Arctoa (2010) **19**: *31-50*

MOLECULAR INSIGHT ON PHYLOGENY AND SYSTEMATICS OF THE LOPHOZIACEAE, SCAPANIACEAE, GYMNOMITRIACEAE AND JUNGERMANNIACEAE

ФИЛОГЕНИЯ И СИСТЕМАТИКА LOPHOZIACEAE, SCAPANIACEAE, GYMNOMITRIACEAE И JUNGERMANNIACEAE С ПОЗИЦИИ МОЛЕКУЛЯРНОЙ ФИЛОГЕНЕТИКИ

A.A. Vilnet[1], N.A. Konstantinova[1] & A.V. Troitsky[2]

А.А. Вильнет[1], Н.А. Константинова[1], А.В. Троицкий[2]

Abstract

The aim of the study is an expanded molecular phylogenetic analysis of the Holarctic taxa traditionally classified to the families Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. Also we will provide a justification of some nomenclatural changes suggested recently by Konstantinova & Vilnet (2009). The nuclear ITS1-2 and chloroplast *trn*L-F DNA sequences of 134 taxa (189 samples) from suborders Jungermanniineae and Cephaloziineae were analyzed. The topologies of phylogenetic trees constructed from combined sequences by maximum parsimony and Bayesian methods are congruent. The separation of family Diplophyllaceae from Scapaniaceae is not supported. The recently described family Solenostomataceae appears to be paraphyletic: the genus *Nardia* is in a sister relation to Gymnomitriaceae. The inclusion of the genus *Isopaches* in the family Anastrophyllaceae is questionable. Position of *Obtusifolium* and *Protolophozia elongata* in Scapaniaceae is not strongly supported. Phylogenetic relations within the genus *Scapania* are not fully resolved, but monophyly of sections *Undulatae* and *Calcicolae* is supported. Species assigned by some authors to a separate genus *Scapaniella* are scattered in different clades of the genus *Scapania*. *Macrodiplophyllum imbricatum* and *M. plicatum* can either be treated as *Douinia* or all these taxa included in *Scapania.* The distribution of species from the family Gymnomitriaceae on phylogenetic trees is congruent with the level of development or reduction of the perianth and perigynium. Taxonomically the species of *Marsupella* with reduced perianth are referred to *Gymnomitrion*, whereas the species called *G. apiculatum* that has a distinct perianth is transferred to *Marsupella*. The species status for *Scapania tundrae*, *S. paludosa*, *S. crassiretis* and *Marsupella aquatica* is supported. Genera *Lophozia* s.str., *Schistochilopsis, Tritomaria, Protolophozia, Orthocaulis* and *Crossogyna* are polyphyletic. The data support segregation of the recently described genera *Pseudotritomaria*, *Heterogemma, Lophoziopsis, Pseudolophozia, Schljakovianthus, Schljakovia* and *Biantheridion*.

Резюме

Целью данной работы является расширение представлений о молекулярной филогении и систематике наиболее крупных Голарктических таксонов печеночников, традиционно относимых к семействам Lophoziaceae, Scapani-

[1] – Polar-alpine Botanical Garden-Institute of Kola SC RAS, Kirovsk, 184236 Russia – Россия 184236, Кировск, Полярно-альпийский ботанический сад-институт Кольского НЦ РАН; e-mail: anya_v@list.ru, nadya_50@list.ru

[2] – A. N. Belozersky Institute of Physicochemical Biology, Moscow State University, Moscow, 119991, Russia – Россия, 119991, Москва, Московский государственный университет, Институт физико-химической биологии им. А.Н. Белозерского; tav@genebee.msu.su

aceae, Gymnomitriaceae и Jungermanniaceae. В работе приводится обоснование некоторых таксономических изменений, опубликованных ранее (Konstantinova & Vilnet, 2009). Нами проанализированы последовательности ITS1-2 ядДНК и *trn*L-F хпДНК 134 видов и внутривидовых таксонов печеночников, представленных 189 образцами, из подпорядков Jungermanniineae и Cephaloziineae. Топологии филогенетических деревьев, построенных по комбинированной матрице последовательностей методом максимальной экономии и методом Байеса, во многом сходны. Выделение семейства Diplophyllaceae из Scapaniaceae нецелесообразно. Недавно описанное семейство Solenostomataceae полифилетично: род *Nardia* формирует кладу, сестринскую семейству Gymnomitriaceae. Включение рода *Isopaches* в семейство Anastrophyllaceae не нашло твердой поддержки, так же как положение *Obtusifolium* и *Protolophozia elongata* в семействе Scapaniaceae. Филогенетические связи в роде *Scapania* выявлены не четко, однако поддержано выделение секций *Undulatae* и *Calcicolae*. Виды рода *Scapaniella* локализованы в разных кладах рода *Scapania* и не обособлены от него. *Macrodiplophyllum imbricatum* и *M. plicatum* могут быть отнесены к роду *Douinia*, либо все эти таксоны следует включить в *Scapania.* Распределение видов из семейства Gymnomitriaceae на филогенетических деревьях согласуется с признаком развития или редукции периантия и перигиния. Таксономически виды рода *Marsupella* с редуцированным периантием отнесены к роду *Gymnomitrion*, в то время как вид, традиционно относившийся к последнему роду, *G. apiculatum,* характеризующийся развитым периантием – к *Marsupella*. Роды *Lophozia* s.str., *Schistochilopsis, Tritomaria, Protolophozia, Orthocaulis* и *Crossogyna* полифилетичны. Полученные данные подтверждают целесообразность выделения новых родов *Pseudotritomaria*, *Heterogemma, Lophoziopsis, Pseudolophozia, Schljakovianthus, Schljakovia* и *Biantheridion*. Видовой статус *Scapania tundrae*, *S. paludosa*, *S. crassiretis* и *Marsupella aquatica* поддержан.

KEYWORDS: Hepaticae, Jungermanniales, ITS1-2, molecular phylogeny, *trn*L-F

INTRODUCTION

Families Scapaniaceae Mig., Gymnomitriaceae H. Klinggr. and Jungermanniaceae Reichenb. (including Lophoziaceae Cavers) were for a long time treated in suborder Jungermanniineae R.M. Schust. (Schuster, 1984). However Schuster (1966) wrote, "the suborder Jungermanniineae is the most difficult of the groups of Jungermanniales H. Klinggr. to circumscribe, perhaps because it is "still heterogeneous". One of the largest families, Lophoziaceae, was distinguished as a distinct one by Schuster (1969), Kitagawa (1965, 1966), Schljakov (1980) and Grolle & Long (2000) or it was included in Jungermanniaceae (Schuster, 1984; Grolle, 1983). Results of modern molecular phylogenetic studies were mainly unexpected but allowed to clarify relation within this group. Both suborder Jungermanniineae sensu Schuster (1984) and many families and genera were shown to be polyphyletic (Davis, 2004; Yatsentyuk et al., 2004; Heinrichs et al., 2005; Forrest et al., 2006; He-Nygren et al., 2006; Hentschel et al., 2007). Taxa that were previously treated in the family Jungermanniaceae, are classified now in suborders Jungermanniineae and Cephaloziineae Schljakov (Crandall-Stotler et al., 2009).

Solenostoma Mitt., *Plectocolea* (Mitt.) Mitt. and *Nardia* Gray were excluded from the Jungermanniaceae s. str. and combined in a new family Solenostomataceae Stotler & Crand.-Stotl. in suborder Jungermanniineae (Crandall-Stotler et al., 2009). Heinrichs et al. (2005) suggested to include family Lophoziaceae into Scapaniaceae and He-Nygren et al. (2006) transferred the latter taxon into suborder Cephaloziineae. The genus *Jamesoniella* (Spruce) F. Lees s. lat. was transferred from Jungermanniaceae to the Jamesoniellaceae (He-Nygren et al., 2006) or to the Adelanthaceae (Joerg) Grolle subfam. Jamesonielloideae (De Roo et al., 2007) that was placed in suborder Cephaloziineae.

The inclusion of Lophoziaceae into Scapaniaceae (Heinrichs et al., 2005) was questionable due to only *Lophozia* (Dumort.) Dumort. s. str., *Tritomaria* Loeske, *Saccobasis* H. Buch and *Schistochilopsis* (Kitag.) Konstant. were clustered with Scapaniaceae, whereas other genera composed a robust clade (Vilnet et al., 2009a) that was described as a separate family Anastrophyllaceae L. Söderstr., De Roo & Hedd. (Söderström et al., 2010).

It was shown that chloroplast *trn*L-F sequence data on *Lophozia, Anastrophyllum* (Spruce) Steph. and *Jungermannia* L. support the narrow generic concept (Yatsentyuk et al., 2004). Nevertheless, some genera, for example, *Lophozia* s.str., *Schistochilopsis, Tritomaria,* etc. even in narrow sense (Buch, 1933; Schljakov, 1980) appear to be polyphyletic (De Roo et al., 2007; Vilnet et al., 2009a).

In this paper we discuss taxonomic rearrangements within the largest boreal hepatic families basing on analysis of nuclear ITS1-2 and chloroplastic *trn*L-F sequences. The present set of taxa is expanded comparatively with the previous analysis being enlarged by a number of taxa and samples that include recently described and rare arctic species.

Material and methods

Taxa

The ITS1-2 nrDNA and *trn*L-F cpDNA sequences of 134 taxa (189 samples) of jungermaniioid liverworts were analyzed (Table 1). Many species were represented by two specimens collected mainly in geographically distant regions.

DNA isolation, amplification and sequencing

DNA was extracted from dried liverwort tissues using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). The *trn*L-F region of the chloroplast genome, including the part of the 5'-terminal exon, intron, the 3'-terminal exon of the *trn*L gene, the *trn*L-F intergenic spacer and part of the *trn*F gene, was amplified and sequenced using primers suggested by Taberlet et al. (1991). The ITS1-2 region of the nuclear genome containing part of the 26S rDNA gene, ITS1, 5,8S rDNA gene, ITS2 and part of the 18S rDNA gene was amplified and sequenced using pairs of external and internal primers (White et al., 1990).

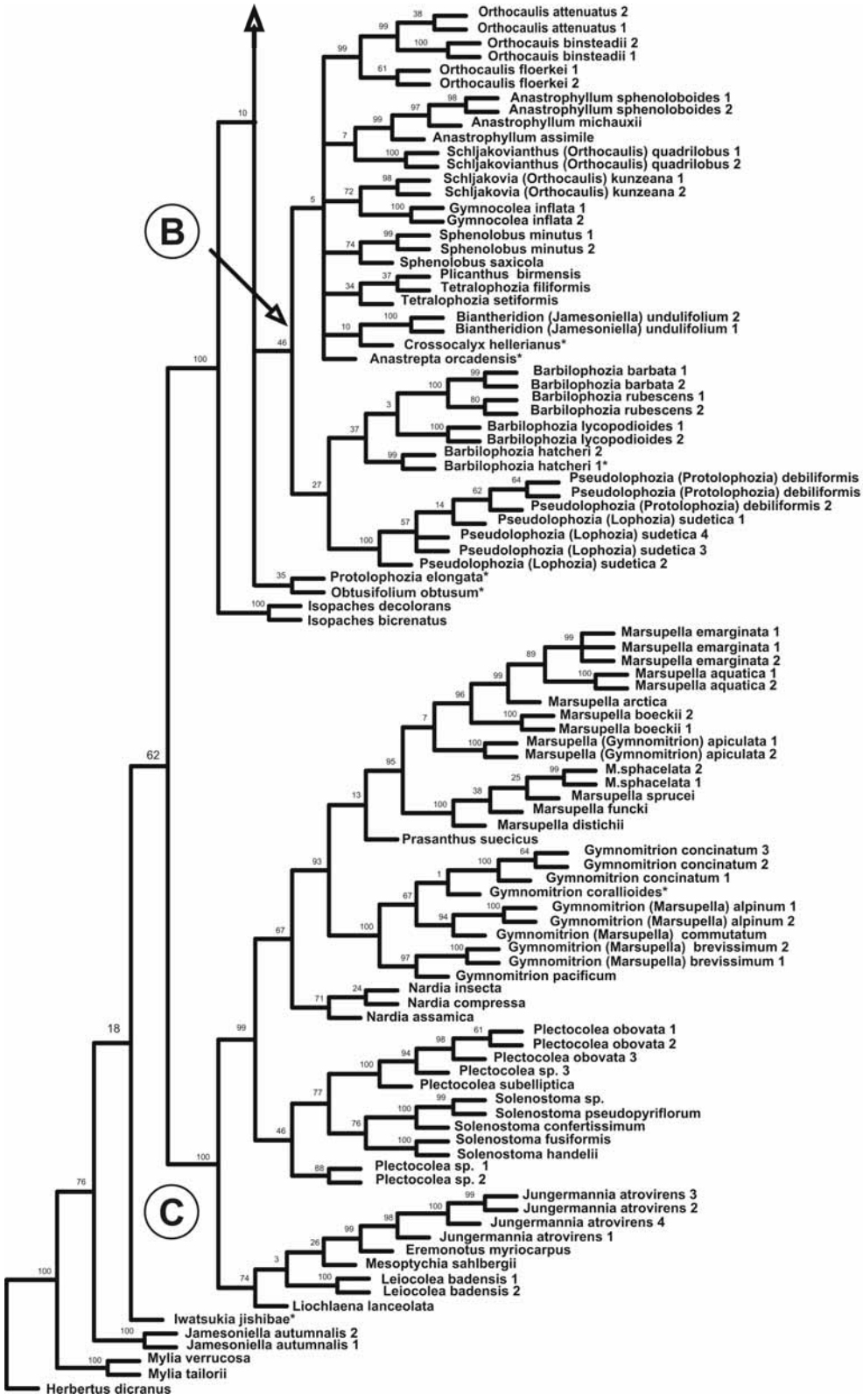
PCR were carried out in 20 mkl volumes according to the following procedure: 3 min at 94°C, 30 cycles (30s 94°C, 40s 58°C, 60s 72°C) and 2 min of extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the GFX™ PCR DNA and Gel Band Purification Kit (Amersham Biosciences, U.S.A.), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA). GenBank accession numbers are in Table 1.

