

## An unexpected record of the European liverwort *Scapania aspera* (Scapaniaceae, Marchantiophyta) in East Siberia

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**Abstract** – A morphological study, supplemented by molecular analysis (ITS1-2 nrDNA, and *trnL-F* cpDNA) revealed *Scapania aspera* M.Bernet & Bernet, a species that is typically distributed throughout Europe, in samples collected from Anabar Plateau, Taimyr District, Subarctic East Siberia. The ecology and distribution of this species are discussed, and images of Siberian specimens of *Scapania aspera* are provided. This finding of the species is both the easternmost and the northernmost in Eurasia and is at least 3000 km from the nearest European localities. The territory is remarkable due to extensive outcrops of calcareous rocks. A number of rare calcareous bryophytes with disjunctive distribution have been observed in this area. Despite the significant distance and probable isolation, the molecular distances between newly identified Siberian population and the European populations are extremely low.

*Scapania aspera* / Hepaticae / phytogeography / Siberia / Taimyr District

### INTRODUCTION

Cyclic climate fluctuations during late Tertiary and Quaternary periods have resulted in dramatic changes in the landscapes of north Eurasia in terms of the vegetation, flora and fauna. The species distribution has undergone periods of expansion and regress that are frequently associated with survival in refugia. Since molecular phylogenetic approaches have become widely used to estimate genetic distances among populations, a number of studies focused on reconstructions of the species distribution in Europe, including both vascular plants (Taberlet *et al.*, 1998; Vogel *et al.*, 1996; Vogel *et al.*, 1998; Barker *et al.*, 2003) and bryophytes (Werner

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& Guerra, 2004; Sabovljevic *et al.*, 2006; Sabovljevic & Frahm, 2008; Heinrichs *et al.*, 2010; Patino *et al.*, 2016). In terms of glacial history, northern Asia stands in marked contrast to Europe, as ice shields did not cover this area and this has increased consequent on the regression of the arctic coastline. In addition, cold and xeric climates and the wide distribution of the permafrost provide conditions reminiscent of glacial periods. These features might provide suitable conditions for the preservation of relict populations, particularly those attributed to glacial relicts. However, the north Asian distribution of species has not been sampled in most phytogeographical studies to date.

The recent exploration of Anabar Plateau in East Siberia has revealed an unexpectedly rich and interesting bryophyte flora along the upper course of the Eriechka River (Fedosov *et al.*, 2015). Reflecting recent revision of the liverwort collections from the Eriechka River area, several specimens of *Scapania*, which differ from all known northern *Scapania* species, have been discovered. These specimens were subsequently identified as *Scapania aspera*, an European species with few localities in Western Asia. Other rare bryophytes with disjunct distributions were also observed (Fedosov *et al.*, 2011, 2015, Ellis *et al.*, 2014; Potemkin *et al.*, 2015), but the *S. aspera* disjunction was new and most unexpected. Presented here is a molecular phylogenetic analysis of this and other *Scapania* collections. In the light of this we discuss whether the Eriechka River *Scapania aspera* is a relict isolated remnant of a wider area of distribution or is the result of a recent dispersal event.

## MATERIALS AND METHODS

Accessible specimens of *S. aspera* from KPABG (see section specimens examined) were used for the morphological studies. The ITS1-2 nrDNA and *trnL-F* cpDNA sequences were obtained from two Siberian specimens according to the protocols for DNA isolation, PCR amplification and DNA sequencing, described in Konstantinova & Vilnet (2011). BLAST searches with megablast algorithms (<http://blast.ncbi.nlm.nih.gov>) were used to confirm the morphological determination of Siberian specimens as *Scapania aspera*. The ITS1-2 and *trnL-F* sequences for 14 European specimens of *Scapania aspera*, obtained by Feldberg *et al.* (2010), Vilnet *et al.* (2010) and Heinrichs *et al.* (2012), were downloaded from GenBank to assess the level of molecular genetic divergence (*p*-distances) between remote populations using Mega 5.1 (Tamura *et al.*, 2011). The phylogenetic affinity of Siberian *Scapania* accessions was further studied using the maximum likelihood method (ML) implemented in PhyML v. 3.0 (Guindon *et al.*, 2010) and an alignment of ITS1-2 and *trnL-F* sequences from *S. aspera* and related species (totally 25 specimens), according to the results of previous studies (Vilnet *et al.*, 2010; Heinrichs *et al.*, 2012). Two datasets, ITS1-2 and *trnL-F*, were automatically aligned using BioEdit 7.0.1 (Hall, 1999) with a ClustalW option followed by manual correction. The preliminary phylogenetic analyses revealed a lack of incongruence between ITS1-2 and *trnL-F*, and subsequently, both datasets were combined. All positions of the final alignment were included in the phylogenetic analysis, and the lacking parts of sequences were coded as missing. The program ModelGenerator (Keane *et al.*, 2004) determined that the GTR+I+G model was the best-fit evolutionary model of nucleotide substitutions for the produced alignment according to

