

RAUIELLA THUIDIOIDES, SP. NOV. (LESKEACEAE, BRYOPHYTA), A NEW SPECIES
FROM THE RUSSIAN FAR EAST

RAUIELLA THUIDIOIDES, SP. NOV. (LESKEACEAE, BRYOPHYTA), НОВЫЙ ВИД
С РОССИЙСКОГО ДАЛЬНЕГО ВОСТОКА

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Abstract

Molecular barcoding of a morphologically unfamiliar thuidiaceus moss, known so far from two specimens collected in the Sikhote-Alin mountain range suggested the affinity with the genus *Raiiella*. Subsequent evaluation in a broader phylogenetic context of Leskeaceae s. lat. using nuclear ribosomal ITS and chloroplast *trnF-trnS* regions confirmed that the plants which morphologically substantially differ from known representatives of *Raiiella* are molecularly likewise distinctive. It is therefore described and illustrated here as a new species, *Raiiella thuidioides*. We further discuss the morphological differences from its congeners and other similar taxa, as well as its ecology and geographical affinities. Finally, we also touch the delimitation of the genus *Raiiella* and advocate the synonymy of Thuidiaceae with Leskeaceae.

Резюме

Предварительное изучение с помощью молекулярных маркеров двух образцов неизвестного вида из семейства Thuidiaceae, собранных на хребте Сихоте-Алинь в Приморском крае, показало их сходство с родом *Raiiella*. Последующая оценка их положения в более широком филогенетическом контексте семейства Leskeaceae s. lat. с помощью ядерного участка ITS и хлоропластного *trnF-trnS* подтвердила их принадлежность к этому роду; при этом были показаны существенные морфологические и молекулярные отличия этих образцов от известных представителей *Raiiella*. Эти растения описаны и проиллюстрированы как новый вид *Raiiella thuidioides*. Обсуждаются его отличия от других видов *Raiiella* и морфологически сходных видов из других родов, а также особенности экологии и распространения нового вида. Рассмотрены также объем и границы рода *Raiiella* и приведены доводы в пользу синонимизации семейства Thuidiaceae с Leskeaceae.

KEYWORDS: Hypnales, molecular barcoding, ITS, *trnF-trnS*, cryptic diversity

INTRODUCTION

In course of identification of specimens collected in 2013 at the well-known locality of Elomovsky Klyuch valley beneath Benevskie waterfalls (Sikhote-Alin mountains, Primorsky Territory, Russian Far East), the second author (EA) was puzzled by a thuidiaceus moss, which combined the characteristics of *Raiiella fujisana* (Paris) Reimers (pluripapillose lamina cells) with the branching pattern unknown in this species (sparse but at least partly bipinnate branching) and pointing thus rather towards *Thuidium* Schimp. s.str., although such sparse

branching is also unknown in the Far East Asian representatives of *Thuidium* with pluripapillose cells, i.e., *T. submicropteris* Cardot, *T. subglaucinum* Cardot, and *T. kanedae* Sakurai. Several years later, JK and VF visited the site again and JK happened to collect the same moss again and was puzzled in the same way when attempting at naming this collection. Molecular barcoding using the nrITS and chloroplast *rps4* regions pointed towards the affinity with *Raiiella fujisana*, rather than with *Thuidium*, but only sequences of *R. fujisana*, *R. lagoensis* (Hampe) W.R. Buck, and *R. praelonga* (Schimp. ex Besch.) Wijk

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& Margad. were publicly accessible (the latter two only for *rps4*, mitochondrial *nad5* intron, and nuclear LSU) at that time, and the representation of the East Asian *R. fujisana* in GenBank was very scarce. We decided therefore to sample molecularly a few additional specimens of *R. fujisana* and add the eastern North American *R. scita*, which is the type of the genus but has not yet been sampled for molecular data. Published molecular phylogenetic accounts with greater emphasis on Thuidiaceae or Leskeaceae s.lat. are sparse and include a smaller account by García-Ávila *et al.* (2009), who used chloroplast *rbcL* and *rps4-trnS* regions, the unpublished dissertation by Soares (2015), who used the combination of chloroplast *rps4*, mitochondrial *nad5* intron and nuclear ribosomal LSU, the arXiv-indexed paper by Cai *et al.* (2019), who used the combination of nuclear ribosomal ITS with the plastid *trnL-trnF*, *rps4*, and *atpB-rbcL*, and a small account published on the occasion of the description of a new thuidiaceae genus, *Lazarenkoa* Ignatov & Ignatova *nom. illeg.* (Ignatov *et al.*, 2019), now replaced by *Ignatovia* U.B. Deshmukh (Deshmukh, 2021); here the molecular dataset was based on the combination of nuclear ribosomal ITS with the plastid *trnL-trnF*.

The genus *Raiiella* was in fact described by Austin (1880) [as *Rauia* Aust.] to accommodate the eastern North American species which was then recognized as *Thuidium scitum* (P. Beauv.) Austin. He considered the 'leskeaceous' capsule form and peristome as diagnostic characters worth segregating it from *Thuidium*. Unfortunately, he has not noticed that the name has already been in use for a rutaceous plant described in 1823 and this failure was corrected by Reimers (1937), who coined a replacement name, *Raiiella* Reimers, and added the second species to the delimitation of the genus, the east Asian *R. fujisana*. His concept was already close to the modern one, having emphasized the monoicy, simple pinnate branching of plants, dense paraphyllia, pluripapillose cells, and erect cylindrical capsule with short operculum and 1–2 endostome cilia between teeth. Several new combinations to the genus were added by Wijk & Margadant (1962) without a dedicated study, and the last addition to the concept of *Raiiella* was made by Buck (1991), who newly combined into the genus the chiefly neotropical species, *R. lagoensis*. The genus is currently rather generally accepted, based probably on the reasoning provided by both Buck & Crum (1990) and Touw (2001), although Noguchi *et al.* (1991) preferred the broad delimitation of the genus *Thuidium*, which included *Pelekium* Mitt., *Bryochenea* C. Gao & K.C. Chang, *Abietinella* Müll. Hal., and *Raiiella*. *Raiiella* has not yet been studied in broader phylogenetic context and sadly, the neotropical species, *R. lagoensis* and *R. praelonga*, which differ in several morphological aspects from the northern temperate species, *R. scita* and *R. fujisana* (Touw 2001), were never included together in one of the above-mentioned phylogenetic studies but doubts on the phylogenetic coherence

