Arctoa (2026) **35**: *1–20*
doi: 10.15298/arctoa.35.01

SPHAGNUM KUSHIROENSE, S. MICROPORUM AND *S. SUBOBESUM* IN RUSSIA

SPHAGNUM KUSHIROENSE, S. MICROPORUM И *S. SUBOBESUM* В РОССИИ

Anna V. Shkurko[1], Oxana I. Kuznetsova[1], Elena D. Lapshina[2], Elena A. Ignatova[3], Rui-Liang Zhu[4] & Michael S. Ignatov[1,2]

Анна В. Шкурко[1], Оксана И. Кузнецова[1], Елена Д. Лапшина[2], Елена А. Игнатова[3], Руи-Лианг Жу[4], Михаил С. Игнатов[1,2]

Abstract

Sphagnum microporum, S. kushiroense and *S. subobesum* are reported for the first time from Russia. Molecular phylogenetic analysis based on plastid *trn*G marker found them in the clade with the GenBank accessions of *S. microporum* and *S. kushiroense* from China and Japan. Nuclear RAPD-A sequences also support this position for Russian samples of *S. microporum* and *S. kushiroense*. These two species do not differ from each other in the studied molecular markers, but can be distinguished by few morphological traits. *Sphagnum kushiroense* appeared to be locally common in mires in the continental southern Russian Far East, extending westwards to the Czara River basin in Transbaikalia. *Sphagnum microporum* is currently known in Russia from three localities in Khabarovsk Territory. Russian specimens referred to *Sphagnum subobesum* are supposed to be of hybrid origin, where maternal species is likely *S. microporum* or S. *kushiroense* and paternal one is another species of *Sphagnum* subgen. *Subsecunda*. *Sphagnum subobesum* was found in Russia in few localities, including eastern Yakutia, Kamchatka, Khabarovsk Territory, and Kunashir Island, where it grew mainly in heavily flooded sites of mires at lake shores. Presence of *Sphagnum denticulatum* in the Russian Far East region is not confirmed, as the specimen from the Amurskaya Province, where it was collected deeply submerged in lake, contains the mixture of *S. subobesum* and *S. kushiroense*.

Резюме

Sphagnum microporum, S. kushiroense и *S. subobesum* приводятся впервые для территории России. По результатам филогенетического анализа последовательностей хлоропластного локуса *trn*G они оказываются в кладе вместе с последовательностями *S. microporum* и *S. kushiroense* из Китая и Японии, которые были взяты из Генбанка. Ядерный локус RAPD-A также поддерживает эту топологию для российских образцов *S. microporum* и *S. kushiroense*. Эти два вида не отличаются друг от друга по этим двум молекулярным маркерам, однако они имеют определенные морфологические отличия. *Sphagnum kushiroense* оказался местами нередким на болотах в континентальной части российского Дальнего Востока, достигая на западе бассейна реки Чара в Забайкалье. *Sphagnum microporum* в настоящее время известен в России из трех местонахождений в Хабаровском крае. Предполагается, что российские образцы *Sphagnum subobesum* имеют гибридное происхождение; при этом материнским видом, по-видимому, является *S. microporum* или S. *kushiroense,* а в качестве отцовского вида выступает другой вид из подрода *Subsecunda*. *Sphagnum subobesum* был найден в России в немногих местонахождениях, включая восточную Якутию, Камчатку, Хабаровский край и о. Кунашир, где он чаще всего рос в сильно обводненных местах на заболоченных берегах озер. Присутствие *Sphagnum denticulatum* на российском Дальнем Востоке не было подтверждено, поскольку его единственный сбор из Амурской области представляет собой смесь *S. subobesum* и *S. kushiroense*.

KEYWORDS: molecular barcoding, RAPD-A, *trn*G, taxonomy, morphology, *S. contortum, S. denticulatum*

Introduction

The genus *Sphagnum* remains unevenly studied in Russia. First comprehensive catalogue of mosses of the Russsian Empire (Warnstorf, 1913, 1914) included its records almost totally from European Russia and the Caucasus, while the data on the distribution of *Sphagnum* species in Asian Russia were fairly scarce. They were based on collections from the lower course of Yenissey River made

[1] – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow, 127276 Russia. E-mails: shenku@bk.ru; oikuznets@gmail.com; misha_ignatov@list.ru. ORCID: (AS) 0000-0001-7682-9323; (OK) 0000-0002-5513-1329; (MI) 0000-0001-6096-6315

[2] – Yugra State University, 16 Chekhov St., Khanty-Mansiysk, 628012 Russia. E-mail: e_lapshina@ugrasu.ru. ORCID: (EL) 0000-0001-5571-7787

[3] – Lomonosov Moscow State University, Faculty of Biology, Leninskie Gory Str. 1–12, Moscow 119234 Russia. E-mail: arctoa@list.ru. ORCID: (EI) 0000-0001-6287-5660

[4] – Bryology Laboratory, School of Life Sciences, East China Normal University, 500 Dongchuan Road, Shanghai 200241, China. E-mail: rlzhu@bio.ecnu.edu.cn. ORCID: (RZ) 0000-0002-0163-8255

by H.W. Arnell and J. Sahlberg during the trip of 1876 and published in the "Musci Asia borealis. II" (Lindberg & Arnell, 1890). Also, samples of A. Cajander from Lena River and of A. Sapehin from Irkursk surroundings were cited. Only two species of *Sphagnum* sect. *Subsecunda*—*S. subsecundum* Nees and *S. platyphyllum* (Lindb. ex Braithw.) Warnst.—were recorded by Warnstorf (1913) based only on Arnell's collections.

Later, Savicz-Lyubitskaya (1932) reported *S. contortum* Schultz from Kamchatka, and then she described two new species, *S. orientale* L.I. Savicz and *S. perfoliatum* L.I. Savicz from Asian Russia (Savicz-Lyubitskaya, 1951). The descriptive flora of *Sphagnum* of the Soviet Union (Savicz-Lyubitskaya, 1952), included seven species of *Sphagnum* sect. *Subsecunda*, five of which were reported for Asian Russia: *S. subsecundum*, *S. platyphyllum*, *S. contortum, S. orientale*, and *S. perfoliatum*.

The "Handbook of the *Sphagnum* of the USSR" published later (Savicz-Lyubitskaya & Smirnova, 1968) provided only general information on species distribution, adding to the previous list *S. denticulatum* Brid. from the Russian Far East region, without any reference to more definite data. The only specimen-based record of *S. denticulatum* from the Russian Far East has been published by Abramova & Abramov (1977), who identified it in the collection from Amur Province, gathered in a lake at two meter deep.

Subsequent publications in the end of the 20th century followed mostly the treatment by Savicz-Lyubitskaya & Smirnova (1968), referring collections with multilayered stem hyalodermis and small, scattered comissural pores in hyalocysts of branch leaves to *S. contortum*.

Shortly after Shaw *et al*. (2008) described from Alaska one more species of *Sphagnum* subgen. *Subsecunda*, *S. beringiense* A.J. Shaw, E.R.Andrus & B. Shaw, Maksimov *et al*. (2016) revised collections from Asian Russia and found that most samples referred to *S. contortum* from the northern part of Asian Russia actually belong to that species. At the same time, some samples from southern Russian Far East were found by Maksimov *et al*. as belonging to *S. inexspectatum* Flatberg, a species similar to *S. contortum* by partially 2-layered hyalodermis, though clearly different in pores in branch leaves, which are most similar to *S. inundatum* Russow (Flatberg, 2005).

In 2025, during the field trip in Khabarovsk Territory, numerous specimens of *Sphagnum* subgen. *Subsecunda* were collected by E.D. Lapshina and I.V. Philippov in the course of the study of mire vegetation. An attempt to identify them revealed that their features do not fit any species known from Russia, as plants with minute, scattered comissural pores in hyalocysts of branch leaves were associated with mainly unistratose hyalodermis. Their identity with *S. microporum* Warnst. ex Cardot was presumed; moreover, this species was known from North-East China (Li & He, 1999) and has been supposed to occur in Asian Russia (Maksimov, 2023). A considerable variation of such plants, however, invoked a molecular phylogenetic study with a broader sampling of similar specimens from eastern Russia. East Asian species of *Sphagnum* subgen. *Subsecunda* were recently in a focus of taxonomical studies by, e.g., Flatberg (2005), and various molecular phylogenetic studies provided a copiose sequence data (Shaw *et al*., 2008a, 2008b, 2013, 2015; Kirkjeeide *et al*., 2019), which make possible a wider comparison of Russian and Chinese specimens.

MATERIAL AND METHODS

Sampling

For molecular phylogenetic study we sampled 32 specimens of *Sphagnum* subgen. *Subsecunda* from MHA and HSNU herbaria, which were preliminarily inferred to *S. beringiense* (2), *S. contortum* (1), *S. orientale* (9), *S. subsecundum* (4), *S. perfoliatum* (5) and new collections presumably referred to *S.* cf. *microporum*, from Russia (10) and China (1).

Laboratory protocol

For DNA extraction, one shoot per specimen was chosen and its capitulum was used. Total genomic DNA was extracted from dry plants using the NucleoSpin Plant DNA extraction kit (Macherey-Nagel, Germany) following the manufacturer's instructions. We obtained Sanger sequences of *Sphagnum*-specific anonymous nuclear region identified by Shaw *et al.* (2003), originally called RAPDa, but referred here as RAPD-A following GenBank naming. RAPD-A was demonstrated to be variable and useful for molecular phylogenic reconstructions at the species and infraspecific levels (Shaw *et al*., 2005a,b, 2008a,b). Additionally, we obtained sequences of *trn*G plastid marker. The laboratory protocols of amplification follow Fedosov *et al*. (2016) for *trn*G and Shaw *et al*. (2003) for RAPD-A regions.

Molecular phylogenetic analysis

Both RAPD-A and *trn*G sequences are well represented in GenBank for *Sphagnum* subgen. *Subsecunda*, therefore we added our dataset with 37 sequences of RAPD-A region representing *S. beringiense, S. contortum, S. kushiroense* H. Suzuki*, S. microporum, S. miyabeanum* Warnst.*, S. orientale, S. platyphyllum, S. subsecundum*; and 50 sequences of *trn*G of the same species plus *S. denticulatum, S. inundatum* Russow*, S.* × *lydiae* Flatber & K. Hassel and *S. perfoliatum*. As an outgroup, accessions for one isolate from GenBank and original sequenses for the one specimen of *S. fallax* (H. Klinggr.) H. Klinggr. were added to both datasets. The list of GenBank accession numbers of the included specimens and vouchers of specimens studied *de novo* are provided in Appendix 1. Sequences were aligned using MAFFT v.7487 for Windows (Katoh *et al.,* 2002) and then alignments were edited manually in BioEdit (Hall, 1999).

Indels in both *trn*G and RAPD-A datasets were scored using the simple indel coding approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1 (Müller, 2005) for Bayesian (BI) reconstructions and in FastGap 1.2 (Borchsenius, 2009) for Maximum Likelihood (ML) analysis.

The dataset used for molecular phylogenetic reconstructions based on *trn*G was composed of 82 accessions, 719 positions plus 6 indels.

The *trn*G alignment lacks ambiguous positions, while RAPD-A data aligning was hampered by a regular presence of polymorphic regions in electropherograms of five samples of plants that are morphologically similar to *S. microporum* (Fig. 2), suggesting their putative hybrid origin (Puglisi *et al*., 2011; Beike *et al*., 2014; Schanzer *et al*., 2020; Hrazdilova *et al*., 2023). These five specimens are called hereafter 'S. sp. × microporum'. Since the speciation through hybridization including allopolyploidisation is well known for *Sphagnum* subgen. *Subsecunda* (Shaw *et al*., 2005b; Ricca & Shaw, 2010; Ricca *et al*., 2011; Shaw *et al*., 2015, *etc*.), we reexamined electropherograms of the RAPD-A sequences obtained for 'S. sp. × microporum'. For each specimen four partially overlapping reads (from internal, external, direct and reverse primers; see Shaw *et al*., 2003) were analyzed visually and then combined in consensus sequences where the 32 positions with double peaks were coded with IUPAC ambiguity codes (Table 1). Consensus sequences for the Table 1 are based on the sequences involved in the analyses of RAPD-A and shown in Figs. 3-4, Additionally, we constructed an artificial sequence of 'putative parent 2', which have in ambiguous positions a nucleotide other than that in *S. microporum*.

The preliminary analyses of the datasets with and without these five samples brought markedly different results, as the inclusion of 'S. sp. × microporum' reduced the resolution of the phylogenetic trees considerably because of ambiguities at the positions with additive signals. Therefore, we conducted two analyses, with and without 'S. sp. × microporum'.

The first analysis of RAPD-A data was conducted for a broader sampling, including four accessions of 'S. sp. × microporum' (the fifth, OK2945, was excluded due less than 75% completeness), generated 'putative parent 2' and accessions of species from five subgenera (Fig. 3). Such sampling makes possible to check the subgeneric position of the putative second parent, which might belong not necessarily to subgenus *Subsecunda*, as intrasubgeneric hybrids with species of the subgenera Cuspidata and Acutifolia are known (Shaw *et al*., 2016; Meleshko *et al*., 2018; Kyrkjeeide *et al*., 2019). Altogether, this dataset included 47 accessions, 1140 positions, and 12 coded indels. The resulted tree was rooted on *S. compactum*.

The second analysis was conducted without 'S. sp. × microporum' accessions; it included the dataset of *Sphagnum* subgen. *Subsecunda* species and two accessions of *S. fallax* from subgen. *Cuspidata* as an outgroup. This RAPD-A dataset included 59 accessions, having 1123 positions of the alignment plus 5 coded indels.

