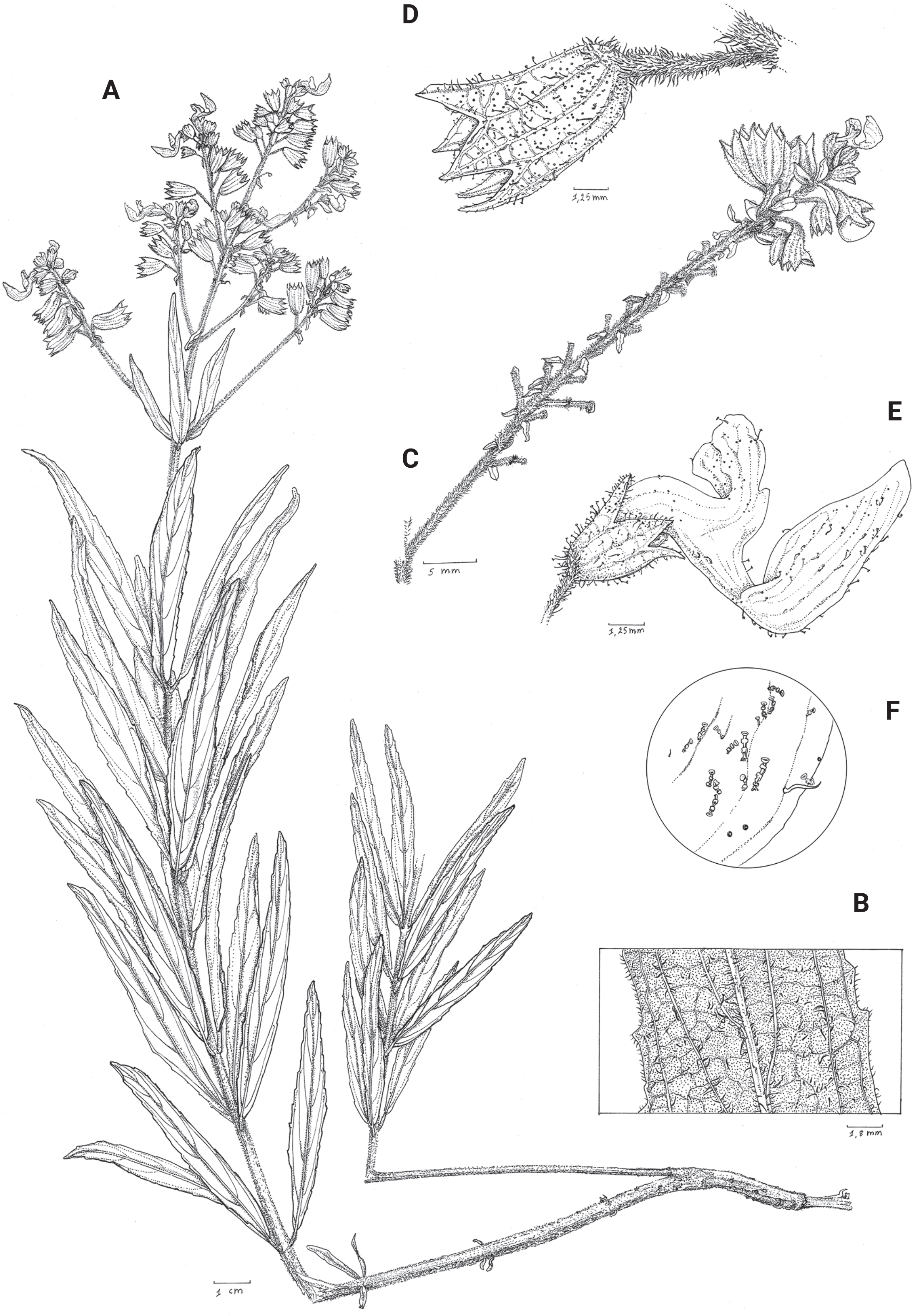

Figure 3. *Coleus duvigneaudii* Meerts & A.J.Paton **A** habit **B** detail of leaf blade undersurface **C** inflorescence branch **D** fruiting calyx **E** flower **F** detail of corolla pubescence (*P.Duvigneaud 5080L*). Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 1.8 mm (**B**); 5 mm (**C**); 1.25 mm (**D, E**).

patent or ascending eglandular hairs and pale sessile glands. Leaves ternate, ascending, subsessile; blade narrowly elliptic, oblong-elliptic to almost linear, 6–9 × 0.5–1.3 cm, length/width ratio ca. 6–10, base mostly cuneate, but almost rounded in upper leaves, apex acute, ca. 8 pairs of secondary veins, margin slightly recurved, distantly serrate, both surfaces somewhat harsh to the touch, pubescent, more densely so on veins underneath, glandular punctate on upper surface, with dense red sessile glands on undersurface; petiole 0–1 mm long. Inflorescence lax to moderately congested at anthesis, laxer at fruiting, paniculiform, with opposite or ternate branches on the uppermost 4–6 nodes of the stem, branches ascending, stiff, 4–12 cm, the longest branches themselves branching; 1 flower in the axil of each bract, lowermost flowers opposite, rachis purplish tomentose, bracts narrowly ovate-elliptic, 3 × 1 mm, obtuse, thin, membranous, pedicels ascending, ca. 2–3 mm long at anthesis, up to 5 mm in fruit, densely pubescent over whole its length, with an inconspicuous joint in the upper third, breaking at the joint at maturity, occasionally not breaking, obliquely adnate to calyx base and eccentrically inserted in front of upper lobe, thickened at fruiting. Flower: calyx ca. 3 mm long at anthesis, densely brownish to purplish pubescent, with eglandular and glandular hairs (these with cup-shaped apical cell in herbarium) and pale sessile glands, campanulate to tubular in fruit, ca. 8–9 mm long, teeth subequal, triangular, acute, the middle lobes of lower lip slightly longer (3 mm long) and more sharply pointed. Corolla blue to purplish, ca. 14 mm long, tube strongly sigmoid, ca. 6 mm long, upper lip 3 mm long, lower lip 8 mm long, 3 mm deep, cucullate, acute at tip, curving upwards, with pale sessile glands and purplish glandular hairs, enclosing stamens and style; anther pouch-like, 1 mm long; style entire. Nutlets ovoid, ca. 1.5 mm long, brown.

Etymology. Dedicated to Paul Duvigneaud (1913–1991), Belgian botanist, who made important contributions to the knowledge of the flora and the vegetation of Katanga (DR. Congo).

Distribution. Endemic of SE DR. Congo (Haut-Katanga); Mitwaba and Kundelungu Plateau.

Habitat and ecology. Savannah, steppic savannah, often on rocky soil; 1500–1700 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Sud du point Kisonsa, savane herbeuse, 24 Mar 1954, *R.Desenfans 5443* (BRLU); id., *R.Desenfans 5451* (BRLU); 15 km N de Mitwaba, steppe frais de plaine, 16 Jan 1960, *P.Duvigneaud 5082L* (BRLU); Kundelungu, près du gîte Rack, 5 Feb 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 1058* (BR) & *1058a* (POZG); Kundelungu, près du gîte Rack, 5 Feb 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 1247* (BR) & *1270* (POZG); same locality, steppe arbustive, 6 Feb 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 1072* (POZG); Kundelungu, au bord de la rivière Kalembe, steppe à suffrutex, 1550 m elev., 12 Jan 1971, *S.Lisowski, F.Malaisse, J.-J.Symoens 12857* (POZG).

Note. *C. duvigneaudii* is very closely related to and arguably only a variety of *C. foliatus*, differing in the ternate, narrower leaves, blade base cuneate, not clasping, apex acute, blade length/width ratio 6–10 (vs. 3–5 in *C. foliatus*). It is also related to the Angolan *C. strictipes*, differing in the ternate leaves, much more pubescent inflorescence and shorter pedicels. See note under *C. foliatus*.

Coleus efoliatus De Wild., Contr. Fl. Katanga: 173. & Ann. Soc. Sci. Bruxelles 41(2): 47. 1921.

≡ *Plectranthus efoliatus* (De Wild.) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 289. 2009. Type: DR. Congo, Welgelegen, 6 Jun 1912, *J.Bequaert 486* (lectotype BR [BR0000006261856], designated by Paton et al. [2009]).
= *Plectranthus leviculus* N.E.Br., Bull. Misc. Inform. Kew 1921: 296. 1921. Type: DR. Congo, Elisabethville [Lubumbashi], Jun 1920, *F.A.Rogers 26211* (holotype K [K000431879]).
= *Coleus kassneri* (T.C.E.Fr.) Robyns & Lebrun, Ann. Soc. Sci. Bruxelles, Sér. B 49: 106. 1929. Type: DR. Congo, Mt Morumbe, between rocks, 12 May 1908, *T.Kassner 2951* (holotype B destroyed; isotype BM, BR [BR0000006262532], E, K, P).

Description. Paton et al. (2009: 289); Paton et al. (2013: 237), as *Plectranthus efoliatus* (De Wild.) A.J.Paton.

Distribution. Rwanda to S Tropical Africa.

Habitat and ecology. *Brachystegia* miombo woodland, dry evergreen forest, steppic savannah, often on rocky outcrops or gravelly soil, occasionally on copper-rich soil; 1250–1400 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Welgelegen, 6 Jun 1912, *J.Bequaert 486* (BR); Tantara, 7 Aug 1956, *P.Duvigneaud & J.Timperman 2235Col* (BRLU); Katende, 50 km S Dilolo, 1957, *P.Duvigneaud 2458Col* (BRLU); Elisabethville [Lubumbashi], May 1912, *H.Homblé 290* (BR); Lubumbashi, Katuba, 24 May 1927, *P.Quarré 450* (BR).

Rwanda, Akagera, Lac Ihema, 15 Aug 1974, *P.Van der Veken 10806* (BR).

Coleus elliotii (S.Moore) A.J.Paton, Phytokeys 129: 43. 2019.

≡ *Pycnostachys elliotii* S.Moore, J. Linn. Soc., Bot. 38: 275. 1908. Type: Uganda, Ruwenzori E, 10 Feb 1906, *A.F.R.Wollaston s.n.* (holotype BM [BM000910111]).
= *Pycnostachys cinerascens* Robyns & Lebrun, Rev. Zool. Bot. Africaines 16: 352. 1928. Type: DR. Congo, Ruwenzori, vallée Lamia, 14 May 1914, *J.Bequaert 4287* (holotype BR [BR0000008910073]; isotype K fragment).
= *Pycnostachys butaguensis* De Wild., Pl. Bequaert. 4: 389. 1928. Type: DR. Congo, Ruwenzori, Vallée Butagu, 15 Apr 1914, *J.Bequaert 3715* (holotype BR [BR0000008909749], isotype K fragment).
= *Pycnostachys bequaertii* De Wild., Pl. Bequaert. 4: 393. 1928., nom. illeg., non *Pycnostachys bequaertii* De Wild., Contr. Fl. Katanga: 171. 1921.

Description. Paton et al. (2009: 406), as *Pycnostachys elliotii* S.Moore.

Distribution. DR. Congo to Uganda (Ruwenzori Mts.).

Habitat and ecology. *Erica* shrubland; 2000–3170 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, NW du Ruwenzori, E de Kalasabango, 13 Sep 1952, *H.Frédéricq in G.F.de Witte 8053* (BR, WAG); Piste Kalonge-Mahungu, 12 May 1953, *H.Frédéricq in G.F.de Witte 8990* (BR); Mont Muhi, 28 Jul 1955, *U.Kinet 63* (BR); Ruwenzori, crête de la Mososa, 4 Aug 1948, *W.Robyns 3321* (BR).

Coleus eminii **(Gürke) A.J.Paton, Phytokeys 129: 43. 2019.**

≡ *Pycnostachys eminii* Gürke, Bot. Jahrb. Syst. 22: 145. 1895. Type: Tanzania, west of Lake Victoria, Kanessa, 14 Nov 1890, *F.Stuhlmann 943* (lectotype B designated by Bruce (1940) destroyed; isolectotype K [K000405740] fragment).

= *Pycnostachys rotundatodentata* De Wild., Pl. Bequaert. 4: 391. 1928. Type: DR. CONGO, Ruwenzori, Kisuki, 6 Jun 1914, *J.Bequaert 4701* (lectotype: BR, designated by Bramley in Paton et al. (2009) [BR0000008909756], [BR0000008910080]).

Description. Paton et al. (2009: 407), as *Pycnostachys eminii* Gürke.

Distribution. Cameroon to Ethiopia and NW Tanzania.

Habitat and ecology. Savannah; 1100–2600 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Kisuki, pied du Ruwenzori, 6 Jun 1914, *J.Bequaert 4701* (BR, K fragment); Rutshuru, 19 Oct 1914, *J.Bequaert 6052* (BR); Bwito, Kikuku, 1 Jun 1954, *A.Deru 264* (BR); Dorsale du Mont Bikingi, 16 Jun 1949, *J.de Wilde 284* (BR); Luofu, 10 Dec 1934, *G.F.de Witte 2186* (DE); Entre Beni et Lubero, Oct 1931, *J.Lebrun 4275* (BR); Rutshuru, Mont Katale, Dec 1937, *J.Lebrun 9167* (BR, LWI, US).

Burundi, Piste de la faille des Allemands, 20 May 1988, *J.Saintenoy 158* (BR).

Coleus engleri **(Briq.) A.J.Paton, Phytokeys 129: 44. 2019.**

≡ *Anisochilus engleri* Briq., Bot. Jahrb. Syst. 19: 190. 1894. Type: DR. Congo, between Nyangwe and Kimbundo, 15 Jun 1882. *P.Pogge 1019* (lectotype K [K000405621], designated by Paton et al. [2009]).

= *Plectranthus africanus* (Baker) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 308. 2009. Type: Sierra Leone, Freetown, Jan 1899, *G.F.Scott Elliot 5033* (holotype K [K000405622]).

Description. Paton et al. (2009: 308), Paton et al. (2013: 251), as *Plectranthus africanus* (Baker) A.J.Paton.

Distribution. W Tropical Africa to Uganda and NE Angola.

Habitat and ecology. Swampy savannah, marshland, edge of riparian forest; 300–1200 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Entre Ngoma et Kikwansa, 5 May 1959, *L.Pauwels 2779* (BR); Kinanga, 6 Jul 1925, *W.Robyns 166* (BR); Dolo, Jun 1899, *R.Schlechter 12469* (BR, K); ***Kasaï***, Toni-Feshi, Kwango, 24 Jun 1955, *R.Devred 2108* (BR); Entre Lufuna et Mbombi, 6 Aug 1944, *R.Germain 2687* (BR); Territ. Dibaya, route Tshimbulu-Hemptinne, 6 Jun 1957, *L.Liben 3101* (BR); Rivière Tudi, route Kinzambi, 8 Aug 1991, *B.Masens 632* (BR, WAG, K); ***Bas-Katanga***, Gandajika, rivière Katamba, 2 Jul 1952, *R.Germain 7939* (BR); Kiabukwa, 9 Jul 1946, *G.Kevers 21* (BR); Entre Nyangwe et Malela, Aug 1932, *J.Lebrun 5940* (BR); Région sud de Kanda Kanda, rive gauche du Lubilash, 28 May 1934, *F.Luxen* 346 (BR); Kaniama, 22 Apr 1947, *W.Mullenders 298* (BR); ***Forestier Central***: Lac Léopold II [Lac Mai Ndombe], Dec 1932, *J.Lebrun 6687* (BR); ***Ubangi-Uele***: Entre Libenge et Gemena, Dec 1930, *J.Lebrun 1765* (BR); Faradje, Aug 1931, *J.Lebrun 3512* (BR); ***Lac Albert***: Kilo, 1921, *J.Claessens 1307* (BR); ***Lacs Edouard et Kivu***, Luamisole, 13 Feb 1939, *F.L.Hendrickx 151* (BR); Mwenga, Mudubwe, 21 May 1959, *A.Léonard 4289* (BR).

Coleus erici-rosenii (R.E.Fr.) A.J.Paton, Phytokeys 129: 44. 2019.

≡ *Pycnostachys erici-rosenii* R.E.Fr., Wiss. Erg. Schwed. Rhod.-Kongo Exped. 1: 281. 1916. Type: DR. Congo, Niragongo, 2000 m elev., 21 Dec 1911. *R.E.Fries 1588* (holotype UPS [V-039931], isotype K [K000405955], MO).

= *Pycnostachys albidoviolacea* De Wild., Pl. Bequaert. 4: 400. 1928. Type: DR. Congo, Kivu, Mukule, 26 Sep 1914, *J.Bequaert 5889* (lectotype BR [BR0000008910011], designated by Paton et al. [2009], isolectotype MO).

= *Pycnostachys robynsii* De Wild., Pl. Bequaert. 4: 398. 1928. Type: Burundi, Busiga, 28 May 1926, *W.Robyns 2356* (holotype BR [BR0000008910356], [BR0000008909695]; isotype K, MO, P).

Description. Paton et al. (2009: 408), as *Pycnostachys erici-rosenii* R.E.Fr.

Distribution. E DR. Congo to Uganda.

Habitat and ecology. Marshland, steppe, savannah, wooded savannah, sclerophyllous mountain forest; 1600–2420 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Haut-Ituri, Kwandruma, 16 Jul 1937, *J.Ghesquière 4731* (BR); ***Lacs Edouard et Kivu***, Boswenda, 23 Oct 1914, *J.Bequaert 6087* (BR, K fragment, MO); Kabare, Lwiro, 17 Aug 1953, *A.Christiaensen 4*0 (BR, LSHI); Chaîne des Mitumba, Hangi-Kipesa, 19 Jan 1956, *J.de Wilde 624* (BR); Bitashimua, 1 Aug 1934, *G.F.de Witte 1725* (BR); Kibumba, route Rutshuru-Goma, 12 Dec 1944, *R.Germain 2993* (BR, U); Kabare, Mulungu, 6 Nov 1958, *A.Léonard 1896* (BR, K, WAG); Kalehe, Mont Kahuzi, 6 Jun 1970, *J.Ntakiyimana 78* (BR).

Rwanda, Buturo, Ruhengeri, Jan 1933, *A.Becquet 362* (BR, MO); Forêt de Nyungwe, env. Gisakura, 12 Jun 1971, *G.Bouxin 993* (BR, WAG); Kabare, colline à l'W de Tshibati, 30 Dec 1969, *Ern 15* (BR, LWI, MO); Nyarutembe, Maraba, 2 Jul 1971, *M.Radoux 19* (BR); Rangiro, Kirambo, 6 May 1980, *B.Runyinya 998* (BR); Mukura, Mont Huye, 17 Jul 1974, *G.Troupin 15122* (BR).

Burundi, Muramvya, 9 Sep 1991, *J.De Laet H82* (BR); Kisozi, 15 Jul 1935, *J.B.Lejeune 314* (BR); Bubanza, 12 Jun 1981, *M.Reekmans 10653* (BR, WAG); Karuzi, 3 Apr 1958, *D.van der Ben 2023* (BR).

Coleus esculentus (N.E.Br.) G.Taylor, J. Bot. 69 (suppl. 2): 158. 1931.

≡ *Plectranthus esculentus* N.E.Br., Bull. Misc. Inform. Kew 1894: 12. 1894. Type: cultivated at K from material sent by J. Medley Wood from KwaZulu-Natal, 1893 (lectotype K [K000975993], designated by Codd (1975); isolectotype BOL).

Note. Our treatment of *C. esculentus* departs from recent floras, which recognised two species (*C. esculentus* and *C. densus*). Variation in DR. Congo is complex, comprising morphs difficult to accommodate into such a scheme. We recognise one species comprising four varieties, including a new one. Evidence from molecular markers is needed to test the validity of this treatment.

Key to the varieties of *Coleus esculentus*

1 Shoot with a pair of opposite branches at the 2–5 upper nodes, forming a panicle; thyrses borne distally on these branches; bracts broadly elliptic, ca. 5 × 3 mm, 5-veined ....***C. esculentus* var. *kolweziensis***
– Shoot unbranched at the upper nodes; thyrses sessile on nodes of the main stem; bracts narrowly obovate or ovate-triangular, ca. 1–3 × 1 mm, mostly 1–3 veined **2**
2 Rachis of the thyrses 8–20 cm long; verticils spaced 2–10 mm; pedicel (2–)3–19 mm long; upper lobe of calyx obovate-elliptic, very different in shape from the other lobes ....***C. esculentus* var. *esculentus***
– Rachis of thyrses 0–5 cm long; verticils spaced 1–2 mm; pedicel 0–2 mm long; upper lobe of calyx triangular, not much different in shape from the other lobes **3**
3 Rachis of thyrses obsolete; thyrses mostly condensed together near the top of the stem into a more or less spiciform inflorescence; upper lobe of calyx 2–3 mm long, equalling the tube .... ***C. esculentus* var. *primulinus***
– Rachis of thyrses 1–5 cm long; thyrses widely spaced along the stem; upper lobe of calyx 1.5–2 mm long, shorter than the tube ....
....***C. esculentus* var. *densus***

Coleus esculentus var. *esculentus*

Description. Paton et al. (2009: 291), Paton et al. (2013: 240), as *Plectranthus esculentus* N.E.Br.

Distribution. Tropical and South Africa.

Habitat and ecology. Degraded miombo woodland, fallow fields, savannah, 300–2285 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Kinwanda, près de Tumba Mani, 23 Aug 1902, *A.Cabra & F.L.Michel 38* (BR); Kisantu, Feb 1913, *J.Gillet s.n.* (BR); Sundi Lutete, 10 Aug 1967, *I.Persson 124* (BR); ***Kasaï***, Kwango, Kahemba, 24 Jul 1955, *R.Devred 2333* (BR); Env. Luluabourg [Kananga], 1910, *A.Sparrano 27* (BR); ***Lacs Edouard et Kivu***, Kaziba, 26 Sep 1952, *J.F.Laurent 574* (BR); ***Haut-Katanga***, Marungu, Kalewe, Apr 1944, *L.Dubois 1200* (BR); 30 km W de Mutshatsha, 28 Aug 1956, *P.Duvigneaud & J.Timperman 2530Co1* (BRLU); Marungu, Kasiki, Nov 1945, *P.Quarré 7363* (BR); Entre Masombwe et Lusinga, 21 Sep 1948, *W.Robyns 3643* (BR); Lubumbashi, 1937, *Salésiens 466* (BR, WAG). Burundi, Gitega, Bufundu, *A.Becquet 766* (BR); Kumuyange, 26 Sep 1971, *J.Lewalle 6132* (BR); Ruvironza, 15 Jul 1958, *G.Michel 5540* (BR); Mosso, Ruyigi, abords de Kinyinya, 13 Aug 1951, *G.Michel & J.Reed 85* (BR).

Notes. 1. Occasionally cultivated for its edible tubers; in Marungu known as “mizumbu” and, in Burundi, as “impombo” (kinyarwanda) or “inumbu” (kirundi).

2. Var. *esculentus* is quite variable in the length of the pedicel and the internodes of the thyrse; some specimens are more or less intermediate between var. *esculentus* and var. *densus* (e.g. *P.Quarré 7085* (BR), *J.Rammeloo 4690* [BR]).

Coleus esculentus var. *densus* (N.E.Br.) Meerts & A.J.Paton, comb. et stat. nov.

urn:lsid:ipni.org:names:77347690-1

Plectranthus densus N.E.Brown in Bull. Misc. Inform., Kew 1894(85): 12. 1894. Type: Tanzania, N of Lake Malawi (Nyassa), Oct 1880, *Thomson s.n*. (holotype K [K000431965]).(Basionym)

≡ *Coleus densus* (N.E.Br.) A.J.Paton, Phytokeys 129: 39. 2019.

= *Plectranthus dekindtianus* De Wild. Ann. Mus. Congo Belge, Bot., sér. 4, 2: 135. 1913. Type: DR. Congo, Bugege (?), Sep 1911. *A.Hock s.n*. (holotype BR [BR0000009824928]), syn. nov.

Description. Paton et al. (2009: 292), Paton et al. (2013: 241), as *Plectranthus densus* N.E.Br., restricted to specimens with inflorescence lax.

Distribution. SW Tanzania to S Tropical Africa.

Habitat and ecology. Dry woodlands, savannah, 1300–2000 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kahemba, route vers l'Angola, 31 May 1948, *P.Duvigneaud 955* (BRLU); ***Haut-Katanga***, Kambove, 17 Aug 1979, *H.Breyne 3735* (BR); Lubumbashi, Kasapa, 15 Sep 1972, *J.Bulaimu 533* (BR); Upemba, piste vers Mitwaba, 12 Apr 1947, *G.F.de Witte 2488* (BR); 10 km W of Mindingi, 21 Jul 1956, *P.Duvigneaud & J.Timperman 2067* (BRLU); Upemba, entre Masombwe et Lusinga, 21 Sep 1948, *J.Lebrun 3644* (BR); Luiswishi, 2 Oct 1974, *F.Malaisse 7965* (BR); Katanga, s.l., 21 Sep 58, *J.Plancke 119/1734* (BRLU); Upemba, 25 Aug 1949, *L.van Meel* in *G.F.de Witte 7555* (BR).

Burundi. Bururi, 21 Sep 1974, *J.Rammeloo 4690* (BR).

Note. *Plectranthus dekindtianus* De Wild. was synonymised with *Plectranthus tetragonus* Gürke by Paton et al. (2009); however, the type specimen lacks bristles on the stem and is better placed here

Coleus esculentus var. *primulinus* (Baker), comb. et stat. nov.

urn:lsid:ipni.org:names:77347691-1

Plectranthus primulinus Baker in Bull. Misc. Inform., Kew 107: 292. 1895. Type: Zambia, Mwero Plateau, 1894, *A.Carson 36* (holotype K [K000430746]).(Basionym)

Description. Closely related to var. *densus*, differing in the much shorter thyrses, with rachis obsolete, mostly grouped into a spiciform inflorescence in the upper part of the stem; calyx lobes 2–3 mm long, equalling the tube.

Distribution. Angola, Zambia, DR. Congo, W Tanzania.

Habitat and ecology. Savannah, wooded savannah, in DR. Congo often on Cu/Co or Mn rich soil, 1170–1830 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Upemba, Piste vers Mitwaba, 12 Apr 1947, *G.F.de Witte 2488* (BR); Kasompi Est, Jul 1956, *P.Duvigneaud & J.Timperman 2051* (BRLU); Kabwelunono copper hill, Jun 1997, *F.Malaisse, E.Kisimba, Y.Muzinga 134* (BR); Kwatebala copper hill, May 2007, *I.Parmentier 4347* (BR; WAG); Upemba, tête de source de la Katuba, Aug 1934, *P.Quarré 4213* (BR); Kipopo, 20 May 1982, *M.Schaijes 1397* (BR); Chabara, 11 Apr 1990, *Tropmetex 224* (BR, MO).

Notes. 1. Previous treatments (Paton et al. 2009, 2013) synonymised *Plectranthus primulinus* with *Coleus densus*. However, in DR. Congo, the two morphs can be readily recognised even though intermediates occur; therefore, we propose to recognise them at varietal rank. They occur in different habitats, var. *primulinus* being particularly frequent in steppic savannah on metal-rich soil in Haut-Katanga, where var. *densus* is rarely observed.

2. Specimens collected in the rainy season consist of leafy shoots without flowers, with leaves steadily decreasing in size upwards, the upper ones bract-like and often forming an apical coma; specimens collected in the dry season are mostly leafless and bear inflorescences in the upper part of the stem. Some specimens have particularly large leaves (up to 20 × 8 cm) with velvety tomentose indumentum (e.g. *G.F.de Witte 2488*).

***Coleus esculentus* var. *kolweziensis* Meerts & A.J.Paton, var. nov.**

urn:lsid:ipni.org:names:77347692-1
Fig. 4A–C

Type. DR. Congo, Haut-Katanga, Piste Nzilo-Kyamasumba, 10°30'29"S, 25°26'12"E, 1435 m elev., 1 Mar 1987, *M.Schaijes 3354* (BR [BR0000021718298], photos).

Diagnosis. Differs from the type in the following combination of traits: thyrses borne on pairs of ascending branches, at the 2–5 upper nodes of the stem, forming a panicle; bracts broadly ovate-elliptic, ca. 5 × 3 mm, 5-veined; rhizome creeping; stem leafy at flowering; leaves narrowly obovate, < 15 mm wide, pubescent on veins beneath, very shortly pubescent above.

Etymology. All collections of this variety originate from the region of Kolwezi in western Upper Katanga.

Distribution. Endemic to SE DR. Congo (Haut-Katanga).

Habitat and ecology. Steppic savannah, dry woodland, rocky slopes; 1300–1475 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Env. de Sakabinda, sources de la Kengere, 9 Apr 1971, *S.Lisowski* 23304 (POZG); Env. Kolwezi, près du village Muilu, 8 Apr 1971, *S.Lisowski* 23703 (POZG); without locality, 1937, *Salésiens 1264* (BR); 19 km SSE of Kolwezi, 13 Mar 1983, *M.Schaijes 1873* (BR); Piste Kolwezi-Musokantanda (Plateau de la Manika), 10°48'42"S, 25°15'59"E, 19 Feb 1989, *M.Schaijes 4305* (BR);

Note. This new variety has a restricted distribution range in the region of Kolwezi.

***Coleus foliatus* (A.J.Paton) A.J.Paton, Phytokeys 129: 46. 2019.**

≡ *Plectranthus foliatus* A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 284. 2009. Type: Tanzania, Sumbawanga District, Tatanda, Mbaa Hill, 25 Apr 1997, *S.Bidgood et al. 3459* (holotype K [K000194843], [K000194844]; isotype C, DSM, K, NHT).

Description. Paton et al. (2009: 284), Paton et al. (2013: 234), as *Plectranthus foliatus* A.J.Paton.

Distribution. SW Tanzania, N Zambia, Burundi, SE DR. Congo.

Figure 4. *Coleus esculentus* var. *kolweziensis* Meerts & A.J.Paton **A** habit **B** detail of inflorescence and bracts **C** detail of calyx **A** *M.Schaijes 3354* **B, C** *Breyne 1197*. Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 5 mm (**B**); 2 mm (**C**).

Habitat and ecology. Steppic savannah, scrub, mostly on highlands, often on shallow rocky soil, occasionally on copper-rich soil; 1500–2000 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Marungu, Kasiki, 20 Jun 1931, *G.F.de Witte 470* (BR); Tenke, *P.Duvigneaud & J.Timperman 2624E* (BRLU); Mitwaba-hôtel, steppe, 9 Sep 1956, *P.Duvigneaud & J.Timperman 2691Co* (BRLU); Marungu, 1 km S Mont Lusale, 27 Jun 1957, *P.Duvigneaud 3738C* (BRLU); Kundelungu, 6.4 km NNW Katshupa, 17 Oct 1966, *F.Malaisse 4660* (BR, LSHI); Poste de Mitwaba, Aug 1945, *G.Mortelmans 96* (BR); Domaine de Muhila, près de Kansimba, 1400 m elev., steppe, 7 Nov 1970, *S.Lisowski 23488* (POZG).

Burundi, Route Matana-Rutovu, km 15, 26 Feb 1966, *J.Lewalle 469* (BR); Bururi, 3 Feb 1968, *J.Lewalle 2760* (BR, P); Luvironza, Bututsi, 3 Mar 1955, *G.Michel 4702* (BR).

Notes. 1. New species record for DR. Congo. Widespread on the Mitwaba and the Marungu Plateau (Haut-Katanga).

2. *Coleus foliatus* is more variable in leaf shape in DR. Congo and Burundi compared to neighbouring regions; specimens with unusually narrow leaves (ca. 45 × 5 mm) are found in Burundi (e.g. *J.Lewalle 469*, *M.Reekmans 8659*); they differ from *C. duvigneaudii* in having opposite leaves, relatively short leaf blade and blunt leaf apex. In Upper Katanga, where *C. foliatus* and *C. duvigneaudii* are sympatric, more or less intermediate specimens occur (e.g. *S.Lisowski, F.Malaisse & J.-J. Symoens 1247*, *S.Lisowski, F.Malaisse & J.-J.Symoens 11295; A.Schmitz 3150*).

Coleus frederici **G.Taylor, J. Bot. 69 (suppl. 2): 159. 1931.**

≡ *Neomuellera welwitschii* Briq., Bot. Jahrb. Syst. 19: 180. 1894., non *Coleus welwitschii* Briq.

≡ *Plectranthus welwitschii* (Briq.) Codd, Fl. Pl. Africa 42: t. 1646. 1972. Type: Angola, Pungo Andongo, 14 Apr 1857, *F.Welwitsch 5544* (holotype BM; isotype C, K, LISU, MEL, PRE).

Description. Short-lived perennial (annual or biennial after Hiern [1900]) herb, not aromatic (after Hiern [1900]), 0.60–1.20 m high. Stem erect, quadrangular, more or less crassulescent, puberulent, with very short retrorse hairs and sparse longer patent hairs and red sessile glands, branched. Leaves opposite, spreading, petiolate; blade ovate, 4.0–10.0 × 3.0–6.0 cm (up to 22 × 18 cm in Angola), base cordate to broadly rounded and shortly attenuate into the petiole, apex subacute, margin flat, crenate, teeth unequal in depth and breadth, with both sides subequal, the largest ones up to 5 mm deep; upper surface subglabrous, lower surface papillate on veins, rarely pubescent and with dense red sessile glands, ca. 5 secondary veins on either side; petiole 1.0–3.5 cm (up to 18 cm in Angola), pubescent as stem. Inflorescence lax, 10–21(–30) cm long, with 6–13 verticils spaced 15–20 mm, cymes on a 5–15 mm long peduncle, dichasial, with two subequal opposite divergent cincinni with 1 median flower, cincinni ca. 5–12 mm long, (3–)5-flowered, bracts ovate, ca. 3 mm long, early deciduous, pedicel 3–4 mm long, inserted eccentrically on calyx behind upper lobe. Flower: calyx ca. 2.5 mm long at anthesis, subglabrous, with red sessile glands, upper lip ovate, acute, ca. 1.4 mm long, upright, lower lobes much shorter, narrowly triangular, calyx at fruiting (in Angolan materials) more or less urceolate, contracted at throat, lobes parallel; corolla white or blue, with red sessile glands, ca. 18 mm long, tube sigmoid, with a narrow parallel-sided lower part ca. 4–5 mm long and a broader progressively dilated part ca. 5 mm long, lower lip ca. 9 mm long, cucullate, 5 mm deep, stamens fused, slightly exserted, anther 0.9 mm long; style undivided. Nutlets not observed (obovoid, slightly compressed, smooth, yellowish, in Angolan materials).

Distribution. Angola, DR. Congo.

Habitat and ecology. Shady places, scrub, forest fringe; 600–1100 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kwango, Tambu [Tambo], près du village, 14 Apr 1953, *H.Callens 1173* (BR); ***Haut-Katanga***, Kundelungu, premier gué sur rivière Kalunda, entre Katwe et Lofoï, 19 May 1984, *A.Bodenghien 139* (BR).

Notes. 1. New species record for DR. Congo.

2. The materials collected in DR. Congo are at an early stage of flowering; however, the diagnostic character of calyx contracted at throat after anthesis is conspicuous in a few flowers in *H.Callens 1173*.

3. The specimen *A.Bodenghien 139* (BR), collected ca. 1000 km east of previously known localities, is unusual in having lower leaf surface pubescent on veins.

Coleus globosus **(Ryding) A.J.Paton, Phytokeys 129: 50. 2019.**

≡ *Plectranthus globosus* Ryding, Bull. Jard. Bot. Natl. Belg. 66: 101. 1997. Type: DR. Congo, Haut-Katanga, Kundelungu Plateau, 20 Mar 1971, *S.Lisowski 23152* (holotype POZG [POZG-V-0100131], C photo).

Description. Herb, probably perennial, 0.30–0.40 m high. Stem quadrangular, pubescent, with thin patent hairs and orange sessile glands. Leaves sessile, ascending to erect, narrowly elliptic to narrowly ovate, the lowermost ones broadly elliptic, 3.0–4.0 × 0.6–0.9 cm, apex obtuse to subacute, base narrowly rounded to subcordate at base, sparsely pubescent, with eglandular hairs on lower surface of veins and orange-red sessile glands on both surfaces, margin shallowly crenate to subentire, ± revolute, secondary veins diverging at a very narrow angle and distally subparallel to the margin. Inflorescence unbranched, of 1 or 2 widely spaced subglobose verticils; bracts broadly ovate ca. 6 × 6 mm, apex acuminate, deciduous; cymes 12–20-flowered; pedicel ca. 1.5 mm long; flower: fruiting calyx only slightly zygomorphic, glandular, pubescent, lobes subequal, ovate-triangular, apex subacute to obtuse, upper lobe slightly decurrent; corolla 12–14 mm long, tube 7–8 mm long, upper lip narrow, 4-lobed, with narrow lateral lobes, lower lip cucullate, 4–5 mm long, stamens connate over ca. 0.5 mm, anthers ca. 0.5 mm diam., with orange sessile glands. Nutlets ± 1.3 × 1.1 mm, dark brown, smooth, glossy.

Distribution. Endemic of SE DR. Congo (Haut-Katanga, Kundelungu Plateau).

Habitat and ecology. Steppic savannah on highlands, on moist soil, riverbanks, often near ponds; 1500–1700 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kundelungu, about 5 km NNE of the western source of Lutshipuka, 19 Feb 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 2669* (POZG); about 6 km WNW of the western source of Lutshipuka, 25 Mar 1969, S.*Lisowski, F.Malaisse & J.-J.Symoens 3793* (POZG); Mont Kabwe, 28 Mar 1971, *S.Lisowski, F.Malaisse & J.-J.Symoens 23610* (POZG).

Coleus goetzenii **(Gürke) A.J.Paton, Phytokeys 129: 50. 2019.**

≡ *Pycnostachys goetzenii* Gürke in Götzen, Durch Afr., reimpr.: 8. 1896. Type: Rwanda, Sabinyo, flanc sud, ca. 2400 m elev, 1 Feb 1972, *P.Auquier 2369* (neotype BR [BR0000013410254] designated here; isoneotype K, LG, MO [MO100924134], WAG).

= *Pycnostachys vulcanicola* Lebrun & L.Touss., Bull. Jard. Bot. État Bruxelles 17: 71. 1943. Type: DR. Congo, Virunga, Volcan Karisimbi, Feb 1932. *J.Lebrun 5006* (holotype BR [BR0000008909725], [BR0000008910059]; isotype K, MO).

Description. Paton et al. (2009: 409), as *Pycnostachys goetzenii* Gürke.

Distribution. EC Tropical Africa (Virunga Mts.).

Habitat and ecology. Mountain forest with bamboo, *Hypericum*, and *Hagenia*; 2300–2800 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Tshakabindi, NE Visoke, 25 Jan 1955, *G.F.de Witte 11548* (BR, WAG); Versant E du Nyiragongo, Nov 1937, *J.Lebrun 8727* (BR); Ruwenzori, entre les gites de Mahangu et de Kalonge, 31 Dec 1977, *J.Lejoly 2570* (BR); Kabara, flanc E du Karisimbi, 21 Aug 1937, *J.Louis 5428* (BR, K, MO, P); Nyamuragira, gegen Biliba, 27 Aug 1954, *Stauffer 230* (BR, K, MO, WAG).

Rwanda, Lac Gando, Mar 1935, *G.F.de Witte 2298* (BR); Route Butare-Cyangugu, km 72, 9 May 1980, *G.Troupin 16246* (BR, K).

Burundi, entre Mabai et la rivière Kavumande, 12 Jun 1950, *H.Renier 238* (BR).

Note. Neotypification of *Pycnostachys goetzenii* Gürke. The holotype has disappeared (Rwanda, Kirunga Volcano [Virunga Mts.], north of Lake Kivu, 7500–8000 ft. elev., *G.Goetzen 98* [holotype B]); no isotype has been found. We select as the neotype *P.Auquier 2369*, matching the protologue, collected in the same region and at about the same altitude as the holotype.

Coleus gracilipedicellatus **(Robyns & Lebrun) A.J.Paton, Phytokeys 129: 51. 2019.**

≡ *Holostylon gracilipedicellatum* Robyns & Lebrun, Ann. Soc. Sci. Bruxelles, Sér. B 49: 103. 1929. Type: DR. Congo, Katanga, Pweto to Baudouinville [Moba], between Kayabala and Lungulungu, 29 Apr 1926. *W.Robyns 2196* (holotype BR [BR0000008908674], [BR0000008908032], [BR0000008908681]; isotype BM fragment, BRLU fragment, E, K).

= *Plectranthus baumii* Gürke in O. Warburg (ed.), Kunene-Sambesi Exped.: 356. 1903, non *Coleus baumii* Gürke. Type: Angola, Kubango, Massaca, 19 Oct 1899. *H.Baum 283* (holotype B destroyed; isotype BM [BM000564009], E (as 238), G [G00437838], K, W [W19010009248], Z [Z-000018989]).

Description. Paton et al. (2013: 233), as *Plectranthus baumii* Gürke.

Distribution. Southern DR. Congo to Botswana.

Habitat and ecology. Miombo woodland, steppic savannah on rocks, 1300–1690 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Katofio, 18 Aug 1948, *P.Duvigneaud 1378* (BRLU); Territ. Sakania, env. Kipushia, Mont Kasamwa, 29 Apr 1971, *S.Lisowski 23485 & 23495* (POZG); Fungurume, 23 Jul 2007, *B.Senterre 4638* (BR); Lubumbashi, 1937, *Salésiens 355* (BR, WAG); Lukafu, Apr 1900, *E.Verdick 455* (BR).

Coleus gracillimus **(T.C.E.Fr.) Robyns & Lebrun, Ann. Soc. Sci. Bruxelles, Sér. B 49: 106. 1929**

≡ *Englerastrum gracillimum* T.C.E.Fr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 69. 1924. Type: DR. Congo, Mt Corva, 15 May 1895, *G.Descamps s.n.* (holotype B destroyed; isotype UPS [V-712081], K fragment).

≡ *Plectranthus gracillimus* (T.C.E.Fr.) Hutch. & Dandy, Bull. Misc. Inform. Kew 1926: 481. 1926.

Description. Paton et al. (2009: 290), Paton et al. (2013: 238), as *Plectranthus gracillimus* (T.C.E.Fr.) Hutch. & Dandy.

Distribution. Widespread in Tropical Africa.

Habitat and ecology. Miombo woodland, savannah, rocks, occasionally on copper-rich soil and on saline soil, 300–1575 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Kimbidi, 21 Apr 1959, *L.Pauwels 2571* (BR); Kibotuka, 2 Sep 1975, *L.Pauwels 5429* (BR, WAG); ***Kasaï***, Mayala, 20 Apr 1953, *H.Callens 1536B* (BR); Kwango-Mela, 20 Mar 1955, *R.Devred 1680* (BR); Kwango, entre Dinga et Mpandi, 5 May 1944, *R.Germain 2238* (BR); ***Bas-Katanga***, 30 km S Kamina, 4 Jul 1948, *P.Duvigneaud 1126Co1* (BRLU); Route Kayembe-Mukulu-Kamina, 9 May 1959, *S.Risopoulos 1071* (BR); N de Mabwe, 2 May 1949, *L.van Meel* in *G.F.de Witte 6279* (BR); ***Lacs Edouard et Kivu***, Ubwari Peninsula, 8 Oct 1979, *Y.&T.Ankei 79/0128* (BR); ***Haut-Katanga***, Kisenge, colline de Kapolo, 1956, *P.Duvigneaud & J.Timperman 2341* (BRLU); Upemba, Ganza, 30 May 1949, *L.van Meel* in *G.F.de Witte 6457* (BR); Tenke, colline Pumpi, 26 May 2007, *I.Parmentier & E.Kisimba 4606* (BR); Mont Mukuen, 6 Jun 1947, *A.Schmitz 698* (BR).

Burundi, Bururi, Rumonge, 5 Jun 1966, *J.Lewalle 892* (BR); Kininya Mosso, 28 Jun 1952, *G.Michel 3104* (BR).

Note. New species record for Burundi.

Coleus guerkei **(Briq.) A.J.Paton, Phytokeys 129: 53. 2019.**

Type. Angola, Cuito (Kuito), 1 Apr 1900. *H.Baum 789* (holotype B destroyed; isotype E [E00193514], G [G00435305], HBG [HBG518375], K, M [M0104725], S [S-G-3335], W [W1901-0009329]).

Description. Paton et al. (2009: 317), Paton et al. (2013: 259), as *Plectranthus guerkei* Briq.

Distribution. Widespread in Tropical & South Africa.

Habitat and ecology. Savannah on moist soil, marshland; 100–1800 m elev.

Additional specimens. DR. Congo, ***Mayumbe***, Gimbi, 17 Jun 1948, *Laurent 713* (BR); ***Bas-Congo***, Ntadi, 21 Apr 1944, *R.Germain 2140* (BR); Kisantu, 1900, *J.Gillet 1337* (BR); Kibotuka, 2 Sep 1975, *N'Kunga 5429* (BR); ***Kasaï***, Gombe ya Tumba, 16 Apr 1953, *H.Callens 1274* (BR); Kananga, 24 Nov 1981, *S.Lisowski 66927* (BR); Kapanga, Jun 1933, *F.Overlaet 923* (BR); Panzi, 1925, *H.Vanderyst 16001* (BR); ***Bas-Katanga***, Gandajika, 12 Oct 1956, *L.Liben 1705* (BR); Katumanga, 29 Oct 1956, *L.Liben 1811* (BR); ***Ubangi-Uele***, Gangala na Bodi, 21 Nov 1942, *C.Cornet d'Elzius et al. 373* (BR); Faradje, 28 Dec 1949, *Costermans 62* (BR); Garamba, piste centrale vers km 82, 18 Feb 1952, *G.Troupin 65* (BR); ***Lac Albert***, Irumu, 9 Mar 1914, *J.Bequaert 2844* (BR); Kerekere, 19 Jan 1960, *D.Froment 649* (BR); ***Haut-Katanga***, Dilolo, riv. Mangoa, 20 Aug 1956, *P.Duvigneaud & J.Timperman 2410* (BRLU); Baudouinville [Moba], 5 May 1926, *W.Robyns 2241* (BR).

Rwanda, Agatete, 19 Nov 1953, *L.Liben 963* (BR).

Burundi, Musumba Mosso, 10 Jun 1952, *G.Michel 2674* (BR); Mosso, Ruyigi, 4 Sep 1951, *G.Michel & J.Reed 178* (BR); Route Rusengo-Cankuso, km 5, 16 May 1978, *M.Reekmans 7003* (BR, WAG).

Coleus hadiensis **(Forssk.) A.J.Paton, Phytokeys 129: 54. 2019.**

≡ *Plectranthus hadiensis* (Forssk.) Schweinf. ex Sprenger, Wiener Ill. Gart.-Zeitung 19: 2. 1894. Type: Yemen, in montibus Hadiensis [Hadiyah], 1763, *P. Forsskål 348* (holotype C [C10002654]).

= *Plectranthus zatarhendii* sensu Troupin & Ayob., Fl. Rwanda 3: 340. 1985., non (Forsskal) E.A.Bruce.

= *Plectranthus fragrans* Lebrun & L.Touss., Bull. Jard. Bot. État Bruxelles 17: 70. 1943. Type: DR. Congo, Katanda, Sep. 1937. *J.Lebrun 7618* (holotype BR [BR0000006262556]; isotype K, P).

Description. Paton et al. (2009: 300), Paton et al. (2013: 247), as *Plectranthus hadiensis* (Forssk.) Sprenger.

Distribution. Widespread, Egypt to South Africa, Arabian Peninsula, Maldives, Sri Lanka.

Habitat and ecology. Savannah, xerophilous scrub, woodland, rocks; 950–2150 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Beni, Kasindi, 10 Aug 1914, *J.Bequaert 5233* (BR); Katanda, Aug 1937, *J.Lebrun 7589* (BR); Katanda, Sep. 1937, *J.Lebrun 7618* (BR); Ruindi, 1937, *J.Lebrun 7933* (BR, YBI); Escarpement de Kabasha, 7 Dec 1934, *G.F.de Witte 2172* (BR); Lac Edouard, baie de Kabale, 24 Dec 1953, *D.van der Ben 972* (BR).

Rwanda, Ibere Rya Bigogwe, 8 Feb 1984, *F.-X.Ayobangira 1673* (BR); Bugesera, env. Karama, 12 Mar 1972, *G.Bouxin 1365* (BR); Mayaga, 27 May 1954, *L. Liben 1202* (BR); Mutara, env. Gabiro, 5 Apr 1957, *G.Troupin 3123* (BR); Akagera, Lac Ihema, 1 May 1973, *G.Troupin 15042* (BR).

Note. In the Flore du Rwanda (Troupin and Ayobangira 1985), *C. hadiensis* is erroneously referred to as *Plectranthus zatarhendii*, a species absent from Central Africa.

Coleus heterotrichus **Briq., Bull. Soc. Roy. Bot. Belgique 40: 40. 1901.**

Figs 1G–H, 2D

= *Coleus claessensii* De Wild., Bol. Soc. Ibér. Ci. Nat. 19: 117. 1920. Type: DR. Congo, Mobwasa, 1910, *J.Claessens 741* (lectotype BR [BR0000006261863]; isolectotype BR [BR0000006262198], designated here), syn. nov.

≡ *Calchas claessensii* (De Wild.) P.V.Heath, Calyx 5: 160. 1997.

= *Coleus ringoetii* De Wild., Contr. Fl. Katanga: 174. & Ann. Soc. Sci. Bruxelles 41(2): 50. 1921. Type: DR. Congo, Shinsenda, Mar 1912, *A.Ringoet 546* (holotype BR [BR0000006262907], [BR0000006263232]), syn. nov.

= *Coleus termetophilus* De Wild., Contr. Fl. Katanga: 175. Ann. Soc. Sci. Bruxelles 41(2): 50. 1921. Type: DR. Congo, Kundelungu, swamps, 13 Mar 1908, *T.Kassner 2618* (lectotype BR [BR0000008732170], right-hand specimen only; designated here; isolectotype Z [Z-000018897]), syn. nov.

= *Coleus quarrei* Robyns & Lebrun, Rev. Zool. Bot. Africaines 16: 3. 1928. Type: DR. Congo, Elisabethville [Lubumbashi], ferme de Kibembe, 30 Jul 1927, *P.Quarré 608* (holotype BR [BR0000006262570]), syn. nov.

= *?C. eetveldeanus* Briq., Bull. Soc. Roy. Bot. Belgique 37: 73. 1899. Type: DR. Congo, Haut-Katanga, M'Toa, 15 May 1899, *G.Descamps s.n*. (holotype BR [BR0000008109156]).

Type. DR. Congo, Bolobo, Jun 1891. *F.Demeuse 455* ["1155" in the protologue in error] (holotype BR [BR0000021454103]; isotype G [G00435192]).

Description. Annual herb, occasionally scrambling, aromatic, (0.15–)0.25–0.90(–2.00) m high; rootstock fibrose, without tubers. Stem erect, simple or branched, quadrangular, somewhat lignified in lower part in robust specimens, in the lower part with very short, papilliform (ca. 0.1 mm long) patent to recurved hairs and sessile red glands or very short glandular patent hairs and sparse longer patent hairs especially at nodes, in the inflorescence with mostly very short (ca. 0.1 mm long, papilliform), patent to slightly recurved eglandular and gland-tipped hairs, and sparse long multicellular patent hairs (ca. 1 mm long), these sometimes almost lacking. Leaves opposite, ascending to spreading, petiole 1.0–4.5(–10) cm long, pubescent like the stem, with dense very short hairs (retrorse or patent) and sparse, much longer patent hairs; blade occasionally with a purplish spot in the middle, ovate to broadly ovate-triangular, (1.0–)3.0–7.0(–12) x (1.0–)2.5–5.0(–8.5) cm, apex acute to obtuse, base broadly rounded, or truncate to subcordate and then shortly attenuate into the petiole, membranous, ca. 4–5 pairs of secondary veins, margin crenate, upper surface with sparse, appressed, antrorse hairs, lower surface very shortly pubescent on veins, (occasionally papillate over the whole surface), rarely with long patent hairs on veins, with red sessile glands. Inflorescence lax, (5–)12–32(–40) cm long, 2–6(–10) cm broad at fruiting, with (2–)7–20(–28) verticils spaced 10–25(–40) mm, bracts whitish, ovate, acuminate, cucullate, 2–7 mm long, ciliate, early deciduous (very rarely persistent at lower verticils), cyme with a 1–2 mm long peduncle, often dichasial, each cyme consisting of two subequal cincinni, diverging at right angle, elongating to 5–20(–50) mm in fruit, lax, each with 4–7(–20) flowers (i.e. cyme with 9–15(–41) flowers), spaced ca. 3 mm, pedicels 2–5(–6) mm long, with very short papilliform, eglandular and gland-tipped hairs and occasional longer multicellular hairs and red sessile glands, pedicel curving at tip, inserted eccentrically in front of calyx upper lobe. Flower: calyx 1.5 mm long at anthesis, 3–5.5 mm in fruit, shortly pubescent and with red sessile glands, tube campanulate ca. 2 mm long, throat truncate, upper lobe broadly ovate to almost round, 1.5–2.5 × 1.5–2.5 mm, apiculate, very shortly decurrent, curving upwards, lateral lobes of lower lip oblong-rectangular, truncate, lower lobes fused into an oblong linear lower lip ca. 2.5–3 mm long with two acute teeth. Corolla blue, with red sessile glands, 8–13 mm long, tube strongly sigmoid 4 mm long, widening near throat, upper lip 1–2 mm long, lower lip 4–7 mm long, 2.5 mm deep, thinly puberulent, stamens fused, tube sigmoid; anther 0.5 mm.

Distribution. Sierra Leone, Ivory Coast, Nigeria, Central African Republic, Ethiopia, Sudan, South Sudan, Tanzania, Mozambique, Malawi, Zambia, Angola.

Habitat and ecology. Rainforest, savannah, dry woodland, dry evergreen forest, fallow fields, ruderal, disturbed ground, rock outcrops, mostly in shady places, occasionally on copper-rich or saline soil; 300–1750 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Kimbuba, 27 Oct 1958, *Pauwels 386* (BR); Kimbidi, 21 Apr 59, *L.Pauwels 2536* (BR); ***Kasai***, Lisha, 28 Apr 1888, *F.Hens C6* (Z, marked as “holotype” in error); Kapanga, 1934, *F.Overlaet 1202* (BR); Thielen Saint-Jacques, *H.Vanderyst 21575* (BR); ***Bas-Katanga***, Tshikamba près Mutombo-Mukulu, Jun 1931, *P.Quarré 2512* (BR); Kamina, 11 Mar 1959, *S.Risopoulos 871* (BR); Kiala, Dec 1954, *Thiébaud 210B* (BR); ***Forestier Central***, Eala, 28 Nov. 1943, *R.Germain 1731* (BR); Entre Bokuma et Bokatola, Sep 1933, *J.Lebrun 1313* (BR); Yangambi, île Yalututcha II, 18 Aug 1938, *J.Louis 10905* (BR, P, U, US); Route Kisangani-Lubutu, 20 Nov 1982, *L.Pauwels 6592* (BR); ***Ubangi-Uele***, Gatanga, Jan 1936, *A.M.De Graer 484* (BR); Garamba, 13 Oct 1951, *H.De Saeger 1438* (BR); Entre Businga et Banzyville [Mobayi-Mbongo], Jan 1930, *J.Lebrun 2009* (BR); ***Lac Albert***, Kurukwata, 4 Nov 1957, *P.Gérard 3586* (BR); ***Lacs Edouard et Kivu***, Ruzizi, Route Uwira-Mbaraka, km 150, May 1950, *Germain 7009* (BR); Ironga, Mutongo, *Gutzwiller 2734* (BR); Lac Mokoto, 21 Jul 1953, *D.van der Ben 634* (BR); ***Haut-Katanga***, Mwashya, May 1939, *H.J.Bredo 2757* (BR); Upemba, riv. Kenia, 28 Mar 1947, *G.F.de Witte 2440* (BR); Kabiashia, 19 Mar 68, *F.Malaisse 5438* (BR, LSHI); Lubumbashi, Mar 1933, *P.Quarré 3159* (BR); Pweto, chutes de la Kafisia, 18 Apr 1926, *W.Robyns 2021* (BR); Luishia, 3 Apr 1990, *Tropmetex 82* (BR, K, MO, MPN, WAG). Burundi, Lac Nyanza, *J.Lewalle 6063* (BR); Route Bugarama, km 8, 2 Jun 1976, *M.Reekmans 5184* (BR); Kabezi, 9 Apr 1978, *M.Reekmans 6892* (BR, WAG); Bururi, Rumonge, 20 Mar 1981, *M.Reekmans 9851* (BR, WAG).

Sierra Leone, Bumban National Park, 25 Sep 1967, *J.K.Morton & S.L.Cole 4920* (SL, K, GC).

Ivory Coast, Inselberg near Duékoué 6°45'N, 7°22'W, 25 Oct 1991, *S.Porembski 1000* (B, K).

Nigeria, Jos Plateau, Naraguta, 18 Oct 1957, *F.N.Hepper 1076* (BR, K). Cameroon, about 15 km. NE of Meiganga, 24 Nov 1964, *W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 4039* (BR).

Sudan, near summit of Gebel Lothir, 27 Nov 1930, *N.D.Simpson 7605* (K).

South Sudan, Kajiko north, 29 Oct 1982, *P.Kosper 128* (K). Ethiopia, Wellega Region, ca. 30 km S of Asosa. 9°55'N, 34°40'E, *E.I.Friis et al. 7878* (AAU, C, K).

Tanzania, Kigoma rural Distr, Gobe Stream Reserve, Kakombe Valley, 04°39'50"S, 29°37'22"E, 15 May 1999, *P.Gobbo et al. 320* (K, MO).

Mozambique, Serra Macula, Mercula, Simba Camp, 12°04.5'S, 37°38'E, 10 Jun 2003, *J.S.Golding, J. Timberlake & P.Clarke 32* (K).

Malawi, St. Kizito Seminary, Mtandere Mission, 14 miles E of main road, 25 Apr 1971, *Pawek 4668* (K, MAL).

Zambia: Choma Distr., Sinazongwe/Choma road, 11.6 km from the junction, 16°52'08"S, 27°16'23"E, 10 Mar 1997, *B.Luwiika, D.K.Harder, H.H. Schmidt, & N.B.Zimba* 608 (BR, K, MO).

ANGOLA. Lunda Norte, 25 km S of Capaia and 55 km WSW of Lucapa, 8°33'25"S, 20°15'13"E, 1 Apr 2013 *D.G.Goyder & I.Darbyshire 7175* (K).

Notes. 1. *Coleus heterotrichus* has been overlooked by recent floras, being synonymised with *C. bojeri*. In the *C. bojeri* complex, it has a most distinctive combination of traits, including long cincinni and stem pubescence of short papilliform hairs and sparse long multicellular hairs; it also tends to have larger leaves with cordate base, but this trait is more variable. Some poorly-grown specimens have short cymes and can be deceptive, for example, *T.Kassner 2652* (BR, P), *J.Bequaert 3100* (BR), but indumentum is typical.

2. *C. heterotrichus* is one of the most widespread *Coleus* species in Central Africa, with a surprisingly broad ecological range, from rainforest to rocky outcrops of Katanga.

3. *C. claessensii* De Wild. is a morphotype with exceptionally long cincinni. *C. quarrei* De Wild. is a dwarf form, branching from the base.

4. *Coleus eetveldeanus* was synonymised with *Plectranthus dupuisii* (= *C. welwitschii*) by Paton et al. (2019); it probably belongs here, differing from typical *C. heterotrichus* in the shorter pedicels (1–2 mm long); however, underground parts are missing and conclusive placement is not possible.

5. Bracts are occasionally more or less persistent (e.g. *M.Micha 349*, *M.Reekmans 436*).

6. Lectotypification of *Coleus claessensii* De Wild. *J.Claessens 741* (BR [BR0000006261863]) is selected as the lectotype because it is the most complete specimen. Remaining syntype: *A.Sapin s.n*. (syntype BR), DR. Congo, Ekuta on the Lua, 1912.

7. Lectotypification of *Coleus termetophilus* De Wild. The very brief protologue published in 1921 without a Latin diagnosis (De Wildeman 1921a) indicates "Elisabethville (Homblé)" as the type. A much more extensive protologue, with a Latin diagnosis (De Wildeman 1921b), indicated the following syntypes: *Homblé 154, Homblé 220, Ringoet 397, Ringoet* in *Homblé 534* and *Kassner 2618*. Of all these specimens, only two sheets are identified as *Coleus termetophilus* in De Wildeman's handwriting, i.e. [BR0000008732170] and [Z-000018897]. The sheet [BR0000008732170] has two collecting labels, i.e. the original label "*Homblé 220*" and a posterior label "*Kassner 2618*". It comprises two specimens marked "a" (right-hand) and "b" (left-hand), respectively. The label in the left-hand corner of the sheet bears the following note in De Wildeman's handwriting: "a) *Coleus termetophilus* De Wild. n.sp.; b) *Coleus homblei* De Wild.". The protologue of *C. termetophilus* ("pétiole atteignant 6 cm de long, limbe ovale, tronqué à la base") corresponds only to the right-hand specimen (*T.Kassner 2618*). The other specimen (*Homblé 220*) is *C. homblei* De Wild. Another sheet in BR is also labelled "*Homblé 220*" [BR0000017710053], with three specimens also corresponding to *Coleus homblei* De Wild., clearly not matching the protologue of *C. termetophilus*. Therefore, *Homblé 220* must be excluded from the original materials of *C. termetophilus*. The right-hand specimen on sheet [BR0000008732170] corresponds to *T.Kassner 2618* and is most likely a duplicate from the gathering *Kassner 2618* in Z [Z-000018897]. In the protologue of *C. termetophilus*, De Wildeman wrote about *T.Kassner 2618*: "ce dernier échantillon provenant de l'herbier de Zürich, mis à notre disposition par le Dr. H. Schinz…" indicating that De Wildeman had indeed received a duplicate. Another sheet in BR [BR0000017710183] is also a duplicate of *T.Kassner 2618*, donated

by P, apparently not seen by De Wildeman. Based on this, I designate *T.Kassner 2618* (right-hand specimen on sheet [BR0000008732170) as the lectotype of *Coleus termetophilus*; *T.Kassner 2618* [Z-000018897]; [BR0000017710183] are isolectotypes.

8. New species record for Sierra Leone, Ivory Coast, Nigeria, Central African Republic, Ethiopia, Sudan, South Sudan, Tanzania, Mozambique, Malawi, Zambia and Angola.

Coleus hildei **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347693-1
Fig. 5A–F

Type. DR. Congo, Haut-Katanga, Parc national de l'Upemba, flancs du muleshi, stream Sense, 1400 m elev., 24 Feb 1948, *G.F.de Witte 3455* (holotype BR [BR0000017707978]; isotype K).

Diagnosis. Related to *Coleus bojeri* and other species formerly referred to the genus *Solenostemon* on account of the lower calyx lobes fused into a lip, differing in the following combination of traits: rootstock bearing fusiform tubers, petiole winged over the whole length, leaf apex acute to acuminate, pedunculate cyme, longer pedicels (mostly 3–7 mm long), longer fruiting calyx (5–7 mm long).

Description. Perennial herb, ca. 0.3–0.9 m high; rootstock fibrose, with a fascicle of fusiform tubers 1–3 cm long (rarely collected). Stem erect, most often simple, occasionally sparingly branched, quadrangular, puberulent, with very short adpressed retrorse hairs and red sessile glands, becoming denser and patent in the inflorescence. Leaves opposite, ascending, petiolate, occasionally with fascicules of young leaves in the axils in robust specimens; blade thin, membranous, ovate to narrowly ovate, apex acute to long acuminate (often obtuse in lowermost leaves), base rounded to cuneate, then attenuate and decurrent on the petiole, margin regularly crenate to serrate (ca. 2–3 teeth/ cm), (2.6–)6–8.5 × (0.8–)1.2–3.8 cm, 3–5 pairs of secondary veins, upper surface subglabrous to very shortly pubescent, with appressed hairs pointing to tip, lower surface very shortly pubescent on mid-vein (retrorse hairs) and reticulation, glabrous elsewhere save numerous red sessile glands (ca. 20/mm^2); petiole 0.7–3.5(–4.5) cm long, very narrowly winged, ciliate. Inflorescence terminal, simple or with 1 or 2 pairs of basal branches, lax, (6–)10–30 cm long, 15–25 mm wide (corollas excluded) at anthesis, up to 4 cm wide in fruit, verticils 10–15(–40) mm apart, bracts membranous, cucullate, ovate-elliptic, ca. 6 b×3 mm, contracted into an acumen, caducous or occasionally persisting, shortly pubescent outside and with red sessile glands; cymes with a 1–8 mm long peduncle, ascending to spreading, the lowermost cymes dichasial, with the basal branches diverging at an open angle, 7–11(–19)-flowered, branches with mixed indumentum of papillae and short spinulose hairs, cincinni elongating to 2 cm in fruit, pedicel variable in length in a cyme, (1–)3–7(–12) mm long, decreasing in length from base to top of cyme, inserted very eccentrically opposite the upper calyx lobe. Flower: calyx ca. 2 mm long at anthesis, very shortly pubescent and with red sessile glands, fruiting calyx 5–7 mm long, tube 1.5–2 mm long, upper lobe ovate, ovate-elliptic to obovate-elliptic, ca. 3 mm long, acute to rounded, recurved, slightly decurrent, lateral lobes ca. 1.5–2 mm long,

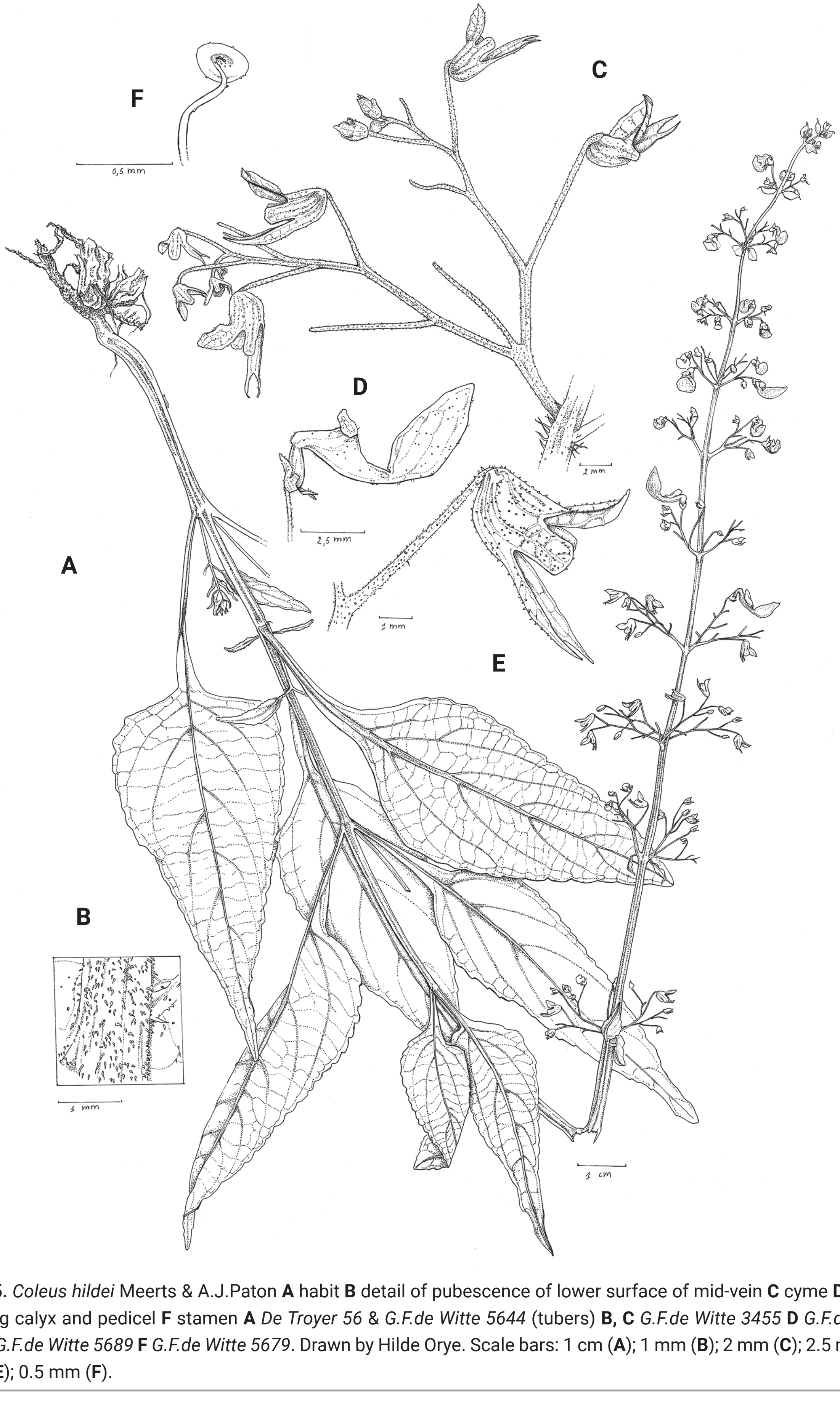

Figure 5. *Coleus hildei* Meerts & A.J.Paton **A** habit **B** detail of pubescence of lower surface of mid-vein **C** cyme **D** flower **E** fruiting calyx and pedicel **F** stamen **A** *De Troyer 56* & *G.F.de Witte 5644* (tubers) **B, C** *G.F.de Witte 3455* **D** *G.F.de Witte 5679* **E** *G.F.de Witte 5689* **F** *G.F.de Witte 5679*. Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 1 mm (**B**); 2 mm (**C**); 2.5 mm (**D**); 1 mm (**E**); 0.5 mm (**F**).

truncate to obtuse, often slightly contracted near middle, lower lobes fused into a linear lip ca. 4 mm long, markedly longer than the other lobes, straight to slightly curved upwards distally, ending in two subaristate teeth ca. 1.5–2 mm long; corolla ca. 12–13 mm long, tube strongly sigmoid, longer than calyx, widening near throat, lower lip. ca. 7 mm long, 3–4 mm deep, with red sessile glands, upper lip ca. 2–3 mm long, bilobate; staminal filaments fused, anthers subglobose, connective often with 2–3 red sessile glands. Nutlets subglobose, smooth, pale brown, densely red-speckled, ca. 1 mm.

Etymology. Dedicated to Hilde Orye, eminent botanical illustrator, chairwoman of the association of Belgian botanical artists, who produced all the original illustrations of this article.

Distribution. Endemic of SE DR. Congo (Haut-Katanga).

Habitat and ecology. Miombo woodland, scree, rocky hills; 800–1500 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Mukulakulu, forêt claire sur sol caillouteux, 24 Mar 1953, *De Troyer 56* (BR); Parc national de l'Upemba, rive droite de la Kalule Nord, contreforts du Mont Kia, près de Biamabwa, 1090 m elev., forêt katangaise d'altitude, 28 Feb 1949, *G.F.de Witte 5644* (BR); Versant N du Mont Kia, rive droite de la Kalule Nord, forêt katangaise d'altitude, saxicole sur éboulis, vers 1090 m elev., 1 Mar 1949, *G.F.de Witte 5679*, *5689*, *5690* (BR); Kundelungu, 830 m elev., forêt claire, exp. SO, pente 45°, 29 Jan 1954, *R.Desenfans 4974* (BRLU); Fungurume, Shandiranzoro west, 21 Mar 2007, *F.Malaisse & E.Kisimba 372* (BR).

Notes. 1. *C. hildei* belongs to the group of species formerly referred to the genus *Solenostemon* (lower calyx lobes fused into a lip). It has affinities with the *Coleus bojeri* complex. It differs in the tuberous roots, the much taller habit, the pedunculate, dichasial cymes, the longer pedicels, the larger fruiting calyx and the winged petiole.

2. Vernacular name: tombwe (in kiluba).

Coleus homblei De Wild., Contr. Fl. Katanga: 174. & Ann. Soc. Sci. Bruxelles 42(1): 49. 1921.

= *Plectranthus sigmoideus* A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 333. 2009., syn. nov.
≡ *Coleus sigmoideus* (A.J.Paton) A.J.Paton, Phytokeys 129: 97. 2019. Type: Zambia, track opposite turning to Mbala (Abercorn) Club, *H.M.Richards 4353* (holotype K [K000070564]), syn. nov.

Type. DR. Congo, Elisabethville [Lubumbashi], brousse, Feb. 1912. *H.Homblé 210* (lectotype BR [BR0000006262181], designated here).

Description. Short-lived perennial herb 0.20–0.40(–0.65) m, rootstock a thin rhizome rooting at nodes, tubers occasionally observed (not collected in Central Africa). Stem erect, quadrangular, with short appressed retrorse hairs (also patent hairs outside Central Africa), yellowish to green, mostly unbranched, rarely with a few erect branches. Leaves opposite, in ca. 5 or 6 pairs, the uppermost pair often much reduced, petiolate, except uppermost pair, ascending, petiole 0.2–2.0(–2.5) cm with short retrorse hairs and a few long cilia, blade ovate, ovate-elliptic to subrhombic, 1.2–4.5(–5.0) × 0.8–2.5(–3.2) cm, apex acute, base cuneate and shortly attenuate into the petiole, margin narrowly recurved, with

4–8 sharp teeth on either side (2–3 mm deep on adaxial side), upper surface pubescent, with a mixed indumentum of antrorse hyaline hairs 0.5–2 mm long and very short papilliform hairs, lower surface very shortly appressed pubescent on veins (hairs often retrorse), also with red sessile glands, 3–5 pairs of secondary veins. Inflorescence lax, 5–13(–17) cm long, with 3–9(–15) verticils spaced 5–25 mm; bracts narrowly ovate, cucullate, 3–7 mm long, acuminate, forming an apical coma, caducous; cymes ascending to spreading, sessile, with 3–7 flowers on a 0–2 mm long rachis; pedicels ca. 4–6 mm long at anthesis, spreading to slightly ascending. Flower: calyx campanulate, ca. 3 mm long at anthesis, shortly pubescent, with red sessile glands, widely open; fruiting calyx 5–6 mm long, lateral teeth obtuse, ca. 2 mm long, lower teeth fused in a ca. 4 mm long very narrow lip, with two acute tips; corolla pale blue or white, with red sessile glands, ca. 9–13 mm long, tube ca. 5 mm long, strongly sigmoid, lower lip ca. 6–7 mm long, 4 mm deep, upper lip ca. 2 mm long; staminal filaments fused, anther ca. 0.5 mm long. Nutlets brown, red-speckled, ovoid, ca. 1 mm long.

Distribution. SW Tanzania to Zambia and SE DR. Congo.

Habitat and ecology. Miombo woodlands, often with *Brachystegia microphylla*, on shallow rocky soil, termite mounds; ca. 1250–1520 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Près de Lubumbashi, colline Kiswishi, 24 Feb 1987, *F.Billet & B.Jadin 4227* (BR, UPS); Dilolo, 1935, *de Wouters d'Oplinter 3* (BR); Lubumbashi, route de la mine de l'Etoile, km 12, 19 Apr 1957 *P.Duvigneaud 2847Co* (BRLU); Entre Welgelegen et Kasumbalesa, 29 Jan 1960, *P.Duvigneaud 5302C* (BRLU); Kasombo, 3 Feb 1960, *P.Duvigneaud 5384Col* (BRLU); 12 km NW de Lubumbashi, 12 Mar 1958, *A.Gathy 300* (BRLU); Elisabethville [Lubumbashi], Mar 1912, *H.Homblé 220* (BR) (about this specimen, see note under *C. heterotrichus*); Kasapa, 26 Feb 1966, *F.Malaisse 4012* (BR, LSHI); Ferme prince Léopold, 21 Feb 1927, *P.Quarré 1032* (BR); Keyberg, 9 km SW of Lubumbashi, 27 Feb 1948, *A.Schmitz 1392* (BR); 14 km from Lubumbashi, 17 Feb 1966, *J.-J.Symoens 12233* (BR, K, LSHI); Likasi, Panda, 25 Mar 1970, *S.Lisowski 23382* (POZG).

Notes. 1. *C. homblei* is superficially similar to *C. bojeri* and was synonymised with it by Paton et al. (2009, 2013). It differs from it in the perennial habit (this often difficult to observe), the more sharply serrate leaf margin, verticils with fewer flowers, longer pedicels and longer calyx at anthesis. The generally unbranched shoot is also typical with only ca. 5 pairs of leaves, the uppermost pair sessile and bracteiform. The species is widespread in miombo woodlands in the region of Lubumbashi.

2. Lectotypification of *Coleus homblei* De Wild. De Wildeman (1921b) cited two syntypes, i.e. *H.Homblé 210* (syntype BR [BR0000006262181], [BR0000006262518]), DR. Congo, Elisabethville [Lubumbashi], brousse, Feb 1912 & *H.Homblé 1259* (syntype BR [BR0000005201518], [BR0000005201846]), Plateau Biano, Tshisinka, partie boisée, Feb 1913. Both syntypes are unusual in having shoots branched from the base. Both match the protologue. *H.Homblé* 210 is more representative of the sharply serrate leaf margin and sheet [BR0000006262181] is designated as the lectotype because the label has "*Coleus homblei*" in De Wildeman's handwriting.

3. The type materials of *Coleus sigmoideus* A.J.Paton show the diagnostic traits of *Coleus homblei* De Wild., differing only in the presence of tubers, while tubers have not been collected in materials from DR. Congo.

4. See also note under C. *heterotrichus*.

Coleus kaminaensis **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347694-1
Fig. 6A–F

Type. DR. Congo, Kamina, la Lovoi, Apr 1932, *P.Quarré 2999* (holotype BR [BR0000017712682], [BR0000017712699], [BR0000017712750], [BR0000017712767]; isotype K).

Diagnosis. Related to *C. gracilipedicellatus*, on account of habit, profusely branched paniculate inflorescence, filiform pedicels jointed near apex and rachis distally zigzagging, differing in the anther not forming a pouch. It is also related to *C. bifidus*, on account of inflorescence architecture and anther structure, differing in the shallowly lobed style and the subentire leaf margin. The calyx of *C. kaminaensis* also differs by having the upper calyx lobe narrower and subulate at apex rather than clearly triangular in shape.

Description. Perennial herb, 1.75–2.25 m high, with a horizontal rootstock (fide Quarré, not observed). Stem erect, thick, woody at base, rounded, slightly striate, pale brownish to purplish, lenticellate, subglabrous to thinly appressed puberulous, with short appressed antrorse hairs in the inflorescence, branching in upper half. Leaves opposite, ascending, subsessile, blade elliptic to ovate-elliptic, 4–8.5 × 1–2 cm, base cuneate to shortly attenuate, apex acute, margin shallowly and remotely crenate, to subentire, recurved, 4–5 pairs of secondary veins, shortly appressed pubescent on veins beneath, with red sessile glands, puberulous on upper surface; petiole 0–0.1 cm. Inflorescence paniculiform, lax, ca. 30 × 20 cm, much branched, flowers solitary in the axil of a small bract, more or less spirally or distichously arranged, occasionally 2 pedicels opposite at a node; inflorescence axis slender and slightly zigzagging at apex, puberulous, bracts narrowly ovate to linear, acute, ca. 1–1.5 mm long, caducous; pedicels 5–25 mm long, filiform, faintly jointed near tip, glabrous below joint, shortly pubescent as calyx above; calyx ca. 5 mm long at anthesis, shortly appressed pubescent and with orange-red sessile glands, tube campanulate ca. 2.5 mm long, faintly 10-veined, lobes subulate, ca. 1.5–2 mm long, separated by broad truncate sinuses, with a short basal membrane; mature calyx not observed. Corolla blue (fide Quarré), ca. 9–11 mm long, tube almost straight, ca. 4–6 mm long, lower lip ca. 5 mm long, distally puberulous, curving upwards and closing throat, upper lip ca. 2 mm, upwardly pointing; stamens not exserted, filaments fused, anthers orbicular, not forming a pouch; style very shallowly lobed. Nutlets not observed.

Etymology. Kamina, locality in DR. Congo where the type specimen was collected.

Distribution. Endemic to SE DR. Congo, known only from the type specimen.

Habitat and ecology. Savannah; ca. 1000 m elev.

Additional specimens. None.

Notes. 1. Corolla structure, with lower lip upwardly curved, almost closing the throat and short stamens, suggest that the species is self-pollinating.

2. The single gathering of this species lacks fruiting calyces, with most flowers detaching at anthesis. Collecting notes indicate that the plant is heavily attacked by some leaf-eating parasite, virtually no leaves being untouched; this might account for the observed early abortion of flowers. The specimen is also galled. The species is said to be widespread in its locality.

