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Research Article

Several new combinations from previous *Didymocarpus* to *Palmatiboea* (Gesneriaceae)

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Abstract

The recently published species, *Didymocarpus pingyuanensis*, is transferred here to the recently re-circumscribed genus, *Palmatiboea*. Two varieties, recently assigned to *Palmatiboea*, have been raised to the rank of species. Their Chinese vernacular names are also revised and provided here.

Key words: China, *Didymocarpus*, *Didymocarpus pingyuanensis*, Gesneriacese, nomenclature, *Palmatiboea*

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Introduction

The genus, *Didymocarpus* Wall., which was established over 200 years ago (Wallich 1819), has become one of the most frequently revised genera within Gesneriaceae. Because of different taxonomic perspectives, morphological evidence has revealed significant macroscopic and even microscopic variation both within and between species of the genus, with highly diverse geographical distributions further complicating its classification. As a result, the genus has gained a reputation as a “repository” or “dumping ground” for morphologically disparate species. At the same time, it has also incorporated a considerable number of species that are highly similar in external morphology (Burtt and Wiehler 1995; Burtt 1997; Vitek et al. 2000; Weber et al. 2000; Liu et al. 2024).

A revision 27 years ago defined the narrow sense of *Didymocarpus* s. str., which includes two sections: *Didymocarpus* sect. *Didymocarpus* and *Didymocarpus* sect. *Elati* Ridl., distributed across Southwest China, the greater Himalayan region, and the Indochinese Peninsula (Weber and Burtt 1997). However, the Chinese species of this genus were divided into two sections: stemmed herbaceous plants (*Didymocarpus* sect. *Didymocarpus*) and stemless herbaceous plants (*Didymocarpus* sect. *Heteroboea* W.T.Wang) (Wang et al. 1990, 1998;

Li and Wang 2005). *Sect. Heteroboea* was originally defined based on morphological characteristics, but recent systematic studies and morphological comparisons have reassigned five species to the genus *Petrocodon* Hance. These species are: *P. bonii* (Pellegr.) A.Weber & Mich.Möller, distributed along the northern edge of the Indochina Peninsula; *P. mollifolius* (W.T.Wang) A.Weber & Mich.Möller, *P. subpalmatinervis* (W.T.Wang) F.Wen & Z.L.Li, and *P. niveolanosus* (D.Fang & W.T.Wang) A.Weber & Mich.Möller, found in Southwest China; and *P. hancei* (Hemsl.) Mich.Möller & A.Weber, distributed in South China (Guangxi and Guangdong) and Central China (Hunan) (Weber et al. 2011; Li et al. 2023).

After the publication of *Flora Reipublicae Popularis Sinicae* (Vol. 69) (Wang et al. 1990), four new taxa were discovered and described within sect. *Heteroboea*: *Didymocarpus dissectus* F.Wen, Y.L.Qiu, Jie Huang & Y.G.Wei (Wen et al. 2013), found in Fujian Province; *D. heucherifolius* Hand.-Mazz var. *yinzhengii* J.M.Li & S.J.Li (Li and Li 2014), found in Hunan Province; *D. heucherifolius* Hand.-Mazz var. *gamosepalus* Xin Hong & F.Wen (Xu et al. 2019), found in Guangdong Province; and *D. lobulatus* F.Wen, Xin Hong & W.Y.Xie (Xie et al. 2020), found in Zhejiang Province.

After multiple revisions, the number of species included in the genus *Didymocarpus* has decreased from over 180 species at its peak to approximately 110 species. However, some unresolved taxonomic issues remain. Recently, the study by Liu et al. (2024) addressed the longstanding taxonomic status of sect. *Heteroboea*, which is endemic to China and has been a subject of debate within *Didymocarpus* s. str.

Liu et al. (2024) conducted phylogenetic analyses with comprehensive sampling across *Didymocarpus* and related genera, utilizing four nuclear ribosomal DNA markers and five chloroplast DNA regions. The results revealed that *Didymocarpus* is not monophyletic. Based on a combination of molecular phylogenetic and morphological data, the circumscription of *Didymocarpus* s. str. was redefined. A new genus, *Palmatiboea* F.P.Liu & Yin Z.Wang, is established to accommodate those species previously assigned to *Didymocarpus* sect. *Heteroboea*. *Palmatiboea* is clearly differentiated from *Didymocarpus* s. str., not only in molecular and morphological characteristics but also in its distinct geographic distribution, as it is restricted to Southeast and South China. Table 1 shows the species originally classified under *Didymocarpus* that have been revised and reassigned to the genus *Palmatiboea* by Liu et al. (2024).

However, Liu et al. (2024) did not elevate the two infraspecific taxa (varieties) listed in Table 1 to species rank. In a nearly concurrent study on *Didymocarpus* sect. *Heteroboea* distributed in southern to southeastern China, two varieties mentioned in Table 1 have already been elevated to the species level: *Didymocarpus heucherifolius* var. *gamosepalus* Xin Hong & F.Wen was revised to *D. gamosepalus* (Xin Hong & F.Wen) Ling H.Yang, Q.Fan & F.Wen, and *D. heucherifolius* var. *yinzhengii* J.M.Li & S.J.Li was revised to *D. yinzhengii* (J.M.Li & S.J.Li) Ling H.Yang, Q.Fan & F.Wen (Yang et al. 2024). The two research teams focused on different taxonomic levels—one at the genus level and the other at the species level—leading to slight discrepancies in their conclusions on the same taxonomic issues.

In the study by Yang et al. (2024), a new species, *Didymocarpus pingyuanensis* Ling H.Yang, Q.Fan & F.Wen, from northeastern Guangdong, China, was described and compared with *D. heucherifolius* var. *gamosepalus* and *D. salviiflorus*, two species that have since been transferred to the genus *Palmatiboea* as *P. heucherifolius* var. *gamosepalus* and *P. salviiflora*. Based on the

Table 1. The species originally from *Didymocarpus* that have been reassigned to *Palmatiboea* in Liu et al. 2024.

No.	The original scientific names of species in *Didymocarpus*	The original Chinese name	The revised species scientific names in *Palmatiboea*	The revised Chinese name
1	*Didymocarpus cortusifolius* (Hance) Lévl.	温州长蒴苣苔	*Palmatiboea cortusifolia* (Hance) F.P.Liu & Y.Z.Wang*	温州掌脉苣苔
2	*Didymocarpus dissectus* F.Wen, Y.L.Qiu, Jie Huang & Y.G.Wei	深裂长蒴苣苔	*Palmatiboea dissecta* (F.Wen, Y.L.Qiu, Jie Huang & Y.G.Wei) F.P.Liu & Y.Z.Wang*	深裂掌脉苣苔
3	*Didymocarpus heucherifolius* Hand.-Mazz.	闽赣长蒴苣苔	*Palmatiboea heucherifolia* (Hand.-Mazz.) F.P.Liu & Y.Z.Wang*	闽赣掌脉苣苔
4	*Didymocarpus heucherifolius* var. *gamosepalus* Xin Hong & F.Wen	合萼长蒴苣苔	*Palmatiboea heucherifolia* var. *gamosepala* (Xin Hong & F.Wen) F.P.Liu & Y.Z.Wang*	合萼掌脉苣苔
5	*Didymocarpus heucherifolius* var. *yinzhengii* J.M.Li & S.J.Li	印政长蒴苣苔	*Palmatiboea heucherifolia* var. *yinzhengii* (J.M.Li & S.J.Li) F.P.Liu & Y.Z.Wang*	印政掌脉苣苔
6	*Didymocarpus lobulatus* F.Wen, Xin Hong & W.Y.Xie	浙东长蒴苣苔	*Palmatiboea lobulata* (F.Wen, Xin Hong & W.Y.Xie) F.P.Liu & Y.Z.Wang*	浙东掌脉苣苔
7	*Didymocarpus sinoprimulinus* W.T.Wang	报春长蒴苣苔	*Palmatiboea sinoprimulia* (W.T.Wang) F.P.Liu & Y.Z.Wang*	报春掌脉苣苔
8	*Didymocarpus reniformis* W.T.Wang	肾叶长蒴苣苔	*Palmatiboea reniformis* (W.T.Wang) F.P.Liu & Y.Z.Wang*	肾叶掌脉苣苔
9	*Didymocarpus salviiflorus* Chun	迭裂长蒴苣苔	*Palmatiboea salviiflora* (Chun) F.P.Liu & Y.Z.Wang*	迭裂苣苔（应更正为迭裂掌脉苣苔） Should be changed as 迭裂掌脉苣苔
10	*Didymocarpus yuenlingensis* W.T.Wang	沅陵长蒴苣苔	*Palmatiboea yuenlingensis* (W.T.Wang) F.P.Liu & Y.Z.Wang*	沅陵掌脉苣苔

*: Inaccurate species namer's abbreviation.

morphological characteristics of this new species, *Didymocarpus pingyuanensis* aligns closely with the concept of *Palmatiboea*, suggesting that it should be transferred to the new genus.

Nomenclature

Palmatiboea pingyuanensis **(Ling H.Yang, Q.Fan & F.Wen) F.Wen & Q.Fan, comb. nov.**
urn:lsid:ipni.org:names:77353132-1

≡ *Didymocarpus pingyuanensis* Ling H.Yang, Q.Fan & F.Wen in Yang et al., Phytokeys 224: 218 (2024).

Type. CHINA • Guangdong Province: Meizhou City, Pingyuan Town, 24°32'N, 115°50'E, 491 m a.s.l., 1 April 2023 (fl.), Qiang Fan, Xing-yue Zhang, Li-Juan Liao, Jie-Hao Jin, Ling-Han Yang DNPC 3352 (holotype: SYS!; isotypes: IBK! IBSC! SYS!)

The Chinese vernacular name. 平远掌脉苣苔 (Píng Yuǎn Zhǎng Mài Jù Tái).

Palmatiboea yinzhengii **(J.M.Li & S.J.Li.) F.Wen & Q.Fan, comb. nov.**
urn:lsid:ipni.org:names:77353133-1

≡ *Didymocarpus heucherifolius* var. *yinzhengii* J.M.Li & S.J.Li, in Phytotaxa 156 (3): 187. 2014.
≡ *Palmatiboea heucherifolia* var. *yinzhengii* (J.M.Li & S.J.Li) F.P.Liu & Y.Z.Wang, in Journal of Systematic and Evolution doi: 10.1111/jse.13124:13.2024.

Type. CHINA • Hunan: near Yongxing County. alt. 300 m, 26°17'10"N, 113°11'25"E, 6 May 2011, Jia-Mei Li 1105062 (holotype: HEAC!); ibid. Jia-Mei Li 11501 (paratype: IBK!).

Palmatiboea gamosepalus **(Xin Hong & F.Wen) F.Wen & Q.Fan, comb. nov.**
urn:lsid:ipni.org:names:77353134-1

≡ *Didymocarpus heucherifolius* var. *gamosepalus* Xin Hong & F.Wen, in PhytoKeys 128: 34. 2019.
≡ *Palmatiboea heucherifolia* var. *gamosepala* (Xin Hong & F.Wen) F.P.Liu & Y.Z.Wang, in Journal of Systematic and Evolution doi: 10.1111/jse.13124: 13. 2024.

Type. China • Guangxi Province, cultivated in the nursery of Gesneriad Conservation Center of China (GCCC), introduced from north of Guangdong Province: Pingyuan County, Meizhou City, growing in rocky crevices at the foot of a calcareous sedimentary rocky hill. 22 February 2019, flowering, WF20190222-05 (holotype: IBK!; isotype: AHU!)

Notes. We have noticed that several newly revised species and genera names use the name abbreviation of the corresponding author Yin-Zheng Wang as “Y.Z.Wang,” such as the names of the two new genera, *Palmatiboea* F.P.Liu & Y.Z.Wang and *Hequnia* Y.Z.Wang & F.P.Liu in Liu et al. (2024). However, the name abbreviation “Y.Z.Wang” originates from Prof. Wang Yun-Zhang, a renowned Chinese mycologist and plant pathologist, whose name abbreviation first appeared in the 1980s when he described 15 new species of Rust Fungi (Wang et al. 1980). Prof. Wang Yin-Zheng, on the other hand, first published a new taxon in the mid-1990s, *Whytockia purpurascens* Yin Z.Wang and *W. hekouensis* Yin Z.Wang (Wang 1995). When *W. purpurascens* and *W. hekouensis* were published, the author’s name abbreviation was mistakenly written as “Y.Z.Wang.” However, the abbreviation “Y.Z.Wang” for Prof. Wang Yun-Zhang appeared 15 years earlier than that of Prof. Wang Yin-Zheng when describing new taxa (IPNI 2024); therefore, for the aforementioned nomenclature, including the new genera *Palmatiboea* and *Hequnia* and their respective species. Additionally, there are quite a few revised species of Gesneriaceae that incorrectly use “Y.Z.Wang” to refer to Prof. Wang Yin-Zheng. For example, *Petrocosmea shilinensis* Y.M.Shui & H.T.Zhao var. *changhuensis* T.F.Lü & Y.Z.Wang should be changed as *P. shilinensis* var. *changhuensis* T.F.Lü & Yin Z.Wang (Li et al. 2020), and so on. In summary, the correct name abbreviation should be “Yin Z.Wang,” not “Y.Z.Wang” among the many revised species epithets of Gesneriaceae mentioned above.

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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

Dryopteris × subdiffracta (Dryopteridaceae), a new natural hybrid fern from Guangxi, China

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Abstract

A new natural hybrid fern, *Dryopteris × subdiffracta* (Dryopteridaceae), is reported from Guangxi, China. Molecular phylogenetic analysis based on DNA sequences from the low-copy nuclear marker *Ak1* and plastid genome revealed respectively that *D. polita* and *D. diffracta* are parents of the new hybrid, with *D. polita* as the maternal parent. Cytometric analysis of the nuclear DNA content indicated that *D. × subdiffracta* might be a diploid hybrid. Morphologically, *D. × subdiffracta* shares a high degree of similarity with *D. × subreflexipinna* from Taiwan, especially in zigzag-shaped rachis and deflexed pinna stalks. However, *D. × subdiffracta* is distinguishable in the degree of lamina division and shapes of lamina and pinnulets. A comprehensive taxonomic description accompanied by line drawings are provided.

Key words: *Dryopteris* sect. *Acrorumohra*, hybridization, molecular phylogeny, nuclear gene *AK1*, plastome

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Introduction

Dryopteris Adans. (1763: 20) is the third largest genus of ferns worldwide, comprising about 400 species (Wu et al. 2013). In China, the newly updated fern checklist includes approximately 188 *Dryopteris* taxa (180 species), making it the second largest fern genus after *Polystichum* Roth (Liu et al. 2023). Recent studies have shown that many *Dryopteris* taxa are of hybrid origin (e.g., Juslén et al. 2011; Hori et al. 2014, 2018, 2021; Sessa et al. 2015; Zuo et al. 2021; Wei et al. 2024). The majority of natural interspecific fern hybrids could be detected initially by their abnormal spores and intermediate morphological characteristics between two distinct ferns in the field (Wagner and Chen 1965; Barrington 1990).

In 2018, a suspicious fern was collected in the Dayaoshan Mountains, the largest mountain in the east-center of Guangxi, China. This fern bears a striking resemblance to *Dryopteris × subreflexipinna* M.Ogata (1935), an endemic fern to Taiwan which was assumed to be a hybrid resulting from a cross between *D. diffracta* (Baker) C.Chr. and *D. hasseltii* (Blume) C.Chr. by Moore (2000), and later verified by Chang et al. (2009). However, the former was always found growing together with *D. diffracta* and *D. polita* Rosenst. In addition, *D. hasseltii* has never been recorded in the Dayaoshan Mountains. The closest recorded site of collection of *D. hasseltii* is approximately 93 km away as the crow flies based on our data. These suggested that the newly discovered fern is probably not *D. × subreflexipinna*, but may rather result from a different parental combination. We named this presumptive new hybrid *D. × subdiffracta* herein, and try to determine its parentage through morphology, palynology, cytology and molecular biology.

Materials and methods

Taxon sampling and morphological comparison

Samples included *Dryopteris × subdiffracta* and its two associated species (i.e., supposed parents), *D. diffracta* and *D. polita*, collected at the same location. Additionally, *D. hasseltii*, the maternal progenitor of *D. × subreflexipinna* (Chang et al. 2009; Zhang et al. 2012), and other species demonstrated to be closely related to *D. polita* in *D.* sect. *Acrorumohra* (Li and Lu 2006; Zhang et al. 2012) were also sampled. Morphological traits of *D. × subdiffracta* and *D. × subreflexipinna* were based on specimens in Shanghai Chenshan Herbarium (CSH), Herbarium of Guangxi Institute of Botany (IBK) and Herbarium of Kunming Institute of Botany (KUN), as well as digital images of specimens in network databases, such as CVH (https://www.cvh.ac.cn/), Digital Taiwan (https://digitalarchives.tw/), Plants of TAIWAN (https://tai2.ntu.edu.tw/index.php) and GBIF (https://www.gbif.org/).

DNA extraction, sequencing, and plastome assembly

Plastid DNA was used as the maternal inherited marker and *AK1* as a biparentally inherited low-copy nuclear marker. Total DNA was extracted using an improved extraction CTAB method (Doyle and Doyle 1987) from 20 mg of silica gel-dried leaf material. Library construction, Illumina sequencing and plasmid DNA assembly followed Zuo et al. (2021). Primer design and reaction protocols for low-copy nuclear *AK1* gene followed Hori et al. (2021). GenBank accession numbers for the six new samples are listed in Table 1.

Data matrices and phylogenetic analyses

Two matrices were constructed for the analyses. The first matrix (plastid matrix) was comprised of nine entire chloroplast genome using Geneious 9.1.4 (Kearse et al. 2012), along with additional thirteen plastid regions (including *rbcL*, *trnL-F*, and *rps4-trnS*) obtained from GenBank. The second matrix (*AK1* matrix) included 11 nuclear *AK1* sequences extracted from our nine samples and another ten *AK1* sequences downloaded from GenBank. Alignment and correction of the matrices were performed using MAFFT v.7.017 (Katoh et al. 2002) and Geneious 9.1.4 (Kearse et al. 2012). Maximum likelihood (ML) analysis utilizing IQ-TREE 1.6.12 (Nguyen et al. 2015) was conducted with the GTR+R6 model and 1000 ultrafast bootstrap replicates. Bayesian inference (BI) analysis using MrBayes 3.2.6 (Ronquist et al. 2012) involved ten million generations with sampling every 1000 generations, employing four Markov chain Monte Carlo (MCMC) runs. The first 20% of trees were discarded as burn-in.

Table 1. Taxon, voucher specimen information, GenBank accession numbers, nuclear DNA content, and the number of spores per sporangium of *Dryopteris* samples used in this study.

Taxon	Specimen	Locality	Plastome	*AK1* copies	pg/2C	Spores	Ploidy
D. diffracta	*JSL6261*	Jinxiu, Guangxi, China	PQ167731	PP277076			
D. diffracta	*Zuo1817*	Gongshan, Yunnan, China	OQ649848	PP277077	19.49 ± 0.54	64	2×
D. diffracta	*Zuo5590*	Jinxiu, Guangxi, China	PQ167732	PP277078	20.20 ± 0.71	64	2×
D. hasseltii	*DLJ2019235*	Gongshan, Yunnan, China	OQ649872	PP277079	20.08 ± 0.15	64	2×
D. polita	*JSL6338*	Jinxiu, Guangxi, China	PQ167733	PP277082			
D. polita	*Zuo5577*	Jinxiu, Guangxi, China	PQ167734	PP277083	14.65 ± 0.32	64	2×
D. **×** *subdiffracta*	*JSL6337*	Jinxiu, Guangxi, China	PQ167735	PP277084; PP277085			
D. **×** *subdiffracta*	*JSL6341*	Jinxiu, Guangxi, China	PQ167736	PP277086; PP277087			
D. **×** *subdiffracta*	*Zuo5589*	Jinxiu, Guangxi, China	PQ167737	PP277088; PP277089	16.82 ± 0.17		2×

Estimation of ploidy level and reproductive mode

Flow cytometry was employed to measure the nuclear DNA content (2C value) of individual cells extracted from fresh leaves (Hori et al. 2021). *Zea mays* L. was used as an internal standard. Ploidy level was inferred by comparison of observed nuclear content among samples and with previous reports. The number of spores in three complete sporangia per sample was counted under a small microscope (Yuantu 100×, China). For most of leptosporangiate ferns, sporangia with 64 and 32 spores, respectively, indicate sexual and apomictic reproduction (Manton 1950; Lovis 1977; Walker 1979; Grusz 2016).

Results and discussion

Morphological comparison

Morphological differences (marked with asterisk “*”) and similarities between *Dryopteris* × *subdiffracta* and *D.* × *subreflexipinna* are listed in Table 2. *Dryopteris* × *subdiffracta* shares high similarities with *D.* × *subreflexipinna* in the color and form of scales, pinna shape, degree of sinuosity of rachis, and angle between rachis and pinna stalks. Their zigzag rachis and deflexed pinna stalks are distinctly derived from *D. diffracta*, the only *Dryopteris* species with these characters in China, suggesting that both taxa might share at least an identical parent. However, there are many differences between *D.* × *subdiffracta* and *D.* × *subreflexipinna*. The most important difference lies in the shape of pinnulets, sometimes including pinnules. The pinnulet of *D.* × *subdiffracta* has a blunt or acute apex and a nearly symmetric base, its basalmost pair of lobes are nearly equal in size. In contrast, *D.* × *subreflexipinna* has a round or obtuse apex and an asymmetric base, with the spreading basalmost acroscopic pinnulet or lobe obviously larger than the ascending basiscopic one. This trait seemingly originated from one of its parents with the same characters, *D. hasseltii*. In terms of morphological intermediacy of hybrids, *D. diffracta* is a quadripinnate species which occasionally has one or two nearly free lobes on the base of some tertiary pinnules, whereas *D.* × *subdiffracta* is a tripinnate-pinnatifid plant with at most one or two free lobes at the bases of larger pinnulets, on the same level in lamina division as *D. hasseltii* rather than intermediate between the latter and *D. diffracta*. *Dryopteris polita* has bipinnate-pinnatipartite fronds, and in theory, is more likely the other parent of *D.* × *subdiffracta*, which also explains why *D.* × *subdiffracta* often has triangular laminae, like those of *D. polita* and *D. diffracta*. In contrast, *D.* × *subreflexipinna* generally has ovate-oblong laminae and shares the same lamina shape with its maternal parent *D. hasseltii*.

Phylogenetic analyses

Phylogenetic analysis of the plastid matrix showed that three samples of *Dryopteris* × *subdiffracta* were fully supported to nest in the clade of *D. polita* (Fig. 2A). Meanwhile, three samples of *D.* × *subreflexipinna* were fully supported to nest in the clade of *D. hasseltii*. All three samples of *D.* × *subdiffracta* were found with two copies of *AK1*. Copy 1 was the same as *D. polita*, while copy 2 was the same as *D. diffracta* (Fig. 2B). This supports the hypothesis that *D.* × *subdiffracta* originated from hybridization between *D. polita* and *D. diffracta*.

Table 2. Morphological comparison between *Dryopteris* × *subdiffracta* and *D.* × *subreflexipinna*.

Characters		***D.* × *subdiffracta***	***D.* × *subreflexipinna***
Scales	color	brown	brown
	shape	lanceolate	lanceolate
	margin	entire	entire
Frond length*		42–99 cm	65–123 cm
Lamina	division*	tripinnate to tripinnate-pinnatisect	4-pinnate
	shape*	triangular or ovate-triangular	ovate-oblong or ovate
	size*	22–44 × 15–34 cm	25–66 × 22–50 cm
	base	broadly cuneate* or rounded	rounded
Rachis form		slightly zigzag	slightly zigzag
Shape of lowest pinna		deltoid	deltoid
Included angle between rachis and deflexed pinna stalk		70–85°	70–85°
Size of basal basiscopic pinnule on lowest pinna*		36–90 × 17–37 mm	45–180 × 22–80 mm
Middle pinnules of pinnae	shape	deltoid-lanceolate	oblong-lanceolate* or deltoid-lanceolate.
	base*	nearly symmetrical; broadly cuneate acroscopically, broadly cuneate to cuneate basiscopically.	asymmetrical; truncate acroscopically, broadly cuneate to cuneate basiscopically.
	apex	shortly acuminate	shortly acuminate, acute or obtuse*
Pinnulets nonadjacent to costae	shape*	ovate to ovate-oblong	rhombic-ovate
	base*	cuneate to rounded-cuneate, nearly symmetrical	rounded-cuneate, asymmetrical
	apex	blunt* or obtuse	rounded* or obtuse
Relative size of proximal pair of pinnulets)*		acroscopic one nearly as large as or slightly larger than basiscopic one	acroscopic one significantly larger than basiscopic one
Relative size of proximal pair of ultimate pinnules (or lobes)*		acroscopic one nearly as large as or slightly larger than basiscopic one	acroscopic one significantly larger than basiscopic one

Estimation of ploidy level and reproductive mode

The mean DNA contents of *D.* × *subdiffracta* and related species are presented in Table 1. *Dryopteris polita* displayed the lowest value (14.65 ± 0.32 pg), whereas *D. diffracta* and *D. hasseltii* exhibited significantly higher values (approximately 20 pg), but still less than twice that of *D. polita*. *Dryopteris diffracta* occurring in Taiwan had been reported to be tetraploid (Tsai and Shieh 1975, 1985; Chang et al. 2009), however, our samples from Guangxi possessed approximately 80 chromosomes per cell (data not shown), indicating that *D. diffracta* is highly likely diploid. *Dryopteris hasseltii*, in our study, shared the similar DNA contents with *D. diffracta*, and so it was probably also diploid, which was in accord with some previous researches (e.g., Shimura et al. 1982; Kato and Nakato 1999). We also infer that *D. polita* is diploid.

All the samples of *D. diffracta*, *D. hasseltii* and *D. polita* were observed with 64 spores per sporangium and considered to be sexual. The DNA content of samples of *D.* × *subdiffracta* was 16.82 ± 0.17 pg, and these samples were also estimated as being diploid. Most of sporangia of *D.* × *subdiffracta* were abortive. Some sporangia had a few normal spores occasionally, but most of these spores were misshapen (Fig. 1), which suggested that *D.* × *subdiffracta* is most likely sterile.

Previous studies reported that *Dryopteris* × *subreflexipinna* is a pentaploid hybrid produced from hybridization between diploid sexual *D. hasseltii* and tetraploid apogamous *D. diffracta* (Chang et al. 2009). Despite sharing some morphological similarities with *D. subreflexipinna*, our results indicate that *D.* × *subdiffracta* is a sterile diploid hybrid originating from the hybridization between two diploid sexual species, *D. polita* and *D. diffracta*.

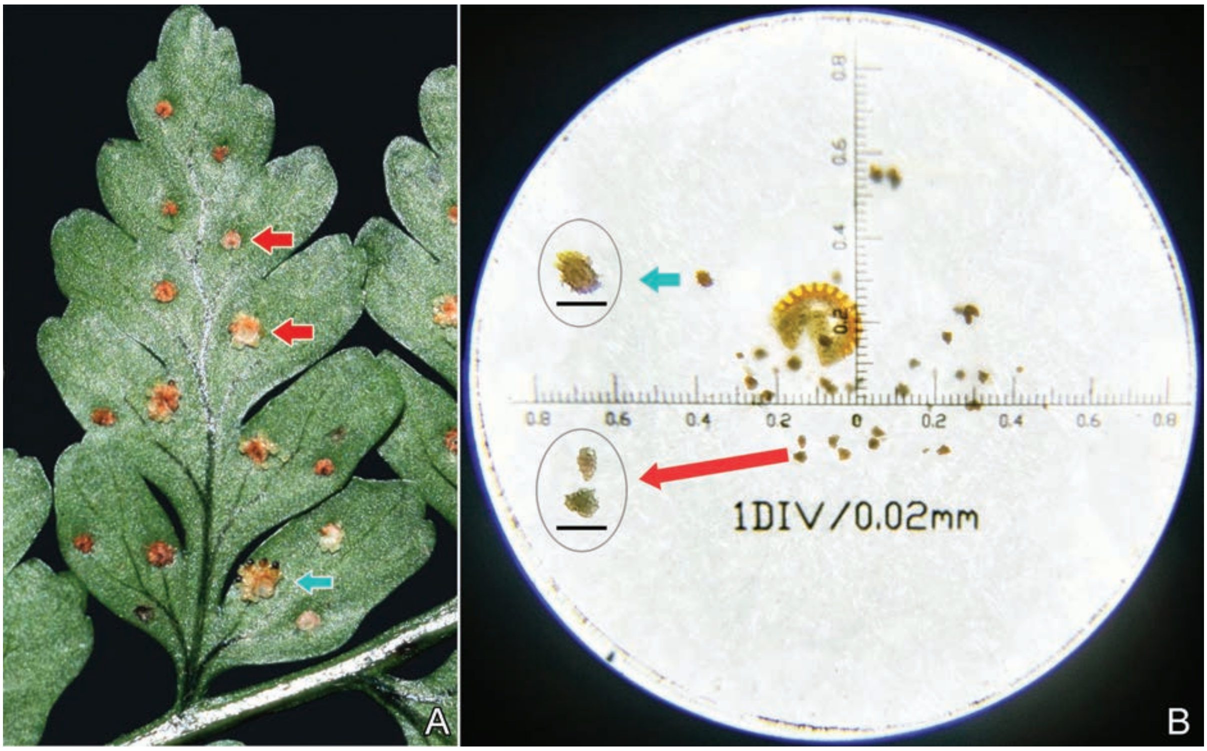

Figure 1. *Dryopteris* × *subdiffracta* **A** pinnules showing fertile sori (blue arrow) and infertile sori (red arrows) **B** sporangium showing mostly misshapen spores (red arrow) and a few normal spores (blue arrow), insets (circles) show detail. Photographed by Zheng-Yu Zuo. Scale bars: (in circles) 0.05 mm.

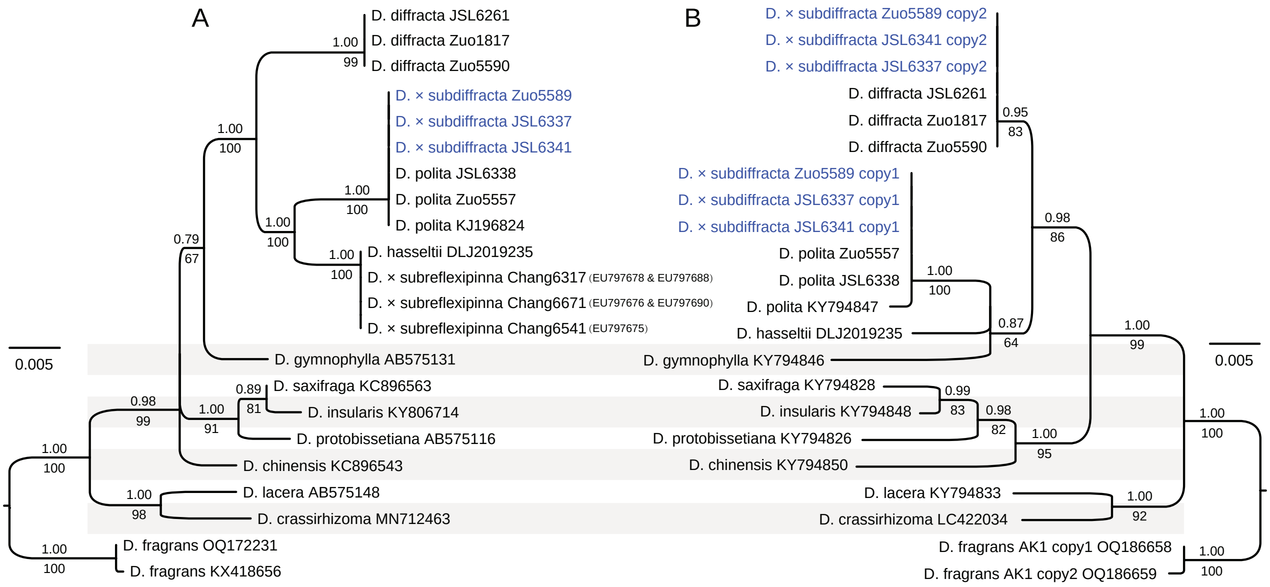

Figure 2. Maximum likelihood phylogram of *Dryopteris* sect. *Acrorumohra* based on (**A**) plastid matrix and (**B**) nuclear *AK1* gene sequences. Support values, including bootstrap support values (BS) and Bayesian confidence values (PP), are depicted along the branches, with PP over the branches and BS under the branches. The NCBI accession numbers of sequences obtained from GenBank are given after the taxon names.

Taxonomy treatment

***Dryopteris* × *subdiffracta* H.J.Wei & Z.Y.Zuo, nothosp. nov.**
urn:lsid:ipni.org:names:77353653-1
Figs 3, 4, 5C, D

≡ *D. diffracta* (Baker) C. Chr. × *D. polita* Rosenst.

Type. China • Guangxi: Jinxiu county, Mt. Shengtangshan, in broad-leaved forest, 23°58'11"N, 116°6'54"E, elev. 1156 m, 9 May 2018, *She-Lang Jin, Jing Liu, Qi-Ming-Tang & Xu Yan JSL6337* (holotype: CSH0200999!; isotypes: CSH!, IBK!, KUN!).

Diagnosis. *Dryopteris* × *subdiffracta* is similar to *D.* × *subreflexipinna* in having slightly flexuous rachis and deflexed pinna stalks, but the former has a tripinnate to tripinnate-pinnatisect frond, narrowly ovate or oblong pinnulets with obtuse apex and nearly symmetric base, while the latter has 4-pinnate frond, ovate pinnulets with round or obtuse-rounded apex and asymmetric base.

Description. ***Rhizome*** erect, densely covered with brown scales at apex. ***Frond*** (42–)50–84 cm; stipe stramineous, (23–)26–56 cm, (1–)1.5–3 mm in diam. at middle part, sparsely covered with scale at base, upwards glabrous, grooved adaxially; scales lanceolate, ca. 16 × 2.4 mm, brown, entire; ***lamina*** 3-pinnate to nearly 4-pinnate, deltoid to ovate-deltoid, (22–)27–43 × (15–)25–34 cm, base round or broadly cuneate, apex acuminate, rachis somewhat flexuous; ***pinnae*** 8–12 pairs, triangular-lanceolate, slightly falcate, alternate, lowest pair sometimes opposite to nearly opposite, stalked, stalks of lower pinnae slightly deflexed, bases forming an angle of ca. 70–85° with rachis, upswept distally, 2–6.5 cm apart from each other, stalks of middle pinnae spreading; ***lowest pinna*** largest, deltoid, (9–)12–21 × (6–)7–13 cm, base broadly cuneate or truncate, apex acuminate, stalk (1.5–)2–4 cm; ***pinnules*** 8–12 pairs, often anadromous, 1- or 2-pinnate, alternate, spreading, triangular-lanceolate, apex shortly acuminate,

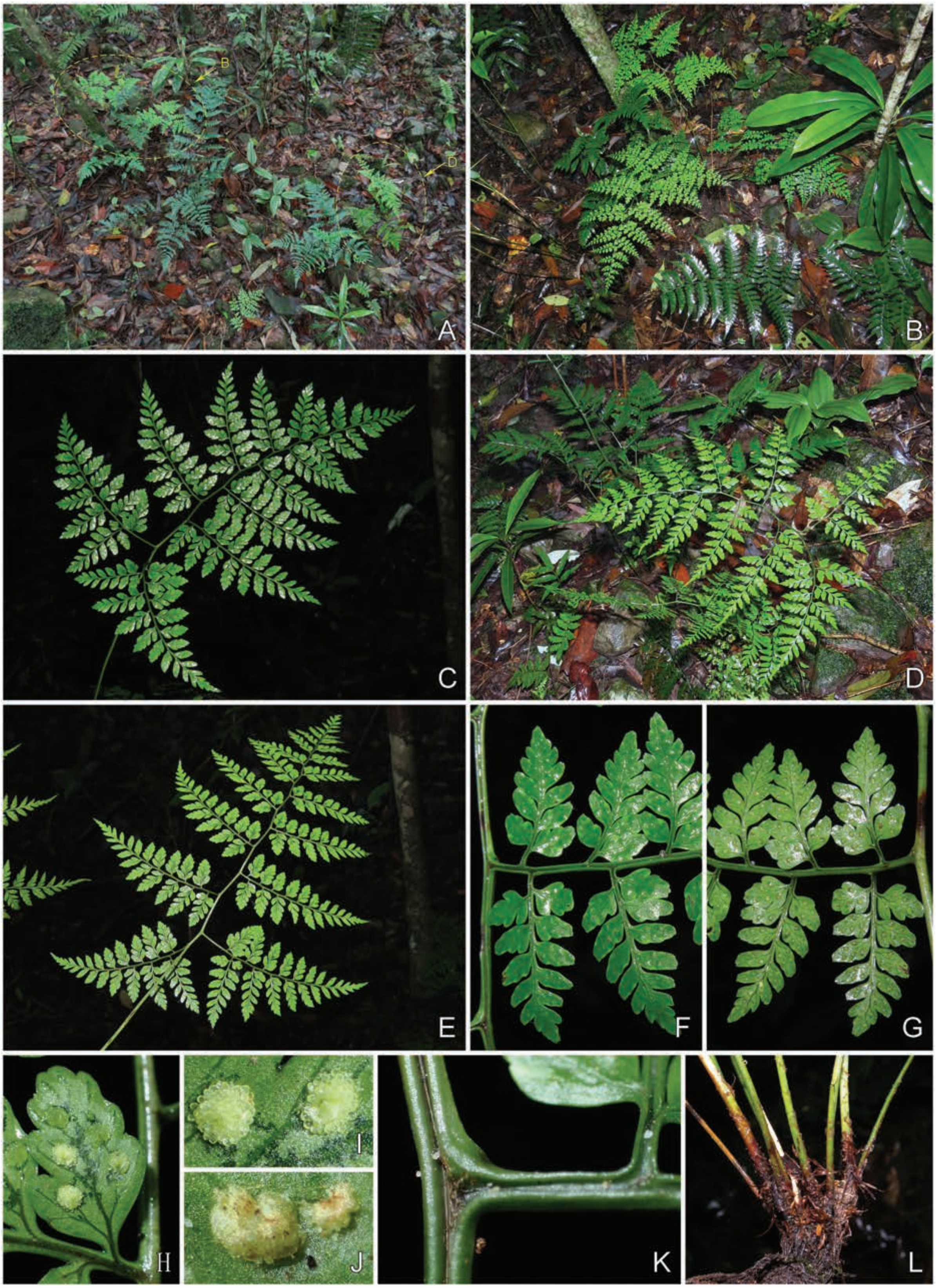

Figure 3. *Dryopteris* × *subdiffracta* **A** habitat showing the plant growing together with parents (arrows inset) **B** *Dryopteris diffracta* and *D. polita* **C** adaxial view of lamina **D** habit **E** abaxial view of lamina **F** adaxial view of lower portion of middle pinna with portion of rachis **G** adaxial view of lower portion of middle pinna with portion of rachis **H** ultimate pinnule **I** sori **J** indusium **K** adaxial view of portion of rachis with lower portion of costae **L** rhizome with lower portion of stipes. Photographed by Hong-Jin Wei.

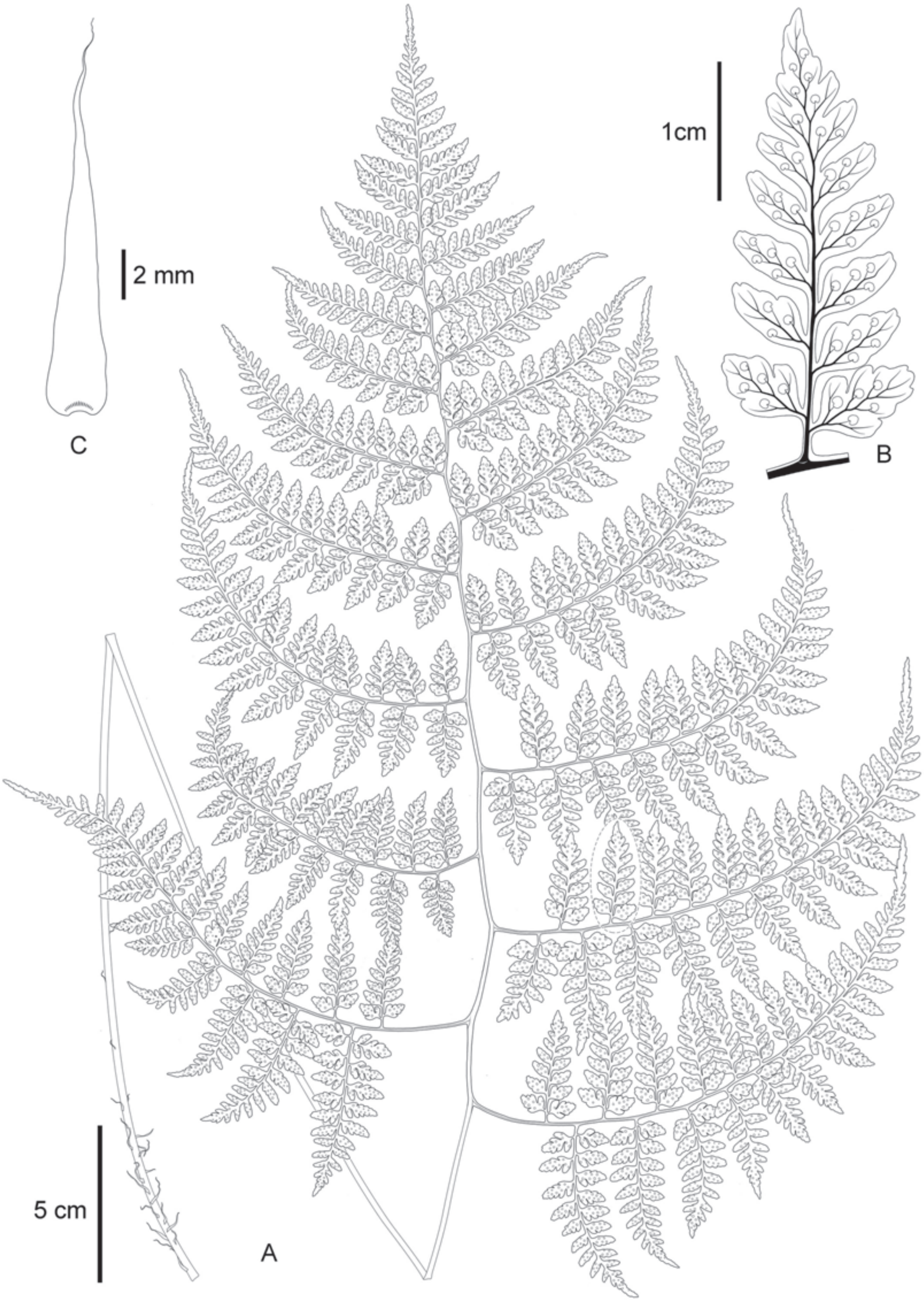

Figure 4. *Dryopteris* × *subdiffracta* **A** habit **B** portion of costa with pinnule showing veins and sori **C** scale from stipe base. Illustrated by Hong-Jin Wei.

proximal pairs shortly stalked, bases broadly cuneate or shallowly cordate, nearly symmetrical, distal pairs of pinnules nearly sessile, bases asymmetrical, acroscopically broadly cuneate, basiscopically cuneate, basal acroscopic pinnule of pinna as large as or slightly smaller than adjacent ones, basal basiscopic pinnule on lowest pinna largest, (3.6–)5.5–7.5(–9) × (1.7–)2–3.7 cm, shortly acuminate, stalklet (1.5–)2–4 mm; ***pinnulets*** 6–10 pairs, often anadromous, proximal 2–5 pairs free, alternate, spreading to ascending, ovate to ovate-oblong, basal acro-

Figure 5. *Dryopteris diffracta* (top), *D.* × *subdiffracta* (middle) and *D. polita* (bottom) **A**, **C**, **E** habit **B** portion of rachis with portion of upper pinna **D** portion of rachis with portion of middle pinna **F** portion of middle pinna. Photographed by Hong-Jin Wei.

scopic one as large as or slightly larger than basiscopic one, bases of proximal pair rounded-cuneate, nearly symmetrical, bases of others rounded-cuneate to cuneate acroscopically, cuneate to narrowly cuneate basiscopically, apex blunt, acute to subacute, with 1 or 2 short obtuse teeth, larger pinnules (9.5–)11–18 × (5.5–)6.5–11 mm, stalklet 0.5–2 mm, pinnatifid or pinnatisect at base, with 1 or 2 free lobes proximally; ***lobes*** 1–3 pairs, ovate, narrowly ovate or oblong, ascending, margin undulant to entire, base narrowly cuneate, apex obtuse, entire or with 1 or 2 short obtuse teeth, larger lobes 3–6 × 2–3 mm; upper pinnae

Figure 6. Geographical distributions of *Dryopteris* × *subdiffracta* (centers of rings) in Guangxi Zhuang Autonomous Region, China.

gradually reduced, spreading to oblique; ***lamina*** herbaceous, green on adaxial surface and light green on abaxial surface when dry, both surfaces glabrous, rachis and rachillae of every order stramineous, nearly glabrous expect for several hair-like scales on midribs and rachillae on abaxial surface, grooved adaxially; ***veins*** indistinct on adaxial surface, visible on abaxial surface, pinnate on pinnulets, veinlets forked or simple on lobes, not reaching margin; ***sori*** medial or slightly nearer to margin than to costa, terminal on veinlets, 1–3 pairs on each ultimate lobes; ***indusium*** brown, papery, entire, fugacious.

Geographical distribution and ecology. *Dryopteris* × *subdiffracta* was found in Jinxiu, Shangling and Wumin County, Guangxi Zhuang Autonomous Region, South China (Fig. 6), always growing together with *D. diffracta* and *D. polita* in broad-leaved forests at the elevation of 800–1200 m.

We noticed that two specimens of *D.* × *subreflexipinna* (TAI270081, TAI270101) collected from Taiwan are consistent with the characteristics of the new hybrid. There is a strong possibility that these two specimens were collected in the area where *D. diffracta* coexisted with *D. polita*. *Dryopteris* × *subdiffracta* might be distributed to Taiwan.

Etymology. The specific name is derived from the Latin prefix sub- (close to), and diffracta, epitheton of a species, referring the new species is closely related to *Dryopteris diffracta*.

Chinese name. 曲轴鳞毛蕨 (qū zhóu lín máo jué).

Paratypes. China • Guangxi: Same place as the holotype, 1100–1200 m, 9 May 2018, *She-Lang Jin, Jing Liu, Qi-MingTang & Xu Yan JSL6341* (CSH!), *Jing Liu, She-Lang Jin, Qi-MingTang & Xu Yan DYS426, DYS427, DYS428* (IBK!) • ibid., 15 Aug. 2023, *Zheng-Yu Zuo Zuo5589* (KUN!) • ibid., 2 Mar. 2024, *Ming-jin Wei & Yu-jin Wei JSL9482* (CSH!).

Additional specimens examined. China • Guangxi: Wumin County, Mt. Damingshan, Gannanhe (Ganlanhe), elev. 800–1000 m, 14 Sep. 1991, *Hou-Gao Zhou & Hua Li 2769* (IBK!) • Shangling County, Mt. Damingshan, Ganlanhe, elev. 900 m,16 Jul. 2011, *Lei Wu & She-Lang Jin D2760* (IBK!).

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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: HJW, ZYZ. Investigation: HJW, ZYZ. Funding acquisition: ZYZ. Methodology: ZYZ. Software: ZYZ. Supervision: ZYZ. Writing - original draft: HJW, ZYZ. Writing - review and editing: HJW, ZYZ.

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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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Monograph

Africa and Arabia encompass a much greater species diversity in the *Achyranthes aspera* aggregate (Amaranthaceae, achyranthoid clade): Evidence from morphological and chorological data

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Abstract

Achyranthes in its traditional sense (excluding *Achyropsis* that phylogenetically falls into *Achyranthes*) has been considered to contain a restricted (three to four) number of species in Africa and one or two species in the Arabian Peninsula. The morphology of the type species of the genus, *A. aspera*, has been treated as highly polymorphic, with several varieties recognised by various authors. Not surprisingly, a recent extended phylogeny revealed a non-monophyly of *A. aspera*. We present a deeper insight into morphological characters of the *A. aspera* aggregate together with taxonomic, nomenclatural, ecological, and chorological data based on field investigations and herbarium studies. Instead of one polymorphic species, we accept *A. aspera* s.str., *A. abyssinica*, *A. acuminata*, *A. annua*, *A. mauritiana*, *A. porphyrostachya*, *A. sicula*, and *A. seychellensis* **sp. nov.**, all being native to different parts of Africa. In most herbaria, the vast majority of African specimens labelled as *A. aspera* belong to other species, which are being reinstated here. In addition, two well-recognized species, *A. fasciculata* and *A. talbotii* from Tropical East and West Africa, respectively, are also discussed. Moreover, we found that the type of *A. aspera* var. *pubescens* as listed in the African and Arabian floras and checklists belongs in fact to an American species *A. fruticosa*, which is absent in the Old World. In place of the misapplied *A. aspera* var. *pubescens*, we accept *A. porphyrostachya*, a species described from Myanmar, as a correct name for the populations growing in Africa and Arabia. According to our results, at least 10 native species of *Achyranthes* occur in Africa (or 16 species if *Achyropsis* is merged with *Achyranthes*), which is a major diversity center of the genus. Four species are recorded from the Arabian Peninsula (*A. abyssinica*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*), and two of them (*A. abyssinica* and *A. annua*) reach their easternmost range limit in this region. As a result, the distribution as well as ecological conditions of each species is now clarified or circumscribed for the first time.

Key words: *Achyranthes*, Africa, Arabian Peninsula, Old World, taxonomy

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Introduction

Achyranthes L. is a genus widely distributed in the tropical and warm temperate regions of the world. Since the morphology-based generic circumscription of *Achyranthes* had been settled, the total number of species varied from three to five (Cavaco 1953; Stoffers 1980), six to eight (Cavaco 1962; Townsend 1985, 1993a, 1993b) or even 8 to 12–15 (Robertson 1981; Iamonico 2014). Recently, a phylogenetic analysis of the entire achyranthoid clade (Di Vincenzo et al. 2018) showed that the genus is paraphyletic to *Achyropsis* Benth. & Hook.f. (with six species in Africa: Townsend 1980a) and *Nototrichium* Hillebr. (with three species in the Hawaiian Islands: Lorence 1996).

Concomitantly, *Achyranthes aspera* L., the type species of *Achyranthes* s.str., also appeared non-monophyletic (Di Vincenzo et al. 2018), apparently because of its historically broad taxonomic concept. The heterogeneous circumscription of this species was laid down already in its original description by Linnaeus (1753), who established two varieties in *A. aspera*: α [var.] *sicula* L. and β [var.] *indica* L. The latter variety was determined as a synonym of *A. aspera* s.str. (Cavaco 1962; Townsend 1985), while the former was sometimes elevated to species rank as *A. argentea* Lam. (Schweinfurth 1867) or *A. sicula* (L.) All. (e.g., Tutin 1964; Podlech 1966; Lebrun 1973; Hassan et al. 2023).

To complicate matters, some species described from different continents were synonymized with *A. aspera*, with others being forgotten and unresolved, e.g. *A. acuminata* E.Mey. ex Sonder, *A. annua* Dinter, *A. frumentacea* Burm.f., *A. fruticosa* Lam., *A. pedicellata* Lopr., *A. totonaca* Sessé & Moc., *A. virgata* Poir., and *A. viridis* Lopr. Infraspecific taxa of *A. aspera* were usually distinguished on the basis of life form, leaf shape and color, and perianth length (Moquin-Tandon 1849; Boerlage 1891; Suessenguth 1952; Cavaco 1962; Townsend 1985; Townsend and Darbyshire 2004; Brundu and Camarda 2013; Hassan et al. 2023).

As expected in such a broad circumscription, *A. aspera* exhibits large morphological variability, occurs in a vast geographical range across the tropics and subtropics, and shows a wide ecological amplitude by growing in deserts, evergreen forests, riverine habitats, and agricultural and urban environments. Worryingly, under this taxonomic uncertainty, plants collectively called *A. aspera* have been widely used in traditional healing with numerous applications (Maiden 1889; Hauman 1951; Burkill 1985; Naidu et al. 2006; Ndhlala et al. 2015; Yadav et al. 2016; He et al. 2017), and are being studied for conventional medicine (Zanzabil et al. 2023; Lin et al. 2024).

Currently, based on the literature, the number of *Achyranthes* species in Africa is estimated at 4 to 5. Traditionally, two species were reported as widely distributed: *A. aspera* (Hooker 1849; Lebrun and Stork 2003; Klopper et al. 2006; APD 2024) including var. *pubescens* auct. (Townsend 1985, 2000; Germishuizen and Meyer 2003; Gibreel and Darbyshire 2015; Odorico et al. 2022), and *A. sicula* (Lebrun 1973; Townsend 2000). The latter was named *A. argentea* in early taxonomic works (Hooker 1849) or accepted occasionally at varietal level as *A. aspera* var. *sicula* L. (Maire 1962; Townsend 1985, 2000; Germishuizen and Meyer 2003; Gibreel and Darbyshire 2015; Odorico et al. 2022; Gosline et al. 2023) or *A. aspera* var. *argentea* Eggers (Baker and Clarke 1909; Hauman 1951), or even treated under both varietal names simultaneously (Sunding 1973). Two other accepted species have a limited distribution: *A. talbotii* Hutch. & Dalziel in Tropical West Africa (Hutchinson and Dalziel 1927; Keay 1954; Townsend and Darbyshire 2004), and *A. fasciculata* (Suess.) C.C.Towns. in Tropical East Africa (Townsend 1980a, 1985). Some authors also reported the presence of the Asian *A. bidentata* Blume in tropical Africa (Baker and Clarke 1909; Hutchinson and Dalziel 1927; Keay 1954; Lebrun and Stork 1991; Phiri 2005; Klopper et al. 2006).

Even within a single floristic area, as in the 'Flora Zambesiaca' (Malawi, Mozambique, Zambia, Zimbabwe, and Caprivi Strip [northeastern corner of Namibia]), taxonomic concepts in *Achyranthes* are fairly diverse (Podlech 1966; Townsend 1988; Mapaura et al. 2004; Phiri 2005; Setshogo 2005; Odorico et al. 2022); see also Table 1 for comparison. In the Arabian Peninsula, Miller (1996) accepted a single species, *A. aspera* with three varieties: var. *aspera*, var. *pubescens*, and var. *sicula*. Lately, Hassan et al. (2023) accepted *A. aspera* (incl. var. *aspera* and var. *pubescens*) and treated var. *sicula* at the species rank, as *A. sicula*.

From this brief overview, it is clear that the taxonomy of the *A. aspera* group is far from stable. Field observations of populations called *A. aspera* in Africa by the first author (APS) revealed striking differences, prompting us to undertake an in-depth study of this aggregate. Based on the phylogenetic paraphyly of *A. aspera*, and the previously noted variability, a morphological examination was chosen. Here, we look into the African and Arabian specimens housed in different herbaria and cited in the literature under the name *A. aspera*, including its varieties (*A. aspera* var. *sicula*, *A. aspera* var. *pubescens*), and neglected taxa described, e.g. by Moquin-Tandon (1849), Suessenguth (1938, 1952) and Suessenguth and Merxmüller (1951). In general, this aggregate includes plants with an upright stem; broad (ovate, obovate, rhombic, or elliptical) leaves; elongated spikes; glabrous, non-hooked bracteoles; and a glabrous, narrowly conical, indistinctly veined perianth that is strongly deflexed at fruiting.

Our aim is to study the African and Arabian *A. aspera* group in order to (1) provide clear morphological characters to distinct taxa, (2) resolve nomenclatural problems, and, if necessary, propose taxonomic changes, and (3) clarify the ecology and distribution of the accepted species. Although in Africa *A. fasciculata* and *A. talbotii* are morphologically distinct and do not belong to the *A. aspera* group, they will also be discussed here because of the former ambiguities.

Material and methods

The field investigations were carried out by the first author (APS) in Zambia (2020) and Tanzania including Zanzibar (Unguja Island) and the continental part of the country (Arusha, Kilimanjaro, and Manyara Regions; 2020–2022). Ripe fruits were harvested from selected taxa for further indoor cultivation to obtain more information about the morphological variability and life form.

Taxonomic and nomenclatural synonyms were comprehensively recorded and nomenclaturally evaluated. When an infraspecific name was assigned to a higher-level infraspecific taxon in the original publication, a name of that taxon is indicated in square brackets in the nomenclatural citation. Type designations follow the requirements and procedures established in Turland et al. (2018).

Herbarium specimens were checked and determined in BM, BOL, BR, FI (incl. FI-WEBB), FT, K, LE, M, MW, MHA, MSB, RAB, W, and WU. The virtual herbaria of AMD, B, DR, CHAMB, ECWP, F, FR, G, GZU, JSB, L, MA, MAU, MPU, NY, P, S-LINN, TOG, U, UCJ, US, WAG, and Z were also checked and included in the taxonomic part with citations of the relevant specimens when the images allowed identification. We also contacted the staff of BIF and G in search for the type material of *A. frumentacea* Burm.f. Commercially distributed herbarium specimens are cited with references (in square brackets) to the published exsiccata. Herbaria codes are as per Thiers (2024).

Reproductive diaspores were photographed with a Nikon DS-Vi1 camera at the Department of Higher Plants (Moscow State University). Fruits and leaf portions were observed using scanning electron microscopy (JSM-6380LA, JEOL Ltd., Japan) at 20 kV. Prior to SEM, to restore the soft tissues, the material was dehydrated in aqueous ethyl alcohol solutions of increasing concentrations, followed by alcohol-acetone solutions and pure acetone. After critical point drying, the samples were sputtercoated with gold-palladium. Cross-sections of leaves were prepared with a sliding microtome (Microm HM 355S, Thermo Fisher Scientific, Whaltham, Massachusetts, USA) after soaking of the material in a mixture of water–alcohol–glycerin (1:1:1). After sectioning, the tissues were stained using toluidine blue.

Distribution maps were prepared using SimpleMappr online tool (http://www.simplemappr.net). For a better understanding of the distribution patterns of each species across the studied area, we provided a background map based on the major vegetation zones. The zonal patterns were compiled from different sources (Ghazanfar and Fisher 1998; Steele 2013; Dinerstein et al. 2017; Nzabarinda et al. 2021; Loidi and Vynokurov 2024), not always agreeing with each other in details, although relatively similar to the scale used here. The resulting scheme includes the following subdivisions: (1) Mediterranean zone, (2) Deserts, (3) Sahel zone, (4) Grassland and savanna, (5) Rainforest zone, and (6) South Arabian woodlands, shrublands and dunes.

The remote Chagos Archipelago is not included in the treatment due to the very limited collections available, but some specimens from this territory were revised when accessible.

Results

In agreement with the molecular data (Di Vincenzo et al. 2018), our morphological revision confirmed a non-uniformity of *A. aspera*, revealing eight species growing in Africa and Arabia, instead of a single variable one. Surprisingly, as a result of this study, only a small number of the African and Arabian specimens in the herbaria belong to *Achyranthes aspera* s.str. as circumscribed here, although it is commonly or frequently found in some parts of the continent, e.g. in Tropical East Africa. The majority of specimens were assigned to other taxa with different morphology, ecological preferences and geographic ranges (Table 1). Within the *A. aspera* aggregate, morphometric parameters of the reproductive structures are fundamental for identification, especially because in many cases only the upper part of a plant was collected as a herbarium voucher. The best characters to differentiate these taxa are: (1) life form, (2) perianth length (Fig. 1), (3) anther length, and (4) style length (Fig. 2). These are the characters used in our identification key. The revised circumscription gives a clearer understanding of the ecology and distributions, allowing for sustainable long-term conservation and potential use of the species.

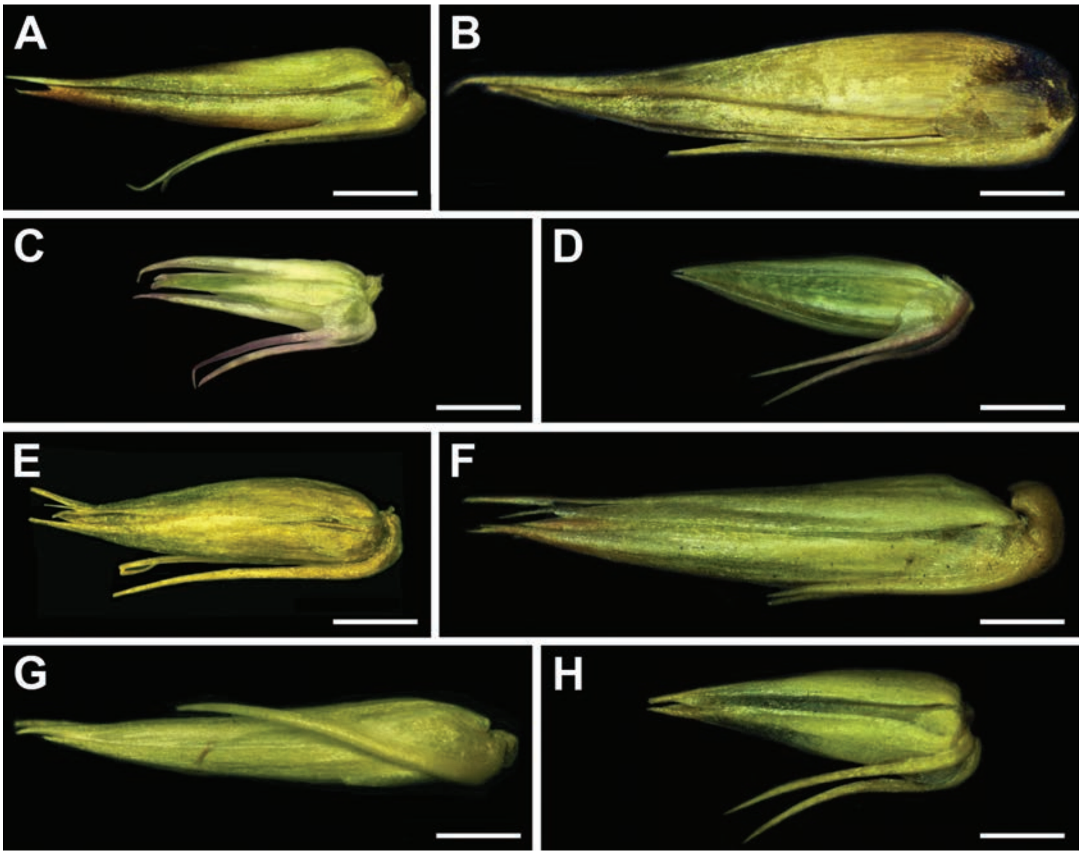

Figure 1. Reproductive diaspore units (perianth and two bracteoles): **A** *Achyranthes abyssinica* **B** *Achyranthes acuminata* **C** *Achyranthes annua* **D** *Achyranthes aspera* **E** *Achyranthes mauritiana* **F** *Achyranthes porphyrostachya* **G** *Achyranthes seychellensis* **H** *Achyranthes sicula*. Scale bar: 1 mm.

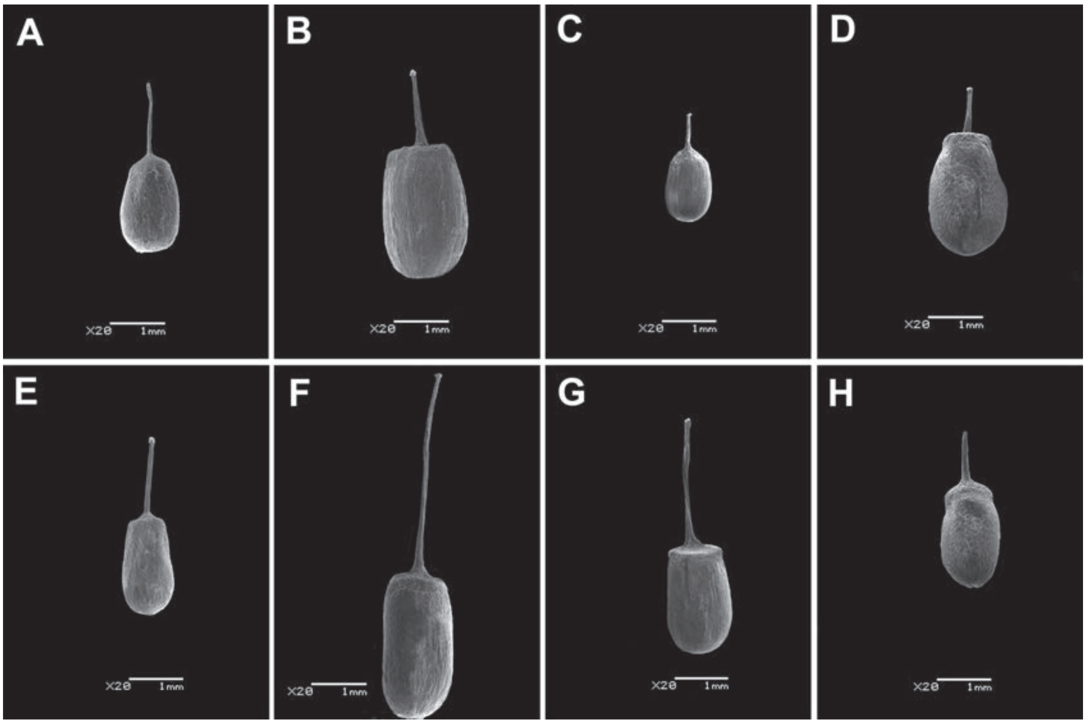

Figure 2. SEM images of a fruit with style and stigma: **A** *Achyranthes abyssinica* **B** *Achyranthes acuminata* **C** *Achyranthes annua* **D** *Achyranthes aspera* **E** *Achyranthes mauritiana* **F** *Achyranthes porphyrostachya* **G** *Achyranthes seychellensis* **H** *Achyranthes sicula*. Scale bar: 1 mm.

Table 1. Comparisons of the taxonomic composition of the *Achyranthes aspera* aggregate in various regions and countries.

Country or floristic region	Previously accepted taxonomy (with references)	New taxonomic circumscription (present paper)
Africa		
Angola	*Achyranthes aspera* s.str., *A. aspera* var. *porphyrostachya*, *A. aspera* var. *sicula*, *A. bidentata* (Figueiredo and Smith 2008)	*Achyranthes abyssinica*, *A. acuminata*, *A. annua*, *A. porphyrostachya*
Burkina Faso	*Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Lebrun et al. 1991); *A. aspera* s.str. (Thiombiano et al. 2012)	*Achyranthes annua*
Cape Verde	*Achyranthes aspera* (var. *argentea* and var. *sicula*) (Sunding 1973); *Achyranthes aspera* (Arechavaleta et al. 2005)	*Achyranthes annua*, *A. aspera* s.str., *A. porphyrostachya*, *A. sicula*
Central African Republic	*Achyranthes aspera*, *A. aspera* f. *argentea* (Boulvert 1977)	*Achyranthes acuminata*, *A. annua*
Chad	*Achyranthes aspera* s.l. (Lebrun et al. 1972); *Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Brundu and Camarda 2013; César and Chatelain 2019)	*Achyranthes annua*, *A. aspera* s.str., *A. porphyrostachya*
Comoros and Madagascar	*Achyranthes aspera* var. *indica*, *A. aspera* var. *argentea*, *A. mauritiana* (Cavaco 1953)	*Achyranthes acuminata* (Madagascar), *A. annua* (Madagascar), *A. aspera* s.str., *Achyranthes* sp. (“velutina”) (Comoros)
Djibouti, Eritrea, Ethiopia	*A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Audru et al. 1994; Townsend 2000)	*Achyranthes abyssinica*, *A. acuminata* (Ethiopia), *A. annua*, *A. aspera* s.str. (Ethiopia), *A. porphyrostachya*
Flora Zambesiaca area (Botswana, Malawi, Mozambique, Zambia, Zimbabwe, and northeastern corner of Namibia)	*Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Townsend 1988); *Achyranthes aspera* s.str., *A. aspera* var. *indica* f. *excelsa*, *A. aspera* var. *porphyrostachya* (Da Silva et al. 2004); *A. aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Mapaura et al. 2004); *Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Setshogo 2005); *Achyranthes aspera*, *A. bidentata* (Phiri 2005); *Achyranthes aspera* var. *porphyrostachya*, *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Odorico et al. 2022)	*Achyranthes abyssinica* (Malawi), *A. acuminata*, *A. annua*, *A. aspera* s.str. (Zimbabwe), *A. porphyrostachya*
Gabon	*Achyranthes aspera* (Sosef et al. 2006)	*Achyranthes acuminata*
Guinea	*Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Gosline et al. 2023)	*Achyranthes acuminata*, *A. annua*
Guinea-Bisau	*Achyranthes aspera* (Catarino et al. 2006)	*Achyranthes annua*
Mascarenes (Mauritius, Réunion, Rodrigues)	*Achyranthes aspera* (Townsend 1994)	*Achyranthes annua* (Réunion), *A. aspera* s.str., *A. mauritiana*
Mali	*Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Boudet and Lebrun 1986)	*Achyranthes annua*, *A. porphyrostachya*
Mauritania	*Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Barry and Celles 1991)	*Achyranthes annua*
Mayotte	*Achyranthes aspera* (Barthelat 2019)	*Achyranthes acuminata*, *A. aspera* s.str.
Namibia	*Achyranthes aspera* s.str., *A. sicula* (Podlech 1966); *Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Klaassen and Kwembeya 2013)	*Achyranthes acuminata*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*
Niger	*Achyranthes sicula* (Peyre de Fabregues and Lebrun 1976)	*Achyranthes annua*, possible records of *A. porphyrostachya*
North Africa (Algeria, Egypt, Libya, Morocco, Tunisia)	*Achyranthes aspera* var. *sicula* (Maire 1962); *A. aspera* s.str., *A. aspera* var. *pubescens* (Boulos 1995)	*Achyranthes annua* (rare: Egypt), *A. sicula* (Mediterranean part), *A. aspera* s.str. (an old record for Egypt), *A. porphyrostachya* (Egypt)
São Tomé and Príncipe	*Achyranthes aspera* s.str. (Figueiredo et al. 2011)	*Achyranthes acuminata*, *A. aspera* s.str.
Senegal	*Achyranthes argentea*, *A. aspera* (Berhaut 1971); *A. aspera*, *A. sicula*, and probably *A. porphyrostachya* (Lebrun 1973)	*Achyranthes annua*, *A. aspera* s.str., *A. porphyrostachya*
Seychelles	*Achyranthes aspera* s.str., *A. aspera* var. *fruticosa*, *A. aspera* var. *velutina* (Friedmann 1994)	*Achyranthes aspera*, *A. seychellensis*, *A.* sp. (*“velutina”*).
Somalia	*Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Townsend 1993b)	*Achyranthes abyssinica*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*
South Sudan and Sudan	*Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Gibreel and Darbyshire 2015)	*Achyranthes abyssinica*, *A. annua*, *A. aspera* s.str. (South Sudan), *A. porphyrostachya*
South Africa	*Achyranthes aspera* s.str.; *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Germishuizen and Meyer 2003)	*Achyranthes acuminata*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*

Country or floristic region	Previously accepted taxonomy (with references)	New taxonomic circumscription (present paper)
Tropical East africa (Kenya, Tanzania, Uganda)	*Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Townsend 1985)	*Achyranthes abyssinica*, *A. acuminata*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*, *A. reptans*
Tropical West-Central Africa (Burundi, DR Congo, Rwanda)	*Achyranthes aspera* s.str., *A. aspera* var. *argentea* (Hauman 1951); *Achyranthes aspera* s.str., *A. aspera* var. *sicula* (Lejoly et al. 2010)	*Achyranthes abyssinica*, *A. acuminata*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*
West Tropical Africa (Benin, Cameroon, Ghana, Ivory Coast, Liberia, Nigeria, Sierra Leone, Togo)	*Achyranthes aspera* s.str., *A. bidentata* (Keay 1954)	*Achyranthes abyssinica* (Cameroon, Nigeria), *A. acuminata*, *A. annua* (no data from Ivory Coast), *A. aspera* s.str. (Benin, Cameroon, Ghana), *A. porphyrostachya* (Benin, Far North Cameroon)
Arabian Peninsula (the genus is present in Oman, Saudi Arabia, UAE, and Yemen)	*Achyranthes aspera* (Ghazanfar 1992); *Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. aspera* var. *sicula* (Miller 1996; Wood 1997); *Achyranthes aspera* s.str., *A. aspera* var. *pubescens*, *A. sicula* (Hassan et al. 2023)	*Achyranthes abyssinica*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*

Key to accepted species of the *Achyranthes aspera* group occurring in Africa and Arabia

1 Perianth usually 6.0–7.5(8.0) mm long **2**
– Perianth up to 5.0(5.5) mm long **3**
2(1) Annual or perennial herbs not rooting or rooting at lower nodes; leaves often nigrescent when dry; anthers 0.35–0.6 mm long; style (1.3)1.6–2.1 mm .... ***A. acuminata***
– Subshrubs, not rooting; leaves not nigrescent when dry; anthers ~ 1 mm long; style (2.5)3.0–4.0 mm long .... ***A. porphyrostachya***
3(1) Perianth 3.0–3.5(3.6–4.1) mm long; anthers minute, 0.15–0.25 mm long .... ***A. annua***
– Perianth (3.5)4.0–5.5 mm long; anthers 0.35–1.0 mm long **4**
4(3) Leaf blades obovate, ovate, rhombic or elliptic, ± concolored **5**
– Leaf blades oblong to ovate, bicolored (green above and white or grey below) **7**
5(4) Anthers 0.75–1.0 mm long .... ***A. seychellensis***
– Anthers up to 0.6(0.75) mm long **6**
6(5) Leaf blades obovate or ovate, ± hirsute on both sides, green or greyish .... ***A. aspera* s.str.**
– Leaf blades rhombic or elliptic, almost glabrous, green or nigrescent .... ***A. mauritiana***
7(4) Perianth (3.5)4.0–4.5(5.0) mm long; style (1.3)1.8–2.5(3.0) mm long; Tropical Africa and South Arabia .... ***A. abyssinica***
– Perianth 3.5–4.0 mm long; style (1.2)1.5–1.8 mm long; North Africa .... ***A. sicula***

Taxonomic treatment

Achyranthes abyssinica Nees, Del. Sem. Hort. Vratisl. 1850: 3 (1851).

= *Achyranthes aspera* f. *rubella* Suess., Bull. Jard. Bot. État Bruxelles 15: 56 (1938). Lectotype (designated here): DR Congo, [South Kivu Prov.,] Kizozi, 1935, *Lejeune 190* (BR0000008819512!, isolectotype BR0000008819192!).

= *Achyranthes aspera* [var. *sicula*] f. *latifolia* Suess., Mitt. Bot. Staatssamml. München 1: 70 (1951). Holotype: Kenya, pr. Forest Station in silva montana, 2350 m, 5 January 1922, *R.E. Fries & Th.C.E. Fries 781* (K000243724!, isotypes BR0000008819922!, S07-12310 – image!).

= *Achyranthes argentea* var. *albissima* Suess., Mitt. Bot. Staatssamml. München 2: 70 (1955). Lectotype (designated here): Kenya, Northern Prov., Furroli [Mount], Mt. top: granite with *Olea* & *Juniperus*, 6600 ft, occasional, 20 September 1952, *J.B. Gillett 13957* (K000243722!, isolectotype K000243723!).

– *Achyranthes sicula* auct. div.

Neotype (designated here). Ethiopia, [Tigray Region,] Scholoda [Soloda Mt. near Adwa Town], 12 November 1838, *Schimper 1144* [Schimper, Iter Abyssinicum, ser. 2 (1842)] (BM!, isoneotypes G00688998, BR00000083356949!, FI!, K005771057! – central twig, LE!, M0241524!, WU!).

Description. (Fig. 3). Annual, stout or rarely delicate herb up to 1.0(1.5–2.0) m, not rooting at nodes, very rarely creeping at lower nodes; stem four-angled, sparsely pubescent, sometimes scrambling; lateral branches long and ± horizontally spreading; leaf petioles 10–25 mm long, blades 20–100(120) × 10–40(50) mm, broadly cuneate or truncate, ovate, entire, tip acuminate, bicolored: ± green, slightly to moderately pubescent above, whitish or grey below (sparsely pubescent and green when cultivated indoor); inflorescence 50–250 mm long, sometimes pendulous; bract ~2.0 mm long; bracteoles 2.5–3.0 mm long, reflexed; perianth (3.5)4.0–4.5(5.0) mm long,

Figure 3. *Achyranthes abyssinica* **A** an indoor cultivated plant in vegetative stage (grown from seeds from Arusha Region, Tanzania) **B** flowering twig in bushy vegetation in Meru area, Arusha Region, Tanzania. Photographer: A. Sukhorukov.

green or purplish inside; pseudostaminodes 0.6–1.0 mm long, short, white or pink, fimbriate or not; stamens 5, with pink filaments, anthers 0.4–0.7 mm long, pink or magenta; style (1.3)1.8–2.5(3.0) mm long, pink; fruit (without style) (1.3)1.8–2.5(3.0) mm long.

Taxonomic notes. Morphologically, *A. abyssinica* is similar to *A. sicula* but differs from the latter by a slightly longer perianth and style, although a few specimens from tropical Africa have the same style length as in *A. sicula*. Although these two species are very similar in morphology, as also shown in our identification key, they take different positions in the molecular phylogeny (unpublished). Both species have clearly different and non-overlapping distributions, with *A. abyssinica* growing in mountainous areas of East and Central Africa and South Arabia, whereas *A. sicula* is a subtropical species found in areas with a Mediterranean climate.

Nomenclatural notes. Unfortunately, the whereabouts of the type specimens of *Achyranthes abyssinica* in the Nees herbarium are mostly unknown because this collection had been split into numerous parts, which were sold to institutions or private individuals (Stafleu and Cowan 1981). The contents of these parts are not always certain; besides, the collection was heavily affected by extensive losses in German herbaria during the Second World War. Our request to Bonn, where these type specimens were possibly kept, was unsuccessful because that Herbarium was completely destroyed during the war (Thomas Joßberger, pers. comm.). There are also no authentic specimens in STR (Gisele Haan-Archipoff, pers. comm.) and LE (Sukhorukov, pers. obs.), where large parts of Nees collections are housed.

In the absence of any original material, we designate Schimper's collection from Ethiopia, which was prepared in numerous duplicates and commercially distributed to many Herbaria under the name *A. argentea*, as the neotype of *A. abyssinica*.

The label of the isolectotype of *A. aspera* f. *rubella* Suess. gives no exact location information, but both specimens belong to a single gathering (*Lejeune 190*). No other specimens of the original material are known, and the type choice is therefore rather formal.

Suessenguth in Suessenguth and Merxmüller (1951) cited the type of *A. aspera* f. *latifolia* Suess. as kept at Kew. The duplicates in BR and S are, therefore, isotypes.

Achyranthes argentea var. *albissima* Suess. comprises mountainous plants with small white leaves. Suessenguth in Suessenguth and Merxmüller (1951) designated two specimens of a single gathering at Kew as "typus". These specimens are syntypes; a lectotype is designated here to restrict the typification to a single specimen.

Habitat. Open or slightly shady grassy slopes, bushy vegetation, calcareous outcrops, sometimes as a weed, at elevations of 1000–3500 m a.s.l. in arid or seasonally moist areas.

Distribution. (Fig. 4; see also Appendix 1). **Africa**: Angola, Burundi, Cameroon, DR Congo, Eritrea, Ethiopia, Guinea, Kenya, Madagascar, Malawi, Nigeria, Rwanda, Somalia, South Sudan, Sudan, Tanzania, Uganda.

Arabian Peninsula: Oman, Saudi Arabia, Yemen.

General distribution. The species is only known from tropical Africa and Arabia.

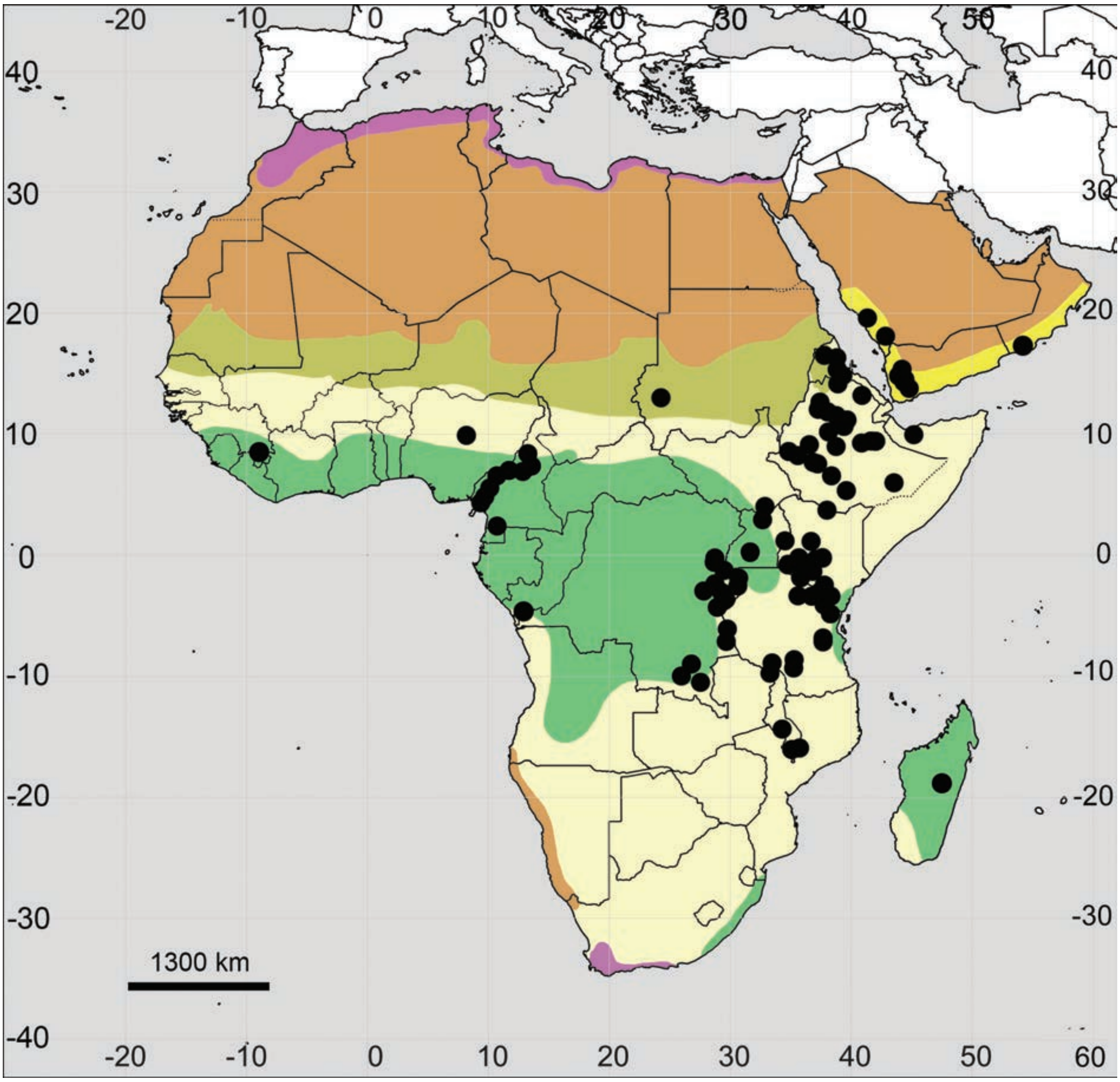

Figure 4. Distribution map of *Achyranthes abyssinica*.

Achyranthes acuminata **E.Mey. ex Sonder, Linnaea 23: 96 (1850).**

= *Achyranthes aspera* f. *nigrescens* Suess., Bull. Jard. Bot. État Bruxelles 15: 56 (1938). Lectotype (designated here): DR Congo, [Équateur Prov.,] Environs d'Eala, July 1930, *J. Lebrun 1230* (BR0000008819543!, isolectotypes BR000000881923!, K!).

– *Achyranthes aspera* var. *rubrofusca* auct. in herb. BM, K.

– *Achyranthes bidentata* var. *africana* Cavaco, nom. nud. in herb. BM, K.

– *Achyranthes bidentata* auct.: Baker and Clarke (1909), Hutchinson and Dalziel (1927), Keay (1954), Lebrun and Stork (1991), Figueiredo and Smith (2008), Phiri (2005), Klopper et al. (2006).

– *Achyranthes africana* Sukhor., nom. nud. in herb. BM, BR, K.

Lectotype (designated here). South Africa, Port Natal [Durban], schattige Waldplätze, 400 ft, 9 April 1832, *Drège 4679* (P01029520 – image!).

Description. (Figs 5, 6). Annual or short-lived perennial herb up to 1.5(2.0) m tall occasionally creeping and rooting at lower nodes; stem sparsely pubescent, obscurely quadrangular turning angular in the inflorescence; leaf petioles 10–40(60) mm, blades 30–260 × 20–110 mm, cuneate, ovate or rhombic or even obovate, entire, tip short or long acuminate, deep green or olivascent and almost glabrous above, pale green or purplish and slightly to moderately pubescent below, usually turning blackish when dry; inflorescence 80–270 mm long, dense, paracladies always present, in early stages thin and delicate similar to inflorescences of some willows (e.g. *Salix triandra*); bract 3.0–4.0 mm long; bracteoles (3.0)4.0–5.0 mm long, reflexed; perianth segments slightly unequal, (4.5–5.0)6.0–7.0(8.0) mm long (two segments longer than three others), green outside and purple-red inside at least at the tip, turning dark brown when dry, three inner segments keeled; pseudostaminodes brownish (when dry), 0.8–1.1 mm, not or slightly fimbriate; stamens 5, filaments purple, anthers 0.35–0.6 mm long, magenta; style (1.3)1.6–2.1 mm long, pink or mauve; fruit (without style) 1.7–2.5 mm long.

Taxonomic note. For a long time, specimens of *A. acuminata* were identified as *A. aspera* or its varieties, e.g. *A. aspera* var. *rubrofusca* in the DR Congo, or as *A. aspera* var. *nigrescens* (Suessenguth in Suessenguth and Merxmüller 1951), and, in some cases in tropical Africa, as *A. bidentata* (e.g., Baker and Clarke 1909; Hutchinson and Dalziel 1927; Townsend 1973; Lebrun and Stork 1991; Klopper et al. 2006). Nonetheless, Townsend (1985) claimed that the Asian *A. bidentata* did not occur in East Tropical Africa and referred specimens of *A. acuminata* to *A. aspera* var. *pubescens* (Moq.) C.C.Towns. Lebrun and Stork (2003) vaguely discussed some morphological differences between *A. aspera* s.l. and *A. bidentata* from Asia and Africa, concluding that there are differences between both species as well as differences between Asian and African populations of *A. bidentata*.

Achyranthes acuminata differs from the Asian *A. bidentata* and *A. japonica* (Miq.) Nakai by its obovate leaves turning blackish when dry (facultative character) and longer (1.6–2.1 mm) styles. The two Asian species are rhizomatous perennial plants with ovate leaves, which do not turn black when dry, and have

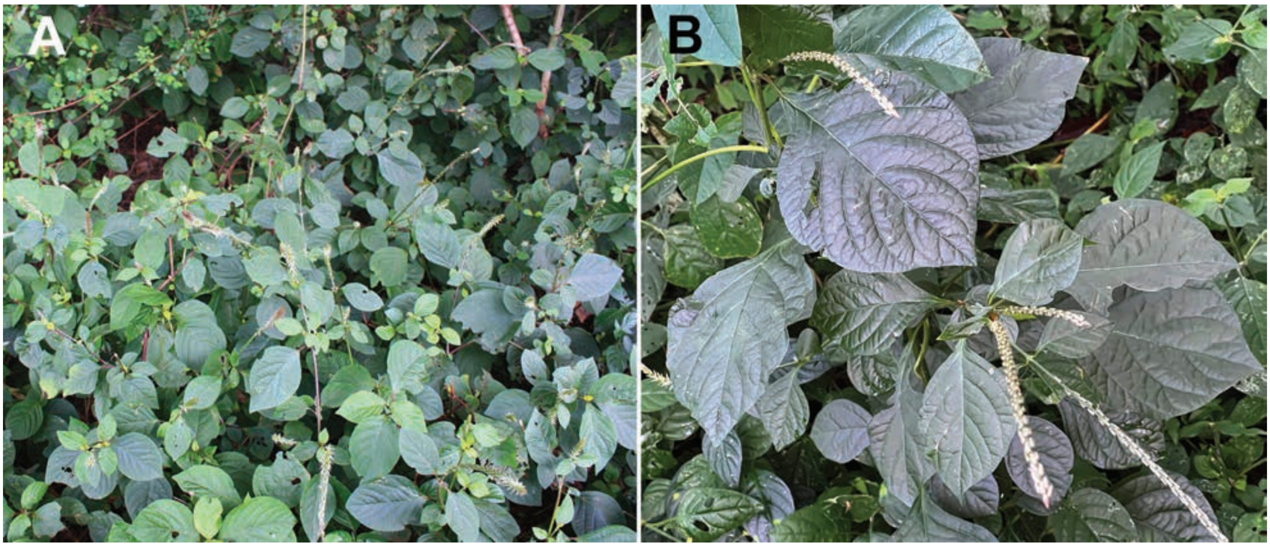

Figure 5. *Achyranthes acuminata* **A** general view of the plants (Meru area, Arusha Region, Tanzania. Photographer: A. Sukhorukov) **B** close-up of the leaves and inflorescences (KwaZulu-Natal Province, near Durban, South Africa. Photographer: Errol Douwes).

Achyranthes aspera L.
var. pubescens (Moq.) C.C.Townsend
DET. I. Darbyshire (fls small for var.) 11 IV 2006

FLORA OF TANZANIA

Name: Achyranthes aspera L.

Growth form: Herb, 70 cm tall.

Habitat: Moist Coastal Forest

Altitude: 200m

Description: Height – 70cm, Mid Green Leaves. Many small pink Flowers

Local Name (Kizigua): Lutala

Date: 31/7/91

Gendagenda Forest, Handeni District, Tanga Reg. 5°32'S 38°38'E. Diverse Coastal Forest types on an escarpment to 300m and an inselberg to 545m.

No. 2377 Collected by the Frontier-Tanzania Coastal Forest Research Programme

Figure 6. A herbarium specimen of *Achyranthes acuminata* (Tanzania, Tanga Region, Gendagenda Forest, 200 m a.s.l., 31 Jul 1991, *Frontier Tanzania team* 2377, K).

shorter styles (1.0–1.5 mm long). To date, the presence of any species of the Asian *A. bidentata* group is not confirmed in Africa, and the native distribution of this group of species is restricted to tropical and warm temperate Asia (South and East China, Japan, South-East Asia, and countries located in the Himalayas). *Achyranthes japonica* is reported as an alien and naturalized plant in temperate North America (Medley et al. 1985).

Achyranthes aspera var. *rubrofusca* was erroneously reported from Africa (Suessenguth in Suessenguth and Merxmüller 1951). Its basionym *A. rubrofusca* (Wight 1852) was described from India and belongs to the *A. bidentata* group.

Nomenclatural notes. The name *A. acuminata* was only mentioned (as *nomen nudum*) in Drège (1843), who cited a number of plant species (incl. *A. acuminata*) growing in forests and woodlands ('Wälder und Holzungen'), and it was later validated by Sonder (1850). Cavaco (1962: 127) considered *A. acuminata* as a putative synonym of the subshrubby *A. aspera* var. *porphyrostachya* (≡ *A. porphyrostachya*) probably based on similar leaf shape. Authentic specimens of *A. acuminata* have obovate leaves, different from *A. porphyrostachya*, which has oblong or ovate leaves. Moreover, *A. acuminata* and *A. porphyrostachya* can be separated based on their ecology.

An authentic specimen of *A. acuminata* kept at W ([without exact location and date] E. M.[eyer] (W18393!) has a perianth shorter (4.5–5.0 mm long) than usual (6.0–7.0 mm). A shorter perianth length was also observed in specimens from dryer areas (e.g., growing in Ethiopia and Benin). On the other hand, the length of anthers (±0.5 mm long) and style (±1.8 mm) long is constant in the species.

Suessenguth (1938) cited two specimens of *A. aspera* f. *nigrescens* Suess., which were collected in the Belgian Congo [now DR Congo]: Matadi [Kongo Central Prov.] and Eala [Équateur Prov.]. Both specimens represent the same species. Suessenguth was probably the first to mention its remarkable character: leaves turning black when dry.

Habitat. Riverine and primary rain forests, forest margins and other wet shady places at elevations of 0–2000 m a.s.l.

Distribution. (Fig. 7; see also Appendix 1). **Africa**: Angola, Benin, Botswana, Burundi, Cameroon, Central African Republic, Comoros, Congo Republic, DR Congo, Equatorial Guinea, Ethiopia, Gabon, Guinea, Ivory Coast, Kenya, Lesotho, Madagascar, Malawi, Mayotte, Mozambique, Namibia, Nigeria, Rwanda, São Tomé and Príncipe, Sierra Leone, Somalia, South Africa, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

General distribution. Tropical Africa.

Achyranthes annua Dinter, Repert. Spec. Nov. Regni Veg. 15: 82 (1917).

≡ *Achyranthes argentea* var. *annua* (Dinter) Suess., Mitt. Bot. Staatssamml. München 1: 152 (1952).

≡ *Achyranthes aspera* [var. *sicula*] f. *annua* (Dinter) Cavaco, Mém. Mus. Nat. Hist. Nat. 13, ser. B (Botanique): 122 (1962).

= *Achyranthes argentea* var. *viridescens* Moq. in DC., Prodr. 13(2): 315 (1849). Lectotype (designated here): [Egypt] Cairo, Rudach [Roda] Island, [1818], *F.W. Sieber s.n.* (G-DC [image!]; isolectotypes M0241528!, M0241529!, K! [left-hand specimen, mounted together with *A. sicula* from Tanger, Morocco]).

