SPHAGNUM WARNSTORFII COMPLEX IN NORTHERN ASIA
КОМПЛЕКС ВИДОВ *SPHAGNUM WARNSTORFII* НА СЕВЕРЕ АЗИИ

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Abstract

An identity of the North Asian *Sphagnum* plants, which combine macroscopical aspect of *S. rubellum* and microscopical traits characteristic to *S. warnstorfii,* was assessed using molecular phylogenetic and morphological data. Molecular phylogenetic reconstruction based on RAPD-A, RAPD-B and *trn*G sequences found a lineage sister to *S. warnstorfii,* which includes two highly supported lineages, well-defined morphologically. One of these lineages comprises plants different from the other red *Sphagnum* sect. *Acutifolia* species in having (1) often slightly curved branches with 5-ranked leaves, (2) triangular-lingulate stem leaves with faint fibrils at apical part, and (3) small, rounded-elliptical pores at apical part of the branch leaves at convex surface. Morphological traits and ecological preferences of these plants agree *S. talbotianum* R.E. Andrus described from Alaska and also correspond to the arctic morphotype of *S. warnstorfii* revealed and described by Yousefi et al. Therefore we refer such Asian plants to *S. talbotianum*, and described and illustrate them based on material from North Asia. The plants from the second lineage differ from *S. warnstorfii* s.str. and *S. talbotianum* by lingulate stem leaves with more lacerate apex and the large round pores at apical part or sometimes scattered throughout at concave side of the branch leaves.

Резюме

Видовая принадлежность североазиатских образцов сфагновых мхов, сочетающих в себе внешний облик, напоминающий *Sphagnum rubellum,* и микроскопические признаки, свойственные *S. warntsorfii*, была оценена с использованием данных молекулярно-филогенетического анализа и морфометрии. Результаты молекулярно-филогенетической реконструкции, основанной на последовательностях участков RAPD-A, RAPD-B и *trn*G, выявили отдельную филогенетическую линию, сестринскую *S. warnstorfii* и включающую в себя две хорошо поддержанные клады, образованные образцами, различающимися морфологически. Растения одной из этих клад отличаются от других родственных видов (1) часто изогнутыми веточками с 5-ти рядным листорасположением, (2) треугольно-языковидными стеблевыми листьями со слабыми фибриллами в апикальной части и (3) мелкими округло-эллиптическими порами в апикальной части веточных листьев с внешней стороны. Морфологические признаки и экологические предпочтения этих растений соответствуют *S. talbotianum,* описанному Эндрюсом из Аляски, а также арктическому морфотипу *S. warnstorfii,* выделенному Юзефи с соавторами. Таким образом, мы отнесли Азиатские растения из этой клады к *S. talbotianum,* и описали и проиллюстрировали их, основываясь на Североазиатском материале. Растения из второй клады отличаются от вышеупомянутых растений языковидной формой стеблевого листа с более широко надорванной верхушкой и крупными круглыми порами на внутренней стороне веточного листа, расположенными в апикальной части или иногда рассеянными по всей внутренней поверхности листа.

KEYWORDS: arctic, Asiatic Russia, biodiversity, morphological variability, phylogeny, *Sphagnum*

INTRODUCTION

Despite the growing number of the regional biodiversity surveys (Ignatov *et al.*, 1994; 2014, Ignatova *et al*., 2011; Fedosov *et al*., 2011; 2020 and many others), exploration of the flora of Asiatic Russia is still irregular and insufficient, especially in case of bryophytes. In the arctic and subarctic regions bryophytes play an essential role in biodiversity and total biomass (Ogureeva *et al*., 2020, Fedosov *et al*., 2020). The genus *Sphagnum* L. has a prominent biodiversity in subpolar region of the northern hemisphere, and in the last few decades a number of new species has been described from this area; most of these species were described from European and North American north and subsequently found in Asian sector: *S. arcticum* Flatb. & Frisv. (Flatberg & Frisvoll, 1984); *S. beringiense* A.J. Shaw, R.E. Andrus, & B. Shaw (Shaw

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et al., 2008, Maksimov *et al.*, 2016); *S. concinnum* Flatb. (Flatberg, 2007a; Fedosov *et al.*, 2020); *S. ×lydiae* Flatberg & K. Hassel (Kyrkjeeide *et al.*, 2019); *S. mirum* Flatberg & Thingsgaard and *S. olafii* Flatberg (Flatberg & Thingsgaard, 2003; Flatberg, 1993; Flatberg *et al.*, 2016); *S. tescorum* Flatberg (Flatberg, 2007b, Fedosov *et al.*, 2012), etc. However, *Sphagnum* specimens problematically assignable to any of the already known species still occur.

In particular, while identifying the *Sphagnum* collections from Taimyr Peninsula we found a number of red-colored plants combining macroscopical aspect of *S. rubellum* Wilson and microscopical traits characteristic to *S. warnstorfii* Russow. Moreover, such plants were collected from rich tundra fens, whereas *S. rubellum* is typically ombrotrophic. Probably, this morphotype was first recognized by Savicz-Lyubitskaya (1952), who mentioned it as an arctic form of *S. rubellum.* Also, similar plants were described by Yousefi *et al.* (2019) as an arctic form of *S. warnstorfii*, which corresponds to our plants morphologically in having pinkish coloration with pale tips of branches, less stellate capitula, somewhat curved branches, and slightly bigger (than in typical *S. warnstorfii*) pores at the convex side of the branch leaf apices. Thus, we considered such plants as an "arctic" *S. warnstorfii* until later revision revealed such plants in non-Arctic North Asian specimens from Yakutia, Sakhalin, Amur Province and Khabarovsk Territory; they were previously assigned to *S. rubellum*, *S. andersonianum* R.E. Andrus (= *S. rubellum*) (Shaw *et al.*, 2005), *S. warnsorfii,* and *S. capillifolium* (Ehrh.) Hedw. These plants have similar ecological preferences and several stable traits: branches with mostly 5-ranked leaves, triangular-lingulate stem leaves with weak fibrils in apical part, and small, round to elliptical pores at the apical part of the branch leaves at convex side.

It is widely known that *Sphagnum* species demonstrate a high morphological plasticity which depends on ecological conditions; it complicates species delimitation based solely on morphological traits (Stenøien *et al.*, 1997; Såstad *et al.*, 1999). Thus, after introduction of the molecular methods, along with newly described species as *S. beothuk* (Kyrkjeeide *et al.*, 2015), *S. beringiense* (Shaw *et al.*, 2008), *S. divinum* Flatberg & K. Hassel (Hassel *et al.*, 2018), *S. incundum* (Kyrkjeeide *et al.*, 2018), etc., a number of earlier described species were synonymized: *S. andersonianum* (= *S. rubellum*), *S. bartlettianum* Warnst. (= *S. rubellum*), *S. subtile* (Russow) Warnst. (= *S. capillifolium* (Ehrh.) Hedw.) (Shaw *et al.*, 2005), *S. isoviitae* Flatberg (= *S. fallax* H. Klinggräff) H. Klinggräff cf. Duffy et al., 2020) etc. These studies demonstrated the necessity of the complex morpho-molecular approach to species delimitation. Thus, we decided to apply the molecular phylogenetic approach to the North Asian plants that correspond in morphology to the "arctic" *S. warnstorfii"* according to Yousefi *et al.* (2019).

MATERIALS AND METHODS

Dataset. While preparing the dataset for molecular phylogenetic study, we revised *S. andersonianum, S. capillifolium, S. rubellum* and *S. warnstorfii* collections from different regions of Russia in MHA and MW and took 40 specimens to be included in an ingroup (Table 3). The two nuclear markers RAPD-A and RAPD-B (Shaw *et al.*, 2003) and one plastid marker *trn*G were then obtained for each specimen to be compared with the GenBank accessions, studied by Shaw *et al.* (2003, 2005) by means of phylogenetic analysis. A set of outgroups, representing other lineages of the subg. *Acuifolia* was included based on data from GenBank and added with our specimens of *S. quinquefarium* (Lindb. ex Braithw.) Warnst. and *S. subfulvum* Sjörs; two accessions of *S. squarrosum* Crome and three of *S. teres* (Schimp.) Ångstr. ex C. Hartm. were introduced in the alignment to be used for rooting trees. While compiling the combined dataset, we added sequences of *trn*LF and LEAFY genes for involved GenBank accessions (used in Shaw *et al.*, 2003, 2005) to improve the resolution of the deeper nodes of trees. GenBank accession numbers of the included specimens and vouchers of specimens studied de novo are compiled in Appendix 1.