3. Vernacular name: Lutoti na pori.

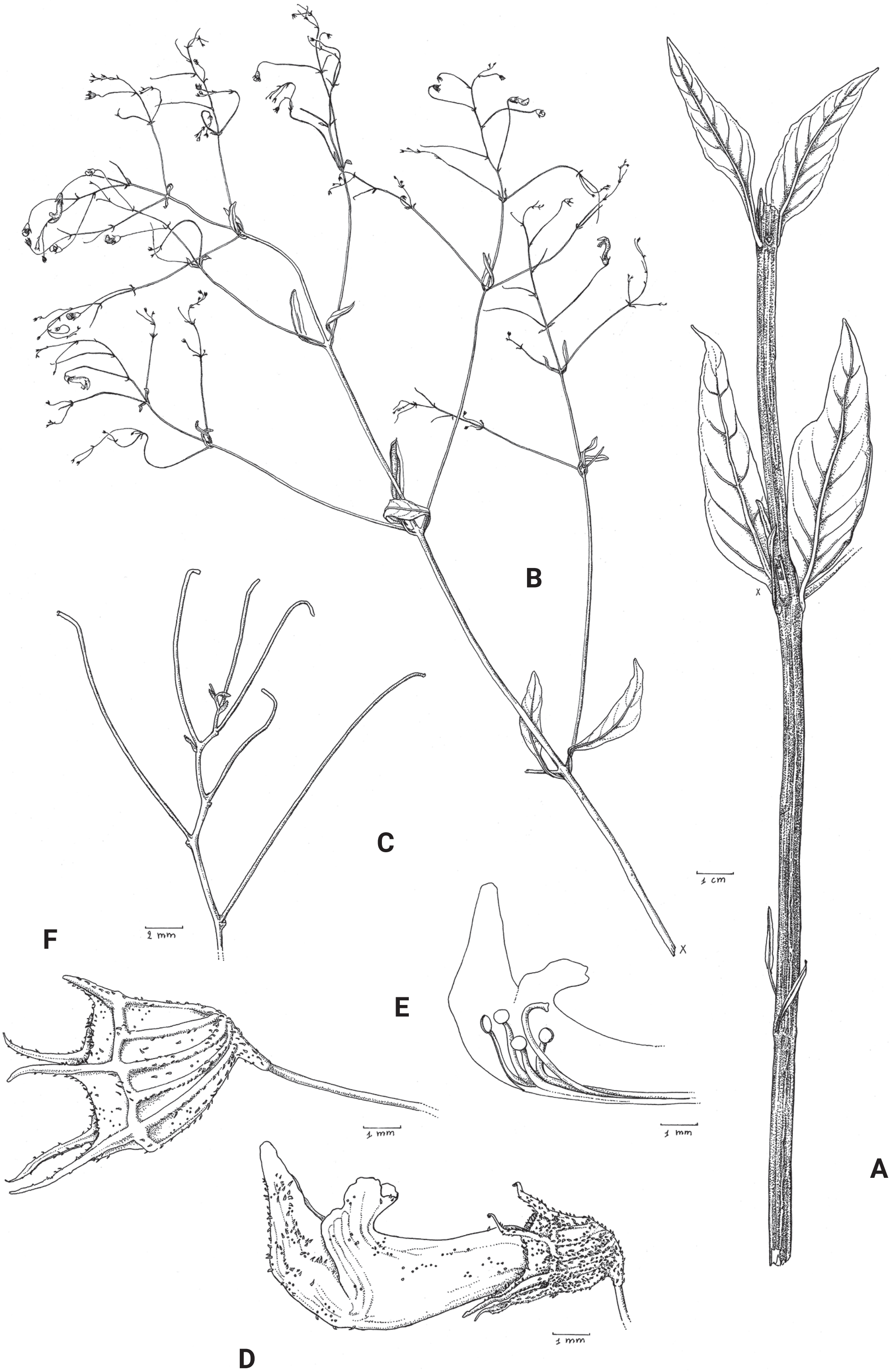

Figure 6. *Coleus kaminaensis* Meerts & A.J.Paton **A** stem and leaves **B** inflorescence **C** detail of inflorescence **D** flower **E** section of a corolla **F** fruiting calyx (*P.Quarré 2999*). Drawn by Hilde Orye. Scale bars: 1 cm (**A, B**); 2 mm (**C**); 1 mm (**D, E, F**).

Coleus kapatensis **R.E.Fr., Wiss. Erg. Schwed. Rhod.-Kongo Exped. 1: 283. 1916.**

≡ *Plectranthus kapatensis* (R.E.Fr.) J.K.Morton, Novon 8: 265. 1998. Type: Zambia, Bangweulu [Bangwelo], in Peninsula Kapata pr. Kamindas, 5 Oct 1911. *R.E.Fries 871* (holotype UPS [V-046475]; isotype K, Z).

Description. Paton et al. (2009: 275), Paton et al. (2013: 242), as *Plectranthus kapatensis* (R.E.Fr.) J.K.Morton.

Distribution. S. Tanzania to S. Tropical Africa.

Habitat and ecology. Miombo woodland, more rarely savannah on rock outcrops and dry evergreen woodland (muhulu); 1050–1570 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Keyberg, 1 Apr 1957, *E. Detilleux 736* (BR); Luiswishi, 4 Apr 1972, *F.Malaisse 7618* (BR); Fungurume, colline Bilima, 29 Aug 2007, *I.Parmentier & Kila 4744* (BR); Kyamasumba, 42 km NNW of Kolwezi, 19 Sep 1982, *M.Schaijes 1521* (BR); 12 km NNW of Lubumbashi, 19 Apr 1962, *A.Schmitz 7711* (BR).

Burundi, Dunga (Osso), 21 Sep 1977, *M.Reekmans 6402* (BR).

Notes. 1. New to DR. Congo and Burundi.

2. This species has been collected in DR. Congo and Burundi either in the rainy season in vegetative state (leafy shoots bearing propagules) or completely leafless and in flowers at the end of the dry season.

Coleus kivuensis **Lebrun & L.Touss., Bull. Jard. Bot. État Bruxelles 17: 72. 1943.**

≡ *Plectranthus kivuensis* (Lebrun & L.Touss.) R.H.Willemse, Kew Bull. 40: 96. 1985. Type: DR. Congo, Kivu, Rutshuru, Dec 1937, *J.Lebrun 9031* (holotype BR [BR0000006262563]; isotype K [K000431876], [K000431875], P [P00450798]).

= *Plectranthus neochilus* sensu Troupin & Ayob., Fl. Rwanda 3: 339. 1985., non Schltr.

Description. Paton et al. (2009: 346), as *Plectranthus kivuensis* (Lebrun & L.Touss.) Willemse.

Distribution. Eritrea to N. Tanzania and E DR.Congo.

Habitat and ecology. Shrub savannah, fallow fields, steppe; 900–1400(–2200) m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Kengele, pied du Ruwenzori, 27 Apr 1914, *J.Bequaert 3969* (BR); Keshero, 23 Sep 1958, *Crispiels-Thonon 124* (BR); Près de Kambukabakali, rive droite de la Semliki, 27 Oct 1954, *G.F.de Witte 11278* (BR); Kaliba, pied du Kasali, 11 Mar 1957, *G.F.de Witte 14035* (BR); Rutshuru, 16 Nov 1971, *C.Evrard 6827* (BR); Rutshuru, 30 Dec 1936, *J.Ghesquière 3573* (BR, K).

Rwanda, Mulehe (Bugesera), 15 Mar 1954, *L.Liben 1268* (BR, WAG); Parc national de l’Akagera, plaine de Nyaruhuru, 14 Apr 1969, *G.Bouxin & M.Radoux 167* (BR); Région du Matara, environs de Mimuli, 23 May 1957, *G.Troupin 3205* (BR); Région du Mutara, environs de Nyagatare, colline Rutare, 1 May 1958, *G.Troupin7239* (BR).

Coleus kundelunguensis **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347695-1
Fig. 7A–D

Type. *S.Lisowski, F.Malaisse & J.-J.Symoens 7626*, DR. Congo, Katanga, Kundelungu, 1650 m elev., steppe humide, 28 Oct 1969 (holotype POZG [POZG-V-0073133]).

Diagnosis. Related to *C. foliatus*, differing in the very lax inflorescence with verticils spaced 10–25 mm, the longer pedicel jointed near the middle, the anthers not forming a pouch and the bifid style.

Description. Perennial herb 0.30–0.50 m high, shoots more or less tufted, more or less woody at base, rootstock rhizomatous. Stem subterete, erect to ascending, simple or sparingly branching, shortly pubescent with patent eglandular hairs of different lengths, almost papilliform in the inflorescence, sparse glandular hairs and yellow sessile glands. Leaves opposite, ascending to erect, sessile to subsessile, ca. 4–6 pairs to a stem, widely spaced, petiole 0–0.2 cm long, blade ovate to ovate-elliptic, or obovate-elliptic, (1.2–)2.0–5.5(–7.5) × (0.5–)0.6–2.0 cm, base broadly cuneate to rounded, occasionally truncate to subauriculate in the uppermost leaves, apex acute to obtuse, more rarely acuminate, margin crenate to subentire, narrowly recurved, very shortly pubescent near margin and on lower surface of mid-vein, punctuate on both surfaces, drying dark reddish-green especially on veins. Inflorescence mostly unbranched, occasionally with a pair of branches at base, 4–20 cm long, very lax, rachis somewhat flexuose, verticils spaced 10–25 mm, flower solitary in the axil of each bract, with 1 or 2 flowers at each node, bract narrowly ovate to linear, 2–5 mm long, acute, pedicel 5–7 mm long at anthesis, elongating to 8–17 mm in fruit, very shortly pubescent (hairs almost papilliform, eglandular), conspicuously jointed and slightly angled slightly above middle, inserted asymmetrically in front of upper calyx lobe. Flower: calyx 4 mm long at anthesis, 9–10 mm long in fruit, tube straight to very slightly curved, 6–7 mm long, shortly pubescent, with eglandular and glandular hairs and sparse sessile orange glands, veins prominent, throat truncate, upper lip triangular, 1.5–2.5 mm long, slightly curving upwards, not decurrent, lower lobes narrowly triangular, the middle ones longer, 2.5–3.5 mm long, all lobes shortly ciliate. Corolla ca. 12 mm long, tube 6–7 mm long, sigmoid, lower lip carenate, 5–7 mm long, slightly pubescent on carena, upper lip 4 mm long, pubescent; anthers not forming a pouch, style bifid. Nutlets pale brown, smooth, dull, ovoid to globose, ca. 1.5 mm long.

Distribution. Endemic to the DR. Congo, Haut-Katanga, Kundelungu Plateau.

Habitat and ecology. Steppic savannah, often on moist soil, 1600–1700 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kundelungu, près de la source occidentale de la Lutshipuka, 1600 m elev., steppe arbustive, 6 Jan 1969, *S.Lisowski 773* (POZG); Kundelungu, bord de la Kalembe, 1600 m elev., 8 Jan 1971, *S.Lisowski 23701* (POZG); Kundelungu, 1600 m elev., près du gîte Rack, 6 Feb 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 1286* (POZG); Kundelungu, rivière Lualala, 1700 m elev., à 3 km au SE du poste de Lualala, 16 Feb 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 2149* (BR, POZG) *& 2149d* (POZG); Kundelungu, 1700 m elev., à 3 km à l'W du poste de Lualala, steppe herbacée, 27 Oct 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 7468* (POZG); Kundelungu,

Figure 7. *Coleus kundelunguensis* Meerts & A.J.Paton **A** habit **B** inflorescence verticil with one fruiting calyx **C** flower **D** stamen (**A** *S.Lisowski, F.Malaisse & J.-J.Symoens* 773 & *6722* **B** S.*Lisowski, F.Malaisse, J.-J.Symoens 6722* **C, D** S.*Lisowski, F.Malaisse, J.-J.Symoens 7468*). Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 5 mm (**B, C**); 1 mm (**D**).

à 3 km de la barrière, 1590 m elev., bord de la rivière Kalunda, 9 Jan 1971, *S.Lisowski, F.Malaisse & J.-J.Symoens 12592A* (POZG).

Notes. 1. Most of the cited specimens had been hitherto misidentified in collections as the Angolan *C. strictipes*, from which *C. kundelunguensis* differs in the smaller habit, flexuous shoot, very lax inflorescence with verticils spaced 10–25 mm, the anthers not forming a pouch and the bifid style.

2. The anthers not forming a pouch and the bifid style are rare in the group of species formerly referred to *Holostylon*, being observed only in *C. kundelunguensis* Meerts & A.J.Paton and *C. bifidus* (A.J.Paton) A.J.Paton.

Coleus lactiflorus **Vatke, Linnaea 43: 89. 1881.**

≡ *Plectranthus lactiflorus* (Vatke) Agnew, Upland Kenya Wild Fl.: 637. 1974. Type: Kenya, Taita District, Mbololo Forest, May 1985, *H.J.Beentje et al. 1042* (neotype K [K000975978]; isoneotype EA, designated by Paton et al. [2009]).

Description. Paton et al. (2009: 351), as *Plectranthus lactiflorus* (Vatke) Agnew.

Distribution. Ethiopia to N. and NW Tanzania, E DR. Congo.

Habitat and ecology. Savannah fallow fields; 1400–1600 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Ituri, SE of Ngolu, N of Nioka, 18 Dec 1951, *T.Sperry 335* (BR).

Rwanda, Territ. Kibungu, Rwinkwavu, 13 Apr 1966, *J.Lewalle 685* (BR).

Note. 1. New to DR. Congo. Rare in Central Africa, known from only two collections.

Coleus lanuginosus **Hochst. ex Benth. in A.P.de Candolle, Prodr. 12: 79. 1848.**

≡ *Plectranthus lanuginosus* (Hochst. ex Benth.) Agnew, Upland Kenya Wild Fl.: 638. 1974.

= *Coleus sodalium* Baker, Fl. Trop. Afr. 5: 526. 1900. Type: Eritrea, Mogad (Magod) Valley, 8 Apr 1892. *G.Schweinfurth & D.Riva 1810* (holotype K; isotype BR [BR0000006245825], FT, Z).

Type. Ethiopia, in montibus et vallibus prope Aduam [Adua], 4 Oct 1842. *G.W.Schimper III.1915* (lectotype K [K000431915]; isolectotype B, BM, E, FT, G, KIEL, MPU, P, UPS, W, designated by Ryding [2000]).

Description. Paton et al. (2009: 347), Paton et al. (2013: 278), as *Plectranthus lanuginosus* (Hochst. ex Benth.) Agnew.

Distribution. Eritrea to N Tanzania, SW Arabian Peninsula. Naturalised in Zimbabwe.

Habitat and ecology. Dry woodlands, steppe, shrub savannah; 1800–2500 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Rutshuru, 19 Apr 1914, *J.Bequaert 6051* (BR); Nyamgaleka, versant droit de la Haute Lume, 14 Apr 1953, *G.F.de Witte 8783* (BR); Kikomero, Nov 1937, *J.Lebrun 8447* (BR); Entre les rivières Molindi et Rutshuru, 21 Feb 1958, *M.Heine 220* (BR).

Rwanda, Kidaho, Rukoro, 29 Mar 1962, *C.Nshorere 116* (BR); Bweramvula, 20 Jun 1933, *G.Molitor 37* (BR).

Note. Many materials cited in the Flore du Rwanda by Troupin and Ayobangira (1985) were errors for *Equilabium wollastonii* (S.Moore) Mwany. & A.J.Paton.

Coleus linarioides Meerts & A.J.Paton, sp. nov.

urn:lsid:ipni.org:names:77347696-1
Fig. 8A–D

Type. *S.Lisowski 23150* (holotype POZG [POZG-V-0072770]), DR. Congo, Haut-Shaba [Haut-Katanga], Plateau des Kundelungu, env. 3 km au NW de la source occidentale de la Lutshipuka, steppe, 11 Jan 1971.

Diagnosis. Belongs in the group of species formerly comprising the genus *Holostylon* on account of the undivided style; closely related to *C. foliatus*, differing in the linear leaves, 1–4 mm wide, with strongly revolute margin.

Description. Herb, annual or perennial, ca. 0.20–0.30 m high, roots not observed. Stem ascending to erect, subterete, simple, with short ascending hairs and sessile red glands, internodes ca. 1 cm. Leaves opposite or ternate, more rarely scattered, ascending to erect, sessile, blade linear, 1.5–3.5 × 0.1–0.4 cm, base truncate to rounded, apex blunt, margin strongly revolute, glabrous and punctate above, slightly pubescent on mid-vein and margins underneath and with many red sessile glands. Inflorescence simple, lax, 2–6 cm long, verticils spaced ca. 5 mm, mostly 2-flowered, rachis shortly pubescent with ascending glandular and eglandular hairs, bracts ovate, acute, ca. 3 mm long, pedicels 5–7 mm long, with short ascending hairs, without a conspicuous joint. Flower: calyx 4 mm long at anthesis, elongating to ca. 9 mm in fruit, campanulate to tubular, tube straight to slightly curved, with orange sessile glands and short glandular and eglandular hairs, upper lip ovate-triangular, slightly recurved, 2 mm long, lateral lobes of lower lip triangular, median lobes of lower lip narrowly triangular, slightly longer; corolla ca. 12 mm long, purplish, tube sigmoid ca. 5 mm long, lower lip strongly keeled, ca. 7 mm long, shortly pubescent and with sessile pale glands, upper lip ca. 4 mm long. Anthers pouch-like; style undivided. Nutlets not observed.

Etymology. Habitus and leaf shape are reminiscent of several species of *Linaria* (Plantaginaceae).

Distribution. Endemic to DR. Congo, Haut-Katanga, Kundelungu Plateau.

Habitat and ecology. Steppic savannah, ca. 1600 m elev.

Additional specimens. None.

Note. A very distinct species on account of the ternate linear leaves with strongly revolute margin.

Coleus lisowskii Meerts & A.J.Paton, sp. nov.

urn:lsid:ipni.org:names:77347697-1
Fig. 9A–E

Type. DR. Congo, Katanga, Marungu, 1900 m elev., près du poste Luonde, steppe herbacée, 15 Jun 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 5908* (holotype POZG [POZG-V-0072834]; isotype POZG [POZG-V-0072833]).

Figure 8. *Coleus linarioides* Meerts & A.J.Paton **A** habit **B** leaf undersurface **C** detail of inflorescence **D** stamen (*S.Lisowski 23150*). Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 5 mm (**B, C**); 1 mm (**D**).

Diagnosis. Belongs in the group of species formerly comprising the genus *Pycnostachys*, closely related to *Coleus descampsii* and *Coleus parvifolius*, on account of the short, narrow leaves, the very pubescent calyx and the ciliate bracts; it differs in the lack of small leaf fascicles in the axils and in the heteromorphic leaves.

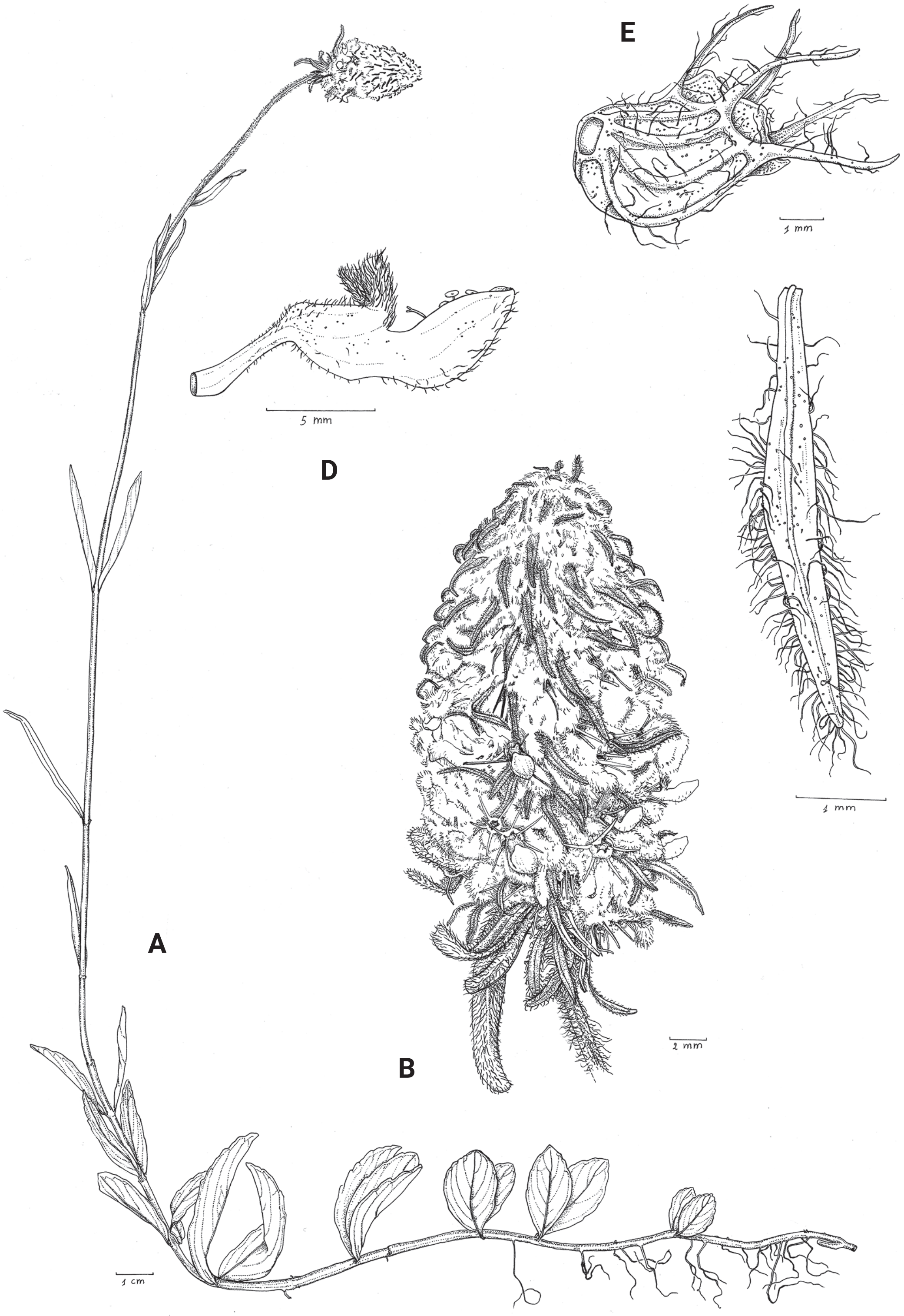

Figure 9. *Coleus lisowskii* Meerts & A.J.Paton **A** habit **B** inflorescence **C** bract **D** corolla **E** fruiting calyx (**A** *S.Lisowski, F.Malaisse & J.-J.Symoens 6148a* **B–E** S.*Lisowski, F.Malaisse, J.-J.Symoens 5908*). Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 2 mm (**B**); 1 mm (**C, E**); 5 mm (**D**).

Description. Perennial herb, 0.50–1.00 m high, rhizome creeping. Stem with a prostrate basal part (0–)1–10 cm, rooting at nodes, then abruptly erect, terete to obscurely quadrangular, shortly pubescent with retrorse hairs in lower half, upwardly more or less villous, also with pale sessile glands, simple or sparingly branched only near tip. Leaves opposite or ternate, sessile to very shortly petiolate, heteromorphic, the ones on the lower part of the stem spreading to recurved, ovate-elliptic, obovate-elliptic, to broadly elliptic, 1.5–3.5 × (0.5–)1.0–1.5 cm, the lowermost (juvenile) ones almost round, ca. 0.5 × 0.5 cm, base broadly cuneate to rounded, apex rounded, obtuse or subacute, margin shallowly crenate to subentire, somewhat thickened by a marginal vein, shortly ciliate, with 4 or 5 pairs of secondary veins, arching and more or less parallel to margin, prominulent on both surfaces, shortly pubescent on veins on lower surface, subglabrous on upper surface; petiole 0.1–0.3 cm; leaves on the erect part of the stem ascending to erect, more rarely recurved, subsessile, blade very narrowly lanceolate or oblanceolate-elliptic, to almost linear, 1.8–5.0 × 0.2–0.6(–0.8) cm, flat or more or less folded in length, base cuneate to truncate, apex subacute, margin subentire to shallowly crenate distally, ciliate to denticulate, veins 3–5 pairs, prominulent on both surfaces, diverging at a narrow angle and more or less parallel, subglabrous to shortly pubescent on both surfaces (antrorse hairs), more densely so in upper leaves, also with sessile orange and red glands on both surfaces. Inflorescence spicate, capitate to shortly ovoid, 12–30 × 10–16 mm (corolla excluded), apex subacute to obtuse, bracts subtending inflorescence narrowly lanceolate to almost linear, reflexed, persistent, ca. 10 × 0.8–1.5 mm, lower surface villous, upper surface glabrous; bracts of individual flowers purplish, narrowly elliptic to almost linear, the uppermost ones forming a coma, outwardly curving, ca. 4–7 × 0.5–0.8 mm, villous on abaxial surface, densely ciliate, with a fringe of undulate or curly cilia 0.5–1 mm. Flower: calyx tube ca. 2 mm long at anthesis, tomentose and with orange sessile glands, fruiting calyx tube elongating to 4–5 mm long, somewhat compressed on upper side, gibbous on lower side, villous, with long eglandular hairs, also with yellow sessile glands, lobes more or less spreading, ca. 3–4 mm long at fruiting, somewhat flattened and sharp-edged near base, with long curly eglandular hairs ca. 0.6 mm long on margins and outer surface and sessile orange glands, scales at mouth triangular ca. 0.8–1 mm long, somewhat outwardly curving at maturity, with short eglandular hairs; corolla ca. 11–15 mm long, colour unknown (pale coloured in herbarium), tube sigmoid, with a narrow basal part ca. 4 mm long and a broader distal part 3–4 mm long, lower lip 4–6 mm long, pubescent and with yellow-orange sessile glands, upper lip 3–4 mm long, with 4 narrowly triangular lobes. Nutlets pale brown, dull, smooth, ovoid, somewhat compressed, ca. 1.5 mm long.

Etymology. Dedicated to Stanislaw Lisowski (1924–2002), Polish botanist, who made important contributions to the flora of tropical Africa.

Distribution. Endemic to the DR. Congo, Haut-Katanga, Marungu Massif.

Habitat and ecology. Steppic savannah, woodlands, dambos, ca. 1400–2000 m elev.

Additional specimens. DR. CONGO, ***Haut-Katanga***, Marungu, à env. 3 km à l'W de Kasiki, 12 Jun 1969, *S.Lisowski, F.Malaisse & J.-J.Symoens 6148a* (POZG); Plateau de Muhila, bord de la rivière Muizia, 13 May 1971, *S.Lisowski 23728* (POZG); Marungu, 20 km NE de Kapulo, dembo frais dans la forêt claire à *Brachystegia*, 25 Jun 1957, *P.Duvigneaud 3710P* (BRLU); Entre Kapulo et Pepa, base du plateau des Marungu, muulu autour d'une termitière, 25 Jun 1957, *P.Duvigneaud 3713bis* (BRLU).

Notes. 1. This species is superficially similar to *C. lancifolius*, on account of the narrow ascending leaves, differing in the capitate inflorescence, the tomentose calyx and the long ciliate bracts. The prostrate basal part of the stem, with broader leaves, is less typical in *P.Duvigneaud 3710P* & *3713bis*, but the four cited collections are quite similar in all the other characters and there is little doubt that they are conspecific.

2. There are intermediates with *C. descampsii*, with very short leaves in some axils, for example, S.*Lisowski 23727, 23728* (POZG), Plateau de Muhila, bord de la rivière Muizia, 1450 m elev., 13 May 1971; *S.Lisowski 23719* (POZG), Plateau de Muhila, 5 km N du poste de Kitu, 1420 m elev., bord marécageux d'un ruisseau, 16 May 1971.

3. *S.Bidgood et al. 3358* (K, P), from Tanzania, is probably the same taxon.

Coleus longipetiolatus Gürke, Bot. Jahrb. Syst. 19: 214. 1894.

= *Plectranthus leptophyllus* (Baker) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 284. 2009. Type: Kenya, Ribe (Ribi) to Galla country, *T.Wakefield s.n.* (holotype K [K000431957]).

Type. Tanzania, Usambara Mts, Kwa Mshusa, 15 Aug 1893, *C.Holst 9076* (holotype B destroyed; isotype COI [COI00005780], G, HBG [HBG518665], K [K000431956], KFTA, M [M0104723], P [P00450800], W, Z).

Description. Paton et al. (2009: 284), Paton et al. (2013: 231), as *Plectranthus leptophyllus* (Baker) A.J.Paton.

Distribution. E & S Tropical Africa.

Habitat and ecology. Wooded savannah, forest; 1040–1300 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Virunga, Katuka, 26 May 1948, *J.de Wilde 70* (BR); Virunga, Rivière Mati, affluent gauche de la rivière Talya, 24 Apr 1956, *G.F.de Witte 13179* (BR); Karunda, Nyabiondo, 24 Jul 1957, *R.Gutzwiller 1369* (BR).

Note. New species record for DR. Congo.

Coleus maculosus (Lam.) A.J.Paton, Phytokeys 129: 68. 2019.

≡ *Galeopsis maculosa* Lam., Encycl. 2: 601. 1788. Type: cultivated, from Africa. (holotype P-Lam).

Note. *Coleus maculosus* is variable in petiole length, leaf blade shape and corolla length. Earlier authors (e.g. Robyns (1947): Troupin and Ayobangira (1985)), recognised three taxa: a taxon with large corolla and oblong sessile leaves (corresponding to the type specimen of *Coleus edulis* Vatke), a taxon with large corolla and ovate petiolate leaves (type of *Coleus fimbriatus* Lebrun & L.Touss.) and a taxon with small corolla and ovate petiolate leaves (type of *Plectranthus punctatus* L'Hér.). Recent authors, however, give priority to corolla size and recognise only two subspecies; we follow this treatment, but further work is needed.

Key to the subspecies of *Coleus maculosus*

1 Corolla 6–8 mm long; tube 3–5 mm long, almost straight to shallowly sigmoid; leaf petiolate, blade ovate ....***C. maculosus* subsp. *maculosus***

– Corolla (11–)13–18 mm long; tube 6–8 mm long, shallowly to conspicuously sigmoid; leaf sessile to petiolate, blade ovate to oblong-elliptic........ ....***C. maculosus* subsp. *edulis***

Coleus maculosus (Lam.) A.J.Paton, subsp. *maculosus*

= *Coleus serrulatus* Robyns, Bull. Jard. Bot. État Bruxelles 17: 78. 1943.

≡ *Plectranthus serrulatus* (Robyns) Troupin & Ayob., Bull. Jard. Bot. Natl. Belg. 55: 299. 1985. Type: DR. Congo, Visoke, R. Susa, 2 Feb 1935, *G.F.de Witte 2214* (holotype BR [BR0000006263263], [BR0000006262624]; isotype K [K000431883]).

= *Plectranthus punctatus* L'Hér. subsp. *punctatus*, Fl. Trop. E. Afr., Lamiac.: 350. 2009. Type: Ethiopia ("Abyssinia"), cultivated from seed sent by Bruce at Hort. Kew, 1774 (neotype BM; isoneotype G; designated by Hedge et al. [1998]).

Description. Paton et al. (2009: 349), as *Plectranthus punctatus* (L.f.) L'Hérit. subsp. *punctatus*.

Distribution. Cameroon, to Eritrea and Tanzania, Madagascar.

Habitat and ecology. Marshland, mountain grassland, fallow field, mountain forest, regrowth; 1700–3050 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Beni, Vayana, Aug 1938, *P.Gille 108* (BR); Entre les Lacs Kivu et Edouard, Apr-May 1929, *H.Humbert 7907* (BR); Mont Kahuzi, 13 Jun 1971, *S.Lisowski 23824* (POZG).

Rwanda, Piste allant de Kinigi au pied du Visoke, 3 Feb 1972, *P.Auquier 2415* (BR); Flanc sud du Sabyinayo, 3 Feb 1972, *P.Bamps 3071* (BR); Remera, Buliza, Kigali, Nov 1932, *A.Becquet 326* (BR); Bunyereri, Nyungwe, 13 May 1971, *G.Bouxin 698* (BR); Forêt de Mushabarara, Apr 1939, *G.Gilbert 2361* (BR); Rukura, Bumbogo, Mar 1933, *G.Molitor 23* (BR); Mont Kisoni, 6 Mar 1935, *J.B.Lejeune 210* (BR); Route Bukavu-Astrida [Butare], km 94, 4 May 1959, *G.Troupin 9909* (BR); Ruhengeri, Kinigi, 24 Feb 1972, *P.Van der Veken 9530* (BR).

Burundi, Kitega, 4 Dec 1922, *O.A.J.Elskens 214* (BR); Bujumbura, Mayuyu, 28 Feb 1971, *J.Lewalle 5249* (BR); Muramwya, Ryarusera, 27 Feb 1972, *M.Reekmans 1577* (BR); Rwasave, rivière Murwuya, 14 May 1957, *D.van der Ben 1567* (BR).

Coleus maculosus subsp. *edulis* (Vatke) A.J.Paton, Phytokeys 129: 69. 2019.

≡ *Coleus edulis* Vatke, Linnaea 37: 319. 1872.

≡ *Plectranthus edulis* (Vatke) Agnew, Upland Kenya Wild Fl.: 640. 1974.

≡ *Coleus maculosus* subsp. *edulis* (Vatke) A.J.Paton (2019) 69. Type: Ethiopia ("Abyssinia"), near Gaffat, Oct 1863, *G.W.Schimper 1212* (holotype B destroyed; isotype BM [BM000514932], K [K000431925], [K000431923]).

≡ *Plectranthus punctatus* subsp. *edulis* (Vatke) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 350. 2009.

= *Coleus fimbriatus* Lebrun & L.Touss., Bull. Jard. Bot. État Bruxelles 17: 79. 1943.

≡ *Plectranthus fimbriatus* (Lebrun & L.Touss.) Troupin & Ayob., Bull. Jard. Bot. Natl. Belg. 55: 299. 1985. Type: DR. Congo, Mt Mushumangabo, Aug 1937, *J.Lebrun 7163* (holotype BR [BR0000006262945], [BR0000006263270]).

Description. Paton et al. (2009: 350), as *Plectranthus punctatus* subsp. *edulis* (Vatke) A.J.Paton.

Distribution. Ethiopia, Kenya, Uganda, Tanzania, Burundi, Rwanda and DR. Congo.

Habitat and ecology. Mountain forest, savannah, fallow field, marshland, swamp, river banks, riparian forest; 1600–3100 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Nioka, 27 Oct 1934, *A.P.De Craene 229** (BR, WAG); ***Lacs Edouard et Kivu***, Tshirunge, 5 Oct 1914, *J.Bequaert 5997* (BR); Parc National Albert [Virunga], volcan Niamlagyra, aux environs de Mushumangabo, 17 Jan 1942, *R.Germain 1258* (BR); W du Lac Kivu, Feb-Mar 1929, *H.Humbert* 7527* & 7528 (BR); Mont Kahuzi, 28 May 1960, *Meurillon 953** (BR, LWI); ***Haut-Katanga***, Parc National de l'Upemba. Lubanga, 17 Apr 1948, *G.F.de Witte 03726* (BR).

Rwanda, Mukono, Byumba, Dec 1932, *A.Becquet 189** (BR); Rwasenkoko, route Butare-Cyangugu, km 67, 1 Mar 1980, *D.Bridson 468* (BR, K); Gikongoro, Kivu, Rubyiro, 16 Aug 1999, *C.Ewango & Ngayabahiga 2195** (BR, GIS, M, MO, WAG); Route Astrida [Butare]-Shangugu, km 65, 7 Mar 1958, *M.Reynders 239* (BR); Route Bukavu-Astrida [Butare], env. Uwinka, colline Bunyereri, 7 Aug 1959, *G.Troupin 10566** (BR).

Burundi, Muramvya, Mont Manga Mugongo, 4 Jun 1966, *J.Lewalle 883* (BR); Muramvya, Nyabigonde, 3 Apr 1966, *J.Lewalle 642** (BR); Nyakirwa, 21 Jan 1977, *M.Reekmans 5647** (BR); Province: Ngozi, Commune: Mukora (Rwegura), 27 Apr 1977, *M.Reekmans 6046* (BR); Ijenda, 8 May 1981, *M.Reekmans 10137** (BR, WAG).

Note. Subsp. *edulis* is variable in petiole length and blade shape; morphs with subsessile leaves and oblong-elliptic blade up to 14 cm long (specimens indicated "*" hereabove) correspond to the type of *C. edulis*; morphs with ovate, petiolate leaves correspond to the type of *C. fimbriatus*.

Coleus mannii Hook.f., J. Proc. Linn. Soc., Bot. 7: 211. 1864.

= *Coleus giorgii* De Wild., Bol. Soc. Ibér. Ci. Nat. 19: 120. 1920. Type: DR. Congo, Likimi, *S.De Giorgi 1511* (lectotype BR [BR0000021453984], designated by Champluvier & Dowsett-Lemaire [1999]).

Type. Cameroon, Mt Cameroon, 1862, *G.Mann 1967* (holotype K [K000025010]).

Description. Paton (2022: 51).

Distribution. W Tropical Africa to DR. Congo and Sudan.

Habitat and ecology. Swamps, riparian forest, savannah on wet soil, often near watercourses and ponds; 400–1200 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Mandzambe, s.d., *J.Claessens 326* (BR); ***Kasaï***: Kebiya, Dec 1951, *Flamigni 10350* (BR); Bokoro, 22 May

1948, *Jans 695* (BR); Luluabourg [Kananga], 1930, *H.Vanderyst 21130 & 21135* (BR); ***Forestier central***, Yaekama, territ. Isangi, 7 Feb 1959, *P.Bamps 337* (BR); Avakubi, 9 Jan 1914, *J.Bequaert 1847* (BR); Ligasa-Mangala, 9 Dec 1956, *C.Evrard 2045* (BR); Banzingi, 22 Jul 1954, *G.F.de Witte 10739* (BR); Marais de la Bukotsa, 27 Nov 1952, *H.Fredericq* in *G.F.de Witte 8421* (BR); 6 km W de Yangambi, 6 Jul 1938, *J.Louis 10212* (BR, P); ***Ubangi-Uele***, Dungu, rivière Nambasa, Oct 1936, *A.M.De Graer 749* (BR); Entre Banzyville [Mobayi-Mbongo] et Pambwa, 14 Oct 1954, *C.Evrard 109bis* (BR); Entre Libenge et Gemena, Dec 1930, *J.Lebrun 1841* (BR); Dida, Gombari, 22 Dec 1906, *F.Seret 711* (BR); ***Lacs Edouard et Kivu***, Virunga, Bakotsa, près confluent Byangolo-Molidi, 23 Sep 1954, *G.F.de Witte 11129* (BR); Sinamboro, affl. droit Balembi, 4 Feb 1955, *G.F.de Witte 11668* (BR).

Coleus marunguensis **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347698-1
Fig. 10A–F

Type. DR. CONGO, Haut-Katanga, Kasiki, 20–27 Jun 1931, *G.H.de Witte 493* (holotype BR [BR0000016835344]).

Diagnosis. Closely related to the species formerly comprising the distinct genus *Solenostemon* (middle lobes of lower calyx lip fused over most of their length), differing in the beige tomentose flowers, the stem with antrorse hairs, the shortly petiolate leaves with blade truncate at base, upper surface glabrous and with impressed veins.

Description. Perennial herb or shrub, woody in lower half, height unknown (> 0.40 m). Stem erect, branched, markedly quadrangular, very shortly puberulent with appressed antrorse eglandular hairs and sparse long patent hairs in lower part and also with sparse red sessile glands. Leaves opposite, spreading, petiolate, with or without fascicles of small leaves in the axils; petiole 0.7–1.6 cm long, pubescent like the stem or villous; blade discolorous, broadly ovate-triangular, 2.0–5.0 × 1.4–4.0 cm, base truncate to slightly cordate, apex acute, margin serrate, recurved, teeth rounded, lower surface with very short appressed hairs on veins and softly pubescent to sparsely villous between the veins and with red sessile glands, upper surface subglabrous, veins impressed on upper surface and prominent on lower surface. Inflorescence 5–20 cm long, lax, verticils spaced 10–25 mm, cymes sessile, cincinni 1–2 mm long (pedicel not included), 6–8 flowered, bracts puberulous on outer surface, ovate, cucullate, contracted into a point, ca. 4 mm long, forming a small apical coma, pedicel ascending, 3–4 mm long in fruit, curving at tip, inserted very eccentrically on calyx in front of upper lobe. Flower: calyx ca. 1.5 mm long at anthesis, densely beige tomentose and with red sessile glands, 4–5 mm long in fruit, pubescent all over, tube ca. 1.5 mm long, contracted at throat, sulcate, upper lip purplish, obovate, ca. 2 mm long, curving upwards, obtuse-rounded, margin often irregularly undulate and with 1 tooth on either side and with a short apical mucro, lateral lobes oblong, ca. 1.5 mm long, truncate to rounded, lower middle lobes fused into a lip ca. 2.5 mm long, with two ovate apical lobes contracted into a point; corolla wholly beige tomentose when in bud, ca. 9–13 mm long at anthesis, pubescent to tomentose and with sparse red sessile glands, tube slightly sigmoid, ca. 3.5 mm long, lower lip 4–8 mm long, 2–3 mm deep, cucullate,

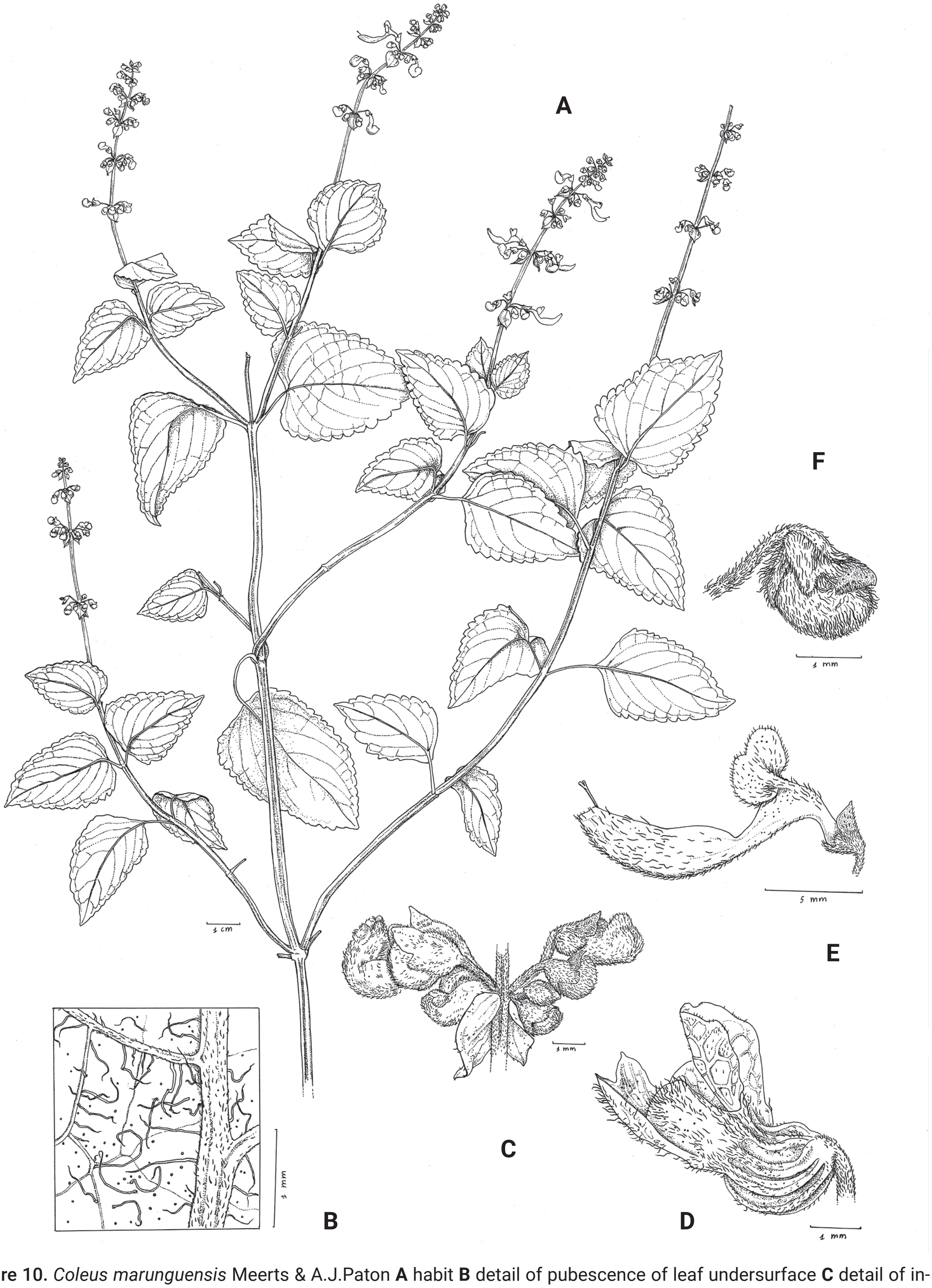

Figure 10. *Coleus marunguensis* Meerts & A.J.Paton **A** habit **B** detail of pubescence of leaf undersurface **C** detail of inflorescence **D** fruiting calyx **E** flower **F** flower bud (**A, B, C, E** *G.H.de Witte 493* **D, F** *S.Lisowski, F.Malaisse & J.-J.Symoens 10339a*). Drawn by Hilde Orye.Scale bars: 1 cm (**A**); 1 mm (**B, C, D, F**); 5 mm (**E**).

upper lip 1.5–3 mm long, 4-lobed; stamen filaments fused, anther ca. 0.7 mm long, style bifid. Nutlets not observed.

Etymology. The Marungu Plateau, where the type specimen was collected, is a hotspot of biodiversity in DR. Congo.

Distribution. Endemic to DR. Congo (Haut-Katanga, Marungu Plateau).

Habitat and ecology. Wetlands, 1850–2200 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Plateau des Marungu, Env. de Luonde, mare Buzanza, 1850 m elev., 20 Feb 1970, *S.Lisowski, F.Malaisse & J.-J.Symoens 10339* (POZG).

Note. There is a second specimen in BR labelled "*G.F.de Witte 493*" [BR0000016835351]; however, it is a different species, i.e. *Equilabium stolzii*, that was probably growing intermingled with *Coleus marunguensis*. *Equilabium stolzii* is known to occur in wetlands on the Marungu Plateau; the second sheet has been labelled by us *G.F.de Witte 493bis*.

Coleus melleri **(Baker) A.J.Paton & Phillipson, Phytokeys 129: 73. 2019.**

≡ *Plectranthus melleri* Baker, J. Bot. 20: 243. 1882. Type: Madagascar, between Toamasina (Tamatave) and Antananarivo, 3 Aug 1862. *C.J.Meller s.n.* (holotype K [K000430814]).

= *Plectranthus luteus* Gürke, Bot. Jahrb. Syst. 28: 468. 1900.

≡ *Coleus luteus* (Gürke) Staner, Bull. Agric. Congo Belge 25: 426. 1934. Type: Tanzania, Morogoro District: SE Uluguru Mts, *F.Stuhlmann 8790* (holotype B destroyed).

Description. Paton et al. (2009: 293), Paton et al. (2013: 242), as *Plectranthus melleri* Baker.

Distribution. Liberia, Gabon, Uganda to S. Tropical Africa, Madagascar.

Habitat and ecology. Dense evergreen mountain forest, riparian forest, Ericaceae scrub; 850–2600 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kwango, 21 Jul 1955, *R.Devred 2317* (BR); ***Lac Albert***, Lekwa (Djugu), 11 Mar 1959, *Deville 229* (BR); Mt. Dia, 13 Oct 1937, *G.C.Gilbert 557* (BR); ***Lacs Edouard et Kivu***, Lake Kivu, Idjwi Island, 6 Aug 1959, *Cambridge Congo Expedition 275* (BR, US); Ruwenzori, versant ouest, vallée de la Lume, Jul 1929, *H.Humbert 8980* (BR, P); Terr. Kabare, Kahuzi, 11 Feb 1959, *A.Léonard 2981* (BR, WAG); Wimbi, 26 km S Lubero, 21 Jul 1937, *J.Louis 4631* (BR); Mont Biega, 10 Aug 1972, *Ntakiyimana 318* (BR, LWI); Route Bukavu-Walikale, km 48, 17 Mar 1960, *J.Petit 9* (BR, LWI); Zwischen Nyamuragira und Mikeno, 17 Sep 1964, *H.U.Stauffer 371* (BR, WAG, Z). ***Haut-Katanga***, Lusinga, route Mitwaba, 14 Sep 1948, *W.Robyns 3591* (BR); Kundelungu, 10°26'S, 27°53'E, 5 Oct 1950, *A.Schmitz 3201* (BR).

Rwanda, Près de Pindura, piste de l'Ibigugu, 29 Jul 1974, *P.Auquier 3526* (BR); Flanc sud Sabyinyo, 3 Jul 1972, *P.Bamps 3049* (BR); Uwinka, Nyungwe, 9 Aug 1969, *G.Bouxin & M.Radoux 554* (BR); Volcan Sabyinyo, 4 Feb 1972, *G.Troupin 14339* (BR, WAG); Route Butare-Cyangugu, 2 km avant Gisakura, 24 Aug 1974, *P.Van der Veken 10942* (BR, GENT, WAG).

Burundi, Bugarama, 29 Jun 1969, *J.Lewalle 3860* (BR); Bururi, rives de la Siguvyaye, 2 May 1966, *J.Lewalle 761* (BR, MO, WAG); Bujumbura, Mt. Manga, 14 Sep 1947, *M.Reekmans 3520* (BR).

Notes. 1. The specimen *W.Robyns 3591* (BR) from Haut-Katanga (Upemba) is larger than usual in all its parts including corolla and leaf blade base is obtuse-rounded instead of acute-attenuate; it could be a different taxon.

2. The specimen *A.Léonard 3526* (BR) differs in having a white corolla (fide collector), being almost glabrous in all parts and lacking propagules; it is almost certainly a distinct taxon, but more materials are needed.

Coleus meyeri (Gürke) A.J.Paton, Phytokeys 129: 73. 2019.

≡ *Pycnostachys meyeri* Gürke, Abh. Königl. Akad. Wiss. Berlin 1891: 362. 1892. Type: Tanzania, Kilimanjaro, Rua stream, *H.Meyer 279* (holotype B destroyed; isotype K [K000405982] fragment).

= *Pycnostachys longibracteata* De Wild., Pl. Bequaert. 4: 388. 1928. Type: DR. Congo, Ruwenzori, Vallée du Lanuri, 26 Mar 1914, *J.Bequaert 4490* (holotype BR [BR0000008909763]; K fragment).

= *Pycnostachys ovoideoconica* De Wild., Pl. Bequaert. 4: 396. 1928. Type: DR. Congo, Mukule–Mokoto, *J.Bequaert 6325* (holotype BR [BR0000008910097]; K fragment).

Description. Paton et al. (2009: 412), as *Pycnostachys meyeri* Gürke.

Distribution. W. Tropical Africa to Ethiopia and Tanzania.

Habitat and ecology. Savannah, Bambusa thickets, mountain forest, riparian forest; 1500–2400 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Blukwa, Sep 1949, *A.P.De Craene 351* (BR, K); Aye Kibali, Djugu, 11 Jun 1959, *D.Froment 520* (BR); ***Lacs Edouard et Kivu***, Ruwenzori, Lanuri, 26 May 1914, *J.Bequaert 4490* (BR, K fragment); Mukule-Mokoto, 19 Dec 1914, *J.Bequaert 6325* (BR, K fragment); Terr. Masisi, Dondo, May 1957, *R.Gutzwiller 1063* (BR, K); Ruwenzori, vallée de la Muboka, Nov 1931, *J.Lebrun 4412* (BR); Kahuzi, 1 Jul 1959, *A.Leonard 4816* (BR, K); Flanc NW du Karisimbi, 17 Aug 1937, *J.Louis 5250* (BR); Mont Bugulumiza, 26 Jul 1955, *R.Pierlot 665* (BR); Busenene, 13 Nov 1953, *R.Van Ysacker 75* (BR).

Rwanda, Wisumo, Gisovu, 21 Feb 1980, *D.Bridson 433* (BR); Route Astrida [Butare]-Bukavu, km 93, *G.Troupin 11533* (MO); Env. Rangiro, Kirambo, 4 Jun 1981, *G.Troupin 16271* (BR); Ruhengeri, Kinigi, 24 Feb 1972, *P.Van der Veken 9531* (MO).

Burundi, Mont Teza, 9 Jul 1974, *J.Rammeloo 3753* (BR).

Coleus mirabilis Briq., Bot. Jahrb. Syst. 19: 183. 1894.

≡ *Ascocarydion mirabile* (Briq.) G.Taylor, J. Bot. 69 (suppl. 2): 162. 1931.

≡ *Plectranthus mirabilis* (Briq.) Launert, Mitt. Bot. Staatssamml. München 7: 299. 1968. Type: Angola, Malanje (Malandsche), Mar 1880, *A.von Mechow 489* (lectotype Z not seen; isolectotype W [W 1889-0054590], designated by Codd [1975]).

= *Coleus mirabilis* var. *poggeanus* Briq., Bot. Jahrb. Syst. 19: 184. 1894. Type: DR. Congo, River Lulua, 9°30'S, *P.Pogge 350* (holotype B destroyed).

Description. Paton et al. (2013: 258), as *Plectranthus mirabilis* (Briq.) Launert

Distribution. S DR. Congo to NE Namibia.

Habitat and ecology. Swamp savannah, riparian forest; ca. 900–1100 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Panzi, 1925, *H.Vanderyst 16117* (BR); ***Bas-Katanga***, Mutombo-Mukulu, Jun 1931, *P.Quarré 2534* (BR); Kamina, Lovoi, Apr 1932, *P.Quarré 3007* (BR); ***Haut-Katanga***, Manika, route Kolwezi-Kasaji, 4 Apr 1955, *J.Brynaert 393* (BR); Territ. Dilolo, Kisenge, marais de la Mukuleshi, en bordure de galerie forestière, 19 May 1957, *P.Duvigneaud 3237La* (BRLU).

Coleus minusculus **Meerts & A.J.Paton, sp. nov.**

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Fig. 11A–C

Type. DR. Congo, Haut-Katanga, 28 km NE de Lubumbashi, Savane de la Luiswishi, 1208 m elev., 30 Aug 1972, *J.Bulaimu 520* (holotype BR [BR0000017733526]).

Diagnosis. Related to *Coleus modestus* on account of inflorescence structure, differing in being a dwarf plant (< 10 cm high), leafless at flowering, rootstock a small tuber.

Description. Perennial herb, 0.04–0.10 m, leafless at flowering, glutinous; rootstock a fusiform tuber 1–2 × ca. 0.5 cm. Stem 1 or several, purplish, erect, simple or branched, terete to subquadrangular, with dense short glandular hairs and sparse eglandular hairs. Leaves not observed. Inflorescence terminal, lax, racemiform, flowers solitary in the axil of each bract, mostly subopposite, bracts linear, ca. 1 mm long, persistent, ciliolate; pedicel 2–3 mm long, extending to 4–5 mm in fruit, slightly ascending to patent, slightly curving downwards at tip, inserted slightly eccentrically on calyx. Flower: calyx 2–2.5 mm long at anthesis, to 4 mm in fruit, with yellow-orange sessile glands and short glandular hairs, tube shortly cylindrical to campanulate, 10-veined, straight or slightly curved upwards, lobes subequal, narrowly triangular, ca. 1 mm long, the upper one slightly broader, slightly recurved, not decurrent; corolla 5–7 mm long, bluish, with yellow-orange sessile glands, tube straight, ca. 2 mm long, progressively broadening to throat, lower lobe 2.5–4 mm long, ca. 2 mm deep, upper lobe ca. 1.5 mm long, 4-lobed; anther ca. 0.6 mm; style bifid. Nutlets pale brown, ca. 0.9 mm diam., smooth, flattened, red-speckled.

Etymology. Latin *minusculus -a -um*, very small, on account of the dwarf habit of the species.

Distribution. Endemic of SE DR. Congo (Haut-Katanga).

Habitat and ecology. Miombo woodlands, savannah; 1200–1300 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Guba (territ. Lubudi), 30 km E of Kolwezi, dépression incendiée sur terre très dure dans les Mutobo [*Isoberlinia* div. sp.], 29 Aug 1956, *P.Duvigneaud & J.Timperman 2549Co* (BRLU); Luiswishi, savane, 20 Sep 1982, *F.Malaisse 12350* (BR).

Note. *C. minusculus* is a very distinctive species, on account of its dwarf habit. It shares similarities with *C. modestus*, which also has tubers, a single flower in the axil of each bract, often subopposite and inflorescence with glandular hairs.

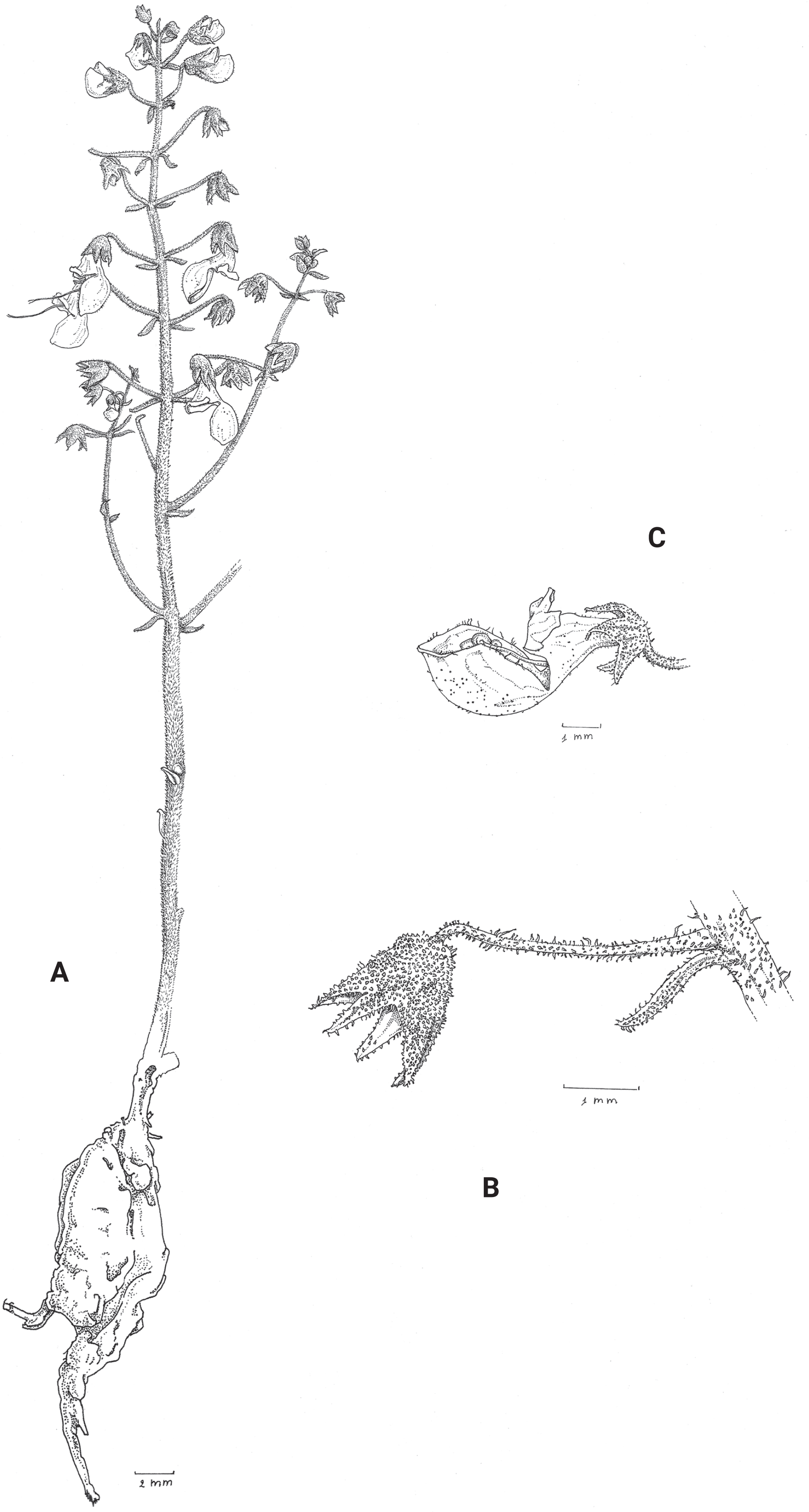

Figure 11. *Coleus minusculus* Meerts & A.J.Paton **A** habit **B** fruiting calyx **C** flower. *J.Bulaimu 520*. Drawn by Hilde Orye. Scale bars: 2 mm (**A**); 1 mm (**B, C**).

Coleus mitwabaensis **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347700-1
Fig. 12A–F

Diagnosis. Differing from all other species by the following combination of traits: corolla yellow, rootstock a small tuber, leaves not exceeding 2.7 × 1.0 cm.

Type. DR. Congo, Haut-Katanga, Kaziba (rive gauche Mweleshi, affluent rive gauche Senze), 1140 m elev., forêt katangaise, 12 Feb 1948, *G.F.de Witte 3333* (holotype BR [BR0000017707961]; isotype K).

Description. Perennial herb, with a single shoot, 0.12–0.40(–0.50) m high, from a globose to irregularly knobby ovoid tuber ca. 10 mm diam. Stem erect or more or less straggling, puberulent, with very short patent or retrorse eglandular hairs and yellow sessile glands; inflorescence axis abruptly becoming densely covered with purplish papillae and very short glandular hairs. Leaves opposite, spreading to ascending, occasionally grouped near stem base, blade mostly elliptic to narrowly elliptic, the lowermost ones shorter, obovate to obovate-elliptic, (1.0–)1.5–2.7 × (0.1–)0.3–1.0 cm, base cuneate to attenuate, apex obtuse to rounded, subglabrous above or strigillose (with short upward pointing hairs), very shortly appressed pubescent on veins beneath, with pale sessile glands, margin shallowly crenate to entire, very narrowly recurved, papillate to ciliolate, ca. 3 pairs of secondary veins diverging at a very acute angle; petiole 0(–0.3) cm. Inflorescence terminal, lax, unbranched or with 1 or 2 branches at lowermost node, 5–15 cm long, rachis with short papilliform hairs, glandular and eglandular, often reddish tinged, verticils spaced 5–15 mm, 2-flowered, flowers solitary in the axil of each bract, bract narrowly ovate, ca. 1 mm long, more or less persistent, pedicel 1–2 mm long, inserted slightly eccentrically. Flower: calyx at right angle with the pedicel, tubular, with pale sessile glands, short glandular hairs and conical papilliform purplish hairs on veins, ca. 3 mm long at anthesis, accrescent to 4–5 mm in fruit, throat truncate, posterior lobe ovate-triangular, ca. 1–1.5 mm long, not decurrent, lateral lobes triangular ca. 2 mm long, median lobes of lower lip narrowly triangular, ca. 2.5 mm long, with the sinus between median lobes deeper than between median and lateral lobes. Corolla yellow, 10–13 mm long, tube slightly curved to almost straight, widening from base to throat, ca. 3 mm diam. near throat, upper lip ca. 1 mm long, lower lip shortly pubescent, with yellow sessile glands and thin flexuous marginal cilia, ca. 4 mm long, cucullate, ca. 2 mm deep, enclosing stamens. Nutlets globose, very slightly compressed, brown, ca. 1 mm diam.

Etymology. Mitwaba Plateau, in the north of Upper Katanga, where the type specimen was collected, hosts a very original flora.

Distribution. Endemic of SE DR. Congo (Haut-Katanga, Mitwaba Plateau).

Habitat and ecology. Savannah, seasonally moist soil on river banks, miombo woodland; 1140–1400 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Route Mitwaba-Manono, km. 45, riv. Kalumengongo (zone Mitwaba), 1140 m elev., 8°19'S, 27°16'E, sable périodiquement inondé en bordure de rivière, 3 Feb 1986, *P.Bamps & F.Malaisse 8613* (BR); Kankunda (affl. rive gauche du Lupiala), 1400 m elev., forêt, 26 Nov 1947, *G.F.de Witte 3104* (BR); Route automobile pour le Shinkulu, 1450 m elev., savane arbustive, 21 May 1948, *G.F.de Witte 3863* (BR, K).

Notes. 1. *C. mitwabensis* is strikingly distinct on account of the yellow corolla, tuberous rootstock, small leaves and 2-flowered verticils.

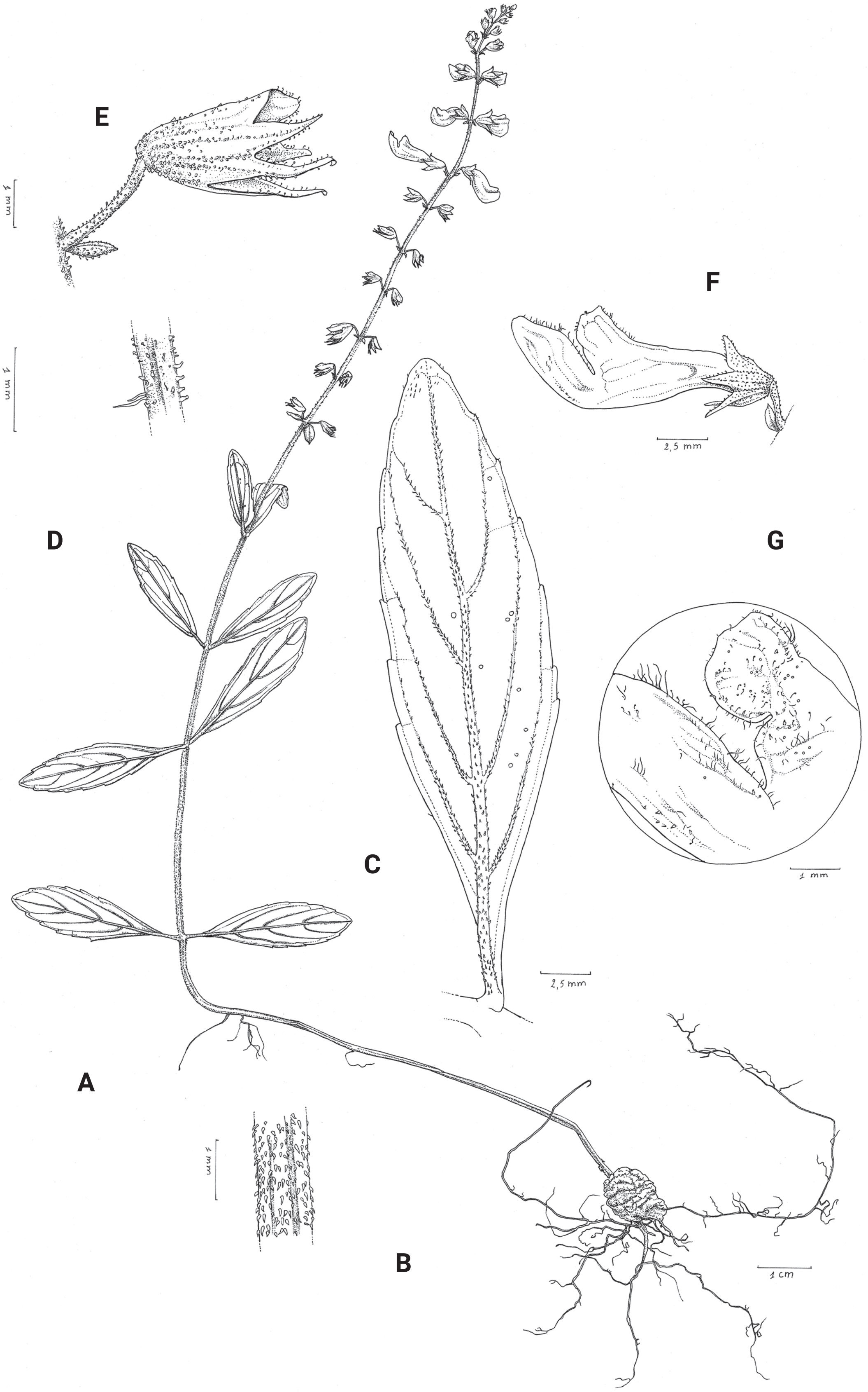

Figure 12. *Coleus mitwabaensis* Meerts & A.J.Paton **A** habit **B** detail of stem pubescence **C** leaf undersurface **D** detail of rachis pubescence **E** fruiting calyx **F** flower **G** detail of corolla pubescence. *P.Bamps & F.Malaisse 8613*. Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 1 mm (**B, D, E, G**); 2.5 mm (**C, F**).

2. Vernacular name: tulamalama, sansala (in kiluba).

3. The sap is used to impregnate fishing nets to attract fish. The tubers are edible.

Coleus modestus **(Baker) Robyns & Lebrun, Ann. Soc. Sci. Bruxelles, Sér. B 49: 106. 1929.**

≡ *Plectranthus modestus* Baker, Bull. Misc. Inform. Kew 1895(99): 72 (1895). Type: Zambia, Mbala District: Tanganyika Plateau, 1889, *A.Carson s.n.* (holotype K [K000430767]).

Description. Paton et al. (2009: 282), Paton et al. (2013: 229), as *Plectranthus modestus* Baker.

Distribution. SW Tanzania to Zambia.

Habitat and ecology. Highland savannah, dry woodlands, dambos; 1250–1950 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Keyberg, 6 Dec 1956, *E. Detilleux 222* (BR); Marungu, près de Kibobwa, 8 Nov 1970, *S.Lisowski, F.Malaisse, J.-J.Symoens 11875* (BR, POZG); Forêt de la Luiswishi (NE Lubumbashi), 3 Dec 1971, *F.Malaisse 7595* (BR); Marungu, Mulongoshi, Nov 1945, *P.Quarré 7211* (BR); Kimilolo, 23 Jun 1927, *P.Quarré 938* (BR); Kipopo, 12 Apr 1958, *A.Schmitz 6018* (BR); Kiunda, Sept 1944, *L.Dubois 1260* (BR).

Coleus monostachyus **(P.Beauv.) A.J.Paton, Phytokeys 129: 76. 2019.**

Type. Benin, *A.Palisot de Beauvois s.n.* (holotype G [G00018077]).

Coleus monostachyus **(P.Beauv.) A.J.Paton subsp. *monostachyus***

= *Solenostemon monostachyus* var. *amplifrons* Briq. Bull. Herb. Boissier, sér. 2, 6: 826. 1906. Type: DR. Congo, Bangala, 26 May 1888, *F.Hens ser. C, 33* (holotype Z [Z-000021117]).

Description. Paton et al. (2022: 52).

Distribution. W Tropical Africa to S Chad and Cabinda.

Habitat and ecology. Disturbed ground, cultivated fields, fallow fields, rainforest, wetland, occasionally epiphytic on palm stipe; 60–800 m elev.

Additional specimens. DR. Congo, ***Mayumbe***, Gimbi, vallée de la Mvuzi, 5 Jan 1949, *L.Toussaint 720* (BR); ***Bas-Congo***, Kinsonia, 9 Mar 1960, *P.Compère 1589* (BR); Kitobola, 15 May 1910, *A.Flamigni 176* (BR, US); Terr. Masina, Kimbangu, 20 Dec 1978, *L.Pauwels 6093* (BR, WAG); ***Kasaï***, Kutu, 30 Oct 1903, *Em.&M. Laurent s.n.* (BR); Kapanga, Apr 1934, *F.Overlaet 1213* (BR); ***Forestier central***: Mulumbela, 27 Jan 1980, *Y.&T.Ankei 79/1042* (BR); Bambesa, 16 Sep 1958, *A.Blomme 122* (BR); Bongabo, 6 Jun 1971, *H.Breyne 1695* (BR); Territ. Banalia, route Kole-Kanwa, km 24, 13 Jun 1932, *Galdermans 10* (BR); Territ. Ekota-Bakutu, Sep 1934, *L.Dubois 565* (BR); Karawa, Apr 1924, *V.G.Goossens 4485* (BR);

Bokuma, 26 Feb 1941, *G.Hulstaert 61* (BR); Eala, 22 May 1946, *J.Léonard 164* (BR); Yangambi, 29 Oct 1913, *A.Michiels 32* (BR); Barumbu, 29 Aug 1938, *J.Louis 11061* (BR, U, US); ***Ubangi-Uele***, Bodangabo, 15 Feb 1955, *C.Evrard 200* (BR); Digba, 13 Sep 1952, *P.Gérard 252* (BR); Tukpwo, 9 Jul 1959, *P.Gérard 3984* (BR);

Note. Specimens with unusually large leaves (e.g. *W.Robyns 4263*) correspond to "var. *amplifrons*', but variation is continuous and this variety is not retained here.

Coleus mystax **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347701-1
Fig. 13A–E

Type. DR. Congo, Haut-Katanga, Parc national de l'Upemba, Ganza, près de la riv. Mware, 24 Jun 1949, *G.F.de Witte 6990* (holotype BR [BR0000016835726]; isotype K).

Diagnosis. Closely related to *Coleus efoliatus* De Wild., differing in the long patent smooth hairs on the calyx, pedicel and rachis, the shorter, more congested, inflorescence and the calyx lobes all similar in shape.

Description. Annual herb, ca. 0.3 m high, leafless at flowering. Stem erect, sharply quadrangular, puberulent (hairs appressed, antrorse), with a tuft of hairs at the nodes, shiny, with yellow sessile glands, sparingly branched. Leaves not observed. Inflorescence lateral, moderately congested, 6–20 mm long, peduncle ca. 5 mm long, 9 to 20 flowers arranged in a spiral, with a single flower between an opposite or subopposite pair, each bract subtending a single flower; rachis with straight, smooth 1–4 mm long long cilia and short glandular hairs; bract narrowly elliptic, ca. 0.3 mm long; pedicel 1–2.5 mm long, pubescent as the rachis, inserted eccentrically in front of upper calyx lobe; calyx tubular, 3–4 mm long at anthesis, slightly accrescent to 4–5 mm long in fruit, pale whitish-green with dark green veins, with patent smooth cilia 2–5 mm long, short glandular hairs and sessile yellow glands, tube truncate, lobes purplish-tinged, all lobes almost similar in shape and length, narrowly triangular-subulate, 1–2 mm long, upper lobe slightly recurved, not decurrent; corolla sky-blue, ca. 6 mm long, tube straight, ca. 3 mm long, not exceeding calyx, progressively widening to throat, upper lip ca. 1 mm long, sparingly pilose, anterior lip ca. 2 mm long, 1 mm deep, cucullate, sparingly pilose, stamens included. Fruit: Nutlets rounded, compressed, shiny brown, ca. 0.8 mm diam.

Etymology. Latin *mystax -acis*, whisker, on account of the long stiff hairs on calyx and pedicel.

Distribution. Endemic of SE DR. Congo (Haut-Katanga).

Habitat and ecology. Steppic savannah, miombo woodland, often on rocky soil; 1100–1400 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Colline de Kungumarembe, à l'Est de Kasompi, forêt claire à *Brachystegia floribunda*, 30 Jul 1956, *P.Duvigneaud & J.Timperman 2183E* (BRLU); Entre Shinkolobwe et Tantara, forêt claire sur roches dures, 7 Sep 1956, *P.Duvigneaud & J.Timperman 2643H* (BRLU); Jadotville [Likasi], forêt claire à *Brachystegia utilis* sur grand conglomérat, 15 Jun 1957, with *Coleus efoliatus*, *P.Duvigneaud 3580C1* (BRLU); 7 km à l'ouest de Nzilo, sur la piste Nzilo-Kyamasumba, 1200 m elev., forêt claire sur affleurement rocheux, 17 Jun 1984, *M.Schaijes 2323* (BR).

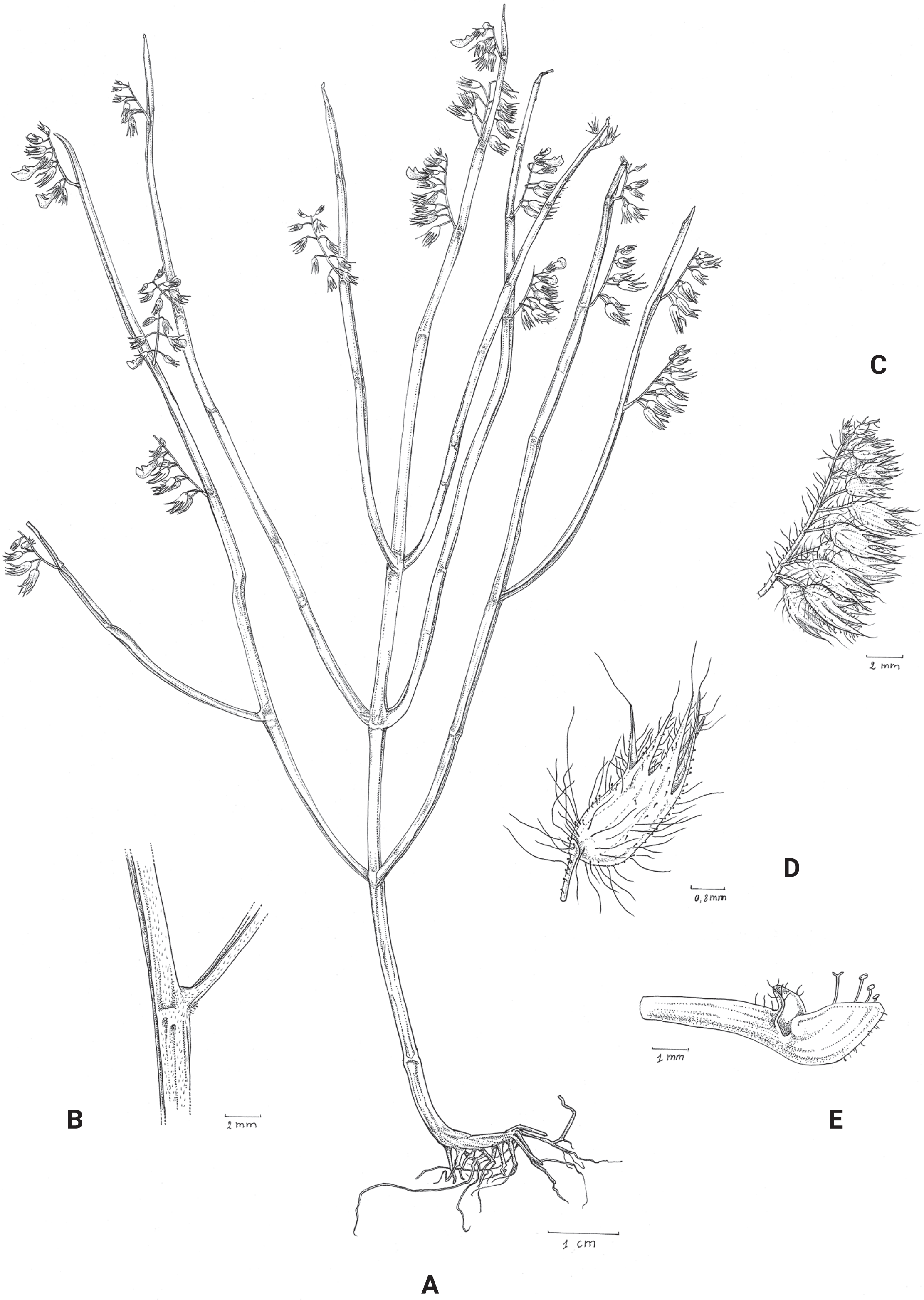

Figure 13. *Coleus mystax* Meerts & A.J.Paton **A** habit **B** detail of stem **C** inflorescence **D** fruiting calyx **E** corolla. *G.F.de Witte 6990*. Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 2 mm (**B, C**); 0.8 mm (**D**); 1 mm (**E**).

Notes. 1. *C. mystax* is closely related to *C. efoliatus*, with which it sometimes co-exists; it shares with it the annual habit, early deciduous leaves, strongly quadrangular stem, inflorescence architecture and short corolla. It differs from it in the very conspicuous long smooth cilia on inflorescence (vs. cilia lacking or occasionally sparse in *C. efoliatus*), the calyx lobes all more or less equal in size and shape (vs. upper lobe ovate), the shorter, more congested inflorescence (6–20 mm long vs. 15–50 mm) and the shorter calyx (4–5 mm long vs. 5–10 mm).

2. Vernacular name: tulamalama (in the Upemba National Park).

Coleus parvifolius **(Baker) Meerts & A.J.Paton, comb. nov.**

urn:lsid:ipni.org:names:77347702-1

Pycnostachys parvifolia Baker, Bull. Misc. Inform. Kew 1895: 72. 1895. Type: Zambia, Northern Province, Fwambo, 1894, *A.Carson 103* (lectotype K [K000405989], designated by Bruce [1940]).(Basionym)

= *Coleus capitatus* A.J.Paton, Phytokeys 129: 33. 2019, nom. illeg., syn. nov.

Description. Paton et al. (2009: 388), Paton et al. (2013: 317), as *Pycnostachys parvifolia* Baker.

Distribution. W and S Tanzania to Zambia and SE DR. Congo.

Habitat and ecology. Steppic savannah on highlands, on moist soil (1200–) 1700–2000 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kundelungu, 1968, *T.Coget 116* (BR); 50 km NE Lubumbashi, bord de la Luiswishi, 11 Apr 1969, *S.Lisowski 23447* (POZG); Lwamisamba, 28 Mar 1975, *F.Malaisse 8641* (BR); Marungu, Kipiri, Nov 1945, *P.Quarré 7337* (BR).

Note. 1. *C. parvifolius* and *C. descampsii* are closely related and intermediates occur.

2. The new name *C. capitatus* A.J.Paton was superfluous because the binomial *Coleus parvifolius* has never been published before.

Coleus pengbelensis **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347703-1

Fig. 14A–I

Type. DR. Congo, Bas-Uele, Route Digba-Gwane, 700 m, sur pengbele, Dec. 1945, *R.Germain 4397* (holotype BR [BR0000016836068]; isotype K).

Diagnosis. Related to *Coleus bojeri* and other species formerly referred to the genus *Solenostemon* on account to the lower calyx lobes fused into a lip, differing in the upper calyx lobe narrowly ovate-triangular, long attenuate, horizontal or somewhat recurved, much exceeding the lower lobes, indumentum papillate and tuberculate nutlets.

