RESEARCH ARTICLE

Taxonomic revision of *Disporum* Salisb. (Colchicaceae, Uvularioideae) of Taiwan

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Abstract

A taxonomic revision of *Disporum* of Taiwan is presented with two species and one variety being recognised. The diagnostic characters of *Disporum* include the colour of tepals, stolon morphology, the trichomes of filaments and style and leaf morphology. These characters, along with karyotype and pollen morphology, are discussed and evaluated amongst different taxa. As a result, *D. kawakamii* and *D. shimadae* are treated as independent species, rather than varieties of *D. cantoniense* and *D. sessile*, respectively. *Disporum nantouense* is treated as a synonym of *D. sessile* var. *intermedium* **stat. nov.** Detailed descriptions, type information, diagnostic key, line drawings, photos and distribution maps are provided.

Keywords

Introduction

Disporum Salisb. comprising of about twenty species, is distributed from the Himalayas through Vietnam, China, Japan, Korea and Russia. More than fourteen species have been found in China (Chen et al. 2000), four species are recorded in Japan (Tamura 2016) and four species are recorded in Taiwan (Ying 2000). Some new species have recently been described (Hu et al. 2016; Hareesh et al. 2018). This genus is characterised by having fleshy roots, erect stems with scale leaves at the lower part, pendulant flowers

and berries, diagnostic characters of intrageneric taxa dependent on whether stolons are present, tepals spreading or not, colour and shape of tepals, length and trichome type of filaments and styles and colour of fruits (Hara 1988; Chen et al. 2000).

Taiwanese species have been studied by several authors from a morphological and karyological standpoint (Matsumura and Hayata 1906; Kawakami 1910; Hayata 1911; Chao et al. 1963; Liu and Ying 1978; Hara 1988; Ying 1989; Ying 1990ab; Wang 1997; Ying 2000), but each author had his/her own way of treating different ranks. Chao et al. (1963) recognised two species, *D. kawakamii* and *D. shimadae*, Liu and Ying (1978) three species, *D. kawakamii*, *D. pullum* Salisb. & Hook. f., and *D. shimadae* and Hara (1988) recorded two varieties and one form, *D. cantoniense* (Lour.) Merr. var. *kawakamii* (Hayata) Hara, *D. sessile* (Thunb.) D. Don & Schult. var. *shimadae* (Hayata) Hara and *D. sessile* var. *shimadae* f. *intermedium* Hara. Ying (2000) treated the genus as consisting of four species *D. kawakamii*, *D. nantouense* Ying, *D. shimadae* and *D. taiwanense* S. S. Ying.

Recently, in studying Liliaceae s. l. of Taiwan, we found that the diagnostic characters of *Disporum* were highly variable; moreover, the taxonomy of the species occurring in Taiwan has been confused by different authors. Therefore, we deemed that a revision of *Disporum* of Taiwan was necessary. In this study, we revise the genus by reviewing the literature and examining type specimens in herbaria, along with comparisons of the morphology, chromosome number and pollen morphology of specimens and establishing their distribution.

Materials and methods

The study materials were collected from the field and from herbarium specimens. Living plants were cultivated in the greenhouse of the Department of Forestry, NCHU. All voucher specimens were deposited in the herbarium of the Department Forestry, National Chung Hsing University (TCF). Specimens from the following herbaria specimens were examined: CHIA, HAST, KYO, PPI, TAI, TAIE, TAIF and TI (acronyms following Thiers, 2019, continuously updated).

Pollen morphology

Pollen was collected from fresh anthers of flowers in anthesis. Voucher specimens (Table 1) were deposited in TCF. The pollen samples were fixed in 70% ethanol (EtOH) and serially dehydrated with 80%, 90%, 95%, 99.5% EtOH and lastly with acetone. After drying with the Quorum E3100 critical-point dehydrator, the pollen specimens were observed and photographed with a scanning electron microscope (HITACHI S-3400N). Descriptions of pollen morphology used the terminology of Punt et al. (2007) and Hesse et al. (2009).

Table 1. Pollen materials of *Disporum* in this study.

Taxa	Coll. location	Coll. no.
D. kawakamii	Hualien: Yenhai forest track	Chao 1376
D. sessile var. *intermedium*	Hsinchu: Yuanyang lake	Chao 1400
D. shimadae	Keelung: Tawulun fort	Chao 1285

Distribution and conservation rank rvaluation

The distribution of each taxon was determined from the data on herbarium sheets and from our own field records. Only recognised specimens were marked on the map. The conservation rank evaluation followed the protocols of The Red List of Vascular Plants of Taiwan, 2017 (editorial committee of The Red List of Vascular Plants of Taiwan 2017).

Results

Taxonomic diagnostic characters

Habit

The habit of *Disporum* in Taiwan includes two types, evergreen and deciduous. The evergreen type includes only *D. kawakamii* and the deciduous type includes two other taxa. The above-ground part of the deciduous types dies back in winter, leaving a dormant bud above the roots. The bud sprouts in the spring and grows up to form a new stem. The evergreen species produces similar buds at the same position, but the above-ground parts do not die back in winter and last into the next year.

Roots and stolons

The roots of *Disporum* are fleshy and glabrous without root hairs, which is a diagnostic character of the genus. Amongst the Taiwanese species, stolons are present in *D. sessile* var. *intermedium* and *D. shimadae*, but absent in *D. kawakamii*. The stolon is subterranean and creeping and the terminal bud becomes the new individual plant.

Leaves

The leaves of *Disporum* are simple, alternate, subsessile, glabrous and with an entire margin and stipules. The shape could be classified into two types, lanceolate to linear-lanceolate and elliptic to oblong. The former includes *D. sessile* var. *intermedium* and *D. shimadae* and the latter *D. kawakamii*. Although the leaf shape of *D. kawakamii* is often elliptic to oblong, narrower leaves could be found on some individuals.

Inflorescence and flowers

The inflorescences of *Disporum* are pseudo-terminal and umbellate, with pendulous flowers. The flower is comprised of six tepals, six stamens and a pistil. The tepals are variable in shape and have a short gibbous spur and nectary. They are variable in colour, but in Taiwan are white, yellow or variable in colour. White tepals are found in *D. sessile* var. *intermedium*, yellow in *D. kawakamii* and *D. shimadae*. The apices of the tepals of *D. sessile* var. *intermedium* often have purplish or reddish spots, respectively. Some populations of *D. kawakamii* have deeper colouration and these had been described as a new species, *D. taiwanense*, based on this character; but the colour can vary with the habitat: the more exposed location it is growing in, the more sunlight and the deeper the colour and vice versa.

Pollen morphology

The pollen grains of *Disporum* taxa of Taiwan are medium-sized monads, monosulcate, prolate, with the length of the equatorial and polar axes being 36.57–44.76 µm and 26.77–28.91 µm, respectively. Sculptural type varies amongst taxa: *D. kawakamii* and *D. sessile* var. *intermedium* are foveolate and areolate, while *D. shimadae* is rugulate. Huang (1972) studied the pollen morphology of *D. kawakamii* and *D. shimadae* by light microscopy and his results showed that the pollen grains of two species were monads, monosulcate, subspheroidal and the sculpture was reticulate. Most of his results are similar to ours, but he sometimes recognised different sculptural types. The different types of microscopy used may lead to the different results (Fig. 1) (Table 2).

Chromosome number

The chromosome number of *Disporum* of Taiwan had been determined by Chuang et al. (1962), Chao et al. (1963), Hsu (1971), Chang and Hsu (1974), Tamura et al. (1992) and Wang (1997). The results revealed that *D. kawakamii* and *D. sessile* var. *intermedium* had 2n = 16 chromosomes, while Hsu (1971) reported tetraploidy (2n = 32) for *D. kawakamii*. *Disporum shimadae* was reported as 2n = 14 in the studies of Tamura et al. (1992) and Wang (1997), but Chang and Hsu (1974) reported the chromosome number as 2n = 16 (Table 3).

Table 2. Pollen morphology of Disporum of Taiwan.

	D. kawakamii	*D. sessile* **var.** *intermedium*	*D. shimadae*
polar axis (µm)	29.12±0.97	26.90±0.20	27.41±1.32
equatorial axis (µm)	43.31±2.02	37.45±3.30	39.77±2.21
P/E	0.67±0.02	0.78±0.08	0.69±0.03
shape	oblate	oblate	oblate
size	medium	medium	medium
aperture	1-sulcate	1-sulcate	1-sulcate
sculpture	foveolate	areolate	rugulate

Table 3. Previous chromosome count of Disporum of Taiwan.

Taxon	Chromosome number		Reference
	n	2n	
D. kawakamii	8		Chuang et al. 1962
		16	Chao et al. 1963; Tamura et al. 1992; Wang 1997
		32	Hsu 1971
D. sessile var. *intermedium*		16	Tamura et al. 1992 (as *D. taipingense*); Wang 1997 (as *D. nantouense*)
D. shimadae		14	Chao et al. 1963; Chang and Hsu 1974; Tamura et al. 1992; Wang 1997
		16	Chang and Hsu 1974
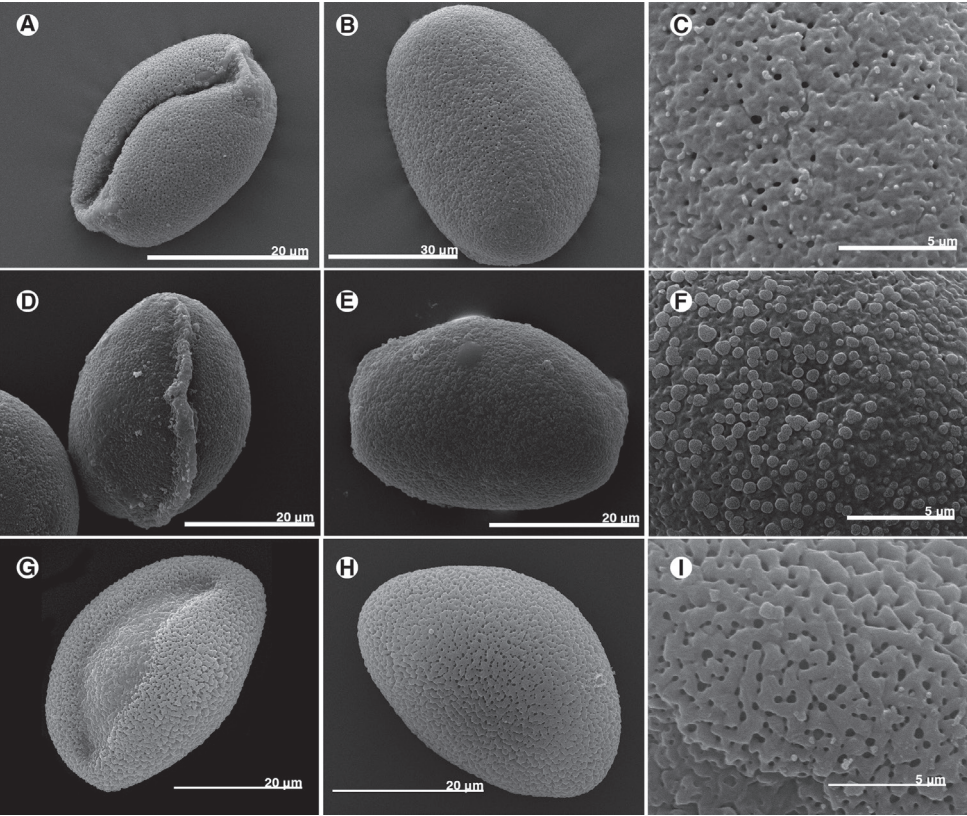
Figure 1. Pollen morphology of *Disporum* of Taiwan. **A–C** *D. kawakamii* **D–F** *D. sessile* var. *intermedium* **G–I** *D. shimadae*. **A, B, D, E, G, H** polar view **C, F, I** sculpture.

Distribution

Disporum taxa are found from near sea level to about 2900 m in the mountainous regions of Taiwan, but each species has a different distribution pattern. *Disporum kawakamii* is found in low to medium altitude mountain areas, often grows as an

understorey plant in a forest or at the edge of a forest, but sometimes even appears on an exposed roadside. *Disporum sessile* var. *intermedium* is found primarily at medium altitudes, from 1500 m to 2900 m in moist and shady areas of forest. *Disporum shimadae* is only found in the north-eastern part of Taiwan, from sea level to low-lying mountains or hills (Table 4) (Figs 2–4).

Evaluation of conservation rank of *Disporum*

According to a study by the editorial committee of The Red List of Vascular Plants of Taiwan (2017), the conservation rank of *D. kawakamii* and *D. shimadae* was least concern (LC), whereas *D. nantouense* (= *D. sessile* var. *intermedium*) and *D. taiwanense* (= *D. kawakamii*) were data deficient (DD). The results of our study were similar, but we determined that the rank of *D. sessile* var. *intermedium* was LC. This was a poorly know taxon, the specimens often being misidentified as another species. During our
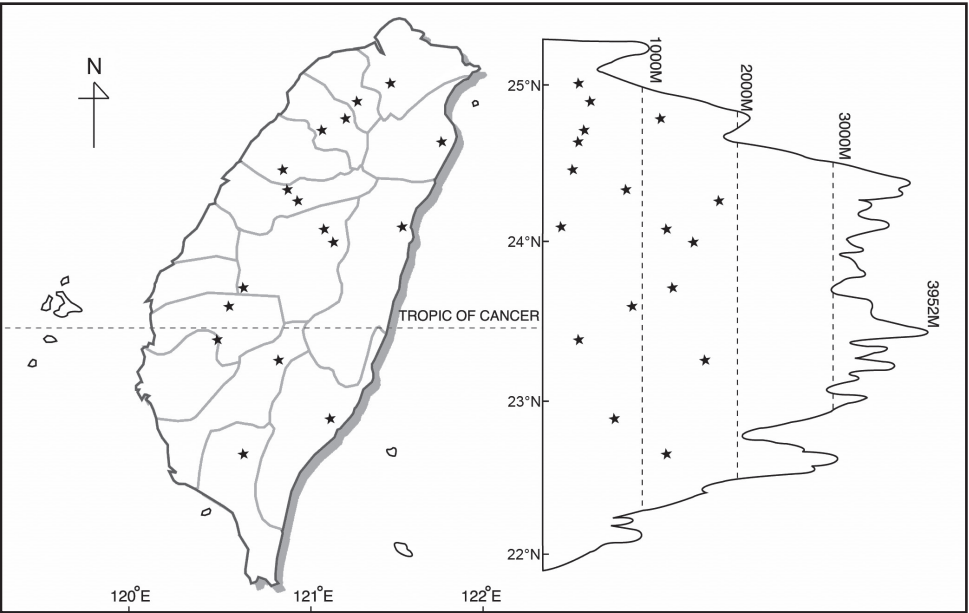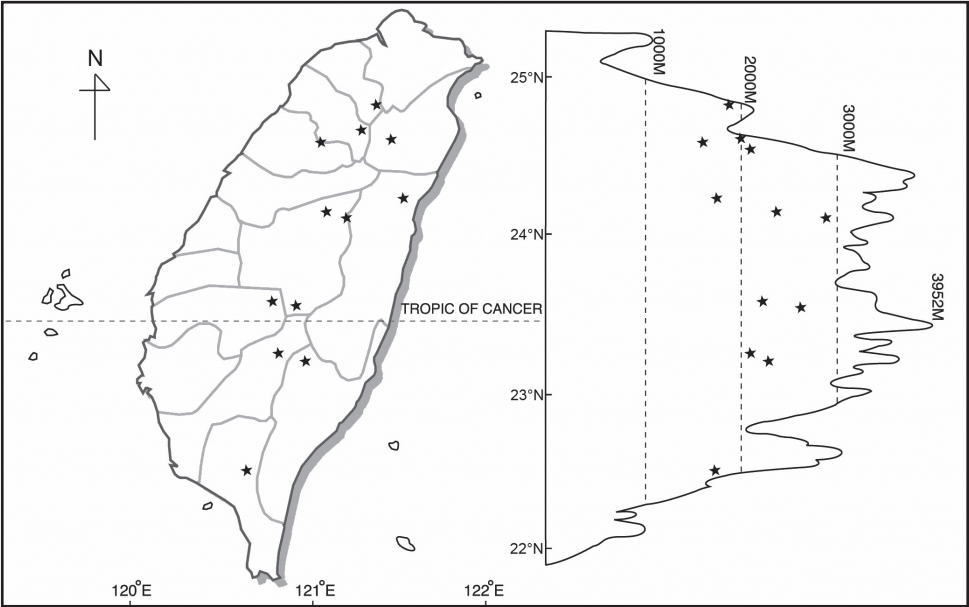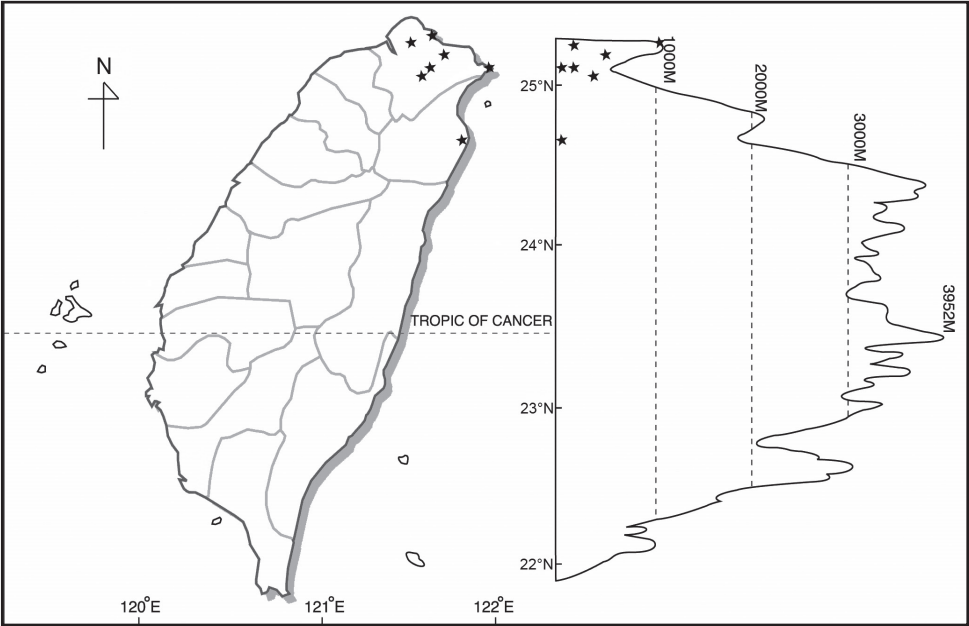

Figure 2. Distribution of *Disporum kawakamii*.

Table 4. Comparisons of Disporum species of Taiwan.

	D. kawakamii	*D. sessile* var. *intermedium*	*D. shimadae*
habit	evergreen	deciduous	deciduous
stolon	absent	present	present
leaf shape	elliptic to oblong	linear-lanceolate	linear-lanceolate
color of tepal	pale-yellow with reddish apex	white with green base and apex	yellow
distribution	low to medium altitude mountain area	medium altitudes ca. 1500–2900m	north-eastern part, seashore to low altitude mountains

Figure 3. Distribution of *Disporum sessile* var. *intermedium*.

Figure 4. Distribution of *Disporum shimadae*.

field survey, we found many populations at a medium altitude, in good habitats with little disturbance. Therefore, we suggest changing the conservation rank of *D. sessile* var. *intermedium* from DD to LC.

Discussion

Comparison of *D. cantoniense* and *D. kawakamii*

Disporum cantoniense is a widely distributed species, found from the Himalayas of northern India to Sikkim, Burma, Thailand, Vietnam and China. Hara (1988) listed four varieties of this species: one of them was *D. cantoniense* (Lour.) Merr. var. *kawakamii* (Hayata) Hara. The main characters of this variety include glabrous pedicels, apices of tepals obtuse or short acute and densely papillate (Hara 1988). Our observations show that, except for *D. cantoniense* var. *kawakamii*, other varieties had acuminate to acute tepals somewhat reflexed when in anthesis. *D. cantoniense* var. *kawakamii* was also the only variety with yellow tepals; the others had green, purple or purplish-brown tepals. The karyological study of Tamura et al. (1992) suggested different karyotypes for *D. cantoniense* (type A and C3) and *D. kawakamii* (type D). Molecular studies (Shinwari et al. 1994; Tamura et al. 2013) also revealed that the two species were placed in different clades. In conclusion, *D. kawakamii* is different from *D. cantoniense* on morphological, karyological and genetic levels and should be treated as an independent species rather than a variety as Hara (1988) published.

Ying (1989) described a new species, *D. taiwanense*, from eastern Taiwan that was distinguished by its usually reddish petioles and yellow tepals with reddish tips, especially on the inner surface. As we mentioned before, the colour of tepals can vary depending on the habitat conditions; therefore, this character would seem to be a poor one for distinguishing them. Since the distribution of the two taxa is also similar, we chose to consider *D. taiwanense* as a synonym of *D. kawakamii*.

The taxonomic status of *D. nantouense* and *D. shimadae*

Disporum nantouense has been treated as a form *D. sessile* var. *shimadae* f. *intermedium* (Hara 1988) or as an independent species (Ying 1990a). These treatments were evaluated and considered, but none of them was found suitable for this taxon. The diagnostic characters of this taxon include lanceolate to narrow lanceolate leaves, white tepals, sub-papillose filaments and chromosome number of 2n = 16. These characters are different from those of *D. shimadae*, therefore, this taxon should not be considered simply as another form of *D. sessile* as Hara (1988) proposed. These specific characters are, however, found in *D. sessile* and the molecular study of Tamura et al. (2013) also suggested close affinity between them. Thus, the proposal of Ying (1990a) that this is an independent species lacks sufficient evidence.

Tamura (2016) distinguished two varieties of *D. sessile*, namely *D. sessile* D. Don *ex* Schult. var. *micranthum* Hatsu. *ex* M. N. Tamura & M. Hotta and *D. sessile* D. Don *ex* Schult. var. *minus* Miq. The Taiwanese taxon resembled *D. sessile* var. *micranthum* in that they both had small flowers (1.5 to 2.2 cm in length) and sub-papillose filaments, but otherwise they were distinguished by the subterranean stolons, lanceolate to nar-

row lanceolate leaves and tepals greenish at the apex. Based on the study of Tamura et al. (2013) and Tamura (2016), the Taiwanese taxon was merged into the monophyletic group of *D. sessile*, with the different morphological characters mentioned above. Thus, we treated this taxon as a variety of *D. sessile*, rather than a species or a form of *D. sessile*.

Disporum shimadae was first described by Hayata (1911) as a separate species, but Hara (1988) considered it a variety of *D. sessile*. Although the two taxa have similar morphological characters, such as leaf shape, long creeping stolons and deciduous habit, *D. shimadae* could be distinguished by its yellow flowers, thicker leaves and glabrous filaments. Furthermore, as mentioned above, the chromosome number of *D. shimadae* is 2n = 14, while that of *D. sessile* is 2n = 16 (Tamura et al. 1992; Wang 1997). This evidence would imply they are not conspecific, similar to the results of the molecular study of (Tamura et al. 2013); consequently, we chose to treat *D. shimadae* as an independent species, not a variety of *D. sessile*.

The status of *D. taipingense*

Another taxon, related to *D. sessile* var. *intermedium*, was *D. taipingense* M. N. Tamura & S. Kawano, nom. nud. This name had been cited in the studies of Tamura et al. (1992) and Shinwari et al. (1994), where they stated that this species was collected from Mt. Taipingshan, at an altitude of 1900 m in a coniferous forest but provided limited morphological description. They cited an article, in press, that could possibly be the original publication of the name (Tamura and Kawano 1994, Biosystematic Studies in *Disporum*, Liliaceae-Polygonateae V., A Taxonomic Revision of Species in Taiwan in Acta Phytotaxonomica et Geobotanica), but we could not find the article in the journal or the description and the type specimen. Thus, this name is *nomen nudum* due to its invalid publication. *Disporum taipingense* was treated as a synonym of *D. nantouense* in Flora of China (Chen et al. 2000). In consideration of the facts that the collectors of the plant had deposited the specimens labelled as *D. taipingense* by M. N. Tamura in the TI herbarium and the plant materials were from Mt. Taipingshan, but morphological descriptions were inadequate and the "in press" journal article could not be found, we chose to treat this taxon as a synonym of *D. sessile* var. *intermedium*.

According to the results, the following taxonomic treatments are made:

Taxonomic treatment

Key to *Disporum* species in Taiwan

1	Plant deciduous, with stolon; leaves lanceolate to linear-lanceolate **2**
–	Plant evergreen, without stolon; leaves elliptic to oblong...... **1. *D. kawakamii***
2	Tepals yellow, without spots.. **3. *D. shimadae***
–	Tepals white, often with purplish spots, apex green...................................... .... **2. *D. sessile* var. *intermedium***

Disporum Salisb. *ex* D. Don, Prodr. Fl. Nepal. 50. 1825

Perennial herbs, often with short rhizome, sometimes with long creeping stolon, often glabrous, sometimes scabrous. Roots fleshy, glabrous. Stem erect, simple or branched at the upper part, with scale leaves at the lower nodes, persistent. Leaves evergreen or deciduous, simple, alternate, sessile or subsessile, linear to suborbicular, 3–several-nerved, estipule. Inflorescences pseudoterminal, solitary to umbel, bract absent. Flowers bisexual, actinomorphic, pendulate to spread, tepals 6, free, 2-whorled, subequal, white, green, yellow or purple, often saccate or spurred at basal part. Stamen 6, inserted at base of tepals. Filaments usually slightly flattened, glabrous of papillose. Anthers basifixed, to innate, extrorse, 2-loculed. Ovary superior, 3-loculed, ovules 2–6 per locule. Style straight, 3-lobed to 3-fid apically. Fruits berry, dark purple to black, 2–6 seeds.

About 20 species, from Himalaya region, India, Myanmar, Bhutan, Sikkim, Thailand, Vietnam, China, Taiwan, Japan to Korea.

1. ***Disporum kawakamii*** **Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 365. 1911**
Figs 5, 6
臺灣寶鐸花

Disporum kawakamii Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 365. 1911. Hayata, Gen. Ind. 85. 1917; Sasaki, List Pl. Form., 106. 1928; Masamune and Simada, Short Fl. Form. 269. 1936; Masamune, List Vasc. Pl. Taiwan. 132. 1954; Chao et al., Bot. Bull. Acad. Sin. New Series 4(2):81; Ying, The Liliaceae of Taiwan. 25. 1969; Wang, Cytotaxonomy of Liliaceae in Taiwan (II) Polygonateae and Tricyrteae. 41. 1997; Liu & Ying, Fl. Taiwan. 5:52. 1978; Ying, Liliaceae of Taiwan. 27. 1990; Chen et al., Fl. China 22:157, 2000; Ying, Fl. Taiwan 2nd ed. 5:44. 2000; Boufford et al., Fl. Taiwan 2nd ed. 6:111. Lectotype: Kagi, Suitoryo, 20 Mar. 1908, T. Kawakami 3493. (lectotypification: Hara, 1988) (TI!) Syntype: in monte Morrison, 13 Oct. 1906, T. Kawakami & U. Mori 1726. (TI)
Disporum cantoniense (Lour.) Merr. var. *kawakamii* (Hayata) Hara, Univ. Mus. Univ. Tokyo Bull. 31:187. 1988.
*Disporum pullum* auct. non. Salisb. *ex* Hook. f.: Matumura & Hayata, J. Coll. Sci. 1Imp. Univ. Tokyo 22: 443. 1906.
Disporum taiwanense S. S. Ying, J. Jap. Bot. 64(5):151. 1989. Ying, Liliaceae of Taiwan. 29. 1990; Ying, Fl. Taiwan 2nd ed. 5:46. 2000; Boufford et al., Fl. Taiwan 2nd ed. 6:111. Type: Hualien county, Taroku to Talishih, 4 Apr. 1988, Ying s. n. (Holotype: NTUF!)

Perennial herbs. Stem erect, up to 1.3 m, branched at the upper part, lower nodes covered with persistent scale leaves. Leaves evergreen, simple, alternate, elliptic to oblong, 6–8 cm long, 3–6 cm wide, 3–5 nerved, apex acuminate, base attenuate, petiole short, 3–5 mm long, green, sometimes reddish, glabrous, estipulate. Inflorescence pseudoterminal, solitary to 3–5 flowers fascicled, peduncle short, 3–5 mm long, bract absent. Te-

pals 6, arranged into 2-whorls, spathulate, 1.5–2 cm long, 5–8 mm wide, light yellow to yellow, often with reddish spots near apex, papillate at the base of the inner surface and margin, 3-nerved, base with a short spur, 1–2 mm long, nectary inside. Stamens 6, inserted at the base of tepals, filaments ca. 1 cm long, expansion at the lower part, slightly papillose at proximal part, anthers 2-loculed, basifixed, ca. 3 mm long, longitudinally dehiscent. Ovary superior, ovate to orbicular, ca. 3 mm long, 3-loculed, style slender, 7–9 mm long, stigma 3-fid, pubescent. Fruits berry, globose or compress globose, 6–7 mm long, 4–6 mm in diam., purplish-black. Seeds numerous. 2n = 16.

Endemic to Taiwan. Distributed in low to medium altitude mountains up to 2,000 m.

Additional specimens examined. Chiayi county: Alishan-Fengshan, 8 Sep 1993, C. M. Wang W00265 (TNM); Yuntan Rest Station-Shuisheliao, 10 Sep 2004, C. M. Wang & Y. M. Hsu 7730 (TNM); Tatienyupupu, 28 Oct 1997, M. Y. Shen 1980 (TAIE); en route from Chiehtung "Villa" to Tienyunshan, 850 m alt., 1 Nov 1985, C. I Peng 8873 (HAST); Juili, 860 m alt., 26 Jan 1997, T. Y. A. Yang et al. 7838 (PPI); Hsinchu county: Kenliaoping, 26 Apr 1994, C. M. Wang W00733 (TNM); on the way from Shihlu to Chingchuan, 27 Jul 1994, K. Y. Wang & T. Y. Liu 75 (TNM); Niaotsui, 21 Oct 2001, C. M. Wang & C. Y. Li 5300 (TNM); Shakaro ancient trail, 1500–1700 m alt., 10 May 2016, P. H. Chen 1096 (PPI); Luoshan forest track, 1000 m alt. 20 Dec 2002, Y. Y. Huang 1309 (HAST); Hualien county: Sanchan, 7 Sep 1996, C. K. Liou et al. 539 (TNM); Yenhai-lindao, 3 Apr 1991, T. Y. Yang et al. 5506 (TNM); Mt. Paliwanshan, 28 Jul 2007, C. H. Chen et al. 8339 (TNM); Shakadang forest road 2 km, 30 Mar 2008, T. Y. A. Yang et al. 20106 (TNM); Huitouwan, 9 Dec 1983, T. C. Huang & S. F. Huang 10200 (TAI); Lanshan, 1900 m alt. 16 Aug 1967, S. C. Hsu 3539 (TAI); Yushan National Park Nanan Recreation Center to Walami, 365 m alt., 16 Apr 1995, H. Y. Shen 683 (HAST); Mukuashan, 700–1000 m alt., 16 Apr 2003, P. J. Lin et al. 159 (HAST), Taorko to Tali, 15 Jun 2007, P. F. Lu 13967 (HAST); Ilan county: Mingchih-Chilan, 15 Apr 2002, C. M. Wang 5468 (TNM); Taipingshan, 5 Apr 2005, C. H. Wu et al. 343 (TNM); Chunchien, 1500–1600 m alt., 30 Jul 1996, Y. C. Chen et al. 17 (HAST); Ssuchi forest road, 1360 m alt., 18 Jul 1999, C. I Huang 399 (HAST). Nanao, 28 Apr 2001, W. F. Ho 1215 (TNM); Mt. Tuli, 450 m alt., 31 Mar 1985, S. Y. Lu 15610 (PPI); Kaohsiung city: Tenchih, 28 Jun 2000, C. M. Wang 4321 (TNM); same loc., 21 May 2016, S. Z. Yang 77621 (PPI); Nanfengshan, 18 Dec 1961, J. M. Liao 788 (TAI); Meilan forest road 8.6 km, 1300 m alt., 10 May 1994, T. Y. Liu et al. 419 (HAST); Southern cross highway, 26 Dec 2000, S. Z. Yang 29567 (PPI); Miaoli county: Shihmen, 20 Mar 1997, M. Y. Shen 1557 (TAIE); Nanchuang shenmiku, 24 Mar 2001, J. H. Lii 428 (TAIF); Taian hot-spring, 300–400 m alt., 30 Jun 1992, J. C. Wang et al. 7707 (HAST, PPI); Tahu, 200–400 m alt., 27 Jan 2007, H. Y. hsieh 138 (PPI); Nantou county: Bihhwu, 2 Sep 1993, C. M. Wang W00160 (TNM); Kunglingshan, 1 May 1991, H. Y. Chen et al. 1118 (TNM); Chitou, 15 May 1988, S. L. Shern & H. M. Su 42 (TNM); same loc., 5 Feb 2010, C. T. Chao 1323, 1324 (TCF); Wushe to Aowanda, 20 Mar 2009, C. T. Chao 496, 497, 498 (TCF); Chioufengershan, 14 Apr 2010, C. T. Chao 607, 608, 609, 610 (TCF); Aowanda, 7 Nov 2009, C. T. Chao 1129 (TCF); Fenghuangshan, 1225 m alt., 4 Sep 1997, T. W. Hsu 8806 (TAIE); Ching Shui Kou Treet, 14 Dec 1960, T. C. Huang 1937 (TAI); Shalishien river, 1120 m alt., 15 May 1985, C. I Peng 7775 (HAST); en
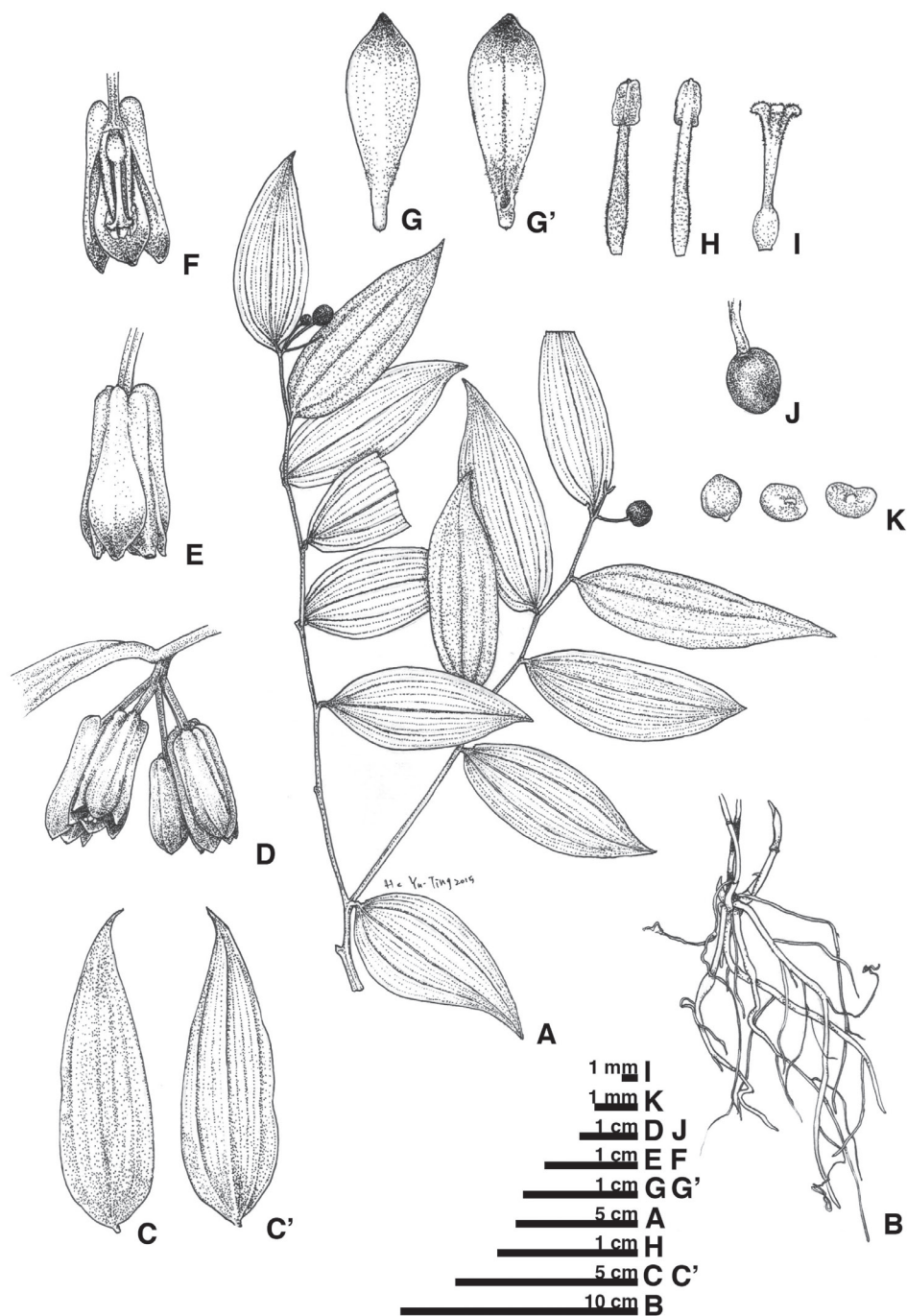
Figure 5. *Disporum kawakamii*. **A** habit **B** underground part **C** leaf adaxial surface **C'** leaf abaxial surface **D** inflorescence **E** flower **F** flower section (with tepals and stamen removed) **G** tepal outer surface **G'** tepal inner surface **H** stamen **I** pistil **J** fruit **K** seeds.
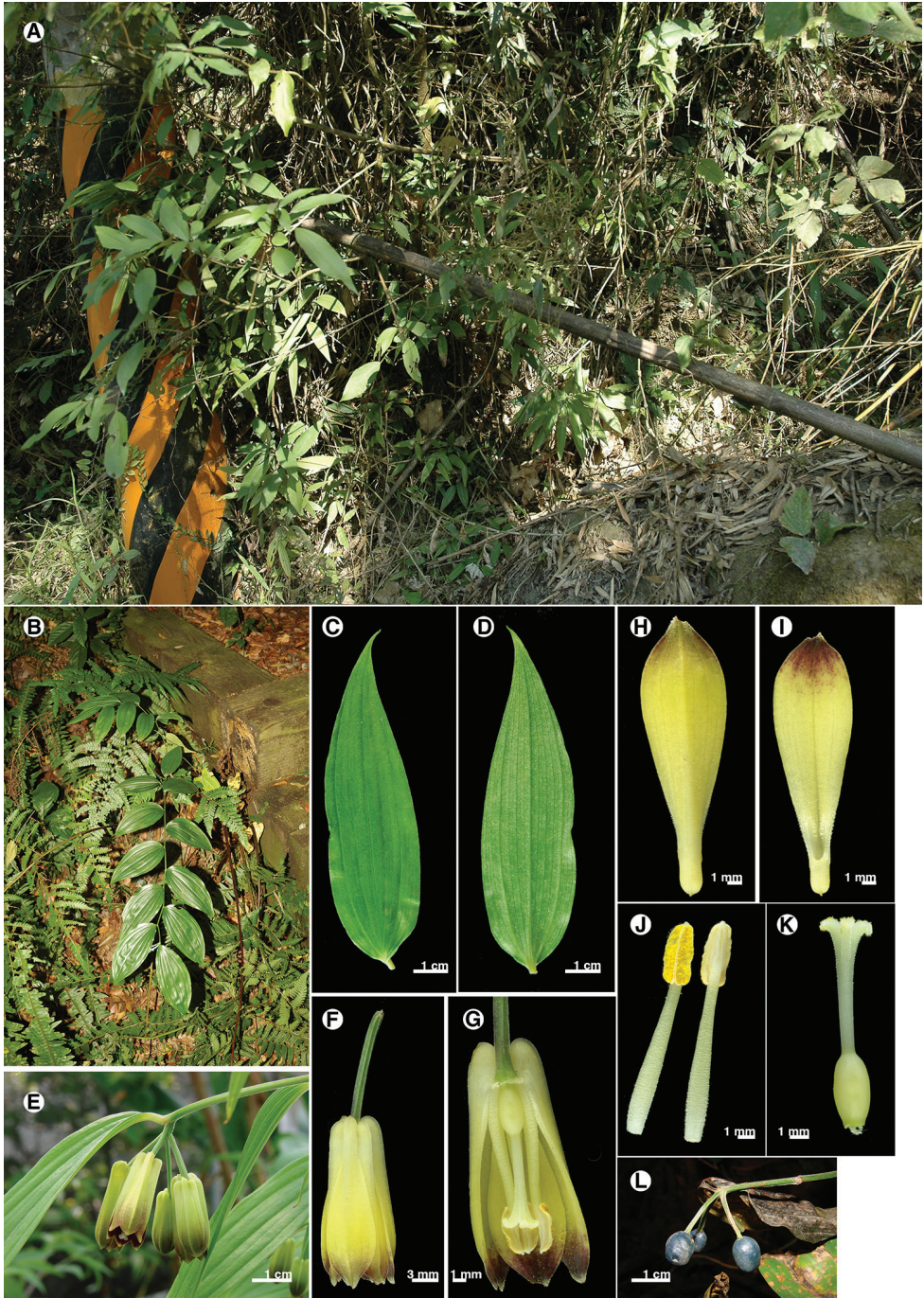
Figure 6. *Disporum kawakamii*. **A** habitat **B** habit **C** leaf adaxial surface **D** leaf abaxial surface **E** inflorescence **F** flower **G** flower section (with tepals and stamen removed) **H** tepal outer surface **I** tepal inner surface **J** stamen **K** pistil **L** fruits.