Laboratory protocols of DNA extraction and sequencing follow Fedosov *et al.* (2016), primers and protocols of amplification follow Shaw *et al.* (2003). Sequences were aligned and edited manually in BioEdit (Hall, 1999).

Phylogenetic analysis. At first, three regions, RAPD-A, RAPD-B and *trn*G were considered separately; the trees were built without and with scored indel data using the simple indel coding (SIC) approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1. (Müller, 2005) to check the repeatability of the resulting topologies. The best-fit models of nucleotide evolution were estimated in Mega11 (Tamura *et al.*, 2021), which suggested the GTR+I+G model for the RABD-A, RAPD-B and LEAFY-like genes, and T92 for plastid partitions. Since no supported conflicts of topologies appeared, the concatenated dataset of six loci (including sequences of two LEAFY-like genes and plastid *trn*L-F, downloaded from GenBank) composed of 95 accessions, 4117 positions of the alignment plus 47 indels, coded with binary code, was analysed. Due to unknown chromosome localization of RAPD markers, they were considered as separate partitions, two LEAFY-like genes were assigned to a separate partition rather based on limited representation in the dataset, and plastid data (*trn*G plus *trn*L-F) were considered as a separate partition.

Phylogenetic reconstructions under Bayesian inference (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
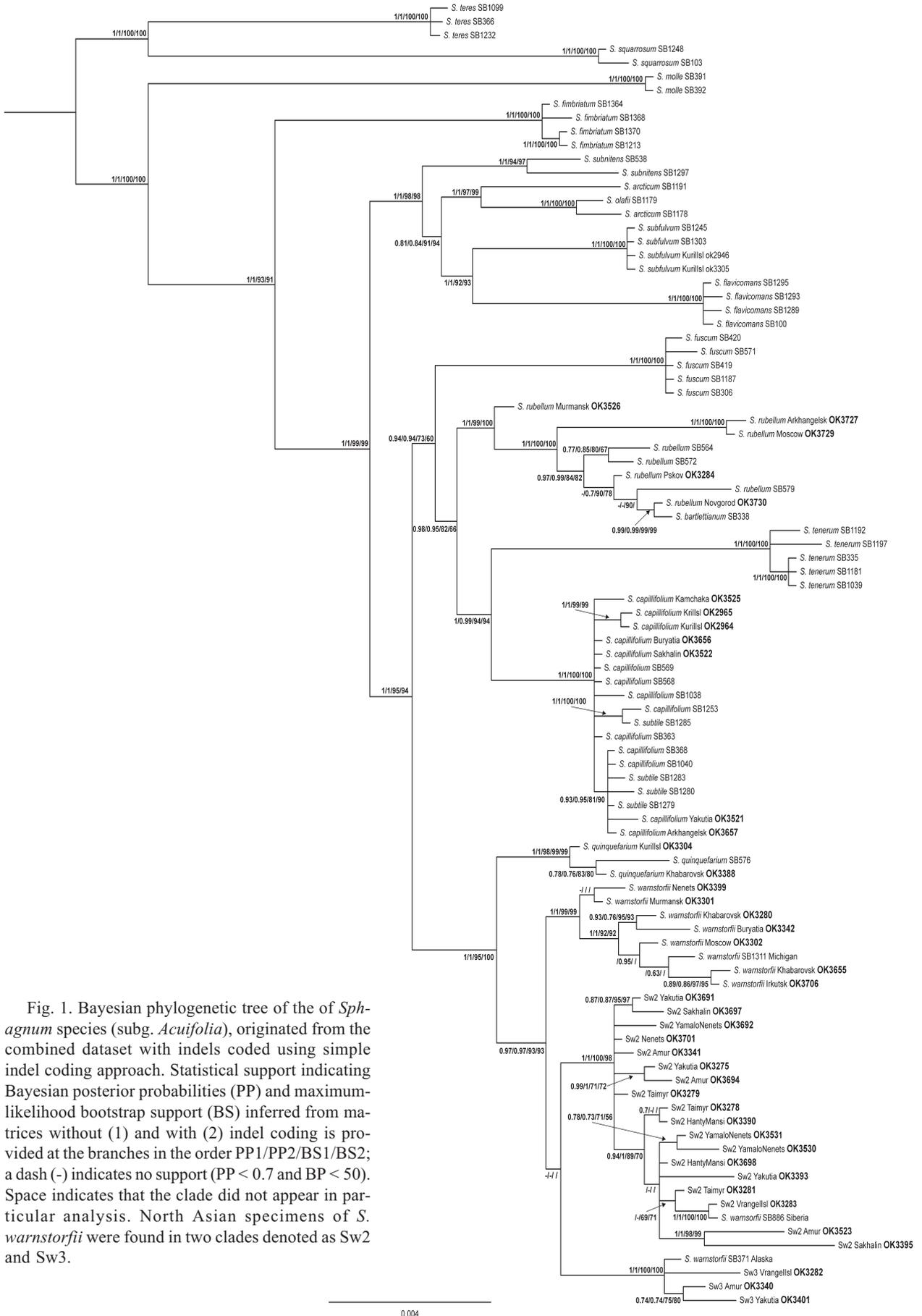
Fig. 1. Bayesian phylogenetic tree of the of *Sphagnum* species (subg. *Acuifolia*), originated from the combined dataset with indels coded using simple indel coding approach. Statistical support indicating Bayesian posterior probabilities (PP) and maximum-likelihood bootstrap support (BS) inferred from matrices without (1) and with (2) indel coding is provided at the branches in the order PP1/PP2/BS1/BS2; a dash (-) indicates no support (PP < 0.7 and BP < 50). Space indicates that the clade did not appear in particular analysis. North Asian specimens of *S. warnstorfii* were found in two clades denoted as Sw2 and Sw3.

Fig. 2. Splits tree of the *Sphagnum* species (subg. *Acuifolia*), originated from the combined nr RAPD-A and RAPD-B sequences. Sw2 and Sw3 – North Asian *S. warnstorfii*.
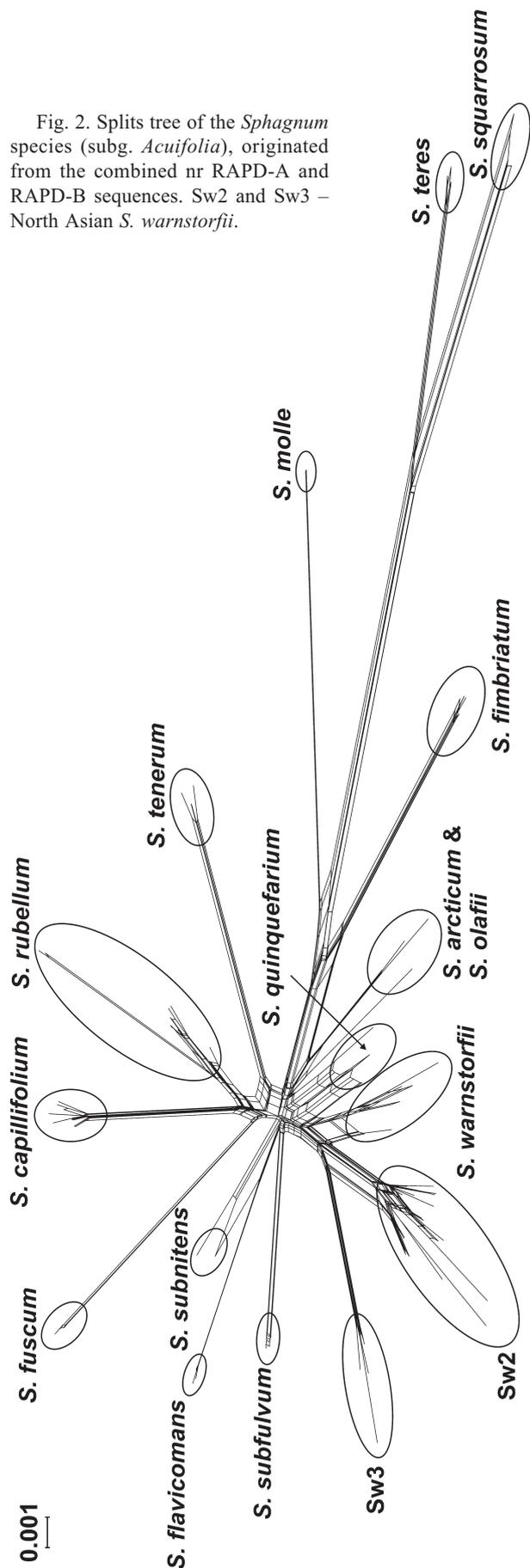
model space (setting nst = mixed). Consensus trees were calculated after omitting the first 25% of trees as burnin. The convergence between runs previously assessed as an average split deviation frequency lower than 0.01 was reached after 0.5 – 1.5 million generations. Additionally, ESS values were checked using Tracer v.1.7.2 (Rambaut *et al*. 2018) to be higher than 200.

