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MOLECULAR PHYLOGENY AND SYSTEMATICS OF THE SUBORDER CEPHALOZIINEAE WITH SPECIAL ATTENTION TO THE FAMILY CEPHALOZIACEAE S.L. (JUNGERMANNIALES, MARCHANTIOPHYTA)

МОЛЕКУЛЯРНАЯ ФИЛОГЕНИЯ И СИСТЕМАТИКА ПОДПОРЯДКА CEPHALOZIINEAE И В ОСОБЕННОСТИ СЕМЕЙСТВА CEPHALOZIACEAE S.L. (JUNGERMANNIALES, MARCHANTIOPHYTA)

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Abstract

Molecular phylogenic analysis of the suborder Cephaloziineae is performed, with the special attention to the family Cephaloziaceae s.l. and its implications for taxonomy are discussed. A combined alignment of nuclear ITS1-2 and chloroplast *trn*L-F DNA sequences of 121 species (209 samples) from the families Scapaniaceae, Anastrophyllaceae, Cephaloziaceae s.l., Cephaloziellaceae, Adelanthaceae, and Jamesoniellaceae are analyzed. The topologies of phylogenetic trees constructed by maximum parsimony, maximum likelihood and Bayesian methods show the principal congruence with previously achieved phylogenies, with exception of ambiguous position of the Cephaloziellaceae. The genus *Hygrobiella* does not reveal affinity to the Cephaloziaceae s.l., which supports its segregation in the monotypic family Hygrobiellaceae. The Odontoschismataceae are resolved sister to the Cephaloziaceae s.str., supporting their classification into two families expedient also from morphological evidences. The former family preliminarily includes, besides *Odontoschisma* and *Cladopodiella,* the genera *Iwatsukia* and *Alobiellopsis* from the subfamily Alobielloideae. The relationships of the subfamily Schiffnerioideae remain uncertain. The genera *Cephalozia*, *Odontoschisma* and *Cladopodiella* appear to be polyphyletic, but the existing section subdivisions for *Cephalozia* and *Odontoschisma* are partly supported. The genus *Nowellia* is found in the sister position to *Cephalozia bicuspidata*-complex and *C. macoinii*. The rest of studied *Cephalozia* species compose an intermingled clade with the monotypic genera *Pleurocadula* and *Schofieldia.* Thus only species of the *Cephalozia bicuspidata*-complex and *C. macoinii* are accepted in *Cephalozia*, whereas other *Cephalozia* species and *Schofieldia* are transferred into the genus *Pleurocadula.* Infraspecific nucleotide sequence variation suggests the species status for *Cephalozia affinis* and *Odontoschisma elongatum*, whereas *O. prostratum* and *O. sphagni* appear to be conspecific.

Резюме

Проведен молекулярно-филогенетический анализ печеночников подпорядка Cephaloziineae и, в особенности, семейства Cephaloziaceae s.l., и на его основе предложены изменения в систематике данной группы. Анализ осуществлен по объединенным нуклеотидным последовательностям ITS1-2 ядерной и *trn*L-F хлоропластной ДНК 121 вида (209 образцов) из семейств Scapaniaceae, Anastrophyllaceae, Cephaloziaceae s.l., Cephaloziellaceae, Adelanthaceae и Jamesoniellaceae. Топологии деревьев, реконструированные с помощью методов максимальной экономии, максимального правдоподобия и метода Байеса сходны как между собой, так и с ранее полученными данными, за исключением нестабильного положения семейства Cephaloziellaceae. Род *Hygrobiella* не является филогенетически близким к Cephaloziaceae s.l., его следует относить к самостоятельному монотипному семейству Hygrobiellaceae. Odontoschismataceae выявлено в сестринском положении к Cephaloziaceae s.str., так что их целесообразно рассматривать в качестве самостоятельных семейств, что подтверждается и морфологическими данными. Кроме родов *Odontoschisma* и *Cladopodiella* к семейству Odontoschismataceae предварительно отнесены роды *Iwatsukia* и *Alobiellopsis* из подсемейства Alobielloideae. Филогенетические связи подсемейства Schiffnerioideae остаются неясными. Роды *Cephalozia*, *Odontoschisma* и *Cladopodiella* являются полифилетичными, однако существующие внутриродовые классификации для *Cephalozia* и

