



The recovery of *Selaginella flaccida* based on morphological and molecular data, with the description of *S. khokhrjakovii* from Indo-China and Peninsular Malaysia

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ABSTRACT

Selaginella delicatula is one of the most widespread and polymorphic species in Asia. Recent molecular-phylogenetic studies have been shown that this species is not monophyletic. Traditionally, two species described from India as *Lycopodium flaccidum* Bory and *L. curvatum* Dalz. have long been recognized as synonyms of *S. delicatula* (Desv. ex Poir.) Alston. However, results of this study based on morphological and micromorphological data, coupled with molecular-phylogenetic evidences is showed that both of these synonyms represent a distinct species and resurrected here under name *S. flaccida* (Bory) Spring and to be distinct from *S. delicatula*. Furthermore, examination of the morphology of specimens collected in Vietnam and Cambodia, combined with additional examination of digital images from various locations in Indo-China and Peninsular Malaysia, has led us to describe a new species (*S. khokhrjakovii* Shalimov **sp. nov.**), which is similar to *S. flaccida* (Bory) Spring from India in size, habitus, general morphology, and lax branch system, but differs in leaf morphology and micromorphological features of mega- and microspores, which is also confirmed by molecular evidences.

Keywords: *Selaginella delicatula*, taxonomy, morphology, spore morphology, synonymy

РЕЗЮМЕ

Шалимов А.П., Зайков В.Ф., Калюжный С.С., Чжан М.-Х., Чжан С.-Ч. Восстановление *Selaginella flaccida* на основе морфологических и молекулярных данных, с описанием *S. khokhrjakovii* из Индокитая и полуострова Малайзия. *Selaginella delicatula* – один из самых распространенных и полиморфных видов в Азии. Недавние молекулярно-филогенетические исследования показали, что этот вид не монофилетичен. Традиционно, два вида описанных из Индии: *Lycopodium flaccidum* Bory и *L. curvatum* Dalz. давно признаны синонимами *S. delicatula* (Desv. ex Poir.) Alston. Однако результаты, основанные на данных морфологии и микроморфологии, в сочетании с молекулярно-филогенетическими доказательствами показали, что оба этих синонима представлены самостоятельным видом и восстанавливаются здесь под названием *S. flaccida* (Bory) Spring и отличаются от *S. delicatula*. Более того, изучение морфологии образцов, собранных во Вьетнаме, и Камбоджа, в сочетании с дополнительно изученными цифровыми изображениями из различных мест Индокитая и полуострова Малайзия, привело нас к описанию нового вида (*S. khokhrjakovii* Shalimov **sp. nov.**), который схож с *S. flaccida* (Bory) Spring из Индии в размере, габитусе, общей морфологии, и рыхлых веточках, но отличающиеся морфологией листьев, признаками микро морфологии мега- и микроспор, что также подтверждается молекулярными данными.

Ключевые слова: *Selaginella delicatula*, таксономия, морфология, морфология спор, синонимика

The genus *Selaginella* P. Beauv. (Selaginellaceae Willk.) is the largest genus within lycophytes with a cosmopolitan distribution, which mostly occurs in tropical and subtropical areas around the world. The genus is most diverse present in the tropical and subtropical Old and New Worlds. Most authors nowadays accept ca. 700–800 species (Jermy 1986, Valdespino 1993, Zhang et al. 2013, Zhou et al. 2015, PPG I 2016; Weststrand & Korall 2016, POWO 2023), but the boundaries of some groups of species remain unclear, although a molecular-phylogenetic studies have been the subject of several recent studies (Arrigo et al. 2013, Zhou et al. 2015a, Weststrand & Korall 2016, Zhang et al. 2020).

During herbarium research in two Moscow herbaria (i.e., A.K. Skvortsov Herbarium of the Main Botanical Garden of the Russian Academy of Sciences (MHA) and Syreyschchikov Herbarium of the Moscow State University

(MW, Russia), we discovered a few herbarium specimens from Vietnam and Cambodia that were not familiar to us.

Further study of the morphology of these samples, the study of flora and publications devoted to the study of *Selaginella* species from Indochina and Malaysia, and the analysis of digital images from GBIF made it possible to understand that the samples found at MW and MHA are closely related to *S. delicatula* (Desv. ex Poir.) Alston, which is a widespread species in Asia. The distribution range of this species extends from the western and southern coasts of India, further to the north of Bhutan, most of China, the entire territory of Indo-China, Malaysia, Indonesia, the Philippines, and up to New Guinea and Polynesia (Wong 1983, 2010, Zhang et al. 2013, Fraser-Jenkins et al. 2017, Chang et al. 2012). A critical analysis of literary sources (Ridley 1919, Alston 1934a, b, 1935, 1945, 1951, Iwatsuki

1975, 1988, Tagawa & Iwatsuki 1979, Dixit 1992, Ghosh et al. 2004, Chang et al. 2012, Fraser-Jenkins et al. 2015, 2017, Wong 1983, 2010, Zhang et al. 2013), did not allow us to get closer to the definition of the species. Further analysis of all synonyms associated with the name of *S. delicatula* s.l. showed that the specimens that are closest morphologically are the two species described from India under the names *Lycopodium flaccidum* Bory (Bory 1833) and *L. curvatum* Dalz. (Dalzell 1852). In taxonomic revisions of the genus for several floras, Alston (1934a, b, 1935, 1945, 1951) recognized *L. flaccidum* and *L. curvatum* as synonyms of *S. delicatula*, and his treatment has been broadly accepted (Dixit 1992, Zhang et al. 2013, Fraser-Jenkins et al. 2015, 2017).

Recent molecular-phylogenetic studies of *Selaginella* (Zhou et al. 2015a) showed that *S. delicatula* form a monophyletic subclade, however, results of the study performed by Weststrand & Korall (2016) and later Zhang & Zhang (2021) showed this species as nonmonophyletic. The search and study of the samples used in the study performed by Weststrand & Korall (2016) allowed us to limit our search to the sample *S. delicatula* (B) "P. Korall 2006:56 (S)", a sample of which we managed to find in the DUKE herbarium (DUKE10152423). The sample used in the molecular phylogenetic study by Weststrand & Korall (2016) had some common features with the samples we found.

