Arctoa (2019) **28**: *203–209*
doi: 10.15298/arctoa.28.17

NEW RECORDS OF *SCAPANIA SPHAERIFERA* H.BUCH ET TUOM. IN EUROPE WITH DESCRIPTION OF GLOBAL DISTRIBUTION AND ECOLOGY OF THE SPECIES

НОВЫЕ НАХОДКИ *SCAPANIA SPHAERIFERA* H.BUCH ET TUOM. В ЕВРОПЕ С ОБСУЖДЕНИЕМ ЭКОЛОГИИ И ГЛОБАЛЬНОГО РАСПРОСТРАНЕНИЯ

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Abstract

Scapania sphaerifera known in Europe only from the type specimen collected 85 years ago, has been found in three sites in the Urals including its European part. The taxonomic position and differences from morphologically similar species are discussed, and the distribution and ecology are significantly reevaluated.

Резюме

Scapania sphaerifera, долгое время известная в Европе только по типовому образцу, собранному 85 лет назад, выявлена в трех точках на Урале, в том числе в европейской его части. Обсуждается таксономическое положение вида, его отличия от морфологически сходных видов, приводятся существенно уточненные распространение и экология, цветные фотографии.

KEYWORDS: *Scapania*, liverworts, Russia, rare species

Introduction

During the study of collections by A. Bezgodov from the western slopes of Ural (European part of Russia, Perm Territory) and by Elena Lapshina from the eastern slopes of Ural (Asian part of Russia) the senior author identified *Scapania sphaerifera* H.Buch et Tuom. Until now the species was known in Europe only from the type specimen collected in 1934 (Buch & Tuomikoski, 1936). Repeated attempts to find this species both at the type locality and in Europe as a whole have been unsuccessful. However, *Scapania sphaerifera* has been found in Asian part of Russia where it occurs in Siberia (Konstantinova and Savchenko, 2008; Afonina *et al*., 2012; Mamontov & Konstantinova, 2018, Mamontov *et al*., 2018, *etc*.) as well as in the Russian Far East (Choi *et al*., 2012a) and Korea (Choi *et al*., 2012b). The species has recently been included in the European Red List of Threatened Species as Critically Endangered (Konstantinova, 2019) and "it is recommended to undertake repeated surveys in order to confirm whether the species may still be present in Europe" (l.c.). Based on this we find it useful to describe the new records of the species in Europe. Despite the fact that *Scapania sphaerifera* recently has been described and discussed in several publications (Potemkin & Sofronova, 2018; Choi *et al*., 2012a), a number of important points were in our opinion overlooked. Therefore it appears practical to discuss in more detail the variability, ecology and distribution of the species based both on the most complete collection of the species stored in KPABG (http://kpabg.ru/cris) and literature sources.

Materials and methods

Two recently collected specimens from the western (European) and one from the eastern (Asian) slopes of Ural were studied using light microscopes equipped with digital cameras and compared with specimens of *Scapania sphaerifera* from Siberia and the Russian Far East preserved in KPABG (http://kpabg.ru/cris). To illustrate the quite characteristic appearance and most important morphological features of *Scapania sphaerifera* we took pictures of shoots using Nikon SMZ 800 and of gemmae, cells etc. using Axioplan2 ZEI88. The distribution map is based on literature sources and the specimens studied and incorporated in Cryptogamic Russian Information System (CRIS, Melekhin *et al*., 2019) available on internet (http://kpabg.ru/cris).

To detect molecular variability of *S. sphaerifera* we sequenced two nucleotide markers – ITS1-2 nrDNA and *trn*L-F cpDNA of one of the specimen from Ural – and compared them with previously studied specimen from South Siberia (Buryatiya Republic) and three unpublished earlier specimens from Far East of Russia (Primorsky

