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Selaginella pseudorepanda (Selaginellaceae), a new spikemoss from southern Vietnam

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Keywords: morphology, new species, phylogenetic analysis, *rbc*L, *Selaginella repanda*, spores.

Summary. A morphological and molecular phylogenetic study of *Selaginella* specimens from Khanh Hoa, Dong Nai, and Dak Lak Provinces of Vietnam, previously identified as *S. repanda*, was conducted. As a result, it was concluded that these specimens represent a new species described here as *S. pseudorepanda*. Morphologically, this species resembles *S. kurzii* and *S. repanda*, but it is easily distinguished from them by having creeping main stems, a contiguous and imbricate arrangement of dorsal and ventral leaves on the main stems and branchlets, margins of ventral and axillary leaves densely long-ciliate, and ovate dorsal leaves with acuminate apex. The molecular phylogenetic analysis resolves *S. pseudorepanda* as a sister to *S. minutifolia*. Moreover, results of the spore morphology study also confirm that *S. pseudorepanda* is a distinct species.

Selaginella pseudorepanda (Selaginellaceae) – новый вид из южного Вьетнама

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Ключевые слова: морфология, новый вид, споры, филогенетический анализ, *rbc*L, *Selaginella repanda*.

Аннотация. Проведены морфологические и молекулярно-филогенетические исследования образцов *Selaginella* из провинций Кханьхоа, Донгнай и Даклак (Вьетнам), идентифицированных ранее как *S. repanda*. В результате был сделан вывод, что эти образцы представляют собой новый вид, который описан здесь как *S. pseudorepanda*. Морфологически он похож на *S. kurzii* и *S. repanda*, но легко отличается от них ползучим основным стеблем, смежным и черепитчатым расположением дорсальных и вентральных листьев на основных стеблях и веточках, вентральными и пазушными листьями длинно реснитчатыми по краю и дорсальными листьями яйцевидной формы с заострёнными верхушками. Молекулярно-филогенетический анализ показал, что *S. pseudorepanda* является сестринским видом к *S. minutifolia*. Кроме того, результаты изучения морфологии спор также подтверждают, что *S. pseudorepanda* является самостоятельным видом.

Introduction

The first treatment of *Selaginella* P. Beauv. in Indochina was performed by Alston (1951), where he recognized 36 species in Vietnam. Later, Pham (1999) recognized 43 species. Since this, several new species and new records have been reported from Vietnam (Wu et al., 2017; Phan et al., 2019; Ye et al., 2020; Zhang et al., 2022; Chen et al., 2023; Shalimov et al., 2024). Recently, Kalyuzhny et al. (2024) reported 54 species of *Selaginella* in Vietnam.

During the study of herbarium collections of *Selaginella* from Southeast Asia at the Herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences (LE), we discovered two sterile specimens from Vietnam that were morphologically similar to *S. repanda* (Desv. ex Poir.) Spring. A subsequent examination of collections at the Vietnamese herbaria allowed us to find several specimens with similar leaves, adding new information on the morphology of the strobili and spores. Further analysis of these samples morphology and review of relevant literature (Alston, 1934, 1945, 1951; Tagawa, Iwatsuki, 1979; Wong, 1982, 2010; Zhang et al., 2013; Fraser-Jenkins et al., 2017; Shalimov et al., 2019; Zhang et al., 2020) indicated that the specimens were most similar to *S. repanda* but differ in some features, such as having densely imbricate ventral leaves and axillary and ventral leaf margins that are more densely long-ciliolate. Additionally, it is well known that *S. repanda* has ascending stems from a decumbent base. However, our examined collections showed that the specimens had creeping main stems. Additional studies of digital images of *S. repanda* from Vietnam at the herbarium of the "Muséum national d'Histoire naturelle" (P) allowed us to conclude that the specimens we found represent a new, undescribed species. Furthermore, our conclusion aligns with the findings of French pteridologist Prince Roland Napoleon Bonaparte (1858–1924), who, 104 years ago, while studying the morphological features of herbarium specimens similar to those we have found, also concluded that they represented a new species. He intended to name and describe them as *S. longiciliata* (non Hieron., 1913), but he never published it. To confirm that the undescribed species is new, we performed macro- and micromorphological comparisons with the closest species, *S. repanda* and *S. kurzii* Baker, as well as phylogenetic analysis of 45 anisosporophyllous *Selaginella* species from mainland Asia, using the plastid marker *rbc*L.

Material and methods

This study was based on morphological analysis of specimens deposited at herbaria CSH, HN, HNU, KUN, LE, MHA, MW, PE, PYU, VNM, and VNMN (herbarium acronyms follow Thiers, 2025), and studies on digital images of selected herbarium sheets deposited in P.

All morphological characters were observed and photographed using an Olympus LC30 camera connected to a stereomicroscope (Olympus SZX7) and a computer; measurements were taken using LCmicro 2.2 software (Olympus).

Spore surfaces were observed using scanning electron microscopy (SEM). The spores were collected from mature sporangia, mounted on double-sided sticky tape, and sputter-coated with a gold-palladium alloy.

Spores were photographed and measured under different magnifications using a Hitachi S3400N at 10–20 kV in the microscopy and X-ray spectroscopy of the Institute for Water and Environmental Problems SB RAS. The morphological terminology of spores followed Lellinger (2002) and Zhou et al. (2015). The samples used for spore morphology studies of *S. pseudorepanda* were obtained from the paratype Tagane et al., No. 304 (VNM00072393).

Phylogenetic analysis

To reconstruct the phylogenetic position, we sampled 79 sequences representing 48 species, downloaded from GenBank (see Supplementary, Table 1 on the journal website). Outgroups were selected based on recent classifications of *Selaginella* (Zhou et al., 2015; Weststrand, Korall, 2016), including *S. kraussiana* (Kunze) A. Braun, *S. laxistrobila* K. H. Shing, *S. nipponica* Franch. et Sav., *S. obovata* S. Y. Dong (with *S. obovata* included as representatives of the *S. bisulcata* – *S. nipponica* clade according to Huang et al., 2022), *S. remotifolia* Spring, and *S. selaginoides* (L.) P. Beauv. ex Schrank et Mart.

Total genomic DNA of two samples 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 plastid genes (*rbc*L), and the phylogenetic analysis was conducted as described in Shalimov et al. (2019). Amplified fragments were purified using MAXLIFE MagnetDNA magnetic particles (MVM-Diagnostic, Russia) according to the manufacturer's protocol.