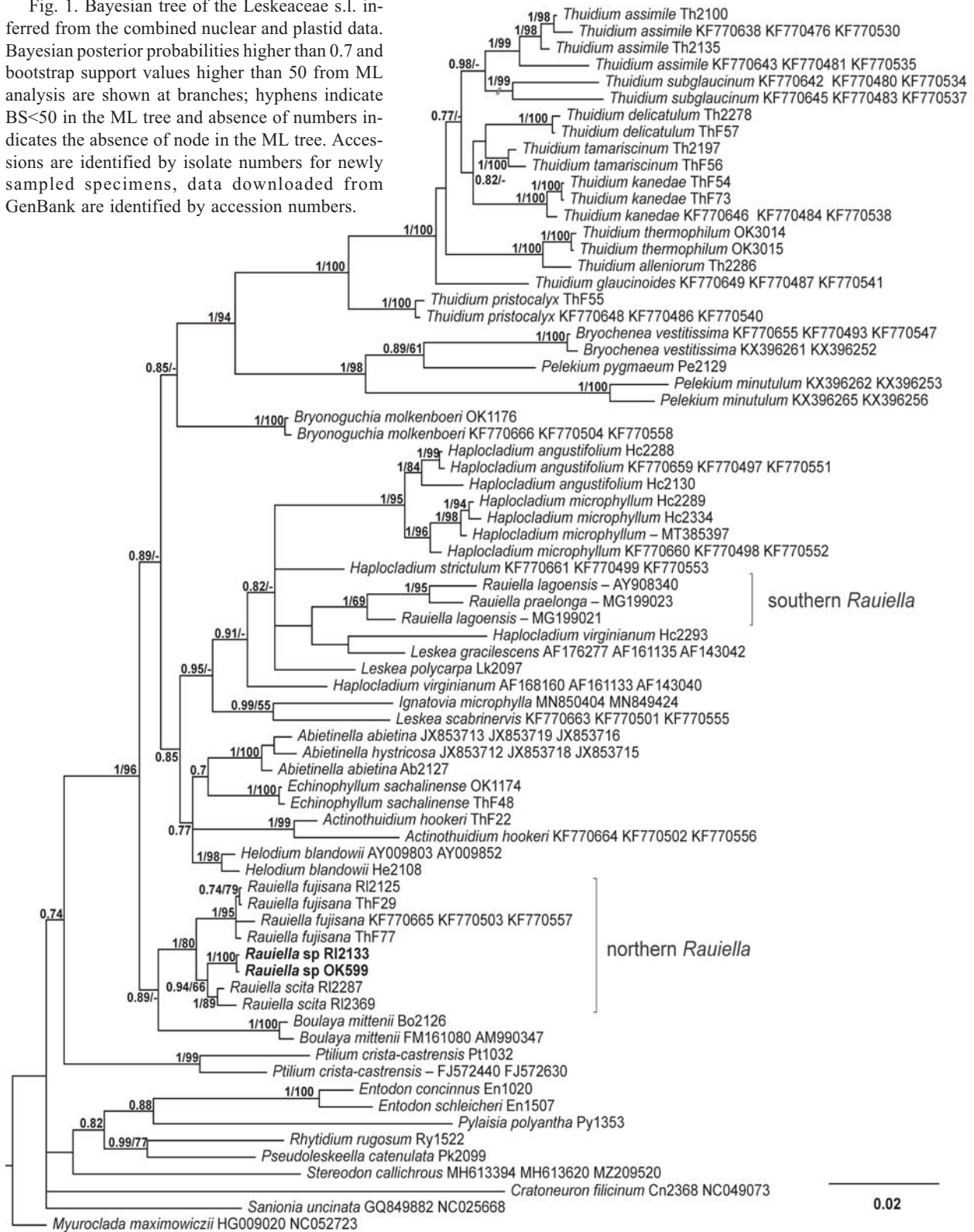
of the groups can be deduced from the markedly different affinities of *R. lagoensis*, which appears mostly closely related to *Haplocladium microphyllum* (Sw. ex Hedw.) Broth. (García-Avila *et al.*, 2009), while *R. fujisana* appears closest to *Abietinella* and *Bryonoguchia* (Cai *et al.*, 2019; Ignatov *et al.*, 2019). The acceptance of the whole family Thuidiaceae with respect to Leskeaceae appears controversial, as the Thuidiaceae comprising at least the genera accepted in the broad *Thuidium* concept of Noguchi *et al.* (1991) are firmly rooted among bryologists, but the above-mentioned phylogenetic studies strongly favour the concept of broad Leskeaceae, as adopted by Allen (2018).

MATERIAL AND METHODS

Based on the published molecular data in Leskeaceae s.lat. with respect to the phytogeographic focus of the sampling, we decided that the most logical combination of loci to use in this study would be the combination of nrITS and chloroplast *trnF-trnS* regions. These loci were used in the treatments by Cai *et al.* (2019) and Ignatov *et al.* (2019), although none of them employed the complete *trnF-trnS* region; the variability of the *trnL-trnT* and *trnT-rps4* spacer was, however, found phylogenetically informative, e.g., in the recent molecular-phylogenetic study of *Orthothecium* (Ignatov *et al.*, 2020). Use of the region however enables employing accessions for which only *trnL-trnF* or *rps4-trnS* part is available. We used the datasets published by Cai *et al.* (2019) and Ignatov *et al.* (2019) as a basis for the matrix, and supplemented it with the newly obtained sequences of *Raiiella* and other Leskeaceae s.lat., as specified in the Appendix.