Best-scoring maximum likelihood (ML) trees for combined dataset with and without indel data were estimated using IQtree (Trifinopoulos *et al*., 2016) with GTR+G+I model. Robustness of the nodes was assessed using 2000 pseudoreplications of the ultrafast bootstrapping algorithm implemented in IQtree. Trees were rooted on the joint clade of *S. squarrosum* and *S. teres* according to topology, published by Shaw *et al*. (2016), and visualized using FigTree 1.4.3 (Rambaut, 2009).

Since phylogenetic reconstruction of *Sphagnum* mosses was shown to be complicated by the hybridization, effect of the incomplete lineage sorting and other effects appearing as reticulate evolution (Shaw & Goffinet, 2000; Ricca & Shaw, 2010; Meleshko *et al*., 2018, 2021), to assess and visualize possible affinities within the dataset, which could not be reflected by the dichotomous tree topology we built the splitstree based on concatenated RAPD-A and RAPD-B sequences using Splitstree v.4.16.2 (Huson & Bryant, 2006)

Morphological analysis

For morphological investigation we took the same 40 specimens used for molecular investigation and added them with 4 specimens of *S. rubellum* collected from Europe, which were too old for sequencing, but demonstrated a typical morphology of *S. rubellum*. For measurements we used a mature portion of stems, i.e., starting from 1 cm below a capitulum from one shoot per specimen. We made temporal slides with several branch leaves obtained from the middle part of each spreading branch from three different fascicles, and several stem leaves stained in gentian violet. For the measurements five branch leaves and five stem leaves were chosen randomly on the slides. Eight traits were measured with the light microscope (Table 1). The width of stem leaves and branch leaves was measured at the half of their length; the width of stem leaf border averaged from both leaf sides at median part of the borders; length (maximal measure of pore which is parallel to the cell wall) and width (maximal measure of pore which is perpendicular to the cell wall) of commissural pores at the apical part of 3 branch leaves (one middle pore per cell, 10 cells per leaf, 30 pores per specimen in total) were measured. Additionally, we used five calculated metrics which reflect the relative characteristics of morphological traits, and four categorical traits ranged from 0 to 2 (0 – absence, 1 – slightly/partially, 2 – strongly). As a result, we obtained 13 numerical and 4 categorical variables (Table 1).

For the statistical treatment we used Past ver. 4.0 (Hammer *et al*., 2001). Each trait of five investigated
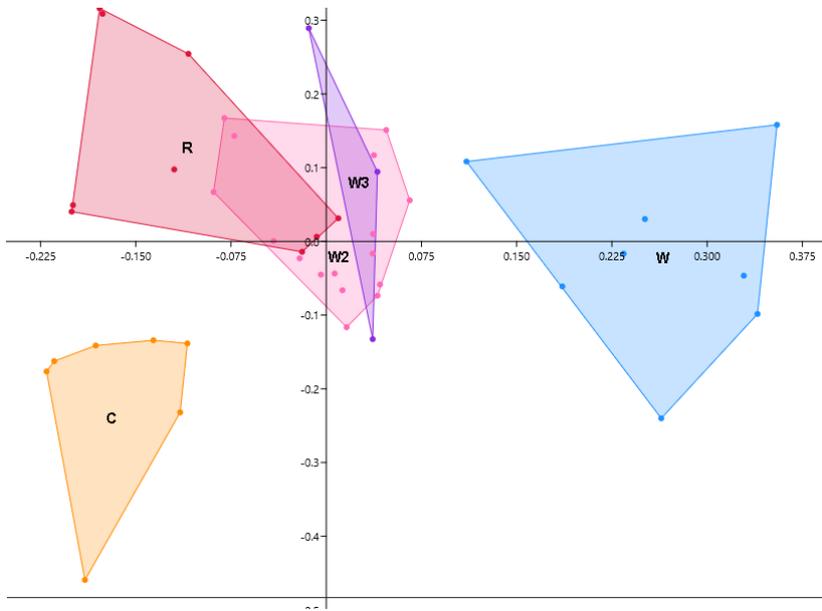
Fig. 3. PCoA plot of the five studied lineages, based on morphometric data: C – *S. capillifolium*, R – *S. rubellum*, W – "typical" *S. warnsorfiii*; W2 and W3 – "arctic *S. warnstorfii*"; loadings on Axis 1 – 43.4%, on Axis 2 – 15.3%.

lineages was tested for significant of medians difference through Mann-Whitney pairwise test since we compared more than two groups we also useed Bonferroni correction of p-values. Then the variables with p-values <0.05 between at least two species were normalized and tested for cross-correlations. The final set consisting of 5 non-correlated traits (SLL, PLW, FRB, BV, and FSL) with the lower p-values were used for the principal components analysis (PCoA) with the Gower distances, since the set of traits included categorical metrics.

RESUTLS

Molecular results. Since the trees, obtained from the single gene based reconstructions show similar topologies without cases of supported conflict between them, we consider below only the tree inferred from the concatenated dataset. The trees inferred from analyses of the combined dataset are well resolved and show good supports of the backbone phylogeny within the subgenus *Acuifolia*, and for the clades corresponding to the species level. Indel data largely improved supports of nodes, revealed by analyses without indel coding (Fig. 1).

After splitting fully supported clades corresponding to *S. molle* and *S. fimbriatum*, the well supported clade composed of *S. subnitens, S. subfulvum, S. flavicomans, S. arcticum,* and *S. olafii* splits, while the remaining accessions are found in two major clades. The weakly supported one comprises the *S. fuscum* clade, and the moderately supported grouping of *S. rubellum* (including *S. bartlettianum*), *S. capillifolium* and *S. tenerum*. Within the *S. rubellum* clade no Asian specimens appeared. The newly studied specimen from Murmansk Province appeared remarkably different from the other European and North American accessions, which form the fully supported clade. Within the latter one a better supported, remarkably diverged nested clade is composed by the newly studied specimens from Arkhangelsk and Moscow Provinces (and rather close American accession from

South Carolina, SB1322 not included in final analyses), while the specimens from Novgorod and Pskov Provinces were found intermingled with the GenBank accessions. The *S. capillifolium* clade is weaker differentiated and our originally studied specimens correspond well to the GenBank accessions.

The second major clade is well supported; it comprises nearly fully supported clade *of S. quinquefarium*, where two newly added specimens from the Russian Far East appear remarkably different from each other and from the GenBank accessions, and not supported clade where originally studied accessions of *S. warnstarfii* s.l. fall. The latter comprises two clades: the well supported one, which includes specimens from European Russia, southern Siberia, southern part of Russian Far East, and the North American GenBank accession SB1311 from Michigan, and not supported one, represented mostly by the North Asian accessions. Morphologically, representatives of the first clade completely correspond to the *S. warnstorfii* s.str., as recognized by Yousefi *et al.* (2019), while the second one largery agrees well with their morphological conception of the North Asian *S. warnstorfii* (see below).