DNA alignment was performed using MUSCLE (Edgar, 2004) in the MEGA X software (Kumar et al., 2018). Phylogenetic schemes were constructed using Maximum Likelihood (ML) and Bayesian Inference (BI) models. For BI analysis, GTR+G+I was selected as the best-fitting model using the Akaike information criterion (AIC) in the jModelTest2 (Darriba et al., 2012). MrBayes v.3.2.6 (Ronquist, Huelsenbeck, 2003) was used for BI analysis with 5000000 generations (random trees sampled every 1000 generations), discarding the first 25 % trees as burn-in, and a majority-rule consensus tree was obtained along with posterior probabilities (PP). Topology was built using MrBayes. For ML, the program raxmlGUI 2.0 (Edler et al., 2020) was used, with 1000 bootstrap replicates. iTOL webserver (Letunic, Bork, 2024) was employed for tree visualization.

Results

Phylogenetic analysis

The matrix of single plastid marker (*rbc*L) was 969 bp. The topologies obtained from both ML and BI analyses are identical, hence the BI tree is shown in Fig. 1. Our results indicated that two individuals of the new species formed a well-supported clade (PP = 0.97, BP = 84) that is sister to the clade of *Selaginella minutifolia* Spring (PP = 1.0, BP = 78). These two clades are, in turn, sister to the *S. subvaginata* X. C. Zhang et Shalimov clade (PP = 0.95, BP = --), but the new species, described below as *S. pseudorepanda* Shalimov, is quite distinct from the *S. minutifolia* rather than *S. repanda* in morphological characters. Although *S. pseudorepanda* and *S. repanda* share some morphological similarities, our phylogenetic analysis indicates they belong to two different clades (Fig. 1). Furthermore, our results also showed that *S. pseudorepanda* is phylogenetically quite distant from *S. kurzii* (Fig. 1).

Morphological observations
Spore morphology

The micromorphology of spores of *Selaginella kurzii*, *S. pseudorepanda*, and *S. repanda* were observed (Fig. 2). Megaspores of *S. kurzii* had verrucate-reticulate ornamentation on the distal faces (Fig. 2A–C). Zhou et al. (2015) reported that *S. kurzii* megaspore surfaces were covered with large or small verrucae and sometimes vermiculate. In contrast, megaspores of *S. pseudorepanda* are verrucate with irregularly sized verrucae (Fig. 2D–F), the distal surfaces verrucate and finely verrucate (Fig. 2E, F), which is different from the megaspores of *S. repanda* which are reticulate (Fig. 2G–I). It is worth mentioning, however, that other studies have reported three other sculpturing patterns for the megaspores of *S. repanda*: verrucate (Huang, 1981; Minaki, 1984; Chang et al., 2002; Liu et al., 2003; Zhou et al., 2015), reticulate (Singh et al., 2014), and granulate (Wang et al., 2018).

The microspores of these three species are also different. The microspores of *S. kurzii* are verrucate with dense spinulose micro-sculptures (Fig. 2J–L), our results are in accordance with previous studies (Zhou et al., 2015). The microspores of *S. pseudorepanda* are rugulate, with granulate micro-sculptures (Fig. 2M–O). Finally, the microspores of *S. repanda* are finely verrucate with reticulate and blunt spinulose micro-sculptures (Fig. 2P–R), which are in accordance with data previously reported (Liu et al., 2003; Xia et al., 2013; Zhou et al., 2015; Yan et al., 2016; Wang et al., 2018).

The results of the study on the morphology of spores of *S. pseudorepanda* and related species have shown clear differences in their ornamentation and micro-sculpture of both types of spores. These differences are summarized in Table 1.

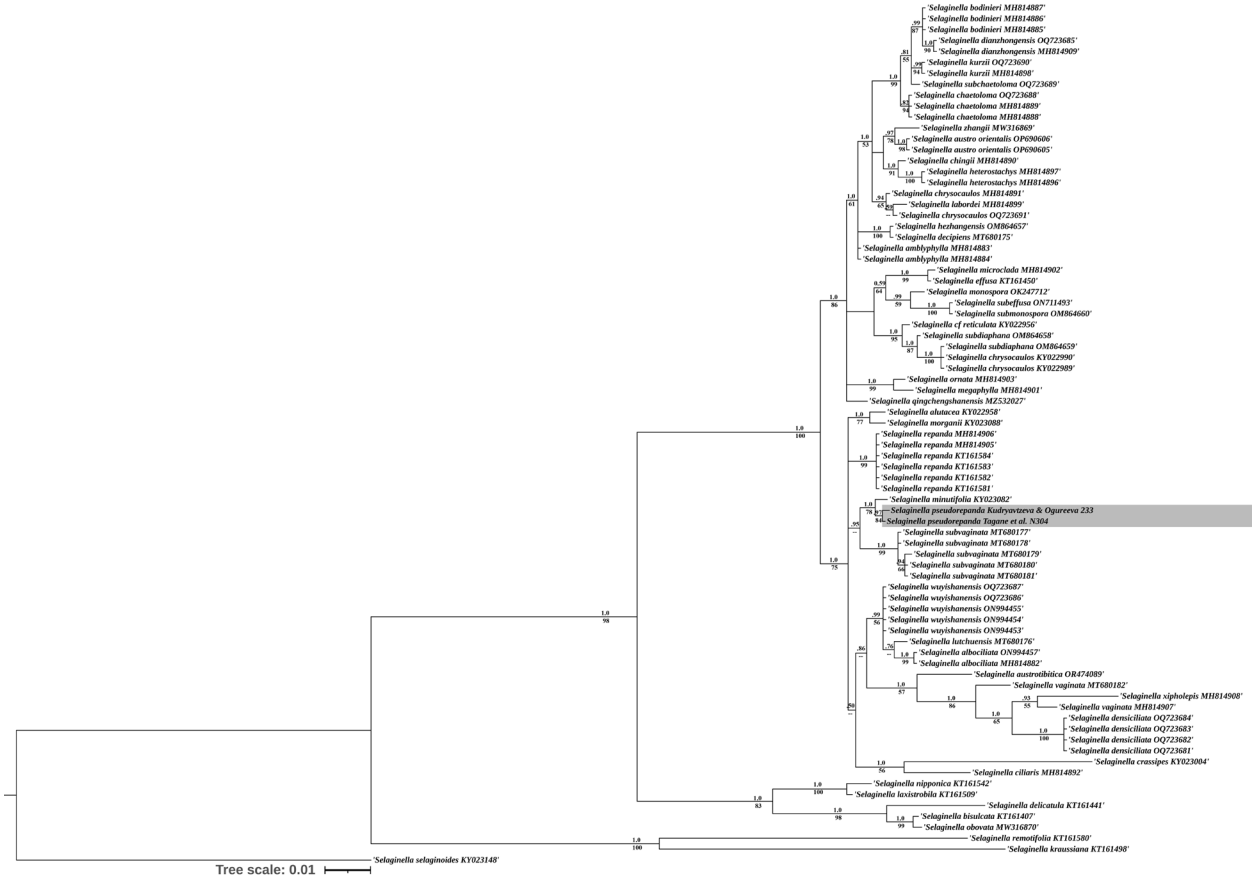

Fig. 1. The Bayesian inference (BI) tree of the new species and related species. Bayesian posterior probabilities and bootstrap supporting values calculated by maximum likelihood (ML) analysis are shown on the branches, respectively; the dash (–) indicates BS < 50 %. The new species name is highlighted in grey.