Phylogenetic reconstructions under BI were performed using MrBayes v.3.2.7 (Ronquist *et al.,* 2012), with two parallel runs each consisting of eight Markov chains, 5 000 000 generations with default number of swaps and sampling frequency one tree each 1000 generations, the chain temperature was set at 0.02 and models were sampled throughout the GTR model space (nst = mixed). Consensus trees were calculated after omitting first 25% of trees as burn-in. The convergence between runs previously assessed as an average split deviation frequency decreased lower than 0.01 was checked to have reached after 0.5–1.5 million generations. Maximum likelihood trees were estimated using IQ-TREE 3.0.1. application for Windows (Trifinopoulos *et al.,* 2016) with auto estimation of the best-fit models of nucleotide evolution which suggested the HKY+G4 model for the nuclear markers RAPD-A, F81+F for plastid and F81+F+ASC for indel partitions. Robustness of the nodes was assessed using 10000 pseudoreplications of the ultrafast bootstrapping algorithm (Minh *et al.,* 2013). The final trees were visualized using FigTree 1.4.3.

Morphological studies

All sequenced specimens were studied using common morphological methods, including light microscopy and SEM observations. For light microscopy, dry plants were soaked in water and stained with Methylene Blue. Specimens were studied and photographed under light microscope BX-63P with camera DP74, Z-stacks of several images were generated using HeliconFocus 4.50 (Kozub *et al*., 2008). Some photographs were taken with Stereomicroscope Nikon SMZ-25, camera Nikon DS-Fi3m stacking photos with the NIS-element, 05.30.00 version. SEM micrographs were obtained from Ciqtek SM-3200, on herbarium specimens without special preparation except the gold coating, ca. 30 nm and observed at 20 kv in high vacuum.

Results

Molecular phylogenetic analysis

In the tree inferred from the plastid *trn*G region, affinities within the ingroup (subgen. *Subsecunda*) are weakly resolved as a whole, but the monospecific clades are mostly well supported (Fig. 1). As an exception, nine involved accessions of *S. perfoliatum* do not form a clade. *Sphagnum microporum* was found in a moderately supported clade (PP=0.99, BS=89) that included also *S. kushiroense* and five specimens of 'S. sp. × microporum'. The most Russian specimens have *trn*G sequences identical to those from Japan and China, excepting OK4504 that possesses additional molecular autapomorphies.

The first phylogenetic tree based on RAPD-A (Fig. 3) resolves all subgenera as clades with maximal posterior probability and bootstrap supports varying from 76 to 100. The clade of the subgen. *Subsecunda* consists of three subclades, while the 'S. sp. × microporum' and 'putative parent 2' samples remain in the unresolved polytomy within this clade. At the same time, *S. microporum* (including five Russian accessions) and *S. kushiroense* form a fully supported clade in the terminal position within the maximally supported clade, which also included *S. pylaesii* Brid. and *S. contortum*.

Fig. 1. Bayesian phylogenetic tree based on *trn*G sequences for the *Sphagnum* subgen. *Subsecunda*. Bayesian posterior probabilities (>70) and Maximum Likelihood bootstrap supports (>80) are shown at branches.

Table 1. Polymorphic positions revealed in electropherograms within RAPD-A sequences of 'S. sp. × microporum' specimens and the nucleotide substitutions at the same positions in sequences of hypothetical 'putative parent 2' and other species of subg. *Subsecunda*. The presented data are fromed accounting all RAPD-A sequences used in analyses (Fig. 4). The position numbers are provided according to the alignment, 1123 bp, started from AGCTTACATCCTTAGCCCC.

lineage	101	153	181	194	195	201	203	230	231	318	426	510	551	640	661	694	720	730	732	736	755	758	784	855	981	1006	1009	1019	1034	1046	1052	1062
microporum	G	G	A	A	G	A	C	T	G	C	C	A	A	C	C	A	C	C	G	G	A	G	T	A	G	C	A	C	C	A	G	G
kushiroense	G	G	A	A	G	A	C	T	G	C	C	A	A	C	C	A	C	C	G	G	A	G	T	A	G	C	A	C	C	A	G	G
'sp. x microporum'	A+G	A+G	A+G	A+G	A+G	A+G	C+T	C+T	A+G	C+T	C+T	G+A	A+G	C+T	G+C	A+G	C+T	G+C	A+G	G+C	A+G	G+T	C+T	A+C	G+C	C+T	A+T	A+C	T+C	A+G	A+G	A+G
'putative parent 2'	A	A	G	G	A	G	T	C	A	T	T	G	G	T	G	G	T	G	A	C	G	T	C	C	C	T	T	A	T	G	A	A
beringiense	A	A	G	A/G	A/T	G	T	T	A/C	T	T	G	G	T	G	G	T	G	G	C	G	T	C	C	C	T	A	A	T	G	A	G
contortum	A	G	G	A	A	A	C	T	G	T	C	A	A	T	C	A	C	C	G	G	G	G	T	A	G	C	A	C	C	G	A	G
orientale	A	A	G	A	A	G	T	T	A	T	T	G	G	T	G	G	T	G	G	C	G	T	C/T	A/C	C	T	A	A	T	G	A	G
platyphyllum	A	A	G	A	A	G	T	T	A	T	T	G	G	T	G	G	T	G	G	C	G	T	C	C	C	T	A	A	T	G	A	G
miyabeanum	A	A	G	G/A	A	A	C	T	A	T	T	G	G	T	G	G	T	G	G	C	G	T	C	C	C	T	T	A	T	G	A	G
subsecundum	A	A	G	G/A	A	A	C	T	A	T	T	G	G	T	G	G	T	G	G	C	G	T	C	C	C	T	T	A	T	G	A	G

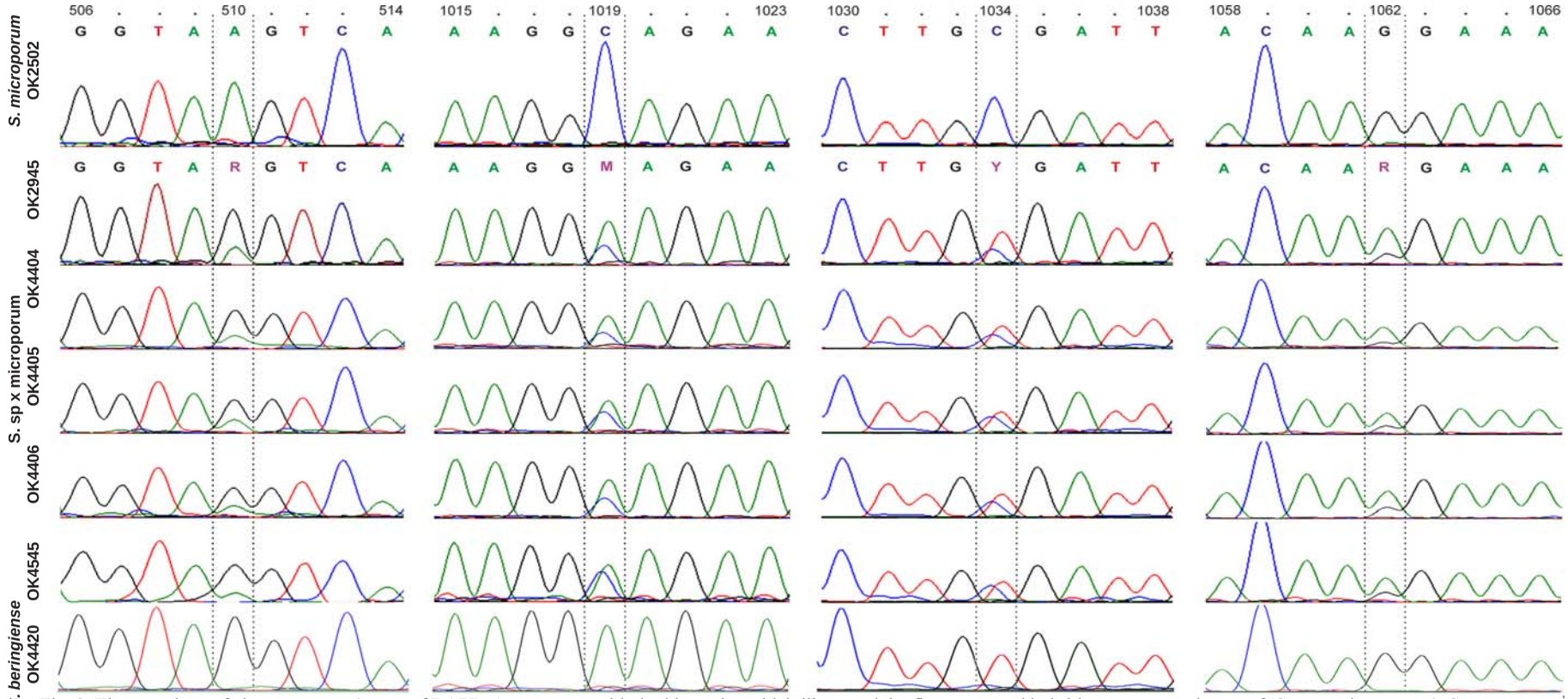

Fig. 2. The snapshots of chromatograms' parts of RAPD-A sequences with double peaks, which illustrated the five suggested hybridogeneous specimens of 'S. sp x microporum', *S. microporum* and one of possible parents, *S. beringiense* (specimesn OK4420), though one of its positions (#1062) contradits this, pointing the lack of unequivocal parent among studied species (cf. Table 1).

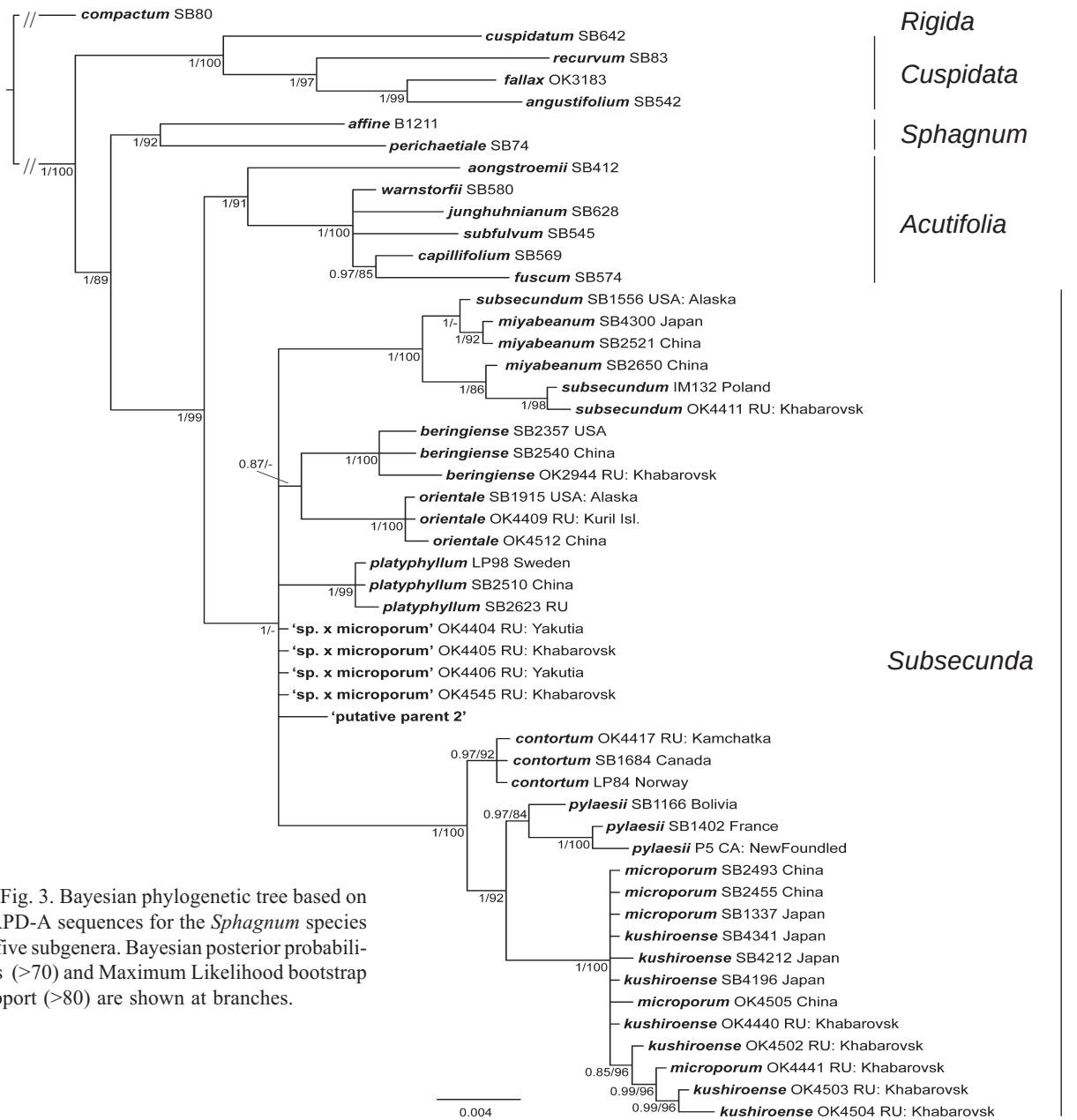

Fig. 3. Bayesian phylogenetic tree based on RAPD-A sequences for the *Sphagnum* species of five subgenera. Bayesian posterior probabilities (>70) and Maximum Likelihood bootstrap support (>80) are shown at branches.