The not supported clade of the North Asian *S. warnstorfii* consists of two fully or nearly so supported ones. The larger one (Sw2) is composed by many specimens from Asian cryolithozone (including the GenBank *S. warnstorfii* accession SB886 from Siberia) and also from Amur Province and Sakhalin Island. The smaller one (Sw3) includes three originally studied North Asian specimens, from Amur Province (Stanovoy Range), Oymyakon District of Yakutia and Wrangel Island, and GenBank accession SB371 from Alaska. The latter clade is completely supported and appears on a long branch resulted from ten synapomorphic substitutions in RAPD-A, otherwise combining molecular traits of "typical *S. warnstorfii*" and Sw2. Two of the three originally stud-

Table 1. The mean and standard deviation of 17 parameters measured/calculated in five lineages; * – categorical metrics.

Character	*S. capillifolium*	*S. rubellum*	Sw2	Sw3	*S. warnstorfii*
N	7	9	16	3	7
Stem leaf length (SLL), μm	1177±97	1070±155	987±66	920±148	1042±98
Stem leaf width (SLW), μm	572±50	596±70	538±51	508±98	583±59
SLW at the base (SLWb), μm	646±43	629±97	603±57	560±84	692±62
Border width (SLBW), μm	144±34	165±29	164±57	167±31	176±43
Branch leaf length (BLL), μm	1291±329	891±157	1033±123	876±196	1012±164
Branch leaf width (BLW), μm	455±124	383±66	408±57	405±58	385±57
SLW/SLL	0.49±0.04	0.56±0.07	0.55±0.04	0.56±0.08	0.56±0.03
SLBW/SLWb	0.22±0.05	0.27±0.04	0.27±0.04	0.29±0.01	0.25±0.05
SLL/BLL	0.95±0.20	1.21±0.13	0.97±0.12	1.06±0.08	1.05±0.15
BLW/BLL	0.35±0.03	0.43±0.06	0.40±0.04	0.47±0.07	0.38±0.03
Pore length (PLL), μm	9.9±1.3	6.8±0.7	5.9±0.9	5.9±0.5	3.9±0.8
Pore width (PLW), μm	4.9±0.7	4.2±0.4	3.6±0.6	3.4±0.2	2.6±0.5
PLW/PLL	0.50±0.03	0.61±0.03	0.62±0.05	0.57±0.03	0.67±0.03
Pentastichous branches (FRB)*	0	2	2	1.5	2
Bud visibility (BV)*	0	0	0	0	1
Subsecund branch leaves (SBL)*	0	2	1	1	1
Fibrills in stem leaf cells (FSL)*	2	1.5	1	0	0.5

ied specimens from this clade, OK3340 (from Amur Province) and OK3401 (from Yakutia) have identical RAPD-B sequences, while OK3282 from Wrangel Island is closer to Alaskan SB371 and has several substitutions common with one specimen of Sw2 from Yamalo-Nenetsky Autonomous District.

Morphology

During measuring, two specimens of hemiisophyllous plants of the Sw2 lineage were excluded from the statistical analysis, since they demonstrated strong mor-

phological deviations; such plans will be discussed later (see Discussion section). The rest 39 specimens were grouped according to the molecular data and consist of 7 specimens of *S. capillifolium*, 5 of *S. rubellum*, which were added with 4 specimens from Europe without molecular data (9 in total), 16 specimens from Sw2 lineage, 8 specimens of the "typical *S. warnstorfii*" and 3 representatives of the Sw3 clade (Table 1). As PCoA plot (Fig. 3) shows, Sw2 plants are fairly morphologically different from *S. capillifolium* and "typical *S. warnstorfii*", but overlaps with *S. rubellum* and Sw3. The Mann-Whitney pairwise test also reveals only few traits which consistently (p<0.01) differ between Sw2 and *S. rubellum*: PLW and SLL/BLL. Although, the three specimens from Sw3 lineage do not show any statistically supported morphological differentiation from Sw2 in the present analysis (Table 1, Fig. 3), they still have a number of distinctive traits (Table 2) such as main shape of the stem leaves and degree of it's apex laceration, shape of the branch leaves and their pore-pattern from the concave side.

DISCUSSION

The backbone topology of the subg. *Acutifolia* obtained in course of our study completely agree with the previously published one (Shaw *et al.*, 2005), therefore we limit our discussion to the *S. warnstorfii* s.l. clade. First of all, morphologically studied specimens of the Sw2 and Sw3 clades demonstrates similarity with an arctic form of *S. warnstorfii* as it described by Yousefi *et al.* (2019) and these plants are close to *S. warnstorfii* molecularly, according to our data they are remarkably delimited phylogenetically, while their joint clade with the "typical *S. warnstorfii*" clade is not supported statistically. Taking into account stable morphological differentiation of Sw2 and

Fig. 4. Macroscopic photograph of the North Asian *S. talbotianum* (from Taimyr, Fedosov 17-2-19, 2017, MHA9102970).
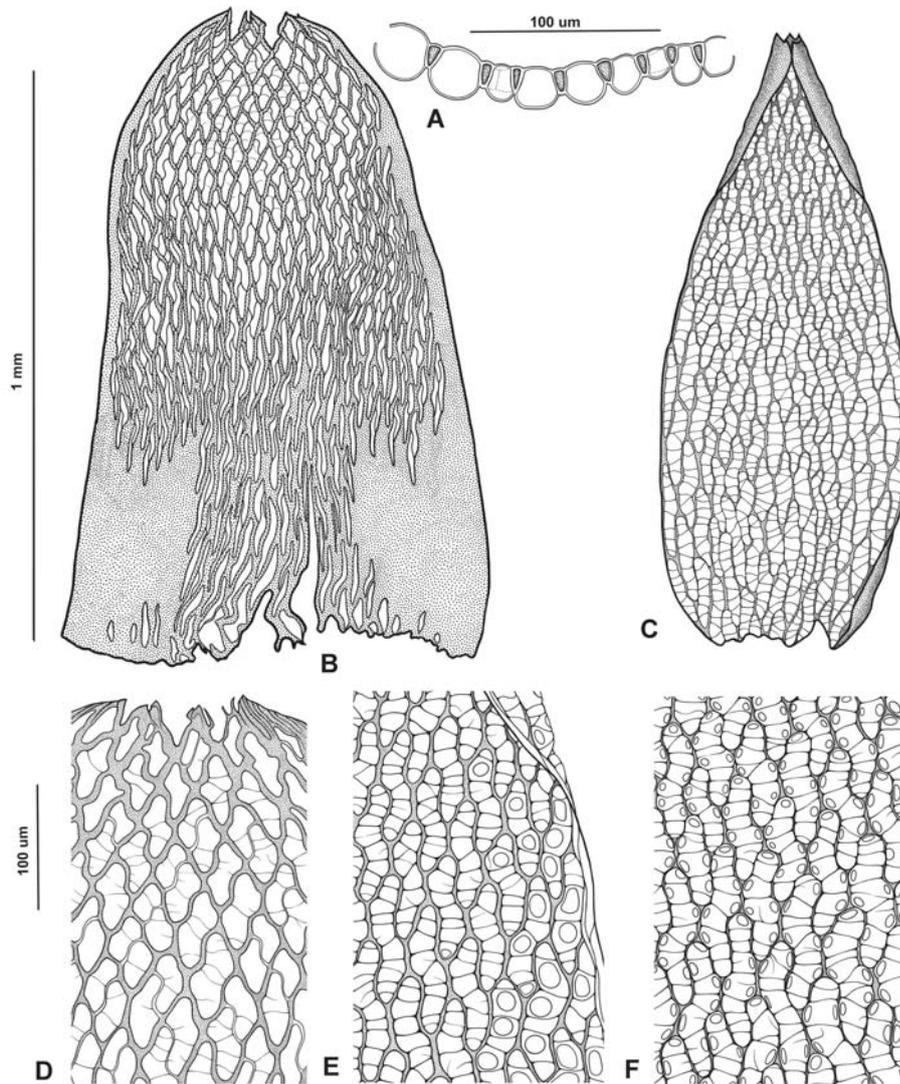
Fig. 5. Asian *S. talbotianum* (from Taimyr, Fedosov 17-2-19, 2017, MHA9102970): A: transverse section of the branch leaf; B: stem leaf; C: branch leaf; D: apical part of the stem leaf, E: marginal part of the branch leaf at the concave side, F: median part of the branch leaf at the convex side.