Phylogenetic analyses

Phylogenetic reconstructions are based on the combined ITS1-2 and *trn*L-F data. Combined sequences for *Lophoziopsis (Lophozia) polaris*, *Lophozia silvicola*, *L. silvicoloides* (Spitsbergen), *Obtusifolium obtusum, Douinia ovata* are derived from two specimens of each (cf. Table 1). Nucleotide data for both samples of *Schistochilopsis incisa* include the *trn*L-F sequences only. The ITS1-2 of *Heterogemma (Schistochilopsis) laxa* and *Scapania tundrae* are presented by two partitions ITS1 and 5.8SrDNA-ITS2, sequenced from one sample. The sequences were aligned manually using the BioEdit program (Hall, 1999). All positions of alignment were included in the phylogenetic analyses.

Two analytical procedures were implemented for the analyses: a maximum parsimony method (MP) with the TNT program (Goloboff et al., 2003) and Bayesian method with the MrBayes v 3.1.2. (Ronquist & Huelsenbeck, 2003). In both cases *Herbertus dicranus* was used as an outgroup. The parsimony analysis with TNT involved a New Technology Search with search minimal length tree by five reiterations and 1000 bootstrap resamplings, for other parameters the default setting was used. Gaps were treated as missing data, indels were taken into account by a modified complex coding algorithm in SeqState (Müller, 2005).

For Bayesian (BA) analysis initially a best-fit evolutionary model of nucleotide substitutions was determined using the Modelgenerator software (Keane et al., 2004). The general time-reversible model with invariable sites and a gamma-distributed rate heterogeneity parameter


B
C
Orthocaulis attenuatus 2
Orthocaulis attenuatus 1
Orthocauis binsteadii 2
Orthocauis binsteadii 1
Orthocaulis floerkei 1
Orthocaulis floerkei 2
Anastrophyllum sphenoloboides 1
Anastrophyllum sphenoloboides 2
Anastrophyllum michauxii
Anastrophyllum assimile
Schljakovianthus (Orthocaulis) quadrilobus 1
Schljakovianthus (Orthocaulis) quadrilobus 2
Schljakovia (Orthocaulis) kunzeana 1
Schljakovia (Orthocaulis) kunzeana 2
Gymnocolea inflata 1
Gymnocolea inflata 2
Sphenolobus minutus 1
Sphenolobus minutus 2
Sphenolobus saxicola
Plicanthus birmensis
Tetralophozia filiformis
Tetralophozia setiformis
Biantheridion (Jamesoniella) undulifolium 2
Biantheridion (Jamesoniella) undulifolium 1
Crossocalyx hellerianus*
Anastrepta orcadensis*
Barbilophozia barbata 1
Barbilophozia barbata 2
Barbilophozia rubescens 1
Barbilophozia rubescens 2
Barbilophozia lycopodioides 1
Barbilophozia lycopodioides 2
Barbilophozia hatcheri 2
Barbilophozia hatcheri 1*
Pseudolophozia (Protolophozia) debiliformis 3
Pseudolophozia (Protolophozia) debiliformis 1
Pseudolophozia (Protolophozia) debiliformis 2
Pseudolophozia (Lophozia) sudetica 1
Pseudolophozia (Lophozia) sudetica 4
Pseudolophozia (Lophozia) sudetica 3
Pseudolophozia (Lophozia) sudetica 2
Protolophozia elongata*
Obtusifolium obtusum*
Isopaches decolorans
Isopaches bicrenatus
Marsupella emarginata 1
Marsupella emarginata 1
Marsupella emarginata 2
Marsupella aquatica 1
Marsupella aquatica 2
Marsupella arctica
Marsupella boeckii 2
Marsupella boeckii 1
Marsupella (Gymnomitrion) apiculata 1
Marsupella (Gymnomitrion) apiculata 2
M.sphacelata 2
M.sphacelata 1
Marsupella sprucei
Marsupella funcki
Marsupella distichii
Prasanthus suecicus
Gymnomitrion concinatum 3
Gymnomitrion concinatum 2
Gymnomitrion concinatum 1
Gymnomitrion corallioides*
Gymnomitrion (Marsupella) alpinum 1
Gymnomitrion (Marsupella) alpinum 2
Gymnomitrion (Marsupella) commutatum
Gymnomitrion (Marsupella) brevissimum 2
Gymnomitrion (Marsupella) brevissimum 1
Gymnomitrion pacificum
Nardia insecta
Nardia compressa
Nardia assamica
Plectocolea obovata 1
Plectocolea obovata 2
Plectocolea obovata 3
Plectocolea sp. 3
Plectocolea subelliptica
Solenostoma sp.
Solenostoma pseudopyriflorum
Solenostoma confertissimum
Solenostoma fusiformis
Solenostoma handelii
Plectocolea sp. 1
Plectocolea sp. 2
Jungermannia atrovirens 3
Jungermannia atrovirens 2
Jungermannia atrovirens 4
Jungermannia atrovirens 1
Eremonotus myriocarpus
Mesoptychia sahlbergii
Leiocolea badensis 1
Leiocolea badensis 2
Liochlaena lanceolata
Iwatsukia jishibae*
Jamesoniella autumnalis 2
Jamesoniella autumnalis 1
Mylia verrucosa
Mylia tailorii
Herbertus dicranus

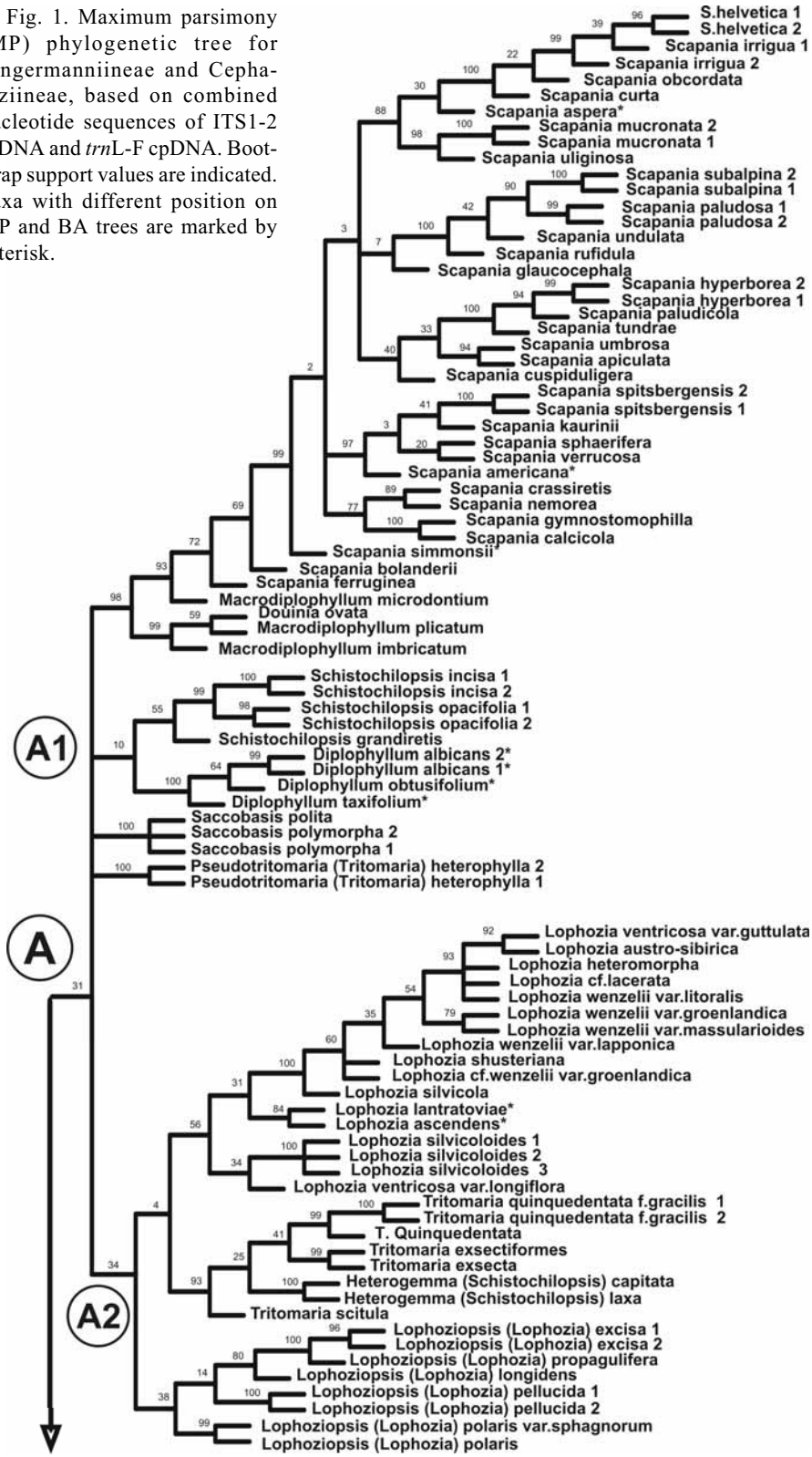
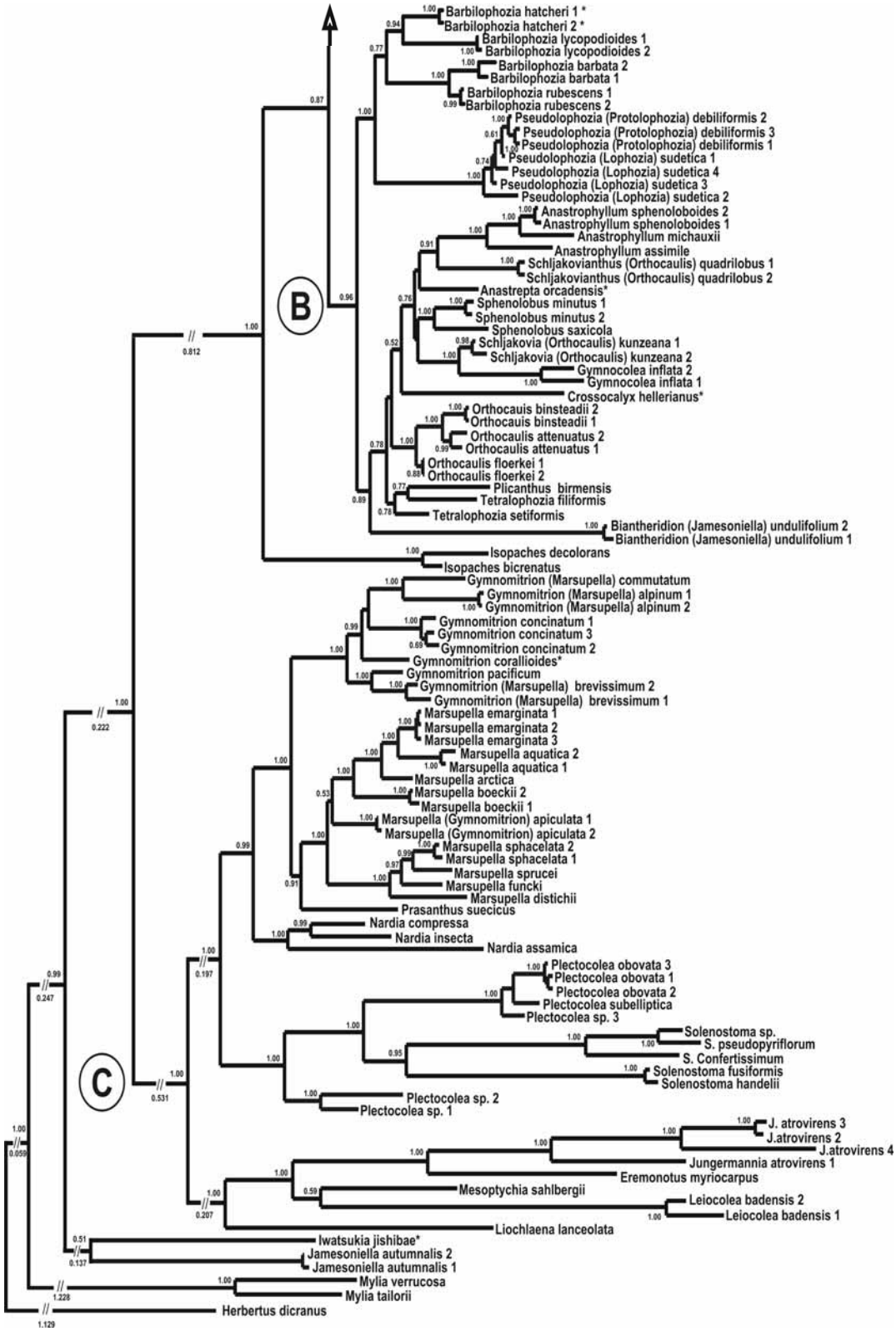


Fig. 1. Maximum parsimony (MP) phylogenetic tree for Jungermanniineae and Cephaloziineae, based on combined nucleotide sequences of ITS1-2 nrDNA and *trn*L-F cpDNA. Bootstrap support values are indicated. Taxa with different position on MP and BA trees are marked by asterisk.