Retrieval of sequences followed the laboratory protocols specified in Kučera *et al.* (2019) and Ignatov *et al.* (2020). Raw sequences were trimmed from primer complements, checked and corrected for reading errors and inserted into preliminary matrices based on the above-mentioned phylogenetic studies, observing our later achievements, particularly the larger study by Kučera *et al.* (2019). ITS and chloroplast matrices were initially aligned and evaluated in phylogenetic context separately. We used the online interface of Mafft ver. 7 (<https://mafft.cbrc.jp/alignment/server/>) to align our matrices using the E-INS-i aligning strategy with otherwise default options and checked the results for obvious inconsistencies manually. We employed Bayesian inference (BI) and Maximum Likelihood (ML) analysis for the phylogenetic inference. The analyses were calculated in MrBayes v. 3.2.7a (Ronquist *et al.*, 2012) and RAxML v. 8.2.12 (Stamatakis, 2014) software packages, run at the cluster facilities of Metacentrum VO (see acknowledgement), following the algorithms specified in Kučera *et al.* (2019). Chloroplast and ITS matrices were not further partitioned but upon inspection of inconsistencies between the results from these partial analyses, we have not discovered discrepancies at supported nodes which would prevent us from concatenation and therefore we

Fig. 1. Bayesian tree of the Leskeaceae s.l. inferred from the combined nuclear and plastid data. Bayesian posterior probabilities higher than 0.7 and bootstrap support values higher than 50 from ML analysis are shown at branches; hyphens indicate BS<50 in the ML tree and absence of numbers indicates the absence of node in the ML tree. Accessions are identified by isolate numbers for newly sampled specimens, data downloaded from GenBank are identified by accession numbers.



used the concatenated data matrix, which was partitioned between nuclear and plastid partitions. Indel data were not scored following the initial inspection of result differences between the included and not included indel data.

RESULTS

Analysis of separate ITS and chloroplast matrices yielded nearly identical topologies, differing mostly in more abundant unresolved lineages resulting from the chloroplast dataset. We present and describe here there-

fore only the results obtained from the analysis of concatenated matrices (Fig. 1). All sampled Thuidiaceae and Leskeaceae accessions form together a well-supported monophyletic unit. The type of Leskeaceae, *Leskea polycarpa*, appears nested in a weakly supported lineage containing accessions of *Haplocladium*, *Raiiella lagoensis* and *R. praelonga*, and *Ignatovia*. Members of *Thuidium*, on the other hand, appear in a fully supported clade which is sister to fully supported *Pelekium* clade that also includes *Bryochenea*. The composite lineage of *Thuidium* and *Pelekium*+*Bryochenea* appears sister to *Bryonoguchia* to form a virtually unsupported clade. All other relationships at supra-generic rank are poorly supported or not supported at all. Members of *Raiiella* form two markedly distant lineages, the northern lineage (PP 1/BS 80) comprising the temperate representatives *R. scita*, *R. fujisana* and the two accessions of plants from Elomovsky Klyuch which form a weakly supported monophylum (PP 0.94/BS 66) with the North American *R. scita*, while *R. fujisana* is sister to this lineage. The whole northern *Raiiella* lineage appears sister to *Boulaya*, comprising a very weakly supported clade (PP 0.89/BS-). The undescribed *Raiiella* shares *rps4-trnS* sequence with *R. scita* but differs in five substitutions in the remaining part of *trnF-rps4* region and five in ITS. *Raiiella fujisana* differs in additional 10 substitutions in *trnF-rps4* region, two substitutions in the *rps4-trnS* region and 8 in ITS. The southern *Raiiella* representatives appear within a poorly supported clade that includes analysed accessions of *Haplocladium*, *Leskea* and *Ignatovia*.

DISCUSSION

The morphologically distinct plants collected several times in the valley of Elomovsky Klyuch in the southern part of Sikhote-Alin mountain range were molecularly confirmed to be a member of the “northern *Raiiella* lineage”, i.e., the genus *Raiiella* in the strict sense. The structure of molecular variability in this lineage fully supports the recognition of three identically evaluated taxa, showing little infraspecific variation and substantially larger divergence among taxa. The undescribed member of *Raiiella* is more closely related to the eastern North American *R. scita* than to the sympatrically occurring *R. fujisana*. At the same time, *R. scita* is not known to occur outside its endemic distribution range between North Carolina and Quebec, eastern Atlantic coast and Iowa in the west (Buck, 2014). The polyphyly of *Raiiella*, as currently delimited, calls for the re-evaluation of the genus, as already suggested by Touw (2001), who stated that the neotropical *Raiiella* members possess character states he considered as derived with respect to northern species, including irregular branching pattern, paraphyllia with few and short branches, weakly differentiated stem and branch leaves, mucous stem leaves, strong costae with dorsal superficial costa cells chlorophyllose, similar to adjacent lamina cells, long and

sheathing perichaetial leaves and reduced peristomes. They also share the acute, sharp terminal cell of branch leaves in contrast to truncate and pluripapillose cells of the northern species (Buck, 2014). We have not had the possibility of studying the tropical representatives of the genus and the phylogenetic affinities are assessed only from the *rps4* part of the *trnF-trnS* region which we employed in most other cases. The comprehensive revision of *Raiiella* is nevertheless far beyond the scope of the current paper.

The results from our phylogenetic analysis also fully support the idea of merging the traditionally recognized family of Thuidiaceae with Leskeaceae (Allen, 2018). Should the two families be maintained, it would necessitate either segregating several new families with low support and hardly any morphological substantiation (one of them containing probably the northern *Raiiella* clade with *Boulaya*), or the acceptance of monophyletic crown group of Thuidiaceae containing probably only *Thuidium* and *Pelekium* at the cost of paraphyletic Leskeaceae represented by the grade of all basal thuidiaceae/leskeaceous genera. Neither of these solutions seems to be more convenient than the somewhat unusual broad delimitation of Leskeaceae, where however only the genus *Leskea* is retained in the classical delimitation of the family (Brotherus, 1925).

TAXONOMY

Raiiella thuidioides Jan Kučera & Ignatova, spec. nov. Fig. 2, 3A–D, 4A–D.

Holotype: Russian Federation, Primorsky Territory, Lazo Distr.: Elomovsky Klyuch valley, 43°13'39.3"N, 133°45'47.6"E, 250 m a.s.l., on mossy rocks in mixed conifer-broadleaved forest, 5 September 2013, coll. Ignatov, Ignatova & Malashkina 13-1264 (MHA9101928). Isotype MW9092266.