Description. Annual herb ca. 0.3–1.0 m high, not reported to be aromatic; tubers absent or not collected. Stem erect, quadrangular, thinly papillate, simple or branched. Leaves opposite, ascending, often with fascicles of small leaves in the axils; blade narrowly ovate to narrowly elliptic, 3.5–6 × 0.8–1.6(–2.2) cm, base attenuate, apex acute, margin crenate, densely papillate on both surfaces

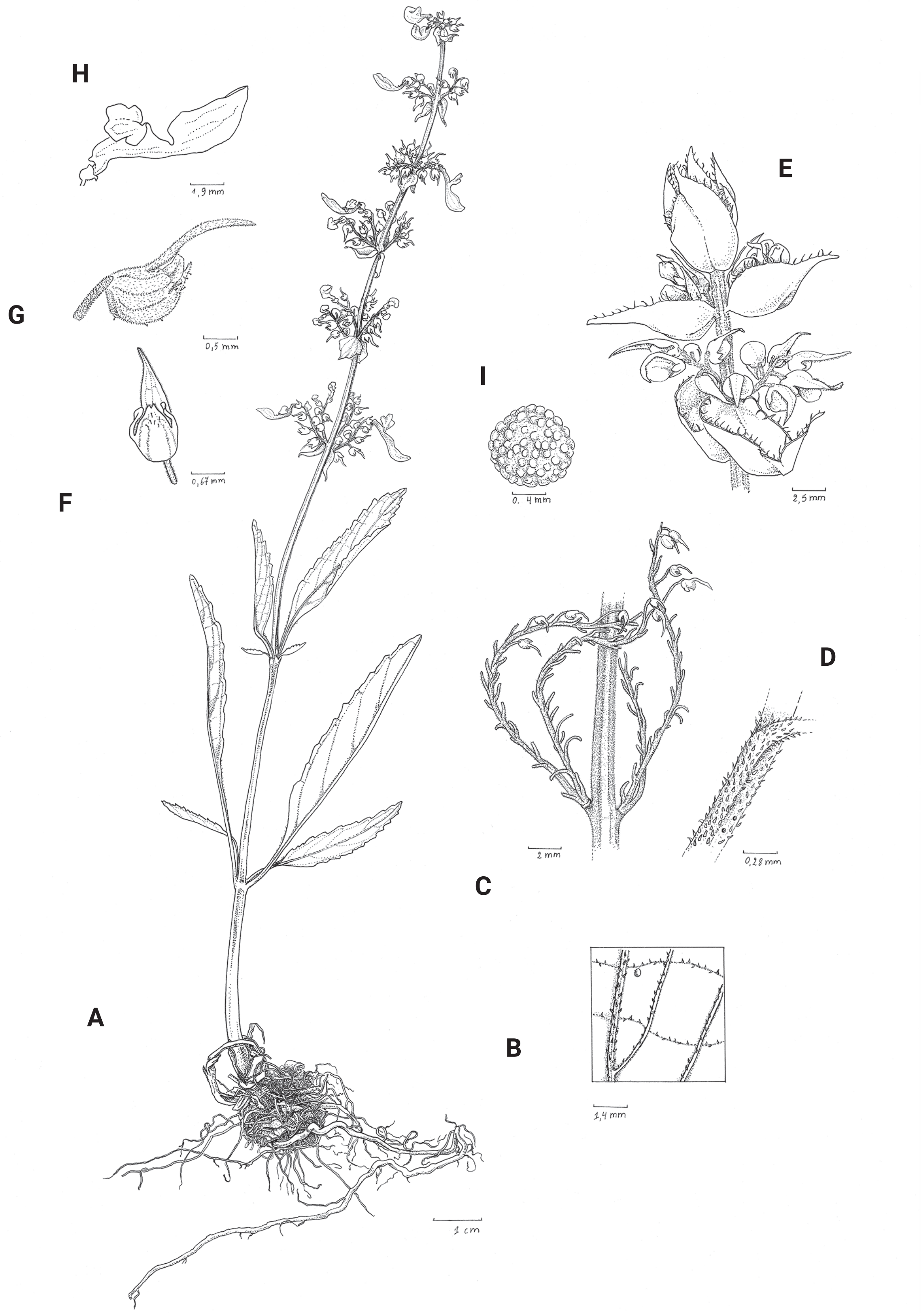

Figure 14. *Coleus pengbelensis* Meerts & A.J.Paton **A** habit **B** detail of lower surface of leaf blade **C** detail of infrutescence **D** detail of pubescence of inflorescence branch **E** detail of tip of inflorescence with bracts **F** flowering calyx seen from below **G** fruiting calyx, side view **H** corolla **I** nucule (**A** *A.De Wulf 264* & *G.Le Testu 338* (roots) **B** *A.De Wulf 264* **C** *G.Le Testu 338* **E** *A.De Wulf 264* **D, F** I *R.Germain 4397*). Drawn by Hilde Orye. Scale bars: 1 cm (**A**); 1.4 mm (**B**); 2 mm (**C**); 0.28 mm (**D**); 2.5 mm (**E**); 0.67 mm (**F**); 0.5 mm (**G**); 1.9 mm (**H**); 0.4 mm (**I**).

and with sessile red glands, 4–6 pairs of veins diverging at a very acute angle, veins prominent on lower surface; petiole 0.5–1.6(–2.5) cm long, narrowly canaliculate, occasionally with long patent cilia. Inflorescence terminal, simple, (3–)9–16 cm long, lax, verticils spaced 5–25 mm, the uppermost ones contiguous, cymes consisting of two opposite cincinni, ca. 20–50 flowered, subsessile, very short at first, markedly elongating up to 30 mm in fruit and then flexuous, bracts narrowly to broadly ovate, ca. 5–7 × 2–5 mm, cucullate, occasionally with long cilia in lower half, contracted into a 2 mm point, persistent, the uppermost ones forming a coma, the others reflexed; pedicel 0.5 mm long at anthesis, elongating to 1.5 mm in fruit, inserted eccentrically in front of posterior lobe. Flower: calyx campanulate to shortly tubulate, 2 mm at anthesis, accrescent up to 4–5 mm in fruit, very shortly pubescent and with red sessile glands, tube truncate, upper lobe narrowly ovate-triangular, long attenuate, horizontal or somewhat recurved, much exceeding the lower lobes, margin occasionally ciliate, shortly pubescent also on inner surface, lateral lobes of lower lip triangular, ca. 1.2 × 1 mm, obtuse, median lobes fused for most of their length into a triangular lip ca. 1.5 × 1.5 mm, with 1 or 2 apical teeth; corolla blue or pale mauve, ca. 8 mm long, tube ca. 3 mm long, slightly curved, upper lip perpendicular, ca. 2–3 mm long, lower lip ca. 5 mm long, 2 mm deep, shortly pubescent, occasionally with sessile red glands, stamens fused. Nutlets almost globular, ca. 0.9 mm in diam., light brown, verrucose-tuberculate.

Etymology. Pengbele (also spelled pembele) is the local name of the particular vegetation type in which the species occurs i.e. open herbaceous vegetation on seasonally flooded lateritic crust (Bamps 1975).

Distribution. N DR. Congo, Central African Republic.

Habitat and ecology. Open savannah, scrub, seasonally moist soil on lateritic crust with impaired drainage in the rainy season and drying out in the dry season (pengbele); 600–700 m elev.

Additional specimens. DR. Congo, ***Ubangi-Uele***, Région de Gwane, sur pengbele, 8 Jul 1955, *R.Boutique 148* (BR); Bas-Uélé, en savane, 13 Oct 1934, *A.De Wulf 264* (BR); Tukpwo, sur pengbele, 1 Aug 1953, *P.Gérard 989* (BR); Tukpwo, savane, 17 Apr 1954, *P.Gérard 1269* (BR); Tukpwo, sur cuirasse latéritique, Nov 1945, *R.Germain 4281* (BR); Tukpwo, un peu au-delà de la bifurcation de Bengo, îlot forestier sur pembele, 18 Jun 1942, *Gilbert* in *H.Dubois 100* (BR).

Central African Republic, ***Oubangui-Chari***, Haute-Kotto, entre Zazo et Lutari (?), plateau de latérite, 30 Oct 1921, *G.Le Testu 3385* (BR); Région de Zemio-Obo, à Obo, 27 Dec 1963, *B.Descoings 11936* (MPU); Entre Kitessa et Zemio, 01 Jan 1964, *B.Descoings 12365* (MPU); entre Zemio et Rafaï, dalle latéritique suintante à 21 km à l'ouest de Zemio, 01 Jan 1964, *B.Descoings 12407* (MPU); route entre Zemio et Rafaï, à 48 km à l'ouest de la Ouarra, 03 Jan 1964, *B.Descoings 12502* (MPU).

Notes. Vernacular name: akonki-pia (in azande).

Coleus penicillatus **(A.J.Paton) A.J.Paton, Phytokeys 129: 82. 2019.**

≡ *Plectranthus penicillatus* A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 325. 2009. Type: Zambia, Mbuzi–Kaluza, 23 Aug 1938, *P.J.Greenway & C.G.Trapnell 5627* (holotype K [K000431999]).

Description. Paton et al. (2009: 325), Paton et al. (2013: 265) as *Plectranthus penicillatus* A.J.Paton.

Distribution. S Tanzania to E Zambia and SE DR. Congo.

Habitat and ecology. Rock outcrop (in DR. Congo; elsewhere: savannah). ca. 2300 m elev., (elsewhere 300–800 m elev.).

Additional specimens. DR. Congo, ***Haut-Katanga***, Marungu, 12 km ESE Kasiki, 23 Sep 1959, *A.Schmitz 6577* (BR).

Notes. 1. New species record for DR. Congo.

2. The specimen cited was collected at a much higher elevation compared to the rest of the range (2300 m vs. 300–800 m). It departs somewhat from other materials in having denser inflorescence, with more flowers.

Coleus piscatorum **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347704-1
Fig. 15A–D

Type. DR. Congo, Haut-Katanga, Upemba National Park, Munoï, bifurcation Lupiala, 890 m elev., 2 Jun 1948, *G.F.de Witte 3897* (holotype BR [BR0000017708043]).

Diagnosis. Closely related to *Coleus efoliatus* De Wild., differing in the shorter pedicels (1.5 vs. 2–6 mm), shorter fruiting calyx (4.5 mm long vs. 5–10 mm), with all 5 subequal triangular lobes (vs. upper lobe ovate) and the longer corolla (ca. 10 mm long vs. 3–5(–6) mm); also closely related to *C. mystax*, differing in the lack of long cilia in the inflorescence, the longer corolla and the divaricate branching pattern.

Description. Annual herb, ca. 0.30 cm high. Stem erect, sharply quadrangular, shiny, sparsely pubescent, with very short retrorse and long patent hairs, with a tuft of hairs at nodes, branched in the upper two-thirds, with 3–5 pairs of opposite branches, almost horizontal to ascending at a broad angle, divaricate, slender, 1–8 cm long, each with 1 or 2 levels of dichotomous ramifications. Leaves almost all absent at flowering; blade ovate, ca. 2 × 1 cm, base rounded, apex narrowly subobtuse, somewhat pubescent on both surfaces, with pale sessile glands on lower surface, margin entire, secondary veins ca. 2 pairs, inconspicuous; petiole 0–1 mm long. Inflorescence seemingly terminal, actually lateral on ultimate node of twigs, slightly congested, 3–7 mm long, racemiform, rachis with short patent eglandular and glandular hairs, 1(–2) flower(s) in the axil of each bract, occasionally subopposite, bracts linear, ca. 1 mm long, pedicels 1–1.5 mm long, pubescent as rachis, inserted slightly eccentrically in front of upper calyx lobe. Flower: calyx ca. 2.5 mm long at anthesis, with short patent glandular and eglandular hairs and pale sessile glands, fruiting calyx ca. 4.5 mm long, whitish-membranous or chartaceous, tube tubular to campanulate, ca. 2 mm long, all lobes more or less similar in shape and size, narrowly triangular, ca. 2–2.5 mm long, acute, with thickened margin; median lobes of lower lip slightly longer; corolla blue, ca. 10 mm long, tube straight, ca. 3 mm long, progressively expanding to throat, lower lobe ca. 5 mm long, 3 mm deep, cucullate, enclosing stamens, thinly puberulent, upper lobe ca. 2 mm long. Nutlets pale brown, shiny, smooth, somewhat lenticular, ca. 1 mm.

Etymology. Latin *piscator -oris*, fisherman; the species is used to impregnate fishing nets to attract fishes.

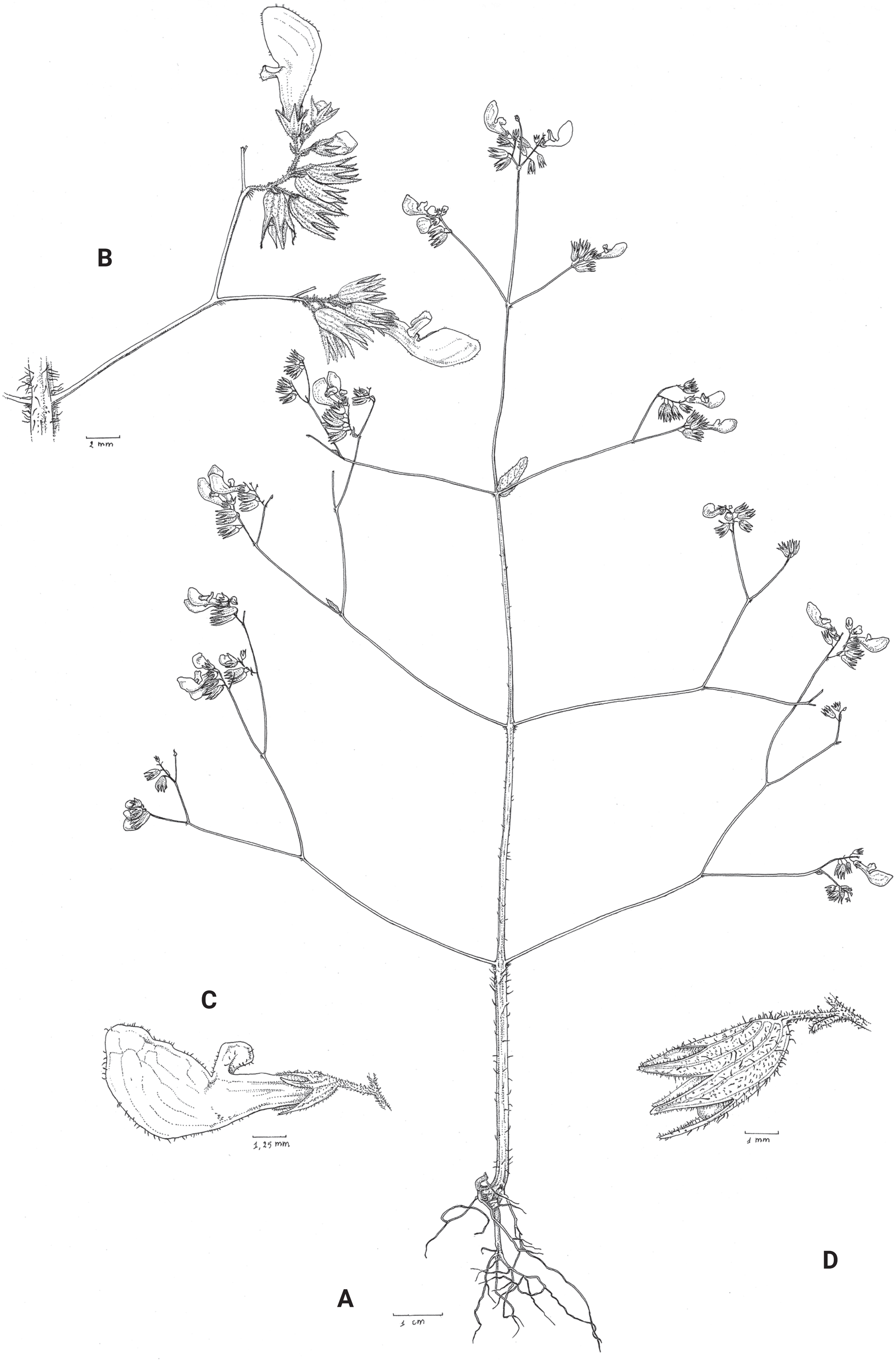

Figure 15. *Coleus piscatorum* Meerts & A.J.Paton **A** habit **B** detail of inflorescence **C** flower **D** fruiting calyx (*G.F.de Witte 3897*). Scale bars: 1 cm (**A**); 2 mm (**B**); 1.25 mm (**C**); 1 mm (**D**). Drawn by Hilde Orye.

Distribution. Endemic of SE DR. Congo (Haut-Katanga).

Habitat and ecology. Shrub savannah, 890 m elev.

Additional specimens. None, known only from the type specimen.

Note. Vernacular name: lukakatjila (in kiluba).

Coleus prittwitzii **(Perkins) A.J.Paton, Phytokeys 129: 86. 2019.**

≡ *Pycnostachys prittwitzii* Perkins, Notizbl. Bot. Gart. Berlin-Dahlem 8: 68. 1921. Type: Tanzania, Iringa District, Ndembera flood plain, near Gominyi, 2 Aug 1901, *G.von Prittwitz 28* (holotype B destroyed; isotype K [K000405965] fragment).

Description. Paton et al. (2009: 398), Paton et al. (2013: 324), as *Pycnostachys prittwitzii* Perkins.

Distribution. SW Tanzania to N Zambia.

Habitat and ecology. Savannah on moist soil; ca. 1200 m elev.

Additional specimens. Burundi, Mutara, Mosso, 12 Aug 1952, *G.Michel 3686* (BR, K); Kiofi, Mosso, 16 Sep 1952, *G.Michel 3907* (BR).

Note. The two cited specimens differ from other materials of *C. prittwitzii* in having opposite (not ternate), broader, leaves and shorter inflorescence; they could represent a different taxon.

Coleus pseudoschizophyllus **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347705-1
Fig. 16A–F

Type. DR. Congo, Haut-Katanga, Marungu, Katomia, 18 Apr 1939, *P.J.J.Vanden Brande 55* (holotype BR [BR0000016832183]).

Diagnosis. Closely related to *C. schizophyllus* on account of pinnatisect leaves and tuberous rootstock, differing by the conspicuously exserted sigmoid corolla tube, larger leaves, exserted stamens, tightly appressed indumentum and lack of glandular hairs in the inflorescence. It is also very closely related to *C. welwitschii*, differing by the jagged to pinnatisect leaves and rootstock with tubers.

Description. Perennial herb, or suffrutex, 0.30–0.80 m high, from a thick rhizomatous rootstock, with fusiform tubers up to 5 cm long. Stem ascending to erect, the lower part woody, defoliated, purplish, strongly quadrangular, thinly puberulous with short adpressed retrorse hairs, upwards more densely puberulous and with red sessile glands, with a few long patent hairs at nodes, branched. Leaves opposite, petioled, often with fascicles of young leaves in the axils, ascending to spreading; blade ovate to trullate, 1.0–2.8 × 0.6–2.5 cm, apex acute, base more or less abruptly contracted and then attenuated into the petiole, margin markedly recurved, jagged to pinnatisect, with 3 to 6 lobes on either side, apical lobe narrowly oblong-triangular 3–5 mm long, upper surface dark green in herbarium, appressed pubescent, ca. 3 pairs of secondary veins, markedly impressed, lower surface markedly paler, pubescent on venation, this prominent, with dense red sessile glands; petiole 0.5–1.5 cm long, narrowly winged over the whole length, canaliculate, margin strongly recurved. Inflorescence lax, 8–10 cm long, 9–16 mm wide at anthesis (corolla excluded), with 12–15

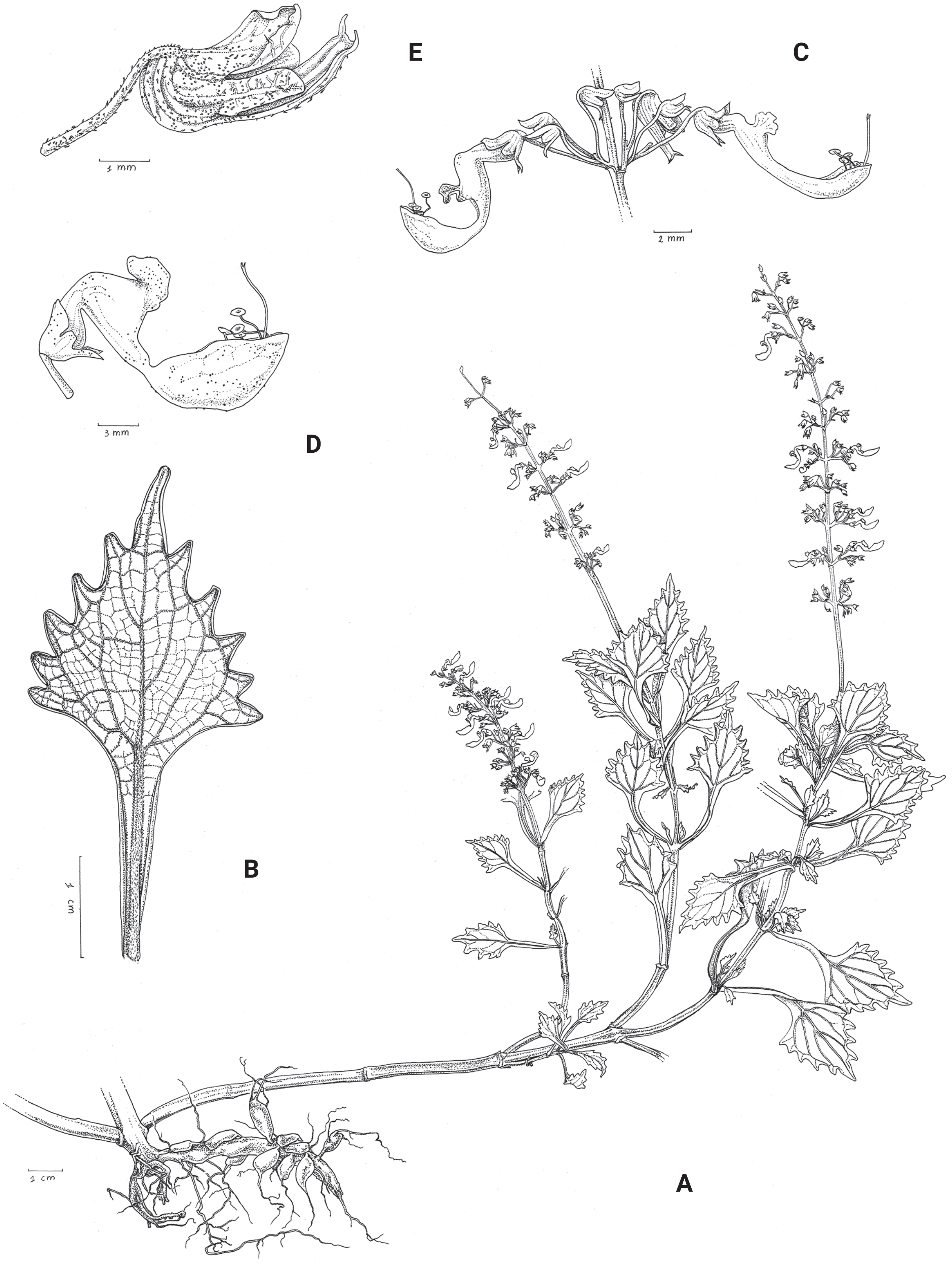

Figure 16. *Coleus pseudoschizophyllus* Meerts & A.J.Paton **A** habit **B** leaf **C** detail of inflorescence **D** flower **E** fruiting calyx **A** (except roots) **B–D** *L.Dubois 1140* **A** (roots only) **E** *P.J.J.Vanden Brande 55*. Drawn by Hilde Orye. Scale bars: 1 cm (**A, B**); 2 mm (**C**); 3 mm (**D**); 1 mm (**E**).

verticils, spaced 6–10 mm, bracts ovate, cucullate, acuminate, 2–3 mm long, not forming a coma, ciliate, soon caducous, cymes sessile or with 1-mm long peduncle, of 5–12 flowers, cincinni 2–4 mm long, pedicels 2–4 mm, appressed pubescent, curved at tip, inserted very eccentrically in front of calyx upper lobe. Flower: calyx ca. 1.5 mm long at anthesis, pubescent, with red sessile glands, fruiting calyx 4–5 mm long, tubular, tube with 10 prominent ridges, throat truncate; posterior lip obovate, slightly recurved, very shortly decurrent, rounded to apiculate, ca. 2 mm long, lateral lobes oblong, ca. 2 mm long, rounded to truncate, median lobes of anterior lip fused into a 3–4 mm long linear lip, with teeth acute. Corolla white, 7–11 mm long, very shortly pubescent or puberulent on lobes, with red sessile glands, tube strongly sigmoid, 3–5 mm long, the sigmoid part long exserted, upper lip ca. 1 mm long, shallowly 4-lobed, much shorter than lower, lower lip ca. 4–5 mm long, 1.5–2 mm deep, somewhat upwardly curving, stamens exserted, filaments fused, anther ca. 0.5 mm long, style very shortly bifid, the branches often not divergent. Fruit: nutlets not observed.

Etymology. The species superficially resembles *Coleus schizophyllus* (Baker) A.J.Paton on account of the deeply lobed leaves.

Distribution. Endemic of SE DR. Congo (Haut-Katanga, Marungu Massif).

Habitat and ecology. Rock crevices on mountains, scrub, steppic savannah on rocky soil (rhyolite); ca. 1600–2450 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Marungu, Ndawa, 2200 m elev., Apr 1944, *L.Dubois 1140* (BR); Marungu Massif, Katomia, 18 Apr 1939, *P.J.J.Vanden Brande 67* (BR); Marungu, Katuba, broussailles sur affleurement de rhyolithes, 27 Jun 1957, *P.Duvigneaud 3744L* (BRLU); Marungu, Env. Kasiki, Mont Kilonge, 12 Jun 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 6518* (POZG); Marungu, 10 km NNE Kasiki, sommet Lusale, 2450 m elev., 26 Nov 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens* 8460 & 8460a (POZG); Marungu, 7 km WSW de Luonde, 16 Feb 1970, *S.Lisowski, F.Malaisse, J.-J.Symoens 9768* (POZG); Marungu, Mont Zuiba, steppe, 21 Feb 1970, *S.Lisowski, F.Malaisse, J.-J.Symoens* 10483 (POZG).

Coleus pseudospeciosus (Buscal. & Muschl.) A.J.Paton, Phytokeys 129: 87. 2019.

≡ *Pycnostachys pseudospeciosa* Buscal. & Muschl., Bot. Jahrb. Syst. 49: 486. 1913. Type: Zambia, Lake Bangweulu, s.d, *E.D'Aosta 1002* (lectotype K [K000405996] fragment, designated by Ryding [2001]).

= *Pycnostachys ballotoides* Perkins, Notizbl. Bot. Gart. Berlin-Dahlem 8: 72. 1921. Type: DR. Congo, Katanga, Mt Senga, May 1908 ["1906" in protologue], *T.Kassner 2930a* (holotype B destroyed).

= *Pycnostachys mausaensis* De Wild., Notes Fl. Katanga 7: 47. 1921. Type: DR. Congo, Katanga, Mt Senga, mt. slope, 31 May 1908, *T.Kassner* 2920a (holotype BR [BR0000013409814]; isotype K [K000405742]).

Description. Paton et al. (2013: 326), as *Pycnostachys pseudospeciosa* Buscal. & Muschl.

Distribution. S DR. Congo to N. Zambia.

Habitat and ecology. Steppic savannah on seasonally set soil (dilungu), pond margin, more rarely dry woodland; 1400–1750 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Au-delà de Kakera vers Baudouinville [Moba], 29 Jun 1957, *P.Duvigneaud 3773* (BRLU); Buyé Bula, affl. Muye, 30 Mar 1948, *G.F.de Witte 3595* (BR, WAG); Mont Senga, 31 May 1908, *T.Kassner 2920a* (K); Près de la rivière Mutungulu, 16 May 1971, *F.Malaisse 1357* (BR).

Coleus repens **Gürke, Bot. Jahrb. Syst. 19: 213. 1894.**

Type. Cameroon, Mt Kupe, Nyasoso, nature trail above the Government High School, *B.Pollard 83* (neotype K [K000051084]; isoneotype KUPE, WAG, YA, designated by Pollard [2005]).

Description. Paton (2022: 53).

Distribution. W & WC Tropical Africa.

Habitat and ecology. Rain forest; ca. 500 m elev.

Additional specimens. DR. Congo, ***Forestier Central***, Katako Kombe, Jan 1910, *J.Claessens 406* (BR).

Note. This species is known from a single collection in DR. Congo, ca. 1000 km east of nearest localities in the Republic of Congo; the materials from DR. Congo departs from typical materials in having lateral calyx teeth obtuse at tip, not acuminate.

Coleus rhodesianus **(N.E.Br.) A.J.Paton, Phytokeys 129: 88. 2019 (“*rhodesianum*”).**

≡ *Englerastrum rhodesianum* N.E.Br., Bull. Misc. Inform. Kew 1922: 31. 1922. Type: Zambia, Mumbwai, *M.A.Macaulay 637* (syntype K), & Zambia, Livingstone, *F.A.Rogers 7205* (syntype, not seen).

= *Englerastrum schweinfurthii* Briq., Bot. Jahrb. Syst. 19: 178. 1894, non *Coleus schweinfurthii* Vatke. Type: South Sudan (“Ghasallquellengebiet, Lande der Bongo”), Addai, 19 Oct 1869, *G.Schweinfurth 2532* (K, P, PRE, W).

= *Plectranthus djalonensis* (A.Chev.) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 286. 2009. Type: Guinea, sur les plateau ferrugineux arides entre Timbo et Kouria, Sept 1907, *A.Chevalier s.n.* (holotype P [P00466389]; isotype K).

Description. Paton et al. (2009: 286), Paton et al. (2013: 236), as *Plectranthus djalonensis* (A.Chev.) A.J.Paton.

Distribution. Tropical Africa to Caprivi Strip.

Habitat and ecology. River-bank, ruderal, open vegetation on wet soil, savannah, palm oil plantation, mostly on wet soil; forests, rarely on copper rich soil; very broad ecological amplitude in terms of light and soil moisture; 100–1750 m elev.

Additional specimens. DR. Congo, ***Mayombe***, Lukula, 1 Sep 1913, *J.Bequaert 671* (BR); Luki, 3 Apr 1947, *R.Devred 3363* (BR, POZG); ***Bas-Congo***, Kisantu, 4 Mar 1959, *L.Pauwels 2005* (BR, WAG); Dolo [Ndolo], Jun 1899, *R.Schlechter 12490* (AMD, BM, BR, E, G, L, P); ***Kasaï***, Lusambo, 15 Mar 1939, *P.Casier 54 & 56* (BR); Suka, Jul 1975, *M.Dujardin 401* (BR); ***Bas-Katanga***, Mwene-Ditu, Kele, 13

May 1957, *L.Liben 2946* (BR); Gandajika, 18 Mar 1954, *S.Risopoulos 196* (BR); ***Forestier Central***, Yangambi, Ile Tukutu, 10 Jul 1963, *D.Bolema 1178* (BR); Kisangani, Ile Kongolo, 3 Mar 1978, *J.Lejoly 2747* (BR, BRLU, K, WAG); Yoambole, entre Lileko et Basoko, 28 Sep 1938, *J.Louis 11437* (BR); Bikoro, Gombe, 20 May 1959, *L.Toka 79* (BR, WAG); ***Ubangi-Uele***, Doruma, Oct 1936, *A.M.De Graer 754* (BR, K, WAG); Camp Garamba, 10 Oct 1955, *M.Micha 296* (BR, WAG); ***Lacs Edouard et Kivu***, Ruzizi, May 1967, *J.Loumaye s.n*. (BR); ***Haut-Katanga***, Upemba, riv. Manda, 20 Apr 1948, *G.F.de Witte 3736* (BR); Entre Mulubi et Kashika, 29 Apr 1926, *J.Lebrun 2119* (BR); Kwatebala, 24 Apr 2006, *F.Malaisse, E.Kisimba, L.Saad 21* (BR).

Rwanda, Route Nyamasheke-Kibuye, km 19, 29 Mar 1972, *G.Bouxin 1527* (BR); Mushao, May 1929, *H.Humbert 8460* (BR); Rwinkwavu, Plaine de Matinza, 21 May 1969, *G.Bouxin & M.Radoux 450* (BR).

Burundi, Aérodrome de Bujumbura, 16 Mar 1967, *J.Lewalle 1680* (BR, MO); Kabuyekere, 5 Jun 1980, *M.Reekmans 9282* (BR, MO, US); Kigwena, 13 May 1982, *M.Reekmans 11199* (BR, MO, WAG).

Coleus rotundifolius **(Poir.) A.Chev. & Perrot, Veg. Ut. Afr. Trop. Franç. 1: 101. 1905.**

≡ *Germanea rotundifolia* Poir. in J.B.A.M.de Lamarck, Encycl. 2: 763. 1788.

≡ *Plectranthus rotundifolius* (Poir.) Spreng., Syst. Veg., ed. 16. 2: 690 (1825). Type: Mauritius (“Isle de France”), *P.Commerson s.n.* (holotype P [P00152706]; isotype FI).

Description. Paton et al. (2009: 330); Paton et al. (2013: 269), as *Plectranthus rotundifolius* (Poir.) Spreng.

Habitat and ecology. Fallow field; ca. 400 m; in Africa, always in cultivation or as a relic of old cultivation.

Additional specimens. DR. Congo, ***Bas-Congo***, Kasangulu, 22 Apr 1960, *P. Compère 1991* (BR).

Rwanda, Nyabarsingo, *Simpson s.n*. (TCD, not seen, cited in Suddee et al. 2004).

Notes. 1. New species record for DR. Congo.

2. This species belongs in the difficult group of *C.bojeri-C. welwitschii*, in which identification requires carefully collected underground organs. The collecting notes on the label of *P.Compère 1991* mention the presence of tubers, but these have not been collected. Apart from tubers, the species differs from *C. bojeri* in having somewhat thicker and more pubescent leaves.

3. See note under *C. welwitschii*.

Coleus ruandensis **(De Wild.) A.J.Paton, Phytokeys 129: 90. 2019.**

≡ *Pycnostachys ruandensis* De Wild., Pl. Bequaert. 4: 401. 1928. Type: Rwanda, between Kirinda and Lubengera, 6 Jun 1926. *W.Robyns 2449* (holotype BR [BR0000008910424], [BR0000008909770]; isotype K [K000405731], P [P00541261]).

Description. Paton et al. (2009: 389), Paton et al. (2013: 318), as *Pycnostachys ruandensis* De Wild.

Distribution. Uganda, Burundi, Rwanda, DR. Congo and Malawi.

Habitat and ecology. Rainforest, riparian forest, fallow field, savannah; 900–2460 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Kabare, Ludaha, s.d., *Gilon 3*3 (BR); Nya Kaziba, 17 Apr 1952, *J.F.Laurent 462* (BR); ***Haut-Katanga***, Upemba, Mbuye-bala, 15 Apr 1948, *G.F.de Witte 3748* (BR, K, WAG); Marungu, Kaboto, Apr 1944, *L.Dubois 1126* (BR, WAG); Marungu, 3 km W de Kasiki, 12 Jun 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 6147* (POZG).

Rwanda, Murambi-Kivumu, 14 May 1983, *F.-X.Ayobangira 1618* (BR).

Burundi, Nyakakaro, 30 Jun 1993, *C.Carème s.n.* (BR); Mwaro, Mont Mugero, 27 Apr 1966, *J.Lewalle 733* (BR, LSHI, MO); Bujumbura, 19 May 1971, *J.Lewalle 5733* (BR); Kisozi, 3 Jun 1934, *J.B.H.Lejeune 86* (BR, K, WAG); Butare, Mosso, Pont de Musasa, 13 May 1981, *M.Reekmans 10273* (BR, US); Kiganda, 24 May 1981, *M.Reekmans 10373* (BR, MO, WAG).

Coleus ruziziensis Meerts & A.J.Paton, sp. nov.

urn:lsid:ipni.org:names:77347706-1

Fig. 17A–F

Type. Burundi. Usumbura [Bujumbura], 800 m elev., Dec 1934. *A.Becquet 834* (holotype BR [BR0000016830684]; isotype K).

Diagnosis. Differing from all other *Coleus* species by the following combination of traits: leaves grouped in the lower third of the shoot, almost forming a rosette, roots produced into fusiform tubers, cymes (3–)4-flowered.

Description. Perennial herb, somewhat succulent, aromatic (scent reminiscent of *Lavandula*), 0.2–0.5 m high; roots dilated into fusiform tubers up to 40 × 8 mm. Stem erect, leafy in the lower third, quadrangular, sulcate, with patent eglandular hairs and shorter glandular hairs, these denser in the inflorescence, simple or sparingly branched in the inflorescence. Leaves present at flowering, at three to four nodes in the lower part of the shoot, with short internodes and often almost rosulate, spreading, with or without fascicles of small leaves in the axils; blade ovate-elliptic to elliptic or obovate-elliptic, (3–)6–13 × (1–)2–7 cm, base obtusely cuneate to attenuate, apex obtuse to rounded, margin undulate to shallowly crenate, ca. 6 secondary veins on either side diverging at an acute angle, main veins flattened on lower surface, upper surface velvety pubescent, lower surface tomentose to villous and with red sessile glands; petiole canaliculate, 2–4(–5) cm long, long pubescent to villous. Inflorescence terminal, lax, (9–)12–28 cm from lowermost node, simple or branched at the lowermost node, verticils laxly disposed, spaced 1–2(–4) cm, cymes sessile, 3–4-flowered; bracts broadly ovate, rounded at tip, ca. 2 × 2 mm, soon caducous, not forming a coma; pedicels 1–2 mm long, elongating to 4–5 mm in fruit, ascending to patent, curved near apex, shortly pubescent and with sparse glandular hairs, eccentrically inserted on calyx in front of upper lobe. Flower: calyx campanulate, at anthesis ca. 2 mm long, in fruit 4–5 mm, pubescent with broad-based short hairs on the veins and with sparse orange or red sessile glands, teeth margin ciliolate, inner side papillate, with pedicel attached asymmetrically in front of upper lip, throat truncate to slight-

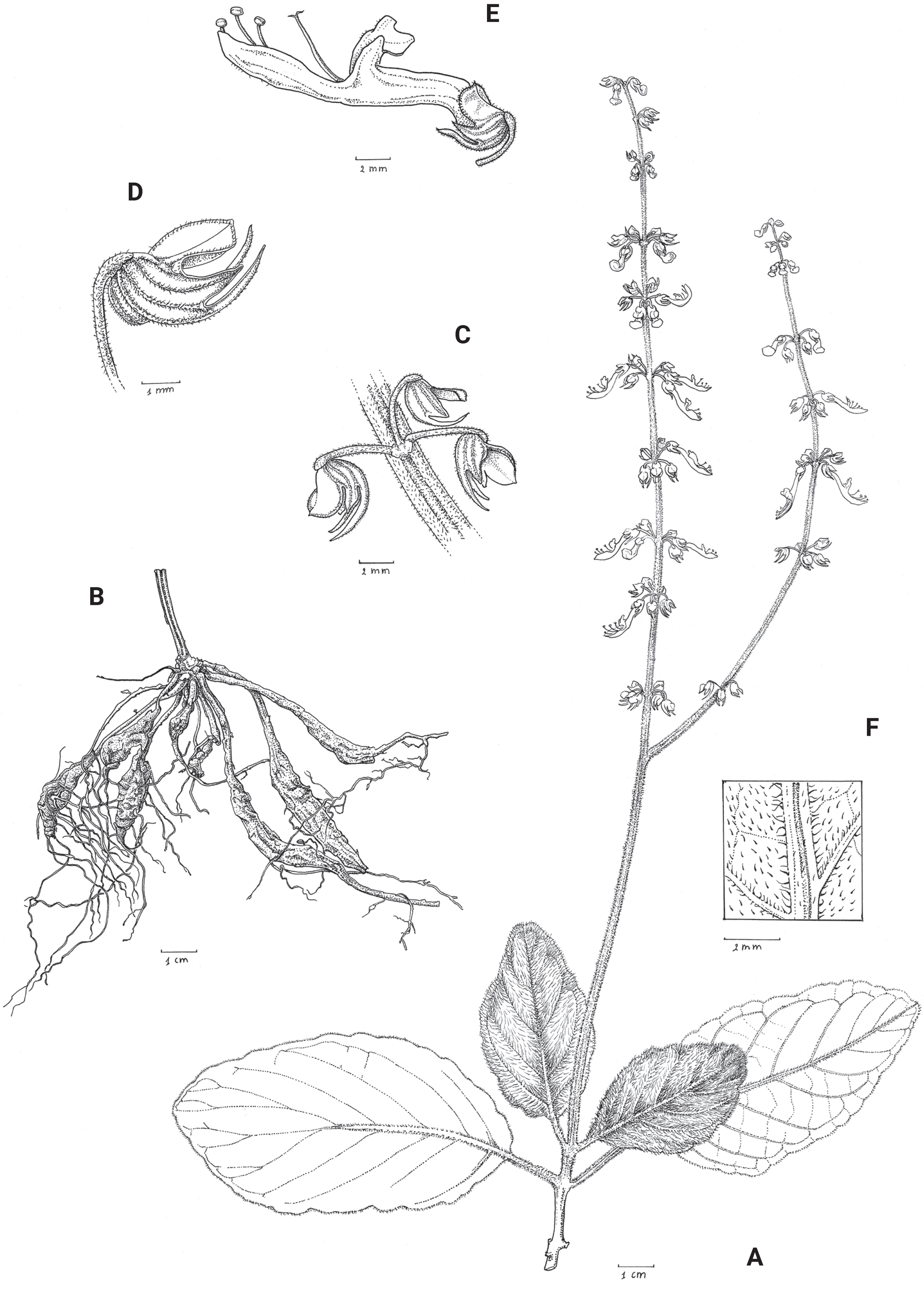

Figure 17. *Coleus ruziziensis* Meerts & A.J.Paton **A** habit **B** roots with tubers **C** detail of inflorescence **D** fruiting calyx **E** flower **F** detail of pubescence of leaf undersurface **A** *A.Becquet 834*, *M.Reekmans 149*, *H.Humbert 7314* **B, C, D** *A.Becquet 834* **E** *J.Lewalle 2401* **F** *J.Lewalle 2401*). Drawn by Hilde Orye. Scale bars: 1 cm (**A, B**); 2 mm (**C, E, F**); 1 mm (**D**).

ly oblique, posterior lip broadly obovate to almost rounded, 2–3 × 2–3 mm, apex rounded to apiculate or emarginate, curving upwards, not or shortly decurrent, lateral lobes midway between upper lip and median lobes of lower lip, triangular, ca. 1.2 mm long, margin narrowly recurved, median lobes narrowly triangular, ca. 3 mm long, curving upwards in fruit; corolla pale mauve to blue, (10–)12–15 mm long, sparsely pubescent, obliquely hanging, tube almost straight to slightly sigmoid, subglabrous, 5–6 mm long, progressively dilated near throat, upper lip 2–3 mm long, shortly pubescent, lower lip shortly pubescent, 5–7 mm long, ca. 2 mm deep, enclosing stamens, anthers ca. 0.5 mm long, round; style bifid. Nutlets brown, shiny, rounded, slightly compressed, ca. 1 mm diam.

Etymology. All collections of the species originate from the Ruzizi River plain.

Distribution. E DR. Congo (Kivu) and W Burundi; endemic of the Ruzizi River plain.

Habitat and ecology. Savannah, steppe, often on rocky or sandy soil; association à *Loudetia simplex* et *Crabbaea velutina*; 800–950 m elev.; flowers in the first half of the rain season.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Plaine de la Ruzizi, route Costermansville-Uvira, 20 Feb 1950, *R.Germain 6159* (BR); Plaine de la Ruzizi, savane à *Heteropogon-Chloris*, 24 Feb 1950, *R.Germain 6234* (BR); Plaine de la Ruzizi, Nyakikumba, env. 900 m elev., savane arborée brûlée, Nov. 1948, *F.L.Hendrickx 5678* (BR); Plaine de la Ruzizi, ca. 800 m elev., env. d'Uvira, Jan. 1929, *H.Humbert 7314* (BR, P); Matiaso, 28 Dec 1950, *P.Liégeois 347* (BR).

Burundi, Ferme de la Randa, 03°07'S, 29°22'E, 950 m elev., prairie en pente faible, pâturée, 14 Nov 1965, *J.Lewalle 16* (BR, MO); Ruzizi, km. 35, prairie sableuse, 25 Nov. 1967, *J.Lewalle 2401* (BR); Plaine de la Ruzizi, Ruziba, 900 m elev., savane arbustive, 5 Dec1969, *J.Lewalle 4152* (BR); Bubanza, Cibitoke, 900 m elev., steppe rocheuse, 21 Feb 1971, *M.Reekmans 149* (BR); Bubanza, Cibitoke, steppe rocheuse, 21 Nov 1971, *M.Reekmans 1183* (BR); Bujumbura, Randa, savane, 900 m elev., 30 Jan 1972, *M.Reekmans 1499* (BR); Bubanza, Kagongwe, vallée Katunguru, 26 Nov 1972, *M.Reekmans 2136* (BR, K).

Notes. 1. *C. ruziziensis* has a very original combination of characters, i.e. fusiform tubers, a rosette of ovate leaves and 4-flowered cymes. Calyx characters are close to *C. hadiensis*. It superficially resembles *Orthosiphon allenii* in having a rosette and tubers.

2. Vernacular name: mwendekere (in kirundi); katjudju, mutuzo (in bashi).

Coleus schliebenii **(Mildbr.) A.J.Paton, Phytokeys 129: 92. 2019.**

≡ *Pycnostachys schliebenii* Mildbr., Notizbl. Bot. Gart. Berlin-Dahlem 11: 405. 1932. Type: Tanzania, Njombe District: Lupembe, stromgebiet des oberen Ruhudje, landschaft Lupenbe, nördlich des Flusses, Apr 1931, *H.J.Schlieben 713* (holotype B destroyed: isotype BM [BM000884009], BR [BR0000006410650], G [G00435269], K [K000405738] fragment, MA [MA384632], P [P00541260]).

Description. Paton et al. (2009: 410), Paton et al. (2013: 330), as *Pycnostachys schliebenii* Mildbr.

Distribution. Tanzania to Zambia and E DR. Congo.

Habitat and ecology. Mountain forest with *Arundinaria*, *Erica* scrub, river bank, more rarely wooded savannah; in Burundi also in savannah and fallow fields, (950–)1750–2500 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Katana, 10 Jul 1959, *Cambridge Congo Expedition 80* (BR, US); Chaîne des Mitumba, W Lac Edouard, piste Mangi-Kipesa, 19 Jan 1956, *J.de Wilde 623* (BR); Entre Kasindi et Lubango, Dec 1931, *J.Lebrun 4690* (BR); Kalehe, Mont Kahuzi, 7 Jul 1971, *J.Ntakiyimana 92* (BR); ***Haut-Katanga***, Upemba, galerie de la Kalumengongo, 18 Apr 1947, *G.F.de Witte 2518* (BR); Marungu, env. Kasiki, fourré de la source de la rivière Lunanga, 12 Jun 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 6429* (POZG); Upemba, tête de source de la riv. Kadidika, près de la piste Lusinga-Mitwaba, 11 May 1949, *van Meel* in *de Witte 6321* (BR).

Burundi, Mont Manga, 21 Apr 1982, Missumba, 4 Jun 1970, *J.Lewalle 4676* (BR); Rushubi, Mont Bona, 26 Apr 1977, *M.Reekmans 6025* (BR, WAG); Kitwe Rumonge, 12 May 1977, *M.Reekmans 6211* (BR, WAG); Kabuyekere, 5 Jun 1980, *M.Reekmans 9287* (MO, WAG); Bujumbura, Mont Manga, 21 Apr 1982, *M.Reekmans 10994* (BR, WAG); Bukemba-Muzye, 12 May 1981, *M.Reekmans 10220* (BR, MO, WAG).

Notes. 1. This species is variable in Burundi; a particular morphotype occurring in savannah has long ciliate bracts, calyx tube with a ring of hairs inside the throat, short inflorescence (1 cm at anthesis) and short calyx teeth (e.g. *J.Lewalle 1912, G.Michel 2408, 2715, 2956, M.Reekmans 486, 5074, 6211, 7035, 9287, 10220, J.Saintenoy 158*); such plants were identified *in schedis* as "*P. bruceae* Gatheri" (unpublished designation); further work is needed to assess their taxonomic status.

2. In the Marungu Massif (Haut-Katanga), the species is represented by a large-flowered phenotype (corolla up to 20 mm long) e.g. *S.Lisowski, F.Malaisse, J.-J.Symoens 6428* (POZG) which could deserve taxonomic recognition; further work is needed on this polymorphic species.

3. The specimens *J.F.Laurent 489* and *Bytebier & Luke 3128* (BR, EA) could represent *Coleus livingstonei* A.J.Paton, a species not yet recorded in Central Africa; however, the materials are poor and the presence of this species needs confirmation.

Coleus scruposus A.J.Paton, Phytokeys 129: 92. 2019.

≡ *Pycnostachys kassneri* De Wild., Contr. Fl. Katanga: 172. & Ann. Soc. Sci. Bruxelles 41(2): 54. 1921., non *Coleus kassneri* Robyns & Lebrun.

= *Pycnostachys congensis* Gürke, Bull. Herb. Boissier 4: 819. 1896. Type: DR. Congo, Lusambo, 1891, *G.Descamps 27* (lectotype Z [Z-000021015], **designated here**).

≡ *Coleus congensis* (Gürke) A.J.Paton, Phytokeys 129: 35. 2019.

Type. DR. Congo, Katanga, West Kundelungu, 17 May 1908, *T.Kassner 2794* (holotype BR [BR0000009824614]; isotype BM [BM000838018], HBG, K [K000405735]).

Description. Paton et al. (2009: 390), Paton et al. (2013: 318), as *Pycnostachys kassneri* De Wild.

Distribution. Tanzania to Zambia.

Habitat and ecology. Savannah, riparian forest, scree, dry woodland; 950–1650 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Sandoa, près de Kambungu, 23 Apr 1959, S.Risopoulos 970 (BR, K, WAG); ***Bas-Katanga***, Samba, 1891, *G.Descamps 28* (BR); Kamina, Lovoi, Mar 1932, *P.Quarré 2971* (BR); ***Haut-Katanga***, Upemba, Mont Muye, 3 May 1948, *G.F.de Witte 3774* (BR); Vallée de la Kalumengongo, près des chutes, 12 Apr 1949, *G.F.de Witte 6071* (BR, K, WAG); Mugila, 23 May 1908, *T.Kassner 2967* (K); Kundelungu, 17 km NW Sampwe, 24 Apr 1970, *S.Lisowski, F.Malaisse, J.-J.Symoens 11072* (BR, POZG); Route Kolwezi-Kamina, km 75, 5 Apr 1948, *A.Schmitz 1780* (BR).

Notes. 1. Calyx teeth length is variable; specimens from DR. Congo and Zambia with very short calyx teeth (< 2 mm) also tend to have calyx throat that is tomentose inside (e.g. *A.Schmitz 1780*, *J.-J.Symoens 10239*). Further work is needed to decide if this represents a distinct taxon or just one extreme of a continuous variation.

2. Lectotypification of *Pycnostachys congensis* Gürke. Gürke (1896) cited two syntypes of *Pycnostachys congensis* Gürke (*G.Descamps 27* (syntype B destroyed; isosyntype Z), DR. Congo, Lusambo & *G.Descamps 28* (syntype B destroyed; isotype BR), DR. Congo, Samba, 1891. We select *G.Descamps 27* (Z) as the lectotype because it comprises a whole plant.

Coleus seretii De Wild., Bol. Soc. Ibér. Ci. Nat. 19: 122. 1920.

≡ *Plectranthus seretii* (De Wild.) Vollesen, Opera Bot. 59: 84. 1980. Type: DR. Congo, route Buta–Bima (Bali), 13 Oct 1905, *F.Seret 68* (lectotype BR [BR0000006262600], **designated here**).

Description. Paton et al. (2009: 313), as *Plectranthus seretii* (De Wild.) Vollesen.

Distribution. Ethiopia, DR. Congo, Tanzania, NW. Madagascar.

Habitat and ecology. Secondary forest, road verge; 450–600 m elev.

Additional specimens. DR. Congo, ***Bas-Katanga***, Kasongo, Mobanga, 18 Jun 1952, *R.Germain 7695* (BR); ***Forestier Central***, Route Benalia-Buta, 1 Nov 1945, *R.Germain 4267* (BR); Route Buta-Banalia, km 38, 23 May 1976, *S.Lisowski 42922* (POZG); Entre Buta et Lekada, 9 Jan 1926, *W.Robyns 1320* (BR).

Note. Lectotypification of *Coleus seretii* De Wild. De Wildeman (1920) cites two syntypes (*F.Seret 68 & 420* (erroneously cited as "120" in the protologue), both matching the protologue; *F.Seret 68* (sheet [BR0000006262600] is selected here as the lectotype because it has better preserved leaves. Remaining syntype: *F.Seret 420* (syntype BR; isosyntype K), Suronga Forest, 26 Dec 1905.

Coleus shirensis Gürke, Bot. Jahrb. Syst. 19: 216. 1894.

≡ *Plectranthus shirensis* (Gürke) A.J.Paton, SABONET Rep. Ser. 31: 189. 2005. Type: Malawi, 1891, *J.Buchanan 376* (lectotype K [K000070492]; isolectotype E [E00193509], designated by Mathew [1976]).

Description. Paton et al. (2009: 336), Paton et al. (2013: 272), as *Plectranthus shirensis* (Gürke) A.J.Paton.

Distribution. SW & S Tanzania to S Tropical Africa.

Habitat and ecology. Riparian forest, swamp savannah, forest margins; 1000–1800 m elev.

Additional specimens. DR. Congo, ***Bas-Congo***, Kinkosi, 26 Feb 1959, *L.Pauwels 1600* (BR); ***Kasaï***, Entre Kwango-Lufuna, 4 Aug 1944, *R.Germain 2643* (BR); Kwango, 21 Jul 1955, *R.Devred 2290* (BR); ***Bas-Katanga***, Gandajika, 20 Jun 1951, *Chalon 326* (BR); Kindele, Sep 1951, *R.Desenfans 2013* (BR, BRLU); 10 km SW Gandajika, 9 Aug 1945, *F.Luxen 534* (BR); Lovoi, Kamina, Mar 1932, *P.Quarré 2929* (BR); ***Haut-Katanga***, Mulumbi, riv. Dona, 30 Aug 1953, *R.Desenfans 3731* (BRLU); 14 km N de Mitwaba, 16 Jan 1960, *P.Duvigneaud 5077Co* (BRLU); Kundelungu, 6 km NNW poste Katshupa, 29 Jul 1966, *F.Malaisse 4213a* (BR; LSHI); Kisanga, Aug 1933, *P.Quarré 3466* (BR); Upemba, Lusinga, route de Mitwaba, 14 Sep 1948, *W.Robyns 3590* (BR); Keyberg, 24 Jun 1947, *A.Schmitz 732* (BR).

Note. At the northern limit of the distribution range, some specimens are unusual in lacking long hairs on pedicel and calyx (*Herman 2308*, *M.Schaijes 1885, P.Quarré 2929*).

Coleus sphaerocephalus (Baker) A.J.Paton, Phytokeys 129: 98. 2019.

≡ *Pycnostachys sphaerocephala* Baker, Bull. Misc. Inform. Kew 1898: 162. 1898. Type: Malawi, Nyika Plateau, Jul 1896, *A.Whyte 139* (holotype K [K000406000]).

Description. Paton et al. (2009: 402), Paton et al. (2013: 327), as *Pycnostachys sphaerocephala* Baker.

Distribution. Tanzania to Zambia.

Habitat and ecology. Near springs, ca. 2200 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Marungu, Musipi, Apr 1945, *L.Dubois 1402* (BR); Mont Mugila, 23 May 1908, *T.Kassner 2991a* (HBG, K).

Coleus stachyoides (Oliv.) E.A.Bruce, Bull. Misc. Inform. Kew 1934: 306. 1934.

≡ *Plectranthus stachyoides* Oliv., Trans. Linn. Soc. London 29: 136. 1875. Type: Uganda, West Nile District: Madi, Dec 1862, *J.A.Grant 732* (holotype K [K000431982]).

= *Plectranthus cylindrostachys* Robyns & Lebrun, Rev. Zool. Bot. Africaines 16: 356. 1928. Type: Burundi, Irubura, Akanguru Valley, 31 May 1926, *W.Robyns 2403* (holotype BR [BR0000006263294]; isotype K [K000431886]).

Description. Paton et al. (2009: 323), as *Plectranthus stachyoides* Oliv.

Distribution. Central African Rep. to E Tropical Africa.

Habitat and ecology. *Hyparrhenia-Loudetia* savannah, wooded savannah, sclerophyllous scrub, rock crevices; 800–3045 m elev.

Additional specimens. DR. Congo, ***Bas-Katanga***, Kasengi, May 1947, *W.Mullenders 2405* (BR); Kisamba, Jan 1931, *P.Quarré 2377* (BR); ***Lacs Edouard et Kivu***, Ruzizi, Tsamate, Apr 1950, *R.Germain 6458* (BR); Mont Muhi, 31 Jul 1955, *U.Kinet 93* (BR); ***Haut-Katanga***, Kando, Mar-Apr 1931, *G.F.de Witte 204* (BR); Marungu, Kasiki, Mont Kilonge, 12 Jun 1969, *S.Lisowski, F.Malaisse, J.-J.Symoens 6388* (POZG); Muhila, Mont Mwango, 12 May 1971, *S.Lisowski 23526* (POZG).

Rwanda, S Kagera, Rwinkwavu, 13 Apr 1966, *J.Lewalle 686* (BR, MO); Rubona, 25 Apr 1958, *G.Michel 5311* (BR, MO); Kagera, colline Rwanyerajana, 5 Apr 1958, *G.Troupin 6833* (BR, LWI); Kibungu, Parc National Kagera, colline Gwenjange, 17 Jun 1958, *G.Troupin 7470* (BR, WAG); Kibungo, Mbuye, 28 Jun 1978, *G.Troupin 16166* (BR). BURUNDI, Gitega, route vers Karuzi, 27 Apr 1971, *J.Lewalle 5793* (BR, WAG); Kininya Mosso, 12 Jun 1952, *G.Michel 2785* (BR); Bubanza, Rugazi, 3 May 1981, *M.Reekmans 10091* (BR, WAG); Bukemba, Muzye, 12 May 1981, *M.Reekmans 10232* (WAG, MO, BR).

Coleus stenostachys **(Baker) A.J.Paton & Phillipson, Phytokeys 129: 100. 2019.**

≡ *Pycnostachys stenostachys* Baker in D.Oliver & auct. suc. (eds.), Fl. Trop. Afr. 5: 380. 1900. Type: Uganda, Bunyoro District: sides of Nile, Nov 1862, *J.A.Grant* in *J.H.Speke & J.A.Grant s.n.* (holotype K [K000405970]).

= *Pycnostachys coerulea* Hook. Exot. Fl. 3: t. 202. 1826, non *Coleus coeruleus* Gürke. Type: Madagascar, cultivated in Kew from seeds sent by *W.Bojer & Helsinger* (holotype K [K000406006]; isotype M [M0104752]).

= *Pycnostachys brevipetiolata* De Wild., Pl. Bequaert. 4: 394. 1928. Type: DR. Congo, Kivu, rivière Rutshuru, Kaitafu, 4 Oct 1914, *J.Bequaert 5972* (holotype BR [BR0000008910363], [BR0000008909718]).

Description. Paton et al. (2009: 393), Paton et al. (2013: 321), as *Pycnostachys coerulea* Hook.

Distribution. Ethiopia to South Africa, Madagascar.

Habitat and ecology. River banks, lake shores, Papyrus marshland and swamps, *Pennisetum-Phragmites* savannah on moist soil; 900–1900 m elev.

Additional specimens. DR. Congo, ***Lac Albert***, Nioka, 5 May 1952, *L.Liben 245* (BR, K); Nioka, rivière Duda, 22 Oct 1947, *A.Taton 666* (BR); ***Lacs Edouard et Kivu***, Kaitafu, rivière Rutshuru, 4 Oct 1914, *J.Bequaert 5972* (BR, K fragment); Lac Magera, 1 Mar 1934, *G.F.de Witte 1416* (BR); Lushadu, bord du Lac Kivu, 10 Jun 1960, *F.L.Hendrickx 7981* (BR, BRLU); Nyamunyunye, 22 Sep 1952, *R.Pierlot 391* (BR); Lac Lukulu, 22 Jul 1953, *D.van der Ben 654* (BR); ***Haut-Katanga***, Kapumfi, rive du Lac Moero, 31 Dec 1965, *J.-J.Symoens 12003* (BR, LSHI).

Rwanda, Lac Bulera, Butaro, 17 Feb 1972, *P.Auquier 2578* (BR); Butare, Jun 1933, *A.Becquet 714* (BR, WAG); Environs de Butare, rivière Nyamogari, 3 May 1957, *D.van der Ben 1547* (BR); Rubona, 16 Feb 1960, *G.Michel 6387* (BR); Akagera, marais Kajumbura, 30 Mar 1973, *G.Troupin 14897* (BR).

Burundi, Kanyanya, Lac Rwihinda, 18 Apr 1971, *J.Lewalle 5547* (BR); Gitwenge, 17 May 1978, *M.Reekmans 7056* (LG, WAG).

Coleus stuhlmannii (Gürke) A.J.Paton, Phytokeys 129: 101. 2019.

≡ *Pycnostachys stuhlmannii* Gürke in H.G.A.Engler, Pflanzenw. Ost-Afrikas, C: 345. 1895. Type: Tanzania, Bukoba District: Karagwe, Ngaramo, 6 Feb 1891, *F.Stuhlmann 1630* (holotype B destroyed; isotype K [K000405975] fragment).

= *Pycnostachys bequaertii* De Wild., Contr. Fl. Katanga: 171. & Ann. Soc. Sci. Bruxelles 41(2): 52. 1921. Type: DR. Congo, Katanga, Shinsenda, *J.Bequaert 425* (lectotype BR [BR0000008910103]; designated by Bramley in Paton et al. [2009]).

= *Pycnostachys longifolia* De Wild., Contr. Fl. Katanga: 172. Ann. Soc. Sci. Bruxelles 41(2): 55. 1921. Type: DR. Congo, Katanga, Welgelegen, *J Bequaert 562* (holotype BR [BR0000008909787]; isotype K fragment).

Description. Paton et al. (2009: 392), Paton et al. (2013: 319), as *Pycnostachys stuhlmannii* Gürke.

Distribution. Kenya to S. Tropical Africa.

Habitat and ecology. Marshland, dilungu savannah on moist soil, dambos, on organic soil; 850–1300 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Shinsenda, 8 May 1912, *J.Bequaert 425* (BR, K fragment); Keyberg, 17 Apr 1957, *E.Detilleux 831* (BR); Dikuluwe, 10 May 1957, *P.Duvigneaud 3118P4* (BRLU), 1.5 km E of Kabiashia, dembo Kandale, 23 May 1969, *F.Malaisse 6435* (BR, LSHI, P); Route Lubumbashi-Kasenga, 2 km après Kumanua, 25 May 1985, *F.Malaisse & Goetghebeur 1144* (BR, K, P); Kipila, May 1929, *P.Quarré 1693* (BR, K, P); Env. Lubumbashi, May 1934, *H.Humbert 15906* (BR, P); Kipopo, 17 Apr 1962, *A.Schmitz 7700* (BR, K); Tumbwe, dembo de la Kasompa, 30 Apr 1960, *J.-J.Symoens 7608* (BR, LSHI).

BURUNDI, Lac Nyanza, 27 Jun 1971, *J.Lewalle 6050* (BR, K); Kinyinya Mosso, 5 Jun 1981, *M.Reekmans 10532* (BR, US, WAG).

Coleus succulentus Pax, Bot. Jahrb. Syst. 39: 646. 1907.

= *Plectranthus pseudomarrubioides* R.H.Willemse, Kew Bull. 40: 93. 1985. Type: Ethiopia, Debre Libanos, 2 Nov 1965, *W.J.J.O.de Wilde & de Wilde-Duyfjes 8656* (holotype WAG [WAG0001746]; isotype BR [BR0000005232543]).

Type. Ethiopia, Zuquala Mt., *O.Ryding & C.Puff 1657* (neotype UPS [V-057092]; isoneotype ETH, designated by Ryding [2000]).

Description. Paton et al. (2009: 320), as *Plectranthus pseudomarrubioides* R.H.Willemse.

Distribution. Ethiopia to N. Tanzania, Arabian Peninsula.

Habitat and ecology. Saxicolous, near riparian forest, ca. 900 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Kundelungu, Sampwe, galerie forestière de la rivière Mufungwe, 10 Apr 1949, *G.F.de Witte 6005* (BR).

Notes. 1. New species record for DR. Congo.

2. The locality in Katanga is remarkably disjunct, ca. 1000 km in the SW of the nearest locations in N Tanzania.

3. Another collection from Upemba National Park (Katanga) (*G.F.de Witte 6449*), is intermediate between *C. succulentus* and *C. cylindraceus*.

Coleus sylvestris (Gürke) A.J.Paton & Phillipson, Phytokeys 129: 103. 2019.

≡ *Plectranthus sylvestris* Gürke, Bot. Jahrb. Syst. 19: 205. 1894. Type: Tanzania, Kilimanjaro, Rifinika Hill on Mawenzi, 14 Sep 1893, *G.Volkens 965* (holotype B destroyed; isotype BM [BM000999974], G).

= *Coleus ferrugineus* Robyns, Bull. Jard. Bot. État Bruxelles 17: 77. 1943. Type: DR. Congo, Karisimbi, Feb 1932, *J.Lebrun 5005* (holotype BR [BR0000006262617]; isotype K).

= *Plectranthus ferrugineus* (Robyns) Troupin & Ayob., Fl. Rwanda 3: 336. 1985., nom. inval.

= *Coleus subulatus* Robyns, Bull. Jard. Bot. État Bruxelles 17: 76. 1943. Type: DR. Congo, Kivu, Tschamugussa. 13 Aug 1934, *G.F.de Witte 1854* (holotype BR [BR0000006262952]; isotype LWI).

Description. Paton et al. (2009: 295), Paton et al. (2013: 243), as *Plectranthus sylvestris* Gürke.

Distribution. Tropical Africa, Madagascar.

Habitat and ecology. Mountain evergreen forest, often with *Hagenia* and bamboo; 2300–3400 m elev.

Additional specimens. DR. Congo, ***Lacs Edouard et Kivu***, Karisimbi, vallée Visoke, 22 Jan 1955, *G.F.de Witte 11568* (BR); Kabara, Mikeno, 16 Jul 1934, *G.F.de Witte 1777* (BR, LWI); Mont Muhi, Jun 1948, *F.L.Hendrickx 5273* (BR); Mont Bukulumiza, 26 Jul 1955, *R.Pierlot 666* (BR); ***Haut-Katanga***, Marungu, Ndawa, Apr 1944, *L.Dubois 1165* (BR). Rwanda, Forêt de Nyungwe, vers km 100, 21 Aug 1969, *G.Bouxin & M.Radoux 716* (BR); Kareba, 10 Oct 1974, *P.Auquier 4514* (BR); Karisimbi, versant Sud, 27 Feb 1935, *G.F.de Witte 2255* (BR); Karisoke, 3 Jan 2006, *Luksenberg & A.Nsanzurwimo s.n.* (BR).

Burundi, Bukeye, Teza, 19 Jun 1971, *J.Lewalle 6024* (BR); Muramvya, bois sacré de Mpotsa, 9 Jun 1979, *M.Reekmans 8245* (BR, WAG).

Coleus tenuicaulis Hook.f., J. Proc. Linn. Soc., Bot. 7: 211. 1864.

Type. Cameroon, Mt Cameroon, Dec 1862, *G.Mann 1939* (holotype K [K000431854]).

Description. Perennial herb 0.3–0.65(–1.50) m high, rootstock weakly rhizomatous. Stem erect, quadrangular, variously pubescent, often with short retrorse hairs, occasionally with patent eglandular hairs, short glandular hairs and papillae, densely glandular pubescent in the inflorescence, erect, branched. Leaves opposite, patent, often with young leaves in the axils, petiolate, upper ones subsessile; blade ovate-triangular, (narrowly ovate out of Central Africa), 1.5–6.5(–7.5) × 1.0–5.0(–6.5) cm, base broadly rounded, truncate or subcordate, more rarely cuneate, shortly attenuate in the petiole, apex acute, margin serrate, upper surface densely pubescent (very short papilliform hairs), lower surface pubescent on veins, ca. 4–5 pairs of secondary veins; petiole 1.0–3.5(–4.0) cm long, with very short retrorse hairs and often also long patent hairs. Inflorescence terminal, lax, 4–18 cm long, with 5–14 verticils spaced 7–30 mm, bracts narrowly ovate, ca. 3 mm long, acuminate, caducous or rarely persistent, cymes ascending, ca. 9–25-flowered, pedunculate, peduncle 1–15 mm long, with two opposite cincinni ca. 5–50 mm long, densely papillate, pedicel 1–4 mm long, widely spaced, inserted eccentrically. Flower: calyx 2 mm long at anthesis, densely papillate and with red sessile glands, ca. 5–6 mm long in fruit, tube slightly curved, slightly constricted at throat, upper lip ovate, ca. 2–3 mm long, markedly curved, subacute, slightly decurrent, lobes of lower lip narrowly triangular, sharply acute, the lateral ones 2 mm long, the middle ones 3 mm long. Corolla pale blue to violet, with pale sessile glands, ca. 10–15 mm long, tube strongly sigmoid, ca. 4 mm long, lower lip ca. 6–8 mm long, 3–4 mm deep, enclosing stamens; filaments fused, anther ca. 0.8 mm, style entire. Nucule pale brown, round, compressed, ca. 1 mm diam., dull, smooth.

Distribution. W Tropical Africa to Cameroon, SW Tanzania to S Tropical Africa.

Habitat and ecology. Dembo, wooded savannah, most often on moist soil; 800–1815 m elev.

Additional specimens. DR. Congo, ***Kasaï***, Kwango, Twana, 12 Sep 1953, *H. Callens 4223* (BR); Kwango, Kibunda, 27 Apr 1953, *H.Callens 4001* (BR); 50 km W of Kimvula, 12 Apr 1948, *P.Duvigneaud 715* (BRLU); ***Haut-Katanga***, Upemba, riv. Lusinga, 21 Oct 1948, *L.van Meel* in *de Witte 4566* (BR); Upemba, 29 Jul 1949, *L.van Meel* in *G.F.de Witte 7128* (BR); Kasombo, 22 Jan 1957, *E.Detilleux 457* (BR); Kundelungu, 6 km NNW poste de Katshupa, rivière Luanza, 29 Jul 1966, *F.Malaisse 4213b* (BR, LSHI); Kundelungu, rivière Kabunda, 28 Mar 1971, *S.Lisowski 23387* (POZG); Dembo de la Katuba, Feb 1934, *P.Quarré 3833* (BR).

Notes. 1. New species record for DR. Congo.

2. *P.Quarré 3833* (BR) and *Lisowski, Malaisse & Symoens 4930* (POZG) are unusual in having lower leaf surface and stem tomentose.

Coleus tetradenifolius (A.J.Paton) A.J.Paton, Phytokeys 129: 104. 2019.

≡ *Plectranthus tetradenifolius* A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 304. 2009. Type: Uganda, Karamoja District, Mt Moroto, Jun 1963, *E.Tweedie 2665* (holotype K [K000430736]).

Description. Paton et al. (2009: 304), as *Plectranthus tetradenifolius* A.J.Paton.

Distribution. Cameroon, S. Sudan to E. Tropical Africa and NE DR. Congo.

Habitat and ecology. Savannah with *Exotheca abyssinica* (out of Central Africa: rocky slopes and cliffs); ca. 2450 m elev. (out of Central Africa: 1350–2700 m elev.).

Additional specimens. DR. Congo, ***Lac Albert***, Mont Aboro, 2450 m elev., 26 Mar 1958, *P.Bamps 147* (BR).

Notes. 1. New species record for DR. Congo.

2. The specimen collected in DR. Congo departs from the type in having the inflorescence axis without glandular hairs and a shorter corolla (ca. 6 mm vs. 8–10 mm).

Coleus thyrsoideus Baker, Bot. Mag. 125: t. 7672 1899.

≡ *Plectranthus thyrsoideus* (Baker) B.Mathew, Kew Bull. 31: 174. 1976. Type: Plant cultivated at Kew, seed from herbarium specimen from N of Lake Malawi collected by Whyte, 3 Jan1899 (holotype K [K000430792]).

Description. Paton et al. (2013: 258), as *Plectranthus thyrsoideus* (Baker) B.Mathew.

Distribution. S Tropical Africa.

Habitat and ecology. Savannah and shrub savannah on rocky slopes; 1200–1300 m elev.

Additional specimens. DR. Congo, ***Haut-Katanga***, Territ. Sakania, SE de Kipushia, Mont Lukanga, 29 Apr 1971, *S.Lisowski 23388* (POZG); Env. Kasumbalesa, colline Kibwe I, 20 Mar 1971, *S.Lisowski 23315* (POZG).

Note. New species record for DR. Congo.

Coleus welwitschii **Briq., Bot. Jahrb. Syst. 19: 185. 1895.**

= *Coleus dupuisii* Briq., Bull. Soc. Roy. Bot. Belgique 37: 70. 1899.

≡ *Plectranthus dupuisii* (Briq.) A.J.Paton, Fl. Trop. E. Afr., Lamiac.: 329. 2009. Type: DR. Congo, Kasai, Mayumbe, Jul 1893, *Dupuis s.n.* (holotype BR [BR0000008109132]).

= *Solenostemon thyrsiflorum* (Lebrun & L.Touss.) Vollesen, Opera Bot. 59: 85. 1980., nom. superfl. Type: Rwanda, Kagera, Nyakayaga, Jan 1938, *J.Lebrun 9447* (holotype BR [BR0000006263003]; isotype K, P).

= ?*Coleus laurentii* De Wild. (1920) 121. Bol. Soc. Ibér. Ci. Nat. 19: 121. 1920. Type: DR. Congo, Gombe, 14 Dec 1903, *E.&M.Laurent s.n.* (holotype BR [BR0000006258580] & [BR0000008109798]).

Type. Angola, Pungo Andongo, *F.Welwitsch 5589* (syntypes BM [BM000564040], [BM000999976], C [C10001537], G, K, LISU [LISU220997], [LISU220998], MEL, P), & *A.von Mechow 75* (syntype, not seen).

Description. Paton et al. (2009: 329), Paton et al. (2013: 268), as *Plectranthus dupuisii* (Briq.) A.J.Paton.

Distribution. Ethiopia to S. Tropical Africa.

Habitat and ecology. Savannah, steppic savannah, often on shallow rocky soil, xerophilous scrub, more rarely forest and woodland (termite mounds); 100–2200 m elev.

Additional specimens. DR. Congo, ***Côtier***, Banana, Mar 1948, *H.Callens 1066* (BR); ***Bas-Congo***, Léopoldvile [Kinshasa], Matete, 5 Aug 1956, *A.Carlier 334* (BR); ***Ubangi-Uele***, Garamba, 14 May 1950, *H.De Saeger 511* (BR); Garamba, route Dungu-Bagbele, km 17 de Bagbele, 27 Aug 1952, *G.Troupin 2028* (BR); ***Lacs Edouard et Kivu***, Plaine de la Ruzizi, sommet Tsamate, Apr 1950, *R.Germain 6826* (BR).

Rwanda, Bugesera, 27 Mar 1970, *G.Bouxin & M.Radoux 1631* (BR); Rusumo, route vers Nyarubuye, 25 Jan 1980, *D.Bridson 299* (BR, WAG); Kibungo, Rusumo, 16 Oct 1974, *J.Lambinon 74/1574* (BR, LG); Route Nyamasheke-Kibuye, 29 Mar 1972, *G.Troupin 6510* (BR, WAG); Kitega, Bweru, Muhweza, 27 Nov 1957, *van der Ben 1727* (BR).

Burundi, Buterama, Gasorwe, 22 May 1959, *van der Ben 2558* (BR); Kameramagambo, 27 Dec 1965, *J.Lewalle 155* (BR, MO); Gitwenge, 2 Jan 1979, *M.Reekmans 7448* (BR); Kagoma, E de Gitwenge, 7 Feb 1979, *M.Reekmans 7639* (BR, WAG); Muramvya, Komwe, 24 May 1981, *M.Reekmans 10355* (BR, MO, WAG).

Notes. 1. *Coleus laurentii* De Wild. is considered as a synonym of *C. welwitschii* by Paton et al. (2019). However, the type material (*E.& M.Laurent s.n.* [BR0000008109798], [BR0000006258580]) is remarkable in being almost glabrous in all vegetative parts; collecting notes on the label indicate the presence of white tubers (not collected); it could represent a different taxon (*C. rotundifolius?*).

2. *L.Liben 2855* is somewhat intermediate between *C. bojeri* and *C. welwitschii*, having robust lignified shoots, but lacking a true rhizome.

3. Many specimens from Rwanda, Burundi and W Tanzania have greyish-tomentose lower leaf surface and thicker leaves, corresponding to the type specimen of *Coleus thyrsiflorus*, but there is no real discontinuity with less pubescent forms.

4. See also note under *C. brazzavillensis*.

Coleus zigzag **Meerts & A.J.Paton, sp. nov.**

urn:lsid:ipni.org:names:77347707-1
Fig. 18A–H

Type. DR. Congo, Ubangi-Uele, Parc national de la Garamba, Ndelele, colline rocheuse, sol humifère dans les dépressions, 26 Aug 1951, *H.De Saeger 1413* (holotype BR [BR0000017707787]; isotype K).

Diagnosis. Related to *Coleus bojeri* and other species formerly referred to the genus *Solenostemon* on account of lower calyx lobes fused into a lip, differing by the pedunculate cyme, subglabrous rachis, divaricate zigzagging cincinni, broadly cordiform to reniform foliar blade.

Description. Annual or perennial herb, 0.5–1.0 m high, more or less tufted, not reported to be aromatic; tubers lacking or not collected. Stem erect or ascending, quadrangular, more or less lignified in lower part, sparingly branched, with a mixed indumentum of very short, papilliform hairs and sparse, long, patent, multicellular hairs, these sometimes almost lacking, also with sparse sessile red glands, becoming subglabrous to papillate in the inflorescence. Leaves opposite, spreading, petiolate, blade broadly ovate to cordiform or almost reniform, shorter than the petiole, (1.0–)2.0–4.5 × (0.8–)1.8–4.0 cm, apex rounded to subacute, base truncate (in the smallest leaves) to cordate, then shortly attenuate into the petiole, margin often recurved, purplish, strongly crenate to serrate, teeth rounded, ca. 4/cm, 4–5 secondary veins on either side, densely covered with very short papilliform hairs on both surfaces, also with sparse long hairs, lower surface also with many red sessile glands, reticulum prominent below; petiole 1.5–6 cm long, canaliculate, pubescent like the stem. Inflorescence unbranched or branching at lower nodes, 15–40 cm long, lax, nodes (5–)15–60 mm apart, verticils (15–)30–50-flowered, cymes all pedunculate, dichasial, peduncle 5–15 mm, with two divaricate cincinni up to 30 mm long in fruit, zigzagging, with 5–22 flowers, papillate, often purplish; pedicel 0.5–1 mm long in flower, ca. 2 mm in fruit, attached eccentrically behind calyx posterior lip. Flower: calyx ca. 1 mm long at anthesis, pubescent, with red sessile glands, fruiting calyx 2.5–3(–4) mm long, shortly tubular or campanulate, papillate and with red sessile glands, throat truncate, posterior lip obovate, ca. 1.5 mm long, obtuse to rounded, apiculate, slightly recurved, not decurrent, lateral lobes rectangular-oblong, truncate to rounded, median lobes of anterior lip linear, fused

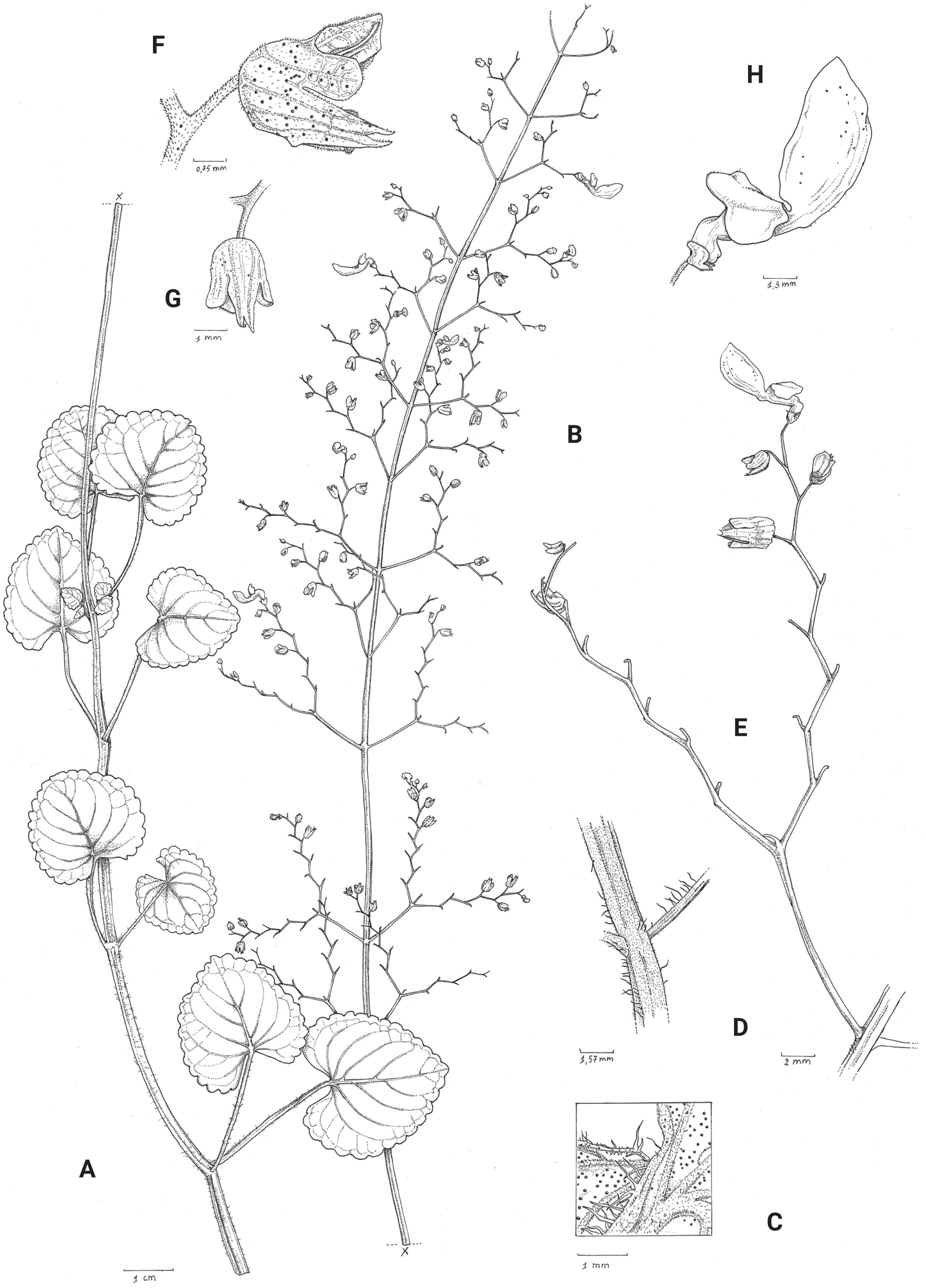

Figure 18. *Coleus zigzag* Meerts & A.J.Paton **A** stem and leaves **B** inflorescence **C** detail of petiole apex **D** detail of pubescence of inflorescence **E** cyme **F** fruiting calyx, side view **G** calyx seen from below **H** flower (**A** *H.De Saeger 1413 & 3849* **B–E** *H.De Saeger 1413* **F, G** *H.De Saeger 3849*). Drawn by Hilde Orye.Scale bars: 1 cm (**A, B**); 1 mm (**C**); 1.57 mm (**D**); 2 mm (**E**); 0.75 mm (**F**); 1 mm (**G**); 1.3 mm (**H**).

into a linear lower lip, straight, projecting well beyond the other lobes, with two fine points curving upwards 0.5–1 mm long. Corolla with red sessile glands, (3–)8–10 mm long, tube sigmoid, ca. 2 mm long, upper lobe 2 mm long, shortly pubescent, lower lip blue to purple, (2–)3–6 mm long, cucullate, 2–3 mm deep, enclosing stamens, shortly pubescent and with red sessile glands, stamens fused in lower half. Nutlets shiny brown, slightly compressed, 0.8–1 mm.