Sw3 plants from those of "typical *S. warnstorfii*" clade, their segregation as a separate species is needed. Although several distinctions between Sw2 and Sw3 were assessed, more representatives of Sw3 lineage and another set of morphological traits are needed to estimate differentiation of the two newly revealed lineages statistically and describe Sw3 as a new species.

Morphology and ecological preferences of plants from Sw2 lineage well correspond to description and illustration of *S. talbotianum* Andrus (Andrus, 2006). Both of the Sw2 plants and *S. talbotianum* have rather small, pink-colored plants with flattered and compact capitula, 5-ranked branches, ovate-lanceolate branch leaves with small pores in the apical part from convex side and tri-

Table 2. Comparison of the morphological traits of *S. talbotianum,* according to Andrus (2006; * means based on illustrations in this publication) and Asian plants of *S. warnstorfii* complex from the two lineages (cf. Figs. 1–3).

| Trait	*S. talbotianum*	Sw2	Sw3
Branch leaf shape	ovate to ovate-lanceolate*	ovate to ovate-lanceolate	ovate to broadly ovate
Branch leaf length, mm	1.0-1.2	0.9-1.1	0.7-1.1
Branch leaf width, mm	0.3-0.35	0.35-0.45	0.35-0.45
Pores in branch leaf concave surface	In proximal side regions	In proximal side regions	**In proximal side regions and apical parts or throughout**
Stem leaf shape	Triangular-lingulate	Triangular-lingulate	**Mostly lingulate**
Stem leaf apex lacerate at	1/5–1/3 leaf width*	1/4–1/3 leaf width	**1/2–2/3 leaf width**
Stem leaf length, mm	0.8-1.05	0.9-1.1	0.9-1.0
Stem leaf width, mm	0.5-0.55	0.45-0.55	0.45-0.55
Stem leaf hyaline cells	Efibrillose (with faint fibrils apically*)	Mostly with faint fibrils apically	Mostly efibrillose
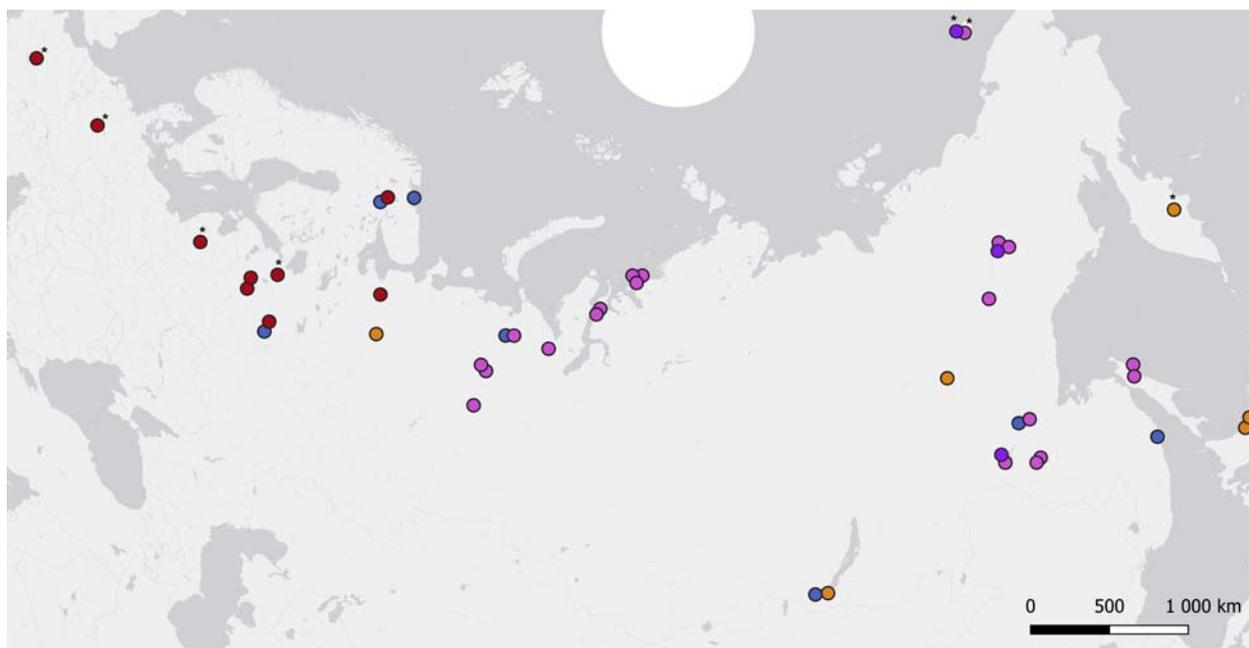
Fig. 6. The distribution map of the studied specimens; the pink dots – Asian specimens of *S. talbotianum*, the red dots – *S. rubellum*, the orange dots – *S. capillifolium*, the blue dots – *S. warnstorfii,* the violet dots – Sw3; * – localities without GPS coordinates, which were drawn approximately to their locality description.

angular-lingulate stem leaves (Table 2, Fig. 4,5). Despite, Andrus (2006) did not mentioned the faint fibrils in the apical part of stem leaves as characteristic traits of *S. talbotianum,* they are illustrated in his protologue and in the Moss flora of North America (McQuen & Andrus, 2007), and North Asian plants from Sw2 lineage have such fibrils as well. Therefore we suggest use this name for our Sw2 clade. Noteworthy, ecology and geographical distribution both of the "arctic *S. warnstorfii*" in Asia, as presented here, and *S. talbotianum* in Alaska correspond to the distribution patterns of the two other species often growing together with our plants from Sw2 lineage, *S. beringiense* and *S. tescorum*. These species also were described from Beringian region which is considered as a glacial refugium for Alaskan and Eastern Russian species (Shaw *et al.*, 2008; Kyrkjeeide *et al.*, 2016). In our opinion, current distributions of these species, predominantly associated with cryolithozone, suggest that this area was the speciation arena during cryoxeric epochs of late Cenosoic as was shown for the genus *Pseudohygrohypnum* by Fedosov *et al.* (2022). Recent discovery of *S. lydiae*, limited to Arctic areas of Beringian Asia underlines importance of this area as a center of *Sphagnum* diversity origin. At the same time, as far as we consider "arctic *S. warnstorfii*" to be conspecific with representatives of our Sw2 clade, its general distribution also includes Svalbard, Greenland and Canadian Arctic Archipelago, thus seeming to be circumpolar.

Noteworthy, many specimens of Asian *S. talbotianum* kept in herbaria were previously assigned to *S. rubellum* for which the oceanic tendency in distribution was mentioned (Daniels & Eddy, 1990). Our results confirm this

point of view since our revision did not reveal Asian specimens of this species yet. Most of *S. rubellum* records in Asian part of Russia (see Ignatov *et al.*, 2006) base on "arctic *S. warnstorfii*", which has not been recognized before 2019. The obtained topology of the phylogenetic tree shows remarkable divergence of the East European populations of *S. rubellum*, which might indicate either ongoing speciation on an eastern boundary of the species distribution, or their survival in isolated glacial refugia. Since eastern European specimens bear a plesiomorphic molecular traits, while their strong divergence can be explained by the bottleneck effect, the second possibility seems more reasonable, which means that the true glacial refugium could have been placed in the Eastern Europe.

Although, the global revision of the two species is still needed; we suppose different patterns of their distribution in Eurasia. For a long time *Sphagnum rubellum* has been considered as having wide distribution in Asia (Savicz-Lyubitskaya & Smirnova, 1968; Ignatov *et al.*, 2006). However, according to our results, it seemingly has predominantly amphiatlantic distribution, being substituted by *S. talbotianum* northwards and inwards. In particular, the latter is widely distributed in Asiatic part of Russia.