Hierarchical Likelihood Ratio Tests, two Akaike Information Criteria and Bayesian Information Criterion. In the ML analysis the GTR+I+G model was used and the rate heterogeneity among sites was modeled using a gamma distribution with four rate categories. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 700 replicates. According to the stopping frequency criterion (FC) for the bootstrapping procedure (Pattengale *et al.*, 2010) for our dataset 500 replicates were sufficient for reaching BS convergence with Pearson average  $p100 = 0.993394$  realized in RAxML v. 7.2.6 (Stamatakis, 2006). The voucher details and GenBank accession numbers for the specimens included in present study are listed in Table 1.

## RESULTS AND DISCUSSION

The ML analysis resulted in a single tree, the arithmetic mean of Log likelihood was  $-3256.04537$ . The Siberian specimens were situated in a polytomous clade with the European accessions of *S. aspera* (Fig. 13). The Overall Mean Distance for the ITS1-2 alignment of *S. aspera* was 0.06%, whereas that for *trnL-F* was 0%. The *Scapania aspera* specimens from Siberia were identical to the majority of European accessions in both DNA loci examined (Table 2). Sequence variability was observed for only two specimens from Germany (JN631379, JN631380), which showed a 1 bp substitution in ITS1, and for a specimen from Italy (JN631381), which showed 1 bp substitutions in ITS1 and ITS2, likely reflecting stochastic mutations. Moreover, this mutation suggests that central and southern Europe might be a centre of infraspecific diversity (and potential origin) of the species, as proposed by Damsholt (2002).

*Scapania aspera* is a well-known European species and has been described in many classic manuals (Müller, 1956; Paton, 1999; Damsholt, 2002). Our specimens fall within the variability of the species, apart from their smaller size and colour (Figs 1-12). Siberian plants are characterized by usually olive-green coloration with red-brown secondary pigmentation, are 2-3 mm wide and 15-25 mm long erect, and have some lateral branching. The stems are rigid, black below, red-brown above; and in cross-section composed of 3-4 layers of outer thick-walled cells and inner cells with thin walls. Leaf lobes are unequal,  $\pm$  ovate, and the keel has 0.2-0.4 of ventral lobe length. The dorsal lobe is weakly convex, has  $\frac{3}{4}$  of the size of the ventral lobe, is shortly decurrent, and only occasionally provided with a few teeth near the apex. The ventral lobe is plane to slightly convex, decurrent at base, and subdentate, dentate to dentate-serrate. Two to six oil-bodies occur per midleaf cell.

Only a few species can be confused with *S. aspera*, particularly *S. koponenii* and *S. aequiloba*. *Scapania aspera* and *S. aequiloba* are closely related and nested in section *Aequilobae*. *Scapania aspera* can be distinguished from the latter by the following features: 1) unequally bilobed leaves vs almost equal size leaf lobes in *S. aequiloba*; 2) shortly decurrent dorsal lobes vs under current dorsal lobes in *S. aequiloba*; 3) subdentate, dentate to dentate-serrate leaf margins vs edentate or distally dentate leaf margins in *S. aequiloba*; and 4) 2-6(-8) oil-bodies per cell vs 2-4 in *S. aequiloba*. Despite morphological similarities, Heinrichs *et al.* (2012) showed that European *Scapania aspera* and Asian *S. koponenii* belong to different main clades of the genus *Scapania*. According to Potemkin (2000), *Scapania aspera* is distinct from *S. koponenii* in the following features: 1) larger size, *Scapania*