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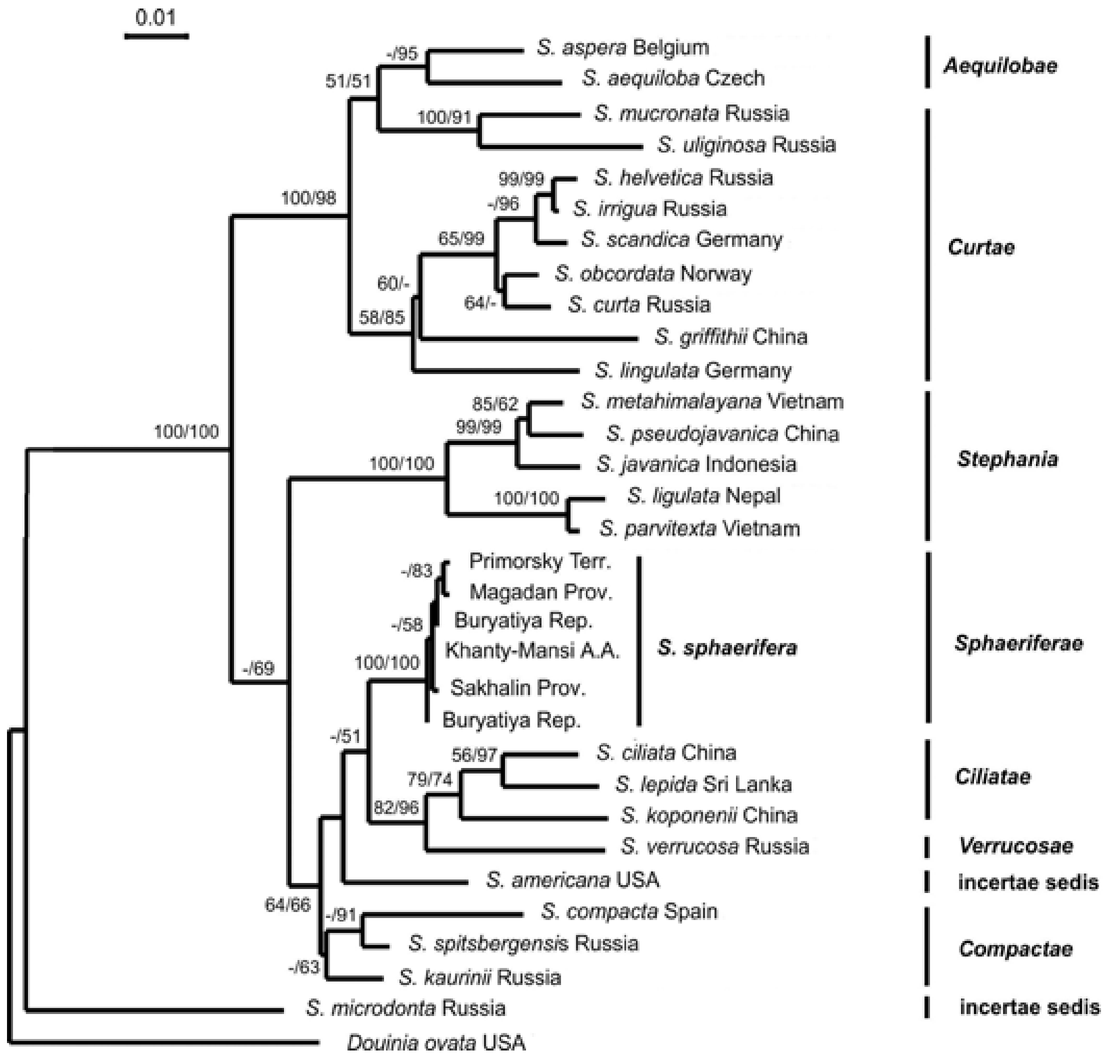

Fig. 1. Maximum likelihood phylogenetic tree inferred from ITS1-2 and *trn*L-F analysis of selected *Scapania* species. Bootstrap support from the maximum parsimony and the maximum likelihood analyses (MP/ML) higher than 50% are indicated above branches. Scale shows substitutions per site.

Territory, Sakhalin and Magadan Provinces). The nucleotide sequences were obtained according to the protocols for DNA isolation, PCR amplification and DNA sequencing published in Vilnet *et al.* (2010). The voucher details and GenBank accession numbers of tested *S. sphaerifera* specimens are placed in Appendix 1.

To illustrate the *Scapania sphaerifera* affinity the ITS1-2+*trn*L-F sequence alignment from Bakalin *et al.* (2019) was reduced to sections *Aequilobae, Curtae, Stephaniae, Verrucosae, Ciliatae* and *Compactae* using BioEdit 7.0.1 (Hall, 1999). In this dataset *Scapania sphaerifera* was represented by six specimens. *Douinia ovata* (Dicks.) H. Buch was chosen as outgroup taxon. Totally, 32 specimens were selected (Appendix 1), all positions were included in the phylogenetic analysis; absent data were coded as missing.