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Odontoschisma частично поддерживаются молекулярными данными. Род *Nowellia* является сестринским комплексу видов *C. bicuspidata* и *C. macoinii.* Остальные исследованные виды рода *Cephalozia* расположены в кладе с монотипными родами *Pleurocadula* и *Schofieldia.* Объем рода *Cephalozia* пересмотрен: только комплекс видов *C. bicuspidata* и *C. macoinii* относятся к *Cephalozia,* в то время как другие изученные виды *Cephalozia* и *Schofieldia* перенесены в род *Pleurocadula*. Исследование вариабельности нуклеотидных последовательностей подтверждает видововой статус *Cephalozia affinis* и *Odontoschisma elongatum*, в то же время *O. prostratum* и *O. sphagni* следует считать одним видом.

KEYWORDS: Cephaloziaceae, Cephaloziineae, Hepaticae, Hygrobiellaceae, infraspecific sequence variability, ITS1-2, molecular phylogeny, Odontoschismataceae, *trn*L-F

INTRODUCTION

In traditional circumscription, suborder Cephaloziineae (Jungermanniales) includes four families: Cephaloziaceae Mig. s.l., Cephaloziellaceae Douin, Adelanthaceae Grolle and Jackiellaceae R.M. Schust. (Schuster, 1984; Crandall-Stotler & Stotler, 2000). Schljakov (1975) added the family Geocalycaceae H. Klinggr., raised the status of the Odontoschismatoideae Buch ex Grolle up to the family level, and also included the family Adelanthaceae into the latter. Molecular phylogenetic studies overturn that circumscription (Yatsentyuk *et al.*, 2004; Heinrichs *et al.*, 2005; He-Nygren *et al.*, 2006; Forrest *et al.*, 2006; De Roo *et al.*, 2007; Vilnet *et al.*, 2010; Feldberg *et al.*, 2010). At present six families compose this suborder: Scapaniaceae Mig., Anastrophyllaceae L. Söderstr., De Roo & Hedd., Cephaloziaceae s.l., Cephaloziellaceae, Adelanthaceae and Jamesoniellaceae He-Nygren (Crandall-Stotler *et al.*, 2009; Södroström *et al.*, 2010).

Phylogenetic tree topologies show some incongruence within the Cephaloziineae. The position of the Cephaloziaceae s.l. sister to the Scapaniaceae+former Lophoziaceae+Cephaloziellaceae-clade was found by Forrest *et al.* (2006), De Roo *et al.* (2007), He-Nygren *et al.* (2006). However, analysis of Hentschel *et al.* (2007) resolved the Cephaloziaceae s.l. in a clade together with the Jamesoniellaceae and Adelanthaceae, whereas the Cephaloziellaceae were retained within the clade of the Scapaniaceae and the former Lophoziaceae.

There are no special studies concerning the Cephaloziaceae s.l. molecular phylogeny. Only some species from several genera of the Cephaloziaceae s.l. were included in phylogenetic analysis. Particulary, *Cephalozia* (Dumort.) Dumort., *Nowellia* Mitt. and *Schiffneria* Steph. were resolved in a sister clade to *Odontoschisma* (Dumort.) Dumort. (Forrest *et al.*, 2006; Hentschel *et al.*, 2007; De Roo *et al.*, 2007). In the mordern morpho-molecular classification Crandall-Stotler *et al.* (2009) included sixteen genera in the Cephaloziaceae s.l. and ten of them were involved in the current study.