route from Tungpu Hot Soring to Kuankao, 1300–2600 m alt., 3 Jul 1985, C. I Peng 8070 (HAST); Patungkuan Ancient Trail, 1150 m alt., 13 Aug 2004, C. C. Wu et al. 725 (HAST); Old Chinai Village, 8 Jul 2007, P. F. Lu 14172 (HAST); Fengshan, 1200 m alt., 29 Jun 1996, T. W. Hsu 7650 (TAIE); Chuoshuihsi River valley by the Yunlong Bridge, 1100 m alt., 15 Jan 1003, M. H. Chen et al. 70 (HAST); en route from Hsini to Hoshe, ca. 950–1200 m alt., 6 Aug 1991, W. P. Leu 1073 (PPI); New Taipei City: Yunsen Falls, 26 Aug 1996, K. C. Yang & W. F. Ho 4982 (TNM); Homei, S. F. Huang 4292 (TAI); Fushan, 300–600 m alt., 3 Apr 2002, Z. W. Lee 77 (HAST); Huangdidian, 450–500 m alt., 2 Feb 2003, S. C. Liu et al. 976 (HAST); Pingtung county: Wutoushan Nature Protected Area, 21 Apr 1995, K. Y. Wang et al. 950 (TNM); Chinshuiying, 1200 m alt., 22 Jun 1999, K. F. Chung 1262 (HAST); Tahanshan, 1100–1200 m alt., 2 May 2006, J. C. Wu 55 (PPI); Shishan forest road, 1600–1650 m alt., 22 Jul 2002, G. P. Hsieh 588 (PPI); Chiupaoshan, 1000–1500 m alt., 28 May 2004, S. H. Hueng 42515 (PPI); Itingshan, 1200–1500 m alt., 23 May 2003, G. P. Hsieh 1069 (PPI); Ali, 14 Jul 1989, S. Z. Yang 24872 (PPI); Hsuehyehkenshan, 800–1200 m alt., 17 May 2014, P. H. Chen 369 (PPI); Wutai, 9 May 1986, C. E. Chang & L. C. Chang 106 (PPI); Dangmanushan, 25 Mar 1990, S. Z. Yang & C. G. Lin 23036 (PPI); Jihmushan, 27 Apr 1991, S. Z. Yang 24604 (PPI); Taichung City: Wushihkeng, 10 Oct 1998, C. M. Wang 3689 (TNM); Yuantsuishan-Shaolaishan, 8 Sep 1998, S. T. Chiu 4913 (TNM); Tzuyukuohsiao (an elementary school), 750 m alt., 6 Jun 1995, Y. H. Tseng 535 (TAIE); under Mt. Izawa, 17 Jul 1935, H. Simada SH 606 (TAI); tausaiibunaraha, H. Simada SH 1307 (TAI); Tainan city: Tatungshan, 2 Apr 1993, T. C. Huang & S. F. Huang 15989 (TAI); Kantoushan Hsienkung temple, 500–700 m alt., 12 Jan 1996, C. C. Liao et al. 1737 (HAST); Zengwen reservoir, 800–1100 m alt., 24 Jul 2008, C. C. Hsiao 17 (PPI); Taoyuan city: en route between Kaopo and Tawan, 9 May 1993, W. P. Liu 1744 (TNM); Hsiehwunao, 700–800 m alt., 10 Sep 2002, Z. W. Lee 378 (HAST); Taitung county: Kuzulun-shan, 29 Aug 1957, Kao et T. I. Chuang 1103 (TAI); Litao-Tienlung Bridge, 4 Apr 1987, S. F. Huang et al. 3642 (TAI); Lichia forest road, 1225 m alt., 16 Oct 1997, Y. C. Kao et al. 137 (HAST); Shawushan, 700–800 m alt., 2 Aug 2005, C. F. Chen 1708 (PPI); Chianaimeishan, 500–700 m alt., 20 Aug 2005, Y. J. Lin 35 (PPI); Preserve area of *Juglans cathayensis*, 9 Feb 1993, S. Z. Yang 30044 (PPI).

2. *Disporum sessile* D. Don *ex* Schult. var. *intermedium* (Hara) Y.H.Tseng & C.T.Chao, comb. nov.

urn:lsid:ipni.org:names:77195641-1
Figs 7, 8
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D. sessile D. Don *ex* Schult. var. *shimadai* (Hayata) Hara f. *intermedium* Hara in Univ. Mus., Univ. Tokyo, Bull. 31:203. 1988. TYPE: Kwarenko, between Tosato and Totokun, 11 Apr. 1940, M. Tagawa 3700 (holotype: TI!, isotype: KYO!)

Disporum nantouense S. S. Ying, Mem. Coll. Argic. Natl. Taiwan Univ. 30(2):59. 1990. Wang, Cytotaxonomy of Liliaceae in Taiwan (II) Polygonateae and Tricyrteae. 44.

1997; Chen et al., Fl. China 22:157, 2000; Ying, Fl. Taiwan 2nd ed. 5:46. 2000. Type: Nantou county, Jenai township, Mt. Hohuanshan, near to Meifeng, alt. 2170 m, 9 Apr. 1989, Ying s.n. (holotype: NTUF), syn. nov.

Disporum taipingense M. N. Tamura & Kawano, nom. nud.

Perennial herbs. Stem erect, 15–45 cm, lower nodes covered with scale leaf, persistent, branched at the upper part, with creeping stolon. Leaf deciduous, simple, alternate, lanceolate to linear-lanceolate, 3-nerved, 5–6 cm long, 2–3 cm wide, apex acuminate, base obtuse, petiole short, 3–5 mm long, green, sometimes reddish, estipule, glabrous. Inflorescences pseudoterminal, solitary to 2–3 flowers, peduncle 3–5 mm, bract absent. Pedicels 1–1.5 cm long, tepals 6, arranged into 2-whorls, spathulate, white, apex green with violet spots, 1.5–2 cm long, 6–8 mm wide, margin papillose, 3-nerved, base spurred, with nectary. Stamens 6, inserted at base of tepals, filaments 1–1.5 cm long, anthers 3 mm long, 2-loculed, longitudinally dehiscent. Ovary superior, 3-loculed, style slender, subglabrous, 1–1.5 cm long, stigma 3-fid, pubescent. Fruits berry, globose, purplish-black when mature. Seeds numerous. 2n = 16

Endemic to Taiwan. Distributed in medium altitudes, ca. 1,500 m to 2,900 m.

Additional specimens examined. Chiayi county: Alishan, near Tziyun temple, 14 Apr 1991, T. Y. Yang et al. 5548 (TNM); Alishan, 9 Jul 1981, C. E. Chang 18237 (PPI); on the road side of Mienyueh railroad, 16 Jul 1986, T. Y. A. Yang 3073 (PPI); Tungpu lodge to Chichung, 2400 m alt., 19 Oct 1987, S. Z. Yang 3767 (PPI); Hsinchu county: Yuanyanghu, 1670 m alt., 28 Apr 1995, K. Y. Wang et al. 1059 (HAST); Hualien county: Mt. Muh-kwa, 24 Jul 1961, M. T. Kao K4146 (TAI); Lanshan, 1 Apr 1994, Y. C. Sun 236 (TAIE); Hoping forest track, 1700–2000 m alt., 24 May 1993, S. F. Huang et al. 5128 (TAI); near Shihtung suspension bridge of Patungkuan ancient trail; 1500–1800 m alt., 7 Apr 2009, J. C. Wu 328 (PPI); Taitung county: Hsiangyang in forest, 2350 m alt., 24 Jul 1988, C. I Peng et al. 11876 (HAST); Ilan county: Mt. Taipingshan, 1970 m alt., 3 Apr 1986, T. C. Huang 10813 (TAI); Nanshan to Chi-li-ting, 1200–1400 m alt., 20 Aug 1969, C. C. Hsu 5834 (TAI); Mt. Nanakotaizan, 14 Jul 1937, SH1330 (PPI); Kaohsiung city: Kuaiku, 5 May 2006, C. M. Wang et al. 8857 (TNM); Chungtzukuan, 20 Dec 2000, S. Z. Yang 25492 (TAIF); Tienchi to Chungchikuang trail, 2000–2400 m alt., 14 Jul 2000, C. C. Hsu 56 (PPI); Nantou county: Tienchi, 16 Jun 1996, S. T. Chiu et al. 3363 (TNM); Tatachiaanbu to entrance of Yushan, 23 Jul 2009, C. T. Chao 838 (TCF); highway no. 18, Tatachia to Shihshan, 24 Jul 2009, C. T. Chao 857 (TCF); Yunhai, 8 May 2004, T. Y. A. Yang 16440 (TNM); May-fong, 17 Apr 1980, Ou & Kao 9316 (TAI); Kun-yang to Yuan-feng, 2700–3000 m alt., 9 Apr 1988, J. C. Wang 5091 (TAI); New Taipei city: Peichatienshan, 26 Feb 2002, S. W. Chung 5134 (TAIF); Pingtung county: en route to Tawushan, 1600–2100 m alt., 16 Jul 1988, T. C. Huang et al. 13618 (TAI); Peitawushan, 1500–1800 m alt., 5 Apr 1997, D. W. Liu 372 (PPI); same loc. 2050–2100 m alt., 29 May 1997, P. F. Sun 56 (PPI); Taichung city: Chinshan-Paikushan, 1 May 1992, H. M. Chang Hunter 14 (TNM); Nankotaizan, Kirittoi to Ekizyu no aida, 8 Jul 1937, H. Simada SH 1308 (TAI); Taitung county: Kuei-hu, 1600 m alt., 29 Jul 1967, C. C. Hsu 3362 (TAI); Hsiangyang, 2200 m alt., 2 Apr 1996, T. Y. Aleck Yang
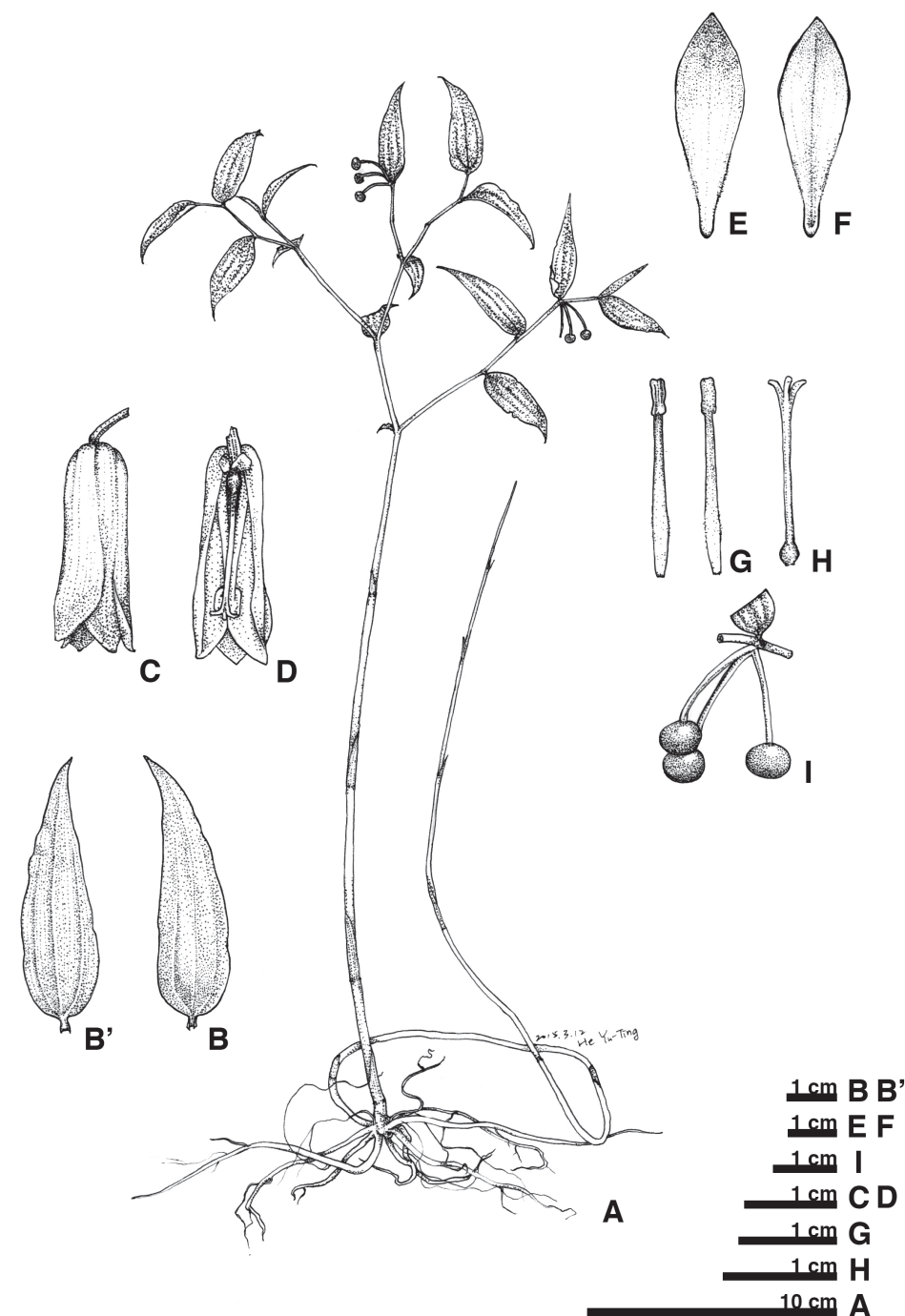
Figure 7. *Disporum sessile* var. *intermedium*. **A** habit **B** leaf adaxial surface **B'** leaf abaxial surface **C** flower **D** flower section (with tepals and stamen removed) **E** tepal outer surface **F** tepal inner surface **G** stamen **H** pistil **I** fruit.

Figure 8. *Disporum sessile* var. *intermedium*. **A** habitat **B** habit **C** leaf adaxial surface **D** leaf abaxial surface **E** inflorescence **F** flower **G** flower section (with tepals and stamen removed) **H** tepal outer surface **I** tepal inner surface **J** stamen **K** pistil.

et al. 6451 (PPI, TNM); Chinlunhsi, 1400–1700 m alt., 10 Mar 2007, J. J. Chen 360 (PPI); Taoyuan city: Paling–Lalashan, 17 Apr 1986, T. Y. Yang et al. 2913 (TNM); Lalashan, 10 Apr 2002, S. C. Wu 2608 (TAI);

3. *Disporum shimadae* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 367. 1911
山寶鐸花
Figs 9, 10

Disporum shimadae Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30(1): 367. 1911. as 'shim-dai'. Hayata, Gen. Ind. 85, 1917; Sasaki, List Pl. Form. 106. 1928; Masamune and Simada, Short Fl. Form. 269. 1936; Masamune, List Vasc. Pl. Taiwan. 132. 1954; Chao et al., Bot. Bull. Acad. Sin. New Series 4(2):81; Ying, The Liliaceae of Taiwan. 24. 1969; Liu & Ying, Fl. Taiwan. 5:54. 1978; Ying, Liliaceae of Taiwan. 28. 1990; Wang, Cytotaxonomy of Liliaceae in Taiwan (II) Polygonateae and Tricyrteae. 46. 1997; Chen et al., Fl. China 22:158, 2000; Ying, Fl. Taiwan 2nd ed. 5:46. 2000; Boufford et al., Fl. Taiwan 2nd ed. 6:111. TYPE: Kelung, Masoku, 6 Mar. 1908, T. Kawakami & Y. Shimada 4311. (isotype: TAI!)

Disporum sessile (Thunb.) D. Don *ex* Schult. var. *shimadae* (Hayata) Hara, Univ. Mus., Univ. Tokyo, Bull. 31:202 1988.

Perennial herbs. Stem erect, 15–45 cm, covered with persistent scale leaf at lower nodes, branch at the upper part. Leaf deciduous, simple, alternate, lanceolate, 4–10 cm long, 2–4 cm wide, apex acuminate, base obtuse, margin entire, 3-nerved at the base, petiole short, 3–5 mm long, glabrous, estipulate. Inflorescences pseudoterminal, solitary to 3–5 flowers fascicled, peduncle short, 3–5 mm long, bract absent. Tepals 6, arranged into 2-whorls, spathulate, 2–3 cm long, 5–8 mm wide, the inner surface of basal part and margin papillose, base with a short spur, 1–2 mm long, nectary inside. Stamens 6, inserted at base of tepals, filament often expansion at proximal part, 10–15 mm long, glabrous, anthers 2-loculed, basifixed, 3 mm long, longitudinally dehiscent. Ovary superior, 3-loculed, obovate, style 1–1.5 cm long, stigma 3-lobed, pubescent. Fruits berry, purplish-black, seed numerous. 2n = 14.

Endemic to Taiwan. Distributed in north-eastern part, from seashore to low altitude mountains.

Additional specimens examined. Ilan county: Tali, 20 Apr 1985, W. S. Tang 1324 (TAI); Kueishan island, 31 May 2003, S. T. Chiu et al. 7542 (TNM); Keelung city: Chyngrenhu, 16 May 2007, T. Y. A. Yang et al. 19220 (TNM), Masu, 6 Mar. 1908, T. Kawakami & S. Simada 4311 (Isotype! TAI); Tawulun Fort, 3 Nov 2009, C. T. Chao 1108, 1111 (TCF); Hoping Island, 12 Mar 1963, S. Y. Lu 643 (TAIF); same loc., 15 Mar 1986, S. Z. Yang 2443 (PPI); Paimiweng Fort, 50 m alt., 4 May 1992, C. C. Liao with C. C. Wang 260 (HAST); New Taipei city: Hsiaotzushan, 21 Mar 1995, H. Y. Shen et al. 560 (TNM); Tatun main peak, 6 Mar 2009, 460, 462, 463, 464, 465 (TCF); Shumeiping, 2 Mar 2002, T. Y. A. Yang et al. 14539 (TNM); Lungtung, 3
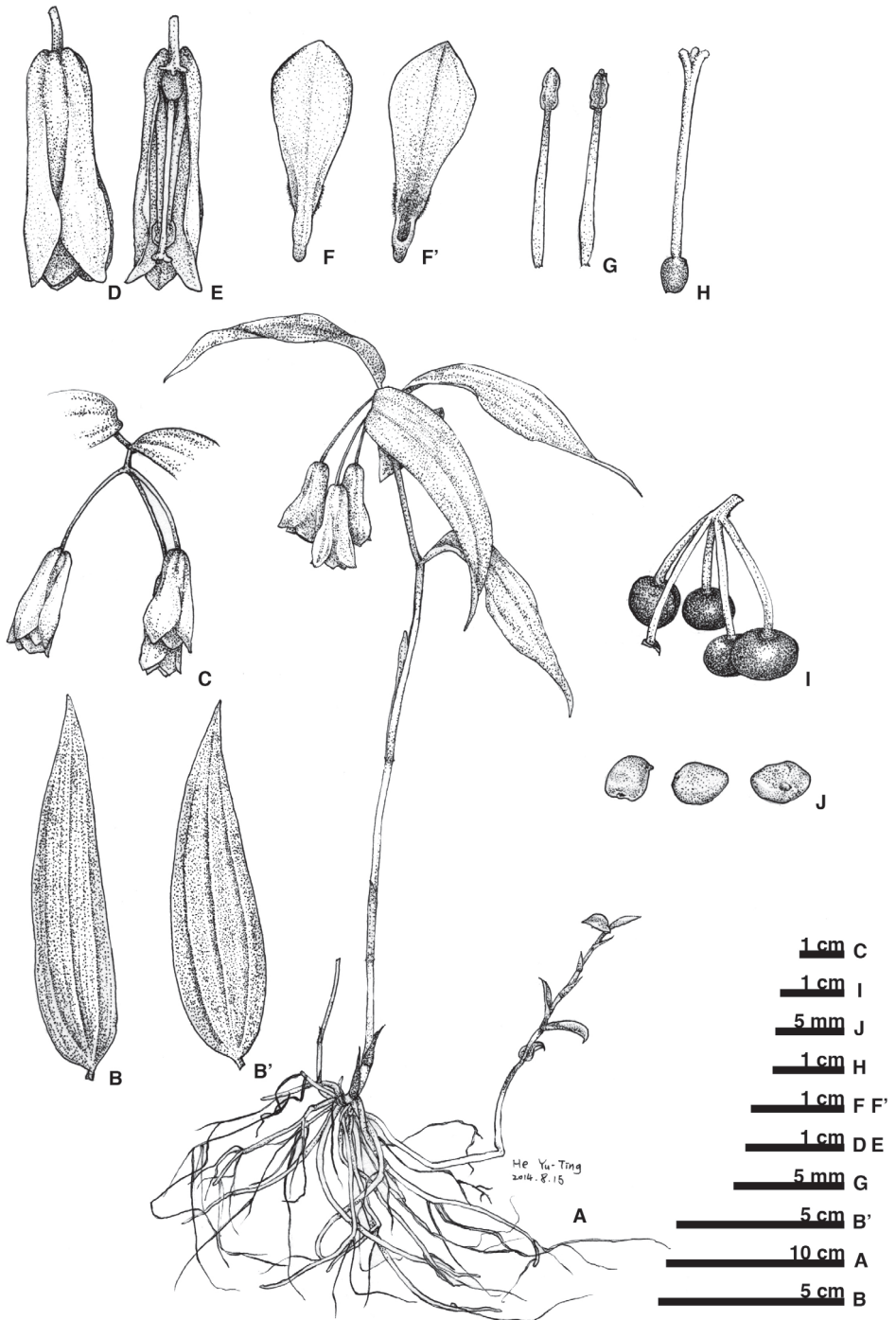
Figure 9. *Disporum shimadae*. **A** habit **B** leaf adaxial surface **B'** leaf abaxial surface **C** inflorescence **D** flower **E** flower section (with tepals and stamen removed) **F** tepal outer surface **F'** tepal inner surface **G** stamen **H** pistil **I** fruit **J** seeds.
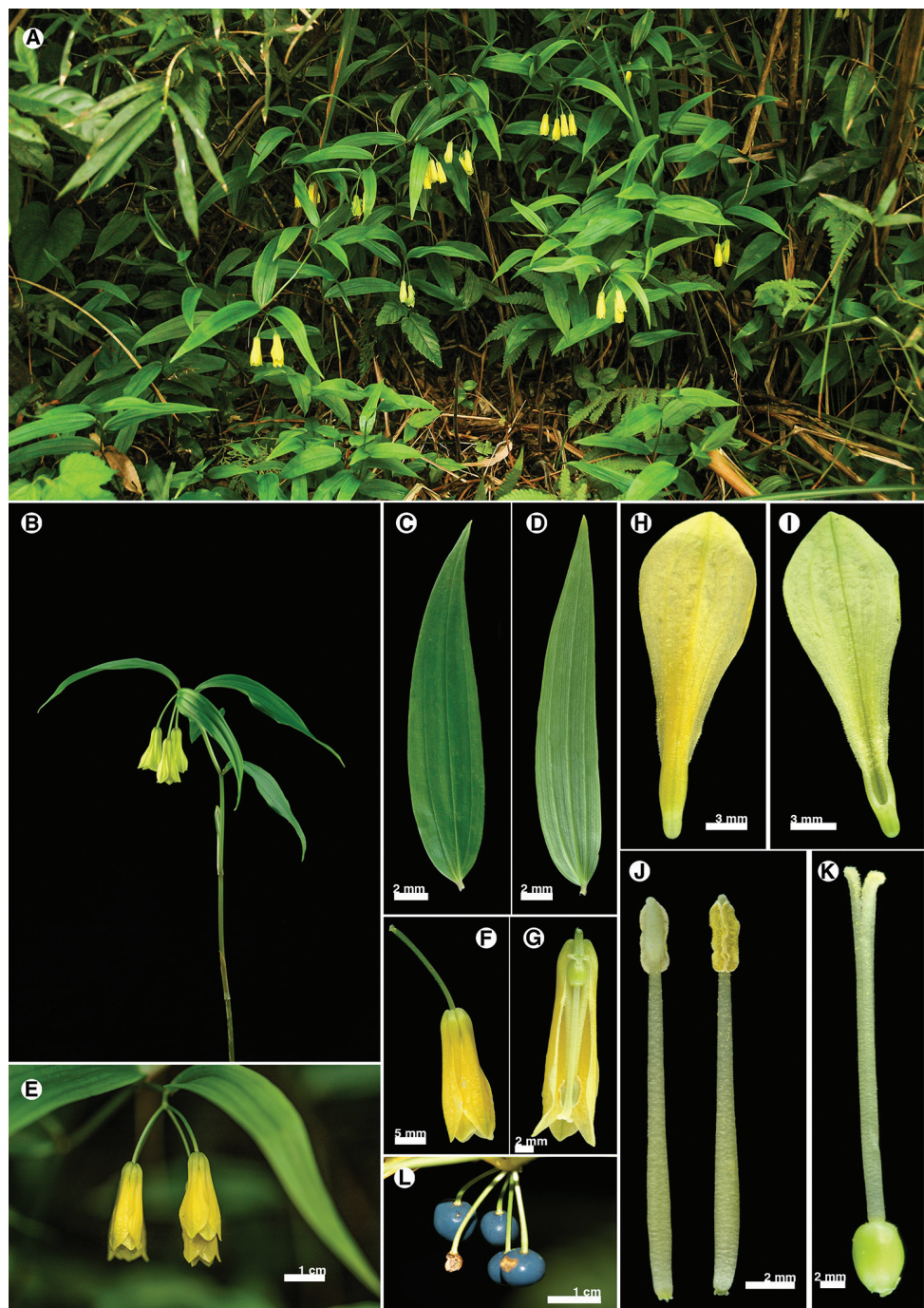
Figure 10. *Disporum shimadae*. **A** habitat **B** habit **C** leaf adaxial surface **D** leaf abaxial surface **E** inflorescence **F** flower **G** flower section (with tepals and stamen removed) **H** tepal outer surface **I** tepal inner surface **J** stamen **K** pistil **L** fruits.

Mar 2002, T. Y. A. Yang et al. 14553 (TNM); Dapishan, 23 May 2003; S. C. Liu et al. 1203 (TNM); Homei, 3 m alt., 16 Jun 2004, Y. H. Tseng 3786 (TAIE); Huangdieden shan, 560 m alt., 2 May 1992, L. F. Huang et al. 29 (TAI); Wututan, 22 Aug 2001, H. L. Chiang 2707 (TAIF); Santiaochiao, 28 Feb 2007, F. C. Kuo 29 (TAIF);

Acknowledgements

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RESEARCH ARTICLE

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Typification of *Oxalis bowiei* W.T.Aiton ex G.Don (Oxalidaceae)

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Abstract

Oxalis bowiei W.T.Aiton ex G.Don (Oxalidaceae) from South Africa was described in 1831, but has not been typified. Although no preserved material was mentioned in the original description, an illustration by Thomas Duncanson painted a few years earlier would have been available to W.T. Aiton at the time he described it and it matches his description. Therefore this illustration is designated as the lectotype for *Oxalis bowiei*.

Keywords

Oxalis bowii, *Oxalis bowieana*, Bowie's woodsorrel, nomenclature, lectotype

Introduction

Oxalis bowiei W.T.Aiton ex G.Don (Oxalidaceae), commonly known as Bowie's woodsorrel, is a bulbous perennial from KwaZulu-Natal and Eastern Cape Province of South Africa. It is an attractive flowering plant and is occasionally grown horticulturally in mild temperate climates (Brickell and Aspden 1994). It has also become naturalised in Australia, Europe, North America and Japan (Carnevali et al. 2018; Conn et al. 1999; Nesom 2017; Thevenot et al. 2018; Yokohata 2002). Indeed, this paper is derived from other research we are conducting on the biology of invasive *Oxalis* in Europe.

Oxalis bowiei was collected by, and named after, James Bowie (circa 1789–2 July 1869) (Loddiges 1832). Bowie was employed by the Royal Botanic Gardens, Kew and

130 O. Bòwɪɪ (Ait. mss.) stemless, hoary-pubescent; leaflets 3, obtuse; peduncles about equal in length to the leaves, umbelliferous. ♃. G. Native of the Cape of Good Hope. Root bulbous. Flowers large, red. An elegant plant.

Bowie's Wood-sorrel. Fl. April, Aug. Clt. 1824. Pl. ¼ ft.

Figure 1. The original description of *Oxalis bowiei* W.T.Aiton ex G.Don from A general history of the dichlamydeous plants by George Don. Taken from the Biodiversity Heritage Library https://biodiversitylibrary.org/page/390566 (Don 1831).

was sent as a botanical collector to the Cape of Good Hope between 1817 and 1823 (Smith and van Wyk 1989). *Oxalis bowiei* was formally named in a publication by George Don (1798–1856) and attributed to W.T.Aiton, who gave the epithet *bowii* (Don 1831) (Fig. 1). The description of George Don refers to a manuscript by Aiton as "Ait. mss.". We know this refers to William Townsend Aiton (1766–1849), rather than his father William Aiton (1731–1793), because the latter would not have not known James Bowie. Bowie was only an infant when William Aiton Sr. died.

Although the original published epithet was *bowii*, this can be legitimately corrected to *bowiei* to form a substantival epithet, *bowiei*, following articles 60.1 and 60.8 of the International Code of Nomenclature for algae, fungi, and plants (ICN) (Turland et al. 2018).

Occasionally the author citations *Oxalis bowiei* Herb. ex Lindl. or solely *Oxalis bowiei* Lindl. are used in the literature (Salter 1944). These are derived from Edward's Botanical Register (Lindley 1833) (Fig. 2). However, this is a superfluous name under article 52 of the ICN, because it was published after Aiton's name.

Likewise, Loddiges (1832) (Fig. 3) uses the name *Oxalis bowieana*, either correcting Aiton's name to the adjectival form or perhaps meaning to establish a new name, but again it was published after Aiton's name (Don 1831). It is clear from the illustrations, names and descriptions that these versions of the name refer to the same taxon. Neither Lindley (1833) nor Loddiges (1832) mention any specimens, nor do they cite W.T.Aiton or G.Don.

Typification

No herbarium specimens are mentioned in the description and the only reference to material, is that plants were cultivated from 1824 ("Clt."), presumably at the Royal Botanic Gardens, Kew, where W.T.Aiton was director (Britten 1885) (Fig. 1). Therefore, this name was published without a holotype. Furthermore, I have been unable to find a subsequent typification where you might expect one, for example in publications on South African *Oxalis*, such as Salter (1944). The lack of a type has also been noted by Nesom (2017).

Figure 2. The illustration of *Oxalis bowiei* from Edward's Botanical Register (Lindley 1833). https://biodiversitylibrary.org/page/239525

Figure 3. The illustration of *Oxalis bowiei* (as *Oxalis bowieana*) from The Botanical Cabinet (Loddiges 1832). https://biodiversitylibrary.org/page/29151292

Figure 4. A painting of *Oxalis bowiei* by Thomas Duncanson deposited at the Royal Botanic Gardens, Kew. It is painted from material collected by James Bowie in the Eastern Cape, South Africa, East of the Great Fish River. Painted October 23rd 1823. Number: 340, Alternative number: 452. Copyright The Trustees of the Royal Botanic Gardens, Kew.

There are no herbarium specimens at Kew for this species during this period. However, Thomas Duncanson was employed by W.T.Aiton at this time to paint plants newly imported and grown at Kew (Britten 1912). Indeed, there is a painting by Thomas Duncanson in the Kew Archives of *Oxalis bowiei* dated 23 October 1823, which may be a suitable type (Fig. 4). The requirements for lectotypification have been revised in the latest Code (McNeill et al. 2016, Turland et al. 2018). It is necessary to show that the illustration was "*available*" to the author and that the author "*associated*" the illustration with the taxon. Given the date and the location, it is clear that this comprises unpublished material that was available to W.T.Aiton prior to the preparation of the description. Also, as W.T.Aiton's description mentions that the species was grown at Kew from 1824 and that the description matches the illustration, this satisfactorily associates the illustration with the description (Fig. 4).

A slight discrepancy is that the description states "*peduncles about equal in length to the leaves*", whereas the Duncanson illustration shows a much longer peduncle. Nevertheless, Salter (1944) indicates that *O. bowiei* can have much longer peduncles and this trait certainly depends on cultural conditions. Otherwise, the Duncanson illustration is also the most accurate of the three illustrations reproduced here (Figs 2–4). It shows the underground structures, which are critical for correct identification. It also shows the absence of apical calli on the sepals (Salter 1944). Furthermore, the other figures imply that the sepals are fused over a third of their length, which is not the case.

Incidentally, other Duncanson illustrations have been used both as lectotypes and as neotypes for several other names of South African species (Figueiredo and Smith 2017; Glen and Hardy 2000; Smith 1990).

Oxalis bowiei W.T.Aiton ex G.Don, Gen. Hist. 1: 761, 1831 [early Aug 1831] (as "Bowii")

Lectotype, designated here: the illustration number 340 preserved at the Royal Botanic Gardens, Kew (K) (Alternative number: 452), painted by Thomas Duncanson, is designated as the lectotype of *Oxalis bowiei* W.T.Aiton ex G.Don (Fig. 4). This was from material collected by Bowie in Caffraria [Kaffraria], East of the Great Fish River and brought home by him in 1823. This illustration is of good quality, shows both above and below ground structures and has good detail and scale.

Acknowledgements

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RESEARCH ARTICLE

Liparis napoensis (Orchidaceae), a new species from Guangxi, China

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Abstract

Liparis napoensis, a new orchid species belonging to section *Cestichis* from Guangxi, China is described and illustrated. It occurs in the karst limestone forest. The new species is morphologically similar to *L. viridiflora* and *L. somae*, but can be readily distinguished by having narrowly oblong-falcate petals; flabellate-quadrate lip distinctly concave at base and emarginate at apex; conspicuously arcuate column with a pair of wedge-shaped wings.

Keywords

Malaxideae, Napo County, orchid, section *Cestichis*, taxonomy

Introduction

The genus *Liparis* L.C. Richard (1817: 21), also known as false twayblade, belongs to the tribe Malaxideae of the subfamily Epidendroideae. It comprises about 320 species with cosmopolitan distribution from the tropics and subtropics to the temperate and alpine regions (Pearce and Cribb 2002, Pridgeon et al. 2005). Since its publica-

tion, various segregate genera have been proposed such as *Alatiliparis* Marg. & Szlach. (2001: 78), *Disticholiparis* Marg. & Szlach. (2004: 175), *Seidenforchis* Marg. (2006: 302) and *Platystyliparis* Marg. (2007: 35). Molecular phylogenetic studies indicated that *Liparis* in broad delimitation is polyphyletic (Cameron 2005, Li and Yan 2013). Pridgeon et al. (2005) concluded that *Liparis* sensu stricto should be restricted to a group of temperate Asian species with the type, *L. loeselii* (L.) Richard. It is as yet unclear whether the recognition of these splits provides a better taxonomy, thus we opted to maintain *Liparis* as a broad concept for the present.

As traditionally delimited, *Liparis* section *Cestichis* Thouars ex Lindley (1831: 29) is characterised by having coriaceous, non-plicate leaves. They are usually epiphytes with distinct pseudobulbs and occur mainly in tropical Asia. In China, the genus *Liparis* is represented by about 70 species (Chen et al. 2009), including eight recently described species (see Jin 2011, Wu et al. 2012, Hsu 2013, Li and Yan 2013, Su et al. 2015, Tang et al. 2015). More than half of the Chinese *Liparis* species (40, about 57%) belong to section *Cestichis*.

The limestone karst area is part of a global biodiversity hotspot. Floristic investigations of limestone areas in southwestern Guangxi, China from April 2012 to July 2015, have yielded the discovery of an interesting *Liparis* species of section *Cestichis*. Morphologically, this species is superficially similar in appearance to *L. viridiflora* (Blume) Lindley (1831: 31) in vegetative habit, but differs significantly from the latter in the floral morphology. On the other hand, it bears yellowish or whitish flowers somewhat resembling those of *L. somae* Hayata (1914: 33), a rare species endemic to Taiwan, but several critical details differ. Over the past three years, the living and cultivated specimens were monitored in the field and in the nursery of South China Botanical Garden (SCBG), Chinese Academy of Sciences (CAS). Careful examinations of diagnostic morphological features of similar taxa and literature surveys (Seidenfaden 1976, Comber 1990, Yang 2006, Averyanov 2013, 2015, Tang et al. 2015) indicated that it represents a species new to science and accordingly described herein.

Materials and method

A total of 450 herbarium specimens of *Liparis* species in the section *Cestichis* were examined from herbaria BM, E, HN, IBK, IBSC, K, PE and US (acronyms according to Thiers 2018). The taxonomic status of *Liparis napoensis* and its close allies were examined by checking the type specimens in these herbaria and online digital image repositories and databases available on JSTOR Global Plants website (http://plants.jstor.org). Relevant literature, including protologue was consulted. Morphological descriptions and measurements of the putative new species were undertaken based on three living specimens in cultivation (South China Botanical Garden). The specimens were observed and photographed under a stereomicroscope (Olympus MD-90). The conservation status of the new species was evaluated following the guidelines in IUCN (2017).

Taxonomic description

Liparis napoensis L.Li, H.F.Yan & S.J.Li, sp. nov.
urn:lsid:ipni.org:names:60478421-2
Figures 1, 2

Type. CHINA. Guangxi Zhuang Autonomous Region, Baise City, Napo County, Yongning Village, Jinlongyan Cave, lithophytic on moss in monsoon evergreen broad-leaved forest, alt. 830 m, 31 May 2012, L. Li 1001, (holotype, IBSC!).