The ITS1-2+*trn*L-F alignment was analyzed by two analytical procedures: the maximum parsimony method (MP) with TNT v. 1.5 (Goloboff & Catalano, 2016) and the maximum likelihood method (ML) with PhyML v. 3.0 (Guindon *et al.*, 2010). The parsimony analysis with TNT included a New Technology Search with search minimal length tree by five iterations and 1000 bootstrap replicates; the default settings were used for other parameters, and gaps were coded as missing. The Model Generator software (Keane *et al.*, 2004) provided the GTR+I+G model as the best-fit evolutionary model of nucleotide substitutions for alignment. The ML analysis was implemented with this model, and the rate of heterogeneity among sites was modelled using a gamma distribution with four rate categories. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 200 replicates. According to the stopping frequency criterion (FC) for the bootstrapping procedure (Pattengale *et al.*, 2010) for our dataset 200 replicates were enough to reach BS convergence with a Pearson average c100 = 0.994880 as estimated by RAxML v. 7.2.6 (Stamatakis, 2006).

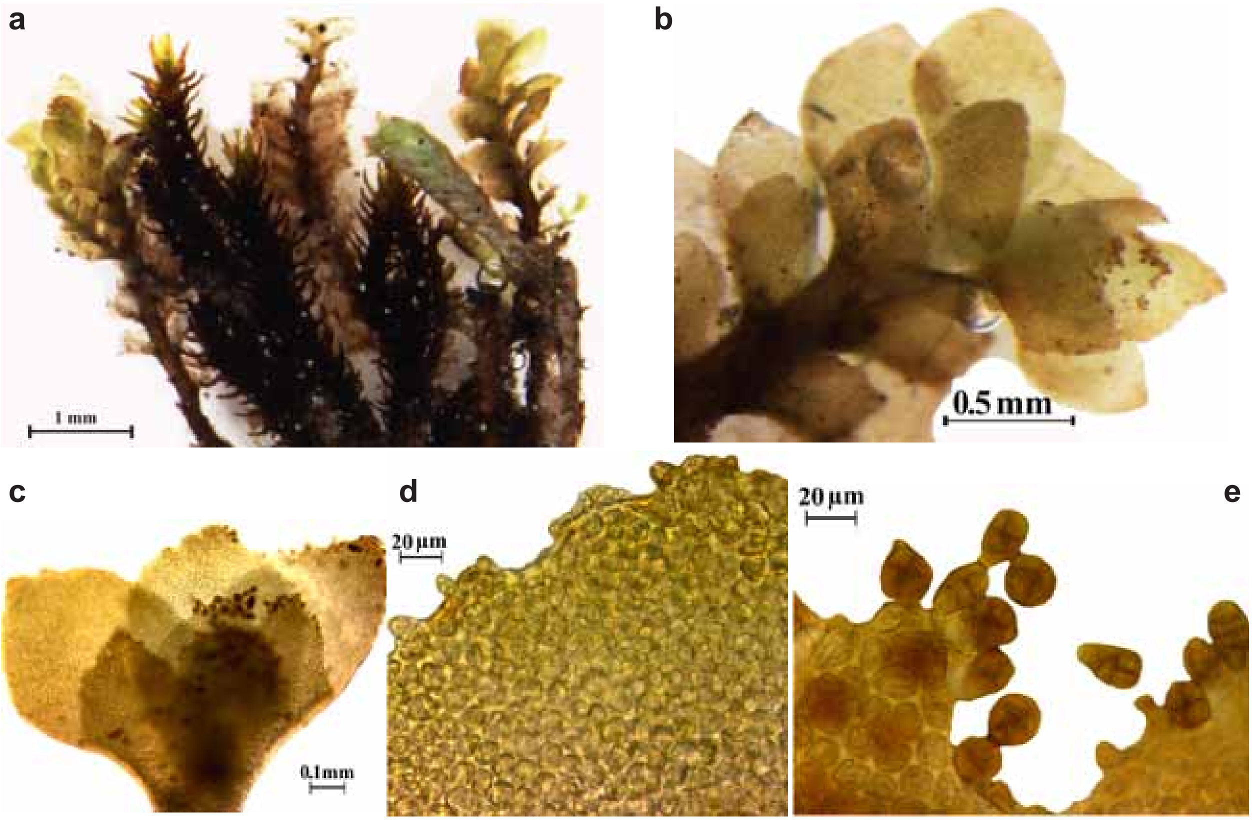

Fig. 2. *Scapania sphaerifera* H.Buch et Tuom. (from: Perm Territory, 01.VIII.2018, *A.G. Bezgodov,* KPABG122124). a – *S. sphaerifera* mixed with *Gymnomitrion concinnatum* (Lightf.) Corda and *Andreaea rupestris* Hedw.; b – upper part of shoot; c – upper leaves with gemmae; d – margin of leaf and cells with papillae; e – gemmae.

The sequence variability of each DNA locus for *S. sphaerifera* was evaluated as *p*-distances between specimens, as calculated in Mega 5.1 (Tamura *et al.,* 2011) using the pairwise deletion option for counting gaps.

Results

Phylogeny. The ITS1-2 and *trn*L-F nucleotide sequences for the Ural specimens as well as previously obtained sequence data for three Far Eastern specimens, totally eight accessions, were deposited in GenBank. The combined ITS1-2+ *trn*L-F alignment for 32 specimens of the selected *Scapania* species consists of 1506 character sites, among them 934 sites belong to ITS1-2 and 572 sites to *trn*L-F. The number of invariable sites in ITS1-2 and *trn*L-F are 557 (59.64%) and 430 (75.17%), variable positions are 299 (32.01%) and 91 (15.91%), parsimony informative positions are 156 (16.70%) and 38 (6.64%) respectively. In the combined alignment there are 987 (65.54%) invariable sites, 390 (25.90%) variable and 194 (12.88%) parsimony informative positions.