TAXONOMY

Sphagnum talbotianum R.E. Andrus, Sida 22: 970, f. 35–40. 2006. (Fig. 4, 5)

Plants small to medium sized, variegated yellow-pink, sometimes to purplish red, capitula flat to slightly rounded, not stellate, apex bud typically not visible. Stems pale to pink, sclerodermis well delimited, superficial cortical cells eporose. Stem leaves triangular-lingulate, 0.9–1.1
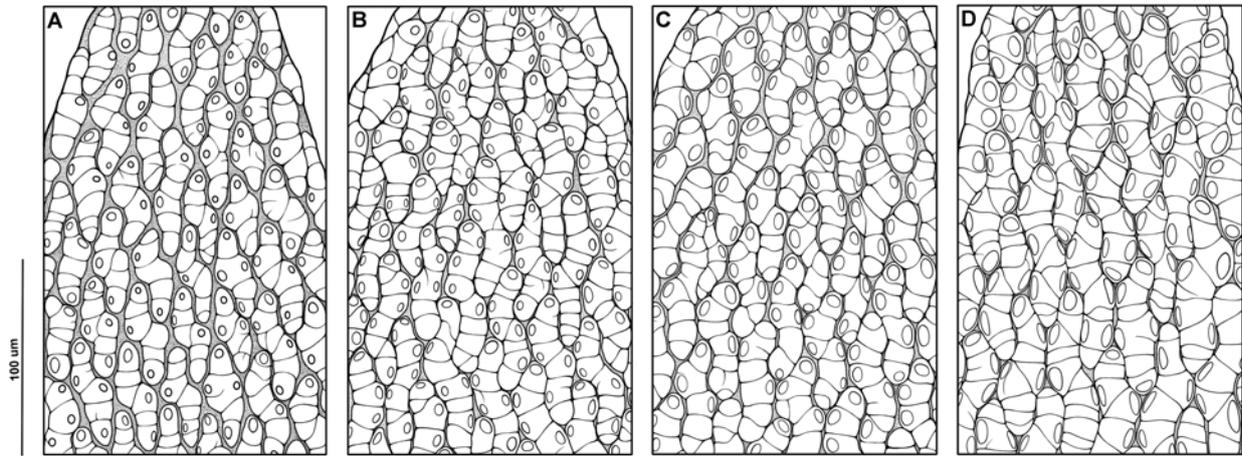
Fig. 7. The differences of the pore size and pattern in A: *S. warnstorfii;* B: Asian *S. talbotianum;* C: –*S. rubellum;* D: –*S. capillifolium.*

mm long and 0.45–0.55 mm wide, apex rounded, narrowly erose, hyaline cells rhomboid, 0-1(-2) septate, typically with weak fibrils at apical part of the leaves, sometimes efibrillose, aporose, border strong, widening at the base to more than 0.25 of the width. Hemiisophyllous plants have more triangular and longer stem leaves with strong fibrils and pores. Branch fascicles with 2 spreading and 1(-2) pendent branches, spreading branches 5-ranked, typically curved or straighten up in plans from compact cushions. Branch leaves straight to slightly subsecund at middle part of branches, ovate to ovate-lanceolate, apex involute, 0.9–1.1 mm long and 0.35–0.45 mm wide, hyaline cells on convex surface with rounded to elliptical pores along commissures, grading from small (4–6 µm) pores near the apex to larger ones at the base, concave surface with large round pores in proximal margins of the leaf. Chlorophyllous cells triangular to trapezoidal in transverse section, broadly exposed on concave surface. Sexuality and sporophytes unknown.

Ecology. The plants assigned to this species were collected from arctic fens, wet moss dominated tundra and eutrophic bogs, in localities dispersed from low maritime areas to high mountain elevations up to 1500 m a.s.l.

Distribution in Russia (Fig. 6): *S. talbotianum* is widely distributed in Asiatic part of Russia from the western foothills of Ural Mountains in Nenets Autonomous District to the Russian Far East. We also expect it's presence in western and middle Siberia, and in inland Chukotka. For now, we proved the west boundary of *S. talbotianum* distribution in inland Eurasia to be situated in Nenets AD (however, its occurrence along northern shore of Kola Peninsula is possible) and the southern one in Amur Province. Along the boundaries of its distribution, *S. talbotianum* occurs sympatrically with *S. warnstorfii*, which, however, does not occur in Asian cryolithozone.

Differentiation. S. talbotianum vs *S. capillifolium.* Although the distributions of the two species overlap, even when growing mixed they readily differ morpho-logically. In contrast to *S. capillifolium*, S. *talbotianum* mostly has 5-ranked branches, smaller and more rounded pores at the apical part of the branch leaves (Fig. 7), and weaker fibrils (or its total absence) in the hyaline cells of the stem leaves. Hemyisophyllous plants of *S. talbotianum* which are very similar to *S. capillifolium* in morphology of stem and branch leaves and often lack typical small pores, still have more or less prominent 5-ranked branch foliage and slightly subsecund leaves, lacking in *S. capillifolium.*

S. talbotianum vs *S. warnstorfii*

In most cases, *S. warnstorfii* readily differs from *S. talbotianum*. Macroscopically plants of *S. warnstorfii* often has a flat star-shaped capitulum with a slightly visible apical bud, straight 5-ranked divergent branches and straight branch leaves, while plants of *S. talbotianum* are more compact with less star-like aspect of capitulum and hidden apical bud, divergent branches slightly curved or straighten up, often with somehow subsecund branch leaves. Microscopically the two species also differ well, since the tiny (3–4 µm) ringed pores often runs lower towards median part of the branch leaves in *S. warnstorfii* becoming mixed with bigger ones proximally (Fig. 7A). *Sphagnum talbotianum* commonly has slightly bigger pores (5–6 µm) at apices of the branch leaves, which become bigger towards median part of the leaf rather gradually (Fig. 7B). Sometimes, *S. talbotianum* also has few tiny pores, however they are more oval, less ringed and often placed closer to commissures than the tiny pores of *S. warnstorfii*. Similar morphological differentiation was mentioned for the "arctic" vs "boreal" plants of *S. warnstorfii* in the study of Yousefi *et al.*, 2019, which contributed a lot to our feeling of *S. talbotianum*.

S. talbotianum vs *S. rubellum.* Despite the clear phylogenetic differentiation, these two are very similar morphologically (Fig. 3), which has resulted in numerous reports of *S. rubellum* from the continental areas of North Asia (Ignatov *et al.*, 2006; Fedosov *et al.*, 2011). Macroscopically both have pink to sometimes red coloration,

flattering capitula, and mostly 5-ranked branches with slightly subsecund branch leaves; however the shoots of *S. rubellum* typically more weak and slender in contrast to commonly compact plants of *S. talbotianum*. The shape of the stem leaves is rather triangular in *S. talbotianum* with weak fibrils at the apical part or without them similarly to *S. warnstorfii*, while *S. rubellum* has more lingulate stem leaves, the marginal parts of which runs rather parallel to each other basally and commonly has strong fibrils in upper hyaline cells or throughout the stem leaves. Also, according to our measurements (Table 1), *S. rubellum* mostly has higher stem/branch leaf length ratio than *S. talbotianum* has, which can be used as an additional trait for separating the two species. The apical pores at the convex side of branch leaves also can help to differentiate these species, since *S. talbotianum* typically has smaller pores, rather similar to tiny pores of *S. warnstorfii* (Fig. 7). Ecological preferences of the two species also differ, *S. rubellum* commonly grows in ombrotrophic bogs, *S. talbotianum* prefer richer habitats as arctic bogs and rich fens.