Barbilophozia hatcheri 1 *
Barbilophozia hatcheri 2 *
Barbilophozia lycopodioides 1
Barbilophozia lycopodioides 2
Barbilophozia barbata 2
Barbilophozia barbata 1
Barbilophozia rubescens 1
Barbilophozia rubescens 2
Pseudolophozia (Protolophozia) debiliformis 2
Pseudolophozia (Protolophozia) debiliformis 3
Pseudolophozia (Protolophozia) debiliformis 1
Pseudolophozia (Lophozia) sudetica 1
Pseudolophozia (Lophozia) sudetica 4
Pseudolophozia (Lophozia) sudetica 3
Pseudolophozia (Lophozia) sudetica 2
Anastrophyllum sphenoloboides 2
Anastrophyllum sphenoloboides 1
Anastrophyllum michauxii
Anastrophyllum assimile
Schljakovianthus (Orthocaulis) quadrilobus 1
Schljakovianthus (Orthocaulis) quadrilobus 2
Anastrepta orcadensis*
Sphenolobus minutus 1
Sphenolobus minutus 2
Sphenolobus saxicola
Schljakovia (Orthocaulis) kunzeana 1
Schljakovia (Orthocaulis) kunzeana 2
Gymnocolea inflata 2
Gymnocolea inflata 1
Crossocalyx hellerianus*
Orthocauis binsteadii 2
Orthocauis binsteadii 1
Orthocaulis attenuatus 2
Orthocaulis attenuatus 1
Orthocaulis floerkei 1
Orthocaulis floerkei 2
Plicanthus birmensis
Tetralophozia filiformis
Tetralophozia setiformis
Biantheridion (Jamesoniella) undulifolium 2
Biantheridion (Jamesoniella) undulifolium 1
B
Isopaches decolorans
Isopaches bicrenatus
Gymnomitrion (Marsupella) commutatum
Gymnomitrion (Marsupella) alpinum 1
Gymnomitrion (Marsupella) alpinum 2
Gymnomitrion concinatum 1
Gymnomitrion concinatum 3
Gymnomitrion concinatum 2
Gymnomitrion corallioides*
Gymnomitrion pacificum
Gymnomitrion (Marsupella) brevissimum 2
Gymnomitrion (Marsupella) brevissimum 1
Marsupella emarginata 1
Marsupella emarginata 2
Marsupella emarginata 3
Marsupella aquatica 2
Marsupella aquatica 1
Marsupella arctica
Marsupella boeckii 2
Marsupella boeckii 1
Marsupella (Gymnomitrion) apiculata 1
Marsupella (Gymnomitrion) apiculata 2
Marsupella sphacelata 2
Marsupella sphacelata 1
Marsupella sprucei
Marsupella funcki
Marsupella distichii
Prasanthus suecicus
Nardia compressa
Nardia insecta
Nardia assamica
Plectocolea obovata 3
Plectocolea obovata 1
Plectocolea obovata 2
Plectocolea subelliptica
Plectocolea sp. 3
Solenostoma sp.
S. pseudopyriflorum
S. Confertissimum
Solenostoma fusiformis
Solenostoma handelii
Plectocolea sp. 2
Plectocolea sp. 1
C
J. atrovirens 3
J.atrovirens 2
J.atrovirens 4
Jungermannia atrovirens 1
Eremonotus myriocarpus
Mesoptychia sahlbergii
Leiocolea badensis 2
Leiocolea badensis 1
Liochlaena lanceolata
Iwatsukia jishibae*
Jamesoniella autumnalis 2
Jamesoniella autumnalis 1
Mylia verrucosa
Mylia taylorii
Herbertus dicranus
A
0.812
0.222
0.247
0.197
0.531
0.059
0.207
0.137
1.228
1.129

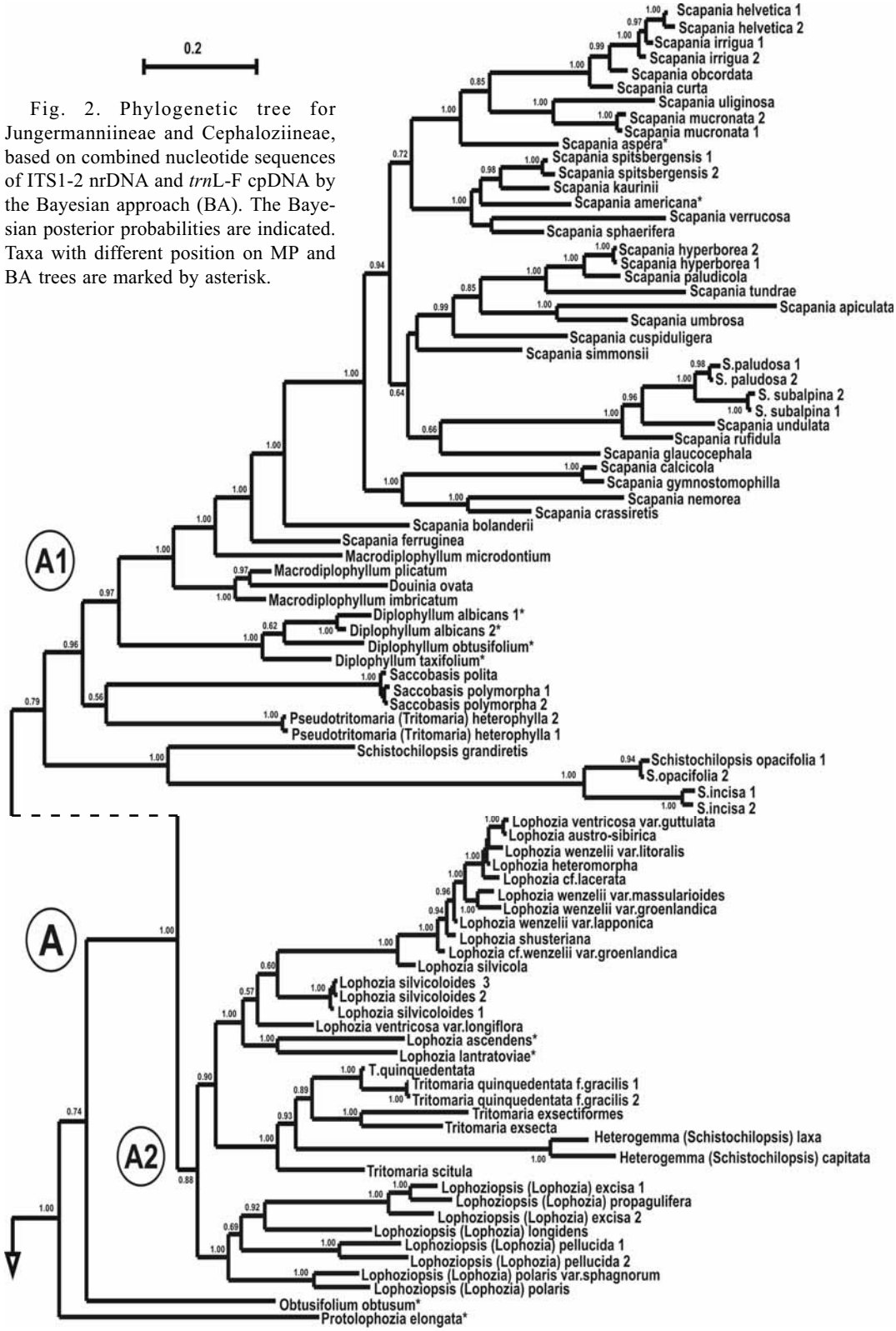


Fig. 2. Phylogenetic tree for Jungermanniineae and Cephaloziineae, based on combined nucleotide sequences of ITS1-2 nrDNA and *trn*L-F cpDNA by the Bayesian approach (BA). The Bayesian posterior probabilities are indicated. Taxa with different position on MP and BA trees are marked by asterisk.

(GTR+G+I) was selected. Sequence alignment was divided into six partitions: 5.8S plus *trn*F, ITS1, ITS2, *trn*L 5'-terminal exon plus *trn*L 3'-terminal exon, *trn*L intron and *trn*L-F spacer. Each of these partitions was separately assigned the GTR+G+I model, gamma distributions were approximated using four categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run includes three heated chains and one unheated, and two starting trees were chosen randomly. The number of generations was 10,000,000, and trees were saved once every 100 generations. The first 25000 trees were discarded in each run, and 15000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated as branch support values. The genetic p-distances referred anywhere in a text below calculated by MEGA 3.1 (Kumar et al., 2004) (see supplement at the electronic version on www.arctoa.ru).

RESULTS

ITS1-2 sequences for 147 samples and *trn*L-F sequences for 129 samples were determined in this study. Additionally, 41 sequences of ITS1-2 and 61 sequences of *trn*L-F were taken from previous studies (Yatsentyuk et al., 2004; Vilnet at al., 2007a; Vilnet at al., 2008). The ITS1-2 alignment consists of 1365 positions. Among them, 787 (57.7%) are variable and 644 (47.2%) are parsimony informative. The *trn*L-F alignment consists of 660 sites, the 335 (50.8%) positions are variable and 260 (39.4%) are parsimony informative. The entire alignment of 189 sequences consists of 2025 sites that were included in the analyses. There are 1122 (55.4%) characters that are variable, and 904 (44.1%) are parsimony informative. In the MP analysis the alignment contained 78 additional indel coded positions.

The MP analysis with TNT yielded from 11 to 20 equally parsimonious trees at different runs with a length of 6076 steps, the tree resulted after 1000 bootstrap resamplings with indicated bootstrap support values (BS) is shown in Fig. 1.

In the BA analysis, trees were sampled after reaching stationarity; average standard deviation of split frequencies between two runs was 0.008618. Arithmetic means of Log likelihoods for runs sampled were -30551.73 and -30534.00. 95% and 99% credible sets contain 64794 and 70794 trees, respectively. The BA tree with means of posterior probabilities (PP) is presented in Fig. 2.

The topologies of MP and BA trees are in a good agreement. The discrepancies are caused by unresolving of some groupings in MP tree (see below) and by low supports in MP tree positions of some species inside highly supported clades. Taxa with different position in MP and BA trees are marked by asterisk in Figs. 1-2. Three main clades A, B and C are found in both analyses (Figs. 1-2). Clade A (BS=31, PP=1.00) is subdivided into subclades A1 and A2 in BA tree (Fig. 2), while A1 is partly presented as an unresolved polytomy in MP tree (Fig.1). Family Scapaniaceae in its traditional circumscription is resolved as a monophyletic group, A1, with PP=0.97 in the BA analysis (Fig. 2), whereas in MP tree the genus *Diplophyllum* (Dumort.) Dumort. is segregated in unsupported clade with *Schistochilopsis* section *Incisae* (C.E.O. Jensen) Potemkin (Fig. 1). The latter taxon composes a small clade sister to the rest of A1 subclade in BA tree (Fig. 2). The genus *Saccobasis* and *Pseudotritomaria (Tritomaria) heterophylla,* traditionally assigned to the family Lophoziaceae, either form separate branches within unresolved polytomy in A-clade in the MP tree (Fig.1), or compose a low supported clade (PP=0.56) in the BA tree (Fig. 2). The genera *Lophozia, Lophoziopsis, Tritomaria* and *Heterogemma* compose the second subclade, A2 (BS=34, PP=0.88).

Other taxa refered usually to Lophoziaceae (excluding *Leiocolea* (Müll. Frib.) H. Buch) compose clade B (PP=0.96) with two subclades. The first subclade, B1 (PP=1.0) contains *Barbilophozia* Loeske*, Pseudolophozia (Protolophozia) debiliformis* and *P. (Lophozia) sudetica*, and the second subclade, B2 (PP=0.89) includes *Anastrophyllum* s.l., *Gymnocolea* Dumort., *Anastrepta* (Lindb.) Schiffn., *Orthocaulus* H. Buch, *Schljakovia* Konstant. & Vilnet, *Schljakovianthus* Konstant. & Vilnet, *Biantheridion* (Grolle) Konstant. & Vilnet, *Tetralophozia* (R.M. Schust.) Schljakov, *Plicanthus* R.M. Schust.