Table 1. Specimens used in the molecular investigation with details of specimen vouchers and GenBank accession numbers. The sequences obtained de novo are provided in italic

| <i>Species</i>                            | <i>Specimen voucher</i>                                                         | <i>GenBank accession numbers</i>                                   |                 |
|-------------------------------------------|---------------------------------------------------------------------------------|--------------------------------------------------------------------|-----------------|
|                                           |                                                                                 | <i>ITS1-2</i>                                                      | <i>trnL-F</i>   |
| <i>S. aequiloba</i> (Schwägr.) Dumort.    | Austria, Tyrol, Lermos – Biberwier Duell 14-8-2002.1/14 (JE)                    | JN631359                                                           | JN631497        |
| <i>S. aspera</i> 1                        | Austria, Schaefer-Verwimp & Verwimp 27469 (GOET)                                | JN631370                                                           | JN631508        |
| <i>S. aspera</i> 2                        | Belgium, Konstantinova, 2-20-3-99 (KPABG)                                       | EU791735                                                           | EU791627        |
| <i>S. aspera</i> 3                        | Bulgaria, Hentschel Bryo762 (GOET)                                              | GQ900012                                                           | GQ900222        |
| <i>S. aspera</i> 4                        | Germany, Marstaller 13-3-2002 (JE)                                              | JN631371                                                           | JN631509        |
| <i>S. aspera</i> 5                        | Germany, Schaefer-Verwimp & Verwimp 28588 (GOET)                                | JN631372                                                           | JN631510        |
| <i>S. aspera</i> 6                        | Germany, Heinrichs <i>et al.</i> 3700 (GOET)                                    | JN631373                                                           | JN631511        |
| <i>S. aspera</i> 7                        | Germany, Duell 3-12-1994-1 (JE)                                                 | JN631374                                                           | JN631512        |
| <i>S. aspera</i> 8                        | Germany, Marstaller 8-10-2004 (JE)                                              | JN631375                                                           | JN631513        |
| <i>S. aspera</i> 9                        | Germany, Meinunger 12-4-2001 (JE)                                               | JN631377                                                           | JN631514        |
| <i>S. aspera</i> 10                       | Germany, Schroeder 17-8-1999 (JE)                                               | JN631378                                                           | JN631515        |
| <i>S. aspera</i> 11                       | Germany, Schaefer-Verwimp & Verwimp 28888 (GOET)                                | JN631379                                                           | JN631516        |
| <i>S. aspera</i> 12                       | Germany, Marstaller 15-7-2002 (JE)                                              | JN631380                                                           | JN631517        |
| <i>S. aspera</i> 13                       | Italy, Duell & Duell 17a.05-06-1990 (JE)                                        | JN631381                                                           | JN631518        |
| <i>S. aspera</i> 14                       | Italy, Marstaller 6-9-2001 (JE)                                                 | JN631382                                                           | JN631519        |
| <i>S. aspera</i> 15                       | Russia, Krasnoyarsk Territory, Taimyr, Fedosov 13-3-0962 (KPABG)                | <i>KU516682</i>                                                    | <i>KU516684</i> |
| <i>S. aspera</i> 16                       | Russia, Krasnoyarsk Territory, Taimyr, Fedosov 13-3-0957 (KPABG)                | <i>ITS1:</i><br><i>KU516683</i><br><i>ITS2:</i><br><i>KU516681</i> | <i>KU516685</i> |
| <i>S. curta</i> (Mart.) Dumort.           | Germany, Saxony-Anhalt, Breitenbach Hentschel Bryo 3174 (GOET)                  | JN631404                                                           | JN631542        |
| <i>S. helvetica</i> Gottsche              | Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova K414-1-05 (KPABG) | EU791728                                                           | EU791620        |
| <i>S. irrigua</i> (Nees) Nees             | Russia, Murmansk Prov., Konstantinova 219-4-02 (KPABG)                          | EU791733                                                           | EU791625        |
| <i>S. lingulata</i> H. Buch               | Russia, Magadan Prov., Bakalin, Mag-22-17-10 (KPABG)                            | JX630059                                                           | JX629930        |
| <i>S. mucronata</i> H. Buch               | Russia, Karelia, Bakalin 43-8-01 (KPABG)                                        | EU791738                                                           | EU791630        |
| <i>S. obcordata</i> (Berggr.) S.W. Arnell | Norway, Svalbard, Konstantinova 123-1-04 (KPABG)                                | EU791734                                                           | EU791626        |
| <i>S. uliginosa</i> (Lindenb.) Dumort.    | Russia, Murmansk Prov., Bakalin 25-7-01 (KPABG)                                 | EU791739                                                           | EU791631        |
| <i>S. verrucosa</i> Heeg                  | Russia, Karachaevo-Cherkessian Rep., Konstantinova & Savchenko 609/6-05 (KPABG) | EU791763                                                           | EU791654        |