The treatment of the Cephaloziaceae s.l. "remains difficult and thoroughly subjective, owing to the fact that the *Cephalozia*-complex (subfamily Cephalozioideae sensu R.M. Schuster (1974)) seems to show reticulate connections to many other groups, some of which (*Schiffneria, Jackiella, Odontoschisma, Hygrobiella*) are often placed in separate families, or at least in other existing families" (Schuster, 1974: 643). Majority of hepaticologists accepted the Cephaloziaceae in a broad sense, with segregation of six subfamilies: Alobielloideae R.M. Schust., Cephalozioideae, Hygrobielloideae (Jørg.) R.M. Schust. ex Grolle, Odontoschismatoideae H. Buch, Schiffnerioideae R.M. Schust., Trabacelluloideae (Fulford) R.M. Schust. (Schuster, 1974, 2002; Grolle, 1983; Damsholt, 2002), some of them were treated as families, particularly the Hygrobiellaceae (Müller, 1954; Arnell, 1956) and Odontoschismataceae (Schljakov, 1975).

The present study is focused on molecular phylogeny of the suborder Cephaloziineae with special attention to the family Cephaloziaceae s.l., in order to make its taxonomy more evolutionary based.

MATERIAL AND METHODS

Taxa selection

Totally 121 species (209 samples) were taken for this study (Table 1), among them 47 species (126 samples) were sequenced for the first time. We analyzed 27 species (110 samples) from the family Cephaloziaceae s.l., 52 species (53 samples) from the Scapaniaceae, 19 species (19 samples) from the Anastrophyllaceae, 11 species (11 samples) from the Cephaloziellaceae, 5 species (8 samples) from the Jamesoniellaceae, 3 species (3 samples) – from the Adelanthaceae. Ten genera of the Cephaloziaceae s.l. (Crandall-Stotler *et al.*, 2009) were analyzed, including the largest genus of the family *Cephalozia* (13 species), as well as *Odontoschisma* (Dumort.) Dumort. (6 species), *Cladopodiella* H. Buch (2 species), and 6 mostly oligo- or monotypic genera that were represented in our study by one species: *Alobielopsis parvifolia, Hygrobiella laxifolia*, *Iwatsukia jishibae, Nowellia curvifolia*, *Pleurocladula albescens*, *Schiffneria hyalina* and *Schofieldia monticola.* With the exception of *A. parvifolia, C. macounii, C. macrostachya, I. jishibae* and *S. hyalina* all species of the Cephaloziaceae s.l. are presented by multiple accessions from geographically distant regions. Thus, almost all known Holarctic genera of the Cephaloziaceae s.l. and related families were analyzed. Basing on previous phylogenetic reconstructions (Forrest *et al.*, 2006, Heinrichs *et al.*, 2005), the genera *Calypogeia* Radii and *Metacalypogeia* (S. Hatt.) Inoue (Calypogeiaceae Arnell) were selected as an outgroup.