Diagnosis. *Liparis napoensis* differs from its closest allies: *L. viridiflora* and *L. somae* in the clustered ovoid-cylindrical or narrowly pyriform pseudobulbs, narrowly oblong-falcate petals; a flabellate-quadrate lip with a distinctly concave base, an emarginate apex and erose margins; a conspicuously arcuate column with a pair of wedge-shaped wings.

Description. Lithophytic herbs. Pseudobulbs clustered, ovoid-cylindrical or narrowly pyriform, 5–10 cm × 5–8 mm, attenuate toward apex, base covered with 3–4 fibrous remnant sheaths. Leaves 2, terminal, blade oblanceolate or oblong-spatulate, thin coriaceous, base contracted into a very short petiole less than 1 cm or subsessile, apex acute and minutely apiculate, 7–12× 1.5–2 cm. Inflorescence terminal, often recurved, 15–20 cm, densely racemose, pedunculate; rachis 10–15 cm with densely arranged numerous flowers; floral bracts linear-lanceolate, 3.5–4 mm, membranous, greenish-white. Flowers resupinate, spreading, 4–4.5 mm across, white, tinged with pale yellow in the centre; pedicel and ovary 3.5–4 mm, pale yellow or greenish-yellow. Dorsal sepal ovate-oblong, margins often revolute, apex obtuse, 2.5–3 × 0.8–1 mm, translucent white, becoming yellowish towards the base. Lateral sepals obliquely ovate-elliptic, margins often revolute, 2.5–3 × 0.8–1 mm, translucent white, becoming yellowish towards the base. Petals narrowly oblong-falcate, margins revolute, 2–2.5 × 0.3–0.5 mm, translucent white, becoming yellowish towards the base. Lip nearly flabellate-quadrate, 2–2.5 × 1.5–2 mm, base shallowly concave and distinctly recurved from the middle, indistinctly divided into hypochile and epichile; hypochile ecallose, adaxially slightly thickened and fleshy towards the margins on each side; epichile emarginate, apical margins inconspicuously erose, translucent white, furnished with pale yellow at base. Column terete, conspicuously incurved or arcuate above the middle, apex with 2 short, wedge-shaped wings, with the base slightly dilated, 1.0–1.5 mm long, greenish-white, tinged with pale yellow at base. Stigma concave, subelliptic. Rostellum approximately truncate, apex obtuse, yellowish. Anther terminal, 2-celled, persistent, compressed ovoid, ca. 0.5 mm long. Pollinia 4, hard, waxy, yellow, ca. 0.3 mm. Capsule obovoid-ellipsoid, ridged, 4–6 × 2–3 mm; fruiting pedicel 3–5 mm.

Distribution and habitat. Endemic to Guangxi in China. Lithophytes in rocks crevices where soil or organic matter has accumulated at elevations from ca. 650 m to 900 m in karst limestone forest.

Etymology. The epithet "napoensis" is derived from the type locality: Napo County, Guangxi, located at China's southwest border, where the species was discovered.

Phenology. Flowering and fruiting in January–February.

Conservation status. Based on careful field investigations in the past years, this species is rare and only known from the type locality. Plants grow in sparsely scattered

Figure 1. *Liparis napoensis* **A** Habit in bloom **B** Flower, lateral view **C** Flower, front view **D** Column, ventral view **E** Column, lateral view **F, G** Lip **H** Dorsal sepal **I** Petal **J** Lateral sepal. Line drawing by Yun-Xiao Liu. Scale bars: 2.5 cm (**A**), 2 mm (**B, C**), 1 mm (**D–I**).
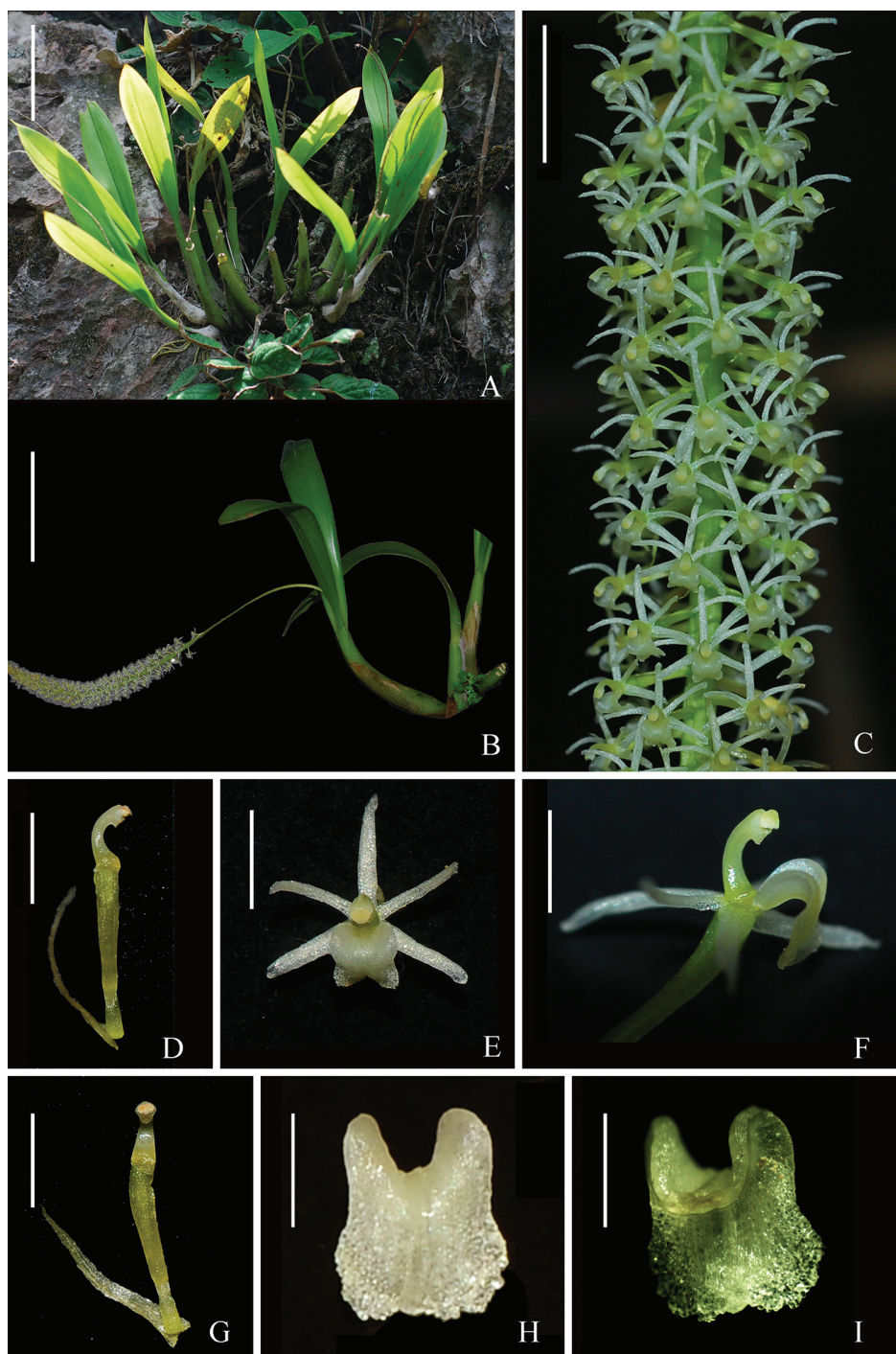
Figure 2. *Liparis napoensis* **A** Habitat **B** A plant in bloom **C** Inflorescence **D** Column, lateral view, showing bract **E** Flower, frontal view **F** Flower, lateral view **G** Column, ventral view, showing bract **H, I** Lip. Scale bars: 5 cm (**A–C**), 2 mm (**D–G**), 1 mm (**H, I**).

Table 1. Comparison of the diagnostic characters of *L. napoensis* and its allies.

Characters	*L. napoensis*	*L. somae*	*L. viridiflora*
Growth habit	lithophytes	epiphytes	epiphytes or lithophytes
Pseudobulbs	ovoid-cylindrical or narrowly pyriform	ovoid or clavate	elongate-cylindrical
Leaves	oblanceolate or oblong-spatulate, apex acute and minutely apiculate	oblanceolate or spatulate, apex acute	linear-oblanceolate, apex acuminate and apiculate
Petiole	less than 1 cm or subsessile	2–3 cm	1–4 cm
Dorsal sepal	ovate-oblong	lanceolate	elliptic-oblong
Lateral sepals	obliquely ovate-elliptic	obliquely ovate	ovate-elliptic
Petals	narrowly oblong-falcate	linear	narrowly linear
Lip	flabellate-quadrate, base concave, slightly thickened on each side, apex emarginate, apical margin inconspicuously erose	ovate, base slightly contracted, apex acute, apical margin slightly crisped-denticulate	ovate-oblong, base contracted, apex subacute or mucronate, apical margin slightly undulate
Column	conspicuously arcuate, apex with 2 wedge-shaped wings	slightly arcuate, apex with 2 obtusely dentate wings	slightly arcuate, apex with rounded wings

groups and the known population of two colonies consists of only a few dozen individuals (density less than one plant per 20 m^2). In addition, the location is not in a protected area and accessible to casual hikers. According to the guidelines for using the IUCN Red List Categories and Criteria (IUCN 2017), the species is categorised as Critically Endangered [CR B2ab(iii)] due to its rarity and the threat of disturbance.

Taxonomic notes. The new species in its general appearance has some superficial similarity with *Liparis viridiflora*, but the latter differs in longer petioles, narrowly linear petals, ovate-oblong lip with a mucronate tipped apex and a column with rounded wings. It also superficially resembles *L. somae*, but is characterised by having ovoid-cylindrical or narrowly pyriform pseudobulbs, a flabellate-quadrate lip with a distinctly concave base and an emarginate apex. A detailed morphological comparison between *L. napoensis* and its closely related taxa *L. viridiflora* and *L. somae* is presented in Table 1.

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SHORT COMMUNICATION

Sisymbrium linifolium and *Sisymbriopsis schugnana* (Brassicaceae), two new records from Xinjiang, China

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Abstract

Sisymbrium linifolium and *Sisymbriopsis schugnana*, previously confined to western North America and Tajikistan, respectively, were discovered in Xinjiang during a recent field trip to this autonomous region of China. The identity of these two species was subsequently confirmed by extensive morphological and molecular studies. The biogeographical significance of these new floristic records is briefly addressed.

Keywords

Brassicaceae (Cruciferae), China, new records, North America, *Sisymbriopsis*, *Sisymbrium*, Tajikistan

Introduction

Although mainly distributed in the temperate regions, species of the mustard family (Brassicaceae / Cruciferae; authorised alternative names, Art. 18.5 and 18.6 of the ICN: Turland et al. 2018) are found in all continents except Antarctica. In total there are 341 currently recognised genera, and about 4050 species worldwide (BrassiBase: https://brassibase.cos.uni-heidelberg.de, accessed 20 July 2018; Koch et al. 2012a, 2018, Kiefer et al. 2014, DA German pers. com.). For the Flora of China, 102 genera and 412 species were recorded by Zhou et al. (2001) but these numbers are out of date due to taxonomic status changes for some taxa and discoveries of new species. These include the reduction of *Desideria* Pamp., *Phaeonychium* O.E.Schulz, and *Eurycarpus* Botsch. to

synonymy of *Solms-laubachia* Muschl. (Yue et al. 2008, German and Al-Shehbaz 2010), and the merging of *Neomartinella* Pilger, *Platycraspedum* O.E.Schulz, *Taphrospermum* C.A.Mey., and *Thellungiella* O.E.Schulz with *Eutrema* R.Br. (Al-Shehbaz and Warwick 2005, Al-Shehbaz et al. 2006). Besides, several new genera have since been proposed, including *Shangrilaia* Al-Shehbaz, J.P.Yue & H.Sun (Al-Shehbaz et al. 2004), *Metashangrilaia* Al-Shehbaz & D.A.German, *Rudolf-kamelinia* Al-Shehbaz & D.A.German, and *Anzhengxia* Al-Shehbaz & D.A.German (Al-Shehbaz and German 2016), *Shehbazia* D.A.German (German and Friesen 2014), *Sinoarabis* R.Karl, D.German, M.A.Koch & Al-Shehbaz (Koch et al. 2012b), *Sinalliaria* X.F. Jin, Y.Y.Zhou & H.W.Zhang (Zhou et al. 2014), as well as new species in *Solms-laubachia* (Yue et al. 2005, 2008, Chen et al. 2018a), *Draba* L. (Al-Shehbaz 2002, 2007, Al-Shehbaz et al. 2014), *Cardamine* L. (Al-Shehbaz and Boufford 2008, Al-Shehbaz 2015a, 2015b, 2015c), *Eutrema* (Gan QL and Li XW 2014, Xiao et al. 2015, Hao et al. 2015, 2016, 2017), and new records, i.e. *Cardamine bellidifolia* L. (Chen et al. 2011), *Pterygostemon spathulatus* (Kar. & Kir.) V.V.Botschantz. [reported as *Fibigia spathulata* (Kar. & Kir.) B. Fedtsch. (German et al. 2012)], *Rhammatophyllum erysimoides* (Kar. & Kir.) Al-Shehbaz & O. Appel (German et al. 2006), and *Erysimum croceum* Popov (Ya et al. 2018). According to our most recent compilation, there are 101 genera and 490 species of Brassicaceae in China.

Two of the authors (H.L.C and J.P.Y) have conducted a botanical expedition to Xinjiang and Xizang from 15 June to 22 July 2017, during which we collected about 130 species of 25 genera of Brassicaceae. Subsequent molecular and morphological studies supported the addition of two species as new records to China. *Sisymbrium linifolium* (Nutt.) Nutt. (Figure 1) and *Sisymbriopsis schugnana* Botsch. & Tzvelev (Figure 2) were previously known only from western North America and Tajikistan, respectively (Figure 3).

Materials and methods

Plant materials and molecular data

Collected specimens were deposited in KUN, and species identification was based on the floras of China (Zhou et al. 2001), Pan-Himalaya (Al-Shehbaz 2015d), and North America (Al-Shehbaz et al. 2010) and studies on *Sisymbrium* L. (Al-Shehbaz 1988, 2006, Warwick and Al-Shehbaz 2003) and *Sisymbriopsis* (Al-Shehbaz et al. 1999).

The *nr*ITS sequence of *Sisymbriopsis schugnana* was included in our previous study on the phylogeny of the tribe Euclidieae (Chen et al. 2018b), while *nr*ITS sequences of four individuals of *Sisymbrium linifolium* were generated and analysed in this study. An additional 48 sequences, representing 19 *Sisymbrium* species (mostly from Warwick et al. 2002) and seven sequences of five species (*Capsella bursa-pastoris* (L.) Medik., *Erucastrum supinum* (L.) Al-Shehbaz & S.I.Warwick, *Neotorularia torulosa* (Desf.) Hedge & J.Léonard, *Neuontobotrys lanata* (Walp.) Al-Shehbaz, and *Polypsecadium solidagineum* (Triana & Planch.) Al-Shehbaz) were downloaded from GenBank (Appendix A). Following Mutlu and Karakuş (2015), *N. torulosa* and *C. bursa-pastoris* were used as outgroups.

DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted from silica gel-dried leaf materials using the Plant Genomic DNA Kit (Tiangen Biotech, Beijing, China) following the manufacturer's protocol. The ITS region was amplified with the primers ITS-18F as modified by Mummenhoff et al. (1997) and ITS-4 (White et al. 1990). All polymerase chain reactions (PCR) were performed in a 25 µl volume consisting of 1µl sample DNA (approx. 5–10 ng), 12.5µl Premix Taq (Takara Biomedical Technology, Beijing, China), 1µl of 10 µM stock of each primer, adjusted to 25 µl with ddH$_2$O. The PCR protocol of the ITS region involved a hot start with 4 min at 94 °C, and 32 cycles of amplification (1 min denaturing at 94 °C, 45 s annealing at 53 °C, 60 s extension at 72 °C), and a final elongation step for 10 min at 72 °C. The sequencing primers are the same as amplified primers.

Phylogenetic analyses

Original chromatograms were evaluated with Sequencher 4.1.4 (Gene Codes Corporation, 2002) for base confirmation and contiguous sequences editing, and sequences were aligned with MAFFT v7.311 (Katoh et al. 2002; Katoh and Standley 2013) and were manually adjusted with MEGA 7.0.14 (Kumar et al. 2016). The aligned sequences were analysed with maximum parsimony (MP) and Bayesian Inference (BI).

Parsimony analysis was performed with heuristic searches of 1000 replicates with random stepwise addition using tree bisection reconnection (TBR) branch swapping as implemented in PAUP* 4.0a161 (Swofford 2018). All characters were weighted equally, and gaps were treated as missing data. For Bayesian Inference analysis, jModeltest v2.1.7 (Darriba et al. 2012) was used to select the best-fitted model of nucleotide substitution based on the Akaike information criterion (AIC), and the SYM+I+G model was selected for the ITS dataset. Bayesian Inference based on the Markov chain Monte Carlo methods (Yang and Rannala 1997) was performed using MrBayes v3.2.5 (Ronquist et al. 2012), four simultaneous Monte Carlo Markov chains (MCMCs) were run for 3 million generations, and one tree sampled every 1000 generations. The first 750 trees (25% of total trees) were discarded as burn-in. The remaining trees were summarised in a 50% majority-rule consensus tree, and the posterior probabilities (PP) were calculated.

Results

The aligned ITS dataset comprised 24 species (59 accessions) with 584 characters, of which 192 were variable and 152 (26.03%) were parsimony-informative. Four individuals of the newly collected *Sisymbrium* from Xinjiang have exact sequences, and sequence divergence between them and *S. linifolium* ranged from 0–0.2%, which was lower than that of 1.5% compared with *S. polymorphum* (Murray) Roth.

The generated MP trees had a very similar topology to the Bayesian tree, thus only the BI topology, which is almost as same as the result of Mutlu and Karakuş (2015), is shown. The four Xinjiang *Sisymbrium* clustered with *S. linifolium* (PP/BS = 1/97), and then clustered with *S. polymorphum* (PP/BS = 0.65/63) and *S. loeselii* L. (PP/BS = 0.78/54) (Figure 4b). Furthermore, sequences alignment revealed that the Xinjiang plants and North American *S. linifolium* shared several specific nucleotide residues that are different from *S. polymorphum* (Figure 4a), which further their identity as *S. linifolium*.

Discussion

Sisymbrium linifolium (Nutt.) Nutt

The generic placement of *Sisymbrium linifolium* has long been in dispute. It was originally placed in *Nasturtium* W.T.Aiton (Nuttall, 1834), and then transferred to *Sisymbrium* (Nuttall in Torrey and Gray, 1838) and *Schoenocrambe* Greene (Greene, 1896). Though several authors claimed that, on aspects of habit, leaves and flowers morphology, this species is very similar to the Eurasian *S. polymorphum* and retained it in *Sisymbrium* (Payson 1922, Schulz 1924, A1-Shehbaz 1973), while others kept it in *Schoenocrambe* (Rollins 1982, 1993). Molecular phylogenetic study on *Sisymbrium*, using ITS sequence data, revealed that *S. linifolium* is most closely related to *S. polymorphum* within the Old World *Sisymbrium* clade of tribe Sisymbrieae, while all other New World *Sisymbrium* were placed in various genera of the tribe Thelypodieae (Warwick et al. 2002). These results prompted Warwick and Al-Shehbaz (2003) to propose nomenclatural adjustments for some *Sisymbrium* species and further delimit *Sisymbrium* to include only 40 Old World species, plus North American *S. linifolium*, instead of the 96 species previously assigned to it (Al-Shehbaz, 2006).

Based on morphology, the Xinjiang *Sisymbrium* material we collected could be identified as *S. polymorphum*, but both phylogenetic analyses and sequence alignments supported its placement in *S. linifolium* (Figure 4). This conclusion makes the distribution range of *S. linifolium* extended from North America into north-western China, with a large range disjunction (Figure 3). One possible explanation for such distribution is a recent introduction of seeds of *S. linifolium* from North America to China by unintentional human activities. Many weeds of the mustard family (e.g., *Capsella bursa-pastoris*, *Thlaspi arvense* L., and *Sisymbrium orientale*) are invasive in both continents under preferable habitats (Zhou et al. 2007) such as farmlands, construction sites and ruins, waste places, disturbed sites, and roadsides. The Xinjiang *S. linifolium* was collected from a rocky hillside near the provincial road S229 in Jeminay County (Figure 1C). This locality is far from any villages or towns and, therefore, the possibility that its occurrence was the result of human activity is less likely. However, introduction with road construction material cannot be excluded as well.
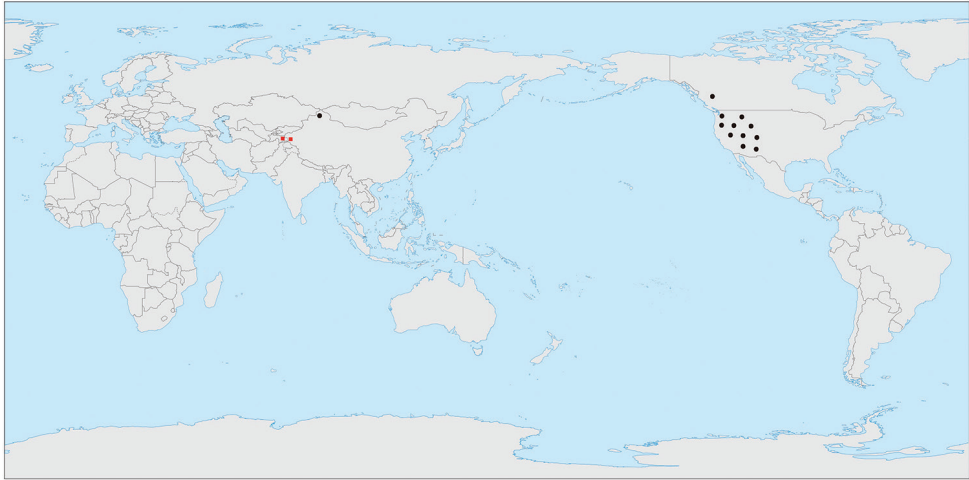
Another possible explanation is that *Sisymbrium linifolium* actually has both North American and Central Asian distribution, and most, if not all, of its Asian populations

Figure 1. *Sisymbrium linifolium* (Nutt.) Nutt. **A** flowering plant **B** fruits **C** habitat.

Figure 2. *Sisymbriopsis schugnana* Botsch. & Tzvelev. **A** flowering plant **B** flowers **C** immature fruits.

Figure 3. Distribution of *Sisymbrium linifolium* and *Sisymbriopsis schugnana*. Black dots: *Sisymbrium linifolium* in North America (modified from Al-Shehbaz et al. 2010) and the new population in Xinjiang, China; red squares: *Sisymbriopsis schugnana* in Tajikistan and Xinjiang, China.

were misidentified as the very similar species, *S. polymorphum*. Further molecular phylogenetic studies and crossing experiments on more populations from both continents are needed to determine whether a single species or two are in fact involved. If it turned out that the species grows on both continents, then the name for the combined species should be the earlier-published one, *S. polymorphum*.

Sisymbriopsis schugnana Botsch. & Tzvelev

Sisymbriopsis Botsch. & Tzvelev was originally recognised as a monospecific genus including *S. schugnana* as its type (Botschantsev and Tzvelev 1961). A second species, *S. mollipila* (Maxim.) Botsch., was transferred from *Sisymbrium* by Botschantsev (1966), and Al-Shehbaz et al. (1999) recognised three other species. Of the five species currently assigned to the genus, *S. schugnana* is endemic to Tajikistan, *S. mollipila* occurs in China, Kyrgyzstan, and Tajikistan, and the other three species are endemic to China. However, in a molecular phylogenetic study by Warwick et al. (2004), *S. mollipila* and *S. yechengensis* (C.H.An) Al-Shehbaz, C.H.An & G.Yang were found unrelated to each other, and the former was close to some *Neotorularia* species, whereas the position of *S. yechengensis* was unresolved. In a later phylogenetic study (Warwick et al. 2007), *S. mollipila* was found nested within a clade containing species of the genera *Desideria*, *Rhammatophyllum* O.E.Schulz, and *Solms-laubachia*, whereas *S. yechengensis* formed a solitary clade. Based on the distant genetic position and clear morphological differentiation, Al-Shehbaz and German (2016) transferred *S. yechengensis* to the new genus *Anzhengxia*.
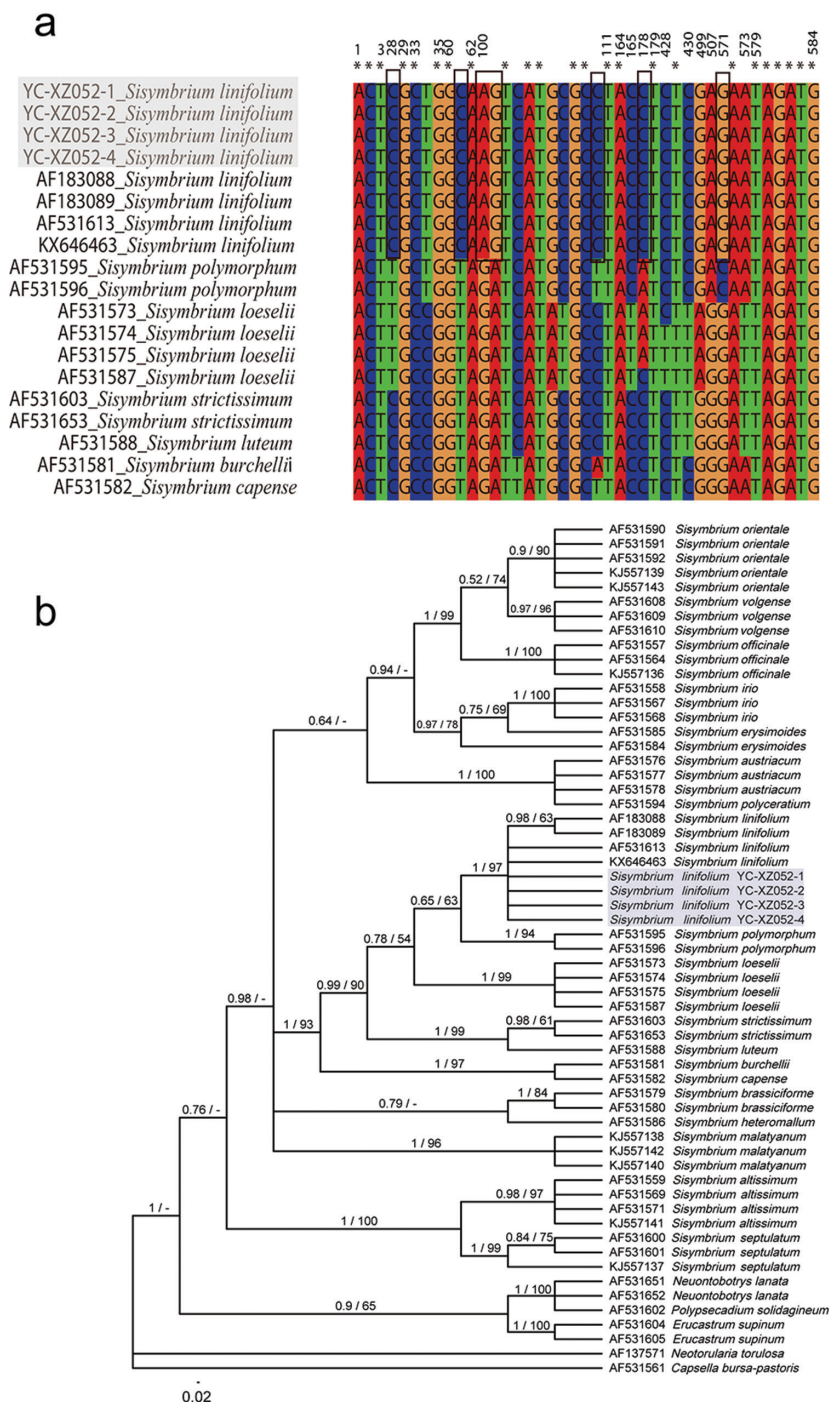
Figure 4. Multiple sequence alignment (**a**) and molecular phylogeny (**b**) based on ITS sequences. Bayesian posterior probability (PP) and MP bootstrap values (BS) are showed above branches in a following of PP / BS (only shown if > 50%). The newly found *Sisymbrium linifolium* were in grey.

The material studied here was collected from alluvium of the Muztagata (also Mugtag Ata) Glacial Public Park in Tashkurgan County, Xinjiang, an area close to the borders of Tajikistan. The plant has decumbent stems, dentate and palmately veined leaves, linear and latiseptate secund fruit, and white to pink flowers (Figure 2). Our initial morphological studies failed to identify the plant using Zhou et al. (2001), but subsequent molecular sequence comparison narrowed its identity to *Sisymbriopsis*, and its unique secund fruits led to its recognition as *S. schugnana* and a new record from China. In addition, species of *S. pamirica* (Y.C.Lan & C.H.An) Al-Shehbaz, C.H.An & G.Yang, *S. mollipila*, and *Anzhengxia yechengnica* (C.H.An) Al-Shehbaz & D.A. German were recently included in a phylogenetic study on the tribe Euclidieae (Chen et al. 2018b). Three *Sisymbriopsis* species formed a monophyletic subclade embedded in the *Solms-laubachia* s.l. clade, and *A. yechengnica* was close to *Pycnoplinthus uniflora* (Hook.f. & Thomson) O.E.Schulz., these findings suggesting that the real identity of *Sisymbriopsis* is still awaiting further studies (Chen et al. 2018b).

Sisymbriopsis schugnana is narrowly distributed in the eastern Pamir (Figure 3), a dry and cold desert plateau currently subjected to severe desertification caused by extensive exploitation of dwarf shrub resources, a phenomenon termed "Teresken Syndrome" (Kraudzun et al. 2014). Discovery of the first population of *S. schugnana* within the poorly explored Chinese mountains bordering Tajikistan should promote further botanical explorations in similar areas of adjacent neighbouring countries.

Acknowledgements

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Appendix A

Taxa and GenBank accession numbers for the nrITS sequences downloaded from GenBank and used in the phylogenetic analyses; an asterisk (*) indicates the new species record.

Capsella bursa-pastoris (L.) Medik. (AF531561), *Erucastrum supinum* (L.) Al-Shehbaz & S.I.Warwick (AF531604, AF531605), *Neotorularia torulosa* (Desf.) Hedge & J.Léonard (AF137571), *Neuontobotrys lanata* (Walp.) Al-Shehbaz (AF531651, AF531652), *Polypsecadium solidagineum* (Triana & Planch.) Al-Shehbaz (AF531602); *Sisymbrium altissimum* L. (AF531559, AF531569, AF531571), *S. austriacum* Jacq. (AF531576, AF531577, AF531578), *S. brassiciforme* C.A.Mey. (AF531579, AF531580), *S. burchellii* DC. (AF531581), *S. capense* Thunb. (AF531582), *S. erysimoides* Desf. (AF531584, AF531585), *S. heteromallum* C.A.Mey. (AF531586), *S. irio* L. (AF531558, AF531567, AF531568), *S. linifolium* Nutt. (AF183088, AF183089, AF531613, KX646463), *S. loeselii* L. (AF531573, AF531574, AF531575, AF531587), *S. luteum* (Maxim.) O.E.Schulz (AF531588), *S. malatyanum* Mutlu & Karakuş (KJ557138, KJ557140, KJ557142), *S. officinale* (L.) Scop. (AF531557, AF531564, KJ557136), *S. orientale* L. (AF531590, AF531591, AF531592, KJ557139, KJ557143), *S. polyceratium* L. (AF531594), *S. polymorphum* (Murray) Roth (AF531595, AF531596), *S. septulatum* DC. (AF531600, AF531601, KJ557137), *S. strictissimum* L. (AF531603, AF531653), *S. volgense* M.Bieb. ex E.Fourn. (AF531608, AF531609, AF531610),**S. linifolium* (Nutt.) Nutt. (MK419926, MK419927, MK419928, MK419929).

RESEARCH ARTICLE

The genus *Indigofera* (Leguminosae) in New Caledonia: two new species and a key for the species

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Abstract

Indigofera monieriana M.Pignal & L.P.Queiroz, **sp. nov.** and *Indigofera dumbeana* M.Pignal & L.P.Queiroz, **sp. nov.**, two new species from New Caledonia, are described and illustrated. Both new species have been collected for a long time, but most herbarium specimens were named as the Australian species *Indigofera australis*, even though they clearly stand apart from this species and the other New Caledonian species of the genus. *Indigofera monieriana* can be diagnosed by the tall virgate shrubby habit, leaves with an articulate rachis and 7–11 widely obovate to orbiculate leaflets with greyish undersurface and almost invisible venation. *Indigofera dumbeana* can be recognized by the arborescent habit, leaves with 15–19 elliptical leaflets, small, c. 6 mm long flowers, and ellipsoid seeds. Preliminary IUCN assessments are provided for both species. A key is provided for all species of *Indigofera* recorded from New Caledonia.

Keywords

Indigofereae, Fabaceae, New-Caledonia, Papilionoideae, taxonomy

Résumé

Indigofera monieriana M.Pignal & L.P.Queiroz, **sp. nov.** et *Indigofera dumbeana* M.Pignal & L.P.Queiroz, **sp. nov.**, deux nouvelles espèces de Nouvelle-Calédonie, sont décrites et illustrées. Toutes deux sont récoltées depuis longtemps, mais la plupart des spécimens d'herbier sont rapportés à *Indigofera australis*, une espèce australienne, même si elles se distinguent clairement de cette espèce et des autres espèces du

genre de la Nouvelle-Calédonie. *Indigofera monieriana* peut être caractérisée par son port arbustif élevé, ses feuilles avec un rachis articulé et 7–11 folioles largement obovales à orbiculées, une face abaxiale grisâtre et une nervation presque invisible. *Indigofera dumbeana* se reconnaît à son port arborescent, à ses feuilles avec 15–19 folioles elliptiques, à ses fleurs de petite taille (environ 6 mm de long) et à ses graines ellipsoïdes. Des statuts UICN préliminaires sont proposés. Une clé est fournie pour toutes les espèces d'*Indigofera* répertoriées en Nouvelle-Calédonie.

Mots-clefs

Indigofereae, Fabacées, Nouvelle-Calédonie, Papilionoidées, taxonomie

Introduction

New Caledonia is a sui generis French collectivity located in the southwest Pacific Ocean, 1210 km east of Australia. It is an archipelago of about 18,600 km^2 in Melanesia subregion with a mostly subtropical climate. Most of New Caledonia's native vegetation can be classified into three major types: dense rainforests, savannas and maquis vegetation, the latter a kind of low, sclerophyllous, evergreen vegetation largely restricted to ultramafic substrates (Jaffré et al. 2012).

The New Caledonian native flora includes more than 3300 species of seed plants with an extraordinarily rich endemism, including several examples of relictual Gondwanan elements, such as gymnosperms, of which 42 out of 44 native species are endemic (de Laubenfels 1972, Gargominy et al. 2018). The flowering plant families Amborellaceae, Oncothecaceae and Phellinaceae are also restricted to New Caledonia. According to the French taxonomic repository (Gargominy et al. 2018), Leguminosae are represented by 39 genera (5% endemic to the island), 103 species (32% endemic), 6 subspecies and 13 varieties. General endemism in this collectivity is estimated at c. 76.4% (Jaffré 1993) and no doubt many taxa still remain to be described (Morat 2010, Gâteblé et al. 2018). New Caledonia also includes 2008 introduced species (Héquet et al. 2009).

Indigofera L. is a legume genus belonging to the tribe Indigofereae, subfamily Papilionoideae (Schrire 2005, LPWG 2017). The genus is characterized by a combination of the presence of medifixed T-shaped hair, pulvinate leaves, axillary simple racemes, anthers with appendiculate connective, and flowers with an explosive pollen display (Hutchinson 1964; de Kort and Thijsse 1984). *Indigofera* is the third largest genus in Leguminosae, embracing c. 750 species with a worldwide distribution, but with a major diversity center in Africa and Madagascar (Schrire 2005; Schrire et al. 2009). In Tropical Asia to Pacific region, the genus is represented by c. 100 species with several species endemic to each region (de Kort and Thijsse 1984; Wilson and Rowe 2004; Schrire 2005).

Indigofera was known in New Caledonia by seven species: *I. atropurpurea* Buch.-Ham. ex Hornem., *I. australis* Willd., *I. hirsuta* L., *I. linifolia* (L.f.) Retz., *I. spicata* Forssk., *I. suffruticosa* Mill., and *I. zollingeriana* Miq. Interestingly, all species except *I. australis* are introduced, weedy and widespread plants, contrasting with the high endemicity of the Caledonian flora. *Indigofera spicata* (as *I. endecaphylla* Jacq.) is used

as forage plant (*Sarlin 18*, P03615827). *Indigofera hirsuta*, *I. linifolia* and *I. suffruticosa* are considered invasive by the Pacific Islands Ecosystems at Risk (PIER 2013) and in New Caledonia by Meyer et al. (2006).

The Australian *I. australis* is commonly cited as occurring in New Caledonia (Guillaumin 1936, Jaffré et al. 2002). However, during fieldwork in New Caledonia, one of us (MP) had the chance to survey plants that match specimens identified as *I. australis*. After a careful review of morphological variation of all New Caledonian specimens identified as *I. australis* and their comparison to the Australian ones, we concluded that they belong to the two new species described in this work and that *I. australis* does not occur in New Caledonia.

Materials and methods

Plant material

We studied the material kept at the National Herbarium of Paris (**P**) and the IRD herbarium of New Caledonia in Nouméa (**NOU**).

Measurements, observations and abbreviations

We used the tool "collaboratoire" of the national French infrastructure e-ReColNat (ANR-11-INBS-0004) for specimen comparisons. All measurements were taken on adult structures. We took measurements using a stereomicroscope, based only on fully developed and mature organs from dried specimens except for rehydrated floral parts. Extremes of variation are presented in descriptions. Virtual herbarium can be consulted on the research infrastructure RECOLNAT (https://explore.recolnat.org/search/botanique/type=index), P herbarium (https://science.mnhn.fr/institution/mnhn/collection/p//list?lang=en_US) and NOU herbarium (http://herbier-noumea.plantnet-project.org/list.php).

We used the following abbreviations in examined material to indicate the phenological state of the specimen: bt. (with flower buds); fl. (flowering); fr. (fruiting).

Geographical tools

The distribution map was generated in ArcGis 9.3 software (ESRI 2008), based on data from specimen labels. For old material where the coordinates do not appear, data points were calculated from the data on the specimen labels with the help of the site https://www.geoportail.gouv.fr/carte. The extent of occurrence (EOO) and area of occupancy (AOO) were assessed using GeoCat (Geospatial Conservation Assessment

Tool; Bachman et al. 2011) and the preliminary conservation status was assessed using IUCN (2017) criteria. Status will be submitted to IUCN New Caledonian Red List Authority to validate it and make an official IUCN assessment.