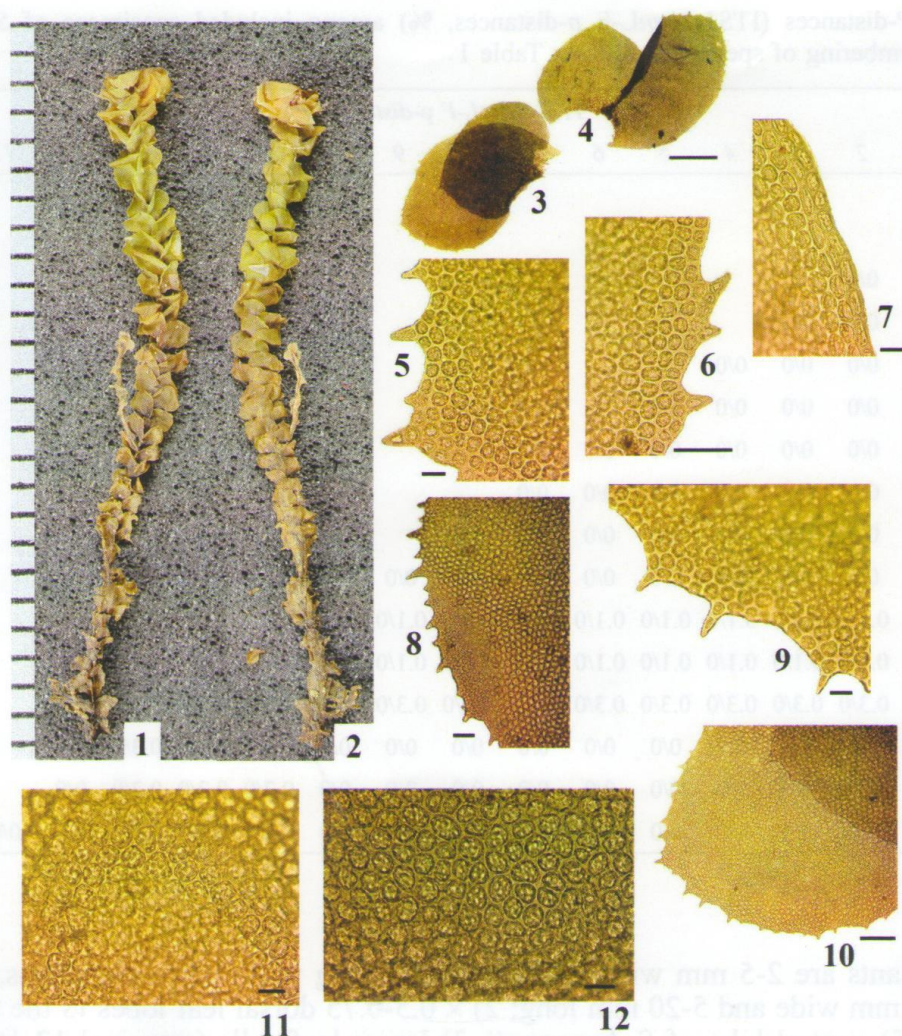
Table 2. *P*-distances (ITS1-2/trnL-F *p*-distances, %) among included specimens of *Scapania aspera*. Numbering of specimens follows Table 1