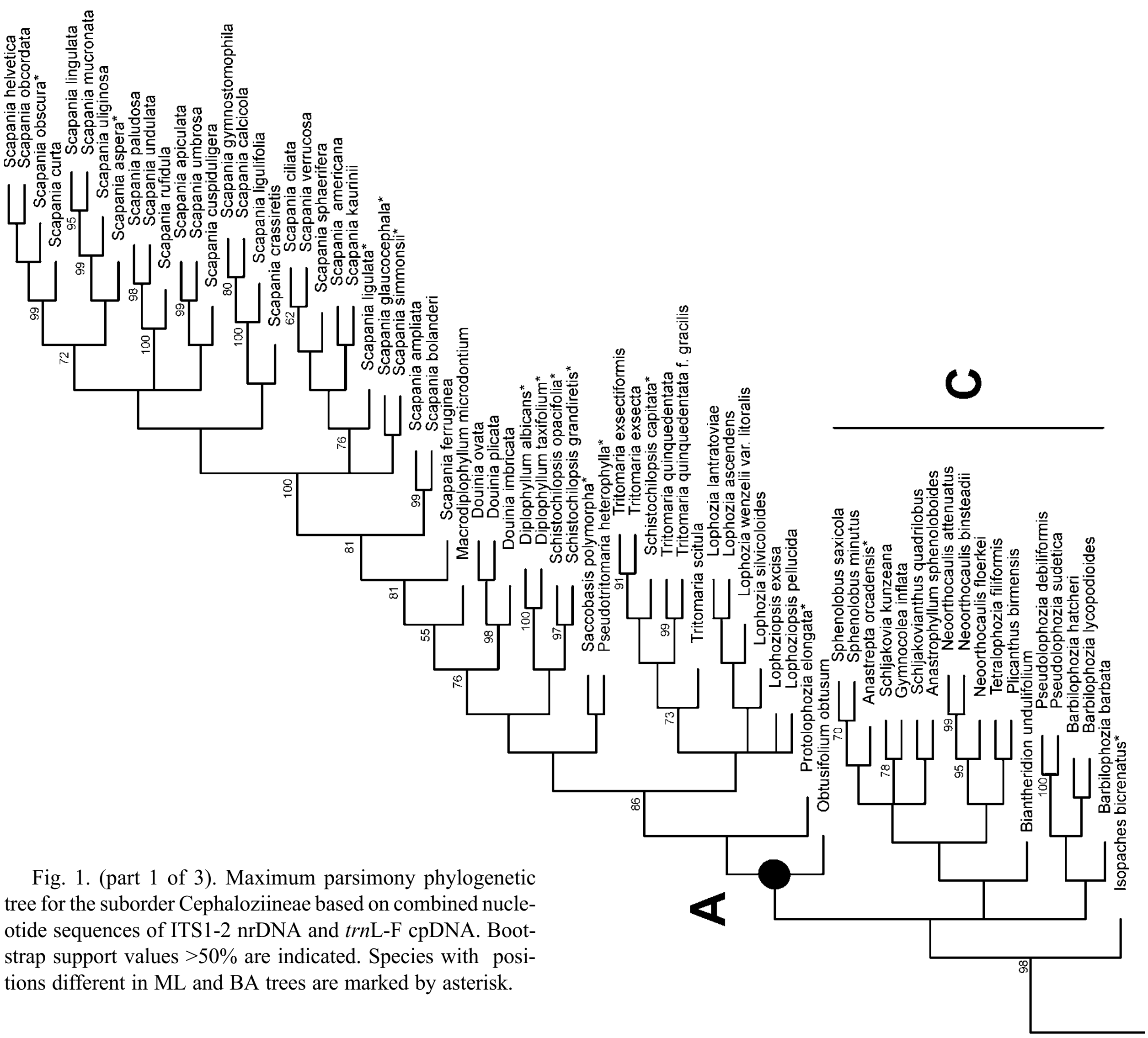


Fig. 1. (part 1 of 3). Maximum parsimony phylogenetic tree for the suborder Cephaloziineae based on combined nucleotide sequences of ITS1-2 nrDNA and *trn*L-F cpDNA. Bootstrap support values >50% are indicated. Species with positions different in ML and BA trees are marked by asterisk.

DNA isolation, amplification and sequencing

DNA was extracted using the NucleoSpin Plant Kit (Macherey-Nagel, Germany) from herbarium samples. The amplification and sequencing were performed using the primers suggested by Taberlet *et al.* (1991) for *trn*L-F cpDNA and White *et al.* (1990) for ITS1-2 nrDNA.

PCRs were carried out in 20 mkl volumes contained about 10-20 ng of template DNA, 10 pmol of each primer, and 1.2U of Smart Taq polymerase (DIALAT Ltd, Russia) in a buffer supplied by the manufacturer. DNA amplification was performed according the following procedure: 3 min at 94°C, 30 cycles (30 s at 94°C, 40 s at 58°C, and 60 s at 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 GFX^{TM} 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 the 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analyses

The initial alignment for ITS1-2+*trn*L-F combined sequences was automatically created by ClustalW implemented by BioEdit 7.0.1 (Hall, 1999). Ambiguously aligned position at 3'-end of ITS2 and P8 stem-loop region of *trn*L-intron were excluded from the alignment. Then alignment was improved using SATé v. 2.2.4 (Liu *et al.*, 2012) with Mafft aligner option, GTR+G20 model for RAxML tree estimation with ten improvement iterations, and finally corrected by eye.