Taxonomic treatment

Selaginella pseudorepanda Shalimov **sp. nov.** (Figs. 2D–F, 2M–O, 3, 4)

Diagnosis. *Selaginella pseudorepanda* is morphologically similar to *S. repanda* and *S. kurzii*, from which differs by having the main stems creeping (vs. ascending from a decumbent base in *S. repanda* and creeping with erect fertile branches in *S. kurzii*), axillary and ventral leaves margins long-ciliolate from the base to the apex (vs. ciliolate up to the middle part of the leaves in *S. repanda* and *S. kurzii*).

Type. "СРВ [Социалистическая Республика Вьетнам], пров. Phu Khanh [Khanh Hoa]. Hon Tre, 12°14′N, 109°31′E. По сыроватым местам во вторичном низкогорном лесу. 1 X 1990. Е. Кудрявцева, Г. Огуреева. Flora Vietnamica N 233" / "SRV [Socialist Republic of Vietnam], Prov. Phu Khanh [Khanh Hoa], Hon Tre, 12°14′N, 109°31′E. In damp places in secondary lowland forest. 1 X 1990. E. Kudryavtzeva, A. Ogureeva. Flora Vietnamica No. 233" (LE 01284123) (Fig. 3).

Description

Plants terrestrial or epilithic, evergreen or seasonally green, creeping, 5–10(15) cm tall. Rhizophores borne at intervals throughout the length of the creeping stems and branches, borne on the ventral side in the axils of branches. Main stems pinnately branched from near the base upward; primary leafy branches 3–6 pairs, once or twice pinnately branched, secondary branches once or twice forked, branchlets dense, adjacent primary branches on main stem 1–1.5(2) cm apart, leafy portion of main stem including leaves 5–7 mm wide at middle, ultimate branches 3.5–5 mm wide including leaves. Axillary leaves on main stem larger than those on branches, ovate-lanceolate to ovate-triangular, 0.6–1.5 × 0.3–0.8 mm, bases obtuse, margins long-ciliate from the base to near the apex, otherwise distally denticulate, apex acuminate (Fig. 4A). Dorsal leaves symmetrical, ovate, 0.2–1.6 × 0.3–0.8 mm, bases rounded, margins ciliate at base, thereafter denticulate-ciliate along the mid-section to the apex, conspicuously white-margined, apex acuminate (Fig. 4B). Ventral leaves asymmetrical,