Etymology. The epithet refers to the characteristic zigzagging rachis of the cymes.

Distribution. W Uganda and NE DR. Congo.

Habitat and ecology. Rock crevices, savannah on shallow rocky soil; ca. 700–850 m elev.

Additional specimens. DR. Congo, ***Ubangi-Uele***, Parc national de la Garamba, Ndelele, fissures et dépressions rocheuses, 27 Sep 1952, *H.De Saeger 3849* (BR); Mont Genze, sur la roche, 30 Sep 1953, *P.Gérard 847* (BR); Entre Faradje et Dungu, savane rocheuse au bord du Kibali, crevasses dans les roches, Aug 1931, *J.Lebrun 3458* (BR, K); Parc National de la Garamba, frontière du Soudan, près de Ndelele, affleurement rocheux, pelouse rase à *Cyanotis* et *Sporobolus*, 13 Aug 1952, *G.Troupin 1848* (BR); ***Forestier Central***, Haut-Zaïre, Ituri, env. de Nduye, Mont Mukonza, rochers, 8 Aug 1975, *S.Lisowski 40451* (POZG); Same locality, 5 Jan 1976, *S.Lisowski 41509, 41738* (POZG); Haut-Zaïre, Ituri, env. de Nduye, au-dessus du village Maitatu, Mont Mukonza, 12 Apr 1976, *S.Lisowski 42315, 42498* (POZG).

Uganda, West Nile Distr., Rokosa Hill, ¾ mile SE of Maracha [illegible] Camp, 6 Aug 1953, *R.J. Chancellor 113* (K).

Note. The specimens from Ituri (region of Nduye), ca. 250 km south of the range of the species in the Garamba Region, match the type in all traits except for the almost straight, not zigzagging cincinni; we consider them as conspecific.

Unplaced names

Coleus poggeanus Briq., Bot. Jahrb. Syst. 19(2–3): 182. 1894. Type: DR. Congo, Mussumba des Muata Jamwo [Mosumba Kekese], S08°1/2, Jan 1876, *P.Pogge 364* (holotype B destroyed).

Coleus viridis Briq., Bot. Jahrb. Syst. 19(2–3): 181. Type: DR. Congo, Mussumba des Muata Jamwo [Mosumba Kekese], S08°1/2, Jan 1876, *P.Pogge 365* (holotype B destroyed).

Species excluded

Coleus schizophyllus (Baker) A.J.Paton was reported from DR. Congo in error, based on *M.Schaijes 1889* (BR) and *F.Malaisse & E.Robbrecht 2356* (BR), which are *Equilabium pulcherrimum* (A.J.Paton) Mwany. & A.J.Paton.

Coleus tetragonus (Gürke) Robyns & Lebrun, was reported from DR. Congo in error, based on *A.Hock s.n.* [BR0000009824928], the type specimen of *Plectranthus dekindtianus* Gürke. However, this specimen clearly belongs in *C. esculentus* var. *densus* (see note under that variety). The specimen *W.Robyns 2061* (BR) was also misidentified as *C. tetragonus*, while it is actually *C. conglomeratus*. A specimen of *C. tetragonus* was collected in Zambia very close to the DR. Congo border (*Brédo 3123* [BR]). However, no authentic materials of *C. tetragonus* have been seen from DR. Congo, Rwanda and Burundi so far.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

PM contributed to Conceptualisation, Methodology, Investigation, Data Curation, Writing – Original draft, Writing – Review and Editing.

AJP contributed to Validation, Investigation, Writing – Review and Editing, Supervision.

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Data availability

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

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Supplementary material 1

Herbarium specimens examined

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Research Article

Salvia penghuana (Lamiaceae), a new species from Guizhou, China

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Abstract

Salvia penghuana, a new species from Guizhou Province of southwestern China, is described and illustrated. Morphologically, *Salvia penghuana* is similar to *S. filicifolia*, but can be easily distinguished from the latter by ovate-lanceolate bracts, purple corolla, and foot-shaped fused lower arms of connective. In addition, *S. penhuana* is morphologically similar to *S. cavaleriei*, but differs by having 3–4-pinnate leave, ovate-lanceolate bracts, puberulent calyx, and longer upper arms of connective. Based on the fibril root, small calyx and corolla, and completely reduced posterior thecae, *S. penghuana* should be placed in section *Sobiso* of subg. *Glutinaria*.

Key words: *Salvia cavaleriei*, *Salvia filicifolia*, sect. *Sobiso*, stamen movement, Subg. *Glutinaria*

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Introduction

As currently defined, the genus *Salvia* L. includes the five traditionally defined genera (*Dorystaechas* Boiss. & Heldr. ex Benth., *Meriandra* Benth., *Perovskia* Kar., *Rosmarinus* L., and *Zhumeria* Rech. f. & Wendelbo) and is classified into 11 subgenera (Drew et al. 2017; Hu et al. 2018; Kriebel et al. 2019; Moein et al. 2023). With approximately 1000 species, *Salvia* is the largest genus within Lamiaceae (Walker et al. 2004; Wei et al. 2015; Hu et al. 2018), and has a subcosmopolitan distribution, but mainly radiates in Mesoamerica/South America, Southwestern Asia and the Mediterranean region, and Eastern Asia (Walker and Sytsma 2007; Wei et al. 2015; Hu et al. 2018). Recently, a large number of new species or hybrids of this genus have been reported around the world (Celep et al. 2020; González-Gallegos et al. 2021, 2023; Ilçim et al. 2023; Jin et al. 2023; Huang et al. 2024).

In East Asia, ca. 100 *Salvia* species have been recorded, most of which are found in China. To date, 89 native species (Li and Hedge 1994; Hu et al. 2014, 2017; Hu and Peng 2015; Chen et al. 2016; Wang et al. 2016; Xiang et al. 2016; Ding et al. 2019; Wei et al. 2019, 2021; Jin et al. 2023; Huang et al. 2024) and three naturalized species from the New World (viz. *S. coccinea* Buc'hoz ex Etl., *S. reflexa* Hornem., and *S. tiliifolia* Vahl) have been reported in China (Li and Hedge 1994; Hu et al. 2013; Shao et al. 2019). Based on the staminal morphology, *Salvia* in East Asia had been placed in subg. *Salvia*, subg. *Sclarea* (Moench) Benth., and subg. *Allagospadonopsis* Briq. (Sun and Wu 1977; Murata and Yamazaki 1993). Recently, based on molecular and morphological evidence, Hu et al. (2018, 2020) classified East Asiatic *Salvia* into two subgenera. *Salvia grandifolia* (endemic to the Hengduan Mountains) and *S. deserta* (distributed in Xinjiang of China, and Central Asia) are retained in the subg. *Sclarea* that includes ca. 120 species mainly from Southwestern Asia, Europe, Mediterranean region (Kriebel et al. 2019; Hu et al. 2020), and the other East Asiatic *Salvia* species were placed in the newly established subg. *Glutinaria* (Raf.) G.X.Hu, C.L.Xiang & B.T.Drew (Hu et al. 2018, 2020).

In January 2021, we were attracted by a *Salvia* population with 3–4-pinnately compound leaves in Libo, southern Guizhou, China. The plants without flowers morphologically resemble *S. filicifolia* Merr. Another population was later found in Kuankuoshui National Nature Reserve (northern Guizhou, China) in April 2021 and some living materials were collected and cultivated at Guizhou University. After careful observation of the flower morphology of the cultivated plants, we confirmed that these collections are not *S. filicifolia*, and may represent a new species. Over the next three years, we continued to observe the species in the field and carefully compared it with other species of *Salvia*. Finally, we confirmed that the new collections represented an undescribed species, and therefore described the new species here.

Materials and methods

Specimens of the potential new species were collected in Libo and Suiyang counties, Guizhou Province, China. Morphological comparisons between the new species and its morphologically similar species (*S. cavaleriei* and *S. filicifolia*) were performed based on fresh materials as well as herbarium specimens deposited at GACP and KUN. Ten diagnostic characters involved in leaf, verticillaster, bract, calyx, corolla, stamen, and nutlet were selected to conduct the comparisons (Table 1). Morphological descriptions mainly referred to the Flora of China (Li and Hedge 1994).

Table 1. Comparison of morphological characters between *Salvia penghuana* and its morphologically similar species.

Characters	*Salvia penghuana*	*Salvia filicifolia*	*Salvia cavaleriei*
Leaves	3–4-pinnate	3–4-pinnate	simple to 2-pinnate
Verticillasters	6-flowered	6–10-flowered	2–6-flowered
Bracts	ovate-lanceolate	linear-lanceolate	lanceolate
Calyx tube	sparsely glandular or puberulent along veins outside, glabrous or apically fine strigose inside	sparsely glandular or villous along veins outside, sparsely villous annulate inside	glabrous outside, apically fine strigose inside
Corolla color	purple	yellow or white	blue-purple to purple-red or white
The middle lobe of the lower lip of corolla	subrectangular	obcordate	obcordate
Lower arm	foot-shaped, fused	subulate, separated	foot-shaped, fused
Upper arm length	ca. 5 mm	ca. 5 mm	ca. 3 mm
Lower arm length	ca. 1.5 mm	ca. 1.8 mm	ca. 1.5 mm
Nutlets	pale brown, ca. 2 mm	brown, ca. 1.5 mm	black, ca. 0.8 mm

Taxonomy treatment

***Salvia penghuana* G.X.Hu & C.L.Xiang, sp. nov.**
urn:lsid:ipni.org:names:77347687-1
Figs 1, 2

Type. China • Guizhou Province: Libo County, Yaoshan Town, Pobashao, karst forest margin, elevation 790 m, 1 May 2022, *G. X. Hu & Y. F. Geng 758* (holotype: GACP!; isotypes: GACP!, KUN!).

Diagnosis. *Salvia penghuana* is similar to *S. filicifolia*, but differs in having 6-flowered verticillasters (vs. 6–10-flowered verticillasters), ovate-lanceolate bracts (vs. linear-lanceolate), purple corolla (vs. yellow or white), foot-shaped fused lower arms of connective (vs. subulate separated lower arm). It is also similar to *S. cavaleriei*, but differs by having 3–4-pinnate leaves (vs. simple to 2-pinnate), ovate-lanceolate bracts (vs. lanceolate), puberulent calyx (vs. glabrous), longer upper arms of connective (ca. 5 mm vs. ca. 3 mm).

Description. Perennial herbs. Roots fibrous, 5–15 cm long. Stems erect, 10–60 cm tall, finely minutely pubescent or glabrous, simple, or branched from the base. Leaves mostly basal, cauline leaves absent or 1–2 paired; the most basal leaves 1–2-pinnate, usually 1-paired, caducous, petiole 4–10 cm long, terminal leaflets ovate, margin serrate; other basal leaves 3–4-pinnate, petiole 6–12 cm long, leaf blades ovate, 9–16 × 8–13 cm, lobes numerous, elliptic to linear-lanceolate, margin entire or few lobulate, terminal leaflets lanceolate, ca. 7 × 2 mm, adaxially dark green, glabrous or sparsely puberulent, abaxially greenish or purplish-brown, glabrous or villous along veins. Verticillasters 6-flowered, in racemes or panicles; rachis puberulent and glandular pilose. Bracts ovate to lanceolate, 4–6 × 1.5–2.5 mm, apex acuminate, margin entire, glabrous; bracteoles similar to bracts in shape but smaller. Pedicels 2–3 mm long, puberulent. Calyx tubular-campanulate, 4–6 mm long, bilabiate to one-fourth its length, pale purple, sparsely glandular or puberulent along veins outside, glabrous or apically fine strigose inside; upper lip semicircular-triangular, ca. 2 × 3 mm, margin entire; lower lip ca. 2 × 2.5 mm, shallowly 2-toothed, teeth triangular, apex acuminate. Corolla purple, 9–13 mm long, densely puberulent or glandular hairs; corolla tube 6–9 mm long, creamy yellow inside calyx tube, ca. 1 mm wide, densely puberulent annulate, gradually dilated after extending out of the calyx tube, purple, ca. 2 mm wide at the throat, sparsely villous; lips subequal, upper lip oblong, 3–4 × 2–3 mm, apex emarginated; lower lip 3-lobed, middle lobe subrectangular, 3–4 × 2.5–3.6 mm, lateral lobes oval-triangular. Fertile stamens 2, purple, glabrous, filament ca. 1.5 mm long; connective ca. 6.5 mm long, upper arm ca. 5 mm long, the lower arm ca. 1.5 mm long; anterior thecae oblong, ca. 1.5 mm long, fertile, connivent; posterior thecae boot-shaped, sterile, fused. Staminodes 2, 0.7–1.1 mm long. Style exerted slightly, stigmatic lobes unequal, posterior lobe shorter. Nutlets ellipsoid, pale brown, glabrous, ca. 2 mm long.

Distribution and habitat. The new species is currently only known from Libo and Suiyang counties, Guizhou Province, China, at elevations between 770 and 1220 m (Fig. 3). Both populations grow in karst evergreen and deciduous broad-leaved mixed forest. The common companion species include *Handeliodendron bodinieri* (H. Lév.) Rehder, *Sarcococca ruscifolia* Stapf, *Selaginella uncinata*

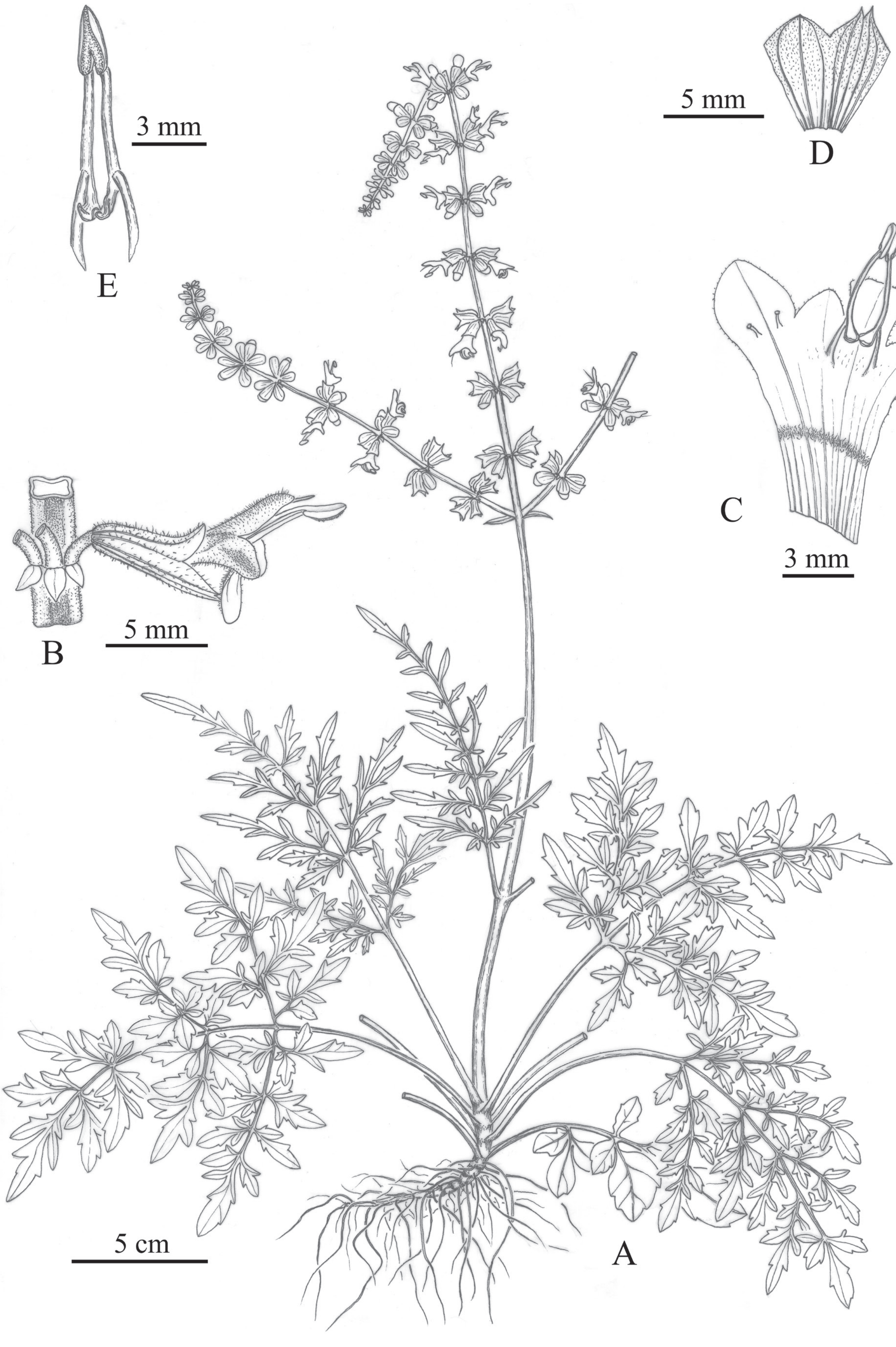

Figure 1. *Salvia penghuana* sp. nov. **A** habit **B** flower **C** dissected corolla **D** dissected calyx **E** fertile stamens. Drawn by Xiao-Yu Wang from the holotype.

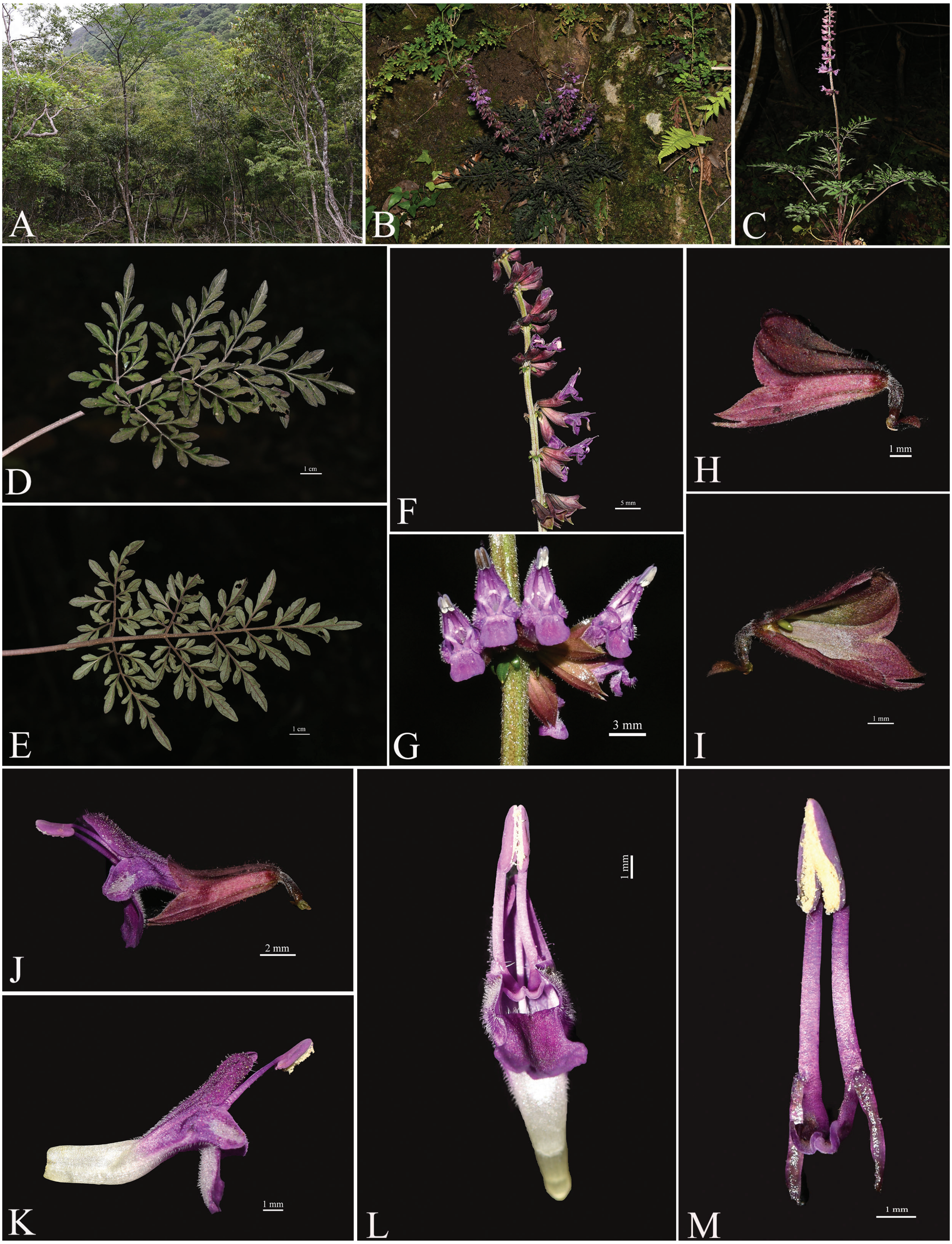

Figure 2. *Salvia penghuana* sp. nov. **A** habitat **B, C** plant **D** leaf (adaxial surface) **E** leaf (abaxial surface) **F** inflorescence **G** verticillaster **H** calyx (external view) **I** calyx (internal view) **J–K** corolla (side view) **L** (front view) **M** fertile stamens. Photographs by Guo-Xiong Hu.

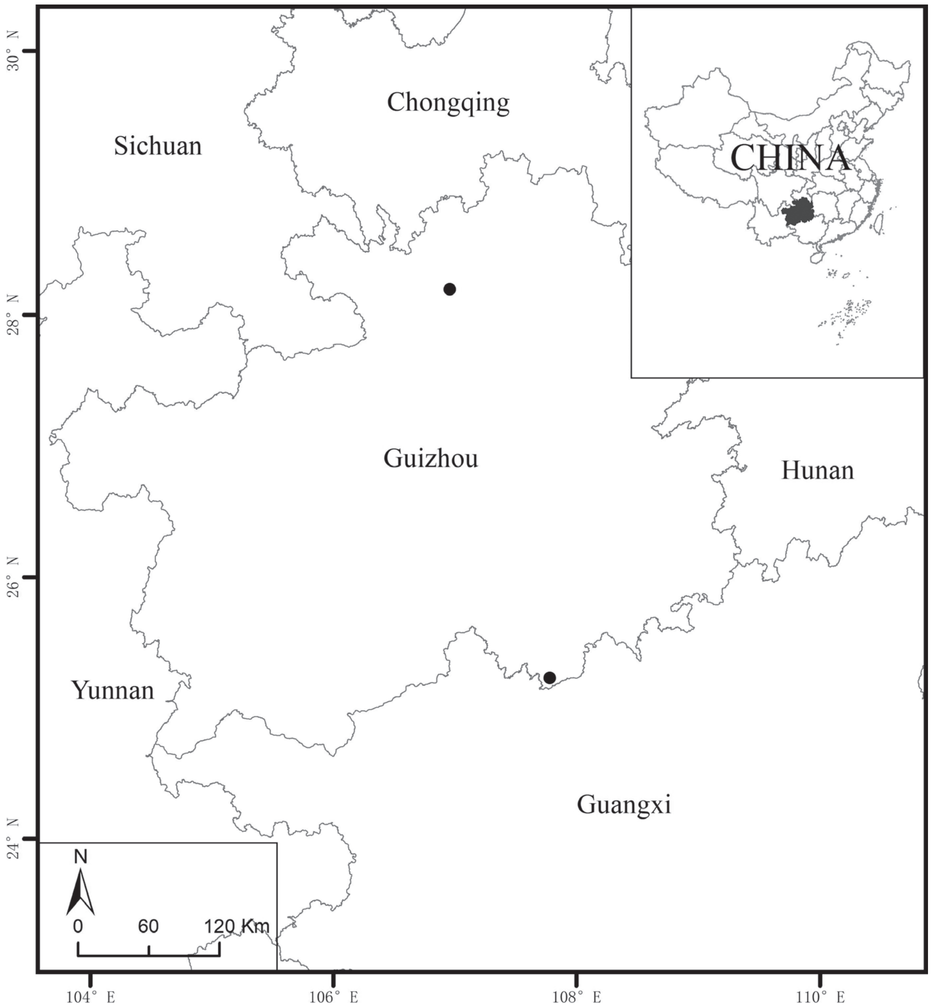

Figure 3. Known geographic distribution of *Salvia penghuana*.

(Desv.) Spring, *Hedera nepalensis* var. *sinensis* (Tobler) Rehder, *Aster ageratoides* Turcz., and *Ajuga decumbens* Thunb.

Phenology. Flowering from April to June, and fruiting from May to June.

Etymology. The specific epithet ‘penghuana’ was selected to honor Prof. Hua Peng, who is a renowned expert on plant taxonomy at the Kunming Institute of Botany, Chinese Academy of Sciences, China.

Vernacular name. Chinese Mandarin: Péng huá shǔ wěi cǎo (彭华鼠尾草)

Conservation status. Currently, two populations are found in Guizhou, China. The population in Libo is close to Maolan National Nature Reserve, and another population in Suiyang is located in the Kuankuoshui National Nature Reserve. Two populations have no plausible threats, and the area is relatively well-known. Under IUCN criteria, the species was categorized as “Least Concern” (IUCN 2024).

Additional specimens examined (Paratypes). CHINA • Guizhou: Suiyang County, Kuankuo Town, Honghe village, elevation 1182 m, 4 May 2024. W. Wu & L. Chen *sy01* (GACP) • Guizhou Province: Libo County, Yaoshan Town, Pobashao, karst forest margin, elevation 790 m, 1 May 2023, G. X. Hu & W. Wu 779.

Notes. Based on molecular and morphological evidences, Hu et al. (2018) established the subg. *Glutinaria*, of which eight sections were recognized. Sect.

Sobiso (Raf.) G.X.Hu, A.Takano & B.T.Drew is characterized by fibril roots, small calyx (4–7 mm), small corolla (5–10 mm), and completely reduced posterior thecae. *Salvia penghuana* has these synapomorphies and therefore should be included in this section. Within sect. *Sobiso*, two lineages were recognized. The *Salvia chinensis* group mainly consists of species distributed to China and a total of 17 species were reported (Hu et al. 2018; Wei et al. 2019). This group is characterized by the stamen movement whereby the upper connective arms bend downward from the upper lips at early anthesis to the middle lobe of the lower corolla lips at the end of flowering (Hu et al. 2018). This stamen movement is considered to be a diagnostic between the *S. chinensis* group and *S. lutescens* group endemic to Japan and Taiwan Island. A similar phenomenon is also observed in this new species, so *S. penghuana* should be placed in the *S. chinensis* group.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: GXH. Formal analysis: GXH, FJQ, YFG, CLX. Resources: DLY, HBL, MTA, GXH. Writing-original draft: FJQ, DLY, HBL, YFG, GXH. Writing-review and editing: GXH, CLX. Funding acquisition: MTA, GXH, YFG.

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Data availability

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

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Research Article

Studies on *Typhonium* (Araceae) of Thailand I: *Typhonium vinicolor*, a new species from Khon Kaen Province, Northeastern Thailand

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Abstract

Typhonium vinicolor from Khon Kaen Province (Northeastern Thailand), is described and illustrated as a species new to science. Color plates, phenology, distribution, discussion of similar taxa, and conservation status assessment are provided.

Key words: Areae, Aroideae, Indochina, Northeastern Thailand, plant taxonomy

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Introduction

Typhonium Schott (1829) (Araceae Juss.) is a genus of tuberous (sometimes rhizomatous or stoloniferous), terrestrial, and seasonally dormant herbs that inhabit forest floors, rocky areas, wet sites, stream sides, and grassy places in tropical and subtropical humid and seasonal forests, as well as in agricultural land (Mayo et al. 1997; Low et al. 2020). Hay et al. (2022) transferred most of the Australian *Typhonium* species to *Lazarum* A.Hay, so, according to these authors *Typhonium* (*sensu stricto*) would refer to species mainly distributed in Indochina (see e.g., Low et al. 2020; Hay and Hein 2022). Among the genera of tribe Areae, *Typhonium s.str.* is the largest one, with more than 70 species (100 based on Boyce and Croat 2011; 72 in POWO 2024). The highest species diversity of *Typhonium* is found in Thailand, with 32 species, 24 of which are endemic (Boyce et al. 2012). Later than Boyce et al. (2012), six new species have been described from Thailand (Galloway 2012, 2015; Hetterscheid 2013; Sookchaloem and Maneeanakekul 2018), increasing the total number of species in the country to 38. However, the current number of species occurring in Thailand is undoubtedly much higher (Boyce et al. 2012).

During our botanical survey in Khon Kaen Province (Northeastern Thailand), an unknown species of *Typhonium* was collected by the second author (SS). After meticulously examining its morphology and comparing it with protologues and relevant literature, as well as with digitized type specimens from Thailand and neighboring countries, it became apparent that the collected specimen does not match any other known *Typhonium* species. Thus, we consider it to represent a taxonomic novelty, which is described and illustrated in the present paper.

Materials and methods

The measurements and descriptions were based on freshly collected and/or alcohol-preserved material, processed according to the methods established by Davies et al. (2023). The species description follows Hay and Hein (2022), while Araceae morphological terminology follows Mayo et al. (1997) implemented by the descriptive terminology of Beentje (2016). Relevant type specimens of *Typhonium* species from Thailand and neighboring countries were examined in different herbaria (A, AAU, B, BK, BKF, C, CAL, CMU, E, HITBC, K, KKU, KUN, L, M, MO, P, PE, QBG, SING, and WAG; acronyms follow Thiers 2024) through high-resolution images from https://plants.jstor.org/ and Global Biodiversity Information Facility (GBIF) accessed from https://www.gbif.org. An assessment of conservation status was carried out following IUCN (2024), based on our current knowledge and the respective terminology on categories, criteria, and subcriteria. The photographs in the plate were taken with an iPhone 13 (iOS version 17.5.1, 2021, Apple Inc., Cupertino, CA, USA). The figure in this study was created using Pixelmator Pro (Version 3.6.5, Archipelago, 2023, Pixelmator Team, Vilnius, Lithuania) on a MacBook Pro (13-inch, M1, 2020, Apple Inc., Cupertino, CA, USA).

Taxonomic treatment

***Typhonium vinicolor* P.Saensouk, K.Z.Hein & Saensouk, sp. nov.**
urn:lsid:ipni.org:names:77347851-1
Fig. 1

Type. THAILAND • Northeastern – Khon Kaen Province, 13 May 2023, *Surapon Ara001* (holotype KKU!; isotypes FOF!, MSU!).

Diagnosis. *Typhonium vinicolor* is easily distinguishable from the other *Typhonium* species by having narrowly elliptic to elliptic-lanceolate leaf blades with a reddish-purple abaxial surface. An only exception is *T. laoticum* Gagnep. (Gagnepain 1942), which shows similar leaf blades. However, *T. vinicolor* differs from *T. laoticum* by its reddish-purple abaxial surface of leaf blades (*vs*. pale green), white or pale green spathe with dark purple mottling externally (*vs*. pink spathe with brown mottling externally), pistillate zone with 5–6 pistil rows (*vs*. 2–3 pistil rows), and staminodes more or less loosely arranged in 4–5 spirals (*vs*. staminodes densely arranged in 2–3 spirals).

Description. Small, deciduous, herbs, to 15 cm tall. ***Stem*** hypogeal, subglobose or depressed globose tuber, 1.2–1.5 cm in diameter, externally pale brown, internally white. ***Roots*** filiform, 0.6–1.0 mm in diameter, white. ***Leaves*** 1–2(–3) together; ***petioles*** 6.5–8.5 cm long, ca. 0.2 cm in diameter, erect, slender, terete, glabrous, basal subterranean portion white, upper aerial portion pale green with numerous longitudinal dark purple striations and spots; ***petiolar sheath*** 2.5–3.0 cm long, ca. 1/3 of petiole length; ***leaf blade*** 8.0–13.0 × 1.8–4.2 cm, narrowly elliptic to elliptic-lanceolate, or elliptic-oblanceolate, chartaceous, adaxially medium green, abaxially reddish-purple, glabrous on both sides, base cuneate or obtuse, margin entire, apex acute and mucronate, mucro ca. 1 mm long; ***midrib*** adaxially impressed, abaxially raised, rounded, 1.5–1.8 mm wide at the base, ca. 1.0 mm wide at center, then narrowing towards blade apex; ***primary lateral veins*** 5–7 per side, adaxially impressed, abaxially raised, diverging from the midrib at 15–30°, anastomosing at 0.5–1.5 mm from margin into an intramarginal collective vein; ***higher order venation*** reticulate. ***Inflorescence*** solitary, subtended by a cataphyll; ***cataphyll*** up to 3.0 cm long, linear-lanceolate, membranous, semi-hyaline, greenish white or white, later withering brown; ***peduncle*** 2.8–3.2 cm long, ca. 0.2 cm in diameter, almost entirely subterranean, white, terete, glabrous; ***spathe*** 8.5–9.5 cm long, strongly differentiated into a spathe tube and a spathe limb by a constriction; ***spathe tube*** ca. 1.2 cm long, 0.6–0.7 cm in diameter, convolute, ellipsoid-ovoid, externally white or greenish white with a dense dark purple mottling, internally greenish white; ***spathe limb*** 7.3–8.3 cm long, 0.6–0.7 cm in diameter at base, linear-lanceolate, tapering towards apex, externally green or yellowish-green with dark purple mottling, internally pale yellowish green, basal part of limb shortly convolute and erect, upper part reflexed and then strongly coiled at anthesis, apex narrowly acute. ***Spadix*** sessile, 8.0–9.0 cm long, nearly as long as or shorter than spathe; ***pistillate zone*** ca. 2 mm long, ca. 3 mm in diameter at the base, shortly conical, with 5–6 rows of congested pistils; ***ovary*** ca. 0.7 mm high, ca. 0.5 mm in diameter, obovoid, white, unilocular with one basal ovule held obliquely on a funicle, on a basal placenta; ***style*** very short, ca. 0.1 mm high, ca. 2.5 mm in diameter; ***stigma*** ca. 0.3 mm in diameter, discoid, red, papillate; ***sterile interstice*** between pistillate and staminate zones 0.8–1.0 cm long, ca. 0.1 cm in diameter, upper part naked, terete, glabrous, glossy white, lower ca. 0.2 cm covered with 4–5 spirals of staminodes; ***staminodes*** 1.2–1.5 mm long, 0.5–0.7 mm in diameter at widest point, clavate-fusiform, shortly beaked with acute apex, free, slightly distant from each other, perpendicular to the spadix axis or slightly curved downwards, glabrous, yellow; ***staminate zone*** 0.7–1.0 cm long, ca. 0.3 cm in diameter, cylindric; ***stamens*** congested, not ostensibly arranged into staminate flowers, irregularly 4-lobed, 0.6–0.7 mm in diameter, pink or yellow, dehiscing by an apical pore; ***appendix*** sessile, 6.2–7.0 cm long, 1.5–2.0 mm in diameter, narrowly elongate-conical, tapering towards apex, erect or weakly arching, glabrous, ivory-colored, base slightly attenuate, apex acute. ***Infructescence*** not seen.

Etymology. The specific epithet is derived from the Latin “*vinicolor*” (wine-coloured), referring to the reddish-purple abaxial surface of the leaves.

Proposed vernacular name. Uttapit-See-Wine.

Phenology. Flowering time in May.

Distribution and habitat. The newly discovered species is found exclusively at its type locality in Khon Kaen Province (Northeastern Thailand). It thrives in shaded to semi-shaded areas of tropical deciduous forests at elevations ranging from 200 to 250 m a.s.l. The species shows optimal growth in sandy loam soil mixed with rocks.

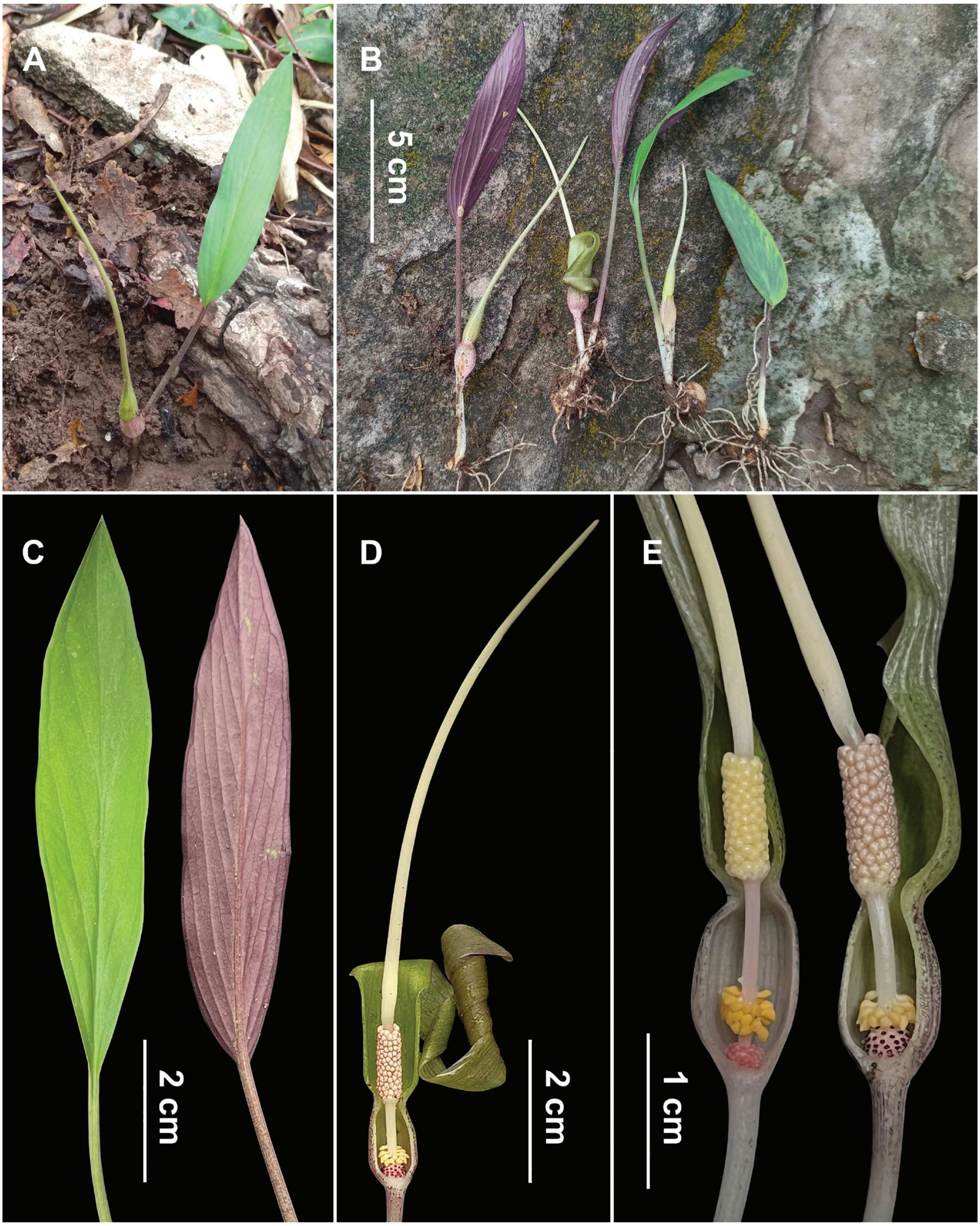

Figure 1. *Typhonium vinicolor* **A** plant in habitat **B** excavated flowering plants **C** leaf blade (left showing adaxial surface, right showing abaxial surface) **D** inflorescence at pistillate anthesis, nearside spathe artificially removed **E** spadix at pistillate anthesis, nearside spathe artificially removed. Photos by: Surapon Saensouk and Thawatphong Boonma.

Conservation status. This new species is known exclusively from its type locality, and no sufficient information there is regarding potential threats to its habitat. In accordance with the Red List criteria of the IUCN Standards and Petitions Subcommittee (2024), we propose classifying this species as 'Data

Deficient' (DD). Further research is necessary, as there is inadequate information to assess the conservation status of this species. Currently, data is limited regarding its distribution, with no details on population size, trends, or potential threats to its habitat.

Taxonomic notes. Based on overall morphology, this new species is also similar to *Typhonium griseum* Hett. & Sookch. (Hetterscheid et al. 2001), which is a sister species of *T. laoticum* (Low et al. 2020). But *T. vinicolor* is strikingly different from *T. griseum* in having the leaf blade base cuneate or obtuse (vs. with rounded posterior lobes), spadix nearly as long as, or shorter than, spathe (vs. longer than spathe), clavate-fusiform and yellow staminodes (vs. narrowly fusiform, sickle-shaped, white staminodes), longer staminate zone (ca. 1 cm vs. ca. 0.5 cm long), and erect or weakly arching, ivory-colored appendix (vs. strongly arching, pale brown appendix).

Regarding spathe and spadix structures, the new species also resembles *Typhonium huense* V.D.Nguyen & Croat (Nguyen and Croat 1997), *T. lineare* Hett. & V.D.Nguyen (Hetterscheid and Nguyen 2001) and *T. stigmatilobatum* V.D.Nguyen (Nguyen 2008) from Vietnam. However, the latter three species differ from *T. vinicolor* by having horizontally flexed spathe limb at anthesis (vs. only the upper part of spathe limb reflexed and then strongly coiled at anthesis in *T. vinicolor*) and strongly arching, dark brown or violet, stipitate appendix (vs. erect or weakly arching, ivory, sessile appendix in *T. vinicolor*). A more detailed comparison between *T. vinicolor* and its morphologically allied species is presented in Table 1.

Additional specimens examined (paratypes). THAILAND • Northeastern – Khon Kaen Province, 18 May 2024, *Saensouk, Boonma & Sengthong, SS 24518* (FOF!).

Table 1. Morphological comparison of *Typhonium vinicolor* and its allied species, *T. griseum* (Hetterscheid et al. 2001), *T. huense* (Nguyen and Croat 1997), *T. laoticum* (Gagnepain 1942; Boyce et al. 2012), *T. lineare* (Hetterscheid and Nguyen 2001) and *T. stigmatilobatum* (Nguyen 2008).

	T. griseum	*T. huense*	*T. laoticum*	*T. lineare*	*T. stigmatilobatum*	*T. vinicolor*
Leaf blade	orbicular, triangular cordate or narrowly ovate	triangular-cordate to deeply trilobed	lanceolate or elliptic-oblong	pedatisect with linear or linear-lanceolate lobes	deeply trilobed or pedatisect with ovate to oblong-ovate lobes	narrowly elliptic to elliptic-lanceolate
Spathe tube	ca. 1 cm long, externally dirty white with brownish-red spots	ca. 1.5 cm long, externally pale green with purplish violet spots	1.3–1.5 cm long, externally pink with brown striations and spots	up to 1.8 cm long, externally whitish-gray with blackish-gray striations and spots	ca. 1.3 cm long, externally pale green or dull white with black or brown spots	ca. 1.2 cm long, externally white or greenish-white with a dense dark purple mottling
Spathe limb	ca. 10 times longer than spathe tube	ca. 6 times longer than spathe tube	4–5 times longer than spathe tube	7–8 times longer than spathe tube	10–12 times longer than spathe tube	6–7 times longer than spathe tube
Spadix	longer than spathe, ca. 13 cm long	as long as or slightly longer than spathe, up to 11 cm long	shorter than the spathe, ca. 7 cm long	as long as or slightly shorter than spathe, up to 17 cm long	as long as spathe, up to 17 cm long	nearly as long as or shorter than spathe, 8.0–9.0 cm long
Staminodes	narrowly fusiform, sickle-shaped, curved downwards, white	fusiform, variously directed, yellowish white	clavate, perpendicular to the spadix axis or curved upwards, white	subulate or fusiform, variously directed, white or yellow	fusiform, perpendicular to the spadix axis or slightly curved downwards, dull white	clavate-fusiform, perpendicular to the spadix axis or slightly curved downwards, yellow
Appendix	sessile, ca. 12 cm long, strongly arching, pale brown	stipitate, ca. 9 cm long, strongly arching, brown or violet	sessile, ca. 5 cm long, erect, pale brown	stipitate, ca. 15 cm long, strongly arching, brown or golden yellow	sessile, 14–15 cm long, strongly arching, dark brown	sessile, 6.2–7.0 cm long, erect or weakly arching, ivory-colored

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization PS, SS, and KZH; Data curation PS, SS, KZH, TB; Formal analysis PS, SS, KZH; Funding acquisition SS; Investigation SS, TB, and AS; Methodology PS, SS, KZH, and TB; Project administration PS and SS; Resources SS, TB, and AS; Supervision SS; Validation PS, SS, KZH, and TB; VisualizationPS, SS, KZH, and TB; Writing - original draft KZH and TB; Writing - reviewing and editing PS, SS, KZH, TB, AS, and SR.

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Data availability

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

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Research Article

Six new species of *Globba* L. (Zingiberales, Zingiberaceae) from the Eastern Himalayas and Northeast India

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Abstract

We describe six new species in the genus *Globba* L.: *Globba corniculata* **sp. nov.**, *Globba paschimbengalensis* **sp. nov.**, *Globba polymorpha* **sp. nov.**, *Globba tyrnaensis* **sp. nov.**, *Globba janakiae* **sp. nov.**, *and Globba yadaviana* **sp. nov.** collected from the Indian part of the Eastern Himalayas (West Bengal) and Northeast India. We provide a detailed morphological description of all six species along with photographic plates, distribution maps, and tentative conservation assessments. We also provide a dichotomous identification key for all the Indian *Globba* species and discuss the newly described species in relation to those that are morphologically similar to them. Finally, we highlight the taxonomic collection challenges in the ecologically sensitive Eastern Himalayas and Northeast regions of India.

Key words: dancing girls ginger, Meghalaya, Mizoram, taxonomy, West Bengal

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Introduction

Zingiberaceae is the largest family within the order Zingiberales, which comprises at least 114 genera and 4022 species (https://www.worldfloraonline.org/). Members of Zingiberaceae are tropical, perennial, rhizomatous herbs that usually grow in moist shady places (Saha et al. 2020). *Globba* L. is the fourth largest genus with about 136 species (POWO 2024; Fig. 1A) within Zingiberaceae, and it is one of the three genera within the tribe Globbeae, the other two being *Gangnepainia* K.Schum. and *Hemiorchis* Kurz (Cao et al. 2019). The genus *Globba* is distinguished from the other two genera by the presence of anther appendages, the absence of central stripe/point on labellum, the labellum being partially fused with the floral tube or free, the reflexed floral tube and flowering throughout the rainy season (Williams et al. 2004). Species within this genus are popular as ornamental plants, often known as: dancing girls, weeping goldsmith, snowball, singapore gold, white dragon, and ruby queen, all of which highlight the attractive and delicate flowers. The type species for the genus *Globba* - *G. marantina* L. was described by Linnaeus in 1771, and subsequent exploration of this genus can be accorded to Smith (1805) and Roxburgh (1820), followed by more regional-level studies throughout Southeast

Asia (Sakai et al. 1999; Takano and Okada 2003; Williams et al. 2004; Sakai and Nagamasu 2006; Sakai et al. 2013; Sangvirotjanapat et al. 2019, 2020, Newman and Sangvirotjanapat 2023). Most *Globba* spp. are terrestrial, a few are lithophytes, and only one species is known to be epiphytic (*G. bokorensis* Nob. Tanaka & Tagane). Morphologically, vegetative traits do not vary as much as reproductive traits, as most of the species are small herbaceous plants with short stature and an understory growth habit. However, there is a high diversity in their reproductive traits, such as in inflorescence type and size, floral morphology (lateral staminode, labellum), presence of andromonoecy, and presence and morphology of bulbils. The flower is characterized by a long, curved filament with a terminal anther, having zero, two, four, or six appendages. Stigma is present between the anther lobes, and style is held in the ventral furrow of the filament. The anther appendages have been shown to be an important morphological trait that defines infrageneric taxonomy in *Globba*, and it has also been used along with molecular markers to identify both subgeneric and sectional delimitations (Williams et al. 2004; Sangvirotjanapat et al. 2019).

The genus *Globba* currently includes seven sections (*Haplanthera* Horan., *Ceratanthera* (Horan.) Petersen, *Globba* (formerly *G.* sect. *Marantella* (Horan.) Benth. & Hook.f.), *Nudae* K.Larsen, *Substrigosa* K.J.Williams, *Sempervirens* K.J.Williams, and *Mantisia* (Sims) K.J.Williams). It is distributed in Sri Lanka, India, Nepal, Bhutan, Bangladesh, tropical China, and all of Southeast Asia (Fig. 2) and can be found as far east as Australia and Solomon Islands.

In recent years (2019–2022, Fig. 1A), an increased field exploration in Southeast Asia has led to a drastic increase in the number of species, making this region truly the center of diversity for this genus. In India, a total of 19 species (Suppl. material 1) have been documented, all of which are confined to the tropical forests of the Western Ghats across four states (Maharashtra, Karnataka, Kerala, and Tamil Nadu), the seven states of Northeast India (Arunachal Pradesh, Assam, Meghalaya, Nagaland, Manipur, Mizoram, and Tripura), Sikkim, and West Bengal (Alfred et al. 2019; Dalisay et al. 2022).

Based on molecular phylogenetic studies (Williams et al. 2004), eight of the Indian species have been assigned to the following three sections: *Haplanthera* (five species: *G. multiflora* Wall. ex Baker, *G. racemosa* Sm., *G. sessiliflora* Sims, *G. orixensis* Roxb., *G. macroclada* Gagnep.), *Ceratanthera* (one species: *G. pendula* Roxb.), and *Globba* (two species: *G. marantina* and *G. schomburgkii* Hook.f.). There are eight *Globba* species described from different parts of India. Williams Roxburgh described the first species from India, *G. orixensis* from Odisha, in 1810 (Roxburgh 1810), and the most recently published species, *G. kanchigandhii* A.Joe & M.Sabu is from Nagaland in 2019 (Alfred et al. 2019).

The northeast region of India is geographically seen as a ‘gateway’ for much of India’s flora and fauna because it shares its geographic borders with China and Bhutan to the north and Bangladesh and Myanmar to the south and southeast (Chakravarty et al. 2012; Ashokan et al. 2022). It has been shown for the genus *Hedychium* J.Koenig (Zingiberaceae) that the multistage uplift of the Himalayas created new geophysical environments along with climatic changes such as an intensification of monsoons which led to high speciation rates in these newly created ecological niches (Ashokan et al. 2022).

Similarly, other gingers in the northeast region of India may also have witnessed high speciation events, making this region a unique habitat for diverse

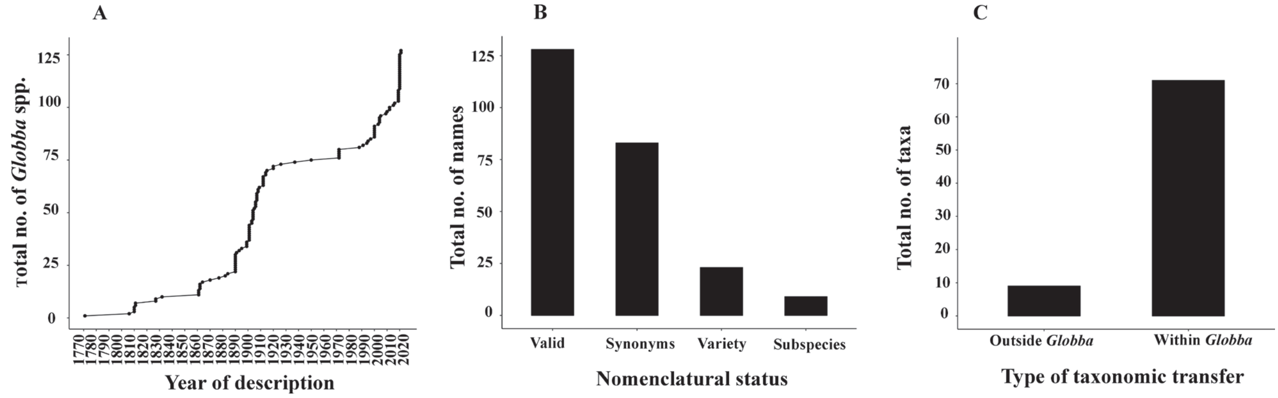

Figure 1. A yearly trend in the number of reported *Globba* spp. **B, C** nomenclatural status (**B**), and type of taxonomic transfer (**C**) in *Globba*.

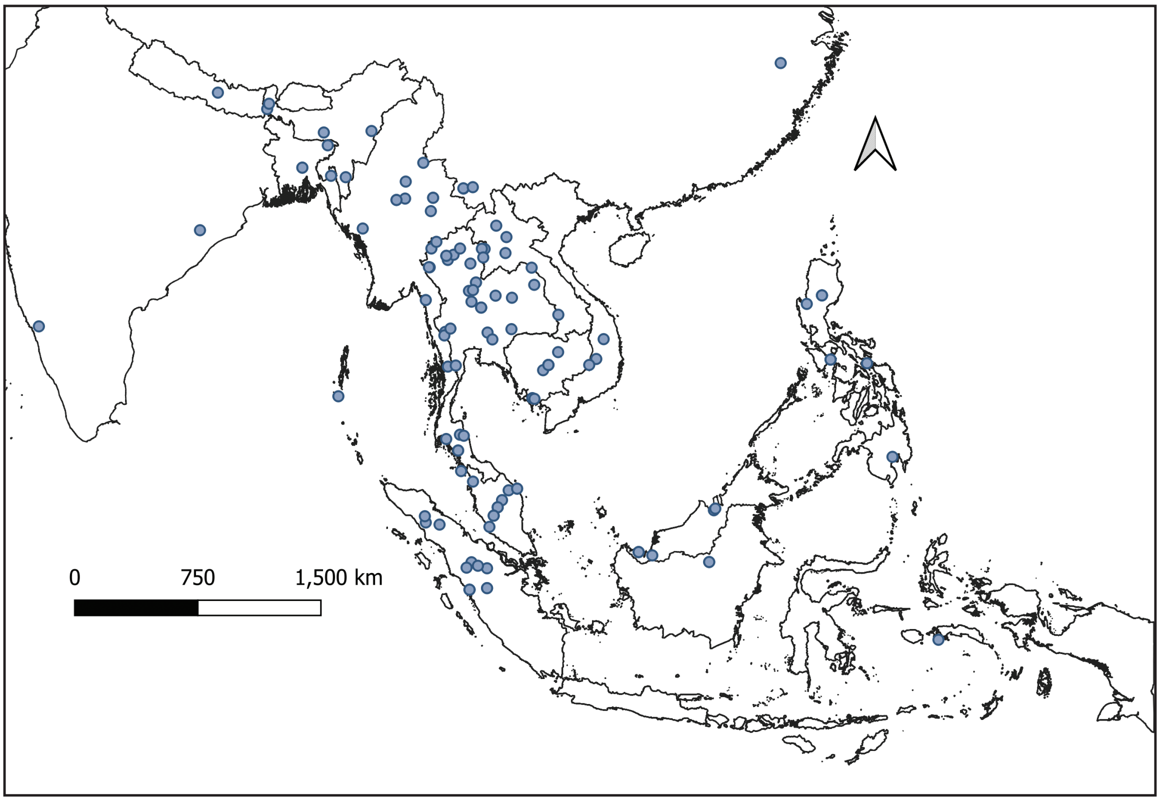

Figure 2. Comprehensive map showing the distribution of all type localities for *Globba* spp. in Asia.

flora with a high level of endemism (Chatterjee et al. 2006; Ashokan et al. 2022). Based on floristic composition and local climate, the northeast region of India can be divided into two biogeographic zones: Eastern Himalaya and Northeast India (Fig. 3 based on Rodgers and Panwar 1988). The Eastern Himalaya region includes (from west to east) the Indian states of West Bengal (five northern districts including Darjeeling), Sikkim, and Arunachal Pradesh and the country Bhutan, and the region of Northeast India includes the states of Assam, Meghalaya, Nagaland, Manipur, Mizoram, and Tripura (Fig. 3, Chatterjee et al. 2006).

Both of these regions have distinct climates, geology, topography, and floristic history. The state of West Bengal is further divided into five geographical regions: the Darjeeling, the Terai-Duars, the Western undulating highland plateau,

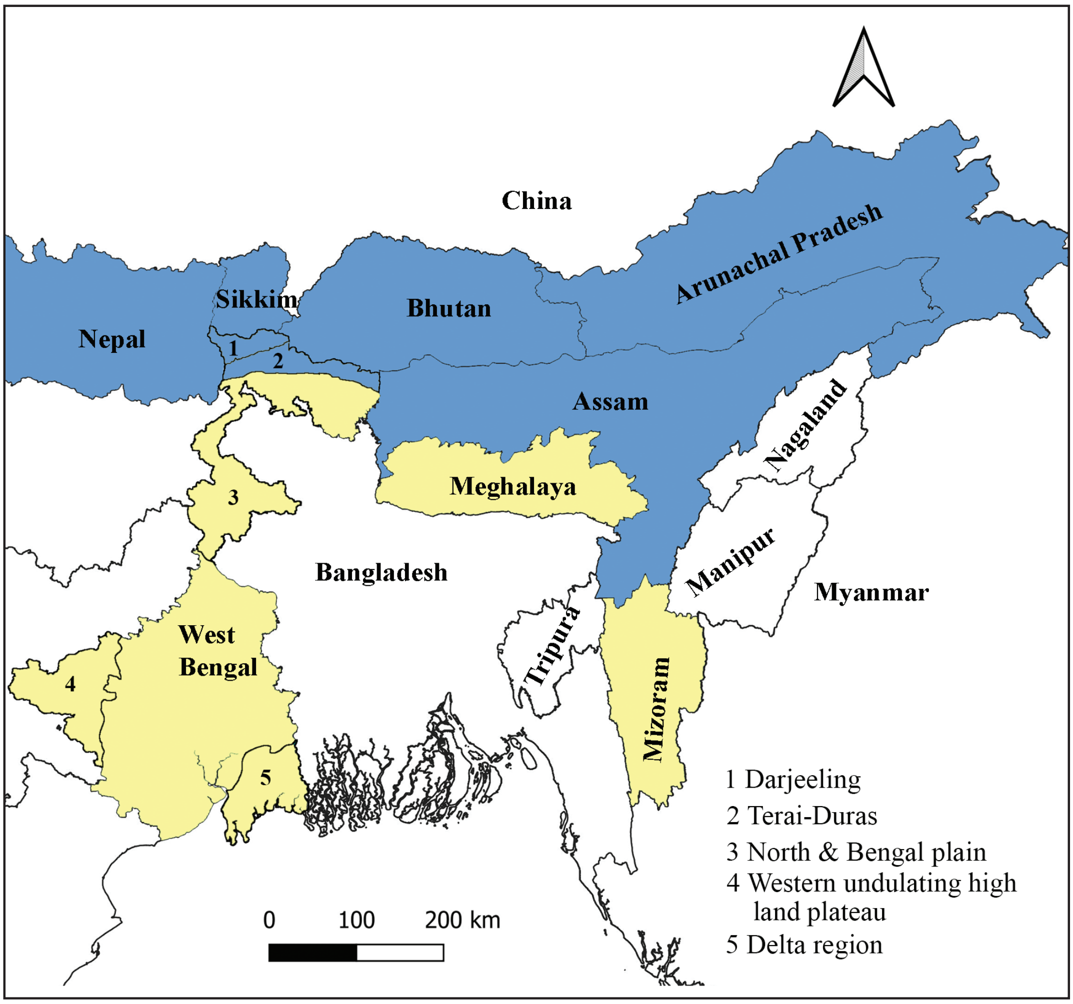

Figure 3. Map illustrating the Eastern Himalayas hotspot zone (highlighted in blue) and the various states of Northeast India. The states from which species are described in this study are highlighted in yellow. Additionally, the state of West Bengal is divided into five geographical regions, represented by the numbers 1, 2, 3, 4, and 5.

the North & Bengal plain, and the Delta (Fig. 3). Among these five vegetational zones, the Darjeeling-Himalayan zone belongs to the Eastern-Himalayan Hotspots zone, and it is the richest floristic zone of the state (Mitra et al. 2021). In this study, we describe six new species of the genus *Globba* from the states of West Bengal (Darjeeling region), Meghalaya, and Mizoram in India.

Materials and methods

Floristic surveys were conducted in the state of West Bengal, Meghalaya, and Mizoram during the monsoon months of August and September 2022, which is the flowering season for most of the *Globba* spp., and these surveys were also used to formulate the conservation assessment for all the six species described here. Morphological measurements for all six species were taken in situ from freshly dissected specimens, and from pickled flowers kept in Copenhagen solution using a digital caliper and under a stereomicroscope (Leica S8 APO), and also from digital images using the ImageJ software (Schneider et al. 2012). We also took morphological measurements from protologues, type specimens, and all available herbarium vouchers of the morphologically similar taxa (that is allied species) for comparative morphometrics with our new species. We have measured the flower length from the base of the ovary to the tip of the anther for all six newly described species. All herbarium vouchers and pickled specimens are deposited at BHPL (IISER Bhopal), and duplicates will be deposited at ASSAM (BSI Shillong). We examined specimens of *Globba*, including relevant type materials from the digitized herbarium collections of various international herbaria, such as E, K, and the JSTOR Global Plants collection (https://plants.jstor.org/), and all relevant *Globba* protologues were studied. The conservation status of the newly described species was evaluated based on guidelines listed by the International Union for Conservation of Nature (IUCN 2022), and terminologies for describing different morphological characters follow Gowda et al. 2012.

Taxonomic treatment

***Globba corniculata* Y.Ritu & V.Gowda, sp. nov.**
urn:lsid:ipni.org:names:77347881-1
Fig. 4

Type. India. West Bengal: Darjeeling district, Takdah forest, 27.0493, 88.3555, elevation 1220 m, 20 August 2022, *Y. Ritu, S. Goray & Rhuthuparna S. B. VG2022WB3803* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *Globba corniculata* is morphologically similar to *G. ruiliensis* and *G. multiflora* but differs in having sessile, oblong-narrowly ovate leaves, absence of inflorescence bracts and bracteoles, orange flower, cuneate labellum with cornicula (Fig. 4F), long pedicel, the presence of bulbils throughout the inflorescence vs. petiolate, ovate to narrowly ovate leaves, presence of inflorescence bracts and bracteole, yellow to orange flowers, and obcuneate labellum with cornicula.

Description. Terrestrial herbs, 100–160 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non tuberulous, creamish white. Leafy shoot with 9–12 leaves; sheath ligulate, ligule 3 mm long, bilobed, margin densely pubescent; lamina 25–32 × 6–10 cm, sessile, oblong–narrowly ovate, base rounded, apex caudate, margin entire, adaxially pubescent along veins and margins, abaxially densely pubescent. Inflorescence terminal to the leafy shoot, 25–53 cm long, erect; peduncle 18–23 mm long, light green, glabrous; rachis, dark green, glabrous, with white dots, bracts and bracteole absent. Ebracteate cincinni 25–51, flowers maturing from base to apex of inflorescence, each cincinni with 2–3 flowers. Floral pedicel for basal flowers 2.2–2.7 cm long, for terminal flowers 0.4–0.6 cm long, dark green, white dotted, glabrous. Flowers 4.2–4.9 cm long, orange, recurved; calyx 9–10 mm long, pale yellow with maroon patches; floral tube 1.5–1.8 cm long, dark orangish red, densely pubescent, curved upwards holding the flower upright; dorsal corolla lobe 8–9 × 3–4 mm, ovate, apex cucullate, dark maroon with orange tip, densely pubescent; lateral corolla lobes 7–8 × 5–5.5 mm, ovate, apex acute, dark maroon with orange apex, glabrous; labellum 1.3 × 0.6–0.8 cm, cordate, corniculate, orange, linear structures scattered on ventral surface; lateral staminodes 9–10 × 3–4 mm, narrowly ovate, apex attenuate, orange, glabrous. Stamen 2.1–2.4 cm long, filament 1.5–1.8 cm long, orange tinged red, glabrous,

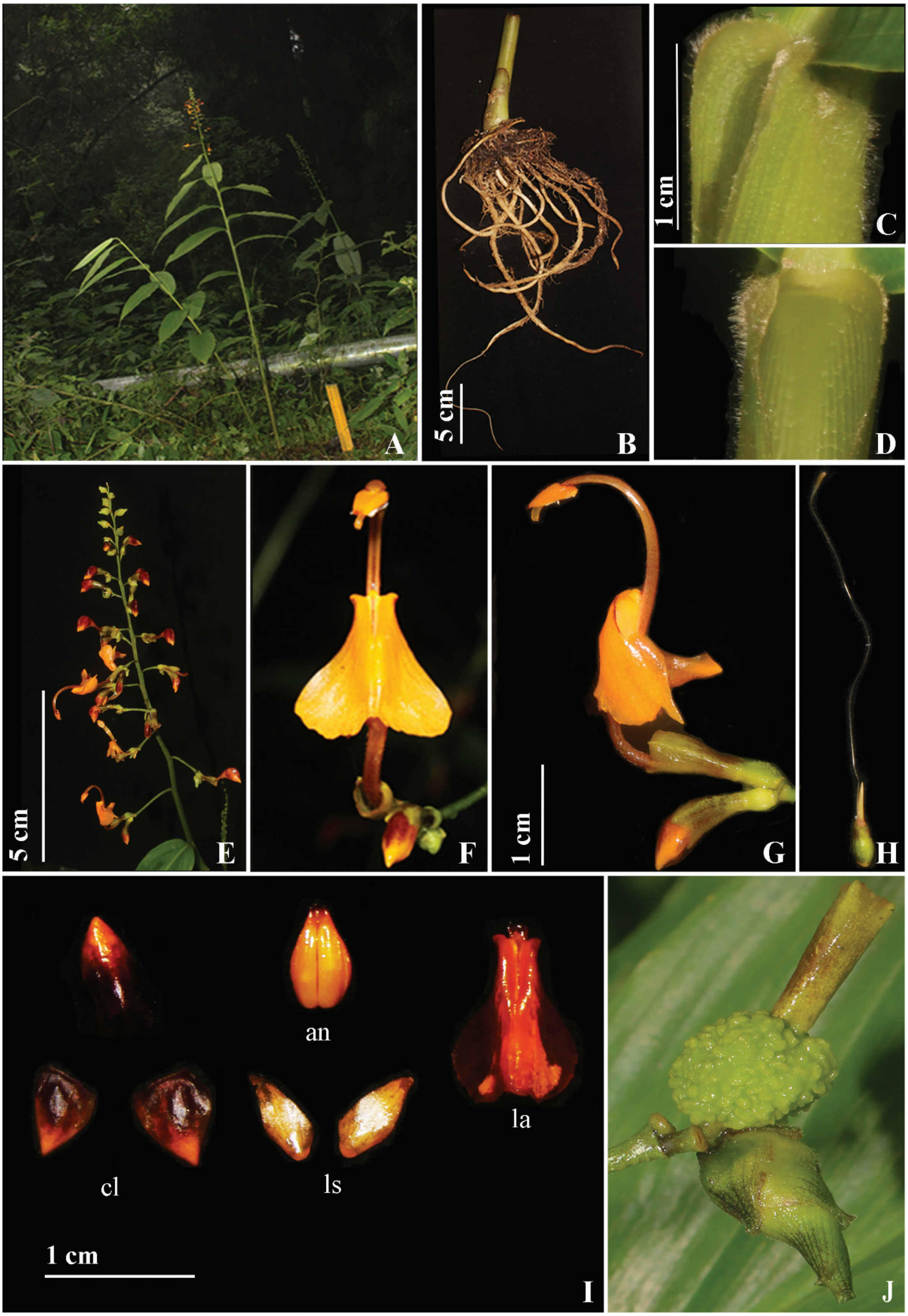

Figure 4. *Globba corniculata* sp. nov. **A** habit **B** rhizome **C, D** ligule **E** inflorescence **F** flower (front view) **G** flower (side view) **H** gynoecium **I** dissected flower, cl (corolla lobes), an (anther), ls (lateral staminodes), la (labellum) **J** fruit. Photographs by Y. Ritu.

fulvous with red dots, arching; anther 5–6 mm long, ovate, apex acute, orange tinged red, crest 0.8–0.9 mm long, non-appendaged; style 4.3–4.8 cm, filiform, apex broader than base, stigma 4–5 mm long, cylindrical, apex ciliate. Ovary 0.4–0.5 × 0.3 cm, obovate, pale green, verrucose; epigynous glands 2, 0.4–0.5 cm long, linear, cream. Fruit 1.5 cm in diameter, globose, green, verrucose, calyx persistent. Bulbils 1.2–2 × 0.5–0.8 cm, narrowly ovoid, yellowish green with dark maroon lines, pubescent, bulbils often at the base within a cincinni, but present throughout the inflorescence.

Distribution and ecology. At present, *G. corniculata* is known only from the Takdah Forest in West Bengal, which is a tropical evergreen, lower montane forest at an elevation of ca. 1220 m. It is terrestrial, mostly growing in open habitats along the edge of roads. The current location has ca. 70 individuals within an area of ca. 400 m^2. Other sympatric ginger species were *G. racemosa* and *Hedychium spicatum* Sm. We have observed several species of bees and butterflies visiting the flowers of this species.

Phenology. Flowering and fruiting were observed in the month of August.

Etymology. The species epithet ‘corniculata’ refers to the presence of horn-shaped structure at the base of labellum.

Informal conservation status. *G. corniculata* is known only from one population, which is a protected area with limited or no anthropogenic disturbance. The population was spread across 2–3 km along the edge of the road, where we counted 1500–2000 individuals. We surveyed six potential locations in Darjeeling, which is 50 km^2 around the type locality (Takdah forest) and could not locate any population in northern West Bengal. Based on the IUCN (2022) guidelines, we hypothesize that if a formal conservation assessment were performed, its conservation status would probably be Critically Endangered according to criteria B1. (a) (B1: extent of occurrence is less than 100 km^2, a: = 1 location).

Specimens of allied species examined. *G. ruiliensis*: China. Yunnan Province: Ruili City, Nongdao Town, Dengga village, 23.95 N, 97.55 E, elevation 854 m, 21 October 2019, *Jian-Yong Shen, Wen-Guang Wang & Xing-Da Ma 1666* (holotype: HITBC!)

***G. multiflora*: India. Sikkim**: Regio Trop, (PL0092 1837), (P01743164). **Assam**: Khasia Hills (L0487990), Khasi Hills, Nambar Forest, 3 July 1949, elevation 91.44 m, *F. Kingdon-Ward 18619* (NY02650821), *Jenkins F Jenkins, F s.n.* (L0487989).

Taxonomic notes. The new species is similar to the two species in flower color and presence of cornicula at the base of the labellum. The new species differs from *G. ruiliensis* in its large inflorescence 25–53 cm (vs. 10–35 cm), short peduncle 1.8–2.3 cm (vs. 3–15 cm), glabrous rachis (vs. hirsute) and absence of inflorescence bracts (vs. present). The new species differs from *G. multiflora* in its large lateral staminodes 9–10 mm (vs. 3–4 mm), length of lateral staminodes equal to corolla lobes (vs. shorter than corolla lobes), and production of bulbils throughout the inflorescence (vs. only at the lower portion of inflorescence). The detailed morphological comparisons between *G. corniculata* and *G. ruiliensis*, *G. multiflora* are presented in Table 1.

Notes. *G. ruiliensis* is distributed in Yunnan province, China and *G. multiflora* is distributed in Meghalaya, Assam, and Sikkim states, India and Bangladesh (Fig. 5).

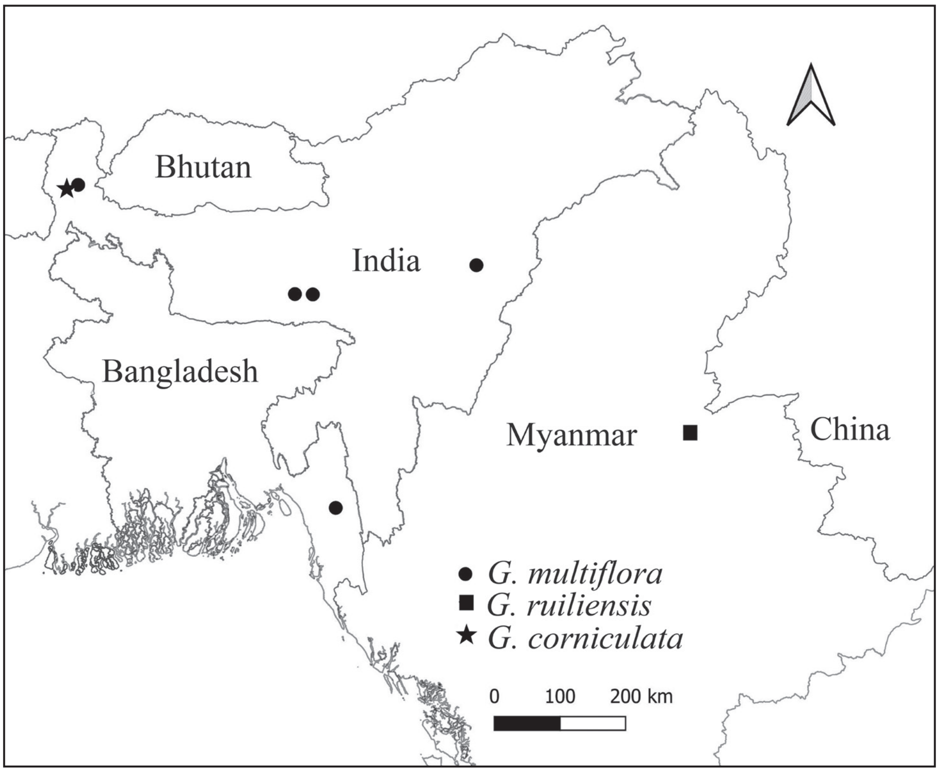

Figure 5. Map showing the distribution of *G. multiflora*, *G. ruiliensis*, *and G. corniculata* sp. nov.

Table 1. Comparison of morphological characteristics of *G. corniculata* sp. nov. with *G. ruiliensis* and *G. multiflora*. Characters not described in the original protologue or in subsequent descriptions of the same species are alternatively marked as not known.

Characters	***G. corniculata*** **Y.Ritu & V.Gowda**	***G. ruiliensis*** **X.D.Ma, W.G.Wang & J.Y.Shen (Ma et al. 2021)**	***G. multiflora*** **Wall. (Alfred et al. 2019, Lal and Verma 1987)**
Ligule length (mm) and indumentum	3, densely pubescent	2, margin ciliate	1–1.6, pubescent
Lamina	Sessile	Subsessile or shortly petiolate	Sessile
Peduncle length (cm) and indumentum	1.8–2.3, glabrous	3–15, hirsute	4.9–5.6, densely pubescent
Inflorescence length (cm) and orientation	25–53, erect	10–35, erect	9.5–25, erect
Rachis indumentum	Glabrous	Hirsute	Not known
Inflorescence bracts	Absent	Present	Absent
Calyx length (mm)	9–10	7–9	8–9
Flower color	Orange	Yellow to orange	Orange
Labellum dimensions (mm) and shape	13 × 6–8, cordate	Not known, obcuneate	8–10, obcuneate
Labellum color	Orange	Yellow to orange	Saffron yellow with two red blotches
Lateral staminode dimensions (mm) and shape	9–10 × 3–4, ovate, apex attenuate	7–8 × 3–4, ovate-oblong, apex rounded	3–4 × 1.5–2, ovate-narrowly ovate, apex acute
Length of lateral staminodes with respect to corolla lobes	Nearly equal to corolla lobes	Nearly equal to corolla lobes	Shorter than (half the length) to corolla lobes
Filament length (cm)	1.5–1.8	1.2–1.7	1.5–1.7
Anther length (mm) and shape	5–6, ovate, apex acute	3–4, elliptic, apex acute	4, narrowly ovate, apex capitate
Anther crest length (mm)	0.8–0.9	Not known	Minutely crested
Ovary dimensions (mm) and shape	3.7–4.5 × 2.6–3, obovoid	4–5 × 2.5, oblong	3
Bulbil position	Throughout the inflorescence	2–4 at the lower part of inflorescence	3–5 at the lower part of inflorescences

***Globba paschimbengalensis* Y.Ritu & V.Gowda, sp. nov.**

urn:lsid:ipni.org:names:77347882-1
Fig. 6

Type. India. West Bengal: Darjeeling district, Latpuncher, 26.9159, 88.4028, elevation 1200 m, 26 August 2022, *Y. Ritu, S. Goray VG2022WB3852* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *G. paschimbengalensis* is morphologically similar to *G. andersonii* but differs in having off-white flowers with a faint tinge of yellow, deeply notched ligule with unequal lobes (Fig. 6C) reduced or no peduncle vs. white flowers, ligule with equal lobes and with peduncle.

Description. Lithophyte herbs, 50–70 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non-tuberulous, creamish-white. Leafy shoot with 10–12 leaves; sheath ligulate, ligule 0.9–1.1 cm long, bilobed, lobes unequal, margin minutely pubescent; lamina 24–30 × 4–8 cm, sessile, narrowly ovate, base obtuse, apex caudate, margin entire, adaxially pubescent along veins and margins, abaxially glabrous, veins prominent. Inflorescence terminal to the leafy shoot, 8–12 cm long, erect; peduncle absent or reduced; rachis, dark maroon at the base and terminally light green, densely pubescent; bracts 1.6–1.7 × 1.4–1.5 mm, obovoid, pale yellow, pubescent adaxially, glabrous abaxially, persistent; bracteole 5.5–8.3 × 1.9–7.3 mm, ovoid, pale yellow, glabrous. Cincinni 7–10 per inflorescence, each cincinni with 2–5 flowers. Floral pedicel for basal flowers 2–2.5 cm long, for terminal flowers 0.2–0.4 cm, dark maroon, densely pubescent. Flowers 4.2–4.5 cm long, pale dull yellow, recurved; calyx 5–6 mm long, gray-green; floral tube 8.3–10 mm long, off-white tinged yellow, densely pubescent, curved upwards holding the flower upright; dorsal corolla lobe 5–6 × 2.4–2.5 mm, ovate, apex cucullate, off-white tinged green, sparsely pubescent; lateral corolla lobes 4.5–5 × 3–4 mm, ovate, apex acute, off-white tinged green, glabrous; labellum 9–10 × 2.4–2.5 mm, decurrent, sagittate, off-white with orange spot in center, glabrous, labellum notch with echinate structures; lateral staminodes 7.8–8.8 × 2.6–3.2 mm, narrowly ovate, apex acute, off-white tinged faintly yellow, glabrous. Stamen 2.4–2.5 cm long, filament 1.9–2 cm long, off-white tinged yellow, glabrous, arching; anther 4–5 mm long, largely ovate, off-white, crest 0.4 mm long, obtuse, non-appendaged; style filiform, apex broader than base, stigma 3–4 mm long, cylindrical, apex ciliate. Ovary 1.7 × 1.3 mm, ovoid, cream; epigynous glands 2, 1.2–1.2 mm, linear, cream. Fruit 1.5 cm in diameter, globose, greenish yellow, verrucose, calyx persistent. Bulbils absent.