Results

Key for the New-Caledonian species of *Indigofera*

1	Leaves simple, elliptic to linear; racemes contracted, to 15 mm long, the flowers tightly clustered in the leaf axil; calyx lobes longer than the tube ....***I. linifolia***
–	Leaves imparipinnate with three to many leaflets; racemes elongated; calyx lobes shorter or equalling the tube **2**
2	Leaflets alternate ....***I. spicata***
–	Leaflets opposite **3**
3	Inflorescence much shorter than the subtending leaf; pod curved and descending, deflexed against the raceme axis ....***I. suffruticosa***
–	Inflorescence equaling or longer than the subtending leaf; pod straight, spreading or ascending **4**
4	Branches, petiole, leaf rachis, inflorescences and pod covered by erect, long (c. 1 mm long) and dark hairs...***I. hirsuta***
–	Branches, petiole, leaf rachis and inflorescences covered with adpressed and white or brown hairs, visible only with the aid of a lens, or glabrescent.......**5**
5	Leaflets mostly obovate or orbicular with an emarginate apex, whitish or greyish at the lower surface; petals white, sometime tinged pink; standard petal straight or slightly spreading at the anthesis.......................................**6**
–	Leaflets elliptic or ovate with apex acuminate, obtuse or rounded; petals pink, red or purple; standard petal reflexed at the anthesis **7**
6	Virgate shrub or subshrub, 0.5–2.5 m high; leaves usually with (5-)7–11 leaflets; leaflets mostly 4–12 mm long, venation almost invisible adaxially; leaf rachis articulated; petiolules light brown on dry specimens, of the same color as the rachis; flowers 8–10 mm long ....***I. monieriana* sp. nov.**
–	Small tree or shrub, 3–5 m high; leaves with 15–19 leaflets; leaflets mostly 27–32 mm long, secondary veins 6–7 visible on the both sides; leaf rachis not articulated; petiolules dark brown in dry specimens, presenting a different color as the rachis; flowers c. 6.5 mm long...................***I. dumbeana* sp. nov.**
7	Leaflet elliptic, apex rounded and mucronate; flowers 8–10 mm long; bracts much longer than the flower bud, persistent; seeds 6–8, circular in cross section and arranged linearly...***I. atropurpurea***
–	Leaflet ovate or elliptic-lanceolate, apex acuminate; flowers 4.5–6.5 mm long; bracts shorter than the flower bud, early caducous; seeds c. 16, lens-shaped, compressed in cross section, arranged like a stack of coins.......***I. zollingeriana***

Taxonomic Treatment

### *Indigofera monieriana* M.Pignal & L.P.Queiroz, sp. nov.

urn:lsid:ipni.org:names:77195679-1
Figs 1, 4a; Table 1

Type. NEW CALEDONIA. Province Sud, Tontouta, 21°57.9336'S; 166°14.9166'E, pousse dans l'ombre, à la base des arbustes, fleurs blanches, 15 Apr 2004, fl., fr., *M. Pignal 2245* (holotype, P! [P02288351]; isotypes HUEFS! [243158], K!, NOU!).

Diagnosis. *Ab aliis speciecibus* Indigoferarum *Novae-Caledoniae species nova facile differt fruticoso virgato habitu, foliis cum 7–11 foliolis oppositis, late obovalibus vel orbiculatis apice emarginato, nervatione obsolescenti, margine revoluto, pagina infera cinareo-albida, floribus 8–10 mm longis petalis plerumque albis.*

Description. *Virgate shrub* or *subshrub*, 0.5–2.5 m high, with slender and thin stems, young stems flexuous, with short internodes (sometimes up to 3 mm long) at the base, slightly quadrangular becoming terete; indumentum of young branches and leaves of straight, white, adpressed T-shaped hairs. *Stipules* 1–1.5 × 0.4–0.5 mm, narrowly triangular to falciform, pubescent. *Leaves* 3–6 cm long, pinnate, (5–)7–11-foliolate, sometimes 3-foliolate towards the base of the stem; petiole furrowed, 5–12 × c. 0.6 mm; rachis furrowed, quadrangular in cross section, articulated, thick black multicellular hairs (colleters) at the leaflets attachments, segments 3–7 mm long; stipels 0.1–0.5 × c. 0.2 mm, brown, thick, forming the 2 lateral apices of the rachis articles; leaflets opposite, widely obovate to orbicular, dark green above, greyish to whitish pale green below, base rounded to obtuse, apex mostly emarginate, rarely rounded, mucronate, the mucron c. 0.2 mm long, brown, margin entire, slightly revolute, secondary veins 2–5, brochidodromous, invisible adaxially, obscure to invisible abaxially; terminal leaflet 7–17 × 6–12 mm, lateral leaflets (4–)9–12 × 4–6 mm; petiolules 0.6–1.5 mm long, of the same color as the rachis. *Inflorescence* a 5–7 cm long raceme (6–13 cm long in fruiting state); peduncle 10–15 mm long, pubescent; bracts 1.1–8 mm long, triangular, shortly acuminate, pubescent; pedicel 2–3 × 0.2–0.25 mm. *Flower* 8–10 mm long; calyx 2–2.5 mm long, campanulate, asymmetrical, 5-lobed, the vexillary (upper) lobes shorter and deltoid, the carinal (lower) lobe longer and acuminate; petals white, sometimes tinged with pink, never red, standard petal c. 8–9.4 × 4.5–5 mm, elliptical or ovate, apex emarginate, pubescent outside with appressed T-shaped hairs, wing petals c. 7–7.5 × 1.5–2.5 mm, slightly shorter than the keel, narrowly obovate to oblong-linear, apex rounded, keel petals 7–9 × 2–2.5 mm, narrowly obovate, spathulate, apex rounded, valvately connate along the lower margin halfway to the tip; androecium diadelphous (9 stamens fused and the vexillary one free), staminal tube 7.5–9 × c. 2 mm; ovary c. 6-ovulate, c. 5.5 mm long, sessile, glabrous, style c. 3.5 mm long, hook-shaped at apex (hook c. 1.2 mm), stigma capitate. *Pod* 27–38 × c. 3 mm, straight, linear, apex acuminate by 2–4 mm, indehiscent or late dehiscent; valves reddish brown in the living plants, glabrescent or with white appressed T-shaped hairs. *Seeds* 2–4, c. 2.5 × 1.2–1.5 mm, rectangular; testa black.
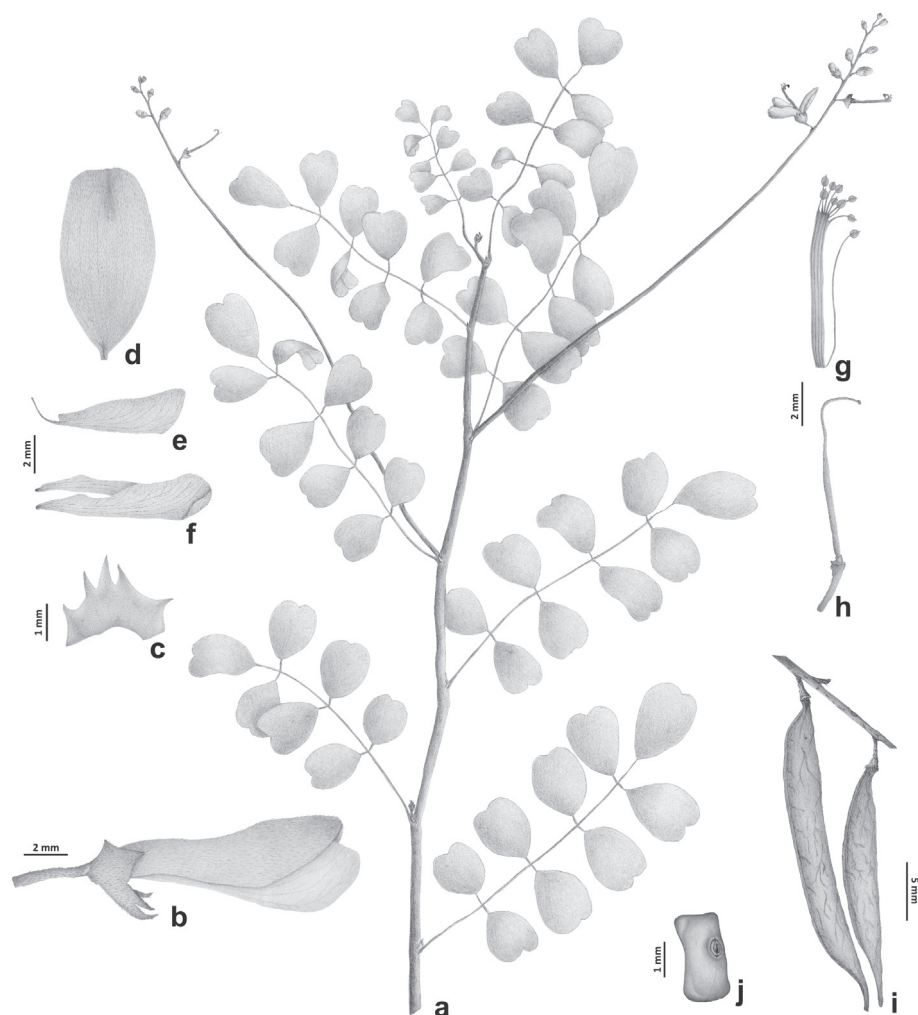
Figure 1. *Indigofera monieriana* sp. nov. **a** Flowering branch **b** Flower before anthesis **c** Calyx (open) **d** Standard petal **e** Wing petal **f** Keel petals **g** Androecium **h** Gynoecium **i** Fruits **j** Seeds. Drawn by Felipe Santos based on *Pignal 2245*.

Distribution and habitat. *Indigofera monieriana* occurs in shrubby maquis vegetation or low forests on schisto-serpentine soil or ferritic soil. It is found in low altitudes on coastal formations from sea level up to about 700 m. Although it occurs in an open environment, it grows under the shadow of higher bushes (See Fig. 2). Coastal formations, especially sclerophyll forests, have greatly reduced (Bouchet et al. 1995, Jaffré et al. 2002).

Phenology. Flowering from January to March, fruiting from May to November.

Etymology. This species is dedicated to Louis-Guillaume Lemonnier (1717–1799), "*associé de l'Institut, ci-devant membre de l'Académie des sciences, conseiller d'État honoraire, et premier médecin du Roi*" (Cuvier 1861) [Associate of the French Institute, former member of the Academy of Sciences, Honorary State Councilor, and First

Table 1. Comparison between the new species of *Indigofera* from New Caledonia with the Australian *I. australis* and the widespread species *I. zollingeriana*.

	I. australis	*I. dumbeana*	*I. monieriana*	*I. zollingeriana*
Habit	Shrub	Shrub or small tree with plagiotropical branches	Virgate shrub	Shrub or small tree
Stipules	Stipules linear	Stipules triangular to falciform	Stipules narrowly triangular or falciform	Stipules linear
Leaf	Leaf 8–10 cm long, rachis only flat (not furrowed) and not articulate, lacking ferruginous colleters fields, at leaflets attachment. Leaflets 17–25.	Leaf, 10.5–11.3 cm, rachis strongly furrowed and not articulate, with brown ferruginous colleters fields, at leaflets attachment. Leaflets 15–19.	Leaf, 3–6 cm long, rachis furrowed and articulate dense colleters fields, dark ferruginous, at leaflets attachment. Leaflets 7(–11).	Leaf 23–26 cm long. Leaflets 11–23.
Leaflet	Petiolule dark brown on dry specimens, same or different color as the rachis; leaflets green below, usually 10–40 mm long, mostly elliptical, apex rounded or obtuse margins thick but not revolute, secondary and sometimes also tertiary venation visible as darker lines at both (but mostly at lower) surfaces, 6–8 pairs of secondary veins.	Petiolule dark brown on dry specimens, different as the rachis; leaflets discolor, greyish green below, usually 17–32 mm long, obovate, apex slightly emarginate, mucronate, margins not revolute, secondary and sometimes also tertiary venation visible at both surfaces, 6–7 pairs of secondary veins.	Petiolule light brown on dry specimens, same color as the rachis; leaflets discolor, whitish or greyish green below, usually 4–12 mm long, mostly obovate or orbiculate with apex emarginate margins slightly revolute discolour, the lower surface grayish venation not visible, 2–4 secondary veins often not visible.	Petiolule dark brown on dry specimens, same color as the rachis; leaflets discolor, greyish green below, usually 35–85 mm long, mostly elliptical-lanceolate with acuminate apex, margins not revolute, c. 10 pairs of secondary veins.
Flower	Calyx truncate; petals pink to purple; standard petal reflexed, keel petals oblong to narrowly obovate.	Calyx 5-lobate, the two upper lobes very short; petals white; standard petal patent, keel petals obovate.	Calyx 5-lobate, the lower lobe as long as or longer than the tube standard petal straight keel petals narrowly obovate.	Calyx 5-lobed, the lower lobe much shorter than the tube; petals pink to red; standard petal straight, keel petals oblong with a 90° upcurved apex.
Pod	Pod straight; endocarp forming translucent envelopes around the seeds; seeds rectangular and arranged linearly.	Pod slightly sinuous; endocarp forming translucent envelopes around the seeds; seeds ellipsoid and arranged linearly.	Pod straight; endocarp forming translucent envelopes around the seeds; seeds rectangular and arranged linearly.	Pod strongly sinuous; seeds naked, lens-shaped and arranged like a pile of coins.

Physician of the King] who herborised with C. Linnæus, J.-J. Rousseau, Antoine and Bernard de Jussieu. We adopt the spelling "Monier" used by J.-B. Fusée Aublet in his herbarium kept at the Paris Museum and known as "Jean-Jacques Rousseau herbarium" (P-JJR), from the name of its most famous owner.

Conservation status. *Indigofera monieriana* was provisionally assessed as vulnerable based on IUCN (2017) criterium B as it presents a restricted EOO (7070 km²) and AOO (32 km²), and its estimated range covers about half of New Caledonia's main island.

Discussion. Guillaumin (1936) noted that several virgate specimens from New Caledonia could not be reported to the typical *Indigofera australis* and he preferred to determine them as *I. australis* var. *gracilis* DC. However, a careful examination of the type collection of this variety (*Sieber Fl. Novae. Holl. 380*, G, K, P) shows that the New Caledonian material is clearly distinguished from *I. australis* by the less numerous leaflets (5–9 vs. 17–25 in *I. australis*), mostly obovate with an emarginate apex, lower surface whitish or greyish green and inconspicuous venation (vs. leaflets mostly elliptical with acute to rounded apex, green lower surface and raised venation; see Table 1 for further distinctive characters). Besides, *I. australis* is restricted to Australia and, although presenting a broad morphological variation (Wilson and Rowe 2010),

its diagnostic features do not overlap with *I. monieriana*. The new taxon is also remarkable for its articulate leaf rachis and its dark ferruginous colleters (multicellular thick secretory hairs) at the insertion of petiolules on the rachis.

Paratypes. NEW CALEDONIA. Province Nord: Arbrisseau de 2–3 m de hauteur, NaKéti [=Nakety], sur les collines schisto-serpentineuses, [21°32.814'S; 166°2.532'E], Oct 1869, fr., *B. Balansa 2471* (P [P03615799, P03615800]); Mont Poumé [=Poum], [20°15.282'S, 164°1.584'E], May 1871, fr., *B. Balansa 3332* (P [P03615852, P03615853]; Village de Voh, [20°59.055'S, 164°39.3881'E], 25 Jul 2015, fr., *D. Fleurot 53* (P [P00993550]); Kaala-Gomen, Taom, au-dessus de l'ancienne carrière, Mt. Homédéboa, 720 m, maquis arbustif, sol ferrallitique ferritique sur pente forte érodée, [20° 46.998'S, 164°34.002'E], 16 Jan 2007, fl., *R. Barrière & F. Rigault 71* (NOU [NOU016084]); Village de Voh, Tribu de Gatope, presqu'île de Gatope, forêt de 2 à 4 m de hauteur à *Terminalia* et *Homalium*, [20°59.148'S, 164°40.368'E], 17 Nov 2004, fr., *J.-N. Labat et al. 3511* (P [P00454773]; Voh, Vavoutou, forêt sèche, 10 m, [21°0.45'S, 164°41.283'E], 18 Nov 2009, fr., *J.-N. Labat et al. 4050* (P [P00749569]; Voh, Gatope, presqu'île de Gatope, maquis minier. Serpentine. Strate inférieure, [20°59.683'S, 164°40.133'E], 20 Nov 2009, fr., *J.-N. Labat et al. 4082* (NOU, P [P00749614]; Au-dessus de Gomen, Mt. Kaala, 500–700 m, maquis sur pente raide serpentineuse, [20°38.55'S, 164°23.448'E], 18 Mar 1966, fl., *H.S. MacKee 14586* (NOU [NOU070814], P [P03615845, P03615846, P03615847]; Pente S Mt. Kaala, [20°38.55'S, 164°23.448'E], 27 Mar 1980, fl. *H.S. MacKee 37971* (NOU [NOU070811], P [P03055971]); suffrutex 0,5 met, Montagne de Gomouen, Gatope, [20°58.014'S, 164°39.786'E],1867, fl, fr., *E. Vieillard 2535* (P [P00888525 to P00888532]); **Province Sud:** Collines ferrugineuses situées à l'embouchure du Dotio [=Dothio], [21°36.882'S, 166°12.684'E], 1 Nov 1870, fr, *B. Balansa 3003* (P [P03615854, P03615855], MO); Tontouta: col de Mo, 400 m [c. 21°58'S, 166°11'E], 27 Jan. 1969, fr, *H.S. MacKee 20168* (P [P00888523]); Tontouta [c. 21°58'S, 166°11'E], 25 Dec. 1971, fr, *H.S. MacKee 24758* (P [P03615805]); Basse Tontouta (rive gauche) [c. 21°58'S, 166°11'E], 14 Jan. 1982, fl., *H.S. MacKee 40197* (P [P03615806]) .

Indigofera dumbeana M.Pignal & L.P.Queiroz, sp. nov.

urn:lsid:ipni.org:names:77195680-1
Figs 2, 3, 4b; Table 1

Type. NEW CALEDONIA. Province Nord, Bois des collines schisteuses près de l'embouchure de la Dumbéa, [22°9.7668'S, 166°26.4336'E], May 1870, bt, fl, *B. Balansa 2807* (holotype: P! [P03615849], isotype, P! [P03615850]).

Diagnosis. Indigoferae zollingerianae *Miq. similis, floribus parvis (c. 4.5−6.5 mm longis) foliisque cum aliquot foliolis (11−23), sed brevioribus 10.5–11.3 cm longis foliis cum valde canaliculata rachidi, brevioribus plerumque 17–32 mm longis, ovatis vel obovatis (vs. elliptico-lanceolata) apice obtuso vel leviter emarginato, secundorum nervorum 6–7 paribus, (vs. 9–10 secundorum nervorum paria), fructu tantum 5–6 seminibus contiguis,*
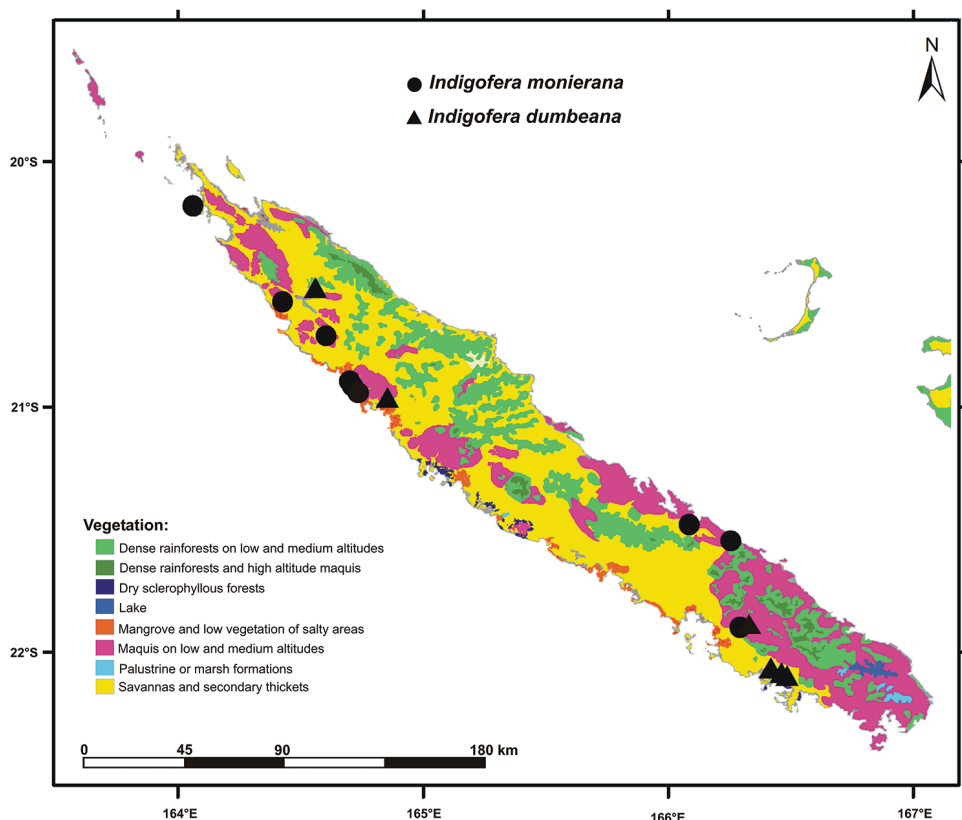
Figure 2. Map of the New Caledonia archipelago showing the major vegetation types (from Jaffré et al. 2012) and the distribution of the new species *Indigofera monieriana* and *I. dumbeana*.

ellipsoideisque, versus 23–26 cm longa folia leviter vel haud canalicalata rachidi, 35–85 mm longa elliptica vel lanceolata foliola acuminato apice, 9–10 secundorum nervorum paria atque circa 16 nuda in cumulo disposita semina), praecipue differt.

Description. *Small tree or shrub* 3–5 m high, branches mostly plagiotropic and horizontal (*Veillon 7138*, P), young stems flexuous, quadrangular or terete, internodes 10–15 mm long (but c. 5 mm long for the flexuous parts); indumentum of young branches and leaves of straight, white, adpressed T-shaped hairs. *Stipules* 1–1.5 × c. 0.2 mm, narrowly triangular to falciform, pubescent. *Leaves* 10.5–11.3 cm long, pinnate, 15–19-foliolate; petiole 10–15 mm long, furrowed, sparsely pubescent; rachis yellowish to light brown, strongly furrowed, non articulated and with thin appressed hairs, thick brown multicellular hairs (colleters) at the leaflets attachments, segments at the leaflets attachments 10–14 mm long; stipels 0.2–0.3 mm long, setiform, early caducous, mostly absent; leaflets opposite, secondary veins visible on both sides of the lamina, upper and lower surfaces with dense, white hairs; terminal leaflet 27–34 × 15–19 mm, ovate to obovate, apex rounded to slightly emarginate, mucronate, base acute,
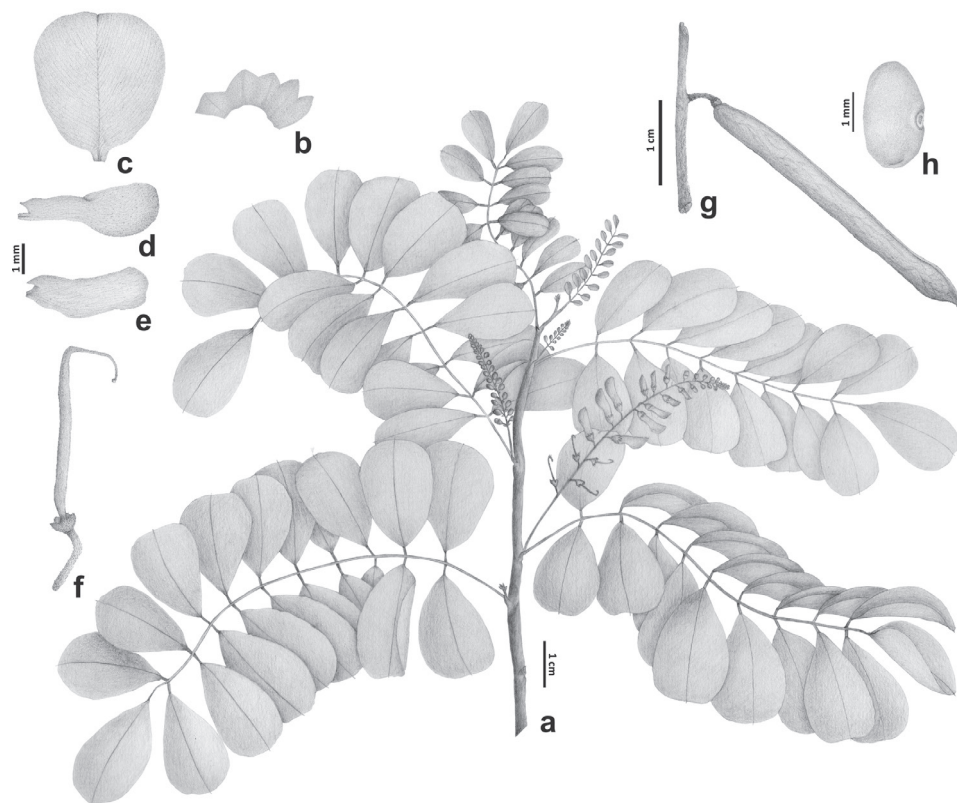
Figure 3. *Indigofera dumbeana* sp. nov. **a** Flowering branch **b** Calyx (open) **c** Standard petal **d** Wing petal **e** Keel petals **f** Gynoecium **g** Fruit **h** Seeds **a–f** after *Balansa 2807* **g–h** after *Nothis 440.* Drawn by Felipe Santos.

secondary veins 7–12 pairs, lateral leaflets 20–17 × 12–14 mm, obovate, apex slightly emarginate, mucronate, secondary veins 6–7 pairs, petiolules 1.2–2 × 0.4–1.5 mm, dark brown on dry specimens, not furrowed. *Inflorescence* a c. 50 mm long raceme, with more than 40 flowers; peduncle pubescent, quadrangular, c. 10 mm long; pedicel c. 1.5 × 0.2 mm. *Flower* c. 6.5 mm long; calyx c. 1.5 mm long, campanulate, asymmetrical, 5-lobed, the vexillary (upper) lobes shorter and shallow deltoid, the carinal (lower) lobe longer and acuminate; petals white; standard petal c. 5–6 × 4.5 mm wide, obovate, apex slightly emarginate, pubescent outside with appressed T-shaped hairs; wing petals c. 4 × 1.5 mm, slightly shorter than the keel, narrowly obovate to oblong-linear, apex rounded; keel petals 5–5.5 × 2 mm, obovate, apex rounded, valvately connate along the lower margin halfway to the tip; androecium diadelphous (9 stamens fused and the vexillary one free), staminal tube c. 6 × 1.5 mm; ovary c. 5-ovulate, c. 5 mm long, sessile, glabrous, style c. 2.5 mm long, hook-shaped at apex, stigma capitate. *Pod* c. 38 × 3 mm, straight, linear, apex acuminate, indehiscent; valves brown, pubescent with appressed white T-shaped hairs. *Seeds* 5–7, c. 3.5 × 5 mm, ellipsoid; testa black.

Distribution and habitat. *Indigofera dumbeana* grows in lowland forests, mostly in wood edges areas (fide *Veillon 7138*, P and *Veillon 7482*, P).
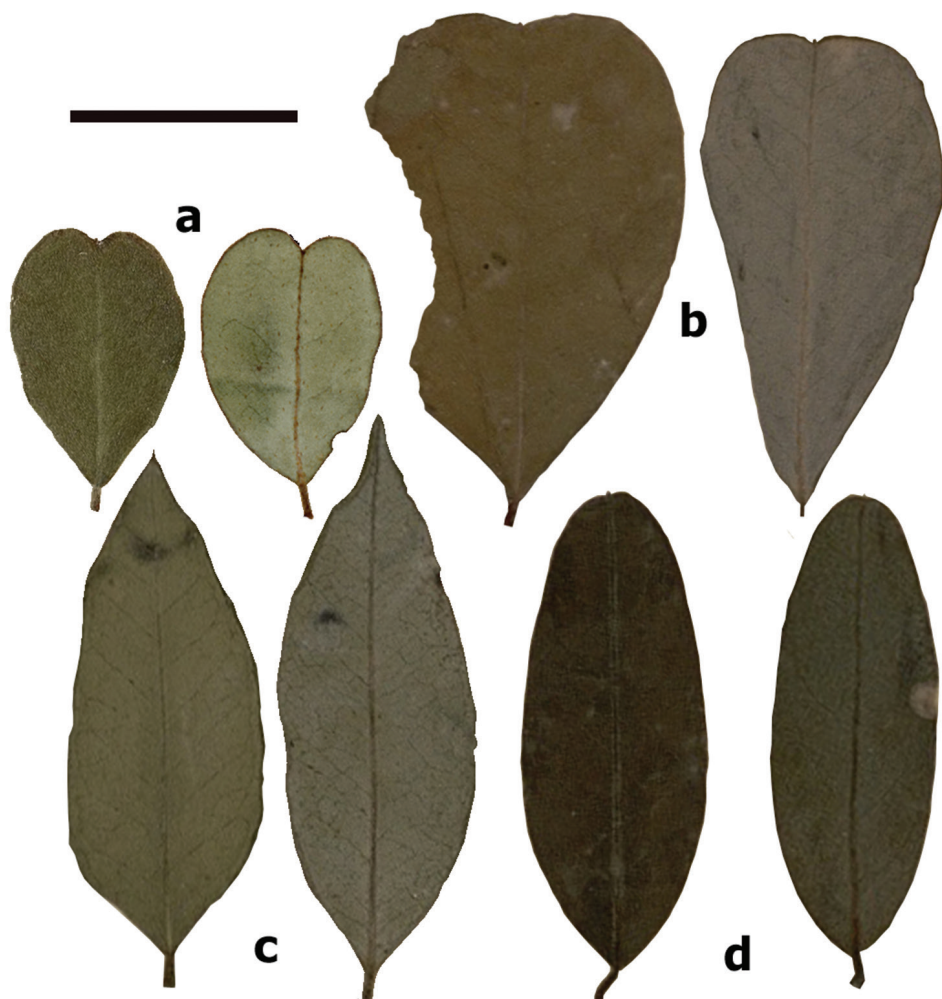
Figure 4. Leaflets comparison of the two new New Caledonian species of *Indigofera* in and their most related species. **a** *Indigofera monieriana* (*M. Pignal 2245*) **b** *I. dumbeana* (*B. Balansa 2807*) **c** *I. zollingeriana* (*B. Balansa 1222*) **d** *I. australis* (*C. Walter s.n.*). Left: adaxial surface, right: abaxial surface. Scale bar: 1 cm.

Phenology. Flowering in March and April, fruiting in May to November.

Etymology. The specific epithet refers to the Dumbéa River in the mouth of which B. Balansa collected the type material.

Conservation status. We assessed *I. dumbeana* as endangered both because it presents small EOO (2358 km^2) and AOO (20 km^2), and it is located rather in sclerophyllous forests that are perhaps the most endangered formations in New Caledonia, especially at low elevation (Bouchet et al. 1995). Additionally, this species is known by few and rather old collections which could indicate its rarity in the island.

Discussion. We agree with B. Schrire who annotated in 2004 the P00379654 specimen (*M. Debray 2296*) as a new species allied to *I. australis* Willd. Specimens

of *Indigofera dumbeana* were previously referred to *I. australis* by Guillaumin (1936). These species are clearly rendered distinct by the habit as *I. dumbeana* presents plagiotropical, almost horizontal branches, stipules triangular or asymmetrical and falciform (vs. linear), and flowers with a five lobate calyx and white petals (vs. flowers with a truncate calyx and pink to purple petals). *Indigofera dumbeana* is more similar to *I. zollingeriana*, both occurring as a tall shrub or small tree habit with plagiotropical branches, but they are clearly distinct by the fruit straight with rectangular seeds linearly arranged (vs. fruit sinuous with transversely compressed seeds arranged like a stack of coins in *I. zollingeriana*). Additionally, they present important differences in leaf and flower traits as presented in Table 1.

Paratypes. NEW CALEDONIA. Tronc grêle, hauteur 4 m, cime légère, croissant en massifs, 200 mètres au dessus du niveau de la mer, localisé, s.d., fr., *I. Pancher s.n.* (P! [P03615856]); **Province Nord:** Forêt derrière Ouéholle, [20°35.316'S, 164°31.464'E], 17 Aug 1967, fr, *A. Nothis 440* (NOU [NOU070806], P! [P02851253]); Pouembout: commun, localisé en lisière de forêt, forêt plate, vers 500 m, forêt dense de moyenne altitude, substrat schistes, [21°1.998'S, 164°49.002'E], 18 June 1992, fr., *J.-M. Veillon 7482* (NOU [NOU070809], P! [P02851258, P02851259]); **Province Sud:** Tontouta [c.22S; c.166°13'E], 29 Sept. 1975, fr, *M. Debray 2296* (NOU, P [P00379654]; Sur un monticule de la région de Païta, [22°7.95'S, 166°22.566'E], s.d., fr, *I. Pancher (Mus. Néocal. 177)* (P! [P00888524, P03615848, P03615857]); sur les monticules argilo-schisteux de Païta, [22°7.95'S, 166°22.566'E], s.d., fr, *I. Pancher s.n.* (P [P03615844]; Nakutakoin: vallée au sud du pic Jacob, exposition S.W, vers 300 m, en lisière de forêt vallicole (vu aussi à l'intérieur), substrat phtanites, sol brun, [22°0.9'S; 166°25.002'E], 24 Aug 1989, fr., *J.-M. Veillon 7138* (P [P03567480, P03615801], NOU [NOU070810]).

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Appendix

Other examined material

***Indigofera australis* Willd.: AUSTRALIA.** Nova Hollandia, *s.c. in herb. Delacourt* (P! [P03567468]); New South Wales, Macleay R., *H. Beckler s.n.* (K image seen [K000217365]); Nova Hollandia, *s.c. s.n.*, 1821, (G-DC image seen [G00497647]); Belair, South Australia, [34°59.886'S, 138°37.35'E], fl, Sept. 1902, *M. Koch 568* (P! [P02949887]); Emu Bay & Lea Coast generally, 1864, *J. Milligan 21* (P! [P02949882]); Nouvelle-Hollande, fl, *F.W. Sieber s.n. in herb. van Heurk* (P! [P02949870 p.p.]; Nouvelle-Hollande, 1825, *F.W. Sieber 379* (P! [P02949883, P02949854, P02949868]); Nova Hollandia, 1825, *F.W. Sieber 380* (G image seen [G00418819, G00418820, G00418821], G-DC image seen [G00497743], K image seen [K000217368], P! [P02141690, P02949867]); Mt Macedon (Victoria, Australia), fl, 21 october 1882, *C. Walter s.n.* (P! [P02949870 p.p., P02949889]);

***Indigofera zollingeriana* Miq. VIETNAM.** Tonkin, Ouonbi [Núi Tản Viên, 21°3.6'N; 105°21.6'E], dans les broussailles, fl, 12 Sept. 1885, *B. Balansa 1222* (P! [P02958234]); Lat Son (HN), [20°31.8'N; 105°53.4'E], fl, 19 Aug. 1891, *H. Bon 4859* (P! [P03026363]); Tonkin, Bois de Co-Phah, entre le canal des rapides et Bac-Ninh, fl, 20 Aug. 1891, *B. Balansa 4881* (P! [P03026356]); Tonkin: pr. Lang Son, Cai Kinh, fr., s.d., *A. Chevalier 27682* (P! [P03026361]).

RESEARCH ARTICLE

A morphometric analysis of *Tobleria bicuspis*, a Voltziales seed cone from the early Permian Jambi palaeoflora, Sumatra (Indonesia)

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Abstract

Tobleria bicuspis, a coniferophyte seed cone, is described from the Jambi Palaeoflora, Sumatra of Asselian (early Permian) age. A morphometric analysis based on cones, paired fertile units, and fertile and sterile scales, demonstrates their close relationship. Small paired fertile units occur mainly in cones. Medium-sized paired fertile units occur mainly on scales. And large paired fertile units are mainly dispersed. The cones are considered female and the paired fertile units are considered to represent the seeds. The cones are composed of helicoidal, bilaterally symmetrical and deeply incised scales with paired seeds. A comparison can be made with the Voltziales female taxon *Schizolepis* from the Triassic and Jurassic. *Tobleria* is regarded as having a voltzian Voltziales affinity and dates from approximately 16 to 26 million years before any other such cones.

Keywords

Asselian, Cathaysia, mesic-xeric, early conifer cones

Introduction

The evolutionary trend from early to late conifers is that of a radial fertile shoot in the axil of a leaf to a fertile scale fused to, or free from, a subtending bract (Florin 1951, Meyen 1997). Radial fertile shoots (walchian Voltziales) occur in late Pal-

aeozoic taxa, while scales with sessile seeds and a (partly) fused subtending bract typify the Mesozoic and Cenozoic conifers (Anderson et al. 2007). The transition between the two took place in the voltzian conifers during the late Palaeozoic. Here the informal group of the walchian Voltziales is typified by radial shoots while the informal group of the voltzian Voltziales is defined by a fertile scale carrying sessile seeds (Rothwell et al. 2005). More precisely, the proliferous Pennsylvanian Hamilton Quarry produces chiefly walchian Voltziales (Anderson et al. 2007) while the Majonicaceae, belonging to the voltzian Voltziales (Rothwell et al. 2005), have been demonstrated to occur in the late Early Permian, thus indicating that evolution of the scale architecture and diversification among conifers took place before that period (Looy 2007).

Jongmans and Gothan (1925, 1935) described co-occurring organs from the early Permian Jambi palaeoflora, which they indicated as 'seeds' and scales. As these seeds and scales are often found superimposed, Jongmans and Gothan (1925) considered them to represent one functional organ, which they called *Tobleria bicuspis*. Van Waveren et al. (2007) reviewing the Early Permian Jambi palaeoflora, and noting three cones in the collection found in association with *Tobleria bicuspis,* suggested they were related, and considered a conifer affinity for the scales, seeds and cones. As the early conifer transition between walchian and voltzian Voltziales took place between the Pennsylvanian and the Early Permian, the voltzian or walchian affinity of *Tobleria bicuspis*, appearing between the two in the Asselian, is of interest and requires verification.

A detailed morphometric analysis of the fertile units and scales, dispersed, superimposed and inside the cones, is presented. The statistical treatment of the fertile unit, and scale width and length, is used to demonstrate the coherence of the cones and the dispersed material. Details of the fertile units, scales and cones are presented to support an interpretation of *Tobleria bicuspis* as a seed cone displaying features indicating a voltzian Voltziales affinity.

Material and methods

Geographical and geological context

The Jambi palaeoflora is composed of impressions and coalified compressions that are kept at Naturalis, the Netherlands Center for Biodiversity. The samples are small in size (commonly 100 mm long, but sometimes up to 400 mm). Some cuticles could be retrieved from the samples, but no diagnostic features were observed.