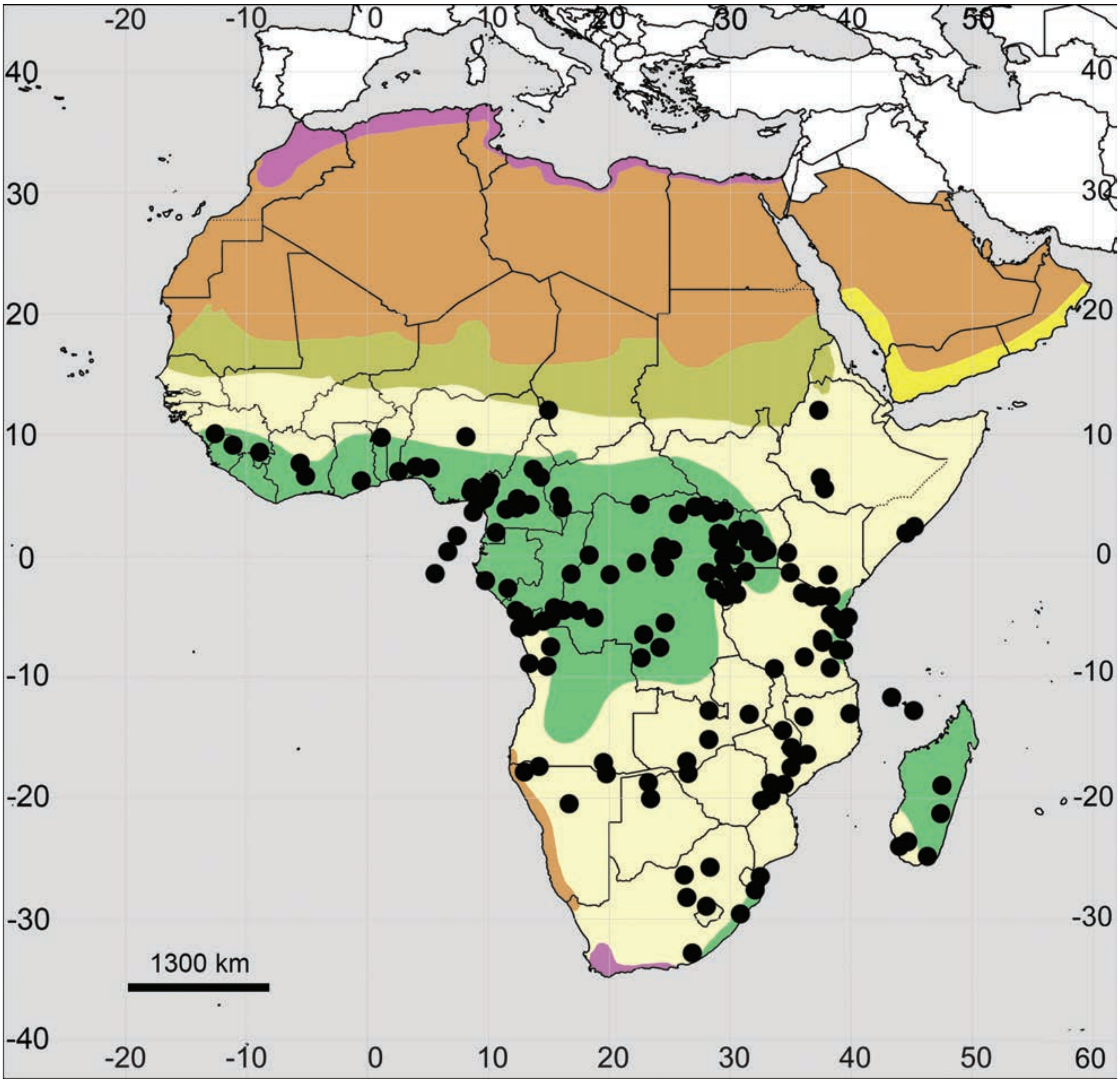

Figure 7. Distribution map of *Achyranthes acuminata*.

= *Achyranthes asperoides* Pires de Lima, Brotéria. Sér. Bot. 19: 116 (1921). Lectotype (designated here): Mozambique. Na planície inculta junto de Palma, 26 February 1917, *A. Pires de Lima 118* (PO69282 – image!; isolectotype PO69283 – image!).

= *Achyranthes aspera* f. *annulosa* Suess., Mitt. Bot. Staatssamml. München 1: 69 (1951). Holotype: Uganda, Ishasha, 4000 ft, November 1946, *J.W. Purseglove 2284* (K!).

= *Achyranthes aspera* [f. *annulosa*] subf. *angustifolia* Suess., Mitt. Bot. Staatssamml. München 1: 69 (1951). Holotype: Sierra Leone, [Southern Prov.,] Njala, 28 December 1932, *F.C. Deighton 2584* (K000243721!).

– *Achyranthes argentea* auct.: Berhaut (1971).

– *Achyranthes aspera* var. *argentea* auct.: Hauman (1951), Cavaco (1953), Sunding (1973).

– *Achyranthes aspera* auct. in herb. div.

- *Achyranthes aspera* var. *sicula* auct.: Boudet and Lebrun (1986), Barry and Celles (1991), Lebrun et al. (1991), Audru et al. (1994), Townsend (1985, 1988, 1993b, 2000), Miller (1996), Wood (1997), Germishuizen and Meyer (2003), Mapaura et al. (2004), Setshogo (2005), Figueiredo and Smith (2008), Brundu and Camarda (2013), Klaassen and Kwembeya (2013), César and Chatelain (2019), Odorico et al. (2022), Gosline et al. (2023).
- *Achyranthes sicula* auct.: Podlech (1966), Lebrun (1973), Peyre de Fabregues and Lebrun (1976), Hassan et al. (2023).

Type. Namibia, [Otjozondjupa Region] Otjihua b.[y] Okandja Dtr. [District] Eahero [Farm], *Dinter 3303* (B, destroyed). ***Neotype*** (selected here): Namibia, [Oshikoto Region] Tsumeb, April 1934, *Dinter 7434* (K005771734!). Fig. 8.

Description. (Fig. 9). Annual, rather delicate herb, 20–100(150) cm tall, not rooting; stems four-angled; lateral branches at acute angle with the main axis; leaf petioles 10–30 mm long, blades 20.0–80.0 × 10.0–60.0 mm, ovate, base truncate, tip ± attenuate, green, often turning red later, sometimes gray or pale green abaxially because of abundant silvery and appressed hairs, pendulous at night (at least in cultivation indoors); young leaves often with small red gland-like outgrowths on the veins adaxially (Fig. 9C–E) turning yellow and then pale white (indoor cultivated plants); inflorescence with ± equal main and lateral branches, with fruits rather distant at least in lower part; bract 1.5–2.0 mm long, bracteoles 2.0–3.0 mm long, pinkish, reflexed; perianth 3.0–3.5(3.6–4.1) mm long, segments ± equal, one-veined with indistinct two lateral veins; stamens 5 with white or mauve filaments, anthers 0.15–0.25 mm long, yellow or pink, pseudostaminodes 0.5–1.2 mm long, apically ± fimbriate, white; style with stigma 0.5–0.8(1.0) mm long; fruit (without style) 1.0–1.5(1.8) mm long.

Taxonomic note. Dinter (1917) described the species from Namibia and correctly noted that there are no intermediates between *A. aspera* and *A. annua*. However, the characters mentioned in the protologue – life form and inflorescence length – cannot be considered as delimiting traits. Both *A. annua* and *A. aspera* are annuals, although the latter species often resembles a perennial herb reaching 2 m tall and having long (up to 70 cm) inflorescences under favorable conditions (e.g., in a humid climate with enough precipitation). Habitually, *A. annua* is similar to *A. abyssinica* and *A. sicula* but differs by the minute anthers and much shorter styles. In addition, *A. annua* has leaves usually green on both sides, but sometimes their abaxial surface may be pale green or gray due to abundant simple hairs, especially in the populations growing in the Desert and Sahel zones. The name *Achyranthes annua* was not retained after its description (Dinter 1917: 82). Podlech (1966) synonymized it with *A. sicula*, mentioning that *A. sicula* in Namibia is an annual plant. The recent checklist of Namibian plants (Klaassen and Kwembeya 2013) did not include *A. annua*, with only a single species with two varieties listed (*A. aspera* var. *aspera* and var. *sicula*). Our study reveals that *A. annua* is not only present in Namibia but is widely distributed across semi-arid regions of Africa reaching up to the Arabian Peninsula.

The gland-like outgrowths on the leaves (Fig. 9C) were detected only in some individuals of *A. annua* cultivated indoors; they were not observed in other species of the genus.

Figure 8. Neotype of *Achyranthes annua* (Namibia, Oshikoto Region, Tsumeb, April 1934, *Dinter 7434*, K005771734). The image was provided by RBG Kew (available at http://specimens.kew.org/herbarium/K005771734).

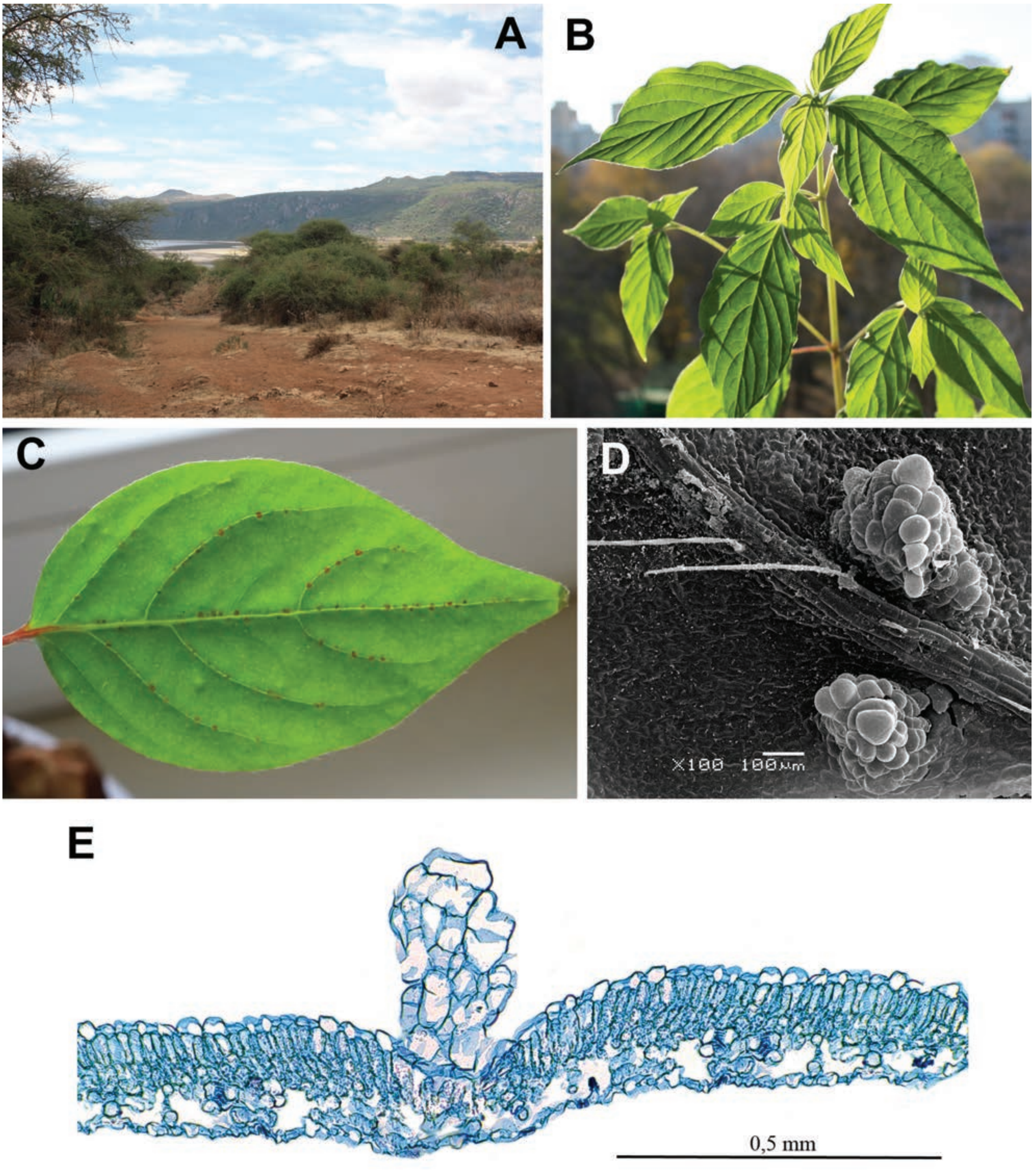

Figure 9. *Achyranthes annua* **A** typical habitat with *Vachellia* trees, Manyara Region, Tanzania **B** an indoor cultivated plant in vegetative stage (grown from seeds from Manyara Region, Tanzania) **C** adaxial side of the leaf with red gland-like outgrowths on the veins (indoor cultivated plant) **D** close-up view of gland-like outgrowths and simple hairs **E** cross-section of a leaf showing bifacial anatomy and structure of an outgrowth. Scale bars: 100 μm (**D**); 0.5 mm (**E**). Photographers: **A–D:** A. Sukhorukov, **E** M. Nilova.

Nomenclatural notes. The type of *Achyranthes annua*, previously kept at B, was lost during the Second World War, and no other original material has been traced in other herbaria visited or digitized. There are no duplicates of *A. annua* in the HBG herbarium, which contains many duplicates of K. Dinter (pers.

comm. M. Schultz). Nevertheless, the first author (APS) has found a specimen collected and labelled by K. Dinter in K, which is selected here as a neotype.

Moquin-Tandon (1849) cited two gatherings of *A. argentea* var. *viridescens* Moq. ("prope Catanam", Heldreich; "in Aegypto", Sieber) in personal collections of Poiret and Candolle, which are, therefore, syntypes. A specimen collected by Sieber and kept at G-DC is designated as lectotype here. This specimen was collected in 1818, when Sieber travelled across Crete, Egypt and Palestine (Sieber 1823), and commercially distributed within a set of dried specimens of 230 species in 1819 (Sieber 1821).

Pires de Lima (1921) cited a single gathering in the protologue of *A. asperoides*, *Pires de Lima 118*, but the original material also comprises an uncited gathering, *Pires de Lima 306*, which was collected on another date. The cited collection is therefore not the holotype but a syntype, and lectotypification is warranted in this case. The plants collected are rooting at the lower nodes, with long lateral inflorescence's branches. Such specimens are sometimes present in *A. annua*, but the exact measurements of reproductive characters are not known yet. In any case, the species cannot be synonymized with *A. acuminata*, *A. aspera*, or *A. porphyrostachya*.

Habitat. A typical shade-loving plant usually collected in *Vachellia*–*Commiphora* bushlands (in East Africa), sometimes in rocky, sandy, volcanic habitats or in degraded plant communities in drier regions at elevations of 0–2400 m a.s.l. Dinter (1917) also indicated that *A. annua* is a common plant in under the canopy of *Vachellia* bushlands in SW Africa [Namibia]. N.M. Otto (in labels at herb. M) noted that *A. annua* (as *A. aspera*) is also common in KwaZulu-Natal (South Africa) as a weed in cultivated areas, where the farmers called it "wild buckwheat". Reports of the common presence of *A. aspera* in subcanopy communities in the tropical part of South Africa (Leistner 1996) should probably belong to *A. annua*. Plants of this species are eaten by livestock.

Distribution. (Fig. 10; see also Appendix 1). **Africa**: Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Cape Verde, Central African Republic, Chad, Djibouti, DR Congo, Egypt, Eritrea, Eswatini, Ethiopia, Gambia, Ghana, Guinea, Guinea-Bisau, Kenya, Lesotho, Liberia, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Réunion, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe.

Arabian Peninsula: Oman, Saudi Arabia, Yemen.

General distribution. Africa and Arabia.

Achyranthes aspera L., Sp. Pl. 1: 204 (1753), nom. cons.

≡ *Achyranthes aspera* var. *indica* L. Sp. Pl. 1: 204 (1753).
≡ *Achyranthes indica* (L.) Mill., Gard. Dict., ed. 8: [unpaged] *Achyranthes* no. 2 (1768).
≡ *Cadelaria indica* (L.) Raf., Fl. Tellur. 3: 45 (1837).
≡ *Stachyarpagophora aspera* (L.) M.Gómez, Anales Inst. Segunda Enseñ. 2: 312 (1896).
≡ *Centrostachys aspera* (L.) Standl., J. Wash. Acad. Sci. 5: 75 (1915).
≡ *Centrostachys indica* (L.) Standl., J. Wash. Acad. Sci. 5: 75 (1915).
= *Achyranthes obtusifolia* Lam., Encycl. 1(2): 545 (1785).

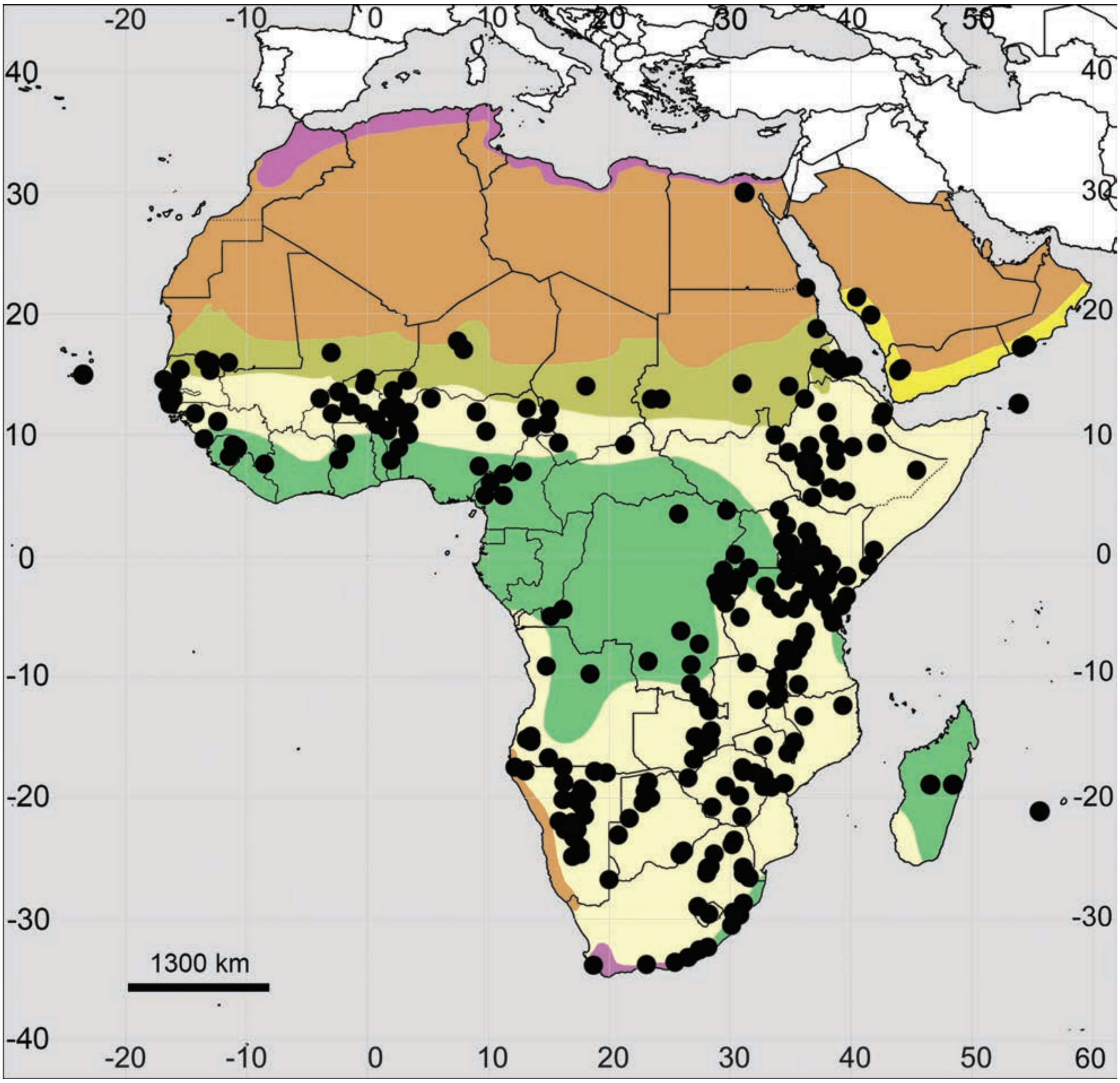

Figure 10. Distribution map of *Achyranthes annua*.

≡ *Achyranthes aspera* var. *obtusifolia* (Lam.) Suess., Mitt. Bot. Staatssamml. München 1(5): 152 (1952). Lectotype (designated here): [India?] leg. *Sonnerat s.n*. (P-LA00380993, image!).

= *Achyranthes argentea* var. *obovata* Moq. in DC., Prodr. 13(2): 316 (1849). Holotype: [Saudi Arabia] “Locis cultis ad pagum Madara vallis Fatme prope Meccam”, 24 November 1833, *W. Schimper 944* [Unio itineraria (1837)] (G00688924!, image available at http://www.ville-ge.ch/musinfo/bd/cjb/chg/adetail.php?id=668392&base=img&lang=en); isotypes HBG503188, M0241524!).

= *Achyranthes aspera* var. *simplex* Millsp., Publ. Field Columb. Mus., Bot. ser. 2: 36 (1900). Holotype: [US Virgin Islands] St. Thomas, Charlotte Amalie, 17–18 January 1899, *C.F. Millspaugh 484* (F – image!, isotype NY658322 – image!).

= *Achyranthes obovata* Peter, Repert. Spec. Nov. Regni Veg. Beih. 40(2, Anhang): 25 (1932) nom. illeg., non (M.Mart. & Gal.) Standl. (1915). Holotype:

Deutsch-Ostafrika [Tanzania, Tanga Region] West-Usambara, Mashewa, Gegend Tunya und Kwatangu, 400 m, 8–9 September 1915, *A. Peter 13869* (B – image!).

Lectotype (designated by Townsend 1974). [Sri Lanka] Herb. Hermann 2: 69, no. 105 (BM000621744!).

Description. (Fig. 11). Annual herb, 30–200 cm tall, stout, not rooting; young stem round, angled at the inflorescence; leaf petioles 10–30 mm, blades 15–110 × 20–80 mm, obovate or ovate, base truncate, pubescent throughout, tip shortly acuminate; inflorescence up to 70 cm long; bract 2.0–2.5 mm long; bracteoles 2.5–3.5 mm long, green, not or slightly reflexed; perianth 4.0–4.5 mm long, segments ± equal, one-veined with two indistinct lateral veins; stamens 5 with white or

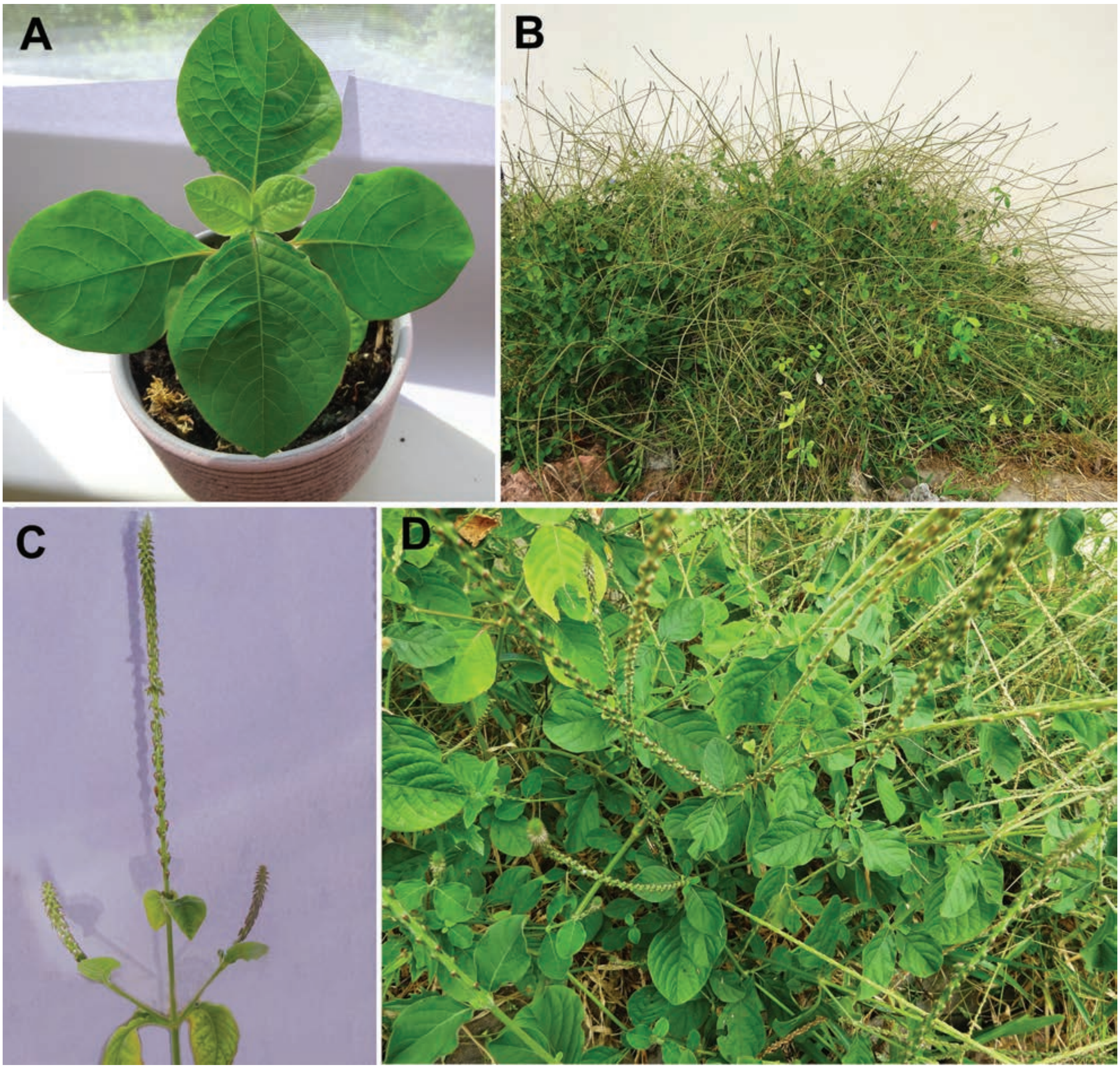

Figure 11. *Achyranthes aspera* **A** an indoor cultivated plant in vegetative stage (grown from seeds from Unguja Island, Tanzania) **B** two bushy plants in fruiting stage (disturbed habitat on Unguja Island, Tanzania) **C** inflorescence of an indoor cultivated plant at fruiting **D** close-up view of a fruiting plant (disturbed habitat on Unguja Island, Tanzania). Photographer: A. Sukhorukov.

mauve filaments, anthers 0.4–0.6 mm long; pseudostaminodes 0.7–1.1 mm long, white; style with stigma 1.0–1.1 mm long; fruit (without style) 1.8–2.2 mm long.

Taxonomic note. Many authors (Podlech 1966; Berhaut 1971; Townsend 1980b; Ghazanfar 1992; Germishuizen and Meyer 2003; De Lange et al. 2004; Gibreel and Darbyshire 2015) indicated that *A. aspera* is a perennial herb occasionally flowering in the first year, but our field observations revealed that the species could be mistaken for a perennial based on its height and much branched habit in the moist regions (e.g., Zanzibar, Tanzania; Haryana, India: pers. obs. APS), but is a robust annual.

Nomenclatural notes. The lectotype of *Achyranthes aspera* designated by Townsend (1974) and proposed for conservation by Jarvis (1992), although only represented by the upper part of a plant, clearly shows the characters typical of the taxon (obovate leaves, short bracteoles and flowers). Fawcett and Rendle (1914: 136) indicated that the type of *A. aspera* var. *indica* is kept at the Natural History Museum (BM) and referred to Hermann's Flora Zeylanica. This choice was formalised by Townsend (1985), who, therefore, made this varietal name a homotypic synonym of the type variety. Jarvis (2007) disagreed with Townsend (1985) and noted that Burman (1737) is the nomenclatural source of this Linneaen variety and should provide a type. Iamonico (2014) selected a lectotype of *A. aspera* var. *indica* in the herbarium S-LINN (IDC 100.19) that is annonated by Linnaeus as "β *aspera*". This sheet contains a fragment of the plant with three obovate leaf pairs and an inflorescence in early blooming stage. We have doubts whether this plant is the annual *A. aspera*, and we assume that the specimen in S-LINN rather belongs to *A. porphyrostachya* (although its leaf shape is not characteristic for the latter species). Despite these doubts, the protologue of *A. aspera* var. *indica* (Linnaeus 1753) contains a separate diagnosis plus the indication that the variety occurs in "India" ("Zeylona" = Sri Lanka). This information links the Hermann's specimen with the protologue and makes it part of the original material, thus eligible for lectotypification. For this reason, the type designation made by Townsend (1985) is formally correct and has priority over Iamonico's choice; it stabilises the nomenclature of *A. aspera* as established by Townsend (1974, 1985) and universally accepted.

The protologue of *A. obtusifolia* (Lamarck 1785) includes a number of cited illustrations which constitute its original material together with the specimens in the personal collection of Lamarck. A lectotype is therefore designated here.

Hassan et al. (2023) synonymized *A. argentea* var. *obovata* Moq. with *A. sicula*. Nevertheless, the holotype represents a branched specimen of *A. aspera* s.str. This lectotype is the only specimen used for and cited in the protologue (Moquin-Tandon 1849), which is thus a holotype by definition; the lectotypification with the same specimen made by Hassan et al. (2023) was therefore superfluous.

The holotype of *A. aspera* var. *simplex* Millsp. is an unbranched specimen with a terminal inflorescence; its leaves are very typical of *A. aspera*.

Habitat. Waste, mostly sunny places; frequent in the regions with humid climate (e.g., Unguja Island, Tanzania) at elevations of 0–1500 m a.s.l.

Distribution. (Fig. 12; see also Appendix 1). Surprisingly, herbarium collections from the western part of Africa are scarce, indicating that it might be a scattered alien in the West Tropical Africa. The majority of collections are from the eastern tropical part of Africa and the islands in the western Indian Ocean, where it is usually considered as alien.

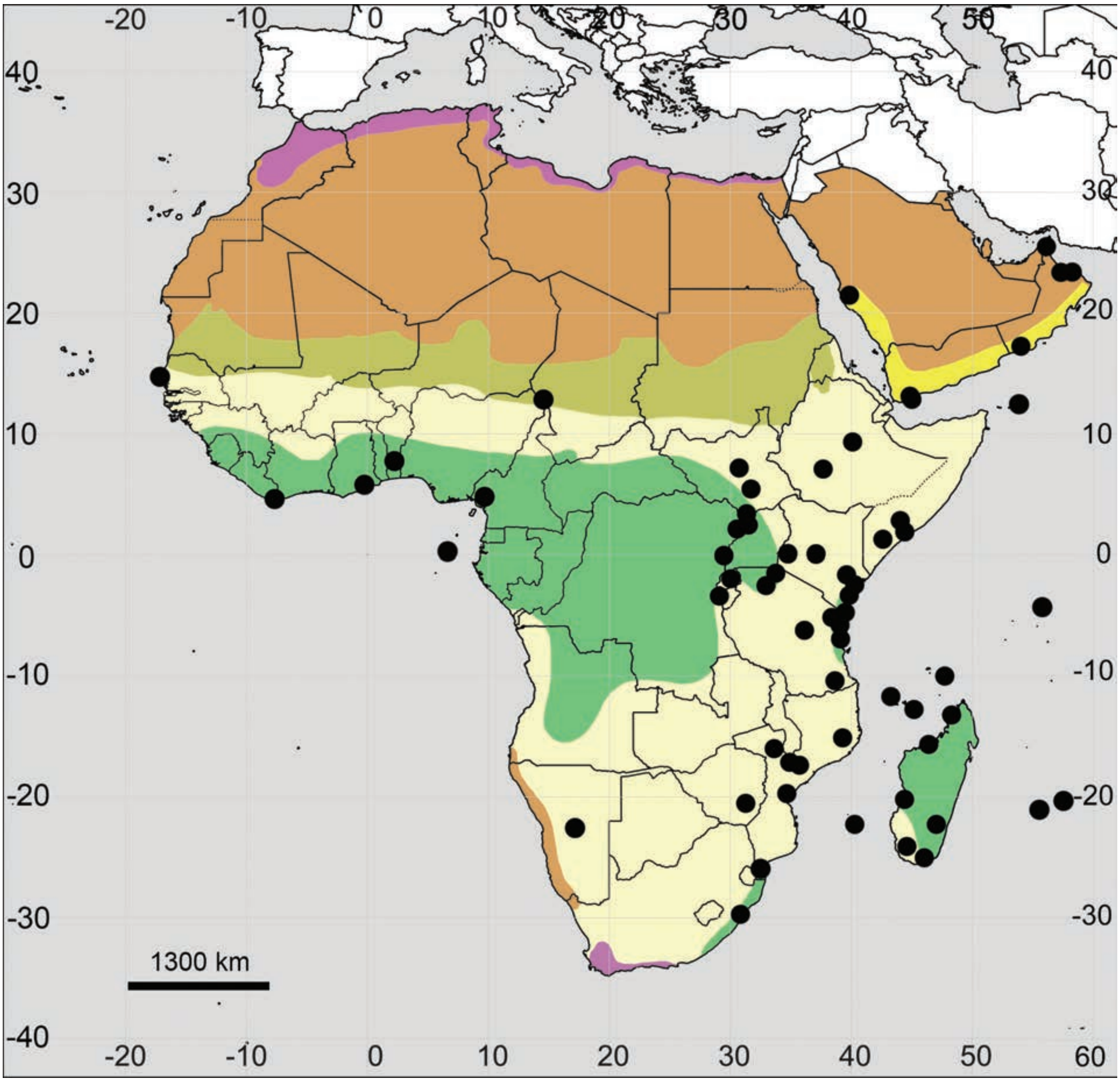

Figure 12. Distribution map of *Achyranthes aspera*.

Africa: Benin, Cameroon, Chad, Comoros, DR Congo, Egypt (old record), Europa Island, Ethiopia, Ghana, Kenya, Liberia, Madagascar, Mauritius, Mayotte, Mozambique, Namibia, Réunion, Rwanda, São Tomé and Príncipe, Senegal, Seychelles, Somalia, South Africa, South Sudan, Tanzania, Uganda, Zimbabwe.

Arabian Peninsula: see Appendix 1.

General distribution. The exact origin of the species is unknown, but it seems to be native in tropical South and South-West Asia. Because of the confusion of *A. aspera* s.str. with other species and varieties, we have detailed its distribution across the World based on the specimens seen in the herbaria visited and online collections.

Africa: see Appendix 1.

Asia: Bangladesh, Bhutan, Cambodia, tropical China including Hong Kong and Taiwan, India, Indonesia, Laos, Malaysia, Maldives, Myanmar, Nepal, Oman, Pakistan, Philippines, Saudi Arabia, Singapore, Sri Lanka, Thailand, UAE, Vietnam, Yemen (incl. Socotra).

Australasian Realm: tropical Australia, Papua New Guinea.

Melanesia: New Caledonia (probably other islands).

Polynesia: Pitcairn Island, Samoa. Also reported for many other islands of Polynesia (Florence 2004).

America: Antigua and Barbuda, Bahamas, Barbados, Bolivia, British Virgin Islands, Brazil (tropical regions, e.g. States of Bahia, Espírito Santo, Minas Gerais, Pará), Colombia, Costa Rica, Cuba, Cayman Islands, Dominica, Dominican Rep., French Guiana, Grenada, Guadeloupe, Guatemala, Guyana, Haiti, Jamaica, Kingdom of the Netherlands (Aruba, Bonaire, Curaçao, St.-Eustatius, St.-Martin), Martinique, Mexico, Montserrat (British Overseas Territory), Nicaragua, Panama, Puerto Rico, Salvador, St. Barthélemy (French Overseas Territory), St. Kitts and Nevis, St. Lucia, St. Vincent and the Grenadines, Suriname, Trinidad and Tobago, USA (Alabama, Florida, Louisiana, Texas, and Hawaii), US Virgin Islands.

It is common or frequent in disturbed places at lower altitudes in tropical America (e.g., Millspaugh 1900, as *A. aspera obtusifolia*; Robertson 1981; Acevedo-Rodríguez and Strong 2012; pers. obs. of APS in Grenada in 2016).

Achyranthes mauritiana **Moq. in DC., Prodr. 13(2): 313 (1849).**

Lectotype (designated here). Mauritius, [1768–1773], [*Commerson*] *s.n.* (P00487020 [image!]; isolectotypes FI-WEBB154894!, G-DC G00688999 [image!]).

Description. (Fig. 13). Annual (?); stem upright, with spreading lateral branches; leaf petioles 20–40 mm long, blades 30–100 × 20–40 mm, rhombic or elliptic, tip attenuate, almost glabrous or sparsely pubescent at the veins, green, sometimes turning black when dry; inflorescence up to 30 cm long; bract 2.5–3.0 mm long, bracteoles 3.0–3.5 mm; perianth 4.0–5.0 mm long; stamens 5, anthers ~ 0.4 mm long; style 1.0–1.2 mm long; fruit 1.7–2.1 mm long.

Taxonomic notes. The specimens seen are represented by upper twigs only, and our present description is based on the scarce material available in the collections FI-WEBB and MAU. A description provided by Cavaco (1954) is insufficient for any comparison of the material from the Mascarenes, Madagascar and Comoros, because the morphometry of the reproductive characters was not indicated. So far, *A. mauritiana* is still poorly known. Townsend (1994) synonymized *A. mauritiana* with *A. aspera* var. *porphyrostachya* [≡ *A. porphyrostachya*], but this synonymy cannot be accepted due to their different leaf shape and morphometry of the reproductive characters. Only a few old collections cited below were from the Mascarenes, with a more recent collection from Agaléga (Mauritian territory). Nevertheless, *A. mauritiana* seems to be a distinct species due to its rhombic or elliptic, almost glabrous leaves as compared with *A. aspera* s.str. Its reproductive characters are the same as in *A. aspera* s.str. The leaf characters are quite similar to those of *A. acuminata*, but the morphometry of the reproductive characters is different. Further studies are needed to explore the morphology, phylogenetic relationships and ecology of *A. mauritiana*.

Townsend (1994) reported *A. aspera* var. *velutina* (Hook. & Arn.) C.C.Towns. (≡ *A. velutina* Hook. & Arn.) from Réunion. This robust species with villous leaves occurs only in the Pacific. The plants from the Mascarenes resembling *A. velutina* seem to belong to a different species whose name may be *A. borbonica* Willd. in Roem. & Schult., Syst. Veg., ed. 15 bis 5: 549 (1819) ≡ *A. aspera*

Figure 13. A herbarium specimen of *Achyranthes mauritiana* (Réunion, Rivière des Galets, Jul 1851, *Boivin s.n.*, MAU0017619).

var. *borbonica* (Willd. ex Schult.) C.C.Towns., Kew Bull. 29(3): 474 (1974). The holotype of *A. borbonica* ("Insula Borbon" [Réunion]) kept at B-W 05-005-010 is represented by a small fragment showing villous leaves and an inflorescence collected in a premature stage. This species is also very poorly known, and no other material except for the type of *A. borbonica* is seen from the Mascarenes.

Nomenclatural notes. Moquin-Tandon (1849) based his *A. mauritiana* on two specimens from Mauritius without exact label information (seemingly collected by P. Commerson during his residence on Mauritius in 1768–1773: Frodin 2001), which were kept in the Paris Museum of Natural History and the personal herbarium of Labillardière. Townsend (1994) designated a specimen at G-DC as lectotype. This specimen belongs to the collection from Mauritius, which was previously kept in Paris but obtained by A.P. de Candolle for his private herbarium by exchange in 1821 (cf. de Candolle 1862). Although this specimen is part (a duplicate) of the collection which was used for the original description, it was not cited in the protologue and therefore has no precedence over cited syntypes in lectotype designation. A specimen at P, which was examined by Moquin-Tandon and is accompanied with his analytical drawing, is designated here as a new lectotype in agreement with Art. 9.12.

Distribution. Mauritius: [without exact location and date] *herb*. *Moquin-Tandon s.n*. (FI-WEBB154894); Agaléga, North Island, 19 Jul 1976, *D.R. Stoddart 7237* (US03544411);

Réunion (French Overseas Department): Rivière des Galets, Jul 1851, *Boivin s.n.* (MAU0017619).

General distribution. The species seems to be endemic to the Mascarenes (Mauritius and Réunion), but recently collected in Agaléga. Cavaco (1954) cited some records from Madagascar, but all material seen belongs to other species.

Achyranthes porphyrostachya **Wall. ex Moq. in DC., Prodr. 13(2): 316 (1849), as "porphyristachya".**

≡ *Achyranthes aspera* var. *porphyrostachya* (Wall.) Hook.f., Fl. Brit. India 4(12): 730 (1885).

= *Achyranthes robusta* C.H.Wright, Fl. Cap. (Harvey) 5(1.2): 428 (1901). Lectotype (designated here): South Africa, [KwaZulu-]Natal, near Durban, 100 ft, [without date] [*Wood*] *7202* (K000243729!).

= *Achyranthes aspera* var. *procera* Fiori, Giorn. Bot. Ital., n.s., 19: 437 (1912). Holotype: [Ethiopia, Tigray Region] in vallibus juxta fruticeta 4–8 pedalis prope Adoa [Adwa], 5 November 1838, *Schimper 1234* [Iter Abyssinicum, ser. 2 (1842)] (FI000824!, isotypes BM!, BR0000008356987!, FI-WEBB154842!, K!, L1673915, M0241518!).

= *Achyranthes aspera* [var. *argentea*] f. *suffruticosa* Fiori, Giorn. Bot. Ital., n.s., 19: 438 (1912). Lectotype (designated here): Eritrea, [Dek'emhare] Hamasen, Ghinda – Baresa, 960 m a.s.l., 26 January 1909, *A. Fiori 52* (FT001025!; isolectotypes FT001026!, FI!).

= *Achyranthes aspera* f. *robustiformis* Suess., Mitt. Bot. Staatssamml. München 1: 70 (1951). Lectotype (designated by Townsend 1985): Tanganyika area [Tanzania], Ngorongoro crater, 5000 ft, 9 April 1941, *P.R.O. Bally 2273* (K!).

– *Achyranthes aspera* auct. in herb. div.

- *Achyranthes aspera* var. *pubescens* auct.: Townsend (1985, 1993b, 1988, 2000), Audru et al. (1994), Boulos (1995), Miller (1996); Wood (1997), Germishuizen and Meyer (2003), Mapaura et al. (2004), Setshogo (2005), Gibreel and Darbyshire (2015), Odorico et al. (2022), Hassan et al. (2023).
- *Achyranthes aspera* f. *fruticosa* auct. in herb. div.
- *Achyranthes aspera* var. *late-ovata* auct. in herb. K.
- *Achyranthes aspera* var. *pinguispicata* Clarke, nom. nud. in herb. K.

Lectotype (designated here). Myanmar. “Tong Dong” [“towards the Hills” = on the way from Sagaing to Shan Hills], 23 November 1826, *N. Wallich in Herb. Wallich 6925/841* (K000848076!; possible isolectotypes G-DC [image!], E00317548!). Other syntype: Myanmar. “Tong Dong” [Thone Taung], 24 November 1826, *N. Wallich in Herb. Wallich 6925/841* (K001126247!).

Description. (Fig. 14). Subshrub to 2.5(3.0) m tall, stout, not rooting at the nodes; young stem round or indistinctly four-angled; leaf petioles 10–20 mm long, blades 40–140 × 40–80 mm long, ovate (rarely oblong) and entire, dark green above and gray below, both sides hirsute especially below (some individuals probably growing under more humid conditions as well as cultivated indoors may be sparsely pubescent resembling *A. acuminata*); inflorescence long, up to 120 cm, stout, bract 3.5–4.0 mm long; bracteoles 3.0–3.3 mm long; perianth (5.0–5.5)6.0–7.5 mm long, green or pale outside and rose or pink inside, tip often violet; stamens 5 with pink filaments, anthers 0.9–1.1 mm long oblong; pseudostaminodes 1.5–3.5 mm long, white or pink, fimbriate or not; style with stigma (2.5)3.0–4.0 mm long (slightly less than perianth or equalling the perianth); fruit (without style) (2.0)2.3–2.7 mm long.

Taxonomic notes. The variety *Achyranthes fruticosa* var. *pubescens* Moq. was described from East Mexico (Moquin-Tandon 1849), and the data about its native status in the Old World, including African references (Wunderlin and Hansen 2011), are erroneous. Two further combinations under *A. aspera* were made: *A. aspera* var. *pubescens* (Moq.) M.Gómez, Noc. Bot. Sist.: 58 (1893), and the isonymic *A. aspera* var. *pubescens* (Moq.) C.C.Towns., Kew Bull. 29: 473 (1974). The plants growing in Central America have different reproductive characters compared with *A. porphyrostachya* (e.g., Sánchez-Del Pino et al. 2013, as *A. aspera* var. *pubescens*). This varietal name cannot be applied to the plants in the Old World, although it was widely used for the perennial African and Arabian populations of *Achyranthes*. A lectotype of *A. fruticosa* var. *pubescens* was selected by Townsend (1974) [Tampico de Tamaulipas, 1827, *Berlandier 79-104-105* (G00236794 – image!], and a later lectotypification with the same specimen undertaken by Hassan et al. (2023) is superfluous.

A plant of *A. porphyrostachya* cultivated by APS indoors (seeds originating from Manyara Region, Tanzania) has much more glabrous leaves (Fig. 14B) compared to the voucher specimen located in MW.

Nomenclatural notes. The original spelling “porphyristachya” (Moquin-Tandon 1849) is a correctable error under Art. 60.10. The species name was established on the basis of Wallich’s collections from present-day Myanmar. Moquin-Tandon studied specimens in the personal herbarium of Candolle, which were indicated as “v. s. in h. DC.” in the protologue, and other specimens with the Wallich distribution number, which was cited in the protologue

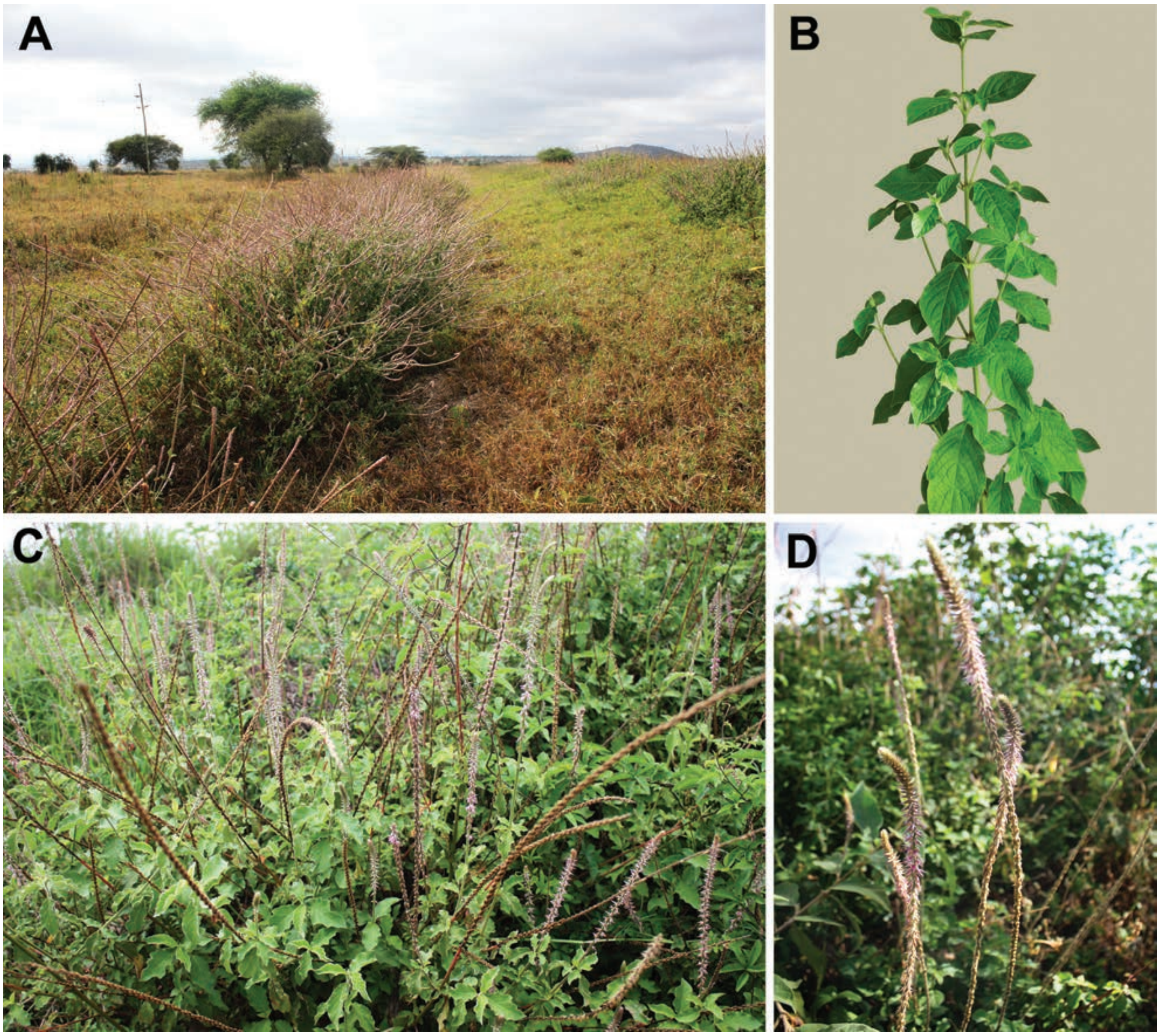

Figure 14. *Achyranthes porphyrostachya* **A** population in the open semi-disturbed habitat in Arusha Region, Tanzania **B** an indoor cultivated plant in vegetative stage (grown from seeds from Manyara Region, Tanzania) **C** plant in blooming stage (Kilimanjaro Region, Tanzania) **D** fragment of the inflorescences (Kilimanjaro Region, Tanzania). Photographer: A. Sukhorukov.

(“Wall.! list n. 6925”). The original material of *Achyranthes porphyrostachya* was collected for and subsequently distributed on behalf of the Honourable East India Company (E.I.C.).

A.P. de Candolle obtained a large set of Wallich specimens (34 packages: Krieger 2023) in 1830, when his son Alphonse visited Wallich in London and negotiated herbarium distribution and taxonomic treatments for himself and his father (Candolle and Radcliffe-Smith 1981). The specimens of *Achyranthes* were dispatched to Candolle prior to their regular distribution from the E.I.C., which was ready in 1832 (Wallich 1832). Labels for the specimens received in 1830 by Candolle had been copied and numbered separately, and were renumbered for the regular distribution later (cf. a note on the double numeration in Compositae: Wallich 1831). On the labels of *A. porphyrostachya*, the Candolle number is 841 (K001126247, G00688936, G00688937), whereas its corresponding Wallich number is 6925 (E00317548, K001126247, K000848076).

The labels of *Wallich 6925* say it is from “Tong Dong 1826”, or Thone Taung Village, Mandalay Region, Myanmar. The Candolle labels are more detailed and informative, and apparently preserve the original field information which was generalised when distribution numbers were formed. Two specimens at G-DC (G00688936, G00688937) have identical labels reading “towards the Hills, 23 Nov. 1826”, indicating the route between the Irawadi River at Sagaing, from which Wallich proceeded towards the Shan Hills on 22 November, being the next day on the way to the Hills “through villages, rice and cotton fields” (Krieger 2023: 178). One specimen at Kew, which also bears a regular distribution label, was originally labelled as “road to Tong Dong” and “Tong Dong, 24 Nov.”, seemingly indicating the arrival at the hilly area of Thone Taung (Candolle and Radcliffe-Smith 1981). This specimen was kept in the Wallich herbarium until its transfer to the Linnean Society in 1857 (Candolle and Radcliffe-Smith 1981), and therefore was not seen by Moquin-Tandon. Two more specimens examined (E00317548, K000848076) bear the standard lithographed distribution labels without further detailed information. The Kew specimen (K000848076) belongs to the set acquired by J.D. Hooker from the possessions of the E.I.C., which was examined in entirety by Moquin-Tandon.

The original material of *A. porphyrostachya* includes two specimens in the personal herbarium of Candolle, which belong to the Wallich collection and bear the species name on original labels with Candolle numbers (examined by Moquin-Tandon according to the protologue), and one specimen in the personal herbarium of Hooker, which was labelled with a lithographed distribution label and annotated by Moquin-Tandon. The latter specimen was directly indicated in the protologue by its distribution number and therefore has precedence in lectotypification. This specimen is formally designated as lectotype here. The two specimens at G-DC and a specimen at E are similar in their appearance and may be treated as isolectotypes.

Achyranthes aspera f. *suffruticosa* Fiori as lectotypified here is a more glabrous form of *A. porphyrostachya*. Another specimen of the original material (Hamasen: Ghinda, 960 m a.s.l., 26 January 1909, *A. Fiori 954*, FT001027! as *A. aspera* var. *argentea* f. *suffruticosa*) is referable to *A. annua*.

Habitat. Various disturbed areas, especially near roadsides, in disturbed savanna communities and bush thickets, mostly in the arid and semi-arid regions of Africa, S and SW Asia at elevations of (0)500–2700 m a.s.l. Common in the open ± disturbed highland vegetation types in Tanzania (APS, pers. obs.). A common appearance of *A. aspera* in the mountain steppe-like vegetation in Rwanda, as reported by Mildbraed (1911), probably also belongs to *A. porphyrostachya*. The species is not eaten by livestock according to herbarium collectors.

Distribution. (Fig. 15; see also Appendix 1). **Africa**: Angola, Benin, Botswana, Burundi, Cameroon, Cape Verde, Chad, Djibouti, DR Congo, Egypt, Eritrea, Eswatini, Ethiopia, Lesotho, Malawi, Mali, Mozambique, Namibia, Rwanda, Senegal, Somalia, South Africa, South Sudan, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

Arabian Peninsula: Oman, Saudi Arabia, Yemen.

General distribution. Africa, South-West Asia and Indian subcontinent (see also full list of specimens from Asia in Appendix 1).

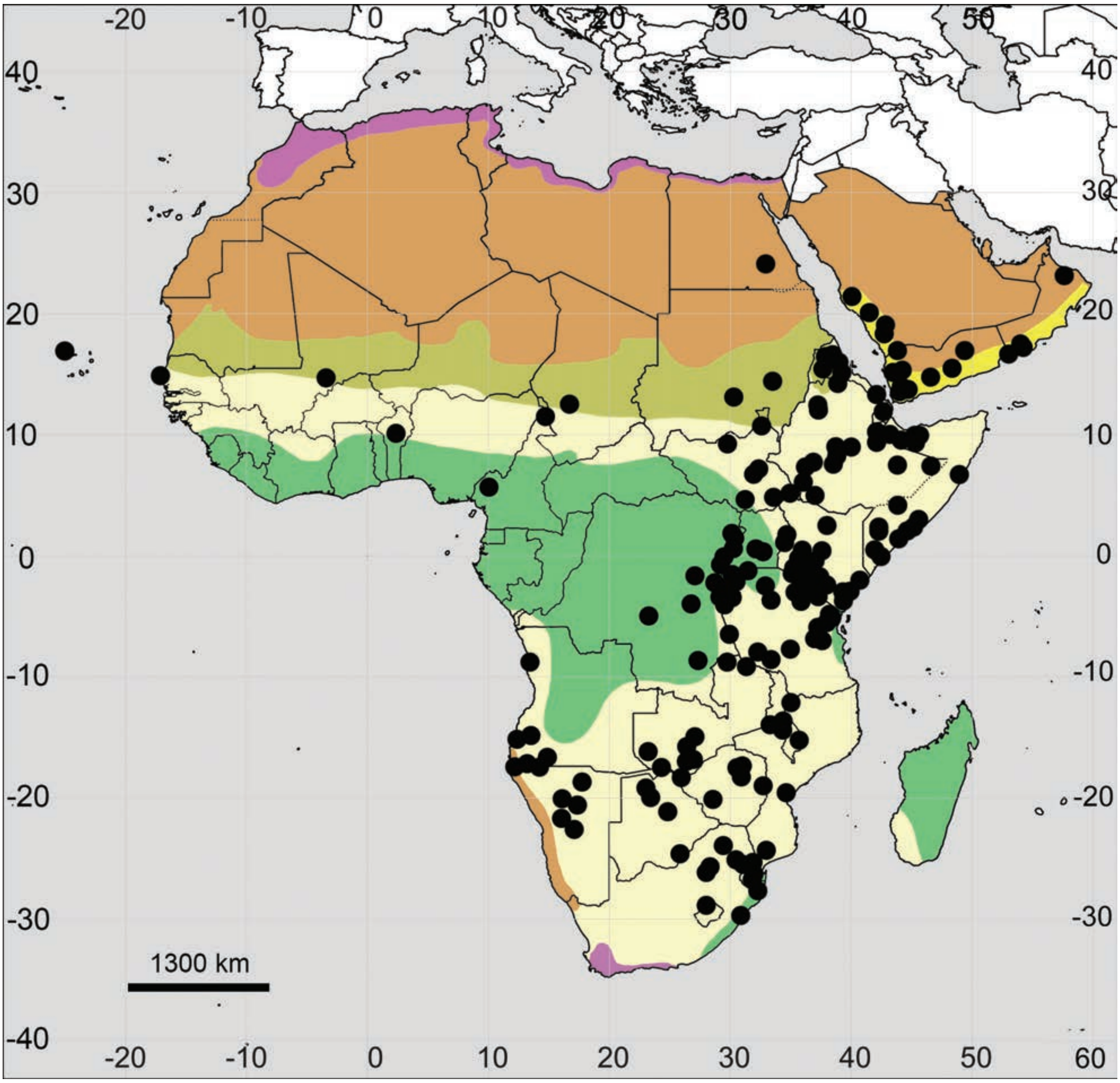

Figure 15. Distribution map of *Achyranthes porphyrostachya*.

Achyranthes seychellensis **Sukhor., sp. nov.**
urn:lsid:ipni.org:names:77353796-1

Holotype. Seychelles, Farquhar Atoll, coconut plantation, 18 August 1984, *G. Ogureeva 608* (MW0586306!, isotype LE00019370!).

Description. (Fig. 16). Annual herb up to 1.5 m tall; stem stout, basally ± roundish, four-angled in the inflorescence; leaf petioles 10–25 mm long, blades 80–120 × 30–60 mm, cuneate, tip shortly acuminate, green above and pale green below, slightly pubescent on veins; inflorescence up to 25 cm long with hirsute axis; bract 3.5–4.0 mm long; bracteoles 3.2–4.0 mm long; perianth 4.5–5.5 mm long, ± equal, deep rose or purple inside; stamens 5, anthers 0.75–1.0 mm long; pseudostaminodes 1.25–2.0 mm long, brownish or white when dry, fimbriate; style with stigma 2.2–2.7 mm long; fruit (without style) ± 2.0 mm long.

Figure 16. Holotype of *Achyranthes seychellensis* Sukhor., sp. nov. (Seychelles, Farquhar Atoll, coconut plantation, 18 Aug 1984, *G. Ogureeva 608*, MW0586306).

Habitat. Calcareous and rocky areas at elevations of 0–200 m a.s.l. It can be a common weed in coconut plantations.

Flowering at fruiting. Around the year.

Additional specimens seen. Seychelles: Sèche Island, 23 Jan 1938, *Ves 6149* (K); St. Pierre Island, Oct 1960, *C.J. Pigeott s.n.* (K); Aride Island, Feb 1983, *F. Friedmann 4469* (P00804851) & Apr 1987, *F. Friedmann 5455* (P00804847); Bird Island, 28 Sep 1952, *E.S. Brown s.n*. (BM); Cousin Island, 25 Jan 1970, *F.R. Fosberg 52173* (K); Fouquet Island, 5 Apr 1976, *D.R. Stoddart 7148* (K); Farquhar Atoll (South), 2 Oct 1967, *Gwynne & Wood 1189* (K); Farquhar Atoll (North), 19 Sep 1968, *D.R. Stoddart 1376* (K); Aride Island, Jul 1975, *Warman 23* (K); Rémire [Eagle] Island, 25 Oct 1976, *S.A. Robertson 2319* (K); Bird Island, Mar 1976, *D.R. Stoddart 7079* (K); Denis Island, 10 Dec 1977, *D.R. Stoddart 8086* (K); Platte Island, 26 Feb 1980, *S.A. Robertson 3021* (K); Poivre Island, 6 Aug 1984, *L. Averyanov & al. s.n*. (LE, MHA); Farquhar Atoll, 16 Aug 1984, *L. Averyanov & al. 580* (LE).

Mauritius: Chagos Archipelago, Diego Garcia Atoll, East Island, 26 Jul 1967, *D.R. Stoddart 875* (K); Diego Garcia, near north coast, 30 Mar 1971, *A.M. Hutson 15* (BM); Sea Cow Island, 21 Feb 1975, *M.J.D. Hirons 50* (K).

Relationship. Friedmann (1994) reported three varieties of *A. aspera*: var. *aspera*, var. *velutina*, and var. *fruticosa* from the Seychelles. The specimens seen were identified as var. *aspera* or var. *velutina*. From *A. aspera*, the new species differs by longer leaf blades (80–120 × 30–60 mm vs. 15–110 × 20–80 mm), and longer anthers (0.75–1.0 mm vs. 0.4–0.6 mm) and styles (2.2–2.7 mm vs. 1.0–1.1 mm). The true *A. velutina* Hook. & Arn. from the Pacific (Samoa, Tahiti, Tuamotu etc.) is a hirsute shrub with longer (ca. 7 mm long) perianths, but some other characters, i.e. length of anthers and styles are similar. Several specimens from the Aldabra Islands identified as 'var. *fruticosa'* represent plant fragments with a woody base and need further evalution.

General distribution. Endemic to the Seychelles and Chagos Archipelago.

***Achyranthes sicula* (L.) All., Auct. Syn. Meth. Stirp. Hort. Regii Taur.: 41 (1773).**

≡ *Achyranthes aspera* var. *sicula* L., Sp. Pl. 1: 204 (1753).
≡ *Achyranthes argentea* Lam., Encycl. 1(2): 545 (1785), nom. illeg. superfl.
≡ *Cadelaria sicula* (L.) Raf., Fl. Tellur. 3: 39 (1837).
≡ *Cadelaria argentea* Raf., Autik. Bot.: 154 (1840), nom. illeg. superfl.
≡ *Achyranthes aspera* var. *argentea* Eggers, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1876: 140 (1877), nom. illeg. superfl.; Boiss., Fl. Orient. 4: 994 (1879), isonym; C.B.Clarke in Th.-Dyer, Fl. Trop. Afr. 6(1): 63 (1909), isonym.
– *Achyranthes aspera* [var. *sicula*] f. *albida* Maire & Weiller, Fl. Afr. Nord. 8: 219 (1962), nom. inval. descr. gall.

Lectotype (designated by Townsend 1994). "Amaranthus radice perpetua" in Herb. Boccone (P).

Description. (Fig. 17). Annual (probably also short-lived perennial), 30–200 cm tall; stem stout, four-angled; leaves shortly petiolate (petioles 5.0–15.0 mm long), blades 25–100 × 15–40 mm, ovate, base broadly cuneate or truncate, tip attenuate, bicolored, green above and white silvery below; inflorescence up to 30 cm long; bract 3.0–4.0 mm long; bracteoles 3.0–4.0 mm long, slightly

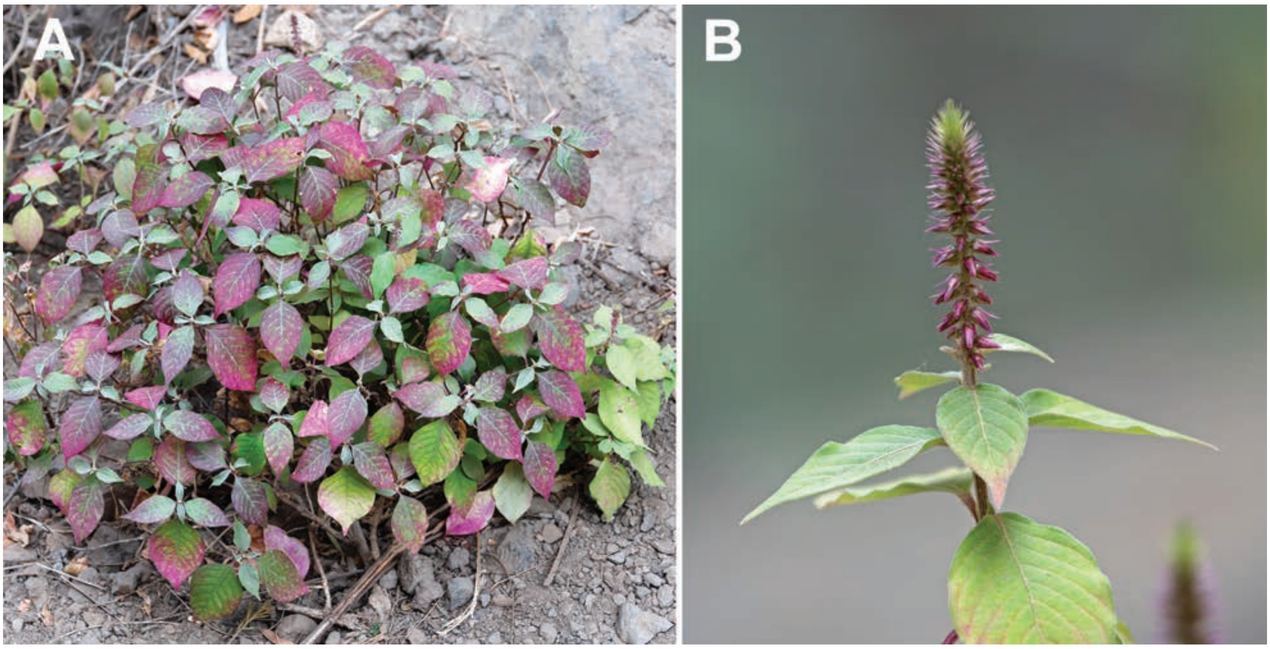

Figure 17. *Achyranthes sicula* **A** plant in vegetative stage (Santa Cruz de Tenerife, Canary Islands) **B** close-up of the inflorescence (Santa Cruz de Tenerife, Canary Islands). Photographer: F. Bednár.

reflexed, green or usually pink; perianth (3.5)4.0–5.0 mm long, segments ± equal, white, pinkish or green and then turning gray; stamens 5 with white or mauve filaments, anthers 0.5–0.8 mm long; pseudostaminodes 0.5–1.2 mm long, fimbriate, white or pink, style with stigma (1.2)1.5–1.8 mm long; fruit (without style) 1.7–2.0 mm long.

Taxonomic note. Only a limited number of specimens were collected with subterranean parts, and the species seems to be annual despite literature references where it is considered as a perennial or suffruticose herb (e.g., Maire 1962, as *A. aspera*; Zohary 1966, as var. *sicula*).

Nomenclatural notes. Linnaeus (1753) validly published *Achyranthes aspera* var. *sicula* without a description or diagnosis but with a citation of "Amaranthus siculus spicatus. *Bocc. sic. 16. t. 9. Pluk. phyt. 260. f. 2*". This pre-Linnaean polynomial is not diagnostic because its only descriptive word, "spicatus", is part of the polynomials similarly cited under another variety of this species, var. *indica*. For this reason, a validating description of the Linnaean variety is one of the descriptions provided by Boccone (1674) and Plukenet (1691), which were referred to in the protologue. Both descriptions are also accompanied by illustrations, directly cited by Linnaeus (1753), which are part of the original material of the variety. Another part is the specimens associated with the descriptions, namely the herbarium collection of L. Plukenet at BM (Herb. Sloane!) and that of P. Boccone at P. Townsend (1994: 21) accepted Boccone (1674) as a source for the validating description and designated the corresponding specimen "Amaranthus radice perpetua" in Herb. Boccone at P. Although Townsend (1994) made it clear that he designated a herbarium specimen at P, Iamonico (2014) doubted his citation and designated another specimen in Herb. Linnaeus (287.1) at LINN as a new lectotype. The latter specimen is not linked to the validating description of the variety (which is not Linnaean), and therefore Iamonico's choice is not effective. The lectotype designated by Townsend is technically correct and should be accepted.

When publishing his *A. argentea*, Lamarck (1785) included a full and direct reference to the pre-Linnaean polynomial in its protologue, which was the sole basis of *A aspera* var. *sicula*. Under Art. 52.3, Lamarck's species name is an illegitimate replacement of *A. sicula* (L.) All. The lectotype of *A. argentea* designated by Raus (2022), a specimen from cultivation in the Botanical Garden in Paris and kept at SEV, therefore has no standing.

Habitat. Calcareous soils, rocks, disturbed areas at elevations of 0–1500 m a.s.l.

Distribution. (Fig. 18; see also Appendix 1). **Africa**: Algeria, Cape Verde, Egypt, Morocco, Spain (Canary Islands), Tunisia, and probably Libya (no specimens seen).

General distribution. Mediterranean basin: Algeria, Egypt, Malta, Morocco, Tunisia, British Overseas Territory [Gibraltar], Greece (very rare: Raus 2022), Israel/Palestine, Lebanon, Portugal (Azores and Madeira), Syria, southern part of Italy, Spain. The records of *A. aspera* from Jordan (Taifour and El-Oqlah 2017) probably belong to *A. sicula*.

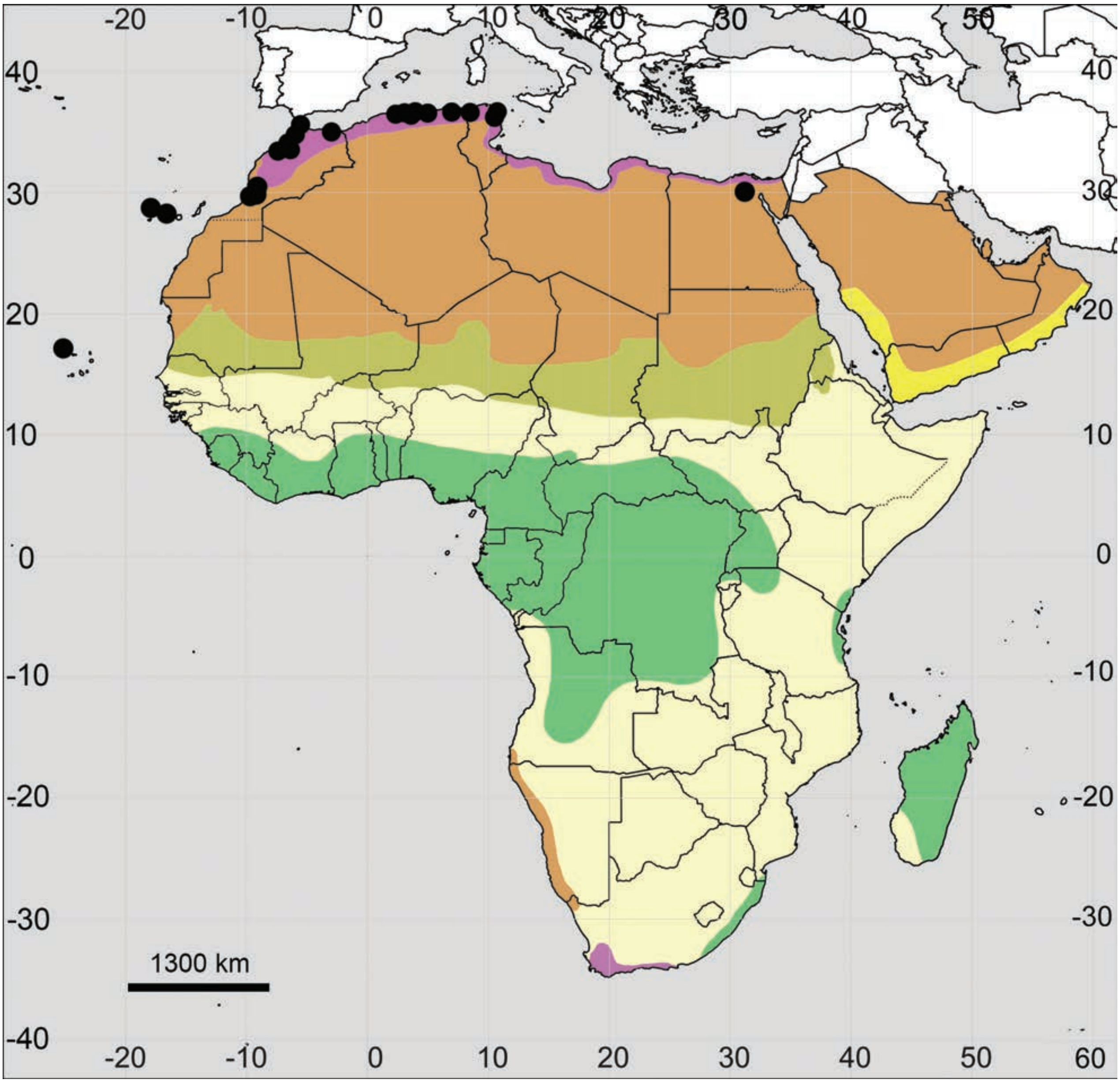

Figure 18. Distribution map of *Achyranthes sicula*.

Notes on other species growing in the regions under study

Two other *Achyranthes* s.str. in Africa have been accepted because of their unique characters: *A. fasciculata* (e.g., Townsend 1985) and *A. talbotii* (Cavaco 1962; Townsend and Darbyshire 2004). The first species is a mountainous scandent shrub with fasciculate inflorescences. *Achyranthes talbotii* is a perennial rheophytic herb frequently rooting at lower nodes, with lanceolate or narrowly oblong leaves. Below we provide currently known localities and distribution maps for both species.

Achyranthes fasciculata **(Suess.) C.C.Towns., Kew Bull. 34(3): 424 (1980).**

≡ *Pandiaka fasciculata* Suess., Kew Bull. 4: 477 (1949).

Holotype. Tanganyika Territory [Tanzania, Manyara Region], Mbulu distr., SE slopes of Mt. Hanang, Nangwa, 8000 ft, 6 February 1946, *P.J. Greenway 7620* (K000243725!, isotype BM!).

Habitat. Upland grassland and mist forests at elevatios 1800–2800 m a.s.l.

Distribution. (Fig. 19). **Tanzania** (selected): Ngorongoro crater, 8000 ft, 12 Sep 1932, *B.D. Burtt 4308* (K); Ngorongoro rest camp, 6000 ft, 3 Apr 1941, *P.R.O. Balley 2232* (K); Ngorongoro crater, 7400 ft, 13 Jul 1966, *P.J. Greenway & K. Kanuri 1256662* (BR0000013708887, K); Empakaai crater, 2150 m a.s.l., 10 Aug 1972, *G.W. Frame 27* (BR0000013708870, K); Masai distr., Ngorongoro crater, 2350 m a.s.l., 15 Sep 1977, *J. Raynal 19052* (K, WAG01404450); Arusha Region, Monduli distr., Ketumbeine Forest Reserve, 2330 m a.s.l., 2 Apr 2000, *R.E. Gereau & al. 6428* (CM, MO).

General distribution. Only known from Tanzania. Records from Kenya are also possible.

Achyranthes talbotii **Hutch. & Dalziel, Fl. W. Tr. Afr.: 127 (1927).**

Holotype. Nigeria, [probably Osun State] Oran district, 1911–1912, *P.A. Talbot s.n*. (K000243719!).

Habitat. Forests and along streams, often on rocky or volcanic substrates at elevations of 0–1000 m a.s.l. as in *J.P.M. Brenan 9497* (in many herbaria), who adds: “Lava rocks by cataracts above water level, frequent; perennial herb with woody base, ± cespitose stem, purplish-green; leaves papery, dull green ± purple tinged; inflorescence erect, pale green”. *M. Cheek et al. 10401* (K000051090 & WAG1404466) also added: “Lowland evergreen forest around series of waterfalls in river gorge; rheophyte erect herb 15–45 cm tall, rooting in rock crevices and on the surface”.

Distribution. (Fig. 20). **Cameroon**: [West Region] Toké, 20 Mar 1948, *J.P.M. Brenan 9497* (BM, BR0000013708900, K000025614, M, P06651712); [Littoral Region] Loum, 20 Dec 1957, *H.C.D. de Wit 392* (WAG0185720); [Littoral Region] 35 km E of Yabassi, 9 Jan 1972, *R. Letouzey 10938* (K, P06651714, YA); Southwest Region, Mt. Cameroon, 350 m a.s.l., 20 Oct 1993, *M. Cheek & al. 5013* (BR0000005004102, K000518867, WAG0255392); Southwest Region, Mokoko,

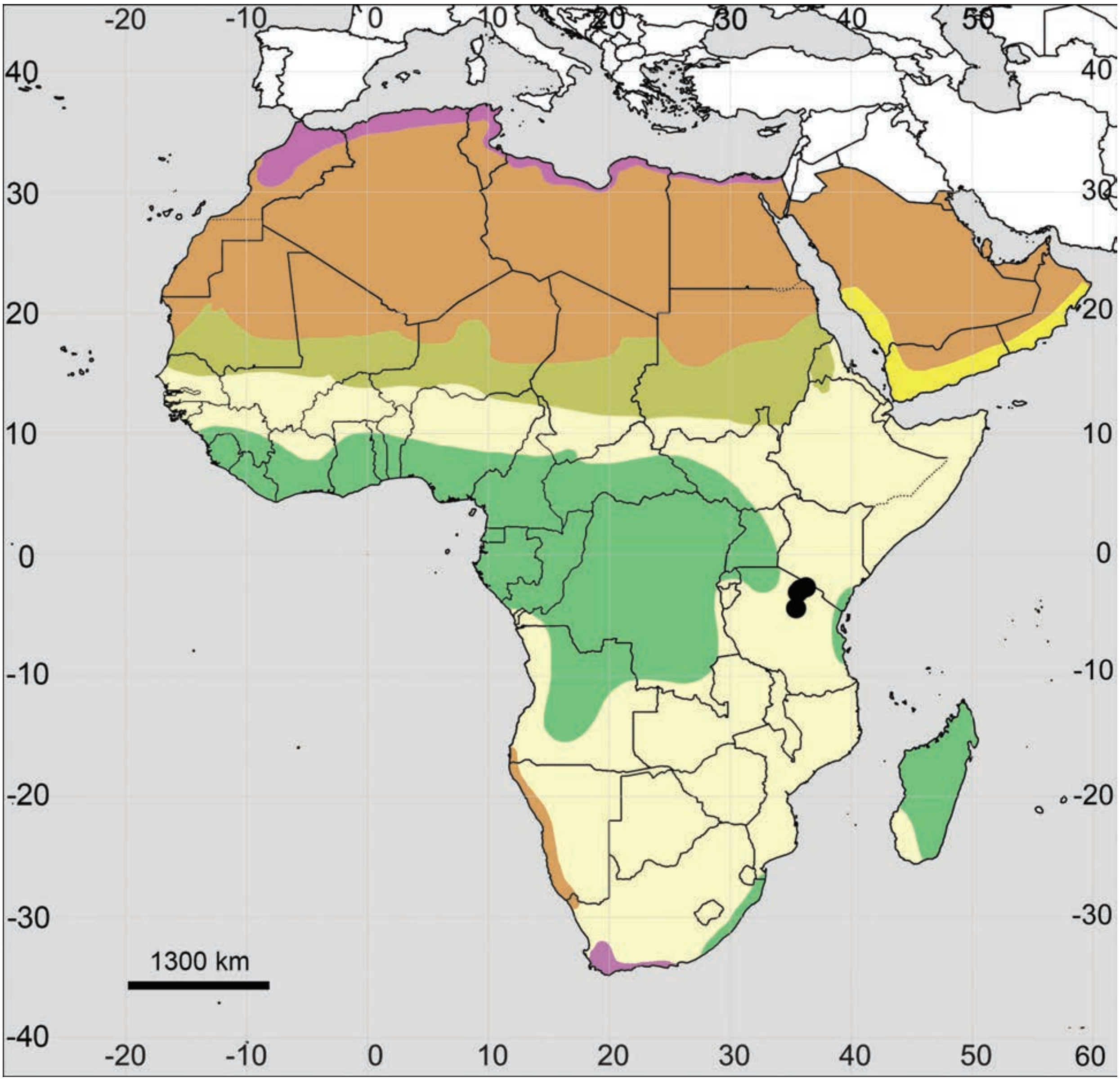

Figure 19. Distribution map of *Achyranthes fasciculata*.

280 m a.s.l., 26 May 1994, *D.W. Thomas 10167* (K000875887); Southwest Region, Mount Cameroon, Bomana, 400 m a.s.l., 20 Oct 1993, *N. Ndam 742* (K000518868); Kupe-Muanenguba Division, Baseng, 750 m a.s.l., 16 Dec 1999, *M. Cheek & al. 10401* (K000051090, WAG1404466); [Southwest Region] Kumba to Loum, 26 Jan 1986, *H. Breyne 5062* (BR0000013709051, YA); Northwest Region, Bamenda, 620 m a.s.l., 14 Nov 2000, *B.J. Pollard 483* (K001422626); Southwest Region, Mbu River, 27 Nov 2000, *M. Cheek & al. 10635* (K001422627, P00940016); Southwest Region, Nyandong, 400 m a.s.l., 27 Mar 2003, *M. Cheek & al. 11466* (K001518827).

Note. Two additional records kept at YA (bank of Nkam River, near Sake, 3 km southwest of Nkondjok, 4°77'N, 10°17'E, 07 Jan 1972, *R. Letouzey 11163*; Kombon at the bank of Kombon River, 4°59'N, 9°26'E, 23 Mar 2011, *F. Kuetegue 316*) and cited by Kuetegue et al. (2019) were also added to the Fig. 20.

Liberia: 30 miles W of Bomi Hills, bank of Lofa River, 12 Nov 1969, *J.W.A. Jansen 1486* (BR0000013833961, K);

Nigeria: see holotype.

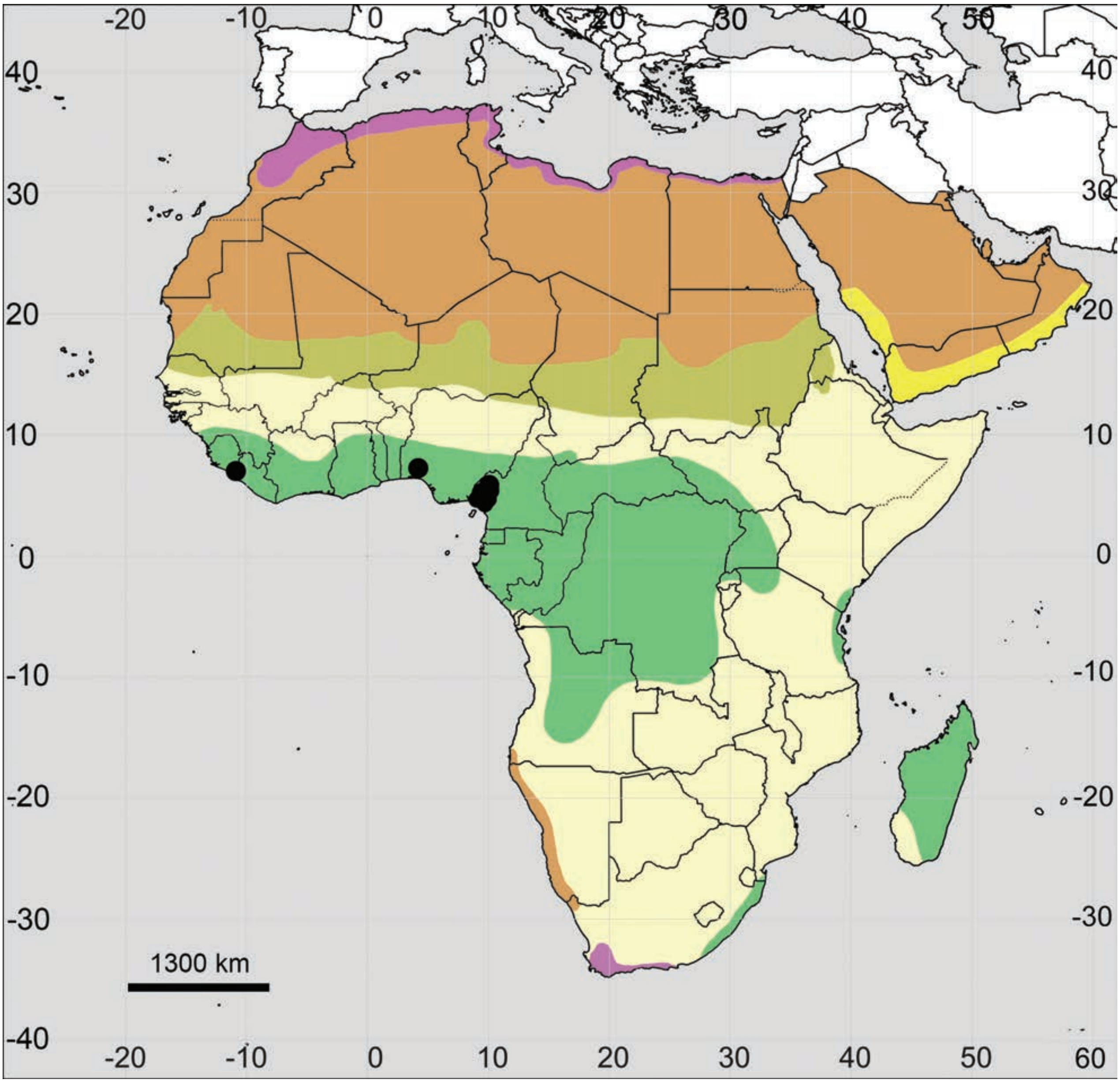

Figure 20. Distribution map of *Achyranthes talbotii*.

General distribution. Tropical West Africa. Probably present at least in the countries located between Liberia and Nigeria (Benin, Ghana, Ivory Coast, and Togo) with a similar climate and vegetation. A specimen from Nigeria (Ogoja Prov., Ikom distr., 17 Dec 1950, *R.W.J. Keay 26284*, K000243718!) with wider oblong leaves was noted by Suessenguth as *Achyranthes talbotii* var. *ogojensis* Suess. A similar specimen was also collected in Cameroon (Mount Cameroon, 1830 m a.s.l., 4 Feb 1962, *F.J. Breteler & al. 202*, K000025642!) with a short annotation: “Herb up to 1 m high, stems obscurely quadrangular, green, above the nodes dark red, leaves dark green, paler beneath, frequent”. The taxonomic status of such plants has not been evaluated so far (records of both specimens are not mapped here).

Note. A report of *A. talbotii* from Madagascar and Europa Islands (Cavaco 1962) is unlikely because of different habitats (open grassy vegetation) and a location very remote from the West Tropical Africa. According to Jean Hivert (pers. comm.), the plants from the French Overseas territories belong to a distinct species.

Nomina incertae sedis vel excludenda

Many names in *Achyranthes* have not been resolved yet owing to the absence of their type material in major herbaria. Some authentic specimens of unresolved names may be dispersed through many herbaria, e.g. those of Burman f. (Wijnands 1992), that makes them difficult to trace when the type material was not recognised and remains unavailable electronically. Among species described from Africa, little is known about *A. frumentacea* Burm.f., *A. pedicellata* Lopr., *A. rubrolutea* Lopr., *A. viridis* Lopr., and *A. winteri* Schinz. They are shortly discussed below.

Achyranthes frumentacea Burm.f., Fl. Ind. [N.L. Burman] Prodr. Fl. Cap.: 7 (1768).

The protologue in “Prodromus Florae Capensis” is very short and incomplete (Burman 1768), and the most informative phrase is “spicis gracilibus frumentaceis” [spikes subtile, grain-like]. The frumentaceous spikes may refer to the small grain-like diaspores that are present, e.g., in *Achyranthes annua*, a reinstated species also known in South Africa (present paper). Nevertheless, this assumption cannot be confirmed at present, and there are no specimens named as *A. frumentacea* in G-PREL (Nicolas Fumeaux, pers. comm.), the major Burman collection in Europe, as well as in Bibliothèque de l’Institut de France (Sabrina Castandet-Le Bris, pers. comm.). This forgotten name was only mentioned in van Hall (1830) who doubted that the plant described is referable to *Achyranthes*.

Achyranthes pedicellata Lopr., Bot. Jahrb. Syst. 27(1–2): 56 (1899).

Lopriore (1899) described this Central African species in the following way: subshrubby; leaves short (up to 3 cm long); bracteoles hairy; flowers very shortly pedicellate; perianth hairy. The description does not match any *Achyranthes* in a traditional sense. Baker and Clarke (1909) and Cavaco (1962) noted that this name may belong to *Pandiaka*, although Klopper et al. (2006) left it under *Achyranthes* as insufficiently known species.

Achyranthes rubrolutea Lopr., Bot. Jahrb. Syst. 27(1–2): 57 (1899). [“*rubro-lutea*”]

This species has been transferred to the genus *Pandiaka* (Townsend 1980a, as *P. rubrolutea* (Lopr.) C.C.Towns.) based on the syntypes seen at Z. Therefore, we exclude this species from *Achyranthes*.

Achyranthes viridis Lopr., Bot. Jahrb. Syst. 27(1–2): 56 (1899).

This species described by Lopriore (1899) from Tanzania is characterized by short (up to 2.5 cm) internodes and capitate inflorescences up to 1 cm long consisting of densely arranged flowers with glabrous perianth segments. Cavaco (1962) thought that *A. viridis* more likely belongs to *A. aspera* var. *sicula*, but the short internodes and capitate inflorescences are not characteristic of any *Achyranthes* and may refer to *Alternanthera*, although Klopper et al. (2006) left it under *Achyranthes* as insufficiently known species.

Achyranthes winteri Schinz ex Peter, Repert. Spec. Nov. Regni Veg., Beiheft 40(2,3): 240 (1938), nom. inval. Schinz (in Peter 1938) briefly described this new species (in German) as having ovate leaves and solitary flowers with fimbriae. Such characters are not informative, and the species is absent in a diagnostic key provided by Peter (1938). The key includes *Achyranthes* in a traditional sense as well as the species with a pubescent perianth (not belonging to *Achyranthes* s.str.) and *Centrostachys aquatica*. Klopper et al. (2006) consider it as an insufficiently known species, probably based on Townsend (1985) who noted that the original specimens cited in the protologue (Peter 1938) were probably destroyed in Berlin during the WW2.

Discussion

Species richness and geographical pattern of *Achyranthes* (excluding *Achyropsis*) in Africa and Arabia

The specific diversity of *Achyranthes* in Africa is not as small as previously thought. Instead of 3–4 species reported, we accept 10 species that are morphologically well-distinguished (*Achyropsis* is not included in this number, but if this genus is synonymized with *Achyranthes*, the number of species will increase to 16). Almost all species have large ranges covering many regions of the continent except *A. fasciculata* that seems to be restricted to Tanzania (with possible records in Kenya) and *A. talbotii* Hutch. & Dalziel that possesses a relatively small range in West Tropical Africa (Cameroon, Liberia, and Nigeria). *Achyranthes mauritiana* and *A. seychellensis* are restricted to the islands of the Western Indian Ocean.

The optimal ecological conditions in some parts of Africa and Arabia enabled the evolution of *Achyranthes*, and its spiny bracteoles attaching the seed-containing diaspore to animals or humans promoted ± long-distance epizoochorous dispersal (Bullock and Primack 1977). Additionally, the diaspores can also be dispersed by water (nautochory: Müller-Schneider 1983), e.g. in riverine areas for *A. acuminata*. Each species in the former *A. aspera* aggregate, despite extensive distribution, has different geographical patterns and ecology.

Mediterranean zone (mauve color in the distribution maps)

It stretches along the Mediterranean coast in North Africa (Algeria, Egypt, Libya, Morocco, and Tunisia) as well as a small strip near the Cape Peninsula in South Africa. Only *Achyranthes sicula* is found in this small zone in North Africa, where it grows on rocky substrates, in woodlands and sclerophyllous environments, or as a weedy plant with summer dormancy. Based on the general distribution of this species along the Mediterranean Sea (Tutin 1964; Zohary 1966; Jalas and Suominen 1980) with radiations into Macaronesia, it is supposed that *A. sicula* is a true subtropical species native to the Mediterranean basin. *Achyranthes annua* reaches the Mediterranean zone, but it seems to be rare in North Africa based on its scattered records and is more frequently found in the Cape Peninsula. No specimens of *A. aspera* s.str. were found from North Africa in the herbaria visited despite some recent reports (Greuter et al. 1984; Iamonico 2015; Iamonico and El Mokni in Raab-Straube and Raus 2018), with the exception of an old and unconfirmed record from Egypt, which is more likely to have been collected in the southern part of the country.

Deserts (brown color in the distribution maps)

The Desert zone lies between the Mediterranean and Sahel zones in North Africa and covers almost all parts of the Arabian Peninsula, except small coastal strips. The largest Sahara Desert (including North Saharan woodlands) as well as Namib Desert in south western Africa belong here too. Scattered records of drought-adapted species (e.g., *A. aspera* s.str., *A. porphyrostachya*) are known from this zone, and they are confined to irrigated places or the Nile River valley, e.g. a single old record of *A. porphyrostachya* from Aswan town (K! also cited by Boulos (1995) as *A. aspera* var *pubescens*). In general, no *Achyranthes* species are common in the desert zone.

The Sahel zone (olive-green color in the distribution maps)

This zone with the hot semi-arid climate and mainly flat topography is suitable for drought-adapted *Achyranthes* species such as *A. annua* and *A. porphyrostachya*. Being a shade-loving annual species, *A. annua* is usually found in *Vachellia* bushland or as a weed under the canopy during the wet season; otherwise, it is collected at higher elevation (e.g. the Marrah Mountains, Sudan). Records of the subshrubby *A. porphyrostachya* are more frequent in the eastern part of the Sahel zone in open and semi-shaded disturbed plant communities. *Achyranthes abyssinica* is confined to the eastern part of the Sahel, growing in the mountains at elevations of 1400–2500 m a.s.l., where it has its northern distribution limit.

Grassland and savanna (pale color in the distribution maps)

Various types of grassland and savanna are widespread in eastern and southern Africa with low rainfall and longer dry seasons (Huntley 1982). This zone incorporates all species of the former *A. aspera* aggregate, and they are mostly growing at elevations between 1000–2200 m a.s.l. under different ecological conditions (*A. abyssinica* in various transitional landscapes; *A. acuminata* in shady wet places, mainly near streams; *A. annua* in *Vachellia*–*Commiphora* shrublands; *A. porphyrostachya* in various secondary areas). *Achyranthes aspera* s.str. is a common weed below 500 m a.s.l. (e.g., in the coastal regions of Kenya and Tanzania).