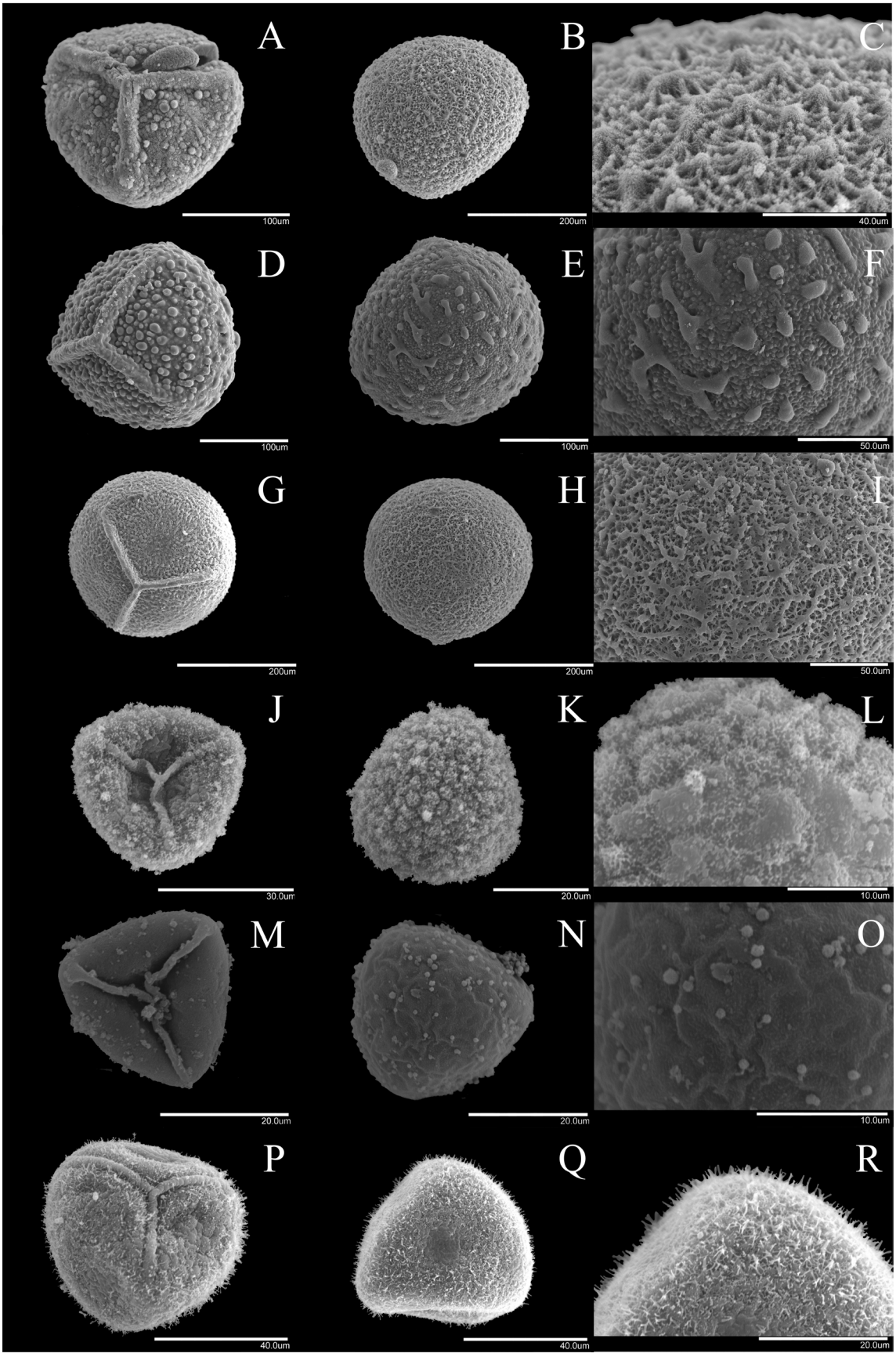

Fig. 2. Spore morphology of *Selaginella kurzii* (A–C – Megaspores, J–L – Microspores; F. G. Dickason 8164, LE); D–F, M–O – *S. pseudorepanda* (D–F – Megaspores, M–O – Microspores; S. Tagane et al. No. 304 (VNM00072393, paratype); G–I, P–R – *S. repanda* (G–I – Megaspores, P–R – Microspores; L. Averyanov et al. VH 1566 (LE); A, D, G, J, M, P – Proximal face, B, E, H, K, N, Q – Distal face, C, F, I, L, O, R – Close-up of surface, distal face.

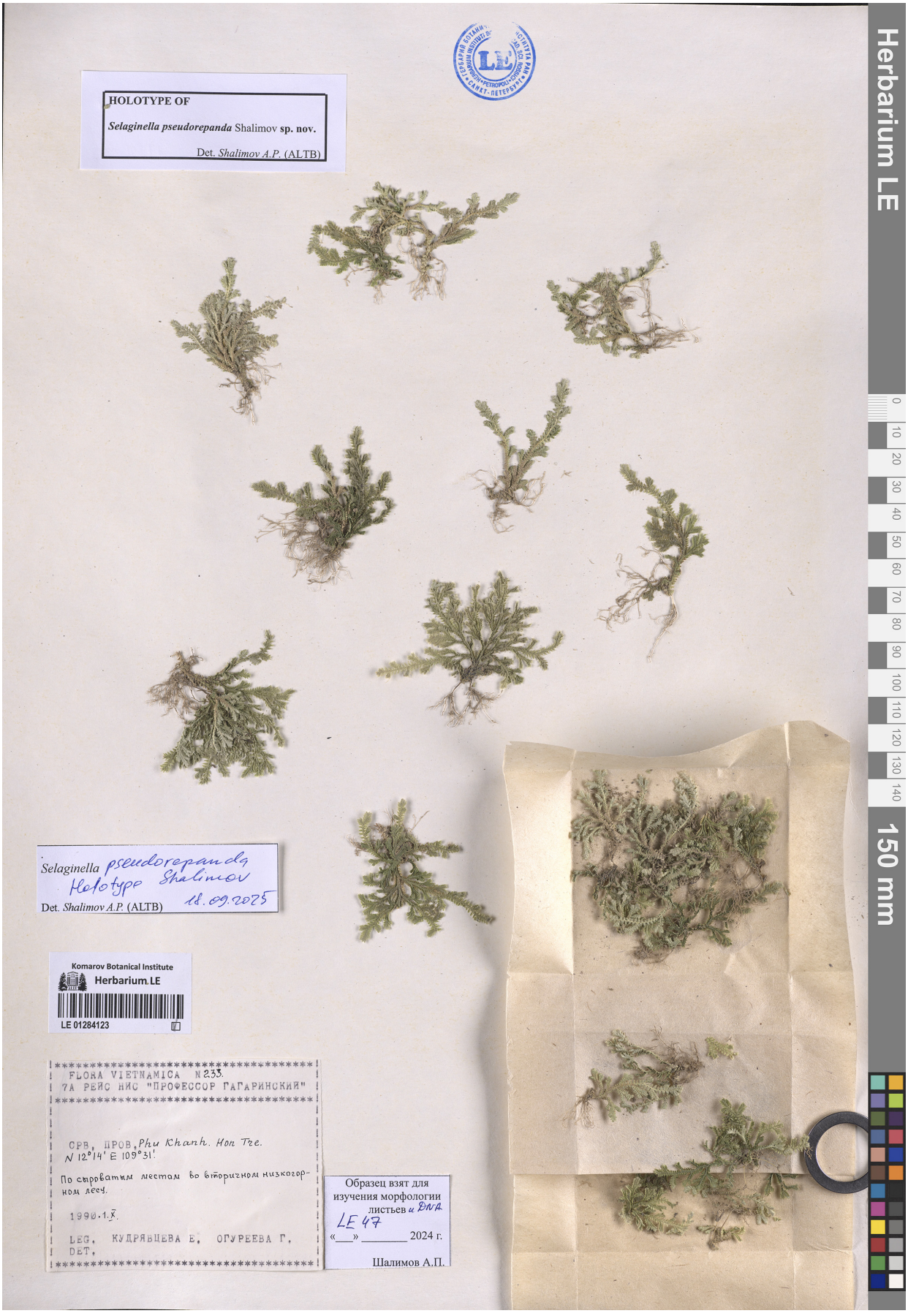

Fig. 3. *Selaginella pseudorepanda* Shalimov, sp. nov. Digitized images of holotype: E. Kudryavtzeva, G. Ogureeva No. 233 (LE 01284123).