Three genera of Gymnomitriaceae studied here compose a robust subclade in the clade C

(BS=93, PP=1.0) sister to taxa traditionally placed to Jungermanniaceae s.str. The genera *Gymnomitrion* Corda and *Marsupella* Dumort. are resolved as not monophyletic, but composing of two intermingled subclades. The family Jugermanniaceae s.str. is found to be polyphyletic: *Nardia* is a sister to the Gymnomitriaceae (BS=67, PP=0.99), while *Solenostoma* and *Plectocolea* form a clade (BS=46, PP=1.00). The close relationship of *Mesoptychia* (Lindb.) A. Evans., *Eremonotus* Lindb. & Kaal. ex Pearson, *Liochlaena* Nees and *Leiocolea* to *Jungermannia* s. str. is evident in both obtained topologies (BS=74, PP=1.00). The genus *Mylia* Gray has a basal position in both trees.

Protolophozia elongata and *Obtusifolium obtusum* are located as two separate lineages at the base of clade A in the BA tree (with PP=1 and PP=0.74 consequently) or form a weekly supported clade (BS=35) in unresolved relation to clade A and B in the MP tree.

Discussion

The obtained results allow to modify the latest classification of the Jungermanniales (Crandall-Stotler et al., 2009), by including in the analysis many additional northern taxa and samples. There are two main clades within Scapaniaceae (including Lophoziaceae) that allow us to recognize two families, Scapaniaceae and recently discribed Anastrophyllaceae (Söderström et al., 2010) opposite to Scapaniaceae sensu Heinrichs et al. (2005). The family Solenostomataceae with inclusion of *Nardia* (Crandall-Stotler et al., 2009) is not supported by topologies obtained here. In our analysis, the genera *Lophozia* s.str., *Schistochilopsis, Tritomaria, Protolophozia, Orthocaulis*, *Gymnomitrion*, *Marsupella*, and *Crossogyna* are found to be polyphyletic, which resulted in a segregation some new genera (Konstantinova & Vilnet, 2009). We understand that the taxa sampling for some genera is still insufficient, especially for those occurred mainly in South Hemisphere, so only a more reliable results are discussed below.

Clade A

Clade A embraces species of traditionally circumscribed Scapaniaceae and several genera of Lophoziaceae, particularly *Tritomaria*, *Pseudotritomaria*, *Saccobasis*, *Schistochilopsis*, *Heterogemma*, *Lophozia* and *Lophoziopsis* (PP=1). It is divided into subclades A1 (PP=0.97, Fig. 2) and A2 (PP=0.88). In MP tree subclade A1 is represented by four separate linages (Fig. 1). Similar taxa relation was found earlier by De Roo et al. (2007) and mainly agree with a new circumscription of the family Scapaniaceae suggested by Söderström et al. (2010).

The two genera in their former broader circumspriptions, *Tritomatia* and *Schistochilopsis*, are distributed among both subclades A1 and A2, which suggest to split them. So now *Pseudotrotomaria* (*Tritomaria) heterophylla* specimens form a branch in A1, while all other *Tritomaria* species form a clade (with nested *Heterogemma (Schistochilopsis) capitata* and *H. laxa*, see below) in subclade A2. The genus *Saccobasis* that had been treated as subgenus of *Tritomaria* by many authors (Schuster, 1969; Grolle & Long, 2000; Damsholt, 2002; Schumacker & Váňa, 2005; etc.) is located in a separate branch in A1 in MP (Fig. 1) or combined in a clade (PP=0.56) with *Pseudotrotomaria* (*Tritomaria) heterophylla* in BA (Fig. 2). Close affinity of the latter taxon to *Saccobasis* was suggested by Schuster (1969: p.695), however they have a number of important differences in mophology: *Pseudotritomaria* (*Tritomaria) heterophylla* differs from *Saccobasis* (1) by simply transversly inserted leaves versus leaves attached by a complex and sinuous line slightly decurrent both antically and postically in *Saccobasis*; (2) constant presence of red-brown or purplish stellate gemmae versus absent or rare ellipsoidal gemmae in *Saccobasis*; (3) short dentate perianth mouth versus entire one in *Saccobasis.* Also *Pseudotritomaria* differs from both *Saccobasis* and *Tritomaria* in spinose-dentate to ciliate-dentate margins of lobes of female bracts (edentate in *Saccobasis* and *Tritomaria*) and often apiculate or cuspidate lobes of leaves versus obtuse in *Saccobasis* and obtuse to subacute or acute in *Tritomaria*. Taking into account the position in phylogenetic trees, relatively high values of genetic distances (see supplement at the electronic version on www.arctoa.ru) between *Saccobasis* and other *Tritomaria* species counted by studied DNA loci and quite distinct morphological features some of which were men-

tioned above we have proposed to segregate *T. heterophylla* in a monotypic genus *Pseudotritomaria* Konstant. & Vilnet (Konstantinova & Vilnet, 2009).

The section *Incisae* of the genus *Schistochilopsis* is located in A1 subclade, while *S. capitata* and *S. laxa* from the section *Heterogemma* are nested within *Tritomaria* in A2 subclade (Figs. 1-2). The morphological differences between both *Schistochilopsis* sections were discussed in Vilnet et al. (2008), and later *Heterogemma* (Joerg.) Konstant. & Vilnet was rised to generic rank (Konstantinova & Vilnet, 2009). According to our unpublished data, the *trn*L-F sequences of *S. cornuta* (Steph.) Konstant., the type species of the genus *Schistochilopsis,* is highly similar to species of the section *Incisae,* so the latter should be kept in this genus.

Subclade A1

Majority of taxa in subclade A1 belongs to the former Scapaniaceae. The ITS1-2 and *trn*L-F sequences from 30 species of *Scapania* (Dumort.) Dumort. reveal that their distribution in the clades corresponds partially to the subdivision of the genus based on morphological data, but, as a whole, phylogenetic relation within *Scapania* stays unclear due to the dubious position of some clades on the trees (Fig. 1-2).

Scapania undulata, S. paludosa, *S. subalpina*, *S. rufidula* compose a robust clade (BS=100, PP=1.00) that agrees with the section *Undulatae* sensu H. Buch (1928). Thus, the separation of *S. rufidula* in section *Rufidula* together with *S. spitsbergensis* by Schuster (1974) is not supported.

Scapania calcicola and *S. gymnostomophila* form a clade (BS=100, PP=1.00) that corresponds to section *Calcicolae* Müll. Frib. ex R.M. Schust. as it was circumscribed by Potemkin (2002).

All species from the commonly recognized section *Irrigua* (Müll. Frib.) H. Buch (*S. hyperborea*, *S. paludicola*, *S. tundrae*) (Arnell, 1956; Schuster, 1974; Grolle & Long, 2000; Schljakov, 1981), except the type species, *S. irrigua,* were found in one clade (BS=100, PP=1.00). *Scapania irrigua* was combined with species from section *Curtae* sensu Potemkin (2002) i.e. *S. curta*, *S. obcordata*, *S. helvetica*, *S. mucronata*, although without a high support (BS=88, PP=0.85). This arrangement never had been assumed before. Differences between nucleotide sequences of *S. irrigua* and *S. helvetica* include a single substitution in ITS1 and one indel of one nucleotide that corresponds to a level of infraspecific variability in both species. The affinity of *S. uliginosa* to S. *mucronata* revealed in our analysis (BS=98, PP=1.00) is unexpected because their morphology as well as ecology are quite distinct. It is worth to note however, that genetic distance between these species is rather high.

Scapania kaurinii, S. sphaerifera and *S. verrucosa* were classified variously by different authors and even were segregated in monotypic sections by Potemkin (2002). In our analysis they compose a clade with *S. americana* and *S. spitsbergensis* with high support (BS=97, PP=1.00).

Scapania apiculata and *S. glaucocephala,* classified as a subgenus by Schuster (1974) or genus *Scapaniella* by Buch (1928), were found in different subclades, so they are likely not closely related and should not be considered as congeneric (cf. Crandall-Stotler et al., 2009).

Three morphologically similar pairs of species, *Scapania hyperborea* and *S. tundrae*, *S. paludosa* and *S. uliginosa*, *S. crassiretis* and *S. nemorea,* sometimes treated as conspecific (e.g. Potemkin, 1994; 1999a) are clearly separated genetically (Vilnet et al., 2006). Nucleotide sequence data confirm these taxa as distinct species, as was suggested by Buch (1928).

Previous molecular analyses did not clarify the relationships of *Diplophyllum, Macrodiplophyllum* (H. Buch.) Perss. and *Douinia* H. Buch (Schill et al., 2004; Yatsentyuk et al., 2004; De Roo et al., 2007). Our results indicate more definitely that the recently described Diplophyllaceae Potemkin (Potemkin, 1999b) is a paraphyletic assemblage. The genus *Diplophyllum* comprises its own clade with a highest possible support, whereas *Douinia* is combined with *Macrodiplophyllum imbricatum* and *M. plicatum*, also with a high support (BS=99; PP=1.00), while *M. microdontium* is placed at the base of the *Scapania*-clade (Figs. 1-2). Thus, it is reasonable to treat *M. microdontium* in *Scapania* as proposed by Potemkin (1999b). However, contrary to the latter publication, *M. imbricatum* and *M. plica-*

tum are better be placed within *Douinia,* not *Scapania*, unless both species and *Douinia* are included in *Scapania.*

Subclade A2

The genera *Lophozia, Lophoziopsis, Tritomaria* and *Heterogemma* are forming this subclade. In our previous study (Vilnet at al., 2008), *Lophozia* s. str. (excluding *L. sudetica*), was resolved as a monophyletic group with a relatively high support (90% and more). Analysis of enlarged species set shows that the *Tritomaria*+ *Heterogemma*-clade split *Lophozia* s.str. into two clades that have the highest possible posterior probability in BA. Based on tree topologies, we segregated the species of *Lophozia* s.str. with red, purplish and red-brown gemmae to a new genus *Lophoziopsis* Konstant. & Vilnet (Konstantinova & Vilnet, 2009).

Clade B

This clade is formed by genera that were segregated from Lophoziaceae into Anastrophyllaceae by Söderström et al. (2010) that was called as «a new undescribed family». in the Checklist of liverworts of Russia (Konstantinova, Bakalin et al., 2009).

Subclade B1

This subclade composed only by two genera: *Barbilophozia* and recently described *Pseudolophozia* Konstant. & Vilnet (Kostantinova & Vinet, 2009). All four studied species of *Barbilophozia* compose a clade although without high support (PP=0.77). Recently described *B. rubescens* (Schuster & Damsholt, 1987) appears to be a hybrid between *B. barbata* and *B. hatcheri* due to inheritance of the ITS1-2 from the first species and the *trn*L-F from the second species (Vilnet et al., 2009b). *Barbilophozia hatcheri* and *B. lycopodioides*, the species that have been considered as closely related or even conspecific (Schljakov, 1980), are clearly separated in both MP and BA analyses.

Psedolophozia (Protolophozia) debiliformis and *P. (Lophozia) sudetica* form a clade (BS=100; PP=1.00) sister to *Barbilophozia* clade. Söderström et al. (2010) suggested to segregate them as *Barbilophozia* subgen. *Sudeticae* (Schljakov) L. Söderstr., De Roo et Hedd. However p-distances between *P. debiliformis* + *P. sudetica* and the genus *Barbilophozia* is 1.8-4.2%, whereas they are only 1.2% between *Barbilophozia* species. Morphological differences and the level of genetic distances in comparison with other taxa from clade B, convinced us to describe a new genus *Pseudolophozia* Konstant. & Vilnet (Kostantinova & Vinet, 2009). The sequence variation within *Pseudolophozia* is ca. 1%, that is two times higher than in *Barbilophozia* spp., so we hesitate to combine *Pseudolophozia (Lophozia) sudetica* and *P. debiliformis* in one species as it was proposed by Söderström et al. (2010).

Subclade B2

Majority of genera assigned earlier to the Lophoziaceae is located here. The genus *Orthocaulis* in its traditional circumscription includes ca. 10 species (Schaljakov, 1981), but as it is evident from the obtained trees, this genus is polyphyletic. The studied species previously referred to the genus occur in three clades, accepted as genera: *Orthocaulis* (*O. floerkei*+*O. attenuatus*+*O. binsteadii), Schljakovianthus* (*S. quadrilobus*) and *Schljakovia* (*S. kunzeana*) (Figs. 1-2). This correspondes with the quite distinct habitus of taxa. *Schljakovianthus quadrilobus* differs from *Schljakovia* and *Orthocaulis* s. str. in very deeply divided 4-lobed leaves with distinctly reflexed margins and sinus vs. less deeply divided 2-lobed, slightly reflexed margins in *Schljakovia kunzeana* and 3-lobed no reflexed margins in *O. floerkei*+*O. attenuatus*+*O. binsteadii*. Furthermore *Schljakovianthus quadrilobus* develops brownish or blackish brown pigmentation and has coarsely verrucose cuticle while the rest of studied taxa have yellow-brown to chestnut brown secondary pigmentation and faintly delicately (*O. floerkei*+*O. attenuatus)* to slightly striate-verruculose cuticle (*Schljakovia kunzeana, O. binsteadii*). The means of p-distances between these clades (1.2-3%) (see supplement) together with quite distinctive morphology encourage us to separate the monospecific genera *Schljakovianthus* and *Schljakovia* from *Orthocaulis* (cf. Konstantinova & Vilnet, 2009). In trees constructed by De Roo et al. (2007), the genus *Orthocaulis* was also divided into three clades: *O. floerkei*+*O. attenuatus*, *O. atlanticus*+*O. cavifolius* and *O. quadrilobus*. Later a new genus *Neoorthocaulis* L Söderstr., De Roo & Hedd. was described (Söderström et al., 2010). It includes *O. floerkei*, *O. attenuatus*

and *O. binsteadii* whereas *O. atlanticus* and *O. cavifolius* are left in *Orthocaulis.* There is no certainty now in the relation between *Neoorthocaulis* and *Orthocaulis* due to differences of species sampling in our and De Roo et al. (2007)' studies.