The Sahel, grasslands and savannas are more or less arid zones of Africa where the vegetation is influenced by rainfall. For example, field observations near Balangida Lake (~ 1940 m a.s.l., Manyara Region, Tanzania) show that seed germination of *A. annua* starts in the beginning of the rain season (March), with the plants completing their life cycle by mid-June, before the dry season.

Rainforest zone (jade green color in the distribution maps)

It includes areas of the Atlantic Equatorial coastal forests and Congolian lowland forests with no or very short dry season. Remarkably, only *A. acuminata* is widespread in this zone; all other, mostly drought-adapted species (*A. abyssinica*, *A. porphyrostachya*) are absent or grow at margins of rainforests and savannas (e.g., *A. abyssinica* and *A. porphyrostachya* reaching the western branches of the East African Rift). There are a few records of *A. aspera* s.str. in this area, although we expect it should more frequently occur as a weed.

Arabian Peninsula (brown color for deserts and yellow color for shrublands)

Remarkably, all *Achyranthes* (*A. abyssinica*, *A. annua*, *A. aspera*, *A. porphyrostachya*) were collected near the coastlines and in the mountains in the southernmost part of the peninsula which is characterized by milder climatic conditions connected with seasonal rainfalls and diverse topography (Fleitmann and Matter 2009). The inland territories include extremely dry sandy plains with very low precipitation (Almazroui et al. 2012). Among these species, *A. aspera* seems to always grow in ruderal habitats.

Further perspectives for revealing the diversity of the genus in the World

We have shown that Africa has many more species of *Achyranthes* than was previously believed. In the rest of the World, the exact species number is yet to be evaluated. The Pacific contains several shrubby endangered endemics as those from the Hawaiian Archipelago (John 1979), Norfolk Islands (two species: De Lange and Murray 2001) and the extinct *A. mangarevica* Suess. from the Mangareva Island (Gambier Islands, French Polynesia: Florence 2004). Australia, Asia and the Americas lack a recent revision of the genus.

Besides the *A. aspera* aggregate revised here, the *A. bidentata* group that is distributed across the Asian tropics and subtropics should be reviewed. This species group is represented by rhizomatous herbs.

Conclusion

This first in-depth morphological study of *Achyranthes* detected a remarkable taxonomic diversity of the genus in Africa and Arabia, with new nomenclatural changes, and elaborated ecological and chorological information. The systematics of *Achyranthes* has not been fully understood so far, and both morphological and phylogenetic studies are needed to advance knowledge about the diversification and evolution of this genus worldwide. The African continent represents a major centre of the specific diversity of *Achyranthes*.

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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: APS. Data curation: CB, MK, APS. Formal analysis: APS. Funding acquisition: APS. Investigation: MVN, ANS. Methodology: APS. Project administration: APS. Resources: CB. Software: MK. Supervision: APS. Validation: APS, ANS. Visualization: APS, ANS. Writing - original draft: ANS, CB, APS. Writing - review and editing: MK, ANS, CB, MVN, APS.

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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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Appendix 1

Records of *Achyranthes abyssinica*, *A. acuminata*, *A. annua*, *A. aspera* s.str., *A. porphyrostachya*, and *A. sicula* from Africa and Arabia based on the examined herbarium specimens and identifiable online images. Records of *A. mauritiana* and *A. seychellensis* are given in the main text due to the limited number of collections.

Achyranthes abyssinica Nees

Africa

Angola: [Lunda Norte Prov.] Bumba, Mar 1879, *F. Welwitsch 6552* (K);

Burundi (new records; selected): 7 km of Muramvya, 2200 m a.s.l., 31 Mar 1956, *J. Symoens 2362* (BR0000005352647); [Western Prov.] Bugarama, 2200 m a.s.l., 7 Jan 1966, *J. Lewalle 216* (BR0000013837167); [Bujumbura Rural Prov.] Ijenda, 16 Mar 1966, *J. Lewalle 526* (BR0000013837174); Muramwya Prov., Teza, 2200 m a.s.l., 9 Apr 1979, *M. Reekmans 7782* (BR0000013708597); Muramwya Prov., Teza, 2000 m a.s..l, 15 Feb 1981, *M. Reekmans 9605* (K, WAG1404354); [Bubanza Prov.] Bubanza town, 2 May 1981, 2000 m a.s.l., *M. Reekmans 10047* (K, WAG1404353);

Cameroon (new records; selected): [Northwest Region] Bamenda, 8000 ft, 18 Jan 1928, *F.W.H. Migeod 18128* (BM, K, M); [Northwest Region] Ndu, 6400 ft, 5 Jan 1951, *R.W.J. Keay & T.A. Russell 28439* (K); [Southwest Region] Buea, Dec 1952, *G.K. Akpabla s.n.* (K); [West Region] Djuttitsa, 1800 m a.s.l., 16 Jul 1955, *A. Saxer 192* (K); [Adamawa Region] 10 km S of Ngaoundéré, Oct 1960, *F.J. Breteler 804* (BR0000013834197, K); [West Region] Dschang city, 1300 m a.s.l., 6 Dec 1965, *A. Meurillon 203* (BR0000013709020, K); Adamawa Region, Hosséré Sillé, 20 Oct 1967, *H. Jacques-Félix 8742* (K); Mt Hosséré Vokré, 30 Oct 1967, *H. Jacques-Félix 8480* (BR0000013834135); Mt. Kupe, 20 Jan 1972, *A.J.M. Leeuwenberg 9254* (K); Northwest Region, Nkambé, 4 Nov 1974, 2130 m a.s.l., *R. Letouzey 13143* (K); Northwest Region, Nso, 22 Sep 2005, *L.J.G. van der Maesen 59* (K); Southwest Region, Nyassosso, 19 Jan 1996, *M. Etuge 1597* (K);

DR Congo: see (iso)lectotype of *Achyranthes aspera* f. *rubella*; [North Kivu Prov.] Rutshuru, 24 Dec 1936, *J. Ghesquière 3527* (BR0000016287532, K); [Lualaba Prov.] Lubudi, 1937, *D. Cabu 133* (BR000001378832); [Haut-Katanga Prov.] Lukafu, Jun 1939, *P. Quarré 5472* (BR0000013836931); [South Kivu Prov.] Mulungu, 20 Feb 1940, *F.L. Hendrickx 1391* (K); [Tanganyika Prov.] Marungu Highlands, 2300 m a.s.l., Apr 1944, *L. Dubois 1207* (BM, BR0000013707958, K); Upemba NP, Apr 1948, *G.F. de Witte 3706* (K); [South Kivu Prov.] Tshibinda, 27 Feb 1951, *R. Pierlot 55* (BR0000013836597); [South Kivu Prov.] Kalonge, 2000 m a.s.l., 14 Jul 1954, *H.A. Osmaston 3307* (BM); [North Kivu Prov.] Sake town, 6 Aug 1957, *R. Devred 3878* (BR0000013836177, K, W0333212); [North Kivu Prov.] Rumangabo, 16 Feb 1958, *A. Leonard 632* (BR0000013836573); [South Kivu Prov.] Birava, 5 May 1958, A. *Meurillon 551* (BR0000013835774); [South Kivu Prov.] Kilimbwe, 16 Nov 1977, *T. Yamada 177* (K); North Kivu Prov., Rutshuru, Virunga NP, Jun 2009, *J. Mangambu Mokoso 2054* (BR0000016287709);

Eritrea (new records; selected): Bel'ta [Mt.] 1800 m a.s.l., 4 Feb 1893, A. *Terracciano & A. Pappi 952* (FT); [Anseba Region] Gekeb [Subregion], 7 Feb

1893, A. *Terracciano & A. Pappi 1900* (FT); [Debub Region] Urug valley, 22 Mar 1893, *A. Pappi 3337* (FT); [Maekel Region] Az-Nefas, 2 Feb 1902, *A. Pappi 3593* (BR0000016286566, FT, W0333250); [Maekel Region] Ad Rassi, 28 Apr 1902, *A. Pappi 4969* (FT); [Debub Region] Sala Daro, 7 Oct 1902, *A. Pappi 2322* (FT); [Northern Red Sea Region] Comaile valley, 4 Mar 1903, *A. Pappi 5923* (FT); Adi Ugri [Mendefera town], 12 Oct 1903, *A. Pappi 64* (FT); nr Asmara, 7600 ft, 22 Aug 1954, *J.W. Colville 6* (FT, K); nr Asmara, 20 Sep 1956, *C.F. Hemming 1050* (BM, K);

Ethiopia (selected): see neotype; Amhara Region, Dembiya, 26 Sep 1909, *G. Caramelli 2221* (FT); Addis Ababa, Dec 1911, *E.A. Mearns 22* (BR0000016286559); [Amhara Region] Gondar, 3 Jun 1915, *R.E. Massey 42* (K); [nr Tana Lake] Zege Peninsula, 14 Feb 1937, *R. Pichi-Sermolli 1442* (FT); Qounzela [Consuela] town, 23 Feb 1937, *R. Pichi-Sermolli 1444* (FT); [Amhara Region] nr Debre Tabor vill., 12 Mar 1937, *R. Pichi-Sermolli 1439* (FT); [Afar Region] Afrera [Lake], 13 Nov 1937, *A. Vatova 571* (FT); [Amhara Region] Dessie, 10 Aug 1946, *G.P. Hall s.n.* (K); nr Tana Lake, 9 Sep 1953, *anonymus 39* (K); Addis Ababa, 8000 ft, 26 Nov 1954, *H.F. Mooney 6400* (FT, K); French Somalia [Somali Region], Gode, 800 m a.s.l., Mar 1956, *E. Chedeville 1548* (FT); [Somali Region] Mulu town, Sep 1956, *H.R.D. Sanford 65* (FT); [Oromia Region] Dembidolo, 6300 ft, 2 Mar 1957, *H.F. Mooney 6860* (K); [Amhara Region] Wof Washa Forest, 9000 ft, 24 Mar 1957, *H.F. Mooney 6995* (K); [Amhara Region] Gojjam, Choqa Mt., 10000 ft, 6 Aug 1957, *I.M. Evans 472* (K); 35 km W of Addis Ababa, 2400 m a.s.l., 23 Sep 1957, *H. Smeda 566* (FT); [Oromia Region] Alamaya, 4 Apr 1958, *Agriculture College Team B-3* (K); [Oromia Region] between Metu & Gore, 5000 ft, 6 Apr 1958, *F. Piffard 114* (K); [nr Addis Ababa city] Entoto [Mt.], 2500 m a.s.l., 1960, *K. Hildebrandt 45* (WU); [Amhara Region] nr Kobo, 27 Aug 1961, *W. Burger 708* (K); nr Addis Ababa, 2600 m a.s.l., 11 Oct 1963, *W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 8212* (K); 25 km E of Lekemti, 2000 m a.s.l., 1 Jul 1965, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 7179* (BR0000013834418); 8 km N of Addis Ababa, 11 Oct 1965, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 8217* (BR0000013834364); [Oromia Region] nr Kulubi, 2400 m a.s.l., 5 Dec 1968, *J.J.F.E. de Wilde 4140* (BR0000013834449); [Sidama Region] Dara, 9000 ft, 1968, *P.M. Mulwany 87* (K); [Oromia Region] 8 km S of Jimma, 8 Nov 1970, *I. Friis & al. 179* (K); [Oromia Region] Mai Gudo Mt., 2400 m a.s.l., 3 Dec 1972, *K. Vollesen 1547* (K); 7 km on road Worata–Debre Tabor, 31 Dec 1972, *C.J.P. Seegeler 3043* (BR0000016286535, WAG1404368); Haberge, Alemaya, nr Bari vill., 2000 m a.s.l., 31 Aug 1976, *P.C.N. Jansen 7051* (BR0000013834357); [Oromia Region] E of Negele town, 2000 m a.s.l., Nov 1976, *D.R. Chaffey 1102* (K); [Amhara Region] Mekdela, 10500 ft, 11 Oct 1995, *V. Purchon & G. Belachew 37* (K);

Guinea (new record): Simandou Range, May 2009. *P.K. Haba 590* (K);

Kenya (selected): see type of *Achyranthes aspera* f. *latifolia*; Taita Hills, 10000 ft, 1898, J.*W. Gregory s.n.* (BM); [Nyeri County], Nyeri, 18 Dec 1921, *R.E. Fries & Th.C.E. Fries 84* (K); Chyulu Hills, 5200 ft, 24 Apr 1938, *P.R.O. Bally 7970* (K); [Nakuru County] Molo, 28 Jan 1947, *A. Bogdan 171* (K); [Rift Valley Region] Mau Forest, 24 Jan 1948, *P.R.P. Bally 89959* (K); Nakuru County, Eastern Mau Forest Reserve, 2300 m a.s.l., 4 Sep 1949, *R.A. Maas Geesteranus 6113* (BR0000013834616, L1673908); Mt. Elgon, Nov 1949, *Tweedie 802* (M); Furroli Mt., 20 Sep 1952, *J.B. Gillett 13954* (M); [Rift Valley Prov.] Mau Forest, Oct 1961, *O. Kerfoot 2921* (FT); nr Nairobi, 7000 ft, 15 Jun 1963, *J. Stewart 720* (K); Rift Valley Prov., Nakuru County, 15 Nov 1967, *B.E. Perdue & S.P. Kibuwa 9061*

(BR0000013834555); Narok distr., 8 Jul 1972, *P.J. Greenway & K. Kanuri 15021* (K, M); Nyanza Prov., Kisii distr., between Ikoba & Ogembo, 1750 m a.s.l., 29 Oct 1974, *D. Vuyk & F.J. Breteler 41* (W0333203); [Narok County] 9 km NE of Entasekera, 6700 ft, 28 Sep 1977, *C. Fayad 201* (K); [Samburu County] between Barsaloi & Maralal, 2000 m a.s.l., 22 Nov 1977, *S. Carter & B. Stannard 613* (K);

Madagascar (new record): Antananarivo Prov., 15 km NW of Antananarivo city, 11 Sep 1980, *M.A. Fischer & al. 85* (WU);

Malawi (new records; selected): [Southern Region] Cholo Mt., 1200 m a.s..l., 21 Sep 1946, *L.J. Brass 17708* (K); [Northern Region] Mughese Forest Reserve, 6000 ft, Sep 1953, *E.G. Chapman 1637* (BM); Chisongole forest, 4500 ft, 25 Aug 1956, *E.I. Newman & T.C. Whitmore 576* (BR0000013709082); [Central Region] Dedza Mts., 16 Apr 1961, *J. Chapman 1236* (K); Central Region, Dedza Mts., 1780 m a.s.l., 1 Apr 1970, *R.K. Brummitt 9571* (K); Northern Prov., Businande, 6500 ft, 28 Dec 1975, *E. Phillips 757* (K);

Nigeria (new records): [Taraba State] Kamatan Forest Reserve, 5 Dec 1968, *B.O. Daramola 62482* (K); [Taraba State] Chappal Waddi, 7000–7500 ft, 19 Nov 1969, *J.K. Jackson & al. 1985* (K);

Rwanda (new records): [Western Prov.] Shangugu, 1929, *J. Claessens s.n.* (BR0000016287402); Shangugu, Astrida to Bukavu, 12 Feb 1959, *G. Troupin* 11295 (BR0000013708429); Kibungo [Eastern] Prov., Akagera NP, 17 Apr 1969, *G. Bouxin & M. Radoux 224* (BR0000013708214, K); [Western Prov.] Cyangugu, 23 Jul 1974, *P. Aquier 3362* (BR0000013708160); Visoke [Bisoke] Mount, 2700 m a.s.l., 9 Feb 1975, *W.G. D'Arcy 7687* (K);

Somalia (new records): Somaliland, Golis Range, Jun 1895, *E.L. Phillips s.n.* (K); [Sahil Region] Berbera, 1905, *G.W. Bury s.n.* (BM);

South Sudan (new records): Katire to Itibol, 6350 ft, 17 Dec 1935, *anonymous 1637* (BM, K); Imatong Mts., 8000 ft, 10 Feb 1936, *H.N. Johnston 1484* (BR0000016286511, K);

Sudan (new records): Darfur Region, Jebel Marrah, Mar 1921, *H. Lynes 62* (BM); Darfur Region, between Jebel Uo & Nyuringya, 2200–2300 m a.s.l., 4 Jan 1934, *J.E. Dandy 128* (BM, BR0000013834272); Jebel Marrah, 8 Sep 1964, *G.E. Wickens 2425* (K); Central Darfur, 120 km E of Zalingei, Jebel Marrah Mts., 1650 m a.s.l., 20 Jan 1965, *W.J.J.O de Wilde & al. 5437* (BR0000013834296);

Tanzania (new records): Mt. Kilimanjaro, Aug 1893, *G. Volkens 678* (K); [Njombe Region] Lupembe, Mar–Apr 1931, *H.J. Schlieben 633 & 369* (BM, BR0000016286733); Uluguru Mts., 900 m a.s.l., 28 Mar 1933, *H.J. Schlieben 3688* (BM, M); Kilimanjaro, 2200 m a.s.l., 14 Feb 1934, *H.J. Schlieben 4766* (BR0000016286665, M); [Morogoro Region] Morogoro town, 4500 ft, Dec 1934, *E. Bruce 219* (BR0000016286634); [Mbeya Region] Mbeya, 1 May 1935, *H.E. Emson 392* (K); [Kigoma Region] Pasagulu Mt., 4800 ft, 8 Aug 1959, *R.M. Harley 9212* (BR0000013835026); [Kagera Region] Ngara, 5000 ft, 29 Dec 1960, *R. Tanner 5558* (K); Ngorongoro crater, 2450 m a.s.l., Mar 1968, *R. Ravazzano s.n.* (FT); Ngurdoto crater, 1900–2000 m a.s.l., 21 Mar 1968, *R. Ravazzano 28* (FT); [Tanga Region] Lushoto distr., 10 Mar 1969, *S. Shabani 332* (BR0000016286719, K); [Arusha Region] Karatu town, 1750 m a.s.l., 15 Sep 1977, *J. Raynal 19077* (BR0000016286696); Iringa Region, Mufindi, 18 Mar 1986, *S. Bidgood & P. Keeley 302* (K); [Kilimanjaro Region] Chambogo, 6 Jul 1987, *F.R. Kisena 532* (K); Arusha Region. nr Meru NP, -3.314720, 36.880373, ca. 2000 m a.s.l., 16 Jun 2021, *A.P. Sukhorukov 7* (MW, W); Arusha Region, nr Arusha town, Moshono, -3.390028, 36.716360, 16 Jun 2021, A.P. Sukhorukov 5 (MW); Arusha Region, nr Arusha town, Sasi, -3.379505, 36.751847, 1 Dec 2021, *A.P. Sukhorukov s.n.* (MW);

Uganda (new records; selected): [Northern Region] Mt. Rom, 7300 ft, 1936, *W.J. Eggeling 2385* (BR0000016286573); Western Region, Kigezi distr., 22 Apr 1950, *H.C. Dawkins 573* (BR0000016286597, K, M); Kigezi distr. [now Western Region], 12 Jan 1933, *H.M. Gardner 356* (BR0000013834487); Western Prov., 14 Nov 1954, *H. Stauffer s.n.* (BR0000013834470, K); Elgon Mt., 2750 m a.s.l., 6 Jan 1996, *K. Wesche 681* (K); Western Region, Kisoro distr., nr Mgalimnga NP, 1700 m a.s.l., 20 Jun 2005, *B. Rose s.n.* (W0333285).

Arabia

Oman (new record): Dhofar Governorate, Ayn Razat Spring, 24 Sep 1991, *H.D.V. Prendergast s.n.* (K);

Saudi Arabia (new records): Asir Prov., nr Al Habala, 8 Mar 1981, *D. Hillcoat 128* (BM); Al-Baha Region, 230 km S of Taif, 2000 m a.s.l., 14 Apr 1988, *A.A. Fayed 1420* (M);

Yemen (new records): [Dhale Governorate] Ash Shu'ayb distr., 2 Jun 1931, *C. Rathjens s.n.* (BM); Jabal Jihaf Mt., 7500 ft, 4 Oct 1937, *H. Scott & E.B. Britton 126* (BM); Yarim, 9300 ft, 21 Sep 1972, *J.R. Wood 55* (BM); [Dhamar Governorate] Dhamar town, 2420 m a.s.l., 30 Sep 1981, *D. Podlech 36061* (M, MSB122471); nr Sana'a, 2450 m as.l., 30 Sep 1981, *D. Podlech 36039* (M); between Sana'a & Manakha, Mar 1988, *Y. Ghyoot s.n*. (BR0000023108011).

Achyranthes acuminata **E.Mey. ex Sonder**

Africa

Angola (new records): [Cuanza Norte Prov.] Golungo Alto, May 1856, *F. Welwitsch* 6544 (BM, K); [Cuanza Norte Prov.] Cazango, Jul 1911, *J. Gossweiler 5148* (BM); nr Luanda, 750 m a.s.l., Nov 1946, *J. Gossweiler 13670* (K); Cuando Cubango Prov., Cuito River, 1059 m a.s.l., 11 Jun 2015, *N.P. Barker & al. 282* (K); Uige Prov., nr Camancoco vill., 857 m a.s.l., 19 Jul 2015, *T. Lautenschläger 40a* (DR048064);

Benin (new record): [Plateau Dept.] Adja-Ouèrè, 12 Dec 1901, *G. Le Testu 189* (BM, BR0000013834043);

Botswana (new records): [Ngamiland distr.] Maun, 12 Jun 1994, *D.T. Cole 853* (K); Northern Botswana, Selinda Reserve, 30 Mar 2005, *A. Heath & R. Heath 985* (K);

Burundi (new records): Bujumbura Rural, Ijenda, 18 May 1969, *J. Lewalle s.n*. (K); Bubanza Territory, 1500 m a.s.l., 11 May 1971, *M. Reekmans 646* (BR0000013837235); Muramvya Prov., 2000 m a.s.l., 18 Jun 1971, *J. Lewalle 5988* (BR0000013837204); [Cankuzo Prov.] Kigamba, 3 Oct 1974, *P. Auquier 4368* (BR0000013837556); [Muramwya Prov.] Teza, 2200 m a.s.l., 15 May 1988, *J. Saintenoy-Simon 120* (BR0000013835798);

Cameroon (new records): [Centre Region] Ndelle, [without date] *F. Welwitsch 6544* (BM, K); [Southwest Region, nr Barombi Lake] Johann Albrechtshöhe, 1896, *Staudt 586* (K000243720); Mount Cameroon, 3500 ft, 30 Mar 1952, *C.D. Adams* 6741 (K); Kumba distr., Meninger vill. to Beimiko in Southern Bekundu, 21 Feb 1956, *A. Binuyo & B.O. Deramola 35553* (K); [Central Region] Nanga Eboko town, 13 Mar 1959, *R. Letouzey 1569* (BR0000013834173, K); East Region, Doumé, 12 Nov 1960, *F.J. Breteler 675* (BR0000013834180, FT, K, M, WAG1404293); Far North Region, 10 km W of Fort Foureau, Chari River, 28 Sep 1964, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 3507* (WAG1404290); [Adamawa Region] Meiganga town, 23 Nov 1964, *G. Amshoff 4007* (BR0000013834166); Tello River, 27 Nov 1964, *W.J.J.O de Wilde & al. 4321* (BR0000013837594); [West Region] Dschang town, 1300 m a.s.l., 6 Dec 1965, *A. Meurillon 206* (BR0000013709037); Yaoundé, Mount Fébé, 1050 m a.s.l, 26 Feb 1977, *J. Lowe 3255* (K); [Adamawa Region] Ranch de Ngaoundaba, 8 Nov 1984, *S. Lisowski 1557* (BR0000013834081); Southwest Region, Mount Kupe, 900 m a.s.l., 7 Dec 1993, *M. Cheek & O. Ebwekoh 5636* (K000051107, WAG1404282); Southwest Region, Nyassosso, 800 m a.s.l., 15 Jan 1995, *M. Cheek & al. 6023* (K000086513); Southwest Region, Mount Kupe, 1000 m a.s.l., 30 Jan 1995, *S. Williams & al. 136* (K000093768, WAG1404132); Southwest Region, Mount Kupe, 7 Sep 1996, *M. Etuge & al. 2681* (K000051092); West Region, Mezam, Bali Ngemba FR, 1400 m a.s.l., 9 Nov 2000, *M. Cheek & al. 10474* (K000746136, K000746128, WAG1404308);

Central African Rep. (new records): [Mambéré-Kadéï Pref.] nr Bania, 26 Nov 1965, *A.J.M. Leeuwenberg 7042* (BR0000013834241, K, WAG0185573); [Mambéré Pref.] nr Carnot, 6 Dec 1965, *A.J.M. Leeuwenberg 7227* (WAG0185574); [Mbomou Pref.] Toki, Tondomazouma & Ngalakpa vill., 1 Jan 1970, *A. Morel 262* (P01195352);

Comoros (new records): Moroni, May 1830, *Boivin s.n*. (P00196461); Anjouan Island, 1875, *J.M. Hildebrandt 1677* (BM);

Congo Rep. (new record): [Niari Region] Bilala, 21 Jun 1989, *R. Dechamps* 13076 (BR0000013834227);

DR Congo (new records; selected): Stanley Pool [Pool Malebo nr Kinshasa], 23 Jul 1888, *F. Hens 28* (BR0000013835606, BM, L1673924, WU); [Kongo Central Prov.] Boma, Jul 1895, *A. Dewèvre 133* (BR0000013835446); [Kongo Central Prov.] Kisantu, 1900, *G. Justin 1019* (BR0000013813835590); [Kwilu Prov.] Kolokoso, 16 Jun 1906, *A. Sapin s.n*. (BR0000013835682); [Kongo Central Prov.] Kitobola, 26 Aug 1910, *De Cock 261* (BR0000013835583); Équateur Prov., Zambi, 2 Aug 1913, *Bequaert 549* (BR0000013835439); [Lomami Prov.] Penge, 14 Feb 1914, *Bequaert 2473* (BR0000013837822); Bankana [nr Kinshasa], Jun 1915, *H. Vanderyst 5480* (BR0000013835613); [Bas-Congo Prov.] Ganda-Sundi, 350 m a.s.l., 25 Jul 1919, *V. Goossens 1086* (BR0000013835545); [Kongo Central Prov.] Pangu, Jun 1921, *H. Vanderyst 9554* (BR0000013835699); [Kongo Central Prov.] Matadi, 6 Oct 1930, *H. Vanderyst 25999* (BR0000013835903); [Kongo Central Prov.] Kiduma, Jul 1932, *H. Vanderyst 32223* (BR0000013835620); [Lualaba Prov.] Kapanga, Aug 1933, *F. Overlaet 705* (BR0000013837785); [Haut-Uélé Prov.] Bangadi River, 29 Jan 1937, *A.M. de Graer 917* (BR0000013837846); [Kasai Central Prov.] Tshimbulu, 21 Apr 1937, *F. Matagne 311* (BR0000013835651); [North Kivu Prov.] Rutshuru, 1937, *J. Lebrun 8872* (K); [North Kivu Prov.] Rutshuru, 25 Feb 1938, *J. Ghesquière 6023* (BR0000013836399); [Tshopo Prov.] Yangambi, 470 m a.s.l., 9 Aug 1938, *J. Louis 10753* (BR0000016287112, K); [Tshuapa Prov.] Lofoli vill., Jul 1939, *P. Quarré 5717* (BR0000013837433); [Tshopo Prov.] nr Lileko, 28 Feb 1940, *R. Ofermain 208* (K); [Haut-Uélé Prov.] Nambiongo vill., Apr 1940, *J.W.G. Wyld 689* (BM); [Orientale Prov.] Nioka, 12 Jul 1945, *R. Germain*

3968 (BR0000013836047); [Equateur Prov.] Boyeka, 19 Nov 1946, *J. Leonard 1030* (BR0000013837419, K); [Haut-Lomami Prov.] Kaniama, 870 m a.s.l., Aug 1947, *W. Mullenders 1224* (BR0000013837815); [Ituri Prov.] Mt. Irumu, Jun 1949, *R. Germain 5189* (BR0000013836054, FT); South Kivu Prov., Kabare, 11 Mar 1951, *R. Pierlot 90* (K); Orientale Prov., Garamba NP, Mar 1952, *G. Troupin 403* (BR0000013837853, K); N'kolo, 26 Aug 1953, *R. Devred 1356* (BR0000013835576); Haut-Katanga Prov., Zawa Mt., 25 Jun 1954, *J. Delvaux 563* (BR0000013837860); [Ituri Prov.] Djugu [Territory], 15 Mar 1957, *A. Froment 91* (BR0000013836030, K); [North Kivu Prov.] Walikale town, Jul 1957, *R. Gutzwiller 1268* (BR0000013836450, M); [North Kivu Prov.] Mutongo, 1 May 1958, *R. Gutzwiller 2650* (BR0000013835910); [Kongo Central Prov.] Lemba to Mayumbe, 27 Aug 1966, *H. Breyne 257* (BR0000013835521); [South Kivu Prov.] Lwiro, 1700 m a.s.l., 29 Dec 1971, *J. Lambinon & G. Troupin 2061* (BR0000013837426, FT, K); [Kongo Central Prov.] Banana [town], 3 Jul 1974, *L. Pauwels 5233* (BR0000013835491, WAG1404154); Virunga NP, 16 Sep 1974, *J.-P. d'Huart 58* (BR0000013836146); [South Kivu Prov.] Kilimbwe, 16 Nov 1977, *T. Yamada 171* (K); [South Kivu Prov.] Lubimbi, 9 May 1978, J. *van Gysel 20* (BR0000013836719); [Tshopo Prov.] Kisangani, 21 Dec 1978, *J. Lejoly 4490* (BR0000013835729); Bas-Uélé Prov., Bambesa Terr., Dindila vill., 30 Jan 1988, *F. Szafranski 1391* (BR000001383535743); [Kiwu Prov.] Kikwit, 7 Nov 1990, *B. Masens 46* (BR0000013835736); [Ituri Prov.] 60 km N of Mambasa, 1000 m a.s.l., mid-1990, *H. Terashima 628* (BR0000013835989);

Equatorial Guinea (new records): Fernando Po [Bioko Island], 1860, *anonymous s.n.* (K); [Bioko Island] Musola, 10 Jan 1947, *E. Guinea 1147* (MA-01-00698962); Annobón Island, 890 ft, 25 Jul 1959, *F. Melville 192* (BM, K); Bioko [Island], 770 m a.s.l., 13 Feb 1989, *J. Fernández Casas 11582* (BR0000013837570, K); [Rio Muni Region] Temelon, 9 Nov 2000, *R. Pérez Viso 4139* (K);

Ethiopia (new records): [Amhara Region] Tana Lake, 14 Nov 1937, *R. Pichi-Sermolli 1437* (FT, K); [Southern Nations, Nationalities, and Peoples Region] Sagan [Segen town], 28 Jul 1939, *R. Corradi 3214* (FT); Gamu-Gofa Region, Between Soda & Arba Minch, 1240 m a.s.l., 28 Sep 1975, *P.C.M. Jansen 3777* (BR000000565821);

Gabon (new records): [Ngouni Prov.] Doussala, 100 m a.s.l., 23 Sep 2000, *H.P. Bourobou Bourobou & al. 452* (WAG0199843); Ogooué-Maritime Prov., Loango NP, 19 Mar 2006, D.*J. Harris & al. 8704* (E00217301, WAG1404159);

Ghana (new records): nr Kibi, Birim River, 2370 ft, 16 Dec 1952, *J.K. Morton 8137* (K); [Eastern Regio] Asiakwa to Pusupusu, 19 Dec 1952, *J.K. Morton 8218* (K);

Guinea (new records): [Kindia Region] Kolante, 10 Nov 1938, *J. Chillou 1035* (BR0000016286443); [Nzérékoré Region] Simandou Range, 1065 m a.s.l., 29 Nov 2008, *P.K. Haba & al. 483* (K000460820);

Ivory Coast (new records): [Bélier Region] between Toumodi & Yamoussoukro, 7 Jan 1954, *L. Aké Assi 7260* (UCJ000581); [Gbêkê Region] Beoumi, 15 Dec 1955, *L. Aké Assi 3515* (UCJ000582);

Kenya (new records): [Rift Valley Prov.] Narok distr., Mara River, 5200 ft, 3 Apr 1961, *P.E. Glover & al. 399* (BR0000013835842, K); [Nyanza Prov.] North Kavirondo distr., Kakamega forest, 1500 m a.s.l., 21 Mar 1977, *S.S. Hooper & C.C. Townsend 1508* (K); [Taita-Taveta County] Ngangao Forest, 1750 m a.s.l., *M. Wakanene 782* (W0333202); Makueni distr., Kibwezi Forest Research, 980 m a.s.l., 21 Nov 2010, *Q. Luke & P. Luke 14895* (K);

Lesotho (new record): Leribe [Hlotse], 1914, *Dieterlen 986* (K, BM);

Madagascar (new records): nr Antatanarivo, Oct 1880, *J.M. Hildebrandt 4108* (BM, K, LE, M, W0333222); [Anosy Region] Berenty Reserve, Oct 1985, *S. O'Conner 108* (K); Tulear Prov., nr Betioky, Beza Mahafaly Reserve, 13 May 1987, *P. Phillipson s.n*. (BR0000013835408, K, WAG1040296); Antsiranana Region, Befalafa, 400 m a.s.l., 13 Jun 1998, *L. Gautier & al. 3351* (K, WAG1404398); Finarantsoa Prov., Ranomafana NP, 20 Nov 1998, *F. Almeda 8211* (K);

Malawi (new records): [Southern Region] Mulanje, 1919, *C. Shinn s.n*. (BM); [Southern Region, Thyolo distr.] Cholo Mountain, 1300 m a.s.l., 20 Sep 1946, *L.J. Brass 17661* (BM, BR0000013837730, K); [Southern Region] Blantyre, 4 Oct 1960, *J. Chapman 936* (K); Central Region, Dedza distr., 12 Jul 1961, *J. Chapman 1427* (K); Central Region, Lifidzi Breeding Center, 21 May 1985, *I.H. Patel & W. Nachamba 2196* (BR0000013835194); Southern Region, Soche Mt., 2 Aug 1985, *A.J. Salubeni & W. Nachamba 4271* (K); Central Region, Lilongwe Nature Sanctuary, 25 Jun 1987, *A.J. Salubeni & E.J. Tawakeli 4964* (K);

Mayotte (French Overseas Department; new record): Grande-Terre. 26 May 2005, *F. Barthelat & al. 1491* (K, P00631148);

Mozambique (new records): nr Sena, Zambezi River, Oct 1883, *Kirk s.n*. (K); [Nampula Prov.] Marenga, Mar 1892, *Menyharth 1179* (WU); [Manica Prov.] Garuso forest, Apr 1935, *H.B. Gilliland 1805* (BM, K); [Maputo Prov.] Salamanga [town], 7 Jun 1948, *A.F. Gomes de Souza 3736* (FT, K, M); [Manica Prov.] 10 miles N of Vanduzi, 1900 ft, 27 Apr 1962, *N.C. Chase 7694* (BM, K); Cabo Delgado Prov., 20 km NE of Ancuabe, 18 Aug 1983, *E.M.C. Groenendijk 623* (BR0000013835262); Zambezia Prov., Chiperone Mt., 29 Nove 2006, *H. Patel & J. Bayliss 7179* (K000545142); Zambezia Prov., Mabu Mt., 18 Oct 2008, *Mphamba & al. 81* (K); [Sofala Prov.] Muanza distr., Gorongosa NP, 112 m a.s.l., 4 May 2013, *B. Wursten 703* (BR0000027318294V); Manica Prov., Moribane Forest Reserve, 26 Jun 2015, *M. Cheek & al. 17900* (K);

Namibia (new records): [Otjozondjupo Region] Waterberg, 5 Feb 1939, *O.H. Volk 1054* (M); [Kavango East Prov.] nr Rundu, 10 May 1939, *O.H. Volk 1960* (M); [Kunene Region] nr Etanga, 4 Apr 1957, *B. de Winter & O.A. Leistner 5439* (K, M); [Omusati Region] Ruacana Falls, 29 Apr 1962, *T.F. Kotze 1714* (K, M); Windhoek, 26 Mar 1963, *R. Seydel 2217* (M);

Nigeria (new records): Oban distr., 1911–1912, *P.A. Talbot 2311* (BM, K); nr Ibadan, 600 ft, Oct 1936, *R. Newberry & al. 139* (K); Ondo Prov., Akure division, 5 Jan 1948, *J.P.M. Brenan & E.W. Jones 8726* (BM, K, M0241526); [Taraba State] Kamatan Forest Reserve, 5 Dec 1968, *B.O. Daramola 62483* (K); [Cross River State] Nyaje to Mkpot, 5 Mar 1973, *Latilo & Oguntayo 70501* (K);

Rwanda (new records): [Southern Prov.] Kabgayi, 1800 m a.s.l., 14 Mar 1970, *G. Bouxin & M. Radoux 1550* (BR0000013837518); [Southern Prov.] Butare town, 19 Jul 1974, *P. Auquier 3244* (BR0000013837457); [Western Prov.] Bweyeye, 17 Aug 1974, *P. Auquier 3814* (BR0000013837471); [Northern Prov.] nr Ruhengeri, 1850 m a.s.l., 9 Oct 1974, *P. Auquier 4438* (BR0000013837495, WAG1404304); nr Kigali, 13 Oct 1974, *P. Auquier 4560* (BR0000013837501); Kigali, 1500 m a.s.l., 11 Aug 1984, *J. Lejoly 220* (BR0000013837068);

São Tomé & Príncipe (new records): São Tomé, 1885, *A. Moller 684* (BM); Guadalupe, 17 Jul 1956, *T. Monod 11893* (BM); [Principe Island] Santo Antonio, 17 Jul 1990, *V. Sequeira 7* (K);

Sierra Leone (new record): Loma Mountains, 29 Dec 1963, *J.K. Morton 355* (K);

Somalia (new records): [Middle Shebella Region] Balad town, 28 Dec 1919, *G. Scassellati 13* (FT); [Lower Shabelle Region] 25 km S of Merca town, Gungi vill., 12 Sep 1975, *R. Ravazzano 1166* (FT);

South Africa: see type of *A. acuminata*; nr Durban, 14 May 1895, *J. Wood 7203* (K); Vet River [Vetrivier] [without date] *Burke s.n.* (K); [North-West Prov.] Hakboslaagte, 28 Feb 1943, H. *Klinges 1667* (M); [KwaZulu Natal Prov.] Hawaan Forest, 100 ft, 16 Mar 1966, *E.J. Moll 3115* (K); [KwaZulu-Natal Prov.] Mtubatuba, 12 May 1970, *R.G. Stray 9777* (K); [KwaZulu-Natal Prov.] Ubombo, 15 Feb 1976, *J.P.M. Brenan 14275* (K); Transvaal Prov., Silverton, 16 Feb 1979, *A. Balsinhas 3379* (K); [Eastern Cape Prov.] nr Alice town, 1800 ft, 16 Mar 1985, *P.B. Phillipson 1053* (K); nr Durban, 29.8612277°S, 30.979105555°E, *E. Douwes* (Fig. 5B);

Tanzania (new records): [Zanzibar] Pemba [Island], Ngezi Forest, [without date] *G.H. Vaughan 552* (K); [Kilimanjaro Region] Marangu, 1560 m a.s.l., Nov 1893, *G. Volkens 1390* (K); [Mbeya Region] Kyimbila distr., 22 Jun 1911, *A. Stolz 778* (K, M, L1673914); [Morogoro Region] Mchombe, 28 Sep 1931, *anonymous 357* (FT); [Kilimanjaro Region] Lyamungo, 21 Aug 1932, *P.J. Greenway 3065* (K); Tanga Region, Pangani, 20 Jul 1955, *R. Tanner 1974* (BR0000013834876, K); [Morogoro Region] nr Mgeta vill., 980 m a.s.l., 17 Jul 1958, *A. Gilli 155* (W0333233) together with *A. porphyrostachya*; [Kigoma Region] Kabesi, 4 Sep 1958, 4500 ft, *J. Newbould & T.G. Jefford 2323* (K); Zanzibar [Unguja Island] Marahubi, 9 Jul 1963, *H.G. Faulkner 3209 & 3258* (BR0000013837716, K); Arusha Region, Tengeru, 10 Mar 1968, *R. Ravazzano 16* (FT); [Tanga Region] Lushoto distr., 19 Apr 1968, *S.A. Renvoize 1592* (K); [Morogoro Region] Morogoro town, 1800 ft, 19 Jul 1969, *B.J. Harris 2971* (K); Kibiti [distr.] 150 km on Dar–Kilwa road, 19 Jun 1970, *A.N. Minjas & M.D.I. Raya 1900* (BR0000013835064); Lushoto distr., Buhurula, 10 Jul 1970, *Shabani 581* (BR0000013835057); Masai distr., nr Engaruka vill., 3600 ft, 11 Feb 1971, *H.M. Richards & S. Arasululu 26645* (BR0000013834944, K); [Morogoro Region] Makanga camp, nr Shiri River, 16 May 1986, *anonymous 1747* (K); Tanga Region, East Usambara Mts., Kwamkoro FR, 930 m a.s.l., 27 Oct 1986, *S.T. Iversen & al. 86220* (K); Coast Region, [Rufiji distr.] Mchungu forest, 4 Aug 1990, *anonymous 1203* (K); Tanga Region, Gendagenda Forest, 200 m a.s.l., 31 Jul 1991, *Frontier Tanzania team 2377* (K); [Lindi Region] Litipo forest, 25 Jul 1993, *L. Mwasumbi & P. Clarke 3621* (K); Kagera, Bukba distr., Mabuye vill., 1166 m a.s.l., 29 Apr 2001, *L. Festo & al. 1460* (K); Kilimanjaro Region, nr Machame vill., -3.219119, 37.222290, ca. 2000 m a.s.l., 15 Jun 2021, *A.P. Sukhorukov s.n.* (MW);

Togo (new record): [Kara Region] Baga, 19 Dec 1985, *Koumantega s.n.* (TOGO01602);

Uganda (new records): Ruwenzori Expedition, 1893–1894, *G.F. Scott Elliot 7248* (K); [Central Region] Mulange [Hill], 4000 ft, Sep 1920, *R.A. Dummer 4480* (K); nr Kampala, Sep 1931, *anonymous 2210* (K); Budongo, Nov 1935, *W.J. Eggeling 2286* (BM); [Central Region] Wabusana, 28 Jul 1956, *L. Brown 2252* (K); Rabongo, Kibale NP, 4800 ft, 26 Jun 1957, *L. Brown 66* (BR0000013834463); Kampala, 2 Sep 1960, *R. Kendall & J. Richardson 60* (K); [Mpigi distr.] Mpanga forest, 2 Sep 1974, *A.B. Katende 2316 & 2318* (K); [Bwindi NP] Rushaga [sector], 5 May 1992, *A.B. Cunningham & Mihanda 4045* (K); Kabalaga [Murchison] NP, 5 Oct 1992, *D. Sheil 1393* (K); Murchinson Falls NP, Rabongo forest, 7 May 1993, *D. Sheil 1495* (K);

Zambia (new records): Southern Prov., Machipapa, 9 Mar 1962, *W.L. Astle 1458* (K); [Copperbelt Prov.] Kataba, 3 Jul 1963, D.B. Fanshawe 7901 (K); [Copperbelt Prov.] Kitwe, 4 Feb 1964, *J.M. Mutimushi 576* (K); [Lusaka Prov.] Luangwa Game Reserve, 7 May 1965, *B.L. Mitchell 2889* (K); North Luangwa NP, 22 Apr 1994, *P.P. Smith 518* (K);

Zimbabwe (new records): [Manicaland Prov.] Chirinda Forest, 3700–4000 ft, 1906, *C.F.M. Swynnerton 1510* (BM); [Manicaland Prov.] Chiringa Forest, 3600 ft, Jun 1967, *B. Goldsmith 77* (BR0000013837747, K); Victoria Falls, Jul 1908, *Schwarz 13405* (BOL0291974).

Achyranthes annua **Dinter**

Africa

Angola (new records): [Lunda Norte Prov.] nr Bumba, [without date, probably late 19th century] *F. Welwitsch 6573* (BM); [Cuanza Norte Prov.] Golungo Alto [town], [without date, probably mid-19th century], *F. Welwitsch 6547* (BM – right-handed specimens); nr Kunere River between Kiteve and Humbe, 3 Jun 1900, *H. Baum 961* (K0002437271, M); Huila Prov., Hungueria, 1300 m a.s.l., 10 Jun 1937, *A.W. Exell & F.A. Mendonça 2448* (BM); [Cunene Prov.] nr Humbe, 1100 m a.s.l., 10 Jun 1937, *A.W. Exell & F.A. Mendonça 2889* (BM); Huila Prov., Lubango, 2220 m a.s.l., 22 Apr 1960, *E.J. Mendes 3817* (BR0000013835088, M, P05047982); Huila Prov., Sá da Bandeira [Lubango], 4 May 1965, *C. Henriques 371* (K); [Namibe Prov.] Bruco, 14 May 1965, *C. Henriques 412* (BM); [Cunene Prov.] Xangongo to Mujombe vill., 18 Mar 1989, J.*M. Daniel & al. s.n.* (FT);

Benin (new records): [Borgou Dept.] Kalalé, Sep 1987, *M. Kreis 98* (BR000000547056); [Borgou Dept.] Sakabansi [town], 5 Nov 1987, *J. Lejoly 527* (BR0000005470266); [Borgou Dept.] Kalalé town, 15 Oct 1988, *J. Lejoly 146* (BR000000547046); Zou Dept., Savalou, 19 Nov 1998, *L.J.G. van der Maesen 6511* (WAG1404341); Atakora Dept., Kouandé, 22 Oct 2001, *A. Akoegninou & al. 5601* (WAG1404334); [Borgou Dept.] Tchaourou, 22 Sep 2005, *P. Houngnon 7169* (WAG1404338); Ailbori Dept., Banikoara, 26 Sep 2007, *K. Jurisch 141* (FR-0009269);

Botswana (new records; selected): [Kgatleng distr.] Mochudi, 1914, *C.C. Harbor 6599* (BOL0291967, K); Ngamiland [North-West distr.], Mwakupan vill., nr Ngami Lake, 7 Mar 1969, *R.J. de Hoogh 126* (WAG1404397); [Ghanzi distr.] Ghanzi pan, 11 Mar 1970, *M.C. Cole 8798* (K); Moremi Wildlife Reserve, Okavango swamps, 3 Mar 1972, *H. Biegel & G. Russell 3841* (K, M); [Ngami distr.] nr Maun, 7 Apr 1975, *P.A. Smith 1340* (K); nr Gaborone, 31 Mar 1977, *O.J. Hansen 3102* (K); Kalahari, 23°05'S, 20°46'E, 21 Mar 1980, *C. Skarpe 422* (K); Ngamiland distr., Aba Hills, 1110 m a.s.l., 20 Mar 1987, *D.G. Long & D.A.H. Rae 392* (K); Selinda Reserve, 26 Mar 2005, *A. Heath & R. Heath 975* (K);

Burkina Faso (new records; selected): nr Ouagadougou, 6 Nov 1976, *L. Aké Assi 13492* (UCJ000583); [Balé Prov.] Boromo, 13 Nov 1980, *J. Lejoly 12* (BR0000013833992); Ouagadougou, 31 Aug 1982, *J. Lejoly 209* (BR0000013834005); [Oubritenga Prov.] Gampela, 14 Sep 1982, *J. Lejoly 498* (BR0000013834012); Tapoa Prov., Maadaga, 12 Sep 1991, *R. Martin 241* (FR-0010160); Tapoa Prov., Diapaga to Tansarga, 14 Sep 1991, *K. Hahn 517* (FR-0010164); Boulgou Prov., 7 km NW of Tenkodogo, 7 Nov 1991, *U. Kéré 434* (FR-0010165); [Kompienga Prov.], Pama, 28 Oct 1993, *M. Ataholo 329* (FR-0017535); Seno Prov., Djigo, 23 Sep 1994, *K. Küppers 1302* (FR-0010171); Oudalan Prov., Menegou vill., 250 m a.s.l., 21 Sep 1996, *J.E. Madsen 5766* (WAG1404197); Oudalan Prov., Kissi, 7 Sep 1999, *J. Müller 337-5* (FR-0010173); Kossi, Nauna, 2 Oct 2004, *B. Bako & J. Boussim 386* (K); Yatenga [Prov.], N of Ouahigouya, 16 Aug 2005, *L.J.G. van der Maesen & al. 8277* (WAG0203842); Tapoa Prov., Kaabougou, 26 Sep 2007, *A. Zwarg 45* (FR-0025046);

Burundi (new records): Bururi Prov., 1850 m a.s.l., 2 Jun 1979, *M. Reekmans 8151* (L3709558); Bubanza town, 1150 m a.s.l., 3 Jun 1980, *M. Reekmans 9279* (BR0000013708610, K);

Cameroon (new records): [Northwest Region] Bamenda, 14 Jan 1928, *F.W.H. Migeod 302* (K, M); [Northwest Region] Bambui, 1 Jan 1951, *R.W.J. Keay 28355* (K000025623); [Northwest Region] Bamenda, 1 Jan 1951, *R.W.J. Keay 28335* (M); [Far North Prov.] 15 km N of Mokolo town, 18 Sep 1964, *M. Binolong 144* (K); [Far North Prov.] 25 km WNW of Fort Foureau [Kousséri], 28 Sep 1964, *R. Letouzey 7101* (K); [Far North Prov.] nr Guirvidig, 10 Oct 1964, *R. Letouzey 7247* (K); West Region, Bafou, 2 Dec 1969, *anonymous 1732* (K); Mogode town, 1000 m a.s.l., 8 Oct 1972, *A.J.M. Leeuwenberg & W.E.K. van Beek 10414* (BR0000013834104, WAG1404365); [Adamawa Region] Léré, Oct 1996, *C. Milan 6* (BR0000013834074); Southwest Region, Kodmin vill., 1400 m a.s.l., 20 Jan 1998, *Ghogue & al. 68* (K000051118); Northwest Region, Mantoum vill., 1560 m a.s.l., 4 Oct 2001, *B.J. Polard 609* (K000875617); [Northwest Region] Mezam, 11 Apr 2004, *M. Etuge & al. 5367* (K);

Cape Verde (new records): Santiago Island, 8 km of Praia, 190 m.s.l., 29 Nov 1955, *L.A. Grandvaux Barbosa 5749* (BM);

Central African Republic (new record): 6 km N of Gounda town, 10 Feb 1982, *J.M. Fay 3667* (K);

Chad (new records): [Batha Region] Ouadi-Rimé, 10 Sep 1962, *H. Gillet s.n.* (P00958623); [Tandjilé Ouest Dept.] road Kélo to Pala, 3 Sep 1984, *S. Lisowski 377* (BR0000016286498); N'Djamena, 23 Dec 1984, *S. Lisowski 1652* (BR0000016286504);

Djibouti (new records): [Arta Region] Ras Korali, 9 Mar 1893, *A. Terracciano 10* (FT); French Somalia [Tadjourah Region], Day vill., 1400 m a.s.l., 4 Jun 1953, *E. Chedeville 327 & 360* (FT); French Somalia [Randa distr. [Randa [vill.], 900 m a.s.l., 9 Jan 1956, *E. Chedeville 1039* (FT); ibidem, May 1959, *E. Chedeville 1340* (FT);

DR Congo (new records; selected): [South Kivu Prov.] Uvira, 1908, *J. Rouling s.n.* (BR0000016287488); [nr Kinshasa] Bankana, Jun 1915, *P.H. Vanderyst & P.J. Lambrette 5493* (BR0000016287006); [South Kivu Prov.] Panzi vill., 1925, *E. Vanderyst 17207* (BR0000016287044); [Haut-Katanga Prov.] Karavia [nr Lubumbashi town] Jun 1929, *P. Quarré 1761* (BR0000013708009); [Haut-Katanga Prov.] Katuba, Jun 1933, *P. Quarré 3223* (BR0000013708016); [Bas-Uélé Prov.] Bambesa territory, Apr 1934, *H. Brédo 1220* (BR0000016287105); [Haut-Katanga Prov.] Elizabethville [Lubumbashi], 1937, *Salésiens 318* (BR0000013708122); [Haut-Katanga Prov.] Kasenga town, May 1939, *H. Brédo 2916* (BR0000013836764); Haut-Uélé Prov., N'ganga [Ganga], 14 Dec 1944, *Tecno 88* (BR0000013836092); [Kasai-Occidental Prov.] Mwango, 6 Jun 1947, *G. Kevers 129* (BR0000016287051); [Lualaba Prov.] Upemba NP, Apr 1948, *G.F. de Witte 3706* (L1695061); [Haut-Uélé Prov.] Faradje, 19 Dec 1949, *J. Costermans 30* (BR0000016287167); [Tanganyika Prov.] nr Manono, Kiala, Jul 1957, *A. Thiebaud 665-39* (BR0000013835705); [North Kivu Prov.] Rutshuru, 10 Dec 1958, *G. Troupin 8928* (BR0000013836672); South Kivu, Katana, 1959, *Cambridge Congo Expedition 11* (BM); Haut-Katanga Prov., Kasenga Territory, Kaselele, 890 m a.s.l., 19 May 1960, *M. Streel 847* (BR0000013837877); South Kivu Prov., Kabare Territory, 2300–2400 m a.s.l., 30 Dec 1969, *H. Ern 25* (BR0000013836344); [Haut-Katanga Prov.] Likasi, 13 Jul 1977, *R. Wechuysen 385* (BR0000013708993); Madimba Territory, 18 Jul 1981, *Nkunga 6488* (BR0000016286986);

Egypt: see lectotype of *A. argentea* var. *viridescens*; [Halaib Triangle] Gebel [Gabal] Elba, 18 Mar 1928, *Khattab 6305* (K); [Halaib Triangle] Gebel [Gabal] Elba, 24 Jan 1933, *J.R. Shabetai 12* (K);

Eritrea (new records; selected): [Northern Red Sea Region] Dahlak Island, Mar 1892, A. *Terracciano 792* (FT); [Northern Red Sea Region] Saati vill., 8 Mar 1893, *V. Ragazzi & A. Pappi s.n.* (FT); [Northern Red Sea Region] Damas valley, 14 Apr 1893, *A. Pappi 4106* (FT); Dogali vill. [nr Massaua town], 2 Mar 1902, *A. Terracciano & A. Pappi 18* (FT); [Debub Region] Mai Daro [vill.] 25 Sep 1902, *A. Pappi 3041* (FT); Keren town, Nov 1902, *A. Tellini 930* (FT); [Northern Red Sea Region] Sabar Guma, 1903, *A. Tellini 1566* (FT); [Dek'emhare] Hamasen, Ghinda, 960 m a.s.l., 14 Jan 1909, *A. Fiori s.n.* (FT001027); [Northern Red Sea Region] Samhar, 10 Apr 1910, *A. Pappi 8654* (FT); [Anseba Region] Karkabet town, 1915, *I. Baldrati 1137* (FT); [Northern Red Sea Region] between Massaua & Ghinda, 26 Mar 1938, *Bologna 22* (FT); [Northern Red Sea Region] Archico [Arkiko], 17 Jan 1952, *H.B. Gilliland & W. Stower 4094* (K); Senafı to Asmara, 16 Augt 1973, *G. Aweke & M.G. Gilbert 673* (WAG1404374); Asmera town, 2350 m a.s.l., 5 May 1988, *O. Ryding 1177* (K);

Eswatini (new records): Mbabane, 23 Mar 1956, *R.H. Compton* 25825 (K); -26.235145°S, 31.178688°, 17 May 2018, *K. Braun*; image available at: https://www.gbif.org/ru/occurrence/4901375172;

Ethiopia (new records): [Semien Gondar Zone] nr Matemma [Metema], 1865, *G. Schweinfurth 646* (BM); [South West Region, Telo distr.] Kolla, 1863–1868, *Schimper 188* (BM);]Oromia Region] Neghelli town, 1937, *G. Cufodontis 250* (FT); [Sidamo Region] Ruscello di el Dire, 15 May 1939, *R. Corradi 3323* (K); [Southern Nations, Nationalities, and People's Region] Asile, 30 Jul 1939, *R. Corradi 3349 & 3350* (FT); [Somali Region, Dollo Zone] Bulleh Sirrauw, 21 Nov 1944, *P. Glover & H. Gilliland 377* (BM); [Oromia Region] Agheremariam [Bule Hora], 1 Dec 1952, *J.B. Gillett 14524* (M); [Oromia Region] nr Jimma town, 11 Feb 1956, *R.B. Stewart s.n.* (FT, K); [Oromia Region] Adami Tullu town, Sep 1956, *H.R.D. Sanford 8* (FT); [Oromia Region] nr Dembidolo town, 6300 ft, 2 Mar 1957, *H.F. Mooney 6860* (FT); [Oromia Region] 25 km E of Lekemti, 2000 m a.s.l., 1 Jul 1965, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 7179* (WAG1404384); 60 km S of Addis Ababa, 2800 m a.s.l., 30 Oct 1965, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 8621* (BR0000013834395); [Afar Region] 50 km W of Awash station, 800 m a.s.l., 8 Apr 1966, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 10678* (BR0000013834371, K, WAG1404376); [Harari Region] nr Harar, ca. 1700 m a.s.l., 18 Mar 1968, *E. Westphal & J.M.C. Westphal-Stevels 3506* (BR0000013834319, WAG0185680); Blue Nile Gorge, 1700 m a.s.l., 25 Sep 1969, *C. Parker 339* (K); Kaffa Prov., 8 km S of Jimma, 1700 m a.s.l., 8 Nov 1970, *I. Friis & al. 179* (BR000001384333); 7 km on road Worata – Debre Tabor, 31 Dec 1972, *C.J.P. Seegeler 3043* (WAG1404368); [Afar Region] nr Awash, 900 m a.s.l., 26 Sep 1976, *L. Boulos 9360* (FT); Shewa Prov., Omo River, 900 m a.s.l., 11 Oct 1984, *R.E. Gereau 1231* (K);

Gambia (new record): Yundum town, 29 Oct 1974, *P.J. Terry 3192* (K);

Ghana (new records): [Bono Region] between Band & Menji vill., 23 Dec 1953, *J.K. Morton 25242* (K); Larabanga [town], 12 Oct 1959, *R. Rose Innes 1414* (K);

Guinea (new records): nr Conakry, Jun 1913, *Ch. D'Allerizette s.n*. (L1673910); [Mamou Region] Pita, 17 Oct 1956, *J.G. Adam 12548* (P00695162);

Guinea-Bisau (new record): [Gabu Region] Madina do Boé, 2 Feb 1962, *J. Alves Pereira 2948* (MA778959);

Kenya (new records): [Kisumu County] Muhoroni, 26 Sep 1950, *Haggie & Turbo 7988* (K); 10 km SE of Meru, Giaki Farm, 3700 m a.s.l., 16 Aug 1958, *A. Bogdan 4628* (K); 15 km N of Kilifi, 17 Sep 1958, *J.C. Moomaw 888* (K); nr Maralal town, 7 Oct 1960, *D.R.M. Stewart 358* (K); Narok distr., Narosura, 6200 f, 16 Aug 1961, *P.E. Glover & al. 2427* (K); Enekidongo, 3000 ft, 16 Jun 1962, *P.E. Glover & al. 2831* (K); [Narok Region] Kipleleo, 21 Jun 1962, *P.E. Glover & Samuel 2875* (FT, K); [Rift Valley Prov.] nr Nakuru town, 6000 ft, 4 Aug 1967, *O.M. Mwangangi 70* (FT, K); Kwale distr., Shimba Hills, 1450 ft, 20 Feb 1968, *F. Magogo & P.E. Glover 153* (BR0000013834548, FT, K); Kitui distr., Uthekethe, nr Mutomo, 1050 m a.s.l., 12 Aug 1968, *Z.J. Kimani 40* (BR0000013834525, K); South Turkana, Loriu Plateau, 4000 ft, 2 Jun 1970, *B. Mathew 6583* (K); Nyanza Prov., Kisii distr., between Ikoba & Ogembo, 1750 m a.s.l., 29 Oct 1974, *D. Vuyk & F.J. Breteler 44* (BR0000013834562, K, WAG1404174); Masai distr., 23 km E of Oloitokitok, 10 Mar 1977, *S.S. Hoopeer & C.C. Townsend 1290* (K); N of Ngomeni, 720 m a.s.l., 25 May 1977, *J.B. Gillett 21087* (FT, K); Nanyuki distr., 18 km NE of Nanyuki, 1850 m a.s.l., 22 Oct 1977, *M.G. Gilbert 4881* (K); Nyanza Prov. [Kisii County], 9 km E of Kisii town, 23 Mar 1978, *A.C. Plaizier 1067* (WAG1404125); Kibwezi–Kitui road, 900 m a.s.l., 26 May 1979, *M.G. Gilbert 5408* (K); Nairobi to Magadi, 1400 m a.s.l., 17 May 1981, *M.G. Gilbert 6145* (K); [Rift Valley Prov.] Trans-Nzoia distr., 1800 m a.s.l., 1988, *G.M. Mungai 520* (K); Rift valley, Bogoria Lake, 1000 m a.s.l., 15 Aug 1988, *P. Pilsl 9156* (HPILSL 009156); Tana River distr., Tana River National Primate Reserve, 16 Mar 1998, *D. Luke & al. 464* (K);

Lesotho (new records): Leribe [Hlotse], [without date and collector] *41* (K); "Basutoland", 1913, *Dieterlen s.n.* (K);

Liberia (new record): [Northern Nimba County] Yekepa vill., 14 Dec 1964, *J.G. Adam 20071* (M);

Madagascar (new records): Central Plateau, 1914, *H/T. Hodgkin & C.E. Stansfield 134* (K); [Prov. of Toamasina] Périnet [Andasibé], 14 Dec 1985, *A.J.M. Leeuwenberg 13810* (BR0000013835316);

Malawi (new records; selected): [Northern Region] Karonga, 28 Jul 1952, *Williams s.n*. (BM); Northern Prov., Chilumba, 22 Apr 1969, *J. Pawek 2285* (K); Nyika Plateau, 7500 ft, 30 Aug 1969, *W.M. Fitzpatrick 77* (BM); Southern Region, Lengwe Game Reserve, 9 Mar 1970, *R.K. Brummitt & A.J. Hall-Martin 8978* (K); [Northern Region] Mzuzu town, 4500 ft, 2 Jul 1974, *J. Pawek 8781* (BR0000013835187, WAG1404184); Northern Region, Chikangawa, 5900 ft, 14 Jul 1978, *E. Phillips 3556* (K, WAG1404389); Zomba distr., Zomba Plateau road, 8 Aug 1978, *H.G. Msiska 51* (BOL0291976); Southern Region, Zomba distr., 24 Jul 1984, *K. Kaunda & E.J. Tawakali 93* (K);

Mali (new record): [Tombouktou Region] Timbuktu, 27 Aug 1927, *O. Hagerup 284* (BR0000013833947, K);

Mauritania (new records): [Gorgol Region] Kaedi, 1972, *A. Naegele 188* (K); [Gorgol Region] Rinndiao, 16 Oct 1972, *A. Naegele 160* (K); Sixth Region, Hassei

Ould Babouh, 20 Nov 1975, *D. Dupont 126* (BR0000016286351); Assaba Region, Kankossa distr., El Awje, 9 Sep 2008, *J.-N. Labat & al. 3970* (P00577631);

Mozambique (new records): [Nampula Prov.] Boroma River, Marenga, Apr 1892, *Menyharth 666* (WU); Cabo Delgado, 9 Apr 1964, *A.R. da Torre & Paiva 11811* (BR0000013837754, WAG1404328); Tete Prov., Cabora Bassa, 21 Apr 1972, *A. Pereira & M.F. Correia 2192* (WAG1404244); [Manica Prov.] nr Chimoio town, 710 m a.s.l., 22 Oct 2013, *B. Wursten 814* (BR0000027322529V); Sofala Prov., Gorongosa NP, 17 May 2015, *B. Wursten 15160* (BR0000027330548V);

Namibia (selected): see neotype of *Achyranthes annua*; [Otjozondjupa Region] Omuramba, Otjenga, 14 Mar 1939, *O.H. Volk 1405* (M-0293179); Kavango-East Region] nr Rundu, 8 May 1939, *O.H. Volk 1871* (M); [Khomas Region] Khomas Highland, 18 May 1939, *G. Gassner 194* (M); Okavango-Nord, 28 Jun 1939, *O.H. Volk 2356* (M); [Hardap Region] Rehoboth, 10 Apr 1949, *K.G. Strey 2534* (K); [Otjozondjupa Region] Grootfontein, 30 Mar 1953, *H. Klinges 2863* (M); [Oshikoto Region] Tsumeb, 29 Mar 1955, *B. de Winter 2990* (K, M); [Hardap Region] nr Kalkrand, 10 May 1955, *B. de Winter 3497* (K. M); [Kavango West Region] nr Tondoro, 5 Mar 1956, *B. de Winter & W. Marais 4998* (M); [Otjozondjupa Region] Erichsfelde Farm, 13 Mar 1956, *O.H. Volk 11826 & 11828* (BR0000016286863, M); [Hardap Region] Haribes, 9 Apr 1956, *O.H. Volk 12296* (M); [Kunene Region] Kaokoveld, 27 Mar 1957, *B. de Winter & O.A. Leistner 5192* (K, M); [Kunene Region] nr Etanga, 7 Apr 1957, *B. de Winter & O.A. Leistner 5436* (K, M); [Erongo Region] Karibib, 1150 m a.s.l., 17 May 1957, *R. Seydel 1143* (Z-000033456); [Hardap Region] Bergland, 1575 m a.s.l., 10 May 1961, *R. Seydel 2858* (L1673883, M, WAG1404405); Windhoek distr., Farm Voigtland, 10 Mar 1963, *H. Leippert 4351* (FT); Windhoek, 12 Mar 1963, *R. Seydel 3424* (BR0000016286870, K, M); [Kunene Region] Etosha Pan, 8 miles N of Namutoni, 18 May 1963, *B. Nordenstam 2688* (M); [Hardap Region] Maltahöhe, 1969, *O.H. Volk 6421* (M); [Ohangwena Region] Oshandi, 19 Mar 1973, *R.J. Rodin 9110* (K, M); [Otjozondjupa Region] Okahandja, 28 Apr 1976, *G. Woortman 2116* (K, M); [Kunene Region] N of Outjo, 12 Mar 1997, *G. Germishuizen 9710* (WAG1404427);

Niger (new records): [Tilaberi Region] Toukounous vill., Jul–Aug 1967, *B. Bartha 31-10* (K, M, MSB122467); [Agadez Region] 30 km NW of Agadez town, 520 m a.s.l., 19 Sep 1977, *P. van der Veken 12727* (BR0000013834067); NP of West Niger, Mékrou, 2 Dec 1986, *E. Robbrecht & N. Leman 3467* (BR0000016286474); Niamey, 28 Sep 1987, *N. Leman 181* (BR0000016286467); [Agadez Region] nr Sekiret, 24 Sep 1988, *E. Schulz s.n.* (GZU000274163); Nianey Prov., 22 km N of Niamey, 20 Sep 1989, *K. Küppers 9* (FR-0010167);

Nigeria (new records): Sokoto [State], May 1921, *B. Moiser 14* (K); [Bauchi State] Nabardo, 21 Sep 1921, *H.V. Lely 620* (K); [Taraba State] Gembu, 1620 m a.s.l., 29 Jan 1958, *F.N. Hepper 1815* (K); [Benue State] Buruku vill., 9 Oct 1961, *J. Olorunfemi 55048* (WAG1404188); [Benue State] Buruku vill., 9 Oct 1964, *J. Olorunfemi 55048* (K); [Kano State] Gaya, Sep 1979, *Sharland 658* (K); Borno State, nr Gajiganna, 4 Sep 1992, *K. Neumann 1280* (FR-0010175); Borno State, Maiduguri to Monguno, 2 Oct 1994, *B. Zach 20* (FR-0010161); Borno State, Lake Tilla, 22 Oct 1994, *U. Salzmann 58* (FR-0010177);

Réunion (French Overseas Department; new record): Dos d'Ane, Mar 1974, *F. Friedmann 2294* (K);

Rwanda (new records): [Eastern Prov.] nr Biharagu, 1400 m a.s.l., 12 Jun 1958, *G. Troupin 7900* (K); [nr Gisenyi town] Rubona [Peninsula], 1700 m a.s.l., 12 Sep 1958, *G. Michel 5637* (BR0000013708306, K); Kibungo Prov., Akagera NP, 19 May 1969, *G. Bouxin & M. Radoux 442* (BR0000013708221, FT); [Southern Prov.] Muhura, 26 Jun 1972, *L. van Puyvelde 29* (BR0000013708504); [Southern Prov.] Butare town, 19 Jul 1974, *P. Auquier 3268* (WAG1404394); [Western Prov.] Bugarama, 1000 m a.s.l., 13 Jun 1975, *B. Runyinya 99* (BR0000013837891);

Senegal (new records; selected): Kaolack town, 1950–1951, *R.P. Berhaut 490* (BR0000016286405); [Louga Region] nr Dahra, 17 Sep 1961, *J.A. Raynal 7582* (BR0000016272811); [Casamance Region] Kabrousse, 4 Nov 1978, *C. Vanden Berghen 2969* (BR0000016286382); [Ziguinchor Region] Badiouré, 16 Nov 1983, *C. Vanden Berghen 6111* (BR0000013833893); [Basse-Casamance Region] Badiouré, 18 Nov 1983, *C. Vanden Berghen 6183* (BR0000013833909); Guires Lake, 12 Nov 1984, *P. Bamps 7623* (BR0000016286368); [Casamance Region] Abéné vill., 2 Nov 1987, *C. Vanden Berghen 8039* (BR0000016286399); Vindou-Tingoli area, 20 m a.s.l, Sep 1989, *J.E. Lawesson 5367* (K); [Basse-Casamance Region] Fegroum, 8 Nov 1990, *C. Vanden Berghen 9293* (BR0000013833916, WAG1404191); Sine Saloum Prov., Delta du Saloum NP, Sep 1991, *A.M. Lykke & al. 503* (K); [Basse-Casamance Region] Abéné, 18 Oct 1995, *C. Vanden Berghen 10103* (BR00000162286436); Bandia Reserve, 25 Sep 1996, *A. Druart 29* (BR0000016286429); Diaoulé vill., 19 Sep 2005, *E. Faye 54* (BR0000016286375);

Sierra Leone: see type of f. *annulosa* subf. *angustifolia*; Loma Mts., 29 Dec 1963, *J.K. Morton 357* (WAG14042000); [Southern Prov.] Njala, 19 Jan 1964, *J.K. Morton 654* (WAG1404202); Tingi Mts., 15 Dec 1965, *J.K. Morton & D. Gledhill 3122* (K);

Somalia (new record): [Lower Jubba Region] 27 km of Badadda [Bad Adda] town, Ola Uager, 28 Aug 1959, *G. Moggi & R. Ravazzano 1722* (K, MA-01-00516272);

South Africa (new records): [Eastern Cape Prov.] Uitenhage, 1847, *R.C. Alexander s.n.* (BM); [KwaZulu-Natal Prov.] Karkloof, 1875–1880, *A. Rehmann 7405* (Z-000033307); [Mpumalanga Prov.] Barberton, 2800 ft, 1890, *E.E. Galpin 920* (K); [Eastern Cape Prov.] Komgha, Mar 1891, *H.G. Flanagan 733* (BM); [Western Cape Prov.] Wynberg, 9 May 1892, *B. Schlechter 735* (BR0000013835309, FI, WU); Grahamstown [Makhanda] town, May 1893, *B. Schlechter 2634* (BM, BR0000013835385, K, WU); nr Capetown, 1895, *H. Bolus 2913* (K); nr Pretoria, 24 Mar 1906, *R. Leendertz 799* (K); [Eastern Cape Prov.] Centane, Mar 1911, *A. Pegler 1499* (BM, K); [Western Cape Prov.] Knysna, Apr 1912, *W.G. Worsdell s.n.* (K); [Limpopo Prov.] Tzaneen, 30 Oct 1913, *A.O.D. Inogg 9548* (K); Western Cape, Kirstenbosch, Apr 1917, *M.M. Page s.n.* (BOL0222316); [Eastern Cape Prov.] Krom River, Mar 1922, *H.G. Fourcade 2136* (BOL73890); Johannesburg, 9 Mar 1924, *C.E. Moss 9302* (BM); [Western Cape Prov.] Wynberg Hill, 2 Jun 1931, *T.M. Salter 795* (BM, K); [KwaZulu-Natal Prov.] Durban, Sep 1933, *A. Meebold 13054* (M); Pretoria, 5 Apr 1934, *A.O.D. Mogg 14934* (BR0000013708764); KwaZulu-Natal Prov., Ixopo, Mar 1935, *N.M. Otto 19A* (M); KwaZulu-Natal Prov., Durban, Apr 1936, *H.M.L. Forbes 1281* (BOL0291980); [Northern Cape Prov.] Rietfontein, 25 Nov 1939, *anonymous s.n.* (M); [Gauteng Prov.] Baviaanspoort, 15 Apr 1946, *W. Giess 15828* (M); [Eastern Cape Prov.] Stutterheim, 11 Dec 1948, *A.P.H. Acocks 9461* (K); Rehoboth distr., 19 Apr 1949, *R.G. Strey 2534* (BOL0291970); [Western Cape Prov.] Claremont, Feb 1950, *Pillans 10034* (BR0000013835378); [Limpopo Prov.] Letaba [Municipality], 18 Aug 1958, *G.C. Scheepers 164* (BM, M); nr Pretoria, 11 Apr 1962, *L. Bernardi 9058* (LE); KwaZulu-Natal Prov., Oribi Gorge, 10 Oct

1963, *J. Lanjouw & B. Lanjouw-Raven 450* (U1052435); Free State Prov., Farm Mequatlingsnek, 1600 m a.s.l. Apr 1972, *M. Jacobs 8530* (K, L1695059); Cape Town, 2 Oct 1972, *E. Esterhuizen s.n*. (BOL0222314); Transvaal Prov., Nylsvley NR, 27 Mar 1976, *A.J.M. Leeuwenberg 11003* (BR0000016286894); [Eastern Cape Prov.] Grahamstown [Makhanda town], 1 Mar 1978, *R.D.A. Bayliss 8584* (M); KwaZulu-Natal Prov., Nkandla Forest, 4 Feb 1982, *J. Lambinon & M. Reekmans 257* (BR0000016286917);

South Sudan (new record): [Upper Nile State] Boing, 11 Oct 1951, *M.I. Sherif 2886* (K);

Sudan (new records): Erkowit [Ar Kaweit], 3600 ft, [without date] *anonymous 24* (K); [White Nile State] Mt Arashkol, 9 Oct 1839, *Kotschy 148* (BR0000013835835, BR0000016286528, HBG503187, M0241531, M0241532, WAG1404426, WU); Central Darfur, Zalingei, Oct 1921, *H. Lynes s.n*. (K); Erkowit [Ar Kaweit], 1928, *Maffey 7* (K); [Al Qadarif State] Al Gadaref distr., 5 Sep 1951, *B. Beohir 314* (K); North Kordofan State, Bara distr., 23 Sep 1962, *G.E. Wickens 519* (K); Central Darfur, 120 km E of Zalingei, Jebel Marrah Mts., 1650 m a.s.l., 20 Jan 1965, *W.J.J.O de Wilde & al. 5437* (BR0000013834296);

Tanzania (new records; selected): [Mwanza Region] Mwanza, 1935, *R.H. Davis 33* (K); Shinyanga, 3800 ft, 29 May 1952, *J.R. Welch 178* (K); Malagarasi [River], 5 Aug 1952, *G. Michel 3601* (BR0000013835828); [Mara Region] Ikoma, 30 Feb 1953, *R. Tanner 1849* (K); [Shinyanga Region] Shinyanga town, 3500 ft, 29 May 1953, *J.R. Welch 178* (M); [Ruvuma Region] Songea distr., 1956, *E. Milne-Redhead & P. Taylor 9621* (BR0000016286641, K); between Lembeni & Same, 3000 ft, Jan 1957, *P.R.O. Bally s.n*. (K); [Kagera Region] Kirushya vill., 5500 ft, 5 Apr 1960, *R.E.S. Tanner 4827* (BR0000013834760, WAG1404267); Mbeya distr., Igawa, 4000 ft, 1 Apr 1962, *R. Polhill & S. Paulo 1964* (BR0000013835002, K); [Rift Valley Region] Lake Manyara NP, 3 Apr 1962, *H. Dingle 191* (K); [Kilimanjaro Region] Kilimanjaro Mt., 1524 m a.s.l., 25 Feb 1968, *R. Ravazzano 5* (FT); [Iringa Region] Mdonya River, 24 Apr 1970, *P.J. Greenway & K. Kanuri 14414* (M); [Dodoma Region] Mtera, 600 m a.s.l., 5 May 1971, *B. Mhoro 1106* (K, WAG1404264); Dodoma Region, Ikowa Reservoire, 20 May 1975, *I. Backéus 1311* (BR0000013834982, K); [Tanga Region] Lushoto, 17 Mar 1979, *J. Grabner 244* (W0333295); [Singida Region] Mgela vill., 1340 m a.s.l., 14 May 1983, *Kisena & Ruffo 86* (K, WAG1404206); Tanga Region, Lushoto distr., West Usambara Mts., Mazumbai Field Station, 1520 m a.s.l., 17 Jan 1985, *S.T. Iversen 85013* (K); Iringa Region, Iringa distr., Ruaha NP, 850 m a.s.l., 17 May 1987, *J. Lovett & al. 2166* (K); Iringa Region, Mufindi distr., 1830 m a.s.l., 20 May 1987, *J. Lovett 2188* (K); Tanga Region, Handeni distr., Gendagenda Forest, 7 Sep 1991, *anonymous s.n.* (K); Kagera, Bakuba Rural distr., W of Minziro vill., 1130 m a.s.l., 20 Mar 2001, *L. Festo & J. Francis 1061* (K); Arusha Region, nr Longido township, 1430 m a.s.l., 15 Jun 2012, *C.J. Kajombo & C. Makyao 7686* (WAG1404203); Manyara Region, Mt. Hanang area, nr Gidewari vill., -4.357316, 35.373525, 14 Jun 2022, *A.P. Sukhorukov s.n*. (MW, W);

Togo (new records): [without exact location and date] *J.F. Brunel 6708* (BR0000013834029); [Savanes Region] Mandouri, 19 Nov 1983, *anonymous 7875* (TOGO01604);

Uganda: see type of *A. aspera* f. *annulosa*; Morungole Mt., 7500 ft, 11 Nov 1939, *A.S. Thomas 3261* (K); Moroto town, 4600 ft, Sep 1956, *Wilson 256* (K); West Buganda distr., Mpanga Forest, 2 Sep 1974, *A.B. Katende 2317* (K);

Zambia (new records; selected): [Central Prov.] Mumbwa, 1911, *Macaulay 687* (K) together with *A. porphyrostachya*; [Southern Prov.] Mazabuka [town], 1934, *J.D. Martin 603* (BR0000013708740, K); [Copperbelt Prov.] Mufulira, 23 May 1948, *A.W. Cruse 350* (K); [Southern Prov.] Mapanza, 3300 ft, 4 Apr 1953, *E.A. Robinson 154* (K); Lusaka, 4000 ft, 22 May 1955, *E.B. Best 101* (BR0000013835132, K); [Southern Prov.] Mazabuka [town], 28 Mar 1963, *H.J. van Rensburg 1848* (BR0000013835163); [Copperbelt Prov.] Kitwe, 16 Apr 1963, *D.B. Fanshawe 7772* (K); [Luapula Prov.] Chibembe River, 2000 ft, 22 Mar 1967, *S.D. Prince 410* (K); [Northern Prov.] nr Mbala, 25 Apr 1968, *M. Richards 23249* (K); Luangwa Valley, Apr 1971, *N.O.G. Abel 247* (BR0000016286764); [Northern Prov.] Mbala, 29 May 1978, *M. Sanane* 1199 (BR0000013835156); [Central Prov.] Kabwe town, 1250 m a.s.l., 21 Apr 1998, *B. Leteinturier & al. 156* (BR0000013835118);

Zimbabwe (new records; selected): Mazowe distr., Mar 1906, *F. Eyles 298* (BM); [Manicaland Prov.] Chirinda, 22 May 1906, *C.F.M. Swinnerton 512* (K); Salisbury [Harare], 17 Jul 1913, *anonymous s.n.* (K); [Manucaland Prov.] Umtali [Mutare], Odrani River valley, 1914, *A.G. Teague 81* (BOL0291973); [Matabeleland South Prov.] Matopos [Matobo] distr., 14 Apr 1931, *anonymous 3965* (BM); [Manicaland Prov.] nr Nuza Mt., 3850 ft, 15 Jun 1934, *H.B. Gilliland 344* (BM); Bvumba [Mts.], 5300 ft, 21 Apr 1950, *N.C. Chase 2151* (BM); [nr Bulawayo town] Matobo, 4000 ft, May 1959, *O.B. Miller 5934* (M); [Midlands Prov.] 18°29'S, 29°00'E, 17 Feb 1967, *M.C. Cole 246* (K); [Masvingo Prov.] Nuanetsi, 1500 ft, 20 Jan 1972, *J.I. Barnes 146* (K); [Matabeleland South Prov.] Matobo distr., 14 Apr 1973, *G. Norrgrann 326* (BR0000016286856); [Masvingo Prov.] Makoholi Exp. Station, 13 Sep 1978, *E. Senderayi 205* (BR0000016286825); [Manicaland Prov.] Nyanga, 1650 m a.s.l., 6 Mar 1981, *D. Philcox & al. 8871* (BR0000016286832, K); [Matabeleland North Prov.] Hwange distr., 14 Apr 1999, *C. Wengler 165* (BR0000013835217).

Arabia

Oman (new records): [Planta culta] Cultivated voucher originated from Dhofar Governorate, Ayn Rizat Spring, *H.D.V. Prendergast s.n.* (K); Dhofar, Salalah, 21 Sep 2001, *M. Raffaelli & al. 43* (FT); Dhofar Region, between Salalah & Mirbat Pista, 11 Sep 2002, *M. Raffaelli & al. 1023* (FT); Dhofar Region, Salalah to Mirbat, 600 m a.s.l., 22 Sep 2002, *M. Raffaelli & al. 269* (FT);

Saudi Arabia (new records): Wadi Kharar, nr the foot of the Taif escarpment granite, 1500 ft, 10 Feb 1980, *I.S. Collenette 1768* (K); [Mecca Prov.] 30 km SW of Taif town, 1830–2050 m a.s.l., 30 Jan 1988, *A.A. Fayed 1343* (M); Al-Baha Region, SE of Baljurashi, 7 Apr 1988, *A.A. Fayed 1394* (M);

Yemen (new records): Socotra Island, Aug 1880, *B. Balfour 39* (BM, K, LE); Socotra, 1897, *Th. Bent s.n.* (K); North Yemen, Jebel al Abid, 27 Aug 1937, *C. Rathjens 104* (BM); 14 km NW of Sana'a, 26 Sep 1981, *D. Podlech 35827* (MSB122469).

***Achyranthes aspera* L.**

Africa

Benin: Zou Dept., Dassa, 4 Nov 1998, *V. Adjakidjè & al. 2197* (BR0000016286450, K, W0333254, WAG1404336);

Cameroon: Southwest Region, Kupe vill., 24 Jan 1995, *M. Cheek & al. 7151* (WAG0075654);

Chad: Hadjer-Lamis Region, Djimlilo vill., 13 Dec 1969, *F.N. Hepper 4184* (BR0000013834210, K);

Comoros: Moroni, 30 Jul 1981, *H. Doutrelepont 1049* (BR0000013709099);

DR Congo: [Orientale Prov.] Nioka, 27 Jan 1946, *A.S. Taton 18* (K); [South Kivu Prov.] Uvira town, 780 m a.s.l., Aug 1951, *Marlier 1327* (WAG1404151); Virunga NP, Lulimbi Camp, 19 Dec 1981, *J. Van Gisel s.n.* (BR000000905112);

Egypt: [without location and date; old specimen from 19th century] *Fischer s.n.* (M) [Not shown on map due to unknown location];

Europa Island (French Southern and Antarctic Islands): Territory of a military camp, 10 Apr 2015, *J. Hivert & al. 1195* (P00956454);

Ethiopia: Omo-Bottego River, 11 Aug 1939, *R. Corradi 8594* (FT); [Afar Region] Amibara [distr.] Melka Sede, 1968–1969, *N. Longhitano s.n.* (FT, K);

Ghana: Legon [Accra], May 1985, *D.K. Abbiw 47250* (K, US03544302);

Kenya: nr Mombasa, Nov 1909, *E.A. Mearns s.n.* (BM); Kisumu, Feb 1915, *R.A. Dümmer s.n.* (BM, K); Mombasa town, 25 Aug 1981, *N. Tzvelev 424* (LE); Mombasa to Kilifi, road to Kaloleni vill., 16 Dec 1969, *J.M. Reitsma 440* (BR0000013834579, WAG1404166); Tana River distr., nr Tana River, 3 Mar 1977, *S.S. Hooper & C.C. Townsend 1163* (K); [Laikipia County] 18 km NE of Nanyuki town, 22 Oct 1977, *M.G. Gilbert 4881* (WAG1404402); Kilifi County, Kilifi, 23 Nov 1981, *V. de Meester-Manger Cats 210* (WAG1404209); Msambweni, 20 m a.s.l., 5 Aug 1982, *S.A. Robertson 3333* (K); [Nandi County] Kaimosi vill., 2 Nov 1984, *A. Hohl 106* (W0333211); Tana River distr., Tana Delta, 6 Aug 2010, *C. Leauthaud & al. 64* (K);

Liberia: [Maryland County] Cape Palmas, 17 Jun 1970, *J.G. Adam 25987* (P00695158);

Madagascar: Majunga [Mahajanga], 23 Apr 1912, *K. Afzelius s.n.* (K); [Androy Region] Ambovombe, 1931, *R. Decary s.n.* (BM); [Androy Region] Ambovombe, 9 Aug 1931, R. *Decary s.n.* (K); Nosy Be Island, 28 Jun 1983, *J. Frazier 661* (K); Ambahatra, 13 Jun 1998, *L. Gautier & al. 3352* (K); [Atsimo-Andrefana Region] Betioky to Ampanihy, 25 Aug 2003, *M. Andriamahay 603* (K); Menabe Region, Bekonazy, 5 Jun 2015, *N. Rakotonirina & al. 1079* (P01048115);

Mauritius (selected): [without exact location and date, early 19th century] *Hilsenberg s.n.* (BR0000013835422); [without exact location] 1819–1821, *F. Cohaut s.n.* (BM); 1879, [without exact location] *Sieber 146* (K, M0241516); Rose Hill, Jan 1953, *E. Rochecouste 3* (MAU0017605); Rodrigues Island, Jul 1970, *Th. Cadet 2754* (K); Albion, 18 Feb 1972, *J. Guého s.n.* (K, MAU0017611); Rodrigues Island, 1 May 1982, *J. Guého 20374* (MAU0017618); Gunners Quoin, Jul 1982, *D. Bullock & S. North 20508* (MAU0017612); Round Island, 29 Jul 2003, *M.C. Johansson 23547* (MAU0017613); Flat Island, 16 Apr 2005, *K. Pynee & J.C. Sevathian 24534* (MAU0017615);

Mayotte (French Overseas Department): Dzoumogne, [without date] *anonymous 4* (P00290533); [without exat location] 1855, *Boivin s.n.* (FI-WEBB154851); Bandrele, 29 Nov 2000, *J.-N. Labat & F. Barthelat 3320* (K);

Mozambique: [Nampula Prov.] Zambesi River, Boroma, 1892, *Menyharth 1197* (WU); [Sofala Prov.] Nova Chupanga [probably Chemba distr.] 22 Jul 1933, *Lawrence 55* (K); Beira town, Nov 1939, *A. Scarpa s.n.* (FT); [Maputo] Villa Luisa, 17 May 1965, *G. Caldeira & A. Marques 405* (WAG1404239); Tete distr., Tete–

Songo road, 7 Apr 1972, *J.M. de Aguiar Macodo 5257* (K); Nampula, 20 Jul 1979, *S. Macitela 25* (WAG1404231); Maputo, 26 Dec 1983, *D. Zunguse & al. 481* (BM);

Namibia: Windhoek Farm Finkenstein, 11 April 1966, *R. Seydel 4412* (LE);

Réunion (French Overseas Department): [without exact location, date and collector] *3* (MAU0017616); Saint-Leu, 3 Apr 2019, *E. Bidault & al. 4573* (P01085572);

Rwanda: nr Kigali, 1450 m a.s.l., 13 Oct 1974, *P. Auquier 4560* (WAG1404298);

São Tomé and Príncipe: São Tomé Island, Aug 1885, *A.F. Moller 684* (BR0000013833985);

Senegal: Dakar, Nov 1925, *L. Hauman s.n*. (BR0000013833879); Dakar, Oct 1950, *R.P. Berhaut 2093* (BR0000016286412);

Seychelles: Christmas Island, [without year] *J. Jackson s.n*. (BM); [without exact location] Sep 1871, *J. Horne 338* (K); Denis Island, 10 Mar 1962, *C. Jeffrey 1210* (K); Astove Atoll, 5 Mar 1968, *F.R. Fosberg 49707* (K); La Digue Island, 22 Dec 2005, *V. Bochkin & N. Bokal s.n*. (MHA);

Somalia: [Middle Juba Region] Bidi, 30 Jun 1913, *G. Paoli 448* (FT); [Bay Region] Burhakaba [town], 21 Sep 1929, *L. Senni 856* (FT); [Lower Shabelle Region] Merca town, 17 Nov 1935, *F. Bigi 108* (FT); [Lower Shabelle Region] South Qoryoley distr., Beynax Barre farm, 14 Jul 1989, *A.M.I. Barkhadle 276* (FT);

South Africa: [KwaZulu-Natal Prov.] nr Durban, Sep 1933, *A. Meebold 13051* (M);

South Sudan: [Central Equatoria state] Bahl al-Jabal, Terekeka [community], 7 Jul 1929, *N.D. Simpson 7267* (K); [Lakes Region] Shambe, 14 Jul 1929, *N.D. Simpson 7376* (BM);

Tanzania (selected): [Zanzibar] Pemba Island, [without date] *G.H. Vaughan 655* (K); Zanzibar, Sep 1873, *J.M. Hildebrandt 1150* (LE – right-hand specimen, M); [Tanga Region] Pangani, Jun 1890, *F. Stuhlmann 105* (M); [Tanga Region] Mashewa, 400 m a.s.l, Sep 1915, *A. Peter 13869* (B 10 0153181); [Mwanza Region] Mwanza town, 21 Oct 1925, *R.L. Davis 60* (K); [Lindi Region] Nachingwea, 1500 ft, 19 Apr 1955, *B. Anderson 1051* (BR0000013834777, K); Tanga Region, Boza, 3 Jul 1956, *R.E.S. Tanner 2972* (BR0000013834838, K); [Mara Region] Musoma town, 1 May 1959, *R.E.S. Tanner 4225* (K); Zanzibar [Unguja Island], Chukwani, 9 Apr 1961, *H.G. Faulkner 2805* (BR0000013835859, K); [Tanga Region] Korogwe town, 25 Nov 1962, *M.E. Archbold 14* (K); Tanga distr., Sawa, 14 May 1965, *H.G. Faulkner 3521* (BR0000013835071); [Kagera Region] Karagwe distr., Segora forest, 9 Feb 1968, *H. Faulkner 4073* (WAG1404277); Dodoma Region, Ikowa Dam, 900 m a.s.l., 29 Jul 1970, *M. Thulin & B. Mhoro 519* (K); Dar es Salaam, Oyster Bay, 11 Aug 1974, *J. Frazier 1067* (K); Tanga Region, Pangani town, 8 Jan 1993, *Limbach & Mshana 204* (M); [Tanga Region] Tanga town, 1 Sep 1995, *Waziri 152* (M); Zanzibar, Unguja Island, 22 Jun 2022, *A.P. Sukhorukov s.n*. (MW);

Uganda: West Nile distr., 10 Aug 1953, *R. Chancellor* 155 (K, M); 20 km W of Pakwach, 5 Oct 1974, *A.B. Katende 2338* (K);

Zimbabwe: [Masvingo Prov.?] Sabi, 800 ft, 14 Jun 1950, *H. Wild* 28079 (BM, M).

Arabia

Oman: Muscat, [without date] *Aucher-Eloy 9294* (P04559070); Bohar Farm, 20 Feb 1973, *C. Parker 158* (BM); Wadi Sahtan, 1400 m a.s.l., 4 Apr 1975, *J.P. Mandaville 6227* (BM); Dhofar, Salalah, 26 Sep 2015, *P. Escobar Garcia 1073* (W);

Saudi Arabia: see type of *Achyranthes argentea* var. *obovata*; Fatme [probably Wadi Fatimah near Jeddah], [without date, 19th century] *S. Fischer 95* (BR0000013457310);

United Arab Emirates: Emirate of Fujairah, Al Badiyah, 15 May 2020, *V.V. Byalt & M.V. Korshunov 2978* (LE01194673);

Yemen: Lahadj [Lahidj city], 26 Dec 1889, A. Deflers 180 (P04559065); Socotra Island, 21 Feb 1953, *G. Popov 99* (BM); Aden, Shaikh Uthman, Jan 1963, *J. Waring 185* (BM); Lahij Gov., Lahij town, 20 Mar 1988, *L. Boulos 17386* (BM).

Achyranthes mauritiana Moq. – see main text.

Achyranthes porphyrostachya Moq.