In the second phylogenetic tree (Fig. 4) inferred from nuclear RAPD-A, subgen. *Subsecunda* is represented by two major clades. The first one (PP=1 BS=86) includes accessions of *S. platyphyllum, S. beringiense, S. orientale, S. subsecundum,* and *S. miyabeanum*; its topology is not considered in details. The second major clade is maximally supported; it splits into two, not supported one (PP=0.81, BS=92) with six accessions of *S. contortum* and maximally supported one with all included accessions of *S. microporum* and *S. kushiroense.* Its further topology again does not allow separating these two: one Russian accession, OK4440, is found in a polytomy with Japanese specimens of the both species and Chinese specimens of *S. microporum*, while the rest of Russian accessions form a grade nested within this polytomy.

Electropherogram analysis

Observation of the polymorphic regions in RAPD-A electropherograms reveals 32 positions with double peaks recurrent for the four 'S. sp. × microporum' accessions and 22 in the available part of 'S. sp. × microporum' sample OK2945, while any polymorphic sites in electropherograms of *S.* cf. *microporum* studied de novo are absent (Table 1, Fig. 2). Since both peaks in these polymorphic regions are uniformly repeated in the sequences of different accessions including overlapping parts of different reads obtained from the same PCR product, we suggest the presence of two different copies of the nuclear RAPD-A region in 'S. sp. × microporum' rather than sequencing artifact (Fig. 2). A comparison with some other species of *Sphagnum* subg. *Subsecunda* revealed a clear correspondence between one of the two nucleotide peaks in these

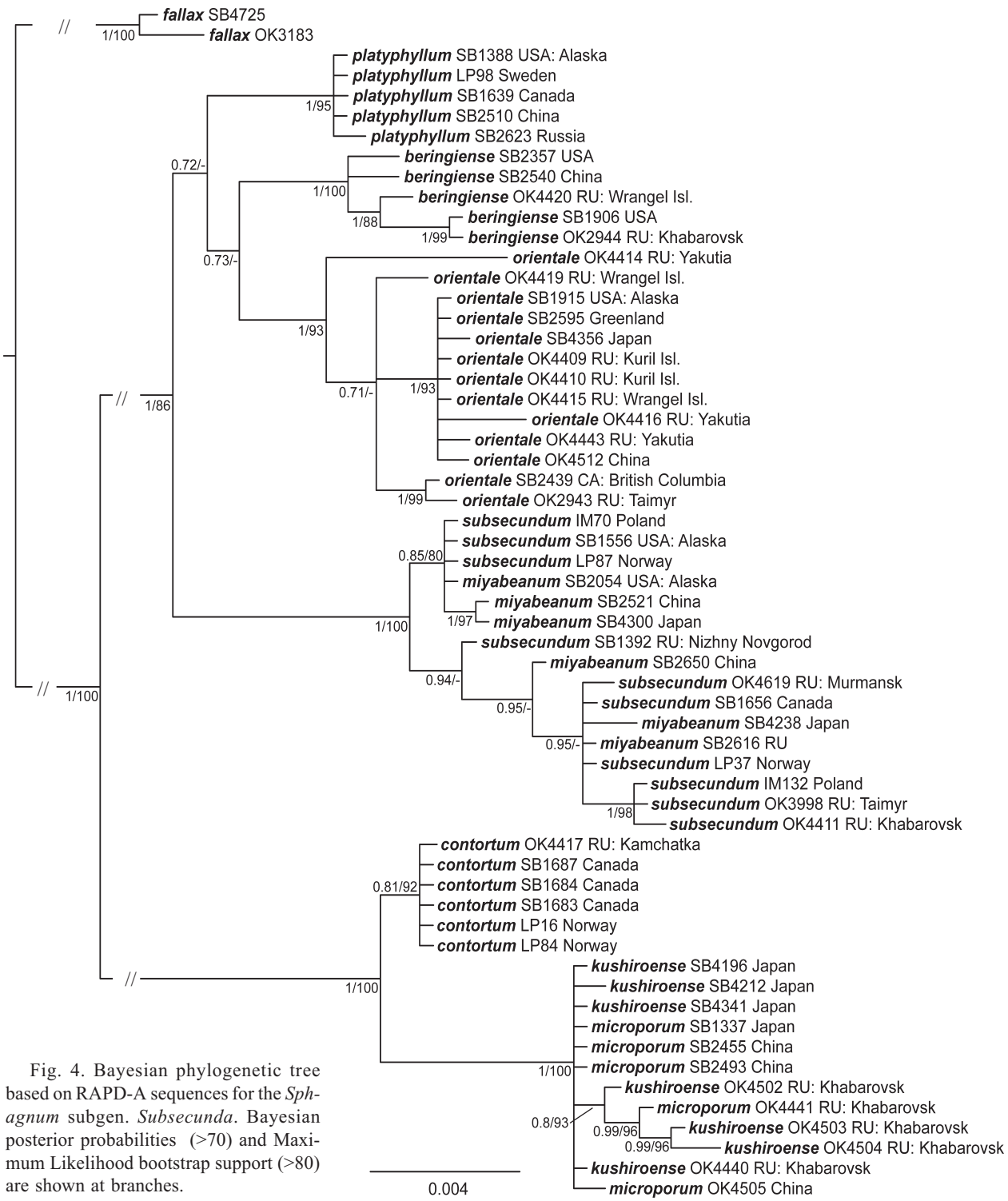

Fig. 4. Bayesian phylogenetic tree based on RAPD-A sequences for the *Sphagnum* subgen. *Subsecunda*. Bayesian posterior probabilities (>70) and Maximum Likelihood bootstrap support (>80) are shown at branches.

polymorphic positions and the nucleotides at the same positions in all sequences of *S. microporum* and *S. kushiroense* (Table 1). No one of the involved species fully match the alternative read where *S. microporum* signal was excluded from double peaks, and thus represented 'putative parent 2' sequence (Table 1). However, the inclusion of this 'putative parent 2' in the analysis showed its position in the clade of the subg. *Subsecunda* (Fig. 3). The most similar to 'S. sp. × microporum' is one of the haplopypes of *S. beringiense,* differing from it only by 4 substitutions. *Sphagnum orientale, S. platypyllum*, *S. subsecundum, S. miyabeanum* and other haplotypes of *S. beringiense* differ from the 'putative parent 2' in 5 substitutions, while *S. contortum* is the most distant with 24 substitutions.

Morphological studies

The samples of *S.* cf *microporum* resolved in a clade with GenBank accessions of *S. microporum* and *S. kushiroense* in both *trn*G and RAPD-A trees share some morphological traits. Their stem hyalodermis is mainly 1-layered, rarely at places 2-layered; the stem leaves have fibril stubs or, rarely, fibrils in the distal 1/3–1/2 of leaves; and the branch leaf hyalocysts on the dorsal surface have few pores of small size arranged in discontinuous rows (Fig. 5A–F). The few small pores are also typical for *S. contortum* (Fig. 6A–C) that, however, can be readily distinguished by having 3–4-layered stem hyalodermis. *Sphagnum beringiense* possesses pores larger, more even in size, arranged in more continuous rows (Fig. 6G–I). *Sphagnum orientale* is similar to *S. microporum* s.l. in smaller pore size, but its branch leaves are short and subobtuse, and pores in branch leaves are numerous, arranged in continuous rows, and more even in size than in the latter (Fig. 6D–F). However, the studied specimens of *S.* cf *microporum* were found quite variable in pores on the ventral surface of stem leaves in distal 1/3 leaf part (cf. Fig. 9). Some of them fit well the circumscription of *S. microporum* s. str., while most other specimens correspond to *S. kushiroense*, as it has been circumscribed and illustrated by Suzuki (1958) and Kyrkjeeide *et al.* (2019).

The plants of 'S. sp. × microporum' are more robust and have larger stem leaves (1.1–1.5 mm long) than those of the latter; moreover, their branch leaves are widely acute and neither strongly falcate nor secund (Figs. 7A–H, 8A–C). The overall morphology of 'S. sp. × microporum' conforms to *S. subobesum* Warnst. circumscription of Suzuki (1958) and Flatberg (2005) and to the Japanese specimens collected and identified by Suzuki (dupl. from H.S. 23923, 19545; LE).

Morphological study of the only specimen from the Russian Far East region identified as *S. denticulatum* showed that it represents a mixture of two plants different in size, but both belonging to the discussed group with 1(2)-layered stem hyalodermis and discontinuous rows of minute pores in branch leaf hyalocysts. The larger one, with stem leaves over one millimeter corresponds to morphology of *S. subobesum* (Fig. 8I, K), while the smaller one can be referred to *S. kushiroense* (Fig. 8J, L).

DISCUSSION

Sphagnum microporum and ***S. kushiroense***

The morphological variation of *Sphagnum microporum* was discussed in detail by Suzuki (1958), who found it to be significant and therefore merged with it two species, *S. okamurae* Warnst. and *S. oligoporum* Warnst. However, the Hokkaido population of this group was found by him to be morphologically distinct enough for segregation it to the new species, *Sphagnum kushiroense*. The most detailed study of genetic diversity of *S. kushiroense* and *S. microporum* has been done by Shaw *et al*. (2015). Their microsatellite analysis showed that *S. kushiroense* is haploid, while *S. microporum* includes both haploid and diploid populations. Moreover, haploid *S. microporum* specimens from China were found to be identical with *S. kushiroense*, while the diploid specimens of *S. microporum* from Japan differed. Although they suggested that the new species should be described, this remains unresolved, as the molecular data for the type collections of *S. microporum* from North Korea are not available.

Since our results also do not contribute to the resolving of this question, further we treat *S. kushiroense* and *S. microporum* as the two species based on their morphology, admitting that they might be conspecific. At the same time, the morphological variation of *S. microporum* in Japan—as can be seen from herbarium collection study (Fig. 9D–G)—the presence of undescribed species, as proposed by Shaw *et al*. (2015), is also possible.

The novelty of our results is the considerable range extension of *S. kushiroense* that appears to be a widespread species in mires in the lower course of Amur River, which remained poorly studied because of difficulty to access. One studied collection of *S. kushiroense* is from Jilin Province of China (Figs. 8D, 9I), though that plant was from a pond side and not optimally developed, thus reported now only with question mark. At the same time, plants referred here to *S. microporum* s. str. according to Suzuki (1958)' definition were found in a few localities in Russia and in Heilongjiang in China.

Sphagnum subobesum

Molecular phylogenetic studies conducted by Shaw (2000) resolved *S. subobesum* in a clade with *S. khasianum* Mitt., albeit with a low support. The only ITS of *S. subobesum* available in GenBank for a plant from Japan (AF193736) by BLAST search is maximally similar to the three specimens: *S. khasianum* from China, Guangdong Province, and Japanese specimens of *S. microporum* and *S. subsecundum*.

Despite the lack of molecular references of RAPD-A and *trn*G markers for *S. subobesum* to compare, we suggest referring the putative allopolyploid plants of 'S. sp. × microporum' to this species based on the morphological traits as it was discussed above. Noteworthy, the studied plants have quite large stem leaves (Figs. 7A–H); in Russia among species of *Sphagnum* subgen. *Subsecunda,* leaves of a similar size are known only in *S. denticulatum* and *S. platyphyllum.* However, the latter species differs in its constantly 2-layered stem hyalodermis, branches usually not differentiated into divergent and pendent, and stem and branch leaves similar in shape, with fibrils and pores extending almost to the leaf base. Plants of *S. denticulatum* differ in larger pores arranged in continuous rows along the commissures.

Illustration of *S. subobesum* by Suzuki (1958) shows its branch leaves as ovate-lanceolate and long acuminate, while in our sequenced plants branch leaves are ovate and shorter acuminate (Fig. 12K, M–O), and only the

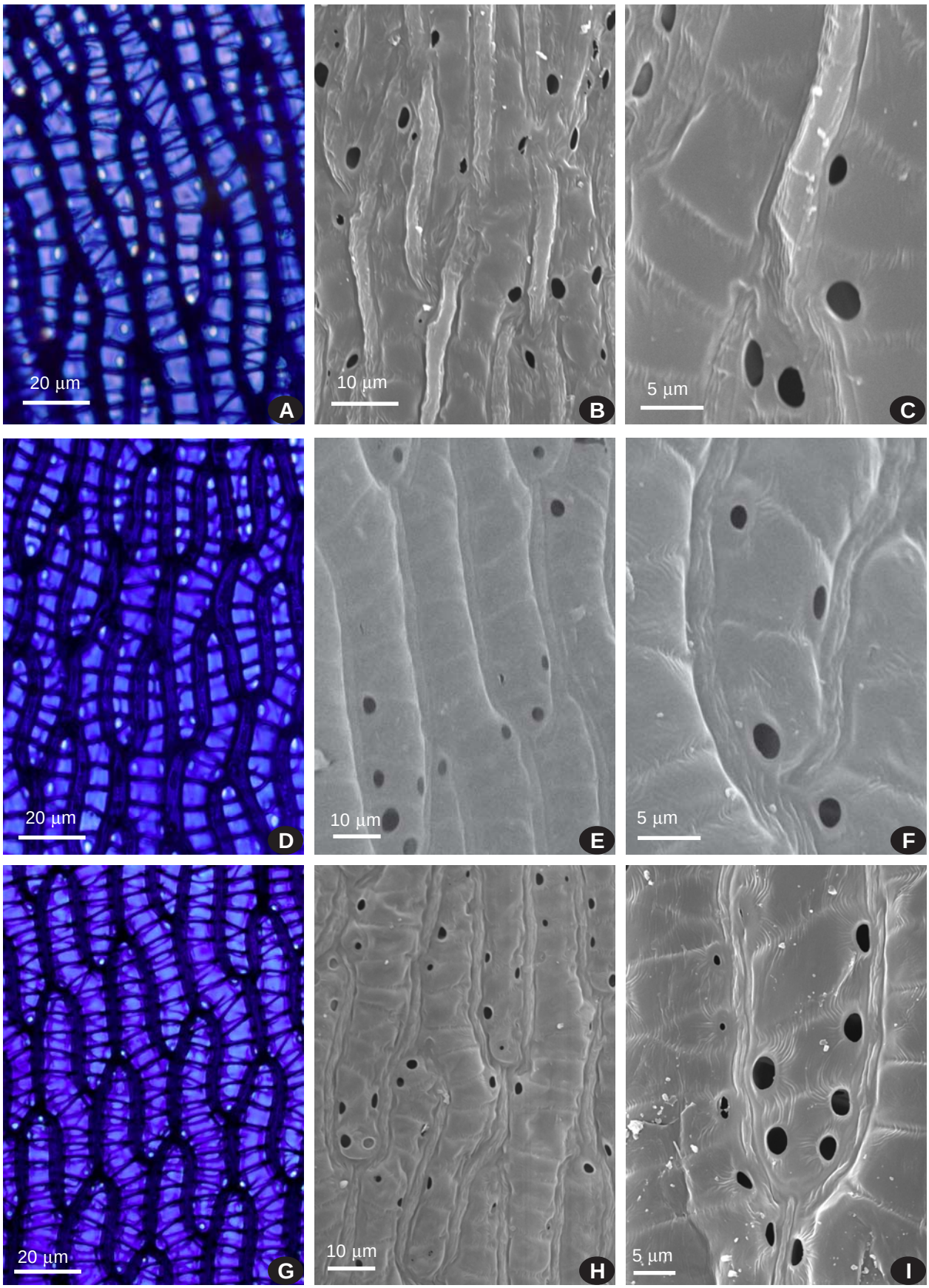

Fig. 5. *Sphagnum kushiroense* (A–C): from Khabarovsk Territory, isolate OK4502; *S. microporum* (D–F) from Khabarovsk Territory, isolate OK4441; *S. subobesum* (G–I): from Yakutia, isolate OK4406. All photos are made from dorsal (convex) surface of branch leaves showing pores in hyalocysts. A, D, G: light microscope; B–C, E–F, H–I: SEM.