The samples originated from outcrops along several rivers and their tributaries. These rivers cut into silicified Permian volcaniclastic rocks from the westerly mountainous region of the province of Jambi (Zwierzycki 1935, Tobler 1917, 1922). *Tobleria bicuspis* was found in localities situated along tributaries of the Merangin, namely the Karing and the Ketidoeran Siamang (see Fig. 1). These localities belong to the Mengkarang Formation (Suwarna et al. 1998).
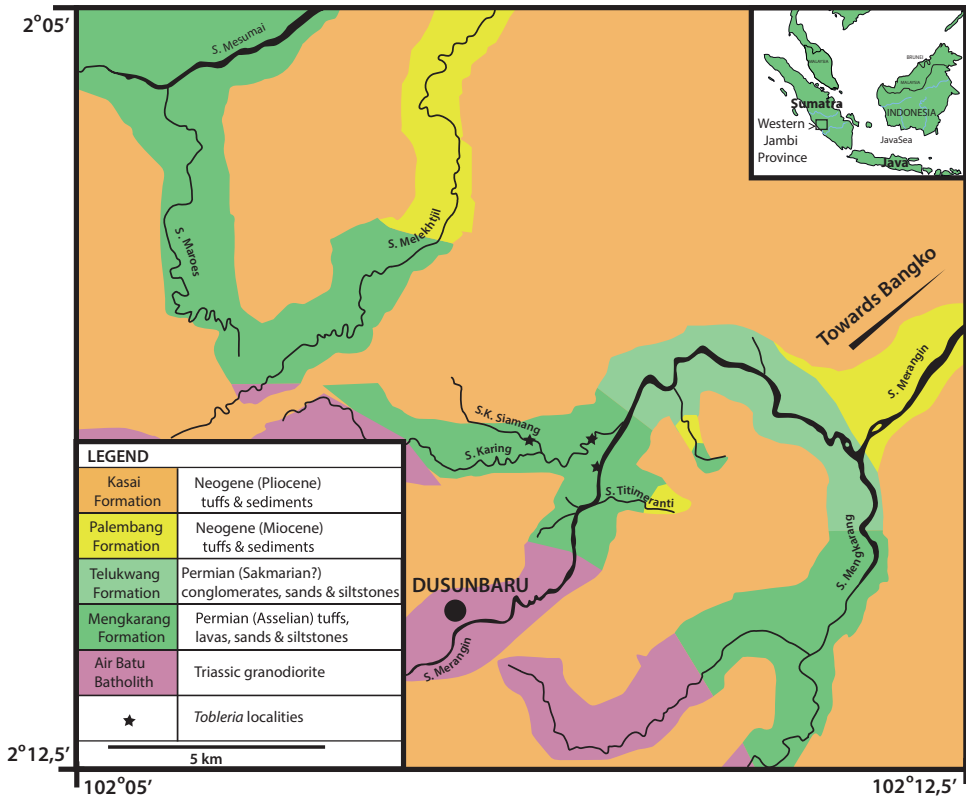
Figure 1. Map of the Bangko area showing the outcrops of the Mengkarang Formation along the distributaries of the Merangin River where *Tobleria bicuspis* was found.

The 500 m thick Mengkarang Formation is represented by eight fining-upwards intervals, each formed at the base of the formation by a basal pyroclastic accretion wedge composed of tuffs, and overlain by tuffaceous sandstones, organic shales and limestones, while at its top the tuffaceous sandstones are more common and basalts form the base of the intervals (Van Waveren et al. 2018). Fusulinids from the Merangin section suggest a late Asselian age (Vachard 1989) and, lately, isotopic age evaluation has indicated an Asselian age between 296.77 and 296.14 million years (Van Waveren et al. 2018). The Mengkarang Formation is overlain by the Telukwang Formation that is characterized by thick polymict conglomerates alternating with tuffaceous sandstones and shales (Suwarna et al. 1998). The Mengkarang and the Telukwang formations are intruded by the Triassic Air Batu granodioritic batholith (Zwierzycki 1935). The Miocene Palembang Formation, consisting of shales, sandstones and coals, is found discordantly on the Permian (Zwierzycki 1935). The Pliocene Kasai Formation, consisting of more than 400 m of tuffs, tuffaceous sandstones and siltstones, tuff breccia, lignites and peats (Suwarna et al. 1998), in turn, overlays the Palembang Formation discordantly (Zwierzycki 1935). *Tobleria* occurs in the upper half of the

Mengkarang Formation. These occurrences and their mesic-xeric palaeoecological context were recently described in Van Waveren et al. (2018).

Palaeomagnetic results indicate that the Mengkarang Formation, in which the *Tobleria* remains were found, was positioned approximately fifteen degrees north of the equator (Suwarna et al. 2000). The presence of reefs and the absence of growth rings in wood (Van Waveren et al. 2005, Crippa et al. 2014) support the palaeomagnetic results, indicating that the Jambi flora grew in a tropical environment. The petrography of the section indicates that the Jambi palaeoflora was caught in the tuffs, pyroclastic flows and gravity flows of an active volcano from a volcanic arc where fluvially reworked tuffs and ashes form an apron to the more central volcaniclastic deposits (Donovan et al. 2013, Matysova et al. 2017, Van Waveren et al. 2018).

Material

A total of 17 samples from the 1925 Jambi collection held *Tobleria bicuspis* organs. These organs consisted of cones, fertile units and scales, fertile and barren. Fertile units were defined as paired, closed, darker circular rims or paired, dark, disc-like areas, respectively. Scales were considered to be bilateral symmetrical, sub-rounded, darker areas with two apices. The possible nature of these barren scales as bracts is fully developed in the discussion. Scales were found in all 17 samples (old collection: 45308-20, 45468, 45471, 45617; and 2006 collection: KS 28). All samples from the 1925 collection had comparably fine-grained lithologies. The sample found in 2006 along the Ketidoeran Siamang stream is composed of light grey medium – to fine-grained tuffaceous sandstones and was collected from a bed of 30 to 40 cm in thickness that was formed by a volcanic mass flow. The remaining samples found in 1925 were also collected from that stream and have the same lithology. Three samples (45468, 45471 and 45311) were collected along the Karing River. These samples consist of light beige, finely banded, tuffaceous mud – and siltstone. They comprise the cones. One of the cones is under an angle to the bedding, indicating that it fell into the soft mud that kept seeds, scales and cones in the same vicinity. A number of coarser-grained tuffs from the old Naturalis Jambi collection did hold relatively large, faintly bifid scales, but preservation was too poor for any type of data acquisition.

Sample 45311 consisted of five fragments that could be reassembled into a single specimen (Aa, Ab, B, C, D). Two cones were observed in fragment 45311A, both on part (Aa) and counterpart (Ab). The cone (C1) positioned centrally is largest and its structure can best be described using the Aa side (Fig 2A). The second cone (C2) is positioned on Aa left of the central cone along the edge and only the right side of that cone is visible (Fig. 2B). On the counterpart Ab, C2 is observed to the right of the central cone. A third cone C3 in sample B is indicated by an apical portion (Fig. 2C). Fragments B and C (Fig. 3A and B) have both fertile units and bifid scales, with or without the fertile units. Fragment D only has a *Pecopteris hemitelioides* fragment.

Figure 2. The three cones from sample 45311: **A** cone C1 from 45311 Aa, the black frame indicates the area that is detailed in Figure 5 **B** *Tobleria bicuspis* right edge of cone C2 fragment showing bicuspid scale and seeds **C** *Tobleria bicuspis* cone C3 fragment showing bicuspid scale. Arrows 1–4 in Figure A indicate scales in side view, arrow 5 indicates the cone axis. The arrow in Figure C indicates a bifid scale. Scale bars: 10 mm (**A**); 2,5 mm (**B**); 5 mm (**C**).

Preparation of cone C1 on sample Aa allowed the visualization of its apex that was buried a bit deeper in the shale, thus indicating that the cone was positioned under at an angle to the bedding before compaction. A scale apex was also prepared on the left apical border of Cone 1 (sample Aa). Dispersed fertile scales and fertile units were found in seven samples (45308, 45310, 45311, 45313, 45320, 45468 and KS 28) (Fig. 3A–C).
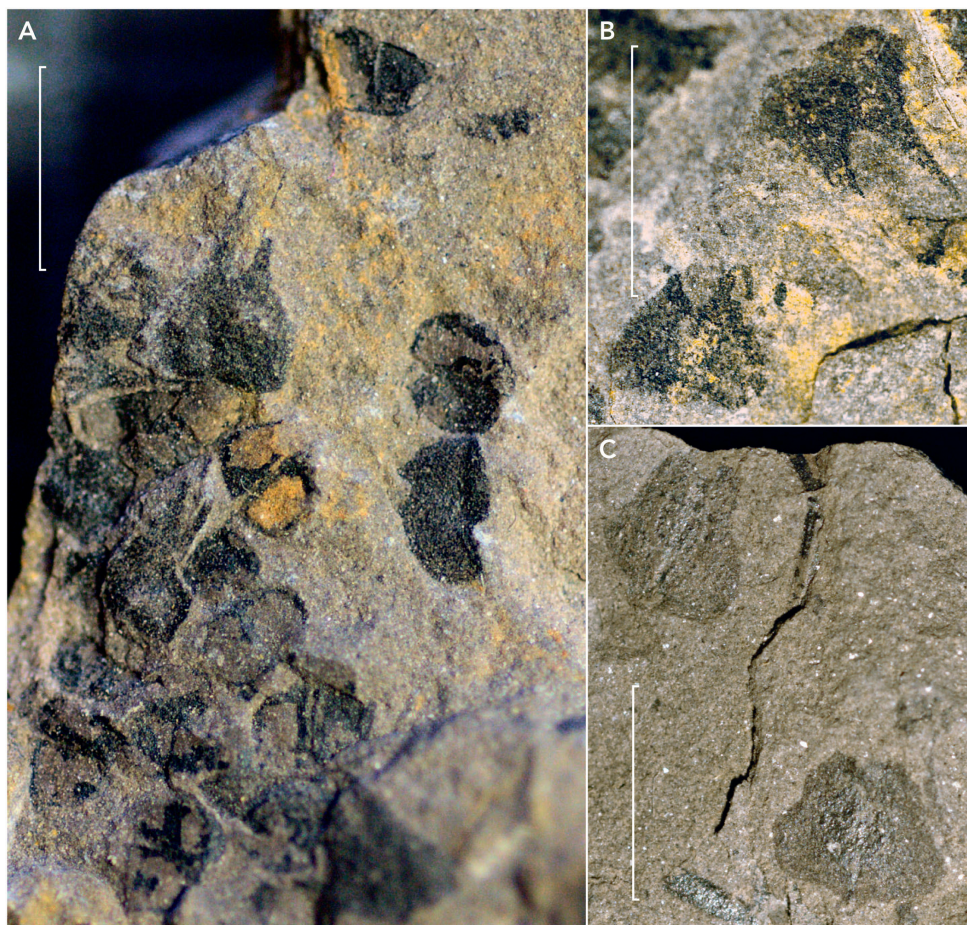
Figure 3. Associated seeds and scales **A** Dispersed seeds and scales (sample 45311a) **B** Scale with hart shaped scar and scale with darker central area (sample 45471) **C** Scale seen from adaxial side showing striation pattern and scale seen from adaxial side showing seed remains (sample 45313). Scale bars: 5 mm.

Quantitative and statistical analysis

Pictures and measurements were made with a multi-stack Zeiss SteREO Discovery V20 microscope with a Zeiss AxioCam MRc 5 for photography, and the associated program AxioVision. Measurements were preserved on the pictures and data were exported into an Excel file. The lengths and widths of the fertile units (Fig. 4A) were measured while noting if they were free (dispersed), on a scale or in a cone. The length and width of the scales (Fig. 4) was measured while it was noted if they were dispersed, empty, fertile or in a cone. Two proxies were used for the size (length x width) of the scale (1) and fertile unit (2).
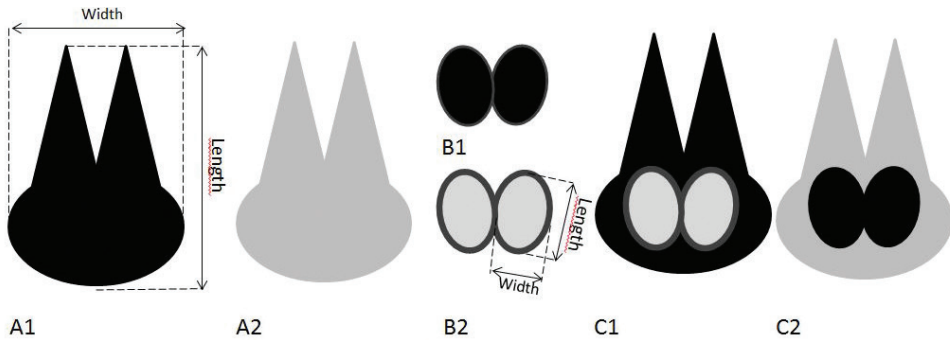
Figure 4. Diagram showing empty scale, opaque (**A1**) or lighter (**A2**), fertile units as dark discs (**B1**) or dark circular rims (**B2**), and fertile scale with lighter fertile units on darker scale (**C1**) or darker fertile units on lighter scale (**C2**) (see also Figure 6). It is indicated how length and width of scale and fertile unit are measured.

For all the data handling, the program PAST (PAleontological STatistics) version 2.12 (Hammer et al. 2001) was used. To analyze the data distribution NIST/SEMAT-ECH e-Handbook of Statistical Methods (http://www.itl.nist.gov/div898/handbook/, 29/11/2017) was used. The degree of skewness was given in Excel.

Fluorescence analysis

As the samples were too large for a fluorescence microscope, they were analyzed with the Diamondview. The instrument illuminates the surface of the sample with intense ultraviolet light specially filtered such that almost all of the light reaching the sample is of wavelengths shorter than 230 nm. To examine a sample, it is inserted into the stone holder from the port at the front of the unit. The stone is first exposed to visible light in order to focus the camera to the area of interest, after which it is illuminated with ultraviolet light and the fluorescence image is recorded to be exported to the computer (Welbourn et al. 1996).

Descriptions

Cones

All three samples displayed compact cones with densely packed scales. The most complete cone fragment C1 has the apical portion preserved and is positioned on the central part of sample 45311 Aa and 45311 Ab. It is 24 mm long and 8–9 mm wide at the base, representing its broadest point, and tapering apically to a width of 4–5 mm

at 2 mm from the apex. The rock sample was broken at the base of the cone and the length of the intact cone remains unknown (Fig. 2A).

Fertile units and scales in cones C1 and C2, on sample 45311 Aa and Ab, were too numerous to each be rendered photographically, but were all measured and are treated (below) in the statistical analysis. On cone C1 (Fig. 2A) the fertile unit size decreases slightly in the apical direction. On cone C2 (Fig. 2B) fertile units are more equally sized in apical direction, suggesting that the fragment is more central in the cone. The more conspicuous fertile units and scales on the cones are discussed in the descriptions below.

A fertile scale complex occurs in facial view (Figs. 2A and 5) central-basally in cone C1 on sample 45311 Aa. This scale was 3 mm wide and 5 mm long, broad at its base, bifid and elongated. The two apices are bluntly acute and not fully symmetrical. Centrally on the scale is a darker, heart-shaped structure. Apically on the left side of cone C1 on sample 45311Aa, a 2 to 3 mm scale could be observed in side view on the cone-edge (see arrow 1, Fig. 2A). Below this point on cone C1, three scales can be observed along the left cone edge, each with their apices pointing towards the cone apex. At approximately one third of the cone base of C1 on sample 45311Aa, on the left side, a larger scale in side view carries two adaxial fertile units (see arrow 4, Fig. 2A). Basally to the left side of the cone, a dark oval area is observed and considered to represent the cone axis (see arrow 5, Fig. 2A). On the right cone side (sample 45311Aa), no scales apices can be seen to protrude, but four fertile unit pairs can be observed; a thin rim abaxially to the third pair from the top indicates these fertile units are subtended by a scale. Throughout the cone, paired rounded units can be observed, indicating the cone is densely packed with seed scale complexes.

The second incomplete cone C2 on sample 45311 Aa left of the central C1 cone described above, consists of six equally sized overlapping scales (Fig. 2B). No gradual size change was observed for these fertile scales either in basal or apical direction. Here, a bifid scale is adaxially covered by another one that carries paired fertile units. This indicates that the rock split from within the cone in such a way that the fertile units are viewed from the axis and are generally positioned adaxially on top of the scales. Abaxially to the central fertile unit pairs on the right side of the cone is a scale with two long apices; abaxially from this scale is a thin rim possibly representing a subtending scale (Fig. 2A, see arrows).

The third and last, smallest incomplete cone C3 on 45311 B, is an apical fragment where three bifid scales could be recognized (Fig 2C). Here, the rock split in such a way as to preserve the external contours of the strobilus. This cone is 6 mm wide and 10 mm in length, and the scales are approximately 3 mm wide and 3 mm long. The cone width decreases apically. Most visible scales are bifid and no convincing fertile units were observed.

Fertile units

The paired fertile units showed a variety of transitional forms from two closely adpressed hemispheres (Fig. 6A, B), to two almond – and (as a pair) heart-shapes attached both centrally and in the narrowest point (Fig. 6D, E, F). For various smaller paired fertile units there are two hemispheres, which display two very thin darker
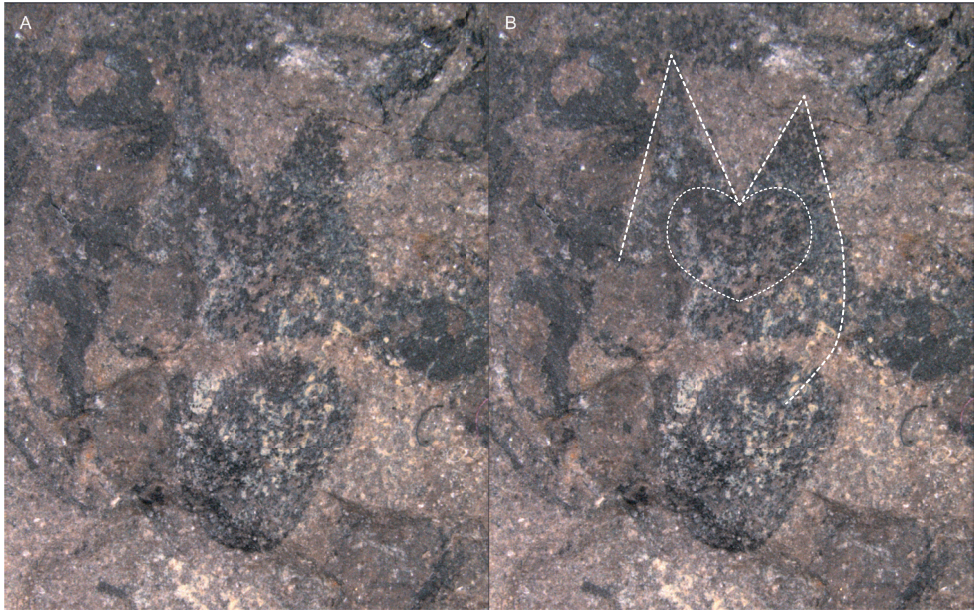
Figure 5. Details from Cone C1: A Facial view of the scale in the cone from sample 45311 Aa (see frame in Figure 2A) B Contours of Facial view of scale and seeds indicated by dashed lines.

walls (see Fig. 6A). In various cases the smaller attached side of the seed pair displays a smaller triangular micropylar protrusion (Fig. 6C). Fertile units vary in length between 0.6 and 2.6 mm, and in width between 0.4 and 1.6 mm.

Scales

The scales are bicuspid (Fig. 6G, H, I). The apices are either short (possibly broken or hidden by the rock) or can be up to half of the total length of the scales. The scales have a broadly rounded to slightly cordate base, uncommonly with a small constriction or a stalk. Length of the scales varies between 1.4 and 7.8 mm, and the width varies between 1.8 and 8.7 mm. The small constriction at the base can be 0.5 to 1.0 mm long. Scales sometimes display a striation (Fig. 3C). They can be empty or carry paired fertile units positioned centrally on the scale. Along the cone C1 on sample 45311Aa, scales all have approximately the same length.

Fertile unit pairs on scales

On the scales the pair of fertile units forms an oval consisting of two hemispheres or a heart-shape pointing adaxially on the scale (Fig. 5, Fig. 6J, K, L), sometimes sprouting from the scale stalk. Other fertile units form two oval shapes attached centrally to the scale.

Figure 6. Details of dispersed seeds, scales and fertile scales: **A** paired seeds with double wall (sample 45311C) **B** paired seeds with triangular micropylar protrusion (sample 45311 E) **C** detail of triangular micropylar protrusion from paired seeds (sample 45311 E) **D** heart shaped paired seeds/ovules (sample 45311 D) **E** heart shaped paired seeds/ovules (sample 45311 B) **F** juxtaposed almond shaped seeds/ovules (sample 45311 B) **G** bicuspid scale (sample 45311 Aa) **H** bicuspid scale (sample 45311D) **I** bicuspid scale (sample 45471) **J** bicuspid scale with contour of two seeds/ovules (sample 45315) **K** bicuspid scale with darker organic contour of seed (sample 45310) **L** bicuspid scale with heart shaped contour of seeds/ovules (sample 45471).

Quantitative analysis

The search for measurable organs resulted in 263 fertile units and 158 scales. Fertile units were observed in the cones, on scales or dispersed; scales were observed in the cones, dispersed fertile or empty (Suppl. materials 1, 2).

Fertile unit, length, width and size proxy (n=263)

The set of 263 data points for the fertile unit length and width have a correlation coefficient of, respectively, 0.9976 and 0.9966 from the normal probability plot (Fig. 7). At the 5% significance level, the critical value for 260 to 270 data points varies between 0.9945 and 0.9947. Since 0.9976 and 0.9966 are larger than the critical values of 0.9947 and 0.9945, we cannot reject the null hypothesis that the fertile units came from a population with a normal distribution. This indicates that the isolated fertile units, the fertile units on the dispersed scales and those in the cone, all belong to the same population showing normal distribution.

The histogram of the proxy for size (length x width) of all fertile units, for example, in cones, on fertile scale and dispersed (Fig. 8), indicates a slight positive skewness. Calculated in excel it is 0.54, and indicates that smaller fertile units appear slightly more commonly than larger ones.

The box charts of the fertile unit size proxies (Fig. 9) indicate that, on average, the fertile units in the cones are smallest and the dispersed fertile units without the scale are the largest. Fertile units on the scales have an average size, but their size range is the largest.

The distribution of the proxy for the size of the fertile units ranked in ascending order can be described with a polynomial function of the third order. In the lower part of the spectrum, fertile units are chiefly positioned in cones. In the central part, fertile units can be positioned either in cones, on dispersed scales or are free, while in the upper part of the spectrum fertile units are either free or on dispersed scales, but more commonly free (Fig. 10).

Scale length, width and size proxy (n = 158)

The set of 158 data points for the scale length and width have a correlation coefficient of, respectively, 0.9975 and 0.9821 from the normal probability plot (Figs 11, 12). At the 5% significance level, the critical value for 150 to 160 data points varies between 0.9909 and 0.9915. Since 0.9975 for the scale length is greater than their respective critical values of 0.9909 and 0.9915, we cannot reject the null hypothesis that the scales came from a population with a normal distribution. This indicates that the length of empty scales, fertile scales and scales in cones belong to the same normally distributed population. As the width of the scales has a high PPCC, yet lower than the critical value, the width of the scales is not normally distributed. When taking the four widest scales out of the analysis, the PPCC is higher than the critical value, indicating that most scale widths are normally distributed and, consequently, most scales, in cones, fertile scales and empty dispersed scales, belong to the same normally distributed population with respect to their width.

The histogram of the proxy for size of all scales – for example, dispersed either empty or fertile – and in cones (Fig. 13), compared to the normal distribution curve, indicates a positive skewness for the fertile unit surface proxy, yet more pronounced; in Excel it has a value of 1.3. It indicates that smaller scales are more common than larger ones.
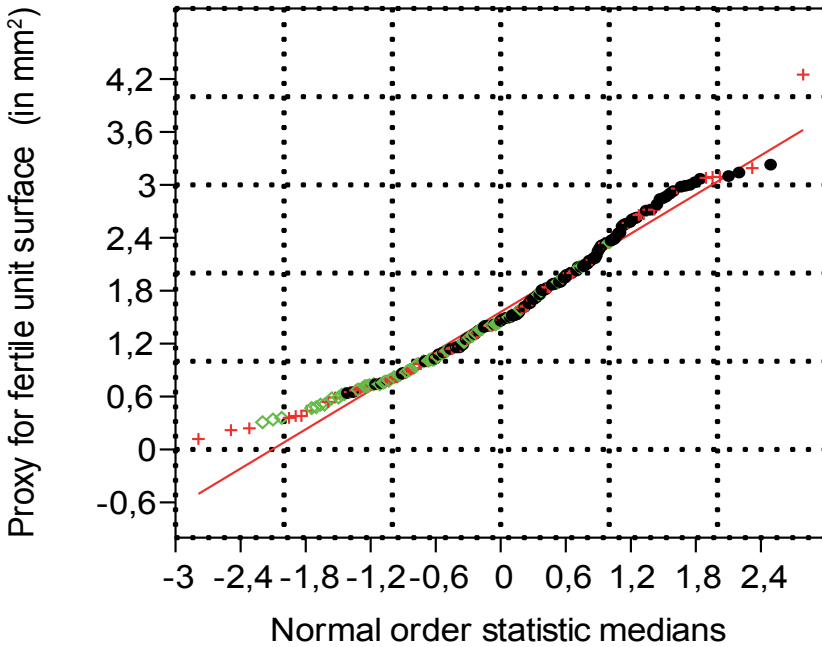
Figure 7. Normal probability plot for the seed surface (length x width) proxy (n=263) (green represents seeds in cone, red represents seeds on scales, and black represents dispersed paired seeds).
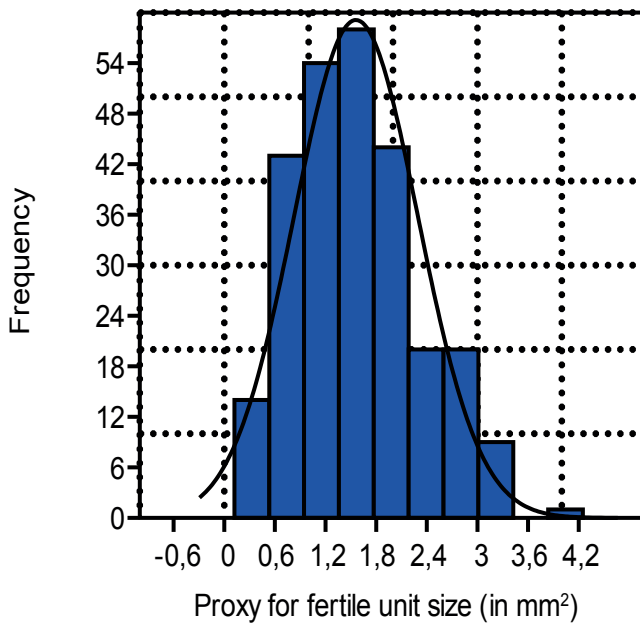
Figure 8. Histogram for the seed surface (length x width) proxy distribution compared to the normal distribution curve (n=263).
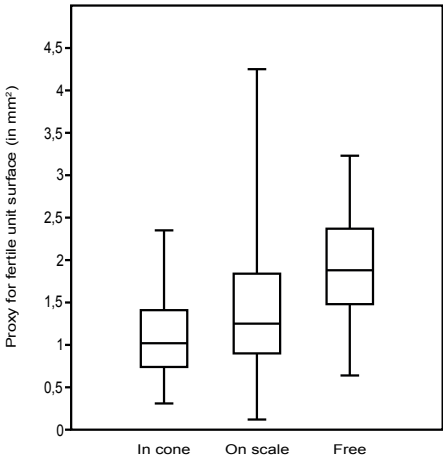
Figure 9. Comparison between the box charts of the proxy for seeds size (length x width) in cones, on scales and free.

3,033E-07x3-0,0001005x2+0,01695x+0,2636
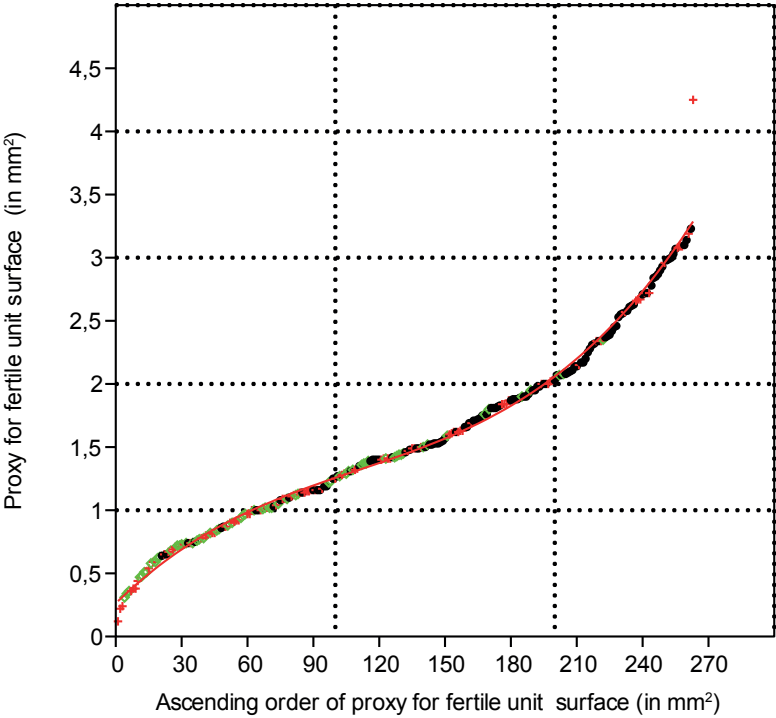
Figure 10. Proxy for seed surface (length x width) organised in ascending order with the superimposed polynomial function describing it (n=263).
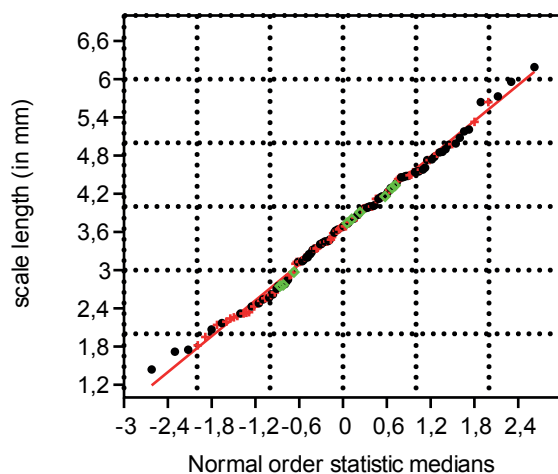
Figure 11. Normal probability plot for the scale length (n=158). Green represents scales in cone, red represents dispersed fertile scales, and black represents dispersed empty scales.
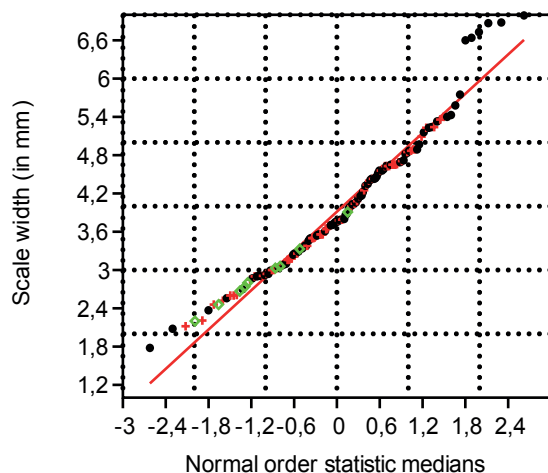
Figure 12. Normal probability plot for the scale width (n=158) (green represents scales in cone, red represents dispersed fertile scales, and black represents dispersed empty scales).

The box charts of the scale size proxies (Fig. 14) indicate that, on average, the scales in the cones are smallest while the dispersed empty scales are largest. The size of fertile scales is in between the two.

The distribution of the proxy for the size of the scales (Fig. 15), ranked in ascending order, diverges from the polynomial function depicted above for the proxy distribution of the fertile units size. It can best be described as three linear fragments: an initial segment with small scales; a second fragment with a lower angle with medium sized scales; and a third steep segment with the largest scales. This first segment holds scales from all three
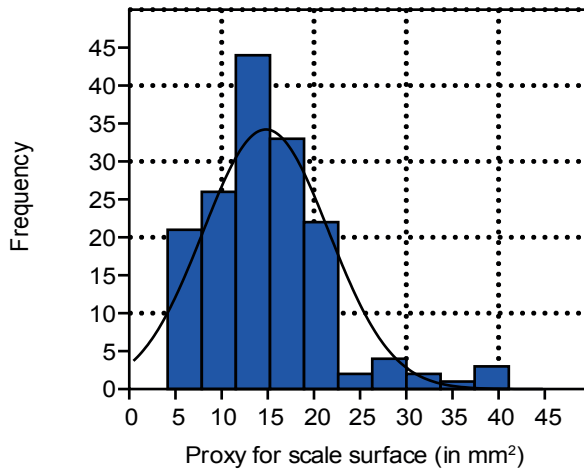
Figure 13. Histogram for the proxy for scale surface (length x width) distribution compared to the normal distribution curve (n=158).
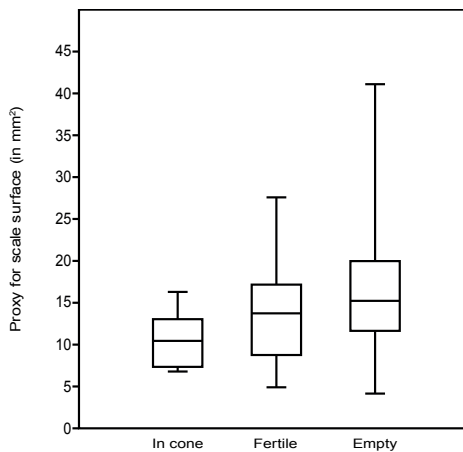
Figure 14. Comparison between the box charts of the proxy for seeds surface (length x width) in cones and dispersed, fertile and empty (n=158).

categories, that is, in cones, fertile and empty; the second segment as well, but scales from cones are less common; and the third segment holds but two fertile scales, while all others are empty scales. The 15 widest, empty scales all fit in one linear segment also comprising two fertile scales. The segment itself has a PPCC of 0.9619, well above the critical value for 15 specimens of 0.9376, indicating the segment itself has a normal distribution and that each specimen from this segment (including the fertile specimen) belongs to the same normally distributed population. As fertile scales are by definition what Jongmans and Gothan (1925, 1935) considered *Tobleria bicuspis*, scales from this last normally distributed linear segment are also considered to belong to *T. bicuspis* with confidence.
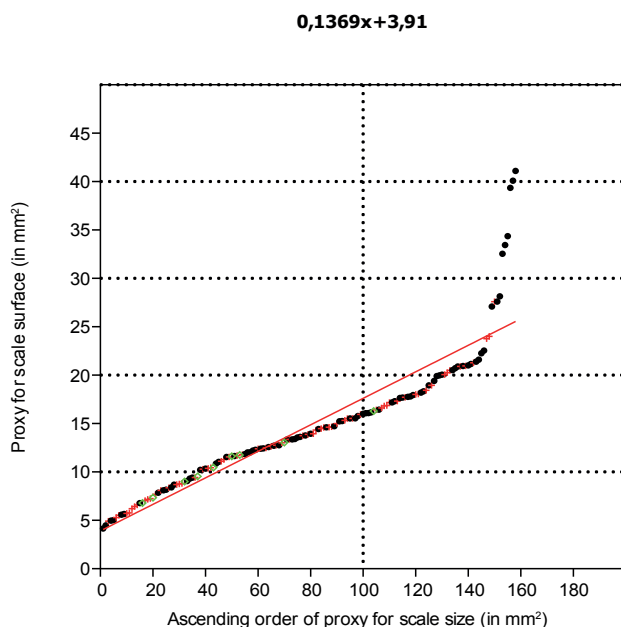
Figure 15. Proxy for scale surface (length x width) organised in ascending order (n=158).

Results of fluorescence analysis

The scales and seeds, both dispersed and in the cone, were exposed to fluorescent light. While the sedimentary rocks holding the plant fossils displayed fluorescence, the scales and seeds were totally inert (Fig. 16A, B, see arrows).

Interpretation and discussion

Seed cones

The statistical analysis conducted above indicates that the paired fertile units and bifid scales belong to one population also represented in the cones. From the box charts it appears that the larger they are, the more the fertile units are dehisced. The fertile units are initially attached to the cone and then dispersed still on a scale to final dispersal without the scale. Considering size generally as a measure for maturity, it appears that more mature fertile units are more easily released. This relation is interpreted here as a natural shedding strategy and as such is applicable to an ontogenetic development from ovules to ripened seeds. The present box charts, indicating a gradual release of the fertile units, supports such an interpretation as seeds. This is often seen in younger cones; numerous Mesozoic seed cones have been found falling apart, and in *Cedrus* and *Abies* the seeds become loose as the cone matures (Harris 1976). Jongmans and Gothan (1925, 1935) also considered *Tobleria bicuspis* as 'seeds' on scales rather than
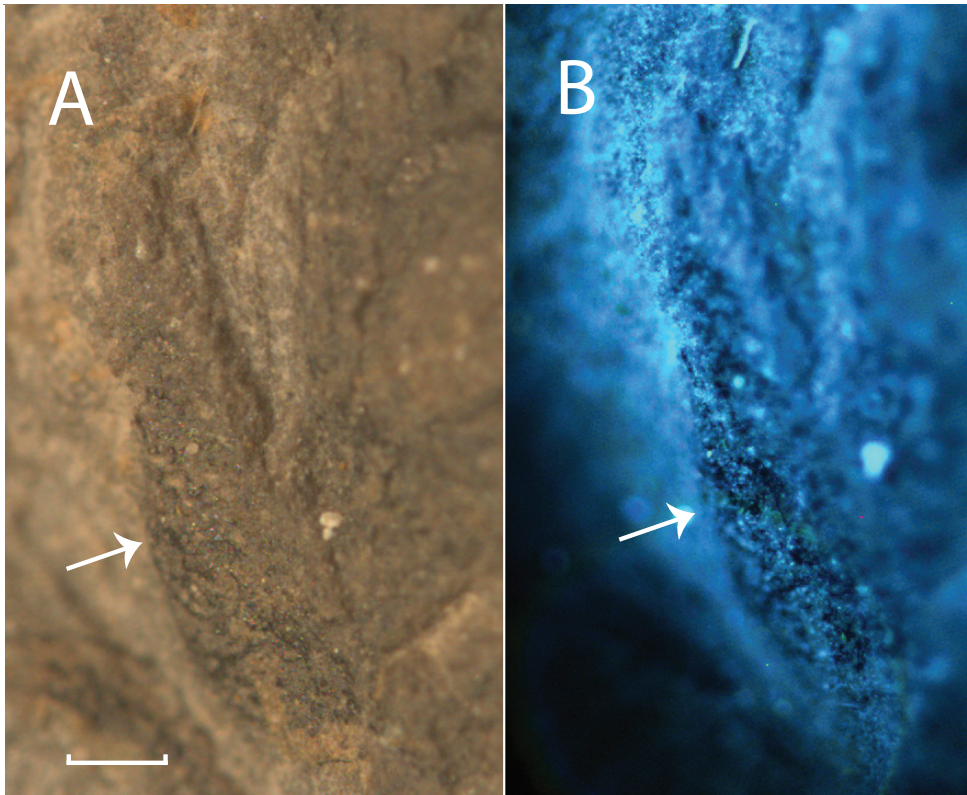
Figure 16. Absence of fluorescence in a scale from the Cone C1 from 45311 Aa: **A** scale under normal light showing the scale as being slightly darker than the rock **B** identical scale with fluorescent light showing the scale as being opaque while the rock around it shows some fluorescence (arrows indicate the scale).

sporophylls bearing microsporangia because they found no pollen grains in their palynological preparations.

Two thin walls were observed around the smaller dispersed fertile units (Fig. 6A, see arrow). As some ovules display a small, darker, cone-like protrusion interpreted here as a micropyle enclosing a small pollen chamber, the outer wall is considered as the integument and the inner wall as the nucellus. The micropylar protrusions were observed on the smaller side of the heart-shaped paired seeds (Fig. 6C, see arrow) which were pointing towards the base of the scale (see Fig. 5A, with interpretation in B); the ovule is consequently interpreted as inverted. No wing was observed on the seeds. *Tobleria bicuspis* is, in consequence, interpreted as a compact cone composed of helicoidally-placed, paired anatropous ovules/seeds sessile on a bifid scale.