Paratypes: (1) Russian Federation, Primorsky Territory, Lazo Distr.: Elomovsky Klyuch valley, 43°13'10"N, 133°46'31"E, 200 m a.s.l., broad-leaved alluvial wood; on half-shaded siliceous boulder, 5 September 2019, coll. J. Kučera 21299 (CBFS). (2) The same area, without exact coordinates, ca. 200 m a.s.l., on rocks in a mixed flood-valley forest, 6 September 2006, coll. Ignatov, Ignatova & Cherdantseva 06-2175 (MHA9131243, MW9092267).

Etymology. The specific epithet refers to thuidioid appearance which results from the presence of sparsely bipinnate branching.

Diagnosis. The species differs from its congeners, and particularly from *R. fujisana* and *R. scita*, in its sparse branching which reveals rich paraphyllia present on stem, the occasional production of second order branches from the primary ones, and the larger stem leaves, mostly exceeding 1 mm in length and 0.5 mm in width. The differences from *Thuidium* species with pluripapillose cells (*T. submicropteris*, *T. subglaucinum*, *T. kanadae*, *T. alleniorum*) include autoicous gametangia and less regular and less dense, mostly unipinnate branching. *Boulaya*

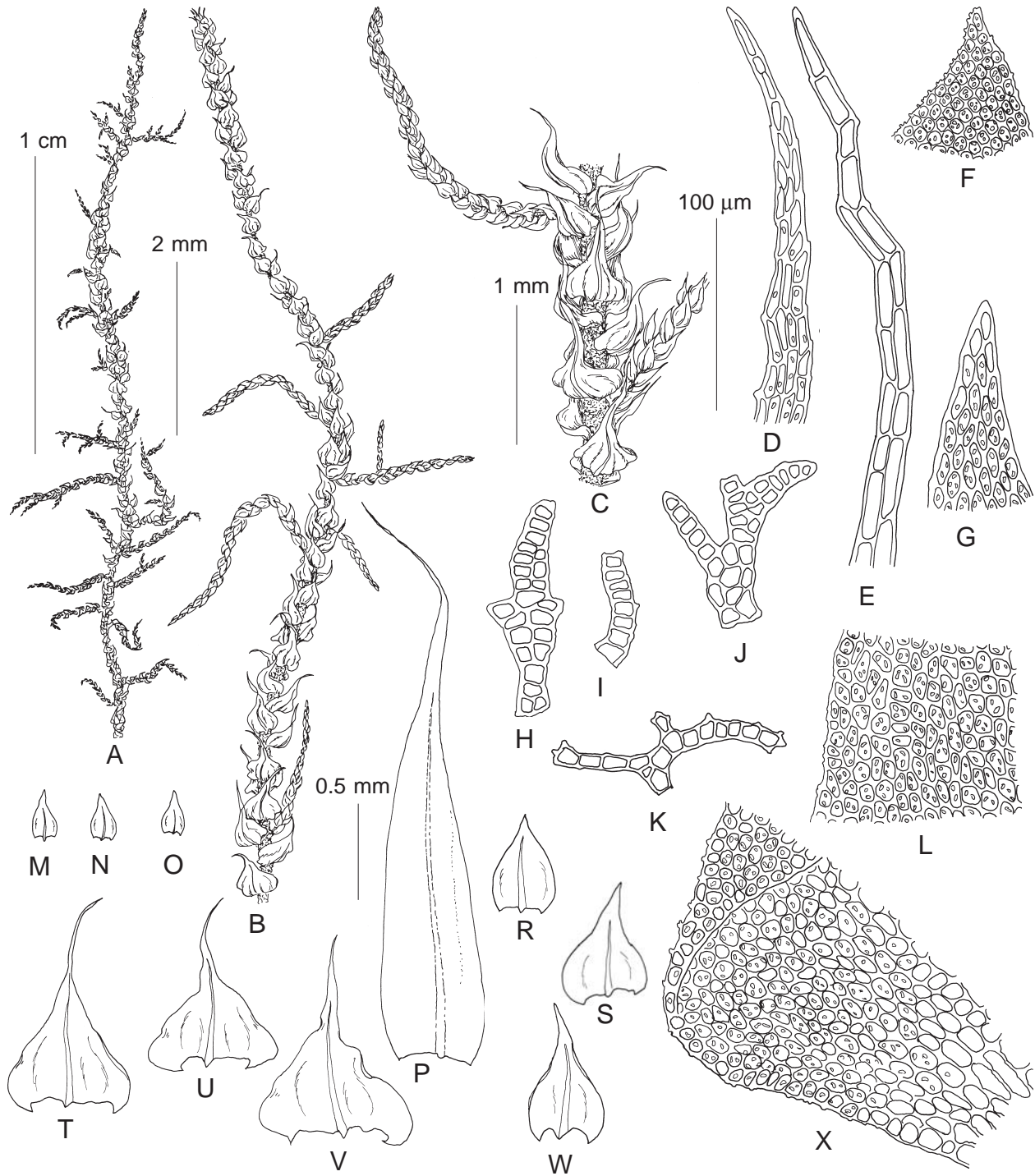


Fig. 2. *Raiiella thuidioides* (from holotype). A–C: habit, dry; D–E: cells of stem leaf acumina; F: cells of the apical portion of the secondary branch leaf; G: cells of the apical portion of the primary branch leaf; H–K: paraphyllia; L: median cells of stem leaf; M–O: branch leaves from secondary branches; P: inner perichaetial leaf; R–S, W: branch leaves from primary branches; T–V: stem leaves; X: basal cells of stem leaf. Scale bars: 1 cm for A; 2 mm for B; 1 mm for C; 0.5 mm for M–W; 100 µm for D–L, X.

mittenii is more densely, unipinnately branched, has unipapillose cells and is dioicous.