| <i>n</i> | ITS1-2/trnL-F <i>p</i> -distances, % |       |       |       |       |       |       |       |       |       |       |       |       |       |     |     |
|----------|--------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-----|-----|
|          | 1                                    | 2     | 3     | 4     | 5     | 6     | 7     | 8     | 9     | 10    | 11    | 12    | 13    | 14    | 15  | 16  |
| 1        |                                      |       |       |       |       |       |       |       |       |       |       |       |       |       |     |     |
| 2        | 0/0                                  |       |       |       |       |       |       |       |       |       |       |       |       |       |     |     |
| 3        | 0/0                                  | 0/0   |       |       |       |       |       |       |       |       |       |       |       |       |     |     |
| 4        | 0/0                                  | 0/0   | 0/0   |       |       |       |       |       |       |       |       |       |       |       |     |     |
| 5        | 0/0                                  | 0/0   | 0/0   | 0/0   |       |       |       |       |       |       |       |       |       |       |     |     |
| 6        | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   |       |       |       |       |       |       |       |       |       |     |     |
| 7        | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   |       |       |       |       |       |       |       |       |     |     |
| 8        | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   |       |       |       |       |       |       |       |     |     |
| 9        | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   |       |       |       |       |       |       |     |     |
| 10       | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   |       |       |       |       |       |     |     |
| 11       | 0.1/0                                | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 |       |       |       |       |     |     |
| 12       | 0.1/0                                | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 | 0.1/0 |       |       |       |     |     |
| 13       | 0.3/0                                | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.3/0 | 0.4/0 | 0.4/0 |       |     |     |
| 14       | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0.1/0 | 0.1/0 | 0.3/0 |     |     |
| 15       | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0.2/0 | 0.2/0 | 0.2/0 | 0/0 |     |
| 16       | 0/0                                  | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0/0   | 0.2/0 | 0.2/0 | 0.2/0 | 0/0 | 0/0 |

*aspera* plants are 2-5 mm wide and 10-60 mm long vs *S. koponenii* plants, which are 1.2-2 mm wide and 5-20 mm long; 2)  $\times 0.5$ -0.75 dorsal leaf lobes vs the  $\times 0.45$ -0.55(-0.65) ventral lobe of *S. koponenii*; 3) larger leaf cells (marginal 12-16  $\times$  12-18  $\mu$ m, median 16-25  $\times$  18-30  $\mu$ m) vs smaller leaf cells (marginal 8-14  $\times$  11.5-17  $\mu$ m, median 13-16  $\times$  16-20  $\mu$ m); 4) moderately and rather irregularly coarse papillose cuticles with  $\pm$  flattened papillae vs the more coarse papillose cuticles with dense  $\pm$  hemispherical papillae of *S. koponenii*; and 5) mostly triangular, not spinose terminal tooth cells in the leaf margins vs the more elongated,  $\pm$  spinose terminal tooth cell in the leaf margins of *S. koponenii*.

## ECOLOGY

*Scapania aspera* is a well-known element of bryophyte communities of different calcareous as well as limestone outcrops and is rather tolerant of habitat desiccation (Watson, 1914, 1918; Clausen, 1964; Damsholt 2002); the species is also a characteristic element of bryophyte communities (ass. *Scapanietum asperae* Rose & Porley 2001) that occur on north-facing, grazed calcareous grasslands on chalk outcrops in England (Porley & Rose, 2001). Based on a multivariate analysis of bryophyte distribution, Callaghan & Ashton (2008) showed that *S. aspera* is positively associated with geological trends.



Figs 1-12. *Scapania aspera* M.Bernet & Bernet from Taimyr District, Fedosov #13-3-0962 (KPABG). 1. habit of plant, ventral view; 2. habit of plant, dorsal view; 3-4. leaves; 5-6, 8-10. leaf margin (ventral lobe); 7. leaf margin (dorsal lobe); 11-12. median leaf cells with oil-bodies. Scale bars: 1 mm for 1-2; 0.5 mm for 3-4; 50 µm for 6, 8-10; 20 µm for 5, 7, 11-12.