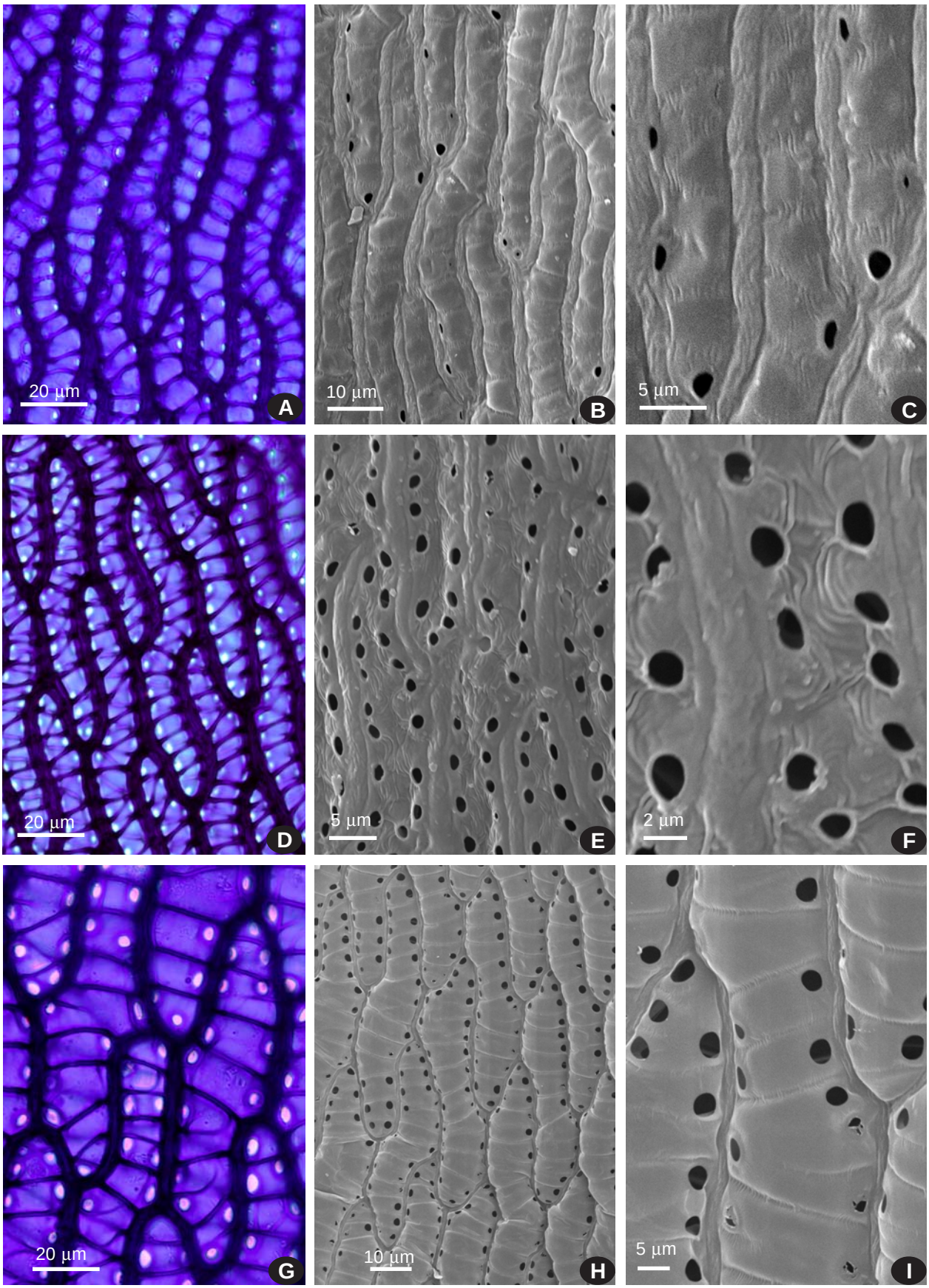

Fig. 6. *Sphagnum contortum* (A: from Russia, Moscow Province, MHA9022804; B–C: from Russia, Kamchatka, isolate OK4417), *S. orientale* (D–F: from Russia, Yakutia, MHA9015782) and *S. beringiense* (G–I: from Russia, Yakutia, MHA9015738). All photos are made from dorsal (convex) surface of branch leaves showing pores in hyalocysts. A, D, G: light microscope; B–C, E–F, H–I: SEM.

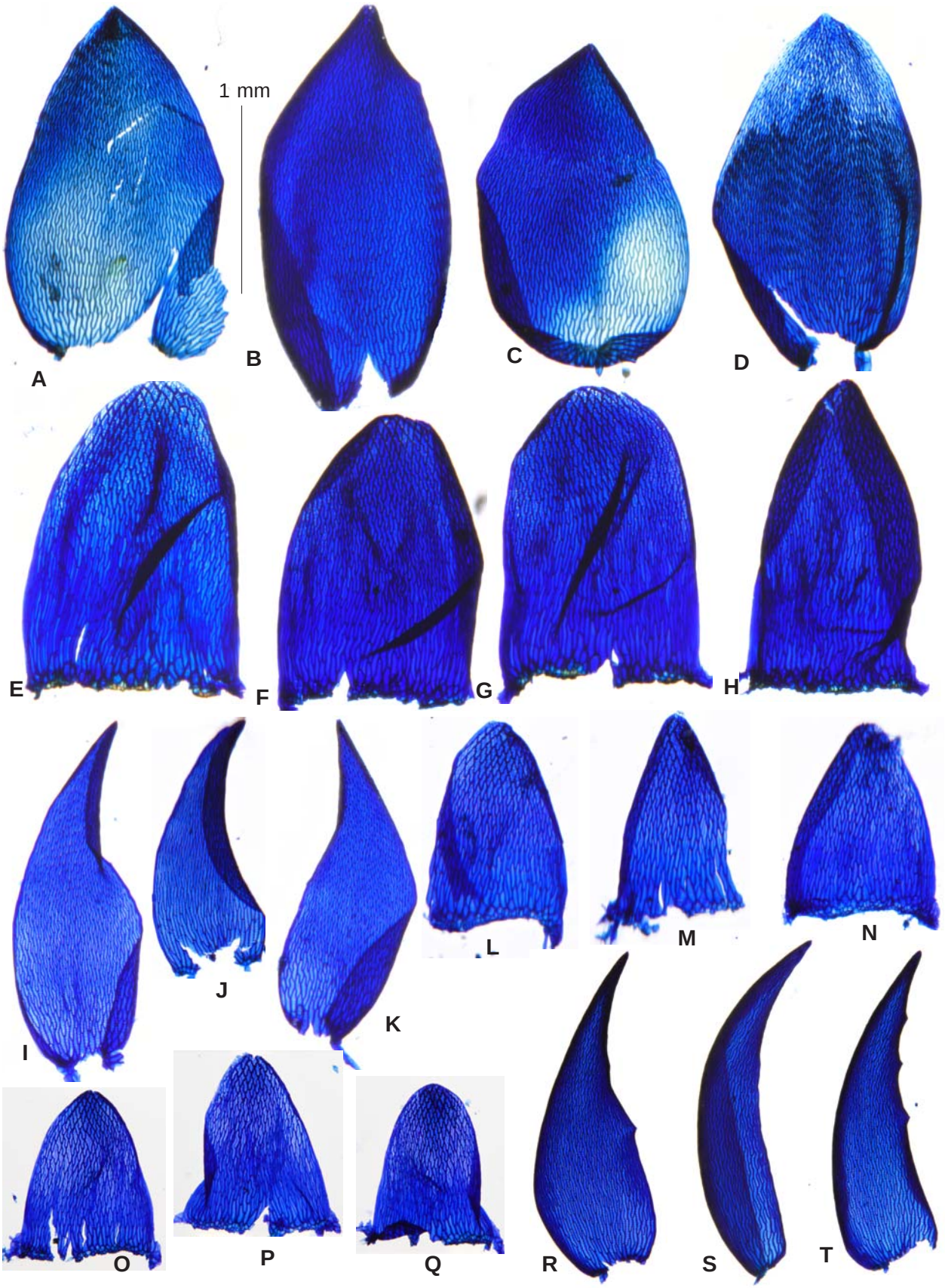

Fig. 7. Leaves (wet) from plants shown in Fig. 8A–H: A–H: *Sphagnum subobesum* (Russia, Yakutia, *Ignatov & Ignatova 18-1629*, MHA9191140); I–N: *S. kushiroense* (Russian Far East, Primorsky Territory, *Ignatov #77*, MHA9063731); O–T: *S. microporum* (Russia, Khabarovsk Territory, isolate OK4441). A–D, I–K and R–T: branch leaves; E–H and L–Q: stem leaves. Scale bar: 1 mm for all.

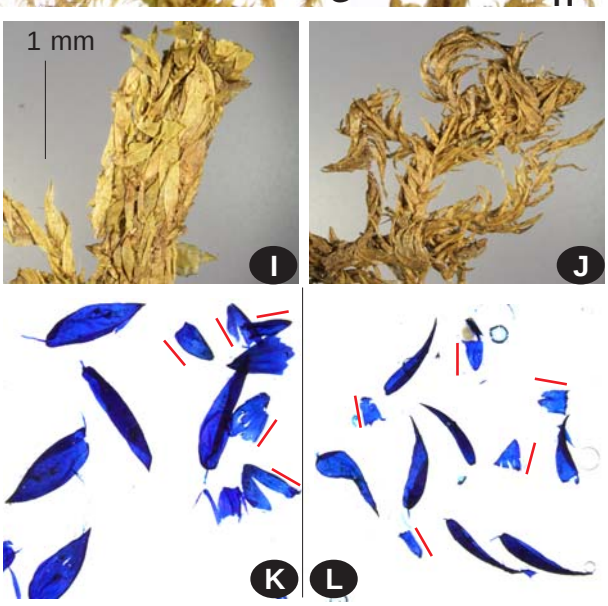

Fig. 8. Habit of herbarium specimens from mire carpet collections (A–H) and from mixed collection of plants growing in lake at 2 m deep (I–J), and leaves from these submerged plants (K– L), showing their shape and size variation (red bars near stem leaves = 1 mm). A–C: *Sphagnum subobesum* (Russia, Yakutia, *Ignatov & Ignatova 18-1629*, MHA9191140); D–F: *S. kushiroense* (D: China, Jilin Prov., *Jin Kou 383*, ex HSHU; E, F: Russian Far East, Primorsky Territory, *Ignatov #77*, MHA9063731), and G–H: *S microporum* (G: Russia, Khabarovsk Territory, isolate OK4441; H: Khabarovsk, Gambaryan, MHA9063732); I–L: Amurskaya Province: Umanskoe Lake, 3 July 1974, *Katanskaya s.n.* (LE). a). Scale bars: 5 mm for A–H; 1 mm for I–J; 1 mm red bars for K–L.

specimen from Khabarovsk Territory collected at 2 m depth in the lake (Fig. 8I) possesses branch leaves most similar to Japanese plants.