Africa

Angola: Luanda, [without date, probably mid-19th century] *F. Welwitsch 6530* (BM, BR0000013835101, K); [Namibe Prov.] Bero River, Aug 1859, *F. Welwitsch 6499* (BM, K); Benguela, Jul 1891, *Menyharth 12* (WU); Near the Kunere River between Kiteve and Humbe, 3 Jun 1900, *H. Baum 961* (BM – left-hand specimens, K0002437271, M); nr Cunene Revier, Ruacaná, 9 Jun 1937, *A.W. Exell & F.A. Mendonça 2798* (BM); Huila Prov., Lubango, 29 May 1974, *A. Borges & al. 409* (K);

Benin: without exact location and date, *G. le Testu 189* (BR0000013834050, left-handed specimen);

Botswana: N'Garni, 13 May 1930, *Vernay-Lang Kalahari Expedition 28743* (BM, M); [Central district] nr Mopipi, 850 m a.s.l., 17 Apr 1973, *G. Glanville 537* (BR0000013835286, K, M); Kwara floodplain, 1 May 1973, *P.A. Smith 561* (K); Gaborone, 3250 ft, 12 Feb 1974, *P.J. Mott 153* (K); Kwando, 1000 m a.s.l., 19 Apr 1977, *D.T. Williamson 127* (K); Ngamiland distr., N of Maun, 920 m a.s.l., 28 Mar 1987, *D.G. Long & D.A.H. Rae 444* (K);

Burundi (selected): [Bururi Prov.] nr Kitete [Gatete] vill., Nov 1922, *Elskens 137* (BM); Bujumbura, 850 m a.s.l., 28 Sep 1966, *J. Lewalle 1040* (BR0000013837181); Bujumbura, Sep 1967, *J. Lewalle 1040* (K, WAG1404281); [Bubanza Prov.] Rukoko, 20 Feb 1980, *J. Bouharmont 12955* (BR0000013837143); [Rumonge Prov.] Gitaza, 780 m a.s.l., 5 Aug 1980, *P. Ndabaneze 980* (BR0000013837228); Bujumbura, 5 May 1988, *J. Saintenoy-Simon 8* (BR0000013835781);

Cameroon (first records): [Far North Prov.] Waza Wild Life Reserve, 22 Jan 1966, *A.J.M. Leeuwenberg 7484* (K, WAG1404136); West Region, Baranka, 27 Apr 2005, *B. Tchiengue & al. 2147* (K);

Cape Verde: São Vicente Island, Monte Verde, *herb. Hookerianum 65* (K001134168);

Chad: [Hajer-Lamis Region] Djimtilo, 13 Dec 1969, *F.N. Hepper 4184* (BR0000013834210);

Djubouti: French Somalia, [Tajourah Region] Randa, 1000 m a.s.l., 29 Sep 1956, *E. Chedeville 1655* (FT);

DR Congo: [South Kivu Prov.] Luvungi, Dec 1907, *P. Aguzzi 56* (BR0000016287327); [South Kivu Prov.] Kabare [Territory] 25 Aug 1914, *J. Bequaert 5447* (BR0000016287389); Albert [Mwitanzige] Lake, Aug 1935, *H. Bredo 1505* (BR0000016287204); [Ituru Prov.] Kasenyi, Nov 1935, *H. Brédo 1793* (BR0000016287228); Katanda [Territory], Sep 1937, *J. Lebrun 7617* (K); [North

Kivu Prov.] Ruindi, Oct 1937, *J. Lebrun 7997* (K); [Maniema Prov.] Kalulu vill., May 1939, *H. Brédo 2874* (BR0000013836740); [Lualaba Prov.] Kasumbi, Apr 1940, *P. Quarré 6297* (BR0000013837334); Virunga NP, Lake Edward, 19 Jun 1945, *R. Germain 3937* (BR0000013836375); Ruzizi Plain, Jan 1950, *R. Germain 5558* (BR0000013836382); [Haut-Katanga Prov.] Mitwaba [Territory], 17 Jun 1955, *J. Brynaert 395* (BR0000013708948); [South Kivu Prov.] Uvira town, 27 Aug 1955, *J.-J. Symoens 1340* (BR0000013836634); [South Kivu Prov.] Kalonge, 1060 m a.s.l., Oct 1956, *G.F. de Witte 13638* (K); [Maniema Prov.] Kalinga, 1050 m a.s.l., Nov 1956, *G.F. de Witte 13931* (K); nr Lake Albert, 5 Nov 1956, *G.F. de Witte 13790* (BR0000013836245); North Kivu Prov., Albert [Virunga] NP, Nov 1956, *G.F. de Witte 13901* (K); South Kivu Prov., Kalehe Territory, Kifunga, 1000 m a.s.l., Jan 1957, *G.F. de Witte 13990* (K); North Kivu Prov., Rutshuru town, Feb 1957, *G.F. de Witte 14173* (K); [South Kivu Prov.] Kahuzi, 20 Jul 1976, *L. Pauwels 5641* (BR0000013836580); [North Kivu Prov.] Beni Zone, Ishango, 28 Nov 1979, *H. Breyne 3859* (BR0000013835750);

Egypt: Aswan, nr Nile River, Jan 1904, *R. Muschler s.n*. (K);

Eritrea (selected): [Debub Region] Akrur, 1900 m a.s.l., 10 Mar 1892, *G. Schweintfurth & D. Riva 1025* (K); [Northern Red Sea Region] Nakfa town, 19 May 1892, *A. Terracciano & A. Pappi 913* (FT); [Debub Region] Lebca, 22 May 1892, *A. Terracciano & A. Pappi 1036* (FT); [Southern Rea Sea Region] Adarte vill., 26 Jan 1893, *A. Terracciano & A. Pappi 2762* (FT); [Northern Red Sea region] Agametta vill., 19 Mar 1893, *A. Pappi 3127* (FT); [Debub Region] Sala Dharo, 2500 m a.s.l., 7 Oct 1902, *A. Pappi 2310* (FT); nr Dwarba [town], 1900 m a.s.l., 8 Oct 1902, *A. Pappi* 504 (FT); [Anseba Region] Garassi, 13 Oct 1905, *A. Pappi 6508* (FT); [Gash-Barka Region] Algata, 450 m a.s.l., 31 Mar 1909, *A. Fiori 955* (FI); Habab, Oazat, 21 Apr 1909, *A. Pappi* 8388 (FT);

Eswatini: nr Mankaiana, 19 Mar 1959, *R.H. Compton 28663* (BM); Lubombo Region, 27 Apr 2024, *L. Loffler* (image available at: https://www.inaturalist.org/photos/375635369);

Ethiopia (selected): see type of *A. aspera* var. *robusta*; Amhara Region, Dembia, 8 Sep 1909, *Chiovenda 1951* (FT); [Rift Valley Prov.] Zuai Lake, 24 May 1937, *L. Senni 615* (FT); [Southern Nations, Nationalities, and Peoples Region] Bonga, Nov 1937, *D. Saccardo s.n*. (FT); [Oromia Region] Bishoftu [Debre Zeit] town, 1938, *P. Benedetto 57* (FT); Omo River basin, Rive del Caschei, 3 Jul 1939, *R. Conradi 3223* (K); [Oromia Region] Bishoftu town, 6000 ft, Oct 1951, *C. Curli 164* (BM); Idli valley, 45 km ESE of Harar, 1550 m a.s.l., 26 Jul 1961, *W. Burger & A. Getahun 371* (K); Shoa Prov., 17 km S of Addis Ababa, 6830 ft, 24 Nov 1961, *F.G. Meyer 7517* (K); [Oromia Region] 4 km S of Alem Tena town, 1720 m a.s.l., 13 Jul 1963, *E. Beals 262* (K); 8 km N of Addis Ababa, 2800 m a.s.l., 11 Oct 1965, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 8217* (BR0000013834364); [Afar Region] 50 km W of Awash station, 800 m a.s.l., 8 Apr 1966, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 10663* (BR0000013834388, WAG1404312); Harari Region, 20 km SE of Harar town, 5 Nov 1966, *W.J.J.O de Wilde & B.E.E. de Wilde-Duyfjes 9962* (WAG1404313); nr Alemaya, 2030 m a.s.l., 10 Jul 1967, *E. Westphal & M.C. Westphal-Stevels 509* (BR0000013834432); Shao Prov., E of Maki town, 5440 ft, 6 Jun 1968, *D. Hundessa 15* (K); Awash valley, 4 miles W of Metehara, 10 Aug 1968, *P.M. Headley 225* (K); NE shore of Lake Abiyata, 1550 m a.s.l., 15 Apr 1969, *J.J.F.E. de Wilde 4908* (BR0000013834425, WAG1404315); Extreme South West, Omo River valley, 1300 ft, 1 Jul 1969, *C.J. Carr 640* (BR0000013834326, K); [Harari Region] Fafan River, 1590 m a.s.l., 7 Jun 1972, *C.J.P. Seegeler 2305* (BR0000013837631, WAG1404320); [Oromia Region] Jimma, 20 Aug 1972, *C.J.P. Seegeler 2397* (BR0000013837648, WAG1404317); [Somali Region] 70 km from Dire Dawa town, 18 Oct 1972, *C.J.P. Seegeler 2700* (WAG1404316); [Oromia Region] Zwai Lake, Feb 1973, *O. Polunin 11594* (K); [Oromia Region] Debre Zeit town, 1800 m a.s.l., 6 Oct 1976, *L. Boulos 9725* (WAG1404318); [Somali Rergion] Sheekh distr., Bokh Reserve, 20 Nov 1979, *C.J. Hansen & al. 6456* (K); Omo NP, 3 Aug 2007, *C. Godefroid 83* (BR000001384340);

Kenya (selected): [Makueni County] Kibwezi town, 9 Sep 1906, *G. Scheffler s.n.* (AMD24172, BM, K, WAG1404333); Nairobi, 1915, *W.J. Dowson 288* (K); Nairobi distr., 14 Jul 1924, *J. MacDonald 769* (FT); nr Mariakani town, Mombasa, Feb 1930, *Thomas s.n.* (BR0000013834630); [Narok County?] Maasai Nature Reserve, 15 Sep 1947, *P.R.O. Bally 5361* (K); Nairobi, 1700 m a.s.l., 30 May 1949, *R.A. Maas Geesteranus 4857* (BR0000013834623, L1673905); Meru, Feb 1951, *A.D. Hancock 121* (K); [Baringo County] 10 miles E of Eldama Ravine, 5400 ft, 8 Feb 1952, *A. Bogdan 4459* (K); [Marsabit County] Mayale, 3700 ft, 21 Apr 1952, *J.B. Gillett 12868* (FT, K, M); [Baringo County] Hannington [Bogoria] Lake, 19 Jul 1953, *P.R.O. Bally 9036* (K); Narok distr., Narosura, 6200 f, 16 Aug 1961, *Glover & al. 2431* (BR0000013837693); [Narok County] Oltarakwai, 8000 ft, 18 Aug 1961, *Glover & al. 2525* (BR0000013834517, K); Meru Game Reserve, 16 Jun 1963, *S.G. Mattenge 86* (K); [Machakos County] Kutumani, 5300 ft, 23 May 1966, *P. Ndunda 37* (BR0000013834692); Naivasha distr., 6200 ft, 27 Aug 1966, *E. Polhill 192* (K); [Nakuru County] Nakuru Lake, 2200 m a.s.l., Oct 1966, *Duvignaud s.n.* (BR0000013834500); [Makueni County] N of Nunguni, 1890 m a.s.l., 10 Mar 1968, *O.M. Mwangangi 869* (K); Isiolo distr., 14 Apr 1971, *Z.J. Kimani 269* (BR0000013834531, K); [Kilifi County] nr Malindi, 20 Mar 1973, *G.W. Sangai 15585* (M); Nyeri distr., Nyeri–Kiganjo road, 1770 m a.s.l., 1 Jun 1974, *D.B. Faden & al. 673* (K); [Tana River County] Galana Ranch, 18 Jun 1975, *P.R.O. Bally 16885* (BR0000013834586, FT); Kalisia Hills, 6300 ft, 14 Aug 1977, *Ichikawa 745* (K); [Rift Valley Prov.] West Suk [West Pokot County], Sigor, 3000 ft, 30 Jul 1978, *E. Meyerhoff 91* (K); Coast Prov., nr Gotani vill., 30 Nov 1979, *J.M. Reitsma 374* (BR0000013834678); [Baringo County] Marigat [town], 14 Apr 1983, *A. Mather 9* (K);

Lesotho: Leribe [Hlotse], 1914, *Dieterlen 986* (BM);

Malawi: Ntandamula Mt. 30 May 1903, *W. Busse 2738* (BR0000013834869); Central Region, Lilongwe distr., 1240 m a.s.l., 21 Mar 1970, *R.K. Brummitt 9250* (K); Central Region, Mchinji distr., nr Namitete, 1130 m a.s.l., 30 Mar 1970, *R.K. Brummitt 8430* (K); Southern Region, nr Lake Chilwa, 640 m a.s.l., 1 Jun 1970, *R.K. Brummitt & C.H. Williams 11206* (K); Lifidzi Goat Breeding Centre, 18 May 1985, *A.J. Salubeni & al. 4203* (K); [Central Region] Salima distr., 19 May 1985, *I.H. Patel & W. Nachamba 2160* (W0333210); Lake Chilwa, 1989, *anonymous 2* (K);

Mali: [Mopti Region] Sarredina, 7 May 1952, *J.T. Davey 96* (K);

Mozambique: Lourenço Marques Prov., Bombay, Jun 1893, *F. Quintas 150* (BR0000013835248); East coast of Nyassa [Malawi] Lake, 22 Sep 1900, *W.P. Jonson 144* (K); [Gaza Prov.] Guijá, 6 Jun 1947, *J.J. Pedrogão 247* (BR0000013835279);

Namibia: Kaokoveld, Otyrtambi, 3 Mar 1885, *W. Belik 43* (WU); Amboland [Ovamboland], Sep 1886, *H. Schinz 7* (Z-000070709); [Otjozondjupo Region] Hamakari, 21 Jan 1939, *O.H. Volk 1182* (M); [Kunene Region] Omuramba, 6 Apr 1953, *H. Walter & E. Walter 240* (M); [Kunene Region] nr Outjo, 4 Apr 1955, *B. de*

Winter 3039 (K, M); Windhoek Bergland, 1400 m a.s.l., 26 Mar 1963, *R. Seydel 3467* (BR0000013835323); Windhoek Bergland, Finkenstein [Estate], 2000 m a.s.l., 11 Apr 1966, *R. Seydel 4412* (M); [Erongo Region] Otjimbojo, [without date] *H. Kinges 3383* (M);

Rwanda (selected): Kigali, 1600 m a.s.l., Feb 1933, *A. Becquet 411* (BR0000013708924); [nr Kigali] Gabiro, 1500 m a.s.l., 4 Feb 1942, *R. Germain 1133* (BR0000013837037); [Western Prov.] Rubona 22 Jul 1956, *G. Michel 4722* (BR0000013837051); [Northern Prov.] Byumba, 1400 m a.s.l., 4 Apr 1957, *G. Troupin 3115* (K); [Eastern Prov.] Kibungo, 1450 m a.s.l., 7 Apr 1958, *G. Troupin 6860* (BR0000013837112, K); Kibungo [Eastern Prov.] 1300 m a.s.l., 17 Sep 1969, *G. Bouxin & M. Rodoux 902* (FT); [Northern Prov.] Shyorongi, 15 Apr 1970, *G. Bouxin & M. Radoux* 1723 (BR0000013837020); [Western Prov.] Bugarama, 10 Aug 1974, *P. Auquier 3627* (BR0000013837006); Kigali, 5 Sep 1974, *J. Lambinon 1093* (BR0000013837884); [Eastern Prov.] Isle Mareba, 1300 m a.s.l., 22 Jul 1978, *G. Troupin 16189* (K); [Northern Prov.] Nyagahanga, 16 May 1982, *M. Aubroeck 5094* (BR0000013836993);

Senegal: [without location and date] *Sieber 57* (G00688993, K, M0241521); [without exact location] 1906, *L. Farmar 23* (BM); Dakar, 1948, *J.G. Adam s.n*. (K); Dakar, 1950–1951, *R.P. Berhaut 2094* (BR0000013833818); Cap Vert-Thiès Region, 8 Nov 1974, *D. Thoen 7322* (BR0000013833886);

Somalia: [Middle Shabelle Region] Mahaadei Uen [Mahaday Weyne], 1922, *R. Confalone 55* (FT); Jubba River, 1926, *P. Gorini 180* (FT); [Bakool Region] Xudur town, 17 Aug 1929, *L. Senni 658* (FT); Somaliland, Hargeisa, 4300 ft, 21 May 1932, *J.B. Gillett 3924* (FT, K); [Lower Shabelle Region] Merca town, May 1953, *T. Sacco & al. 56* (FT); [Jubaland State] Bardera, 30 Sep 1953, *P.R.O. Bally 9404* (K); Sagaleh Region, Migiurtinia, 23 Jan 1954, *G. Merla & al. s.n*. (FT); [Middle Shabelle Region] nr Mahaddei Uen [Mahaday Weyne] town, 13 Sep 1959, *G. Moggi & R. Ravazzano 2529* (FT); [Lower Shabelle Region] nr Danane, 21 Sep 1959, *G. Moggi & R. Bavazzano 2727* (FT, K); between Brava & Modun, 23 Sep 1959, *G. Moggi & R. Ravazzano 2783* (FT); [Lower Juba Region] Jubbada Hoose, Lake Salamo, 28 Oct 1971, *G. Moggi & R. Ravazzano s.n.* (FT); [Sahil Region] Sheikh town, 4600 ft, 6 Jun 1973, *J.R. Wood 137* (K); Mogadisho, 8 Sep 1975, *R. Ravazzano 1105* (FT); [Somaliland, Togdheer Region] Burao distr., 23 Dec 1977, *Kazmi & al. 126* (BR0000013834456, M); Central Rangelands, near sea coast, 5°57'N, 48°57'E, 28 May 1979, *J.B. Gillett & al. 22131* (K); [Sahil Region] Northern Rangelands, 9°59'N, 43°08'E, 1540 m a.s.l., 13 Jul 1981, *J.J. Beckett 1275* (K); [Lower Shabelle Region] Afgooye, 11 Aug 1981, *S. Pignatti s.n.* (FT); [Middle Shebelle Region] Mahaday Weyne vill., 28 Feb 1983, *R.J. Douthwaite 1* (K); [Lower Juba Region] nr Goobweyn vill., 15 Aug 1986, *C.F. Hemming & I. Deshmukh 187* (K); Middle Juba Region, 8 Sep 1986, *J. Madgwick 63* (K); [Lower Shabelle Region] Genale, Uebi Scebeli, 11 Nov 1986, *M. Tardelli 461* (FT); Shabeellaha Hoose Region, 47 km SW of Afgol [Afgooye], 60 m a.s.l., 11 Jun 1987, *V. Alstrup & A. Michelsen 146* (BR0000013837600, K);

South Africa: see type of *A. robusta*; [Mpumalanga Prov.] Lydenburg town, Dec 1894, *F. Wilms 1263* (AMD24173, BM, L1673919, M, WU); Johannesburg, Jan 1903, *Rand 1148* (BM); [Limpopo Prov.] nr Petersburg [Polokwane], 4000 ft, Feb 1904, *H. Bolus 11155* (BOL0291963); [North West Prov.] Rustenburg, 4500 ft, 13 Feb 1904, *O. Nation 168* (BOL0291962); [Mpumalanga Prov.] Nelspruit [Mbombela], Mar 1931, *Lieberberg 2363* (K); [Limpopo Prov.] Pietersburg, 28

Jun 1961, *Strey & Schlieben 8593* (M); Johannesburg, 14 Mar 1962, *M. Macnae 1471* (BOL0291956); KwaZulu-Natal Prov., Nsumu, 6 Apr 1966, *E.J. Moll 3149* (BR0000013835354); Transvaal Region, Johannesburg distr., 5300 ft, 29 Jul 1967, *J. Scheegers 1443* (M); Transvaal Prov., Silverton [nr Pretoria], 16 Feb 1979, A. *Balsinhas 3379* (BR0000013835293); Kruger NP, nr Crocodile Bridge, 24 Mar 2007, *O. Maurin 1393* (WAG1487727);

South Sudan: [Central Equatoria state] Bahl al-Jabal 22 Feb 1901, *anonymous 71* (K); Upper Nile State, Khor Daleib, 17 Jun 1929, *N.D. Simpson 7207* (BM, K); [Unity State] nr Bentiu, Nov 1936, *E.E. Evans-Pritchard 1* (K); [Eastern Equatoria State] nr Kapoeta, 30 Aug 1941, *Myers 13979* (K); [Jonglei State] Jongol's Post, 30 Aug 1951, *M.I. Sherif 3993* (K); Ilemi Triangle, 1350 ft, 10 Aug 1969, *C.J. Carr 737* (BR0000013834258); 80 km N of Bor town, Djam-Djam, 440 m a.s.l., 19 Feb 1981, *J.M. Lock 41* (K);

Sudan: nr El Obeid town, Jul 1875, *J. Pfund 876* (K); Kordofan, Malbeis, 1879, *J. Pfund 286* (K); Khartoum, Dec 1902, *Broun 476* (K); El Gezira [Al Jzirah] State, Wad Medani town, 11 Nov 1965, *W.J.J.O de Wilde & al. 5731* (BR0000013834289, WAG1404410);

Tanzania (selected): [Kilimanjaro Region] Moshi distr., 9300 ft Oct 1927, *anonymous 788* (K); [Kagera Region] Bunazi vill., 1935, *H. Gillman 508* (K); [Katavi Region] Rukwa Lake, 3 May 1935, *Michelmore 1137* (K); [Shinyanga Region] Shinyanga town, Nov 1938, *anonymous 8155* (K); Rukwa valley, Kasanga Mbuga, Mar 1952, *W. Siame 132* (BM); [Mwanza Region] Mwanza, 22 Apr 1952, *R.E.S. Tanner 676* (K); [Tanga Region] Korogwe, 14 Jul 1952, *H.G. Faulkner 994* (BR0000013837709); nr Kwakuchinja, 1080 m a.s.l., 21 Jul 1956, *E. Milne-Redhead & P. Taylor 11192* (BR0000013835873, K); Tanga Region, Kigoma Region, Kibwesa town, Tanganyika Lake, 10 Jul 1958, *T.G. Jefford & al. 55* (BR0000013834999, K, WAG1404269); [Morogoro Region] nr Mgeta vill., 980 m a.s.l., 17 Jul 1958, *A. Gilli 155* (W0333233) together with *A. acuminata*; Lushoto distr., Mombo Forest Reserve, 1300 ft, 10 Sep 1960, *S.R. Semsei 3091* (K); [Tabora Region] Nzega distr., Webbere Plain, 1050 m a.s.l., 1961, *H.M. Richards 13472* (K); [Arusha Region] Olongogo, 14 Dec 1962, *J.B. Newbould 6384* (K); Tanga Region, Kideleko, 2000 ft, 29 Jun 1965, *M.E. Archbold 459* (K); Arusha Region, Arusha NP, 1371 m a.s.l., 17 Nov 1968, *H.M. Richards 23312* (K, M); [Iringa Region] Great Ruaha River, Msembe, 2700 ft, 20 Aug 1969, *P.J. Greenway & K. Kanuri 13781* (K); road from Longido to Engare Naibor, 1524 m a.s.l., 25 Mar 1970, *H.M. Richards 25680* (BR0000013837723, K); [Morogoro Region] Kilosa distr., 1700 ft, 25 Jun 1973, *P.J. Greenway & K. Kanuri 15235* (K); [Ngorongoro Conservation area] Ang'ata Kiti Plain, 30 Oct 1989, *S. Cuwa 3006* (K); Manyara Region, nr Babati vill., -4.053593, 35.775181, 29 Nov 2021, *A.P. Sukhorukov s.n.* (MW); Kilimanjaro Region, Moshi distr., way from Arusha town to Moshi vill., -3.335736, 37.284384, 15 Jun 2022, *A.P. Sukhorukov s.n.* (MW);

Uganda (selected): [Central Region] Kipayo vill., Aug 1914, *R. Dümmer 1006* (BM); 100 miles NW of Kampala, 4200 ft, Jun 1915, *E. Boernmueller 2681* (K); base of Debasien [Katam] Mount, Jan 1936, *W.J. Eggeling 2527* (K); Kasenyi, 27 May 1953, *D. van der Ben 472* (K); Tooro [sub-region], 25 Jan 1962, *J.P. Loveridge 459* (K); nr Kasanda, 10 Aug 1974, *A.B. Katende 2235* (K); Mt. Elgon, Sasa Trail, 3150 m a.s.l., 7 Jan 1997, *K. Wesche 739* (K); [Central Region] Mawokota County, Nkozi Hill, 20 Feb 2011, *S. Santini 393* (FT);

Zambia: [Western Prov.] Sesheke, 1910, *A.E. Gardner 486* (K); [Central Prov.] Mumbwa, 1911, *Macaulay 687* (K) together with *A. annua*; [Southern Prov.] Bambwe Forest, 1934, *J.D. Marin 643* (K); [Southern Prov.] Namwala distr., 1934–1935, *J.G. Read 36* (BM, K); [Western Prov.] Kalangola, Jul 1939, *H.J. Bredo 3168* (BR0000013708825); [Southern Prov.] Mapanza, 12 Mar 1953, 3500 ft, *E.A. Robinson 124* (BR0000013835149, K); Lusaka distr., 22 Jun 1956, A. *Angus 1348* (K); Tanganyika Lake, Casawa sand dunes, 1050 m a.s.l., 14 Apr 1957, *H.M. Richards 9219* (K); Northern Prov., Kampinda, 2950 ft, 25 Jul 1962, *P.J. Tyrer 113* (BM);

Zimbabwe (selected): Salisbury [Harare], 4800 ft, Mar 1906, *F. Eyles 299* (BOL0291961); Salisbury [Harare], 27 May 1914, *O. Craster 129* (K); Bulawayo distr., 1930, *E. Cheeseman 29* (BM); [Central Prov.] Concession town, Apr 1931, *R.W. Jack 3932* (BM); Salisbury [Harare] city, 27 Jul 1931, *H.B. Gilliland 85* (BM); Bulawayo town, Nov 1933, *A. Meebold 11801* (M); [Manicaland Prov.] Umtali [Mutare] city, 1956, *N.C. Chase 207* (BM); [Midlands Prov.] Gokwe [town], 23 Apr 1964, *M.G. Bingham 1292* (BR0000013835200, M); [Mashonaland East Prov.] Beatrice farm, 18 Apr 1972, *L.C. Leach 14885* (BR0000013835224); [Matabeleland North Prov.] Matetsi, 23 May 1975, *P. Gande 26* (K); [Mashonaland West Prov.] Great Dyke, 19 Feb 2000, *Th. Baudesson 154* (BR0000009048782, WAG1404330).

Arabia

Oman: nr Shurayjab, 6000 ft, 19 Mar 1972, *J.P. Mandaville 3619* (BM); nr Bani Habib vill., 5700 ft, 19 Mar 1972, *J.P. Mandaville 3640* (BM); 43 km North of Salalah, nr Aqabat al Hatab, 600 m a.s.l„ 21 Sep 1977, *A. Redcliffe-Smith 5126* (K); Dhofar, Jebel Qara, 180 m a.s.l., 23 Sep 1992, *S. Ghazanfar 2098* (BR0000023108004); Dhofar, Salalah to Thumrayt, 730 m a.s.l., 14 Sep 2002, *M. Raffaelli & al. 1196* (FT);

Saudi Arabia: nr Mekkah, 21 Nov 1857, *W. Schimper 944* (HBG503188, L1673920); 14 km E of Khamis Mushait town, 20 Oct 1969, *J.P. Mandaville 2522* (BM); Jeddah–Taif road, 3500 ft, 3 Feb 1980, *I.S. Collenette 1709* (K); Asir, 1984, *H.A. Fatih 35* (BM); Al-Bahah Region, 19 Feb 1987, *A.A. Fayed 1285* (M);

Yemen: Hadramaut, 15 May 1939, *H. Wissmann 3025* (BM); Kharaiba, Wadi Duan [Dawan], 26 Aug 1950, *K.M. Guichard 395* (BM); between Sana'a & Hodeidah, 13 Nov 1962, *G. Popov 20* (BM); T'aiz, Ibb road, 19 Nov 1971, *M. Brunt 2381* (BM); Jibla, 8 Jan 1974, *J.R.I. Wood 253* (BM); Sa'dah Prov., nr Furlanis camp, 22 May 1981, *P. Cuccuini 32-278* (FT); [Sanaa Governorate] 31 km ENE of Manacha [Manakhah], 5 Oct 1981, *anonymous 36453* (MSB122470); Ibb Governorate, nr Ibb, 2000 m a.s.l., 22 Jul 1983, *R. Spellenberg s.n.* (K); Dhala town, 1450 m a.s.l., 10 Jun 1987, *L. Boulos & al. 16717* (BM); Wadi Mursel, 2 km W of Hadaba Assufla vill., 14 Jan 1996, *M. Van Slageren & W. Saeed 189* (K); nr Sana'a, Wadi Dhar, 2500 m a.s.l., 9 Mar 1996, *P. Hein & E. von Raab-Straube 154 & 917* (W0333236, M); Al Mahrah Governorate, between Al Faydami & Hawf vill., 950–1150 m a.s.l., 23 Nov 1999, *P. Hein 6745* (E00540183, W0333225).

Other Asian countries

India: Madras [Chennai city] [without date, probably mid-19th century, *anonymous s.n.*] (K); [Sate of Karnataka] Southern Maratha County & North Canara, 1879, *Schlagintweit s.n*. (BM); Kashmir Region (disputed area between India &

Pakistan] Darar vill., 2 Sep 1887, *J.R. Drummond 26471* (K); [State of Karnataka] Hassan distr., 20 Sep 1971, *K.N. Gandhi 2058* (K); [State of Tamil Nadu] Dgarmapuri, 900 m a.s.l., 13 Nov 1979, *K.M. Matthew 24561* (K); [State of Karnataka] Mandya distr., 12 Feb 2014, *K.S. Rao & al. 139* (JSB-0278 – image!).

Pakistan: Punjab, [without date, mid-19th century] *T. Thomson s.n.* (M); nr Karaha Lake [probably nr Sakesar], 3500 ft, 14 Sep 1902, *J.R. Drummond 14572* (K).

Achyranthes seychellensis Sukhor.

– see main text.

Achyranthes sicula (L.) All.

Africa

Algeria (selected): Algiers, Feb 1832, *W. Schimper s.n.* (L1673836); La Calle, 24 Jul 1843, *Durieu s.n.* (P04992333); Cherchell town, 1875, *E. Cosson s.n.* (K); El-Kettar, nr Dellys, 40 m a.s.l., 1877, *A. Meyer 1828* (FI, K); nr Algiers, Apr 1879, *C. Allard 2601* (K); Kouba, Jun 1879, *M. Gandoger s.n.* (BM); Bougie [Bejaia], May 1896, *E. Reverchon 84* (M, P0518080, WU); Guyotville [Ain Benian], 29 May 1919, *Ch. D'Alleizetti s.n.* (M, MA-01-00030124); [nr Algiers] Bouzaréah, 20 Apr 1953, *L. Delvosalle 3278* (BR0000023107991); Philippeville [Skikda town] 17 Aug 1954, *Doppelbaur 259* (M); between Algier & Bouira, 6 May 1971, *P.H. Davis 51963* (BM);

Cape Verde: Santo Antão Island, Agua das Caldeiras, 1430 m a.s.l., 23 Apr 2008, *J. Lambinon 77* (BR000000508604);

Egypt: Cairo, Nile valley, 1880, *G. Schweinfurth 229* (K); Cairo, 1886, *anonymous s.n.* (BR0000023108622);

Morocco (selected): Tanger, Apr 1871, *J. Ball s.n.* (K); Bou Regreg River, 1888, *anonymous s.n.* (K); Tanger, 25 Jun 1913, *C.-J. Pitard 1494* (K); Rabat, 21 Apr 1921, *E. Jahandiez s.n.* (RAB101204); Chaouia, 21 Apr 1924, *E. Jahandiez 167* (BM); Jebel Zem-Zem, 17 May 1930, *Pont Quer 174* (BM); Yassin, 25 Jun 1930, *Sennen & Mauricio 7700* (FI, RAB101207); Fedala [Mohammedia], Mar 1933, *anonymous 17* (K); Segangan, May 1934, *Sennen & Mauricio 9555* (BM); Douar Zyatene, 9 Jun 1956, *Bertault 157* (RAB101208); Oued Mellah [River], NE of Casablanca, 13 Apr 1972, *P.H. Davis 54423* (BM); Rabat, 19 May 1973, *J. Lewalle 7153* (BR0000023107984, M); Temara, 3 Mar 1976, *J. Lewalle 8195* (BR0000023108448, FI, RAB50567); Mehdia, 13 May 1978, *M. Naya s.n.* (BR0000024611862); Ain Harrouda, 5 Feb 1981, *D. Petit s.n.* (RAB64080); nr Rabat, 2 May 1987, *D. Podlech 43475* (M); Ladera NE of Jebel Imzi, 1150 m a.s.l., 16 Apr 2007, *T. Buira & J. Calvo 255* (MA-01-00758373, W0333274); Tiznit-Aït o Abderrahmane, 29.77347, -9.27243, 680 m a.s.l., 1 Feb 2021, *M. Chambouleyron s.n.* (CHAMB); Labaarir, 30.47088, -9.11964, 30 Dec 2021, *J.-F. Léger s.n.* (ECWP); Moullay Bousselham, Dlalha, 34.84363, -6.15838, 10 m a.s.l., 6 Oct 2023, *M. Chambouleyron s.n.* (ECWP);

Spain (Canary Islands; selected): Tenerife, Feb 1845, *E. Bourgeau 23* (BM, K005770144); La Palma, 400 m a.s.l., 13 Oct 1934, *M. Dinklage 3181* (BM, BR0000023108424, K005770160); Gran Canaria, 31 Jul 1940, *R.J. Andrews 29* (K005770154); Tenerife, Punte del Ancon, 26 Mar 1972, *J.L. de Sloover 72* (BR0000022706492); Hierro, 500 m a.s.l., 17 Mar 1973, *A.E. Aldridge 1317* (BM); Tenerife, Candelaria, 15 Mar 2004, *F. Verloove 5571* (BR0000012253821); Tenerife, 29 Nov 2008, *A. Seregin & I. Seregina s.n.* (MW10586318);

Tunisia: [Cape Bon] Sidi Rais, 24 Apr 1953, *Pottier-Alapetite s.n.* (MPU000626); [Nabeul Governorate] Hammamet, 9 Apr 1968, *H. Hertel 8221* (M); Ichkeul NP, 1978–1979, *J.M. Fay 932* (K).

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Research Article

Revisiting the genus *Tulipa* (Liliaceae) in Kazakhstan, the country with the richest tulip diversity worldwide

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Abstract

The genus *Tulipa* L., belonging to the Liliaceae family, has significant economic, horticultural, and ecological importance and is culturally revered in various regions worldwide. The total number of *Tulipa* species, including 90–120 taxa, varies based on different sources. Globally, Kazakhstan has one of the highest diversities of *Tulipa* species, most of which are threatened. In this study, we update and revise the *Tulipa* species in Kazakhstan based on field observations and an extensive herbarium specimens' survey. A total of 41 taxa were identified, including 13 species endemic to Kazakhstan, among which seven species have been assessed as threatened globally. Furthermore, we gathered 1,942 occurrence records of 41 *Tulipa* taxa to analyze spatial arrangement of *Tulipa* species richness in Kazakhstan. Based on these results, we identified 22 grid cells with a high diversity of tulip species in southern Kazakhstan. We also present taxonomic key for all *Tulipa* species occurring in Kazakhstan, along with comments on their general distribution, habitat, phenology, distribution map, and conservation status. In addition, a color plate for each species is provided. Overall, our study provides valuable insights into the conservation status, distribution patterns, and biodiversity of *Tulipa* species in Kazakhstan, laying a foundation for targeted conservation efforts and further research in the region.

Key words: Conservation, endemism, species pattern, threatened species, *Tulipa*

Introduction

Tulipa L. species, belonging to the Liliaceae family, have significant economic, horticultural, ecological, and aesthetic importance, are culturally revered in various regions worldwide (Pavord 1999). However, the total number of *Tulipa* species varies among sources; for example, 104, and 95 taxa have been accepted in the World Checklist of Selected Plant Families (WCSP 2024) and

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Plants of the World Online (POWO 2024), respectively. Although Christenhusz et al. (2013) revised the *Tulipa* genus to include 76 accepted species, several new *Tulipa* species have since been discovered (de Groot and Zonneveld 2020; Rukšāns and Zubov 2022; de Groot and Zonneveld 2024).

The bulbs of *Tulipa* spp. are covered with a thin tunic that is glabrous or hairy. Typically, large flowers are trimerous, comprising two whorls of three brightly colored tepals, with the two whorls sometimes differing in color or having differently colored blotches at the base of each tepal (Hall 1940; Botschantzeva 1962). In addition, *Tulipa* species are identified based on various characteristics including capsule length, diameter, and shape; carpophore size, shape, and color; narrowed sterile upper portion of the capsule; and stigma shape, color and position (Botschantzeva 1962). More recently, Dekhkonov et al (2022) studied the morphological characteristics of 48 species from Central Asia, which are well supported at the section level.

Species of this genus occur naturally in temperate habitats, ranging from the Middle East, Central Asia, and North China to southern Europe and North Africa (Botschantzeva 1962; Zonneveld 2009; Christenhusz et al. 2013; Everett et al. 2013). *Tulipa* originated in Central Asia (Vvedensky and Kovalevskaya 1971); specifically, areas bounded by the Pamir-Alay and Tian Shan mountain ranges (Hoog 1973) are considered the primary centers of the genus diversity (Botschantzeva 1962; Dekhkonov et al. 2022). In particular, Kazakhstan has a high diversity of *Tulipa* species, with over 40 taxa (Ivashchenko and Belyalov 2019), followed by 34 taxa in Uzbekistan (Dekhkonov et al. 2021, 2022; Tojibaev et al. 2022) and 20 taxa in Turkey (Eker et al. 2014). Numerous researchers have studied the genus *Tulipa* based on conservation, prediction modeling, morphology, and molecular evidence. For example, Eker et al. (2014) revised the *Tulipa* species in Turkey based on many herbarium records and field observations. Similarly, Tojibaev et al. (2022) updated Uzbekistan *Tulipa* species using a taxonomic key and distribution. Meanwhile, Wilson et al. (2021) investigated the prediction modeling of several *Tulipa* species in Central Asia. Several studies have investigated the phylogenetic relationships among *Tulipa* species based on their plastomes and nuclear DNA sequences (Hajdari et al. 2021; Eker et al. 2024; Samartza et al. 2024; Sutula et al. 2024). In addition, complete plastome and comparative analyses have been conducted on several *Tulipa* species (Li et al. 2021; Yuan et al. 2022; Xing et al. 2023; Almerekova et al. 2024a, b; Tussipkan et al. 2024)

A brief history of *Tulipa* in Kazakhstan

In the late 18th century, P.S. Pallas surveyed Western Siberia and the adjacent territories and was the first to describe herbarium specimens of tulips from Kazakhstan (Ivashchenko and Belyalov 2019). A more detailed study of the diversity of *Tulipa* species in Kazakhstan began in the 19th century by A. Lehman, I. Kirilov, I. Borshchow, L. Shrenk, and S. Karelin and E.A. von Regel, whose herbarium specimens have since been preserved, serving as invaluable materials for studying tulips. Accordingly, many plant species, including tulips, have been named after these scientists, including *Tulipa schrenkii* Regel, *T. borszczowii* Regel, and *T. lemmersii* Zonn., Peterse & J.de Groot (Ivashchenko and Belyalov 2019).

Specifically, in the second half of the 19th century, E.L. Regel made an invaluable contribution studying Kazakhstani tulips by describing 17 tulip species (Ivashchenko and Belyalov 2019). One of the most remarkable species of tulips in terms of leaf shape, *Tulipa regelii* Krasn, is named in his honor. He distinguished the presence or absence of pubescence on the inner leaflets of the perianth and the base of the stamens as the main characteristics for species identification (Botschantzeva 1962). Aleksey Ivanovich Vvedensky also contributed greatly to the study of wild tulips in Central Asia, describing 17 new species of tulips in the 20th century, of which six species were described in Kazakhstan. He provided the account of tulips in “Flora of USSR” (Vvedensky 1935), with changes in the tulip classification system including distinguishing two monotypic sections *Spiranthera* Vved. and *Lophophylon* Vved. He also processed the genus *Tulipa* in “Flora of Uzbekistan” (Vvedensky 1941), “Flora of Tajikistan” (Vvedensky 1963), and “Conspectus Florae Asiae Mediae” (Vvedensky and Kovalevskaya 1971).

Zinaida Petrovna Botschantzeva devoted her life to studying tulips in Central Asia, describing five new species and publishing a monograph, “Tulips: morphology, cytology and biology” (Botschantzeva 1962). Her study provided a detailed description of 61 species of Central Asian wild tulips, including data on the geography, morphology, biology, and karyosystematics of tulips. Accordingly, *Tulipa zenaidae* Vved. and *T. botschantzevae* S.N.Abramova & Zakal were named in honor of Z.P. Botschantzeva. Meanwhile, A.A. Ivashchenko has studied wild bulbous plants, including tulips, in Kazakhstan since 1963 (Ivashchenko 1987, 2005, 2007; Ivashchenko and Belyalov 2019). In addition to numerous publications on floristic studies in South Kazakhstan, she has published two monographs devoted to “Tulips and other bulbous plants of Kazakhstan” (Ivashchenko 2005) and “Kazakhstan is the birthplace of Tulips” (Ivashchenko and Belyalov 2019). In “Tulips and other bulbous plants of Kazakhstan” Ivashchenko described the cultivation, morphology and ecology peculiarities, geographical distribution, practical importance, and existing protection measures of 50 bulbous plants, including 34 species of tulips in Kazakhstan (Ivashchenko 2005). More recently, “Kazakhstan is the birthplace of Tulips” included 42 species of tulips, including colorful illustrations and maps of species distribution ranges in Kazakhstan (Ivashchenko and Belyalov 2019).

According to various sources, the number of tulips in Kazakhstan ranges from 32 to 42. For example, Polyakov (1958) revised the classification of wild tulips in “Flora of Kazakhstan” to include 32 species. Similarly, Abdulina (1999) updated the list of flora in Kazakhstan to include 34 tulip species. Later, Baitenov (2001), in treating the genus synopsis of the flora of Kazakhstan, reported 33 species of tulips. Recently, Ivashchenko and Belyalov (2019) updated and revised the tulips of Kazakhstan to include 42 species. Over the past 20 years, the new species of tulips have been described in Kazakhstan: *T. kolbintsevii* Zonn. (Zonneveld and de Groot 2012), *T. lemmersii* Zonn., Peterse & J.de Groot (Veldkamp and Zonneveld 2012), *T. ivasczenkoae* Epiktetov & Belyalov (Epiktetov and Belyalov 2013), *T. auliekolica* Perezhogin, *T. turgaica* Perezhogin (Perezhogin 2013), *T. annae* J.de Groot & Zonn, *T. dianaeverettiae* J.de Groot & Zonn. (de Groot and Zonneveld 2020), *T. salsola* Rukšāns & Zubov (Rukšāns and Zubov 2022), *T. jansii* J.J. de Groot & Zonn., and *T. kujukense* J. de Groot & Zonn. (de Groot and Zonneveld 2024). According to the latest checklist of endemic vascular plants, 13 species are endemic to Kazakhstan (Kubentayev et al. 2024). However, our understanding of overall distribution, species diversity, and conservation issues on Kazakhstan *Tulipa* is far from complete.

In the present study, we revisited the genus *Tulipa* in Kazakhstan based on field surveys (2020–2024) and extensive herbarium specimens. The primary aims of this study are to (i) provide an updated synopsis with the taxonomic keys and taxonomic notes on all species along with photographic documentation of wild plants, (ii) determine species diversity and distribution using all known occurrence records from various sources across Kazakhstan, and (iii) discuss future conservation actions for tulips.

Materials and methods

Plant distribution data

Species occurrences data were gathered from four main sources: (i) field survey observations between 2020 and 2024; (ii) literature (i.e. Ivashchenko and Belyalov 2019; de Groot and Zonneveld 2024) survey; (iii) herbarium collections from AA, ALTB, BRNU, CO, E, GB, KFTA, KG, KNU, KSPI, KUZ, L, LE, LECB, MHA, MW, NUR, O, TALL, TASH, TK, US (Thiers 2023) and (iv) the iNaturalist and Plantarium platforms. We collected herbarium specimens, which were deposited in the NUR, during the field surveys. Photographs of wild *Tulipa* species populations were captured by the authors during field surveys. Moreover, additional tulip photographs from the iNaturalist (https://www.inaturalist.org/) and Plantarium (https://www.plantarium.ru/) platforms were used.

A total of 2,496 occurrence records were gathered, including 821 herbarium specimens and 1,675 observations from iNaturalist (accessed on 01 Apr 2024). The coordinates and misidentification of each observation were critically examined on iNaturalist. After removing duplicates and doubtful records, 1,942 occurrence records were retained for species pattern analysis.

For the characterization of each species distribution, the floristic division of Kazakhstan (Fig. 1) was divided into 29 regions and 7 sub-regions, based on Pavlov (1956).

Species richness and conservations

We created a grid net for Kazakhstan with a spatial resolution of 0.5° × 0.5° grid size (equivalent to approximately 50 × 50 km^2) using the FishNet tool in ArcGIS 10.3 (Esri 2012). The country was divided into 1294 grid cells. Additionally, three diversity measures were estimated using Biodiverse v.4.1 software: species richness (SR), weighted endemism (WE), and corrected weighted endemism (CWE), (Laffan et al. 2010). The WE was estimated by considering the presence or absence of a species within a cell, whereas the CWE was determined by calculating the proportion of endemic species within a cell relative to the total endemic SR of the cell (Laffan and Crisp 2003).

The conservation status of each species followed the Red Book of Kazakhstan (Baitulin 2014), which assumes three categories of rarity, i.e., I – very rare and critically endangered species, II – very rare species, and III – a rare species with a shrinking range. In addition, the global conservation status of the species, if assessed, was defined using the IUCN (2024) criteria.

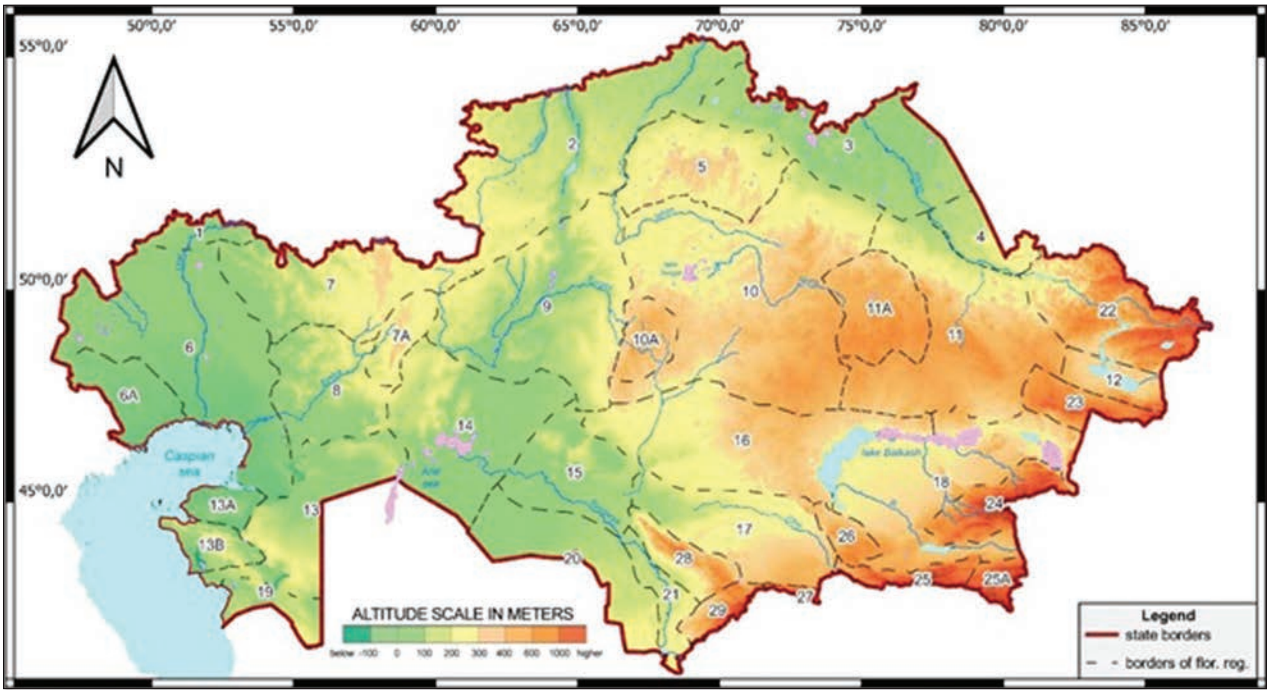

Figure 1. Map of the floristic division of Kazakhstan based on Pavlov (1956): 1 – Syrt, 2 – Tobol-Ishim, 3 – Irtysh, 4 – Semipalatinsk pine forest, 5 – Kokchetav, 6 – Caspian region, 6A – Bukeev, 7 – Aktobe, 7A – Mugojary, 8 – Emba, 9 – Turgay, 10 – Western Upland, 10A – Ulutau, 11 – Eastern Upland, 11A – Karkaraly, 12 – Zaysan, 13 – Northern Ustyrt, 13a – Buzachi, 13B – Mangyshlak, 14 – Aral region, 15 – Kyzylorda, 16 – Betpak -Dala, 17 – Moiynkum, 18 – Balkhash-Alakol, 19 – Southern Ustyrt, 20 – Kyzylkum, 21 – Turkestan, 22 – Altai, 23 – Tarbagatai, 24 – Dzungarian Alatau, 25 – Trans-Ili Kungey Alatau, 25A – Ketmen -Terskey Alatau, 26 – Chu-Ili Range, 27 – Kyrgyz Alatau, 28 – Karatau, 29 – Western Tian Shan.

Phylogenetic analysis

To explore the evolutionary relationship of *Tulipa* spp. in Kazakhstan, internal transcribed spacer (ITS) sequences for 30 *Tulipa* species, collected only from Kazakhstan and belonging to three subgenera, were downloaded from the National Center for Biotechnology Information (NCBI) GenBank (Suppl. material 1: table S1). *Amana edulis* (Miq.) Honda and *Erythronium sibiricum* (Fisch. & C.A.Mey.) Krylov were selected as the outgroup based on previous studies. Briefly, the sequences were aligned using Clustal Omega (Sievers et al. 2020) as implemented in a Geneious Prime 2024.0.5 (http://www.geneious.com). The phylogenetic analyses were conducted using the maximum likelihood (ML) method in RAxML v.8.2.11 (Stamatakis 2006) with the best-scoring ML tree algorithm and 1000 bootstrap replicates. The reconstructed trees were visualized using Figtree v.1.4.2 (Rambaut 2012).

Results and discussion

Diversity of *Tulipa* in Kazakhstan

In this study, 41 *Tulipa* taxa, including 1 hybrid, *Tulipa × tschimganica* Botschantz., were identified (Suppl. material 1: table S2) in Kazakhstan, currently the highest number of taxa reported for a particular country in terms of the number of species and endemics. According to our previous study (Kubentayev et al. 2024), a total of 13 species— i.e., *T. alberti*, *T. auliekolica*, *T. annae*, *T. brachystemon*, *T. berkariensis*, *T. dianaeverettiae*, *T. ivasczenkoae*, *T. kolbintsevii*, *T. lemmersii*, *T. orthopoda*, *T. regelii*, *T. salsola*, and *T. turgaica* — were identified as being endemic to the country. However, two previously described endemic tulips from the present study, i.e., *T. annae* and *T. berkariensis* (Kubentayev et al. 2024) were excluded from the current study's list of endemic tulips in Kazakhstan as *T. annae* also occurs in China (de Groot and Zonneveld 2020) and *T. berkariensis* is a synonym of *T. kaufmanniana* (Christenhusz et al. 2013; Everett et al. 2013; Sennikov and Tojibaev 2021). Instead, two newly described species endemic to Kazakhstan, *T. jansii* and *T. kujukense* (de Groot and Zonneveld 2024), were included on the list. Finally, a point distribution map was generated based on the herbarium (black dot) and observation records (red triangles) across the country for each species. A distribution map of *Tulipa* × *tschimganica* was created based on the *T. kaufmanniana* record, a parent species.

Tulipa collection efforts in Kazakhstan

The number of occurrences and collection years between the herbarium specimens and the observations were compared (Fig. 2). Most herbarium collections were found to be conducted before 2000. In contrast, the number of *Tulipa* observations on the iNaturalist platform has dramatically increased, owing to the efforts of numerous citizen scientists. Specifically, over 1,600 occurrences of 29 *Tulipa* species have been recorded by iNaturalist. Meanwhile, herbarium collections of *Tulipa* species in Kazakhstan have declined over the past 20 years, primarily due to many *Tulipa* species being threatened. In contrast, observations via photographic evidence have recently increased, which is beneficial for protecting threatened species and monitoring the current distribution of *Tulipa*.

Phylogenetic relationship of *Tulipa* spp. in Kazakhstan

A phylogenetic tree was generated for 43 accessions of 31 *Tulipa* species, including 7 endemic species (Fig. 3). The phylogenetic analysis of *Tulipa* was based on the nuclear ITS region with a length of 475 bp, of which 85 bp were parsimony-informative. *Tulipa* species from Kazakhstan formed a monophyletic phylogenetic tree with strong bootstrap values (Fig. 3). In general, *Tulipa* species were clustered into two main clades. The first included species of the subgenus *Orithyia* (Fig. 3), while the second clade was divided into two groups represented by species of the subgenera *Eriostemones* and *Tulipa* (Fig. 3), similar to the results of previous studies (Christenhusz et al. 2013; Hajdari et al. 2021; Chernysheva et al. 2023; Eker et al. 2024). Finally, about 90% of total tulip species from Kazakhstan were successfully sequenced (nrITS) and available on NCBI (Suppl. material 1: table S1). In addition, several studies have been investigating the complete plastome analysis (Almerekova et al. 2024a, b) and the population genetic (Yermagambetova et al. 2024) of *Tulipa* species in the country.

Species richness and conservation of *Tulipa* in Kazakhstan

Three different indices were analyzed (i.e., SR, WE, and CWE, for *Tulipa* species using 1,942 occurrences across the country (Fig. 4). The spatial distribution of records was assessed with most tulips collected in eastern Kazakhstan (Fig.

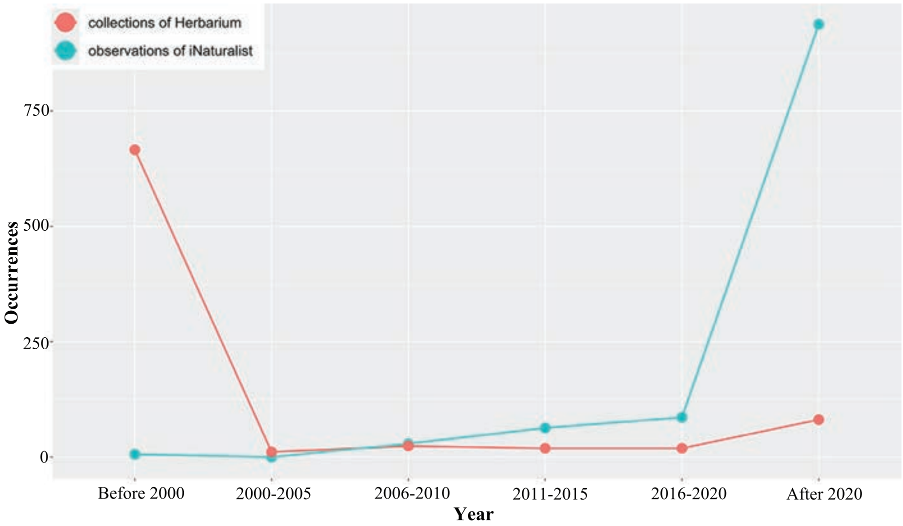

Figure 2. Number of herbarium specimen collection and observations on iNaturalist of *Tulipa* species in Kazakhstan.

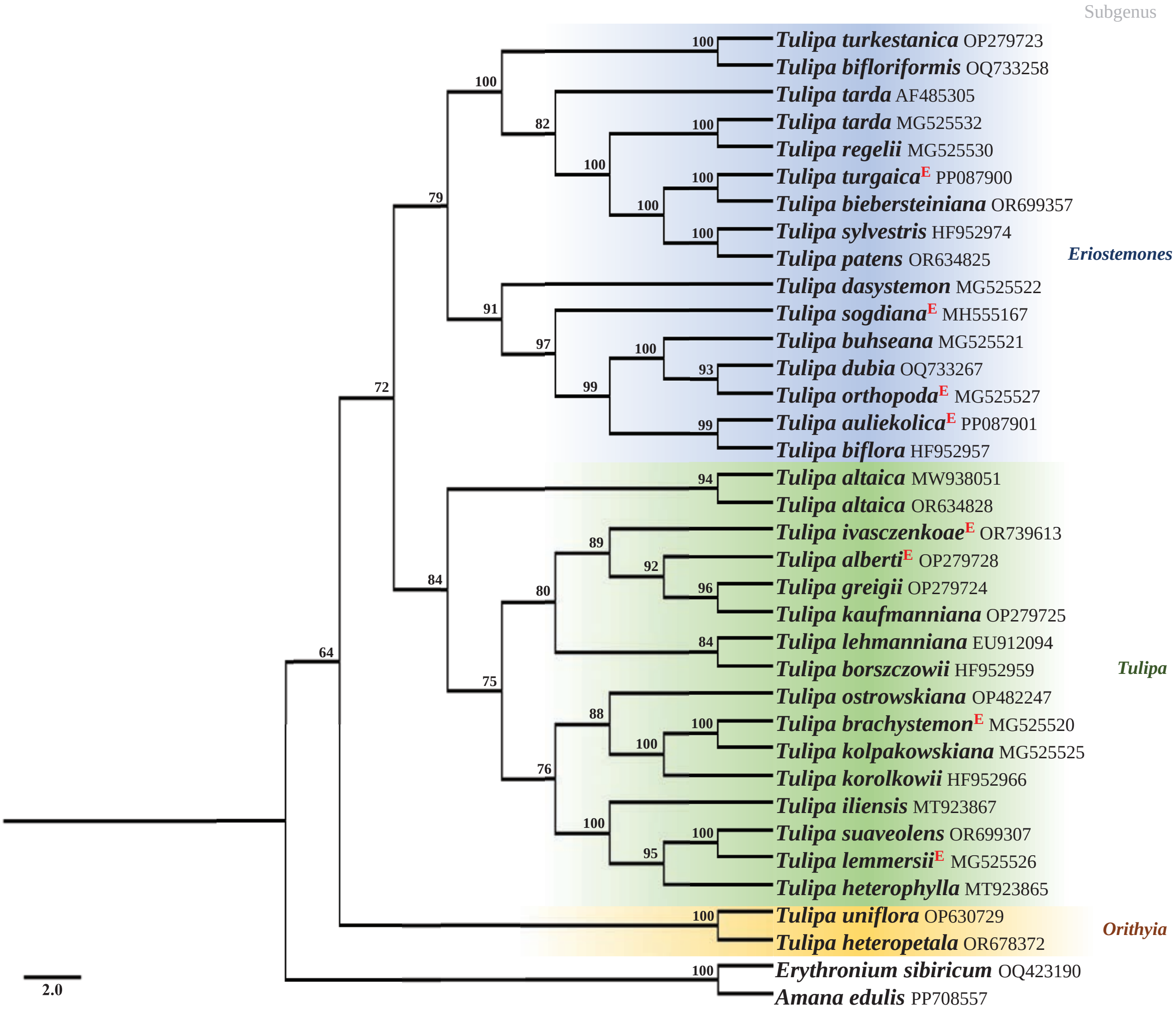

Figure 3. Phylogenetic tree of the *Tulipa* species based on the ITS sequence using the maximum parsimony method. Each subgenus is indicated as follows: *Orithyia* in yellow, *Eriostemones* in blue, and *Tulipa* in green. The endemic *Tulipa* species are indicated by E in red color.

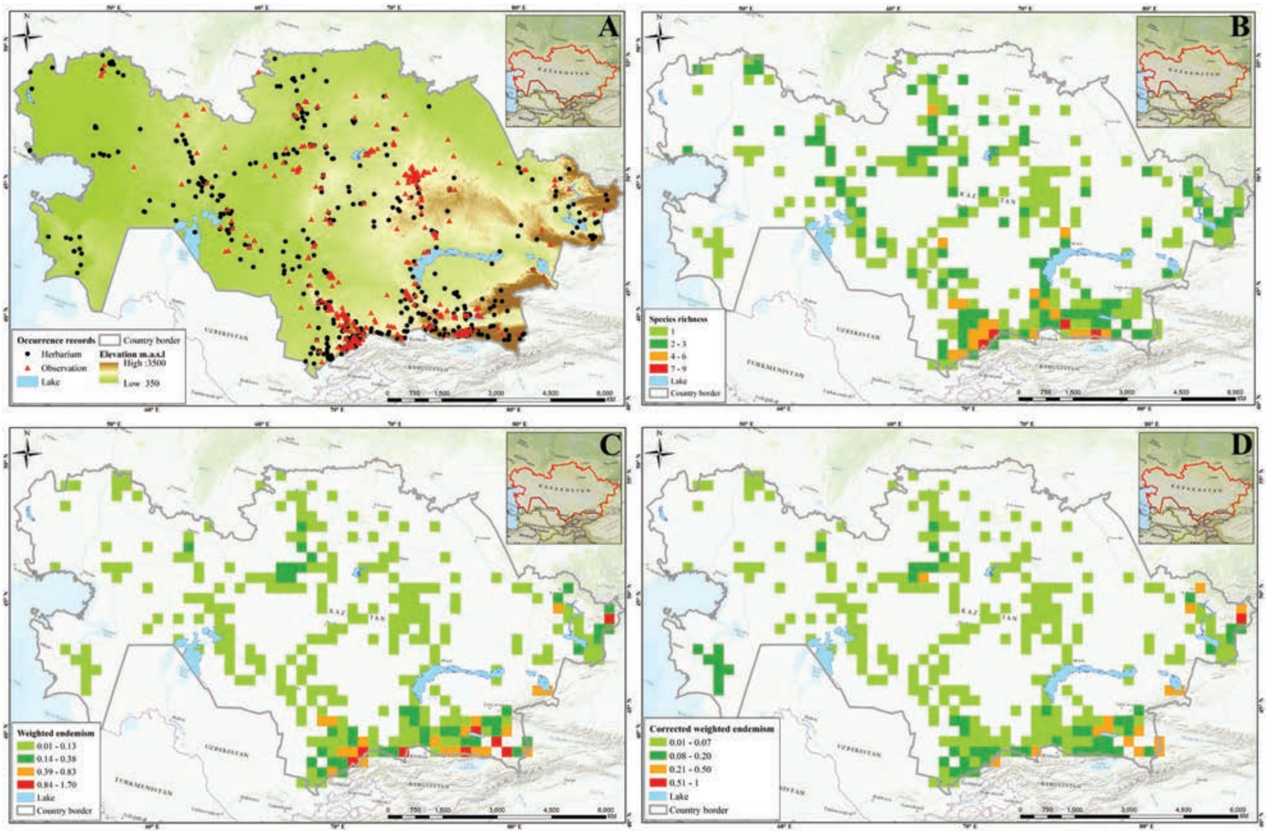

Figure 4. Species diversity of *Tulipa* in Kazakhstan **A** distribution map based on all records **B** species richness (SR) **C** weighted endemism (WE) **D** corrected weighted endemism (CWE).

4A). In general, *Tulipa* species were unevenly distributed in the 295 grid cells across the country (Fig. 4B). For the SR, we identified 22 grids with high tulip SR, with 4–9 species concentrated in these grids, particularly in eastern Kazakhstan (Fig. 4B). The CWE ranged between 0.001 and 1, and the maximum values of 0.51–1 in a single grid cell were recorded for CWE. The WE ranged between 0.01 and 0.13, but a WE maximum value of 0.84–1.70 was recorded for the eight grid cells. In conclusion, based on the SR, WE, and CWE indices, most *Tulipa* species are distributed in the high mountains of southern and eastern Kazakhstan.

The distribution of *Tulipa* species in Kazakhstan was uneven, with most species recorded on the ridges of Western Tian Shan. The fewest species were recorded in the desert areas of southwestern Kazakhstan and the steppe regions of Northern and Central Kazakhstan. The highest concentrations of *Tulipa* species were documented in three floristic regions: Western Tian Shan (12 species), Trans-Ili Kungey Alatau (10 species) and Dzungarian Alatau (8 species). Additionally, 5–7 species were observed in 11 other floristic regions, namely Karatau (7 species), Moiynkum (7 species), Turgay (7 species), Altai (6 species), Betpak-Dala (6 species), Chu-Ili Range (6 species), Kyrgyz Alatau (6 species), Turkestan (6 species), Western Upland (6 species), Aral region (5 species), and Balkhash-Alakol (5 species); 2–4 species were identified in 15 floristic regions: Aktobe (4 species), Eastern Upland (4 species), Ketmen-Terskey Alatau (4 species), Mugojary (4 species), Tobol-Ishim (4 species), Zaysan (4 species), Bukeev (3 species), Caspian region (3 species), Kyzylorda (3 species), Syrt (3 species), Tarbagatai (3 species), Ulutau (3 species), Emba (2 species), Karkaraly

(2 species), and Northern Ustyrt (2 species); and 1 species each was identified in Irtysh, Kokchetav, Kyzylkum, Mangyshlak, Semipalatinsk Pine Forest, and Southern Ustyrt. Meanwhile, no *Tulipa* species were detected in Buzachi (Suppl. material 1: table S2).

Generally, the distribution of tulip species was consistent with the findings of Asatulloev et al. (2023), who mapped and analyzed the distribution patterns in ecoregions and phytogeographic regions in Central Asia. The results also aligned with the studies of Ivashchenko and Belyalov (Ivashchenko 2005; Ivashchenko and Belyalov 2019), who distinguished two mountainous centers of species diversity in Kazakhstan (Tian Shan Zhetusy and Altai-Tarbagatai) and one plain center of tulip diversity, covering vast areas of steppes and deserts.

However, a new location for *T. altaica* was found in the current study in the Western Upland and Betpak-Dala in Kazakhstan, significantly extending the species' general distribution range. Additionally, new localities of *T. auliekolica* were established in Northern Kazakhstan. Previously, this species was only reported in two localities, including the classical locality (15 km from the Karamendy). Moreover, *T. annae* was listed for the first time in the Dzungarian Alatau (Taskora Gorge), based on photographic observations by Kolbintsev (2016).

Of all 41 species of tulips in Kazakhstan, 18 species are listed in the Red Data Book of Kazakhstan (Baitulin 2014), including: Category I – two species (*T. biflora* and *T. lehmanniana*); Category II – eight species (*T. alberti*, *T. borszczowii*, *T. brachystemon*, *T. heteropetala*, *T. korolkowii*, *T. regelii*, *T. tarda*, and *T. zenaidae*); Category III – eight species (*T. greigii*, *T. kaufmanniana*, *T. kolpakowskiana*, *T. ostrowskiana*, *T. patens*, *T. suaveolens*, and *T. uniflora*) (Suppl. material 1: table S2). This categorization does not correspond to the current state of tulip rarity in Kazakhstan, requiring radical revision. Hence, a regional reassessment of all tulips according to the IUCN assessment criteria is required for the next edition of the Red Data Book of Kazakhstan. Additionally, according to long-term observations, *T. biflora*, *T. patens* and *T. biebersteiniana* should be excluded from the Red Data Book of Kazakhstan; they do not require protection. Meanwhile, the following five species should be included in the next edition of the Red Data Book of Kazakhstan: *T. dubia*, *T. iliensis*, *T. ivasczenkoae*, *T. lemmersii*, and *T. orthopoda.* Additionally, the regional conservation status for the potential protection of nine tulip species in Kazakhstan requires reassessment: *T. annae*, *T. jansii*, *T. kujukense*, *T. kolbintsevii*, *T. salsola*, *T. turgaica*, *T. auliekolica*, *T.* × *tschimganica*, and *T. dianaeverettiae*.

Based on the IUCN (2024) criteria, 27 tulips species from Kazakhstan were assessed at the global level. This analysis identified seven threatened species, comprising two critically endangered (CR) species (*T. dianaeverettiae* and *T. ivasczenkoae*), two endangered (EN) species (*T. regelii* and *T. kolbintsevii*), and three vulnerable (VU) species (*T. lemmersii*, *T. orthopoda* and *T. zenaidae*). The remaining 20 species were assessed as near threatened, comprising 10 near threatened (NT) species (*T. alberti*, *T. borszczowii*, *T. dubia*, *T. iliensis*, *T. kaufmanniana*, *T. kolpakowskiana*, *T. korolkowii*, *T. lehmanniana*, *T. ostrowskiana* and *T. uniflora*) and 10 least concern (LC) species (*T. altaica*, *T. bifloriformis*, *T. brachystemon*, *T. dasystemon*, *T. greigii*, *T. heteropetala*, *T. heterophylla*, *T. tarda*, *T. tetraphylla*, and *T. turkestanica*).

Taxonomic key of *Tulipa* in Kazakhstan

Identification key for the sections of *Tulipa* in Kazakhstan

1 Filaments glabrous, flowers generally bowl-shaped with a rounded base and predominantly with red or yellow color, if white ovary as long as stamens, with a very long style..**2**

– Filaments with hairs at the base and/or soft hairs along their length; flowers funnel-shaped, with a slight constriction just above the base, and predominantly white or whitish-yellow color **7**

2 Bulb tunics typically papery and glabrous inside; leaves 2; ovary as long as stamens, with a very long style .... **sect. *Orithyia***

– Bulb tunics typically of varying consistency, from papery to coriaceous and covered with varying degrees of hair on the inside; leaves usually 2 to numerous; ovary slightly shorter than stamens, with sessile style............**3**

3 Anthers opening gradually and slowly (during 2–3 days) from tip to base and becoming contorted.. **sect. *Spiranthera***

– Anthers opening rapidly, not becoming contorted **4**

4 Leaves narrow, glaucous; bulb tunic extended, sometimes up to soil level .... **sect. *Kolpakowskianae***

– Leaves often broad; bulb tunic not extended up to soil level **5**

5 Leaves with anthocyan markings..................................... **sect. *Vinistriatae***

– Leaves without anthocyan markings **6**

6 Bulb tunics scales leathery, long hairy inside, more densely hairy basally and apically; stem pubescent; leaves erect-ascending, the lower leaf base is as high above the ground, glossy, pubescent adaxially, whitish-reddish margined, keeled; tepals red with yellow 3-dentate spot at base .... **sect. *Lanatae***

– Bulb tunics weakly coriaceous, blackish-brown, more or less hairy all over; stem glabrous to more or less pubescent; leaves more or less spreading, scattered, glaucous, rather crisp, glabrous or pubescent; tepals polychrome in color, usually red, yellow or white, basal blotch black or yellow or absent .... **sect. *Tulipa***

7 Bulb tunics covered inside with some short, sometimes adpressed hairs on the top, middle part glabrous or ± glabrous; anthers oblong and without cusp... **sect. *Sylvestres***

– Bulb tunics covered inside with woolly, sometimes densely adpressed hairs on the top and base anthers terminating in a short cusp ....**sect. *Biflores***

Subgenus *Tulipa*

Sect. *Tulipa* L.

Tulipa suaveolens Roth in Ann. Bot. (Usteri) 10: 44 (1794).

Type. —*Tulipa gesneriana* L., Sp. Pl. 1: 306 (1753).

Sect. *Lanatae* (Raamsd.) Zonn. in Pl. Syst. Evol. 298: 90 (2012).

Tulipa ivasczenkoae Epiktetov & Belyalov in Turczaninowia 16: 5 (2013).

Basionym. *Tulipa* ser. *Lanatae* van Raamsd., van Raamsd. & T. de Vries, Pl. Syst. Evol. 195: 40 (1995).

Type. —*Tulipa lanata* Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 647 (1884).

Sect. *Kolpakowskianae* Raamsd. ex Zonn. & Veldkamp., Pl. Syst. Evol. 298: 90 (2012).

Type. —*T. kolpakowskiana* Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 5: 266 (1877).

Identification key for *Tulipa* sect. *Kolpakowskianae* in Kazakhstan

1 Bulb tunic fibrous, splitting, black to tawny, prolonged to soil surface, inside densely covered with curly woolly hairs; stamens one-third to two-fifths the length of perigone; filaments black to purple **2**

– Bulb tunic not fibrous and splitting, black to dark brown, not prolonged or slightly prolonged (if prolonged up to soil surface, then lined with woolly hairs at the top and glabrous below); stamens two or three times shorter than the perigone, filaments yellow **3**

2 Upper leaves exceeding or at least reaching the flower; aboveground part one-half to two-thirds as long as the underground part; tepals with a dark violet blotch on both surfaces .... ***T. borszczowii***

– Upper leaves do not exceed the flower; aboveground part as long as or slightly longer than the underground part; tepals usually with a dark basal blotch on the inner surface, rarely on both surfaces ....***T. lehmanniana***

3 Stem in upper part and peduncle pubescent.. **4**

– Stem and peduncle glabrous **5**

4 Stem up to 7.5 cm long, reddish green leaves usually lying on the soil surface ; tepals with short hairs on both sides near the base, tepals outside dull pinkish-red with yellow margins .... ***T. annae***

– Stem up to 35 cm long, green; leaves usually scattered on the stem, never lying on the soil surface, glabrous; tepals glabrous, outer tepals outside yellowish-gray with a pinkish haze between the center and narrow yellow margins .... ***T. altaica***

5 Tepals usually red, sometimes yellow-red or yellow; filaments black in the lower part and purple in the upper part, rarely in yellow form entirely yellow .... ***T. korolkowii***

– Tepals usually yellow or yellowish, sometimes red filaments commonly concolorous **6**

6 Filaments gradually dilated at base, expanded in the middle part............ **7**

– Filaments with nearly parallel margins, abruptly narrowed at apex........... **9**

7 Leaves (3–4) 5 up to 7, very close together, all sublorate, surpassing the flower; flowers 1 or 2, up to 4 .... ***T. tetraphylla***

– Leaves (3) 4, spreading, commonly not surpassing the flower; flower usually solitary..**8**

8 Bulb tunics coriaceous; lowest leaf sublorate to linear-lanceolate, 0.7–1.5 cm broad; tepals mostly acute or acuminate; anthers half as long as filaments .... ***T. iliensis***

– Bulb tunics papery, sometimes subcoriaceous; lowest leaf linear-lanceolate, 2–3 cm broad; tepals mostly obtuse; anthers as long as filaments.... .... ***T. brachystemon***

9 Tepals yellow, not blotched; leaves commonly surpassing the flower....**10**

– Tepals usually red with a black basal blotch, sometimes yellow-red or yellow; leaves commonly not surpassing the flower **12**

10 Plants small, up to 7 cm tall; tepals usually incurved .... ***T. lemmersii***

– Plants taller, 10–15 cm tall; tepals usually not incurved **11**

11 Bulb ovoid or usually slightly prolonged with fibers above the bulb; outer tepals oblong to oblong-rhomboidal, inner tepals oblong-oblanceolate to oblong; filaments straight, orange-yellow....................... ***T. kolpakowskiana***

– Bulb pear-shaped, tunics not prolonged and without fibers; outer tepals lanceolate, the tip and nearby margins covered with short hairs, inner tepals obovate; filaments ovate to almost straight, yellow, mottled with grayish.. ***T. jansii***

12 Tepals usually yellow, lower-most leaf oblong-lanceolate to oblong, 3–6 cm broad .... ***T. zenaidae***

– Tepals usually red, lower-most leaf linear-lanceolate to lanceolate, 1–4 cm broad ....***T. ostrowskiana***

Sect. *Vinistriatae* (Raamsd.) Zonn., Pl. Syst. Evol. 298: 91 (2012).

Type. —*Tulipa greigii* Regel in Gartenflora 22: 290, t. 773. (1873).

Identification key for *Tulipa* sect. *Vinistriatae* in Kazakhstan

1 Inner tepals obovate and slightly longer than the outer; leaves profusely violet-speckled on upper side..***T. greigii***

– Inner tepals triangular-obovate and shorter than the outer; leaves without violet-speckled on upper side... ***T. alberti***

Sect. *Spiranthera* Vved. ex Zonn. & Veldkamp, Pl. Syst. Evol. 298: 90 (2012).

Type. —*Tulipa kaufmanniana* Regel in Gartenflora 26: 194 (1877).

Identification key for *Tulipa* sect. *Spiranthera* in Kazakhstan

1 Relatively small plants, sometimes with almost sessile flowers; leaves curled or undulate; anthers almost equal in length with filaments or up

to 1.5 times longer, not becoming strongly incurved or twisted; filaments rather thick .... ***T. dubia***

– Relatively tall plants; flowers usually not sessile; leaves not curled or slightly undulate; anthers 2–4 times longer than filaments, when ripe the tips are curved down and outwards; filaments narrowly triangular **2**

2 Anthers becoming strongly incurved or twisted; filaments yellow, dilated at the base; widespread in various habitats on all ranges of Kazakhstan part of Western Tian-Shan .... ***T. kaufmanniana***

– Anthers not becoming strongly incurved or twisted; filaments yellow with brown apex, narrow, slightly dilated at the base; grows on stony-gravelly slopes of Karzhantau Range..***T. tschimganica***

Subgenus *Orithyia* (D.Don) Baker, J. Linn. Soc. Bot. 14: 277 (1874).

Lectotype. *Tulipa uniflora* (L.) Besser ex Baker.

Sect. *Orithyia* (D. Don) Vved., Brit. Fl. Gard. [Sweet] Ser. 2: 336 (1836).

Type. —*Tulipa uniflora* Besser ex Baker, J. Linn. Soc., Bot. 14: 295 (1874).

Identification key for *Tulipa* sect. *Orithyia* in Kazakhstan

1 Bulb elongate-ovoid, tunics naked, leaves opposite .... ***T. heterophylla***

– Bulb ovoid, tunics with appressed hairs inside at apex; leaves alternate; anthers 3–6 mm long..**2**

2 Leaves narrowly linear-lanceolate, usually slightly surpassing the flower with brown margins; tepals obtuse or subobtuse; filaments gradually attenuate from base .... ***T. uniflora***

– Leaves much scattered, linear, glabrous, not surpassing the flower with reddish margins; tepals very acute; filaments dilated below the middle; anthers up to 9 mm long...***T. heteropetala***

Sect. *Sylvestres* in Gard. Chron. 20: 233 (1883).

Type. —*Tulipa sylvestris* Pall., Sp. Pl.: 305 (1753).

Identification key for *Tulipa* sect. *Sylvestres* in Kazakhstan

1 Tepals yellow, the outer often violet tinged on the outside **2**

– Tepals white, yellow at base, the outer greenish-gray on the outside, becoming darker toward the base..***T. patens***

2 Bulb tunics ca. 2–2.5 cm; ovary slightly shorter than stamens; forest lawns and meadows in river valleys................................ ***T. biebersteiniana***

– Bulb tunics up to 4.5 cm; ovary equal to or longer than stamens; dry steppe or semi-desert plains .... ***T. turgaica***

Sect. *Biflores* A.D.Hall ex Veldkamp & Zonn., Pl. Syst. Evol. 298: 89 (2012).

Type. —*Tulipa biflora* Pall., Reise Russ. Reich. 3: 727 (1776).

Identification key for *Tulipa* sect. *Biflores* in Kazakhstan

1 Filaments glabrous .... ***T. sogdiana***

– Filaments with a ring of hairs at the base or scattered hairs along their length **2**

2 Leaf solitary, with raised undulating ridges along its length .... ***T. regelii***

– Leaves 2 to several, never with undulating ridges along its length **3**

3 Bulb tunics glabrous; leaves 3–7, very close together; flowers 1–8 .... ***T. tarda***

– Bulb tunics always hairy to varying degrees, sometimes with few appressed hairs at apex (*T. dasystemon*); leaves commonly 2 or sometimes 3, scattered, spreading **4**

4 Bulb tunics papery or nearly so **5**

– Bulb tunics coriaceous or sub-coriaceous **9**

5 Flowers commonly yellow; bulb tunics blackish-brown .... ***T. auliekolica***

– Flowers commonly white, creamy white with a yellow (whitish yellow) blotch; bulb tunics brown or grayish-brown **6**

6 Stem 30–50 mm long, covered with short hairs; bulb tunics reddish-brown with woolly hairs at the top; capsule with a small dome on the top; at an altitude of 1800 m .... ***T. dianaeverettiae***

– Stem up to 20–25 cm long, glabrous; bulb tunics light to dull brown, inside glabrous or covered with woolly hairs more densely at the top; capsule without dome on the top; below an altitude of 1800 m **7**

7 Stamens slightly longer than ovary; anthers 2–3 mm long .... ***T. biflora***

– Stamens shorter or equal to ovary; anthers 5–7 mm long **8**

8 Bulbs globose or pear-shaped, inside glabrous, at the neck with some hairs; flowers solitary; stamens longer than the ovary; low bushes in Taskora and adjacent Kolasu Valleys of Dzjungarian Ala-Tau .... ***T. kolbintsevii***

– Bulbs ovoid, inside in upper third thinly covered with thin, more or less parallel hairs, becoming more densely hairy apically; flowers 2(3); stamens shorter or equal to ovary; stabilized fixed and hilly-ridged sands over brown and gray-brown soils, in depressions of takyrs and solonchaks with sparse semi-desert/desert vegetation in Zhetysu region, extreme southern part of Dzungarian Alatau .... ***T. salsola***

9 Leaves almost opposite, very close together; style very short or practically absent; flower buds and flowers upturned; endemic of Karatau Ridge .... ***T. orthopoda***

– Leaves mostly distant or more or less approximate; style short or with a rather long style; buds and flowers are not inverted; plants are more widespread in the desert and mountainous parts of Kazakhstan **10**

10 Upper part of stem and peduncle pubescent; flower whitish with yellow blotch; style short; plants of plains, foothills and mid-mountains, up to 2400–2500 m **11**

– Upper part of stem and peduncle glabrous; flower pale yellow or whitish; style long; plants of high mountains, above 2400–2500 m **14**

11 Leaves very scattered, usually shorter than flower; sandy and clay soils in predominantly arid plains .... ***T. buhseana***

– Leaves more or less distant, commonly longer than the flower; foothills and mid-mountains of West Tian Shan... **12**

12 Bulb tunic brown-gray or reddish-brown, covered with woolly hairs........ **13**

– Bulb tunic dark brown, at the upper part densely covered with more appressed long silky hairs .... ***T. turkestanica***

13 Bulb tunic reddish-brown or pink, densely covered with woolly hairs on the inside, most of which are at the top and base filaments narrow triangular with hairs above the hairy rim.. ***T. bifloriformis***

– Bulb tunic brown-gray, covered with felt-like short woolly hairs concentrated at the top; leaves narrower; filaments narrow triangular, glabrous above the hairy rim .... ***T. kujukense***

14 Bulb tunic usually light-brown or brown, papery, glabrous or covered with few straight, adpressed, white hairs at tip; anthers oblong; ovary scarcely shorter than stamens.. ***T. dasystemon***

– Bulb tunic black to tawny, thin coriaceous, densely lined with woolly hairs at tip; anthers linear-oblong; ovary about the length of stamens................ .... ***T. dasystemonoides***

Taxonomic status of *Tulipa* in Kazakhstan

Detailed taxonomic notes are provided for each species with phenology, conservation status, distribution, and type information. In addition, capsule characteristics are important for identifying *Tulipa* species, according to Botschantzeva (1962). Therefore, the capsules of 34 *Tulipa* species are illustrated based on our own and other sources (Fig. 5). According to Fig. 5, the capsule shape relatively differs among the studied species; however, further morphological studies on capsules of *Tulipa* species are needed.

Tulipa alberti **Regel, Gartenflora 26: 257, t 912 (1877).**

Fig. 6

Type. Kazakhstan • Illustration t. 912 in Gartenflora 26 (1877) [lectotype designated by Christenhusz et al. 2013: 303].

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Balkhash-Alakol, Betpak-Dala, Chu-Ili Range, Dzungarian Alatau, Eastern Upland, Karatau, Moinkym, Trans-Ili Kungey Alatau, and Western Upland. Grows on dry rubbly and stony slopes of low mountains.

Conservation status. *Tulipa alberti* is assessed near threatened at the global level (IUCN 2024) and is included in the Red Book of Kazakhstan (Category II).

Phenology. Flowering in April–May; fruiting in May–June.

Notes. Eduard Regel described *T. alberti* in 1877, based on materials collected by his son Albert Regel, who worked as a doctor in Kulja, from the Karatau Mountains in 1876 (Ivashchenko and Belyalov 2019). The locus classicus of this species in the Chirchik River Valley was incorrectly stated when describing *T. alberti* (Vvedensky and Kovalevskaya 1971). More recently, Sutula et al. (2024) reported the

Figure 5. Capsules of *Tulipa* species in Kazakhstan **A** *T. alberti* **B** *T. altaica* **C** *T. annae* **D** *T. auliekolica* **E** *T. biflora* **F** *T. bifloriformis* **G** *T. borszczowii* **H** *T. brachystemon* **I** *T. buhseana* **J** *T. dasystemon* **K** *T. dubia* **L** *T. greigii* **M** *T. heteropetala* **N** *T. heterophylla* **O** *T. ivasczenkoae* **P** *T. kaufmanniana* **Q** *T. kolbintsevii* **R** *T. korolkowii* **S** *T. kolpakowskiana* **T** *T. lehmanniana* **U** *T. lemmersii* **V** *T. orthopoda* **W** *T. ostrowskiana* **X** *T. patens* **Y** *T. regelii* **Z** *T. salsola* **ZA** *T. sogdiana* ZB *T. biebersteiniana* **ZC** *T. tarda* **ZD** *T. tetraphylla* **ZE** *T. turgaica* **ZF** *T. turkestanica* **ZG** *T. uniflora* **ZH** *T. zenaidae*.

hybridization of *T. alberti* and *T. patens* and the possible existence of a new undescribed species of hybridogenic origin. However, given that these species are morphologically different and belong to different subgenera, we believe that hybridization between these taxa is highly unlikely. Moreover, the distribution ranges of the species do not overlap, excluding the possibility of spontaneous hybridization in nature. Meanwhile, spontaneous hybrids of *T. alberti* and *T. greigii* exist in the wild (Ivashchenko and Belyalov 2019; Vvedensky and Kovalevskaya 1971). Recently, Yermagambetova et al. (2024) studied the genetic diversity and gene flow of *T. alberti* in Kazakhstan. In this work, the more isolated populations were determined to be genetically distinct with low genetic diversity (Yermagambetova et al. 2024).

Tulipa altaica **Pall. ex Spreng., Syst. Veg., ed. 16 [Sprengel] 2: 63 (1825).**
Fig. 7

Type. • 'Mons Imaus' *Pallas* (not located). Neotype: Ledebour, Ic. Pl. Ross. 2: t. 134 (1830) [designated by Christenhusz et al. 2013: 304].

Figure 6. *Tulipa alberti* in Kazakhstan **A, B** general habits **C** flower **D** tepals **E** gynoecium **F** stamens **G** bulb sheath. (Photos: **A–G** by S. Kubentayev).

General distribution. China (Xinjiang), Kazakhstan and Russia (Altai, west Siberia) (POWO 2024).

Distribution in Kazakhstan and habitat. Altai, Betpak-Dala, Eastern Upland, Tarbagatai, Western Upland, and Zaysan. This species grows on stony slopes of low mountains and steppe areas at the foot of mountains, as well as among shrubs on rubbly slopes.

Conservation status. *Tulipa altaica* is assessed as least concern at the global level (IUCN 2024).

Phenology. Flowering in April–May; fruiting in May–June.

Notes. This species was first collected by P.S. Pallas in Altai (Mount Imaus) in the late 18th century. However, it was first described in 1825 by the German botanist Kurt Sprengel (Ivashchenko and Belyalov 2019). In the past, this species was recorded only in the Bektauata Mountain, Eastern Upland of Kazakhstan (Ivashchenko and Belyalov 2019; Kupriyanov 2020). In this study, however, a new location was found in the Kokshetau Mountains (Karamysheva *s.n.* LE), Western Upland of Kazakhstan, which significantly extended its distribution range.

Figure 7. *Tulipa altaica* in Kazakhstan **A** general habits **B** general appearance **C**, **D** flowers **E** tepals **F** gynoecium **G** stamens **H** bulb **I** bulb sheath. (Photos: **A–I** by S. Kubentayev).

Tulipa annae **J.de Groot & Zonn., Int. Rock Gard. 122: 10 (2020).**
Fig. 8

Type. Kazakhstan • Marble Pass, Altai region, north-eastern Kazakhstan, 2008, *JJ de Groot* (holotype L 3986814).

General distribution. China (Xinjiang) and Kazakhstan (de Groot and Zonneveld 2020).

Distribution in Kazakhstan and habitat. Altai and Dzungarian Alatau. This species grows on cliffs, rocky and rubbly slopes, and mountainous plumes.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa annae* was described in 2020 from plants grown in a cultural collection in the Netherlands and bulbs collected at the Marble Pass in eastern Kazakhstan. This species is morphologically similar to *T. altaica* but differs by the presence of short hairs on the leaves, a smaller overall habit, the ovary shorter than the stamens and a tunic on the bulb elongated into a long spout. *Tulipa annae* is named after Anna Ivaschenko, a well-known botanist living and working

Figure 8. *Tulipa annae* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by J.J. de Groot).

in Almaty, Kazakhstan (de Groot and Zonneveld 2020). Based on the results of our research, this species was listed for the first time in the Dzungarian Alatau (Taskora Gorge) based on the photographic observations by Kolbintsev (2016). Due to the relative paucity of information on *T. annae* in the literature, further studies are needed regarding its distribution, abundance, and conservation status.

***Tulipa auliekolica* Perezhogin, Novosti Sist. Vyssh. Rast. 45: 145 (2014).**

Fig. 9

Type. Kazakhstan • Prov. Kostanay, Auliekol distr., 25 April 2009, *Yu. Perezhogin s.n.* (LE).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Tobol-Ishim and Turgay. This species grows in cereal steppes on plains.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in April; fruiting expected from May to June.

Notes. *Tulipa auliekolica* was first described in 2013 by Yu. V. Perezhogin from Kostanay region, Northern Kazakhstan. Morphologically, this species is similar to *T. biflora* but differs in its darker blackish-brown bulb tunics and yellow flower petals (Perezhogin 2013). The independence of this species raises doubts, as the known morphological characteristics are insufficient to assign the species rank. Additionally, *T. biflora* and *T. auliekolica* were placed in the same clade on the phylogenetic tree constructed using data from GenBank (Fig. 3). Accordingly, we consider it necessary to conduct phylogenetic and morphological studies to establish the taxonomic position of *T. auliekolica* in *Tulipa* genus. New localities of this species were established in Northern Kazakhstan during this study, according to herbarium collections of Yu. V. Perezhogin in the herbarium of the KSPI. Previously, the distribution of this species was only reported for two localities, including the type locality (15 km from the Karamendy turnoff) (Perezhogin 2013) and FR Turgay, north of the Akkuma sands (Perezhogin et al. 2015).

Figure 9. *Tulipa auliekolica* in Kazakhstan **A, B** general habits **C** flower **D** tepals **E** gynoecium **F** stamens **G** bulb and bulb sheath. (Photos: **A–G** by S. Kubentayev).

Tulipa biebersteiniana **Schult.f., Syst. Veg., ed. 15 bis [Roemer & Schultes] 7: 382 (1829).**
Fig. 10

Type. Russia • 'In hortis et vineis ad fluvium Terek inter Mosdok et Kisljar', April, Bieberstein (not found).

General distribution. Kazakhstan, Krym, North Caucasus, and Transcaucasus (Kutlunina et al. 2013).

Distribution in Kazakhstan and habitat. Aktobe, Mugojary, Aral region, Western Upland, Ulytau, Syrt, Tobol-Ishim, Bukeev, Turgay, and Caspian region.

Conservation status. The IUCN conservation status of this species requires assessment. It is included in the red book of Kazakhstan (CategoryIII).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa biebersteiniana* was described in 1829 by J.H. Schultes from specimens from the North Caucasus (between Mozdok and Kizlyar). The species was named in honor of Russian botanist F. K. Biberstein-Marshall (Ivashchenko and Belyalov 2019). Some taxonomists classified *T. biebersteiniana* and *T. patens* as synonyms of the widespread European

Figure 10. *Tulipa biebersteiniana* in Kazakhstan **A** general habits **B, C** flowers **D** ovary and stamen **E** bulb (Photos: **A–E** by S. Kubentayev).

T. sylvestris subsp. *australis* (Christenhusz et al. 2013; Everett et al. 2013). However, according to Zonneveld (2009), the difference in genome size between *T. biebersteiniana* (56.7 pg) and *T. sylvestris* (62.3 pg) may differentiate *T. biebersteiniana*. In 2013, Perezhogin (2013) described a new species, *T. turgaica* Perezhogin, similar to *T. biebersteiniana* and grows in arid conditions. It was suggested that *T. biebersteiniana*, should form its own subgenus based on hierarchical cluster analysis of genetic profiles of taxa conducted on Iranian tulips using AFLPs (Asgari et al. 2020). However, this hypothesis requires further investigation. Wilson (2023) included *T. biebersteiniana* on the list of tulips, which may require reinstatement if evidence confirms their uniqueness.

Tulipa biflora **Pall., Reise Russ. Reich. 3: 727 (1776).**
Fig. 11

Type. Russia • Described from southern Russia, *Pallas* (lectotype BW000528948) [lectotype designated by Eker et al. 2014].