Comparison of digital images of *S. delicatula* specimens collected from different localities in Asia and India with type material and analyzed protologue information showed those representing *S. delicatula* from India and named *S. flaccida* (Bory) Spring could be resurrected and distinguished from *S. delicatula* on the basis of several morphological characters recognized in this study. Further investigation showed that specimens collected from Vietnam and Cambodia, with additional re-examination of digital images from different locations in Indo-China and Malaysia, is a new species (*S. kbokbrjakovii*) as described below, which has the same habitus and simple lateral branches as in *S. flaccida* but differs in some morphological and micromorphological characters.

MATERIALS AND METHODS

Morphology

This study was based on morphological analysis of specimens deposited at MHA, MW, and PE and also additionally analyzed digital images from online databases such as JSTOR Global Plants (<http://plants.jstor.org>), Chinese Virtual Herbarium (<http://www.cvh.ac.cn/>), and GBIF (Global Biodiversity Information Facility, <http://www.gbif.org>), including different herbariums such as BSI, DUKE, H, K, L, MICH, MO, NY, P, PH, UC, and US (acronyms according to Thiers 2023), were carefully analyzed and studied. All morphological characters were observed and photographed with an Olympus LC30 camera connected to a stereomicroscope (Olympus SZX7) and computer, measurements were done by D 3.10 (<http://www.nikoninstruments.com>). Digital images of close-up morphology features of the type specimens of *Selaginella flaccida* (P00677428) were provided by the Muséum national d'Histoire naturelle (MNHN; Paris, France).

Spore surfaces were observed using scanning electron microscopy (SEM) without treatment in herbarium spe-

cimens. The spores were taken from mature sporangia, mounted on double-sided sticky tape, and sputter-coated with gold palladium. Spores were photographed and measured under different magnifications using a Hitachi – S3400 N at 10–20 kV in the Shared research facilities of microscopy and X-ray spectroscopy of the Institute for Water and Environmental Problems SB RAS (Barnaul, Russia). The morphological terminology of spores followed Lellinger (2002) and Zhou et al. (2015). The samples used for spore morphology studies of *S. kbokbrjakovii* were obtained from Savinov s. n. (paratype) and Khokhryakov s. n. (holotype) from MHA. For *S. flaccida*, the description of the mega- and microspores was taken from Singh et al. (2014, 2016) for Indian species under the name *S. delicatula*.

Phylogenetic analyses

Total genomic DNA of one sample from the new species was extracted from herbarium specimen using the Diamond DNA plant genomic DNA extraction kit (ABT, Russia) following the manufacturers protocols. Primers, PCR condition of one chloroplast genes (*rbcl*), and the phylogenetic analysis was conducted as described in Shalimov et al. (2019). Amplified fragment were purified with using MAXLIFE MagnetDNA magnetic particles (MVM-Diagnostic, Russia) according to the manufacturers protocol. For the phylogenetic position of the new *Selaginella*, inside *S. delicatula* group, a total of 21 accessions representing 5 species of *S. delicatula* group were included, *S. dianzhongensis* X.C. Zhang were included as outgroup taxa. Matrix included 17 accessions from Zhang & Zhang (2021) representing 3 species of *S. delicatula* group, *S. delicatula* 'B' from Weststrand & Korall (2016), and one accession of *S. delicatula* from India. Maximum likelihood (ML) and Bayesian inference (BI) methods were used to reconstruct the phylogenetic trees. ML analyses were performed using RAxML v.7.2.6 (Stamatakis 2014), and BI analyses were carried out using MrBayes v.3.2.6 (Ronquist et al. 2012). ML and BI analyses were conducted on Cipres (Miller et al. 2010).

RESULT AND DISCUSSION

Examination of morphological characters of specimens from MHA and MW, review of literature sources for Asian *Selaginella* species (Ridley 1919, Alston 1934a, b, 1935, 1945, 1951, Iwatsuki 1975, 1988, Tagawa & Iwatsuki 1979, Dixit 1992, Hō 2003, Ghosh et al. 2004, Chang et al. 2012, Fraser-Jenkins et al. 2015, 2017, Wong 1983, 2010, Zhang et al. 2013, Sun et al. 2014), including the study of the type specimens belonging to synonyms of *S. delicatula*, showed that unknown samples in general morphology were similar to the two synonyms of *S. delicatula* described from India.

Lycopodium flaccidum Bory was validly published by Bory (Bory 1833, non Fée 1872) based on material collected by C.P. Bélanger from "Mahe" on the Côte de Malabar in the West Coast of India (Fig. 1A). In the protologue, Bory (1833) described *L. flaccidum* as a plant with erect stems, weak, ramose, paniculate; leaves arranged in two rows, ovate-acuminate, at the apex subserulate, leaves at apex mucronate; strobili cylindrical, long (Caule erecto, debile, ramoso, paniculato; foliis disticho-complanatis, ovato-acutiusculis



Figure 1 The type specimens: A – *Lycopodium flaccidum* Bory (P00677428), B – *L. curvatum* Dalz. (K000880404)

extrimete subserrulatis, foliis adpressis mucronatis; spicis longiusculis cylindraccis). Then, Spring (1843) and later Kuntze (1891) transferred it to the genera *Selaginella* and *Lycopodioides* and made appropriate combinations.

Several years later, Dalzell (1852) described *Lycopodium curvatum* based on material collected from “India, Crescit in umbrosis prov. Malwan” (Fig. 1B). However, this name is illegitimate being a later homonym of *L. curvatum* Sw. (Swartz 1801). However, Alston (1934a; 1945) considered *Lycopodium flaccidum* Bory and *L. curvatum* Dalz. as synonyms of *S. delicatula*, and this treatment was preserved in subsequent floristic and taxonomic studies.

A detailed examination of digital images of the type material and additional specimens, relevant literature, including the protologue, for these two species of *Lycopodium flaccidum* Bory (P00677428, WAG.1901915) and *L. curvatum* Dalz. (K000880404), showed that descriptions of plants matched in all morphology features (Figs 1, 2). Both of these plants were described from the West Coast of India. These plants are characterized by having suberect main stems, sulcate, transparent, main stems branched from lower part upward, lateral branches lax, ventral leaves oblong, acroscopic base oblique, sub-acute at apex, margin entire at base, minutely denticulate towards apex; dorsal leaves sub-falcate, ovate or



Figure 2 Close-up of the type specimen of *Lycopodium flaccidum* Bory. A – section of upper surface of stem, B – section of lower surface of stem, C – strobilus, D – section of strobilus (from C.P. Bélanger, P00677428). Scalebar: 1 mm

oblong-lanceolate, cuspidate at apex, oblique at base, margin entire, denticulate at top; strobili tetragonal, sporophylls uniform, broadly ovate, apex acuminate, margin entire.

