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Sorbus gongshanensis (Rosaceae), a new species from the Hengduan Mountains, China

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Abstract

Sorbus gongshanensis **sp. nov.**, a new species from the Hengduan Mountains China, is described and illustrated. It is similar to *S. kurzii* from China (Yunnan & Xizang), Nepal, and Sikkim in the size of the leaflets, glabrous veins, persistent (sometimes) herbaceous stipules and reddish brown villous inflorescences and red fruits, but differs in its serrate leaflet margins toothed in the distal half or often almost to their base, reddish brown villous to glabrous hypanthium and reddish brown villous infructescences, among other characteristics.

Keywords

Flora of China, taxonomy, Yunnan, Xizang

Introduction

Sorbus L. *sensu lato* (*s.l.*; Rosaceae) comprises about 260 species distributed in the temperate zone of the Northern Hemisphere (Aldasoro et al. 1998; Lu and Spongberg 2003; Zika and Bailleul 2015; Sennikov and Kurtto 2017). Both molecular (Campbell et al. 2007; Lo and Donoghue 2012) and morphological evidence (Zheng and Zhang 2007) suggests that *Sorbus s.l.* is polyphyletic. *Sorbus sensu stricto* (*s.s.*) includes ca. 80 species and is characterized by pinnately compound leaves. Recent molecular study of *Sorbus s.s.* suggests that the most recent common ancestor originated in eastern Asia (Li et al. 2017). The greatest diversity of species of *Sorbus s.s.* (ca. 60 species) is found in the mountains of southwestern China (principally the Hengduan mountains) and adjacent areas of Myanmar, Nepal, and the eastern Himalaya (Long 1987; Lu and Spongberg 2003; McAllister 2005; Watson and Manandhar 2012). This region is one of the world's biodiversity hotspots, as it also is for the genus *Sorbus* (Myers et al. 2000; Li et al. 2017).

While studying *Sorbus* for the *Flora of Pan-Himalaya* Project, we found several accessions from Yunnan and Xizang, China, at the Harvard University Herbarium (GH) that were markedly different from other species of *Sorbus*. After detailed morphological examination, field investigation and literature study, it was concluded that these specimens represent an undescribed species, which we name *S. gongshanensis*. The description of *S. gongshanensis* is based on dried herbarium specimens stored at GH (all herbarium acronyms in this paper follow Thiers 2019).

Material and methods

Morphological study was based on specimens deposited in the following herbaria: A, BM, CAS, CDBI, G, GH, K, KUN and NF. Macroscopic descriptions were based on the specimen sheets and notes made in the field. Detailed observations were conducted using an optical microscope. For scanning electron microscopy (SEM), dried pollen grains and stomata were mounted on metal stubs and sputtered with technical gold, and then were observed under Phenom proX SEM at 10 kV accelerating voltage at the Chengdu Institute of Biology, CAS. Pollen grains come from the field collection from Motuo [China, Xizang, *Meng Li 00281*(NF)]. Terminology of descriptive terms followed Flora of China vol. 9 (Lu and Spongberg 2003). Conservation assessment was based on the known distribution data and followed the IUCN red list category criteria (IUCN 2017).

Results

Taxonomic description

Sorbus gongshanensis Xin-Fen Gao & Meng Li, sp. nov.
urn:lsid:ipni.org:names:77208266-1
Figs 1, 2

Type. China. Yunnan: Gongshan County, Bingzhongluo Xiang. Vicinity of Fucai, on the north side of Nianwaluo River, ca. 10.8 direct km of Bingzhongluo, east side of Gaoligong Mountains, 28°0.47'N, 98°31.11'E, alt. 2780 m, 1 Sept. 2006. *Gaoligong Shan Biodiversity Survey (2006) 31749* (holotype: GH; isotypes: CAS, KUN).

Diagnosis. Similar to *S. kurzii*, but differs in its serrate leaflet margins toothed in the distal half or often almost to their base, reddish brown villous to glabrous hypanthium and reddish brown villous infructescences.

Description. Shrubs or trees, 2–3 m tall. Bark gray. Branchlets tomentose when young, glabrous when old. Buds ovoid. Leaves pinnately compound, 8–10 × 5–5.5 cm;

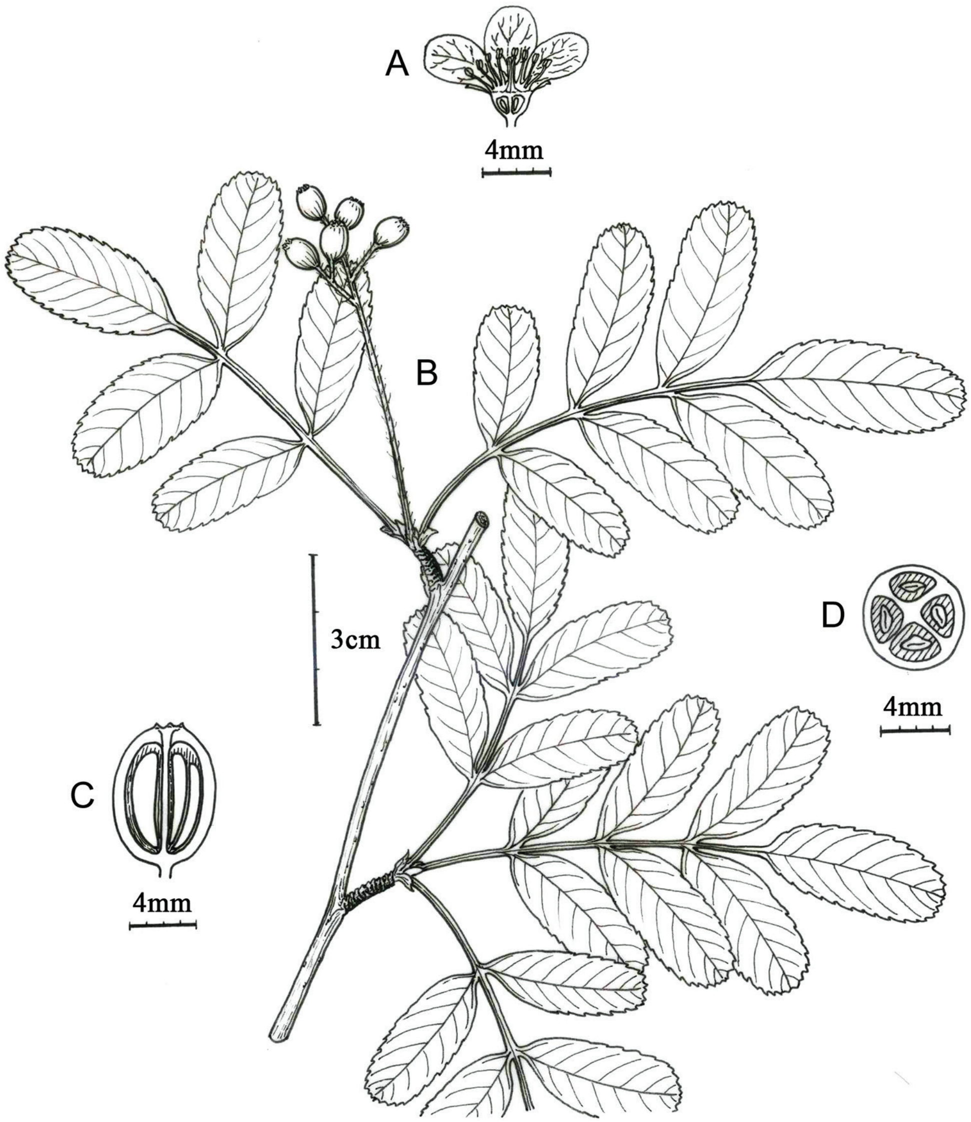

Figure 1. Main morphological characters of *Sorbus gongshanensis* **A** flower, longitudinal section **B** fruiting branch **C** fruit, longitudinal section **D** fruit, cross section.

petiole 1.5–3 cm long; stipules membranous, caducous; rachis slightly winged, sulcate, sparsely tomentose; leaflets 2–4 pairs, opposite, elliptic, oblong to oblong-ovate, 2.8–3.5 × 1–1.5 cm, length/width ratio 2.4–3, surfaces essentially glabrous or sparsely (moderately) villous at flowering, usually glabrescent thereafter; blade paler abaxially, dull green adaxially; lateral veins 8–11 pairs, margins serrate, in the distal half or often almost to their base; base rounded or oblique, apex acute. Inflorescences corymbose, 4–5 × 2–3 cm, 3–15 flowered, sparsely reddish brown villous; stipules semi-orbicular, 0.5–0.8 × 1–1.3 cm, herbaceous, persistent in fruit; pedicels sparsely reddish brown

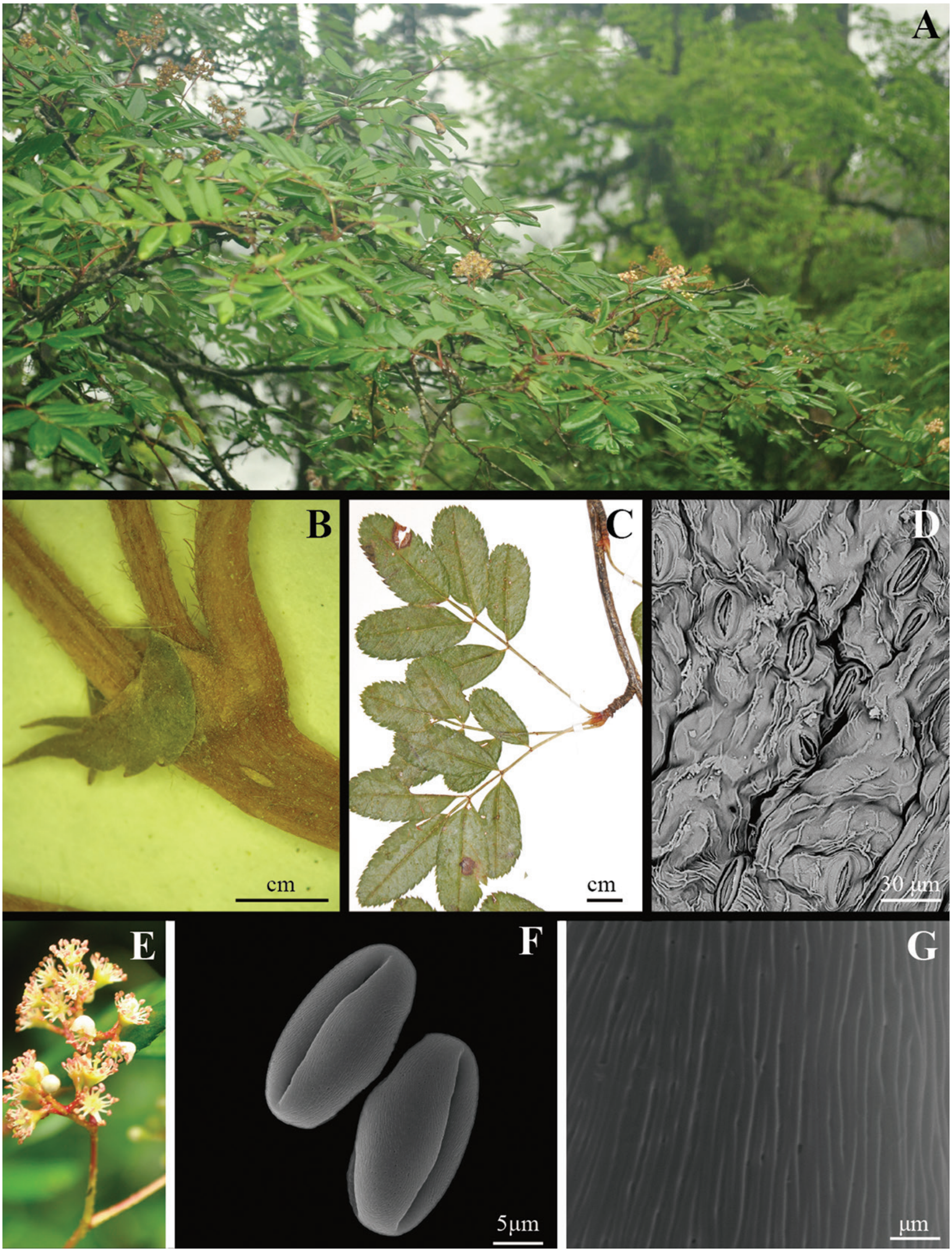

Figure 2. *Sorbus gongshanensis* **A** habit **B** stipules and reddish-brown hairs on infructescences **C** leaves **D** stomata of abaxial blade surface **E** inflorescence **F** perprolate shape pollen, length of polar axis (33.03 ± 2.67 μm) and equatorial (16.61 ± 2.44 μm) diameter **G** striate-perforate ornamentation of pollen grains.

villous. Flowers 6–8 mm in diam.; hypanthium reddish brown villous or glabrous, sepals 1–1.5(–2) mm long, margins entire; petals white, orbiculate to obovate, 3–4 mm long; stamens 15–20; carpels 1/2 adnate to hypanthium, styles 3–5. Infructescences

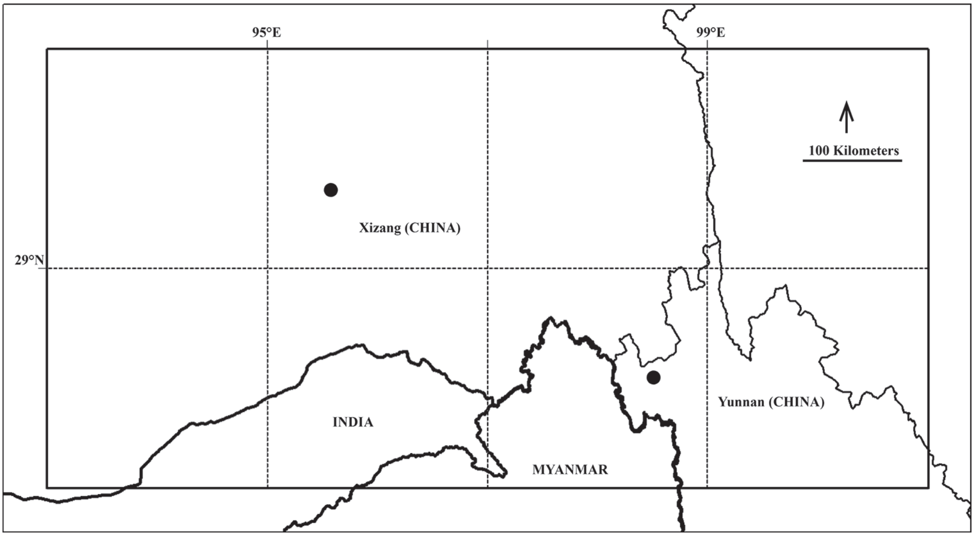

Figure 3. Geographical distribution map of *Sorbus gongshanensis* from Yunnan and Xizang province, China.

sparsely reddish brown villous; pomes red, globose to subglobose, 6–8 mm in diam.; sepals inconspicuous, incurved when fruiting. Seeds brown, ovoid-lanceoloid, 3–4 × 1.2–1.5 mm, slightly asymmetric.

Etymology. The specific epithet refers to the type locality, Gongshan County.

Phenology. Flowering May–July, fruiting September–October.

Distribution and ecology. *Sorbus gongshanensis* is known from the Yunnan & Xizang Province, China (Fig. 3). It grows in broad-leaved forests or on rocky slopes; 2500–3000 m.

Specimens examined. China. Yunnan: Gongshan County, Cikai Xiang, east side of Gaoligong Mountains, along the Danzhu River, on the roadside from Nu Jiang to Danzhu, 27°37.82'N, 98°37.30'E, alt. 2650 m., 2 July 2000. *Li Heng 11905* (GH, CAS, KUN). Xizang: Motuo County, 80k to Galung La, 29°42.30'N, 95°34.24'E, alt. 2782 m., 2 June 2015. *Meng Li 00281* (CDBI, NF).

Conservation status. The distribution of *S. gongshanensis* is based on three collections. The collection notes mention that *S. gongshanensis* is occasional in forests among boulders. There is no direct or indirect information about its current conservation status or possible threats. We therefore assign the conservation status of *S. gongshanensis* as 'Data Deficient (DD)' according to the IUCN red list criteria (IUCN 2017).

Discussion

Sorbus species show a high level of similarity in flower structure and color. The numbers of leaflets and fruit color are also fairly consistent across the group (Li et al. 2017). The number of leaflet pairs in *Sorbus* range between 2 and 21 pairs, and fruit color ranges between white, pink, red and orange-red (Lu and Spongberg 2003). While

Figure 4. Type materials of four similar species distinguishing *Sorbus gongshanensis* **A** *Sorbus kurzii* (G barcode 00437217) **B** *Sorbus macallisteri* (BM barcode 000602118) **C** *Sorbus helenae* (A barcode 00046019) **D** *Sorbus insignis* (K barcode 000758177).

useful floral morphological characteristics are limited, pairs of leaflets, leaflet size, serra position, stipule shape and fruit color can provide valuable information for the identification of *Sorbus* at the species level.

A few species in the Hengduan Mountains have few pairs of leaflets. This group includes *S. helenae* Koehne (3–4 pairs), *S. insignis* (Hook. f.) Hedl. (3–6 pairs), *S. kurzii* (Watt ex Prain) C. K. Schneid (3–6 pairs) and *S. macallisteri* Rushforth (1–2 pairs) (Hedlund 1901; Hooker 1878; Koehne 1913; Prain 1904; Rushforth 1991; Schneider 1906) (Fig. 4 and Table 1). *Sorbus gongshanensis* is easily distinguished from all others by several distinctive characteristics (Long 1987; Lu and Spongberg 2003; Watson and Manandhar 2012) (Table 1). The red fruits distinguish *S. gongshanensis* from all species except *S. kurzii*. However, *S. gongshanensis* differs in its serrate leaflet margins toothed in the distal half or often almost to their base, the hypanthium reddish brown villous or glabrous and infructescences reddish brown villous. In all other species (exclude *S. gongshanensis* and *S. kurzii*), the fruits are typically white. *Sorbus gongshanensis* is also distinguished from *S. macallisteri*, *S. helenae*, and *S. insignis* by its persistent herbaceous stipules when fruiting (Table 1). Furthermore, *S. gongshanensis* have 2–4 pairs of leaflets which have serrate margins. *Sorbus macallisteri* only has 1–2 pairs of leaflets with few teeth. *Sorbus helenae* and *S. insignis* both have more pairs of leaflets (3–6 pairs) with the leaflets also longer and broader (10–20 cm long, 1.7–4 cm wide) than *S. gongshanensis* (Table 1).

There are also several species sometimes with few pairs of leaflets found in other geographic regions. They are *S. gracilis* (Siebold et Zucc.) K. Koch [3–6 pairs of leaflets, distributed in Japan (Honshu, Shikoku, and Kyushu)], *S. sargentiana* Koehne (3–5 pairs of leaflets, distributed in southwest Sichuan Province, and northeast Yunnan Province), *S. sambucifolia* (Chamisso & Schlechtendal) M. Roemer (3–5 pairs of leaflets, distributed in Alaska, Japan, and the Russian Far East), and *S. sitchensis* M. Roem. (3–5 pairs of leaflets, distributed in the Pacific Northwest) (Chamisso and

Table 1. Comparison of characters distinguishing *Sorbus gongshanensis* and similar species.

	Sorbus gongshanensis	***S. kurzii***	***S. macallisteri***	***S. helenae***	***S. insignis***
Leaf & petiole length (cm)	8–10 & 1.5–2.5	7–11 & 1.2–2.8	3.5–6 & 1–1.8	13–20 & 2.5–4	10–15 & 1.7–3
Pairs of leaflets	2–4	3–6	1–2	3–4	3–6
Leaflet size (cm)	2.8–3.5 × 1–1.5	1.8–3.2 × 0.8–1.8	1.7–3 × 0.7–1.4	5–9 × 2–3	3–5 × 1–2
Margins	Deep toothed 1/2 way and often almost to base	Finely toothed in upper 1/2	Few teeth	Serrate or doubly serrate	Finely toothed in upper 1/2 or 1/4
Veins	Glabrous	Glabrous	Glabrous	Reddish brown villous along veins	Glabrous
Stipules	Herbaceous, semiorbicular, persistent	Herbaceous, lanceolate, persistent	Membranous, lanceolate, caducous	Membranous, lanceolate, caducous	Membranous, lanceolate, caducous
Inflorescences	Reddish brown villous	Reddish brown villous	Glabrous	Reddish brown villous	Slightly pubescent
Hypanthium	Reddish brown villous to glabrous	Glabrous to pubescent	Glabrous	Glabrous	Glabrous to pubescent
Infructescences	Reddish brown villous	Glabrous	Glabrous	Glabrous to pubescent	Glabrous
Fruits color	Red	Red	White	White	White

Schlechtendal 1827; Koch 1853; Koehne 1913; Roemer 1847; Siebold and Zuccarini 1846). *Sorbus sargentiana*, *S. sambucifolia*, and *S. sitchensis* have larger infructescences when fruiting (more than 30 fruits), while *S. gracilis* has large stipules (1.5 × 1.5 cm) at the nodes of the inflorescences. *Sorbus gongshanensis* can be easily distinguished from these four species by its few fruits and small stipule size.

Acknowledgments

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Onosma fuyunensis (Boraginaceae), a new species from Xinjiang, China

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Abstract

Onosma fuyunensis, a new species of Boraginaceae from northern Xinjiang, China, is described and illustrated here. *Onosma fuyunensis* is similar to *O. simplicissima* and *O. gmelinii*; it differs in having a particularly bristly indumentum, unbranched stems, white and yellow corollas, anthers united only at base, and nutlets with a stipitate cicatrix. An updated key to the species of *Onosma* from Xinjiang and Altai Mountains is also provided.

Keywords

Boraginaceae, new species, *Onosma fuyunensis*, Xinjiang

Introduction

Onosma L. (Boraginaceae-Lithospermeae), one of the largest genera in Boraginaceae, is primarily distributed in the temperate zones of the Old-World, with the main center of diversity in the Irano-Turanian region (Weigend et al. 2016). In recent years, several new species of *Onosma* have been described (Riedl et al. 2004, Binzet and Orcan 2007, Kandemir and Turkmen 2010, Aytac and Turkmen 2011, Almasi and Ranjbar 2015, Tarimcilar et al. 2015, Binzet 2016a, Binzet 2016b, Cecchi et al. 2016, Binzet and Eren 2018, Dehshiri 2018, He et al. 2018, Mehrabian and Mozaffarian 2018, Mehrabian and Rad 2018), which increases the total number of *Onosma* species to nearly 240. The northeastern region of the geographic distribution of the genus ranges from Turkestan to Altai (Johnston 1951), with the Altai Mountains running through Russia, China, Mongolia and Kazakhstan. In this area, four species and one subspecies of *Onosma* have been described (Krylov 1907, Popov 1953, Rybinskaya 1997, Baitulin and Kotukhov 2011, Urgamal et al. 2014). Furthermore, five species and one subspecies of *Onosma* are recorded in Xinjiang (Riedl 1995, Zhu et al. 1995, Pan and Nurbay 2004), a region of China that includes the southern part of Altai Mountains.

In Flora of the USSR, Popov (1953) provided the classification of sect. *Aponosma* DC. and sect. *Euonosma* DC (subsect. *Haplotricha* Boiss. and subsect. *Asterotricha* Boiss.), which was a combination of Candolle (1846) and Boissier (1875). On a sectional level, the morphology of the calyx in fruit and of the leaf indumentum are considered as the main diagnostic characters, but recent molecular data does not support the monophyly of these sections or subsections (Cecchi et al. 2016, Nasrollahi et al. 2019). On a specific level, the morphology of the flowers, the indumentum inside the corolla, and the morphology of the filaments and anthers have demonstrated to be useful characters (Johnston 1951, Liu 1989). Nutlet and pollen morphology also may be important characters to clarify similar species in *Onosma* taxonomy. (Binzet et al. 2014, Mehrabian et al. 2012, He et al. 2018).

In the process of a taxonomic revision of Chinese *Onosma* species, the identification of specimens from Xinjiang was extremely confusing, especially those specimens collected from Fuyun and Qinghe County, Altay City. Some of the specimens were identified as *O. simplicissima*, while others were assigned to *O. gmelinii*. However, within this group of *Onosma* is clearly another distinct taxon with a combination of characters that could not be associated with either *O. simplicissima* or *O. gmelinii*. Further detailed literature examination and field trips to Northern Xinjiang convinced us that this neglected taxon has been mistakenly mixed within those two species for more than half a century. To our best knowledge, it is not any other known species from the Altai Mountains and nearby regions. Here, we clarify the confusion by describing and illustrating this new species. An updated key of genus *Onosma* from Altai Mountains and Xinjiang is also provided for further study.

Materials and methods

A total of 37 herbarium specimens of *Onosma fuyunensis* were collected from four populations in Northern Xinjiang, China in July, 2017. Type photos of accepted names and their synonyms from Xinjiang and adjacent regions were examined and compared along with 133 herbarium specimens from BNU, KUN, N, NAS, PE, XJA, XJBI, YUKU and 731 specimen pictures from BM, E, FL, K, KW, L, G, MO, MW, P and W. Images of morphological features were taken by Nikon digital camera with macro lens. Dried leaves, nutlets, and pollen grains were settled on stubs using double-sided adhesive tape and were coated with gold by Hitachi E-1045 ion sputter, photographed by Cam Scan Hitachi SU4800 Electron Microscope. For pollen studies, 30 pollen grains were measured for polar axis (P) and equatorial axis (E). Voucher information for the plant materials used was shown in Table 1. Terminology for pollen was used under Erdtman (1952) and Punt et al. (1994). The main characters for comparison of related species are presented in Table 2, which were measured by Image J 1.52a (Abràmoff et al. 2004). Conservation assessments were made according to the IUCN Standards and Petitions Committee (2019) guidelines.

Table 1. Voucher information for the plant materials used.

Taxa	Voucher information	Locality
O. fuyunensis	Y. He & Y. Zhou XJ133 (BNU)	China, Xijiang, Fuyun
O. gmelinii (corolla and pollen)	Anonymous 80617-1 (XJU)	China, Xijiang, Hebukesaier
O. gmelinii (nutlet)	Anonymous 803220 (XJU)	China, Xinjiang, Buerjin
O. simplicissima	Anonymous 19492 (YUKU)	USSR, Voronezh

Table 2. Comparison of *Onosma fuyunensis* with *O. gmelinii* and *O. simplicissima*.

Organ	Character	*O. fuyunensis*	*O. gmelinii*	*O. simplicissima*
Habit	life form	perennial herb with rosettes	perennial herb with rosettes	subshrub with woody branching base and sterile shoots, without rosettes
Leave	indumentum	spreading bristles	spreading bristles	appressed bristles
	venation	reticulate	obscure	obscure
Inflorescence	length (cm)	slightly elongating and straightening in fruit, 5–11	markedly elongating and straightening in fruit, 10–22	markedly elongating and straightening in fruit, 5–9
Bract	shape	lanceolate to linear-oblanceolate	lanceolate	lanceolate to linear-oblanceolate
	size (mm)	12–20 × 1.2–4.5	13–31 × 3.5–10	7–15 × 1.5–3.5
Calyx	lobe	parallel in fruit	converging in fruit	angular in fruit
	size (mm)	15–23 × 1–2	13–22.5 × 1.5–3	6–13 × 0.8–1.2
Corolla	length (mm)	22–27	19–30	15–20
	color	cream and light yellow	pale yellow	cream and light yellow
Androecium	anther (mm)	united only at base, included, 7–8	united into a tube, apex exserted, 8–10	united only at base, included, ca. 5
	filament (mm)	9–11	7–9	ca. 8
	pollen shape	isopolar	heteropolar	unknown
	polar axis (μm)	21.91 ± 1.19	14.41 ± 1.03	unknown
	equatorial axis (μm)	13.83 ± 0.17	9.98 ± 0.12	unknown
Nutlet	length (mm)	ca. 5	ca. 5	ca. 2.5
	cicatrix	stipitate	complanate	unknown
	epidermis cells	rectangular	reticulate	unknown

Taxonomic treatment

Onosma fuyunensis Y. He & Q.R. Liu, sp. nov.

urn:lsid:ipni.org:names:77208267-1
Figs 1C, D, 2, 3B, C, G, I, 4

Onosma gmelinii auct. non Ledeb.: Fl. Reipub. Popul. Sinicae 64(2): 54. 1989. p.p.; Fl. China 16: 352. 1995. p.p.; Clavs Plantarum Xijiangensis. 428. 2000. p.p.; Fl. Xinjiangensis 4: 157. pl. 50. 2004. p.p.

Onosma simplicissima auct. non L.: Fl. China 16: 351. 1995; Fl. Xinjiangensis. 4: 157. 2004.

Type. China. Xinjiang: Between Fuyun County and Keketuohai Town, *Y. He & Y. Zhou BNU2017XJ133*, 7 July 2017, 1270 m a.s.l., rocky slopes, 46°59'01"N, 89°41'42"E. (Holotype: BNU 0041549; Isotype: BNU, PE).

Diagnosis. Closely allied to *O. simplicissima* L., a widespread species distributed from E Europe to E Siberia. It is differentiated by being perennial herb with rosettes (v.s. mostly subshrub with woody branching base and sterile shoots, Fig. 1B), having leaves with spreading bristles (Fig. 2 C–F, v.s. densely silky appressed pilose), larger nutlets (ca. 5 mm v.s. 2.5–3 mm), longer calyx (15–22 mm v.s. 6–13 mm) and corolla (22–27mm v.s. 18–20 mm). Also nearly to *O. gmelinii* Ledeb., but different through having obvious reticulate venation (v.s. obscure lateral veins), slightly elongating and straightening inflorescences in fruit (v.s. markedly elongating and straightening), longer and parallel calyx lobes in fruit (1.2–2 mm v.s. ca. 4mm, lobes converging), cream and pale yellow corolla (v.s. pale yellow), included anthers united only at base (v.s. united into a tube, Fig. 3D), nutlet with stipitate cicatrix and elongated, rectangular surfaces epidermis cells (v.s. complanate cicatrix and reticulate cells, Fig. 3A, F) and isopolar pollen grains (v.s. heteropolar, Fig. 3H).

Description. Herbs perennial, 15–40 cm tall, hispid, strigose. Stems single or several (1–4) arise from rosettes, caspitose, erect, not branched, usually pale straw to light brown, densely covered with long white spreading bristles. Basal leaves short petiolate, linear to linear-oblanceolate, 10–23 cm × 3–10 mm, abaxially densely pubescent and hispid along rised midrib and margin, reticulate venation, adaxially densely appressed hispid and short strigose, base attenuate, apex acute; Cauline leaves sessile, lanceolate, 2–5 cm × 1.5–5 mm. Inflorescences terminal, solitary or dichotomously branched, 4–8 cm wide at anthesis, length to 11 cm in fruit, flowers 5–20; bracts lanceolate to linear-oblanceolate, 1.2–2 cm × 1.2–4.5 mm, densely hispid, short strigose. Pedicel short, ca. 5 mm. Calyx 1.5–2.3 cm × 1–2 mm, densely hispid, short strigose, parted nearly to base; lobes linear. Corolla cream above middle, light yellow below middle, clavate, 2.2–2.7 cm, base ca. 2 mm wide, gradually expanded upward; throat ca. 5 mm wide, obscurely pubescent outside, glabrous inside; lobes broadly triangular, ca. 1.5 × 3 mm. Filaments subulate, 9–11 mm, decurrent; anthers united only at base, 7–8 mm, included, apex sterile, ca. 2 mm. Style 2.4–2.8 cm, glabrous. Nectary ca. 1 mm, glabrous. Pollen grains isopolar, tricolporate and prolate, polar axis (P) 21.91 ± 1.19 μm, equatorial axis (E) 13.83 ± 0.17 μm, P/E ratio 1.58. Nutlets gray-brown, ca. 5 mm × 3 mm, lustrous, smooth, ventral keeled, stipitate cicatrix.

Phenology. Flowering and fruiting occurs from May to July.

Etymology. The specific epithet of the new species refers to its type locality, Fuyun County, Xinjiang, China.

Distribution and habitat. *Onosma fuyunensis* is mainly distributed in Fuyun County, Qinghe County and Altay Prefecture (Fig. 4), it is also known from W Mongolia near the border (Khovd aimag), according to the photo record by Peter Kosachev (http://www.plantarium.ru/page/image/id/128255.html). It prefers dry rocky screes and upland meadows along the hillside, from 500–1400 m a.s.l. Species growing nearby are: *Echinops gmelinii* Turcz, *Goniolimon speciosum* (L.) Boiss., *Artemisia rutifolia* var. *altaica* (Kryl.) Krasch. and *Carex turkestanica* Regel.

Figure 1. Type specimens of *Onosma gmelinii* (**A** syntype, W 1899-0213498), *O. simplicissima* (**B** lectotype, LINN No. 187.1) and *O. fuyunensis* (**C** holotype, BNU 0041549 **D** isotype, BNU 0041547).

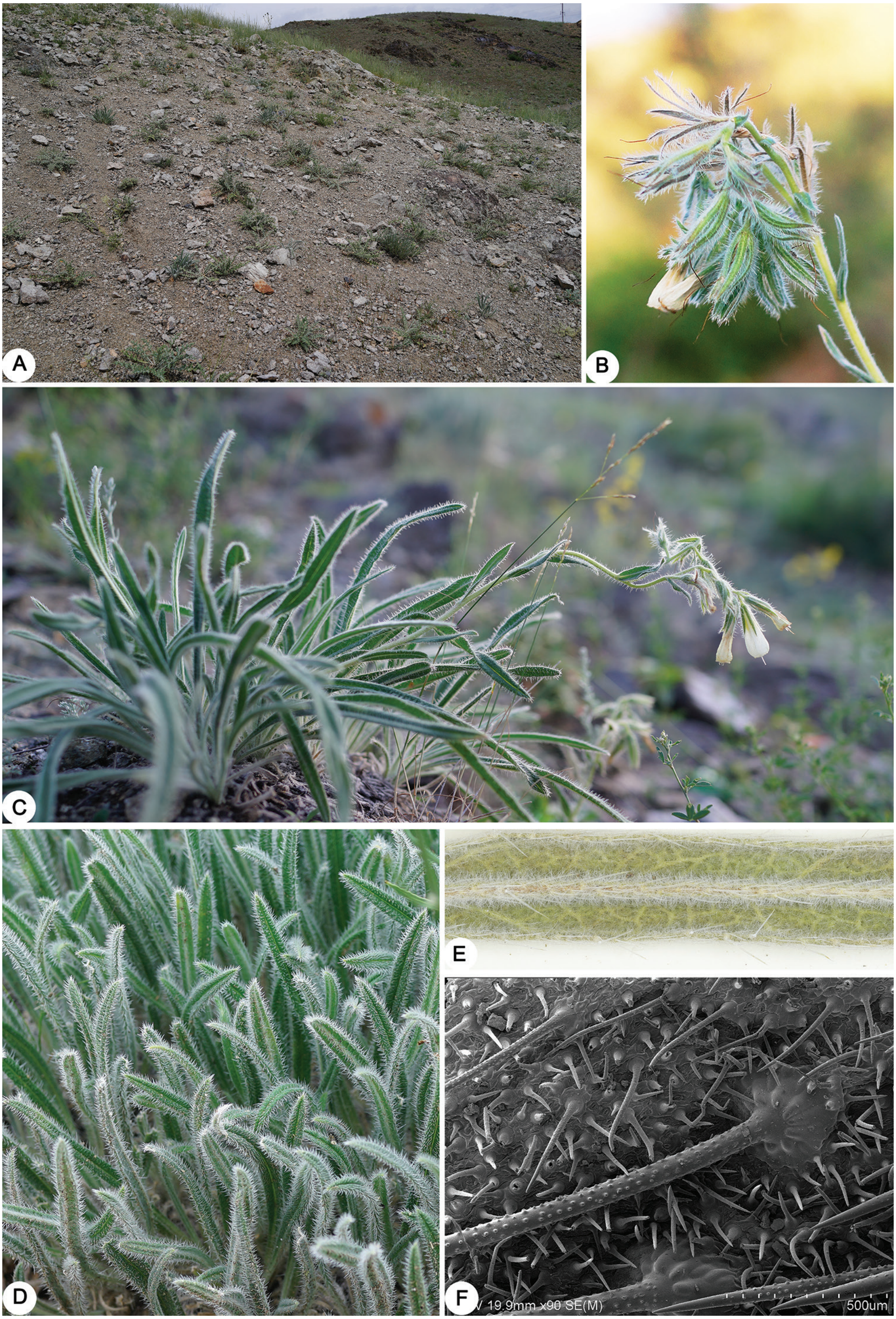

Figure 2. Photographs of *O. fuyunensis*. **A** Habitat **B** inflorescence during late flowering season **C** habit **D** basal leaves (show spreading bristles) **E** leaves in abaxial view (show netted venation) **F** scanning electron micrographs of leaves in adaxial view. Photo by Yi He.

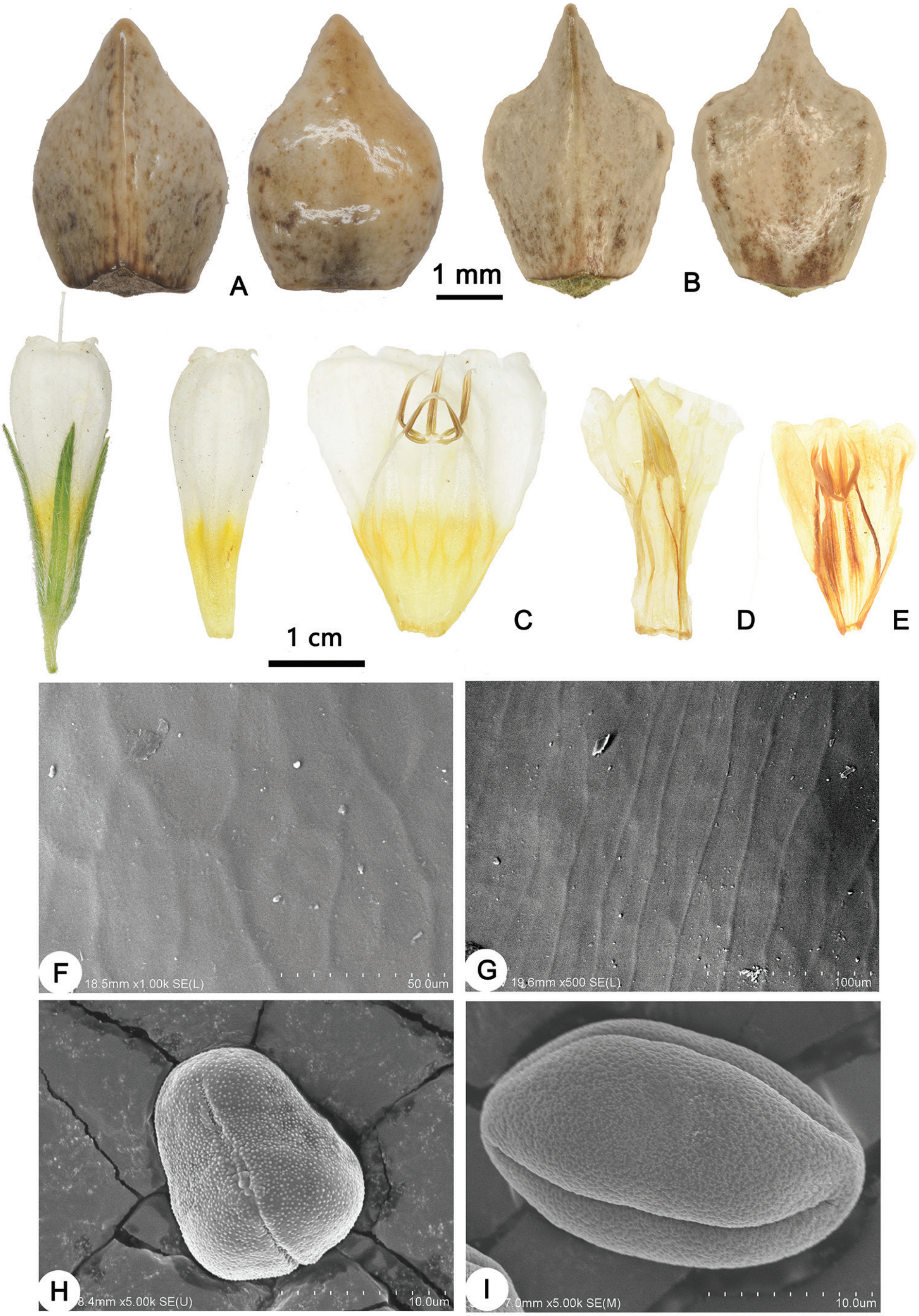

Figure 3. Characters comparison of *O. fuyunensis* and related species **A** nutlets of *O. gmelinii* (in adaxial and abaxial view) **B** nutlets of *O. fuyunensis* (in adaxial and abaxial view) **C** flowers of *O. fuyunensis* **D** corolla of *O. gmelinii* **E** corolla of *O. simplicissima* **F** scanning electron micrograph of nutlets of *O. gmelinii* **G** scanning electron micrograph of nutlets of *O. fuyunensis* **H** scanning electron micrograph of pollens of *O. gmelinii* **I** scanning electron micrograph of pollen of *O. fuyunensis*. Photo by Yi He.