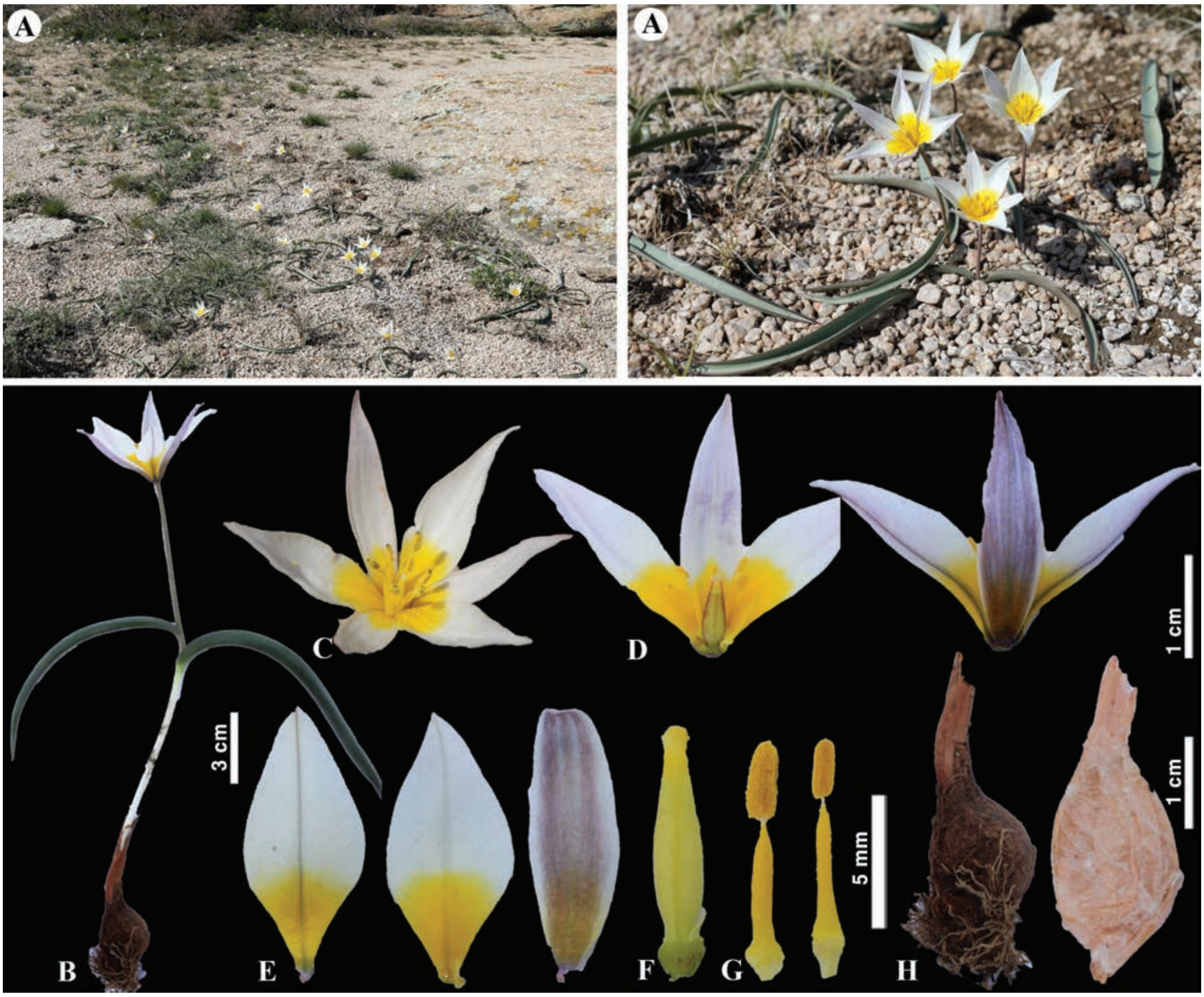

Figure 11. *Tulipa biflora* in Kazakhstan **A, B** general habits **C**, **D** flower **E** tepals **F** gynoecium **G** stamens **H** bulb and bulb sheath. (Photos: **A–H** by S. Kubentayev).

General distribution. Kazakhstan, Uzbekistan (Northern Ustyurt), China (northern part), the south of Russia, Transcaucasia, and Crimea (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Aktobe, Aral region, Betpak-Dala, Bukeev, Caspian region, Eastern Upland, Karkaraly, Mugojary, Northern Ustyrt, Turgay, Western Upland, and Zaysan. It grows on solonetz, clay steppe, and desert areas and less often on the stony and rubbly slopes of hills.

Conservation status. The IUCN conservation status of this species requires assessment. It is included in the red book of Kazakhstan (Category I).

Phenology. Flowering in April–May; fruiting in May–June.

Notes. The species was described in 1776 by P. S. Pallas from specimens collected from the Caspian deserts. The location of the type specimens is unknown (Ivashchenko and Belyalov 2019). According to the latest system of *Tulipa* (Christenhusz et al. 2013), many species from the section *Biflores* A.D.Hall ex Veldkamp & Zonn., including *T. buhseana* and *T. sogdiana*, are considered synonyms of the *T. biflora s.l.* complex. However, we propose that *T. buhseana* and *T. sogdiana* should be considered independent taxa based on their complex morphological characteristics, ecology, and distribution range. In addition, these taxa were arranged in a separate clade from *T. biflora* in the phylogenetic tree (Fig. 3). The southern boundaries of the *T. biflora* range in Kazakhstan from west to east pass through the Northern Ustyurt, Aral region, Sarysu region sands, and the northern Balkhash region. Perezhogin (2013) considered the reports of *T. biflora* from Tobol-Ishim and Turgay erroneous. In his opinion, *T. biflora* was replaced with *T. auliekolica*. Given that it is impossible to distinguish *T. biflora* from *T. auliekolica* based on herbarium material, it is impossible to confirm or deny this statement.

Tulipa bifloriformis **Vved., Opred. Rast. Sred. Azii 2: 320 (1971).**
Fig. 12

Type. UZBEKISTAN • Tian-Schan occidentalis, in collibus argillosis circa urb. Taschkent, 19 March 1923, *M.G. Popov & A.I. Vvedensky* 1036 (holotype TASH000502!; isotypes BM, H1200916, K).

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Karatau, Kyrgyz Alatau, Kyzylorda, Moiynkum, Turkestan, and Western Tian Shan. This species grows on the clay, stony, and rubbly slopes of hills, steppes and semi-desert foothill plains.

Conservation status. *Tulipa bifloriformis* is assessed as least concern at the global level (IUCN 2024).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa bifloriformis* was described by Vvedensky in 1935 from herbarium material collected near Tashkent in 1923. Later, a complete diagnosis of this species was published in ‘Conspectus Florae Asiae Mediae’ (Vvedensky and Kovalevskaya 1971). This species is morphologically similar to *T. biflora*, differing in its leathery bulb sheaths and drooping buds before flowering. Externally, *T. bifloriformis* is similar to *T. buhseana* but differs in its tomentose bulb sheaths on the inner side (Vvedensky and Kovalevskaya 1971). This species often inhabits open slopes after landslides and forms dense carpets that spread vegetatively (Tojibaev et al. 2022).

Figure 12. *Tulipa bifloriformis* in Kazakhstan. **A** habitat **B** habit. (Photos: **A, B** by K.Tojibaev).

Tulipa borszczowii **Regel, Bull. Soc. Imp. Naturalistes Moscou 41: 438 (1868).** Fig. 13

Type. Kazakhstan • Steppe Kara-Kum am Aralsee, *Borszczow 677* (holotype LE!; photograph K).

General distribution. Kazakhstan and Uzbekistan (POWO 2024).

Distribution in Kazakhstan and habitat. Aral region, Betpak-Dala, Kyzylkum, Kyzylorda, Moiynkum, and Turkestan. This species grows in sandy and clay-sandy deserts.

Conservation status. *Tulipa borszczowii* is a near threatened species at the global level (IUCN 2024). It is included in the red book of Kazakhstan (Category II).

Phenology. Flowering in April–May; fruiting in May–June.

Notes. *Tulipa borszczowii* was described by E.L. Regel in 1868 from the collections of Russian botanist I.G. Borshchow from Aral Karakum. The species is morphologically similar to *T. lehmanniana*, differing in its flower stalk that does not droop in buds, leaves exceeding or reaching the flower, and a shorter above-ground stem part that is 1.5–2 times shorter than the underground part (Ivashchenko and Belyalov 2019). This species was considered endemic to Ka-

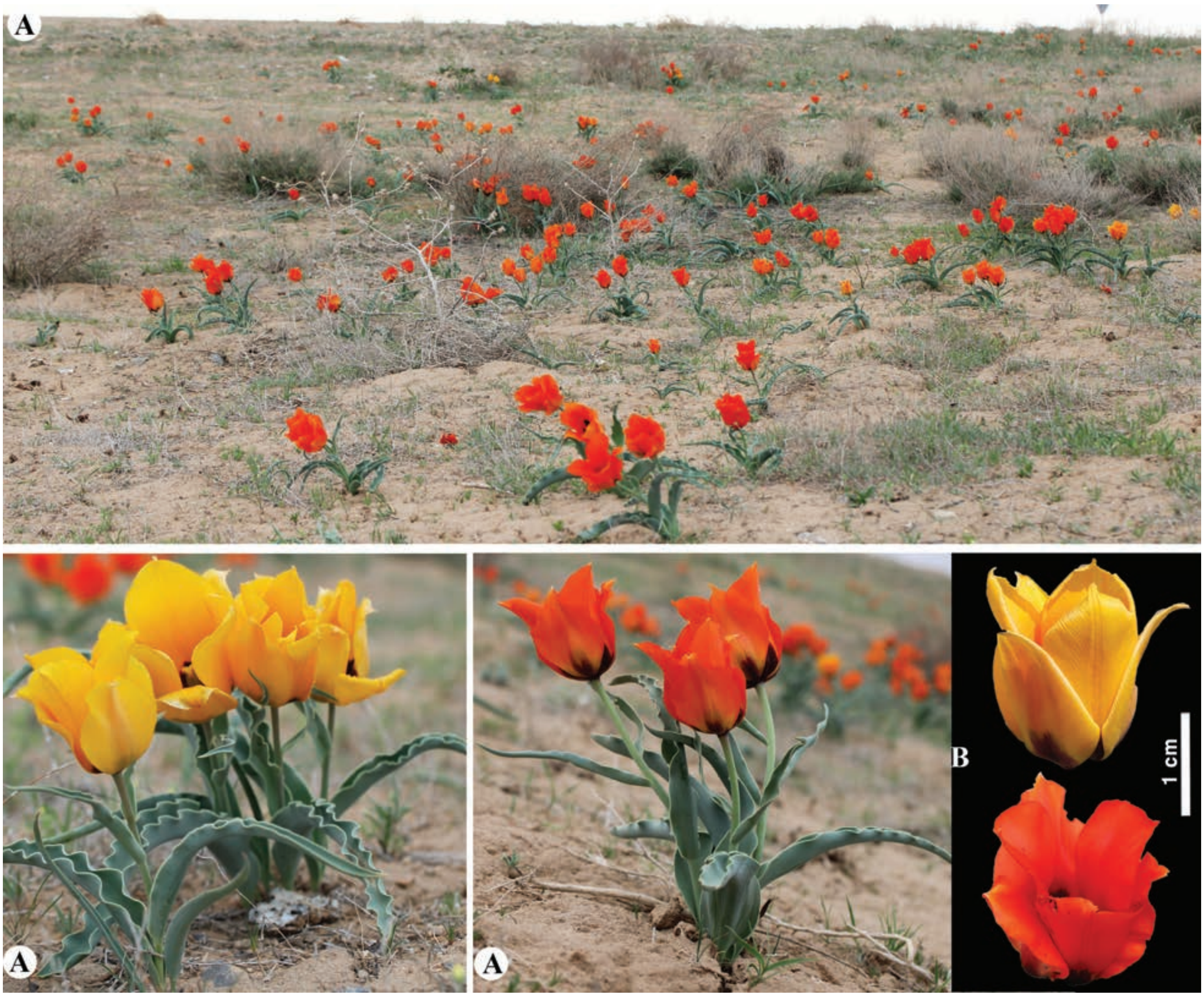

Figure 13. *Tulipa borszczowii* in Kazakhstan **A** general habits with different color forms **B** flowers. (Photos: **A, B** by S. Kubentayev).

zakhstan until 2002, when it was found in Uzbekistan (from the western part of the Hungry Steppe) (TASH), and elsewhere in the Uzbek part of Kyzylkum (Abduraimov et al. 2020). The southernmost limit of its total range is in Uzbekistan, the northernmost limit is in the northern Aral region, and the range reaches the Transkaratau foothill plain in the east (Kyzylkol and Akkol lakes).

Tulipa brachystemon **Regel, Gartenflora 323 (1882).**

Fig. 14

Type. • Illustration t. 1099, f. 2 in Gartenflora 31 (1882) [lectotype designated by Christenhusz et al. 2013: 325].

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Dzungarian Alatau. It grows on stony, rubbly slopes of the lower and middle belt of mountains in Dzungarian Alatau (up to 1700 m a.s.l.).

Conservation status. *Tulipa brachystemon* is a least concern species at the global level (IUCN 2024). It is included in the red book of Kazakhstan (Category II).

Phenology. Flowering in April–May; fruiting in May–June.

Notes. *Tulipa brachystemon* was described by E.L. Regel in 1882, without the precise location of the type specimens. The LE herbarium contains collections of A. E. Regel from Schengeldy (Ivashchenko and Belyalov 2019). *Tulipa brachystemon* is listed as a synonym of *T. tetraphylla* in POWO (2024) and according to Christenhusz et al. (2013) and Everett et al. (2013). However, Zonneveld (2009) distinguished *T. brachystemon* as an independent taxon based on DNA barcoding. In addition, *T. brachystemon* and *T. tetraphylla* clustered in different clades based on our phylogenetic tree (Fig. 3). Thus, we consider it necessary to conduct further morphology and phylogeny studies to resolve the taxonomies of these two species.

Figure 14. *Tulipa brachystemon* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by V. Epiktetov)

Tulipa buhseana **Boiss., Diagn. Pl. Orient. ser. 2, 4: 98 (1859).**

Fig. 15

Type. Iran • ‘Prope Yezd Persiae’, *Buhse* (holotype G).

General distribution. Afghanistan, China, Kazakhstan, Iran, Turkmenistan, and Uzbekistan (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Aral region, Balkhash-Alakol, Betpak-Dala, Chu-Ili range, Karatau, Kyzylorda, Moiynkum, Trans-Ili Kungey Alatau, Turgay, Turkestan, and Western Tian Shan. This species grows on sandy and clay deserts, and semi-deserts also occur on the rubbly slopes of lowlands.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa buhseana* was described by P.E. Boissier in 1859 based on the collections of V.A. Buhse from Iran. Collections of *T. buhseana* from the northern Balkhash region had filaments with sparse pubescence, while the collections from the vicinity of the Shieli town, Kyzylorda region had glabrous filaments. According to Christenhusz et al. (2013), Zonneveld (2009), Everett et al. (2013) and POWO (2024), *T. buhseana* is considered a synonym of *T. biflora*. However, these species are morphologically distinguished by the lowering of bulb sheaths on the inner. Additionally, the bulb sheaths of *T. buhseana* are densely hairy on the inner side, whereas those of *T. biflora* are tomentose. In

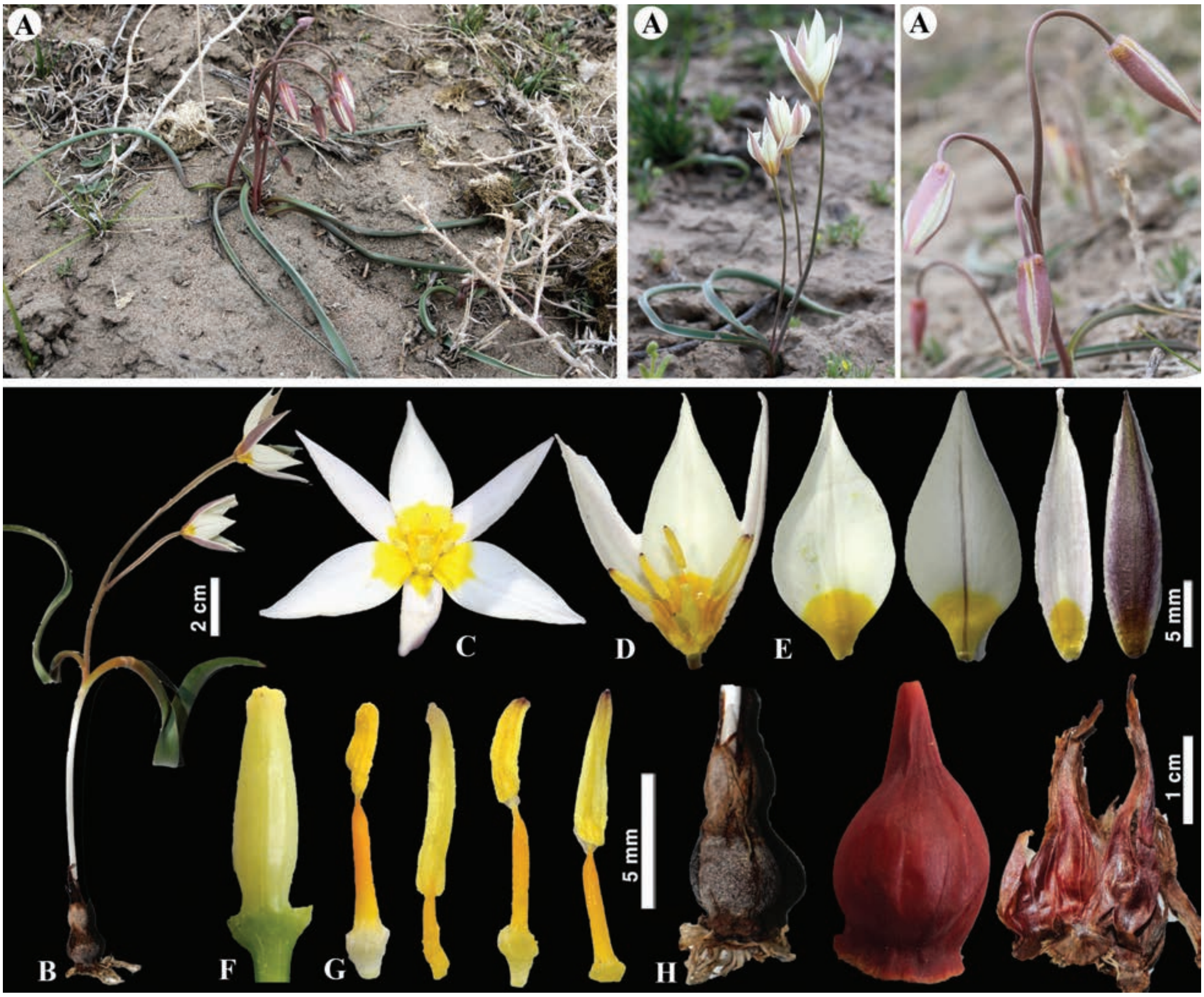

Figure 15. *Tulipa buhseana* in Kazakhstan **A, B** general habits **C, D** flower **E** tepals **F** gynoecium **G** stamens **H** bulb and bulb sheath. (Photos: **A–H** by S. Kubentayev).

the phylogenetic tree, *T. buhseana* and *T. biflora* were placed in different clades (Fig. 3). Therefore, additional studies are required to determine the taxonomic position of *T. buhseana*.

Tulipa dasystemon **(Regel) Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 6: 507 (1879).**

Fig. 16

Type. Kazakhstan • 'In montibus prope Wernoje ad fluvium Almatinka', *A. Regel* (holotype LE; isotype PRC454341).

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, and China (Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Ketmen Terskey Alatau, Kyrgyz Alatau, Trans-Ili Kungey Alatau. This species grows on steppe and meadow slopes, as well as on forest glades from the middle to the alpine belt (1900–3000 m a.s.l.).

Conservation status. *Tulipa dasystemon* is a least concern species at global level (IUCN 2024).

Phenology. Flowering in April–June; fruiting in May–August.

Note. *Tulipa dasystemon* was described by E.L. Regel in 1879 from the Almaty vicinity (in the valley of the Almatinka River) (Regel 1879). Originally described as *Orithyia dasystemon* Regel, this species was later classified as *Tulipa* due to its long, narrow stems. In addition to the present *T. dasystemon*, A.I. Vvedensky (1935) wrote about a close species in Fergana Valley, which occurs at a lower rate and is characterized by strong and leathery bulb sheaths, potentially representing an undescribed species or demonstrating the ecological variability of *T. dasystemon*.

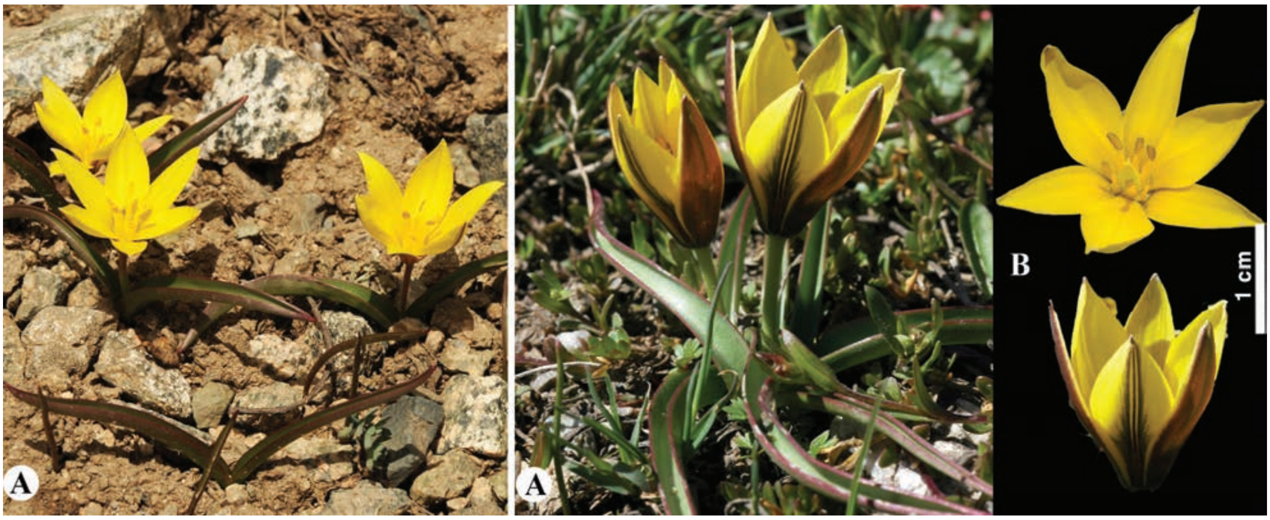

Figure 16. *Tulipa dasystemon* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by V. Epiktetov).

Tulipa dasystemonoides **Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 147 (1935).**

Fig. 17

Type. Kazakhstan • 'Altai Talac', 11 June 1909, *Minkwitz 1365* (holotype LE!).

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan (POWO 2024).

Distribution in Kazakhstan and habitat. Kyrgyz Alatau, and Western Tian Shan. This species grows in meadows in the alpine belt of mountains and is sometimes found at the lower limit of the sub-alpine belt.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in May–June; fruiting in June–August.

Notes. *Tulipa dasystemonoides* was described by A.I. Vvedensky in 1935, based on herbarium material collected from the valley of the Maidantal River in Talas Alatau. Christenhusz et al. (2013) referred to *T. dasystemonoides* as being synonymous of *T. dasystemon*. However, *T dasystemonoides* is distinguished from *T. dasystemon* primarily by its dense woolly bulb sheaths and cream-colored flowers (Vvedensky 1935; Everett et al. 2013). In addition, the two species have different genome sizes (57.7 pg for *T. dasystemonoides* and 51.5 pg for *T. dasystemon*) (Zonneveld 2009). Therefore, we propose that *T. dasystemonoides* is an independent species.

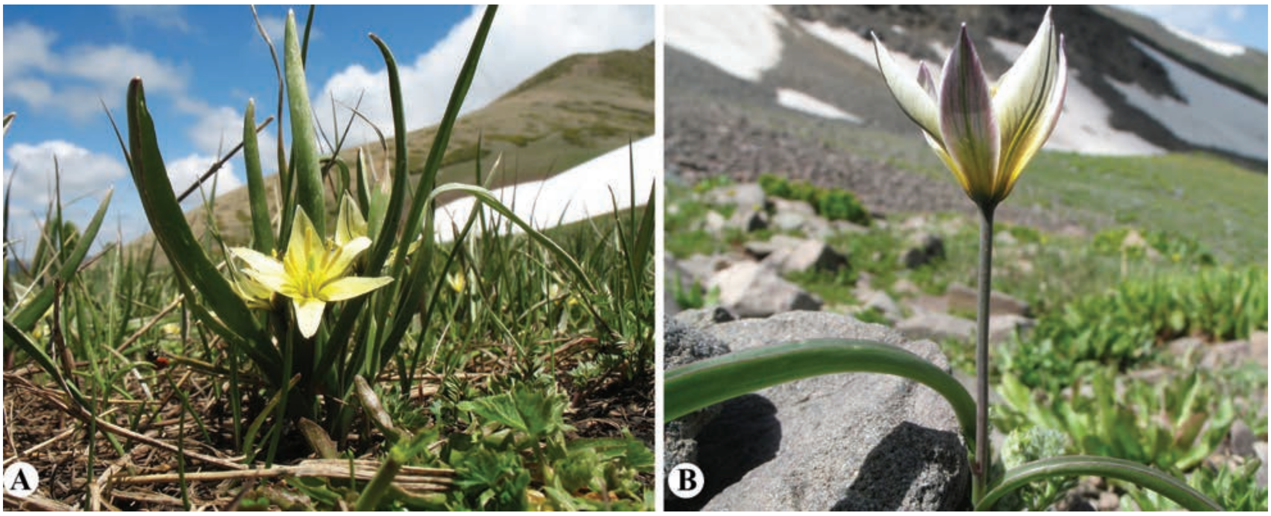

Figure 17. *Tulipa dasystemonoides* in Kazakhstan **A** general habits. (Photos: **A, B** by V. Kolbintsev).

***Tulipa dianaeverettiae* J.de Groot & Zonn., Int. Rock Gard. 122: 7 (2020).**
Fig. 18

Type. Kazakhstan • Altai. Altai Pass, approximately 1800 m altitude, cult. *J.J. de Groot* (L 3986813).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. This species grows in open sunny places in dry sandy soil mixed with stones in the Altai.

Conservation status. *Tulipa dianaeverettiae* is a critically endangered species globally (IUCN 2024).

Phenology. Flowering in April– May; fruiting in May–June.

Notes. *Tulipa dianaeverettiae* was described in 2020 by de Groot and Zonneveld (2020) from cultivated plants grown in the Netherlands from seeds collected by W. Lemmers in Kazakhstan (Alatai Pass Kurchumskiy Ridge) in 2001. *Tulipa dianaeverettiae* is distinguishable from other closely related species

Figure 18. *Tulipa dianae-verettiae* in Kazakhstan. (Photo by J.J. de Groot).

(*T. biflora*, *T. kolbintsevii* and *T. patens*) by the presence of short hairs on the stem, particularly on the leaf margin, and by a distinct capsule with a small dome at the apex. The authors reported that this is the only species of the sect. *Biflores* growing at an altitude of 1800 m a.s.l. in the Altai Mountains. The flowers of *T. dianaeverettiae* have a sweet odor (de Groot and Zonneveld 2020). Currently, little information is available on the distribution and population status of this species.

Tulipa dubia Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 148 (1935).

Fig. 19

Type. Tashkent district • Chotan river gorge, slope near the confluence of Kashka-su brook into Chotan, 10 June 1909, *Z. von Minkwitz* (holotype LE00053022!).

General distribution. Kazakhstan, Kyrgyzstan, and Uzbekistan (POWO 2024).

Distribution in Kazakhstan and habitat. Western Tian Shan. This species grows on fine-grained and rubbly-small-grained slopes in the upper belt of the mountains.

Conservation status. *Tulipa dubia* is an assessed near threatened species at the global level (IUCN 2024).

Phenology. Flowering in April–June; fruiting in May–August (depending on the elevation).

Notes. *Tulipa dubia* was described by A.I. Vvedensky in 1935 from herbarium material collected by Z. Minkwitz in 1909 from the Tashkent district,

Figure 19. *Tulipa dubia* in Uzbekistan **A** general habits **B** flowers (Photos: A–B by K. Tojibaev).

Chotan River gorge. Typically, *T. dubia* populations occur in higher altitudinal zones than *T. kaufmanniana* and *T. tschimganica*. However, all three species grow at similar elevations but occupy different habitats in the Aksay Valley (Greater Chimgan). The main characteristic distinguishing *T. dubia* from the other species of *Tulipa* sect. *Spiranthera* is the shape of the stamen filaments and anthers (Tojibaev et al. 2022). This species forms spontaneous hybrids with *T. kaufmanniana* in common habitats (Vvedensky 1935). The main range of this species is Uzbekistan with a few populations in Western Tian Shan. In addition, high genetic variability has been reported in *T. greigii* in Kazakhstan (Yermagambetova et al. 2024).

Tulipa greigii **Regel, Gartenflora 290: 773 (1873)**

Fig. 20

Type. • Illustration t. 773 in Gartenflora 22 (1873) [lectotype designated by Christenhusz et al. 2013: 312].

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Chu-Ili Range, Karatau, Kyrgyz Alatau, Moiynkum, Trans-Ili Kungey Alatau, Turkestan, and Western Tian Shan. This species grows on clay and rubbly slopes up to 2400 m a.s.l., as well as on foothill plains and mountain flutes.

Conservation status. *Tulipa greigii* is a least concern species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in April–June; fruiting in June–July.

Notes. *Tulipa greigii* was described by E.L. Regel in 1873 from the Karatau Mountains, based on herbarium collections of A. Sivertsev and B. Fedtschenko, initially as a variety of *T. altaica* var. *karatavica* Regel. In the same year, it was described by the same author as an independent species (Ivashchenko and Belyalov 2019; Tojibaev et al. 2022). The species is named in honor of S.A. Greig, president of the Russian Botanical Society of Gardeners. It contains unusual speckles on its leaves that serve as the progenitors of hundreds of

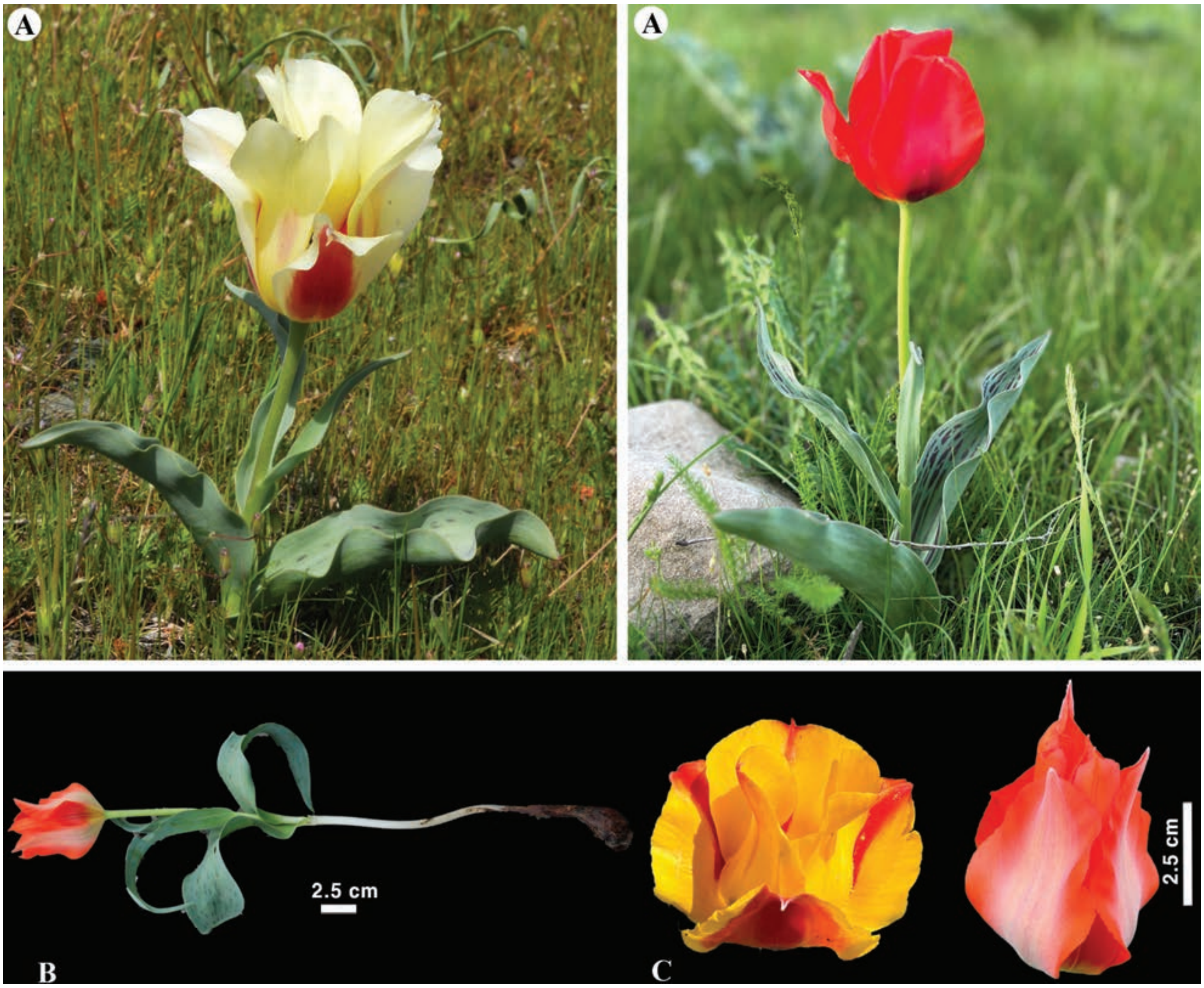

Figure 20. *Tulipa greigii* in Kazakhstan **A, B** general habits with different morphological form **C** flowers with different color. (Photos: **A** by V. Epiktetov, **B, C** by S. Kubentayev).

tulip varieties. This species often hybridizes with *T. kaufmanniana* and *T. alberti* in nature (Ivashchenko and Belyalov 2019). Vvedensky (1935) noted that the collection of this species from Syrdarya deserves a separate study as it differs from the northern (typical) *T. greigii* in that it has longer pedicels and gradually decreasing leaves at the top. In our opinion, this population represents the ecological variability in this species.

Tulipa heteropetala **Ledeb., Icon. Pl. [Ledebour] 1: 21, t. 85 (1829).**

Fig. 21

Type. Kazakhstan • 'Bukhtarminsk et Mont Kurtschum', *Ledebour* (holotype LE).

General distribution. China (Xinjiang), Kazakhstan, and Russia (Altai) (POWO 2024).

Distribution in Kazakhstan and habitat. Altai, Tarbagatai, and Zaysan. This species grows on steppes and semi-deserts on stony and rubbly slopes.

Conservation status. *Tulipa heteropetala* is a least concern species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category II).

Figure 21. *Tulipa heteropetala* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by G. Bolbotov and V. Kolbintsev).

Phenology. Flowering in April–May; fruiting in June–July.

Notes. *Tulipa heteropetala* was described by C.F. Ledebour in 1829 using herbarium material from the vicinity of Bukhtarma (East Kazakhstan). This species is morphologically similar to *T. uniflora* but different by its strong spreading, deviated leaves, very sharp tepals, and expanded stamen filaments below the middle (Vvedensky 1935). Some authors (Mordak 1990, 1992; Cherepanov 1995) consider *T. heteropetala* a synonym of *T. uniflora*. However, most authors consider it an independent species (Vvedensky 1935; Abdulina 1999; Zonneveld 2009; Christenhusz et al. 2013; Everett et al. 2013; Ivashchenko and Belyalov 2019). According to recent morphological analyses of *Tulipa* species of the subgenus *Orithyia*, *T. heteropetala* does not grow in South Siberia, and the previously reported tulips in this region, under the name *T. heteropetala* are large individuals of *T. uniflora* (Chernysheva et al. 2023).

***Tulipa heterophylla* Baker, J. Linn. Soc., Bot. 14: 295 (1874).**

Fig. 22

Type. China • 'Tianshan: Trens Ui Ala-Tau', *Semenow* (holotype LE).

General distribution. Kazakhstan, Kyrgyzstan, and China (Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Trans-Ili Kungey Alatau, Ketmen Terskey Alatau. This species grows on gravelly slopes, forest clearings, and subalpine meadows.

Conservation status. *Tulipa heterophylla* is a least concern species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category II).

Phenology. Flowering in April– July; fruiting in June–August (depending on the elevation).

Notes. *Tulipa heterophylla* was initially described by E.L. Regel in 1868 from Zailiyskiy Alatau as *Orithyia heterophylla* Regel. In 1874, Baker assigned this species to the genus *Tulipa*. Notably, M.G. Popov allocated *T. heterophylla* to a new genus, *Eduardoregelia* Popov, in 1936 due to its unusual flower appearance

Figure 22. *Tulipa heterophylla* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by V. Epiktetov).

(Ivashchenko and Belyalov 2019). This species is distinguished from other species of the subgenus *Orithyia* by the fact that its flower stalks are curved at the top of the stem resulting in flowers in a more or less horizontal position (Zonneveld 2009; Everett et al. 2013). More recently, *T. heterophylla* was found to have a lower level of intrachromosomal asymmetry than other species of the subgenus *Orithyia* (Chernysheva et al. 2023). The main range of this species does not extend beyond the Tian Shan.

Tulipa iliensis Regel, Gartenflora 28: 162 (1879).

Fig. 23

Type. Kyrgyzstan. ‘Sarybulak’, 23 Apr 1878, *A. Regel* (lectotype P-00730916; isolectotype BM) [lectotype designated by Christenhusz et al. 2013: 315].

General distribution. Kazakhstan, Kyrgyzstan, and China (NW-Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Ketmen, and Terskey Alatau. This species grows on steppe slopes and among shrubs in the altitude range of 1300–1500 m a.s.l.

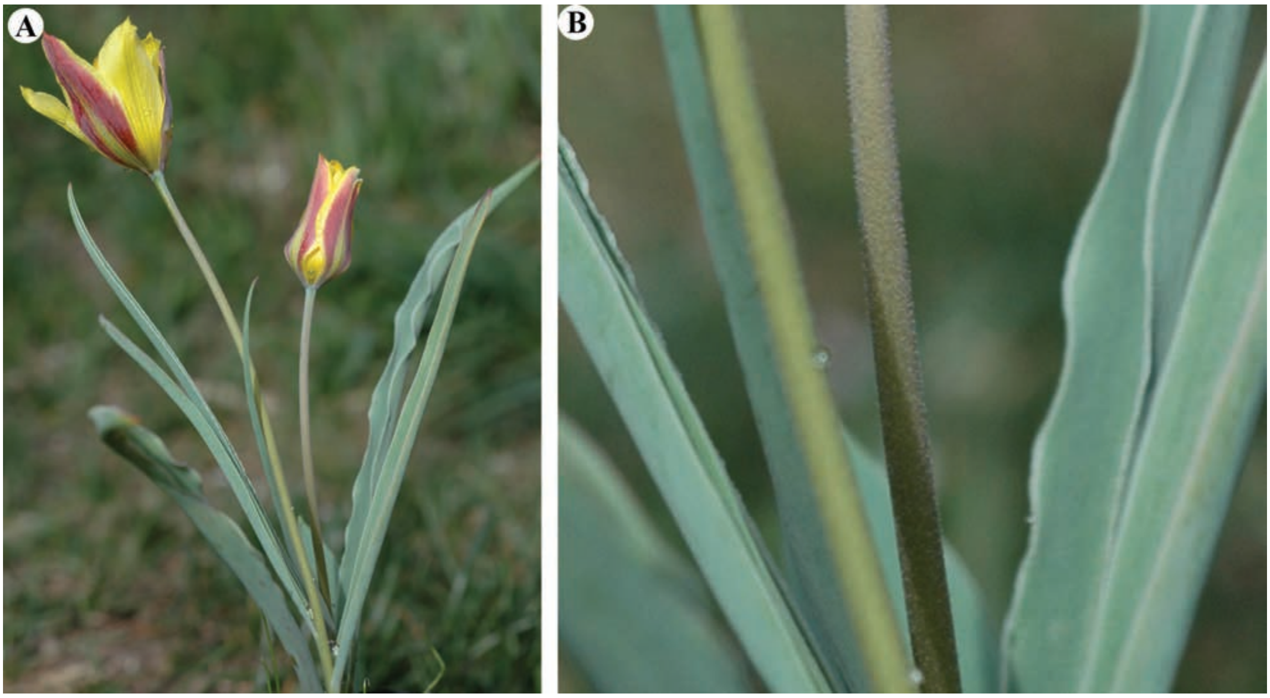

Figure 23. *Tulipa iliensis* in Kazakhstan **A** general habits **B** stem with short pubescences and leaves with flat edge. (Photos: **A, B** by V. Epiktetov).

Conservation status. *Tulipa iliensis* is near threatened species at the global level (IUCN 2024).

Phenology. Flowering in April–May; fruiting in June–July.

Notes. *Tulipa iliensis* was described by E.L. Regel in 1879 based on collections by A. Regel from the upper reaches of the Ile River. This species is morphologically similar to *T. altaica*, differing by the appressed hair-like pubescence at the apex and base of the bulb sheaths and linear (linear-lanceolate) leaves with a flat margin (Vvedensky 1935). Van Raamsdonk and De Vries (1995) listed *T. iliensis* and *T. kolpakowskiana* as synonyms of *T. altaica*. However, this species is recognized as independent according to the latest classifications of the genus *Tulipa* (Zonneveld 2009; Christenhusz et al. 2013; Everett et al. 2013). *Tulipa iliensis*, *T. kolpakowskiana*, *T. altaica*, and *T. thianschanica* are closely related species, as confirmed by molecular genetic data (Christenhusz et al. 2013; Li et al. 2021). The main range of *T. iliensis* is in China (Xinjiang) (Qin et al. 2024). In Kazakhstan, only a few localities of this species are known on the Ketmen Terskey Alatau.

***Tulipa ivasczenkoae* Epiktetov & Belyalov, Turczaninowia 16: 5 (2013).**
Fig. 24

Type. Kazakhstan • SW part of Dzhungarian Alatau, mts. Chulak; Aiyrkezen, upper third of stony northern slope (1100 m. a. s. l.), between bushes, 26 April 2013, *V.G. Epiktetov & O.V. Belyalov* (ALTB, iso – LE).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Dzungarian Alatau. This species grows on dry stony slopes among shrubs in low-desert mountains (1100 m a.s.l.).

Figure 24. *Tulipa ivasczenkoae* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by V. Epiktetov).

Conservation status. *Tulipa ivasczenkoae* is a critically endangered species at the global level (IUCN 2024).

Phenology. Flowering in April–May; fruiting in June.

Notes. *Tulipa ivasczenkoae* was described in 2013 from the south-western part of the Dzungarian Alatau, Chulak Mountain, Ayyrkezen. The species was named in honor of the Kazakhstani scientist Anna Andreyevna Ivasczenko, who has been studying wild bulbous plants of Kazakhstan, including tulips, since 1963. This species is closely related to the Pamir-Alai endemic *T. fosteriana* Irw. and *T. carinata* Vved. It is distinguished from the former by keeled leaves and from the latter by blunt or short pointed rather than long-pointed perianth leaflets and larger broad leaves (Epiktetov and Belyalov 2013). This species has not been encountered in other areas since its description; thus far, it is known only from its type locality.

Tulipa jansii **J.J.de Groot & Zonn., Int. Rock Gard. 168: 1 (2024).**

Fig. 25

Type. • Wild collected material from the Ily Valley north of Kapchagay. *J.J. de Groot and B.J.M. Zonneveld* (holotype L4513065).

General distribution. Endemic to Kazakhstan (de Groot and Zonneveld 2024).

Distribution in Kazakhstan and habitat. Balkhash-Alakol and Dzungarian Alatau. This species grows on dry, stony slopes at the foot of mountains.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in April–May; fruiting in June.

Notes. *T. jansii* was recently described from the Ili River valley north of Kapchagai (de Groot and Zonneveld 2024). This species was named after Harry Jans, a famous world traveler. The main difference between *T. jansii* and other representatives of *T.* sect. *Kolpakowskianae* is the pear-shaped bulb with stolons, non-elongated tunic without fibers, narrower lanceolate leaves and narrow, almost straight filaments (de Groot and Zonneveld 2024).

Figure 25. *Tulipa jansii* in Kazakhstan, general habits. (Photos by J.J. de Groot).

***Tulipa kaufmanniana* Regel, Gartenflora 26: 194 (1877).**

Fig. 26

Type. Uzbekistan • 'In Turkestaniae montibus fluvium Tschirtschik [Chirchiq] adjacentibus', *A. Regel* (LE!).

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan (POWO 2024).

Distribution in Kazakhstan and habitat. Western Tian Shan, Karatau, and Kyrgyz Alatau. This species grows on shaded slopes, meadow areas, and scrub thickets and less often on rocky slopes from the lower to the upper mountain belts.

Conservation status. *Tulipa kaufmanniana* is a near threatened species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in March–May; fruiting in June–July.

Notes. *Tulipa kaufmanniana* was described by E.L. Regel in 1877 from the Chirchik River basin. The species was named in honor of Kaufmann, Governor-General of the Turkestan region (Ivashchenko and Belyalov 2019). *Tulipa berkariensis* Rukšāns, described from the Berkari Gorge by Rukšāns (2019), differs from *T. kaufmanniana* by the globular bulb shape and the presence of horizontal stolons. Currently, many researchers consider *T. berkariensis* a synonym of *T. kaufmanniana* (Christenhusz et al. 2013; Everett et al. 2013; Sennikov and Tojibaev 2021). However, *T. berkariensis* has a slightly smaller genome size than the authentic *T. kaufmanniana* from Uzbekistan (Zonneveld 2009). Further research is needed to study *T. berkariensis* and establish its taxonomic status.

***Tulipa kolbintsevii* Zonn., Pl. Syst. Evol. 298: 1294 (2012).**

Fig. 27

Type. Kazakhstan • Grown in the Netherlands from material collected at Dzjungarian Ala-Tau, Taskora Valley, cult. *J.J. de Groot* (holotype L 0821329!).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Figure 26. *Tulipa kaufmanniana* in Kazakhstan **A, B** general habits **C** flower **D** tepals **E** gynoecium **F** stamens **G** bulb and bulb sheath. (Photos: **A** by S. Kubentayev and V. Epiktetov, **B–G** by S. Kubentayev).

Figure 27. *Tulipa kolbentsevii* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by Zh. Nurgozhanova and V. Epiktetov).

Distribution in Kazakhstan and habitat. Dzungarian Alatau. This species grows among shrubs at an altitude of 650 m a.s.l.

Conservation status. *Tulipa kolbintsevii* is an endangered species at the global level (IUCN 2024).

Phenology. Flowering in March–June; fruiting in May–June.

Notes. *Tulipa kolbintsevii* was described from the cultural collection of J.J. de Groot in the Netherlands, collected from Taskora Valley, 650 m from Dzjungarian Ala-Tau, Kazakhstan (Zonneveld and de Groot 2012). The main difference between *T. kolbintsevii* and other *Tulipa* species in the section *Biflores* is that the sepals have a pilose margin at the base rather than a pilose band. This species was named in honor of V. Kolbintsev, who guided the expedition leading to discovery (Zonneveld and de Groot 2012). *Tulipa kolbintsevii* is diploid, with a 48.0 pg genome size, smaller than that of other species in *T.* sect. *Biflores*, ranging from 51.5 to 76.3 pg (Zonneveld 2009). The distribution of this species is poorly studied, and known from only two localities, including "locus classicus".

Tulipa kolpakowskiana **Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 5: 266 (1877).**

Fig. 28

Type. Kazakhstan • 'In Turkestania prope Verniy et in valle fluvii Almatinka', *A. Regel* (holotype LE; possible isotype K).

General distribution. Afghanistan, Kazakhstan, Kyrgyzstan, and China (Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Trans-Ili Kungey Alatau, Moiynkum, Chu-Ili range, Dzungarian Alatau, Kyrgyz Alatau, and Ketmen Terskey Alatau. This species grows on clayey, less often gravelly, slopes of steppe and desert foothills.

Conservation status. *Tulipa kolpakowskiana* is a near threatened species at the global level (IUCN 2024). It is included in the red book of Kazakhstan (Category III).

Phenology. Flowering in April–May; fruiting in June–July.

Notes. *Tulipa kolpakowskiana* was first described by E.L. Regel in 1877 from Verniy vicinity (Almaty). This species was named in honor of G. A. Kolpakowskiy, an honorary member of the Russian Geographical Society (Ivashchenko and Belyalov 2019). Van Raamsdonk et al. (1997) classified this species as a synonym of *T. altaica* var *altaica*. However, after studying wild material, Zonneveld (2009), distinguished it as a separate species of the section *Kolpakowskianae* (Everett et al. 2013). In nature, this species often hybridizes with *T. ostrowskiana*, *T. tetraphylla*, and *T. brachystemon* (Vvedensky 1935; Ivashchenko and Belyalov 2019).

Tulipa korolkowii **Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 3: 295 (1875).**

Fig. 29

Type. Uzbekistan • 'Habitat in solo lutoso in desertis inter Turkestaniam et Khiwam prope Farisch', *Korolkow et Krause* (holotype LE!).

Figure 28. *Tulipa kolpakowskiana* in Kazakhstan **A, B** general habits **C, D** flower **E** tepals **F** bulb. (Photos: **A–F** by S. Kubentayev).

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Turkestan, and Western Tian Shan. This species grows on dry gravel and stony surfaces, sandy ceilings, slopes, and plains at the outlet (opening), and in the lower belt of the mountain (up to 1800 m a.s.l.).

Conservation status. *Tulipa korolkowii* is a near threatened species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category II).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa korolkowii* was first described by E.L. Regel in 1875 from Forish (Uzbekistan). This species was named in honor of amateur botanist N. I. Korolkow, who lived and worked in the Turkestan region from 1868 to 1905 (Ivashchenko and Belyalov 2019). Vvedensky (1935) distinguished *T. korolkowii* and two related species, *T. rosea* Vved. and *T. nitida* Hoog, as geographically isolated species (Tojibaev et al. 2022). Based on the flow cytometry results, Zonneveld (2009) considered *T. korolkowii* and *T. nitida* two different species and *T. rosea* as *T. korolkowii* f. *rosea* (Vvedensky). Christenhusz et al. (2013) considered *T. nitida* and *T. rosea* as synonyms of *T. korolkowii*. Based on long-term studies in natural habitats and observations in *ex situ* living collections in TASH

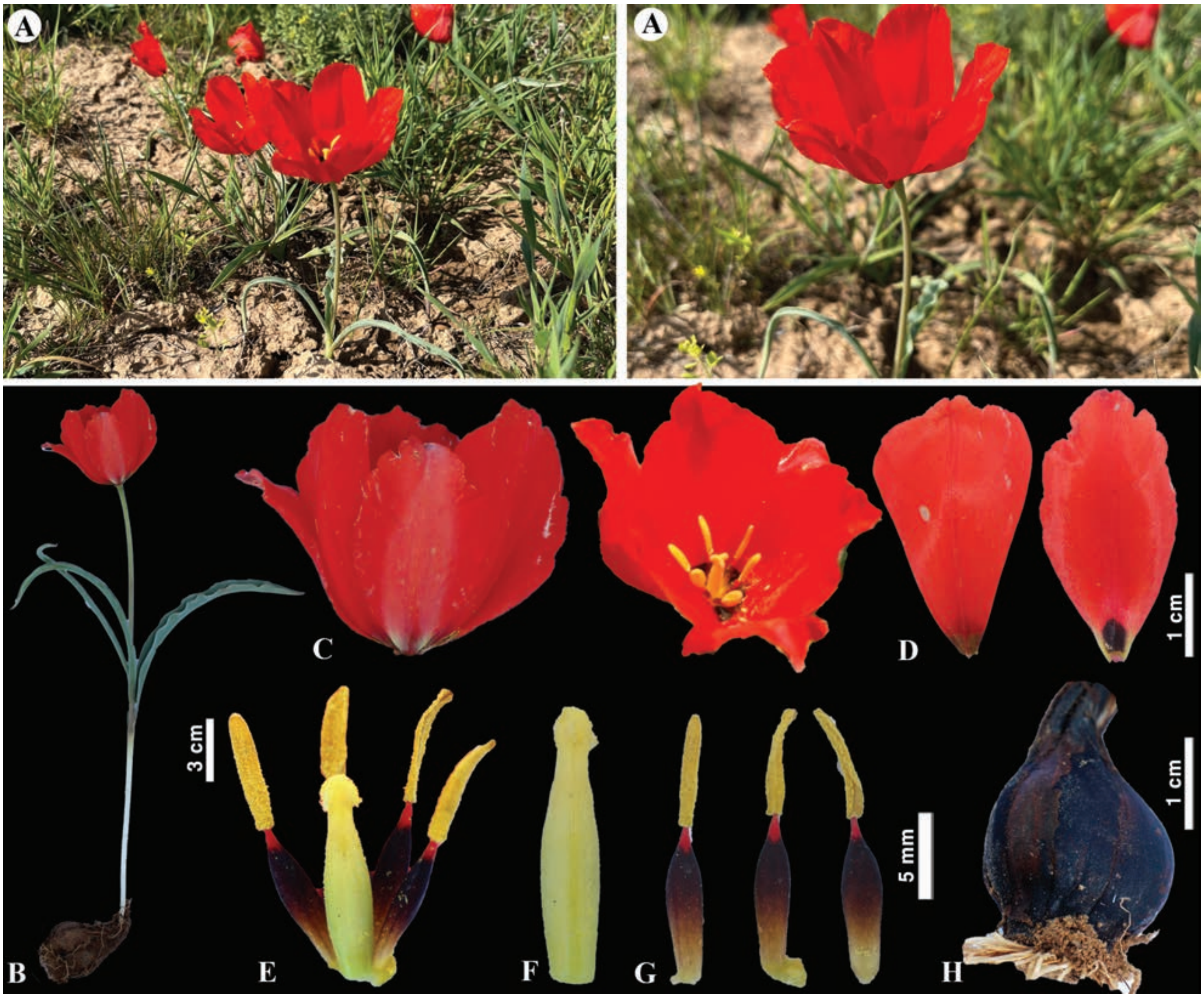

Figure 29. *Tulipa korolkowii* in Kazakhstan **A, B** general habits **C** flower **D** tepals **E** gynoecium and stamens **F** gynoecium **G** stamens **H** bulb. (Photos: **A–H** by S. Kubentayev).

and Tashkent Botanical Garden, Tojibaev et al. (2022) found that morphological characters between *T. korolkowii* and *T. nitida*, vary depending on habitat and climatic conditions. In addition, they did not find any evidence to confirm the presence of *T. rosea* within the present-day boundaries of Uzbekistan.

Tulipa kujukense **J.J. de Groot & Zonn.**

Fig. 30

Type. Kazakhstan • Vegetative progeny of wild collected material grown in the collection of *J.J. de Groot*, collection number G05-8 (holotype L4513067).

General distribution. Endemic to Kazakhstan (de Groot and Zonneveld 2024).

Distribution in Kazakhstan and habitat. Karatau. This species grows among shrubs.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in March–April; fruiting in May–June.

Figure 30. *Tulipa kujukense* in Kazakhstan, general habits. (Photo by J.J. de Groot).

Notes. *Tulipa kujukense* was first described in 2024 from Karatau (Kuyuk Pass). *Tulipa kujukense* is morphologically similar to *T. orthopoda* and *T. bifloriformis* but differs in size and by bulb with gray-brown tunica, characteristic of the Turkestanica species group. In addition, *T. kujukense* has a large genome size (60.7 pg) compared with other species of *T.* sect. *Biflores* (de Groot and Zonneveld 2024).

Tulipa lehmanniana **Merckl., A.A.von Bunge, Beitr. Fl. Russl. 7: 337 (1852).**
Fig. 31

Type. UZBEKISTAN • *A. Lehmann sn*., *Bunge Rel. Lehm. 337* (K-000844622) [lectotype designated by Christenhusz et al. 2013: 316].

General distribution. Afghanistan, Eastern Iran, Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan (POWO 2024).

Distribution in Kazakhstan and habitat. Balkhash-Alakol, Betpak-Dala, Chu-Ili range, Kyzylkum, Moiynkum, Turkestan, and Western Tian Shan. This species grows on sand and variegated rock outcrops, in sandy and stony deserts.

Conservation status. *Tulipa lehmanniana* is a near threatened species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category I).

Phenology. Flowering in April; fruiting in May–June.

Notes. *Tulipa lehmanniana* was described by Merklin in 1854 from collections made near Bukhara. The species was named in honor of A. Lehmann, a Russian botanist, who collected plants from Central Asia on behalf of the St. Petersburg Botanical Garden (Ivashchenko and Belyalov 2019). Christenhusz et al. (2013) considered *T. zenaidae* a synonym of *T. lehmanniana*, which we strongly disagree with. These species are distinct morphologically, ecologically, and geographically. Eduard Ludvigovich Regel described *T. behmiana* Regel in 1880 from the vicinity of the Iliysk settlement (Kapchagai). This species was classified as a synonym of *T. lehmanniana* according to the latter classifications (Van Raamsdonk and De Vries 1995; Zonneveld 2009; Christenhusz et al. 2013; Everett et al. 2013).

Figure 31. *Tulipa lehmanniana* in Kazakhstan **A, B** general habits **C, E** flowers with different color variants **D** tepals of different color variants **F** gynoecium **G** stamens **H** bulb (Photos: **A–H** by S. Kubentayev).

Tulipa lemmersii **Zonn., Peterse & J.de Groot, Pl. Syst. Evol. 298: 91 (2012).**
Fig. 32

Type. Kazakhstan • Chimkent: Mashad Pass, cult. *A. Peterse* (holotype L 0822655).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Western Tian Shan. This species grows on dry stony slopes with outcrops or shallow deposits of conglomerate rocks, on a plateau or canyon sites.

Conservation status. *Tulipa lemmersii* is a vulnerable species at the global level (IUCN 2024).

Phenology. Flowering in March–April; fruiting in May.

Notes. *Tulipa lemmersii* was first found in 2007 by A. Peterse, at the top of steep cliffs on Mashat Pass, when he accompanied a tulip expedition organized by W. Lemmers (the species is named in his honor). *Tulipa lemmersii* can be distinguished from *T. iliensis*, *T. ferganica*, *T. anisophylla*, and *T. tetraphylla* by its glabrous stems, thin tunic, and single flowers. It can be distinguished from other species of the *T.* sect. *Kolpakowskianae* as they have mostly red and yellow flowers. It is a diploid species with the smallest genome size (36 pg) among

Figure 32. *Tulipa lemmersii* in Kazakhstan **A, B** general habits **C, D** flower **E** tepals **F** gynoecium **G** stamens **H** bulb and bulb sheath. (Photos: **A–H** by S. Kubentayev).

all species in the section *Kolpakowskianae* (Zonneveld 2009). The species was later validated using type designation in 2012 (Veldkamp and Zonneveld 2012).

Tulipa orthopoda **Vved., Opred. Rast. Sred. Azii 2: 320 (1971).**
Fig. 33

Type. Kazakhstan • Turkestan, 5 April 1930, *Lipschitz & Pavlov 32* (holotype TASH!).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Karatau, Western Tian Shan. This species grows in clay, gravel and stony slopes of the lowlands.

Conservation status. *Tulipa orthopoda* is a vulnerable species at the global level (IUCN 2024).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa orthopoda* is a narrowly localized endemic species to Kazakhstan (Kamelin 1990). This species was first mentioned by Vvedensky (1935) in Flora of the USSR in a note on *T. bifloriformis* Tulip specimens from Karatau

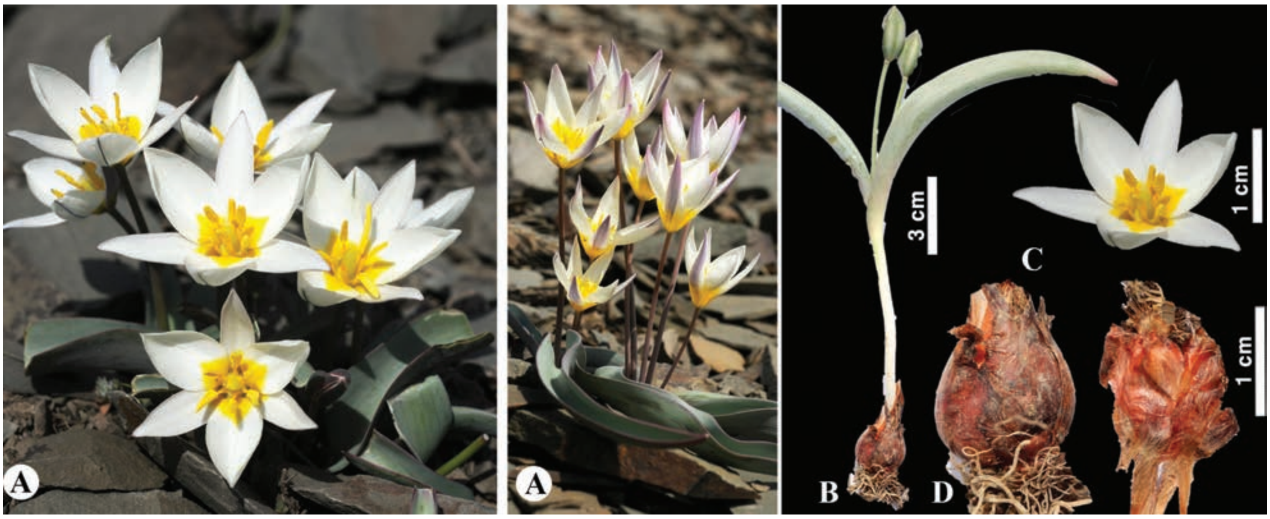

Figure 33. *Tulipa orthopoda* in Kazakhstan **A, B** general habits **C** flower **D** bulb and bulb sheath. (Photos: **A, C** by V. Epiktetov; **B, D** by S. Kubentayev).

are reportedly characterized by drooping buds, lower height, and more pubescent leaves. A detailed description in Latin was first published in 1971 in the Conspectus Florae Asiae Mediae (Vvedensky and Kovalevskaya 1971). Christenhusz et al. (2013) reported that *T. orthopoda* is a synonym of *T. bifloriformis*; however, later indicated that it deserves recognition. According to Zonneveld (2009), the genome size of *T. orthopoda* is 59.3 pg, while that of *T. bifloriformis* is 56.6 pg. This difference was sufficient to distinguish between two representatives of the same group (Everett et al. 2013). Wilson (2023) listed *T. orthopoda* as an independent taxon in his updated list of recognized tulip species. We agree that *T. orthopoda* should be recognized as an independent taxon based on several morphological characteristics and different flowering times (*T. orthopoda* flowers earlier than *T. bifloriformis*).

Tulipa ostrowskiana **Regel, Gartenflora 33: 34 (1884).**
Fig. 34

Type. Kazakhstan • ‘Iter Turkestanicum, Kl. Almaty Schlucht bei Werny’, 2 April 1879, *A. Regel* (K).

General distribution. Kazakhstan, and Kyrgyzstan (POWO 2024).

Distribution in Kazakhstan and habitat. Kyrgyz Alatau and Trans-Ili Kungey Alatau. This species grows on slopes with deep nutritious soil (less often gravelly), in the lower and middle mountain belts.

Conservation status. *Tulipa ostrowskiana* is assessed near threatened at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in April– May; fruiting in June– July.

Notes. *Tulipa ostrowskiana* was described in 1884 by E.L. Regel from collections near Verny (Almaty). This species was first collected in 1879 by A.E. Regel and A.M. Fetisov (the chief gardener of Pishpek (Bishkek) in charge of the Treasury Garden in Verny) (Ivashchenko and Belyalov 2019). Zonneveld (2009) suggested that *T. ostrowskiana* may be an allotetraploid originating from *T. kolpakowskiana* and *T. lemmersii* based on genome size. Spontaneous

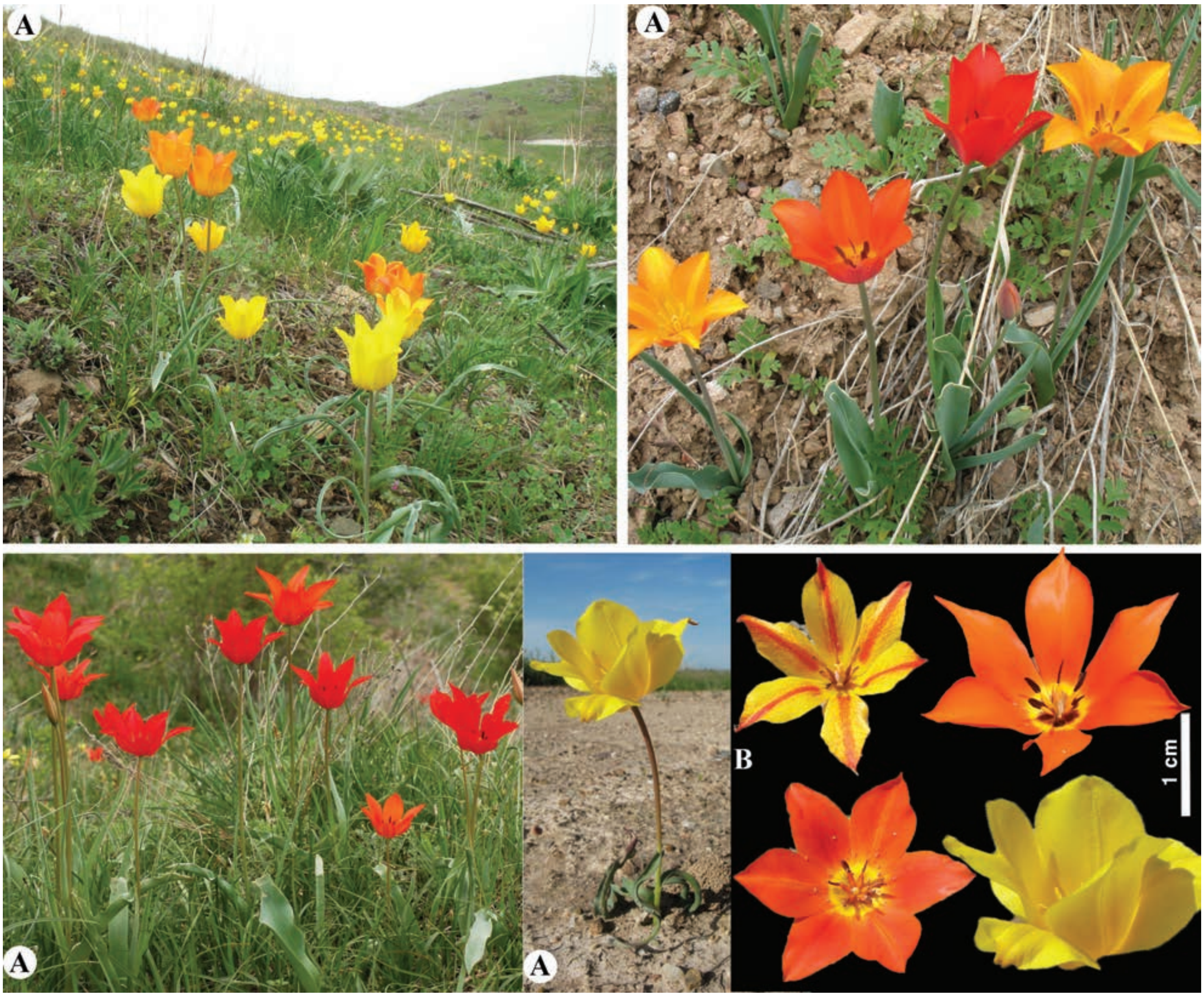

Figure 34. *Tulipa ostrowskiana* in Kazakhstan **A** general habits **B** flowers showing different color morphs. (Photos: **A, B** by V. Kolbintsev and V. Epiktetov).

hybrids of *T. ostrowskiana* and *T. kolpakowskiana* with intermediate flower coloration and habit traits are known in nature (Vvedensky 1935; Ivashchenko and Belyalov 2019).

Tulipa patens **C.Agardh, Syst. Veg., ed. 15 bis [Roemer & Schultes] 7: 384 (1829).**

Fig. 35

Type. 'In Sibiria', Agardh (LD?, not found).

General distribution. Kazakhstan, and Russia.

Distribution in Kazakhstan and habitat. Syrt, Tobol-Ishim, Irtysh, Semipalatinsk pine forest, Kokchetav, Mugojary, Turgay, Western Upland, Ulytau, Zaysan, Eastern Upland, Karkaraly, and Altai, Tarbagatai. This species grows in steppe, semi-desert and shrub land on gravelly clayey slopes.

Conservation status. The IUCN conservation status of this species requires assessment. It is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in April–May; fruiting June.

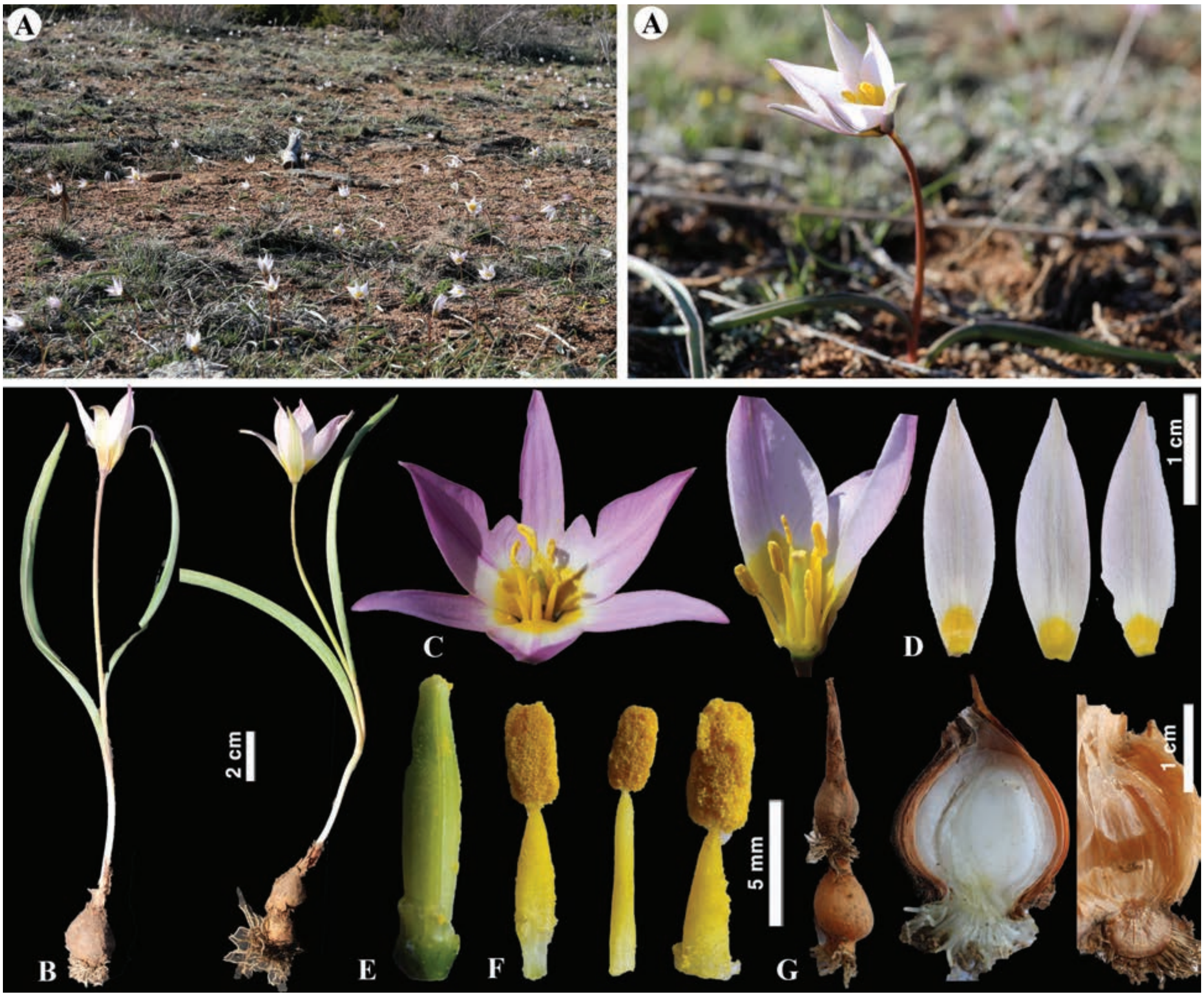

Figure 35. *Tulipa patens* in Kazakhstan **A, B** general habits **C** flower **D** tepals **E** gynoecium **F** stamens **G** bulb and bulb sheath. (Photos: **A–G** by S. Kubentayev).

Notes. A complete species description of *T. patens* was published in 1829 by J. Roemer and J. Schultes (Ivashchenko and Belyalov 2019). Subsequently, C. F. Ledebour described it as *T. tricolor* Ledeb. The taxonomic position of *T. patens* is relatively controversial. Some authors (Christenhusz et al. 2013; Everett et al. 2013; Li et al. 2021) place it in synonymy of *T. sylvestris* subsp. *australis*, while other authors (Polyakov 1958; Cherepanov 1995; Zonneveld 2009; Kutlunina et al. 2013; Wilson 2023) consider this species an independent taxon. We believe that *T. patens* deserves recognition based on its complex morphological characteristics and ecology.

Tulipa regelii **Krasn., Bot. Zap. 2: 21 (1888).**
Fig. 36

Type. Kazakhstan • 'Prope fauces fluminis Kurtu inter saxa non rara in montibus Andrakai rarior', April 1886, *A. Krassnow s.n.* (LE).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Balkhash-Alakol, and Chu-Ili range. This species grows on rocky, gravelly slopes and scree (800–1100 m a.s.l.).

Figure 36. *Tulipa regelii* in Kazakhstan **A** general habits **B** leaf blade **C** flower. (Photos: **A–C** by V. Epiktetov).

Conservation status. *Tulipa regelii* is an endangered species at the global level (IUCN 2024). It is included in the Red Book of Kazakhstan (Category II).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa regelii* was described in 1887 by the prominent Russian botanical geographer A. N. Krasnov, who surveyed the Shu-Ili Mountains (where the species was collected from the Anyrakai and Kurti tracts). The species is named in honor of E.L. Regel, the director of the botanical garden in St. Petersburg (Ivashchenko and Belyalov 2019). It is one of the most distinctive tulips due to the leaf blade surface having many parallel ridge-like outgrowths. However, the position of this species in the genus *Tulipa* remains controversial. Vvedensky (1935) classified *T. regelii* into a separate section, *T.* sect. *Lophophyllon* Vved, due to the unique structure of its leaf blade. Meanwhile, Zonneveld (2009) placed it in the section *Biflores* based on its genome size and flower structure. However, Christenhusz et al. (2013) assigned *T. regelii* to the subgenus *Eriostemones*. Later, Wilson (2023) placed *T. regelii* in the section *Sylvestres* (Baker) Baker.

Tulipa salsola Rukšāns & Zubov, Int. Rock Gard. 148: 11 (2022).

Fig. 37

Type. Kazakhstan • Zhetysu region, the extreme southern part of Dzungarian Alatau (44°10'N, 79°31'E); sandy, saline soils within semi-desert habitat, c. 880 m.a.s.l.; leg. 05 May 2012, *Rukšāns*; cult. (12KZ-059 specimen grown in J. Rukšāns garden, Latvia), fl. 11 Apr. 2021, *Rukšāns* (holotype GB).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Dzungarian Alatau, and Trans-Ili Kungey Alatau. This species grows on fixed and hilly-ridged sands over brown and gray-brown soils, in depressions of takyrs and solonchaks with Saxaul.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa salsola* was described relatively recently in 2022 from the southern part of Dungarian Alatau, Zhetysuyskaya Oblast, Kazakhstan. It is

Figure 37. *Tulipa salsola* in Kazakhstan. **A** general habits **B** flower **C** tepals **D** gynoecium and stamens **E** stamens **F** bulb and bulb sheath. (Photos: A–F by J. Rukšāns).

morphologically similar to *T. kolbintsevii* but differs by the presence of 2(–3) flowers, an adaxially strongly woolly bulb tunic, absent elongated bulb tunic, and stamens shorter or equal to the ovary (vs. one flower, naked on the neck with some hairs on the bulb tunic adaxially, elongated bulb tunic, and stamens longer than the ovary in *T. kolbintsevii*) (Rukšāns and Zubov 2022).

Tulipa sogdiana **Bunge, Beitr. Fl. Russl. 338 (1852).**
Fig. 38

Type. Uzbekistan • Inter Bukhara et Kermine, A. Lehmann *s.n.* (holotype LE; isotypes K 000844627, P00730919, P00730920).

General distribution. Kazakhstan, Tajikistan, Turkmenistan, and Uzbekistan (Tojibaev et al. 2022).

Distribution in Kazakhstan and habitat. Kyzylkum, Southern Ustyrt, Northern Ustyrt, and Mangyshlak. This species grows in deserts on sandy and clay soils.

Conservation status. The IUCN conservation status of this species requires assessment.

Figure 38. *Tulipa sogdiana* in Kazakhstan **A** general habitat **B** flowers. (Photos: **A** by F. Shakula; https://www.plantarium.ru/page/image/id/766687.html); **B** by V. Epiktetov).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. *Tulipa sogdiana* was first described in 1854 by A.A. Bunge from a desert region between Bukhara and Kermin (Uzbekistan). In “Flora of Kazakhstan” (Polyakov 1958), this species was listed in Kyzylkum. Although we did not identify herbarium materials in this area, we believe that it is in Kzyzlkum, as there are numerous confirmed localities of this species in the Uzbekistan part of Kyzylkum (Tojibaev et al. 2022). *Tulipa sogdiana* differs from similar species of the subgenus *Eriostemones* by its glabrous filaments of stamens (Everett et al. 2013; Ivashchenko and Belyalov 2019; Tojibaev et al. 2022). Christenhusz et al. (2013) and Everett et al. (2013) placed *T. sogdiana* in synonymy of *T. biflora* s.l. However, some authors consider it an independent taxon (Abdulina 1999; Zonneveld 2009; Tojibaev et al. 2022). Wilson (2023) believed that *T. sogdiana* can be recognized if its uniqueness is proven. Additional studies of this species under natural growing conditions are required to establish its taxonomic position.

Tulipa suaveolens Roth, Ann. Bot. (Usteri) 10: 44 (1794).

Fig. 39

Type. Kazakhstan • ‘Deserta Caspica’, *Pallas* (neotype BM!) [neotype designated by Christenhusz et al. 2013: 320].

General distribution. Kazakhstan, Krym, North Caucasus, and Transcaucasus (POWO 2024).

Distribution in Kazakhstan and habitat. Aktobe, Turgay, Bukeev, Emba, Mugojary, Caspian region, Syrt, Tobol-Ishim, Western Upland, Aral region, and Ulytau. This species grows on steppe and semi-desert areas.

Conservation status. The IUCN conservation status of this species has not yet been assessed. It is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in March–April; fruiting in May–June.

Notes. This species is usually reported under *T. schrenkii* Regel, which was first described from the Yesil River valley in 1873. However, the older name *T. suaveolens* takes precedence (Christenhusz et al. 2013). Christenhusz et al.

Figure 39. *Tulipa suaveolens* in Kazakhstan **A, B** general habits **C** flowers showing color variation of the species **D** tepals of two different color morphs **E** gynoecium **F** stamens **G** bulb and bulb sheath. (Photos: **A–G** by S. Kubentayev).

(2013) provided lectotyping of *T. suaveolens* from a specimen collected in the wild, securing the name for wild plants. In Kazakhstan, this species is found in the Caspian region to the Eastern Shallow Basin and from the northern borders of the country to the northern part of Mangystau (Ivashchenko and Belyalov 2019).

Tulipa tarda **Stapf, Bot. Mag. 156: t. 9321 (1933).**

Fig. 40

Type. Cultivated • Bulbs sent to Firma Van Tubergen, originally from Iran (Urmia) in 1928. A preserved flower from the Van Tubergen garden and associated original illustration are labeled as presented by the Editor of the Botanical Magazine to the Kew Herbarium (K).

General distribution. Kazakhstan, and Kyrgyzstan.

Distribution in Kazakhstan and habitat. Trans-Ili Kungey Alatau. This species grows on stony-gravelly and rocky slopes, steppe areas and thickets of shrubs in the lower mountain belt.

Conservation status. The IUCN conservation status of this species has not yet been assessed. It is included in the Red Book of Kazakhstan (Category II).

Figure 40. *Tulipa tarda* in Kazakhstan **A** general habits **B** flowers (Photos: **A, B** by A. Tolenova).

Phenology. Flowering in April–May; fruiting June.

Notes. Christenhusz et al. (2013) formally synonymized *T. tarda* into a taxon with the older name *T. urumiensis* Stapf when revising the genus. However, the name *T. tarda* has become entrenched in literature, horticultural trade, and conservation assessments, leading to nomenclatural destabilization and confusion. For these reasons, it has been suggested that the name *T. urumiensis* should be rejected so that *T. tarda* becomes the correct name for this species (Christenhusz and Wilson 2022). *Tulipa tarda* is endemic in northern Tien-Shan and grows in the western part of the Zailiyskiy Alatau ridge and adjacent regions of northern Kyrgyzstan, i.e., the valley of the Chu and Chon-Kemin rivers with the adjacent northern slopes of the Kyrgyz ridge and Kungey Alatau (Tolenova et al. 2021).

Tulipa tetraphylla **Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 3: 296 (1875).**
Fig. 41

Type. Kyrgyzstan • Turkestaniae in valle Kotschkura, Kaulbars, *Baro* (holotype LE, not located).

General distribution. Kazakhstan, Kyrgyzstan, and China (Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Ketmen Terskey Alatau, and Trans-Ili Kungey Alatau. This species grows on stony slopes, and steppe areas in the lower and middle zones of the mountains.

Conservation status. *Tulipa tetraphylla* is a least concern species at the global level (IUCN 2024).

Phenology. Flowering in April–May; fruiting in June –July.

Note. *Tulipa tetraphylla* was described by E.L. Regel in 1875 from collections from Central Tian Shan (Kochkur River basin, Kyrgyzstan). Spontaneous hybrids with *T. kolpakowskiana* have also been reported (Ivashchenko and Belyalov 2019; Vvedensky 1935). *Tulipa tetraphylla* is often found in its autotetraploid form (Wilson 2023), although it also has a diploid form (Botschantzeva 1962). The new species *T. toktogulica* B.D.Wilson & Lazkov from Jalal-Abad province was described in 2022. It is morphologically similar to *T. tetraphylla* but differs by fewer leaves (3 leaves) and weakly fragrant flowers.

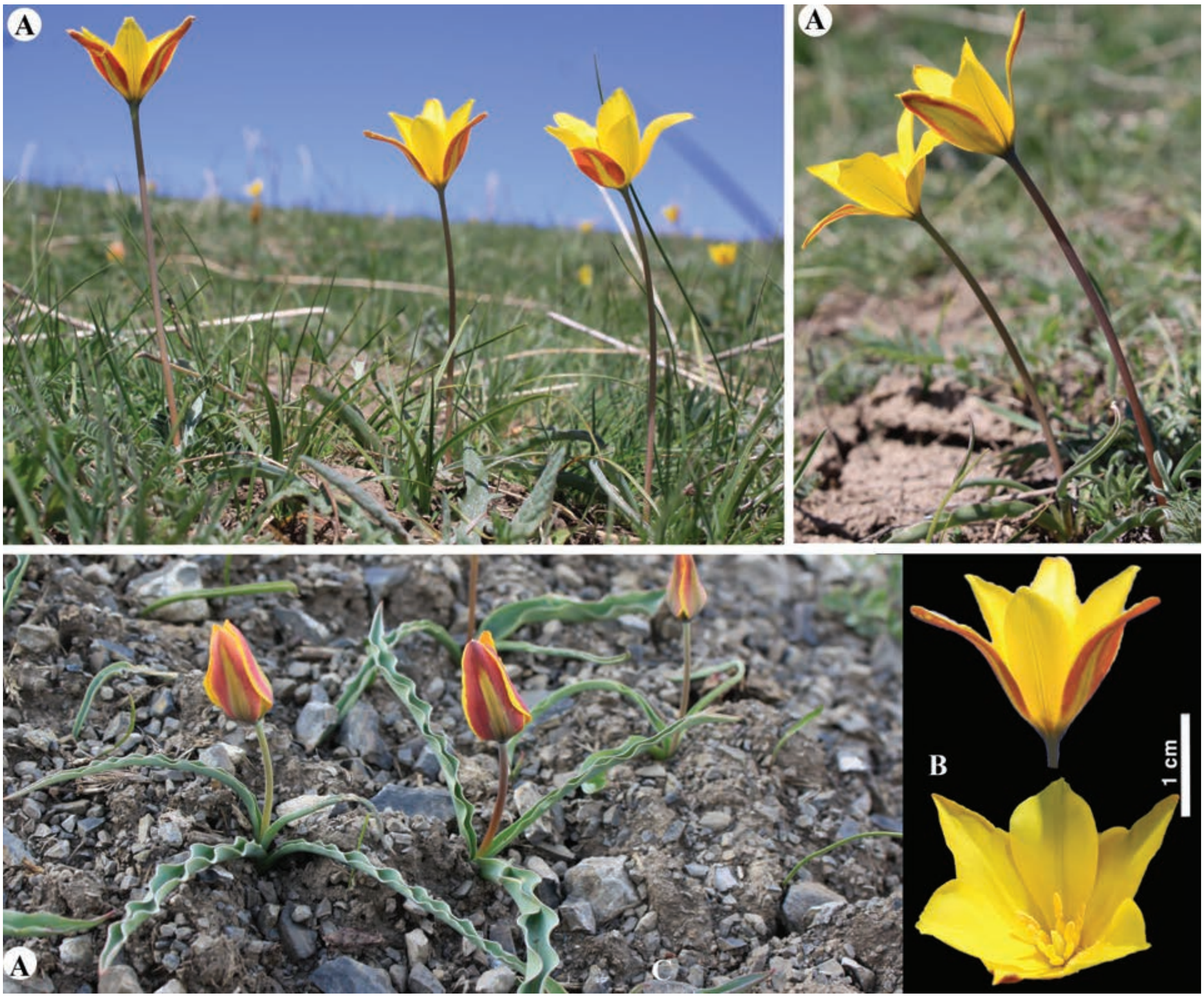

Figure 41. *Tulipa tetraphylla* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by S. Mukhtubayeva).

Tulipa turgaica **Perezhogin, Novosti Sist. Vyssh. Rast. 45: 145 (2014).**
Fig. 42

Type. Kazakhstan • Prov. Kostanay, Zhangeldin distr., pag. Turgay, 2 May 2009, *Yu. Perezhogin* (LE).

General distribution. Endemic to Kazakhstan (Kubentayev et al. 2024).

Distribution in Kazakhstan and habitat. Aktobe, and Turgay. This species grows on dry, deserted clay steppes.

Conservation status. The IUCN conservation status of this species requires assessment.

Phenology. Flowering in April–May; fruiting in June–July.

Notes. *Tulipa turgaica* was first invalidly described in 2013 by Yu. V. Perezhogin from Northern Kazakhstan (Turgai) and validated in 2014. This species is morphologically similar to *T. biebersteiniana* but differs by several flowers and grows in drier habitats (Perezhogin 2013). Some taxonomists classified *T. biebersteiniana* as a synonym of the widespread European *T. sylvestris* subsp. *australis* (Christenhusz et al. 2013; Everett et al. 2013). When we studied populations of *T. turgaica* from the type locality, a high frequency of plants with several flowers was not observed. Individuals with 2–3 flowers were found in the population. However, *T. turgaica* differs morphologically from mesophytic

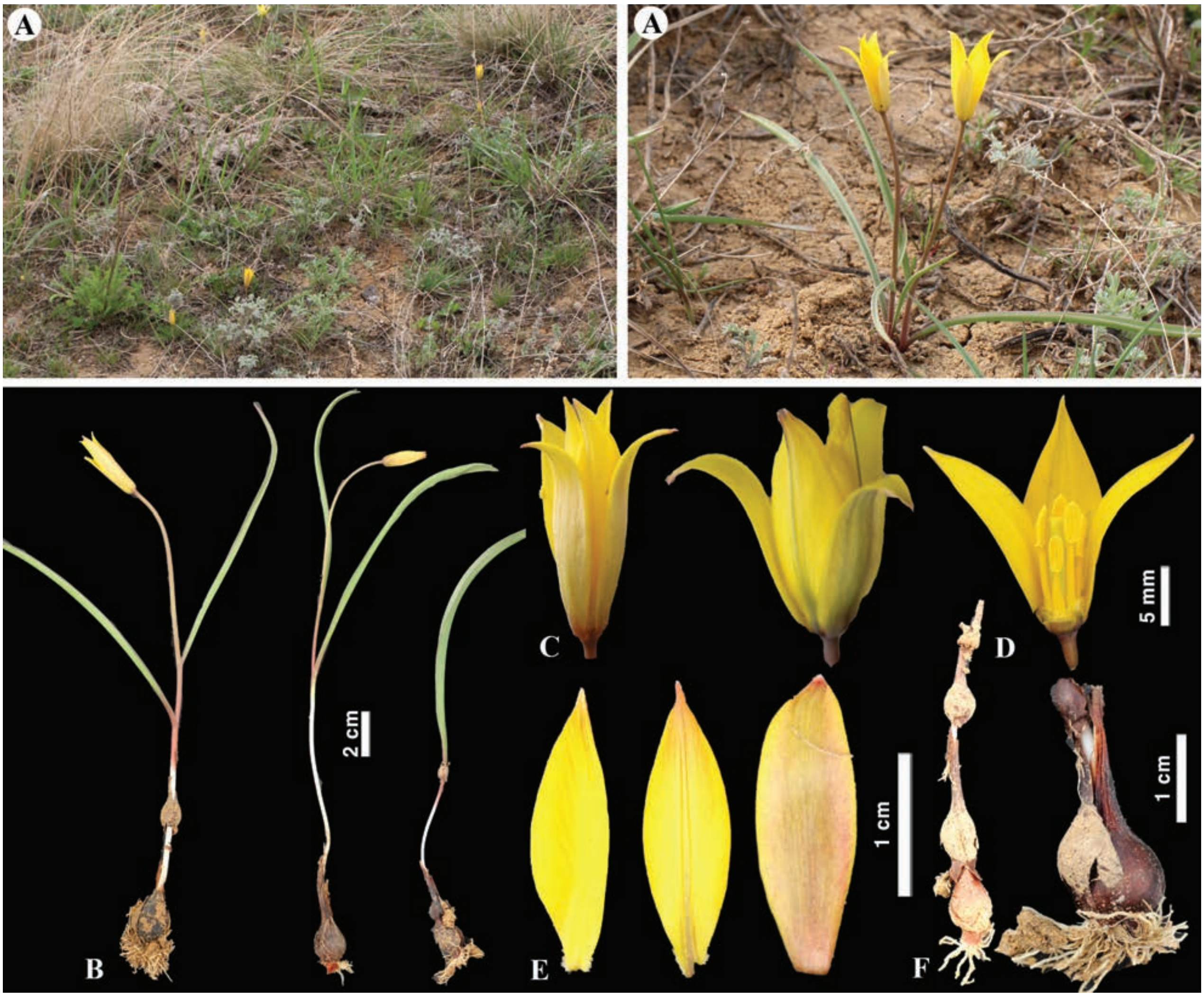

Figure 42. *Tulipa turgaica* in Kazakhstan **A, B** general habits **C, D** flowers **E** tepals **F** bulbs. (Photos: **A–F** by S. Kubentayev).

T. biebersteiniana in that it does not exhibit vegetative propagation and does not form lateral stolons like *T. biebersteiniana*. Further studies are required to investigate the taxonomy of these species.

Tulipa turkestanica **(Regel) Regel, Trudy Imp. S. Peterburgsk. Bot. Sada 3: 296 (1875).**
Fig. 43

Type. Uzbekistan • 'Chiwa', Korolkow & Krause (COI-00050870) [lectotype designated by Christenhusz et al. 2013: 325].

General distribution. Kazakhstan, Kyrgyzstan, Tajikistan, Uzbekistan, and China (Xinjiang) (POWO 2024).

Distribution in Kazakhstan and habitat. Western Tian Shan, Karatau. This species grows in clayey and gravelly slopes from the foothills to the alpine zone (800–3000 m a.s.l.).

Conservation status. *Tulipa turkestanica* is a least concern species at the global level (IUCN 2024).

Phenology. Flowering in March–June; fruiting June –July.

Figure 43. *Tulipa turkestanica* in Kazakhstan **A, B** general habits **C** flowers **D** tepals and stamens **E** gynoecium and stamens **F** stamens **G** bulb and bulb sheath. (Photos: **A–G** by S. Kubentayev).

Notes. Eduard Ludvigovich Regel originally described *T. turkestanica* as *Tulipa sylvestris* var. *turkestanica* Regel in 1873, but later reclassified it as an independent species in 1875 (Ivashchenko and Belyalov 2019). Morphologically, this species is similar to *T. bifloriformis*, which differs by its erect buds and woolly pubescence at the top of the bulb scales (Vvedensky 1935). Transitional forms close to *T. bifloriformis* and *T. orthopoda* occur in nature (Ivashchenko and Belyalov 2019), making identifying these taxa difficult. These forms have been poorly studied and require additional research. The range of *T. turkestanica* might be restricted to Pamir-Alai, and this species might have been replaced by *T. bifloriformis* in Kazakhstan. However, this hypothesis requires further confirmation.

Tulipa × tschimganica Botschantz., Bot. Mater. Gerb. Inst. Bot. Akad. Nauk Uzbeksk. SSR. 16: 10 (1961).

Fig. 44

Type. Uzbekistan • Grown in the Botanical Garden of the Academy of Sciences of Uzbek SSR from bulbs collected by Z.P. Botschantzeva in 1959 in the gorge in piedmonts of Greater Chimgan, on fine earth among stones, Botschantzeva 99 (holotype TASH000526!).

General distribution. Kazakhstan, Kirgizstan, and Uzbekistan.

Distribution in Kazakhstan and habitat. Western Tian Shan. This species grows on rubbly and stony slopes in lower and middle mountain belts (1400–1700 m a.s.l.).

Conservation status. Not assessed at the global level. However, this nothospecies is not protected in Kazakhstan.

Phenology. Flowering in April–May; fruiting June–July.