Like Indian species, *S. kbokbrjakovii* has the same habitus and lax branches, but its ventral leaves are ovate, margin entire to subentire (with spaced teeth at the margin), apex acuminate; dorsal leaves are narrowly ovate-elliptic or falcate, base oblique-cuneate, margin entire to subentire (with spaced teeth), apex acuminate; strobili are tetragonal, sporophylls are uniform, broadly ovate, apex acuminate, margin entire.

In contrast, *S. delicatula* has similar morphological features of leaves and strobili in shape and structure with species mentioned above. However, it has a more robust main stem, lateral branches are denser and regular, in combination with secondly and thirdly placed branches, form a feather-like appearance. A morphological comparison among these three species is presented in Table 1.

Micromorphology of spores

Comparison of our results for *S. kbokbrjakovii* with previous studies confirmed the micromorphological differences of mega- and microspores between *S. delicatula* and *S. flaccida* (in previous studies as *S. delicatula* from India, Singh et al. 2014a, b). The proximal and distal surfaces of megaspores of *S. delicatula* are covered with verrucae ornamentation (see Zhou et al. 2015b, p. 23, and Fig. 23I–J; Xia et al. 2013, Liu et al. 1989, Huang 1981, Alston 1951, Zhang & Zhang 2021) with interconnected and fine cribrate ornamentation, although Singh et al. (2014, p. 204, and Fig. 3) has shown that Indian species of *S. delicatula* are covered with verrucae ornamentation "locally, verrucae elongate to form rugulae on the distal surface" on the proximal and

distal sides. The surface with verrucae or forming a honeycomb-like network microstructure. Our observation of *S. kbokbrjakovii* showed verrucae ornamentation of megaspores on the proximal and distal sides, with coarse reticulate ornamentation on the surface, which was covered by bacillate micro-sculptures (Fig. 3 A–D).

Microspores of *S. delicatula* on proximal and distal sides had verrucae ornamentation, surface covered blunt spines on proximal sides, and blunt spines with dense spines on the distal sides (see Zhou et al. 2015b, p. 23, and Fig. 23K–L; Xia et al. 2013, Liu et al. 1989, Huang 1981, Alston 1951, Zhang & Zhang 2021). As reported by Singh et al. (2016), microspores of *S. delicatula* from India (here as *S. flaccida*) had a baculate ornamentation, micro-sculptures are baculate-echinulate. However, Singh et al. (2014b) have not noted the presence of short irregular ridges around the proximal side of microspores (Singh et al. (2014b, Pl. 2-1), which are not typical for Chinese specimens of *S. delicatula* reported by Zhou et al. (2015b). Our observation of microspores of *S. kbokbrjakovii* showed that proximal surface had verrucae or papillate ornamentation around the laesurae zones, with three prominent equatorial ridges (Fig. 3 E, F). The distal side covered are irregular ridges with praemorse at top (Fig. 3 G, H).

A comparison of the results of the study for Indian and Chinese representatives of *S. delicatula* showed clear differences in the morphology of micro- and megaspores and in the structural features of their microsculpture. The analyses of the morphology of spores show that these two species can be separated from *S. kbokbrjakovii* by using the morphological features of mega- and microspores to separate them. A summary of the difference between mega- and microspores of *S. delicatula*, *S. flaccida* (incl. *Lycopodium curvatum*), and *S. kbokbrjakovii* is summarized in Table 2.

Table 1. Morphological comparisons among *Selaginella delicatula*, *S. flaccida* and *S. kbokbrjakovii*.

Characters/Species	<i>Selaginella delicatula</i>	<i>Selaginella flaccida</i> (incl. <i>Lycopodium curvatum</i>)	<i>Selaginella kbokbrjakovii</i>
Habit and size (cm)	erect, suberect, or ascending from suberect, 15–70 decumbent base, 35–50		erect, 7–20(30)
Axillary leaves	shape size (mm) apex margin	oblong-ovate or narrowly elliptic 2.2–3.6 × 0.8–2.4 acuminate entire	ovate or elliptic to broadly elliptic 1.4–2.9 × 0.5–1.8 acute minutely denticulate towards apex
Dorsal leaves	shape size (mm) margin apex base of dorsal leaf	narrowly elliptic or falcate 1.8–2.4 × 0.8–1.2 entire acuminate, acute, mucronate, or cuspidate oblique	broadly ovate or ovate-elliptic 1.4–3.6 × 0.8–2.2 acuminate entire to subentire (with spaced teeth) acuminate to cuspidate oblique-cuneate
Ventral leaves	shape size (mm) apex margin	oblong-ovate or oblong 3–4 × 1.2–1.6 acute or apiculate minutely dentate	oblong-ovate 2–4 × 1–1.9 subacute entire at base, minutely denticulate towards at apex
Strobili	size (mm)	5–10(–20) × 1.4–2.8	6–16(–30) × 2–3
Sporophylls	shape apex margin	broadly ovate acuminate entire	broadly ovate acuminate entire