The MP analysis with TNT yielded a single parsimonious tree with a length of 1336 steps, with CI = 0.669333 and RI = 0.731892 calculated in Mega 5.1. The ML calculation resulted in a tree; the arithmetic means of Log likelihood was -6271.568893. Both trees possess a similar topology, thus on Fig. 1 we provide the ML tree with indication of BS values obtained in MP and ML calculations. The six specimens of *S. sphaerifera* comprise a clade with the highest BS (100/100) on both trees. The phylogenetic affinity of *S. sphaerifera* to clade of the section *Ciliatae* is poorly supported.

Below the Cryptogamic Russian Information System numberrs (kpabg.ru›cris/ ?q=node/16) are given in brackets.

Recently studied specimens: **Perm Province**, Vishera State Nature Reserve, western slopes of Ural Mountains: Chuval Ridge, watershed of Zyryanka River and left tributary of Kuryksarka River, rock outcrop at the top, on northern cliff, 60°59’N, 58°56’E, alt. 740 m, 31.VI.2017 *A.G. Bezgodov 439-17*, some stems with gemmae in mats with dominance of *Gymnomitrion concinnatum* (Lightf.) Corda and admixture of *Trilophozia quinquedentata* (Huds.) Bakalin*, Tetralophozia setiformis* (Ehrh.) Schljakov*, Andreaea rupestris* Hedw.*, Pohlia cruda* (Hedw.) Lindb., *etc.* [122122]; Kuryksar Ridge near the northern part. Cliffs on eastern slope, on dry light cliff, 61°02’02”N-58°50’21”E, alt. 760 m, 01.VIII.2018 *A.G. Bezgodov 266-2-18*, scattered in mats with dominance of *Racomitrium lanuginosum* (Hedw.) Brid., lichens and admixture of *Tetralophozia setiformis, Barbilophozia sudetica* (Nees ex Huebener) L. Söderstr., De Roo & Hedd.*, Cephaloziella* sp. [122124]; Khanty-Mansi Autonomous Okrug -Yugra, Beresovskiy District, Eastern spur of subpolar Ural, Upper Khulga River Basin, 4 km upstream of the mouth of Tykotlova River, rock outcrop on gentle north-east facing slope, on fine earth on rock, 65.27757N°, 62.11185°E, 12.VII.2018 *E.D. Lapshina 057-8.1-18* [122121].