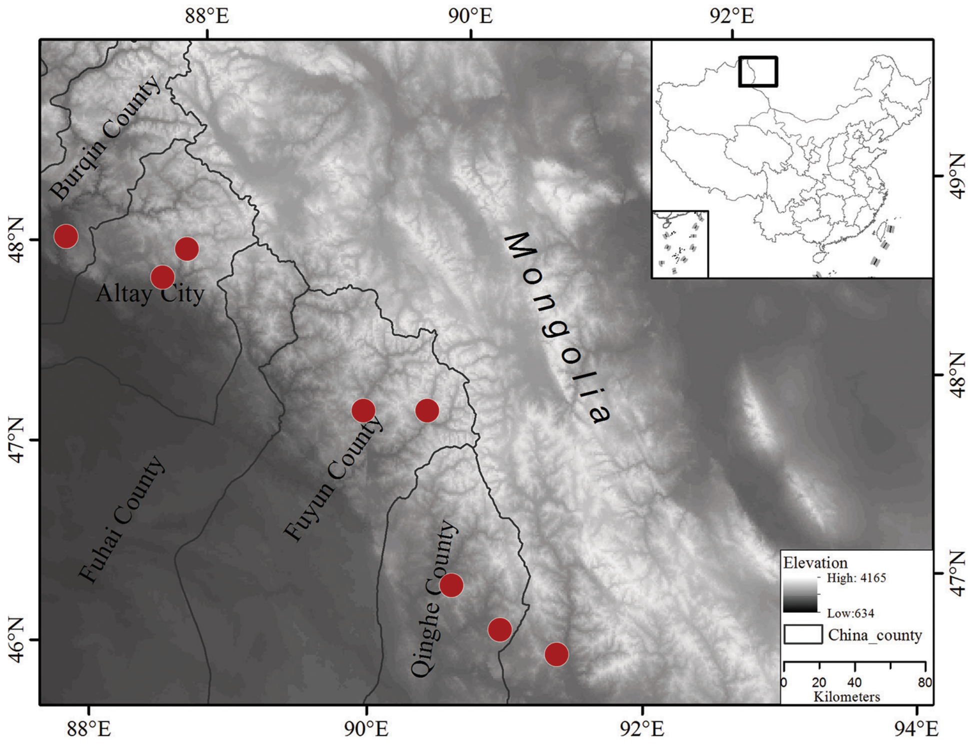

Figure 4. Distribution map of *O. fuyunensis*. Red points denote localities. Illustrated by Feng Xue and Yi He.

Conservation status. According to current data, *Onosma fuyunensis* grows in a large area of ca. 70, 000 km^2 between N Xinjiang and W Mongolia. Similar habitats are common in this area. During our field investigation, four large populations (at least 50 mature individuals) of this species were easily found even at the end of its flowering season. *Onosma fuyunensis* could be the dominant species in some screes and meadows. In this area, human activities are infrequent, and grazing pressure is low. Historical specimens of this taxon are also abundant (from 16 different locations). According to the IUCN Standards and Petitions Committee (2019) criteria, we justify a preliminary status of 'Least Concern' (LC). More accurate quantitative analyses should be used for assessment after more field works in the future.

Additional specimens examined. China. Xinjiang: Altay Prefecture, Dahe forestry station, 1400 m, 5 July 1985, *Anonymous 85-5751* (XJU00016072B); Altay Prefecture, Dahe forestry station, 1200 m, 5 July 1985, *Anonymous 85-0225* (XJU00016073B); Altay Prefecture, Dahe forestry station, 1400 m, 12 June 1985, *Pi 85018* (XJU00016076B); Altay Prefecture, Dahe forestry station, 900 m, 6 July 1985, *Pi 85017* (XJU00016086B); Altay Prefecture, Aweitan Police checkpoint, 815 m, 8 July 2017, *Y. He et Y. Zhou BNU2017XJ153* (BNU0041544); Altay Prefecture, Xiaodonggou forest park, 1000 m, 8 July 2017, *Y. He et Y. Zhou BNU2017XJ159* (BNU0041543); Altay Prefecture, Xiaoxigou, 1 July 1973, *Anonymous Altay197* (XJBI00031718); Fuyun County, roadside to Qinghe County, 1200 m, *G.J. Liu et al. Altay901* (XJBI00031717);

Altay Prefecture, suburban areas, 900–950 m, 29 May 1987, *X.Y. Chen et Q.X. Liu 87061* (NAS00214133); Altay Prefecture, Television tower mountain, 780 m, 30 May 1991, *Z.J. Ma #* (XJA00058804); Altay Prefecture, Dahe forestry station, 900 m, 10 June 1984, *C.Y. Yang 84008* (XJA00058805); Altay Prefecture, suburban areas, 800 m, 6 June 1989, *B. Wang 89-0038* (XJA00058808); Fuyun County, Akequtadao Mountain, 1200 m, 8 June 1959, *Xinjiang Expedition Team 10417* (XJBI00031710, XJBI00031711, PE01354749); Fuyun County, 73 km roadside to Fuhai County, 850 m, 5 June 1974, *Anonymous 00959* (XJBI00031714; XJBI00031715); Fuyun County, 1100 m, 9 July 1977, *Anonymous 11247* (XJBI00031713); Fuyun County, Kemuqi, 800 m, 22 August 1965, *Anonymous 652179* (XJBI00031712); Fuyun County, hydropower station, 750 m, 9 July 1988, *X.Y. Chen et Q.X. Liu 88210* (N138252360, N138252361); Qinghe County, road side from Areletuobie to town, 1170 m, 10 July 2017, *Y. He et Y. Zhou BNU2017XJ083* (BNU0041564); Qinghe County, Kuosirele Village, Areletuobie town, 1143m, 6 July 2017, *Y. He & Y. Zhou BNU2017XJ089* (BNU0041561); Qinghe County, near the checkpoint, 1140m, 7 July 2017, *Y. He et Y. Zhou BNU2017XJ123* (BNU0041554); Qinghe County, Buergen Beaver National Nature Reserve, 11 June 1989, *B. Wang 89-153* (XJA00058826); Buerjin County, Gaochao Commune, 500 m, August 1972, *C.Y. Yang A720295* (XJA00058802, XJA00058803).

Discussion

This species is widely distributed in the middle and low altitude mountains in the eastern part of the Altai Mountains. In the past 60 years, multiple specimens of this taxon have been collected; however, they were not recognized correctly.

According to its nature of indumentum, *O. fuyunensis* belongs to subsect. *Haplotricha* Boiss. Morphologically, in the color and shape of the corolla, this species is close to *O. simplicissima*. The upper part of the fresh corolla is milky white, and the part below the calyx is light yellow. The whole corolla turns pale yellow after drying. The filaments are slightly longer than the anthers, which are united only at base and not exserted from the corolla. The calyx of this species is longer, nearly half to 2/3 of the length of the corolla, while the calyx of *O. simplicissima* is shorter, only ca. 1/3 of the length of the corolla. There is a large difference in the vegetative features of the plants of this newly described species. *O. fuyunensis* is perennial herb with highly-developed rosettes, lacking sterile shoots, covered with long and spreading bristles, while *O. simplicissima* is subshrub with differentiation of flowering shoots and sterile shoots (without rosettes) and its indumentum is appressed. The vegetative parts of *O. fuyunensis* are similar to those of *O. gmelinii*. Both of these species are perennial herbs with rosettes and spreading bristles. The species could not be easily distinguished without the presence of cymes. In addition to the significant differences in aforementioned floral morphology, the stems of *O. gmelinii* are usually bluish, and those of *O. fuyunensis* are generally straw-colored to light-brown.

Geographically, *O. fuyunensis* is mainly distributed in the southeastern part of the Altai Mountains in China and Mongolia. *O. simplicissima* was recorded in Northern Xinjiang by Zhu et al. (1995) and Pan and Nurbay (2004); however, after we examined multiple specimens *of Onosma* collected from China, no specimen should be identified to this taxa. Those previous records were misidentified as either *O. fuyunensis* or *O. gmelinii*. According to Popov (1953), *O. simplicissima* can range eastward to the upper reaches of the Yenisei River and to the northern part of Kazakhstan, so there is no overlap between these two species. *O. gmelinii* is primarily distributed in Central Asia and Siberia. In China, this species is distributed from Kanas Lake, the junction of China and Kazakhstan, to Qinghe County, which makes it sympatric with *O. fuyunensis*.

Key to the species of genus *Onosma* in Altai Mountains and Xinjiang

1	Anthers coherent only at base	**2**
–	Anthers coherent into a tube	**6**
2(1)	Subshrubs or perennial herbs, stems mostly not branched; corolla cream and pale yellow, filaments longer than anthers	**3**
–	Biennial herbs; stems branched; corolla yellow, filaments shorter than anthers	**4**
3(2)	Perennial herbs with rosettes, leaves with spreading bristles, calyx lobes parallel in fruit, 15–23 mm, corolla 22–27 mm	**1. *O. fuyunensis***
–	Mostly subshrubs with sterile shoots, leaves with appressed bristles, calyx lobes angular in fruit,6–13 mm corolla 15–20 mm	**2. *O. simplicissima***
4(2)	Plants strongly whitish gray hirsute; corolla longer than 20 mm	**3. *O. setosa***
–	Plants yellow-green hirsute or sparse whitish hirsute; corolla shorter than 20 mm	**5**
5(4)	Cauline leaves lanceolate, 4–6 cm × 6–11 mm	**4. *O. borysthenica***
–	Cauline leaves linear, 3–5 cm × 3–5 mm	**5. *O. setosa* subsp. *transrhymnensis***
6(1)	Bracts longer than calyx	**6. *O. apiculata***
–	Bracts not longer than calyx	7
7(6)	Plants covered with long horizontally spreading bristles; corolla slightly longer than calyx	**7. *O. irritans***
–	Plants covered with shorter bristles; corolla twice as long as calyx	**8. *O. gmelinii***

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RESEARCH ARTICLE

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A new species of *Dischidia* (Apocynaceae, Asclepiadoideae) from North-eastern Thailand

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Abstract

Dischidia phuphanensis Chatan & Promprom, a new species from north-eastern Thailand, is described and illustrated. The new species is similar to *D. tonkinensis* Costantin, but is distinguished by the shape of its leaves, the apices of the staminal corona lobes, the colour of the corolla and the absence of a corolline corona. The distinguishing characters of similar species are discussed. A key for the identification of those species in Thailand without pitcher-like leaves is provided.

Keywords

Marsdenieae, plant diversity, taxonomy

Introduction

Dischidia Brown (1810: 461) belongs to the tribe Marsdenieae of the Apocynaceae and comprises approximately eighty species, distributed in India, Indochina, Malesia, Melanesia and the eastern Pacific (Rintz 1980; Livshultz et al. 2005). Some members of *Dischidia* are epiphytes living in association with ants (Livshultz et al. 2005; Kidyoo and Suddee 2017). Ants may inhabit the pitcher-shaped leaves of certain species or they may live in the shelter of those with circular leaves which are convex above and concave below. *Dischidia* exhibits umbel-like inflorescences with small, more or less urceolate flowers that usually have a ring of hairs inside the mouth of the corolla tube and an anchor-shaped staminal corona (Rintz 1980, Forster 1996, Hoffmann et al. 2002).

In Thailand, nineteen species of *Dischidia* were reported by Thaithong et al. (2018). During a floristic survey of the forests in north-eastern Thailand conducted between 2009 and 2018, specimens of *Dischidia* were collected in Sakon Nakhon Province. After the living plants and herbarium specimens were carefully investigated, the authors concluded that these could not be referred to any previously named species. Consequently, a new species, *D. phuphanensis*, is described here.

Material and methods

Specimens were collected from Phu Pha Yol National Park, Sakon Nakhon Province, Thailand in 2017. Morphological observations of the new species were carried out on living plants from the field, as well as on herbarium specimens in BK and BKF. Measurements were made with a Vernier caliper or with an ocular micrometer in a dissecting microscope. We consulted the relevant taxonomic literature (e.g. Kerr (1951), Kidyoo and Suddee (2017), Thaithong et al. (2018) etc). We assessed the preliminary conservation status of the new species using our field knowledge and by applying the criteria given by IUCN (2017).

Taxonomy

Dischidia phuphanensis **Chatan & Promprom, sp. nov.**
urn:lsid:ipni.org:names:77208268-1
Figures 1, 2

Diagnosis. *Dischidia phuphanensis* is most similar to *D. tonkinensis*, but the new species differs from the latter in its elliptic or narrowly elliptic or slightly oblanceolate leaves (leaves in *D. tonkinensis* are ovate to ovate elliptic, rarely obovate), apex of corona lobes obtuse (with tips pointing downward in *D. tonkinensis*), yellow base of the corolla tube and light yellow or white apices of the lobes (white or orange-yellow corolla tube and lobes in *D. tonkinensis*) and the absence of a corolline corona (corolline corona present in *D. tonkinensis*). (Figures 1, 2)

Type. Thailand: Sakon Nakhon Province, Phu Pha Yol National Park, 300–400 m, 16°56.126667'N, 104°2.336667'E, 7 August 2017, *W. Chatan 2489* (holotype: BKF!; isotype: BK!).

Description. ***Plant*** epiphytic or lithophytic, sometimes pendulous, fleshy, growing loosely rooted on the host trees or shrubs or on rocks, glabrous except in tube of corolla. ***Branches*** terete, 2.0–2.5 mm thick, green or greenish-purple; internodes 5–15 cm long. Stipular colleters paired, triangular, ca. 0.1 mm long. ***Leaves*** with cylindrical (slightly flattened above), 7–13 × 2.0–2.3 mm petiole; lamina green, dark green or purplish-green, underneath lighter green, slightly fleshy and coriaceous, elliptic, narrowly elliptic or slightly oblanceolate, 3–5 × 1.5–2.0 cm, apex acute-apiculate, base

Figure 1. *Dischidia phuphanensis*. **A** Plant climbing on rock **B** plant climbing on branches of shrub 2–3 m tall **C** branches and leaves **D** inflorescence **E** follicle (nearly mature) **F** dehiscent follicle. Photographed by Wannachai Chatan from *W. Chatan 2489* (**A–D**) and *W. Chatan 2904* (**E, F**).

round or slightly acute, margin entire, gland present on adaxial side near lamina base, midrib and secondary veins inconspicuous on both surfaces. ***Inflorescences*** umbelliform, usually bearing 1–4 open flowers and 2–5 developing buds; bracts 2 subtending each flower, triangular, ca. 0.5 × 0.5 mm, greenish-brown, apex acute; peduncle extra-axillary or apparently axillary, persistent, 0–3 mm long; rachis 1–5 per peduncle, bearing scars of previous flowerings 1–3 × 1.0–1.8 mm; pedicels 1–2 × ± 0.5 mm. ***Sepals*** greenish-white, lobes ovate, 0.6–0.8 × 0.5–0.8 mm, apex round, without colleters. ***Corolla*** broadly urceolate or slightly globose, 2.4–2.6 × 2.4–2.5 mm, basally yellow, progressively fading into light yellow or white at the tips of the lobe, corolla tube with one ring of retrorse hairs in throat; lobes triangular to deltate, light yellow or white, 1.3–1.5 × ca. 1.3 mm, apex acute; corolline corona absent. ***Gynostegium*** conical in outline, 1.8–2.0 mm tall, 1.4–1.6 mm in diameter. subsessile; stipe ca. 0.1 mm tall. ***Staminal corona* lobes** anchor-shaped, stalk ca. 0.8 mm high, apical part ca. 0.6 × 0.8 mm, apex obtuse. ***Pollinarium*** erect, ca. 2 mm long. ***Pollinium*** yellow, 0.6–0.8 × 0.20–0.22 mm, ellipsoidal; translator arms 1.0–1.2 mm long; corpusculum ovate,

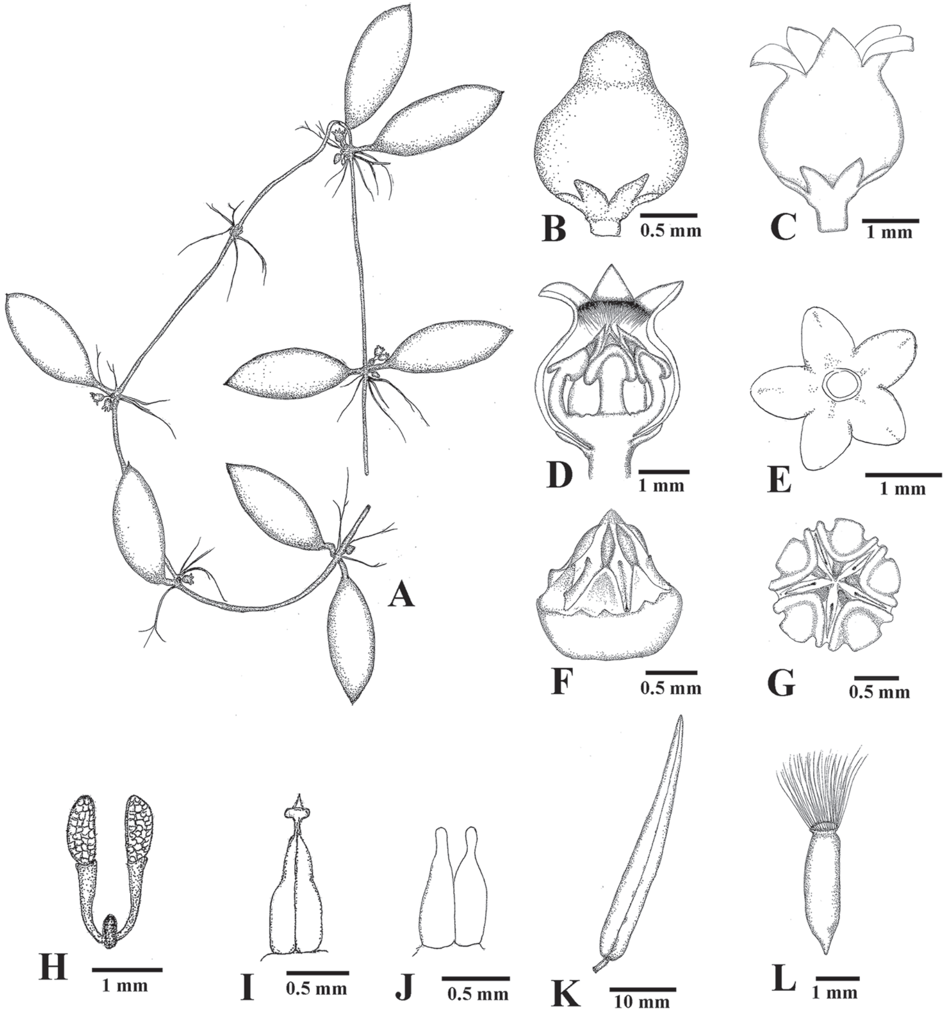

Figure 2. *Dischidia phuphanensis*. **A** Branch with leaves and inflorescences **B** bud **C** flower **D** dissected flower with half of corolla removed **E** calyx from abaxial side **F** gynostegium (side view), with coronal lobes removed **G** gynostegium (from above) **H** pollinarium **I** pistil **J** pistil (style-head removed) **K** follicle **L** seed **A–J** drawn by Wannachai Chatan from *W. Chatan 2489*, and **K, L** from *W. Chatan 2904*.

reddish-brown, 0.15–0.16 × 0.05–0.07 mm. ***Ovary*** bicarpellate, bottle-shaped and slightly flattened, 0.7–1.0 mm long, each carpel ca. 0.2–0.5 mm in basal diameter. ***Follicles*** solitary by abortion. linear, 38–45 × 2.5–3.0 mm, green when immature changing to brown when ripe. ***Seed*** slightly cylindrical, 3.8–4.0 × 1.3–1.5 mm, base obconic, bearing white coma 30–32 mm long.

Additional specimen examined. Thailand, Sakon Nakhon Province: Phu Pha Yol National Park, 300–400 m alt., 16°56'07.2"N, 104°02'21.1"E, 5 September 2017, *W. Chatan 2904* (paratype: BKF).

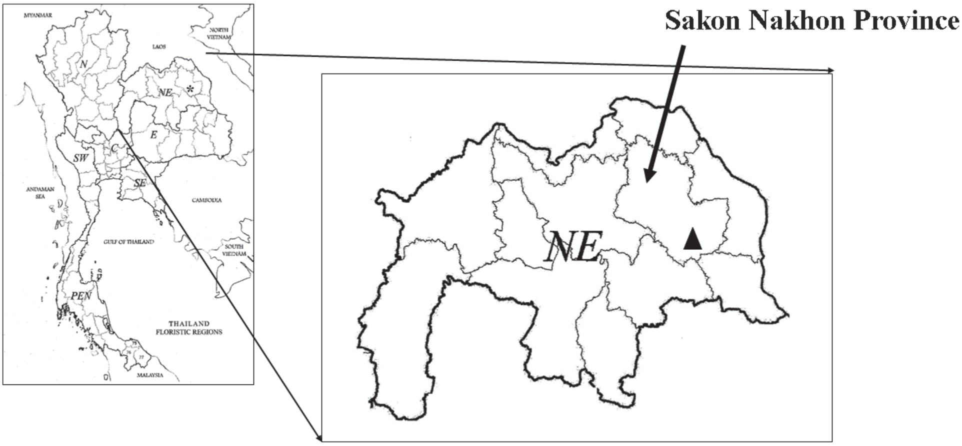

Figure 3. Distribution of *Dischidia phuphanensis* (black triangle) in Phu Pha Yol National Park, Sakon Nakhon Province, Thailand.

Phenology. Flowering in July–September and fruiting in Aug–December.

Distribution. The new species is endemic to Thailand and is known only from the type locality, Phu Pha Yol National Park, Sakon Nakhon Province, north-eastern Thailand (Figure 3).

Ecology. This new species grows in both slightly open and in shaded areas in mixed deciduous forest at an elevation of 300–400 m.

Vernacular name. Thao Rag Noi.

Etymology. The specific epithet of *Dischidia phuphanensis* refers to its type locality, the Phuphan mountain range.

Preliminary conservation status. One population of *Dischidia phuphanensis* was found at the type locality in Phu Pha Yol National Park, Sakon Nakhon Province, north-east Thailand. It is estimated to number fewer than 250 mature individuals. Therefore, it should be considered as "Endangered (EN)" according to the IUCN criteria D (IUCN 2017).

Discussion. *Dischidia phuphanensis* is similar to *D. tonkinensis*, from China, Indochina and Thailand (Thaithong et al. 2018). Similarities include their stems (thick, succulent, 2–3 mm in diameter, glabrous), glabrous petiole and lamina, succulent and coriaceous leaves and their glabrous corolla lobes. However, the new species differs from *D. tonkinensis* in its elliptic or narrowly elliptic or slightly oblanceolate leaves, the obtuse apex of the staminal corona lobes, the yellow base of the corolla tube, the light yellow or white apices of the lobes and absence of a corolline corona. *Dischidia tonkinensis* has ovate to ovate-elliptic, or rarely obovate lamina, the apices of the staminal corona lobes are retuse; it has a white or orange-yellow corolla tube and lobes and possesses a corolline corona. The new species is similar to *D. acuminata* Costantin, from Vietnam, in that they share the 1–5 branches to the inflorescence, the short peduncle 0–3 mm long and the absence of a corolline corona. It differs from *D. acuminata* by

Table 1. Distinguishing features between *Dischidia phuphanensis* and *D. tonkinensis*.

Characters	*D. phuphanensis*	*D. tonkinensis*
1. Leaf shape	elliptic or narrowly elliptic or slightly oblanceolate	ovate to ovate-elliptic, rarely obovate
2. Corolla colour outside	tube yellow at base, light yellow or white towards apices of lobes	white or orange-yellow tube and lobes
3. Corolline corona	Absent	present
4. Staminal corona lobes	stalked, anchor shaped with apex obtuse	stalked, anchor shaped with apex retuse

the triangular to deltate corolla lobes and with acute apices (narrowly shape, thick and abaxial side nose-like in *D. acuminata* (Constantin 1912))

The genus *Dischidia* may be divided into two main groups based on the leaf types, i.e. those with pitcher-like leaves and species with non-pitcher-like leaves. *Dischidia phuphanensis* has non-pitcher-like leaves. The most recent revision of *Dischidia* in Thailand was by Thaithong et al. (2018) and nineteen species were recognised. This was made up of one species with pitcher-like leaves and 18 species with non-pitcher-like leaves. After this new species is added to this group, the number of species with non-pitcher-like leaves is 19. A key to the species with non-pitcher-like leaves in Thailand is provided below and is modified from Thaithong et al. (2018). Details of the morphological differences between *D. phuphanensis* and *D. tonkinensis* are presented in Table1.

Key to species of *Dischidia* with non-pitcher-like leaves in Thailand

1 Leaves broadly ovate or orbicular or orbicular-peltate; if elliptic, then mixed with others that are peltate or orbicular..**2**

– Leaves narrowly ovate, elliptic, narrowly elliptic, obovate, lanceolate, oblanceolate, or spathulate; not mixed with peltate or orbicular leaves.................**5**

2 Leaves broadly ovate or orbicular or elliptic, abaxial sides slightly flattened... .... ***D. nummularia***

– Leaves peltate or orbicular, abaxial sides distinctly concave;.........................**3**

3 Branches pubescent... ***D. astephana***

– Branches glabrous **4**

4 Staminal corona lobes ± absent...***D. imbricata***

– Staminal corona lobes consisting of spreading horn-like projections ....***D. cornuta***

5 Leaves abruptly laterally expanded at the middle or in upper half ....***D. singularis***

– Leaves not expanded in upper half...**6**

6 Leaves linear or narrowly elliptic or spathulate; proportion of length /width is 3.8–16 ....***D. bengalensis***

– Leaves ovate, elliptic, lanceolate, obovate, slightly oblanceolate or broadly obovate; proportion of length/width ratio smaller than 3.8 7

7 Leaves broadly obovate, rarely elliptic; staminal corona lobes broadly saddle-shaped .... ***D. griffithii***

– Leaves ovate, elliptic, slightly elliptic, lanceolate, slightly oblanceolate; staminal corona lobes anchor shaped or sagittate or reduced to minute swellings **8**

8 Branches pubescent, tomentose or hirsute **9**

– Branches glabrous **11**

9 Corolla pink, red, dark red or purple, 6–7 mm long, with two rings of hairs inside around mouth of tube .... ***D. hirsuta***

– Corolla white or creamy white, less than 5.5 mm long, mouth of corolla tube glabrous or with a single ring of hairs **10**

10 Corolla ribbed inside; apices of corona lobes sagittate .... ***D. rimicola***

– Corolla smooth inside; apices of corona lobes cuneiform .... ***D. tomentella***

11 Staminal corona lobes reduced to minute swellings .... ***D. kerrii***

– Staminal corona lobes stalked and anchor-shaped or sagittate **12**

12 Branches and leaves succulent **13**

– Branches and leaves not succulent **14**

13 Apices of staminal corona lobes obtuse .... ***D. phuphanensis***

– Apices of staminal corona lobes retuse .... ***D. tonkinensis***

14 Corolla tube and lobes glabrous inside .... ***D. calva***

– Corolla with hairs at mouth of tube or on adaxial side of lobes **15**

15 Corolla with two distinct rings of hairs only in mouth of tube .... ***D. fruticulosa***

– Corolla with a single ring of hairs around mouth of tube **16**

16 Corolla lobes adaxially pubescent **17**

– Corolla lobes adaxially glabrous **19**

17 Corolla lobes triangular, with a ring of hairs around base only .... ***D. albida***

– Corolla lobes lanceolate, with hairs from base to the middle **18**

18 Leaves 1.5–3.0 × 0.7–1.3 cm; corona lobes anchor-shaped with rounded apices .... ***D. tricholoba***

– Leaves 2.5–6.5 × 0.9–2.5 cm; corona lobes sagittate with obtuse or truncate apices .... ***D. singularis***

19 Corolla greenish-white with purple lines alternating with lobes, mouth of corolla tube hairy throughout .... ***D. punctate***

– Corolla white or creamy white, with a ring of hairs in mouth of tube .... ***D. acutifolia***

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RESEARCH ARTICLE

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Taxonomic revision of the Mesoamerican genus *Spathacanthus* (Justicieae, Acanthoideae, Acanthaceae)

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Abstract

Spathacanthus is a Mesoamerican genus that occurs in tropical and temperate regions from southern Mexico to Costa Rica; its taxonomy has not been updated for two decades. In view of the fact that a new species has been discovered and that the interspecific affinities in this genus have not been addressed to date, the present study aims to revise the genus *Spathacanthus*. Specimens of plants of this genus collected from across the distribution range and deposited in herbaria and digital databases were reviewed. In parallel, a cladistic analysis was carried out, based on morphological characters in order to examine relationships between species. Four species of *Spathacanthus* were recognised: one endemic to Costa Rica, another micro-endemic to Veracruz in Mexico, one more restricted to the forests of Mexico and Guatemala and the last one more widely distributed. Reflecting the previously limited knowledge of the group, many of the specimens that we studied had been misidentified. A key to differentiate these species is provided, supplemented with photographs, drawings and other illustrations, morphological descriptions, synonymy and ecological data. Results, presented here, extend the distribution range of some taxa and a distribution map is presented. The cladistic analysis recovered the genus as monophyletic, showing that *S. hoffmannii* and *S. hahnianus* are sister taxa and *S. magdalenae* was found to be more closely related to *S. parviflorus*. These plants are vulnerable to degradation and habitat loss.

Keywords

conservation, distribution, endemism, phylogeny

Introduction

The family Acanthaceae comprises more than 4,000 species and some 230 genera widely distributed throughout the world. They mostly thrive in tropical and subtropical areas, with the Indo-Malay, African (including Madagascar), South American and Mexican-Central American regions as primary diversity centres. The species of this family thrive in virtually all intertropical habitats, except for high-mountain areas (above 3,000 metres a.s.l.).

Mesoamerica is one of the seven American biodiversity hotpots where species face a high risk of extinction, associated with accelerated deforestation and global warming (Myers et al. 2000; Malcolm et al. 2006). Consequently, an enormous portion of the Mesoamerican flora may well become extinct before species can be described, much less characterised taxonomically and in terms of evolutionary relationships.

Mexico is a major centre of species richness, diversity and endemism for the family Acanthaceae (Daniel 2007), which ranks fifteenth in terms of floristic diversity in the country. Acanthaceae represent 1.6% of the total floristic richness of Mexico (Villaseñor 2016), with around 400 species (47 genera) of herbs, shrubs and trees; of these, 58.8% are endemic to Mexico (Villaseñor and Ortiz 2014), while seven of the 38 native genera documented in Mexico are also endemic to this country. Due to high species richness, no study has covered the entire family and new species are still being discovered (Daniel 2007).

Spathacanthus Baill. is a small genus of shrubs and trees; plants are distinctive amongst Mesoamerican Acanthaceae by having very large capsules and seeds, both of which are amongst the largest known in the family. The genus comprises four species distributed in moist to wet forests of Mexico and Central America. In Mexico, the genus is represented by three native species. Two of them were treated by Daniel (1995) – *Spathacanthus hahnianus* Baill. and *S. parviflorus* Leonard – and also inhabit Guatemala, with *S. hahnianus* reaching Honduras. *Spathacanthus magdalenae* Cast.-Campos was recently discovered in a riparian forest in Veracruz (Castillo-Campos et al. 2013). Meanwhile, *Spathacanthus hoffmannii* Lindau is restricted to Costa Rica (Lindau 1895a). Although currently it is accepted that the genus belongs to subfamily Acanthoideae, tribe Justicieae, *Pseuderanthemum* lineage (McDade et al. 2000), its generic relationships have not been resolved yet and the correct placement of the genus *Spathacanthus* has not been thoroughly assessed.

In addition to issues at the generic level, there is only one previous taxonomic treatment of the entire genus (Daniel 1999). The discovery of a fourth species (Castillo-Campos et al. 2013) clearly calls for re-assessment of the genus; also, interspecific affinities have yet to be addressed. Therefore, the present study aims to provide an updated taxonomic revision of the genus *Spathacanthus*, particularly in Mexico, where three of our species occur.

Methods

This study was based primarily on herbarium specimens deposited in the following herbaria: BIGU, CHAPA, CR, ENCB, IEB, IBUG, MEXU, TEFH, USJ and XAL, as well as field observations of living plants. In total, 97 *Spathacanthus* specimens were examined. Digital specimens from the herbaria at CAS, DS, DUKE, F, K, MO, NY, TEX, US and UT were also consulted, all of them available via the TROPICOS (http://www.tropicos.org) and JSTOR Global Plants (https://plants.jstor.org/collection/TYPSPE) websites. Herbarium acronyms follow Thiers (2019). Protologues and type material of all species and synonyms involved were consulted. This allowed verifying or, where appropriate, re-identifying specimens from morphological features. We used a stereomicroscope (Stemi 2000-C, Carl Zeiss, Cd. Mx., Mexico) to study morphological variations amongst plants of all four species. New descriptions prepared for each species reflect the careful comparative work undertaken.

Specimens were reviewed using the dichotomous keys, descriptions and images provided by Daniel (1995, 1999) and Castillo-Campos et al. (2013). Additionally, all of the major floristic works for Mexico, Guatemala, Honduras and Costa Rica were reviewed (Baillon 1891; Lindau 1895a,b; Leonard 1937; Standley 1938; Standley and Steyermark 1974; Gibson 1974; Durkee 1986; Daniel 1993, 2010; Daniel et al. 2012).

The descriptions, newly presented here, include taxonomic and nomenclatural synonyms of each taxon, along with phenological information, habitat, distribution, elevation and vegetation types. The names of the species were verified on TROPICOS, The International Plant Name Index (https://www.ipni.org/) and Catalogue of Life 2020 Annual Checklist (http://www.catalogueoflife.org/col). Endemism was determined according to the descriptions in specialised studies, floristic listings, distribution data as reported in international databases (IPNI, TROPICOS, Global Biodiversity Information Facility (https://www.gbif.org/)) and information from herbarium specimens. A species was considered endemic if its distribution range is restricted to a given territory and as micro-endemic if exclusive to a limited site within a country. Distribution maps were prepared using geographic data via ARCGIS v.10.2.2 (ESRI 2014), based on the collection data compiled from herbarium specimens.

We also conducted a cladistic analysis, based on morphological characters as a first approach to explore relationships amongst species. We examined all four species of *Spathacanthus* as the in-group, plus *Odontonema callistachyum* Kuntze and *Odontonema cuspidatum* (Nees) Kuntze, as out-groups. Both genera – *Odontonema* and *Spathacanthus* – have been recognised as being the closest American relatives within the *Pseuderanthemum* lineage, in the tribe Justicieae (McDade et al. 2000). Based on the work of Daniel (1999) and after a detailed review of herbarium specimens, morphological characters derived from traditional external morphology were selected to build a matrix of morphological traits for cladistic analysis. A total of 15 binary and multistate characters were scored; the character by taxon matrix was built in MESQUITE v.3.2 (Maddison and Maddison 2017).

Character definitions and states are given in Appendices 1 and 2. A maximum-parsimony analysis (MP) was performed using PAUP* v.4.0a (build 165) (Swofford 2002); to this end, an exhaustive search was conducted involving 15 unordered characters given equal weight; multistate taxa were interpreted as polymorphisms. A total of 1000 replicates were carried out, auto-increased by 100, collapsing zero-length branches and with MulTrees in effect. The shortest trees were saved and a majority-rule consensus tree was produced. Statistical branch support was determined with 1000 non-parametric bootstrap (BS) iterations each with ten replicates, saving five trees per replicate. In addition, a Jackknife analysis (JK) was carried out with a 50% deletion and a full heuristic search; groups with a frequency > 50% were retained, with 1000 replicates and using the TBR branch-swapping algorithm. Finally, the tree was visualised with FIGTREE v.1.4.

Results

Taxonomic treatment

Spathacanthus Baill. Hist. pl. 10: 444. 1891

Type. *Spathacanthus hahnianus* Baill.

Description. Small trees or shrubs, highly branched. Stems sometimes with conspicuous lenticels. Leaves opposite, sessile, subsessile to petiolate, entire, blade usually elongated, oblong or elliptical, membranous. Inflorescence terminal, cymose in the form of a thyrse, with opposite branches, consisting of dichasia or monochasia when one of the buds aborts, sometimes axillary, sessile to pedunculate, subtended by a bract; bracts opposite, small, green, entire. Flowers large, few, subsessile to pedicellate, pedicels usually enlarged in fruit; 2 homomorphic bracteoles; calyx green or yellowish, spathaceous, bilabiate equally or unequally divided into 2 segments; anterior segment with 2 fused lobes, apically entire to bifid; the posterior segment with 3 fused lobes, apically entire to trifid; corolla white or yellow, externally glabrous; tube expanded distally into a distinct throat; corolla with upper lip deeply bilobed, lower lip deeply trilobed; corolla lobes imbricate in bud. Stamens 4, didynamous, adnate at base of corolla throat; anthers monothecous or dithecous, if dithecous, then thecae equal in size, parallel, equally inserted, lacking basal appendages; anterior pair dehiscing towards upper lip, posterior pair dehiscing towards lower lip; staminodes lacking. Style glabrous, included in corolla tube; stigma bilobed, lobes equal. Capsule stipitate, large, glabrous, woody, green when immature, brown when dry. Seeds 4, homomorphic, flattened, glabrous.

The genus *Spathacanthus* consists of four species occurring in humid tropical forests to temperate forests of south-eastern Mexico and Central America (Fig. 1A, B). The genus is easily differentiated from other Acanthaceae genera by the spathaceous calyx divided into 2 segments. The extremely large fruits are also distinctive amongst Neotropical Acanthaceae.

Key to *Spathacanthus* species

1 Calyx divided into 2 equal segments at anthesis **2**
– Calyx divided into 2 unequal segments at anthesis...................................... **3**
2 Leaves subsessile, rarely shortly petiolate; calyx green before fruiting; restricted to Costa Rica.. ***Spathacanthus hoffmannii***
– Leaves petiolate, petiole 10–50 mm long; calyx yellowish before fruiting; restricted to Mexico .... ***Spathacanthus magdalenae***

3 Corolla white, 25–30 mm long, throat 2–6 mm in diameter near midpoint; calyx yellowish before fruiting; distributed in Mexico and Guatemala.......... .... ***Spathacanthus parviflorus***

– Corolla yellow, 31–80 mm long, throat 5–20 mm in diameter near midpoint; calyx green before fruiting; distributed in Mexico, Guatemala and Honduras... .... ***Spathacanthus hahnianus***

Spathacanthus hahnianus **Baill., Hist. pl. 10: 444. Jan-Feb 1981**

Figs 2, 3

Macfadyena simplicifolia Donn. Sm., Bot. Gaz. 16:198 (1891). Type: Guatemala. Alta Verapaz: borders of forest in Pasamalá, 3800 ft a.s.l., Aug 1886, von Tuerckheim 1030 (holotype: US!; isotypes: GH!, K!, M!, US!).

Spathacanthus donnell-smithii Lindau ex Donn. Sm., Bot. Gaz., 20: 293 (1895), nom. nov. superfl.

Spathacanthus donnell-smithianus Lindau, Bull. Herb. Bossier 3: 371 (1895), nom. superfl.

Spathacanthus simplicifolius (Donn. Sm.) Lindau ex Bureau & K. Schum. In C. Martius, Fl. Bras. 8: 294 (1897), basionym *M. simplicifolia*.