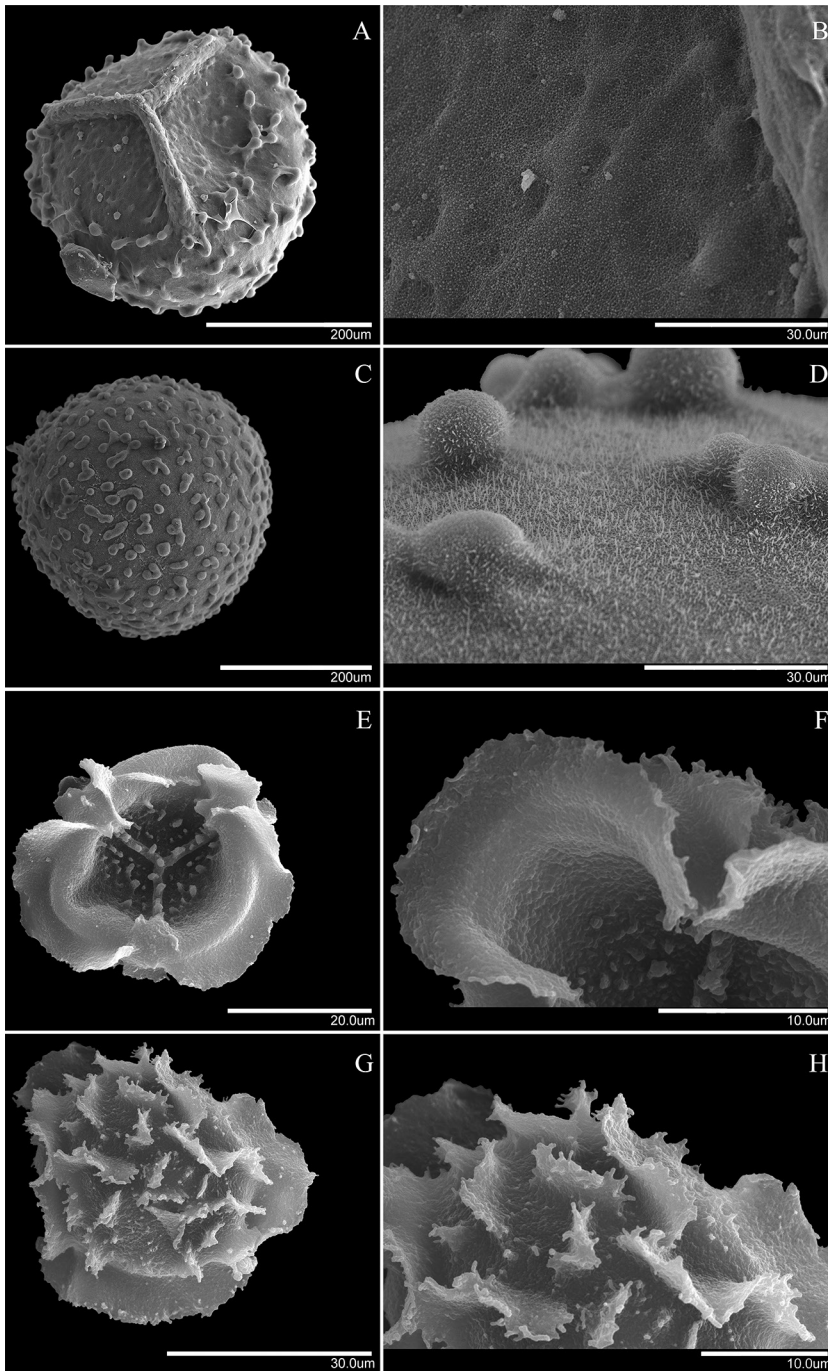


Figure 3 *Selaginella khokhrjakovii* Shalimov **sp. nov.** A – megaspore, proximal face; B – detail of megaspore, proximal face; C – megaspore, distal face; D – detail of megaspore, distal face; E – microspore, proximal face; F – detail of microspore, proximal face; G – microspore, distal face; H – detail of microspore, distal face (A–H, from the holotype, A.P. Khokhryakov s. n. (MHA 0034906))

Phylogenetic analysis

The chloroplast DNA (*rbcL*) matrix had 977 characters, with 41 parsimony informative sites. The topologies obtained from both ML and BI analyses are identical, hence the ML tree is shown in Fig. 4. Unlike the original hypothesis based on morphology characters and habitat, that Peninsular Malaysia (KY023007 as *S. delicatula* "B"), Indo-Chinese (from Vietnam as *S. khokhrjakovii*) and Indian (MK601916 as *S. delicatula*) representatives that all these samples are conspecific. The molecular phylogenetic results

suggested that the new species *S. khokhrjakovii* clustered together with *S. delicatula* "B", from Weststrand & Korall (2016) with strong support ($BS_{ML} = 71$; $PP_{BI} = 1.0$), and nested in subclades with *S. delicatula* and *S. picta*. Moreover, molecular data showed that *S. delicatula* (here as *S. flaccida*) from India, sister to *S. wallichii*. In conclusion, although they are all similar in general morphology, molecular data and spore morphology data have shown that they are two different species.

Taxonomic treatment

Selaginella flaccida (Bory) Spring, 1843, Bull. Acad. Roy. Sci. Bruxelles 10: 145.

≡ *Lycopodium flaccidum* Bory, 1833, in C.P. Bélanger, Voy. Index Or., Both. 2(1): 9, no. 10.

≡ *Lycopodioides flaccida* (Bory) O. Kuntze, 1891, Revis. Gen. Pl. 2: 826.

Type: INDIA "Mahé, sur la terre, dans les lieux ombragés et humides, C.P. Bélanger s.n." (holotype: P [P00677428], image online!; isotype: WAG [WAG.1901915], image online!).

= *Lycopodium curvatum* Dalz., 1852, in Hooker's J. Bot. Kew Gard. Misc. 4: 114, no. 4, nom. illeg., non *L. curvatum* Sw., 1801, J. Bot. (Schrader) 1800(2): 116.

Type: INDIA "Crestis in umbris provinciae Malwan, [no data], N.A. Dalzell s.n." (holotype: K [K000880404], image online!).

Description: Plants terrestrial, evergreen, suberect, 15–70 cm, rhizophores restricted to lower part. Main stems branched from lower part upward, branches copious, lax; thick, fleshy, sulcate, pale-green to stramineous on drying, 0.8–3 mm in diam. in lower part, apex of main stem not blackish, primary leafy branches 6–10 pairs, simple or once pinnately branched, secondary branches not forked, branchlets lax, leafy portion of main stem including leaves 5–8 mm wide at middle, ultimate branches 3–5 mm wide including leaves. Axillary leaves on main stems obviously larger than those on branches, axillary leaves on branches ovate or elliptic to broadly elliptic, 1.4–2.9 × 0.5–1.8 mm, base obtuse, margin minutely denticulate towards apex, apex acute. Dorsal leaves on branches contiguous, oblique, elliptic, 1.3–2.4 × 0.5–1.2 mm, not carinate, base oblique, margin entire, apex acuminate to cuspidate. Ventral leaves on branches contiguous to imbricate, oblong-ovate, 2–4 × 1–1.9 mm, base oblique, margin entire at base, minutely denticulate towards apex, apex subacute. Strobili solitary, terminal, compact, tetragonal, lax, 10–20(30) × 1–2 mm; sporophylls uniform, broadly ovate, margin entire, apex acuminate. Microspores brown, baculate, 26–32 μm, micro-sculpture is baculate-echinulate. Megaspores black, surface verrucate, 225–375 μm, micro-sculpture is verrucate or forming a honeycomb-like network.

