

A taxonomic revision of *Cenchrus* L. (Poaceae) in Thailand, with lectotypification of *Pennisetum macrostachyum* Benth.

Paweena Wessapak^{1,2}, Chatchai Ngernsaengsaruy^{1,2}, Suthee Duangjai³

¹ Department of Botany, Faculty of Science, Kasetsart University, Chatuchak, Bangkok 10900, Thailand

² Biodiversity Center, Kasetsart University (BDCKU), Chatuchak, Bangkok 10900, Thailand

³ Department of Biology, Faculty of Forestry, Kasetsart University, Chatuchak, Bangkok 10900, Thailand

Corresponding author: Chatchai Ngernsaengsaruy (fsciccn@ku.ac.th)

Abstract

A revision of the genus *Cenchrus* (Poaceae) in Thailand is reported. Seven species, i.e. *C. brownii*, *C. ciliaris*, *C. clandestinus*, *C. echinatus*, *C. pedicellatus*, *C. purpureus* and *C. setosus* are described in this taxonomic treatment. This genus is an exotic species and distributed throughout the floristic regions. All the species have become naturalised to Thailand as a weed and found growing in wastelands, open areas by the roadside, disturbed sites, the edge of rice fields and the edge of deciduous and evergreen forests at elevations between 0 and 2,650 m alt. *Pennisetum macrostachyum*, a synonym of *Cenchrus purpureus* is lectotypified. Detailed morphological descriptions, illustrations and a key to the species are presented, along with information on distributions, habitats, ecology, phenology, vernacular names and specimens examined.

Key words: Gramineae, grasses, lectotype, revision, taxonomy



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Introduction

The Poaceae or grass family, also known as Gramineae, is one of the largest families of flowering plants, consists of approximately 12,000 species in 789 accepted genera and is widely distributed around the world (Soreng et al. 2022). This family is able to adapt to a wide range of habitats as it can survive in different environmental stresses. Grasses are both common and important plants. The world's human population relies on grasses, which include rice, wheat, oat and maize and are a valuable source of food for humans as they contain fibres, proteins and some nutrients. Most of them have a short life, fast growth and undergo high biomass accumulation. As such, several species are considered as good fodder and a source of nutrients for the livestock. Many species are also used as ornamental plants in landscaping and gardening, for beautifying the lawns. In addition, some grasses are used as raw materials in manufacturing paper, extracting the essential oils and are also used to prevent soil erosion and surface run-off (Chase 1921; Bor 1960; Gould 1968; McIlroy 1972; Oyen and Dung 1999; Obi Reddy et al. 2014; Chavre and Sonawane 2021).

Grasses have various morphological characters. Their reproductive part consists of a small spikelet which is a significant characteristic used in their

identification. The classification of grass family has been traditionally based on morphological and anatomical data. During recent times, the molecular Deoxyribonucleic acid or DNA data have been also used in several studies to understand the phylogenetic relationship within the family (Mathews et al. 2000; Kellogg 2015; Soreng et al. 2015, 2017). According to a recent report, this family can be phylogenetic classified into 12 subfamilies, 54 tribes and 109 subtribes, with the Panicoideae subfamily being the largest number in terms of the genera (Soreng et al. 2022).

The genus *Cenchrus* belongs to the subtribe Cenchrinae, tribe Paniceae, subfamily Panicoideae (Soreng et al. 2022). It comprises of about 107 species (including the genus *Pennisetum* s. str.). The genus *Cenchrus* L. and *Pennisetum* Rich. have been traditionally considered to be related genera. Both the genera are differentiated by the characteristics of the bristles subtending the spikelets which are fused well above the base in *Cenchrus*, while those in the *Pennisetum* are free or fused only at the base. Recent molecular phylogenetic studies have confirmed that most species of *Cenchrus* are nested in *Pennisetum*. Several studies strongly suggest to combine the two genera. Thus, with the generic name *Cenchrus* given the priority, all species of *Pennisetum* were transferred to *Cenchrus* (Donadio et al. 2009; Chemisquy et al. 2010; Verloove 2012; Veldkamp 2014).

The genus *Cenchrus* is native to the tropical and subtropical Old World and Americas and introduced to several countries for utilisation (POWO 2023). Several well-known species of this genus are widely planted for forage, such as Napier grass (*C. purpureus* (Schumach.) Morrone), Buffel grass (*C. ciliaris* L.) and Pearl millet (*C. americanus* (L.) Morrone). Some species are cultivated for ornamentation, such as Fountain grass (*C. setaceus* (Forssk.) Morrone), Chinese fountain grass (*C. alopecuroides* (L.) Thunb), Feathertop grass (*C. longisetus* M. C. Johnst.) and White fountain grass (*C. orientalis* (Rich.) Morrone), because of their fluffy inflorescences. However, some species are considered invasive species in several countries, such as Southern sandbur (*C. echinatus* L.), Buffel grass (*C. ciliaris* L.) and Mission grass (*C. setosus* Sw.) (Verloove and Sánchez Gullón 2012; Veldkamp 2014; Global Invasive Species Database 2023).

The usefulness of this genus led to its introduction in Thailand, be it for its ornamental usage or for foraging purposes. Some species are naturalised and considered as invasive and noxious weeds. Even though there have been several studies on grasses in Thailand (Chaisongkram et al. 2013; Teerawatananon et al. 2014; Boonsuk et al. 2016; Wessapak & Ngernsaengsaruy 2021, 2022), the identification of some grasses relies on the literature of neighbouring countries. The species of this genus found in Thailand is yet to be revised. Therefore, the taxonomic treatment presented here will contribute to the “Flora of Thailand” project.

Material and methods

The study was based on the herbarium specimens of the following Herbaria: AAU, BK, BKF, BM, C, CMUB, K, KKU, P, PSU and QBG, including digital specimen images from B, BISH, E, G, LINN, S and W. Additional specimens were collected on recent field surveys made throughout Thailand. Plant morphological characters, ecological data and flowering and fruiting periods were also recorded. Most of the grass specimens collected from fieldwork have been submitted to

BK and BKF. The identifications were made using morphological characters observed using a stereomicroscope and the available taxonomic literature available in Thailand and the neighbouring region.

Taxonomic treatment

Cenchrus L., Sp. Pl.: 1049. 1753

Pennisetum Rich. in Pers., Syn. Pl. 1: 72. 1805. Type species: *Pennisetum typhoideum* Rich.

Odontelytrum Hack., Oesterr. Bot. Z. 48: 86. 1898. Type species: *Odontelytrum abyssinicum* Hack.

Snowdenia C. E. Hubb., Bull. Misc. Inform. Kew 1929: 30. 1929. Type species: *Snowdenia microcarpha* C. E. Hubb.

Kikuyuochloa H. Scholz, Feddes Repert. 117: 513. 2006. Type species: *Kikuyuochloa clandestina* (Hochst. ex Chiov.) H. Scholz (Basionym: *Pennisetum clandestinum* Hochst. ex Chiov.)

Type species. *Cenchrus echinatus* L.

Description. Annual or perennial, tufted. **Culms** geniculate ascending or prostrate. **Leaf sheaths** with or without keeled conspicuous, margins hyaline or hairy. **Ligules** ciliolate membrane, ciliolate rim or a fringe of hairs. **Leaf blades** linear, margins scabrous, usually chartaceous. **Inflorescence** spiciform panicle, usually cylindrical; racemes very short or false spike. **Spikelets** 1–8 in cluster, subtended by involucre of bristles and spines, these free at base to forming a cup and burr-like, filiform, terete or flattened, spikelet dorsally compressed; sessile or pedicelled. **Lower glume** shorter than spikelet or absent. **Florets** 2. **Lower floret** male or sterile. **Lower lemma** variable. **Upper floret** bisexual. **Lodicules** present or absent.

A genus of approximately 107 pantropical species, seven species were introduced in Thailand and have become naturalised in the country (the taxonomic treatments and a key to the species excluding the species were introduced so as to be useful in Thailand, but were not found or recorded in their natural habitat).

Key to the species

- 1 Inner involucre connate into a cup and burr-like forming or connate at least the base (*Cenchrus* s.str.) **2**
- Inner involucre free at the base (*Pennisetum* s.str.) **4**
- 2 Involucre of a cup and burr-like forming, coriaceous flattened spines connate at lower part as 1–3 mm long; bristles with retrorsely scabrous; upper glume 3 or 5-nerved **3**
- Involucre of slightly flattened bristles connate only at the base less than 1 mm long; bristles with antrorsely scabrous; upper glume 1-nerved **2. C. ciliaris**
- 3 Raceme crowded on inflorescence axis; axis internode 0.5–2 mm long **1. C. brownii**
- Raceme loose on inflorescence axis; axis internode 2–3 mm long **4. C. echinatus**

- 4 Culms prostrate, mat-forming; inflorescence very short panicle with central axis less than 1 cm long, concealed within the uppermost leaf sheath; 2–3 racemes along central axis; spikelet 1.6–1.8 cm long; upper glume absent; stigma 2–3 cm long **3. *C. clandestinus***
- Culms erect or ascending; inflorescence with central axis more than 1 cm long, exerted from the uppermost leaf sheath; more than 4 racemes along central axis; spikelet less than 1 cm long; upper glume present; stigma less than 1 cm long **5**
- 5 Ligules a fringe of hairs; inflorescence axis terete; upper glume shorter than spikelet; lower lemma apex acuminate and chartaceous; upper floret persistent **6. *C. purpureus***
- Ligules ciliate membrane; inflorescence axis shortly decurrent ribs; upper glume as long as spikelet; lower lemma apex trifid and membranous; upper floret caducous **6**
- 6 Spikelet 2–4 in cluster, one sessile and the other pedicelled spikelets **5. *C. pedicellatus***
- Spikelet solitary, sessile spikelet **7. *C. setosus***

1. *Cenchrus brownii* Roem. & Schult., Syst. Veg. 2: 258. 1817.

Figs 1, 2

≡ *Cenchrus inflexus* R. Br., Prodr. Fl. Nov. Holland.: 195. 1810.

= *Cenchrus viridis* Spreng., Syst. Veg. 1: 301. 1824. Type: West Indies, Guadeloupe, C. G. Bertero s.n. (holotype: B [B100248055] seen on digital image). ≡ *Cenchrus echinatus* L. var. *viridis* (Spreng.) Spreng., Fl. Brit. W. I.: 556. 1864.

= *Cenchrus hexaflorus* Blanco, Fl. Filip.: 36. 1837. Type: Philippines, Manila, Luzon, Feb 1915, E. D. Merrill Sp. Blancoan. 811 (neotype, designated by Merrill 1918, pg. 68: US n.v.; isoneotypes: L n.v., P [P00642071!], W n.v.).

= *Cenchrus dactylolepis* Steud., Syn. Pl. Glumac. 1: 109. 1854. Type: Surinam, 1843, F. W. R. Hostmann 12a (holotype: P [P00642090!]; isotype: BAA n.v.).

Type. AUSTRALIA, Arnheim South Bay, 6 Feb 1803, R. Brown 6140 (lectotype, designated by DeLisle 1963, pg. 280: BM [BM000795713!]; isolectotypes: E [E00381727] seen on digital image, K [K000215260!], P [P00642070!], US (frag.) n.v.).

Description. Annual, tufted, **Culms** geniculate ascending, 30–80 cm high; nodes glabrous; internode subterete, 5–13 cm long, 1–3 mm in diam., glabrous. **Leaf sheaths** 4.5–10 cm long, margins membranous, glabrous. **Ligules** a fringe of hairs, 0.5–1 mm long. **Collar** glabrous. **Leaf blades** linear, 14–38 × 0.6–1 cm, apex acute, base rounded, margins scabrous, chartaceous, usually conduplicate, glabrous on both surfaces. **Inflorescence** spiciform panicle, 14–43 × 0.8–1.2 cm (including bristles); central axis angular, 5.5–10 cm long, axis internode 0.5–2 mm long, scabrous to glabrescent; peduncle terete, 7–34 cm long, glabrous or scabrous; short racemes crowded along central axis; raceme with (1–)2–3 spikelets in cluster, all sessile, subtended by an involucre of burr-like spines and bristles. **Involucre** compose of outer and inner circles; outer circle usually longer than inner circle; outer involucre of bristles, numerous and filamentous, free, 1–6 mm long, one conspicuous longest bristle 4.5–9 mm long, retrorsely scabrous; inner involucre of 6–10 flattened spines,

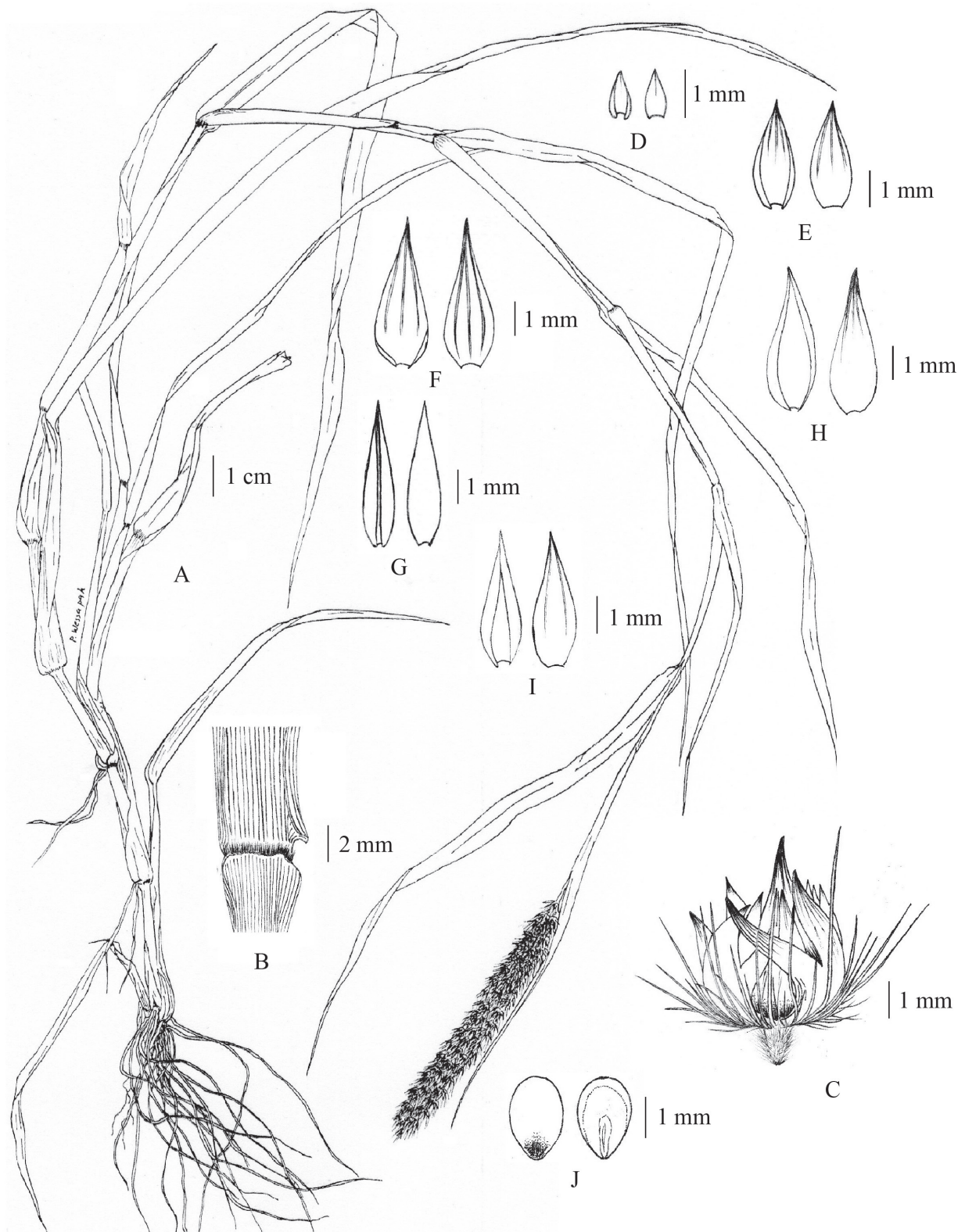


Figure 1. *Cenchrus brownii* Roem. & Schult **A** habit **B** ligule **C** spikelets with involucre **D** lower glumes **E** upper glumes **F** lower lemmas **G** lower paleas **H** upper lemmas **I** upper paleas **J** caryopsis. (Drawn from P. Wessapak 365 by Paweena Wessapak).

4–5.2 mm long, connate at lower part 1–3 mm long, burr-like forming, a cup up to 5 mm in diam., coriaceous, puberulose and retrorsely scabrous; involucre falling with spikelets; stipe (raceme-based) 1–2 mm long, hairy. **Spikelets**

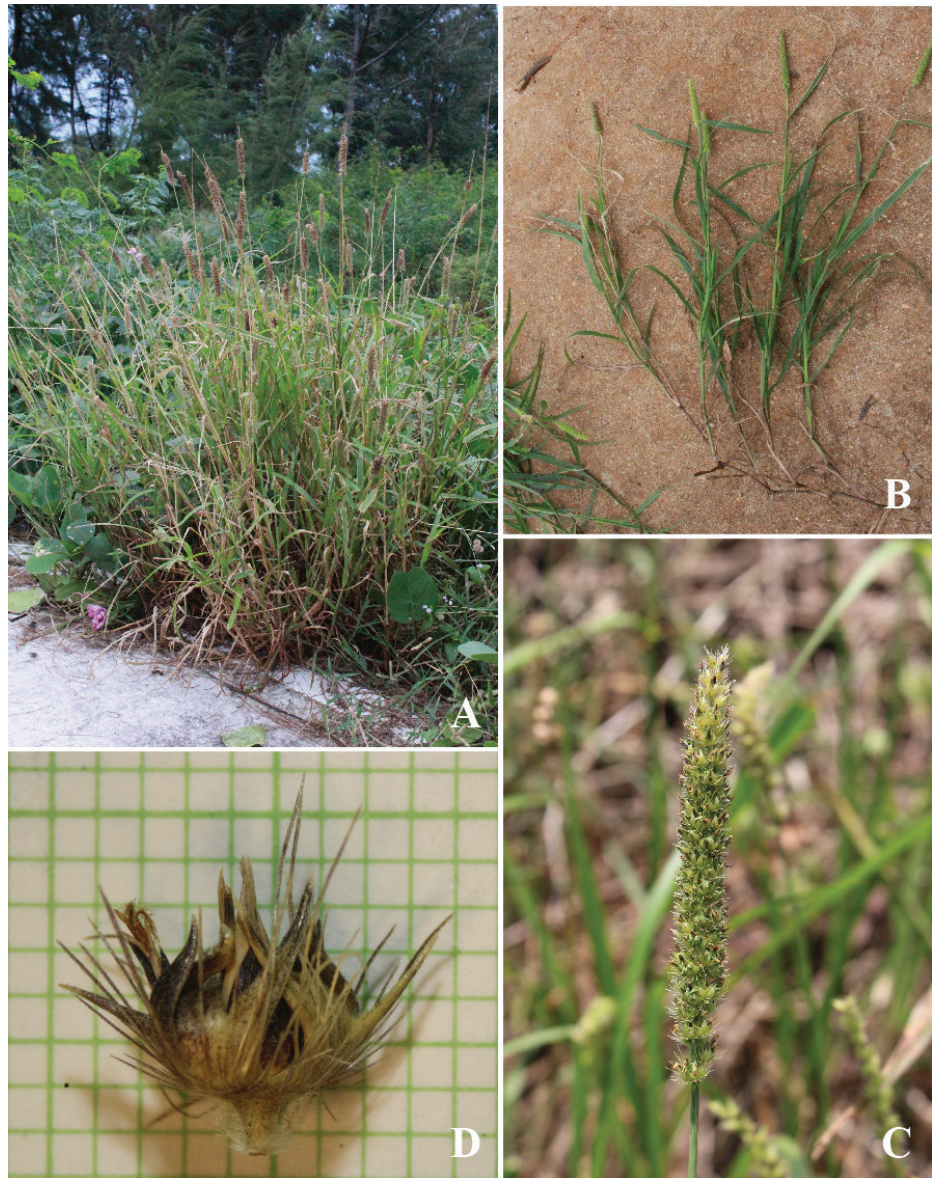


Figure 2. *Cenchrus brownii* Roem. & Schult **A** habitat **B** habit **C** inflorescence **D** spikelets with involucre. (Photographs: Paweena Wessapak).

dorsally compressed, lanceolate, $3.6\text{--}5.5 \times 1\text{--}1.7$ mm. **Lower glume** usually absent, if well-developed, ovate, $0.6\text{--}1.2 \times 0.3\text{--}0.5$ mm, apex acute, membranous, glabrous, 1-nerved. **Upper glume** ovate or lanceolate-ovate, $3\text{--}4 \times 1.2\text{--}1.8$ mm, apex acute or acuminate, membranous to chartaceous, glabrous, 3 or 5-nerved. **Florets** 2. **Lower floret** male or sterile. **Lower lemma** lanceolate, $3.5\text{--}5 \times 1\text{--}1.5$ mm, apex acute or acuminate, membranous to chartaceous, glabrous, 3 or 5-nerved. **Lower palea** lanceolate-oblong, $3.2\text{--}5 \times 0.8\text{--}1$ mm, apex acute or acuminate, margins folded with antrorsely scabrous, membranous, glabrous, 2-nerved or palea absent. **Upper floret** bisexual. **Upper lemma** lanceolate or ovate-lanceolate, $2.5\text{--}5 \times 1\text{--}1.8$ mm, apex acute or acuminate, margins hyaline, coriaceous, glabrous, 5-nerved. **Upper palea** lanceolate, $2.5\text{--}5 \times 0.9\text{--}1.5$ mm, apex acuminate, margins hyaline, coriaceous, glabrous, 2-keeled, 2-nerved. **Lodicules** 2, ca. 0.5 mm long, truncate. **Stamens** 3; filament ca. 3 mm long; anther yellow 1–1.6 mm long. **Pistil** ovary elliptic, $0.6\text{--}1 \times$

0.2–0.3 mm; style 2; stigma plumose. **Caryopsis** obovoid or ellipsoid, gibbous, 1.5–2.5 × 1–1.7 mm.

Distribution. Native to tropical and subtropical America. Introduced to South-east Asia and Oceania.

Distribution in Thailand. NORTHERN: Chiang Mai (Mae Rim, Doi Suthep-Pui, Mueang Chiang Mai), Tak (Wang Chao Forest, Bhumibol Dam), Sukhothai (Sawan Khalok), Kamphaeng Phet (Phran Kratai), Nakhon Sawan; NORTH-EASTERN: Khon Kaen (Chum Phae); EASTERN: Nakhon Ratchasima (Pak Chong), Amnat Charoen; SOUTH-WESTERN: Uthai Thani (Khao Phraya Phai Ruea), Kanchanaburi (Sai Yok, Ban Kao), Ratchaburi (Huai Yang), Prachuap Khiri Khun (Pran Buri, Hat Sai Noi); CENTRAL: Lop Buri (Sap Champa), Suphan Buri (U Thong, Bang Pla Ma), Samut Prakan (Pak Nam), Bangkok (Phu Khao Thong, Chatuchak); SOUTH-EASTERN: Chon Buri (Sattahip, Si Racha), Rayong (Klaeng); PENINSULAR: Chumphon, Ranong (Kraburi), Phuket (Hat Nai Yang), Nakhon Si Thammarat, Satun (Tarutao), Songkhla (Hat Yai).

Habitat and ecology. In wastelands, open areas by the roadside, the edge of rice fields and the edge of deciduous and evergreen forests at elevations between 0 and 500 m above mean sea level (a.m.s.l.). Flowering and fruiting throughout the year.

Vernacular name. Ya bung (หญ้าบัง); Brown's burgrass, Brown's sandbur, Fine-bristle burgrass, Fine-bristle sandbur, Slim-bristle sandbur (English).

Specimens examined. THAILAND. Amnat Charoen: 28 Oct 2001, *S. Laegaard & M. Norsaengsri* 21856 (AAU, BKF, QBG); **Bangkok:** Bang Khen, 12 Nov 1952, *K. Suvatabandhu* 33 (BK); Chatuchak, Lat Yao, 26 Dec 2016, *P. Wessapak* 346 (BK); Kasetsart University, 12 Sep 2017, *P. Wessapak* 393 (BK); Phu Khao Thong, 18 Dec 1955, *T. Smitinand* 3147 (BKF); 14 Mar 1920, *A. F. G. Kerr* 4063 (BM, K); 5 Jan 1958, *Th. Sørensen, K. Larsen & B. Hansen* 22 (C, K); 4 Apr 1958, *Th. Sørensen, K. Larsen & B. Hansen* 7904 (BKF, C, K); **Chiang Mai:** Doi Suthep-Pui, 7 Nov 1988, *W. Nanakorn et al.* 2296 (QBG); Mae Rim, 8 Aug 1994, *W. Nanakorn et al.* 2167 (QBG); *ibid.*, 15 Sep 1995, *W. Nanakorn et al.* 4219 (QBG); *ibid.*, 28 Nov 1995, *W. Nanakorn et al.* 5377 (QBG); Mueang Chiang Mai, 13 Sep 1995, *W. Nanakorn et al.* 4277 (QBG); **Chon Buri:** Sattahip, 26 Nov 1964, *S. Sutheesorn* 224 (BK); Si Racha, 8 Nov 1992, *J. F. Maxwell* 92-709 (P); 30 May 1964, *C. Hambananda* 218 (BKF); **Chumphon:** 6 Apr 1967, *S. Sutheesorn* 2127 (BK); **Kamphaeng Phet:** Phran Kratai, Khui Ban Ong, Ban Rai Dong, 22 Oct 1992, *J. F. Maxwell* 92-648 (AAU, BKF, P); **Kanchanaburi:** Ban Kao, 8 Nov 1961, *K. Larsen* 8044 (C, K); Sai Yok, 15 Aug 2004, *S. Sirimongkol* 136 (BKF); Sai Yok, Lum Sum, 17 Feb 2000, *J. F. Maxwell* 00-61 (BKF); Sai Yok, Sai Yok Noi, 5 Nov 1979, *T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara & C. Niyomdham* T-21696 (BKF); **Khon Kaen:** Chum Phae, 29 Oct 2001, *S. Laegaard & M. Norsaengsri* 21870 (AAU, BKF, QBG); Khon Kaen University, 24 Oct 1982, *P. Chantharanonthai* 247 (KKU); *ibid.*, 20 Nov 1997, *S. Saensuk s.n.* (KKU); **Lop Buri:** Sap Champa, 19 Nov 1984, *G. Murata, C. Phengklai, S. Mitsuta, T. Yahara, H. Nagamasu & N. Nantasana* T-68121 (AAU, BKF); **Nakhon Ratchasima:** Pak Chong, 5 May 1971, *P. Wisuthasom* 10 (BK); *ibid.*, 10 Oct 1979, *T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara & T. Santisuk* T-18228 (BKF); **Nakhon Sawan:** 21 Jul 1973, *G. Murata, N. Fukuoka & C. Phengklai* T-16582 (BKF); **Nakhon Si Thammarat:** 27 May 1995, *W. Nanakorn et al.* 3626 (QBG); **Phuket:** Thalaeng, Hat Nai Yang, 12 Sep 1996, *W. Nanakorn et al.* 7455 (QBG); **Prachuap Khiri Khun:** Hat Sai Noi, 12 Nov 2017, *P. Wessapak* 435 (BK);

Pran Buri, 11 Nov 2017, *P. Wessapak* 430 (BK); 14 Sep 1926, *Put* 241 (BK, BM, K); 18 Aug 1967, *T. Shimitzu, N. Fukuoka & A. Nalampoon T-7644* (BKF); **Ranong**: Kraburi, 17 Jan 1987, *J. Supapol* 284 (PSU); **Ratchaburi**: Huai Yang, 9 Aug 1966, *K. Larsen, T. Smitinand & E. Warncke* 1326 (AAU, C, K, P); **Rayong**: Klaeng, 30 Apr 2017, *P. Wessapak* 365 (BK); **Samut Prakan**: Pak Nam, 22 Apr 1924, *A. Marcan* 1692 (BM); **Satun**: Tarutao, 23 Oct 1979, *G. Congdon* 99 (AAU, PSU); **Songkhla**: Hat Yai, Prince of Songkhla University, 11 Mar 1986, *J. F. Maxwell* 86-163 (AAU, PSU); **Sukhothai**: Sawan Khalok, *D. E. Paray* 17 (K); **Suphan Buri**: Bang Pla Ma, Phai Kong Din, 17 Sep 2017, *P. Wessapak* 399 (BK); U Thong, 26 Mar 2017, *P. Wessapak* 355 (BK); **Tak**: Ban Na, 20 May 1959, *T. Smitinand* 513 (BK); Rahaeng, 9 Jan 1904, *E. Lindhard* 56 (C, K); **Uthai Thani**: Khao Phraya Phai Ruea, 7 Sep 1975, *S. Sutheesorn* 3426 (BK).

Note. This species is similar to *Cenchrus echinatus* in terms of having involucre burr-like formation, but differing from the species by having a denser inflorescence, with the involucre usually having a longer outer bristle. In Thailand, it was introduced for foraging and has since become naturalised and is treated as a weed.

2. *Cenchrus ciliaris* L., Mant. Pl. Altera 2: 302. 1771.

Figs 3, 4

≡ *Pennisetum ciliare* (L.) Link, Hort. Berol. 1: 213. 1827.

= *Pennisetum petraeum* Steud., Syn. Pl. Glumac. 1: 106. 1854. Type: Iran, Mar 1842, *C. G. T. Kotschy* 170 (lectotype, designated by Gutiérrez and Morone 2012, pg. 264: P [P00642074] seen on digital image; isoelectotypes: K [K000244671!], P [P00642073] seen on digital image).

= *Cenchrus longifolius* Hochst. ex Steud., Syn. Pl. Glumac. 1: 109. 1854. Type: Sudan, Arasch-Cool, 16 Oct 1839, *C. G. T. Kotschy* 190 (holotype: P [P00442947!]; isotypes: BM [BM000923378!], E [E00200302] seen on digital image, G n.v., K [K000281252!], P [P00442951!, P00442948!]).

Type. SOUTH AFRICA, Cape, *Koenig* s.n. (lectotype, designated by Clayton & Renvoize in Polhill (ed.) (1982, pg. 691): LINN [LINN-1217.9] seen on digital image).

Description. Perennial, tufted, **Culms** geniculate ascending, 45–75 cm high; nodes glabrous; internode subterete, 4–13 mm long, 1–2 mm in diam., glabrous. **Leaf sheaths** keeled conspicuous, 4–8 cm long, margins hairy, glabrous or hairy. **Ligules** a fringe of hairs, 1–1.5 mm long. **Collar** glabrous. **Leaf blades** linear, 16–32 cm × 2–7 mm, apex acute, base rounded, margins scabrous, chartaceous, both surfaces hairy or lower surface glabrous and upper surface pilose. **Inflorescence** spiciform panicle, 17–33 × 1.5–2.2 cm (including bristles); central axis angular, 6–11 cm long, axis internode 0.5–1.5 mm long, scabrous and puberulose; peduncle terete, 8–25 cm long, scabrous; short raceme along central axis; raceme with (1–)2–3(–4) spikelets in cluster, all sessile, subtended by an involucre of bristles. **Involucre** composed of outer and inner circles; outer circle usually shorter than inner circle; outer involucre of bristles, numerous and filamentous, free, 1–7 mm long, antrorsely scabrous; inner involucre of 8–13 slightly flattened bristles with 6–11 mm long, connate only at the base less than 1 mm long, one conspicuous longest bristle 0.9–1.4 cm long, hairy and

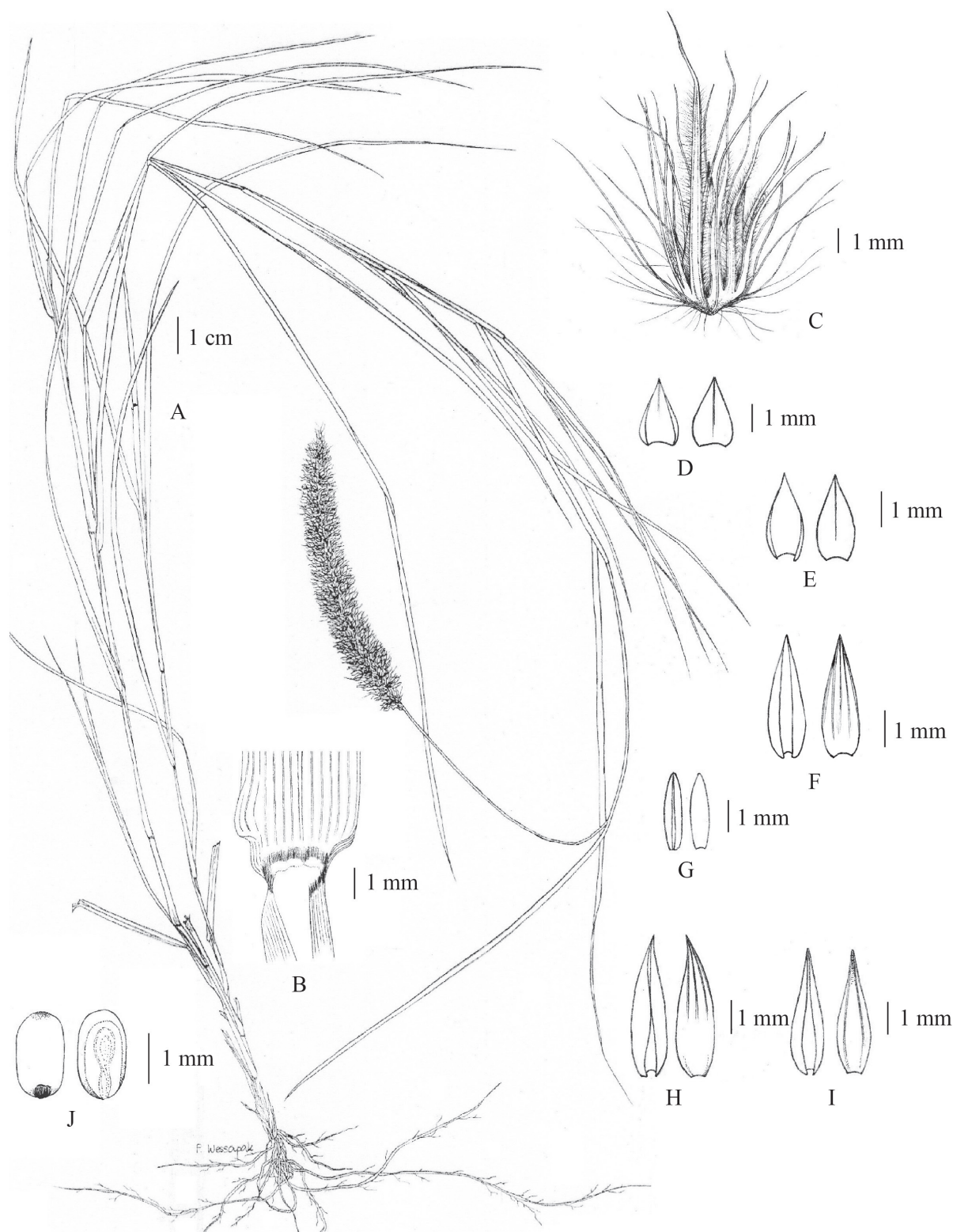


Figure 3. *Cenchrus ciliaris* L. **A** habit **B** ligule **C** spikelets with involucre **D** lower glumes **E** upper glumes **F** lower lemmas **G** lower paleas **H** upper lemmas **I** upper paleas **J** caryopsis. Drawn from P. Wessapak 376 by Paweena Wessapak.

antrorsely scabrous; involucre falling with spikelets; stipe (raceme-based) ca. 0.5 mm long, hairy. **Spikelets** dorsally compressed, lanceolate, 3–4.4 × 1–1.1 mm. **Lower glume** ovate, 1.7–2.4 × 0.8–1.2 mm, apex acute, membranous, gla-



Figure 4. *Cenchrus ciliaris* L. **A** habitat **B** inflorescence **C**, **D** spikelets with involucre. (Photographs: Paweena Wessapak).

brous, 1-nerved. **Upper glume** ovate, $2-3 \times 1-1.3$ mm, apex acute, membranous, glabrous, 1-nerved. **Florets** 2. **Lower floret** sterile, rarely male. **Lower lemma** lanceolate or ovate-lanceolate, $3-4 \times 1-1.5$ mm, apex acute or mucronate, membranous, glabrous, 5 or 7-nerved. **Lower palea** elliptic or oblong, $2-3 \times$ ca. 0.6 mm, apex obtuse or acute, margins folded with antrorsely scabrous, membranous, glabrous, 2-nerved or palea absent. **Upper floret** bisexual. **Upper lemma** lanceolate, $3.2-4.3 \times 1-1.2$ mm, apex acute or acuminate, margins hyaline, chartaceous or coriaceous, glabrous, 5-nerved. **Upper palea** lanceolate, 3–4

× 0.7–1.2 mm, apex acuminate, margins hyaline, chartaceous or coriaceous, glabrous 2-keeled, 2-nerved. **Lodicules** absent. **Stamens** 3; filament ca. 3 mm long; anther yellow 1.5–2.5 mm long. **Pistil** ovary elliptic, 0.4–0.8 × 0.2–0.5 mm; style 2; stigma plumose. **Caryopsis** ellipsoid, 1.4–1.8 × ca. 1 mm.

Distribution. Native to Africa, Greece, Sicilia, Middle East, Afghanistan, Pakistan, India and Bangladesh. Introduced to America, Australia and Southeast Asia.

Distribution in Thailand. South-Western: Kanchanaburi (Sai Yok); CENTRAL: Nakhon Pathom (Kamphaengsaen, Mueang Nakhon Pathom).

Habitat and ecology. In open areas by the roadside and the edge of rice fields. This species is cultivated for forage at elevations between 0 and 250 m a.m.s.l. Flowering and fruiting from May to September.

Vernacular name. Ya khi khrok rayang phu (หญ้าขี้ครอกทรายงศ์ฟู); African foxtail grass, Buffel grass (English).

Specimens examined. THAILAND. **Kanchanaburi:** Sai Yok, 17 May 2005, *P. Porkar* 17 (BKF, CMUB); **Nakhon Pathom:** Kamphaengsaen, 22 Jul 2017, *P. Wessapak* 373, 374 (BK); Mueang Nakhon Pathom, Thap Luang, 22 Jul 2017, *P. Wessapak* 376 (BK).

Notes. This species has been planted as fodder and to prevent soil erosion. It is considered as invasive in some countries. In Thailand, this species commonly escapes planting, but is not widely naturalised like the other species of the *Cenchrus*.

3. *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone in Ann. Bot. (Oxford) 106: 127. 2010.

Fig. 5

Pennisetum clandestinum Hochst. ex Chiov., Annuario Reale Ist. Bot. Roma 8: 41. 1903. Basionym.

≡ *Kikuyuochloa clandestina* (Hochst. ex Chiov.) H. Scholz in Feddes Repert. 117: 513. 2006.

= *Pennisetum inclusum* Pilg., Bot. Jahrb. Syst. 45: 209. 1910. Type: Uganda, Lamuru, 3,000 m alt., 30 Jun 1909, *Scheffler* 294 (holotype: B [B100168617]; isotypes: BM [BM000923356] seen on digital images, K [K000281293], P [P00442923] seen on digital image).

Type. ETHIOPIA, Semien, 27 Oct 1852, *G. H. W. Schimper* 2084 (lectotype, designated by Thulin and Phillips (2015, pg. 174): G [G00022569] seen on digital image; isolectotype: S [S-G-4663] seen on digital image).

Description. Perennial, mat-forming, stoloniferous. **Culms** prostrate, 5–15 cm high; nodes glabrous; internodes terete or semi-terete, channelled, 1–1.5 cm long, 1–2.5 mm in diam., glabrous. **Leaf sheaths** 1.1–1.3 cm long, usually distichous, margins hyaline with hairs, hairy or glabrous on both surfaces. **Ligules** a fringe of hairs, 1–2 mm long. **Collar** glabrous. **Leaf blades** linear, 1.7–7 cm × 2–3.5 mm, apex acute, based rounded or obtuse, chartaceous, usually folded, with or without pilose on both surfaces. **Inflorescence** very short spiciform panicle, ca. 2 × 0.2–0.3 cm (including bristles); central axis flattened, 4–5 mm long, scabrous; peduncle very short or sessile; 2–3 short racemes along central axis; raceme with solitary sessile spikelet subtended by an involucre

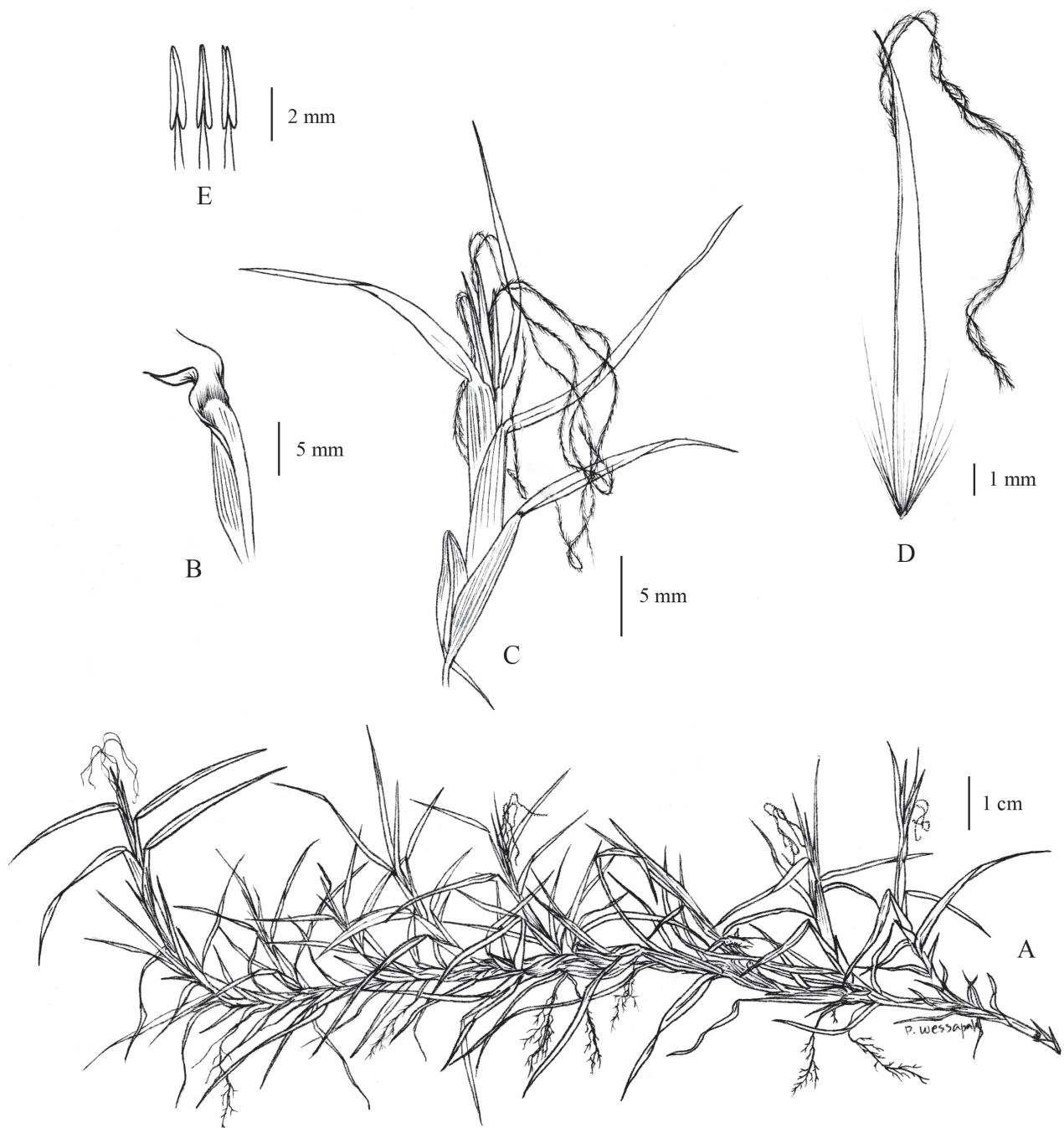


Figure 5. *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone **A** habit **B** ligule **C** inflorescence enclosed by terminal sheath **D** spikelet with involucre **E** stamens. (Drawn from S. Laegaard & M. Norsaengsri 21727 by Paweena Wessapak).

of bristles. **Involucre** composed of numerous bristles, slender and filiform, 0.2–1.4 cm long, antrorsely scabrous; involucre falling with spikelet; stipe (raceme-based) absent. **Spikelets** dorsally compressed, lanceolate-linear, 1.6–1.8 cm × 1.2–1.8 mm, slightly curved. **Lower and upper glumes** absent. **Florets** 2. **Lower floret** sterile. **Lower lemma** lanceolate-linear, ca. 1.5 cm × 1.2–1.8 mm, apex acute, margins folded and membranous, chartaceous, glabrous, 9- or 11-nerved. **Lower palea** absent. **Upper floret** bisexual, persistent. **Upper lemma** lanceolate-linear, 1.6–1.7 cm × 1.2–1.5 mm, apex acute, margins folded

and membranous, chartaceous, glabrous, 10- or 11-nerved. **Upper palea** lanceolate-linear, 1.4–1.6 cm × 1.2–1.5 mm, apex acute, membranous, glabrous, 4-nerved. **Lodicules** absent. **Stamens** 3; filament 3.5–5 mm long; anther yellow 2–3.5 mm long. **Pistil** ovary lanceolate, 1.8–2 × 0.3–0.4 mm; style 2; stigma plumose, 2–3 cm long, terminally distinct exerted. **Caryopsis** not seen.

Distribution. Native to central-eastern tropical Africa and widely introduced and cultivated elsewhere.

Distribution in Thailand. NORTHERN: Chiang Mai (Doi Inthanon, Mae Taeng).

Habitat and ecology. This species is cultivated as a lawn grass. It grows well on upland and escapes to nearby areas at elevations of 1100–2650 m a.m.s.l. Flowering and fruiting from June to January.

Vernacular name. Kikuyu grass (English).

Specimens examined. THAILAND. Chiang Mai: Doi Inthanon, 16 Oct 2001, S. Laegaard & M. Norsaengsri 21727 (AAU); Mae Taeng, Huai Thung Cho, 13 Jan 1986, Y. Paisooksantivathana y1760-86 (BK); Mae Taeng, Pa Pae, Thung Cho, 3 Jun 1981, Y. Paisooksantivathana & T. Chuaycharoern y616-81 (BK).

Note. This species is unique to the *Cenchrus* as it has a short spiciform inflorescence, partially exerted from the uppermost leaf sheath. Originally, this species was native to the tropical parts of Africa and has been widely introduced elsewhere for forage, urban landscaping, preventing soil erosion and is also considered as a weed in some countries (Hosaka 1958; Cudney et al. 1993; Arango-Gaviria et al. 2019). In Thailand, there are a few specimens recorded in the natural habitat, maybe because its inflorescence is difficult to notice and its vegetative part is similar to other lawn grasses.

4. *Cenchrus echinatus* L., Sp. Pl.: 1050. 1753.

Figs 6, 7

- = *Cenchrus pungens* Kunth, Nov. Gen. Sp. 1: 115. 1816. Type: Peru, Guyaquil, F. W. H. A. von Humboldt & A. J. A. Bonpland s.n. (holotype: P [P00669360] seen on digital image).
- = *Cenchrus brevisetus* E. Fourn., Mexic. Pl. 2: 50. 1886. Type: Mexico, Orizaba, 1866, E. Bourgeau 3140 (lectotype, designated by Gutiérrez and Morrone 2012, pg. 266: G [G00099346], seen on digital image; isoelectotypes: BR n.v., K [K000643125!]). ≡ *Cenchrus echinatus* L. var. *brevisetus* (E. Fourn.) Scribn., Publ. Field Columb. Mus., Bot. Ser. 2: 26. 1900.
- = *Cenchrus insularis* Scribn. ex Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 26. 1896. Type: Mexico, Yucatan, Pagaros Island, 8 Mar 1899, C. F. Millspaugh 1759 (holotype: F n.v.; isotypes: B [B100278941] seen on digital image, US n.v.).
- = *Cenchrus hillebrandianus* Hitchc., Mem. Bernice Pauahi Bishop Mus., Honolulu 8: 211. 1922. Type: Hawaii, Oahu, Waikiki, 19 Jun 1916, A. S. Hitchcock 13801 (holotype: US n.v.; isotypes: B [B100278942], BISH [BISH-439425] seen on digital images, K [K001056124!], P [P00698357] seen on digital image). ≡ *Cenchrus echinatus* L. var. *hillebrandianus* (Hitchc.) F. Br., Bull. Bernice P. Bishop Mus. 84: 65. 1931.
- = *Cenchrus echinatus* L. var. *glabratus* F. Br., Bull. Bernice P. Bishop Mus. 84: 66. 1931. Type: Marquesas Islands, Nuku Hiva, F. Brown 745 (lectotype, designated by St. John 1976, pg. 419: BISH [BISH-92743] seen on digital image).

= *Cenchrus echinatus* L. var. *pennisetoides* F. Br., Bull. Bernice P. Bishop Mus. 84: 66. 1931. Type: Marquesas Islands, Nuku Hiva, Hakau, 15 Jul 1921, *F. B. H. Brown & E. D. W. Brown* 657 (holotype: BISH [BISH-92748] seen on digital image).

Type. JAMAICA, 'Habitat in Jamaica, Curassa', *Anonymous* s.n. (lectotype, designated by Veldkamp in Jarvis et al. (ed.) (1993, pg. 31): L [Herb. A. van Royen No. 912.356-116] n.v.; isolectotype: L [Herb. A. van Royen No. 912.356-103] n.v.).

Description. Annual, tufted, **Culms** geniculate ascending, 15–75 cm high; nodes glabrous; internode subterete, 5–15 cm long, 1–2 mm in diam., glabrous. **Leaf sheaths** keeled conspicuous, 5–9 cm long, margins hyaline, glabrous. **Ligules** a fringe of hairs, 0.8–1.2 mm long. **Collar** glabrous. **Leaf blades** linear, 14–32 cm × 4–8 mm, apex acute, base rounded, margins scabrous, chartaceous, glabrous on both surfaces, sometimes upper surface pilose. **Inflorescence** spiciform panicle, 16–35 × 0.9–1.6 cm (including bristles); central axis angular, 5–11 cm long; axis internode 2–3 mm long, scabrous to subglabrous; peduncle terete, 10–27 cm long, glabrous or scabrous; short racemes loose along central axis; raceme with 2–4(–6) spikelets in cluster, all sessile, subtended by involucre of burr-like spines and bristles. **Involucre** composed of outer and inner circles; outer circle usually shorter than inner circle; outer involucre of bristles, numerous and filamentous, free, 1–4(–5) mm long, retrorsely scabrous; inner involucre of 7–11 flattened spines, 4–7 mm long, connate at lower part as 1–3 mm long, burr-like forming, a cup up to 5 mm in diam., coriaceous, puberulose and retrorsely scabrous; involucre falling with spikelets; stipe (raceme-based) 0.5–1.3 mm long, hairy, falling with raceme. **Spikelets** dorsally compressed, lanceolate, 4.5–6 × 1–2 mm. **Lower glume** ovate or lanceolate, 1–3 × 0.3–1.6 mm, apex acute or obtuse, membranous, glabrous, 1-nerved or nerveless, rarely absent. **Upper glume** lanceolate, 3.2–5.5 × 1.2–1.8 mm, apex acute or obtuse, membranous to chartaceous, glabrous, 3 or 5-nerved. **Florets** 2. **Lower floret** male or sterile. **Lower lemma** lanceolate, 3.8–5.8 × 1–2 mm, apex acute or acuminate, membranous to chartaceous, glabrous, 5-nerved. **Lower palea** lanceolate-oblong, 3.5–5.5 × 0.5–1 mm, apex acute to acuminate, margins folded with retrorsely scabrous, membranous, glabrous, 2-nerved, sometimes palea absent. **Upper floret** bisexual. **Upper lemma** lanceolate, 3.3–6 × 1–2 mm, apex acute or acuminate, margins hyaline, coriaceous, glabrous, 3 or 5-nerved. **Upper palea** lanceolate, 3–5.7 × 1–2 mm, apex acute or acuminate, margins hyaline, coriaceous, glabrous, 2-keeled, 2-nerved. **Lodicules** absent. **Stamens** 3; filament ca. 3 mm long; anther yellow, 1–2 mm long. **Pistil** ovary elliptic, 0.4–0.8 × 0.2–0.3 mm; style 2; stigma plumose. **Caryopsis** ellipsoid and gibbous or obovoid and slightly flattened, 1.5–3 × 1–2 mm.

Distribution. Native to North America and South America. Introduced and naturalising elsewhere in tropical and temperate zones worldwide.

Distribution in Thailand. NORTHERN: Tak (Thararak Waterfall); NORTH-EASTERN: Loei (Phu Ruea, Na Haeo), Udon Thani (Ban Dung), Khon Kaen (Mueang Khon Kaen, Phu Wiang, Khok Pho Chai); EASTERN: Nakhon Ratchasima; SOUTH-WESTERN: Kanchanaburi (Thong Pha Phum), Prachuap Khiri Khan (Pran Buri); CENTRAL: Saraburi (Muak Lek), Bangkok (Chatuchak); SOUTH-EASTERN: Chon Buri (Samaesan, Phanat Nikhom), Rayong (Klaeng); PENINSULAR: Songkhla (Mueang Songkhla, Hat Yai).

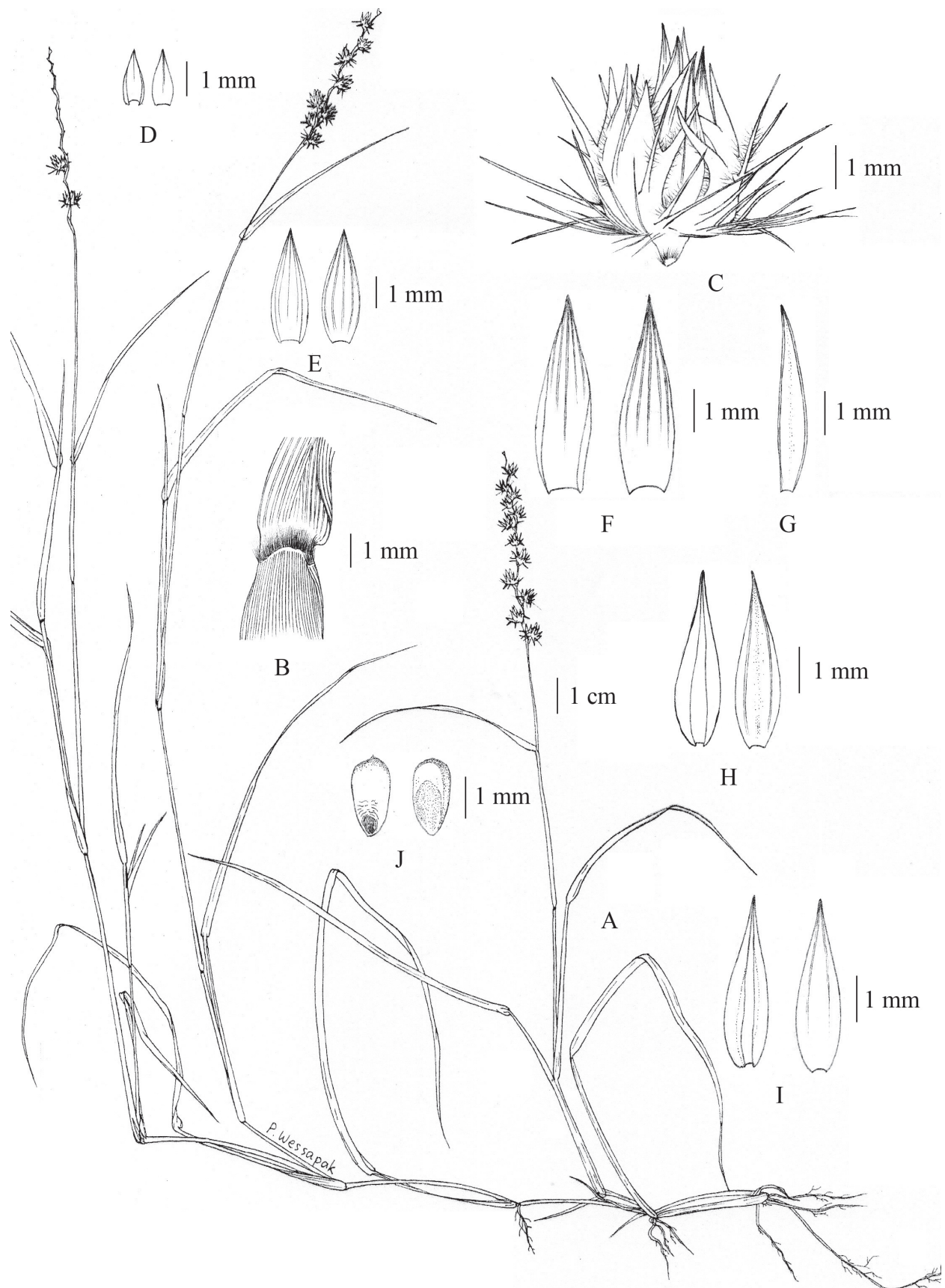


Figure 6. *Cenchrus echinatus* L. **A** habit **B** ligule **C** spikelets with involucre **D** lower glumes **E** upper glumes **F** lower lemmas **G** lower paleas **H** upper lemmas **I** upper paleas **J** caryopsis. (Drawn from P. Wessapak 361 by Paweena Wessapak).



Figure 7. *Cenchrus echinatus* L. **A** habitat **B** inflorescence **C** spikelets with involucre. (Photographs: Paweena Wessapak).

Habitat and ecology. In wastelands, open areas by the roadside, the edge of rice fields and the edge of deciduous and evergreen forests at elevations between 0 and 600 m a.m.s.l. Flowering and fruiting throughout the year.

Vernacular name. Ya khi khrok (หญ้าขี้ครอก), **Ya son krachap** (หญ้าสอนกระจับ); Hedgehog grass, Mossman river grass, Southern sandbur, Spiny sandbur (English).

Specimens examined. THAILAND. Bangkok: Chatuchak, Kasetsart University, 25 Dec 2016, *P. Wessapak* 347 (BK); *ibid.*, 12 Sep 2017, *P. Wessapak* 394 (BK); 2 Mar 1987, *J. Lambinon* 87/10 (AAU)]; **Chon Buri:** Phanat Nikhom, Kut Ngong, 29 Apr 2017, *P. Wessapak* 361 (BK); Samaesan, 8 Aug 1998, *T. Wongprasert s.n.* (BKF); **Kanchanaburi:** Thong Pha Phum, Pilog, Ban Pilog, 29 Jun 2004, *S. Sirimongkol* 123 (BKF); **Khon Kaen:** Khok Pho Chai, 24 Feb 2010, *P. Thongson* 14 (QBG); Mueang Khon Kaen, 25 Oct 2001, *S. Laegaard & M. Norsaengsri* 21791 (AAU, BKF, K, SING, QBG); Phu Wiang, 15 Sep 1994, *W. Nanakorn et al.* 1730

(QBG); **Loei**: Na Haeo, 20 Jun 1995, *W. Nanakorn et al.* 3829 (QBG); Phu Ruea, 24 Jul 2004, *C. Jaroenchai* 76 (KKU); **Nakhon Ratchasima**: 4 Sep 1989, *Pasikarn & Prayad* 41 (BK); **Prachuap Khiri Khan**: Pran Buri, 11 Nov 2017, *P. Wessapak* 431 (BK); **Rayong**: Klaeng, 30 Apr 2017, *P. Wessapak* 364 (BK); **Saraburi**: Muak Lek, Sap Sanun, 9 Jul 2017, *P. Wessapak* 372 (BK); **Songkhla**: Hat Yai, 23 Nov 2016, *P. Wessapak, C. Ngernsaengsaray, N. Meeprom & W. Boonthasak* 337 (BK); Mueang Songkhla, 6 Oct 1990, *B. Aksorn* 6 (PSU); Sadao, 30 Jul 2013, *H. Soh* 24 (PSU); **Tak**: Mae Sot, Thararak Waterfall, 22 Jun 2005, *R. Pooma, K. Phattarahirankanok, S. Sirimongkol & M. Poophat* 5426 (BKF); *ibid.*, 21 Aug 2010, *M. Norsaengsri* 7094 (QBG); **Udon Thani**: Ban Dung, Ban Dung Yai, 4 Dec 2008, *M. Norsaengsri* 4550 (QBG).

Note. The species is considered as a noxious weed in some countries (Ensbey 2014; Verloove and Sánchez Gullón 2012). In Thailand, it was introduced for forage and has become naturalised and treated as a weed.

5. *Cenchrus pedicellatus* (Trin.) Morrone in Chemisquy et al., Ann. Bot. (Oxford) 106: 128. 2010.

Figs 8, 9

Pennisetum pedicellatum Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3(2): 184. 1834. Basionym.

= *Pennisetum lanuginosum* Hochst., Flora 27: 252. 1844. Type: Sudan, Oct 1839, *C. G. T. Kotschy* 394 (lectotype, designated by Gutiérrez 2015, pg. 164: TUB [TUB018061-cb006519] n.v.; isolectotypes: BM [BM000923370!], K [K000281241!], W [W0000305, W18890244992] seen on digital images).

= *Pennisetum amoenum* Hochst. ex A. Rich., Tent. Fl. Abyss. 2: 386. 1850. Type: Ethiopia, Oct 1839, *G. H. W. Schimper* 641 (lectotype, designated by Gutiérrez and Morrone 2012, pg. 267: P [P03471044!]; isolectotypes: B [B100167868] seen on digital image, BM [BM000923371!], W [W18890244973] seen on digital image).

Type. CAPE VERDE ISLANDS, St. Iago, *D. Peters s.n.* (holotype: LE [Herb. Trinius 1102.1] n.v.).

Description. Annual, tufted. **Culms** erect or ascending, 0.5–2 m high; nodes glabrous; internodes subterete, sometimes slightly flattened, 5.5–30 cm long, 1.5–9 mm in diam., glabrous. **Leaf sheaths** 7–13 mm long, margins with hairs or tubercle-base hairs, glabrous. **Ligules** ciliate membrane, 2–4 mm long. **Collar** glabrous. **Leaf blades** linear, 20–50 × 0.5–1.7 cm, apex acute, base rounded with tubercle-base hairs, margins scabrous, chartaceous, hairy on both surfaces. **Inflorescence** spiciform panicle, 22–35 × 2.5–3 cm (including bristles); central axis with shortly decurrent ribs, 11–19 cm long, scabrous or pubescent; peduncle terete, 10–20 cm long, villose or scabrous; short racemes along central axis; raceme with 2–4 spikelets in cluster, one sessile and the other pedicelled, sessile spikelet smaller than pedicelled spikelet; pedicels 1–3 mm long, hairy; subtended by the involucre bristles. **Involucre** composed of outer and inner circles, numerous and free at base, outer circle shorter than inner circle; outer involucre 2–5 mm long; inner involucre 1–2 cm long, one conspicuous longest bristle 1.6–2.5 cm long, antrorsely scabrous and woolly hairs; involucre falling

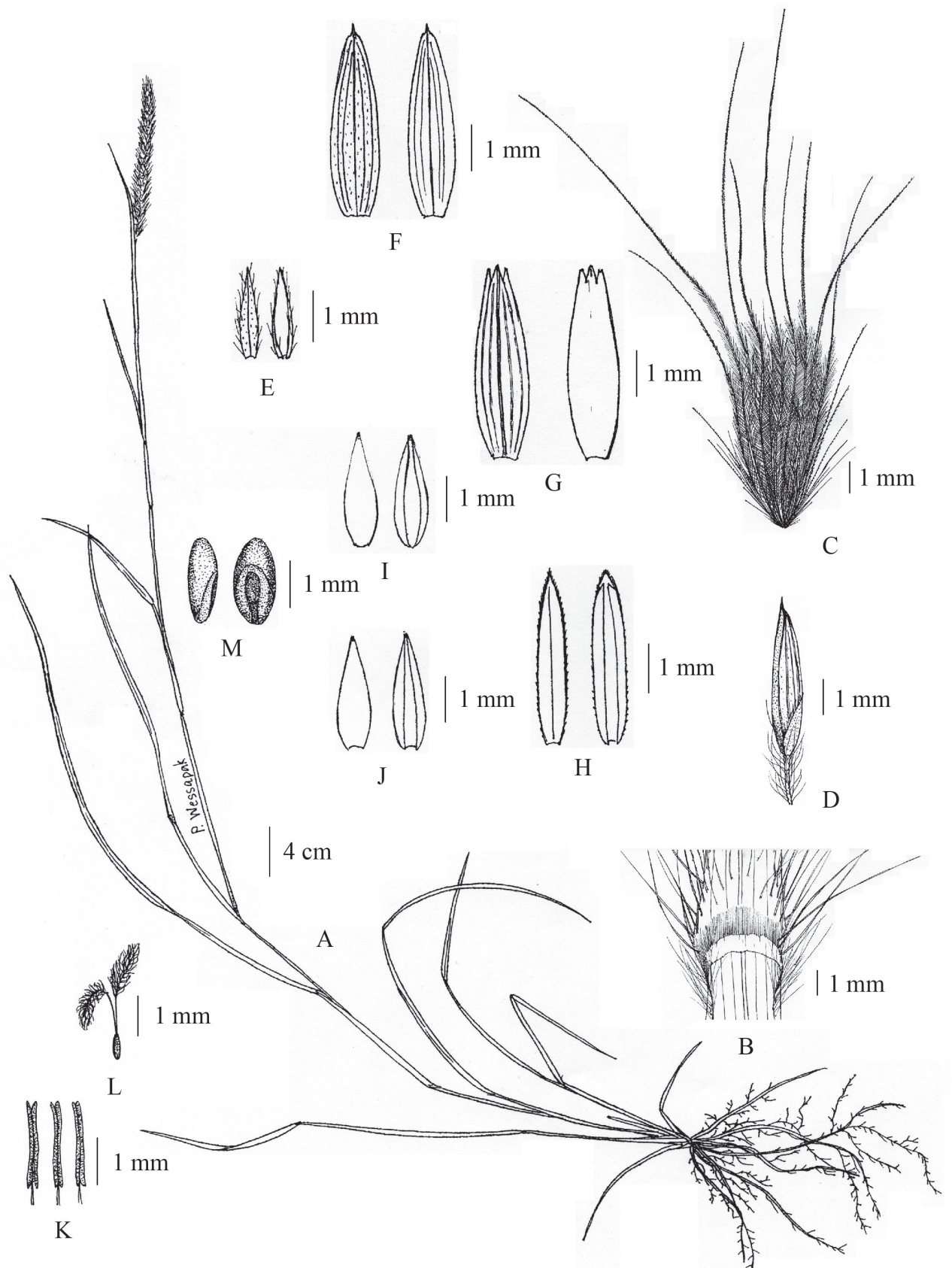


Figure 8. *Cenchrus pedicellatus* (Trin.) Morrone **A** habit **B** ligule **C** spikelet with involucre **D** pedicelled spikelet **E** lower glumes **F** upper glumes **G** lower lemmas **H** lower paleas **I** upper lemmas **J** upper paleas **K** stamens **L** pistil **M** caryopsis. (Drawn by Paweena Wessapak).



Figure 9. *Cenchrus pedicellatus* (Trin.) Morrone **A** habitat **B** inflorescence **C** spikelets with involucre **D** spikelets. (Photographs: Paweena Wessapak).

with spikelets; stipe (raceme-based) absent. **Spikelets** dorsally compressed, lanceolate, $3.5\text{--}5 \times 0.8\text{--}1.4$ mm. **Lower glume** lanceolate or lanceolate-elliptic, $1\text{--}2.5 \times 0.5\text{--}1$ mm, apex bifid, hyaline, pubescent, nerveless or 1-nerved. **Upper glume** lanceolate or elliptic, $3.5\text{--}5 \times 1\text{--}1.3$ mm, apex acuminate, cuspidate or mucronate, membranous, glabrous or scabrous, 5-nerved. **Florets** 2. **Lower floret** male. **Lower lemma** lanceolate, $3\text{--}4 \times 0.8\text{--}1.2$ mm, apex trifid, membranous, glabrous or scabrous, 5-nerved. **Lower palea** lanceolate or oblong-lanceolate, $3\text{--}4 \times 0.4\text{--}0.6$ mm, apex acute to acuminate, margins folded, membranous, glabrous, 2 or 3-nerved. **Upper floret** bisexual, caducous. **Upper lemma** lanceolate, $1.8\text{--}2.8 \times 0.5\text{--}1$ mm, apex obtuse with ciliate, coriaceous, glabrous, 3-obscure or 5-nerved. **Upper palea** lanceolate, $1.8\text{--}2.8 \times 0.5\text{--}1$ mm, apex obtuse with ciliate, coriaceous, glabrous, nerveless. **Lodicules** absent. **Stamens** 3; filament $1.5\text{--}2$ mm long; anther yellow, $1.5\text{--}2.2$ mm long. **Pistil** ovary oblong or elliptic,

0.4–0.8 × 0.1–0.2 mm; style 2; stigma plumose, 2.8–4 mm long. **Caryopsis** ellipsoid, 1.3–2 × 0.6–1 mm.

Distribution. Originally from Tropical Africa, India and Macronesia and introduced elsewhere.

Distribution in Thailand. NORTHERN: Chiang Mai (Mae Rim, Doi Suthep-Pui, Doi Saket, Mae Chaem, Samoeng, Mueang Chiang Mai), Lamphun (Doi Khun Tan), Tak; NORTH-EASTERN: Loei (Phu Luang, Phu Ruea, Phu Kradueng), Udon Thani (Ban Dung, Phu Kao), Nong Khai, Maha Sarakham, Khon Kaen (Phu Wiang, Tha Phra); EASTERN: Nakhon Ratchasima (Pak Thong Chai, Pak Chong), Buri Ram (Chaloem Phra Kiat), Si Sa Ket (Khao Phra Wihan), Ubon Ratchathani (Pha Taem, Phu Chong Na Yoi); SOUTH-WESTERN: Kanchanaburi (Thong Pha Phum); CENTRAL: Bangkok, Suphan Buri (Mueang Suphan Buri), Nakhon Nayok (Khao Yai), Samut Prakan (Phra Pradaeng); SOUTH-EASTERN: Prachin Buri (Khao Khiao), Chon Buri (Ko Si Chang, Sattahip), Sakaeo (Aranyaprathet).

Habitat and ecology. In open areas by the roadside, open areas in disturbed or deciduous forest at elevations of 25–1100 m a.m.s.l. Flowering and fruiting from October to March.

Vernacular name. Ya kha chon chop (หญ้าजरจบ), **Ya kha chon chop dok yai** (หญ้าजरจับดอกใหญ่); Annual kyasua grass, Deenanath grass, Dinanath grass, Hairy fountain grass (English).

Specimens examined. THAILAND. Bangkok: 16 Dec 1990, *K. Larsen, S. S. Larsen, W. Nanakorn, W. Ueachirakan & P. Sirirugsa* 42014 (AAU); **Buri Ram:** Chaloem Phra Kiat, Isan Khet, 21 Oct 2017, *P. Wessapak* 409 (BK); **Chiang Mai:** Doi Saket, Ban Pang Faen, 10 Dec 1998, *F. Konta & S. Khao-lam* 4422 (BKF); Doi Suthep, 21 Oct 1987, *J. F. Maxwell* 87-1218 (AAU, BKF); Doi Suthep-Pui, 21 Nov 1996, *S. K. Kafle* 13 (CMUB); Mae Chaem, Ban Mae Wak, 19 Dec 1998, *F. Konta, C. Phengklai & S. Khao-lam* 4813 (BKF); Mae Rim, 10 Feb 2006, *C. Glamwaewwong* 466 (QBG); Mueang Chiang Mai, 5 Dec 1989, *C. Lek-korbkul* 602 (CMUB); Samoeng, 21 Oct 2001, *S. Laegaard* 21763 (AAU, BKF, K, QBG); **Chon Buri:** Ko Si Chang, 29 Nov 1992, *J. F. Maxwell* 92-785 (CMUB, P); Sattahip, Thung Brong, 10 Jun 1971, *J. F. Maxwell* 71-416 (AAU, BK); **Kanchanaburi:** Thong Pha Phum, Pilok, 23 Oct 2004, *S. Sirimongkol* 166 (BKF); **Khon Kaen:** Phu Wiang, Khok Phu Ta Ka, 30 Nov 2003, *C. Jaroenchai* 36 (KKU); Tha Phra, 3 Nov 1971, *T. Smitinand* 11518 (BKF); **Lamphun:** Mae Tha, Doi Khun Tan, 18 Nov 1993, *J. F. Maxwell* 93-1376 (BKF, CMUB); **Loei:** Phu Kradueng, 25 Dec 2011, *M. Norsaengsri & N. Tathana* 8424 (QBG); Phu Luang, 19 Dec 2001, *V. Chaemchumroon* 1204 (BKF); Phu Ruea, 27 Nov 2005, *C. Jaroenchai* 243 (KKU); **Maha Sarakham:** 30 Oct 1965, *S. Sutheesorn* 705 (BK); **Nakhon Nayok:** Khao Yai, 13 Oct 1984, *G. Murata, C. Phengklai, S. Mitsuta, H. Nagamasu & N. Nantasan* T-52211 (BKF); *ibid.*, 15 Oct 1984, *G. Murata, C. Phengklai, S. Mitsuta, H. Nagamasu & N. Nantasan* T-52591 (BKF); **Nakhon Ratchasima:** Pak Chong, 14 Jan 1965, *Umpai* 172 (BK); Pak Thong Chai, Nov 1970, *Ch. Charoenpol, K. Larsen & E. Warncke* 4535 (BKF, K); 9 Dec 1962, *C. Phengklai* 408 (BKF); 6 Nov 1963, *T. Smitinand* 8398 (BKF); **Nong Khai:** 10 Nov 1984, *G. Murata, S. Mitsuta, T. Yahara, H. Nagamasu & N. Nantasan* T-40452 (BKF); **Prachin Buri:** Mueang Prachin Buri, Khao Khiao, 25 Oct 2000, *S. Watthana & T. Riyapun* 963 (QBG); **Sakaeo:** Aranyaprathet, 20 Nov 1984, *Chabeuf s.n.* (P); **Samut Prakan:** Phra Pradaeng, Song Khanong, 25 Mar 2012, *P. Wessapak & C. Ngernsaengsaruy* 205 (BK); **Si Sa Ket:** Khao Phra Wihan, Pha Mo I Daeng, 21 Dec 2005, *R. Pooma, K. Pattarahirankanok, S. Sirimongkol & K.*

Poopath 6002 (BKF); 10 Oct 1984, G. Murata, C. Phengklai, S. Mitsuta, H. Nagamasu & N. Nantasen T-38118 (BKF)]; **Suphan Buri**: Mueang Suphan Buri, Don Masang, 30 Dec 2016, P. Wessapak 352 (BK)]; **Tak**: Mae Sot-Umphang road, 23 Oct 1997, Anonymous s.n. (QBG); **Ubon Ratchathani**: Pha Taem, 28 Oct 2001, S. Laegaard, M. Norsaengsri, P. Pornpongrungrueng & S. Khoomkrathok 21857 (AAU, QBG); Phu Chong Na Yoi, Phalan Kong Kwian, 6 Nov 2010, P. Wessapak, Y. Buangam & W. Sareemongkonnimit 158 (BK); **Udon Thani**: Ban Dung, Ban Dung Yai, 4 Dec 2008, M. Norsaengsri 4561 (QBG); Phu Kao, Non Sung, 3 Jan 1968, K. Bunchuai 1519 (BKF, C).

Note. This species has been used for improving pasture quality, in soil remediation and erosion control (Asmare et al. 2016; Umer et al. 2019; Kumar and Fulekar 2022). It was introduced to Thailand from India for forage. At present, it has become naturalised as a weed and is distributed to almost all Thai floristic regions. *Cenchrus pedicellatus* is a close relative of *C. setosus*, but differs in terms of having a pedicelled spikelet, while *C. setosus* only has one sessile spikelet. Furthermore, its hairs on bristles are usually fluffier than the latter.

6. *Cenchrus purpureus* (Schumach.) Morrone in Chemisquy et al., Ann. Bot. (Oxford) 106: 129. 2010.

Figs 10, 11

Pennisetum purpureum Schumach., Beskr. Guin. Pl.: 44. 1827. Basionym.

= *Pennisetum macrostachyum* Benth. in W. J. Hooker, Niger Fl.: 563. 1849, non (Brongn.) Trin. (1834). Type: Nigeria, Aboh, Vogel s.n. (lectotype, designated here: K [K000281312!]; isoelectotype: K [K000281311!]).

= *Pennisetum flavicomum* Leeke, Z. Naturwiss. 79: 46. 1907. Type: Tanzania, von Prittwitz & Gaffron 199 (holotype: B [B100167864] seen on digital image).

= *Pennisetum pruinsum* Leeke, Z. Naturwiss. 79: 46. 1907. Type: Tanzania, Mtemere am Rufidji, W. Goetze 66 (holotype: B [B100167822] seen on digital image).

= *Pennisetum pallescens* Leeke, Z. Naturwiss. 79: 47. 1907. Type: Togo, Nov 1902, O. Kersting 719 (holotype: B [B100167821] seen on digital image).

Type. Ghana, P. Thonning 355 (lectotype, designated by Hepper (1976, pg. 149): C [C10004308!]; isoelectotype BM n.v.).

Description. Perennial, tufted. **Culms** erect or ascending, 1.8–4 m high; nodes glabrous or hairy; internodes terete or subterete, 7–32 cm long, 2–10 mm in diam., glabrous. **Leaf sheaths** 9–20 cm long, glabrous. **Ligules** a fringe of hairs, 2–5 mm long. **Collar** glabrous. **Leaf blades** linear, 26–100 × 0.4–3(–3.5) cm, apex acute, base rounded glabrous or with tubercle-base hairs, margins scabrous, chartaceous, scabrous on both surfaces (sometimes hairy on upper surface). **Inflorescence** spiciform panicle, 45–80 × 2–4 cm (including bristles); central axis terete, 15–40 cm long, pubescent; peduncle terete, 25–55 cm long, glabrous or pubescent; short racemes along central axis; raceme with 1–4 spikelets in cluster, one sessile and the other pedicelled (if solitary, it is sessile or subsessile spikelet), pedicelled spikelets smaller than sessile spikelet; pedicels 0.5–2.2 mm long, scabrous; subtended by involucre bristles. **Involucre** composed of outer and inner circles, numerous and free at base, outer circle shorter than inner circle; outer involucre 2–4 mm long; inner involucre 1–1.4 cm

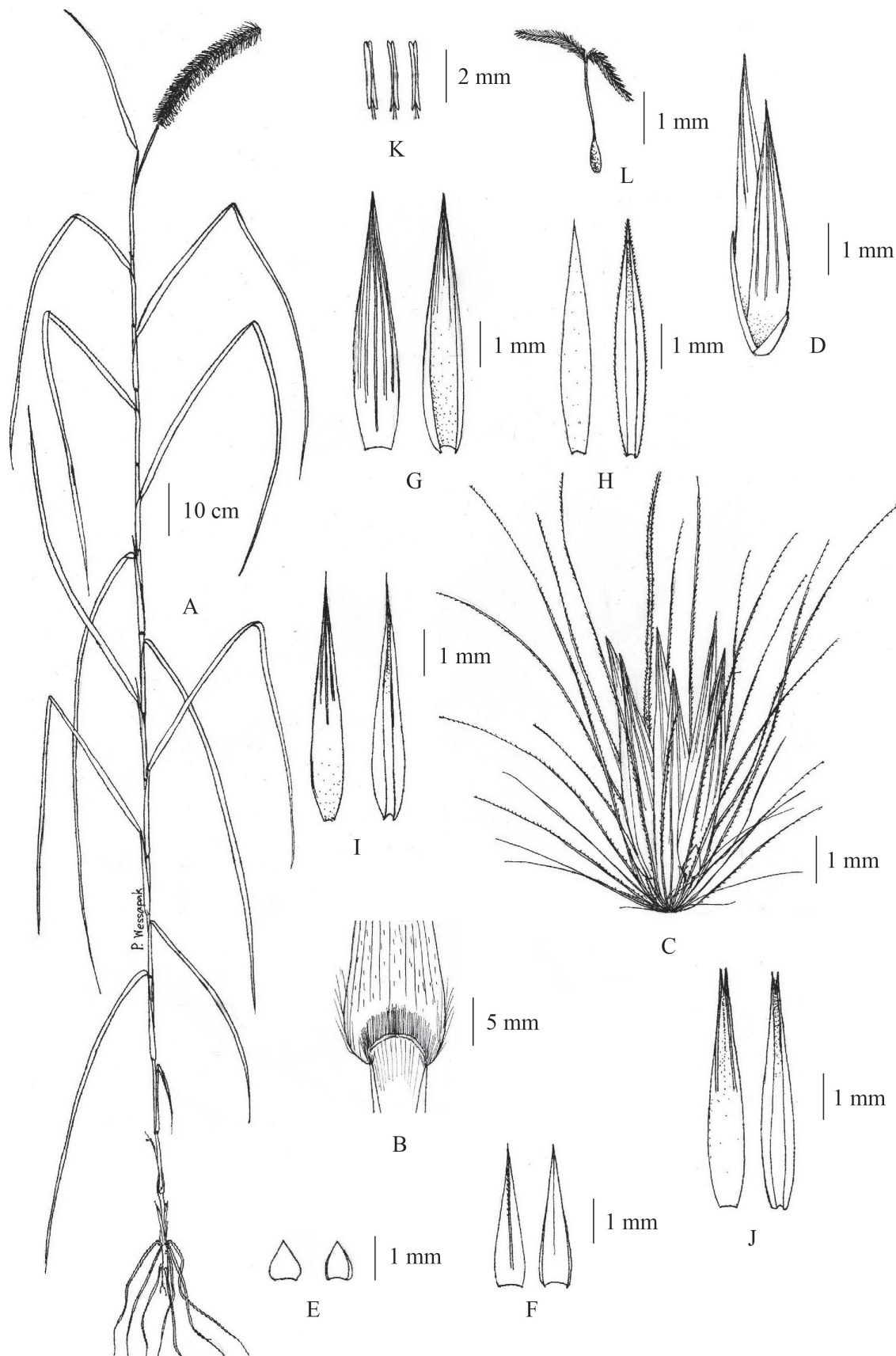


Figure 10. *Cenchrus purpureus* (Schumach.) Morrone **A** habit **B** ligule **C** spikelets with involucre **D** spikelet **E** lower glumes **F** upper glumes **G** lower lemmas **H** lower paleas **I** upper lemmas **J** upper paleas **K** stamens **L** pistil. (Drawn by Paweena Wessapak).

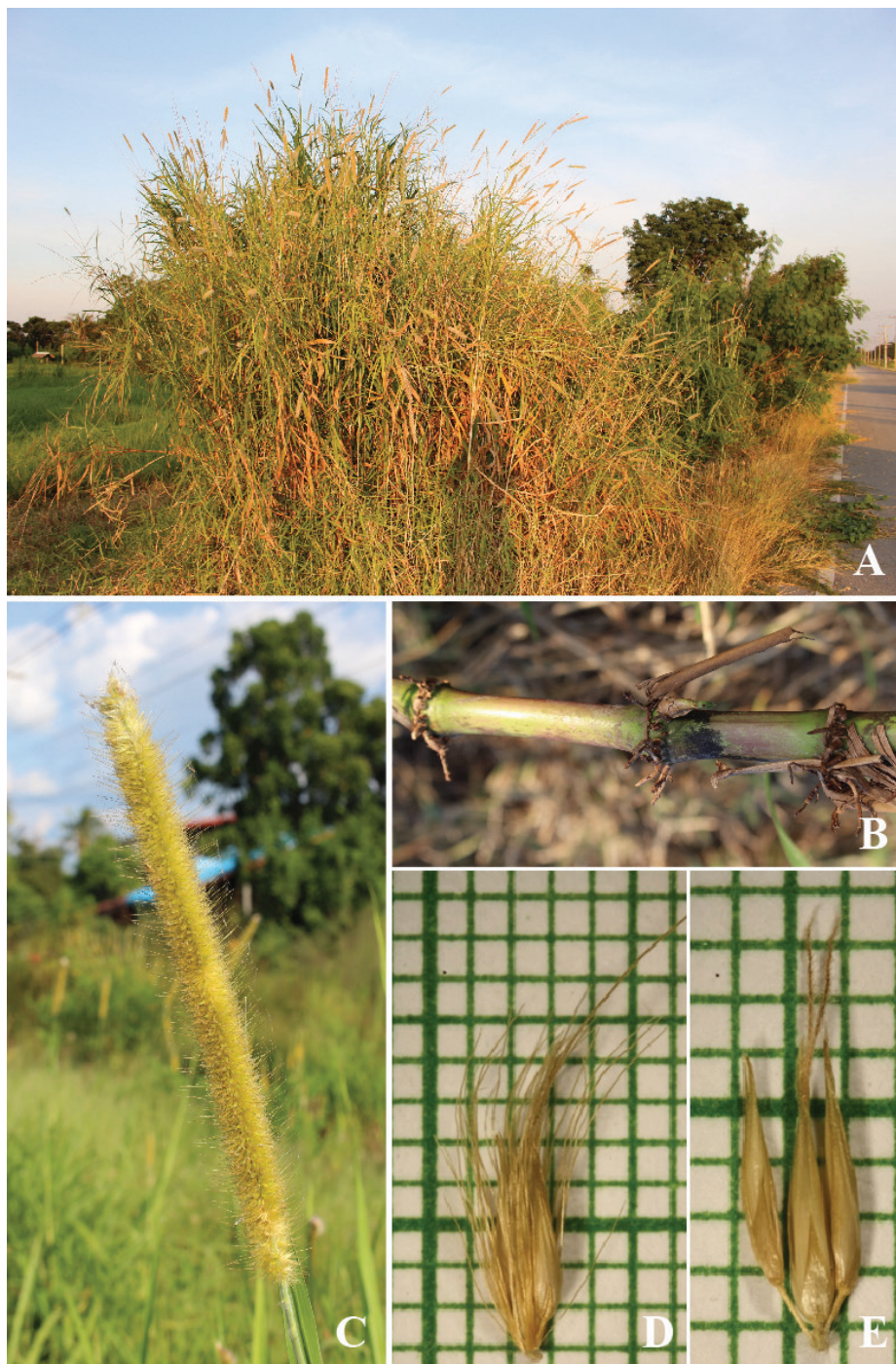


Figure 11. *Cenchrus purpureus* (Schumach.) Morrone **A** habitat **B** culm with node rooting **C** inflorescence **D** spikelets with involucre **E** spikelets. (Photographs: Paweena Wessapak).

long (sometimes up to 2.6 cm long), one conspicuous longest bristle 1.1–2.3 cm long, antrorsely scabrous; involucre falling with spikelets; stipe (raceme-based) 0.2–0.3 mm long, hairy, persistent on axis. **Spikelets** dorsally compressed, lanceolate, 4–6.5 × 0.8–1.3 mm. **Lower glume** ovate or lanceolate, 0.5–1.5 × 0.2–0.6 mm, apex acute or acuminate, sometimes obtuse, chartaceous, glabrous, nerveless or 2-obscure-nerved. **Upper glume** lanceolate or ovate-lanceolate, 1.8–4.2 × 0.4–1 mm, apex acute or acuminate, chartaceous, glabrous with or without scabrous along nerve, 1- or 3-nerved or nerveless. **Lower floret** male

or sterile. **Lower lemma** lanceolate, 3–6 × 0.8–1.3 mm, apex acuminate, chartaceous, glabrous with or without scabrous along nerve, 3- or 5-nerved. **Lower palea** mostly absent or lanceolate, 4.5–5.2 × 0.8–1 mm, apex acute, margins fold with or without scabrous, membranous, glabrous, 2- or 3-nerved. **Upper floret** bisexual, persistent. **Upper lemma** lanceolate, 4–6.5 × 0.8–1.2 mm, apex acuminate, margins with ciliate, coriaceous, glabrous and scabrous near tip, 3- or 5-nerved. **Upper palea** lanceolate, 4.3–6.5 × 0.8–1.2 mm, apex acuminate, coriaceous, glabrous with or without scabrous near tip, 2-, 3- or 5-nerved. **Lodicules** absent. **Stamens** 3, filament 0.3–3 mm long, anther yellow, 1.5–2.8 mm long. **Pistil** ovary oblong-lanceolate, 0.6–1.5 × 0.1–0.5 mm; style 2, 1.5–4 mm long; stigma plumose, 2–6 mm long. **Caryopsis** ellipsoid, 1.5–2 × 0.8–1 mm.

Distribution. Native from Sahara to Tropical Africa and introduced to China, India, Myanmar, Indo-China, Malaysia, Australia, New Zealand, North America and South America.

Distribution in Thailand. NORTHERN: Mae Hong Son (Pang Ma Pha, Mae Rim, Doi Suthep-Pui), Chiang Rai (Doi Tung, Mae Sai, Tham Luang-Khun Nam Nang Non), Lampang (Ngao); NORTH-EASTERN: Khon Kaen; EASTERN: Nakhon Ratchasima (Pak Chong), Si Sa Ket (Phrai Bueng); CENTRAL: Nakhon Pathom (Kampheangsaen); SOUTH-EASTERN: Chon Buri (Sattahip), Rayong (Klaeng); PENINSULAR: Surat Thani (Tha Chang), Krabi (Khlong Thom), Trang (Khao Chong), Songkhla (Sadao), Yala (Bannang Sata), Narathiwat (Sungei Kolok).

Habitat and ecology. In open areas by the roadside, disturbed sites and the edge of deciduous forests. They are also cultivated for forage at elevations of 50–1350 m a.m.s.l. Flowering and fruiting from October to March.

Vernacular name. Ya hang chang (หญ้าหางช้าง), **Ya Napier** (หญ้าเนเปียร์); Elephant grass, Napier grass (English).

Specimens examined. THAILAND. Chiang Mai: Doi Suthep-Pui, 23 Jan 1991, J. F. Maxwell 91-95 (AAU); *ibid.*, 1 Jan 2001, J. F. Maxwell 01-1 (BKF, CMUB); Doi Suthep, 4 Nov 1958, Th. Sorensen, K. Larsen & B. Hansen 2633 (BKF, C, K); *ibid.*, 24 Dec 1965, E. Hennipman 3478 (BKF, C); *ibid.*, 19 Mar 1997, K. Chayamarit & C. Pattanacharoen 732 (BKF); Mae Rim, 28 Nov 1995, Anonymous 5378 (QBG); Mae Rim, Queen Sirikit Botanic Garden, 10 Feb 2006, C. Glamwaewwong 463 (QBG); **Chiang Rai:** Doi Tung, Mae Fa Luang, 23 Dec 2006, J. F. Maxwell 06-989 (QBG, CMUB); Mae Sai, Pong Pha, Ban Nam Cham, 2 Dec 2008, M. Norsaengsri 4475 (QBG); Tham Luang-Khun Nam Nang Non, 13 Feb 2012, M. Norsaengsri & N. Thatana 8876 (QBG); **Chon Buri:** Sattahip, 11 Oct 1969, J. F. Maxwell s.n. (BK); **Khon Kaen:** Khon Kaen University, 25 Dec 1997, U. Pattaramanon 18 (KKU); **Krabi:** Khlong Thom, Khlong Thom Tai, 12 Nov 2011, P. Wessapak 202 (BK); **Lampang:** Ngao, Ban Huat, 9 Dec 2014, J. F. Maxwell 14-19 (CMUB, PSU); **Mae Hong Son:** Pang Ma Pha, Ban Tha Khrai, 16 Feb 2005, K. Pruesapan KP2005-9 (BK); **Nakhon Pathom:** Kampheangsaen, 28 Dec 2016, P. Wessapak 348, 350 (BK); **Nakhon Ratchasima:** Pak Chong, Oct 1931, A. F. G. Kerr s.n. (BM, BK); **Narathiwat:** Sungei Kolok, Nikhom Waeng, 6 Mar 1974, K. Larsen & S. S. Larsen 33030 (AAU, BKF, K); **Rayong:** Klaeng, Chak Pong, Ban Phlong Sawai, 13 Jan 2009, P. Wessumritt & M. Norsaengsri 160 (QBG); **Si Sa Ket:** Phrai Bueng, Suk Sawat, 26 Dec 2004, A. Virapongse 194 (BKF); **Songkhla:** Sadao, Samnak Tao, 24 Oct 2010, P. Wessapak & C. Ngernsaengsaruy 153 (BK, BKF); 11 Nov 1959, T. Smitinand 6124 (BKF); **Surat Thani** Tha Chang, Tha Koei, Ban Thong Sai, 2 Nov 2011, P. Wessapak 200 (BK); **Trang:** Khao Chong, 18 Nov 1990, K.

Larsen, S. S. Larsen, M. S. Barfod, W. Nanakorn, W. Ueachirakan & P. Sirirugsak 41606 (AAU, BKF, PSU); **Yala:** Bannang Sata, 12 Dec 1961, *Ploenchit* 1775 (BKF).

Notes. Napier grass is a multipurpose forage crop. It is mainly used to feed livestock and is also used for ornamentation and soil erosion control. Its fibres are used to make pulp and in papermaking. Furthermore, its biofuel producing potential is being researched because all the parts of this species produce lignocellulose biomass which can be used to produce cheap biofuel (Obi Reddy et al. 2014; Chavre and Sonawane 2021). This species was introduced to Thailand from Malaysia for forage. At present, it has become naturalised to almost all Thai floristic regions.

The synonym, *Pennisetum macrostachyum*, was described by George Benth in 1849 and is based on the Vogel's specimens from Aboh (Nigeria) and Fernando Po (Equatorial Guinea). He did not choose any specimens to be the holotype. We located the Vogel's specimen in three sheets at K which was collected from Aboh (Nigeria) [K000281311 and K000281312] and Fernando Po (Equatorial Guinea) [K000281310] and, according to Art 9.6 of the ICN (Turland et al. 2018), they constitute syntypes. The sheet K000281312 is a well-preserved specimen with more leaves and spikelets and, therefore, it is herein designated as the lectotype for the synonym *P. macrostachyum*. (Fig. 12)



Figure 12. Lectotype of *Pennisetum macrostachyum* Benth. Digital image The Board of Trustees of the Herbarium of the Royal Kew Botanic Garden (K).

7. *Cenchrus setosus* Sw., Prodr.: 26. 1788.

Figs 13, 14

≡ *Pennisetum setosum* (Sw.) Rich, Syn. Pl. 1: 72. 1805.

≡ *Pennisetum polystachion* (L.) Schult. subsp. *setosum* (Sw.) Brunken, Bot. J. Linn. Soc. 79(1): 63. 1979.

Type. JAMAICA, O. Swartz s.n. (lectotype, designated by Hitchcock (1908, pg. 143): S [S-R-969] seen on digital image; isoelectotypes: BM [BM000938799], G [G00168094], S [S-R-968, S06-637] seen on digital images).

Description. Annual or perennial, tufted. **Culms** erect or ascending, 0.5–3 m high; nodes glabrous; internodes subterete, sometimes slightly flattened, 5.5–34 cm long, 1–8 mm in diam., glabrous. **Leaf sheaths** 0.7–2.5 cm long, glabrous. **Ligules** ciliate membrane, 1.5–3 mm long. **Collar** ciliate or hairs 1–2 mm long. **Leaf blades** linear, 10–85 × 0.4–2.2 cm, apex acute, base rounded with tubercle-base hairs, margins scabrous, chartaceous, hairy on both surfaces. **In-florescence** spiciform panicle, 22–55 × 1.5–4.5 cm (including bristles); central axis with shortly decurrent ribs, 12–23 cm long, scabrous or almost glabrous; peduncle terete, 10–35 cm long, scabrous or almost glabrous or glabrous; short racemes along central axis; raceme with solitary sessile spikelet subtended by an involucre bristle. **Involucre** composed of outer and inner circles, numerous and free at base, outer circle shorter than inner circle; outer involucre 1–5 mm long; inner involucre 1–1.4 cm long, one conspicuous longest bristle 1.2–3.3 cm long, antrorsely scabrous and hairy. Involucre falling with spikelet; stipe (raceme-based) absent. **Spikelets** dorsally compressed, lanceolate, 3.3–4.5 × 0.8–1.2 mm. **Lower glume** absent, minute ca. 0.1 mm long or triangular, 0.5–0.8 × 0.1–0.6 mm, apex acute, membranous, nerveless. **Upper glume** lanceolate, 3.3–4.5 × 0.8–1.2 mm, apex acuminate or mucronate, membranous, glabrous or slightly scabrous, 5-nerved. **Florets** 2. **Lower floret** male or sterile. **Lower lemma** lanceolate-elliptic or lanceolate, 2.8–3.5 × 0.8–1.2 mm, apex trifid, membranous, glabrous or slightly scabrous, 3- or 5-nerved. **Lower palea** oblong or oblong-lanceolate, 2.2–3.2 × 0.3–0.8 mm, apex acute, margins folded, membranous, glabrous, 2 or 3-nerved or nerveless, sometime palea absent. **Upper floret** bisexual, caducous. **Upper lemma** lanceolate, 1.9–2.5 × 0.4–0.8 mm, apex obtuse with ciliate, coriaceous, glabrous, nerveless or 5-obscure-nerved. **Upper palea** lanceolate, 1.9–2.5 × 0.3–0.8 mm, apex obtuse with ciliate, coriaceous, glabrous, nerveless or 5-obscure-nerved. **Lodicules** absent. **Stamens** 3; filament 1–1.5 mm long; anther yellow or brown 1.3–2.2 mm long. **Pistil** ovary oblong or elliptic, 0.3–0.6 × 0.1–0.2 mm; style 2, 1–2 mm long; stigma plumose, 2–3 mm long. **Caryopsis** ellipsoid, 1.2–1.7 × 0.5–0.8 mm.

Distribution. Native to India and Tropical Africa and introduced to Indo-China, Malaysia, Australia, North America and South America.

Distribution in Thailand. NORTHERN: Chiang Mai (Doi Saket, Mae Ya Waterfall, Chom Thong, Mae Rim, Doi Chiang Dao, Hang Dong), Chiang Rai (Mae Chan, Mae Sai, Mueang Chiang Rai), Phrae (Song), Nan (Tham Sa Koen), Lampang (Doi Luang), Phitsanulok (Thung Salaeng Luang), Kamphaeng Phet (Pang Sila Thong); NORTH-EASTERN: Phetchabun (Nam Nao), Loei (Phu Ruea, Wang Saphung), Udon Thani (Kumphawapi), Khon Kaen (Waeng Yai, Phu Wiang, Nam Nao); EASTERN: Nakhon Ratchasima (Pak Thong Chai, Sakaerat, Pak Chong,

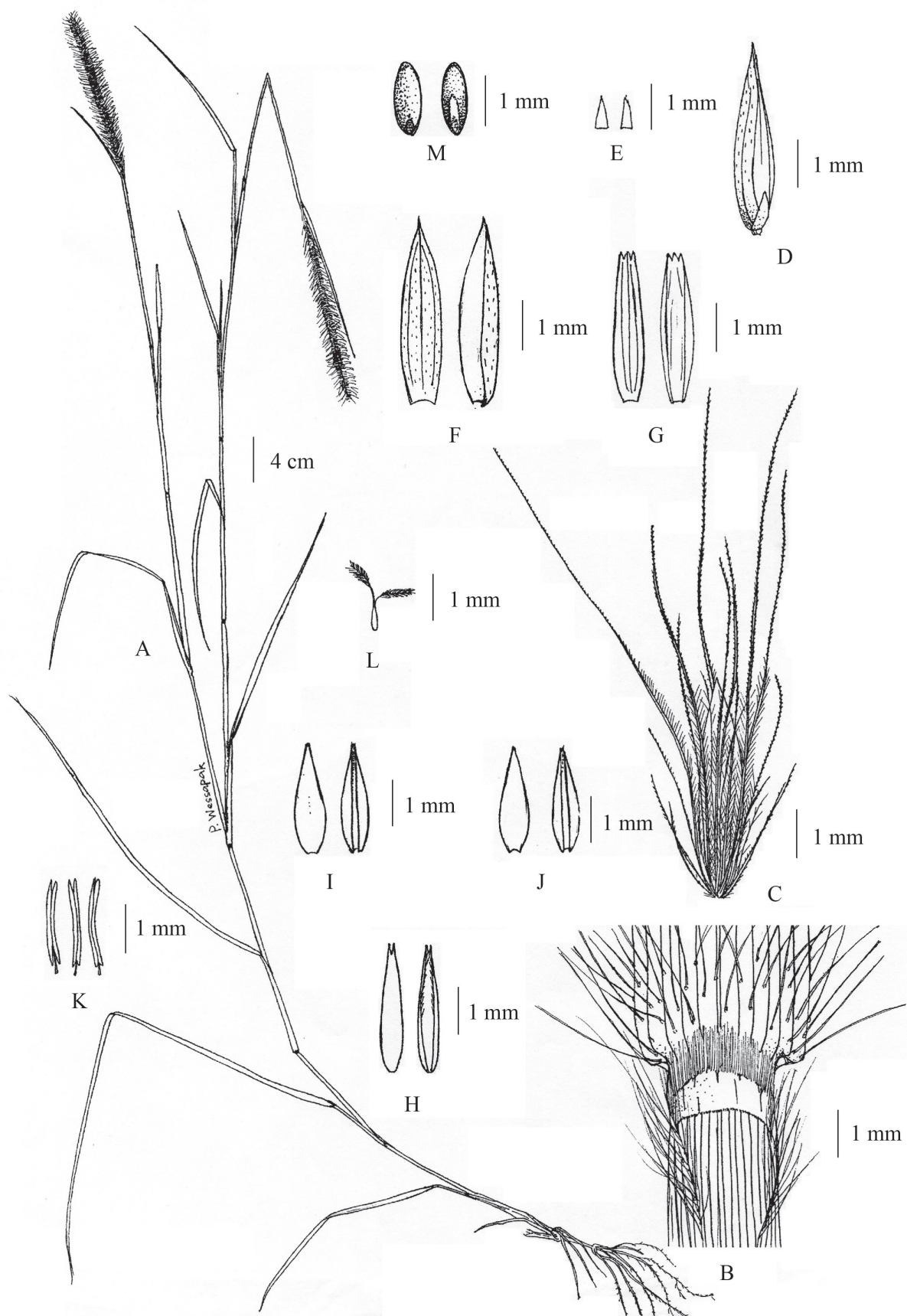


Figure 13. *Cenchrus setosus* Sw. **A** habit **B** ligule **C** spikelet with involucre **D** spikelet **E** lower glumes **F** upper glumes **G** lower lemmas **H** lower paleas **I** upper lemmas **J** upper paleas **K** stamens **L** pistil **M** caryopsis. (Drawn by Paweena Wessapak).