The topology of trees obtained in the present analysis supports the narrow generic concept for the genus *Anastrophyllum* s.l. with segregation of three genera: *Anastrophyllum* s.str., *Sphenolobus* (Lindb.) Berggr. and *Crossocalyx* Meyl. that was previously suggested on cpDNA loci data by Yatsentyuk et al. (2004) and De Roo et al. (2007).

Plicanthus birmensis was found within *Tetralophozia* (R.M. Schust.) Schljakov, although differences between nucleotide sequences of these taxa are relatively high (1.8%) and correspond with differences between genera in clade B. Due to insufficient species sampling the taxonomical status of *Plicanthus* is not discussed here.

Jamesoniella, a genus with predominantly South Hemispheran distribution, has been placed, in a distinct subfamily of Jungermanniaceae by Schuster (1970) and Schljakov (1980) or in a subfamily of Lophoziaceae by Grolle & Long (2000). Two Northern Hemisphere species, *Jamesoniella undulifolia* and *J. autumnalis,* were placed in the subgenus *Crossogyna* by Schuster (1969) and later in the genus *Crossogyna* by Schljakov (1981). Molecular phylogenetic studies suggested to place *Jamesoniella* in a separate family Jamesoniellaceae (He-Nygren et al., 2006) or in the family Adelanthaceae (Feldberg et al., 2010). The genus *Jamesoniella* was shown to be polyphyletic with one of the two mostly North Hemisphaeran species *J. autumnalis* separated in its own lineage (De Roo et al., 2007; Hentschel et al., 2007) or clustered with morphologically similar *J. nipponica* (Feldberg et al., 2010). Recently based on molecular data the most species of *Jamesoniella* were transferred to the genus *Syzigiella* Spruce (Feldberg et al., 2010). We have studied two predominantly Holarctic species of genus/subgenus *Crossogyna* including worldwide rare and morphologically isolated *C. undulifolia* that was never analyzed molecularly before. In obtained trees *C. undulifolia* forms a separate lineage within clade B, whereas *C. autumnalis* is found in basal grade as a separate lineage or together with *Iwatsukia* Kitag. (Figs. 1-2). Based on these data as well as on morphological peculiarities of *C. undulifolia* that were discussed by Schuster (1969) and Schljakov (1981*)*, this species is segregated in monotypic genus, *Biantheridion* (Grolle) Konstantinova & Vilnet (Konstantinova & Vilnet, 2009).

The systematic position of oligotypic genus *Isopaches* H. Buch is questionable. Both MP and BA analyses put it at a base of (A+B) clade (BS=100, PP=1.00) (Figs. 1-2). De Roo et al. (2007) found it within "Anastrophyllaceae"-clade only in BA tree, whereas in MP tree it is located in "Scapaniaceae"-clade. Söderström et al. (2010) placed *Isopaches* in Anastrophyllaceae. Additional study is needed to resolve the problem with this genus.

The treatment of *Obtusifolium obtusum* and *Protolophozia elongata* as a members of Scapaniaceae (Söderström et al., 2010) is not confirmed due to unstable position of these taxa in obtained trees.

Clade C

Clade C is composed by members of the families Gymnomitriaceae, Jungermanniaceae s.str. and recently described Solenostomataceae (Crandall-Stotler et al., 2009). The terminal position in this clade is occupied by the family Gymnomitriaceae. Earlier, with more limited taxa sampling, this family was recognized as monophyletic (Yatsentyuk et al., 2004; Schill et al., 2004). However, the genus *Eremonotus* classified for a long time in the Gymnomitriaceae (Schuster, 1984; Grolle, 1983; etc.), was found here within the clade formed by *Jungermannia* s. str., *Mesoptychia*, *Leiocolea* and *Liochlaena* (Figs. 1-2), which generally agrees with the results of Henstchel et al. (2007) and with the placement of *Eremonotus* in Jungermanniaceae by Crandall-Stotler et al. (2009).

The genera *Gymnomitrion* and *Marsupella* are found to be polyphyletic, with the species intermingled and distributed into two main clades (Figs. 1-2) that have some morphological definition. The main *Marsupella* clade is formed by species with well-developed perianth and perigynium, including *Marsupella apiculata (*previously treated as *Gymnomitrion apiculatum)* that has perianth and perigynium similar to that in most *Marsupella* species. Contrary to that, three spe-

cies with more or less reduced perianth and perigynium, *Gymnomitrion alpinum, G. brevissimum* and *G. commutatum,* which usually are placed in *Marsupella,* are located in the *Gymnomitrion* clade. Based on these results the rearrangement of Gymnomitriaceae species was made in Checklist of liverworts of Russia (Konstantinova, Bakalin et al., 2009) and later accepted in the study of Gymnomitriaceae by Váňa et al. (2010).

Three morphologically allied species, *Marsupella arctica, M. aquatica* and *M. emarginata*, are combined in a clade. *Marsupella aquatica* has been classified as a variety of *M. emarginata* by some authors (e.g. Schuster, 1974; Grolle & Long, 2000). The *trn*L-intron of *M. emarginata* is characterized by unique 43 base pairs deletion compared to both *M. aquatica* and *M. arctica* (Vilnet et al., 2007b). The value of p-distances between *M. arctica* and *M. emarginata* is higher than between *M. aquatica* and *M. emarginata* (2.4 and 1.2% correspondingly). Nevertheless, it would be more reasonable to recognize these taxa at one rank taking into account morphological features listed by Schuster (1972), Schljakov (1981) etc., and to accept *Marsupella aquatica* as a distinct species.

The monotypic genus *Prasanthus* Lindb. is characterized by presence of fleshy perigynium and lacking of perianth. It forms a basal lineage in a clade composed by Gymnomitriaceae species with developed perianth and perigynium in both trees (Figs. 1-2).

The studied species of *Nardia* compose a clade sister to Gymnomitriaceae with 0.99 support in BA tree (Fig. 2) and a low support (BS=67%) in MP tree (Fig. 1). Crandall-Stotler et al. (2009) placed *Nardia* in the recently described family Solenostomataceae. However our data show that the inclusion of *Nardia* makes Solenostomataceae paraphyletic and suggest either to place *Nardia* in Gymnomitriaceae or segregate it to its own family.

In the trees obtained here and those of Hentschel et al. (2007), *Solenostoma* and *Plectocolea* compose an intermingled clade. Majority of authors included *Plectocolea* in *Solenostoma* following modern molecular data (Crandall-Stotler et al., 2009; Váňa & Long, 2009). However, species sampling seems to be not enough for the final decision on taxonomic position of *Solenostoma* and *Plectocolea.*

Genera *Jungermannia* s.str., *Eremonotus, Mesoptychia, Leiocolea* and *Liochalena* form a subclade within clade C. In general it corresponds to Jungermanniaceae sensu Hentschel et al. (2007), although differs from the family circumscription of Crandall-Stotler et al. (2009) that placed *Liochalena* and *Delavayella* in a separate oligotypic family Delavayellaceae.

Conclusions

Our molecular data support segregation of the family Anastrophyllaceae, but the position of the genus *Isopaches* remains uncertain, as well as the position of *Obtusifolium* and *Protolophozia elongata* in the family Scapaniaceae.

The position of the genus *Nardia* within Solenostomataceae is not supported; this genus is better be placed in Gymnomitriaceae or to its own family.

The genera *Lophozia* s.str., *Schistochilopsis, Tritomaria, Protolophozia, Orthocaulis* and *Crossogyna* in their traditional circumscription are found to be polyphyletic. The segregation of genera *Pseudotritomaria*, *Heterogemma, Lophoziopsis, Pseudolophozia, Schljakovianthus, Schljakovia* and *Biantheridion* are suggested by molecular data.

Species of *Marsupella* with more or less reduced perianth and perigynium should be referred to *Gymnomitrion*, whereas *G. apiculatum* that has distinct perianth and perigynium is transferred to *Marsupella*.

The subdivision of the genus *Scapania* based on morphological data is partially supported.

The segregation of *Scapaniella* as a genus is not supported. *Macrodiplophyllum imbricatum* and *M. plicatum* could be placed in the genus *Douinia,* unless all of these taxa be included in *Scapania.*

The status of *Scapania tundrae*, *S. paludosa*, *S. crassiretis* and *Marsupella aquatica* as a separate species is supported.

Acknowledgments

We thank Dr. Michael S. Ignatov for helpful suggestions and discussion, Dr. Diana Horton for comments and improving the English of the first version of manuscript and Dr. Lars Söderström for careful reading and useful comments. This research has been supported by Russian Foundation for Basic Researches grants (09-04-00281,

09-04-01324, 10-04-00050) and program for Basic Research of Russian Academy of Science "Biodiversity and dynamics of gene pools" (subprogram "Gene pools and genetic diversity").

LITERATURE CITED

ARNELL, S. 1956. Illustrated moss flora of Fennoscandia. I. Hepatacae. – *Gleerup, Lund. 314*.

BUCH, H. 1928. Die Scapanien Nordeuropas und Sibiriens 2. Systematischer teil. – *Soc. Sci. Fenn., Comm. Biol*. **3**: *1-177*.

BUCH, H. 1933. Vorarbeiten zu eineer Lebermoosflora Fenno-Scandien. I. Ein Versuch zur Aufteilung der Gattungen *Lophozia* Dum. und *Sphenolobus* Step. – *Memoranda Soc. Fauna Fl. Fenn.* **8**: *282-297*.

CRANDALL-STOTLER, B., R.E. STOTLER & D.G. LONG 2009. Phylogeny and classification of the Marchantiophyta. – *Edinburgh J. Bot.* **66**: *155-198*.

DAMSHOLT, K. 2002. Illustrated flora of Nordic liverworts and hornworts. – *Nord. Bryol. Soc., Lund*. *840*.

DAVIS, E.C. 2004. A molecular phylogeny of leafy liverworts (Jungermanniidae: Marchantiophyta). – *In: (Goffinet B., V. Hollowell & R. Magill eds.) Molecular Systematics of Bryophytes. Monogr. Syst. Bot. St. Louis, Missouri Bot. Gard. Press,* **98**: *61-86*.

DE ROO, R.T., T.A. HEDDERSON & L. SÖDERSTRÖM 2007. Molecular insights into the phylogeny of the leafy liverwort family Lophoziaceae Cavers. – *Taxon* **56**: *310-314*.

FELDBERG, K., J. VÁŇA, D. LONG, A.J. SHAW, J. HENTSCHEL & J. HEINRICHS 2010. A phylogeny of Adelanthaceae (Jungermanniales, Marchantiophyta) based on nuclear and chloroplast DNA markers, with comments on classification, cryptic speciation and biogeography. – *Mol. Phylogenet. Evol*. **55**: *293-304*.

FORREST, L.L., E.C. DAVIS, D.G. LONG, B.J. CRANDALL-STOTLER, A. CLARK & M.L. HOLLINGSWORTH 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta): multiple taxa, genomes and analyses. – *Bryologist* **109**: *303-334*.

GOLOBOFF, P., S. FARRIS & K.NIXON 2003. TNT (Tree analysis using New Technology) (BETA) ver. 1.0. – *Program and documentation, available from the authors, and at www.cladistics.com/aboutTNT.html.*

GROLLE, R. 1983. Nomina generica Hepaticarum: references, types and synonymies. – *Acta Bot. Fenn*. **121**: *1-62*.

GROLLE, R. & D.G. LONG 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. – *J. Bryol.* **22**: *103-141*.

HALL, T. A. 1999. BioEdit: a user-friendly biological sequence aligment editor and analysis program for Windows 95/98/NT. – *Nucl. Acids. Symp.* **41**: *95-98*.

HEINRICHS, J., S.R. GRADSTEIN, R.WILSON & H. SCHNEIDER 2005. Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene rbcL. – *Cryptog. Bryol*. **26**: *131-150*.

HENTSCHEL, J., J.A. PATON, H. SCHNEIDER & J. HEINRICHS 2007. Acceptance of *Liochlaena* Nees and *Solenostoma* Mitt., the systematic position of *Eremonotus* Pearson and notes on *Jungermannia* L. s.l. (Jungermanniidae) based on chloroplast DNA sequence data. – *Pl. Syst. Evol.* **268**: *147-157*.