Distribution: INDIA (Maharashtra, Kerala, Karnataka, Tamil Nadu, Goa).

Table 2. Morphological comparison of mega- and microspores *Selaginella delicatula*, *S. flaccida* and *S. khokhrjakovii*.

Character	<i>Selaginella delicatula</i>	<i>Selaginella flaccida</i> (incl. <i>Lycopodium curvatum</i>)	<i>Selaginella khokhrjakovii</i>
Megaspores			
the proximal and distal surfaces	verrucae	verrucae ornamentation (locally, verrucae elongate to form rugulae on the distal surface)	verrucae
micro-sculptures	interconnected and fine cribrate ornamentation	verrucate or forming a honeycomb-like network	coarse reticulate ornamentation with bacillate micro-sculptures
equatorial × polar axis (µm)	(238.1–350.7) 309.1 × 254.9 (217.4–281.4)	225–375 × n/d	(214.8–392.2) 341.7 × 320.5 (174.8–368.0)
Microspores			
the proximal surfaces	verrucae and blunt spines	baculate	verrucae or papillate
the distal surface	blunt spines with dense spinules	baculate-echinulate	prominent equatorial ridges, irregular ridges with praemorse at top
equatorial × polar axis (µm)	(18.65–26.69) 21.90 × 12.53 (10.19–14.86)	26–32 × n/d	(27.4–46.2) 38.4 × 21.4 (18.4–26.5)

Habitat. In shade, on moist soil, at sloping grounds or on roadside banks, or near streams, in a semi-evergreen forest at 100–1000 m.

Specimens examined: INDIA: KARNATAKA STATE: Hasan distr.: “1 km below bridge at bottom of Bisle ghat. In shade, on sloping grounds, in a semi-evergreen forest at 300 m, 3 XII 1970, C. Saldanha, T.P. Ramamoorthy, HFP 1155” (MICH-V-1578178); “Bisle ghat. Fairly common slender herbs with green stem. In shade, on moist soil, in a semi-evergreen forest. 6 X 1970, F.M. Jarrett, C. Saldanha, T.P. Ramamoorthy, HFP 867” (MICH-V-1578180; US 01392606); “Mysore, above Kempuhole bridge, 12 IX 1970, F.M. Jarrett, C. Saldanha, HFP 771” (MICH-V-1578179; US 01392603); “Mysore, Panorama point, Bisle ghat, F.M. Jarrett, C. Saldanha, T.P. Ramamoorthy, HFP 673” (US 01392602); Dakshina Kannada distr.: “Kanara Distr., Ullal, 2 miles S of Mangalore at sea level. At foot of low wall close to sea shore, 8 X 1970, M. Frances, F.M. Jarrett, 512” (US 01392495); “Belthangady, 13°07'129"N 75°19'474"E, 26 XI 2016, D. Tripathi, 202501” (BSI0000016317); “Kadambi Falls, 19 XI 2015, D. Tripathi, 197930” (BSI0000016309); “Londa, 3 XI 1970, G.A. Gammie, 15857” (BSI0000016321). KERALA STATE: “Malabar, Concan, regio trop., J.E. Stocks, J.S. Law” (U.1034892); Palakkad distr.: “Palakkad, Dhoni Hill, north of Palghat, South Malabar. Shady grassy glen, alt. 800 ft., 21 XII 1933, E.W. Erlanson, 5228” (MICH-V-1578557); Thiruvananthapuram distr.: “Trivandrum, Lower reaches of Western Ghats above Kallar, towards Ponmudi (east of Trivandrum). By road cut in not too dry semi-evergreen forest at 350 m. Shaded place. Common, erect, stems very pale green, leaves light green, especially beneath, 5 I 1978, K.U. Kramer, G.B. Nair, 6594” (U.1603283); “Ponmudi ghat road, mile 10. Abundant on roadside banks and growing very vigorously, near stream in forest. Main axis stout. 3 XI 1970, F.M. Jarrett, 619” (US 01392605); “Kollar (Trivandrum), 11 X 1958, G.S. Puri, 41338” (BSI000000784). MAHARASHTRA STATE: “Kasare R.F., 20 IX 1968, K.V. Billore, 116781”

(BSI0000000777; BSI0000029031); “Koyna Rest House, Koyna, 30 VIII 1978, R.K. Kochhar, 152503” (BSI0000000778); “Tamboxm in Pennem, 18 XI 1962, R.S. Rao, 84932” (BSI000000781, plant A); “Amboli Ghat, 20 IX 2013, Dr. A. Benniamin, 195263” (BSI0000029022); “Amboli Ghat, alt. 2456 ft., 19 IX 2013, Dr. A. Benniamin, 195257” (BSI0000029023; BSI0000029032); “Koyna Wildlife Sanctuary, 22 IX 2013, Dr. A. Benniamin, 195291” (BSI0000029024); “Chaukul, alt. 2069 ft., 19 IX 2013, Dr. A. Benniamin, 195236” (BSI0000029025; BSI0000029026); “Sagdand, Jawhar Range, 04 IX 1967, K.V. Billore, 11742” (BSI0000029027); “Choukul, 17 IX 2013, Dr. A. Benniamin, 195210” (BSI0000029029; BSI0000029033); “Chalami Forest, 26 X 1967, K.V. Billore, 113030” (BSI0000029030; BSI0000029034). GOA STATE: “Satrem, 25 IX 1970, N.P. Singh, 124581” (BSI0000000785; BSI0000000794); “Dudhsagar along Railway Line, 18 IX 1970, M.Y. Ansari, 124082” (BSI0000000786; BSI0000000791); “Budsari, Goundugarha, 10 XI 1962, R.S. Rao, 84580” (BSI0000000787); “Ordoford, Butpal, 11 XI 1962, R.S. Rao, 84652” (BSI0000000788); “Butpal, Goa, 11 XI 1962, R.S. Rao, 84640” (BSI0000000789); “Dolura, 04 X 1963, M.Y. Ansari, 94158” (BSI0000000790; BSI0000000793);