Figure 14. *Cenchrus setosus* Sw. **A** habitat **B** inflorescences **C** spikelet with involucre. (Photographs: Paweena Wessapak).

Khao Yai), Buri Ram (Chaloem Phra Kiat), Ubon Ratchathani (Phu Chong Na Yoi); SOUTH-WESTERN: Kanchanaburi (Thong Pha Phum); CENTRAL: Saraburi (Wang Muang), Nakhon Pathom (Phutthamonthon), Nakhon Nayok (Khao Yai), Samut Prakan (Phra Pradaeng); SOUTH-EASTERN: Prachin Buri (Kabin Buri), Chon Buri (Si Racha, Ban Bueng), Rayong (Klaeng), Chanthaburi (Tha Mai, Khlong Nong Khla, Laem Sadet), Trat (Ko Chang); PENINSULAR: Surat Thani (Chaiya), Phuket (Thalaeng), Krabi (Ao Ma Ya, Khlong Thom), Nakhon Si Thammarat (Thung Song, Tha Yang), Phatthalung (Phanang Tung), Trang (Sikao), Satun (Mueang Satun), Songkhla (Hat Yai, Khao Phra, Rattaphum, Sadao, Na Mhom).

Habitat and ecology. In open areas by the roadside, disturbed and open areas in deciduous forests at elevations between 0 and 1200 m a.m.s.l. Flowering and fruiting throughout the year.

Vernacular name. Ya kha chon chop (หญ้าजरจบ), **Ya kha chon chop dok lek** (หญ้าजरจับดอกเล็ก), Ya kha chon chop dok lueang (หญ้าजरจับดอกเหลือง); Mission grass (English).

Specimens examined. THAILAND. Buri Ram: Chaloe Phra Kiat, Isan Khet, 21 Oct 2017, *P. Wessapak* 410 (BK); **Chanthaburi:** Tha Mai, 2 Jan 1971, *S. Sutheesorn* 1947 (BK); *ibid.*, 8 Nov 1971, *S. Sutheesorn* 2017 (BK); Tha Mai, Khlong Nong Khla, 16 Feb 2009, *M. Norsaengsri* 4894 (QBG); Tha Mai, Laem Sadet, 24 Feb 2008, *M. Norsaengsri* & *K. Wangwasit* 3487 (BKF, QBG); **Chiang Mai:** Chom Thong, 3 Dec 1991, *J. F. Maxwell* 91-1092 (AAU); Doi Chiang Dao, 21 Nov 1999, *P. Suksathan* 2221 (QBG); Hang Dong, 21 Mar 2009, *S. Watthana* 3007 (QBG); Doi Saket, Ban Pang Faen, 10 Dec 1998, *F. Konta* & *S. Khao-lam* 4421 (BKF); Mae Rim, 3 Oct 1994, *W. Nanakorn et al.* s.n. (QBG); Mae Ya Waterfall, 15 Dec 1998, *F. Konta*, *C. Phengkklai* & *S. Khao-lam* 4529 (BKF); **Chiang Rai:** Mae Chan, 20 Jan 1981, *Y. Paisooksantivatana* y492-81 (BK, CMUB, KKU); *ibid.*, 1 Dec 2008, *M. Norsaengsri* 4470 (QBG); Mae Sai, Pong Pha, Ban Nam Cham, 2 Dec 2008, *M. Norsaengsri* 4477 (QBG); Mueang Chiang Rai, Ban Pa Rai, 24 Jan 1981, *Y. Paisooksantivatana* 561-81 (BK); **Chon Buri:** Ban Bueng, 3 Jun 1989, *Y. Paisooksantivatana* 2327-89 (BK); Si Racha, Thung Sukhla, 8 Dec 2003, *J. F. Maxwell* 03-482 (CMUB); **Kamphaeng Phet:** Pang Sila Thong, 13 Nov 2007, *M. Norsaengsri* 2986 (QBG); **Kanchanaburi:** Thong Pha Phum, 15 Nov 1971, *C. F. van Beusekom*, *C. Phengkklai*, *R. Geesink* & *B. Wongwan* 3788 (BKF, C, K, P); Thong Pha Phum, Huai Khayeng, Bueng Nam Thip, 3 Dec 2003, *S. Sirimongkol* 67 (BKF); Thong Pha Phum, Pilo, 23 Oct 2004, *S. Sirimongkol* 164 (BKF); **Khon Kaen:** Nam Nao, 10 Mar 1979, *P. J. O'Corner* & *C. Niyomdham* 15724 (AAU, BKF); Phu Wiang, 21 Feb 1993, *P. Chantaranonthai*, *D. Middleton*, *J. Parnell* & *D. Simpson* 826 (K, KKU); Phu Wiang, Khok Phu Ta Ka, 30 Nov 2003, *C. Jaroenchai* 37 (KKU); Waeng Yai, 26 Dec 2007, *M. Norsaengsri* 3255 (AAU, CMUB, QBG); Waeng Yai, Ban Khao Nai, 7 Nov 2008, *M. Norsaengsri* 4384 (QBG); **Krabi:** Ao Ma Ya, 24 Nov 1998, *C. Niyomdham* 5646 (BKF); Khlong Thom, Khlong Phon, 29 Nov 1986, *J. Supapol* 288 (PSU); Khlong Thom, Khlong Thom Tai, 29 Oct 2011, *P. Wessapak* 196, 197 (BK, BKF); **Lampang:** Doi Luang, 12 Dec 1998, *O. Petrmitr* 400 (BKF, CMUB); **Loei:** Phu Ruea, 6 Dec 2004, *C. Jaroenchai* 133 (KKU); *ibid.*, 27 Nov 2005, *C. Jaroenchai* 163 (KKU), *ibid.*, 12 Nov 2005, *C. Jaroenchai* 210 (KKU), *ibid.*, 13 Nov 2005, *C. Jaroenchai* 228 (KKU); *ibid.*, 27 Nov 2005, *C. Jaroenchai* 245 (KKU); Wang Saphung, 26 May 2009, *M. Norsaengsri* & *W. La-ongsri* 5560 (QBG); **Nakhon Nayok:** Khao Yai, Hin Tung, 23 Jan 2002, *J. F. Maxwell* 02-35 (BKF, CMUB); **Nakhon Pathom:** Phutthamonthon, Salaya, 22 Nov 2002, *J. F. Maxwell* 02-418 (BKF, CMUB); **Nakhon Ratchasima:** Khao Yai, 23 Oct 1970, *T. Smitinand* 11040 (BKF); Pak Chong, 14 Jan 1965, *Umpai* 173 (BK); Pak Thong Chai, Nov 1970, *Ch. Charoenpol*, *K. Larsen* & *E. Warncke* 4535 (C); Sakaerat, 4 Dec 1983, *N. Fukuoka* & *M. Ito* T-35013 (BKF); **Nakhon Si Thammarat:** Tha Yang, Thung Yai, 2 Nov 2011, *P. Wessapak* 201 (BK); Thung Song, 18 Dec 1965, *J. Sada-korn* 2 (BK); **Nan:** Tham Sa Koen, 30 Nov 2011, *W. La-ongsri*, *M. Norsaengsri*, *P. Panyachan*, *P. Tatiya* & *S. Satatha* 2002 (QBG, PSU); **Phatthalung:** Phanang Tung, Khuan Khanun, 2 Dec 2012, *P. Na Sawat* 2 (PSU); **Phitsanulok:** Thung Sa-laeng Luang, 25 Jul 1973, *G. Murata*, *N. Fukuoka* & *C. Phengkklai* T-17144 (BKF); *ibid.*, 21 Oct 1984, *G. Murata*, *C. Phengkklai*, *S. Mitsuta*, *T. Yahara*, *H. Nagamasu* & *N. Nantasan* T-38399 (BKF); **Phetchabun:** Nam Nao, 25 Oct 2001, *S. Laegaard* & *M. Norsaengsri* 21787 (AAU, BKF, QBG); **Phrae:** Song, Mae Yom, 10 Nov 1991, *J. F. Maxwell* 91-1003 (AAU); **Phuket:** Thalaeng, Thap Kasattri, Ban Mai Kao, *J. Supapol* 100 (PSU); **Prachin Buri:** Kabin Buri, 13 Feb 2009, *M. Norsaengsri* 4854 (QBG); **Rayong:** Klaeng, 15 Feb 2009, *M. Norsaengsri* 4877, 4891 (QBG); Klaeng,

Chak Don, 18 Nov 2008, *P. Wessumritt & M. Norsaengsri* 147, 148 (QBG); **Samut Prakan:** Phra Pradaeng, Song Khanong, 25 Mar 2012, *P. Wessapak & C. Ngernsaengsaruy* 204 (BK); **Saraburi:** Wang Muang, Kham Phran, 1 Dec 2011, *P. Wessapak* 203 (BK); **Satun:** Mueang Satun, Phi Man, 24 Oct 2010, *P. Wessapak & C. Ngernsaengsaruy* 154 (BK, BKF); **Songkhla:** Hat Yai, 2 Feb 1979, *G. Congdon* 247 (AAU, PSU); Hat Yai, Ban Nong Bua, 3 Jul 2012, *S. Aya* 26 (PSU); Hat Yai, Khao Kho Hong, 24 Oct 2010, *P. Wessapak & C. Ngernsaengsaruy* 151 (BK, BKF); Khao Phra, 28 May 2001, *A. Boonprom* 1 (PSU); Na Mhom, Klong Rhang, 23 Nov 2016, *P. Wessapak, C. Ngernsaengsaruy, N. Meeprom & W. Boonthasak* 344, 345 (BK); Rattaphum, Ban Khao Rak Kiat, 15 Oct 2012, *K. Jamnongjit* 27 (PSU); Sadao, Samnak Taao, 9 Jan 2014, *H. Soh* 36 (PSU); **Surat Thani:** Chaiya, Pak Mak, 2 Nov 2011, *P. Wessapak* 198 (BK); Chaiya, Pa We, 2 Nov 2011, *P. Wessapak* 199 (BK, BKF); **Trang:** Sikao, Mai Fat, Ban Khuan Hen Le, 27 Oct 2011, *P. Wessapak* 195 (BK, BKF); **Trat:** Ko Chang, Ban Khlong Son, 22 Mar 2001, *K. Chayamarit, T. Wongprasert, R. Pooma, V. Chaemchumroon, K. Pattarahirank-anok & M. Newman* 2735 (BKF)]; **Ubon Ratchathani:** Phu Chong Na Yoi, Phalan Kong Kwian, 6 Nov 2010, *P. Wessapak, Y. Buangam & W. Sareemongkonnimit* 159 (BK)]; **Udon Thani:** Kumphawapi, Huai Koeng, 4 Dec 2008, *M. Norsaengsri* 4582 (QBG).

Notes. This species was introduced to Thailand from India and Philippines as a fodder grass. At present, it has become a major weed and naturalised throughout the country.

Previously, this species was identified as *Pennisetum polystachion* (L.) Schult. The name was established by J. A. Schultes in 1824, based on the basionym *Panicum polystachion* L. After the genera were combined, based on the molecular phylogenetic studies (Donadío et al. 2009; Chemisquy et al. 2010), *Pennisetum* was merged into *Cenchrus*. The name of this species in *Cenchrus* is *Cenchrus polystachios* (L.) Morrone coined by Morrone in Chemisquy et al. (2010). Turner et al. (2019) reported that the lectotypification of the basionym *Panicum polystachion* L. by Merrill in 1917 was based on the plate cited by Linnaeus, which is identified as *Setaria flava* (Nees) Kunth. (now treated as a synonym of *Setaria parviflora* (Poir.) Kerguelen). Therefore, the name of *Cenchrus*, based on *Panicum polystachion* L., is not correct. The correct name of this species is considered as *Cenchrus setosus* Sw., which has the next priority.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: CN. Data curation: CN, PW. Formal analysis: PW. Funding acquisition: CN. Investigation: PW, CN. Methodology: PW, CN. Project administration: CN. Resources: PW, CN. Supervision: SD, CN. Writing – original draft: PW. Writing – review and editing: SD, CN.

Author ORCIDs

Chatchai Ngernsaengsaruy  <https://orcid.org/0000-0002-7131-976X>

Suthee Duangjai  <https://orcid.org/0000-0002-1490-759X>

Data availability

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

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Bryophyte flora of Mount Tebu Forest Reserve, Terengganu, Peninsular Malaysia

Nur Saidatul Atiqah¹, Elizabeth Pesiu¹ , Muhammad Syafiq Sarimi¹, Nor Aishah Shafie¹, Chin Wen Koid¹, Nik Norhazrina² , Nur Syazwana², Gaik Ee Lee^{1,3} 

¹ Faculty of Science and Marine Environment, 21030 Kuala Nerus, Universiti Malaysia Terengganu, Terengganu, Malaysia

² Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 Selangor, Malaysia

³ Institute of Tropical Biodiversity and Sustainable Development, 21030 Kuala Nerus, Universiti Malaysia Terengganu, Terengganu, Malaysia

Corresponding author: Gaik Ee Lee (gaik.lee@umt.edu.my)

Abstract

A checklist of the bryophyte flora of Mount Tebu Forest Reserve in Terengganu, Peninsular Malaysia, is presented. A total of 189 taxa in 71 genera and 26 families were enumerated. This figure represents 63% of the 298 bryophyte species recorded so far for the State of Terengganu. Out of 189 taxa of bryophytes, 26 liverworts are new additions to the bryoflora of Terengganu. The most prominent liverwort family is represented by Lejeuneaceae, with 54 species from 17 genera, while the moss family is the Sematophyllaceae, with 34 taxa in 13 genera. The majority of the species are epiphytes, either corticolous or ramicolous. Almost half of the bryophyte species have wider elevational ranges and occur from the lowlands to the summit of Mount Tebu.

Key words: Biodiversity, bryophytes, checklist, Malaysia, Marchantiophyta, taxonomy



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Introduction

Mount Tebu (1039 m) is the second-highest mountain after Mount Lawit (1519 m) in the northernmost part of Terengganu (Fig. 1). It is located within one of the primary mountain ranges of Peninsular Malaysia, known as the Timur Range (Banjaran Timur). The mountain comprises undulating lowlands, hill and upper hill dipterocarp forest. It has been gazetted as one of the state forest reserves, including the lowlands of Lata Belatan Recreational Forest at the base of Mount Tebu. Geologically, Mount Tebu is composed of unconsolidated alluvium, metasedimentary and igneous rocks in the lowlands to the summit of the mountain (Mohamed and Ali 2014). The unique landscape feature provides ample habitat for a diverse flora and fauna community with high conservation value (see Abdul Rahim et al. (2014) for several extensive floristic and ecological studies). It also offers a variety of vegetation and habitats favourable to the growth and diversity of bryophytes. The history of bryophyte

exploration in Terengganu has been reviewed by Lee et al. (2019). The early investigation was conducted by British and Japanese bryologists and yielded only a few bryophyte species, nine being mosses and two were liverworts (Dixon 1926; Yamada 1979; Inoue 1984). Subsequently, more recent collections of bryophytes from this region have been carried out, of which 11 species of bryophyte have been reported for the first time in Peninsular Malaysia and 77 taxa are new records to Terengganu (Lee et al. 2018, 2022; Pesiu et al. 2021; Sarimi et al. 2021).

Study area

Mount Tebu Forest Reserve is located at latitude 5.5914°N and longitude 102.6122°E in the Besut District, the northern part of Terengganu. The highest peak reaches 1039 m above sea level, including Lata Belatan Recreational Forest at its base, an entering point to the forest reserve. The foot of this mountain is often shaded by riparian forests where bryophytes are easily found within this area, ranging from 40–100 m a.s.l. with medium canopy cover. The closest rivers are Sungai Besut, Sungai Keluang Besar and Sungai Setiu. Most trees are

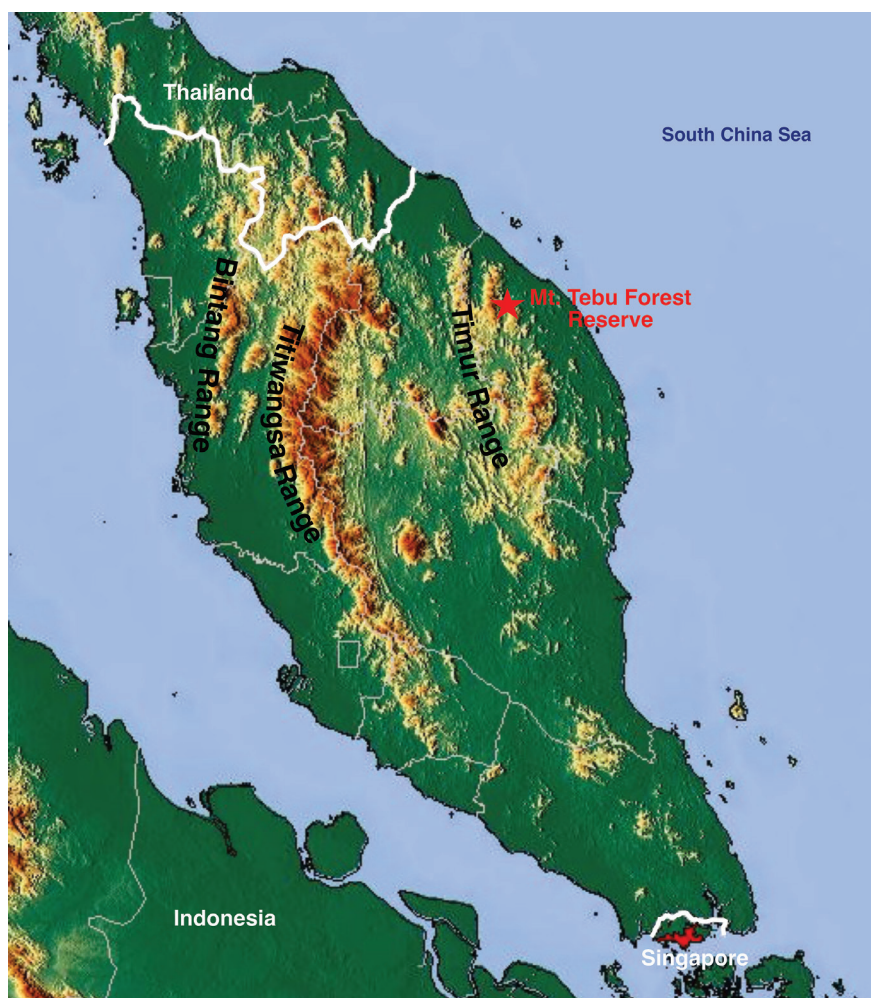


Figure 1. The map of Peninsular Malaysia shows the study area, Mt. Tebu Forest Reserve. Map modified from Dr Blofeld - <http://www.maps-for-free.com>, CC BY 3.0.

from the families Dipterocarpaceae, Euphorbiaceae, Annonaceae, Lauraceae and Myrtaceae. They grow on both sides of a valley and throughout the trails. Streams are moderate to fast water currents, often creating a few natural pools on the granite surfaces.

Materials and methods

This study is based on the authors' intensive bryophyte explorations from April 2019–November 2021 in Terengganu and a re-examination of previous moss collections of A. Damanhuri was made during the Mount Tebu scientific expedition in 2012. All the bryophyte samples were collected from various microhabitats along the trails within the study area, including tree trunks and branches, rocks, soils, fallen logs, rotten wood and leaves. Liverwort specimens were deposited in the Herbarium of Universiti Malaysia Terengganu (UMTP) and moss specimens were deposited in the Herbarium of Universiti Kebangsaan Malaysia (UKMB). About 1000 samples of bryophytes were collected from the study area and were examined by light microscopy. The drawing of the specimen was produced using an Olympus BX43 microscope, equipped with a drawing tube.

Results and discussion

A total of 189 taxa in 71 genera and 26 families were found in the Mount Tebu Forest Reserve, of which 109 are mosses and 80 are liverworts (Figs 2–4). This represents 63% of the 298 bryophyte species recorded so far for the State of Terengganu (Pócs and Lee 2016; Pesiu et al. 2021; Sarimi et al. 2021; Lee et al. 2022). Out of 80 species of liverworts, 26 are reported for the first time for Terengganu. The largest liverwort family found is the Lejeuneaceae, with 54 species, followed by Lepidoziaceae (eight species) and Radulaceae (seven species). The largest moss family is the Sematophyllaceae, with 34 taxa, followed by Calymperaceae (32 taxa) and Hypnaceae (seven taxa). The smallest liverwort and moss families were represented by only one species, for example, liverworts: Calypogeiaceae, Pallaviciniaceae, Plagiochilaceae, Solenostomataceae and Schistochilaceae and mosses: Diphysciaceae, Myuriaceae, Neckeraceae and Thuidiaceae. As expected, the distinct dominance of species is from the family Lejeuneaceae and mosses Sematophyllaceae and Calymperaceae, representing about 60% of all the bryophyte species found in Mount Tebu. They are the most common bryophyte families in the lowland tropical rainforests with high light intensity, dense canopy, high temperatures and many evergreen tree species.

Our study found that the diversity of moss species was higher than that of liverworts, a scenario similar to all the states in Peninsular Malaysia (Fig. 5). Reasons may be lower liverwort collecting, difficulty identifying liverwort species and lack of comprehensive field guides and local bryologists dealing with liverwort. The moss flora of Peninsular Malaysia has been well-studied taxonomically, in which exploration and species inventory of mosses have been more intensive and detailed. Thus far, 524 moss species have been reported from Peninsular Malaysia and all but Perlis and Malacca are well-represented



Figure 2. Mosses and their habit **A** *Diphyscium mucronifolium* Mitt **B** *Leucobryum sanctum* (Schwägr.) Hampe **C** *Fissidens ceylonensis* Dozy & Molk **D** *Pyrrhobryum latifolium* (Bosch & Sande Lac.) Mitt **E** *Arthrocnemum schimperii* (Dozy & Molk.) Dozy & Molk **F** *Octoblepharum albidum* Hedw **G** *Mitthyridium fasciculatum* (Hook. & Grev.) H. Rob **H** *Ectropothecium buitenzorgii* (Bél.) Mitt. **I** *Syrrhopodon muelleri* (Dozy & Molk.) Sande Lac.

with above 100 species (Yong et al. 2013; Ellis et al. 2019a, b). In comparison, only 491 taxa of liverworts are known from Peninsular Malaysia, suggesting that several States, particularly the northern regions, such as Perlis, Kedah and the east coast (Kelantan), have been under-collected and understudied (Lee and Gradstein 2021; Lee et al. 2022). The State of Pahang seems to be the centre of bryophyte diversity in Peninsular Malaysia (Fig. 5). The presence of major highlands and montane forests in Pahang often provides more favourable and more varied microhabitats for a rich bryophyte flora.

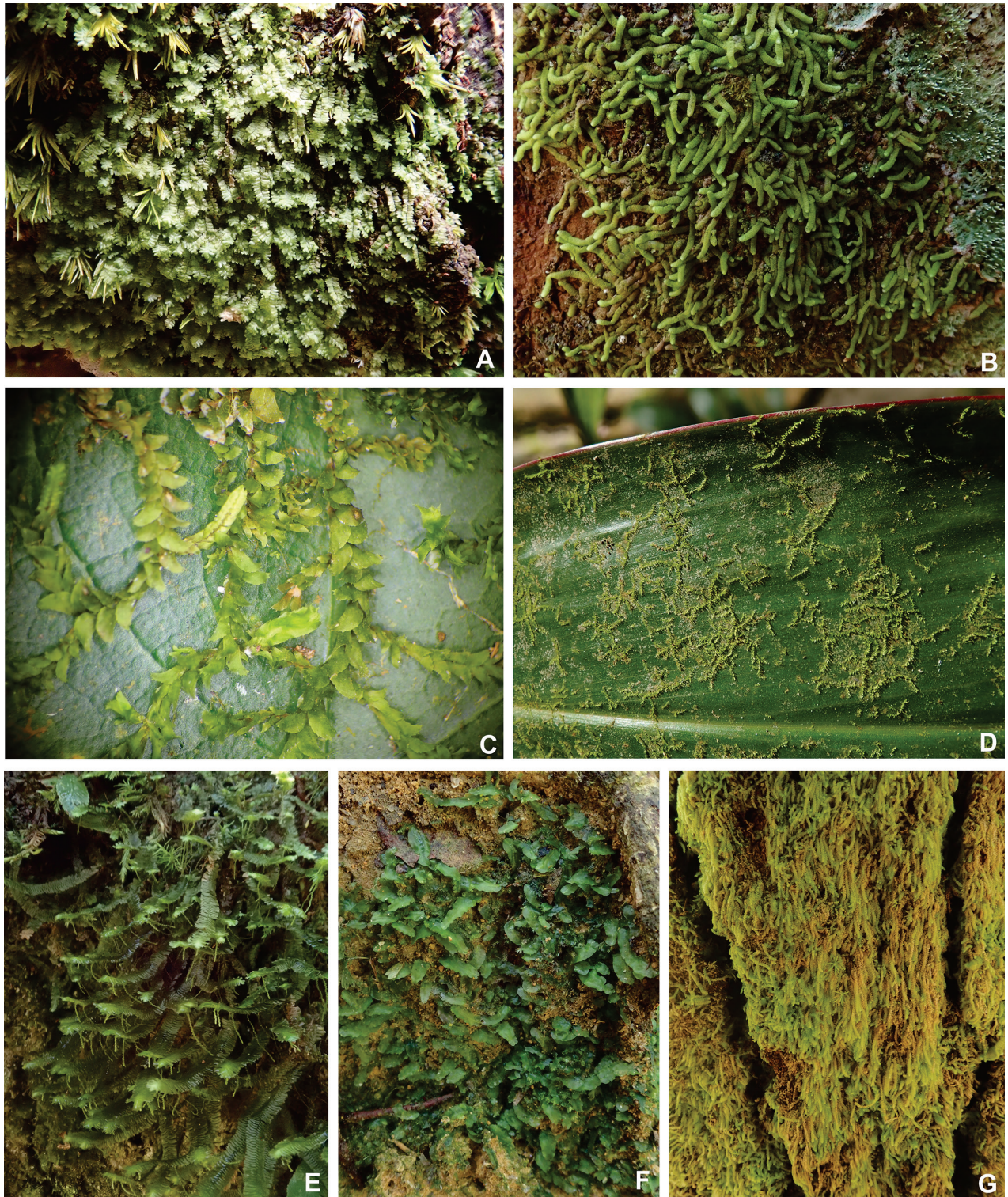


Figure 3. Liverworts and their habit **A** *Bazzania uncigera* (Reinw., Blume & Nees) Trevis **B** *Pycnolejeunea grandiocellata* Steph **C** *Caudalejeunea reniloba* (Gottsche) Steph **D** *Leptolejeunea epiphylla* (Mitt.) Steph **E** *Bazzania densa* (Sande Lac.) Schiffn **F** *Pallavicinia lyellii* (Hook.) Gray **G** *Drepanolejeunea pentadactyla* (Mont.) Steph.

Most of the bryophyte species in Mount Tebu are epiphytic, growing on the bark of tree trunks, on branches or tree stumps and the base of trees (Fig. 6). About half (49%) of ca. 1000 specimens examined were collected on trees

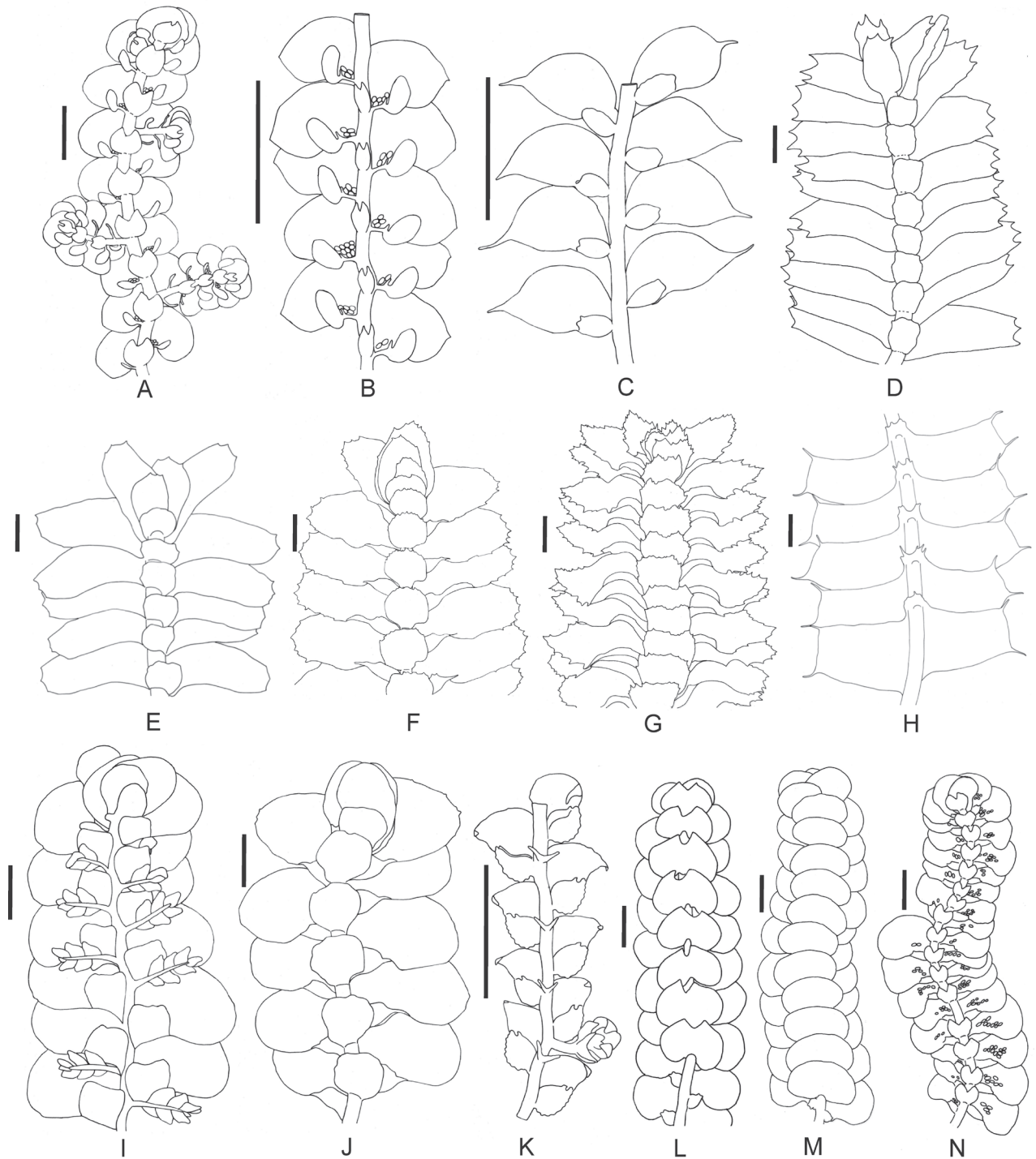


Figure 4. Liverworts from Mount Tebu Forest Reserve, all in ventral view **A** *Frullania gracilis* (Reinw. et al.) Nees **B** *Frullania trichodes* Mitt **C** *Cololejeunea wightii* Steph **D** *Bazzania longicaulis* (Sande Lac.) Schiffn **E** *Bazzania albifolia* Horik **F** *Ptychanthus striatus* (Lehm. & Lindenb.) Nees **G** *Thysananthus spathulistipus* (Reinw. et al.) Lindenb **H** *Heteroscyphus coalitus* (Hook.) Schiffn **I** *Radula formosa* (Spreng.) Nees **J** *Spruceanthus polymorphus* (Sande Lac.) Verd **K** *Drepanolejeunea vesiculosa* (Mitt.) Steph **L** *Lejeunea sordida* (Nees) Nees **M** *Lepidolejeunea integristipula* (J.B. Jack & Steph.) R.M. Schust **N** *Pycnolejeunea grandiocellata* Steph. (Scale = 0.5 mm).

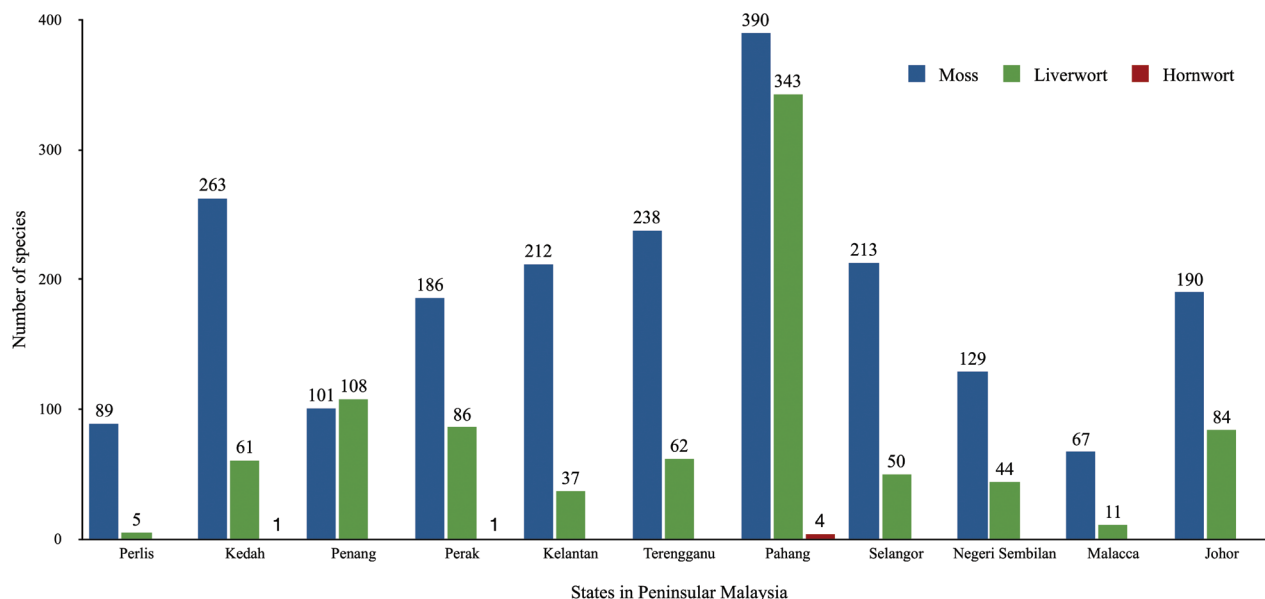


Figure 5. The number of bryophyte species reported from the States of Peninsular Malaysia.

(trunks, branches, twigs), while 22% were from leaves, 14% from rocks, 9% from soil or humus and 6% from rotten logs. About 18 species had broad substrate preferences and occurred on bark and branches of trees, leaves, soils and decaying logs. Others had more narrow preferences and occurred on only one substrate type, for example, *Pallavicinia lyellii* and *Solenostoma comatum* were always found on soil, *Ephemeropsis tjobodensis* and *Leptolejeunea epiphylla* occurred exclusively on leaves and *Diphyscium mucronifolium* grew only on rock (Appendix 1).

The distribution of the bryophyte species in Mount Tebu shows a distinct elevational differentiation from sea level to the mountain's summit (Fig. 7). About half of the moss species have wide elevational ranges and occur from the lowlands to the summit of Mount Tebu. The remaining half of the species have more narrow elevational ranges and are restricted to a lower range, below 500 m. Liverwort species have wider elevational ranges and occur in all elevation belts. However, both groups show a similar trend where most of the species are elevational generalist species, occurring in most rainforest belts and lowland specialists, being found only below 500 m. Of 189 taxa, only 29 species are restricted to the submontane rainforest and occur exclusively at 700–1000 m a.s.l. For example, *Acroporium condensatum* and *Mastopoma uncinifolium* are obligate highland species known only from Cameron Highlands, Mount Jerai and Mount Tebu (this study) (Tixier 1980; Yong et al. 2006). Other moss species typical of high elevations found in Mount Tebu are *Campylopus exasperatus*, *Leucoloma molle*, *Pogonatum cirratum* subsp. *macrophyllum*, *Acroporium stramineum* and *Trichosteleum saproxylophilum* and liverworts are *Frullania gracilis*, *F. trichodes*, *Cheilolejeunea ceylanica*, *C. trifaria*, *Cololejeunea aequabilis*, *C. appressa*, *C. equalbi*, *C. falcata*, *C. inflectens*, *C. metzgeriopsis*, *C. obliqua*, *C. ocelloides*, *C. sigmoidea*, *C. stephaniai*, *Drepanolejeunea dactylophora*, *Ptychanthus striatus*, *Schistochila aligera*, *Spruceanthus polymorphus* and *Tuyamaella molischii*.



Figure 6. Habitats of bryophyte species of Mount Tebu Forest Reserve **A** lowland dipterocarp forest **B** area around the summit **C–E** bryophytes on tree bases, branches, trunks **F** on rocks **G, H** on leaves.

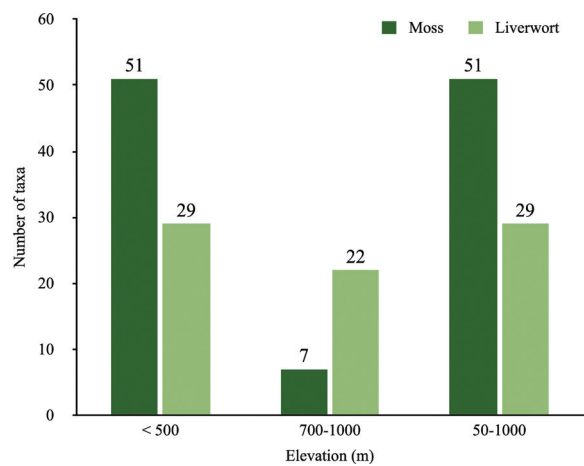


Figure 7. The elevational distribution of bryophyte taxa found in Mount Tebu Forest Reserve.

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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: GEL. Data curation: NN, MSS, NSA, NS, CWK, GEL, NAS, EP. Investigation: NN, GEL. Methodology: MSS, NS, EP, GEL, NN. Supervision: GEL. Writing - original draft: GEL. Writing - review and editing: EP, NAS, NN, CWK, NSA, MSS, NS.

Author ORCIDs

Elizabeth Pesiu  <https://orcid.org/0000-0003-4063-3489>

Nik Norhazrina  <https://orcid.org/0000-0001-9068-8192>

Gaik Ee Lee  <https://orcid.org/0000-0001-5161-6196>

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

Table A1. Substrate preferences and elevational distributions of bryophyte taxa in Mount Tebu. Corti: Corticolous (tree trunk), Epi: Epiphyllous (leaf), Ligni: Lignicolous (rotten log), Rami: Ramicolous (tree branch), Saxi: Saxicolous (rock), Terri: Terricolous (soil). An asterisk indicates new additions to the State of Terengganu (*).

No.	Taxon	Substrate preference	Elevation (m)
Bryophyta (Mosses)			
I.	Calymperaceae Kindb.		
1	<i>Arthrocnemum schimperi</i> (Dozy & Molk.) Dozy & Molk.	Corti, Saxi	60–110
2	<i>Calymperes afzelii</i> Sw.	Corti	50–130
3	<i>Calymperes boulayi</i> Besch.	Corti	60–110
4	<i>Calymperes erosum</i> Müll. Hal.	Corti, Saxi	50–1005
5	<i>Calymperes fasciculatum</i> Dozy & Molk.	Corti, Rami	50–1005
6	<i>Calymperes graeffeanum</i> Müll. Hal.	Corti	60–110
7	<i>Calymperes lonchophyllum</i> Schwägr.	Corti, Ligni	50–970
8	<i>Calymperes lonchophyllum</i> Schwägr. subsp. <i>beccari</i> (Hampe) M.Menzel	Ligni	110–940
9	<i>Calymperes mollucense</i> Schwägr.	Corti, Rami, Saxi, Ligni	50–130
10	<i>Calymperes porrectum</i> Mitt.	Corti	60–110
11	<i>Exostratum blumii</i> (Hampe) L.T.Ellis	Corti, Saxi, Ligni	60–110
12	<i>Leucophanes augustifolium</i> Renauld & Cardot	Corti, Saxi, Terri	50–1005
13	<i>Leucophanes glaucum</i> (Schwägr.) Mitt.	Corti	50–130
14	<i>Leucophanes octoblepharioides</i> Brid.	Corti, Rami, Saxi	50–970
15	<i>Mitthyridium constrictum</i> (Sull.) H.Rob	Corti, Epi, Rami	60–110
16	<i>Mitthyridium fasciculatum</i> subsp. <i>cardotii</i> (M.Fleisch.) B.C.Tan & L.T.Ellis	Corti	50–130
17	<i>Mitthyridium fasciculatum</i> (Hook. & Grev.) H.Rob.	Corti, Rami	50–1005
18	<i>Mitthyridium flavum</i> (Müll. Hal.) H.Rob.	Corti	50–130
19	<i>Mitthyridium junquilianum</i> (Mitt.) H.Rob.	Corti, Rami	50–130
20	<i>Mitthyridium repens</i> (Harv.) H.Rob.	Corti	50–970
21	<i>Mitthyridium undulatum</i> (Dozy & Molk.) H.Rob.	Corti, Rami	50–970
22	<i>Octoblepharum albidum</i> Hedw.	Corti	50–130
23	<i>Syrrhopodon albo-vaginatus</i> Schwägr.	Ligni	50–130
24	<i>Syrrhopodon aristifolius</i> Mitt.	Corti	50–1005
25	<i>Syrrhopodon confertus</i> Sande Lac.	Corti	50–1005
26	<i>Syrrhopodon croceus</i> Mitt.	Corti, Saxi	50–1005
27	<i>Syrrhopodon muelleri</i> (Dozy & Molk.) Sande Lac.	Corti	50–970
28	<i>Syrrhopodon prolifer</i> Schwägr.	Corti, Ligni	110–940
29	<i>Syrrhopodon spiculosus</i> Hook. & Grev.	Corti, Ligni	50–970
30	<i>Syrrhopodon stoneae</i> W.D.Reese	Corti	50–130
31	<i>Syrrhopodon trachyphyllus</i> Mont.	Corti	50–940
32	<i>Syrrhopodon tristichus</i> Schwägr.	Corti	60–940
II.	Daltoniaceae Schimp.		
33	<i>Distichophyllum cuspidatum</i> (Dozy & Molk.) Dozy & Molk.	Corti	110–940
34	<i>Distichophyllum nigricaulis</i> var. <i>cirratum</i> (Renauld & Cardot) M.Fleisch	Corti, Saxi	110–940
35	<i>Ephemeropsis tjibodensis</i> K.I.Goebel	Epi	60–110
III.	Dicranaceae Schimp.		
36	<i>Campylopus ericoides</i> (Griff.) A.Jaeger	Saxi	100–1005
37	<i>Campylopus exasperatus</i> (Nees & Blume) Brid.	Saxi	940–1005
38	<i>Dicranella coarctata</i> (Müll. Hal.) Bosch & Sande Lac.	Terri	110–940
39	<i>Leucoloma amoene-virens</i> Mitt.	Saxi	50–130
10	<i>Leucoloma molle</i> (Müll. Hal.) Mitt.	Corti	940–1005

No.	Taxon	Substrate preference	Elevation (m)
IV.	Diphysciaceae M.Fleisch		
41	<i>Diphyscium mucronifolium</i> Mitt.	Saxi	60–970
V.	Fissidentaceae Schimp.		
42	<i>Fissidens ceylonensis</i> Dozy & Molk.	Saxi	60–110
43	<i>Fissidens crassinervis</i> Sande Lac.	Terri	50–970
44	<i>Fissidens hollianus</i> Dozy & Molk.	Corti	60–110
45	<i>Fissidens javanicus</i> Dozy & Molk.	Saxi	60–110
46	<i>Fissidens oblongifolius</i> Hook. f. & Wilson	Corti	70–80
47	<i>Fissidens pellucidus</i> Hornsch.	Terri	70–80
VI.	Hypnaceae Schimp.		
48	<i>Ectropothecium buitenzorgii</i> (Bél.) Mitt.	Corti, Ligni, Saxi, Terri	50–970
49	<i>Ectropothecium ichnotocladum</i> (Müll. Hal.) A.Jaeger	Corti, Saxi	50–940
50	<i>Isopterygium albescens</i> (Hook. in Schwägr.) A.Jaeger	Corti	50–130
51	<i>Pseudotaxiphyllum pohliaecarpum</i> (Sull. & Lesq.) Z.Iwats.	Terri	110–940
52	<i>Vesicularia dubyana</i> (Müll. Hal.) Broth.	Corti, Saxi, Terri	50–130
53	<i>Vesicularia miquelii</i> (Sande Lac.) M.Fleisch.	Corti	60–110
54	<i>Vesicularia reticulata</i> (Dozy & Molk.) Broth.	Saxi	70–80
VII.	Hypnodendraceae Broth.		
55	<i>Hypnodendron dendroides</i> (Brid.) Touw	Saxi	110–940
56	<i>Hypnodendron subspinervium</i> (Müll. Hal.) A.Jaeger subsp. <i>arborescens</i> (Mitt.) Touw	Corti	110–940
VIII.	Leucobryaceae Schimp.		
57	<i>Leucobryum aduncum</i> Dozy & Molk.	Corti, Ligni, Saxi, Terri	50–970
58	<i>Leucobryum aduncum</i> var. <i>scalare</i> (M.Fleisch.) A.Eddy	Corti	50–970
59	<i>Leucobryum bowringii</i> Mitt.	Corti, Saxi	50–970
60	<i>Leucobryum candidum</i> (P.Beauv.) Wilson	Corti, Saxi	50–970
61	<i>Leucobryum chlorophyllosum</i> Müll. Hal.	Corti	50–970
62	<i>Leucobryum javense</i> (Brit.) Mitt.	Corti, Terri	100–1005
63	<i>Leucobryum microleucophanoides</i> A.Johnson	Corti	100–970
64	<i>Leucobryum sanctum</i> (Schwägr.) Hampe	Corti, Saxi, Terri	50–970
IX.	Meteoriaceae Kindb.		
65	<i>Aerobryidium crispifolium</i> (Broth. & Geh.) M.Fleisch.	Corti, Rami	60–110
66	<i>Aerobryopsis longissima</i> (Dozy & Molk.) M.Fleisch.	Corti	50–130
X.	Myuriaceae M.Fleisch.		
67	<i>Oediciadium pseudorufescens</i> (Hampe) B.C.Tan & Mohamed	Corti, Saxi	50–970
XI.	Neckeraceae Schimp.		
68	<i>Himantocladium plumula</i> (Nees in Brid.) M.Fleisch.	Corti	60–110
XII.	Polytrichaceae Schwägr.		
69	<i>Pogonatum cirratum</i> subsp. <i>fuscum</i> (Mitt.) Hyvönen	Terri	110–940
70	<i>Pogonatum cirratum</i> subsp. <i>macrophyllum</i> (Dozy & Molk.) Hyvönen	Saxi	940–1005
XIII.	Pottiaceae Hampe		
71	<i>Barbula consanguinea</i> (Thwaites & Mitt.) A.Jaeger	Saxi	60–110
72	<i>Hyophila involuta</i> (Hook.) A.Jaeger	Saxi, Terri	50–130
XIV.	Rhizogoniaceae Broth.		
73	<i>Pyrrhobryum latifolium</i> (Bosch & Sande Lac.) Mitt.	Corti	50–130
74	<i>Pyrrhobryum medium</i> (Besch.) Manuel	Corti	60–110
XV.	Sematophyllaceae Broth.		
75	<i>Acanthorrhynchium papillatum</i> (Harv.) M.Fleisch.	Corti, Ligni	50–130
76	<i>Acroporium adpersum</i> (Hampe) Broth.	Corti	60–110
77	<i>Acroporium condensatum</i> E.B.Bartram	Saxi	940–1005

No.	Taxon	Substrate preference	Elevation (m)
78	<i>Acroporium diminutum</i> (Brid.) M.Fleisch.	Corti	60–1005
79	<i>Acroporium joannis-winkleri</i> Broth.	Corti, Ligni, Terri	60–1005
80	<i>Acroporium lamprophyllum</i> Mitt.	Corti	50–130
81	<i>Acroporium rigens</i> (Dixon) Dixon	Saxi, Terri	50–1005
82	<i>Acroporium stramineum</i> (Reinw. & Hornsch.) M.Fleisch.	Terri	940–1005
83	<i>Acroporium strepsiphyllum</i> (Mont.) B.C.Tan	Corti, Saxi	60–1005
84	<i>Clastobryophilum bogoricum</i> (Bosch & Sande Lac.) M.Fleisch.	Corti	50–130
85	<i>Clastobryum caudatum</i> (Sande Lac.) M.Fleisch.	Corti	70–80
86	<i>Clastobryum cuculligerum</i> (Sande Lac.) Tixier	Corti	60–110
87	<i>Clastobryum epiphyllum</i> (Renauld & Cardot) B.C.Tan & Touw	Corti, Rami	60–110
88	<i>Gammiella tonkinensis</i> (Broth. & Paris) B.C.Tan	Rami	100–970
89	<i>Isocladia surcularis</i> (Dixon) B.C.Tan & Mohamed	Corti	60–110
90	<i>Mastopoma uncinifolium</i> (Broth.) Broth.	Rami	940–1005
91	<i>Meiothecium microcarpum</i> (Harv.) Mitt.	Corti	50–130
92	<i>Papillidiopsis bruchii</i> (Dozy & Molk.) W.R.Buck & B.C.Tan	Corti	60–110
93	<i>Papillidiopsis complanata</i> (Dixon) W.R.Buck & B.C.Tan	Corti, Ligni	50–1005
94	<i>Papillidiopsis luxurians</i> (Dozy & Molk.) W.R.Buck & B.C.Tan	Corti, Ligni, Saxi	50–940
95	<i>Papillidiopsis malesiana</i> W.R.Buck & B.C.Tan	Corti	50–130
96	<i>Rhaphidostichum bunodicarpum</i> (Müll. Hal.) M.Fleisch.	Corti, Saxi	50–130
97	<i>Rhaphidostichum piliferum</i> (Broth.) Broth.	Corti	60–110
98	<i>Taxithelium instratum</i> (Brid.) Broth.	Corti	50–130
99	<i>Taxithelium isocladium</i> (Bosch & Sande Lac.) Renauld & Cardot	Corti, Epi, Rami	50–130
100	<i>Taxithelium kerianum</i> (Broth.) Broth.	Corti, Rami	60–940
101	<i>Taxithelium lindbergii</i> (A.Jaeger) Renauld & Cardot	Epi, Rami	110–1005
102	<i>Taxithelium nepalense</i> (Schwägr.) Broth.	Corti	60–110
103	<i>Trichosteleum boschii</i> (Dozy & Molk.) A.Jaeger	Corti, Ligni, Rami, Saxi	50–1005
104	<i>Trichosteleum saproxylophilum</i> (Müll. Hal.) B.C.Tan et al.	Terri	940–1005
105	<i>Trichosteleum singaporense</i> M.Fleisch.	Corti	70–80
106	<i>Trichosteleum stigmosum</i> Mitt.	Corti, Ligni, Rami	50–130
107	<i>Trismegistia lancifolia</i> (Harv.) Broth.	Corti, Saxi	50–970
108	<i>Trismegistia lancifolia</i> var. <i>pseudoplicata</i> (Harv.) Broth.	Corti, Ligni	60–940
XVI. Thuidiaceae Schimp.			
109	<i>Thuidium pristocalyx</i> (Müll. Hal.) A.Jaeger	Saxi	50–940
Marchantiophyta (Liverworts)			
I. Calypogeiaceae Arnell			
1	<i>*Asperifolia arguta</i> (Nees & Mont.) A.V.Troitsky et al.	Terri	63–340
II. Frullaniaceae Lorch			
2	<i>Frullania apiculata</i> (Reinw. et al.) Nees	Epi	850–1000
3	<i>*Frullania gracilis</i> (Reinw. et al.) Nees	Corti	980
4	<i>*Frullania trichodes</i> Mitt.	Epi	800
III. Lejeuneaceae Cavers			
5	<i>Caudalejeunea reniloba</i> (Gottsche) Steph.	Corti, Epi, Rami	40–1039
6	<i>Ceratolejeunea minor</i> Mizut.	Epi	100
7	<i>Ceratolejeunea singaporensis</i> (Lindenb.) Schiffn.	Epi	100
8	<i>Cheilelejeunea ceylanica</i> (Gottsche) R.M.Schust. & Kachroo	Corti, Epi	900–1000
9	<i>Cheilelejeunea trapezia</i> (Nees) Kachroo & R.M.Schust.	Corti, Epi, Rami	80–1000
10	<i>Cheilelejeunea trifaria</i> (Reinw. et al.) Mizut.	Epi	1006
11	<i>Cololejeunea aequabilis</i> (Sande Lac.) Schiffn.	Epi	900–1000
12	<i>Cololejeunea appressa</i> (A.Evans) Benedix	Epi	600–1000
13	<i>Cololejeunea equalbi</i> Tixier	Epi	880–1000

No.	Taxon	Substrate preference	Elevation (m)
14	<i>Cololejeunea falcata</i> (Horik.) Benedix	Epi	600–1000
15	<i>Cololejeunea floccosa</i> (Lehm. & Lindenb.) Schiffn.	Epi	80–1000
16	<i>Cololejeunea inflata</i> Steph.	Epi	80–1000
17	<i>Cololejeunea inflectens</i> (Mitt.) Benedix	Epi	900–1000
18	<i>Cololejeunea lanciloba</i> Steph.	Epi	80–500
19	<i>Cololejeunea metzgeriopsis</i> (K.I.Goebel) Gradst. et al.	Epi	780
20	<i>Cololejeunea obliqua</i> (Nees & Mont.) Schiffn.	Epi	800–1000
21	<i>Cololejeunea ocelloides</i> (Horik.) Mizut.	Epi	900–1000
22	<i>Cololejeunea planissima</i> (Mitt.) Abeyw.	Epi	80–1000
23	<i>Cololejeunea schmidtii</i> Steph.	Epi	300–1000
24	<i>Cololejeunea sigmoidea</i> Jovet-Ast & Tixier	Epi	800–1000
25	<i>Cololejeunea stephanii</i> Benedix	Epi	900–1006
26	<i>Cololejeunea verrucosa</i> Steph.	Epi	100–900
27	* <i>Cololejeunea wightii</i> Steph.	Corti	100–900
28	<i>Colura acroloba</i> (Prantl) Jovet-Ast	Epi	100–900
29	<i>Colura ari</i> (Steph.) Steph.	Epi	100–1000
30	<i>Colura conica</i> (Sande Lac.) K.I.Goebel	Corti, Epi	100–900
31	<i>Colura corynophora</i> (Nees et al.) Trevis.	Corti, Epi	100–1000
32	<i>Colura inuii</i> Horik.	Epi	100–1000
33	<i>Drepanolejeunea dactylophora</i> (Nees et al.) J.B.Jack & Steph.	Epi	850–1006
34	<i>Drepanolejeunea levicornua</i> Steph.	Epi	80–1000
35	<i>Drepanolejeunea longicornua</i> (Herzog) Mizut.	Epi	100–1000
36	<i>Drepanolejeunea pentadactyla</i> (Mont.) Steph.	Epi	100–1000
37	<i>Drepanolejeunea spicata</i> (Steph.) Grolle & R.L.Zhu	Corti, Epi, Rami	100–1000
38	<i>Drepanolejeunea ternatensis</i> (Gottsche) Schiffn.	Corti, Epi, Rami	100–1000
39	<i>Drepanolejeunea thwaitesiana</i> (Mitt.) Steph.	Epi	80–1000
40	* <i>Drepanolejeunea vesiculosa</i> (Mitt.) Steph.	Epi	60–100
41	<i>Lejeunea adpressa</i> Nees	Corti, Epi	90–500
42	<i>Lejeunea micholitzii</i> Mizut.	Epi	900–1000
43	* <i>Lejeunea sordida</i> (Nees) Nees	Corti	89
44	<i>Lepidolejeunea bidentula</i> (Steph.) R.M.Schust.	Corti, Epi	63–340
45	* <i>Lepidolejeunea integristipula</i> (J.B.Jack & Steph.) R.M.Schust.	Corti	63–340
46	<i>Leptolejeunea amphioththalma</i> Zwickel	Epi	80–1000
47	<i>Leptolejeunea subacuta</i> A.Evans	Epi	300–1000
48	<i>Leptolejeunea epiphylla</i> (Mitt.) Steph.	Epi	80–1000
49	<i>Leptolejeunea maculata</i> (Mitt.) Schiffn.	Epi	80–1000
50	<i>Leptolejeunea vitrea</i> (Nees) Schiffn.	Epi	80–1000
51	<i>Lopholejeunea eulopha</i> (Taylor) Schiffn.	Epi	100–900
52	<i>Metalejeunea cucullata</i> (Reinw. et al.) Grolle	Epi	900–1000
53	<i>Microlejeunea punctiformis</i> (Taylor) Steph.	Corti, Epi	89–940
54	* <i>Ptychanthus striatus</i> (Lehm. & Lindenb.) Nees	Corti	980
55	* <i>Pycnolejeunea grandiozellata</i> Steph.	Corti	60–100
56	* <i>Spruceanthus polymorphus</i> (Sande Lac.) Verd.	Corti	980
57	<i>Tuyamaella molischii</i> (Schiffn.) S.Hatt.	Epi	780–1006
58	* <i>Thysananthus spathulistipus</i> (Reinw. et al.) Lindenb.	Rami	48
IV.	Lepidoziaceae Limpr.		
59	* <i>Bazzania albifolia</i> Horik.	Corti	89–700
60	* <i>Bazzania asymmetrica</i> (Steph.) N.Kitag.	Corti, Rami	100–200
61	* <i>Bazzania calcarata</i> (Sande Lac.) Schiffn.	Corti	100
62	* <i>Bazzania densa</i> (Sande Lac.) Schiffn.	Corti	89–700

No.	Taxon	Substrate preference	Elevation (m)
63	<i>*Bazzania longicaulis</i> (Sande Lac.) Schiffn.	Corti, Terri	89–700
64	<i>*Bazzania uncigera</i> (Reinw. et al.) Trevis.	Corti, Saxi	89–700
65	<i>*Kurzia gonyotricha</i> (Sande Lac.) Grolle	Terri	89
66	<i>*Lepidozia trichodes</i> (Reinw. et al.) Nees	Terri	89
X.	Lophocoleaceae Vanden Berghen		
67	<i>*Heteroscyphus aselliformis</i> (Reinw. et al.) Schiffn.	Corti	89
68	<i>*Heteroscyphus coalitus</i> (Hook.) Schiffn.	Terri	89
69	<i>*Heteroscyphus succulentus</i> (Gottsche) Schiffn.	Corti	89
XI.	Pallaviciniaceae Mig.		
70	<i>*Pallavicinia lyellii</i> (Hook.) Gray	Terri	60
XII.	Plagiochilaceae Müll.Frib.		
71	<i>Plagiochila bantamensis</i> (Reinw. et al.) Mont.	Corti,	89
XIII.	Radulaceae Müll.Frib.		
72	<i>Radula acuminata</i> Steph.	Epi	80–1000
73	<i>Radula assamica</i> Steph.	Epi	60–100
74	<i>*Radula formosa</i> (Spreng.) Nees	Corti	60–100
75	<i>Radula grandilobula</i> Promma & Chantanaorr.	Epi	100
76	<i>Radula javanica</i> Gottsche	Corti, Epi	60–100
77	<i>Radula nymannii</i> Steph.	Epi	60–100
78	<i>Radula tjibodensis</i> K.I.Goebel	Epi	80–1000
IX.	Solenostomaceae Stotler & Crand.-Stotl.		
79	<i>*Solenostoma comatum</i> (Nees) C.Gao	Terri	60
X.	Schistochilaceae H.Buch		
80	<i>*Schistochila aligera</i> (Nees & Blume) J.B.Jack & Steph.	Corti	994

Panax siamensis J. Wen, a new species of the ginseng genus (*Panax*, Araliaceae) from northern Thailand

Jun Wen¹, Gary Krupnick¹, Hans-Joachim Esser²

¹ Department of Botany, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA

² Botanische Staatssammlung München, Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB), Menzinger Straße 67, 80638 München, Germany

Corresponding author: Jun Wen (WENJ@si.edu)

Abstract

We herein describe a new species, *Panax siamensis* J. Wen, from the tropical monsoon forests in northern Thailand. *Panax siamensis* is characterized by a combination of characters including horizontally elongated rhizomes with thick internodes, 3–5 whorled leaves each with 7–9 sessile and lanceolate leaflets, lanceolate bracteoles not persisting at the fruiting stage, 2-locular ovaries, and red fruits with a black top. The new species is most closely related to *Panax zingiberensis* C.Y. Wu & Feng from south-eastern Yunnan province of China, sharing the character of sessile leaflets, but differing in that *P. siamensis* has well developed, elongated rhizomes (vs. compact, ginger-like rhizomes and rootstock in *P. zingiberensis*), and 7–9 leaflets (vs. (3–) 5–7 leaflets in *P. zingiberensis*). We also compare *Panax siamensis* to other related Asian *Panax* species, including *P. assamicus* Banerjee, *P. bipinnatifidus* Seem., *P. pseudoginseng* Wallich, and *P. vietnamensis* Ha & Grushv. The new taxon is preliminarily assessed as Vulnerable (VU D2), according to the IUCN Red List criteria. A taxonomic key is provided to facilitate the identification of *P. siamensis* and its close allies.

Key words: Araliaceae, conservation, ginseng genus, *Panax*, *Panax siamensis* J. Wen



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Introduction

Panax L., the ginseng genus, is an economically important lineage with several medicinally significant species, e.g., *Panax ginseng* C.A.Meyer (ginseng), *P. quinquefolius* L. (American ginseng), *P. notoginseng* (Burkill) F. H. Chen ex C. Y. Wu et al. (sanchi), *P. zingiberensis* C.Y. Wu & Feng (ginger-like sanchi), and *P. vietnamensis* Ha & Grushv. (Vietnamese ginseng) (Zhou et al. 1975; Ha and Grushvitzky 1985; Wen and Zimmer 1996). The genus consists of c. 18 species disjunctly distributed in eastern Asia to the Himalayas and eastern North America, showing a classical eastern Asian – eastern North American biogeographic disjunction (Wen and Zimmer 1996; Wen 1999, 2001; Lee and Wen 2004; Zuo et al. 2015). It is one of the c. 50 genera of the ginseng family Araliaceae (Wen et al. 2001; Plunkett et al. 2018; Gallego-Narbón et al. 2022).

In spite of its economic (Hu 1976; Proctor 1996) and biogeographic (Wen 1999; Zuo et al. 2017) importance, the species delimitation of Asian *Panax* has been controversial, largely involving the circumscription of *Panax japonicus*

C.A. Meyer and *Panax pseudoginseng* Wallich (Li 1942; Hara 1966, 1971; Zhou et al. 1975; Hoo and Tseng 1978; Yang 1981; Xiang and Lowry 2007). Molecular phylogenetic analyses have strongly suggested that *Panax japonicus* is endemic to Japan and forms a clade with two of the medicinally important species: *Panax ginseng* and *P. quinquefolius* (Wen and Zimmer 1996; Lee and Wen 2004; Zuo et al. 2011, 2017). A number of studies have supported the distinctiveness of *Panax pseudoginseng* as a species that is narrowly distributed in Nepal and adjacent areas of Xizang, China, and as closely related to *Panax stipuleanatus* Tsai & Feng, which is from southwestern China and northern Vietnam (Lee and Wen 2004; Zuo et al. 2011, 2017). Zhou et al. (1975) also described *Panax zingiberensis* from southeast and southern Yunnan that has ginger-like roots persistent in older plants, and leaflets without petiolules.

During our revisionary studies of *Panax*, we discovered a new species from northern Thailand. This species had been recognized as *Aralia pseudoginseng* (Wallich) Benth. ex C. B. Clarke var. *angustifolia* (Burkill) Craib (Craib 1931). Hara (1971) and more recently Esser and Jebb (2019) treated it in the genus *Panax* [as *P. pseudoginseng* Wallich var. *angustifolius* (Burkill) H. L. Li], which has been treated as *Panax bipinnatifidus* Seem. (Zuo et al. 2015, 2017). The new species is highly distinct from *Panax bipinnatifidus* and several related species from Asia (see Discussion below).

Material and methods

Descriptions and measurements of morphological characters of the new species were based on field observations of living plants and herbarium specimens at A, BKF, CMUB, E, K and US. For comparative studies with other *Panax* species, we examined herbarium specimens from the following herbaria: A, ABD, ASSAM, B, BKF, BM, BSHC, C, CAL, CAS, CMUB, E, GH, IBSC, K, KATH, K-W, KUN, L, LBG, LE, MO, NBU, NY, P, PE, PH, TCD, TI, U, UC, US, W, WH, and WU (abbreviations following Thiers 2020). We also examined images of type specimens and other herbarium specimens on JSTOR Global Plants (<http://plants.jstor.org>), the Chinese Virtual Herbarium Website (<http://www.cvh.ac.cn/>), and National Specimen Information Infrastructure (<http://www.nsii.org.cn/>).

Taxonomic treatment

Panax siamensis J. Wen, sp. nov.

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Figs 1, 2

Type. THAILAND. Chiang Mai. A southerly ridge of Doi Pa Mawn, an easterly spur of Doi Angka (i.e., Doi Inthanon), ca. 1350 m, berries bright red with a black top, 30 Dec 1926, in fr, H. B. G. Garrett 364 (holotype: BKF!; isotypes: ABD!, C!, E!, K!, TCD!).

Diagnosis. Rhizomes horizontally elongated with thick internodes. Leaves 3–5 at the tip of stem, exstipulate, with 7–9 leaflets; leaflets sessile or nearly so, tapering toward the base, lanceolate, long acuminate at apex, long acute at base, serrulate to doubly so at margin, membranaceous, bristly along veins and veinlets on both surfaces. Ovary 2-locular. Fruits subglobose, bright red with a black top, persistent stigmas recurved, 1–2 seeded, 5–6 mm long, 7–8 mm



Figure 1. Illustration of *Panax siamensis* J. Wen based on J. Wen 7371 (US) **A** habit **B** horizontal rhizome with base of stem **C** leaflet margin **D** leaflet abaxial surface **E** infructescence **F** enlarged infructescence **G** bracteoles subtending pedicels at flowering stage **H** older flowers after petals falling off, showing 2-locular ovary **I** young fruiting stage **J** seed **K** seed surface.

wide, 3–3.5 mm thick. Seeds ovate, 5–5.5 mm long, 3–4 mm wide, 2.5–3.5 mm thick, surface rough.

Description. Perennial herb, 60–70 cm, hermaphrodite. Rhizomes horizontally elongated with thick internodes, brown outside, whitish inside; stems light green,



Figure 2. Field images of *Panax siamensis* and its habitat **A** habitat in monsoon evergreen forest **B** infructescence showing red fruits with a black top **C** habit. Photo credit: **A** (Ricky Ward), **B**, **C** (Jun Wen).

30–45 cm. Leaves 3–5 at the tip of the stem, with 7–9 leaflets, exstipulate, petioles 7–11 cm, glabrous; leaflets sessile or nearly so, tapering toward the base, lanceolate, basal leaflets 7–10 cm long, 2–2.5 cm wide, upper leaflets 13–17.5 cm long, 2–3 cm wide, long acuminate at apex, long acute at base, serrulate to doubly so at margin, membranaceous, bristly along veins and veinlets on both surfaces, bristles or setae 1–2.5 mm long, lateral veins 17–25 per side. Inflorescence consisting of a terminal umbel, sometimes with 1–2 lateral umbels, peduncle 15–20 cm, glabrous, terminal umbels with 70–90 flowers, lateral umbels with 20–30 flowers; pedicels puberulent to slightly so, pale light green, with dark violet color at both ends at late flowering to fruiting stage, 10–13 mm in terminal umbels, 6–8 mm in lateral umbels; bracteoles lanceolate, membranaceous, glabrous, 1.3–1.6 mm long, 0.2–0.3 mm wide, mostly not persistent at fruiting stage. Sepals 5, triangular, 0.4–0.5 mm long, 0.6–0.7 mm wide; petals light green, 1.6–2 mm long, 1–1.1 mm wide; anthers white, filaments pale light green, 2–2.2 mm; ovary 2-locular, stigma white. Fruits subglobose, bright red with a black top, persistent stigmas recurved, 1–2 seeded, 5–6 mm long, 7–8 mm wide, 3–3.5 mm thick. Seeds ovate, 5–5.5 mm long, 3–4 mm wide, 2.5–3.5 mm thick, surface rough.

Additional specimens examined. Thailand. CHIANG MAI: Mae Soi Ridge, Mae Soi Subdistrict, near Ban Bah Cluary (Meo Village), 1475 m, 11 Aug 1991, in fl, shaded place, mixed evergreen hardwood and pine forest, *J. F. Maxwell* 91-722 (A, CMUB, E); Ob Luang National Park, Mae Soi Conservation Area, Bah Gluay (Hmong) village area, between the Ranger Station and the village, on the N side of the road passing through the Bah Gluay village, elev. 1550 m, evergreen forest, plant c. 60–70 m tall, fruits red with a black top, 04 Nov 2003, fr. *J. Wen* 7371 (KUN, US).

Phenology. Flowering in August; fruiting in November to December.

Distribution. Northern Thailand; elevation 1350–1550 m.

Ecology. In shaded areas of monsoon evergreen hardwood forests, or in mixed evergreen hardwood and pine forests, granite bedrock.

Etymology. The species epithet denotes the geographic distribution of the species in Thailand.

Conservation

The area of occupancy (AOO) of this species as measured with a 2×2 grid is estimated to be 12 km²; the extent of occurrence (EOO) is estimated to be 39.54 km². Apart from habitat destruction, no specific threats are known. It is not found in cultivation, and it is not known from any *ex situ* collections. With a restricted area of occupancy, only three known locations, and a plausible future threat due to stochastic events or habitat disturbance brought about by human activities near villages, *Panax siamensis* is preliminarily assessed with a status of Vulnerable (VU D2) according to IUCN Red List Criteria (IUCN 2012, 2022).

Discussion

The new species *Panax siamensis* is distinguished from other *Panax* species by a combination of characters including horizontally elongated rhizomes with thick internodes, 3–5 whorled leaves each with 7–9 sessile and lanceolate leaflets, lanceolate bracteoles not persisting at the fruiting stage, 2-locular ovaries, and red fruits with a black top. The new taxon is sister to *Panax zingiberensis*

from southeastern Yunnan province of China (J. Wen, unpublished), sharing the character of sessile leaflets. The two species differ in that *P. siamensis* has elongated rhizomes (vs. compact ginger-like rhizomes in *P. zingiberensis*), and 7–9 leaflets (vs. 5–7 leaflets in *P. zingiberensis*). As *P. zingiberensis* is medicinally important (Zhou et al. 1975), it is important to explore the chemistry of *P. siamensis* to test its medicinal value.

Panax siamensis is similar to *Panax vietnamensis* from Vietnam and southwestern China in that both species have bamboo-like horizontally elongated rhizomes and 2-locular ovaries. They can be easily differentiated in that *P. vietnamensis* usually has 5 (–7) leaflets (vs. 7–9 leaflets in *P. siamensis*) that are ovate to elliptic (vs. lanceolate in *P. siamensis*), petiolules 8–15 mm long (vs. sessile leaflets without conspicuous petiolules in *P. siamensis*), and glandular pedicels (puberulent pedicels in *P. siamensis*) (Ha and Grushvitzky 1985; Wen 2001; Duy et al. 2016).

Even though *Panax siamensis* was recently treated as part of *P. pseudoginseng* (Esser and Jebb 2019), the new species is highly distinct from *Panax pseudoginseng*, which is narrowly distributed in Nepal and neighboring Xizang of China (Wallich 1829; Wen 2001). *Panax pseudoginseng* has fusiform tubers that are single or fascicled (vs. tubers absent in *P. siamensis*), rhizomes short and upright (vs. elongate and horizontal in *P. siamensis*), leaves with stipules (stipules absent in *P. siamensis*), and fruits that are red throughout (vs. fruits red with a black top in *P. siamensis*) (Wen 2001; Yoo et al. 2001).

Panax pseudoginseng var. *angustifolius* is now considered as part of *Panax bipinnatifidus* Seem. (Wen 2001; Zuo et al. 2015). Burkill (1902) originally described *Aralia quinquefolia* var. *angustifolia* Burkill as a taxon from the Sikkim, Bhutan and Khasia Hills (Assam), citing specimens belonging to two species, *P. bipinnatifidus* Seem. and *P. assamicus* R.N. Banerjee. *Panax siamensis* resembles *P. assamicus* in the lanceolate leaflets that are sessile or nearly so. They differ in that *P. assamicus* has mostly 5 (–7) leaflets (vs. 7–9 leaflets in *P. siamensis*), persistent bracteoles (vs. bracteoles mostly not persisting in fruiting stage in *P. siamensis*), pilose pedicels (vs. puberulent pedicels with extremely short hair-like structures in *P. siamensis*), oblong sepals (vs. triangular sepals in *P. siamensis*), and 2–3 (–4) locular ovaries (vs. 2-locular ovaries in *P. siamensis*). *Panax assamicus* is also a much taller herbaceous species that is 70–150 cm tall (vs. *P. siamensis* 60–70 cm tall). Their habitats are also highly distinctive, with *P. siamensis* in tropical monsoon forests and *P. assamicus* in temperate deciduous or mixed forests.

Panax siamensis can be easily distinguished from *P. bipinnatifidus* in that the latter has horizontal rhizomes with slender internodes and subglobose nodes (vs. horizontal rhizomes with thick and short internodes, i.e., bamboo-like, in *P. siamensis*), leaves with 5 (–7) leaflets (vs. 7–9 leaflets in *P. siamensis*), and terminal umbels with fewer flowers (25–50 flowers in *P. bipinnatifidus*, vs. 70–90 flowers in *P. siamensis*). Ecologically, *Panax bipinnatifidus* occurs in deciduous or mixed deciduous and coniferous forests in western China to the Himalayas at higher elevations of 2000–3600 m (Wen 2001), while *P. siamensis* occurs in monsoon evergreen hardwood forests, or in mixed evergreen hardwood and pine forests around 1350–1550 m.

We herein provide a key to *Panax siamensis* and its close allies to help differentiate the species.

Key to *Panax siamensis* and its close congeneric allies

- 1 Rhizomes elongate and creeping; fruits red with a black top.....2
- Rhizomes short and upright; fruits red throughout.....8
- 2 Rhizomes with slender internodes and subglobose nodes...*P. bipinnatifidus*
- Rhizomes with short and thick internodes3
- 3 Leaflets usually with petiolules4
- Leaflets usually without petiolules.....6
- 4 Leaves subtended by stipules, leaflets usually divided at the margin*P. stipuleanatus*
- Leaves without stipules, leaflets usually undivided, only occasionally divided.....5
- 5 Leaves with 5 (rarely 3 or 7) leaflets, leaflets oblong or ovate, occasionally lanceolate, light green; ovaries 2-locular*P. vietnamensis*
- Leaves with 7–9 (rarely 5) leaflets, leaflets lanceolate to narrowly so, dark green; ovaries 2–4-locular *P. wangianus*
- 6 Roots ginger-like, persistent in older plants; leaflets elliptic to obovate*P. zingiberensis*
- Roots tuberous, decayed in older plants; leaflets lanceolate7
- 7 Plant 70–150 cm tall; leaflets usually 5 to occasionally 7; bracteoles subtending pedicels persistent into fruiting stage; ovaries 2–3 (–4) –locular.*P. assamicus*
- Plant 60–70 cm tall; leaflets 7–9; bracteoles subtending pedicels mostly not persisting at fruiting stage; ovaries 2–locular..... *P. siamensis*
- 8 Roots singly, sometimes forked; stipules linear in shape; each umbel mostly with 80–100 flowers *P. notoginseng*
- Roots usually fascicled; stipules ovate in shape; each umbel mostly with 40–65 flowers.....*P. pseudoginseng*

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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All authors have contributed equally.

Author ORCIDs

Jun Wen  <https://orcid.org/0000-0001-6353-522X>

Gary Krupnick  <https://orcid.org/0000-0002-1357-4826>

Hans-Joachim (Hajo) Esser  <https://orcid.org/0000-0001-6518-8612>

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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Generic concepts and species diversity within the Gynoxyoid clade (Senecioneae, Compositae)

Belen Escobari^{1,2}, Thomas Borsch^{1,3}, Norbert Kilian¹

¹ Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Berlin 14195, Germany

² Herbario Nacional de Bolivia, Universidad Mayor de San Andres, Casilla, La Paz, 10077, Bolivia

³ Institut für Biologie, Systematische Botanik und Pflanzengeographie, Freie Universität Berlin, Berlin 14195, Germany

Corresponding author: Belen Escobari (b.escobari@bo.berlin)

Abstract

The Gynoxyoid clade of the Senecioneae (Asteraceae) until now included the five genera *Aequatorium*, *Gynoxys*, *Nordenstamia*, *Paracalia* and *Paragynoxys* as diagnosed using selected morphological characters. In their pre-phylogenetic circumscription, the genera *Aequatorium* and *Paragynoxys* were considered to inhabit the northern Andes in contrast to *Nordenstamia* and *Paracalia* that occur in the central Andes. The most species-rich genus, *Gynoxys*, was believed to be distributed throughout the Andes. We use a recently established plastid phylogenomic framework that rendered *Gynoxys* paraphyletic to further evaluate the delimitation of genera in the Gynoxyoid clade. We examine the morphological variation of all members of the Gynoxyoid to identify characters potentially informative at genus level. This results in a matrix of eleven, mostly multistate characters, including those originally used to diagnose these genera. The ancestral character state inference displays a high level of homoplasy, but nevertheless supports the recognition of four genera. *Aequatorium* is characterised by white radiate capitula. *Paracalia* and *Paragynoxys* share white flowers and floral characteristics, such as flower opening and length of disc flowers lobes, as plesiomorphic states, but differ in habit (scandent shrubs vs. trees). *Paracalia* also retained white flowers, but its two species are characterised by the absence of outer phyllaries. The genera *Gynoxys* and *Nordenstamia* comprise species with yellow capitula which appear to be a derived feature in the Gynoxyoids. The genus *Nordenstamia*, with eight species, is synonymised under *Gynoxys* since molecular evidence shows its species nested within various parts of the *Gynoxys* subclade and the morphological variation of *Nordenstamia* falls well within that of *Gynoxys*. With the goal to assign all species to four genera (*Aequatorium*, *Gynoxys*, *Paracalia* and *Paragynoxys*), we assess the states for the eleven characters for all members of the Gynoxyoids and generate new ETS and ITS sequences for 171 specimens belonging to 49 species to further support their generic placement. We provide a taxonomic treatment for the four genera recognised here including amended diagnoses and morphological descriptions. Furthermore, a species-level taxonomic backbone is elaborated for all genera using electronic tools that list 158 currently accepted names and synonyms (209 names in total) with the respective protologue and type information, as well as notes on the current understanding of species limits. Eleven names are newly synonymised, two are lectotypified and eight are newly transferred to other genera.



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Key words: Andes, Asteraceae, character evolution, chloroplast capture, EDIT Platform, morphology, phylogeny, taxonomic backbone, taxon concepts

Introduction

The Gynoxyoid group is a New World clade of the subtribe Tussilaginiinae (Senecioneae, Asteraceae) that was estimated to comprise around 150 species in five genera (Nordenstam et al. 2009). The clade includes shrubs, trees and, more rarely, lianas, growing at the higher elevations of the Andes, in humid mountain forests, subalpine forests and in the paramo. Originally, Jeffrey (1992) suggested the existence of this group of putatively related genera, based on cylindrical anther-collars, polar endothelial thickening and high chromosome numbers, based on $x = 10$. He included *Capelio* B.Nord. (as *Alciope* DC.) from South Africa (Nordenstam 2002), the Andean genera *Paracalia* Cuatrec., *Paragynoxys* (Cuatrec.) Cuatrec., *Gynoxys* Cass. and *Aequatorium* B.Nord. and the Caribbean genus *Herodotia* Urb. & Eckm. Subsequently, Robinson et al. (1997) restricted the group to the South American genera and pointed out that it is characterised by a chromosome number of $2n = 80$. The *Roldana* clade, sister to the *Gynoxys* clade (Pelser et al. 2007, 2010), in contrast, has a chromosome number of $2n = 60$ (Jeffrey 1992). These high chromosome numbers can be explained by ancient polyploidisation in the Tussilaginiinae. The genus *Nordenstamia* Lundin was later erected to accommodate certain species previously placed in *Aequatorium* and *Gynoxys* (Lundin 2006).

The first phylogenetic data for the Gynoxyoid group were provided by Pelsner et al. (2007) in the context of inferring relationships within the Senecioneae, based on sequences of the nrITS region. The authors resolved a clade with the genera *Aequatorium*, *Gynoxys*, *Nordenstamia* and *Paragynoxys* and found *Nordenstamia* (2 species) nested within *Gynoxys* (4 species). Pelsner et al. (2010) extended the taxon sampling with a representative of *Paracalia* and increased the number of molecular markers (nrITS and nrETS and plastid *ndhF*, *psbA-trnH*, *rbcL*, 5' and 3' *trnK*, *trnL* and *trnL-F* regions) and essentially confirmed their earlier results. Recently, Escobari et al. (2021) provided a comprehensive plastid phylogenomic framework, based on 17 complete plastid genomes representing all five genera and close American relatives within the Tussilaginiinae. Their results corroborated the Gynoxyoid group as monophyletic with high support. The three representatives of the genus *Nordenstamia* were found nested within a broadly paraphyletic genus *Gynoxys*. Additionally, the plastid genome sequence of *Paracalia jungioides* appeared as sister to *G. baccaroides* and *G. violacea* within *Gynoxys*, whereas *P. pentamera* was retrieved as sister to all other members of the Gynoxyoids. The second diverging clade was comprised of the monophyletic *Paragynoxys* and the only representative of the genus *Aequatorium*.

The Gynoxyoid group represents one of the speciose Andean plant lineages and, thus, contributes significantly to the high species diversity and endemism in the Andes as one of the global biodiversity hotspots (Myers et al. 2000; Padilla-Gonzalez et al. 2021). The uplift of the Andes led to shifts in ecosystem barriers (Luebert and Weigend 2014; Bacon et al. 2022) and enabled the creation of new habitats (Colwell et al. 2008; Moreira-Munoz et al. 2020; Perez-Escobar et al. 2022) which seem to have triggered rapid speciation of Andean plants (e.g. Madriñán et al. 2013; Zhang et al. 2021; Perez-Escobar et al. 2022). Amongst the studies focusing on the evolution of Andean plant groups (see Hughes and Atchison (2015)), several dealt with genera of the sunflower family, such as *Diplostephium* Kunth (Vargas et al. 2017), *Espeletia* Mutis ex Bonpl. (Pouchon

et al. 2018) and *Loricaria* Wedd. (Kandziora et al. 2022). In all three cases, the authors reported low genetic distances, complicating the study of species relationships and species limits. Moreover, frequent events of reticulate evolution and incomplete lineage sorting have been reported from rapidly evolving Andean plant groups (Garcia et al. 2014; Vargas et al. 2017; Schley et al. 2021; Kandziora et al. 2022). Low genetic distances were also observed amongst plastid genomes in the Gynoxyoid clade in our previous study (Escobari et al. 2021). Consequently, we demonstrated that complete plastid genome sequences, including the more variable intron and spacer partitions, were needed to achieve resolution at species and even genus level. The results of Escobari et al. (2021) underscored that *Gynoxys* is not monophyletic as currently circumscribed and that an evaluation of morphological characters hitherto used to diagnose the genera of the Gynoxyoid clade in an evolutionary context is warranted.

Cassini (1827) described the genus *Gynoxys* as having a tree-like habit, opposite leaves, the presence of an indumentum on the lower leaf surface, corymbiform capitula and the apex of style branches vested by papillose hairs as diagnostic characters. Weddell (1855) subdivided *Gynoxys* into two sections: one with radiate and the other with discoid capitula, which has lately been adopted by Correa (2003). The first taxonomic treatment including a larger number of species was made by Herrera (1980) who dealt with the 30 species distributed in Peru. That author redefined the genus by having usually opposite leaves, an indumentum on the lower leaf face, discoid or radiate capitula with up to 32 yellow disc flowers, an inconspicuously sagittate anther base and a conical, hispid and caudate style-branch apex. According to published regional checklists, *Gynoxys* is distributed from Bolivia to Venezuela at altitudes between 1600 and 4700 m above sea level and estimated to comprise about 180 species (Brako and Zarucchi 1993; Jorgensen and Leon-Yanez 1999; Beck and Ibañez 2014; Bernal et al. 2019).

Paragynoxys was first described by Cuatrecasas (1951) as *Senecio* sect. *Paragynoxys*, but raised to generic rank shortly thereafter (Cuatrecasas 1955). It is characterised by a tree- or shrub-like habit, subcoriaceous petiolate alternate leaves, a corymbose-paniculate terminal synflorescence, few-flowered discoid capitula, white corollae with the limb divided to its base, conical style-branches and a distribution in Colombia and Venezuela. The only taxonomic revision by Correa (2003) recognised 12 species and extended its diagnosis by having radiate capitula with five or more inner phyllaries and up to 12 flowers.

Paracalia was segregated by Cuatrecasas (1960) from *Paragynoxys* because of its scandent habit, smaller leaves and involucre lacking outer phyllaries. The genus comprises two species distributed in Bolivia and Peru (Cuatrecasas 1960; Nordenstam 2007; Hind 2007).

Aequatorium was published by Nordenstam (1978) to accommodate two shrubby species with alternate leaves, a rusty tomentum of stellate hairs, white corollae, sagittate or auriculate anther bases and blunt style-branches apices. Subsequently, several new species were added (i.e. Díaz-Piedrahita and Cuatrecasas 1990; Jeffrey 1992; Díaz-Piedrahita and Cuatrecasas 1994; Nordenstam 1997), resulting in an ongoing discussion on morphological features suitable for circumscribing the genus (see Nordenstam 1997). Based on the presence of stellate hairs and the differently-shaped involucre, Jeffrey (1992) transferred

Gynoxys section *Praegynoxys* to *Aequatorium*. Nordenstam (1997) concurred with this hypothesis and divided *Aequatorium* in two subgenera. *Aequatorium* subg. *Aequatorium* included species with (generally) alternate leaves, peltate trichomes forming two layers, white flowers, apically obtuse style branches; distributed in Ecuador and Colombia. *Aequatorium* subg. *Praegynoxys* included species with opposite or alternate leaves, irregular branching trichomes, absence of the overlying brownish tomentum, yellow flowers and apically pointed style branches and distributed in Argentina, Bolivia, Peru and southern Ecuador. Interestingly, he even suspected that the latter subgenus may be closer to *Gynoxys* than to *Aequatorium*. These concerns were taken up by Lundin (2006), who raised *Aequatorium* subg. *Praegynoxys* to a genus of its own, *Nordenstamia*, including 14 species.

Since the establishment of *Gynoxys*, the first genus in the clade, almost 200 years ago, new species continue to be described in this conspicuous Andean plant group (Cuatrecasas 1950, 1951, 1954, 1955; Robinson and Cuatrecasas 1992; Beltrán and Baldeón 2009; Beltrán and Calvo 2020). However, monographic work aiming at a synthesis of taxonomic data was largely limited to *Gynoxys* and *Paragynoxys* (Herrera 1980; Robinson and Cuatrecasas 1984; Nordenstam 1997; Correa 2003) or to geographically-confined areas (Dillon et al. 1993; Nordenstam and Lundin 1999; Badillo et al. 2008; Beck and Ibáñez 2014; Avila et al. 2016). The considerable species number, the shallow morphological differentiation within the clade and the absence of a robust phylogenetic hypothesis added considerable uncertainty and instability to the circumscription of the genera of the Gynoxyoids, which has found its expression in frequent transfers of species between genera. A consistent taxonomic synthesis is, therefore, needed for the whole Gynoxyoid clade.

The availability of electronic sources for names and protologue citations (IPNI, www.ipni.org; TROPICOS, www.tropicos.org), as well as online access to digitised type specimens (JSTOR Global Plants, <https://plants.jstor.org/>) and electronic tools to support the taxonomic workflow (EDIT Platform; Berendsohn (2010)) has facilitated the way taxonomic treatments are undertaken. More recently, a comprehensive name source is available through the World Flora Online Plant list which is regularly updated (worldfloraonline.org). Therefore, names can be imported into an electronic taxonomic working tool so that the actual taxonomic research can focus on checking validity of names and testing taxon concepts at species level. At the same time, the taxonomic workflows are revolutionised by structured data (Kilian et al. 2015) and evolutionary approaches to investigate species limits (Stuessy and Lack 2011; Marhold et al. 2013).

For the Gynoxyoid clade, we have taken on the task to check all names and to present a consistent classification at species level as a baseline hypothesis for the whole clade using the available data. While our approach is still largely based on morpho-species, it utilises some phylogenetic data that could be generated for specimens representing part of the species. Our goal was to elaborate an expert-revised taxonomic backbone for a plant group throughout its range of distribution in the sense of the workflow of the World Flora Online (WFO; see Borsch et al. (2020)), ideally including all validly-published names assigned to a status as accepted name or synonym. Such a taxonomic backbone also provides the best possible taxonomic knowledge in time as this is needed for conservation status assessments, biodiversity monitoring etc.

Considering this situation, the aims of this investigation are: [1] to revise the generic classification of the Gynoxyoids making use of molecular (plastome and nrDNA) and morphological data and [2] to provide a revised species inventory of the Gynoxyoids for the entire range of distribution.

Materials and methods

Plant material and sources for specimen data

The study was based on plants observed, collected and photo-documented in the field during three collecting trips in Bolivia and Peru, as well as physical specimens loaned to B from AAU, F, G, K, LPB, MA, MO, NY and P (Thiers, continuously updated). Specimens that were physically examined are listed in Suppl. material 1. In addition, high resolution digital images of herbarium specimens, in particular types, were consulted online either accessed through JSTOR Global Plants (<https://plants.jstor.org/>), GBIF (<https://www.gbif.org/>) or directly through online databases of the individual herbaria.

Sources of names and compilation into a checklist of the species of the Gynoxys clade

The species inventory of the Gynoxyoids was built in a database using the EDIT Platform for Cybertaxonomy (Berendsohn 2010), based on imports of names and associated data (authors, protologue citations) from the International Plant Names Index (IPNI) (<https://www.ipni.org/>) supplemented by TROPICOS (<https://tropicos.org/home>), the Global Asteraceae Database (<https://www.Asteraceae.org/aphia.php?p=stats>) and the World Flora online (<http://www.worldfloraonline.org/>)

Definition and assessment of morphological characters and states

The first round of assessing the morphological variation in the Gynoxyoid group included all species of the genera *Aequatorium*, *Nordenstamia*, *Paracalia* and *Paragynoxys* and a representative selection in terms of morphological diversity of *Gynoxys* species, altogether 65 species. We examined the diagnostic characters stated in the protologues and in other studies of the five genera, but also compared specimens to detect morphological variance to develop a list of characters and their states. For this investigation, a character state was considered taxonomically relevant and selected for further processing if its expression marked morphological discontinuities at supra-specific level. For each such character, unordered categorical states were defined following the terminology by Roque et al. (2009) and Beentje (2010). In cases where a more detailed homology statement was needed due to conflicting or unclear use of character definitions or terms, a description and illustration were included. For later reconstruction of character evolution, a specimen-based matrix of characters and states suitable for reliable delimitation and characterisation of supra-specific entities was constructed using the specimens included in the plastid phylogenomic analysis of Escobari et al. (2021). For certain characters, for example, the plant habit, the respective states were recorded from literature if not given on the specimen label.

Ancestral character state reconstruction

Only Bayesian trees obtained from complete plastome sequences with indels coded and alignments manually corrected as provided by Escobari et al. (2021) were used as the hypothesis of the phylogenetic relationships in the Gynoxyoids, because lack of resolution rendered the use of nrDNA marker trees impossible. The reconstruction of character states at ancestral nodes was performed with a Bayesian approach using BayesTraits version 2.0 (Pagel and Meade 2006), which uses a selection of post-burn-in trees obtained from the t.files of the Bayesian analysis. This random selection of 800 of the total of 1600 post-burn-in trees taken from Escobari et al. (2021) was obtained through Mesquite version 3.7 (Maddison and Maddison 2021). The file stating the relevant nodes of the tree to be addressed by the analyses of BayesTraits was generated with TreeGraph v.2.14beta (Stöver and Müller 2010). The inference of the ancestral character state reconstruction was performed using the reverse jump MCMC approach with 5,050,000 iterations, with a burn-in of 50000, a sample frequency of 1000 and, following the recommendation by Pagel and Meade (2006), a hyper-prior where the mean of the exponential is drawn from a uniform 0–100 distribution. TreeGraph v.2.14beta (Stöver and Müller 2010) was used to plot the results from the BayesTraits output log file with the function Import BayesTraits data on the Bayesian major consensus tree. We excluded the other genera of the Tussilagineae that were present in the plastid phylogenomic investigation, considering that the outgroup sampling in their dataset is incomplete with respect to the morphological diversity.

Extraction, amplification and phylogenetic tree inference of nuclear ribosomal DNA

To achieve a better overview on species-level phylogenetic relationships within the Gynoxyoid clade and to test if groups of samples identified with the same species name appeared in terminal subclades, 171 samples belonging to 50 species (Suppl. material 1) were included into an extended molecular dataset. These samples were selected to cover morphological and geographical variation as much as possible and also included the samples that were already part of the plastid phylogenomic study. The nrITS and nrETS regions were used as they provided some variable and informative characters in a short marker that was possible to sequence with little effort per sample. Additionally, by representing the nuclear genome, the dataset could be used to test for incongruence between trees inferred from different genomic compartments. Plastid regions often applied to assess the tree space of speciose clades (Mansion et al. 2012) were not suitable in the Gynoxyoid clade due to extremely low genetic distances (Escobari et al. 2020). Genomic DNA was extracted using the CTAB method by Doyle and Doyle (1987), with three fractions for each sample as modified by Borsch et al. (2003). PCR amplification of ITS followed White et al. (1990), ETS was amplified with the primers AST-1 (f) and 18-S-ETS (r) (Markos and Baldwin 2001), following Pelser et al. (2010). PCR was performed in a peqSTAR Thermocycler 1107D (PiqLab, Erlangen, Germany). The PCR products were electrophoresed on 1.5% agarose, the bands were cut out and cleaned with the GenepHlow Gel/PCR kit (Geneaid, New Taipei, Taiwan). Samples were se-

quenced by Macrogen Europe (Amsterdam, The Netherlands). Sequence files were aligned using MAFFT v.7.394 (Katoh and Standley 2013) and manually edited using PhyDE version 0.9971 (Müller et al. 2010), following the rules of Löhne and Borsch (2005). Indels were coded as binary characters using the simple-indel-coding method (Simmons and Ochoterena 2000) in SeqState version 1.4.1 (Müller 2005). Altogether, 146 ETS and 166 ITS sequences were newly generated and the sequences were deposited in the European Nucleotide Archive (ENA) using the *annonex2embl* submission pipeline (Grünstäudl 2020) and can be retrieved from ENA under study number PRJEB53579 (<https://www.ebi.ac.uk/ena/submit/webin/study/PRJEB53579>).

Phylogenetic trees were inferred from the ITS, ETS and a concatenated matrix of both belonging to the corresponding samples in the plastid tree presented in Escobari et al. (2021). A Bayesian analysis was performed with MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003), using four parallel Markov Chain Monte Carlo (MCMC) runs for a total of 50 million generations under the GTR+G+I model. The convergence of the Markov chains was checked with Tracer v.1.7 (Rambaut et al. 2018). The initial 25% of all trees were discarded as burn-in and the remaining trees were used to summarise the 50% majority consensus tree.

Assignment of all species to genera and evaluation of taxon concept at species level

Despite the extended nuclear ribosomal sequence dataset generated in this investigation, not all species could be included into phylogenetic analysis. This was largely due to the unavailability of suitable material, for example, in species only known from type or historical specimens. We, therefore, used our set of eleven morphological characters with their states in conjunction with the results from ancestral state reconstruction, to assign all species to a genus and, in the case of *Gynoxys* species, also to informal infrageneric groups of morphologically similar species that can be used as a hypothesis on close relationships. The genera and informal infrageneric entities were described and a taxonomic key for their determination was created. At species level, all protologues were consulted to check for the correct typification of names. Type specimens of all names, with the exception of only a few unavailable ones (indicated in the taxonomic treatment part, below), were examined from high resolution digital images provided by JSTOR Global Plants, GBIF and the herbarium websites of individual herbaria. The digital images of type specimens were referenced in the checklist to the type citation. Where necessary, new combinations were made and names were lectotypified. As a general principle, a morpho-species concept, delimiting species purely based on morphological discontinuities, was applied. Type specimens and additional specimens (see Suppl. material 1) were examined to assess the qualitative differences and possible infraspecific variation with the aim to hypothesise a name as accepted or as a synonym. The citation of authors follows the international standards by Brummitt and Powell (1992); the citation of publications follows BPH (Bridson et al. 2004) and TL-2 (Stafleu and Cowan 1976–1986; Stafleu and Mennega 1992–2009); the latter was also consulted for actual publication dates. Accepted names were provided with full synonymies and type citations. Type specimens that were online include only the herbarium acronym. Specimens that were physically examined are marked with (!).

Results

Morphological characters of taxonomic relevance on supra-specific level

The evaluation of morphological characters with respect to discontinuities at supra-specific level resulted in a matrix of eleven characters. These characters and their states are defined in Table 1 and, where appropriate, illustrated in Fig. 1.

Morphological characterisation of the members of the Gynoxys clade

Our evaluation for consistent presence and absence of sets of diagnostic character states in Gynoxyoid species resulted in the recognition of four morphologically and phylogenetically defined genera. The morphological matrix with the diagnostic characters applied to the genera and species of the Gynoxyoids represented in the sampling for the plastome tree is given in Table 2.

Table 1. Morphological characters selected for the ancestral character reconstruction analysis with their respective character abbreviation (Abbr.) and character states with a respective abbreviation and definition when needed.