Distribution and ecology. *G. paschimbengalensis* is recorded only from Latpuncher, Darjeeling district, West Bengal, where we observed ca. 30 individuals in an area of an estimated 400 m^2. *G. paschimbengalensis* is lithophytic, mostly growing along the edge of roads at an elevation of ca. 1200 m. We have observed bumblebees visiting the flowers of this species.

Phenology. Flowering and fruiting were observed in the month of August.

Etymology. The species epithet refers to the Indian state of West Bengal, where this species was found.

Informal conservation status. We have only found one population that was not in a protected area. The population was spread across a 20–25 m^2 area

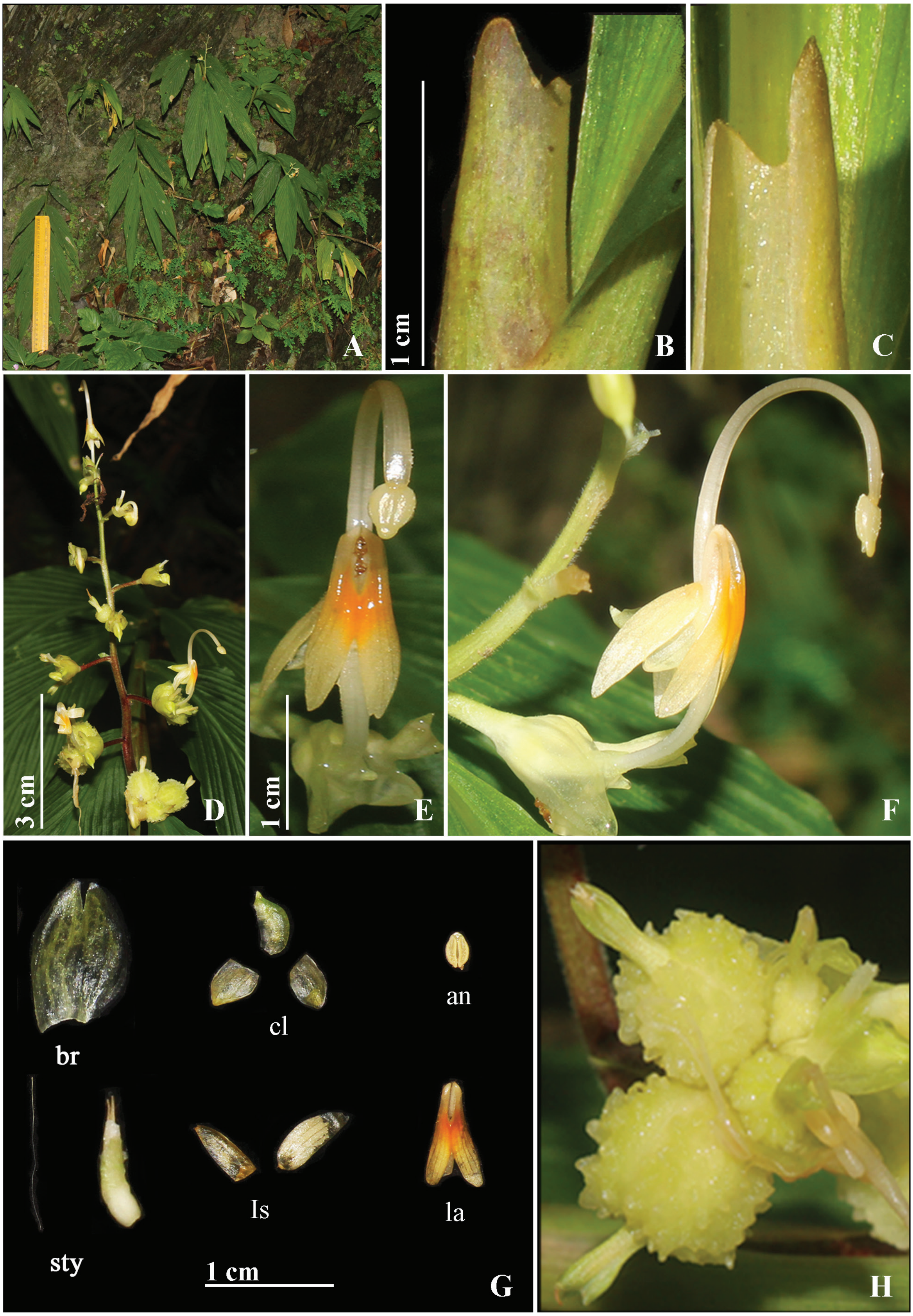

Figure 6. *Globba paschimbengalensis* sp. nov. **A** habit **B, C** ligule **D** inflorescence **E** flower (front view) **F** flower (side view) **G** dissected flower, br (bracteole), cl (corolla lobes), an (anther), sty (style with stigma, ovary and epigynous gland), ls (lateral staminodes), la (labellum) **H** fruit. Photographs by Y. Ritu.

with a total of 60–70 individuals only. We surveyed six potential locations in Darjeeling in a 40 km^2 area around the type locality (Latpuncher) and did not find any population in northern West Bengal. Based on the IUCN (2022) guidelines, we informally assess the status as Critically Endangered according to criteria B1. (a) (B1: extent of occurrence is less than 100 km^2, a: =1 location), and C. (C: fewer than 250 mature individuals).

Specimens of allied species examined. *G. andersonii*: India. West Bengal: Darjeeling Himalaya, around Baghpul, elevation 200–300 m, 6 July 2011, *S. Nirola & AP Das 1334A* (holotype: CAL!), Sivok Hill Forest, Near Coronation Bridge in the ghat region, 2 July 2011, *Sachin A. Punekar s.n.* (CALI!), elevation 914 m, 15 July 1913 (E00095574), Mongpoo, elevation 914.4 m, 12 July 1884, *Williams* (P00411420), Mongpoo, 914.4 m, 12 July 1884, *Williams* (P00252245), Darjeeling, Pankabari, elevation 762 m, July 1874, *J. S. Gamble 8130* (K000640559). **Sikkim**: elevation 305 m, 6 July 1915 (E00095573), Regio Trop (P00686468).

Taxonomic notes. The new species is similar to one species in inflorescence length, presence of inflorescence bracts, and absence of bulbils. This species differs from *G. andersonii* in having unequal lobes, deeply notched ligule (vs. equal lobes and slightly notched), absence of peduncle (vs. presence of peduncle), and large lateral staminodes 7.8–8.8 mm (vs. 5–6 mm). The detailed morphological comparisons between *G. paschimbengalensis and G. andersonii* are presented in Table 2.

Table 2. Comparison of morphological characteristics of *G. paschimbengalensis* sp. nov. and *G. polymorpha* sp. nov. with *G. andersonii*. Characters not described in the original protologue or in subsequent descriptions of the same species are alternatively marked as not known.

Characters	***G. paschimbengalensis* Y.Ritu & V.Gowda**	***G. polymorpha* Y.Ritu & V.Gowda**	***G. andersonii* C.B.Clarke ex Baker (according to Nirola and Das 2015, Thachat et al. 2020)**
Ligule length (mm) and indumentum	0.9–1.1, minutely pubescent, unequal lobes, deeply notched	1.5–1.8, densely pubescent, deeply notched at center	0.8–1.2, pubescent externally, entire, slightly notched at center
Lamina	Sessile	Sessile	Sessile
Peduncle length (cm) and indumentum	Absent	1.56, densely pubescent	Densely pubescent
Inflorescence length (cm)	8–12	7.5–16	8–16
Bract dimensions (mm), shape, and color	1.6–1.7 × 1.4–1.5, obovate, pale green	4.6–9.2 × 2.2–3.4, elliptic, olive green with brown tinge	5–6 × 1.5–2, narrowly ovate, pale green
Calyx length (mm) and color	5–6, gray green	4–5, maroon	5–6, greenish
Flower color	Off-white with a hint of yellow	Pale dull yellow	White
Lateral staminode dimensions (mm) and shape	7.8–8.8 × 2.6–3.2, narrowly ovate	6–6.5 × 2–2.5, narrowly ovate	5–6 × 2, narrowly ovate
Length of lateral staminodes with respect to corolla lobes	Longer than corolla lobes	Slightly longer than corolla lobes	Slightly longer than corolla lobes
Filament length (cm) and color	1.9–2, off-white with a hint of yellow	1.6–1.8, off white with a hint of yellow	1.5–1.8, white
Anther length (mm) and color	4–5, gray green	2.5–3, pale yellow	1.5 × 1, white
Anther crest length (mm)	0.4	0.3	Not known
Ovary dimensions (mm)	1.7 × 1.3	2.9 × 1.7	3 × 2
Bulbil	Absent	Absent	Absent

Globba polymorpha **Y.Ritu & V.Gowda, sp. nov.**

urn:lsid:ipni.org:names:77347883-1
Fig. 7

Type. India. West Bengal: Darjeeling district, Pankhabari, 26.8326, 88.2662, elevation 600 m, 6 September 2022, *Y. Ritu, & P. A. Shangreiphao VG2022WB3906* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *G. polymorpha* is morphologically similar to *G. andersonii* but differs in having pale yellow flower, densely pubescent ligule with long white hairs (Fig. 7C), red or green-colored bracteole, large anther (4–5 mm) vs. white flowers, ligule pubescent externally, white color bracteole and small anther (1.5 mm).

Description. Lithophytic herbs, 42–68 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non-tuberulous, creamish white. Leafy shoot with 6–12 leaves; sheath ligulate, ligule 1.5–1.8 cm long, bilobed, densely pubescent; lamina 22–28 × 5–9 cm, sessile, narrowly ovate, base attenuate, apex caudate, margin entire, adaxially pubescent along veins and margins, abaxially pubescent. Inflorescence terminal to the leafy shoot, 7.5–16 cm long, erect; peduncle 1.5 cm long, green with red dots to dark maroon, densely pubescent; rachis, green with red to dark maroon spots, densely pubescent; bracts 4.7–9.2 × 2.2–3.4 mm, elliptic, olive green with brown tinge, glabrous; bracteole 6.4–8.7 × 2.9–4.7 mm, obovoid to ovoid, brown with purple tinge, glabrous. Cincinni 7–17, each cincinni with 4–6 flowers. Floral pedicel for basal flowers 1.2–1.4 cm long, for terminal flowers 0.6–0.8 cm long, dark maroon, sparsely pubescent. Flowers 4–4.5 cm long, pale dull yellow, recurved; calyx 4–5 mm long, maroon; floral tube 8–9.3 mm long, pale yellow tinged pink, densely pubescent, curved upwards holding the flower upright; dorsal corolla lobe 5–6 × 2.5 mm, ovate, apex cucullate, light maroon, pubescent; lateral corolla lobes 3–3.5 mm × 2.2 mm, ovate, apex acute, yellow tinged maroon, pubescent; labellum 7–8 × 1.5–1.8 mm, decurrent, linear, pale dull yellow, glabrous, labellum notch with echinate structures; lateral staminodes 6–6.5 × 2–2.5 mm, narrowly ovate, apex acute, pale dull yellow, glabrous. Stamen 1.9–2.1 cm long, filament 1.6–1.8 cm long, off-white tinged yellow, glabrous, arching; anther 2.5–3 mm long, largely ovate, apex attenuate, pale yellow, crest 0.3 mm long, non-appendaged; style, filiform, stigma 4–5 mm wide, funnel-shaped, apex ciliate. Ovary 2.9 × 1.7 mm, ovoid, maroon, verrucose; epigynous glands 2, 1.2–1.3 mm, linear, cream. Fruit 1.5 cm in diameter, globose, greenish yellow, verrucose, calyx persistent. Bulbils absent.

Distribution and ecology. *G. polymorpha* is recorded only from Pankhabari, Darjeeling district, West Bengal. At Pankhabari, we have observed ca. 21 individuals in a ca. 400 m^2 area. *G. polymorpha* is lithophytic, mostly growing along the edge of roads at an elevation of ca. 600 m. We observed floral color polymorphism in this species, with red bracteole and yellow bracteole individuals growing within the same population. We have observed different species of bees and butterflies visiting the flowers of this species.

Phenology. Flowering and fruiting were observed in the month of September.

Etymology. The species epithet refers to the floral color variation due to bracteole color variations among individuals within the same population, which can be seen in Fig. 7A (top left and bottom left).

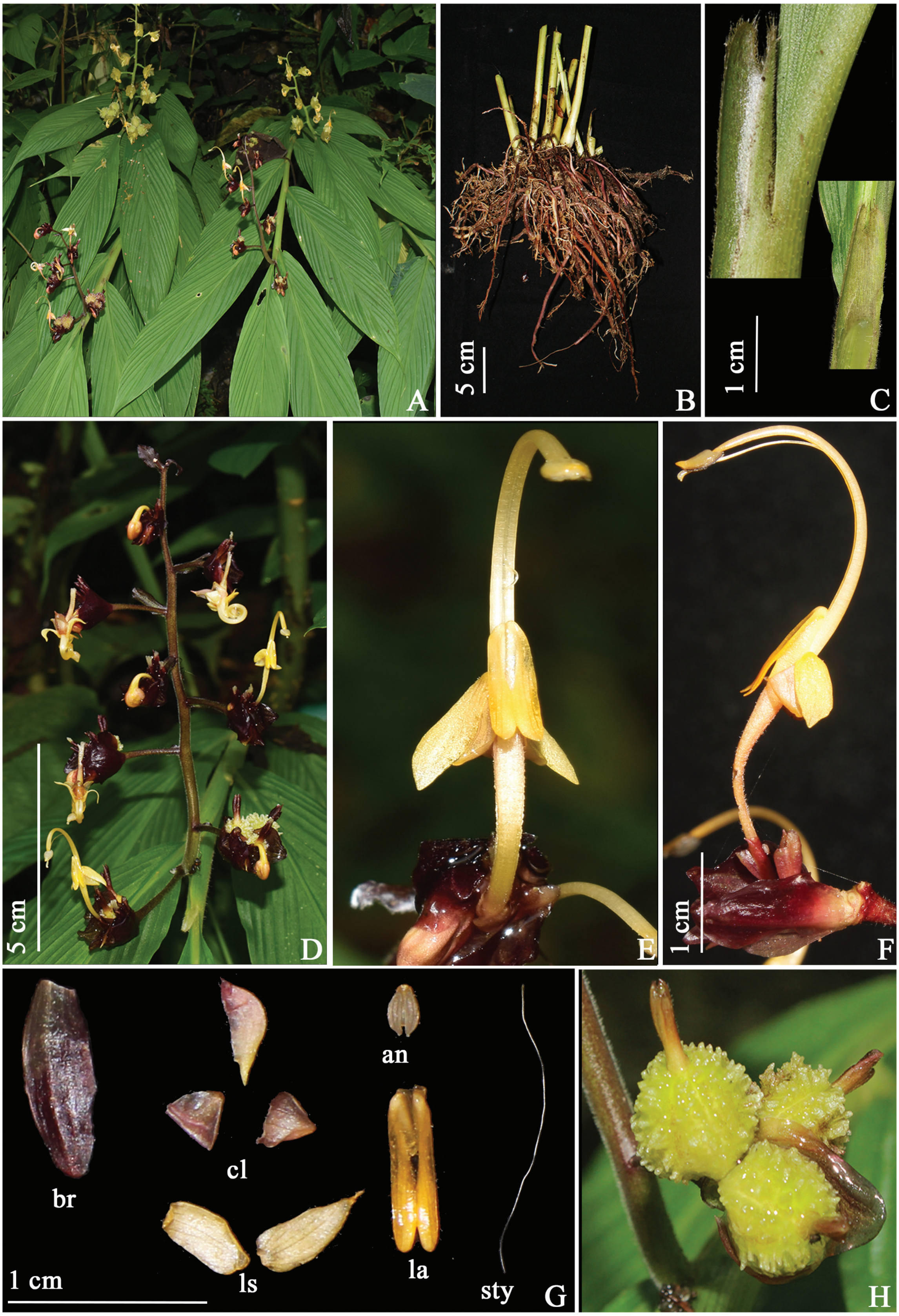

Figure 7. *Globba polymorpha* sp. nov. **A** habit **B** rhizome **C** ligule **D** inflorescence **E** flower (front view) **F** flower (side view) **G** dissected flower, br (bracteole), cl (corolla lobes), an (anther), ls (lateral staminodes), la (labellum), sty (style and stigma) **H** fruit. Photographs **A, D** and **E** by Rhuthuparna SB, rest by Y. Ritu.

Informal conservation status. *G. polymorpha* is known from only one population, which was not a protected habitat or area. The population was spread across a 10–15 m long stretch along the roadside with 20–25 individuals. We surveyed six potential locations in the Darjeeling district, which is 40 km^2 around the type locality (Pankhabari), and we did not locate any population in northern West Bengal. Based on the IUCN (2022) guidelines and a formal conservation assessment based on the known distribution and number of individuals present, we propose its conservation status to be critically endangered according to criteria B1. (a) (B1: extent of occurrence is less than 100 km^2, a: =1 location), and D. (D: number of mature individuals <50). In 2022, we observed 20–25 individuals at the type location, most of which were cleared for road extension, which led to a decrease in the number (10) of individuals, suggesting that the species is at risk of extinction.

Specimens of allied species examined. *G. andersonii*: India. West Bengal: Darjeeling Himalaya, around Baghpul, elevation 200–300 m, 6 July 2011, *S. Nirola & AP Das 1334A* (holotype: CAL!), Sivok Hill Forest, Near Coronation Bridge in the ghat region, 2 July 2011, *Sachin A. Punekar* s.n. (CALI!), elevation 914 m, 15 July 1913 (E00095574), Mongpoo, elevation 914.4 m, 12 July 1884, *Williams* (P00411420), Mongpoo, elevation 914.4 m, 12 July 1884, *Williams* (P00252245), Darjeeling, Pankabari, elevation 762 m, July 1874, *J. S. Gamble 8130* (K000640559). **Sikkim**: elevation 305 m, 6 July 1915 (E00095573), Regio Trop (P00686468).

Taxonomic notes. The new species is similar to one species in inflorescence height, sessile leaves, densely pubescent peduncle, and absence of bulbils. This species differs from *G. andersonii* in its large ligule 1.5–1.8 mm (vs. 0.8–1.2 mm), pale dull yellow flowers (vs. white), and large anther 2.5–3 mm (vs. 1.5 mm). Detailed morphological comparisons between *G. polymorpha* and *G. andersonii* are presented in Table 2.

Notes. *G. andersonii* is distributed to West Bengal, India (Fig. 8).

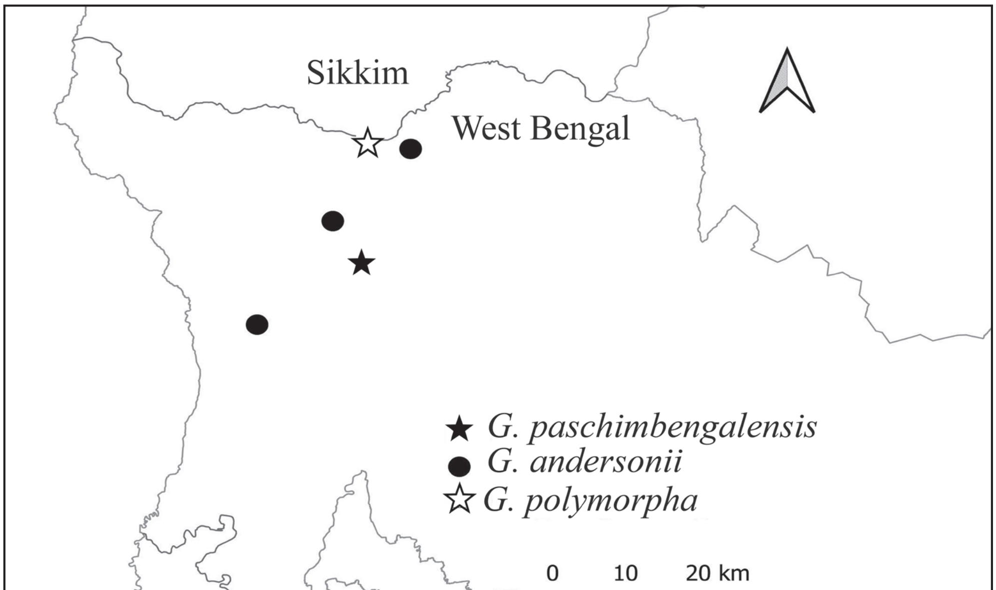

Figure 8. Map showing the distribution of *G. paschimbengalensis*, *G. andersonii*, *and G. polymorpha* sp. nov.

Globba tyrnaensis **Y.Ritu & V.Gowda, sp. nov.**

urn:lsid:ipni.org:names:77347884-1
Fig. 9

Type. **India. Meghalaya:** East Khasi Hills district, Tyrna village, Double decker bridge, 25.2513, 91.672, elevation 731 m, 25 July 2022, *Y. Ritu VG2022WB3725* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *G. tyrnaensis* is morphologically similar to *G. orixensis and G. macroclada* but different in having short inflorescence, absence of inflorescence bracts, petiolate lamina, short filament, large anther (Fig. 9) vs. large inflorescence, presence of inflorescence bracts, sessile lamina, large filament and small anther.

Description. Terrestrial herbs, 32–59 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non-tuberulous, creamish-white. Leafy shoot with 6–11 leaves; sheath ligulate, ligule 3 mm long, bilobed, translucent margin and green in center, turns papery when dry, pubescent; lamina 13–18 × 2.8–3.2 cm, subsessile, petiole 0.5 cm, green with cream color stripes, glabrous, narrowly ovate, base obtuse, apex caudate, margin entire, glabrous. Inflorescence terminal to the leafy shoot, 3–8 cm long, erect; peduncle 18 mm long, light green with maroon dots, glabrous; rachis, green with maroon patches, glabrous, bracts and bracteoles absent. Ebracteate cincinni 5–16, each cincinni with 2–3 flowers. Floral pedicel 0.15–0.5 cm, light green, glabrous. Flowers 3–3.9 cm long, orange, recurved; calyx 8–9 mm long, yellowish orange; floral tube 1.2–1.3 mm long, dull orangish red, densely pubescent, bent upwards holding the flower upright; dorsal corolla lobe 5.2–5.5 × 2.3–3.2 mm, ovate, apex cucullate, orange, glabrous; lateral corolla lobes 5.7 × 3.3 mm, ovate, apex acute, yellow, glabrous; labellum 7 × 5 mm, corniculate, ovate, orange in center with lighter orange margin, labellum notch with echinate structures, cornicula 0.2–0.3 mm in length, glabrous; lateral staminodes 4.7–4.8 × 2.7 mm, narrowly ovate, apex acute, orange, hairs on margin. Stamen 2.1 cm long; filament 1.8 cm long, orange, glabrous, arching; anther 3.7 mm long, ovate, apex truncate, orange, crest 0.7–0.8 mm long, non-appendaged; style filiform, apex broader than the base, stigma 4–5 mm, cylindrical, apex ciliate. Ovary 3.1–3.6 × 2.5 mm, obovate, yellow, verrucose, epigynous glands 2, 0.3 cm long, linear, cream. Fruit 1.2 cm in diameter, globose, green, verrucose, calyx persistent. Bulbils 1.2–2 × 0.5–0.8 cm, ovoid, light green to light yellow, pubescent, bulbils present in the inflorescence and axil of leaves.

Distribution and ecology. At present, we have seen *G. tyrnaensis* in the Double decker bridge, Tyrna village, and Thangkharang Park, Cherrapunji, Meghalaya. We have observed 150–200 individuals in Tyrna village and 10–15 individuals in Thangkharang Park, and the overall area of these two populations is ca. 400 m^2 each. *G. tyrnaensis* is terrestrial mostly growing in understory habitats inside forests at an elevation of ca. 731 m. We have observed different species of bees visiting the flowers of this species.

Phenology. Flowering and fruiting were observed in the month of July.

Etymology. The species epithet refers to the type locality for this species, which is at the Tyrna village, Cherrapunji, Meghalaya.

Informal conservation status. We have documented *G. tyrnaensis* from two populations within the state of Meghalaya: at Double decker bridge (Cherrapunji district) and near Thangkharang Park (Cherrapunji district). Both populations were in community-protected areas with limited anthropogenic disturbance. The first

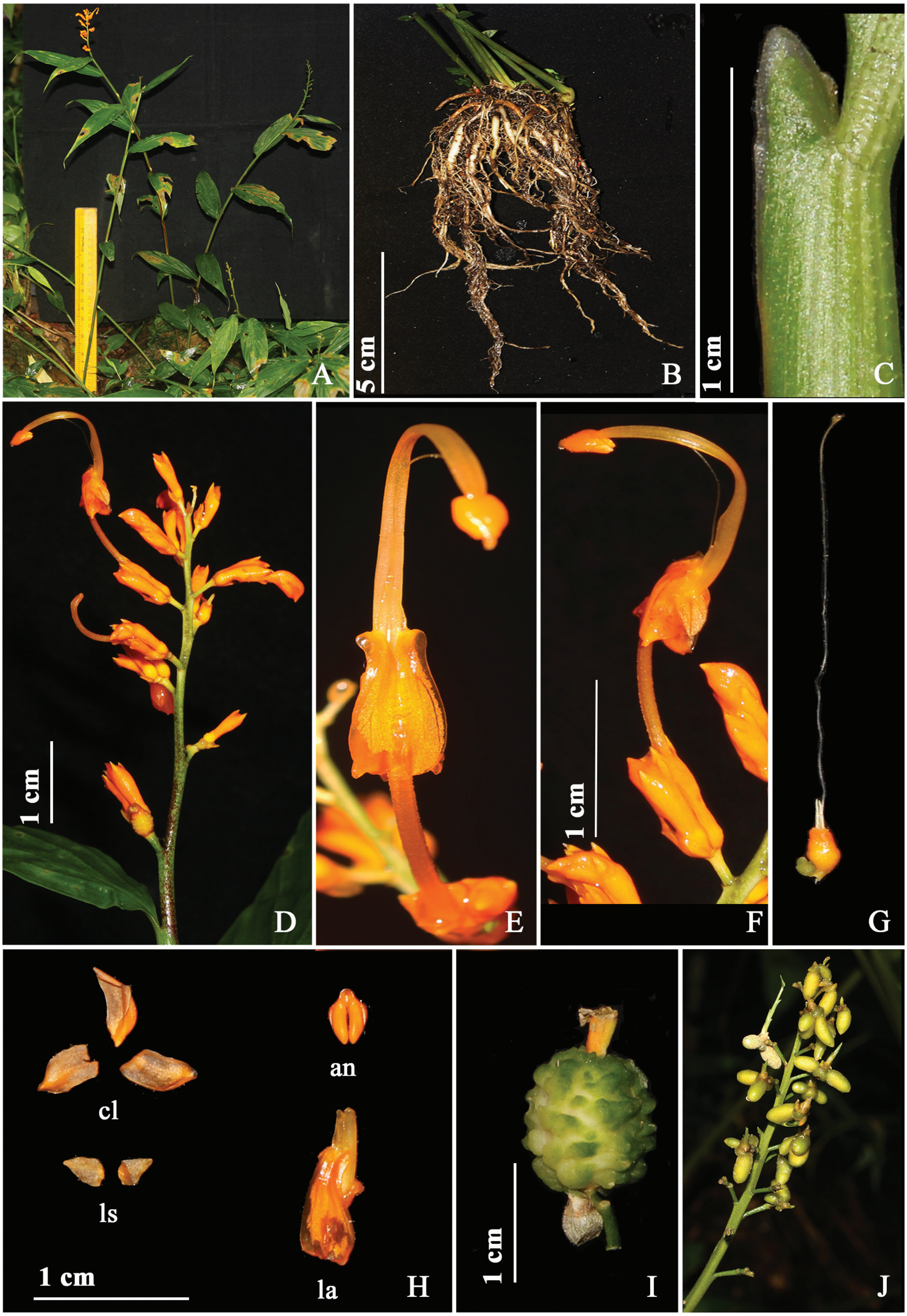

Figure 9. *Globba tyrnaensis* sp. nov. **A** habit **B** rhizome **C** ligule **D** inflorescence **E** flower (front view) **F** flower (side view) **G** gynoecium **H** dissected flower, cl (corolla lobes), an (anther), ls (lateral staminodes), la (labellum) **I** fruit **J** Bulbils. Photographs by Y. Ritu.

population was spread across 20–30 km along the edge of the road, where 300–400 individuals were counted. The second population was spread across 5–6 km with 10–15 individuals. We surveyed seven potential locations in Meghalaya, which accounts to ~50 km^2 around the type locality (Double decker bridge), and we did not locate any other population of this species in this region. Based on the IUCN (2022) guidelines and observed population sizes and area of occupancy, we propose the conservation status of *G. tyrnaensis* to be Endangered according to criteria B1. (a) (B1: extent of occurrence is less than 100 km^2, a: less than or equal to 5 locations).

Specimens of allied species examined. *G. orixensis*: India. Assam: Barak valley, Cachar district, Kumbhirgram, 21 July 2009, Coll.: *D. Bhattacharyya 2501*, Fl. & Fr.; Dargakona, Assam University Silchar Campus, behind Life Science and Bioinformatics Department, along the trek path to ecoforest, 24.6870 N & 92.7521E, 13 July 2010, Coll.: Fl. (Herbarium of Department of Life Science & Bioinformatics, Assam University, Silchar), *L. Darlong & D. Bhattacharyya 10063*,

28 May 1808 (E00095817), 13 June 1920 (E00095807), (E00097427), elevation 610 m, 31 May 1882 (E00097430), 13 June 1920 (E00095807), elevation 610 m, 31 May 1882 (E00097430), 28 May 1808 (E00095817), 28 May 1809 (E00095821), (E00095820), (E00097427), (E00095812), 25.583 N, 91.633 E (L0487999), *Wallich N* (L0487998), Nayagarh, 5 August 1936, *H. F. Mooney 528* (L0487991). **Odisha**: Keonjhar, *H. F. Moooney 152* (L0488000). **Meghalaya**: Khasia, Regio Trop, *Hooker J. D.* (L0488002), Regio Trop, 28 September 2001, *Hooker J. D*. (P01743148) Hort Bot. Calcutta et Serampore, *Voigt, J.O. 101* (P00252266), East Himalaya, *5634* (P01743147). **Myanmar.** 13 August 1908 (E00097420), elevation 137 m, 13 August 1909 (E00097421), 13 August 1908 (E00097420), Sagaing Division, *W. J. Kress 2-7123* (US00605376). **Bangladesh.** Elevation 40 m, 3 September 1999 (E00189266), 22.695 N, 92.237 E, elevation 40 m, 5 September 1999 (E00189267), Sreemangal, Lawachera forest, 24.25 N, 91.583 E, 8 May 1997, *Williams K J* (L0413463)

***G. macroclada*: India.** *Wallichn 6411* (L0487998), **Assam**: Khasia, 25.583 N, 91.633 E, 5 August 1936, *Tea Deputation Tea Deputation s. n.* (L0487999), Nayagarh, 8 May 1997, *Mooney H. F. 528* (L0487991). **Sikkim**: East Himalaya, *Griffith W 5639* (L0041113), *Herb. Watt 8702* (E00095812), (E00097427), *6536G* (E00095820), 28 May 1808, 7 (E00095821), elevation 610 m, 31 May 1882, *6931* (E00097430), 13 June 1920, 277 (E00095807), Khasia, *Hooker J. D.* (P01743148), East Himalaya, *Herb. Griffith 5634* (P01743147), Hort. Bot. Calcutta et Serampore, *Voigt, J. O. 101* (P00252266), East Himalaya, 12 July 1884, *Griffith, W. 5639* (P032726), Mogpoo, Silake, elevation 3000 m, 12 July 1884, s.c.|Boissier, P.E. (P00686490), Silake, elevation 609.6 m, *Buissier, P. E.* (P00686489). **Bangladesh.** 24.25, 91.583, elevation 35 m, 1 March 1971, *Huq AM; Mia MK* (L0413463), elevation 40 m, 3 September 1999, 972 (E00189266). **Myanmar.** 13 August 1908, elevation 137 m, 4195 (E00097420). **Nepal.** 26.816 N, 87.3 E, elevation 500 m, 13 August 1972, *1427* (E00500193). **United States of America. Maryland**: NMNH Botany Research Greenhouses. Suitland, 28 September 2001, *W. J. Kress & M. Bordelon 02-7123* (US3432988).

Taxonomic notes. The new species is similar to two species in flower color, and absence of anther appendages. This species is different from *G. orixensis* in its petiolate leaves 0.5 mm (vs. subsessile), absence of inflorescence bracts (vs. present), short filament 1.8 cm (vs. 2.4 cm), and large anther 3.7 mm (vs. 2 mm). The species is different from *G. macroclada* in its petiolate leaves (vs. sessile), short inflorescence 3–8 cm (vs. 15 cm), and

Table 3. Comparison of morphological characteristics of *G. tyrnaensis* sp. nov. and *G. janakiae* sp. nov. with their two closely related taxa. Characters not described in the original protologue or in subsequent descriptions of the same species are alternatively marked as not known.

Characters	***G. tyrnaensis*** **Y.Ritu & V.Gowda**	***G. janakiae*** **Y.Ritu & V.Gowda**	***G. orixensis*** **Roxb. (according to Darlong and Bhattacharyya 2011)**	***G macroclada*** **Gagnep.**
Ligule length (mm)	3	1	1–3	2–3
Petiole (cm)	0.5	0.3	Subsessile	Sessile
Peduncle length (mm)	18	12	Not known	Not known
Inflorescence length (cm)	3–8	4–6	6.5	15
Rachis color and indumentum	Green, glabrous	Green, glabrous	Not known	Not known
Bract dimensions (mm) and color	Absent	Absent	Narrowly ovate, 5–7 × 2–3, acute at apex	Narrowly ovate, white or yellowish
Calyx length (mm)	8–9	8–9	5–10	8
Flower color	Orange	Orange	Orange yellow	Yellow
Labellum base	Decurrent on filament	Decurrent on filament	Not known	Not known
Lateral staminode dimensions (mm) and shape	4.7–4.8, narrowly ovate	3.2, ovate	Narrowly ovate	Narrowly ovate
Length of lateral staminodes with respect to corolla lobes	Shorter than corolla lobes	Shorter than corolla lobes	Shorter than corolla lobes	Equal
Filament length (cm)	1.8, orange	2, white- orange	2.4, yellow	Not known
Anther length (mm)	3.7	3.8	2	6–7
Anther crest	Yes	Yes	Not known	Not known
Ovary dimensions (mm)	3.1–3.6	3.4	Not known	Not known
Epigynous glands length (mm)	3	4	Not known	4
Fruit shape	Globose	Not observed	Globose	Not observed
Bulbil	Present	Present	Present	Absent
Bulbils shape	Ovoid	Narrowly ovate	Not Known	Linear

absence of inflorescence bract (vs. present). The detailed morphological comparisons between *G. tyrnaensis* and *G. orixensis* are presented in Table 3.

Globba janakiae Y.Ritu & V.Gowda, sp. nov.

urn:lsid:ipni.org:names:77347885-1
Fig. 10

Type. **India. Meghalaya:** East Khasi Hills district, Tyrna village, Double decker bridge, 25.2513, 91.672, elevation 731 m, 25 July 2022, *Y. Ritu VG2022WB3727* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *G. janakiae* is morphologically similar to *G. orixensis* and *G. macroclada* but different in having short inflorescence, absence of inflorescence bracts, petiolate lamina, short filament, large anther, heart-shaped labellum with cornicula (Fig. 10F) vs. large inflorescence, presence of inflorescence bracts, sessile lamina, large filament, small anther, and labellum without cornicula.

Description. Terrestrial herbs, 40–46 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non-tuberulous, creamish-white. Leafy shoot with 8–10; sheath ligulate, ligule 1 mm long, bilobed, margin translucent and green in the center, pubescent; lamina 13 × 2.8 cm, subsessile, petiole 0.3 cm, green, glabrous, narrowly ovate, base obtuse, apex caudate, margin entire, glabrous. Inflorescence terminal to the leafy shoot, 4–6 cm

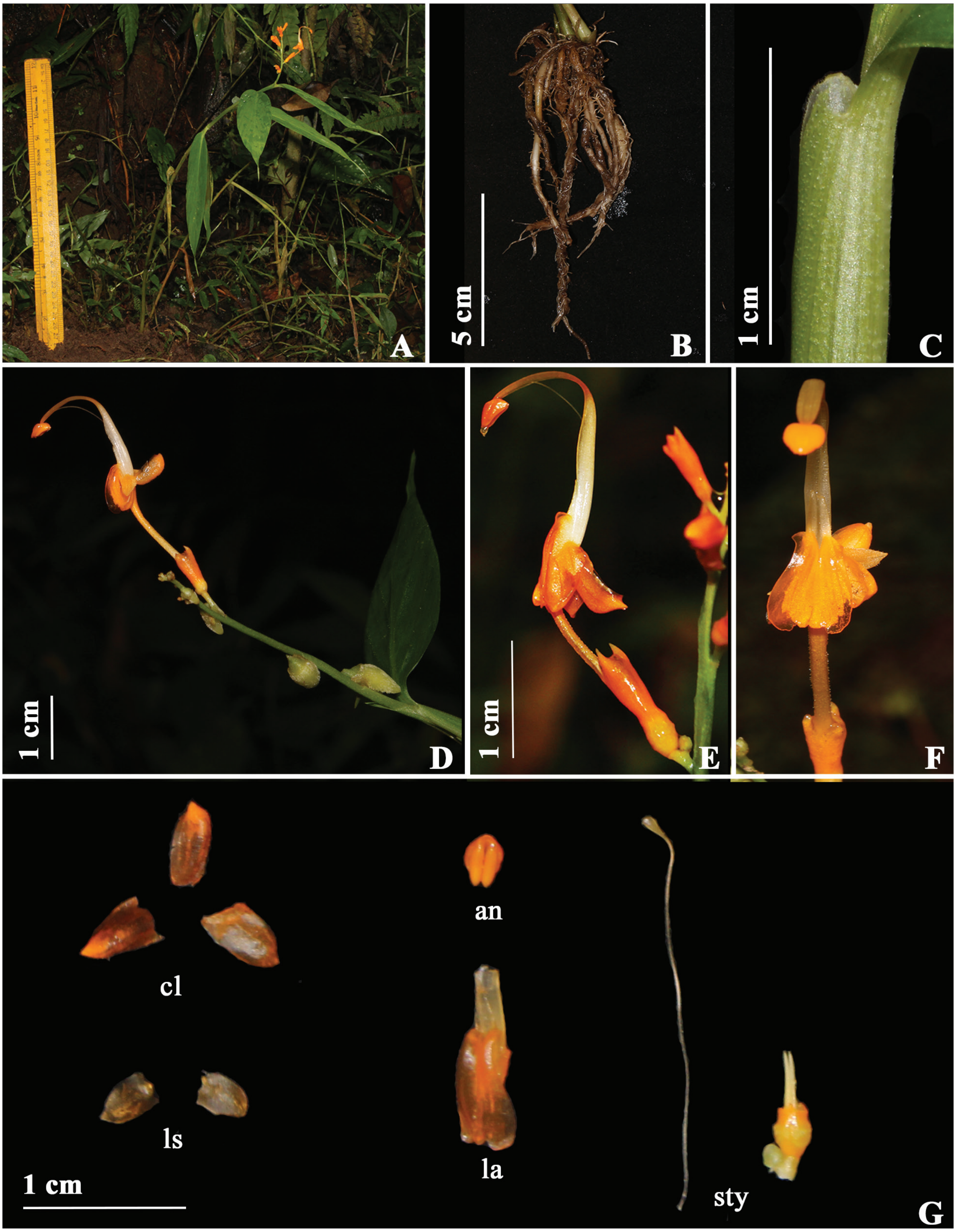

Figure 10. *Globba janakiae* sp. nov. **A** habit **B** rhizome **C** ligule **D** inflorescence **E** flower (side view) **F** flower (front view) **G** dissected flower, cl (corolla lobes), an (anther), ls (lateral staminodes), la (labellum), sty (style with stigma and ovary with epigynous glands). Photographs by Y. Ritu.

long, erect; peduncle 12 mm long, green, glabrous; rachis, green, glabrous, bracts and bracteole absent. Ebracteate cincinni 6–8, glabrous, each cincinni with 1–2 flowers. Floral pedicel 0.1–0.5 cm long, light green, glabrous. Flowers 3–3.9 cm long, orange, recurved; calyx 8–9 mm long, yellowish orange; floral tube 0.5–0.6 cm long, dull orangish red, densely pubescent, curved upwards holding the flower upright; dorsal corolla lobe 6.6–7 × 2.5–3 mm, ovate, orange, densely pubescent; lateral corolla lobes 5.4 × 3 mm, ovate, apex acute, dark maroon with orange apex, glabrous; labellum 8.6 × 3 mm, cordate, corniculate, orange in center with light orange margins, labellum notch texture echinate, cornicula 0.3 mm in length, glabrous lateral staminodes 3.2 × 2.5 mm, ovate, orange, glabrous. Stamen 2.3 cm long, filament 2 cm long, orange, glabrous, arching; anther 3.8 mm long, ovate, apex truncate orange, crest 0.2–0.3 mm long, non-appendaged; style, filiform; stigma 4–5 mm, cylindrical, apex ciliate. Ovary 3.4 × 2.4 mm, obovate, pale green, verrucose; epigynous glands 2, 0.4 cm long, linear, cream. Fruits - not observed. Bulbils 1.2–2 × 0.5–0.8 cm, narrowly ovate, light green to light yellow, pubescent, bulbils present in inflorescence and axil of leaves.

Distribution and ecology. At present, we have seen this species only in the Double decker bridge, Tyrna village, Cherrapunji, Meghalaya. We have observed 5–6 individuals in an overall area of ca. 400 m^2. This species is terrestrial, mostly growing in understory habitats inside forests with an elevation of ca. 731 m. We have observed different species of bees visiting the flowers of this species.

Phenology. Flowering was observed in the month of July.

Etymology. The species is named in honor of Dr. E. K. Janaki Ammal. She was a pioneering Indian woman botanist who challenged the norms of caste, gender and race. She was critical about deforestation carried out to make way for development projects and advocated preservation of native plants.

Informal conservation status. *Globba janakiae* is currently known from one population in Double decker bridge (Cherrapunji district) within the state of Meghalaya, wherein the population was spread across 2–3 km along the edge of the road and has approximately 5–6 individuals. We surveyed seven potential locations in Meghalaya, which is 50 km^2 around the type locality (Double decker bridge) and could not locate any population. Based on the IUCN (2022) guidelines, we hypothesize that if a formal conservation assessment were performed, its conservation status would probably be Critically Endangered according to criterias B1. (a) (B1: extent of occurrence is less than 100 km^2, a: = 1 location) and D. (D: number of mature individuals <50).

Specimens of allied species examined. *G. orixensis*: India. Assam: Barak Valley, Cachar district, Kumbhirgram, 21 July 2009, Coll.: *D. Bhattacharyya 2501*, Fl. & Fr.; Dargakona, Assam University Silchar Campus, behind Life Science and Bioinformatics Department, along the trek path to ecoforest, 24.6870 N & 92.7521E, 13 July 2010, Coll.: Fl. (Herbarium of Department of Life Science & Bioinformatics, Assam University, Silchar), *L. Darlong & D. Bhattacharyya 10063*, 28 May 1808 (E00095817), 13 June 1920 (E00095807), (E00097427), elevation 610 m, 31 May 1882 (E00097430), 13 June 1920 (E00095807), elevation 610 m, 31 May 1882 (E00097430), 28 May 1808 (E00095817), 28 May 1809 (E00095821), (E00095820), (E00097427), (E00095812), 25.583 N, 91.633 E (L0487999), *Wallich N* (L0487998), Nayagarh, 5 August 1936, *H. F. Mooney 528* (L0487991). **Odisha**: Keonjhar, *H. F. Moooney 152* (L0488000). **Meghalaya**:

Khasia, Regio Trop, *Hooker J. D.* (L0488002), Regio Trop, 28 September 2001, *Hooker J. D*. (P01743148) Hort Bot. Calcutta et Serampore, *Voigt, J.O. 101* (P00252266), East Himalaya, *5634* (P01743147). **Myanmar.** 13 August 1908 (E00097420), elevation 137 m, 13 August 1909 (E00097421), 13 August 1908 (E00097420), Sagaing Division, *W. J. Kress 2-7123* (US00605376). **Bangladesh.** Elevation 40 m, 3 September 1999 (E00189266), 22.695 N, 92.237 E, elevation 40 m, 5 September 1999 (E00189267), Sreemangal, Lawachera forest, 24.25 N, 91.583 E, 8 May 1997, *Williams K J* (L0413463)

***G. macroclada*: India.** *Wallichn 6411* (L0487998), **Assam**: Khasia, 25.583 N, 91.633 E, 5 August 1936, *Tea Deputation Tea Deputation s. n.* (L0487999), Nayagarh, 8 May 1997, *Mooney H. F. 528* (L0487991). **Sikkim**: East Himalaya, *Griffith W 5639* (L0041113), *Herb. Watt 8702* (E00095812), (E00097427), *6536G* (E00095820), 28 May 1808, 7 (E00095821), elevation 610 m, 31 May 1882, *6931* (E00097430), 13 June 1920, 277 (E00095807), Khasia, *Hooker J. D.* (P01743148), East Himalaya, *Herb. Griffith 5634* (P01743147), Hort. Bot. Calcutta et Serampore, *Voigt, J. O. 101* (P00252266), East Himalaya, 12 July 1884, *Griffith, W. 5639* (P032726), Mogpoo, Silake, elevation 3000 m, 12 July 1884, s.c.|Boissier, P.E. (P00686490), Silake, elevation 609.6 m, *Buissier, P. E.* (P00686489). **Bangladesh.** 24.25, 91.583, elevation 35 m, 1 March 1971, *Huq AM; Mia MK* (L0413463), elevation 40 m, 3 September 1999, 972 (E00189266). **Myanmar.** 13 August 1908, elevation 137 m, 4195 (E00097420). **Nepal.** 26.816 N, 87.3 E, elevation 500 m, 13 August 1972, *1427* (E00500193). **United States of America. Maryland**: NMNH Botany Research Greenhouses. Suitland, 28 September 2001, *W. J. Kress & M. Bordelon 02-7123* **(**US3432988).

Taxonomic notes. The new species is similar to two species in color of the flower, and absence of anther appendages. This species is different from *G. orixensis* in its petiolate leaves 0.3 mm (vs. subsessile), absence of inflorescence

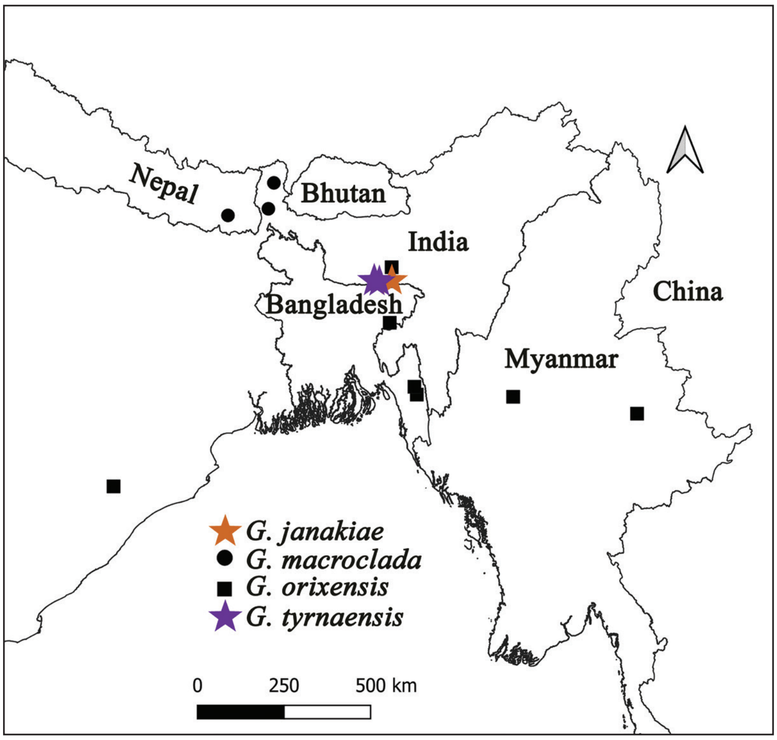

Figure 11. Map showing the distribution of *G. janakiae* sp. nov., *G. macroclada*, *G. orixensis*, *and G. tyrnaensis* sp. nov.

bracts (vs. present), and large anther 3.8 mm (vs. 2 mm). This species is different from *G. macroclada* in its short ligule 1 mm (vs. 2–3 mm), small size inflorescence 4–6 cm (vs. 15 cm), and short anther 3.8 mm (vs. 6–7 mm). Detailed morphological comparisons between *G. janakiae* and *G. orixensis* are presented in Table 3.

Notes. *G. macroclada* is distributed in Nepal and West Bengal, India, and *G. orixensis* is distributed in Bangladesh, Assam and Odisha states, India, and Myanmar (Fig. 11).

Globba yadaviana **Y.Ritu & V.Gowda, sp. nov.**

urn:lsid:ipni.org:names:77347887-1
Fig. 12

Type. India. Mizoram: Mamit district, Reiek Tlang road, 23.6777, 92.6037, elevation 300 m, 28 September 2022, *Y. Ritu & P. A. Shangreiphao VG2022MZ3958* (holotype: BHPL!; isotype: ASSAM!).

Diagnosis. *Globba yadaviana* is morphologically similar to *G. rahmanii*, *G. expansa* and *G. lancangensis* but clearly different in pod shape fruit (Fig. 12I), absence of andromonoecy, reduced peduncle, large inflorescence, short calyx vs. oblong, globose ellipsoid fruit, presence of andromonoecy, large peduncle, small inflorescence, and large calyx.

Description. Lithophytic herbs, 35–70 cm tall including inflorescence height, pseudostem swollen at the base. Rhizomes compact, non-tuberulous, creamish-white. Leafy shoot with 5–10 leaves; sheath ligulate, ligule 4–5 mm long, bilobed, light green, sparsely pubescent; lamina 26–35 × 6.5–11 cm, sessile, narrowly ovate, base obtuse, apex caudate, margin entire, glabrous. Inflorescence terminal to the leafy shoot, 6–35 cm long, erect; peduncle reduced, light green, glabrous; rachis, green, pubescent; bracts 2.3–2.5 × 0.7–0.8 mm, elliptic, green, pubescent and bracteoles 2.5–2.6 × 1–1.3 mm, ovate, light green, glabrous. Cincinni 5–39, each cincinni with 7–18 flowers. Floral pedicel for basal flowers 2.5–4 cm long, for terminal flowers 0.6 –1.5 cm long, light green, pubescent. Flowers 3–3.6 cm long, yellow-orange, recurved; calyx 2–2.5 mm long, grayish green; floral tube 3.2 mm long, yellow, densely pubescent, slightly curved at the middle; dorsal corolla lobe 6.8 × 2.6–2.8 mm, ovate, yellow tinged green, glabrous; lateral corolla lobes 4.8–4.9 × 2.2 mm, ovate, apex obtuse, yellow green tinged, glabrous; labellum 11.5 × 3 mm, sagittate, yellow, labellum notch texture echinate; lateral staminodes 14–15 × 5.5–5.6 mm, ovate, apex acute, yellow, hairs on margins and on veins. Stamen 2.2 cm long; filament 2 cm long, yellow, glabrous, arching; anther 1.9–2 mm long, elliptic, apex truncate, yellow, crest absent, appendaged; style, filiform, tip broader than base, stigma 4–5 mm wide, clavate, ciliate. Ovary 0.4–0.5 × 0.2–0.3 cm, obovate, pale green, verrucose; epigynous glands 2, 0.4–0.5 cm long, linear, cream. Fruit 1.5 cm in length, linear, base obtuse, green, texture undulate, calyx persistent. Bulbils absent.

Distribution and ecology. At present, we have seen this species in Reiek Tlang road, Mamit, Mizoram. We have observed ca. 30 individuals in an overall area of ca. 400 m^2. This species is lithophytic, mostly growing along the edge of roads with an elevation of ca. 300 m. We have observed different species of bees and butterflies visiting the flowers of this species. We have observed ants as seed dispersal for this species.

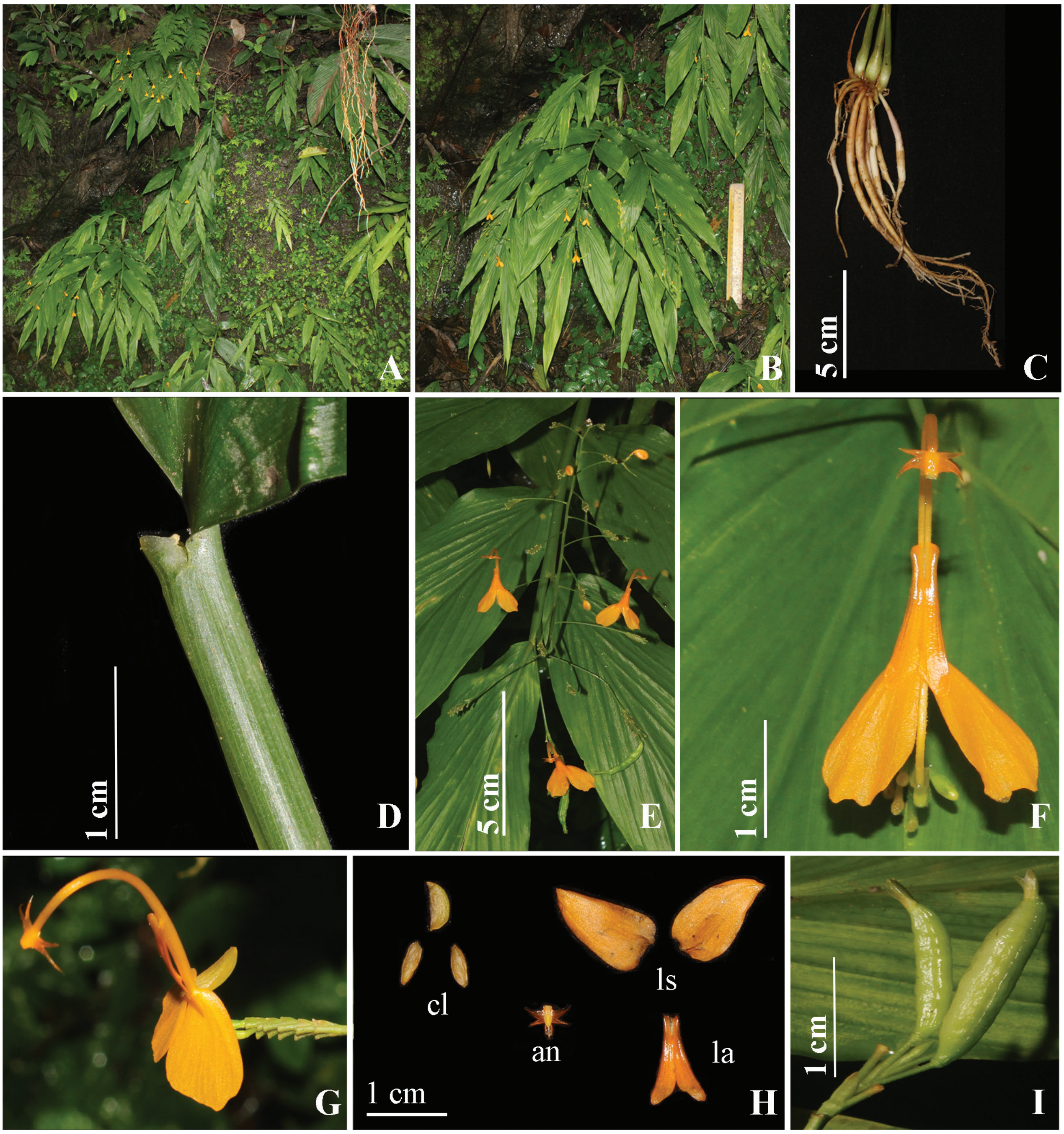

Figure 12. *Globba yadaviana* sp. nov. **A** habitat **B** habit **C** rhizome **D** ligule **E** inflorescence **F** flower (front view) **G** flower (side view) **H** dissected flower, cl (corolla lobes), an (anther), ls (lateral staminodes), la (labellum) **I** fruit. Photographs by Y. Ritu.

Phenology. Flowering and fruiting were observed in the month of August.

Etymology. This species epithet is in the memory of the late Mr. Rajesh Yadav, who was the father of the first author and was instrumental in the author's progress in science and education.

Informal conservation status. This species is currently known from 4–5 small populations across Reiek-Tlang road (Mamit district) within the state of Mizoram, wherein each population is spread across 1–2 km along the edge of the road and has approximately 30 individuals each. Although this species is known only from the type locality, it could be more widespread in neighboring countries with similar habitats, we, therefore, assess it as Data Deficient (DD).

Specimens of allied species examined. *G. rahmanii*: Bangladesh. Khagrachari: Dighinala- Marissha road, Teentila, 30 August 1997, *Rahman et al., 1878* (HCU)

***G. expansa*: India. Assam**: *Jenkins F, Jenkins, F s.n.* (L0487987), 1 May 1908, *Alleizette AC d', Alleizette, AC d' 7115* (L0488012), 1 July 1909, *Alleizette AC d'. Alleizette AC d' s.n.* (L0487993), 12 June 1910 (E00097428), *Tea Deputation* (NYBG04355596). **West Bengal**: Hortus Botanicus Calcuttensis, 22.559 N, 88.291 E, *Anon 6536E* (BM013718590), Circa Calcuttam, *J. W. Helfer 192* (NYBG04355597). **Thailand. Chiang Mai**: Mae Rim, 19.166 N, 98.833 E, elevation 700 m, 8 August 1990, *J. F. Maxwell 89-912* (L0413531), Mua ng, 18.833 N, 98.883 E, elevation 400 m, 3 July 1992, *J. F. Maxwell 90-847* (L0413571), Maerim, 19.166 N, 98.833 E, elevation 700 m, 15 September 1995, *J. F. Maxwell 92-358* (L0413518), Doi Intanon, 18.533 N, 98.566 E, elevation 1100-1200 m, 17 May 1995, *Larsen K; Larsen SS; Tange C; Sookchaloem D, 46485* (L0413547), *Sahngahmpang, Mae Awn*, elevation 1050 m, 31 May 2006, *J. F. Maxwell 95-403* (L0413491), Doi Suthep-Pui National Park, elevation 960 m, *A.F.G. Kerr* (E00097516), 18.55 N, 98.6 E, elevation 710 m, 19 September 2008, *4513* (E00533779), 18.855 N, 100.734 E, elevation 300 m, 16 August 2012, *5614* (E00680827), *Fleuve Petchaponai, Pierre, L.* (P00234360), *Neeckey près Wangka*, elevation 150 m, 9 May 1946, *Hoed, G. den 246* (P00234428), elevation 10 km *W Fang*, 19.95 N, 99.183 E, elevation 600 m, 24 July 968, *Larsen, K. Santisuk, T.Warncke, E. 2650* (P00234440), Bo Luang, 18.75 N, 98.416 E, elevation 1050 m, 12 June 1973, *Geesink, R. Phanichapol, D. Santisuk, T. 5886* (P00234419), Mai Rim, Nae Rin, Doi Sutop Pui Natl. Park, elevation 700 m, 3 July 1992, *J. F. Maxwell 92-356* (P00234313), Doi Suthep, elevation 975.36 m, 12 June 1910, *1214* (BM013718611), Ang-ka-noi, 26 June 1978, *C. Phengklai, 4121* (NYBG04347253). **Lao People's Democratic Republic. Khammouan**: Laos P.D.R., 18.394 N, 103.075 E, elevation 199 m, *Newman MF; Thomas PI; Armstrong KE; Lamxay V; Sengdala K LAO-1529* (L0811897), Laos, 14.949 N, 106.886 E, elevation 105 m, 15 July 2009, *VL1957* (E00640106), Phabat, 18.3944 N, 103.0758 E, elevation 199 m, 31 May 2006, *Newman, M.F., Thomas, P., Armstrong, K., Lamxay, V., Sengdala, K. LAO1529* (P01743264), Luang Prabang, Mekong river, 19.8669 N, 102.0630 E, elevation 303 m, 12 June 2012, *Jana Leong-Skornickova; Tran Huu Dang; Ota Sida; Kittisack Phoutthavong; Somdy Oudomsack JLS1688* (P00840173). **Cambodia. Mondulkiri**: 13.429 N, 103.763 E, elevation 491 m, 2 November 2006, *Long, C. Cheng, K.C. Leti, M. CL435* (P00626289)

***G. lancangensis*: China.** 22.061 N, 100.194 E, elevation 1210 m, 14 July 2000, *00-253* (E00187763), 22.543 N, 99.943 E, elevation 1080 m, 13 July 2000, *00-241* (E00187762).

Taxonomic notes. The new species is similar to three species in flower color, and presence of four anther appendages. This species is different from *G. rahmanii* in its large inflorescence 6–35 cm (vs. 8–19 cm), small calyx 2–2.5 mm (vs. 3.5–5 mm), large ovary 3.5–3.7 mm (vs. 1 mm) and dorsal corolla lobes with a keel (vs. without a keel). This species is different from *G. lancangensis* and *G. expansa* in its inflorescence length 6–35 cm (vs. 10–27 cm), small calyx 2–2.5 mm (vs. 4 mm), absence of anther crest (vs. present), and pod shape fruit (vs. globose and ellipsoid). The detailed morphological comparisons between *G. yadaviana* and *G. rahmanii*, *G. lancangensis*, *G. expansa* are presented in Table 4.

Notes. *G. rahmanii* is distributed to Bangladesh, *G. lancangensis* is distributed to China, and *G. expansa* is distributed to Thailand, Laos, and Cambodia (Fig. 13).

Table 4. Comparison of morphological characteristics of *G. yadaviana* sp. nov. with *G. rahmanii*, *G. lancangensis* and *G. expansa*. Characters not described in the original protologue or in subsequent descriptions of the same species, are marked as not known.

Characters	***G. yadaviana*** **Y.Ritu & V.Gowda**	***G. rahmanii*** **Yusuf (Yusuf 2004)**	***G. lancangensis*** **Y.Y.Qian (according to Sangvirotjanapat et al. 2019)**	***G. expansa*** **Wall. (according to Sangvirotjanapat et al. 2019)**
Ligule length (mm)	4–5	3	2	1–6
Peduncle length (cm)	Absent	Not known	1.5–3	3
Inflorescence length (cm)	6–35	8–19	10–20	10–27
Rachis color and indumentum	Green, densely pubescent	Green, pubescent	Light green, minutely pubescent;	Green, glabrous
Bract dimensions (mm) and color	2.3–2.5 × 0.7–0.8, elliptic, green, pubescent	2–5–3 × 2, ovate, green, sparsely hairy	1.5 × 1–2, caducous	10, caducous
Calyx length (mm)	2–2.5	3.5–5	4	4
Flower color	Yellowish orange	Yellow	Primrose or pale yellow	Yellowish orange
Lateral staminode dimensions (mm)	14–15 × 5.5–5.6	13–19 × 9–10	10–13 × 4–5	11–12 × 4–5
Dorsal corolla lobe keel	Present	Absent	Present	Present
Filament length (mm)	20	18	23	26–28
Anther length (mm)	1.9–2	2	2	1–2
Crest length (mm)	Absent	Not known	1	1
Ovary dimensions (mm)	3.5–3.7	1	3	4
Fruit shape	Pod shape, more linear with undulate margins	Oblong, with smooth margins	Globose	Ellipsoid
Bulbil	Absent	Absent	Absent	Bulbils occasionally

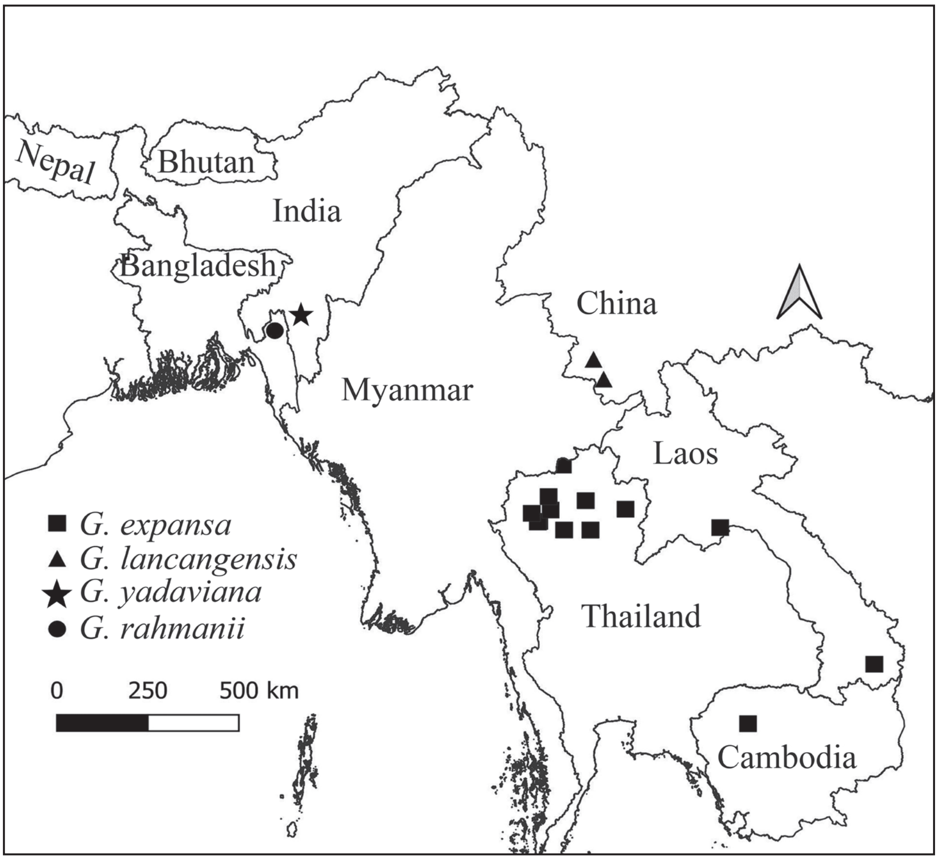

Figure 13. Map showing the distribution of *G. expansa*, *G. lancangensis*, *G. yadaviana* sp. nov., and *G. rahmanii*.

Taxonomic key to the Indian *Globba* species

1 Prominent bracts; anther appendages present **2**
– Not prominent bracts; anther appendages absent **12**
2 Bracts large imbricating then spreading; 4 anther appendages **3**
– Bracts small not imbricating; 2 anther appendages **7**
3 Pendant inflorescence; red spot at the center of labellum **4**
– Erect inflorescence; red spot absent at the center of labellum **5**
4 Leaves elliptic or ovate/narrowly ovate; inflorescence bracts oblong; green .... ***G. schomburgkii***
– Leaves elliptic; inflorescence bract narrowly ovate; white .... ***G. sherwoodiana***
5 Bracts persistent; ovate; bulbils present .... ***G. marantina***
– Bracts deciduous; bulbils absent **6**
6 Leaves oblong; inflorescence short (<5 cm); cincinni lax with few flowers .... ***G. pauciflora***
– Leaves narrowly ovate; inflorescence long (6–35 cm); cincinni crowded with numerous flowers .... ***G. yadaviana***
7 Inflorescence pendent; lateral staminodes attached below labellum **8**
– Inflorescence erect; lateral staminodes attached above labellum **9**
8 Leaves oblong; bulbils absent .... ***G. bracteolata***
– Leaves narrowly ovate; bulbils present .... ***G. pendula***
9 Flowering precedes the onset of vegetative shoot **10**
– Flowering occurs on vegetative shoot **11**
10 Bracteole light pink; flowers generally white; labellum yellow .... ***G. spathulata***
– Bracteole light green; flowers yellow; labellum yellow .... ***G. wengeri***
11 Leaves narrowly ovate; bracts ovate; purple; floral tube yellow; lateral staminodes facing upwards .... ***G. radicalis***
– Leaves cardio-acuminate; bracts elliptic; violet; floral tube reddish purple; lateral staminodes facing downwards .... ***G. wardii***
12 Ovary long (>0.3 cm); bulbils present **13**
– Ovary small (<0.3 cm); bulbils absent **22**
13 Inflorescence bracts persistent; flower bracteole present **14**
– Inflorescence bracts caducous or absent; flower bracteole absent **15**
14 Flower yellow; lateral staminodes erect; backwardly positioned .... ***G. kanchigandhii***
– Flower white; lateral staminodes not erect; downward positioned .... ***G. andersonii***
15 Inflorescence short (<12 cm); latera staminodes short (<0.5 cm) cornicula present **16**
– Inflorescence long (>12 cm); lateral staminodes long (>0.5 cm); cornicula absent **18**
16 Labellum obcuneate; labellum saffron yellow with 2 red blotches .... ***G. multiflora***
– Labellum not obcuneate; labellum without red blotch **17**
17 Ligule 3 mm; labellum ovate; lateral staminodes narrowly ovate .... ***G. tyrnaensis***
– Ligule 1 mm; labellum cordate; lateral staminodes ovate .... ***G. janakiae***

18 Fruit smooth; bulbils only in the axil of leaves; lateral staminodes longer than corolla lobes .... ***G. macroclada***

– Fruit warted; bulbils produced on the inflorescence; lateral staminodes equal to corolla lobes **19**

19 Calyx brown; floral tube yellow with a tinge of brown; bulbils produced on the upper part of inflorescence .... ***G. clarkei***

– Calyx not brown; floral tube yellow; bulbils produced all over the inflorescence **20**

20 Inflorescence crowded; leaves oblong; labellum narrowly obovate with outwards curled; lateral staminodes longer than corolla lobes .... ***G. sessiliflora***

– Inflorescence lax leaves not oblong; labellum not narrowly obovate with outwards curled; lateral staminodes equal to corolla lobes.................... **21**

21 Inflorescence long (>10 cm); calyx dark purple; flower yellow..... ***G. racemosa***

– Inflorescence up to 6.5 cm; calyx yellow, flower orange yellow..... ***G. orixensis***

22 Ligule with unequal lobes; labellum sagittate; off-white with orange spot at center .... ***G. paschimbengalensis***

– Ligule with equal lobes; labellum linear; orange with no orange spot in center .... ***G. polymorpha***

One species, *G. platystachya*, is not included in the above taxonomic key since anther characters were not described in its protologue, and anther characters are very critical for subgeneric classification in *Globba*. To the best of our knowledge there has been no subsequent record of this species. Since the description of this species is incomplete, we did not include it in this dichotomous key.

A note on the taxonomic collection challenges in the ecologically sensitive Eastern Himalayas and northeast region of India, and recommendations:

In the past few decades, the Eastern Himalayas and the Northeast India are two biodiversity-rich regions that have been constantly threatened by rapid development projects. The effects of ecological destruction caused in this region need special mention and attention because these regions are among the least explored areas in India for their flora, fauna, ecology, and evolutionary patterns, and they remain one of the most challenging regions for collection-based studies, both logistically and politically. Based on our decade-long experience of working in this region, we discuss below two main challenges in collection-based floristic and taxonomic studies: 1) access to study areas and associated logistic challenges, and 2) safety in the field.

1) *Access to study areas*—The only mode of transportation within Northeast India is by road, with a single rail line that connects Guwahati (Meghalaya) to Tinsukia (Arunachal Pradesh). The roadways within Northeast states are well-connected, but they are difficult to traverse due to poor road quality, and unpredictable landslides that can completely isolate large parts of this region for an indefinite time (Fig. 14). Lastly, the lack of frequent public transportation means that fieldwork can only be carried out using privately hired vehicles, which significantly increases fieldwork budgets.

Figure 14. Images depicting common logistic hurdles in field collections when working in the Northeast states of India **A** Willong Road, Manipur **B** mining in Cherrapunji road, Meghalaya **C** forest clearing, on the way to Thanamir, Nagaland **D** stone cutting Ziro road, Arunachal Pradesh **E** Mawphlang Sacred Grove, Meghalaya **F** roadblock because of a landslide in Lachen, Northern Sikkim. Photographs **A, D** by Ajith Ashokan **B** by N S Prasanna **C** by Aleena Xavier **E, F** by Y. Ritu.

One of the forest types that is challenging to access in the northeastern states is the sacred groves (Fig. 14E). Sacred groves cover over 40000 hectares of natural forest area across five states (Upadhyay et al. 2019) and they represent a valuable practice in conserving biodiversity, where local communities preserve a specific site untouched out of reverence for religious or cultural reasons. This conservation method is essential in protecting threatened flora and fauna from extinction as well as preserving socio-ecologically important species. While it is possible to access most sacred groves via research permits from the indigenous guardian communities, collecting samples within the groves is restricted. This presents a significant challenge in identifying species from these sacred groves since voucher collections from these locations are prohibited.

Other logistic challenges include scarcity of paid accommodations and access to basic amenities such as electricity for drying herbarium specimens. The high humidity in this region makes it difficult to dry specimens, especially in areas like Cherrapunji, Meghalaya, where rainfall can reach up to 450 inches (11430 mm). Finally, the absence of a continuous electrical power source also means that charging of field equipment such as cameras, GPS devices, power banks, and mobile phones becomes challenging here.

2) *Safety in the field*—The safety of researchers has been a major concern in the northeastern states due to the combination of natural disasters and political conflicts. This region shares political boundaries with five countries, making it a politically sensitive area, especially in regions closer to the political borders.

The Northeast states are biodiversity corridors between the Indian subcontinent and Southeast Asia (Ashokan et al. 2022, Prasanna et al. 2020). With the region's needs to focus on development, it is very critical to take active measures in documenting the biodiversity present in this area. Our discovery of six new species highlights the importance of documenting and preserving the flora of this biodiverse region. Here, we have briefly discussed the research challenges in this region to highlight and emphasize the need for an active dialogue towards building local facilities for taxonomic studies such as botanical gardens, herbaria, and tissue collections. Based on our studies in the northeast region we suggest that a collective effort from local communities, researchers, taxonomists, forestry personnel, and policymakers are the need of the hour in order to mitigate biodiversity loss in this region.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Ritu Yadav collected the specimens, both authors analyzed the specimens and protologues, and wrote the manuscript together.

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Data availability

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

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Supplementary material 1

Type localities of Indian *Globba* spp.

Authors: Ritu Yadav, Vinita Gowda

Data type: csv

Explanation note: Table contains the occurence data for type localities of all 19 Indian *Globba* spp.

Link: https://doi.org/10.3897/phytokeys.246.118751.suppl1

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Research Article

Temochloa (Poaceae, Bambusoideae), a newly-recorded bamboo genus for China and Vietnam, with new taxa and a re-interpretation of flowering structures

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Abstract

Neomicrocalamus and *Temochloa* are closely-related genera for which 'inflorescence' structures were incompletely understood and difficult to reconcile. After re-examining the inflorescence morphology, the so-called 'spikelets' of both genera as described should instead be recognised as pseudospikelets with mostly inactive axillary buds. The new bamboo taxa, comprising two varieties of a new species, are placed in *Temochloa*, representing a new genus record for China and Vietnam.

Key words: Bambusoideae, morphology, pseudospikelet, taxonomy

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Introduction

Neomicrocalamus Keng f. and *Temochloa* S. Dransf. are two climbing bamboo genera (Poaceae, Bambusoideae, Bambuseae) only distributed in limestone areas (Dransfield 2000; Li and Stapleton 2006; BPG 2012). Phylogenetically, they are sister groups (Ruiz-Sanchez and Sosa 2015; Zhou et al. 2017). In morphology, *Neomicrocalamus* possesses some characters in common with *Temochloa*, such as short-necked pachymorph rhizomes, scrambling culms and even the ambiguous inflorescence structures (Dransfield 2000; Li and Stapleton 2006).

When Keng (1983) established the genus *Neomicrocalamus*, he considered that the 'inflorescence' is semelauctant (determinate, characterised by true spikelets), meaning it completes its development within a single grand period of growth (McClure 1966). However, at the same time, he considered that the inflorescence basic unit is a pseudospikelet (typically with basal bracts subtending buds that will produce similarly branching lateral units, these then repeating the process, giving what has been called an iterauctant or indeterminate development; McClure (1934, 1966)), as indeed the basal prophyll and bracts are present. Stapleton (1994) held the same opinion as Keng. These descriptions are very confusing, as the semelauctant and iterauctant conditions would seem to be fundamentally contrasting. In the protologue of *Temochloa*, it was diagnosed as having a determinate ‘inflorescence with bracteate and prophyllate branches’ (Dransfield 2000).

With some newly-collected flowering material from China and Vietnam, it becomes possible for us to re-examine the ‘inflorescence’ structure of *Neomicrocalamus* and *Temochloa*. Furthermore, during the examination, we recognised that some taxa are new to science. These taxa are described and illustrated here.

Materials and methods

Flowering material was dissected under a stereomicroscope (Mshot-MZ101) and images were taken with the camera attachment (Mshot-MSX2). Morphological comparisons and descriptions were based on the relevant literature including protologues, as well as herbarium specimens and living plants.

Results

The newly-discovered bamboo plants are characterised by short-necked pachymorph rhizomes, scrambling culms, solitary and almost circular primary branch buds, branch complement with many short and subequal branches with an occasional dominant central branch that reiterates and approaches the size of the culm, pseudospikelets with 2–4 fertile florets; 6 stamens with emarginate anther apices, 3 stigmas and caryopses.

Discussion

Flowering structures in the three groups

The pseudospikelet should be interpreted as a condensed flowering branch which terminates in a spikelet proper and is basally supplied with a prophyll and bracts (reduced sheaths) subtending buds (McClure 1934, 1966). Typically, these subtended buds are able to develop as secondary pseudospikelets, which in turn lead to higher-order lateral pseudospikelets. This is termed an iterauctant or indeterminate development (McClure 1966). In contrast, a semelauctant or determinate development refers to a single episode of development of the flowering branch, conventionally associated with true spikelets (McClure 1966). However, it should be noted that McClure (1966) mentioned that the axillary buds of primary pseudospikelets of *Arundinaria prainii* Gamble, equivalent to *Neomicrocalamus prainii* (Gamble) Keng f., may remain dormant. Perhaps because of this, Keng (1983) employed the term ‘semelauctant’ for the ‘inflorescence’ of *Neomicrocalamus*. Afterwards, in the *Flora Reipublicae Popularis Sinicae*, inflorescence development was not discussed, but it was stated that, although axillary buds of the pseudospikelet type are present, they have never been known to develop as secondary pseudospikelets (Geng and Wang 1996). Probably for much the same reason, the ‘inflorescence’ of *Temochloa* was also regarded as being of a determinate nature, but its description in the protologue states it is “usually comprising one spikelet, in inflorescences with more than one spikelet . . . the axis [is]. . . terminated by a spikelet and a single branch . . . borne at each node, subtended by a bract/sheath and a prophyll . . .” (Dransfield 2000). It should be noted that Dransfield (2000) avoided using the term ‘semelauctant’ in her very careful description.

In fact, according to our observation, pseudospikelets of *Neomicrocalamus* do produce secondary pseudospikelets, although it happens only occasionally (Fig. 1A). Therefore, the pseudospikelet development of *Neomicrocalamus* is still iterauctant rather than semelauctant, the latter conventionally linked to true spikelets. It would be confusing if the semelauctant condition is also said to develop pseudospikelets. Hence, the ‘spikelets’ of both *Neomicrocalamus* and *Temochloa* could be properly recognised as a variant (possibly extreme reduction) of the typical pseudospikelet structure, in which axillary buds are not as active as in the typical condition.

The new species of *Temochloa*

The morphological characters of our newly-discovered bamboos are more similar to *Temochloa*. The primary branch buds of both the newly-discovered bamboos and *Temochloa* are nearly circular and their culm leaf sheaths are shallowly grooved, whereas *Neomicrocalamus* has lanceolate buds and plane culm leaf sheaths (Dransfield 2000; Li and Stapleton 2006). Besides, the anther apices of the newly-discovered bamboos are emarginate (Fig. 1L, left), while those of *Neomicrocalamus* are conspicuously cuspidate due to prolongation of the connective (Fig. 1L, right). However, to date, some characters, including stamens, of *Temochloa* are still unknown.

On the other hand, the newly-discovered bamboos and *Temochloa* occur at very low elevations, 50–250 m, rarely reaching 700 m, whereas *Neomicrocalamus* taxa have hitherto only been found above 1000 m (Dransfield 2000; Li and Stapleton 2006).

The similar morphology and distribution, in terms of elevation, of the newly-discovered bamboos and *Temochloa* are also commensurate with their close phylogenetic affinities. The phylogenetic evidence indicates that the newly-discovered bamboos originate from introgressive hybridisation between *Temochloa liliana* S. Dransf. and *N. prainii* (Cai et al. 2023; the newly-discovered bamboo accessions referred as *BH85*, *2018VNB018* and *2018VNB040*). The newly-discovered bamboos inherited most (80.7%) of its genome from *T. liliana*; therefore, genetically, these two groups are closer related (Cai et al. 2023).

Given the present evidence accrued from a combination of morphological, phylogenetic and biogeographical evidence, we propose that the newly-discovered bamboos are an undescribed species with a variety best placed in *Temochloa*, which then represents a newly-recorded genus for both China and Vietnam.

Taxonomic treatment

***Temochloa elegans* N.H.Xia, Y.Y.Zhang, Z.Y.Cai & Y.H.Tong, sp. nov.**
urn:lsid:ipni.org:names:77347888-1
Figs 1, 2

Diagnosis. The new species resembles *Temochloa liliana*, but differs by its subsolid (vs. hollow) culm internodes, hairy (vs. glabrous) prophylls of the pseudospikelets, paleae longer than (vs. as long as) lemmas and acute to slightly obtuse (vs. 2-lobed) palea apices.