Notes. *Tulipa* × *tschimganica* was described in 1961 by Z.P. Botschantzeva from specimens grown in the Tashkent Botanical Garden from bulbs collected in Bolshoi Chimgan Gorge (Uzbekistan) (Ivashchenko and Belyalov 2019). In Kazakhstan, the species was first discovered in 2003 in the territory of the Keles Forestry, Karabausai tract (Karzhantau Ridge) along the rubbly hollows of the northwestern and north-eastern slopes at an altitude of 1600–1700 m a.s.l. (Ivashchenko et al. 2006). The origin of this species is relatively controversial; some consider it a separate species (Botschantzeva 1962; Van Raamsdonk et al. 1997;Pratov et al. 2006; Zonneveld 2009), whereas others consider it a hybrid of *T. greigii* and *T. kaufmanniana* (Vvedensky and Kovalevskaya 1971) or a hybrid of *T. dubia* and *T. kaufmanniana* (Christenhusz et al. 2013). Tojibaev (2010) and Tojibaev and Beshko (2014) previously considered this species a subspecies of *T. kaufmanniana* subsp. *tschimganica* but it was listed as a separate species later in the synopsis of the genus *Tulipa* (Liliaceae) in Uzbekistan (Tojibaev et al. 2022).

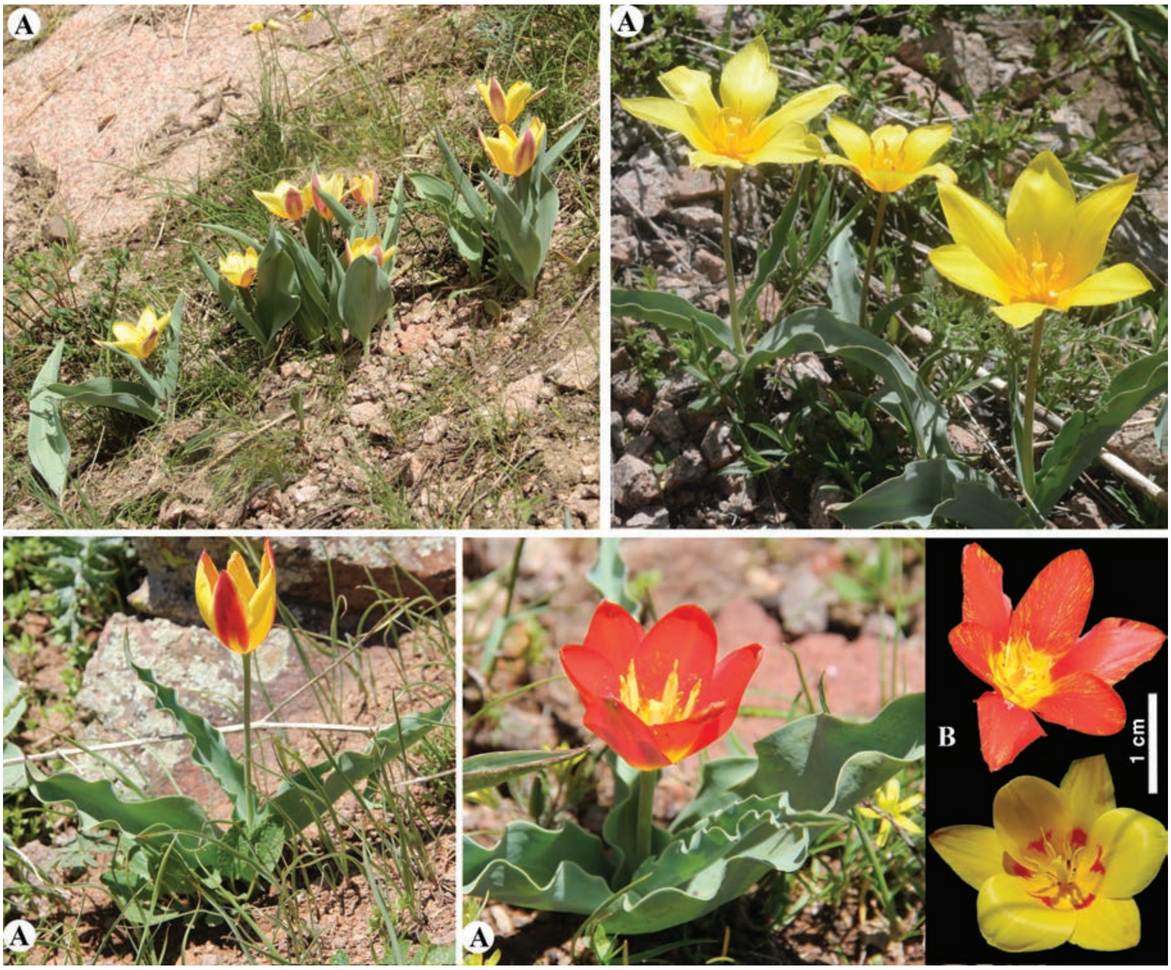

Figure 44. *Tulipa* × *tschimganica* in Uzbekistan **A** general habits **B** flowers. (Photos: **A, B** by K. Tojibaev).

Figure 45. *Tulipa uniflora* in Kazakhstan **A** general habits **B** flowers. (Photos: **A, B** by Sh. Baasanmunkh).

Tulipa uniflora **(L.) Besser ex Baker, J. Linn. Soc., Bot. 14: 295 (1874).**
Fig. 45

Type. Russia • “In Siberiae montis Sini Sopka”, *E. Laxmann* (LE; isoneotype K-000844631) [neotype designated by Levichev, 1997].

General distribution. China (Inner Mongolia, Xinjiang), Kazakhstan, Russia (Altay, Chita, Irkutsk, Krasnoyarsk, Tuva), and Mongolia (Baasanmunkh et al. 2022).

Distribution in Kazakhstan and habitat. Altai, Tarbagatay, and Zaysan. This species grows in sandy places, gravelly slopes, and as shrubs from desert foothills to the upper belt of mountains.

Conservation status. *Tulipa uniflora* is a near threatened species at the global level (IUCN 2024); it is included in the Red Book of Kazakhstan (Category III).

Phenology. Flowering in April–May; fruiting June –July.

Notes. This species was first described by Linnaeus in 1767 as *Ornithogalum uniflorum* L. from specimens collected from the Altai Mountains. Don (1836) described the new genus *Orithyia* D.Don. from specimens of *Ornithogalum uniflorum*. It was not until 1874 that Ch. Bassey assigned this species to *Tulipa*. *Tulipa uniflora* is similar to *T. heteropetala*; their differences are outlined in the description of *T. heteropetala* above.

Tulipa zenaidae **Vved., Byull. Sredne-Aziatsk. Gosud. Univ. 21: 150 (1935).**
Fig. 46

Type. Kyrgyzstan • ‘Habitat in montibus Alexandricis (Tian-Shan)’, 14 June 1932, *Vvedensky 280* (TASH).

General distribution. Kazakhstan, and Kyrgyzstan (Sennikov and Tojibaev 2021).

Distribution in Kazakhstan and habitat. Kyrgyz Alatau. This species grows in fine earth and gravelly slopes, usually with thickets of bushes, in the lower mountain belt.

Conservation status. *Tulipa zenaidae* is a vulnerable species at the global level (IUCN 2024); it is included in the Red Book of Kazakhstan (Category II).

Phenology. Flowering in April–May; fruiting May–July.

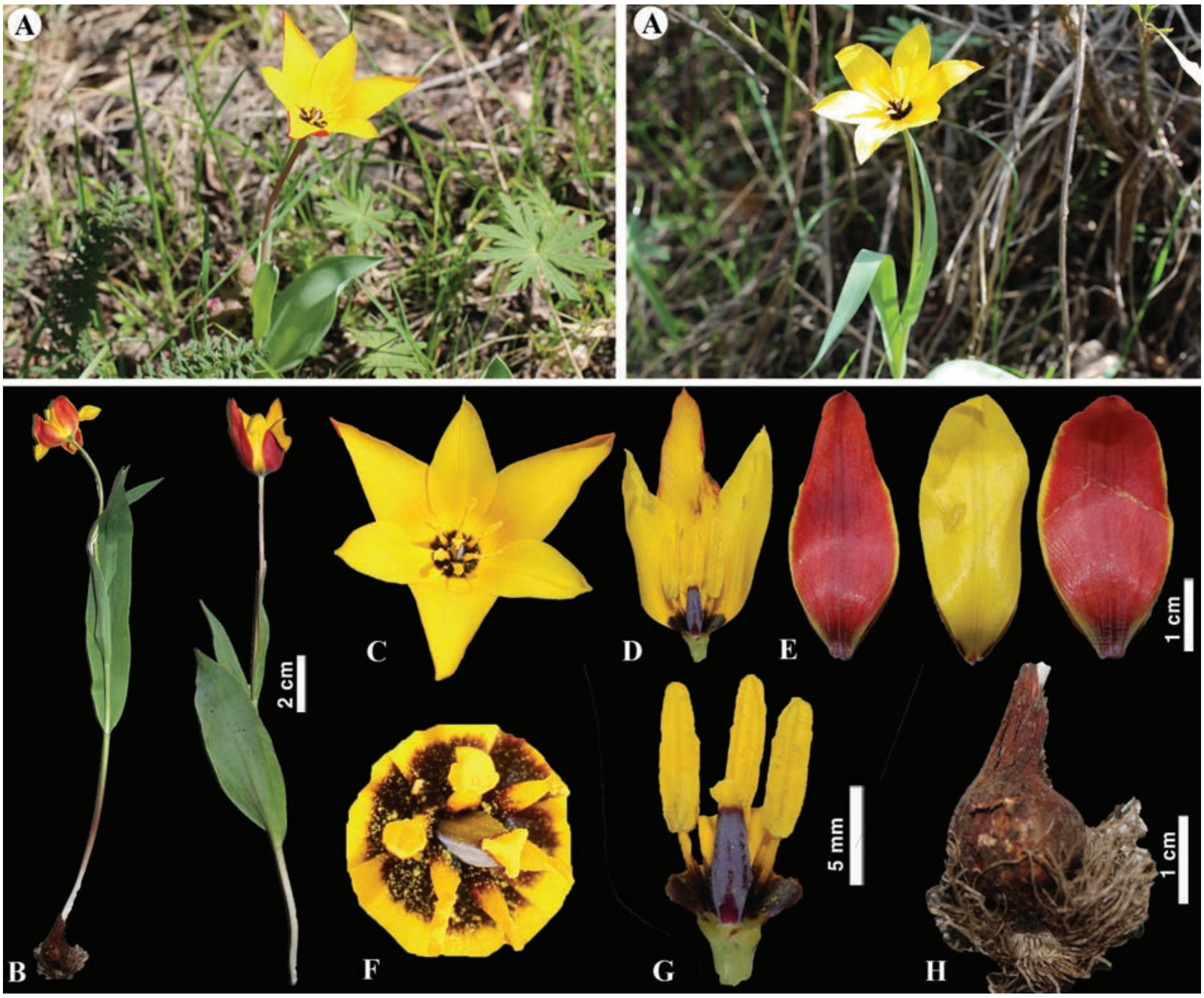

Figure 46. *Tulipa zenaidae* in Kazakhstan **A, B** general habits **C, D** flowers **E** tepals **F, G** gynoecium and stamens **H** bulb (Photos: **A–H** by S. Kubentayev).

Notes. *Tulipa zenaidae* was described by A.I. Vvedensky in 1935 from Kyrgyz Ridge (Mount Shekule). The species was named in honor of Zinaida Botschantzeva, who devoted her life to studying Central Asian tulips (Ivashchenko and Belyalov 2019). According to the latest classification, this species was assigned the synonym of *T. lehmanniana* (Christenhusz et al. 2013; Everett et al. 2013). Wilson (2023) later confirmed that *T. zenaidae* is a different species from *T. lehmanniana* which we agree with in this study.

Conclusion

The total number of *Tulipa* species varies according to the source, representing 90–120 species worldwide. Similarly, the number of tulips in Kazakhstan is 32–42, according to various sources. Therefore, we revisited the species diversity of *Tulipa* in Kazakhstan based on field observations, extensive herbarium specimens, and literature data. We confirmed that 41 tulip taxa are currently distributed in Kazakhstan, of which 13 species are endemic. The present study provides valuable information on the tulip species richness in Kazakhstan, focusing on taxonomic keys, historical notes, species diversity, point distribution maps (Figs 47–51), phylogenetic analysis, and photographs of the wild plants.

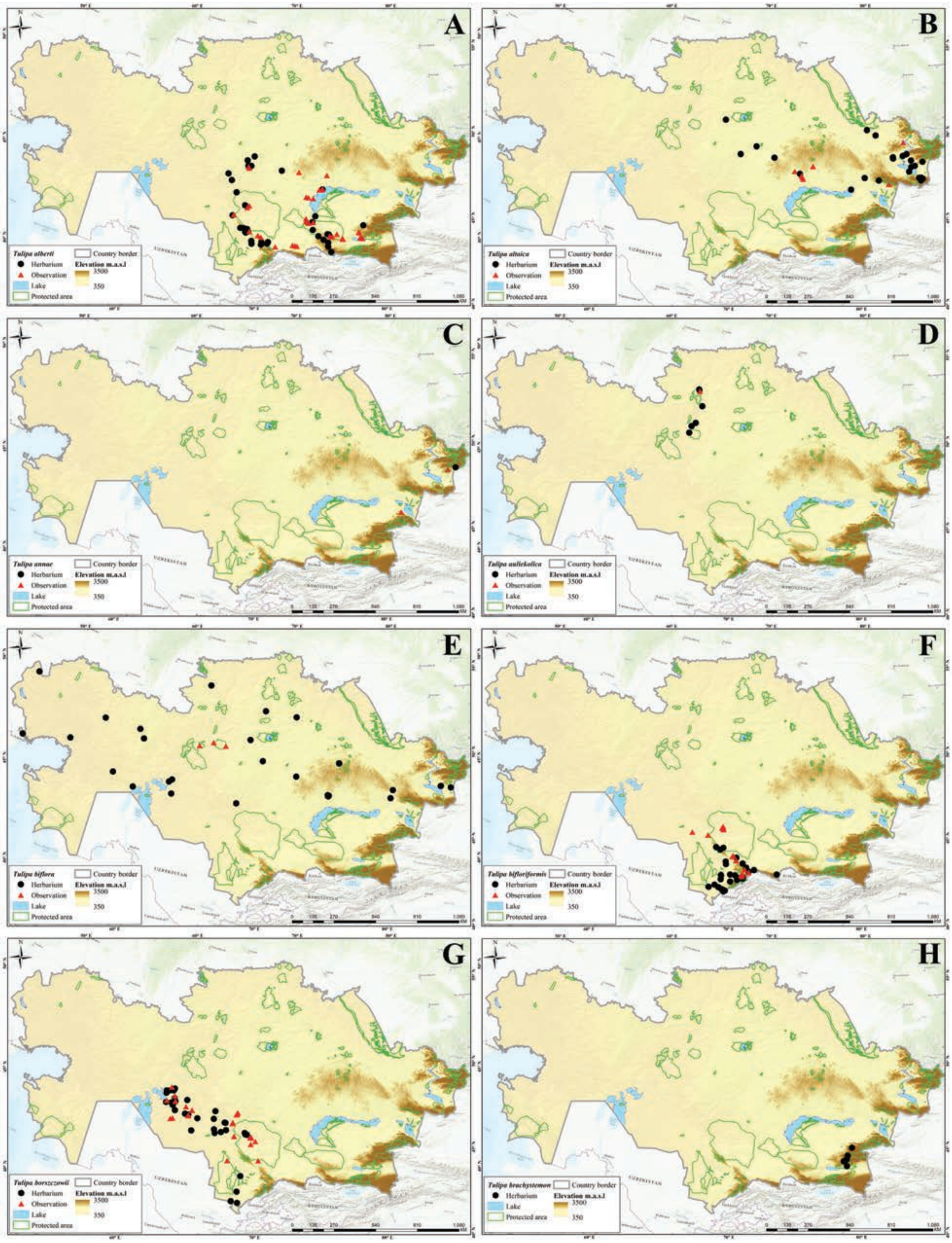

Figure 47. Distribution maps of *Tulipa* in Kazakhstan **A** *T. alberti* **B** *T. altaica* **C** *T. annae* **D** *T. auliekolica* **E** *T. biflora* **F** *T. bifloriformis* **G** *T. borszczowii* **H** *T. brachystemon*.

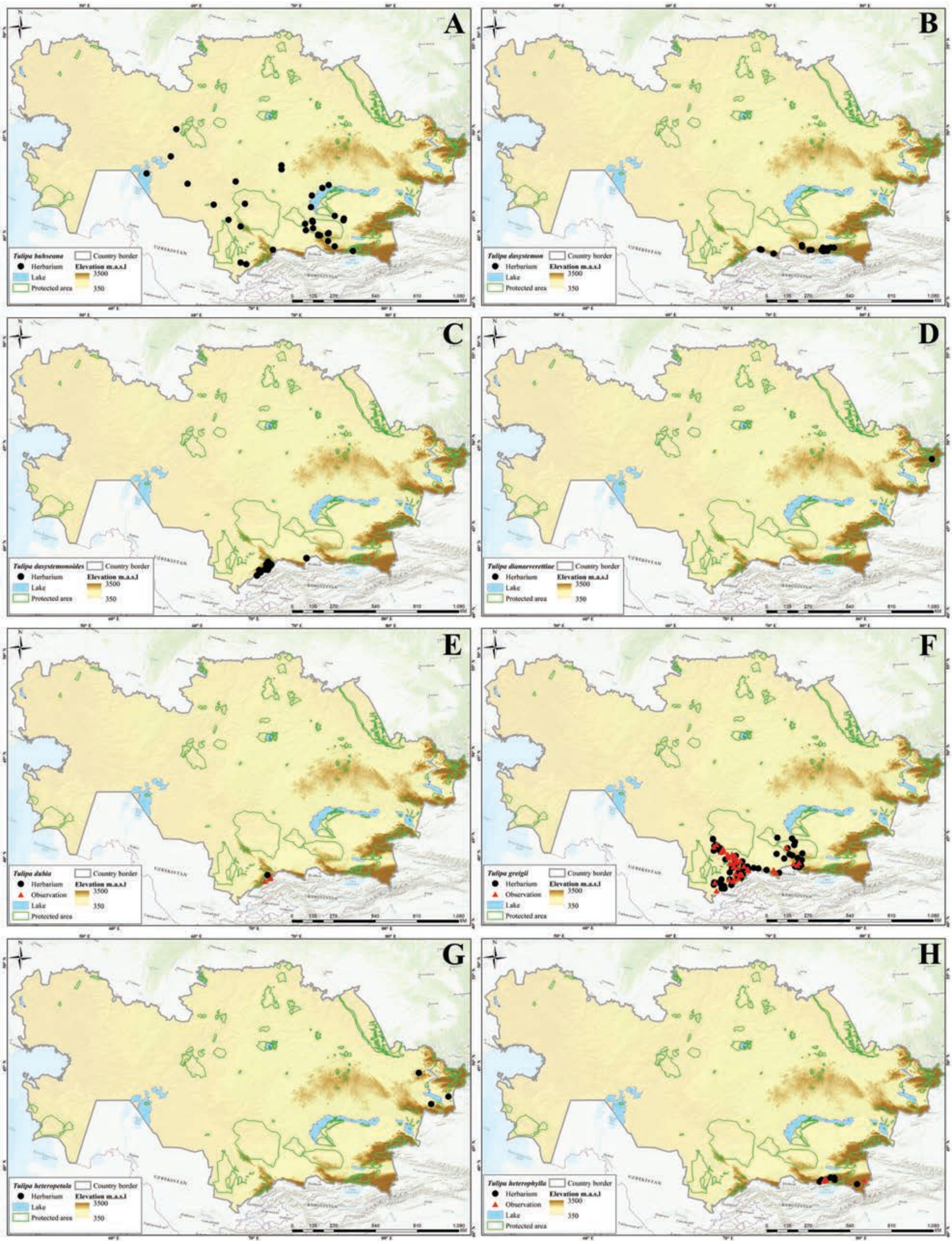

Figure 48. Distribution maps of *Tulipa* in Kazakhstan **A** *T. buhseana* **B** *T. dasystemon* **C** *T. dasystemonoides* **D** *T. dianae-verettiae* **E** *T. dubia* **F** *T. greigii* **G** *T. heteropetala* **H** *T. heterophylla*.

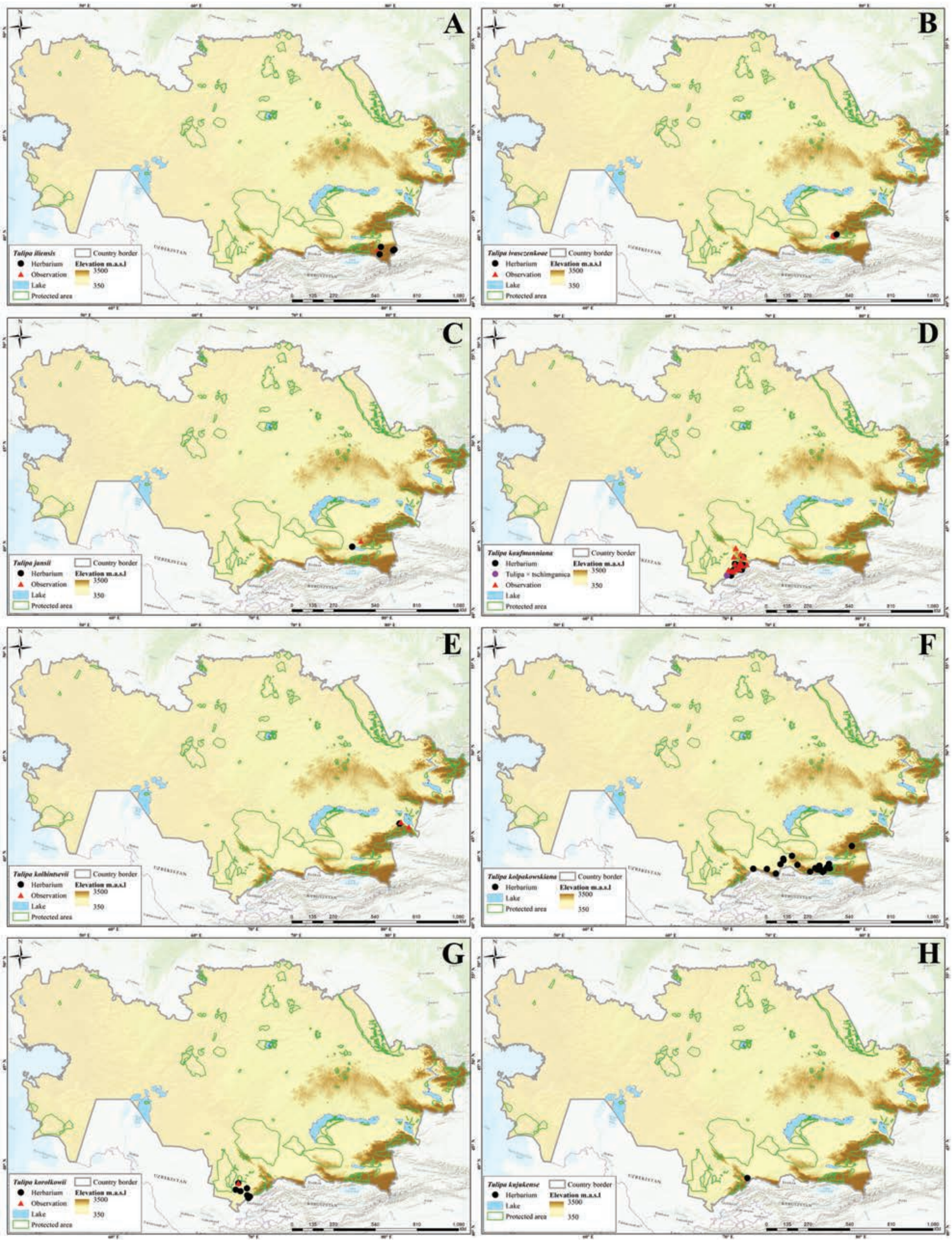

Figure 49. Distribution maps of *Tulipa* in Kazakhstan **A** *T. iliensis* **B** *T. ivasczenkoae* **C** *T. jansii* **D** *T. kaufmanniana* **E** *T. kolbintsevii* **F** *T. kolpakowskiana* **G** *T. korolkowii* **H** *T. kujukense*.

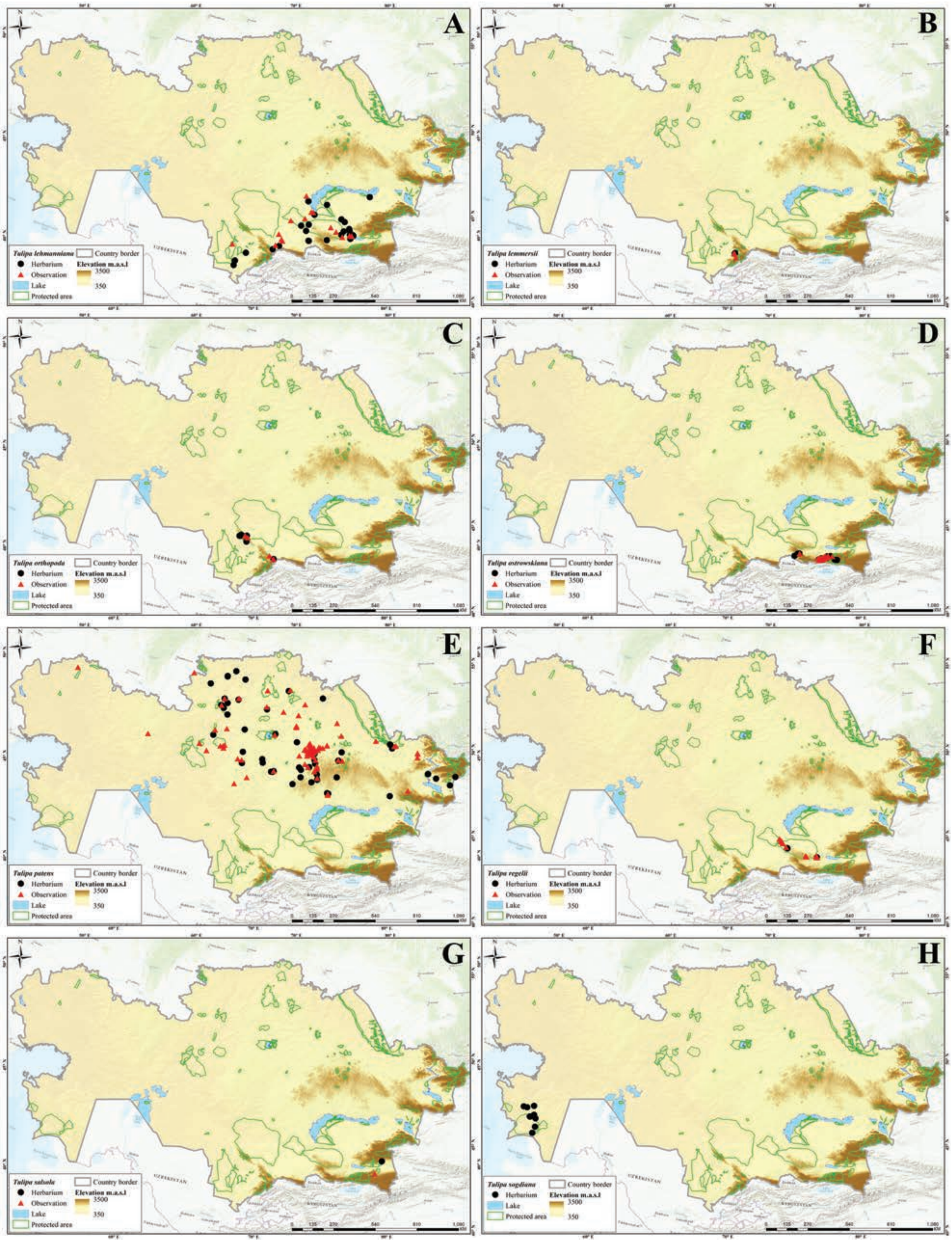

Figure 50. Distribution maps of *Tulipa* in Kazakhstan **A** *T. lehmanniana* **B** *T. lemmersii* **C** *T. orthopoda* **D** *T. ostrowskiana* **E** *T. patens* **F** *T. regelii* **G** *T. salsola* **H** *T. sogdiana*.

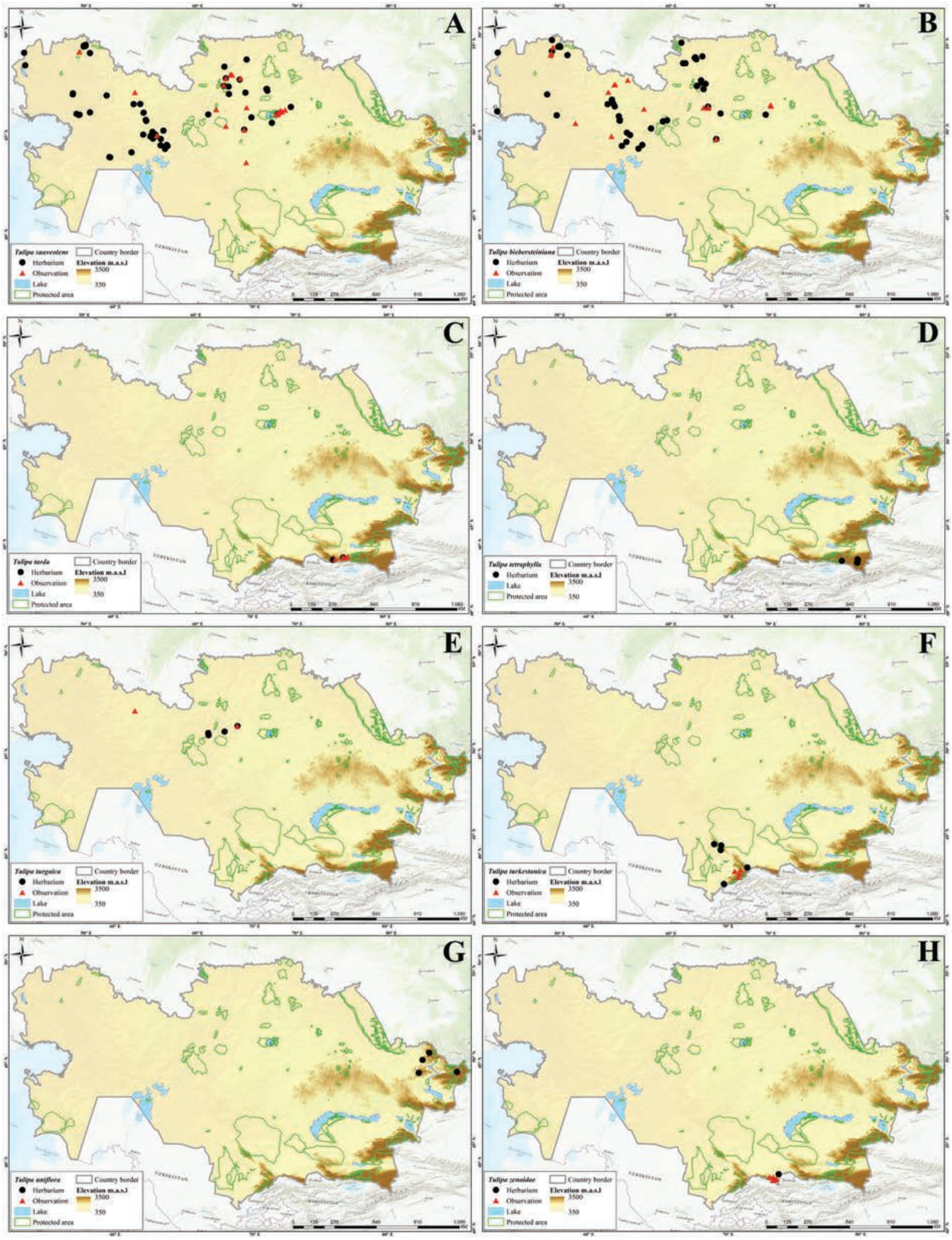

Figure 51. Distribution maps of *Tulipa* in Kazakhstan **A** *T. suaveolens* **B** *T. biebersteiniana* **C** *T. tarda* **D** *T. tetraphylla* **E** *T. turgaica* **F** *T. turkestanica* **G** *T. uniflora* **H** *T. zenaidae*.

Notably, we identified several high-biodiversity hotspots, particularly in the floristic regions of Western Tian Shan and Trans-Ili Kungey Alatau. We compared herbarium data and iNaturalist observations of tulips, revealing interesting trends in collection periods and observation frequencies. Although herbarium specimens were predominantly collected before 2000, the number of iNaturalist observations has since steadily increased demonstrating the growing contribution of citizen scientists to biodiversity research.

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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

SAK and SB designed this study. SAK, DTA, VGE, and SKM collected the samples. NBA, ZTI, KSI, and GTS prepared the data. SB, SAK, NN, and ZT analyzed the data. SB, SAK, and NN wrote the original draft of the manuscript. SAK, SB, KT, AAI, HYG, and HJC revised the manuscript. All the authors have revised and agreed to the published version of the manuscript.

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Data availability

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

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Supplementary material 1

Supplementary Information

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Research Article

A new marine diatom (Bacillariophyceae) species – *Halamphora lombokensis* sp. nov. and the first observation for *H. banzuensis* from Kuta Beach Lombok, West Nusa Tenggara, Indonesia

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Abstract

This paper describes a new species of Halamphora – *Halamphora lombokensis* **sp. nov.** and records for the first time *Halamphora banzuensis* for the coasts of Indonesia. The study utilized light and scanning electron microscopy to meticulously examine the morphology. These species were found at Kuta Beach on the island of Lombok in Indonesia in highly saline sandy environments. The newly identified species, *H. lombokensis* **sp. nov.**, is characterized by its semi-lanceolate to narrowly semi-elliptic shape with a straight ventral and convex dorsal margin. The study contributes to our understanding of marine diatom flora in Indonesia's coastal regions.

Key words: Diatoms, *H. Lombokensis*, *H. banzuensis*, Mandalika, Microalgae, new record, new species

Introduction

Over the past decades, considerable effort has been expended to enhance our understanding of the diversity of marine and freshwater diatoms (Bacillariophyceae) in Indonesian aquatic ecosystems, starting with the classical work of Hustedt in 1943. In subsequent years, numerous new marine and freshwater diatom taxa were reported from islands throughout the Indonesian Ocean (Risjani et al. 2021), including those attributed to the *Luticola* D.G. Mann taxa from Maluku (Rybak et al. 2021, 2024), *Hantzschia* species from rural areas

(Southeast Asia) (Rybak et al. 2022), *Achnanthidium* spp., from Lake Bratan, Bali (Kapustin et al. 2022), and from Temple Lake and Matano Lake (Tseplik et al. 2021a, b), *Catenula* species from Java and Sulawesi (Kryk et al. 2021), *Nupela brevistriata* from soil and tree bark in Palambak and Sumatra (Rybak et al. 2019), *Gomphonema matanensis* ancient Lake Matano (Kociolek et al. 2018), and 11 new taxa of Surirella from The Malili Lakes, Sulawesi (Bramburger et al. 2006). The richness of diatom taxa across Indonesia is well established with hotspots like the fossil deposits of Lake Toba (Sumatra) and the endemic assemblages of the Maili Lakes (Sulawesi) focal points for future investigations. Despite the existence of these discoveries, there is still a lack of understanding about littoral marine diatoms in Indonesia.

The genus *Halamphora*, a group of diatoms within the family Amphipleuraceae, has been extensively researched and revised over the past few decades. In addition to the classical literature on the subgenus *Halamphora* (Cleve 1895), Levkov (2009) studied an extensive number of *Amphora* species and officially elevated *Halamphora* to the level of genus. Stepanek and Kociolek (2013) have more recently made further extensive contributions to the discovery of marine *Halamphora* species using a combination of morphological examinations with electron and light microscopes and genetic analyses. *Halamphora* is distributed globally in freshwater and marine environments; there are 155 accepted species names and 8 accepted varieties (Algaebase). Genetically, *Halamphora* is monophyletic and positioned within the Family Amphipleuraceae next to the sister Rhopalodiaceae (Stepanek and Kociolek 2014). *Halamphora* is morphologically similar to the genus *Amphora* (Family Catenulaceae) but can be identified by distinct features, among which are the raphe ledge that exists only on the dorsal side in the genus *Halamphora*, while the areolae have round, elliptical, or transversely elongated shapes occluded by hymenes or vela and internally with small pores (Levkov 2009; An et al. 2022).

The reliability of identifying fine features in *Halamphora* species using light microscopy is enhanced by using scanning or transmission microscopy which is often essential for accurate identifications. The objective of this study is to describe a new species *Halamphora lombokensis* sp. nov. and record for the first time *Halamphora banzuensis* for the coasts of Indonesia, Kuta Beach, West Nusa Tenggara, Lombok Island.

Materials and methods

Study area

Kuta Beach is one of many beaches on Lombok Island, located on the east side of the larger Bali Island (Fig. 1). The sampling station is located in Mandalika in the southern region of the Central Lombok District, West Nusa Tenggara Province with coordinates 8°53'41.132"S, 116°17'0.042"E. In contrast to other Indonesian beaches which collect extensive garbage and plastics, the coastal location with exposure to the Indian Ocean has clean and clear seawater. The beach is famous for its beautiful scenery and is a top choice for many tourists. This location is part of a unique eco-tourism management area, which includes the tourism zone, the open-access zone, and the support facilities near the Mandalika Circuit, an international-standard racing circuit. The beach is shaped

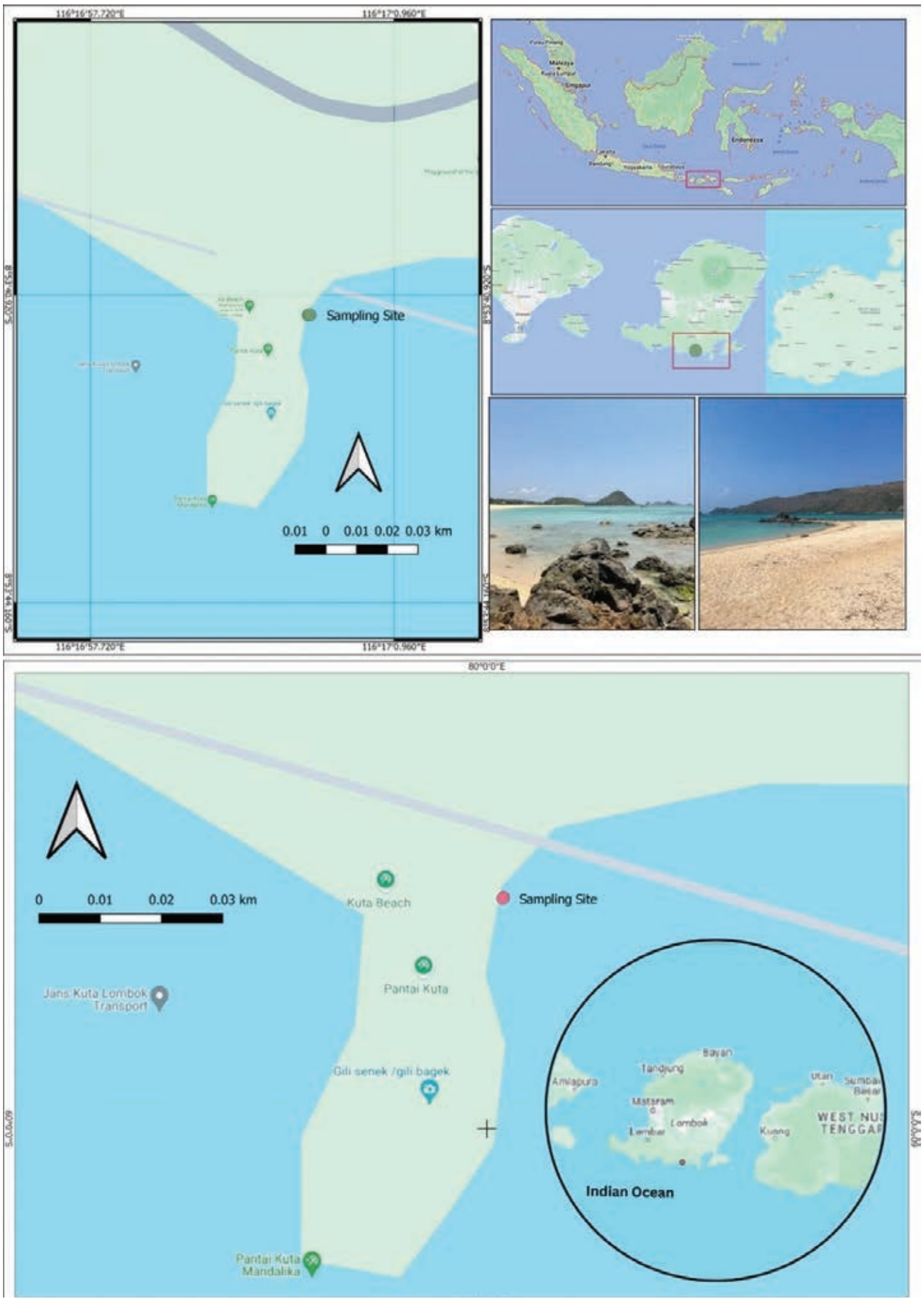

Figure 1. Sampling site of this study in Kuta Beach, Lombok Island, Indonesia.

like a bay and is approximately 3000 m long from west to east. It is bordered by hills and composed of white, ball-shaped sand from abraded coral reefs. The bathymetric in front of the beach is shallow across 2/3 of the eastern part, which can be dry during low tide, descending about 800 m from the beachline (Pradjoko et al. 2015).

Sampling

Samples were collected in November 2023 from sandy and rocky substrata. The sampling sites along the seashore revealed seashore depths ranging from approximately two to five centimeters, clearly indicating relatively shallow substrate conditions. Epilithic samples were separated from the substrate using a toothbrush and epipelic samples were collected using a plastic pipette (Taylor et al. 2007). Rock substrates of varying random size and flatness were selected from Kuta Beach and thoroughly brushed clean over the andesitic, basalt, and granite stones. Water temperature (°C), dissolved oxygen (mg.L-1), oxygen saturation (%), pH, electrical conductance (μS.cm-1), and salinity (%) were measured in situ using a Lange Hach 40d multi-parameter meter. Samples were immediately transported back to the lab for study. The collected type materials are deposited at the Center for Algae and Environment (ALGAEN Center) at the Department of Aquatic Resources Management, Faculty of Fisheries and Marine Science, Brawijaya University, Malang, East Java, Indonesia. The holotype slide and material are deposited in the Canadian Museum of Nature (CANA), Ottawa, Ontario, Canada, and isotype slides in Kütahya Dumlupınar University (DPU), Türkiye.

Sample preparation

Light (LM) and scanning electron microscope (SEM) materials were prepared by treatment with 10% HCl and 30% H2O2 to remove organic material following the method described in Swift (1967). To obtain permanent microscopic slides, cleaned material was mounted in Naphrax®. The slides were analyzed using a Nikon Ci Light microscope in the Diatom Laboratory at Kütahya Dumlupınar University (DPU), Türkiye. Observations were completed at 1000x magnification with a 100x Plan Apochromat oil immersion objective (NA = 1.4). The ultrastructure morphological observations were done using SEM. For that purpose, cleaned material was filtered through a polycarbonate membrane filter with a pore diameter of 5 μm. These membrane filters were fixed on aluminum stubs after air–drying. Stubs were sputter-coated with a gold layer reaching a thickness of ~20 nm and studied using a ZEISS Ultra field emission scanning electron microscope at the University of Eskişehir Technical University, Türkiye. Stubs of the type material are stored at the Center of Algae and Environment (ALGAEN Center), Faculty of Fisheries and Marine Science, University of Brawijaya, Malang, East Java, Indonesia, and Kütahya Dumlupınar University (DUP), Türkiye.

Results

In this study, some environmental variables were measured during sampling in November 2023. The temperature was 33.3 °C, pH 7, salinity 32 ppt, and dissolved oxygen 18.5 mg.L^{-1}.

Two species of seven *Halamphora* were present in large numbers from Kuta Beach. The frustules of *Halamphora banzuensis* Stepanek, Mayama and Kociolek 2018: 73 (Figs 2, 3) are wedge-shaped with semi-elliptical valves showing subcapitate ends that deflect dorsally, 13.0–16.5 μm in length and 3.0–4.0 μm in width. The axial conopeum and raphe ledge are broad and even throughout and the striae are biseriate. A primary identifying feature in SEM for this species is a distinct silica rib extending the length of the internal valve near the axial area on the dorsal side (Fig. 2G, H). The other common species is new and here described below.

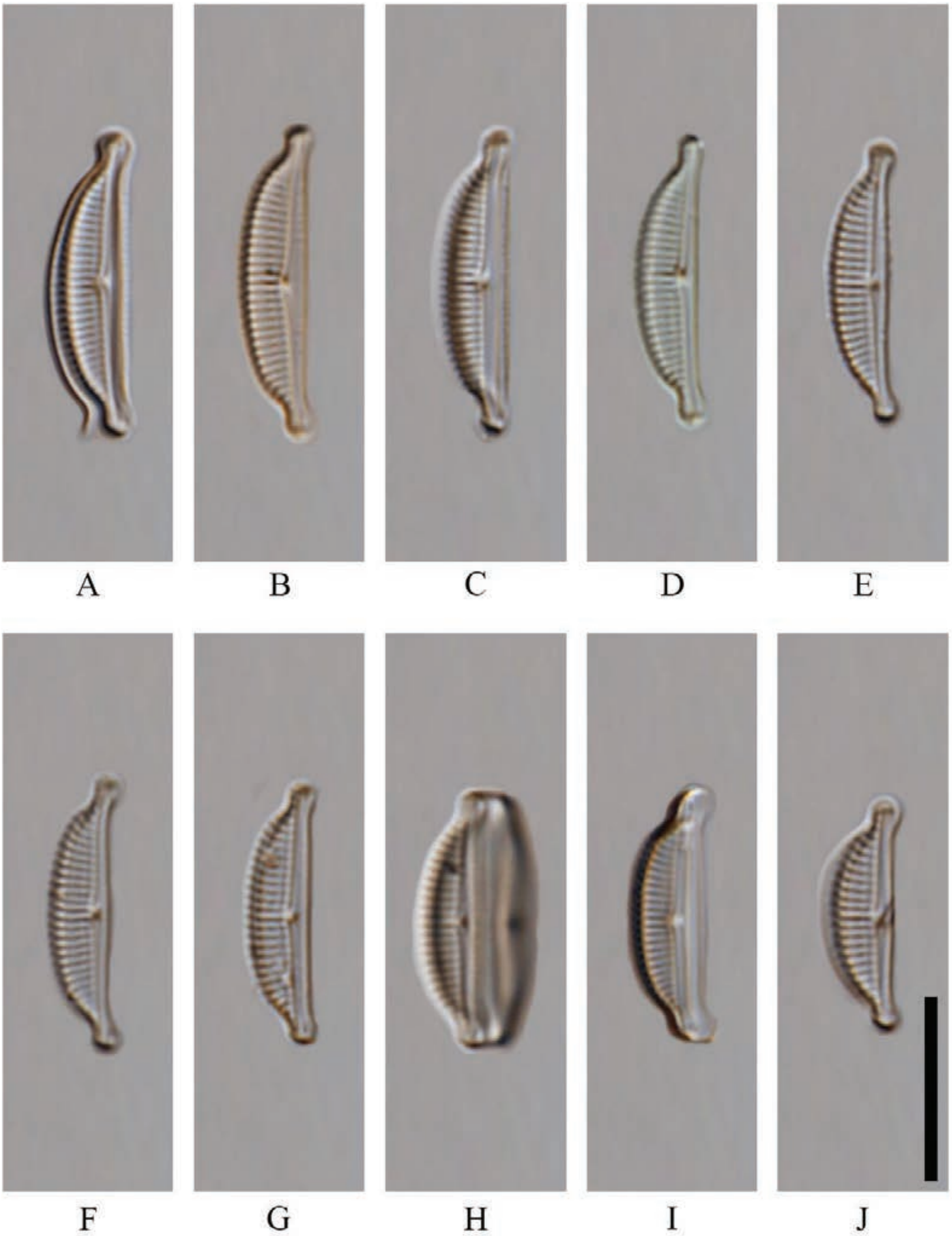

Figure 2. *Halamphora banzuensis* from Lombok Kuta, Indonesia. LM micrographs of valves showing the size diminution series. Scale bar: 10 μm.

Ochrophyta Cavalier-Smith, 1995
Bacillariophyceae Haeckel, 1878
Thalassiophysales D.G. Mann, 1990
Catenulaceae Mereschkoewsky, 1902

***Halamphora lombokensis* P.B.Hamilton, E.P.Pane, Y.Risjani & C.N.Solak, sp. nov.**

Description (LM). Valves semi-lanceolate to narrowly semi-elliptic with straight ventral and distinctively convex dorsal margins. Valve length 11.0–13.0 μm, breadth 2.0–3.0 μm. Valve ends slightly ventrally bent, rostrate to

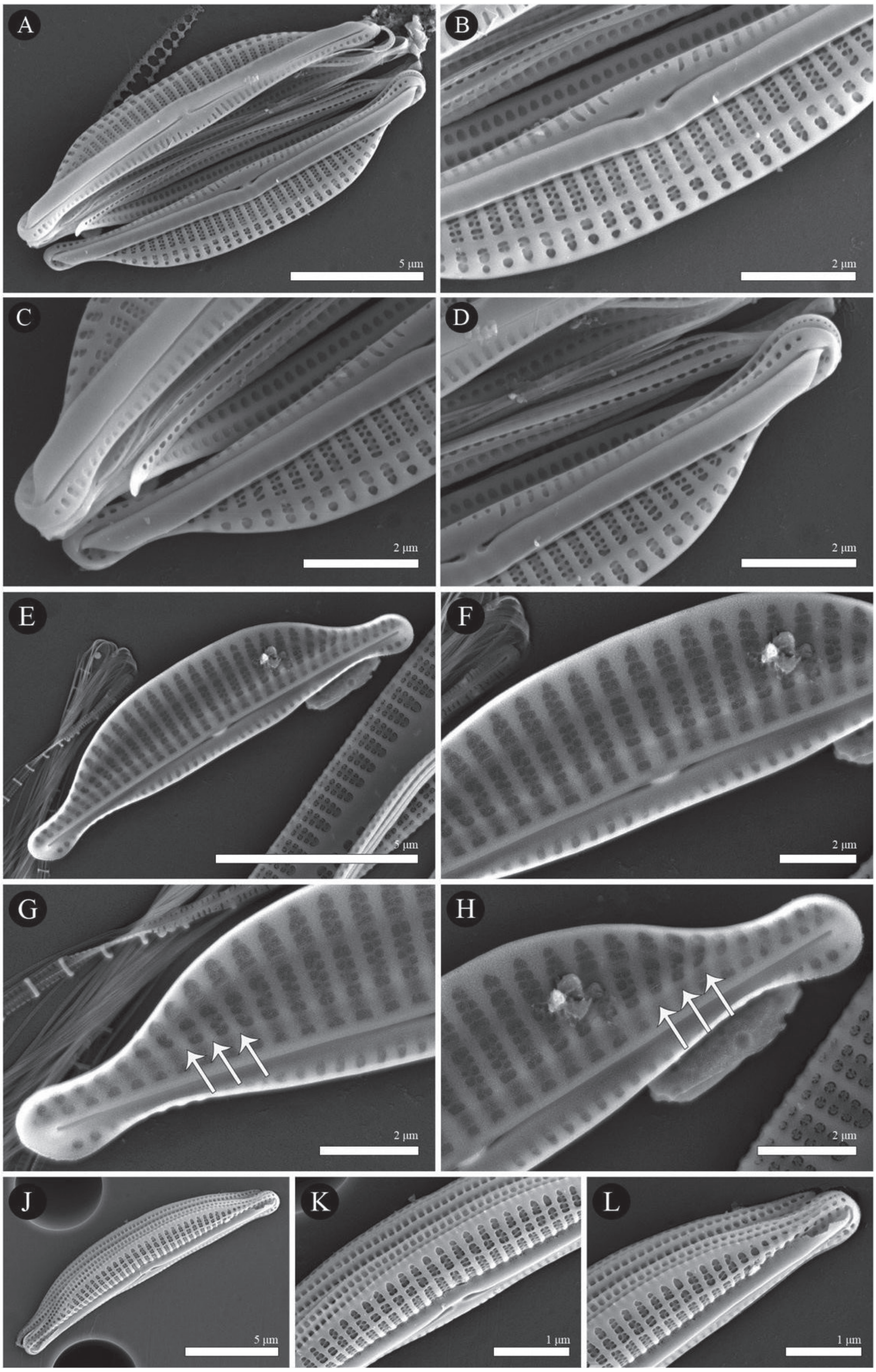

Figure 3. SEM micrographs of external view of *Halamphora banzuensis* **A** general external view of a valve **B** details of the central area showing proximal raphe endings **C, D** details of the apices showing distal raphe endings **E–H** SEM micrographs of internal view of *Halamphora banzuensis* **E** general internal view of a valve **F** details of the central area showing proximal raphe endings **G, H** details of the apices showing distal raphe endings and axial ridge. Arrows identify silica rib extending the length of the internal valve near the axial area on dorsal side. **J–L** SEM micrographs of external girdle view of *Halamphora banzuensis* **J** general external view of a valve **K** details of central area showing proximal raphe endings **L** details of the apices showing distal raphe endings. Scale bars: 5 µm (**A, E, J**); 2 µm (**B–D, F–H**); 1 µm (**K, L**).

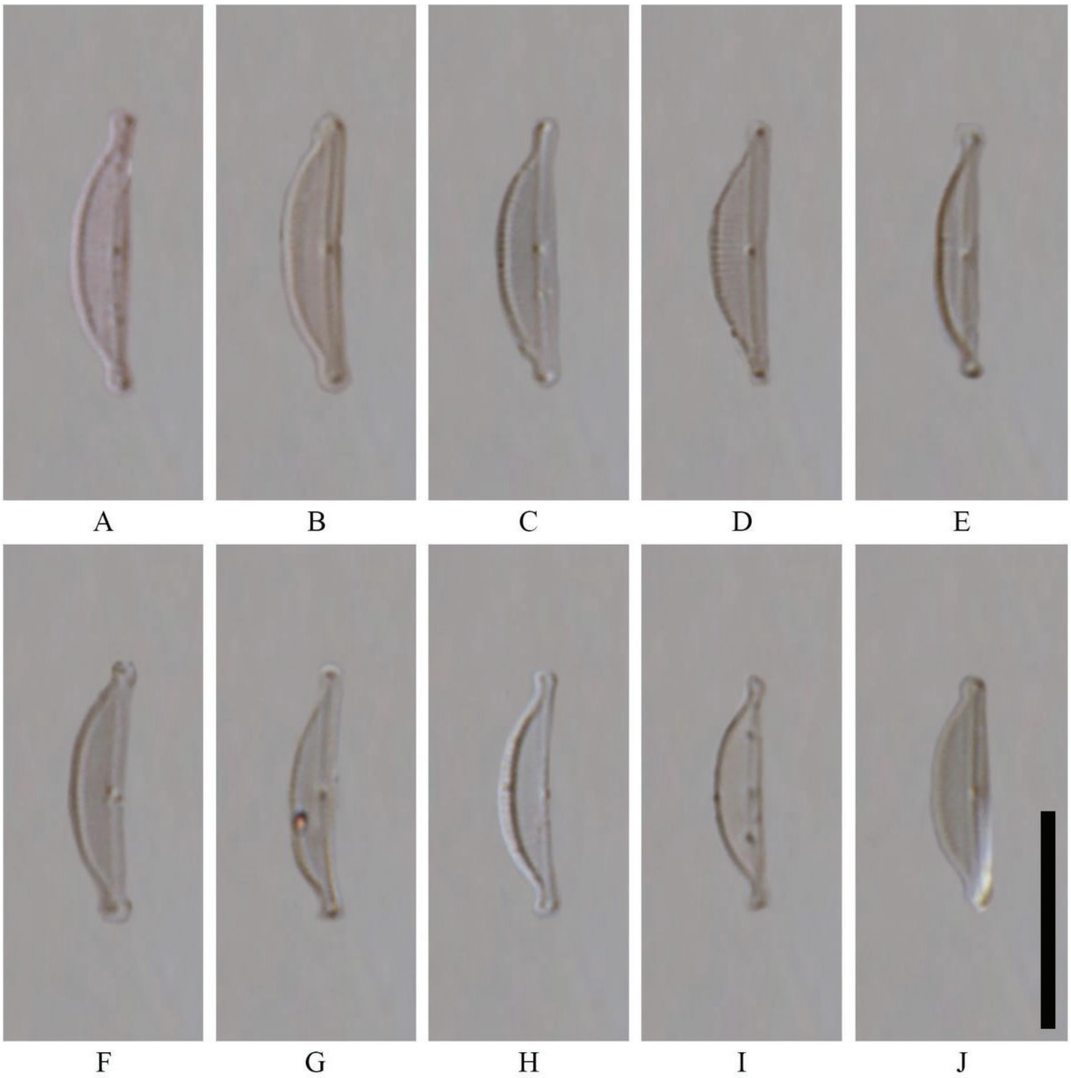

Figure 4. Type material of *Halamphora lombokensis* Hamilton, Pane, Risjani & Solak, sp. nov. from Lombok Kuta, Indonesia. LM micrographs of valves showing the size diminution series. Scale bar: 10 µm.

almost subcapitate. Raphe branches straight. Proximal raphe endings linear, distal raphe fissures not discernible in LM. The axial area narrow and the central area is almost absent. Striae is only visible under SEM. Dorsal striae density 28–32 in 10 µm (Fig. 4A–J).

SEM. Externally, valves are dorsiventral with narrowly convex dorsal margin and straight concave ventral margin. Central area absents on dorsal side and semi-lanceolate on ventral side. Raphe ledge extends from end to end, moderate, more or less equal width and weakly expanded towards the ends. Raphe branches weakly arched. Proximal raphe endings slightly expanded into straight central depressions. Distal raphe endings are hook-shaped. Dorsal striae are composed of uniseriate areolae; areolae elongated to become rounded towards margin. Areolae are composed of two elongated forms. Ventral striae with slit-like areola. Internally, areolae are round to elongate and divided into two pieces. Distal raphe endings terminating with poorly developed helictoglossae. Proximal raphe fissures fused into central helictoglossae. A distinct longitudinal band of silica runs from end to end near the dorsal axial area (Fig. 5A–H).

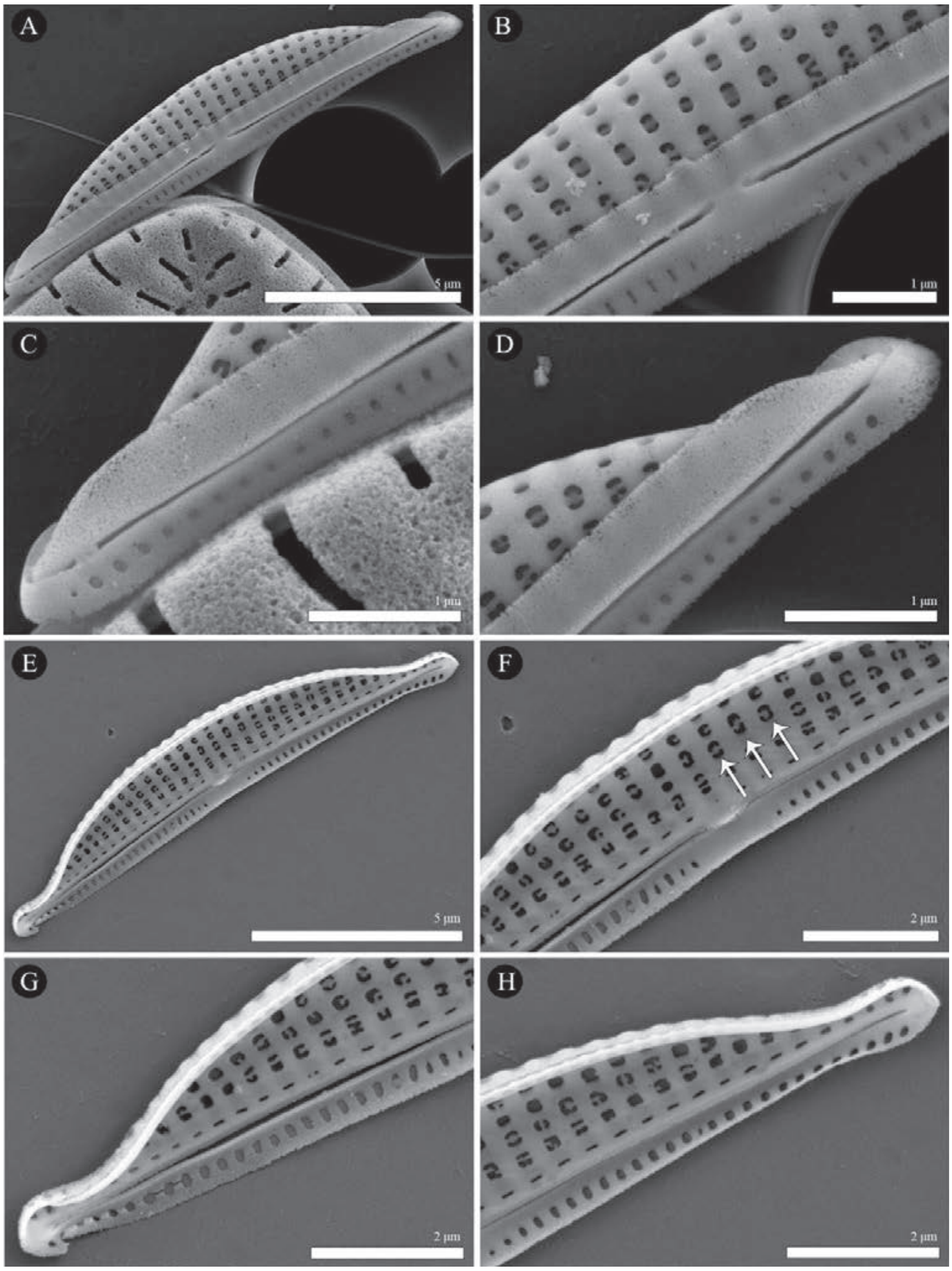

Figure 5. Type **A–D** SEM micrographs of external view of *Halamphora lombokensis* Hamilton, Pane, Risjani & Solak **A** general external view of a valve **B** details of central area showing simple depressed proximal raphe endings **C, D** details of the apices showing distal raphe endings. A small grove extends from the terminal raphe end towards the apex. **E–H** SEM micrographs of internal view of *Halamphora lombokensis* **E** general external view of a valve **F** details of central area showing proximal raphe endings. Arrows highlight thick verminae separating the areolae. **G, H** details of the apices showing distal raphe endings. Scale bars: 5 µm (**A, E**); 2 µm (**F–H**); 1 µm (**B–D**).

Material examined. ***Holotype:*** slide number CANA 131860 (microscope slide designed as a holotype) in the collection of Nature Museum of Canada.

Isotype: Slide No. UB04 KUTA PSAL stored at the Center of Algae and Environment (ALGAEN Center) at the Faculty of Fisheries and Marine Science, University of Brawijaya, Malang, East Java, Indonesia • Slide no: INDO_Lombok Kuta_B2_(E.Pane)_Nov2023 observed at Kütahya Dumlupınar University Herbarium (DUP), Türkiye.

Type material. Type material stored at the Center of Algae and Environment (ALGAEN Center), at Faculty of Fisheries and Marine Science, University of Brawijaya, Malang, East Java, Indonesia; subsample CANA 131860, analyzed at the Canadian Museum of Nature.

Type locality. Indonesia, Kuta Beach, Lombok Island (GPS 8°53'41.132"S, 116°17'0.042"E), collector: Elya Putri PANE 11.11.2023.

Etymology. Named for the Island of Lombok, where the species was found.

Distribution and ecology. Observed from the type locality (Temperature 33.3 °C, pH 7.0, salinity 32 ppt. and dissolved oxygen 18.5 mg.L^{-1}).

Differential diagnosis. The species is similar to *Halamphora angustiformis* Stepanek and Kociolek (2018: 68), *H. attenuata* Stepanek and Kociolek (2015: 32), *H. borealis* (Kützing) Levkov (2009: 175), *H. pellicula* Stepanek and Kociolek (2018: 50), *H. salinicola* Levkov & Díaz (Levkov 2009: 220), *H. tenuis* Stepanek and Kociolek (2018: 45) and *H. valdeminutissima* Zidarova et al. (2023: 202). Regarding striae density, *Halamphora pellicula*, *H. tenuis* and *H. valdeminutissima* have higher stria densities while the other comparable taxa have lower stria densities. Moreover, *H. angustiformis*, *H. attenuata* and *H. borealis* are larger while *H. pellucula* and *H. valdeminutissima* have smaller dimensions and typical long areolae. *Halamphora tenuis* is distinguished by biseriate areolae.

Associated diatom flora. Unidentified species of another *Halamphora*, *Tabularia*, and *Navicula* were other frequent taxa in the sample.

Discussion

The two species of *Halamphora* are identified from Kuta Beach on the island of Lombok Island, Indonesia; one is a new species. These marine taxa prefer highly saline epipsammic environments. The physicochemical results indicate marine coastal conditions with high temperature, high oxygen, and a circumneutral pH. The two species from the same microbiome are different in morphology and easy to distinguish through LM observations. Five additional poorly documented *Halamphora* taxa were abundant in Kuta beach (Fig. 6).

Taxonomically, these valve shapes (Fig. 6) are similar to a number of brackish and marine diatom taxa. Valve shape along with the formation of the raphe ledge, and striae and areolae (internal and external) are the primary characteristics that distinguish these *Halamphora* taxa. *Halamphora lombokensis* sp. nov., with a semi-lanceolate to narrowly semi-elliptic outline and capitate ends is a common valve outline. The new species is similar to the halophilous/brackish species (*H. salinicola*, *H. attenuata*), brackish species (*H. angustiformis*, *H. borealis*, *H. valdeminutissima*) and true marine species (*H. pellicula*, *H. tenuis*). *Halamphora angustiformis*, like *H. lombokensis*, has a wide continuous dorsal raphe ledge and the areolae are uniseriate and unevenly distributed. *Halamphora angustiformis* is distinguished by an expanded raphe ledge around the central area, deflected proximal and distal raphe ends toward the dorsal side, and larger valves with fewer striae. *Halamphora attenuata* is a salt lake taxon from Dakota, USA (Stepanek and Kociolek 2015) and was identified by the large valves with a higher stria density, linear-elliptic dorsal valve margins, and protracted, not capitate ends. This saline lake taxon is distinguished by the higher density of areolae, differential formation of the areolae adjacent to the external dorsal axial area, and the absence of an internal silica rib next

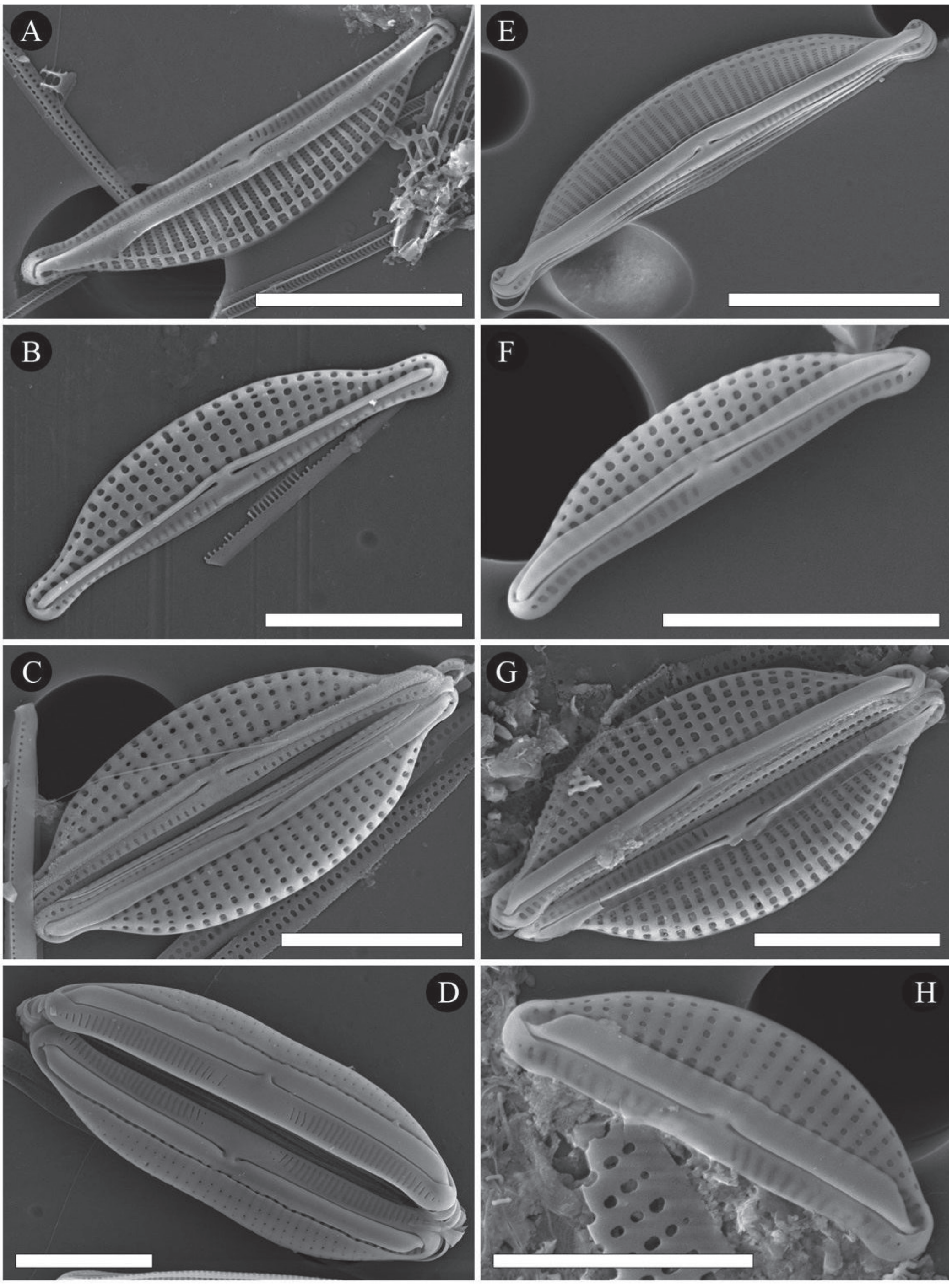

Figure 6. Five additional undescribed *Halamphora* taxa from Kuta Beach. A. *Halamphora* cf. *hybrida*. Scale bars: 10 µm.

to the axial area. *Halamphora borealis* was first described as *Amphora borealis* by Kützing (1844: 108) and later changed to *Halamphora* by Levkov (2009). Distinctively, *H. lombokensis* and *H. borealis* have similar valve outlines, wide continuous raphe ledges from end to end, and irregularly spaced uniseriate dorsal areolae externally. Internally *H. borealis* has recessed biporoid pores between interrupted costae and continuous striae on the ventral side, whereas *H. lombokensis* has well-structured cribra over the areolae and interrupted striae on the ventral side at the central area. Also *H. borealis* has larger specimens (>19.0 µm length, >3.0 µm width) with a lower stria density (<25 in 10 µm).

Halamphora pellicula was described from St. Joseph Bay in Florida, USA (Stepanek and Kociolek 2018). Valves of *H. pellicula*, like *H. lombokensis*, have a long, wide and continuous raphe ledge but the striae on the external valve face are not interrupted (uneven areolae distribution), there is a silica ridge at the valve face mantle junction (not in *H. lombokensis*) and the striae are finely biseriate. Internally, the striae are also finely biseriate between thickened costae, unlike the singular cribra covered areolae of *H. lombokensis*. *Halamphora pellicula* also has a higher striae density (>41 in 10 μm). *Halamphora salinicola* was described from a salt lake in Atacama, Chile by Levkov and Díaz (Levkov 2009). This taxon has a broad continuous raphe ledge, and the central and dorsal raphe ends deflect dorsally. *H. salinicola* is distinguished from *H. lombokensis* by the biseriate poroid striae without cribra. The taxon is longer (>20.0 μm), has a lower stria density (<26 in 10 μm) and with shortly protracted and capitate endings. The marine *Halamphora tenui*s (Stepanek and Kociolek 2018) from Biscayne Bay Florida, USA is longer (>13.0 μm) and has a higher striae density (>32 in 10 μm). *Halamphora tenuis* is easily separated by the densely biseriate striae that are continuous across the valve face. *Halamphora valdeminutissima* was described from Black Sea by Zidarova et al. (2023). The taxon has smaller specimens (<11.0 μm length, <3.0 μm width) and with a higher striae density (about 45 in 10 μm) (Table 1). This Black Sea taxon has a flat valve (curved in *H. lompokensis*), continuously biseriate striae with the marginal ridge sporadically interrupted by the striae. The secondary side of the central raphe ledge is also thickened.

Halamphora banzuensis from Banzu Flats in Tokyo Bay, Japan (Stepanek and Kociolek 2018) is geographically close and environmentally similar to the Kuta Beach assemblage, documenting a range extension for this species from 35 to 8°N which is a broad range extension from the East China Sea to the Timor Sea. The new documented range for this taxon is additional evidence that marine *Halamphora* species in the Indo-Pacific can have wide geographic distributions. It is worth noting that the population from Banzu flats is marginally larger and the dorsal side of the valve is continuously arched, while the Kuta population has more flattened dorsal valve margins.

Although the valve outlines of these two taxa from Kuta beach are common (linear-elliptic dorsal margin to more broadly rounded valve margin with protracted rostrate to capitate apices), fine structural features of the areolae, raphe ledge development and formation of silica ridges (or partial ridges) help distinct these species. Taxa with uniseriate taxa, like *H. lombokensis*, have a diverse assemblage of areolae structure, while species with recessed biseriate striae are less morphologically diverse with continuous or disrupted areolae along the striae. At present, species from inland saline waters, brackish waters and marine waters appear to be taxonomically separated.

Other new species of the genus Halamphora have been described recently, for example *Halamphora minima*, new brackish diatom species from the mudflat of Korea (An et al. 2022) and two species from Livingstone Islands, Antarctica (Zidarova et al. 2022). The new and rare species from Lombok, Indonesia contribute to the new records of species from marine tropical regions. Kuta beach is a strict marine environment and the extended geographical distribution of *H. banzuensis* suggests that marine *Halamphora* species in Asian waters likely have broad distributions.

Table 1. Morphological and meristic characteristics of *Halamphora lombokensis* (Hamilton, Pane, Risjani & Solak), sp. nov., and other *Halamphora* taxa sharing similar morphological features.

	Species valve length (µm)	Valve width (µm)	Dorsal stria density (in 10 µm)	Valve ending	Raphe ledge	Axial area	References
Halamphora lombokensis Hamilton, Pane, Risjani & Solak sp. nov.	**11.0–13.0**	**2.0–3.0**	**28–32**	**protracted, narrowly rounded to subcapitate**	**broad, and linear**	**narrow with ventral fasica**	**this study**
Halamphora banzuensis (this study)	**13.0–16.5**	**3.0–4.0**	**22–23**	**protracted, narrowly rounded to subcapitate**	**broad, slightly dorsally elevated at centre**	**narrow dorsally and difficult to distinguish along the ventral side**	**this study**
H. banzuensis Stepanek, Mayama & Kociolek	16.0–17.0	3.0–3.5	20–22	protracted, narrowly rounded to subcapitate	broad, linear	narrow dorsally and difficult to distinguish along the ventral side	Stepanek and Kociolek 2018
Halamphora acutiuscula (Kützing) Levkov	27.0–40.0	5.0–7.5	15–18	protracted, capitate	broad, linear, elevated dorsally	narrow throughout, widening ventrally	Levkov 2009
Halamphora angustiformis Stepanek & Kociolek	15.0–33.0	3.0–4.0	20–22	protracted, narrowly rounded to subcapitate	broad, elevated dorsally	narrow throughout, widening ventrally	Stepanek and Kociolek 2018
H. aponina (Kützing) Levkov	23.0–40.0	3.0–4.5	20–22	protracted, capitate	narrow linear	narrow, widening ventrally	Levkov 2009
H. attenuata Stepanek & Kociolek	20.0–33.0	3.5–4.5	23–25	protracted, narrowly rounded	broad linear	narrow throughout, expending slightly ventrally	Stepanek and Kociolek 2015
H. banzuensis Stepanek, Mayama & Kociolek	16.0–17.0	3.0–3.5	20–22	protracted, narrowly rounded to subcapitate	broad, linear	narrow dorsally and difficult to distinguish along the ventral side	Stepanek and Kociolek 2018
H. borealis (Kützing) Levkov	19.0–40.0	3.0–4.0	20–24	protracted, capitate	narrow linear	narrow, widening ventrally	Levkov 2009
H. crenulatoides Stepanek & Kociolek	16.0–23.0	3.0–4.0	17–23	protracted, subcapitate	broad, linear	narrow dorsally and ventrally expanded	Stepanek and Kociolek 2018
H. nagumoi Stepanek, Mayama & Kociolek	16.0–24.0	3.0–3.5	18–20	weakly protracted, narrow, rounded	very broad, linear	narrow dorsally and ventrally expanded	Stepanek and Kociolek 2018
H. pellicula Stepanek & Kociolek	10.0–18.0	2.5–3.5	41–42	protracted, subcapitate	broad, linear	not well defined	Stepanek and Kociolek 2018
H. salinicola Levkov & Díaz	20.0–34.0	2.5–3.7	21–26	shortly protracted and capitate	narrow, expanded on both valve sides	narrow, widening ventrally	Levkov 2009
H. tenuis Stepanek & Kociolek	13.0–19.0	2.5–3.0	31–32	protracted, subcapitate	moderate, linear	narrow throughout	Stepanek and Kociolek 2018
H. valdeminutissima Zidarova et al.	6.0–13.5	1.5–3.0	about 45	protracted, subcapitate	narrow, slightly widening at centre and apices	narrow, widening ventrally	Zidarova et al. 2022

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

Conceptualisation: YR, CNS, EPP. Data curation: PBH. Funding acquisition: EPP, CNS, YR. Investigation: EPP, CNS, NE. Methodology: CNS, EY. Project administration: EPP. Supervision: YR, CNS, Y. Visualization: CNS, NE. Writing – original draft: EPP. Writing – review and editing: YR, CNS, PBH, EY, Y.

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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

Ctenophora hunanensis sp. nov. (Bacillariophyta) from the Yongle River in Hunan Province, China

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Abstract

A new species, *Ctenophora hunanensis* Bing Liu & Rioual, **sp. nov.**, found in the Yongle River, a tributary of the Xiang River (Hunan Province, southern China) is described on the basis of morphological observations made under light and scanning electron microscopes. *Ctenophora hunanensis* is distinguished from other *Ctenophora* taxa by a unique combination of characters that includes its lanceolate valve outline with rostrate apices, sternum gradually becoming wider from valve apices to center, and a greater valve width than the other members of the genus. *Ctenophora hunanensis* inhabits the epilithic community in the headwaters of a freshwater river. Many abnormal valves of *C. hunanensis* were observed in the samples investigated and the most frequent morphological abnormalities consisted in a lack of symmetry relative to the apical axis caused by a unilateral incising in the middle part of the valve.

Key words: abnormal valve, central area, cribrum, *Ctenophora*, sternum

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Introduction

In recent years, the diatom flora of Hunan Province in southern China (Fig. 1) has been investigated by Dr. Liu from Jishou University and his collaborators and their research led to the descriptions of several species new-to-science (e.g. Liu et al. 2016, 2017a, 2017b, 2017c, 2018a, 2018b, 2018c, 2019a, 2019b, 2019c, 2020a, 2021; Long et al. 2021, 2022a, 2022b; Liu 2023; Yuan et al. 2023; Xu et al. 2024). Many of these new species were described from Dongting Lake, the second largest freshwater lake in China that is located in the northeast of Hunan and drains the entire river system of this province with only a few exceptions. By contrast, the diatom flora of the rivers of Hunan, such as the Xiang River and its tributaries, has been relatively underexplored until now with only a few reports available in the literature (Long et al. 2022c, Liu 2023, Yuan et al. 2023, Zheng et al. 2023). Thus, as part of an ongoing investigation on the Xiang River and its tributaries, epilithon samples were collected from the Yongle River (Fig. 1) and analysed. The analyses revealed the presence of specimens of the genus *Ctenophora* (Grunow) D.M. Williams & Round that could not be attributed to any known species from this genus.

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[*] These authors contributed equally to this work.

Figure 1. Map of Hunan Province, in southern China, showing the location of the Yongle River, a tributary of the Xiang River and Dongting Lake. The Yongle River is the type locality of *Ctenophora hunanensis* sp. nov.

Ctenophora was raised to the generic level by Williams and Round (1986). As a genus, it is distinguished from other related genera by the type of valve striation (with transverse, uniseriate striae composed of poroids closed externally by complex cribra), the cribrum structure and the robust plain area (i.e. without perforations in the silica wall) that usually occupies the entire width of the valve in its center. For more than three decades, *Ctenophora* was thought to be monotypic, only represented by the species *Ctenophora pulchella* (Kützing) Williams & Round, which was originally described from England but considered as cosmopolitan. This situation changed with the discovery of *Ctenophora sinensis* Bing Liu & D.M. Williams (Liu et al. 2020b) from samples collected in Lake Qinghai (China). More recently, Williams and Van de Vijver (2023a, 2023b) re-examined type material from European historical collections and proposed the re-combination and transfer to *Ctenophora* of three species. An exhaustive discussion on the structural characters useful for the description of *Ctenophora* taxa and on the phylogenetic relationships of this genus with other genera such as *Tabularia* (Kützing) Williams & Round and *Catacombas* Williams & Round was also proposed in Williams and Van de Vijver (2023b).

This paper describes *Ctenophora hunanensis* Bing Liu & Rioual sp. nov., as a new freshwater species from China and further contributes to the under-appreciated diversity of *Ctenophora* as well as to the investigation of the diatom flora of Hunan Province.

Materials and methods

The diatom samples of this study were collected from the Yongle River which runs through Anren County in the south of Hunan Province (Fig. 1). The Yongle River is a headwater tributary of the Xiang River which is the largest river in Hunan. Benthic diatom samples were collected on March 24, 2024. 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. Immediately after being retrieved from the river bed, each stone was placed on a plastic plate and its surface was brushed using a toothbrush, with the brushed-off diatom samples being washed into 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, water temperature, pH, and conductivity were measured in situ with a portable multimeter (HQ40D, Hach Company, USA).

The laboratory methods are also the same as in Liu (2023) and consist as follows: "The collected diatom samples which were 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 acronyms follow Index Herbarium http://sweetgum.nybg.org/science/ih/). Samples were further examined using a field emission scanning electron microscope (SEM, Carl Zeiss Microscope, model Sigma HD) available at Huaihua University, China. For SEM analysis, several drops of the cleaned diatom material were air-dried onto glass coverslips. The coverslips were attached to aluminum stubs using double-sided conductive carbon strip and sputter-coated with platinum (Cressington Sputter Coater 108auto, Ted Pella, Inc.). The terminology used in the description and in the discussion mainly follows Round et al. (1990) and Liu et al. (2020b).

Results

Ctenophora hunanensis **Bing Liu & Rioual, sp. nov.**
Figs 2–5

Holotype. Specimen circled on slide DIA2024010 (= Fig. 2B), deposited in the Herbarium of Jishou University (JIU), China. Registration: http://phycobank.org/105130.

Type locality. China. Hunan Province: Anren County, Yongle River, sampling site with the coordinates 26°50'12"N, 113°35'59"E, and an elevation of 123 m asl. Diatom samples collected by Bing Liu, March 24, 2024.

Description. ***LM*** (Fig. 2). Valves lanceolate with rostrate apices. Valve dimensions (n = 30): length 48–78 µm, width 6.5–8.5 µm at center. Sternum clearly visible, gradually widening when approaching central area. Central area distinct, rectangular to square, sometimes with ghost striae. Striae parallel, uniseriate, perpendicular to central sternum, opposite one another across sternum. Stria density 13–16 in 10 µm. Areolae punctate, 20 in 10 µm. Many

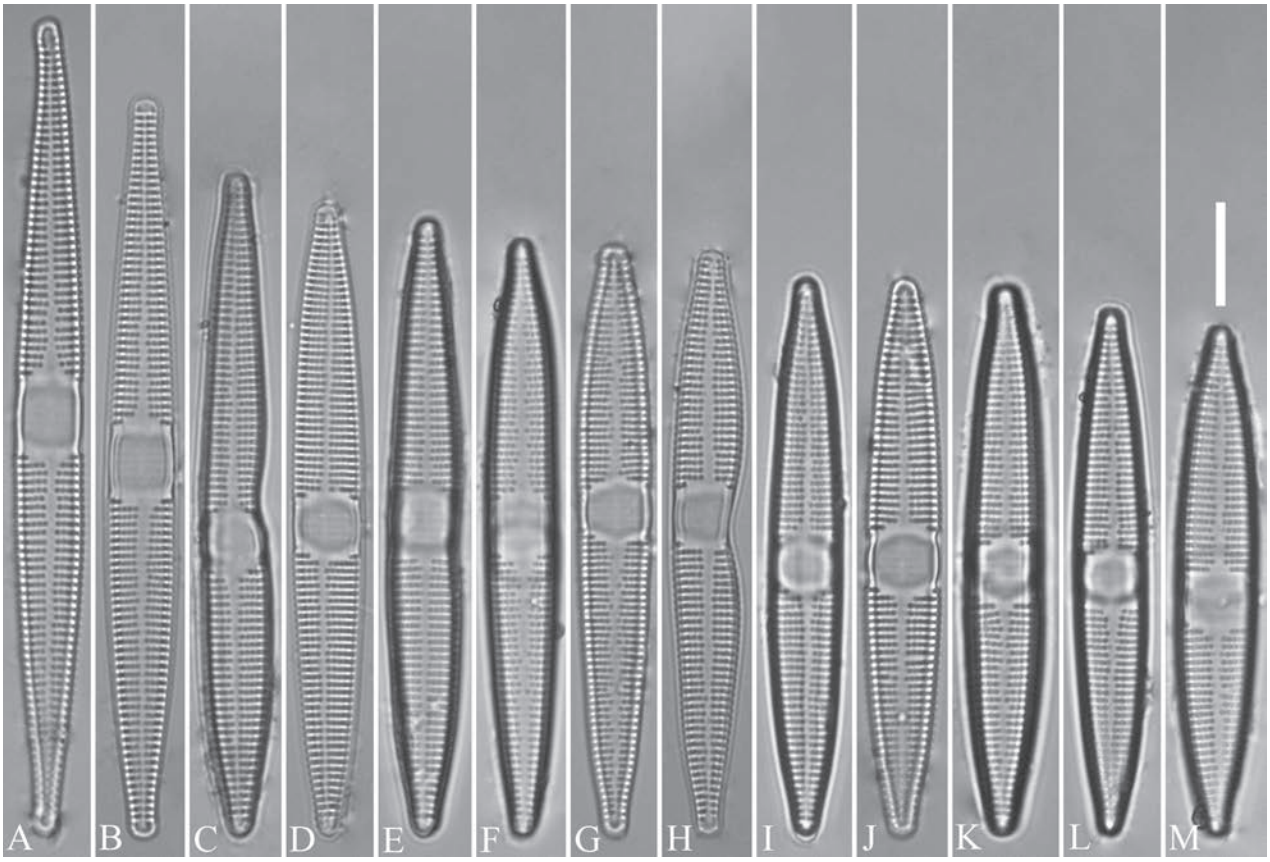

Figure 2. *Ctenophora hunanensis* sp. nov., LM × 1000 **A–M** thirteen valves showing a size diminution series, note three abnormal valves (**C, E, H**) **B** illustration of holotype specimen. Scale bar: 10 μm (**M**).

abnormal valves are found, all of which exhibit the asymmetry relative to the apical axis due to the V-shaped incising of valve margin only occurring at one side (Fig. 2C, E, H).

SEM (Figs 3–5). Sternum meeting and integrated with virgae, vimines reduced in size relative to virgae. Virgae and vimines join to form square to rectangular areolae that are closed externally by complex cribra appearing as sieve-like closing plates composed of pegged struts (Fig. 3D–F). Inner openings of areolae appear rounded (Fig. 4C, D). Central area distinctive, externally a broad plain area (Fig. 3D), internally thickened around its periphery, ghost striae within (Fig. 4D). One rimoportula present at each apex, externally expressed as a simple hole (Fig. 3E, F), internally bilabiate, situated close to sternum (Fig. 4E, F). Ocellulimbus produced at each apex, typically sunken below surface of valve margin (Fig. 3E, F). Valvocopula open, lacking ornamentation, distinctly deeper than copulae (Fig. 5). On its advalvar edge, valvocopula bears a row of serrated projections, each corresponding internally to a virga (Fig. 5, three arrows). Copulae with row of poroids situated at pars media (Fig. 5, two wavy arrows).

Etymology. Named after Hunan Province where the species was found.

Distribution and ecology. Known only from the type locality. The samples that included this species were scraped off the surface of stones collected in the Yongle River. Hence this is a benthic, epilithic species. The relative abundance of this new species is ca. 3%. The associated taxa include

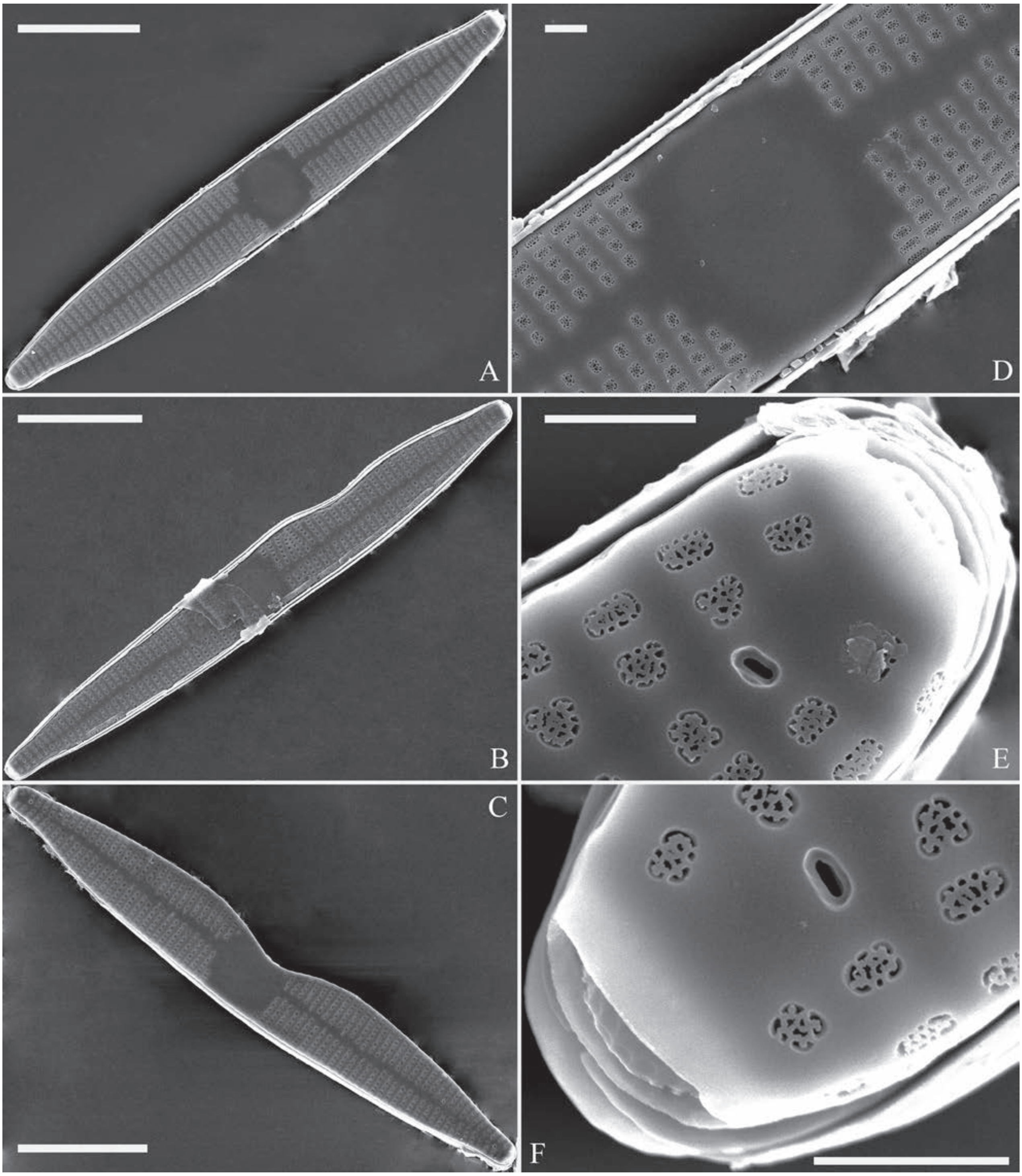

Figure 3. *Ctenophora hunanensis* sp. nov., external view, SEM **A** normal frustule **B, C** two abnormal frustules **D** middle part, detail from **A** note the central area and sternum **E, F** details of the two apices of the valve shown in **A** note the complex cribrae, the external openings of the rimoportulae (one on each apex), and the ocellulimbi. Scale bars: 10 µm (**A–C**); 1 µm (**D–F**).

Gomphonema parvulum (Kützing) Kützing, *Luticola* spp., *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot, *Tryblionella* spp., *Nitzschia* spp., among others. The following environmental parameters were measured in the field with three replications: Conductivity = 85.9 ± 0.1 µS cm^{-1}; pH = 8.9 ± 0.1; Water temperature = 22.3 ± 0.3 °C.