Description: Plants in loose, interwoven mats, rigid, green or yellowish-green, dull but with glossy stem leaf apices. Stems to 8 cm long, 0.5–1.0 mm wide with leaves, sparsely and irregularly branched, often with secondary branchlets on primary branches; central strand absent;

medullary cells firm-walled, cortical cells in 3–4 layers thick-walled, brown, hyalodermis absent; paraphyllia numerous on stems and primary branches, filamentose and foliose, branched. Stem leaves incurved when dry, widely spreading when moist, 0.9–1.2 × 0.6–0.8 mm, from wide triangular or cordate-deltoid bases abruptly narrowed into long, narrow triangular acumina, with unise-

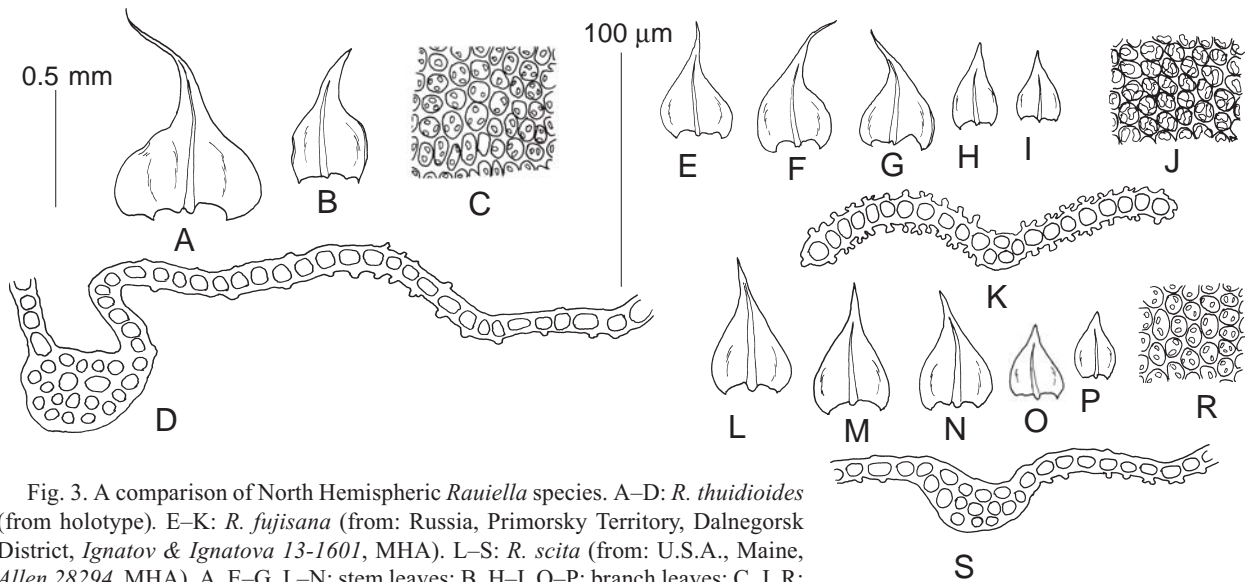


Fig. 3. A comparison of North Hemispheric *Raiiella* species. A–D: *R. thuidioides* (from holotype). E–K: *R. fujisana* (from: Russia, Primorsky Territory, Dalnegorsk District, Ignatov & Ignatova 13-1601, MHA). L–S: *R. scita* (from: U.S.A., Maine, Allen 28294, MHA). A, E–G, L–N: stem leaves; B, H–I, O–P: branch leaves; C, J, R: median laminal cells; D, K, S: leaf transverse sections. Scale bars: 0.5 mm for A–B, E–I, L–P; 100 µm for C–D, J–K, R–S.

riate apices 2–4 cells long, abruptly rounded to the insertion, strongly plicate; costae extending to the base or middle part of narrow acumina, gradually tapered distally; margins entire, plane or recurved at places in basal half; median laminal cells irregularly polygonal and transversely ovate, with moderately thickened walls, slightly collenchymatous, with several round and 0-shaped, low papillae over lumina mainly on dorsal side of leaf lamina, 5–12×7–10 µm; cells of acumina elongate, 25–30×5–8 µm, smooth. Primary branch leaves with ovate base and triangular acumina, 0.55–0.70×0.3–0.4 mm, apical cell sharp, smooth; secondary branch leaves ovate, 0.2–0.25×0.12–0.14 mm, apical cell truncate, papillose. Autoicous. Perichaetia on stem, conspicuous. Inner perichaetial leaves narrowly lanceolate, ca. 2.5–3.0×0.5 mm, not plicate, with long, filiform, flexuose acumina, uniseriate apices 3–4 cells long; margins plane, serrulate throughout; costa to 0.7 the leaf length, weakly delimited from adjacent cells; laminal cells oblong, smooth. Perigonia on stem close to perichaetia, small, inconspicuous. Setae 1.8–2.2 mm long, yellowish or yellow brown. Capsules inclined, cylindrical, slightly curved, 1.8–2 mm long and 0.8–0.9 mm wide. Opercula and annuli not seen. Exostome teeth ca. 500 µm long, light yellow, cross-striolate below, papillose above. Endostome with basal membrane ca. 250 µm high; segments as long as exostome, narrow, not or scarcely perforated; cilia in groups of 2–3, nodose. Spores 9–11 µm, very finely papillose. Calyptrae not seen.

Differentiation. *Raiiella thuidioides* can be rather easily differentiated from the co-occurring common East Asian *R. fujisana* by the longer, up to 8 cm long stems, much sparser branching with somewhat irregularly long primary branches and particularly by the sparse but rather regular appearance of short secondary branches arising from the primary ones (cf. Fig. 4C). Stem leaves

are larger, 0.9–1.2×0.6–0.8 mm vs. to 0.9×0.45 mm (as specified by Noguchi *et al.*, 1991), are more strongly plicate and have typically longer, piliferous apices (Fig. 3), although this character is rather variable in *R. fujisana*. Leaf laminal cells of *R. fujisana* are covered by dense, coarse, forked papillae on both leaf surfaces (Fig. 3K), while in *R. thuidioides* the papillae are smaller, less massive, simple or indistinctly bifid (0-shaped), more numerous on dorsal surface of leaf lamina (Fig. 3D). *Raiiella thuidioides* also differs from *R. fujisana* in longer setae (1.8–2.2 vs. 1.0–1.2 mm), longer exostome teeth (500 vs. 350 µm), and smaller, finer papillose spores (9–11 vs. 12–15 µm). *Raiiella scita* is presently only known from eastern North America and can also be differentiated by the absence of secondary branches and more regular and dense branching pattern (Fig. 4G), although less regular than in *R. fujisana*, and with only few secondary branches. Its leaves are also much smaller than those of *R. thuidioides* – 0.6–0.8 mm long (Allen, 2014). The papillae on leaf lamina of *R. scita* are more similar to those of *R. thuidioides*; cells are described by Allen (2014) as densely pluripapillose on dorsal surface, bulging or unipapillose on ventral surface (cf. Fig. 3S). *Raiiella scita* has shorter setae, 0.8–1.4 mm vs. 1.8–2.2 mm long), and its spore size is similar to *R. thuidioides* (8–12 µm). *Raiiella thuidioides* possibly most resembles members of the genus *Haplocladium* at casual observation with respect to similar, irregular and sparse branching pattern. In particular, stem leaves of *R. thuidioides* are strikingly similar in shape, size and strong plication to plants named *Haplocladium microphyllum* in northeastern Asia, although such plants differ from typical Central American plants representing the type of *H. microphyllum*. Species of *Haplocladium* can, however, be differentiated by the unipapillose cells, dioicous gametangia distribution