Our findings also expand the distribution range of *S. subobesum,* which up to now was thought to be restricted to Japan. The species was once reported from Queen Charlotte Islands, an archipelago off the northern Pacific coast of British Columbia, Canada (Schofeild, 1969; Andrus & Vitt, 1977; Andrus, 1979). In the latter paper, this species was described and illustrated based on North American

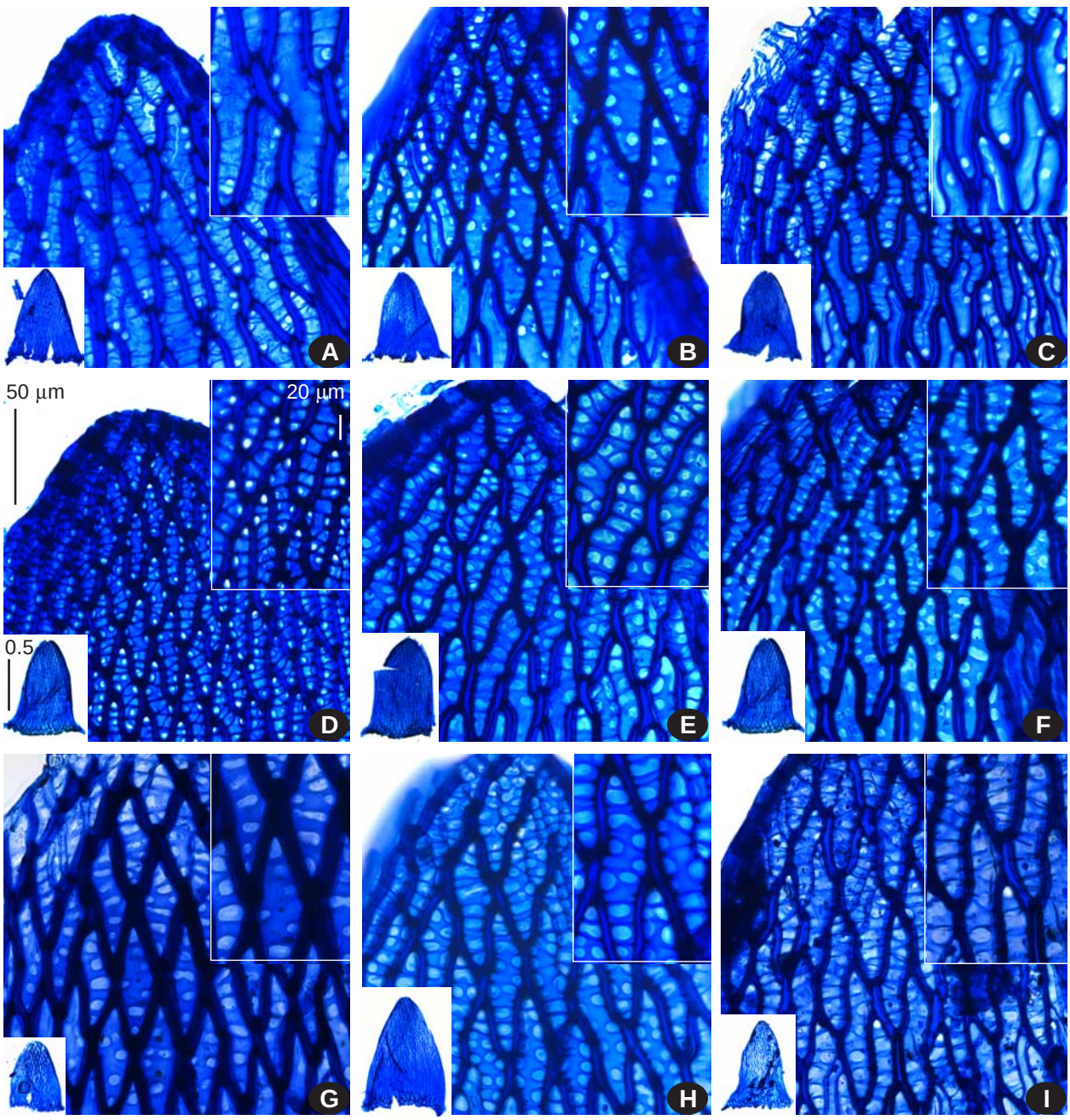

Fig. 9. *Sphagnum microporum* (A–D) and *S. kushiroense* (E–I). Upper part of stem leaf from ventral side with insets, showing whole leaf and close up of selected cells. Specimens A: Russia, Khabarovsk Territory, Gambaryan (MHA9063732); B: Russia, Khabarovsk Territory, *Lapshina*, isolate OK4505; C: Russia, Khabarovsk Territory, *Lapshina*, isolate OK4441; D: Japan, Honsu, *Suzuki 26442* (LE); E–F: two leaves from same plant from Japan, *Suzuki 43182* (LE); G: Japan, Hokkaido, Suzuki 21124 (LE); H: Russia, Khabarovsk Territory *Lapshina*, isolate OK4504; I: China, Jilin, *Jin Kou 383* (HSNU, dupl. MHA). Scale bars: 0.5 mm (leaf), 50 µm (leaf part), 20 µm (cells) for all.

specimens and compared with *S. subsecunsum*. However, Flatberg (2005) revised these collections and referred them to *S. andrusii* (Crum) Flatberg (=*S. subsecundum* var. *andrusii* Crum), thus returning to *S. subobesum* the status of Japanese endemic. He discussed in details and illustrated the distinctions between *S. subobesum*, *S. andrusii* and *S. inexspectatum*. Large stem leaves, usually 1.2–1.6 mm long, make *S. andrusii* similar to *S. subobesum*, but they are readily distinguished by numerous pores in stem leaves on dorsal side in the former and on ventral one in the latter, as well as by large (7–9 µm) pores in continuous rows vs. small (1–2 µm) pores in discontinuous rows in hyalocysts on dorsal surface of branch leaves. However, later McQueen & Andrus (2007) in their treatment of the genus *Sphagnum* in Flora of North America placed *S. subsecundum* var. *andrusii* into the synonymy of *S. inexspectatum*; furthermore, Buck & Goffinet (2024) placed *S. subobesum* into synonymy of *S. miyabeanum* Warnst., referring to Shaw *et al.* (2015), where *S. subobesum*, however, is not mentioned.

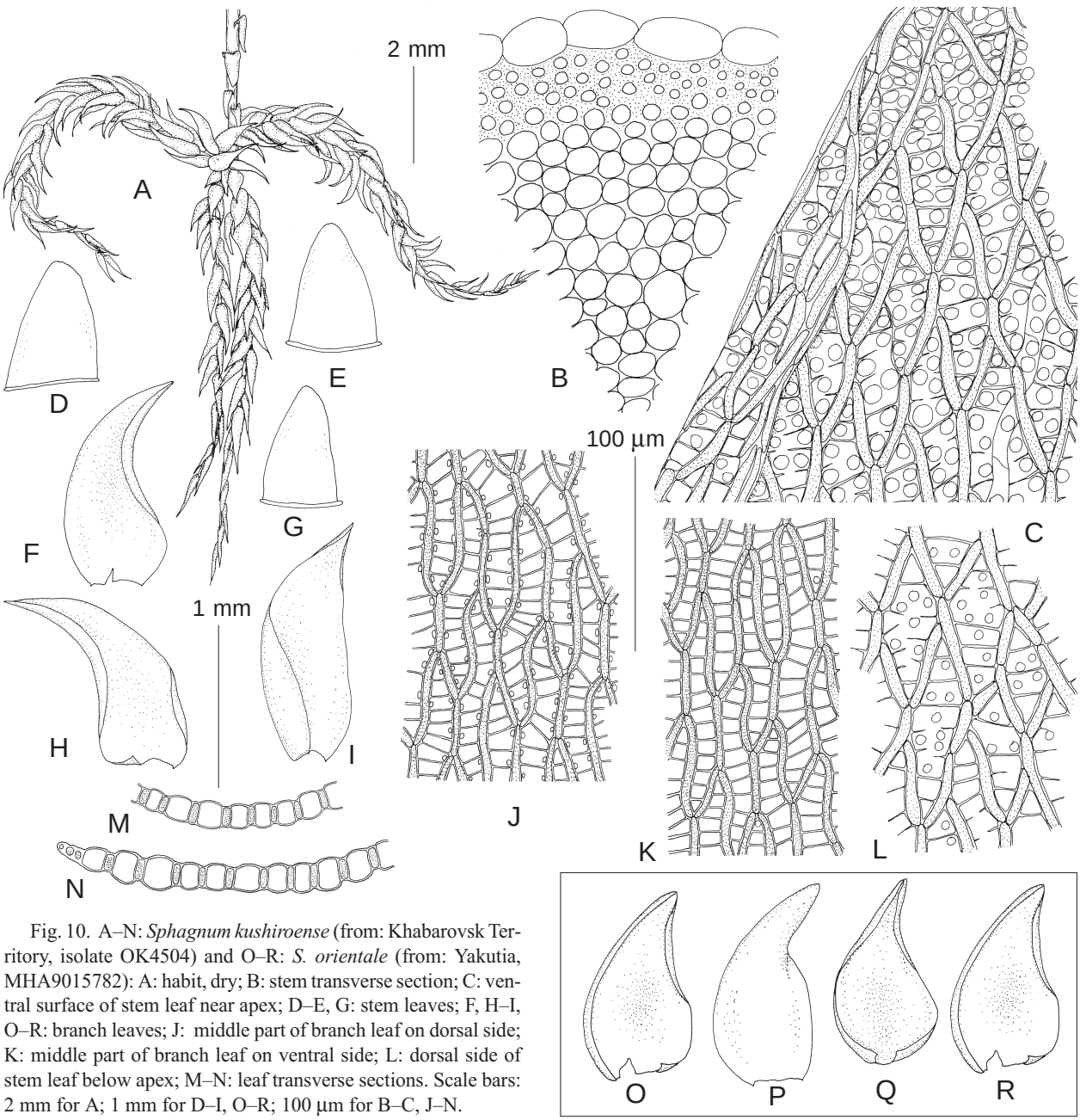

Fig. 10. A–N: *Sphagnum kushiroense* (from: Khabarovsk Territory, isolate OK4504) and O–R: *S. orientale* (from: Yakutia, MHA9015782): A: habit, dry; B: stem transverse section; C: ventral surface of stem leaf near apex; D–E, G: stem leaves; F, H–I, O–R: branch leaves; J: middle part of branch leaf on dorsal side; K: middle part of branch leaf on ventral side; L: dorsal side of stem leaf below apex; M–N: leaf transverse sections. Scale bars: 2 mm for A; 1 mm for D–I, O–R; 100 µm for B–C, J–N.

TAXONOMY

Sphagnum kushiroense H. Suzuki, Jap. J. Bot. 16: 258. 1958. Figs. 5A–C; 7I–N; 8E–F; 9E–I; 10A–N.

Holotype: Japan, Hokkaido, Prov. Kushiro, Shiranuka, Shiranuka-gun, Shiranuka-machi, Shoro, coll. H. Suzuki July 19, 1956, HIRO 21135). Not seen.

Plants medium-sized, in loose tufts, green, yellowish-brown to fuscous. *Capitula* small, flat to slightly convex, not stellate, apical bud inconspicuous; inner branches curved and ascending, outer branches arcing downwards, gradually attenuate. *Stems* rigid, light green to light brownish; *hyalodermis* unistratose to irregularly at places bistratose, usually with 1–2 pores at distant end. *Stem leaves* pendent-spreading or obliquely pendent-appressed, lingulate-triangular, 0.7–1.0×0.4–0.7 mm, rounded-obtuse at apex, occasionally slightly fringed, narrowly bordered by elongate cells; hyalocists with few septae, in distal 1/3–1/2 with fibrills or, more often, with fibrill stubs, on dorsal surface with few pores at cell angles, on ventral surface in distal 1/3–1/2 with numerous pores along comissures, 10–15 per cell, unringed, round or irregular in shape, 5–9 µm in diameter, in distalmost part of leaf occupying most of the lumen width. *Branch fascicles* with 2 divergent and 1–2 pendent branches, not crouded on stem; divergent branches arcuate, to 8 mm long; pendent branches slightly thinner, equal in length or sligtly longer than divergent branches. *Branch leaves* loosely appressed, slightly or strongly falcate-secund, 1.2–1.6×0.5–0.6 mm, lanceolate or ovate-lanceolate, moderately concave; hyalocists on dorsal surface with small, round, ringed pores 1–2(–3) µm in diameter in discon-