Type. Mexico. Veracruz: Misantla, forêt de montagne, Santa Rita, 3 Jul 1866, L. Hahn 349 (holotype: P!).

Description. Small trees or shrubs, up to 10 m height, branched, internodes glabrous. Stems quadrate to compressed when young, pubescent at nodes with eglandular trichomes. Leaves petiolate, petioles 5–45 mm long, blades elliptic to obovate-elliptic, 40–260 mm × 10–143 mm, apically acute-to-acuminate, basally acute, margin entire, adaxial surface glabrous, abaxial surface glabrous to pubescent along main veins with eglandular trichomes, flattened to flexuous. Inflorescences terminal, rachis nearly glabrous or pubescent with eglandular trichomes; bracts triangular to subulate, 1.5–6 mm × 1–2.3 mm, abaxial surface nearly glabrous or pubescent like rachis; bracteoles triangular, subulate to linear-lanceolate, 1.6 mm × 0.8–1.5 mm, abaxial surface nearly glabrous or pubescent like rachis. Flowers subsessile to pedicellate, pedicels 2–8 mm long, glabrous; calyx green, 20–40 mm × 8–19 mm, abaxially glabrous, unequally divided into 2 prominent elliptic to ovate segments, 16–30 mm long on posterior side and 3–15 mm long on anterior side; the anterior segment bilobed, lobes triangular, 0.4–2 mm long; the posterior segment trilobed, triangular lobes, 0.4–4 mm long, acute to apiculate; corolla yellow, 31–80 mm long × 20–40 mm wide, externally glabrous and internally pubescent, throat 19–33 mm long × 5–20 mm in diameter near midpoint, upper lip 12–19 mm long, lobes elliptic, (5)9–10.5 mm × 4.5–8.5 mm, lower lip 15–18 mm long, lobes linear-elliptic to elliptic, 8–15 mm long × (3.5–)7–8.5(–11) mm. Stamens whitish, longer pair 16–18.5 mm long from the base to the apex of the thecae, shorter pair 12–14.5 mm long; anthers dithecous, thecae 3.3–4.2 mm long; style glabrous 28–35 mm long; stigma lobes 0.7 mm long. Capsule 45–70 mm long, stipe 25–37 mm long, head 20–33 mm long. Seeds subcircular to subcordate, 5–10 mm long, 5.7–8 mm wide, surface roughened.

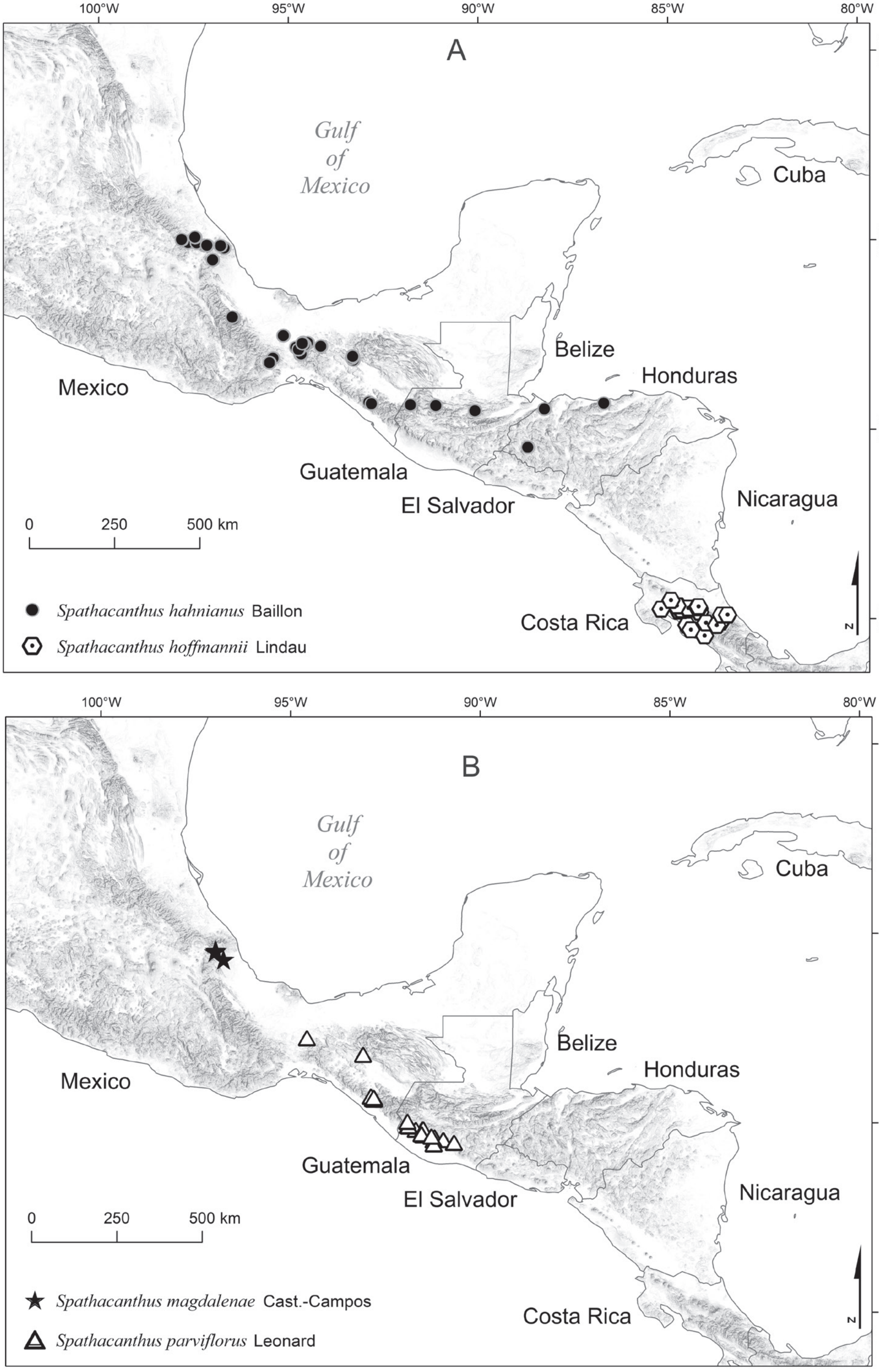
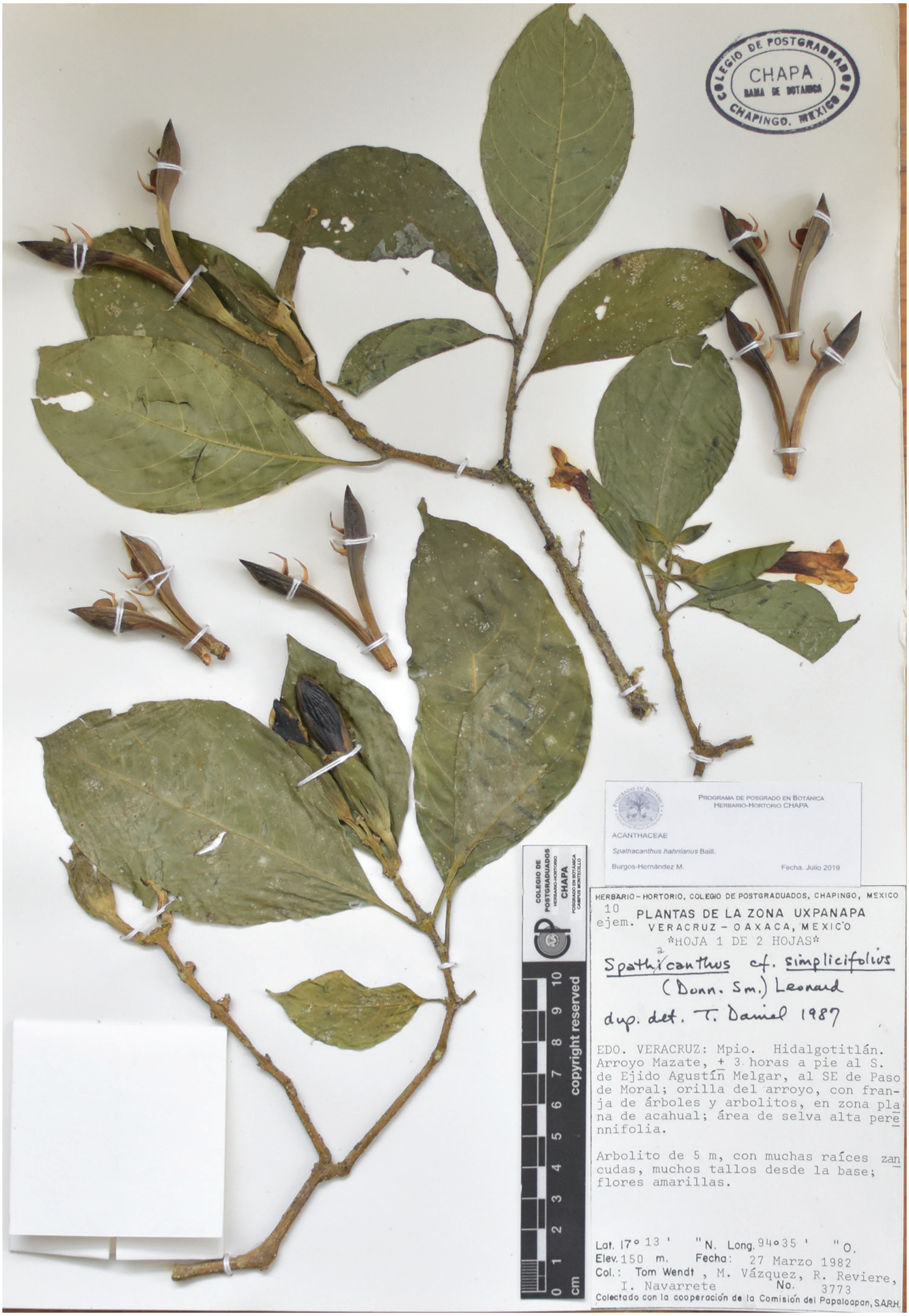


Figure 1. Distribution of the Mesoamerican genus *Spathacanthus* Baillon. **A** Distribution of *S. hahnianus* and *S. hoffmannii* **B** distribution of *S. magdalenae* and *S. parviflorus*.



PROGRAMA DE POSGRADO EN BOTÁNICA
HERBARIO-HORTORIO CHAPA
ACANTHACEAE
Spathacanthus hahnianus Baill.
Burgos-Hernández M. Fecha. Julio 2019

HERBARIO – HORTORIO, COLEGIO DE POSTGRADUADOS, CHAPINGO, MEXICO
10 ejem. PLANTAS DE LA ZONA UXPANAPA
VERACRUZ – OAXACA, MEXICO
HOJA 1 DE 2 HOJAS
Spathicanthus cf. simplicifolius
(Donn. Sm.) Leonard
dup. det. T. Daniel 1987

EDO. VERACRUZ: Mpio. Hidalgotitlán. Arroyo Mazate, ± 3 horas a pie al S. de Ejido Agustín Melgar, al SE de Paso de Moral; orilla del arroyo, con franja de árboles y arbolitos, en zona plana de acahual; área de selva alta perennifolia.

Arbolito de 5 m, con muchas raíces zancudas, muchos tallos desde la base; flores amarillas.

Lat. 17° 13 ' " N. Long. 94° 35 ' " O.
Elev. 150 m. Fecha: 27 Marzo 1982
Col.: Tom Wendt, M. Vázquez, R. Reviere, I. Navarrete No. 3773
Colectado con la cooperación de la Comisión del Papaloapan, S.A.R.H.

Figure 2. *Spathacantus hahnianus* Baillon, *T. Wendt, M. Vázquez, R. Reviere & I. Navarrete 3773* (CHAPA), Mexico: Veracruz, Hidalgotitlan. Note that specimen was identified as *S.* cf *simplicifolius*, a name that is synonymous of *S. hahnianus*.

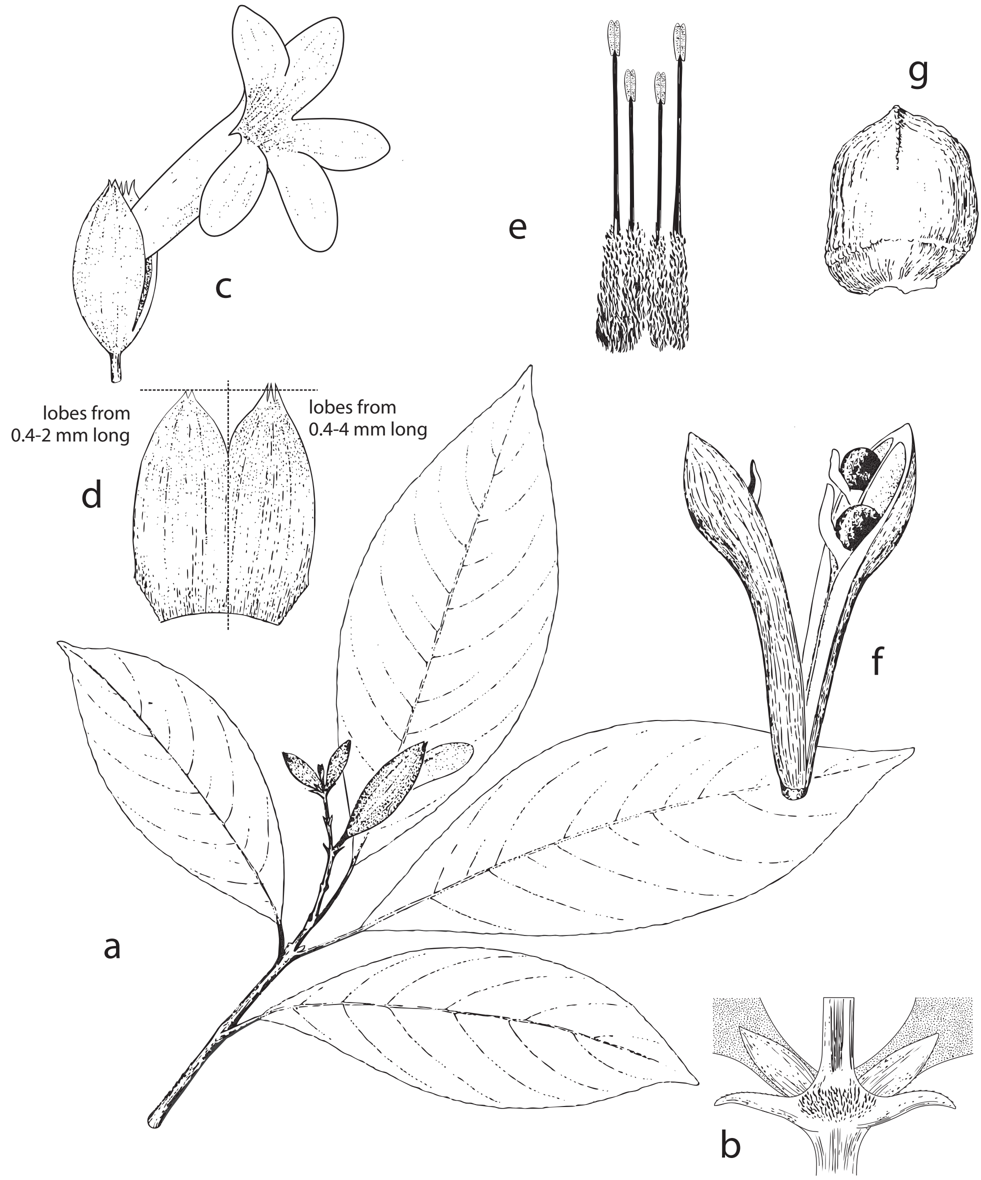


Figure 3. *Spathacantus hahnianus* Baillon. Image and legend modified from Daniel (1995) Flora of Chiapas, Part 4, page 131 **a** habit, × 0.5 **b** inflorescence node, × 3.5 **c** flower, × 1.1 **d** calyx split, × 1.3 **e** androecium showing didynamous stamens, × 1.8 **f** capsule, × 1 **g** seed, × 3.9. Illustration: Ellen del Valle.

Distribution, habitat and phenology. *Spathacanthus hahnianus* occurs in southern Mexico (Chiapas, Oaxaca, Puebla, Veracruz), Guatemala (Alta Verapaz, Quinché) and northern Honduras (Cortés, Lempira, Yoro) (Fig. 1A). It inhabits humid low to middle elevation forests and oak forests in flooded plains, near streams and in ravines, at 100 to 2000 m a.s.l. Flowering takes place all year round, fruiting from November to June.

Specimens examined. Mexico. Chiapas: Mpio. Berriozábal, 13 km N of Berriozábal near pozo Turipache and finca El Suspiro, 1000 m a.s.l., 02 Nov 1971, D.E. Breedlove & A. Smith 21618 (DS, DUKE, F, MEXU, MO, NY, TEX); 900 m a.s.l., 25 Dec 1972, D.E. Breedlove & R. Thome 30868 (ENCB, MO); a 12 km N de Berriozábal, 600 m a.s.l., 16 May 1989, E. Martínez & M. Soto 24241 (MEXU); La Aduana, cerca de rancho Flor de Corazón, hacia El Cairo, 800 m a.s.l., 06 Sep 1990, E. Palacios E. 1726 (IBUG, MEXU); a 13 km al N de Berriozábal, 29 Mar 1984, O. Téllez V. et al. 7598 (MEXU); Mpio. La Concordia, camino de El Triunfo para la Finca Prusia, 1940 m a.s.l., 14 May 1982, J.I. Calzada 8935 (IBUG, MEXU, XAL); Mpio. Ángel Albino Corzo, sendero Palo Gordo, Reserva de la Biosfera El Triunfo, 2000 m a.s.l., 14 May 2004, F. González-García s.n. (XAL). **Oaxaca:** Mpio. San Felipe Usila, campamento cerro Verde, carr. para arroyo Tambor, 450 m a.s.l., 02 Nov 1990, J.I. Calzada et al. 16596 (MEXU); Mpio. Santiago Lachiguiri, Distr. Tehuantepec, cerro de Buenavista, 2 km SO de crucero Buenavista, 27 Oct 1991, A. Campos V. & R. Torres 4103 (CHAPA, MEXU); Mpio. Santa María Chimalapa, Uxpanapa region, between Esmeralda (17 km E of Sarabia) and Río Verde, 1.1 mi S of Esmeralda, 100 m a.s.l., 10 Jan 1987, T.B. Croat & D.P. Jhmnon 63303 (BM, ENCB, MO, TEX); Mpio. Sta. María Chimalapa, arroyo Matzpac, N de Sta. María por la vereda al Río Verde, 250 m a.s.l., 29 Oct 1985, H. Hernández G. & C. González L. 1777 (MEXU, MO, TEX); Río Verde por la vereda a la cabecera, ca. 7 km N de Sta. María, 280 m a.s.l., 21 Nov 1985, H. Hernández G. & C. González L. 1855 (CAS, MEXU, MO, TEX); Mpio. San Felipe Usila, Nuevo Santa Flora, 22 Nov 1993, R. de Santiago & A.M. Hanan 247 (MEXU); Mpio. Guevea de Humboldt, Distr. Tehuantepec, recorrido La Cumbre-arroyo Seco, 13.4 km N de Guevea de Humboldt, 29 Mar 1991, R. Torres C. & A. Campos V. 13897 (CHAPA, MEXU); Mpio. Matías Romero Avendaño, en la estación del río Azul a 16.6 km al E de la Colonia Cuahutémoc, 1500 m a.s.l., 23 Jan 2003, E. Martínez 36091 (MEXU). **Puebla:** Mpio. Ahuacatlán, 4.5 km al SE de Ahuacatlán, brecha a Zapotitlán, 1250 m a.s.l., 24 May 1986, P. Tenorio L. et al. 11413 (MEXU); Mpio. Cuetzalan del Progreso, Tzitzinapan, Yancuictlalpan, 11 Jul 1981, F. Basurto & R. Patron 454 (MEXU); Mpio. Hueyapan, cerca de Atexcaco, 1300 m a.s.l., 12 Jul 1953, D. Gold 324 (MEXU); Mpio. Xochitlán de Vicente Suárez, 1 km al E de Pahuata, camino a Huahuaxtla, 1150 m a.s.l., 05 Aug 2014, J.L. Contreras 5604 (XAL); **Veracruz:** Mpio, Atzalan, La Calavera, 1000 m a.s.l., 07 Jul 1975, F. Ventura A. 11601 (ENCB, IEB, MEXU, XAL); La Calavera, puente La Calavera, km 12 carretera Atzalán-Tlapacoyan, 1010 m a.s.l., 08 Jul 2008, T. Krömer & J. Viccon-Esquivel 3495 (MEXU, MO, XAL); Mpio. Coatepec, Barranca de Ramírez, 1500 m a.s.l., 28 Jun 1990, P. Zamora C. 2540 (IEB, XAL); Mpio. Jesús Carranza, 3 km al este de río Chalchijapa, por la carretera Sarabia-Cedillo, 09 Jan 1975, M. Vázquez T. 1584 (IEB, XAL); Mpio. Juchique de Ferrer, cerro de La Botella, parte mediana San Alfonso, 847 m a.s.l., 24 Jul 2008, M. Vázquez T. 8635 (XAL); Mpio. Uxpanapa, km 4 camino Cedillo-La Escuadra, 150 m a.s.l., 06 Dec 1974, J. Dorantes et al. 3766 (ENCB); km 4 del camino Hnos. Cedillo-La Hulera, 150 m a.s.l., 21 Jan 1975, J. Dorantes et al. 4058 (ENCB, IEB, XAL); río Soloxúchil, 1.5 km O del campamento Hnos. Cedillo, 150 m a.s.l., 02 Jan 1975, M. Vázquez et al. 1611 (ENCB, IEB, MEXU, XAL); río Uxpanapa, cerca del límite con Oaxaca, 180 m a.s.l., 27 Sep 1980, T. Wendt et al. 2769 (CHAPA, IEB, MEXU, MO, TEX, XAL); arroyo Mazate al S de ejido Agustín Melgar, al SE de Paso de Moral, 150 m a.s.l., 27 Mar 1982 T. Wendt et al 3773 (CHAPA, MEXU, MO, TEX); 4.5 km O de Uxpanapa, sobre terracería a La Laguna, 120 m a.s.l., 17 Oct 1983, T. Wendt & I. Almaraz G. 4194 (CHAPA, MEXU, MO, NY, TEX, XAL); 1.5 km N del Poblado Dos, ejido F.J. Mina, 180 m a.s.l., 02 Feb 1983, O. Zambrano C. 1184 (CHAPA); Mpio. Yecuatla, entre La Unión y Roca de Oro, 900 m a.s.l., 21 Aug 1989 C. Gutiérrez B. 3584 (IEB, MEXU, XAL). **Guatemala. Alta Verapaz:** Pasmala, 1159 m a.s.l., Aug 1886, H. Von Tuerckheim 1030 (MEXU); **Quiché:** Chajul, La Perla, E. Tribouillier & I. Pedro 409 (BIGU); Chajul, La Perla, E. Tribouillier & I. Pedro 436 (BIGU); Chajul, aldea Chel, E. Tribouillier & I. Pedro 469 (BIGU). **Honduras. Cortés**: 2 km NW de la quebrada de Cantiles, 1700 m a.s.l., 26 Sep 1993, C. Nelson et al. 16631 (MO, TEFH). **Lempira**: Parque Nacional Montaña de Celaque, cerro Aguacatal. Las Chimis, San Manuel Colohete, P. House et al. 185 (EAP). **Yoro**: ca. 16 km from Yaruca on Quebrada de Oro to cerro Búfalo, W. Holmes 4392 (NY, TEX).

Spathacanthus hoffmannii **Lindau, Bull. Herb. Boissier 3: 370. 1895**

Figs 4, 5

Type. Costa Rica. Alajuela: prope Aguacate, Aug 1857, C. Hoffmann 842 (holotype: B destroyed, photos F!, GH!, US!).

Description. Small trees or shrubs, up to 8 m height, highly branched, internodes glabrous. Stems quadrate to flattened when young, glabrous or pubescent at nodes with flexuose eglandular trichomes. Leaves subsessile to rarely short petiolate, petioles 2–5 mm long, blades elliptic to obovate-elliptic, 72–285 mm × 25–110 mm, apically acute to acuminate, basally acute, margin undulate, glabrous on both surfaces. Inflorescences terminal, sometimes axillary, rachis pubescent; bracts triangular to lanceolate, subulate, 1–8 mm × 1–1.3 mm, abaxial surface glabrous; bracteoles lanceolate to subulate, 2.5 mm × 1–1.5 mm, abaxial surface glabrous. Flowers pedicellate, pedicels 9 mm long, glabrous; calyx green before fruiting, 10–40 mm × 10–16 mm, abaxially glabrous, equally divided into 2 prominent elliptic to obovate-elliptic segments; each segment 11–30 mm long; anterior segment entire, the posterior entire to bilobed; triangular lobes, 1.5–5 mm long, acute to apiculate; corolla white, 52–110 mm long × 30–50 mm wide, externally glabrous and internally pubescent, throat 35–50 mm long × 9–20 mm in diameter near midpoint, upper lip 15–26 mm long, bilobed, lobes ovate to elliptic, 10–20 mm × 11–18 mm, lower lip 18–25 mm long, three-lobed, lobes ovate to elliptic, 15–20 mm × 12–16 mm. Stamens whitish, longer pair 24–34 mm long from the base to the apex of the thecae, shorter pair 18–28 mm long; anthers dithecous, thecae 4–6 mm long; style glabrous 44–59 mm long; stigma lobes 0.3–0.6 mm long. Capsule 50–89 mm long, stipe 20–40 mm long, head 22–39 mm long. Seeds subcordate, 7.5–13 mm × 7.5–11 mm, surface roughened.

Figure 4. *Spathacanthus hoffmannii* Lindau. *R. Liesner, E. Judziewicz & B. Pérez G. 15444* (MEXU), Costa Rica: Cartago.

Figure 5. *Spathacanthus hoffmannii* Lindau. Image modified from Durkee (1986) Flora Costaricensis, No. 18, page 19. The image shows an elliptic leaf of *S. hoffmannii*, flowers with a five-lobed corolla and the 2-segments of calyx equally or subequally divided, with its large woody fruit.

Distribution, habitat and phenology. *Spathacanthus hoffmannii* is known only from Costa Rica where it has been reported from all provinces (Fig. 1A). It occurs along the banks of watercourses and on cliffs in humid forests, rain forests and cloud forests at 350 to 1750 m a.s.l. Flowering takes place from January to October, fruiting from December to September.

Specimens examined. Costa Rica. Alajuela: Est. Biol. Reserva Forestal de San Ramón, valley of Río Lorencito, Burger et al. 12439 (F); Bajos de Jamaical, Reserva de San Ramón, I. Chacón 1768 (CR, DUKE); finca Los Ensayos ca. 11 mi NW of Zarcero, 900 m a.s.l., 15 Aug 1977, T.B. Croat 43516 (MO); San José de Naranjo, I. García s.n. (CR, F); río San Lorencito, límite E de la Reserva Forestal de San Ramón, J. Gómez-Laurito 10263 (CR, F); Est. Biol. Res. Forestal de San Ramón, valley of río

Lorencito on Caribbean slope, J. Gómez-Laurito & K. Swangel 12439 (CR); Reserva Forestal de San Ramón, río San Lorencito, 800–1000 m a.s.l., 05 Dec 1983, G. Herrera 362 (CR, MEXU, MO, US); Buena Vista de San Carlos, L. Holdridge 6790 (CR); Quebrada Lajas, finca Los Ensayos, Buena Vista de San Carlos, A. Jiménez M. 2319 (CR, F, MO, NY); near road to Laguna Hule, R. Lent 3243 (CR, F, MO); Cordillera de Tilarán, río La Balsa, 500 m a.s.l., 07 Mar 1994, V. Ramírez & Q. Jiménez 273 (CR, MO, NY); road to Colonia Virgen del Socorro, barranca of río Sarapiquí, 700–800 m a.s.l., 08 Aug 1979, W. Stevens 13547 (DUKE, F, MEXU, MO). **Cartago:** carretera entre Turrialba y Siquirres, a la vera del río Chitaría, J. Gómez-Laurito 6801 (CR, USJ); cerros de La Carpintera, 1600 m a.s.l., 14 Oct 1973, R, Lent 3657 (CR, F, MO); 13 km E of Turrialba on hwy to Limón, canyon of Río Chitaría, R. 750–800 m a.s.l., 10 May 1983, Liesner et al. 15444 (CR, DUKE, MEXU, MO); above Turrialtica restaurant, 36.5 km from Turrialba, R. Read & G. Daniels 74–63 (US); vicinity of Pejivalle, P. Standley & J. Valerio 46759 (F, US); 9.5 mi E of Turrialba, on rocky banks of río Chitaría, 762 m a.s.l., 12 Aug 1977, G. Webster 22253 (DUKE, F, MEXU). **Guanacaste:** El Silencio, near Tilarán, P. Standley & J. Valeria 44745 (F, US). **Heredia:** Virgen del Socorro, río Sarapiquí, Cariblanco, 600–800 m a.s.l., 31 Aug 1983, I. Chacón & G. Herrera 1211 (CAS, CR, DUKE, MO); barranca del río Sarapiquí, Colonia Virgen del Socorro, J. Gómez-Laurito 9868 (CR, F); canyon of río Sarapiquí, just upstream from bridge on rd to La Virgen del Socorro, 05 Aug 1983, B. Hammel 13304 (CR, DUKE, F, MO); camino a la Colonia de la Virgen del Socorro, rumbo a Pto. Viejo, L. Poveda 985 (CR); Vara Blanca de Sarapiquí, N slope of Central Cordillera, 1500–1750 m a.s.l., Jul 1937, A. Skutch 3325 (K, MO, NY, US). **Limón:** La Florida, voie ferrée atlantique, H. Pittier 11286 (US); río Hondo, H. Pitiier 16641 (K). **Puntarenas:** Miramar, Quebrada seca, cerro Zapotal, 18 Sep 1985, L.D. Gómez et al. 23990 (CAS, CR, DUKE, MEXU, MO). **San José:** Terrazú, Pérez Zeledón. estribaciones del cerro Diamante, 500–600 m a.s.l., 22 Sep 1998, A. Estrada et al. 1730 (MEXU); zona protectora La Cangreja, Santa Rosa de Puriscal, Q. Jiménez 482 (CR, K); zona protectora cerro Turrubares, Q. Jiménez 543 (CR).

Spathacanthus magdalenae Castillo-Campos, Nordic J. Bot. 31: 449. 2013.

Figs 6, 7

Type. Mexico. Veracruz: San Andrés Tlalnelhuayocan (previously Coatepec as a publication error), Piedras Blancas, eastern slopes of the volcano Cofre de Perote, riparian vegetation, 1666 m a.s.l., 7 Mar 2012. G. Castillo-Campos et al. 27235 (holotype XAL!; isotypes ENCB!, MEXU!).

Description. Small trees or shrubs, up to 12 m height, highly branched, internodes glabrous. Stems quadrate to flattened when young, glabrous or pubescent at nodes with eglandular trichomes. Leaves with petioles 10–50 mm long, blade elliptic to obovate-elliptic, 110–280 mm × 42–129 mm, apically acute to acuminate, basally acute, margin undulate, tomentose when very young along veins, then glabrous on both surfaces.

Figure 6. *Spathacanthus magdalenae* Castillo-Campos. *G. Castillo-Campos 27235* (XAL), Mexico: Veracruz, San Andrés Tlalnelhuayocan.

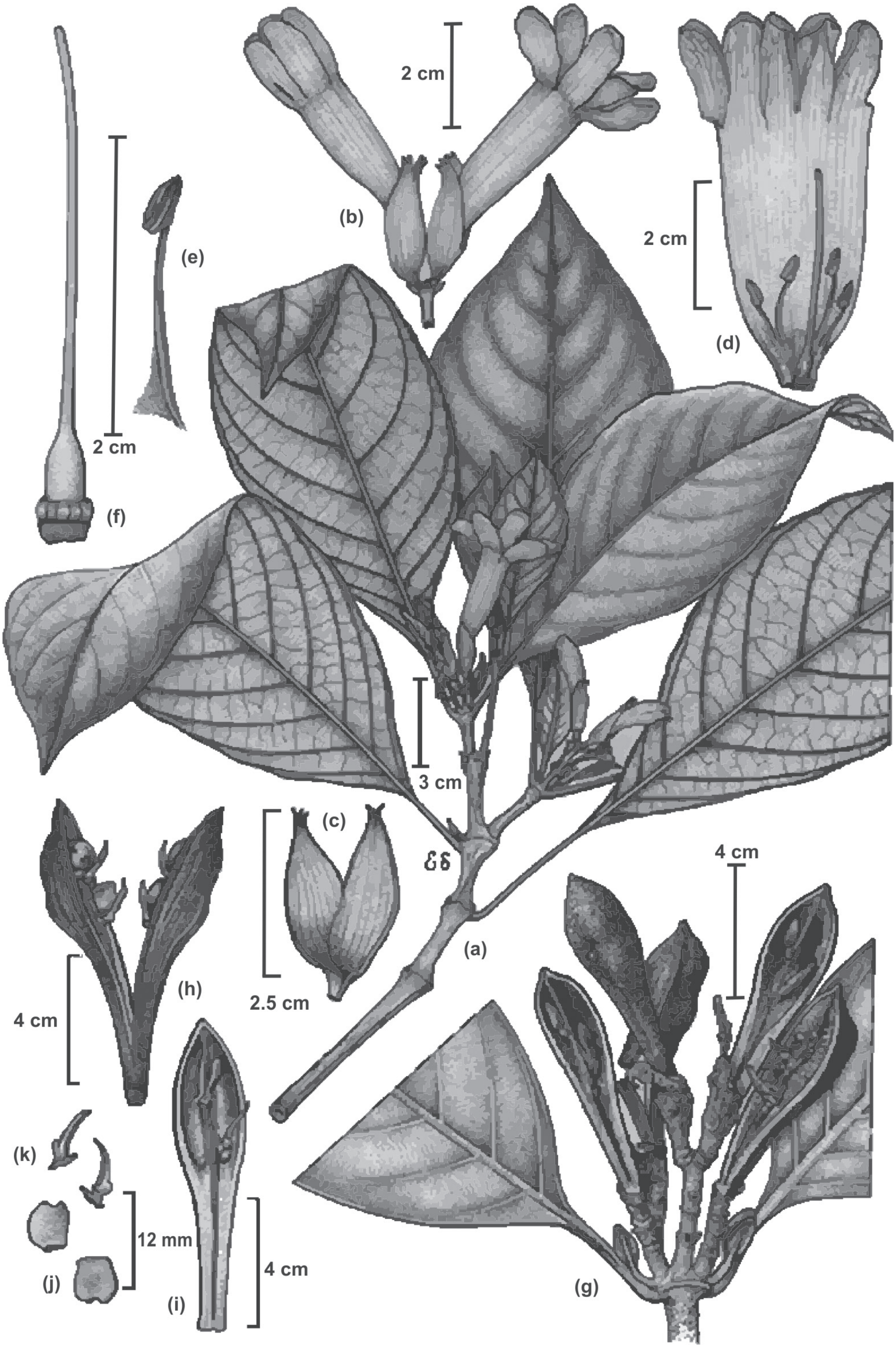


Figure 7. *Spathacanthus magdalenae* Castillo-Campos. Image and legend modified from Castillo-Campos et al. (2013), page 450. **a** Branch showing insertion of the leaves and position on the branch, inflorescences with flowers and buds **b** flowers, **c** calyx **d** open flower with stamens and style **e** stamen **f** style **g** branch with open capsules **h** open capsule with retinacula subtending seeds in both valves of fruit **i** interior of half of a capsule **j** seeds **k** retinacula removed from the capsules. Illustration: E. Saavedra.

Inflorescences terminal, rarely axillary, rachis glabrous; bracts triangular to subulate, 7 mm × 1 mm, abaxial surface tomentose; bracteoles triangular to subulate, 3.5 mm long, abaxial surface tomentose. Flowers subsessile to short pedicellate, pedicels to 6 mm long, glabrous; calyx yellowish before fruiting, turning green in ripe fruit, 18–25 mm × 13 mm, equally divided into 2 prominent elliptic to ovate segments; anterior segment bilobed, the posterior segment trilobed; lobes triangular, 15 mm long, apically acute to apiculate; corolla white, 58–100 mm long × 38–44 mm wide, externally glabrous and internally pubescent, throat 10–12 mm long × 3–6 mm in diameter near midpoint, upper lip bilobed, oblong, lower lip trilobed, both lobes 10–17 mm long, glabrous. Stamens whitish, longer pair about 16 mm long from the base to the apex of the thecae, shorter pair about 10 mm long; anthers monothecate, 3.5 mm long; style glabrous, 26 mm long, stigma lobes 0.3–0.7 mm long. Capsule 65–89 mm long; stipe 35–49 mm long, head 30–40 mm long. Seeds subcircular to subcordate, 8 mm × 9 mm long, surface roughened.

Distribution, habitat and phenology. *Spathacanthus magdalenae* is endemic to southern Mexico where it is restricted to the riparian vegetation of central Veracruz (Fig. 1B). It is frequent near rivers or humid canyons in cloud forests and oak forests in tropical to temperate zones, at 1300 to 1700 m a.s.l. Flowering takes place from November to March; mature fruits can be found from January to March.

Specimens examined. Mexico. Veracruz: Mpio. San Andrés Tlalnelhuayocan, Piedras Blancas, Eastern slope of the volcano Cofre de Perote, 1666 m a.s.l., 7 Mar 2012, G. Castillo-Campos et al. 27189 (XAL, MEXU, ENCB); Piedras Blancas, Eastern slope of the volcano Cofre de Perote, 1666 m a.s.l., 30 Apr 2012, G. Castillo-Campos et al. 27377 (XAL, MEXU, ENCB); San Antonio, 1350 m a.s.l., 06 Feb 1982, F. Ventura A. 19361 (ENCB, IEB, XAL); Mpio. Jacomulco, barranca de Actopan, road to Buena Vista, 1 km after Jalcomulco, 646 m a.s.l., 12 Jun 1991, G. Castillo-Campos et al. 8206 (XAL).

Spathacanthus parviflorus **Leonard, Proc. Biol. Soc. Washinton 50: 15–16. 1937.**
Figs 8, 9

Type. Guatemala. Quetzaltenango: in heavy forest of volcán Zunil, 1750 m a.s.l., 7 Aug 1934. A. Skutch 961 (holotype US!; isotypes A!, BM!, L!, NY!, US!).

Description. Small trees or shrubs, up to 8 m tall, branched, internodes glabrous or nearly glabrous. Stems subquadrate to somewhat compressed when young, nodes sparsely pubescent with rigid to flexible eglandular trichomes. Leaves petiolate, petioles 5–45 mm long, blade elliptic to obovate-elliptic, 20–155 mm × 11–100 mm, apically acute to acuminate, basally acute, marginally entire, both surfaces glabrous or with eglandular trichomes along main veins, these conspicuous on abaxial surface. Inflorescence terminal, rarely axillary, rachis glabrous to pubescent with eglandular trichomas; bracts triangular to subulate, 1.3–6 mm × 0.8–1.4 mm, abaxial surface glabrous or pubescent like rachis; bracteoles triangular to subulate, 1–4 mm × 0.6–1 mm, abaxial surface glabrous or pubescent like rachis. Flowers pedicellate, pedicels 1–13 mm long,

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ACANTHACEAE
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CALIFORNIA ACADEMY OF SCIENCES
Plants of Mexico

Spathacanthus parviflorus Leonard

Chiapas: El Triunfo Biosphere Reserve, vicinity of Deslave along trail from El Paval to Camp. El Triunfo, ca. 15°38'N, 92°50'W. Cloud forest with *Quercus*, *Cyathea*.
Shrub to tree to 4 m; calyx at anthesis lemon yellow, turning green in fruit; infrequent to locally frequent from 1940-2030 m.
Elevation 1940 m.