Taxonomic affinity

Seed cones from the Carboniferous-Permian transition have either a cycadalean, a gnetalean or a peltaspermalean affinity; or, within the conifers, may belong to the Cord-

aitanthales, the Ferugliocladales, the Dicranophyllales or the Voltziales. Early Permian cycadalean fertile scales differ from those of *T. bicuspis* as their seeds are positioned laterally to the sporophyll base (Gao and Thomas 1989). The gnetalean cones from the late Permian of China (Wang 2004) differ from those of *T. bicuspis* as they have a lanceolate bract and a single megaspore adnate to the bract. Peltaspermales are, as their name indicates, peltate, which is not the case in *Tobleria*. Cordaitanthalean seed cones differ from those of *Tobleria bicuspis* because entire scales subtend shoots with erect ovules form a seed with a conspicuous wing (Ignatiev and Meyen 1989). Early Permian Ferugliocladales seed cones are characterized by an orthotropous ovule attached directly to the cone axis while *T. bicuspis* has sessile anatropous ovules. Cheirolepidiales cones have trifid scales encapsulating a single seed, while the bract is entire (Anderson et al. 2007).

Cones with paired anatropous ovules occur in the voltzian conifers. Most typically the seeds/ovules of *Tobleria bicuspis* are sessile on the scale, similar to the informal group coined by Rothwell et al. (2005) of the voltzian Voltziales, like, for instance, *Majonica*, *Dolomitia*, *Ullmannia*, *Voltzia*, *Pseudovoltzia*, *Voltziopsis and Schizolepis*, amongst others. They are not carried directly by the fertile shoot axis as is the case in the informally coined group of walchian Voltziales (Rothwell et al. 2005) like in *Emporia* or *Ernestiodendron*. *Tobleria bicuspis* consequently is most reminiscent of a voltzian Voltziales.

Dicranophyllales also represent early conifers with paired seeds on a helicoidally-placed scale in a compact cone, but the seeds are erect and winged (Noll 2011). In Rothwell et al. (2005), *Dicranophyllum hallei* still appears as transitional between the Cordaithantales and the Voltziales, but would, considering the latest description (Noll 2011), rather fit in the Voltziales. As the seeds in *T. bicuspis* are inverted and carried by a scale, they have characters of the voltzian Voltziales.

Bract adnate, closely packed or absent

Voltzian Voltziales are generally described with a bract, but there is little evidence available for *T. bicuspis* to establish the presence of a bract subtending the scale. There are more dispersed empty scales than dispersed paired seeds, thus indicating that all paired seeds are accounted for by a scale while only 55% of the dispersed paired seeds are accounted for by a second empty scale that can be hypothesized to represent a bract. Various solutions can be offered for the discrepancy between the proportion of fertile and empty scales. A taphonomic rationale can explain this bias by considering that scales are relatively lighter than seeds and that they are more easily transported, leaving relatively more seeds behind. Another solution resides in the fact that the fertile scales and bracts can be expected to be adnate or closely packed; therefore, it is difficult to distinguish one from the other in the dispersed material.

The Voltziales *Schizolepis moelleri* and *S. planidigesita* from the Middle Jurassic of the Liaoning (Wang et al. 1997) have been figured with a bifid bract subtending an equally bifid scale. Scales and bracts having a comparable shape masking their function can consequently be expected in the Voltziales.

Schizolepis permensis, from the Kupferschiefer of Funfkirchen, based on one scale only with a pair of inverted seeds, was described without a bract (Heer 1876); this is not an isolated case as the same is the case for the early Cretaceous *Schizolepis longipetiolus* of which the cone is reconstructed without bracts (Xu et al. 2013), while in Zhang et al. (2011, table 1) 17 out of 23 listed *Schizolepis* species are without bract description. Moreover, various *Schizolepis* species have reduced bracts (Wang et al. 1997) suggesting that bract reduction may also have led to bract absence or to difficulties in observing the bract. The absence of a bract is consequently a common feature for various *Schizolepis* species. *Schizolepis* has been placed in the Voltziaceae (Schweitzer and Kirchner 1996, Anderson et al. 2007); Voltziaceae are typified by a fertile scale, rather than a fertile shoot, and belong consequently to the informal group coined by Rothwell et al. (2005) as the voltzian Voltziales.

Comparison to Schizolepis

Comparably to *Schizolepis* species, *Tobleria bicuspis* is characterized by deeply incised scales (Schweitzer and Kirchner 1996, Wang et al. 1997, Heer 1876, Zhang et al. 2011, Xu et al. 2013). In this respect *T. bicuspis* differs from *Gomphostrobus* (Marion 1890) which has an apically bifurcating scale. It also contrasts with the bracts of *Emporia, Ernestiodendron, Otovicia* and *Barthelia* (Anderson et al. 2007), all of which display a minor apical bifurcation.

Consider the suite of features shown by *Tobleria bicuspis*: an apically compact cone composed of helicoidally-placed scales, seeds being shed, ovules with a double wall and a small micropyle, scales with adaxially paired anatropous sessile ovules, deeply incised scales, and the absence of a seed wing. These features indicate that *Tobleria bicuspis,* in spite of the difficulties in unequivocally demonstrating the presence of bracts, mostly resembles the voltzian Voltziales and is reminiscent of *Schizolepis,* but differs from it in that the latter's cones are generally lax (Wang et al. 1997, Zhang et al. 2011).

The resemblance to *Schizolepis* is remarkable as it is commonly found in Mesozoic strata (Schweitzer and Kirchner 1996, Zhang et al. 2011, Xu et al. 2013, Wang et al. 1997) and is often considered as a Pinaceae (Krassilov 1982, Wang et al. 1997, Zhang et al. 2011) because of the discovery of a wing to its seed (Wang et al. 1997, Zhang et al. 2011). It should be mentioned that this pinaceous affinity is disputed by some (Anderson et al. 2007) or found to be very distant (Xu et al. 2013).

An early voltzian Voltziales in an early extrabasinal palaeoflora?

An evolutionary development from a radial ovuliferous shoot to an ovuliferous scale is a common concept for the origin of the voltzian Voltziales (Meyen 1997, Anderson et al. 2007, Taylor et al. 2009). Taxa with an ovuliferous shoot in a leaf axil are found in late Pennsylvanian strata (Anderson et al. 2007), while derived Voltziales with only one scale and sessile seed like the Ullmanniaceae are described from the early Permian (Roadian)

Kupferschiefer (Schweitzer 1963). Transitional taxa with paired seeds and bifid scales can consequently be expected between the Pennsylvanian and the Roadian. *Tobleria bicuspis* represents such a transitional taxon and is found in the Mengkarang Formation. The Mengkarang Formation is late Asselian, for which an isotopic age was measured between 296.77 and 296.14 million years (Van Waveren et al. 2018). *Lebowskia*, the earliest voltzian Voltziales described until now, was found in the slightly younger strata of the late early Permian Leonardian (270 to 280 million years old) (Looy 2007). *Tobleria bicuspis* can consequently be seen to represent a voltzian Voltziales occurring 16 to 26 million years earlier than was described until now. *Dicranophyllum hallei* from the 290.7 million years old Donnersberg Formation (Lippolt and Hess 1989) represents a voltzian Voltziales, as seen above, only 6 million years younger than *Tobleria bicuspis*.

The early occurrence of *Tobleria bicuspis* is not as surprising as it may seem as it was found in the Mengkarang Formation where gravity flows from the extrabasinal volcanic slope environment are characterized by very early seed fern occurrences (Booi et al. 2008, 2009a, 2009b). Earliest American gigantopterids (Koll et al. 2017), for instance, are 12 million years younger than *Gothanopteris,* a gigantopterid from the Mengkarang Formation gravity flows. *Tobleria bicuspis*, consequently, is part of the extrabasinal environment where Rothwell et al. (2005) expected greater evolutionary innovations in conifers. It illustrates, in particular, the traditional view that stressed environments, such as those of the volcanic slopes from the Karing Volcanic Complex (Van Waveren et al. 2018) must have been, are especially prone to morphological novelties.

Late Palaeozoic conifer diversity

Voltziales with ovuliferous shoots and those with only ovuliferous scales are not necessarily mutually exclusive. *Molyostrobus texanum* from the early Permian of Texas has a single erect ovule carried by a flattened shoot (Miller and Brown 1973), while the paired seeds in the Sakmarian *Dicranophyllum hallei* are carried by a scale (Noll 2011). This indicates that Voltzialean conifers with shoots and scaled Voltzialeans co-existed at the Permo-Carboniferous transition. It has even been suggested that co-occurrence of Palaeozoic coniferophytes, for example, *Pseudovoltzia*, with a complete reduction of the dwarf shoot with others like *Buriadia* or *Ferugliocladus* with stalked ovules attached directly to the cone axis (Archangelsky and Cuneo 1987), may indicate that there were two or more distinct lineages present at this time (Serbet et al. 2010). Considering the diversity of coniferophytes from the late Palaeozoic, the assumption of Florin (1951) that they all can be traced to a single ancestor is, perhaps, debatable.

Early accidental cone shedding or matured cone?

The positive skewness in the histogram for seeds and scales size proxies in *Tobleria bicuspis* indicates that smaller fertile units and scales occur more commonly than larger ones. Fossils cones, in general, can be represented by numerous separate scales, while

accidentally detached cones, on the contrary, still can hold seeds and scales (Harris 1976). In the case of *T. bicuspis*, the dominance of smaller seeds and scales can be explained by accidental early cone shedding arresting all developments. Accidentally shed cones are expected to be intact (Harris 1976), which is not the case for *Tobleria bicuspis* that partly fell apart as has been demonstrated by the statistical study conducted above. On the other hand, the size distribution of ovules or seeds may also relate to poor fertilisation success in a fully grown cone. In the absence of size studies of seeds in conifers, comparison is drawn here with extant Zamiaceae where the ovule/seed size is represented by three categories: the ovules that have not been pollinated which are smallest, the pollinated ovules and abortive seeds that are medium-sized, and the mature seeds that are largest (Mora et al. 2013). In the fertile unit size proxy distribution (Fig. 10), three diagram segments appear, a segment with small fertile units, a segment with middle-sized fertile units and a steep segment with largest fertile units. These three segments can be hypothesized as indicating that the smallest fertile units are not pollinated, the medium-sized are aborted or pollinated but not matured, while the last segment represents matured seeds. For *Dioon edule* seed efficiency was only 42.5% which was considered to indicate that major seed loss was attributable to ineffective pollination (Mora et al. 2013). The positive skewness of *T. bicuspis* seeds and scales consequently may indicate either that cones were shed while being immature, or that there was ineffective pollination, or a mixture of both. Considering the low number of large seeds, cone shedding while the cone was chiefly immature seems to have been the case for *Tobleria bicuspis*.

In extant taxa, *Cedrus* and *Abies for example*, scales and seeds disperse separately when the cone ripens while in *Araucaria* the seed, enclosed in the cone scale, disperses as one unit (Harris 1976). The relation between size and the degree of release of seeds/ovules as described for *T. bicuspis* above suggests both seed shedding strategies, on scales or separate seeds and scales, operate simultaneously, while the latter dominates because the fertile scales are fewer.

Reconstruction of the *Tobleria bicuspis* cone

The scale size proxy curve is also represented by three segments with three different steepnesses, but these are clearly linear: (1) small scales with a steep size distribution; (2) medium-sized scales with a moderately steep size distribution; and (3) large scales with a steep size distribution. Considering growth to be apical, the largest scales are interpreted as representing the scales near the cone base. As these large scales are chiefly empty and because a steep diagram fragment was also observed for the fertile unit size distribution, indicating that the largest paired seeds were often dehisced from the scale (Fig. 10), these larger empty scales are hypothesized to have shed their seeds. Because both the large paired seeds and the large scales belong to a steep segment of their size distributions, it is hypothesised to represent a zone of rapid maturation.

The second segment of the scale size distribution comprising empty scales, fertile scales and scales in the cones is expected to represent the central part of the cone. As

the largest scales still attached to the cones are only found in the lower half of the second segment of the scale size proxy distribution, cones are expected to be twice the length of the longest fossil cone fragment found in the Jambi collection. The first segment with the smallest ones comprises most scales found in the cones and is expected to chiefly represent its apical part, last developed. Such smaller scales, when being dispersed, may also represent a constricted cone base, but there is insufficient evidence to allow for its reconstruction. In consequence, the reconstruction presented here does not comprise the very base of the cone, but a zone of large empty scales hypothesized to represent fertile scales that have shed their seeds (Fig. 17).

In some cones of *Compsostrobus*, there is a fertile zone where the scales and bracts are attached at a less acute angle, a feature that is considered to be associated with maturation (Delevoryas and Hope 1973). Because of the sudden and steep positive excursion of the proxy for scale size at the high end of its distribution, and because of the presence of relatively large dispersed ones in the fertile unit distribution, it is suggested here that such a zone of rapid maturation was also found in *T. bicuspis*. This suggestion adds an explanation for the positive skewness of the fertile unit size proxy distribution, as it is speculated that dominance of smaller fertile units follows from functional protection from pollination and ripening due to a more acute positioning of the scales for most of the cone.

Associated palaeoflora

Tobleria seeds were found in association with the mesic-xeric elements from the Jambi palaeoflora. Gymnosperm leaves from these localities are *Cordaites principalis*, *Macralethopteris hallei*, *Sphenopteris* sp., *Dicranophyllum molle* and Peltaspermales. *Gothanopteris boschana* and taeniopterids of which the taxonomic affinities are unknown, are also part of this mesic-xeric association from the Mengkarang Formation (Booi et al. 2008, 2009a, 2009b). *Dicranophyllum molle* is a leaf species found on specimens holding *Tobleria bicuspis* scales and seeds (Van Waveren et al. 2007). Considering that the early conifer *Dicranophyllum hallei* with a comparable leaf habit (Barthel et al. 1998) carries cones on its axis, *Dicranophyllum molle* appears to be a good model for the vegetative form of *Tobleria bicuspis*.

Associated pollen and spores

Palynological analysis of only one sample from the base of the Mengkarang Formation gives good results (Crippa et al. 2014). The sample is dominated by lycopsids like *Laevigatosporites* spp., indeterminate bisaccate pollen representing a broad range of gymnospermous taxa, *Florinites* representing the cordaites and *Convolutispora* sp. representing ferns. The assemblage also contains very small numbers of other taxa of which
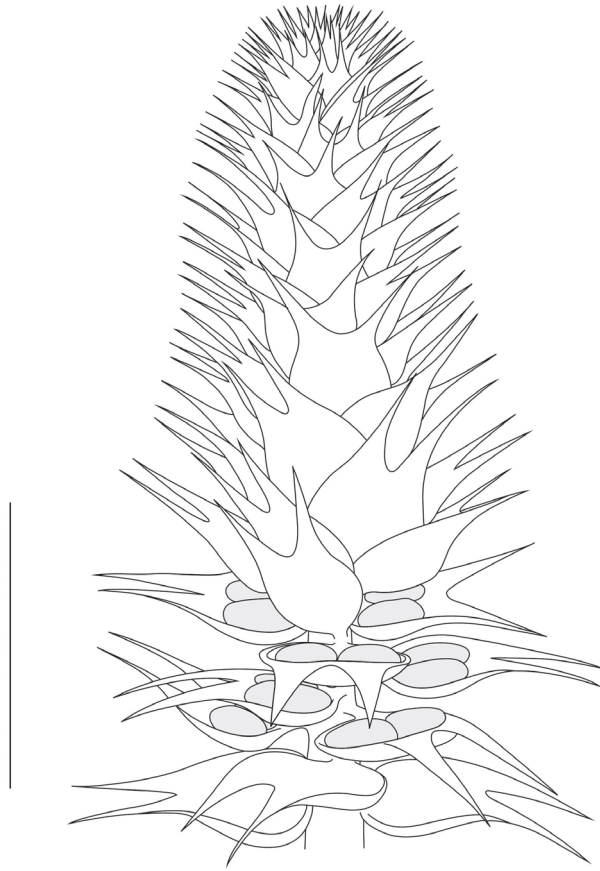
Figure 17. Reconstruction of *Tobleria bicuspis*. Scale bar: 1 cm.

Alisporites spp., ?*Divarisaccus* sp., *Circumstriatites* spp. and *Protohaploxypinus* cf. *limpidus* represent gymnosperms, while the remaining *Punctatisporites* spp., *Raistrickia* sp., *Calamospora* spp. and *Sulcatisporites ovatus* represent spore forming plants. *Tobleria bicuspis* has a robust axis and it is considered to represent an erect cone with, as said above, inverted ovules. According to Leslie (2008), such erect cones with inverted ovules are likely to have been pollinated by bisaccate pollen, leaving a broad range of possibilities within the palynological sample described above for the pollinator of *Tobleria bicuspis*. It should be stressed that, in contrast to the palynological sample described above, *T. bicuspis* was found in the upper half of the Mengkarang Formation during which time, according to Van Waveren et al. (2018), ecological circumstances were more xeric. Indeed, *T. bicuspis* was found in strata at least half a million years later than the time of origin of the palynological sample and it is questionable if *Tobleria bicuspis* was already part of an upland palaeoflora during the climatic circumstances from the base of the section which were depicted by Van Waveren et al. (2018) as tropical wet.

Palaeoecological implication of the taphonomy of the samples

The *Tobleria bicuspis* seeds and scales that are from the Ketidoeran Siamang River locality, representing the upper half of the Mengkarang Formation, are considered to have originated from the source area of the gravity flows and are consequently allochtonous. The cones from the Karing River, at the top of the Mengkarang Formation, have not been transported significantly and are considered to be parauchtonous. This indicates that *Tobleria bicuspis* grew on the slope of the Karing Volcanic Complex during what was indicated by Van Waveren et al. (2018) as the falling stage of a third order eustatic sea level fluctuation, while during the low stand *T. bicuspis* grew at the foot of the volcano. This palaeoecological habitat transition can be hypothesized as being climatically induced as mesic-xeric taxa, occupying the volcanic slope during periods of climate deterioration, appeared to move to wetlands at the base of the volcanic slope when climate deteriorated.

Petrography and fluorescence

The *Tobleria bicuspis* samples were not exposed to petrographic analysis, unlike 33 samples from the Merangin section through the Mengkarang Formation. Ten out of these 33 organic-rich samples clearly contain leaf remains and indicate between 36 and 89% of inertinite, the remaining percentages being vitrinite and in four cases also low ratios of liptinite. The inertinite in these samples was chiefly composed of fusinite, but also semi-fusinite, macrinite, detrinite and inertodetrinite (Sýkorová and Šulc 2009). As none of the 33 samples subjected to petrographic analysis is composed for a 100% of inertinite (fusinite in particular), forest fire, considered to form inertinite and fusain (Scott 2000), probably played little to no part in the preservation of the Jambi palaeoflora.

On the other hand, the seeds, scales and cones of *Tobleria bicuspis* displayed no fluorescence at all. Inertinite, as opposed to vitrinite and leptinite, displays no fluorescence (Tyson 1995); thus, the *T. bicuspis* remains are inertinite. The detailed morphology even suggests they are composed of a particular category of inertinite, namely fusinite. The early appearance of voltzian Voltziales in the Asselian can therefore not only be explained by a unique depositional setting giving a rare window into the palaeoecological consequences of a low stand within an icehouse period in the tropics (Van Waveren et al. 2018), but also by the outstanding preservation circumstances that follow from the formation of inertinite or fusinite by forest fires.

Conclusion

Tobleria bicuspis is regarded as a compact cone, with helicoidal paired seeds on bifid scales. The cone dehisced (dispersed) and released fertile scales, scales and seeds. The

most important aspect of the present description is the demonstration of the existence, in early Permian times, of a coniferophyte with scales, if not scale/bract complexes, with a derived voltzian Voltzialean architecture. The radial symmetry of ovuliferous shoots of the walchian Voltziales, common to the late Palaeozoic, cannot be detected. *Tobleria bicuspis* is part of the mesic-xeric Jambi palaeoflora from the West Sumatra volcanic region, where other gymnosperm taxa also appeared relatively early.

Acknowledgements

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Supplementary material 1

Measurements of 263 fertile units

Authors: Isabel M. Van Waveren

Data type: measurement

Explanation note: Column 1: "cone" indicates the fertile units found in cones, "on scale indicates the fertile units found on dispersed scales, "free" indicates the fertile units found dispersed free from scale; column 2 gives the length of the fertile units in mm; column 3 gives the width of the fertile units in mm; column 4 gives length x width and represents a proxy for the fertile unit size.

Link: https://doi.org/10.3897/phytokeys.119.29555.suppl1

Supplementary material 2

Measurements of 158 scales

Authors: Isabel M. Van Waveren

Data type: measurement

Explanation note: Measurements of 158 scales: Column 1: "In cone" indicates the scales found in cones, "fertile dispersed" indicates the dispersed scales that are fertile, "empty dispersed" indicates the empty dispersed scales. Column 2 gives the length of the scales in mm; column 3 gives the width of the scales in mm; column 4 gives length x width and represents a proxy for the scale size.

Link: https://doi.org/10.3897/phytokeys.119.29555.suppl2

RESEARCH ARTICLE

Sorbus lushanensis, a new species of Rosaceae from China

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Abstract

Sorbus lushanensis Xin Chen & Jing Qiu, **sp. n.** (Rosaceae), a new simple-leaved species belonging to *Sorbus* subg. *Aria* sect. *Alnifoliae*, is described from Anhui and Jiangxi provinces in China. Illustrations, photographs of wild plants and a distribution map are presented. The new species is morphologically similar to *S. folgneri*, but can be distinguished easily by its abaxially greenish-grey tomentose leaves, scale-like stipules and glabrous styles.

Keywords

Sorbus, new species, taxonomy, China

Introduction

Species of *Sorbus* are mainly distributed in the temperate areas of the Northern Hemisphere, with a centre of the highest diversity in East Asia, especially in China. The genus comprises about 100 (Lu and Spongberg 2003) to more than 250 (Phipps et al. 1990) species, 67 of which are native to China (Lu and Spongberg 2003). During fieldwork carried out in recent years for wild germplasm resources of the genus, a new simple-leaved species from Anhui and Jiangxi provinces in China was discovered and is described here.

Materials and methods

The description was based on data and specimens collected in the field between 2015 and 2018 from Anhui and Jiangxi provinces. Geographical coordinates and elevations were determined using Holux m-241. Voucher specimens were deposited at the Herbarium of Nanjing Forestry University (**NF**).

Taxonomic treatment

Sorbus lushanensis Xin Chen & Jing Qiu, sp. n.

urn:lsid:ipni.org:names:77195769-1

Figures 1–3

Type. China. Jiangxi: Lushan City, Lushan National Park, Xianren Cave, 993 m alt., 29°34'06.24"N, 115°57'42.84"E, 05 May 2018, *J. Qiu 1219* (holotype NF-2005029!; isotypes NF-2005027!, NF-2005028!, NF-2005030!, NF-2005031!, NF-2005032!, NF-2005033!, NF-2005034!, NF-2005035!)

Diagnosis. *Sorbus lushanensis* is morphologically most similar to *S. folgneri* (C. K. Schneid.) Rehd., but differs by its leaf blade abaxially greenish-grey tomentose, stipules smaller, pedicels longer, petals larger and styles glabrous.

Description. Tree up to 12 m tall, 14.6 cm in DBH; bole straight, bark grey to dark grey, smooth when young, with fissures, particularly at the base of trunk when mature. Branchlets greyish-brown, sparsely tomentose when young, glabrous or glabrescent at maturity, with pale brown to ochraceous lenticels. Buds turbinate or ovoid, pointed; scales reddish-brown, with white pubescent along margins. Leaves simple; stipules scale-like, 1–1.5 mm long, early deciduous; petiole (9–)13–16 (–19) mm long, greenish-grey tomentose; blades elliptic to broadly ovate, 5.9–9.2 cm long, (3–)4–5.6 cm wide, base cuneate to subcordate, apex acute to shortly acuminate, margin serrate to double serrate, densely greenish-grey tomentose abaxially, sparsely white tomentulose when young, gradually glabrous or glabrescent adaxially; venation craspedodromous, secondary veins 11–16 pairs, slightly impressed adaxially, raised abaxially. Inflorescence a compound corymb, terminal or axillary in the terminal 1–3 leaves, loosely 11–17(–26)-flowered; peduncles 3.9–6 cm long, pedicels 9.4–18.6 mm long, both sparsely white vilous. Flowers 12.5–14.2 mm in diam.; hypanthium campanulate, sparsely white vilous abaxially; sepals triangular-ovate, apex acute, 2.3–3.1 mm long, 2–2.9 mm wide, white vilous on both sides; petals white, broadly ovate or subrounded, apex obtuse, 5.9–7.1 mm long, 4–6.1 mm wide, glabrous, with a short claw at base. Stamens 17–20, 4.9–6.2 mm long, filaments whitish, anthers cream white to slightly yellow. Ovary 2-loculed, white tomentose apically. Styles 2, 3.1–4.6 mm long, connate to 1/3–1/2 of their length, glabrous. Infructescence glabrous, with numerous

Figure 1. Holotype of *Sorbus lushanensis* sp. n. Scanned by Xiaochen Zhang.

Figure 2. *Sorbus lushanensis* sp. n. **A** habit (A plant at Wulao Peak, Lushan National Park, Jiangxi province) **B** flowering branch and leaves (from the plant of type specimen) **C** young inflorescence (from the same plant as habit).

lenticels. Fruit orange-red, oblong to ovoid-oblong, 7.8–11.3 mm long, 4.2–7 mm in diam., 2-loculed, sparsely lenticellate, with an annular scar of the deciduous sepals and white tomentose inside it apically. Seeds brown, 5.46–6.48 mm long, 2.88–3.62 mm in diam., 2.04–2.72 mm thick.

Phenology. Flowering from late April to early May, fruiting from September to October.

Etymology. The name "*lushanensis*" refers to the type locality, Lushan Mountain, Jiangxi Province, China.

Vernacular name. 庐山花楸 (lu shan hua qiu).

Figure 3. *Sorbus lushanensis* sp. n. **A** flower branch and leaves **B** flower **C** petal **D** styles **E** stamens **F** fruit **G** seed. Drawn by Yuxuan Bao.

Distribution, ecology and conservation status. *Sorbus lushanensis* is presently known only from Anhui and Jiangxi provinces (Figure 4). It was observed growing in broad-leaved and mixed conifer broad-leaved forests at altitudes between 853 m
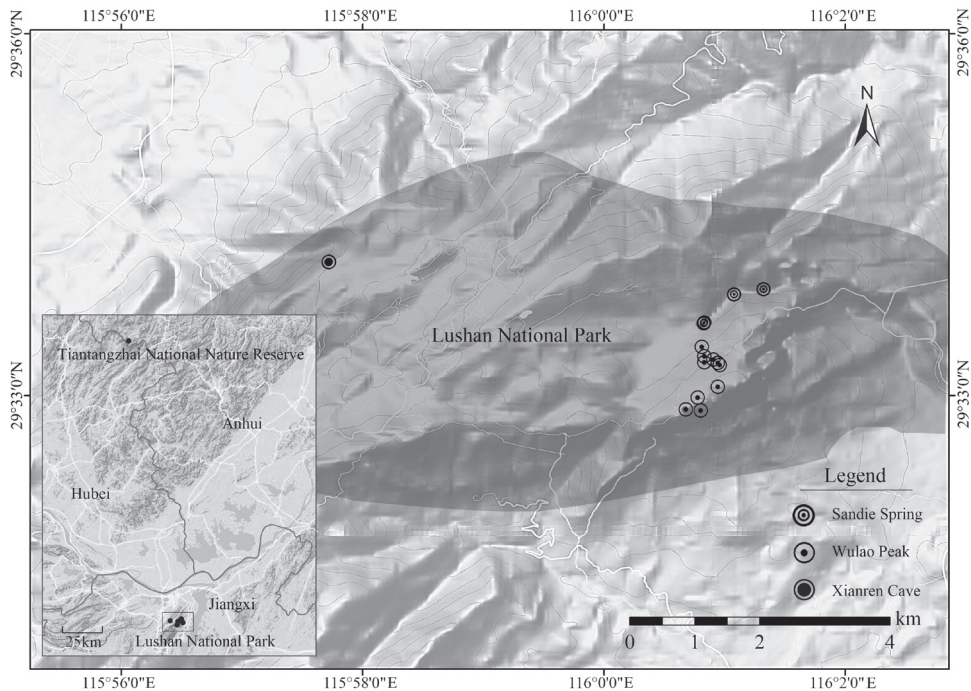
Figure 4. Geographic distribution of *Sorbus lushanensis* sp. n. Drawn by Junsheng Shu.

and 1354 m, together with *S. alnifolia* (Siebold & Zucc.) K. Koch and *S. folgneri* from the same genus and *Pinus taiwanensis* Hayata, *Carpinus cordata* var. *chinensis* Franch., *Cornus kousa* subsp. *chinensis* (Osborn) Q. Y. Xiang, *Cyclobalanopsis glauca* (Thunb.) Oerst., *Fraxinus chinensis* Roxb., *Litsea elongata* (Nees ex Wall.) Benth. & Hook. f., *Prunus serrulata* Lindl. etc. Its natural habitat is at core Lushan National Park and Tiantangzhai National Nature Reserve, which are perfectly protected. No threats were identified though only about 26 individuals were found along the collection routes. The diameter of individuals ranged from 1.5 to 14.6 cm, denoting the species regenerated well naturally. Adequate data on its distribution and population status need to be further collected for we investigated just along the tourist route without entering the inner forest. At present, we assign the conservation status of *S. lushanensis* as "Data Deficient (DD)" following the IUCN Red List Criteria and Categories (IUCN 2017).

Additional specimens examined. China. Anhui: Lu'an City, Tiantangzhai National Nature Reserve, 853 m alt., 31°09'00.84"N, 115°46'07.39"E, 8 May 2015, *W. Du* & *F. Wang 0125* (NF). Jiangxi: Lushan City, Lushan National Park, Wulao Peak, 1354 m alt., 29°32'52.23"N, 116°00'47.78"E, 14 May 2016, *X. Chen, X. X. Fu* & *Q. L. Liu 0285* (NF); Wulao Peak, 1334 m alt., 29°33'04.00"N, 116°00'56.31"E, 14 May 2016, *X. Chen, X. X. Fu* & *Q. L. Liu 0289* (NF); Wulao Peak, 1246 m alt., 29°33'14.84"N, 116°00'57.31"E, 14 May 2016, *X. Chen, X. X. Fu* & *Q. L. Liu 0298* (NF); Wulao Peak, 1210 m alt., 29°33'17.49"N, 116°00'54.14"E, 14

Table 1. Comparison of main features separating *S. lushanensis* and *S. folgneri*.

	S. lushanensis	*S. folgneri*
Leaf blade	denssely greenish-grey-tomentose abaxially	densely white-tomentose abaxially
Stipule	scale-like, 1–1.5 mm long	lanceolate, 3–4.5 mm long
Petiole	sparsely greenish-grey-tomentose	densely white-tomentose
Inflorescence	sparsely white vilous	densely white tomentose
Pedicel	9.4–18.6 mm long	5–8 mm long
Petal	5.9–7.1 mm× 4–6.1 mm	5–5.8 mm× 2.5–4.2 mm
Style	glabrous	tomentose basally

May 2016, *X. Chen, X. X. Fu* & *Q. L. Liu 0302* (NF); Wulao Peak, 982 m alt., 29°33'16.12"N, 116°00'49.56"E, 14 May 2016, *X. Chen, X. X. Fu* & *Q. L. Liu 0316* (NF); Wulao Peak, 1234 m alt., 29°33'15.88"N, 116°00'56.26"E, 25 April 2015, *X. Chen* & *W. Du 0069* (NF); Wulao Peak, 1089 m alt., 29°33'23.85"N, 116°00'48.32"E, 10 May 2015, *W. Du* & *F .wang 0085* (NF); Wulao Peak, 1306 m alt., 29°32'52.74"N,116°00'40.44"E, 15 October 2015, *X. Chen, W. Q. Liu*; *M. W. Geng 0154* (NF); Wulao Peak, 1101 m alt., 29°33'19.14"N, 116°00'49.64"E, 15 October 2015, *X. chen, W. Q. Liu* & *M. W. Geng 0155* (NF); Wulao Peak, 1310 m alt., 29°32'58.59"N, 116°00'46.29"E, 15 October 2015, *X. chen, W. Q. Liu* & *M. W. Geng 0157* (NF); Sandie Spring, 1021 m alt., 29°33'36.10"N, 116°00'49.59"E, 25 April 2015, *X. Chen* & *W. Du 0063* (NF); Sandie Spring, 927 m alt., 29°33'49.98"N, 116°00'56.31"E, 25 April 2015, *X. chen* & *W. Du 0064* (NF); Sandie Spring, 897 m alt., 29°33'52.56"N, 116°01'19.04"E, 15 October 2015, *X. Chen, W. Q. Liu* & *M. W. Geng 0156* (NF); Sandie Spring, 983 m alt., 29°33'35.62"N, 116°00'49.31"E, 15 October 2015, *X. Chen, W. Q. Liu* & *M. W. Geng 0158* (NF); Xianren Cave, 987 m alt., 29°34'06.06"N, 115°57'42.78"E, 14 May 2016, *X. Chen*, *X. X. Fu* & *Q. L. Liu 0267* (NF).

Discussion. Morphological characters, such as sepals persistent or deciduous, leaves glabrous or with white or brown hair, venation craspedodromous or camptodromous, styles free or connate, are of taxonomic significance and useful in classification and delimitation of simple-leaved *Sorbus* taxa (Hedlund 1901, Yu and Lu 1974, Gabrielian 1978, Lu and Spongberg 2003, Aldasoro et al. 2004). In the latest revision of simple-leaved species of *Sorbus* (Aldasoro et al. 2004), species in China are assigned to one subgenus and five sections. The new species is morphologically a member of *S.* subg. *Aria* Persoon sect. *Alnifoliae* (Yu) Aldasoro et al., for it shares the common characters of this section, such as craspedodromous venation, spreading and white petals, coalescent styles and red pomes. *Sorbus* sect. *Alnifoliae* contains five species: *S. alnifolia*, *S. japonica* (Decne.) Hedl., *S. zahlbruckneri* C. K. Schneid., *S. yuana* Spongberg and *S. folgneri*, mainly distributed in China, Japan and Korea (Aldasoro et al. 2004). The new species is morphologically similar to *S. folgneri* in leaf form (Figure 5) and the difference between the two species is summarised in Table 1.

Sorbus lushanensis and the two sympatric species, *S. alnifolia* and *S. folgneri* are all diploid (2n=2x=34) sexual species (Chen et al. unpubl. data). Our preliminary

Figure 5. Leaf abaxial surface of **A** *Sorbus lushanensis* and **B** *S. folgneri*, show the similar of leaf form and the differences of hairs.

molecular work, based on two chloroplast gene fragments, atpB-rbcL and trnL and four nuclear gene fragments, GBSSI, PGIP, PPO and WD, resolved that *S. lushanensis* formed as sister to *S. alnifolia* var. *angulata* S. B. Liang and they two together were resolved as sister to *S. folgneri*, suggesting that *S. lushanensis* is not most closely related to *S. folgneri* (Chen et al. unpubl. data). The new species can be distinguished from the other five species by its abaxially greenish-grey tomentose laminae.

Key to the species of *Sorbus* sect. *Alnifoliae*

1	Leaves tomentose abaxially...	**2**
–	Leaves glabrous or sparsely hairy abaxially..................................	**4**
2	Leaves orbicular-ovate or suborbicular, margins lobed...............	***S. japonica***
–	Leaves elliptic to broadly ovate, margins serrate to double-serrate	**3**
3	Leaves densely white tomentose abaxially....................................	***S. folgneri***
–	Leaves densely greenish-grey tomentose abaxially..................	***S. lushanensis***
4	Fruits with a small annular scar apically, sepals deciduous...........	***S. alnifolia***
–	Fruits with persistent sepals apically...	**5**
5	Leaves elliptic to broadly ovate; fruits much larger, 10–16 × 6–13 mm	***S. yuana***
–	Leaves lanceolate; fruits much smaller, 6–10 × 4–7 mm.....	***S. zahlbruckneri***

Acknowledgements

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DATA PAPER

Taxonomic studies of pteridophytes of Ambon and Seram (Moluccas) collected on Indonesian-Japanese botanical expeditions 1983–1986. XIII. Hymenophyllaceae

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Abstract

Identifications are given for 713 specimens of Hymenophyllaceae collected on Ambon and Seram islands, the Moluccas, Indonesia, during 1983–86. The collection is composed of forty-seven species and one variety belonging to seven genera. The dataset is deposited in GBIF and available at https://www.gbif.jp/ipt/resource?r=seram_hymen.

Introduction

The flora of Seram and Ambon islands, the Moluccas, covering bryophytes, pteridophytes and seed plants, was investigated during field expeditions in 1983, 1984–85 and 1986. As the Moluccan islands, in particular Seram, have been explored very sparsely, the expeditions aimed to make general collections of the land plants in the area. More than 11,000 field numbers of vascular plant and 5,000 bryophyte specimens were collected, mainly from east, central and west Seram (Kato 1990a).

The pteridophyte flora of Seram and Ambon was revised by Kato (1990a), who has continuously contributed to this topic, based on his taxonomic studies in identi-

fying our collections. Kato (1990a) provided an overview of the fern flora of Seram and implied that well over 700 species of pteridophytes occur on the island, based on the collection of nearly 700 species on only three explorations. The collection lists of pteridophytes, excluding Hymenophyllaceae, were already published by M. Kato and his collaborators (Kato 1988, 1989a, 1989b, 1990b, 1992, 1994, 1996, 1997, 2007, Kato and Kramer 1990, Kato and Parris 1992, Kato and Price 1990).

Description

The GBIF dataset is a list of specimens of Hymenophyllaceae collected in Seram and Ambon from 1983 to 1986. The first two sets of specimens of this family are kept in TI and BO; the third more or less incomplete set will be in L, with a few more duplicates to be distributed to other herbaria. In total, 47 species of the Hymenophyllaceae are recorded.

Seram has an area of about 17,000 km^2 with many mountain peaks reaching 2,000 to 3,000 m elevation, the highest being 3,019 m. When the collections were made in 1980s, most mountainous areas were still natural and undeveloped, covered mostly with primary forests. Mountains over 1500 m elevation are in a cloud zone of mossy forests where filmy ferns prefer to grow. For the species enumerated here, the habitat of each species is summarised and edited from the field notes on the collection labels. There are widespread calcareous areas on Seram Island and most collections are from such areas. Ambon is a much smaller island, located southwest of Seram. The flora of Ambon had been relatively better known than Seram's because of the epoch-making pre-Linnean work of G. E. Rumphius' Herbarium Amboinense. However, the island is now well populated and has been deforested. A small number of Hymenophyllaceae were collected on Ambon. On Seram Island, no particular species of filmy fern necessarily grow in limestone areas. For the epiphytic species, calcareous habitats appear to be of less concern. The epipetric species cited in the following list usually grow on very wet, often moss-covered limestone as facultative calcareous species.

Data published through GBIF

https://www.gbif.jp/ipt/resource?r=seram_hymen

Geographic coverage

Ambon Island and Seram Island (the Moluccas), Indonesia.

Taxonomic coverage

Hymenophyllaceae.

Study area

Ambon and Seram islands, the Moluccas, Indonesia. The collection route map for the 1983 trip is given in Kato et al. (1984: 150–151). The collection sites on Seram Island are given in Kato (1990a).