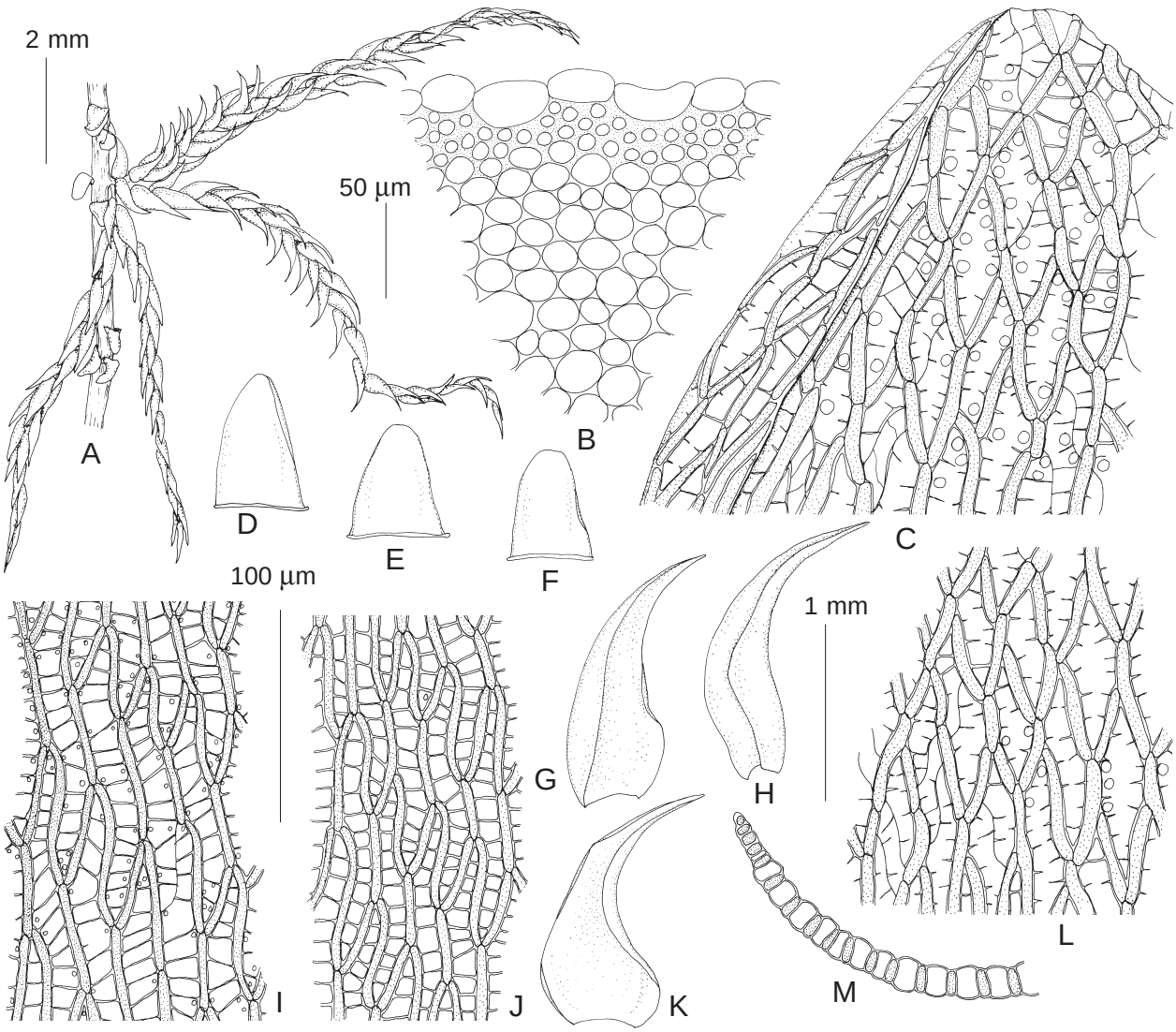

Fig. 11. A–N: *Sphagnum microporum* (from: Khabarovsk Territory, isolate OK4441): A: habit, dry; B: stem transverse section; C: ventral side of stem leaf near apex; D–F: stem leaves; G–H, K: branch leaves; I: middle part of branch leaf on dorsal side; J: middle part of branch leaf on ventral side; L: dorsal side of stem leaf below apex; M: leaf transverse section. Scale bars: 2 mm for A; 1 mm for D–H, K; 50 µm for B; 100 µm for C, I–J, L–M.

tinuous rows along comissures, on ventral surface eporose or with few round pores at cell angles; chlorocysts in leaf transverse section elliptic or rectangular, exposed on both surfaces, with moderaterly thickened outer walls. *Dioicous*. *Sporophytes* unknown in Russia. [*Antheridia* on pendent branches. *Capsules* 1.87–1.95 mm in diameter. *Spores* 30–32 µm].

Distinction. Suzuki (1958) described *Sphagnum kushiroense* distinguishing it from *S. microporum* in several sporophytic and gametophytic characters. The sporophytic characters include the dimensions of capsule and spores: *S. kushiroense* has larger capsules, 1.87–1.95 mm vs. 1.3–1.5 mm in diameter in *S. microporum*, and larger spores, 30–32 µm vs. 20–25 µm, correspondingly. However, sporophytes were not found in Russia, and also in China (Li & He, 1999), thus now we may rely only on the gametophytic distinctions.

Suzuki (1958) included in the key to identification two gametophytic characters. One of them, anisophyllous vs. hemiisophyllous stem leaves, was found difficult to apply to our collections from Russia and China, because plants of both species from China and Russia have stem leaves markedly smaller than branch leaves (cf. Figs. 7I–T, 10, 11), while in Japan, according to Suzuki (1958, Fig. 3), the hemiisophyllous plants of *S. microporum* prevail.

The second gametophytic distinction, the pore pattern on ventral surface of stem leaves in their distal 1/3 subdivide our collections into two groups in a way suggested and illustrated by Suzuki (1958, Fig. 8I and 9H) for distinguishing *S. kushiroense* and *S. microporum*. In *S. microporum*, pores are (3–)5–10 per cell, round, not occupuing most of the lumen width (Fig. 9A–D), while in *S. kushiroense* pores are more numerous, (7–)10–15

per cell, often enlarged and irregular in shape, occasionally fusing and becoming of the whole cell width and occupying most of the lumen (Fig. 9E–I). Pores themselves are either small and regular in shape (Fig. 9D), or of moderate size, mostly regularly round and few, filling only a small part of lumen (Fig. 9A–B), or irregular, filling most on the hyalocyst lumen (Fig. 9D, H), and unltimately with oblate pores prevailing (Fig. 9G).

Suzuki' key to identification mention only large pores vs. small pores. Our observation shows that such traits as the regularly round pore vs. irregularly shaped are probably also important. This maybe is what Suzuki considered differently, as his specimen '*S. microporum,* Suzuki 43182' (two its leaves are illustrated here in Fig. 9E–F), seems to be better corresponding to his illustration of *S. kishiriense* by Suzuki (1958, Fig. 9H) and Kyrkjeeide *et al.* (2019, Fig. 5), despite the 43182 specimen is from southern Honshu, Hiroshima area, not Hokkaido where the species was thought to be confined.

Distribution and ecology. *Sphagnum kushiroense* has been described from Hokkaido, Japan and was hitherto considered its endemic. However, it appeared to be sporadically distributed in the southern Russian Far East (Primorsky and Khabarovsk Territories, Amurskaya Province), reaching north-east of Zabaikalsky Territory westwards. We also found one specimen of this species in China, Jilin Province (growing on soil near the garden pond). Furthermore, two specimens from Honshu, Hiroshima-ken) have numerous pores in distal parts of stem leaves (Fig. 9E–F) are referred here to *S. kushiroense,* not *S. microporum*, as they were named by Suzuki.

In Khabarovsk Territory, the species occurs in herb-tussock sedge (*Carex cespitosa* subsp. *minuta*) mires in flood valleys of small rivers and in closed or weakly flowing depressions; it usually grows together with *Sphagnum oriental*e or, less often, forms pure turfs. It was also repeatedly noted in small abundance in herb-sedge (*Carex meyeriana*) communities of waterlogged hollows in extensive aapa-like string-flark floating mire systems. About other localities, only scarce information from labels is available. In Primorsky Territory it was collected in transitional mires on sea terrace and in river valleys, and on wet grass meadow; in Zabaikalsky Territory on flood-valley sedge meadow.

Additional specimens examined: **RUSSIA: Zabaikalsky Territory**, Czara River, 5 Aug 1964, coll. *Garashchenko s.n.* (LE); **Amurskaya Province:** Umanskoe Lake, 2 m deep, left bank of Bureya River, 3 July 1974, *Katanskaya s.n.* (LE); **Primorsky Territory**: Posiet District, 1 June 1928 *Sewerkin s.n.* (LE); [Vladivostok] Vtoraya Reczka 30 June 1932, coll. *Luchkin s.n.* (LE); [Vladivostok] Lyanchikhe River, 26 Sep 1950, coll. *Voroshilov 5180* (MHA9105523); Kavalerovo Distr., mouth of Tadusha (Zerkalnaya) River, 1 Aug 1973, coll. *Kudryashov* (LE); Khasan Distr., Ryazanovka, 15 Sep 1985, coll. *Ignatov #77* (MHA9063731). **CHINA:** Jilin Province, Antu Co., Chanbaishan, 11 January 2021, Jin Kou 383 (ex HSHU). **JAPAN**: Hokkaido, Suzuki 21124 (LE); Honsu, Suzuki 43182 (LE, as *S. microporum*).

Sphagnum microporum Warnst. ex Cardot, Beih. Bot. Centralbl. 17: 3. f. 1. 1904. Figs. 5D–F; 7O–T; 8G–H; 9A–D; 11.

Type: [North Korea, Wonsan], Ouen-San, #61 [coll. Faurie, from June to October 1901]. Not seen.

Plants medium-sized, in loose tufts, light-green, yellowish-brown to brownish. *Capitula* small, slightly convex, not stellate, apical bud inconspicuous; inner branches curved and ascending, outer branches arcing sideway or downwards, attenuate. *Stems* rigid, light to brownish to dark brown; *hyalodermis* unistratose or, very rarely, at few places bistratose, usually with one pore at distant end. *Stem leaves* pendent-spreading or obliquely pendent-appressed, triangular-lingulate, 0.7–0.9[–1.0]×0.4–0.6(–0.7) mm, rounded-obtuse at apex, occasionally slightly fringed, narrowly bordered by elongate cells; hyalocists often with 1–2 septae, in distal 1/3–1/2 with fibrills or, more often, with fibrill stubs, on dorsal surface eporose or with few pores at cell angles, on ventral surface in distal 1/3–1/2 with 5–10 pores per cell along comissures, unringed, 5–6 μm in diameter. *Branch fascicles* with 2 divergent and 1–2 pendent branches, not crouded on stem; divergent branches arcuate, to 8 mm long; pendent branches slightly thinner, usually longer than divergent branches. *Branch leaves* loosely appressed, strongly falcate-secund, 1.3–1.4(–1.6)×0.5–0.6 mm, lanceolate or ovate-lanceolate, concave, with incurved distal margins; hyalocists on dorsal surface with small, round, ringed pores 1–2(–3) μm in diameter in discontinuous rows along comissures, on ventral surface eporose or with few round pores at cell angles; chlorocysts in leaf transverse section elliptic or rectangular, exposed on both surfaces, with moderaterly thickened outer walls. *Dioicous*. *Sporophytes* unknown in Russia. [*Antheridia* on divergent, rarely pendent branches. *Capsules* 1.3–1.5 mm in diameter. *Spores* 20–25 μm].

Distinction. The differences of *S. microporum* from the most closely related and morphologically similar *S. kushiroense* are discussed in the comments to the latter species. Its distinction from other species of subgen. *Subsecunda* are discussed in the Result section.

Distribution and ecology. *Sphagnum microporum* has been described from Korea. It is widespread in China: Fujian, Heilongjiang, Jilin, Jiangsu, Nei Mongol, Yunnan Provinces (Li & He, 1999) and Japan: Honshu, Shikoku, Kyushu (Suziki, 1958; Iwatsuki, 2004). In Russia it was revealed in three localities in Amur River valley (Khabarovsk Territory). In Bolshekhekhtsirsky Nature Reserve, it grew on sedge-cotton-grass meadow; in the vicinity of the Selgon railway station it was found in dwarf shrub-sedge (*Carex lasiocarpa*)-sphagnum fen, and in Sanboli surroundings it was collected in sphagnum mire with *Chamaedaphne calyculata* and *Carex lasiocarpa*.

Additional specimens examined: RUSSIA: **Khabarovsk Territory**: Lazo Distr., Bolshekhekhzirsky Nature Reserve, 11.VII.1975, *Gambaryan* (MHA9063732); Amur Distr., Sel-

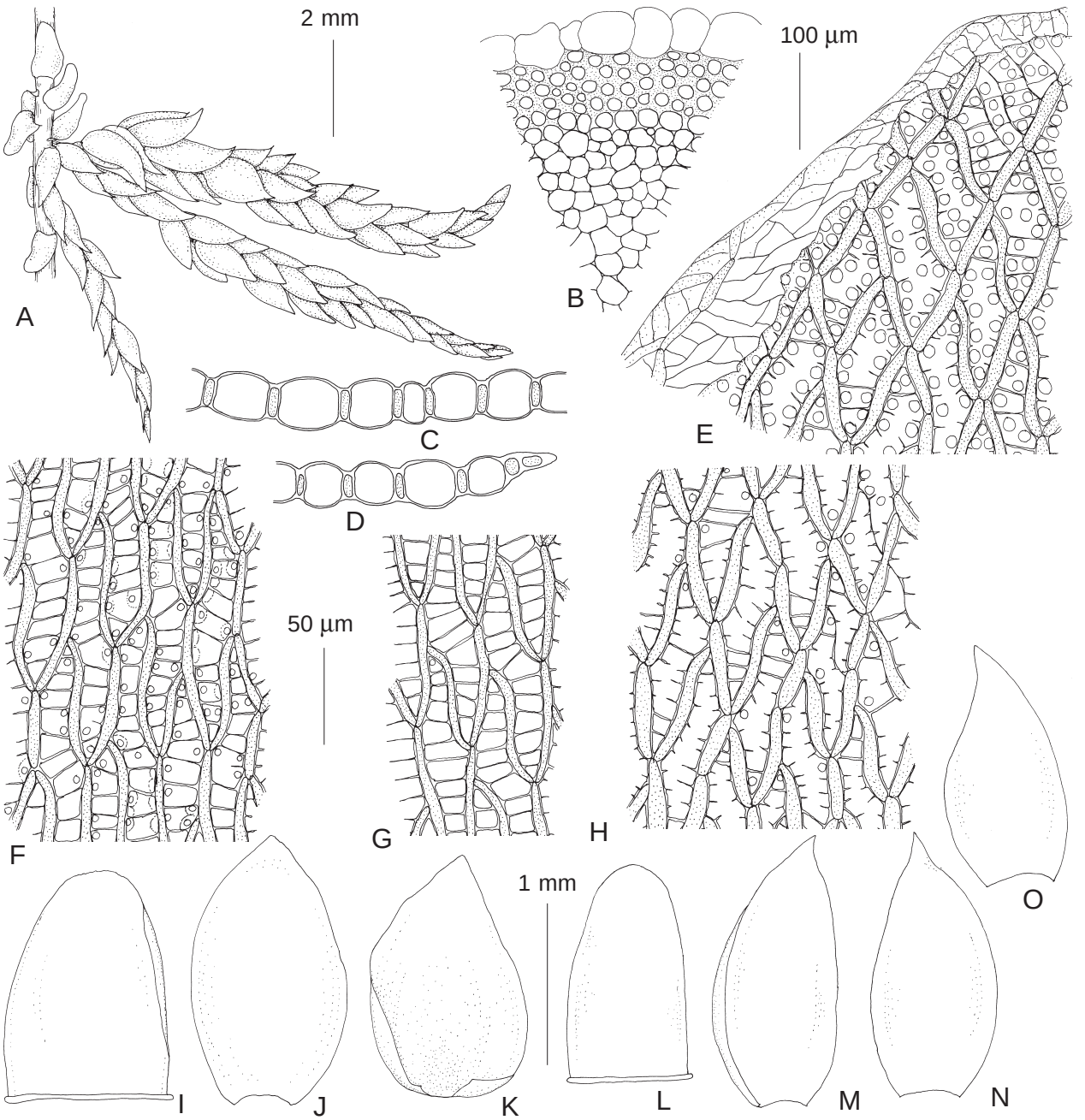

Fig. 12. *Sphagnum subobesum,* A–K: from Yakutia, isolate OK4404; L–N: from Kunashir isolate OK2945; O: from Khabarovsk Territory, isolate OK4545. A: habit, dry; B: stem transverse section; C–D: leaf transverse sections; E: ventral surface of stem leaf near apex; F: middle part of branch leaf on dorsal side; G: middle part of branch leaf on ventral side; H: dorsal side of stem leaf below apex; I, L: stem leaves; J–K, M–O: branch leaves. Scale bars: 2 mm for A; 1 mm for I–O; 100 µm for B; 50 µm for C–H.

gon surroundings, 4.VIII.2025, *Lapshina #069E-1* [07425 YSU]; Amur Distr., Sanboli surroundings, Alga River valley, 1.VIII.2025, *Lapshina #037E-6* [07297 YSU]. JAPAN: Nagano Pref., Suwa city, Kirigamine Mt., Kurumayama-moor, ca 1750 m, 29 August 1960, coll. H. Suzuki (LE ex H.S. 26442).