T.F. Daniel 8403 10-12 November 1996
w/M. González E., N. Ramírez-Marcial, & M. Martínez-Icó

Figure 8. *Spathacanthus parviflorus* Leonard. *T.F. Daniel 8403* (MEXU), Mexico: Chiapas, Reserva de la Biosfera El Triunfo.

glabrous; calyx yellowish before fruiting, turning green in ripe fruit, 20–30 mm × 6.5–11 mm, abaxially glabrous, unequally divided into 2 prominent lanceolate-ovate to ovate segments, 25 mm long on posterior side and 7–17 mm on anterior side; anterior segment bilobed, lobes triangular, 0.3–0.7 mm long; the posterior segment trilobed, triangular lobes, 0.6–0.8 mm long; corolla white, 25–30 mm long × 15–25 mm wide, externally glabrous and internally pubescent, throat 12–18 mm long × 2–6 mm in diameter near midpoint, upper lip 2–3 mm long, lobes rounded, 1.5–3 mm × 1.5–2 mm, lower lip 2.5–3.5 mm long, lobes rounded, 1.3 mm × 1.5–2.5 mm. Stamens whitish, longer pair 11–15 mm long from the base to the apex of the thecae, shorter pair 8–12 mm long; anthers dithecous, thecae 3–4.5 mm long; style glabrous 10–17 mm long; stigma lobes, 0.4–0.9 mm long. Capsule 37–60 mm long, stipe 20–35 mm long, head 17–25 mm long. Seeds subcircular to subcordate, 6–10 mm long, 6–8 mm wide, surface roughened.

Distribution, habitat and phenology. *Spathacanthus parviflorus* occurs in Mexico (Veracruz, Chiapas) and Guatemala (Chimaltenango, Quetzaltenango, San Marcos, Sololá and Suchitepéquez) (Fig. 1B), along streams and flooded areas, mainly in cloud forest, less frequently in other humid forests. It has been collected at 1000 to 2300 m a.s.l. Flowering takes place throughout the year, with ripe fruits from September to February.

Specimens examined. Mexico. Chiapas: Mpio. Mapastepec, El Triunfo Biosphere Reserve, along trail from El Paval to camp. El Triunfo, 1940–2030 m a.s.l., 10 Nov 1996, T. Daniel et al. 8403 (ENCB, K, MEXU, MO, NY, US); Mpio. Mapastepec, El Triunfo Reserve. Trail NNW from El Triunfo camp toward Palo Gordo Camp., 1–3 km from El Triunfo camp. El Triunfo Reserve, 2000 m a.s.l., 21 Feb 1990, R.J. Hampshire et al. 522 (MEXU); Reserva El Triunfo (campamento/HQ), near campamento El Triunfo, 2000 m a.s.l., Sep 1989, M. Heath & A. Long MA84 (CHIP, MEXU); Reserva El Triunfo, polígono 1, campamento /HQ - finca Prusia, 1900 m a.s.l., 11 Dec 1989, M. Heath & A. Long 491 (CHAPA, MEXU); between Cañada Honda and El Triunfo, slopes of sierra de Soconusco, 1300–2100 m a.s.l., 06 Nov 1945, E. Xolocotzi & A. Sharp 338 (DS, MEXU); Reserva de la Biosfera El Triunfo, polígono zona núcleo I, 1800 m a.s.l., 06 Aug 2005, N. Martínez 1149 (MEXU); Reserva El Triunfo, Palo Gordo-finca Catarrinas, M. Heath et al. 738 (CHIP); Mpio. La Concordia, camino entre finca Custepec and San Antonio Miramar (pass), M. Heath & A. Long 834 (CHIP); Reserva de la Biosfera El Triunfo, N. 1850 m a.s.l., 16 Jun 1994, Ramírez-Marcial & P. Quintana-Ascencio 507 (CAS, MEXU); Mpio. Undetermined, Mt. Pistar, 03 Aug 1937, E. Matuda 1696 (F, MO, NY, UT, US). **Veracruz:** Mpio. Uxpanapa, Arroyo Zarco, 15 km al S de La Laguna, 200 m a.s.l., 24 Nov 2012, G. Castillo-Campos & L. Aragón A. 27651 (XAL). **Guatemala. Chimaltenango:** SW slope of volcán Fuego above finca Montevideo, J. Steyermark 52100 (F, US). **Quezaltenango:** 1400–2250 m a.s.l., 14 Jun 2005, M. Pérez 563 (MO); Pacific escarpment, 3 km S of Santa María Planta eléctrica on Hwy 9S, K. Roe et al. 715 (BM, US); volcán Zunil, 1737 m a.s.l., 07 Aug 1934, A. Skutch 961 (F, IEB); along Quebrada San Gerónimo, finca Pirineos, lower S-facing slopes of volcán Sta. María, between Sta. María de Jesús and Calahuaché, J. Steyermark 33359 (F); lower S-facing slopes of volcán Santa María, between Santa María de Jesús and Calahuaché, J. Steyermark 33507 (F). **San Marcos:** La Trinidad, ca.

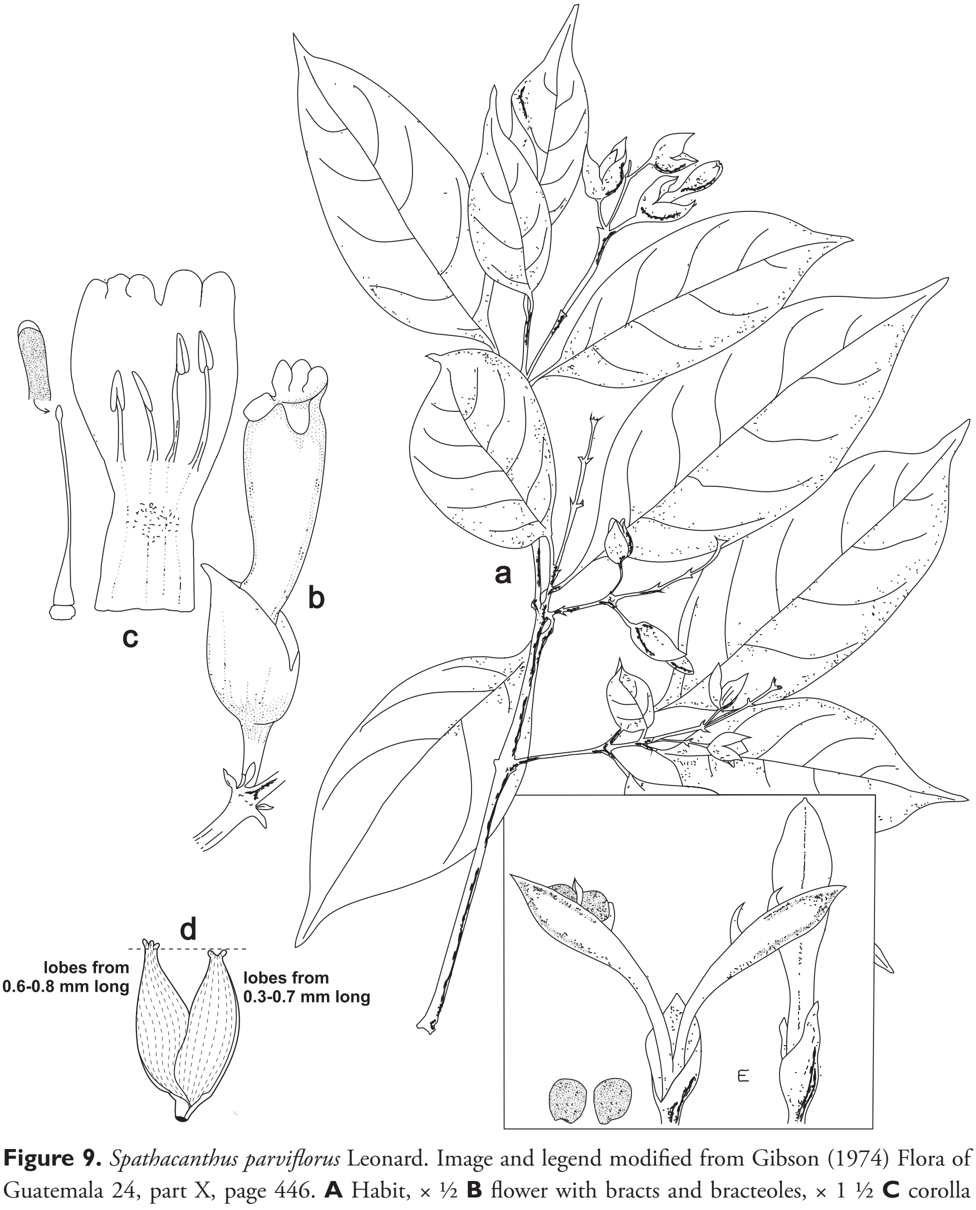

Figure 9. *Spathacanthus parviflorus* Leonard. Image and legend modified from Gibson (1974) Flora of Guatemala 24, part X, page 446. **A** Habit, × ½ **B** flower with bracts and bracteoles, × 1 ½ **C** corolla opened, with pistil removed, to show didynamous stamens, × 1 ½ **D** opened calyx, × 1 ½ **E** capsules with calyces, one opened to show retinacula and seeds, × 1.

2 km from finca Armenia above San Rafael, 1100–1250 m a.s.l., 12 Jul 1977, T.B. Croat 40846 (CAS, MEXU, MO); finca Armenia, San Rafael Pie de la Cuesta, 1524 m a.s.l., 06 Jul 1977, J.D. Dwyer 14412 (CAS, MO); finca Armenia, San Rafael Pie de la Cuesta to Carrizal, past finca África, 1300–1600 m a.s.l., 09 Aug 1980, J.D. Dwyer 15340 (MEXU, MO); volcán Tajumulco, above finca Porvenir on "Todos Santos Chiquitos", J. Steyermark 37204 (F). **Sololá:** sin localidad, 1000 m a.s.l., Aug 1993, M. Flores, 27

(MO); finca Mocá, Guatalón, S slope of volcán Atitlán, W. Hatch & C Wilson 342 (F). **Suchitepéquez:** Sta. Bárbara, finca Sta. Adelaida, K. Lind 69 (F); volcán Sta. Clara, between finca El Naranjo and upper slopes, J. Steyermark 46632 (CAS, F, NY, US).

Phylogenetic relationships

A total of 15 characters were analysed, 14 (93.3%) of which were parsimony-informative. The MP analysis resulted in five most parsimonious trees of 24 steps, a consistency index (CI) of 0.88 (excluding uninformative characters) and a retention index (RI) of 0.80. The majority rule consensus tree is shown in Fig. 10.

The monophyly of the genus *Spathacanthus* was strongly supported (BS and JK = 100%). Within the genus, two clades were recovered, the first one includes the species *S. hahnianus* and *S. hoffmannii* as more closely related, with moderate support (BS = 60% and JK = 50%) (Fig.10). In the second clade, two of the white flower species, *S. parviflorus*, and *S. magdalenae* were recovered as sister taxa, with support values of BS = 60% and JK = 52%.

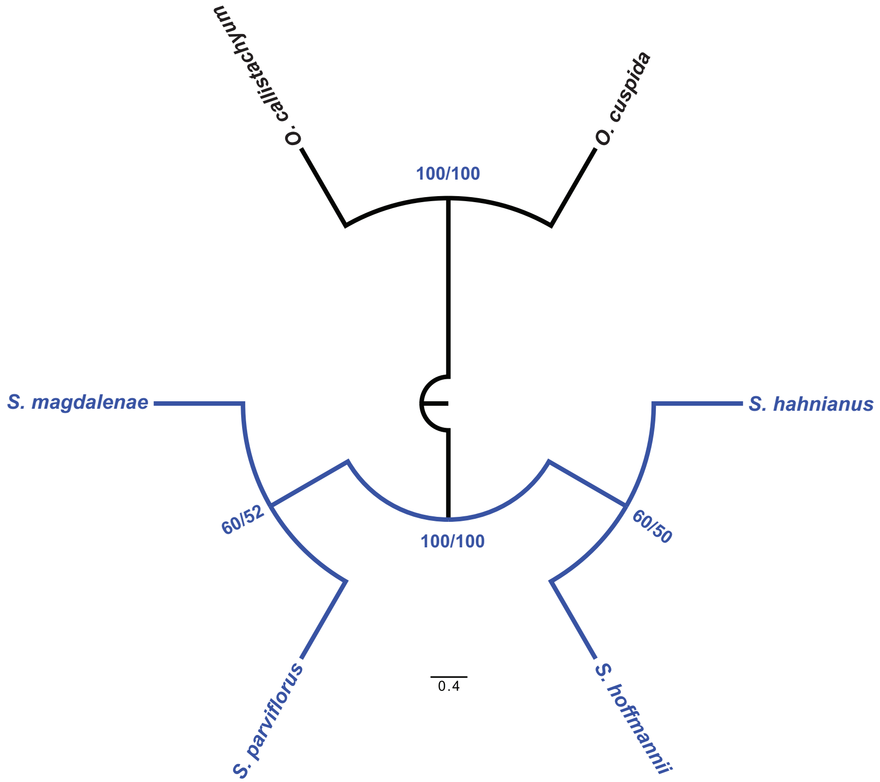

Figure 10. Majority-rule consensus tree inferred from parsimony analysis of 15 morphological characters for four species of *Spathacanthus* (tree length = 24 steps, CI = 0.88 and RI = 0.80). Bootstrap values (BS; left) and Jackknife values (JK; right) are shown above branches. Only support values above 50% are shown. Representatives of the genus *Odontonema* were used as out-group.

Discussion

Spathacanthus is composed of four recognised species, all of which are restricted to Mesoamerica. *Spathacanthus hahnianus* is the most widely distributed species, spanning from southern Mexico and Guatemala to Honduras. *Spathacanthus parviflorus* occurs only in southern Mexico and Guatemala; *S. magdalenae* and *S. hoffmannii* are geographically restricted, the first as micro-endemic to the centre of Veracruz, Mexico and the second as endemic to Costa Rica, where it is widely distributed throughout that country. Narrowly distributed species like *S. magdalenae* are of conservation concern as they may be threatened by the effects of environmental deterioration and habitat loss (Castillo-Campos et al. 2005; Mooers and Redding 2009). Despite this, none of these species has been formally assessed using the IUCN Red List standard. This highlights the need for more studies on each of the species in the group that allow us to know if it is necessary to take measures for conservation.

Plants of *Spathacanthus* occur mainly in tropical rainforests and cloud forests and at elevations between 100 and 2,300 m a.s.l. Of the four species, *S. hahnianus* and *S. hoffmannii* thrive in areas below 1,000 m a.s.l. Plants occur less commonly in higher elevation temperate forests. Particularly, *S. parviflorus* is restricted to cloud forests, *S. hoffmannii* inhabits humid tropical forests and *S. magdalenae* is usually found in cloud forests and oak forests. Meanwhile, *S. hahnianus* occurs in all of these environments. This information is relevant because, globally, montane cloud forests and tropical rainforests are threatened ecosystems. Particularly, the first is considered rare due to its restricted extent of coverage. A mere 2.5% of the total area of the tropical forests worldwide is cloud forest (Bruijnzeel et al. 2010; Sánchez-Ramos and Dirzo 2014). Three of the four species occur naturally in Mexico where tropical forests occupy only 1% of the territory; nevertheless, these ecosystems harbour a large number of species, representing 27% of the floristic richness of the country (Gual-Díaz and Rendón-Correa 2014). Worldwide, Central America is one of the regions most affected by deforestation. An important issue is that no collections of *Spathacanthus* have been made from Nicaragua or El Salvador. It is not clear whether these countries remain inadequately known botanically or whether plants of *Spathacanthus* are genuinely absent from these countries. Based on proximity and shared climate and vegetation types, further botanical exploration is warranted.

The detailed taxonomic review of the four species revealed a number of specimens that were misidentified. For example, Daniel (1999) noted that a white corolla had been reported for *S. hahnianus* by *Ventura A. 19361* (XAL, IEB). However, this specimen corresponds to *S. magdalenae* (revised and corrected in this study). Other records of plants with white corollas, such as *L.D. Gómez et al. 23990* (MEXU) and *A. Estrada et al. 1730* (MEXU) from Costa Rica, correspond to *S. hoffmannii*. Specimens of *S. hahnianus* (e.g. *C. Gutiérrez B. 3584* (IEB, MEXU, XAL); *J. Dorantes 3766* (XAL), *4058* (ENCB, IEB, XAL); *M. Vázquez T. 1584* (IEB, XAL); *J.I. Calzada 8935* (IBUG, MEXU, XAL); *F. Gónzalez-García s.n.* (XAL)) have been misidentified as *S. parviflorus*. As species are circumscribed here, intraspecific variation in corolla colour can be ruled out (see Daniel 1999 for discussion). This study demonstrates corolla colour is a key morphological character for differentiating species (see the identification key above). However, since the work by Daniel (1999), no taxonomic has been carried out on *Spathacanthus*, such that such errors were perpetuated. Consequently, we also find labels with scientific names that are no longer valid today. In addition, our study found that only *S. magdalenae* has monothecate anthers, an autapomorphy for the species. Therefore, this and other slight modifications were made in the description of the genus, since it was originally described as having dithecate anthers only. These results highlight the importance of taxonomic research as we report here.

Until recently, *S. hahnianus* was known only from Mexico and Honduras. Daniel (1999) reported a single specimen of *Spathacanthus* from Guatemala but the condition of the specimen did not allow it to be identified. A decade later, Daniel (2010) suggested that the species was either rare or extirpated in Guatemala. In 2012, in a report on new distribution records of Acanthaceae in Guatemala, the same author noted the presence of the species in the montane cloud forests of Quiché. Similarly, in Honduras, the species was only known from Yoro, but is here reported also from the provinces of Cortés and Lempira. Thus, this species is now known to range more widely in Guatemala and Honduras than had been previously recognised.

Phylogenetic analysis

The parsimony phylogenetic analysis retrieved *Spathacanthus* as a monophyletic group, which is consistent with the results of Daniel (1999). In his previous cladistic analysis, *S. hoffmannii* was more closely related to *S. hahnianus* because both species have long corollas and the lower lip ends in relatively long lobes. On the other hand, based on similarities and differences according to the morphological key proposed by Castillo-Campos et al. (2013), it is suggested that *S. magdalenae* was closest to *S. parviflorus*, although the former has longer flowers, fruits and seeds, as well as wider leaves, relative to *S. parviflorus*.

Our results are concordant with those suggested from both of these works. However, the basal position of *S. parviflorus*, resulting from Daniels's analysis, changes when *S. magdalenae* is included, supporting the hypothesis, proposed by Castillo-Campos et al. (2013), that *S. magdalenae* and *S. parviflorus* are closely related species; both share white corollas (as does their sister taxon, *S. hoffmannii*) and leaves petiolate. The plants of these species are mainly distributed in the cloud forest of the Pacific regions, only above 1000 m a.s.l. For their part, *S. hahnianus* and *S. hoffmannii* share long corollas and they are the most widely distributed species in terms of habitats and altitude. *Spathacanthus hahnianus* is the most widely distributed geographically, meanwhile, *S. magdalenae* and *S. hoffmannii* have a more limited distribution on the Mexican Pacific slopes and in Costa Rica, respectively. Although the results are concordant with previous studies, it should not be forgotten that the cladistic analysis, presented here, is only exploratory, so increased character sampling and the acquisition of molecular data integrated into a framework of total evidence will support a test of the phylogenetic hypothesis proposed herein.

Conclusions

Our analysis yielded a more in-depth insight into the distribution, characters and ecological features of plants of the Mesoamerican genus *Spathacanthus*; however, this genus remains poorly known in Mexico and Central America. Future research should specifically seek to collect plants of *Spathacanthus* species in suitable habitats across the Mesoamerican region. We expect that extensive fieldwork will reveal new areas of distribution and perhaps new species of *Spathacanthus*. Molecular data should be gathered to test the phylogenetic hypothesis presented here; notably, strategic sampling within species would shed light on the processes of speciation.

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Appendix 1

Morphological characters and character states used in this study.

Characters	Character states			
	0	1	2	3
Calyx color	Yellowish	Green	Purple	Reddish
Shape of divisions of the calyx	Homomorphic	Heteromorphic		
Pubescence in calyx	Glabrous	Pubescent		
Calyx length	1–9mm	13–40mm		
Type of calyx	Spathaceous	Pentamer		
Apex of calyx segments	Entire	Bifid	Trifid	
Corolla color	Yellow-yellowish	White	Pinkish-purple	Red
Corolla length	17–30mm	31–110mm		
Outer corolla surface	Glabrous	Pubescent		
Number of stamens	2	4		
Type of stamens	Homogeneous	Didynamous		
Style length	5–17mm	21–38mm	44–59mm	
Margin of leaves	Entire	Undulate		
Pedicel type	Pedicellate	Subsessile		
Capsule length	9–27mm	40–89		

Appendix 2

Matrix of morphological characters of *Spathacanthus* and out-groups used for the cladistic analysis.

Characters	*S. hahnianus*	*S. hoffmannii*	*S. parviflorus*	*S. magdalenae*	*O. callistachyum*	*O. cuspidatum*
Calyx color	1	1	0	0	2	3
Shape of divisions of the calyx	1	1	1	1	0	0
Pubescence in calyx	0	0	0	0	1	1
Calyx length	1	1	1	1	0	0
Number of segments in calyx	0	0	0	0	1	1
Apex of calyx segments	2	1	2	2	0	0
Corolla color	0	1	1	1	2	3
Corolla length	1	1	1	0	0	0
Outer corolla surface	1	1	1	1	0	0
Number of stamens	1	1	1	1	0	0
Type of stamens	1	1	1	1	0	0
Style length	1	2	0	1	0	0
Margin of leaves	0	1	0	1	0	0
Pedicel type	1	0	0	1	1	1
Capsule length	1	1	1	1	0	0

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Revision of *Fothergilla* (Hamamelidaceae), including resurrection of *F. parvifolia* and a new species, *F. milleri*

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Abstract

Fothergilla is a small genus of deciduous shrubs native to the southeastern United States that depending on circumscription comprises two to four species. Recent treatments recognized only two species in the genus: *F. gardenii* (tetraploid) and *F. major* (hexaploid). Until recently, no diploid taxon of *Fothergilla* was known. However, recent investigations identified a number of diploid populations in Alabama, Florida, Georgia, and South Carolina. A subsequent phylogenomic analysis showed that the diploids segregated into two, well-supported lineages, corresponding to largely allopatric populations. A re-examination of the morphology of diploid plants, in combination with the genetic evidence, has led us to the recognition of two species of diploids in the genus – a resurrected *F. parvifolia* and a new species (*F. milleri* W.D. Phillips & J.E. Haynes, **sp. nov.**) – bringing the total number of recognized species in *Fothergilla* to four. A revised taxonomic treatment of the genus is provided.

Keywords

Coastal Plain, Fothergilleae, Hamamelidoideae, southeastern United States

Introduction

Fothergilla L. (Hamamelidaceae, Hamamelidoideae, Fothergilleae) is a small genus of deciduous shrubs native to the southeastern United States that depending on circumscription comprises two to four species (Small 1903; Britton 1905; Small 1913; Harms

1930; Small 1933; Bailey 1949; Weaver 1969). The genus was erected based on *F. gardenii* L., the latter based on material sent to Linnaeus by Dr Alexander Garden of Charleston, South Carolina (lectotype: LINN.-693.1). Loddiges (1829) segregated *F. major* based on "having a spike of flowers, three inches or more in length; [...] later flowering, and [...] leaves [...] very broad, and much more toothed" (Weaver 1969). Subsequently, two more names were validly published at the rank of species: *F. monticola* Ashe (1897) and *F. parvifolia* Kearney in Small (1903), a segregate of *F. gardenii*.

Ashe (1897) published the name *Fothergilla monticola*, under the mistaken impression that *F. major* Lodd. represented a robust form of coastal *F. gardenii*, rather than applied to the primarily mountain populations of *Fothergilla*. This circumscription was followed by Hesse (1909), Rehder (1910), Bailey (1949), Harms (1930), Anderson and Sax (1935), and Ernst (1963), but not Small (1903, 1913, 1933) or Radford et al. (1968), who recognized only *F. major*. In revising the genus, Weaver (1969) recognized *F. monticola* as a synonym of *F. major*, a treatment that has been followed ever since (Meyer 1997; Weakley 2015).

Kearney (in Small 1903) segregated *Fothergilla parvifolia* from *F. gardenii* on the basis of leaf width (about as broad as long in *F. parvifolia* vs. longer than broad in *F. gardenii*), leaf base (cordate in *F. parvifolia* vs. cuneate to rounded in *F. gardenii*), and leaf margin (toothed from below the middle to the apex in *F. parvifolia* vs. toothed only near the apex in *F. gardenii*). This circumscription was followed by Britton (1905), Small (1913, 1933), and Harms (1930), though more recent authors apparently found these characters uninformative and treated *F. parvifolia* as a synonym of *F. gardenii* (Weaver 1969; Meyer 1997; Weakley 2015). In fact, recent treatments recognized only two species in the genus: *F. gardenii* (incl. *F. parvifolia*) and *F. major* (incl. *F. monticola*) (Weaver 1969; Meyer 1997; Weakley 2015).

As circumscribed by most recent authors, *Fothergilla gardenii* is found in wet savannas and pocosins in the coastal plains of North Carolina, South Carolina, Georgia, Florida, and Alabama, whereas *F. major* occurs primarily in woodlands, bluffs, and riverbanks of the upper Piedmont and mountains of North Carolina, South Carolina, Georgia, Alabama, Tennessee, and Arkansas (Weaver 1969; Meyer 1997; Weakley 2015). Recent authors generally distinguish *F. gardenii* from *F. major* by the smaller stature (3–10 dm vs. 10–80 dm in *F. major*), smaller leaves (<5.2 cm wide vs. > 5.2 cm wide in *F. major*), leaf dentations (tending towards the upper half of the leaf vs. extending below the middle in *F. major*), base symmetry (symmetric vs. asymmetric in *F. major*), hypanthium length (3–4.5 mm vs. 4–9.2 mm in *F. major*), number of stamens per flower (12–24 vs. 22–32 in *F. major*), and seed size (4.8–6.3 mm long vs. 6.2–7.8 mm long in *F. major*) (Radford et al. 1968; Weaver 1969; Weakley 2015). Weaver (1969) recognized *Fothergilla gardenii* as a tetraploid with $2n = 4x = 48$, and *F. major* as a hexaploid with $2n = 6x = 72$.

Although *F. major* and *F. gardenii* sensu Weaver (1969) have allopatric distributions, they have been grown together in cultivation, where they will freely hybridize. Ranney et al. (2007) concluded that the majority of cultivars represented in commerce was pentaploid with ($2n = 5x = 60$) and named the nothospecies *F.* ×*intermedia* Ranney & Fantz, a finding that cleared up previous controversy as to whether common cultivars (such as ‘Mount Airy’) represented *F. major* or *F. gardenii*. No pentaploids have been identified in nature.

Until recently, no diploid taxon of *Fothergilla* was known. However, recent sampling and cytometric analysis identified a number of diploid populations in Alabama, Florida, Georgia, and South Carolina (Ranney et al. 2012). This work was followed by phylogenomic analyses, examining the origins of *F. gardenii* and *F. major* and their relationship to the diploid populations (Qi et al. 2015). These analyses identified 11 haplotypes of plastid DNA, five of ETS, and 13 of combined plastid-ETS sequences. Of these, no haplotypes were shared between the diploid populations and polyploid taxa (i.e., *F. gardenii* and *F. major*). Furthermore, the diploid OTUs segregated into two, well-supported lineages, corresponding to largely allopatric populations. A re-examination of the morphology of diploid plants, in combination with the genetic evidence, has led us here to the recognition of two species of diploids in the genus: a resurrected *F. parvifolia* and a new species (*F. milleri*) as described below. A revised taxonomic treatment of the genus is provided.

Methods

Specimens studied in the course of preparing this revision included: (1) 34 accessions of *Fothergilla* from throughout the southeastern United States, planted and grown in a common garden at the Mountain Horticultural Crops Research and Extension Center in Mills River, North Carolina (Table 1), and (2) 207 specimens from the following herbaria: AUA, BRIT/VDB, DOV, F, FLAS, GEO, HTTU, KNK, LINN, MISS, MO, NCSC, NCU, NY, OS, US, and UWFP. The accessions from the Mountain Horticultural Crops Research and Extension Center are particularly important because ploidy level is known for all individuals (Table 1). The Phylogenetic Species Concept (PSC) sensu Nixon and Wheeler (1990), and its method of discovery–Population Aggregation Analysis–was applied to determine if taxa could be recognized. Thirteen binary and three multi-state morphological characters were assessed (Table 2). These included several novel characters not heretofore explicitly employed in study of the genus, such as the orientation of blades on living plants (e.g., spreading, erect, or drooping) and the ratio of: (1) the width, at the widest point, of the intervening leaf surface between the lowermost secondary vein and the leaf margin (IW), and (2) the length of the midvein interval between the junction of the midvein and lowermost secondary vein and the junction of the midvein and the next-most distal secondary vein on the same side of the leaf (IL; Fig. 1). To determine the IW:IL ratio for the Population Aggregation Analysis, respective measurements were taken from the largest measurable leaf of each of 34 accessions of known ploidy (Table 1). Subsequent to our post-analysis decisions regarding taxon recognition, we took additional IW and IL measurements from 96 loaned herbarium specimens (marked by ^{m} in the list of exsiccatae below). We also searched the SERNEC portal (http://sernecportal.org) to identify any additional specimens of the diploid taxa we recognized. This search resulted in six additional specimens, which we added to the list of exsiccatae in the taxonomic treat-

Table 1. Accessions grown at the Mountain Horticultural Crops Research and Extension Center and examined in the present study. F# and genome size as reported from Qi et al. (2015).

F#	Accession	Ploidy	Species sensu Weaver (1969)/Meyer (1997)	Species sensu present study	Native Location	Genomic Size (pg) +/- Standard Error
01	2011-083	2x	*F. gardenii*	*F. milleri*	Okaloosa Co., FL	1.70 +/- 0.03
02	2011-087	2x	*F. gardenii*	*F. milleri*	Baldwin Co., AL	1.78 +/- 0.02
03	2011-088	2x	*F. gardenii*	*F. milleri*	Walton Co., FL	1.74 +/- 0.00
04	2011-168	2x	*F. gardenii*	*F. parvifolia*	Tattnall Co., GA	1.74 +/- 0.05
05	2011-170	2x	*F. gardenii*	*F. parvifolia*	Emanuel Co., GA	1.75 +/- 0.10
06	2011-171	2x	*F. gardenii*	*F. parvifolia*	Long Co., GA	1.73 +/- 0.02
07	2011-178	2x	*F. gardenii*	*F. milleri*	Taylor Co., GA	1.74 +/- 0.02
08	2012-060	2x	*F. gardenii*	*F. milleri*	Walton Co., FL	1.76 +/- 0.01
09	2012-084	2x	*F. gardenii*	*F. parvifolia*	Aiken Co., SC*	1.82 +/- 0.04
11	2011-085	4x	*F. gardenii*	*F. gardenii*	Richmond Co., NC	3.69 +/- 0.02
12	2011-096	4x	*F. gardenii*	*F. gardenii*	Carteret Co., NC	3.64 +/- 0.08
13	2011-097	4x	*F. gardenii*	*F. gardenii*	Hoke Co., NC	3.57 +/- 0.00
14	2011-103	4x	*F. gardenii*	*F. gardenii*	Carteret Co., NC	3.69 +/- 0.00
15	2011-123	4x	*F. gardenii*	*F. gardenii*	Richmond Co., NC	3.68 +/- 0.04
16	2012-075	4x	*F. gardenii*	*F. gardenii*	Charleston Co., SC	3.40 +/- 0.01
17	2012-076	4x	*F. gardenii*	*F. gardenii*	Horry Co., SC	3.33 +/- 0.16
18	2012-077	4x	*F. gardenii*	*F. gardenii*	Charleston Co., SC	3.76 +/- 0.05
19	2012-078	4x	*F. gardenii*	*F. gardenii*	Effingham Co., GA	3.61 +/- 0.02
20	2008-009	6x	*F. major*	*F. major*	Dekalb Co., AL	5.27 +/- 0.02
21	2011-082	6x	*F. major*	*F. major*	Searcy Co., AR	5.22 +/- 0.12
22	2011-091	6x	*F. major*	*F. major*	Oconee Co., SC	5.40 +/- 0.04
23	2011-092	6x	*F. major*	*F. major*	Marshall Co., AL	5.23 +/- 0.11
24	2011-093	6x	*F. major*	*F. major*	Blount Co., AL	5.29 +/- 0.03
25	2011-105	6x	*F. major*	*F. major*	Burke Co., NC	5.09 +/- 0.05
26	2011-112	6x	*F. major*	*F. major*	Transylvania Co., NC	5.12 +/- 0.02
28	2011-122	6x	*F. major*	*F. major*	Montgomery Co., NC	5.27 +/- 0.06
29	2011-124	6x	*F. major*	*F. major*	Orange Co., NC	5.15 +/- 0.10
30	2011-131	6x	*F. major*	*F. major*	Transylvania Co., NC	5.13 +/- 0.05
31	2011-146	6x	*F. major*	*F. major*	Walker Co., GA	5.36 +/- 0.02
32	2011-147	6x	*F. major*	*F. major*	Marshall Co., AL	5.17 +/- 0.05
33	2011-163	6x	*F. major*	*F. major*	Rutherford Co., NC	5.27 +/- 0.01
34	2011-164	6x	*F. major*	*F. major*	Lumpkin Co., GA	5.31 +/- 0.01
35	2011-169	6x	*F. major*	*F. major*	Fulton Co., GA	5.17 +/- 0.17
36	2012-065	6x	*F. major*	*F. major*	Scott Co., TN	5.24 +/- 0.28

* Reportedly from Aiken County, SC, but the population could not be relocated in a recent survey.

ment below (only two of these represented a county not represented in our original loan of specimens). The combined sets of specimens of known ploidy (Table 1) and available to us from the herbaria identified above were the source of the morphological data we provide in our species descriptions.

Results and discussion

Population Aggregation Analysis revealed four distinct aggregate profiles, each corresponding to one of the major lineages identified by Qi et al. (2015) (Table 3; Fig. 2). In contrast to the tetraploids and hexaploids, which bear leaves mostly spreading (profiles

Table 2. Binary and multi-state morphological character states assessed in *Fothergilla*.

Character	Character State
1. Stem: Pubescence color	(0) White/Gray, (1) Brown
2. Leaf color	(0) Green, (1) Blue-green/Gray-green
3. Leaf orientation	(0) Spreading, neither drooping nor erect, (1) Erect, (2) Drooping
4. Leaf shape	(0) Obovate, (1) Ovate
5. IW:IL ratio	(0) < 0.5, (1) > 0.5
6. Leaf base	(0) Cordate, (1) V-cordate/V-rounded, (2) Rounded/truncate, (3) Cuneate
7. Leaf apex	(0) Acute, (1) Obtuse
8. Leaf dentation	(0) Top 1/3 of leaf only, (1) Begins at middle, (2) Begins below middle
9. Leaf dentation type	(0) Crenate, (1) Dentate/Serrate
10. Lamina: Adaxial waxy bloom	(0) Present (i.e., lamina glaucous), (1) Absent
11. Lamina surface: Pubescence color	(0) White/Gray, (1) Brown
12. Lamina midvein: Pubescence color	(0) White/Gray, (1) Brown
13. Floral bract color	(0) Tan/White/Pink, (1) Dark Brown
14. Constriction between filament and anther	(0) Present, (1) Absent
15. Style pubescence	(0) Present, (1) Absent
16. Seed apex shape	(0) Rounded/Obtuse, (1) Acute/Acuminate

3 and 4), diploids bear leaves either distinctly drooping (profile 1) or erect (profile 2) (Fig. 3). Diploids with drooping leaves (profile 1) also exhibit green, ovate laminas with marginal dentation beginning at the middle of the blade, as well as obtuse seed apices, in contrast to diploids bearing erect leaves (profile 2), which exhibit blue-green or gray-green, obovate laminas with marginal dentation beginning only at the top third of the blade and seed apices that are acute.

A re-examination of type material revealed that a name already exists for the drooping-leaved diploids representing profile 1: *F. parvifolia* Kearney (holotype: *Kearney s.n.*, NY-02514026; Fig. 4). This name was originally published in Small (1903), but lumped beneath *F. gardenii* by subsequent authors (Ernst 1963; Radford et al. 1968; Weaver 1969; Meyer 1997 and Weakley 2015). The mean IW:IL ratio for *F. parvifolia* accessions from the common garden at the Mountain Horticultural Crops Research and Extension Center (Table 1; known ploidy) is 0.86 (s.d. = 0.25, n = 4) and 0.96 (s.d. = 0.22, n = 7) when including additional herbarium specimens. There are no prior names applicable to plants referred to profile 2, which we here recognize as representing a new species, described as *F. milleri* below. The mean IW:IL ratio for *F. milleri* accessions from the common garden at the Mountain Horticultural Crops Research and Extension Center (Table 1; known ploidy) is 0.26 (s.d. = 0.13, n = 4) and 0.29 (s.d. = 0.10, n = 14) when including additional herbarium specimens.

Fothergilla gardenii is the appropriate name for the tetraploids representing profile 3. With the removal of the diploid components previously lumped under that name, our taxon concept of *F. gardenii* is necessarily narrower than that of recent authors such as Weaver (1969) and Meyer (1997). The mean IW:IL ratio for *F. gardenii* accessions from the common garden at the Mountain Horticultural Crops Research and Extension Center (Table 1; known ploidy) is 0.29 (s.d. = 0.09, n = 10) and 0.33 (s.d. = 0.09, n = 49) when including additional herbarium specimens.

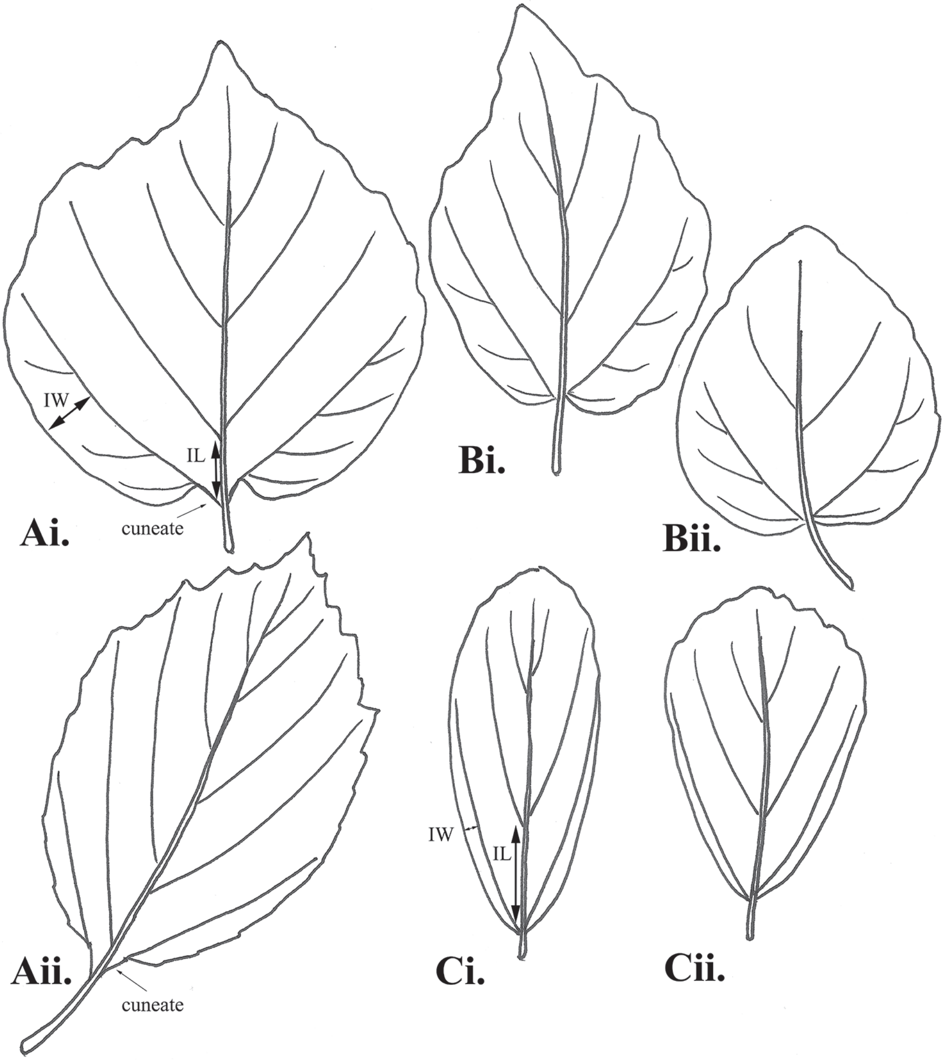
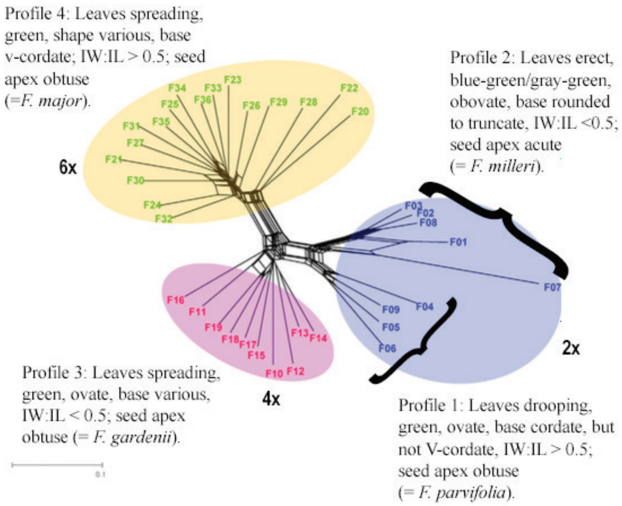


Figure 1. Leaf shape and base variation in *Fothergilla*: **Ai–Aii** *Fothergilla major* (V-cordate/V-rounded, i.e. with distinct cuneate portion at extreme blade base that broadens out laterally to cordate [Ai.] or rounded [Aii.]) **Bi–Bii** *Fothergilla parvifolia* (note the neatly cordate bases without well-defined cuneate portions at extreme blade base) **Ci–Cii** *Fothergilla milleri* (bases rounded). *Fothergilla gardenii* not shown as bases are variably rounded, cuneate, or cordate. IL = the length of the midvein interval between the junction of the midvein and lowermost secondary vein and the junction of the midvein and the next-most distal secondary vein on the same side of the leaf; IW = the width, at the widest point, of the intervening leaf surface between the lowermost secondary vein and the leaf margin. Illustrations by A. Krings based on *Lynch 29* (Ai.), *Lynch 21* (Aii.), *Phillips 56* (Bi.), *Lynch 18* (Bii.), *Lynch 68* (Ci.), and *Lynch 69* (Cii.).