Sampling methods

Pteridophytes specimens, including those of Hymenophyllaceae, were collected in Seram and Ambon islands on the expeditions 1983–1986.

The pteridophyte flora of Ambon and Seram (Ceram) was comprehensively explored in the 1980s and was studied by M. Kato and his colleagues during 1985 and 2007. Most of the pteridophyte collections have already been studied, but the specimens of Hymenophyllaceae remained unprocessed. After identification of the specimens by the authors, following the classification system by Ebihara et al. (2006), seven genera and 47 species are here recorded. The diversity of species is equivalent to nearly half of all species in Malesia, where 108 species have now been identified and recorded (Iwatsuki and Ebihara in prep.).

The field research was organised as a joint survey by the Botanical Gardens, the University of Tokyo and Herbarium Bogoriense, LIPI. Along with the work on the Hymenophyllaceae for Flora Malesiana, this taxonomically interesting family has been revised and the taxonomy of the species has been determined, including the identification of the collections cited here. A modern system, including information based on molecular systematics, was proposed by Ebihara et al. (2006), although further study is continuing. This list of Ambon and Seram species is arranged according to the system proposed there, except for the order of the infrageneric taxa.

Key to the subgenera and species

See Ebihara et al. (2006) for key to the genera.

Hymenophyllum Sm.

1	Stellate hairs present on fronds, and/or fronds dichotomously divided (subgen. *Sphaerocionium*) **2**
–	Stellate hairs absent on fronds and/or fronds not dichotomously divided....**4**
2	Fronds nearly glabrous or with occasional soft hairs at margin ....**2. *H. nitidulum* (Blume) Ebihara & K. Iwats**
–	Obvious hairs present on fronds **3**

3	Fronds with soft stellate hairs on costae and margin of segment .... **3. *H. palmatifidum* (Bosch) Ebihara & K. Iwats**	
–	Fronds setose, at margin of segments, hairs dark brownish........................... ....**4. *H. digitatum* (Müll. Berol.) Ebihara & K. Iwats**	
4	Fronds glaucous or covered with whitish multicellular hairs (subgen. *Pleuromanes*) ....**1. *H. pallidum* (Blume) Ebihara & K. Iwats**	
–	Fronds neither glaucous nor covered with whitish multicellular hairs..........**5**	
5	Rhizome more than 0.4 mm in diameter, nearly glabrous or with scattered pale hairs (subgen. *Globosa*) **6**	
–	Rhizome filiform, less than 0.4 mm in diameter, with scattered short brown hairs..**16**	
6	Receptacles filiform to columnar, involucres triangular to subdeltoid, longer than wide or rarely reniform, nearly as long as wide **7**	
–	Receptacles capitate, involucre distinctly broader than long **12**	
7	Wings of axes flat or undulate, lips of involucre entire or at most crenulate (or toothed in *H. productum*) **8**	
–	Wings of axes and ultimate segments distinctly crisped at margin **9**	
8	Lips of involucre entire or at most crenulate ......**5. *H. angulosum* H. Christ**	
–	Lips of involucre toothed; segments often laxly placed with some irregularly elongated ones .... **6. *H. productum* Kunze**	
9	Lips of involucre entire to crenate **10**	
–	Lips of involucres toothed to fimbriate..**11**	
10	Lamina of fronds > 8cm; wings of axes distinctly crisped ....**7. *H. reinwardtii* Bosch**	
–	Lamina of fronds < 8(-10) cm; wings exceedingly crisped, margin of narrower segments appearing toothed..**8. *H. thuidium* Harr.**	
11	Margin of segments flat or undulate, lips of involucres toothed ....**9. *H. javanicum* Spr.**	
–	Margin of segments distinctly crisped, lips of involucre fimbriate ....**10. *H. fimbriatum* J. Sm.**	
12	Margin of wings and ultimate segments flat..**13**	
–	Margin of wings and ultimate segments more or less crisped........................ ....**11. *H. badium* Hook. & Grev.**	
13	Fronds in general ovate to oblong-ovate...**14**	
–	Fronds narrowly lanceolate .... **13. *H. longifolium* Alderw.**	
14	Head of receptacles widened **15**	
–	Head of receptacles globose................................**14. *H. imbricatum* Blume**	
15	Involucres crenate; wings usually narrower than or the same as segments...... ....**11. *H. badium* Hook. & Grev.**	
–	Involucres entire; wings of rachis broad, often > 1 mm wide, flat and entire . ...**12. *H. junghunii* Bosch**	
16	Margin of segments toothed (subgen. *Hymenophyllum*)............................**17**	
–	Margin of segments entire...**24**	

17   Rachis terete basally, wings of upper part of rachis narrow and flat............**18**

–   Rachis winged throughout, wings more or less crisped, lips of involucre entire or serrate...**21**

18   Mature fronds normally > 3 cm long **19**

–   Mature fronds < 3 cm long .... **19. *H. blandum* Racib.**

19   Fronds normally > 6 cm long, more or less lax; sori < 4 mm long, not blackish **20**

–   Fronds < 6 cm long, more or less compact; sori about 4 mm long, blackish ..

     ....**24. *H. melanosorum* (Copel.) C. V. Morton**

20   Segments about 7–10 mm broad, sori < 3 mm long, fronds not dark when dried .... **16. *H. serrulatum* (C. Presl) C. Chr.**

–   Segments about 7 mm broad, sori 3–4 mm long, dark brownish when dried ....

     ....**17. *H. klabatense* H. Christ**

21   Wings not toothed...**22**

–   Wings toothed **23**

22   Fronds not black when dried, ultimate segments about 1 mm broad, dentation regular, with few cells ....**18. *H. holochilum* (Bosch) C. Chr.**

–   Fronds blackish when dried, ultimate segments 0.3–0.7 mm broad, dentation sharp and distinct, with several rows of cells........**23. *H. rosenstockii* Brause**

23   Wings more or less crisped.................................... **20. *H. denticulatum* Sw.**

–   Wings plane......................................**21. *H. acanthoides* (Bosch) Rosenst.**

24   Laminar cell walls thin and straight; receptacles included (subgen. *Mecodium*)....

     ....**15. *H. polyanthos* (Sw.) Sw., s.l.**

–   Laminar cell walls more or less thick; receptacle extruded beyond lips of involucres (subgen. *Hymenophyllum*) **25**

25   Fronds usually > 10 cm long, axes of fronds sparsely hairy ....**22. *H.* sp. 1**

–   Fronds usually < 7 cm long, axes of fronds rather densely hairy ....

     ....**25. *H. pachydermicum* Cesati**

Didymoglossum Desv.

1   1. Submarginal false veinlets absent (subgen. *Didymoglossum*) **2**

–   1. Submarginal false veinlets present (subgen. *Microgonium*).........................

     ....**28. *D. bimarginatum* (Bosch) Ebihara & K. Iwats.**

2   Fronds simple, stipitate, attached at base (or not peltate), the lower surface glabrescent.............................**26. *D. motleyi* (Bosch) Ebihara & K. Iwats.**[*]

–   Fronds sessile, circular and subentire, peltate, lower surface with hairs along veins .... **27. *D. tahitense* (Nadeaud) Ebihara & K. Iwats.**

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[*] Senterre et al. (2017) proposed a hypothesis that *D. beccarianum* Senterre & Rouhan can be segregated from *D. motleyi* sensu stricto (type collection only), based on morphological characters. Here, we accept *D. motleyi* in a broad sense, including *D. beccarianum*.

Crepidomanes (C. Presl) C. Presl

1　Rhizome slender, < 2 mm in diameter, long creeping, fronds < 10 cm long (subgen. *Crepidomanes*) **2**

–　Rhizome thick, > 2 mm in diameter, erect or creeping, fronds > 10 cm long (subgen. *Nesopteris*) **10**

2　False veinlets present, if absent, without differentiated marginal cells and gemmae (sect. *Crepidomanes*) **3**

–　Segments without false veinlets **8**

3　Mature fronds usually > 5 cm long, texture more or less firm **4**

–　Mature fronds smaller, usually < 4 cm long, texture soft and delicate **6**

4　Submarginal veinlets continuous without any interruption, the additional oblique striae none or few ....**29. *C. bipunctatum* (Poir.) Copel.**

–　Submarginal veinlets, if any, not continuous, oblique striae present **5**

5　Submarginal veinlets continuous but interrupted...................................
....**29. *C. bipunctatum* (Poir.) Copel.**

–　Submarginal veinlets obsolete, with abundant oblique striae ....
....**30. *C. latealatum* (Bosch) Copel.**

6　Submarginal veinlets present, continuous or interrupted..........................**7**

–　Submarginal veinlets obsolete; fronds simple to pinnately compound...........
....**33. *C. pervenulosum* (Alderw.) Copel.**

7　Two rows of normal cells present outside submarginal strands ....
....**31. *C. brevipes* (C. Presl) Copel.**

–　Only one row of normal cells present outside submarginal strands...............
....**32. *C. kurzii* (Bedd.) Tagawa & K. Iwats.**

8　Marginal cells not differentiated...**9**

–　One or two marginal rows of cells differentiated from others (sect. *Crepidium*)....
....**36. *C. humile* (G. Forst.) Bosch**

9　Fronds sessile to subsessile; stipe never gemmiferous (sect. *Crepidomanes*) .....
....**34. *C. vitiense* (Baker) Bostock**

–　Fronds never sessile to subsessile; stipe always distinct, wingless and often gemmiferous (sect. *Gonocormus*) ....**35. *C. minutum* (Blume) K. Iwats.**

10　Without abortive fronds....**37. *C. intermedium* (Copel.) Ebihara & K. Iwats.**

–　With abortive fronds at base of normal fronds ....
....**38. *C. aphlebioides* (H. Christ) I. M. Turner**

Vandenboschia Copel.

1　Terrestrial or saxicolous plants or at most on base of tree trunks; fronds de-compound, at least tripinnate (subgen. *Vandenboschia*) ....
....**39. *V. maxima* (Blume) Copel.**

–　Scandent plants, usually on branches of trees; fronds lanceolate to narrowly so, simply pinnate (subgen. *Lacosteopsis*).........**40. *V. auriculata* (Blume) Copel.**

Abrodictyum C. Presl

1   Rhizome short-creeping; laminar cells up to 1 mm long, tetragonal to elongate, variously arranged (subgen. *Abrodictyum*) **2**

–   Rhizome erect or ascending; laminar cells up to 0.2 mm long, almost all tetragonal, close to each other (subgen. *Pachychaetum*) ....
....**44. A. obscurum (Blume) Ebihara & K. Iwats.**

2   Ultimate segments narrow, setaceous, in several planes in cubic arrangement, laminar cells obsolete or only in one row at each side of costa......................
.... **42. A. pluma (Hook.) Ebihara & K. Iwats.**

–   Ultimate segments narrow but not setaceous, arranged in one plane, laminar cells in 2–4 rows at each side of costa...**3**

3   Terrestrial ferns with erect or short ascending rhizome; fronds < 10 cm long; stipes rather sparsely hairy; ultimate segments narrow, with 2–4 rows of cells on each side of costa .... **43. A. idoneum (C. V. Morton) Ebihara & K. Iwats.**

–   Epiphytic or epipetric ferns with creeping rhizome; fronds usually 20–50 cm long; stipes with dense bristles throughout, bristle > 8 mm in length; ultimate segments various, forming more or less cubic construction of fronds, broader, usually with 3–6 larger, elongate cells rather obliquely arranged on each side of costa .... **41. A. schlechteri (Brause) Ebihara & K. Iwats.**

Cephalomanes C.Presl

1   Mouth of involucre dilated ....**45. C. atrovirens C. Presl**
–   Mouth of involucre truncate or hardly dilated **2**
2   Sori on acroscopic margin of pinnae, not on basiscopic margin ....
...................................**46a. C. javanicum (Blume) C. Presl var. javanicum**
–   Sori on distal portion of pinnae and distributed towards acroscopic margin or sometimes on basiscopic margin ....
....**46b. C. javanicum (Blume) C. Presl var. asplenioides (C. Presl) K. Iwats.**

Callistopteris Copel. (a single species in the area)

47. C. apiifolia (C. Presl) Copel.

Dataset description

Object name: A Specimen List of Hymenophyllaceae of Seram and Ambon collected on Indonesian-Japanese botanical expeditions 1983–1986

Character encoding: UTF-8
Metadata Language: English

Acknowledgements

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RESEARCH ARTICLE

Allium albanicum (Amaryllidaceae), a new species from Balkans and its relationships with *A. meteoricum* Heldr. & Hausskn. ex Halácsy

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Abstract

A new species, *Allium albanicum*, is described and illustrated from Albania (Balkan Peninsula). It grows on serpentines or limestone in open rocky stands with a scattered distribution, mainly in mountain locations. Previously, the populations of this geophyte were attributed to *A. meteoricum* Heldr. & Hausskn. ex Halácsy, described from a few localities of North and Central Greece. These two species indeed show close relationships, chiefly regarding some features of the spathe valves, inflorescence and floral parts. They also share the same diploid chromosome number $2n =16$ and similar karyotype, while seed testa microsculptures and leaf anatomy reveal remarkable differences. There are also several morphological features that allow them to be differentiated at specific level. The inclusion of both species into a newly described section *Pseudoscorodon* of the subgen. *Allium* is proposed. An analytic key to the species, included in the new section, is also provided.

Introduction

One of the richest and largest genera of Monocotyledons is *Allium* L. and it is almost exclusively widespread in the northern hemisphere, where it is represented by ca. 1200 taxa (Govaerts et al. 2018). This genus is characterised by a high rate of endemism, especially observable in North America, Asia and the Mediterranean area, which represent the main centres of diversity.

In the context of cytotaxonomical research on the genus *Allium* in the Mediterranean territories, especially regarding the subgen. *Allium* (Bogdanović et al. 2008, 2009, 2011a, 2011b, Brullo et al. 1997a, 1997b, 1999, 2001, 2003a, 2003b, 2004, 2007, 2008a, 2008b, 2009, 2010, 2014, 2017, 2018, Özhatay et al. 2018), a peculiar population occurring in Albania, previously attributed to *A. meteoricum* Heldr. & Hausskn. ex Halácsy, is examined. *Allium meteoricum* s. str. was described from Meteora in Central Greece by Halácsy (1904) and later also recorded from Assopos, Greece (Tzanoudakis 1983, Tzanoudakis and Vosa 1988, Brullo et al. 2001). Extensive morphological investigations, carried out on herbarium material and living specimens coming from Albania (Devoli river near Berat on serpentines) and Greece (Meteora on sandstones), allowed us to verify that the Albanian populations are very different from those of Meteora, which is the locus classicus of *A. meteoricum*. Detailed analyses regarding the chromosome complement and karyotype structure, seed testa micro-morphology and leaf anatomy provided relevant discriminant features. Based on these data, the Albanian populations were referred to a species new to science, named *Allium albanicum*.

Materials and methods

Plant morphology was analysed on 20 living mature plants. Qualitative and quantitative morphological characters, considered as diagnostic in *Allium,* were analysed and scored (Table 1) on fresh material. Comparison of *A. albanicum* with *A. meteoricum* was based on living plants coming from the type locality of both species, collected by S. Cambria in Albania (June 2017) and by S. Brullo and C. Cambria in Greece (June 2018), as well as on several herbarium specimens (BM, CAT, G, K, W, WU) in order to check the correct sample identification. Literature data were also considered. Collected specimens are preserved in CAT.

For the karyological study, living bulbs were collected and potted at the Botanical Garden of Catania University. Root tips were pre-treated with 0.3% (w/v) colchicine water solution for 3 h at room temperature and then fixed overnight in fresh Farmer's fixative (3:1 v/v, absolute ethanol: glacial acetic acid). Root tips were hydrolysed in 1N HCl at 60 °C for 7 min, washed and stained with Feulgen for 1 h. Microphotographs of good quality metaphase plates were taken with a Zeiss Axioskop2 light microscope equipped with an Axiocam MRc5 high resolution digital camera. Chromosome number and karyotype details were analysed from 10 well spread metaphase plates from 5 individuals, the mean values being used for the karyotype characterisation. Metaphase chro-

Table 1. Main diacritic features of *Allium albanicum* and *A. meteoricum*.

Characters	A. albanicum	A. meteoricum
Bulb size (mm)	8–10 × 5–10	10–14 × 8–12
Bulb outer coat colour	brownish	blackish-brown
Stem height (cm)	14–28(-30)	10–25
Stem diameter (mm)	1	1–1.2
Stem coverage by leaf sheaths	1/4	1/2
Leaf number	3	3–4
Leaf length (cm)	up to 10	up to 12
Spathe valves length (mm)	subequal, 8–12	unequal, 7–11
Spathe valve appendage length (mm)	1–2.5	1–4
Spathe valves arrangement	fused up to 1/2	free
Larger spathe valve nerves (no.)	3–5	5
Smaller spathe valve nerves (no.)	3	3–5
Pedicel length (mm)	6–25	6–15
Tepal colour	white tinged with pink	purplish-pink
Tepal midvein colour	greenish-purple	purplish
Tepal length (mm)	5.5–6.5	6–7.5
Tepal apex	eroded	rounded
Stamen filament colour	yellowish above, white below	white
Outer stamen filament length (mm)	1.7–2.1	2.7–3.3
Inner stamen filament length (mm)	2.5–3.2	3.5–4
Anther colour	greenish-pale yellow	yellow
Anther apex	rounded	apiculate
Annulus height (mm)	0.5–0.6	0.7–0.9
Ovary colour	yellow	green
Ovary apex	slightly wrinkled	smooth
Ovary nectariferous pores height	about 1/2 ovary	about 1/4 ovary
Style length (mm)	2.7–2.8	1.5–2
Capsule length (mm)	4–4.5	3–3.5
Capsule shape	subglobose-obovate	subglobose
Seed size (mm)	3.5–4.0 × 2.4–2.5	2.2–2.5 × 1.9–2.0

mosomes were measured using the image analysis system Zeiss Axiovision 4.8, while karyotyping was performed by CROMOLAB 1.1 software Brullo (2002). The chromosome types were named according to the position of the centromere: r = 1–1.3 (m) median, r = 1.3–1.7 (msm) median-submedian, r = 1.7–3 (sm), r = 3–7 (st) subterminal (Tzanoudakis 1983). All measured karyomorphometric parameters are given in Table 2. Karyotype symmetry indices followed Paszko (2006) and Peruzzi and Eroğlu (2013).

Leaf anatomy was studied on living materials coming from the type locality and cultivated in the Botanical Garden of Catania University. Leaf blades of maximum size, in their optimal vegetative development, usually before the flowering stage, were taken from the middle part and fixed in Carnoy. Leaf cross sections were double stained with ruthenium red and light green, analysed and photographed with a light microscope (Zeiss Axioskop2 and Axiocam MRc5 digital camera).

Seed testa micro-morphology was analysed on mature and dry material taken from individuals coming from the type locality, using a scanning electron microscope (SEM) Zeiss EVO LS10, according to the protocol reported by Stork et al. (1980). Terminology of the seed coat sculpturing follows Barthlott (1981, 1984) and Gontcharova et al. (2009).

Taxonomy

Allium albanicum Brullo, C. Brullo, Cambria, Giusso & Salmeri, sp. nov.
urn:lsid:ipni.org:names:60478500-2
Figs 1, 7B–D

Allium meteoricum auct. fl. Albania non Halacsy, Consp. Fl. Graec. 3(1): 250. 1904, **Syn.**

Type. ALBANIA. Devoli river, near Berat, serpentines, ca. 700 m elev., 40°43'12.00"N, 20°32'18.00"E, 26 June 2017, *S. Cambria s.n.* (Holotype: CAT; Isotypes: CAT, FI, G).

Diagnosis. Allio meteoricum similis sed bulbis minoribus tunicis exterioribus brunneis, scapo ad 1/4 longitudinem vaginis foliorum tecto, spathae valvis in dimidio inferiore connatis, appendice usque ad 2,5 mm longa, majore 3–5 nervata, minore 3 nervata, tepalis albo-roseis, minoribus, apice erosis, filamentis staminorum minoribus, luteis superne, annulo breviore, antheris viridulis- pallide luteis, apice rotundatis, ovario luteo leviter apice rugoso, poris nectariferis majoris, capsula majore subglobosoobovata, differt.

Description. Bulb ovoid, 8–10 × 5–10 mm, with outer tunics coriaceous, brownish, the inner membranous, whitish. Stem 14–28(30) cm tall, cylindrical, flexuous, 1–1.5 mm in diameter, glabrous, erect, covered for 1/4 of its length by the leaf sheaths. Leaves 3, rather flat, glabrous, green, ribbed, up to 10 cm long and 1–2.2 mm wide, denticulate at margins. Spathe persistent, with 2 valves subequal, 8–12 mm long, shorter than the inflorescence, fused to half of their length, with an appendage 1–2.5 mm long, the larger 3–5-nerved, the smaller 3-nerved. Bostryces 12. Inflorescence laxly hemispheric, 2–3 cm in diameter, many flowered, with unequal pedicels 6–25 mm long. Perigon cylindrical-urceolate, with tepals of equal length, white tinged with pink, mid-vein greenish-purple, the inner ones linear-elliptical, the outer ones sublanceolate, rounded and slightly eroded at the apex, 5.5–6.5 mm long and 1.7–2 mm wide. Stamens included, with simple filament yellowish above and whitish below, the outers 1.7–2.1 mm long, the inners 2.5–3.2 mm long, below connate into an annulus 0.5–0.6 mm high. Anthers greenish-pale yellow, elliptical, 1–1.1 × 0.6 mm, rounded at the apex. Ovary subglobose-ovoid, yellow, slightly wrinkled at the apex, 1.5–1.7 × 1.4–1.7 mm, with large nectariferous pores, long about half the ovary. Style white, 2.7–2.8 mm long, stigma capitate. Caspule trivalved, subglobose-obovate, 4–4.5 mm, with evident nectariferous pores.

Phenology. Flowering and fruiting from June to July.

Etymology. The epithet refers to the Latin "*Albanicum*", coming from Albania, the country where the species grows.

**Karyology.** The investigated specimens of *A. albanicum* from the type locality revealed a diploid chromosome number with $2n = 16$. The karyotype obtained from somatic metaphase plates (Fig. 2A) is mostly characterised by nearly metacentric chromosomes; specifically, the mean karyogram (Fig. 2B) reveals 4 typical metacentric (m) pairs (III, V, VI, VIII), 3 meta- submetamentric (msm) pairs (I, II, VII), having an arm ratio

Table 2. Karyomorphometric parameters and symmetry indices for *Allium albanicum* and *A. meteoricum*. Mean values were calculated from 10 good metaphase plates from individuals of the type locality.

Pairs	LA (µm)	SA (µm)	TAL (µm)	TRL%	AR	CI	CA	Type
Allium albanicum								
I	5.00 ± 1.43	3.74 ± 1.07	8.74 ± 2.48	7.87 ± 0.59	1.34	42.82	0.14	msm
II	4.52 ± 0.94	3.38 ± 1.05	7.91 ± 1.71	7.16 ± 0.34	1.34	42.80	0.14	msm
III	4.03 ± 0.87	3.48 ± 0.73	7.53 ± 0.58	6.84 ± 0.34	1.16	46.20	0.07	m
IV	4.67 ± 0.99	1.99 ± 0.38	6.79 ± 1.31	6.19 ± 0.27	2.35	29.30	0.40	sm[sat]
V	3.56 ± 0.40	3.09 ± 0.34	6.78 ± 0.66	6.26 ± 0.59	1.15	45.57	0.07	m[sat]
VI	3.48 ± 0.77	2.93 ± 0.61	6.44 ± 1.34	5.86 ± 0.42	1.19	45.56	0.09	m
VII	3.33 ± 0.75	2.10 ± 0.38	5.43 ± 0.38	4.91 ± 0.81	1.58	38.69	0.23	msm[sat]
VIII	2.87 ± 0.42	2.33 ± 0.42	5.33 ± 0.77	4.90 ± 0.47	1.23	43.68	0.10	m[sat]

TCL: 109.88 ± 21.7 µm; **MCL:** 6.87 ± 1.2 µm; **d-value:** 16.83; **DRL%:** 3.28; **S%:** 57.95; **MAR**: 1.37; **MCI**: 41.83; Cv_{CL}: 17.12; Cv_{CI}: 13.00; M_{CA}: 15.63

Pairs	LA (µm)	SA (µm)	TAL (µm)	TRL%	AR	CI	CA	Type
Allium meteoricum								
I	4.05 ± 0.21	3.23 ± 0.30	7.27 ± 0.31	7.78 ± 0.02	1.26	44.35	0.11	m
II	3.87 ± 0.44	3.06 ± 0.73	6.94 ± 1.01	7.42 ± 0.35	1.26	44.19	0.12	m
III	3.79 ± 0.43	2.74 ± 0.23	6.53 ± 0.34	6.99 ± 0.37	1.38	41.98	0.16	msm
IV	4.15 ± 0.16	1.69 ± 0.11	6.16 ± 0.27	6.59 ± 0.29	2.45	27.49	0.42	sm[sat]
V	2.90 ± 0.35	2.58 ± 0.11	5.48 ± 0.11	5.87 ± 0.12	1.13	47.06	0.06	m[sat]
VI	2.90 ± 0.23	2.50 ± 0.34	5.40 ± 0.57	5.78 ± 0.61	1.16	46.27	0.07	m
VII	2.66 ± 0.11	1.85 ± 0.11	4.52 ± 0.23	4.83 ± 0.24	1.43	41.07	0.18	msm
VIII	2.42 ± 0.23	2.02 ± 0.42	4.44 ± 0.57	4.74 ± 0.51	1.20	45.45	0.09	m

TCL: 93.48 ± 21.7 µm; **MCL:** 5.84 ± 1.06 µm; **d-value:** 14.13; **DRL%:** 3.5; **S%:** 55.31; **MAR**: 1.36; **MCI**: 42.21; Cv_{CL}: 18.16; Cv_{CI}: 14.48; M_{CA}: 15.21

Abbreviations: LA = long arm; SA = short arm; TAL = total absolute length; TRL = total relative length; AR = arm ratio; CI = centromeric index; CA = centromeric asymmetry; Type=chromosome nomenclature; sat = satellited; TCL = total chromosome length; MCL = mean chromosome length; d-value = difference between Long arms and Short arms; DRL% = difference of relative length; S% = Relative length of shortest chromosome; MAR = mean arm ratio; MCI = mean centromeric index; Cv_{CL} = coefficient of variation of chromosome length; Cv_{CI} = coefficient of variation of centromeric index; MCA = mean centromeric asymmetry.

between 1.30 and 1.67 and one submetacentric (sm) pair (IV). Microsatellites were detected on the short arms of two metacentric chromosome pairs, one meta-submetacentric pair and the submetacentric one. Thus, the chromosome formula can be expressed as $2n = 2x = 16$: 4 m + 4 m[sat] + 4 msm + 2 msm[sat] + 2 sm[sat]. Chromosomes have a total length varying from 8.90 ± 2.5 µm of the longest chromosome to 5.16 ± 0.8 µm of the shortest one, while the relative length ranges from 8.01% to 4.73%. As already emphasised by Tzanoudakis (1983) and Brullo et al. (2001), *A. meteoricum* also has a diploid chromosome complement with $2n = 16$ (cf. Brullo et al. 2001, Fig. 6A), which is characterised by 5 metacentric chromosome pairs, two of which microsatellited on the short arm, 2 msm pairs and one submetacentric microsatellited pair (cf. Brullo et al. 2001, fig. 8A). Chromosomes vary in total length from 7.29 µm of the longest chromosome to 4.03 µm of the shortest one, while the relative chromosome length ranges from 7.8% to 4.3%. Table 2 shows the mean values for all measured karyomorphometric parameters and symmetry indices of *A. albanicum* and *A. meteoricum* from the type locality.
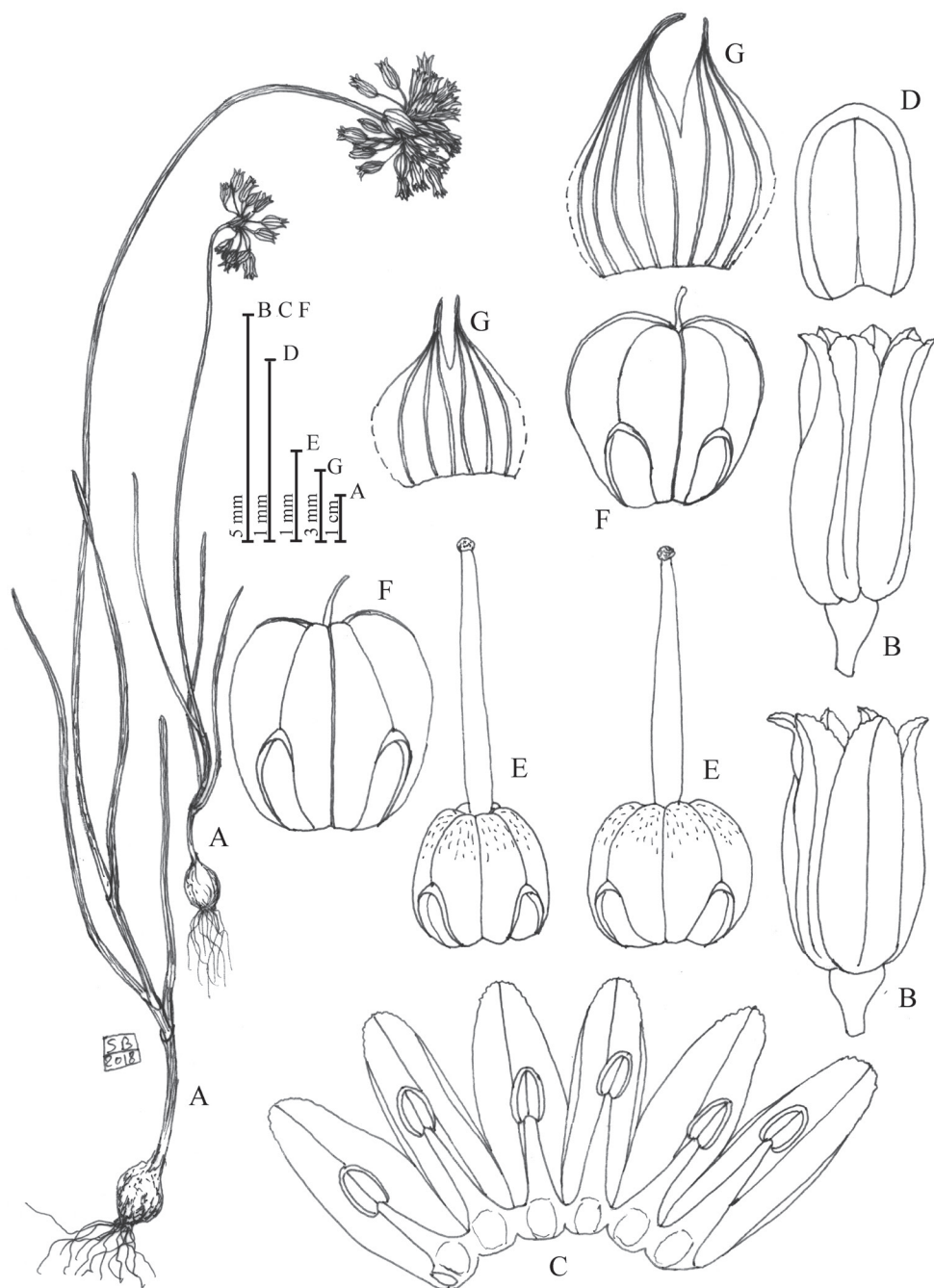
Figure 1. *Allium albanicum* Brullo, C. Brullo, Cambria, Giusso & Salmeri sp. nov. **A** Habit **B** Flower **C** Perigon and stamens open **D** Anther **E** Ovaries **F** Capsule **G** Spathe valves. Drawing by S. Brullo based on living material coming from the type locality.
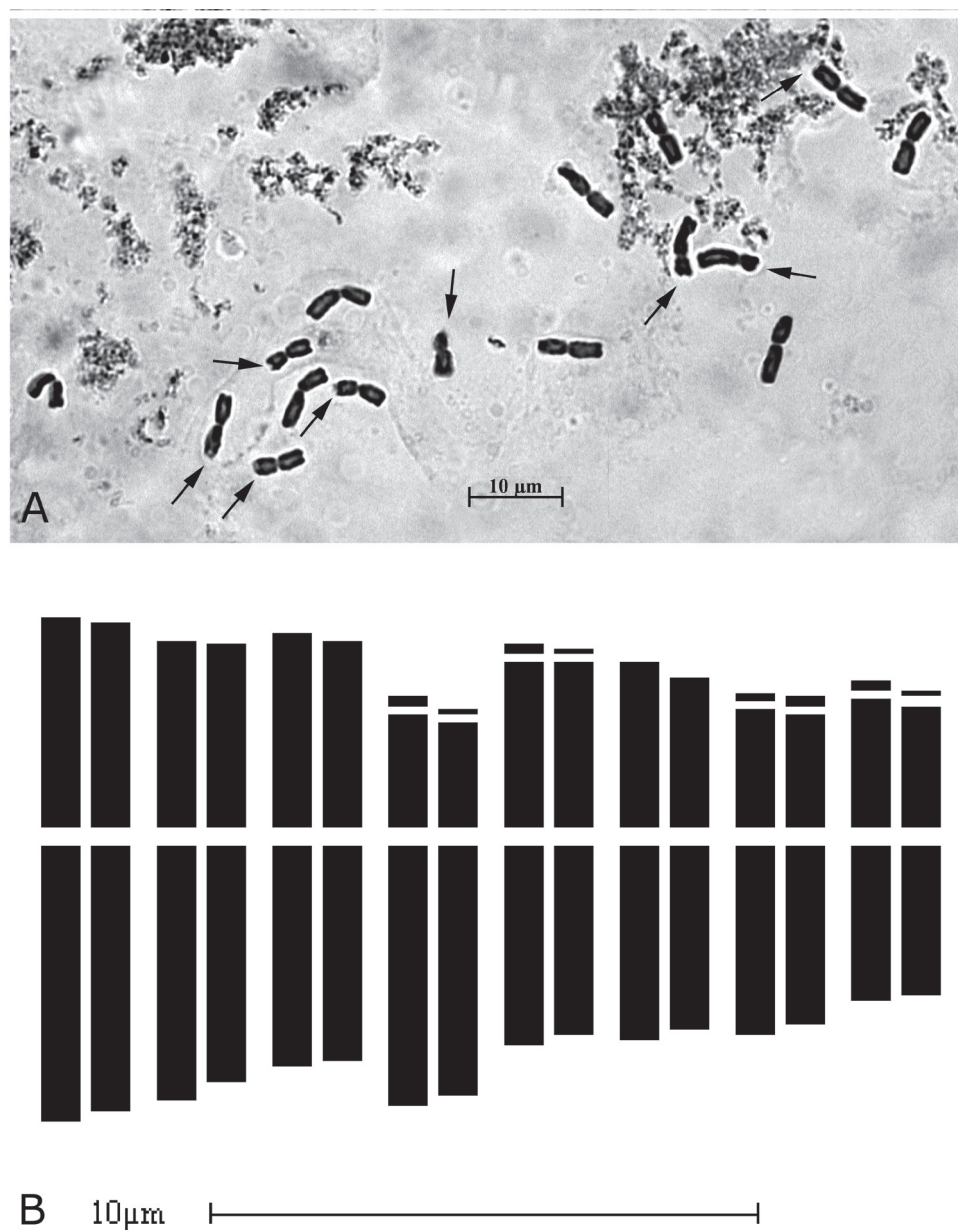
Figure 2. Chromosome complement ($2n = 2x = 16$) of *Allium albanicum*. **A** Mitotic metaphase plate from type locality; arrows indicate satellited chromosomes **B** idiogram.

Leaf anatomy. The leaf cross section of *A. albanicum* shows a flat outline, with some dorsal ribs. The epidermis is formed by small cells covered by a well-developed cuticle externally more thickened. Stomata are numerous and distributed along the whole leaf perimeter. The palisade tissue is regular and compact, arranged in one layer
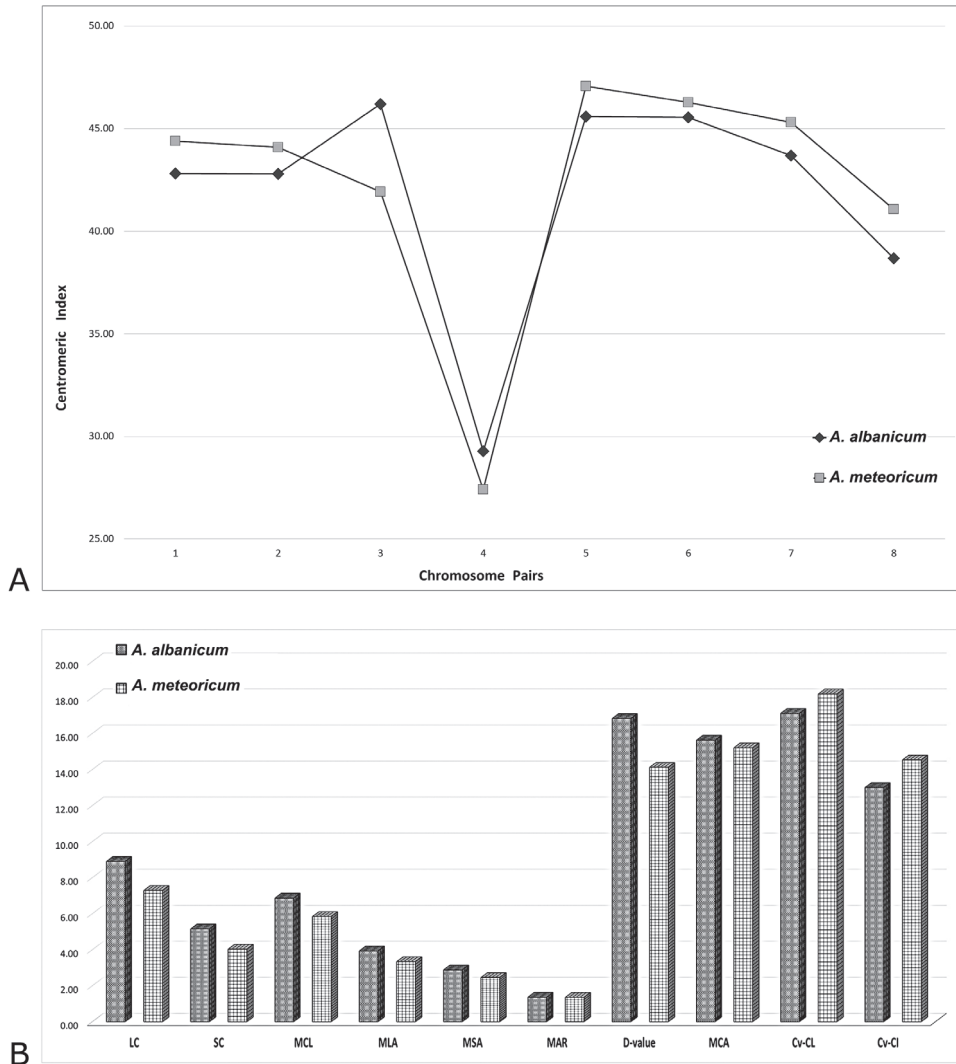
Figure 3. Comparison of karyotype morphometric data between *Allium albanicum* and *A. meteoricum*. **A** Variation of centromeric index for each chromosome pair **B** Variation of the main karyomorphometric parameters and symmetry indices (*LC* longest chrom., *SC* shortest chrom.; *MCL* mean chromosome length; *MLA* mean long arm; *MSA* mean short arm; other abbreviations see Table 2).

of long cylindrical cells, more developed on the adaxial face. The spongy tissue is rather compact and slightly lacunose, in the peripheral part many secretory canals occur. The maximum number of vascular bundles is 20, 11 of which are very small and are localised on the adaxial face, while on the abaxial face, there is one large central vascular bundle and 4 smaller ones for each side (Fig. 4).