Other selected specimens studied: Krasnoyarsk Territory [109051, 16385]; Buryatiya Republic, Khamar-Daban Ridge [104378, 104242, 104249, 102500, 102497, 112394], Magadan Province [115235], Sakhalin Province [115233], Primorsky Territory [115234, 115618, 19143]

DISCUSSION

Taxonomy. The species is placed in the monotypic section *Sphaeriferae* Konstant. et Potemkin (Konstantinova & Potemkin, 1994). This has recently been confirmed by molecular phylogenetic studies that clearly show the strictly isolated position of the species. In the earliest study of *Scapania* molecular phylogeny *S. sphaerifera* was found in unsupported relation with *S. verrucosa* Heeg (Vilnet *et al*., 2010). Later, with extended species sampling *S. sphaerifera* was placed in affinity to sections *Stephaniae* Amakawa et S.Hatt. ex Potemkin and *Ciliatae* Grolle without support (Heinrichs *et al*., 2012). The recently published phylogeny with inclusion a number of Asiatic specimens resolved *S. sphaerifera* in relation to section *Compactae* (Müll. Frib.) H. Buch and *S. americana* Müll. Frib. with 0.55 Bayesian posterior probabilities (PP) (Bakalin *et al*., 2019). Thus, the attribution of the species to the section *Aequilobae* (Müll. Frib.) H. Buch, which some researchers follow (Arnell, 1956; Choi *et al*., 2012a) is not confirmed.

Variability. All studied specimens are very similar both morphologically and genetically. The length of ITS1-2 for six *S. sphaerifera* specimens from widely separated geographical regions was stable and counted 743 base pairs, the length of *trn*L-F achieved 471 base pairs. The length of ITS1-2 and *trn*L-F for specimen of *S. verrucosa* were 747 and 484 base pairs. The *p*-distances among *S. sphaerifera* specimens varied from 0% to 0.5% in ITS1-2 and from 0% to 0.4% in *trn*L-F (Table 1). The specimen from the Urals differed from the other ones in 0-0.4% in both sequenced DNA loci. Thus, molecularly *S. sphaerifera* is a species with a low variability.

The morphology of the studied specimens corresponds well to the description of the species (Buch & Tuomikoski, 1936) but plants from Ural differ in slightly smaller size being mostly around 7–10 mm long and 1.5-2 mm wide, whereas it is described as "bis 12 mm lang und 3 mm breit" (l.c.). Moreover in the Russian Far East the species can reach 20 mm in length (Choi *et al*., 2012a). At the same time, the size of the gemmae and cells do not differ from that described before (l.c.) or cells are slightly smaller being in midlobes 12–15 μm wide, whereas described as 14–18 μm (Buch & Tuomikoski, 1936). To the greatest extent Ural samples differ in dentation of leaves. Leaves of plants from Ural are almost toothless. Only some of them have single blunt protrusions (Fig. 2), whereas the species is described and illustrated as having dentate margins (Buch & Tuomikoski, 1936: fig.7; Choi *et al*., 2012a: figs. 45, 46). This is probably due to the fact that the plants in Ural are found in drier conditions compared to other collections. In most studied Asian specimens margins of leaves are clearly dentate.

Differentiation. *Scapania sphaerifera* is characterized by a combination of specific features that allow it to be distinguished at once from other species of the genus even in the field. The plants are characteristically dark yellow or brown-yellow, more rare yellow-green. Their leaves have straight keel, almost transversely inserted dorsal lobe, the upper leaves always develop light brown or golden-brown large gemmae. Of microscopic features the most distinctive are strongly papillose cuticle and almost spherical 4- or even 8-celled gemmae always present that are quite unusual in *Scapania* (Fig. 2). This form of gemmae is not found in any of the other species of the genus, although they are very similar to gemmae of *Scapania microdonta* (Mitt.) Müll. Frib. The latter species differs from *S. sphaerifera* in size of plants (being 4–4.5 mm wide and up to 70 mm long), in not decurrent ventral lobes, and much larger cells of leaves. In the color and size of plants, long decurrent ventral lobes, densely covered by large round papilla surface of leaf cells *Scapania sphaerifera* looks more like *S. verrucosa.* But *S. verrucosa* has angular, mostly 2-celled gemmae, cells along the margin of leaves in 2–3 rows thick-walled versus not thick-walled in *S. sphaerifera*. It differs as well in non plicate perianth versus plicate in *S. sphaerifera* and different habitats. *S. sphaerifera* is the plant of dry outcrops in coniferous forests or tundra. By contrast *S. verrucosa* is restricted to low mountains, mostly to zones of deciduous or mixed forests where it occurs in crevices of moist cliffs on banks of streams, often near waterfalls, sometimes on decaying logs in running water.