Sphagnum subobesum Warnst., Hedwigia 39: 104. 1900. Figs. 5G–I, 7A–H, 8A–C, I, K; 12.

Type: [Japan. NE Honshu, Prov. Mutsu], Aomori. Faurie No. 56. 18 June, 1897, leg. Urbain Faurie) (Lectotype KYO, selected by Flatberg, 2005). Not seen.

Plants robust, in loose tufts, often submergent, yellowish-brown to pale brown, sometimes pale green at places above, with slight metallic luster when dry. *Capitula* small, 7–10 mm in diameter, flat to slightly convex, not stellate, apical bud inconspicuous; inner branches upwards directed and incurved, outer branches arcing sideway and downwards, gradually attenuate. *Stems* rigid, yellowish below capitulum, brown to dark brown below; *hyalodermis* unistratose to irregularly bistratose at places, usually with 1–2 pores or wall thinnings at distant end. *Stem leaves* pendent-spreading or pendent-appressed, ovate-lingulate, 1.0–1.6[–2.6]×0.7–0.9 mm, con-

cave, rounded-obtuse at apex, margins often involute in upper part, occasionally slightly fringed, narrowly bordered by elongate cells; hyalocysts with few septae, in distal 1/4–1/3[2/3] with fibrills or with fibrill stubs, on dorsal surface with few pores at cell angles, on ventral surface in distal 1/4–1/3 with numerous, 8–15 per cell, unringed pores 5–7(–9) µm in diameter along comissures and, occasionally, on free surface. *Branch fascicles* with 2 divergent and 1(2) pendent branches, not crouded on stem; divergent branches arcuate, to 7–10[–15] mm long; pendent branches slightly thinner and shorter than divergent branches. *Branch leaves* loosely appressed, straight or slightly secund, 1.4–1.8[2.5]×[0.7–] 0.9–1.0[–1.8] mm, ovate, moderately to strongly concave; hyalocists on dorsal surface with small, round, ringed pores 1–2(–3) µm in diameter in discontinuous rows along comissures and pseudopores scattered along comissures, on ventral surface eporose or with few small round pores at cell angles and few pseudopores; chlorocysts in leaf transverse section elliptic or rectangular, exposed on both surfaces, with moderaterly thickened outer walls. *Dioicous*, plants with pearichaetia were found in Yakutia. *Sporophytes* unknown in Russia. [*Capsules* 1.5–1.7 mm in diameter. *Spores* 36–39 µm].

Variability. Plants from Yakutia are more robust, with larger stem leaves, 1.4–1.6 mm long, having more numerous pores on the ventral surface of hyalocysts in distal 1/3, whereas plants from Khabarovsk Territory have stem leaves 1.0–1.3 mm long, with fewer pores. However, pores and pseudopores in hyalocysts of branch leaves are similar in all studied specimens.

Distinction. *Sphagnum subobesum* is most similar to a European *S. denticulatum*; their differences are discussed above in the Discussion section. It is unlikely to confuse *S. subobesum* with another large species occasionally occurring in Asian Russia and being somewhat similar habitually–*S. platyphyllum*–since the latter species has 2(3)-layered hyalodermis and weakly differentiated branches in fascicles. Differences from the North American *S. andrusii,* which is also very similar to *S. subobesum* are provided in the Discussion section.

Distribution. In Japan, *S. subobesum* is known from Honshu (northern part) and Hokkaido (Suzuki, 1958). In Russia, it has generally more northern distribution area than *S. kushiroense* and *S. microporum*: it reaches latitude 64°51'N in Ulakan-Chistai Mt. Range in Yakutia and 53°25'N in Kamchatka, but is also known from Khabarovsk Territory and Kunashir Island at 44°N (Fig. 13). Records of *S. subobesum* from North America, in British Columbia were referred to other species (Flatberg, 2005), and not mentioned in the Flora of North America (McQueen & Andrus, 2007). In Khabarovsk Territory, the species was found in the vicinity of the Selgon railway station on dwarf shrub-sedge (*Carex lasiocarpa*)-sphagnum fen with *S. microporum*, *S. olafii*, *S. subsecundum*, and *S. imbricatum*, in zone of temporary flooding up to the side of the mire stream; in the second locality on the territory of the Udyl' Nature Reserve it grew in the waterlogged *Menyanthes*-sedge (*Carex meyeriana*)-*Sphagnum* hollows together with *Sphagnum orientale*, *S. majus*, and *S. obtusum* on the vast aapa-like mire system. In Kunashir Island it was found in *Carex–Equisetum–Comarum–Menianthes* bog community near Lake Serebryanoe. In Yakutia and Kamchatka it was collected in heavily flooded sites of mires at lake shores.

Additional specimens examined: **RUSSIA: Yakutia**: Momsky District, Ulakhan-Chistai Mt. Range, middle course of Tirekhtyakh River, lake between Chugulukka-Yuryuie and Meltekh-Yuryuie Creeks, *Ignatov & Ignatova 18-1653* (MHA9029596). **Kamchatsky Territory**: Levyi Kikhchik River, 19 Aug 2001 *Neshataeva s.n.* (LE); **Amurskaya Province:** Umanskoe Lake, 2 m deep, left bank of Bureya River, 3 July 1974, *Katanskaya s.n.* (LE). JAPAN: Honshu, Aomori Pref., Kominato-Cho, North of Tsubakiyama, 5 September 1958, col. H. Suzuki (LE ex H.S. 23923); Aomori Pref., Kamikita-gum, Yokohama-cho, Fukkoshi, 2 September 1954, coll. H. Suzuki (LE ex H.S. 19545).

ACKNOWLEDGEMENTS

We are grateful for curators of LE bryophyte herberium for specimen loans. We also thank V.E. Fedosov for his contribution to the molecular-phylogenetic analysis and comments. The work of Shkurko, Kuznetsova, Lapshina, Ignatov and Zhu was supported by the NSFC-RSF project 25-44-02076 and W2512083 (laboratory work and sequencing, phylogenetic analysis and manuscript preparation). The work of Ignatova was carried out within the MSU state assignment #121032500090-7. SEM studies were carried out at the Shared Research Facility "Electron microscopy in life sciences" at Moscow State University.

LITERATURE CITED

[ABRAMOVA, A.L. & I.I. ABRAMOV] АБРАМОВА А.Л., И.И. АБРАМОВ. 1977. К бриофлоре Дальнего Востока. – [On the bryoflora of the Far East] *Новости систематики низших растений* [*Novosti Sistematiki Nizshikh Rastenij]* **14**: *212–219.*

ANDRUS, R.E. & D.H. VITT. 1977. Sphagnotheca Boreali-americana: fascicle II. – *Bryologist* **80**: *645–647*.

ANDRUS, R.E. 1979. *Sphagnum subobesum* Warnst. in North America. – *Phycologia* **41**: *377–383*.

BORCHSENIUS, F. 2009. FastGap 1.2. – *Department of Biosciences, Aarhus University, Denmark. Published online at* http://www.aubot.dk/FastGap_home.htm

BEIKE, A.K., M. VON STACKELBERG, M. SCHALLENBERG-RÜDINGER, S.T. HANKE, M. FOLLO, D. QUANDT, S.F. MCDANIEL, R. RESKI, B. C. TAN & S.A. RENSING. 2014. Molecular evidence for convergent evolution and allopolyploid speciation within the Physcomitrium-Physcomitrellaspecies complex. – BMC Evolutionary Biology 14: 158 https://doi.org/10.1186/1471-2148-14-158

BUCK, W.R. & B. GOFFINET. 2024. A new checklist of the mosses of the continental United States and Canada. – *Bryologist* **127**(4): *484–549*.

FEDOSOV, V.E., A.V. FEDOROVA, V.E.FEDOSOV & M.S. IGNATOV. 2016. Phylogenetic inference and peristome evolution in haplolepideous mosses, focusing on Pseudoditrichaceae and Ditrichaceae sl. – *Botanical Journal of the Linnean Society* **181**(2): *139–155*. https://doi.org/10.1111/boj.12408

FLATBERG, K.I. 2005. The taxonomic identity of *Sphagnum subobesum* and *S. andrusii*, stat. et sp. nov. (sect. *Subsecunda*), with phytogeographical implications. – *Lindbergia* **30**: *97–106*.

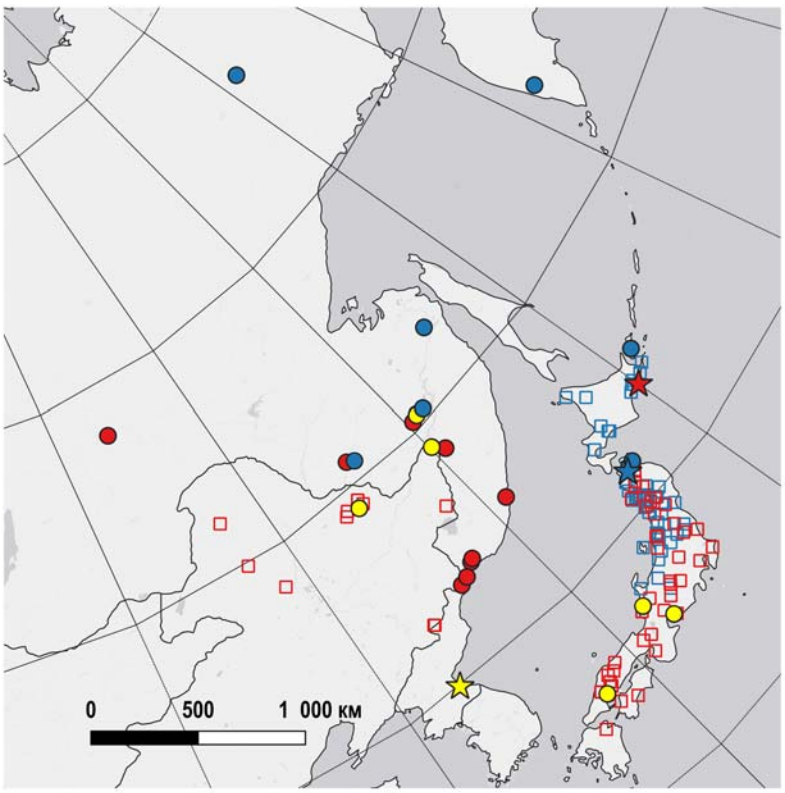

Fig. 13. Distribution of *Sphagnum kushiroense* (red), *S. microporum* (yellow), and *S. subobesum* (blue) in eastern Russia, North-East China, Japan and North Korea. Solid circles show studied herbarium specimens for *S. kushiroense* (red), *S. microporum* (yellow), and *S. subobesum* (blue). Empty squares represent the data from GBIF and literature records for *S. subobesum* (blue), while literature records for both *S. kushiroense* and *S. microporum* are given in red. Stars indicate type localities of these species.

HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucleic Acids Research Symposium Series* **41**: *95–98.*

HRAZDILOVA, K., O. DANEK, A. HRBATOVA, B. CERVENA, E. NOSKOVA, P. ADAMIK, J. VOTYPKA, A.D. MIHALCA, M. NOUREDDINE, D. MODRY & L. ZUREK. 2023. Genetic analysis challenges the presence of Ixodes inopinatus in Central Europe: development of a multiplex PCR to distinguish I. inopinatus from I. ricinus. – Parasites Vectors 16: 354. https://doi.org/10.1186/s13071-023-05971-2

IWATSUKI, Z. 2004. New catalog of the mosses of Japan. – *Journal of the Hattori Botanical Laboratory* **96**: *1–182*.

KATOH, K., K. MISAWA, K. KUMA & T. MIYATA. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. – *Nucleic Acids Research* **30**: *3059–3066*.