HE-NYGREN, X., A. JUSLEN, D. GLENNY & S. PIIPPO 2006. Illuminating the evolutionary history of liverworts (Marchantiophyta) – towards a natural classification. – *Cladistics* **22**: *1-31*.

KEANE, T.M., T.J. NAUGHTON & J.O. MCINERNEY 2004. ModelGenerator: amino acid and nucleotide substitution model selection. – *National University of Ireland, Maynooth*. *http://bioinf.may.ie/software/modelgenerator/*

KITAGAWA, N. 1965. A revision of the family Lophoziaceae of Japan and its adjacent region. I. – *J. Hattori Bot. Lab.* **28**: *239-293*.

KITAGAWA, N. 1966. A revision of the family Lophoziaceae of Japan and its adjacent region. II. – *J. Hattori Bot. Lab.* **29**: *101-149*.

KONSTANTINOVA N.A., V.A. BAKALIN ET AL. 2009. Checklist of liverworts (Marchantiophyta) of Russia. – *Arctoa* **18**: *1-64*.

KONSTANTINOVA, N.A. & A.A. VILNET 2009. New taxa and new combinations in Jungermanniales (Hepaticae). – *Arctoa* **18**: *65-67*.

KUMAR, S., K. TAMURA & M. NEI 2004 MEGA3: Integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. – *Briefings in Bioinformatics* **5**: *150-163*.

MÜLLER, K. 2005. SeqState. Primer design and sequence statistic for phylogenetic DNA datasets. – *Appl. Bioinformatics* **4**: *65-69*.

POTEMKIN, A.D. 1994. Studies on *Scapania*, Hepaticae sectio *Rufidulae* and sectio *Nemorosae*. – *J. Hattori Bot. Lab.* **77**: *273-285*.

POTEMKIN, A.D. 1999a. An analysis of the practical taxonomy of some critical northern species of *Scapania* (Scapaniceae, Hepaticae). – *Bryologist* **102**: *32-38*.

POTEMKIN, A.D. 1999b. Circumscription of the family Scapaniaceae, with segregation of the new family Dipophyllaceae (Hepaticae). – *Ann. Bot. Fennici* **36**: *271-283*.

POTEMKIN, A.D. 2002. Phylogenetic system and classification of the family Scapaniaceae Mig. emend. Potemkin (Hepaticae). – *Ann. Bot. Fennici* **39**: *309-334*.

RONQUIST, F., & J.P. HUELSENBECK 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. – *Bioinformatics* **19**: *1572-1574*.

SCHILL, D.B., D.G. LONG, M. MOELLER & J. SQUIRRELL 2004. Phylogenetic relationships between Lophoziaceae and Scapaniaceae based on chloroplast sequences. – *In: (Goffinet B., V. Hollowell & R. Magill eds.) Molecular Systematics of Bryophytes. Monogr. Syst. Bot. St. Louis, Missouri Bot. Gard. Press:* 98: *141-149*.

[SCHLJAKOV, R.N.] ШЛЯКОВ Р.Н. 1980. Печеночные мхи Севера СССР. – [The Hepatics of the North of the USSR] *Л., Наука* [*Leningrad, Nauka*] **3**: *1-188*.

[SCHLJAKOV, R.N.] ШЛЯКОВ Р.Н. 1981. Печеночные мхи Севера СССР. – [The Hepatics of the North of the USSR] *Л., Наука* [*Leningrad, Nauka*] **4**: *1-221*.

SCHUMACKER, R. & J. VÁŇA 2005. Identification keys to the liverworts and hornworts of Europe end Macaronesia (distribution and status). – *Poznan, Sorus*: *1-212*.

SCHUSTER, R.M. 1966. The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 1. – *New York, Columbia University Press*: *1-802*.

SCHUSTER, R.M. 1969. The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 2. – *New York, Columbia University Press*: *1-1062*.

SCHUSTER, R.M., 1970. Studies on Hepaticae. XVIII. The family Jungermanniaceae, s. lat.: a reclassification. – *Trans. British Bryol. Soc.* **6**: *86-107*.

SCHUSTER, R.M., 1974. The Hepaticae and Anthocerotae of North America east of the hundredth meridian, Vol. 3. – *New York, Columbia University Press*: *1-880*.

SCHUSTER, R.M. 1984. Evolution, phylogeny and classification of the Hepaticae. – *In:* (*Schuster, R.M. eds.*) *New manual of Bryology*. *J. Hattori Bot. Lab*. Vol. 2: *892-1071*.

SCHUSTER, R.M. & K. DAMSHOLT 1987. Some new taxa of Jungermanniales. – *Phytologia* **63**: *325-328*.

SÖDERSTRÖM, L., R. DE ROO & T. HEDDERSON 2010. Taxonomic novelties resulting from recent reclassification of the Lophoziaceae/Scapaniaceae clade. – *Phytotaxa* **3**: *47-53*.

TABERLET, P., L. GIELLY, G. PAUTOU & J. BOUVET 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. – *Plant Mol. Biol.* **17**: *1105-1109*.

VÁŇA, J. & D.G. LONG 2009. Jungermanniaceae of the Sino-Himalayan region. – *Nova Hedwigia* **89**: *485-517*.

VÁŇA, J., L. SÖDERSTRÖM, A. HAGBORG, M. KONRAT J. 2010. Early land plants today: taxonomy, systematics and nomenclature of Gymnomitriaceae. – *Phytotaxa* **11**: *1-80*.

VILNET, A.A., N.A. KONSTANTINOVA & A.V. TROITSKY 2006. The molecular divergence between some closely allied taxa of genus *Scapania* (Dumort.) Dumort. – *Sustainable of ecosystems and problems of preservation of biological diversity in the North. Proceedings of the International conference*, *Kirovsk*: *49-53*.

VILNET, A.A., N.A. KONSTANTINOVA & A.V. TROITSKY 2007b. On molecular phylogeny of Gymnomitriaceae H. Klinggr. (Hepaticae). – *Computational Phylogenetics and molecular systematics. Conference proceedings, Moscow: 27-29*.

VILNET, A.A., N.A. KONSTANTINOVA & A.V. TROITSKY 2008. Phylogeny and systematics of the genus *Lophozia* s. str. (Dumort.) Dumort. (Hepaticae) and related taxa from nuclear ITS1-2 and chloroplast trnL-F sequences. – *Mol. Phylogenet. Evol.* **47**: *403-418*.

VILNET, A.A., N.A. KONSTANTINOVA & A.V. TROITSKY 2009a. Genosystematics and new insight into the phylogeny and taxonomy of liverworts. – *Molecular biology* **43**: *845-855*.

VILNET, A.A., N.A. KONSTANTINOVA & A.V. TROITSKY 2009b. Systematics of *Barbilophozia* Loeske (Marchantiophyta): evidence from DNA sequences data. – *Programme and Abstracts of 17th Symposium «Cryptogamic botany»*, *Tomar: 77-78*.

VILNET, A.A., I.A. MILYUTINA, N.A. KONSTANTINOVA, M.S. IGANTOV & A.V. TROITSKY 2007a. Phylogeny of the genus *Lophozia* (Dumort,) Dumort. inferred from nuclear and chloroplast sequences ITS1-2 and trnL-F. – *Russian J. Genetics* 43: *1306-1313*.

WHITE, T.J., T. BRUNS, S. LEE & J. TAYLOR 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. – *In: (Innis M.A., D.H. Gelfand, J.J. Snisky & T.J. White eds.) PCR protocols: a guide to methods and applications. San Diego, CA: 315-322*.

YATSENTYUK, S.P., N.A. KONSTANTINOVA, M.S. IGNATOV, J. HYVÖNEN & A.V. TROITSKY 2004. On phylogeny of Lophoziaceae and related families (Hepaticae, Jungermanniales) based on trnL-trnF intron-spacer sequences of chloroplast DNA. – *In: (Goffinet B., V. Hollowell & R. Magill eds.) Molecular Systematics of Bryophytes. Monogr. Syst. Bot. St. Louis, Missouri Bot. Gard. Press:* **98**: *150-167*.

Table 1. The list of taxa, specimens vouchers and GenBank accession numbers

Taxon	Herbarium voucher	Accession no.	
		*trn*L	ITS
Anastrepta orcadensis (Hook.) Schiffn.	Russia, Buryatia, Konstantinova, 59-1-01 (KPABG)	DQ875088	DQ875126
Anastrophyllum assimile (Mitt.) Steph.	USA, Konstantinova, A 137-18-95 (KPABG)	EU791664	EU791776
A. michauxii (F. Weber) H.Buch	Russia, Buryatia, Konstantinova, 17-1-02 (KPABG)	DQ875087	DQ875125
A. sphenoloboides R.M. Schust. 1	Norway, Spitsbergen, Konstantinova, K 50-3-06 (KPABG)	EU791662	EU791777
A. sphenoloboides R.M. Schust. 2	Russia, Murmansk Prov., Bakalin, 23-03-01 (KPABG)	EU791663	EU791778
Barbilophozia barbata (Schmidel ex Schreb.) Loeske 1	Netherlands, Konstantinova, 3b-5-99 (KPABG)	EU791676	EU791779
B. barbata (Schmidel ex Schreb.) Loeske 2	Russia, Kamchatka Prov., Bakalin, 56-8-01-VB (KPABG)	EU791677	EU791780
B. hatcheri (A. Evans) Loeske 1	Russia, Kamchatka Prov., Bakalin, K 7-3-03 (KPABG)	EU791675	EU791782
B. hatcheri (A. Evans) Loeske 2	Norway, Spitsbergen, Konstantinova, K 60-4-06 (KPABG)	EU791674	EU791781
B. lycopodioides (Wallr.) Loeske 1	Russia, Kuril Is., Paramushir, Bakalin, K 100-13-04 (KPABG)	EU791673	EU791783
B .lycopodioides (Wallr.) Loeske 2	Russia, Murmansk Prov., Konstantinova,16-4-00 (KPABG)	EF090627	EF090632
B. rubescens (R.M. Schust. & Damsh.) Kartt.et L. Söderstr. 1	Russia, Murmansk Prov., Konstantinova, 409-92 (KPABG)	EF090628	EF090633