Distribution. *S. sphaerifera* was described from Europe, but its main range is Asia where it occurs from the coniferous forest zone up to the tundra zone. As mentioned above the species is extremely rare in Europe and is known from the type locality where it was collected 85 years ago and a locality in Ural described in this paper. However in Siberia and the Russian Far East *Scapania*

Table 1. The value of *p*-distances for *Scapania sphaerifera*.

	Specimen	Infraspecific *p*-distances, ITS1-2/trnL-F, %					
		1	2	3	4	5	6
1	Khanty-Mansi A. A.						
2	Buryatiya Rep. EU791765+EU791656	0.1/0					
3	Buryatiya Rep. JN631471+JN631605	0.1/0	0.3/0				
4	Primorsky Terr.	0.4/0	0.3/0	0.5/0			
5	Magadan Prov.	0.4/0	0.3/0	0.5/0	0.3/0		
6	Sakhalin Prov.	0/0.4	0.1/0.4	0.1/0.4	0.4/0	0.4/0	

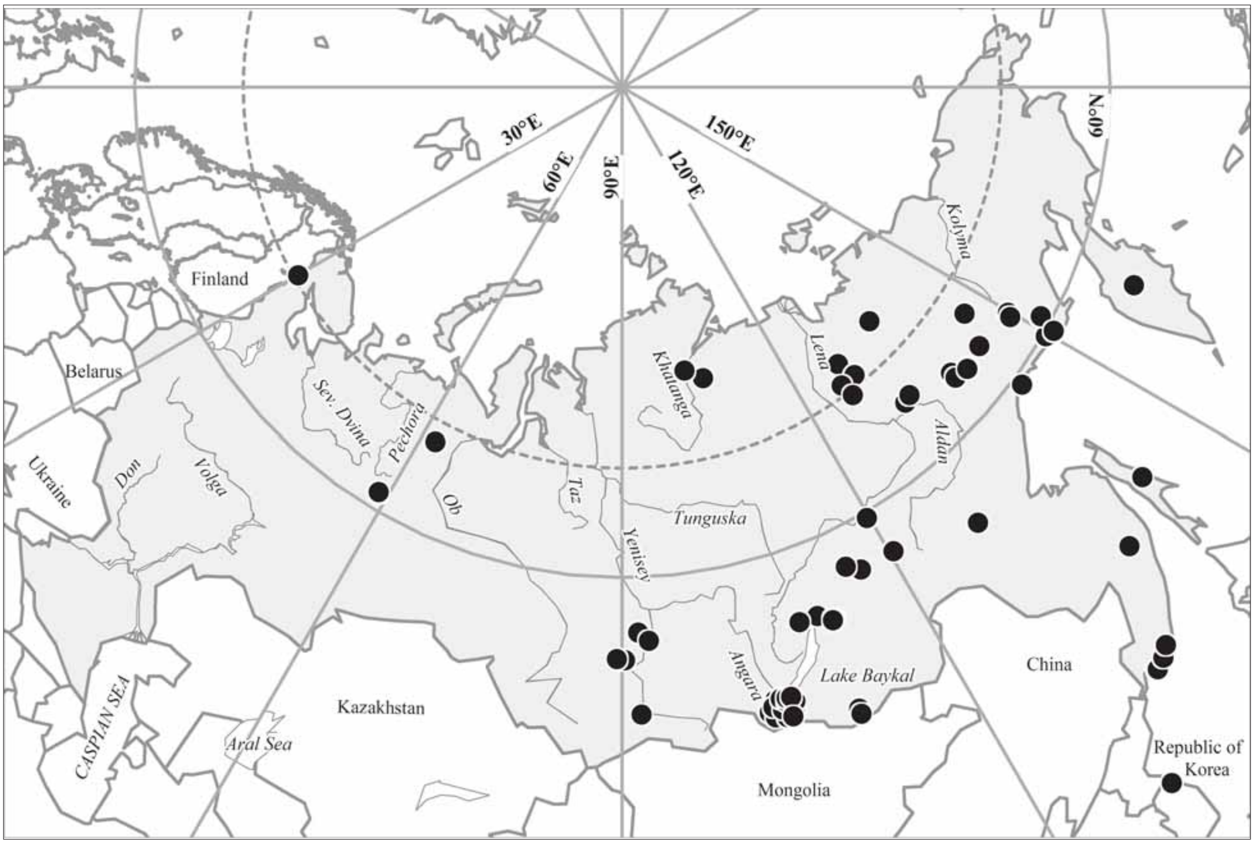

Fig. 3. Worldwide distribution of *Scapania sphaerifera* H. Buch et Tuom.

sphaerifera is not rare in some regions. In the South and East Siberia *S. sphaerifera* was collected in almost all studied mountains (Afonina *et al*., 2012; Konstantinova & Savchenko, 2008, Mamontov *et al*., 2018; Sofronova & Potemkin, 2018, *etc*.). In South Siberia the species is not rare in the Khamar-Daban Mountains where it has been collected many times in valleys of Pereemnaya River, Anosovka River, Osinovskiy Golets Mountains (Konstantinova & Savchenko, 2008; Mamontov & Konstantinova, 2017, see also specimens examined). But in most mountains of the South Siberia the species is recorded as rather rare (l.c.), that is probably at least partly explained by incomplete knowledge. The species occurs sporadically in Yakutia from the Tokinsky Stanovik Range (ca. 55°46'N) in the south (Sofronova, 2013) where it is known from single locations at the altitudes of about 950 m, up to 67°04'N in the Orulgan Sis Range in the north, where it is rather frequent (Sofronova *et al*., 2015). The northernmost recently known locations of the species 71°15' are in Taimyr (Fedosov *et al*., 2015). In the Far East of Russia the species is known from the North in the Magadan Province up to the south of the Primorsky Territory (Choi *et al*., 2012a) whereas the most southern locality is recorded in South Korea (Choi *et al*., 2012b). In general the range of species can be described as holarctic Eurasian (Fig. 3).