Fothergilla major is the appropriate name for the hexaploids referred to profile 4. The average IW:IL ratio for *F. major* accessions from the common garden at the Mountain Horticultural Crops Research and Extension Center (Table 1; known ploidy) is

Table 3. Population Aggregation Analysis population profiles for *Fothergilla* and corresponding taxa. (–) = populations exhibited mixture of characters.

	Attributes							
	Seed apex	**Leaf color**	**Leaf orientation**	**Leaf shape**	**Leaf base**	**Leaf dentation**	**IW:IL ratio**	**Ploidy**
Aggregate profile 1 (*F. parvifolia*)	Obtuse	Green	Drooping	Ovate	Cordate (but not V-cordate)	Begins at middle	> 0.5	2x
Aggregate profile 2 (*F. milleri*)	Acute	Blue-green/ gray-green	Erect	Obovate	Rounded to truncate	Only top 3rd of leaf	< 0.5	2x
Aggregate profile 3 (*F. gardenii*)	Obtuse	Green	Spreading	Ovate	–	–	< 0.5	4x
Aggregate profile 4 (*F. major*)	–	Green	Spreading	–	V-cordate/V-rounded	Begins below middle	> 0.5	6x



Profile 4: Leaves spreading, green, shape various, base v-cordate; IW:IL > 0.5; seed apex obtuse (=*F. major*).

Profile 2: Leaves erect, blue-green/gray-green, obovate, base rounded to truncate, IW:IL <0.5; seed apex acute (= *F. milleri*).

Profile 3: Leaves spreading, green, ovate, base various, IW:IL < 0.5; seed apex obtuse (= *F. gardenii*).

Profile 1: Leaves drooping, green, ovate, base cordate, but not V-cordate, IW:IL > 0.5; seed apex obtuse (= *F. parvifolia*).

Figure 2. Phylogenetic network of *Fothergilla* cytotypes from Qi et al. (2015; generated by NeighborNet method using SplitTree 4 based on 165 SNP dataset), corresponding morphological population aggregation profiles, and associated names recognized herein (Table 3). For accession details, including localities, see Table 1.

0.99 (s.d. = 0.37, n = 16) and 0.96 (s.d. = 0.32, n = 60) when including additional herbarium specimens. Our taxon concept of *F. major* is consistent with that of Weaver (1969) and Meyer (1997). However, it should be noted that although the leaf bases of *F. major* have often been generally described as cordate or rounded (if sometimes asymmetrically so), the shape is actually a combination of a short cuneate section adjoining the petiole that broadens out laterally into the more general cordate or rounded shape. We here use the terms V-cordate and V-rounded to describe this type of base (the "V" representing the cuneate section) and consider it structurally distinct from the neatly cordate leaf bases of *F. parvifolia* (Fig. 1).

Based on these results, *Fothergilla* is here recognized as a genus of four species endemic to the southeastern United States: *F. gardenii* (4x), *F. major* (6x), *F. milleri* (2x), and *F. parvifolia* (2x). An updated taxonomic treatment follows.

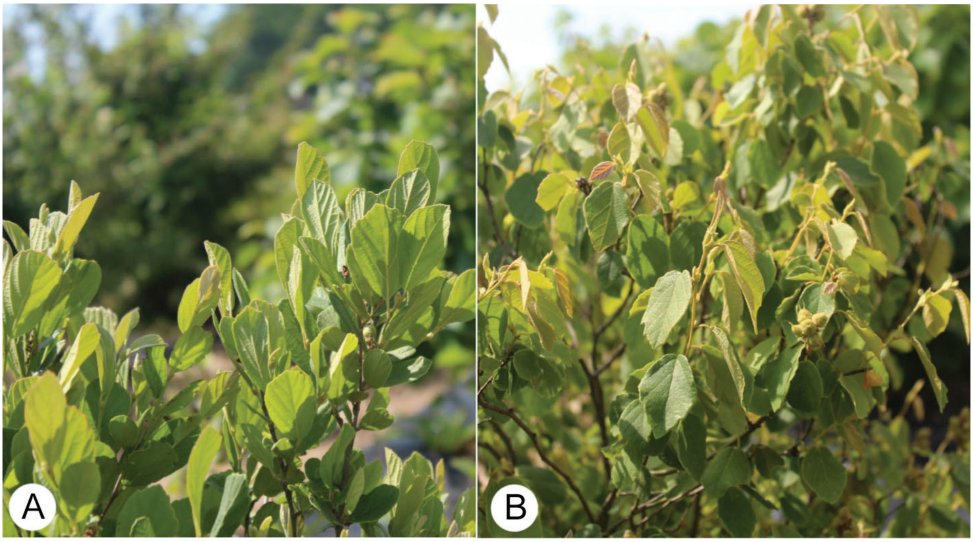


Figure 3. The two leaf orientations found in the diploid lineages of *Fothergilla* **A** erect leaves of *F. milleri* (aggregate profile 2) **B** drooping leaves of *F. parvifolia* (aggregate profile 1). Photos by J. Haynes of plants at the Mountain Horticultural Crops Research and Extension Center, Mills River.

Taxonomic treatment

Fothergilla L., Syst. Veg. ed. 13. 418. 1774

Type. *Fothergilla gardenii* L., Syst. Veg. ed. 13. 418. 1774 [as *F. Gardeni*] (***Lectotype***: LINN-693.1, LINN [online!], designated by Reveal in Jarvis et al. 1993).

Description. ***Shrubs***, rhizomatous, perennial, to 8 m tall; clump forming, usually multi-stemmed. ***Bark*** smooth, gray to reddish-brown. ***Stems*** stellate-pubescent when young, sparsely pubescent to glabrate when mature. ***Vegetative buds*** naked, densely stellate-pubescent. ***Leaves*** deciduous, simple, alternate, petiolate; stipules lanceolate to ovate; blades pinnately-veined, ovate, obovate, or oblong, bases oblique to symmetric, rounded, truncate, V-cordate or cordate, margins crenate to serrate from at or below middle to apex, or only near apex, apices acute to obtuse, surfaces sparsely to densely stellate-pubescent or glabrous, abaxially glaucous or not. ***Inflorescence*** terminal, spikes, erect, appearing with or before leaves. ***Flowers*:** mostly perfect, proximal often staminate; calyx lobes 5–7, connate, forming shallow hypanthium; apetalous; stamens 10–32, adnate to hypanthium, filaments white, anthers yellow, basifixed, 2-loculed; gynoecium, adnate to hypanthium, 2-carpellate, connate below, divergent near apex into separate styles, semi-inferior. ***Fruit*:** capsules, in groups of 3 or more, loculicidal, gray to brown, densely stellate-pubescent throughout with long, simple trichomes mixed in predominantly on and above persistent hypanthium; remnant style beaks conspicuous, abscising with maturity. ***Seeds*:** 2 per capsule, glossy, hard, nearly white, mottled, or solid red-brown to brown, ellipsoid to slightly ovoid, round to slightly flattened near apex in cross-section, apex round, obtuse, or acute to acuminate, when acuminate often recurved.

Figure 4. Holotype of *Fothergilla parvifolia* Kearney (*Kearney s.n.*, NY-02514026). Note the identifying characteristics of *F. parvifolia*: leaves drooping, bases neatly cordate, and margins with the crenation/serration from the midpoint to the apex.

Notes. *Fothergilla* seeds vary in color and shape, but the surface texture is consistent throughout. The seed surface is smooth and glossy with a conspicuous hilum scar at the base. In *F. major*, seeds are variable in color: completely white, mottled, or brown. In *F. gardenii*, seeds are mottled white-brown, with white conspicuously appearing around the margins of the seeds. In both diploid taxa, seeds are consistently red-brown to brown. In *F. gardenii* and *F. major*, it appears that color is affected by age and storage, as older herbaria specimens have nearly completely white seeds.

Key to the species of *Fothergilla*

1 Leaves spreading **2**

– Leaves erect or drooping **3**

2 Shrub usually <1 m tall; leaf blades narrowly ovate to ovate, to 5.3 cm wide, bases usually rounded to cuneate, sometimes shallowly cordate, IW:IL ratio < 0.5; petioles 3.9–10.5 mm long; Coastal Plain (Carolinas and e Georgia) .... **1. *F. gardenii***

– Shrub usually >1 m tall and often taller (to 8 m); leaf blades broadly ovate or elliptic to suborbiculate, to 13.0 cm wide, bases usually V-cordate or V-rounded, IW:IL ratio > 0.5; petioles 8.0–17.1(–18.9) mm long; mountains and Piedmont (rarely in Coastal Plain-like seep communities) .... **2. *F. major***

3 Leaves erect, blue-green or gray-green, blades obovate, bases rounded to truncate, margins crenate to serrate above middle, mainly near apex, IW:IL ratio < 0.5, petioles 1/3–1/2 the length of the IL; seed apex acute to acuminate, if acuminate often recurved; Alabama, nw Florida, and w Georgia .... **3. *F. milleri***

– Leaves drooping, mostly green, blades ovate, bases cordate, margins coarsely crenate to serrate mostly from the middle to the apex, IW:IL ratio > 0.5, petioles nearly as long to longer than the IL; seed apex obtuse; Georgia and South Carolina .... **4. *F. parvifolia***

Alternate key to the species of *Fothergilla*

1 IW:IL ratio < 0.5........ **2**

– IW:IL ratio > 0.5........ **3**

2 Leaves spreading, blades green, narrowly ovate to ovate, petioles usually ¾ the length of the IL or longer; seed apex rounded or obtuse; Carolinas and e Georgia .... **1. *F. gardenii***

– Leaves erect, blades blue-green or gray-green, obovate, petioles 1/3–1/2 the length of the IL; seed apex acute to acuminate, if acuminate often recurved; Alabama, nw Florida, and w Georgia........ **3. *F. milleri***

3 Leaves spreading, bases usually V-cordate or V-rounded; Piedmont and Mountains (rarely in Coastal Plain-like seep communities)........ **2. *F. major***

– Leaves drooping, bases cordate; Coastal Plain (Alabama, Georgia, South Carolina) .... **4. *F. parvifolia***

1. *Fothergilla gardenii* L. Syst. Veg. ed. 13. 418. 1774 [as *F. gardeni*]

Hamamelis virginiana L. var. *carolina* L., Mant. 2: 333. 1771. Type. Unknown.

Type. Habitat in Carolina, *Garden s.n.* (***Lectotype*****:** LINN-693.1, LINN [online!], designated by Reveal in Jarvis et al. 1993). Figs 5, 9.

Description. ***Shrub***, rhizomatous, usually <1m in height; clump forming, multi-stemmed, branching. ***Leaves*****:** stipules ovate to lanceolate, 1.8–4.6(–7.7) × 0.9–2.7(–4.3) mm; petioles 3.9–10.5 mm long, usually ¾ the length of the IL or longer, brown-yellow pubescent; blades mostly spreading, green, narrowly ovate to ovate, (1.8–)2.8–8.7 × (1.0–)2.5–5.3 cm, pinnately 8–11-veined, bases asymmetrical or symmetrical, usually rounded to cuneate, sometimes shallowly cordate, margins crenate to serrate above middle, teeth 3–10, apices acute to obtuse, both surfaces stellate-pubescent, rarely glabrous, abaxial surface sometimes glaucous, IW:IL < or = 0.49 ($\bar{x}$ = 0.33). ***Inflorescences*** appearing before leaves, spikes terminal, appearing lateral on short lower branches, sessile or on short peduncles. ***Flowers*****:** stamens 10–24, filaments 3.6–13.8 mm long. ***Capsules*** 6.6–9.0 × 5.5–6.6 mm. ***Seeds*** white to mottled brown or red-brown, ellipsoid to slightly ovoid, 5.1–5.8 × 2.5–3.5 mm, apices mostly obtuse. ***Genome size and ploidy*** 3.33–3.76 pg, tetraploid (2n = 4x = 48).

Phenology. Flowering beginning late Mar; fruiting by late Apr through Jul.

Distribution and habitat. This species can be found along the Atlantic coastal plains of North Carolina, South Carolina, and Georgia (Fig. 5). It occurs in pocosins, savannas, and ecotones. It can be found in both sandy and peaty soils from mesic to wet conditions. It has been found in association with *Acer rubrum* L., *Amelanchier obovalis* (Michx.) Ashe, *Aronia arbutifolia* (L.) Pers., *Clethra alnifolia* L., *Cyrilla racemiflora* L., *Gaylussacia dumosa* (Andrews) Torr. & A. Gray, *G. tomentosa* (A. Gray) Pursh ex Small, *Ilex coriacea* (Pursh) Chapm., *I. glabra* (L.) A. Gray, *I. vomitoria* Aiton, *Kalmia cuneata* Michx., *K. latifolia* L., *Liquidambar styraciflua* L., *Lyonia* Nutt. spp., *Magnolia virginiana* L., *Persea palustris* (Raf.) Sarg., *Pinus serotina* Michx., *Pteridium aquilinum* (L.) Kuhn, *Quercus laevis* Walter, *Q. virginiana* Mill., *Rhododendron viscosum* (L.) Torr., *Vaccinium crassifolium* Andrews, *V. myrsinites* Lam., and *Zenobia pulverulenta* (W. Bartram ex Willd.) Pollard (fide colectoris).

Notes. *Fothergilla gardenii* was apparently cultivated in England as early as 1765, grown at Kew Gardens by 1789, and English and French plant nurseries were offering seeds for sale by the early 1800s (Weaver 1971).

The species appears well adapted to periodic fires and is shade intolerant. Populations found in recently burned sites appear more abundant and robust, while populations in sites that have not been burned are generally outcompeted by other plants.

Fothergilla gardenii s.l. is known to attract pollinators such as honey bees and bumblebees (Dumroese and Luna 2016). The authors have also observed numerous Lepidoptera visiting the sweetly-fragranced blooms. Other members of the Hamamelidaceae, such as *Hamamelis* and *Liquidambar*, also attract those pollinators, in addition to hover flies (Syrphidae) (Dumroese and Luna 2016).

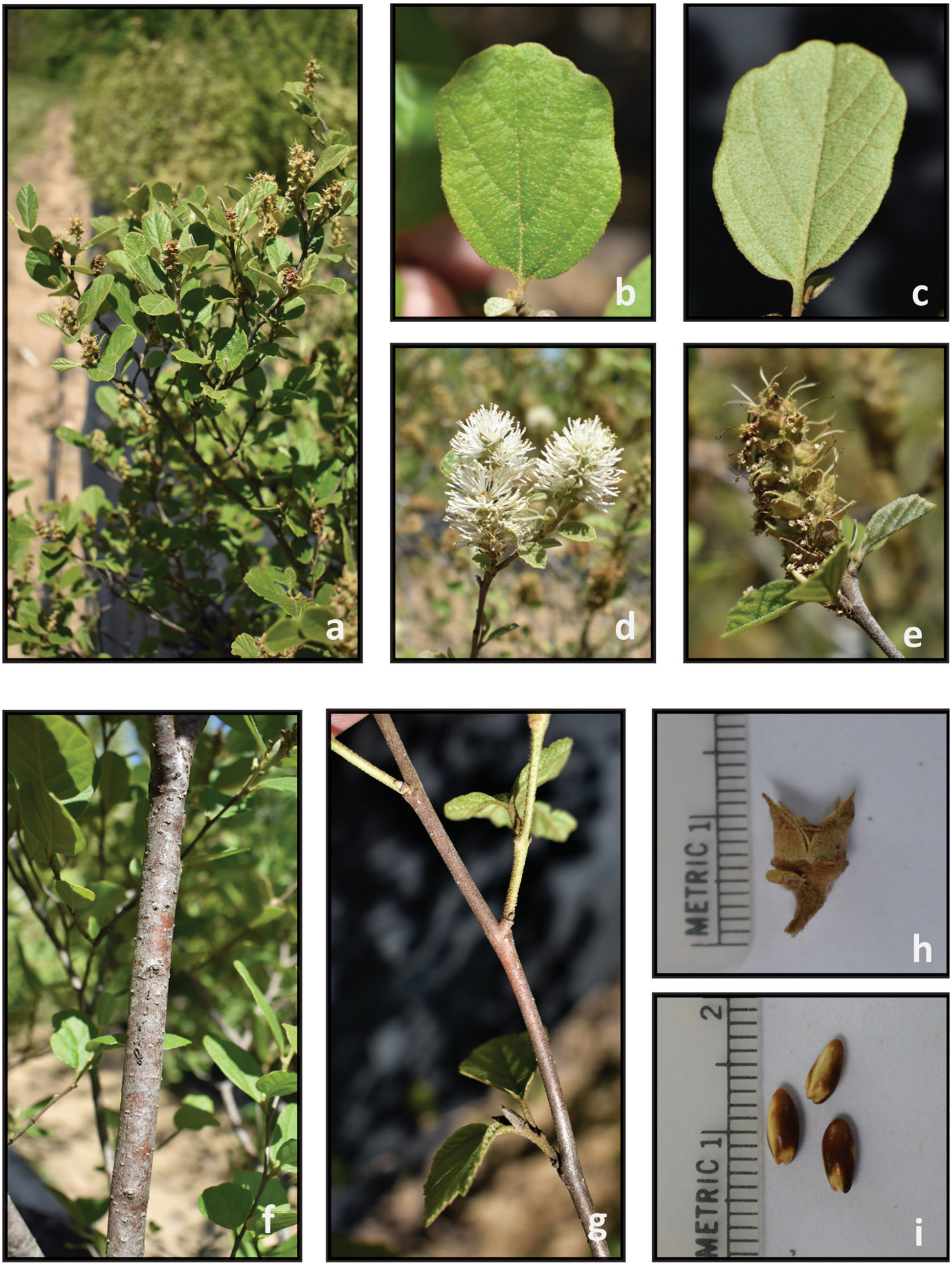


Figure 5. *Fothergilla gardenii* **a** plant form and leaf orientation **b** adaxial leaf surface **c** abaxial leaf surface **d** inflorescence **e** young infructescence **f** stem **g** twig **h** capsule, and **i** seeds. Photos by J. Haynes of plants at the Mountain Horticultural Crops Research and Extension Center, Mills River.

Conservation. *Fothergilla gardenii* s.l. is considered Vulnerable, currently ranked by NatureServe as follows: G3G4; Alabama (S1), Florida (S1), Georgia (S2), Mississippi (SNR), North Carolina (S3S4), South Carolina (SNR) (http://explorer.natureserve.org/, accessed 11 Dec 2019). In light of the removal of the diploid taxa *F. milleri* and *F. parvifolia* from the broader historical concept of *F. gardenii*, the conservation status of this species, as well as that of the diploid taxa, warrants re-evaluation; such re-evaluation is likely to result in a more imperiled ranking than the G3G4 current assessment, following removal of a significant number of populations and a narrower distribution following its narrower taxonomic circumscription. Due to its sensitive status, we provide only skeletal collections data below.

Additional specimens seen [(V) = vegetative only, (FL) = in flower, (FR) = in fruit].

Georgia. Effingham: 2012-078, 15 Apr 2014 (FL), *Lynch 43* (NCSC); 2012-078, 13 Jun 2014 (V), *Phillips 49* (NCSC^{m}); 12 Jul 1997 (V), *Sorrie 9349* (NCU^{m}). McDuffie: Jun 1911 (V), *Bartlett 2636* (NCU, VDB^{m}).

North Carolina. Beaufort: 27 Mar 1949 (FL), *Coker s.n.* (NCU); 14 May 1966 (FL), *Blair 415* (NCSC); 21 Jun 1965 (FR), *Sawyer 2475* (NCU^{m}); 5 Nov 1956 (V), *Ahles & Leisner 21471* (NCU^{m}); 20 Apr 1957 (FL), *Ahles & Ramseur 23593* (NCU^{m}); 31 May 2003 (FR), *Horn 4437* (BRIT^{m}); 25 Jan 1937 (FL), *Melvin 3613* (BRIT^{m}); 7 Jul 1994 (V), *Nifong 400* (NCU^{m}). Brunswick: 8 Jun 1951 (FR), *Boyce & Wells 1656* (NCSC); 13 May 1950 (FL), *Godfrey & Wiebe 50341* (BRIT^{m}, NCSC, NCU); 18 Apr 1999 (FL), *Hill 31327* (BRIT); 6 Mar 1974 (V), *Kologiski 54* (NCSC^{m}); 7 May 1974 (FL), *Kologiski 125* (NCSC); 23 Jul 1974 (V), *Kologiski 311* (NCSC); 6 Jun 1975 (FR), *Kologiski 423* (NCSC); 27 Apr 1976 (FL), *Kologiski 551* (NCSC); 18 Apr 1965 (FL), *Mullen s.n.* (NCSC). Carteret: 2011-096, 26 Mar 2012 (FL), *Lynch 9* (NCSC); 2011-096, 2 Jul 2012 (V), *Lynch 76* (NCSC^{m}); 2011-096, 13 Jun 2014 (FR), *Phillips 50* (NCSC); 2011-103, 21 Mar 2012 (FL), *Lynch 3* (NCSC); 2011-103, 2 Jul 2012 (V), *Lynch 75* (NCSC^{m}); 22 May 1976 (V), *Wilson 1792* (NCU^{m}); 9 Apr 1977 (FL), *Wilson 3067* (NCU). Columbus: 25 Apr 1958 (FL), *Bell 11417* (NCU). Craven: 19 Apr 1958 (Fl), *Radford 31924* (NCU). Cumberland: 11 Oct 1957 (V), *Ahles 36621* (NCU^{m}); 28 Apr 1933 (FL), *Tallin & Harbison s.n.* (NCU). Duplin: 27 Apr 1957 (V), *Ahles & Ramseur 23990* (VDB^{m}); 27 Apr 1957 (FR), *Radford & Ramseur 23990* (NCU^{m}). Harnett: 10 Apr 1957 (FL), *Laing 843* (NCU); 30 Jun 2005 (FR), *Sorrie 11634* (NCU^{m}). Hoke: 2011-097, 21 Mar 2012 (FL), *Lynch 4* (NCSC); 2011-097, 2 Jul 2012, (V), *Lynch 72* (NCSC^{m}); 2011-097, 13 Jun 2014 (FR), *Phillips 71* (NCSC); 16 May 1976 (V), *Kral 58099* (VDB ^{m}); 26 Jun 1975 (FR), *Ahles & Haesloop 29627* (NCU^{m}). Lee: 19 Apr 1958 (FL), *Stewart 149* (NCU); 7 Jun 1958 (FR), *Stewart 451* (NCU^{m}). Montgomery: 9 Oct 1956 (V), *Radford 19633* (NCU^{m}). Moore: 17 Jul 1942 (FR), *Wicker s.n.* (NCU^{m}); 8 Apr 1973 (FL), *Carter 449* (NCU); 24 Apr 1949 (FL), *Woods 2256* (NCSC). New Hanover: 6 Jun 1929 (FR), *Wells s.n.* (NCSC^{m}); 29 Jun 1963 (V), *McCrary 607* (NCU ^{m}); 30 Mar 1991 (FL), *Pyne & Seneca 91-013* (NCSC). Onslow: 11 May 1948 (FR), *Boyce & Moreland 647* (NCSC); 28 Apr 1951 (FL), *Beaman s.n.* (NCSC); 2 June 1948 (FR), *Boyce & Moreland 700* (NCSC^{m}); 24 Jun 1965 (FR), *Wilbur 8398* (BRIT^{m}). Pamlico: 12 Oct 1957 (V), *Radford 42285* (NCU^{m}). Pender: 17 May 1925 (FR), *A.C.W. s.n.* (NCSC); 1 Jun 1945 (V), *Wells s.n.* (NCSC); 19 Apr 1957 (FL), *Ahles & Ramseur 23440* (NCU); 25 Apr 1947 (FL), *Fox & Wells 162* (NCSC); 12 May 1951 (FR), *Fox 4621* (NCSC);

26 Aug 1983 (V), *Leonard 8199* (UWFP^{m}); 14 Apr 1925 (FL), *Wells s.n.* (NCSC). Richmond: 2011-123, 11 Apr 2012 (FL), *Lynch 13* (NCSC); 2011-123, 21 Aug 2012 (V), *Lynch 74* (NCSC^{m}); 2011-085, 21 Mar 2012 (FL), *Lynch 5* (NCSC); 2011-085, 2 Jul 2012 (V), *Lynch 73* (NCSC); 2011-085, 13 Jun 2014 (V), *Phillips 55* (NCSC^{m}); 19 May 2007 (FL), *Boyle 1* (NCU). Robeson: 18 Apr 1956 (FL), *Terrell 3019* (NCU). Sampson: 10 Apr 1938 (FL), *Godfrey 3394* (NCSC). Scotland: 20 Apr 1999 (FL), *Hill 31345* (BRIT^{m}); 20 Jun 1957 (FR), *Ahles & Haesloop 28637* (NCU); 20 Jun 1957 (FR), *Ahles & Haesloop 28601* (NCU^{m}); 4 Jun 2004 (FR), *Sorrie 11264* (NCU^{m}).

South Carolina. Berkeley: 9 Apr 1944 (FR), *Duncan 5923* (NCSC). Charleston: 2012-075, 15 Apr 2014 (FL), *Lynch 42* (NCSC); 2012-075, 13 Jun 2014 (FR, V), *Phillips 48* (NCSC ^{m}); 2012-77, 15 Apr 2014 (FL), *Lynch 37* (NCSC); 2012-077, 21 Aug 2012 (V), *Lynch 30* (NCSC^{m}); 2012-77, 13 Jun 2014 (FR), *Phillips 53* (NCSC); 2 Apr 1944 (FL), *Duncan 5885* (NCSC). Chesterfield: 25 Apr 1968 (FR), *Ewel 666* (NCSC); 5 Jun 1956 (V), *Radford 12431* (NCU^{m}); 5 Apr 1968 (FL), *Leonard & Radford 1219* (NCU). Clarendon: 20 Apr 1957 (FL), *Radford 21097* (NCU). Colleton: 5 Apr 1956 (FL), *Bell 1862* (NCU); 17 Apr 1974 (FL), *Hardin 13420* (NCSC, VDB^{m}). Darlington: 25 Mar 1935 (Fl), *Matthews s.n.* (NCU); 26 Mar 1935 (FL), *Matthews & Smith s.n.* (NCU); 10 Apr 1940 (FL), *Smith 1378* (NCU). Dillon: 7 Apr 1940 (FL), *Radford & Stewart 56* (NCU). Dorchester: 20 Jul 1957 (V), *Ahles & Leisner 31966* (NCU^{m}). Georgetown: 18 Apr 1987 (FL), *Taggart 78* (NCU); Near Georgetown, 28 Jul 1928 (FR), *Ashe s.n.* (NCU^{m}). Horry: 2012-076, 15 Apr 2014 (FL), *Lynch 41* (NCSC); 2012-076, 13 Jun 2014 (FR, V), *Phillips 51* (NCSC ^{m}). Lee: 26 Jul 1957 (V), *Radford 27396* (NCU^{m}). Marlboro: 4 May 1968 (FL), *Leonard & Radford 1218* (NCU).

2. *Fothergilla major* Lodd., Bot. Cab. 16: Pl. 1520. 1829

F. monticola Ashe, Bot. Gaz. 24: 374. 1897. Type. North Carolina, mountains, *W.W. Ashe 1509* (***Lectotype*:** MO-247915 [online!], designated here; ***isolectotypes*:** DOV [online!]; OS [online!], US [online!])

Type. *C. Loddiges* Illustration Pl. 1520. Figs 6, 9.

Description. ***Shrub***, erect, robust, frequently >1 m tall (to 8 m); stems in clumps of 3 or more, branching. ***Leaves*:** stipules ovate to lanceolate, 3.5–11.8 × 1.9–4.0 mm; petioles 8.3–17.1(–18.9) mm, ½ as long or longer than the IL, brown-yellow pubescent; blades mostly spreading, green, broadly ovate or elliptic to suborbiculate, rarely obovate, 3.6–13.7 × 3.2–13.0 cm, most within the upper end of those ranges, pinnately 7–12-veined, bases oblique, occasionally symmetrical, usually V-cordate, rarely nearly rounded, margins crenate or serrate to nearly entire, toothed from at or below middle to the apex, teeth 11–24, apices acute to obtuse, often pubescent, both surfaces glabrous to sparsely stellate-pubescent, abaxial surface sometimes glaucous, IW:IL >

or = 0.51 ($\bar{x}$ = 0.96). ***Inflorescences*** usually appearing with leaves, spikes sessile or on short peduncles. ***Flowers*:** stamens 14–32, filaments 7.3–16.2 mm long. ***Capsules*** 6.8–12.7 × 6.5–8.6 mm. ***Seeds*** nearly white to completely brown or red-brown, usually ellipsoid, 5.3–7.4 × 2.7–3.6 mm, apices rounded to obtuse. ***Genome size and ploidy*** 5.21–5.25 pg, hexaploid ($2n = 6x = 72$).

Phenology. Flowering beginning late Mar; fruiting late May through mid-Jul.

Distribution and habitat. This species can be found in the mountains and Piedmont of Alabama, Arkansas, Georgia, North Carolina, South Carolina, and Tennessee (Fig. 5). Habitat in which this species is found is variable, from rocky/xeric to peaty/mesic, but generally upland deciduous forest (typically oak-dominated) with mountain and Piedmont-associated species. However, in the Uwharrie National Forest, Montgomery County, North Carolina, *F. major* can be found growing in seepage community with Coastal Plain-affinity species. In this habitat, where burning is frequent, this species may be <1 m in height. However, height variance is apparently not simply a factor of fire frequency. *Fothergilla major* varies considerably in habit, ranging from colonial shrubs less than 2 m tall, typically found growing on sandy dampish sites in the southwestern part of the range and lower elevations (for example populations from Marshall Co., Alabama and Blount Co., Alabama) to larger tree forms growing to 6 m, with offsets but no rhizomes, typically found in more upland mountain dry forest sites with igneous geology found to the North and East (for example populations in Scott Co., Tennessee). Commonly associated upland species include *Acer rubrum*, *Aesculus sylvatica* W. Bartram, *Alnus serrulata*, *Aronia arbutifolia* (Aiton) Willd., *Calycanthus floridus* L., *Carpinus caroliniana* Walter, *Cornus florida* L., *Gaylussacia frondosa* (L.) Torr. & A. Gray, *Hamamalis virginiana* L., *Hepatica americana* (DC.) Ker Gawl, *Hypericum nudiflorum* Michx. ex Willd., *Ilex opaca* Aiton, *Kalmia latifolia*, *Liquidambar styraciflua*, *Liriodendron tulipifera* L., *Magnolia acuminata* (L.) L., *Polystichum acrostichoides* (Michx.) Schott, *Quercus alba* L., *Q. rubra* L., *Rhododendron catawbiense* Michx., and *Stewartia ovata* (Cav.) Weath. (fide colectoris).

Conservation. *Fothergilla major* is considered Vulnerable rangewide, ranked by NatureServe as follows: G3; Alabama (S2), Arkansas (S1), Georgia (S1), North Carolina (S3), South Carolina (S2), Tennessee (S2); http://explorer.natureserve.org/, accessed 11 Dec 2019). Due to its sensitive status, we provide only skeletal collections data below.

Additional specimens seen [(V) = vegetative only, (FL) = in flower, (FR) = in fruit].

Alabama. Blount: 2011-093, 2 Jul 2012 (V), *Lynch 91* (NCSC^{m}). Cherokee: 12 Apr 1969 (FL), *Kral 34269* (NCU, VDB); 10 May 1970 (FL), *Kral 39052* (BRIT^{m}); 14 Jul 1966 (FR), *Clark & Landers 5122* (BRIT^{m}, NCSC). Cullman: 17 Apr 1931 (FL), *Ashe s.n.* (NCU); 16 Apr 1924 (FR), *Wolf s.n.* (AUA^{m}); 4 Jul 1911 (FR), *Wolf 813* (AUA^{m}); 28 May 1931 (V), *Wolf s.n.* (VDB). DeKalb: 2008-009, 21 Mar 2012 (FL), *Lynch 7* (NCSC); 2008-009, 2 Jul 2012 (V), *Lynch 81* (NCSC^{m}); 14 Jul 1966 (FR), *Clark & Landers 5023* (BRIT ^{m}, NCU); 22 May 1972 (FL), *Whetstone 1935* (NCU^{m}). Marshall: 2011-092, s.d. (FL), *Lynch 79* (NCSC); 2011-092, 2 Jul 2012 (V), *Lynch 17* (NCSC^{m}); 2011-147, 21 Aug 2012 (V), *Lynch 24* (NCSC^{m}); 15 Apr 1973 (FL), *Kral 49636* (AUA, VDB ^{m}). St. Clair: 31 May 1947 (FL,FR), *McVaugh 8594* (BRIT ^{m}): Unspecified: n.d. (FL), *Buckley s.n.* (FLAS).

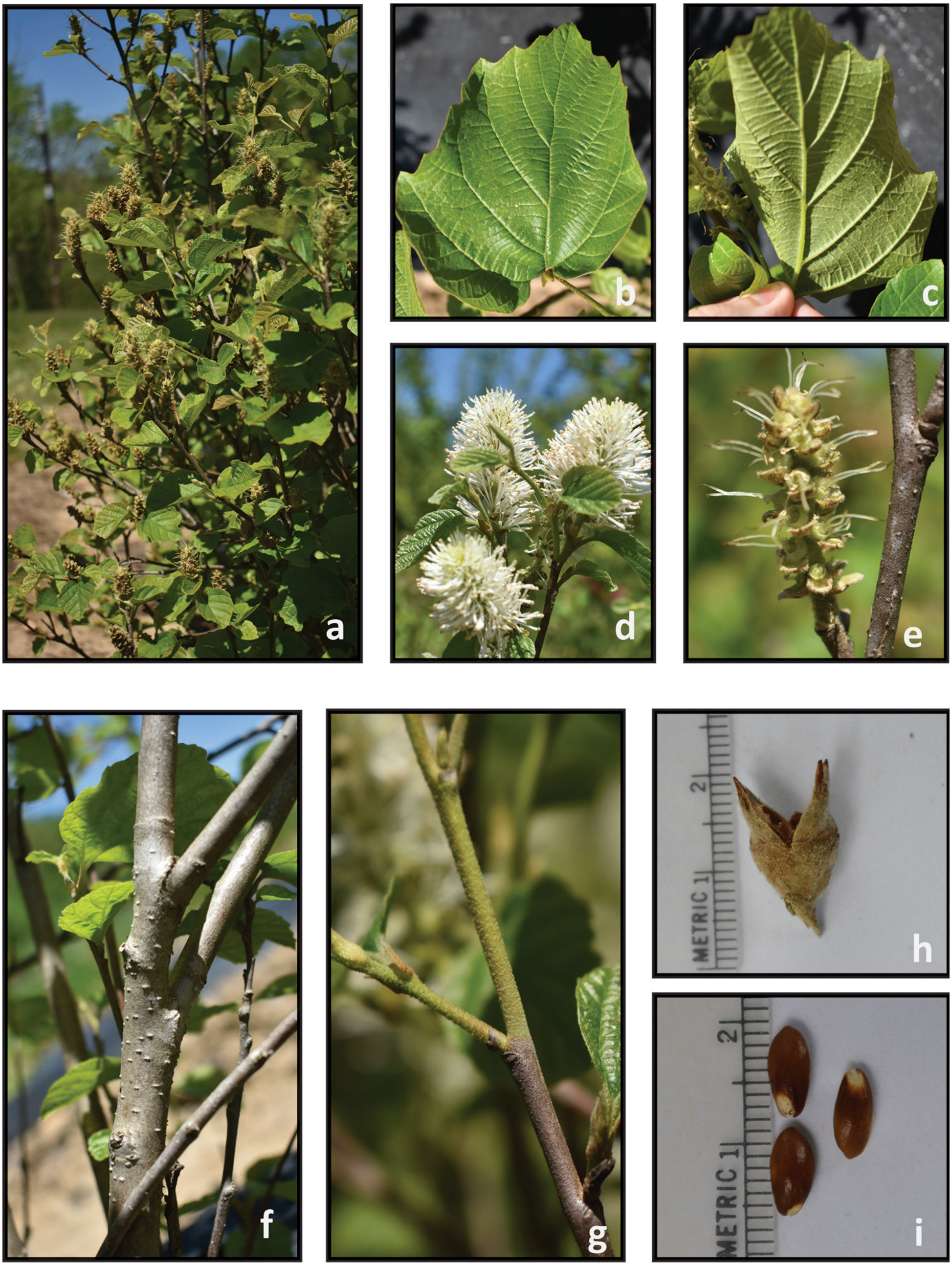


Figure 6. *Fothergilla major* **a** plant form and leaf orientation **b** adaxial leaf surface **c** abaxial leaf surface **d** inflorescence **e** young infructescence **f** stem **g** twig **h** capsule, and **i** seeds. Photos by J. Haynes of plants at the Mountain Horticultural Crops Research and Extension Center, Mills River.

Arkansas. Searcy: 2011-082, 26 Mar 2012 (FL), *Lynch 10* (NCSC); 2011-082, 2 Jul 2012 (FR), *Lynch 80* (NCSC^{m}).

Georgia. Bartow: 30 Mar 1951 (FL), *Duncan & McDowell 12200* (NCU); 30 Mar 1951 (FL), *Duncan & McDowell 12200* (BRIT, FLAS, NCSC); 6 May 1951 (FL), *Duncan & Venard 12339* (BRIT ^{m}). Fulton: 2011-169, 21 Aug 2012 (V), *Lynch 28* (NCSC). Lumpkin: 2011-164, 21 Aug 2012 (V), *Lynch 27* (NCSC^m). Walker: 2011-146, 21 Aug 2012 (V), *Lynch 25* (NCSC); 15 Apr 1986 (FL), *Coile 4547* (NCSC).

Illinois. DuPage: Cultivated at Morton Arboretum, 9 May 1990 (FL), *Gavalak 3306V90* (BRIT ^{m}).

Massachusetts. Suffolk: Cultivated at Arnold Arboretum, Harvard University, 13 May 1968 (FL), *Dewolf & Bruns 2235* (BRIT).