Type. China, Guangxi, Jingxi, near Bandan Village, limestone, 22°53'23"N, 106°21'16"E, 703 m elev., fl. (floret, flower), fr. (fructus, fruit), 10 June 2020, *N.H. Xia et al. BH85* (holotype: IBSC!).

Description. Clumps unicaespitose, open, spreading. Rhizomes short-necked, pachymorph. Culms scrambling; internodes subsolid, 15–30(–35) cm long, 4–5 mm diam., glabrous; supranodal ridges slightly prominent; sheath scar prominent with a persistent sheath-base collar. Primary branch bud solitary, nearly circular, compressed, 7–8 mm long, puberulent, the lateral edges ciliolate. Culm leaf sheath deciduous, narrowly triangular, green when young, margins glabrous, abaxial surface glabrous and white pubescent at the base, with shallow longitudinal grooves, grooves with white pubescence becoming glabrous; ligule inconspicuous; auricles and oral setae absent; culm leaf blade persistent, erect, acicular. Branches intravaginal, many and subequal at each node, central branch sometimes dominant, reiterating and approaching the size of the culm. Foliage leaves 6–13 per ultimate branch; foliage leaf sheath pubescent, margins glabrous; ligule truncate, no longer than 0.5 mm high, puberulent, ciliolate; auricles and oral setae absent; foliage leaf blades papery, lanceolate to oblong, 5–8 cm long, 0.4–0.8 cm wide, abaxial surface glabrous, adaxial surface (sub)glabrous, one margin entire, the other serrulate, base rounded-obtuse to rounded-truncate, apex acicular, acuminate, secondary longitudinal veins 2–3 pairs, transverse veins inconspicuous.

Pseudospikelets solitary, secondary pseudospikelets rarely produced, slightly compressed, prophyll oblong, 3–3.5 mm long, papery, 2-keeled, keels ciliate, puberulent between keels, adaxial surface apically puberulent, apex acute; bracts 4–5, papery to leathery, gemmiferous or not, triangular to lanceolate, 2.5–5 mm long, abaxial surface glabrous or puberulent above the middle, adaxial surfaces glabrous or apically puberulent, 7–9-veined, apex acute and mucronate; fertile florets 2–4, uppermost floret not fully developed; rachilla segments compressed, 4–5 mm long, glabrous; glumes absent; lemma leathery, lanceolate, ca. 6–8 mm long, both surfaces glabrous or adaxial surface apically puberulent, 9–11-veined, apex acute and mucronate, callus inconspicuous, no more than 0.5 mm long, glabrous; palea longer than lemma, ca. 7–9 mm long, glabrous, 2-keeled, 2–3-veined between keels, each side 3–4-veined, apex acute to slightly obtuse; lodicules 3, the anterior two, broadly ovate, ca. 2 mm long, 3–4-veined, the posterior one, lanceolate, ca. 2 mm long, 1–3-veined; stamens 6, filaments free, anthers yellow, ca. 3.5–4.5 mm long, apex emarginate; stigmas 3, 2–2.5 mm long, plumose, ovary ellipsoid, ca. 1.5 mm long. Caryopsis ellipsoid, ca. 7–8 mm long.

Phenology. New shoots around May.

Etymology. The specific epithet refers to its elegant habit.

Chinese name. 雅竹 (yǎ zhú).

Distribution and habitat. This species occurs in the limestone area of southwest Guangxi, China and northeast Vietnam, at elevations of 210(–700) m.

Conservation status. Up to now, *T. elegans* is known from only two locations in China and Vietnam. It is not very common at those locations so the number of mature clumps appears to be limited. The Vietnamese population is well protected in the Nature Reserve, while the Chinese population is distributed along

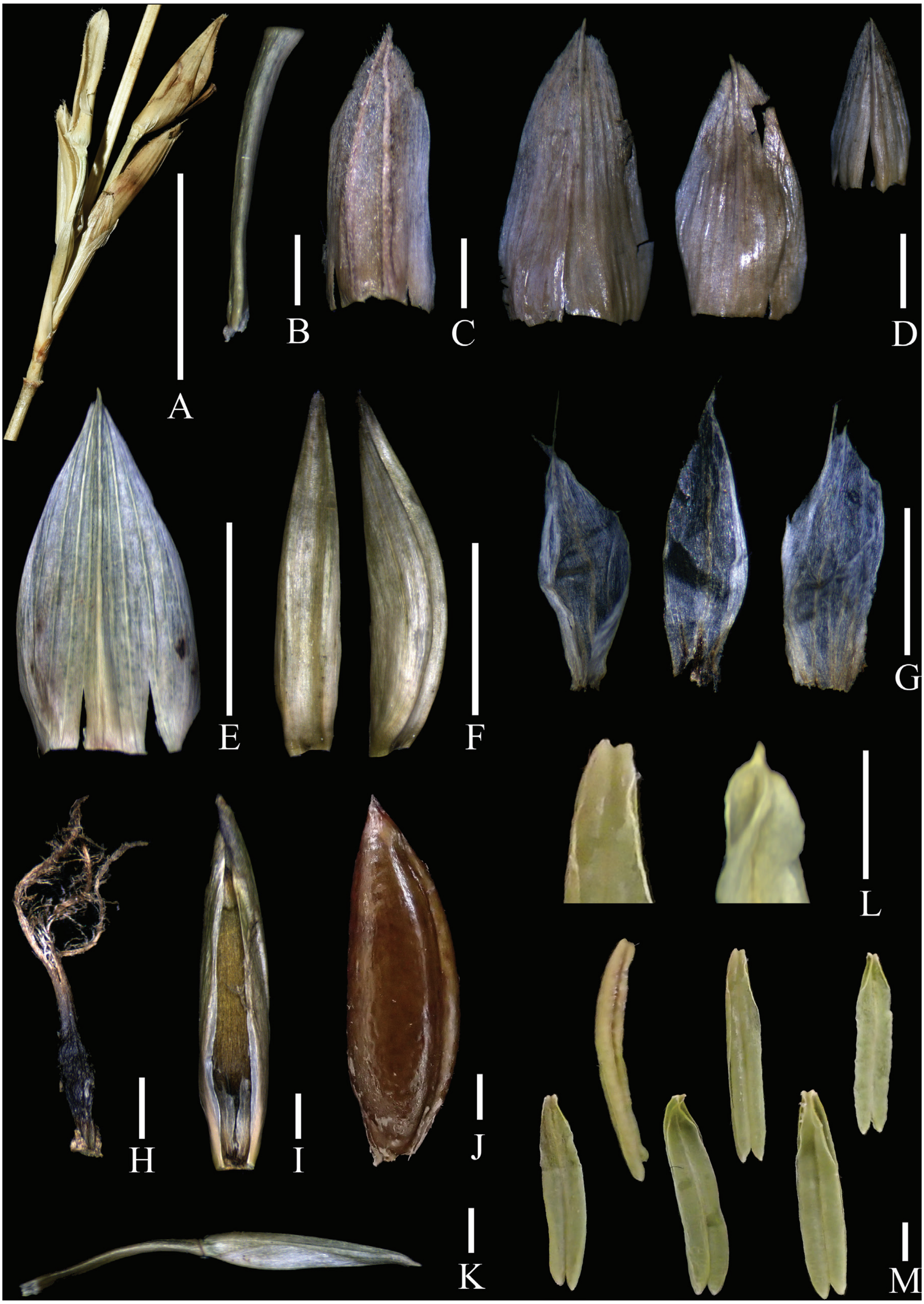

Figure 1. Floral morphology of *Temochloa elegans* **A** pseudospikelets of *Neomicrocalamus* sp. showing the secondary pseudospikelet (left) developed from the base of the primary pseudospikelet (right) **B** rachilla segment **C** prophyll (abaxial view) **D** bracts (abaxial view) **E** lemma (abaxial view) **F** palea (left: back view; right: side view) **G** lodicules **H** pistil **I** young fruit subtended by a palea **J** mature fruit **K** apical not fully developed floret **L** anther apices (left from *Temochloa elegans*; right from *Neomicrocalamus* sp. included for comparison) **M** anthers.

Figure 2. Morphology of *Temochloa elegans* **A** habit **B** foliage leaves **C** branch complement without a dominant central branch **D** branch complement with a developing dominant central branch **E** primary branch bud **F** culm internode section **G** culm leaf (upper half) **H** culm leaf (lower half) **I** flowering branches **J** spikelet proper.

the highway and not in any protected area. It should probably be categorised as Near Threatened (NT) (IUCN Standards and Petitions Committee 2022).

Additional specimens examined (paratypes). Vietnam, Bac Kan, Ba Be Lake, limestone, 22°25'15"N, 105°36'53"E, 170 m elev., 20 May 2018, *N.H. Xia* et al. *2018VNB018* (IBSC!, VNMN!).

***Temochloa elegans* var. *glabra* N.H.Xia, Z.Y.Cai, Y.Y.Zhang & J.B.Ni, var. nov.**
urn:lsid:ipni.org:names:77347889-1

Diagnosis. This variety can be differentiated from *Temochloa elegans* var. *elegans* in its glabrous foliage leaf sheaths and glabrous foliage leaf ligules.

Type. Vietnam, Ha Giang, Minh Ngoc Village, limestone, 22°43'19"N, 105°11'36"E, 210 m elev., 24 May 2018; *N.H. Xia et al. 2018VNB040* (holotype: IBSC!, isotype: VNMN!).

Etymology. The specific epithet refers to its glabrous foliage leaf sheaths and glabrous foliage leaf ligules.

Chinese name. 光雅竹 (guāng yǎ zhú).

Distribution and habitat. This species occurs in the limestone area of northeast Vietnam, at elevations of 140–210 m.

Conservation status. Up to now, *T. elegans* var. *glabra* is known from only one location in Vietnam. Less than 10 clumps were found. Due to the insufficient field survey, it should probably be categorised as Data Deficient (DD) (IUCN Standards and Petitions Committee 2022).

Additional specimens examined (paratypes). Vietnam, Ha Giang, Minh Ngoc Village, limestone, 22°43'48"N, 105°12'25"E, 140 m elev., 2018 *N.H. Xia* et al. *2018VNB032* (IBSC!, VNMN!)

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

Planothidium pseudolinkei sp. nov. (Bacillariophyta), a new marine monoraphid diatom species from the coast of Guangxi, China

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Abstract

A new marine monoraphid diatom species, *Planothidium pseudolinkei* **sp. nov.**, is described from the coast of Guangxi, China. The detailed morphology of this epipsammic diatom is studied by using both light and scanning electron microscopy. *P. pseudolinkei* differs from congeners by a combination of morphological features including capitate apices, multiseriate striae, a small central area on the raphe valve and an oblong sinus on the rapheless valve. Ecological preferences of *Planothidium* are also briefly discussed.

Key words: China, Guangxi, monoraphid diatom, new species, *Planothidium*

Introduction

Monoraphid diatoms represent a large assemblage of species which is characterized by the presence of a single raphe system on one valve. Over the past 40 years, 12 marine monoraphid genera have been described: *Bennettella* R.W.Holmes, *Epipellis* R.W.Holmes, *Astartiella* A.Witkowski et al., *Pogoneis* Round & Basson, *Pauliella* Round & Basson, *Vikingea* A.Witkowski et al., *Scalariella* Riaux-Gob., *Madinithidium* A.Witkowski et al., *Majewskaea* Van de Vijver, *Navithidium* Al-Handal & Romero, *Xenobennettella* A.Witkowski & Riaux-Gob. and *Vallithidium* J.A.Nienow & A.K.S.K.Prasad (Holmes 1985; Round and Basson 1997; Witkowski et al. 2000, 2022; Riaux-Gobin et al. 2012, 2013; Desrosiers et al. 2014; Van de Vijver et al. 2020; Al-Handal et al. 2021; Nienow and Prasad 2023). According to Round et al. (1990), all monoraphid species should be included in the order Achnanthales Silva. But Kulikovskiy et al. (2016) suggested that this order was not a monophyletic group.

As a monoraphid diatom genus, *Planothidium* Round & Bukht. was erected and separated from *Achnanthes* Bory based on its morphological features of bi- to multiseriate striae, internally raised virgae, elongated terminal fissures and unilaterally asymmetrical central areas on the rapheless valves in many species (Round and Bukhtiyarova 1996). At present, AlgaeBase lists a total of 123 taxonomically accepted *Planothidium* species and infraspecific names (Guiry and Guiry 2024). Morales (2006) divided this genus into four groups by the features of

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the central area of the rapheless valve. The first group is commonly represented by *Planothidium delicatulum* (Kützing) Round & Bukht., which presents continuous striae on the rapheless valve. The species in second group are characterized by a clear space without any depression at the central area such as in *Planothidium minutissimum* (Krasske) Morales. The other two groups are marked by a sinus (a rimmed depression) or a cavum (a hood) and represented species are *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot and *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, respectively. However, a molecular investigation of *Planothidium* confirmed two distinct clades within the genus, one of them possessing a sinus or a cavum on the rapheless valve and the other lacking either additional structure (Jahn et al. 2017). So far, Marine and brackish *Planothidium* have been rarely investigated. The current divisions, which are prepared for freshwater species, may not reflect the morphological diversity and phylogenetic relationship of marine and brackish species. Apart from *Planothidium*, the cavum can also be seen in another four monoraphid genera: *Xenobennettella*, *Gliwiczia* Kulikovskiy et al., *Skabitschewskia* Kuliskovskiy & Lange-Bertalot and *Planoplatessa* Kulikovskiy et al. (Kulikovskiy et al. 2022; Witkowski et al. 2022). It was suggested that the cavum might work as a lens for utilization of sunlight in the *Planothidium* cells (Bukhtiyarova and Lyakh 2014). But the function of the sinus is poorly known. Up to now, there are six species of *Planothidium* recorded from marine environments in China (Li 2019; Chen et al. 2022). Most of them live in sandy sediments from coastal areas of Fujian (Chen et al. 2022), no *Planothidium* taxa has been reported from Guangxi.

During a survey of the epipsammic diatom flora along the coast of Guangxi, China, an unknown *Planothidium* species was found on the sand grains from two sampling sites. Under the light microscope (LM), this taxon is very similar to *Planothidium linkei* (Hustedt) Lange-Bertalot. But the ultrastructural observations reveal that it is quite different from the latter. Therefore, we describe the new species as *Planothidium pseudolinkei* sp. nov. brief information on its ecology is also provided.

Materials and methods

Sampling was conducted along the coast of Fangchenggang City, Guangxi Province, China on 10 January 2021. We selected two locations as sampling sites in our study (Fig. 1). The first location is the Jin Beach (21°31.85'N, 108°10.95'E), which is located at the southern part of Wanwei Island and faces south. The second location is the Bailang Beach (21°32.27'N, 108°17.43'E), which lies in the middle part of Jiangshan Peninsula and faces east. Fangchenggang is situated in the north of Beibu Gulf with an average precipitation of 2362.6 mm (Du et al. 2022). The city has a subtropical monsoon climate and an average temperature ranging from 14 °C to 29 °C (Du et al. 2022). Its coastal region is dominated by irregular diurnal tides with maximum and average tidal ranges exceeding 4.5 m and 2.5 m, respectively (Huang et al. 2023).

At each site, sand samples were scraped by a hand shovel from the low intertidal zone of the beach during low tide and then placed into polyethylene ziplock bags with some air for transporting. Upon return to the laboratory, sub-samples were pretreated in an ultrasonic bath at 700 W for 3 minutes to separate diatoms attached to the sand grains. Prior to observation and analysis, diatom samples were digested with concentrated nitric acid (65%–68%) at 100 °C for 20 minutes to eliminate

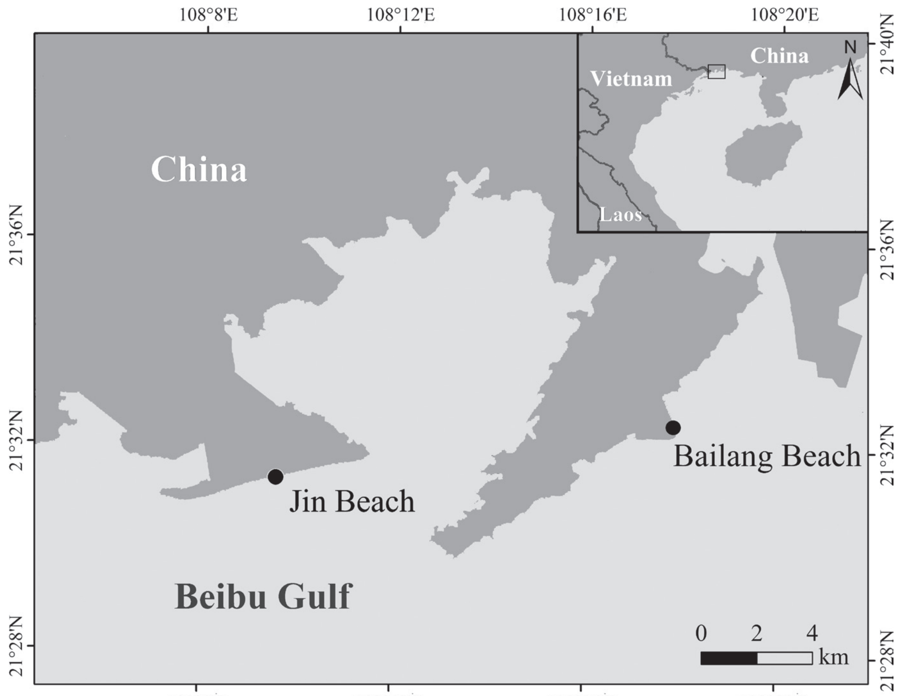

Figure 1. Locations of the sampling sites in this study.

organic matter. After several rinses with Milli-Q water, cleaned materials were dried onto coverslips and permanently mounted onto slides with Naphrax®. Diatoms were examined and identified at a magnification of 1,000× using a Zeiss Imager Z2 (Carl Zeiss, Germany) microscope equipped with differential interference contrast (DIC) and Zeiss Axiocam 512 color digital camera. Measurements were taken from 75 individuals for the new species. Relative abundance data was based on LM counts of at least 1500 valves. Valve ultrastructure was observed and imaged by a Hitachi S-3400 scanning electron microscope (SEM) (Hitachi, Japan) operated at 10 kV and 6 mm working distance. For SEM, small aliquots of suspensions were air-dried onto coverslips or membrane filters attached to aluminum stubs with conductive tape, and then sputter coated with 10 nm of gold in a Hitachi MC 1000.

Terminology follows Morales (2006), Jahn et al. (2017), Van de Vijver et al. (2018) and Van de Vijver and Bosak (2019).

Results

Division Bacillariophyta
Class Bacillariophyceae
Order Achnanthales
Family Achnanthidiaceae
Genus *Planothidium*

***Planothidium pseudolinkei* Lang Li, Yuhang Li & Junxiang Lai, sp. nov.**
Figs 2–4

Holotype. Slide MBMCAS286907 deposited in the Marine Biological Museum, Chinese Academy of Sciences (MBMCAS), Qingdao, China, represented here by Fig. 2B (Rapheless valve) and Fig. 2H (Raphe valve).

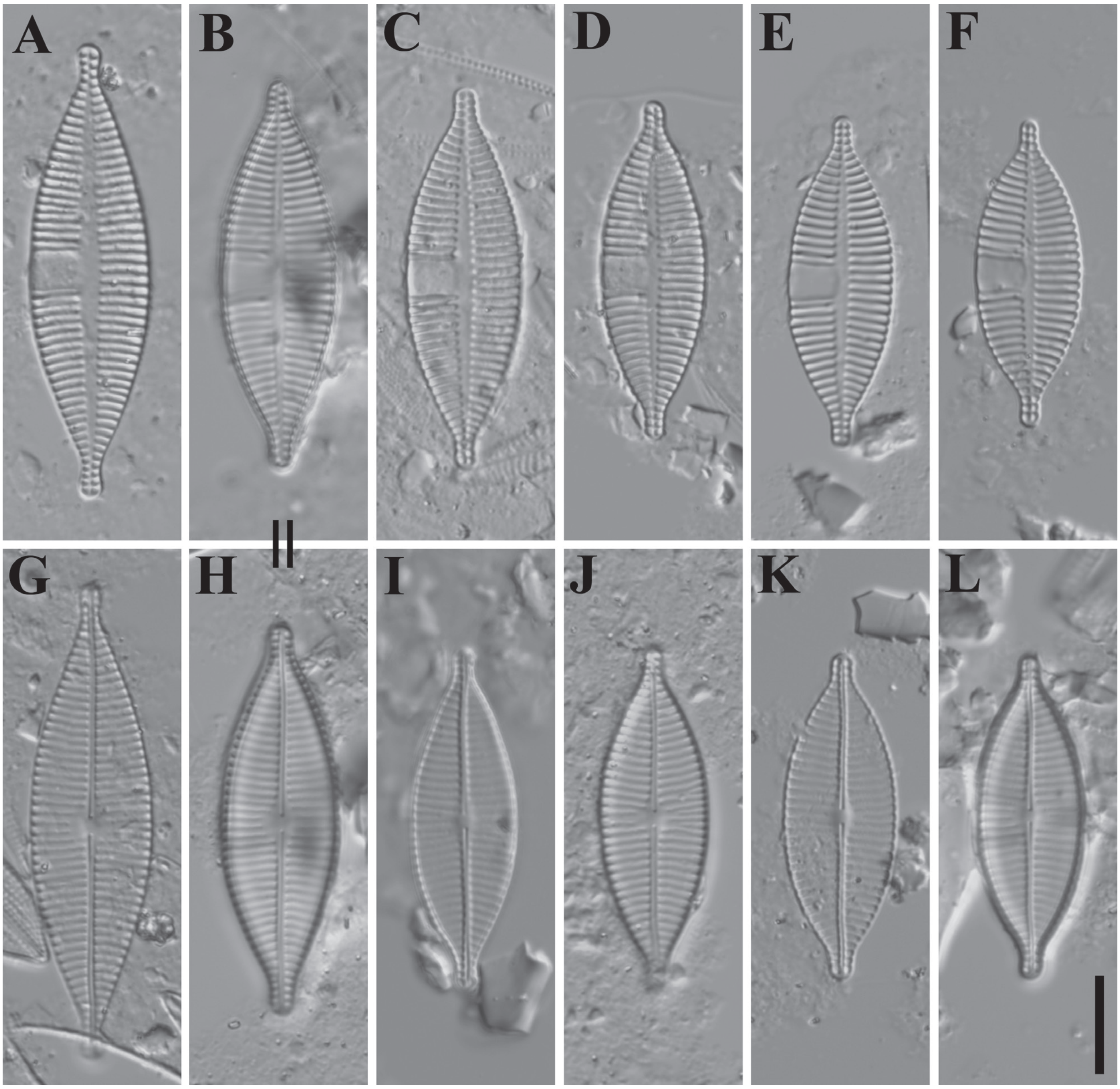

Figure 2. *Planothidium pseudolinkei* sp. nov. LM **A–F** rapheless valves **G–L** raphe valves **B, H** holotype designated. "=" indicates the different valves of the same frustule. Scale bars: 10 μm.

Type locality. Jin Beach, Wanwei Island, Guangxi Province, China, 21°31.85'N, 108°10.95'E, surface sand samples, collected by Lang Li on 10 January 2021.

Description. ***LM*** (Fig. 2A–L). Valves lanceolate to elliptic-lanceolate with convex margins and protracted, capitate to rostrate apices. Valve dimensions (n = 75): length 26.5–50.0 μm, width 10.0–13.0 μm. Rapheless valve (Fig. 2A–F): Axial area linear and narrowly lanceolate, slightly expanded in the middle of the valve. Central area asymmetrical with a unilateral large hyaline area; on the opposite side, striae barely shortened near the axial area. Striae weakly radiate at the center and more strongly radiate towards the apices, 11–12 in 10 μm. Raphe valve (Fig. 2G–L): Axial area very narrow, linear, slightly widened near the middle of the valve. Central area very small, slightly transapically expanded, bordered by 3–4 shortened striae on each side. Raphe straight, filiform with slightly enlarged central raphe endings. Terminal

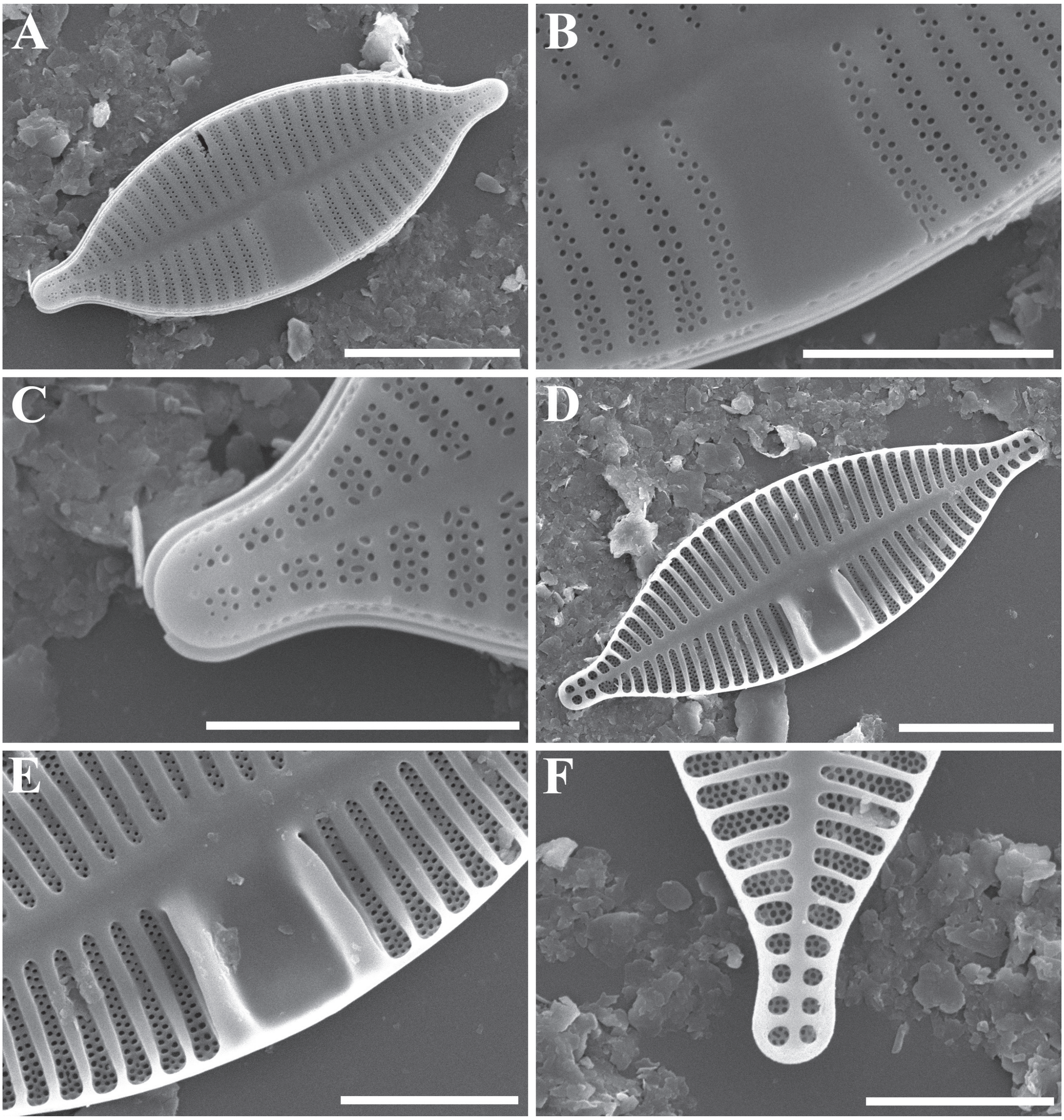

Figure 3. *Planothidium pseudolinkei* sp. nov. SEM **A** external view of an entire rapheless valve **B** external detail of the interruption of the striae on the rapheless valve **C** external detail of the valve apex **D** internal view of an entire rapheless valve **E** internal detail of the sinus depression **F** internal detail of the valve apex. Scale bars: 10 μm (**A, D**); 5 μm (**B, C, E, F**).

fissures not discernible in LM. Striae radiate throughout the entire valve, 12 in 10 μm. Areolae not discernible in LM.

SEM (Figs 3A–F, 4A–F). Rapheless valve (Fig. 3A–F): Externally, valve face generally flat, with a slightly linear depression in the axial area (Fig. 3A). Central area large, unilateral (Fig. 3A, B). Striae multiseriate, composed of three rows of small, rounded areolae at the apices, varying from three rows near the valve face/mantle junction to biseriate towards the axial area (Fig. 3B, C). Striae portion near the axial area often composed of one or two areolae (Fig. 3B). Striae extending onto the valve mantle, but interrupted by the valve face-mantle

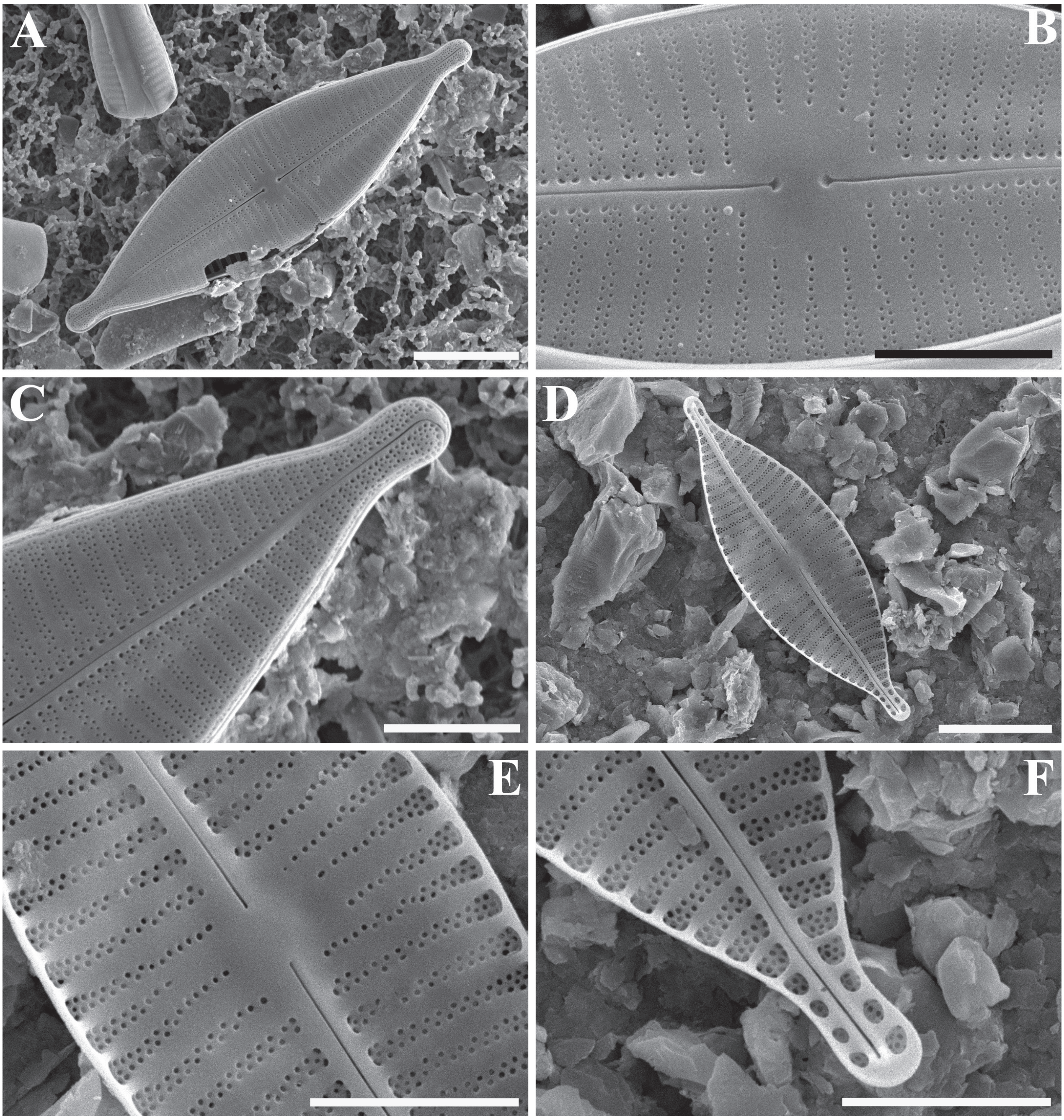

Figure 4. *Planothidium pseudolinkei* sp. nov. SEM **A** external view of an entire raphe valve **B** external detail of the central area of the raphe valve **C** external detail of the valve apex **D** internal view of an entire raphe valve **E** internal detail of the central area of the raphe valve **F** internal detail of the valve apex. Scale bars: 10 µm (**A, D**); 5 µm (**B, C, E, F**).

junction (Fig. 3B, C). Internally, axial area elevated and striae sunken between the raised virgae (Fig. 3D–F). A well-developed sinus distinctly present on one side of the central area, with the borders fusing with lateral virgae, forming a deep oblong depression (Fig. 3D, E). Raphe valve (Fig. 4A–F): Externally, valve face flat (Fig. 4A). Striae composed of one to four rows of small, rounded areolae, clearly broader than virgae at the apices (Fig. 4B, C). Striae portion along the axial area composed of two larger areolae than other ones (Fig. 4B, C). Central raphe endings straight, simple, expanded and pore-like (Fig. 4B). Terminal fissures bent, continuing shortly onto the valve mantle (Fig. 4C). Internally, virgae poorly developed (Fig. 4D–F). Raphe hook-shaped, branches situated on a slightly elevated raphe-sternum (Fig. 4D). Terminal raphe endings terminated by small helictoglossae (Fig. 4F).

Etymology. The specific epithet, *pseudolinkei*, was referring to the morphological and habitat similarities with *P. linkei*.

PhycoBank registration. http://phycobank.org/104835.

Distribution and ecology. In addition to the type locality, *P. pseudolinkei* also occurs in the surface sand sample from the Bailang Beach of Jiangshan Peninsula. This taxon is a marine epipsammic diatom. In the type material, *P. pseudolinkei* was very rare and only found in abundance of 0.14%. The associated diatom flora is composed of *Amphora* spp., *Navicula* spp., *Diploneis* spp., *Fallacia* spp., *Cocconeiopsis* spp., *Gyrosigma* sp., *Planothidium* sp., *Anorthoneis hummii* Hustedt, *Biremis ambigua* (Cleve) D.G.Mann, *Cymatoneis margarita* A.Witkowski, *Moreneis coreana* J.Park et al. and *Halamphora coffeiformis* (C.Agardh) Levkov.

Discussion

Planothidium is a species-rich genus which is widespread in freshwater, brackish and marine environments. Most representatives can be found in freshwater habitats, only a few taxa are marine or brackish species (Marquardt et al. 2021). In marine environments, however, the diversity of *Planothidium* species was suggested to be higher than that which has been found (Riaux-Gobin et al. 2018; Van de Vijver and Bosak 2019; Lai et al. 2021). It has been supported by several recently discovered marine *Planothidium* species, such as *P. galaicum* Álvarez-Blanco & S. Blanco, *P. juandenovense* Riaux-Gob. & A.Witkowski and *P. kaetherobertianum* Van de Vijver & Bosak (Álvarez-Blanco and Blanco 2013; Riaux-Gobin et al. 2018; Van de Vijver and Bosak 2019). Van de Vijver and Bosak (2019) pointed out that most marine and brackish species of the genus *Planothidium* had completely symmetrical central areas. In this genus, the presence/absence of a cavum or sinus is the most important taxonomic criterion, followed by the valve outline and morphometric data (Jahn et al. 2017). But Stancheva et al. (2020) reported that the striae density is often useless for distinguishing similar cavum- or sinus-bearing species. Given the importance of ultrastructural details, the SEM observation is necessary to illustrate the morphology of the *Planothidium* species (Stancheva et al. 2020).

P. pseudolinkei has a unique combination of morphological features of capitate apices, multiseriate striae, thickened virgae and internal depressions in the central areas of rapheless valves. All these characters justify its separation from all other species in the genus *Planothidium*. Our new taxon shares some similarities with a few previously described species, such as *P. apiculatum* (R.M.Patrick) Lange-Bertalot, *P. dispar* (Cleve) A.Witkowski et al., *P. iberense* L.Rovira & A.Witkowski, *P. lanceolatoides* (Sovereign) Lange-Bertalot, *P. oculatum* (Hustedt) A.Witkowski et al. and *P. rostrolanceolatum* Van de Vijver et al. A detailed comparison of these taxa is summarized in Table 1. *P. apiculatum* and *P. lanceolatoides* differ from *P. pseudolinkei* by having apiculate apices, a large central area on the raphe valve and a cavum on the rapheless valve (Patrick 1945; Sovereign 1958; Potapova 2010, 2015). In *P. dispar*, the central area on the raphe valve is also moderately large and the striae on the rapheless valve are continuous (Witkowski et al. 2000). *P. iberense* has a smaller cell size

Table 1. Comparison of morphological characteristics of *Planothidium pseudolinkei* sp. nov. and similar species.

	P. apiculatum	***P. dispar***	***P. iberense***	***P. lanceolatoides***	***P. oculatum***	***P. rostrolanceolatum***	***P. linkei***	***P. pseudolinkei***
Length (µm)	28.0	16.0–55.0	17.0–26.0	22.0–35.0	10.0–20.0	15.0–28.0	34.0–38.0	26.5–50.0
Width (µm)	10.0–11.0	6.0–15.0	6.5–9.5	10.0–12.0	4.0–5.0	5.6–7.8	12.0–15.0	10.0–13.0
Striae in 10 µm (rapheless valve)	10–12	14–20	14–16	11–13	12–16	14–16	11	11–12
Striae in 10 µm (raphe valve)	10	14–20	12–15	11–14	20–24	13–15	11	12
Apices	Apiculate	Rostrate	Broadly rounded, slightly capitate	Apiculate	Slightly rostrate	Rostrate, protracted	Markedly protracted	Protracted, capitate to rostrate
Central area (raphe valve)	Large	Moderately large	Rather large	Large	Small	Large	Large	Small
Axial area (rapheless valve)	Narrow	Narrow	Narrow	Narrow	Broad	Narrow	Narrow	Narrow
Additional structure	Cavum	Absent	Absent	Cavum	Absent	Sinus	Absent	Sinus
Striae pattern	Multiseriate	Unknown	Multiseriate	Multiseriate	Unknown	Multiseriate	Biseriate	Multiseriate
References	Patrick 1945; Potapova 2010	Witkowski et al. 2000	Rovira et al. 2011	Sovereign 1958; Potapova 2015	Witkowski et al. 2000	Van de Vijver et al. 2013	Andrews 1981	This study

(17.0–26.0 µm long, 6.5–9.5 µm wide) and denser striae on both valves (raphe valve: 12–15/10 µm, rapheless valve: 14–16/10 µm), no additional structures are formed in the central area of the rapheless valve (Rovira et al. 2011). *P. oculatum* differs by its smaller cell size (10.0–20.0 µm long, 4.0–5.0 µm wide), denser striae on both valves (raphe valve: 20–24/10 µm, rapheless valve: 12–16/10 µm), broad axial area on the rapheless valve and absence of a sinus (Witkowski et al. 2000). Though *P. rostrolanceolatum* shows a sinus with circular depression on the rapheless valve, it has a large central area on the raphe valve and denser striae on both valves (raphe valve: 13–15/10 µm, rapheless valve: 14–16/10 µm) (Van de Vijver et al. 2013).

P. pseudolinkei is easily confused with *P. linkei* under LM, as they have the same valve outlines, overlapping valve dimensions, similar striae densities and unilateral central areas of the rapheless valves. Additionally, both species occur in marine habitats (Andrews 1981). *P. linkei* was originally reported by Schulz (1926) and described as *Achnanthes linkei* Hustedt in Hustedt (1939). Lange-Bertalot transferred it into the genus *Planothidium* (Lange-Bertalot 1999). Recently, Van de Vijver et al. (2018) re-examined the type material of *P. delicatulum* and found that most specimens are *P. linkei*. Based on the LM observations in Hustedt (1939) and Van de Vijver et al. (2018), *P. linkei* has a larger central area on the raphe valve and a narrower unilateral hyaline area on the rapheless valve than those of *P. pseudolinkei*. The ultrastructural features of *P. linkei* was firstly revealed in Andrews (1981) by using SEM. It can be seen that the clear space on the rapheless valve of *P. linkei* is actually a gap between the central striae without any depression (Andrews 1981). Thus *P. linkei* should be belonging to the *P. minutissimum*-group (Morales 2006; Rovira et al. 2011). In addition, the two species can also be distinguished by the striae pattern (multiseriate striae in *P. pseudolinkei* vs. biseriate striae in *P. linkei*). Witkowski et al. (2000) published three *P. linkei* LM photographs (plate 48, figs 42–44). However, the morphology of their specimen does not entirely correspond with the type material, because both raphe and rapheless valves have a relatively large central area (Hustedt 1939; Simonsen 1987; Witkowski et al. 2000). Most likely, these valves belong to an unknown *Planothidium* species, which needs to be further investigated.

Planothidium is a typical benthic diatom genus which has diverse ecological preferences, whether in freshwater, brackish or marine habitats (Kulaš et al. 2020). Species within the genus can attach to various inorganic and biotic substrates by their raphe valves (Spaulding et al. 2008; Wetzel et al. 2019; Morais et al. 2020). For example, *P. delicatulum* and *P. deperditum* (Giffen) A.Witkowski et al. are two epipsammic diatom species, *P. galaicum* and *P. hinzianum* C.E.Wetzel et al. are two epiphytic diatom species, and *P. africanum* Van de Vijver et al. and *P. wetzelii* Schimani et al. are two epilithic diatom species (Witkowski et al. 2000; Álvarez-Blanco and Blanco 2013; Wetzel et al. 2019; Juchem et al. 2023; Van de Vijver et al. 2023). Interestingly, Van de Vijver and Bosak (2019) also described an epizoic species, *P. kaetherobertianum*, which was on the carapace of one sea turtle. In the present study, the newly documented species is an epipsammic diatom collected from the intertidal zone in the city of Fangchenggang. As a unique benthic community, epipsammic diatoms are able to adapt to sandy environments with unstable substrates and insufficient nutrients and have only recently started to receive domestic research attention in China, such as Zhao et al. (2017), Zhang et al. (2020), Li et al. (2021) and Liu et al. (2022). Their results had illustrated the biodiversity of diatoms in this specific habitat and improved our understanding of marine epipsammic diatoms in China. We speculate that more newly described epipsammic taxa will be found along with the further investigation of sand samples from different coastal areas in China.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

Xantolis weimingii (Sapotaceae), a new species from the Yuanjiang River basin, Yunnan, southwest China

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Abstract

Xantolis weimingii **sp. nov.** (Sapotaceae) is described and illustrated from Yunnan, southwest China. The new species is morphologically most similar to *X. tomentosa* (Roxb.) Raf., but differs from the latter in the ovate or obovate leaves, entirely glabrous corollas, lanceolate, ca. 5 mm long staminodes, fringed at the base. We provided a distribution map and a preliminary conservation assessment for the new species. Additionally, an updated dichotomous key to all known species of *Xantolis* is presented.

Key words: Central Yunnan, critically endangered, dry-hot valley, endemism, staminode

Introduction

Xantolis Raf. (Sapotaceae, Chrysophylloideae) is a small genus of trees and shrubs that comprises approximately 14 species (van Royen 1957; Swenson and Anderberg 2005). Its distribution ranges from the eastern Himalayas to the Philippines in tropical Asia (van Royen 1957; Li 1987; Li and Pennington 1996). This genus is morphologically characterized by having obvious spines, acute anther appendages, lanceolate lobes of calyx and corolla, and aristate staminodes (Swenson and Anderberg 2005). Some members of the genus are of significant economic importance due to their edible fruits and high-quality timber (Li 1987).

The systematic position of *Xantolis* has been controversial. Pennington (1991) classified it as a member of the large tribe Chrysophylleae. Recent studies based on molecular data have demonstrated that *Xantolis* is recovered as a sister to the rest of the subfamily Chrysophylloideae, being a very isolated and poorly understood genus (Anderberg and Swenson 2003; Bartish et al. 2005, 2011; Swenson and Anderberg 2005). Therefore, further extensive sampling is still required to test the monophyly and synapomorphic characters, generic status, and phylogenetic position of *Xantolis* (Triono et al. 2007; Stride et al. 2014; Swenson et al. 2023).

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The Yuanjiang River is the mainstream of the upper reaches of the Hong (Red) River, while the Luzhijiang River, situated in central Yunnan in southwest China, is an upper tributary of the Hong River. The rain shadow effect created by the Ailao-Wuliang Mountains and the Yunnan-Guizhou Plateau results in a distinctive hot and dry climate in these valleys, in contrast to most of the surrounding regions (Jin and Ou 2000; Li et al. 2016). The climate in this region is characterized by a dry season (which can be further divided into a cool dry season from November to February and a hot dry season from March to April), with an annual average temperature of 24 °C and a mean annual evaporation capacity of 2700–3800 mm, which is three to six times higher than the mean annual precipitation (600–800 mm). There is also a wet season from May to October, during which 80–90% of the precipitation is concentrated (Jin 2002; Shen et al. 2010; Zhou et al. 2017). The relatively closed environment of the area has led to the formation and retention of a large number of rare and endangered plants and endemic species (Li et al. 2008; Ma 2016). Knowledge of biodiversity in the region seems far from complete, with many new species being described in recent years in different lineages of organisms (Bai et al. 2015; Zhou et al. 2017; Qiao et al. 2018; Yang et al. 2019; Ding et al. 2020; Liu et al. 2022; Ma et al. 2022; Wang et al. 2022; Yang et al. 2022a, 2022b, 2022c; Ma et al. 2023).

The new species of *Xantolis* described here, *X. weimingii* Huan C. Wang & Feng Yang, was first collected in the Luzhijiang Valley in August 2015. During our subsequent fieldwork, we encountered this species several times. However, only sterile or fruiting specimens were collected. In April 2022, the specimen with flowers was finally gathered in Wadie, Yuanjiang County. After a detailed comparison with morphologically similar species, we confirmed its novelty to science and describe it here as *Xantolis weimingii* Huan C. Wang & Feng Yang.

Materials and methods

Based on the morphological species concept defined by Cronquist (1978), the morphological studies of the new species were conducted on living plants and specimens coming from the four localities corresponding to the holotype and paratypes. The digital specimen images of similar species available at JSTOR Global Plants (https://plants.jstor.org/), the Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/botany/), and the Global Biodiversity Information Facility (https://www.gbif.org/) were extensively reviewed. Pertinent taxonomic literature (e.g. Clarke 1882; van Royen 1957; Aubréville 1963; Luo 1974; Wu 1977; Li 1987; Luo 1991; Li and Pennington 1996; Pham 1999; Santisuk et al. 2014; Sankara et al. 2019; Turner 2021) were extensively consulted. Measurements were taken using a ruler and a metric vernier caliper under a stereomicroscope (Olympus SZX2, Tokyo, Japan). The dot-distribution map was compiled from all specimens studied and generated with ArcGIS version 10.4 (ESRI, Inc., Redlands, USA). The conservation status was assessed using GeoCAT (online tool available at https://geocat.iucnredlist.org/) (Bachman et al. 2011) to estimate the extent of occurrence (EOO) and the area of occupancy (AOO) of the species, followed by applying the IUCN Red List Categories and Criteria (IUCN 2022) for conservation status assessment. The characters used in the identification key for the congeners mainly followed those of Van Royen (1957) and Li and Pennington (1996).

Taxonomy

Xantolis weimingii **Huan C. Wang & Feng Yang, sp. nov.**
urn:lsid:ipni.org:names:77348184-1
Figs 1–4

Type. China • Yunnan Province: Yuanjiang County, Wadie village, Luozhi village, near the junction of the Yuanjiang River and Hedihe River, 23°25'51.9"N, 102°18'42.4"E, alt. 1100 m, 14 April 2022, *C. Chen & Z. X. Li YJ19450* (holotype: YUKU 02074716!; isotypes: YUKU!).

Diagnosis. *Xantolis weimingii* is most similar to *X. tomentosa* (Roxb.) Raf., but can be easily distinguished by its ovate or obovate (vs. elliptic or elliptic-oblong in *X. tomentosa*) leaves, base broadly cuneate or nearly round (vs. cuneate), apex acute or acuminate (vs. obtuse, short obtusely or acutely acuminate), corollas entirely glabrous (vs. densely hairy at throat), 7.7–9.7 (vs. 4–8) mm long, lanceolate staminodes, ca. 5 (vs. 3–3.5) mm long, apex acuminate into an awn, fringed at the base (vs. broad base, not fringed), glabrous (vs. hairy).

Description. Shrubs or small trees, 2–4 m tall, evergreen, acanthaceous, laticiferous. Bark pale gray, cracked, shallowly and vertically fissured. Branches terete, gray to grayish black; branchlets densely ferruginous arachnoid-lanate, more or less glabrescent when old. Acantha usually axillary, straight, cuspidate, ca. 7 mm long. Petioles 4–8 mm long, with a slight furrow on the adaxial side, densely ferruginous arachnoid-lanate when young, gradually shedding, sparse or glabrescent when old. Leaves ovate to obovate, alternate, leathery, 2.0–8.5 cm long, 1.5–5.0 cm wide, base broadly cuneate or nearly round, apex acute to acuminate, slightly revolute, margin entire, adaxially dark-green, shiny, densely ferruginous arachnoid-lanate when young, glabrescent, abaxially densely ferruginous arachnoid-lanate when young, gradually faded to gray-green sericeous, or to glabrescent when old; midrib flat, obvious adaxially, prominent abaxially, lateral veins 6–9 pairs, arcuate, rising at an angle of 35°–50°, apex bifurcation near the margin, irregularly connected, tertiary and reticulate veins convex abaxially. Flowers in 1–5-flowered clusters in leaf axils or along old branches, pendant. Pedicels stout, terete, 3–4 mm long, densely ferruginous arachnoid-lanate. Calyx cup-shaped, 5-lobed, rarely 4-lobed; sepals imbricate, ovate to triangular, 6–7 mm long, 3.5–4.5 mm wide, apex acute, inside white pubescent on the upper part, outside densely ferruginous arachnoid-lanate. Corolla sympetalous, 5-merous, glabrous, slightly fleshy, tube ca. 4 mm long, lobes lanceolate, 3.7–5.7 mm long, apex acuminate, margin slightly involute, dentate at the base. Stamens 5, adnate to corolla tube at the base, opposite to lobes, filaments white, linear, 2.8–3.5 mm long; anthers sagittate, yellow, ca. 3 mm long, dorsifixed, longitudinal, apex acuminate, base cordate. Staminodes 5, glabrous adnate to corolla tube at the base, alternate to lobes, white, lanceolate, ca. 5 mm long, 1–2 mm wide at the base, apex acuminate into an awn, fringed at the base, glabrous. Ovary ovoid, densely brown pilose; style terete, yellow-green, ca. 8 mm long. Fruits ovoid, oblong or elliptic, with ferruginous arachnoid-lanate hairs, 2.2–4.5 cm long, 1.2–1.5 cm in diam., with persistent calyx, apex sometimes beaked, with persistent style, 1-seeded. Seeds oblong to ellipsoid, slightly compressed, 2–2.5 cm long, ca. 8 mm in diam., both ends truncate, pericarp woody, shiny yellowish brown, scar elliptic, 1.5–2 cm long, ca. 3 mm wide, whitish.

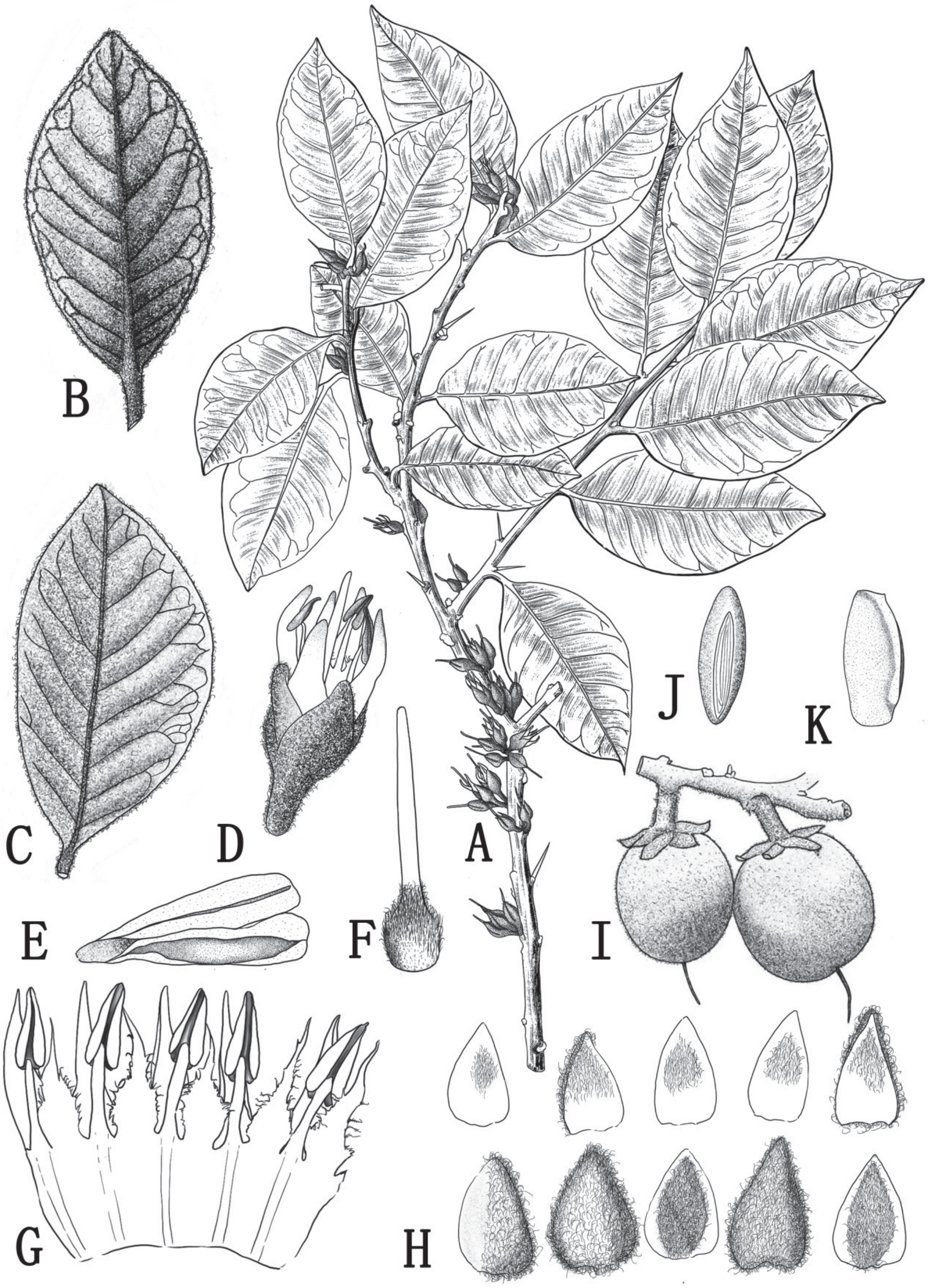

Figure 1. *Xantolis weimingii* sp. nov. (drawn by Qiu-Ping Wang) **A** habit **B** abaxial surface of leaf **C** adaxial surface of leaf **D** flower in blooming **E** anthers **F** pistil **G** corolla dissected to show stamens and staminodes **H** calyx lobes (the upper line is the inner view, the lower line is the outer view) **I** fruits **J** side view of seed to show scar **K** front view of seed.

Phenology. Flowering from April to May, and fruiting from May to October.

Etymology. The new species is named after Professor Weiming Zhu (朱维明-Wei Ming Chu, 1930–2023), a renowned botanist from Yunnan University, in recognition of his outstanding contributions to the study of China's flora of Lycophytes and Ferns and to the Herbarium of Yunnan University (Kunming, China).

Distribution and habitat. *Xantolis weimingii* is a rarely and poorly collected species endemic to the central Yunnan province in southwest China. As of now, it has been discovered in four different sites, all situated in the dry and hot valleys of both the Yuanjiang River and its primary tributary, the Luzhijiang River

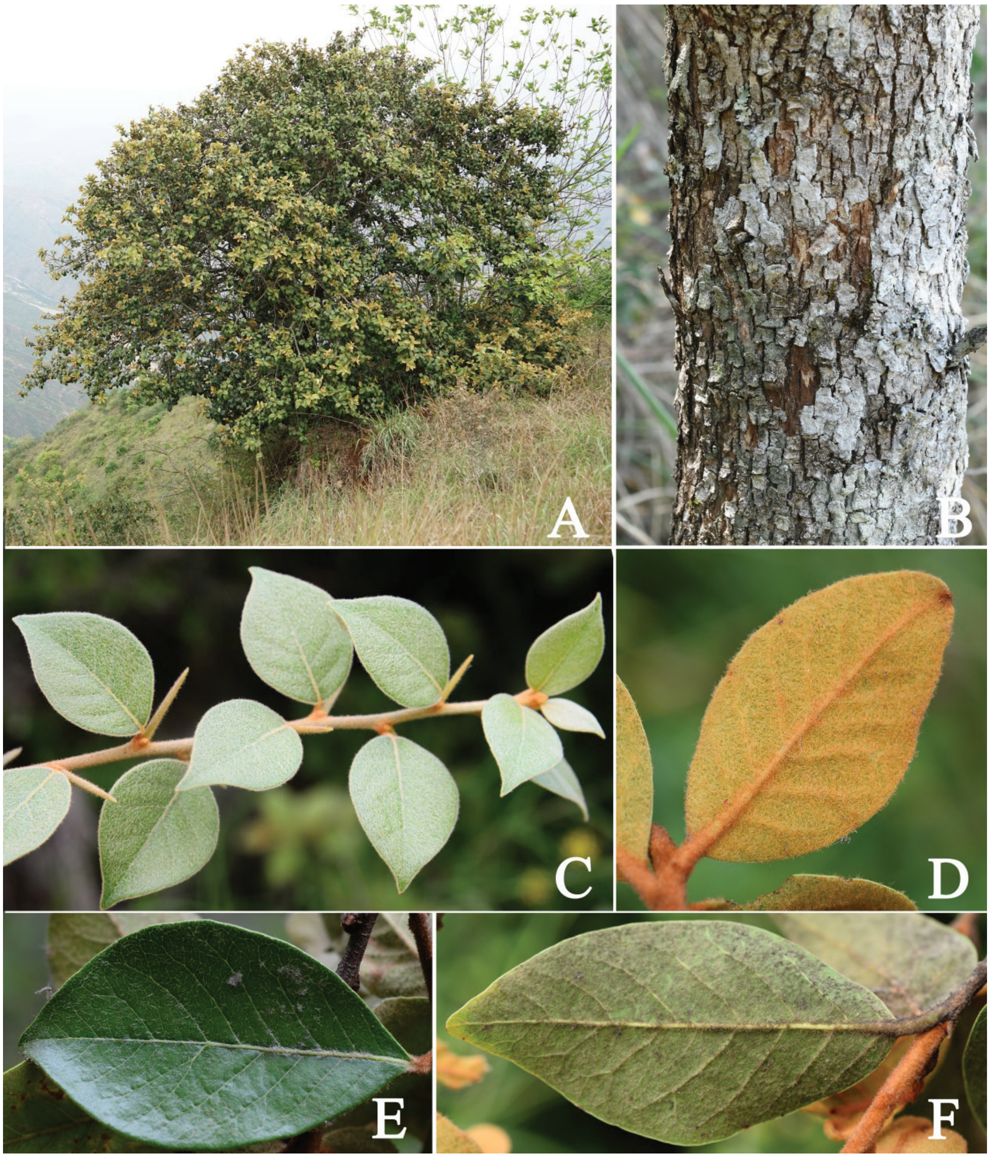

Figure 2. *Xantolis weimingii* sp. nov. **A** habit **B** trunk showing bark texture **C** branchlet **D** abaxial surface of tender leaf **E** adaxial surface of leaf **F** abaxial surface of leaf.

(Fig. 5). This new species grows in savanna habitats on the mountain slopes at elevations ranging from 1100 to 1400 m (Fig. 6).

Preliminary conservation assessment. *Xantolis weimingii* is at a restricted geographic range, with an estimated extent of occurrence (EOO) of 139.594 km^2 and an area of occupancy (AOO) of 12 km^2. Four populations of the new species have been discovered: two of them from the same locality (Yimen County), and one in the Yuanjiang National Nature Reserve. Unfortunately, these populations are typically small, ranging from three to a maximum of eight plants. So far, we have not found any saplings or seedlings in the Yuanjiang and Fawu populations, and we judged that the self-renewal capacity of the wild population of this species is low. The other populations in the Luzhijiang River valley at Yimen County are most threatened. The hillside land here is highly degraded and soil erosion is serious due to mining operations. Furthermore, residents had been harvesting the plant for firewood, resulting in the plant becoming a shrub-like appearance. Therefore, *Xantolis weimingii* is at a high risk of extinction due to

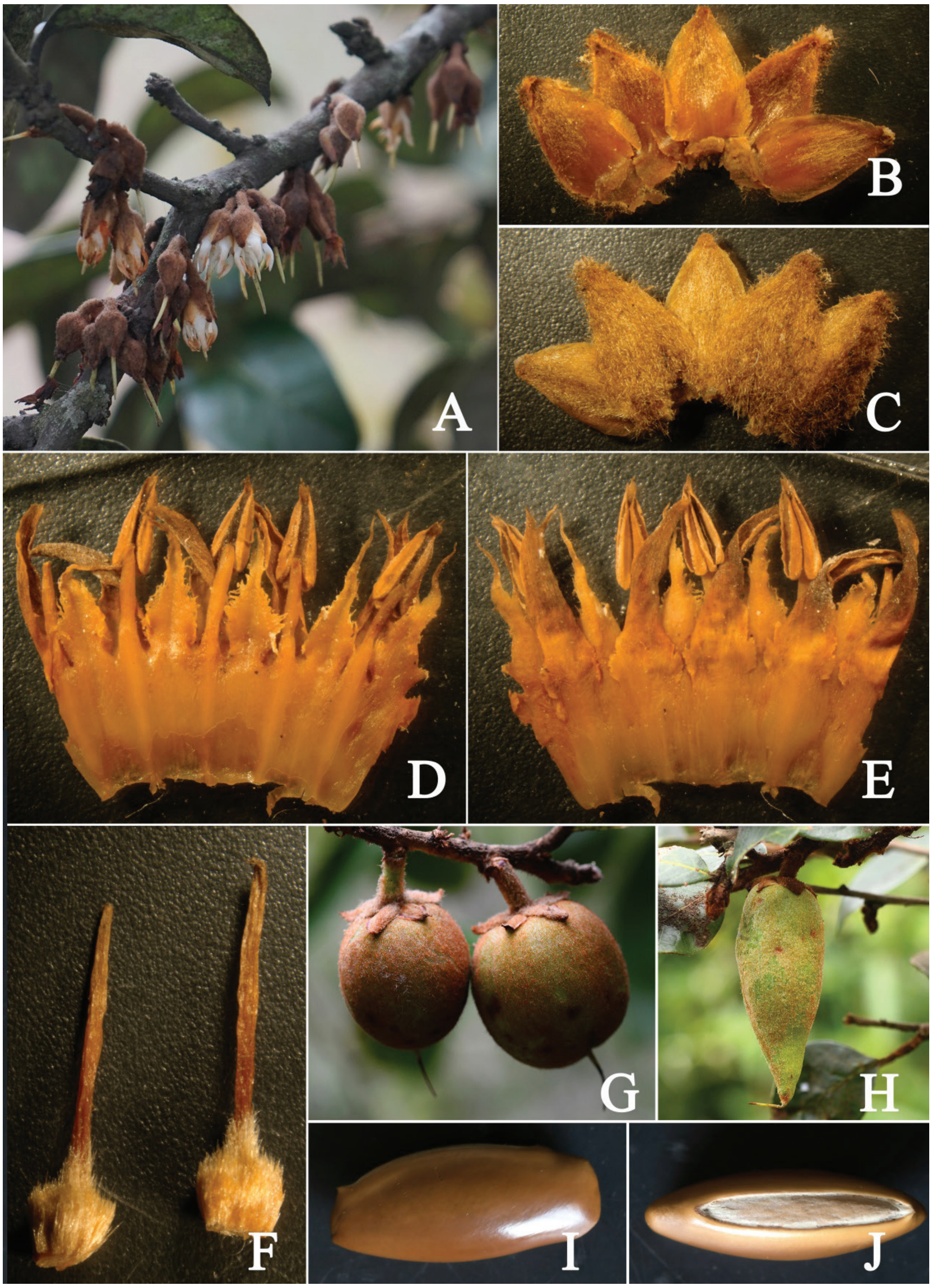

Figure 3. *Xantolis weimingii* sp. nov. **A** flowering branch **B** adaxial view of sepals **C** abaxial view of sepals **D** corolla dissected to show five stamens and five staminodes **E** corolla dissected to show five lobes **F** pistils **G–H** fruits **I** front view of seed **J** side view of seed to show scar.

a restricted geographic range, fragmented distribution, small population sizes, and fragile living environment. Based on IUCN Red List Categories and Criteria (IUCN 2022), we suggest a Critically Endangered (CR) category for the species.

Discussion. *Xantolis weimingii* can be easily distinguished from its congeners by the following combination of characters: plants densely covered with ferruginous arachnoid-lanate, leaves ovate or obovate, and staminodes fringed at the base. It is most similar to *X. tomentosa* (excluding the synonym *Planchonella dongnaiensis* Pierre ex Dubard), which is widely distributed in Sri

Figure 4. Holotype of *Xantolis weimingii* sp. nov. (YUKU-02074716).

Lanka, India, and Myanmar. However, it differs clearly from the latter by having pale gray (vs. light reddish brown in *X. tomentosa*) barks, ovate or obovate (vs. elliptic, elliptic-oblong) leaves, 2–8 (vs. 4–14) cm long, 1.5–5.0 (vs. 2–6) cm wide, base broadly cuneate or nearly round (vs. cuneate), apex acute or acuminate (vs. obtuse or short obtusely or acutely acuminate), 6–9 (vs. 8–l6) pairs lateral veins, 4–8 (vs. 3–20) mm long petioles, 3–4 (vs. 4–7) mm long pedicels, entirely glabrous (vs. throat densely hairy) corollas, 7.7–9.7 (vs. 4–8) mm long, lanceolate (vs. lanceolate-oblong or ovate) lobes, staminodes ca. 5 (vs. 3–3.5) mm long, 1–2 mm wide at the base, apex acuminate into an awn, fringed at the base (vs. broad base, not fringed), glabrous (vs. hairy).

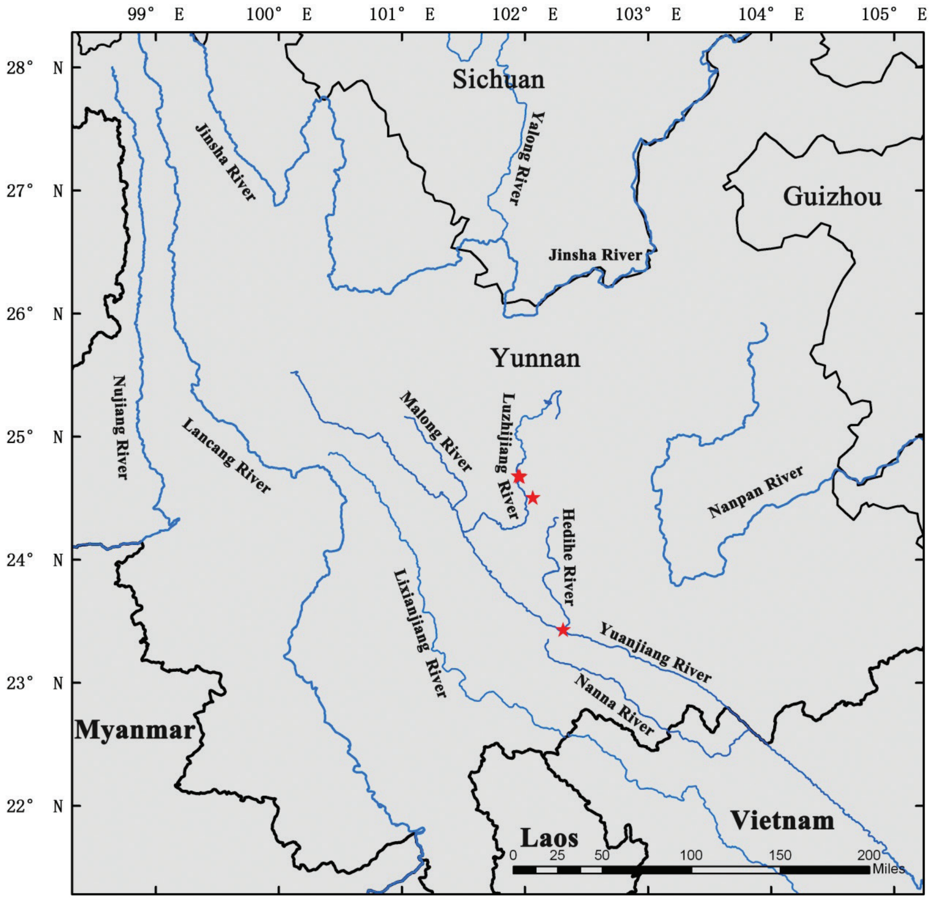

Figure 5. Known geographical distribution of *Xantolis weimingii* (red stars). Based on all known collections.

Xantolis weimingii is also morphologically similar to *X. cambodiana* (Pierre ex Dubard) P. Royen from Indo-China. Nevertheless, *X. weimingii* differs from *X. cambodiana* in having ovate to obovate (vs. rhomboid-obovate or elliptic, sometimes lanceolate in *X. cambodiana*) leaves, base broadly cuneate or nearly round (vs. tapering towards the base), apex acute to acuminate (vs. obtuse, entire or retuse, sometimes short obtusely acuminate), ovate to triangular (vs. ovate or oblong) sepals, 6–7 (vs. 2.5–4) mm long, 3.5–4.5 (vs. 1–2) mm wide, lanceolate (vs. lanceolate or linear) staminodes, ca. 5 (vs. 2–3) mm long, 1–2 (vs. ca.0.5) mm wide at the base. *Xantolis weimingii* shares similar fruits with *X. assamica* (C.B. Clarke) P. Royen, a species occurring in Assam to Bangladesh, but differs from the latter in its 4–8 (vs. 5–15) mm long petioles, ovate to obovate (vs. ovate, elliptic or broadly lanceolate) leaves, 2.0–8.5 (vs. 6–16.5) cm long, 1.5–5.0 (vs. 2–7) cm wide.

Additional specimens examined. China • Yunnan: Yimen County, near Xiaoluzhi village, the west side of Luzhijiang valley, 24°40'46.21"N, 101°56'49"E, 25 September 2015, *H. C. Wang et al. YM241* (YUKU, plant in vegetative period); same location, 27 April 2016, *H. C. Wang et al. YM863* (YUKU, plant in vegetative period); Luzhijiang valley, near Luzhi town, 12 November 2019, *H. C. Wang et al. YM8317* (YUKU, plant in vegetative period); • Luzhijiang valley, near Xiaoluzhi village, Maomao mountain, on the limestone of the dry-hot valley, 24°40'30.9"N, 101°57'37.21"E, elev. 1392.46 m, 25 December 2021, *H. C. Wang et al. YM14630* (YUKU, plant in vegetative period); • Eshan County, Dalongtan, the mountain

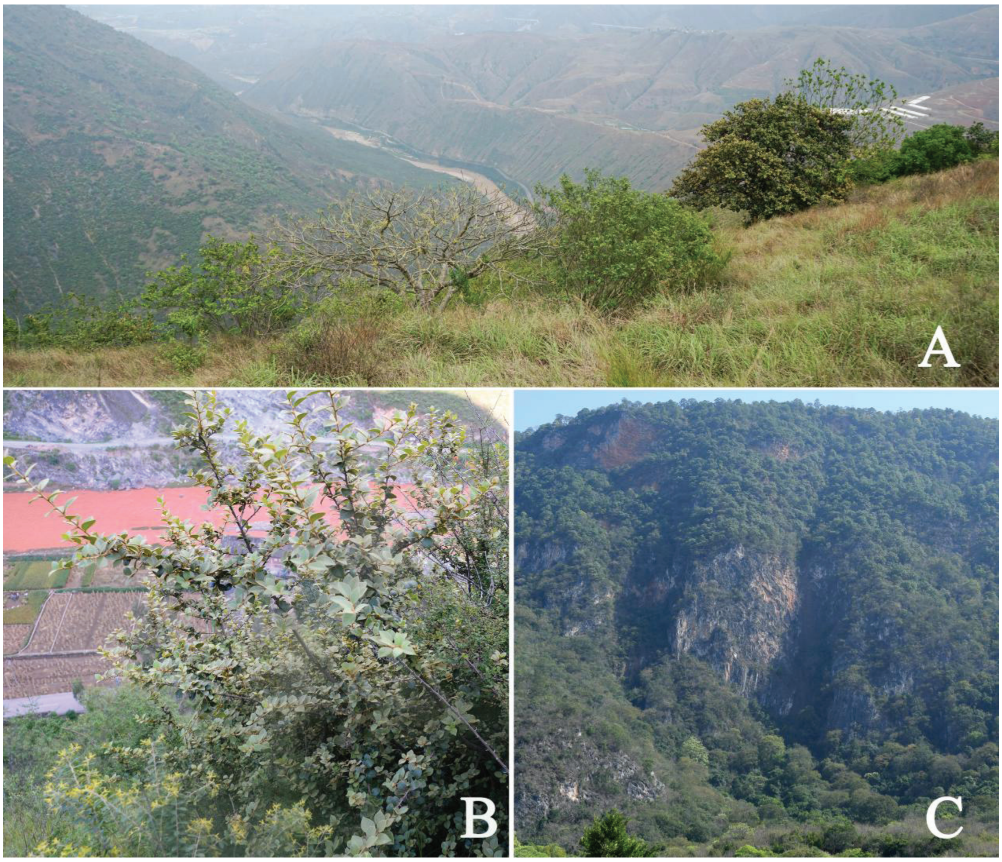

Figure 6. Habitat of *Xantolis weimingii* **A** habitat of the Yuanjiang population **B** habitat of the Yimen population **C** habitat of the Eshan population.

behind the Fawu village, 24°30'14.17"N, 102°03'46.60"E, alt. 1400 m, 20 August 2015, *H. C. Wang et al. ES173* (YUKU, plant during grain-filling period); • same location, 9 June 2016, *H. C. Wang et al. ES866* (YUKU, plant in late flowering and fruiting period); • same location, 17 September 2017, *H. C. Wang et al. ES2450* (YUKU, plant during grain-filling period); • same location, 27 April 2022, *H. C. Wang et al. YM16402* (YUKU, plant in vegetative period).

Identification key to the species of *Xantolis*

1 Lateral veins numerous, not convex abaxially **2**
– Lateral veins few, conspicuously elevated abaxially **5**
2 Sepals glabrous adaxial, staminodes pubescent adaxial ...... ***X. baranensis***
– Sepals pubescent adaxial, staminodes glabrous adaxial **3**
3 Stems sometimes creeping, with numerous spines; leaves suborbicular .. .. ***X. maritima***
– Stems not creeping, sometimes with occasional spines; leaves spatulate, obovate-oblong, obovate or elliptic **4**
4 Flowers small, corolla 6–9 mm long, lobes lanceolate, 5–6 mm long, ca. 1.5 mm wide, stamens 4–5 mm long, staminodes lanceolate, ca. 3 mm long.. ***X. parvifolia***
– Flowers slightly larger, corolla 10–14 mm long, lobes linear, 7–10.5 mm long, 2–3 mm wide, stamens 6–8.5 mm long, staminodes ovate, 4–7.5 mm long .... ***X. longispinosa***

5 Aspect ratio of mature leaves 1.3–2.5.. **6**
– Aspect ratio of mature leaves 2–4.. **11**
6 Pedicels 7–11 mm long.. ***X. burmanica***
– Pedicels 3–7 mm long.. **7**
7 Staminodes fringed at the base.. **8**
– Staminodes not fringed at the base.. **10**
8 Flowers in clusters along 0.7–3 cm long axillary shoots........ ***X. racemosa***
– Flowers solitary or in clusters along branchlets.. **9**
9 Leaf blades ovate or obovate, apex acute to acuminate; staminodes longer than or equal to stamens.. ***X. weimingii***
– Leaf blades rhomboid-obovate or elliptic, apex obtuse, entire or retuse; staminodes shorter than stamens.. ***X. cambodiana***
10 Leaves spatulate or elliptic, sometimes rhomboid-oblong, 2–3.5 cm long, (0.6–) 1–2 cm wide, base tapering into petioles; secondary nerves 5–10, ascending at an angle of 40°–45°.. ***X. siamensis***
– Leaves elliptic-oblong, ovate or obovate, 4–14 cm long, 2–6 cm wide, cuneate at the base, decurrent; secondary nerves 8–16, ascending at an angle of 50°–80°.. ***X. tomentosa***
11 Leaves 12–22 cm long, 2–7 cm wide, secondary nerves 10–17; pedicels pubescent.. **12**
– Leaves 6–12 cm long, 2.8–5.5 cm wide, secondary nerves 5–13; pedicels glabrous.. **15**
12 Sepals ovate, apex subobtuse; corolla lobes 7–9 mm long, 2.5–3.5 mm wide; staminodes 6–7 mm long.. ***X. hookeri***
– Sepals lanceolate, apex acute; corolla lobes 3–6 mm long, 1.5–2 mm wide; staminodes 2.5–4 mm long.. **13**
13 Leaves ovate, elliptic or broadly lanceolate, 6–16.5 cm long, 2–7 cm wide; secondary veins of leaf 9–15, ascending at an angle of 60°–85°.. ***X. assamica***
– Leaves lanceolate, oblanceolate or oblong-lanceolate, 5–18 cm long, 2–5 cm wide; secondary veins of leaf 15–17, ascending at an angle of 40°–55°.. **14**
14 Sepals lanceolate to ovate-lanceolate, 4–6 mm long, 1.5–3 mm wide; fruit ferruginous, sericeous to pubescent.. ***X. stenosepala***
– Sepals ovate, 3–4 mm long, 2–3 mm wide; fruit subglabrous.. ***X. stenosepala* var. *brevistylis***
15 Corolla lobes fimbriate at the base.. ***X. shweliensis***
– Corolla lobes entire.. **15**
16 Fruits glabrous; secondary veins of leaf 5–8, ascending at an angle of 35°–55°.. ***X. boniana***
– Fruits pubescent; secondary veins of leaf 9–13, ascending at an angle of 50°–65°.. **17**
17 Scar of seed as long as the seed, seeds 2–3 cm long.. ***X. boniana* var. *rostrata***
– Scar of seed 2/3 the length of the seed, seeds up to 2 cm long.. ***X. boniana* var. *pavieana***

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

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

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Research Article

George Gardner's enigmatic species *Goyazia villosa* (Gesneriaceae) finally rediscovered

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Abstract

Tapina villosa (Gesneriaceae) was published by George Gardner in 1842, based on material he collected in Serra de Natividade (Tocantins, Brazil) in 1840. The species is now recognized as *Goyazia villosa* (Gardner) R.A. Howard. Since Gardner's travels in Central Brazil, this species had not been collected again and the taxon was considered as possibly extinct. After a long time, we report the discovery of two new populations of *G. villosa* in the municipality of Palmas and in the Estação Ecológica Serra Geral do Tocantins, ca. 200 and 100 km north of the Serra de Natividade, respectively. The newly collected materials allow us to better characterize the morphology and infer the phylogenetic placement of this poorly-known species. Here we demonstrate that *G. villosa* is closely related to *G. rupicola* in a clade including *Goyazia* and *Mandirola* species, and provide an updated description of the species, including field images, photographic plate, information on its distribution and habitat, and a taxonomic key for the species of *Goyazia*.

Key words: Cerrado, Gloxiniinae, protected area, savanna

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Introduction

George Gardner (1812–1849), a Scottish botanist, intensively explored the Brazilian Cerrado between the years 1836 and 1841, collecting thousands of plant specimens. He also described and published many new plant species from this phytogeographic region, most of them published in the illustrated botanical magazine named Icones Plantarum (Gardner 1842). Between October 1839 and February 1840, Gardner stayed at Vila de Natividade, a locality today known as the county town Natividade in Tocantins State (Fig. 1), to explore and describe the flora and geology of the mountains east of the town (Gardner 1942: 283). It is where Gardner collected plant specimens that he later described as *Tapina villosa* Gardner. This species is currently classified as *Goyazia villosa* (Gardner) R.A. Howard and was until now only known by Gardner's type collection.

Since the first description of *Tapina villosa*, this species was subsequently classified into different genera: *Tapeinotes villosa* (Gardner) Walp., *Ligeria villosa* (Gardner) Hanst., *Anetanthus villosus* (Gardner) Benth. & Hook.f. ex B.D. Jacks., and *Gloxinia villosa* (Gardner) Wiehler. The latter is an illegitimate name because *Gloxinia villosa* (Gardner) Wiehler is a later homonym with *Gloxinia villosa* (Lindl.) Mart., which is currently placed in *Sinningia villosa* Lindl. The current classification of *Tapina villosa* in *Goyazia* Taubert was proposed by Howard (1975), based on characters such as “shape and lobing of the corolla, adherence of all four anthers, pubescent ovary, and the scaly rhizomes”. The genus *Goyazia* also includes two other species endemic to Brazil (*G. rupicola* Taub. and *G. petraea* (S.M. Phillips) Wiehler) that are also found on rocky outcrops within the Cerrado phytogeographic domain (Araujo 2007, 2024). The genus belongs to the subtribe Gloxiniinae and has strong morphological and phylogenetic affinities with *Mandirola* Decne. (Araújo et al. 2010). Currently, *Goyazia villosa* is an accepted name in the Flora e Funga do Brasil (Araujo 2024), although Roalson et al. (2005) treated the species as *incertae sedis* and possibly related to *Phinaea* Benth. Therefore, the taxonomic placement of *G. villosa* was ambiguous and needed to be reexamined based on additional morphological and phylogenetic data.