Reflecting the extensive calcareous outcrops, the area in which this species was recently revealed can be identified from small-scale earth images obtained from space, as a light arc, southeast of the Taimyr Peninsula. Calcareous sedimentary rocks, diverse both in composition and age, were also observed in this area. In general, the area represents a gentle plateau with an altitudinal range from *ca* 165 m to 470 m a.s.l. (Fedosov *et al.*, 2015), comprising a white to grey terrigenous-marine Proterozoic siliciclastic limestone with a  $\text{SiO}_2$  content of *ca.* 10-18% and a CaO content of *ca* 50%. Numerous rock outcrops and steep rocky slopes alternate with relatively gentle slopes that are covered by forests or mountain tundra vegetation. The species occurring in this area are primarily observed on moist fine-soil in shaded niches at the base of limestone cliffs and in limestone cliff crevices in deep canyons with snowbeds. The area and ecotope, as well as a list of bryophytes and bryophyte communities in this area have been previously described (Fedosov *et al.*, 2015).

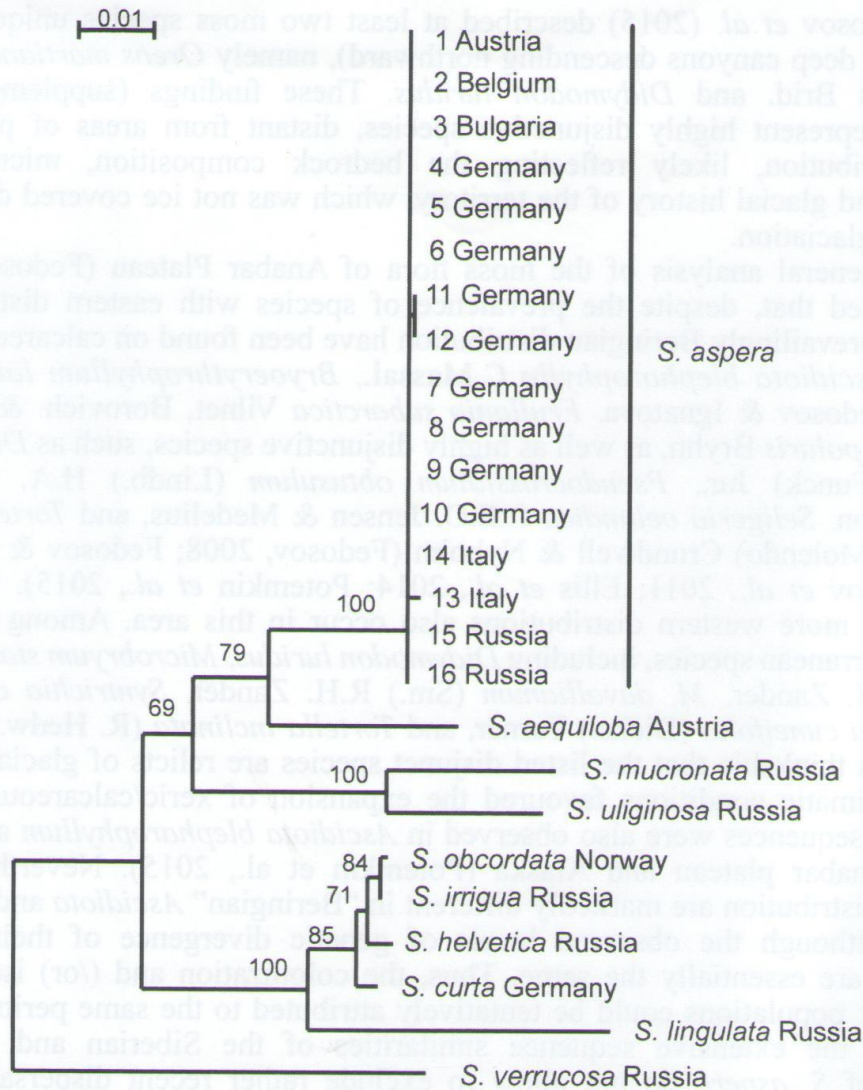


Fig. 13. Maximum likelihood phylogenetic tree for *Scapania aspera* and related species based on combined ITS1-2+trnL-F dataset. Bootstrap support values > 50% are indicated. The numbering of *S. aspera* specimens conforms with Table 1.

## DISTRIBUTION

*Scapania aspera* is distributed throughout Europe. In Scandinavia it occurs at 67°N and is then rather common in hemiboreal southern Scandinavia, to the Mediterranean (Damsholt, 2002; Söderström *et al.*, 2002; Górski & Váňa, 2015). Eastward, *S. aspera* extends to the Crimea and West Caucasus (Söderström *et al.*, 2002). In Russia, this species is known only from the Western Caucasus – Caucasian State Nature Reserve (Konstantinova *et al.*, 2009). To date, Turkey is the only Asian country where it has been recorded (Kürschner & Erdağ, 2005).