Taxon	Herbarium voucher	Accession no. *trn*L	ITS
B. rubescens (R.M. Schust. et Damsh.) Kartt.et L. Soderstr. 2	Russia, Magadan Prov., Mochalova & Bakalin, G106852 (KPABG)	EU791678	EU791784
Biantheridion undulifolium (Nees) Konstant. &Vilnet 1	Russia, Kemerovo Prov., Konstantinova, 56-1-00 (KPABG)	EU791671	EU791794
B. undulifolium (Nees) Konstant. &Vilnet) 2	Russia, Buryatia, Konstantinova, 85-1-02 (KPABG)	EU791672	EU791795
Crossocalyx hellerianus (Nees) Meyl.	Russia, Karelia Rep., Bakalin, 6.VIII.1997 (KPABG)	AY327780	EU791788
Diplophyllum albicans (L.) Dumort. 1	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K446-7-05 (KPABG)	EU791659	EU791773
D. albicans (L.) Dumort. 2	Norway, Spitsbergen, Konstantinova, K 121-6-06 (KPABG)	EU791660	EU791774
D. obtusifolium (Hook.) Dumort.	Russia, Amur Prov., Bakalin, 14.VII.2000 (KPABG)	AY327782	EU791775
D. taxifolium (Wahlenb.) Dumort.	Russia, Karelia, Bakalin, 28.VII.1998 (KPABG)	AY327762	EU791772
Douinia ovata (Dicks.) H. Buch	USA, Washington, A. Potemkin, 95/401 (KPABG)	AY327778	—
D. ovata (Dicks.) H. Buch	USA, Washington, Konstantinova, A116-95 (KPABG)	—	EU791771
Eremonotus myriocarpus (Carrington) Pearson	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K446-6-05 (KPABG)	EU791716	EU791839
Gymnocolea inflata (Huds.) Dumort. 1	Norway, Spitsbergen, Konstantinova 118-1-04 (KPABG)	EU791661	EU791787
G. inflata (Huds.) Dumort. 2	Russia, Nizhny Novgorod Prov.. Konstantinova, 129-2a-03 (KPABG)	GQ220785	GQ220783
Gymnomitrion alpinum (Gottsche ex Husn.) Schiffn. 1	Russia, Buryatia, Konstantinova, 83-2-02 (KPABG)	EU791707	EU791828
G. alpinum Gottsche ex Husn.) Schiffn. 2	Russia, Sakhalin Prov., Bakalin, 58-30-05 (KPABG)	EU791706	EU791827
G. brevissimum (Schleich. ex Dumort.) Warnst. 1	Russia, Murmansk Prov. Konstantinova, G8171 (KPABG)	EU791711	EU791833
G. brevissimum (Schleich. ex Dumort.) Warnst. 2	Russia, Kamchatka Prov., Bakalin, HRE	EU791712	EU791834
G. commutatum (Limpr.) Schiffn.	Russia, Khabarovskiy Kray, Ignatov, 97-1025 (KPABG)	EU791708	EU791829
G. concinatum (Lightf.) Corda 1	Russia, Murmansk Prov., Konstantinova, 366-00 (KPABG)	AF519202	EU791832
G. concinatum (Lightf.) Corda 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K465a-05 (KPABG)	EU791710	EU791831
G. concinatum (Lightf.) Corda 3	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K493-05 (KPABG)	EU791709	EU791830
G. corallioides Nees	Norway, Spitsbergen, Konstantinova, 155-04 (KPABG)	EU791705	EU791826
G. pacificum Grolle	Russia, Commander Is., Bakalin, K-26-4-02-VB (KPABG)	EU791713	EU791835
Herbertus dicranus (Tayl.) Trev.	Russia, Primorskiy Kray, Bakalin, P-74-15-05 (KPABG)	EU791724	EU791849
Heterogemma capitata (Hook.) Konstant. &Vilnet	Russia, Nizhny Novgorod Prov., Konstantinova, 132-03 (KPABG)	DQ875080	DQ875119
H. laxa (Jørg.) Konstant. &Vilnet)	Russia, Murmansk Prov., Konstantinova, 40-6-94 (KPABG)	DQ875084	DQ875053
Isopaches bicrenatus (Hoffm.) H. Buch	Russia, Yakutia, Bakalin, 18.VII.2000 (KPABG)	AY327788	EU791797
I. decolorans (Limpr.) H. Buch	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K464-3-05 (KPABG)	EU791680	EU791798
Iwatsukia jishibae (Steph.) Kitag.	Russia, Buryatia, Konstantinova 48-1-01 (KPABG)	EU791680	EU791798
Jamesoniella autumnalis (DC.) Steph. 1	Russia, Maryi-El Rep., Konstantinova, K 448-5-04 (KPABG)	EU791720	EU791844
J. autumnalis (DC.) Steph. 2	Russia, Buryatia, Konstantinova, 103-1-01 (KPABG)	EU791721	EU791845
Jungermannia atrovirens Dumort. 1	Russia, Caucasus, Karachayevo-Cherkessian Rep., Ignatov & Ignatova, 4.VIII.2002 (KPABG)	GQ220766	GQ220782
J. atrovirens Dumort. 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 421- 6-05 (KPABG)	GQ220763	GQ220779
J. atrovirens Dumort. 3	Russia, Kamchatka Prov., Bakalin K-74-13a-04 (KPABG)	GQ220764	GQ220780
J. atrovirens Dumort. 4	Russia, Buryatia, Konstantinova, 21-4-02 (KPABG)	GQ220765	GQ220781
Leiocolea badensis (Gottsche) Jörg. 1	Russia, Amur Prov., Bakalin, 33-1-00 VB (KPABG)	EU791718	EU791842
L. badensis (Gottsche) Jörg. 2	Russia, Komi Rep., Dulin, Konstantinova, 101313 (KPABG)	EU791717	EU791841
Liochlaena lanceolata Nees	Russia, Murmansk Prov., Konstantinova, 206-2-02 (KPABG)	EU791719	EU791843
Lophozia ascendens (Warnst.) R. M. Schust.	Russia, Buryatia, Konstantinova, 109-3-01 (KPABG)	DQ875054	DQ875089
L. austro-sibirica Bakalin	Russia, Buryatia, Bakalin, B 15-9-99 (KPABG)	DQ875069	DQ875105
L. heteromorpha R. M. Schust.	Russia, Kamchatka Prov., Bakalin, K-47-3-02 (KPABG)	DQ875068	DQ875104
L. cf. lacerata N. Kitag.	Russia, Commander Island, Bakalin, K-3-2-02-VB (KPABG)	DQ875071	DQ875107
L. lantratoviae Bakalin	Russia, Buryatia, Bakalin, 76-7-01 (KPABG)	DQ875055	DQ875090

Taxon	Herbarium voucher	Accession no. *trn*L	ITS
L. schusteriana Schljakov	Russia, Murmansk Prov., Bakalin, G9331 (KPABG)	DQ875067	DQ875103
L. silvicola H. Buch	Russia, Karelia, Bakalin, 02.VIII.1998 (KPABG)	AF519197	—
L. silvicola H. Buch	Russia, Nizhny Novgorod Prov., Konstantinova, 124-1-03 (KPABG)	—	DQ875102
L. silvicoloides N. Kitag. 1	Russia, Murmansk Prov., Konstantinova, 356-4-00 (KPABG)	DQ875064	DQ875099
L. silvicoloides N. Kitag. 2	Russia, Kamchatka Prov., Bakalin, K -57-23-02-VB (KPABG)	DQ875063	DQ875098
L. silvicoloides N. Kitag. 3	Norway, Spitsbergen, Konstantinova, 150-6-04 (KPABG)	DQ875065	—
L. silvicoloides N. Kitag. 3	Norway, Spitsbergen, Konstantinova, 150-2-04 (KPABG)	—	DQ875100
L. cf. *wenzelii* (Nees) Steph. var. *groenlandica* (Nees) Bakalin	Russia, Kemerovo Prov., Konstantinova, 67-3-00 (KPABG)	DQ875070	DQ875106
L. ventricosa (Dicks.) Dumort. var. *guttulata* (Lindb. et S.W. Arnell) Bakalin	Russia, Buryatia, Konstantinova, 81-1-01 (KPABG)	DQ875072	DQ875108
L. ventricosa (Dicks.) Dumort. var. *longiflora* (Nees) Macoun	Russia, Chita Prov., Bakalin, 11-5-00 (KPABG)	DQ875066	DQ875101
L. wenzelii (Nees) Steph. var. *groenlandica* (Nees) Bakalin	Russia, Murmansk Prov., Konstantinova, 9329 (KPABG)	DQ875073	DQ875109
L. wenzelii (Nees) Steph. var. *lapponica* H. Buch et S.W. Arnell	Norway, Spitsbergen, Konstantinova,124-2-04 (KPABG)	DQ875076	DQ875112
L. wenzelii (Nees) Steph. var. *litoralis* (S.W. Arnell) Bakalin	Russia, Murmansk Prov., Bakalin,12-3-02 (KPABG)	DQ875074	DQ875110
L. wenzelii (Nees) Steph. var. *massularioides* Bakalin	Russia, Caucasus, V. Onipchenko, 31.VIII.83 (MHA)	DQ875075	DQ875111
Lophoziopsis excisa (Dicks.) Konstant. &Vilnet 1	Russia, Murmansk Prov., Konstantinova, 41-2-97 (KPABG)	DQ875057	DQ875092
L. excisa (Dicks.) Konstant. &Vilnet 2	Norway, Spitsbergen, Konstantinova, K-21-2-05 (KPABG)	DQ875058	DQ875093
L. longidens (Lindb.) Konstant. &Vilnet	Russia, Murmansk Prov., Konstantinova, 360-2-00 (KPABG)	DQ875059	DQ875094
L. pellucida (R. M. Schust.) Konstant. &Vilnet 1	Russia, Komi Rep., M. Dulin, 103640 (KPABG)	EF065686	EF065694
L. pellucida (R. M. Schust.) Konstant. &Vilnet 2	Russia, Murmansk Prov., Konstantinova, 39-2a-03 (KPABG)	EF065687	EF065695
L. polaris (R. M. Schust.) Konstant. &Vilnet) 1	Russia, Kamchatka Prov., Bakalin, 30-01-02 (KPABG)	DQ875060	—
L. polaris (R. M. Schust.) Konstant. &Vilnet) 1	Norway, Spitsbergen, Konstantinova, K-9-2-05 (KPABG)	—	DQ875095
L. polaris (R. M. Schust.) Konstant. &Vilnet 2	Russia, Yakutia, Bakalin, 23-11-00 (KPABG)	DQ875061	DQ875096
L. propagulifera (Gottsche) Konstant. &Vilnet)	Russia, Kamchatka Prov., Bakalin, K-53-6-02-VB (KPABG)	DQ875062	DQ875097
Macrodiplophyllum imbricatum M. Howe	USA, Alaska, Konstantinova, 110-2-92a (KPABG)	EU791658	EU791770
M. microdontium (Mitt.) Perss.	Russia, Buryatia, Konstantinova, 146/12-01 (KPABG)	AF519199	EU791769
M. plicatum (Lindb.) Perss.	Russia, Kamchatka Prov., Bakalin, 22.VIII.2001	AF519198	EU791768
Marsupella apiculata Schiffn. 1	Norway, Spitsbergen, Konstantinova, K93-1-06 (KPABG)	EU791699	EU791819
M. apiculata Schiffn. 2	Russia, Chita Prov., Bakalin, 5-13-00 (KPABG)	EU791698	EU791818
M. aquatica (Lindenb.) Schiffn. 1	Russia, Murmansk Prov., Konstantinova, 152/5-87 (KPABG)	AF519201	EU791813
M. aquatica (Lindenb.) Schiffn. 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 517-4-05 (KPABG)	EU791694	EU791814
M. arctica (Berggr.) Bryhn et Kaal.	Norway, Spitsbergen, Konstantinova, 128-04 (KPABG)	EU791695	EU791815
M. boeckii (Austin) Kaal. 1	Russia, Murmansk Prov., Konstantinova, 367-2-00 (KPABG)	EU791696	EU791816
M. boeckii (Austin) Kaal. 2	Norway, Spitsbergen, Konstantinova, K93-2a-06 (KPABG)	EU791697	EU791817
M. distichii Steph.	Japan, Deguchi & Yamaguchi, Bryophytes of Asia #170 (2000) (KPABG)	EU791703	EU791824
M. emarginata (Ehrh.) Dumort. 1	Russia, Murmansk Prov., Konstantinova, 354-4-00 (KPABG)	EU791693	EU791812
M. emarginata (Ehrh.) Dumort. 2	Russia, Buryatia, Konstantinova, 44-01 (KPABG)	EU791691	EU791810
M. emarginata (Ehrh.) Dumort. 3	Russia, Buryatia, Konstantinova, 23-4-02 (KPABG)	EU791692	EU791811
M. funckii (F. Web. et D. Mohr) Dumort.	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 516-1-05 (KPABG)	EU791700	EU791820