Ecology. *S. sphaerifera* is a strictly petrophytic species that grows almost exclusively on rocks but always in sites with relatively high humidity, e.g. in deep gorges as in the type locality in the Murmansk Province, or in many sites in Khamar-Daban, Sayan and Primorsky Territory. However it probably avoids areas with strictly oceanic climate, as stressed by Choi *et al*. (2012a) and confirmed by the distribution of the species particularly its occurrence in Siberia and Ural. More often the species occurs in rock fields on mountain slopes, in gorges or on plateaus where it grows on thin soil layers between rocks in crevices or just on sides of huge rock blocks, often in floodplains of mountain rivers or in coniferous forests in valleys of rivers. In their most southern locations the species occurs at high altitudes. So in South Korea the species has been collected at the altitude of 1449 m "on shaded rocks in stony slope at top of mountain in coniferous forest" (Choi *et al*., 2012b). The species reaches about the same heights in Primorsky Territory, where it occurs in the range of heights from 700 to 1600 m (Olkhovaya Mountain). The highest known location of the species is in South Siberia in Khamar-Daban (Kamushinskiy Pass, 2048 m alt., http://kpabg.ru/h/?q=node/400726). *Scapania sphaerifera* is rather basiphilous species, but in its northernmost location it occurs in moist crevices of limestone cliffs (Fedosov *et al*., 2015) which is quite unusual for the species. Here it grows mixed with *Trilophozia quinquedentata.* The species can be characterized as xeromesophyte and occurs with other bryophytes tolerant of dry conditions. The most common of its associated liverwort species are *Tetralophozia setiformis* (Ehrh.) Schljakov, *Trilophozia quinquedentata, Sphenolobus minutus* (Schreb.) Berggr.*, Sphenolobus saxicola* (Schrad.) Steph. and among moss *Andreaea rupestris.* In Siberia the list of the most frequent associates also includes *Scapania microdonta* (Mitt.) Müll.Frib.