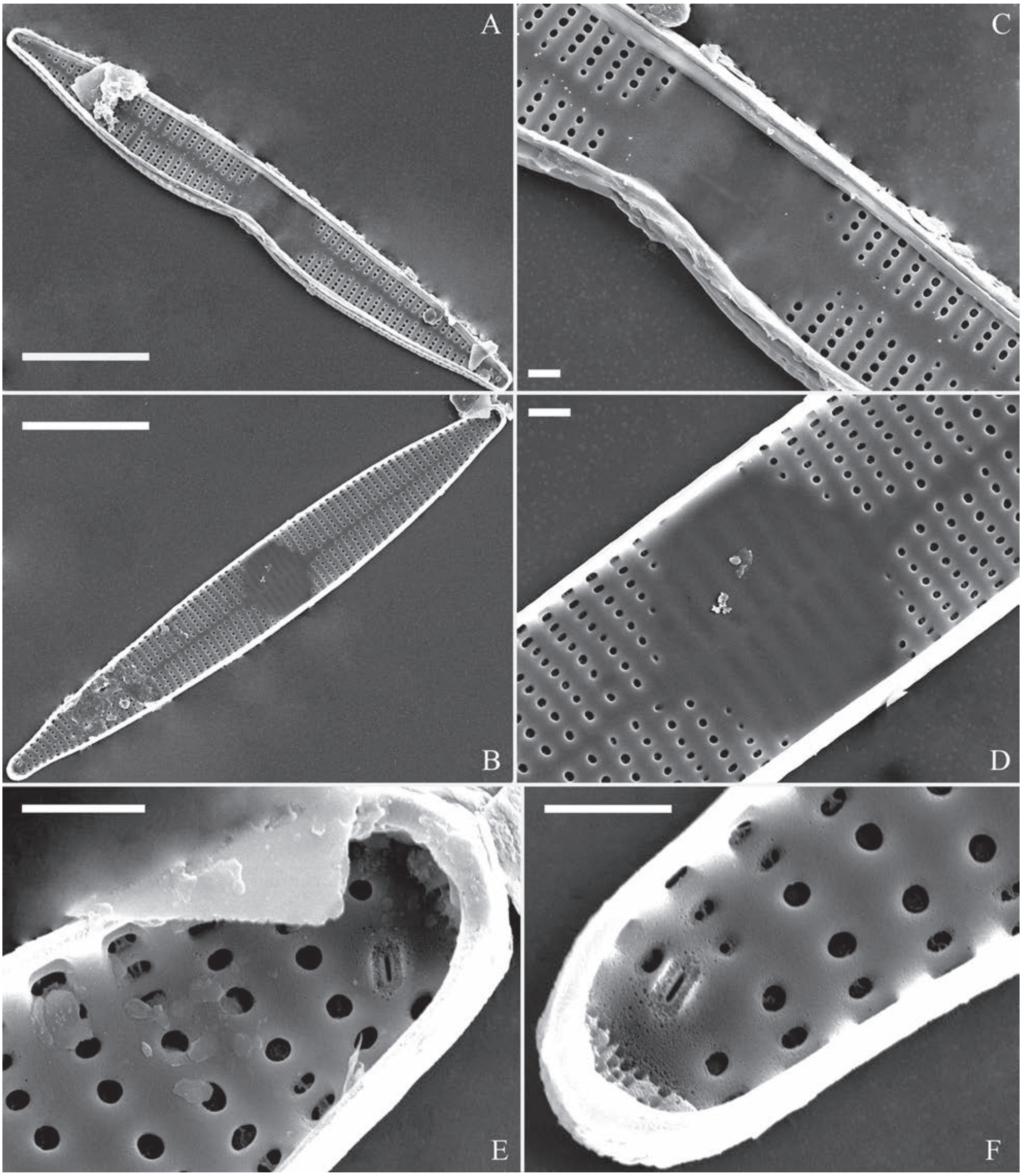

Figure 4. *Ctenophora hunanensis* sp. nov., internal view, SEM **A** abnormal valve **B** normal valve **C** middle part, detail from **A** showing the central area **D** middle part, detail from **B** showing the central area **E, F** details of the apices from **B**. Scale bars: 10 µm (**A, B**); 1 µm (**C–F**).

Discussion

The general morphology of *Ctenophora hunanensis* Bing Liu & Rioual sp. nov. has all the characteristic features of the genus *Ctenophora*, including transverse, uniseriate striae composed of poroids closed externally by complex cribra, and the robust plain area that usually occupies the entire width of the

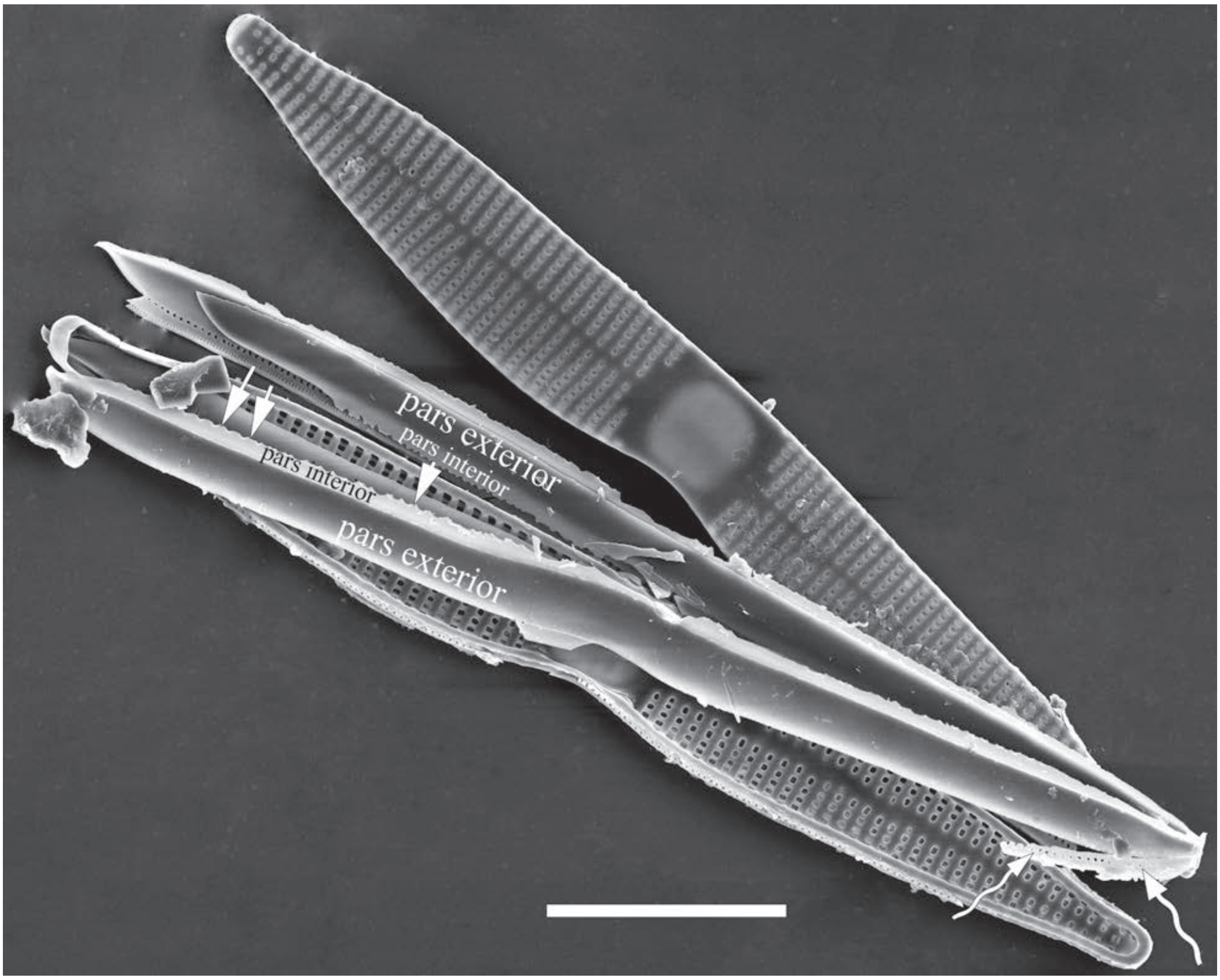

Figure 5. *Ctenophora hunanensis* sp. nov., SEM A dissembled frustule, note the distinctive central area, open, unornamented valvocopula, on its advalvar edge, valvocopula bears a row of serrated projections, each corresponding internally to a virga (three white arrows). Copulae with row of poroids situated at pars media (two white wavy arrows). Scale bar: 10 µm.

valve in its center. Currently in AlgaeBase (Guiry in Guiry and Guiry 2023) for the genus *Ctenophora* there are five names taxonomically accepted as species. The five species include *C. pulchella*, the type species of the genus, *C. saxonica* (Kützing) D.M. Williams & Van de Vijver, *C. sinensis* B. Liu & D.M. Williams, *C. subula* (Sande Lacoste & Suringar) D.M. Williams & Van de Vijver, and *C. vertebra* (W. Gregory) D.M. Williams & Van de Vijver. Compared to the five other species of *Ctenophora* listed above, *C. hunanensis* is distinguished by its valve outline (lanceolate with rostrate apices), a sternum gradually becoming wider from the valve poles to center, and a much greater valve width than the other *Ctenophora* taxa (Table 1). *Ctenophora sinensis* and *C. vertebra* have very different valve outlines and can therefore be easily distinguished from *C. hunanensis*. *Ctenophora hunanensis* could be possibly confused with the smaller valves of *C. pulchella* and *C. saxonica* (and possibly *C. subula*?), but the difference in valve width remains (i.e., the ranges in width do not overlap). In addition, the central area of *C. hunanensis* is not buttressed while those of *C. pulchella* and *C. subula* are strongly buttressed.

Table 1. Comparisons between *Ctenophora hunanensis* sp. nov. and the other species of the genus *Ctenophora*.

Feature	*C. hunanensis* sp. nov.	*C. pulchella*	*C. saxonica*	*C. sinensis*	*C. subula*	*C. vertebra*
Valve outline	Lanceolate with rostrate apices	Lanceolate with sub-capitate apices	Lanceolate with sub-capitate apices	Lanceolate with capitate to sub-capitate apices	Lanceolate, tapering towards the poles	Lanceolate with capitate apices
Valve length (L) and width (W) (μm)	L: 48–78; W: 6.5–8.5	L: ca. 48–59; W: ca. 2–4	L: ca. 51–97; W: ca. 4–6	L: 70–136; W: 4–6	L: 65–80; W: 2–5	L: ca. 44–104 μm; W: 2–4 μm
Striae in 10 μm	13–16	13–14	13–14	15–19	13–14	No data
Areolae in 10 μm	20	ca. 20	ca. 20	26–28	ca. 20	No data
Cribrum	Sieve-like closing plates	Mesh-work with ca. 4–8 strutted closing plates	Mesh-work with ca. 6–8 closing plates	Sieve-like closing plates	Mesh-work with ca. 8–12 strutted closing plates	No data
Sternum	Gradually widening from pole to center	Gradually widening from pole to center	Very narrow, linear	Very narrow, linear	Relatively narrow, linear	Very narrow, linear
Central area	Square to rectangular, not butressed	Square to broadly circular-oblong, butressed	Square to broadly circular-oblong, not butressed	Rectangular to square, weakly butressed	Square to oblong, heavily butressed	Ovoid
Habitat	Freshwater	Freshwater to brackish	Fresh to salty water	Brackish water	Freshwater	Freshwater (?)
References	This study	Williams and Van de Vijver (2023b)	Williams and Van de Vijver (2023b)	Liu et al. (2020b)	Williams and Van de Vijver (2023a)	Williams and Van de Vijver (2023b)

Regarding the ultrastructure of the cribra, *C. hunanensis* possesses sieve-like closing plates composed of pegged struts that appear similar to those of *C. sinensis*, the other species described from China. In the three species described from Europe for which the structure has been illustrated, i.e. *C. pulchella*, *C. saxonica*, *C. subula*, the cribra appear as mesh-like structures. This difference in cribra structure may however be an artifact of the valve preservation, as the specimens illustrated by Williams and Van de Vijver (2023a, 2023b) were taken from historical collection at least 160 years old and may have been eroded to some extent.

Until recently as the genus was thought to be monotypic, *Ctenophora* was generally considered as an indicator of high electrolyte content in brackish waters, in marine coasts and river estuaries. When found in inland waters, *Ctenophora* was encountered in saline springs and salinized running waters. Its presence in freshwater was possible, but only in low numbers. It was also considered tolerant of polluted water, up to the α-mesosaprobic level (Lange-Bertalot et al. 2017). The discovery (or re-discovery) of other species of *Ctenophora* already suggested that populations of this genus could live in freshwater habitats. For example, Williams and Van de Vijver (2023a) reported that *Ctenophora subula* was found in the Netherlands as epiphytic on the filamentous green alga "*Cladophora Sandii*" (syn.: *Cladophora rivularis* (L.) Kuntze), which is a freshwater species. The salinity preference of *Ctenophora vertebra* is difficult to assess precisely although the type location "lacustrine sands, Glenshira, near Inveraray" in Scotland, also suggests it comes from a freshwater habitat (Williams and Van de Vijver, 2023b). The discovery of *C. hunanensis* in the headwaters of the Yongle River therefore confirms that the ecological niche of the genus *Ctenophora* is very broad, not just restricted to brackish conditions but also includes low-conductivity, unpolluted freshwater habitat.

Interestingly, the type population of *C. hunanensis* includes many abnormal valves (e.g., Figs 2C, E, H; 3B, C; 4A) which in the samples we investigated represented 23% of the specimens observed (7 abnormal valves out of 31). Most abnormal valves of *C. hunanensis* exhibit abnormal valve outlines lacking symmetry relative to the apical axis due to the incising of valve margin only occurring at one side (Figs 2C, E, H, 3B, C, 4A), which is a type of abnormality commonly reported in araphid diatoms (Falasco et al. 2009, 2021).

These observations further illustrate the morphological plasticity reported for some araphid genera such as *Hannaea*, *Ulnaria* and *Fragilaria*. For *Ulnaria* in particular, Zheng et al. (2024) also reported a large percentage of abnormal valves, with an asymmetrical incision on one margin of the valve, from the type population of *Ulnaria shun-biseriata* Bing Liu & Rioual, which was also described as a new species from a river in Hunan province. Further research is required to explain why diatom populations with large proportions of abnormal valves appear to be common in rivers of Hunan.

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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: BL. Data curation: DQX, YZ, RY. Formal analysis: PR, BL. Funding acquisition: BL. Writing - original draft: DQX, RY. Writing - review and editing: PR.

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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

Cryptantha acrimuricata (Boraginaceae), a distinctive new taxon of series *Muricatae*

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Abstract

In the process of studying the species *Cryptantha muricata* and its varieties, we discovered a unique taxon of the genus that resembles *C. muricata* but differs in having a mostly densely white-strigose stem vestiture (sometimes with spreading trichomes) and tuberculate to muricate nutlets with often whitish tubercles that are, in comparison with typical *C. muricata*, larger, with a wider base and more pointed apex, and more densely spaced. We believe this form to be different enough to describe as a new species, *Cryptantha acrimuricata*. This new species occurs in southwestern North America: in California and Arizona of the United States and in northern Baja California, Mexico. It occurs in mid- to relatively high elevation mountain regions of mostly desert transition/escarpment in the Transverse and Peninsular Ranges, in the Sonoran and Mohave Deserts, and with some populations scattered in the southern Sierra Nevada. We believe this new species to be closely related to *C. clokeyi*, *C. martirensis*, *C. muricata*, and possibly *C. hooveri*, of *Cryptantha* series *Muricatae*. Detailed molecular phylogenetic are needed to better establish their interrelationships.

Key words: Boraginaceae, *Cryptantha*, *Cryptantha muricata*, series *Maritimae*, series *Muricatae*, taxonomy

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Introduction

The genus *Cryptantha* (Boraginaceae, subtribe Amsinckiinae, after Chacón et al. 2016), as currently delimited, consists of approximately 110 species and 125 minimum-rank taxa, with 64 species native to North America, 47 species native to South America, and one of these found on both continents (see Hasenstab-Lehman and Simpson 2012; Guilliams et al. 2017; Simpson et al. 2017a; Amsinckiinae Working Group 2024). The numerous species in the genus are delimited from one another by duration (perennial versus annual), stem habit/branching pattern and vestiture, inflorescence cymule number, leaf position/morphology, floral bract presence, calyx shape/size/vestiture, corolla shape/size/color, and fruit (nutlet) morphology. The last feature is often most important in taxonomic circumscription. Nutlets of different *Cryptantha* species may vary markedly in several features, including: number per fruit (1–4), heteromorphism [with some species having one nutlet different from the other(s)], size, shape, and sculpturing types; the last feature includes smooth, papillate, muricate/tuberculate, spinulose, and/or winged (see Simpson and Hasenstab 2009).

Recent molecular phylogenetic analyses (Hasenstab-Lehman and Simpson 2012; Simpson et al. 2017b; Mabry and Simpson 2018) have clarified generic circumscriptions within subtribe Amsinckiinae, to which *Cryptantha* belongs (see Chacón et al. 2016). These studies provided evidence for the segregation of *Eremocarya*, *Greeneocharis*, *Johnstonella*, and *Oreocarya* from the traditional concept of *Cryptantha* s.l., which had been circumscribed in having a ventral groove attachment scar. Several taxonomic studies (Mabry et al. 2016; Simpson et al. 2013, 2014, 2016, 2019; Simpson and Kelley 2017; Simpson and Rebman 2013, 2021a, b; Rebman and Simpson 2022; and Simpson and York 2024) have contributed to an understanding and recognition of new species and infraspecies within *Cryptantha* and its close relatives.

In the process of studying the species *Cryptantha muricata* (Hook. & Arn.) A.Nelson & J.F.Macbr. and its varieties (work in progress), we discovered a unique form that resembles aspects of the three varieties of *C. muricata* in calyx shape and in nutlet shape and presence of a median ridge. However, the new species differs from all *C. muricata* varieties in stem vestiture and in nutlet sculpturing. We believe that these differences warrant its description as a species new to science, based on a taxonomic (morphologic) concept (Cronquist 1978, 1988).

Methods

Herbarium specimens of what originally had been identified as *Cryptantha muricata* from **ARIZ**, **ASU**, **BCMEX**, **BSCA**, **CAS/DS**, **GMDRC**, **HSC**, **JOTR**, **LOB**, **PUA**, **RSA/POM**, **SBBG**, **SD**, **SDSU**, **UC/JEPS**, and **UCR** (herbarium acronyms after Thiers 2024) were examined, with focus on nutlet morphology. This new species was identified as distinct from the three recognized varieties of *Cryptantha muricata* (Table 1), after comparative study of those specimens. In order to verify that this entity had not been previously named, we studied online images of type specimens of all heterotypic synonyms of *Cryptantha muricata* varieties: *C. horridula* Greene, *C. densiflora* A.Nelson & P.B.Kenn., and *C. vitrea* Eastw. (Table 1; see Amsinckiinae Working Group 2024).

All known specimens corresponding to this new species were assembled, and their associated collection data were collated in a spreadsheet. A similar spreadsheet was prepared using selected specimen data for the three varieties of *Cryptantha muricata*. Point distribution maps, at two scales, were prepared of the localities of these collections, the georeference data either recorded directly from herbarium sheet label data or estimated from recorded locality information of these labels. Maps were prepared using the Berkeley multi-mapper tool (https://ucjeps.berkeley.edu/consortium/load_mapper_multi.html). Stem and leaf morphology, mature (fruiting) calyx, and nutlets of selected specimens were photographed from field observations and from herbarium specimen material. High magnification images were produced using a Macropod Pro 3D camera system (Macroscopic Solutions, East Hartford, CT, USA) or an Infinity 2 camera on an Olympus SZ61 boom-mounted dissecting microscope. All specimens were studied in generating a description of the new taxon. A key was prepared to separate this new species from *Cryptantha muricata* and close relatives.

Table 1. *Cryptantha* series *Muricatae*. Diagnosis and classification, with 5 species and 7 minimum-rank taxa. Heterotypic synonyms, only occurring for the varieties of *C. muricata*, are also listed. *=Included in the molecular phylogenetic studies of Simpson et al. 2017 and Mabry and Simpson 2018. †=Placement tentative.

Series *Muricatae*: Nutlets 4 per fruit, homomorphic, ovate to triangular, papillate and turberculate to muricate, style extending beyond nutlets at maturity
Cryptantha acrimuricata J.M.André, L.M.Simpson, & M.G.Simpson
**Cryptantha clokeyi* I.M.Johnst., J. Arnold Arbor. 20: 387 (1939)
†*Cryptantha hooveri* I.M.Johnst., J. Arnold Arbor. 18: 23 (1937)
**Cryptantha martirensis* M.G.Simpson & Rebman, Madroño 60: 35 (2013)
**Cryptantha muricata* (Hook. & Arn.) A.Nelson & J.F.Macbr. var. *muricata*, Botanical Gazette 61: 42 (1916)
[*Cryptantha horridula* Greene, Pittonia 5: 55 (1902)]
Cryptantha muricata var. *denticulata* (Greene) I.M.Johnst., Contr. Gray Herb. 74: 71 (1925)
[*Cryptantha densiflora* A.Nelson & P.B.Kenn., Proc. Biol. Soc. Washington 19: 156 (1906)]
Cryptantha muricata var. *jonesii* (A.Gray) I.M.Johnst., Pl. World 22: 114 (1919)
[*Cryptantha vitrea* Eastw., Proc. Calif. Acad. Sci., ser. 3, 2: 292 (1900)]

Taxonomic treatment

Cryptantha acrimuricata **J.M.André, L.M.Simpson, & M.G.Simpson, sp. nov.**
urn:lsid:ipni.org:names:77354339-1

Type. United States • California, San Bernardino County, New York Mountains: Mojave Natl. Preseve; Caruthers Canyon, 2.3 road miles north of junction New York Mtns Rd, at base of steep ascent to Giant Ledge Mine (historic), along closed dirt road paralleling perennially moist drainage, California, San Bernardino Co., 35.24875, -115.299217, 1768 m elevation, pinyon-juniper-oak woodland, among granitic outcrops, associates: *Pinus monophylla*, *Quercus turbinella*, *Garrya flavescens*, *Arctostaphylos pungens*, *Bouteoua gracilis*, *Yucca baccata*, *Brickellia californica*, *Opuntia phaeacantha*, *Dudleya saxosa aloides*, *J. M. André 40457*, 10 May 2019 (**holotype: RSA**0633491; **isotypes: ASU**, **GMDRC**, **SBBG**, **SD**, **SDSU**, **UC**, **UCR**).

Diagnosis. *Cryptantha acrimuricata* resembles *C. muricata* and varieties in having ovoid fruiting calyces with nutlets that are typically four per fruit, homomorphic, ovate in shape, with margins thickened and bearing tuberculate to muricate processes, with a median dorsal ridge, and with surfaces densely tuberculate to muricate. *Cryptantha acrimuricata* differs from *C. muricata* and varieties in having dense whitish-strigose stems, with spreading trichomes absent to sparsely present, and in having nutlets with relatively large and densely spaced, conic, often whitish, muricate processes with relatively wide bases and sharp apices, surfaces between the processes often shiny.

Description. (Figs 1, 2). ***Plants*** annual herbs, 10–35 cm tall, mostly gray-green. ***Root*** a taproot, brown to red-purple, sometimes staining paper. ***Stems*** generally erect to ascending, some plants with a dominant, erect primary axis bearing several short to elongate, ascending, secondary branches, others with numerous, subequal, inclined to ascending branches arising from plant base; stem surface light green, vestiture strigose with dense, white, tapered, antrorsely appressed, basally white-pustulate trichomes, ca. 0.5–0.7 mm long; hispid vestiture scattered to absent, if present with few, white, tapered, spreading (horizontal to inclined), basally white-pustulate trichomes, ca. 1 mm long.

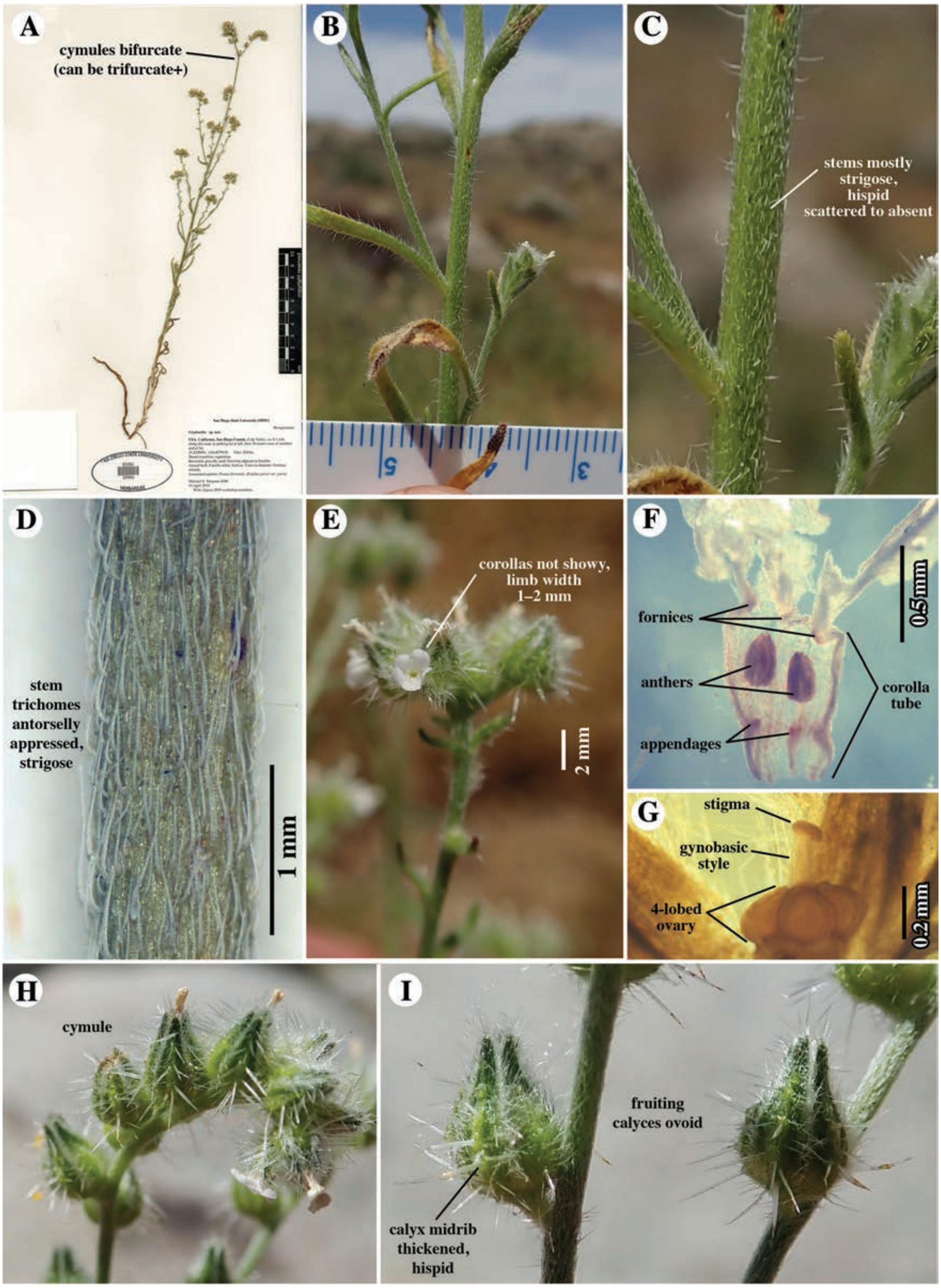
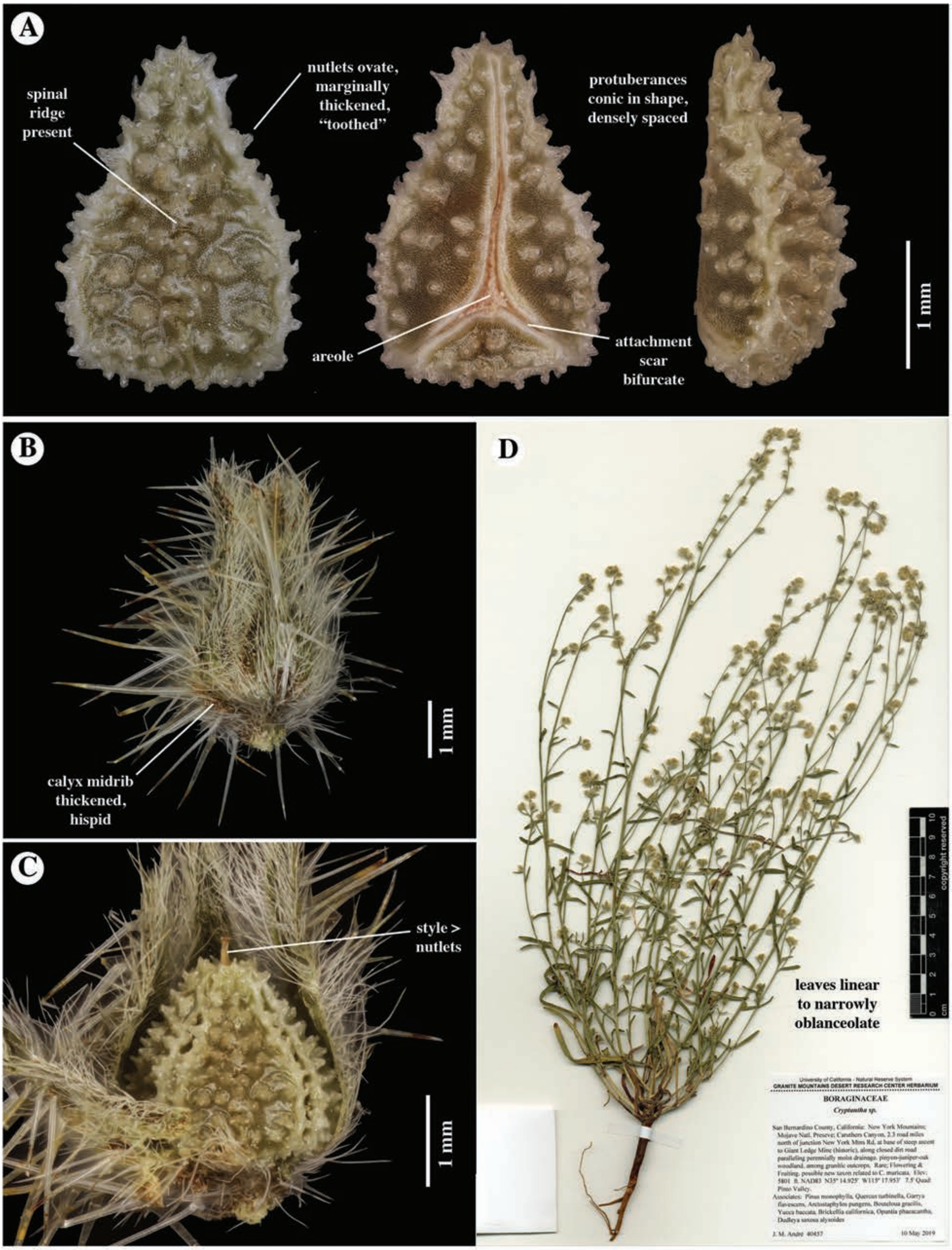


Figure 1. *Cryptantha acrimuricata*. Images of collection: *M.G. Simpson 4186*, 14 April 2019, **SDSU**22965 **A** herbarium specimen. Note dominant primary stem terminating in bifurcate cymules **B–E, H, I** field photographs **B** primary stem, showing cauline leaves and lateral branches **C** close-up of primary stem, the vestiture primarily strigose plus scattered spreading-hirsute **D** extreme close-up of primary stem, showing predominantly whitish strigose vestiture (trichomes antrorsely oriented) **E** close-up of cymule tip, showing relatively small corolla, this one slightly < 2 mm wide **F, G** flower removed and dehydrated **F** corolla, showing fornices, anthers adnate to corolla tube, and basal appendages **G** gynoecium, showing 4-lobed ovary, gynobasic style, and discoid stigma **H** cymule of primary stem **I** close-up of mature fruiting calyces. Note ovoid shape and spreading-hispid, pustulate trichomes of thickened sepal midribs.

Leaves mostly gray-green, sessile, linear to narrowly oblanceolate, midrib grooved adaxially, thickened abaxially, apex rounded to obtuse, both surfaces and margin appressed to ascending hirsute, trichomes white pustulate, especially in basal leaves; basal-most leaf pair apparently opposite, perhaps remnants of cotyledons, all others alternate-spiral; basal leaves 2–5 cm × ca. 2–3 mm, in a loose rosette withering at anthesis, cauline leaves 1–2 cm × ca. 1 mm, extending to base of cymule inflorescence units, slightly reduced upwards. ***Inflorescence*** cymules mostly in clusters of 2–3 (bifurcate or trifurcate), occasionally solitary, rarely up to 5, a terminal flower/fruit typically at junction of cymule bases; bracts occasionally at base of cymules, these linear to narrowly oblong; cymules elongated in fruit, 2–12 flowers per unit, lower fruits not touching at maturity. ***Flowers*** mostly ebracteate, pedicellate, pedicels in fruit more elongate, ascending, thickened apically, 0.5–1 mm long, surface densely hirsute, trichomes horizontal to ascending. ***Calyx*** symmetric, ca. 3 mm long at anthesis, sepals distinct; fruiting calyx ovoid, base truncate, apex acuminate, 3.5–5 mm long, sepals lance-ovate to lanceolate, apices erect; abaxial surface densely hirsute ascending along margins, marginal surfaces hirsute appressed, midrib strongly thickened, hispid, the trichomes stout, straight, tapered, pustulate, inclined, horizontal, or reflexed; adaxial surface glabrous basally, appressed short hirsute on surface of extreme apex. ***Corolla*** rotate, inconspicuous, white, fornices white, tube as long as calyx, limb 1–2 mm wide, not showy, appendages present ca. 1/3 from base of corolla tube in vertical line with anthers. ***Androecium*** of five stamens, attached at slightly different levels ca. 2/3 from base of corolla tube between and below fornices; anthers ca. 0.4 mm long, ellipsoid, dithecal, introrsely dehiscent, dorsifixed; filaments filiform, ca. 0.1 mm long. ***Gynoecium*** four-lobed, lobes ca. 0.3 mm long, globose, style gynobasic, ca. 0.7 mm long, protruding ca. 0.4 mm beyond ovary; stigma minute, discoid. ***Gynobase*** narrowly pyramidal, extending nearly to nutlet apices; style extending 0.1–0.3 mm beyond nutlet apices. ***Nutlets*** 4, erect, homomorphic, ca. 2–2.4 mm × 1.7 mm (at widest width), whitish to tan, sometimes dark brown-mottled, surface typically shiny, appearing varnished, ovate, abaxially flattened to low convex, adaxially shallowly 2-planed-convex, base truncate, margins sharp-angled with a thickened, usually whitish rim appearing “beaded”/”toothed” from marginal tuberculate to muricate protuberances, nutlet apex acute-rounded (blunt), surface irregularly transversely ridged, papillate and densely white tuberculate to muricate, these processes generally widely conic, densely spaced on surface, especially abaxially; spinal ridge present, sometimes obscure; attachment scar edges abutted at upper two-thirds, strongly bifurcate in lower one-third, delimiting a narrowly triangular, basal areole.

Distribution and habitat. *Cryptantha acrimuricata* occurs in the eastern part of the Peninsular Ranges, in the eastern and central Transverse Ranges, in higher elevations of the Mohave and Sonoran Deserts, and in scattered regions of the Sierra Nevada, of California and Arizona in the United States and Baja California in Mexico (Fig. 3). Its habitat ranges from sandy to coarsely gravelly substrates, usually granitic, sometimes limestone, sometimes adjacent to boulders, of chaparral, desert scrub/wash, pinyon-juniper woodland, or pine/oak woodland vegetation. The documented elevation range is 180–2621 m (average 1270 m).



University of California - Natural Reserve System
GRANITE MOUNTAINS DESERT RESEARCH CENTER HERBARIUM

BORAGINACEAE
Cryptantha sp.

San Bernardino County, California: New York Mountains; Mojave Natl. Preseve; Caruthers Canyon, 2.3 road miles north of junction New York Mtns Rd. at base of steep ascent to Giant Ledge Mine (historic), along closed dirt road paralleling perennially moist drainage. pinyon-juniper-oak woodland, among granitic outcrops. Rare; Flowering & Fruiting. possible new taxon related to C. muricata. Elev: 5801 ft. NAD83 N35° 14.925' W115° 17.953' 7.5' Quad: Pinto Valley.
Associates: Pinus monophylla, Quercus turbinella, Garrya flavescens, Arctostaphylos pungens, Bouteloua gracilis, Yucca baccata, Brickellia californica, Opuntia phaeacantha, Dudleya saxosa alysoides

J. M. André 40457 10 May 2019

Figure 2. *Cryptantha acrimuricata*. Images from holotype specimen: *J.M. André 40457*, 10 May 2019, **RSA**0633491 **A** nutlet, in (left to right) dorsal, ventral, and lateral views. Note ovate shape (dorsal and ventral outlines); truncate base; thickened, "toothed" or "beaded" margins; whitish, conic surface tubercles; and narrow ventral groove, which is widely bifurcate at the base, delimiting small areole **B** fruiting calyx, showing appressed marginal trichomes and spreading hispid along midrib **C** fruit opened, showing prominent style, protruding well beyond nutlets **D** herbarium specimen.

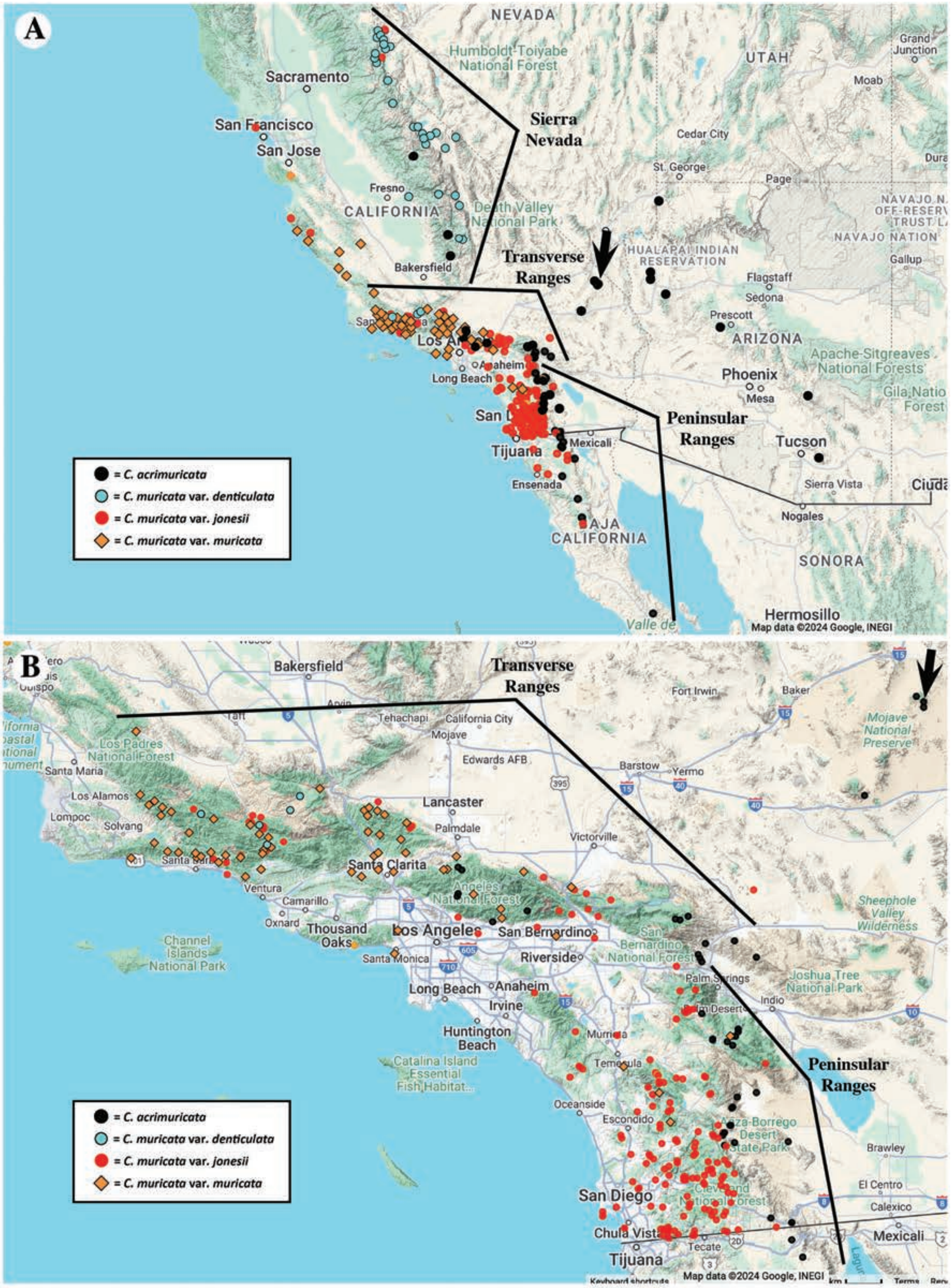


Figure 3. Distribution maps of *Cryptantha acrimuricata* from specimens cited here, plus of the three varieties of *C. muricata* from preliminary data, in two scales **A** showing overall distribution and **B** in a larger scale map highlighting the Transverse Ranges and northern Peninsular Ranges. See text for distribution summaries of the taxa. Arrow indicates location of holotype/isotypes specimens of *Cryptantha acrimuricata*. Map data @2024 Google, INEGI.

Phenology. Based on data from available specimens, the species typically flowers April–July, rarely in the fall following warm-seasonal rains (J. M. André, personal observation).

Rarity and conservation status. *Cryptantha acrimuricata* has been somewhat sparsely collected compared to the close relative *Cryptantha muricata*. Where encountered, populations of *C. acrimuricata* tend to be relatively isolated and restricted in areal extent, with few total numbers of individual plants. Though we are not aware of any imminent threats to existing populations, based upon its fairly limited distribution and small populations, this taxon may warrant conservation status.

Etymology. The specific epithet *acrimuricata* means "sharply muricate," from the Latin *acri-*, sharp, and *muricata* (derived from Latin *murex*, conch), hard-pointed. The name refers to the stout, widely-based, and sharply pointed conic tubercles, shaped like miniature mountain peaks, as contrasted with the more cylindrical or rounded tubercles of the varieties of *Cryptantha muricata*.

Suggested common name. We suggest Sharp-Pointed Prickly Cryptantha as a common name.

Paratypes

Arranged by country, then alphabetically by collector; *=estimated from label data.

Mexico • Baja California. San Rafael, Sierra San Pedro Mártir; west side of Cerro Blanco; 3k SSW of San Rafael, Baja California, 31.09333, -115.65167, 1550 m elevation, west facing slope, granite rock and gravel, associates: *Adenostoma fasciculatum*, *Arctostaphylos*, *Chorizanthe fimbriata*, *Eriogonum fasciculatum*, *Lotus rigidus*, *Lupinus concinnus*, *Mimulus pilosus*, *Rhus ovata*, *Salvia apiana*, *Swertia albomarginata*, and *Trichostemma parishii*, *M. A. Baker 12915 with Robert Johnson*, 12 May 1998 (**ASU**0014635!, **BCMEX**11466!); • Cerro San Luis, Baja California, 29.3167, -114.1167, 1300 m elevation, open gravelly place, north side, gravelly, *R. Moran 10296 with Jim Henrickson*, 2 March 1963 (**RSA**165004!, **SD**54579, **UC**1235600); • Sierra Juarez, 5 km W of La Rumorosa, Baja California, 32.55, -116.1, 1325 m elevation, colony under piñon, granitic area, associates: Piñon, *R. Moran 24108*, 15 May 1977 (**CAS**612817!, **SD**97068!); • Sierra Juarez, 1 km NW of Tres Pozos, Baja California, 32.37917, -116.075, 1350 m elevation, under shrubs along arroyo, *R. Moran 27383*, 26 May 1979 (**RSA**292842!, **SD**103648!); • Sierra Juarez, 1.5 km NW of El Mezquite, Baja California, 32.35833, -116.0667, 1400 m elevation, semishade of piñones, piñon-juniper-pine wood, associates: piñon-juniper-pine wood, *R. Moran 27437*, 27 May 1979 (**POM**369185!, **SD**103689); • Sierra Juarez, arroyo Agua Grande, 10 km south of La Rumorosa, Baja California, 32.4625, -116.0333, 1225 m elevation, in semishade, among rocks, *R. Moran 30751*, 16 May 1982 (**SD**110999!); • San Salvador: Bridge over branch of Rio San Carlos near Rancho San Salvador, Baja California, 31.8333, -116.0667, 1000 m elevation, *R. F. Thorne 60086 with Dave Charlton*, 19 April 1985 (**RSA**346809!); • Canon de Guadalupe, Baja California, 32.15, -115.8, 450 m elevation, dry slopes along canyon above resort area, sandy areas and rocky, *R. F. Thorne 61750 with Steve Boyd*, *etc.*, 23 March 1986 (**RSA**349247!); 1.5 mi NW Village of Valle Trinidad, Baja California, 31.423618*, -115.739987*, 989 m elevation*, granitic hillside, *I. L. Wiggins 16061A*, 3 April 1960 (**DS**506948!);

United States • New York Mtns, [above Brant Siding] in canyon above old mine site, California, San Bernardino Co., 35.27667, -115.34556, 1364 m elevation, granite, talus, gravel, *J. M. André 4153 with G.L. Clifton*, 7 May 2003 (**GMDRC**1194!, **UCR**-164170!); • New York Mountains: growing in bottom of main drainage, just above main parking area/camp. Caruthers Canyon, Mojave National Preserve, California, San Bernardino Co., 35.224817, -115.303467, 1675 m elevation, at base of boulders in creek bottom, granite, alluvium, gravel, associates: *Salix exigua*, *Baccharis sergiloides*, *Carex alma*, *Ericameria cuneata*, *Pinus monophylla*, *J. M. André 9554 with T. La Doux*, *G.L. Clifton*, 5 May 2008 (**GMDRC**2793!, **SDSU**18622!); • Joshua Tree National Park, Little San Bernardino Mountains: Long Canyon, up side canyon approx. 400 m. west of main canyon drainage, California, Riverside Co., 34.063517, -116.443033, 1172 m elevation, south-facing slope, decomposed granite, alluvium, associates: *Juniperus californica*, *Ephedra nevadensis*, *Coleogyne ramosissima*, *Mentzelia involucrata*, *Calycoseris parryi*, *Eriophyllum confertiflorum*, *J. M. André 21088 with T. La Doux*, *R.B. Kelley*, 4 May 2011 (**GMDRC**5506!, **GMDRC**5507!, **UCR**0005646!); • Hualapai Mountains: along dry creekbed at Moss Wash trailhead, just below Wild Cow Campground, 4.0 mi. south of Hualapai Mtn Ranger Sta., Arizona, Mohave Co., 35.064183, -113.8672, 1836 m elevation, yellow pine - oak woodland, granite, alluvium, gravel, associates: *Pinus ponderosa*, *Quercus turbinella*, *Q. gambelii*, *Q. chysolepis*, *Ptelea trilobata*, *Symphoricarpos rotundifolius*, *Prunus virginiana*, *Eriogonum davidsonii*, *J. M. André 30870*, 29 May 2014 (**ASU**0307471!, **GMDRC**6806!); • Cerbat Mountains: west side of range c. 12 mi north of Kingman, 0.3 mi along faint dirt road north of Mineral Park Road, 2.7 mi east of Hwy 93, Arizona, Mohave Co., 35.35557, -114.17613, 1166 m elevation, upper alluvial fan, mixed, alluvium, gravel, associates: *Juniperus californica*, *Coleogyne ramosissima*, *Larrea tridentata*, *Salvia dorrii*, *Acamptopappus sphaerocephala*, *Krameria erecta*, *Camissoniopsis pallida*, *J. M. André 32653*, 24 April 2015 (**GMDRC**7523!, **UCR**-275600!); • Granite Mountains; UC GM Desert Research Center; upper Granite Cove in wash 0.1 mile south of Granite Cove Spring, 0.2 mile north of Staples cabin, California, San Bernardino Co., 34.786, -115.65863, 1338 m elevation, under granite boulder, sand, associates: *Acacia greggii*, *Ambrosia eriocentra*, *Prunus fasciculata*, *Eriophyllum wallacei*, *Plagiobothrys arizonicus*, *Descurainia pinnata*, *J. M. André 33209*, 4 April 2015 (**GMDRC**7681!, **RSA**0087609!, **UCR**0004260!); • Peninsular Ranges: along north side of Hwy 74 approx 1 mile east of Pinyon Flats, south facing slopes of Sugarloaf Mtn, California, Riverside Co., 33.583617, -116.437467, 1210 m elevation, granitic gravelly soils among boulders, granite, alluvium, gravel, associates: *Juniperus californica*, *Adenostoma sparsifolium*, *Arctostaphylos glauca*, *Cercocarpus betuloides*, *Mentzelia veatchiana*, *Phacelia fremontii*, *Saltugilia latimeri*, *J. M. André 41103*, 5 April 2019 (**GMDRC**11665!); • Peninsular Ranges: southeastern end of San Jacinto Mountains, along Hwy 74, 12.6 miles SW of Palm Desert (Hwy 111), 1.2 miles NNE of Sugarloaf Mtn, California, Riverside Co., 33.603767, -116.4199, 1081 m elevation, granitic boulders, granite, alluvium, gravel, associates: *Pinus monophylla*, *Rhus ovata*, *Ericameria linearifolia*, *Encelia actoni*, *Phacelia distans*, *Chaenactis fremontii*, *Acmispon argophyllus*, *Cryptantha lepida*, *J. M. André 42565*, 14 April 2020 (**GMDRC**12668!); • Peninsular Ranges; Anza Bench region: Hills north of Warner Springs, Indian Flats Campground of Cleveland National Forest along Road 9S05, California, San Diego Co., 33.349, -116.661, 1097 m elevation, slopes and shallow draws bordered by *Quercus agrifolia*, thin soils over granitic bedrock with extensive boulder outcrops and on sandy benches, associates: *Adenostoma sparsifolium*, *Ceanothus greggii*, *C. perplexans*, *Adenostoma fasciculatum*, *Gutierrezia sarothrae*, *Muhlenbergia rigens*, *Lonicera subspicata*, *Rosa californica* and *Rhus trilobata*, *S. Boyd 11034 with LeRoy Gross*, 4 May 2004 (**RSA**726843!, **UCR**0004357); • Kernville, California, Kern Co., 35.755333*, -118.425998*, 812 m elevation*, *T. S. Brandegee s.n.*, 13 May 1892 (**UC**79312!); Canon wash, 1 mi w of Morengo, California, San Bernardino Co., 34.047071*, -116.621009*, 898 m elevation*, *J. R. Bruff 99a*, 2 April 1928 (**RSA**699336!); • Local landmark: Cerbat Mountains, Chloride Quad, Arizona, Mohave Co., 35.464472, -114.179333, 1584 m elevation, Rocky Hillside; Slope Aspect: North, Slope Position: Lower Third; Vertical Slope Shape: Smooth; Horizontal Slope Shape: Smooth, *G. L. Clifton 14473*, 28 April 1986 (**PUA**32315(Card#64080)!); • Whitewater Canyon Rd. (exit from Interstate-10 ca. 2.5 mi. W of jct I-10 with State 62); near start of Angeles [Pacific] Crest Trail, California, Riverside Co., 33.99178*, -116.663304*, 610 m elevation, riparian woodland (through creosote bush scrub) along rocky sandy stream channel joining the main Whitewater wash, rocky, sandy, associates: *Encelia farinosa*, *Baccharis*, *Quercus*, *C. Davidson 5578 with B. Gustafson*, 7 April 1977 (**RSA**499703!); • Near Dos Palmas Spring, San Jacinto Mts, California, Riverside Co., 33.61841*, -116.424376*, 914 m elevation, *H. & M. Dearing 4851*, 29 March 1942 (**SBBG**6266!); • Rincon Mountains, Chimenea Canyon above Madrona Ranger Station, Arizona, Pima Co., 32.183772*, -110.593461*, 1219 m elevation, riparian forest in desert scrub, associates: *Quercus*, *Juglans*, *Fraxinus*, *Baccharis*, *Ambrosia*, *M. Fishbein 2013*, 15 April 1994 (**ARIZ**315946!); • South fork of San Joaquin river, California, Madera Co., 37.437614*, -119.239026*, 2621 m elevation, *H. M. Hall 650B with H. P. Chandler*, July 1900 (**UC**79530!); 0.5 west of Peg Leg monument along Henderson Canyon Road, Anza Borrego Desert State Park, California, San Diego Co., 33.3004, -116.314, 180 m elevation*, sandy wash, sandy wash, overlain with dry silty ash from 2003 fire above Coyote Canyon, associates: *Larrea tridentata*, *Atriplex lentiformis*, *Phacelia brachyloba*, *Melilotus indica*, *Palafoxia arida* var. *arida*, *Geraea canescens*, *Abronia villosa* var. *villosa*, *Antirrhynum coulterianum*, *Calycoseris parryi*, *Chaenactis artemisiifolia*, *L. Hendrickson 53 with L. Louise Jee*, 9 April 2004 (**SD**161807!); • San Felipe Valley. Cigarettes Hills. San Felipe Wildlife Area, California Department of Fish & Game property. 1.8 air miles W of SW intersection of State Hwy. 78 and County Rd S-2 and .7 mile N of hwy 78, on south side of prominent hill (2765), California, San Diego Co., 33.0963, -116.5064, 769 m elevation, decomposing pegmatite dike, coarse gravel and sandy soil, associates: *Agave deserti*, *Juniperus californica*, *Prunus fremontii*, *Ziziphus parryi*, *Ericameria brachylepsis*, *Eriogonum fasciculatum* var *polifolium*, *L. Hendrickson 3928*, 10 May 2009 (**BSCA**1213, **SD**214894!); 5 mi. se. of Nevada-Arizona border along Lime Kiln Canyon BLM rd. 242, Arizona, Mohave Co., 36.680548*, -114.009796*, 1000 m elevation, mixed desert shrub community, gravelly limestone soils, associates: *Quercus*, *Juniperus*, *L. C. Higgins 25212*, 6 April 2004 (**BRYV**0155702, **HSC**202913!, **KHD**00031415); • Lime Kiln Canyon, Virgin Mountains, Arizona, Mohave Co., 36.646315, -114.019191, 1250 m elevation, Pinyon, juniper, oak community, limestone soil., *L. C. Higgins 25402 with G. Green*, 4 May 2004 (BRYV0155701, **RENO**81684!, **UNM**0026372); • Arizona, Skull valley, Arizona, Yavapai Co., 34.504684*, -112.687251*, 1311 m elevation, *M. E. Jones 7028*, 28 April 1903 (**UC**78720!); • Arizona, Skull valley, Arizona, Yavapai Co., 34.504684*, -112.687251*, 1311 m elevation, *M. E. Jones s.n.*, 1 May 1903 (**POM**71271!); • Arizona, Skull valley, Arizona, Yavapai Co., 34.504684*, -112.687251*, 1311 m elevation, *M. E. Jones s.n.*, 1 May 1903 (**POM**71274!); • Pinal Mts. above road to Madera Peak on road to Signal Peak and Pinal Peak, Arizona, Gila Co., 33.2822*, -110.821*, 2384 m elevation*, upper south facing slopes, *D. Keil 4628*, 12 May 1969 (**ASU**69306!); • Little San Bernardino Mountains, ridge along Upper East Deception Canyon, Joshua Tree National Park, California, Riverside Co., 33.97936, -116.30985, 1319 m elevation, associates: *Yucca schidigera*, *Juniperus californica*, *Eriogonum wrightii nodusum*, *Peucephyllum schotii*, *T. LaDoux 3724 with E. Babich*, *N. Pietrasiak*, 21 April 2008 (**JOTR**00914!); 2 miles east of Banner on San Felipe Wash, California, San Diego Co., 33.083288*, -116.516252*, 773 m elevation, *K. McCully 92*, 17 May 1925 (**POM**97231!); • Traverse Ranges; San Bernardino Mountain region: Whitewater Canyon; Along Whitewater River drainage and adjacent slopes below Whitewater Visitor Center (Whitewater Trout Farm) in the vicinity of Bonnie Bell, California, Riverside Co., 33.95477, -116.64248, 525 m elevation, riparian woodland along water course to desert sage scrub on adjacent flats and slopes, *O. Mistretta 4627 with Duncan Bell*, *Jill Beckman*, *Joy England*, *Katie Kane*, *Jamie Hall*, *Chris McDonald*, *Lucila Reccia*, *Lonnie Rodriguez*, *April Sall*, *Tracy Tennant*, 12 April 2010 (**RSA**772061!); • Traverse Ranges; San Bernardino Mountain region: Whitewater Canyon; Along Whitewater River drainage and adjacent slopes below Whitewater Visitor Center (Whitewater Trout Farm), California, Riverside Co., 33.97538, -116.65119, 600 m elevation, riparian woodland along water course to desert sage scrub on adjacent flats and slopes, *O. Mistretta 4702a with Duncan Bell*, *Jill Beckman*, *Joy England*, *Katie Kane*, *Jamie Hall*, *Chris McDonald*, *Lucila Reccia*, *Lonnie Rodriguez*, *April Sall*, *Tracy Tennant*, 12 April 2010 (**RSA**771786!); • Northwest slope of Santa Rosa Mtns., California, Riverside Co., 33.555223*, -116.487153*, 2134 m elevation, dry banks, northwest slope, *P. A. Munz 15086*, 30 May 1937 (**BRYV**0155683, **RSA**0079225, **UC**662529!); • Pines to Palms Highway #74, 15 miles west of Palm Desert, California, Riverside Co., 33.581968*, -116.459557*, 1219 m elevation, *D. Myrick 833*, 30 April 1964 (**SBBG**28428!); • Colorado Desert, California, San Diego Co., 33.05*, -116.12*, m elevation, *C. R. Orcutt s.n.*, April 1889 (**UC**280510!); Walker Canyon Ecological Preserve: between Boulevard and Jacumba on the north side of Interstate 8, along arroyo bottom near stream, California, San Diego Co., 32.66306, -116.22333, 915 m elevation, Chaparral/desert transition, granitic substrates, associates: *Quercus cornelius mulleri*, *Adenostoma sparsifolium*, *Rhus ovata*, *Juniperus californica*, *Cylindropuntia ganderi*, *J. P. Rebman 8530 with Jeannie Gregory*, 17 April 2003 (**SD**159509, **UC**1787644!, **UCR**0004378); • San Jacinto Mountains, along the trail toward Spitler Pk from the Hurkey Crk camp to Bonita Vista Rd, California, Riverside Co., 33.6961*, -116.6392*, 1707 m elevation, along trail; chaparral & some yellow pine forest, *A. C. Sanders 6537*, 1 June 1986 (**DES**00030658, **OBI**131801, **SBBG**87639!, **UCR**0004196, **UNLV**23020); • Along FS road 22S82, east base of the Needles, approx. 3 miles from Pyles Camp., California, Tulare Co., 36.10939*, -118.484532*, 2419 m elevation, granitic sandy soils, *J. R. Shevock 5114*, 18 June 1976 (**LOB**100364!); • SW Imperial Co, near SE boundary of San Diego Co., In-Ko-Pah Mountains, access road to Valley of the Moon, California, Imperial Co., 32.639288*, -116.100194*, 1031 m elevation, transition area from scrub oak-yucca to diverse high desert scrub, steep N-facing bouldery drainage, rocky slopes, steep N-facing bouldery drainage; granitic outcrops and soils, mostly coarse particle size;, associates: *C. pterocarya* var. *cycloptera*, *C. p.* var. *purpusii*, *C. clevelandii*, *C. intermedia*, *Microsersis douglasii*, *Gilia caruifolia*, *Phacelia distans*, *Lotus scoparius*, *Quercus cornelius-muelleri*, *Yucca schidigera*, *Nolina parryi*, *Rhus ovata*, *Simmondsia chinensis*, *Acacia greggii*, *Encelia actoni*, *Salvia apiana*, *Cylindropuntia ganderi*, *C. wolfii*, *Ericameria brachylepsis*, and *Lupinus excubitus* var. *medius*, *D. Silverman 3964 with Jon Rebman*, 23 April 2001 (**JEPS**103093!, **SBBG**116573!); • Wash adjacent to and just west of jeep road, Rodriguez Canyon, ca. 2.0 miles southwest of Granite Mtn. peak., California, San Diego Co., 33.03111, -116.50361, 946 m elevation, wash adjacent to exposed, sparse desert scrub, sandy, gravelly soil, associates: *Prunus fremontii*, *Rhus ovata*, *Baccharis sergiloides*, *Quercus* sp., *M. G. Simpson 2790 with K. Hasenstab*, *M. Silveira*, *and L. Simpson*, 7 April 2007 (**SDSU**19296!); • Wash adjacent to and just west of jeep road, Rodriguez Canyon, ca. 2.0 miles southwest of Granite Mtn. peak., California, San Diego Co., 33.03111, -116.50361, 946 m elevation, wash adjacent to exposed, sparse desert scrub, sandy, gravelly soil, associates: *Prunus fremontii*, *Rhus ovata*, *Baccharis sergiloides*, *Quercus* sp., *M. G. Simpson 2794 with K. Hasenstab*, *M. Silveira*, *and L. Simpson*, 7 April 2007 (**SDSU**17573!); • Pacific Coast Trail, ca. 0.1 mile north of parking area at Hwy 74., California, Riverside Co., 33.56416, -116.57673, 1499 m elevation, beneath Adenostoma fasciculatum. Adjacent to open *Adenostoma sparsifolium - Adenostoma fasciculatum - Ceanothus greggii* scrub, coarse sand, associates: *Adenostoma sparsifolium*, *Adenostoma fasciculatum*, *Ceanothus greggii*, *M. G. Simpson 3080 with Lori Simpson*, 26 April 2009 (**SDSU**21885!); • Pacific Coast Trail, ca. 0.6 mile north of parking area at Hwy 74., California, Riverside Co., 33.56977, -116.57572, 1526 m elevation, side of trail. Open *Adenostoma sparsifolium - A. fasciculatum - Ceanothus greggii* scrub., coarse sand, associates: *Adenostoma sparsifolium*, *Adenostoma fasciculatum*, *Ceanothus greggii*, *M. G. Simpson 3085 with Lori Simpson*, 26 April 2009 (**SDSU**21647!); • Anza Borrego Desert State Park. Wash of Bitter Creek Canyon, ca. 1.0 mile north of Grapevine Mountain peak., California, San Diego Co., 33.13444, -116.46798, 739 m elevation, along base of canyon wall rocks of wash, open scrub of desert wash, gravelly sand, associates: *Agave deserti*, *Chenopodium* sp., *Encelia farinosa*, *Opuntia basilaris*, *Senegalia greggii*, *M. G. Simpson 3790 with Amanda Everett*, *Andy Siekkinen*, *Lee Ripma*, *Matt Newcomb*, 15 February 2014 (**SDSU**20519!); • Anza Borrego Desert State Park, Cool Canyon, ca. 1,000 m west-southwest of parking area at end of dirt road, ca. 1.8 km east-southeast of Granite Mountain peak., California, San Diego Co., 33.04362, -116.44427, 869 m elevation, desert succulent scrub, brown, sandy loam, associates: *Juniperus californica*, *Cylindropuntia ganderi*, *Prunus fremontii*, *Encelia farinosa*, *Bahiopsis parishii*, *M. G. Simpson 3795 with SDSU Taxonomy of California Plants Class*, 29 March 2014 (**SDSU**23021!); • Anza Borrego Desert State Park, Bitter Creek Canyon, ca. 2.3 kilometers southwest of Grapevine Canyon Road (dirt)., California, San Diego Co., 33.13402, -116.47022, 745 m elevation, wash of canyon, desert succulent scrub, silty, coarse sand, associates: *Prosopis glandulosa*, *Encelia farinosa*, *Chenopodium murale*, *Bromus rubens*, *M. G. Simpson 3800 with Makenzie*

E. Mabry, 3 April 2014 (**SDSU**23020!); • Anza Borrego Desert State Park, Culp Valley, along hiking trail at camping area., California, San Diego Co., 33.22376, -116.45312, 1033 m elevation, flat, coarse sand/fine gravel, organic material beneath, associates: *Rhus ovata*, *Ziziphus parryi var. parryi*, *Cylindropuntia ganderi* scrub, *M. G. Simpson 3856 with Makenzie Mabry & Andy Siekkinen*, 1 April 2015 (**SDSU**23271!); • Culp Valley, ca. 0.1 mile along dirt road, to parking lot at left, then 10 meters west of northern end of lot., California, San Diego Co., 33.22209, -116.45791, 1014 m elevation, desert transtion vegetation, brownish, gravelly sand, growing adjacent to boulder, associates: *Prunus fremontii*, *Ziziphus parryi* var. *parryi*, *M. G. Simpson 4186 with Jepson 2019 workshop members*, 14 April 2019 (**SDSU**22965!); • San Gabriel Mountains, east side of Cabin Canyon, c. 200 m north of canyon mouth, west of Aliso Cyn. Rd., 0.5 mi west of Angeles Forest Hwy, California, Los Angeles Co., 34.4169444, -118.0925, 1183 m elevation, shallow canyon bottom with flowing stream; chaparral dominant, associates: *Ceanothus leu.*, *Adenostoma f.*, *Quercus wis.*, *Prunus ili.*, *Eriodictyon tri*., with *Layia gla.*, *Phacelia fre.*, *Calyptridium mon*., *Penstemon cen.*, *Malacothrix gla.*, *Camissoniopsis hir.*, *Bromus tec.*, *Antirrhinum cou.*, *Cirsium occ.*, *Chaenactis gla*., etc, *R. G. Swinney 14663*, 12 May 2011 (**RSA**0091168!, **SDSU**22957!); • San Gabriel Mountains, 0.3–0.5 miles south of Aliso Canyon Road, 2 miles west of Angeles Forest Hwy., nameless cyn. To the east of Beartrap Cyn., California, Los Angeles Co., 34.42778, -118.11639, 1066 m elevation, Station Fire burn of 2009, shallow ravine and adj. slopes, chaparral, associates: *Adenostoma f.*, *Prunus i.*, *Lonicera su.*, *Rhus ar.*, *Cercocarpus b.*, *also w/ Opuntia ba.*, *Malacothamnus fr.*, *Lupinus bi*., *Camissonia s.*, *Uropappus*, *Mentzelia co.*, *Delphinium pat.*, *Phacelia fr.*, *Leptosiphon a*., etc, *R. G. Swinney 14845*, 26 May 2011 (**RSA**0092147!, **SDSU**22955!); • San Gabriel Mountains: Colby Ranch (Camp Colby), S end of Inspiration Canyon tr., in a N-flowing tributary of upper Coldwater Cyn., California, Los Angeles Co., 34.29861, -118.11361, 1226 m elevation, Station Fire burn of ‘09, canyon wih slopes; chaparral, coarse granite and fine brown loam, associates: *Ceanothus*, *Eriodictyon*, *Quercus*, *Pinus*, *Nicotiana*, *Eschscholzia*, *Phacelia*, *Adenostoma*, *Mimulus*, *Chaenactis*, *Keckiella*, *Calyptridium*, *Salvia*, *Galium*, *Penstemon*, *Argemone*, *Erhendorferia*, *Dendromecon*, *Eriogonum*, *Mentzelia*, *Solanum*, *R. G. Swinney 15440*, 7 July 2011 (**RSA**0091783!, **SDSU**22954!, **UCR**0004166!); • San Gabriel Mountains: Colby Ranch (Camp Colby), S end of Inspiration Canyon tr., in a N-flowing tributary of upper Coldwater Cyn., California, Los Angeles Co., 34.29861, -118.11361, 1226 m elevation, Station Fire burn of ‘09, canyon wih slopes; chaparral, coarse granite and fine brown loam, associates: *Ceanothus*, *Eriodictyon*, *Quercus*, *Pinus*, *Nicotiana*, *Eschscholzia*, *Phacelia*, *Adenostoma*, *Mimulus*, *Chaenactis*, *Keckiella*, *Calyptridium*, *Salvia*, *Galium*, *Penstemon*, *Argemone*, *Erhendorferia*, *Dendromecon*, *Eriogonum*, *Mentzelia*, *Solanum*, *R. G. Swinney 15442*, 7 July 2011 (**RSA**0091784, **SDSU**22946!, **UCR**0039547); • San Gabriel Mountains: Strawberry Peak summit (Chilao Flat)., California, Los Angeles Co., 34.28389, -118.12028, 1869 m elevation, Station Fire burn of 2009, entire summit burned; resprouting chaparral, associates: *Eriodictyon trichocalyx*, *E. parryi*, *Quercus wislizeni*, *Q. chrysolepis*, *Penstemon centranthifolius*, *Eriastrum densifolium*, *Ericameria nausiosa*, *Camissoniopsis hirtella*, *Bromus tectorum*, *B. carinatus*, *Eriophyllum confertiflorum*, *Cryptantha muricata*, *Garrya flavescens*, *Tauschia parishii*, *Eriogonum saxatile*, *Orobanche fasciculata*, *Sidotheca trilobata*, etc, *R. G. Swinney 15527*, 21 July 2011 (**RSA**0089514, **SDSU**22959!, **UCR**0004165); • San Gabriel Mts., n. e. boundary ridge top of San Dimas Experimental Forest, c. 0.14 miles s.w. of summit at far s.e. end of ridge, 1.7 air miles w. of Cow Cyn. Saddle at Glendora Ridge Rd. to 1.8 land miles ESE along SDEF boundary ridge to ridge top at 5595 ft. (1706 m.), and east via level ridge connection to ridge top at 5560 ft., 04 air miles NNE of Sunset Pk. summit. This is the highest elev. within SDEF, Mt. Baldy Quad, California, Los Angeles Co., 34.209722, -117.695278, 1695 m elevation, Ridge top, chaparral, Big Cone Spruce/*Quercus* woodland, associates: *Pseudotsuga macrocarpa*, *Quercus wislizeni subsp. frutescens*, *Q. chrysolepis*, *Ceanothus crassifolius*, *Eriogonum fasciculatum* subsp. *foliolosum*, *Bromus tectorum*, *R. G. Swinney 18319*, 4 May 2016 (**SDSU**23973!); • North of Azusa, WCA's Azusa Foothills Open Space, ridgetop overlooking mouth of San Gabriel Cyn., within 50 meters of Vasquez Ranch Flagpole, last burned 2014 - Cobly Fire, 0.55 air miles n. of jct. of Sierra Madre Ave. and Hilltop Dr., Azusa Quad 7.5', California, Los Angeles Co., 34.156355, -117.904528, 450 m elevation, ridge top, coastal sage scrub and chaparral surrounding previously slightly-disturbed area, granitic-loam, associates: *Malosma laurina*, *Bromus diandrus*, *Encelia farinosa*, *Artemisia californica*, *Hirschfeldia incana*, *Malacothrix saxatilis* var. *tenuifolia*, *R. G. Swinney 24723A*, 5 May 2021 (**SDSU**25595!, **UCR**0164808); • San Bernardino Mountains: unnamed ridgetop (7,582') and adjacent slope just W of Heart Bar Peak and SE of Cienaga Seca Creek., California, San Bernardino Co., 34.1667, -116.775, 2222 m elevation, ridgetop recently bulldozed for firebreak; adjacent N and W slopes w/ *Quercus chrysolepis* and *Pinus jeffreyi*, etc., *Quercus chrysolepis* and *Pinus jeffreyi*, etc., *S. D. White 13324 with Marissa Caringella*, 24 July 2009 (**RSA**752962!, **UC**1949977, **UCR**0004334, **UCSB**029502); • Peninsular Ranges: Santa Rosa Mountains, California, Riverside Co., 33.539*, -116.457*, 2310 m elevation, *R. S. Woglum 3072*, 12 June 1941 (**RSA**611564!); • San Bernardino Mountains: Unnamed canyon and ridgeline immediately SW of Cienega Seca (Blue Sky Meadow), California, San Bernardino Co., 34.1833, -116.725, 2476 m elevation, yellow pine forest with somes areas of pinyon/juniper woodland, *J. M. Wood 948 with Dustin Ray*, 18 June 2009 (**RSA**752329!); • San Bernardino Mtns., Santa Ana River, unnamed canyon and ridgeline E of Wildhorse Canyon, N of Hwy 38, California, San Bernardino Co., 34.17083, -116.8, 2100 m elevation, dry canyon wash, riparian woodland and adjacent uplands, *J. M. Wood 1013 with Dustin Ray*, 30 June 2009 (**RSA**750733!); • Borrego Palm Canyon, California, San Diego Co., 33.276836*, -116.426169*, 322 m elevation, *F. Youngberg 103*, 11 April 1935 (**POM**209514!).

Discussion

Cryptantha acrimuricata is morphologically distinctive, but is an obvious close relative of *C. muricata*, given its similarity in fruiting calyx shape (ovoid), style length (typically longer than the nutlets), nutlet number (four per fruit), nutlet shape (ovate, typically with a dorsal ridge, this sometimes obscure), and nutlet sculpturing pattern (tuberculate to muricate). As noted by Johnston (1925), *C. muricata* has the edges of the nutlets thickened to form a "beaded" or "toothed" margin (Fig. 4), this feature also seen in *C. acrimuricata* (Fig. 2).

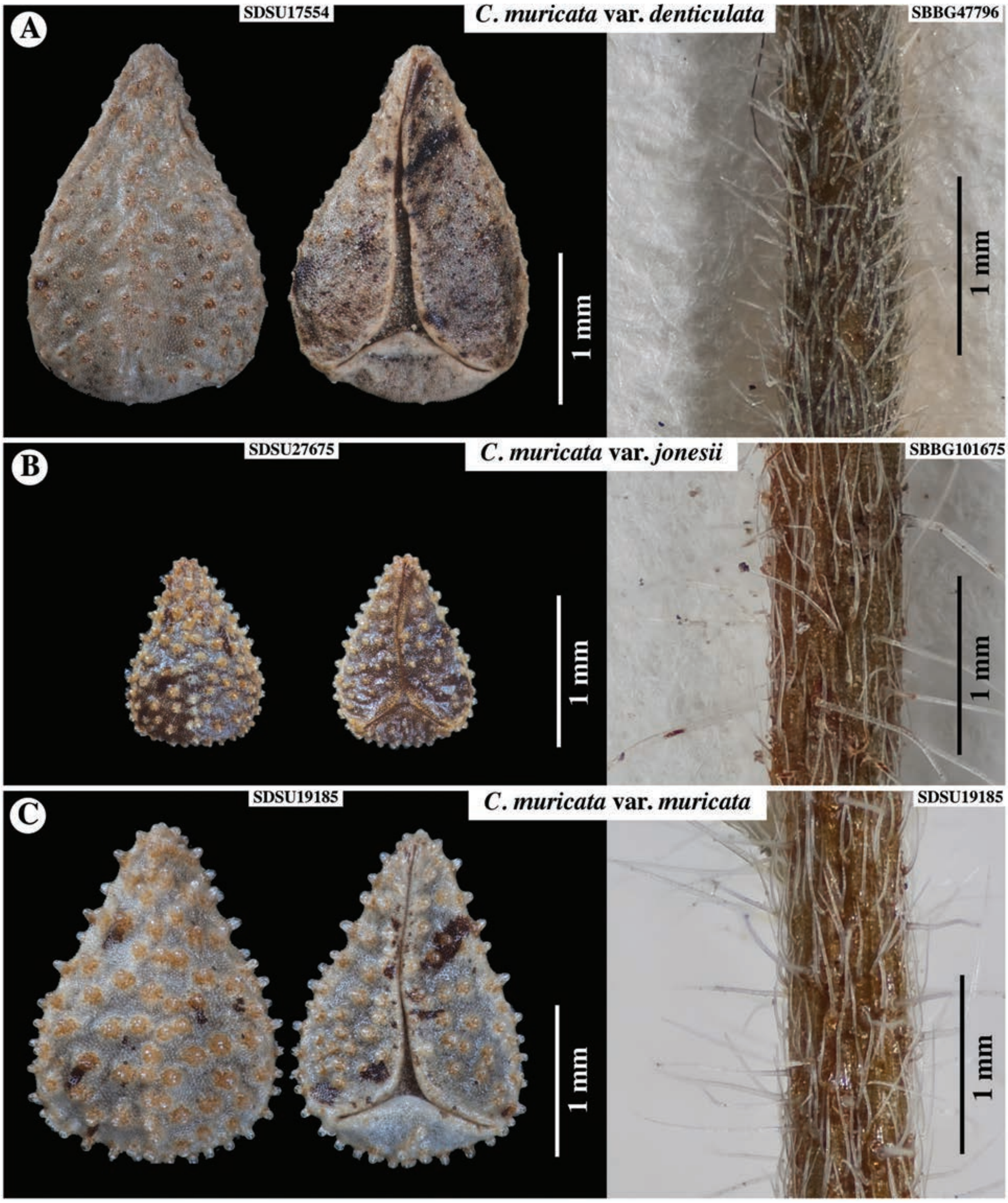


Figure 4. Nutlets (dorsal view at left, ventral at right) and stem morphology of the three recognized varieties of *C. muricata*, series *Muricatae* **A** *Cryptantha muricata* var. *denticulata* **B** *Cryptantha muricata* var. *jonesii* **C** *Cryptantha muricata* var. *muricata*. Accession numbers of specimens sampled indicated. Note variation in nutlet sculpturing and stem vestiture that is strigose and hispid.

We confirmed that the type specimens of the three heterotypic varietal synonyms of *C. muricata* (Table 1) did not conform to the morphology of *C. acrimuricata* and thus feel confident that our new species had not been previously named. We considered treating *C. acrimuricata* as a fourth variety of *C. muricata*.

However, we felt justified in treating it as a separate species for two reasons. First, it is different from the other species in two major features: stem vestiture and nutlet sculpturing, characters which, based on our observations, appear to be stable. Second, we have no evidence that it is more closely related to one or more of the varieties of *C. muricata* than to other species of the complex (see below). In fact, future studies may support elevation of one or more varieties of *C. muricata* to species status (see below). Thus, we think it more stable to recognize this unique taxon as its own species, pending more detailed molecular phylogenetic studies. *Cryptantha muricata*, with its three currently recognized varieties, is a taxonomically challenging complex. Preliminary data indicate that one or more of the currently recognized varieties—*C. m.* var. *denticulata* (Greene) I.M.Johnst. (Fig. 4A), *C. m.* var. *jonesii* (A.Gray) I.M.Johnst. (Fig. 4B), and *C. m.* var. *muricata* (Fig. 4C)—may eventually be elevated to species status or split into more than one taxon. The complex is currently under study by members of the Amsinckiinae Working Group (2024).

The distributions of *Cryptantha acrimuricata* and of the three varieties of *C. muricata* show some discrete geographic clustering but also overlap in some regions. *Cryptantha acrimuricata*, as cited before, occurs in the eastern part (escarpment) of the Peninsular Ranges of California and Baja California, Mexico, in higher elevations of the Mohave and Sonoran Deserts of California and Arizona, and in localities of the eastern and central Transverse Ranges and southern Sierra Nevada of California (Fig. 3). *Cryptantha muricata* var. *jonesii* is most common in the western part of the Peninsular Ranges westward to the coast, as well as in parts of the Transverse Ranges. *Cryptantha muricata* var. *muricata* is most common in the western part of the Transverse Ranges, Central Coast Ranges, and northward to the San Francisco Bay area of California. *Cryptantha muricata* var. *denticulata* is mostly restricted to the southern and central Sierra Nevada but also has populations in the western Transverse Ranges (Fig. 3).

We believe *Cryptantha acrimuricata* should be classified in series *Muricatae* of Johnston (1925). This subgeneric group was diagnosed by him as "Nutlets 4, verrucose or coarsely tuberculate, triangular-ovate, decidedly homomorphous, back obtuse and bearing a suggestion of a medial ridge, with sides evidently angles and beaded; style usually surpassing the nutlets though rarely only equally them" (Johnston 1925: 69–70). Another possible feature that could be added as a diagnostic feature of this series is a style extending beyond the nutlets in fruit. Series *Muricatae* originally included only *C. muricata*, with its currently recognized three varieties. Later, Johnston (1939) suggested that *C. clokeyi* I.M.Johnst. (Fig. 5A) be placed in *Muricatae*. Subsequently, Simpson and Rebman (2013: 41) stated that their newly described *C. martirensis* M.G. Simpson & Rebman (Fig. 5B) "...may be tentatively placed in section *Muricatae*; however, molecular phylogenetic studies are needed to verify the monophyly of this group." Indeed, the subsequent molecular phylogenetic analyses of Simpson et al. 2017b and Mabry and Simpson 2018 confirmed the composition of three members of series *Muricatae*, as it is delimited here (Table 1). In both studies *C. muricata* var. *muricata* is sister to *C. clokeyi*, with these two sister to *C. martirensis*, all with strong support.

One species of *Cryptantha* whose relationships has been a bit of a mystery is *C. hooveri* I.M.Johnst. In the protologue for *Cryptantha hooveri*, Johnston (1937: 24) stated "I can suggest no close relative for this very distinct species."

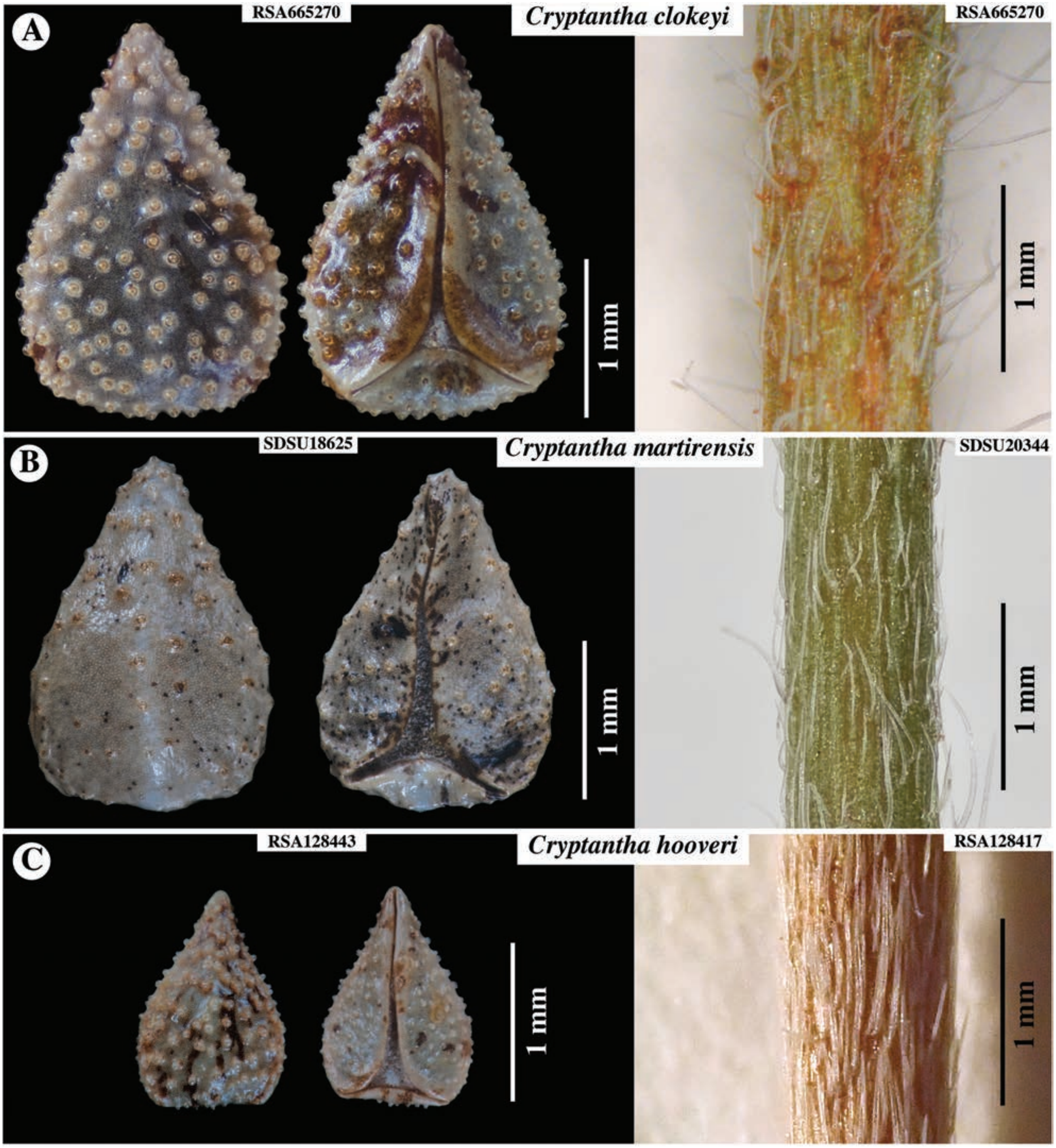


Figure 5. A, B Nutlets (dorsal view at left, ventral at right) and stem morphology of three additional *Cryptantha* species of series *Muricatae* **A** *Cryptantha clokeyi* **B** *Cryptantha martirensis* **C** *Cryptantha hooveri,* tentatively placed in series. Accession numbers of specimens sampled indicated.

Cryptantha hooveri does have a number of unique features, such as clustered, head-like cymes and bracteate flowers, the bracts very narrow ("thread-like"). Subsequently, however, Johnston (1939: 388) suggested that *Cryptantha clokeyi* is "perhaps most closely related to *Cryptantha hooveri* Johnst. of the Sierran foothills of central California." *Cryptantha hooveri* does resemble *C. clokeyi* in having ovate to deltate nutlets with a similar, tuberculate sculpturing (Fig. 5C), and it does have the elongate style, extending beyond the nutlets in fruit, characteristic of series *Muricatae*. However, aside from its unique features, *C. hooveri* differs from *C. clokeyi* in having calyces and nutlets about half the size of the latter species (Fig. 5B, C). Unfortunately, *C. hooveri* is presumed extinct (CNPS Inventory 2024), having been last collected in 1939 and not observed since.

These three additional members of series *Muricatae*—*C. clokeyi*, *C. hooveri*, and *C. martirensis*—are somewhat restricted in range (not mapped here), occurring, respectively, in regions of the Mohave Desert and Transverse Ranges, in the Central Valley, and in the San Pedro Martir mountains of Baja California, Mexico. They are not sympatric with *C. acrimuricata* or varieties of *C. muricata*.

The subgeneric classification of *Cryptantha* is an ongoing project of research (Amsinckiinae Working Group 2024). Although most of Johnston's series do not correspond to monophyletic groups (Mabry and Simpson 2018), series *Muricatae*, as expanded here, does and should be accepted (Table 1). Interestingly, from the aforementioned molecular phylogenetic studies of Simpson et al. 2017b and Mabry and Simpson 2018, series *Muricatae* itself appears to be sister to a modified series *Maritimae* (Johnston 1925), named after *Cryptantha maritima*. The two series, *Muricatae* and *Maritimae*, were together termed the "*Maritimae* clade" in those studies. Further studies are needed to refine these relationships. It seems clear, however, that based on the phylogenetic studies to date, our new species should be placed in series *Muricatae* of the *Maritimae* clade, the latter a monophyletic group separate from the bulk of the genus *Cryptantha*, which may in the future warrant a formal name (Simpson et al. 2017b, Mabry and Simpson 2018).

Given the evidence for the relationships of *Cryptantha acrimuricata*, we here present a key to our accepted members of *Cryptantha* series *Muricatae* (tentatively including *C. hooveri*).

Key differentiating *Cryptantha* taxa within series *Muricatae* (See Figs 1, 2, 4, 5 for images of nutlets and other diagnostic features)

1 Cymules tightly clustered, head-like, only lowest flowers in each cymule developing fruit; flower bracts mostly present, filiform in shape .... ***C. hooveri***
– Cymules elongate at maturity, most flowers developing fruit; flower bracts absent **2**
2 Calyx 5–9(–10) mm long; nutlets without dorsal ridge, (1.8–)2.4–2.8(–3) mm long .... ***C. clokeyi***
– Calyx 2–5 mm long; nutlets with dorsal ridge, 1.1–2.2 mm long **3**
3 Corolla limb showy, 3–8 mm wide .... ***C. muricata* var. *muricata***
– Corolla limb generally inconspicuous, 1–2(3.5) mm wide **4**
4 Nutlet tubercles conic in shape, very densely spaced, often whitish, intervening surfaces often shiny, appearing shellacked; stems mostly strigose, occasionally also spreading hispid, appearing whitish to gray-green in color .... ***C. acrimuricata***
– Nutlet tubercles terete to rounded in shape, less densely spaced, brownish, intervening surfaces generally not shiny; stems strigose and densely hispid, generally green or yellow-green in color **5**
5 Nutlets 1.1–1.3(1.9) mm long, muricate, tubercles generally elongate .... ***C. muricata* var. *jonesii***
– Nutlets 1.8–2.2 mm long, tuberculate, tubercles generally low, rounded..... **6**

6 Primary stem axis 11–53 cm long, not obviously different from secondary axes; inflorescence cymules, including stalk, 12–140 mm long .... ***C. muricata* var. *denticulata***

– Primary stem axis 35–68 cm long, prominent, elongate, virgate; inflorescence cymules, including stalk, 5–10 mm long .... ***C. martirensis***

Conclusions

Research on the taxonomy and phylogenetic relationships of *Cryptantha* and other members of the "Popcorn Flowers" (subtribe Amsinckiinae) is an ongoing project of the Amsinckiinae Working Group (2024). We point out that new species of *Cryptantha* continue to be discovered; in addition to this new taxon, five new species and one new variety have been described in the last 11 years. *Cryptantha acrimuricata* was originally recognized as a distinct form from the study of herbarium specimens and subsequently from field collections. The majority of herbarium records of this new species had been housed in herbarium cabinets for years, most identified as *C. muricata*. As we have emphasized before, the discovery of this new species highlights the need for continued field collections of plant specimens, their storage and databasing in herbaria, and the study of those specimens by scientific experts. There are undoubtedly many more species yet to be named, some lying in herbarium collections, waiting to be discovered (Bowdler 2010).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Author contributions

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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

Xanthophytum antoanense (Rubiaceae, Ophiorrhizeae), a new species from Vietnam

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Abstract

Xanthophytum antoanense is described as a new species endemic to Central Vietnam. It is morphologically closest to *X. capitatum* in having setose hairs on the abaxial leaf surface and a pedunculate head-like inflorescence but differs from the latter by a number of characteristics: shorter stem, 3-lobed stipules, narrowly lanceolate leaf blades with a cuneate-oblique base and 20–22 pairs of secondary veins, 3.5–4.5 cm long peduncle, spatulate calyx lobes, larger corollas with a 5–5.4 mm long tube and 2.4–3 mm long lobes, and an apically hairy style. A detailed description, an illustration, and information on distribution, ecology and phenology, and a provisional assessment of the conservation status of the new species are provided.

Key words: An Toan Nature Reserve, Central Vietnam, endemic, head-like inflorescence, indumentum, setose

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Introduction

Xanthophytum was initially proposed as a genus of the Rubiaceae by Blume (1823) but was only validly described in his subsequent work (Blume 1826). Its taxonomic position varied according to authors, being assigned to different tribes over time, such as Pomazoteae (Bremekamp 1952), Hedyotideae (Robbrecht 1988), and either Hedyotideae or Ophiorrhizeae (Tange 1995, published 1996). More recently, it has been placed in Ophiorrhizeae (Bremer and Manen 2000). Most recent molecular phylogenetic analyses confirm its placement in Ophiorrhizeae (Razafimandimbison and Rydin 2019, 2024). The genus was revised by Axelius (1990), who recognized 30 species. Later, Tange (1995 [published 1996]) asserted that *Myrioneuron borneense* Stapf (Stapf 1894) and *Siderobombyx kinabaluensis* Bremek. (Bremekamp 1947) were synonymous and should be included in *Xanthophytum*, based on their distinctive small brown seeds with tuberculate exotesta cell thickenings and ferruginous hairs. Consequently, he reduced the monospecific genus *Siderobombyx* to a synonym of *Xanthophytum*. Since the combination *X. borneense* (Valeton) Axelius was already established (Axelius 1990), he provided the new combination *X. kinabaluense* (Stapf) Tange for this species. However, the correct name should be *X. kinabaluense* (Bremek.) Tange, as the epithet was originally used by Bremekamp (1947). Additionally, he described a new species, *X. bullatum* Tange, from Sarawak, Malaysia. Currently, the genus comprises 32 accepted species distributed across tropical and subtropical Asia to the Southwest Pacific (POWO 2024).

Prior to this study, five species of *Xanthophytum* had been documented in Vietnam (Axelius 1990; Pham-Hoang 2003; Chen and Taylor 2011): *X. attopevense* (Pierre ex Pitard) H.S.Lo (Lo 1986; Pitard 1922), *X. balansae* (Pitard) H.S.Lo (Lo 1986; Pitard 1922), *X. johannis-winkleri* Merrill (Merrill 1937), *X. kwangtungense* (Chun & F.C.How) H.S.Lo (Chun and How 1939; Lo 1986), and *X. polyanthum* Pitard (Pitard 1922). Notably, the distribution of *X. attopevense* and *X. johannis-winkleri* in Vietnam remains uncertain. The collection *d'Alleizette s.n.*, June 1909 (P) from Nha Trang, was provisionally assigned to *X. attopevense* and may represent an unknown species (Axelius 1990). Meanwhile, *X. johannis-winkleri* was reported by Pham-Hoang (2003) to occur in Nha Trang, but no vouchered specimens were included; this record is likely followed by POWO (2024). Axelius (1990) documented this species' distribution in West Borneo, which is considerably disjunct from mainland Southeast Asia. Given this context, these two species should be excluded from the flora of Vietnam until their distribution in the country is reliably confirmed.

During our botanical inventory at An Toan Nature Reserve in Central Vietnam in May 2023, we encountered a *Xanthophytum* plant exhibiting a striking red ferruginous indumentum on its stem, leaves, and head-like inflorescence. Detailed morphological examination confirmed that it represents a new species, which we describe below.

Materials and methods

The studied material was collected from Binh Dinh Province, Central Vietnam. Specimens were sampled and processed using methods described by the Royal Botanic Gardens, Kew (Bridson and Forman 1999). Herbarium acronyms follow Thiers (2024). Detailed photographs and the description of taxonomically important characters of the new species were based on fresh material. Taxonomic identification was based on vegetative and reproductive morphological characters following the aforementioned literature, primarily Axelius (1990) and Chen and Taylor (2011).

Taxonomic treatment

Xanthophytum antoanense Luu, H.C.Nguyen, X.B.Nguyen-Le & Q.D.Nguyen, sp. nov.

urn:lsid:ipni.org:names:77354340-1
Fig. 1

Type. Vietnam • Binh Dinh Province, An Lao District, An Toan Commune, An Toan Nature Reserve, coordinates 14°31'31"N, 108°42'48"E, 838 m elevation, 17 May 2023, Nguyen Le Xuan Bach, Nguyen Quoc Dat, Nguyen Hieu Cuong *BN1015* (Holotype: SGN!, barcode SGN006396).