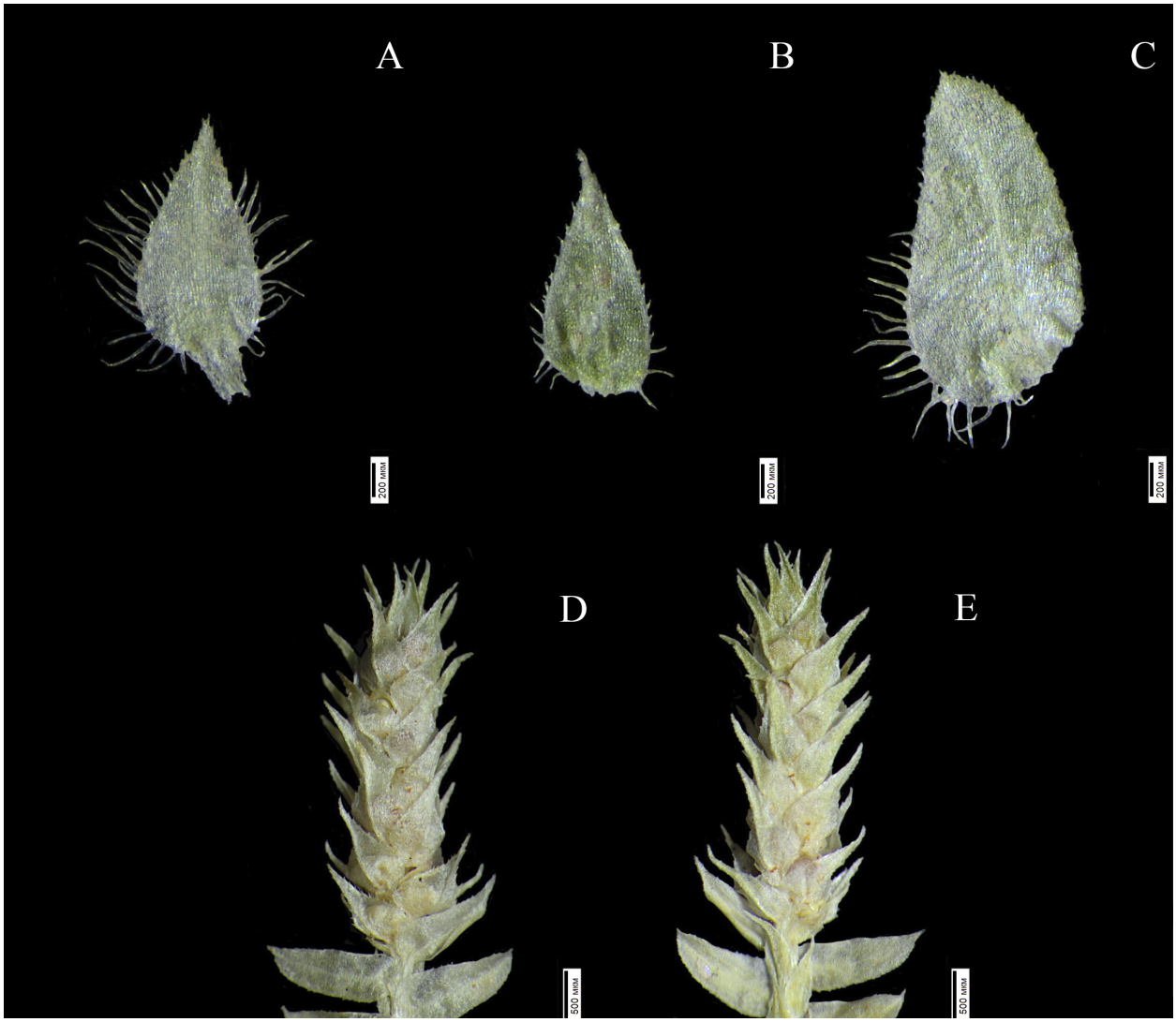

Fig. 4. *Selaginella pseudorepanda* Shalimov: A – Axillary leaf, lower surface; B – Dorsal leaves, upper surface; C – Ventral leaf, lower surface; D – Strobilus, lower surface; E – Strobilus, upper surface; A–C – Scalebar = 200 μm; D, E – Scalebar = 500 μm. A–C – Taken from the holotype E. Kudryavtzeva, G. Ogureeva 233 (LE); D, E – Taken from the paratype S. Tagane et al. No. 304 (VNM00072393).
Note: The measurement on figures 4 and 5 is designated in Russian transcription as "mkm", which stands for "μm" in the International System of Units (SI).

strongly imbricate on main stems and lateral branches, oblong-falcate to broadly oblong-falcate, 1.2–1.9 × 0.6–1 mm, basiscopic bases rounded, margins denticulate-ciliolate with few short cilia at base, each ca. 1 mm long, and denticulate distally; acroscopic bases rounded, almost completely overlapping the stem and the axis of the branches, margins densely long-ciliate from the base to the middle part of the leaf lamina, denticulate-ciliate from the middle to the apex (Fig. 4C). Strobili solitary or paired, terminal, compact, subtetragonal or subcomplanate, 3–8 × 1–1.5 mm; sporophylls unlike sterile leaves, submonomorphic or sometimes dorsal sporophylls longer, obviously white-margined; dorsal sporophylls ovate, carinate, the margins ciliate, the apex acuminate, with a complete, ciliate to ciliate-denticulate, well-formed laminar flap; ventral sporophylls ovate, carinate, inconspicuously white-margined, margins ciliate to ciliate-denticulate (Fig. 4D, E); megasporophylls in basal portion on the underside of the strobili; microsporophylls throughout the upper side of the strobilus and on the underside from the middle part onward to the apex; microsporangia orbicular, relatively thin and composed of uniform cells; megaspores yellowish, 170.3–271.2 × 146.7–242.7 μm, proximal and distal surfaces irregularly verrucate, the distal surfaces verrucate (with large irregular in sizes and small

verrucae) ornamentation (Fig. 2D–F); microspores orange-red, 24.9–30.4 × 16.5–20.8 μm**,** proximal and distal surface rugulate, with granulate microsculptures (Fig. 2M–O).

Distribution and habitat. On June 12, 2025, the Vietnam National Assembly's 9th session passed a resolution to merge, Phu Yen Province and Dak Lak Province, Ninh Thuan Province and Khanh Hoa Province, and Binh Phuoc Province and Dong Nai Province. *Selaginella pseudorepanda* is only known in Khanh Hoa, Dong Nai, and Dak Lak Provinces of Vietnam. It grows in open places on clay or rocky soil, in rock outcrops, or on dry clay coastal slopes, in open forest and scrub among xerophytic shrubs, and in semi-deciduous forests at elevations of 50–800 m a. s. l.

Etymology. The specific epithet refers to morphological similarity of the new species and *S. repanda*.