At high altitudes in South Siberia *S. sphaerifera* occurs with the widespread *Barbilophozia sudetica*, *Scapania microdonta*, *Sphenolobus minutus*, *Lophoziopsis excisa* (Dicks.) Konstant. et Vilnet. In some areas in South Siberia the species can be abundant in valleys of mountain rivers with relatively high humidity in zones of coniferous forests where it grows on walls of huge boulders. In such habitats its associates are other mountain species, particularly *Marsupella emarginata* (Ehrh.) Dumort., *Herbertus* sp., *Tritomaria exsecta* (Schmidel) Schiffn. ex Loeske, *etc*. Although mainly found in relatively dry habitats, the species has once been found in a very deep gorge on moist cliff as admixture in mats with *Diplophyllum taxifolium* (Wahlenb.) Dumort., *Mylia taylorii* (Hook.) Gray, and *Tetralophozia filiformis* (Steph.) Urmi. In general 16 species of liverworts occur with *S. sphaerifera*.

Conclusion

Numerous new records of *S. sphaerifera* in Asia, including South Korea, suggest that the species has a wider range than is currently known and it is likely to be found in China as well. We suggest that at least some records of *Scapania verrucosa* from China (Piippo, 1990; Piippo *et al*., 1997) should be referred to *S. sphaerifera*. It is necessary to revise the specimens cited for China as *S. verrucosa* (l.c.), since *S. sphaerifera* is a poorly known species and can easily be confused with *S. verrucosa* as has been done before (cf. Schljakov, 1981). On the other hand the isolated taxonomic position of *S. sphaerifera*, and its distribution largely limited to areas of Siberia and Far East of Russia not glaciated in the Pleistocene, indicate the ancient age of the species and its relict range.

Acknowledgements

Anders Hagborg is gratefully acknowledged for correction of English and some useful suggestions. We also thank A.G.Bezgodov for sending collections and useful comments on collecting sites. A. N. Savchenko is thanked for the preparing map of collecting sites. The study was partly supported by RFBR 18-04-00594, and of E.D. Lapshina also by the Government of the Khanty-Mansi Autonomous Region under project 18-44-86001.

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Appendix 1. Specimens used in the molecular phylogenetic analysis, ITS1-2/*trn*L-F (for newly generated ones, the specimen voucher information is added).

Douinia ovata EU791771/AY327778; *Scapania aequiloba* JN631362/JN631500; *Scapania americana* EU791764/EU791655; *Scapania* aspera EU791735/EU791627; *Scapania ciliata* JN631390/JN631527; *Scapania compacta* JN631399/JN631537; *Scapania curta* EU791628/EU791736; *Scapania griffithii* MH930835/MH931422; *Scapania helvetica* EU791728/EU791620; *Scapania irrigua* EU791729/EU791621; *Scapania javanica* JN631436/JN631572; *Scapania kaurinii* EU791759/EU791650; *Scapania koponenii* JN631437/JN631573; *Scapania lepida* JN631439/JN631575; *Scapania ligulata* JN631442/JN631578; *Scapania lingulata* JN631444/-; *Scapania metahimalayana* MH930836/MH931423; *Scapania microdonta* EU791769/AF519199; *Scapania mucronata* EU791737/EU791621; *Scapania obcordata* EU791734/EU791626; *Scapania parvitexta* MH930841/MH931428; *Scapania pseudojavanica* MH930840/MH931427; *Scapania scandica* JN631469/JN631603; *Scapania sphaerifera* (Russia, Khanty-Mansi Autonomous Area, Lapshina E. KPABG 122121) MK811447/MK820695;*Scapania sphaerifera (*Russia, Magadan Prov., Bakalin V. KPABG 115235, VBGI 313995) MK811448/MK820696; *Scapania sphaerifera* (Russia, Primorsky Terr., Bakalin V. KPABG 115234) MK811449/MK820697; *Scapania sphaerifera* (Russia, Sakhalin Prov., Bakalin V. KPABG 115233, VBGI 312957) MK811450/MK820698; *Scapania sphaerifera* EU791765/EU791656; *Scapania sphaerifera* JN631471/JN631605; *Scapania spitsbergensis* EU791760/EU791751; *Scapania uliginosa* EU791739/EU791631; *Scapania verrucosa* EU791763/EU791654.