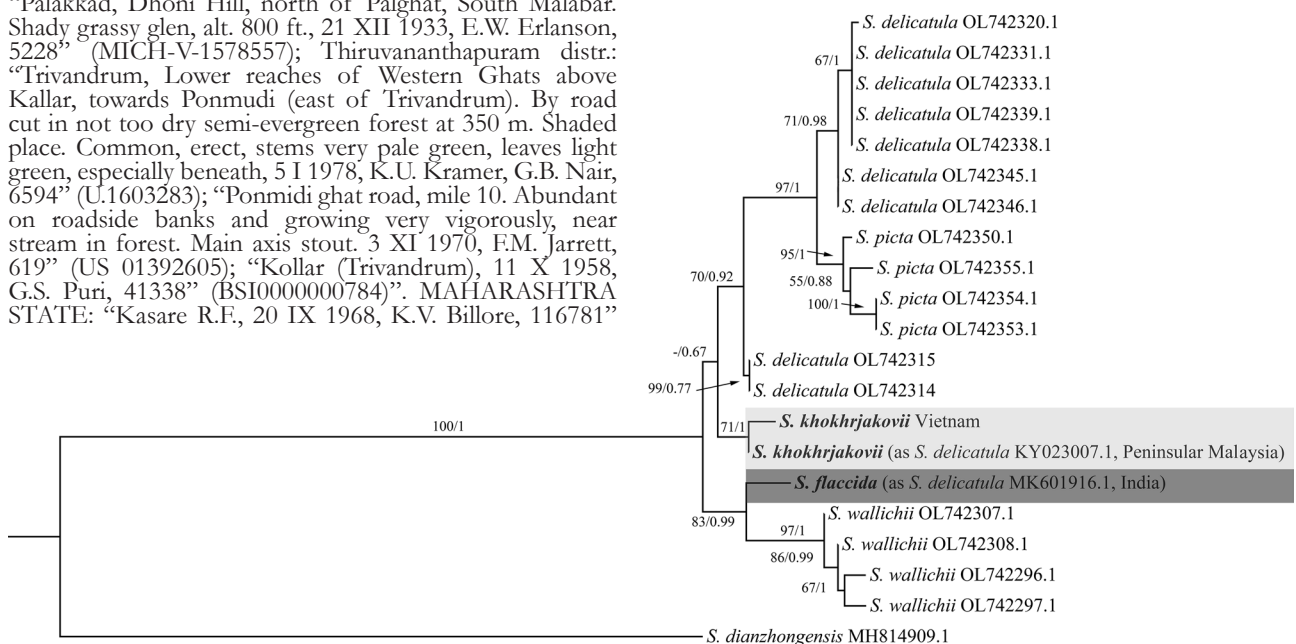


Figure 4 The 50% majority rule consensus tree derived from maximum likelihood showing the position of *Selaginella khokhrjakovii* and *S. flaccida* inside the *S. delicatula* group. Support values (BS_{ML}/PP_{BI}) are shown above the main branches; the dash (–) indicates BS < 50%. The two morphologically comparable species are shown in grey and light grey

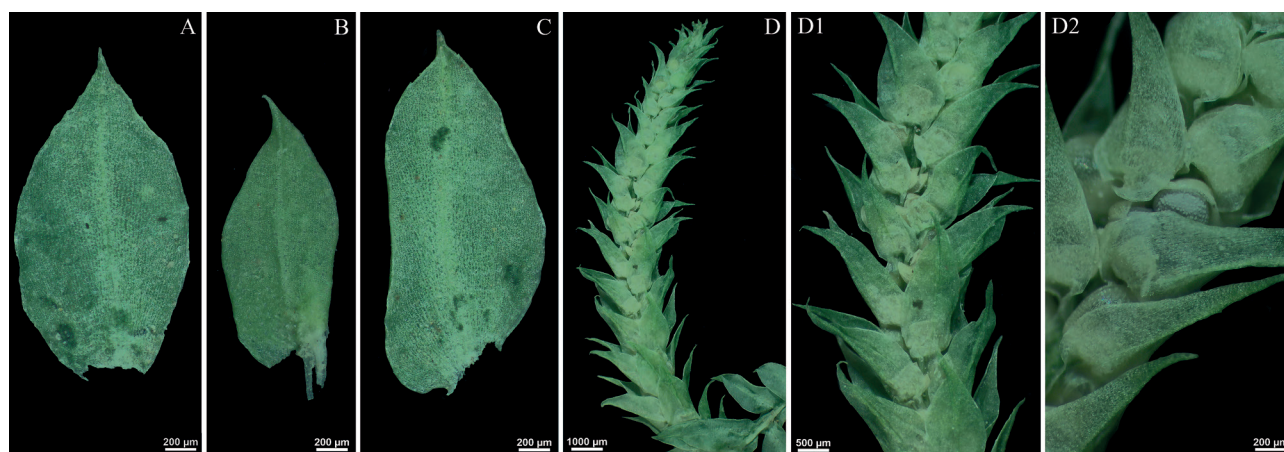


Figure 5 *Selaginella khokhrjakovii* Shalimov **sp. nov.**: A – axillary leaf, lower surface; B – dorsal leaves, upper surface; C – ventral leaf, lower surface; D – strobilus, lower surface, D1 – close-up section of strobilus, D2 – close-up section of strobilus with megaspores, A–D from the holotype, A.P. Khokhrjakov s. n. (MHA 0034906)

“Nanecha Dongar (Codal, alt. 1000 m, 23 IX 1970, N.P. Singh, 123375” (BSI0000000792); “Ordoxford-Tudal, 11 X 1962, R.S. Raghavan, 103503” (BSI0000000795); “Ordoxford-Tudal, 11 X 1964, R.S. Raghavan, 103503” (BSI0000000796; BSI0000000797); “Tamboxm in Pemem, 18 XI 1962, R.S. Rao, 84932” (BSI0000000797); “Dina-Rai Forest, 2 IX 1963, K.C. Kanodia, 89733” (BSI0000000798; BSI0000000799); “Budsari, Goundugarha, 10 XI 1962, R.S. Rao, 84580” (BSI0000000800).

***Selaginella khokhrjakovii* Shalimov **sp. nov.** Figs 3, 5, 6**

Diagnosis. *Selaginella khokhrjakovii* is morphologically similar to *S. flaccida* in habitus, general morphology and branches system, but it is different in dorsal leaves narrowly ovate-elliptic or falcate (vs. oblique or elliptic in *S. flaccida*), with margins entire to subentire or with spaced teeth (vs. entire), and acuminate (vs. acuminate to cuspidate) at apices; ventral leaves ovate (vs. oblong-ovate); megaspores with verrucae ornamentation and coarse reticulate ornamentation with bacillate micro-sculptures (vs. verrucate or forming a honeycomb-like network); microspores on the distal surface with prominent equatorial ridges, irregular ridges with praemorse at top (vs. baculate-echinulate).