Additional specimens examined (paratypes): **Khanh Hoa Province:** "Phu Khanh [Khanh Hoa] Prov., Nha Trang, 12°12′N, 108°58′E. 9 VI 1989. L. Averyanov, E. Kudryavtzeva 45" (LE 01284122); "Annam: Massif de Co-Inh Nhatrang [Khanh Hoa Prov., Mt. Co Inh near Nha Trang], 700 m. 27 X 1922. Poilane 4974" (VNM00021539; P01229669 photo!); "Annam: Nui Han Heo pres de Nhatrang [Khanh Hoa Prov., Mt. Hon Heo near Nha Trang], 200 m. alt., dans la presqu'ile en face Ninh-Hoa. 27 IX 1922. Poilane 4765" (VNM00021542; P01229672, P01237220 photo!); "Annam: [Khanh Hoa Prov.] route de Nhatrang a Ninh Hoa. 21 IX 1922. Poilane 4653" (VNM00021541, VNM00021544; P01229670, P01229671 photo!); "Annam: [Khanh Hoa Prov.] Village Mol. lle Tre pres de Nhatrang, 200 m. 19 IV 1922. Poilane 3081" (VNM00021546); "Annam: Massif de Co Hin pres de Nhatrang [Khanh Hoa Prov., Mt. Co Hin], 50 m. 10 III 1922. Poilane 2763" (P01229665 photo!); "Ninh Thuan [Khanh Hoa] Prov., Nui Chua National Park, N11.72679°, E109.18567°, alt. 58 m. 21 XII 2023. S. Tagane, V. S. Dang, P. Souladeth, B. V. Truong, T. V. Nguyen, Q. T. Pham, Q. B. Nguyen, D. Kongxaisavath, T. Yamamoto, K. Yamazaki No. 304" (VNM00072393); "Annam: Ca-Na, Phanrang [Khanh Hoa] Prov., 100 m. 8 III 1923. Poilane 5689" (VNM00021535; P01229745 photo!); "Ninh Son district, Unnamed Road Petite colline, 12°41′24″N, 108°52′48″E, alt. 50 m. 28 IV 2018. J. Wolff, M. Pignal 55" (P02275916 photo!); "Ninh Hai District, Vinh Hy Townlet, alt. 200 m a. s. l. 1 XI 2024. L. Averyanov, V. C. Nguyen, T. Maisak AL3512" (LE 01277997). **Dong Nai Province:** "Cochinchine: Gia ray [«Gia Ray»] prov. de Bien Hoa, Montagne de Chua chan [Mt. Chua Chan], 840 m. 21 I 1921. Poilane 2438" (P01229673; P01229674 photo!); "Cochinchine: Montagne de Chua chan [«Mt. Chua Chan»], Gia ray [«Gia Ray»] prov. de Bien Hoa, 800 m, Poilane 2463" (P01229676, P01254293 (exclude right plant it is *S. kurzii* Baker) photo!). **Dak Lak Province** "[Phu Yen Prov.], Dong Ha District, Deo Ca Pass, at elev. 100–150 m a. s. l. 4 XI 2024. L. Averyanov, N. V. Canh, T. Maisak AL3545" (LE 01277912); ibid. "4 XI 2024. L. Averyanov, N. V. Canh, T. Maisak AL3543" (LE 01277910; LE 01277909; LE 01277911).

Discussion

The results of this study show that *Selaginella pseudorepanda* is morphologically similar to *S. repanda* but differs by its creeping main stems (vs. ascending from a decumbent base in *S. repanda* and creeping with erect fertile branches in *S. kurzii*). Additionally, the shape of the axillary and ventral leaves of the new species resembles those of *S. repanda* and *S. kurzii*. However, *S. pseudorepanda* can be easily distinguished from these similar species by the margins of its ventral and axillary leaves, which are more densely covered with long cilia than those of *S. repanda* and *S. kurzii* and with cilia that are noticeably shorter. The shape of the dorsal leaves is more variable in *S. pseudorepanda*. It has ovate leaves that are rounded at the base and acuminate at the apex (in contrast to *S. repanda*, which has obliquely ovate, obliquely subcordate leaves at the base and long acuminate to shortly aristate apex, and *S. kurzii*, which has ovate or ovate-elliptical leaves, subcordate or blunt at the base with acuminate or aristate apex). *Selaginella pseudorepanda* and *S. repanda* are similar in strobili shape; both species have subtetragonal or subcomplanate strobili, but they differ from *S. kurzii*, which has strongly dimorphic strobili. A comparison of morphological characters between *S. pseudorepanda* and its related species is shown in Table 1 and Fig. 5.

Table 1. Morphological characters of *Selaginella kurzii*, *S. pseudorepanda*, and *S. repanda*

Characters	*S. kurzii*	*S. pseudorepanda*	*S. repanda*
Stem habit	Stem creeping, 10–20 cm long, fertile stems erect 5–15(25) cm long	Stem creeping, 5–10(15) cm long	Stem ascending to erect from decumbent base, 8–30 cm long
Axillary leaves	Ovate or ovate-lanceolate, 1–2.5 × 0.6–1.6 mm, margin rather long ciliate at base	Ovate-lanceolate to ovate-triangular, 0.6–1.5 × 0.3–0.8 mm, margin long ciliate at base	Ovate to ovate-lanceolate, 2–3 × 1–1.4 mm, margin short ciliate at base
Dorsal leaves	Ovate or ovate-elliptic, 1–1.2 × 0.4–0.8 mm, base subcordate or obtuse, margin ciliate, apex acuminate or aristate, arista 0.3–0.6 mm	Ovate, 0.2–1.6 × 0.3–0.8 mm, base rounded, margin long ciliate at base, denticulate-ciliate from middle to apex; apex acuminate	Obliquely ovate, 0.7–1.6 × 0.4–0.9 mm, base obliquely subcordate, margin denticulate; apex long acuminate to shortly aristate
Ventral leaves	Ovate-triangular, 1.6–3.8 × 0.6–1.6 mm	Oblong-falcate to broadly oblong-falcate, 1.2–1.9 × 0.6–1 mm	Oblong-falcate, 2.5–3 × 1–1.5 mm
Acroscopic margin of ventral leaves	Long ciliate at base, subentire to the apex	Densely long ciliate from base to middle part, denticulate-ciliate from middle to apex	Ciliate at base
Strobili	6–8 × 2–3 mm, strongly dimorphic	3–8 × 1–1.5 mm, subtetragonal or subcomplanate	3–7 × 1.5–3 mm, subtetragonal or subcomplanate
Dorsal sporophylls	Ovate-lanceolate, margin ciliate	Ovate, carinate, margin ciliate	Ovate, sharply carinate, margin ciliate
Ventral sporophylls	Ovate, margin ciliate	Ovate, margin ciliate to ciliate-denticulate	Ovate, margin ciliate
Megaspores: proximal and distal surfaces	Verrucate-reticulate	Verrucate (with large irregular in sizes and small verrucae)	Reticulate
Microspores: proximal and distal surfaces	Verrucate	Rugulate	Finely verrucate
Microspores: microsculptures	Dense spinulose	Granulate	Reticulate and blunt spinulose