Character	Abbr.	Character states
Plant habit	H	tree (T), shrub (S), scandent (C)
Phyllotaxis	P	alternate (A), opposite (O)
Trichome architecture	T	Trichomes absent (G), unicellular hairs (S), multicellular hairs (M)
		Unicellular hairs: unicellular simple hair.
		Multicellular hairs: branched or unbranched hairs. Differences between multicellular hairs were avoided since several types of these can be present in a same specimen (Fig. 1F).
Corolla colour	CF	white (W), yellow (Y)
		This character state describes both ray and disc flowers since it is always shared by both flower types in a capitulum.
Outer phyllaries	OP	absent (A), present (P)
		As outer phyllaries were considered all phyllaries attached at the base of the involucre and not at the peduncle of the capitulum
Number of inner phyllaries	InP	≤ 5 (F), 6–8 (M)
		The following categories are based on the stability of a defined number of phyllaries for the genera
Radiate flowers	RF	absent (D), present (R)
		The states implicitly define the architecture of the capitulum. The absence of ray flowers (0 = A) represents a discoid capitulum (Fig. 1A). A number > 0 represents a radiate capitulum
Number of disc flowers	DF	≤ 8 (F), > 8 (M)
		The following categories are based on the stability of a defined number for the genera
Ratio corolla lobe/tube length	Rat	≤ 0.6 (S), > 0.6 (D)
		This character describes the opening depth of the corolla. Length of lobes in relation to the length of the corolla tube (shortly vs. deeply lobed corolla) (Fig. 1C).
Anther-base shape	AB	sagittate (S), obtuse (O)
		The base of the anthers is defined as obtuse when no appendage can be distinguished (Fig. 1e). We ignored the difference between acute (small appendages) vs. sagittate (large appendages) since both can be present in a same specimen and this may be unstable depending on the state of the specimen
Style branch apex shape	SA	acute (A), rounded (R)
		The style branch apex is described as acute when the branches tips have a conspicuously pointed tip (Fig. 1D). We use rounded in a wider sense also including an apex described as truncate, as the presence of papillose hairs makes the distinction unreliable

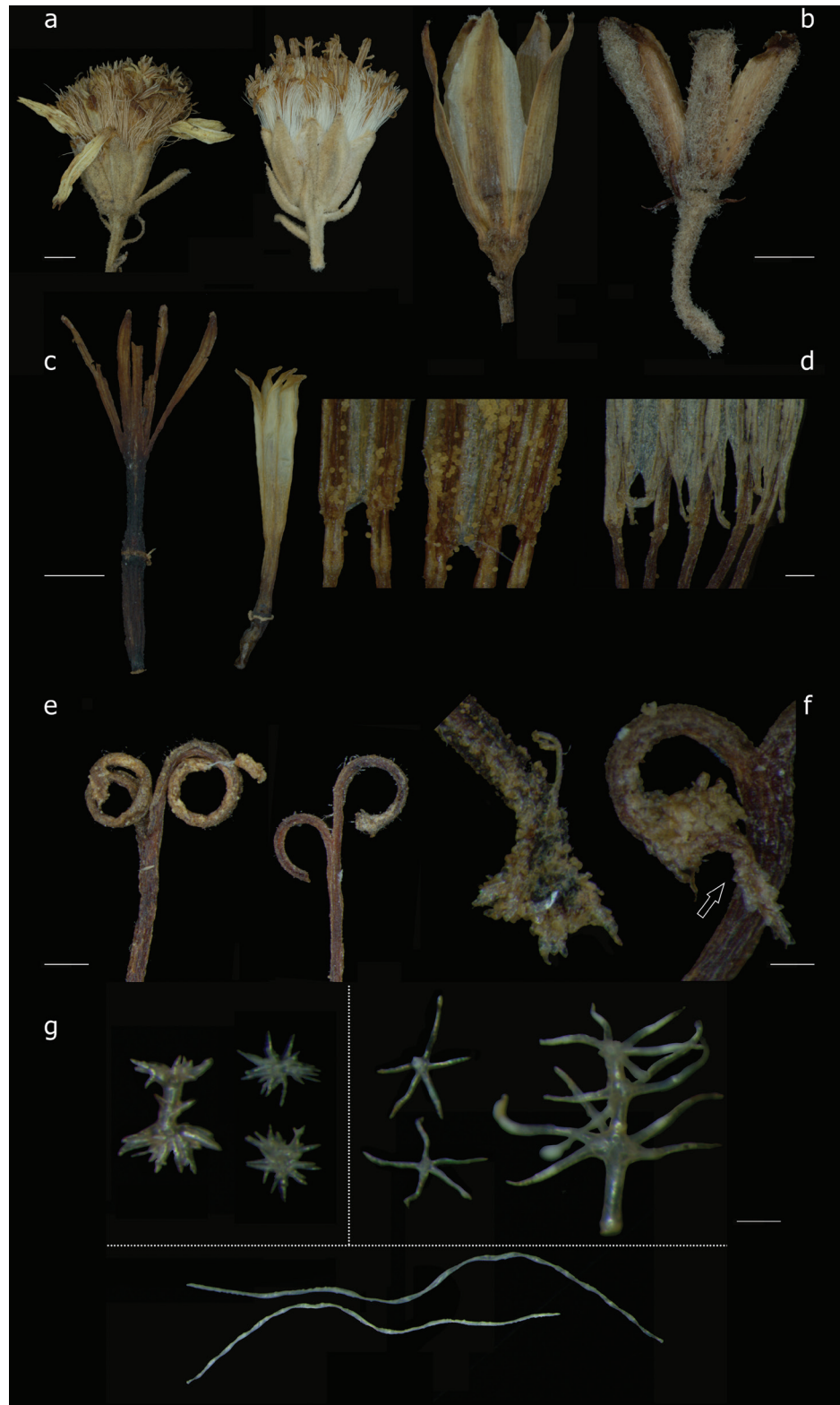


Figure 1. Characters and states from floral morphology and indumentum for the Gynoxyoid clade **a** capitula: radiate (*Gynoxys calyculisolvans* left), discoid (*G. longifolia* right) **b** involucral outer phyllaries: absent (*Paracalia pentamera* left), present (*Paragynoxys martingrantii* right) **c** ratio corolla lobe/tube length: deeply lobed (*Paragynoxys venezuelae* left) (ratio > 0.6), shortly lobed (*G. asterotricha* right) (ratio < 0.6) **d** anther-base shape: obtuse (*Paracalia jungioides* left), sagittate (*G. ignaciana* right) **e** length of style branches: large (*P. jungioides* left), short (*G. ignaciana* right) **f** style branches apex shape: rounded (*G. ignaciana* left), acute (*G. baccharoides* right) **g** trichome architecture: multicellular hairs (*A. jamesonii* left above, *N. kingii*, right above), unicellular hairs (*G. violacea* below line). Scale bars: 2 mm (**a–c**); 200 μ m (**d**); 500 μ m (**e**); 100 μ m (**f, g**).

Table 2. Assessment of characters and their states for the species within the Gynoxyoid clade as included in the phylogeny inferred by Escobari et al. (2021). The codes of characters and states are noted in Table 1, (?) indicates missing data.

Species	H	P	T	CF	OP	InP	RF	DF	Rat	AB	SA
<i>Gynoxys megacephala</i>	S	O	M	Y	P	M	D	M	S	S	A
<i>Nordenstamia cajamarcensis</i>	T	O	M	Y	P	M	R	F	S	O	R
<i>Gynoxys ignaciana</i>	S	O	S	?	P	M	R	M	S	S	R
<i>Gynoxys longifolia</i>	S	O	S	Y	P	M	D	M	S	S	R
<i>Nordenstamia repanda</i>	T	A	M	Y	P	M	R	F	S	S	A
<i>Nordenstamia kingii</i>	S	A	M	Y	P	M	R	M	S	S	A
<i>Gynoxys violacea</i>	S	O	S	Y	P	M	R	M	?	S	R
<i>Gynoxys asterotricha</i>	S	O	S	Y	P	M	R	M	S	S	A
<i>Gynoxys baccharoides</i>	S	O	S	Y	P	M	R	M	S	S	A
<i>Gynoxys calyculisolvens</i>	S	O	S	Y	P	M	R	M	S	S	A
<i>Gynoxys tomentosissima</i>	S	O	S	Y	P	M	R	M	S	S	A
<i>Gynoxys mandonii</i>	T	O	S	Y	P	M	R	M	S	S	A
<i>Aequatorium jamesonii</i>	S	O	M	W	P	M	R	F	S	O	R
<i>Paragynoxys martingrantii</i>	T	A	M	W	P	F	D	F	D	O	R
<i>Paragynoxys venezuelae</i>	T	A	M	W	P	F	D	F	D	O	R
<i>Paracalia jungioides</i>	C	A	S	W	A	F	D	F	D	O	R
<i>Paracalia pentamera</i>	C	A	G	W	A	F	D	F	D	O	A

The first of these four genera is *Aequatorium* with all species sharing the combination of multicellular trichomes, radiate capitula, white flowers, a low number of disc flowers (< 8) and an obtuse shape of the anther base. Diagnostic for this genus is the unique combination of white flowers and radiate capitula.

Further genera are *Paracalia* and *Paragynoxys*, the species of which are differentiated from the other Gynoxyoid genera by a deep-lobed corolla, white flowers and discoid capitula. *Paracalia* can be distinguished from *Paragynoxys* by a scandent habit, absence of outer phyllaries and a central Andean distribution. In contrast, *Paragynoxys* has a woody habit, an involucre with outer phyllaries and a north-Andean distribution.

The genus *Nordenstamia* cannot be delimited morphologically. The presence of stellate hairs by which this genus was originally distinguished from *Gynoxys* (Lundin 2006) is not only highly variable amongst the *Nordenstamia* species, but also shared with many *Gynoxys* species. If *Nordenstamia* is included in *Gynoxys*, this genus can be differentiated from all the others by the combination of yellow flowers and a shallowly divided disc corolla.

Gynoxys is notably the most diverse taxon within the Gynoxyoid clade, displaying a wide range of morphological variation. Within the genus, three informal groups can be discerned, based on distinct characteristics, including phyllotaxis, the number of ray flowers and the type of trichomes. The first group encompasses species with discoid capitula. In contrast, the second group comprises species with multiseriate stellate hairs, primarily featuring alternate leaves. Finally, the third and largest group is characterised by opposite leaves, radiate capitula and simple hairs.

Phylogenetic trees inferred from nuclear ribosomal markers

In addition to the trees of the Gynoxyoids, based on a representative set of complete plastid genome sequences (Escobari et al. 2021), this study attempted to provide further phylogenetic evidence from nrDNA, amongst many others also including the same set of samples present in the plastid tree. Three phylogenetic analyses were performed, based on the ribosomal nuclear markers ETS, ITS and a concatenation of both (Suppl. material 2). In contrast to the tree, based on the plastid genome (Suppl. material 2: appendix 2a), the Bayesian ETS and ITS trees are poorly resolved (Suppl. material 2: appendix 2d). In all trees, the members of the *Gynoxys* clade form a single polytomy. The sister group relationship between the two species of *Paragynoxys* is the only clear congruence between the two nuclear ribosomal trees (however, with low support in the ITS inference) and is, moreover, in conformity with the plastid genome tree. Only the ETS tree resolved the two species of *Paracalia* as a (moderately supported) clade (Suppl. material 2: appendix 2c), whereas they were resolved in separate clades in the ITS (Suppl. material 2: appendix 2b) and in the concatenated ETS+ITS tree (Suppl. material 2: appendix 2d).

Character evolution in the Gynoxyoids based on the phylogenetic hypothesis of the plastome tree

Employing the eleven characters of Table 1, a species-based matrix was created for the 17 members of the Gynoxyoid clade represented in the phylogenetic tree by Escobari et al. (2021) (Table 2) and used for ancestral character reconstruction. Two character states for *G. ignaciana* (colour of flowers) and *G. violacea* (length ratio disc flower corolla lobe/tube) were coded as missing because they were not accessible in the material at hand. The accession *Gynoxys* sp. in Escobari et al. (2021) was identified as *G. calyculisolvens* during this study. The ancestral character reconstructions for the eleven characters in the Gynoxyoid clade are presented in Figs 2–4.

The Gynoxyoids exhibit various evolutionary changes in their characteristics. The shrubby habit was initially considered primitive, but two independent shifts to a scandent habit occurred in the two *Paracalia* species, while a shift from shrub to tree habit was observed in *Paragynoxys* and within the *Gynoxys* clade. Opposite phyllotaxis was revealed as the ancestral state, but shifts to alternate phyllotaxis occurred in *Paracalia pentamera*, the stem node of *Paragynoxys*, two (out of three) species of *Nordenstamia* and *Paracalia jungioides*. Unicellular trichomes were revealed as ancestral for all Gynoxyoids, but *Paracalia pentamera* became glabrous. Multicellular hairs emerged in the most recent common ancestor of *Aequatorium* and *Paragynoxys*, as well as in certain species within the *Gynoxys* clade. White flowers were revealed as the ancestral state, retained by the earliest diverging clades (*Aequatorium*, *Paragynoxys* and *Paracalia pentamera*), while yellow flowers appeared at the stem node of *Gynoxys* and *Nordenstamia*. A reversal to white flowers occurred in *Paracalia jungioides*, nested within the *Gynoxys* clade. A higher number of inner phyllaries was ancestral, but both *Paracalia* and *Paragynoxys* species showed a decrease in this number. Radiate flowers were ancestral, but discoid capitula emerged in all *Paracalia* and *Paragynoxys* species, with additional losses of ray flowers in some *Gynoxys* species.

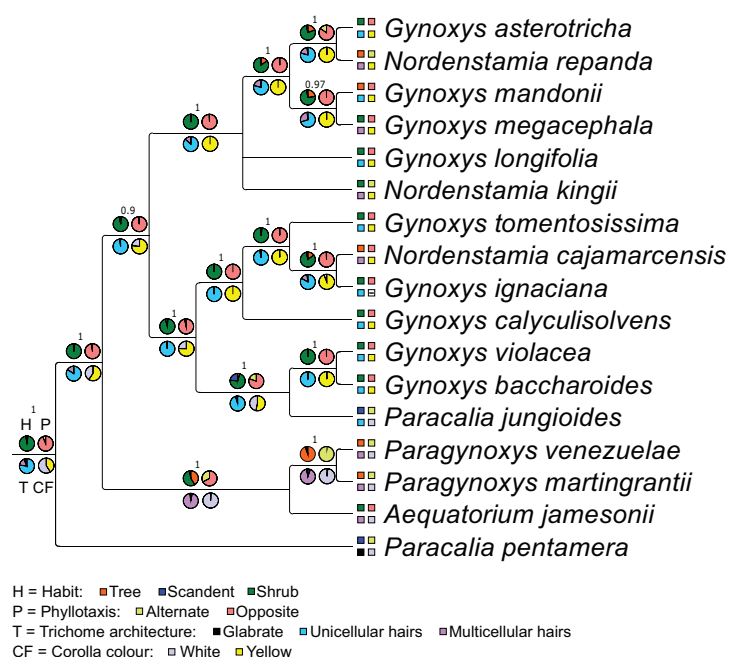


Figure 2. Bayesian inference of ancestral character state reconstruction of four morphological characters of the Gynoxyoid clade in the consensus plastome tree by Escobari et al. (2021). Each pie chart represents a single character and each colour represents a character state as described in the legend. The actual state of the characters is represented by boxes next to the species names. The pie charts at the stem of the tree show the character abbreviations as mentioned in Table 1. Missing data are represented (-).

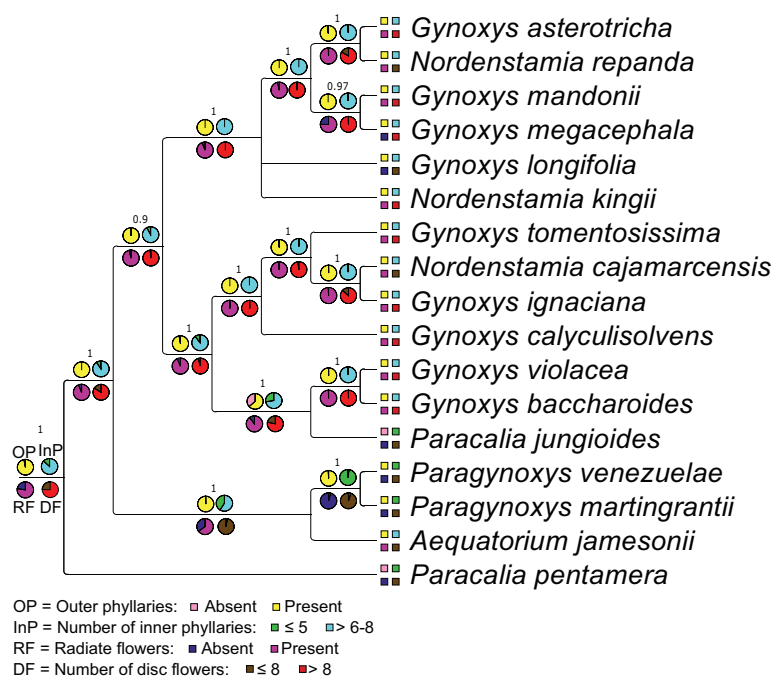


Figure 3. Bayesian inference of ancestral character state reconstruction of four morphological characters of the Gynoxyoid clade in the consensus plastome tree by Escobari et al. (2021). Each pie chart represents a single character and each colour represents a character state which is described in the legend. The actual state of the characters is represented by boxes next to the species names. The pie charts at the stem of the tree show the character abbreviations as mentioned in Table 1.

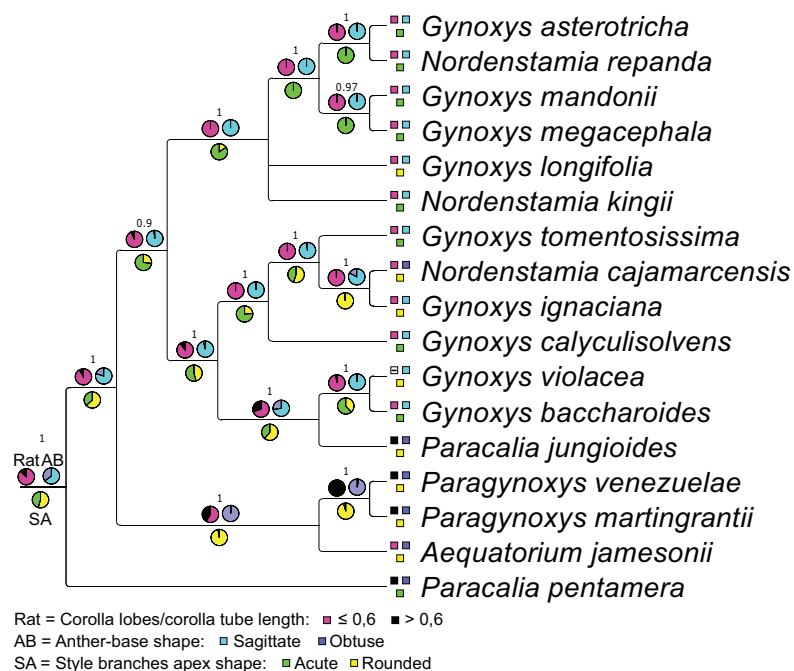


Figure 4. Bayesian inference of ancestral character state reconstruction of four morphological characters of the Gynoxyoid clade in consensus plastome tree by Escobari et al. (2021). Each pie chart represents a single character and each colour represents a character state which is described in the legend. The actual state of the characters is represented by boxes next to the species names. The pie charts at the stem of the tree show the character abbreviations as mentioned in Table 1. Missing data are represented as (-).

A high number of disc flowers was the ancestral state, but reductions occurred at the stem node of *Aequatorium* and *Paragynoxys* and in all *Paracalia* species, partially within the *Gynoxys* clade. A shallow division of the corolla into lobes was revealed as plesiomorphic and retained in *Aequatorium* and all *Gynoxys*, but changed in *Paracalia* and *Paragynoxys* to a deep division. The style branch apex was rounded ancestrally, retained in *Aequatorium* and *Paragynoxys*, but an acute apex appeared in the earliest diverging species, *Paracalia pentamera*, with further shifts and reversals in *Gynoxys*, *Nordenstamia* and *Paracalia jungioides*.

A summary of the BayesTraits analysis of all state shifts for each character in Figs 2–4 is given in Fig. 5. Characters are represented by numbers and states with the codes given in Table 1. A high number of shifts occur in the two species of *Paracalia* because the genus is retrieved as non-monophyletic in the plastid topology, although its species share most morphological character states. The clade represented by both *Paragynoxys* species shared all derived characters with *Aequatorium jamesonii* in addition to five derived characters that characterise the clade. A single character (corolla colour) was retrieved as synapomorphic for the clade containing *Aequatorium*, *Gynoxys*, *Paragynoxys*, *Nordenstamia* and *Paracalia jungioides* and even this character shows several reversals at the MCRA of *Aequatorium* and *Paragynoxys* and of both species of *Paracalia*. The analysis retrieved most of the morphological characters as highly homoplastic with the style branch apices being the most variable character throughout the tree at many nodes. A summary of the BayesTraits analysis with each character at each node is given in Suppl. material 3.

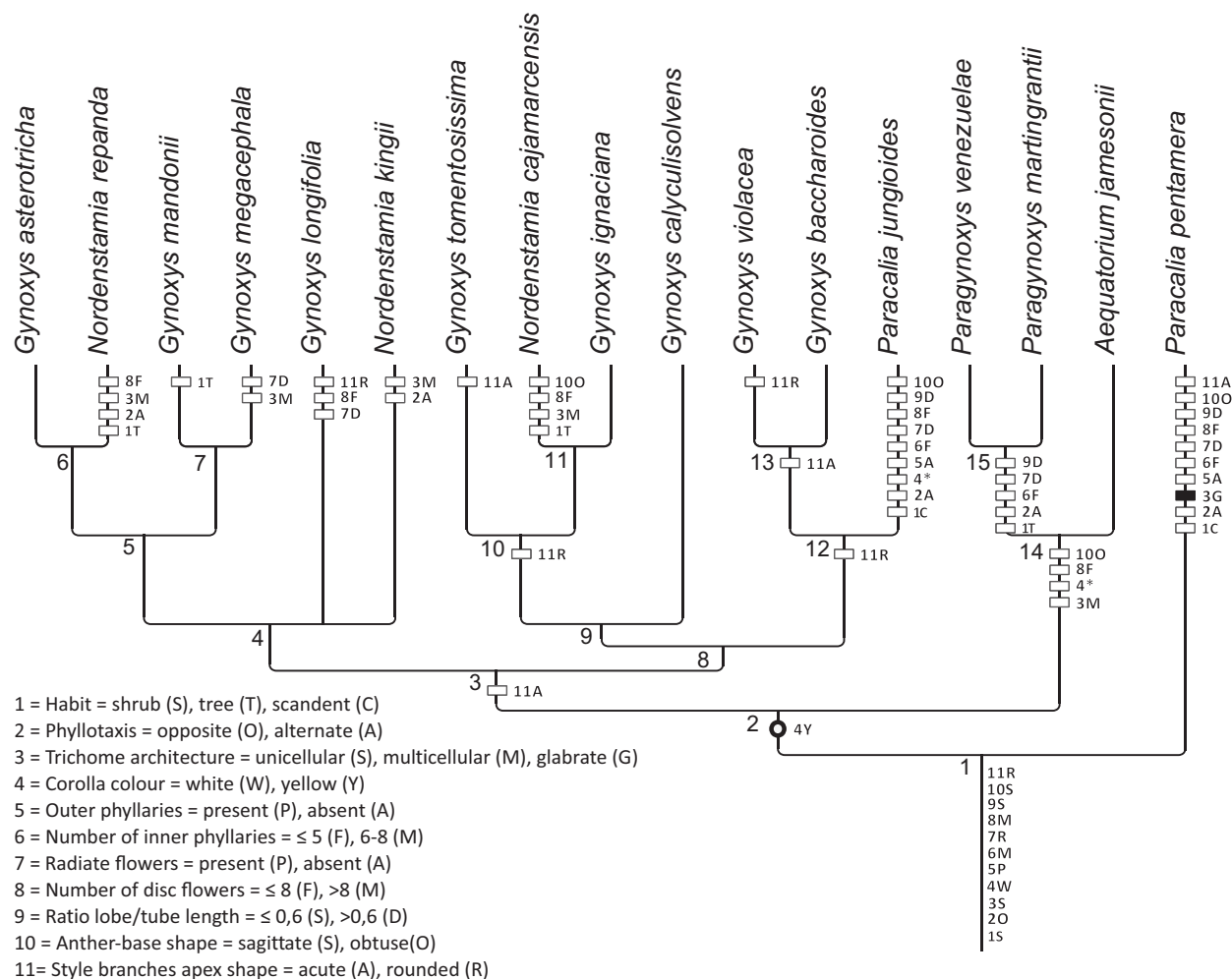


Figure 5. Summary tree based on the results of the BayesTraits analysis (Figs 2–4) of state shifts in morphological character. A threshold of 0.75 was used to define the character shifts between states. Characters with multiple state shifts (homoplasies) are shown with white boxes, reversals are indicated by * and unresolved shifts are indicated by an open circle. Numbers at the left of the branches represent the nodes in Suppl. material 3.

Checklist of the Gynoxys clade

The initial revision of the different databases resulted in a variable number of species. The Compositae Global Database lists 270 names (May 2023), The World Flora online includes 257 (Dec 2022), IPNI registers 242 (May 2023) and Tropicos has 243. This study resulted in a checklist comprising a total of 209 names of which 158 are accepted. Additionally, eleven names were newly synonymised, two were lectotypified and eight were newly transferred to other genera.

Discussion

Trees inferred from plastid genomes and putative cytonuclear discordance

In the present investigation, we attempted to compare, for the members of the Gynoxyoid clade, tree reconstructions, based on the plastid genome and on the ITS and ETS nuclear ribosomal regions. Variation amongst the plastid genomes

was extremely low (Escobari et al. 2021) and even more so in the nuclear ribosomal DNA. The lack of resolution in the nuclear ribosomal trees severely limits the comparison of phylogenetic signal from the organellar and nuclear genomic compartments. Nevertheless, there are some noteworthy exceptions. One is the unequivocal support for the sister group relationship of the two *Paragynoxys* members. The second is the missing support for the monophyly of the three *Nordenstamia* members in all three trees. The most significant result is, however, the gene tree incongruence concerning the two *Paracalia* species. The plastid tree placed *Paracalia jungioides* within *Gynoxys* and far distant from the second species, *P. pentamera* (Escobari et al. 2021). In contrast, the two species of *Paracalia* are supported as monophyletic in the ETS tree in conformity with morphology, although not in the ITS nor in the concatenated ETS-ITS tree (Suppl. material 2: appendix 2d). This finding is surprising because *Paracalia jungioides* is morphologically very distinct from all members of *Gynoxys*. It is scandent (instead of a tree or shrub), has white (instead of yellow) flowers and an involucre without outer phyllaries (instead of present). Moreover, *P. jungioides* and *P. pentamera* are morphologically very similar and the plastome phylogeny would suggest that these species have accumulated a high number of independent parallel state shifts (i.e. scandent habit, alternate leaves, absent outer phyllaries, few inner phyllaries, discoid capitula, few number of disc flowers, deep-lobed corolla, obtuse anther base) (Figs 3, 5). We assume that the incongruence with respect to the position of the two *Paracalia* species between the morphological data and the ETS topology on the one hand and the plastome tree topology on the other hand, is best explained by a chloroplast capture event. Chloroplast capture occurs when two species hybridise and go through extensive backcrossing to one of the ancestors (Rieseberg and Soltis 1991). The hybridisation event followed by extensive backcrossing swamp out the nuclear signal, but the captured plastid remains (Kandziora et al. 2022). In our case, we assume that *P. jungioides*, after introgression with a *Gynoxys* species, has captured the plastome of a member of the latter genus.

Nuclear-cytoplasmic incongruences have been reported in several studies within the Asteraceae family at higher and specific levels (Kilian et al. 2017; Pascual-Díaz et al. 2021; Senderowicz et al. 2021), especially in the Senecioneae (Pelser et al. 2007, 2010). It has also been shown by Stull et al. (2020) for the asterids that conflicts between nuclear and plastome trees are a relevant issue even at higher evolutionary scales. Phylogenetic inferences on nuclear data recovered different placements for several asterid lineages compared to topologies on plastid data (Yin et al. 2021; Kandziora et al. 2022). This is of some significance when we consider that current backbones of angiosperm phylogeny are largely based on plastid phylogenies (APG IV 2016). Amongst the principal reasons for these incongruences, horizontal gene flow amongst lineages, introgression, hybridisation and incomplete lineage sorting were suggested (Rieseberg and Soltis 1991; Maddison 1997; Vargas et al. 2017). The inclusion of different markers of different origins in a phylogenetic analysis has the capacity to elucidate signals of such events. Pelser et al. (2010) analysed potential causes for tree incongruences in the tribe Senecioneae comparing two nuclear (ITS/ETS) and six plastid markers. They concluded that hybridisation is a much more likely explanation than ILS, long-branch attraction or sampling error. Lee-Yaw et al. (2018) focused their study on or-

ganelle discordances by sequencing whole plastomes and over 1000 nuclear single-nucleotide polymorphisms in *Helianthus* L. The authors showed that incongruences in this genus can be expected at species level and amongst individuals of the same species. The Gynoxyoid clade is a further example of short molecular distances on plastid and ribosomal markers amongst species. The lack of molecular variability hampers the reconstruction of well-supported clades on this type of data; nevertheless, the great morphological variation enables the definition of morpho-species in many cases. On the other hand, the phylogenetic reconstruction, although with moderate support, can give evidence to support the assignment of morphologically similar individuals to the same entities (i.e. hypothesised species).

Gene tree discordance is expected to be more likely in rapid radiating lineages that can be found in young biodiversity hotspots, such as the Andean Region (Madriñán et al. 2013; Kandziora et al. 2022). The fast succession and accumulation of descendant species are prone to inter-breeding before reproductive barriers develop, increasing the probability of incomplete lineage sorting (ILS) (Vargas et al. 2017). In addition, young radiating groups have shown whole genome duplication and hybridisation events in the tropical high-altitude areas of South America (*Lachemilla*: Morales-Briones et al. 2018; *Lupinus*: Nevado et al. 2018; *Diplostephium*: Vargas et al. 2017; Espeletiinae: Cortés et al. 2018). Hybridisation may be a result of sexual selection, ecological adaptation, pollinator changes (Moreira-Munoz 2020; Kandziora et al. 2022) or due to the dynamic changes in habitat connectivity in this ecosystem with multiple topography changes during the Pleistocene (Flantua et al. 2019) which facilitated the contact between geographically isolated species before exhibiting strong barriers to gene flow (Vargas et al. 2017; Kandziora et al. 2022). Vargas et al. (2017) revealed complex patterns of reticulate evolution at generic and species level of *Diplostephium*.

Evolution and significance of morphological characters in the Gynoxys clade

Previous generic classifications of the Gynoxyoid group were based on morphological similarities and discontinuities between species assemblages. In this study, we tested these hypotheses by optimising character states on the full plastome phylogeny (Escobari et al. 2021, see also Suppl. material 2: appendix 2a). Morphological differentiation amongst the Gynoxyoids is shallow and limited to comparatively few and often rather subtle characters. The most recent ancestor of the Gynoxyoid had a shrubby habit, opposite leaves and it was vested by unicellular simple hairs. The capitula was radiate, equipped with outer phyllaries and 6–8 inner phyllaries and had up to eight disc flowers. The corolla was whitish and the corolla lobes were remarkably shorter than the corolla tube. Most of these plesiomorphic states (except the whitish corolla) were retained by most of the species of the genus *Gynoxys* during its evolution. Shifts in the character states are evident in the rest of the Gynoxyoid members. Specially, the switch from whitish to yellowish corolla (which is apparently the only synapomorphy under the given tree inference) resulted as unresolved due to a small difference of the PP values (59% yellow vs. 41% white). All shifts reconstructed under the ancestral character recon-

struction were retrieved as highly homoplasious and are, therefore, unsuitable for genera characterisation under the given plastid inference presented in Escobari et al. (2021).

Species diversity of the Gynoxyoid clade

Our taxonomic backbone provides the best estimate of species diversity in the Gynoxyoid clade. Type information has been synthesised here for the first time in a comprehensive way. Further taxonomic knowledge turnover is expected at species level once species limits are tested in an integrative approach in a separate paper. Specially the examination of a reduced group of Bolivian species depicted shallow morphological differences, making the taxonomy complicated and predicting further nomenclatural changes. Additionally, the low number of collections available hinders a full examination of the species limits.

Taxonomic conclusions

Gynoxyoid clade

158 species

Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela

Trees, shrubs or scandent vines. Indumentum tomentose, of unicellular (simple) or multicellular trichomes (simple, stellate, T-shaped, multi-branched), becoming rusty or greyish-white with age on petioles, abaxial side of the leaves and involucres. Leaves alternate, opposite or subopposite, petiolate or subsessile; margin angulate, dentate, denticulate, entire, sinuate or repand, callous-tipped teeth present or absent; base acute, cordate, cuneate, obtuse, oblique, rotund or truncate; apex acute, acuminate, attenuate, mucronate, obtuse or rotund; coriaceous or papyraceous; leaf indumentum on abaxial leaf surfaces rusty-brownish or greyish-white with age. Synflorescence terminal, subterminal or axillary, thyrsoïdiform, paniculiform or corymbiform, peduncles bracteolate. Capitula heterogamous or homogamous, numerous, Receptacle flat to convex. Involucre campanular or tubular; outer phyllaries 0–8; inner phyllaries 5–10 (–13), uni- or biseriate. Ray flowers 0–8 (–13), female; tube cylindrical, glabrous; ligule white, cream-coloured or yellow, almost equalling the tube in length, 3–4-veined, 3-toothed at the apex, with a papillate upper surface. Style bifid, fertile. Disc flowers 5–32 (–36), hermaphrodite; corolla campanulate or funnel-shaped, white, pale greenish-yellow or yellow, shortly or largely lobed; lobes ovate, triangular or oblong, straight, recurved to the outside or helically twisted. Anthers exerted; apical appendage oblong-ovate or obtuse; base obtuse, auriculate or sagittate; filament collar narrowly cylindrical, uniform or thicker than the filament; with polar endothelial thickenings (Jeffrey 1992). Style-base gradually dilated, placed on a nectary; style branches straight or contorted, apically obtuse, truncate or acute, with papilliform sweeping-hairs. Achenes homomorphic, oblong, glabrate, ribbed. Pappus bristles pluriserial, persistent, coarse, shortly barbellate, off-white or somewhat brownish-fulvous. $n = \text{ca. } 40$ (Watanabe 2002).

Key to the genera of the Gynoxyoid clade

- 1a Flowers white.....2
- 2a Leaves, stems (in young shoots) and involucres with peltate-stellate hairs; capitula radiate..... **Aequatorium**
- 2b Leaves, stems (in young shoots) and involucres glabrous, with single or stellate hairs; capitula discoid.....3
- 3a Trees; leaves, stems (in young shoots) and involucres with stellate hairs; outer phyllaries present. Colombia and Venezuela..... **Paragynoxys**
- 3b Scandent shrublets; leaves, stems (in young shoots) and involucres with hairs absent or simple; outer phyllaries absent. Bolivia and Peru..... **Paracalia**
- 1b Flowers yellow..... **Gynoxys**

Revised classification of the genera and species of the Gynoxyoid clade

1. *Aequatorium* B.Nord. in *Opera Bot.* 44: 59. 1978 (Fig. 1f)

Type: *Aequatorium asterotrichum* B.Nord.

12 species

Colombia, Ecuador

Erect shrubs or trees, sometimes with sub-scandent branches. Indumentum tomentose, of subsessile stellate trichomes (with 1–3-tiered, irregularly star-shaped, subtended by a narrow pluricellular uniseriate stalk), with age, glabrescent, but with persistent greyish-white tomentum on petioles, abaxial side of leaves and sometimes involucres. Leaves alternate or subopposite or rarely opposite, petiolate, rounded-elliptic to lanceolate; margin entire, sinuate-dentate or denticulate, with small callous-tipped teeth; base acute, cuneate to rounded-truncate, subcordate or oblique; apex acute or rotund; coriaceous; leaves indumentum rusty-brownish on the adaxial side with two layers of peltate-stellate hairs, internal layer with sessile hairs and outer layer with subsessile hairs in patches, becoming grey-tomentose with age. Synflorescence terminal, rarely subterminal, (thyrsoid-) paniculiform or corymbiform. Capitula heterogamous. Receptacle flat or slightly convex. Involucre campanular; outer phyllaries usually < 6; inner phyllaries 5–10, biseriate. Ray flowers usually < 5 (–8); ligule white or cream-coloured. Disc flowers 5–10; corolla campanulate or funnel-shaped, white or pale greenish-yellow, shortly lobed, ratio lobes/tube < 0.8; lobes narrowly ovate, triangular or oblong, recurved to the outside or straight. Anther base sagittate-auriculate; filament collar narrowly cylindrical, uniform, not thicker than the filament. Style branches half contorted, apically obtuse or truncate. Distribution: Colombia, Ecuador.

Notes: We exclude *Aequatorium venezuelanum* from this genus, based on its yellow flowers and distribution and transfer this species to *Gynoxys*.

Aequatorium albiflorum (Wedd.) Cuatrec. & S.Díaz, *Revista Acad. Colomb. Ci. Exact.* 17(67): 665. 1990 ≡ *Gynoxys albiflora* Wedd., *Chlor. Andina* 1(3): 78. 1856 [“1855”]. – Syntypes: Colombia. Mariquita, sur la lisière du volcan de Tolima, 3900 m, Jan 1843, *J. Linden* 907 (F: V0076792F V0076793F (photo & fragments), K: K000497659, NY 178788, P: P00711390 P00711391 P02273078).

- Aequatorium asterotrichum*** B.Nord., Opera Bot. 44: 59. 1978. – Holotype: Ecuador. Pichincha, lago Papallacta, thicket, 3300 m, 31 Oct 1955, E. Asplund 18263 (S: S-R-8297; isotypes: K: K000497658, LD 1821970, MO: MO-3237504, NY, P: P00971087, R, S: S18-7665, UPS, US).
- Aequatorium caucanum*** S.Díaz & Cuatrec., Revista Acab. Colomb. Ci. Exact. 73: 248. 1994. – Holotype: Colombia. Cauca, Macizo Central Colombiano, Páramo de las Papas, El Boquerón, 3200–3510 m, 7–27 Sep 1958, J. Idrobo et al. 3221 (COL: COL000004758).
- = *Aequatorium caucanum* var. *abbreviatum* S.Díaz & Cuatrec., Revista Acab. Colomb. Ci. Exact. 73: 248, f. 2. 1994. – Holotype: Colombia. Cauca, Volcán Puracé, alrededores de la Laguna San Rafael, 3340 m, 6 Jan 1972, A. M. Cleef & A. Fernandez 526 (COL: COL000004759).
- Aequatorium jamesonii*** (S.F.Blake) C.Jeffrey, Kew Bull. 47(1): 61. 1992 ≡ *Gynoxys jamesonii* S.F.Blake, Acad. Sci. 18: 34. 1928. – Holotype: Ecuador. Pichincha, west side of Mount Pichincha, 3050 m, 2 Aug 1926, Jameson 227 (K: K000497657; isotype: US 00122911 (fragments & photo)).
- = *Senecio simulans* Benoist, Bull. Soc. Bot. France 83: 808. 1937, nom. illeg. [non *Senecio simulans* Chiov. 1935] ≡ *Gynoxys simulans* Cuatrec., Brittonia 8: 158. 1955. – Syntype: Ecuador. Pichincha, 12 Jul 1931, Benoist 4572 (P: P02273075).
- Aequatorium latibracteolatum*** S.Díaz & Cuatrec., Revista Acad. Colomb. Ci. Exact. 17(67): 661, 663, f. 1. 1990. – Holotype: Colombia. Cauca, Municipio de Puracé, Parque Nacional Natural del Puracé, cercanías de la Laguna San Rafael, 3300 m, 6 Oct 1984, C. G. Lozano 4667 (COL: COL000004762; isotypes: COL: COL000004760 COL000004761).
- Aequatorium lepidotum*** B.Nord., Compositae Newslett. 31: 6, f. 3. 6B. 1997. – Holotype: Ecuador. Carchi, El Mirador, 15 km S of San Francisco, 00°37'N, 77°31'W, 3300 m, 2 Aug 1990, W. Palacios & D. Rubio 5286 (MO: MO-037535; isotype: US 01919680).
- Aequatorium palealbum*** S.Díaz & A.Correa, Revista Acad. Colomb. Ci. Exact. 26(100): 345–346, f. 3. 2002. – Holotype: Colombia. Nariño, Ospina, páramo de Paja Blanca, alrededores de la bocatoma del acueducto, 1°58'N, 77°34'W, 3200 m, 2 Dic 1995, B. Ramirez-P. et al. 8904 (PSO: PSO0000058; isotype: MO: s.n.).
- Aequatorium polygonoides*** B.Nord., Opera Bot. 44: 63. 1978 ≡ *Senecio polygonoides* Cuatrec., Notas a la Flora de Colombia 6: 20, f. 14. 1944, nom. illeg. [non *Senecio polygonoides* Muschl. 1911]. – Holotype: Colombia. Caldas, Cordillera Central, vertiente occidental, vertiente SE del Nevado del Ruiz, Termales, 3400 m, 4 May 1940, J. Cuatrecasas 9243 (COL).
- Aequatorium repandiforme*** B.Nord., Compositae Newslett. 31: 9, f. 4. 1997. – Holotype: Ecuador. Pichincha, over high pass en route to Quito, 92 km E of Quevedo, 3400 m, 19 Sept 1959, B. Maguire & C. Maguire 44246 (NY 3468431; isotypes: K: K000497656, US 01919679).
- Aequatorium sinuatifolium*** S.Díaz & A.Correa, Revista Acad. Colomb. Ci. Exact. 19(73): 251–252, f. 3. 1994. – Holotype: Colombia. Quindío, Mun. de Salento, arriba de Guayaquil, 3680 m, 10 Jan 1994, W. G. Vargas 1335 (COL: COL000004764; isotype: COL: COL000004763).
- Aequatorium tatamanum*** S.Díaz & A.Correa, Revista Acad. Colomb. Ci. Exact. 23(88): 332, f. 1. 1999. – Holotype: Colombia. Risaralda, Municipio de Santua Río, Macizo de Tatamá, 200 m arriba del campamento El Reposo, 3700 m, 8 Feb 1983, J. H. Torres et al. 1720 (COL: COL000004765).

Note: This species is probably conspecific with *A. albiflorum*.

Aequatorium verrucosum (Wedd.) S.Díaz & Cuatrec., Revista Acad. Colomb. Ci. Exact. 17(67): 659–666. 1990 ≡ *Gynoxys verrucosa* Wedd., Chlor. Andina 1(3): 77. 1856 [“1855”] [non *Gynoxys verrucosa* V.M.Badillo 1946]. – Lectotype (Díaz & Cuatrecasas 1990: 663): Colombia. Nueva Granada, Mariquita, Cordillere de Quindiu, a Los Volcancitos, 3200 m, Jan 1843, *Linden 1050* (P: P02273077; isolectotypes: F: V0076796F V0076797F V0076798F, K: K000497655).
= *Senecio verrucosus* Klatt, Abh. Naturf. Ges. Halle 15(2): 332. 1881 [1882]. – Syntypes: *Triana s.n.* (P; photo: F).

2. *Paracalia* Cuatrec., Brittonia 12: 183. 1960 (Fig. 1b, e)

Type: *Paracalia pentamera* (Cuatrec.) Cuatrec.

2 species

Bolivia, Peru

Scandent shrublets. Indumentum glabrate to glabrescent, of simple hairs, glabrate with age. Leaves alternate, petiolate, ovate; margin entire or angulate, with or without small callous-tipped teeth; base rotund or cordate; apex acuminate or mucronate; coriaceous; leaves glabrous or pilose on the adaxial site, but glabrescent with age. Synflorescence terminal or axillar, paniculiform or corymbiform. Capitula homogamous. Receptacle flat. Involucre tubular; outer phyllaries absent; inner phyllaries 5, uniseriate. Ray flowers absent. Disc flowers 5; corolla campanulate, white or pale greenish, deeply lobed, ratio lobes/tube ≈ 1; lobes linear, helically twisted. Anther base auriculate or obtuse; filament collar cylindrical, thicker than the filament. Style branches half contorted, apically obtuse or subtruncate. Distribution: Peru, Bolivia.

Note: Although the phylogenetic inferences suggest this genus to be not monophyletic, we kept the circumscription of *Paracalia* including two species. We substantiate this decision based on shared morphological characters, such as deeply lobed and white-flowered corolla and the central Andean distribution beginning from lowlands (800 m). *Paracalia jungioides* which is nested in the *Gynoxys* clade strikingly differs morphologically from the true *Gynoxys* species and its inclusion in this genus would break the continuity of the morphological characters and altitudinal distribution in this group. A possible explanation for the contradiction between morphological/ecological and molecular data may be chloroplast capture and this needs to be further studied and better understood before further nomenclatural decisions are made. In this context, we think the best practice is to retain the current circumscription of *Paracalia* and avoid suggesting further possibly wrong hypotheses of relationships of these species.

Paracalia jungioides (Hook. & Arn.) Cuatrec., Brittonia 12: 183. 1960 ≡ *Pentanthus jungioides* Hook. & Arn., Companion Bot. Mag. 1: 33. 1835. – Holotype: Perú. Purruhuca, Jun 1833, *Matthews 1016* (K: K000497546(!); isotypes: E: E00414051 E00414052, K: K000497547(!)).
= *Cacalia mikaniifolia* DC., Prodr. 6: 328. 1837 ≡ *Senecio mikaniifolius* (DC.) Sch. Bip., Flora 28: 498. 1845. – Syntypes: Peru. San Buenaventura, *Nee & Thibaud s.n.* (not traced in G-DC, F: s.n. (photo)).

***Paracalia pentamera* (Cuatrec.) Cuatrec., Brittonia 12: 183. 1960** $\equiv$ *Senecio pentamerus* Cuatrec., Fieldiana, Bot. 27: 57. 1951. – Holotype: Bolivia. La Paz, Larecaja, Copacabana (ca. 10 km. south of Mapiri), 850–950 m, 08 Oct – 15 Nov 1939, B. A. Krukoff 11150 (NY 259336(!); isotypes: A: A00010877, F: V0077069F, K: K000497545(!), S: S-R-7986, U 0105750, US 00123446).

3. *Paragynoxys* (Cuatrec.) Cuatrec., Brittonia 8: 153. 1955. (Fig. 1b, c)

$\equiv$ *Senecio* sect. *Paragynoxys* Cuatrec., Fieldiana, Bot. 27(2): 72. 1951.

Type: *Paragynoxys neodrendoides* (Cuatrec.) Cuatrec.

13 species

Colombia, Venezuela

Erect shrubs or trees. Indumentum tomentose of (always?) stellate T-shaped trichomes, persistent in all age states, becoming greyish-white on petioles, abaxial side of leaves and involucres. Leaves alternate or rarely opposite, petiolate, oblong-elliptic, obovate-elliptic or ovate; margin entire or repand, with or without small callous-tipped teeth; base cordate, obtuse or rarely cuneate; apex obtuse, attenuate or rarely acute; coriaceous; leaf indumentum shaggy rusty-brownish in the adaxial site, persistent with age. Synflorescence terminal rarely subterminal, (thyrsoid-) paniculiform or corymbiform. Capitula homogamous. Receptacle flat. Involucre campanular; outer phyllaries < 6; inner phyllaries 5 or 8, uniseriate. Ray flowers absent. Disc flowers 5–11; corolla campanulate, white, deeply lobed, ratio lobes/tube $\Rightarrow$ 1; lobes linear, helically twisted. Anther base auricular or obtuse; filament collar cylindrical, thicker than the filament. Style branches fully contorted (forming a complete loop or even two), apically obtuse to subacute. Distribution: Colombia, Venezuela.

Note: We support the view of Correa (2003) who transferred *Paragynoxys regis* back to *Gynoxys* (as it was originally described), based on its radiate capitula with yellow flowers and distribution.

***Paragynoxys angosturae* (Cuatrec.) Cuatrec., Brittonia 8: 154. 1955** $\equiv$ *Senecio angosturae* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 55: 132. 1953. – Holotype: Colombia. Antioquia, Angostura, just outside town, 2000 m, 11 Mar 1944, F. R. Fosberg 21603 (US 00123252; isotypes: US 00123253 00123254).

***Paragynoxys corei* (Cuatrec.) Cuatrec., Brittonia 8: 154. 1955** $\equiv$ *Senecio corei* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 55: 136. 1953. – Holotype: Colombia. Antioquia, Alto El Oso, n. of Yarumal, 2320 m, 4 Mar 1944, E. L. Core 624 (F: V0051295F; isotype: US 00123277).

Paragynoxys cuatrecasasii Ruiz-Teran & López-Fig., Revista Fac. Farm. Univ. Andes 14: 14, f. 3, 4. 1974. – Holotype: Venezuela. Merida, Rangel, norte de la población Las Piedras, Cuenca del río Aracay, afluente del Santo Domingo, 2550–2700 m, 16 Dic 1972, Ruiz-Terán et al. 8258 (MERF; isotype: US).

Paragynoxys magnifolia Cuatrec., Brittonia 8(2): 154. 1955. – Holotype: Venezuela. Merida, Culata, 7000 ft., May 1847, N. Funck & Schlimm 1522 (P: P00711443 P00711444; isotypes: G: G00301285, P: P00711445 P00711446, US 00811048, VEN: VEN118056 (fragments of holotype)).

- Paragynoxys martingrantii*** (Cuatrec.) Cuatrec., Brittonia 8: 156. 1955 $\equiv$ *Senecio martingrantii* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 55: 139. 1953. – Holotype: Colombia. Magdalena, Sierra de Perijá, Casacará Valley 23 km. East of Codazzi, 2 km from the Venezuelan border, 2450, 15 Feb 1945, M. L. Grant 10949 (F: V0051336F V0051337F; isotypes: COL: COL000005419, HUA: HUA0000364, NY 259292 259293, US 00123324 00123323, VEN: VEN209193, WIS: WISv0256984WIS WISv0256985WIS).
- Paragynoxys meridana*** (Cuatrec.) Cuatrec., Brittonia 8(2): 156. 1955 $\equiv$ *Gynoxys verrucosa* V.M.Badillo, Bol. Soc. Venez. Ci. Nat. 10: 312. 1946, nom. illeg. [non *Gynoxys verrucosa* Wedd. 1855] $\equiv$ *Senecio steyermarkii* Cuatrec., Fieldiana, Bot. 27: 32–33. Jun 1950, nom. illeg. [non *Senecio steyermarkii* Greenm. Apr 1950] $\equiv$ *Senecio meridanus* Cuatrec., Fieldiana, Bot. 27(2): 38. 1951. – Syntypes: Venezuela. Merida, Paramo de Pozo Negro between San José and Beguilla, 2590–3220 m, 3 May 1944, A. Steyermark 56268 (NY 259418, US 00123361).
- Paragynoxys neodendroides*** (Cuatrec.) Cuatrec., Brittonia 8(2): 156, f. 13, 14. 1955 $\equiv$ *Senecio neodendroides* Cuatrec., Notas Fl. Colombia 6: 19, f. 13. 14. 1944. – Holotype: Colombia. Santander, Cordillera Oriental, Páramo de la Rusia, vertiente noroeste, 3300–3500 m, 4 Ago 1940, J. Cuatrecasas 10435 (COL; isotypes: F: V0051343F V0051344F V0051345F, P: P01816686).
- Paragynoxys pileolanata*** S.Díaz, Caldasia 12(59): 379–381, f. 1. 1979. – Holotype: Colombia. Santander, Municipio de Onzaga, vereda Chaguaz, finca de Oliverio Mesa, en robledal, 2820 m, 29 Mar 1976, J. H. Torres et al. 500 (COL: COL000005310).
- Paragynoxys santurbanensis*** (Cuatrec.) Cuatrec., Brittonia 8(2): 156. 1955 $\equiv$ *Senecio santurbanensis* Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 55: 145. 1953. – Holotype: Colombia. Santander, Páramo de Santurbán, vert. W, 3100 m, 27 Jul 1940, J. Cuatrecasas & H. García Barriga 10326 (F: V0051361F V0051362F; isotype: P: P01816508).
- Paragynoxys steyermarkii*** Cuatrec., Phytologia 40(1): 34. 1978. – Holotype: Venezuela. Táchira, Between Las Copas de Alto de Fila de Tierra Negra at the ridge dividing headwaters of rivers Quinimarí, Riofrio, Uribante and Talco (Oirá), 2870–2880 m, 16 Jan 1968, J. A. Steyermark & E. Dunsterville 101014 (US 00115958; isotypes: MA 638740, US 00115959, VEN: VEN74042).
- Paragynoxys undatifolia*** Cuatrec., Proc. Biol. Soc. Washington 74: 15. 1961. – Holotype: Colombia. Magdalena, Sierra Nevada de Santa Marta. South-eastern slope: Hoya del Río Donachuí, below Sabanita Diricune, 3200 m, 29 Sep 1959, J. Cuatrecasas & R. Romero-Castañeda 24485 (US: US00115961 US00115962 US00115963 US00115964 US00115965; isotypes: COL: COL000005311 COL000005312 COL000005313 COL000005314, P: P00711449 P00711450, US: US00115960 US00930968).
- Paragynoxys uribei*** Cuatrec., Phytologia 40(1): 33. 1978. – Holotype: Colombia. Boyaca, Arcabuco, 4 km. NE of town, 08 Jun 1966, L. U. Uribe 5633 (US: US00115966 US00115967; isotypes: COL: COL000005315 COL000005316).
- Paragynoxys venezuelae*** (V.M.Badillo) Cuatrec., Brittonia 8(2): 156. 1955 $\equiv$ *Cacalia venezuelae* V.M.Badillo, Bol. Soc. Venez. Ci. Nat. 10: 319. 1947 $\equiv$ *Senecio venezuelae* (V.M.Badillo) Cuatrec., Fieldiana, Bot. 27(1): 31. 1950. – Holotype: Venezuela. Merida, Below páramo above San Isidro Alto, 1820 m, 14 May 1944, J. Steyermark 56560 (VEN: VEN32772; isotypes: F: V0049135F, NY 162855).

4. *Gynoxys* Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827. (Fig. 1a, c–f)

Lectotype (Flann et al. 2010: 1225): *Gynoxys baccharoides* (Kunth) Cass.
= *Nordenstamia* Lundin, Compositae Newslett. 44: 15–16, f. 1. 2006, syn. nov.
Type: *Nordenstamia repanda* (Wedd.) Lundin [= *Gynoxys repanda* Wedd.]

130 species

Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela

Erect shrubs or trees. Indumentum absent or tomentose, of simple or multicellular simple trichomes, glabrescent with age, but with persistent greyish-white tomentum on abaxial side of all leaves and involucres. Leaves alternate or opposite, petiolate or sessile, elliptic, lanceolate, ovate, obovate; margin entire, repand, sinuate, sparsely angular or denticulate, with small callous-tipped teeth; base acute, attenuate, cordate, cuneate, obtuse, rotund, truncate or oblique; apex acute, acuminate, obtuse or mucronate; coriaceous or papyraceous; leaf indumentum absent, white or rusty-brownish in the adaxial site, persistent with age. Synflorescence terminal or axillar, paniculiform or corymbiform. Capitula homogamous (Sec 1) or heterogamous. Receptacle flat or convex. Involucre campanular; outer phyllaries 1–8; inner phyllaries usually 5–8(–13), biseriate. Ray flowers usually < 8 (–10–13); ligule yellow. Disc flowers usually 5–32 (–36); corolla tubular, campanulate or funnel-shaped, yellow, usually shortly lobed, ratio lobes/tube usually < 0.5; lobes triangular, oblong or narrowly ovate, recurved to the outside or straight. Anther base sagittate, auriculate or rarely obtuse; filament collar narrowly cylindrical, usually thicker than the filament. Style branches straight or half contorted, apically obtuse, truncate or acute.

Note: *Gynoxys alternifolia* and *G. mandonii* were described in literature as scandent. This information is certainly erroneous; in the field, we had a chance to trace several individuals of *G. mandonii* as large trees with thick branches and the type specimen of *G. alternifolia* also shows thick and erect branches with no sign of a liana-like growth.

- 1a Capitula discoid.....***Gynoxys*, discoid group**
- 1b Capitula radiate**2**
- 2a Leaves, stems (in young shoots) and involucres with stellate hairs
.....***Gynoxys*, *Praegynoxys* group**
- 2b Leaves, stems (in young shoots) and involucres with simple hairs.....
.....***Gynoxys*, *Gynoxys* s.str. group**

Gynoxys campii Cuatrec., Brittonia 8(1): 39. 1954. – Holotype: Ecuador. Cañar, Near El Tambo (ca. 69 km. by railroad south of Sibambe), 9500–10000 ft., 5 Jul 1945, W. H. Camp E–3970 (F: V0076704F; isotypes: G: G00223899, GH: GH00008575, K: K000497540, NY 178793, P: P00711407, US 00122893, VEN: VEN34418).

Gynoxys dielsiana Domke, Biblioth. Bot. 116: 169. 1937. – Syntype: Ecuador. Chimborazo, Tipococha, untere Rand des Paramo, ca. 3230 m, 20 Aug 1933, L. Diels 675 (B, destroyed).

Gynoxys hutchisonii H. Rob. & Cuatrec., Novon 2(4): 414. 1992. – Holotype: Perú. Piura, above Huancabamba, road to Piura, 3000 m, 10 Oct 1957, P. C. Hutchison 1609 (US 00409556; isotype: F: V0076714F).

Gynoxys induta Cuatrec., Fieldiana, Bot. 27: 9. 1950. – Syntypes: Colombia. Valle, Cordillera Central, Hoya del río Bugalagrande, Barragán, Páramo de Bavaya, corrales, 3550–3400 m, 9 Apr 1946, J. Cuatrecasas 20546 (COL: COL000005215 COL000005216, F: V0076715F V0076716F V0076717F, P: P00711414, US 00122909, WIS: WIS00001047MAD).

Gynoxys leiotheca S.F.Blake, J.Wash. Acad. Sci. 18: 35. 1928. – Holotype: Ecuador. Borma, Sep 1904, Rivet 671 (P: P00711416; isotypes: US 00122915 (photo & fragments)).

Gynoxys littlei Cuatrec., Revista Acad. Colomb. Ci. Exact. 9: 242. 1954. – Holotype: Colombia. Huila, on foot of Cordillera Oriental, 20 km. SE of gigant, 103000 ft., 15 Sep 1944, E. L. Little 8658 (F: V0076752F; isotypes: COL: COL000005220, US 00650427).

Note: This species is described as having “pale flowers” in the protologue; nonetheless, the label of the type specimen describes the flowers as “pale yellow”.

Gynoxys longifolia Wedd., Chlor. Andina 1(3): 79. 1855. – Syntypes: Perú. Cuzco, Andes de Cuzco, Oct 1839 – Feb 1940, Gay s.n. (F: V0076718F, P: P00711417 P00711418 P00711419, US 00122917 (fragments)).

Gynoxys lopezii M.O.Dillon & Sagást., Brittonia 40(2): 223, f. 2. 1988 ≡ *Paragynoxys lopezii* (M.O. Dillon & Sagást.) Cuatrec., Phytologia 69(5): 314. 1990 ≡ *Paracalia lopezii* (M.O. Dillon & Sagást.) A.Correa, Brittonia 55(2): 167. 2003. – Holotype: Perú. La Libertad, Patáz, Yaupa (Llaupa), entre Chagual-Retanas, carretera a Tayabamba, en borde carretera, pedregoso, 2300 m, 24 Jan 1974, A. López & A. Sagástegui 8160 (HUT; isotypes: F: V0076719F, MO: MO–176388 s.n.).

Note: The taxonomic assignment of this species was discussed by Cuatrecasas (1990) and Correa (2003). Its ratio of corolla lobe and tube length resembles the genus *Paracalia*, but we agree with Correa (2003) that this species belongs to *Gynoxys* because of its yellow flowers, shrubby (non-climbing) habit and central Andean distribution.

Gynoxys megacephala Rusby, Bull. New York Bot. Gard. 4: 398. 1907. – Syntypes: Bolivia. M. Bang 1959 (F: V0076754F (fragments), GH: GH00008597, K: K000497526, MICH: MICH1107432, MO: MO–1183133, NY 178867 178868, PH: PH00013514, US 00122920, WIS: WISv0256704WIS). Bolivia. Huaycani, 11000 ft., May 1866, Pearce s.n. (MO: s.n.).

= *Diplostephium foliosum* Rusby, Bull. New York Bot. Gard. 8(28): 128–129. 1912. – Syntypes: Bolivia. Cargadira, 8000 ft., 29 Jul 1902, W. Roberts 1529 (BM: BM001024073, F: V0076745F, K: K000497534, NY 168221).

Gynoxys moritziana Sch.Bip. ex Wedd., Chlor. Andina 1: 79. 1855. – Syntypes: Venezuela. Merida, Sierra Nevada, 1844, Moritz 1385 (GH: GH00008598 GH00008599 (drawing & fragment), K: K000497525, P: P00711421 P00711422 P00711423, US 00122924 (fragments)).

Gynoxys pendula Sch.Bip. ex Wedd., Chlor. Andina 1(3): 78. 1855. – Syntypes: Colombia. Nouvelle-Grenade, Mariquita, Boqueron, Tolima, Jan 1843, J. J. Linden 954 (F: V0076760F V0076761F, GH: GH00008601, K: K000497523, NY 178870, P: P00711425 P00711426, US 00122929 (fragments)).

= *Gynoxys pendula* var. *sinuata* Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 29: 38. 1935. – Syntypes: Colombia. Tolima, Andes, Cordillera Central, vert. merid. monte Tolima, loc. dict. Las Mesetas, 3600 m, 13 May 1932, J. Cuatrecasas 2851 (MA: MA240997 MA240997–2 (fragments)).

- Gynoxys regis*** H.Rob. & Cuatrec., *Phytologia* 56: 370(–371), f. 1984 ≡ *Paragynoxys regis* (H.Rob. & Cuatrec.) H.Rob. & Cuatrec., *Novon* 2(4): 415. 1992. – Holotype: Ecuador. Azuday, 30 km S of cumbé on the road to Saraguro at an elevation of 9800 ft., 26 Jan 1979, *R. M. King & F. Almeda* 7804 (US 00122934; isotypes: K: K000497542, QCA: QCA17841).
- Gynoxys soukupii*** Cuatrec., *Bull. Soc. Bot. France* 101: 245. 1954. – Holotype: Perú. Amazonas, Chachapoyas, cerro Puma Urco, Jun 1952, *Soukup* 4072 (F: V0076774F; isotype: US 00122939).
- Gynoxys subhirsuta*** Cuatrec., *Notas Fl. Colombia* 6: 35. 1944. – Holotype: Colombia. Santander, Cordillera Oriental, Páramo de Tamá, alrededores ed la Cueva, 3000–3200 m, 28 Oct 1941, *J. Cuatrecasas et al.* 12714 (COL: COL000005229; isotypes: BC: BC634998, F: V0076778F, GH: GH00008611, U: U0001284, US 00122942).

Gynoxys, *Praegynoxys* group

- Gynoxys azuayensis*** Cuatrec., *Brittonia* 8(1): 39. 1954. – Holotype: Ecuador. Azuay, Eastern Cordillera, 4–6 km N of Sevilla de Oro, 9000–10000 ft., 16 Aug 1945, *Camp E-4724B* (F: V0076733F; isotypes: GH: GH00008572, K: K000497543, NY 178791, P: P00711396, US 00122890).
- Gynoxys cajamarcense*** (H.Rob. & Cuatrec.) B.Escobari & N.Kilian, **comb. nov.** ≡ *Aequatorium cajamarcense* H.Rob. & Cuatrec., *Novon* 2(4): 411. 1992 ≡ *Nordenstamia cajamarcensis* (H.Rob. & Cuatrec.) B.Nord., *Compositae Newslett.* 44: 20. 2006. – Holotype: Perú. Cajamarca, Cutervo, Dist. San Andrés de Cutervo, Parque Nacional de Cutervo, caserío „Pajonal“ camino hacia Jaén, 2600 m, 10 Aug 1987, *Díaz & Osore*s 2585 (US 00409567; isotypes: F: V0043642F, MO: MO–2940604).
- Gynoxys carpishensis*** Cuatrec., *Brittonia* 12: 185. 1960 ≡ *Aequatorium carpishense* (Cuatrec.) H.Rob. & Cuatrec., *Novon* 2(4): 412. 1992 ≡ *Nordenstamia carpishensis* (Cuatrec.) B.Nord., *Compositae Newslett.* 44: 20. 2006. – Holotype: Perú. Carpish, between Huánuco and Tingo María, 2800 m, 10 Jul 1957, *H. Ellenberg* 2211 (U: U.1610531; isotypes: GOET010400 GOET010401).
- Gynoxys chingualensis*** H.Rob. & Cuatrec., *Novon* 2(4): 414. 1992. – Holotype: Ecuador. Sucumbíos, Paramo mirador SW of Playón de San Francisco, S del Río Chingual headwaters, 3400–3600 m, 15 May 1990, *P. King & Judziewicz* 10131 (US 00409557; isotypes: F: V0076702F, K: K000497538, MO, S: S-R–2685).
- Gynoxys congestiflora*** Sagást. & M.O.Dillon, *Brittonia* 37(1): 8, f. 3. 1985. – Holotype: Perú. Huánuco, ca. 46 Km NNE of Huánuco on road to Tingo María, Carpish Pass, E slope, 14 Jul 1981, *M. Dillon* 2608 (F: V0043633F; isotypes: HUT, MO: MO–2940531, NY 178795, TEX00374263, US 00122897, USM: USM000112).
- Gynoxys cuatrecasasii*** B.Herrera, *Bol. Soc. Perúana Bot.* 8(1–2): 40, f. 30. 1980. – Holotype: Perú. Amazonas, Chachapoyas, Cerros Calla Calla, east side, 19 km. above Leimebamba on road to Balsas, 3100 m, 4 Jun 1964, *P. C. Hutchison & J. Kenneth Wright* 5519 (USM: USM000114; isotypes: US 00122898, F: V0076740F, NY 804137).
- Gynoxys fabrisii*** Cabrera, *Bol. Soc. Argent. Bot.* 15(4): 332, f. 6. 1974. ≡ *Aequatorium fabrisii* (Cabrera) C.Jeffrey, *Kew Bulletin* 47(1): 61. 1992 ≡ *Nordenstamia fabrisii* (Cabrera) B.Nord., *Compositae Newslett.* 44: 20. 2006. – Holotype: Argentina. Jujuy, Valle Grande, Serranía de Calilegua, senda Alto Calilegua, 2500 m, 18 Feb 1964, *H. A. Fabris et al.* 5338 (LP: LP000275).

Note: Jeffrey (1992) and Nordenstam (2006) incorrectly cited a paratype as holotype and isotype.

Gynoxys jaramilloi H.Rob. & Cuatrec., Novon 2(4): 415. 1992. – Holotype: Ecuador. Loja, Loma del Oro, 2800–3200 m, 4 Aug 1986, Z. Jaramillo & Valencia 8799 (US 00409555; isotypes: MO: MO–1891634, QCA: QCA17836).

Gynoxys juninensis (H.Rob. & Cuatrec.) B.Escobari & N.Kilian, **comb. nov.** ≡ *Aequatorium juninensis* H.Rob. & Cuatrec., Novon 2(4): 412. 1992 ≡ *Nordenstamia juninensis* (H.Rob. & Cuatrec.) B.Nord., Compositae Newslett. 44: 20. 2006. – Holotype: Perú. Junin, Carpata, above Huacapistana, 2700–3200 m, 7 Jun 1929, Killip & Smith 24434 (US 00409566).

Gynoxys kingii (H.Rob. & Cuatrec.) B.Escobari & N.Kilian, **comb. nov.** ≡ *Aequatorium kingii* H.Rob. & Cuatrec., Novon 2(4): 412. 1992 ≡ *Nordenstamia kingii* (H.Rob. & Cuatrec.) B.Nord., Compositae Newslett. 44: 20. 2006. – Holotype: Bolivia. Cochabamba, 15 km from Colomi, on the road to Tunari, 10600 ft., 7 Feb 1978, King & Bishop 7680 (US 00409565).

Gynoxys limonensis (B.Nord.) B.Escobari & N.Kilian, **comb. nov.** ≡ *Aequatorium limonensis* B.Nord., Compositae Newslett. 31: 14, f. 7. 1997 ≡ *Nordenstamia limonensis* (B.Nord.) B.Nord., Compositae Newslett. 44: 21. 2006. – Holotype: Ecuador. Morona-Santiago, 49 km from Limón on road to Gualaceo, 2300 m, 16 Jul 1996, Stahl & Knudsen 2882 (S: S18–7653; isotype: QCA: QCA148693).

Gynoxys pascoensis (H.Beltrán & H.Rob.) B.Escobari & N.Kilian, **comb. nov.** ≡ *Aequatorium pascoense* H.Beltrán & H.Rob., Compositae Newslett. 42: 5–7, f. 1. 2005 ≡ *Nordenstamia pascoensis* (H.Beltrán & H.Rob.) B.Nord., Compositae Newslett. 44: 22. 2006. – Holotype: Perú. Pasco, Oxapampa, trail to summit of Cordillera Yanachaga via Río San Daniel, 10°23'S, 75°27'W, 2600 m, 18 Jul 1984, D. N. Smith & H. Botiger 7884 (USM; isotypes: AMAZ, MO: MO–037539, US 00810884).

Gynoxys repanda Wedd., Chlor. Andina 1(3): 77. 1855 ≡ *Aequatorium repandum* (Wedd.) C.Jeffrey, Kew Bull. 47(2): 292. 1992 ≡ *Nordenstamia repanda* (Wedd.) Lundin, Compositae Newslett. 44: 16. 2006. – Syntypes: Bolivia. La Paz, Larecaja, Vallée de Tipuani, 1851, M. Weddell s.n. (F: V0076768F (fragments), P: P02273082, US 00122936 (fragments)).

Note: We consider the locality designation in the protologue “dans les tail-lis, sur le versant orientale du mont Illampù” to correspond to the (upper) Valle de Tipuani given on the label of the above specimen, because of its location east of Mt. Illampu. No specimen with the locality indication in the protologue could be found.

= *Schistocarpha triangularis* Rusby, Bull. New York Bot. Gard. 4: 392. 1907. – Syntypes: Bolivia. La Paz, Unduavi, Sep 1894, M. Bang 2477 (F: V0076813F, GH: GH00549665, US 00122819 00955547).

= *Gynoxys alternifolia* Sch.Bip. ex Rusby, Mem. Torrey Bot. Club 6(1): 67. 1896; Sch.Bip., Linnaea 34: 531. 1865, nom. nud. ≡ *Senecio alternifolius* (Sch.Bip. ex Rusby) Greenm., Ann. Missouri Bot. Gard. 10: 76. 1923. – Syntypes: Bolivia. La Paz, Vic. Mapiri, 8000 ft, Sep 1892, Bang 1574 (A: A00008569, F: V0076725F, GH: GH00549664, K: K000634163, NDG: NDG62631, NY 114876 114877, PH: PH00013520, PUL: PUL00000344, US 00122884). Bolivia. La Paz, Larecaja, Viciniis Sorata, inter Laripata et tani, in nemoribus, 3000–3200 m, Apr 1858–May 1859, Mandon 131 (BR: BR0000005318605, GH: GH00012072, K: K000497519, MPU: MPU016063, P: P02273079 P04099622 P00711394 P00711395).

Gynoxys rimachiana Cuatrec., Phytologia 52(3): 164. 1982 $\equiv$ *Aequatorium rimachianum* (Cuatrec.) H.Rob. & Cuatrec., Novon 2(4): 413. 1992 $\equiv$ *Nordenstamia rimachiana* (Cuatrec.) B.Nord., Compositae Newsletter 44: 22. 2006. – Holotype: Perú. Huanuco, Carretera de Tingo Maria - Huanuco, El Mirador, near Carpish, 2600–2700 m, 21 Mar 1980, *M. Rimachi* 4908 (US 00324004; isotypes: F: V0043643F, US 00324003).

Gynoxys stellatopilosa (Greenm. & Cuatrec.) B.Escobari & N.Kilian, **comb. nov.** $\equiv$ *Senecio stellatopilosus* Greenm. & Cuatrec., Collect. Bot. (Barcelona) 3: 264. 1953 $\equiv$ *Aequatorium stellatopilosum* (Greenm. & Cuatrec.) C.Jeffrey, Kew Bull. 47(1): 62. 1992 $\equiv$ *Nordenstamia stellatopilosa* (Greenm. & Cuatrec.) B.Nord., Compositae Newslett. 44: 22. 2006. – Holotype: Perú. Villcabamba, hacienda on río Chinchao, 6000 ft., 17 Jul 1923, *F. Macbride* 4966 (F: V0043600F).

Gynoxys tovarii (H.Rob. & Cuatrec.) B.Escobari & N.Kilian, **comb. nov.** $\equiv$ *Aequatorium tovarii* H.Rob. & Cuatrec., Novon 2(4): 413. 1992 $\equiv$ *Nordenstamia tovarii* (H.Rob. & Cuatrec.) B.Nord., Compositae Newslett. 44: 22. 2006. – Holotype: Perú. Huancavelica, Tayacaja, arriba de Marcavalle, entre Huachocolpa y Tintay, 3300 m, 21 Apr 1964, *O. Tovar* 4781 (US 00409564).

Gynoxys tuestae (Cuatrec.) Cuatrec., Brittonia 8: 158. 1955 $\equiv$ *Senecio tuestae* Cuatrec., Fieldiana, Bot. 27: 46. 1951 $\equiv$ *Aequatorium tuestae* (Cuatrec.) H.Rob. & Cuatrec., Novon 2: 413. 1992 $\equiv$ *Nordenstamia tuestae* (Cuatrec.) B.Nord., Compositae Newslett. 44: 22. 2006. – Holotype: Perú. Huanuco, Pillao, 2700 m, 17 Feb 1946, *D. Tuesta Díaz* & *J. Woytkowski* 34095 (F: V0043646F).

Note: This species is very likely conspecific with *G. repanda* and will be treated in a forthcoming work.

Gynoxys valenzuelae (H.Beltrán & J.Calvo) B.Escobari & N.Kilian, **comb. nov.** $\equiv$ *Nordenstamia valenzuelae* H.Beltrán & J.Calvo, Phytotaxa 474(3): 294, f. 1 & 2. 2020. – Holotype: Perú. Junín, Jauja, Monobamba, comunidad campesina Marancocha, zona de amortiguamiento del Bosque de Protección Pui-Pui, 11°18'39"S, 75°11'01"W, 3470 m, 25 Oct 2014, *L. Valenzuela et al.* 28791 (USM: USM306000; isotypes: HOXA68690, MO: MO-2951169).

Gynoxys venezuelana (V.M.Badillo) B.Escobari & N.Kilian, **comb. nov.** $\equiv$ *Aequatorium venezuelanum* V.M.Badillo, Ernstia, ser. 2, 10(1): 16, f. 9. 2000. – Holotype: Venezuela. Edo. Trujillo. Mun. Carache, Parque Nacional Dinira, arriba de Mesa, debajo del Pico Cendé, 9°53'N, 70°07'W, 3000 m, 1 Apr 1999, *Duno & Riina* 783 (MY; isotype: VEN).

Gynoxys s. l.

Gynoxys acostae Cuatrec., Feddes Repert. Spec. Nov. Regni Veg. 55: 129. 1953. – Holotype: Ecuador. Tunguragua, Alta de Pasa, 3500 m, 28 Oct 1944, *M. Acosta Solís* 8738 (F: V0076722F).

Gynoxys albifluminis Cuatrec., Fieldiana, Bot. 27(2): 12. 1951. – Holotype: Perú. Lima, Río blanco, 15000 ft, 20 Mar 1923, *J. F. Macbride* 3028 (F: V0076723F; isotype: US 00122883).

Gynoxys albivestita Cuatrec., Revista Acad. Colomb. Ci. Exact. 9: 242. 1954. – Holotype: Colombia. Boyacá, Nevada del Cocuy, Las Lagunillas, Pozo Azul, 4300 m, 12 Dic 1938, *J. Cuatrecasas* 1434–A (F: V0076724F; isotype: BC: BC624334).

- Gynoxys apollinaris*** Cuatrec., Fieldiana, Bot. 27(2): 16. 1951. – Holotype: Colombia. Caldas, Salamina, Corregimiento San Félix, Jul 1943, *T. Alberto 1884* (F: V0076726F; isotype: MEDEL: MEDEL000097).
- Gynoxys arnicae*** Cuatrec., Fieldiana, Bot. 27(1): 2–3. 1950. – Syntypes: Colombia. Departamento del Valle, Cordillera Occidental, Los Farallones, vertiente oriental, bajo el filo de la Cordillera en el cerro de La Torre: La Laguna, 3500–3550 m, 1 Aug 1946, *J. Cuatrecasas 21864* (COL: COL000005204 COL000005205 COL000005206, F: V0076728F V0076727F, K: K000497544, P: P00711392, US 00122885).
- = *Gynoxys arnicae* var. *scandens* Cuatrec., Fieldiana, Bot. 27: 3. 1950. – Syntypes: Colombia. Dep. del Valle, Cordillera Occidental, Los Farallones, extremo N. bajando a Las Cascadas, 3100 m, 2 Aug 1946, *J. Cuatrecasas 21923* (F: V0076729F V0076730F, P: P00711393, US 00122886 00122887).
- = *Gynoxys arnicae* f. *subtomentosa* Cuatrec., Fieldiana, Bot. 27: 3. 1950. – Syntypes: Colombia. Dep. del Valle, Cordillera Occidental, Los Farallones, lomas parameras sobre la mina El Diamante, 3000–3120 m, 31 Jul 1946, *J. Cuatrecasas 21834* (COL: COL000005203).
- Gynoxys asterotricha*** Sch.Bip., Linnaea 34: 529. 1865.
Lectotype (designated here): Bolivia. Larecaja, Viciniis Sorata, Lancha de Cochipata in scopulis montis Illampia, 3300 m, 1 Apr 1859, *G. Mandon 84* (P02273125; isoelectotypes: BR: BR0000005318506, F: V0076731F V0076732F, GH: GH00008570(!) GH00008571(!), MPU: MPU012549 MPU012550 MPU012570, NY 178790, P: P02273080(!) P02273126(!)).
Note: The gathering *Mandon 84* is a mixed collection of material representing *G. asterotricha* and *G. mandonii*. The above cited specimens in BR, F, GH, MPU, NY & P represent *G. asterotricha*. The specimen in K (K000497527) & P (P04099621(!)) holds material of both species on the same sheet.
- Gynoxys baccharoides*** (Kunth) Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827 ≡ *Senecio baccharoides* Kunth, Nov. Gen. Sp. (folio ed.) 4: 146. 1818 [“1820”]. – Syntypes: Ecuador. Crescit locis frigidis Andium Quitensium, 3240 m, Jul, *F. W. H. A. Humboldt & A. Bonpland s.n.* (P: P00320174(!) P00320173(!)).
- = *Gynoxys lindenii* Sch.Bip. ex Wedd., Chlor. Andina 1: 76. 1856. – Syntypes: Colombia. New Granada, Mariquita, Pic. de Tolima, 4280 m, *Linden 930* (syntypes; G: G00223897 F: V0076720F, NY 468695; US 00122916 (fragment)).
- Gynoxys bracteolata*** Cuatrec., Notas Fl. Colombia 6: 33, f. 26. 1944. – Holotype: Colombia. Caldas, Cordillera Central, vertiente occidental, faldas sudoeste del Ruiz, El Aprisco, 3500–3600 m, 5 May 1940, *J. Cuatrecasas 9313* (COL; isotypes: BC: BC-Cuatrecasas-635016 BC-Cuatrecasas-634964, F: V0076735F V0076734F, P: P00711406, US: US00122891, U: U 0001282).
- Gynoxys buxifolia*** (Kunth) Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827 ≡ *Senecio buxifolius* Kunth., Nov. Gen. Sp. (folio ed.) 4: 147. 1818 [“1820”]. – Syntypes: Ecuador. Quito, Rucu Pichincha, Crescit cum praecedente: locis frigidis Andium Quitensium., *F. W. H. A. Humboldt & A. Bonpland s.n.* (F: s.n. V0077029F (fragments), HAL: HAL0113451, P: P00320176 P00670367 P00670368).
- = *Gynoxys buxifolia* var. *brevifolia* Hieron., Bot. Jahrb. Syst. 19(1): 63. 1895. – Syntypes: Ecuador. Loja, Alsos de Zoghunes, Oña & Zaraguro, 3000–3300 m, 23 Oct 1888, *F. C. Lehmann 4899* (US 00122892 01101244 (fragments), K: K000497541).

- Gynoxys callacallana*** Cuatrec., Ciencia (Mexico) 23: 146. 1964. – Holotype: Perú. Amazonas, Chachapoyas, Middle eastern Calla-Calla slopes, ca. Kms. 411–416 of Leimebamba-Balsas road, 3100–3250 m, 11 Jul 1962, J. J. Wurdack 1324 (US 00323999; isotypes: GH: GH00008574, LIMA, NY 178792, P, US 00811165).
- Gynoxys calyculisolvens*** Hieron., Bot. Jahrb. Syst. 36: 504. 1905. – Syntypes: Perú. Cajamarca, entre Chota y Cutervo, Jun 1879, C. von Jelski 611 (not traced), C. von Jelski 780 (B, destroyed; photo: F: F0BN018153).
- Gynoxys capituliparva*** Cuatrec., Fieldiana, Bot. 27(2): 6. 1951. – Holotype: Perú. Huanuco, Tambo de Vaca, 12000 ft., 10 Jun 1923, J. F. Macbride 4434 (F: V0076736F; isotype: US 00122894).
- Gynoxys caracensis*** Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 85–86. 1913. – Syntypes: Perú. Ancash, in declivibus Cordillerae blancae Supra Caraz, 3200–3700 m, 9 Jun 1903, A. Weberbauer 3248 (B, destroyed). Perú. Ancash, Formatio aperta, 3600–3700 m, 18 Apr 1903, A. Weberbauer 2909 (B, destroyed; photo: F: F0BN018154).
- Gynoxys cerrateana*** B.Herrera, Bol. Soc. Perúana Bot. 8(1–2): 37, f. 28. 1980. – Holotype: Perú. Amazonas, Chachapoyas, Cordillera Calla-Calla lado del Marañón, 3400–3600 m, R. Ferreyra 15578 (USM).
- Gynoxys chagalensis*** Hieron., Bot. Jahrb. Syst. 28: 630. 1901. – Syntypes: Ecuador. Cuenca, chagal W Andens of Cutca, 2200–2800 m, Sep [no year], F. C. Lehmann 7948 (B, destroyed; photo: F: F0BN018156; F: V0076703F, K: K000497539, US 00122895).
- Gynoxys chimborazensis*** Hieron., Bot. Jahrb. Syst. 29(1): 66. 1900. – Syntypes: Ecuador. Chimborazo, crescit in declivibus montis Chimborazo, 2600 m, Sep 1881, A. Sodiro 60/9 (P: P00711408 (fragments), QPLS: QPLS211069).
- Gynoxys colanensis*** M.O.Dillon & Sagást., Brittonia 40(2): 221. 1988. – Holotype: Perú. Bagua, Cordillera Colán, NE of La Peca, 78.26064N, 5.350383W, 2980–3100 m, 8 Sep 1978, P. Barbour 3409 (F: V0043641F; isotypes: HUT, LSU: LSU00210549, MO: MO-2152935).
- Gynoxys columbiana*** (Klatt) Hieron., Bot. Jahrb. Syst. 28: 631. 1901 ≡ *Liabum columbianum* Klatt, Bot. Jahrb. Syst. 8(1): 47. 1886. – Syntypes: Columbia. Cauca, in silvis densis ad latera montis Páramo de Moras, 2800–3400 m, 16 Mar 1884, F. C. Lehmann 3783 (GH: GH00008578 (fragment), K: K000497537, US 00122695).
- Gynoxys compressissima*** Cuatrec., Fieldiana, Bot. 27(2): 4. 1951. – Holotype: Perú. Huanuco, Tambo de Vaca, ca. 12000 ft., 10–24 Jun 1923, J. F. Macbride 4435 (F: V0076738F; isotype US 00122896).
- Gynoxys corazonensis*** Hieron., Bot. Jahrb. Syst. 29: 65. 1900. – Syntype: Ecuador. Pichincha, Monte Corazón, A. Sodiro 60/8 (P: P00711411 (fragments)).
- Gynoxys costihirsuta*** Cuatrec., Ciencia (Mexico) 23: 146. 1964. – Holotype: Perú. Amazonas, Chachapoyas, upper slopes and summit of Cerro Yama-uma above Taulia, 12–15 km south-southeast (145°) of Molinopampa, 3200–3450 m, 11 Aug 1962, J. J. Wurdack 1670 (US 00324000; isotypes: GH: GH00008580, K: K000497535, LIMA, LP: LP002068, NY 178796, P, US 00811164, USM: USM000113).
- Gynoxys cuicochensis*** Cuatrec., Fieldiana, Bot. 27: 16. 1951. – Holotype: Ecuador. Imbabura, Lake Cuicocha, 3500 m, 27 May 1939, C. W. Pendland & R. H. Summer 722 (F: V0076705F).

- Gynoxys cusilluyocana*** Cuatrec., Fieldiana, Bot. 27(2): 8. 1951. – Syntypes: Perú. Cuzco, Paso de tres Cruces, Cerro de Cusilluyoc, 3500–3800 m, 3 May 1925, F. W. Pennell 13900 (F: V0076741F, GH: GH00008582, PH: PH00013518, US 00122899).
- Gynoxys cutervensis*** Hieron., Bot. Jahrb. Syst. 36: 506. 1905. – Syntypes: Perú. Crescit prope Cutervo, May 1879, C. von Jelski 632 (B, destroyed; photo: F: F0BN018157).
- Gynoxys cuzcoensis*** Cuatrec., Fieldiana, Bot. 27(2): 9. 1951. – Holotype: Perú. Cuzco, Tres Cruces, Pancartambo, 3600 m, 1 Oct 1941, C. Vargas 2253 (NY 178797; isotypes: F: V0076742F (fragment), LP: LP002069 LP002070).
- Gynoxys cygnata*** S.Díaz & A. Correa, Revista Acad. Colomb. Ci. Exact. 26(100): 343–344, f. 2. 2002. – Holotype: Colombia. Caldas, Sur del Nevado del Cisne, cerca a Laguna Verde, 04°50'07"N, 75°21'38"W, 4600–4800 m, 28 Jan 1986, V.A. Funk 8082 (COL: COL000005207; isotype: US 01826640).
- Gynoxys dilloniana*** Sagást. & C. Téllez, Brittonia 39(4): 432, f. 1. 1987. – Holotype: Perú. Lambayeque. Ferreñafe, distrito Incahuasi, Laguna Tembladera-Cerro Negro, 3300 m, 12 Sep 1985, A. Sagástegui et al. 12835 (HUT; isotypes: F: V0043636F, MO: s.n., NY).
- Gynoxys fallax*** Mattf., Repert. Spec. Nov. Regni Veg. 17: 183. 1921. – Syntypes: Perú. Piura, Huancabamba, westhänge der Cordillere östlich von Huancabamba, über der Hacienda Chantaco, 2500 m, 17 Apr 1912, A. Weberbauer 6319b (F: V0076706F V0076707F, GH: GH00008584).
- Gynoxys ferreyrae*** B. Herrera, Bol. Soc. Perúana Bot. 8(1–2): 35. 1980. – Holotype: Perú. Cajamarca, Hualgayoc, Jalca, 16 Aug 1952, 3400 m, R. Ferreyra 8559 (not traced; isotypes USM: USM000115; MO–714138, US 00122903).
Note: The protologue states the holotype specimen to be at USM (not traced online); the specimen in USM (USM000115) digitally available in JSTOR is labelled as isotype by Herrera. In case no other specimen exists in USM, USM000115 would actually be the holotype).
- Gynoxys flexopedes*** Cuatrec., Fieldiana, Bot. 27: 13. 1950. – Syntypes: Colombia. Cundinamarca, Paramo de Guasca, 3000–3500 m, 11 Oct 1939, H. Garcia Barriga 08098 (COL: COL000005209 COL000005208, F: V0076708F V0076709F, US 00122904).
- Gynoxys florulenta*** Cuatrec., Fieldiana, Bot. 27(1): 4–5. 1950. – Syntypes: Colombia. Valle, Cordillera Central, Hoya del río Bugalagrande, Barragán, Páramo de Bavaya, Corrales, 3450–3520 m, 18–20 May 1946, J. Cuatrecasas 20148 (COL000005210, COL000005211, F: V0076743F V0076744F, P: P00711412, US 00122905, WIS: WIS00001046MAD).
- Gynoxys frontinoensis*** S.Díaz & A. Correa, Revista Acad. Colomb. Ci. Exact. 23(88): 333. 1999. – Holotype: Colombia. Antioquia, Municipio de Urrao, Páramo de Frontino, Llano Grande, 3460 m, 1 Jul 1984, R. Lodoño et al. 29 (COL: COL000005212; isotype: MEDEL: MEDEL000047).
- Gynoxys fuliginosa*** (Kunth) Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827 ≡ *Senecio fuliginosus* Kunth, Nov. Gen. Sp. (folio ed.) 4: 146. 1818 [“1820”]. – Syntypes: Colombia. Pasto, Inter pagos Ypidales et Guachucal, 2916 m, Dic, F. W. H. A. Humboldt & A. Bonpland s.n. (F: V0076822F (fragments), P: P00320175 P00670369).
= *Gynoxys fuliginosa* var. *glabriuscula* Domke, Biblioth. Bot. 116: 170. 1937. – Syntype: Ecuador. Cañar, Tipococha, 3200 m, 16 Aug 1933, Diels 551 (B, destroyed).

- Gynoxys huanucona*** (Cuatrec.) Cuatrec., Brittonia 8: 158. 1955 $\equiv$ *Senecio huanuconus* Cuatrec., Fieldiana, Bot. 27: 45. 1951 $\equiv$ *Nordenstamia huanucona* (Cuatrec.) B.Nord., Compositae Newslett. 44: 20. 2006. – Syntypes: Perú. Huanuco, 1927, *M. Sawada* 45 (F: V0076921F, US 00123418).
- Gynoxys hallii*** Hieron., Bot. Jahrb. Syst. 19: 64. 1894. – Syntypes: Ecuador. Quito, crescit in regione suprema silvae Andinum occidentalium 2500–3400 m, Aug 1888, *F. C. Lehmann* 4664 (K: K000634159 K000634160); prope Zurucho et Tambo de Quinoa haud procul ab urbe Cuenca, 3000–3500 m, Sep 1888, *F. C. Lehmann* 4605 (K: K000497532 K000634158); In monte ignivomo Pichincha, 3400 m, *F. Hall* s.n. (B, destroyed; photo: F: F0BN018158).
- Gynoxys henrici*** Mattf., Repert. Spec. Nov. Regni Veg. 17: 178. 1921. – Syntype: Perú. Amazonas, Östlich von Chachapoyas: zwischen dem steppe mit einzelnen Sträuchern, 3200–3400 m, 29 Jul 1904, *Weberbauer* 4413 (B, destroyed).
- Gynoxys hirsuta*** Wedd., Chlor. Andina 1: 79. 1855. – Syntypes: Colombia. Bogotá, Nouvelle-Grenade, *F. W. H. A. Humboldt* & *A. Bonpland* s.n. (F: V0076746F, P: P00670371), *Goudot* s.n. (GH: GH00008586).
- Gynoxys hirsutissima*** Cuatrec., Notas Fl. Colombia 6: 34, f. 27–29. 1944. – Syntypes: Colombia. Cundinamarca, Cordillera oriental, extremo sudeste de la Sabana de Bogota en San Miguel, 2800–3000 m, 10 Sep 1941, *J. Cuatrecasas* & *R. Jaramillo* 12022 (COL: COL000005213 COL000005214, BC: BC–635006, F: V0076711F V0076712F, K: K000497530, LL: LL00374264, NY 178858, P: P00711413, U: U 0001283, US 00122902).
- Gynoxys huasahuasis*** Cuatrec., Fieldiana, Bot. 27(2): 2. 1951. – Holotype: Perú. Huasahuasu, 2900 m, 29 Apr 1940, *F. Woytkowski* 37 (F: V0076713F).
- Gynoxys hypoleucophylla*** Cuatrec., Ciencia (Mexico) 23: 148. 1964. – Holotype: Perú. Amazonas, Chachapoyas, Upper slopes and summit of Cerro Yamauma above Taulia, 12–15 km, south-southeast (145°) of Molinopampa, 3200–3450 m, 11 Aug 1962, *J. J. Wurdack* 1671 (US 00324001; isotypes: GH: GH00008587, K: K000497529, LIMA, LP: LP002071, NY 178860, P, US 00811163).
- Gynoxys ignaciana*** Cuatrec., Fieldiana, Bot. 27(2): 14. 1951. – Holotype: Ecuador. Pichincha, San Ignacio, 11200 ft., 14–19 Aug 1923, *H. E. Anthony* & *G. H. H. Tate* 127 (US 00122908; isotype: F: V0076747F).
- Gynoxys infralanata*** Cuatrec., Fieldiana, Bot. 27(2): 6. 1951. – Holotype: Perú. Cusco. Torontoy, Urubamba Valley, 3900 m, 1915, *E. Heller* 2181 (US 00122910; isotype: F: V0076748F).
- Gynoxys jelskii*** Hieron., Bot. Jahrb. Syst. 36: 507. 1905. – Syntypes: Perú. Crescit prope Cutervo, May 1879, *C. von Jelski* 678 (B, destroyed; photo: F: F0BN018159; F: V0076749F (fragments), US 00122912).
- Gynoxys laurata*** Cuatrec., Fieldiana, Bot. 27: 5. 1950. – Syntypes: Colombia. Valle, Cordillera Central, cabeceras del río Tulu, quebrada de Las Vegas, 3400–3500 m, 23 Mar 1946, *J. Cuatrecasas* 20399 (COL: COL000005217 COL000005218 COL000005219, F: V0076750F V0076751F, P: P00711415, US 00122913).
- Gynoxys laurifolia*** (Kunth) Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827 $\equiv$ *Senecio laurifolius* Kunth, Nov. Gen. Sp. (folio ed.) 4: 146. 1818 [“1820”]. – Syntypes: Ecuador. Loja, Crescit locis subcalidis, umbrosis inter Lucarque et Gonzanama Quitensium, 1908 m, Aug, *F. W. H. A. Humboldt* & *A. Bonpland* s.n. (B, destroyed; photo: F: F0BN018160).

- Gynoxys lehmannii*** Hieron., Bot. Jahrb. Syst. 28: 629. 1901. – Syntypes: Colombia. Cauca, crescit in fruticetis densis in Páramo de las Delicias in Andibus centralibus papayanensibus, 3200–3600 m, Jan-Feb, *F. C. Lehmann* 8501 (B, destroyed; photo: F: F0BN018155; F: V0076721F, PH: PH00013515, S-R-2688, US 00122914 01014476).
- Gynoxys longistyla*** (Greenm. & Cuatrec.) Cuatrec., Chlor. Andina 1(3): 79. 1855
 ≡ *Senecio longistylus* Greenm. & Cuatrec., Collect. Bot. (Barcelona) 3: 292. 1953 ≡ *Nordenstamia longistyla* (Greenm. & Cuatrec.) B.Nord., Compositae Newslett. 44: 21. 2006. – Holotype: Perú. Moquegua, Saylapa near Carumas, 3600–3700 m, 3 Mar 1925, *Weberbauer* 7331a (F: V0076925F).
- Gynoxys macfrancisci*** Cuatrec., Fieldiana, Bot. 27(2): 3. 1951. – Syntypes: Perú. Pachitea, Yanano, ca 6000 ft., 13–16 May 1923, *J. F. Macbride* 3747 (F: V0076753F, US 00122918).
- Gynoxys macrophylla*** Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 88–89. 1913. – Syntypes: Perú. Huanuco, Huamalies, Montes prope Monzon, 2000–2500 m, 8 Aug 1903, *Weberbauer* 3534 (B, destroyed; photo: F: F0BN018161).
- Gynoxys magnifolia*** (H.Beltrán & J.Campos) B.Escobari & N.Kilian, **comb. nov.**
 ≡ *Nordenstamia magnifolia* H.Beltrán & J.Campos, Arnaldoa 16(1): 37. 2009.
 – Holotype: Perú. Amazonas, Luya. Camporredondo, Tullanga, Subiendo del campamento o Pascana hacia el Cerro Huicsocunga, 2700–3000 m, 7 Sep 1989, *C. Díaz & J.Campos* 3830 (USM; isotypes: MO: MO-1962029 MO-1962030, S: S19-3395 S19-3398).
- Gynoxys malcabalensis*** Cuatrec., Ciencia (Mexico) 23: 149. 1964. – Holotype: Perú. Amazonas, Chachapoyas, Summit of Cerro Malcabal (Cerro Tumbe) 3–6 km. southwest of Molinopampa, 2850–2900 m, 20 Jul 1962, *J. J. Wurdack* 1413 (US 00324002; isotypes: GH: GH00008591, LIMA, LP: LP002072, NY 178862, P, USM: USM000117, US 00811161).
- Gynoxys mandonii*** Sch.Bip. ex Rusby, Mem. Torrey Bot. Club 6(1): 67. 1896; Sch.Bip., Bulletin de la Société Botanique de France 12: 80. 1865, nom. nud.
 – Lectotype (designated here): Bolivia. Cochabamba, Chapare, Espiritu Santo, 1891, *M. Bang* 1196 (NY 178865; isolectotypes: BR: BR0000005318933, K: K000634162, NDG: NDG62632, PH: PH00013513). – Syntypes: Bolivia. Larecaja, Viciniis Sorata, Lancha de Cochipata in scopulis montis Illampia, 3300 m, 1 Apr 1859, *G. Mandon* 84 (BR: BR0000005317899, P: P00711420(!), S: S10-31297 S10-31297, US 01117686).
- = *Gynoxys hypomalaca* S.F.Blake, Bot. Gaz. 74: 427. 1922. – Holotype: Bolivia. La Paz, Sorata, higher limit of trees, 22 Apr 1920, *E. W. D. Holway & M. M. Holway* 567 (US 00122907; isotypes: GH: GH00008588(!), NY 178861, US 01100708).
- = *Gynoxys cochabambensis* Cabrera, Notas Mus. La Plata, Bot. 14: 194. 1949. – Holotype: Bolivia. Cochabamba, Chapare, Yanta-Aduana, 3200 m, 10 Jul 1929, *J. Steinbach* 9813 (LP: LP000274; isotypes: E00414368, F: V0076737F, G: G00223898(!), GH: GH00008576 GH00008577, K: K000634161 K000659419, NY 178794, S: S-R-2686).
- = *Gynoxys cruzensis* Cuatrec., Collect. Bot. (Barcelona) 3(3): 295. 1953. – Syntypes: Bolivia. Santa Cruz, Comarapa, Cerro San Mateo, 3400 m, 24 Oct 1928, *J. Steinbach* 8515 (E00414367, F: V0076739F, GH: GH00008581, K: K000497536, PH: PH00013519, S: S-R-2687).

Note: The gathering *Mandon 84* is a mixed collection of material representing *G. asterotricha* & *G. mandonii*. The above cited specimens in BR, P, S, and US represent *G. mandonii*. The specimen in K (K000497527) depicts material of both ". The species are doubtfully distinct and will be treated in a forthcoming work.

Gynoxys marcapatana Cuatrec., Collect. Bot. (Barcelona) 3: 297. 1953. – Holotype: Perú. Cuzco, Quispicanchis, Marcapata, Compi-pampa, on the grade from Huailai to Huallo-hualla, 4100 m, 11 Dic 1938, *C. Vargas 9717* (GH: GH00008596; isotype: F: V0076835F).

Gynoxys meridana Cuatrec., Bol. Soc. Venez. Ci. Nat. 15(81): 109. 1954. – Holotype: Venezuela. Merida, Laguna Negra, 9 Nov 1952, *L. Aristeguieta 970* (F: s.n.; isotypes: US 00122921 00122922, VEN: VEN282322).

Gynoxys metcalfii Cuatrec., Fieldiana, Bot. 27(2): 2. 1951. – Holotype: Perú. Puno, Sandía. Near Limbani, 3200–3450 m, *R. D. Metfcalf 30529* (US 00122923).

Gynoxys miniphylla Cuatrec., Fieldiana, Bot. 27(1): 11. 1950. – Holotype: Ecuador. Azuay, In vicinity of Toreador, between Molleturo and Quinoas, 3810–3930 m, 15 Jun 1943, *J. A. Steyermark 53175* (F: V0076701F; isotype: NY 178863).

Gynoxys monzonensis Mattf., Repert. Spec. Nov. Regni Veg. 17: 180. 1921. – Syntype: Perú. Huanuco, Huamalies, Berge südwestlich von Monzon, 3400–3500 m, 11 Jul 1903, *Weberbauer 3338* (B, destroyed).

Gynoxys multibracteifera H. Rob. & Cuatrec., Phytologia 56: 369, f. 1984. – Holotype: Ecuador. Azuay, Ridge between El Pan and Guachapala, 7500–9800 ft., 4 Sep 1945, *W. H. Camp E-5244* (US 00122925; isotype: NY 178864).

Gynoxys myrtoides Mattf., Repert. Spec. Nov. Regni Veg. 17: 182. 1921. – Syntype: Perú. Piura, Huancabamba, westhänge der Cordillere östlich von Huancabamba, über der Hacienda Chantaco, 5°10'W, 5°20'S, 2500 m, 17 Apr 1912, *Weberbauer 2. Ser., 6319a* (B, destroyed).

Gynoxys neovelutina Cuatrec., Fieldiana, Bot. 27(2): 11. 1951. – Holotype: Bolivia, 3000 m, 1–4 Apr 1892, *O. Kuntze* (NY 178869; isotype: F: V0076755F (fragment)).

= *Gynoxys tablaensis* Cabrera, Blumea 7: 197. 1952. – Syntypes: Bolivia. Cochabamba, Tablas, 3400 m, May 1911, *T. Herzog 2201* (B: B 10 0093559, L: L0001978 L0001979, LP: LP000276, S: S-R-2690, Z: Z-000003473 (fragments)).

Gynoxys nervosa Hieron., Bot. Jahrb. 21: 354. 1895. – Syntypes: Colombia. Boyacá, Crescit prope Muso civitatis Boyacá, Jul 1868, *A. Stuebel 161* (B, destroyed; photo: F: F0BN018162).

Gynoxys nitida Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 86–87. 1913. – Syntypes: Perú. Ayacucho, Supra Quinuam prope Ayacucho, 3300–3500 m, 30 May 1910, *Weberbauer 5535* (F: V0076756F, G: G00223896 (fragments), GH: GH00008600, K: K000497524, US 00122927; photo: US 00122926).

Gynoxys oleifolia Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 89–90. 1913. – Syntypes: Perú. Ancash, Pichiu, provinsia Huari, 4000–4100 m, 20. Apr 1903, *Weberbauer 2937* (photo F: V0076757F, S: S07-10464 (fragments)).

Gynoxys pachyphylla Mattf., Repert. Spec. Nov. Regni Veg. 17: 184. 1921. – Syntype: Perú. Huancabamba, Cordillera östlich von Huacabamba, 5°20'S, 5°10'W, 3400–3500 m, 8 Apr 1912, *Weberbauer 2. Ser. 6082* (B, destroyed).