The present locality of this species is not only the easternmost but also the northernmost area worldwide, at no less than 3000 km from the closest European localities. Although this pattern is surprising, the incidence of *Scapania aspera* is not unique as several species with primarily Mediterranean distributions, such as *Didymodon luridus* Hornsch. have also been found where on calcareous rocks (Ellis *et al.*, 2014).

Fedosov *et al.* (2015) described at least two moss species unique to this locality (*i.e.*, deep canyons descending northward), namely *Oreas martiana* (Hoppe & Hornsch.) Brid. and *Didymodon luridus*. These findings (supplemented by *S. aspera*) represent highly disjunctive species, distant from areas of previously known distribution, likely reflecting the bedrock composition, microclimatic conditions and glacial history of the territory, which was not ice covered during the Pleistocene glaciation.

A general analysis of the moss flora of Anabar Plateau (Fedosov *et al.*, 2011) revealed that, despite the prevalence of species with eastern distributions, others with prevalingly Beringian distribution have been found on calcareous rocks, including *Ascidiota blepharophylla* C.Massal., *Bryoerythrophyllum latinervium* (Holmen) Fedosov & Ignatova, *Frullania subarctica* Vilnet, Borovich. & Bakalin, and *Funaria polaris* Bryhn, as well as highly disjunctive species, such as *Didymodon giganteus* (Funck) Jur., *Pseudocrossidium obtusulum* (Lindb.) H.A. Crum & L.E. Anderson, *Seligeria oelandica* C.E.O. Jensen & Medelius, and *Tortella densa* (Lorentz & Molendo) Crundwell & Nyholm (Fedosov, 2008; Fedosov & Ignatova, 2009; Fedosov *et al.*, 2011; Ellis *et al.*, 2014; Potemkin *et al.*, 2015). However, species with more western distributions also occur in this area. Among these are xeric/Mediterranean species, including *Didymodon luridus*, *Microbryum starckeanum* (Hedw.) R.H. Zander, *M. davallianum* (Sm.) R.H. Zander, *Syntrichia caninervis* Mitt., *Tortula cuneifolia* (Dicks.) Turner, and *Tortella inclinata* (R. Hedw.) Limpr.

It is thinkable that the listed disjunct species are relicts of glacial periods, when the climatic conditions favoured the expansion of xeric/calcareous species. Similar ITS sequences were also observed in *Ascidiota blepharophyllum* accessions from the Anabar plateau and Alaska (Potemkin *et al.*, 2015). Nevertheless the patterns of distribution are markedly different in "Beringian" *Ascidiota* and Eurasian *Scapania*, although the observed levels of genetic divergence of their isolated populations are essentially the same. Thus, the colonization and (/or) isolation of north Asiatic populations could be tentatively attributed to the same period. On the other hand, the extensive sequence similarities of the Siberian and European accessions of *S. aspera* do not allow to exclude rather recent dispersal. Studies involving more variable marker systems may shed further light on the emergence of the observed disjunctions (Ramaiya *et al.*, 2010).

**Specimens examined.** Russia, Krasnoyarsk Territory, Taimyr District, Khatanga settlement outskirts, Ereechka River upper course, Nyamakit-Daldyn creek basin; northern slope of plateau with altitudinal mark 377.8 m, 71°12'N-105°26'E, ca. 300 m alt, leg. 11. XIII.2013, Fedosov, ## 13-3-0962, 13-3-0986, 13-3-0957 (KPABG). **Other examined specimens:** Belgium, Belgian Ardennes, Beverce near Malmedy, calcareous conglomerate rocks, on stone wall near the stairs, leg. 20.X.1999, Konstantinova, #2-20/3-99 (KPABG); Hungary, Comit. Fejer, Montes Vertes, in rupibus dolomitics dumetosis vallis «Csatornavolgy» prope Csakbereny, leg. 30.VI.1935, Boros (KPABG); Crimea, Crimean Economy Warren, Central Basin, on gravel soil, leg. 21.VI.1964, Partyka (KPABG).

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