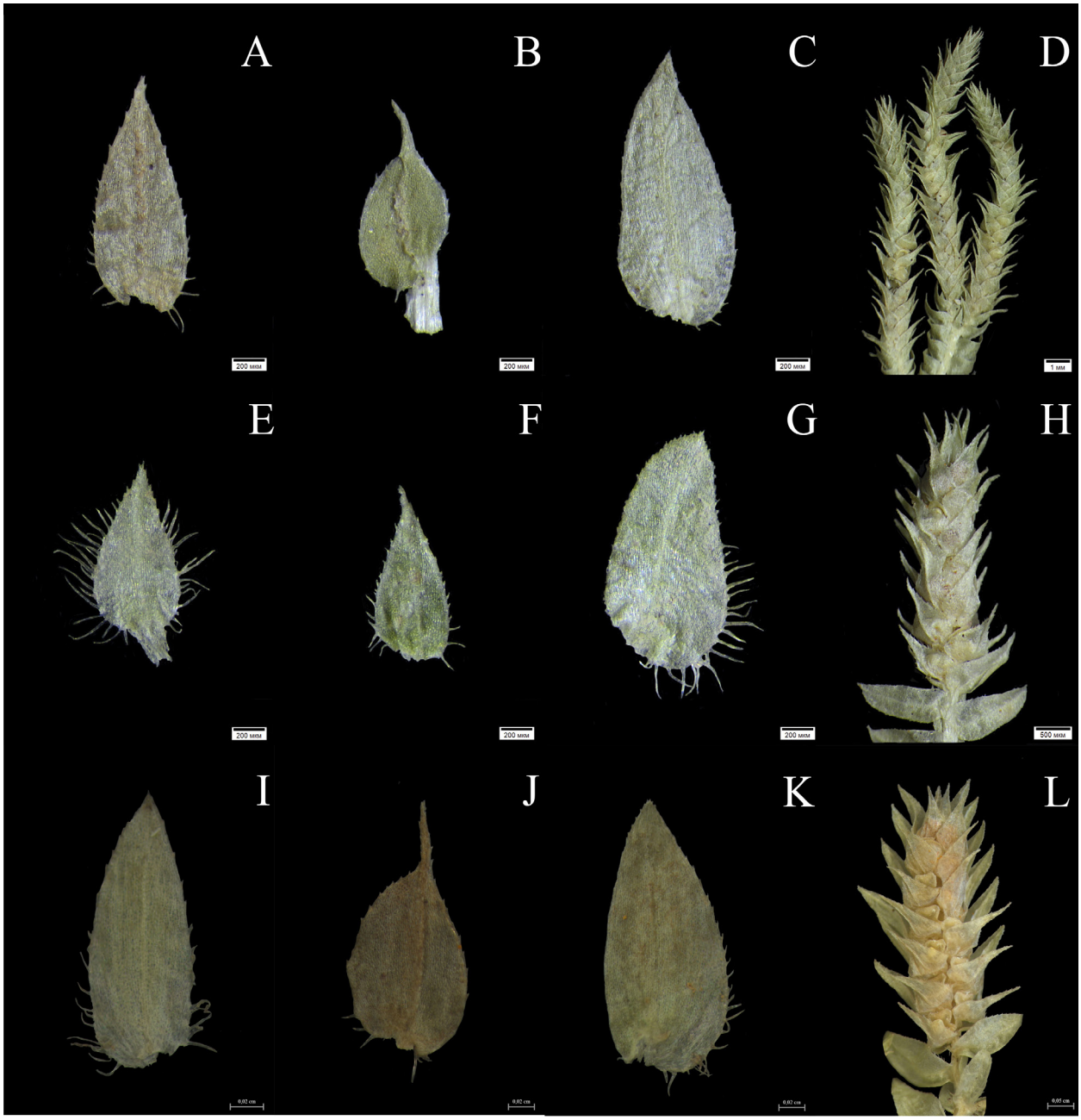

Fig. 5. Leaves and strobili of *Selaginella repanda*, *S. pseudorepanda*, and *S. kurzii*: A–D – *Selaginella repanda* (L. Averyanov et al. VH 1566, LE); E–H – *S. pseudorepanda* (E–G from the holotype of E. Kudryavtzeva, G. Ogureeva 233, LE 01284123; H – from the paratype S. Tagane et al. No. 304, VNM00072393); I–L – *S. kurzii* (F. G. Dickason 8164, LE: A, E, I – Axillary leaves; B, F, J – Dorsal leaves; C, G, K – Ventral leaves; D, H, L – Strobili. Scale bars = 200 μm (A, B, C, E, F, G, I, J, K), 1 mm (D), 500 μm (H, L).

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REFERENCES / ЛИТЕРАТУРА

Alston A. H. G. 1934. An enumeration of the Chinese species of *Selaginella*. *Bull. Fan Mem. Inst. Biol. Bot.* 5(6): 261–294.

Alston A. H. G. 1945. An enumeration of the Indian species of *Selaginella*. *Proc. Natl. Inst. Sci. India, B* 11(3): 211–235.

Alston A. H. G. 1951. Selaginellaceae. In: H. Lecomte (ed.). *Flore generale de I'Indo-Chine*. Paris: Masson. Pp. 555–594.

Chang C. Y., Liu Q. R., Chen X. D. 2002. Megaspore morphology of eight species of *Selaginella*. *Journal of Chinese Electron Microscopy Society* 21(5): 566–567.

Chen C.-W., Hsu T.-C., Doan H. S., Do V.H., Luu H. T., Le V. S., Liu Y.-C., Li C.-W., Huang Y.-M., Chung K.-F. 2023. Studies of Vietnamese Pteridophyte Flora 2. *Syst. Bot.* 48, 2: 159–172. https://doi.org/10.1600/036364423X16847773873161

Darriba D., Taboada G.L., Doallo R., Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. https://doi.org/10.1038/nmeth.2109

Edgar R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res*. 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Fraser-Jenkins C. R., Gandhi K. N., Kholia B. S., Benniamin A. 2017. Selaginellaceae. In: *An annotated checklist of Indian Pteridophytes, Pt. 1 (Lycopodiaceae to Thelypteridace).* Dehra Dun: Bishen Singh Mahendra Pal Singh. Pp. 27–53.

Huang L., Li S.-H., Dong S.-Y. 2022. Two new species of the Lycophyte genus *Selaginella* (Selaginellaceae) from China, with notes on phylogenetic position of related species. *Syst. Bot.* 47, 1: 85–96. https://doi.org/10.1600/036364422X16442668423400

Huang T. C. 1981. *Spore flora of Taiwan*. Taipei: Botany Department Press, National Taiwan University. Pp. 105–111.

Kalyuzhny S. S., Plugatar Y. V., Shalimov A. P. 2024. Modern taxonomic list of Pteridophytes (including Lycopodiopsida class) for the Socialist Republic of Vietnam. *Indian Fern J.* 41, 1: 53–75.