Holotype. VIETNAM: “Hô Chí Minh City (Saigon), plantations, zoo territory, 3 XII 1979, A.P. Khokhrjakov s.n.” – [Вьетнам, провинция Хошмин, Сайгон, плантации, территория зоопарка, 3 XII 1979, А.П. Хохряков] (MHA 0034906; **isotypes** MHA 0034907, MHA 0034908).

Description. Plants terrestrial, evergreen, erect, 7–20(30) cm. Rhizophores restricted to lower part of stem. Main stems branched from lower part, stramineous, 0.9–1.2 mm in diam. in lower part, oval, apex of main stem not blackish; primary leafy branches 5–10 pairs, lateral branches simple or pseudopinnate, leafy portion of main stem including leaves 5–7 mm wide at middle, ultimate branches 4–6 mm wide including leaves. Axillary leaves on main stems obviously larger than those on branches, broadly ovate or ovate-elliptic, 1.4–3.6 × 0.8–2.2 mm; base exauriculate, obtuse; margin entire to subentire (with spaced teeth), apex acuminate. Dorsal leaves on branches contiguous, narrowly ovate-elliptic or falcate, 1.5–2.2 × 0.4–1.2 mm, not carinate, base oblique-cuneate, margin entire to subentire (with spaced teeth), apex acuminate. Ventral leaves on main stems contiguous, on branches contiguous to imbricate, slightly ascending, ovate, 1.5–3 × 0.6–2 mm, apex acuminate; basiscopic base rounded, margin entire; acroscopic base oblique, not overlapping stem and branches, margin entire to subentire (with spaced teeth). Strobili solitary, terminal, compact, tetragonal, 6–16(–30) × 2–3 mm; sporophylls uniform, hyaline at margin, broadly ovate, margin entire, apex acuminate; megasporophylls in middle on lower side of strobilus; microsporangia transversely elliptic, rather thin, cells regular; microspores

pale yellow, surfaces are covered with irregular ridges with praemorse at top (27.4–46.2) 38.4 × 21.4 (18.4–26.5) µm, megaspores light yellow to light black-grey, verrucate, (214.8–392.2) 341.7 × 320.5 (174.8–368.0) µm.

Etymology. *Selaginella khokhrjakovii* is named in honor of Soviet and Russian botanist Professor A.P. Khokhrjakov, who made a great contribution to botanical geography, plant systematics, and evolutionary biomorphology.

Distribution and habitat. Terrestrial. In shaded forests along streams or on dry, open places. Alt. 30–800(–1200) m. Myanmar, Thailand, Cambodia, Vietnam, Malaysia, (?)India (Andaman & Nicobar Islands).

Conservation status. Additional results based on the study of digital images of herbarium collections from GBIF.org and other herbariums showed that the new species *S. khokhrjakovii* has a wide distribution area. It is most widely distributed in Thailand and is known from several collections from Myanmar, Cambodia, Vietnam, and Malaysia.

Paratypes. CAMBODIA: SIEM-REAP PROVINCE: “Bantey Srey Temple, on stones near Temple, 13 XII 2008, I.A. Savinov” (MHA 0034909); VIETNAM: Hô Chí Minh City “Hô Chí Minh City (Saigon), In Hevea plantations. 3 XII 1979. A.P. Khokhrjakov s.n.” (MW 0732043; MW 0732044); PROV. ĐÔNG NAI: “Tân Phú distr., National Park Cattien, near the road, 4 II 2021, S.S. Kalyuzhny” (MHA).

Note: The two specimens from the Moscow State University herbarium that we analyzed had a slightly different label that reads, “Vietnam, Ho Chi Minh City, In Hevea plantations”. Both samples were signed by A.P. Khokhrjakov as *Selaginella proniflora*, collection on 3 XII 1979 (MW 0732043), with the second sample lacking information regarding the location of collection (MW0732044). We attribute both of these samples to paratypes, while they could also represent isotypes.

Other material examined (digital images). MYANMAR: “[Eastern Burma], Dalgroin, alt. 600 m, 27 I 1933. H.M. Smith, 571” (US 01392612); “Kyauk-me-taung, Tavoy Distr., shaded slopes at 300 ft, 1938, F.G. Dickason, 8024” (L.3496654); THAILAND: “Northern Siam, valley of the Melang, 31 XII 1932, H.M. Smith, 565” (US 01392610); “Takaw, 21 XII 1932, H.M. Smith, 533” (US 01392611); PROV. MAE HONG SON: “Mae La Noi, Payar, 18°25'N 97°55'E, alt. c. 375 m, deciduous forest along streamlet, terrestrial, 27 XII 1965, E. Hennipman, 3486” (NY2682135; UC1414537); PROV. PHETCHABUN: “Phu Miang, alt. 800 m, On dry slope along new road in open place, 5 X 1967, T. Shimizu, K. Iwatsuki, N. Fukuoka, M. Hutoh, D. Chaiglom, A. Nalampoorn, T-11702” (L.3496629; US 01392597); PROV. CHIANG MAI: “Kang Dan Tao, canyon leading up to Huey Tard from Me Raming, Chiang Dao, alt. 500–750 m, abundant on cut bank of trail in ravine with moist deciduous forest, 7 XII 1957, F.R. Fosberg,



Figure 6 *Selaginella khokhrjakovii* Shalimov sp. nov. Digitized images of holotype: A.P. Khokhrjakov s. n. (MHA 0034906)