Michigan. Ingham: Cultivated at Michigan State University, 9 May 1979 (FL), *Gillis 15041* (BRIT ^{m}).

North Carolina. Burke: 2011-105, 2 Jul 2012 (V), *Lynch 81* (NCSC^m); 7 Oct 1966 (V), *Downs 408* (NCSC); 2 Aug 1977 (FR), *Kral 60712* (VDB^m); 25 Aug 1989 (FR), *Lance & Wood s.n.* (NCU^m); 1 Sep 1952 (FR), *Radford 6676* (NCU^m); 9 Sep 1976 (V), *Smith 182* (NCSC); 5 Jul 1940 (FR), *Stewart 1554* (NCU); 27 May 1964 (FR), *Wilbur 7012* (VDB^m). Chatham: 25 Apr 1988 (FL), *Swab 75* (NCSC); 4 May 1988 (FL), *Swab 97* (NCSC); 28 May 1988 (FR), *Swab 236* (NCSC). Gaston: 19 May 1919 (FR), *Coker s.n.* (NCU^m). Harnett: 18 Apr 2006 (V), *Sorrie & Hart 11770* (NCU^m). Montgomery: 2011-122, 21 Aug 2012 (V), *Lynch 23* (NCSC^m); 11 Oct 2002 (FR), *Diamond 1606* (NCU^m); 14 Jul 2004 (V), *Schwartzman 30* (NCU^m); 20 Jul 2004 (V), *Weakley s.n.* (NCU^m); 15 Oct 2004 (V), *Weakley s.n.* (NCU). Orange: 2011-124, 19 Apr 2012 (FL), *Lynch 14* (NCSC); 2011-124, 2 Jul 2012, *Lynch 78* (NCSC^m); 2011-124, 24 Jun 2014 (FR), *Phillips 62* (NCSC); Apr 1899 (FL), *Ashe s.n.* (NCU); Jun 1899 (FR), *Ashe s.n.* (NCU); 31 Apr 200 (FL), *Wally & Wichmann 125* (NCU^m); 4 May 1910 (FR), *Clerces s.n.* (NCU). Person: 7 Jul 2005 (FR), *LeGrand s.n.* (NCU^m). Polk: 30 May 1930 (FL), *Ashe s.n.* (NCSC); 20 Apr 1897 (FL), *Biltmore 6565* (BRIT^m); 20 Apr 1897 (FL), *Biltmore 708* (NCU). Randolph: 22 Apr 1958 (FL), *Melvin s.n.* (NCU). Rutherford: 2011-163, 21 Aug 2012 (V), *Lynch 26* (NCSC^m); 2011-163, 15 Apr 2013 (FL), *Lynch 39* (NCSC); 2011-163, 24 Jun 2014 (FR), *Phillips 64* (NCSC); 21 Apr 1956 (FL), *Bell 2118* (NCU). Stokes: 23 Apr 1950 (FL), *Fox et al. 3565* (NCSC); s.d. (FR), *Harbison s.n.* (NCU); 5 May 1936 (FL), *Hunt 13474* (BRIT ^{m}, NCU); 7 Jul 1969 (FR), *Leonard & Russ 2553* (NCU^m); 21 Apr 1974 (FL), *Massey 3900* (VDB); 26 Apr 1958 (FL), *Matthews 54* (BRIT); 15 Jun 1967 (FR), *Radford 45392* (AUA^m, MISS, NCSC, NCU); 4 Jun 1958 (FR), *Radford 34675* (VDB ^{m}); 9 Apr 1933 (FL), *Schallert 3613* (BRIT). Surry: 19 May 1935 (V), *Harbison s.n.* (NCU). Transylvania: 2011-112, 2 Jul 2012 (V), *Lynch 16* (NCSC); 2011-112, 24 Apr 2014 (FL), *Lynch 47* (NCSC); 2011-112, 24 Jun 2014 (FR), *Phillips 63* (NCSC); 2011-131, 21 Aug 2012 (FR), *Lynch 22* (NCSC^m); 19 Jun 1965 (FR), *Eggers 1262* (VDB ^{m}); 26 Jul 1962 (FR), *Rodgers 62064a* (NCU^m); 24 May 2006 (FR), *Schwartzman 29* (NCU^m). Wake: 28 Oct 2005 (V), *Bruhn s.n.* (NCU).

Pennsylvania. Marion: Cultivated at the Arboretum of the Barnes Foundation, 27 Apr 1968 (FL), *Fogg 1* (UWFP).

South Carolina. Greenville: 17 May 1976 (FR), *Kral 58130* (VDB ^{m}); 15 Oct 1988 (V), *Hill 20066* (BRIT ^{m}); 23 May 1996 (V), *Townsend 874* (VDB ^{m}). Oconee: 2011-091, 28 Mar 2012 (FL), *Lynch 12* (NCSC); 2011-091, 2 Jul 2012 (V), *Lynch 77* (NCSC^{m}); 26 Apr 1965 (FL), *Radford 44707* (NCU); 20 Apr 1973 (FL), *Rogers & Green 73078* (FLAS-2). Pickens: 15 June 1992 (FT), *Hill 23387* (BRIT ^{m});

Tennessee. Grainger: 20 Apr 1931 (FL), *Sharp 556* (BRIT, NCSC); 30 Apr 1931 (FL), *Jennison & Sharp s.n.* (NCU); May 3 1936 (Fl), *Sharp & Underwood 4205* (NCU^{m}, NCSC). Greene: 17 May 1970 (FL), *Sharp et al. 45204* (BRIT ^{m}, NCU, VDB). Scott: 2012-065, 21 Aug 2012 (V), *Lynch 29* (NCSC ^{m}); 2012-065, 15 Apr 2014 (FL), *Lynch 44* (NCSC); 23 Apr 1972 (FL), *Clebsch s.n.* (VDB); 19 Apr 1979 (FL), *Whitten & Noss s.n.* (FLAS-2); 23 Jun 1978 (FR), *Wofford et al. 78-112* (VDB ^{m}). Sevier: 1 May 1960 (Fl), *Sharp 26818* (BRIT, NCU); 25 Apr 1970 (FL), *Williams 82* (AUA ^{m}); 25 Apr 1970 (FL), *Pippin 83* (VDB); 2 Apr 1938 (FL), *Jennison 53* (VDB ^{m}); 26 Apr 1957 (FL), *Sharp 21575* (BRIT ^{m}).

Washington D.C. U.S. National Arboretum, 16 Oct 1990 (V), *Meyer 37144* (FLAS).

3. *Fothergilla milleri* W.D.Phillips & J.E.Haynes, sp. nov.

urn:lsid:ipni.org:names:77208304-1

Type. Florida. Walton Co.: Voucher specimen from containerized plant at Mountain Horticultural Crops Research and Extension Center, Mills River, NC (leaves and stem collected 19/7/2012), [living plant originally collected 25 Mar 2011 by Ron Miller from Walton Co., Florida], 2011-088, 19 Jul 2012 (V), *Nathan Lynch 70* (***Holotype*:** NCSC-00102544^{m}, here designated). Figs 1C, 3A, 7, 9.

Diagnosis. *Fothergilla milleri* is morphologically most similar to *F. gardenii*, but differs from the latter by leaves held erect (vs. spreading in *F. gardenii*), blades blue-green or gray-green (vs. green in *F. gardenii*), petioles 1/3–1/2 the length of the IL (vs. ¾ the length of the IL or longer in *F. gardenii*), and seed apices acute to acuminate (vs. rounded or obtuse in *F. gardenii*).

Description. ***Shrub***, rhizomatous, erect, to 1.5 m tall, clump-forming, multi-stemmed, branching. ***Leaves*:** stipules ovate to lanceolate, 2.5–7.8 × 1.0–3.0 mm; petioles 2.6–8.0 mm long, usually 1/3–1/2 the length of the IL, brown-yellow pubescent; blades erect, blue-green to gray-green, obovate, 3.2–8.0 × 3.0–4.8 cm, pinnately 8–10-veined, bases rounded to truncate, margins crenate to serrate above middle and mostly near the apex, sometimes appearing crenate to entire, apices mostly obtuse to acute, both surfaces conspicuously stellate-pubescent, sometimes sparsely so, abaxial surface not glaucous, IW:IL < or = 0.48 ($\bar{x}$ = 0.29). ***Inflorescences*** appearing before leaves, spikes on short peduncles or sessile. ***Flowers*:** stamens 15–22, filaments 4.3–10 mm long. ***Capsules*** 7.0–9.0 × 5.0 –7.0 cm. ***Seeds*** usually completely brown to red-brown, ovoid, 4.5–6.2 × 2.4–3.2 mm, apices acuminate, often recurved. ***Genome size and ploidy*:** 1.70–1.78 pg, diploid ($2n = 2x = 24$).

Phenology. Flowering beginning late Mar; fruiting late May through the end of Jul.

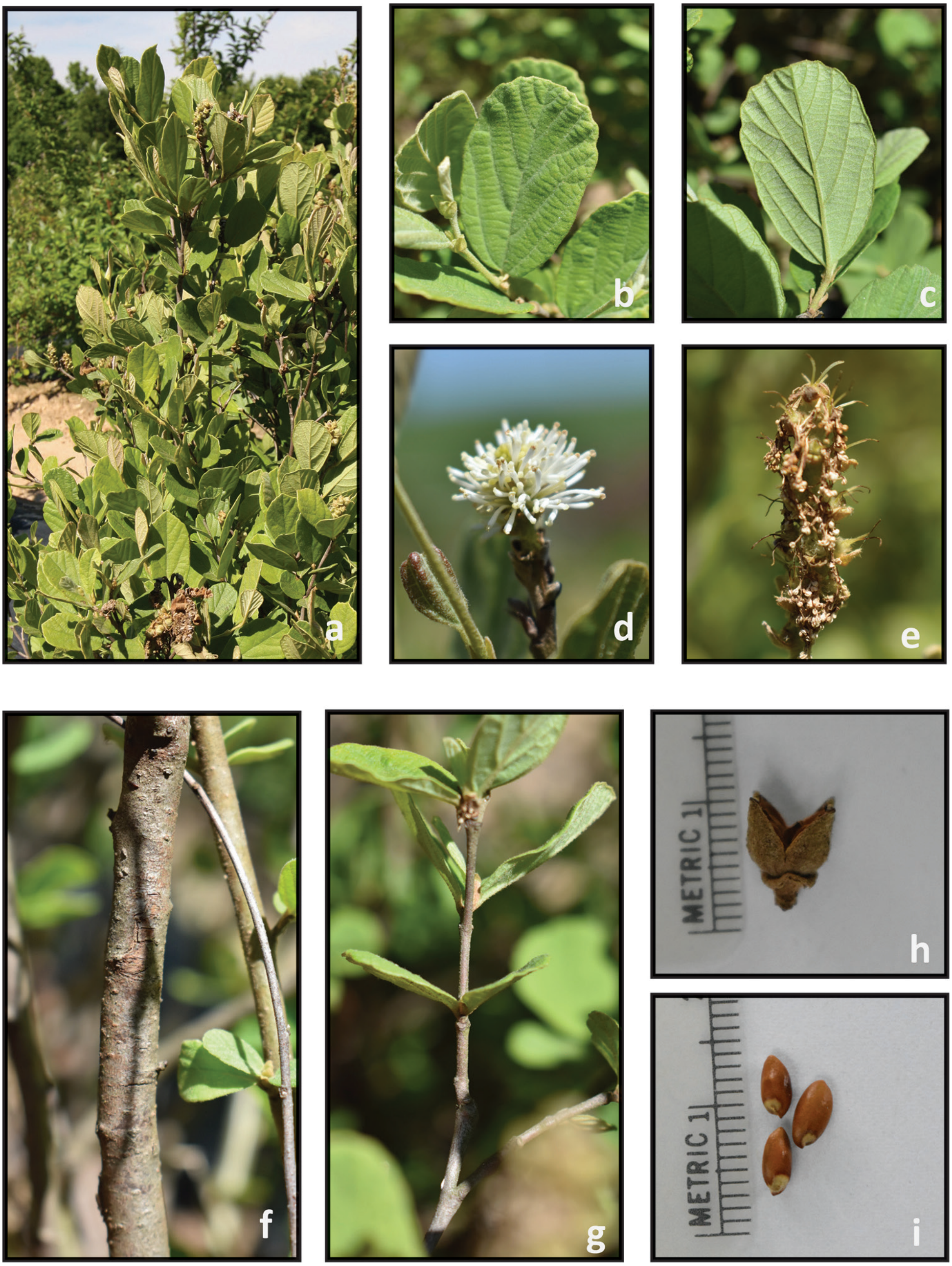


Figure 7. *Fothergilla milleri* **a** plant form and leaf orientation **b** adaxial leaf surface **c** abaxial leaf surface **d** inflorescence **e** young infructescence **f** stem **g** twig **h** capsule, and **i** seeds. Photos by J. Haynes of plants at the Mountain Horticultural Crops Research and Extension Center, Mills River.

Distribution and habitat. This species can be found in the panhandle of Florida, in Alabama in the Gulf coastal plain, and is also known from one county in Georgia (Fig. 5). This species is found in sandy peat shrub bogs, seepages, dry longleaf pine woodlands, and the edge of *Cyrilla racemiflora* or *Taxodium ascendens* swamp forests. Plant associates include *Acer rubrum*, *Arundinaria tecta* (Walter) Muhl., *Clethra alnifolia*, *Hibiscus aculeatus* Walter, *Hypericum cistifolium* Lam., *Juncus trigonocarpus* Steud., *Dichanthelium scoparium* (Lam.) Gould., *Osmundastrum cinnamomeum* (L.) C. Presl, *Rhexia virginica* L., *Rhynchospora chalarocephala* Fernald & Gale, and *Xyris fimbriata* Elliott (fide colectoris).

Etymology. The species is named in honor of Dr Ron Miller, Pensacola, Florida, who championed this project, originally suggested that diploid cytotypes might still exist, and ultimately found them. Dr Miller's extensive effort and field work (with colleagues) provided the foundation for this research and establishment of ex situ living collections, including accessions in the U.S. National Plant Germplasm System.

Conservation. The conservation status of this species must be reassessed. It is presently known from only seven counties, and would appear to have an imperilment status at least as severe as that of *F. major*. Consequently, only skeletal collections data are provided below.

Additional specimens seen [(V) = vegetative only, (FL) = in flower, (FR) = in fruit].

ALABAMA. BALDWIN: 2011-087, 21 Mar 2012 (FL), *Lynch 1* (NCSC); 2011-087, 2 Jul 2012 (V), *Lynch 68* (NCSC^m); 2011-087, 13 Jun 2014 (FR), *Phillips 58* (NCSC); 16 Jun 1984 (FR), *Hedges 156* (UWFP^m); 19 Apr 2001 (FR), *Schotz 1830* (UNA [online!]). COVINGTON: 25 Jun 1906 (FR), *Harper 108* (NY [online!]). ESCAMBIA: 11 Apr 1964 (FL), *Kral 19698* (AUA^m). GENEVA: 25 Jul 1968 (V), *Kral 32029* (VDB^m); 26 Apr 1969 (FL), *Kral 34524* (VDB^m); 7 Sep 1994 (V), *Simmers s.n.* (HTTU [online!]). MONROE: 15 Jun 1959 (V), *Grelen s.n.* (FLAS^m).

FLORIDA. OKALOOSA: 2011-083, 21 Mar 2012 (FL), *Lynch 2* (NCSC); 2011-083, 2 Jul 2012 (FL), *Lynch 67* (NCSC); 2011-083, 13 Jun 2014 (FR), *Phillips 57* (NCSC^m); 20 Apr 1991 (FL), *Burkhalter 12638* (FLAS^m, UWFP); 5 Aug 1990 (V), *Burkhalter 12211* (UWFP^m); 13 Jul 1996 (V), *Burkhalter 15064* (UWFP); 18 May 1993 (FR), *Naczi 3028* (KNK [online!]). WALTON: 8 Apr 1899 (FL), *Biltmore Herbarium 7609b* (FLAS^m); 2011-088, 28 Mar 2012 (FL), *Lynch 11* (NCSU); 2012-060, 19 Mar 2013 (FL), *Lynch 34* (NCSC); 2012-060, 2 Jul 2012 (V), *Lynch 15* (NCSC); 2012-060, 13 Jun 2014 (FR) *Phillips 59* (NCSC); 18 Aug 1990 (V), *Orzell and Bridges 14757* (FLAS^m, NY [online!], USF [online!]).

GEORGIA. TAYLOR: 2011-178, 26 Mar 2012 (FL), *Lynch 8* (NCSC); 2011-178, 2 Jul 2012 (V), *Lynch 69* (NCSC^m).

4. *Fothergilla parvifolia* Kearney in Small, Fl. S.E. U.S. 509, 1331. 1903

Type. Georgia. Wayne Co., Jesup, dry soil, 4 June 1893 (FR), *Kearney s.n.* (***Holotype***: NY!; ***isotype***: F [online!]). Figs 1B, 3B, 8, 9.

Description. ***Shrub***, rhizomatous, erect, to 1 m tall, clump-forming, multistemmed, branching. ***Leaves*:** stipules ovate to lanceolate, 3.5–6.0 × 8.0–13.0 mm, curved downward; petioles 4.4–17.8 mm long, usually nearly as long to longer than the IL, brown-yellow pubescent; blades drooping, green, mostly ovate, 3.2–12.1 ×

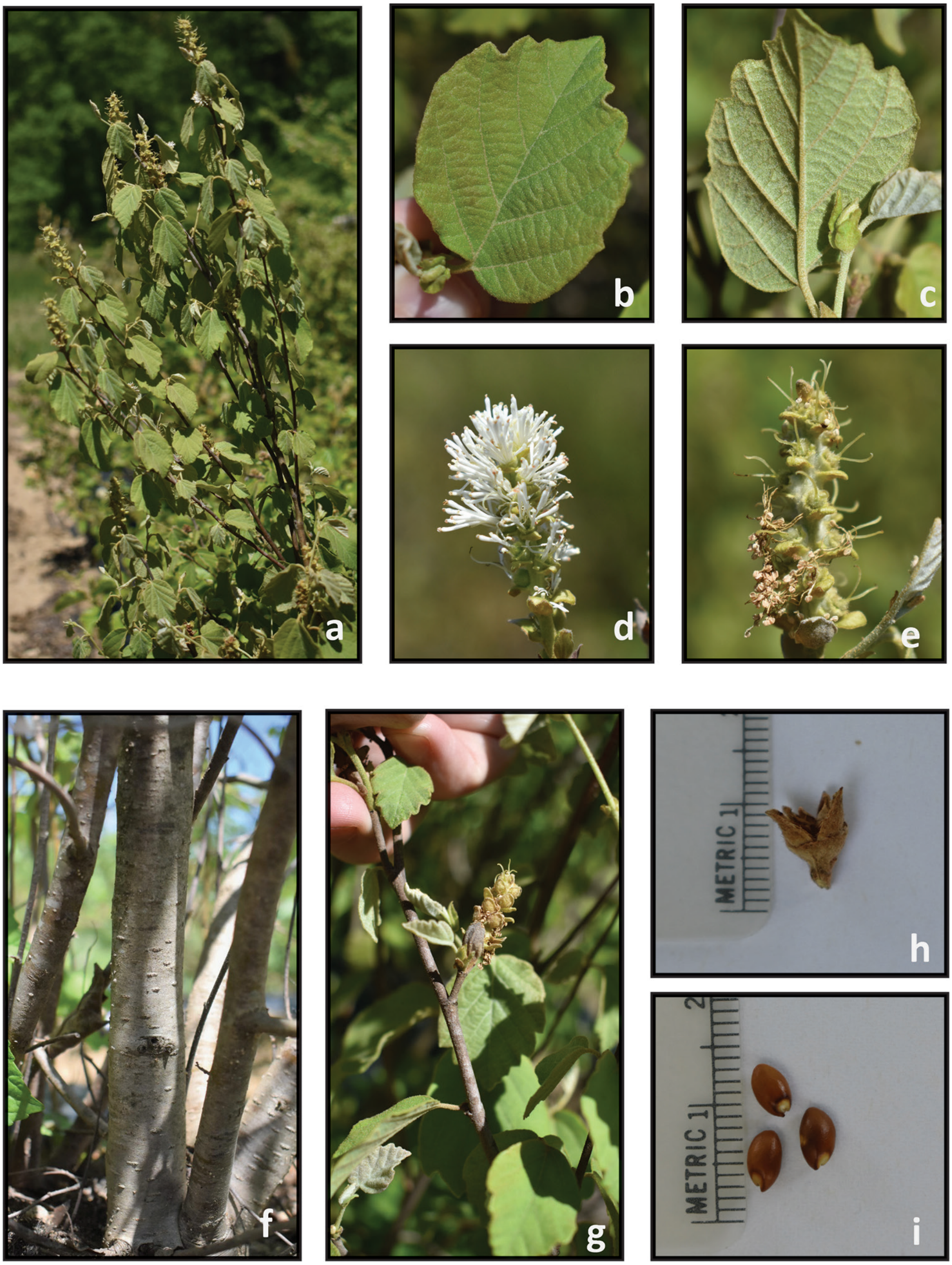


Figure 8. *Fothergilla parvifolia* **a** plant form and leaf orientation **b** adaxial leaf surface **c** abaxial leaf surface **d** inflorescence **e** young infructescence **f** stem **g** twig **h** capsule, and **i** seeds. Photos by J. Haynes of plants at the Mountain Horticultural Crops Research and Extension Center, Mills River.

3.0–6.2 cm, pinnately 8–10-veined, bases cordate, margins crenate to serrate from middle, apices acute, adaxial and abaxial surfaces not glaucous, stellate-pubescent, sometimes sparsely so, IW:IL > or = 0.62 ($\bar{x}$ = 0.96). ***Inflorescences*** appearing before

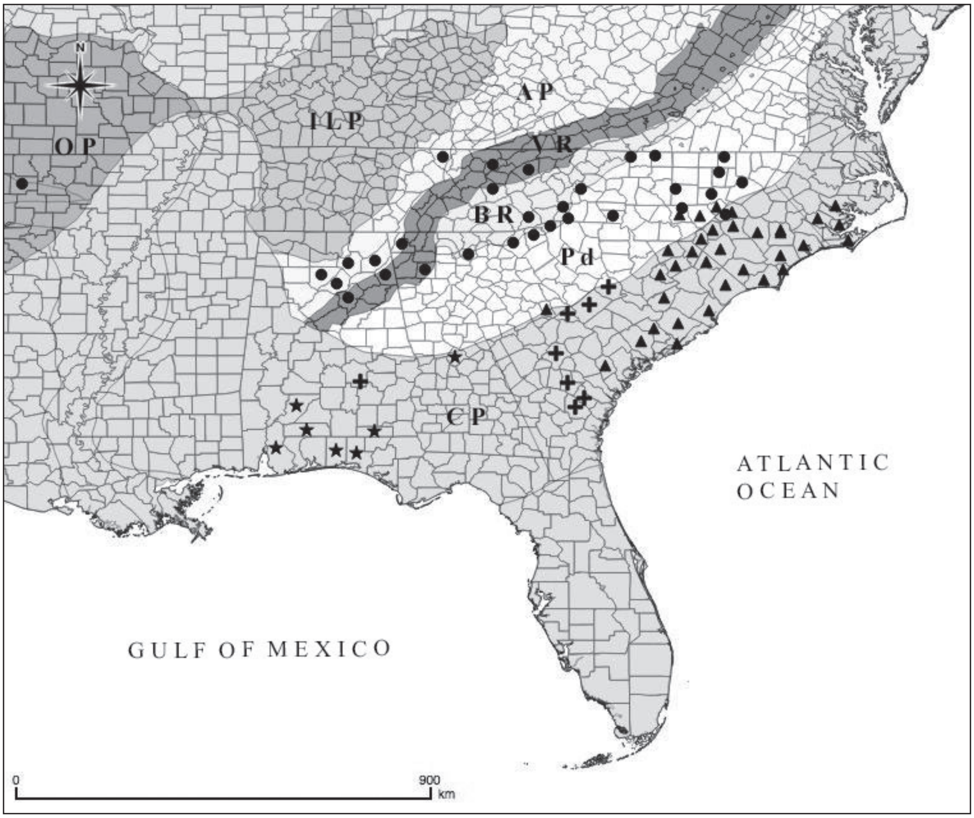


Figure 9. Distribution of *Fothergilla* in the southeastern United States. Circle = *F. major* (6x); triangle = *F. gardenii* (4x); star = *F. milleri* (2x); plus sign = *F. parvifolia* (2x). Physiographic provinces follow Fenneman and Johnson (1946), shape files courtesy of usgs.gov. AP = Appalachian Plateau; BR = Blue Ridge; CP = Coastal Plain; ILP = Interior Low Plateau; OP = Ozark Plateau; Pd = Piedmont; VR = Valley and Ridge. Map generated by A. Krings in QGIS (QGIS Development Team 2019).

leaves, spikes on short peduncles or sessile. ***Flowers*:** stamens 15–20 per flower, filaments 6.6–9.3 mm long. ***Capsules*** 7.5–10.0 × 5.0 –7.6 mm. ***Seeds*** usually completely brown to red-brown, ovoid, apex obtuse, 4.5–6.2 × 2.4–3.2 mm, apices obtuse to acute. ***Genome size and ploidy*** 1.73–1.82 pg, diploid (2n = 2x = 24).

Phenology. Flowering Mar–May; fruiting May–Sep.

Distribution and habitat. This species range is restricted to Georgia, South Carolina, and Alabama (Fig. 5). Because there are few herbarium records for this species, little is known about its exact distribution and environmental restrictions. According to the few notes available on herbarium specimens, it occurs in seepages and margins of bogs, bay swamps, and watercourses.

Conservation. The conservation status of this species needs to be assessed. It is presently known from only eight counties, and would appear to have an imperilment status at least as severe as that of *F. major*. Consequently, only skeletal collections data are provided below.

Additional specimens seen [(V) = vegetative only, (FL) = in flower, (FR) = in fruit].

Alabama. Montgomery: 12 Sep 1899 (FR), *Harbison 1033* (NCU^{m}).

Georgia. Augusta-Richmond: 2 Apr 1898 (FL), *Cuthbert s.n.* (FLAS). Brantley: 23 Aug 1947 (V), *Thorne & Norris 6284* (GEO [online!]). Emanuel: 2011-170, 2 Jul 2012 (V), *Lynch 19* (NCSC^{m}); 2011-170, 15 Mar 2013 (FL), *Lynch 33* (NCSC); 2011-170, 14 Jun 2014 (FR), *Phillips 60* (NCSC). Long: 2011-171, 2 Jul 2012 (V), *Lynch 20* (NCSC^{m}); 2011-171, 14 Mar 2013 (FL), *Lynch 32* (NCSC); 2011-171, 13 Jun 2014 (FR), *Phillips 61* (NCSC); Tattnall: 2011-168, 19 Mar 2013 (FL), *Lynch 35* (NCSC); 2011-168, 2 Jul 2012 (V), *Lynch 18* (NCSC^{m}). Wayne: 31 Aug 1904 (V), *Biltmore Herbarium 14940* (NY [online!]).

South Carolina. Aiken: 2012-084, 15 Apr 2014 (FL), *Lynch 40* (NCSC); 2012-084, 13 Jun 2014 (V), *Phillips 56* (NCSC^{m}). Lexington: 13 Sept 1988 (V), *Pittman 9139817* (BRIT^{m}); 27 May 1957 (FR), *Radford 23378* (NCU^{m}).

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RESEARCH ARTICLE

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A classification of endangered high-THC cannabis (*Cannabis sativa* subsp. *indica*) domesticates and their wild relatives

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Abstract

Two kinds of drug-type *Cannabis* gained layman's terms in the 1980s. "Sativa" had origins in South Asia (India), with early historical dissemination to Southeast Asia, Africa, and the Americas. "Indica" had origins in Central Asia (Afghanistan, Pakistan, Turkestan). We have assigned unambiguous taxonomic names to these varieties, after examining morphological characters in 1100 herbarium specimens, and analyzing phytochemical and genetic data from the literature in a meta-analysis. "Sativa" and "Indica" are recognized as *C. sativa* subsp. *indica* var. *indica* and *C. sativa* subsp. *indica* var. *afghanica*, respectively. Their wild-growing relatives are *C. sativa* subsp. *indica* var. *himalayensis* (in South Asia), and *C. sativa* subsp. *indica* var. *asperrima* (in Central Asia). Natural selection initiated divergence, driven by climatic conditions in South and Central Asia. Subsequent domestication drove further phytochemical divergence. South and Central Asian domesticates can be distinguished by tetrahydrocannabinol and cannabidiol content (THC/CBD ratios, ≥7 or <7, respectively), terpenoid profiles (absence or presence of sesquiterpene alcohols), and a suite of morphological characters. The two domesticates have undergone widespread introgressive hybridization in the past 50 years. This has obliterated differences between hybridized "Sativa" and "Indica" currently available. "Strains" alleged to represent "Sativa" and "Indica" are usually based on THC/CBD ratios of plants with undocumented hybrid backgrounds (with so-called "Indicas" often delimited simply on possession of more CBD than "Sativas"). The classification presented here circumscribes and names four taxa of *Cannabis* that represent critically endangered reservoirs of germplasm from which modern cannabinoid strains originated, and which are in urgent need of conservation.

Keywords

Cannabinoids, *Cannabis sativa*, classification, ecology, germplasm, marijuana, nomenclature

Introduction

Cannabis is an ancient domesticate, a triple-use crop. Archaeologists found fruits ("seeds") in a food context, a kitchen midden, with a calibrated radiocarbon date of 8000 cal BCE (Kudo et al. 2009). Evidence of fiber use is nearly as old, although identifying ancient cordage as *Cannabis* (or pottery impressions of same) is somewhat subjective (McPartland and Hegman 2018). Artifacts from a drug context-burnt residues with cannabinoids in a censer – date to 500 cal BCE (Ren et al. 2019). Early words for *Cannabis* include Chinese *má*, attested *ca*. 750–600 BCE (Qu and Waley 1955), *qunubu*, a Neo-Assyrian loanword from the Scythian language, *ca*. 680 BCE (Seidel 1989), and *κάνναβις*, a Greek loanword from Scythian, *ca*. 440 BCE (Herotodus 2007).

The Latin name *Cannabis sativa* is usually attributed to Leonhart Fuchs, but the binomial was actually coined by Ermolao Barbaro, between 1480 and 1490, published 23 years after he died (Barbaro 1516). Carl Linné adopted the binomial in *Species Plantarum*, the internationally-recognized starting point of botanical nomenclature (Linnaeus 1753). Jean-Baptiste Lamarck broke from Linnaean orthodoxy by recognizing a second species, *C. indica*, for drug-type plants (Lamarck 1785).

Small and Cronquist (1976) proposed a single-species concept. They separated taxa by Linnaeus and Lamarck at the rank of subspecies, as *C. sativa* subsp. *sativa* and *C. sativa* subsp. *indica* (Lam.) E. Small & Cronq. The subspecies were circumscribed on the basis of Δ^9-tetrahydrocannabinol (THC) content. They defined *C. sativa* subsp. *sativa* as containing <0.3% THC in dried flowering tops of female (pistillate) plants, and *C. sativa* subsp. *indica* as containing ≥0.3% THC. Numerous countries have incorporated the 0.3% criterion in regulations governing fiber-type (hemp) plants and drug-type (marijuana) plants.

Some botanists prefer to recognize *C. sativa* L. and *C. indica* Lam. at the rank of species (Hillig 2005a, Clarke and Merlin 2013). Debates over taxonomic rank are notoriously arbitrary. Molecular studies using DNA sequences can make the question of rank less arbitrary. Mandolino et al. (2002) quantified DNA polymorphisms in ten drug- and fiber-type varieties. They found more variability between individuals within a variety than between varieties – data that confirmed "the existence of a single, widely shared gene pool." In a worldwide collection of *Cannabis*, Gilmore et al. (2007) found a low rate of sequence variation (approximately 1 polymorphism per 1 kb sequenced cpDNA) – consistent with a single species.

McPartland (2018) used DNA barcodes as a metric to place the *Cannabis* question of rank in context with other plants. He examined five plant barcodes (*rbcL*, *matK*, *trnH-psbA*, *trnL-trnF*, and *ITS1*), and calculated a mean divergence (barcode gap) of 0.41% between *C. sativa* and *C. indica*. This nearly equaled the mean divergence of 0.43% between five pairs of plants considered different varieties or subspecies (e.g., *Camellia sinensis* var. *sinensis* and *C. sinensis* var. *assamica*). In contrast, a 3.0% barcode gap separated five pairs of plants considered different species (e.g., *Humulus lupulus* and *H. japonicus*). Hebert et al. (2004) proposed a 2.7% difference between two *COI* sequences (the "barcode gap") as the threshold for flagging genetically divergent specimens as distinct animal species.

Sawler et al. (2015) calculated a mean fixation index (F_{ST}) of 0.156 between populations of fiber- and drug-type plants (n = 43 and 81, respectively). F_{ST} values range from 0 to 1; a zero value indicates the two groups freely interbreed; a 1 value indicates the groups are completely isolated from one another. A mean F_{ST} of 0.156 is similar to the degree of genetic differentiation between human populations in Europe and East Asia, which belong to a single species.

Lynch et al. (2016) calculated F_{ST} = 0.099 between fiber- and drug-type groups (n = 22 and 173, respectively). Grassa et al. (2018) calculated F_{ST} = 0.229 between fiber-type accessions and "marijuana," by concatenating data from Sawler, Lynch, and their own sequencing. Hey and Pinho (2012) proposed F_{ST} = 0.35 as a conservative threshold measure for species differentiation; pairs with greater values are identified as separate species, pairs with lesser values are identified as subspecies populations. Clearly, *C. sativa* L. and *C. indica* Lam. are best differentiated at a subspecies rank.

In the 1980s, drug-type plants came to be divided into two categories, widely known by the ubiquitous labels "Indica" and "Sativa". This vernacular taxonomy became widespread after Anderson (1980) published a line drawing of the plants (Fig. 1). He differentiated "Indica" and "Sativa" by morphology and geographical provenance. As summarized by de Meijer and van Soest (1992), "Indica" applied to plants with broad leaflets, short and compact habit, and early maturation, and there is evidence that landrace ancestors of such plants came from Central Asia (primarily Afghanistan). "Sativa" applied to plants with narrow leaflets, tall and diffuse habit, and late maturation, and there is evidence that landrace ancestors of such plants came originally from South Asia (primarily India), with early historical distribution to Southeast Asia, Africa, and the Americas.

Clarke (1981) accepted Anderson's "Indica" concept for plants from Central Asia, "Strains from this area are often used as type examples for *Cannabis indica*." In addition to morphological differences, he noted a phytochemical trait – Central Asian plants uniquely produced an acrid, skunk-like aroma. Clarke (1987) added an organoleptic quality – plants from Afghanistan produced a "slow flat dreary high." Hillig (2005a) referred to Central Asian landraces as wide-leaflet diameter (WLD) biotypes, and landraces of South Asian heritage as narrow-leaflet diameter (NLD) biotypes. WLD and NLD biotypes differed in genetics (Hillig (2005a), morphology (Hillig 2005b), THC-to-cannabidiol (CBD) ratios (Hillig and Mahlberg 2004), and terpenoid content (Hillig 2004).

Recent authors have mistakenly equated the vernacular term "Sativa" with the epithet in the scientific name *C. sativa*, and mistakenly equated the vernacular term "Indica" with the epithet in the scientific name *C. indica*, mismatches first noted by McPartland et al. (2000). Small (2007) stated that "Sativa" and "Indica" were "quite inconsistent" with formal nomenclature. Linnaeus's type specimen of *C. sativa* is a fiber-type (hemp) plant, not a drug-type (marijuana), and so the term "Sativa" has been inappropriately applied to drug-type plants (logically, it should be reserved for

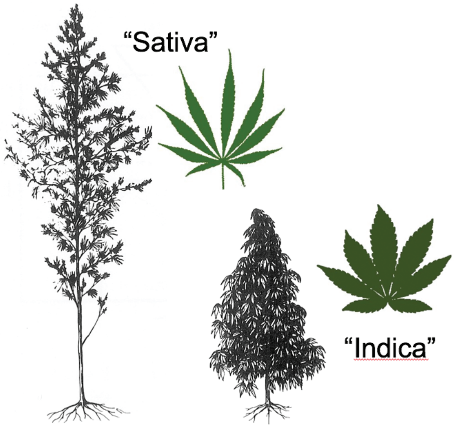

Figure 1. Line drawing adapted from Anderson (1980), courtesy of the Harvard University Herbaria and Botany Libraries.

fiber-type hemp). Lamarck described *C. indica* for drug-type plants from India, and progenies in Southeast Asia and Africa – now counterintuitively called "Sativa" (logically, "Indica" should be reserved for the drug plants described by Lamarck).

The erroneous equivalences of vernacular "Sativa" (denoting plants with cannabinoids mostly or entirely THC) with "*C. sativa*" (in the narrow nomenclatural sense, denoting low-THC hemp forms), and vernacular "Indica" (denoting plants with substantial THC but also often substantial CBD) with "*C. indica*" (in the narrow nomenclatural sense, denoting high-THC, low-CBD forms) have appeared in taxonomic studies and legal documents. Even the pages of "Nature" have been problematically adorned with "Sativa" and "Indica", accompanied by a version of Fig. 1 (Gould 2015). Those unfamiliar with the complexities and subtleties of biological classification can be misled, but in principle the issue is simple: the terms "Sativa" and "Indica" have been employed ambiguously and contradictorily.

In past centuries, landraces of South Asian heritage were grown over a much wider geographical range around the world than Central Asian landraces. The latter did not come to the attention of western *Cannabis* breeders until the early 1970s. Since then, breeders have haphazardly hybridized Central Asian and South Asian landraces, and largely obliterated their phenotypic differences (Clarke and Merlin 2013; Small 2017). Already 35 years ago, unhybridized landraces had become difficult to obtain in the USA and Europe (Clarke 1987). Hybrids of "Sativa" and "Indica" have proved overwhelmingly popular. "Indica" genes are useful for increasing cannabinoid yields, accelerating the maturity of outdoor plants at high latitudes, and reducing the height of plants so they are more easily concealed outdoors and more easily grown indoors. In the burgeoning CBD market, "Indica" genes (often from plants mislabeled "Ruderalis") have increased the proportion of CBD relative to THC in plant products.

Alarmingly, Central and South Asian landraces have been corrupted by the introduction of foreign germplasm into their centers of diversity. Beisler (2006) boasted of importing "Mexican Gold" into Afghanistan around 1972. Casano (2005) noted that Afghani landraces were "disappearing" due to hybridization with other drug-type plants. Conversely, Central Asian landraces were introduced into South Asian centers of diversity in the 1970s – into Nepal (Cherniak 1982), Jamaica (Lamb 2010), and Thailand (Clarke and Merlin 2016). By 1980, Afghani landraces were imported into southern Kashmir, cultivated for sieved *hashīsh*, and escapes grew near crop fields (Clarke 1998). Also in the 1980s, Central Asian genetics were introduced into South Africa (Peterson 2009) and Morocco (Clarke and Merlin 2016). Sharma (1988) wrote about "hybrid *Cannabis*" growing in Kullu, Himachal Pradesh, and he implicated "foreign nationals."

Central and South Asian landraces face extinction through introgressive hybridization. Wiegand (1935) first described this phenomenon in plants. Introgression refers to the infiltration of genes between taxa through the bridge of F_1 hybrids. Fertile offspring from these crosses may display hybrid vigor (enhanced fitness), and replace one or both parental populations (Ellstrand 2003). Recent phylogenetic studies of populations allegedly representing "Indica" and "Sativa" show little or no genetic differences, because these studies primarily analyzed hybrid "strains" (Sawler et al. 2015; Dufresnes et al. 2017; Schwabe and McGlaughlin 2018). These results conflict with studies of landraces collected in the 1970s–1990s, which showed much clearer genetic differences (Hillig 2005a; Gilmore et al. 2007).