Seed micromorphology. As emphasised by numerous authors (Pastor 1981, Češmedžiev and Terzijski 1997, Fritsch et al. 2006a, Neshati and Fritsch 2009, Celep
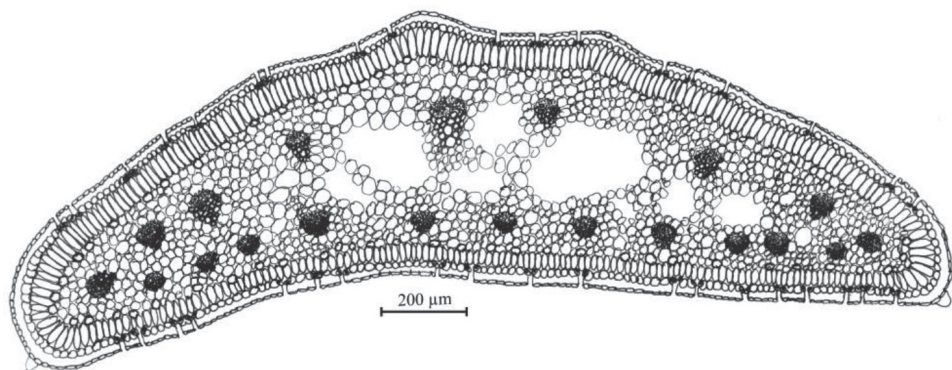
Figure 4. Leaf cross section of *Allium albanicum* from living material coming from the type locality. Drawing by S. Brullo.

et al. 2012, Salmeri et al. 2016, Lin and Tan 2017, Özhatay et al. 2018, Brullo et al. 2018), the micro-sculptures of the seed testa in the *Allium* species represent a very stable and conservative character, showing usually relevant taxonomical and phylogenetical implications. Seeds of *A. albanicum* at low magnification (30×) showed a semiovoid shape (3.5–4.0 × 2.4–2.5 mm), with a rather rugose surface (Fig. 5A, B). The seeds observed at high magnification (600× and 1200×) revealed irregularly polygonal testa cells, having a size of 40–80 × 17–40 μm (Fig. 5C–F). The anticlinal walls appeared flat, rather straight and partly covered by strip-like sculptures forming a widened intercellular region, not or just a little lacerate. The periclinal walls were flat, with few flat and smooth or slightly knobby verrucae, usually arranged along the margin surrounding a central one. Conversely, the seeds of *A. meteoricum* at low magnification (30×) revealed a semi-globose shape and a smaller size (2.2–2.5 × 1.9–2.0 mm), with less pronounced surface roughness (Fig. 6A, B). The seeds observed at high magnification (600× and 1200×) also showed irregularly polygonal testa cells, but with a larger size (60–120 × 15–50 μm) (Fig. 6C–F). The anticlinal walls appeared flat, rather straight and partly covered by strip-like sculptures forming a widened intercellular region, partially lacerate. The periclinal walls were weakly protruding with several knobby verrucae distributed over the whole surface.

Ecology and distribution. The investigated population of *A. albanicum*, previously reported as sub *A. meteoricum* (Pils 2016, Barina 2017), was collected on serpentinic substrata of open stands characterised by rocky outcrops at ca. 700 m of elevation (Fig. 7). Plants grow in shrub vegetation differentiated by some serpentinicolous plants, such as *Acantholimon albanicum* O.Schwarz & F.K.Mey, *Centaurea salonitana* Vis., *Centranthus longiflorus* Steven, *Festucopsis serpentini* (C.E. Hubb.) Melderis, *Forsythia europaea* Degen & Bald., *Iberis umbellata* L., *Salvia ringens* Sibth. & Sm. etc. According to literature (Pils 2016, Barina 2017) and herbarium investigations, *A. albanicum* seems to have a scattered distribution in Albania, though its effective geographic range might be better defined only through further field surveys. Based on Brullo et al. (2001),
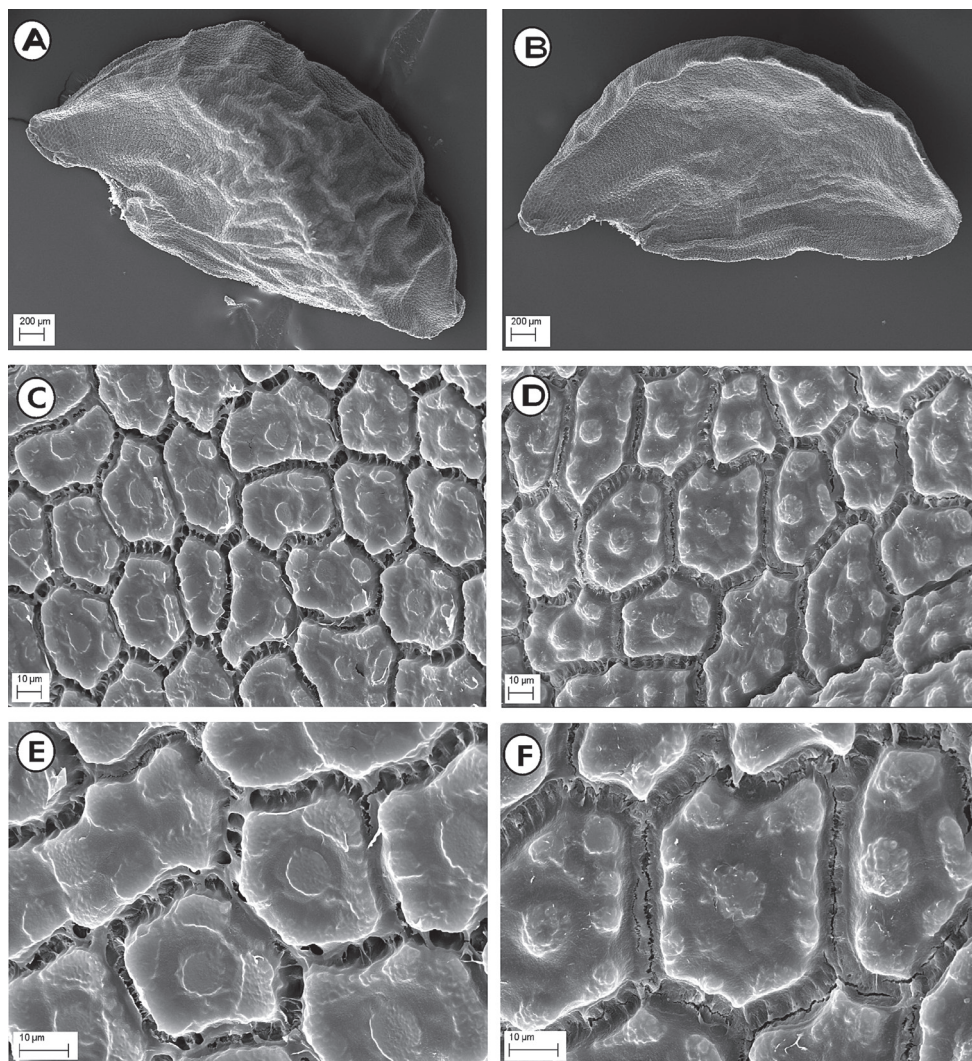
Figure 5. SEM micrographs of the seed coat of *Allium albanicum*. **A** Seed (dorsal face, 30×) **B** Seed (ventral face, 30×) **C** Seed coat (central part of dorsal face, 600×) **D** Seed coat (central part of ventral face, 600×) **E** Seed coat (central part of dorsal face, 1200×) **F** Seed (central part of ventral face, 1200×). Photos from material of type locality (CAT).

Dimopoulos et al. (2013) and personal herbarium surveys, *A. meteoricum* is a Greek endemic, circumscribed to northern and central Greece and further populations reported in other Greek sites or different territories cannot be referred to this species. Therefore, the remaining Albanian populations referred to as *A. meteoricum* should also be checked in detail as regards their taxonomic attribution.

Additional specimens examined. ALBANIA. In humidis collinis serpentinum ad Renci distr. Scutari, 11 June 1897, *Baldacci 85a* (BM, G); In humidis collinis serpentinii ad Renci distr. Scutari, June 1897, *Baldacci 355* (WU); Nordost Albanien,
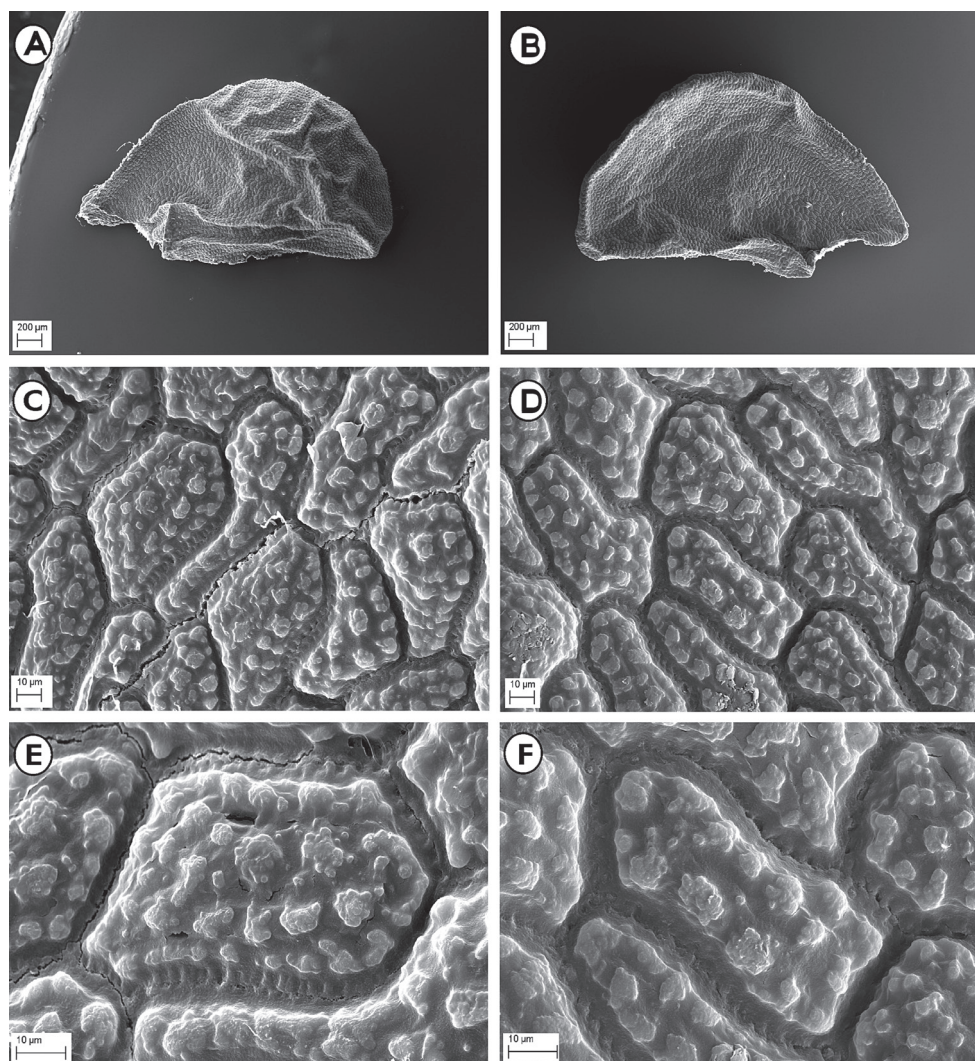
Figure 6. SEM micrographs of the seed coat of *Allium meteoricum*. **A** Seed (dorsal face, 30×) **B** Seed (ventral face, 30×) **C** Seed coat (central part of dorsal face, 600×) **D** Seed coat (central part of ventral face, 600×) **E** Seed coat (central part of dorsal face, 1200×) **F** Seed (central part of ventral face, 1200×). Photos from material of type locality (CAT).

auf Felsen in der subalp. Region des Pastrik ca. 1200 m elev., 31 July 1914, *Dorfler 593* (WU); Nord Albania, Umgebung von Shkodra Abhänge des kleinen Bordans alt. Serpentin, 8 June 1916, *Janchen s. n.* (WU); Hasi Pastrik an Felsen des westlichen Ausläufers, ca. 1200 m elev., 22 July 1918. *Dorfler 908* (BM, K, W, WU).

Examined specimens of *Allium meteoricum*. GREECE, Thessalia superior in collibus circa monasteria Meteora supra Kalabaka (Aeginium veterum), substrata diluviali e saxis conglomeratis, 15/16 July 1885 *Heldreich s. n.*, sub *Allium meteoricum* Heldreich & Haussknecht sp. nova (WU Herbarium Halacsy); this specimen, already
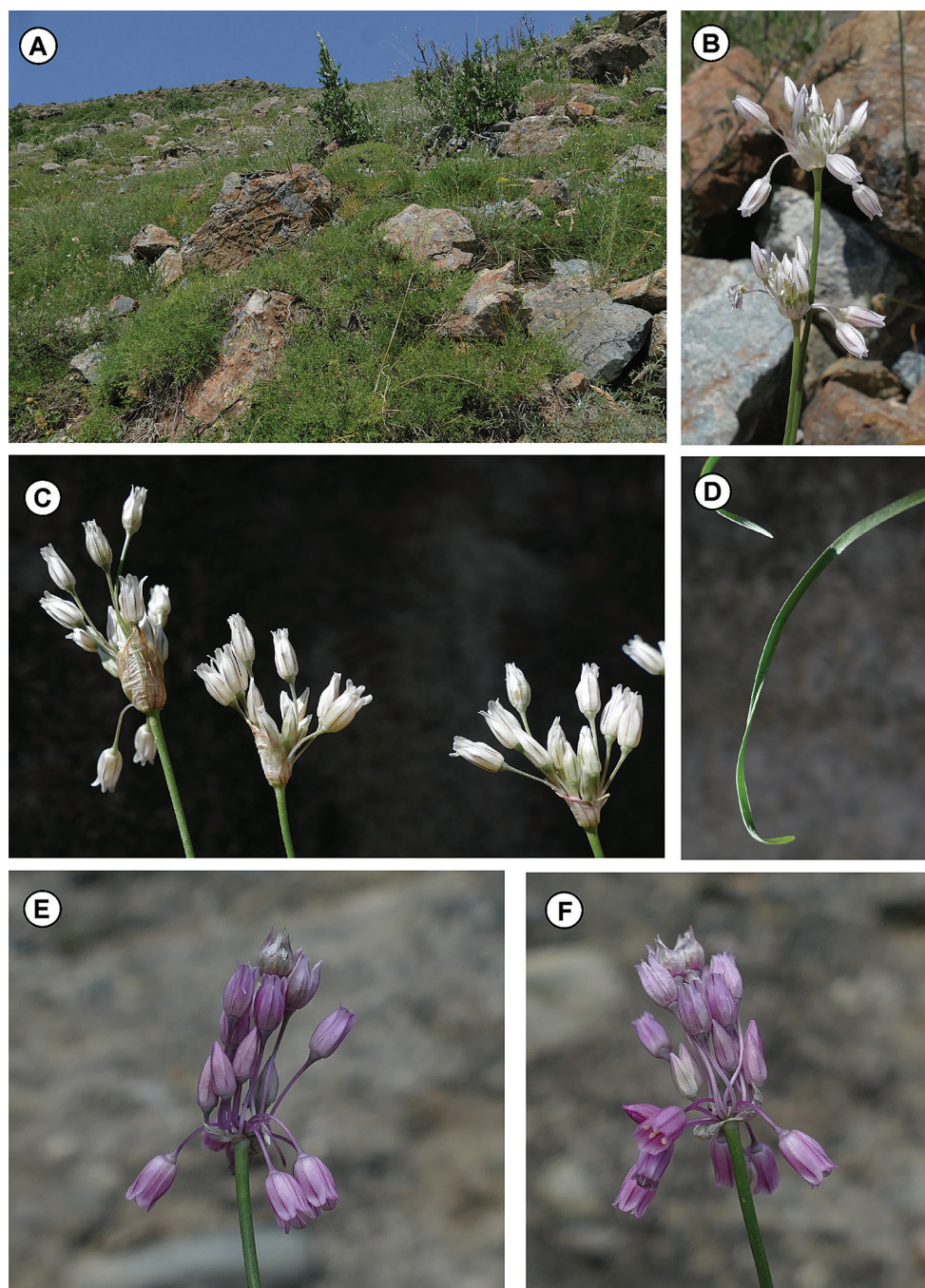
Figure 7. Phenological features of *Allium albanicum* and *A. meteoricum*. **A** Growing habitat of *A. albanicum* in the locus classicus (Albania) **B** Individuals of *A. albanicum* from the locus classicus **C** *A. albanicum* cultivated material in Botanical Garden of Catania **D** Leaf of *A. albanicum*, cultivated material **E, F** Individual of *A. meteoricum*, from Meteora (Greece). Photos by S. Cambria.

quoted by Brullo et al. 2001 as a type of *A. meteoricum*, is more completely reported and here correctly designated as lectotype of *Allium meteoricum*. Thessalia, Trikkala at Meteora above Kalambaki, sunny rocks, 29/06/2018, *S. Brullo & S. Cambria s. n.* (CAT); for other examined specimens, see Brullo et al. (2001).

Discussion. For its general habit and some features such as flat leaves, spathe valves very short, 3–5 nerved, briefly appendiculate, umbel laxly subglobose, perigon cylindrical-urceolate, stamens not exserted, ovary with evident nectariferous pores, the populations of *A. albanicum* were previously referred to as *A. meteoricum* (Halacsy 1904, Hayek 1932, Bornmüller 1933, Stearn 1978, 1980, Meyer 2011, Vangjeli 2015, Pils 2016, Barina 2017).

In light of in-depth taxonomical investigations carried out on living and herbarium material, the analysed Albanian populations are well differentiated from those of *A. meteoricum* coming from the locus classicus, formerly studied by Brullo et al. (2001). Table 1 summarises the most relevant morphological characters differentiating the two species, which mainly consist in the different size and colour of bulbs and tepals, length of the scape covered by the leaf sheaths, shape of spathe valves, colour and size of stamens, ovary and capsule and the shape of nectariferous pores. In particular, *A. meteoricum* differs from *A. albanicum* in having larger bulbs with blackish-brown outer tunics, stem covered up to 1/2 of its length by the leaf sheaths, free spathe valves, with appendage up to 4 mm long, tepals purplish-pink, up to 7.5 mm long, smooth at the apex, staminal filaments longer, whitish, annulus longer, anthers yellow, apiculate at the apex, ovary green, smooth, with much smaller nectariferous pores and smaller capsule. Other relevant differences concern the leaf anatomy, since the leaf cross-section of *A. meteoricum* (cf. Brullo et al. 2001, fig. 11A) is characterised by a thinner cuticle, cells of palisade tissue with uniform size along the entire perimeter, spongy tissue markedly lacunose in the centre and with few vascular bundles in the abaxial face.

According to previous research data (Stearn 1978, Tzanoudakis 1983, Brullo et al. 2001), *A. meteoricum* and *A. albanicum* share the same diploid chromosome complement with $2n = 16$ and their karyotypes are prevalently constituted by more or less metacentric chromosomes (arm ratio less than 1.67), except for one submetacentric pair, microsatellited in the short arm. The chromosome formulae are also rather similar, with some differences regarding the proportion of *m* and *msm* chromosomes, which are, respectively, 10 and 4 in *A. meteoricum*, contrary to 8 and 6 in *A. albanicum* and the number of recognisable satellited chromosomes, consisting in three pairs of chromosomes for *A. meteoricum* (vs. 4 pairs for *A. albanicum*). The high morphological chromosome homogeneity and karyotype symmetry, rather common in closely allied *Allium* species, accounts for the overall karyological similarity between the two species, with no statistically significant differences in their karyomorphometric parameters (Fig. 3).

Based on literature (Stearn 1978, 1980, Tzanoudakis 1983, Tzanoudakis and Vosa 1988, Brullo et al. 2001), *A. meteoricum* was included in the sect. *Scorodon* Koch, but as highlighted by Brullo et al. (2018), this traditional section is actually an assemblage of various and well-differentiated phylogenetic lineages (see Fritsch and Friesen 2002, Friesen et al. 2006, Nguyen et al. 2008, Hirschegger et al. 2010, Li et al. 2010).

In particular, the sect. *Scorodon* s.str., typified by *A. moschatum* L., now belongs to the subgen. *Polyprason* Radić, which groups rhizomatous species (Friesen et al. 2006, Fritsch et al. 2006b), rather than to subgen. *Allium*, to which *A. meteoricum* and *A. albanicum* clearly belong. Effectively, there are several species previously included within the sect. *Scorodon* s.l. which require a taxonomic reassessment, consisting in the recognition of a distinct new section of the subgen. *Allium*, herein proposed and named as sect. *Pseudoscorodon*.

Allium subgen. *Allium* sect. *Pseudoscorodon* Brullo, C. Brullo, Cambria, Giusso & Salmeri, sect. nov.
urn:lsid:ipni.org:names:60478501-2

Type. *Allium obtusiflorum* DC in Redouté (1805).

Diagnosis. Bulbus solitarius vel bulbilliferous, sine basali rhizomate, folia glabra vel pilosa, numquam filiformes, plerumque spathae valvae umbella breviores, persistentes, saltem 3-nervatae, staminum filamenta complanata inferne, interiores saepe 1–2 cuspidibus praedita, ovarium nectariferis poris bene evolutis, plica membranacea praeditis, partim nectariferum porum tegente.

Description. Bulb solitary or bulbilliferous, leaves glabrous to hairy, never thread-like, spathe valves persistent and usually shorter than the inflorescence, at least 3-nerved, stamen filaments flattened and widened in the lower part, the inner ones often uni-bicuspidate, ovary with well-developed nectariferous pores, bordered by a membranous plica, partly covering the nectariferous pore.

Note. Based on current knowledge (Stearn 1978, 1980, Brullo and Pavone 1983, Pastor and Valdes 1983, Brullo and Tzanoudakis 1989, Tzanoudakis and Kollmann 1991, Brullo et al. 1992a, 1992b, 1993, 1994, 2018, Trigas and Tzanoudakis 2000, Khedim et al. 2016), the following species, all having a Mediterranean distribution, can be included in this new section, in addition to *A. meteoricum* and *A. albanicum*: *A. chalkii* Tzanoud. & Kollmann, *A. chrysonemum* Stearn, *A. erythraeum* Griseb., *A. franciniae* Brullo & Pavone, *A. grosii* Font Quer, *A. lagarophyllum* Brullo, Pavone & Tzanoud., *A. maniaticum* Brullo & Tzanoud., *A. obtusiflorum* DC., *A. reconditum* Pastor, Valdes & Munoz, *A. rhodiacum* Brullo, Pavone & Salmeri, *A. rouyi* G. Gautier, *A. runemarkii* Trigas & Tzanoud., *A. seirotrichum* Ducellier & Maire, *A. thessalicum* Brullo, Pavone, Salmeri & Tzanoud., *A. trichocnemis* Gay and *A. valdecallosum* Maire & Weiller. Amongst these species, we designated as type of the new section *Allium obtusiflorum*, since it is the oldest known species within this group and a good representative of the new section.

Based on the descriptions and related iconographies, all of these species share the set of discriminant features that characterise the new section and distinguish it very well from all the known sections of the subgenus *Allium* (Friesen et al. 2006, Khassanov et al. 2011). Altogether, these species markedly differ from *A. moschatum* and consequently from the sect. *Scorodon* s. str., since the latter shows bulbs with a short basal rhizome, 1–3 mm long (Fritsch et al. 2006b), filiform leaves, spathe valves usually 1-nerved,

the larger one rarely obscurely 3-nerved, subulate stamen filaments, ovary with well-developed nectariferous pores which are almost fully covered by a membranous plica.

In order to highlight the morphological similarities and differences amongst the species of the new section, the following analytic key is provided.

Key to the species referable to the sect. *Pseudoscorodon*

1	Leaves hairy	**2**
–	Leaves glabrous or subglabrous	7
2	Tepals and stamen filaments greenish-yellow........................	**3**
–	Tepals and stamen filaments white to pink or purplish............	**5**
3	Tepals thickened at the base, 2.5–3.2 mm wide. Inner stamen filaments with 1–2 cusps at the base. Capsule 5–5.5 mm long	**A. valdecallosum**
–	Tepals not thickened at the base, 1.5–2.5 mm wide. Stamen filaments all simple. Capsule 3.5–4(4.5) mm long..............................	**4**
4	Leaf blade 0.5–1 mm wide. Umbel fastigiate, 3–4.5 mm long. Stamen filaments exserted	**A. chrysonemum**
–	Leaf blade 1.5–2 mm wide. Umbel expanded, 4–6 mm long. Stamen filaments included	**A. rouyi**
5	Spathe valves much shorter than umbel. Perigon 4.5–6 mm long. Stamen filaments all simple, exserted...............................	**A. reconditum**
–	Spathe valves slightly shorter than umbel (sometimes subequal). Perigon 6–8 mm long. Stamen filaments included, the inner ones with two cusps in the middle part	**6**
6	Leaves almost totally densely hairy. Perigon cup-shaped, white to white-pink with tepals 8–8.2 mm long and 3.2–3.3 mm wide...............	**A. seirotrichum**
–	Leaves sparsely hairy in the sheath. Perigon cylindrical-urceolate, pink-lilac with tepals 5–7 mm long and 1–2 mm wide.......................	**A. trichocnemis**
7	Tepals 3.5–5 mm long..	**8**
–	Tepals more than 5 mm long	**12**
8	Outer bulb tunics breaking into parallel fibres, pale brown. Inner stamen filaments with two basal cusps..................................	**A. thessalicum**
–	Outer bulb tunics coriaceous, brown to dark brown. Inner stamen filaments without basal cusps	**9**
9	Spathe valves free. Umbel with flexuous pedicels......................	**10**
–	Spathe valves connate at the base. Umbel with erect or suberect pedicels	**11**
10	Leaves 4–6. Inflorescence dense and compact. Spathe valves both 3-nerved, 5–7 mm long. Anthers purple-violet. Ovary with apical purplish-brown spots. Nectariferous pores about ½ of the ovary length	**A. obtusiflorum**
–	Leaves 2–4. Inflorescence lax. Spathe valves (1)2–4-nerved, 5–20 mm long. Anthers yellowish. Ovary without apical spots. Nectariferous pores about 1/10th of the ovary length....................................	**A. maniaticum**

11 Leaves (3)4–5. Pedicels 2–8 mm long. Tepals whitish-pink. Anthers purplish-violet. Ovary 1.3–2 mm log, with a purplish-brown apical spot...***A. runemarkii***

– Leaves 3. Pedicels 5–20 mm long. Tepals purplish-pink. Anthers pale yellow. Ovary 1.2–1.3 mm long, without apical spot.........................***A. erythraeum***

12 Tepals linear, 5–5.5 × 0.8–1 mm. Ovary 1–1.2 mm long. Capsule max. 3 mm long ....***A. franciniae***

– Tepals linear-elliptical to sublanceolate or oblong-elliptical, 5.5–8 × 1.7–2.5 mm. Ovary 1.5–2 mm long. Capsule 3–5 mm long **13**

13 Spathe valves unilateral, long fused. Inflorescence fastigiate and unilateral....**14**

– Spathe opposite, free or partially fused. Inflorescence expanded, never unilateral..**15**

14 Stem 15–25 cm long. Inflorescence 12–20-flowered. Tepals purplish at the apex. Ovary 1.6–1.8 mm long ....***A. rhodiacum***

– Stem 5–12 cm. Inflorescence 2–12-flowered. Tepals concolorous. Ovary 1.2–1.5 mm long... ***A. chalkii***

15 Stem flexuous. Spathe valves subequal, fused to half of their length. Tepals white-pink. Ovary with very large nectariferous pores...............................**16**

– Stem rigid. Spathe valves unequal, free. Tepals purplish-pink. Ovary with small nectariferous pores **17**

16 Stem 3-leaved, 14–28(30) cm tall. Spathe valves 8–12 mm long, 3–5-nerved. Style 2.7–2.8 mm long ....***A. albanicum***

– Stem 1-leaved, 9–15 cm tall. Spathe valves 5–7 mm long, 1–3-nerved. Style 1 mm long..***A. lagarophyllum***

17 Outer bulb coats blackish-brown. Anthers yellow. Staminal annulus 0.7–0.9 mm high. Capsule 3–3.5 mm long .... ***A. meteoricum***

– Outer bulb coats purplish-brown. Anthers purplish-pink. Staminal annulus 1.5 mm high. Capsule 4–5 mm long ....***A. grosii***

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RESEARCH ARTICLE

Two new records of the fern genus *Coniogramme* (Pteridaceae) from Vietnam

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Abstract

Two new records of the fern genus *Coniogramme* Fée from Vietnam, *C. japonica* and *C. procera*, are presented. In addition, a key to recognising the species of *Coniogramme* in Vietnam is given in this paper.

Keywords

Introduction

Coniogramme Fée, which belongs to the subfamily Cryptogrammoideae in the family Pteridaceae (Christenhusz et al. 2011; Zhang and Ranker 2013; PPG I 2016), is mainly distributed in the tropical and subtropical regions of Asia, extending south to Africa. It is characterised by its large habit with creeping rhizomes and 1–3 pinnate fronds with exindusiate sori borne along the lateral veins.

The genus was first monographed in its modern form by Hieronymus (1916), who accepted 17 species in the world. Dixit and Das (1979) recorded 13 taxa within the genus from India. In the course of the study of pteridophytes in China, some scholars (Ching 1930, 1974, 1982; Shing 1981; Kong 1982; Ching and Liu 1984;

Guo and Chen 2013) have published more than 30 new taxa of *Coniogramme*. Amongst them, Shing (1981) reported 27 new taxa and recognised 39 species and eight varieties in Flora Reipublicae Popularis Sinicae (Shing 1990). In the taxonomic keys, many species are distinguished only by the shape of pinnules, size of serrated teeth from pinnule margins and position of hydathodes at the top of the veins, but these traits are unstable and vary occasionally within normal populations and are difficult to use in practical identification. This taxonomic treatment has been described as the "inclusion of many erroneous new species entirely confusing the variation within species which is easily observable in the field" (Fraser-Jenkins et al. 2015). So far, the genus has long been one of the most problematic fern groups with respect to its specific definition. Fraser-Jenkins (2008) concluded that the taxonomy of *Coniogramme* is very complicated and has been confusing taxonomists in species circumscription.

Although many new taxa have been recorded recently, the fern diversity in Vietnam remains unclear (Lu et al. 2014). In revising the taxonomy of *Coniogramme*, the senior author was fortunate to visit Vietnam and examine the specimens deposited at HNU and HN. Two new records were discovered, i.e. *C. japonica* (Thunberg) Diels and *C. procera* Fée. This work is a contribution to the knowledge of fern flora in Vietnam.

Results

Coniogramme japonica (Thunb.) Diels (1899: 262)
Figures 1, 3

Type. Japan. No exact location. *C. P. Thunberg s.n.* (UPS!).

Specimens examined. Vietnam. Cao Bang Province: Ha Lang District, Dong Loan municipality, vicinities of Ban Lung and Lung Phuc, 22°46'N, 106°44'E, 500–600 m elev., 25 Nov 1998, *L. Averyanov et al. CBL 656* (HN). **Bac Kan Province:** Cho Don District, Ban Thi municipality, Phia Khao village, 22°17'03"N, 105°30'34"E, ca. 800 m elev., 5 Mar 2011, *N.Q. Hieu, N.T. Hiep, P.K. Loc, P.V. The, & N.T. Vinh CPC 1240* (HNU 017603, HNU 017604).

Taxonomic notes. This species is very unique in morphology, differing from other species in its anastomosing veins, which form 1–3 rows of areoles along each side of midrib and hydathodes not extending the base of short serrated teeth. Shing (1981, 1990) considered that pinnules of *Coniogramme japonica* are narrowly lanceolate with a cuneate or rounded-cuneate base and published a similar new species, *C. centrochinensis* Ching, whose pinnules were widely lanceolate with a rounded base. After specimen examination, combined with fieldwork, we found that the morphology of the pinnules was not stable and varied occasionally within normal populations. More research work should be undertaken to elucidate their phylogenetic relationship.

Distribution and habitat. *Coniogramme japonica* is distributed in China, Japan (including Ryukyu Islands), Korea and Vietnam (new record). The species usually grows in shady wet places at an elevation of about 100 to 2000 m.

Figure 1. *Coniogramme japonica* (Thunberg) Diels **A** one of the voucher specimens **B** portion of a pinnule, showing anastomosing veins **C** morphology and habitat.
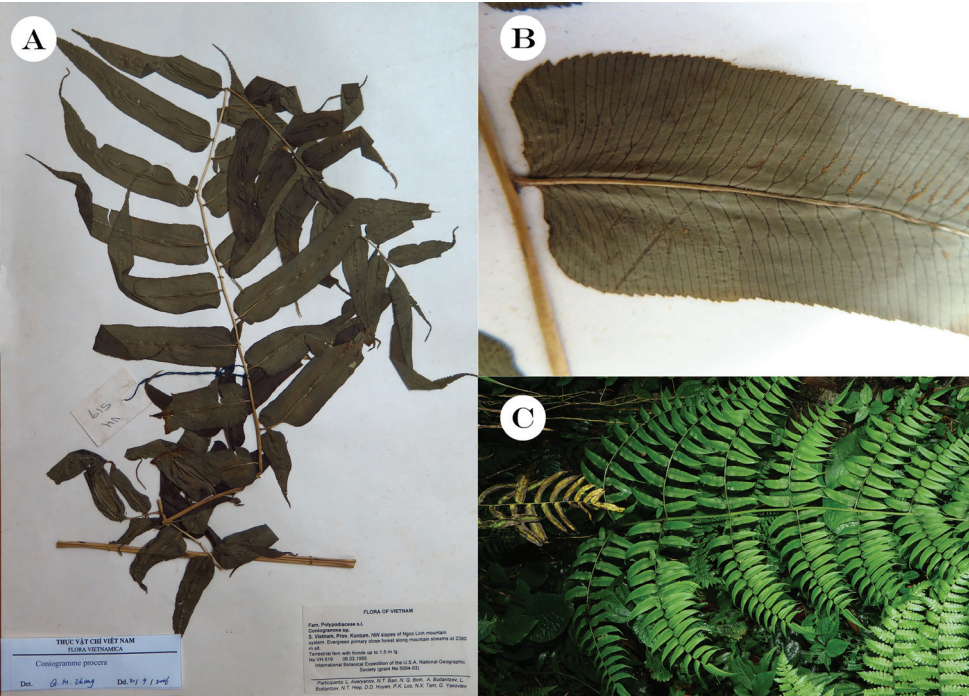
Coniogramme procera Fée (1865: 22)
Figures 2, 3

**Type.** Nepal. April 1821. *Wallich no 3* (K!).

Specimens examined. VIETNAM. **Kon Tum Province:** NW slopes of Ngoc Link mountain, 2380 m elev., 06 Mar 1995, *L. Averyanov et al. VH 519* (HN); W slope of Ngoc Link mountain, 1950 m elev., 10 May 1995, *L. Averyanov et al. VH 1290* (HN).

Taxonomic notes. This species is large and up to 1.8 m tall, differing from other species in its far more dissect laminae, basal pinnae having more than 10 pairs of pinnules, pinnules with rounded-truncate or truncate (sometimes slightly cordate) base and coarsely serrated margin and sori extending only to 1/2–2/3 of veins. Fraser-Jenkins (2008) reported that the species has a characteristically strong odour when the leaves were crushed or broken, similar to that of *Coniogramme fraxinea* (D.Don) Diels.

Distribution and habitat. *Coniogramme procera* was once recorded being distributed in Vietnam in Flora Reipublicae Popularis Sinicae (Shing 1990) and this was followed by Flora of China (Zhang and Ranker 2013). After specimen examination, we found that there were no accounts of *C. procera* in K, BM, P, PE and other major herbaria and we wondered about the basis of this recognition. In addition, the species has never been recorded in the literature on flora of Vietnam (Tardieu-Blot and Christensen 1941;

Figure 2. *Coniogramme procera* Fée. **A** One of the voucher specimens **B** Portion of a pinnule, showing a truncate base **C** Morphology and habitat.
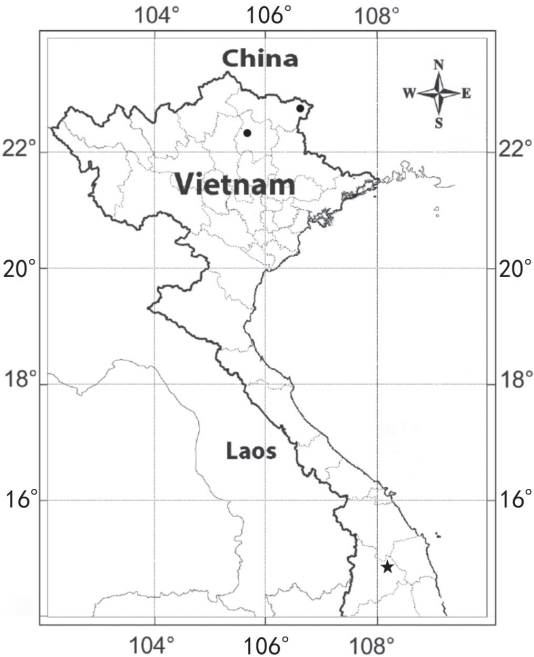
Figure 3. Distribution of *C. japonica* (dots) and *C. procera* (star) in Vietnam.

Pham 1991; Phan 2010), including the recently updated checklist (Phan 2010). *C. procera* is therefore confirmed to be distributed in central Vietnam for the first time. It is also distributed in Bhutan, China, India, Myanmar, Nepal, Philippines and Thailand. The species usually grows by streams in woodlands at a high elevation, about 1400 to 3600 m.

Based on previous literature (Tardieu-Blot and Christensen 1941; Pham 1991; Phan 2010), along with our specimen identification work at HNU, HN and K, six taxa of *Coniogramme* were recognised in Vietnam, namely *C. fraxinea* (D.Don) Diels, *C. intermedia* Hieron., *C. macrophylla* (Blume) Hieron., *C. petelotii* Tardieu, *C. japonica* (Thunberg) Diels and *C. procera* Fée. Their main differences in character were illustrated in the following key:

Key to the species of *Coniogramme* in Vietnam

1	Veins anastomosing to form 1 or 2 continuous rows of areoles on each side of midrib .... ***C. japonica***
–	Veins all free..**2**
2	Pinnule margins entire...**3**
–	Pinnule margins serrate...**5**
3	Hydathodes extending to cartilaginous lamina margin......... ***C. macrophylla***
–	Hydathodes spindle-shaped, not extending to lamina margin **4**
4	Base of pinnules rounded or slightly cordate .... ***C. petelotii***
–	Base of pinnules cuneate or rounded-cuneate..............................***C. fraxinea***
5	Basal pinnae having more than 10 pairs of pinnules; pinnules broadly lanceolate, base rounded-truncate or truncate (sometimes slightly cordate)........ ***C. procera***
–	Basal pinnae having 2–3 pairs of pinnules; pinnules lanceolate, base rounded to rounded-cuneate... ***C. intermedia***

Acknowledgements

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