- Gynoxys paramuna*** Cuatrec., Fieldiana, Bot. 27: 7. 1950. – Syntypes: Colombia. Boyacá, Sierra Nevada del Cocuy, valle de Las Lagunillas, 4110 m, 11 Sep 1938, J. Cuatrecasas & H. García Barriga 1434 (BC: BC-624335, COL: COL000005221, F: V0076758F, P: P00711424, US 00122928).
- Gynoxys parvifolia*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 6: 59, f. 25. 1944. – Holotype: Colombia. Nariño, Páramo de la Laguna del Cumbal, 3475 m, 7 Feb 1942, Miguel de Garganta 418 (COL: COL000005222; isotype: F: V0076759F).
- Gynoxys perbracteosa*** Cuatrec., Fieldiana, Bot. 27(1): 1. 1950. – Syntypes: Colombia. Cauca, Cordillera Central, Cabeceras del Río Páez, Páramo alrededor de la Laguna del Páez, 3450 m, 4 Dic 1944, J. Cuatrecasas 19057 (COL: COL000005223 COL000005224 COL000005225, DUKE10000786, F: V0076762F V0076763F G: G00223895, GH: GH00008602, K: K000497522, MO: MO-714136, NY 178871, P: P00603125 P00711427).
- Gynoxys pillahuatensis*** Cuatrec., Fieldiana, Bot. 27(2): 7. 1951. – Syntypes: Perú. Cuzco, „Pillahuata“, Cerro de Cusilluyoc, 3000–3300 m, 3 May 1925, F. W. Pennell 14134 (F: V0076764F, GH: GH00008603, K: K000497521, NY 178872, PH: PH00013512, US 00122930).
- Gynoxys poggeana*** Mattf., Repert. Spec. Nov. Regni Veg. 17: 179. 1921. – Syntypes: Perú. Junin, Valle del Río Masamerich, abajo del Tambo de Atac. 11°30'S, 3400–3500 m, 25 Apr 1913, Weberbauer 2. Ser. 6645 (F: V0077103F, GH: GH00008605, MO: MO-714135 (fragments), MOL: MOL00006552, US 00122931, USM: USM000118).
- Gynoxys psilophylla*** Klatt, Ann. K. K. Naturhist. Hofmus. 9: 367. 1894 ≡ *Gynoxys glabriuscula* Rusby, Mem. Torrey Bot. Club 6(1): 68. 1896, nom. illeg. – Syntypes: Bolivia. Cochabamba, 1 Jul 1891, M. Bang 1116 (A: A00008585, BR: BR0000005318186 BR0000005318513, E: E00413271, F: V0076765F, GH: GH00008606 GH00008607, US 00122935, WIS: WISv0256703WIS).
- = *Liabum bolivianum* Klatt, Ann. K. K. Naturhist. Hofmus. 9: 362. 1894 ≡ *Gynoxys boliviana* (Klatt) S.F.Blake, Contr. Gray Herb. 53: 28. 1918. – Holotype: Bolivia, Cuming s.n. (W: W18890106172; isotype: GH: GH00008573 (fragment with drawing)).
- = *Gynoxys hoffmannii* Kuntze, Revis. Gen. Pl. 3(3): 156. 1898. – Syntype: Bolivia. Cochabamba, Weg zum Río Juntas, 3000 m, 13–21 Apr 1892, O. Kuntze s.n. (NY 178859).
- Gynoxys pulchella*** (Kunth) Cass. in Cuvier, Dict. Sci. Nat., ed. 2, 48(2): 455. 1827 ≡ *Senecio pulchellus* Kunth, Nov. Gen. Sp. (folio ed.) 4: 146–147. 1818 [“1820”]. – Syntype: Ecuador. Crescit locis frigidis Andium Quitensium., 3240 m, Jul, F. W. H. A. Humboldt & A. Bonpland s.n. (P: P00320177).
- Gynoxys puracensis*** Cuatrec., Notas Fl. Colombia 6: 32. 1944. – Holotype: Colombia. Cauca, Cordillera Central, 2700–3100 m, 11 Jul 1939, J. Cuatrecasas 5958 (COL; isotypes: BC: BC635070, F: V0076766F, P: P00711410; US 00122933).
- Gynoxys reinaldii*** Cuatrec., Fieldiana, Bot. 27(2): 15. 1951. – Holotype: Ecuador. Loja, Cajamuna, 2400 m, 7 May 1946, R. Espinosa 312 (F: V0076767F).
- Gynoxys rimbachii*** Cuatrec., Fieldiana, Bot. 27: 10. 1950. – Syntypes: Ecuador. Eastern Cordillera, inner slope, 3200 m, Dec [no year], A. Rimbach 79 (A: A00008608, F: V0076769F).
- Gynoxys rugulosa*** Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 87–88. 1913. – Lectotype (Herrera de Loja 1980: 39): Perú. Sandia, 3300 m, 11 Apr 1902, Weberbauer 747 (F: F0BN018163 (photo)).

- Gynoxys rusbyi*** Cuatrec., Fieldiana, Bot. 27(2): 10. 1951. – Syntypes: Bolivia. La Paz, Vic. Pongo de Queme, 12500 ft., 2 Jul 1921, *H. H. Rusby* 3 (F: V0076770F (fragments), MO: MO-1508476, NY 178874, US 00122937).
- Gynoxys sancti-antonii*** Cuatrec., Fieldiana, Bot. 27(1): 9. 1950. – Syntypes: Colombia. Comisaría del Putumayo, Páramo de San Antonio del Bordoncillo, entre el Encano y Sibundoy, 3250 m, 3 Jan 1941, *J. Cuatrecasas* 11722 (BC: BC635012, COL: COL000005226, F: V0076771F, P: P00711429, US 00122938). Colombia. Narino, Yacuanquer, 2800–3000 m, 4 Jan 1943, *M de Garganta* 504 (not traced).
- = *Gynoxys sancti-antonii* var. *latifolia* Cuatrec., Brittonia 12: 186. 1960. – Holotype: Ecuador. Chimborazo. Border to Canar (western escarpment), between Sta. Rosa and Joyagahi, 8000–9000 ft., *W. H. Camp* E-4049 (F: V0076772F; isotypes: GH: GH00008609, K: K000497518, MO: MO-714134, NY 178875, S: S-R-2689, VEN: VEN34425).
- Gynoxys seleriana*** Muschl., Bot. Jahrb. Syst. 50(2/3, Beibl. 111): 90–91. 1913. – Syntypes: Perú. Cuzco, Cazeo, in dumetis, 28 Jun 1910, *Seler* 163 (B, destroyed). Perú. Cuzco, Urubamba, 3400 m, 10 Jun 1905, *Weberbauer* 4926 (B, destroyed).
- Gynoxys sodiroi*** Hieron., Bot. Jahrb. Syst. 29: 64. 1900. – Syntypes: Ecuador. In decliv. m. Chimbor. vers. Guaranda, *L. Sodiro* 60/3 (B, destroyed; photo: F: F0BN018164; QPLS: QPLS211119).
- Gynoxys sorataensis*** Cuatrec., Fieldiana, Bot. 27(2): 12. 1951. – Syntypes: Bolivia, La Paz, Sorata, 10000 ft, Feb 1886, *H. H. Rusby* 1638 (F: V0076773F s.n., MO: s.n., NY 178876).
- Gynoxys stuebelii*** Hieron., Bot. Jahrb. Syst. 21: 355. 1895. – Syntypes: Ecuador. Pichincha, Crescit prope Verdecuchu in monte Pichincha, 4000 m, Jul-Aug, *Stuebel* 31 (B, destroyed; photo: F: F0BN018165). Ecuador. Pichincha, Monte Cayambe, 4300 m, *Stuebel* 114 (not traced).
- Gynoxys subamplectens*** Cuatrec., Fieldiana, Bot. 27(2): 1. 1951. – Syntypes: Perú. Cuzco, Paso de Tres Cruces, Cerro de Cusilluyoc, 3800–3900 m, 3 May 1925, *F. W. Pennell* 13825 (F: V0076775F, GH: GH00008610, US 00122940).
- Gynoxys subcinerea*** Cuatrec., Fieldiana, Bot. 27: 6. 1950. – Syntypes: Colombia. Santander, Cordillera Oriental, Hoya del río Chitagá en Vega Colombia, 2880 m, 28 Nov 1941, *J. Cuatrecasas* 13473 (BC: BC634976, COL: COL000005227 COL000005228, LP: LP002075, F: V0076776F V0076777F, P: P00711430, US 00122941).
- Gynoxys szyszlowiczii*** Hieron., Bot. Jahrb. Syst. 36(5): 505. 1905. – Syntypes: Perú. Caldas, Crescit prope Cutervo, May 1879, *Jelski* 607 (B, destroyed); ibid., Apr 1879, *Jelski* 754 (B, destroyed, photo: F: F0BN018166).
- Gynoxys tabaconasensis*** H. Beltrán & S. Baldeón, Compositae Newslett. 47: 14, f. 1. 2009. – Holotype: Perú. Caldas, Province San Ignacio, District Tabaconas, Lagunas Arrebiatadas, Santuario Nacional Tabaconas-Namballe, 3150–3180 m, 9 Apr 2003, *S. Baldeón & L. Adrianzen* 5160 (USM; isotypes: MO, S: S09–3275).
- Gynoxys tetroici*** V.A. Funk & H. Rob., Revista Acad. Colomb. Ci. Exact. 17(65): 243–245, f. 1. 1989. – Holotype: Perú. Piura, Bosque de Huamba, 2950 m, 20 Sep 1987, *Valencia* 1991 (US 00169692; isotype: USM).
- Gynoxys tolimensis*** Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 29: 37–38. 1935. – Syntypes: Colombia. Tolima, Cordillera Central, vert. merid. monte Tolima, El Salto, 3200 m, 15 May 1932, *J. Cuatrecasas* 2850 (F: V0076779F (fragment), MA: MA240999).

- Gynoxys tomentosissima*** Cuatrec., Ciencia (Mexico) 23: 149. 1964. – Holotype: Perú. Amazonas, Chachapoyas, middle eastern Calla-Calla, near Kms. 416–419 of Leimebamba-Balsas road, 3900–3100 m, 9 Jul 1962, J. J. Wurdack 1254 (US00122943; isotypes: F: V0076780F, GH: GH00008612, K: K000497517, LP: LP002076, NY 178878, US 00811162, USM: USM000119).
- Gynoxys trianae*** Hieron., Bot. Jahrb. Syst. 21: 353. 1895. – Syntypes: Colombia. Nueva Granada, Tuquerres, 3000 m, Jun 1853, *Triana 1444* (B, destroyed; photo: F: F0BN018167; E: E00413269 E00413270, NY 77375, P: P00711431 P00711432, US 00122944). Colombia. Santisimo, haud procul a vico Cum-bal, *Stuebel 435a* (not traced).
- = *Gynoxys trianae* var. *nemocona* Cuatrec., Fieldiana, Bot. 27(2): 17. 1951. – Holotype: Colombia. Cundinamarca, Nemocón, 2900–3000 m, 23 Oct 1917, F. W. Pennell 2619 (NY 178879).
- Gynoxys vacana*** Cuatrec., Fieldiana, Bot. 27(2): 5. 1951. – Syntypes: Perú. Pasco, Tambo de Vaca, 13000 ft., 10–24 Jun 1923, J. F. Macbride 4391 (F: V0076782F, US 00122945).
- Gynoxys validifolia*** Cuatrec., Brittonia 8(1): 40. 1954. – Holotype: Ecuador. Azuay, N-NW of the Páramo del Castillo, 6–8 km N-NE of Sevilla de Oro, 10000–11200 ft., 31 Aug 1945, W. H. Camp E–5156 (F: V0076783F; isotypes: GH: GH00008613, K: K000497516, NY 178880, US 00122946).
- Gynoxys vargasiana*** Cabrera, Revista Univ. (Cuzco) 33(87): 121–122, f. 20. 1944. – Holotype: Perú. Cuzco, Calvca, alrededores de Lares, 3200 m, 30 Aug 1943, C. Vargas 3598 (LP: LP000277).
- Note: Probably not a *Gynoxys*. Too many inner phyllaries for a *Gynoxys*.
- Gynoxys venulosa*** Cuatrec., Fieldiana, Bot. 27(1): 8. 1950. – Syntypes: Colombia. Cauca, Cordillera Central, Cabeceras del Río López, Quebrada del Duen-de, 3400–3450 m, 3 Dic 1944, J Cuatrecasas 18945 (COL: COL000005230 COL000005231, DUKE: DUKE10000787, F: V0076784F, GH: GH00008614, K: K000497515, NY 178881, P: P00711433).
- Gynoxys violacea*** Sch.Bip. ex Wedd., Chlor. Andina 1(3): 77. 1855. – Syntypes: Venezuela. Merida, Sierra nevada de Merida, 2920 m, 1 Sep 1846, *Funck & Schlim 1159* (F: V0076789F (fragments), GH: GH00008617 (fragments), K: K000497514, LD 1001683, MPU: MPU012551, P: P00711439 P00711440 P00711441 P00711442, US 00122948 (fragments & photo)).
- Gynoxys visoensis*** Cuatrec., Fieldiana, Bot. 27(2): 13. 1951. – Syntypes: Perú. Viso, 9000 ft., 5–14 May 1922, *Macbride & Featherstone 580* (F: V0076788F, US 00122949).
- Gynoxys weberbaueri*** Mattf., Repert. Spec. Nov. Regni Veg. 17: 181. 1921. – Syntype: Perú. Huancabamba, Cordillere östlich von Huancabamba, 3300–3500 m, 5°10'–5°20'S, 8 Apr 1912, *Weberbauer 2. Ser. 6075* (B destroyed).
- Gynoxys woytkowskii*** (Cuatrec.) Cuatrec., Brittonia 8: 158. 1955 ≡ *Senecio woytkowskii* Cuatrec., Fieldiana, Bot. 27: 49. 1951 ≡ *Nordenstamia woytkowskii* (Cuatrec.) B.Nord., Compositae Newslett. 44: 22. 2006. – Holotype: Perú. Huánuco, vicinity of Tambo de Vacas, 3500 m, 4 Nov 1937, *F. Woytkowski 145* (F: V0076790F).
- Gynoxys yananoensis*** Cuatrec., Fieldiana, Bot. 27(2): 10. 1951. – Holotype: Perú. Huanuco, Yanano, 6000 ft., 20 Jun 1923, J. F. Macbride 4931 (F: V0076791F)..

Excluded names

Gynoxys aquifolia Cuatrec. ≡ *Scrobicaria aquifolia* (Cuatrec.) B.Nord.
Gynoxys auriculata Turcz. = *Aetheolaena patens* (Kunth) B.Nord.
Gynoxys berlandieri DC. = *Pseudogynoxys chenopodioides* (Kunth) Cabrera
Gynoxys cordifolia Cass. ≡ *Pseudogynoxys cordifolia* (Cass.) Cabrera
Gynoxys cummingii Benth. ≡ *Pseudogynoxys chenopodioides* var. *cummingii* (Benth.) B.L.Turner
Gynoxys discolor Rusby = *Pentacalia marinii* (Cabrera) Cuatrec.
Gynoxys fragrans Hook. ≡ *Pseudogynoxys fragrans* (Hook.) H.Rob. & Cuatrec.
Gynoxys haenkei DC. ≡ *Pseudogynoxys haenkei* (DC.) Cabrera
Gynoxys heterophylla Turcz. ≡ *Aetheolaena heterophylla* (Turcz.) B.Nord.
Gynoxys ilicifolia (L.f.) Wedd. = *Scrobicaria ilicifolia* (L.f.) B.Nord.
Gynoxys incana Less. = *Jacmaia incana* (Sw.) B.Nord.
Gynoxys laciniata Less. = *Odontocline laciniata* (Sw.) B.Nord.
Gynoxys lucida Less. = *Dendrophorbium lucidum* (Sw.) C.Jeffrey
Gynoxys oerstedii Benth. ≡ *Pseudogynoxys oerstedii* (Benth.) Cuatrec.
Gynoxys poeppigii DC. ≡ *Pseudogynoxys poeppigii* (DC.) H.Rob. & Cuatrec.
Gynoxys prenanthifolia Turcz. = *Aetheolaena patens* (Kunth) B.Nord.
Gynoxys scabra Benth. ≡ *Pseudogynoxys scabra* (Benth.) Cuatrec.
Gynoxys sinclairii Benth. = *Pseudogynoxys sonchoides* (Kunth) Cuatrec.

Names of doubtful status

For the following names in the Global Compositae Database, no publication is given:

Aequatorium castillense B.Nord.
Aequatorium stellatopilosum Cuatrec.
Gynoxys auriculata Sch.Bip
Gynoxys cumingii Sch.Bip.
Gynoxys glabrata Less.
Gynoxys incana (Sw.) Griseb.
Gynoxys lanceolata Weddel
Gynoxys napoensis H.Rob.
Gynoxys perbracteata Cuatrec.
Gynoxys unduaviana Cuatrec.
Gynoxys verrucosa var. *magna* Cuatrec.

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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: TB, NK. Data curation: BE. Funding acquisition: NK, TB. Investigation: BE. Methodology: NK. Supervision: NK, TB. Writing - original draft: BE. Writing - review and editing: BE, TB, NK.

Author ORCIDs

Belen Escobari  <https://orcid.org/0000-0002-4588-3180>

Tomas Borsch  <https://orcid.org/0000-0002-5724-2786>

Norbert Kilian  <https://orcid.org/0000-0003-0890-4373>

Data availability

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

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Supplementary material 1

List of specimens investigated with full specimen data, lab codes and ENA accession numbers for molecular markers

Authors: Belen Escobari, Thomas Borsch, Norbert Kilian

Data type: xlsx

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Link: <https://doi.org/10.3897/phytokeys.234.107750.suppl1>

Supplementary material 2

Majority consensus tree

Authors: Belen Escobari, Thomas Borsch, Norbert Kilian

Data type: docx

Explanation note: Majority consensus tree on a) Plastid genome (Escobari et al 2021), b) ITS, c) ETS, d) ETS-ITS concatenated under Bayesian inference topology. Posterior probability values.

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Supplementary material 3

Ancestral character analysis: Bayes Traits scores of the of morphological characters state shifts at the tree nodes of Fig. 5.

Authors: Belen Escobari, Thomas Borsch, Norbert Kilian

Data type: xlsx

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Digitization of the historical Herbarium of Michele Guadagno at Pisa (PI-GUAD)

Francesco Roma-Marzio¹, Simonetta Maccioni¹, David Dolci², Giovanni Astuti¹, Nicoletta Magrini¹, Federica Pierotti¹, Roberta Vangelisti¹, Lucia Amadei¹, Lorenzo Peruzzi^{1,2}

¹ Orto e Museo Botanico, Sistema Museale d'Ateneo, Università di Pisa, via Ghini 13, 56126 Pisa, Italy

² PLANTSEED Lab, Dipartimento di Biologia, Università di Pisa, via Derna 1, 56126 Pisa, Italy

Corresponding author: Giovanni Astuti (giovanni.astuti@unipi.it)

Abstract

The herbarium digitization process is an essential first step in transforming the vast amount of data associated with a physical specimen into flexible digital data formats. In this framework, the Herbarium of the University of Pisa (international code PI), at the end of 2018 started a process of digitization focusing on one of its most relevant collections: the Herbarium of Michele Guadagno (1878–1930). This scholar studied flora and vegetation of different areas of southern Italy, building a large herbarium including specimens collected by himself, plus many specimens obtained through exchanges with Italian and foreign botanists. The Herbarium is composed by 547 packages of vascular plants. Metadata were entered into the online database Virtual Herbaria JACQ and mirrored into a personalized virtual Herbarium of the Botanic Museum. After the completion of the digitization process, the number of sheets preserved in the Herbarium amounts to 44,345. Besides Guadagno, who collected 42% of his specimens, a further 1,102 collectors are represented. Most specimens were collected in Europe (91%), but all the continents are represented. As expected, Italy is the most represented country (59%), followed by France, Spain, Germany, and Greece. The specimens cover a time span of 99 years, from 1830 to 1929, whereas the specimens collected by Guadagno range between 1889 and 1928. Furthermore, we traced 134 herbarium sheets associated with documents, among which 75 drawings handmade by Guadagno, 34 letters from various corresponding authors, 16 copies of publications, and 14 copies of published iconographies.

Key words: herbaria, historical botanical collection, history of botany, museology, specimen metadata, taxonomy



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Introduction

Herbarium specimens, as all the other natural history collections, are verifiable records of the presence of a species in a defined place at a specific time (Borsch et al. 2020). Currently, around 396 million specimens are kept in more than 3,000 active herbaria and can be considered as the basic documentation of all formally described plant species (Thiers 2021; Heberling 2022).

The inestimable value of herbaria is widely recognised in the fields of taxonomy, systematics, and biogeography and, in the last decades, they turned out to

be greatly useful for studying ecological shifts (Lang et al. 2019; Garretson and Forkner 2021; Davis 2023; Jaroszynska et al. 2023). Indeed, herbarium studies should not be limited to the most recent specimens, but also to historical ones (e.g., Stefanaki et al. 2019), that have proven to be fundamental in several biological disciplines, from the most traditionally prone to the use of herbaria (Funk 2018) to the most recent approaches dealing with climate change biology (Heberling 2022), biodiversity (Nelson and Ellis 2018), phenology (Park et al. 2023), nature conservation (Nualart et al. 2017), biological invasions (Martin et al. 2014), and phylogenomics (Beck and Sempel 2015). Also, herbaria are the repositories of nomenclatural types, and hold useful data for studies on endangered species or represent a documentation of taxa that have gone extinct in historical times (Lavoie 2013). Actually, herbaria may be the only source for the resurrection of extinct species, or de-extinction, because they may preserve viable diaspores (Albani Rocchetti et al. 2022a, b).

Given the high scientific, historical, and cultural value of herbarium collections, in the last 20 years many efforts have been made towards their digitization, and to make them available to the scientific community and beyond (Tulig et al. 2012). The digitization process – i.e. the capture of images and metadata from specimen labels – is an essential first step in transforming this vast amount of data associated with a physical specimen into flexible digital data formats that are accessible, usable, and useful (Hedrick et al. 2020), since it allows information to be summarised, categorised and manipulated, in order to retrieve specific information, otherwise hidden in an overwhelming pile of specimens. Particularly, historical specimens are often accompanied by fragmentary label information, so that providing a link to correct metadata is crucial to make them accessible for researchers worldwide (Reiner-Drehwald et al. 2022).

However, digitization activities require huge efforts in terms of equipment, personnel training and, consequently, time and money. Although the digitization rates increase in parallel with the experience of technical staff, databasing is the most time-expensive step with effort variable according to the details of metadata to capture, which can vary from a complete databasing including georeferentiation to a minimal subset of label data referred as skeletal (Powell et al. 2021).

In this framework, the Herbarium of the University of Pisa [PI is the international code according to Thiers (2020, and onwards)], started a process of digitization in November 2017. The PI Herbarium, currently preserving more than 350,000 specimens from all over the world, was started by Gaetano Savi (1769–1844), director of the Pisa Botanic Garden from 1814 to 1842. His first collection dates back to the end of the XVIII century, when he collected the first specimens during botanic trips with Giorgio Santi (1746–1822). Furthermore, thanks to the friendship with Ottaviano Targioni Tozzetti (1755–1826), he had access to the collection of Pier Antonio Micheli (1679–1737) and he had also the opportunity to bring to Pisa some of these specimens, which are the oldest specimens currently preserved in the Herbarium. In addition to the general Herbarium, other separate collections are preserved in PI, such as the Herbarium of Michele Guadagno (1878–1930). After his death, in 1939 this Herbarium (PI-GUAD hereafter) was sold by his relatives to PI. In December of the same year, Alberto Chiarugi (1901–1960), the director of the Botanical Institute in Pisa, with the help of his son, personally carried the Herbarium to Pisa, and counted 36,648

specimens only considering those already intercalated (Chiarugi 1950). It has been hence considered one of the richest private herbaria ever recorded in Italy.

Michele Guadagno was born in Naples (Campania, southern Italy) on October 16th 1878 and showed from an early age a special attitude for natural sciences and particularly for botany. In 1905 he graduated as a civil engineer in Naples and then he worked as an engineer at the Municipality of Naples (Trotter 1930; D'Erasmo 1931; Andolfato et al. 2002). During his life, he studied the flora and vegetation of different areas of Campania, which led to seventeen papers between 1909 and 1932, including a monograph on the vegetation of the Sorrento Peninsula and a floristic study of Capri Island, posthumously published by his friend Augusto Béguinot (1875–1940). Unfortunately, the former monograph is incompletely published, as only three out of the six parts planned by the author were published, while the fourth part was only partially published. The complete botanic bibliography of M. Guadagno is available on the online Suppl. material 1: table S1. Alongside the scientific activities resulted in publications, he built a large herbarium including specimens collected by himself mainly in central and southern Italy, plus many specimens obtained through exchanges with Italian and foreign botanists. As a result of these exchanges, specimens collected by Guadagno can be also found in numerous Herbaria like MA, L, SPA, P (a list of all the Herbaria where we were able to track specimens collected by Guadagno is available in Suppl. material 1: table S2). PI-GUAD is accompanied by an index in three volumes compiled by Guadagno, and containing the list of taxa and the corresponding number of specimens annotated into two columns with the heading “G” and “D”, meaning those collected by Guadagno and those donated by other botanists, respectively. Also, Guadagno left a card index, now housed at the Herbarium of Naples [code NAP according to Thiers (2020, and onwards)], containing meticulous taxonomic, nomenclatural and biogeographical annotations about the species he encountered during his more than 200 field trips (Fontanella 2008).

PI-GUAD also preserves original material for taxa described by other botanists (accepted names in square brackets), like *Draba longirostra* var. *guadagnoii* O.E.Schulz (1927; see also Mazzola et al. 2014), *Viola splendida* W.Becker [= *Viola aethnensis* (Ging. & DC.) Strobl subsp. *splendida* (W.Becker) Merxm. & Lippert] (Becker 1902; Portal to the Flora of Italy 2023), *Hieracium sartorianum* var. *lucanicum* Arv.-Touv. [= *Hieracium hypochoeroides* S.Gibson subsp. *lucanicum* (Arv.-Touv.) Di Grist., Gottschl. & Raimondo] (Guadagno 1909; Di Gristina et al. 2015), *Centaurea ×cavarae* Guadagno ex Del Guacchio, Cennamo & P.Caputo (Del Guacchio et al. 2020a), and it has been an important source of data for floristic and taxonomic studies (Ricciardi 1998; Andolfato et al. 2002; Del Guacchio and Caputo 2008; Gottschlich 2009; Peruzzi et al. 2013, 2015a, 2019a; Roma-Marzio et al. 2015, 2017a, 2018; Conti et al. 2019; Del Guacchio et al. 2020b; Gargano et al. 2023).

For all these reasons, at the end of 2018, the Botanic Museum of the University of Pisa started a project in collaboration with the Department of Biology, focused on the digitization of all the vascular plant specimens of the Herbarium of Michele Guadagno. The aim of this paper is to illustrate the process of digitization of the Herbarium Guadagno, which made the collection freely accessible to botanists. The digitization process allowed to extract and summarise information about collectors, localities, collection dates, and taxonomy of the specimens, including nomenclatural types.

Materials and methods

PI-GUAD, stored inside four cabinets of 310 × 270 × 58 cm and another small cabinet of 110 × 68 × 50, is composed by 547 packages of vascular plants, of which 501 organised according to the systematic criterion introduced by Durand (1888), and other 39 organised according to collection localities or correspondents of Michele Guadagno (Fig. 1). Concerning the seven packages of pteridophytes, they were reassembled by extracting the specimens that were previously interspersed in the general Herbarium of Pisa. PI-GUAD also includes specimens of non-vascular plants, algae, fungi, and lichens, not considered in this study.

Prior to the acquisition of the images, all the specimens lacking a scientific name were at least identified at the genus level. Then, a unique identification number (ID hereafter) was stamped on each specimen.

The digitization procedure followed two distinct steps: 1) acquisition of high-resolution digital images and 2) label data (metadata) acquisition.

Concerning the image acquisition, each specimen was scanned using a Bookeye 4 Professional planetary scanner producing a 600 dpi and 24-bit color depth image in .tiff format. Each scan was accompanied by a metric and colorimetric reference. After the acquisition, each image was renamed using the ID assigned to the specimen and uploaded on a web server of the University of Pisa. To produce a backup copy, all the images were also converted in .jpeg format and stored in physical hard disks preserved at the Botanic Museum.

Metadata were entered into the online database Virtual Herbaria JACQ (<http://www.jacq.org/>), a continuously developing consortium of virtual herbaria located in Vienna (Bräuchler et al. 2021). Today JACQ is used by 53 institutions in 18 countries worldwide, mainly in Europe, with a total of approximately 1,400,000 records covering the entire globe and constituting an important source for collection data portals such as GBIF and BioCAsE (Borsch et al. 2020). One of the strengths of this free project is the presence of a query system which allows searching simultaneously all the Herbaria that are partners of the project. The Virtual Herbarium JACQ allows for structured registration of metadata, georeferencing of each specimen, and automatic linking of these data to digital images. In addition, it is possible to download a .csv file containing all the metadata of the recorded specimens, as well as a .kml file containing the geographical data, useful for GIS-based analyses. By means of the .csv file produced by JACQ we also set up a personalized Virtual Herbarium of the Botanic Museum (<https://erbario.unipi.it/>), that mirrors the data inserted into JACQ.

To detect original material and type specimens preserved in the Herbarium, we analysed the literature that directly cites specimens from PI-GUAD, and investigated the protologue of all those taxa whose author(s) were contemporaries of Guadagno or were the collector of the specimens, or when the labels bear annotations like “*sp. nov.*”, “*var. nov.*” or similar. Furthermore, to trace duplicates of types, we also analysed literature with massive data about typification of taxa described between the end of XIX and the first decades of XX century, or described by authors which were collectors in the Herbarium Guadagno (Bartolucci et al. 2013; Peruzzi et al. 2015b; 2019b; Galasso et al. 2018a; Vogt et al. 2018; Raptis et al. 2019; Del Guacchio et al. 2020a, 2020b; Reich et al. 2021). All the type specimens detected were also uploaded in the JSTOR Global Plants, the world’s largest database of digitized plant specimens (JSTOR Global Plants 2019).



Figure 1. Two of the four cabinets where is preserved the Herbarium of Michele Guadagno (PI-GUAD) at the Botanic Museum of the University of Pisa (a), one of the 547 packages of the collection (b), and an example of a specimen collected by Guadagno (c).

At the end of the digitization process, each specimen was marked with a stamp (“D”) to indicate that the digitization process was completed.

Concerning the georeferentiation, coordinates were inferred from the geographical information reported on the label, which range from very precise indications of the locality to very generic indications of a wide geographic area. For collectors, we referred to the Harvard University Herbaria Index of Botanists (https://kiki.huh.harvard.edu/databases/botanist_index.html) as a guide for handwritings hard to decipher. When possible, we inferred the collectors based on the handwriting’s recognition if not explicitly reported (e.g., the many specimens collected by Guadagno).

For the analysis of the plant families, we updated the default taxonomic circumscription used by JACQ according to PPG I (2016) for ferns and fern allies, to Christenhusz et al. (2011) for gymnosperms, and to APG IV (2016) for angiosperms.

Since many specimens are represented or accompanied by drawings, illustrations, manuscripts, correspondences, publications, and other documents, these specimens were marked as “.doc” in the “annotations” field of the database, to facilitate their search.

All the statistical analyses and graphs were carried out by means of PAST version 4.11 (Hammer et al. 2001; Hammer 2022), whereas QGIS 3.10 software was used to draw all the maps.

Results

The number of sheets preserved in PI-GUAD amounts to 44,345, to which a further 65 not digitized sheets, lacking label, should be added. The number of specimens amounts to 41,314. The reason for this discrepancy lies in the admixture of specimens in some sheets, and in the occurrence of specimens composed by two or more sheets. Among the digitized specimens there are also 16 sheets bearing 66 labels of specimens destroyed during the flood of Arno River in 1944.

From a taxonomic point of view, the Herbarium includes pteridophytes (833 specimens corresponding to 2% of the collection), gymnosperms (177; 0.4%),

non-eudicot dicots (114; 0.3%), monocots (6,730; 16.3%), and eudicots (33,457; 81%). Totally, 255 families and 2,380 names at the genus level (including names currently considered as synonyms) can be found in PI-GUAD. The ten most represented families are Asteraceae (5,970; 14.5%), Fabaceae (3,981; 9.6%), Poaceae (3,347; 8.1%), Lamiaceae (2,260; 5.5%), Caryophyllaceae (2,070; 5%), Brassicaceae (1,794; 4.3%), Apiaceae (1,524; 3.7%), Rosaceae (1,330; 3.2%), Ranunculaceae (1,179; 2.9%), Plantaginaceae (1,171; 2.8%). The most represented names at genus level are: *Hieracium* (701; 1.7%), *Carex* (677; 1.6%), *Trifolium* (668; 1.6%), *Centaurea* (646; 1.6%), *Silene* (559; 1.4%), *Vicia* (534; 1.3%), *Ranunculus* (518; 1.3%), *Galium* (423; 1.0%), *Viola* (422; 1%), *Euphorbia* (404; 1%). A complete list of all families, genera and relative number of specimens are available in the online Suppl. material 1: table S3.

From the geographical point of view, although most of the specimens were collected in Europe (91.8%), there are specimens from all the other continents: Africa (4.3%), Asia (1.8%), North America (1.8%), South America (0.2%), and Oceania (0.7%). Overall, there are 90 countries in which at least one specimen was collected: Italy is, of course, the most frequent (24,372; 59.1%), followed by France (2941; 7.1%), Spain (1,618; 3.9%), Germany (1,299; 3.2%), and Greece (1,234; 3%) (Fig. 2a). A complete list of all geographic data is available in the online Suppl. material 1: table S4. As concerns the Italian regions, Campania is the most represented (13,027; 54.2%), followed by Abruzzo (2,628; 10.9%), Calabria (1,800; 7.5%), Veneto (1,042; 4.3%), and Toscana (820; 3.4%) (Fig. 2b). A focus on the specimens collected by Guadagno shows that he collected plants mainly in Campania (12,482), followed by Abruzzo (2,274), Calabria (1,611), Basilicata (365), Lazio (141), Puglia (83), Molise (36), Lombardia (27) and, out of Italy, in Switzerland (17) (Fig. 3).

All the digitized specimens cover a time span of 99 years, from 1830 (48 years before the birth of Guadagno) to 1929 (Fig. 4) (see discussion for further details), whereas the specimens collected by Guadagno range between 1889 and 1928. The variation of the collection effort through years is significantly different between Guadagno (median year 1909; range 39) and the other collectors (1904; 99) (Mann-Whitney test $p < 0.01$).

Besides Guadagno, who collected 42% of the specimens, another 1,103 collectors are present. Nonetheless, 319 specimens (1%) do not report any collector, while for other 90 specimens (0.2%) we were unable to decipher the collector's name. Among the other collectors, the most frequent are A. Noblet (France) with 779 specimens (1.9%), C. Marchesetti (Italy, Slovenia, and Croatia) with 680 specimens (1.6%), W. Behrendsen (Germany, Bosnia and Herzegovina, Poland, Croatia, Montenegro) with 679 specimens (1.6%), C. Bicknell (Italy and France) with 632 specimens (1.5%), J. M. Wood (South Africa) with 561 specimens (1.4%), S. Sommer (Italy) with 539 specimens (1.3%), and G. Rigo (Italy) with 514 specimens (1.2%). Considering only the specimens collected in Italy, there are 217 collectors besides Guadagno, among them the most frequent are: G. Rigo (512 specimens), S. Sommer (497), C. Bicknell (391), A. Fiori (374), A. Béguinot (369), O. Gavioli (346), A. Mazza (336), L. Grande (324), C. C. Lacaita (305), and R. Pampanini (303). A complete list of all collectors and relative data is available in the online Suppl. material 1: table S5.

PI-GUAD hosts 4,291 specimens linked to 133 different series of exsiccata; among them the most represented are "Flora Italica Exsiccata series I" by A. Fiori, A. Béguinot and R. Pampanini (1,072 digitized specimens, 28 of which collected

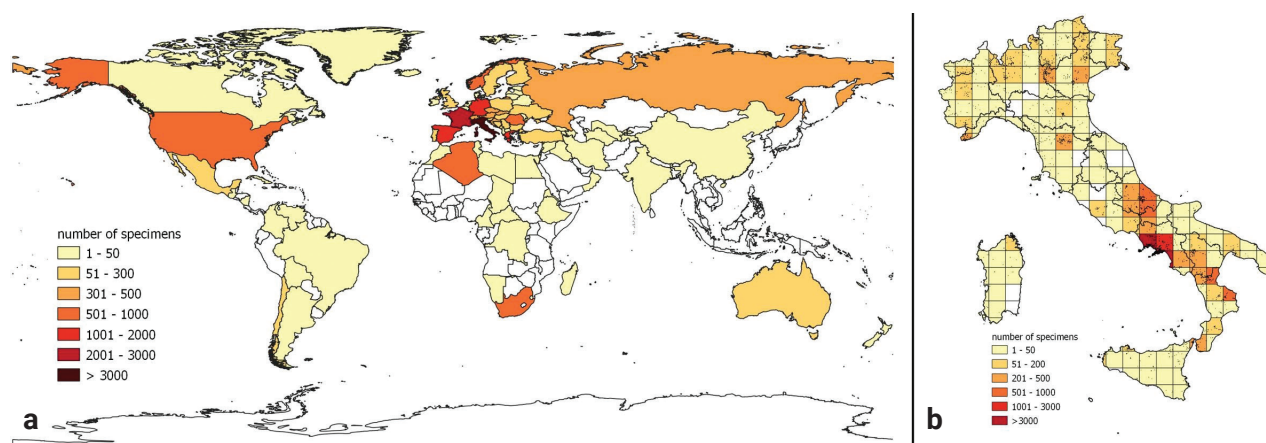


Figure 2. Global geographic coverage of the specimens preserved in the herbarium of Michele Guadagno (PI-GUAD) at the Botanic Museum of the University of Pisa (a), and focus on specimens collected in Italy (b). The number of specimens in Italy is calculated on a grid of 50×50 km.

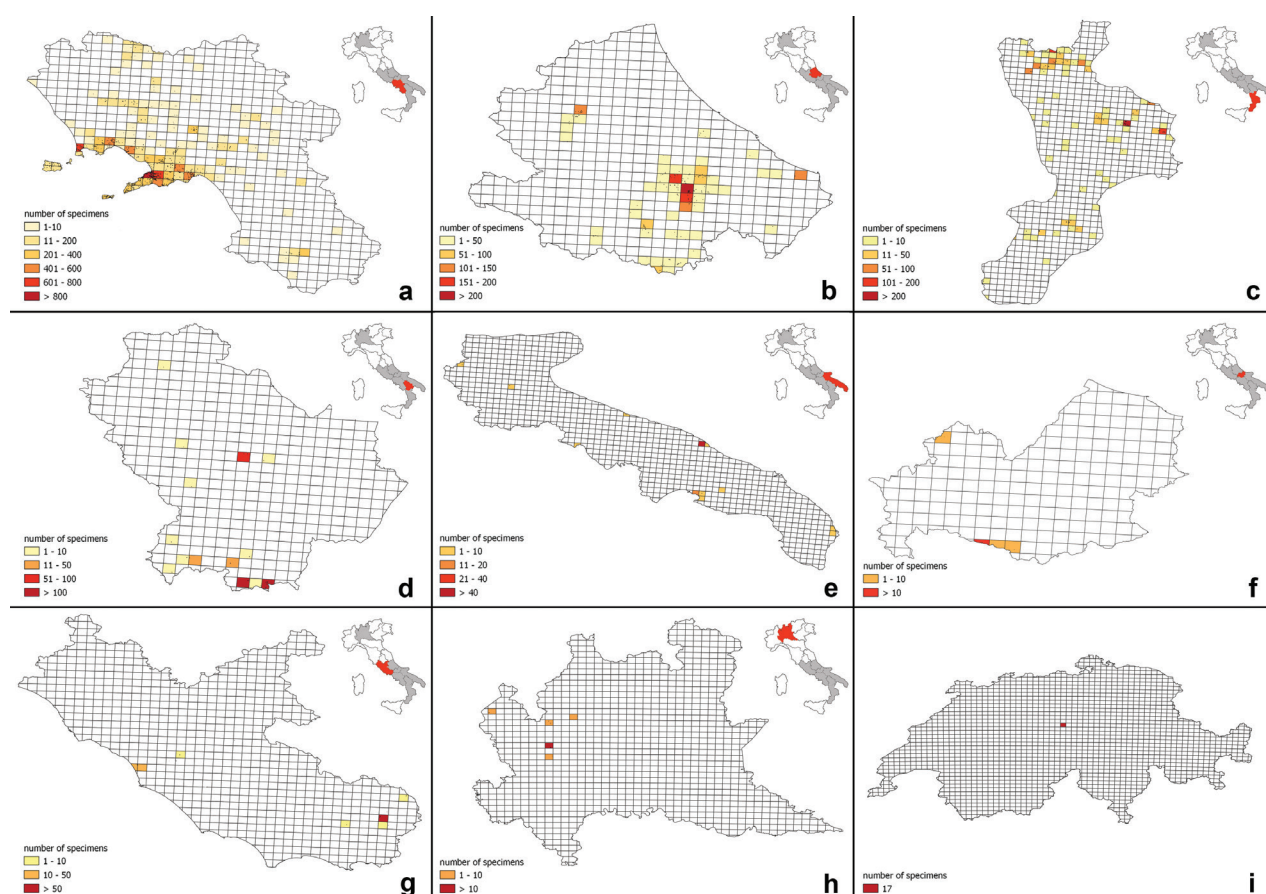


Figure 3. Geographic coverage of the specimens preserved in the Herbarium of Michele Guadagno (PI-GUAD) at the Botanic Museum of the University of Pisa and collected by Michele Guadagno in Italy (a Campania b Abruzzo c Calabria d Basilicata e Puglia f Molise g Lazio h Lombardia) and Switzerland (i). The number of specimens is calculated on a grid of 5×5 km.

by Guadagno himself) and “series II” by A. Fiori and A. Béguinot (1,154, 30 of which collected by Guadagno), “Herbarium Graecum Normale” by T. von De Heldreich (258), “Plantes d’Espagne” by F. Sennen (277), “Plantes d’Espagne” by Elisée Réverchon (176), and “Herbarium Normale” by I. Dörfler (85). A complete list of all the series of exsiccata is available in the online Suppl. material 1: table S6.

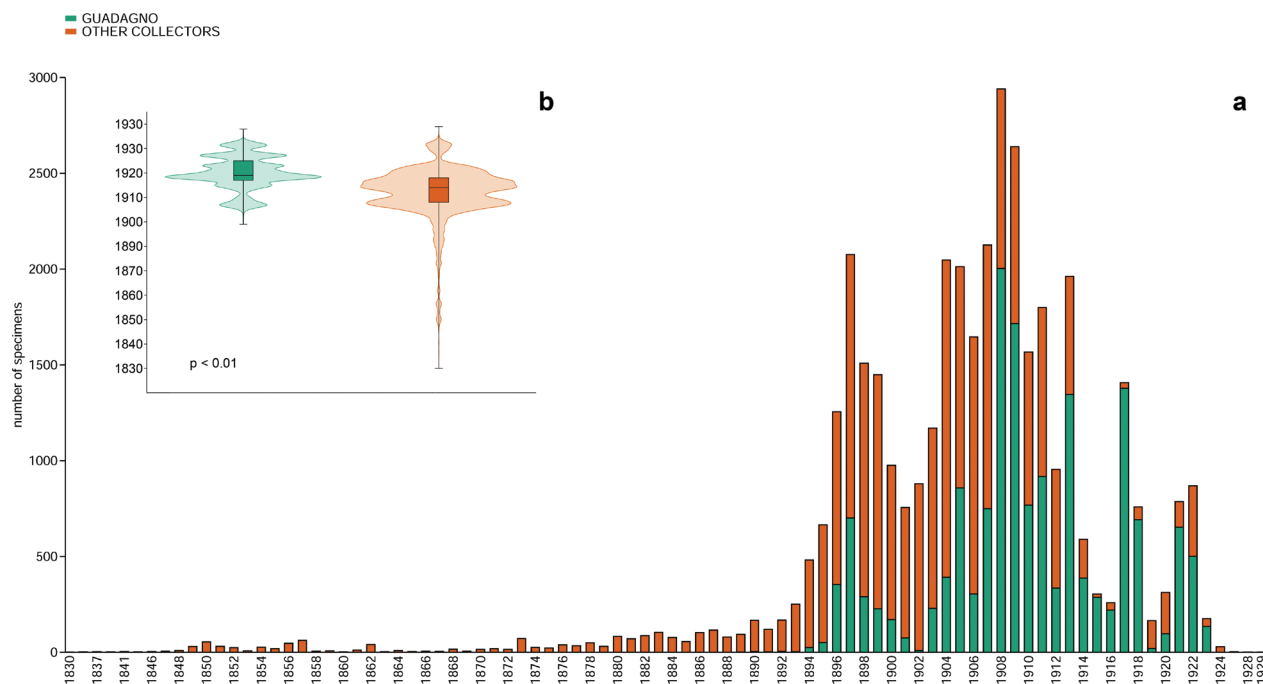


Figure 4. Histograms showing temporal coverage of specimens preserved in the Herbarium of Michele Guadagno (PI-GUAD) at the Botanic Museum of the University of Pisa (a). Boxplots show the differences in the collection year among specimens collected by Guadagno and other collectors (b).

We traced 134 sheets bearing plants associated with documents or only documents. In particular, we found 77 drawings made by Guadagno or by his corresponding authors, 16 copies of publications and 14 copies of published iconographies. All these sheets can be found in JACQ database or in the Virtual Herbarium of the Botanic Museum by typing “_doc” in the field “annotation”.

After the digitization process, we traced 44 specimens that can be considered original material for several names not yet typified, and another 62 type specimens, of which one is a holotype, 15 are isotypes, four are lectotypes, 16 are isolectotypes, 25 are syntypes, and one is an isoeotype.

Discussion

The digitization of PI-GUAD revealed much information hidden in the cabinets, confirming the importance of this procedure to study large natural collections (James et al. 2018).

Considering only the first 501 packages of the Herbarium, which include the material organized according to a systematic criterion, we surveyed 40,748 herbarium sheets, 4,100 more than those previously counted by Chiarugi (1950).

The number of plant families represented in PI-GUAD covers 58% of the 452 families of vascular plants of the world, and the four most represented families in the Herbarium (Asteraceae, Fabaceae, Poaceae, and Lamiaceae) correspond, in this precise order, to the four most represented families at global scale (Christenhusz and Byng 2016).

Besides Italy, which is the country most represented, the geographic data at European scale are considerable, providing useful information for research on plant diversity in this continent, as already emerged by other studies using data from PI-GUAD (Janković et al. 2019). Focusing on Italy, the results of the digitiza-

tion confirmed that most of the specimens were collected by Guadagno and his correspondents in the southern regions, and particularly in Campania (Amadei et al. 2013; Roma-Marzio et al. 2017b). This precious source of data is confirmed also by several publications of floristic records based on specimens preserved in PI-GUAD (Badino and Peruzzi 2009; Del Guacchio 2010; Bartolucci and Santangelo 2015), that contributed to compile the updated checklist of the vascular floras native and alien to Italy (Bartolucci et al. 2018; Galasso et al. 2018b).

PI-GUAD also hosts specimens of taxa that are currently extinct or, according to IUCN criteria (IUCN 2022), evaluated Endangered or Critically Endangered in Italy (Rossi et al. 2013; 2020). An emblematic example is represented by the single specimens of *Ipomoea imperati* (Vahl) Griseb. (under the name *Convolvulus imperati* Vahl; PI nr. 057590), collected by Giulio Avellino on the Ischia Island and donated by Giuseppe Antonio Pasquale (1820–1893) to Guadagno. This species was considered extinct in Campania until the recent rediscovery by Bartolucci et al. (2022) near Naples. The specimen preserved in the Herbarium therefore is a case of useful source of genetic material or propagules for driving practical in situ and ex situ conservation actions (Albani Rocchetti et al. 2021), or for effective recovery of genetic variation and structure of lost population in wild, as already investigated for this species (Cennamo et al. 2013). Another case is represented by the specimen of *Ekokochia saxicola* (Guss.) Freitag & G. Kadereit (under the name *Kochia saxicola* Guss.; PI nr. 038612) collected by Guadagno on the Ischia Island. This species, currently evaluated as Endangered in Italy (Rossi et al. 2013), is only known for three populations, two located in Capri Island and Palinuro in Campania, one in Strombolicchio islet in the Aeolian Archipelago in Sicily, whereas the population from Ischia is currently extinct (Strumia et al. 2021).

As concerns the collectors, although 42% of the specimens were collected by Guadagno, the high number of other collectors and the different series of exsiccata testify to the extensive exchanges among Guadagno and other botanists from all over the world (Trotter 1930; D’Erasmus 1931). This is also testified by the 34 letters we found intermixed with specimens. Another evidence of Guadagno relationships with other prominent botanists throughout Europe is represented by the revisions of many specimens sent to specialists of certain genera or groups of plants, such as Jean-Maurice Casimir Arvet-Touvet (1841–1913) for *Hieracium*, Émile Burnat (1828–1920) for *Rosa*, Eduard Hackel (1850–1926) for *Poaceae*, Hermann Christ (1833–1933) for pteridophytes (see also Marchetti 2021).

The first specimen collected by Guadagno is a plant of *Fallopia convolvulus* (L.) Á. Löve (under the name *Polygonum convolvulus* L.) found in Naples, in July 1889 when he was only eleven years old (PI nr. 024486), the label that reports “*Polvica (Capodimonte) (Prop. Perretti)*” probably refers to an ancient farmhouse near Chiaiano (E. Del Guacchio pers. comm.) property of the family Perretti, surname of the mother of Guadagno Rosa Perretti (D’Erasmus 1931). The last specimen collected by Guadagno (PI nr. 033129) is a plant of *Hyparrhenia hirta* (L.) Stapf, from Mt. Barbaro (Campania) in 1928, two years before his death. The span between the dates of these two specimens covers 75% of the life span of Michele Guadagno, testifying that his passion for natural science maintained until the end of his days (Trotter 1930). The specimens collected by the other collectors cover a wider temporal range and are generally older with respect to those collected by Guadagno. He accumulated a fair number of specimens and had the possibility to exchange some of them with older botanists that started their activities earlier.

The analysis of the collection data revealed some biases in the collection activities made by Guadagno, particularly between 1919 and 1920, when the collections were reduced with respect to other periods, probably because this was the busiest time for Guadagno as an engineer (Trotter 1930). Another significant reduction can be seen between 1915 and 1918 considering the specimens collected by his correspondents, probably due to World War I, a trend also highlighted in other Herbaria (Daru et al. 2017).

Among the specimens collected before the birth of Michele Guadagno, those collected by three notorious Italian botanists like Giovanni Gussone (1787–1866), Filippo Parlatore (1816–1877), and Antonio Bertoloni (1775–1868) are of particular interest. There are seven specimens collected by Gussone, almost all of them with labels handwritten by Loreto Grande, a friend of Guadagno and curator of the Naples Herbarium between 1921 and 1942. In these years, Grande sent many specimens to various botanists for revision (Santangelo et al. 1995) including Guadagno, who was probably unable to return these specimens to NAP because of his sudden death. This hypothesis is also supported by considering that in those years the director of the Botanical Garden of Naples was Fridiano Cavara (1857–1929), a point of reference and friend of both Guadagno and Grande. Two of the specimens collected by Gussone refer to taxa that he described (*Asperula nitens* Guss. PI nr. 061806, and *Sonchus nymanii* Tineo & Guss. PI nr. 035943) and collected in their type localities (Gussone 1843; Del Guacchio and Caputo 2005), whereas the specimen of *Alyssum hispidum* Loscos & J.Pardo (PI nr. 034437) was collected during his journey in Spain (Trotter 1948). In the case of Bertoloni, we traced one specimen (PI nr. 052728) collected in the Botanical Garden of Bologna, where Bertoloni served as Praefectus from 1817 to 1869. It is not clear why this specimen ended up in the hands of Guadagno, but we can hypothesize that Federico Delpino (1833–1905), who was the Praefectus at Bologna's Garden from 1884 to 1894 (Mossetti 2021), and then moved to the Botanical Garden of Naples until 1905 (Catalano 1958), might have acted as the intermediary of this passage. Alternatively, we may infer that this specimen was sent by Bertoloni to Tenore or Gussone (as many others in NAP), and only later came into the hands of Guadagno, who was unable to return them because of his sudden death. The presence of specimens like these may be difficult to trace by researchers. Therefore, the digitization activities, including those concerning private or separate collections, can be very useful to locate specimens otherwise possibly considered as lost.

Among the 62 type specimens traced in the Herbarium, there are 15 types of taxa currently accepted at the original or different rank: an isotype of *Adonis flammea* Jacq. subsp. *cortiana* C.H.Steinb. (PI nr. 015061, Steinberg 1971); a lectotype of *Hieracium sartorianum* Boiss. & Heldr. var. *lucanicum* Arv.-Touv. (PI nr. 019816, Di Gristina et al. 2015), isolectotypes of *Dianthus tarentinus* Lacaita (PI nr. 040642, Bacchetta and al. 2010), *Globularia neapolitana* O.Schwarz (PI nr. 013730, Del Guacchio et al. 2020a), *Muscari longifolium* Rigo (PI nr. 025613, Frattini et al. 1996; Galasso et al. 2018a), *Nepeta heldreichii* Halácsy (PI nr. 039187, Baden 1987; Reich et al. 2021), *Polygala flavescens* DC. var. *maremmana* Fiori (PI nr. 030515, Arrigoni, 2014), *Polygala alpestris* Rchb. var. *valdarnensis* Fiori (PI nr. 051946, Arrigoni 2014), *Viola mercurii* Orph. ex Halácsy (PI nr. 051514, Reich et al. 2021); syntypes of *Centaurea laureotica* Heldr. ex Halácsy (PI nr. 012698, Reich et al. 2021), *C. tuntasia* Heldr. ex Halácsy (PI nr. 012866, Reich et al. 2021), *Helianthemum jonium* Lacaita & Grosser (PI nr. 051105), *Hieracium halacsyi* Heldr. ex Halácsy (PI nr. 019507, Reich

et al. 2021), *Poa timoleontis* Heldr. ex Boiss. (PI nr. 029594, Reich et al. 2021), and an isoeotype of *Cirsium lobelii* Ten. (PI nr. 013207, Del Guacchio et al. 2021).

We also traced original materials of four taxa described by Guadagno himself: *Bromus erectus* Huds. var. *stabianus* Guadagno (Guadagno 1913), *Catapodium liliaceum* (Huds.) Link f. *erectum* Guadagno (Guadagno 1913), *Cerastium hirsutum* Ten. var. *pumilum* Guadagno (Guadagno 1926) and *Rumex pseudoamplexicaulis* Guadagno (Guadagno 1926). In addition, Del Guacchio and al. (2020a) recently described the hybrid *Centaurea ×cavarae* Guadagno ex Del Guacchio, Cennamo & P.Caputo based on a hypothesis that M. Guadagno reported on the label of the holotype PI nr. 034717 about the putative hybrid origin of this plant between *Centaurea deusta* Ten. and *C. montaltensis* (Fiori) Peruzzi (see also De Luca et al. 2023).

The project carried out on the Herbarium Guadagno is part of the ongoing process that was started at the Herbarium of Pisa, currently focused on the digitization of type specimens, historical collections, revised specimens and all the new acquisitions that are being entered in the Herbarium (Astuti et al. 2019; Roma-Marzio et al. 2020; Maccioni et al. 2023). This activity has highlighted the high value of PI-GUAD in terms of geographic and temporal coverage, as well as for the precious material linked to type specimens, and for the historical information linked to documents, iconographies and original drawing found in the Herbarium. The study of PI-GUAD, associated with his card index, will be fundamental for studies concerning the flora of southern Italy and particularly of Campania region. In this framework, although the Herbarium Guadagno represents a small portion of the estimated 400 million specimens deposited across about 3,000 herbaria worldwide, its digitization significantly contributes to the emergence of the so-called open access global metaherbarium, that will be the crucial for guiding the exploration, illumination, and prediction of plant biodiversity change in the Anthropocene, and will facilitate the rapid exploration, synthesis, and dissemination of accurate biodiversity data at unprecedented scales (Davis 2023).

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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

LP and FRM conceived the study; FRM, SM, GA, RV and LA contributed to the deciphering of critical labels, the georeferentiation of the localities, and the standardisation of

entry fields in the database; FRM, SM, DD, NM and FP digitized all the specimens; FRM, SM and GA revised the final database; FRM and GA wrote the paper; LP supervised the final version of the manuscript; all the authors revised the final version.

Author ORCIDs

Francesco Roma-Marzio  <https://orcid.org/0000-0002-2184-0311>

David Dolci  <https://orcid.org/0000-0002-3043-9757>

Giovanni Astuti  <https://orcid.org/0000-0001-5790-3516>

Lorenzo Peruzzi  <https://orcid.org/0000-0001-9008-273X>

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 data

Authors: Francesco Roma-Marzio, Simonetta Maccioni, David Dolci, Giovanni Astuti, Nicoletta Magrini, Federica Pierotti, Roberta Vangelisti, Lucia Amadei, Lorenzo Peruzzi

Data type: xlsx

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Lagerstroemia stenophylla (Lythraceae), a new species from China

Bao-Huan Wu^{1,2,3}, Xing Hu^{1,2,3}, Wen-Hui Tu^{1,2,3}, Wei Wang^{1,2,3}, Se-Ping Dai^{1,2,3}

¹ Guangzhou Institute of Forestry and Landscape Architecture, Guangzhou 510405, China

² Guangzhou Horticultural Plant Germplasm Resource Nursery, Guangzhou 510405, China

³ Guangzhou Collaborative Innovation Center on Science-Tech of Ecology and Landscape, Guangzhou 510405, China

Corresponding author: Se-Ping Dai (daiseping@126.com)

Abstract

Lagerstroemia stenophylla, a new species from southeastern Shaanxi Province and northwestern Hubei Province of China is described. Morphologically, *L. stenophylla* resembles *L. subcostata*, but it differs in having 4-angular, subulate branchlets, elliptic-lanceolate, or narrowly elliptic leaves, and relatively larger flowers.

Key words: China, crape myrtle, Flora, new species

Introduction

Lagerstroemia L. (Lythraceae) is a genus of trees or shrubs with simple leaves, terminal panicles of showy flowers, and woody capsule fruits (Qin and Graham 2007, De Wilde and Duyfjes 2014). *Lagerstroemia* is one of the most popular ornamental flowering trees in China, producing showy flowers in summer. One such is the *Lagerstroemia indica* L., also known as Bairihong (百日红) in Chinese, which can bloom for up to 100 days, and is widely cultivated in China (Wang et al. 2022). In taxonomy, the monograph of this genus was completed by Koehne (1903) and fully revised by Furtado and Srisuko (1969), accepting 53 species. Thereafter, regional taxonomic revisions (Lee and Lau 1983; Hewson 1990; Qin and Graham 2007; De Wilde and Duyfjes 2013, 2014, 2016) and some sporadic taxonomic works (Zhou et al. 2004; Gu et al. 2012; Gu et al. 2015; Deepu and Pandurangan 2017; Pham et al. 2017; De Wilde and Duyfjes 2019) were published successively. In these works, many species were reduced to synonyms, and many new species were described. According to our statistics, the genus *Lagerstroemia* currently comprises about 51 species (excluding subspecies and varieties).

In China, there are 15 *Lagerstroemia* species that have been documented in “Flora of China” (Qin and Graham 2007). *Lagerstroemia parviflora* Roxb. was recorded in Yingjiang County of southern Yunnan Province (Yuan 1983), and *L. minuticarpa* Debberm. ex P.C.Kanjilal was recorded in Motuo County of Tibet Autonomous Region (Tang 1986), but neither of them was included in “Flora of China”. Recently, two new species of China were discovered, including *L. densa* C.H.Gu & D.D.Ma (Gu et al. 2015) from Guangxi Zhuang Autonomous Region and *L. menglaensis* C.H.Gu, M.C.Ji & D.D.Ma (Gu et al. 2012) from Yunnan Province.



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During our examination of *Lagerstroemia* specimens, some collections from south-eastern Shaanxi Province of China, such as Z.B. Wang 16543 from Shanyang County and B.Z. Guo 2225 from Xunyang County, were found likely misidentified as *L. subcostata* Koehne. While morphologically similar, these specimens have conspicuously smaller, narrower leaves. A more extensive examination of specimens and literature survey (Koehne 1903; Furtado and Srisuko 1969; Ho 1974; Lee and Lau 1983; Fu 2002; Zhou et al. 2004; Qin and Graham 2007; Gu et al. 2012; De Wilde and Duyfjes 2013, 2014, 2016; Li and Li 2013; Gu et al. 2015; Liu et al. 2022) were therefore conducted. Field investigation was also conducted, and more specimens were collected. The result of these studies confirmed a new *Lagerstroemia* species from Shaanxi and Hubei Provinces of China, which is described below, bringing the total numbers of species of *Lagerstroemia* to 52.

Material and methods

Morphological descriptions were based on observations of the living plants in the field and dried specimens in herbaria. Measurements were conducted manually with rulers or using Digimizer version 4.6.0 (MedCalc Software, Mariakerke, Belgium), and a total of 53 collections were measured. The voucher specimens were deposited in Guangzhou Institute of Forestry and Landscape Architecture, and the herbarium of South China Botanical Garden (IBSC).

Taxonomic treatment

***Lagerstroemia stenophylla* B.H.Wu, X.Hu & S.P.Dai, sp. nov.**

urn:lsid:ipni.org:names:77328633-1

Fig. 1

Type. CHINA. Shaanxi: Shangluo, Jinsixia Town, Xinglong Country, in ravine, on rocky slopes. 33°26'36.14"N, 110°32'51.13"E, 387 m a.s.l., 6 June 2023 (fl.), B.H. Wu & W.H. Tu Lg202334 (Holotype: IBSC!; isotypes: Herbarium of Guangzhou Institute of Forestry and Landscape Architecture!).

Diagnosis. *Lagerstroemia stenophylla* is morphologically similar to *L. subcostata* Koehne, but distinguished by its branchlets 4-angular, sometimes subalate, leaves elliptic-lanceolate, narrowly elliptic, leaf apex acute, leaf base cuneate, flowers 2.5–3 cm in diameter.

Description. Shrubs or small trees ca. 0.5–3 m tall. Bark reddish brown, longitudinally fissured and slightly peeling to reveal the inner bark when mature; branchlets scabridulous to glabrous, 4-angular, sometimes subalate. Leaves mostly alternate, or subopposite; petiole 1–3 (4) mm long, densely scabridulous to glabrous; leaf blade herbaceous, margin entire, lanceolate to elliptic-lanceolate, rarely ovate or obovate-oblongate, 2–6 (7) × 0.7–2 (2.3) cm, base cuneate, apex acute, sometimes obtuse, rarely apiculate, abaxially pale green, scabridulous (especially along midrib and later veins) to glabrous, adaxially green, sparsely scabridulous to glabrous, lateral veins 4–7 pairs. Inflorescences paniculate, terminal or axillary; panicles (2) 4–7 cm long, densely scabridulous. Flowers sessile or subsessile; flower buds turbinate to subglobose (excluding pseudopedicels). Calyx tubes (excluding pseudopedicels) cup-shaped,

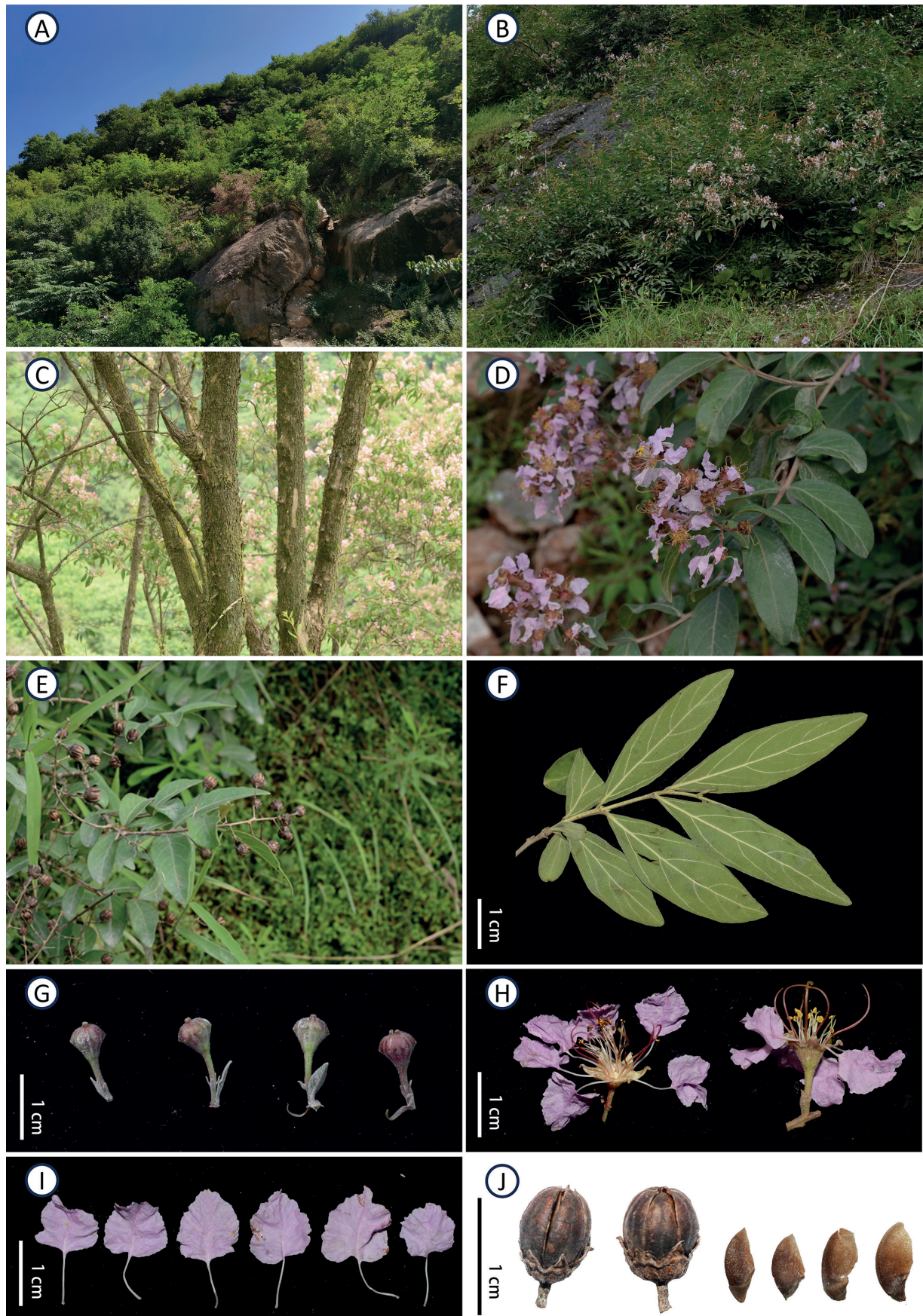


Figure 1. Plate of *Lagerstroemia stenophylla* **A** habitat **B** flowering individuals **C** stems **D** flowering branch **E** fruiting branch **F** leaves **G** flower buds **H** flowers **I** petals **J** capsules and seeds.

3.3–4.2 mm long, outside densely scabridulous to glabrous, with 10–12 distinctly ribs or dark veins (sometimes not obvious), inside glabrous, with glabrous annulus (sometimes absent) in the throat, lobes 6, sometimes 5, triangular, 1–2.3 mm × 1–2.3 mm, erect, epicalyx absent, pseudopedicel 2–9 mm long; petals 6, crumpled, oblong, suborbicular or ovate, base cuneate to broadly cuneate, rounded, or sometimes subcordate, apex obtuse or rounded, 10–18 mm with claws 3–8 mm long; stamens 20–28, dimorphic, with 6 stamens longer (ca. 15 mm long), thicker and red-brown in color, the remaining stamens are shorter (ca. 7 mm long), thinner and white in color, filaments glabrous; ovary glabrous, styles 10–14 mm long, glabrous, stigmas small. Capsules globose to oblong, 6–8 mm long, 4.5–6 mm in diameter, loculicidally dehiscent, 4–7-valved. Seeds ca. 6 mm long including wing.

Phenology. Flowering from May to June, and fruiting after July and fruits persist through winter.

Distribution and habitat. *Lagerstroemia stenophylla* is hitherto known from Baihe County, Danfeng County, Shanyang County, Shangnan County, Xunyang County, Zhashui County, Zhen'an County of south-eastern Shaanxi Province and Baokang County, Fang County and Shiyan City of north-western Hubei Province (Fig. 2). It grows on rocky slopes in ravine, at 290–770 m elevation.

Etymology. The epithet of the new species refers to its narrow leaf blade.

Vernacular name. The Chinese name of the new species is here given as 狭叶紫薇 (xiá yè zǐ wēi).

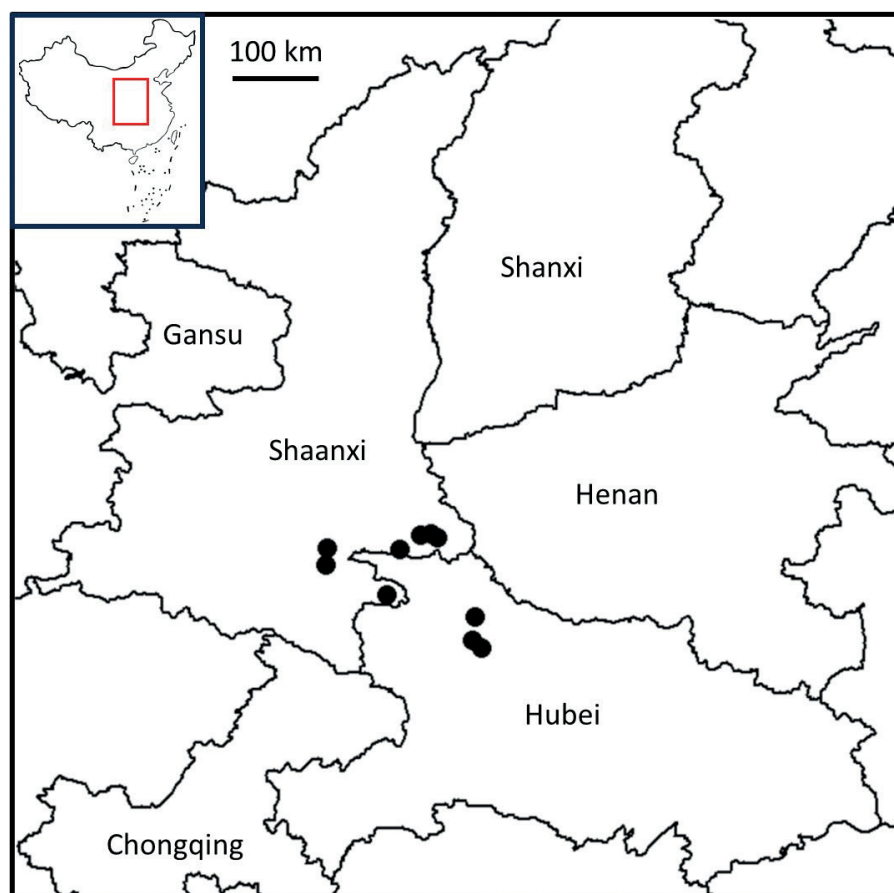


Figure 2. Distribution of *Lagerstroemia stenophylla*.

Note. *Lagerstroemia stenophylla* is formerly misidentified as *L. subcostata* (Li and Li 2013). Morphologically, *L. stenophylla* and *L. subcostata* share many similar characters, including calyx tubes cup-shaped, with ca. 12 ribs or darkened veins, epicalyx absent, and sepals adaxially glabrous, stamens less than 30, leading to misidentify *L. stenophylla* as *L. subcostata*, using the Keys of “Flora Reipublicae Popularis Sinicae” (Lee and Lau 1983) and “Flora of China” (Qin and Graham 2007). However, *L. stenophylla* is a shrub or small tree with conspicuously smaller, narrower leaves and larger flowers, differing distinctly from *L. subcostata*. Detailed morphological comparisons among *L. stenophylla* and its relatives are presented in Table 1.

Additional specimen examined. CHINA. Shaanxi Province: Baihe County, Maoping, 29 September 1969, *Vegetation Team 541* (WUK); *ibid.*, 8 June 2023, *B.H. Wu and W.H. Tu Lg202378, Lg202379, Lg202380, Lg202381*; Danfeng County, Tumen Town, 6 June 2023, *B.H. Wu and W.H. Tu Lg202329, Lg202331*; Danfeng County, Zhulinguan Town, Baijiawan, 6 June 2023, *B.H. Wu and W.H. Tu Lg202332*; Shanyang County, Zhaochuan, 1 July 1960, *Huashan Team 0206* (IBSC); Shanyang County, Manchuanguan, 17 September 1952, *Z.B. Wang 16543* (KUN, PE, WUK); *ibid.*, 1 May 1964, *J.X. Yang 2456* (WUK); *ibid.*, 19 May 2011, *S.F. Li et al. 15016* (XBGH); *ibid.*, 5 June 2023, *B.H. Wu and W.H. Tu Lg202312, Lg202313, Lg202314, Lg202315, Lg202316, Lg202317, Lg202318, Lg202319*; Shangnan County, Jinsixia, 6 June 2023, *B.H. Wu and W.H. Tu Lg202335, Lg202336, Lg202337, Lg202338*; Xunyang County, on the road from Zhaojiawan to Liangheguan, 7 October 1952, *B.Z. Guo 2225* (WUK); Xunyang County, precise locality unknown, 1959, *Xida 019* (WUK); Xunyang County, on the road from Zhangping to Xunyang, 19 August 1959, *P.Y. Li 8962* (WUK); Xunyang County, Guojiacao, 7 May 2012, *S.F. Li et al. 16523* (XBGH); Xunyang County, Liangheguan, 9 June 2023, *B.H. Wu and W.H. Tu Lg202384, Lg202385*,

Table 1. Morphological Comparison of *Lagerstroemia stenophylla* and its relatives.

Characters	<i>L. stenophylla</i>	<i>L. subcostata</i>	<i>L. indica</i>	<i>L. excelsa</i>
Branchlets	4-angular, sometimes subulate	terete to slightly 4-angular	4-angled or subulate	terete
Leaf shape	elliptic-lanceolate, narrowly elliptic, rarely ovate, obovate-oblongate	oblong, ovate-lanceolate, elliptic, obovate-elliptic, or infrequently obovate	elliptic, oblong, obovate, or suborbicular	elliptic to broadly elliptic
Leaf size	2–6 (7) × 0.7–2 (2.3) cm	2–9 (11) × 1–5 cm	2.5–7(10) × 1.5–4 cm	7–13 × 3.5–5 cm
Leaf apex	acute, sometimes obtuse, rarely apiculate	acuminate	acute, obtuse with small mucro, or retuse	narrowly to broadly acuminate
Leaf base	cuneate	broadly cuneate to subrounded	broadly cuneate to rounded	acute
Lateral veins	4–7 pairs	3–10 pairs	3–7 pairs	7–9 pairs
Flower	2.5–3 cm in diameter	less than 1 cm in diameter	3–4 cm in diameter	ca. 0.5 cm in diameter
Calyx-tube	cup-shaped, with 10–12 distinctly ribs or dark veins, sometimes not obvious	cup-shaped, with 10–12 dark veins or faint ribs	campanulate, obscurely to decidedly 6-ribbed	tubular, with 12 dark veins or ribs
Annulus	present, sometime absent	thin or apparently absent	present	absent
Petal	10–18 mm long including claw	2–6 mm long including claw	12–20 mm long including claw	3–3.5 mm long including claw
Stamens	20–28	15–30	36–42	(5)6–12
Seed	ca. 6 mm long including wing	ca. 4 mm long including wing	ca. 8 mm long including wing	3.5–4.8 mm long including wing
Phenology	flowering from May to June, fruiting after July	flowering from June to August, fruiting from July to October	flowering from June to September, fruiting from September to November	flowering in April, fruiting in July

Lg202386, Lg202387, Lg202388; Zhashui County, Shiweng, 8 June 2008, S.F. Li et al. 10463; Zhen'an County, Lengshuihe, 9 June 2023, B.H. Wu and W.H. Tu *Lg202389, Lg202390, Lg202392, Lg202393*. **Hubei Province**: Baokang County, Siping, 21 April 1986, 84*Linxue* 86-1058 (CCAU); *ibid.*, 8 June 2023, B.H. Wu and W.H. Tu *Lg202365, Lg202366, Lg202367, Lg202369, Lg202372*; Fang County, Wanyuhe, 8 June 2023, B.H. Wu and W.H. Tu *Lg202373, Lg202374, Lg202375*; Shiyan City, Wudangshan, 7 June 2023, B.H. Wu and W.H. Tu *Lg202343, Lg202344, Lg202345, Lg202346, Lg202347, Lg202348*.

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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

Bao-Huan Wu is the main author of the article, and everyone else participated in the writing. Xing Hu and Wen-Hui Tu participated in the taxonomic confirmation of the new species and filed investigation, and Se-Ping Dai and Wei Wang are the leaders of the research projects, responsible for promoting the project.

Author ORCIDs

Bao-Huan Wu  <https://orcid.org/0000-0002-0498-0603>

Data availability

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

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Primula xilingensis (Primulaceae), a new species from Sichuan, China

Junjia Luo^{1,2}, Mingke Zhang², Xiaofeng Liu², Hui Chen², Tingyu Li², Xudong Ma²,
Ke Huang², Zhixi Fu^{1,2,3}

¹ Key Laboratory of Land Resources Evaluation and Monitoring in Southwest, Sichuan Normal University, Ministry of Education, Chengdu 610066, China

² College of Life Sciences, Sichuan Normal University, Chengdu 610101, China

³ Sustainable Development Research Center of Resources and Environment of Western Sichuan, Sichuan Normal University, Chengdu 610066, China

Corresponding authors: Ke Huang (542176689@qq.com); Zhixi Fu (fuzx2017@sicnu.edu.cn)

Abstract

A new species, *Primula xilingensis* K.Huang & Z.X.Fu, **sp. nov.** (Primulaceae), is described and illustrated. In gross morphology, it is clearly allied to section *Minutissimae* on account of having stolons, being glabrous, leaf rosette less than or equal to corolla, flower solitary and bract not swollen at base. The new species is easily distinguished by the combination of scape densely yellow farinose, leaf apex acute, rarely broadly obtuse, corolla pale purplish blue and style 3.0–6.0 mm above base of corolla tube, stamens reaching the corolla tube mouth in thrum flower. In addition, the distribution map, morphological comparison of related species and conservation status of the new species are also provided.

Key words: conservation, morphological characters, *Primula* sect. *Minutissimae*, taxonomy

Introduction

The genus *Primula* L. is one of the largest genera in the Primulaceae, encompassing approximately 536 species (Ju et al. 2023; Li et al. 2023; POWO 2023; Wang et al. 2023; Wu et al. 2023a, b; Yang et al. 2023; Zhang et al. 2023). In China, the last comprehensive account of the genus was that of Hu and Kelso (1996) who treated 300 species in the “Flora of China”. The additional several new species of *Primula* were added by e.g., Li and Hu (2009; one species), Xu et al. (2016a, b, 2017, 2022; four species), Wu et al. (2019; one species), Ju et al. (2021; one species), Wang et al. (2022; one species), Li et al. (2023; one species), and Yang et al. (2023; two species), bringing the total number of species in China to c. 340 species.

In China, *Primula* sect. *Minutissimae* Pax has approximately 17 species, and is abundantly distributed to Xizang, Yunnan and Sichuan provinces (Hu and Kelso 1996). This section can be distinguished by a set of morphological characters, in which members are dwarf perennial herbs, glabrous or with glandular hairs, often with stolons, leaf rosette less than or slightly larger than corolla, bracts small and not swollen at base, flower usually solitary, rarely 2–4, and capsule nearly as long as calyx (Hu 1990; Hu and Kelso 1996).



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During a botanical expedition led by the last author to Xiling Snow Mountain, Dayi city, Sichuan Province in May 2022, a population of *Primula* was discovered, photographed and collected. Based on flowering taxon photos, the taxon appears to be closely related to *Primula tenella* King ex G.Watt. and *Primula dujiangyanensis* W.B.Ju, Bo Xu & X.F.Gao. After consultation with relevant literature and morphological examination of closely related taxa, it proved that it is eventually represents an unreported taxon of *P.* sect. *Minutissimae*. The new species can be differentiated from other members of this section by the combination of corolla pale purplish blue, scape densely yellow farinose with a solitary flower, and the style 3.0–6.0 mm above base of corolla tube, and stamens reaching the corolla tube mouth in thrum flower. Thus, it is described and illustrated as new to science below.

Material and methods

The observation and collection of both herbarium and living materials of the new species from Xiling Snow Mountain, Dayi city, Sichuan Province were conducted in May 2022 and June 2023. Morphological comparison of taxonomic literature of the closely related species, i.e. *P. dujiangyanensis* (Ju et al. 2021, herbarium CDBI, holotype, *DJY00272*), *Primula Pengzhouensis* C.M.Hu, G.Hao & Y.Xu (Xu et al. 2017, herbarium IBSC, holotype, *Xu16009*) and morphological comparison of specimens' images from Global Plants JSTOR (<https://plants.jstor.org>), i.e. *P. tenella* (herbarium K, holotype, *K000639442*, photo!, herbarium E, isotype, *E00024523*, photo!) were consulted. Morphological description and measurements of *P. xilingensis* were based on living plants. The taxonomic description follows the terminology used by Beentje (2016). The type and voucher specimens are stored at herbarium SCNU (follows Thiers 2023). The conservation status of the new species was assessed following the guidelines of the IUCN Red List categories and criteria (IUCN 2022).

Taxonomic treatment

Primula xilingensis K.Huang & Z.X.Fu, sp. nov

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Diagnosis. The new species is easily recognised by the following combination of characters: the scape densely yellow farinose, leaf apex acute, rarely broadly obtuse, corolla pale purplish blue and the style 3.0–6.0 mm above base of corolla tube, and stamens reaching the corolla tube mouth in thrum flower (Figs 1–3).

Type. CHINA. Sichuan: Dayi City, Xiling Snow Mountain, growing on moist rock surfaces amidst moss under the forest. 30°41'59.82"N, 103°9'47.63"E, alt. c. 3200m, 7th June 2023 (fl.), K. Huang & Zhixi Fu 7531 (holotype, SCNU!) (Figs 1–3).

Description. A perennial herb, 1.0–4.0 cm tall. **Stolons** dark red, 2.0–6.0 cm long developing onwards leafless flagellate, each with a tiny rosette at the end, and clothed the base by the withered remains of the old leaves. **Roots** numerous, fibrous, without hairs, 3.0–12.0 cm long. **Leaves** in a loose to tight rosette, 1.0–2.0 cm in diameter, leaf rosette less than or equal to corolla; leaf blade ovate to ovate-elliptic, 5.0–8.0 × 3.0–6.0 mm, margin dentate generally in the upper half only, apex acute, rarely broadly obtuse, tapering to base forming a winged

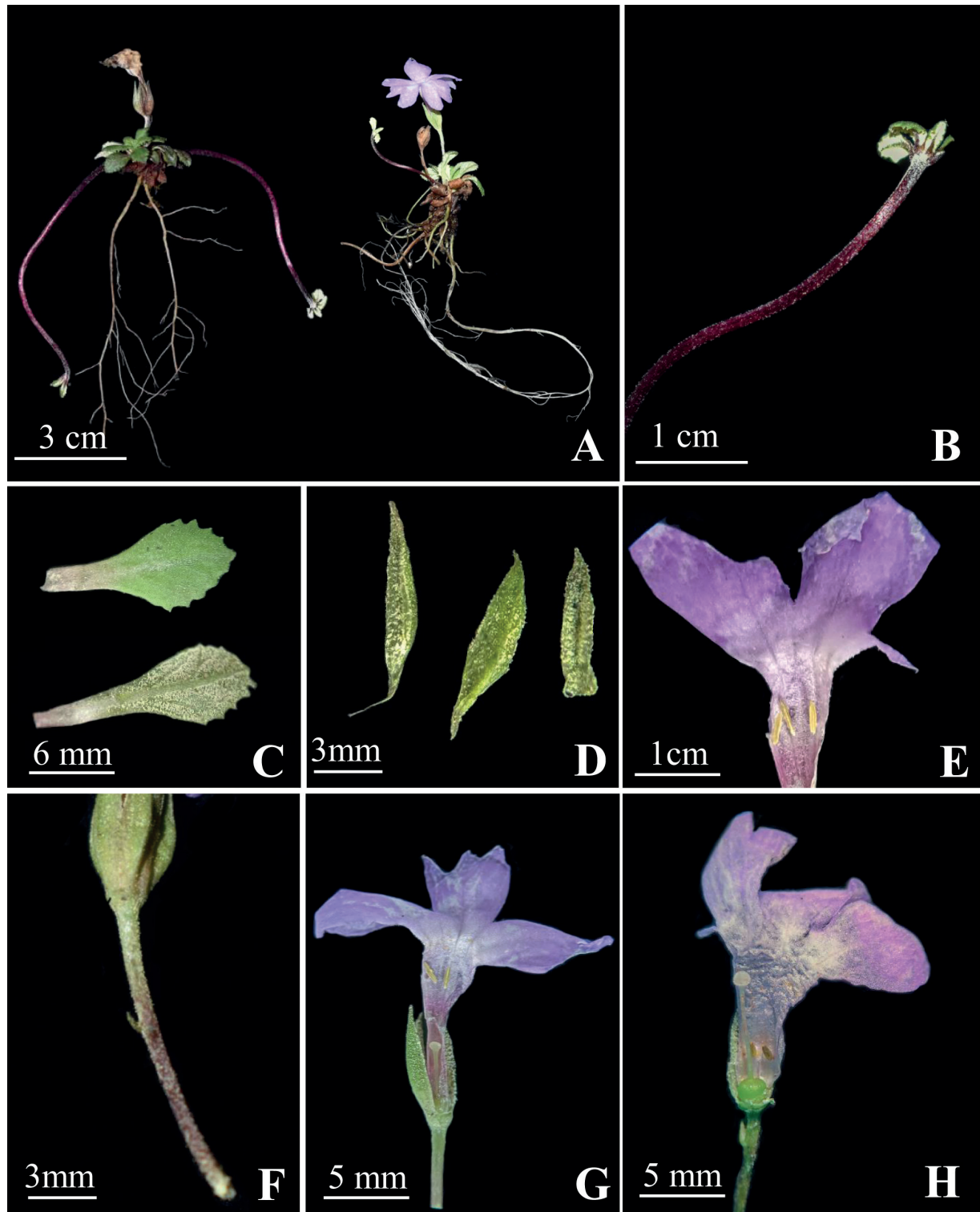


Figure 1. *Primula xilingensis* sp. nov. **A** plant and roots **B** stolon **C** leaves **D** calyx **E** stamens **F** scape and bract **G** thrum flower **H** pin flower. (Photos **A**, **B** by XM, and **C**–**H** by MZ).

petiole, petioles usually shorter than leaf blade and sparingly farinose, densely yellow farinose abaxially, midvein prominent, sparingly yellow farinose adaxially, veins inconspicuous. **Scape** solitary, 0.2–1.5 cm tall, erect, densely yellow farinose, usually with a single flower. **Bracts** solitary, 1.0–2.0 mm long, lanceolate, not swollen at base. **Pedicel** slightly bent, densely yellow farinose. **Flowers**

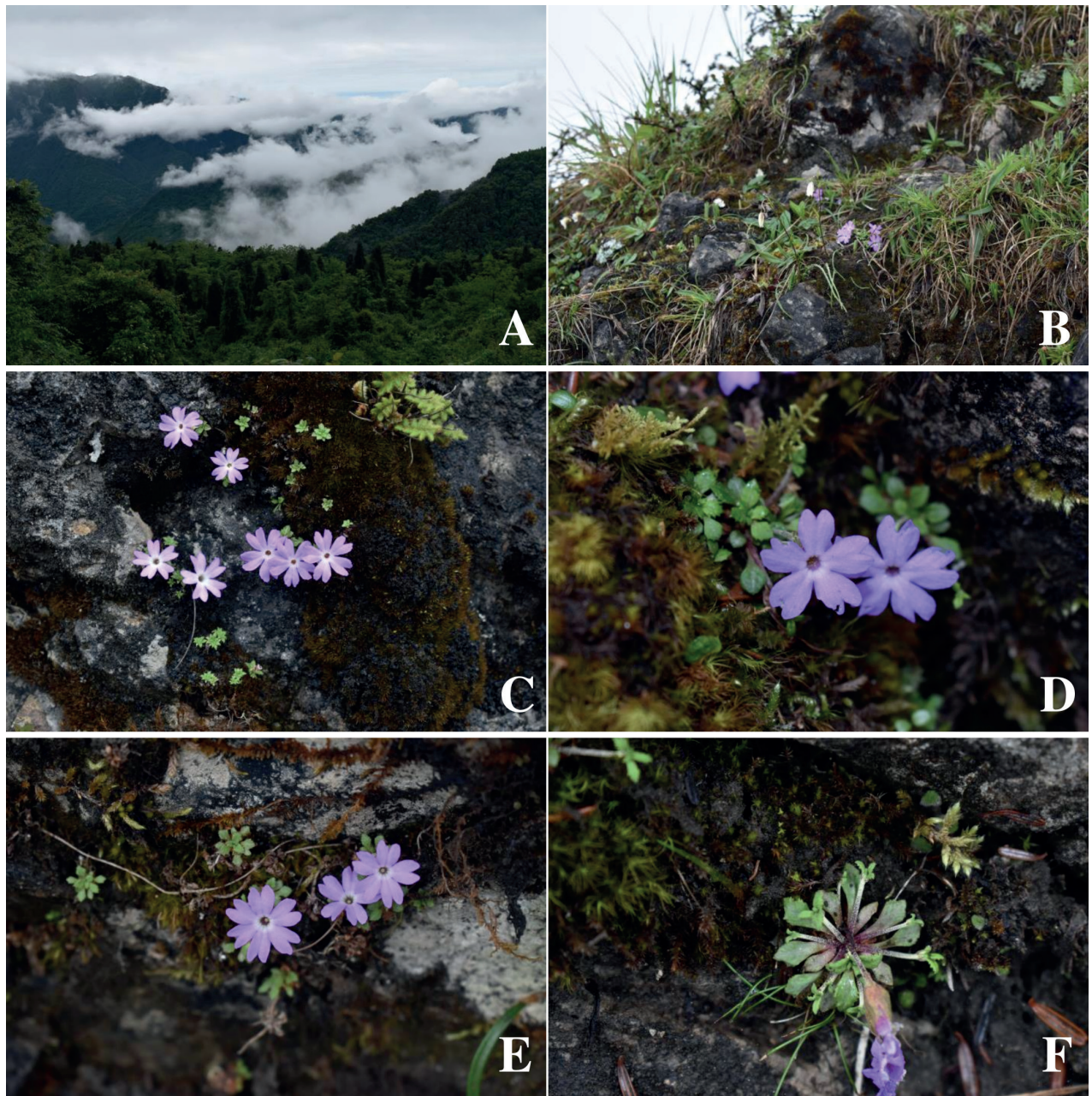


Figure 2. *Primula xilingensis* sp. nov. **A, B** habitat **C** plants of thrum flower **D** habit **E** plants of pin flower **F** stolons. (Photos **A, B** by ZF, **C, D** by KH, and **E, F** by MZ).

heterostylous. **Calyx** narrowly campanulate, prominent 5-veined, 3–9 mm long, densely yellow farinose, parted to 2/3 of its length or slightly below, lobes linear lanceolate to lanceolate, apex acute. **Corolla** pale purplish blue, lacking the appendage on the corolla tube, 5 lobes spreading, obovate, 4.0–8.0 mm long, densely yellow farinose abaxially, efarinose and glabrous adaxially, deeply emarginate. **Pin flower:** corolla tubes 5.0–10.0 mm long in length, 2–3 mm in diameter, longer than calyx, stamens 2.0–5.0 mm above base of corolla tube, style nearly as long as tube. **Thrum flower:** corolla tubes 7.0–13.0 mm long in length, c. 3 mm in diam, longer than calyx, style 3.0–6.0 mm above base of corolla tube, stamens reaching the corolla tube mouth (Figs 1–3). **Capsule** unknown.

Phenology. Flowers collected in May and June.

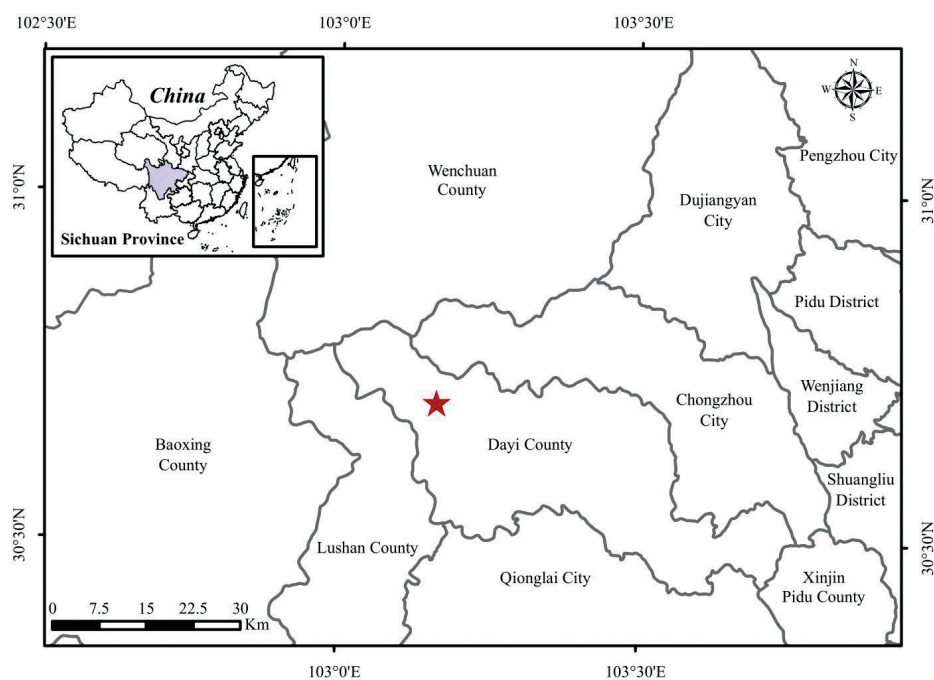


Figure 3. Holotype image of *Primula xilingensis* K.Huang & Z.X.Fu, sp. nov.

Etymology. The epithet “*xilingensis*” is derived from Xiling Snow Mountain, the snow mountain located in Dayi City, Sichuan Province, China.

Distribution and habitat. *P. xilingensis* is currently known only from its type locality in Yingyangjie, Xiling Snow Mountain, Xiling Town, Dayi City, Sichuan Province, China (Map 1). It grows on moist rock surfaces amidst moss under the forest, at elevations of approximately 3200 m (Fig. 2).

Additional specimens examined (paratypes). CHINA. Sichuan: Dayi City, Xiling Snow Mountain, 30°41'59.82"N, 103°9'47.63"E, 21 May 2022 (fl.), Zhixi Fu 6052 (SCNU!); ibid., 7 June 2023 (fl.), K. Huang & Zhixi Fu 7532 & 7533 (SCNU!).



Map 1. Location of the population of *Primula xilingensis* in Dayi County, Sichuan (red star).

Conservation status. Data Deficient (DD). Currently, only one population with more than 100 individuals has been found in the type locality. The population of *P. xilingensis* grows on moist rock surfaces amidst moss, and the Xiling Snow Mountain has corresponding protective measures for the environment and plants. Whilst currently only known from Xiling Snow Mountain, it is very possible that the taxon is found in other localities and, without a more comprehensive collecting programme, and known only from two collections, it would be best to assess the conservation status of the species as Data Deficient (DD) following the IUCN Red List criteria (IUCN 2022).

Relationship with related species. Critical examination of collected specimens, comparison with type material of allied taxa, and relevant taxonomic literature revealed that *P. xilingensis* is a new member of the *P.* sect. *Minutissimae*. Morphologically, *P. xilingensis* shares certain similarities with *P. dujiangyanensis*. However, *P. xilingensis* differs from *P. dujiangyanensis* in having the style nearly as long as tube in pin flowers (vs. the style slightly exceeding the corolla tube mouth in pin flowers), stamens reaching the corolla tube mouth in thrum flowers (vs. stamens inserted on the apex of the corolla tube, scarcely exceeding 1 mm in thrum flowers), lacking an appendage on the corolla tube (vs. a yellow appendage present on the corolla tube), having numerous roots without hairs (vs. few roots with dense white hairs), corolla pale purplish blue (vs. corolla pinkish purple), leaf apex acute (vs. leaf apex broadly obtuse to sub-rounded) and distributed at about 3200 m elevation (vs. 1550–1650 m). To some extent, it also resembles *P. tenella* as a perennial herb with stolons, farinose leaves, margin dentate generally on the upper half only, but differs from *P. tenella* in leaf blade (ovate to ovate-elliptic vs. rhomboid to ovate-spatulate), leaf size (5.0–8.0 × 3.0–6.0 mm vs. 6.0–15.0 × 5.0–8.0 mm), leaf farinose (yellow vs. white) and altitude (at an altitude of approximately 3200 m vs. 4700–5000 m). The species of *P. xilingensis* is similar to *P. pengzhouensis*,

Table 1. Morphological characters comparison between *P. xilingensis* and closely related species of *P. dujiangyanensis*, *P. pengzhouensis* and *P. tenella*.

Features	<i>P. xilingensis</i>	<i>P. dujiangyanensis</i>	<i>P. pengzhouensis</i>	<i>P. tenella</i>
Roots	numerous, without hairs	few, dense white hairs	unknown	unknown
Stolon	2.0–6.0 cm long	3.0–6.0 cm long	absent	short leafy stolons
Leaf blade	ovate to ovate-elliptic, 5.0–8.0 × 3.0–6.0 mm	ovate to ovate-elliptic, 4.0–8.0 × 3.0–5.0 mm	elliptic to ovate elliptic, 2.0–3.5 × 1.5–2.2 cm	rhomboid to ovate-spatulate, 6.0–15.0 × 5.0–8.0 mm
Leaf farinose	abaxially densely yellow farinose, adaxially sparingly yellow farinose	abaxially copiously yellow farinose, adaxially sparingly yellow farinose	abaxially more or less covered with a fugacious yellow farina, adaxially efarinose	abaxially copiously white farinose, adaxially densely glandular and sparingly white farinose
Leaf apex	acute, rarely broadly obtuse	broadly obtuse to sub-rounded	broadly obtuse to sub-rounded	subrounded, rarely acute
Leaf margin	margin dentate generally in the upper half only	margin dentate or crenulate generally in the upper half only	margin serrate–dentate	margin usually denticulate or crenulate above middle
Scape	scape 1, 0.2–1.5 cm tall, usually with a single flower	scape 1, 1.0–2.5 cm tall, usually with a single flower, very rarely two	scape almost obsolete, at most 2.0 mm tall, bearing one terminal flower.	Scape 1, 2.0–5.0 cm tall, bearing 1 (or rarely 2)-flowered
Scape farinose	densely yellow farinose	scarcely farinose	unknown	scarcely farinose
Calyx	narrowly campanulate,	narrowly campanulate	narrowly campanulate	narrowly campanulate
Calyx farinose	densely yellow farinose	sparingly yellow farinose outside, densely so inside	sparingly yellow farinose outside, parted slightly beyond middle	glandular outside, copiously white farinose inside
Corolla	pale purplish blue	pinkish purple	corolla rose or pale purple	corolla blue-violet
Corolla farinose	abaxially densely yellow farinose	unknown	sprinkled with yellow farina outside	unknown
An appendage on the corolla tube or not	absent	yellow appendage	absent	white appendage
Pin flowers	stamens 2.0–5.0 mm above base of corolla tube, style nearly as long as tube	stamens in the middle of corolla tube; style slightly exceeding the corolla tube mouth	stamens c. 3 mm above base of corolla tube, style c. 2/3 as long as corolla tube	stamens c. 3 mm above base of corolla tube, style reaching mouth
Thrum flowers	stamens reaching the corolla tube mouth, style 3.0–6.0 mm above base of corolla tube	stamens inserted on the apex of the corolla tube, scarcely exceeding 1 mm; style in the middle of the corolla tube	stamens up to 2/3 of corolla tube; style c. 3 mm	stamens at middle of corolla tube; style c. 3 mm
Altitude and distribution area	c. 3200 m, Dayi City, Sichuan Province	1550–1650 m, Dujiangyan City, Sichuan Province	c. 1170 m, Pengzhou City, Sichuan Province	4700–5000 m, Southern of Xizang Province

but can be easily distinguished from the former by its stolons (present with 2–6 cm long vs. absent), scape visibility (vs. almost obsolete) and altitude (c. 3200 m vs. c. 1170 m). Further morphological comparisons among the species of *P. xilingensis*, *P. dujiangyanensis*, *P. pengzhouensis*, and *P. tenella* are shown in Table 1.

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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

ZF and KH collected this species. XL, HC, XM and TL performed the data analysis. JL and MZ wrote the manuscript. JL revised the manuscript. All authors have read and approved the final manuscript.