Taxon	Herbarium voucher	Accession no. *trn*L	ITS
M. sphacelata (Gieseke ex Lindenb.) Dumort. 1	Russia, Kemerovo Prov., Konstantinova, 65/1-00 (KPABG)	AF519200	EU791821
M. sphacelata (Gieseke ex Lindenb.) Dumort. 2	Russia, Murmansk Prov., Konstantinova, 58-5-97 (KPABG)	EU791701	EU791822
M. sprucei (Limpr.) Bernet	Russia, Kemerovo Prov., Konstantinova, 54-1-00 (KPABG)	HQ833031	EU791823
Mesoptychia sahlbergii (Lindb.) A. Evans	Russia, Chukotka, Afonina, 10.VIII.1979 (KPABG)	AF519189	EU791840
Mylia taylorii (Hook.) Gray	Russia, Buryatia, S. Kazanovsky, 26.VII.1990 (LE)	AY327779	EU791847
Mylia verrucosa Lindb.	Russia, Primorskiy Kray, Bakalin, P-73-9-05 (KPABG)	EU791723	EU791848
Nardia assamica (Mitt.) Amak.	Russia, Kuril Islands, Iturup, Bakalin, K 54-1a-05 (KPABG)	EU791715	EU791838
Nardia compressa (Hook.) Gray	Canada, Konstantinova, A97/1-95 (KPABG)	AF519188	EU791837
Nardia insecta Lindb.	Belgium, Konstantinova, 102077 (KPABG)	EU791714	EU791836
Obtusifolium obtusum (Lindb.) S.W. Arnell	Russia, Murmansk Prov., Bakalin, 1.VII.2001 (KPABG)	AY327769	—
Obtusifolium obtusum (Lindb.) S.W. Arnell	Russia, Permskiy Kray, Konstantinova, K-315-1-04 (KPABG)	—	DQ875118
Orthocaulis attenuatus (Mart.) A. Evans 1	Russia, Sakhalin Prov., Harpel, Cherdantseva, 105728 (KPABG)	EU722343	EU727538
O. attenuatus (Mart.) A. Evans 2	Russia, Murmansk Prov., Konstantinova, 29-3-97 (KPABG)	EU722344	EU727539
O. binsteadii (Kaal.) H. Buch 1	Russia, Amur Prov., Bakalin, 34-3-00VB (KPABG)	EU722345	EU727540
O. binsteadii (Kaal.) H. Buch 2	Russia, Murmansk Prov., Bakalin, 8-3-02 (KPABG)	EU722346	EU727541
O. floerkei (E. Weber & D. Mohr) H. Buch 1	Russia, Murmansk Prov., Konstantinova, 191-1-02 (KPABG)	EU722348	EU727543
O. floerkei (E. Weber & D. Mohr) H. Buch 2	Russia, Permskiy Kray, Konstantinova, K 322-4-04 (KPABG)	EU722347	EU727542
Plectocolea obovata (Nees) Mitt. 1	Russia, Murmansk Prov., Konstantinova, 196-6-02 (KPABG)	GQ220754	GQ220770
P. obovata (Nees) Mitt. 2	Russia, Kemerovo Prov., Konstantinova, 72-2-00 (KPABG)	GQ220753	GQ220769
P. obovata (Nees) Mitt. 3	Russia, Permskiy Kray, Konstantinova, K 324-1-04 (KPABG)	GQ220755	GQ220771
P. subelliptica (Lindb. Ex Kaal.) A. Evans	Russia, Kamchatka Prov., Bakalin, K-48-13-03 (KPABG)	GQ220752	GQ220768
P. sp. 1	Russia, Murmanka Prov., Konstantinova, 30-1-97 (KPABG)	GQ220761	GQ220777
P. sp. 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova K 495-2-05 (KPABG)	GQ220762	GQ220778
P. sp. 3	Russia, Buryatia, Konstantinova, 70-2-01 (KPABG)	GQ220751	GQ220767
Plicanthus birmensis (Steph.) R.M. Schust.	Russia, Primorskiy Kray, Bakalin, P-76-5-05 (KPABG)	EU791668	EU791791
Prasanthus suecicus (Gottsche) Lindb.	Norway, Spitsbergen, Konstantinova K 121-5-06 (KPABG)	EU791704	EU791825
Protolophozia elongata (Steph.) Schljakov	Russia, Murmansk Prov., Bakalin, 3-1-02 (KPABG)	DQ875078	DQ875116
Pseudolophozia debiliformis (R.M. Schust. & Damsh.) Konstant. &Vilnet 1	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 510-1-05 (KPABG)	EF065685	EF065692
P. debiliformis (R.M. Schust. & Damsh.) Konstant. &Vilnet) 2	Russia, Kamchatka Prov., Bakalin, K 20-2-04 (KPABG)	DQ875079	EF065693
P. debiliformis (R.M. Schust. & Damsh.) Konstant. &Vilnet) 3	Russia, Murmansk Prov., E. Borovichev, 22.VII.04 (KPABG)	EF090623	EF090629
Pseudolophozia sudetica (Nees ex Huebener) Konstant. &Vilnet) 1	Russia, Murmansk Prov., Bakalin, 4.VI.1998 (KPABG)	AF519195	DQ875113
P. sudetica (Nees ex Huebener) Konstant. &Vilnet 2	Russia, Commander Island, Bakalin, K-41-5-04 (KPABG)	EF090624	DQ875115
P. sudetica (Nees ex Huebener) Konstant. &Vilnet) 3	Norway, Spitsbergen, Konstantinova, K 91-4-06 (KPABG)	EU791679	EU791796
P. sudetica (Nees ex Huebener) Konstant. &Vilnet) 4	Russia, Kemerovo Prov., Konstantinova, 90-7-00 (KPABG)	DQ875077	DQ875114
Pseudotritomaria heterophylla (R.M. Schust.) Konstant. &Vilnet 1	Russia, Yakutia, Zolotov & Sofronova, 13.VII.2003 (KPABG)	EU791686	EU791805
P. heterophylla (R.M. Schust.) Konstant. &Vilnet 2	Russia, Krasnoyarskiy Kray, Fedosov, 107960 (KPABG)	EU791687	EU791806
Saccobasis polita (Nees) H. Buch	Russia, Kemerovo Prov., Konstantinova, 61-1-00 (KPABG)	EU791690	EU791809
S. polymorpha (R.M. Schust.) Schljakov 1	Russia, Murmansk Prov., Konstantinova, 21-3b-96 (KPABG)	EU791688	EU791807
S. polymorpha (R.M. Schust.) Schljakov 2	Russia, Murmansk Prov., Konstantinova, 315-8-00 (KPABG)	EU791689	EU791808
Scapania americana Müll. Frib.	USA, Washington, Konstantinova, A 22-6a-95 (KPABG)	EU791655	EU791764
S. apiculata Spruce	Russia, Buryatia, Konstantinova, HRE [1] 49 (KPABG)	EU791633	EU791741
S. aspera Bernet et M. Bernet	Belgium, Konstantinova, 2-20-3-99 (KPABG)	EU791627	EU791735
S. bolanderi Austin	USA, Washington, Konstantinova, A10-4a-95 (KPABG)	EU791657	EU791767
S. calcicola (H. Arnell et J. Perss) Ingham	Germany, Konstantinova, 28.VIII.86	EU791648	EU791757
S. crassiretis Bryhn.	Russia, Murmansk Prov., Konstantinova, 354-5b-00 (KPABG)	EU791646	EU791755
S. curta (Mart.) Dumort.	Russia, Murmansk Prov., Konstantinova, 358-3-00 (KPABG)	EU791628	EU791736
S. cuspiduligera (Nees) Müll.Frib.	Russia, Buryatia, Konstantinova, 24-1-02 (KPABG)	EU791643	EU791752

Taxon	Herbarium voucher	Accession no. *trn*L	ITS
S. ferruginea (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	India, Sikkim, D. Long, 22492 (KPABG)	AF519193	EU791766
S. glaucocephala (Taylor) Austin	Russia, Buryatia, Konstantinova, 64-5-02 (KPABG)	EU791644	EU791753
S. gymnostomophila Kaal.	Russia, Murmansk Prov., Konstantinova, 13-1-98 (KPABG)	EU791649	EU791758
S. helvetica Gottsche 1	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova K414-1-05 (KPABG)	EU791620	EU791728
S. helvetica Gottsche 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, 488-3-05 (KPABG)	EU791619	EU791727
S. hyperborea Jörg. 1	Russia, Murmansk Prov., Konstantinova, 509-3a-04 (KPABG)	EU791635	EU791744
S. hyperborea Jörg. 2	Russia, Yakutia, Bakalin, 1-10-00 (KPABG)	EU791636	EU791745
S. irrigua (Nees) Nees 1	Russia,Permskiy Kray, Konstantinova, K 372-5-04 (KPABG)	EU791624	EU791732
S. irrigua (Nees) Nees 2	Russia, Murmansk Prov., Konstantinova, 219-4-02 (KPABG)	EU791625	EU791733
S. kaurinii Ryan	Russia, Chita Prov., Bakalin, 11-1-00 (KPABG)	EU791650	EU791759
S. mucronata H. Buch 1	Russia, Tuva Rep., Bakalin, 100854 (KPABG)	EU791629	EU791737
S. mucronata H. Buch 2	Russia, Karelia, 43-8-01 (KPABG)	EU791630	EU791738
S. nemorea (L.) Grolle	Belgium, Konstantinova, 1-20-9-99 (KPABG)	EU791645	EU791754
S. obcordata (Berggr.) S.W.Arnell	Norway, Spitsbergen, Konstantinova, 123-1-04 (KPABG)	EU791626	EU791734
S. paludicola Loeske et Müll. Frib.	Russia, Karelia, Bakalin, 11.VIII.1997	AF519196	EU791743
S. paludosa (Müll.Frib.) Müll. Frib. 1	Russia, Permskiy Kray, Konstantinova, K316-2-04 (KPABG)	EU791639	EU791748
S. paludosa (Müll.Frib.) Müll. Frib. 2	Russia, Kemerovo Prov., Konstantinova, 4-3-00 (KPABG)	EU791638	EU791747
S. rufidula Warnst.	Russia, Yakutia, Bakalin, 35-3-00 (KPABG)	EU791637	EU791746
S. simmonsii Bryhn et Kaal.	Russia, Murmansk Prov., Konstantinova, 45-9-98 (KPABG)	EU791653	EU791762
S. sphaerifera H.Buch et Tuom.	Russia, Buryatia, Konstantinova, 92-2-01(KPABG)	EU791656	EU791765
S. spitsbergensis (Lindb.) Müll. Frib. 1	Russia, Buryatia, Konstantinova, 121-6-02 (KPABG)	EU791651	EU791760
S. spitsbergensis (Lindb.) Müll. Frib. 2	Norway, Spitsbergen, Konstantinova, K 90-2-06 (KPABG)	EU791652	EU791761
S. subalpina (Nees ex Lindenb.) Dumort. 1	Russia, Permskiy Kray, Konstantinova, K379-04 (KPABG)	EU791641	EU791750
S. subalpina (Nees ex Lindenb.) Dumort. 2	Russia, Buryatia, Konstantinova, 136-4-01 (KPABG)	EU791640	EU791749
S. tundrae (Arnell) H. Buch	Norway, Spitsbergen, Konstantinova, 140-1-04 (KPABG)	EU791634	EU791725 & EU791742
S. uliginosa (Sw. ex Lindenb.) Dumort.	Russia, Murmansk Prov., Bakalin, 25-7-01 (KPABG)	EU791631	EU791739
S. umbrosa (Schrad.) Dumort.	Russia, Komi Rep., M. Dulin, MD 139-1-99 (KPABG)	EU791632	EU791740
S. undulata (L.) Dumort	Russia, Murmansk Prov., Konstantinova, 208-2-02 (KPABG)	EU791642	EU791751
S. verrucosa Heeg	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, 609/6-05 (KPABG)	EU791654	EU791763
Schistochilopsis incisa (Schrad.) Konstantinova 1	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K411-1-05 (KPABG)	EF065689	—
S. incisa (Schrad.) Konstantinova 2	Russia, Murmansk Prov., Konstantinova,187-1-02 (KPABG)	DQ875083	—
S. grandiretis (Lindb. Ex Kaal.) Schiffn.	Russia, Kamchatka Prov., Bakalin, 99-5-01-VB (KPABG)	DQ875081	DQ875122 & DQ875120
S. opacifolia (Meyl.) Konstant. 1	Norway, Spitsbergen, Konstantinova, K-43-2-05 (KPABG)	DQ875082	DQ875121
S. opacifolia (Meyl.) Konstant. 2	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 468-6b-05 (KPABG)	EF065688	GQ220784
Schljakovia kunzeana (Hübener) Konstant. &Vilnet 1	Russia, Kamchatka Prov., Bakalin, K 56-9-02 VB (KPABG)	EU722350	EU727545
S. kunzeana (Hübener) Konstant. &Vilnet 2	Russia, Murmansk Prov., Konstantinova, 181-02 (KPABG)	EU722349	EU727544
Schljakovianthus quadrilobus (Lindb.) Konstant. &Vilnet 1	Russia, Tuva Rep., Otnyukova, Bakalin, 100805 (KPABG)	EU791666	EU791786
S. quadrilobus (Lindb.) Konstant. &Vilnet 2	Russia, Komi Rep., Dulin, 101302 (KPABG)	EU791665	EU791785
Solenostoma confertissimum (Nees) Schljakov	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 459-8a-05 (KPABG)	GQ220758	GQ220774
S. fusiformis (Steph.)Steph.	Russia, Kamchatka Prov., Bakalin, HRE 42 (KPABG)	GQ220757	GQ220773
S. handelii (Schiffn.) Müll. Frib.	Japan, M. Itouga, Bryophytes of Asia 194 (KPABG)	GQ220756	GQ220772
S. pseudopyriflorum Bakalin &Vilnet	Russia, Buryatia, Konstantinova, 30-2-01 (KPABG)	GQ220759	GQ220775
S. sp.	Russia, Caucasus, Karachayevo-Cherkessian Rep., Konstantinova, K 419- 05 (KPABG)	GQ220760	GQ220776
Sphenolobus minutus (Schreb.) Berggr. 1	Russia, Karelia, Bakalin, 24.VII.1998 (KPABG)	AY327766	EU791790
S. minutus (Schreb.) Berggr. 2	Norway, Spitsbergen, Konstantinova, K 68-1-06 (KPABG)	EU791667	EU791789

Taxon	Herbarium voucher	Accession no. *trn*L	ITS
S. saxicola (Schrad.) Steph.	Russia, Buryatia, Konstantinova ,123-3-02 (KPABG)	DQ875086	DQ875124
Tetralophozia filiformis (Steph.) Urmi	Russia, Buryatia, Konstantinova, 13-24-01 (KPABG)	EU791669	EU791792
T. setiformis (Ehrh.) Schljakov	Russia, Buryatia, Konstantinova, 123-2-02 (KPABG)	EU791670	EU791793
Tritomaria exsecta (Schhmidel) Loeske	Russia, Nizhny Novgorod Prov., Konstantinova, 103-1-03 (KPABG)	EU791682	EU791800
T. exsectiformis (Breidl.) Loeske	Russia, Buryatia, Konstantinova, 83-4-01 (KPABG)	EU791683	EU791801
T. quinquedentata (Huds.) H. Buch	Russia, Karelia, Bakalin, 02.VII.1997 (KPABG)	AY327786	EU791804
T. quinquedentata f. *gracilis* (Jens.) R.M. Schust. 1	Norway, Spitsbergen, Konstantinova, K 118-2-06 (KPABG)	EU791684	EU791802
T. quinquedentata f. *gracilis* (Jens.) R.M. Schust. 2	Norway, Spitsbergen, Konstantinova, K 72-2-06 (KPABG)	EU791685	EU791803
Tritomaria scitula (Tayl.) Jørg.	Russia, Komi Rep., Dulin, G101301 (KPABG)	EU791681	EU791799