39044" (UC1618876); PROV. NAKORN RATCHASIMA: "Prov. Kanchanaburi, Sai Yoke. 14°9'0"N 99°10'0"E, along streamlet in mixed deciduous forest on limestone, alt. ca 150 m, 27 XI 1971, C.F. van Beusekom, R. Geesink, C. Phengkai, B. Wongwan, 3901" (L.3484054; L.3484055); PROV. RANONG: "Kaper dist., Klong Naka Wildlife Sanctuary, tropical rain forest, alt. 30–50 m, 8 XII 1979, T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara, C. Niyomdham, T-26430" (L.3496642; MO-3393838); "Kaper distr., Ban Kam Phuran, open sandy grassland, alt. 30 m, 9°22'0"N 98°25'0"E, 7 XII 1979, T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara, C. Niyomdham, T-26270" (L.3496644; MO-3393834); PROV. TRANG: "Thung Khai, open swampy grassland with spring bogs, sandy acid soil, 7°27'0"N, 99°40'0"E, alt. 50 m, 22 VIII 1995, K. Larsen, S.S. Larsen, C. Tange, R. Moran, C. Niyomdham, P. Puudjaa, 45839" (L.4329271); "Nakawn Sritamarat: lower elevation of Khao Chonh, alt. 100–800 m, on rather dry slope in dense forest, 26 I 1966, M. Tagawa, K. Iwatsuki, H. Fukuoka, T-6699" (US 01392619); "Trang distr., Ban Nam Phari, 20 km north of Trang, limestone hill, alt. 50–200 m, 17 XII 1979, T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara, T. Santisuk, T-27547" (MO-3393831; L.3496638); PROV. SATUN: "Kwan Kah Long distr., near Wam Ran Village, Toong Ngui Subdistrict, alt. 75 m, open disturbed slope, weedy area; limestone bedrock, 7 I 1985, J.F. Maxwell, 85-59" (PH00626132); PROV. SURAT THANI: "Pa Nom Distr., Chong Lom, Khao Sok National Park, evergreen forest on limestone hill, alt. 100–150 m, 12 XII 1979, T. Shimizu, H. Toyokuni, H. Koyama, T. Yahara, C. Niyomdham, T-27123" (MO-3393830). **CAMBODIA:** "Angkor, 14 I 1926, H.M. Smith, 305" (US 01392616). **MALAYSIA:** KEDAH: "Baling. In rubber plantation clearing close to Badak River trailhead, alt. ca 100 m, 5.82360°N 100.46202°E, 29 VIII 2006, P. Korall et al., 2006:53" (DUKE10152423; DUKE10152424; S, n.v.); "Baling. Titi Hayun recreation area, alt. ca 100 m, lowland Dipterocarp Forest, in forest along stream. In high "grass" vegetation. 5.79378°N, 100.40342°E, 29 VIII 2006, P. Korall et al., 2006:56" (DUKE10152425; S, n.v.).

Key to distinguish *Selaginella khokhrjakovii*, *S. flaccida* and related species

1. Main stems 3–5 mm in diam., apical part black when dry; stomata invisible on dorsal leaves *S. picta*
+ Main stems 2–3 mm in diam., apical part not black when dry; stomata on adaxial surface of dorsal leaves visible 2
2. Main stems robust, primary leafy branches long up to 15 cm or more, lanceolate-ovate in shape, secondary branches simple or forked, s.b. closely placed; dorsal leaves oblique, narrowly elliptic or falcate, margin entire; apex acuminate, acute, mucronate, or cuspidate 3
+ Main stems thick, primary leafy branches short 2–8 cm, lax, secondary branches simple or rarely forked, s.b. distantly; dorsal leaves oblique, elliptic, narrowly ovate-elliptic or falcate, margin entire to subentire, apex acuminate to cuspidate 4
3. Lateral branchlets simple or forked, or basal branchlets often forked; dorsal leaves overlapping distally
..... *S. delicatula*
+ Lateral branchlets simple, sometimes with irregular longer branches; dorsal leaves parallel, not overlapping distally *S. wallichii*
4. Ventral leaves oblong-ovate, subacute at apex, margin entire at base, minutely denticulate towards at apex; dorsal leaves, margin entire, apex acuminate to cuspidate
..... *S. flaccida*
+ Ventral leaves ovate, acuminate at apex, margin entire to subentire (with spaced teeth); dorsal leaves entire to subentire (with spaced toothed), apex acuminate
..... *S. khokhrjakovii*

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Appendix

Information of the plant materials used in this study is presented in the following order: taxon name, locality (if available), collection number (if available), rbcL GenBank accession number, * – sequences downloaded from NCBI

Selaginella delicatula (Desv. ex Poir.) Alston, Peninsular Malaysia, P. Korall 2006-56 (S), KY023007.1*; *S. delicatula* (Desv. ex Poir.) Alston, India, –, MK601916.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Hainan, X.C. Zhang 7747 (PE), OL742314.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Yunnan, X.C. Zhang & B. D. Liu 7786 (PE), OL742315.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Yunnan, X.C. Zhang 3018 (PE), OL742320.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Guizhou, X.C. Zhang et al. 7186 (PE), OL742331.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Guizhou, X.C. Zhang et al. 7218 (PE), OL742333.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Guangxi, Y.H. Yan et al. RS68 (PE), OL742338.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Chongqing, J.Q. Sun S19 (PE), OL742339.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Taiwan, YSL5067 (PE), OL742345.1*; *S. delicatula* (Desv. ex Poir.) Alston, China: Fujian, H. Shang & Y. F. Gu SG142 (CSH), OL742346.1*; *S. dianzhongensis* X.C. Zhang, China: Yunnan, Zhang X.-C. 8158 (PE), MH814909.1*; *S. kbokhrjakovii* Shalimov, Vietnam, HỒ Chí Minh City (Saigon), A.P. Khokhryakov s.n. (MHA), OR810627.1; *S. picta* (Griff.) A. Braun ex Baker, Viet Nam, X.C. Zhang & Sino-Vietnam Bot. Exp. 3476 (PE), OL742350.1*; *S. picta* (Griff.) A. Braun ex Baker, China: Hainan, X.C. Zhang 429 (PE), OL742353.1*; *S. picta* (Griff.) A. Braun ex Baker, China: Hainan, X.C. Zhang & Q.P. Xiang 9395 (PE), OL742354.1*; *S. picta* (Griff.) A. Braun ex Baker, Myanmar: Kachin state, T.Y. Nwe TYN225 (NY), OL742355.1*; *S. wallichii* (Hook. & Grev.) Spring, Myanmar: Kachin state, T.Y. Nwe TYN493 (NY), OL742296.1*; *S. wallichii* (Hook. & Grev.) Spring, China: Yunnan, X.C. Zhang & S.Y. Dong 1421 (PE), OL742297.1*; *S. wallichii* (Hook. & Grev.) Spring, China: Guangdong, Y.H. Yan et al. WYD649 (CSH), OL742307.1*; *S. wallichii* (Hook. & Grev.) Spring, China: Guangdong, Y.H. Yan et al. WYD649 (CSH), OL742307.1*.