Author ORCIDs

Junjia Luo  <https://orcid.org/0009-0003-6453-9507>

Mingke Zhang  <https://orcid.org/0009-0007-2494-7695>

Xiaofeng Liu  <https://orcid.org/0009-0003-2471-6935>

Hui Chen  <https://orcid.org/0009-0003-4786-7453>

Tingyu Li  <https://orcid.org/0009-0005-6873-2114>

Xudong Ma  <https://orcid.org/0009-0006-6303-0006>

Ke Huang  <https://orcid.org/0009-0006-2057-5452>

Zhixi Fu  <https://orcid.org/0000-0002-2789-6287>

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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Karyotype and genome size variation in *Delphinium* subg. *Anthriscifolium* (Ranunculaceae)

Xiao-Yu Luo^{1,2}, Tang-Jie Nie^{1,3}, Heng Liu^{1,2}, Xue-Fei Ding^{1,2}, Ying Huang^{1,2}, Chun-Ce Guo^{1,2}, Wen-Gen Zhang^{1,2}

¹ Forestry College, Jiangxi Agricultural University, Nanchang 330045, China

² Jiangxi Provincial Key Laboratory for Bamboo Germplasm Resources and Utilization, Nanchang 330045, China

³ Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, China

Corresponding author: Wen-Gen Zhang (wgzhang@jxau.edu.cn)

Abstract

Five taxa of *Delphinium* subg. *Anthriscifolium* have been karyologically studied through chromosome counting, chromosomal measurement, and karyotype symmetry. Each taxon that we investigated has a basic chromosome number of $x = 8$, *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, *D. ecalcaratum*, and *D. callichromum* were diploid with $2n = 16$, while *D. anthriscifolium* var. *anthriscifolium* was tetraploid with $2n = 32$. Monoploid chromosome sets of the investigated diploid taxa contained 1 metacentric chromosome, 3 submetacentric chromosomes, and 4 subtelocentric chromosomes. Higher interchromosomal asymmetry (CV_{CL}) was present in *D. ecalcaratum* and *D. callichromum* than in other taxa. The highest levels of intrachromosomal asymmetry (M_{CA}) and heterogeneity in centromere position (CV_{CL}) were found in *D. anthriscifolium* var. *majus*. Diploid and tetraploid genome sizes varied by 3.02–3.92 pg and 6.04–6.60 pg, respectively. Karyotype and genome size of *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, *D. callichromum*, and *D. ecalcaratum* were reported for the first time. Finally, based on cytological and morphological data, the classification of *Delphinium anthriscifolium* was revised.



Key words: Columbines, *Consolida*, genome size, karyotype, ploidy, Ranunculales

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Introduction

Delphinium L., ca. 385 species and 232 species in China (Ilarslan et al. 1997; Wang 2019; Hadidchi et al. 2020), is a species-abundant genus of tribe Delphinieae in the buttercup family (Ranunculaceae) with great economic importance in terms of both horticultural and pharmaceutical value (Ghimire et al. 2015; Wang 2019; Wang et al. 2020). It is usually characterised by the following key traits: (1) In the zygomorphic flower, there are 5 petaloid sepals, with the upper one spurred; (2) a pair of dorsal petals are sessile, free, and spurred in the upper sepal, while a couple of lateral petals (i.e., staminodes) are spurless, each with a slender claw and an expanded limb; (3) follicles 3 (Tamura 1993; Wang and Warnock 2001; Wang 2019). Except for a few species found in tropical Africa's montane regions, the genus is widely distributed in northern temperate regions (Milne-Redhead and Turrill 1952; Chartier et al. 2016; Aleem et al. 2020; Kashin et al. 2021).

To date, the classification of subgenus or groups in *Delphinium* is still controversial. For example, Wang (2019, 2020) divided *Delphinium* into subgenus *Delphinastrum* (DC.) Peterm. comprising sections *Aconitoides* W.T.Wang, *Elaopsis* Huth, *Delphinastrum* DC. and *Oligophyllon* Dimitrova, and subgenus *Delphinium* with section *Anthriscifolium*. However, molecular phylogenetic studies indicated at least four monophyletic subgenera [i.e., *D.* subg. *Consolida* (DC.) Huth, subg. *Delphinium*, subg. *Delphinastrum*, and subg. *Anthriscifolium* (W.T.Wang) Wei Wang] should be accepted (Jabbour and Renner 2011, 2012; Wang et al. 2013; Xiang et al. 2017; DuPasquier et al. 2021). Interestingly, the taxon, including *D. anthriscifolium* Hance, is a monoclade, either a subgenus of *Delphinium* (Xiang et al. 2017) or an independent group included in *Delphinium* (Jabbour and Renner 2012; Wang et al. 2013).

As a recently erected subgenus, *Delphinium* subg. *Anthriscifolium*, including ca. 3 species [i.e., *D. anthriscifolium* Hance, *D. ecalcaratum* S.Y.Wang & K.F.Zhou, and *D. callichromum* Q.L.Gan & X.W.Li], is endemic to East Asia and mainly distributed in the south of Zhongtiao Mountain and Qinling Mountain in China (Ding et al. 1981; Gan and Li 2017; Wang 2019). Moreover, there are three varieties of *D. anthriscifolium* [i.e., *D. anthriscifolium* var. *anthriscifolium*, *D. anthriscifolium* var. *majus* Pamp., and *D. anthriscifolium* var. *savatieri* (Franch) Munz], among which there are obvious differences in flower size, colour, and shape, which cause disagreements in the taxonomic circumscription of this species and associated varieties.

Genome size refers to the amount of DNA contained in the gametes of a species, which is broadly constant within an organism and is primarily indicated by C-value (Pellicer et al. 2018; Twyman and Wisden 2018; Kocjan et al. 2022). C-value estimation is not only crucial for genomic sequencing and analysis (Gregory 2005) but also significant for the identification of species and taxonomic positions (Bourge et al. 2018; Sliwinska 2018). Furthermore, as an important character of genetic material, karyotype, including chromosome number, morphology, length, band type, and centromere position (de Resende 2017; Ning et al. 2018; Vimala et al. 2021; Mahmoudi and Mirzaghadri 2023), was extensively used in the systematic and evolutionary study of plants (Baltisberger and Hörandl 2016; Peruzzi et al. 2017; Wang et al. 2020). So far, there are few reports on the genome size and karyotype of *Delphinium* subg. *Anthriscifolium*.

Here, we aim to: (1) determine the chromosome number, karyotype, and genome size of the above five taxa (i.e., *D. anthriscifolium* var. *anthriscifolium*, *D. anthriscifolium* var. *majus*, *D. anthriscifolium* var. *savatieri*, *D. ecalcaratum*, and *D. callichromum*); (2) evaluate the reliability of flow cytometry in genome size determination to infer ploidy levels in *D.* subg. *Anthriscifolium*; and (3) provide cytological evidence for the taxonomic revision of *D. anthriscifolium*.

Materials and methods

Sampling

Materials of *Delphinium* subg. *Anthriscifolium*, including *D. ecalcaratum*, *D. callichromum*, *D. anthriscifolium* and its varieties (Fig. 1), were collected by field investigations in China during 2017–2021 (see Table 1 in detail), of which rep-

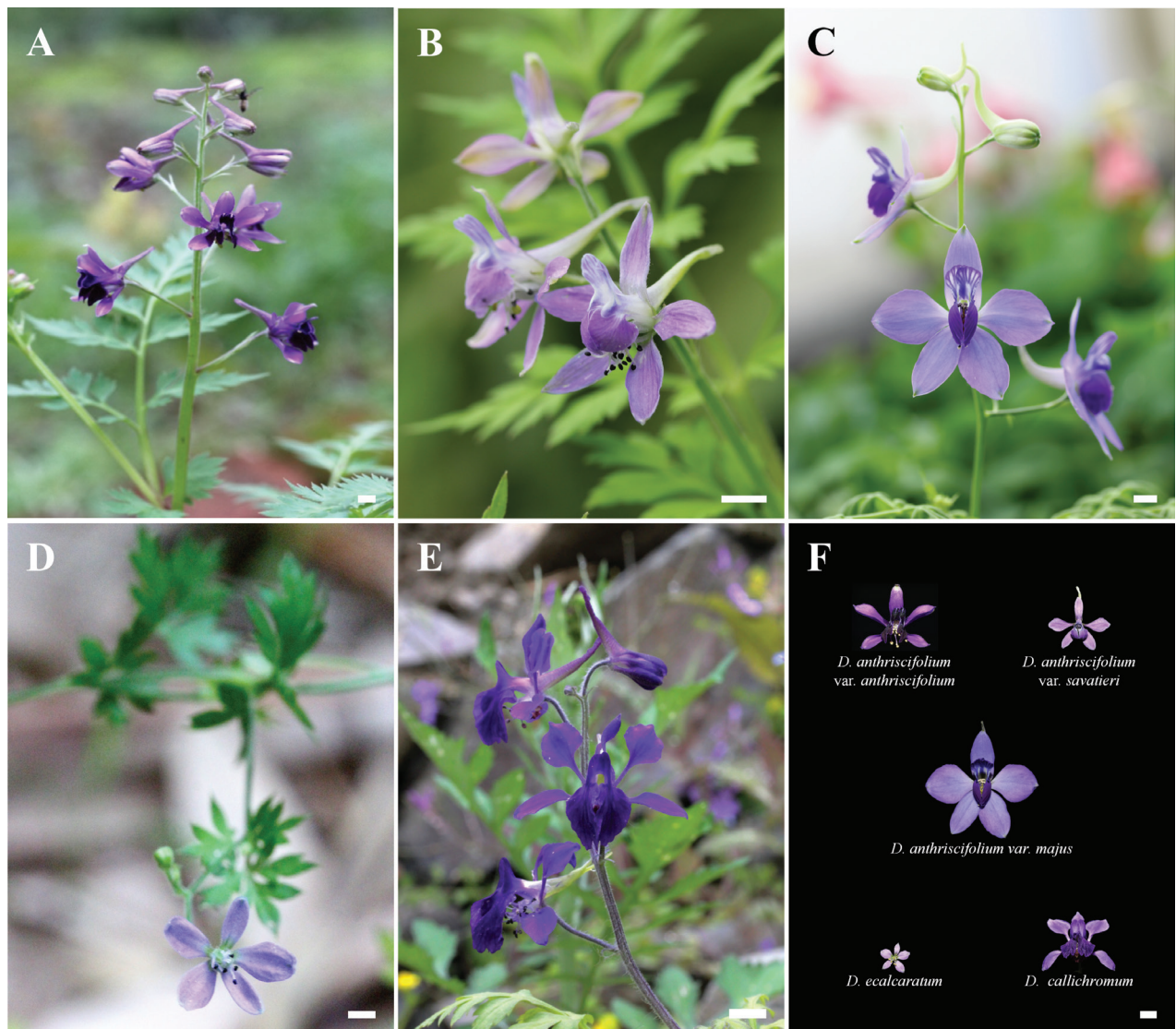


Figure 1. Five taxa of *Delphinium* subg. *Anthriscifolium* **A** *D. anthriscifolium* var. *anthriscifolium* **B** *D. anthriscifolium* var. *savatieri* **C** *D. anthriscifolium* var. *majus* **D** *D. ealcaratum* **E** *D. callichromum* **F** flower front view of the above five taxa. Scale bars: 5 mm.

representatives were transplanted to the garden of Jiangxi Agricultural University. All vouchers were deposited in the herbarium of the College of Forestry, Jiangxi Agricultural University, China (**JXAU**).

Flow cytometry (FCM) analysis

Twenty-two populations of *Delphinium* subg. *Anthriscifolium* were gathered with silica gel-dried leaves for the assessment of genome size by using flow cytometry (FCM; Table 1). In a petri dish containing pre-chilled MG^b dissociation solution, ca. 1 cm² of leaf material was quickly chopped using a sharp blade. After 10 min on ice, the samples were filtered through a 40 µm filter into a tube with pre-chilled PI (50 µg/mL) and RNAase solution (50 µg/mL), which were then placed on ice and kept from light for 0.5 to 1 hour. Using BD FACSCalibur Flow Cytometer (USA), three replicates of each population of *D.* subg. *Anthriscifolium* were estimated with the internal standard

Table 1. Chromosome number, ploidy, and genome size of *Delphinium* subg. *Anthriscifolium* in the study.

Pop	Taxa	Voucher information	2n	Ploidy	2C (pg)	1Cx (pg)
1	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Bamboo Culture Park, Yifeng County, Jiangxi, China, 28°24'31"N, 114°50'3"E, 24 Apr 2018, <i>Liu 1824</i>	32	4x	6.26	1.57
2	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Huacheng Temple, Yichun City, Jiangxi, China, 27°48'40"N, 114°22'44"E, 17 Apr 2019, <i>Zhang 1917</i>	32	4x	6.20	1.55
3	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Guling Town, Lushan City, Jiangxi, China, 29°34'28"N, 115°59'19"E, 17 Apr 2019, <i>Zhang 1904</i>	32	4x	6.33	1.58
4	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Miaofeng Mountain, Fuzhou City, Fujian, China, 26°4'53"N, 119°14'59"E, 2 May 2017, <i>Luo 1705</i>	32	4x	6.39	1.60
5	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Jiaoqiao Town, Nanchang City, Jiangxi, China, 28°46'6"N, 115°50'22"E, 16 Apr 2018, <i>Liu 1816</i>	32	4x*	6.13	1.53
6	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Fujia County, Fuzhou City, Jiangxi, China, 27°45'40"N, 116°26'17"E, 17 Apr 2019, <i>Nie 1917</i>	32	4x*	6.22	1.56
7	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Shangli County, Pingxiang City, Jiangxi, China, 27°50'37"N, 113°49'15"E, 17 Apr 2019, <i>Zhang 1918</i>	32	4x	6.04	1.51
8	<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	Guangxi Botanical Institute, Guangxi, China, 25°4'58"N, 110°18'45"E, 26 Mar 2020, <i>Zhang 2026</i>	32	4x	6.60	1.65
9	<i>D. anthriscifolium</i> var. <i>savateri</i>	Hanfeng, Liuyang County, Shaanxi, China, 33°20'26"N, 105°59'43"E, 11 Apr 2020, <i>Gao 2011</i>	16	2x	3.32	1.66
10	<i>D. anthriscifolium</i> var. <i>savateri</i>	Baisha River, Zhuxi County, Hubei, China, 32°5'27"N, 109°55'25"E, 18 Apr 2019, <i>Zhang 1818</i>	16	2x*	3.36	1.68
11	<i>D. anthriscifolium</i> var. <i>savateri</i>	Sun Yat-sen Mausoleum, Nanjing City, Jiangsu, China, 32°5'23"N, 118°52'28"E, 19 Apr 2019, <i>Nie 1919</i>	16	2x	3.40	1.70
12	<i>D. anthriscifolium</i> var. <i>savateri</i>	Baohua Mountain, Gourong City, Jiangsu, China, 32°8'8"N, 119°5'40"E, 19 Apr 2019, <i>Nie 1920</i>	16	2x*	3.43	1.72
13	<i>D. anthriscifolium</i> var. <i>savateri</i>	Nanjing Zhongshan Botanical Garden, Jiangsu, China, 32°3'38"N, 118°50'16"E, 19 Apr 2019, <i>Nie 1921</i>	16	2x*	3.36	1.68
14	<i>D. anthriscifolium</i> var. <i>savateri</i>	Zhongtiao Mountain, Yuncheng City, Shanxi, China, 32°46'44"N, 107°34'30"E, 21 May 2019, <i>Ren 1921</i>	16	2x	3.32	1.66
15	<i>D. anthriscifolium</i> var. <i>savateri</i>	Jiaoqiao Town, Nanchang City, Jiangxi, China, 28°46'6"N, 115°50'22"E, 15 May 2021, <i>Luo 2115</i>	16	2x	3.31	1.66
16	<i>D. anthriscifolium</i> var. <i>majus</i>	Hefeng County, Enshi City, Hubei, China, 30°3'57"N, 110°8'45"E, 18 Apr 2019, <i>Zhang 1919</i>	16	2x	3.92	1.96
17	<i>D. anthriscifolium</i> var. <i>majus</i>	Songbai Town, Shennongjia, Hubei, China, 31°45'11"N, 110°40'5"E, 18 Apr 2019, <i>Zhang 1925</i>	16	2x*	3.80	1.90
18	<i>D. anthriscifolium</i> var. <i>majus</i>	Jiaoqiao Town, Nanchang City, Jiangxi, China, 28°46'6"N, 115°50'22"E, 15 May 2021, <i>Luo 2116</i>	16	2x	3.75	1.88
19	<i>D. ecalcaratum</i>	Jiaoqiao Town, Nanchang City, Jiangxi, China, 28°46'6"N, 115°50'22"E, 15 May 2021, <i>Luo 2117</i>	16	2x	3.02	1.51
20	<i>D. ecalcaratum</i>	Lingshan Mountain, Xinyang City, Henan, China, 31°54'46"N, 114°13'19"E, 19 Apr 2019, <i>Luo 1919</i>	16	2x*	3.03	1.52
21	<i>D. callichromum</i>	Baisha River, Zhuxi County, Hubei, China, 32°5'27"N, 109°55'25"E, 18 Apr 2019, <i>Luo 1918</i>	16	2x	3.10	1.55
22	<i>D. callichromum</i>	Jiaoqiao Town, Nanchang City, Jiangxi, China, 28°46'6"N, 115°50'22"E, 15 May 2021, <i>Luo 2118</i>	16	2x*	3.10	1.55

* Chromosome number and ploidy were validated by experimental analysis in the study, while others were inferred according to the genome size by flow cytometry. **Pop** = population.

(*Solanum lycopersicum* L., 900 M bp; The Tomato Genome Consortium 2012). According to Tian et al. (2011), the 2C-value of each sample was calculated as the fluorescence intensity ratio. To remove the effect of genome size resulting from recent polyploidisation, monoploid genome size value (1Cx; Greilhuber et al. 2005) was used and calculated through the 2C-value.

Karyotype analysis

Somatic chromosomes were studied from the root tip cells of young seedlings. About 1–2 cm long roots were first pretreated in a 0.1% colchicine solution at 15 °C for 2–3 hours, then fixed in Carnoy I (absolute ethyl alcohol and glacial acetic acid in the proportions 3:1) for 30 minutes. After cleaning in purified water, they were hydrolysed in a mixture of 1 M HCl and 45% acetic acid (1:1) at 60 °C for 3–5 min and then stained with improved phenol magenta for 2 h. Five mitotic cells per species were examined and photographed using an Axio Imager A.1 microscope (Carl Zeiss, Germany) with ZEN software at 1000× magnification.

Short arm length (s) and long arm length (l) were measured using Image J (Collins 2007). Excel was used to determine additional chromosomal characteristics such as arm ratio ($r = l/s$), centromeric indices (CI), mean chromosome length (CL), relative chromosome length (RL), and total haploid length (THL). The coefficient of variation of chromosome length (CV_{CL}) [$(S_{CL} / X_{CL}) \times 100$, where S_{CL} : standard deviation; X_{CL} : mean chromosome length] (Lavana and Srivastava 1992; Paszko 2006), coefficient of variation of the centromeric index (CV_{CI}) [$(S_{CI} / X_{CI}) \times 100$, where S_{CI} : standard deviation; X_{CI} : mean centromeric index] (Paszko 2006), and mean centromeric asymmetry (M_{CA}) ($A \times 100$; the calculation of A is detailed in Watanabe et al. 1999) (Peruzzi and Eroğlu 2013) were calculated.

To infer the formulas of karyotype, the arm ratio (r), as defined by Levan et al. (1964), was used to categorise the chromosomes, and the homologous chromosome was allocated based on the similarity in length and centromere position using Photoshop CS6 software. The idiogram was constructed according to the arm ratio and relative length of the chromosomes. In order to illustrate karyotypic correlations between organisms, a bidimensional scatter plot was also created, in which the parameters CV_{CL} and M_{CA} are plotted on the x- and y-axes, respectively, and dots indicate each sample.

Results

Genome size of *Delphinium* subg. *Anthriscifolium*

In the FCM analysis, all studied taxa and the internal standards exhibited clear and sharp peaks (Fig. 2), and coefficients of variation were lower than 5%, supporting the reliability of the flow cytometric assessments. Twenty-two populations of *D.* subg. *Anthriscifolium*, including five taxa, i.e., *D. anthriscifolium* var. *anthriscifolium*, *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, *D. ecalcaratum*, and *D. callichromum*, showed remarkable variation (3.02–6.60 pg) in genome size (Table 1). Nearly twice as large as the others, *D. anthriscifolium* var. *anthriscifolium* had the greatest 2C-values (6.27 ± 0.17 pg). In contrast, *D. ecalcaratum* (3.03 pg) and *D. callichromum* (3.10 pg) had the lowest values (Fig. 3A). The 1Cx values were highest in *D. anthriscifolium* var. *majus* (1.91 ± 0.04 pg), while lower in *D. anthriscifolium* var. *anthriscifolium* (1.57 ± 0.04 pg), *D. ecalcaratum* (1.51 pg), and *D. callichromum* (1.55 pg) (Fig. 3B). Additionally, the monoploid genome sizes of tetraploids (mean 1Cx = 1.57 pg) are smaller than those of diploids (mean 1Cx = 1.69 pg). Thus, genome loss or duplication events have occurred in the evolution of *D.* subg. *Anthriscifolium*.

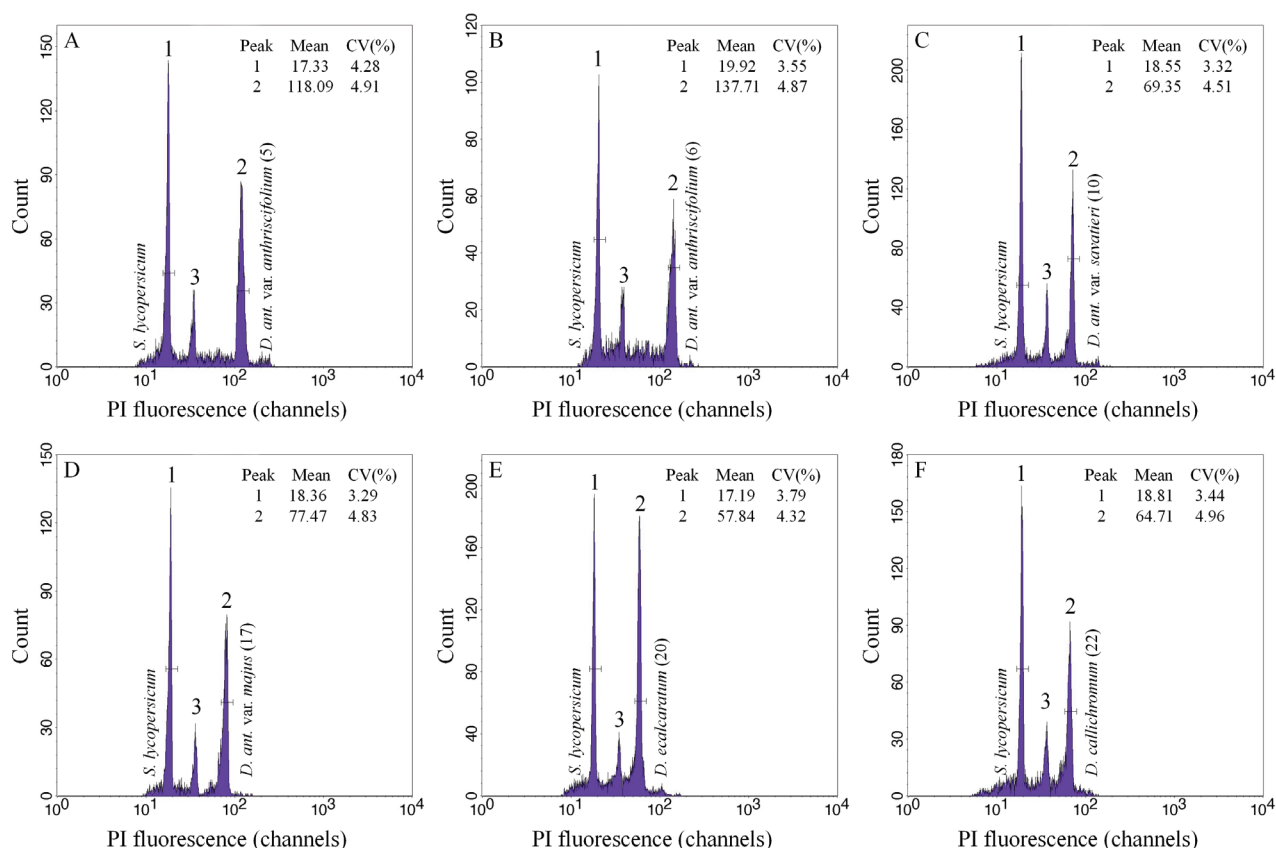


Figure 2. Flow cytometric histograms of *Delphinium* subg. *Anthriscifolium* was analysed simultaneously with the internal standard *Solanum lycopersicum*. In each histogram, the peaks are marked as follows: 1, nuclei of the internal standard at the G₁ phase; 2, nuclei of the sample at the G₁ phase. The mean channel number (PI fluorescence) and coefficient of variation value (CV, %) of each peak are also given; 3, nuclei of the internal standard at the G₂ phase.

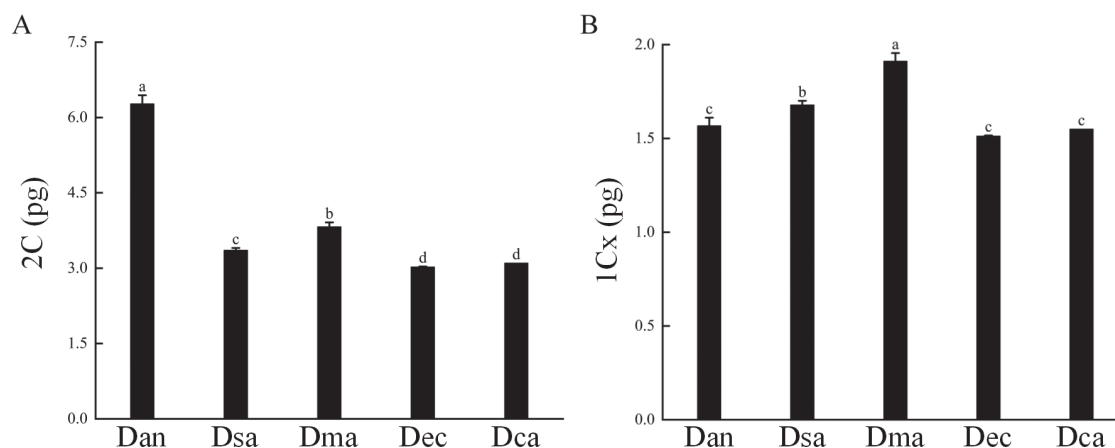


Figure 3. Comparison of the 2C and 1Cx mean values among *Delphinium* subg. *Anthriscifolium*. The columns marked with different index letters are significantly different at $P < 0.05$; those marked with the same index letters are not significantly different at $P < 0.05$ (one-way ANOVA followed by Tukey's test). Error bars represent standard deviation.

Karyotypes of *Delphinium* subg. *Anthriscifolium*

Eight representative populations of *D. subg. Anthriscifolium*, including the above five taxa, were karyologically studied. Karyomorphometric data, microphotographs of metaphase plates, and idiograms are presented here (Tables 1–3; Figs 4–6).

Table 2. Karyomorphological parameters of *Delphinium* subg. *Anthriscifolium* in the study.

Taxa	Pop	Chromosome pair	CL (μm)	r	CI	RL (%)	Type
<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	5	I	7.42 ± 0.72	1.28 ± 0.06	0.44	14.47	m
		II	6.35 ± 0.48	1.59 ± 0.05	0.39	12.38	m
		III	5.85 ± 0.12	2.10 ± 0.42	0.33	11.40	sm
		IV	4.28 ± 0.25	2.45 ± 0.55	0.29	8.35	sm
		V	3.25 ± 0.50	2.79 ± 0.26	0.26	6.34	sm
		VI	2.76 ± 0.08	2.06 ± 0.42	0.33	5.38	sm
		VII	2.54 ± 0.02	3.34 ± 0.21	0.23	4.95	st
		VIII	2.41 ± 0.02	3.15 ± 0.00	0.24	4.71	st
		IX	2.34 ± 0.03	3.38 ± 0.27	0.23	4.57	st
		X	2.19 ± 0.01	3.26 ± 0.13	0.23	4.27	st
		XI	2.06 ± 0.07	2.88 ± 0.19	0.26	4.01	sm
		XII	1.95 ± 0.02	2.73 ± 0.76	0.20	3.79	sm
		XIII	1.76 ± 0.08	3.02 ± 0.06	0.25	3.42	st
		XIV	1.61 ± 0.09	3.08 ± 0.29	0.25	3.14	st
		XV	1.40 ± 0.01	1.82 ± 0.14	0.30	2.72	sm
		XVI	1.31 ± 0.06	1.88 ± 0.13	0.35	2.56	sm
	6	I	5.60 ± 0.05	1.22 ± 0.09	0.45	13.90	m
		II	4.14 ± 0.13	1.14 ± 0.13	0.47	10.27	m
		III	4.62 ± 0.16	1.90 ± 0.02	0.35	11.45	sm
		IV	3.43 ± 0.52	2.12 ± 0.03	0.32	8.50	sm
		V	2.75 ± 0.20	1.90 ± 0.17	0.35	6.81	sm
		VI	2.24 ± 0.23	2.33 ± 0.75	0.31	5.55	sm
		VII	1.81 ± 0.08	3.09 ± 0.04	0.33	4.49	st
		VIII	1.90 ± 0.04	3.01 ± 0.00	0.37	4.70	st
		IX	1.78 ± 0.29	2.03 ± 0.43	0.24	4.42	sm
		X	1.88 ± 0.04	1.73 ± 0.01	0.25	4.66	sm
		XI	1.76 ± 0.25	3.25 ± 0.01	0.24	4.37	st
		XII	1.56 ± 0.01	3.08 ± 0.07	0.24	3.86	st
		XIII	1.76 ± 0.50	3.23 ± 0.24	0.26	4.37	st
		XIV	1.32 ± 0.20	3.10 ± 0.02	0.28	3.28	st
		XV	1.59 ± 0.20	2.91 ± 0.06	0.24	3.94	sm
		XVI	1.68 ± 0.22	2.60 ± 0.12	0.24	4.16	sm
<i>D. anthriscifolium</i> var. <i>savatieri</i>	13	I	7.65 ± 0.53	1.05 ± 0.04	0.49	28.15	m
		II	5.14 ± 0.43	2.71 ± 0.31	0.27	18.91	sm
		III	2.87 ± 0.11	4.23 ± 0.91	0.19	10.54	st
		IV	2.73 ± 0.03	3.36 ± 0.03	0.23	10.05	st
		V	2.67 ± 0.03	3.60 ± 0.49	0.22	9.84	st
		VI	2.15 ± 0.26	3.53 ± 0.14	0.22	7.90	st
		VII	1.53 ± 0.08	2.90 ± 0.01	0.26	5.64	sm
		VIII	1.39 ± 0.00	2.90 ± 0.13	0.26	5.12	sm
	12	I	8.15 ± 1.58	1.24 ± 0.17	0.45	27.24	m
		II	6.14 ± 0.20	2.04 ± 0.06	0.33	20.52	sm
		III	3.13 ± 0.16	3.80 ± 0.01	0.21	10.45	st
		IV	2.62 ± 0.08	4.47 ± 1.41	0.19	8.75	st
		V	2.46 ± 0.09	3.75 ± 0.02	0.21	8.23	st
		VI	2.37 ± 0.02	3.05 ± 0.02	0.25	7.93	st
		VII	1.82 ± 0.00	2.82 ± 0.18	0.26	6.09	sm
		VIII	1.55 ± 0.24	2.89 ± 0.14	0.26	5.20	sm

Taxa	Pop	Chromosome pair	CL (μm)	r	CI	RL (%)	Type
<i>D. anthriscifolium</i> var. <i>savatieri</i>	10	I	10.43 ± 0.11	1.13 ± 0.03	0.47	30.34	m ^{sat}
		II	6.77 ± 0.49	2.95 ± 0.01	0.25	19.70	sm
		III	3.60 ± 0.16	4.31 ± 1.43	0.20	10.49	st
		IV	3.30 ± 0.03	3.25 ± 0.32	0.24	9.59	st
		V	2.89 ± 0.14	4.60 ± 0.23	0.18	8.40	st
		VI	2.45 ± 0.10	3.23 ± 0.02	0.24	7.14	st
		VII	2.18 ± 0.10	2.55 ± 0.40	0.28	6.36	sm
		VIII	1.84 ± 0.15	2.64 ± 0.18	0.28	5.34	sm
<i>D. anthriscifolium</i> var. <i>majus</i>	17	I	11.08 ± 0.48	1.05 ± 0.05	0.49	28.96	m
		II	7.10 ± 0.04	2.97 ± 0.01	0.25	18.58	sm
		III	4.40 ± 0.06	3.43 ± 0.10	0.23	11.51	st
		IV	3.75 ± 0.31	3.43 ± 0.34	0.23	9.81	st
		V	3.26 ± 0.15	4.75 ± 1.40	0.18	8.53	st
		VI	3.07 ± 0.00	4.03 ± 0.84	0.20	8.03	st
		VII	2.67 ± 0.05	2.86 ± 0.01	0.26	6.97	sm
		VIII	1.86 ± 0.31	2.84 ± 0.06	0.26	4.87	sm
<i>D. ecalcaratum</i>	20	I	8.17 ± 0.10	1.06 ± 0.05	0.49	30.99	m
		II	5.39 ± 0.03	2.66 ± 0.26	0.27	20.45	sm
		III	2.61 ± 0.02	3.14 ± 0.04	0.24	9.92	st
		IV	2.51 ± 0.04	3.12 ± 0.10	0.24	9.53	st
		V	2.27 ± 0.02	3.21 ± 0.09	0.24	8.62	st
		VI	1.95 ± 0.07	3.65 ± 0.72	0.22	7.38	st
		VII	1.70 ± 0.00	2.65 ± 0.31	0.28	6.43	sm
		VIII	1.50 ± 0.09	2.73 ± 0.09	0.27	5.70	sm
<i>D. callichromum</i>	22	I	9.47 ± 1.40	1.20 ± 0.14	0.46	29.21	m
		II	6.48 ± 0.12	2.50 ± 0.62	0.29	19.99	sm
		III	3.36 ± 0.17	3.25 ± 0.33	0.24	10.36	st
		IV	3.14 ± 0.10	3.45 ± 0.46	0.23	9.70	st
		V	2.56 ± 0.45	3.23 ± 0.07	0.24	7.90	st
		VI	2.07 ± 0.01	3.74 ± 0.25	0.21	6.38	st
		VII	1.96 ± 0.09	2.01 ± 0.27	0.33	6.05	sm
		VIII	1.66 ± 0.09	1.77 ± 0.01	0.36	5.11	sm

CI = centromeric index; CL = chromosome length, mean value ± standard deviation; m = metacentric chromosome; Pop = population, numbers shown in Table 1; r = arm ratio, mean value ± standard deviation; RL = relative chromosome length; sat = chromosome showing secondary constriction; sm = submetacentric chromosome; st = subtelocentric chromosome.

Table 3. Karyotype parameters of *Delphinium* subg. *Anthriscifolium* in the study.

Taxa	Pop	Ploidy	2n	Karyotype formula	THL	CV _{CL}	M _{CA}	CV _{CI}
<i>D. anthriscifolium</i> var. <i>anthriscifolium</i>	5	4x	32	2n = 4m + 16sm + 12st	51.30	60.13	40.32	22.07
	6	4x	32	2n = 4m + 16sm + 12st	40.33	50.93	37.18	27.08
<i>D. anthriscifolium</i> var. <i>savatieri</i>	13	2x	16	2n = 2m + 6sm + 8st	27.18	62.81	46.58	34.01
	12	2x	16	2n = 2m + 6sm + 8st	29.91	65.20	47.18	30.83
	10	2x	16	2n = 2m ^{sat} + 6sm + 8st	34.37	68.27	46.05	33.27
<i>D. anthriscifolium</i> var. <i>majus</i>	17	2x	16	2n = 2m + 6sm + 8st	38.24	63.10	47.59	35.79
<i>D. ecalcaratum</i>	20	2x	16	2n = 2m + 6sm + 8st	26.35	68.87	44.65	29.84
<i>D. callichromum</i>	22	2x	16	2n = 2m + 6sm + 8st	32.42	69.63	40.11	29.09

CV_{CI} = Coefficient of Variation of Centromeric Index; CV_{CL} = Coefficient of Variation of Chromosome Length; m = metacentric chromosome; M_{CA} = Mean Centromeric Asymmetry; Pop = population, numbers shown in Table 1; sat = satellite chromosome; sm = submetacentric chromosome; st = subtelocentric chromosome; THL = total haploid length, μm.

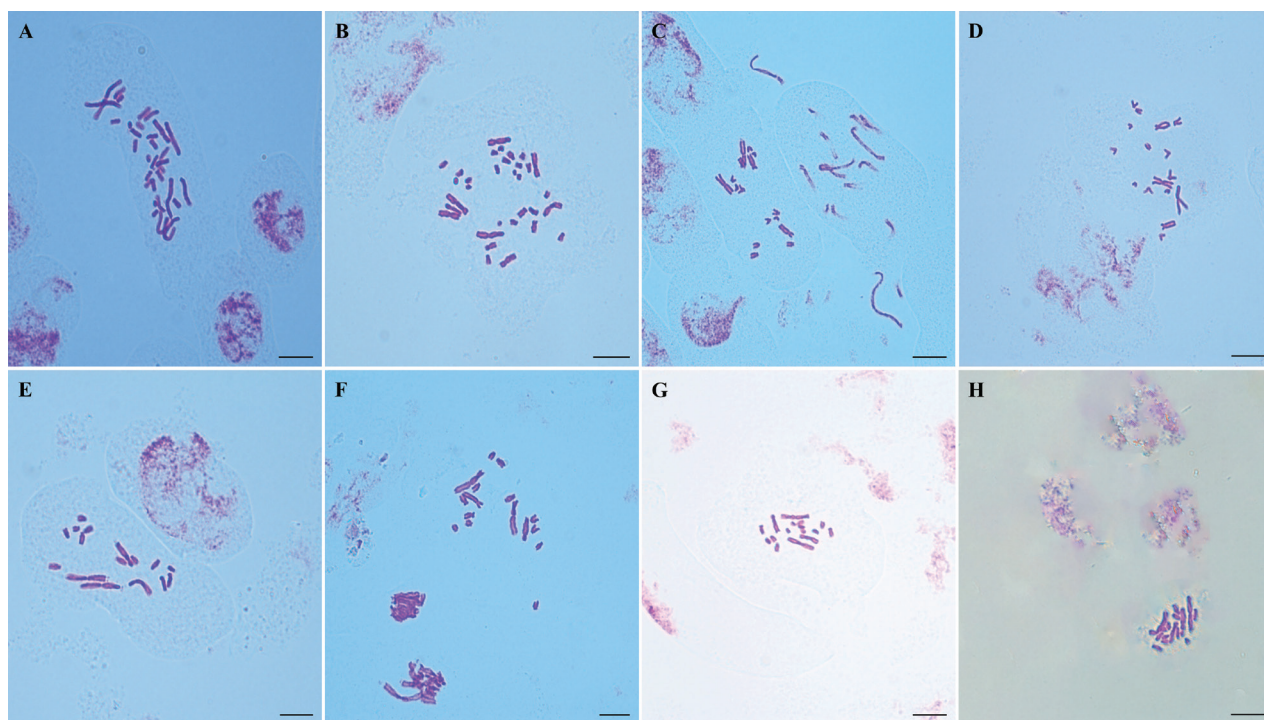


Figure 4. Somatic metaphases of *Delphinium* subg. *Anthriscifolium* **A** *D. anthriscifolium* var. *anthriscifolium* (5), $2n = 32$ **B** *D. anthriscifolium* var. *anthriscifolium* (6), $2n = 32$ **C** *D. anthriscifolium* var. *savatieri* (13), $2n = 16$ **D** *D. anthriscifolium* var. *savatieri* (12), $2n = 16$ **E** *D. anthriscifolium* var. *savatieri* (10), $2n = 16$ **F** *D. anthriscifolium* var. *majus* (17), $2n = 16$ **G** *D. ecalcaratum* (20), $2n = 16$ **H** *D. callichromum* (22), $2n = 16$. Numbers in brackets represented populations shown in Table 1. Scale bars: 10 μ m.

1. *Delphinium anthriscifolium* var. *anthriscifolium*

In two populations (Pop 5 and Pop 6) of *D. anthriscifolium* var. *anthriscifolium* from Jiangxi, China, the somatic and basic chromosome numbers were $2n = 32$ and $x = 8$, respectively (Table 1; Fig. 4A, B). Two pairs of chromosomes (i.e., I–II) are metacentric, eight pairs (i.e., III–VI, XI–XII, and XV–XVI) are submetacentric, and six pairs (i.e., VII–X and XIII–XIV) are subtelocentric (Tables 2, 3; Figs 5A, B, 6A, B). Thus, the karyotype formula is $2n = 4x = 32 = 4m + 16sm + 12st$.

2. *Delphinium anthriscifolium* var. *savatieri*

In three populations (i.e., Pop 10 from Hubei, Pop 12 and Pop 13 from Jiangsu), the somatic and basic chromosome numbers are $2n = 16$ and $x = 8$, respectively (Table 1; Fig. 4C–E). Pop 12 and Pop 13 have more similar karyotypes: one pair of chromosomes (i.e., I) is metacentric, three pairs (i.e., II, VII, and VIII) are submetacentric, and four pairs (i.e., III–VI) are subtelocentric (Tables 2 and 3; Figs 5C, D, 6C, D). The karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$. However, Pop 10 differed from Pop 12 and Pop 13 in that it has a secondary constriction on the first pair of chromosomes (Figs 5E, 6E), so its karyotype formula is $2n = 2x = 16 = 2m^{sat} + 6sm + 8st$.

3. *Delphinium anthriscifolium* var. *majus*

In Pop 17, the somatic and basic chromosome numbers are $2n = 16$ and $x = 8$, respectively (Table 1; Fig. 4F). Its chromosome set includes one pair of

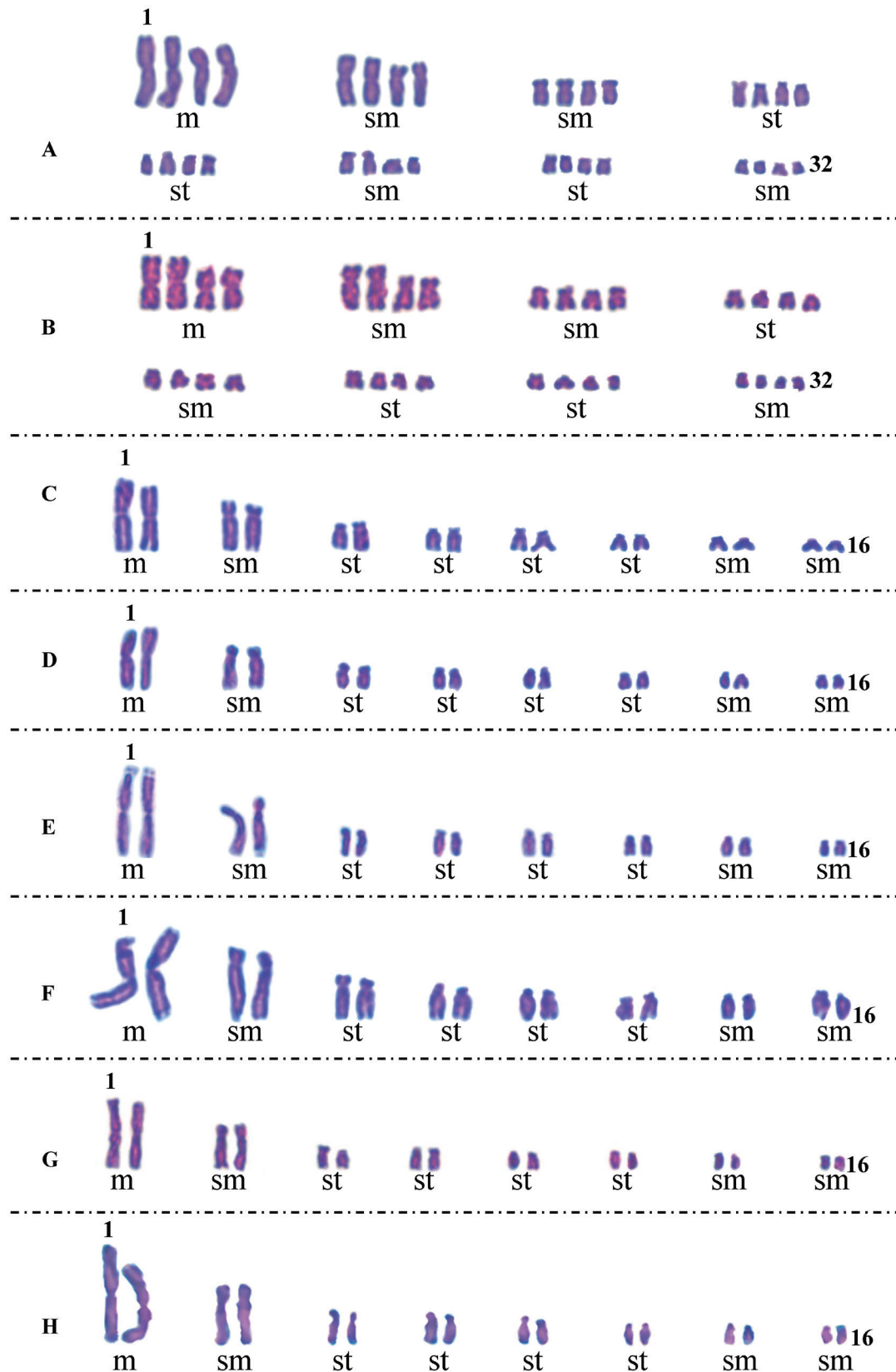


Figure 5. Karyotypes of *Delphinium* subg. *Anthriscifolium* **A** *D. anthriscifolium* var. *anthriscifolium* (5), $2n = 32$ **B** *D. anthriscifolium* var. *anthriscifolium* (6), $2n = 32$ **C** *D. anthriscifolium* var. *savatieri* (13), $2n = 16$ **D** *D. anthriscifolium* var. *savatieri* (12), $2n = 16$ **E** *D. anthriscifolium* var. *savatieri* (10), $2n = 16$ **F** *D. anthriscifolium* var. *majus* (17), $2n = 16$ **G** *D. ecalcaratum* (20), $2n = 16$ **H** *D. callichromum* (22), $2n = 16$. Numbers in brackets represented populations shown in Table 1. **m** = metacentric chromosome; **sat** = satellite chromosome; **sm** = submetacentric chromosome; **st** = subtelocentric chromosome.

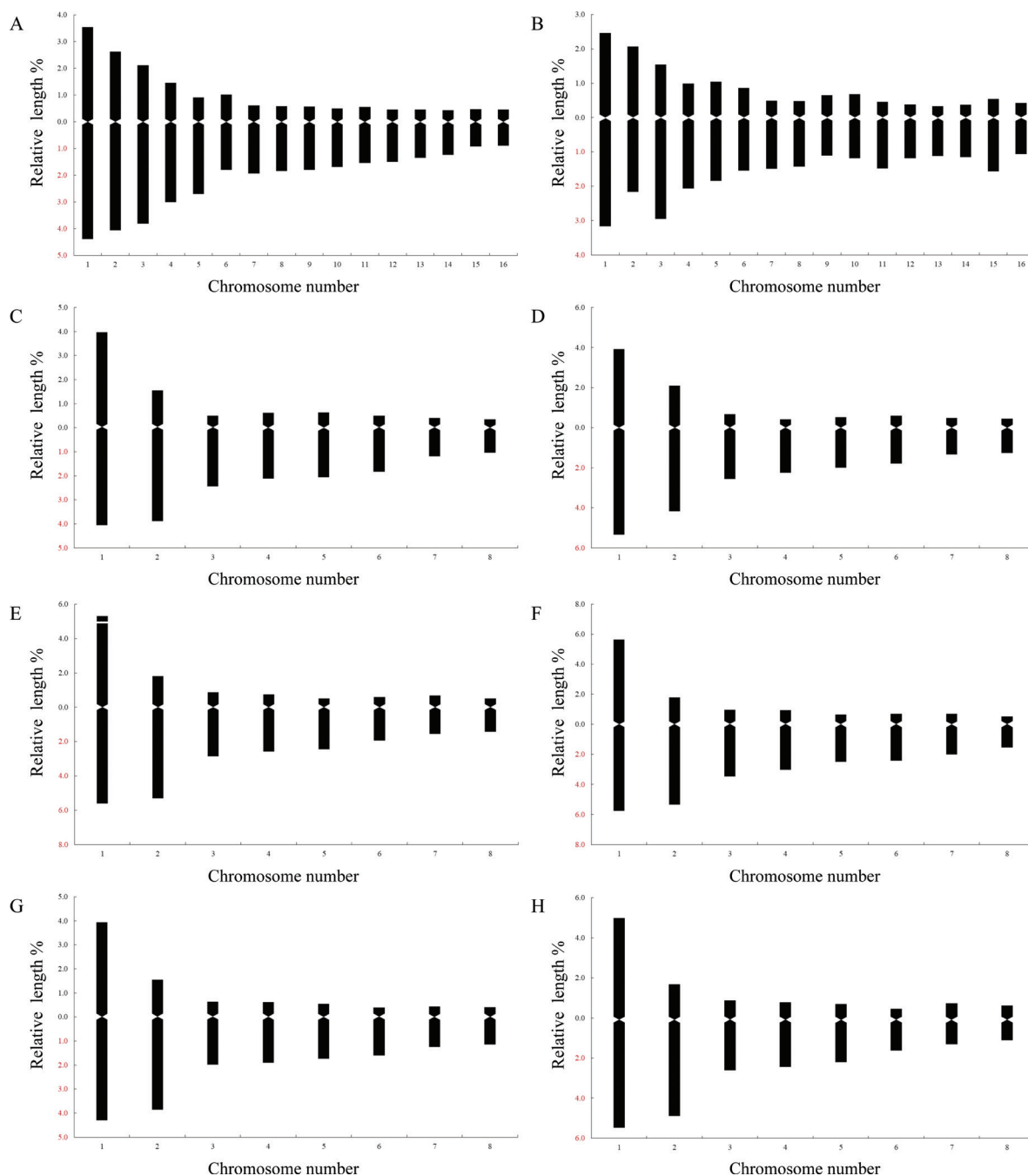


Figure 6. Haploid idiograms of *Delphinium* subg. *Anthriscifolium* **A** *D. anthriscifolium* var. *anthriscifolium* (5) **B** *D. anthriscifolium* var. *anthriscifolium* (6) **C** *D. anthriscifolium* var. *savatieri* (13) **D** *D. anthriscifolium* var. *savatieri* (12) **E** *D. anthriscifolium* var. *savatieri* (10) **F** *D. anthriscifolium* var. *majus* (17) **G** *D. ecalcaratum* (20) **H** *D. callichromum* (22). Numbers in brackets represented populations shown in Table 1.

metacentric chromosomes (i.e., I), three submetacentric (i.e., II, VII, and VIII), and four subtelocentric chromosomes (i.e., III–VI; Tables 2, 3; Figs 5F, 6F). Hence, the karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$.

4. *Delphinium ecalcaratum*

In Pop 20 from Xinyang City of Henan, China, the somatic and basic chromosome numbers are $2n = 16$ and $x = 8$, respectively (Table 1; Fig. 4G). One pair of

metacentric chromosomes (i.e., I), three pairs of submetacentric chromosomes (i.e., II, VII, and VIII), and four subtelocentric chromosomes (i.e., III–VI) make up the chromosome set of *D. ecalcaratum* (Tables 2, 3; Figs 5G, 6G). Therefore, the karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$.

5. *Delphinium callichromum*

In Pop 22 collected from the type locality of Zhuxi County, Hubei, China, the somatic and basic chromosome numbers are $2n = 16$ and $x = 8$, respectively (Table 1; Fig. 4H). Its chromosome set includes one pair of metacentric chromosomes (i.e., I), three submetacentric (i.e., II, VII, and VIII), and four subtelocentric chromosomes (i.e., III–VI) (Tables 2, 3; Figs 5H, 6H). Accordingly, the karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$.

Karyotype asymmetry analysis

In all five taxa of *Delphinium* subg. *Anthriscifolium*, the total haploid length (THL) of *D. ecalcaratum* was probably the shortest (26.35), while that of *D. anthriscifolium* var. *majus* was the longest (up to 38.24). The highest level of interchromosomal asymmetry, estimated via CV_{CL} , was found in *D. callichromum* (69.63). In contrast, the lowest level of CV_{CL} was found in *D. anthriscifolium* var. *anthriscifolium* (its mean value was 55.53). The highest values of both the heterogeneity in centromere position (CV_{CI}) and intrachromosomal asymmetry (M_{CA}) were found in *D. anthriscifolium* var. *majus* (47.59 and 35.79, respectively; Table 3). As seen in the scatter diagram (Fig. 7) drawn based on the parameter CV_{CL} vs M_{CA} , compared to *D. anthriscifolium* var. *anthriscifolium* and *D. callichromum*, *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, and *D. ecalcaratum* gathered together, indicating that they might be more closely related.

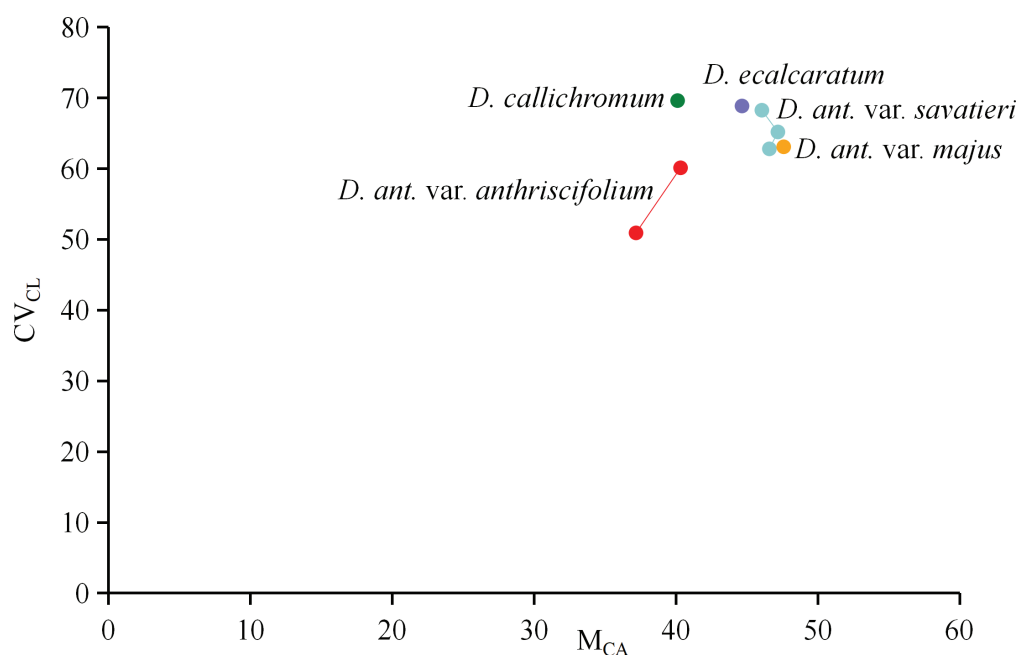


Figure 7. Scatter diagram of *Delphinium* subg. *Anthriscifolium* based on karyotype parameters CV_{CL} vs. M_{CA} . CV_{CL} = Coefficient of Variation of Chromosome Length; M_{CA} = Mean Centromeric Asymmetry.

Discussion

In Ranunculaceae, taxonomic position and evolutionary history were generally inferred by using chromosomal data (Tamura 1993; Yang 2001; Cires et al. 2010; Soza et al. 2013; Orooji et al. 2022). So far, nearly 60 species of *Delphinium* have been karyologically studied (Tjebbes 1927; Kolar et al. 2012; Gupta et al. 2018; Bosch et al. 2019; see www.iaptglobal.org/chromosome-data). The basic number of haploid chromosomes in *Delphinium* was typically 8 (Legro 1961; Orellana et al. 2007; Yuan and Yang 2008), with 9 (Blanché and Molero 1983; Bosch 1999; Bosch et al. 2002) and 10 (Sarkar et al. 1982) occasionally occurring in some circumstances. The chromosome number of most *Delphinium* plants was $2n = 16$, while a few were $2n = 32$, such as *D. denudatum* (Al-Kelidar and Richards 1981), *D. chrysotrichum* (Yuan 2006), and *D. spirocentrum* (Yuan and Yang 2008). Here, chromosome numbers of five taxa in *D.* subg. *Anthriscifolium* (i.e., *D. anthriscifolium* var. *anthriscifolium*, *D. anthriscifolium* var. *majus*, *D. anthriscifolium* var. *savatieri*, *D. ecalcaratum*, and *D. callichromum*) are reported. All studied taxa have a basic chromosome number of $x = 8$, *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, *D. ecalcaratum*, and *D. callichromum* are diploid with $2n = 16$, while *D. anthriscifolium* var. *anthriscifolium* is tetraploid with $2n = 32$.

Furthermore, the karyotypes of *Delphinium* taxa were very consistent, typically consisting of one pair of large metacentric, one pair of large submetacentric, five pairs of medium-sized subtelocentric, and one pair of smaller submetacentric (rarely subtelocentric) chromosomes (Lewis et al. 1951; Yang 2001; Yuan and Yang 2008; Kolar et al. 2012). In the study, we found that the karyotype of the diploid cytotype in *D.* subg. *Anthriscifolium* shared the traits listed below: (1) the first pair (metacentric chromosomes) and the second pair (submetacentric chromosomes) of chromosomes are significantly larger than the remaining six pairs; (2) the proportion of subtelocentric chromosomes is relatively high; and (3) intrachromosomal asymmetry and interchromosomal asymmetry are both high. Two pairs of large metacentric, eight pairs of submetacentric, and six pairs of subtelocentric chromosomes make up the tetraploid cytotype in *D. anthriscifolium* var. *anthriscifolium*. The karyotype formula of *D. anthriscifolium* var. *anthriscifolium* is $2n = 4m + 16sm + 12st$, consistent with the results of Yuan and Yang (2008). The karyotype formulas of *D. anthriscifolium* var. *savatieri*, *D. anthriscifolium* var. *majus*, *D. ecalcaratum*, and *D. callichromum* are $2n = 2m + 6sm + 8st$, consistent with the karyotype formulas of *D. caeruleum*, *D. maximowiczii*, *D. kamaoense* var. *glabrescens*, *D. nangchienense*, and *D. candelabrum* var. *monanthum* (Yang 1996; Liu and Ho 1999).

On the genome size of Ranunculaceae, few related studies involving ten genera (i.e., *Ranunculus*, *Eranthis*, *Helleborus*, *Hepatica*, *Thalictrum*, *Delphinium*, *Anemone*, *Ficaria*, *Adonis*, and *Trollius*), showed that the 2C-value of diploid taxa significantly ranged from 0.5 to 57.3 pg and from 14.8 to 89.2 pg for tetraploid taxa (Zonneveld 2001; Mabuchi et al. 2005; Cires et al. 2009; Cires et al. 2010; Zonneveld 2010; Soza et al. 2013; Zonneveld 2015; Mitrenina et al. 2020; Mitrenina et al. 2021; Salvado et al. 2022; Seidl et al. 2022). According to Salvado et al.'s (2022) report on the genome size of *Delphinium*, the tetraploid *D. montanum* had a 1C value of 10.32 pg. Here, the 2C-value of *D.* subg. *Anthriscifolium* was 3.02–3.92 pg for diploids and 6.04–6.60 pg for tetraploids, respectively. Chromosome counts were completed for selected taxa to confirm

ploidy and further calibrate the flow cytometry results. However, the above data lacks comparability due to the difference in experimental conditions and reference genome species.

Interestingly, in the study, the monoploid genome sizes of tetraploids (mean $1Cx = 1.57$ pg) are less than those of diploids (mean $1Cx = 1.69$ pg; see Fig. 3B), maybe showing a general tendency toward genome downsizing in the evolution of *Delphinium* subg. *Anthriscifolium*. Following polyploidisation, chromosome counts and genome size may change independently or dependently due to sequence loss and gain, chromosomal elimination, or chromosome fusions and fissions (Heslop-Harrison et al. 2023). Typically, the loss of repetitive DNA, such as retroelements or retrotransposons, caused the decline in monoploid genomes (Leitch and Bennett 2004; Bennetzen et al. 2005; Simonin and Roddy 2018). In addition, genome size data can be used to estimate ploidy in closely related taxa when properly calibrated with known cytological standards (Shearer and Ranney 2013; Lattier et al. 2014; Hembree et al. 2019). *Delphinium anthriscifolium* var. *anthriscifolium* is tetraploid with a genome size of about 6.28 pg. In comparison, the remaining diploid taxa have a genome size of approximately 3.38 pg, meaning that polyploidisation occurred in the *D.* subg. *Anthriscifolium*.

Taxonomic treatment

1. *Delphinium anthriscifolium* Hance. In J. Bot. 5: 207. 1868.

= *D. calleryi* Franch. in Bull. Mens. De la Soc. Linn. De Paris, 1: 329. 1882. ≡ *D. anthriscifolium* var. *calleryi* (Franch.) Fin. & Gagnep. in Bull. Soc. Bot. Fr. 51: 471. 1904. syn. nov. Type: China: Aomen (Macao), 1841, *Callery* 6 (Holotype P!); Aomen, 1844, *Callery* 51 (Isotypes P!).

= *D. cavaleriense* Lévl. et Vant. in Bull. Acad. Géog. Bot. 11: 49. 1902., syn. nov. Type: China: Guizhou (Kweichow), “environs de Tou-chan, belles fleurs bleues”, 2 June 1898, *J. Cavalerie* 2344 (Holotype E!; Isotypes K!).

= *D. cerefolium* Lévl. et Vant. in Bull. Acad. Géog. Bot. 11: 49. 1902., syn. nov. Type: China: Guizhou (Kouy-Tcheou), Guiyang (Kouy-Yang), “mont du College”, 2 June 1898, *Chaffanjon* s.n. (Holotype E!).

Type material. Lectotype: CHINA: Guangdong (Kwantung), “necnon prope rupem calcaream kai-kun-shek, secus eundem fluvium”, June 1867, *Sampson*, *Hance* no. 10125 (Holotype K!; Isotypes BM! NY! P! JE! GH).

2. *Delphinium savatieri* Franch. In Bull. Mens. De la Soc. Linn. De Paris 1: 330. 1882.

≡ *D. anthriscifolium* var. *savatieri* (Franchet) Munz., J. Arnold Arbor. 48: 261. 1967. Type: China: Zhejiang (Tche-kiang/Chekiang), “in siccis ad pedem montium Shao-Shin, prope Ning-po”, May 1863, *Lud. Savatier* (Holotype P!; Isotype P!).

= *D. robertianum* Lévl. et Vant. in Bull. Acad. Géog. Bot. 11: 49. 1902., syn. nov. Type: China: Guizhou (Kouy-tcheou), Guiyang (Kouy-yang), 9 Dec 1897, no. 2025 (Holotype E!).

- = *D. minutum* Lévl. et Vant. in Bull. Herb. Boiss. sér. 2, 6: 505. 1906., syn. nov.
Type: China: Guizhou, 2 Mar 1904, Jos. Esquirol no. 23 (Holotype E!).
- = *D. kweichowense* W.T.Wang in Acta Bot. Sin., 10: 283. 1962., syn. nov. Type:
China: Guizhou, Huishui, 18 July 1930, Y. Jiang 8571 (PE!).

Note. Morphologically, *D. savatieri* differs from *D. anthriscifolium* in that the staminode limb is ovate (vs. dolabriform), 2-lobed (vs. 2-parted), and its base is broadly cuneate (vs. subtruncate). Cytologically, *D. savatieri* also differs from *D. anthriscifolium* in that its karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$ (vs. $2n = 4x = 32 = 4m + 16sm + 12st$).

3. *Delphinium zanlanscianense* W.G.Zhang & X.Y.Luo, nom. nov.

urn:lsid:ipni.org:names:77328947-1

- ≡ *Delphinium anthriscifolium* var. *majus* Pamp. in Nuovo Giorn. Bot. Ital., n.s., 20: 288. 1915.
- = *D. anthriscifolium* f. *latilobulatum* W.T.Wang in Acta Bot. Sin., 10: 279. 1962., syn. nov. Type: China: Hunan, Xue-Feng-Shan, 1954, Z. T. Li 2371 (Holotype PE!; Isotype PE!).

Type material. Lectotype: CHINA: Hubei (Hu-peh), Zhanglang County (Zan-lan-scian), 1913, P. C. Silvestri no. 3917 (Holotype FI!).

Note. Morphologically, *D. anthriscifolium* var. *majus* differs from *D. anthriscifolium* var. *anthriscifolium* in that the flowers are 2.3–3.4 cm long (vs. 1.0–1.8 cm), spur 1.7–2.2 cm (vs. 0.5–2.2 cm) and its base 3.0–4.0 mm (vs. 1.5–4.0 mm) in diam., other sepals 1.2–1.6 cm (vs. 0.6–1.6 cm), staminode limb broadly ovate (vs. dolabriform or ovate). Cytologically, *D. anthriscifolium* var. *majus* differs from *D. anthriscifolium* var. *anthriscifolium* in that its karyotype formula is $2n = 2x = 16 = 2m + 6sm + 8st$ (vs. $2n = 4x = 32 = 4m + 16sm + 12st$).

When elevating *D. anthriscifolium* var. *majus* to the rank of species, the name is already occupied by *D. majus* (W.T.Wang) W.T.Wang (Wang and Hsiao 1965), making it necessary to propose a replacement name. Thus, we propose the name '*zanlanscianense*' based on the locality of its lectotype.

Conclusions

In the present study, comparative karyomorphological analyses and genome size determinations of five taxa of *Delphinium* subg. *Anthriscifolium* have been carried out. The chromosome numbers of *D. savatieri*, *D. zanlanscianense*, *D. callichromum*, and *D. ecalcaratum* were determined for the first time. Karyotypes of *D.* subg. *Anthriscifolium* were shown to have both common and species-specific features related to chromosome number, size, and morphology. All studied taxa have the basic chromosome numbers $x = 8$, diploid, or polyploid cytotypes, and the monoploid genome size (C-value) determined by flow cytometry varies more than twice. Additionally, the monoploid genome sizes of tetraploids (mean $1Cx = 1.57$ pg) are smaller than those of diploids (mean $1Cx = 1.69$ pg). Thus, genome loss or duplication events have occurred in the evolution of *D.* subg. *Anthriscifolium*. Finally, based on

cytological and morphological evidence, *D. anthriscifolium* var. *savatieri* was restored to species rank, and *D. anthriscifolium* var. *majus* was elevated and renamed as *D. zanolanscianense*.

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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, Data curation, Writing – original draft: XYL. Methodology, Visualization: TJN. Data curation, Visualization: HL, YH, XFD. Conceptualization, Resources, Supervision, Writing – review and editing: WGZ, CCG.

Author ORCIDs

Xiao-Yu Luo  <https://orcid.org/0009-0005-8153-7348>

Tang-Jie Nie  <https://orcid.org/0000-0003-2405-8904>

Heng Liu  <https://orcid.org/0009-0008-4900-4025>

Xue-Fei Ding  <https://orcid.org/0009-0008-2034-5459>

Ying Huang  <https://orcid.org/0009-0004-7731-6916>

Chun-Ce Guo  <https://orcid.org/0000-0003-3376-1116>

Wen-Gen Zhang  <https://orcid.org/0000-0003-0946-8614>

Data availability

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

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Lithocarpus tapanuliensis (Fagaceae), a new stone oak from northern Sumatra and its role as an important resource for critically endangered orangutans

Try Surya Harapan^{1,2,3}, Wei Harn Tan⁴, Thoriq Alfath Febriamansyah³, Nurainas³, Syamsuardi³, Joeri Sergej Strijk⁵

1 Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences & Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China

2 Yunnan International Joint Laboratory of Southeast Asia Biodiversity Conservation & Yunnan Key Laboratory for Conservation of Tropical Rainforests and Asian Elephants, Menglun, Mengla, Yunnan, 666303, China

3 Herbarium Andalas, Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Andalas, Jl. Universitas Andalas, Limau Manis, Padang 25163, West Sumatra, Indonesia

4 Faculty of Science, Universiti Brunei Darussalam, Jalan Tungku Link, Gadong BE1410, Darussalam, Brunei

5 Alliance for Conservation Tree Genomics, Pha Tad Ke Botanical Garden, 06000 Luang Prabang, Laos

Corresponding author: Try Surya Harapan (surya@xtbg.ac.cn)

Abstract

A new species of stone oak, *Lithocarpus tapanuliensis* Harapan, W.H.Tan, Nurainas & Strijk from South Tapanuli, North Sumatra, Indonesia is described. We provide colour photographs, a distribution map and a new IUCN conservation status assessment for inclusion on the global Red List. The unique cupule morphology, particularly the shape, placement and distinctness of the cupule protuberances, are distinctive from other *Lithocarpus* species in the region. Ecological interactions (e.g. consumption and nesting) with Tapanuli orangutans were recorded in the field.

Key words: Batang Toru, Hoteng, *Lithocarpus tapanuliensis*, Sumatran Fagaceae, Tapanuli orangutan, food habits



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Introduction

The tropical rainforest of Sundaland is one of the most megadiverse regions on the Planet (Myers et al. 2000), with the island of Sumatra as one of the larger remaining land masses in this submerged continental shelf. Sumatra serves as a refugium for many Sundaic flora and fauna species (Woodruff 2010). Some of the world's most critically endangered megafauna (Sumatran elephant (*Elephas maximus sumatranus* Temminck, 1847); Sumatran rhinoceros (*Dicerorhinus sumatrensis* Fischer, 1814); Sunda tiger (*Panthera tigris sondaica* Temminck, 1844) and Sumatran and Tapanuli orangutans ((*Pongo abelii* Lesson, 1827) and (*Pongo tapanuliensis* Nurcahyo, Meijaard, Nowak, Fredriksson & Groves, 2017)) are found here. Sumatra is also botanically diverse, with an estimated number of 10,600 plant species and more than 300 endemics (Roos et al. 2004). Moreover, the plant diversity of Sumatra is hypothesised to be as diverse

as Borneo and much richer than the other neighbouring islands of Java and Sulawesi (Meijer 1981). However, floristic studies in Sumatra have been neglected in the past, with the mistaken assumption of being well documented due to its similarity with flora from the Malay Peninsula (Whitten 1984; Laumonier 1997). Recent discoveries in various taxa prove otherwise, sparking renewed interest in the island's rich untapped diversity.

Lithocarpus Blume (Stone oaks) is the second largest genus in the Fagaceae family (Camus 1952–1954), with approximately 347 species recorded globally, including 32 found in Sumatra, of which five species are endemic to the island (POWO 2023; Strijk 2023). Species from this genus are commonly found throughout Sumatra, inhabiting many different altitudinal habitats, from lowland to montane forest (Laumonier 1997; Fujii et al. 2006). Fujii et al. (2006) found a great species diversity of *Lithocarpus* in Sumatra between 400 and 700 m above sea level, with several species having distributions limited to certain elevations. Along with several families like Lauraceae and Myrtaceae, Fagaceae are a major component of the lower tropical montane rainforest between 900 and 1500 m above sea level (Cockburn 1972; Laumonier 1997). Species such as *Lithocarpus pallidus* (Blume) Rehder and *Lithocarpus pseudomoluccus* (Blume) Rehder often constitute the canopy layer of submontane forest in Sumatra (Laumonier 1997). Eight species of *Lithocarpus* were also recorded in Sumatra's upper montane forest (1400–2500 m a.s.l.) by Fujii et al. (2006), further highlighting the flexibility of the genus in occupying different ecological niches.

South Tapanuli is one of the three forest blocks that make up the Batang Toru Ecosystem and is the last refuge for the recently described, Critically Endangered and extremely rare Tapanuli orangutans (Kuswanda et al. 2020). The land cover within the Batang Toru Ecosystem consists of a mosaic of mixed plantations and primary and secondary forests (Meylia and Mustari 2022). During a field survey conducted in South Tapanuli in February 2023, specimens of an unknown *Lithocarpus* were discovered. Further morphological comparisons with other relatives in Malesia clearly distinguish it as a new species due to its distinctive cupule morphology (Cockburn 1972; Soepadmo 2000; Phengklai 2008). Hence, we describe and name it as *Lithocarpus tapanuliensis*, providing a description, accompanied by photographs and a morphological comparison with closely-related species, as well as an exploration of its interactions with Tapanuli orangutans.

Taxonomy

***Lithocarpus tapanuliensis* Harapan, W.H.Tan, Nurainas & Strijk, sp. nov.**

urn:lsid:ipni.org:names:77329008-1

Fig. 1

Type material. Holotype. INDONESIA, North Sumatra Province, South Tapanuli Regency, Sipirok District, Bulu Mario Village, Pilar Forest (Fig. 2). 1°34'53.9"N, 099°11'38.2"E, elevation 894 m, 23 February 2023, **Holotype:** ANDA [ANDA00000051794]; **Isotypes:** ANDA [ANDA00000051793].

Diagnosis. *Lithocarpus tapanuliensis* distinguishes itself from similar species through its presence and placement of unique bullate protuberances



Figure 1. *Lithocarpus tapanuliensis* Harapan, W.H.Tan, Nurainas & Strijk, sp. nov. **A** fresh fruits from field collection **B** fresh fruits in the canopy **C** bark and sapwood **D** fresh leaves **E** dried mature and immature infructescence **F** base of tree next to an animal wallow **G** cupule- bottom view, top view and nut bottom view and cross-section. Pictures by T.S. Harapan & T.A Febriamansyah, edited by W.H. Tan.

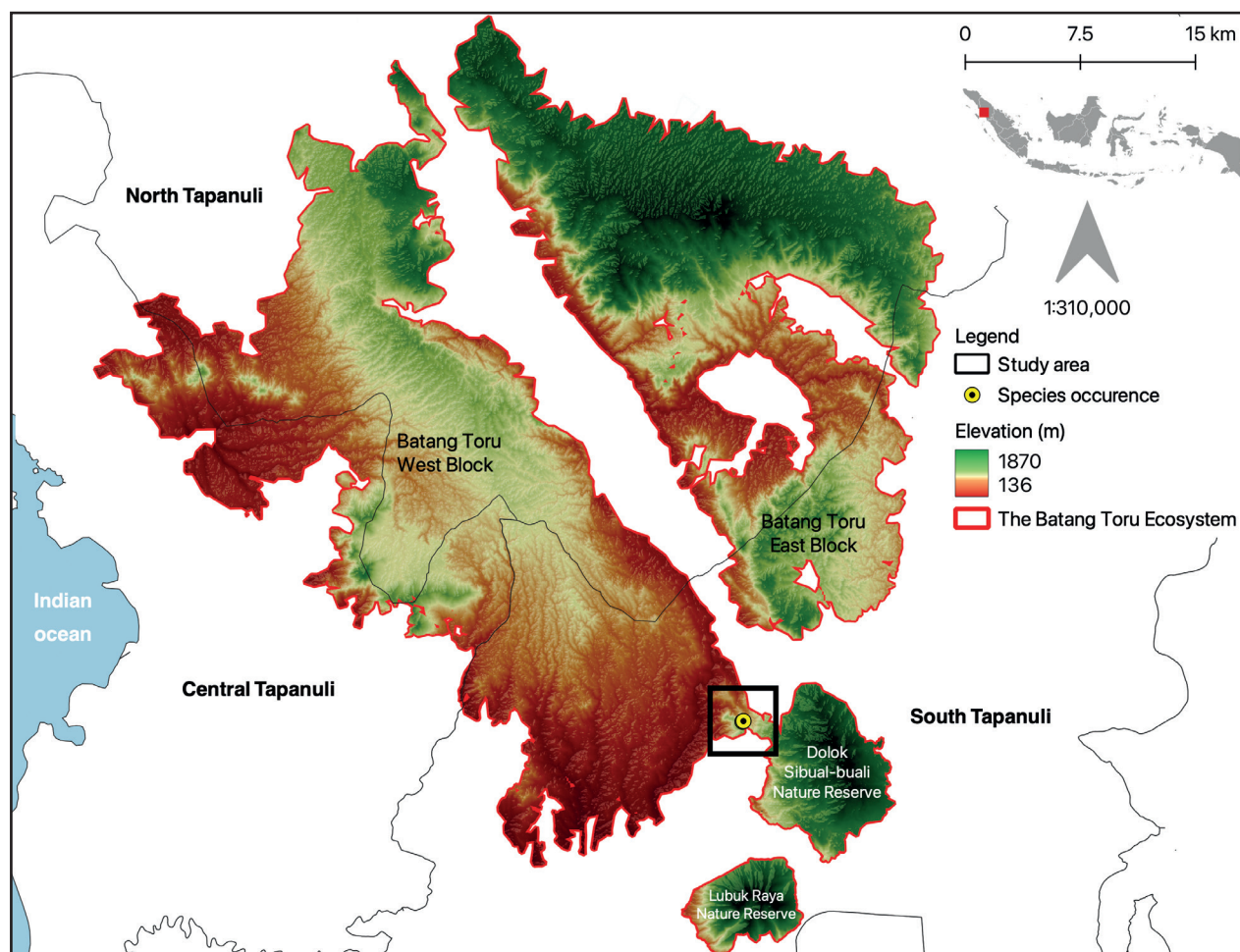


Figure 2. Distribution map of *Lithocarpus tapanuliensis* sp. nov. in South Tapanuli, North Sumatra. The inset map shows the location of the sampling region on Sumatra Island, Indonesia. Elevation was obtained from SRTM (2023). Map by T.S. Harapan.

covering the cupule and the distinct presence of a narrow ring of small denticulated plates around the rim. It differs from *L. elegans* (Blume) Hatus. ex Soepadmo with tiny, pointed scale-like appendages, *L. confragosus* (King ex Hook.f.) A.Camus with close-set warts, *L. corneus* (Lour.) Rehder with the diamond-like pattern and *L. pulcher* (King) Markgr. with tuberculate cupules. The cupule of *L. tapanuliensis* covers almost 3/5 of the nut (in contrast with *L. pulcher* and *L. confragosus*, whose cupule encloses almost the entire nut). The surface of the cupule is slightly tomentose and dark brown with distinct protuberances (whereas *L. confragosus*, *L. corneus* and *L. pulcher* lack such because of the absence of lamellae) (Table 1).

Description. A large tree without buttresses, up to 35 m tall. **Bark** rough, lightly fissured, greyish-green with whitish lenticel. Inner bark is dark red forming longitudinal slits. **Twigs** diameter 0.2–0.4 cm, smooth, striate, bud imbricate 0.5 mm. **Branches** dark brown. **Leaves** simple, underneath tomentose, dark green above and fawn green below when fresh; above, dull greyish-brown, lightly brown when dry. Blade elliptic-oblong, 16.5–20 (L) × 6–8.5 (W) cm; margin entire; apex cuspidate tip; bases attenuate. Petiole: striate, glabrous, 1.3–1.5 cm in length. **Venation** mid-rib wide, raised on both sides; pinnately veined, secondary

Table 1. Morphological differences between *Lithocarpus tapanuliensis* sp.nov and other species of *Lithocarpus* in the surrounding region from literature (Cockburn 1972; Soepadmo 2000; Phengklai 2008).

Characters	<i>Lithocarpus tapanuliensis</i> Harapan, W.H. Tan, Nurainas & Strijk	<i>L. confragosus</i> (King ex Hook.f.) A.Camus	<i>L. corneus</i> (Lour.) Rehder	<i>L. luteus</i> Soepadmo	<i>L. elegans</i> (Blume) Hatus. ex Soepadmo	<i>L. pulcher</i> (King) Markgr.
1. Cupule surface	Up to ½ covered with bullate protuberances; upper ½ with narrow ring of small denticulated plates. The surface of the cupule is slightly tomentose	Outside irregularly set with rounded to pointed short tubercles.	Outside with triangular to rhomboid bracts, the centre and margin ridged or fused with cupule and ± united into concentric rings.	Woody, tomentose, lamellate; thick, hairy, enclosing up to half of the acorn; lamellae obscure or slightly distinct, edge denticulate, set in 8–10 regular lines.	Adpressed tomentose, scale-like appendages distinct, appressed, woody imbricate, set in regular lines.	Woody, tomentose, covered in distinct sturdy tuberculate, irregularly and densely set on the upper part of cupule, spreading out towards the base.
2. Nut scar	Concave.	Flat to concave, basal only.	Scar covering ½ to most of nut, convex.	Flat.	Flat to concave, basal only.	Scar covering ¾ of the nut, deeply convex.
3. Size of acorns (<i>l</i> × <i>w</i>)	1.9–2.9 cm long, 2.6–3.4 cm in diam.	1.5–2.5 cm long, 2–4 cm in diam.	2.5–3.4 cm long, 3.3–4.9 cm in diam.	1–1.5 cm long, 2–2.5 cm in diam.	1.5–2.5 cm in length, 1.5–3 cm in diam.	2–4 cm long, 4–5 cm in diam.
4. Acorn position	Sessile, solitary along the rachis and spaced.	Sessile or with stalk up to 1 cm.	Sessile, singular or in 2s, 3s or 4s.	Sessile, solitary or more common in clusters.	Sessile or with stalk up to 0.5 cm, solitary.	Sessile, solitary along the rachis.
5. Nut surface	Sparsely tomentose.	Glabrous, smooth.	Tomentose around the apex.	Densely fulvous to greyish-tomentose.	Glabrous, smooth.	Sparsely tomentose, brown.
6. Wall; nut covering extent of the cupule.	Free from the cupule; up to half of the nut covered.	For the greater part free from the cupule; enclosing greater part of the nut, except for opening.	Free from the cupule; enclosing ca. ½ of the nut.	Free from the cupule; enclosing ca. ½ of the nut.	Free from the cupule; enclosing ca. ½ nut.	Mostly adnate to the cupule; enclosing greater part of the nut except for opening.
7. Nut shape	Obovoid (more flat at the apex)	Depressed, ovoid-globose, top rounded and depressed umbonate at the centre, base truncate	Subglobose to turbinate, apex rounded, flat, or slightly concave	Ovoid to sub hemispherical	Ovoid or depressed ovoid to subglobose, apex rounded	Obconical-hemispherical. Top flat or convex. Base deeply convex
8. Leaf shape; size (<i>l</i> × <i>w</i>)	Elliptic to oblong, (14) 16–17(20) × (4.7) 6–7(8.5) cm, margin entire, apex cuspidate, base attenuate.	Elliptic to oblong, to broadly elliptic, (10–)12–18(–27) × (3.5–)5–7(–10) cm, broadest around the middle line.	Elliptic to oblong, (5–)10–15 × 2–4.5 cm. Base cuneate to subrounded and symmetric or oblique, margin dentate, shallowly undulate, or rarely entire, apex acuminate to acute.	Elliptic to obovate, (7–)9–12 (–15) × (2.5 –) 3.5–5 (–6) cm, broadest at or slightly below the middle, base acute to cuneate, top acute to 1 cm acuminate.	Narrowly to broadly obovate or elliptic, (9–)12–17(–21) × 3–6(–8) cm base acute or cuneate, margin revolute, apex bluntly acute or acuminate.	Broadly elliptic to oblong, (10–)15–20(–30) × (4–)6–8(–12.5) cm, base acute to cuneate, margin revolute, apex acute to acuminate.

venation eucamptodromous. Pairs of secondary nerves 10–11 pairs, raised on the underside. Tertiary veins sub-scalariform. **Male and female inflorescences** not seen. **Peduncles** up to 2–4 cm long and between 0.3 and 0.5 cm in diameter. **Infructescence** rachis diameter 0.4–0.5 cm. **Acorn** solitary along the rachis and spaced both in immature and mature stages. **Cupule** solitary and sessile, greenish-brown when fresh, mature cupules cup-shaped covering half of the nut, diameter 2.8–3.4 cm, cupule thickness 2.4–2.8 cm. thick-walled woody, cupule surface irregular, with a narrow ring of small denticulated plates around the rim, rest of cupule covered in distinct bullate protuberance gradually fusing into large tumour-like masses towards the base. Protuberances, specifically the rim, have resin burn marks with blackish shiny colour when dried. Immature cupules thin, cup-shaped covering 80% of the nut, covered in small protuberances ranging from relatively flat lines to bullate. **Nut** obovoid, length 1.9–2.3 cm, diameter



Figure 3. **A** Acorns consumed by orangutan **B** orangutan nest in a neighbouring tree. Pictures by T.S. Harapan & T.A. Febriamansyah, edited by W.H. Tan.

2.2–2.6 cm, sparsely tomentose around the basal scar, fawn-green when ripe, brownish-grey when dried, basal scar depressed, nut scar diameter 1.6–1.7 cm, thickness 0.3–0.4 cm. Resin leaking on the nuts. Apex flattened obtuse.

Phenology. Fruiting was observed in February 2023 with fresh fruits recovered from the tree and from the ground.

Distribution, habitat and ecology. During our fieldwork in Pilar Forest, a primary forest near the Bulu Mario District, we recorded two individuals of *Lithocarpus tapanuliensis*. The lower-montane forest is characterised by the abundance of meranti gunung (*Shorea platyclados* Slooten ex Endert). Additional Fagaceae species were recorded, namely *Lithocarpus javensis* Blume, *Quercus oidocarpa* Korth. and *Castanopsis tungurrut* (Blume) A.DC. Interactions with Tapanuli orangutans were observed with a nest and remnants of consumed fruits were recorded near the tree (Fig. 3). Sipirok Regency precipitation typically varies during different sections of the year. Maximum monthly precipitation is 296.5 mm and the minimum monthly precipitation is 67 mm, with an average temperature around 28 °C (Badan Pusat Statistik 2023).

Vernacular name. Hoteng (Tapanuli language).

Etymology. The epithet is derived from its type locality, Tapanuli, South Tapanuli District, Sipirok Regency, North Sumatra Province, Indonesia.

Conservation status. Using the guidelines established by the IUCN Red List (IUCN Standards and Petitions Committee 2022), we provide an initial conservation assessment of the species as Critically Endangered (B1ab(iii) + B2ab(iii), D), based on only two recorded individuals within Pilar Forest, its limited range and extensive habitat alteration and forest clearance in the immediate vicinity of the forest and throughout Sumatra. Pilar Forest does not have any legal protection or governance, but is immediately adjacent to Dolok Sibual-buali Nature Reserve. Both are part of the wider Batang Toru ecosystem landscape (150,000 ha; Fredriksson and Usher (2017)). Under this programme, the area is targeted for protection, ecosystem restoration and sustainable tourism development through a combination of NGOs and the State. More information and images are available on the species webpage (www.asianfagaceae.com/lithocarpus_tapanuliensis/) and GBIF.

Discussion

There are an estimated 32 species of *Lithocarpus* documented in Sumatra (Soepadmo 1972; Purwaningsih and Polosakan 2016; POWO 2023; Strijk 2023). *Lithocarpus tapanuliensis* sp. nov. is distinguished from other *Lithocarpus* in the region by its distinctly large acorn and a cupule covered in unique bullate protuberances and the distinct presence of a narrow ring of small denticulated plates around its rim. The possibilities of hybrids between stone oaks are rare because of the limited contact zone between closely-related taxa in our field sites (primary forest). A study in Mexico shows hybridisation of *Quercus* occurs in areas with high levels of disturbance (Tovar-Sánchez and Oyama 2004). Exposed and disturbed areas by humans may establish the hybrid zone (Howard et al. 1997; Tovar-Sánchez and Oyama 2004) and enhance opportunities for contact and cross-pollination (Arnold et al. 1990; Klier et al. 1991).

The flora of Sumatra has garnered more interest over the last decade with a variety of plant species being described, like the iconic rafflesia (Susatya et al. 2017), enigmatic pitcher plants (Victoriano 2020), several begonias (Hughes et al. 2015)

and a peculiar pipevine (Mustaqim and Arico 2022). To the authors knowledge, the discovery of *L. tapanuliensis* is the first new Sumatran *Lithocarpus* to be described in the last decade. This is a major contrast with other neighbouring botanical countries, in which a significant number of Fagaceae have been described in the last decade (e.g. Tan et al. (2023); Zhang et al. (2023)). The hotspots of *Lithocarpus* diversity are well-known to be in Indochina and NE Borneo, but the diversity of Sumatran Fagaceae has remained understudied. With further efforts in the future, the number of species confirmed for this island is expected to significantly increase.

During fieldwork, acorn remains of *L. tapanuliensis* and *C. tungurrut* consumed by Tapanuli orangutans were collected (Fig. 3A). It has been well documented that the acorns, leaves and bark of Fagaceae (i.e. *Lithocarpus*, *Castanopsis* and *Quercus*) are consumed by all three orangutan species (Russon et al. 2009; Kuze et al. 2011; Payne and Zainudin 2023). Fruit scarcity is a common occurrence in the seasonal Sundaic rainforest, due to the supra-annual fruiting cycle (within a period of 2–10 years) of many major tree families (e.g. Wong et al. (2005); Tan et al. (2021)). Although often overlooked, Sundaic Fagaceae are often a fall-back resource for many animals in periods of fruit scarcity, being one of the few families to have annual asynchronous fruiting (Araye et al. 2022). Besides the well-documented rodents, several large Asian megafaunal species, such as the Asian black bear (*Ursus thibetanus* Cuvier, 1823) and Malayan sun bear (*Helarctos malayanus* Raffles, 1821) (Wong et al. 2002; Fredriksson et al. 2006; Steinmetz et al. 2013) often consume fruits of Fagaceae, especially in times of famine. The great migrations of the bearded pig (*Sus barbatus* Müller, 1838) across Borneo are dictated by the fruiting of several species, including those from Fagaceae (Lusking and Ke 2017). The importance of Fagaceae as a food supply for many species in times of famine should warrant greater protection for the family throughout its range in Southeast Asia as the loss of matured Fagaceae would have detrimental trophic effects.

An orangutan nest was also observed in a neighbouring tree to *L. tapanuliensis* (Fig. 3B). Orangutans are known to make their nest close to food sources and can be very selective of the tree species used. Species from families like Fagaceae and Dipterocarpaceae, with dense branching and tall, straight boles with thick diameters, are often favoured by orangutans for nest building, as they are relatively stable and provide good vantage points across the canopy (Kuswanda et al. 2020; Patana et al. 2021; Meylia and Mustari 2022). However, orangutans will avoid building nests in fruiting trees to avoid disturbance from other animals that also used the same resources (Sugardjito 1983; Van Casteren et al. 2012). The ecological interactions we recorded in the field further highlight the importance of Fagaceae to orangutans. Hence, we strongly recommend future conservation plans in the region to incorporate the family, not only for orangutans, but also for the myriad of other species that rely upon it for resources.

We provide an initial IUCN conservation assessment for *L. tapanuliensis* as Critically Endangered, as only two individuals were recorded in a small section of South Tapanuli, specifically in Pilar Forest (West Block of Batang Toru Ecosystem). The Batang Toru ecosystem suffers from habitat fragmentation and habitat loss due to massive infrastructure projects, such as mining, agroforestry plantations and hydropower in important corridor areas (e.g. Rahman et al. (2019)). Most of the Batang Toru area has been gazetted as protected forest, but some key forest areas are still unprotected (Fredriksson 2017; Sloan et al. 2018; Rahman et al. 2019). Recent infrastructure development near the study

area could further fragment important habitats, increasing the risk of damaging the unique biodiversity found within this landscape. Conserving the remaining forest within the Batang Toru ecosystem is important to safeguard orangutans and many other mammals that depend on seasonal fruit production in highland and lowland forest areas of Batang Toru (Buij et al. 2002).

Our findings make an important contribution to the discovery of new Fagaceae species, highlighting the importance of preserving Indonesia's unique habitats of the Batang Toru landscape. A comprehensive understanding of the species, along with further surveys and spatial distribution analysis, is crucial for protecting against potential extinction. Future strategies must focus on the long-term survival of the species through ex situ conservation in suitable habitats combined with in situ conservation efforts (Volis and Blecher 2010; Harapan et al. 2022).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

TSH conceived the study, conducted the field survey, and wrote first draft of manuscript. WH wrote first draft of the manuscript, revised the manuscript and prepared the figures. TAF photographed the specimens, supported the field survey, and measured the specimens. NN & SS coordinated field survey, commented on the manuscript, and revised the herbaria collection. JSS wrote the first draft of manuscript, commented on, and revised the manuscript.

Author ORCIDs

Try Surya Harapan  <https://orcid.org/0000-0002-6513-0012>

Wei Harn Tan  <https://orcid.org/0000-0002-0971-7820>

Syamsuardi  <https://orcid.org/0000-0001-8351-6528>

Joeri Sergej Strijk  <https://orcid.org/0000-0003-1109-7015>

Data availability

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

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Ardisia krauensis, a new species of Primulaceae (Myrsinoideae) from Peninsular Malaysia

Avelinah Julius¹, Suhaimi Syahida-Emiza², Timothy M. A. Utteridge³

¹ Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia

² Forest Research Institute Malaysia, Kepong, Selangor, 52109, Malaysia

³ Royal Botanic Gardens, Kew, Richmond, TW9 3AE, UK

Corresponding author: Avelinah Julius (plagiovel80@gmail.com; avelinah.julius@ums.edu.my)

Abstract

Ardisia krauensis, a new species of Primulaceae from Peninsular Malaysia, is described and illustrated. The new species is assignable into subgenus (§) *Pyrgus* on account of specialised lateral reproductive branches bearing a terminal inflorescence subtended by foliose bracts. Morphologically, the new species mostly resembles *Ardisia rigida* in having elliptic leaves. However, the new species can be distinguished by the combination of its lateral veins number, the inflorescence branching pattern, the rachis and flower colour, and the stigma shape. *Ardisia krauensis* is found in an entirely protected habitat, thus, it is assessed as Least Concern (LC).

Key words: *Ardisia rigida*, conservation, endemic, Krau Wildlife Reserve, Pahang, SE Asia, subgenus *Pyrgus*, taxonomy

Introduction

Ardisia Sw., comprising about 730 species (POWO 2023) is one of the largest genera in the subfamily Myrsinoideae of the enlarged Primulaceae (APG 2016). The genus is morphologically classified into 14 subgenera by Mez (1902), with three additional proposed subgenera by Stone (1993: §*Scherantha* B.C.Stone, endemic to the Philippines), Larsen and Hu (1995: §*Tetradisia* (Mez) K.Larsen & C.M.Hu) and Yang and Hu (2022: §*Odontophylla* (Y.P.Yang) C.J.Yang & J.M.Hu) using characters of habit, leaf morphology, disposition of flowers at inflorescence branch apices (racemes, umbels, corymbs), inflorescence position and floral morphology. Of these, eleven subgenera are present in Peninsular Malaysia (for the grouping discussion see Stone 1989a; Larsen and Hu 1995; Yang and Hu 2022).

A flowering plant of *Ardisia* was collected during a botanical survey led by the second author in Krau Wildlife Reserve, Pahang in 2022. The plant is assignable to §*Pyrgus* (Lour.) Mez, which is defined by the combination of the small, woody shrub habit (rarely trees), entire leaves lacking bacterial nodules, and specialised lateral reproductive branches bearing a terminal inflorescence subtended by leaf-like foliose bracts (or referred to as ‘reproductive shoot’) (see Julius et al. 2021a; Utteridge and Julius 2022). This subgenus only has two species in Peninsular Malaysia: *Ardisia calophylla* Furtado and *A. rigida* Kurz s.l.; the latter is widespread



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from Peninsular Malaysia, through the Andamans (the type locality of *A. rigida*) and into the western side of Thailand. In the last treatment of the genus in Peninsular Malaysia, Stone (1989a) listed *A. calophylla* and *A. vaughanii* Ridl. as the two members of §*Pyrgus*. However, comparison of the types of *Ardisia vaughanii* and *A. rigida* shows clearly that they are conspecific, with *A. rigida* the older name, and both taxa were sampled for a recent molecular study and were found to be sister taxa with little or no support to maintain them as distinct species (Julius et al. 2021b). In addition, *A. oxystemon* Ridl. ex H.R. Fletcher was described from Peninsular Thailand but is conspecific with *A. rigida* and was placed as a synonym of the latter in the recent Flora of Thailand treatment (Larsen and Hu 1996).

After morphological comparison to closely related species and consultation with relevant literature (Furtado 1959; Stone 1989a, 1989b; Larsen and Hu 1996), the new taxon is an undescribed species and is thus described and illustrated here as new to science.

Material and methods

Morphological comparison with related species, viz. *Ardisia calophylla* and *A. rigida* s.l. (including *A. oxystemon* and *A. vaughanii*), was based on the study of herbarium material at K and KEP (acronyms according to Thiers 2016). In addition, specimen images online were also consulted (<http://plants.jstor.org/>). Floral measurements were made from rehydrated specimens. Morphological description of the new species is following Utteridge and Julius (2022). Flowering and fruiting material is indicated by 'fl.' and "fr.", respectively. The conservation status of the new species was assessed following IUCN standards (IUCN 2012, 2022), including guidelines and procedures developed by FRIM for the Malaysia Plant Red List (Chua and Saw 2006).

Taxonomy

Ardisia krauensis Julius, Syahida-Emiza & Utteridge, sp. nov. (§*Pyrgus*)

urn:lsid:ipni.org:names:77329057-1

Figs 1, 2

Diagnosis. Similar to *Ardisia rigida* in having elliptic leaves but differs in the lateral veins arranged more or less in parallel (vs. ascending), the specialised lateral branch with only 1 or 2–3 foliose bracts along its length (vs. 2–4), its inflorescence branched to 3-ordered (vs. branched to 2-ordered), pendulous with the rachis green and thinner (vs. erect, pink and stout), corolla lobes spreading (vs. recurved) and the stigma trilobed (vs. punctiform).

Type. MALAYSIA. Peninsular Malaysia: Pahang, Temerluh, Krau Wildlife Reserve, Sg. Teris, Plot 2 (UPM Resource Assessment for Flora in Krau Wildlife Reserve), 3°42.20'N, 102°03.95'E, alt. 131 m, 29 March 2022 (fl. & young fr.), Syahida-Emiza et al. FRI 95127 (holotype KEP!; isotype BORH!) (Fig. 2).