The use of "strain" names for Indica–Sativa hybrids began with Watson (1985). A database of strain names currently lists 14,348 of them (Seedfinder 2019). This crowd-sourced enterprise – crossing and re-crossing hybrids of largely clandestine parentage – has resulted in a loss of genetic diversity (Mudge et al. 2018). Most strains sold by seed companies are characterized as "Sativa-dominant" or "Indica-dominant." The arbitrariness of these designations is illustrated by "AK-47", a hybrid strain that won "Best Sativa" in the 1999 Cannabis Cup, and won "Best Indica" four years later (McPartland 2017). Conceptually, a "strain" is equivalent to a "cultivar," the latter being a taxonomic rank recognized by the "International Code of Nomenclature for Cultivated Plants" (ICNCP, Brickell et al. 2016). However, few commercial "strains" of drug-type *Cannabis* have met ICNCP requirements for cultivar recognition (Small 2015).

The ICNCP clusters cultivars into "Groups". Consistent with ICNCP requirements, Small (2015) designated Central Asian landraces as "Cannabis Group Narcotic, THC/CBD Balanced," and South Asian landraces as "*Cannabis* Group Narcotic, THC Predominant." Some botanists argue that plants with traits created by human selection should be assigned cultivar status under the ICNCP, rather than assigned taxa under the "International Code of Nomenclature for Algae, Fungi, and Plants" (ICN, Turland 2018). However, for pragmatic reasons, botanists use the ICN framework to assign taxa to artificially selected plants (e.g., Hammer and Gladis 2014).

The above information has dealt basically with domesticated material. In addition, "wild" plants are also of concern. *Cannabis* "wild-type" traits were first described by

Zinger (1898): small achene size, a persistent perianth with camouflagic mottling, and an elongated base – drawn out in the shape of a short, tapered stub with a well-developed abscission layer. In contrast, domesticated plants express a suite of phenotypic traits (the "domestication syndrome") absent in wild-type plants, such as enlarged seed size, a lack of seed shattering (from reduction of the abscission zone), and reduction of perianth adherence.

Domesticated *Cannabis* easily escapes cultivation and goes "feral." Domesticated *C. sativa* reverted to a wild-type phenotype in Canada just 50 generations (years) after cultivation was prohibited (Small 1975). This rapid phenotypic evolution makes it difficult to distinguish truly wild plants from formerly cultivated plants that have reverted to wild-type phenotypes. Thus *Cannabis* plants growing outside of cultivation could be (1) "volunteers" (escaped very recently from cultivation, maintaining their domesticated characteristics, and growing near where they were cultivated); (2) "escapes" that have readapted to wild existence (growing in various habitats, typically in disturbed or weedy places); or (3) "aboriginal" (unaltered by domestication and growing in their indigenous areas).

Aboriginal populations of several of the world's most important crops do not seem to have survived, and *Cannabis* may be of this nature. Regardless, the wild-growing plants of Asia that are near (sympatric or parapatric) to the domesticates are of special significance. They may be direct ancestors of the domesticates, although this remains to be ascertained – many ancient domesticates were domesticated in locations distant from their sites of origin (Jarvis et al. 2016). In any event, there is considerable likelihood that the nearby wild plants of the domesticates share genes, since *Cannabis* produces massive quantities of pollen that is distributed for vast distances, and all *Cannabis* populations are capable of cross-pollination and completely interfertile (Small 1972). Accordingly, the wild varieties recognized in this publication represent very significant potential sources of genes representative of the endangered "Sativa" and "Indica" genomes.

This study does not address the European subspecies, *C. sativa* subsp. *sativa*. Small and Cronquist (1976) segregated this subspecies into two varieties – domesticated and wild-type plants. The domesticated variety is composed of fiber-type and oilseed landraces and cultivars. The wild-type variety has nomenclatural issues regarding *C. sativa* var. *spontanea* Vavilov (1922) and *C. ruderalis* (Janischevsky 1924). Vavilov and Janischevsky assigned these separate taxa to the same population of wild-type plants growing near Saratov, Russia. "Ruderalis" has become a mainstay of today's vernacular taxonomy (Anderson 1980). See Suppl. material 1: SF.2 for a discussion of these nomenclatural issues, and an elaboration of "wild-type nominalism" in SF.3b.

Worldwide introgressive hybridization of "Indica" and "Sativa" threatens the agrobiodiversity of *C. sativa*. Seen pessimistically, the varieties described here are components of a vanishing world, and classifying them is like an exercise in renaming dinosaurs. Optimistically, the formal recognition of indigenous Central and South Asian varieties will provide them with unambiguous names, and may help prevent their extinction.

Methods

Taxonomic characters for analysis included aspects of morphology, phytochemistry, genetics, and host-parasite relationships. Some data are new (morphological studies of herbarium specimens), whereas phytochemical and molecular data were extracted from previously published studies. Most of those studies employed common garden experiments (CGEs). CGEs grow plants from different places in a single location, under common environmental conditions, with uniform processing (Grassi and McPartland 2017).

Morphological characters

Approximately 1,100 herbarium specimens were examined, at 15 herbaria, designated by herbarium acronyms in Index Herbariorum (Suppl. material 1: SF.4). Additionally, we extracted morphological data from CGEs that compared Central and South Asian germplasm collected in the previous century (e.g., Vavilov and Bukinich 1929, Small et al. 1976, Anderson 1980, de Meijer 1994, Hillig 2005b). We also drew on morphological data from archaeobotanical studies. In the spirit of open access, extracted morphological data are provided in Suppl. material 1: SF.8, permitting readers to synthesize the raw data for themselves. CGE studies provided data often absent in herbarium specimens, such as plant height, internode length, stalk thickness, and branch angle or divarication.

Branch angle or divarication measured the angle, in degrees, that a branch came off the vertical shoot; it generally ranged between 35° to 85° from vertical. Branch angle may be a function of internode length, which was also assessed. Branch flexibility is a qualitative measure of the ability of a branch to bend or droop without snapping. Flexibility likely reflects the ratio of bast fiber (flexible) to wood fiber (inflexible). Leaf morphology was assessed in “fan leaves” (i.e. larger palmately compound leaves) near the base of inflorescences. The sampled leaves conformed to the concept of 1st order branching off the main shoot, as presented by Spitzer-Rimon et al. (2019). Central leaflet length/width ratio (L/W) is expressed as a quotient. Leaflet shape was either lanceolate (the widest part is less than midway down the length of the leaflet from its base), or oblanceolate (where the widest location is more than half way down the length). This was measured as the distance to the widest point (WP) divided by the entire length (WP/L). A leaflet with $WP/L > 0.5$ is oblanceolate (Anderson 1980).

The perigonal bract (also called bracteole, perigonium, or inappropriately “calyx”) is the floral bract enclosing the female flower and later the achene (Small 2015). Inflorescence density was qualitatively assessed using the “perigonal bract-to-leaf index” (i.e., the “calyx-to-leaf ratio,” Clarke 1981). Inflorescences with a low index have a predominance of leaf material – interstitial “sugar leaves” (relatively small leaves with few leaflets occurring in the inflorescence) between clusters, subtending 2nd order to 7th order branchlets (Spitzer-Rimon et al. 2019). A low index is associated, in part, with short internode length and broad leaflet width.

The density of capitate-stalked glandular trichomes (CSGTs) was qualitatively assessed (i.e. visually evaluated) on perigonal bracts. CSGT density was mentioned by Christison (1850) in one of the first CGEs that compared *C. sativa* (Scottish hemp) and *C. indica* (Indian *gunjuh*). He noted that *C. indica* inflorescences felt resinous when touched, "Floral leaves, bracts, and perianth covered with glandular pubescence." He also noted that *C. indica* leaves produced "both sessile glands and glandular hairs [CSGTs]." CSGT density on sugar leaves was also qualitatively assessed, based on the method by Potter (2009).

As used here, the "fruit" includes the achene and its more or less adherent perianth. In female flowers of *Cannabis*, the perianth does not produce a corolla, but instead adheres to the exocarp (outermost layer of the achene wall). Dimensions and appearance of the fruit were assessed.

For each herbarium specimen, a standardized form was used to record specimen label data (collector name, date, location, annotations) and morphological data. During the course of this study, morphological characters were added (e.g., branch angle, inflorescence density, CSGT density), necessitating return visits to some herbaria (BM, ECON, GH, IND, K). Morphological data were synthesized qualitatively (e.g., branch flexibility, leaf color, inflorescence density, CSGT density, perianth adherence), or quantitatively (e.g., plant height, internode length, leaflet L/W and WP/L ratios, achene size). Quantitative data provided bracket measurements for each described taxon.

Phytochemical characters

A widely-cited paper by Turner et al. (1980) listed 420 phytochemicals isolated from *C. sativa* – the 420 plant. Few phytochemicals provide useful taxonomic information, however. Our study focused on cannabinoids and terpenoids. In living plants and freshly harvested tissues, cannabinoids exist predominantly in the form of carboxylic acids. THC occurs as tetrahydrocannabinolic acid (THCA); cannabidiol (CBD) occurs as cannabidiolic acid (CBDA). Decarboxylation of the cannabinoids into their neutral counterparts occurs relatively slowly with aging, and rapidly with heat. Thus THCA converts to THC, and CBDA converts to CBD. In addition, when THC ages (unless appropriately stored) it substantially transforms to cannabinol (CBN), an oxidation product. In this paper when THC and CBD are mentioned it should be understood that depending on context, "THC" may mean THCA + THC + CBN, and "CBD" may mean CBDA + CBD.

Rather than cannabinoid *quantity* (i.e., THC% w/w), we report a parameter measuring cannabinoid *quality*: the THC/CBD ratio (THC% w/w divided by CBD% w/w). The THC/CBD ratio is a quite conservative (stable) character, whereas THC% correlates with morphology, such as trichome density (Potter 2009), as well as inflorescence density and gland head size. These morphological differences do not alter the THC/CBD ratio. The ratio is determined by a single gene with codominant alleles (de Meijer et al. 2003), or two tightly-linked yet separate *THCAS* and *CBDAS* genes (Van Bakel et al. 2011, Laverty et al. 2019). Weiblen et al. (2015) identified a single quantitative trait locus (QTL) associated with the THC/CBD ratio.

In contrast, THC% expression is polygenic, altered by many genes that contribute to morphological differences. Environmental factors (light intensity, temperature, soil nutrients, etc.) alter THC%, but have much less effect on THC/CBD. As a dimensionless ratio, THC/CBD provides a more valid comparison of many studies that grew plants under different conditions (Grassi and McPartland 2017).

Tetrahydrocannabivarin (THCV) and cannabidivarin (CBDV) are short-tailed C_{19} analogs of THC and CBD. The biosynthetic pathway leading to THCV and CBDV diverges early, on the resorcinol side of the cannabinoid pipeline. Some researchers add C_{19} analogs to THC/CBD ratios, as THC+THCV/CBD+CBDV (e.g., Turner et al. 1980). Here, the percentage of C_{19} analogs (THCV%+CBDV%) is treated as a separate character.

Terpenoids constitute the "essential oil" of *Cannabis*. Terpenoids include hydrocarbon terpenes and their oxygenated derivatives, which form alcohols, ethers, aldehydes, ketones, and esters. They are volatile, and give the plant its characteristic smell. Christison (1850) noted that Indian *gunjuh* emitted a balsamic odor, lacking in Scottish hemp. South Asian landraces often smell "herbal" or "sweet," whereas Central Asian landraces give off an acrid or "skunky" aroma (Clarke 1981).

Genetic characters

Molecular genetic studies of Central and South Asian populations – which have not been significantly hybridized in recent times – are limited in number. Twenty years ago, when unhybridized landraces were much more readily available, molecular methods were blunt instruments. Today, we can decode the DNA sequence of whole genomes, but a good representation of the range of unhybridized biodiversity is not available for analysis, although collection of genuinely representative germplasm from Asia may still be possible. Herbaria of course are invaluable repositories of older specimens, but collections from Asia are relatively limited, and for various reasons, curators have often been unable to allow sampling of older collections.

Herbarium voucher specimens were deposited for some CGE studies (Small and Beckstead 1973; Turner et al. 1973, 1979; de Meijer et al. 1992; de Meijer 1994; Hillig 2004, 2005a; Hillig and Mahlberg 2004; Gilmore et al. 2007), which we examined to ascertain correlations with morphology. For other phytochemical and genetic studies, we relied upon reports of geographic provenance of their accessions.

Results

The electronic version of this article in Portable Document Format (PDF), in a work with an ISSN or ISBN number, represents a published work according to the ICN

(Turland 2018). Hence the new names contained in the electronic publication of this article are effectively published under the ICN from the electronic edition alone. New names contained in this work have been submitted to the International Plant Names Index (IPNI, http://www.ipni.org), from where they will be made available to the Global Names Index.

An example of a taxonomic trait shifting over the past 50 years, as Central Asian landraces hybridized into "Indica", is provided in Fig. 2. It illustrates a convergence in THC/CBD ratios over the past 50 years. In studies of accessions collected in the 1970s–1990s, Central Asian landraces (study numbers in unitalicized red font), the THC/CBD ratio, expressed as a quotient, was always < 7 (study size weighted mean = 3.56). In studies of South Asian landraces collected in the 1970s–1990s (study numbers in italicized green font), the THC/CBD ratio was ≥ 7 (study size weighted mean = 97.14). Since then, THC/CBD ratios have skyrocketed in accessions purportedly representing Central Asia (i.e., "Indica"). Now there is little or no difference between "Indica" and "Sativa".

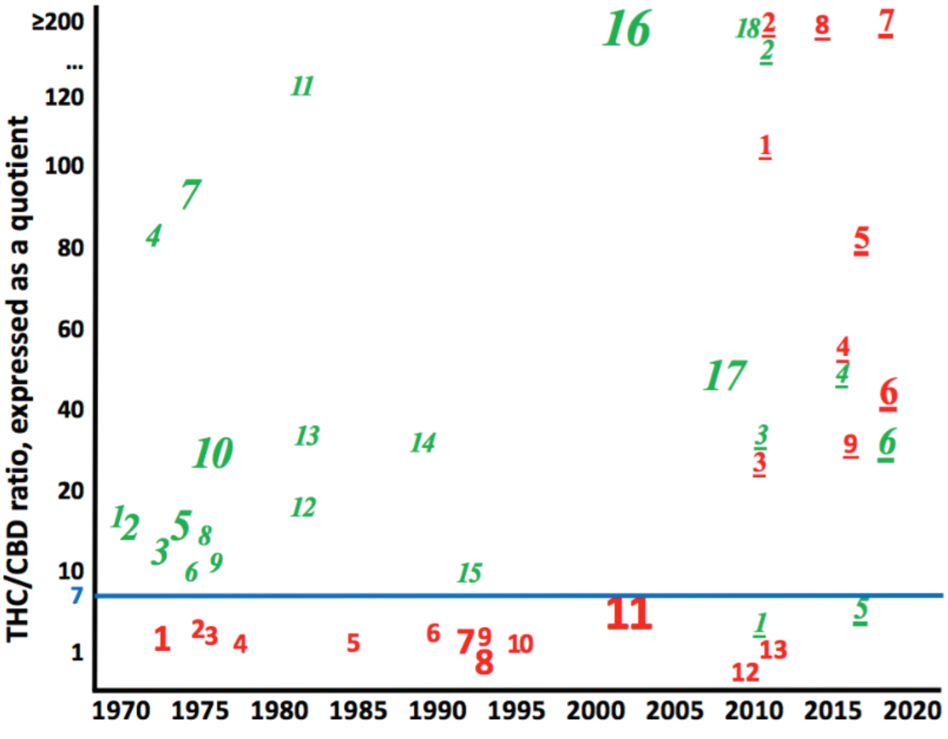

Figure 2. Shifts in THC/CBD ratios over time; data from 47 numbered studies in Suppl. material 1: SF.9. Central Asian landraces in unitalicized red (n =13 studies); "Indica" in underlined unitalicized red (n= 9); South Asian landraces in *italicized green* (n =18 studies); "Sativa" in *underlined italicized green* (n =7 studies). Size of numeral reflects the number of accessions analyzed in that study.

Taxonomic analysis

We classified *C. sativa* subsp. *indica* into four varieties (in the formal nomenclatural sense, i.e., varietas). Two varieties express traits of domestication (identical to "Indica" and "Sativa" in the original narrow meanings of these terms), and two varieties have wild-type traits. We followed precedent set by Small and Cronquist (1976) who segregated *C. sativa* subsp. *indica* into two varieties – domesticated and wild-type plants. They did not place these varieties in an ancestor–progeny relationship, however, because they could not verify putative ancestral relationships.

Key to four varieties of *C. sativa* subsp. *indica*[1]

1. Plants usually with a THC/CBD ratio ≥7; terpenoid profile usually lacks sesquiterpene alcohols, fresh aroma often pleasant. Plants ≥ 2 m tall in good habitats; branches flexible, diverging from the shoot at a relatively acute angle (<45° from vertical). Fresh leaves medium green in color; central leaflets narrow (length/width usually >6), lanceolate to linear-lanceolate; margins with fine to coarse serrations, sometimes biserrate. Mature female inflorescence somewhat compact (flowering stems producing small to medium "buds"), with relatively obscure sugar leaves (a high perigonal bract-to-leaf index); sugar leaves with capitate-stalked glandular trichomes (CSGTs) usually limited to the proximal half of the leaves; perigonal bracts express a moderate to high density of CSGTs. Mature achene exocarp color (beneath the perianth) often green-brown.

A THC/CBD ratio always ≥7, often much more. Mature achenes usually ≥ 3.6 mm long (Fig. 3e, f); perianth mostly sloughed off, but often persistent in places (appearing as irregular spots or stripes); exposed exocarp exhibiting prominent venation; lacking a prominent protuberant base; not readily disarticulating from plant................. **var. *indica*** ("Sativa" in the historical sense[2])

B THC/CBD ratio usually ≥7, sometimes less. Mature achenes usually <3.6 mm long (Fig. 3g, h); perianth persistent (covering exocarp and its venation), with strong pigmentation in a mottled or striped pattern; with a protuberant base; readily disarticulating from plant .... **var. *himalayensis***

2. Plants with a THC/CBD ratio <7; terpenoid profile includes sesquiterpene alcohols, fresh aroma often acrid or "skunky." Plants < 2 m tall in good habitats, and often *ca.* 1 m; branches not flexible, branching sometimes nearly 90° from the stalk axis, producing a menorah-shaped habitus. Fresh leaves dark green in color, leaflets of larger leaves sometimes overlap; central leaflets broad (length/width usually <6), often oblanceolate; margins with coarse serrations, rarely biserrate. Mature female inflorescence compact (flowering stems producing medium to large "buds") with prominent

sugar leaves (a low perigonal bract-to-leaf index); sugar leaves have CSGTs extending more than half way down their length; perigonal bracts densely covered with CSGTs. Mature achene exocarp color (beneath the perianth) often a lighter shade of olive green to gray.

A THC/CBD ratio <7 (almost always >2). Mature achenes usually ≥ 3.6 mm long (Fig. 3a, b); perianth mostly sloughed off (appearing as irregular spots or stripes); exposed exocarp exhibiting prominent venation; lacking a prominent protuberant base; not disarticulating from plant, and often trapped in the dense inflorescence ....**var. *afghanica*** ("Indica" in the historical sense[2])
B THC/CBD ratio often <2. Mature achenes usually < 3.6 mm long (Fig. 3c, d); perianth persistent (covering exocarp and its venation), with strong pigmentation in a mottled or striped pattern; with a protuberant base; readily disarticulating from plant ....**var. *asperrima***

[1] As emphasized in the text, the differences presented here represent unhybridized plants, before extensive recent hybridization between them.

[2] Historically, as discussed in the text, "Sativa" formerly represented landraces of South Asian heritage, and "Indica" formerly represented Central Asian landraces. This key is not intended for the identification of "Sativa" and "Indica" strains commercially available today.

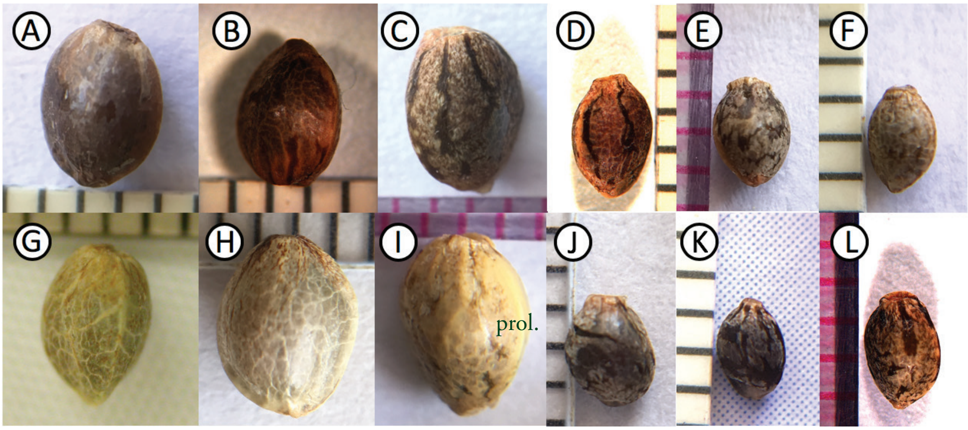

Figure 3. Representative achenes of four varieties **A** *indica*, Rajshahi (Bangladesh), *Clarke* 1877 (BM) **B** *indica*, Coimbatore (India), *Bircher* 1893 (K) **C** *indica*, South Africa, *Hillig* 1996; (IND) **D** *himalayensis* neotype **E** *himalayensis*, Bareilly (India), *Roxburgh* 1796 (K). **F** *himalayensis*, East Bengal (Bangladesh) *Griffith* 1835 (GH) **G** *afghanica* neotype **H** *afghanica* epitype **I** *afghanica* Yarkant (Xīnjiāng), *Henderson* 1871 (LE) **J** *asperrima* lectotype **K** *asperrima* Nuristān (Afghanistan), *Street* 1965 (F) **L** Kailiyskiy Alatau (Kazakhstan), *Semenov-Tyan-Shansky* 1857 (LE).

Taxonomic treatment

Please note that light quality varied among herbaria, so photographs of herbarium specimens and achenes at different herbaria varied somewhat in their tint, hue, and tone. For protologues of the four varieties (everything associated with a basionym at its time of publication), see Suppl. material 1: SF.6. For additional representative herbarium specimens of the four varieties, see Suppl. material 1.

Variety 1: South Asian domesticate

***Cannabis sativa* subsp. *indica* var. *indica* (Lam.) Persoon, *Synopsis Plantarum* 2: 618, 1807.**

Figure 4a

Cannabis indica Lamarck, Encyclopédie Méthodique 1(2): 694–695, 1785 Basionym. See McPartland (1992) for justification of citing Persoon as the authority in the comb. nov, not Wehmer as treated in Small and Cronquist (1976).

≡ *C. sativa* var. *indica* (Lam.) Fristedt, Upsala Läkareförenings Förhandlingar 5: 504, 1869–1870.

≡ *C. sativa* f. *indica* (Lam.) Voss in Siebert & Voss, Vilmorin's Blumengärtnerei 1: 912, 1896.

≡ *C. sativa* var. *indica* (Lam.) Wehmer, Die Pflanzenstoffe p. 248, 1911.

= *C. sativa* var. *indica* Blume, Bijdragen tot de flora van Nederlandsch Indië, p. 515, 1825.

= *C. macrosperma* Stokes, *Botanical Materia Medica* 4: 539, 1812.

≡ *C. sativa* B *macrosperma* (Stokes) Ascherson & Graebner, Synopsis Mitteleuropäischen Flora 4: 599, 1911.

≡ *C. sativa* var. *macrosperma* (Stokes) Chevalier, Revue de Botanique Appliquée et d'Agriculture Coloniale 24: 64, 1944.

= *C. sativa* γ *crispata* Hasskarl, Neuer Schlüssel zu Rumph's Herbarium amboinense p. 112, 1886.

= *C. sativa* β *vulgaris* de Candolle, Prodromus 16(1):31, 1869 (en part, based on plants cultivated in India).

= *C. americana* Houghton & Hamilton, Proc. Am. Pharm. Assoc. 55: 445, 1907, nomen nudum.

≡ *C. americana* Wehmer, Die Pflanzenstoffe, 2: 157, 1911, nomen nudum.

= *C. madagascar* Pearson, Proc. Penna. Pharm. Assoc. 1909: 179, 1909, nomen nudum.

= *C. africana* Glickman, Mulford's Veterinary Bulletin 4(2): 88, 1912, nomen nudum.

≡ *C. sativa* var. *africana* Wehmer, Die Pflanzenstoffe 2: 39, 1935.

= *C. mexicana* Stanley, Am. J. Police Science 2(3): 252, 1931, nomen nudum.

Figure 4. Two varieties of *C. sativa* subsp. *indica* from South Asia. On left **a** var. *indica*. On right **b** var. *himalayensis*.

Holotype. India, likely Pondicherry, *Lamarck*, no date, annotated "Chanvre rapporte de l'Inde par M. Sonnerat" (herb. P). Most of Pierre Sonnerat's herbarium specimens at herb. P were collected around Pondicherry between 1775 and 1778.

Diagnosis. Plants with THC% ≥0.3% in inflorescence and a THC/CBD ratio always ≥7, often much more; central leaflet length:width ratio ≥6 in fan leaves near the base of inflorescences; mature achenes usually ≥ 3.6 mm long, the perianth mostly sloughed off, lacking a prominent protuberant base, and lacking a well-developed abscission zone that allows easy disarticulation.

Morphology. Plants usually >2.0 m tall (shorter in inhospitable situations). Central stem (stalk) internodes relatively long (often >12 cm, shorter in shorter plants), somewhat hollow (up to 1/3 stem diameter). Branches flexible, diverging from the stalk at relatively acute angles (around 45°). Leaf palmately compound, largest leaves typically with at least 7 leaflets, leaflet edges not overlapping. Central leaflet long and narrow, lanceolate or linear-lanceolate in shape; margins with moderately coarse serrations, and rare secondary serrations. Female inflorescence (and infructescence) elongated and somewhat diffuse, with relatively obscure sugar leaves (a high perigonal bract-to-leaf index). Sugar leaves with CSGTs limited to the proximal half. Perigonal bract covered with a moderate density of CSGTs. Perianth membranous, hyaline with pigmented areas (brown and mottled or marbled in appearance); mostly sloughed off but sometimes persistent. Achene, usually ≥ 3.6 mm long, globose to elongate, exocarp green-brown; abscission zone poorly developed.

Phytochemistry. Dried female inflorescences: THC ≥0.3%, in late 20th century accessions, nearly always >1.0%; literature weighted x̄ = 3.97%, up to 12.5%. THC/CBD ratio ≥7, and often >100. THCV is commonly present, especially in landraces from South Asia and Africa. Hillig and Mahlberg (2004) report THCV+CBDV% content x̄ = 0.25%. Terpenoid profile often imparts an "herbal" or "sweet" aroma, with terpinolene, *β*-caryophyllene, trans-*β*-farnesene, and *a*-guaiene content significantly higher than Central Asian plants.

Genetics. Landraces of South Asian heritage segregated from Central Asian landraces in an allozyme analysis (Hillig 2005a) and cpDNA haplotype study (Gilmore et al. 2007). "Sativa" and "Indica" were segregated with STR loci (Knight et al. 2010), RAPD markers (Piluzza et al. 2013), and nDNA SNP haplotypes (Henry 2015; Lynch et al. 2016). Other studies showed little or no genetic differences between "Sativa" and "Indica" (Sawler et al. 2015; Dufresnes et al. 2017), or their phenotypes matched poorly with their purported genotypes (Schwabe and McGlaughlin 2018).

Other characters. Generally late maturing; monoecious plants relatively common compared to the other varieties; susceptible to black mildew caused by *Schiffnerula cannabis*.

Provenance and uses. Originally cultivated in India for *gañjā*, and spread at an early date to southeast Asia, Africa, and the Americas.

Variety 2: South Asian wild-type

Cannabis sativa subsp. *indica* var. *himalayensis* (Cazzuola) McPartl. & E.Small

Figure 4b

Cannabis sativa var. *hymalaiensis* Cazzuola, Il Regno vegetale tessili e tintoriale, p. 49, 1875 (misspelling corrected *apud* ICN Article 60.1) Basionym.

≡ *C. sativa* var. *hymalaiensis* Cazzuola, Nuovo Giornale Botanico Italiano 5: 262, 1873, nomen nudum.

≡ *C. sativa* var. *himalayensis* Cazzuola, Dizionario di botanica, p. 105, 1876 (later homonym).

= *C. sativa* var. *himalayensis* Koch, Annales des Sciences Naturelles Botanique (Series 4) 1: 352, 1854, nomen nudum.

= *C. sativa* β *vulgaris* de Candolle, *Prodromus* 16(1):31, 1869 (*en part*, based on plants growing spontaneous in northern India and Burma).

= *C. sativa* α *indica* f. *montana* Fristedt, Upsala Läkareförenings Förhandlingar 5: 507, 1869- 1870, nomen nudum.
= *C. himalyana* Zinger, Flora oder Allgemeine Botanische Zeitung 85: 207, 1898, nomen nudum.
= *C. sativa* subsp. *indica* sect. *spontanea* var. *spontanea* Clarke, *Cannabis* Evolution p. 224, 1987, nomen invalidum.

Neotype. Designated herein, INDIA: Himachal Pradesh, Shimla or Kinnaur ("Himalaya Boreal. Occident., Regio Temp."), *T. Thompson*, 1847 (GH). No *himalayensis* specimens exist in the herbaria of Cazzuola or Koch (pers. communications, Lucia Amadei, herb. PI; Robert Vogt, herb. B). Thompson's specimen was designated as neotype because it represents the best of several collections he made in the Himalaya. It was distributed as an exsiccatum, with duplicates at several herbaria, providing isoneotypes (BM! K! LE! US!).

Diagnosis. Plants with THC% ≥0.3% in inflorescence and a THC/CBD ratio often ≥7, sometimes less; central leaflet length:width ratio ≥6 in fan leaves near the base of inflorescences; mature achenes usually <3.6 mm long, with a persistent perianth and a protuberant base, and readily disarticulating from plant by a well-developed abscission zone.

Morphology. Plants 1.0–3.0 m tall. Central stem (stalk) internodes relatively long (often >10 cm, shorter in shorter plants), somewhat hollow (up to 1/2 stem diameter). Branches flexible, diverging from the stalk at relatively acute angles (around 45°). Leaf palmately compound, larger leaves usually with at least 7 leaflets, leaflet edges not overlapping. Central leaflet long and narrow, lanceolate in shape; margins with moderately coarse serrations, and rare secondary serrations. Female inflorescence (and infructescence) elongated and somewhat diffuse, with relatively obscure sugar leaves (a high perigonal bract-to-leaf index). Sugar leaves with CSGTs limited to the proximal half. Perigonal bract covered with a moderate density of CSGTs. Perianth membranous, hyaline with pigmented areas (brown and mottled or marbled in appearance); always persistent. Achene usually <3.6 mm long, exocarp green-brown; with an elongated base and abscission zone that is relatively narrow.

Phytochemistry. Dried female inflorescences: THC ≥0.3% (although two studies report plants with THC <0.3%); weighted $\bar{x}$ = 1.49%, range between 0.06% and 9.3%. THC/CBD ratios vary; two studies (those with THC <0.3%), who shared accessions, reported ratios of only 1.28 and 1.56; these accessions may represent East Asian fiber-type domesticates that reacquired wild-type traits. Ratios in other studies are >10, even >100. THC content and THC/CBD ratios are skewed by THCV%+CBDV%, which is higher than any other variety: $\bar{x}$ = 0.90% (Hillig and Mahlberg 2004). The terpenoid profile is similar to that of var. *indica*, except for higher levels of *β*-myrcene, *cis*-ocimene, and *β*-caryophyllene.

Genetics. Allozyme analysis (Hillig 2005a) partially segregated wild-type accessions from South Asian domesticates. He proposed that wild-type accessions from the Himalaya represented the ancestral source of South Asian domesticates.

Other characters. Generally late maturing; achenes fall from plant at maturity. Bast fiber content (as a percent of stalk dry weight) in Himalayan plants is higher than plants grown exclusively for drugs in southern India (Bredemann 1952; de Meijer 1994).

Provenance and uses. Wild-growing (possibly indigenous) populations occur throughout montane India, Nepal, and Bhutan, where they are harvested for bast fiber (stalks), *bhāng* (leaves), hand-rubbed *charas* (*hashīsh*), or achenes (seeds). Achenes in some herbarium specimens from the Himalaya were relatively large with a reduced abscission mechanism, indicating the presence of genes from domesticated plants.

Basionym notes. Cazzuola spelled the epithet *himalayensis* variously between 1873 and 1876. His earliest publication did not provide a clear diagnosis, a nomen nudum, not validly published (*ICN* Art. 38.2, Turland 2018). Koch also proposed a taxon *himalayensis* without a clear diagnosis, and he equated it with the South Asian domesticate – an erroneous concept.

Variety 3: Central Asian domesticate

***Cannabis sativa* subsp. *indica* var. *afghanica* (Vavilov) McPartl. & E.Small, stat. nov.**

urn:lsid:ipni.org:names:77208272-1
Figure 5

Cannabis sativa f. *afghanica* Vavilov, *Trudy po Prikladnoi Botanike*, *Genetike i Selektsii* 16(2): 227, 1926 (Basionym).
≡ *C. indica* var. *afghanica* Vavilov in Vavilov & Bukinich, *Trudy Po Prikladnoi Botanike*, *Genetike i Selektsii* 33 (Suppl.): 380, 1929, orthographic variant.
≡ *C. indica* var. *kafiristanica* f. *afghanica* Vavilov in Vavilov & Bukinich, *Trudy Po Prikladnoi Botanike*, *Genetike i Selektsii* 33: 381, 1929.
= *C. sativa* subsp. *culta* prol. *asiatica* var. *narcotica* Serebriakova in Serebriakova & Sizov, *Kul'turnaya Flora SSSR* 5: 36, 1940 (no Latin diagnosis and not typified).
= *C. afghanica* var. *turkistanica* Clarke, *Cannabis Evolution* p. 225, 1987, *nomen invalidum*.
= *C. sativa* var. *afghanica* McPartland, *Hemp Diseases & Pests* p. 4, 2000, nomen nudum.
= *C. sativa* var. *afghan*, Sands, U.S. patent 6,403,530, 2002, nomen nudum.

Neotype. Designated herein: AFGHANISTAN: Ghazni Province (formerly Kandahar Province), Gui-Akhen (Гуй-Ахен) village near Qala-i Murvardar (Кала-и Мурвардар), on the Ghazni-Kandahar road, *Vavilov*, 1924, from seed sown by Serebriakova in 1926 at North Caucasus Experiment Station, Maikop, Krasnodar Krai (labeled *Cannabis sativa*, WIR 609, 3945). Fig. 5a. No specimen labeled *afghanica* exists at WIR (McPartl., pers. observation, WIR 2010). The achene illustration in Vavilov and Bukinich

(1929) cannot serve as lectotype because it is not part of the protologue, which appears in Vavilov (1926).

Epitype. Designated herein, explicitly supporting the neotype: Afghanistan: Kandahar Province, near Kandahar, *Schultes*, XII.13–20.1971 (ECON 26505). Fig. 5b. The ICN defines an epitype as a specimen selected as an interpretive type when the holo-/lecto-/neotype is suboptimal for critical identification (Turland 2018). ECON 26505 serves as an epitype because its morphology unambiguously agrees with the widespread concept of "Indica". ECON 26505 also serves as a typotype – a photograph of the specimen, when alive and in the ground, which appears in Schultes et al. (1974), and is reproduced in Suppl. material 1: SF.8.

Diagnosis. Plants with THC% ≥0.3% in inflorescence and a THC/CBD ratio <7 (almost always >1); central leaflet length:width ratio <6 in fan leaves near the base of inflorescences; mature achenes usually ≥ 3.6 mm long, the perianth mostly sloughed off, lacking a prominent protuberant base, and lacking a well-developed abscission zone that allows easy disarticulation.

Morphology. Plants usually < 2 m tall, often <1 m. Central stem (stalk) internodes short (often 5–11 cm), mostly solid, central hollow usually less than 20% of stalk diameter. Branches in well-developed plants begin close to ground level, at an angle sometimes nearly 90° from the stalk axis, producing a menorah-shaped habitus. Leaf palmately compound, largest leaves typically with 7–11 leaflets, leaflet edges often overlapping, color dark green ("black hemp" Vavilov 1992). Central leaflet long and broad, often oblanceolate in shape; margins with coarse serrations, secondary serrations rarely seen. Female inflorescence (and infructescence) compact, often agglutinated with trichome exudate, with prominent sugar leaves (a low perigonal bract-to-leaf index); short internode length causes axillary racemes become confluent and coalesce into collective congested colas. Sugar leaves with dense CSGTs on the proximal half, often present beyond the midpoint of the leaflet. Perigonal bract densely covered with CSGTs. Perianth membranous, usually sloughed off, with a fringe of striped or irregularly mottled pigmentation near the base of the fruit. Achene usually ≥ 3.6 mm long, exocarp green to gray; base blunt and lacking well-developed abscission zone.

Phytochemistry. Dried female inflorescences: THC ≥0.3, in late 20th century accessions nearly always >1.0%; literature weighted $\bar{x}$ = 5.69%, up to 14.5%. This variety expresses the highest total THC%+CBD% (a measure of relative resin content of the plants, since these two cannabinoids usually dominate the resin) of all varieties, which correlates with its dense covering of glandular trichomes. Its THCV%+CBDV% content is lower than South Asian populations; Hillig and Mahlberg (2004) report a mean of 0.14%. Terpenoid profile imparts an acrid or "skunky" aroma, and uniquely expresses sesquiterpene alcohols, such as guaiol, *γ*-eudesmol, *β*-eudesmol, and the monoterpene alcohol nerolidol, as well as hydroxylated terpenoids, such as *γ*-elemene, *a*-terpineol, and *β*-fenchol.

Genetics. Allozyme and DNA studies that segregated Central Asian and South Asian domesticates are detailed in the genetics section of Variety 1. Onofri et al. (2015)

Figure 5. Type specimens of *C. sativa* subsp. *indica* var. *afghanica*. Neotype on left (**a**), epitype on right (**b**).

identified a SNP in the gene that encodes THCA synthase that was unique in two Afghani accessions and a Moroccan "*hashīsh* landrace" (their SNP accession code no. 1179, A→T transversion). It was not present in 16 other accessions of fiber- and drug-type plants.

Other characters. Generally early maturing, with greater late-season frost tolerance than South Asian domesticates. Late-season cold triggers anthocyanin production in leaves and inflorescences – the sought-after "purple weed." Achenes are mostly retained on plants, trapped by surrounding parts of the dense infructescence. Plants are more susceptible to gray mold (*Botrytis cinerea*) and powdery mildew (*Golovinomyces cichoracearum*) than South Asian domesticates.

Provenance and uses. Herbarium specimens from the 19th-early 20th centuries come from Afghanistan, northwest Pakistan, Turkestan (Uzbekistan, Tajikistan, Kyrgyzstan, Xīnjiāng Region in China), and Iran. These plant were cultivated for sieved *hashīsh* (*nasha*, *charas*) and sometimes for seed oil.

Comments. Vavilov (1926) characterized *afghanica* as "a morphological link between the wild and the cultivated races of hemp." However, evidence in Vavilov and Bukinich (1929) suggests a domesticated phenotype (argued in Suppl. material 1: SF.6). Small and Cronquist (1976) treated *afghanica* as a domesticate, synonymized under *C. sativa* subsp. *indica* var. *indica*. Small (2018) commented, "The characteristics of indica type marijuana are highly consistent with those of an advanced cultigen. Like modern oilseed cultivars, they are short and compact, an architecture reducing diversion of energy into stem production and increasing harvest index for the desired product (inflorescence). Even the foliage (with very large, wide leaflets) is consistent with the trend described earlier of advanced cultigens often manifesting larger leaves than their wild and more primitive cultivated relatives. When indica type strains are allowed to set seed (they are normally harvested for flowering material) the infructescences are very dense, preventing most of the seeds from falling away and being distributed naturally – another indication of considerable domestication." The prominent sugar leaves in the inflorescence may be another indication of domestication, as these likely increase photosynthate production very close to the developing flowers and their perigonal bracts.