Specimens used for molecular and morphological study:

Sphagnum capillifolium: **Arkhangelsk Province**, Verkhneoemky Disrict, vicinity of Tymoshino Village, oligotrophic bog, 61.94°N, 45.28°E, 19.VII.1999, Churakova 497 (OK3657, MHA9112619); **Buryatia Republic**, Kabansk Disrict, Khamar-Daban Range, valley of Bolshoy Mamai Creek, minerotrophic bog, 51.37°N, 104.83°E, 1100 m a.s.l., 6.IX.2018, Ignatov, Ignatova, & Kolenikova 18-4238 (OK3656, MHA9027234); **Yakutia**, Khangalasskiy District, "Lenskye stolby" National Park, hanging sphagnum bog, 61.15°N, 127.60°E, 05.VIII.2016, Ignatov & Ignatova 16-488 (OK3521, MW9113201); **Sakhalin Province**, Sakhalin Island, Nogliksky Disrict, oligotrophic bog, 51.43°N, 143.43°E, 28.IX.2016, Dudov & Kozhin Br_0113 (OK3522, MW9079504); Kunashir Island, Doktorskiy Stream valley, fir-spruce-bamboo forest near the thermal Lake Faust, on rock outcrops near the lake water, 43.99°N, 145.77°E, 20.IX.2020, Mamontov 833-1-s34 (OK2964, MHA9121196); the same place, 833-1-s40 (OK2965, MHA9121197); **Kamchatka Province**, Milkovsky Disrict, Kostin Mountain, rocky slope, on soil, 04.IX.2010, Fedosov, 10-4-58 (OK3525, MW9065671);

Sphagnum rubellum: **France**, Sainte-Croix-Hague, 14.VI.1888, Cobiere, 3399 (MW9014338); **Germany**, Berlin, Sumpfe zwischen Hundekehle und Grunewald, IX.1902, Prager 40 (MW9014329); **Lithuania**, Kaunas, 12.IV.1953, Tyuremnov (MW9014344); **Russia**, **Murmansk Province**, Apatity City outskirts, north shore of Imandra Lake, aapa-bog, 67.60°N, 30.00°E, 27.VI.2012, Ignatov & Ignatova 12-14, (OK3526, MW9014350); **Leningradskaya Province**, Laryanskoe bog, 06.X.1935, Tyuremnov (MHA9014357); **Pskov Province**, Polistovsky National Reserve, Bezhanitskiy District, southern part of Polistovskiy peatland, oligotrophic bog, 57.23°N, 30.43°E, 18.VI.2021, Shkurko & Fedosov T5-s1 (OK3284, MHA); **Novgorod Province**, Rdeyskiy National Reserve, Kholmskiy Disrict, eastern part of Polistovskiy peatland, oligotrophic bog, 57.09°N, 30.73°E, 18.VI.2022, Shkurko & Korolkova, 169, (OK3730, MHA9121195); **Moscow Province**, Klinskiy District, "Zavidovo", minerotrophic bog, 56.33°N, 36.15°E, 28.VI.2008,

Ignatov & Notov 08-21 (OK3729, MHA9022810); **Arkhangelsk Province**, Primorskiy District, Yagry Lake, oligotrophic bog, 10.IX.2001, Churakova 2037 (OK3727, MW9014412);

Sphagnum talbotianum: **Russia, Nenets** Autonomous District, Middle course of Adzva River, moss tundra, 67.09°N, 60.59°E, 04.VIII.2009, Ivanov & Donskov 09-344 (OK3701, MHA9102281); **Khanty-Mansiysk** Autonomous District, Berezovsky District, eastern slope of Ner-Oyka Mountain, sedge-sphagnum bog with willows, 64.57°N, 59.59°E, 914 m a.s.l., 06.VIII.2013, Lapshina 13-525 (OK3390, MHA9015818); the same area, sedge-sphagnum bog, 64.58°N, 59.59°E, 960 m a.s.l., 01.VIII.2013, Lapshina 13-507 (OK3698, MHA9015873); **Yamalo-Nenets** Autonomous District, Baydara River basin, sedge-sphagnum tundra, 67.53°N, 67.93°E, 31.VII.2018, Popov 307 (OK3692, MHA9102182); the same area, sedge mire, 70.85°N, 73.93°E, 27.VIII.2022, Dudov, Poloshevetz & Kopeina 15-2 (OK3531, MHA); Tazovsky District, tundra, 70.93°N, 74.13°E, 21.VIII.2022, Dudov, Poloshevetz & Kopeina 19-8 (OK3530, MHA); **Krasnoyarsk Territory**, Taimyrsky District, Dikson village area, Kara Sea shore near Velbotov Bay, rich fen 73.56°N, 80.62°E, 07.VIII.2019 Fedosov & Koltysheva 291-3 (OK3278, MHA9102973); the same area, vicinity of Dikson settlement, wet tundra at base of ridge slope, rich fen, 73.48°N, 80.57°E, 08.VII.2017, Fedosov 17-2-19-6 (OK3279, MHA9102970); the same area, Bol'shoy Arctichesky State Reserve, vicinity of Meduza Bay, poor fen, 73.39°N, 80.59°E, 24.VII.2019, Fedosov & Koltysheva 274-8 (OK3281, MHA9102982); **Yakutia**, Momsky District, Ulakhan-Chistay mountain ridge, forestless bog, on side of a hummock, 64.9°N, 146.417°E, 840 m a.s.l., 19.VII.2018, Ignatov & Ignatova 18-1915 (OK3275, MHA9028536); Tyrekhtyakh River downstream, wet larch forest near a lake, 64.17°N, 146.69°E, 25.VII.2018, Ignatov & Ignatova 18-2476 (OK3691, MHA9028800); Tomponsky district, Kyurbelyakh Creek, wet tundra, 63.13°N, 139.07°E, 950 m a.s.l., 8.VII.2011, Ignatov & Ignatova 11-2170 (OK3393, MHA9102061); **Amur Province**, Zeyskiy National Reserve, Tukuringra Mountain Ridge, the sphagnum bog with sparse trees, 54.21°N, 126.98°E, 28.VIII.2016, Dudov & Kozhin Br_0112 (OK3523, MW9079503); Norsky Nature Reserve, mire with *Larix*, 52.97°N, 130.17°E, 6.VII.2010, Bezgodov 220 (OK3694, MHA9105692); Zeya District, Stanovoy Ridge, Tokinsky-Stanovoy National Park, tundra peat bog, 55.74°N, 130.78°E, 1529 m a.s.l., 16.VII.2021, Dudov TSMF0247-355 (OK3341, MHA); **Sakhalin Province**, Nogliksky District, Bolshoy-Gamoray River range, sphagnum bog, 52.52°N, 143.12°E, 24.VIII.2009, Pisarenko op03309 (OK3697, MHA9102843); Smirnykh District, Nature Reserve "Vaida Mountain", northern slope of mountain, 49.88°N, 143.47°E, 750 m a.s.l., 21.VIII.2006, Ignatov & Teleganova 06-3607 (OK3395, MHA9101781); **Chukotka**, Vrangel Island, tundra, 2020, D20m2 (OK3283, MHA).

Sphagnum warnstorfii: **Russia, Murmansk Province**, Apatity City outskirts, north shore of Imandra Lake, aapa-bog, 67.60°N, 30.00°E, 27.VI.2012, Ignatov & Ignatova 12-16 (OK3301, MHA9105709); Pechengskiy District, sedge mire with willows, 69.64°N, 32.43°E, 13.VII.2009, Popova 118-m-27 (MW9014349); **Moscow Province**, Klinskiy District, "Zavidovo", minerotrophic bog, 56.33°N, 36.15°E, 28.VI.2008, Ignatov & Notov 08-23 (OK3302, MHA9015728); **Nenets** Autonomous District, Middle course of Adzva River, tundra with willows, 67.09°N, 60.60°E, 04.VIII.2009, Ivanov & Donskov 09-687 (OK3399, MHA9102309); **Irkutsk Province**, Khamar-

Daban Mountains, Vicinity of Chersky Peak, minerotrophic bog near lake, 51.49°N, 103.60°E, 1700 m a.s.l., 05.IX.2022, Fedosov & Shkurko 274-1 (OK3706, MHA); **Amur Province**, Zeya District, Stanovoy Ridge, Tokinsky-Stanovoy National Park, tundra peat bog, 55.74°N, 130.79°E, 1548 m a.s.l., 26.VII.2021, Dudov TSMF0265-393 (OK3342, MHA); **Khabarovk Territory**, Badzhal Mountains, Yarap River tributary upper course, lover subalpine belt, minerotrophic bog, 50.35°N, 134.63°E, 1400 m a.s.l., 08.VIII.2016, Fedosov 16-40-s6 (OK3280, MHA9120573); Botchinsky National Reserve, pine forest, along stream, 48.30°N, 139.57°E, 12.VIII.2013, Ignatov & Ignatova 13-365 (OK3655, MHA9101775).