Description. Shrub c. 1.2 m tall. **Indumentum** of sessile, circular and rusty scale on vegetative part and multi-cellular ginger-brown hairs with two clavate lobes, and simple hairs of various lengths, either arranged singly or in groups of 2 or 3 on petiole and reproductive part. **Leaves** pseudowhorl of 3; petioles 1.5–1.7 cm long, covered with dense, rusty, simple and forked glandular hairs

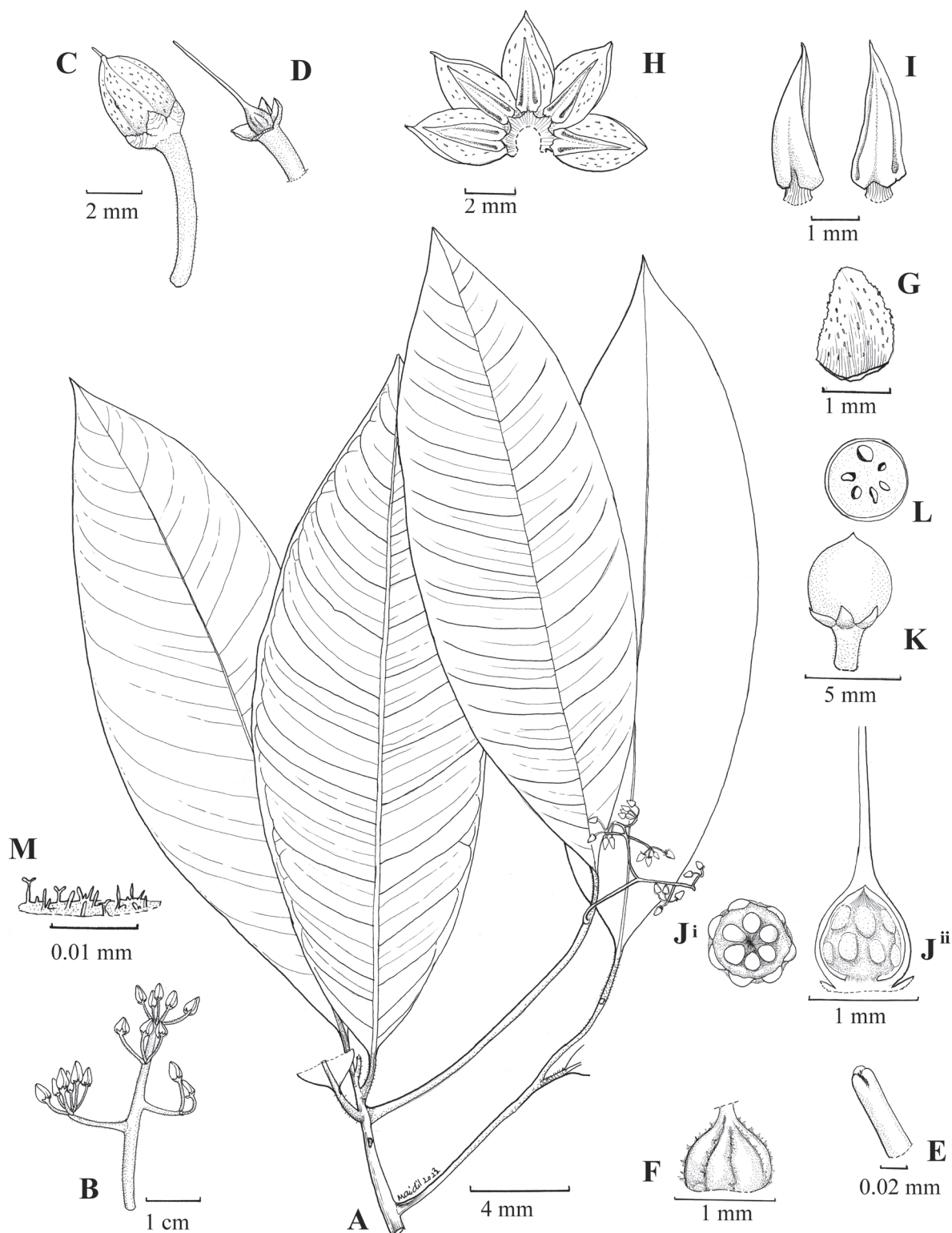


Figure 1. *Ardisia krauensis* **A** flowering branches **B** inflorescence **C** flower bud **D** corolla removed showing pistil **E** close-up of stigma **F** the grooved and hairy young ovary **G** abaxial view of calyx lobe **H** flower (spread) showing the stamen arrangement **I** abaxial (left) and adaxial (right) view of anther **J** dorsal (left) and ventral (right) view of placenta with ovules **K** young fruit **L** cross-section of young fruit **M** hair details. Illustration by Mohd Aidil Nordin.

when young, glabrous when mature; lamina chartaceous, raised between venation giving a somewhat bullate appearance, elliptic, 18.5–26 × 5–9 cm, base cuneate, margin entire, apex acuminate, acumen 1–1.5 cm long, glabrous on both



Figure 2. The holotype image of *Ardisia krauensis*.

surfaces, but densely scaly beneath; midrib flat above, raised beneath; lateral veins 15–21 pairs, joining towards the margin, and 1–2 intersecondary veins, prominent on both surfaces; intercostal veins obscure above, faintly reticulate beneath. **Inflorescences** terminal on specialised lateral branches arising directly from the stem, with 1–3 foliose bracts along the length of the branch and only one subtending the inflorescence, bracts elliptic, 16–26 × 5.5–9 cm, base cuneate, apex acuminate with acumen c. 1 cm long, petiole 7–10 mm long, densely hairy when young, glabrous when mature; inflorescences pendulous, branched to 3-orders, 5–6.2 cm long; peduncle and rachis green, thin, covered with dense, rusty, simple and forked glandular hairs throughout. **Flowers** 5-merous; pedicels 4–7 mm long, densely hairy and scaly towards calyx; calyx-lobes, ovate, c. 1.5 × 1 mm, margin erose, apex obtuse, spreading at anthesis, glabrous adaxially, densely hairy abaxially; corolla tube c. 0.2 mm long, lobes spreading, ovate, 3.8 × 2–3 mm, margin entire, one side slightly curve inward, apex appears acuminate but obtuse when flatten, glabrous on both surfaces but densely gland dotted throughout abaxially; stamens 5, filaments short c. 0.5 mm long at the basal part of anther, anthers ovate, c. 3 × 1.5 mm, connective acute, thecae not locellate, dehiscent by longitudinal slits; ovary subglobose, 0.5 × 0.8 mm, grooved at young stage, hairy on the groove, becoming smooth and glabrous with age, ovules c. 13 arranged in 2-series, stigma and style slender, 3.6–3.8 mm long, stigma trilobed, hairy with simple multicellular hairs adaxially, glabrous abaxially. **Young fruit** green, globose, c. 5 × 4.8 mm, glabrous, mature fruit unseen.

Distribution. Endemic to Peninsular Malaysia, Pahang. Thus far known only from Krau Wildlife Reserve (Fig. 3).

Ecology. In lowland forest, flat land near small river under a semi-shaded area, at 131 m altitude. Flowers and young fruits in March.

Etymology. The species epithet 'krauensis' refers to the type locality Krau Wildlife Reserve where it was collected.

Conservation status. Least Concern (LC). This new species was collected during a general survey in Krau Wildlife Reserve in 2022. There is no survey conducted specifically for this species yet, therefore we could not estimate the number of mature individuals and assessed it against Criterion D. As for D2, although this species is only known from one locality, but the habitat is protected and no plausible threat is identified, so it does not meet D2 also. Therefore, this species is currently best assessed as of Least Concern.

Notes. *Ardisia* subgenus *Pyrgus* is one of the smallest groups comprising only two known species in Peninsular Malaysia. This latest addition brings the number of *Pyrgus* species native to Peninsular Malaysia to three including *A. calophylla* and *A. rigida*. The new species resembles *A. calophylla* in that both have inflorescences branched to three orders, but the leaves of the former species are much smaller (to 10 cm long and 4 cm wide), obovate with an acute to rounded tip and a coriaceous lamina, whereas the leaves of *A. krauensis* are larger (18.5–26 cm long and 5–9 cm wide), elliptic with a long acuminate tip and a chartaceous lamina. Compared to *A. rigida*, the new species differs in the denser venation comprised of more lateral vein pairs (15–21 pairs vs. usually less than 15 pairs in *A. rigida*, though occasionally up to 18 pairs) as well as 1–2 intersecondary veins. The leaves of *A. rigida* usually dry and sandy-brown with the venation somewhat obscure, giving a very 'flat' and dull appearance in the herbarium, whereas the leaves of *A. krauensis* are olive green when dry, are

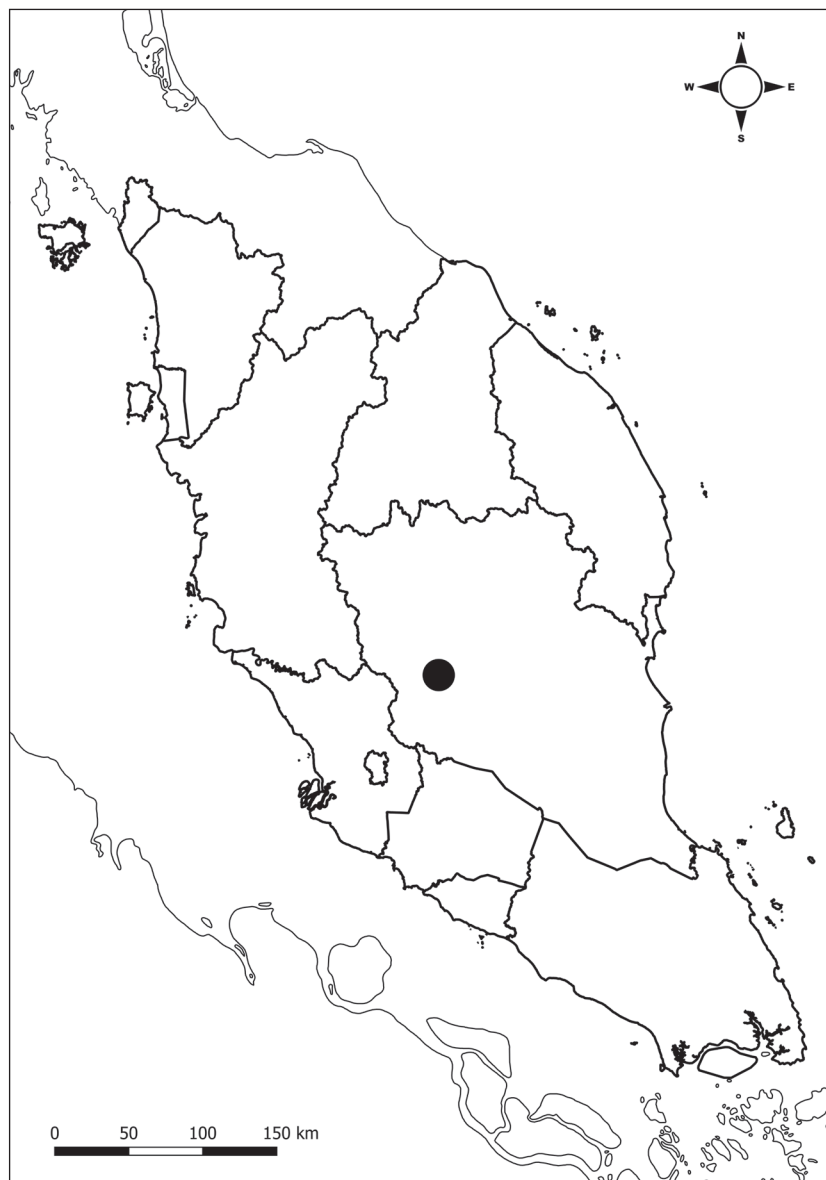


Figure 3. The type locality of *Ardisia krauensis* in Pahang, Peninsular Malaysia (Black Dot).

slightly thinner and dry with a ‘puckered’ appearance along the conspicuous venation. In *A. rigida*, the specialised lateral branches have up to 4 foliose bracts along their length and the terminal inflorescence is stout with a rigid rachis to 15 cm long; this is very different from the lateral branches with 1–3 foliose bracts and a thinner and more pendulous inflorescence rachis to only 5–6.2 cm long. The flowers of the new species differ with the filaments that are positioned at the base of the anther (vs. peltate), and the anther connective acute (vs. connective elongated, narrowly acute and becoming recurved at anthesis).

The stigma of *Ardisia* has variously been described as punctiform (Stone 1989a) or apiculate (Utteridge 2021), but *A. krauensis* possesses a stigma that is distinct in that it is divided into three lobes, closed, and hairy with simple multicellular hairs adaxially but glabrous abaxially. For any species within the genus that we previously studied, the ovary often exhibits a constant shape and degree of hairiness. The ovary of *A. krauensis*, however, is grooved and hairy at the groove when young (Fig. 1F), but gradually becomes smooth and glabrous with age (Fig. 1Jⁱⁱ).

Key to Peninsular Malaysian species of *Ardisia* subgen. *Pyrgus*

- 1 Leaves up to 10 cm long, lamina obovate with acute to rounded apex, coriaceous; foliose bracts in a pseudowhorl of 3–5 just below the inflorescence..... ***Ardisia calophylla***
- Leaves > 10 cm long, lamina elliptic with obtuse or acuminate apex, chartaceous; foliose bracts alternately arranged 1–4..... **2**
- 2 Foliose bracts 2–4; inflorescences erect, branched to 2-ordered; rachis pink and stout; corolla lobes recurved; stigma punctiform..... ***Ardisia rigida***
- Foliose bracts 1–3; inflorescences pendulous, branched to 3-ordered; rachis green and thinner; corolla lobe spreading; stigma trilobed ***Ardisia krauensis***

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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

AJ & TMAU: paper writing, plant identification & examination. AJ & SES: conservation assessment. SES: fieldwork.

Author ORCIDs

Avelinah Julius  <https://orcid.org/0000-0003-1991-1915>

Suhaimi Syahida-Emiza  <https://orcid.org/0000-0002-9321-2779>

Timothy M.A. Utteridge  <https://orcid.org/0000-0003-2823-0337>

Data availability

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

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A new species of *Mollinedia* (Monimiaceae, Laurales) from the Quadrilátero Ferrífero, Brazil

Danilo Alvarenga Zavatin¹, Renato Ramos^{1,2}, Mauricio Takashi Coutinho Watanabe²,
Luciano Gonçalves Pedrosa³, Elton John de Lório²

¹ Universidade de São Paulo, Instituto de Biociências, Rua do Matão 277, Edifício Sobre-as-ondas (Herbário), São Paulo, SP, 05508-900, Brazil

² Instituto Tecnológico Vale, Rua Boaventura da Silva 955, Belém, PA, 66055-090, Brazil

³ Departamento de Biodiversidade, Evolução e Meio Ambiente, Universidade Federal de Ouro Preto, Campus Morro do Cruzeiro, ICEB III, Ouro Preto, MG, 35400-000, Brazil

Corresponding author: Danilo Alvarenga Zavatin (danilozavatin@ib.usp.br)

Abstract

Monimiaceae comprises approximately 26 genera and 250 species, with a pantropical distribution, predominantly occurring in humid forests. In Brazil, it is represented by five genera and 47 species, most of which are found in the Atlantic Forest, particularly in dense ombrophilous forest. Nevertheless, studies on this family in other biomes and vegetation types in Brazil are still scarce. The Quadrilátero Ferrífero (QF), a region located in the state of Minas Gerais, exhibits high plant species richness and endemism. During collections and analysis of herbarium materials from this region, some specimens of *Mollinedia* caught our attention due to a combination of characteristics that do not match those of any described species within the genus. For this reason, we describe this new taxon and assess its risk of extinction. Additionally, we review the occurrences of Monimiaceae in the QF and provide maps of its geographical distribution. With the description of this new species, the region now hosts eight species of Monimiaceae, two from the genus *Macropelplus* and six from *Mollinedia*. The new species is the first endemic species of the Monimiaceae family to be described in the QF. Concerning the extinction risk assessment, the new species was assessed as critically endangered.

Resumo

Monimiaceae abrange c. 26 gêneros e 250 espécies, tem distribuição pantropical e suas espécies ocorrem predominantemente em florestas úmidas. No Brasil está representada por cinco gêneros e 47 espécies, a maior parte das quais com ocorrência na Mata Atlântica, em floresta ombrófila densa. Estudos com a família em outros biomas e vegetações ainda são escassos no Brasil. O Quadrilátero Ferrífero (QF), região localizada no estado de Minas Gerais, possui alta riqueza e endemismo de plantas. Durante coletas e análise de materiais herborizados da região, alguns espécimes de *Mollinedia* nos chamaram a atenção devido a uma combinação de caracteres que não coincidem com nenhuma espécie descrita para o gênero. Este novo táxon é aqui descrito e tem seu risco de extinção avaliado, além disso, revisamos as ocorrências de Monimiaceae no QF, e fornecemos mapas de distribuição geográfica. Com a descrição desta nova espécie, a região apresenta agora oito espécies de Monimiaceae, duas do gênero *Macropelplus* e seis de *Mollinedia*. A nova espécie é a primeira da família endêmica do QF. Em relação à avaliação do risco de extinção, a nova espécie foi categorizada como Criticamente em Perigo.



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Key words: Flora of Brazil, Magnoliidae, Mollinedieae, new taxon

Palavras-chave: Flora do Brasil, Magnoliidae, Mollinedieae, novo taxon

Introduction

Monimiaceae is a pantropical family of shrubs, trees or lianescent plants with opposite leaves showing acuminate-convex teeth on the margin and venation entering the tooth medially and not joined by lateral veins, called “monimioid teeth” (Hickey and Wolf 1975). The family has 26 genera and c. 250 spp. occurring mainly in humid forests (Philipson 1993; Renner et al. 2010; Lírío et al. 2020a). On the American continent, ca. 60 species occur in six genera: *Grazielanthus* Peixoto & Per.-Moura, *Hennecartia* J. Poiss., *Macrotorus* Perkins, *Macropeplus* Perkins, *Mollinedia* Ruiz and Pavón and *Peumus* Molina (Lorence 1999; Lírío et al. 2020a, b). *Mollinedia* is the richest Neotropical genus of the family, with c. 45 species, occurring in southern Mexico and Central and South America (Lírío et al. 2015, 2020a). *Mollinedia* is characterized by staminate flowers with nearly rounded buds, tepals with a ratio of ca. 1:1 in relation to the length of the flower, ovate or rounded stamens, and locules with two longitudinal openings and an extended connection or confluence at the apex, making the anther horseshoe-shaped (Perkins 1898, 1900; Lírío et al. 2020a). However, phylogenetic analyses suggest that this morphologically well-circumscribed genus is not monophyletic, albeit with low statistical support (Renner et al. 2010). In Brazil, there are 38 species of *Mollinedia*, 33 of which occur in the Atlantic forest, four in the Amazon forest, three in the Cerrado, and one in Pantanal (Lírío et al. 2020a). To date, 28 species of *Mollinedia* have been officially assessed at the national level following IUCN criteria, with 11 of them being considered threatened with extinction and one as deficient data (Lírío et al. 2023a). In addition, many *Mollinedia* species are microendemic, known by few collections in herbaria and/or considered rare (Lírío et al. 2018, 2023a).

The “Quadrilátero Ferrífero” (QF) region belongs to Minas Gerais state (Brazil) and is situated in a transition zone between the Atlantic Forest and Cerrado domains. The total area is approximately 7,200 km² and has significant iron ore reserves (Jacobi et al. 2007; Messias et al. 2012). At the highest altitudes, ironstone outcrop vegetation (named “canga”) can be found. This ecosystem is considered a center of high diversity, including the occurrence of poorly known, endemic and endangered plant and animal species (Jacobi et al. 2007; Zappi et al. 2017).

Seven species of Monimiaceae have been registered in the QF region, none of which are restricted to this area, five of which belong to *Mollinedia* and two of which belong to *Macropeplus* (Fig. 1). Here, a new species of *Mollinedia* endemic to the QF is described and illustrated. Additionally, its conservation status is evaluated, and its morphological affinities are discussed.

Material and methods

The newly described species was recognized by a unique combination of features (Donoghue 1985) identified through comparisons with morphologically similar taxa and a literature review (Peixoto 2002; Lírío and Peixoto 2017; Lírío et al. 2020a). A 10–60× magnification stereomicroscope was used to analyze the

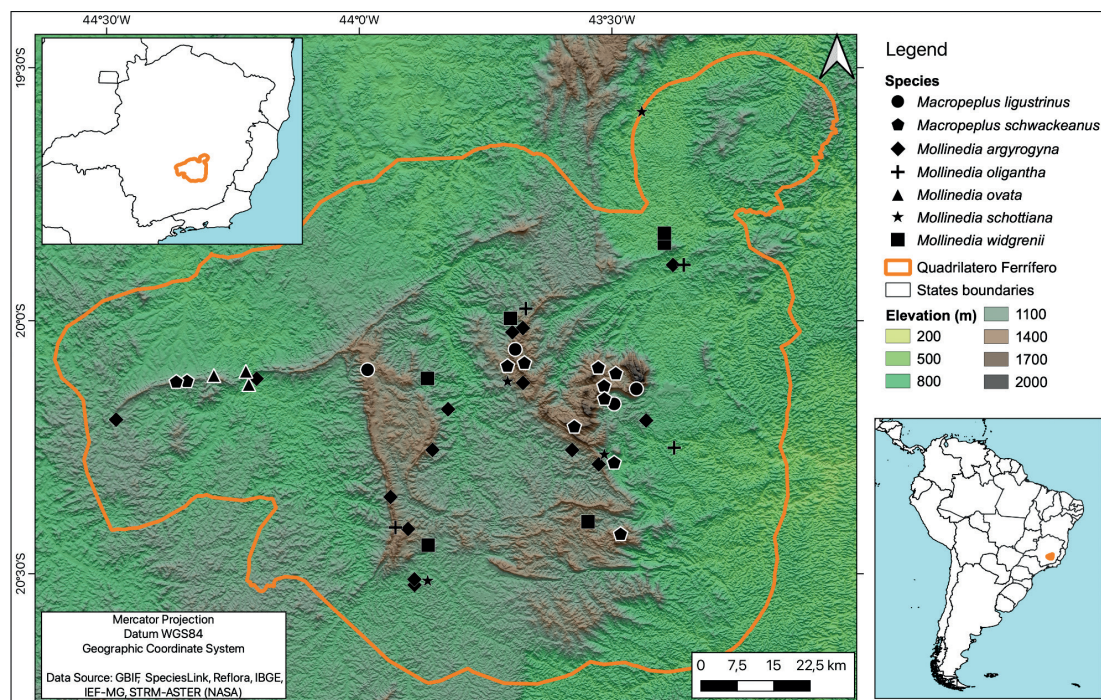


Figure 1. Geographic distribution map of Monimiaceae species in the Quadrilátero Ferrífero, state of Minas Gerais, Brazil, showing the limits of the region, mountainous areas and elevations.

morphological features of the specimens. Terminology follows that of Harris and Harris (2001) for general morphology, except for characters unique to Monimiaceae, which are described according to Hickey (1973), Hickey and Wolfe (1975) and Perkins (1898, 1900). Herbarium acronyms follow Thiers (2023, continuously updated). The comparison with similar species was conducted through analysis of collections deposited in the following herbaria: BHCB, BHZB, GH, HAS*, ICN*, INPA, LZ*, MA, MBM, MBML, MO*, NY*, OUPR, SP, SPF, P, RB and W. Specimens from collections indicated with “*” were studied based on digital images available in virtual herbaria (REFLORA 2023; SpeciesLink 2023). IUCN (2012, 2022) conservation status was applied to assess and analyze the threat criteria at the interface with the anthropogenic factors fire (INPE 2023) and land natural or anthropogenic cover (IDE-SISEMA 2019). Species area values were determined using GEOCAT (Bachman et al. 2011). Environmental characteristics were mapped using soil data (UFV 2010a, b), elevation data (NASA et al. 2019) and 10-meter-resolution normalized difference vegetation index (NDVI) data from the Sentinel-2 databases processed in the *rgee* package (Aybar et al. 2020) of R (R core Team 2018). A distribution map was produced in QGIS version 3.16 (QGIS Development Team 2021).

Taxonomic treatment

Mollinedia fatimae Zavatin & Lírío, sp. nov.

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Figs 2–4

Type. BRAZIL, Minas Gerais: Ouro Preto, Parque Estadual do Itacolomi, mata em frente à capela, 20°26'04"S, 43°30'37"W, 1343 m elev., 28 Nov 2022, mal. fl.

D.A. Zavatin & L.G. Pedrosa 1327 (holotype: SPFI, isotypes (to be distributed to): ALCB!, B!, BHCBI, BHZBI, DIAM!, HUFU!, HURBI, KI, MEXU!, MO!, NY!, OUPRI!, PI, PTBRI!, RBI, UBI!).

Diagnosis. *Mollinedia fatimae* resembles *Mollinedia boracensis* due to its coriaceous leaf consistency; however, it can be easily differentiated by the leaves glabrate on the abaxial surface (vs. glabrous), flowers farinose-pilose (vs. puberulous), stamens 14–20 (vs. 22–24) and carpels 12–20 (vs. 26–30).

Trees, ca. 6–15 m tall, dioecious; rhytidome rough, twigs cylindrical, young branches strigulose, covered by whitish and long simple trichomes; older branches reddish, glabrescent, with conspicuous lenticels. **Leaves** 5.5–12.5 × 1.5–2.8 cm, opposite, narrowly elliptic, apex attenuate or usually rounded, base attenuate, margin entire or with 1–5 teeth per side, not in pairs, irregularly distributed between sides, from the upper half to the apex, coriaceous, discolored, brown when dried, lighter on the abaxial surface, young leaves white-strigose on both surfaces; denser on primary vein of the abaxial surface, then glabrate on the abaxial surface and glabrous on the adaxial surface, primary vein apparent on the adaxial surface and prominent on the abaxial surface, whitish pubescence adpressed on the abaxial surface, mostly along the basis of the primary vein, secondary veins 4–6 pairs, not apparent or only slightly apparent on the adaxial surface and prominent on the abaxial surface, petiole 0.5–1.1 cm long, canaliculated, puberulous or glabrous on older leaves. Inflorescences in thyrses or fascicles with up to 3 cymes (3-florous), axillary or terminal. **Staminate flowers** greenish, 5 × 5 mm, indumentum of two types, farinose and pilose, caducous on anthesis, rachis 1.5–3 cm, peduncle 3–8 mm, pedicel 4–8 mm, bracts ovate, apex acute or rounded, c. 1 mm long, bracteoles lanceolate, apex acute, 2–3 mm long, whitish tomentose or when absent, with a ferruginous scar, receptacle campanulate, tepals c. $\frac{3}{4}$ of the flowers length, externals ovate, apex obtuse, internals ovate, apex truncate or acuminate, stamens, 14–20, ovate, locules confluent at the apex, filament short. **Pistillate flowers** greenish, 5 × 6 mm, fascicles up to 2 flowers, rarely solitary, indumentum of two types, farinose and pilose, peduncle 0.4–2 cm, pedicel 1–1.7 cm, bracts ovate, apex acute or rounded, c. 1 mm long, bracteoles lanceolate, apex acute, 2–3 mm long, whitish tomentose or when absent, with a ferruginous scar, receptacle cupuliform, internally puberulous, tepals c. $\frac{3}{4}$ of the flower length, externals ovate with a caudate apex, margin entire, internals ovate with truncate or acuminate apex, carpels 12–20, ovary oblong, stigma c. $\frac{1}{3}$ of the carpel length. **Drupelets** ellipsoid, 0.8–1.5 × 0.7–1.3 cm, not stipitate, apex rounded, stigma persistent, brown when dried, fruiting receptacle 0.6–1 cm wide, reflexed, fruit scars prominent, peduncle plus pedicel 1–1.7 cm long.

Phenology. The species was collected with flowers in November and fruits in March.

Etymology. The epithet of this species is a homage to Dra. Fátima Otavina de Souza Buturi, an inspiring Brazilian botanist who dedicates her career studying Asteraceae, mentoring several biologists and botanists, including the first author of this paper (DAZ).

Habitat and distribution. *Mollinedia fatimae* occurs at an average altitude of 1527 m (min.: 1354 m; max.: 1673 m), on mountain slopes or in river drainage ravines (Fig. 4A), predominantly in Haplic Cambisols – typical dystrophic, texture medium (code RLd10 in Fig. 4B), formed from matrix rocks of phyl-

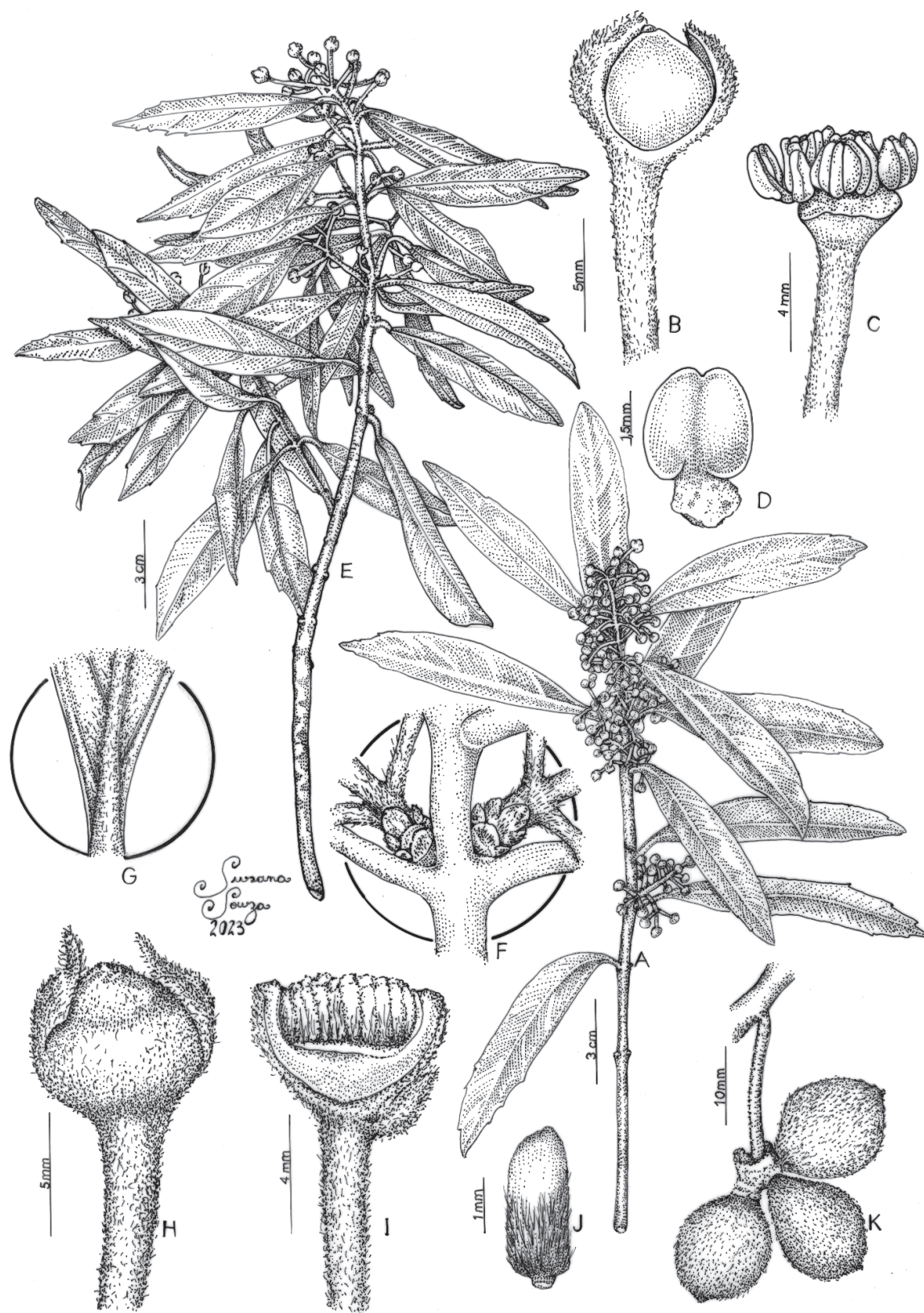


Figure 2. **A** branch with staminate flowers **B** staminate flower in lateral view **C** staminate flower with tepals removed, showing the stamens **D** stamen **E** branch with pistillate flowers **F** detail of cataphylls **G** detail of leaf abaxial surface **H** pistillate flower in lateral view **I** pistillate flower dissected, showing the carpels **J** carpel **K** composed fruit. (Illustrated by Susana Souza based on Zavatin 1326 and 1327 and Pedrosa 46 specimens).

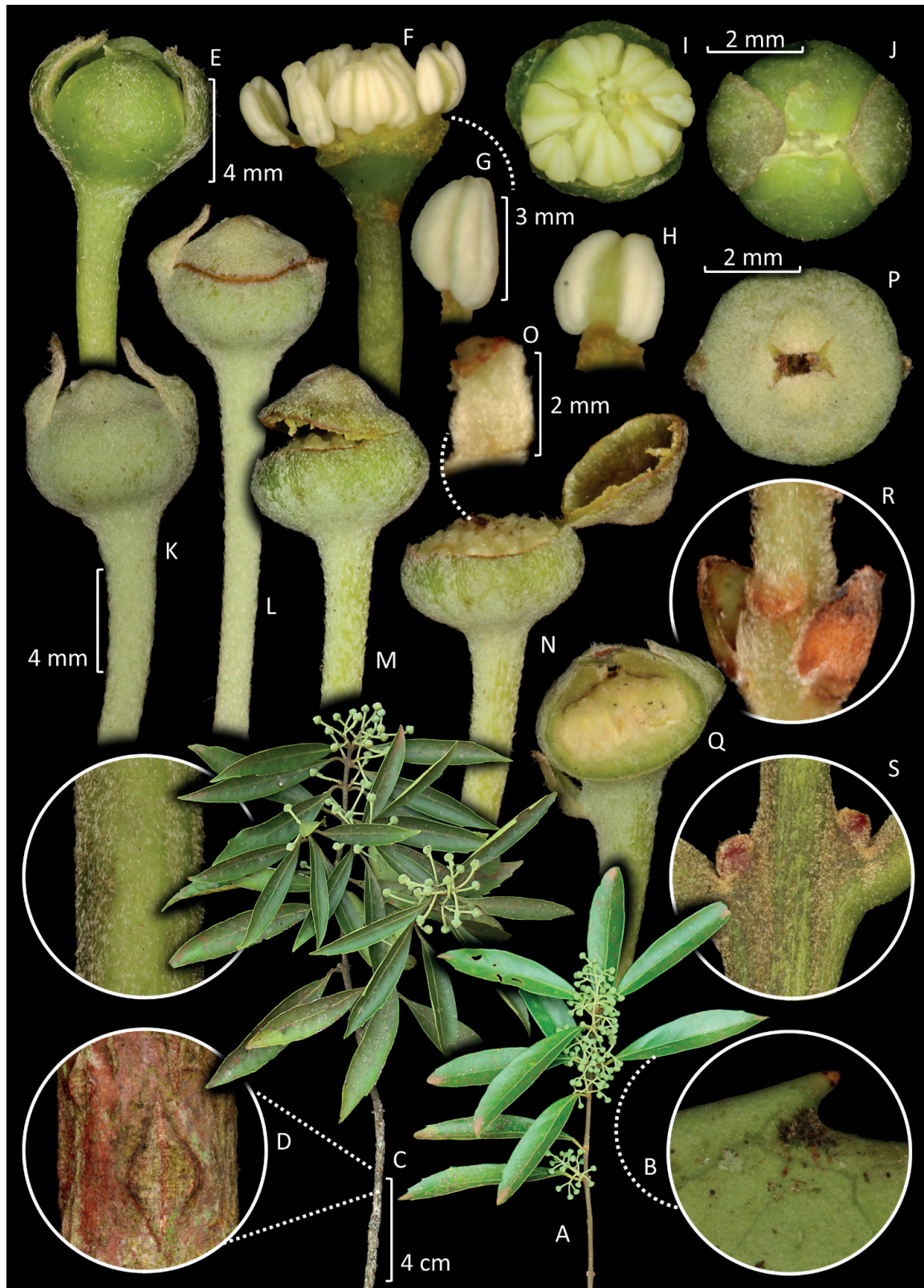


Figure 3. **A** branch with staminate flowers **B** monimiod tooth **C** branch with pistillate flowers **D** magnification of a young reddish branch showing a lenticel **E** staminate flower **F** staminate flower with the removal of tepals showing the androecium **G-H** stamens **I** staminate flower with removed tepals in upper view **J** staminate flower in upper view, almost complete anthesis **K** pistillate flower **L** pistillate flower starting scission in the tepals **M** early opening of calyptra **N** opened calyptra exposing the carpels **O** carpel **P** pistillate flower in upper view in anthesis **Q** pistillate flower in longitudinal section **R** bractlets **S** cataphylls. (Image authorship: Danilo A. Zavatin).

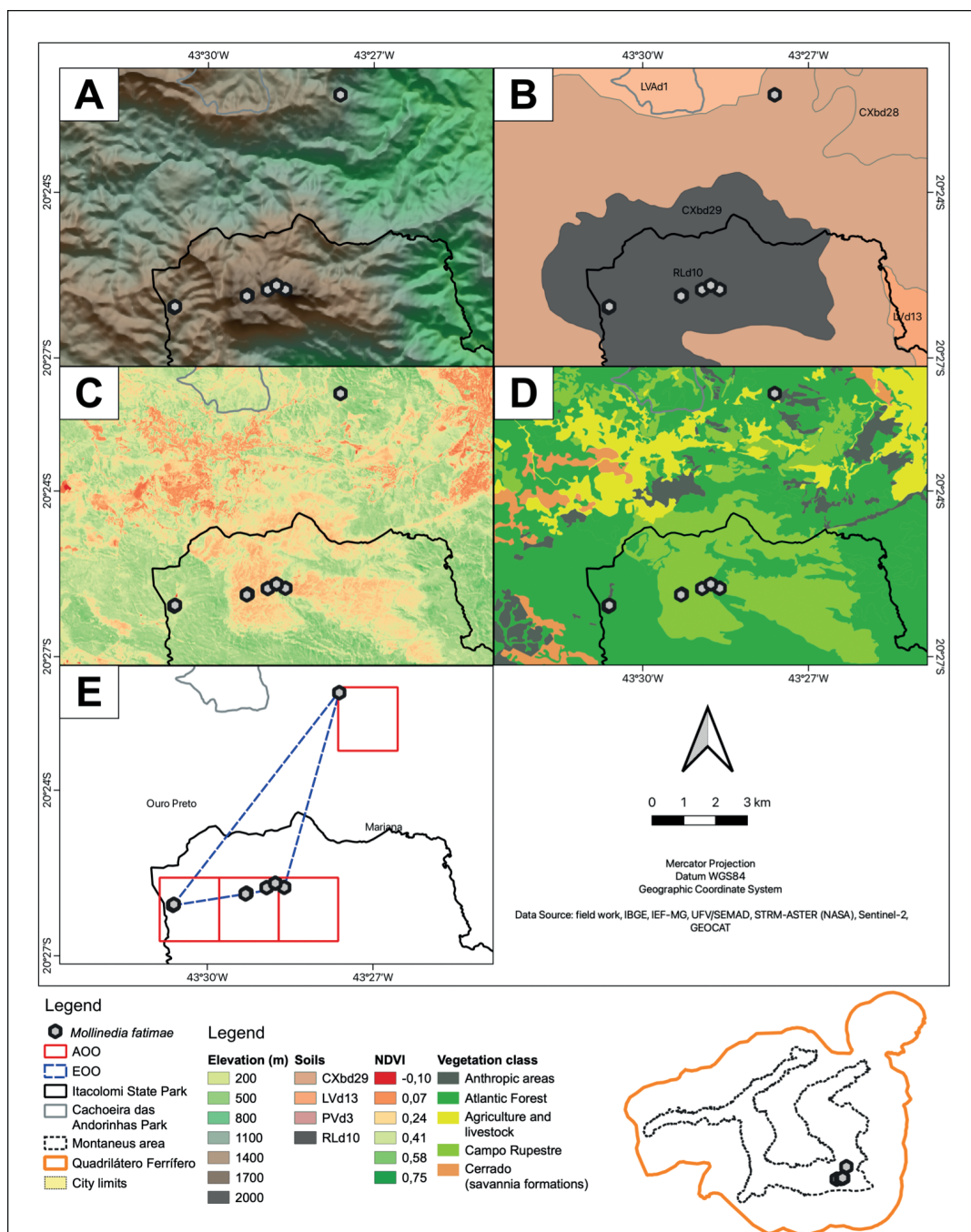


Figure 4. Environmental and Conservation spatial data **A** digital elevation model of the terrain **B** soil classes **C** normalized difference vegetation index (NDVI) **D** natural vegetation and anthropic use classes **E** AOO and EOO analyses.

lite, schist, dolomite and quartzite. The vegetation is defined as mountainous semideciduous seasonal forest in intermediate to advanced stages of regeneration, with perceptible variations in the NDVI (Fig. 4C). Its individuals grow in extensive forest fragments at lower elevations but with most occurrences in small forest enclaves in areas with a predominance of “campo rupestre”, where vegetation indices indicate open formations in the surroundings (Fig. 4D).

Conservation status. Most species’ populations are inside the integrally protected Itacolomi State Park, on the boundaries of the Ouro Preto and Mariana municipalities, with an EOO of 11.06 km² and AOO of 16 km² (Fig. 4E). Accord-

ing to the B1ab (iii, iv) criteria (IUCN 2012, 2022), the species should be considered critically endangered (CR). The main threats are stochastic events due to seasonal variations and climate change but mainly due to fires in the region. In high areas, fire is ignited by rare natural phenomena (i.e., lightning) and mainly by artificial fires (Schumacher et al. 2022). These fires spread quickly through campo rupestre, invading forests with significant dry biomass accumulation. Four of the six species records occur in these vegetation contact zones, with severe population decline projections if fires intensify in the region. The expansion of burned areas and the calorific power of fires have intensified in the last five years (INPE 2023). Furthermore, restricted endemism impacts potentialize the overall occurrence of the species, even with localized events.

Additional specimens examined. BRAZIL. Minas Gerais: Ouro Preto, Parque Estadual do Itacolomi, mata em frente à capela, 20°26'04"S, 43°30'37"W, 1343 m elev., 28 Nov 2022, fem. fl., D.A. Zavatin & L.G. Pedrosa 1326 (ALCB!, B!, BHCB!, BHZB!, DIAM!, HUEFS!, HUFU!, HURB!, INPA!, K!, MEXU!, MO!, NY!, OUPR!, SPFI!, P!, PTGB!, R!, RB!, UB!, UCI!, UEC!); Cratera no topo da montanha à esquerda antes do Pico do Itacolomi, 20°25'46.2"S, 43°28'56.1"W, 1594 m elev., 28 Nov 2022, mal. fl., D.A. Zavatin & L.G. Pedrosa 1334 (BHCB!, MEXU!, OUPR!, P!, RB!, SPFI!); Cratera em frente ao Pico do Itacolomi, 20°25'41.2"S, 43°28'46.1"W, 1588 m elev., 7 Nov 2022, mal. fl., D.A. Zavatin & L.J. Sauthier 1284 (BHCB!, MEXU!, OUPR!, RB!, SPFI!) Cratera no topo da montanha à esquerda antes do Pico do Itacolomi, 20°25'52.4"S, 43°29'18.1"W, 1590 m elev., 8 Nov 2022, mal. fl., D.A. Zavatin & L.J. Sauthier 1285 (BHCB!, MEXU!, P!, RB!, SPFI!); Cratera no topo da montanha à esquerda antes do Pico do Itacolomi, 20°25'52.2"S, 43°29'17.4"W, 1590 m elev., 8 Nov 2022, mal. fl., D.A. Zavatin & L.J. Sauthier 1286 (BHCB!, MEXU!, NY!, OUPR!, P!, RB!, SPFI!); Cratera no topo da montanha à esquerda do Pico do Itacolomi, 20°25'43.7"S, 43°28'36.0"W, 1596 m elev., 8 Nov 2022, mal. fl., D.A. Zavatin & L.J. Sauthier 1287 (B!, BHCB!, HURB!, K!, MEXU!, NY!, OUPR!, P!, PTGB!, RB!, SPFI!); Fazenda do Manso, 20 Mar 2018, fr., L.G. Pedrosa 46 (OUPR!); Serra do Espinhaço, Ouro Preto, disturbed vegetation on a S-SE exposed place in the area of "Campo Grande" along the road to Cachoeira das Andorinhas, 1470–1500 m elev., 17 Sep 1990, ste., G.L. Esteves, W. Morawetz, B. Wallnofer & J.L. da Silva 15456 (NY, W).

Similar species and remarks. *Mollinedia fatimae* does not co-occur with other species of the genus. The new species resembles *Mollinedia boracensis* Peixoto due to its coriaceous leaves; however, it can be easily differentiated by the length of the petioles and the indumentum of leaves and flowers. Additionally, the farinose-pilose flower indumentum in *Mollinedia fatimae* resembles that in *Mollinedia arianae* Lirio & M. Pignal and *Mollinedia leucantha* M. Molz & D. Silveira, but the species can be differentiated from *M. arianae* by the branch indumentum, leaf consistency, and color when dried and can be distinguished from *M. leucantha* mainly by its leaf consistency, indumentum, color when dried and number of carpels. The new species was recorded in herbaria as *Mollinedia engleriana* Perkins, probably due to the dark-brown color of the leaves when dried (darkish in *M. engleriana*), but it can be differentiated from this species mainly by its leaves and flower indumentum and the length proportion of the staminate tepals in relation to the receptacle. All the comparisons with related species are summarized in Table 1.

Table 1. Comparison of *Mollinedia fatimae* sp. nov. with the similar species *Mollinedia boracensis* Peixoto and *Mollinedia engleriana* Perkins. Characters based on additional specimens examined and Peixoto (2002), Lirio and Peixoto (2017), Molz and Silveira (2021), and Lirio et al. (2020a) and (2023b).

Characters	<i>Mollinedia fatimae</i>	<i>Mollinedia arianeae</i>	<i>Mollinedia engleriana</i>	<i>Mollinedia leucantha</i>	<i>Mollinedia boracensis</i>
branch indumentum	glabrescent	tomentose	glabrous	glabrescent	glabrescent
leaf consistency	coriaceous	chartaceous	chartaceous or coriaceous	chartaceous	coriaceous
leaf width	1.5–2.8 cm	1.8–4 cm	2–10 cm	1.8–5.4 cm	3–5.5 cm
leaf color when dried	dark brown, lighter on the abaxial surface	olivaceous	Black	green-brownish, grayish brown on the abaxial surface	dark brown, lighter on the abaxial surface
leaf indumentum below	pubescent	tomentose	glabrous	tomentose	glabrous
flower indumentum	farinose and pilose	farinose and pilose	pubescent or glabrous	farinose and pilose	puberulous
tepala length in relation to flower length	tepals c. 3/4 of the flower length	tepals c. 3/4 of the flower length	tepals c. 1/2 of the flower length	tepals c. 1/4 of the flower length	tepals c. 1/2 of the flower length
number of stamens	14–20	16–21(–24)	10–20	19–20	22–24
number of carpels	12–20	unknown	12–23	22–34	26–30
geographic distribution	endemic to the Quadrilátero Ferrífero, state of Minas Gerais	endemic to Itatiaia National Park, state of Rio de Janeiro	states of Espírito Santo, Rio de Janeiro and São Paulo	states of Rio Grande do Sul and Santa Catarina	states of Rio de Janeiro and São Paulo

Supplementary material examined. *Macropeplus ligustrinus*. BRAZIL. Minas Gerais: Santa Bárbara, RPPN Santuário do Caraça, Trilha após a capela do Sagrado Coração, 4 Nov 2023, mal. fl., D.A. Zavatin, R. Ramos & L.J. Sauthier 1244 (SPF!). Belo Horizonte, Parque da Serra do Curral, Interior de mata sentido escritório da Vale, 22 May 2023, fr., D.A. Zavatin 1765 (SPF!). Distrito Federal: Brasília, Jardim Botânico de Brasília, 28 Sep. 2021, fem. fl., D.A. Zavatin 362 (SPF!). *Macropeplus schwackeanus*. Minas Gerais: Santa Bárbara, RPPN Santuário do Caraça, 3 Nov. 2022, mal. fl., D.A. Zavatin, R. Ramos & L.J. Sauthier 1214 (SPF!). RPPN Santuário do Caraça, 3 Nov. 2022, fem. fl., D.A. Zavatin, R. Ramos & L.J. Sauthier 1215 (SPF!). Monte Azul, Pico da Formosa, 28 Apr. 2023, fr., D.A. Zavatin, F.R. de Souza & J.C.B. dos Anjos 1700 (SPF!). *Mollinedia argyrogyna*. Minas Gerais: Ouro Preto, Camarinhas, 30 Jul. 1979, mal. fl., J. Badini s.n. (OUPR15501!). Ouro Preto, Camarinhas, 12 Sep. 1984, fem. fl., J. Badini s.n. (OUPR15500!). Santa Bárbara, RPPN Santuário do Caraça, 3 Nov. 2022, fr., D.A. Zavatin, R. Ramos & L.J. Sauthier 1216. (SPF!) *Mollinedia arianeae*. Rio de Janeiro: Serra da Mantiqueira, Maciço do Itatiaia, Parque Nacional do Itatiaia, Mata secundária entre a cascata de Maromba e cascata Véu de Noiva, 13 Aug. 1978, mal. fl., G. Gottsberger & W. Morawetz 15-13878 (GH!, LZ!, MA!, MO!, NY!, PI!, WI!). Parque Nacional do Itatiaia, borda de mata rente a trilha sentido cachoeira Véu da Noiva, 6 Jun. 2022, mal. fl., D.A. Zavatin & C. Gentile 780 (PI!, NY!, SPF!). Interior de mata rente à trilha, sentido cachoeira Itaporani, 7 Jun. 2022, mal. fl., D.A. Zavatin & C. Gentile 781 (PI!, NY!, SPF!). *Mollinedia boracensis*. Rio de Janeiro: Petrópolis, Floresta IBDF, Estrada Floresta Inglesa-Pati do Alferes, 23

Apr. 1980 fr., G. Martinelli 6729 (INPA!, MBM!, MO!, NY!, RB!). São Paulo: Santo André, Alto da Serra, Estação Biológica do Alto da Serra de Paranapiacaba, 19 Oct. 1931, mal. fl., C. Lemos s.n (SP29813!). Bananal, Fazenda Resgate, 22 Jun. 2005, mal. fl., J.L. Vieira 320 (RB!). *Mollinedia engleriana*. Brazil. Espírito Santo: Santa Teresa, Estação Biológica Santa Lúcia, trilha do indaiacú, 1 Nov. 2011, mal. fl., E. J. Lírio 47 (RB!, MBML!). Rio de Janeiro: Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, picada para Pedra Bicuda, 25 Jun. 1989, fem. fl., C.M.B. Correia 34 (RB!). Minas Gerais: Lima Duarte, Parque Estadual do Ibitipoca, 21 Sep. 2006, fr., R.C. Forzza, J.C. Silva, R.A.X. Borges, M.M. Saavedra & F.M. Ferreira 4289 (RB!). *Mollinedia leucantha*. Rio Grande do Sul: Três Cachoeiras, Lado esquerdo da RS-494, 1, 480 m da BR-101, 04 Nov. 2013, fem. fl., D. Silveira, F. Gonzatti & L. Machado 86 (ICN!, RB!, HAS!). Morrinhos do Sul, Pixirica, Rio do Mengue, 21 Apr. 2013, fr., D. Silveira, M. Molz & B.O. Boeni 43 (ICN!, RB!). *Mollinedia oligantha*. Minas Gerais: Santa Bárbara, EPDA de Peti, 16 Apr. 2005, fr., R.M. Ferreira & G.S. França 96 (BHCB!). Espírito Santo: Santa Teresa, Estação Ecológica Santa Lúcia, 17 Ago. 2022, mal. fl., D.A. Zavatin, H.L. Fonseca, A. Suzuki & E.J. Lírio 936 (SPF!). *Mollinedia ovata*. Minas Gerais: Coronel Pacheco, Estação Experimental de Café, 27 Feb. 1944, mal. fl., E.P. Heringer 1324 (RB!). Brumadinho, Inhotim, 11 Feb. 2009, fr., J.G. Oliveira & F.M. Rodrigues 431 (RB!). Rio de Janeiro: Silva Jardim, Reserva Biológica de Poço das Antas, 26 Nov. 1992, fem. fl., H.C. de Lima 4496 (RB!). *Mollinedia schottiana*. Minas Gerais: Ouro Preto, APA Cachoeira das Andorinhas, 27. Sep. 1999, mal. fl., M.C.T.B. Messias 234 (OUPR!). Ouro Preto, APA Cachoeira das Andorinhas, 26 Feb. 2000, fr., A.L. Silveira 98 (OUPR!). São Paulo: Americana, Parque da Gruta Dainese, 1 Dec. 2019, fem. fl., D.A. Zavatin & E.Z. Viana 153 (SPF!). *Mollinedia widgrenii*. Minas Gerais: Barroso, Mata do Baú, 21 Oct. 01, mal. fl., A.S.M. Valente, L.C.S. Assis, R.M. Castro, M.C.M. Garcia, G.E.P. Silva & R.C. Forzza 32 (CESJ! RB!). Tiradentes, Refúgio Estadual de Vida Silvestre Libélulas de São José, 12 Nov. 2022, fem. fl., D.A. Zavatin & L.J. Sauthier 1323 (SPF!). São Paulo: Piracicaba, ESALQ-USP, Mata próxima ao herbário, 18 Apr. 2022, fr., D.A. Zavatin 670 (SPF!).

Monimiaceae in the QF. Seven species of Monimiaceae occur in the QF region, two of the genus *Macropeplus* [*Macropeplus schwackeanus* (Perkins) I.Santos & Peixoto and *Macropeplus ligustrinus* (Tul.) Perkins] and four of *Mollinedia* [*Mollinedia argyrogyna* Perkins, *Mollinedia oligantha* Perkins, *Mollinedia ovata* Ruiz & Pav., *Mollinedia schottiana* (Spreng.) Perkins and *Mollinedia widgrenii* A.DC.]. *Mollinedia fatimae* sp. nov. is the eighth Monimiaceae species reported to occur in the QF and the only species endemic to this region.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: DAAZ. Data curation: RRR. Funding acquisition: RRR. Investigation: DAAZ. Methodology: LGP, MTCW. Project administration: DAAZ. Writing - original draft: DAAZ. Writing - review and editing: EJJ.

Author ORCIDs

Danilo Alvarenga Zavatin  <https://orcid.org/0000-0002-8851-0202>

Renato Ramos  <https://orcid.org/0000-0001-5957-3573>

Mauricio Takashi Coutinho Watanabe  <https://orcid.org/0000-0001-9690-5565>

Elton John de Lrio  <https://orcid.org/0000-0002-9986-9640>

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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Anoectochilus zhongshanensis (Orchidaceae), a new species from Guangxi, China

Yan-Bin Wu¹, Yu Han^{1,2*}, Xu-Hui He², Hui-Ling Chen¹, Jin-Zhong Wu¹, Qi Ye³, Cheng-Jian Zheng^{2,4}

¹ School of Pharmacy, Fujian University of Traditional Chinese Medicine, 1 Qiuyang Road, Fuzhou 350122, China

² Department of Chinese Medicine Authentication, Faculty of Pharmacy, Naval Medical University, 325 Guohe Road, Shanghai 200433, China

³ College of Life Sciences, Fujian Agriculture and Forestry University, Fuzhou 350001, China

⁴ State Key Laboratory for Quality Ensurance and Sustainable Use of Dao-di Herbs, Beijing 100700, China

Corresponding author: Cheng-Jian Zheng (cjzheng1984@126.com)

Abstract

A new species of *Anoectochilus* (Orchidaceae) from Guangxi, China, *A. zhongshanensis*, is described here, which was identified based on phylogenetic studies adopting combined plastid markers (*rbcL-matK-trnL-F*), morphological observation and chemical analysis. Molecular phylogenetic results support the systematic status of *A. zhongshanensis* as a new species in *Anoectochilus* genus. Morphologically, this new species is similar to *A. zhejiangensis* and *A. malipoensis*, but differs by its characteristic labellum and column, including the hastate or scalpel-shaped lobes of epichile, forward curved and pinnately divided cristate lobes at both sides of the mesochile and inverted triangle column wings. Furthermore, HPLC-ELSD analysis of these three species revealed the interesting chemotaxonomic difference that the principle and characteristic lactone glycoside in this new species was kinsenoside, rather than its diastereoisomer, goodyeroside A, a major glycoside in *A. zhejiangensis* and *A. malipoensis*.

Key words: *Anoectochilus*, new species, phylogeny, taxonomy



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Introduction

The genus *Anoectochilus* Blume (Goodyerinae, Cranichideae, Orchidaceae) consists of about 40 reported species in the world, distributed mainly from south and southeast Asia to Australia and the southwest Pacific islands (Jin et al. 2021; POWO 2023). To date, a total of 20 species (including 11 endemics) have been recorded from China (Tian and Xing 2008; Tian et al. 2014; Jin et al. 2021; POWO 2023). These *Anoectochilus* species, along with certain members of *Goodyera* and some related genera, are famous as Jewel Orchids in English (Cavestro 1994), and known as “Jin Xian Lian” in Chinese for their “golden lines” on leaves, with both medicinal and edible values.

In the course of our comprehensive resource survey of *Anoectochilus* species in China from 2015 to 2021, we have reported three new record species: *A. elatus* (Zheng et al. 2018), *A. papillosus* (Zheng et al. 2019) and *A. brevibris* (Wu et al. 2017), mainly based on their plant morphology. Chemical diversity could also provide some taxonomic evidence for the quality control

* These authors contributed equally to this work.

and authentication of *Anoectochilus* species using kinsenoside and goodyeroside A (a pair of diastereoisomers) as promising chemotaxonomic markers (Wu et al. 2020). However, species delimitation in this genus is still a big challenge and interspecific relationships among *Anoectochilus* species remain unclear. Molecular markers have therefore been more and more explored and utilized to solve those phylogenetic issues. ITS2 region as DNA barcode has been commonly adopted for distinguishing those related species, and also for the rapid discrimination of *A. roxburghii* and its counterfeits (Lv et al. 2015). Our recent study also indicated that both ITS2 and *psbA-trnH* sequences can be used to distinguish *A. roxburghii* from its related species with larger genetic distances (Wu et al. 2022b). By analyzing 20 species containing 58 samples, Han et al found that the combination of chloroplast gene fragments (*rbcl-matK-trnL-F*) was more helpful in exploring the infrageneric relationships among *Anoectochilus* species than any of those three individual DNA sequences (Han 2019). A similar strategy has been more recently adopted to identify a new *Anoectochilus* species, *A. medogensis*, from Tibet, China (Jin et al. 2021).

During our plant resource investigation in Zhongshan, Guangxi Province, China in Aug 2020, an *Anoectochilus* species was found to be difficult to identify, which was finally clarified as a new species on the basis of detailed morphological, molecular and chemical studies, and described below as *A. zhongshanensis* C.J. Zheng & Y.B. Wu. In this study, we deciphered the morphological differences between the new species and its nearest congener, *A. zhejiangensis* Z. Wei & Y. B. Chang. We also used three combined cpDNA sequences (*matK*, *trnL-F* and *rbcl*) to infer the phylogenetic relationships and substantiate the systematic status of *A. zhongshanensis* as a new species in *Anoectochilus*. In addition, potential chemotaxonomic markers, kinsenoside and goodyeroside A, were also employed to disclose the chemical difference between the new species and its nearest congeners, *A. zhejiangensis* and *A. malipoensis*.

Materials and methods

Voucher specimens of *A. zhongshanensis* were collected in Zhongshan, Guangxi Province, and preserved at the herbarium of Fujian Agriculture and Forestry University (FAFU!). Fresh leaves were washed and dried with filter paper in the field, and then stored in a plastic bag with silica gel for molecular experiments. The living plants of *A. zhongshanensis* were carefully observed for detailed morphological description and local observation of the plant's small parts was performed using a stereo microscope (SZ61). Tissue cultures of all collected *Anoectochilus* species in our lab have been successfully established for resource protection and further chemical and biological studies.

A total of 42 samples representing 18 *Anoectochilus* species were included for molecular analysis, and all sequences used for constructing the phylogenetic tree were downloaded from GenBank (Suppl. material 6) except those of the new species. *Zeuxinella vietnamica* was selected as an outgroup according to previous phylogenetic studies (Averyanov 1988; Averyanov and Averyanova 2003). To investigate the phylogenetic status of the new species within the genus *Anoectochilus*, four DNA markers, including internal transcribed spacer (ITS) and three plastid DNA regions (*matK*, *rbcl* and *trnL-F*), were selected to

reconstruct the phylogenetic tree based on previous studies (Jin et al. 2021; Tong et al. 2022).

Ezup column plant tissue genomic DNA extraction kit (Sangon B518261) was used to extract the total genomic DNA from silica gel-dried leaves of the new species. The concentration of DNA samples used in this study were ≥ 20 ng/ μ L, and the working DNA was stocked in refrigerator at 4 °C for use. Polymerase Chain Reaction (PCR) amplification was performed on a Veriti 96-well thermal cycler (Verity, ABI, USA) using a 25 μ L reaction system containing 2.5 μ L 10 $\times$ Taq Buffer (with $MgCl_2$), 0.2 μ L Taq enzyme, 1.0 μ L Dntp (mix), 1.0 μ L forward and reverse primers, 1.0 μ L target DNA template and 18.3 μ L ddH₂O. Information on primers and amplification protocols for each DNA region is listed in Suppl. material 7.

DNA quality was detected by electrophoresis using 1% agarose and 1 $\times$ TAE buffer solution (voltage 120–180V). The concentration and purity were detected by spectrophotometer, and gel imager FR-980A (Shanghai Furi Technology Co., LTD.) was used to record and take photos. The qualified PCR products were sequenced bi-directionally on a 3730XL sequencer (ABI, USA) after purified by a SanPrep column DNA gel extraction kit (Sangon B518131). Sequences were first assembled and edited with SEQMAN (DNA STAR package, USA), followed by sequence alignment with MEGA11 to trim the irregular bases at both ends of the aligned sequences. Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP) methods were used to construct the dataset of multi-gene tandem (*rbcL-matK-trnL-F*). All characters are considered as unordered and equally weighted, while the indels were processed as missing data after sequence alignment.

MP analysis was performed using MEGA11 (Felsenstein 1985; Tamura et al. 2021). Bootstrap values were generated with 1000 bootstrap replicates with the Subtree-Pruning-Regrafting (SPR) algorithm, with a search level of 1 in which the initial trees were obtained by the random addition of 10 sequences and a limit of 1000 trees, and branch lengths were calculated using the average pathway method. ML analysis of concatenated cpDNA by IQ-TREE-1.6.2 runs with aligned partitions and allows ModelFinder (Kalyaanamoorthy et al. 2017) to identify the best model for each partition (Table 1). Node support was estimated using 1,000 bootstrap iterations and other parameters were set as default for the searches. The BI analysis was performed using MRBAYES-3.2.7-WIN (Ronquist and Huelsenbeck 2003) with best-fit evolutionary models selected under the Bayesian Information Criterion (BIC) also using ModelFinder (Table 1), and the analysis consisted of 2,000,000 generations of four simultaneous Monte Carlo Markov chains. We increased the number of generations (typically 1,000,000) until the average standard deviation of split frequencies falls below 0.01 (3,000,000 generations in total). Phylogenetic trees were sampled every 1000 generations. When the average standard deviation of split frequencies consistently fails to reach the ideal values, the *run.1.p file can be viewed by Tracer v.1.6. The effective sample size (ESS) of all parameters were > 200 . Posterior probability (PP) ≥ 0.95 or bootstrap values (BS_{ML} , BS_{MP}) ≥ 85 indicates strong support, whereas $0.95 > PP \geq 0.85$ or $85 > BS_{ML}$, $BS_{MP} \geq 70$ suggests moderate support and weak support otherwise.

HPLC-ELSD was performed using EasySep®-3030 HPLC system (Shanghai Tongwei Analytical Technology Co., LTD., China) equipped with an AQ-

Table 1. nr/cpDNA data partitions and best-fit models estimated by IQ-TREE model selection for BI analysis.

Partition	Model
ITS	K80
<i>rbcL</i>	HKY
<i>matK</i>	GTR+I+G
<i>trnL-F</i>	HKY

C18 chromatographic column (3 μ m, 4.6 $\times$ 250 mm) and an ELSD detector. The mobile phase was ultrapure water (100%) and the flow rate was set at 0.5 mL/ min. The column temperature and ELSD spray chamber temperature were 30 °C and 70 °C, respectively, while the nitrogen flow rate was 2.5 mL/ min (Wu et al. 2020). Tissue cultured plant samples of *A. zhongshanensis*, *A. zhejiangensis* and *A. malipoensis* were dried and ground into powder. 0.1 g powder of each sample was accurately weighed and ultrasonically extracted with 20 mL distilled water for 45 min. The extract was subsequently passed through a 0.22 μ m PTFE syringe filter for HPLC-ELSD analysis.

Results

Since ITS2 sequence alone could not confirm the systematic status of the new species with convincing infrageneric relationships in the tested *Anoectochilus* species (Suppl. materials 1–3), combined cpDNA sequences (*matK*, *trnL-F* and *rbcL*) were used to construct datasets that may provide more discriminative information in phylogenetic analysis. By comparing the phylogenetic trees of BI, MP and ML, it was found that the topologies of ML and BI analysis were almost the same, and the topology of MP tree was also congruent with those of ML and BI, only with slight differences in the largest clade including the new species (Suppl. material 4). Here, the topology diagram generated by BI is displayed as Fig. 1, with most of the major clades receiving relatively strong support ($PP_{BI} \geq 0.95$). This BI phylogenetic tree revealed that two endemic species of Hainan Island, *A. hainanensis* and *A. baotingensis*, split off first and formed a branch as the sister clade of the other 16 species from mainland China with relatively strong support ($PP = 0.99$, $BS_{ML} = 61$, $BS_{MP} = 86$). The other 16 species separated into two large clades. Our two samples of *A. zhongshanensis* clustered into a well-supported subclade ($PP_{BI} = 1$, $BS_{MP} = 94$, $BS_{ML} = 99$), which is nested in the clade consisting of seven other *Anoectochilus* species, including *A. brevilabris*, *A. zhejiangensis*, *A. longilobus*, *A. roxburghii*, *A. malipoensis*, *A. nandanensis*, and *A. formosanus*. These phylogenetic analyses therefore supported the recognition of *A. zhongshanensis* as a new species of the genus *Anoectochilus*.

In addition, HPLC-ELSD analysis displayed interesting chemotaxonomic difference that the principle and characteristic lactone glycoside in *A. zhongshanensis* was kinsenoside rather than its diastereoisomer, goodyeroside A, a major glycoside in *A. zhejiangensis* and *A. malipoensis* (Fig. 2). Though morphologically similar, these three species are genetically and chemically different. Especially, those HPLC profiles revealed that *A. malipoensis* probably only

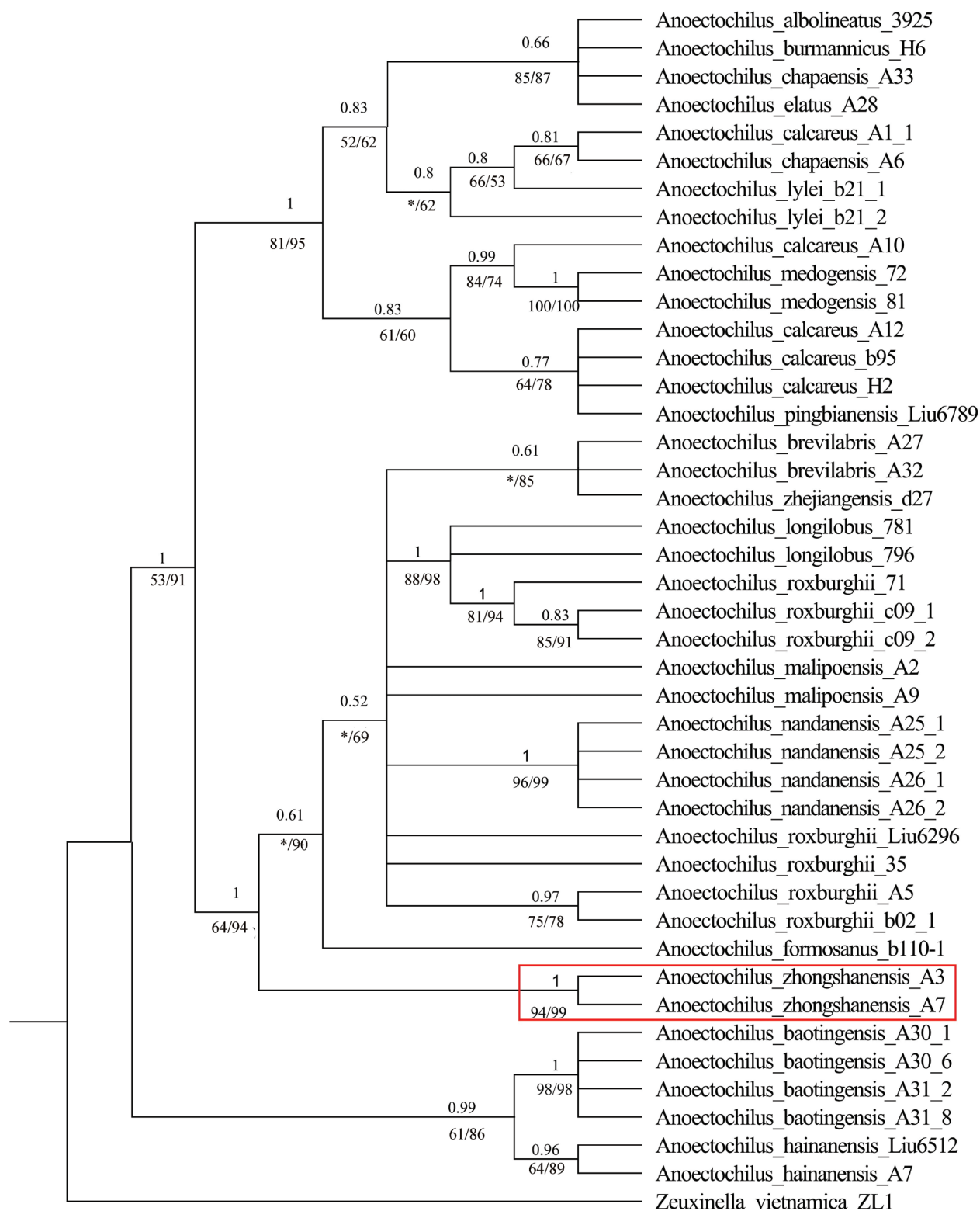


Figure 1. Phylogenetic relationships based on concatenated *rbcL*, *matK* and *trnL-F* sequences in *Anoectochilus* species inferred by Bayesian inference. PP_{BI} is shown above the branches, while BS_{ML} and BS_{MP} are displayed below the brancher (left, BS_{MP}; right, BS_{ML}). “*” indicates that the value is not supported or is smaller than 50.

contained goodyeroside A or with trace amounts of kinsenoside that cannot be detected, whereas the other two species have a mixture of goodyeroside A and kinsenoside but with inverse proportion.

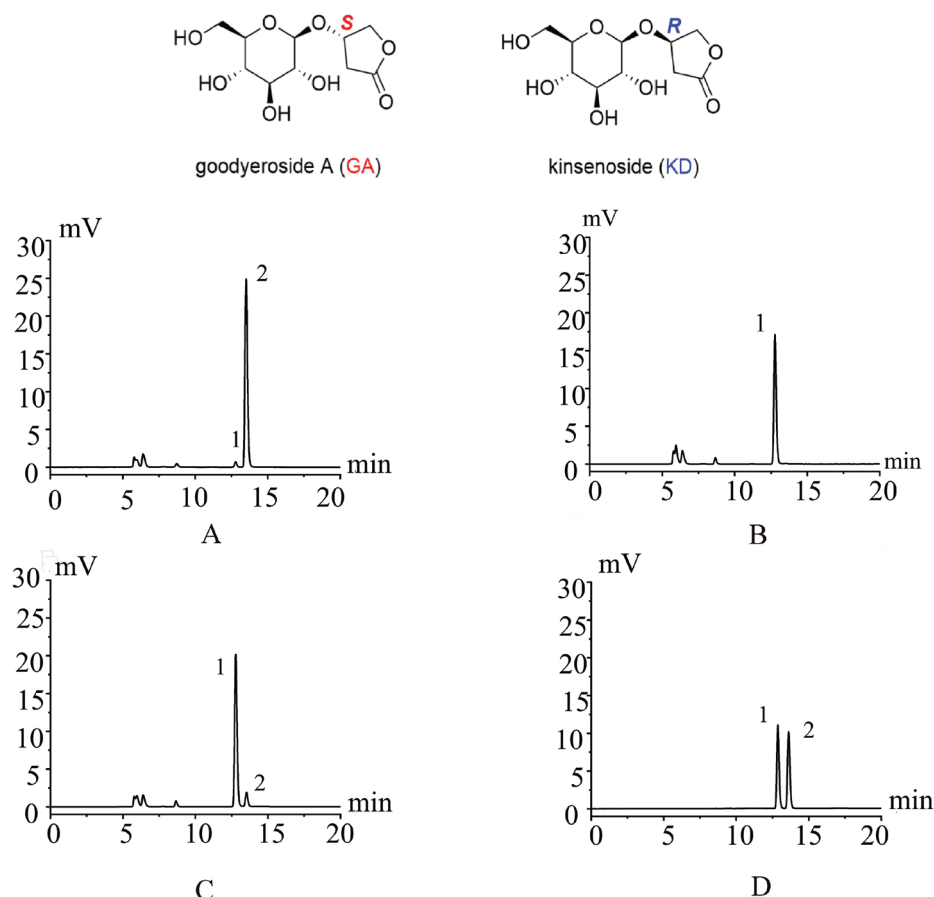


Figure 2. HPLC-ELSD chromatograms of *A. zhongshanensis* (A), *A. malipoensis* (B), *A. zhejiangensis* (C), and standards mixture (D) of goodyeroside A (1) and kinsenoside (2).

Taxonomic treatment

Anoectochilus zhongshanensis C.J.Zheng & Y.B.Wu, sp. nov.

urn:lsid:ipni.org:names:77329347-1

Figs 3, 7

Type. CHINA. Guangxi province: Zhongshan County, Hezhou City, under ever-green broad-leaved forest or shady and humid valleys, cultivated at the Medicinal Botanical Garden of the Second Military Medical University, 12 August 2020, Wu20200812003 (holotype: FAFU!).

Diagnosis. *A. zhongshanensis* is similar to *A. zhejiangensis*, but can be distinguished by the hastate or scalpel-shaped lobes of epichile (vs. semiovoid), forward curved and pinnately divided cristate lobes at both sides of the mesochile (vs. backward curved, the same orientation as the spur), unbowed conical spur (vs. bowed) and inverted triangle column wings (vs. squarish) (Fig. 6). *A. zhongshanensis* is also similar to *A. malipoensis*, but can be distinguished by the hastate or scalpel-shaped lobes of epichile (vs. obovate lobes with acuminate apex and crenulate margins), pinnately divided cristate lobes at both sides of the mesochile (vs. obliquely subquadrate and serrate lobes) and inverted triangle column wings (vs. elliptic) (Chen and Shui 2010).

Description. Terrestrial herb, 8~22 cm tall, with an erect stem and 2~6 leaves. Leaf ovate or orbicular, 1.2~4.0 × 1.0~2.8 cm, adaxially black with fine

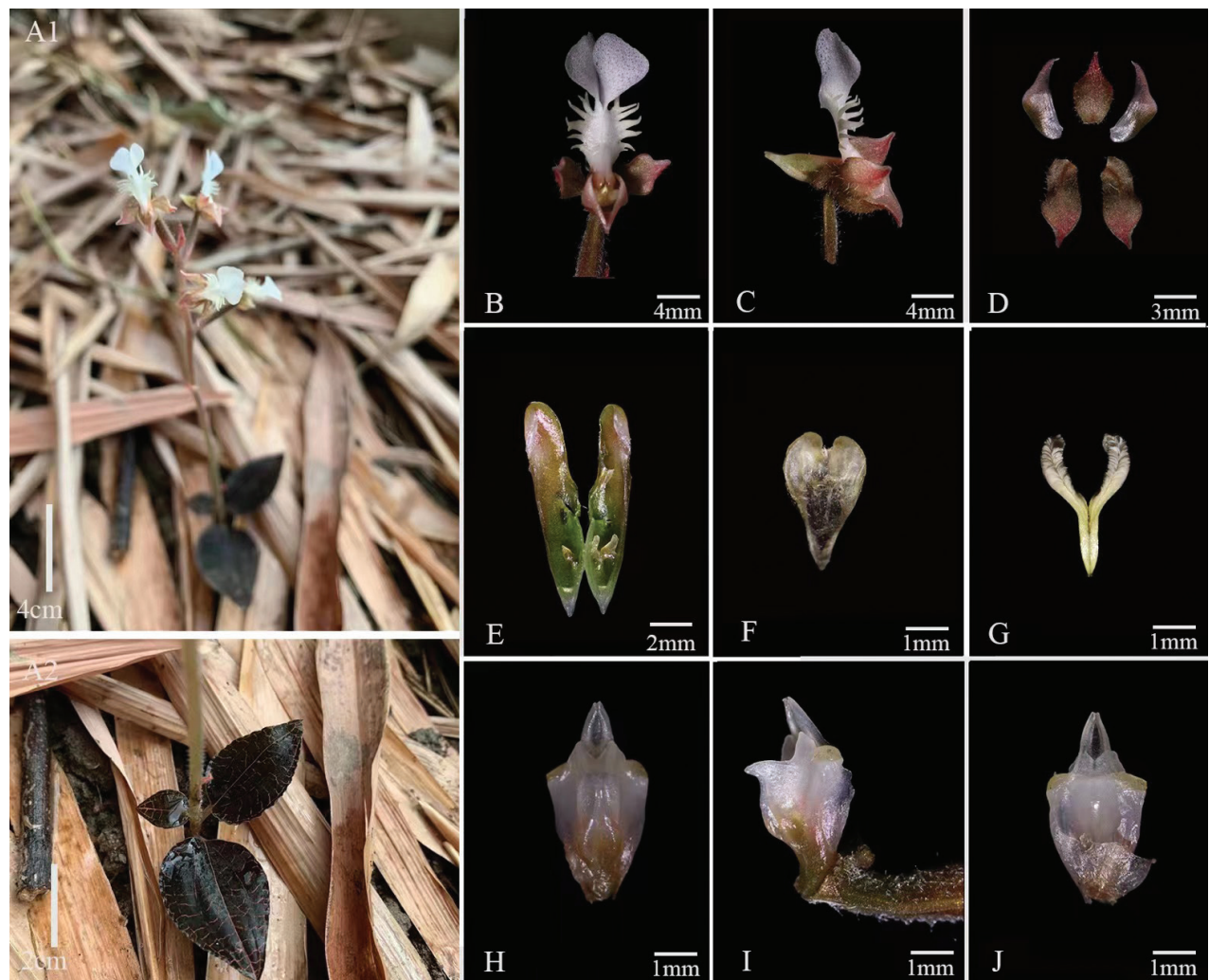


Figure 3. *Anoectochilus zhongshanensis* **A1** and **A2** habit **B** flower (front view) **C** flower (lateral view) **D** sepals and petals **E** spur **F** anther cap **G** pollinia **H** column (front view) **I** column (lateral view) **J** column (rear view). Photographs by Yan-Bin Wu.

golden red net veins with silk luster, abaxially purplish red, apex acute, base subtruncate or rounded, abruptly narrowed into a stalk; petiole 4–12 mm long, base enlarged into a cauline sheath. Racemose inflorescence, 1–6 flowered, inflorescence rachis pubescent; peduncle long and slender, mauve red, pubescent, with 2–4 mauve sheath-like bracts; floral bracts reddish, ovate-lanceolate, ca. 6 × 3 mm, apex acuminate, abaxially pubescent, subequal length as the ovary or slightly longer; ovary cylindrical, not twisted, reddish brown, white pubescent, connected with pedicel ca. 13 mm long; flowers not resupinate (labellum held uppermost); sepals reddish, subequal, ca. 5 mm long, abaxially puberulent; dorsal sepal ovate, sunken navicular, apex acute, joined with petals to form a hood; lateral sepals oblong, slightly oblique; petals white greenish, obliquely falcate, ca. 5 mm long, middle part ca. 1.5 mm wide, base narrow, apex acute; lip white, upstretched, Y-shaped, 13 mm long, epichile longitudinally dilated, 2-lobed, lobes hastate or scalpel-shaped, 5 mm long, ca. 2 mm wide, apex blunt, diverging at an acute angle; mesochile ca. 4 mm long, flange bearing forward curved and pinnately divided cristate lobes at both sides; conical spur, ca. 10 mm long, obliquely upward, subvertical to ovary, apex shallowly bilobed, containing 2 subcuneate calli. Column ca. 4 mm long, ventrally with an inverted

triangular column wing on both sides. Anther cap ovate, ca. 3 mm. Pollinia 2, yellow, obliquely clavate, ca. 3 mm long. Rostellum erect, apical concave and bifurcated. Stigma lobes 2, distinct, located to the sides of the rostellum. Fruit not seen.

Etymology. Referring to the locality (Zhongshan County) where this new species was found.

Vernacular name. 钟山金线兰 (Chinese pinyin: zhong shan jin xian lan).

Distribution and habitat. *A. zhongshanensis* is currently known only from Zhongshan County, Hezhou City, Guangxi Province, China. This species grows in evergreen broad-leaved forests or shady and humid valleys, elev. 500–1200 m.

Conservation status. During our three surveys in April, August and September 2020, *Anoectochilus zhongshanensis* was found in the forests or shady and humid valleys of Zhongshan County only at two separate locations, where we counted fewer than 100 individuals at each site. Due to the highly medicinal and edible value of *Anoectochilus* plants (Ye et al. 2017; Wu et al. 2022a; Shi et al. 2023), over exploitation and collection remains a high-risk factor for continuing resource decline and thus the major threat to these species, especially those with restricted distribution and small population size. All *Anoectochilus* plants have already been listed as potentially endangered species in the ‘List of National Key Protected Wild Plants in China’ (Level II) issued on Sep 7, 2021 by the National Forestry and Grassland Administration, and Ministry of Agriculture and Rural Affairs of the People’s Republic of China (http://www.gov.cn/zhengce/2021-09/07/content_5727413.htm). Though the comprehensive population assessment of *A. zhongshanensis* in the whole Zhongshan County has not been conducted, conservation status of this new species is best classified as ‘Endangered’ (En) (IUCN guidelines 2020) based on the discovered small population size of less than 200 mature individuals and potential risk of continuing decline in the number of mature individuals.

Phenology. Flowering in August–October.

Discussion

Anoectochilus zhongshanensis (Fig. 3), collected from Guangxi, China, possesses typical features of *Anoectochilus* species, characterized by golden-vein foliage, conical spur, separated stigma-lobes, and the pair of lamellae on column. This new species shows close morphological similarity to *A. zhejiangensis* and *A. malipoensis* (Figs 4, 5), but can be distinguished by the hastate or scalpel-shaped lobes of epichile, forward curved and pinnately divided cristate lobes at both sides of the mesochile, and inverted triangle column wings. Molecular studies based on cpDNA (*rbcL-matK-trnI-F*) combined with chemical analysis on characteristic lactone glycoside further supported the uniqueness of this new species. The key for identifications of 20 already reported species of genus *Anoectochilus* in China has been recently and systematically established by Jin et al (Jin et al. 2021), and *A. zhongshanensis* is thus the 21st member that can be distinguished from its nearest congeners, *A. zhejiangensis* and *A. malipoensis*.

The single use of nrDNA (ITS) (Suppl. materials 1–3) or concatenation of both nrDNA and cpDNA (ITS, *rbcL*, *matK*, *trnI-F*) (Suppl. material 5) failed to establish distinguishable relationships among those tested *Anoectochilus*



Figure 4. *Anoectochilus zhejiangensis* **A** habit **B** flower (front view) without petals and sepals **C** flower (lateral view) without petals and sepals **D** sepals and petals **E** spur **F** anther cap **G** pollinia **H** column (front view) **I** column (lateral view) **J** core column (rear view). Photographs by Yan-Bin Wu.



Figure 5. *Anoectochilus malipoensis* **A** transplant **B** flower (front view) **C** flower (lateral view) **D** sepals and petals **E** spur **F** anther cap **G** pollinia **H** column (front view) **I** column (lateral view) **J** core column (rear view). Photographs by Yan-Bin Wu.

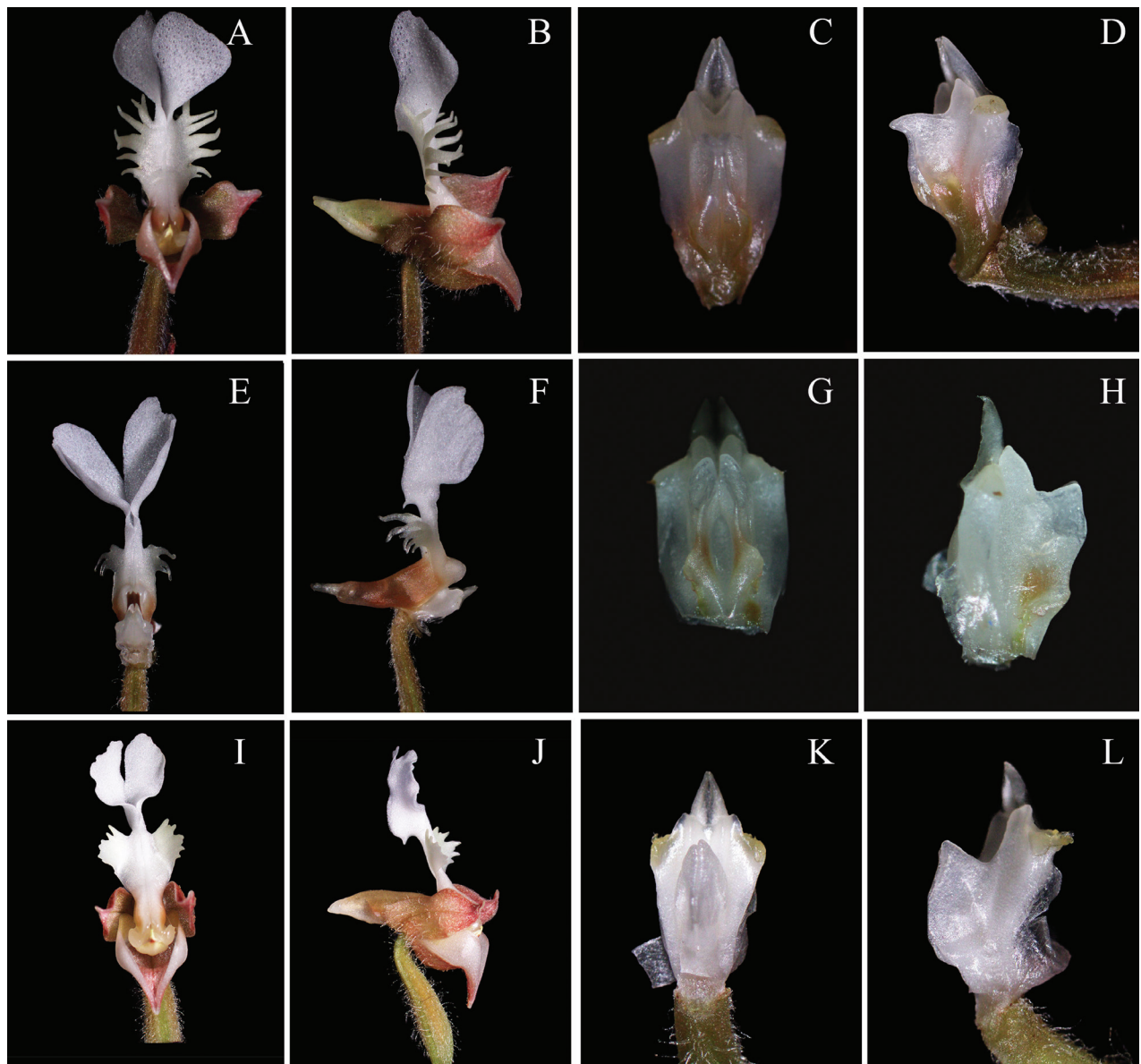


Figure 6. Diagnostic morphologic characteristics comparing *A. zhongshanensis* (A–D), *A. zhejiangensis* (E–H) and *A. malipoensis* (I–L) A, E, I flower (front view) B, F, J flower (lateral view) C, G, K column (front view) D, H, L column (lateral view). Photographs by Yan-Bin Wu.

species. However, only combined cpDNA resulted in a more resolved topology with a reliable phylogenetic result consistent with previous studies (Han 2019; Jin et al. 2021). These inconsistencies can be explained by the varied evolution between nuclear ribosomal DNA and chloroplast DNA (Clegg et al. 1994; Pérez-Escobar et al. 2020), which makes nrDNA ITS much more suitable for genetic diversity analysis due to its faster evolutionary rate and cpDNA better for genetic relationship investigation in virtue of their prolific hereditary information. Based on a series of new species (Tian and Xing 2008; Chen and Shui 2010; Tian et al. 2014; Qu et al. 2015) and new records for China (Hu et al. 2012; Wu et al. 2017; Zheng et al. 2018; Jin et al. 2019; Zheng et al. 2019; Jin et al. 2021), there are currently 21 *Anoectochilus* species known from China. And more distinguishable DNA molecular markers are needed to be developed to provide convincing species delimitation in the *Anoectochilus* genus.

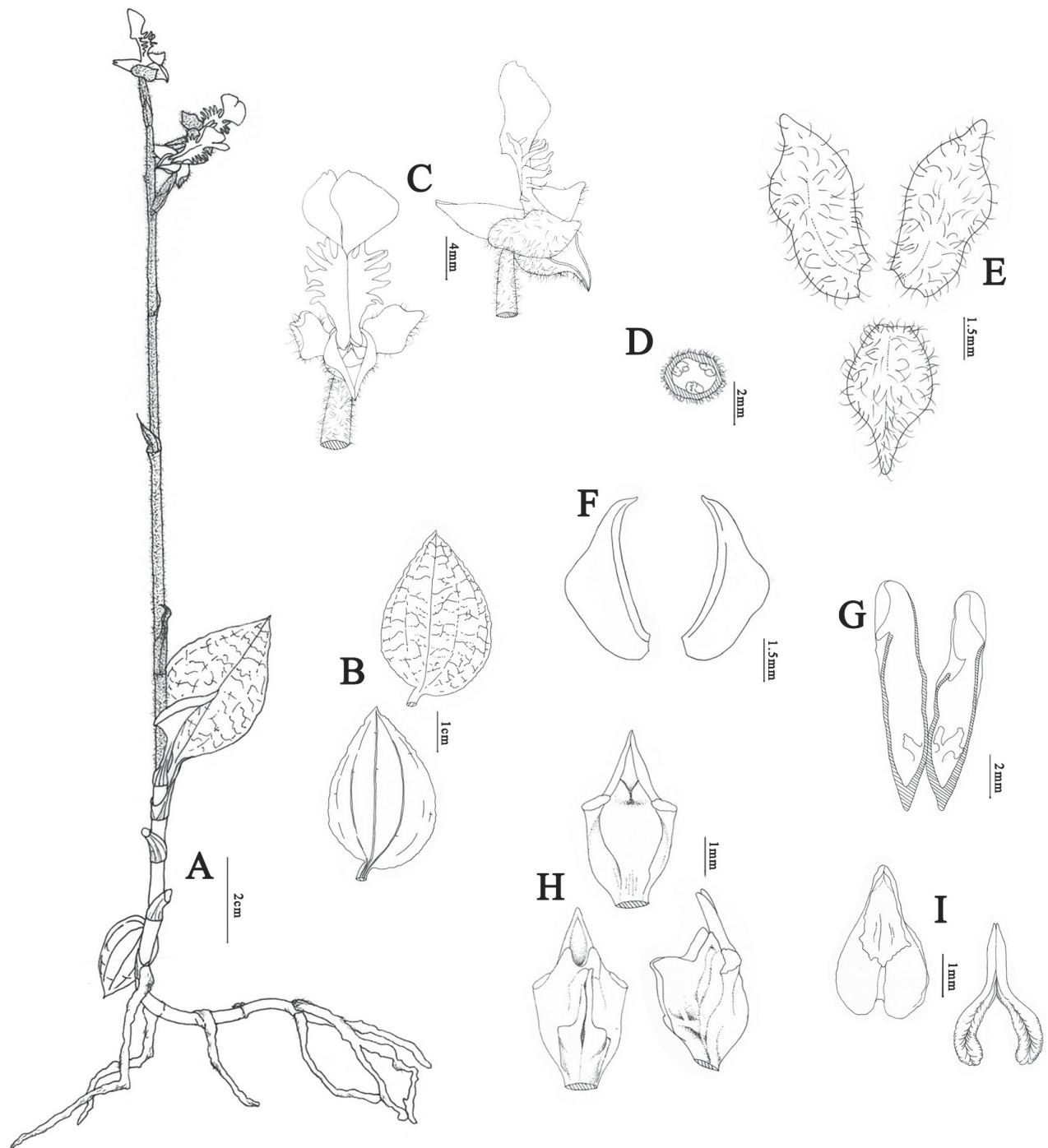


Figure 7. *Anoetochilus zhongshanensis* **A** habit **B** leaves **C** flower (front view and lateral view) **D** ovary (cross section) **E** sepals **F** petals **G** spur **H** core column (front view, lateral view and rear view) **I** anther cap and pollinia. Drawn by Li-Xiang Zheng.

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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: YBW, CJZ. Data curation: HLC, YBW, YH, JZW, QY, XHH. Funding acquisition: CJZ. Investigation: XHH. Methodology: YH. Resources: YBW. Supervision: CJZ. Writing – original draft: YH. Writing – review and editing: YBW, CJZ.

Author ORCIDs

Yan-Bin Wu  <https://orcid.org/0000-0001-9401-366X>

Cheng-Jian Zheng  <https://orcid.org/0000-0002-7867-3438>

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

Phylogenetic relationships based on nrDNA (ITS) in *Anoectochilus* species inferred by maximum likelihood (ML)

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

Data type: jpg

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Link: <https://doi.org/10.3897/phytokeys.234.111106.suppl1>

Supplementary material 2

Phylogenetic relationships based on nrDNA (ITS) in *Anoectochilus* species inferred by Bayesian inference (BI)

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

Data type: jpg

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Supplementary material 3

Phylogenetic relationships based on nrDNA (ITS) in *Anoectochilus* species inferred by maximum parsimony (MP)

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

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Supplementary material 4

Phylogenetic relationships based on concatenated *rbcL*, *matK* and *trnL-F* sequences in *Anoectochilus* species inferred by maximum parsimony (MP)

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

Data type: png

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Link: <https://doi.org/10.3897/phytokeys.234.111106.suppl4>

Supplementary material 5

Phylogenetic relationships based on concatenated ITS, *rbcL*, *matK* and *trnL-F* sequences in *Anoectochilus* species inferred by Bayesian inference (BI)

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

Data type: jpg

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Link: <https://doi.org/10.3897/phytokeys.234.111106.suppl5>

Supplementary material 6

Information of samples for phylogenetic analysis in this study

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

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Supplementary material 7

Primers and amplification protocols used in this study

Authors: Yan-Bin Wu, Yu Han, Xu-Hui He, Hui-Ling Chen, Jin-Zhong Wu, Qi Ye, Cheng-Jian Zheng

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Walsura guangxiensis (Meliaceae), a new species from Guangxi, China

You Nong¹ , Chuan-Gui Xu¹ , Gui-Yuan Wei¹ , Ke-Jian Yan¹ , Xin-Cheng Qu¹ ,
Zhan-Jiang Zhang², Ren-Chuan Hu¹ , Yun-Feng Huang¹

¹ Guangxi Key Laboratory of Traditional Chinese Medicine Quality Standards, Guangxi Institute of Chinese Medicine & Pharmaceutical Science, No. 20-1 Dongge Road, Nanning, Guangxi, China

² Guangxi Key Laboratory of Medicinal Resources Protection and Genetic Improvement, Guangxi Botanical Garden of Medicinal Plant, Nanning 530023, China
Corresponding author: Yun-Feng Huang (huangyunfeng2000@126.com)

Abstract

Walsura guangxiensis (Meliaceae), a new species from Guangxi, China, is here described and illustrated. The new species is easily distinguishable from the other two Chinese members of the genus by its petals being pale yellow, filaments being connate into tubes above the middle, the berry being oval and glabrous. An identification key of *Walsura* for 17 species is also provided.

Key words: China, Meliaceae, new species, taxonomy, *Walsura guangxiensis*

Introduction

Researchers have been continuously enhancing the classification of the Meliaceae family through various studies (Muellner et al. 2003, 2005, 2009a, b; Muellner and Mabberley 2008; Pennington and Muellner 2010; Köcke et al. 2015; Clarkson et al. 2016; Gama et al. 2020). Furthermore, new species are still being uncovered and documented (Pannell et al. 2020). *Walsura* Roxb. is a small genus of the family and, according to the International Plant Names Index (IPNI), 53 binomials are referable to *Walsura*, but most of them now considered synonyms of *Walsura pinnata* Hassk. In POWO 16 species are accepted. Clark (1994), in his monography of the genus, recognized 13 species and 3 insufficiently known species, the same as Mabberley in Flora Malesiana (Mabberley et al. 1995). The species of *Walsura* occur in India (west to the Western Ghats and north to Darjeeling), Sri Lanka, the Andaman Islands, Burma, Thailand, Indo-China, Yunnan, Hainan, the Malay Peninsula, Sumatra, Java, Borneo, the northern and western Philippines (Luzon to Palawan), Sulawesi, Halmahera and western New Guinea (Manokwari). Medicinal plants of the genus *Walsura* are native to tropical zones of a number of Asian countries and have been used for local medicines; in addition, the genus has received increasing attention due to its bioactive limonoids and triterpenoids (Son 2022).

Species of the genus grow as trees, sometimes small. Leaves are arranged in spirals, odd-pinnate or occasionally a single leaflet; leaflets are opposite. Flowers are bisexual and male or unisexual (then plants dioecious). The calyx is short,



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deeply (4)5(6)-lobed, imbricate in bud. Petals 5, much longer than the calyx, distinct, broad and expanding, valvate or imbricate in bud. Stamens 10; filaments flat, broad, usually basally connate into a tube or sometimes discrete, shorter than petals; anthers introrse, inserted on apex or between 2 lobes of filament.

Walsura can be distinguished from all other genera in the Meliaceae by its fruit being a berry, indehiscent; its stamen filaments being connate for $\pm$ basal half into a staminal tube; its corolla usually being imbricate; loculi uniovulate or with 2 collateral ovules; its anthers inserted apically on filaments or on margin of staminal tube; its disk being annular, fleshy (Pennington and Styles 1975; Clark 1994).

To date, only two species have been recognised in China, *Walsura robusta* and *Walsura pinnata* (Peng and Mabberley 2008). Very recently, however, eight individuals of a distinctive plant have been found by the first author on limestone in Guangxi, which we describe as a new species below, based on measurements of three individuals.

Materials and methods

Morphology

The new species is described, based on field observations and examination of herbarium specimens at KUN, PE, IBK, IBSC, GXMI and HITBC. Other *Walsura* species were examined online from the Kew Herbarium (<http://apps.kew.org/herbcat/gotoHomePage.do>) and Museum national d'histoire naturelle (<https://www.mnhn.fr/fr>). Morphological characters that distinguish it from all other species in the genus of *Walsura* are used. We observed living plants of the new species at flowering and fruiting time (April to August). We observed characters of stems, leaves, pedicels, flowers, receptacles, petals, stamens, gynoecium, carpels, size of flowers, size and shape of petals, number of stamens and the shape of gynoecium and fruit by studying three individuals.

Descriptions were written based on herbarium specimens. Measurements were made with a tape measure and callipers. The structure of the indumentum and its distribution were observed and described under a dissecting microscope at magnifications of more than 20 $\times$. Additional information on locality, habitat, ecology, plant form, bark and wood characters and fruits was collected in the field and taken from herbarium labels. The conservation threat assessment followed IUCN Categories and Criteria (IUCN 2022).

Results and discussion

Taxonomy

***Walsura guangxiensis* Y.Nong & Y.F. Huang, sp. nov.**

urn:lsid:ipni.org:names:77329399-1

Figs 1, 2

Chinese name: guǎng xī gē shé shù (广西割舌树)

Diagnosis. *Walsura guangxiensis* is readily distinguishable from the other two Chinese species of *Walsura*, *Walsura guangxiensis* is similar to *W. pinnata* and *W. robusta* regarding secondary veins 3–9 (vs. secondary veins 8–11 /

secondary veins 5–8); but differs with petals being pale yellow (vs. petals white / petals white); stamen filaments undivided, connate into tubes above the middle (vs. stamen filaments broad, basal to middle part connate into a tube, tip 2-lobed / stamen filament base or basal to middle part connate into a tube); berry oval, 1–2 cm long and 1–1.2 cm wide, glabrous, thin peel, yellow and shiny when mature (vs. berry globose to ovoid, ca. 1.5 cm in diam., densely covered with yellowish gray trichomes / berry globose to ovoid, 1–2 cm in diam., densely covered with yellowish gray trichomes).

Holotype. CHINA. Guangxi: Fengshan, 24°24'29.02"N, 106°50'23"E, alt. 866 m, in subtropical evergreen broad-leaved forest, limestone, 7 June 2022, R.C. Hu, HRC210424001 (holotype: GXMI!; isotypes:IBK! GXMI!).

Description. Trees 3–5 m tall. Branches grey-brown, glabrous or sometimes young branches yellow pubescent or glabrescent, with grey-white lenticels. Leaves 10–26 cm; petioles (1.5) 3–7 cm; with fine hairs. Leaflets 3 or 5, subsessile, papery or thinly leathery, elliptic or oblong-lanceolate, tapering at the apex, descending at the base or cuneate or broadly cuneate, glabrous on both sides, 3–9 pairs of lateral veins, obvious protrusions on both sides of reticular veins and entire edges of leaflet blades; lateral leaflets are 3–14 cm long and 1.5–5 cm wide and the apical leaflets are larger. Petiole 2–5 mm long, terminal up to 1 cm, glabrous. Panicle axillary or terminal, with cyme-like branches, shorter leaves, appressed yellow pubescence, with total pedicels, small pedicels 1–3 mm long, jointed at the lower part and puberulent, 3 triangular bracteoles at the base, pubescence. Calyx short, 4- or 5-lobed, lobes ovate, apex acute, puberulent or glabrous. Petals 4 or 5, pale yellow, puberulent outside; elliptical, much longer than sepals, free, imbricate in bud. Stamen filament tube 8–10 split; filaments are tapered at the top, undivided, connate into tubes above the middle, with short bristles on the upper part of the inner surface and anthers 8–11, yellow and oval, inserted at the top of filaments. Disc cup-shaped, fleshy. Ovary glabrous, 1-loculed, with 2 ovules in each locule, as long as or slightly longer than the ovary. Style cylindrical; stigma globose, tip not divergent. Berry is oval, stipitate, 1–2 cm long and 1–1.2 cm wide, glabrous, 1 loculed, with 1 or 2 seeds, thin peel, yellow and shiny when mature.

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

Etymology. Guangxi is located in the southwest of China and is a biodiversity hotspot where many new species or new species records have been found (Hu et al. 2019; Luo et al. 2020; Feng et al. 2021; Xin et al. 2021; Huang et al. 2022). The new species, *W. guangxiensis*, is found in this region and is named after the geographic location.

Distribution and habit. Known only from the southwest of Guangxi, China. The new species mainly occurs at elevations of 800 m and is usually found together with *Cinnamomum saxatile* H. W. Li, *Myrsine kwangsiensis* (E. Walker) Pipoly & C. Chen, *Platycarya strobilacea* Sieb. et Zucc., *Wrightia sikkimensis* Gamble. It often grows in stone crevices with barren soil.

IUCN Red List Category. Data available for the new species are still insufficient to assess its conservation status. According to the IUCN Criteria (IUCN 2022), it is considered Data Deficient (DD) until more information becomes available. Although *W. guangxiensis* currently has relatively good growth and protection status, further collection and monitoring are necessary to allow more conclusive estimations about the rarity and vulnerability of the species. Therefore, special attention should be given to the conservation of the new species of *Walsura*.