Variety 4: Central Asian wild-type

***Cannabis sativa* subsp. *indica* var. *asperrima* (Regel) McPartl. & E.Small**
Figure 6

Cannabis sativa γ asperrima Regel, *Acta Horti Petropolitani* 6 (1): 476, 1879 (Basionym).
≡ *C. sativa* var. *asperrima* Regel in Herder, *Acta Horti Petropolitani* 12(1): 34, 1892.
= *C. indica* var. *kafiristanica* Vavilov in Vavilov & Bukinich, *Trudy Po Prikladnoi Botanike*, *Genetike i Selektsii* 33 (Suppl.): 381, 1929.
≡ *C. sativa* subsp. *indica* var. *kafiristanica* (Vavilov) Small & Cronquist, *Taxon* 24: 429, 1976.
≡ *C. kafiristanica* (Vavilov) Chrtek, *Časopis Národního Muzea v Praze*, *Rada Přírodovědna* 150(1–2): 22, 1981.

Lectotype. Designated herein: Kyrgyzstan, Issyk-Kul Region, near Karakol, leg.: A. Regel; det.: E. Regel, 1.X.1877 (LE). Fig. 6a.

Epitype. Designated herein, explicitly supporting the neotype: Afghanistan, Kunar Province, Chekhosarai (now Asadābād), *Vavilov*, 1924, from seeds sown by Serebriakova in 1927 at Pushkin Experiment Station, Detskoye Selo, St. Petersburg (WIR 599, 3952). Fig. 6b.

Diagnosis. Plants with THC% ≥0.3% in inflorescences and a THC/CBD ratio <7 (almost always >1); central leaflet length:width ratio <6 in fan leaves near the base of inflorescences; mature achenes usually <3.6 mm long, with a persistent perianth and a protuberant base, and readily disarticulating from plant by a well-developed abscission zone.

Morphology. Plants usually < 1.5 m tall. Central stem (stalk) internodes short (often 5–11 cm, shorter in shorter plants), mostly solid, central hollow, if present, usually less than 20% of stalk diameter. Branches in well-developed plants begin close to ground level, at an angle sometimes nearly 90° from the stalk axis, producing a menorah-shaped habitus. Leaf palmately compound, dark green, larger leaves with 5–7 leaflets, sometimes overlapping. Central leaflet relatively short and broad, often oblanceolate in shape; margins with coarse serrations, secondary serrations rarely seen. Female inflorescence small but somewhat compact, with moderately prominent sugar

Figure 6. Type specimens of *C. sativa* subsp. *indica* var. *asperrima*. Lectotype on left (**a**), epitype on right (**b**).

leaves (a moderate perigonal bract-to-leaf index). Sugar leaves with moderately dense CSGTs on the proximal half. Perigonal bract densely covered with CSGTs. Perianth membranous, with dark brown pigmentation in a mottled or sometimes linear pattern; persistent but easily flaked off with manual manipulation. Achene small, oval to elongate, exocarp dark olive colored, with an elongated base.

Phytochemistry. Dried female inflorescences: THC ≥0.3, literature weighted $\bar{x}$ = 1.49%, range between 0.4% and 4.47%. THC/CBD ratio literature weighted $\bar{x}$ = 2.23%, range 0.77 to 4.75 (one outlier 9.43). Terpenoid profile likely approximates that of the Central Asian domesticate, but has not been reported in the literature.

Provenance and uses. Herbarium specimens resembling *afghanica*, but with a wild-type phenotype, have provenance from northwestern Pakistan, Afghanistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan, and Xīnjiāng Region in China. The mountains in this region are a biodiversity "hotspot," harboring significant numbers of wild crop relatives, and over 1000 species of endemic plant species (Critical Ecosystem Partnership Fund 2017).

Comments. Herder (1892) retained *C. sativa γ asperrima* as a distinct variety, whereas he synonymized *C. erratica* and *C. sativa β davurica* under *C. sativa*. This taxon's publication date has priority over Vavilov's *kafiristanica*, but Vavilov's specimen is much better preserved, and serves as an epitype.

Discussion

Cannabis populations have undergone both natural and human selection. Fossil pollen studies show that Central and South Asian populations occupied their separate ecological niches for at least 32,600 years (McPartland et al. 2019). Their phenotypes may be presumed to have diverged, due to environmental adaptation and natural selection. Generally, Central Asia has cooler and drier Köppen climates, and shorter growing seasons. South Asia has warmer and wetter Köppen climates, and longer growing seasons (Kottek et al. 2006).

Ecological adaptions to Central and South Asian conditions probably gave rise to habitat isolation, a prezygotic reproduction barrier. Central Asian plants transplanted to South Asian conditions suffer reduced fitness (reproductive success). When their heavily-flowered branches are exposed to monsoonal rainfall, they may snap under the load, because of their brittle, menorah-shaped branching habitus. This does not occur in South Asian plants, whose branches are more flexible, and come off the stalk at more acute angles. The dense, leafy inflorescences of Central Asian plants have poor resistance to fungi that proliferate in high humidity, such as *Botrytis cinerea.* In comparison, the looser, less leafy inflorescences of South Asian plants better tolerate necrotrophic fungi (McPartland et al. 2000). See Suppl. material 1: SF.1 for more examples of prezygotic reproduction barriers.

We mapped the distribution of herbarium specimens identified as wild-type var. *asperrima* and var. *himalayensis*, using ArcGISPro 2.2 (Fig. 7). The distribution of *himalayensis* and *asperrima* herbarium specimens can be compared to two previous publications that mapped these geographic ranges, by Indian Hemp Drugs Commission (1894) and Breckle and Koch (1982), reproduced in Suppl. material 1: SF.4.

The distributions of *himalayensis* and *asperrima* are parapatric – their ranges do not significantly overlap, but are adjacent to each other. Their interface lies between the Indus River watershed (the northwestern border of var. *himalayensis*) and the Kunar/Chitral River watershed (the southeastern border of var. *asperrima*). Parapatry supports our hypothesis of habitat isolation. The distribution of wild-type plants sweeps through an arc of mountains in Central Asia (Hindu Kush, Karakoram, Pamir, and Tian Shan) and in South Asia (Himalaya and Purvanchal Range).

Contrasting climates in Central Asia and South Asia give rise to distinctive flora, and biogeographers assign Central Asia and South Asia to separate floristic regions. Floristic regions are well-defined areas of the world, recognized by their relatively uniform composition of plants species, including endemic flora. The floristic regions mapped in Fig. 7 are based on Djamali et al. (2012). Herbarium specimens of var. *asperrima* localize in the Irano-Turanian region, whereas herbarium specimens of var. *himalayensis* localize in the Indian region. Their parapatric interface lies in the Saharo-Sindian region. Outliers in other floristic regions likely represent herbarium specimens of naturalized escapes (formerly domesticated plants that reacquired wild-type traits).

Note that the Indian floristic region by Djamali et al. (2012) was updated and simplified from White and Léonard (1991), who separated peninsular India from the Hima-

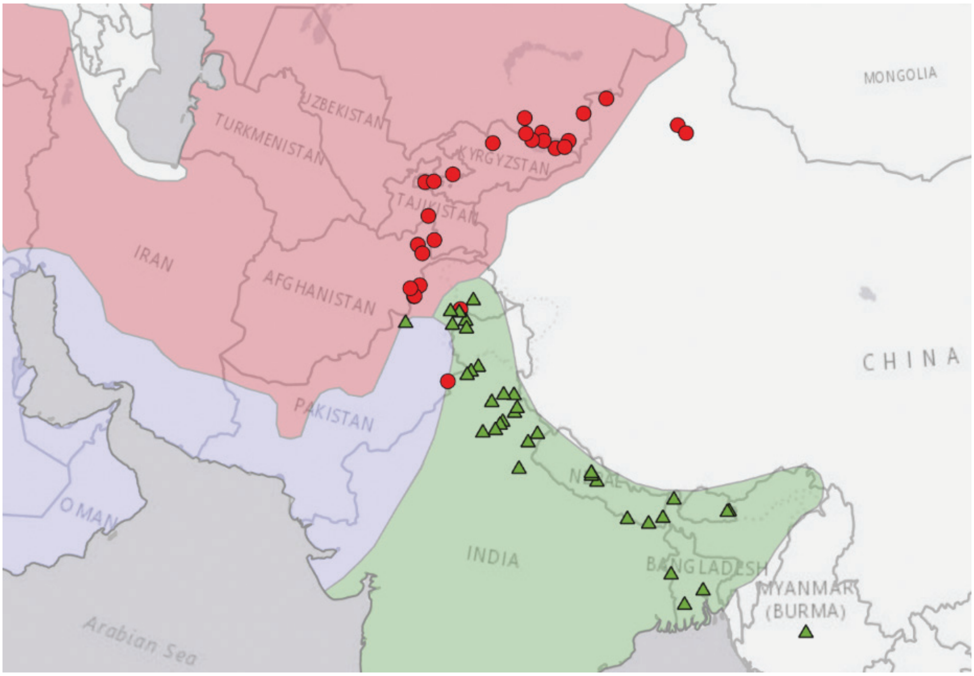

Figure 7. Distribution of herbarium specimens. Red circles: var. *asperrima*; green triangles: var. *himalayensis*. Floristic zones based on Djamali et al. (2012): Red area: Irano-Turanian region; green area: Indian region; lilac area: Saharo-Sindian region. Other floristic regions not demarcated and unlabeled. Background base map by Natural Earth, free open-source map data (https:// www.naturalearthdata.com).

laya range. They, in turn, simplified Takhtajan (1986), who split the Himalaya range into eastern and western provinces, with Kali Gandaki in Nepal at the divide. Takhtajan separated the "Eastern Himalayan Province" due to an influx of flora from China. We hypothesize that this was the route taken by *Cannabis* into the Himalaya, hence into peninsular India. It arrived relatively recently, the oldest fossil pollen in all of South Asia dates back only 32,600 years (McPartland et al. 2019). The morphology of var. *himalayensis* shares traits with East Asian hemp, such as tall height, relatively hollow shoots with a high percentage of bast fiber and little wood; leaflets with moderately coarse serrations; inflorescences elongated and somewhat loose, with a high perigonal bract-to-leaf index. Himalayan plants and East Asian hemp share similar THC/CBD ratios (Suppl. material 1: Table S11) and terpenoid profiles (Suppl. material 1: Table S15).

Early agriculturalists launched *Cannabis* on its next round of evolution. Floristic regions became "centers of diversity" (CODs), where wild-type plants were domesticated. Vavilov (1935) named eight CODs around the world, and mapped them. He presciently named two separate CODs for *Cannabis indica*: the "Central Asiatic COD," which corresponds with the Irano-Turanian floristic region, and the "Indian COD," which corresponds with the Indian floristic region.

Central and South Asian populations diverged further, under different human management regimes (which were also under climatic selection). Central Asians produced sieved *hashīsh*, where bulk processing likely limited the selection of individual high-THC plants (de Meijer 1999). Thus THC/CBD ratios remained close to wild-type. South Asians produced *gañjā*, where plants could be individually harvested, and South Asians selected seeds from choice, high-THC plants, thereby increasing THC/CBD ratios over the course of a millennium (Clarke and Merlin 2013).

South Asian germplasm was carried to Southeast Asia and East Africa by the 13th century, and to Brazil during the African slave trade (Clarke and Merlin 2013). The Central Asian domesticate had a restricted range prior to the 1970s, limited to Afghanistan, Pakistan, and Turkestan. Plants from Turkestan are sometimes classified as South Asian domesticates (Clarke and Merlin 2013; Small 2015), although Clarke (1987) erected *C. afghanica* var. *turkistanica* [sic] for Turkestani domesticates. Herbarium collections from the 19th century indicate that cultivated Turkestani plants were Central Asian domesticates, not South Asian domesticates.

The goal of this investigation was to identify "practical and natural" taxa within *C. sativa* subsp. *indica.* Our decision to cleave the subspecies into four varieties raises debates regarding nomenclatural priorities, nested hierarchies, and practical applications. We address these issues in Suppl. material 1: SF.13. Our emphasis has been on the domesticates, representing landraces of South Asian heritage (*C. sativa* subsp. *indica* var. *indica*), and Central Asian landraces (*C. sativa* subsp. *indica* var. *afghanica*). Several features tend to differentiate these taxa (Table 1). They are best segregated by their THC/CBD ratios and terpenoid profiles.

Few trends in Table 1 that distinguish the landraces remain true for "Indica" and "Sativa" strains in commerce today. In particular, THC/CBD ratios have converged in material allegedly representing "Indica" and "Sativa" (Fig. 2). Some recent studies of "Indica" and "Sativa" show reversals from their landrace ancestors. Whereas landraces from Central Asia expressed THC/CBD ratios lower than landraces from South Asia; six recent studies reported the reverse in "Indica" and "Sativa" (Fischedick et al. 2010; Hazekamp and Fischedick 2012; Elzinga et al. 2015; Hazekamp et al. 2016; Lynch et al. 2016; Jikomes and Zoorob 2018). This prompted Hazekamp and Fischedick (2012) to abandon "Indica"/"Sativa" nomenclature, in favor of "chemovars."

Terpenoid profiles, surprisingly, have largely remained distinct. "Indica" hybrids uniquely express sesquiterpene alcohols, like their Central Asian ancestors. These are absent in South Asian landraces and their "Sativa" descendants (Suppl. material 1: SF.9). Centuries of artificial selection for THC content apparently did not alter sesquiterpene alcohol content. The same may be true for THCV. Limited evidence suggests that THCV, a marker of South Asian landraces and South Asian wild-types (Hillig and Mahlberg 2004), is retained in "Sativa" (Hazekamp and Fischedick 2012; Aizpurua-Olazizolo et al. 2016).

Intermediate forms are often observed between varieties, which are capable of interbreeding and gene exchange under the biological species concept. Where varieties overlap geographically, they frequently generate intermediate forms. Intermediate forms are commonly seen in herbarium specimens from Pakistan, which is the

Table 1. Trends distinguishing the domesticated high-THC varieties *C. sativa* subsp. *indica* var. *indica* and *C. sativa* subsp. *indica* var. *afghanica*.[1]

Character	*C. s.* var. *indica*	*C. s.* var. *afghanica*
THC/CBD ratio	≥7	<7
THCV+CBDV content	Often present	Often absent
terpenoid profile	"herbal" or "sweet" aroma, with no sesquiterpene alcohols	acrid or "skunky" aroma, with the presence of guaiol, γ-eudesmol, and β-eudesmol
height, branching	well-grown plants usually ≥ 2 m; branching flexible (with upward-angled habitus)	well-grown plants usually < 2 m; branching inflexible (with menorah-shaped habitus)
leaves at the base of inflorescences	lighter green, usually 7 leaflets, with gaps between leaflet margins	darker green, usually 9 leaflets, with overlapping margins
central leaflets of multifoliolate leaves	long and narrow, lanceolate or linear-lanceolate in shape; margins finely serrate, biserrate margins sometimes seen	long and broad, often oblanceolate in shape; margins coarsely serrate, biserrate margins rarely seen
pistillate inflorescences	relatively diffuse & open, sugar leaves relatively obscure (with a high perigonal bract-to-leaf index)	compact and with prominent sugar leaves (with a low perigonal bract-to-leaf index)
stalked glandular trichome density	few on the proximal end of floral leaves; moderately dense on perigonal bracts	many on the proximal end of floral leaves, extending at least half way down floral leaves; very dense on perigonal bracts
perianth	perianth with mottled pigmentation, sometimes persistent over entire achene	perianth with mottled pigmentation, rarely persistent, limited to base of achene
achene	exocarp color green brown (darker than *afghanica*), lower range of size smaller than *afghanica*; loosely embedded in perigonal bract and sugar leaves	exocarp color olive green to gray (lighter than *indica*), upper range of size larger than *indica*; tightly embedded in perigonal bract and sugar leaves
maturation time	later maturing	earlier maturing
other characters	susceptible to black mildew (*Schiffnerula cannabis*), monoecious plants occasionally seen	susceptible to gray mold (*Botrytis cinerea*) and powdery mildew (*Golovinomyces cichoracearum*), monoecious plants rarely seen

[1] As emphasized in the text, the differences presented here represent the historical, unhybridized forms of "Indica" and "Sativa" landraces, before extensive recent hybridization between them.

center of diversity for subspecies *indica* – all four varieties occur there. Many herbarium specimens from the Middle East (Turkey, Syria, Lebanon, Palestine, Israel, Jordan, Iraq, western Iran) and north Africa (Egypt to Morocco) also show intermediate phenotypes. Clarke and Merlin (2013) classified Middle Eastern and north African populations as ancestors of South Asian landraces. However, Central Asian germplasm may have reached the Middle East in the 1200s, and again in the 1600s (Suppl. material 1: SF.11).

Several quantitative phenotypic traits await measurement in *Cannabis*, such as glandular trichome density per mm^2 surface area, glandular trichome size, and gland head abscission. An unambiguous genetic "barcode" differentiating *C. indica* and *C. afghanica* awaits discovery. See "Future directions" in Suppl. material 1: SF.13. Lastly, this study has not addressed East Asian hemp. Cannabinoid and genetic data segregate East Asian *Cannabis* as a subset of the *C. indica* subsp. *indica* genepool (Hillig 2005b). See Suppl. material 1: SF.12 for more about East Asian *Cannabis*, particularly regarding biodiversity in Yúnnán.

Conclusions

The four *Cannabis* varieties circumscribed and named here merit formal recognition. Recognizing infraspecific taxa helps to identify populations vulnerable to extinction (e.g., Ellstrand 2003; Haig et al. 2006). In the wake of the United Nations Biodiversity Convention, infraspecific variation has become a focus for conservation efforts (Coates et al. 2018). Recognizing the four *Cannabis* varieties and their unique morphological and chemical characters also provides "prior art," thwarting claims of originality in *Cannabis* utility patents.

Collection and conservation of germplasm of indigenous populations of Central and South Asian landraces in their centers of diversity is urgently needed. The germplasm base outside their centers of diversity has become genetically contaminated by widespread crossbreeding. In the context of climate change and unpredictable future needs, in situ conservation of agrobiodiversity is much preferable for crop plants and their wild relatives, but given the precarious continued existence of unaltered aboriginal wild populations of *Cannabis* in Asia, preservation in seed banks is an immediate priority. Hopefully the unambiguous names provided may help prevent extinction of these taxa.

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Supplementary material 1

A classification of endangered high-THC cannabis (*Cannabis sativa* subsp. *indica*) domesticates and their wild relatives

Authors: John M. McPartland, Ernest Small

Data type: species data

Explanation note: Description of species concepts, level nominalism, wild-type nominalism, protologues, nomenclatural priority, intermediate forms, and elaboration of methodology. List of taxonomic characters and their respective coding, used in the morphological and total evidence analyses.

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RESEARCH ARTICLE

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Poa magellensis (Poaceae), a new species from Central Apennine (Italy)

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Abstract

A new species, *Poa magellensis* **sp. nov.**, is described and illustrated based on collections from the Majella Mountains in Central Apennine, Italy. It is morphologically similar to *P. ligulata* Boiss., but can be distinguished by green leaves, the basal ones adaxially lightly scabrous or sparsely hairy, longer ligules particularly in the upper leaves, panicles denser with primary branches sub-erect to erect, glumes with broader scarious margin, more acute glumes and lemmas, lemmas and paleas longer, rachilla hairy, calluses usually with a crown of hairs or shortly webbed, caryopses longer. A distribution map of the species is also presented.

Keywords

Abruzzo, endemic, Italy, Majella National Park, new species, *Poa*, Poaceae

Introduction

The genus *Poa* L. (Poaceae, Pooideae, Poeae, Poinae), one of the largest genera of grasses, has a cosmopolitan distribution, principally in temperate regions of both hemispheres and in mountainous regions of the tropics (Soreng et al. 2017; Peterson and Soreng 2018). It is a monophyletic genus and comprises approximately 550 annual and perennial species (Soreng 1990; Gillespie et al. 2007, 2008; Soreng et al. 2017). Based on molecular phylogenetic studies, *Poa* has been divided into five subgenera: *P.* subg. *Ochlopoa* (Asch. & Graebn.) Hyl., *P.* subg. *Poa*, *P.* subg. *Pseudopoa* (K.Koch) Stapf, *P.* subg. *Stenopoa* (Dumort.) Soreng & L.J.Gillespie and *P.* subg. *Sylvestres* (V.L.Marsh ex Soreng) Soreng & L.J.Gillespie (Gillespie et al. 2007, 2008; Soreng et al. 2010; Giussani et al. 2016). As concerns Italy, the genus *Poa* is represented by 29 taxa (species and subspecies) (Bartolucci et al. 2018). Recently, two other species have been added to the flora of Italy: *P. jubata* A.Kern. (Brullo et al. 2019) and *P. ligulata* Boiss. (Conti et al. 2019). This latter taxon belonging to *P.* subg. *Ochlopoa* sect. *Alpinae* (Hegetschw. ex Nyman) Stapf, occurs in Spain and NW Africa (Buschmann 1942; Ortega-Olivencia and Devesa 2018) and recorded in France (Greuter and Raus 2005) by mistake (Tison and de Foucault 2014). Its recent discovery in Central Apennine was considered as a confirmation for Italy; in fact, this species had already been collected by G. Rigo in Central Apennine on Majella Mountains "*Iter in Aprutio anno 1905. Poa magellensis mihi, proxima P. ligulata Bss. In pascuis alpinis di M. Amaro, calc. 2600 m, Jul. exeunte G. Rigo* " (BP). Buschmann (1942) quoted the specimen preserved at BP and listed *P. magellensis* Rigo *in sched.* (this name was never validly published) as a doubtful synonym of *P. ligulata* and regarded the collecting site of the specimen doubtful. After this record the species was no longer reported for Italy until the discovery by Conti et al. (2019). The specimen traced in BP and others collected by us in Majella were provisionally attributed to *P. ligulata* (Conti et al. 2019). Indeed, on the basis of a preliminary morphological analysis, the population from Majella showed peculiar features that led us to compare it with those from Spain and Morocco referable to *P. ligulata*.

Materials and methods

This study is based mainly on field surveys, on an extensive analysis of relevant literature, and on careful examination of herbarium specimens preserved at APP, BC, BP, SALA (acronyms follow Thiers 2019). In order to investigate the morphological variability of *Poa ligulata* and to correctly classify the population from Italy, morphological analyses were carried out on 40 selected specimens including *Poa* from Central Apennine (20 specimens) and *P. ligulata* from Spain and Morocco (20 specimens). The individuals were studied measuring 20 quantitative characters (see Table 1). Other qualitative characters were studied: shape of ligule, shape of glume, shape of lemma, shape of palea, rachilla hairness, callus hairness. Morphological observations and measurements were conducted on living and dried (primarily) specimens. All morphological characters were observed and photographed with a Leica MZ16 stereoscopic microscope and a Canon S50 camera.

Table 1. Morphological quantitative characters studied.

Character
culm height (mm)
number of culm nodes
blade length (basal leaf) (mm)
blade width (basal leaf) (mm)
ligule length (basal leaf) (mm)
ligule length (upper leaf) (mm)
panicle length (mm)
panicle width (mm)
rachis diameter (mm)
spikelet length (mm)
spikelet width (mm)
number of flowers in each spikelet (mm)
lower glume length (mm)
upper glume length (mm)
scarious margin width of glume (mm)
lemma length (mm)
length of hair strip on the lemma keel (mm)
palea length (mm)
anther length (mm)
caryopsis length (mm)

Taxonomy

***Poa magellensis* F.Conti & Bartolucci, sp. nov.**
urn:lsid:ipni.org:names:77208269-1
Figs 1–3

Type. Italy. Abruzzo, Fara S. Martino (Chieti), Majella, M. Acquaviva (WGS84 42°06'11.1"N, 14°07'55.9"E), 2720 m, pendii rupestri, 30 Jul. 2019, *F. Conti, L. Di Martino & V. Di Cecco s.n.* (holotype: APP 65502; isotype: APP 65501).

Diagnosis. *Poa magellensis* differs from *P. ligulata* by: basal leaves adaxially lightly scabrous or sparsely hairy vs glabrous, longer ligules particularly in the upper leaves (2.5)4–6.9(9) vs. (1.8)2–5(6) mm long, panicles denser with primary branches suberect to erect, glumes with broader scarious margin 0.1–0.4(0.5) vs. 0–0.2 mm wide, more acute glumes and lemmas, longer lemmas (2.7)2.9–3.5(3.6) vs. (2.1)2.3–2.9(3) mm long, longer paleas (2.2)2.5–3.1(3.2) vs. 2–2.8(3) mm long, rachilla hairy vs glabrous, calluses usually with a crown of hairs or shortly webbed vs glabrous, longer caryopses 1.7–2.2 vs. 1.4–1.7 mm long.

Description. Perennials; without horizontal or downward tending cataphyllous shoots, densely tufted, bicolour, green and white because of the brightness of large exerted ligules; tillers erect or ascending, intravaginal. *Culms* 20–150 mm tall, 0.25–0.5 mm in diameter, erect to ascending slender, terete, smooth, weakly sulcate, nodes (1)2 exerted, thickened at the base with old leaf-sheaths. *Leaves* green, leaves-sheaths

Figure 1. *Poa magellensis* F.Conti & Bartolucci, sp. nov. **A** panicle (Cima delle Murelle, Abruzzo, Italy; photo by F. Conti) **B** tuft bicoloured, green and white because of the brightness of the large exerted ligules (Cima delle Murelle, Abruzzo, Italy; photo by F. Bartolucci) **C** species habitat (Cima delle Murelle, Abruzzo, Italy; photo by F. Conti).

Figure 2. *Poa magellensis* F.Conti & Bartolucci, sp. nov. **A** habit **B** spikelet without glumes **C** palea **D** glumes **E** ligules.

terete, smooth, glabrous, ribbed; collars smooth, glabrous; blades of basal leaves (8)8.6–19.4(20) mm long, 0.8–1.5(1.6) mm wide, linear, usually folded, abaxially rough, margins lightly scabrous, adaxially lightly scabrous or sparsely hairy, prow-tipped, blades strongly graduated or reduced distally, blades of uppermost leaves 3.5–12 mm long, ligules of the basal leaves (4)4.7–10.2(12) mm long, smooth, glabrous, whitish-pearly, lacerate, apices acuminate, decurrent on the sheaths; ligules of the uppermost leaves

FLORA DEL PARCO NAZIONALE DELLA MAJELLA

Poa magellensis F.Conti & Bartolucci

POACEAE

regione Abruzzo CH **cod.** 65502
comune Fara San Martino
località M. Acquaviva
habitat pendii rupestri **alt.** 2720
data 30/07/2019 **coord.** 428290E 4661495N WGS84
legit F. Conti, L. Di Martino e V. Di Cecco
det. F. Conti, F. Bartolucci
oss. HOLOTYPE

Figure 3. Holotype of *Poa magellensis* F.Conti & Bartolucci (APP, reproduced with permission of the Herbarium, Centro Ricerche Floristiche dell'Appennino, Italy).

(2.5)4–6.9(9) mm long. *Panicles* compact, narrowly ellipsoid, (11)11.6–22.4(23) mm long, 5–10(13) mm wide, dense, with 3–7 nodes, rachis with 1–2(–3) branches per node; primary branches sub-erect to erect, sulcate or few-angled, scabrous 0.1–0.3 mm in diameter, longest branches up to 5 mm, with 1–3 spikelets, pedicels 0.1–4 mm. *Spikelets* 3.2–5(5.4) mm long, (1.3)1.4–3.2(3.5) wide, laterally compressed; bulbifery absent, violaceous and green, not pruinose, florets 2–4(5); rachilla hairy to sparsely hairy. *Glumes* subequal (1–)3 veined, not reaching lemma apices, lanceolate, with scarious margin 0.1–0.4(0.5) mm, glabrous, distinctly keeled, keels moderately scabrous in the distal part, apices sharply-acute; lower glumes (2.1)2.2–3.3(3.4) mm long; upper glumes (2.4)2.5–3.6 mm long; calluses with a crown of hairs (0.1–0.3 mm) or shortly webbed; *lemmas* (2.7)2.9–3.5(3.6) mm long, 1–5 weakly veined, lanceolate, violaceous or sometimes green, with scarious margin broader in the distal part, distinctly keeled, keels short villous in proximal part (1–2 mm), scaberulous along distal keel and sparsely in the upper sides, apices acute; paleas (2.2)2.5–3.1(3.2) mm long, scabrous along the keels, between keels glabrous. *Anthers* 1–2 mm long. *Caryopses* 1.7–2.2 mm long.

Distribution and habitat. *Poa magellensis* is endemic to Majella Mountains (Mt. Amaro, Mt. Focalone, Mt. Acquaviva, between Mt. Focalone and Mt. Acquaviva, Cima delle Murelle) in Central Apennine (Italy). It grows on limestone rocky slopes from 2200 up to 2730 m a.s.l. (Fig. 4).

Phenology. Flowering in July, fruiting July to August.

Chromosome number. A single population (Majella, Cima delle Murelle) of *P. magellensis* is resulted diploid with 2n = 14 chromosomes (Astuti et al. 2019 under the name *P. ligulata*).

Conservation status. The populations of *P. magellenis* are included in NATURA 2000 network within the Site of Community Interest "IT140203 Majella" in the Majella National Park. The extent of occurrence (EOO) is 6.86 km^2 calculated with minimum convex hull polygon in QGIS and area of occupancy (AOO) is 16 km^2 calculated with a 2×2 km cell fixed grid. The species occurs in only one location (definition according to IUCN 2019), but the population is not declining, and there are no extreme fluctuations. According to IUCN criterion B (2019) we propose to include *P. magellensis* in the following category: Near Threatened (NT).

Etymology. The specific epithet of the new species is derived from the type locality, Magella Mountains (currently Majella Mountains).

Taxonomic notes. The new species *P. magellensis* is similar to *P. ligulata* but can be distinguished by several characters as shown in Table 2.

Additional specimens examined. ***Poa magellensis*** F.Conti & Bartolucci (paratypes): Italy. Abruzzo: in pascuis alpinis di M. Amaro, calc., m. 2600, Jul exeunte, *G. Rigo s.n.* [Iter in Aprutio anno 1905] (BP); Majella, sotto l'anfiteatro delle Murelle e il Fusco, verso il Blockhaus, Pennapiedimonte (Chieti), pendii rupestri, 2250–2500 m, 04 Aug. 1991, *F. Conti s.n.* (APP 12455); Majella, dal Blockhaus al Focalone, Caramanico Terme (Pescara), pendii rupestri, 2350 m, 30 Jul. 2009, *F. Conti, L. Gubellini & R. Soldati s.n.* (APP 59356); salendo a Cima delle Murelle in loc. La Carozza, Pennapiedimonte (Chieti), rupi e pendii rupestri, 2300 m, 02 Sep. 2011, *F. Bartolucci & F. Conti s.n.* (APP 59212, 59214); Majella, Cima delle Murelle, Pen-

Figure 4. Map showing distribution of *Poa magellensis* F.Conti & Bartolucci, sp. nov. in Central Apennine, Abruzzo (Italy).

napiedimonte (Chieti), pendii rupestri, 2250 m, 17 Jul. 2019, *F. Conti & L. Di Martino s.n.* (APP 65242, 65243, 65244, 65245, 65246, 65247, 65248, 65249, 65250, 65251, 65252, 65254, 65253, 65255). ***Poa ligulata*** Boiss.: Morocco. c38 km from Chefchaouen, 14 km above Bab Taza on track to Djbel Talamssemtane (35°9'N, 5°12'W), forest of *Abies maroccana* and *Cedrus atlantica*, on limestone, 1765–1900 m, 26 Jun. 1992, *Achhal et al. n. 64.2260* [Optima Iter Mediterraneum V] (APP 45892; SALA 144759); Tanger-Tétouan: Bab Taza, pr. Refugio del Jbel Lakraa, 35°8'11,7"N, 5°8'13,6"W, 1693–2000 m, substrato calizo dolomitico, 16 Jun. 2008, *S. Andrés et al. n. AQ2695* (SALA 159115); Spain. Aznattin W. (Macizo de Magina pr. Jaén) 1710 m. riscas, 20 Jun. 1926, *Cuatrecasas s.n.* (BC-70613); Carceles in decliv. NW, rupestr. 1950 m. alt., 17 Jun. 1826, *Cuatrecasas s.n.* (BC-70612); Sierra Tejeda, Málaga, 10 Jun. 1919, *Gros s.n.* (BC-70615); Cadiz: Grazalema, 30 Jun. 1925, *Font i Quer & Gros s.n.* (BC-914825); Baetica: in graminosis l. Cerrecillos del Sabinal dicto, montis Sierra de Gador (Almeria), ad 2000 m alt., 27 May 1921, *Gros n. 108* [Flora Iberica selecta Cent. II] (BC-86523,BC-61436, BC-86524); *ibidem*, *Gros s.n.* (BC-70614); Cerro de la Laguna, Sierra de Cazorla, 1550 m, (J) WG0295, in locis lapidosis cacuminalis, 25 May 1981, *A.M. Hernández s.n.* (BC-641787); Teruel: Palomar de Arroyos, port de Sant Just, entre Escucha i Palomar de Attoyos, UTM 30T 687830 4515699, 1486 m, 02 Jun. 2010, *S. Pyke & M. Aixart s.n.* (BC-904950); Sierra de Javalambre (España, prov. Teruel), 30S

Table 2. Comparison of the key features of *Poa ligulata* and *P. magellensis*. Quantitative continuous characters are expressed in mm and are reported as mean ± standard deviation and 10–90 percentiles (extreme values in brackets). For quantitative discrete cardinal characters, 10–90 percentiles are given (extreme values in brackets).

Character	*Poa ligulata*	*Poa magellensis*
Leaves	green or glaucous	green
adaxial blade (basal leaf)	glabrous	lightly scabrous or sparsely hairy
blade width (basal leaf)	(0.9)1–2.5(2.7)	0.8–1.5(1.6)
	1.53±0.49	1.07±0.23
ligule length (upper leaf)	(1.8)2–5(6)	(2.5)4–6.9(9)
	3.35±1.13	5.35±1.44
panicle width	(8)8.5–20	5–10(13)
	13.81±4.22	7.6±2.13
number of flowers in each spikelet	3–6(7)	2–4(5)
upper glume length	2–2.8(3)	(2.4)2.5–3.6
	2.45±0.25	3.08±0.3
scarious margin width of glume	0–0.2	0.1–0.4(0.5)
	0.08±0.07	0.28±0.11
apex of glume	acute	sharply-acute
lemma length	(2.1)2.3–2.9(3)	(2.7)2.9–3.5(3.6)
	2.6±0.23	3.23±0.24
palea length	2–2.8(3)	(2.2)2.5–3.1(3.2)
	2.37±0.28	2.87±0.23
caryopsis length	1.4–1.7	1.7–2.2
	1.52±0.12	1.94±0.16
hairs on rachilla	absent	present
hairs on callus	absent	present

XK 74, alt 1850 m, pastizal subnitrófilo de alta montaña, *Festuco-Pojon ligulatae* Rivas Goday & Rivas Martínez, 01 Jun. 1985, *M. Costa et al. n. 13853* (SALA 83393); La Rioja: Turruncún, Sierra de Préjano, Peña Isasa, 30T WM7068, 1450 m, en crestones y pequeñas repisas con suelo esquelético, caracterizando los céspedes xerofiticos del *Festuco-Pojon ligulatae* Rivas Goday & Rivas Martínez 1966, 29 Jun. 1988, *Amich, Fdez. Diez & Sanchez Rodriguez n. 97* [Exsiccata Selecta Flora Ibericae] (SALA 83963, 45290); Villafeliz de Babia (León), 20 May 1983, *J. Andrés & Fllamas s.n.* (SALA 68424); Granada: Sierra Nevada, Puerto de la Ragua, suelos pedregosos, 17 Jul. 1971, *Ladero & E. Valdés s.n.* (SALA 64021); Valporqueto (Espagne, prov León, Cordillera Cantábrica), alt. 1250 m, pâturages pierreux dans la zone subalpine cantabrique, fissures et replats des rochers calcaires, communautés du *Festuco-Pojon ligulatae*, 06 Jul. 1980, *J.M. Losa Quintana n. 11026* (SALA 70101); Segovia: Navares de las Cuevas, Peñacuero, 08 Jun. 1985, *Rico, T. Romero & Sánchez Rodriguez s.n.* (SALA 49384); Pastizales pedregosos en el Cerro de San Cristobal, Grazalema (Cádiz), Jun. 1961, *Borja s.n.* (SALA 1747); Ciudad encantada (Cuenca), 13 May 1977, *Fernández Diez, Rico, Amich & Sánchez s.n.* (SALA 11599); Guadalajara: Saúca, 30T WL 4041, 1150 m, páramo calizo con *Genista pumila*, 22 Jun. 1987, *L. Villar & P. Montserrat s.n.* (SALA 125139); Cádiz, Grazalema base del Cerro de San Cristobal, 23 May 1966, *E.F. Galiano s.n.* (SALA 22260); Teruel: nacimiento del rio

Tajo, 15 Jun. 1982, *Rico & Sánchez s.n.* (SALA 32128); León: Ponferrada, Peñalba de Santiago, en calizas, 25 Jun. 1984, *S. Castroviejo, J.L. Fernández Alonso, Gonzalo & Valdes s.n.* (SALA 103309); Prado Martín, Penyagolosa prov. Castellón, 1550 m, *Poo-Festucetum hystricis*, 20 Jun. 1980, *I. Soriano s.n.* (SALA 71015); Granada: Sierra Nevada, Barranco de San Juan, en suelos pedregosos, 3200 m, 10 Jul. 1980, *M. Ladero, López-Guadalupe & Molero* (SALA 61347); Castellon: El Toro (L'Alt Palància), la Halmarja, 30S XK82, 1500 m, patizales ralos de Minuartio-Pojon, 18 May 1984, *A. Aguilella n. 15828* (SALA 90109); Segovia: villar de Sobrepeña, Cerro del Valdemuela, 15 May 1983, *T. Romero s.n.* (SALA 40608); Segovia; Sepúlveda, 01 Jun. 1986, *X. Giraldez & T. Romero s.n.* (SALA 41703); Segovia: Prádena, Peña Corva, 02 Jun. 1984, *T. Romero s.n.* (SALA 40607); Burgos: Hontorio de la Cantera, 30T VM 4769, 950 m, frecuente, encinar, calizas de cantera subterraneas, 16 May 2004, *J.L.B. Alonso s.n.* (SALA 124549); Cadiz: Sierra de Grazalema, 12 Jun. 1976, *A.M. Hernandez s.n.* (SALA 31879).

Key to identification of species of *Poa* sect. *Alpinae* in Europe (from Edmondson 1980 modified)

1 Lemma hairy between veins **2**

– Lemma glabrous between veins **4**

2 Culm below the panicle 0.7–1 mm in diameter; leaves 4–10 cm long; lower cauline and basal leaves with a short, ± truncate ligule; panicle ± pyramidal .... ***P. alpina***

– Culm below the panicle 0.2–0.5 mm in diameter; leaves (1.5)2.5–6 cm long; cauline and basal leaves with an elongate, acute ligule; panicle ± ovoid **3**

3 Leaves 2–4.5 mm wide, flat to weakly folded .... ***P. badensis***

– Leaves 1.5–2.5 mm wide, canaliculate to strongly folded .... ***P. molinerii***

4 Stem (15)20–30(40) cm; panicle 3.5–5 cm, ellipsoid-oblong .... ***P. media***

– Stem 3.5–20(30) cm; panicle 1–5 cm, ellipsoid, ovoid to pyramidal **5**

5 Ligule of the basal leaves 1–2 mm, hyaline **6**

– Ligule of the basal leaves 2.5–12 mm, milky white **7**

6 Lemma callus glabrous .... ***P. thessala***

– Lemma callus woolly .... ***P. pumila***

7 Leaves green, adaxially lightly scabrous or sparsely hairy, ligule of the upper leaves (2.5)4–6.9(9) mm, panicle narrowly ovoid, glume with scarious margin 0.1–0.4(0.5) mm, glume sharply acute, lemma (2.7)2.9–3.5(3.6) mm, rachilla hairy, callus usually with a crown of hairs or shortly webbed, caryopsis 1.7–2.2 mm .... ***P. magellensis***

– Leaves green or glaucous, adaxially glabrous, ligule of the upper leaves (1.8)2–5(6) mm, panicle ovoid to pyramidal, glume without or with scarious margin up to 0.2 mm, glume acute, lemma (2.1)2.3–2.9(3) mm, rachilla glabrous, callus glabrous, caryopsis 1.4–1.7 mm .... ***P. ligulata***

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