Recent floristic exploration in the savannas of the Jalapão region (Tocantins) has resulted in a large number of new species described, as well as new records of poorly known taxa (e.g. Yamamoto et al. 2008; Araújo et al. 2016; Borges and Antar 2016; Mendes et al. 2017; Antar et al. 2018; Pastore and Antar 2021; Santana and Simon 2022). However, most of this vast area remains poorly collected (Antar and Sano 2019; Santana and Simon 2022). To fill gaps in floristic knowledge, we organized expeditions to different localities in the state of Tocantins in 2017, and also carried out a survey of the vascular flora of the Estação Ecológica Serra Geral do Tocantins (EESGT) between 2018 and 2022. Several floristic novelties that resulted from these expeditions have already been published (Alves et al. 2018; Guimarães et al. 2021; Mendes et al. 2022; Schindler et al. 2023).

In the context of these expeditions, we discovered two populations of *G. villosa* in the central and eastern parts of Tocantins, more than a century and a half after Gardner first collected this species. In this paper, we present an updated and detailed morphological description of *G. villosa* including field images, distribution maps, habitat preferences, as well as a taxonomic key for the species of *Goyazia*. Phylogenetic analyses were also conducted using newly obtained nrDNA ITS sequences to verify the placement of *G. villosa* within the Gloxiniinae.

Material and methods

In 2005 and 2013, expeditions aiming to collect *G. villosa* were carried out in the type locality at Serra de Natividade and surrounding areas by two of the authors (AOA and AC). However, no plants of *G. villosa* were located in this area. Subsequent field expeditions were carried out in different parts of the state of Tocantins in 2017. Field expeditions to survey the flora of EESGT were conducted by three of the authors (BS, MF, and MFS) between 2018 and 2022 (Schindler et al. 2023). EESGT is a large protected area (716,306 hectares) located in the eastern portion of the state of Tocantins and the extreme west of the state of Bahia (Fig. 1). According to Köppen’s classification, the climate corresponds to

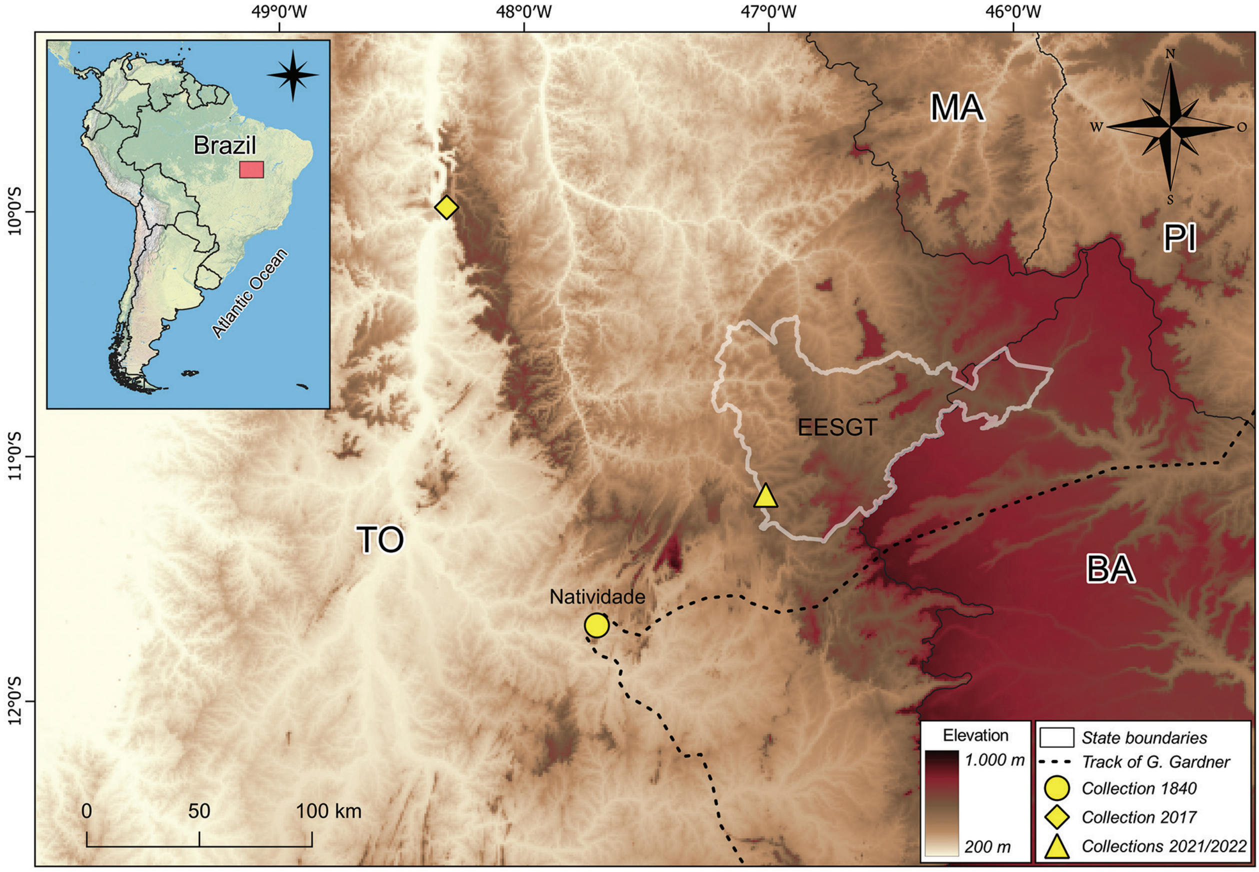

Figure 1. Location of the type collection of *Goyazia villosa* made in 1840 (circle) and new records made in the municipality of Palmas in 2017 (diamond) and Estação Ecológica Serra Geral do Tocantins (EESGT) in 2021 and 2022 (triangle). Brazilian states: BA (Bahia), MA (Maranhão), PI (Piauí), TO (Tocantins). Track of G. Gardner based on the Atlas dos Viajantes no Brasil (https://viajantes.bbm.usp.br/). Map produced with QGIS (QGIS Development Team 2024).

a tropical climate with dry winter, with rain from November to April and marked dry season from May to October (*Aw*) (Alvares et al. 2014), and altitudes range from 400 to 730 m. Vegetation types in EESGT include savannas and grasslands, which dominate the landscape, as well as riverine forests and swamps along water courses (Franke et al. 2018).

Observations and photographic records of the species were carried out in the field in 2017, 2021, and 2022. Collections were deposited in the CEN, G, R, RB, and SORO herbaria (acronyms according to http://sweetgum.nybg.org/science/ih/). Identification of the specimens collected was based on the protologue (Gardner 1842) and comparisons with digital images of the types deposited at BM, CGE, E, FI, G, K, P, and W. Morphological terminology used in the description follows Beentje (2010) and Font Quer (2001) for general morphology, and Ellis et al. (2009) for leaf venation. The assessment of the species conservation status followed the IUCN guidelines (IUCN 2024) using criterion B (geographic range). Estimates of Area of Occupancy (AOO) and Extent of Occurrence (EOO) were calculated using QGIS, version 3.28 (QGIS Development Team 2024). We used land cover maps from the Mapbiomas platform (Projeto MapBiomas, 2024) to estimate *G. villosa* habitat availability and reduction based on the variation of native vegetation and anthropic areas within the EOO of the species between 1986 and 2021.

The ribosomal DNA internal transcribed spacer (ITS) of a newly collected sample of *G. villosa* (*B. Schindler et al. 41*) was sequenced to estimate the phylogenetic placement of this species within the Gloxiniinae. Leaves from a plant collected in the field were immediately dried in silica gel. DNA was extracted from tissues samples using the SILEX method (Vilanova et al. 2020). Amplification and sequencing of ITS follow the procedures described in Araújo et al. (2010). The newly acquired sequence was deposited in EMBL/GenBank (no PP468351) and was added to the ITS alignment generated by Araújo et al. (2010), which includes 13 Gloxiniinae genera. Maximum likelihood analysis of this dataset was conducted using the software RAxML (Stamatakis 2014) through the web-server of the Swiss Institute of Bioinformatics (Kozlov et al. 2019). The unpartitioned sequence alignment was analyzed using the GTR + GAMMA model. The robustness of the tree was evaluated with bootstrap resampling and 1000 replicates.

Results

Taxonomic treatment

***Goyazia villosa* (Gardner) R.A. Howard, J. Arnold Arbor. 56(3): 367. 1975.**

≡ *Tapina villosa* Gardner. Type: Brazil. Goyaz [Tocantins]: in dry clefts of rocks near the summit of the Serra de Natividade, February 1840, *G. Gardner 3875* (lectotype: K [barcode] K000509791 image!; isolectotypes BM [barcodes] BM000793292, BM000883802 images!, CGE [barcode] CGE00055228 image!, E [barcodes] E00062346, E00062347 images!, FI [barcode] FI009756 image!, G [barcodes] G00365532, G00365534, G00365541 images!, P [barcodes] P00587409, P00587410, P00587411 images!, W [barcodes] W0005013, W0192283 images!).

Description. Herb, rupicolous, with a perennial scaly rhizome at the base of the roots, stem 1–10 cm long, erect, unbranched, green *in vivo*, villous. Leaves in basal pseudo-rosette or opposite and arranged in 2–5 pairs along the stem, anisophyllous, internodes 0.2–3 cm long, petiole 2–8 mm long, terete, green, villous, blade 1–3.5 × 0.3–2.5 cm, ovate-elliptic or elliptic, symmetrical, membranaceous, pubescent on both faces, tector trichomes unicellular or multicellular uniseriate, base obtuse or cuneate, apex acute or acuminate, margin serrate with 5–14 teeth, lateral veins 4–5 per side. Inflorescence composed of a single flower on leaf axil, pedicel 1.8–3.5 cm long, erect, villous; sepals subequal, 3–4 × 0.5 mm, linear-lanceolate, subulate at the apex, villous; corolla tubular-infundibuliform, pseudo-actinomorphic, 10–12 mm long, white at base, tube dark purple, lobes 5, 3–4 mm long, subequal, marked with 3 lines of purple and faint dots, with white towards the apex, margin subdentate, throat with wine red dots; stamens 4, filaments glabrous, anthers coherent, nectary dehiscent, annular; ovary superior, ovoid, villous, style 3.5–4 mm long, villous at base, glabrous at the apex, stigma stomatomorph. Fruit a dry loculicidal capsule, dehiscent at the apex, seeds black.

Additional specimens examined. Brazil • Tocantins, Palmas, Serra do Lajeado; 09°58'55"S, 48°19'00"W; 295 m, fl.; 5 Apr 2017; *R.J.V. Alves & N.G. Silva 12586* (CEN, R); • Tocantins, Ponte Alta do Tocantins, ESEC Serra Geral do Tocantins, rio das Balsas, Cachoeira da Fumaça; 11°09'22"S, 47°00'43"W; 467 m, fl. and fr.; 2 Mar 2021; *B. Schindler*, *M. Figueira*, *M.F. Simon*, *V.F. Gomes*, *W.B. Silva 41* (CEN, RB); • idem; 11°09'22"S, 47°00'45"W; 465 m, fl.; 15 Mar 2022; *M. Figueira*, *B. Schindler*, *M.F. Simon*, *R.R. Souza*, *V.F. Gomes*, *W.B. Silva 1808* (CEN, G [barcode] G00447873, R, RB, UB).

Distribution and habitat. The species is endemic to the state of Tocantins, Brazil (Fig. 1). It has been recorded in the municipalities of Natividade, Palmas, and Ponte Alta do Tocantins. Recent records were made in a humid and shaded hillside, in the Serra do Lajeado, at around 295 m of altitude (*R.J.V. Alves & N.G. Silva 12586*), and also in a riparian forest on shaded humid sandstone walls in the locality known as Cachoeira da Fumaça, in the southwest corner of the EESGT, at around 470 m of altitude (*B. Schindler et al. 41 and M. Figueira et al. 1808*) (Fig. 3A–C). Description of the habitat by Gardner on the specimen label indicates that the plant was collected "in dry clefts of rocks near the summit of the Serra de Natividade". In contrast, our field observations suggest that *Goyazia villosa* grows in humid and shaded sites. Preference of *G. villosa* for drier sites is however not unlikely because of its rhizomes with fleshy scales (Fig. 2B) that allow the plant to become dormant during the dry season, and grow and reproduce during the rainy season. This feature has already been reported for other genera of Gloxiniinae (Araújo et al. 2010).

Phenology. Flowers and fruits between December and April during the rainy season.

Etymology. The genus name is a reference to the state of Goiás (formerly spelled as Goyaz in old Portuguese orthography). The plant was collected in an area that now belongs to the state of Tocantins. The specific epithet refers to the trichomes found throughout the plant.

Conservation status assessment. *Goyazia villosa* is currently known from only three localities, where it inhabits a very specific habitat. It has an AOO of 12 km^2 and EOO 9103.44 km^2. Analysis of land use within *G. villosa* range (EOO) revealed a reduction of 1616 km^2 over 35 years, which represents an increment of anthropic areas from 9.0% in 1986 to 17.7% in 2021. Considering its AOO < 500 km^2, number of locations ≤5, and continuing decline in extent of occurrence, we preliminary assign a category of endangered (EN) for *G. villosa* under IUCN criterion B2ab(i).

Although known from only three localities and inhabiting a very specific habitat, *G. villosa* occurs in a region that still harbors much of its native vegetation, despite the observed vegetation loss over its range. The two newly reported populations are between 100 and 200 km from the type collection. The area covered within its current range harbors a number of unexplored sites of potential occurrence of *G. villosa*, including several mountain ranges, which could increase its AOO. Recently documented habitats of *G. villosa* are either unsuitable for agriculture (rocky outcrops) or protected by environmental regulations (riparian forests), which reduces the chances of loss of this specific habitat. The overall extent of occurrence of *G. villosa* in eastern Tocantins includes a large protected area (EESGT). One negative aspect in the conservation of this species is that the population found in Cachoeira da Fumaça within the EESGT may suffer from trampling since a patch of individuals of *G. villosa* is located along a trail used by the numerous visitors to the waterfall. The rarity of *G. villosa* is probably a result of strong habitat specificity and insufficient collecting effort across its geographic range, which could explain the paucity of records. Finally, more sampling is needed to understand its entire geographical range.

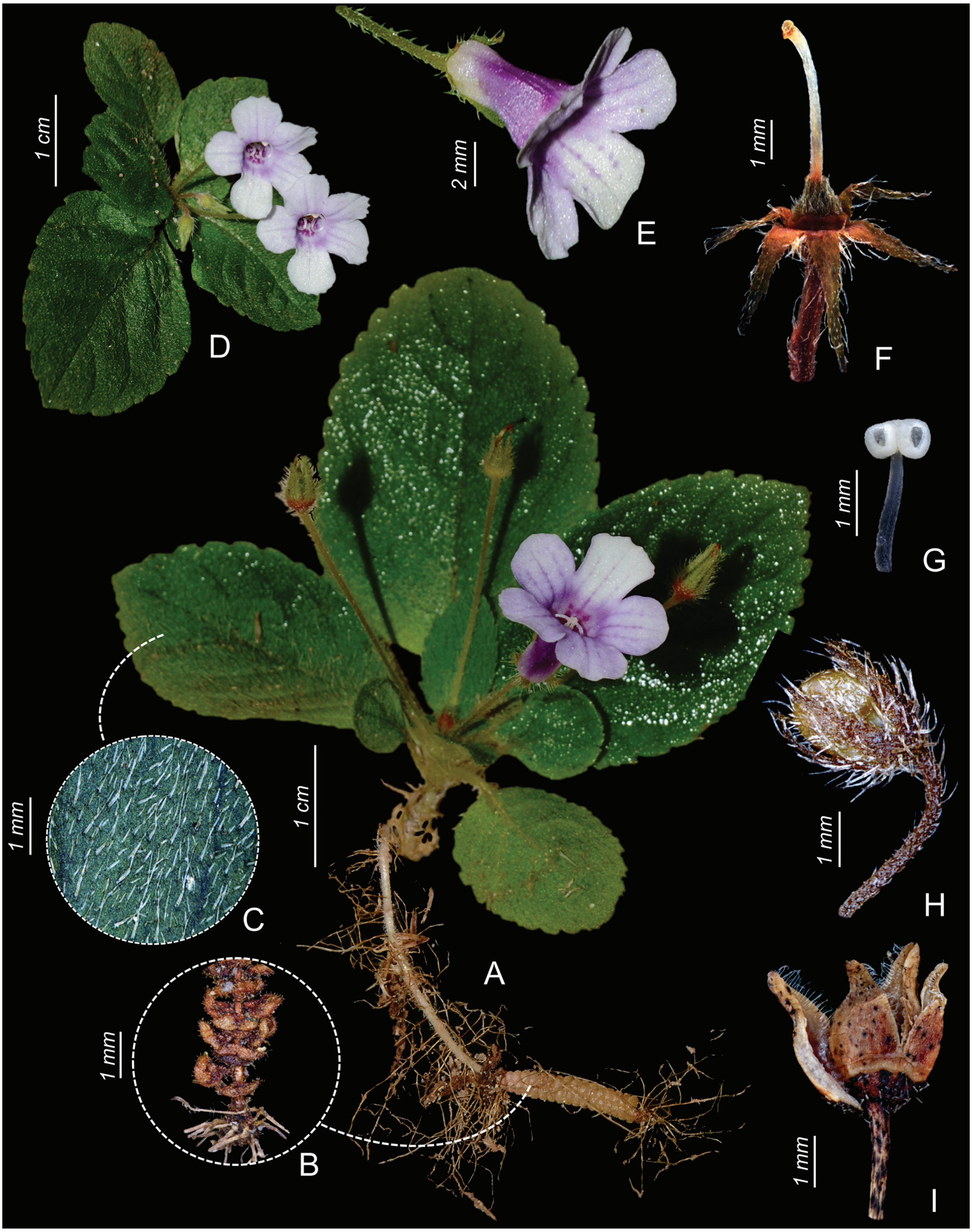

Figure 2. *Goyazia villosa* (Gardner) R.A. Howard **A** habit **B** detail of rhizome with fleshy scales **C** detail of leaf trichomes on the adaxial surface **D** front view of corolla **E** lateral view of corolla **F** detail of sepals, ovary, and ring nectary (corolla removed) **G** stamen **H** immature fruit **I** open capsule. Photographs by M. Figueira and B. Schindler from M. Figueira et al. 1808.

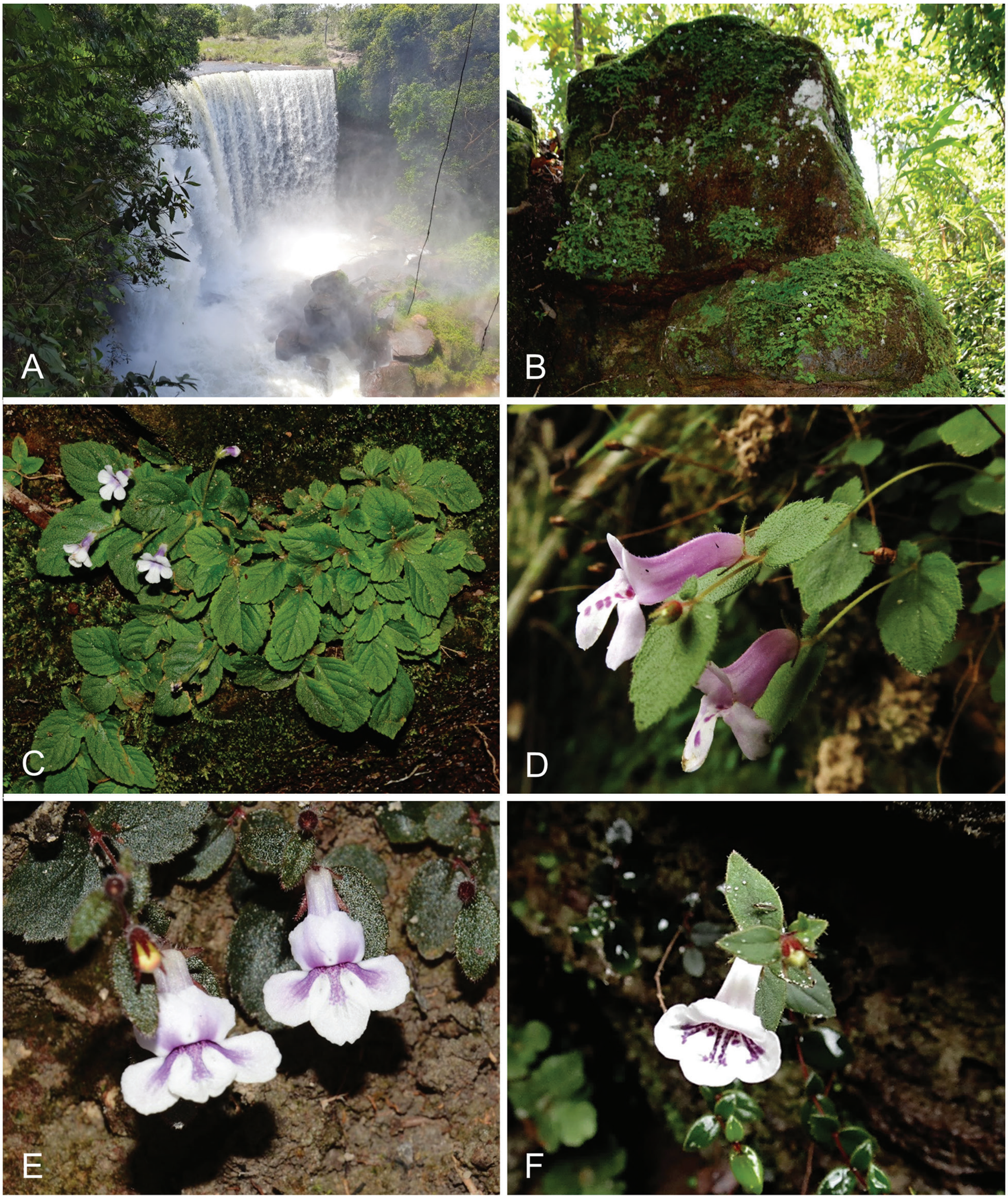

Figure 3. Habitat and habit of *Goyazia* **A** Cachoeira da Fumaça at the Estação Ecológica Serra Geral do Tocantins **B** habitat of *G. villosa* on rocky outcrops **C** frontal view of *G. villosa* attached to sandstone rocks **D** lateral view of individuals of *G. petraea* **E, F** habit of *G. rupicola*. Photographs: **A–C, E** M. Figueira and B. Schindler **D** and **F** A.O. Araujo; photos from collections: **B, C** M. Figueira et al. 1808 **D** A.O. Araujo et al. 1065-24 **E** M. Figueira et al. 1897 **F** A.O. Araujo et al. 1082.

Updated key to species of *Goyazia*

1 Plant rosette-like; stems not-filiform, villose; leaf margin usually bearing more than 5 teeth per side, petioles 2–8 mm long; flowers long-pedicellate, pedicel more than 1.8 cm long, corolla tubular-infundibuliform, pseudo-actinomorphic, macules restricted to the throat with lines of faint dots on the lobes (endemic to the state of Tocantins) .... ***G. villosa* (Figs 2, 3B, C)**

– Plant with developed stem; stems filiform, glabrous or pubescent; leaf margin entire or bearing 2 or 3 teeth per side, petioles inconspicuous or lacking; flowers short-pedicellate, pedicel less than 0.5 cm long, corolla bilabiate, zygomorphic, macules spreading to the lobes (widespread in the Brazilian Cerrado) **2**

2 Corolla tube externally white, light lilac, or with purplish to lilac longitudinal lines; nectary forming a ring (occurring in the states of Goiás, Maranhão, Minas Gerais, Pará, and Tocantins)........................... ***G. rupicola* (Fig. 3E, F)**

– Corolla tube externally pink or lilac; nectary formed by 5 glands, lobed and free from each other (occurring in the states of Mato Grosso and Mato Grosso do Sul) .... ***G. petraea* (Fig. 3D)**

Phylogenetic relationships

The topology of the phylogenetic tree resulting from our RAxML analysis (Fig. 4) is fully congruent with the Bayesian 50% majority rule consensus tree shown in Araújo et al. (2010). *G. villosa* is inferred as sister to *G. rupicola* but this relationship is not statistically supported (BS < 50%). In contrast, *G. villosa* is nested in a strongly supported clade (BS = 100%) that includes all *Goyazia* and *Mandirola* species.

Discussion

The rediscovery of *G. villosa* was made possible by active search and botanical exploration of moist cliffs, and its very specialized habitat. These cliffs are known for hosting vascular plant assemblages, which typically include small species of Gesneriaceae, *Pitcairnia* (Bromeliaceae), *Anemia* (Anemiaceae), and liverworts. Gardner's description of the locality of *G. villosa* as 'dry' may refer to the rocky clefts providing protection from direct insolation, thereby maintaining a relatively humid microclimate. The populations rediscovered between 2017 and 2022 were growing in very humid conditions. These occurrences confirm that the species still persists in the wild and calls for more intensive field surveys of the Cerrado's endemic flora. Analysis of the recent collections of *G. villosa* allowed a better understanding of the morphological traits that characterize this species. The presence of a scaly rhizome is illustrated here for the first time (Fig. 2B). This feature, together with the small habit of the plant, the coherent four anthers, and the pubescent ovary are congruent with the placement of this species in the genus *Goyazia* (Howard 1975). The species can be easily differentiated from the two congeners (*G. petraea* and *G. rupicola*) by serrate leaf margin and long (1.8–3.5 cm) pedicels (Figs 2, 3D).

Recent collections also provided material for ongoing studies on pollen micromorphology that preliminarily show that *G. villosa* shares many characters

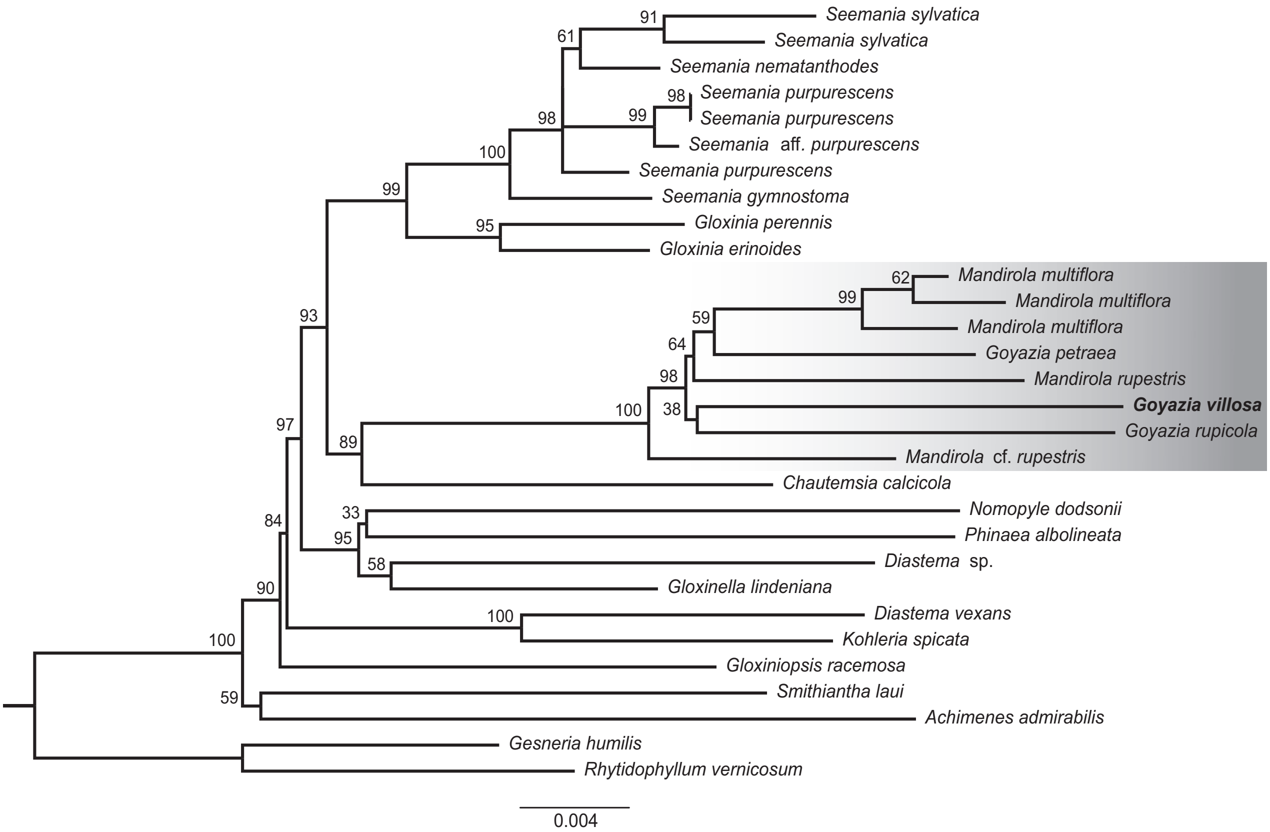

Figure 4. Maximum Likelihood tree resulting from the analysis of the nuclear ribosomal internal transcribed spacer (ITS) of 28 accessions of subtribe Gloxiniinae and two outgroups from subtribe Gesneriinae. The clade containing the rediscovered *Goyazia villosa* is highlighted in gray. Numbers above branches are bootstrap support values.

with the two other species of *Goyazia* and the three species of *Mandirola* (Souza et al., in prep.). In agreement with morphology, our preliminary phylogenetic analysis based on a single nuclear marker (ITS) places *G. villosa* together with *G. rupicola*, the type species of the genus, in a well-supported clade (BS = 100%) including species of *Goyazia* and *Mandirola* (Fig. 4). A natural intergeneric hybrid was recently described under the name *Goydirola* A.O. Araujo & M. Peixoto, indicating the close relationships between the two genera (Araujo et al. 2021). However, a more thorough study of the phylogenetic relationships based on a larger number of genes (Ogutcen et al. 2021) and a larger infraspecific sampling (Fiorini et al. 2020) is still needed to clarify the generic circumscription of *Goyazia* and *Mandirola* and to define the closest relative species of *G. villosa*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: BS, AOA, MFS, AC, MF. Data curation: MP, BS, MF. Formal analysis: MP. Methodology: MP. Resources: AC, MFS. Validation: AC, AOA. Writing – original draft: BS, MF. Writing – review and editing: RJVA, MFS, MP, AC, AOA, NGS.

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Data availability

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

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Research Article

Lysimachia ailaoshanensis (Primulaceae), a new species from Yunnan, China

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Abstract

A new species, *Lysimachia ailaoshanensis* is described and illustrated. In gross morphology it is evidently allied to subgen. *Palladia* sect. *Chenopodiopsis* and is most similar to *L. chenopodioides* and *L. remotiflora*, but is distinguished from *L. chenopodioides* by narrower lanceolate leaf blade and longer pedicel, and longer stamens and styles, and from *L. remotiflora* by narrower leaf blade and longer stamens.

Key words: Ericales, flora, morphological features, taxonomy, Yunnan

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Introduction

Ailao Mountain, located in central Yunnan, China, has rich plant diversity and was designated as a national natural reserve in 1988. In August 2020, Dr. H.F. Yan and colleagues of South China Botanical Garden made a botanical excursion to Ailao Mt., collecting plants of this area for systematic study on Primulaceae. A putatively new species of *Lysimachia* was secured. A subsequent field trip was conducted to confirm its entity. Careful examination revealed that the plant is distinct from all other *Lysimachia* species and represents an undescribed taxon.

Materials and methods

Earlier taxonomic literature has been consulted (e.g. Handel-Mazzetti 1928; Chen and Hu 1979; Chen et al. 1989; Hu 1985, 1992, 1999; Hu and Kelso 1996) to infer allied species and relatedness. The new species was examined in the field and at the herbarium, and measurements of morphological features were conducted with fresh specimens. Flowers were dissected and measured in the laboratory. Morphological comparison with similar species was performed based on living plants and specimens from IBSC, KUN, PE, IBK and from the images of specimens from the JSTOR Global Plants (http://plants.jstor.org/). The conservation status of the new species was assessed following the guidelines for using the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2024).

Taxonomic treatment

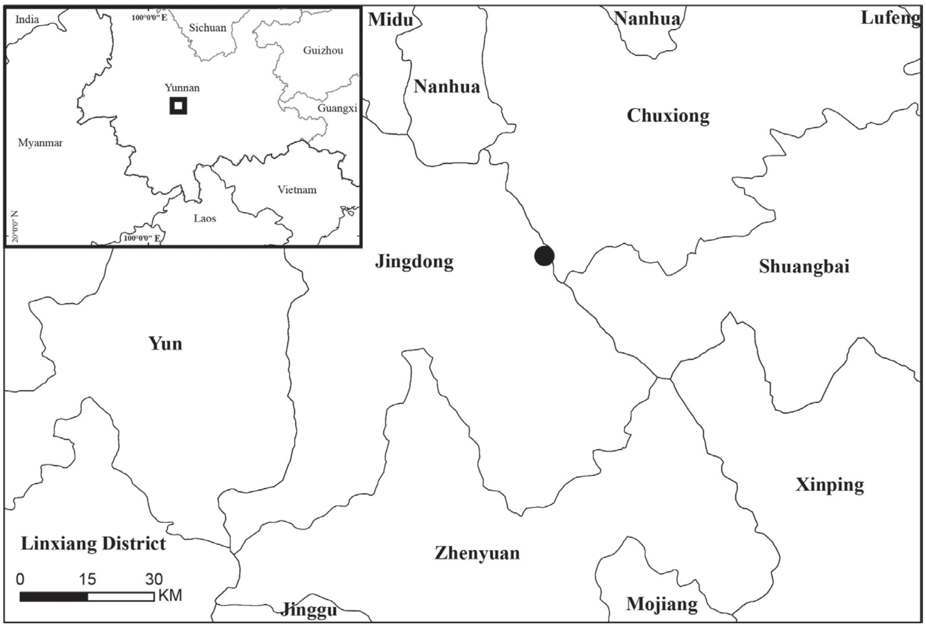
Lysimachia ailaoshanensis **G.Hao & Y.F.Yan, sp. nov.**
urn:lsid:ipni.org:names:77348638-1
Figs 1, 2

Type. China. • Yunnan Province, Jingdong Yi Autonomous County, Xujiaba, near Damenkou; 24°31'N, 101°00'E; alt. 2363 m; 14 Aug. 2020; *Hai-Fei Yan et al. Y2020286* (holotype: IBSC! barcode IBSC1021506; isotypes: IBSC! barcode IBSC1025535, IBSC1025536).

Diagnosis. *Lysimachia ailaoshanensis* is most similar to *L. chenopodioides* Watt ex Hook. f. and *L. remotiflora* C.M. Hu, but differs from *L. chenopodioides* in narrower lanceolate leaf blade and longer pedicel, and longer stamens and styles, and from *L. remotiflora* in narrower leaf blade and longer stamens.

Description. Herbs annual, glabrous, 18 to 58 cm tall. Stems erect to ascending-erect, quadrangular, branches usually few above middle. Leaves alternate; petiole 1–2.8 cm long, narrowly winged; leaf blade narrowly lanceolate, 1.8–6.0 × 0.5–1.5 cm, sparsely dark purple or brown glandular punctate, base attenuate, apex acuminate to acute. Pedicel 0.5–2 cm long. Flowers in axils of upper leaves, always forming a raceme of 5–18 cm, lax. Calyx lobes lanceolate, 4.5–5.5 mm long, split nearly to base, dark purple or black glandular striate outside, apex obtuse to subacute. Corolla white or pink; tube ca. 1 mm long; lobes oblong-spatulate, 4.5–5 mm long, dark purple glandular striate, apex obtuse. Stamens ca. as long as to slightly shorter than corolla lobes; filaments adnate to base of corolla lobes, free parts ca. 4.0 mm; anthers ovate, dorsifixed, ca. 0.5 mm. Ovary glabrous; style ca. 4.5 mm. Capsule globose, ca. 4 mm in diameter, glabrous.

Distribution and habitat. The new species is presently known only from the type locality in Yunnan Province, Jingdong Yi Autonomous County (Map 1). It grows at the edge of secondary mixed-evergreen forests.



Map 1. Location of the population of *Lysimachia ailaoshanensis* in Jingdong, Yunnan.

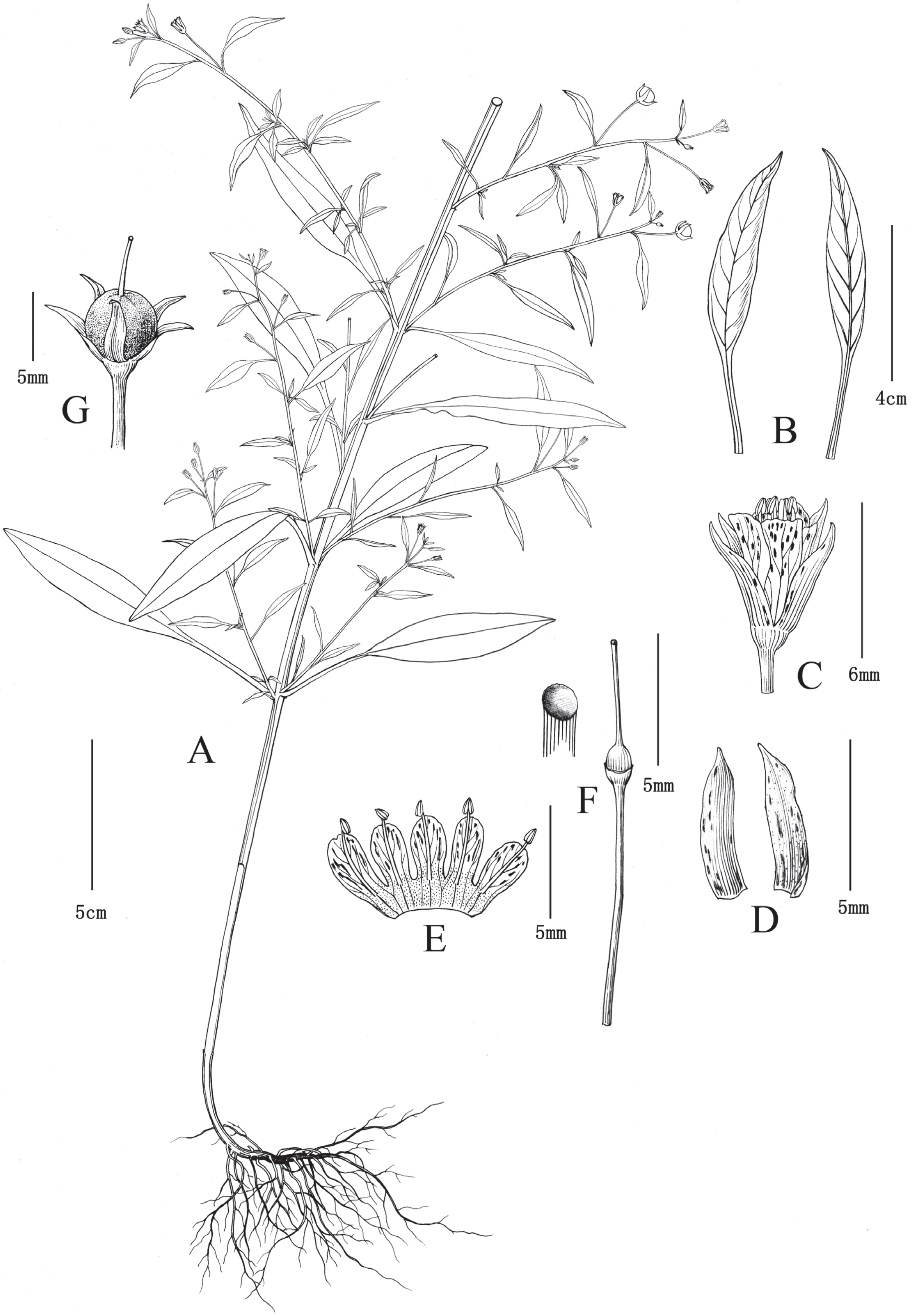


Figure 1. *Lysimachia ailaoshanensis* G.Hao & Y.F.Yan, sp. nov. **A** habit **B** abaxial (right) and adaxial (left) surfaces of a leaf **C** flower **D** calyx lobes **E** dissected corolla **F** pistil and its stigma (enlarged) **G** young fruit with persistent calyx. Drawn by Yun-Xiao Liu from the holotype.

Figure 2. Living plant of *Lysimachia ailaoshanensis* G.Hao & Y.F.Yan, sp. nov. **A** habitat **B** habit **C** leaves on abaxial (right) and adaxial (left) surfaces **D** flower (lateral view) **E** corolla **F** pistil **G** abaxial (left) and adaxial (right) sides of a calyx lobe. Photographed by Hai-Fei Yan.

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

Etymology. The new species is named referring to the type locality where the new species occurs, Ailaoshan National Nature Reserve, Yunnan, China.

Conservation status. Based on our field investigations in Jingdong Yi Autonomous County and adjacent areas in the past three years, only one population with only five individuals of the new species have been found in an area of 10 km^2 in Jingdong Yi Autonomous County. Moreover, the local habitat is under threat by road construction and tourism development. Therefore, the conservation status of the new species is assessed as Critically Endangered (CR) (B2a & bi, iii), according to the guidelines for using the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2024).

Additional specimens examined (paratype). China. The same locality as holotype, 7 August 2023, *Hai-Fei Yan Yan2023054* (IBSC! barcode IBSC1025537, IBSC1025538).

Relationship with similar species. Based on the classification of *Lysimachia* by Handel-Mazzetti (1928) and Chen and Hu (1979), the new species clearly belongs to *Lysimachia* subg. *Palladia* sect. *Chenopodiopsis* Hand.-Mazz., which is characterised by leaves alternate, racemes sparsely flowered or solitary in axils of upper leaves, filaments free, adnate to middle of corolla, and styles usually shorter than corolla. Approximately eight species were recognized in this section, mainly distributed in southwestern China and adjacent regions (e.g., Bhutan, India, Kashmir, N. Myanmar, Nepal, Pakistan), and a few outliers in Thailand, the Mediterranean coast, and southeastern Africa (Handel-Mazzetti 1928; Chen et al. 1989; Hu and Kelso 1996). The new species is morphologically similar to *L. chenopodioides* and *L. remotiflora*, but is distinctive in its leaf shape and heights of stamens and styles (see Table 1, Figs 1–3).

Figure 3. Holotypes of *Lysimachia ailaoshanensis* and two of its allies **A** *L. ailaoshanensis* **B** *L. chenopodioides* **C** *L. remotiflora*.

Table 1. Main morphological differences between *Lysimachia ailaoshanensis* and two similar species.

Features	*L. ailaoshanensis*	*L. chenopodioides*	*L. remotiflora*
Petiole length	1–2.8 cm	0.5–1 cm	ca. 1.1 cm
Lamina shape	narrowly lanceolate	ovate to rhomboid-ovate	ovate-lanceolate
Pedicel length	0.5–2 cm	1–2 mm	1.5–2.5 cm
Filament length	4.5–5 mm	1–1.5 mm	1–1.5 mm
Style length	4.5 mm	1.5 mm	2.5 mm

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

All authors have contributed equally.

Data availability

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

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Research Article

Three new species of *Isodon* (Nepetoideae, Lamiaceae) from China

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Abstract

Three new species of *Isodon* (Lamiaceae) from China are described and illustrated, based on both morphological evidence and our recent phylogenomic studies of the genus. *Isodon attenuatus*, a herbaceous new species known only from the Fanjing Mountain, is shown to be sister to *I. villosus*, but they can be easily distinguished by leaf and inflorescence indumentum, calyx teeth shape and corolla tube morphology. *Isodon gongshanensis*, a herbaceous new species collected from the Hengduan Mountains in southwest China, represents a distinct lineage within the genus. *Isodon sukungii*, a shrubby new species also endemic to the Hengduan Mountains, was previously misidentified as *I. tenuifolius*, but they are phylogenetically distantly related and differ in lamina size and margin, inflorescence type and corolla length and shape.

Key words: dry valley, Hengduan Mountains, Isodoninae, Ocimeae, southwest China

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Introduction

Isodon (Schrad. ex Benth.) Spach (Ocimeae, Nepetoideae, Lamiaceae) is a genus of approximately 140 species mainly distributed in subtropical to tropical Asia, with two disjunct species endemic to Africa (Wu and Li 1977; Li 1988; Li and Hedge 1994). The genus is most diverse in southwest China, particularly in the dry valleys in the Hengduan Mountains (Zhong et al. 2010; Yu et al. 2014; Chen et al. 2022). Morphologically, *Isodon* can be distinguished from other genera of tribe Ocimeae by its pedunculate and bracteolate cymes, slightly or strongly 2-lipped (3/2) calyces, strongly 2-lipped (4/1) corollas and free filaments inserted at the base of the corolla tube (Li 1988; Paton and Ryding 1998; Harley et al. 2004).

Resolving the intrageneric relationships within *Isodon*, based on limited DNA loci (Zhong et al. 2010; Yu et al. 2014; Chen et al. 2019) or plastome sequences (Chen et al. 2022) has been difficult due to the rapid radiation of the genus in southwest China. Recently, we reconstructed a robust phylogeny for 126 *Isodon* taxa using transcriptome and genome-resequencing data (Chen et al. 2024). Except for the four clades (Clade I–Clade IV) recovered consistently in previous molecular phylogenetic studies (Yu et al. 2014; Chen et al. 2019, 2022), four subclades (Clade IVa–Clade IVd) were further recognised within the largest Clade IV which comprises ca. 80% species of the genus (Chen et al. 2024). Meanwhile, Chen et al. (2024) confirmed the statuses of three unidentified species we collected during 2018–2020 as new to science. These species were thus named *I. attenuatus* Y.P.Chen & C.L.Xiang, *I. gongshanensis* Y.P.Chen & C.L.Xiang and *I. sukungii* Y.P.Chen & C.L.Xiang and described below.

Materials and methods

Phylogenetic placements of the three new species within *Isodon* were directly referenced from our recent phylogenomic study of the genus (Chen et al. 2024). Morphological comparisons of these new species and other *Isodon* taxa were conducted, based on our previous field observations, specimen examination and morphological investigations of mericarps (Chen et al. 2022). Specimens from 17 Herbaria (BM, CDBI, E, GXMI, HIB, IBK, IBSC, K, KUN, KYO, LE, MW, NAS, PE, SZ, TI and WUK; abbreviations follow Thiers 2024) and our field collections were examined. Additionally, images of specimens (including type specimens) and living plants of *Isodon* from JSTOR (https://www.jstor.org/), Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn/) and Plant Photo Bank of China (PPBC, http://ppbc.iplant.cn/) were checked. Furthermore, protologues of all published names and related taxonomic and floristic literature on *Isodon* were reviewed. Morphological descriptions of the new species followed the terminology used by Li (1988) and Li and Hedge (1994).

Results and discussion

Isodon attenuatus (corresponding to *Isodon* sp. 1 in Chen et al. (2024)) was collected from the Fanjing Mountain in Guizhou Province, China (Fig. 1) and was recovered in Clade I according to Chen et al. (2024). It shares reddish-brown glands covering the plants as in other taxa of Clade I, a characteristic considered a synapomorphy of this clade (Zhong et al. 2010; Yu et al. 2014; Chen et al. 2022). Phylogenetically, *I. attenuatus* is sister to *I. villosus* Y.P.Chen & H.Peng (Chen et al. 2024) from the adjacent Guangxi Zhuang Autonomous Region. Both species have a declinate corolla, lobes of posterior corolla lip with an acute apex and stamens and style included within the corolla (Fig. 2), differing from the straight corolla, rounded apices of the lobes of posterior corolla lip and/or exserted stamens and style of other taxa of Clade I. However, they can be easily differentiated by the morphology of lamina, which is subglabrous with a decurrent base in *I. attenuatus* (Fig. 2), but densely villose with a non-decurrent base in *I. villosus*. There are also differences in the calyx teeth shape, with *I. attenuatus* having triangular teeth with an acute apex and *I. villosus* having ovate teeth with an obtuse apex. Furthermore, the corolla tube of *I. attenuatus* is significantly attenuate towards the throat, but that of *I. villosus* is not attenuate. More detailed differences between the two species are listed in Table 1. *Isodon attenuatus* is now only known from its type locality, where it grows along hiking trails in subtropical evergreen broadleaf forests. It is possibly threatened by human disturbances, such as tourism and herbicide use. However, more comprehensive investigations are needed to further elucidate its distribution, decline and conservation status.

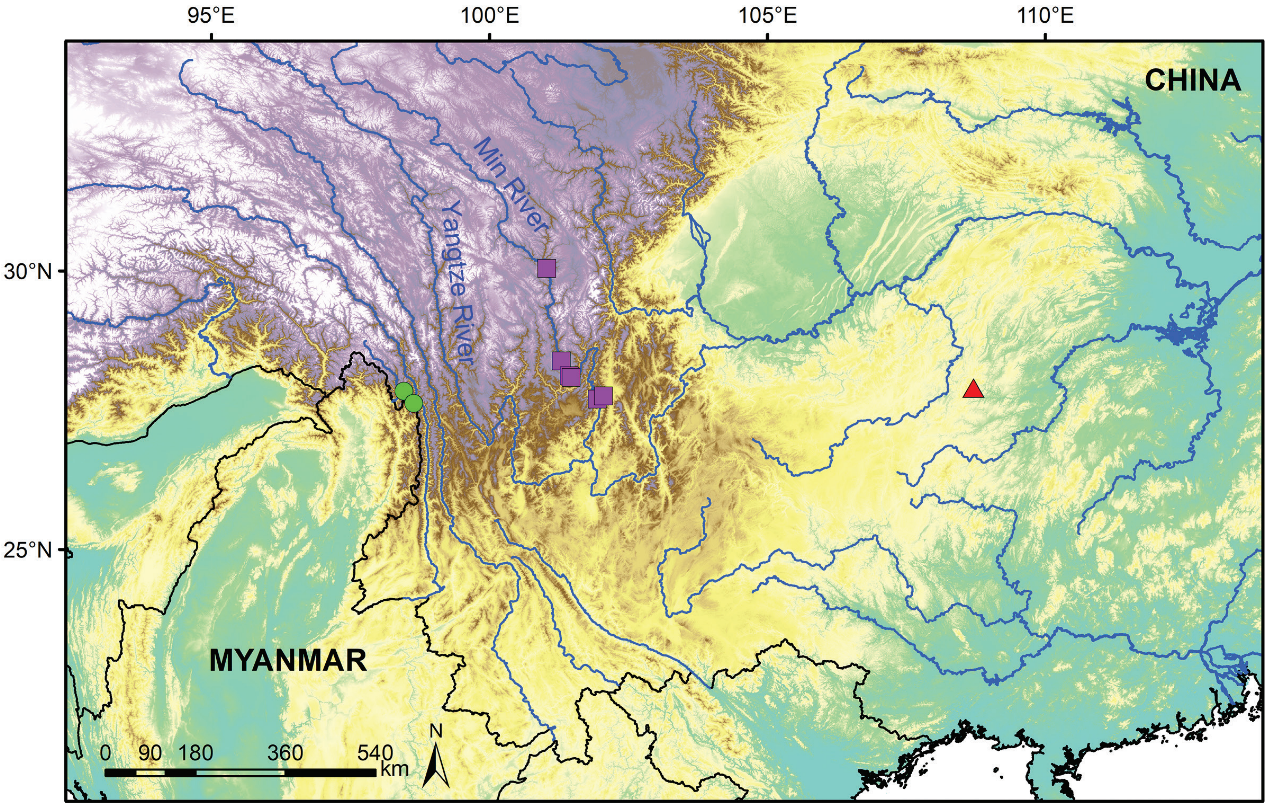

Figure 1. Geographic distribution of *Isodon attenuatus* (red triangle), *I. gongshanensis* (green circles) and *I. sukungii* (purple squares).

Isodon gongshanensis is endemic to Gongshan County in Yunnan Province, southwest China (Fig. 1). It typically grows in mixed needle-leaf and broadleaf forests in the Gaoligong Mountain at altitudes of 2700–2900 m. The new species (corresponding to *Isodon* sp. 11 in Chen et al. (2024)) was identified as a distinct lineage within Clade IVc, serving as the sister group to the remaining herbaceous taxa in this clade (Chen et al. 2024). Morphologically, *I. gongshanensis* is most similar to *I. rosthornii* (Diels) Kudô from the sister clade. While they share similar indumentum and inflorescence types, they exhibit clear differences in the morphology of the calyx and corolla. The calyx teeth of the posterior lip of *I. gongshanensis* are lanceolate and ca. 1 mm long (Fig. 3), in contrast to the triangular teeth of *I. rosthornii*, which are about 0.5 mm long. In *I. gongshanensis*, the corolla is 6–7 mm long with a pink posterior lip lacking spots, whereas in *I. rosthornii*, the corolla is ca. 5 mm long with a white posterior lip marked by reddish-purple spots. Additionally, the ovary of *I. gongshanensis* is glandless, whereas that of *I. rosthornii* is glandular. Other differences between the two species are summarised in Table 2.

Isodon sukungii is a shrubby species restricted to the dry valley along Min River in the Hengduan Mountains (Fig. 1). It was previously misidentified as *I. tenuifolius* (W.W.Sm.) Kudô from a geographically adjacent, but isolated valley along the upper Yangtze River, perhaps due to the small and densely grey tomentose leaves shared by both species (Fig. 4). However, phylogenetic analysis revealed that the two species are distantly related, despite both being placed in Clade IVd (Chen et al. 2024). *Isodon sukungii* (corresponding to *Isodon* sp. 5 in Chen et al. (2024)) is phylogenetically most closely related to morphologically distinct species from the same river valley. The small and densely grey tomentose leaves of *I. sukungii and I. tenuifolius* may represent a case of convergent evolution and adaptation to dry habitats. The two species can be distinguished by their lamina length and margin: in *I. sukungii*, the lamina is 1–4 cm long and serrate, whereas in *I. tenuifolius*, it is 0.5–1 cm long and usually entire. The cymes in *I. sukungii* often form panicles, while in *I. tenuifolius*, they are simple and never arrange into a thyrse or panicle. Additionally, the corolla of *I. sukungii* is 6–7 mm long with a straight anterior lip, compared to the ca. 4 mm long corolla with a strongly reflexed anterior lip in *I. tenuifolius*. Other minute differences between the two species are detailed in Table 3.

Table 1. Morphological comparisons between *Isodon attenuatus* and *I. villosus*.

Characters	*I. attenuatus*	*I. villosus*
Lamina	Subglabrous, base cuneate to broadly cuneate, decurrent	Densely to sparsely villose, base broadly cuneate to shallowly cordate, not decurrent
Inflorescence	Densely puberulent and glandular puberulent	Densely villose and glandular puberulent
Pedicel	4–6 mm long	2.5–4 mm long
Fruiting calyx	Teeth triangular, apex acute, not folded	Teeth ovate, apex obtuse, folded
Corolla	Tube attenuate towards the throat, lips light bluish-purple	Tube not attenuate, lips white

Table 2. Morphological comparisons between *Isodon gongshanensis* and *I. rosthornii*.

Characters	*I. gongshanensis*	*I. rosthornii*
Lamina	Ovate to broadly ovate, apex acuminate, base cuneate to broadly cuneate	Broadly ovate to subrounded, apex acute to obtuse, base broadly cuneate to subrounded
Calyx	2-lipped to 1/2 its length, teeth of the posterior lip ca. 1 mm long, narrowly triangular, apex acuminate	2-lipped to over 1/2 its length, teeth of the posterior lip ca. 0.5 mm long, triangular, apex acute
Corolla	6–7 mm long, posterior lip pink without spots	Approximately 5 mm long, posterior lip white with reddish-purple spots
Ovary	Non-glandular	Glandular

Table 3. Morphological comparisons between *Isodon sukungii* and *I. tenuifolius*.

Characters	*I. sukungii*	*I. tenuifolius*
Lamina	Ovate to oblong, thick papery, 1–4 × 0.5–2 cm, margin serrate	Oblong to subrounded, papery, 0.5–1 × 0.4–0.7 cm, margin entire, rarely serrate
Petiole	0.3–1 cm long	1–3 (–5) mm long
Cymes	Forming secund panicles up to 20 cm long	Single, not forming thyrses or panicles
Corolla	6–7 mm long, tube exerted from the calyx, anterior lip straight	Approximately 4 mm long, tube included within the calyx, anterior lip strongly reflexed
Mericarp	Surface glabrous	Surface sparsely glandular

Taxonomic treatment

Isodon attenuatus Y.P.Chen & C.L.Xiang, sp. nov.

urn:lsid:ipni.org:names:77348680-1
Fig. 2

Type. China – **Guizhou Prov.** • Jiangkou County, Fanjing Mountain, along the hiking trail in forests; 27°53'45.08"N, 108°42'39.09"E; alt. 1635 m; 1 Sep 2018; *Y.P. Chen et al. EM590* (holotype: KUN1628213!; isotypes: K!, KUN1628215!, PE!).

Diagnosis. *Isodon attenuatus* is most closely related to *I. villosus*, but differs by having subglabrous (vs. densely to sparsely villose) laminae with a

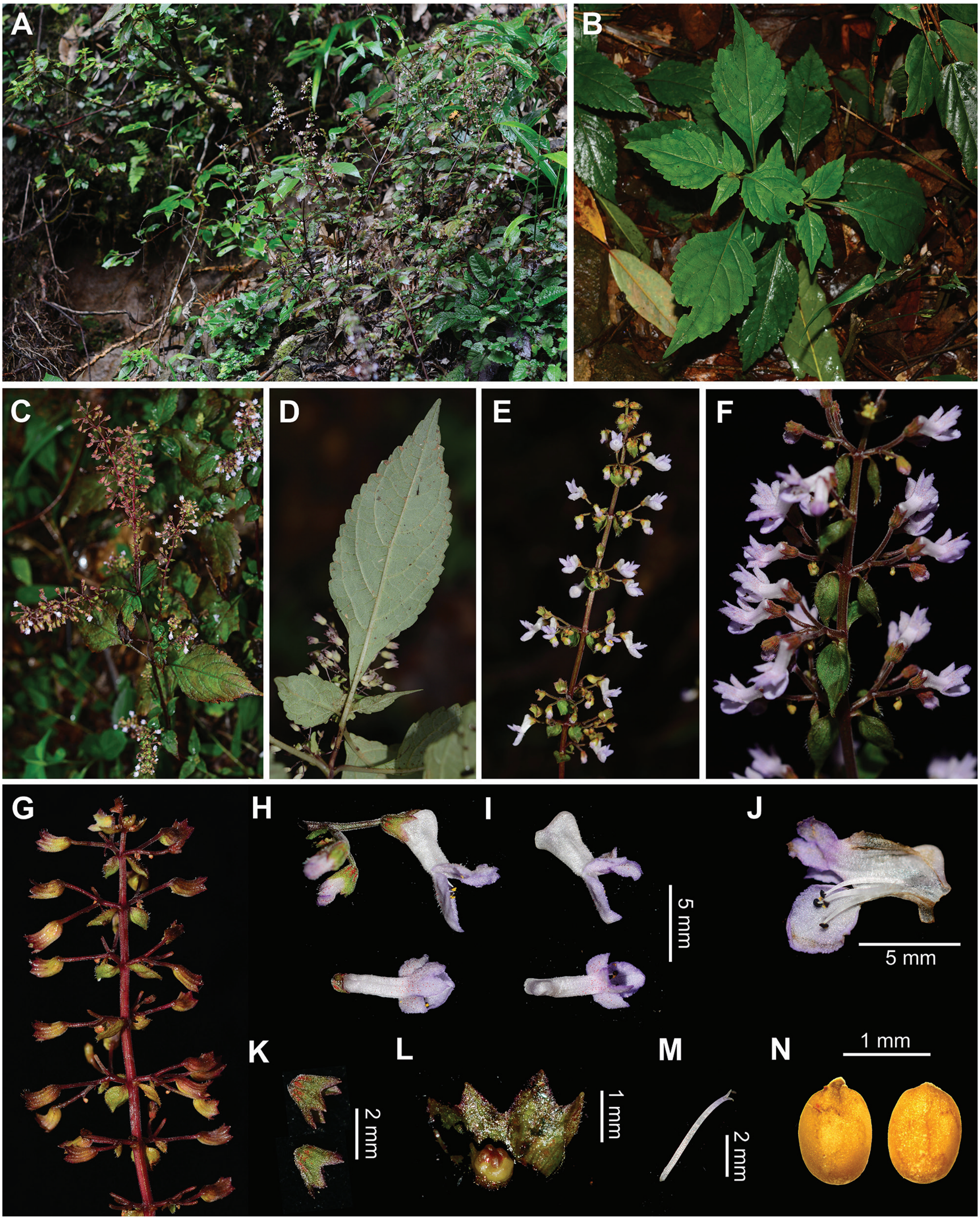

Figure 2. Morphology of *Isodon attenuatus* from the type locality **A** habitat **B, C** habit **D** abaxial view of lamina **E, F** inflorescences **G** infructescence **H** flowers **I** corollas **J** dissected corolla **K** calyces **L** ovary **M** style **N** mericarps (Photographed by Ya-Ping Chen).

decurrent (vs. not decurrent) base, densely puberulent and glandular puberulent (vs. densely villose and glandular puberulent) inflorescences, longer pedicels (4–6 mm vs. 2.5–4 mm long), triangular (vs. ovate) calyx teeth and a corolla tube attenuate towards the throat (vs. not attenuate).

Herbs perennial, 30–70 cm tall. Rhizomes woody, tuberose. Stems erect, branched, quadrangular, densely puberulent and reddish-brown glandular. Leaves decussate; lamina ovate to broadly ovate, papery, 5–15 × 3–7 cm, apex acuminate, base cuneate to broadly cuneate, margin crenulate, adaxially green, subglabrous to sparsely pubescent, reddish-brown glandular, abaxially light green, subglabrous, densely reddish-brown glandular; lateral veins 3–5-paired; petioles 1–5 cm long. Thyrses terminal and axillary, ca. 10 cm long; cymes 3–7-flowered, peduncles 2–3 mm long, pedicels 4–6 mm long, densely puberulent, glandular puberulent and reddish-brown glandular; bracts broadly ovate, sessile, apex lanceolate, margin entire, 3–10 mm long, bracteoles linear, ca. 1 mm long, ciliate, densely reddish-brown glandular. Calyx campanulate, ca. 2 mm long, densely glandular puberulent and reddish-brown glandular outside; 2-lipped to 1/2 its length, teeth triangular, apex acute, fruiting calyx dilated to ca. 5 mm long. Corolla 5–6 mm long, declinate, pubescent and reddish-brown glandular outside; tube 3–3.5 mm long, white, saccate abaxially near base, ca. 2 mm in diameter, attenuating gradually towards throat to ca. 1 mm in diameter; apex 2-lipped, light bluish-purple, posterior lip 4-lobed, ca. 3.5 × 3.5 mm, reflexed, lobes oblong, apex acute, anterior lip entire, subrounded, concave, straight, 2–3.5 mm in diameter. Stamens 4, included; anther cells 2, confluent, divergent; filaments pubescent at base. Style included, glabrous, apex slightly subequally 2-lobed. Mericarps 4, ochre-yellow, oblong, 1.4–1.55 mm long, ca. 1 mm wide, smooth and glabrous.

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

Distribution and habitat. Currently, *I. attenuatus* is only known from the Fanjing Mountain in Guizhou Province, China (Fig. 1). The new species usually grows in evergreen broadleaf forests at altitudes of 1600–2000 m.

Etymology. The specific epithet refers to the gradually attenuating corolla tube of the new species towards the throat.

Chinese name (assigned here). jiàn xiá xiāng chá cài (渐狭香茶菜).

Additional specimens examined. China – **Guizhou Prov.** • Jiangkou County, vicinity of Jinding along the crest of the Fanjing Shan Mountain Range; alt. 2000–2300 m; 28–29 Aug 1986; *Sino-American Guizhou Botanical Expedition 673* (L3902407!, PE00833681!); • ibid.; alt. 1707 m; 20 Oct 2017; Y.P. Chen & L. Chen EM429 (KUN!).

***Isodon gongshanensis* Y.P.Chen & C.L.Xiang, sp. nov.**

urn:lsid:ipni.org:names:77348681-1
Fig. 3

Type. China – **Yunnan Prov.** • Gongshan County, Dulongjiang Town; alt. 2915 m; 27°50'33.93"N, 98°27'27.85"E; at the streamside in forests; 15 Aug 2020; *Y.P. Chen et al. EM1570* (holotype: KUN1628216!; isotypes: K!, KUN1628214!, PE!).

Diagnosis. *Isodon gongshanensis* is morphologically similar to *I. rosthornii*, but differs by having lanceolate (vs. triangular) and longer (ca. 1 mm vs. ca. 0.5 mm long) teeth of the posterior calyx lip, longer (6–7 mm vs. ca. 5 mm long) corollas with a pink (vs. white) posterior lip, but without spots (vs. with reddish-purple spots) and an ovary without glands (vs. with glands).

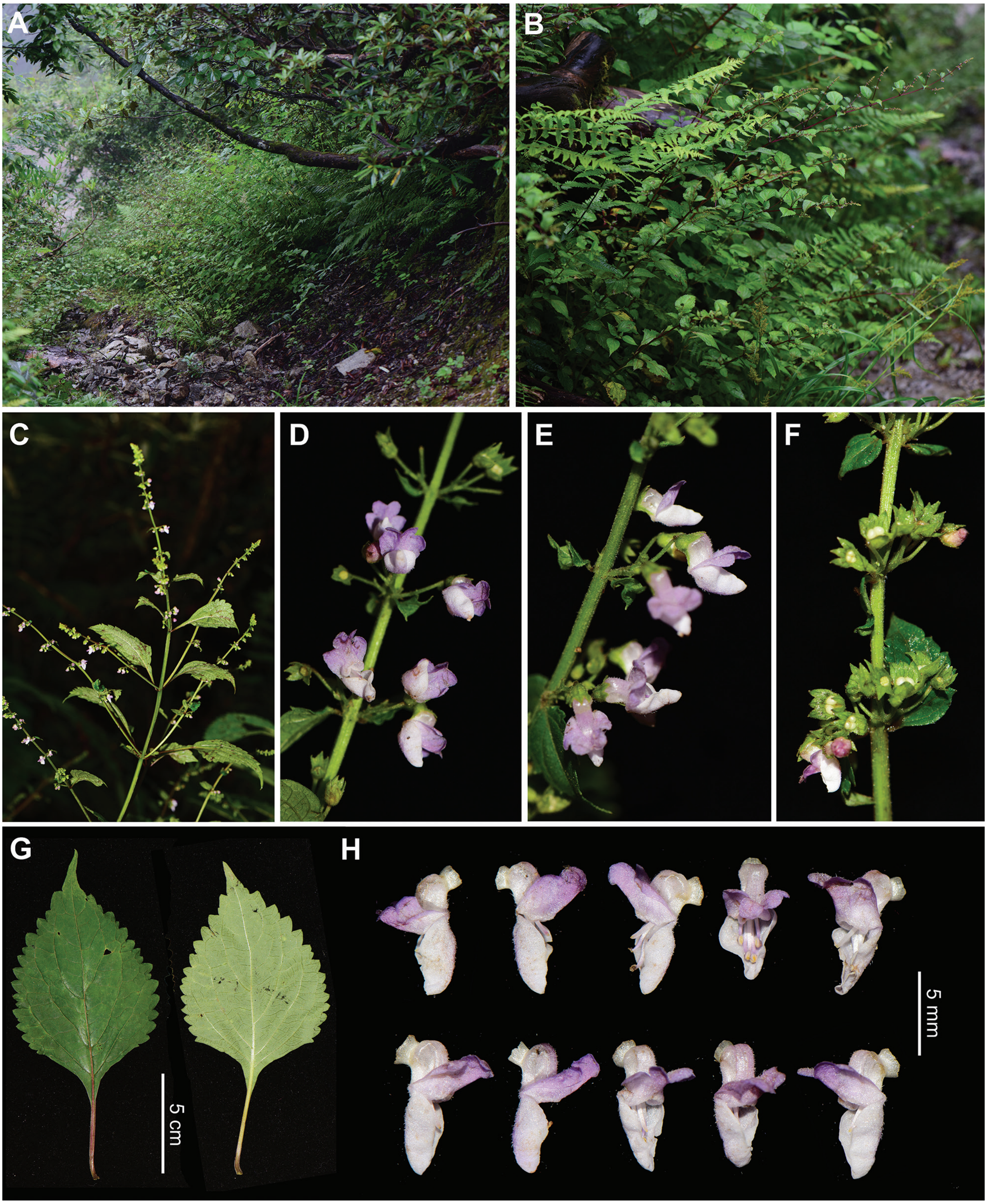

Figure 3. Morphology of *Isodon gongshanensis* from the type locality **A** habitat **B** habit **C–E** inflorescences **F** infructescence **G** leaves **H** corollas (Photographed by Ya-Ping Chen).

Herbs perennial, 50–150 cm tall. Stems erect, branched, quadrangular, 4-sulcate, often claret, subglabrous to densely strigose. Leaves decussate; lamina ovate to broadly ovate, papery, 5–12 × 3–7 cm, apex acuminate, base cuneate to broadly cuneate, margin crenulate, adaxially green, sparsely strigose and glandular, abaxially light green, subglabrous, densely glandular; lateral veins

3–4-paired; petioles 1–5 cm long, claret or green, strigose. Thyrses terminal and axillary, 10–20 cm long; cymes 3–7-flowered, peduncles 1–2 mm long, pedicels 3–5 mm long, strigose; bracts ovate to broadly ovate, 2–30 mm long, apex lanceolate, margin crenulate or entire, petioles 0–5 mm long, bracteoles linear, ca. 1 mm long. Calyx campanulate, ca. 2.5 mm long, strigose and glandular outside; 2-lipped to 1/2 its length, teeth narrowly triangular, apex acuminate, fruiting calyx dilated to ca. 5 mm long, posterior lip strongly reflexed. Corolla white, 6–7 mm long, declinate, strigose and glandular outside; tube 2.5–3 mm long, white, saccate abaxially near base, 1.5–2 mm in diameter; apex 2-lipped, posterior lip pink, 4-lobed, ca. 4 × 4 mm, reflexed, lobes subrounded, anterior lip entire, subrounded, concave, navicular, straight, 3.5–4 mm in diameter. Stamens 4, included; anther cells 2, confluent, divergent; filaments pubescent at base. Style included, glabrous, apex slightly subequally 2-lobed. Ovaries glabrous. Mericarps not seen.

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

Distribution and habitat. *Isodon gongshanensis* is only known from Gongshan County in Yunnan Province, southwest China (Fig. 1). The new species usually grows in mixed needle-leaf and broadleaf forests at altitudes of 2700–2900 m.

Etymology. The specific epithet is derived from the type locality of the new species, i.e. Gongshan County in Yunnan Province, China.

Chinese name (assigned here). gòng shān xiāng chá cài (贡山香茶菜).

Additional specimens examined. China – **Yunnan Prov.** • Gongshan County, Cikai Town, Danzhu Village; alt. 2787 m; 27°37'17.14"N, 98°38'1.04"E; 25 Sep 2022; *Y.J. Zhao et al. 22ZYJ023* (KUN); • Gongshan County, Dulongjiang Town, near the Dulongjiang Tunnel; 2 Jul 2015; *Y.P. Chen & R.L. Stubbs EM203* (KUN!); • ibid.; 16 Oct 2019; *L.Q. Jiang & Y.Y. Li LJ28* (KUN!).

Isodon sukungii **Y.P.Chen & C.L.Xiang, sp. nov.**

urn:lsid:ipni.org:names:77348682-1
Fig. 4

Type. China – **Sichuan Prov.** • Muli County, Sanjiaoya Town, on the way from Biji to Guoquanyan, amongst the thickets on the dry valley slope; 28°04'58.50"N, 101°28'8.77"E; alt. 2041 m; 13 Oct 2018; *Y.P. Chen et al. EM666* (holotype: KUN1628218!; isotypes: K!, KUN1628217!, PE!).

Diagnosis. *Isodon sukungii* is morphologically similar to *I. tenuifolius* but differs by having longer laminae (1–4 cm vs. 0.5–1 cm long) with serrate (vs. entire) margins, cymes that form panicles (vs. single cymes that do not form thyrses or panicles) and a longer corolla (6–7 mm vs. 4 mm long) with a straight (vs. strongly reflexed) anterior lip.

Shrubs 30–120 cm tall. Stems erect, much branched; branches brown, decorticate, subterete, glabrescent; branchlets brown, obtusely 4-angled, densely grey tomentose. Leaves decussate; lamina ovate to oblong, thick papery, 1–4 × 0.5–2 cm, apex acute, base cuneate to subrounded, margin serrate, rarely entire, adaxially green, sparsely minute grey tomentose and glandular, abaxially white, densely grey tomentose and glandular, lateral veins 3–5-paired, conspicuously elevated abaxially; petioles 0.3–1 cm long, densely grey tomentose. Cymes 3–7-flowered, often forming secund panicles up to 20 cm long; bracts leaf-like, gradually reduced towards apex, margin entire, longer than cymes,

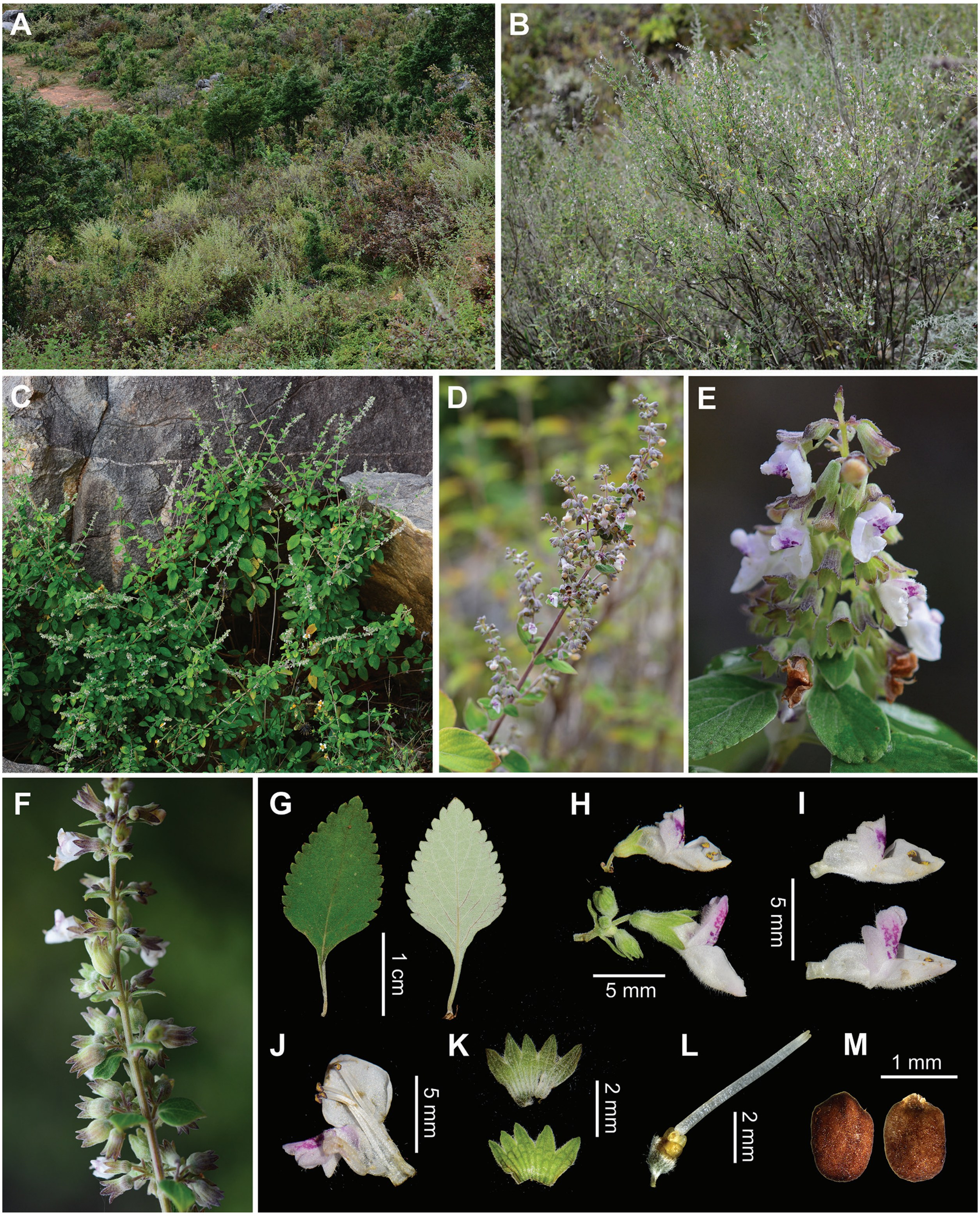

Figure 4. Morphology of *Isodon sukungii* from the type locality **A** habitat **B, C** habit **D, E** inflorescences **F** infructescence **G** leaves **H** flowers **I** corollas **J** dissected corolla **K** dissected calyces **L** pistil **M** mericarps (Photographed by Ya-Ping Chen).

upper ones sessile, lanceolate, bracteoles linear, ca. 1 mm long; peduncles 1–3 (–5) mm long, pedicels 1–2 mm long, densely grey tomentose. Calyx campanulate, 2.5–3 mm long, densely grey tomentose and glandular outside, slightly 2-lipped to 1/3 its length; teeth subequal, ovate-triangular, apex acute, fruiting calyx slightly dilated to ca. 4 mm long. Corolla white, 6–7 mm long, declinate, pubescent and glandular outside; tube 3.5–4 mm long, saccate abaxially near base, ca. 1.5 mm in diameter; apex 2-lipped, posterior lip 4-lobed, dotted with reddish-purple spots, ca. 2.5 mm long, reflexed, lobes subrounded, anterior lip entire, subrounded, concave, navicular, straight, 2.5–3 mm in diameter. Stamens 4, included; anther cells 2, confluent, divergent; filaments pubescent at base. Style included, glabrous, apex slightly subequally 2-lobed. Mericarps 4, brown, oblong, 1.25–1.35 mm long, 0.85–0.95 mm wide, smooth and glabrous.

Phenology. Flowering from July to November, fruiting from September to December.

Distribution and habitat. *Isodon sukungii* is widely distributed in the dry valley along Min River, a tributary of the Yangtze River, in Sichuan Province, southwest China (Fig. 1). The new species usually grows on open dry slopes with savannah-like vegetation at altitudes of 1600–2700 m.

Etymology. The new species is named after the late Prof. Su-Kung Wu, who is one of the earliest Chinese botanists to explore the plant diversity of Muli County.

Chinese name (assigned here). sù gōng xiāng chá cài (素功香茶菜).

Additional specimens examined. CHINA – **Sichuan Prov.** • Muli County, on the way from Moshuogou to Boao; alt. 1900–2290 m; 6 Sep 1959; *S.K. Wu 2419* (KUN0271016!, KUN0271017!); • Muli County, Boao, Baidiao; alt. 2150 m; 20 Sep 1959; *S.K. Wu 3155* (KUN0271018!, KUN0271019!); • Muli County, Housuo Town, Xiagu Village; 26 Jul 2011; *E.D. Liu et al. 2911* (KUN1278979!); • Muli County, Kala Town, Tianzheng Village; alt. 1966 m; 15 Oct 2018; *Y.P. Chen et al. EM689* (KUN!); • Yanyuan County, Ma'anshan Town, Songlinping Village; alt. 1663 m; 15 Oct 2017; *Y.P. Chen & Z.H. Wang EM419* (KUN!); • Yanyuan County, Jinhe Town; 4 Oct 2020; *L.B. Jia s.n.* (KUN!); • Yajiang County; alt. 2570 m; 18 Aug 2011; *W. Fang et al. FW11269* (KUN1340269!, KUN1340270!); • ibid.; alt. 2711 m; 28 Aug 2020; *Y.P. Chen et al. EM1711* (KUN!).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Y-PC and C-LX conceptualised the study. Y-PC, HP and C-LX carried out the field investigation. Y-PC conducted the analyses and drafted the manuscript. All authors read, revised and approved the final manuscript.

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Data availability

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

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Research Article

Glacial history of *Saxifraga wahlenbergii* (Saxifragaceae) in the context of refugial areas in the Western Carpathians

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Abstract

Despite the wealth of data available for mountain phylogeography, local-scale studies focused on narrow endemic species remain rare. Yet, knowledge of the genetic structure of such species biogeographically linked to a restricted area is of particular importance to understand the history of the local flora and its diversity patterns. Here, we aim to contribute to the phylogeographical overview of the Western Carpathians with a genetic study of *Saxifraga wahlenbergii*, one of the most characteristic endemic species of this region. We sampled populations from all discrete parts of the species' distribution range to apply sequencing of selected non-coding cpDNA and nuclear ribosomal DNA (ITS) regions, as well as Amplified Fragment Length Polymorphism (AFLP) fingerprinting. First, while ITS sequences showed weak diversification, the genetic structure based on cpDNA sequences revealed two well-differentiated groups of haplotypes. One of them is restricted to the main center of the distribution range in the Tatra Mountains (Mts), while the second group included a series of closely related haplotypes, which in most cases were unique for particular isolated groups of populations in peripheral mountain ranges and in the south-eastern part of the Tatra Mts. AFLP fingerprinting also revealed a pattern of divergence among populations, while only partly corroborating the division observed in cpDNA. Taking into account all the data, the pattern of genetic structure, supported by the high levels of unique genetic markers in populations, may reflect the historical isolation of populations in several local refugia during the last glacial period. Not only the center of the range in the Tatra Mts, but also other, neighboring massifs (Malá Fatra, Nízke Tatry, Chočské vrchy, Muránska planina), where populations are characterized by separate plastid DNA haplotypes, could have acted as separate refugia.