Additional specimen. Tiane. Southwest Guangxi: limestone hills, fl. 8 May 2020, C.G. Xu, XCG20200508001 (GXMI!); Lingyun. Yuntai Park, fr. 7 June 2013, GXMI063377 (GXMI!); Lingyun. Yuntai Mountain, fr. 12 August 2013, GXMI063363 (GXMI!)

Notes. This new species is represented by eight individuals that have been found so far in the wild, three of which were fruiting and used for species description.

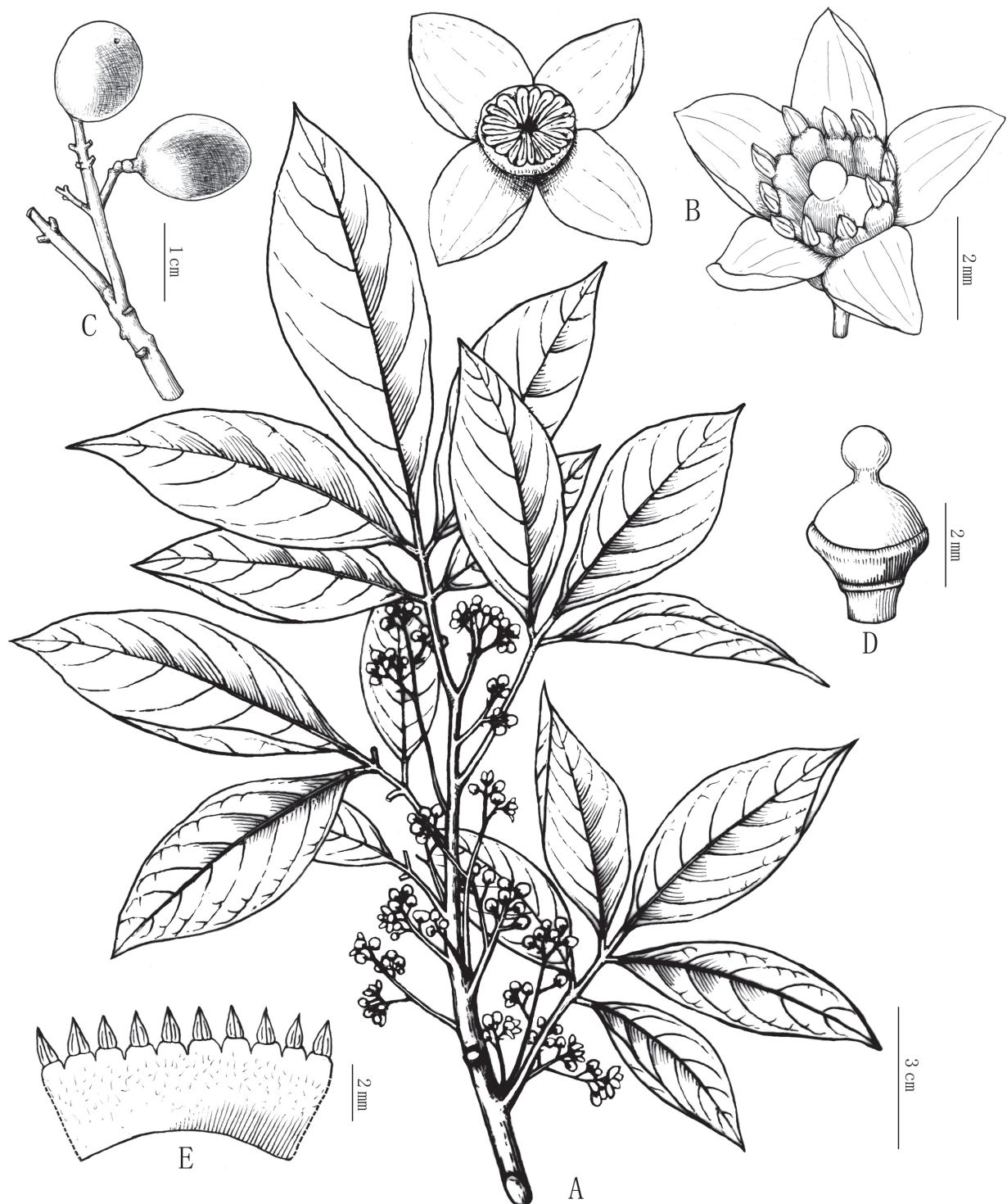


Figure 1. Line drawing of *Walsura guangxiensis* **A** flowering branch **B** flowers **C** fruits **D** style and ovary **E** staminal tube spread out **F** free portion of stamen (Drawn by Xin-Cheng Qu).

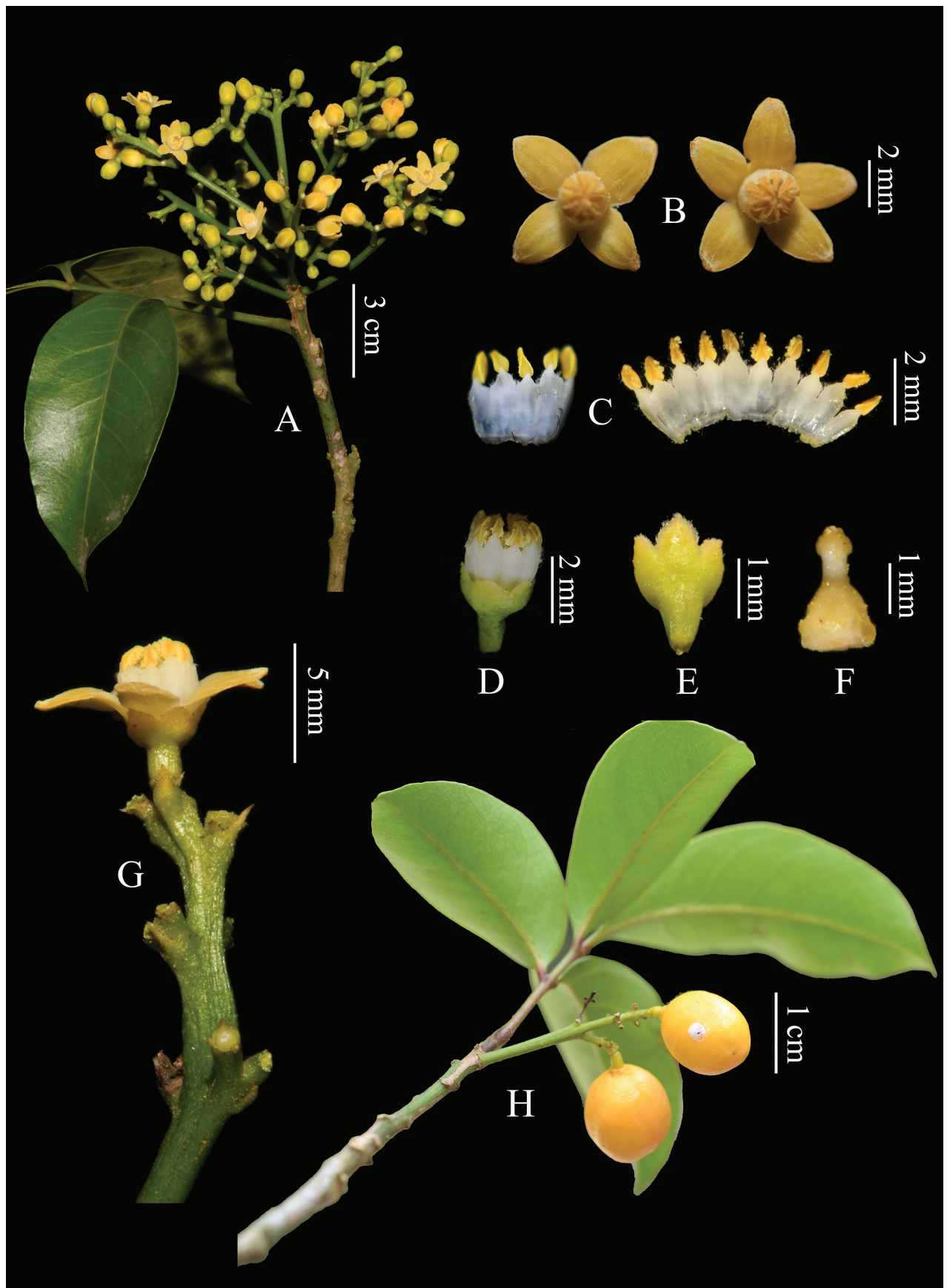


Figure 2. *Walsura guangxiensis* **A** flowering branch **B** flowers **C** staminal filaments **D** staminal tube **E** calyx **F** ovary and stigma **G** flower and stipules **H** fruits (Photographed by You Nong and Ke-Jian Yan, edited by Yuan Fang).

Key to species of *Walsura*

- 1 Single leaf 2
- Compound leaf 3
- 2 Peduncle of inflorescence with 2-armed trichomes; androecium tubular for less than 1/6 of length 1. *W. gardneri*
- Peduncle of inflorescence with simple trichomes only; androecium tubular for more than 1/3 of length 2. *W. monophylla*
- 3 Leaves 1-jugate 4
- Leaves 2-or more-jugate 6
- 4 Leaflets slightly asymmetric; filament apex truncate 3. *W. bonii*
- Leaflets symmetric; filament apex shortly bifid 5
- 5 Leaf apex acuminate 4. *W. tubulata*
- Leaf apex obtuse 5. *W. trifoliolata*
- 6 Leaflet abaxial surface white-dotted (matt/glaucous in islets); stamen filament base or basal to middle part connate into a tube 6. *W. robusta*
- Leaflet abaxial surface not white-dotted (matt/glaucous uniformly); stamen filaments basal to middle part connate into a tube or connate into tubes above the middle 7
- 7 Leaflet abaxial surface velutinous 7. *W. poilanei*
- Leaflet abaxial surface glabrous to subdensely pubescent 8
- 8 Fruit 4-winged to rhomboid (in transverse section) and weakly dehiscent. 8. *W. dehiscens*
- Fruit globose and indehiscent 9
- 9 Fruit slightly beaked 10
- Fruit not beaked 13
- 10 Leaflet blades lanceolate 11
- Leaflet blades ovate, ovate-lanceolate or elliptic 12
- 11 Inflorescences axillary, crowded at ends of branches, puberulous; fruits ovoid to globose, ca 2 cm long, minutely rusty-puberulous with a slightly curved conical apiculus 9. *W. candollei*
- Inflorescences clustered around shoot apex in axils of caducous undeveloped or fully expanded leaves, primary rachis minutely pubescent, branches and all other parts densely puberulous; fruits ovate-oblong, acuminate, ca 1.2 cm long, greyish-velvety 10. *W. oxycarpa*
- 12 Inflorescences subcorymbose cymes, axes densely fulvous pilose; fruits ellipsoid, 2.5–3 cm long, brownish green tomentellous, apex usually apiculate 11. *W. decipiens*
- Inflorescence panicle, pubescent; fruits ovoid to globose, 1.5–2 cm long, brownish yellow tomentellous, apex usually apiculate 12. *W. trichostemon*
- 13 Leaves 2- (or 3-)jugate 14
- Leaves 3- (or 4-) jugate 16
- 14 Leaflet apex obtuse 13. *W. villosa*
- Leaflet apex acute or acuminate 15
- 15 Petals white, filaments of stamens 2-toothed at the top; berry globose to ovoid, ca. 1.5 cm in diam., densely covered with yellowish gray trichomes 14. *W. pinnata*
- Petals yellow, filaments of stamens not divided at the top; berry oval, 1–2 cm long and 1–1.2 cm wide, glabrous 15. *W. guangxinesis*

- 16 Leafy twigs 2.5–8.0 mm diam.; leaves 3-jugate.....**16. *W. sarawakensis***
– Leafy twigs 8–15 mm diam.; leaves 4- (or 5-) jugate
.....**17. *W. pachycaulon***

Discussion

To date, in total, there are 17 species accepted in *Walsura*. Amongst these 17 species, *Walsura guangxinesis* is unusual in the genus with its petals being yellow, filaments not divided at the top, and the berry being oval, stipitate, 1–2 cm long and 1–1.2 cm wide, glabrous, 1-loculed, with 1 or 2 seeds, thin peel, yellow and shiny when mature.

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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

Data curation: YN, RCH. Funding acquisition: YN, RCH, and GYW. Investigation: YN, CGX, GYW, KJY. Methodology: YN, KJY, YGW. Project administration: YN, RCH, ZJZ. Supervision: CGX, GYW, KJY, YGW. Visualization: YN, YF, KJY, YFH. Writing-original draft: YN, YGW. Writing-review and editing: YN.

Author ORCIDs

You Nong  <https://orcid.org/0000-0001-7004-0946>
Chuan-Gui Xu  <https://orcid.org/0009-0000-6263-3821>
Gui-Yuan Wei  <https://orcid.org/0000-0003-0652-1213>
Ke-Jian Yan  <https://orcid.org/0000-0002-4927-4665>
Xin-Cheng Qu  <https://orcid.org/0009-0009-9078-9976>
Ren-Chuan Hu  <https://orcid.org/0000-0002-0941-7203>

Data availability

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

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Checklist

Preliminary checklist of the genus *Festuca* L. (Loliinae, Pooideae, Poaceae) in the Altai Mountains with outlines for further studiesPolina D. Gudkova^{1,2}, Elizaveta A. Kriuchkova^{1,2}, Alexander I. Shmakov², Marcin Nobis³¹ Research laboratory 'Herbarium', National Research Tomsk State University, Lenin 36 Ave., 634050 Tomsk, Russia² Department of Botany, Institute of Biology and Biotechnology, Altai State University, Lenin 61 Ave., 656049 Barnaul, Russia³ Institute of Botany, Faculty of Biology, Jagiellonian University, Gronostajowa 3, 30-387 Kraków, Poland

Corresponding author: Polina D. Gudkova (PDGudkova2017@yandex.ru)

Abstract

Here we present an updated checklist of the genus *Festuca* in the Altai Mountains (AM). The study was carried out on the abundant herbarium material and considered the latest published phylogenetic analyses. *Festuca* was revised within the scope of the fine-leaved group (clade) with two sections, sect. *Aulaxyper* and sect. *Festuca*. Two species, namely *F. richardsonii* and *F. lenensis*, were previously misidentified and are not present in the AM. *Festuca brevissima* is a new record for the Russian part of the AM and for the flora of Mongolia. In total, our revision shows that 17 species of fine-leaved fescues are present in the area of AM. In this paper, we provide a key to species identification, as well as illustrations of plants, habits, leaves, spikelets, and glumes. Information on nomenclature types, synonymy, flowering period, chromosome numbers, habitats, and general distribution along with distribution maps of the particular species within the AM are included.

Key words: Distribution, *Festuca ovina* group, fine-leaved fescue, identification key, taxonomic revision



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Introduction

The fescue genus, *Festuca* L., is one of the largest genera of the Poaceae family and includes more than 600 species with the greatest diversity in the Holarctic zone of Eurasia and North America (Tzvelev 1976; Alexeev 1980; Clayton and Renvoize 1986; Aiken and Darbyshire 1990; Watson and Dallwitz 1992; Soreng et al. 2003, 2022; Clayton et al. 2006; Lu et al. 2006; Stančík and Peterson 2007). The genus is easily recognisable by its perennial caespitose or rhizomatous plant form, paniculate inflorescences, 3–11-floret spikelets, dorsally rounded lemmas with 3–5 veins, a linear hilum, and lack of a hairy appendage on the ovary apex (Kellogg 2015; Ospina-González et al. 2015). A base chromosome number of the genus *Festuca* is $x=7$ (Ospina-González et al. 2015). However, fescues are often polyploids, and even representatives of one species may be characterised by a different number of chromosomes (Šmarda and Kočí 2003; Šmarda et al. 2005; Galli et al. 2006; Enushchenko and Probatova 2020; Kiedrzyński et al. 2021). In the Altai Mountains (AM), the fescues are dip-

loids, tetraploids or hexaploids. Different ploidy level is typical for species such as *F. rubra* L., *F. kryloviana* Reverd., *F. pseudovina* Hach. ex Wiesb., *F. lenensis* Drobow and *F. valesiaca* Schleich. ex Gaudin (Mizianty and Pawlus 1984; Alexeev et al. 1988; Šmarda 2008; Dirihan et al. 2016; Tzvelev and Probatova 2019). It is considered that ploidy level influences the morphological characters including the diagnostic ones, such as the length of the lemma, the length of the spikelet, the width of the vegetative leaves in the way that higher ploidy levels results in generally larger sizes of the particular parts of the plants (Litardière 1923; Levitskii and Kuzmina 1927; Bidault 1968; Rewicz et al. 2018). Therefore, the species whose representatives are characterised by polyploidy are highly polymorphic, which significantly complicates species identification. In the Altai Mountains, the fescues are diploids, tetraploids or hexaploids. Although fescues are widely distributed in the steppe zone and have regional economic importance as forage grasses, due to taxonomic problems and challenging species identifications, the genus is understudied, and thus all the more important (Torrecilla and Catalán 2002; Torrecilla et al. 2003, 2013; Ospina-González et al. 2015; Bednarska and Brazauskas 2017; Ospina and Picca 2019; Enushchenko and Probatova 2020; Boeuf et al. 2022; Vasile et al. 2022).

The Altai Mountains (AM) are located in Russia, Kazakhstan, Mongolia and China. The AM host 2700 species of vascular plants, with Poaceae being one of the most widely distributed families (Kamelin 2005; <http://altaiflora.asu.ru/en/>; Vaganov et al. 2019) including several species of fescues. The first person who listed species of *Festuca* in the AM was Gmelin (1747). Later, Trinius (1829) recorded six species of *Festuca* that belong to subgenera *Festuca*, *Leucopoa* (Griseb.) Hack., and *Schedonorus* Peterman. While the above mentioned authors used only macromorphological characters of flowering, and less often vegetative, shoots for species-identification, Hackel (1882) proposed using anatomical structures of the leaf blade cross-section as diagnostic characters, and these have been shown to be very significant for the taxonomy of the genus. Following Drobow (1915), botanists used these characters for the description and identification of the *Festuca* species in the Altai territory (Krylov 1914; Reverdatto 1936, 1965; Tzvelev 1976; Grubov 1982; Alexeev 1990; Chen et al. 2003; Lu et al. 2006).

In the first synopsis of the genus *Festuca* s.l. in the AM, Chusovljanov (2007) listed 22 species belonging to subgenera *Festuca* and *Leucopoa*, and described two new species for the area, namely *F. kuprijanovii* Czus. and *F. kemberovensis* Czus. (Chusovljanov 1998, 2003). *Festuca kemberovensis* was recorded for the Kemerovo region, outside the AM, but Chusovljanov (2003) mentioned that the new species can be found in the Altai Mountains. To date, 21 species of *Festuca* s. l. (the fine-leaved clade and the broad-leaved clade) are reported in the Russian part of Altai (Alexeev 1990; Chusovljanov 2007; Tzvelev and Probatova 2019), 15 species in the Kazakh part of Altai (Kotukhov 2021), 9 species in the Mongolian part of Altai (Grubov 1955, 1982; Alexeev 1977, 1981; Gubanov 1996; Chusovljanov 2007; Baasanmunkh et al. 2022), and 15 species in the Chinese part of Altai (Chen et al. 2003; Lu et al. 2006). However, the taxonomic approach and treatment of *Festuca* in the AM differs, somewhat, among these countries. We can summarize that the genus *Festuca* s.l. comprises 22 species in the AM, including subgenus *Leucopoa*, sect. *Leucopoa* (Griseb.) Krivot. – *F. sibirica* Hack. ex Boiss.; sect. *Breviaristatae* Krivot. – *F. altaica* Trin., *F. tristis* Kryl. et Ivanitzk.

and subgenus *Festuca*, sect. *Festuca* – *F. rubra*, *F. richardsonii* Hook., *F. borissii* Reverd., *F. kurtzschumica* E. Alexeev, *F. brachyphylla* Schult. et Shult., *F. saurica* E. Alexeev, *F. lenensis*, *F. albifolia* Reverd., *F. tschujensis* Reverd., *F. pseudosulcata* Drob., *F. kemeroensis*, *F. kryloviana*, *F. pseudovina*, *F. valesiaca*, *F. oreophila* Markgr.-Dannenb., *F. rupicola* Heuff., *F. ovina* L., *F. sphagnicola* B. Keller, *F. kuprijanovii*.

Since the beginning of the XXI century, the widespread uptake of molecular sequencing methods has provided many new insights into the phylogenetic relationships within many grasses (Baiakhmetov et al. 2021; Baker et al. 2021; Gallaher et al. 2022; Soreng et al. 2022). Recent phylogenetic analyses on *Festuca* s.l., based on nuclear ITS and *trnL-trnF* loci, *Festuca* is divided into two well-supported clades: narrow- or fine-leaved clade and the broad-leaved clade (Torrecilla and Catalán 2002; Torrecilla et al. 2003, 2013; Catalán et al. 2004, 2006, 2007; Inda et al. 2008; Moreno-Aguilar et al. 2022). In the AM, the fine-leaved clade is represented by the subgenus *Festuca*, which includes two sections: sect. *Aulaxyper* Dumort. (*F. rubra* L. group) and sect. *Festuca* (*F. ovina* group). Broad-leaved fescues comprise subgenus *Drymanthele* V.I. Krecz. & Bobrov, *Schedonorus* (with sections *Schedonorus* and *Plantynia* (Dumort.) Tzvel.), and subgenus *Leucopoa* (with sections *Breviaristatae* and *Leucopoa*). According to the latest taxonomic treatment of grasses (Soreng et al. 2022), subgenus *Schedonorus* is assigned to the genus *Lolium*, and subgenera *Drymanthele* (= *Drymochloa* Holub) and *Leucopoa* are regarded as independent genera. Taking all the above into account, within the genus *Festuca* in the AM, we consider here the fine-leaved fescues only.

According to the results of our molecular studies based on genome-wide genotyping (Kriuchkova et al. 2023), the Altai fescues are divided into five well-supported clades. However, relationships of some species within clades (e.g. *F. ovina*, *F. kryloviana* and *F. valesiaca*) are weakly resolved. There are also no general findings regarding the diversity of fescue species in the AM based on a comparison of the morphology and the molecular data. Therefore, a thorough study of *Festuca* in the AM, including the analysis of its morphological variability corresponding to molecular data, is necessary.

The goal of this paper is to evaluate the morphological and anatomical characteristics of particular species of fine-leaved fescues in the AM. We then present an identification key, detailed distribution maps of the examined species, and illustrations of the most important characters of the examined species.

Materials and methods

Study area

The study was carried out in 2017–2021 in the AM, which straddles the territories of Russia (South Siberia), eastern Kazakhstan, western China (Xinjiang Uygur Autonomous Region), and a part of western Mongolia, and occupies an area of 550,000 km². The elevation varies from 240 m to the highest mountains of North Asia, namely Belukha (4506 m), and Tavan-Bogdo-Ula (4374 m). The AM include five elevational zones: steppe, forest-steppe, forest, subalpine, and alpine tundra. However, depending on the region, the composition and altitudinal boundaries of these zones are different. The AM host 2700 species of vascular plants, and the most widely distributed families are Asteraceae, Poa-

ceae, and Fabaceae, which characterise the boreal flora (Fig. 1; Kamelin 2005; <http://altaiflora.asu.ru/en/>; Vaganov et al. 2019). For the AM, Kamelin (2005) proposed a botanical-geographical subdivision into regions, which we used to describe the distribution of species.

Plant material

This study is based on the revision of the specimens deposited in the following herbaria: ALTB, AA, LE, KRA, KUZ, MW, NS, NSK, and TK. In addition, we conducted a series of field work expeditions into the Russian, Mongolian and Khazakh parts of the Altai Mountains. Herbarium acronyms follow Thiers (2023, continuously updated <http://sweetgum.nybg.org/ih/>). All specimens were compared with the type specimens and protologues. Photos for illustration were taken with a stereo microscope Nikon SMZ800N (Japan), the image of the general habit was taken with a scanner HP Laser Jet M1132 (USA). Maps were generated using DIVA-GIS 7.5 (Hijmans et al. 2001, continuously updated <http://www.diva-gis.org>). In total, more than 800 herbarium sheets of 23 species were used for the preparation of distribution maps. The distribution frequency scale is as follows: very rare – 1–10 localities, rare – 10–20 localities, common – 20–30 localities, wide spread – >50 localities.

The terminology used follows Alexeev (1972, 1978, 1980, 1981, 1983, 1990), Darbyshire and Pavlick (2007), and Lu et al. (2006). The most important key characters are presented in Fig. 2.



Figure 1. The botanical-geographical subdivision of Altai Mountains: A – Altai province (regions: A1 – Northern Altai, A2 – North-Eastern Altai, A3 – Central Altai, A4 – Tchulyshman, A5 – Abakan-Dzhebash, A6 – Khemchik); KAD – Altai-Dzungarian province (regions: KAD1 – North-Western Altai, KAD2 – Kalbinsky, KAD3 – Tarbagatai, KAD4 – Saur, KAD5 – Zaissan, KAD6 – Bukhtarma, KAD7 – Markakol-Kanas, KAD8 – Kara-Irtysh, KAD9 – Altai-Dzungarian); ZM, UM – Tuviniian-Mongolian province (regions: ZM1 – Chuya-Khobdo, ZM2 – Tsagan-Gol, ZM3 – Khobdo-Tonkhil; UM – South-Mongolian).

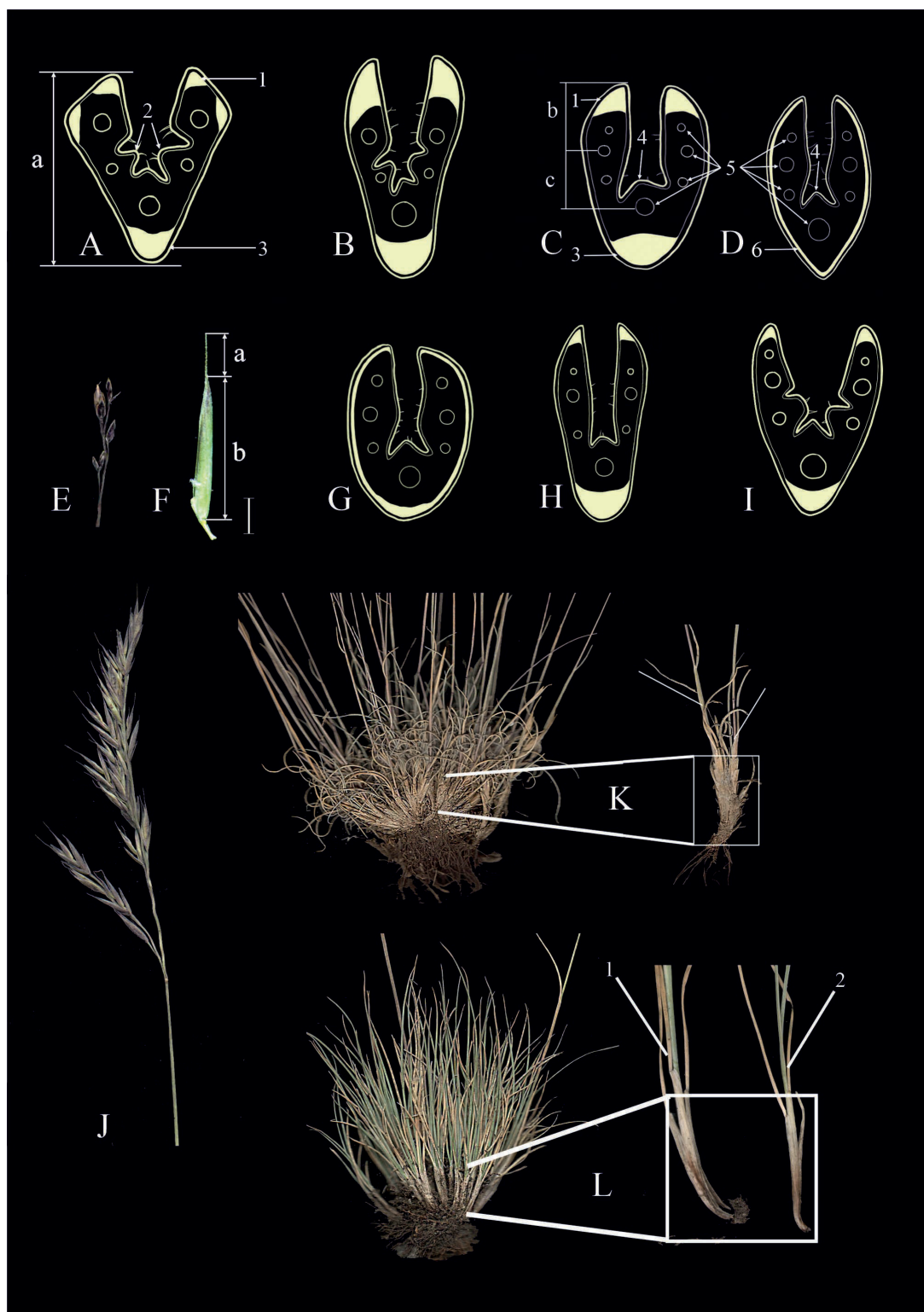


Figure 2. The most important macromorphological and anatomical characters of fescues **A, B, I** a cross-section with three well-defined ribs **C, D, G, H** a cross-section with only midrib or also two lateral ribs weakly defined. Shape of the cross-section leaf blades: **A** 4 angular **B, C, H** obovate **A, C, D** diagram of the leaf blades' anatomical structure of *Festuca* (designed by E.B. Alexeev): a) diameter, b/c) ratio b/c, 1) lateral sclerenchyma strand, 2) lateral ribs, 3) keel sclerenchyma strand, 4) middle rib, 5) vascular bundles, 6) continuous sclerenchyma layer **C** lateral sclerenchyma strands similar middle strand **H** lateral sclerenchyma strands less, than middle strand **F** flower: a) awn, b) lemma **E** panicle with 1–2 spikelets on lower branches, contacted **J** panicle with more than 2 spikelets on lower branches, open **K** grouped shoots (2–3 shoots surrounded by old sheaths) **L** single shoots: 1) flowering shoot, 2) vegetative shoot (AKA tillers).

Taxonomic treatment

Identification key to *Festuca* species occurring in the AM

- 1 Anthers 0.5–1(–1.3) mm long..... **2**
- Anthers 1.4–3 mm long **3**
- 2 Lower branches with more than 2 spikelets..... ***F. brachyphylla***
- Lower branches with 1–2 spikelets (Fig. 2E) ***F. brevissima***
- 3 Sclerenchyma in leaf blade cross-section in a continuous or sometimes discontinuous layer **4 (*F. ovina* aggr.)**
- Sclerenchyma in leaf blade cross-section in discrete strands **6**
- 4 Sclerenchyma layer thickened and wider on the midrib, invariably continuous layer (Fig. 2G); the leaf sheaths of tillers fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length ..
..... ***F. kuprijanovii***
- Sclerenchyma layer of similar width throughout, continuous or sometimes discontinuous layer (Fig. 2D); the leaf sheaths of tillers fused for $\frac{1}{6}$ – $\frac{1}{3}$ their length **5**
- 5 Spikelets brownish ***F. sphagnicola***
- Spikelets greenish or blueish green ***F. ovina***
- 6 Plants usually loosely tufted with extravaginal shoots with usually rhizomatous habit, sheaths of the tillers fused almost to their apex; shape of the leaf blade cross-section 4–6 angular (Fig. 2A) ***F. rubra***
- Plants usually densely tufted with intravaginal shoots; shape of the leaf blade cross-section obovate to elongate (Fig. 2B) **7**
- 7 Groups of 2–3 shoots are surrounded by a cover of previous sheaths (Fig. 2F) **8**
- Groups of 2–3 shoots are not surrounded by a cover of previous sheaths (Fig. 2L) **10**
- 8 Middle sclerenchyma strand two-three times wider than lateral strands (Fig. 2H); the leaf blades flexuose..... ***F. tschujensis***
- Middle sclerenchyma strand similar to lateral strand in terms of diameter; the leaf blades arcuate **9**
- 9 Spikelets brownish. Endemic of Saur Mountains (KAD4)..... ***F. saurica***
- Spikelets purple-green, green to white-green. Distribution in the Central and Northeast AM (A3, A5, A6) ***F. albifolia***
- 10 Spikelets brownish **11**
- Spikelets greenish **14**
- 11 Sheaths of tillers fused for $\frac{2}{3}$ – $\frac{4}{5}$ their length..... **12**
- Sheaths of vegetative leaves fused for less than $\frac{2}{3}$ their length **13**
- 12 Sheaths of vegetative leaves fused for $\frac{4}{5}$ their length; leaf blades with 7 (the narrowest ones with 5) vascular bundles, abaxial surface smooth or somewhat scabrous..... ***F. borissii***
- Sheaths of vegetative leaves fused for $\frac{2}{3}$ – $\frac{3}{4}$ their length; leaf blades with 5 (rarely 7) vascular bundles, abaxial surface distinctly scabrous
..... ***F. kurtzschumica***
- 13 Sheaths of vegetative leaves fused for $\frac{1}{3}$ – $\frac{2}{3}$ their length; lemma (4.5)4.8–5.5(6) mm; leaf blades green, rare bluish-green..... ***F. kryloviana***
- Sheaths of vegetative leaves usually fused for $\frac{1}{4}$ – $\frac{1}{3}$ their length; lemma 3.2–4.2(4.6) mm; leaf blades bluish green..... ***F. musbelica***

- 14 Leaf blade cross-section with only midrib or also two lateral ribs weak defined; sheaths of vegetative leaves fused for less than $\frac{1}{4}$ – $\frac{1}{3}$ their length ..
..... ***F. pseudosulcata***
- Leaf blade cross-section with 3 well-defined ribs; sheaths of vegetative leaves fused for less than $\frac{1}{6}$ their length **15**
- 15 Spikelets and leaf blades bluish and covered by wax..... ***F. valesiaca***
- Leaf blades green or bluish, not or rarely covered by wax..... **16**
- 16 Spikelets 4–6 mm; lemma 2.3–4.5 mm ***F. pseudovina***
- Spikelets 6–10 mm; lemma 4.5–6 mm ***F. rupicola***

***Festuca* L., Sp. Pl. 1: 73. 1753.**

Type species. –*F. ovina* L.

Subgen. *Festuca* sect. *Aulaxyper* Dumort., Observ. Gramin. Belg.: 102. 1824.

Type. *F. rubra* L.

***Festuca rubra* L., Sp. Pl. 1: 74. 1753.**

Type. Lectotype (designated by Jarvis et al. 1987: 302). Habitat in Europae sterilibus siccis (GB).

General distribution. Widespread across North America, Eurasia, Africa, introduced in Australia and South America.

Distribution in the AM. Widespread, all regions (Fig. 3f).

Habitat. Common in a wide range of vegetation types (fallow lands, roadsides, sands, meadows, forests, alpine zone); elev. 500–3500 m.

Flowering period. May–August.

Chromosome number. $2n=42$ (Leningrad region; Alexeev et al. 1987a; Altai; Probatova and Sokolovskaya 1980; o. Vrangeli; Petrovskii and Zhukova 1981; Primorskii Krai, Probatova et al. 2013); $2n=56$ (Chukotka Peninsula; Zhukova and Petrovskii 1976; o. Vrangeli; Petrovskii and Zhukova 1981).

Notes. *Festuca rubra* s.l. is an easily recognised taxon that has mostly extravaginal vegetative shoots (plants usually rhizomatous), the sheaths of the tillers and young leaves on flowering culms being fused almost to the top, 4–6 angular shape of leaf blades in cross-section, five or seven sclerenchyma strands, and well-defined ribs. *Festuca rubra* is a polymorphic species: the plant length is 25–100 cm; the colour of spikelets is greenish to purplish; the surface of lemma is characterised as glabrous or smooth with hooks, prickles or pilose, and the palea keels have hooks or prickles, the number of flowers in a spikelet is 5 to 11; the number of vascular bundles in a leaf blade cross-section of vegetative shoots equals to 5–11; the lemma length is 3.7–7 mm. Recent molecular research revealed that all of the examined *F. rubra* s.l. specimens belong to one clade (Kriuchkova et al. 2023).

Festuca richardsonii was previously recorded for the AM. However, these specimens were misidentified with *F. rubra*. Moreover, the results of our molecular study confirmed that the above mentioned specimens did not show any significant molecular differences (Kriuchkova et al. 2023), thus we here treat

the specimens collected from the AM and previously determined as *F. richardsonii* as representatives of *F. rubra*.

Festuca richardsonii is a species also belonging to sect. *Aulaxyper*. The species has a rather complicated history of records in the study area. Alexeev (1990) was the first who reported *F. rubra* subsp. *arctica* (= *F. richardsonii*) in the AM. He noted that, in the territory of the AM, there were individuals with transitional characters between *F. rubra* subsp. *arctica* and *F. rubra* subsp. *rubra*. A quarter of a century later, Chusovljanov (2007) recorded three more localities of *F. richardsonii* from the AM. Generally, *F. richardsonii* is the most widely distributed grass throughout the Arctic, common throughout Eurasia, North America, and Greenland. It was also recorded in the northern boreal zones, and in the Tarbagatai, Tian Shan, and Pamiro-Alai mountains within Central Asia (Markgraf-Dannenberg 1980; Darbyshire and Pavlick 2007; Chusovljanov 2007). Typical specimens of *F. richardsonii* differ from *F. rubra* in having shorter culm length (10–30(40) cm vs 50–60 cm); shape of the panicle (contracted vs open); smaller number of spikelets on lower panicle branches (1–2 spikelets vs 2 and more spikelets); the shorter awn length (0–1.5 mm vs 1–2.3 mm), respectively.

The taxonomic history of *F. richardsonii* is challenging. In the latest taxonomic revision of the genus *Festuca* in Russia, Tzvelev and Probatova (2019) synonymised *F. cryophila*, *F. kirelowii*, *F. rubra* ssp. *arctica*, *F. rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica* Hack under *F. richardsonii*. Previously, Tzvelev (1972, 1976), Alexeev (1990), Lu et al. (2006) treated *F. richardsonii*, *F. cryophila*, *F. kirelowii*, *F. rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica* Hack as synonyms of *F. rubra* subsp. *arctica*.

Festuca richardsonii, *F. rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica*, *F. kirelowii* were described almost at the same time. *Festuca richardsonii* was described by Hooker (1840) from North America; *F. rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica* was described by Hackel (1882) from Arctic Europe. *Festuca rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica* differs from typical *F. rubra* by the following characters: plant length 13–30 cm; dense to loose tuft; panicle with 1 to 2 spikelets on lower branches, contracted, length 20–60 mm; panicle branches hairy; lemma pubescent (data on the awn length is absent; Reverdatto 1928). *Festuca kirelowii* was described by Steudel (1855) from Tarbagatai, Kazakhstan. Krechetovich and Bobrov (1934) described a new species of *F. cryophila* from Yugorsky Strait, and mentioned *F. rubra* subsp. *eu-rubra* var. *arenaria* f. *arctica* as its synonym.

Specimens examined. RUSSIA. Republic Altai, Ust-Kanskii district, village Vladimirovka 50°44'4"N, 86°22'30"E, 4 June 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK; used to create Fig. 3a–e); Altai, Ust-Koksu, peschano-galechnikovy bereg r. Katuni, 9 July 1932, B.K. Shishkin (LE); Altai, Oirotiya, Chuiskaya step, boloto v usti r. Elongash – na vershinah, 11 August 1937, Akamin (LE); Vostochnyi Altai, khr. Kurkure, oz. Sarykul, yu.v. sklon, oзерная пойма mohovo-osokovo-travyanyi ernik, 16 August 1976, A. Galanik (LE); Altai, Oirotiya, Koshagachskii aimak, Kuraiskii hr., ushch. r. Tobozhok, severo-zap. Sklon, krai osypi, 30 August 1937, B.A. Shtakelberg, I.G. Kiorring (LE); Altaiskii zapovednik, bereg Teletskogo ozera naprotiv sel. Yailyu, vysokotravnyi lug, 22 July 1945, L. Tyulish (LE); Dolina r. Vaha, srednee techenie, okolo Korolskikh yurt, pesok v sosnovom boru, 17 July 1910, V.I. Ravaelev (LE);

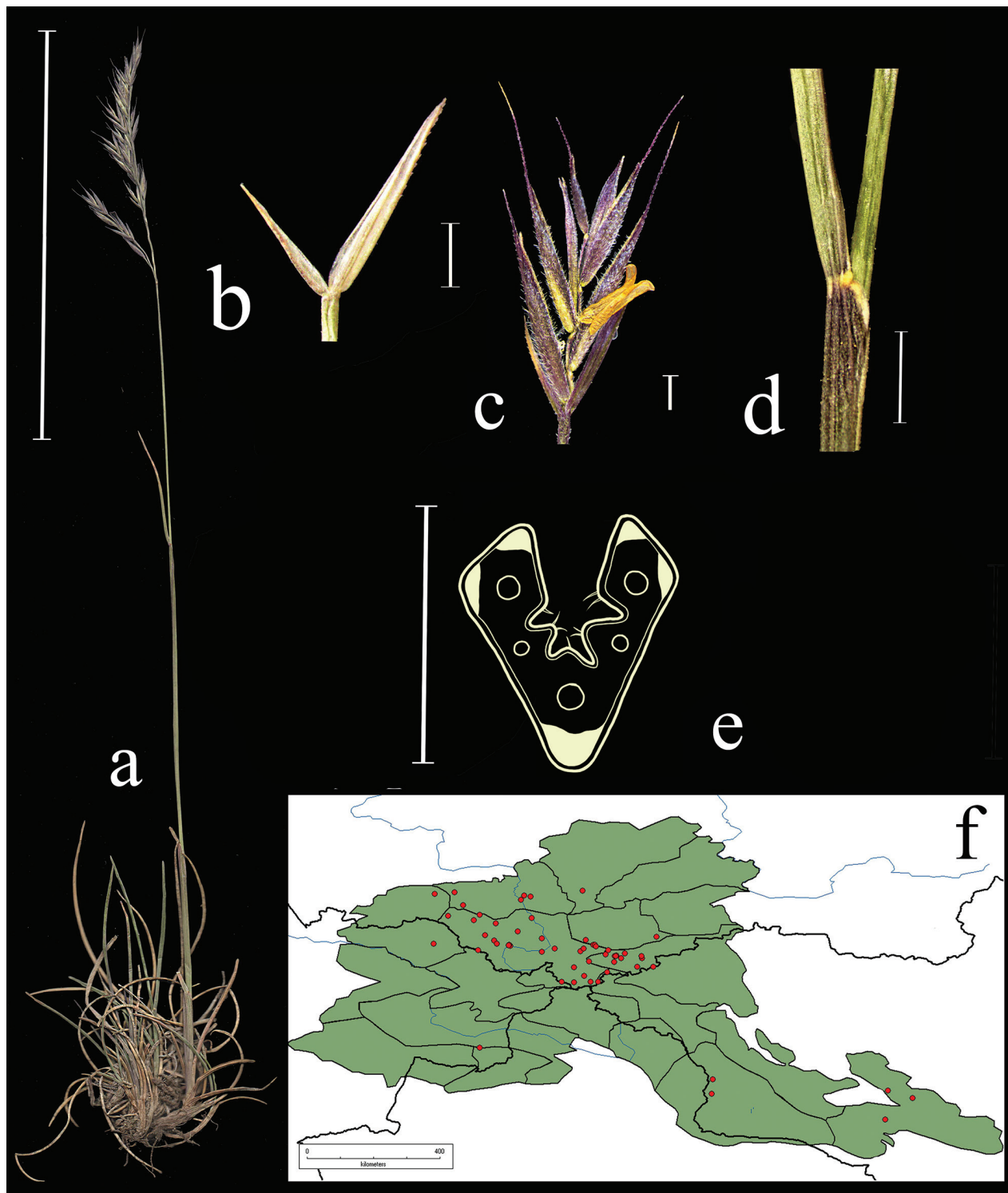


Figure 3. *Festuca rubra* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species distribution in the region known from literature data; red points mark localities confirmed by us during the revision of herbarium materials.

Altai, Oiroitiya, Koshagachskii aimak, gornyi pereval iz dol. Tarhaty v dol. Usai, osokovyi kochkarnik, 27 August 1936, A.V. Kalinina, L.A. Sokolova et B.K. Shishkin (LE); Respublika Altai, Kosh-Agachskii r-on, ploskogor. Ukok, sredn. tech. r. Kalguty, lev. bereg, 49°17'N, 88°03'E, 22 July 1995, R.V. Kamelin et al.

(KUZ); Respublika Altai, Kosh-Agachskii r-on, ploskogor. Ukok, nizhnee tech. r. Argamdzhi(srednei), 49°17'N, 87°50'E, 29 July 1998, R.V. Kamelin et al. (KUZ); Altaiskii krai, Charyshskii r-on, bass. r. Kumir, nizhnee tech. r. Berezovaya prav bereg, 50°53'N, 84°17'E, 3 August 1995, R.V. Kamelin, et al. (KUZ); Respublika Altai, Kosh-Agachskii r-on, dolina r. Ulandryk bliz vyhoda iz gor, 49°42'N, 89°07'E, 22 August 1998, A.I. Shmakov, et al. (ALTB); Altai, Oirotskaya avt. obl. s. Ust-Koksu, yuzhnye kamenistye sklony, 10 July 1931, B.K. Shishkin, L. Chilikina (LE); Altai, Ust-Koksinskii r-n, dolina r. Bannoi, otrogi khr. Holzun, levyi bereg reki, 8 August 1984, M. Lomonosova, Bubnova (NSK); Respublika Altai, Shebalinskii raion, v 3 km po doroge ot sela Barlyk k selu Topuchaya, levyi bereg reki Sema. Raznotravno-zlakovy pribeznyy lug (*Festuca pratensis*, *F. rubra*, *Dactylis glomerata*, *Elymus sibiricus*, *Lathyrus vernum*) 50°27'37"N, 85°34'45"E, 3 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK); Respublika Altai, Ust-Kanskii raion, okolo sela Vladimirovka. Kamenisty bereg reki Charysh (*Poa* sp., *Festuca rubra*, *Potentilla anserina*), 51°3'3"N, 84°12'0"E, 4 June 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK); Respublika Altai, Kosh-Agachskii raion, 4 km zapadnee sela Kurai. V elnike, na beregu reki, 50°14'13.6"N, 87°50'45.2"E, 4 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK); Respublika Altai, Kosh-Agachskii raion, 4 km zapadnee sela Kurai. Turbaza Merkit. Sredi mha, na bolotistom beregu (*Festuca rubra*, *Carex* sp., *Scirpus* sp.), 50°15'15.9"N, 87°51'11"E, 6 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK); Respublika Altai, Ongudaiskii raion, v 10 km ot sela Topuchaya na yug. Lug u dorogi 51°0'31"N, 85°38'17"E, 8 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK); Respublika Altai, Chemsalskii raion, okrestnosti sela Chermal, pravyy bereg reki Chermal, sklon, sosnovy les s vyhodami skal, 18 June 2017, P.A. Kosachev, P.D. Gudkova (TK); Respublika Altai, Kosh-Agachskii raion, 4 km zapadnee sela Kurai. Turbaza Merkit. Sredi mha, na bolotistom beregu (*Festuca rubra*, *Carex* sp., *Scirpus* sp.), 50°15'15.9"N, 87°51'11.0"E, 6 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK).

KAZAKHSTAN. VKO, Ridderskii raion, bliz Riddera, Altaiskii bot. sad., boloto, 21 July 1936, E.P. Matveeva (LE); Semipalatinskaya obl. Semipalatinskii uezd, Chingiz, gory Mashant, gornyy lug, 8 June 1914, C. Kossinsky (LE).

MONGOLIA. Mong. Altai, Hasannu-Hairhan, sev. sklon Uagon-Irmykula, sklon sev ekspozitsii v verh. Hunkerin-ama, kobreznik, elev. 2700–3100 m, v travostoe, 23 August 1972, V. Grubov et al. (LE); Mong. Altai, Hasachtu-Hairhan, sev. sklon Uagan-Irmyk-ula, sklon sev. ekspozitsii v verh. Hunkerin-ama, listvennichnyi les, elev. 2500–2700 m, 23 August 1972, V. Grubov et al. (LE); Zaphanskii aimak, Otgon somon, yuzhn. sklon Otgon-tenger, tipchakovaya pitrogritnaya step, elev. 2450 m, Sair v doline r. Chulut, 15 July 1974, Bagurai, Gambold, Damba, Muibayar (LE); Gobi-Altai aimak, dolina r. Bidzhi-gol v Mongolskom altae v 5 km v verh po techeni. reki na predgornyy lug s reliktovyymi berezami u vyhoda klyucha po sklonu ravniny, 10 August 1947, A.A. Yunatov (LE).

CHINA. Sintszyan-Uigurskaya avt. obl., v. Tian-Shan, sev. sklon, bass. r. Manas, levoberezhie, dol. r. Ulan-Usu, srednyaya chast doliny, lesnoi poyas, po dnishchu doliny na galechnikah, 18 July 1957, A.A. Yunatov, Li Shi-in, Yuan I-fen (LE); KNR, Sintszyan-Uigurskaya avt. obl., v. Tian-Shan, severnyye predgorya khr. Narat plato spuskayushchuyushcheesya v dolinu lonma – pritok Kungesa, subalpiiskii lug, 7 August 1958, A.A. Yunatov, Yuan I-Fen (LE).

Section *Festuca*.

Type species. *F. ovina* L.

***Festuca albifolia* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 3: 2. 1936**

≡ *F. lenensis* subsp. *albifolia* (Reverd.) Tzvel., Bot. Zhurn. 56 (9): 1254. 1971.

Type. Lectotype (designated by Tzvelev 1972: 39) [Russia] Khakasskii okrug, bliz ul. Birzul. Stepnoi lug na gore, 10 July 1929, V.V. Reverdatto (LE!).

General distribution. Russia (Khakassia, Western Sayan), Northern Mongolia.

Distribution in the AM. Very rare; A3, A5, A6 (Fig. 4f).

Habitat. Petrophytic steppes, stony slopes, rock fissures; elev. 500–2000 m.

Flowering period. June–July.

Chromosome number. $2n$ =unknown.

Notes. *Festuca albifolia* was described by Reverdatto (1936) based on herbarium material from Khakassia and Altai. Previously, the species was treated as *F. lenensis* subsp. *albifolia* (Tzvelev 1971, 1972; Alexeev 1990). However, *F. albifolia* differs from *F. lenensis* by the spikelets covered with a thick layer of wax, the color of spikelets (green vs green-brown), the leaf sheaths of tillers (glabrous and smooth vs scabrous), degree of the leaf sheath fusion (fused $\frac{1}{4}$ – $\frac{1}{2}$ their length vs fused $\frac{1}{2}$ their length), ratio b/c (ca. 1 vs ca. 2).

Festuca albifolia morphologically is also close to *F. valesiaca*. However, *F. albifolia* is distinguished from *F. valesiaca* by shoots (grouped by 2–3, surrounded by a cover of the old sheath vs single, not grouped), the leaf blade width (0.6–0.8 mm vs (0.35)0.4–0.6 mm), the number of ribs in a leaf blade cross-section (1 well-defined midrib vs 3 well-defined ribs), the number of vascular bundles (7 vs 5), the leaf sheaths of tillers (fused to $\frac{1}{4}$ – $\frac{1}{3}$ their length vs fused to $\frac{1}{6}$ – $\frac{1}{4}$ their length), the lemma length (4–5 mm vs (2.8)3.2–4.2(4.7) mm).

Specimens examined. RUSSIA. Okr. s. Sonskogo, shchebnistii sklon. 6–8 June 1910, V. Titov; Russkii Altai. Chuiskie belki. R. Sebistei, pritok Kokuze-ka. Sukhie sklony, 7 August 1911, V. Sapozhnikov (syntypes 2 sheaths: TK!); Altai, sev. sklon, khr. Sailyugem, uroch. Kochkor-Bas, sklon yuzhnoi ekspozitsii, 10 June 1967, I. Yemelkin (ALTB; used to create Fig. 4a–e; NSK); Minusinskii uezd, mezhdu oz. Shira i r. Tuimom, na shchebnistom yuzhnom sklone, 10 June 1910, W.I. Smirnow (LE); Khakasskii okrug, bliz ul. Birzul, stepnoi lug na gore, 10 July 1929, V.V. Reverdatto (LE); Oirotskaya avton. obl. Yugo-vostochnyi Altai. Chuiskaya step. V 26 km na yugo-vostok, bereg r. Irbistu, 20 July 1938, M. Albitskaya, V. Eliseeva (LE); Khakasiya, Shirinskii raion, okr. C-u "Borec" oz. Vlasevo, kamenistaya step, 29 June 1966, Neifeld, Kurochkina (ALTB).

***Festuca borissii* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 83: 8. 1965.**

Type. [Russia] Yuzhnyi Altai, okr. Katon-Karagaya, Narymskii khrebet ushchele Ushkungoi, alpiiskaya obl. 1 July 1920, V.V. Sapozhnikov (holotype and isotype TK!).

General distribution. Russian, Kazakh, Mongolian Altai.

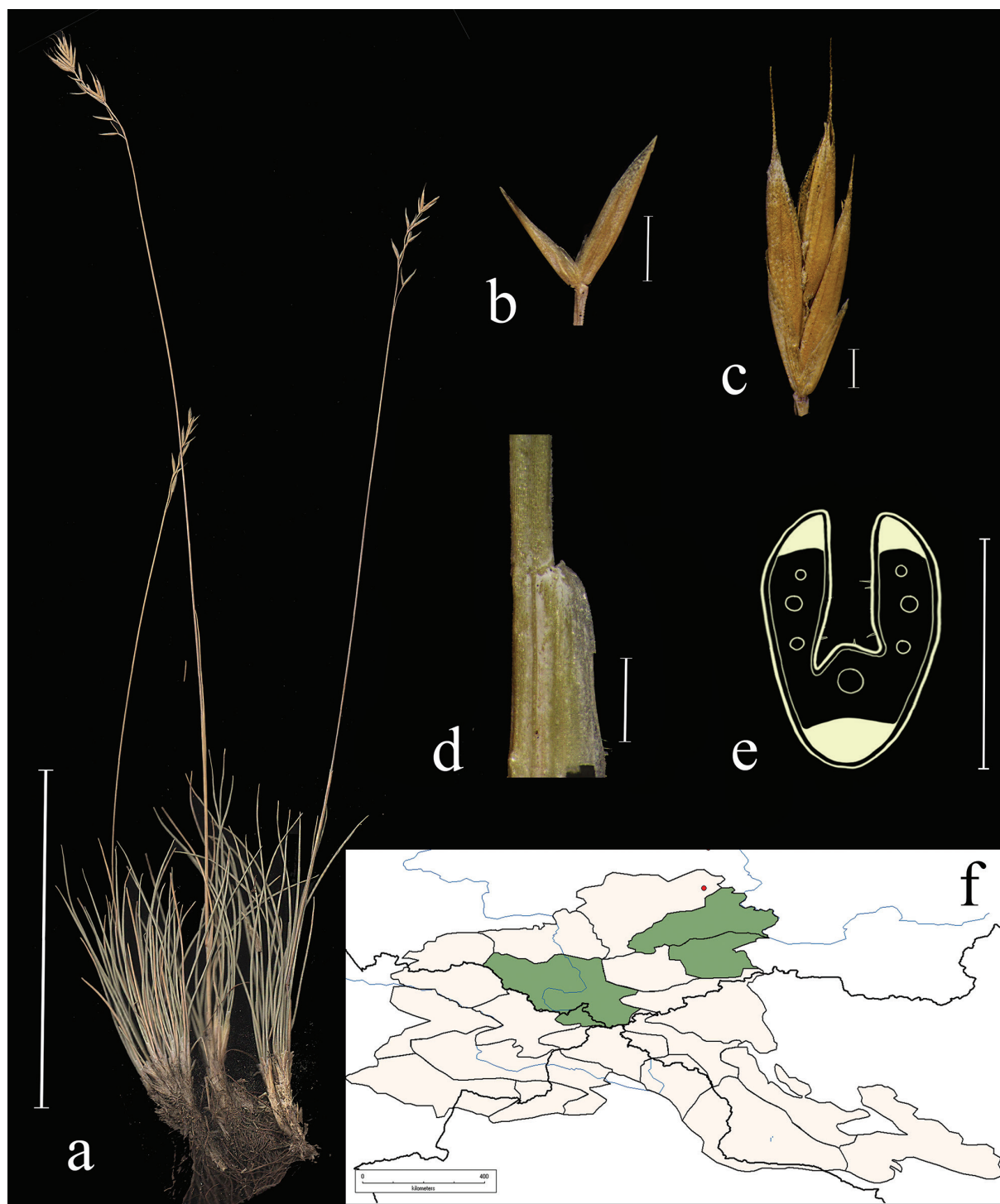


Figure 4. *Festuca albifolia* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map marks information about distribution for the region known from literature data, red points mark localities confirmed by herbarium materials revised during our studies.

Distribution in the AM. Common; A3, ZM1, KAD1, KAD6 (Fig. 5e).

Habitat. Stony slopes, rock fissures, screes; thin larch and cedar-larch forests at the edge of the forest, alpine zone, riversides in mosses; elev. 500–2200 m.

Flowering period. July–August.

Chromosome number. $2n$ =unknown.

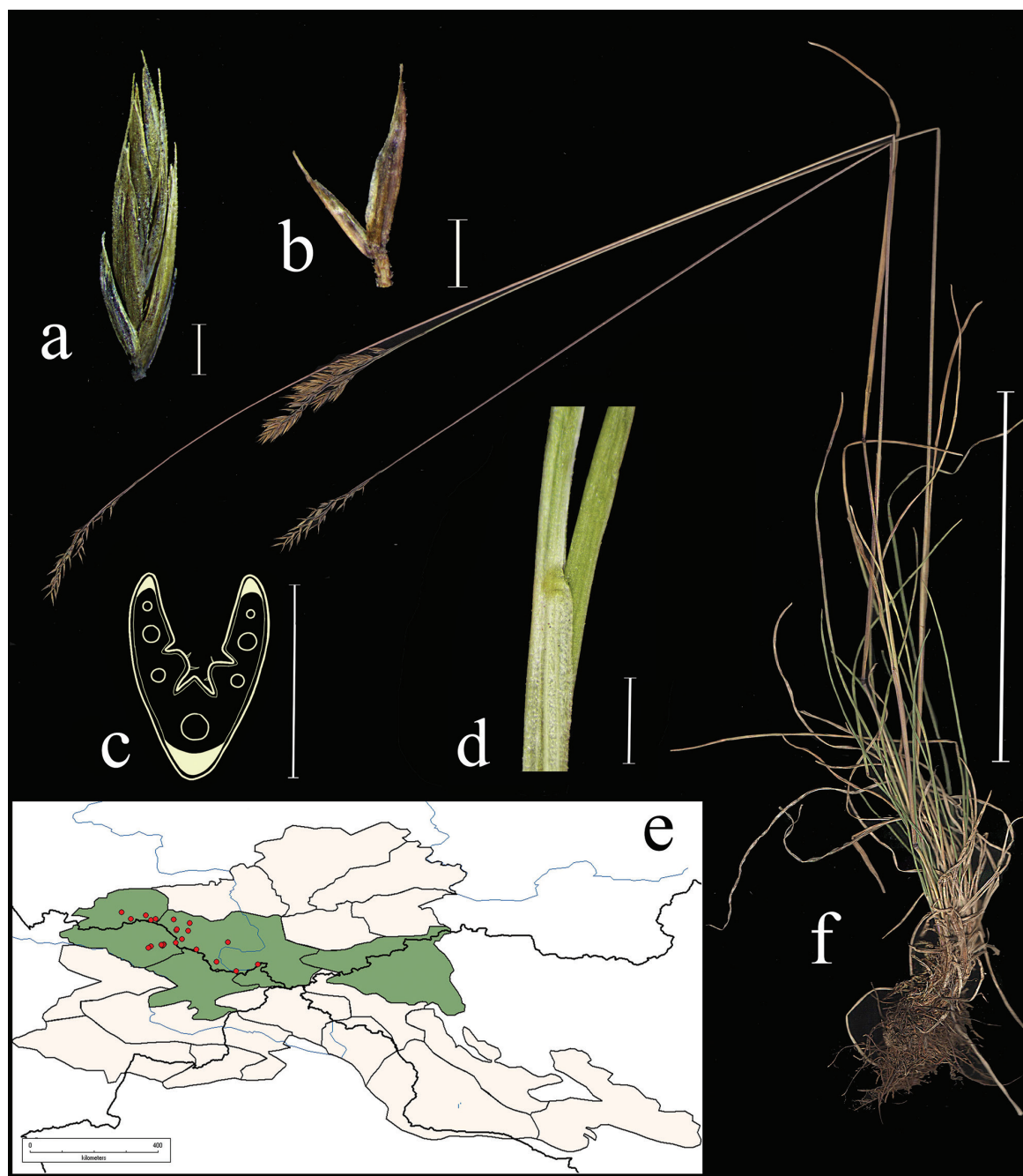


Figure 5. *Festuca borissii* **a** spikelet, lateral view **b** glumes, lateral view **c** leaf-blade cross-section **d** junction of leaf sheath and blade, lateral view **e** distribution map **f** general habit. Scale bars: 10 cm (**f**); 1 mm (**a**, **b**, **d**); 0.5 mm (**c**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Notes. *Festuca borissii* is close to *F. kryloviana*. Some taxonomists have distinguished the species from each other based on characters of the abaxial surface of the leaf blade and panicle branches, but these, in fact, cannot be used for this purpose (Tzvelev 1976; Alexeev 1990; Tzvelev and Probatova 2019). Both species are characterised by glabrous or scabrous leaf blades, scabrous or pubescent panicle branches. *Festuca borissii* differs from *F. kryloviana* by the structure of tillers (loosely tufted with extravaginal shoots vs densely tufted with intravaginal shoots respectively), the shape of the leaf blade cross-section (elongated

elliptical vs obovate), leaf sheaths of tillers (fused for $\frac{4}{5}$ their length vs fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length), the lemma length (3.5–4 mm vs 4–6 mm respectively).

Specimens examined. RUSSIA. Altai. Tigiretskii kkhrebet. Vershina r. Kumir, alpiiskii lug, 5 July 1955, A. Kuminova, M. Mitrofanova (ALTB; used to create Fig. 5a–d, f); Zapadnyi Altai, Kkhrebet Ivanovskii 2.5 km sev-vost. versh. Vysheivanovskii Belok, na skalah, elev. 2100 m, 18 July 1997, D.V. Chusovljanov (KUZ); Altaiskii krai, Zmeinogorskii r-n, kkhrebet Tigiretskii belok, 51°03'N, 82°56'E, 22 July 1997, A.N. Kupriyanov (KUZ); Tomskaya gub., Zmeinogorsk. u., kamen. sklon, subalp. obl., g. Sinyuha, bliz Ridderskogo rud., 19 June 1909, V.S. Ilin (LE); Tomskaya gub., Biiskii uezd: Katunskie belki, dolina r. Prohodnoi, Istvennichnyi les, 1 June 1911, W.L. Nekrassova (LE); Altai, khr. Korgon verh. r. Tatarki, alpiiskii lug, 4 July 1953, A. Kuminova, G. Pavlova (LE); Tomskaya gub. Biiskii u. Katunskie belki, verhove Katuni, vodorazdel s Bel. Berelyu, alpiiskie luga i tundra, 7 July 1911, W.L. Nekrassova (LE); Tomskaya gub. Zmeinogorsk. u. dolina r. Bystruhi, po sklonu k gornomu ruchyu bliz lesnogo predela, 2 August 1910, P. Tomin (LE); Altai, khr. Holzun, istoki r. Bannoi, alpiiskii lug, 8 August 1984, N. Frizen (NSK); Altai, Ust-Koksinskii r-n, Terektinskii hr., istoki r. Kastahta, osokovo-raznotravnyi kobrezev lug, 12 August 1984, Frizen, Bubnova (NSK); Altai, khr. Korgon, verhovya r. Charysha, alpiiskii lug, 2 June 1953, A. Kuminova, G. Pavlova (LE).

KAZAKHSTAN. Vostochnyi Kazakhstan, Ivanovskii hr., okr. Leninogorska, kurumnik, razrezhenyi listvenichnik, 10 September 2001, D. Chusovljanov (KUZ); Vostochnyi Kazakhstan, Ivanovskii hr., okr. Leninogorska, sypuha, 10 September 2001, D.V. Chusovljanov (KUZ); Vostochno-Kazakhstanskaya oblast, Khoazunskii kkhrebet pravyi bereg pravogo pritoka r. Khaidun na lugu na shchebnistoi pochve, 22 June 1939, Paulskaya (LE); Vostochnyi Kazakhstan, Koksinskii hr., elev. 1800 m, nizkotravnye alpiiskie luga, 10 August 2004, Yu. Kotuhov. (KUZ); Zapadnyi Altai, Khrebet Ivanovskii, v raione ozer Beloubinskih, elev. 1600 m, razrezhenyi kedrach, 18 July 1976, Yu. Kotuhov (KUZ); Zapadnyi Altai, Khrebet Ivanovskii, yugo-vostochnye otrogi versh. Vysheivanovskii Belok. Goltsy. elev. 2300 m, 26 July 1997, D.V. Chusovljanov (KUZ); Zapadnyi Altai, kh. Ivanovskii, Vostochnoe podnozhie versh, Vysheivanovskii Belok, shchebnistaya tundra, 26 July 1997, D.V. Chusovljanov (KUZ); Zapadnyi Altai, Khrebet Ivanovskii 3.5 km sev-vost. versh. Vysheivanovskii Belok, alpiiskii lug, elev. 1900 m, 8 July 1997, D.V. Chusovljanov (KUZ).

***Festuca brachyphylla* Schult & Schult fil., Mant. 3: 646. 1827.**

≡ *F. ovina* subsp. *brevifolia* (R. Br.) Hack., Monogr. Festuc. Europ.: 117. 1882.

Type. Lectotype (designated by Frederiksen 1977: 269) Melville Island, 1820, Mr. Edwards (BM; syntypes BM, LE!).

General distribution. Common throughout all arctic parts of NE European Russia, Siberia, Beringia, Canada, and Greenland. It also occurs in the northern boreal zones and in mountains farther south of Central Asia.

Distribution in the AM. Rare; KAD1, KAD4, KAD8, KAD9, A3, ZM1, ZM2, UM (Fig. 6f).

Habitat. Mountain steppes, alpine zone, rocky slopes, rocks and pebbles, screes; elev. (2000)2500–3500 m.

Flowering period. July–August.

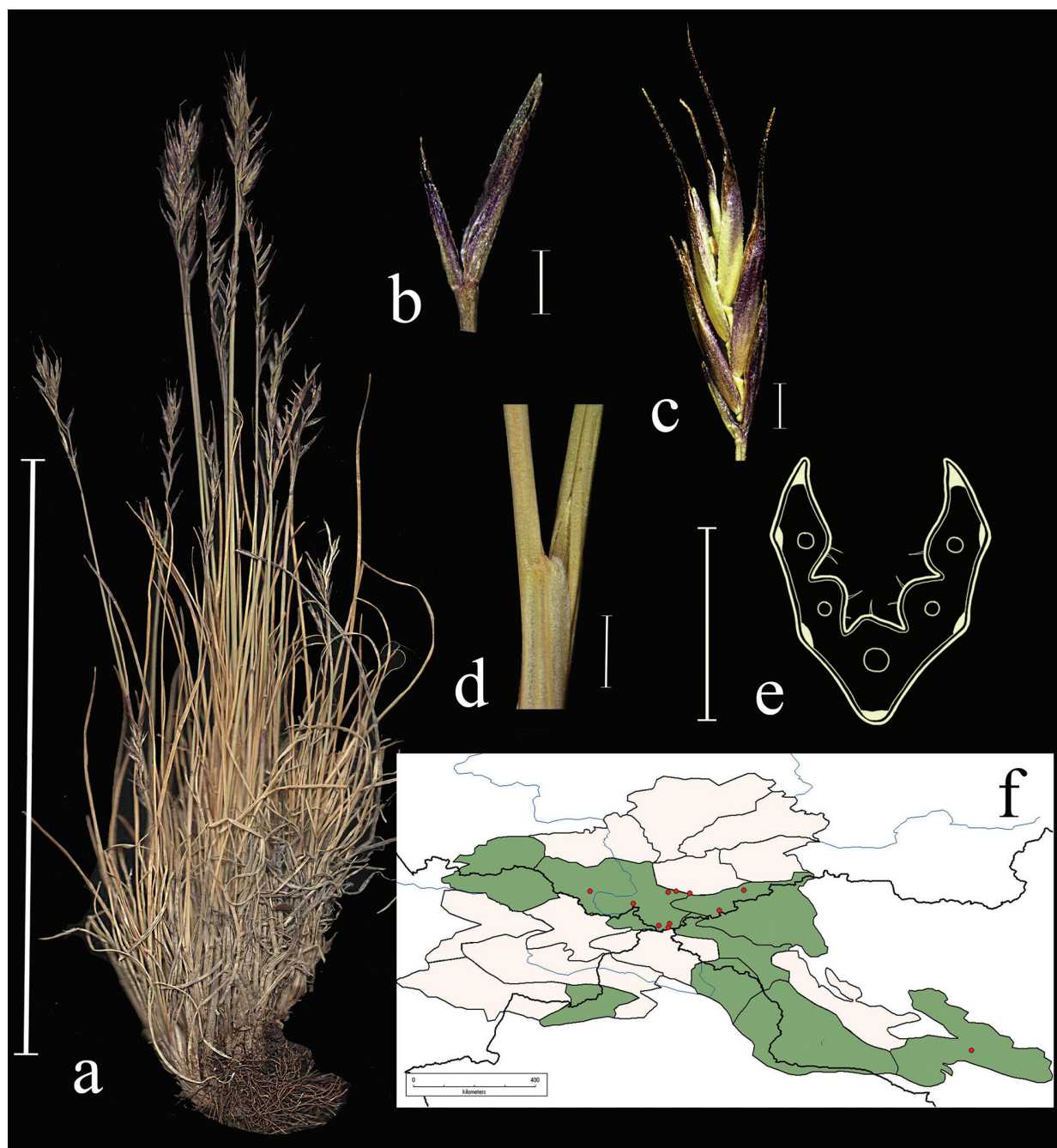


Figure 6. *Festuca brachyphylla* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, while red points mark localities confirmed by us during revision of herbarium materials.

Chromosome number. $2n=42$ (Kamchatskaya obl., Magadanskii obl.; Alexeev et al. 1987b; o. Vrangelya; Zhukova and Petrovskii 1980; Chukotka; Yurtzev and Zhukova 1978; American Arctica; Frederiksen 1981)

Notes. *Festuca brachyphylla* is easily recognised by its panicles with more than 2 spikelets on lower branches, anthers 0.5–1.5 mm in length, scabrid leaf blades, 5 or 7 sclerenchyma strands. Phylogenetically, our molecular study demonstrated that *F. brachyphylla* and *F. brevissima* refer to a separate clade distinct from sect. *Festuca* (Kriuchkova et al. 2023).

Specimens examined. RUSSIA. Kuraiskii khrebet, yuzhnyi makrosklon, alpiiskaya luzhaika, na osypyah. elev. 2850 m, 12 July 1998, *D.V. Chusovljanov* (KUZ; used to create Fig. 6a–e); Respublika Altai, Kuraiskii hr., verhove r. Ortalyk, po beregu ruchya, 2 July 1999, *A.A. Ebel* (KUZ); Altai, Oirotskaya avt. obl. r. Archaly, pritok r. Koksus, alp. mohovo-lishainikovaya tundra, 27 July 1931, *B. Shishkin, L. Chilinina, G. Sumnevich* (LE); Altai, Oirotskaya avt. obl. pereval mezhdru Ak-kemom i Kairom, alpiiskie luga, 18 July 1931, *B. Shishkin, L. Chilinina, G. Sumnevich* (LE); Altai, Oirotskaya avt. obl., istoki r. Kanasa, alpiiskaya tundra, 3 August 1931, *B.K. Shishkin, L. Chilinina, G. Sumnevich* (LE); Respublika Tuva, Mugur-Aksynskii r-n, kotl. oz. Hindiktig-Hol, okr. oz. Durug-Bazhi-Kara-Hol, 50°19'N, 89°55'E, 5 July 1995, *R.V. Kamelin* (ALTB); Altai, Kosh-Agachskii aimak, okr. s. Tashanta, bereg ozera, 15 July 1958, *A. Kuminova* (TK); Gorno-Altayskaya avt. obl. Ulaganskii r-n, verhove r. Yarly Amry, elev. 2700 m, 50°15'N, 87°40'E, driadovaya tundra, 6 August 1981, *M. Danilov, N. Kolesnikova* (NS); Kuraiskii khr. yuzhnyi makrosklon, v verhove Ortolyk, alpiiskii lug, na osypi, elev. 2850 m, 12 July 1998, *D.V. Chusovljanov* (KUZ); Respublika Altai, Kosh-Agachskii raion, plato Ukok, pereval Teplyi klyuch, elev. 2900 m, 49°24'27"N, 88°02'09"E, 7 August 2001, *A.I. Shmakov*; Respublika Altai, Kosh-Agachskii raion, khr. Sailugem, okr. Oz. Karakul, 49°40'N, 88°32'E, 3 July 2001, *M.G. Kucev, D.A. German* (ALTB).

MONGOLIA. Istoki r. Humet, kamenistaya tundra, 10 August 1998, *D.V. Chusovljanov* (KUZ); Kobdoskiy aymak, khr. Munkh-Khayrkhan, bassein r. Ulystyn-gol bliz severnoi chasti lednika Munkh-Khayrkhan, elev. 3250 m 12.08.1991, *G. N. Ogureeva* (MW).

***Festuca brevissima* Jurtzev, Bot. Zhurn. 57 (6): 645. 1972.**

Type. [Russia] Zap. Chukotka, istoki Anadyrya, u yuzhn. berega oz. Edgygytgyn, na yugo-zap. sklone, 20 July 1968, *B. Yurtzev et al. n K-61* (holotype LE!).

General distribution. Arctic parts of Siberia, Beringia, Altai.

Distribution in the AM. Very rare; A3, A4, ZM1 (Fig. 7f).

Habitat. Alpine zone, screes; elev. 2000–3500 m.

Flowering period. July–August.

Chromosome number. $2n=14$ (Russia, Chukotka; Yurtzev and Zhukova 1978; Kamchatka; Probatova et al. 2008).

Notes. *Festuca brevissima* is distributed in Chukotka, Kamchatka, Wrangel Island and Alaska on gravel slopes. As a result of the herbarium revision, we recorded the species much farther to the South in the mountains of Siberia. The specimens have been misidentified as *F. brachyphylla*. *Festuca brevissima* differs from *F. brachyphylla* by the number of spikelets in the panicle (fewer than 8 spikelets vs more than 11 spikelets respectively), the number of spikelets on lower branches (1–2 spikelets vs 2- or more spikelets), the panicle length (0.7–26 mm vs 23–55 mm), the lemma length (2.5–4 mm vs 4.5–5.5 mm), the plant length (up to 120 mm vs 100–550 mm). According to the results of our molecular studies, *F. brevissima* is clearly separated from *F. brachyphylla* (Kriuchkova et al. 2023). All the localities listed above are new records of the species for the AM. Information on the occurrence of species in areas previously unnoticed or misidentified with other species is nowadays very important, because being under increasing pressure from human activities and recently also under

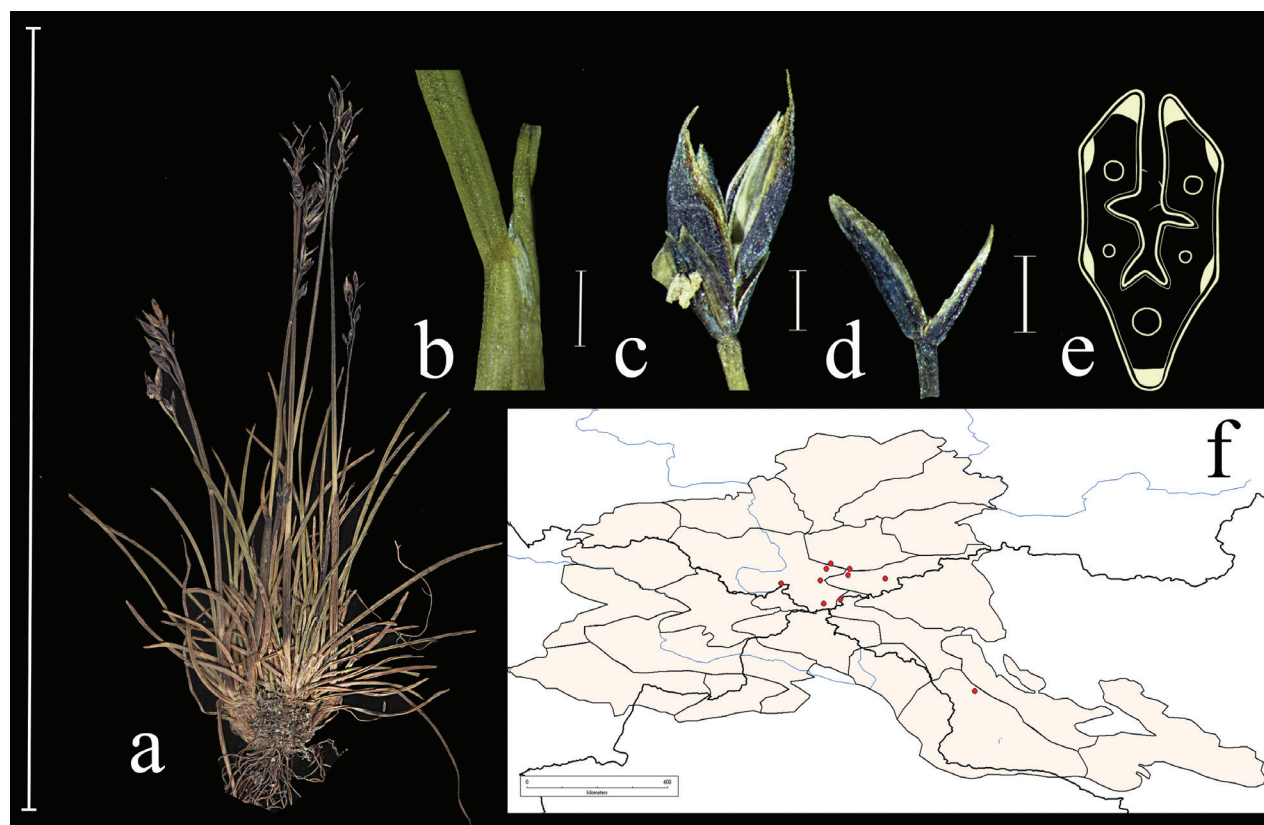


Figure 7. *Festuca brevissima* a general habit b junction of leaf sheath and blade, lateral view c spikelet, lateral view d glumes, lateral view e leaf-blade cross-section f distribution map. Scale bars: 10 cm (a); 1 mm (b–d); 0.5 mm (e).

the negative impact of global climate warming, the dynamics of both flora and vegetation in recent decades is much faster than before (Araújo and Rahbek 2006; Bellard et al. 2012; Vintsek et al. 2022; Nobis et al. 2023).

Specimens examined (New records): RUSSIA. Gorno-Altayskaya A.O., Kosh-Agachskii r-n, urochishche Tueryk, elev. 2900 m, 50°5'N, 88°22'E, osypi kristallicheskikh slantsev, 30 June 1982, *M. Danilov, V. Doronkin* (LE, NS); Gorno-Altayskaya A.O., Ulaganskii r-n, okr. oz. Choibekkol. elev. 2850 m, 50°16'N, 87°25'E, skaly po grebnyu khrebt, 13 July 1982, *M. Danilov, A. Grinev* (LE); Respublika Altai, Kosh-Agachskii raion, Yuzhno-Chuiskii khr., verkhovya r. Taldura bliz lednika, elev. 2480 m, 49°51'N, 87°43'E, 13 July 1993, *R.V. Kamelin et al.* (ALTB); Talduair, alp. poyas, elev. 3000 m, Kobrezievaya pustosh, 10 July 1999, *A. Ebel* (KUZ); Yuzh. makrosl. Kuraiskogo khr. v verkh. Ortolyk, alpiiskaya luzhaika, na osypi, elev. 2850 m, 12 July 1999, *A. Ebel* (KUZ); Gornii Altai, Katunskii kkhrebet, oz. Akkem, severnii sklon starogo kara, osyp, elev. 2400 m, 3 July 1974, *N.V. Revyakina, N. Vorobeva* (NS); Respublika Altai, Kosh-Agachskii raion, khr. Tabyn-Bogdo-Ula, ushchele Kara Chad, verkhovya reki, 49°19'N, 87°42'E, sklony ushchelya, skaly, 13 July 1992, *R.V. Kamelin, A. Shmakov, P. Golyakov, M. Mikhailova, S. Dyachenko, A. Kiselev, T. Krestovskaya, M. Kashcheev* (ALTB); Altai Republic, Koch-Agachskii distr., Ukok Plateau, pass between the rivers Djumala and Usay, elev. 2680 m, 49°25'35"N, 88°07'58"E, 20 July 1999, *A.I. Shmakov, S.V. Smirnov, E.V. Antonyuk, S.A. Kostjukov, V.I. Dorofeyev, I.N. Chubarov, P.A. Kosachev, S.A. Djachenko* (ALTB; used to create Fig. 7a–e).

MONGOLIA. Kobdoskiy aymak, khr. Munkh-Khayrkhan, bassein r. Ulystyn-gol bliz severnoi chasti lednika Munkh-Khayrkhan, elev. 3250 m, 12.08.1991, G. N. Ogureeva (MW).

***Festuca kryloviana* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 2: 3. 1927.**

Type. Lectotype (designated by Tzvelev 1972: 40) [Russia] Gorno-Alt. u., kkhrebet ot r. Berezovki do r. Khaisyna, alpiiskii lug, 1 July 1920, V. Sapozhnikov (LE01011329!).

General distribution. China (Altai, Dzungaria), Mongolia (Altai) and Russia (Altai, Sayan, Ural, Tarbagatai), Kazakhstan (Altai, Tyan-Shan.).

Distribution in the AM. Widespread; A1, A2, A3, A4, A6, ZM1, ZM3, KAD1, KAD3, KAD4, KAD6, KAD8, KAD9, UM (Fig. 8f).

Habitat. Forests, stony slopes, alpine and subalpine zone, petrophytic steppes, screes, riverbanks; elev. 1000–3500 m.

Flowering period. July–August.

Chromosome number. $2n=28, 42$ (Russia, Altai; Probatova and Sokolovskaya 1980); $2n=42$ (Irkutsk region; Chepinoga et al. 2010).

Notes. *Festuca kryloviana* is a morphologically variable species. The surface of lemma can be glabrous and smooth or scabrous, abaxial surface of the vegetative leaf blade is glabrous to scabrous, adaxial surface of the vegetative leaf blade is covered by hooks or prickles, rarely with microhairs present, the number of vascular bundles is 5 to 7, rarely 9 and the number of ribs is 3 to rarely 5, the lemma length equals to 4.3–5 mm, the awn length varies from 2 to 5 mm; the wax on the leaf blades is present or absent.

Specimens examined. RUSSIA. Respublika Altai, Kosh-Agachskii raion, srednee techenie reki Ortolyk, levoberezhie, listvennichnik, elev. 2100 m, 50°17'33.1"N, 87°50'53.8"E, 5 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK; used to create Fig. 8a–e). Yuzhnyi makrosklon Kuraiskogo hrebta, alpiiskaya luzhaika na osypyah, elev. 2850 m, 12 July 1999, A.A. Ebel (KUZ); Altai, Kosh-Agachskii r-n, khr. Sailyugem, verh. r. ZHumaly, elev. 2600 m, okr. rudnika Nov. Kalguty. Nadpoimennaya terrasa, raznotravno-lukovaya alpiiskaya luzhaika v ponizhenii, 51°N, 89°E, 8 August 1982, V. Hanminchun, N. Frizen, V. Petrusenko (NSK); Altaiskii krai, Soloneshenskii r-n, verhovya r. Shepeta, berezkovo-lishainikovaya tundra, 51°16'N, 84°15'E, 25 June 1997, T.O. Strelnikova, D.A. German (ALTB); Altai, Kosh-Agachskii r-n, khr. Sailyugem, verh. r. ZHumaly, elev. 2600 m, okr. rudnika Nov. Kalguty. Nadpoimennaya terrasa, osochkovo-ovsyanitsevaya tundra, 51°N, 89°E, 8 August 1982, V. Hanminchun, N. Frizen, V. Petrusenko (NSK); Respublika Altai, Kuraiskii khr. reka Ortolyk, zakustarenniy sklon, 2 July 1999, A.A. Ebel (KUZ); Altai, Oirotiya, Koshagachskii aymak, Kuraiskii khr., ushchele r. Tobozhok, yugo-zap. travyanisty sklon ushchelya Dzhayat, 3 August 1937, Shtakelberg (LE); Tomskaya gub. Biiskii u. belok mezhdur. Ini i vershinoi Senteleka v 15 km ot d. Pokrovka, 16 July 1913, N.J. Kusnezov (LE); Altai, Oirotiya, Koshagachskii aymak, dol. r. Tarhatty, lev. ber. sklon sev-vost. ekspozitsii, 23 August 1936, A.V. Kalinina, L.A. Sokolova, B.K. Shishkin (LE); Altai, Tigirekskii khrebet, vershina r. Belogolosov, Korgon, vysokogornaya tundra, 12 June 1955, A. Kuminova, G. Pavlova (LE); Altai, Kosh-Agachskii aymak, yuzhn. sklon Kuraiskogo hrebta, alpiiskaya tundra, 23 July 1955, A. Yakubova, E. Tyurina, L. Zubkus (LE); Altai, Oirotskaya avt. obl.

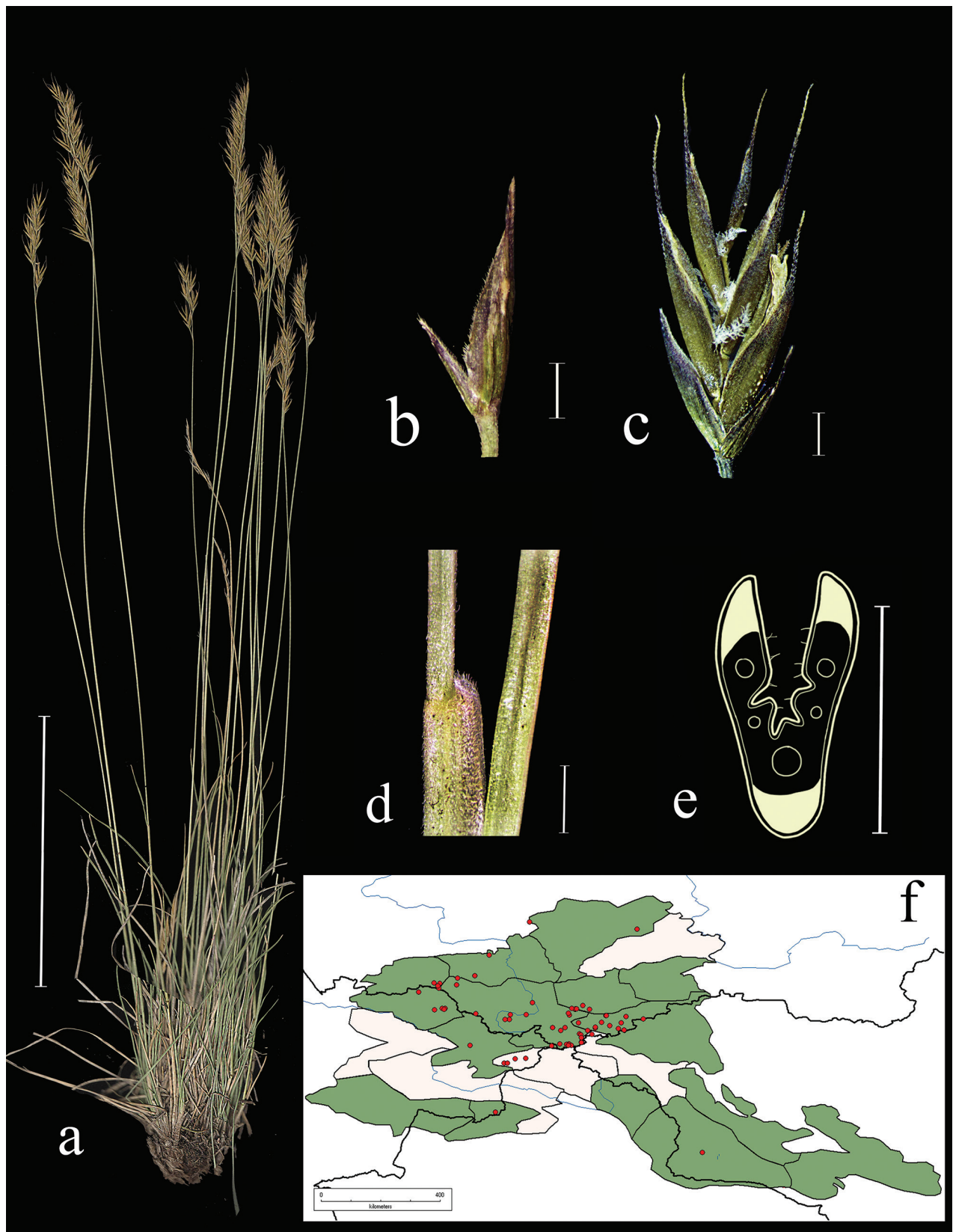


Figure 8. *Festuca kryloviana* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

istoki r. Kanasa, na lednikovyh morenah, 1 August 1931, *B. Shishkin, L. Chilikina, G. Sumnevich* (LE); Centr Altai, khr. Holzun, istoki r. Bannoi, alp. po yas, na shchebnistom lugu, 8 August 1984, *L. Malyshev* (NSK); Khakasiya, Tashtynskii r-n, okr. p. Nizhnie Siry, r. Tashtyi, ostepnennyi sklon, 29 June 1983, *Bondareva* (NSK).

KAZAKHSTAN. Yuzhnyi Altai, khr. Azatau, okresnosti s. Urunhaiki, vostochnyi sklon, razrezhennyi listvennichnyi les, 24 July 1984, *Yu. Kotuhov* (KUZ); Vostochno-Kazakhstanskaya oblast, Zapadnyi Altai, khrebet Ivanovskii, severo-vostochnyi sklon vershiny Vysheivanovskii Belok, shchebnistaya tundra, elev. 2150 m, 22 July 1997, *D.V. Chusovljanov* (KUZ); Zapadnyi Altai, khrebet Ivanovskii, yugo-vostochnye otrogi versh. Vysheivanovskii Belok, goltsy, elev. 2300 m, 26 July 1997, *D.V. Chusovljanov* (KUZ); Yugo-Zapadnyi Altai, VKO, Kolyvanskii hr., vershina sklona v verhovyah Tigireka, 25 July 1939, *Koroitkevich* (LE); Ozero Markakol, gornye luga, vysoko nad ozerom, 7 August 1908, *B.A. Keller* (LE); Khr. Saur, subalpiiskii lug, elev. 1900 m, vodorazdel r.r. B. i Mal. Dusemeneya, 5 July 1931, *N. Goncharov, P. Borisova* (LE).

MONGOLIA. Vostochnaya chast Mongolskogo Altaya, dolina r. Urhugol, listvenichnyi les po vostochnomu sklonu gory, 19 August 1930, *E.G. Pobedimova* (LE).

***Festuca kurtschumica* E. Alexeev, Novosti Sist. Vyssh. Rast. 13: 24. 1976.**

Type. Vostochnii Kazakhstan, Altai, gory u severnogo berega ozero Markakol, vyshe granitsy lesa, 2400–2700 m, 10 July 1912, *A. Sedelnikov* (holotype LE!).

General distribution. Mongolia (Altai), Kazakhstan (Altai), Russia (Altai, Olkhon island, lake Baikal).

Distribution in the AM. Very rare; A3, A5, ZM2, KAD7 (Fig. 9f).

Habitat. Gravelly places, screes; elev. 1500–3500 m.

Flowering period. July.

Chromosome number. $2n$ =unknown.

Notes. The distribution of *Festuca kurtschumica* is restricted to the AM. *Festuca kurtschumica* is similar to *F. kryloviana* but differs by leaf sheaths of tillers (fused for $\frac{2}{3}$ – $\frac{3}{4}$ their length vs fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length), leaf blade width (0.4–0.5 (0.55) mm vs (0.4)0.55–0.85(1) mm), lemma length (3.5–4.5 mm vs 4.5–6 mm), and the number of vascular bundles (5 vs (5)7 respectively). However, in accordance with the results of molecular analysis, *F. kurtschumica* and *F. kryloviana* are grouped into a common clade (Kriuchkova et al. 2023). The species needs a taxonomic revision within its entire distributional range, including the locus classicus, namely the vicinity of Lake Markakol, the Khazakh part of the AM.

Specimens examined. RUSSIA. Altai, Oirotskaya avt. Obl., r. Archaly, pritok r. Koks, alpiiskaya mokhovo-lishainikovaya tundra, 27 July 1931, *B. Shishkin, L. Chilikina, G. Sumnevich* (paratype LE!); Respublika Altai, Kosh-Agachskii r-on, zap. chast ploskogor. Ukok, vostochnyi makrosklon gory Muzdy-Bulak, 49°15'N, 87°14'E, 23 July 1998, *R.V. Kamelin, A.I. Shmakov, S. Kostyukov, I. Chubarov, D. Tihonov, E. Antonyuk* (ALTB); Respublika Altai, Kosh-Agachskii r-on, ploskogor. Ukok, okresnosti oz. Ukok, 49°15'N, 87°23'E, 26 July 1998, *R.V. Kamelin, A.I. Shmakov, S. Smirnov, P. Kosachev, D. Tihonov, E. Antonyuk* (KUZ); Altai, Oirotskaya avt., obl. r. Archaly, pritok r. Koks, alp. mohovo-lishainikovaya tundra, 27 July 1931, *B.K. Shishkin, L. Chilinina, G. Sumnevich* (LE); Respublika Altai, Ulaganskii raion, Kuraiskii hr., verhovya r. Yarly-Amry, elev. 2700–2900 m, 50°20'08"N, 87°44'45"E, 20 July 2012, *A.I. Shmakov et al.* (ALTB).

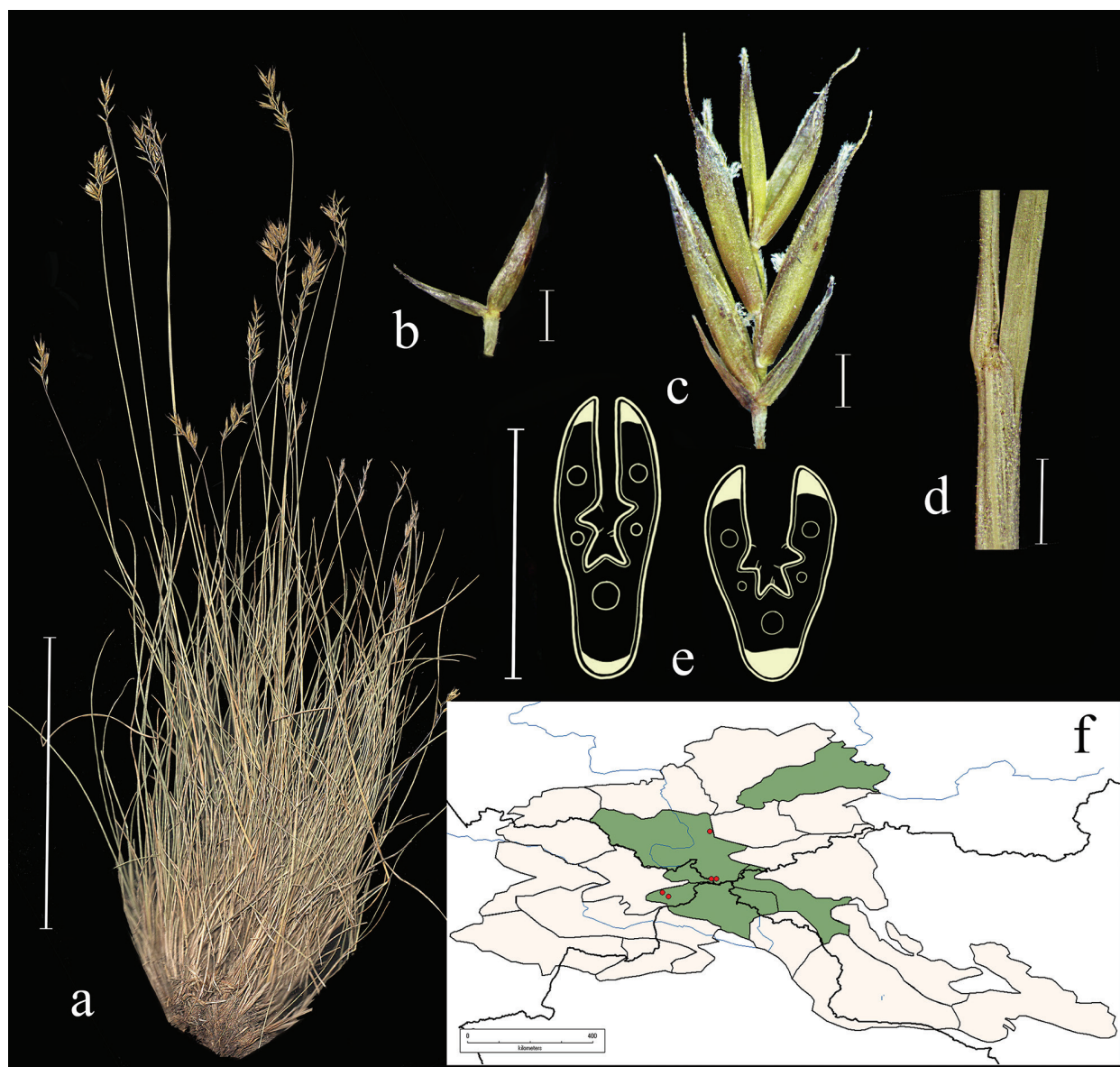


Figure 9. *Festuca kurtschumica* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

KAZAKHSTAN. Yuzhnyi Altai, khr. Azutau, Urunhaiskii pereval, razrezhennyi listvennichnyi les, ostepnennye lugoviny, elev. 1800 m, 20 June 1986, Yu. Kotuhov (ALTB; used to create Fig. 9a–e); Yuzhnyi Altai, khr. Azutau, Urunhaiskii pereval, elev. 1800 m, razrezhennyi listvennichnyi les, ostepnennye lugoviny, 20 June 1986, Yu. Kotuhov (KUZ); Vostochnyi Kazakhstan, Altai, gory u severnogo berega oz. Markakol vyshe granitsy lesa, elev. 2400–2700 m, 10 July 1912, A. Sedelnikov (LE).

MONGOLIA. Sev. Mongolia i Hangai, listvennichnyi les, v dvuh verstah ot Klyucha Hurum-bulyk, 8 July 1926, N. Ikonnikov-Galitzky (LE); Sev. Mongolia i Hangai, okr. TSzain-shaby, v listvennichnom lesu, k zapadu ot klyucha Haltszangyn-bulyk, 17 July 1926, J. Prochanov (LE); Zapadnaya Mongoliya, Bayan-Ulgiiskii aimak. Mongolskiy Altay, 15 km na zapad ot Khoto-Nura, subalpy na granitse s Kitayem, 17 August 1979, I.A. Gubanov, Det. Alexeev E.B. (MW0170759);

Zapadnaya Mongoliya, Kobdoskii aimak, Mongolskii Altai. Vostochnyi makroskion khr. Munkh-Khayrkhan, kotlovina Ikh-Khak v verkhovnykh r. Dolon-Nuryngol bliz yuzhnyi chasti lednika Munkh-Khayrkhan, vykhody slantsev na verkhushke gory, elev. 3020 m, 7 August 1991, G.N. Ogureeva, Det. Dariyma (MW0170755).

***Festuca musbelica* (Reverd.) Iconn. Opred. Vyssh. Rast. Badakhsh.: 75. 1979.**

≡ *F. kryloviana* var. *musbelica* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 2: 4. 1927.

= *F. ovina* subsp. *sulcata* var. *hypsochila* St.-Yves., Candollea 111. 1932; non *F. hypsochila* Phil. Anal. Mus. nac. Chile: 89. 1891.

= *F. oreochila* Markgr.-Dannenb., Willdenowia 11: 208. 1981.

Type. Lectotype (designated by Tzvelev 1972: 168) Armenia, distr. Nor. – Bajazet, in monte Achdagh mior, 16 August 1929, O. Zedelmeyer, T. Heidemann (*F. ovina* subsp. *sulcata* var. *hypsochila*; LE!).

General distribution. The species occurs in mountains, from Turkey, throughout Caucasus, Central Asia (Western, Eastern Siberia), up to Mongolia (Altai).

Distribution in the AM. Very rare; A3, ZM1, ZM3, KAD4, KAD6, KAD9, UM (Fig. 10c).

Habitat. Alpine zone, forests, meadows, petrophytic steppes; elev. 1500–2500 m.

Flowering period. July–August.

Chromosome number. $2n=14$ (Kazakhstan, Kyrgyzstan; Alexeev et al. 1988; TRANS-Baikal territory; Probatova et al. 2013).