Kumar S., Stecher G., Li M., Knyaz C., Tamura K. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molec. Biol. Evol.* 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Lellinger D. B. 2002. A modern multilingual glossary for taxonomic pteridology (English and Spanish Edition). Washington: American Fern Society, Inc. 263 pp.

Letunic I., Bork P. 2024. Interactive Tree of Life (iTOL) v6: recent updates to the phylogenetic tree display and annotation tool. *Nucl. Acids Res.* 52(W1): W78–W82. https://doi.org/10.1093/nar/gkae268

Liu J. X., Sun X. H., Jin Y. Y., Lu L., Yu X. X., Zhang X.-C. 2003. Spore morphology of eight species of Selaginellaceae from Yunnan. *Acta Bot. Yunnan.* 25(3): 303–312.

Minaki M. 1984. Macrospore morphology and taxonomy of *Selaginella* (Selaginellaceae). *Pollen et Spores* 26: 421–480.

Pham H. H. 1999. Selaginellaceae. In: *Cây cỏ Việt Nam: An illustrated Flora of Vietnam*. 2nd ed. Vol. 1. Ho Chi Minh: Tre Publishing House. Pp. 26–36. [In Vietnamese]

Phan K. L., Vu T. D., Nguyen C. T., Pham V. T., Trinh N. B. 2019. A checklist of pteridophytes collected on Cham Chu mountains and adjacent sites. *Acad. J. Biol.* 41(4): 75–89. https://doi.org/10.15625/0866-7160/v41n4.14639

Ronquist F., Huelsenbeck J. P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Shalimov A. P., Zhu Y. M., Zhang M.-H., Zhang X.-C. 2019. *Selaginella dianzhongensis* (Selaginellaceae), a new spikemoss from China. *PhytoKeys* 118: 75–87. https://doi.org/10.3897/phytokeys.118.30375

Shalimov A. P., Zaikov V. F., Kalyuzhny S. S., Zhang M.-H., Zhang X.-C. 2024. The recovery of *Selaginella flaccida* based on morphological and molecular data, with the description of *S. khokhrjakovii from* Indo-China and Peninsular Malaysia. *Bot. Pacifica* 13(1): 45–54. https://doi.org/10.17581/bp.2024.13105

Singh S. K., Yadav B. B., Srivastava M., Shukla P. K., Srivastava G. K. 2014. Micro-morphology of *Selaginella* megaspores from India. *Grana* 53(3): 197–220. https://doi.org/10.1080/00173134.2014.919356

Tagawa M., Iwatsuki K. 1979. Selaginellaceae. In: R. C. Bakhuizen et al. (eds.). *Flora of Thailand.* Vol. 3(1). Pteridophytes. Bangkok: The Tistr Press. Pp. 14–32.

Thiers B. [2025]. *Index Herbariorum: A global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium. URL: http://sweetgum.nybg.org/ih/ (Accessed 16 May 2025).

Wang L. J., Zhang X.-C., Liu J. X. 2018. Studies on the complementary relationship of surface orna-mentations between megaspores and microspores of *Selaginella* P. Beauv. (Selaginellaceae). *Microsc. Res. Tech.* 81(12): 1–15. https://doi.org/10.1002/jemt.23148

Weststrand S., Korall P. 2016. Phylogeny of Selaginellaceae: There is value in morphology after all! *Amer. J. Bot.* 103(12): 2136–2159. https://doi.org/10.3732/ajb.1600156

Wong K. M. 1983. Critical observations on Peninsular Malaysian *Selaginella*. *The Garden's Bulletin, Singapore* 35(4): 107–135.

Wong K. M. 2010. Selaginelaceae. In: B. S. Parris, R. Kiew, R. C. K. Chung, L. G. Saw, E. Soepadmo (eds.). *Flora of Peninsular Malaysia, Series I: Ferns and lycophytes*. Vol. 1 (Malayan Forest Records No. 48). Kepong: Forest Research Institute Malaysia. Pp. 50–86.

Wu Y.-D., Zhang H.-R., Zhang X.-C. 2017. *Selaginella guihaia* (Selaginellaceae): A new spikemoss species from southern China and northern Vietnam around the Gulf of Tonkin. *PhytoKeys* 80: 41–52. https://doi.org/10.3897/phytokeys.80.11126

Yan D., Wang L. J., Song Y. Y., Wang L., Du T. T., Liu J. X. 2016. Microspore morphology of Selaginellaceae in China and its systematic significance. *Pl. Syst. Evol.* 302: 561–574. https://doi.org/10.1007/s00606-016-1284-8

Ye Z.-Y., Lu N. T., Zhang L., Zhou X.-M., Zhang L. B. 2020. *Selaginella coriaceifolia* (sect. *Heterostachys*; Selaginellaceae), a new lycophyte species from central Vietnam. *Phytotaxa* 453(2): 121–129. https://doi.org/10.11646/phytotaxa.453.2.3

Zhang M.-H., Yang J., Luu H. T., Tran G., Zhang X.-C. 2022. *Selaginella pseudotamariscina* (Selaginellaceae), an overlooked rosette-forming resurrection spikemoss from Vietnam. *Guihaia* 42(10): 1632–1640. https://doi.org/10.11931/guihaia.gxzw202104055

Zhang X.-C., Nooteboom H. P., Kato M. 2013. Selaginellaceae. In: Z. Y. Wu, P. H. Raven, D. Y. Hong (eds.). *Flora of China*. Vol. 2–3. Beijing: Science Press, St. Louis: Missouri Botanical Garden Press. Pp. 37–66.

Zhang X.-C., Shalimov A. P., Kang J. S., Zhang M.-H. 2020. *Selaginella subvaginata* (Selaginellaceae), a new spikemoss from China. *Journal of Species Research* 9(3): 221–232. https://doi.org/10.12651/JSR.2020.9.3.221

Zhou X. M., Jiang L. J., Zhang L., Gao X. F., He Z. R., Zhang L. B. 2015. Spore morphology of *Selaginella* (Selaginellaceae) from China and its systematic significance. *Phytotaxa* 237(1): 1–67. https://doi.org/10.11646/phytotaxa.237.1.1

Zhou X.-M., Rothfels C. J., Zhang L., He Z.-R., Pechon T. L., He H., Lu N. T., Knapp R., Lorence D., He X.-J., Gao X.-F., Zhang L.-B. 2016. A large-scale phylogeny of the lycophyte genus *Selaginella* (Selaginellaceae: Lycopodiopsida) based on plastid and nuclear loci. *Cladistics* 32(4): 360–389. https:// doi.org/10.1111/cla.12136