Diagnosis. The new species is morphologically closest to *X. capitatum* Valeton but differs from the latter by its 3-lobed (vs. unlobed) stipules, narrowly lanceolate (vs. oblong to obovate) leaf blades with a cuneate-oblique (vs. symmetrically cuneate to attenuate) base and 20–22 (vs.11–16) pairs of secondary

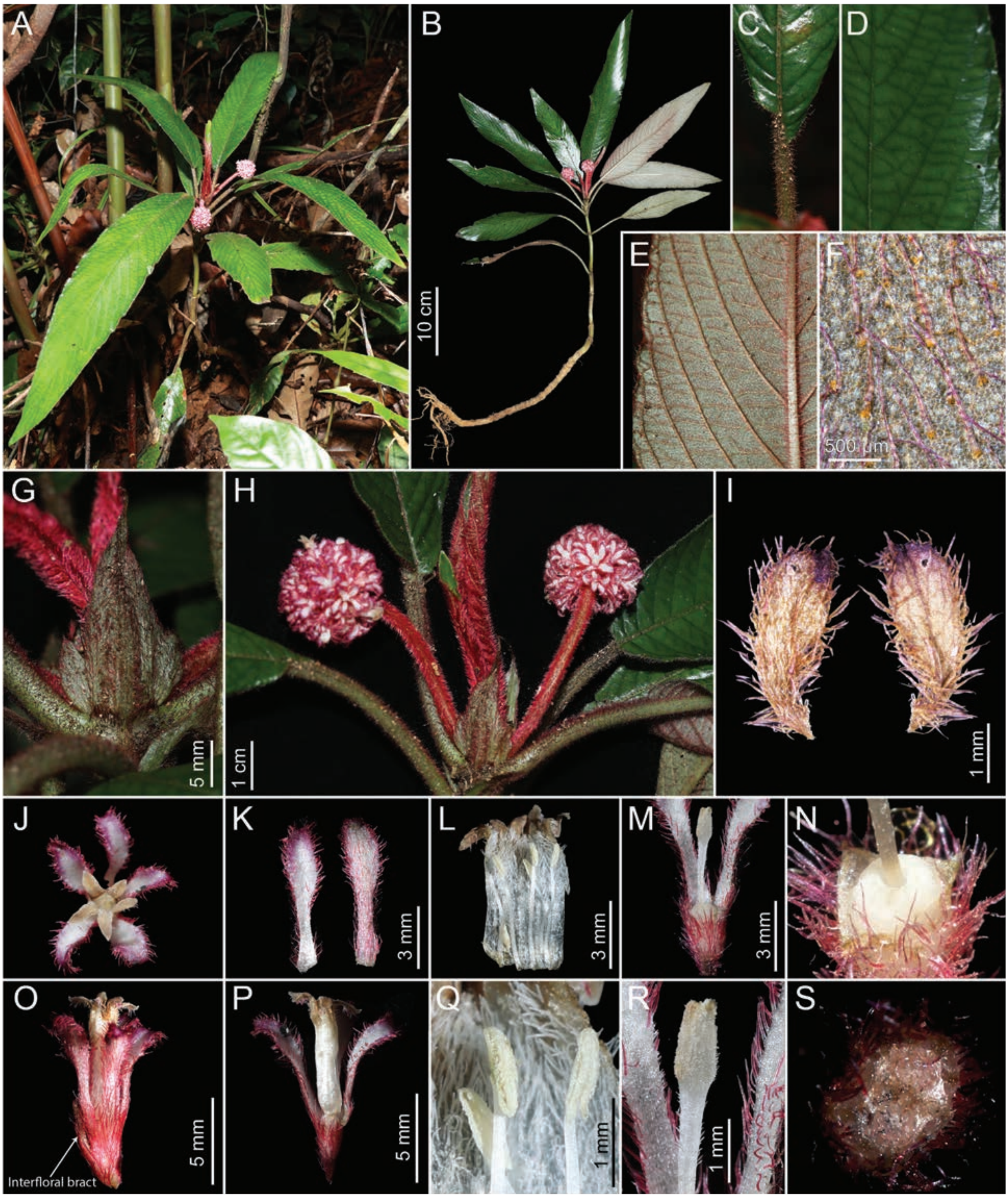

Figure 1. *Xanthophytum antoanense* **A** plant in situ **B** whole plant **C** leaf base **D** leaf, adaxial surface **E** leaf, abaxial surface **F** setose hairs on abaxial leaf surface (dried) **G** stipule **H** inflorescences **I** bracts (dried) **J** flower, top view **K** calyx lobes **L** opened corolla showing stamens **M** pistil **N** ovary, disc and base of style **O** flower, side view, with an interfloral bract (arrow) **P** corolla and calyx, some calyx lobes removed **Q** anthers **R** stigma (corolla removed) **S** cross-section of ovary.

veins, 3.5–4.5 (vs. 0.5–3) cm long peduncle, spatulate (vs. bluntly triangular) calyx lobes, larger flowers with a 5–5.4 (vs. c. 1.8) mm long corolla tube and 2.4–3 (vs. c. 0.7) mm long corolla lobes, and an apically hairy (vs. glabrous) style.

Description. Monocaul dwarf shrublet, sub-herbaceous, to 50 cm tall. ***Stems*** densely hairy, hairs septate, red, c. 1 mm long. ***Leaves*** simple, opposite, decussate;

petiole 4–6 cm long, c. 0.35 cm in diameter, densely hairy with hairs septate, red, c. 1.5 mm long; ***lamina*** elongate-lanceolate, 13–24 cm long, 3–4.5 cm wide, adaxially green, glabrous, abaxially gray, densely hairy, hairs setose, red, c. 1.5 mm long; base cuneate-oblique, apex acute; ***venation*** pinnate, midrib prominent on both surfaces, adaxially sparsely and abaxially densely hairy, hairs c. 1.5 mm long, secondary veins 20–22 pairs, weakly brochidodromous, tertiary veins abaxially prominent. ***Stipules*** 1.7–2.5 cm long, 1.2 cm at widest, ovate, acuminate, slightly 3-lobed, abaxially densely hairy, hairs septate, red, c. 1.5 mm long. ***Inflorescences*** axillary, pseudo-terminal heads, erect then nodding, heads c. 2 cm in diameter, many-flowered; ***peduncles*** 3.5–4.5 cm long, 0.2–0.3 cm in diameter, densely hairy, hairs septate, red, c. 1.3 mm long. ***Bracts*** oblanceolate, 3.0–3.2 mm long, 1.1–1.3 mm wide, white, apically red-violet, ciliate, abaxially densely hairy, hairs septate, red, c. 1 mm long. ***Interfloral bracts*** linear, c. 3.5 mm long, 0.25 mm wide, white, abaxially densely hairy, hairs septate, red, c. 0.6–0.8 mm long. ***Flowers*** bisexual, probably heterostylous, sessile, c. 1.1 cm long. ***Calyx*** 5-lobed, lobes spatulate, white, apically red, 7–8 mm long, c. 1.6 mm at widest, adaxially glabrous, abaxially densely hairy, hairs septate, red, c. 1 mm long. ***Corolla*** white, turning brown, tubiform with spreading lobes; ***tube*** 5–5.4 mm long, 1.2–1.4 mm in diameter, outside glabrous, inside densely white tomentose on upper ¾, hairs 0.4–0.5 mm long; ***lobes*** 5, 2.4–3 mm long, 0.7–1 mm at widest, oblong-lanceolate, acute, outside white to red setose with 0.5–0.6 mm long stiff hairs, inside papillose. ***Stamens*** 5, inserted at corolla base, 5.3–5.5 mm long; filaments c. 5 mm long, glabrous; anthers c. 1 mm long, dorsifixed, longitudinally dehiscent. ***Pistil*** 4.8–5.0 mm long; ***disc*** white, hemispherical, c. 0.5 mm high; ***ovary*** 2-celled, c. 2 mm high, 1.5 mm wide, densely red septate hairy; ***ovules*** numerous on a globose, axile placenta in each cell; ***style*** 2.7–2.8 mm long, gradually thickened towards the apex, sparsely hairy on upper half; ***stigma*** 2-lobed, lobes lanceolate, with obtuse apex, c. 1.3–1.4 mm long. ***Fruit*** unknown.

Etymology. The species epithet is derived from the location where the new taxon was discovered.

Vernacular name. *Hoàng cành An Toàn* (Vietnamese).

Phenology. Flowering observed in May; fruiting is unknown.

Distribution and ecology. The species is known only from An Toan Nature Reserve (Binh Dinh Province, Vietnam). It grows on moist fertile soils in lower montane evergreen forests at elevations around 850 m. The forest is dominated by Rubiaceae, Fagaceae, Lauraceae, Myrtaceae, Clusiaceae, and Fabaceae.

Preliminary IUCN conservation status. Data Deficient (IUCN Standards and Petitions Subcommittee 2024). The new species appears to be rare and was discovered in a small population. Its actual distribution and population size cannot be assessed at present, but the species is likely to occur in adjacent forests in Gia Lai and Quang Ngai Provinces. Further surveys are necessary to determine its precise conservation status.

Taxonomic notes. Axelius (1990) identified ferruginous indumentum as a synapomorphy for *Xanthophytum* species. Despite variations in color and density among species, the indumentum generally consists of two kinds of hairs: multicellular (septate) and unicellular. Septate hairs are found on vegetative parts and the exterior of the calyx and corolla, while unicellular hairs are located inside the corolla. These hairs are further classified into four types, one of which is setose hairs that are characterized as stiff, ferruginous, approximately 0.5 mm long, entirely septate with thick, smooth cell walls. Confined to vegetative parts, setose hairs have an upper part filled with a reddish substance and a swollen basal cell that protrudes from the leaf surface. To date, only two *Xanthophytum* species, *X. capitatum* and *X. setosum* Axelius (Axelius 1990), have been reported to possess setose hairs on their leaves. Therefore, our new taxon represents the third species in this group. Its setose hairs are up to 1.5 mm long, three times as long as those in the other species.

In *Xanthophytum*, flower morphology varies across species, some species having heterostylous flowers and others having homostylous flowers, with different placements of stamens and stigma, as well as varying hair-ring widths inside the corolla. However, many species remain undocumented due to lack of flowering material (Axelius 1990; Chen and Taylor 2011). According to Axelius (1990), in homostylous species with narrow hair-rings, anthers are positioned at the level of the ring with the stigma positioned just above the ring; for those with broad hair-rings, anthers are positioned at the ring's upper margin with the stigma clearly above the hair-ring. Most heterostylous species with narrow hair-rings have the anthers positioned at the level of the ring and the stigma positioned clearly above it, while species with broad hair-rings show more variation: the stigma can be positioned above or at the level of the ring, and anthers in brevistylous flowers may be above, at, or below the hair-ring, whereas in longistylous flowers, anthers are usually at the level of the ring. Our specimen, with a broad hair-ring, has the anthers at the upper part and the stigma at the lower part of the ring, similar to brevistylous flowers in other species like *X. cylindricum* Axelius (Axelius 1990). We thus assume our species is heterostylous, and our studied specimen is likely brevistylous, as we have not encountered longistylous flowers.

Xanthophytum antoanense is morphologically closest to *X. capitatum* (Valeton 1910), sharing the presence of setose hairs on the abaxial leaf surface and a pedunculate head-like inflorescence. However, the two species can be distinguished by key morphological characteristics as outlined in the diagnosis. Additionally, *X. antoanense* differs in having ovate, slightly 3-lobed and 1.7–2.5 cm long stipules (vs. triangular to ovate and c. 0.7 cm long in *X. capitatum*), 4–6 (vs. c. 3.5) cm long petioles, larger flower heads (c. 2 vs. c. 1.5 cm in diameter), adaxially glabrous and 7–8 mm long calyx lobes (vs. pubescent and c. 0.6 mm long), oblong-lanceolate (vs. triangular) corolla lobes, and brevistylous flowers with 5.3–5.5 (vs. c. 2) mm long stamens and a 2.7–2.8 (vs. c. 1.4) mm long style. Furthermore, the corolla tube of brevistylous flowers in *X. antoanense* is densely hairy on the upper three-quarters of the inside, whereas in *X. capitatum*, it has a c. 0.6 mm high ring of hairs in the upper part of the tube.

Xanthophytum setosum is easily distinguishable from the new taxon as it has a paniculate inflorescence. It further differs from the new species in having smaller leaf blades (7–16 cm long in *X. setosum* vs. 13–24 cm long) with 12–19 (vs. 20–22) pairs of secondary veins, shorter petioles (≤ 4 vs. 4–6) cm long, c. 1 cm long and unlobed (vs. 1.7–2.5 cm long and 3-lobed) stipules, minute (vs. c. 3.5 mm long) bracts, an adaxially densely pubescent (vs. glabrous) calyx with bluntly triangular and c. 1 mm long (vs. spatulate and 7–8 mm long) lobes, smaller brevistylous flowers (longistylous flowers unknown) with c. 1.8 (vs. 5–5.4) mm long corolla tube and c. 1.2 (vs. 2.4–3) mm long corolla lobes, shorter stamens (c. 2.8 vs. 5.3–5.5 mm long), and a c. 1.2 mm long and glabrous (vs. 2.7–2.8 mm long and apically hairy) style. Finally, the corolla tube in *X. antoanense* is densely hairy on the upper three-quarters of the inside and

Table 1. Key morphological differences between *Xanthophytum antoanense* and its closest congeners (based on Axelius 1990; Chen and Taylor 2011).

Characteristics	***X. antoanense***	***X. attopevense***	***X. capitatum***	***X. setosum***
Indumentum on stem	septate	sericeous to pilose	septate and setose	septate and setose
Stipules	ovate, 1.7–2.5 cm long, 3-lobed, hairs septate	ovate, c. 1.5 by 0.8 cm, unlobed, hairs sericeous or pilose to glabrescent	triangular to ovate, 0.7 cm long, unlobed, hairs septate	lanceolate, triangular or ovate, c. 1 cm long, unlobed, hairs septate and setose
Leaf blade	13–24 × 3–4.5 cm, narrowly lanceolate, abaxially with dense red setose hairs, base cuneate-oblique	11–20 × 3–5 cm, broadly lanceolate to oblong, abaxially with sericeous hairs, base cuneate to attenuate	8–18.5 × 2.5–7 cm, oblong to obovate, abaxially with setose hairs, base cuneate to attenuate	7–16 × 2.5–6.6 cm, lanceolate to oblong, abaxially with setose hairs, base cuneate to attenuate
Leaf secondary veins	20–22 pairs	20–24 pairs	11–16 pairs	12–19 pairs
Petioles	4–6 cm long, hairs septate	2 cm long, hairs sericeous	3.5 cm long, hairs setose	≤4 cm long, hairs setose
Inflorescence	head-like, heads 2 cm in diameter	head-like, heads c. 1 cm in diameter	head-like, heads ≤1.5 cm in diameter	paniculate
Peduncles	3.5–4.5 cm long, hairs septate	≤1.5 cm long, hairs sericeous	0.5–3 cm long, hairs setose	≤3.5 cm long, hairs septate and setose
Bracts	oblanceolate, 3.0–3.2 mm long	triangular, 1.5–3 mm long	narrow, ≤1 cm long	minute
Calyx	adaxially glabrous	adaxially glabrous	adaxially densely pubescent	adaxially densely pubescent
Calyx lobes	spatulate, 7–8 mm long	band-shaped to broadly spatulate, 1.5–2.5 mm long	bluntly triangular, c. 0.6 mm long	bluntly triangular, c. 1 mm
Corolla tube of brevistylous flowers	5–5.4 mm long, inside densely hairy on upper ¾, outside glabrous	c. 2 mm long, inside with a ring of hairs at the upper part, outside glabrous	1.8 mm long, inside with a 0.6 mm high ring of hairs in the upper part of the tube, outside glabrous	c. 1.8 mm, inside with a narrow ring of hairs a bit down from the throat, outside sparsely hairy
Corolla lobes	oblong-lanceolate, 2.4–3 mm long	shape unknown, c. 1 mm long	triangular, 0.7 mm long	triangular, 1.2 mm long
Stamens of brevistylous flowers	5.3–5.5 mm long	c. 2 mm long	c. 2 mm long	c. 2.8 mm long
Style of brevistylous flowers	2.7–2.8 mm long, sparsely hairy at upper half	c. 2.5 mm long, glabrous	c. 1.4 mm long, glabrous	c. 1.2 mm long, glabrous

glabrous on the outside, whereas in *X. setosum*, it has a narrow ring of hairs below the throat on the inside and is sparsely hairy on the outside.

The leaf size and shape, head-like pedunculate inflorescence, and spatulate calyx lobes in *Xanthophytum antoanense* are reminiscent of those in *X. attopevense* from Laos. However, *X. attopevense* differs in several key characteristics: it has a cuneate to attenuate (vs. cuneate-oblique in *X. antoanense*) leaf base, shorter petioles (c. 2 vs. 4–6 cm long), c. 1.5 cm long and unlobed stipules (vs. 1.7–2.5 cm long and 3-lobed), flower heads c. 1.5 (vs. c. 2) cm in diameter, up to 1.5 (vs. 3.5–4.5) cm long peduncles, adaxially hairy and 1.5–2.5 mm long (vs. glabrous and 7–8 mm long) calyx lobes, a c. 2 (vs. 5–5.4) mm long corolla tube, and c. 1 (vs. 2.4–3) mm long corolla lobes. Notably, *X. attopevense* was not reported to have setose hairs on its leaf blades, although this type of hair is depicted in a drawing illustrating fruits attached to the type specimens *Harmand 1099*, collected in February 1877, Attopeu, Bassac, Laos (P, barcodes 02436251 and 02436253) (JSTOR 2024).

The morphological differences among these four species are summarized in Table 1.

Key to the 4 presently known Vietnamese species of *Xanthophytum*

1 Inflorescence head-like **2**
– Inflorescence paniculate **3**

2	Lateral veins 9–16 pairs	***X. kwangtungense***
–	Lateral veins ≥ 20 pairs	***X. antoanense***
3	Petioles up to 1 cm long; lateral veins 11–15 pairs	***X. balansae***
–	Petioles up to 5 cm long; lateral veins 14–25 pairs	***X. polyanthum***

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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, Hong Truong Luu, Xuan Bach Nguyen-Le; Formal analysis, Hong Truong Luu, Quoc Dat Nguyen, Hieu Cuong Nguyen, Xuan Bach Nguyen-Le, Tran Quoc Trung Nguyen; Funding acquisition, Hong Truong Luu; Investigation, Quoc Dat Nguyen, Xuan Bach Nguyen-Le, Hieu Cuong Nguyen; Methodology, Hong Truong Luu, Xuan Bach Nguyen-Le, Quoc Dat Nguyen; Project admistration, Tran Quoc Trung Nguyen; Supervision, Hong Truong Luu; Visualization, Hong Truong Luu, Hieu Cuong Nguyen, Xuan Bach Nguyen-Le; Writing – original draft, all authors; Writing – review & editing, Hong Truong Luu, Xuan Bach Nguyen-Le. All authors have read and agreed to the published version of the manuscript.

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Data availability

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

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Research Article

Microtoena wawushanensis (Lamiaceae, Lamioideae): A new species from Sichuan, China

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Abstract

Microtoena wawushanensis, a new species from Sichuan, China, is described and illustrated here. The new species is closely related to *M. moupinensis* and *M. prainiana*, but differs distinctly from both in leaf, calyx and bract morphology. It is further distinguished by its highly variable and unstable calyx tooth ratio (1.36–2.13), red-marked lateral lobes on the lower corolla and filaments that are barbate at both the upper and basal parts, with nearly imperceptible hairs in the middle section. Phylogenetic analyses, based on 81 coding regions of the chloroplast genome, suggest that *M. wawushanensis* belongs to sect. *Delavayana* and is sister to a clade formed by *M. urticifolia*, *M. prainiana* and *M. megacalyx*.

Key words: Lamiaceae, *Microtoena*, new taxon, taxonomy

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Introduction

Microtoena Prain was established by David Prain in 1889 (Prain 1889). Recent studies, based on various chloroplast and nuclear gene fragments, consistently show that *Microtoena* belongs to the tribe Pogostemoneae Briq. of the Subfam. Lamioideae Harley within the Lamiaceae Martinov, closely related to *Pogostemon* Desf. and *Anisomeles* R. Br. (Scheen et al. 2010; Bendiksby et al. 2011; Li et al. 2016; Yao et al. 2016; Zhao et al. 2021a, b). Based on the monograph of *Microtoena* (Wang 2018), there are 19 species of *Microtoena* globally, with 18 species widely distributed across China, ranging from Gansu to Hainan. Phylogenetic analyses of 11 species within the genus, based on three chloroplast markers, revealed that *Microtoena* can be divided into two distinct sections, sect. *Microtoena* and sect. *Delavayana*, which are also supported by morphological evidence (Wang 2018).

Biodiversity loss and species extinction are being accelerated globally, largely driven by human-induced population growth and climate change (Huang et al. 2023; Mi et al. 2023). In an effort to mitigate biodiversity degradation, the Chinese government has undertaken numerous initiatives (Mi et al. 2021; Huang et al. 2023; Mi et al. 2023; Ren and Antonelli 2023), amongst which the establishment of national botanical gardens stands out as a significant achievement (Huang et al. 2023; Ren and Antonelli 2023). The Qinghai-Tibetan Plateau is a natural habitat for rare plants and a gene pool of plateau life, recognised globally as a biodiversity hotspot and receiving significant attention (Sun et al. 2017; Lu et al. 2018; Liu et al. 2021; Mi et al. 2021; Zhang et al. 2023). It has also become a focal point of national botanical garden initiatives. As members of the first national botanical garden of China (Ren and Antonelli 2023), we are engaged in the ongoing compilation of the Lamiaceae volume for the Flora of Pan-Himalaya (FPH) project (Wang and Hong 2022). We made an expedition to Sichuan Province last year and encountered a population in the Wawushan Nature Reserve, Meishan City, which could be distinctly differentiated from previously described *Microtoena* species, based on characteristics such as corolla colour, clear presence or near imperceptibility of hair on the middle parts of filaments and calyx morphology. After a comprehensive review of specimens, literature and incorporating detailed morphological and molecular features, we confirmed that this plant represents a new species within the *Microtoena* genus in China.

Materials and methods

Taxa sampling

We selected 13 individuals from the genus *Microtoena* for our analyses, representing nine distinct species. These taxa include representatives from the two sections currently recognised in *Microtoena* (Wang 2018), as well as those that are morphologically similar to newly-described species. For our outgroup, we used *Pogostemon*, *Anisomeles* and *Craniotome* Rchb., following a previous study (Yao et al. 2016; Wang 2018; Yuan et al. 2022). All ingroup samples were newly sequenced for this study, totalling 13 samples, while sequences for the three outgroup species were obtained from public datasets (see Table 1). Amongst the materials used in our research, three samples consisted of silica gel-dried fresh leaves collected from the field and 10 were sourced from herbarium specimens deposited in the herbarium of the Institute of Botany, Chinese Academy of Sciences (PE), with permission. Detailed information regarding the taxa used in this study can be found in Table 1.

DNA extraction, sequencing, genome assembly

DNA extractions were performed using a modified cetyltrimethylammonium bromide (CTAB) method as outlined by Doyle and Doyle (1987) for specimens or with the Magnetic Plant Genomic DNA Kit from TIANGEN BIOTECH (Beijing) Co., Ltd. for silica gel-dried samples. Library preparation and whole genome sequencing (WGS) were carried out at Novogene Bioinformatics Technology Co., Ltd. in Beijing, China. Initially, the genomic DNA samples were fragmented. Following this, the fragments underwent end polishing, A-tailing, ligation with full-length sequencing adapters and PCR amplification. After quality assessment and quantification, the eligible libraries were sequenced using either the DNBSEQ-T7 or Illumina NovaSeq 6000 platform according to the PE150 strategy.

Table 1. Voucher information of samples for phylogenetic analyses and GenBank accession numbers.

	Taxon	Voucher	Sample Form	GenBank accession numbers
1	*Microtoena urticifolia* Hemsl._89	Z.P.Jian et al. *31157* (PE)	specimen leaves	PQ664497
2	*Microtoena urticifolia* Hemsl._90	Z.P.Jian et al. *31157* (PE)	specimen leaves	PQ664498
3	*Microtoena prainiana* Diels_83	Q.Wang *H12079* (PE)	specimen leaves	PQ664495
4	*Microtoena prainiana* Diels_W24-19	Q.Wang *H12079* (PE)	specimen leaves	PQ664500
5	*Microtoena moupinensis* (Franch.) Prain_78	D.Y.Hong et al. *H12056* (PE)	specimen leaves	PQ664493
6	*Microtoena moupinensis* (Franch.) Prain_86	K.J.Guan et al. *3219* (PE)	specimen leaves	PQ664496
7	*Microtoena megacalyx_* C.Y.Wu_*72*	Y.M. Shui *003011* (PE)	specimen leaves	PQ664492
8	*Microtoena robusta* Hemsl._W24-16	J.Q.Fu *2756* (PE)	specimen leaves	PQ664499
9	*Microtoena delavayi* Prain_W037	Q.B.Gong *CPG47960* (PE)	silica gel-dried leaves	PQ664501
10	*Microtoena delavayi* Prain_W038	Q.B.Gong *CPG46899* (PE)	silica gel-dried leaves	PQ664502
11	*Microtoena insuavis* (Hance) Prain ex Briq._71	X.Y.Liu *24836* (PE)	specimen leaves	PQ664491
12	*Microtoena patchoulii* (C.B. Clarke ex Hook. f.) C.Y. Wu & S.J. Hsuan_82	Q.Wang *H&W09011* (PE)	specimen leaves	PQ664494
13	*Microtoena wawushanensis* Xue X. Wu & Qiang Wang	X. X. Wu et al. *WXX23001* (PE)	silica gel-dried leaves	PQ664503
14	*Pogostemon cablin* (Blanco) Benth.	–	–	MF445415
15	*Anisomeles indica* (L.) Kuntze	–	–	NC_46781
16	*Craniotome furcata* (Link) Kuntze	–	–	NC_54194

In this study, we utilised GetOrganelle software (Jin et al. 2020) to assemble the chloroplast genetic sequencing data for the target taxa listed in Table 1. The assembly results were saved as a GFA file and later imported into Bandage (Wick et al. 2015) for visualisation and verification. The assembled genomes were annotated using the Plastid Genome Annotator (Qu et al. 2019), with a re-annotated *Craniotome furcata* (Link) Kuntze (NC_054194) from GenBank serving as the reference.

Molecular phylogenetic analyses

Single gene matrices were generated using Geneious Prime 2022. The matrices for each of the 16 plastomes were aligned using MAFFT v.7.3.1 (Katoh and Standley 2013) in PhyloSuite v.1.2.2 (Zhang et al. 2020). Loci with abnormal high variation were removed using the default parameters of Gblocks (Castresana 2000). The final coding regions (CDS) matrices from the 16 taxa were manually checked using AliView v.1.26 (Larsson 2014). Subsequently, all individual CDS matrices were concatenated into a single supermatrix using PhyloSuite v.1.2.2 (Zhang et al. 2020).

Phylogenetic trees were constructed using Bayesian Inference (BI) methods and Maximum Likelihood (ML) methods. The BI analysis was performed with MrBayes v.3.2.7a (Ronquist et al. 2012), using the MCMC (Markov Chain Monte Carlo) algorithm run for 1,000,000 generations, saving a tree every 1,000 generations. The first 25% of the trees were discarded. The analysis was stopped when effective sample sizes (ESS) exceeded 200 and the average standard deviation (SD) of split frequencies was below 0.01. ML analysis was performed using RAxML v.8.2.12 (Stamatakis 2014) with the GTRGAMMA model and 1000 bootstrap replicates.

Morphological and taxonomy study

Apart from the new species, all morphological samples of the genus *Microtoena* were obtained from the Herbarium PE (Table 1). Photographs of *Microtoena* morphologies were taken using an Olympus EM5 Mark III and a Nikon D7500 digital camera. Details of the filaments of the *Microtoena* were captured using a Leica M205C stereoscopic microscope. Morphological data were collected by measuring specimens indoors with a measuring tape and analysing photographed specimens using MATO software (Liu et al. 2023).

We used analytical indices for the bracts and calyx introduced by Wang (2018): BR (bract ratio) = BW (bract width) / BL (bract length), CLA (calyx length in anthesis), SR (split ratio) = OTL (average of ordinary tooth length of calyx) / CL (calyx length) and TR (tooth ratio) = LLT (length of the longest tooth) / OTL (average of ordinary tooth length of calyx).

Results and discussion

Sequence characterisation

Our ingroup samples were sequenced, yielding a range of 42.12G to 156.18G of raw data, with an average of 79.9G (Suppl. material 1). All of the 13 samples had complete chloroplast genomes assembled. The lengths of *Microtoena* plastomes in this research range from 152742 bp (*M. insuavis* (Hance) Prain ex Briq) to 153004 bp (*M. prainiana* Diels). All individuals of 81 CDS matrices (i.e. CP81) were concatenated into one single 68346 bp-long supermatrix.

Molecular phylogeny results

The phylogenetic tree inferred from Bayesian Inference (BI) methods and Maximum Likelihood (ML) analyses identified the genus *Microtoena* as monophyletic (BI-PP = 0.86, ML-BS = 69%) (Figs 1, 2), consistent with findings from previous studies (Wang 2018). The topologies of the BI and ML phylogenetic trees are largely congruent, with *M. wawushanensis* clustering within sect. *Delavayana*. Within this section, *M. urticifolia* Hemsl., *M. prainiana* and *M. megacalyx* C.Y.Wu formed a clade sister to the potential new species *M. wawushanensis* with high support (BI-PP = 1, ML-BS = 98%). However, the topologies differed between the BI and ML phylogenetic trees in some nodes. The previous clade is sister to *M. moupinensis* (Franch.) Prain and *M. robusta* Hemsl. in BI phylogenetic tree (Fig. 1: BI-PP = 1.00). In the ML tree, the previous clade is sister to *M. moupinensis* with low support (Fig. 2: ML-BS = 48%), then this clade is sister to *M. robusta* (Fig. 2: ML-BS = 100%). *M. robusta*, which shares the characteristic of a white corolla with red markings on the upper lip with the newly-described species. *M. delavayi* Prain, characterised by a pale yellow or yellow corolla with an upper lip that is either densely spotted with purplish-red markings or completely spotless, occupies a basal position within sect. *Delavayana*, supported by high values (BI-PP = 1.00, ML-BS = 100%). In this study, sect. *Microtoena* is resolved as a sister clade to sect. *Delavayana*, comprising *M. patchoulii* (C.B. Clarke ex Hook. f.) C.Y. Wu & S.J. Hsuan and *M. insuavis* with high support (BI-PP = 1.00, ML-BS = 100%) in this study.

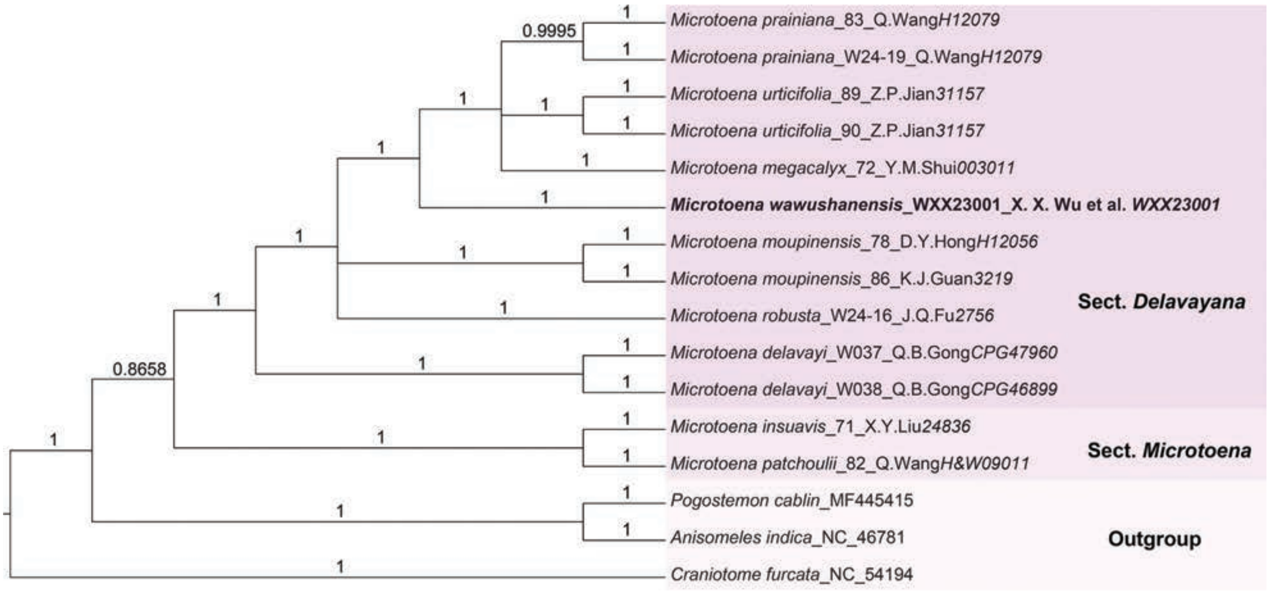

Figure 1. Phylogenetic placement of *Microtoena wawushanensis* sp. nov. within the *Microtoena* inferred by Bayesian Inference (BI), based on 81 coding regions (dataset CP81).

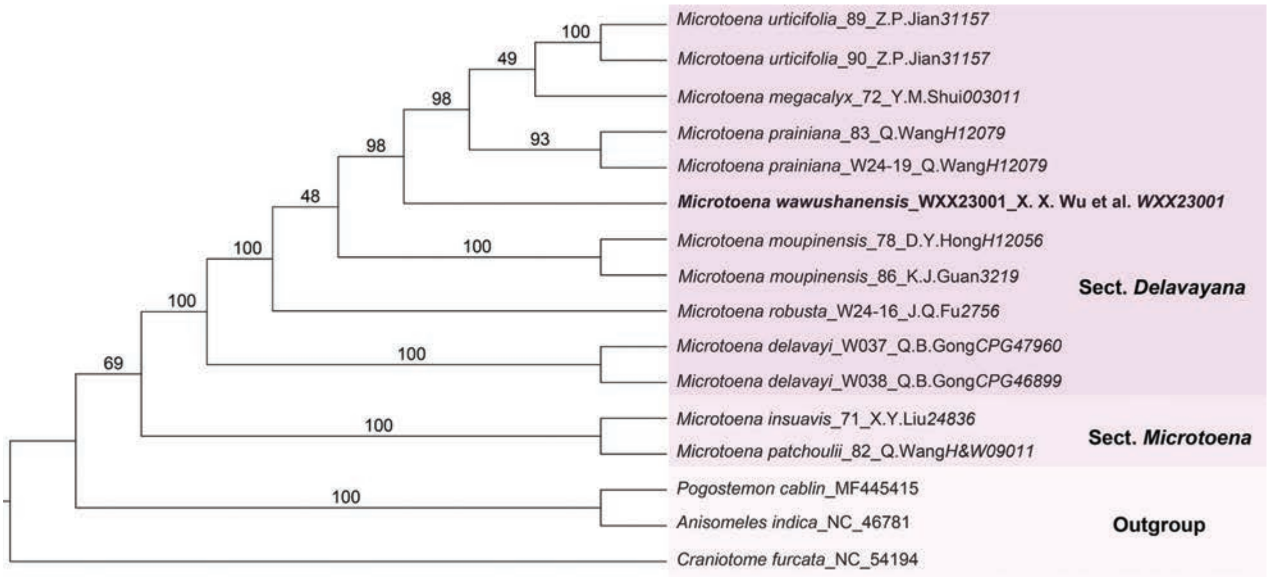

Figure 2. Phylogenetic placement of *Microtoena wawushanensis* sp. nov. within the *Microtoena* inferred by Maximum Likelihood (ML), based on 81 coding regions (dataset CP81).

Morphological comparison

A comprehensive morphological comparison was conducted between the new species and other species of *Microtoena*. Key morphological characteristics of the new species include the inflorescences characterised by lax to more or less compact spike-like panicles (Fig. 3B, C). The corolla is white, marked with red on the upper lip and the lateral lobes of the lower corolla are also red (Fig. 3D). The calyx teeth are triangular-lanceolate to linear-lanceolate or subulate, with the apex typically hooked (Fig. 3E, F). The bracts are linear to lanceolate (Fig. 3G). The leaf base that is cuneate to truncate-subcordate (Fig. 3H). These distinctive traits facilitate the easy differentiation of the new species from all other members of the sect. *Delavayana*.

The size of the calyx and its teeth has been used to subdivide *Microtoena* (Hsuan 1965; Wu and Li 1977); however, both the calyx and its teeth in this genus continue to grow after anthesis. To address this, we applied three analytical indices for the calyx as proposed by Wang (2018): CLA (calyx length in anthesis), SR (split ratio) and TR (tooth ratio). The CLA value of *M. wawushanensis* was found to range from 0.38 to 0.80 cm, which is similar to *M. moupinensis*. Regarding the SR, this value of *M. wawushanensis* ranged from 0.23 to 0.40, shows variability similar to that of *M. moupinensis*, with a much wider range than the other species (Wang 2018). Concerning the calyx tooth ratio (TR), *M. moupinensis* has five unequal calyx teeth, with one tooth slightly longer than the other four. In comparison, *M. wawushanensis* displays a highly variable and unstable TR (Fig. 3E, F), ranging from 1.36 to 2.13, which is comparable to *M. urticifolia* with a range of 1.83 to 2.24.

The bracts of *Microtoena* are typically linear, lanceolate or ovate and are minute, with some being early deciduous (Wang 2018). Upon measurement, the bracts of *M. wawushanensis* range from 2.10, 11.40 mm in length and 0.40, 0.80 mm in width, with a bract ratio (BR) ranging from 0.13 to 0.18, displaying a linear to lanceolate shape (Fig. 3G). In comparison, the bracts of morphologically similar species such as *M. moupinensis* and *M. urticifolia* are linear, with a BR of approximately 0.10, while *M. prainiana* has ovate bracts, with an average BR of 0.45 and *M. megacalyx* has lanceolate bracts, with an average BR of 0.26.

Morphologically, the new species is characterised by a conspicuously elongated corolla tube (Fig. 3I), indicating its placement within the sect. *Delavayana* (Wang, 2018). Our observations revealed that the similar species *Microtoena prainiana* has filaments that are barbate in the middle and lower sections (Fig. 4A), a trait commonly observed within the genus (Wang 2011). In contrast, *M. wawushanensis* exhibits a smooth, glabrous surface, with the hairs being almost imperceptible in the middle region (Fig. 4C), but barbate at both the upper and basal parts of the filaments (Fig. 4B, D).

Microtoena wawushanensis exhibits similarities in corolla colouration with two other species in the genus *Microtoena* that have red markings on the upper lip: *M. robusta* and *M. delavayi*. *M. robusta* has a white corolla featuring red markings on the upper lip, similar to the newly-described species, while *M. delavayi* has a pale yellow or yellow corolla and its upper lip may have dense purplish-red markings or be completely devoid of spots. However, *M. robusta* can be easily distinguished from *M. wawushanensis* by its cymes, which are axillary and terminal, dichotomous and lax, as well as by its tiny linear bracts. Likewise, *M. delavayi* is clearly identifiable by its unequal calyx teeth, with one tooth being notably elongated and its characteristic pale yellow or yellow corolla.

Consequently, the combined evidence from morphological and phylogenetic analyses supports the recognition of a new species in *Microtoea*.

Taxonomic treatment

Microtoena wawushanensis **Xue X. Wu & Qiang Wang, sp. nov.**

urn:lsid:ipni.org:names:77349693-1
Figs 3, 5, 6

Type. China • Sichuan Province Meishan City, Hongya County, Wawushan Nature Reserve, growing under the forest by the edge of a riverside, 29°32.2832'N,

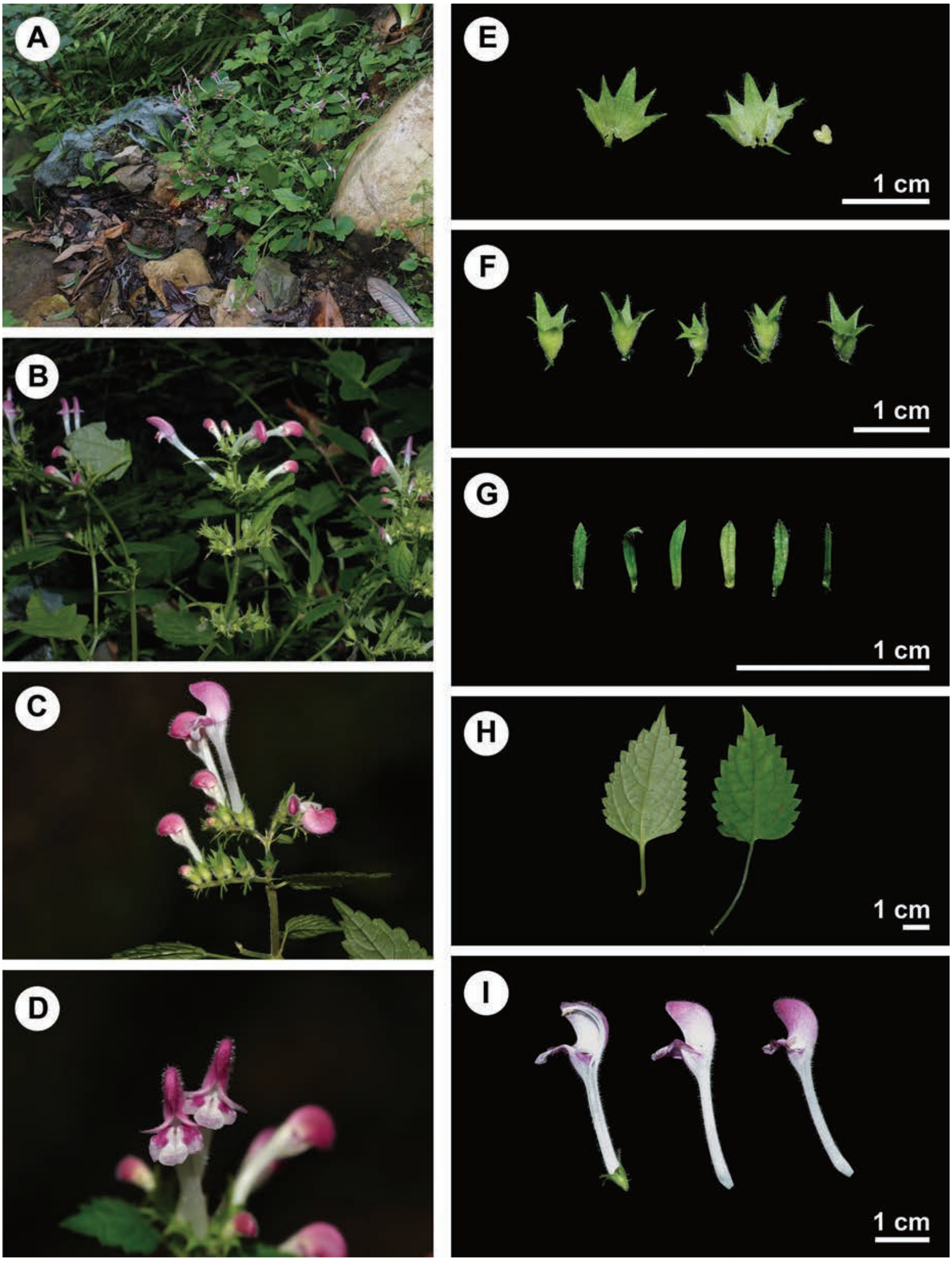

Figure 3. Images of *Microtoena wawushanensis* sp. nov. **A** individual in the flowering period of wild populations **B, C** inflorescence in lateral view **D** lower corolla lip **E** dissected calyxes (outside & inside) **F** calyxes **G** bracts **H** leaves **I** dissected corolla (containing filaments) and corola.

102°55.6359'E, 1500 m alt., 14 September 2023, *X. X. Wu et al. WXX23001* (holotype: PE02462560; isotypes: PE02462561, PE02462562, PE02462563, PE02462564, PE02462565).

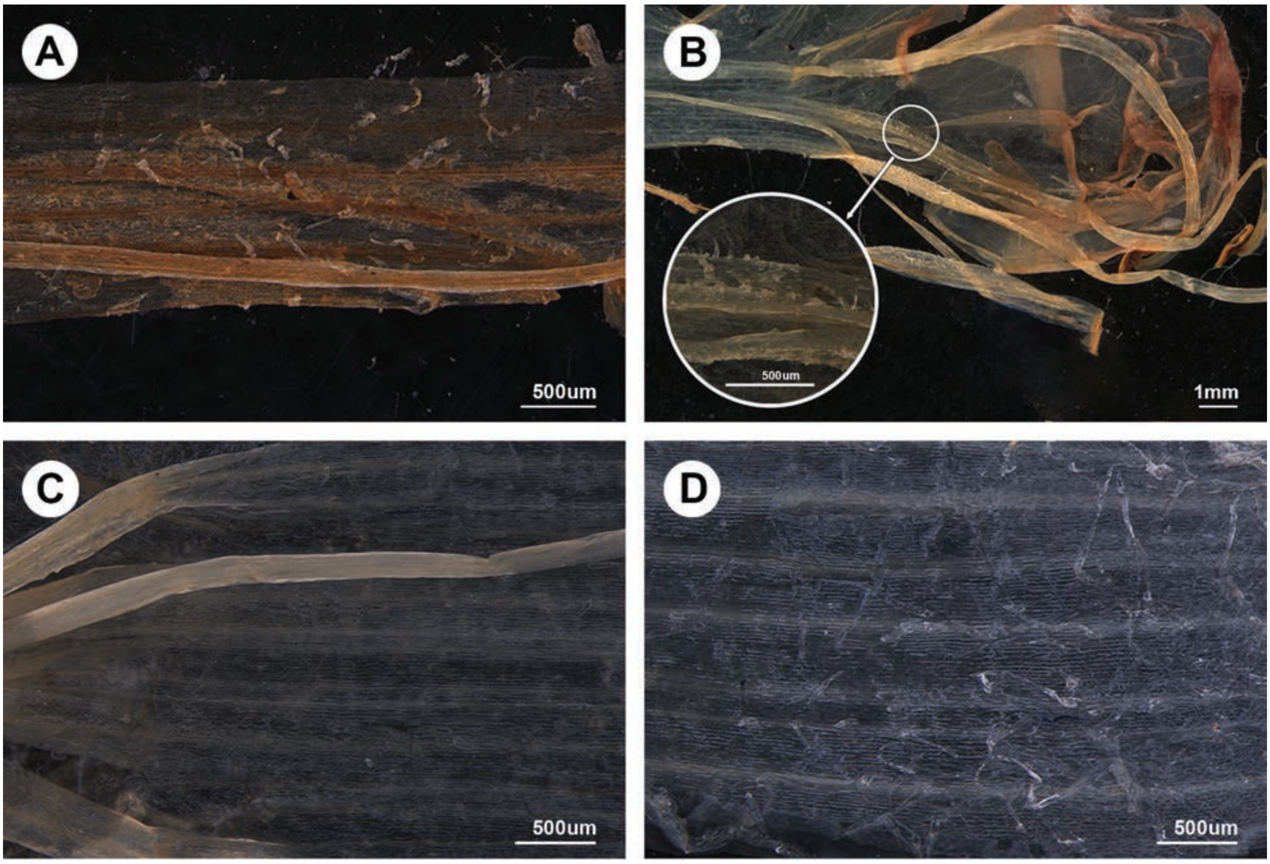

Figure 4. Images of partial filaments morphology of *Microtoena prainiana* and *M. wawushanensis* sp. nov. **A** the middle part of the filaments of *M. prainiana* (PE 01908066) **B** the upper part of the filaments of *M. wawushanensis* **C** the middle part of the filaments of *M. wawushanensis* **D** the basal part of the filaments of *M. wawushanensis*.

Diagnosis. *Microtoena wawushanensis* is morphologically similar to *M. moupinensis* (Franch.) Prain and *M. prainiana* Diels (Table 2), but differs from *M. moupinensis* and *M. prainiana* by having a crenate leaf margin with distinct mucrones (vs. with or dentate without any mucro), a cuneate to truncate-subcordate leaf base (vs. truncate-subcordate or cuneate leaf base), a lax, more or less compact to spike-like panicle inflorescence (vs. inflorescence sometimes with one-sided branches or shortly ovoid panicles), linear to lanceolate bracts (vs. linear or ovate bracts), calyx teeth that are triangular-lanceolate, linear-lanceolate to subulate with an apex usually hooked (vs. similar or calyx teeth subulate with a conspicuously hooked apex), a highly variable and unstable calyx tooth ratio: 1.36–2.13 (vs. 1.03–1.49 or five subequal calyx teeth), a white corolla marked with red on both upper lip and the lateral lobes of the lower corolla (vs. yellow or pale yellow corolla) and filaments are barbate at both the upper and basal parts, with the hairs in the middle section being almost imperceptible (vs. filaments are clearly barbate from the lower to middle part).

Description. Herbs perennial. Stems erect, 0.40–0.80 m tall, base sometimes woody, sparsely puberulent. Leaf petiole 3–9 cm long; leaf blade ovate to oblong-ovate, triangular-ovate, 3.91–9.86 cm long, 3.91–9.86 cm broad, sparse hairs on the adaxial surface, with few hairs visible only along the veins on the abaxial surface and the rest of the abaxial surface glabrous; base truncate or cuneate; margin coarsely serrate to mucronate crenate, with distinct mucrones; apex acuminate to shortly caudate-acuminate. Cymes axillary and terminal, dichotomous,

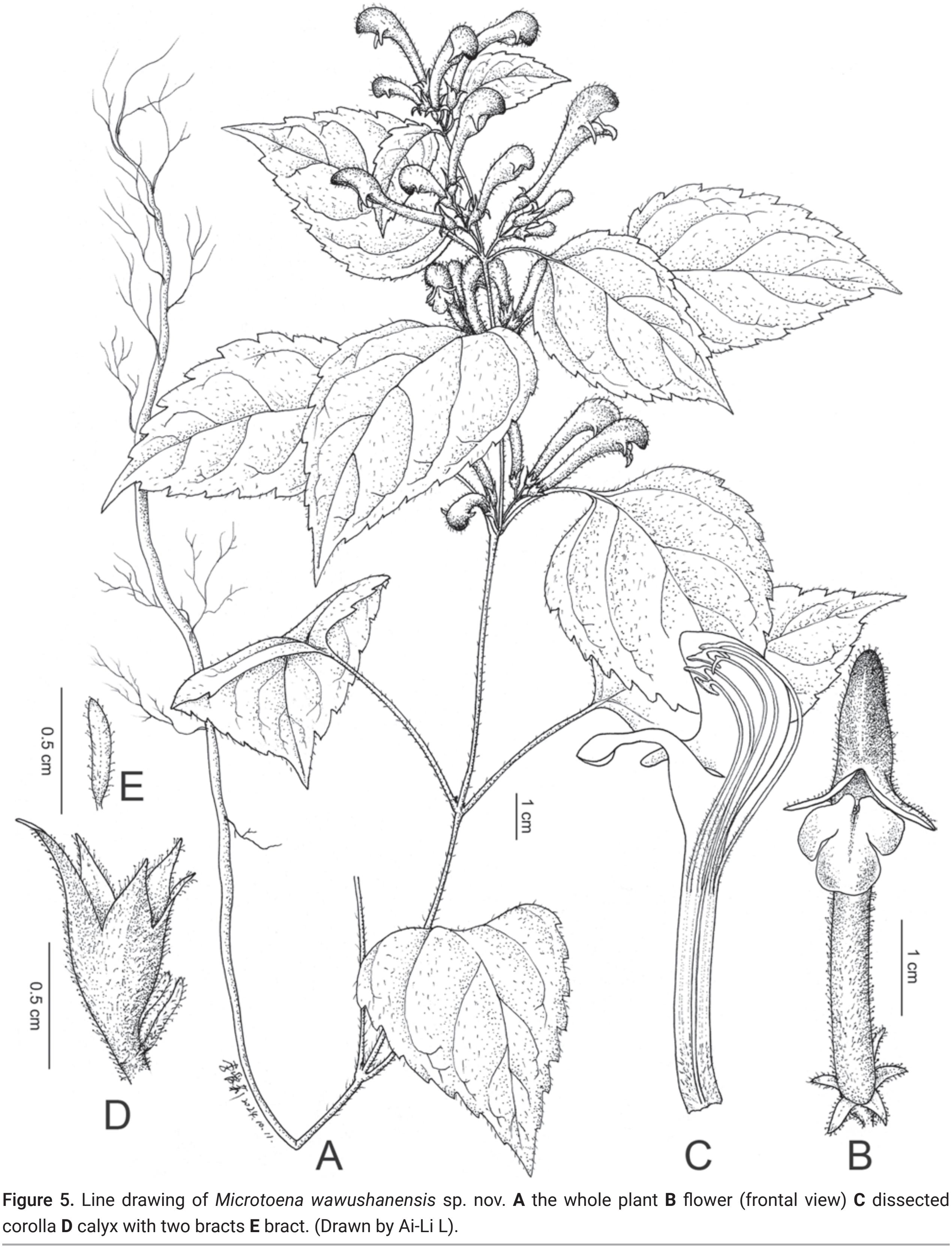

Figure 5. Line drawing of *Microtoena wawushanensis* sp. nov. **A** the whole plant **B** flower (frontal view) **C** dissected corolla **D** calyx with two bracts **E** bract. (Drawn by Ai-Li L).

lax, slightly to very compact in spike-like panicles; peduncle inconspicuous. Bracts usually linear to lanceolate, 2.10–11.40 mm long, 0.40–0.80 mm broad. Calyx is 0.38–0.80 cm long at anthesis, densely puberulent, dilated after anthesis and 5-toothed; calyx teeth are triangular-lanceolate, linear-lanceolate to subulate, with

Figure 6. Holotype of *Microtoena wawushanensis* sp. nov. (PE02462560).

the tooth ratio highly variable and unstable and the apex is usually hooked. Corolla white, marked with red on upper lip, 1.76–3.59 cm long, hirsutulous outside; corolla tube conspicuous; upper corolla lip laterally compressed; lower corolla lip 3-lobed, middle lobe subcircular, wider than lateral lobes, lateral lobes marked with red. Stamens 4, filament barbate at the upper and basal parts, while the middle section has nearly imperceptible hairs. Nutlets dark brown to black, smooth.

Distribution and habitat. Currently, *M. wawushanensis* has been found in Wawushan Nature Reserve, Hongya County, Meishan City, Sichuan Province, China. It occurs by the edge of a riverside with weak light, at an elevation of 1500 m. In the type locality, the companion species mainly include *Bistorta amplexicaulis* (D. Don) Greene, *Urtica fissa* E. Pritz., *Lecanthus peduncularis* (Wall.

Table 2. Morphological comparison amongst *M. wawushanensis*, *M. moupinensis* and *M. prainiana*.

Morphology	*M. wawushanensis*	*M. moupinensis*	*M. prainiana*
Leaf margin	crenate with distinct mucrones	crenate with distinct mucrones	dentate without any mucro
Leaf base	cuneate to truncate-subcordat	truncate-subcordate, cuneate, cordate	cuneate
Inflorescence	lax, more or less compact, to spike-like panicles	lax, more or less compact, to spike-like panicles, sometimes with 1-sided branches	shortly ovoid panicles
Bracts	linear to lanceolate	linear	ovate
Calyx morphology	calyx teeth triangular-lanceolate, linear-lanceolate to subulate, with apex usually hooked	calyx teeth triangular-lanceolate, linear-lanceolate to subulate, with apex usually hooked	calyx teeth subulate, apex conspicuously hooked
Calyx tooth ratio	highly variable and unstable: 1.36–2.13	variable and unstable: 1.03–1.49	five subequal calyx teeth: 1.1
Corolla	corolla white, marked with red on upper lip, the lateral lobes of the lower corolla are marked with red	corolla yellow to pale yellow	corolla uniformly pale yellow
Stamens	filaments are barbate at both the upper and basal parts of the corolla tube, with the hairs in the middle section being almost imperceptible	filament barbate on the lower to middle part	filament barbate on the lower to middle part

ex Royle) Wedd., *Cyathula officinalis* K. C. Kuan, *Sinacalia davidii* (Franch.) Koyama and *Stachyurus chinensis* Franch.

Phenology. Flowering from August to September, fruiting in September.

Etymology. The specific epithet is derived from the type locality of the new species, i.e. the Wawushan Nature Reserve in southwest Sichuan Province, China and the Latin suffix-*ensis*, indicating the place of origin or growth.

Vernacular name. (assigned here). Simplified Chinese: 瓦屋山冠唇花 (Chinese pinyin: wǎ wū shān guàn chún huā).

Conservation assessment. The ongoing field investigation has identified only one population of this taxon that is endemic to the Wawushan Nature Reserve. Additional fieldwork is necessary to gain a better understanding of this species. According to the guidelines of the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022), *Microtoena wawushanensis* is assessed as data deficient (DD).

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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

Resources: XXW, YW, YYC, QW. Investigation: XXW, YW, YYC, QW. Writing - original draft: XXW. Writing - review and Editing: XXW, YW, YYC, QW. Conceptualization, Supervision and Funding acquisition: QW. All co-authors contributed to the manuscript and revised it critically.

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Data availability

All of the data that support the findings of this study are deposited at GenBank.

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Supplementary material 1

Summary of the quality of samples sequencing data

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Research Article

Melicope iolensis (Rutaceae), a new tree species from Kauaʻi, Hawaiian Islands

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Abstract

A newly-discovered endemic tree species of *Melicope* from Kauaʻi, Hawaiian Islands, is described and illustrated with notes on its distribution, ecology, conservation status and phylogenetic placement. A modification to the existing key to Hawaiian *Melicope* is also provided. *Melicope iolensis* **sp. nov.** is a member of Stone's *Megacarpa* group having carpels connate at base, capsules 4-lobed and leaves usually opposite. The new species differs from its Hawaiian congeners by its unique combination of abaxially glabrate to pilose-pubescent leaves with petioles up to 70 mm long, ramiflorous and axillary inflorescences, sepals on staminate flowers 0.3–0.5 mm long, capsules with green and purple streaking, 10–14 mm wide and seeds 3–3.5 mm long. Since its discovery in 2021, 15 individuals have been documented within a single remote windward hanging valley below the Kawaikini Summit of Kauaʻi. *Melicope iolensis* represents a new Critically Endangered (CR) single island endemic species in need of conservation.

Key words: Conservation, discovery, endangered tree species, Hawaiian flora, *Melicope* section *Pelea*, Sapindales, single island endemism

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Introduction

Melicope J.R.Forst. & G.Forst. is the largest genus within Rutaceae (Citrus family) containing ca. 239 species of shrubs and trees distributed across the Malagasy and Indo-Himalayan regions, SE Asia, Australasia and the Pacific Islands (Hartley 2001; Appelhans et al. 2014b, 2017; Wood et al. 2016, 2017). The Hawaiian lineage was initially placed in the genus *Pelea* A.Gray, but both morphological (Hartley and Stone 1989; Hartley 2001) and molecular phylogenetic studies (Harbaugh et al. 2009; Appelhans et al. 2014a) confirm that *Pelea* is nested within the genus *Melicope*.

Hartley (2001) recognised four sections in *Melicope* and placed the Hawaiian lineage in sect. *Pelea* (A.Gray) Hook.f. along with species distributed from Taiwan, Southeast Asia and Marquesas Islands to New Caledonia. Subsequently, Appelhans et al. (2017) merged the Hawaiian endemic genus *Platydesma* H.Mann into *M.* sect. *Pelea* and excluded the New Caledonian species from that section in order to preserve its monophyly. They also suggested the four sections of *Pelea* proposed by Stone (1969) and the former genus *Platydesma* be called subsections of *M.* sect. *Pelea*, but no combinations were made as they were waiting for a better understanding of relationships with Hawaiian *Melicope* (Appelhans et al. 2017). Botanists still use Stone's species groups (sections of *Pelea*) for helping to key out the Hawaiian taxa: *Apocarpa* with carpels distinct in fruit, leaves opposite; *Pelea* with carpels connate at base, leaves in whorls; *Megacarpa* with carpels connate at base, capsules 4-lobed, leaves usually opposite; and *Cubicarpa* with capsules cuboid, leaves opposite (Wagner et al. 1999). However, the species groups are in need of revision since only *Pelea* was resolved as monophyletic (Appelhans et al. 2014a; Paetzold et al. 2019).

Phylogenetic analysis reveals that the Hawaiian lineage was the result of a single long-distance colonisation event, originating from an Australasian ancestor with diversification dating back ca. 7.5 mya to the Late Miocene or Early Pliocene (Appelhans et al. 2018; Paetzold et al. 2019) and pre-dating the oldest current high island of Kauaʻi (i.e. ca. 5 mya, Price and Clague (2002)). *Melicope* rely on birds for long-distance dispersal (Hartley 2001). Despite the isolated position of the Hawaiian Islands, the archipelago is not a dead-end of dispersal for *Melicope* as two independent colonisation events from the Hawaiian to the Marquesas Islands occurred in the genus (Appelhans et al. 2014a, 2018; Paetzold et al. 2019).

Hawaiian *Melicope* are one of the four most species rich plant radiations in the archipelago, having undergone extraordinary morphological and ecological diversification with 54 accepted endemic species (Wagner et al. 1999; Wood et al. 2016, 2017; Appelhans et al. 2017). Many occur throughout dry, mesic and wet forest habitats, including bogs and cliffs and range from 300–1700(–2060) m elevation. Kauaʻi holds the greatest diversity of *Melicope* with 22 species, 16 of which are single island endemics (SIE). Unfortunately, there are now 22 Hawaiian *Melicope* species that are federally listed as endangered and four considered possibly extinct (Wood 2011; Wood et al. 2016, 2019). Having limited land mass, tropical islands are particularly vulnerable to human disturbance, especially the impact of introduced non-native plant and animal species which can quickly spread and degrade remote natural ecosystems.

With Hawaii State, federal and non-government agencies conducting research and protecting the biotic diversity of Kauaʻi, SIE continue to be discovered. The > 1900 *Melicope* collections at PTBG represent a long intensive focus on the genus. The collection includes five recently discovered and described *Melicope* species from Hawaiian, Marquesas and Austral Islands. This collection has helped to guide conservationists with data on the distribution and abundance of rare Pacific Island species and also houses collections representing rediscoveries of species previously thought extinct, including nine Hawaiian *Melicope* (Appelhans et al. 2014b; Wood et al. 2016, 2017; Lorence and Wagner 2020; Wood and Walsh 2022).

In October of 2021, the lead author and members of the Kauaʻi Plant Extinction Prevention Program (PEPP) documented an unusual tree species with exceedingly small 4-lobed capsules (*Megacarpa*) in a remote isolated hanging valley below the central summit peak of Kawaikini (Fig. 1). Further exploration and research subsequently revealed that it differed from all other known *Melicope* species by its unique combination of abaxially glabrate to pilose-pubescent leaves with petioles up to 70 mm long, ramiflorous and axillary inflorescences, sepals on staminate flowers 0.3–0.5 mm long, capsules with green and purple streaking, 10–14 mm wide and seeds 3–3.5 mm long (Table 1). We hereby describe and name this new species *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner, present a summary of its distribution and ecology, provide a diagnostic key with distinguishing characters, evaluate its phylogenetic position, present a table comparing it to other Kauaʻi members of *Megacarpa* and provide a preliminary conservation assessment using IUCN Red List criteria. This publication brings the number of recognised *Melicope* species in the Hawaiian Islands to 55 and attests to the remarkable floristic diversity of Kauaʻi, exceeding all other Hawaiian Islands with its total of 254 SIE vascular plant taxa.

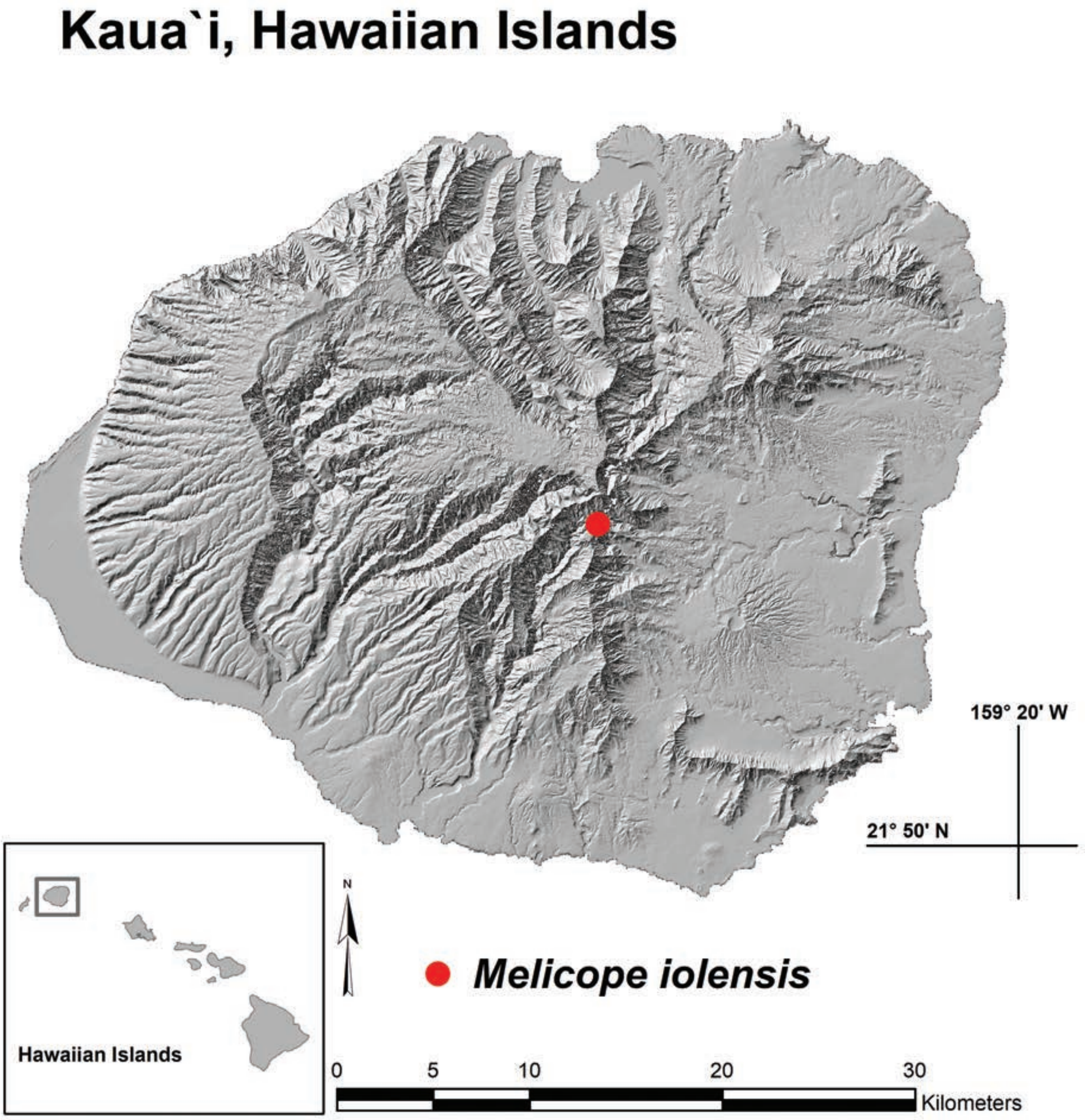

Figure 1. Distribution map (Kauaʻi, Hawaiian Islands) with red dot indicating single known location of *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner in ʻIole Valley.

Methods

Research in the type locality has been conducted from 1994 to present. All morphological measurements were taken from dried herbarium specimens and field notes and are presented in the descriptions as follows: length × width, followed by units of measurements (mm, cm or m). The authors have examined all specimens cited and have worked extensively with *Melicope* specimens at BISH, PTBG and US. We assessed the extinction risk for *Melicope iolensis* following the IUCN Red List Categories and Criteria (IUCN 2012, 2022). The extent of occurrence (EOO) and area of occupancy (AOO) were calculated by using ArcMap 10.6.1 in relation to coordinates recorded while collecting herbarium specimens or making field observations. Lat/Long coordinates have been truncated to protect exact locations from unauthorised access.

Taxonomic treatment

Melicope iolensis **K.R.Wood, Lorence & W.L.Wagner, sp. nov.**
urn:lsid:ipni.org:names:77354456-1
Figs 2, 3, 4A, B, 5

Diagnosis. *Melicope iolensis* is morphologically most similar to *M. wawraeana* (Rock) T.G.Hartley & B.C.Stone, but differs by its combination of leaves abaxially glabrate to pilose-pubescent (vs. glabrous), inflorescence ramiflorous, rarely axillary (vs. axillary), shorter sepals on staminate flowers, 0.3–0.5 mm long (vs. 3.5 mm) and smaller seeds 3–3.5 mm long (vs. 5–8 mm). Phylogenetically, *M. iolensis* is most closely related to *M. nealae* (B.C.Stone) T.G.Hartley & B.C.Stone, yet starkly differs by its tree habit (vs. shrub), flowers usually 9–18 per inflorescence (vs. 1–5), carpels with exocarp glabrous, connate 1/6–1/5 their length (vs. puberulent, connate 1/2–3/4 length) and seeds 3–3.5 mm long (vs. 5–8 mm long).

Type. USA • Hawaiian Islands, Kauaʻi: Līhuʻe District, ʻIole headwaters, ♀, 22.042, -159.497, 872 m alt., 8 Sep 2022 (fr.), *K.R. Wood, S. Heintzman & S. Deans 19143* (holotype: mounted on 2 sheets, PTBG1000096868, PTBG1000096869!; isotype (to be distributed): US!).

Description. ***Trees*** 3–8 m tall, trunks up to 20 cm diameter, bark smooth, mottled grey-brown, ultimate stems brown-red, new growth and young branchlets sparsely tan puberulent, glabrate in age. ***Leaves*** opposite, unifoliolate; petiole (20–)30–70 mm long, strigose-pubescent, adaxially glabrous, shallowly canaliculate; the blade subcoriaceous to coriaceous, ovate, oblong-ovate, oblong-elliptic, (8–)14–25(–33) × (6–)10–18 cm, margin entire; base truncate to obtuse, rarely acute; apex rounded, often emarginate; secondary veins 15–20 pairs, connected by an arched vein 4–20 mm from margin; higher order venation reticulate; adaxial surface glabrous; abaxial surface minutely black glandular punctate, pilose-pubescent, tan-yellow, or glabrate; mid-rib usually densely pilose-strigose; secondary veins pilose-strigose. ***Inflorescences*** in ramiflorous, densely fasciculate cymes, occasionally axillary, (4–)9–18 flowered, to 40 mm long, purple-red when fresh; peduncles 2–5 mm long, glabrate, branched to second degree; primary branches 2–4 pairs; pedicels 4–14 mm long, glabrate; bracteoles triangular-ovate 0.3–0.4 mm long. ***Flowers*** unisexual, 4-merous; perianth glabrate; androecium, nectary disc and gynoecium glabrous; ovary

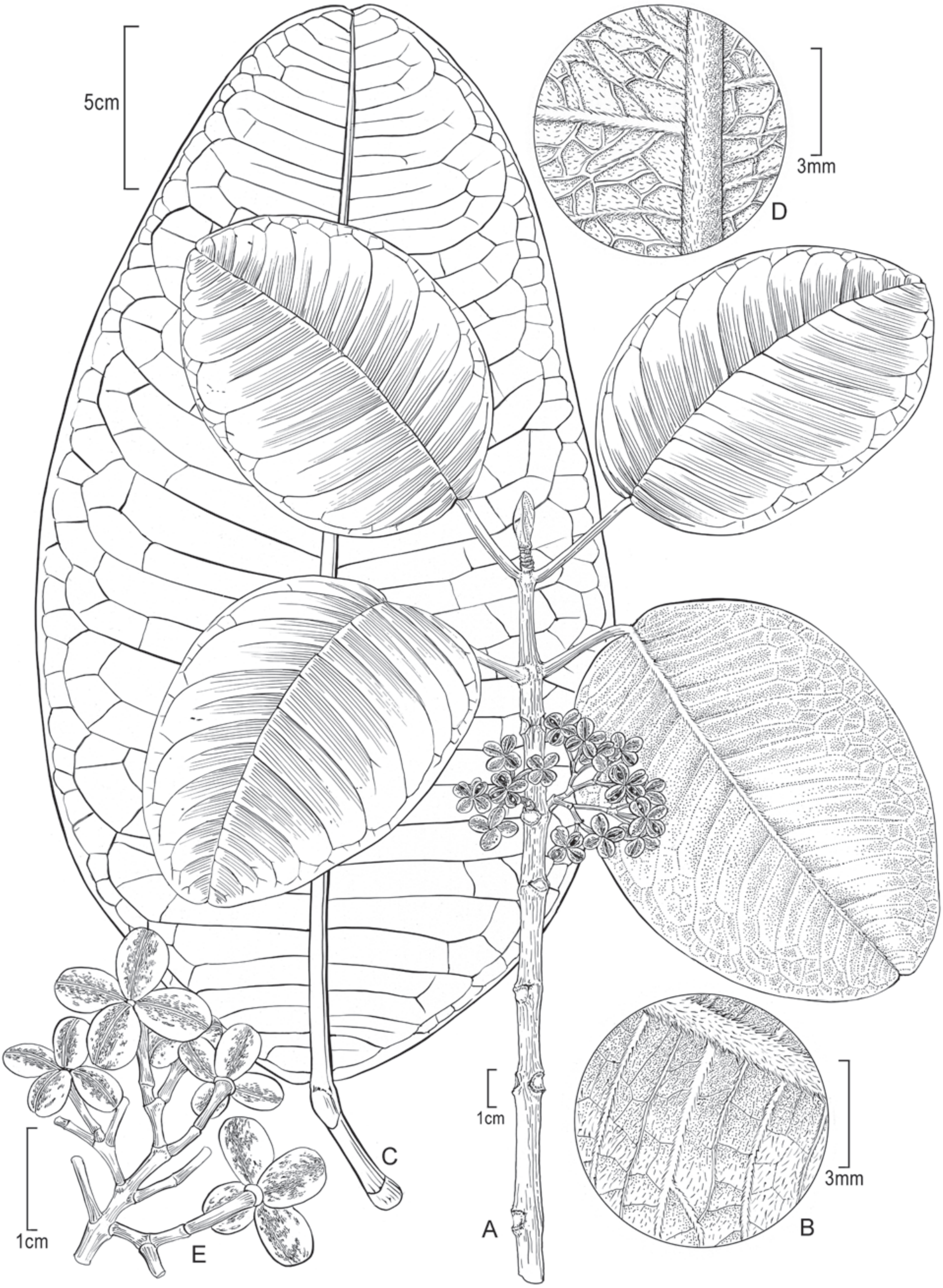

Figure 2. *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner **A** fruiting branch **B** abaxial leaf surface on branch in A showing pubescence **C** abaxial surface of large leaf showing marginal and secondary venation **D** abaxial surface of large leaf in C showing scattered minute pubescence **E** portion of infructescence with connate capsules (*Megacarpa*) showing irregular streaking **A–E** from photos of holotype, *Wood, Heintzman & Deans 19143* (PTBG, US) (Illustration by Alice Tangerini).

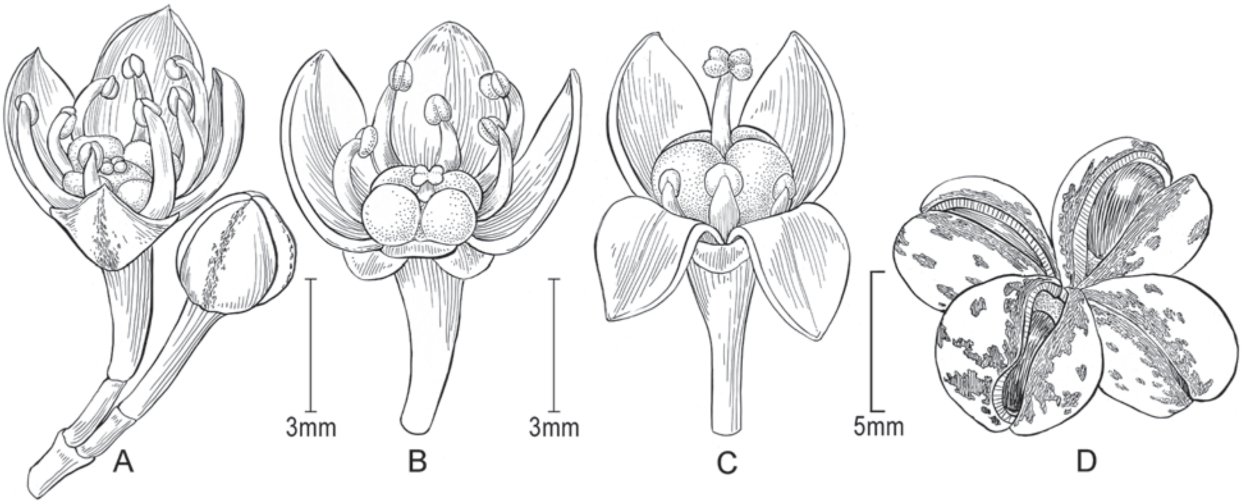

Figure 3. *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner **A** staminate flower and bud **B** staminate flower, lateral view with petal cut away to show antisepalous and antipetalous stamens and two minute sepals **C** pistillate flower, lateral view with two petals folded down to show staminodes and pistil and one minute sepal **D** dehisced fruit, showing seeds **A, B** 20 Oct 2021, from photos of *Wood, Heintzman & Deans 18830* (PTBG) **C** 10 Aug 2023, from photos of *Wood, Heintzman & Deans 19369* (PTBG) **D** from holotype, 8 Sep 2023, *Wood, Heintzman & Deans 19143* (PTBG, US) (Illustration by Alice Tangerini).

greenish glabrous; stigma 4-lobed ca. 0.5 mm diameter; staminate flowers with sepals orbicular-ovate, free, 0.3–0.5 × 0.5–0.7 mm, glabrate; petals green with purple streaks, narrowly deltate to ovate, 2.5–4.0 mm long; stamens 8; antisepalous filaments ca. 3.5 mm long; antipetalous filaments ca. 2.5 mm long; anthers ellipsoid ca. 0.5–0.6 mm long, with pollen; style obsolete; pistillate flowers with sepals orbicular-ovate, free, 1.0 × 1.3–1.5 mm; petals green, dorsally purple, narrowly deltate to ovate, free, 2.8–3.0 mm long; staminodes 8; antisepalous filaments ca. 0.5 mm long; antipetalous filaments ca. 0.4 mm long; anthers ovoid-ellipsoid ca. 0.5–0.6 mm long, no pollen observed; style 1.5 mm long. ***Capsules*** green with purple irregular streaking when fresh, 3–4 × 10–14 mm; carpels basally connate 1/6 to 1/5 their length, exocarp glabrous; endocarp glabrous. ***Seeds*** 1–2 per carpel, ovoid, 3–3.5 mm long.

Additional specimens examined (paratypes). USA. Hawaiian Islands, Kaua'i: Līhu'e District; all collections from 'Iole headwaters • 1 ♂; 884 m alt.; 20 Oct 2021 (fl.); *Wood et al.18830* (PTBG) • 1 ♀; 884 m alt.; 20 Oct 2021 (fr.); *Wood et al. 18831* (PTBG, US) • 1 ♂; 884 m alt.; 20 Oct 2021 (fl.); *Wood et al. 18832* (BISH, PTBG) • 1 ♀; 884 m alt.; 20 Oct 2021 (fr.); *Wood et al. 18833* (PTBG) • 1 ♀; 884 m alt.; 8 Sep 2022; *Wood et al. 19146* (PTBG, US) • 1 ♀; 900 m alt.; 8 Sep 2022 (fl.); *Wood et al. 19148* (UC, PTBG) • 914 m alt.; 8 Sep 2022; *Wood et al. 19151* (BISH, NY, PTBG, UC, US) • 890 m alt.; 29 Dec 2022; *Wood & Perlman 19245* (PTBG) • 1 ♂; 884 m alt.; 10 Aug 2023 (fl.); *Wood et al. 19367* (PTBG) • 1 ♂; 884 m alt.; 10 Aug 2023 (fr.); *Wood et al. 19368* (PTBG); • 884 m alt.; 10 Aug 2023 (fl.); *Wood et al. 19369* (PTBG) • 1 ♀; 911 m alt.; 10 Aug 2023 (fl.); *Heintzman et al. KP08102301* (PTBG).

Phenology. *Melicope iolensis* has been observed with flowers during the months of August and October and with fruit in August, September and October.

Etymology. The name *Melicope* is derived from the Greek *meli*, honey and *kope*, cut in pieces, alluding to the lobed floral nectary (Lorence and Wagner 2020) and the species epithet represents the holotype locale, 'Iole, which literally means "rat" in the Hawaiian language (Pukui et al. 1974).

Affinities. Molecular phylogenetic analyses, based on RADseq datasets (Restriction-Site Associated DNA-sequencing; see Paetzold et al. (2019) for methodology), resolve *Melicope iolensis* in a clade that includes all taxa belonging to *Cubicarpa* and *Megacarpa* and as being most closely related to *M. nealae* (Appelhans et al., in preparation). *Melicope iolensis* can be distinguished from the latter species by its tree habit (vs. shrub); flowers usually 9–18 per inflorescence (vs. 1–5); sepals of staminate flowers 0.3–0.5 mm long (vs. 2.5 mm long); capsules with green and purple streaking, up to 14 mm wide (vs. green, up to 27 mm wide), carpels with exocarp glabrous, connate 1/6–1/5 their length, (vs. puberulent, connate 1/2–3/4 length); and seeds 3–3.5 mm long (vs. 5–8 mm long) (Table 1). *Melicope nealae* was previously thought extinct with only two known collections made in 1909 and 1960 and has long been looked for by NTBG Science staff. It was recently rediscovered in transitional mesic to wet forests of western Kauaʻi (Wood and Walsh 2022), is currently known from only 11 individuals and is being monitored and conserved by PEPP and NTBG.

Morphologically, *Melicope iolensis* is most similar to *M. wawraeana*, but can easily be separated by its combination of leaves abaxially glabrate to pilose-pubescent (vs. glabrous on *M. wawraeana*); inflorescence ramiflorous, rarely axillary (vs. axillary); sepals on staminate flowers glabrous, 0.3–0.5 mm long (vs. puberulent, 3.5 mm long); capsules with endocarp and exocarp glabrous, connate 1/6–1/5 their width, up to 14 mm wide, with green and purple streaking (vs. endocarp and exocarp usually sparsely puberulent, connate 1/2 width, up to 20 mm wide, dark green); and seeds 3–3.5 mm long (vs. 5–8 mm) (Table 1). *Melicope wawraeana* is quite common and known from Kauaʻi and Oʻahu (Wagner et al. 1990, 1999).

Melicope iolensis is not closely comparable morphologically to any of the remaining Hawaiian *Megacarpa* taxa. Specifically on Kauaʻi, as a tree up to 8 m tall, it differs from the shrubs *M. feddei* (H.Lév.) T.G.Hartley & B.C.Stone, *M. kavaiensis* (H.Mann) T.G.Hartley & B.C.Stone and *M. macropus* (Hillebr.) T.G.Hartley & B.C.Stone. It also differs from those three shrub species in having longer petioles and leaves, inflorescence ramiflorous, rarely axillary, shorter sepals and smaller capsules and seeds (Table 1). The only two remaining *Megacarpa* taxa on Kauaʻi are *M. cruciata* (A.Heller) T.G.Hartley & B.C.Stone and *M. puberula* (H.St.John) T.G.Hartley & B.C.Stone, from which *M. iolensis* also starkly differs in having longer petioles and leaves, inflorescence ramiflorous, rarely axillary, shorter sepals, glabrous endocarp and smaller capsules and seeds (Table 1).

Distribution and ecology. *Melicope iolensis* is endemic to the volcanic island of Kauaʻi (Fig. 1), where it is known from only 15 individuals located in the remote, upper headwater valley of ʻIole. The type location is in a hanging valley, having vertical cliffs above and a series of cliffs and waterfalls below, isolating its accessibility (Fig. 4C).

The plant community where *Melicope iolensis* occurs is a *Metrosideros* Banks ex Gaertn. (Myrtaceae) / *Cheirodendron* Nutt. ex Seem. (Araliaceae) montane wet forest with matting ferns of *Dicranopteris* Bernh. and *Diplopterygium* (Diels) Nakai (Gleicheniaceae) and a dissecting riparian drainage. The forested slopes are steep with a diverse mixture of native sedges, grasses, ferns, herbs, shrubs and trees, along with a high density of terrestrial and epiphytic bryophytes throughout. Associated genera of trees include *Polyscias* J.R.Forst. & G.Forst. (Araliaceae); *Pritchardia* Seem. & H.Wendl. (Arecaceae);

Figure 4. *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner **A** habit of young tree **B** fruiting branch with axillary and fasciculate cymes **C** habitat, looking down into hanging valleys below Kawaikini summit. All photos by K.R. Wood. **A** 29 Dec 2022, *Wood & Perlman 19245* (PTBG) **B** from holotype, 8 Sep 2022, *Wood, Heintzman & Deans 19143* (PTBG, US) **C** 28 Jan 2022.

Dubautia Gaudich. (Asteraceae); *Cyanea* Gaudich. (Campanulaceae), *Perrottetia* Kunth (Dipentodontaceae); *Antidesma* L., *Euphorbia* L. (Euphorbiaceae); *Hydrangea* Gronov. (Hydrangeaceae); *Geniostoma* J.R.Forst. & G.Forst. (Loganiaceae); *Eurya* Thunb. (Pentaphylacaceae); *Myrsine* L. (Primulaceae); *Syzygium* Gaertn. (Myrtaceae); *Bobea* Gaudich., *Coprosma* J.R.Forst. & G.Forst., *Kadua* Cham. & Schltdl., *Psychotria* L. (all Rubiaceae); *Melicope* J.R.Forst. & G.Forst.

Figure 5. *Melicope iolensis* K.R.Wood, Lorence & W.L.Wagner **A** infructescence with connate capsules (*Megacarpa*) showing green and purple streaking **B** staminate flower and buds **C** abaxial leaf surface showing close-up of pubescence. All photos by K.R. Wood. **A, C** from holotype, 8 Sep 2022, *Wood, Heintzman & Deans 19143* (PTBG, US) **B** 20 Oct 2021, *Wood, Heintzman & Deans 18830* (PTBG).

(Rutaceae); and *Pipturus* Wedd. and *Touchardia* Gaudich. (Urticaceae). Genera of sedges and grasses include *Carex* L., *Cyperus* L., *Machaerina* Vahl (Cyperaceae); *Eragrostis* Wolf, *Panicum* L. (Poaceae); herbs and shrubs include *Bidens* L. (Asteraceae); *Vaccinium* L. (Ericaceae); *Cyrtandra* J.R.Forst. & G.Forst. (Gesneriaceae); and the woody climber *Freycinetia* Gaudich. (Pandanaceae). Genera of ferns include *Asplenium* L., *Hymenasplenium* Hayata (Aspleniaceae); *Deparia*

Table 1. Comparison of morphological characters of all eight Kauaʻi *Melicope* species with carpels connate at base, capsules 4-lobed, and leaves opposite (i.e., *Megacarpa*).

Character	*M. iolensis*	*M. cruciata*	*M. feddei*	*M. kavaiensis*	*M. macropus*	*M. nealae*	*M. puberula*	*M. wawraeana*
Habit	Tree	Tree	Shrub	Shrub	Shrub	Shrub	Tree	Tree
Leaf length (cm)	(8–)14–25(–33)	8–17	2–8(–14)	5.5–18	10–15	3–18	6–17	4–20(–30)
Abaxial leaf pubescence	Glabrate to pilose–pubescent	Sparsely pilose	Glabrous	Sparsely pilose	Glabrate	Pilose–pubescent	Sparsely pilose	Glabrous
Petiole length (mm)	(20–)30–70	10–35	5–25	10–40	12–20	10–30	20–30	10–50
Inflorescence	Ramiflorous and axillary	Axillary	Axillary	Axillary	Axillary	Axillary	Axillary	Axillary
# of flowers	9–18	3–6(–12)	1–5(–15)	(1–)3–9(–11)	1–3	1–5	3–9(–15)	5–15(–21)
♂ Sepal length (mm)	0.3–0.5	3–3.5	2–2.5	3.5–5.5	Unknown	2.5	3–3.5	3.5
♀ Sepal length (mm)	1.0	3.5–5	2–2.5	2–4	1.5	2.5	2–4.5	3.0
♀ Sepal indumentum	Glabrous	Puberulent	Glabrous to sparsely puberulent	Glabrate to sparsely puberulent	Minutely puberulent	Puberulent	Puberulent	Puberulent
Capsule width (mm)	10–14	24–34	16–25(–30)	(13–)18–40	25–35	20–27	14–20	11–20
Carpel length (mm)	4–6	12–17	7–12(–14)	8–20	12–18	10–12	7–10	6–7
Carpel % connate	1/6–1/5	1/4	1/6–1/4	1/5–1/2	1/6	1/2–3/4	1/2	(1/3–)1/2
Capsule color	Green w/ purple streaking	Green	Reddish green	Green	Green	Green	Dark red	Dark green
Pubescence on exocarp	Glabrous	Glabrous	Glabrous	Glabrous	Sparsely puberulent	Puberulent	Puberulent	Puberulent to glabrous
Pubescence on endocarp	Glabrous	Densely short villous	Glabrous	Glabrous	Glabrous	Glabrous	Short villous	Sparsely puberulent to glabrous
Seed length (mm)	3–3.5	7.5	4–8	6–10	5–6	5–8	5–6	5–8

Hook. & Grev., *Diplazium* Sw. (Athyriaceae); *Sadleria* Kaulf. (Blechnaceae); *Cibotium* Kaulf. (Cibotiaceae); *Microlepia* C.Presl (Dennstaedtiaceae); *Ctenitis* (C.Chr.) C.Chr. (Dryopteridaceae); *Hoiokula* S.E.Fawc. & A.R.Sm. and *Menisciopsis* (Holttum) S.E.Fawc. & A.R.Sm. (Thelypteridaceae).

Modification of existing key to Hawaiian *Melicope* (in Wagner et al. 1990, 1999)

To accommodate *Melicope iolensis*, the following couplets can be inserted into the existing key to Hawaiian *Melicope* (treated as *Pelea*) by Stone, Wagner and Herbst (in Wagner et al. (1990, 1999), p. 1178). Note: K = Kauaʻi; O = Oʻahu.

18(15) Carpels connate 1/6–1/2 their length, sometimes recurved or reflexed before dehiscence; endocarp glabrous or pubescent; leaves rarely inrolled-revolute near base (*Megacarpa*) **19**
18 Carpels connate 2/3 to throughout their length, never recurved; endocarp glabrous; leaves often inrolled-revolute near base (*Cubicarpa*) **64**
19(18) Exocarp sparsely to densely puberulent or tomentose, at least towards base along suture **20**
19 Exocarp glabrous or glabrate, sometimes with a few hairs widely spaced over surface **49**
49(19) Endocarp densely and uniformly short-villous; K .... ***M. cruciata***
49 Endocarp glabrous or sparsely puberulent, especially along suture **50**
50(49) Leaves ternate; O .... ***M. lydgatei***
50 Leaves opposite **51**
51(50) Most petioles 0–10 mm long **52**
51 Most petioles over 10 mm long **58**

58(51) Ovary sparsely to densely puberulent or tomentulose, exocarp glabrate to minutely puberulent **59**
58 Ovary and exocarp glabrous.. **60**
60(58) Inflorescence ramiflorous and axillary, leaves glabrate to pilose-pubescent abaxially, seeds 3–3.5 mm long; K.......................... ***M. iolensis***
60 Inflorescence axillary, leaves glabrous abaxially, seeds 4–8 mm long. **60a**
60a(60) Carpels slightly ascending in fruit, 7–12(–14) mm long, sprawling, prostrate or erect shrubs 1–2 m tall, leaves 2–8(–14) cm long; K..... ***M. feddei***
60a Carpels spreading at 180° or reflexed in fruit, 10–24 mm long, sprawling shrubs or trees 1–10 m tall, leaves usually more than 8 cm long **61**

Preliminary conservation assessment. IUCN Red List Category

Melicope iolensis falls into the Critically Endangered (CR) category according to the criteria (B1ab(iii)+B2ab(iii) which reflects a severely limited EOO of 1 km^2 and AOO of 1 km^2, a severely fragmented population of only one small subpopulation consisting of 15 mature plants and a continued decline in quality of habitat inferred. The continued decline in quality of habitat for *M. iolensis* is evidenced by severe habitat degradation from invasive non-native mammals such as goats (*Capra hircus* L.), pigs (*Sus scrofa* L.) and rats (*Rattus* spp.), along with introduced slugs, insects and disease. In January 2024, we observed the destruction of numerous rare *Cyanea* species in the immediate area by wild goats.

Other serious threats to the habitat include hurricane force winds, flash floods and landslides triggered after torrential rains. Specific invasive non-native plants that displace naturally occurring ones locally include *Erigeron karvinskianus* DC., (Asteraceae); *Buddleia asiatica* Lour. (Buddlejaceae); *Sphaeropteris cooperi* (Hook. ex F. Muell.) R.M.Tryon (Cyatheaceae); *Juncus planifolius* R.Br. (Juncaceae); *Miconia crenata* (Vahl.) Michelang. (Melastomataceae); *Psidium cattleyanum* Sabine (Myrtaceae); *Axonopus fissifolius* (Raddi) Kuhlm., *Paspalum urvillei* Steud., *Paspalum conjugatum* P.J.Bergius (Poaceae); and *Rubus rosifolius* Sm. (Rosaceae).

Seeds of *Melicope iolensis* have been collected by NTBG Science staff and plants are now being cultivated at the NTBG Horticultural Center, Kaua‘i, Hawai‘i.

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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

Kenneth R. Wood / lead author and field research; David H. Lorence / co-author and field research; Warren L. Wagner / co-author; Marc S. Appelhans / co-author, phylogenetic analyses.

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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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