Notes. *Festuca kryloviana* var. *musbelica* was described from the Altai Republic, Russia (Reverdatto 1927), whereas *F. ovina* subsp. *sulcata* var. *hypsochila* was described from Europe (Saint-Yves 1932). Tzvelev (1971), in his taxonomic revision of the genus, proposed new nomenclatural combinations: *F. valesiaca* subsp. *musbelica* and *F. valesiaca* subsp. *hypsochila* and respectively referred *F. kryloviana* var. *musbelica* and *F. ovina* subsp. *sulcata* var. *hypsochila* to the synonyms of the above-mentioned taxa. *Festuca kryloviana* var. *musbelica* is rather well distinguished from *F. kryloviana* var. *kryloviana* by the characters of the leaf sheath surface of tillers (glabrous or smooth and glossy vs scabrous and matte), the leaf sheaths of tillers (fused for $\frac{1}{4}$ their length, rarely $\frac{1}{6}$ their length vs fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length). Considering these major differences, Ikonnikov (1979) proposed to raise *F. kryloviana* var. *musbelica* to the rank of species, *F. musbelica*. Later, Markgraf-Dannenberg (1981) described a new species, *F. oreochila*, and synonymized *F. ovina* subsp. *sulcata* var. *hypsochila* under this new name. In the later taxonomic treatment of the genus *Festuca*, Tzvelev and Probatova (2019) subsumed *F. ovina* subsp. *sulcata* var. *hypsochila*, *F. kryloviana* var. *musbelica*, *F. valesiaca* subsp. *hypsochila*, and *F. oreochila* as synonyms of *F. musbelica*. *Festuca musbelica* is the earliest legitimate name and thus, according to ICBN, chapter 2, article 11.4 (Turland et al. 2018), has priority as the correct name.

Molecular analyses placed *F. musbelica* in the common clade with *F. valesiaca* (Kriuchkova et al. 2023). However, the species differs from *F. valesiaca* by the color of spikelets (brown vs green, bluish green, pinkish green), and the leaf sheath of tillers (fused for $\frac{1}{4}$ – $\frac{1}{3}$ their length vs fused for $\frac{1}{4}$ – $\frac{1}{6}$ their length). The species needs a taxonomic revision over its entire distributional range.

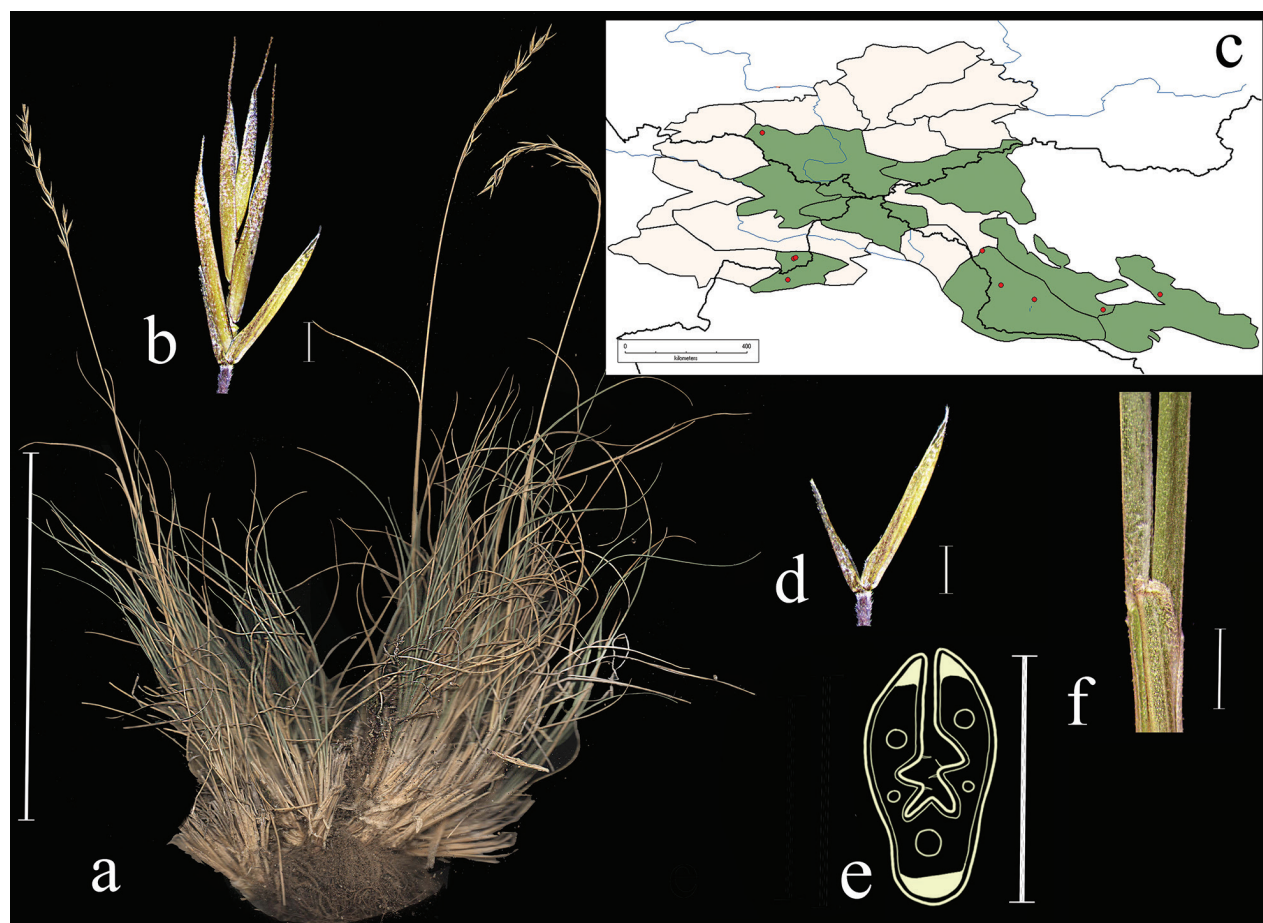


Figure 10. *Festuca musbelica* **a** general habit **b** spikelet, lateral view **c** distribution map **d** glumes, lateral view **e** leaf-blade cross-section **f** junction of leaf sheath and blade, lateral view. Scale bars: 10 cm (**a**); 1 mm (**b**, **d**, **f**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Specimens examined. RUSSIA. Gornyi Altai, Ust-Kanskii r-n, lev. bereg r. Koksas, v 15,5 km vyshe pos. Sauzar 50°28'N, 84°40'E, 24 June 1991, *M. Mihailova* (ALTB; used to create Fig. 10a–e); Altai, Ust-Koksinskii r-n, d. r. Charysh, okr. p. Vladimirovka, kamenistaya step, 21 May 1982, *Doronkin* (LE).

KAZAKHSTAN. Kazahskaya SSR, khrebet Saur, sev. makrosklon, verhovaya r. Terekty bliz pos. Kyzyl-Kiya, melkozemlistye sklony s kobreziei, 16 July 1965, *V.I. Vasilevich et al.* (LE); Kazahskaya SSR, Kalbinskii khrebet, Yuzhnyi Altai, Zaisanskaya kotlovina, khrebet Saur, verhnaya granitsa lesa i vysokogornye kobrezniki, v 3–4 km SZ Kyzyl-Kiya, v 35–40 km YuV goroda Zaisan, 16 July 1965, *A.A. Yunatov* (LE).

MONGOLIA. Gobi-Altai aimak, Hurmin-somon, 10 km k yugo-vostoku ot Yusun-Bulaka, srednyaya chast severnogo belya, khr. Han-Taishiri, raznotravno-zhitnyakovo-kovyl'naya step, 14 July 1948, *A.A. Yunatov* (LE); Hobdoskii aimak, Bulgan somon, verhovaya Haragaitu gala, levoberezhnogo pritoka Buluguna, listvennichnyi les, 24 July 1947, *A.A. Yunatov* (LE); Hobdoskii aimak, Hudiirtu somon, Sairin-gol, sosna na drevnei morene, 25 July 1947, *A.A. Yunatov* (LE); Hobdoskii aimak, Bulgan somon, v 2 km k zapadu ot somona po doroge, na Haragaitu Hutul, step, 24 July 1947, *A.A. Yunatov* (LE); Gobi-Altai aimak, Tamchi somon, 2–3 km yuzhnee oz. Tamchi, v shirokoi mezhgornoi doline, polynno-tipchakovaya gornaya step, 17 July 1947, *A.A. Yunatov* (LE).

CHINA. Sintszyan-Uigurskaya avtonomnaya oblast, khrebet Saur, yuzhnyi sklon, dol. r. Karagaitu, pravoberezhnaya pad Bain-TSagan, subalpiiskii lug vyshe lesnoi granitsy, 23 June 1957, A.A. Yunatov, Li Shi-in, Yuan I-fen (LE).

***Festuca ovina* agg.**

The aggregate comprises three species in the AM, *F. ovina*, *F. sphagnicola* and *F. kuprijanovii*.

Notes. *Festuca ovina* is easily distinguished by green or bluish green spikelets, the leaf blade cross-section with abaxial sclerenchyma in a continuous or sometimes discontinuous in 3 main islets of low profile layer, with only a midrib well defined, and with 5 or 7 vascular bundles. Within the *F. ovina* complex in the territory of the AM, two more species close to *F. ovina* (*F. sphagnicola* and *F. kuprijanovii*) are identified, however molecularly they form a common clade (Kriuchkova et al. 2023).

Festuca kuprijanovii is the next species of the *F. ovina* complex. It was described by Chusovljanov (1998) based on macromorphological and anatomical data. *Festuca kuprijanovii* is known only from the type locality (RUSSIA. Gornyi Altai. Ulaganskii raion, verhovya r. Nizhnyaya Koks, lev. pritoka r. Ulusuk, sklon, na skalah, 31 July 1991, M.V. Olova, M.M. Silanteva and Altaiskii krai, Kosh-Agachskii r-on, okrestnosti s. Kurai, pravyy bereg r. Tyute, 15 July 1982, V.N. Kutafev, T. Ermina (LE)). *Festuca kuprijanovii* is close to *F. ovina* and *F. sphagnicola*. However, *F. kuprijanovii* differs from *F. ovina* in the continuous subepidermal layer consisting of 2–3 cells with a thickening opposite the midrib consisting of 5–6 cells (vs similar continuous subepidermal layer consisting of 2–3 cells), brown spikelets (vs green; Table 1). *Festuca kuprijanovii* differs from *F. sphagnicola* in the continuous subepidermal layer consisting of 2–3 cells with a thickening opposite the midrib consisting of 5–6 cells (vs similar continuous subepidermal layer consisting of 2–3 cells; Chusovljanov 1998). Molecular research, however, grouped *F. kuprijanovii* and *F. ovina* into a common clade (Kriuchkova et al. 2023).

The similar issue refers to another species of the *F. ovina* complex, *F. sphagnicola*. Some botanists treated *F. sphagnicola* as a subspecies of *F. ovina* (Tzvelev 1971, 1976; Probatova and Sokolovskaya 1980; Alexeev 1990; Lu et al. 2006), or independent species (Tzvelev and Probatova 2019). Further, Alexeev considered diploid individuals to be *F. ovina* s. str. and referred polyploid individuals to other species. Consequently, tetraploid individuals of *F. ovina* from the AM were referred to *F. sphagnicola* (Table 1). The last mentioned taxon differs from *F. ovina* by the color of spikelets (brown vs green, respectively), the elevation of occurrence (over 1700 m vs up to 1700 m, respectively), the number of chromosomes (tetraploid vs diploid).

Table 1. Main morphological differences between species of the *F. ovina* aggregate.

Character	<i>F. kuprijanovii</i>	<i>F. sphagnicola</i>	<i>F. ovina</i>
Spikelet	brown	brown	green
Abaxial sclerenchyma	a continuous subepidermal layer thickening opposite the midrib	a continuous subepidermal layer	a continuous subepidermal layer or subcontinuous in 3 main islets of low profile
Count of chromosomes	unknown	28	14

Molecular research, however, grouped *F. sphagnicola*, *F. kuprijanovii* and *F. ovina* into a common clade (Kriuchkova et al. 2023). Thus, further studies including molecular (at the population level), morphological, and cytological analyses are needed on the above mentioned group of taxa from the entire area of their distribution to resolve whether *F. kuprijanovii* and *F. sphagnicola* are separate or conspecific with *F. ovina*.

***Festuca ovina* L., Sp. Pl. 1: 73. 1753.**

= *F. ovina* var. *ruprechtii* Boiss., Fl. Orient. 5: 619. 1884.

≡ *F. ruprechtii* (Boiss.) V. Krecz. et Bobr., Fl. SSSR 2: 507. 1934.

≡ *F. ovina* subsp. *ruprechtii* (Boiss.) Tzvel., Bot. Zhurn. 56 (9): 1255. 1971.

= *F. supina* var. *elata* Drobow, Tr. Bot. Muz. Akad. Nauk 153. 1915.

= *F. supina* auct. non Schur: V. Krechetovich i Bobrov, Fl. SSSR 2: 504. 1934.

Type. Lectotype (designated by Kerguélen in Lejeunia 75: 150 1975) habitat in Alpius Lapponicae, Helvetiae, Scotiae (LINN 92.1); isolectotype (LAPP 55).

General distribution. The species is widely distributed, it is common in the Arctic zone of Eurasia and North America, and occurs also in mountains farther to the south of Eurasia (Kazakhstan, China, Mongolia).

Distribution in the AM. Very rare; A3, ZM1, ZM3, UM (Fig. 11o).

Habitat. Forest, meadows, steppes, sand, rock fissures; elev. 500–1700 m.

Flowering period. May–June.

Chromosome number. $2n=14$ (Altai; Probatova and Sokolovskaya 1980; Irkutskaya Oblast; Probatova et al. 2009).

Notes. See notes under *F. ovina* agg.

Specimens examined. RUSSIA. Respublika Altai, Kosh-Agachskii raion, srednee techenie reki Ortalyk, levoberezhie, listvennichnik s mohovoi podstilkoj, elev. 2100 m, 50°07'28"N, 87°50'19"E, 5 July 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (TK; used to create Fig. 11); Na granitse Tomsk. i Enis. Gub. Vodrazdel r.r. V.S. Lyusa i B. Usy, u lesnogo predela, 22 June 1901, V.S. Titov (LE).

MONGOLIA. Prihubs, per. Sagsain-daba k vostoku Hathyla po doroge na Chindaman-Undursomok, zabolochennyi listvennichnyi les s ernikom po grebnyu, 30 July 1972, V. Grubov et al. (LE); Ubsanurskii aimak, Turun somon, khr. Han-Huhoi, g. TSgan Hairhan, osokovo-kobrezievyi alpiiskii lug, 23 July 1945, A.A. Yunatov (LE).

***Festuca kuprijanovii* Chus. Bot. Zhurn. 83: 113. 1998.**

Type. [Russia] Gornii Altai. Ulaganskii raion, verkhovya r. Nizhnyaya Koku, lev. pritoka r. Ulusuk. Sklon na skalakh. 31 July 91, Olonova, Silanteva (holotype LE01011330!).

General distribution. Altai mountains, endemic.

Distribution in the AM. Very rare; A3, ZM1 (Fig. 11p).

Habitat. Among rocks, petrophytic steppes, elev. 1500–2500 m.

Flowering period. June–July.

Chromosome number. $2n$ =unknown.

Notes. See notes under *Festuca* agg. *ovina*.

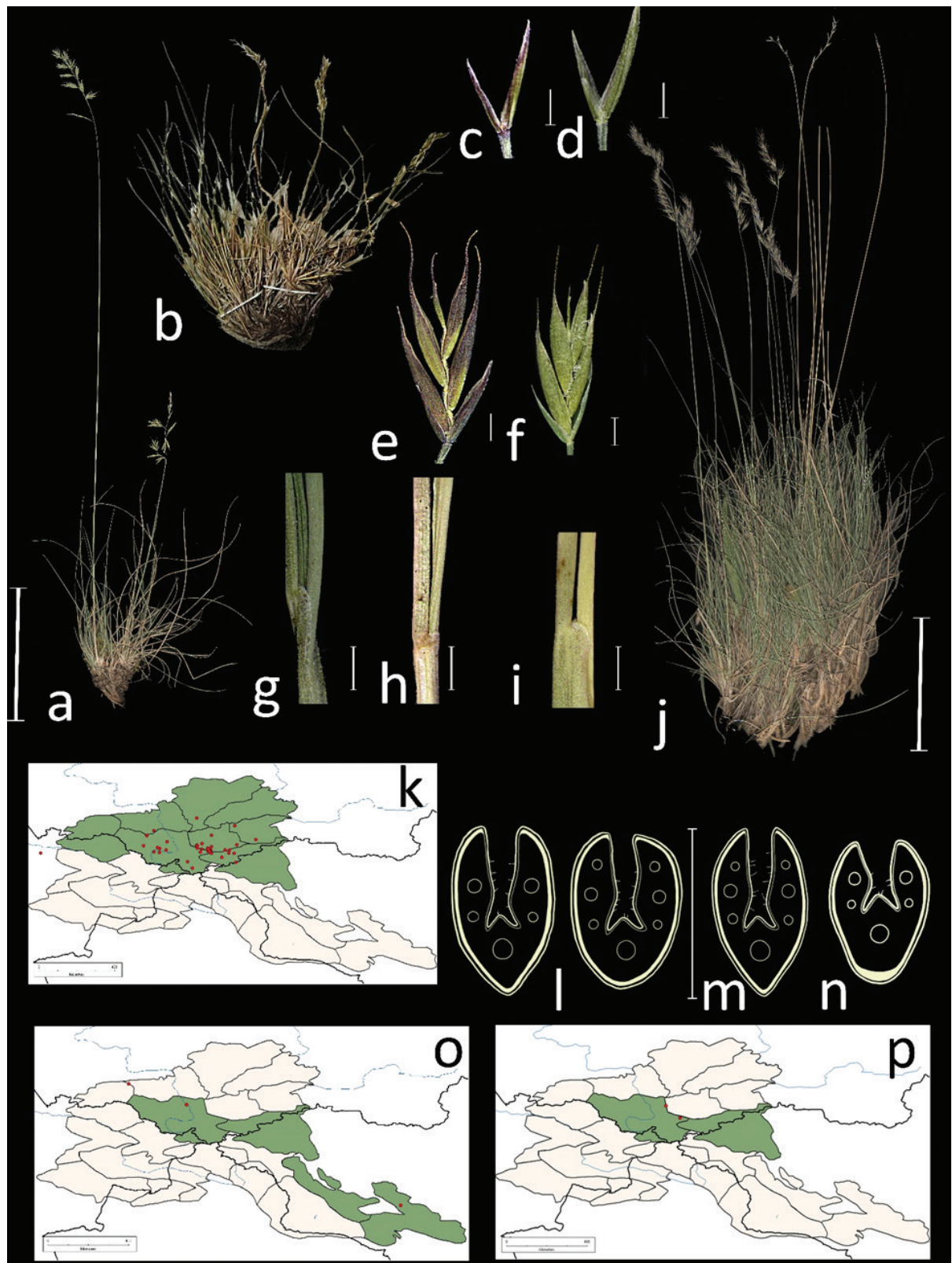


Figure 11. General habit of **a** *F. ovina* **b** *F. kuprijanovii* **j** *F. sphagnicola* glumes, lateral view **c** *F. sphagnicola* **d** *F. ovina* spikelets **e** *F. sphagnicola* **f** *F. ovina* junction of leaf sheath and blade, lateral view **g** *F. sphagnicola* **h** *F. ovina* **i** *F. kuprijanovii* leaf-blade cross-section **l** *F. sphagnicola* (two cross-sections) **m** *F. ovina* **n** *F. kuprijanovii* distribution maps **k** *F. sphagnicola* **o** *F. ovina* **p** *F. kuprijanovii*. Scale bars: 10 cm (**a**, **b**, **j**); 1 mm (**c**–**i**); 0.5 mm (**l**–**n**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Specimens examined. RUSSIA. Altaiskii krai. Kosh-Agachskii r-on, okrestnosti s. Kurai. Pravii bereg r. Tyute. 15 July 1982, *Kutafev V.N., Eremina T.* (paratype LE!); Gornyi Altai. Ulaganskii raion, verhovya r. Nizhnyaya Koksus, lev. pritoka r. Ulusuk, sklon, na skalah, 31 July 1991, *M.V. Olonova, M.M. Silanteva* (LE; used to create Fig. 11); Altaiskii krai, Kosh-Agachskii r-on, okrestnosti s. Kurai, pravii bereg r. Tyute, 15 July 1982, *V.N. Kutafev, T. Eremina* (LE); Respublika Altai, Kosh-Agachskii r-on, verkh. r. Kokorya, lev. bereg. 50°09'N, 88°55'E, 24 August 1995, *A.I. Shmakov, Dyachenko S., Golyakov P., Smirnov S.* (paratype has been lost SSBG).

***Festuca sphagnicola* B. Keller, Zap. Voronezh. Selkokhoz. Inst. 11: 78. 1928.**

Type. Neotype (designated by Alexeev 1979: 129) [Russia] Prov. Tomsk, distr. Biisk, alpinum Karakolskii, tundra muscoso-lichenosa, 19 July 1915, *P. Krylov* (LE!).

General distribution. Middle (northeast) and Central (North) Asia, Russia (Eastern, Western Siberia, Sayans), Mongolia (Altai).

Distribution in the AM. Common; A1, A2, A3, A4, A5, A6, ZM1, KAD1 (Fig. 11k).

Habitat. Alpine zone, steppes, forests; elev. 1700–3500 m.

Flowering period. July–August.

Chromosome number. $2n=28$ (Altai; Probatova and Sokolovskaya 1980).

Notes. See notes under *F. ovina* agg.

Specimens examined. RUSSIA. Respublika Altai, Kosh-Agachskii raion, srednee techenie reki Ortolyk, levoberezhie, elev. 2300 m, alpiiskii lug na opushke listvennichnika, 50°17'59.7"N, 87°50'21.1"E, 5 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (ALTB; used to create Fig. 11a, c–e); Respublika Altai, levii bereg r. Suhoi Tytugem, ernik, elev. 2350 m, 18 July 1999, *D. Chusovljanov* (KUZ); Altai, Ust-Koksinskii raion, okr. s. Abai, verhovya r. Ayuly, alpiiskii lug, 24 June 1955, *N.T. Tzhehanovskaya, V. Efremkov* (ALTB); Terehtinskii khrebet, dol. r. Terekty, alpiiskii lug, 1 July 1951, *G. Pavlova* (LE); Altaiskii zapovednik okr. oz. Dzhulukul. dolina r. Bogoyash, okr. gory Boksy, elev. 2170 m, 23 July 1977, *N.I. Zolotuhin, I. Mahatkov, O.N. Kozlova, N.D. Revushkina* (ALTB); Tomskaya gub. Biiskii u. Karakolskii belok, mohovo-lishainikovaya tundra neskolko vyshe lesnogo predela, 19 July 1901, *P.N. Krylov* (TK); Altai, Oiroitiya, Ongudaiskii aimak, gornii pereval iz loga Kulady v log Altair, ernikovo-lishainikovaya tundra, 12 October 1936, *A.V. Kalinina, L.A. Sokolova et B. Shishkin* (LE); Gornyi Altai, Ulaganskii r-n, bassein Nizhnego Ildugema 50°18'N, 88°15'E, dolina verhnego Yasatera, myatlikovaya step, 22 July 1984, *M. Danilov, I. Ostanina* (NS); Gornyi Altai, Ongudaiskii r-n, elev. 1640 m, 51°10'N, 85°35'E, Seminskii peerval, polyana sredi kedrovogo lesa, 26 June 1981, *D. Shaulo* (NS); Gorno-Altayskaya AO, Kosh-Agachskii r-n, dolina r. Uzuntotygem, 50°6'N, 80°10'E, elev. 2550 m, osochkovo-zlakovaya step na ploskoi vershine, 30 July 1982, *M. Danilov, N. Chernitskaya* (NS); Gornyi Altai, khr. Chihacheva, v verh. r. YUsty, v okr. oz. Kyndykty-Hol, 49°40'N, 89°30'E, elev. 2450 m, ostepnennyi subalpiiskii lug, 30 July 1982, *I. Krasnoborov, L. Mironova* (NS); Gornyi Altai, Ulaganskii r-n, verhovya Oroya, 50°20'N, 88°10'E, elev. 2200 m., subalpiiskii manzhetskovi lug po pologomu sklonu, 15 July 1984, *M. Danilov, N. Chalchikov* (NS); Altai, Kosh-Agachskii r-n, ushchele Kuyahtanar, elev. 1810 m, 50°10'N, 88°15'E, zabolochennaya lozhbina, 7 July 1983, *M. Danilov, O. Babarykina* (NS); Gornyi Altai, Kosh-Agachskii raion, verhovya Bashkausa, elev. 2400 m, 50°15'N, 89°12'E, driadovaya shchebnistaya tundra, 27 July 1983,

M. Danilov, L. Gunderina (NS); Respublika Altai, Ulaganskii raion, 15 km na sever ot Aktasha, Kustarnichkovaya tundra (Kurilskii chai), 50°28'29"N, 87°37'22"E, 7 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Kosh-Agachskii raion, srednee techenie reki Ortolyk, levoberezhie, elev. 2300 m, alpiiskii lug, 50°18'27"N, 87°49'18"E, 5 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Kosh-Agachskii raion, kkhrebet Chikhacheva, dolina r. Karaoyuk v srednem techenii, 49°50'40"N, 89°32'30"E, 2 August 1999, *A.I. Shmakov et al.* (ALTB); Altaiskii zapovednik, okresnosti Yailyu, poberezhie Teletskogo ozera, tundra na vershine, 20 July 1945, *L. Tyulipa* (LE); YUzhnyi makrosklon Kuraiskogo hrebt, verhove r. Ortolyk, subalpiiskii lug, elev. 2000 m, 12 July 1999, *A.A. Ebel* (KUZ); Vostochnyi Altai, khr. Kurkure, r. Turanaya, elev. 2100 m, stenka kara sz eksp., v nizhnei chasti, krupnokamenistaya osyp, 10 August 1977, *L. Marina, Galanin A., Zoloterin N.* (LE); Vost. Altai, khr. Kurkure, pravyy pritok r. B. Kurkure, sklon s-z eksp, kustarnik s ruchem, 7 August 1976, *Marina L., Galanin A., Zolotuhin N.* (LE); Vostochnyi Altai, khr. Kurkure, r. "Luchshaya", elev. 2100 m, sklon yuzhn. eksp., ernik raznoravno-zlakovyy, 14 July 1976, *L. Marina, Galanin A., Zoloterin N.* (LE).

KAZAKHSTAN. Yuzhnyi Altai, khr. Azutau, Urunhaiskii pereval, razrezhennyi listvennichnyi les, ostepnennyye lugoviny, elev. 1800 m, 20 June 1986, *Yu. Kotuhov* (ALTB); Vostochnyi Kazakhstan, Koksinskii hr., elev. 1800 m, nizkotravnye alpiiskie luga, 10 August 2004, *Yu. Kotuhov* (KUZ).

***Festuca pseudovina* Hach. ex Wiesb., Osster. Bot. Zeitschr. 30: 126. 1880.**

Type. Im Thale der reichen Liesing zwischen Kalksburg und dem Rothen Stadel (Austria) (W).

General distribution. Occurs in Europe and Russia.

Distribution in the AM. Common; A1, A2, A3, A4, ZM1, KAD1, KAD2, KAD5, KAD6, KAD9 (Fig. 12f).

Habitat. Steppes, meadows, forests, sand, marshes; elev. 400–3000 m.

Flowering period. May–July.

Chromosome number. $2n=14$ (Perm region; Alexeev 1974), $2n=42$ (Novosibirsk region; Krasnikov, 1991).

Notes. *Festuca pseudovina* is morphologically similar and closely related to *F. valesiaca*. The color of the leaves (bluish-green or green) is the only morphological character that separates these species (Alexeev 1990; Tzvelev 1976; Lu et al. 2006; Tzvelev and Probatova 2019). Most specimens previously identified as *F. pseudovina* have been re-identified by us as *F. valesiaca*, because both are bluish green but are characterised by varying colour saturation of leaf blades. In molecular research, *F. pseudovina* specimens collected from the AM were shown to be hybrids between *F. valesiaca* and *F. rupicola* (Kriuchkova et al. 2023). The species needs further study, including molecular (at the population level), morphological, and cytological analyses.

Specimens examined. RUSSIA. Altaiskii krai, Bystroistokskii raion, 8 km na yug ot s. Priobskoe, raznotravno-zlakovyy lug na sklone (*Fragaria viridis*, *Iris ruthenica*, *Stipa* sp., *Poa* sp., *Achillea* sp., *Artemisia gmelinii*), 52°18'01"N, 84°25'58"E, 13 June 2020, *P.D. Gudkova, Zolotov D.V., E.A. Kriuchkova* (ALTB; used to create Fig. 12a–e); Respublika Altai, Ust-Kanskii raion, okolo sela Vladimirovka. Yuzhnyi kustarnikovyy kamenisty sklon, pravyy bereg reki Charysh

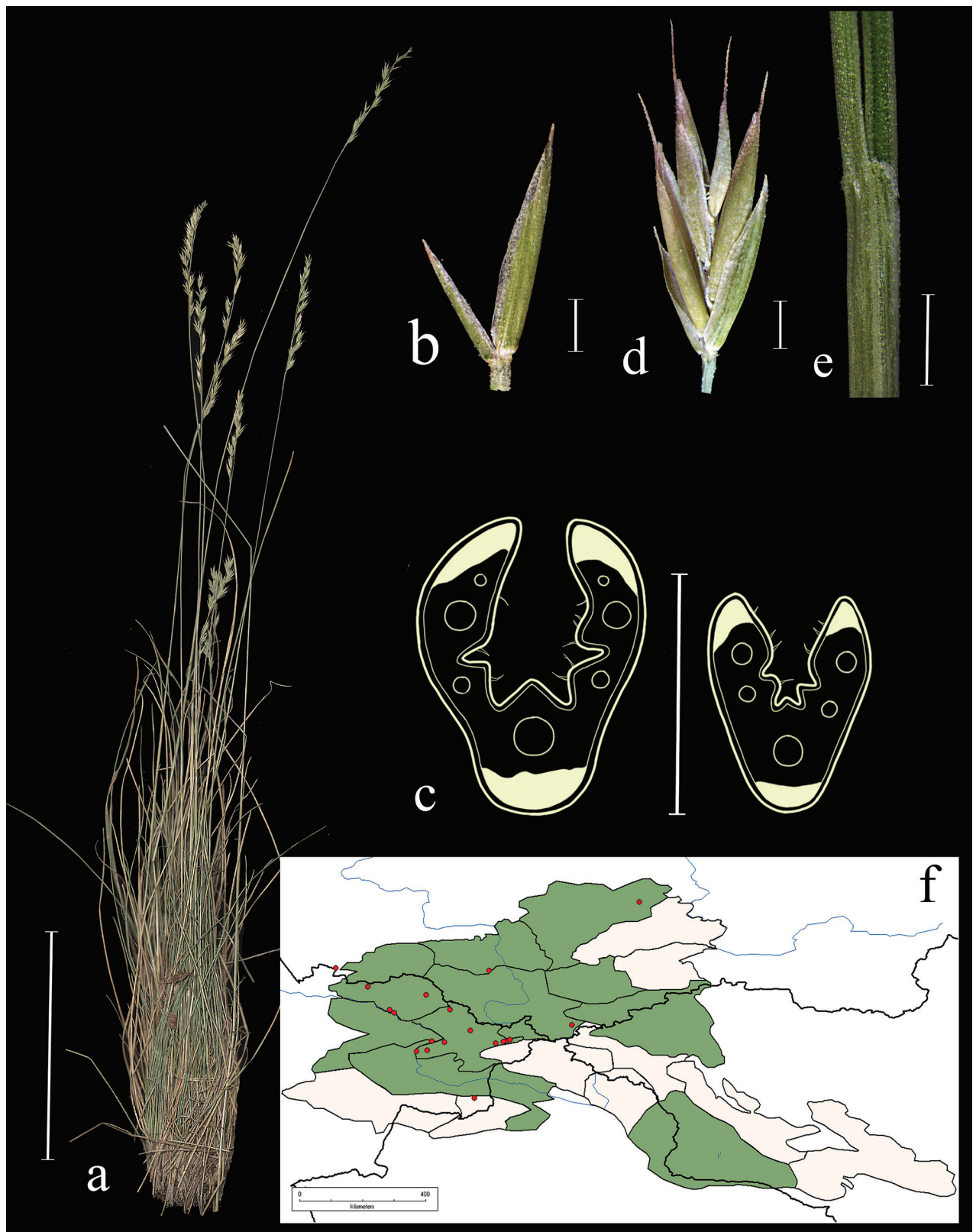


Figure 12. *Festuca pseudovina* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

(*Caragana frutex*, *Spirea* sp., *Achnatherum* sp., *Stipa* sp., *Orostachys spinosa*), 51°3'15"N, 84°11'26"E, 4 June 2020, E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova (ALTB).

KAZAKHSTAN. Yuzhnyi Altai, khrebet Sarym-Sakty, yuzhnyi bort Karakabinskoi vpadiny, yugo-vostochnyi sklon, 11 July 1991, Yu. Kotuhov (KUZ); Khr. Kalbinskii, v raione s. Novo-Timofeevka, vyrovnenne peski, kovyl'naya step, 18 June 1983. Yu. Kotuhov (KUZ); Yuzhnyi Altai, khr. Narymskii, v raione s. Sergeevka, yugo-zapadnyi shchebnisty sklon, elev. 800 m, 31 July 1986, Yu. Kotuhov (KUZ); Yuzhnyi Altai, khr. Kurchumskii, vostochnye otrogi, elev. 1700 m, dolina r. Tautekeli, ostepnennye luga, 3 August 1985, Yu. Kotuhov (KUZ); Vostochno-Kazakhstanskaya obl., Kurchumskii r-n., 10 km severnee p. Kuigan v raione Kaznakovskoi perepravyy, yugo-zapadnye predgorya khr. Narymskii, na kamnyah, 8 June 1998, D.V. Chusovljanov (KUZ); VKO, okr. s. Medvedki, khr. Narymskii, suhodolnyi lug, vershinna gory, 15 July 1978, Kupriyanov A.N. (KUZ); Zapadnyi Altai, khr. Narymskii, uroch. Terekty, v raione s. Novo-Berezovka, elev. 1600 m, ostepnennye alpiiskie luga, 30 July 1970, Yu. Kotuhov (KUZ); Zapadnyi Altai, khr. Ivanovskii, v raione s Poperechnoe, dolina r. Belaya Uba, ostepnennyi lug, 25 July 1970, Yu. Kotuhov (KUZ); Yuzhnyi Altai, khr. Narymskii, sev-zap. Otrogi, v raione s. Sergeevki, vershinna grivy, shchebnistye uchastki, 11 June 1988, Yu. Kotuhov (KUZ); Vostochno-Kazakhstanskaya obl., Kurchumskii r-n, gory Bukumbai, kamenistoe ushchele, zlakovaya step, 9 June 1998, D.V. Chusovljanov (KUZ); Yuzhnyi Altai, khr. Tarbagatai, Karakabinskaya vpadina, elev. 1600 m, ostepnennye luga, 2 August 1985, Yu. Kotuhov (KUZ); Zaisanskaya kotlovina, Bukonskie peski, uste r. Bukoni, vyrovnenne pesky, 8 June 1970, Yu. Kotuhov; Altai, Ust-Kamenogorsk, na sklone v dol. r. Ulby, 2 June 1931, B. Shishkin K., L. Chilikina i Sumnevich G. (LE); Kazahskaya ASSR, Ust-Kamenogorsk, gora Tarabachiha, tipchakovo-kelerievyy sklon k r. Irtyshu, 1 June 1931, Shishkin K.B., Sumnevich G. (LE); Khr. Manrak, v raione s. Priozernoe, kustarnikovo-zlakovaya step, 4 June 1976, Yu. Kotuhov (KUZ); Khr. Saur., dolina r. Terekty, ugolnyi karer, uglisty slantsy, 23 June 1986, Yu. Kotuhov (KUZ).

***Festuca pseudosulcata* Drobow, Tr. Bot. Muz. Akad. Nauk 14: 156. 1915.**

Type. Lectotype (designated by Tzvelev 1968: 168). [Russia] Vilyuiskii okr., r. Chona v 35 km vyshe Ustyia ee pritoka Yagody, 30 July 1914, N°556, V. Drobov (LE!).

General distribution. Russia (Eastern Siberia, Far East), North-Eastern China, Mongolia.

Distribution in the AM. Very rare; A5, KAD9, UM (Fig. 13f).

Habitat. Steppes, stony slopes, rocks, forests; elev. 1000–2500 m.

Flowering period. June–July.

Chromosome number. $2n=28$ (Krasnoyarsk territory, Amur region; Alexeev et al. 1988).

Notes. Morphologically, *F. pseudosulcata* belongs to the *F. valesiaca* group. *Festuca pseudosulcata* differs from *F. rupicola* in the number of ribs in a leaf blade cross-section (one well-defined midrib vs 3 well-defined ribs), the leaf sheaths of tillers (fused for $\frac{1}{4}$ – $\frac{1}{3}$ their length vs fused for $\frac{1}{6}$ their length).

Specimens examined. RUSSIA. Respublika Altai, Kosh-Agachskii raion, Kuraiskii hr., verhnee techenie r. Kokorya, prav. bereg, skl.vost. ekspozitsii, scaly, 50°06,5'N, 88°52'E, 27 June 1993, R.V. Kamelin, A.I. Shmakov, P.V. Golyakov, A.Ya. Kiselev, T.V. Krestovskaya, M. Kashcheev, M.A. Mihailova, A. Solovev (KUZ);

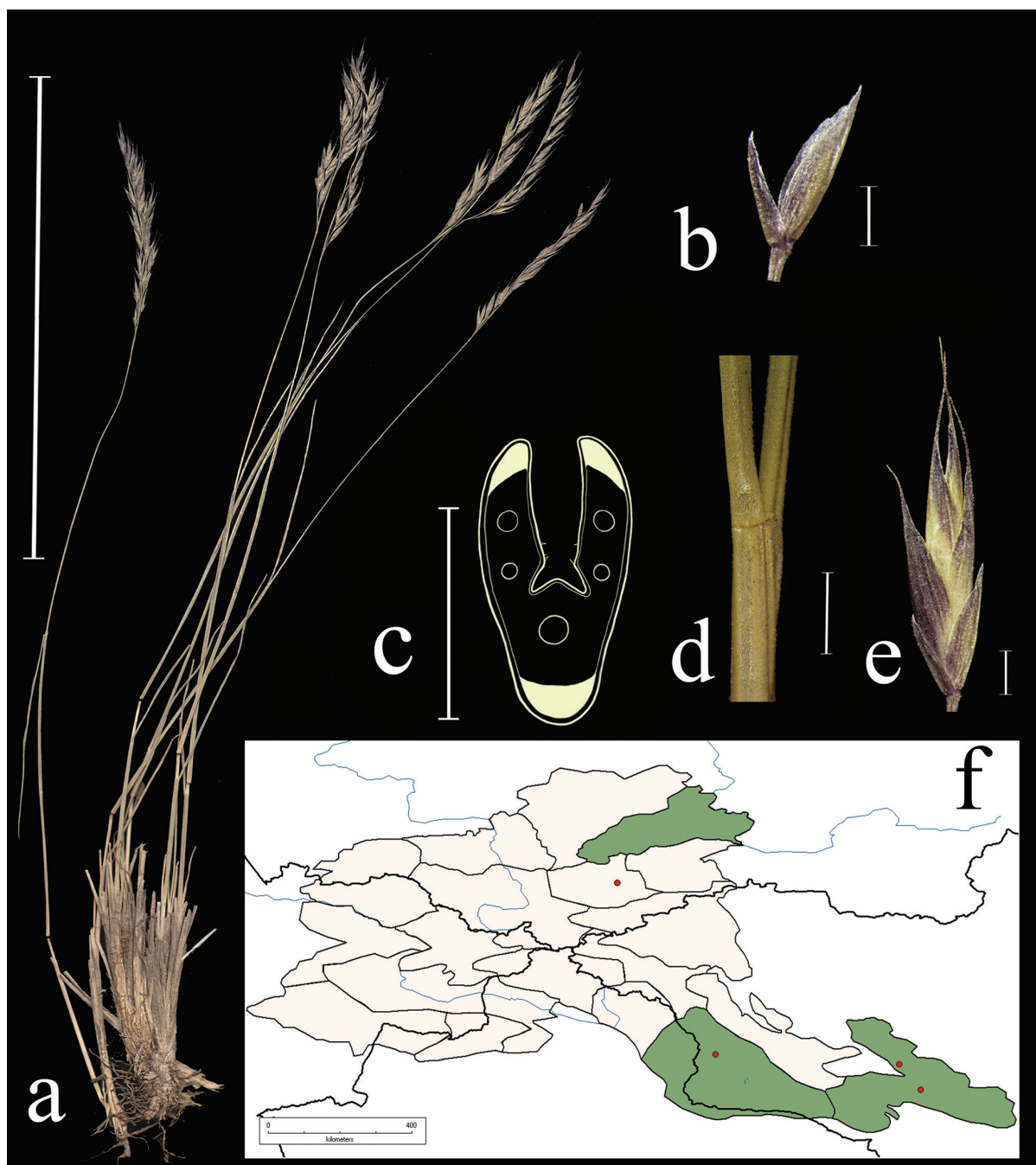


Figure 13. *Festuca pseudosulcata* **a** general habit **b** glumes, lateral view **c** leaf-blade cross-section **d** junction of leaf sheath and blade, lateral view **e** spikelet, lateral view **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b**, **d**, **e**); 0.5 mm (**c**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

used to create Fig. 13a–e); Khakasiya, Shirinskii r-n, okr. p. Sarala, stepnoi sklon, 1984, Rybinskaya (LE).

MONGOLIA. Gobi-Altai aimak, Hurmin-somon, 10 km k yugo-vostoku ot Yusun-Bulaka, srednyaya chast severnogo belya, khr. Han-Taishiri, raznotravno-zhitnyakovo-kovyl'naya step, 14 July 1948, A.A. Yunatov (LE); Gobi-Altai aimak, Tumun somon, severnyi sklon khr. Han-Taishiri, pyatno listvennichnogo lesa km v 15 k yu-v ot Yusun-Bulaha, osokovo-tipchakovyi lug, 11 September 1948, V.I. Grubov (LE).

***Festuca rupicola* Heuff., Verh. Zool.-Bot. Ges. Wien 8: 2335. 1858.**

= *F. ganeschinskii* Drobow, Tr. Bot. Muz. Akad. Nauk 14: 175. 1915.

= *F. recognita* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 3–4: 7. 1928.

= *F. ovina* subsp. *sulcata* var. *genuina* Hack., Monogr. Festuc. Europ. 104. 1882.

= *F. valesiaca* subsp. *sulcata* var. *hirsuta* (Link) E. Alexeev, Byulleten MOIP. Otdel Biologicheskii 78 (3): 109. 1973.

Type. In rupestribus umbrosis montis Domugled ad Thermas Herculis (holotype W).

General distribution. Wide distribution species from Europe, to south Central Siberia.

Distribution in the AM. Very rare; A2, KAD1, KAD4, KAD6, KAD7, KAD9 (Fig. 14f).

Habitat. steppes, forests, rock, limestones, solonchaks; elev. 300–2500 m.

Flowering period. May–June.

Chromosome number. $2n=42$ (Ukraine; Alexeev et al. 1988).

Notes. *Festuca rupicola* is rare in the AM, and Western Siberia. It occurs here at its easternmost distribution limit. *Festuca rupicola* is characterised by green leaf blades; the leaf blade cross-section with three sclerenchyma strands, with 5 or 7 vascular bundles; the leaf blades (0.45)0.55–0.85(1.1) mm wide; the leaf sheaths of tillers fused for $\frac{1}{6}$ their length; the spikelets green; the lemma (4.5)4.8–5(6) mm in length; the spikelets (5.5)6.5–8.5(10) mm in length.

Recent molecular research revealed that *F. rupicola* belongs to the *F. valesiaca* group but forms a separate subclade (Kriuchkova et al. 2023).

Specimens examined. RUSSIA. Altaiskii krai, Zmeinogorskii raion, okr. oz. Kolyvanskoe, na granitnykh ostantsakh, 14 June 1999, O. Maslova, D. Chusovljanov (ALTB, KUZ; used to create Fig. 14a–e); Altaiskii krai, Loktevskii r-n, 2 km severo-vostochnyye s. Pokrovka, sopochnyi massiv, kamenisty ostepnennyi sklon, 20 June 2001, O.M. Maslova, A.V. Grebenyuk, D.V. Chusovljanov (ALTB); Altaiskii krai, Loktevskii r-n, 3 km severo-vostochnyye s. Ustyanka, sopochnyi massiv, shchebnisto-glinisty sklon yuzhnoi ekspozitsii, 20 June 2001, O.M. Maslova, A.V. Grebenyuk, D.V. Chusovljanov (ALTB); Altaiskii krai, Loktevskii raion, okr. s. Ustyanka, melkosopochnyi massiv SV sela, 51°10'N, 81°38'E, 14 August 1998, T.O. Strelnikova, O.M. Maslova, D.V. Chusovljanov, L. Sokolova (ALTB); Altaiskii krai, Zmeinogorskii raion, okr. oz. Kolyvanskoe, Yuzhnyi bereg, sklon severnoi ekspozitsii 51°21'N, 82°12'E, 25 June 1996, A.N. Kupriyanov, E.V. Samusenko (KUZ); Altaiskii krai, Loktevskii raion, 2 km severnee pos. Removskii, sopochnyi massiv, stepnoi sklon, 20 June 2001, O.M. Maslova, A.V. Grebenyuk, D.V. Chusovljanov (ALTB); Altaiskii krai, Tret'yakovskii r-n, okr. s. Kraboliha, kamenisty ostepnennyi sklon sopki, na kamnyakh, 22 June 2001, O.M. Maslova, A.V. Grebenyuk, D.V. Chusovljanov (ALTB); Tuvinskaya ASSR, Ulug-Hemskii r-n, Zap. Sayan, Uyukskii hr., sr. tech. r. Arty-Haya, prav. prit. r. Vayan-Kol, yuzhn. sklon. ovsyantsovo-kovylny-osochnovaya step, 5 July 1975, M. Lomonosova, T. Grushevskaya (NS); Altai, Kosh-Agachskii aimak, Chusiskaya kotlovina, okr. pos. Tashanty, step, 20 July 1931, A. Kuminova, A. Skvortsova (LE); Altaiskii krai, Zmeinogorskii r-n, okr. s. Savvushka, v rasshcheline skaly, 8 June 1983, Frizen, Zuev (NSK); Altaiskii krai, Zmeinogorskii raion, okr. oz. Kolyvanskoe, na granitnykh ostantsakh, 14 June 1999, O.M. Maslova, D.V. Chusovljanov (KUZ); Altaiskii krai, Kurinskii raion, 2 m vverh po lev. ber. r. Charysh ot byvsh. s.

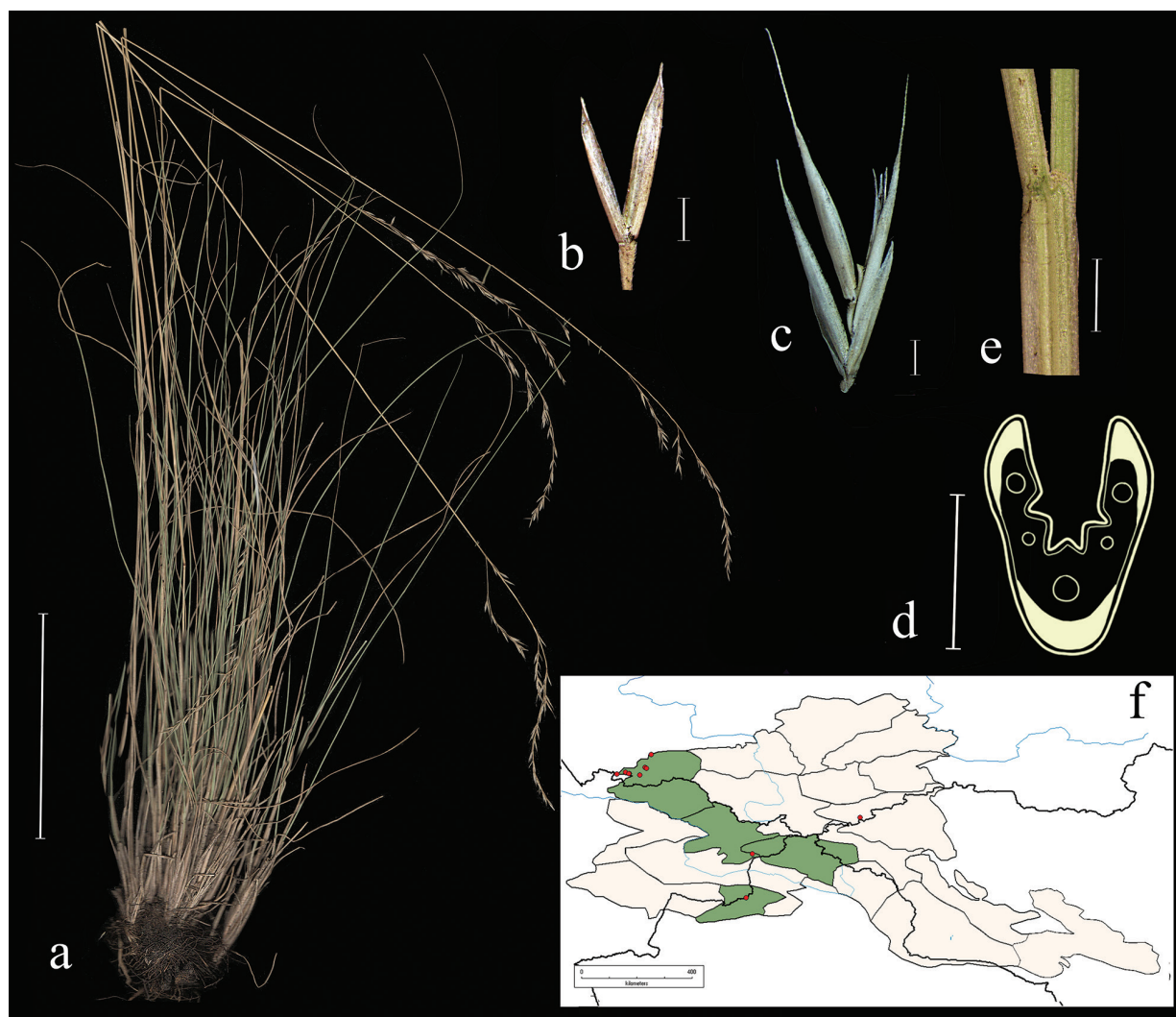


Figure 14. *Festuca rupicola* **a** general habit **b** glumes, lateral view **c** spikelet, lateral view **d** junction of leaf sheath and blade, lateral view **e** leaf-blade cross-section **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b**, **c**, **e**); 0.5 mm (**d**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Vostruha, 51°48'N, 82°22'E, 16 June 1999, *R.V. Kamelin et al.* (ALTB); Altaiskii krai, Smolenskii raion, v 5 km ot sela Berezovo na severo-vostok po doroge, lugovaya kovyl'naya step na yugo-zapadnom sklone (*Stipa* sp., *Potentilla* sp., *Delphinium* sp., *Iris ruthenica*, *Festuca* sp., *Poa* sp., *Bromus inermis*), 51°48'27"N, 82°22'19"E, 6 June 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK).

KAZAKHSTAN. Yuzhnyi Altai, khr. Azutau, Uspenskaya vpadina, dolina r. Yuelezek, ostepnennye luga, 27 July 1983, *Yu. Kotuhov* (KUZ); Khr. Saur, vodora-zdel rek B. i M Dzhemeneya, kovyl'no-raznotrav'naya step, 6 July 1930, *N. Goncharov, A. Borisova* (KUZ).

***Festuca saurica* E. Alexeev, Novosti Sist. Vyssh. Rast. 21. 1976.**

Type. Kazakhstan, khr. Saur, sev. sklon, verkhovya r. Terekty bliz pos. Kyzyl-Kiya, travyanistye skloni s sibaldiei, 16 July 1965, *V. Vasilevich, Z. Karamysheva, N. Nikolskaya, E. Rachkovskaya, I. Safronova* (holotype and isotype LE!).

General distribution. Saur ridge, endemic of Altai.

Distribution in the AM. Very rare; KAD4 (Fig. 15d).

Habitat. Forests, alpine zone; elev. 2000–2600 m.

Flowering period. June–July.

Chromosome number. $2n$ =unknown.

Notes. *Festuca saurica* is an endemic species of the AM. The species is highly variable in morphology: the number of vascular bundles varies from 5 to 7; the leaf blade cross-section may have only one single midrib or two additional lateral well-defined ribs; the shape of ribs varies from rounded to triangular; the shape of the leaf blade cross-section varies from obovate with an elongated keel to wide-lanceolate; the leaf sheaths of tillers may be fused for $\frac{1}{2}$ – $\frac{3}{4}$ their length; the abaxial surface of the leaf blade is characterised as glabrous or scabrous; and shoots are either grouped by 2–3 and surrounded by a cover of old sheaths. According to our molecular research, *Festuca saurica* is separated in an independent clade (Kriuchkova et al. 2023).

Specimens examined. KAZAKHSTAN. Khr. Saur, verh. r. Kyzyl-Kiya, sev.-zap. sklon, razrezhennyy listvennichnyy les, ostepnennyy alpiiskie luzhaiki, elev. 2000 m, 16 July 1992, Yu. Kotuhov (KUZ; used to create Fig. 15a, c–f); Khr. Saur, verh. r. Kyzyl-Kiya, kamenistaya tundra, elev. 2600 m, 14 August 1991, Yu. Kotuhov (KUZ, 3 sheets); Kkhrebet Saur, verhovya r. Kyzyl-Kiya, severo-zapadnyi sklon, elev. 2000 m, razrezhennyy listvennichnyy les, ostepnennyy alpiiskii lug, 16 July 1992, Yu. Kotuhov (KUZ); Kazahskaya SSR, khrebet Saur, sev. makrosklon, verhovya r. Terekty bliz pos. Kyzyl-Kiya na meklozemistom sklone, soobshchestvo tipchaka, 16 July 1965, V.I. Vasilevich, Z.V. Karamysheva, N.I. Nikolskaya, E.I. Rachkovskaya, I.N. Saphronova (LE); Kazahskaya SSR, khrebet Saur, sev. makrosklon, verhovya r. Terekty, bliz pos. Kyzyl-Kiya, dresvyanistye sklonyy s sibbaldiei, 16 July 1965, V.I. Vasilevich, Z.V. Karamysheva, N.I. Nikolskaya, E.I. Rachkovskaya, I.N. Saphronova (LE).

***Festuca tschujensis* Reverd., Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 3: 3. 1936.**

Type. [Russia] Chuiskaya step, na vysokom beregu reki Tarkhatty, vyshe sliyaniya ee s Chegan-Burgazy, v kovylno-polynnoi stepi, 6 July 1935, I. Plotnikov (holotype TK!).

General distribution. Kazakhstan (north of east Kazakhstan region), north Mongolia, Russia (south Siberia). South Siberia is the disjunct northernmost limit in the geographical distribution of *F. tschujensis*.

Distribution in the AM. Common; A3, A5, ZM1, ZM2, ZM3, KAD4, KAD8, KAD9 (Fig. 16b).

Habitat. Petrophytic steppes, stony slopes, rock fissures; elev. 2000–3500 m.

Flowering period. June–July.

Chromosome number. $2n$ =28 (Altai Republic; Agapova et al. 1993).

Notes. The species is easily distinguished by its lemmas 4.5–6 mm long, awns 1.5–4 mm long, leaf blades 0.5–1.1 mm wide, leaf blade cross-section with 3 well-defined ribs, leaf sheaths of tillers fused for $\frac{1}{3}$ – $\frac{1}{2}$ their length; shoots are either grouped by 2–3 and surrounded by a cover of old sheaths. Our recent molecular research revealed that this species might hybridise with the *F. kryloviana* group (Kriuchkova et al. 2023). However, there are no morphological characters distinguishing the hybrids from *F. tschujensis*.

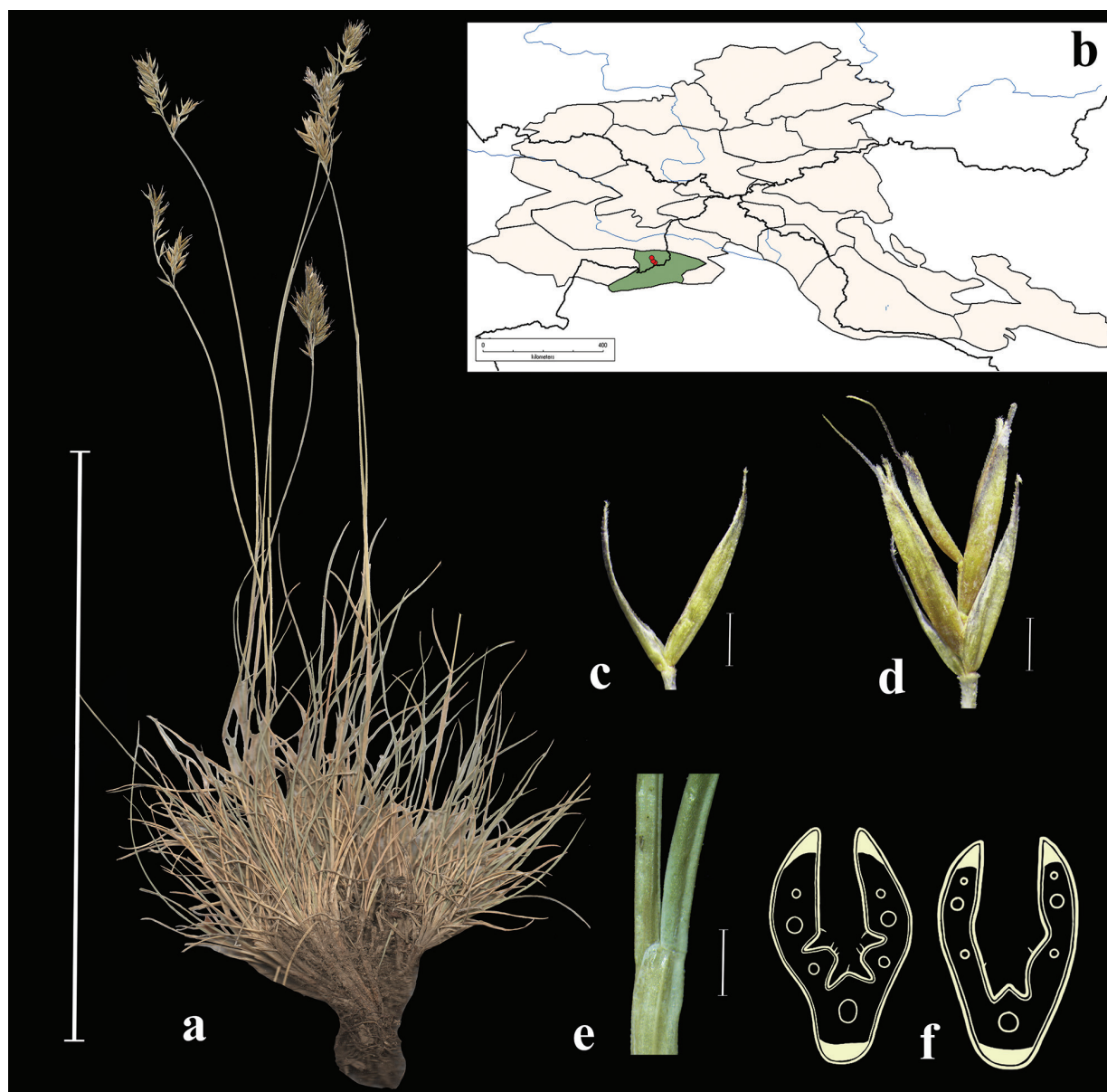


Figure 15. *Festuca saurica* **a** general habit **b** distribution map of the AM **c** glumes, lateral view **d** spikelet, lateral view **e** junction of leaf sheath and blade, lateral view **f** leaf-blade cross-section. Scale bars: 10 cm (**a**); 1 mm (**c–e**); 0.5 mm (**f**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Alexeev (1981) and Chusovljanov (2007) mention that *F. lenensis* grows in the Mongolian part of the AM, and the species differs from *F. tschujensis* by the leaf blade structure (width of middle sclerenchyma strand is similar to lateral strands vs middle sclerenchyma strand is two-three times wider than lateral strands; leaf blades arcuate vs flexuose, respectively). However, during our revision, all the available specimens of *F. lenensis* from the AM were identified by the first author of this paper as *F. tschujensis*. Thus, the presence of *F. lenensis* in the AM needs to be confirmed.

Specimens examined. RUSSIA. Altai, Kosh-Agachskii raion, dol. r. Tarhata okolo perevalochnoi bazy kolhoza im. Lenina, elev. 2150 m, 49°45'N, 88°30'E, 9 June 1982, M. Lomonosova, N. Timukina (LE; used to create Fig. 16a, c–f);

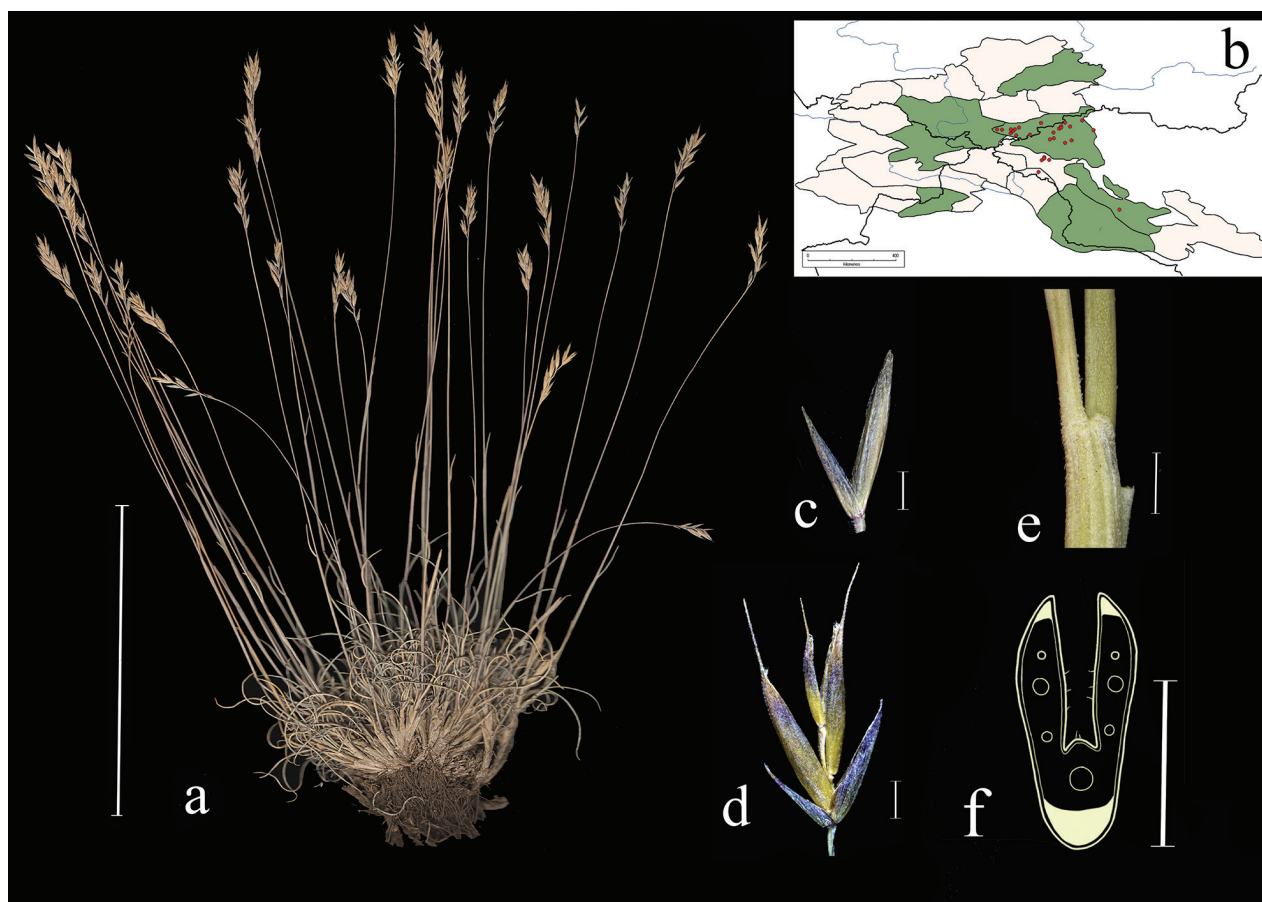


Figure 16. *Festuca tschujensis* **a** general habit **b** distribution map of the AM **c** glumes, lateral view **d** spikelet, lateral view **e** junction of leaf sheath and blade, lateral view **f** leaf-blade cross-section. Scale bars: 10 cm (**a**); 1 mm (**c–e**); 0.5 mm (**f**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

Altai, Oirotiya, Koshagachskii aimak, Chuiskaya step, Kyzylchin, kamenisty sklon, 1 August 1937 (LE); Altai, Oirotiya, Koshagachskii aimak, dol. r. Tarhatty, poimennaya terrasa, galechnikovy otlozheniya, 24 August 1936, A.V. Kalinina, L.A. Sokolova, B.K. Shishkin (LE); Altai, Oirotiya, Chuiskaya step, nizove r. Kok-Uzek, 16 September 1937, Akashimin (LE); Altai, Kosh-Agachskii r-n, dol. r. Tarhata vblizi perevalochnoi bazy kolhoza im. Lenina, raznotravno-zlavkovaya kamenistaya step sredi valunov, elev. 2300 m, vost. sklon, 49°45'N, 88°30'E, 9 June 1982, M. Lomonosova, N. Timukina (NS); Altai, Kosh-Agachskii raion, pravyyi bereg r. Kyzylchin, kamenistaya step po grebnyu shleifa, 13 August 1981, M. Lomonosova, N. Kilinina (NS); Respublika Altai, Kosh-Agachskii r-n, okr. oz. Kara-Kol, kamenistye osypi, elev. 2659 m, 49°54'05"N, 87°56'51"E, 7 July 2006, I. Han, R. Shtengauer (NSK); Altai, Kosh-Agachskii r-n, r. Tarhata, raznotravno-zlakovaya step, 8 July 1982, N. Frizen, V. Doronkin (NSK); Altai, Kosh-Agachskii r-n, r. Tarhata, vblizi perevalochnoi bazy kolhoza im. Lenina, yu-z sklon, zadernovannaya kamenistaya osyp, elev. 2200 m, 49°45'N, 88°30'E, 8 July 1982, M. Lomonosova, A. Vanyayev (NS); Respublika Tuva, Mugur-Aksynskii r-on, dol. r. Mogen-Buren u ustya ruch. Bashky-Kara-Syg, 50°10'N, 89°46'E, 4 July 1995, R.V. Kamelin, et al. (ALTB); Respublika Altai, Kosh-Agachskii r-n, ushchele reki Chagan-Burgazy v srednem techenii, 49°39'N, 88°44'E, 1 August 1998, R.V. Kamelin et al. (ALTB); Talduair,

zлакovo-kovyl'naya step, elev. 2300 m, 8 August 1997, *Ebel* (ALTB); Dzhirialant, Gurvan-Ulleusal, na skalah s-z ekspozicii, subalpiiskii lug (ALTB); Respublika Altai, Kosh-Agachskii r-n, Chuiskaya step, dol. r. Bar-Burgazy bliz vyhoda iz gor, elev. 1990–2100 m, 49°50'N, 89°11'E, 20 July 2000, *R.V. Kamelin et al.* (ALTB).

MONGOLIA. Tolbonur-Ulgii, zлакovo-polyнно raznotrav'naya step, elev. 2300 m, 8 August 1997, *A.A. Ebel* (KUZ); Ubsunurskii aimak, v 48 km k Yugu ot somon Taryalan, ravnina, sev.-zap. chast uroch. Kalhat-Chessen, elev. 1950 m, kserofitnoraznotravno-zhitnyakovo-tyrsovaya step, 19 July 1980, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Ubsunurskii aimak, poima r. Tes v 60 km VSV ot Tes-somona, soobshchestvo s gospodstvom *Leymus* po suhim grivam, 17 June 1978, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Dzabzhanskii aimak v 25 km Z ot somona Erdene-Hairhan, zлакovo-tyrsovaya step s uchastiem polukustarnichkov, 30 June 1980, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Ubsunurskii aimak, v 30 km k SSV ot Umne-gobi, polyнно-petrofitnoraznotravnoe tipchakovaya step na sklone sev. eksp. elev. 2000 m, 21 June 1978, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Bayan-Ulgiiskii aimak, v 12 km k YuYuV ot somona Tolbo, melkosopochnik iz slantsev, polyнно-zлакovaya step, 30 July 1980, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Ubsunurskii aimak, sopki v 33 km k Yugu ot shaht Urhai-Suren, polyнно-melkodernovinnozлакovaya step v doline, 1 July 1977, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Ubsunurskii aimak, v 42 km k SV ot Buh-Murena, melkosopochnik po sev. okraine Achit-Kursk. vpadiny, tipchakovaya step, elev. 2100 m, 8 July 1978, *Z.V. Karamysheva, I.Yu. Sumerina, U. Beket, H. Buyan-Orshih* (LE); Kobdoskii aimak, khr. Mongolskii Altai, pereval Baga-Ulan-Daba, alpiiskii lug, elev. 2900 m, 46°41'N, 92°17'E, 6 July 2009, *I.A. Sherin, P.A. Shalimov* (LE); Zapadnaya Mongoliya, Kobdoskii aimak, Mongolskii Altai, Vostochnyi makrosklon khr. Munkh-Khayrkhan, basseyn r. Dolon-Nuryngol bliz severnoy chasti lednika Munkh-Khayrkhan, elev. 3300 m, 17 August 1991, *G.N. Ogureyeva*, Det. *E.A. Kriuchkova* (W0170756)

***Festuca valesiaca* Schleich. ex Gaudin., Agrost. Helv. 1: 242. 1811.**

Type. *Festuca glauca* marit ? Vill. De Branson (holotype LAU); in Valesia prope Branson, in apricis, Gaudin (syntype LE!).

General distribution. Common in Eurasia, rare in North America (adventive).

Distribution in the AM. Widespread; KAD1, KAD2, KAD3, KAD4, KAD5, KAD6, KAD7, KAD8, KAD9, A1, A2, A3, ZM1, ZM2, ZM3, UM (Fig. 17f).

Habitat. Steppes, among bushes, rarely deserts, meadows, stony slopes, limestones, sands, fellfield, pine forest; elev. 300–3000 m.

Flowering period. May–June.

Chromosome number. $2n=14$ (Russia, Altai; Probatova and Sokolovskaya 1980; Primorskyi kray, Vladivostok; Probatova et al. 1991).

Notes. *Festuca valesiaca* is a polymorphic widespread species. There is considerable variation in plant height (10–40 cm), width of tiller leaf blades (0.4–0.7 mm), length of the lemma (2.8–4.6 mm), awn length (0.5–2.2 mm), and number of florets in spikelets (3–6). The most significant diagnostic characters for *F. valesiaca* are bluish wax covering the entire plant, green spikelets, and three similar sclerenchyma strands in the leaf blade cross-section (Tzvelev 1976; Alexeev 1990; Lu et al. 2006; Tzvelev and Probatova 2019). According to our molecular studies,

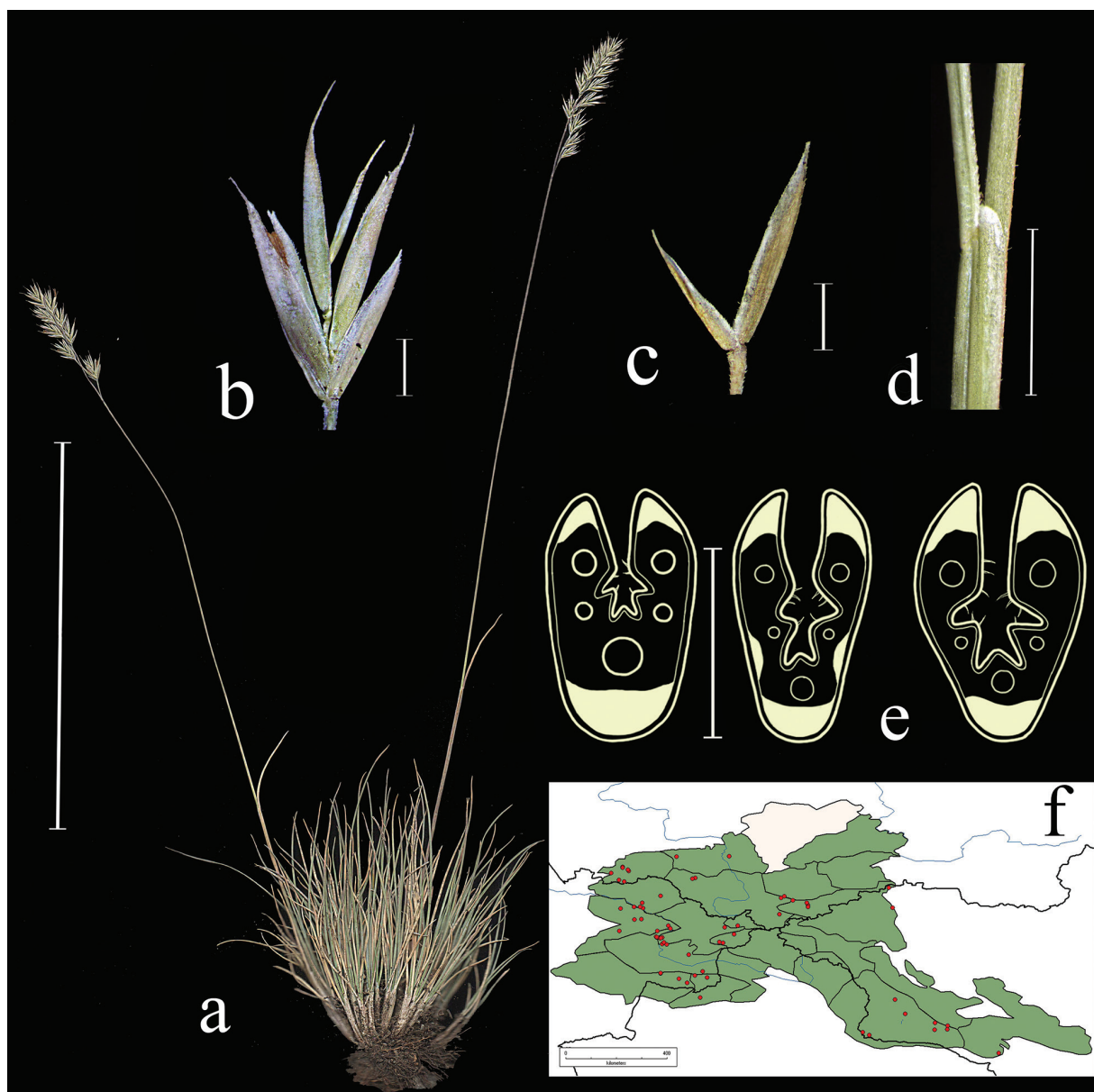


Figure 17. *Festuca valesiaca* **a** general habit **b** spikelet, lateral view **c** glumes, lateral view **d** leaf-blade cross-section **e** junction of leaf sheath and blade, lateral view **f** distribution map. Scale bars: 10 cm (**a**); 1 mm (**b–d**); 0.5 mm (**e**). The green colour on the map refers to information on species-distribution in the region known from literature data, red points mark localities confirmed by us during revision of herbarium materials.

F. valesiaca includes two genetic groups: one from mountains and another from lowland (Kriuchkova et al. 2023). The species needs further study, including molecular (at the population level), morphological, and cytological analyses.

Specimens examined. RUSSIA. Respublika Altai, Kuraiskii khr. r. Ortol'nyy, zakus-tarenniy sklon, 2 July 1999, A.A. Ebel (KUZ; used to create Fig. 17a–e); Altaiskii krai, Zmeinogorskii r-n, 6 km na severo-vostok ot p. Cherepanovskii, podnozhie gory Shish, step, 19 June 1999, *Usik N.A., Strelnikova T.O., Mungalov E.A.* (ALTB); Altaiskii krai, Kurinskii r-n, 5 km k yu-vost. ot d. Kalmytskie Mysy, dolina r. Charysh, 16 June 1999, *Usik N.A., Strelnikova T.O., Mungalov E.A.* (ALTB); Altaiskii krai, Soloneshenskii r-n, okrestnosti s. Sibiryachiha, 3 km k vostoku. 51°44'N, 84°07'E, 17 June 1997, *Strelnikova T.O., Maslova O.M., German D.A.* (ALTB); Altaiskii krai, Zmeinogorskii r-n,

okr. s. Savvushka, rashchelina skaly, 8 June 1983, *Doronkin, Rybinskaya* (ALTB); Altaiskii krai, okresnosti poselka Konyuhi, zlakovyi stravlennyi lug (*Festuca*, *Poa*, *Stipa*, *Leymus*, *Koeleria*, *Astragalus*, *Agropyron*), 53°10'10"N, 83°42'28"E, 20.05.2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Ulaganskii raion, pereval Katu-Yaryk, vysokotravnyi subalpiiskii lug, 50°3'53"N, 87°52'11"E, 7 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Kosh-Agachskii raion, srednee techenie Ortolyk, levoberezhie, elev. 2100 m, petrofitnaya step, 50°17'33"N, 87°50'53"E, 5 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Kosh-Agachskii raion, 4 km zapadnee sela Kurai, petrofitnaya kovyl'naya step (*Stipa capillata*, *S. orientalis*, *S. glareosa*, *S. krylovii*), 50°14'13"N, 87°50'45"E, 4 July 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK); Respublika Altai, Ust-Kanskii raion, selo Ust-Kan, kamenisty tipchakovyi sklon (*Poa* sp., *Koeleria* sp., *Orostachys spinosa*, *Festuca valesiaca*), 50°56'33"N, 84°46'40"E, 5 June 2020, *E.A. Kriuchkova, D.D. Ryzhakova, P.D. Gudkova* (TK).

KAZAKHSTAN. Vostochno-Kazakhstanskaya obl., Zaisanskii r-n, khr. Saikan, Uroch. Koksoldy, zlakovo-raznotravnyi lug, elev. 1650 m, 14 June 1998, *D.V. Chusovljanov* (KUZ); Vostochno-Kazakhstanskaya obl., Zaisanskii r-n, khr. Saikan, Uroch. Koksoldy, peschano-kamenisty sklon zap. ekspoz. elev. 2100 m, 14 June 1998, *D.V. Chusovljanov* (KUZ); Vostochno-Kazakhstanskaya obl., Samarskii r-n, 10 km yu-v s. Kaznakovka, Kulundzhunskie peski, bugristye peski, 7 June 1998, *D.V. Chusovljanov* (KUZ); Khr. Saur, pereval Saikan, elev. 1800 m, severnyi sklon, zlakovye ostepnennye luga, 17 June 1976, *Yu. Kotuhov* (KUZ); Khr. Manrak, gory Katan-Chilik, elev. 800 m, vershina grivy, kamenistaya zlakovaya step, 15 July 1985, *Yu. Kotuhov* (KUZ); Yuzhnyi Altai, khr. Kurchumskii, dolina r. Tautkeli, ostepnennye luga, elev. 1700 m, 3 August 1985, *Yu. Kotuhov* (KUZ); Kazahskaya ASSR, Ust-Kamenogorsk, 1931, *B. Shishkin, G. Sumnevich* (LE); Yuzhnyi Altai, khr. Yuzhnyi Altai, verh. r. Kara-Koba, u grebnya, alpiiskii poyas, elev. 2500–2800 m, 3 August 1987, *A. Ivashchenko* (KUZ); Khr. Kalbinskii, v raione s. Podgornoe, predgornye stepi, 19 June 1983, *Yu. Kotuhov* (KUZ).

MONGOLIA. Hobdoskii aimak, Bulgan somon, Mongolskii Altai, levoberezhnyi sklon v dolinu Inderzhin gola, u letnei stoyanki somona, kamenistaya step, 25 August 1947, *A.A. Yunatov* (LE); Gobi-Altai aimak, Altai somon, mezhdru khr. Adzhi-Bogdo i Alak-Hairhan u perevala v verhovyah Tuhumyin hundo, po opeschanen-nomuberegu, 9 August 1947, *A.A. Yunatov* (LE); Gobi-Altaiskii aimak, Altai somon, Dzhungarskaya Gobi, razrushennyi khrebet, mezhdru Adzhi-Bogdo i Altaem, po lozhbinam, 10 August 1947, *A.A. Yunatov* (LE); Ubsunurskii aimak, Under-Hangai somon, sev. makrosklon Hanhueya, v 32 km k YuV ot Barun-Turun somona, polynno-raznotravno-tipchakovaya step, elev. 1390 m, 24 July 1973, *D. Banzragg, Z.V. Karamysheva, Munhbayar, C. Cegmid* (LE).

CHINA. Sinczyan-Uigurskaya avtonomnaya oblast, Sev. Zap. Dzhungariya. Vost. shleify khr. Saur, v 60 km sev. Hosh-Tologoi (na r. Hobuk) po doroge na Altai, gornaya tipchakovaya step, 4 July 1959, *A.A. Yunatov, Yuan I-fen* (LE).

Conclusion

During our study we confirmed the occurrence of 17 species of genus *Festuca* in the AM. *Festuca brevissima* is a new record to the flora of the AM and at present, its localities in the region are the southernmost within its distribution range. Our revision showed that *F. lenensis* and *F. richardsonii* are not component of the AM

flora. All the available specimens of *F. lenensis* from the AM were identified as *F. tschujensis*, whereas specimens of *F. richardsonii* previously recorded for the AM were identified as *F. rubra*. We found also that *F. oreophylla* was previously listed in the flora of the AM as a synonym of *F. musbelica*, however, *F. musbelica* is the earlier legitimate name. Finally, we did not confirm Chusovljanov's assumption (Chusovljanov 2003) on the presence of *F. kemerovensis* in the AM.

In accordance with our morphological and molecular (Kriuchkova et al. 2023) studies we have revealed three complexes of closely related taxa: *F. kurt-schumica*–*F. kryloviana*; *F. sphagnicola*–*F. kuprijanovii*–*F. ovina*; and *F. musbelica*–*F. valesiaca*. Nevertheless, to resolve whether they are separate or conspecific species, further studies including more advanced molecular, morphological, and cytological analyses are needed on the above mentioned complexes of taxa from the entire area of their distribution.

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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

PG, MN designed the study; EK, AS, PG collected samples in the field; EK conducted revision of herbarium materials, identification of specimens collected in the field and preserved in the herbaria, morphological measurements of samples; PG and EK wrote the manuscript with input of MN. All authors contributed to the final version manuscript and approved the submitted version.

Author ORCIDs

Polina D. Gudkova  <https://orcid.org/0000-0002-6537-8018>

Elizaveta A. Kriuchkova  <https://orcid.org/0000-0003-3704-1730>

Alexander I. Shmakov  <https://orcid.org/0000-0002-1052-4575>

Marcin Nobis  <https://orcid.org/0000-0002-1594-2418>

Data availability

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

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Taxonomic revision of *Camellia langbianensis* (Theaceae) with four new synonyms

Dongwei Zhao¹ 

¹ Department of Forestry, College of Forestry, Central South University of Forestry and Technology, Changsha, 410004, China
Corresponding author: Dongwei Zhao (zhaodw@csuft.edu.cn)

Abstract

Based on analysis of morphologically diagnostic characters, *Camellia langbianensis*, a yellow camellia native to southern Vietnam, is taxonomically revised to include four new heterotypic synonyms: *C. decora*, *C. dongnaiensis*, *C. oconoriana* and *C. tadungensis*. *Camellia vidalii* is retained in the synonymy of *C. langbianensis*. Updated description and distribution map for *C. langbianensis* are provided.

Key words: *Dankia*, endemic, golden camellia, Indochina

Introduction

Gagnepain (1939: 198) established *Dankia* Gagnep. for *Dankia langbianensis* Gagnep. The species was transferred into *Camellia* L. (Theaceae) by Hô (1991: 537) as *Camellia langbianensis* (Gagnep.) P.H. Hô. Accordingly, the monotypic genus *Dankia* became a heterotypic synonym of *Camellia* (Zhao et al. 2017a; Zhao 2022a), which had been overlooked in Ming (2000). Nevertheless, *Dankia* remains listed as an accepted genus in the family Theaceae on the Angiosperm Phylogeny Website (<http://www.mobot.org/MOBOT/research/APweb/genera/theaceaegen.html>). Sealy suggested that a columella was absent in the fruit of *D. langbianensis*, so *Dankia* was distinct from *Camellia*; however, subsequent investigations revealed that the capsule of *D. langbianensis* does bear a columella (Zhao 2019; Quach et al. 2021). Morphological investigations have not revealed any substantial differences between *Camellia* and *Dankia*. Both genera bear a generally globose capsule with the wingless seeds attached to the columella (Zhao 2019; Quach et al. 2021). Molecular phylogenetic analysis suggested that *C. vidalii*, a heterotypic synonym of *C. langbianensis* (Zhao 2019), was nested in the clade Piquetia within the monophyletic genus *Camellia* (Zhao et al. 2023). Therefore, it can be reasonable to conclude that *Dankia* is a synonym of *Camellia*, based on both morphological and molecular data.

Though more than 100 species of *Camellia* have been described since Ming's (2000) latest monograph of the genus and most of them were derived from Vietnam (Zhao et al. 2023), recent research suggested that many of them were merely repeated names for the previously-published species (e.g. Zhao et al. [2017b]; Zhao [2019, 2021, 2022b]). Plants of *Camellia* can vary widely within



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a single species, a remarkable example is that hundreds of cultivars of *C. japonica* L., *C. sasanqua* Thunb. and *C. sinensis* (L.) Kuntze have been recorded (Wang et al. 2019). It would be unreasonable to suppose that a species should vary narrowly in nature, but broadly in cultivation. However, Quach et al. (2021) argued that *C. vidalii* could be distinguished from *C. langbianensis* by the indumentum of the flower parts, which suggested that *C. langbianensis* and *C. vidalii* were distinct species. Additionally, during a revision of camellias in Vietnam, I found that four previously described species (Orel 2006; Orel et al. 2013; Orel and Curry 2015) had a close relationship with *C. langbianensis*. They are discussed below in detail with a taxonomic revision of *C. langbianensis* provided.

Material and methods

Taxonomic literature (e.g. Sealy [1958]; Chang [1981]; Hô [1991]; Ming [2000]), especially protologues of taxa (e.g. Gagnepain [1939]; Rosmann [1999]; Orel [2006]; Orel et al. [2013]; Orel and Curry [2015]), were studied. Types and additional specimens and/or their images conserved at Herbaria DLU, HN, HNU, K, KUN, L, NSW, P, PE, PHH, SGN, TCD, VFM, VNF, VNM and VNMN (acronyms based on Thiers 2023, continuously updated) were examined. Article 11.4 of the Shenzhen Code (Turland et al. 2018) was applied to evaluate the priority of the name of a species. Morphological characters were described or measured, based on collections and/or their images examined and the protologues to make comparisons. Geographic coordinate data were retrieved from the records on specimens and mapped using ArcMap 10.7 and then optimised in Adobe Illustrator.

Taxonomic treatment

***Camellia langbianensis* (Gagnep.) P.H. Hô, Cayco Vietnam 1(1): 537. 1991.**

- ≡ *Dankia langbianensis* Gagnep., Fl. Indo-Chine [P.H. Lecomte et al.] Suppl.: 198. 1939. Lectotype (designated by Zhao et al. [2017a: 173]): Vietnam. [Lam Dong]: entre B. dlé et Dankia, Langbiang, 1200–1300 m elev., 26 October 1930, E. Poilane 18648 (P00754831! Image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p00754831>).
- = *Camellia vidalii* Rosmann, Adansonia 21(2): 319. 1999. Holotype: Vietnam. Lam Dong: Bao Loc, 875 m elev., December 1998, J.C. Rosmann et al. 981 (P00834283! Image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p00834283>).
- = *Camellia dongnaiensis* Orel, Novon 16(2): 244. 2006. Syn. nov. Holotype: Vietnam. Lam Dong: unnamed tributary, the headwaters of Dong Nai River, 17 January 2004, G. Orel et al. 21148 (NSW868472, image!).
- = *Camellia oconoriana* Orel, Curry & Luu, Edinburgh J. Bot. 70(3): 440. 2013. Syn. nov. Holotype: Vietnam. Lam Dong: unnamed mountain about 120 km SW of Dalat, 22 November 2010, G. Orel & A.S. Curry 0720 (NSW900415, image!).
- = *Camellia decora* Orel, Curry & Luu, Pursuit Hidden Camellias Vietnam China 173. 2015. Syn. nov. Holotype: Vietnam. Ninh Thuan, 23 March 2009, H. T. Luu et al. VNM 12381 (NSW901588, image!).

= *Camellia tadungensis* Orel, Curry & Luu, Pursuit Hidden Camellias Vietnam China 256. 2015. Syn. nov. Holotype: Vietnam. Dak Nong: Ta Dung Nature Reserve, 11 January 2011, *H.T. Luu et al.* TD 264 (NSW901888, image!).

Description. Shrubs 4–6 m tall. **New branchlets** puberulous; **terminal buds** pubescent. **Petioles** 6–17 mm long, puberulous to glabrous; **leaf blades** narrowly elliptic, oblong or ligulate, 15–40 × 2.5–15 cm, coriaceous, abaxially yellowish or pale green and puberulous, adaxially dark green and glabrous, mid-rib raised on both surfaces, secondary veins 14–27 on each side of mid-rib, abaxially raised and adaxially impressed, base cuneate, obtuse, rounded or subcordate, margin nearly entire or sparsely serrulate, apex attenuate. **Flowers** solitary or paired, borne in the axils of leaves or on short bracteate shoots; short shoots bearing 3–5 bracts subtending flowers; bracts caducous; flowers 2.5–4.5 cm in diam. **Pedicels** 2–5.5 cm long, puberulous to glabrous. **Bracteoles** 2–4, alternate, narrowly ovate or deltate, 1.5–6 × 1.5–3 mm, outside puberulous, inside glabrous or puberulous, margin ciliolate. **Sepals** 5–6, broadly ovate or ovate, 4–7 × 4–12 mm, outside puberulous to pubescent, inside glabrous or puberulous, margin ciliolate. **Petals** 7–9 in 2 whorls, yellow or with pale red fringe, broadly obovate or elliptic, 1–2.5 × 1–2.2 cm, outer surface pubescent to puberulous, inner surface glabrous or puberulous. **Stamens** 1–2 cm long, outer filaments basally connate for 3–4 mm, adnate to petals for 1–2 mm, glabrous or basally pubescent. **Ovary** oblate or ovoid, densely pubescent. **Styles** 3–6, distinct, 1–2.5 cm long, pubescent or gradually becoming glabrous apically. **Capsule** oblate, 5–7 cm in diam., 2–3.5 cm in height; pericarp 0.5–3 mm thick. **Seeds** reddish-brown or black, hemispherical or polyhedral, 1.5–2 cm in diam., glabrous and shiny.

Phenology. Flowering November–April, fruiting April–October.

Distribution. Endemic to southern Vietnam, in Dak Nong, Khanh Hoa, Lam Dong and Ninh Thuan Provinces (Fig. 1).

Habitat. Evergreen forest, 750–1800 m elev.

Additional specimens examined. VIETNAM. Khanh Hoa: Cam Lam, Hon Ba, 8 April 2012, *L.H. Truong & T. Gioi* KH 86, KH 87 & KH 88 (SGN), 8 April 2013, *L.H. Truong & T. Gioi* KH 1140 (SGN). Lam Dong: Bao Loc, Pu Sapoum près Mt. ageicole de Blao, 1000–1100 m elev., 10 January 1934, *E. Poilane* 23790 (P04500357, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p04500357>); Dam Ri, 11 January 2012, *DL 12.01.02* (DLU), 1 December 2012, *DL 12.12.02* (DLU), 31 January 2015, *DL 15.01.03* (DLU), 11°38'29"N, 107°44'25"E, 780–830 m elev., 30 November 2015, *D.W. Zhao & L.V. Dung* 124 (TCD), 125 (KUN, PHH, TCD) & 126 (TCD); Don Duong, Pro, 15 February 2014, *DL 14.02.01*, *DL 14.02.02*, *DL 14.02.03* (DLU), *DL 15.10.08* (DLU); massif du Braïan près de Djiling, 1700–1800 m elev., 17 January 1935, *E. Poilane* 23959 (P05312544, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p05312544>), 1200–1400 m elev., 3 February 1935, *E. Poilane* 24105 (P06838121, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p06838121>). Ninh Thuan: Ninh Hai, Nui Chua, 22 March 2009, *Truong & Dat* NC 198 (SGN), March 2010, *Luu* 749 (SGN), March 2011, *Luu* 750 (SGN), 20 April 2012, *Luu* 736 (SGN); Ninh Son, Phuoc Binh, 37 km to NE from Dalat City, 12°6'N, 108°43'E, 1300–1400 m elev., 2 April 1997, *L. Averyanov et al.* VH

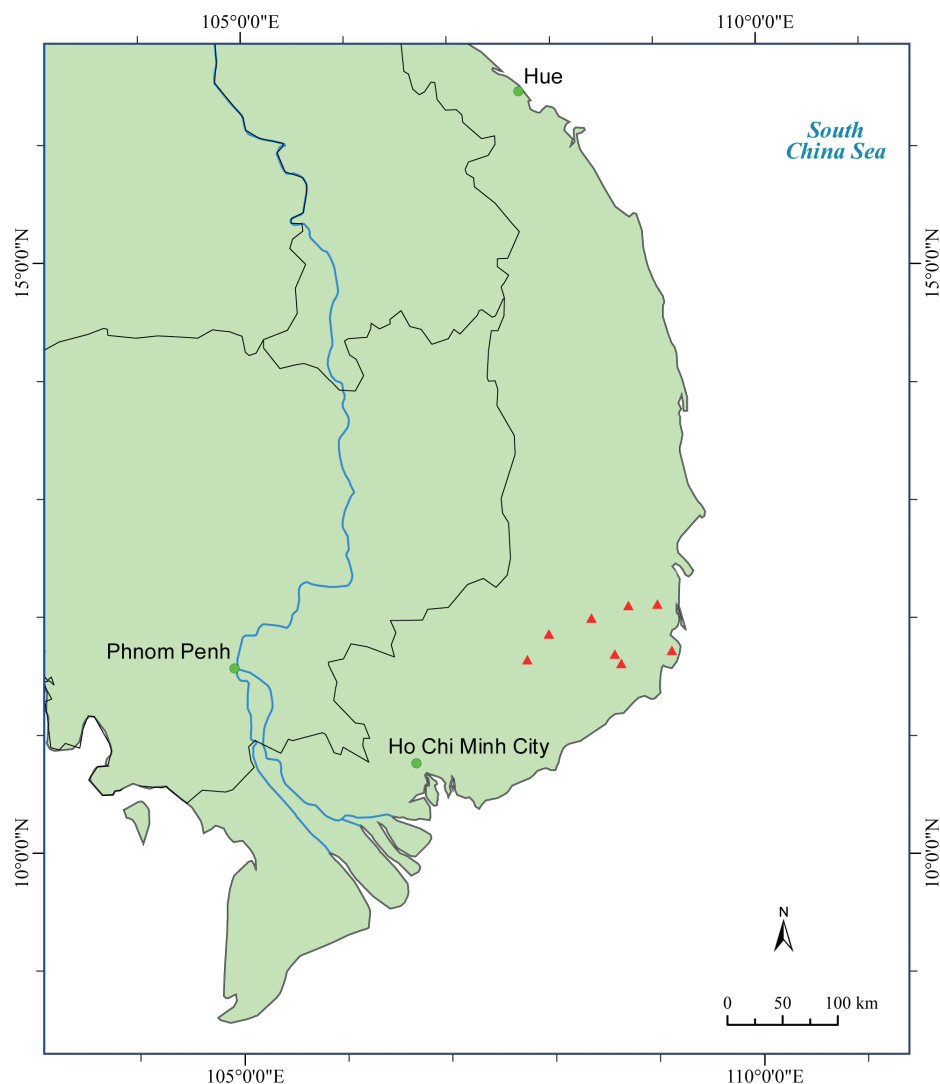


Figure 1. Geographic distribution of *Camellia langbianensis* (red triangle) in Vietnam.

3561 (HN, P05191415, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p05191415>; P05247468, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p05247468>).

Notes. The diagnostic morphological differences amongst the type materials of *C. decora*, *C. dongnaiensis*, *C. langbianensis*, *C. oconoriana*, *C. tadungensis* and *C. vidalii* are shown in Table 1. Quach et al. (2021) argued that *C. vidalii* could be distinguished from *C. langbianensis* by its glabrous pedicel, basal part of filaments, upper part of styles and inside surfaces of the bracteoles, sepals and petals, whereas the latter was hairy on the parts listed. However, the original materials of *C. langbianensis* bear a glabrous to sparsely puberulous pedicel and its bracteoles are glabrous or sparsely puberulous on the inside surface (isolectotypes: K000704329; P00754832, image: <https://science.mnhn.fr/institution/mnhn/collection/p/item/p00754832>). The specimens L. Averyanov et al. VH 3561 at HN and P, cited as *C. langbianensis* in Quach et al. (2021), bear nearly glabrous sepals and much less hairy petals. By contrast, the filaments of the holotype of *C. vidalii*, J.C. Rosmann 981 (P00834283), are basally pubescent. The persistent sepals of L.H. Truong & T. Gioi KH 1140 at SGH, a specimen that is conspecific with *C. vidalii*, are hairy on the inside surface.

Table 1. Morphological comparisons of the types of *Camellia decora*, *C. dongnaiensis*, *C. langbianensis*, *C. oconoriana*, *C. tadungensis* and *C. vidalii*.

Character	<i>C. decora</i>	<i>C. dongnaiensis</i>	<i>C. langbianensis</i>	<i>C. oconoriana</i>	<i>C. tadungensis</i>	<i>C. vidalii</i>
Length of petiole	10–15 mm	10–15 mm	10–17 mm	10–15 mm	10–14 mm	9–13 mm
Size of leaf blade	25–30 × 8–11 cm	29–46 × 9–15 cm	21–28 × 3–5.5 cm	32–35 × 5.5–8.5 cm	24–34 × 6–9 cm	20–36 × 4–7 cm
Pairs of secondary veins	16–19	15–27	14–16	19–24	14–16	17–22
Indumentum of pedicel	glabrous	glabrous to puberulous	glabrous to sparsely puberulous	glabrous	glabrous	glabrous
Indumentum of sepals	outside pubescent, inside glabrous	outside pubescent, inside glabrous	outside pubescent, inside puberulous	outside puberulous, inside glabrous	outside pubescent, inside glabrous	outside puberulous, inside glabrous
Indumentum of petals	outside pubescent, inside glabrous	outside pubescent, inside glabrous	outside pubescent, inside puberulous	outside pubescent, inside glabrous	outside pubescent, inside glabrous	outside pubescent, inside glabrous
Indumentum of filaments	glabrous	Unknown	Unknown	glabrous	glabrous	basally puberulous
Number of styles	3–4	5–6	5	3–5	5–6	4–5
Indumentum of styles	pubescent	glabrous	basally pubescent	basally pubescent	basally pubescent	pubescent
Phenology	flowering March	flowering January	flower buds in October	flowering November	flowering January	flowering December

When more collections are examined, it is hard to ignore the morphological variations of the plants represented by *C. langbianensis* and its synonyms listed above (Table 1). The size of leaves and indumenta of pedicel, sepals, petals and filaments usually vary continuously amongst individuals and a clearly diagnostic breaking point is generally absent. For example, the size of the leaves increases from the type of *C. langbianensis* to that of *C. dongnaiensis*, with those of *C. decora*, *C. oconoriana*, *C. tadungensis* and *C. vidalii* locating between them and overlapping with each other. The type of *C. langbianensis* might be much hairier on the sepals and petals than those of the synonyms recognised above (Table 1; Quach et al. [2021]). The morphological variation is, however, hardly convincing to differentiate species in *Camellia* because this kind of variation can also be found within other taxa, such as *C. sinensis* var. *pubilimba* Hung T. Chang and *C. lanceolata* (Blume) Seem. (Ming 2000). Orel (2006) argued that *C. dongnaiensis* was unique by its yellow petals with pink margin; nevertheless, the fringed pink petals can also be found in *C. langbianensis* (Quach et al. 2021). Therefore, I retain my previous treatment (Zhao 2019) that *C. vidalii* is a heterotypic synonym of *C. langbianensis* before more data are available and treat *C. decora*, *C. dongnaiensis*, *C. oconoriana* and *C. tadungensis* as new heterotypic synonyms of *C. langbianensis*.

Camellia langbianensis is characterised by its generally large leaves, long pedicels, persistent bracteoles and sepals, yellow petals hairy outside, distinct styles, hairy ovaries and glabrous and shiny seeds (Table 1). As a member of sect. *Piquetia* (Pierre) Sealy, it is closely-related with *C. dalatensis* V.D. Luong, Ninh & Hakoda (Tran et al. 2012) and *C. piquetiana* (Pierre) Sealy (Zhao et al. 2023). *Camellia langbianensis* can be distinguished from *C. dalatensis* by its nearly glabrous branchlets, petiole and abaxial surface of the leaf blade, whereas the latter are pubescent on those parts mentioned. *Camellia piquetiana* bears a shorter pedicel and red petals, while *C. langbianensis* has a longer pedicel and yellow petals.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

The author solely contributed to this work.

Author ORCIDs

Dongwei Zhao  <https://orcid.org/0000-0002-7761-7127>

Data availability

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

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