Sphagnum warnstorfii 3: **Russsia, Yakutia**, Oymyakomskiy Disrict, Ust'-Nera Settlement outskirts, grass-sphagnum mire, 64.5°N, 143.72°E, 500 m a.s.l., 5.VIII.2015, Ignatov & Ignatova 15-1564 (OK3401, MHA9102053); **Amur Province**, Zeyskiy National Reserve, Zeya District, Stanovoy Ridge, Tokinsky-Stanovoy National Park, tundra peat bog, 55.74°N, 130.78°E, 1529 m a.s.l., 16.VII.2021, Dudov 355-1 (OK3340, MHA); **Chukotka**, Wrangel Island, tundra, 2020, D25m4n1 (OK3283, MHA).

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Table 3. Voucher information and GenBank accession numbers of *Sphagnum* specimens used for DNA studies.

Species	Isolate	Locality	Voucher	RAPD-A	RAPD-B	*trnG*
S. capillifolium	OK2964	Russia, Kunashir Isl.	Mamontov, 2020, 833-1-s34 (MHA9121196)	OR972432	OR972476	OR972520
S. capillifolium	OK2965	Russia, Kunashir Isl.	Mamontov, 2020, 833-1-s40 (MHA9121197)	OR972431	OR972475	OR972519
S. capillifolium	OK3521	Russia, Yakutia	Ignatov & Ignatova, 2016, 16-488 (MW9113201)	OR972428	OR972472	OR972516
S. capillifolium	OK3522	Russia, Sakhalin Isl.	Dudov & Kozhin, 2016, Br_0113 (MW9079504)	OR972427	OR972471	OR972515
S. capillifolium	OK3525	Russia, Kamchaka	Fedosov, 2010, 10-4-58 (MW9065671)	OR972437	OR972481	OR972525

Species	Isolate	Locality	Voucher	RAPD-A	RAPD-B	*trnG*
S. capillifolium	OK3656	Russia, Buryatia Republic	Ignatov, Ignatova, & Kolesnikova, 2018, 18-4238 (MHA9027234)	OR972430	OR972474	OR972518
S. capillifolium	OK3657	Russia, Arkhangelsk Province	Churakova, 1999, 497 (MHA9112619)	OR972429	OR972473	OR972517
S. quinquefarium	OK3304	Russia, Shikotan Isl.	Shkurko & Fedosov, 2021, 21-2 (MHA)	OR972435	OR972479	OR972523
S. quinquefarium	OK3388	Russia, Khabarovsk Territory	Pisarenko, 2016, x2c (NSK2008493)	OR972436	OR972480	OR972524
S. rubellum	OK3284	Russia, Pskov Province	Shkurko & Fedosov, 2021, T5-s1 (MHA)	OR972438	OR972482	OR972526
S. rubellum	OK3526	Russia, Murmansk Province	Ignatov & Ignatova, 2012, 12-14 (MW9014350)	OR972442	OR972486	OR972530
S. rubellum	OK3727	Russia, Arkhangelsk Province	Churakova, 2001, 2037 (MW9014412)	OR972439	OR972483	OR972527
S. rubellum	OK3729	Russia, Moscow Province	Ignatov & Notov, 2008, 08-21 (MHA9022810)	OR972440	OR972484	OR972528
S. rubellum	OK3730	Russia, Novgorod Province	Shkurko & Korolkova, 2022, 169 (MHA9121195)	OR972441	OR972485	OR972529
S. sp.	OK3282	Russia, Wrangel Isl.	2020, D25m4n1 (MHA)	OR972468	OR972512	OR972554
S. sp.	OK3340	Russia, Amur Province	Dudov, 2021, 355-1 (MHA)	OR972469	OR972513	OR972555
S. sp.	OK3401	Russia, Yakuia	Ignatov & Ignatova, 2015, 15-1564 (MHA 9102053)	OR972470	OR972514	OR972556
S. subfulvum	OK2946	Russia, Kunashir Isl.	Mamontov, 2020, s12 (MHA)	OR972433	OR972477	OR972521
S. subfulvum	OK3305	Russia, Shikotan Isl.	Shkurko & Fedosov, 2021, 581 (MHA)	OR972434	OR972478	OR972522
S. talbotianum	OK3275	Russia, Yakutia	Ignatov & Ignatova, 2018, 18-1915 (MHA9028536)	OR972454	OR972498	OR972540
S. talbotianum	OK3278	Russia, Taimyr Peninsula	Fedosov & Koltysheva, 2019, 291-3 (MHA9102973)	OR972450	OR972494	OR972537
S. talbotianum	OK3279	Russia, Taimyr Peninsula	Fedosov, 2017, 17-2-19 (MHA9102970)	OR972453	OR972497	-
S. talbotianum	OK3281	Russia, Taimyr Peninsula	Fedosov & Koltysheva, 2019, 274-8 (MHA9102982)	OR972445	OR972489	OR972532
S. talbotianum	OK3283	Russia, Wrangel Isl.	2020, DD20m2 (MHA)	OR972444	OR972488	OR972531
S. talbotianum	OK3341	Russia, Amur Province	Dudov, 2021, TSMF0247-355 (MHA)	OR972455	OR972499	OR972541
S. talbotianum	OK3390	Russia, Khanty-Mansiysk AD	Lapshina, 2013, 13-525 (MHA9015818)	OR972451	OR972495	OR972538
S. talbotianum	OK3393	Russia, Yakutia	Ignatov & Ignatova, 2011, 11-2170 (MHA9102061)	OR972447	OR972491	OR972534
S. talbotianum	OK3395	Russia, Sakhalin Isl.	Ignatov & Teleganova, 2006, 06-3607 (MHA9101781)	OR972446	OR972490	OR972533
S. talbotianum	OK3523	Russia, Amur Province	Dudov & Kozhin, 2016, Br_0112 (MW9079503)	OR972443	OR972487	-
S. talbotianum	OK3530	Russia, Yamalo-Nenets AD	Kozhin, 2022, 19-8 (MHA)	OR972452	OR972496	OR972539
S. talbotianum	OK3531	Russia, Yamalo-Nenets AD	Kozhin, 2022, 15-2 (MHA)	OR972449	OR972493	OR972536
S. talbotianum	OK3691	Russia, Yakutia	Ignatov & Ignatova, 2018, 18-2476 (MHA9028800)	OR972458	OR972502	OR972544
S. talbotianum	OK3692	Russia, Nenets AD	Popov, 2018, 307 (MHA9102182)	OR972457	OR972501	OR972543
S. talbotianum	OK3694	Russia, Amur Province	Bezgodov, 2010, #220 (MHA9105692)	OR972460	OR972504	OR972546
S. talbotianum	OK3697	Russia, Sakhalin Isl.	Pisarenko, 2009, op03309 (MHA9102843)	OR972459	OR972503	OR972545
S. talbotianum	OK3698	Russia, Khanty-Mansiysk AD	Lapshina, 2013, 13-507 (MHA9015873)	OR972448	OR972492	OR972535
S. talbotianum	OK3701	Russia, Nenets AD	Ivanov & Donskov, 2009, 09-344 (MHA9102281)	OR972456	OR972500	OR972542
S. warnstorfii	OK3280	Russia, Badzhal Mts.	Fedosov, 2016, 16-40-6 (MHA9120573)	OR972461	OR972505	OR972547
S. warnstorfii	OK3301	Russia, Murmansk Province	Ignatov & Ignatova, 2012, 12-16 (MHA9105709)	OR972467	OR972511	OR972553
S. warnstorfii	OK3302	Russia, Moscow Province	Ignatov & Notov, 2008, 08-23 (MHA9015728)	OR972465	OR972509	OR972551
S. warnstorfii	OK3342	Russia, Amur Province	Dudov, 2021, TSMF0265-393 (MHA)	OR972462	OR972506	OR972548
S. warnstorfii	OK3399	Russia, Nenets AD	Ivantov & Donskov, 2009, 09-687 (MHA9102309)	OR972466	OR972510	OR972552
S. warnstorfii	OK3655	Russia, Khabarovsk Territory	Ignatov & Ignatova, 2013, 13-365 (MHA9101775)	OR972463	OR972507	OR972549
S. warnstorfii	OK3706	Russia, Irkutsk Province	Shkurko & Fedosov, 2022, 274-1 (MHA)	OR972464	OR972508	OR972550