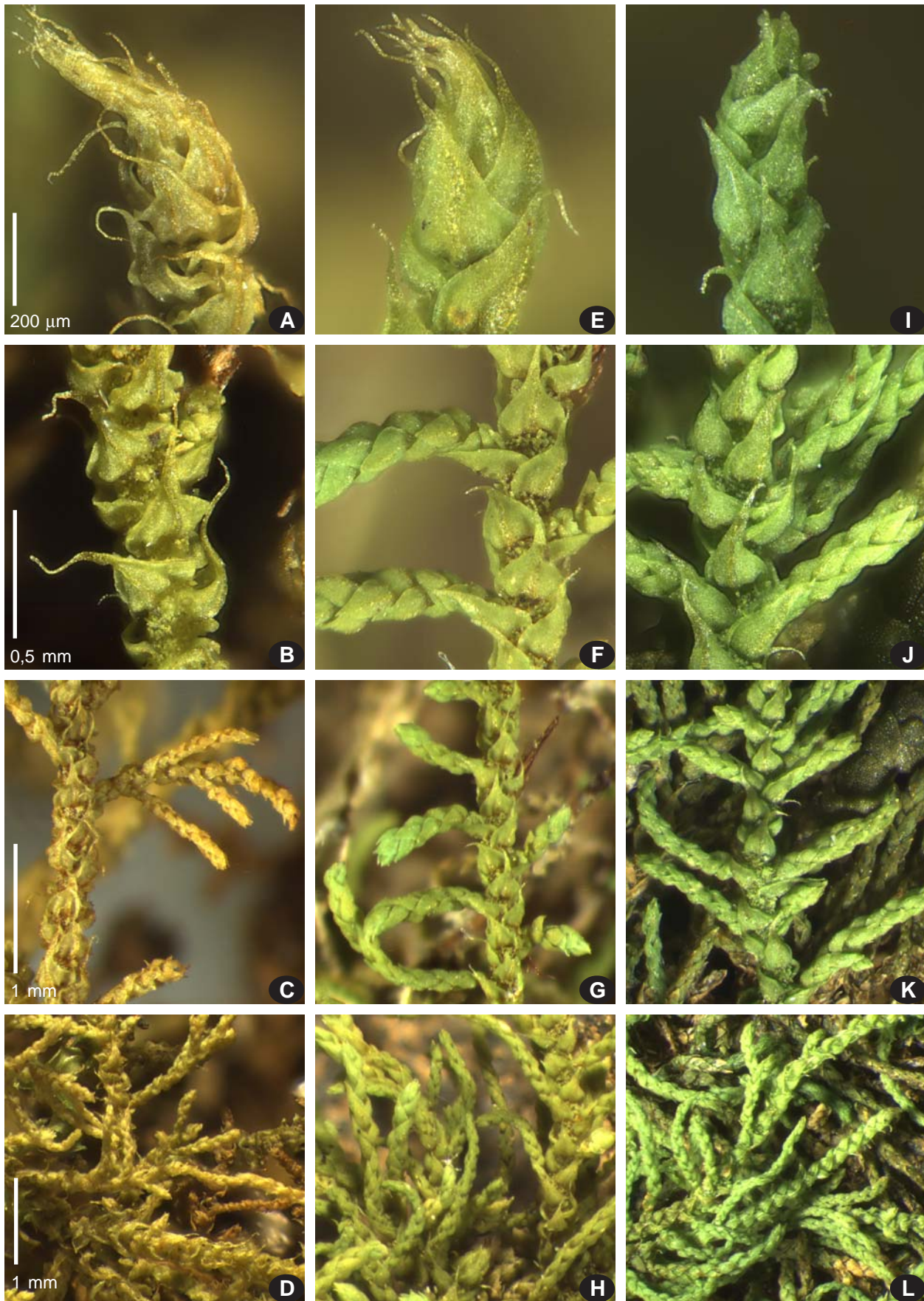


Fig. 4. Habits of *R. thuidioides*, from holotype (A–D), *R. scita* (from: USA, Maine, Allen 28294 MHA9057089; E–H), *R. fujisana* (from: Russia, Primorsky, Ignatov & Ignatova 13-1380, MHA9048227; I–L). Each row at the same magnification.

and mostly sparser paraphyllia, particularly on branches, and secondary branches are also absent. *Boulaya mittenii* is also unipinnate, more densely and regularly branched plant with thicker primary branches, cells are weakly unipapillose and somewhat collenchymatous, the plants are also dioicous. *Thuidium* species are dioicous as well and mostly are more densely and regularly bi- to tripinnate, except for, e.g., *T. alleniorum*, which however has only shortly pointed stem leaves and the branch leaves are incurved.

Ecology and Geography. *Rauiella thuidioides* was collected from half-shaded siliceous boulders in broad-leaved alluvial wood surrounding the brook at 200–250 m a.s.l. It is not known how typical this habitat is for the species; the co-occurring *R. fujisana* is mostly found epiphytically in the same environments, but occasionally is also encountered on stones or bare ground. On the other hand, the habitat of shaded siliceous boulders in humid environment is also typical for the co-occurring species of the genus *Haplocladium* (currently referred to *H. angustifolium*, *H. microphyllum* and *H. strictulum*). The valley beneath Benevskie waterfalls has been well studied for bryophytes and contains many rare mosses of the Eastern element, including *Arrhenopterum heterostichum* Hedw., *Boulaya mittenii* (Broth.) Cardot, *Forsstroemia konoii* (Broth.) Enroth, Fedosov & Ignatov, *Hypopterygium flavolimbatum* Müll. Hal., *Orthotrichum consobrinum* Cardot, *Pylaisia coreana* Nog., *Rhizomnium striatulum* (Mitt.) T.J. Kop. and many others. This discovery confirms that the bryoflora of the north-eastern Asia still contains unnoticed species, which might, however, prove more broadly distributed after previously unassigned material is revised. The use of molecular tools greatly enhances such efforts.