KYRKJEEIDE, M.O., K. HASSEL, B. AGUERO, E.M. TEMSCH, O.M. AFONINA, A. J. SHAW, H. K. STENØIEN & K. I. FLATBERG. 2019. *Sphagnum ×lydiae*, the first allotriploid peatmoss in the northern hemisphere. – *Bryologist* **122**(1): *38–61*.

LI, X.-J. & S. HE. 1999. Sphagnaceae. – *In: Gao Chien et al. (eds.) Moss Flora of China, English Version. Vol. 1. Science Press & Missouri Botanical Garden, Beijing, New York & St. Louis, pp. 3–49.*

LINDBERG, S.O. & H.W. ARNELL. 1890. Musci Asiae borealis. – *Kongliga Svenska Vetenskaps Academiens Handlingar*, n.s. **23**(10): *1–163*.

[MAKSIMOV, A.I.] МАКСИМОВ А.И. 2023. Разнообразиес фагновых мхов России. – [The diversity of *Sphagnum* mosses in Russia] Труды Карельского научного центра РАН [Transactions of the Karelian Research Centre RAS] **8**: *75–80*.

MAKSIMOV, A.I., V.E. FEDOSOV & E.A. IGNATOVA. 2016. *Sphagnum beringiense* (Sphagnaceae, Bryophyta) in Russia. – *Arctoa* **25**(1): *102–106*.

McQUEEN, C.B. & R.E. ANDRUS. 2007. Sphagnaceae. – *In: Flora of North America Editorial Committee (eds.). Flora of North America North of Mexico. Vol. 27. Oxford University Press, New York.* **27**: *45–101*.

MELESHKO, O., H.K. STENØIEN, J.D.M. SPEED, K.I. FLATBERG, M.O. KYRKJEEIDE & K. HASSEL. 2018. Is interspecific gene flow and speciation in peatmosses (*Sphagnum*) constrained by phylogenetic relationship and life-history traits? – *Lindbergia* **41**: linbg.01107. https://doi.org/10.1093/botlinnean/boaf077/8267911

MINH, B.Q., M.A.T. NGUYEN & A. von HAESELER. 2013. Ultrafast approximation for phylogenetic bootstrap. – *Molecular Biology and Evolution* **305**: *1188–1195*. http://dx.doi.org/10.1093/molbev/mst024

MULLER, K. 2005. SeqState. – *Applied Bioinformatic*s **4**: *65–69*.

PUGLISI, C., Y. G. WEI, K. NISHII & M. MOELLER. 2011. Oreocharis× heterandra (Gesneriaceae): a natural hybrid from the Shengtangshan Mountains, Guangxi, China. – Phytotaxa 38(1): 1–18. https://doi.org/10.11646/phytotaxa.38.1.1

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*. DOI: 10.1093/sysbio/sys029.

[SAVICZ-LYUBITSKAYA, L.I. & Z.N. SMIRNOVA] САВИЧ-ЛЮБИЦКАЯ Л.И., З.Н. СМИРНОВА. 1968. Определитель сфагновых мхов СССР. – [The Handbook of Sphagnaceae of the U.S.S.R.] *Л., 112 pp*.

[SAVICZ, L.I.] САВИЧ Л.И. 1932. Флора торфяных мхов Камчатки. – [Flora of peatmosses of Kamchatka] *Известия Ботанического сада АН СССР* [*Izvestiya Botanicheskogo sada AN SSSR*] **30**(3–4): *415–480*.

[SAVICZ-LYUBITSKAYA, L.I.] САВИЧ-ЛЮБИЦКАЯ Л.И. 1951. Два новых вида Sphagnum секции *Subsecunda* Schlieph. из СССР. – [Duo species novae Sphagnorum sectionis *Subsecunda* Schlieph. ex URSS] Ботанические материалы отдела споровых растений Ботанического института им. Комарова АН СССР [Botanicheskie materialy otdela sporovykh rastenij Botanicheskogo instituta imeni Komarova AN SSSR] **7**: *206–211*.

[SAVICZ-LYUBITSKAYA, L.I.] САВИЧ-ЛЮБИЦКАЯ Л.И. 1952. Сфагновые (торфяные) мхи. – [Musci frondosi (I). Sphagnales] *В кн.: Савич В.П. (ред.) Флора споровых растений СССР. I. Листостебельные мхи.* [*In: Savicz, V.P. (ed.) Flora Sporovykh Ras-*

tenij SSSR] *Изд-во АН СССР, М.-Л.* [*Academia Scientarum URSS, Moscow & Leningrad*], *252 pp.*

SCHANZER, I.A., A.V. FEDOROVA, M.A. GALKINA, E.A. CHUBAR, A.V. RODIONOV & V.V. KOTSERUBA. 2020. Is Rosa × archipelagica (Rosaceae, Rosoideae) really a spontaneous intersectional hybrid between R. rugosa and R. maximowicziana? Molecular data confirmation and evidence of paternal leakage. – Phytotaxa 428(2): 93–103. https://doi.org/10.11646/phytotaxa.428.2.3

SCHOFEILD, W.B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. – *Madrono* **20**: *155–207*.

SHAW, A.J. 2000. Phylogeny of the Sphagnopsida based on chloroplast and nuclear DNA. – *The Bryologist* **103**(2): *277–306*.

SHAW, A.J., C.J. COX, & S.B. BOLES. 2003. Polarity of peatmoss (*Sphagnum*) evolution: who says bryophytes have no roots? – AMERICAN JOURNAL OF BOTANY **90**(12): *1777–1787*. https://doi.org/10.3732/ajb.90.12.1777

SHAW, A.J., C.J. COX, & S.B. BOLES. 2005a. Phylogeny, species delimitation, and recombination in *Sphagnum* section *Acutifolia*. – *Systematic botany* **30**: *16–33*. https://doi.org/10.1600/0363644053661823

SHAW, A.J., I. MELOSIK, C.J. COX et al. 2005b. Divergent and reticulate evolution in closely related species of *Sphagnum* section *Subsecunda*. – *The Bryologist* **108**: *363–376*. https://doi.org/10.1639/0007-2745(2005)108[0363:DAREIC]2.0.CO;2

SHAW, A.J., S. BOLES & B. SHAW. 2008a. A phylogenetic delimitation of the "*Sphagnum subsecundum* complex" (Sphagnaceae, Bryophyta). – *American journal of botany* **95**: *731–744*. https://doi.org/10.3732/ajb.0800048

SHAW, A.J., L. POKORNY, B. SHAW et al. 2008b. Genetic structure and genealogy in the *Sphagnum subsecundum* complex (Sphagnaceae: Bryophyta). – *Molecular Phylogenetics and Evolution* **49**: *304–317*. https://doi.org/10.1016/j.ympev.2008. 06.009

SHAW, A.J., B. SHAW, M.G. JOHNSON, M. HIGUCHI, T. ARIKAWA, T. UENO & N. DEVOS. 2013. Origins, genetic structure, and systematics of the narrow endemic peatmosses (*Sphagnum*): *S. guwassanense* and *S. triseriporum* (Sphagnaceae). – *American Journal of Botany* **100**(6): *1202–1220*.

SHAW, A.J., B. SHAW, M.G. JOHNSON, N. DEVOS, H.K. STENIIIIEN, K.I. FLATBERG & B.E. CARTER. 2015. Phylogenetic structure and biogeography of the Pacific Rim clade of *Sphagnum* subgen. *Subsecunda*: haploid and allodiploid taxa. – *Biological Journal of the Linnean Society* **116**(2): *295–311*.

SIMMONS, M.P.& H. OCHOTERENA. 2000. Gaps as characters in sequence-based phylogenetic analyses. – *Systematic Biology* **49**: *369–381*.

SUZUKI, H. 1958. Taxonomical studies in the *Subsecunda* group of the genus *Sphagnum* in Japan, with special reference to variation and geographical distribution. – *Japanese Journal of Botany* **16**: *227–268*.

TRIFINOPOULOS, J., L.-T. NGUYEN, A. VON HAESELER & B.Q. MINH. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. – *Nuclear Acids Research* **44:** *W232–W235*. DOI: 10.1093/nar/gkw256

WARNSTORF, C. 1911. Sphagnales, Sphagnaceae (Sphagnologia universalis). – *In: Engler, H.G.A. (ed.) Das Pflanzenreich. 51. Verlag von Wilhelm Engelmann, Leipzig, 547 pp.*

WARNSTORF, C. 1913. Zur Bryo-Geographie des Russischen Reiches. Eine Erinnerung an Dr. E. Zickendrath – *Hedwigia* **53**: *184–320*.

WARNSTORF, C. 1914. Zur Bryo-Geographie des Russischen Reiches. Eine Erinnerung an Dr. E. Zickendrath (Fortsetzung aus Band LIII). – *Hedwigia* **54**: *22–182*.

Received 23 February 2026 *Accepted 11 June 2026*

Appendix 1. Specimens and Genbank Accession data for newly sequenced samples.

Species	Isolate	Region	Voucher	RAPD-A	*trn*G
S. beringiense	OK4420	Russia, Chukotka, Vrangel Island	*Obabko d14m1*, 2020, MHA	PZ450687	PZ450722
S. beringiense	OK2944	Russia, Khabarovsk Territory	*Fedosov 16-42-s5*, 2016, MHA9120589	PZ450688	PZ450711
S. contortum	OK4417	Russia, Kamchatka	*Klimova & Bakalin K-54-1-21*, 2021, MHA9131609	PZ450709	PZ450719
S. fallax	OK3183	Russia. Moscow Province	*Fedosov & Shkurko 20-8-20*, 2020, MHA9102944	PZ450683	PZ450710
S. kushiroense	OK4504	Russia, Khabarovsk Territory	*Lapshina 72e-1a*, 2025, MHA	PZ450703	PZ450734
S. kushiroense	OK4440	Russia, Khabarovsk Territory	*Lapshina 8e-3*, 2025, MHA	PZ450704	PZ450729
S. kushiroense	OK4502	Russia, Khabarovsk Territory	*Filippov 8f-2ab*, 2025, MHA	PZ450706	PZ450732
S. kushiroense	OK4503	Russia, Khabarovsk Territory	*Lapshina 48e-5a*, 2025, MHA	PZ450707	PZ450733
S. microporum	OK4441	Russia, Khabarovsk Territory	*Lapshina 33e-2*, 2025, MHA	PZ450705	PZ450730
S. microporum	OK4505	China, Heilongjiang	*Xiang et al. 20210422-10*, 2021, MHA ex HSNU	PZ450708	-
S. orientale	OK4414	Russia, NE Yakutia	*Lapshina 136*, 2023, MHA	PZ450689	PZ450716
S. orientale	OK2943	Russia, Taimyr	*Fedosov & Koltysheva 17-2-22-1*, 2017, MHA9102994	PZ450690	PZ450713
S. orientale	OK4409	Russia, Kuril Islands	*Shkurko & Fedosov 70-21*, 2021, MHA	PZ450691	PZ450714
S. orientale	OK4410	Russia, Kuril Islands	*Shkurko & Fedosov 70-7*, 2021, MHA, MW	PZ450692	PZ450715
S. orientale	OK4415	Russia, Chukotka, Vrangel Island	*Obabko d20m3n1*, 2020, MHA	PZ450693	PZ450717
S. orientale	OK4416	Russia, NE Yakutia	*Lapshina 314(03E/4-23)*, 2023, MHA	PZ450694	PZ450718
S. orientale	OK4419	Russia, Chukotka, Vrangel Island	*Obabko d7m5n8*, 2020, MHA	PZ450695	PZ450721
S. orientale	OK4443	Russia, S Yakutia	*Dudov 606-5*, 2024, MHA	PZ450696	PZ450731
S. orientale	OK4512	China, Heilongjiang	*Xiang et al. 20210427-51*, 2021, MHA ex HSNU	PZ450697	PZ450735
S. subsecundum	OK3998	Russia, Taimyr	*Pospelov 2-7*, 2024, MHA	PZ450684	PZ450712
S. subsecundum	OK4411	Russia, Khabarovsk Territory	*Lapshina 51e-3a*, 2025, MHA	PZ450685	PZ450724
S. subsecundum	OK4612	Russia, Ryazan Province	*Volosnova s.n.*, 2008, MHA9102326	-	PZ450737
S. subsecundum	OK4619	Russia, Murmansk Province	*Shkurko & Fedosov x10-1*, 2024, MHA	PZ450686	PZ450739
S. perfoliatum	OK4628	Russia, S Yakutia	*Dudov 394-1*, 2024, MHA	-	PZ450741
S. perfoliatum	OK4627	Russia, Magadan Province	*Pisarenko m14-96*, 2014, MHA ex NSK2007127	-	PZ450740
S. perfoliatum	OK4618	Russia, Yamalo-Nenetsky Autonomous District	*Koroleva N22*, 2017, MHA9102202	-	PZ450738
S. perfoliatum	OK4421	Russia, Kamchatka	*Dudov 335-1*, 2024, MHA	-	PZ450723
S. perfoliatum	OK4418	Russia, NE Yakutia	*Lapshina 26f-1a*, 2023, MHA	-	PZ450720
S. subobesum	OK2945	Russia, Kuril Islands	*Mamontov s18*, 2020, MHA	PZ450702	PZ450725
S. subobesum	OK4404	Russia, E Yakutia	*Ignatov & Ignatova 18-1629*, 2018, MHA9121140	PZ450698	PZ450726
S. subobesum	OK4405	Russia, Khabarovsk Territory	*Filippov 41f-4a*, 2025, MHA	PZ450699	PZ450727
S. subobesum	OK4406	Russia, E Yakutia	*Ignatov & Ignatova 18-1643*, 2018, MHA9029382	PZ450700	PZ450728
S. subobesum	OK4545	Russia, Khabarovsk Territory	*Lapshina 160e-5a*, 2025, MHA	PZ450701	PZ450736