Key words: AFLP, haplotype, high mountain plant, narrow endemic, phylogeography, refugial areas, Tatra Mts

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Introduction

Mountainous systems of temperate Europe are biodiversity hotspots, due, among others, to their high floristic richness, including endemic species that contribute to the natural uniqueness of a given biogeographical unit. The evolution of mountain species is strongly related to historical environmental and climatic factors, including the Pleistocene climatic fluctuations that caused alternating glacial and interglacial periods (Hewitt 2000, 2004; Kadereit et al.

2004). Phylogeographic analysis of various mountain species allowed us to discover genetic patterns and, to some extent, understand mechanisms and dynamics of processes involved in the formation of local floristic hotspots within large mountain massifs. The results have made it possible to determine the scenarios of events and processes related to the survival of species during glaciations, including the location of refugial areas and recolonization routes to the areas currently occupied by these species. The revealed convergence of genetic diversity patterns between mountain species indicates that similar factors had a prevailing role in shaping the history of the flora in different areas, especially with regard to the history of Quaternary glaciations (e.g., Koch et al. 2003; Kropf et al. 2008; Lowe and Allendorf 2010; Ronikier 2011; Schmitt 2017; Šrámková-Fuxová et al. 2017; Konečná et al. 2019).

Endemic species are a special element of the biodiversity of mountain areas. In this group, species with highly limited local ranges are of particular importance, as they most often reflect evolution in specific microclimatic isolation in geographically small and isolated areas (Kochjarová et al. 2006; Cieślak et al. 2007, 2021; Pittet et al. 2020). Their emergence confirms the role of local ecological niche systems (including topography, climate, and bedrock factors) in shaping the regional mountain flora during historical evolutionary processes. In mountain ranges, establishing an understanding of such local systems is crucial to understanding their contemporary distribution and biodiversity. Consequently, it will allow the determination of the response range of these unique, often isolated, local habitat systems to past and ongoing climate fluctuations, such as the Pleistocene glacial/interglacial sequences (Nagy et al. 2003; Stehlik 2003; Kadereit et al. 2004; Tribsch 2004; Schmitt 2009; Gentili et al. 2015).

It has been confirmed that the Western Carpathians are an important, independent center of endemism with both Pan-Carpathian species and a group of endemic species specific to this region (Pawłowski 1970; Kliment 1999; Piękoś-Mirkowa and Mirek 2003; Mráz and Ronikier 2016). Their location close to the northern ice sheet during glacial periods, heterogeneous environments constituting a mosaic of habitats, and microtopographically diverse environments on a regional scale were crucial to the establishment of an important evolutionary center in this region of the Carpathians (Paclová 1977). Recently, phylogeographic analyses of *Cochlearia tatrae*, the endemic species of the Tatra Mts, showed a significant level of intra-specific variability with several geographically arranged genetic groups in this small mountain range (Cieślak et al. 2021). This pattern may reflect the isolation of the populations in several micro-refugia, indicating that the systems of local factors in the Tatra Mts and its outskirts were crucial in formation of the genetic structure of this species.

In this study, we address *Saxifraga wahlenbergii* Ball, one of the most characteristic endemic species of the Western Carpathians, with wide ecological preferences, including a large elevational range and limited bedrock restriction. It occurs in several massifs with its range center in the Tatra Mts (Piękoś-Mirkowa et al. 1996). Recent phylogenetic study based on nrDNA and cpDNA regions revealed a complex hybrid origin of *S. wahlenbergii* with unidirectional introgression and different parental contributions observed in extant genotypes (Tkach et al. 2019). The maternal parent has been shown to belong to the West Eurasian lineage of alpine taxa grouped in the subsection *Androsaceae*, most likely the widespread *S. androsacea*. The putative paternal parent was probably

S. adscendens, which belongs to a distantly related subsection *Tridactylites*. Contribution from both groups was confirmed by a next-generation sequencing (NGS) analysis of within-individual ITS variation (Tkach et al. 2019). The supported topological incongruencies between phylogenies reconstructed from nuclear and plastid DNA regions, as previously found (Tkach et al. 2015; Gerschwitz-Eidt and Kadereit 2020), may suggest that interspecific transfer of adaptive traits through hybridization may have played an important role in the evolution of *Saxifraga* sect. *Saxifraga*. In general, hybrid speciation events involving polyploidization are common in the genus *Saxifraga* and have played an important role in the diversification of this large genus (e.g., Ebersbach et al. 2020).

Interestingly, in the framework of the phylogenetic analysis, regional genetic variation was found in the populations of *S. wahlenbergii* including two distinct cpDNA clades, which was a direct motivation to undertake a more detailed analysis of the species' phylogeographical structure. While unequivocally dating the hybrid origin of *S. wahlenbergii* could not be assessed, it could theoretically precede the Pleistocene and several arguments pointed to a possibly ancient rather than recent age of this species (Tkach et al. 2019), hence also its geographical range.

In the region of the Western Carpathians, with its high topographic and habitat heterogeneity, *S. wahlenbergii*, a plant with a rather wide altitudinal range, could survive in the massifs where it occurs today, over the Pleistocene climatic oscillations, following the altitudinal shifts or persistence in long-term, non-glaciated microrefugia. However, as cold (glacial) periods have led to a significant increase in habitats suitable for alpine plants in the lower parts of the Carpathians (Ronikier 2011), the present range could also result from a recent (Last Glacial Maximum) migration to peripheral massifs.

The main objective of this study is to determine the range-wide genetic structure of *S. wahlenbergii*, to provide insight into its glacial history. For this purpose, an extended sequence analysis of selected nuclear and plastid DNA regions complementing data from Tkach et al. (2019) and supplemented by population genotyping with Amplified Fragment Length Polymorphism method (Vos et al. 1995; Kirschner et al. 2021), were used. The study was based on the analysis of *S. wahlenbergii* populations from the area of their highest density in the Tatra Mts and those from all neighboring mountain massifs, where it occurs less abundantly (sometimes as isolated populations). Genetic diversity and divergence were analyzed to identify potential distinct lineages and areas of genetic discontinuities of species.

Based on the above data, an attempt was made to resolve whether the contemporary distribution results from long-term survival in several isolated areas (local refugia) and thus is a relic of ancient events or whether the species recently spread from a single refugium (likely located in the Tatra Mts – central part of the range).

Materials and methods

Study species

Saxifraga wahlenbergii Ball (sect. *Saxifraga*; Saxifragaceae) is an endemic perennial species of the Western Carpathians (in Poland and Slovakia). Its range includes the massifs of Tatra Mts, Malá Fatra Mts, Chočské vrchy Mts, Nízke

Tatry Mts, and Muránska planina. However, it is a common species only in the Tatra Mts (the highest and environmentally most complex massif of the Western Carpathians) – it is abundant at higher altitudes above the tree line (up to 2540 m a.s.l.) and also descends to lower elevations, e.g., along streams (880 m a.s.l.) (Pawłowska 1966). The species grows on both limestone and granitic substrates, with preference for limestones. Throughout its range, it is found mainly on moist edges of limestone and granite screes, in the shade of rocks, on ledges and in rock crevices or on the edge of forests. It is a characteristic species of the *Saxifragetum wahlenbergii* community (Matuszkiewicz 2005) (described as *Saxifragetum perdurantis* Pawłowski and Stecki 1927). This community is considered an endemic community of the limestone Tatra Mts, Malá Fatra Mts and Chočské vrchy Mts (Matuszkiewicz 2005). Species is a hexaploid with a chromosome number of 2n = 66 (x = 11) (Skalińska 1963).

Population sampling

Plant material of *Saxifraga wahlenbergii* was sampled in natural populations, spanning the entire natural distribution area of this species in the Western Carpathians. Populations were assigned to regional geographical units, which were further assigned into predefined groups: the Western Tatra Mts, the Eastern Tatra Mts and those outside of the Tatra Mts, including localities from: the Malá Fatra Mts, Chočské vrchy Mts, Nízke Tatry Mts and Muránska planina (Kondracki 1989) (Fig. 1A and Table 1 for location details). The number of samples per population varied and depended on population size. Special attention was paid to include samples from all isolated massifs where the species occurs. In total, our dataset comprised 57 individuals collected from 11 populations of *S. wahlenbergii*. Leaves from each individual were placed in a tube or bag with silica gel immediately after collecting and stored at room temperature until the DNA isolation. Herbarium material (vouchers) was collected only from large populations, due to conservation reasons and deposited in the Herbarium of W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków (KRAM).

Laboratory analysis

The total genomic DNA was isolated from 5–10 mg of dried leaf tissue of collected samples using the DNeasy Plant Mini Kit system (Qiagen, Hilden, Germany) according to the manufacturer's protocol (final elution step was carried out using 2×50 µL of elution buffer). DNA quality and concentration were estimated against λ-DNA on 1% agarose gel stained with ethidium bromide. The purified DNA isolates were the basis of DNA sequencing and AFLP analyses. Samples from the Muránska planina population (S11) were collected later than the core sample set and they could only be used in the sequencing analysis.

The non-coding chloroplast DNA regions (cpDNA) – *rps*16-*trn*K and *rpl*32-*trn*L (Shaw et al. 2007) – and nuclear ribosomal DNA region (nrDNA) – ITS (*ITS*1A-*ITS*4, White et al. 1990; Blattner 1999) – were used for DNA sequencing. Primers were selected and analyzed according to the protocols described in detail by Tkach et al. (2015, 2019).

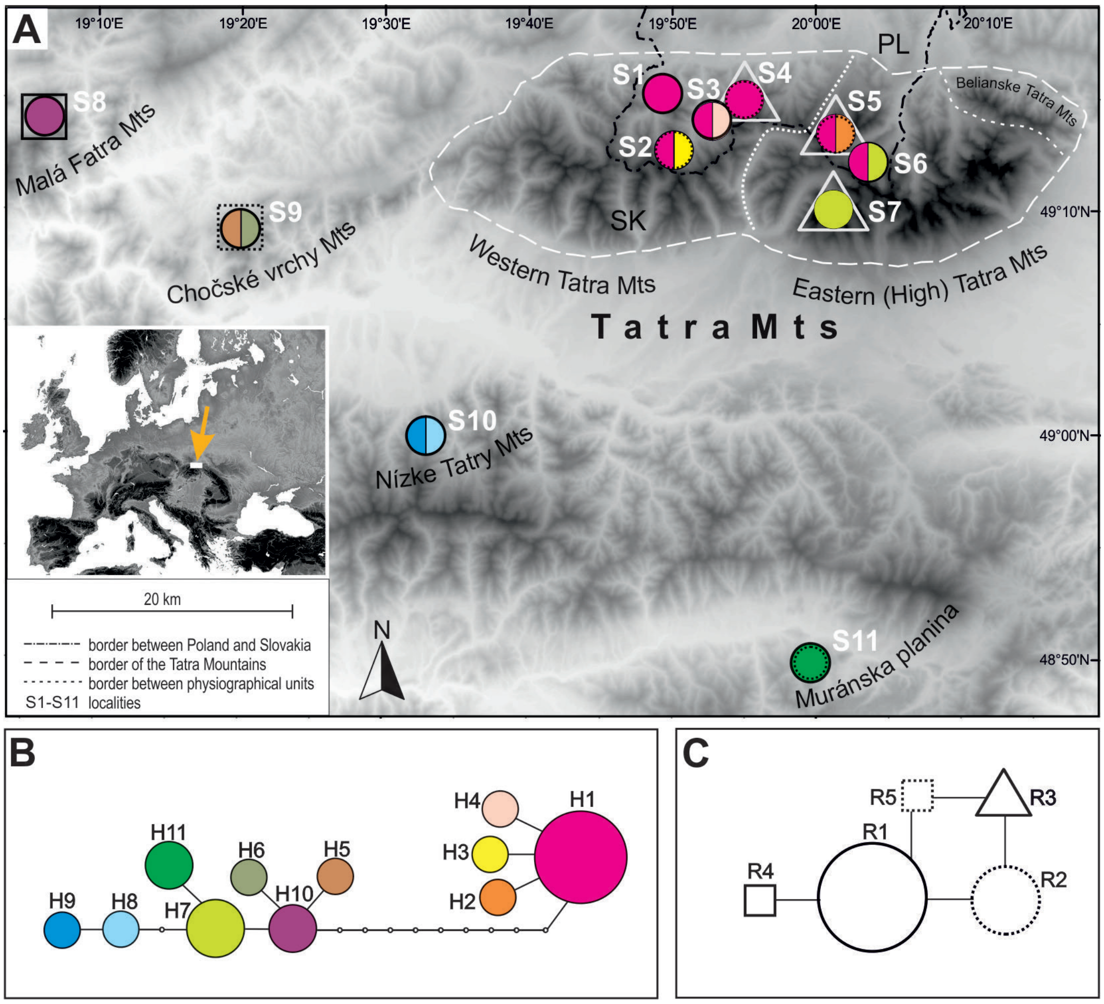

Figure 1. Location of studied populations of *Saxifraga wahlenbergii* and their genetic variability based on DNA sequence data **A** distribution of 11 populations of *S. wahlenbergii* and haplotypes and ribotypes in the populations **B** haplotype network based on the combined chloroplast regions: *rps*16-*trn*K and *rpl*32-*trn*L **C** ribotype network based on ITS region. Networks obtained from TCS based on a 95% connection limit. The relative sizes of circles in networks are proportional to haplotype and ribotype frequencies. For population acronyms see Table 1.

AFLP analysis was performed according to Vos et al. (1995) as described in detail by Cieślak et al. (2007). For high-quality AFLP profiles, we tested selective primer combinations using four individuals from distant populations. All samples were analyzed using three selective primers combinations that yielded clear, unambiguous, and polymorphic profiles – *EcoRI*-AAG/*MseI*-CTG, *EcoRI*-ACT/*MseI*-CAG and *EcoRI*-AGA/*MseI*-CAC. Genotyping reproducibility was tested by including duplicates for each population (Bonin et al. 2004). Amplification products were separated with an internal size standard (GeneScan ROX-500) on the ABI Prism 3100 Avant automated sequencer using POP-4 polymer (Applied Biosystems, Foster City, CA, USA). Obtained AFLP marker sets were imported to Genographer Software (v. 1.6.0; J. Benham, Montana State University, 1998–2001) (Benham et al. 1999), which was used to score the fragments in the range of 50–500 bp. AFLP fragments for primer combination were saved as present (1) or absent (0) for a binary data matrix (see Suppl. material 1).

Table 1. Localities of populations of *Saxifraga wahlenbergii* used in the study and parameters of their genetic variability based on AFLP, nrDNA (ITS) and cpDNA sequences. N_A/N_S – population sampling for AFLP analysis and DNA sequencing; *P*/% – number and percentage of polymorphic markers; *He* – mean (±SD) Nei's gene diversity; *I* – mean (±SD) Shannon's Index; *DW* – frequency down-weighted marker values; R – ribotypes (variants of ITS of nrDNA) and H – haplotypes (variants of cpDNA) in population (the number of individuals representing a particular ribotype or haplotype is given in parentheses). Country code: PL – Poland, SK – Slovakia. Collectors code: AD – Anna Delimat, AR – Anna Ronikier, MR – Michał Ronikier, RL – Roman Letz, PM – Patrik Mráz, PT – Peter Turis.

Code	Locality	N_A/N_S	AFLP				ITS	cpDNA
			P/%	*He*	*I*	*DW*	R(No.)	H(No.)
Western Tatra Mts (Tatry Zachodnie, Západné Tatry)								
S1	PL, Dolina Chochołowska valley, 1370 m a.s.l., 49°14'N, 19°48'E (AD)	5/2	59/27.31	0.10 (±0.18)	0.15 (±0.26)	21.77	R1(2)	H1(2)
S2	PL, between the Gaborowa Przełęcz pass and Bystra Przełęcz pass, ~1930 m a.s.l., 49°12'N, 19°49'E (RL, PM)	4/2	61/28.24	0.12 (±0.19)	0.17 (±0.28)	20.06	R2(2)	H1(1) H3(1)
S3	PL, Przełęcz pod Kopą Kondracką pass, 1500 m a.s.l., 49°14'N, 19°55'E (AD)	5/2	61/28.24	0.11 (±0.18)	0.16 (±0.26)	25.07	R1(2)	H1(1) H4(1)
S4	PL, Piekiełko (Piekło) valley, 1640 m a.s.l., 49°14'N, 19°56'E (AD)	9/2	91/42.10	0.15 (±0.20)	0.23 (±0.28)	58.57	R2(1) R3(1)	H1(2)
Eastern Tatra Mts (High Tatra Mts, Tatry Wysokie, Vysoké Tatry)								
S5	PL, N slopes of the pass Zawrat, 2100 m a.s.l., 49°13'N, 20°01'E (MR)	4/2	79/36.57	0.14 (±0.19)	0.20 (±0.28)	25.46	R2(1) R3(1)	H1(1) H2(1)
S6	PL, Mięguszowiecki Szczyt Czarny Mt., 2220 m a.l.s., 49°11'N, 20°03'E (AD)	7/2	83/38.43	0.14 (±0.20)	0.20 (±0.28)	36.37	R1(2)	H1(1) H7(1)
S7	SK, Hrubý vrch Mt, ~ 2350 m a.s.l., 49°10'N, 20°01'E (MR)	8/2	85/39.35	0.14 (±0.19)	0.21 (±0.28)	40.09	R3(2)	H7(2)
Malá Fatra Mts								
S8	SK, Veľký Rozsutec Mt., 1550 m a.s.l., 49°14'N, 19°06'E (MR, AR)	5/2	76/35.19	0.13 (±0.19)	0.19 (±0.27)	26.90	R1(1) R5(1)	H10 (2)
Chočské vrchy Mts								
S9	SK, Veľký Choč Mt., 1600 m a.s.l., 49°09'N, 19°20'E (MR)	4/2	60/27.78	0.10 (±0.18)	0.15 (±0.26)	23.36	R1(1) R4(1)	H5(1) H6(1)
Nízke Tatry Mts								
S10	SK, Siná Mt., 1422 m a.s.l., 49°00'N, 19°33'E (RL, PT)	4/2	61/28.24	0.11 (±0.19)	0.27 (±0.27)	29.54	R1(2)	H8(1) H9(1)
Spišsko-gemerský kras								
S11	SK, Muránska planina, Veľka Stožka, 1242 m a.s.l., 48°46'N, 19°58'E (PT)	–/2	–	–	–	–	R1(1) R2(1)	H11 (2)

cpDNA and ITS of nrDNA data analysis

Analyses of cpDNA and ITS of nrDNA regions were performed separately. Forward and reverse DNA sequences data were automatically assembled and aligned based on ClustalW algorithm (Thompson et al. 1994; Larkin et al. 2007) using the Geneious Pro 6.0.2 program (Drummond et al. 2011). The obtained sequences are deposited in GenBank with accession numbers: *rps*16-*trn*K – OQ706232–53; *rpl*32-*trn*L – OQ706254–73, OR682717–18 and *ITS*1A-*ITS*4 – OQ678158–79 (see Suppl. material 2).

Gene diversity (*h*) and nucleotide diversity (π) were calculated based on cpDNA and ITS sequence variation for the total sample of *Saxifraga wahlenbergii* and for predefined region groups within the species range using the DNAsp 5.0 program (Librado and Rozas 2009). To detect past demographic expansion, evidence for possible selection and/or genetic bottlenecks, Tajima's *D* neutrality test was implemented (Tajima 1989). Indels were treated as single polymorphic sites. The relationships between nrDNA ITS ribotypes (R) and cpDNA haplotypes (H) were separately analyzed using the statistical parsimony (SP) algorithm (Templeton et al. 1992) as implemented in TCS v1.2 (Clement et al. 2000); coding indels longer than 1 bp were treated as single characters. Statistical parsimony networks and the maximum number of mutational steps were obtained with 95% connection limit approach. Phylogenetic reconstruction using Bayesian inference was accomplished with MrBayes 3.2.7a program (Ronquist et al. 2012). The analysis was completed for four chains, parameter values of nst=6 and rates=invgamma, 50 million generations with sampling trees every 100 generations. 25% of the initial trees were discarded and the remaining 75% were used to build majority consensus tree and to calculate Bayesian posterior probabilities. The tree was visualized using FigTree 1.4.2 (Rambaut 2014).

AFLP data analysis

The genetic diversity of *Saxifraga wahlenbergii* at species and within-species level (populations) was assessed on the basis of binary AFLP data matrix by calculating the genetic parameters, including the number (*P*) and percentage of polymorphic markers (*%)*, Nei's gene diversity (*He*), Shannon's information index (*I*) and gene flow (*Nm*) using POPGENE v. 1.32 software (Yeh et al. 1999). In order to identify long-term isolated and genetically unique populations, frequency down-weighed marker values (*DW*; Schönswetter and Tribsch 2005) were calculated using R-script AFLPdat (Ehrich 2006). The relationships among individuals and populations were analyzed by a Principal Coordinates Analysis (PCoA) based on the Nei-Li genetic distance matrix computed in FAMD v. 1.25 (Schlüter and Harris 2006) and by a split network (Neighbor-Net) also based on the Nei-Li coefficient with branch support estimated by bootstrapping with 1000 replicates, implemented in SPLITStree4 (Huson and Bryant 2006). Further, the model-based Bayesian clustering procedure in STRUCTURE v. 2.3.4 (Pritchard et al. 2000) was used to determine the genetic structure of populations. The analysis was performed by setting the number of populations (*K*) from 2 to 12. The burn-in steps and the number of replicates were 10,000 and 50,000 for each *K*, respectively. All runs were repeated 100 times at each *K* and the optimal *K* value was selected as a point of a marked change in the envelope slope (kink of the curve) of lnP(D) as a function of *K*. Genetic population structure was investigated by a hierarchical analysis of molecular variance (AMOVA), and relationships between populations from different parts of the species' range were assessed based on pairwise genetic divergence (F_{ST}) for all populations, both implemented in Arlequin v. 3.5 (Excoffier and Lischer 2010).

Results

cpDNA and ITS of nrDNA variation

The sequences of cpDNA and ITS of nrDNA regions were obtained from 22 individuals from eleven populations of *Saxifraga wahlenbergii* (Table 1).

The alignments of *rps*16-*trn*K and *rpl*32–*trn*L regions of cpDNA were 796 bp and 655 bp in length, respectively (concatenated cpDNA alignment – 1451 bp in length). 15 variable sites were found – 4 singleton variable sites and 11 parsimony informative sites, which represented transitions (C-T, 3 A-G) and transversions (3 G-T, 2 A-T and 2 A-C). In the *rpl*32–*trn*L region a thirty-one-nucleotide insertion/deletion was also identified. Eleven haplotypes (H1–H11; Fig. 1A, B) determined by these polymorphisms were revealed.

Each population harbored one or two cpDNA haplotypes, mostly specific for individual populations and/or mountain ranges. H1–H4 and H7 haplotypes occurred only in the Tatra Mts, with the most frequent H1 haplotype present in almost all Tatra populations (six out of seven populations) (Fig. 1A, B, Tables 1, 2). On the other hand, H8–H11 haplotypes were detected exclusively in populations from the isolated locations outside the Tatra Mts. Accordingly, the network of cpDNA haplotypes based on statistical parsimony analysis revealed two main groups separated by nine mutations and corresponding to the Tatra Mts versus other mountain ranges (Fig. 1A, B). In the Tatra Mts group, haplotypes displayed a star-like pattern, with H1 as the dominant haplotype, widespread across the Western Tatra Mts and the Eastern Tatra Mts. In the second group from outside the Tatra Mts, haplotypes occurred with comparable frequency. The phylogenetic tree, as inferred through Bayesian analysis, revealed two distinct groups – individuals from the Tatra Mts form a sister genetic group to the group including all other individuals. A certain level of divergence was observed only among individuals from the Eastern Tatra Mts in both clades (Fig. 2).

Overall, *S. wahlenbergii* displays a moderate gene diversity (h = 0.81 ±0.06) and nucleotide diversity (π = 0.0036 ±0.0003) of cpDNA. At the local level of predefined regional groups, the highest gene diversity (h = 0.86 ±0.11) was found in the group of populations outside of the Tatra Mts (i.e., in Malá Fatra Mts, Chočské vrchy Mts, Nízke Tatry Mts and Muránska planina) with low nucleotide diversity (π = 0.0013 ±0.0003; Table 2). Within the Tatra Mts, populations of *S. wahlenbergii* from the eastern part were characterized by higher gene (h = 0.73 ±0.16) and nucleotide diversity (π = 0.0036 ±0.0004) than populations from the western part of this mountain range (h = 0.46 ±0.20; π = 0.0003 ±0.0007, respectively). Testing deviation from neutrality (Tajima's D) revealed no significant indications for departure from neutrality within regions ($P > 0.05$).

The obtained ITS alignment was 730 bp long, with very low sequence diversity. Only four indels (three poly-A and one poly-G stretches) were found and on this basis five ribotypes were established (R1–R5) (Fig. 1A, C). Only R1 ribotype was widespread and shared by seven populations within the species' range. The following ribotypes were specific for geographical regions: R3 for the Tatra Mts, R4 for the Malá Fatra Mts and R5 for the Chočské vrchy Mts (Tables 1, 2). The network analysis indicated close links between five ribotypes, and internal divisions into groups (Fig. 1C).

Table 2. Genetic diversity of nrDNA and cpDNA sequences of *Saxifraga wahlenbergii* calculated for a priori delimitation of regional groups. R – ribotypes (variants of nrDNA ITS) and H – haplotypes (variants of cpDNA); h – mean (±SD) gene diversity; π – mean (±SD) nucleotide diversity; D – Tajima's D statistic value; *non-significant at the 5% level ($P > 0.05$).

Regional groups	ITS				cpDNA			
	R	h	π	D	H	h	π	D
Western Tatra Mts	R1, R2, R3	0.00	0.00	0.00	H1, H3, H4	0.46 (±0.20)	0.0003 (±0.0007)	-1.31*
Eastern Tatra Mts	R1, R2, R3	0.00	0.00	0.00	H1, H2, H7	0.73 (±0.16)	0.0036 (±0.0004)	1.80*
Tatra Mts (as a whole)	R1, R2, R3	0.00	0.00	0.00	H1, H2, H3, H4, H7	0.66 (±0.12)	0.0024 (±0.0008)	-0.15*
Outside of the Tatra Mts	R1, R2, R4, R5	0.00	0.00	0.00	H5, H6, H8, H9, H10, H11	0.86 (±0.11)	0.0013 (±0.0003)	-0.33*

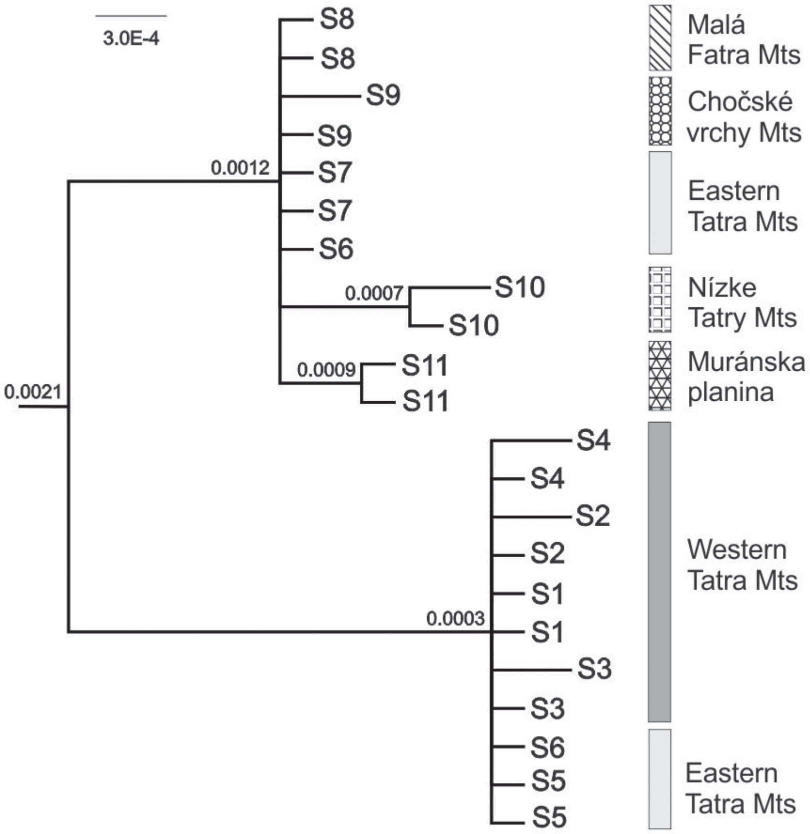

Figure 2. MrBayes tree based on the combined plastid *rps*16–*trn*K and *rpl*32–*trn*L regions of *Saxifraga wahlenbergii* (reduced dataset; see text for details). Numbers at nodes, in the order shown, correspond to posterior probabilities estimated in MrBayes. For population acronyms see Table 1.

AFLP variation

The AFLP analysis yielded 213 DNA markers, of which 181 (84.98%) were polymorphic for 55 individuals from ten populations of *Saxifraga wahlenbergii* (Table 1). Reproducibility of obtained AFLP band profiles was ~96%. The number of polymorphic markers in populations ranged from 59 (S1) to 91 (S4), with a mean of 83 markers (±20.29) per individual. There were no identical AFLP phenotypes among studied individuals. Only in populations from the Veľký Choč Mt. (S9, Chočské vrchy Mts) and Siná Mt. (S10, Nízke Tatry Mts) one private marker in each was identified.

At the species level, Nei's gene diversity (*He*) was 0.16 (±0.17) and ranged from 0.10 (S1) to 0.15 (S4), with an average value of 0.12 (±0.02). The frequency of down-weighted markers (*DW*) was similar across most populations and ranged from 20 to 30, with much higher values in populations S4 (59), S7 (40) and S6 (36) (Table 1).

The further analysis of PCoA performed on the entire dataset revealed that *S. wahlenbergii* populations are not clearly genetically divergent and form partially overlapping groups. In general, the population's scatter is characterized by the west-east gradient across the distribution range of *S. wahlenbergii*. In 1–3 axes arrangement, the populations from the disjunct parts of the range (populations: S1, S8, S9 and S10) are opposite to the highest locations of Hrubý vrch Mt. and Mięguszowiecki Szczyt Czarny Mt. (the

Eastern Tatra Mts). In the central part of plot, individuals from population of the Western Tatra Mts (S3, S4) and Malá Fatra Mts were located. The first three factors of the PCoA accounted for 35.39% of the total variation in the dataset (Fig. 3A).

The Neighbor-Net diagram demonstrated two groups, each consisting of clusters representing single, spatially isolated populations, but with different bootstrap support. The first group included those with higher bootstrap values, such as Nízke Tatry Mts (98%), Dolina Chochołowska valley (96%), Gaborowa Przełęcz pass (85%), Veľký Choč Mt. (62%) and Malá Fatra Mts (61%). The second group consisted of populations with very low support (Fig. 3B). It is characteristic that individuals of *S. wahlenbergii* from the higher altitudes of the Eastern Tatra Mts were closely related with each other and genetically more distant from individuals from slightly lower altitudes in the Western Tatra Mts.

Analysis of genetic variation (AMOVA) showed that a major part of *S. wahlenbergii* variation is attributed to the within-population level – 72.09%, in relation to among-population variation – 27.91% ($F_{ST} = 0.28$, $P < 0.001$). The same pattern can be found when analyzing geographical groups (Table 3, see Suppl. material 3). AMOVA also confirmed low but statistically significant genetic differences between regions ($F_{CT} = 0.05$, $P < 0.01$). Based on the comparison of F_{ST} values between pairs of populations, a gradation in differentiation between the populations of *S. wahlenbergii* from individual range regions was found. The population from Nízke Tatry Mts is the most distinct one, while the population from Malá Fatra Mts shows greater similarity with those from the Tatra Mts compared to the other parts of the range (see Suppl. materials 4, 5). Within the Tatra Mts, populations from the Eastern Tatra Mts presented greater genetic affinity with each other than with populations from the Western Tatra Mts. The greater mean diversity of the population in the Western Tatra Mts is due to the significant distinctiveness of the population from the Dolina Chochołowska valley, where the F_{ST} values between other populations range from 0.36 to 0.49 (see Suppl. material 4).

AFLP data indicates a low level of gene flow between populations of *S. wahlenbergii* ($Nm = 0.66$). In the STRUCTURE analysis of AFLP data, the stable and optimal number of population groups was selected based on the kink in the envelope of lnP(D) values. As can be seen from Fig. 4A, B, a clear change in the slope was found for $K = 3$. In order to further justify the reasons for such a choice, similar analyses were performed both for $K = 2$ and 3. For $K = 2$, the population from Dolina Chochołowska valley, represented a nearly homogeneous and clearly separated genetic group whereas populations from Eastern Tatra Mts, Nízke Tatry Mts and remaining populations from the Western Tatra Mts formed the second one. The populations from Malá Fatra Mts and Veľký Choč Mts displayed genetic admixture with a significant contribution of both genetic pools. For $K = 3$, population from the Dolina Chochołowska valley is even more genetically distinct, while all the populations from the Eastern Tatra Mts, Gaborowa Przełęcz pass in the Western Tatra Mts and Nízke Tatry Mts are similar to each other. Remaining populations from the Western Tatra Mts, as well as from Malá Fatra Mts and Veľký Choč Mts, represent the third group.

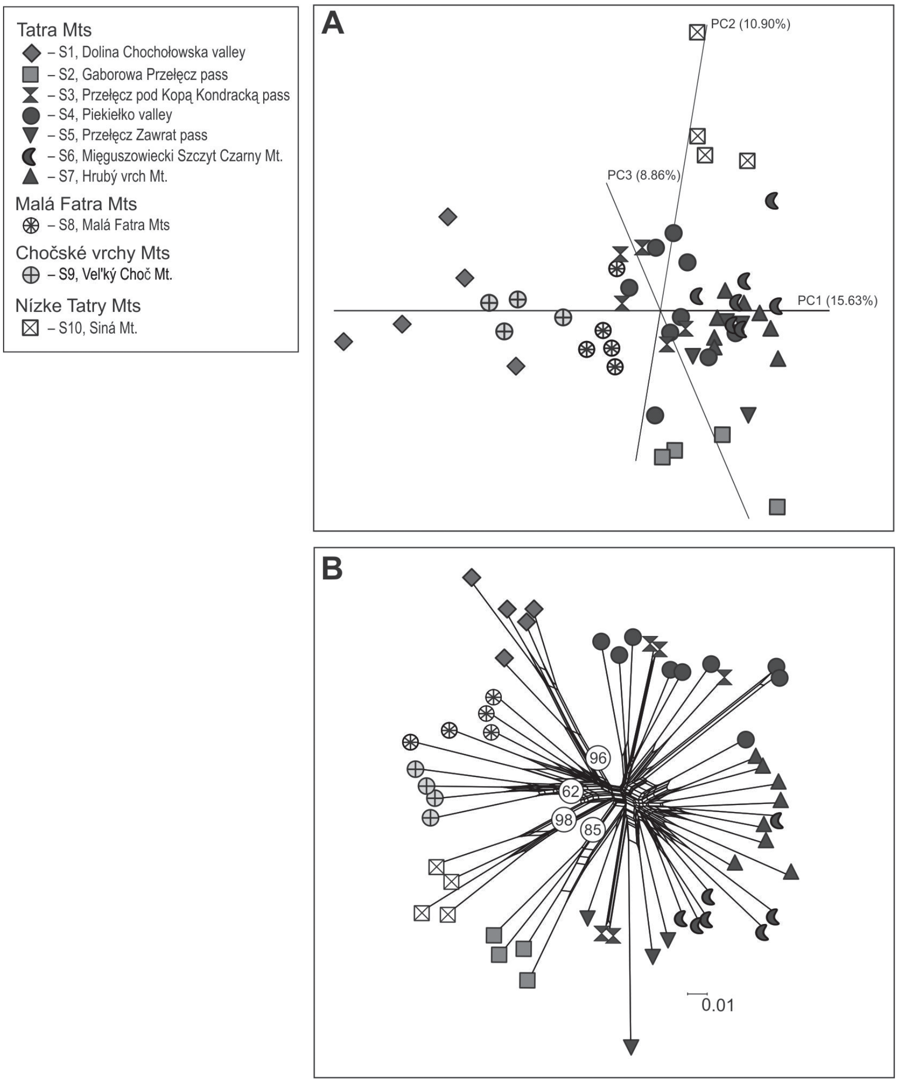

Figure 3. Phylogeographic structure within of *Saxifraga wahlenbergii* based on AFLP dataset (55 individuals from 10 populations) **A** Principal Component Analysis diagram, ordination at 1 *vs* 2 *vs* 3 axes **B** Neighbor-Net diagram with the bootstrap values derived from an analysis of 2,000 replicates above 50% has been given. Both diagrams were prepared based on the Nei-Li coefficient. For population acronyms see Table 1.

Table 3. AMOVA analysis based on AFLP data for the populations of *Saxifraga wahlenbergii* calculated for all populations and a priori delimitation of regional groups. Significance tests based on 1023 permutations, ****P* < 0.001, ***P* < 0.01.

Source of variation	d.f.	Sums of Squares	Variance components	% Total variance	*F* statistics
Among populations	9	487.480	6.753	27.91***	F_{ST} = 0.28
Within populations	45	784.738	17.439	72.09	
Total	54	1272.218	24.192		
Among regional groups – Western Tatra Mts *vs*. Eastern (High) Tatra Mts *vs.* outside of the Tatra Mts	2	145.588	1.206	4.92**	F_{CT} = 0.05
Among populations	7	341.892	5.872	23.95***	F_{SC} = 0.25
Within population	45	784.738	17.439	71.13	F_{ST} = 0.29
Total	54	1272.218	24.517		

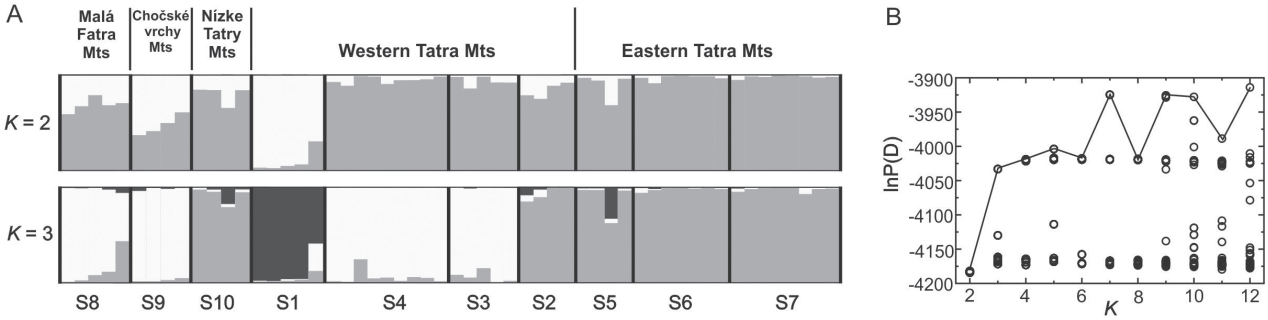

Figure 4. A The histograms representing the assignment of 55 individuals of *Saxifraga wahlenbergii* to different clusters by Bayesian spatial clustering (STRUCTURE software). Each vertical bar corresponds to an individual, highlighted in gray for clarity, contrasting with the cluster assignments, respectively, at *K* = 2 and *K* = 3 **B** in P(Data) values in function of *K* are shown. For population acronyms see Table 1.

Discussion

Phylogenetic analyses of the *Saxifraga* section indicated the hybrid origin of *Saxifraga wahlenbergii* and allowed us to estimate the possible oldest age of its hybrid origin to the late Neogene (4.7 Ma). These analyses also provided insights into its internal diversity (Tkach et al. 2019). Our analysis confirmed two distinct groups of plastid haplotypes corresponding to the geographical locations of populations and revealed additional local phylogeographical structures. This distribution of genetic lineages on a small spatial scale, characteristic of the Tatra Mts, was also observed in the endemic species *Cochlearia tatrae* (Koch et al. 2003; Cieślak et al. 2021). This spatial pattern, along with the presence of unique haplotypes in populations, implies survival in local refugia with limited contact among them.

In mountain conditions, the process of isolation by distance contributed to historical interruption of gene flow between populations, leading to geographically driven groups of populations (e.g., Tribsch and Schönswetter 2003; Schönswetter et al. 2005; Kropf et al. 2006; Christe et al. 2014; Melichárková et al. 2019). Consequently, contemporary populations represent more or less distinct units in the landscape, potentially facilitated by the periglacial environment. This environment consisted of a mosaic of habitats that allowed the survival of various population groups (Birks and Willis 2008; Provan and Bennett 2008). The accumulation of intraspecific diversity in *S. wahlenbergii*, particularly within the cpDNA, among populations from different regions, such as the Malá Fatra Mts, Chočské vrchy Mts, Nízke Tatry Mts, and Muránska planina, points to the scenario that these regions may have acted as distinct glacial refugia for high mountain species in the Western Carpathians. Analyses of AFLP data highlight a weakly resolved but distinct position of spatially isolated populations and groups, further supporting the above interpretation.

In the Tatra Mts, subalpine populations of *S. wahlenbergii* are more closely related to those geographically closest from the same mountain range than to their subalpine counterparts from other mountain ranges. This suggests that the source area of their recolonization could have been populations from low elevations, such as the extant population from the Dolina Chochołowska valley, a site which remained outside the glaciation area (Kłapyta et al. 2016; Kłapyta and Zasadni 2017–2018). In the Tatra Mts, which are clearly different from their periphery, a high genetic diversity of haplotypes is observed. Apart from several haplotypes from both cpDNA groups, the presence of R2 and R3 ITS variants is restricted to populations from the Tatras range. The genetic structure of *S. wahlenbergii* in this area was likely influenced by the topographically complex environment and historical conditions in the glacial periods.

The Tatra Mts, unlike most of the Western Carpathians, were strongly, albeit unevenly, glaciated during the Pleistocene glaciations (Zasadni and Kłapyta 2014; Zasadni et al. 2022). Due to the occurrence of extensive glaciers in the valleys (Kłapyta et al. 2016), available local glacial refugia were physically isolated. Within the mountains, refugia were generally distributed along steep, uncovered rocky crests at the highest altitudes and lower crests below the snowline. Large areas with a mosaic of habitats potentially suitable for high-mountain plants were also available in adjacent low-altitude locations along the entire range. Consequently, survival in lower, periglacial habitats appears appropriate for *S. wahlenbergii*. During cold glacial periods, these could have been places both at the foot and along the glacial moraines, in the glacier ablation zones, as well as in the areas occupied by steppe-tundra. Survival in these areas could have been possible thanks to the ability of species to live in a wide range of habitat conditions, such as moist edges of limestone and granite scree, in the shade of rocks, on shelves and in rock crevices.

On the other hand, low values of F_{ST} (the lowest in relation to the compared pairs of populations) observed in the AFLP data from the Tatra Mts can be the result of the maintenance of gene flow between populations during recolonization of this area after the last glaciation and may counteract incipient differentiation processes, thereby avoiding bottlenecks, genetic drift, and the loss of genetic diversity. Characteristically, the highest values of the F_{ST} were noted between populations from the areas with the highest altitudes, namely the Tatra Mts and the Nízke Tatry Mts. These results suggest that mountain ridges acted as a stronger barrier for gene flow more effectively than the elevation differences between subalpine and lower-lying areas within the same ranges. In addition, the genetic structure of *S. wahlenbergii*, a relic mountain plant species, certainly reflects processes acting in different time periods. Populations that survived when environmental conditions became unfavorable could retain genetic variability. Becoming a source of remigration in new conditions, they could also host new local mutation fixations. Therefore, it can be assumed that both Quaternary climatic oscillations and ecological divergence have played a role in shaping the distribution and divergence patterns observed in *S. wahlenbergii*. Similarly, in the species complex *Alyssum montanum*–*A. repens*, a clear elevational shift was identified, indicating that differential ecological adaptation occurred in the respective mountain areas (Melichárková et al. 2019). It should be emphasized that these findings are consistent with previous results of phylogeographical analyses (Ronikier et al. 2012; Cieślak et al. 2021), which showed the Tatra Mountains as an important, independent area within the Western Carpathians, where the local structure of species was formed. These patterns indicate that the Tatra Mts also served as a refugium or a system of microrefugia, likely due to their high topographical and habitat diversity. However, the genetic position of populations from remaining massifs, especially the series of massif-specific cpDNA haplotypes, also indicates their role supporting the *S. wahlenbergii* populations, forming a system of discrete parts of the range likely over a longer temporal scale. In the case of an allopolyploid species of hybrid origin it cannot also be ruled out that a polytopic hybrid origin may have played a role in the two main intraspecific lineages observed (Melichárková et al. 2019), which have later undergone an internal diversification in the isolated mountain environment.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Elżbieta Cieślak: Research concept and design, Data analysis and interpretation, Writing the article, Critical revision of the article, Final approval of the article. Michał Ronikier: Research concept and design, Collection and/or assembly of data, Critical revision of the article, Final approval of the article. Magdalena Szczepaniak: Data analysis and interpretation, Critical revision of the article, Final approval of the article.

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Data availability

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

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Supplementary material 1

AFLP dataset of *Saxifraga wahlenbergii*

Authors: Elżbieta Cieślak, Michał Ronikier, Magdalena Szczepaniak

Data type: xls

Link: https://doi.org/10.3897/phytokeys.246.118796.suppl1

Supplementary material 2

The datasets of nrDNA and cpDNA of *Saxifraga wahlenbergii*

Authors: Elżbieta Cieślak, Michał Ronikier, Magdalena Szczepaniak

Data type: docx

Link: https://doi.org/10.3897/phytokeys.246.118796.suppl2

Supplementary material 3

AMOVA analysis based on AFLP data for populations of *Saxifraga wahlenbergii* calculated with a priori delimitation of regional groups

Authors: Elżbieta Cieślak, Michał Ronikier, Magdalena Szczepaniak

Data type: docx

Explanation note: Significance tests based on 1023 permutations; *$P < 0.001$. Regional grouping of populations see in Materials and methods.

Link: https://doi.org/10.3897/phytokeys.246.118796.suppl3

Supplementary material 4

Pairwise genetic divergence (F_{ST}) across 10 populations of *Saxifraga wahlenbergii* based on AFLP data

Authors: Elżbieta Cieślak, Michał Ronikier, Magdalena Szczepaniak

Data type: docx

Explanation note: Significance tests based on 1023 permutations; $P < 0.001$. For population acronyms see Table 1.

Link: https://doi.org/10.3897/phytokeys.246.118796.suppl4

Supplementary material 5

Spatial arrangement of varying divergences (F_{ST}) among populations within distribution range of *Saxifraga wahlenbergii*

Authors: Elżbieta Cieślak, Michał Ronikier, Magdalena Szczepaniak

Data type: pdf

Explanation note: Above the line, the average F_{ST} values are given; the line colors correspond to scale in the right corner of the map. For population acronyms see Table 1.

Link: https://doi.org/10.3897/phytokeys.246.118796.suppl5

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Research Article

Ulnaria shun-biseriata sp. nov. (Bacillariophyta) from the Shun River in Hunan Province, China

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Abstract

A new species, *Ulnaria shun-biseriata* **sp. nov.**, was found in the Shun River of Hunan Province, southern China, and its morphology was described based on light and scannning electron microscope obervations. *Ulnaria shun-biseriata* is characterized by its lanceolate valve outline, apiculate valve apices, slightly undulate valve margins, mostly biseriate striae, variable central area, and closed valvocopula. Many abnormal valves of *U. shun-biseriata* were observed in the samples investigated and the most frequent morphological abnormalities consisted of a lack of symmetry relative to the apical axis caused by a unilateral expansion in the middle part of the valve.

Key words: abnormal valve, biseriate striae, pre-normal valve, *Ulnaria*, valvocopula

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Introduction

Hunan Province, is situated in southern China to the south of both the Yangtze River and Dongting Lake. It has an area of 210,500 km^2, is a major rice-producing region with a population that exceeded 66.6 million inhabitants in 2020. Dongting Lake, the second largest freshwater lake in China, locates in the northeast of Hunan, and drains the entire river system of Hunan with only a few exceptions. There are four major rivers in Hunan, i.e. the Xiang, Zi, Yuna and Li Rivers, all of which flow into Dongting Lake.

In recent years, the diatom flora of Hunan has been explored by Dr. Liu from Jishou University and his collaborators and their research led to the descriptions of more than 30 species new-to-science (e.g. Liu 2023; Liu et al. 2016, 2017a, 2017b, 2017c, 2018a, 2018b, 2018c, 2019a, 2019b, 2019c, 2020a, 2021; Long et al. 2021, 2022a, 2022b; Yuan et al. 2023; Xu et al. 2024). However, the diatom flora of the Xiang River has been underexplored until now. The Xiang River is one of the principal tributaries of the Yangtze River, China's largest river, and is the largest and longest river in Hunan with a total length of 800 km. The Xiang River's source is located in the mountains in the northern part of the Zhuang Autonomous Region of Guangxi and flows northeast into Hunan Province. During its course into Dongting Lake, the Xiang River is joined by many tributaries (e.g. the Xiao, Lei and Lu Rivers) to form a very large drainage area. There are very limited reports on the diatom flora of the Xiang River (Long et al. 2022c; Liu 2023; Yuan et al. 2023; Zheng et al. 2023).

The diatom genus *Ulnaria* (Kützing) Compère is a freshwater genus which has been intensively studied by Liu (2023). In this monograph, Liu (2023) provided many insights on the life history and living cells, as well as morphological observations on the ultrastructure of the basal siliceous layer, with details on the central area, ocellulimbus, rimoportula, valvocopula, and configuration of girdle bands for 63 *Ulnaria* taxa. Moreover, 15 new *Ulnaria* species have been found and described from Hunan Province (Liu et al. 2017b, 2019a, 2019c, Liu 2023), one of which (*U. pandurata-uniseriata*) was found in the Shun River – a small tributary of the Xiang River. This paper further contributes to the investigation of the diatom flora of the Xiang River by providing the description of a new *Ulnaria* species, *U. shun-biseriata* sp. nov., collected from the Shun River, one of its tributary.

Materials and methods

The diatom samples of this study were collected from the Shun River, a headwater tributary of the Xiang River, which runs through Lanshan County in the south of Hunan. Epilithic diatom samples were collected on October 5, 2021. The method of collecting the diatom samples is the same as in Liu (2023) and consists of sampling numerous submerged stones showing yellow-brown surfaces that indicate the presence of diatoms. Each stone was placed on a stainless-steel plate and its surface was brushed using a toothbrush, with the brushed-off diatom samples being washed onto the plate. The diatom samples were transferred into two 100 ml sampling bottles. One bottle was fixed with 70% ethanol and the other was left unfixed. At the time of sample collection, temperature, pH, and conductivity were measured in situ with a portable multimeter (HQ40D, Hach, Colorado, USA).

The laboratory methods are also the same as in Liu (2023). To alleviate any plagiarism concerns, we acknowledge the repetition herein: "The collected diatom samples to which was added 70% alcohol were processed (cleaned) for microscopic examination with 10% HCl and 30% H_2O_2. Permanent slides were prepared using Naphrax mountant and examined using a Leica DM3000 light microscope (LM). Slides are deposited in the Herbarium of Jishou University, Hunan, People's Republic of China (**JIU**) (Herbarium acronym according the Index Herbarium http://sweetgum.nybg.org/science/ih/). Samples were also examined using scanning electron microscope (SEM). Several drops of the cleaned diatom material were air-dried onto glass coverslips. The coverslips were attached to aluminium stubs using double-sided conductive carbon strip and sputter-coated with platinum (Cressington Sputter Coater 108auto, Ted Pella, Inc.). Samples were examined and imaged using a field emission scanning electron microscope (Carl Zeiss Microscope, model Sigma HD) available at Huaihua University, China".

The terminology in the diatom descriptions and in the discussion mainly follows Liu (2023). In particular, the term viminule refers to the interconnecting tiny ribs between the two adjacent virgae which define areolae in biseriate or multiseriate striae.

Results

Ulnaria shun-biseriata **Bing Liu & Rioual, sp. nov.**
Figs 1–4

Holotype. A specimen circled on the Slide DIA2024008, deposited in the herbarium of Jishou University (JIU), China, illustrated here as Fig. 1A. Registration. Phycobank http://phycobank.org/104927.

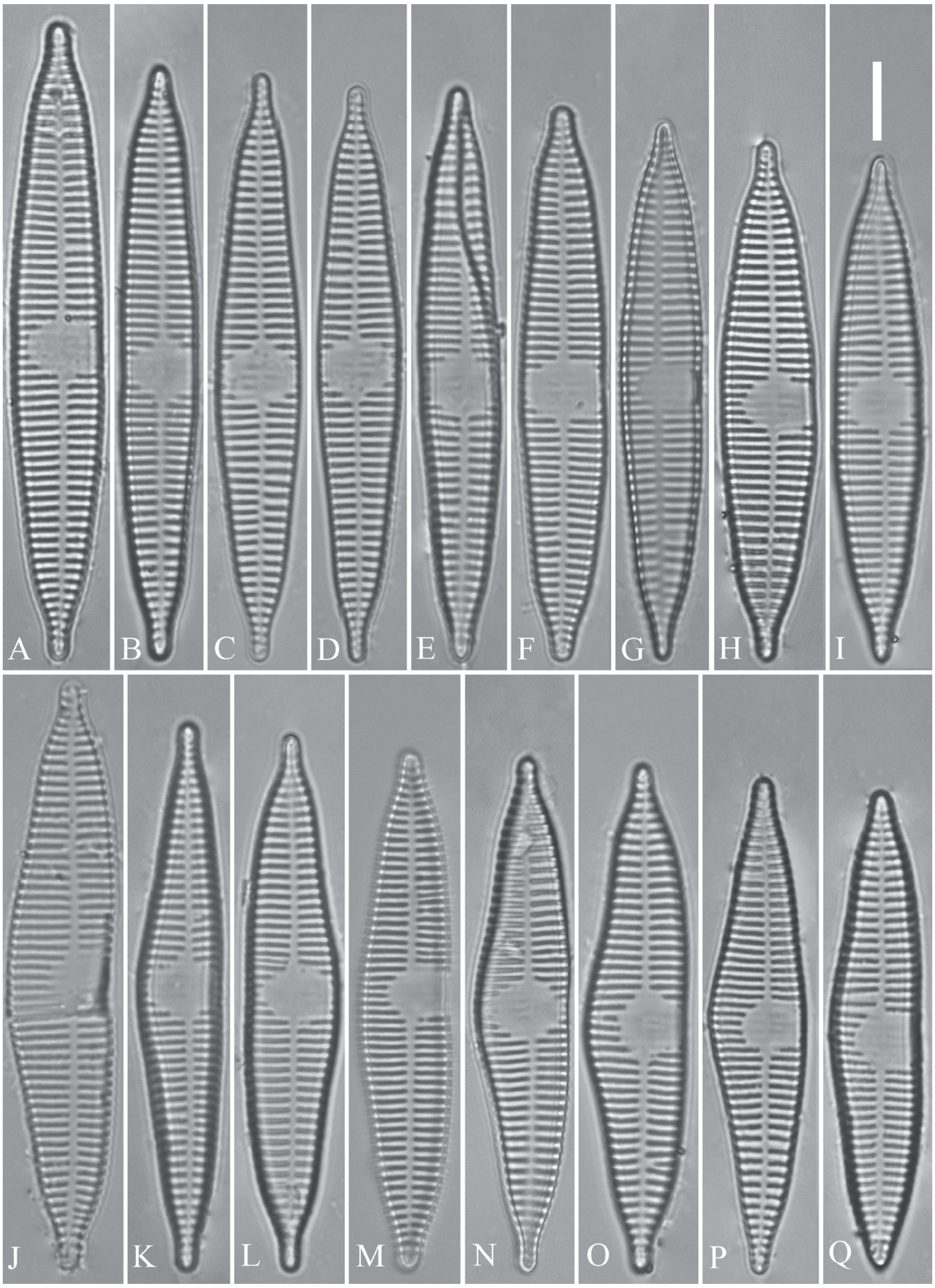

Figure 1. *Ulnaria shun-biseriata* sp. nov., LM **A–I** nine normal valves showing a size diminution series **J–Q** eight abnormal valves **A** illustration of holotype specimen. Scale bar: 10 μm (**I**).

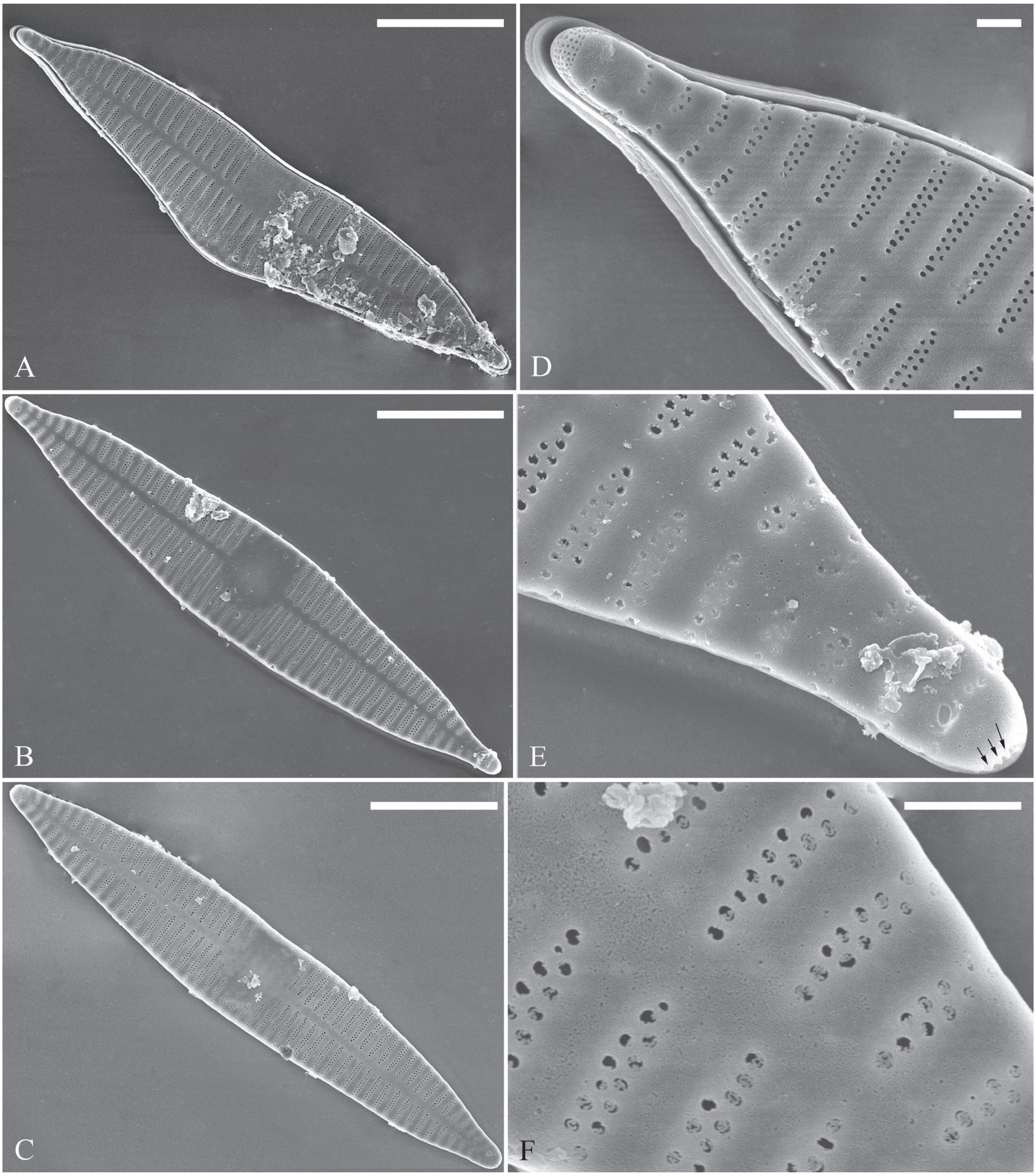

Figure 2. *Ulnaria shun-biseriata* sp. nov., external view, SEM **A–C** three complete valves, note biseriate striae and variable central areas **D, E** two apical details from **A**, note a few serrated projections protruding over the ocellulimbus (three arrows) **F** details of areolae showing the closing plates. Scale bars: 10 µm (**A–C**); 1 µm (**D–F**).

Type locality. China • Hunan Province: Lanshan County, Shun River, at a sampling site (25°14'55"N, 112°8'32"E, 400 m asl.), collected by Bing Liu, October 5, 2021.

Description. *LM* (Fig. 1). Valves lanceolate with slightly undulate valve margins and apiculate apices. Valve dimensions (n = 41): length 48–70 µm, width 8.3–10.7 µm at center. Sternum distinct, extending length of valve. Central

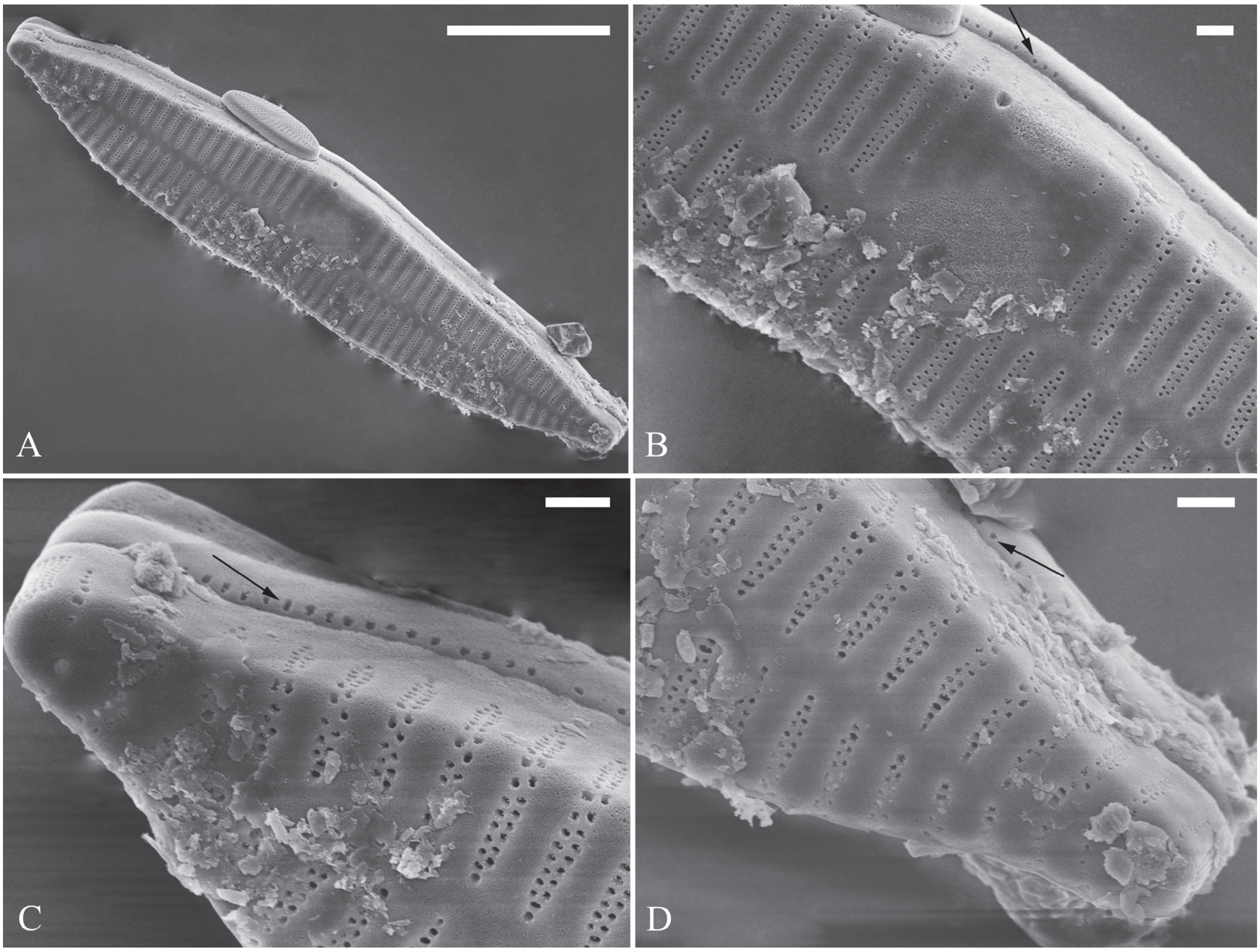

Figure 3. *Ulnaria shun-biseriata* sp. nov., external view, SEM **A** valve with valvocopula **B–D** details from **A** showing the mantle, valvocopula and ocellulimbus. Scale bars: 10 μm (**A**); 1 μm (**C–D**).

area with two arrangements: an asymmetric hyaline region extending to both margins (Fig. 1B–F) or a hyaline area which extends to one margin with the other side bordered with a few shortened striae (Fig. 1A, G–I). Ghost striae sometimes present (e.g. Fig. 1C, D) in the central area. Striae parallel, mostly opposite one another across sternum. Stria density 8.5–11 (often 10) in 10 μm. Many abnormal valves found, all of which exhibit an asymmetry relative to the apical axis due to the valve middle part only expanding on one side, and more undulate valve margins (Fig. 1J–Q) than normal valves (Fig. 1A–I).

SEM (Figs 2–4). Valves characterized by relatively wide virgae, interconnected with thin viminules, areolar closing plates having a few struts fixing them onto the areolar wall (Figs 2–4). Valves with mixed striae, mostly biseriate. Two rimoportulae per valve, one at each pole, externally expressed as simple holes (Fig. 2E), internally bilabiate, situated close to sternum (Fig. 4E). Ocellulimbus composed of pervalvar columns and transverse rows of porelli (Fig. 2D, 3C). A few serrated apical outgrowths protruding over the ocellulimbus (Fig. 2E). Valvocopula is a closed hoop, attached to the mantle interior, surrounding internal valve margin (Fig. 4C–F). Each valvocopula bears a mostly continuous row of poroids dividing the pars interior from pars exterior, located at midline (Fig. 3B–C, arrows); lacking ornamentation at either apex (Fig. 4E, F, arrow respectively). On its advalvar edge, valvocopula

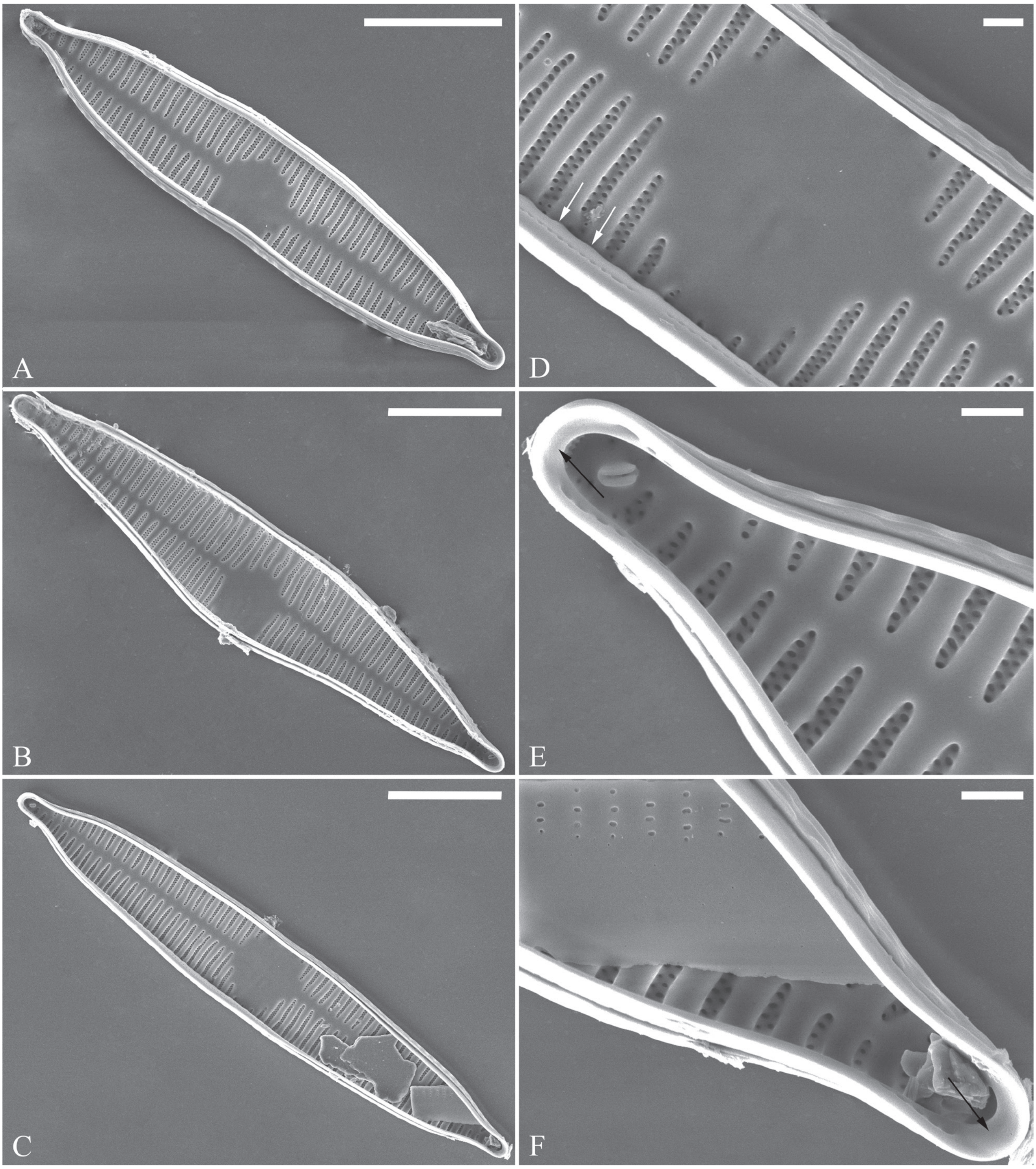

Figure 4. *Ulnaria shun-biseriata* sp. nov., SEM, internal view **A–C** three valves with closed valvocopulae **D** middle part detail from **C** note central area flanked by a few marginal striae only on one side and serrated projections over each virga (two arrows) **E, F** two apical details from **C** note unornamented valvocopula at both apices (arrow respectively). Scale bars: 10 µm (**A–C**); 1 µm (**D–F**).

bears a row of serrated projections, each corresponding internally to a virga (Fig. 4D, two arrows).

Etymology. The specific epithet *shun-biseriata* is a combination of the Shun River and the adjective biseriate to reflect the type locality and the mostly biseriate character of the striae.

Distribution and ecology. Known only from the type locality in which it is a common species with ca. 1% relative abundance. The samples that included this species were scraped off the surface of stones collected in the Shun River. Hence this is a benthic, epilithic species. The associated taxa include *Gyrosigma kuetzingii* (Grunow) Cleve, *Encyonema appalachianum* Potapova, *Pinnularia subgibba* Krammer, *P. borealis* Ehrenberg, *Gomphonema berggrenii* Cleve, *Epithemia* spp., *Nitzschia* spp., *Iconella* spp., among others. The following environmental parameters were measured in the field with three replications: Conductivity = 70.1 ± 0.1 μS cm^{-1}; pH = 8.5 ± 0.1; Water temperature = 24.5 ± 0.1 °C.

Discussion

Ulnaria shun-biseriata sp. nov. can be distinguished from all other species of *Ulnaria* by a unique combination of characters that includes its lanceolate valve outline, slightly undulate valve margins, mostly biseriate striae, and variable central area.

The most similar species to *U. shun-biseriata* is *U. oxybiseriata* D.M. Williams & Bing Liu because both species have overlapping ranges of valve dimensions and are characterized by apiculate apices and biseriate striae (Table 1). *Ulnaria shun-biseriata* however, has generally wider valves and has undulate valve margins which distinguish it from *U. oxybiseriata* whose valve margins are straight (not undulate). Moreover, *U. oxybiseriata* has linear-lanceolate valves, an outline not observed for *U. shun-biseriata*.

Among the other *Ulnaria* species from China whose ranges in valve length partly overlap with those of *U. shun-biseriata*, we should mention *U. gaowangjiensis* Bing Liu & D.M. Williams, *U. sangzhi-biseriata* Bing Liu and *U. chengduoensis* Bing Liu. Besides having generally narrower valves these three species have different valve outlines and different central areas. In addition, *U. chengduoensis* has uniseriate striae (Table 1).

We also checked the “*Synedra*” that the Russian taxonomist Boris Skvortzov described from Chinese material collected in the first part of the 20th century. The list compiled by Kociolek et al. (2020) and again reported in Liu (2023) indicates that Skvortzov described 11 new “*Synedra*” taxa in three different papers published in 1928, 1935 and 1938. From the hand-drawings available in these publications and from the valve dimensions reported by Skvortzov, only *Synedra ulna* var. *tenuirostris* (Skvortzov 1938) appears comparable to *Ulnaria shun-biseriata*. However, *Synedra ulna* var. *tenuirostris* possesses linear-lanceolate valves with abruptly rostrate apices and a rectangular central area. Therefore, this taxon looks much closer to *Ulnaria gaowangjiensis* and/or *Ulnaria sangzhi-biseriata* than to *U. shun-biseriata*.

Like *Ulnaria shun-biseriata*, *U. acus* (Kützing) Aboal, *U. dongtingensis* Bing Liu, *U. menyuanensis* Bing Liu and *U. undulata* (Rabenhorst) Williams, also bear lanceolate valve with undulate margins. However, *U. shun-biseriata* can be differentiated from the latter four species by having generally much shorter and wider valves and by the stria type: the former bears mostly biseriate striae whereas the latter four species possess uniseriate striae (Table 1).

Interestingly, the type population of *U. shun-biseriata* includes many abnormal valves (Fig. 1J–Q) with a proportion of 45% (91 specimens observed in total,

Table 1. Comparisons between *Ulnaria shun-biseriata* sp. nov. and taxa sharing similarities in valve dimensions and/or valve outline.

Species	Valve outline	Valve margin	Valve length (L) and width (W) (μm)	Striae type and density (in 10 μm)	Central area	Valvocopula	Type locality	References
U. shun-biseriata sp. nov.	Lanceolate with apiculate apices	Slightly undulate	L: 48–70; W: 8.3–10.7	Mostly biseriate, 8.5–11	Two arrangements: an asymmetric hyaline region extending to both margins or a hyaline area which extends to one margin with the other side bordered with a few shortened striae	Closed	Shun River, Hunan (China)	This study
U. acus	Lanceolate	Sometimes slightly undulate	L: 90–100; W: 4–6	Uniseriate, 12–15	Sometimes lacking, when present with shorter marginal striae forming a rectangular portion	Closed	Falaise (France)	Williams and Blanco (2019)
U. chengduoensis	Linear with rostrate apices	Not undulate	L: 42–66; W: 6–8	Uniseriate, 12–15	Variable, completely absent or formed by short marginal striae	Closed	Baima River, Qinghai (China)	Liu (2023)
U. dongtingensis	Narrow-lanceolate with rostrate to capitate apices	Sometimes slightly undulate	L: 106–260; W: 5–7	Uniseriate, 10–12	Forming a fascia, almost square	Closed	Dongting Lake, Hunan (China)	Liu et al. (2019c)
U. gaowangjiensis	Linear-lanceolate with protracted-rostrate apices	Gently undulate	L: 61–108; W: 6.5–8.5	Biseriate, 9–11	More or less square	Closed	Maxi stream, Wuling Mts (China)	Liu et al. (2017b)
U. menyuanensis	Lanceolate with cuneate to rostrate apices	Sometimes slightly undulate	L: 60–104; W: 5–7	Uniseriate, 12–14	Not clearly defined due to presence of many ghost striae	Closed	Menyuan county, Qinghai (China)	Liu (2023)
U. oxybiseriata	Linear-lanceolate to lanceolate with apiculate apices	Not undulate	L: 56–78; W: 6–9	Mostly biseriate, 10–12	Mostly forming an incomplete fascia bordered by shortened striae on one side, trapezoid; rarely as a rectangular fascia in larger valve	Closed	Donghe River, Hunan (China)	Liu et al. (2019c)
U. sangzhi-biseriata	Linear-lanceolate with slight middle constriction, capitate apices	Not undulate	L: 49–91; W: 6.5–8.2	Mixed, biseriate to triseriate, 10–12	Rectangular or square with ghost striae	Closed	Li River, Hunan (China)	Liu (2023)
U. undulata	Lanceolate	Gently undulate	L: 60–80; W: 3–5	Uniseriate	Absent	Closed	Dresden (Germany)	Williams (2020)
Synedra ulna var. *tenuirostris*	Linear-lanceolate with abruptly rostrate apices	Not undulate	L: 42–72; W: 6.8–7	Type unknown, 12–13	Rectangular	Unknown	Chengdu, Sichuan (China)	Skvortzov (1938)

including 50 normal and 41 abnormal). Falasco et al. (2009, 2021) reviewed diatom teratological forms and summarized the most frequent types of abnormality: 1) abnormal valve outline (lack of symmetry, bent, incised, swollen, or notched profile); 2) unusual raphe system (fragmented, displaced, and bifurcated); 3) abnormal striation pattern (irregular, altered, fragmented, and branched); and 4) unusual raphe channel system (distorted, curved, and occasionally doubled back). Most abnormal valves of *U. shun-biseriata* exhibit abnormal valve outlines lacking symmetry relative to the apical axis due to the valve middle part only expanding on one side (Fig. 1J–Q), and the other types of abnormality were rarely observed.

These abnormal valves should not be confused with pre-normal frustules/valves as defined in Liu and Williams (2020b) and Liu (2023). During the life history of the araphid genera *Hannaea* and *Ulnaria*, there is a pre-normal vegetative period which is “the time between immediately after the initial cell’s first division and the presence of the first new normal vegetative cells. The cell, frustule, and valve occurring during this period can be termed ‘pre-normal vegetative cell, frustule, and valve” (Liu and Williams 2020b). The pre-normal valves in *Hannaea* and *Ulnaria* are irregularly shaped but they are produced only in the early period of the life history so that the pre-normal valves are larger than the normal valves. In *U. shun-biseriata* small valves also present abnormalities (e.g. Fig. 1P, Q) and therefore cannot correspond to pre-normal valves.

These observations further illustrate the morphological plasticity reported for some araphid genera such as *Hannaea* (Liu and Williams 2020b), *Ulnaria* (Liu 2023) and *Fragilaria*. In the genus *Fragilaria* in particular, occurrence of morphologically abnormal populations has long been reported. For example, Feldt et al. (1973) illustrated a variant population from Lake Superior (USA/Canada) of what they then tentatively identified as *Synedra radians* (Kützing) Grunow. These valves were characterized by being longitudinally asymmetric with a strongly incised central portion. Recently, a similar population from Lake Superior was re-investigated by Alexson et al. (2022), who thought that these valves were teratological forms of (possibly) *Fragilaria limnetica* Alexson & Reavie. Similarly, Cunningham and Whitson (1978) described from a lake in Iowa (USA) apparently stable populations of abnormal valves of *F. cyclopum* (Brutschy) Lange-Bertalot as *Synedra cyclopum* var. *incisa* Cunningham while Hoff et al. (2011) illustrated “notched” and “non-notched” morphotypes of *F. flexura*, a species resembling *F. cyclopum* that they described from a mountain lake in Kamchatka (Russian Far East). Type populations of several needle-shaped *Fragilaria* species were also illustrated with numerous, apparently deformed, valves such as *F. billingsii* Wengrat, C.E. Wetzel & E. Morales (Wengrat et al. 2016), *F. neotropica* P.D. Almeida, E. Morales & C.E. Wetzel (Almeida et al. 2016), *F. huebeneri* A. Schwartz, K.J. Krahn & C.E. Wetzel (Krahn et al. 2021), *F. campyla* (Hilse) Van de Vijver, Kusher & D.M. Williams, *F. pseudofamiliaris* Van de Vijver, T.M. Schuster, Kusber & D.M. Williams and *F. metcalfeana* Van de Vijver, D.M. Williams, Kusber & T.M. Schuster (the latter three species being illustrated in Van de Vijver et al. 2022). Krammer & Lange-Bertalot (1991) also suspected that *F. montana* (Krasske) Lange-Bertalot was not an independent species but teratological valves of *F. crotonensis* Kitton. Besides these long, needle-shaped species, a few small-sized *Fragilaria* species were also diagnosed as including asymmetrical valves such as *F. deformis* (W. Sm.) Van de

Vijver & Ector (Van de Vijver et al. 2020) and *F. irregularis* Chudaev, Jüttner & Van de Vijver (Chudaev et al. 2021).

In summary, natural diatom populations may include initial valves, pre-normal valves, normal valves, and abnormal valves, and this morphological variability should be considered when establishing a new species in araphid diatoms.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Formal analysis: PMR. Investigation: JYL, MZ. Writing - original draft: YZ. Writing - review and editing: BL.

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Data availability

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

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