ACKNOWLEDGEMENTS

Jan Kučera acknowledges the loan of material from the herbarium DUKE arranged by B. Aguero and the effective laboratory work by Dr. Alžběta Manukjanová (University of South Bohemia, České Budějovice). The work of MI, EI, AF, OI and VF was supported by RSF project 18-14-00121. The work of VF was also supported by contract AAAA20-120031990012-4 of the Botanical Garden-Institute FEB RAS. The work of AF was also supported by Tsitsin Main Botanical Garden state assignment no. 19-119012390082-6 and of EI by Lomonosov Moscow State University state assignment no. 121032500090-7. We also thank the Ministry of Higher Education and Science of the Russian Federation for support and the Center of Collective Use “Herbarium MBG RAS”, grant 075-15-2021-678. Computational resources (“Metacentrum VO”) were supplied by the Ministry of Education, Youth and Sports of the Czech Republic under the Projects CESNET (Project No. LM2015042) and CERIT-Scientific Cloud (Project No. LM2015085) provided within the program Projects of Large Research, Development and Innovations Infrastructures.

LITERATURE CITED

- ALLEN, B.H. 2014. Maine mosses: Drummondaceae – Polytrichaceae. *Memoirs of The New York Botanical Garden* **111**: i–xvi, 1–607.
- ALLEN, B.H. 2018. Moss flora of Central America. Part 4. Fabroniaceae–Polytrichaceae. – *Monographs in Systematic Botany from the Missouri Botanical Garden* **132**: i–x, 1–830.
- AUSTIN, C.F. 1880. Bryological notes. – *Bulletin of the Torrey Botanical Club* **7**: 15–16.
- BROTHERUS, V.F. (1925) Musci (Laubmoose) 2. Hälfte. Die natürlichen Pflanzenfamilien, Zweite Auflage. – *Duncker & Humblot, Berlin*, 542 pp.
- BUCK, W.R. 1991. The Generic Placement of *Anomodon lagoensis*. – *The Bryologist* **94**: 82. <https://doi.org/10.2307/3243728>
- BUCK, W.R. 2014. *Rauiella*. – In: *FNA Editorial Committee (eds.). Flora of North America*, pp. 378–380.
- BUCK, W.R. & H.A. CRUM. 1990. An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. – *Contributions from the University of Michigan Herbarium* **17**: 55–69.
- CAI, Q.-Y., B.-C. GUAN, G. GE, & Y.-M. FANG. 2019. Molecular Phylogeny of Chinese Thuidiaceae with emphasis on *Thuidium* and *Pelekium*. – *arXiv:1902.06032 [q-bio]*.
- DESHMUKH, U.B. 2021. *Ignatovia*, a new replacement name for *Lazarenkoa* Ignatov & Ignatova (Leskeaceae, Bryophyta). – *Phytotaxa* **497**: 173–174. <https://doi.org/10.11646/phytotaxa.497.2.11>
- GARCÍA-ÁVILA, D., E. DE LUNA & A.E. NEWTON. 2009. Phylogenetic relationships of the Thuidiaceae and the non-monophyly of the Thuidiaceae and the Leskeaceae based on *rbcL*, *rps4* and the *rps4-trnS* intergenic spacer. – *The Bryologist* **112**: 80–93. <https://doi.org/10.1639/0007-2745-112.1.80>
- IGNATOV, M.S., O.D. DUGAROVA, A.V. FEDOROVA & E.A. IGNATOVA. 2019. *Lazarenkoa* a new moss genus from the Russian Far East. *Arctoa* **28**: 226–230. <https://doi.org/10.15298/arctoa.28.21>
- IGNATOV, M.S., J. KUČERA, L. HEDENÄS, O.I. KUZNETSOVA & E.A. IGNATOVA. 2020. A revision of the genus *Orthohecium* (Plagiotheciaceae, Bryophyta) in northern Eurasia. – *Arctoa* **29**: 10–48. <https://doi.org/10.15298/arctoa.29.02>
- KUČERA, J., O.I. KUZNETSOVA, A. MANUKJANOVÁ & M.S. IGNATOV. 2019. A phylogenetic revision of the genus *Hypnum*: Towards completion. – *Taxon* **68**: 628–660. <https://doi.org/10.1002/tax.12095>
- NOGUCHI, A., Z. IWATSUKI & T. YAMAGUCHI. 1991. Illustrated Moss Flora of Japan Vol. 4. – *Hattori Botanical Laboratory, Nichinan*, pp. 743–1012.
- REIMERS, H.J.O. 1937. Die europäischen *Haplocladium*-Arten mit besonderer Berücksichtigung ihrer außereuropäischen Verbreitung und ihrer Verwandtschaft. – *Hedwigia* **76**: 191–298.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D.L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J.P. HUELSENBECK. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. – *Systematic Biology* **61**: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- SOARES, A.E.R. 2015. A Família Thuidiaceae Schimp. no Brasil, um estudo taxonômico, filogenético e morfológico. – *Universidade de Brasília*, 201 pp.
- STAMATAKIS, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics* **30**: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- TOUW, A. 2001. A review of the Thuidiaceae (Musci) and a realignment of taxa traditionally accommodated in *Thuidium* sensu amplo (*Thuidium* Schimp., *Thuidiopsis* (Broth.) M. Fleisch., and *Pelekium* Mitt.) including *Aequatoriella* gen. nov., and *Indothuidium* gen. nov. – *Journal of the Hattori Botanical Laboratory* **90**: 167–209.
- WIJK, R. & W.D. MARGADANT. 1962. New combinations in mosses VII. – *Taxon* **11**: 221–223. <https://doi.org/10.2307/1216658>

Received 1 December 2021

Accepted 20 December 2021

Appendix. Specimen voucher information and GenBank accession numbers for newly generated sequences. Newly generated sequences are in bold.

Taxon	Provenance	Voucher	isolate	ITS	<i>trnF-trnS</i>
<i>Cratoneuron filicinum</i>	Czech Rep.: Horní Maršov	Kučera 22385 (CBFS)	Cn2368	OL989999	-
<i>Entodon concinnus</i>	Bulgaria: Trigrad gorge	Kučera 14006 (CBFS)	En1020	MH613374	OL960672
<i>Entodon schleicheri</i>	Russia: Irkutskaya Prov., Slyudyanka	Kučera 20340 (CBFS)	En1507	MK327300	OL960673
<i>Rhytidium rugosum</i>	Austria: Mt Waldhorn	Kučera 12871 (CBFS)	Ry1522	MK327361	OL960693
<i>Pseudoleskeella catenulata</i>	Czech Rep.: Křížlice	Kučera 14759 (CBFS)	Pk2099	OL990009	OL960682
<i>Pylaisia polyantha</i>	Czech Rep.: Mikulov	Kučera 19399 (CBFS)	Py1353	MH613484	OL960684
<i>Ptilium crista-castrensis</i>	Czech Rep.: Zliv	Kučera 17064 (CBFS)	Pt1032	MH613481	OL960683
<i>Abietinella abietina</i>	Czech Rep.: Horní Albeřice	Kučera 22358 (CBFS)	Ab2127	OL989996	OL960665
<i>Actinothuidium hookeri</i>	China: Yunnan	Shevock 52072 (MW)	ThF22	OL989997	OL960666
<i>Boulaya mittenii</i>	Russia: Primorsky, Elomovsky	Kučera 21386 (CBFS)	Bo2126	OL989998	OL960667
<i>Bryonoguchia molkenboeri</i>	Russia: Primorsky, Chandolaz	Ignatov & Ignatova 13-1936 (MW)	OK1176	KX396260	OL960668
<i>Echinophyllum sachalinense</i>	Russia: Primorsky, Tadusha	Ignatov et al. 13-1469 (MW)	OK1174	KX396259	OL960671
<i>Echinophyllum sachalinense</i>	Russia: Botchi Reserve	MW9037836	ThF48	OL990000	OL960669 OL960670
<i>Haplocladium angustifolium</i>	South Africa: Amatola Mts	Vanderpoorten 23 (DUKE)	Hc2288	OL990002	OL960675
<i>Haplocladium angustifolium</i>	Russia: Primorsky, Elomovsky	Kučera 21282 (CBFS)	Hc2130	OL990001	OL960674
<i>Haplocladium microphyllum</i>	USA: Florida, Orlando	Majestyk 11418 (DUKE)	Hc2289	OL990003	OL960676
<i>Haplocladium microphyllum</i>	Bolivia: Gran Chaco	A. Fuentes s.n. (DUKE)	Hc2334	OL990004	OL960677
<i>Haplocladium virginianum</i>	USA: NC, Lillington	Aguero 19745 (DUKE)	Hc2293	OL990005	OL960678
<i>Helodium blandowii</i>	Austria: Wanzenau	Kučera 17242 (CBFS)	He2108	OL990006	OL960679
<i>Leskea polycarpa</i>	Czech Rep.: Řeznovice	Kučera 19133 (CBFS)	Lk2097	OL990007	OL960680
<i>Pelekium pygmaeum</i>	Russia: Primorsky, Dalnegorsk	Kučera 21867 (CBFS)	Pe2129	OL990008	OL960681
<i>Raiiella fujisana</i>	Russia: Primorsky, Pidán Mt	Kučera 21698 (CBFS)	R12125	OL990010	OL960685
<i>Raiiella fujisana</i>	Russia: Khabarovsk Territory, Badzhal Range	MW9130131	ThF29	OL990011	OL960686
<i>Raiiella fujisana</i>	Russia: Shikotan Island	Fedosov s.n. 15.VIII.2021 (MW)	ThF77	-	OL960687
<i>Raiiella scita</i>	USA: Maine, Schoodie Bay	Schofield 124652 (DUKE)	R12287	OL990012	OL960688
<i>Raiiella scita</i>	Canada: Nova Scotia	Schofield 97336 (DUKE)	R12369	-	OL960689
<i>Raiiella thuidioides</i>	Russia: Primorsky, Elomovsky	Kučera 21386 (CBFS)	R12133	OL990014	OL960692
<i>Raiiella thuidioides</i>	Russia: Primorsky, Elomovsky	Ignatov et al. #13-1264 (MHA)	OK599	OL990013	OL960690 OL960691
<i>Thuidium alleniorum</i>	USA: NC, Atkinson	B. Shaw 6015 (DUKE)	Th2286	OL990015	OL960694
<i>Thuidium assimile</i>	Czech Rep.: Praha	Kučera 22175 (CBFS)	Th2100	OL990016	OL960695
<i>Thuidium assimile</i>	Russia: Primorsky, Chandalaz	Kučera 21386 (CBFS)	Th2135	OL990017	OL960696
<i>Thuidium delicatulum</i>	USA: NC, Duke Forest	Aguero 19750 (DUKE)	Th2278	OL990018	OL960697
<i>Thuidium delicatulum</i>	Norway: Luster	MW9078688	ThF57	OL990019	OL960698
<i>Thuidium kanedae</i>	Japan: Shikoku Island	MW9075555	ThF54	OL825640	OL960700
<i>Thuidium kanedae</i>	Russia: Shikotan Island	Fedosov s.n. 27.VIII.21 (MW)	ThF73	OL825641	OL960701
<i>Thuidium pristocalyx</i>	Russia: Primorsky, Elomovsky	MW9066364	ThF55	OL990020	OL960699
<i>Thuidium tamariscinum</i>	Czech Rep.: Vidov	Kučera 22544 (CBFS)	Th2197	OL990021	OL960702
<i>Thuidium tamariscinum</i>	Russia: Iturup Island	MW9066363	ThF56	OL990022	OL960703
<i>Thuidium thermophilum</i>	Russia: Kunashir Island	Koroteeva 15-6/1-1 MHA9119722	OK3014	OL990023	OL960704
<i>Thuidium thermophilum</i>	Russia: Koryaksky Distr.	Chernyagina #5 MHA9119753	OK3015	EF368013	OL960705