The final alignment of ITS1-2+*trn*L-F (207 samples) was analyzed by three analytical procedures: the maximum parsimony method (MP) using the TNT program (Goloboff *et al.*, 2003), the Bayesian method (BA) using the MrBayes v. 3.2.1 (Ronquist *et al.*, 2012), and the

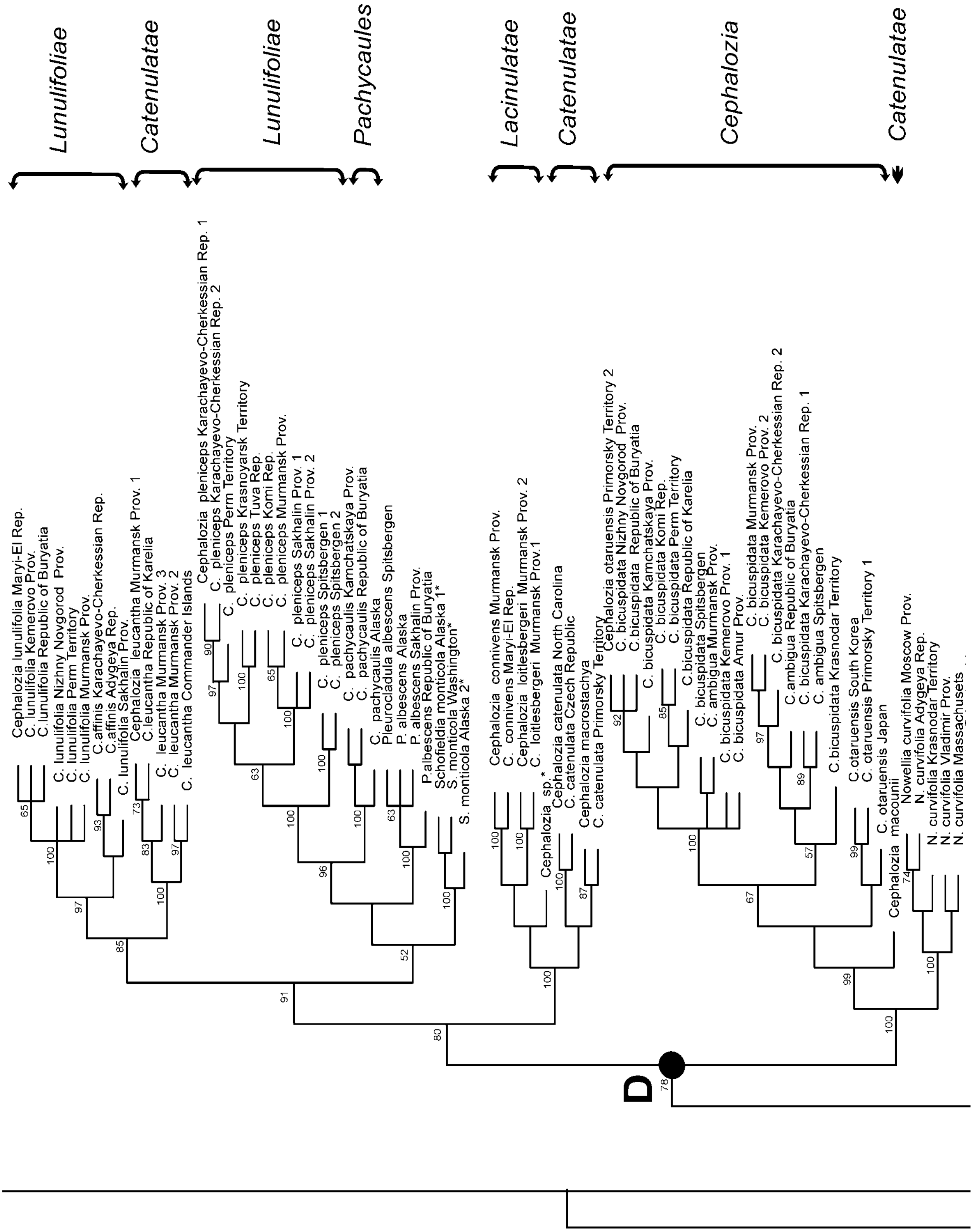


Fig. 1. (part 2 of 3).

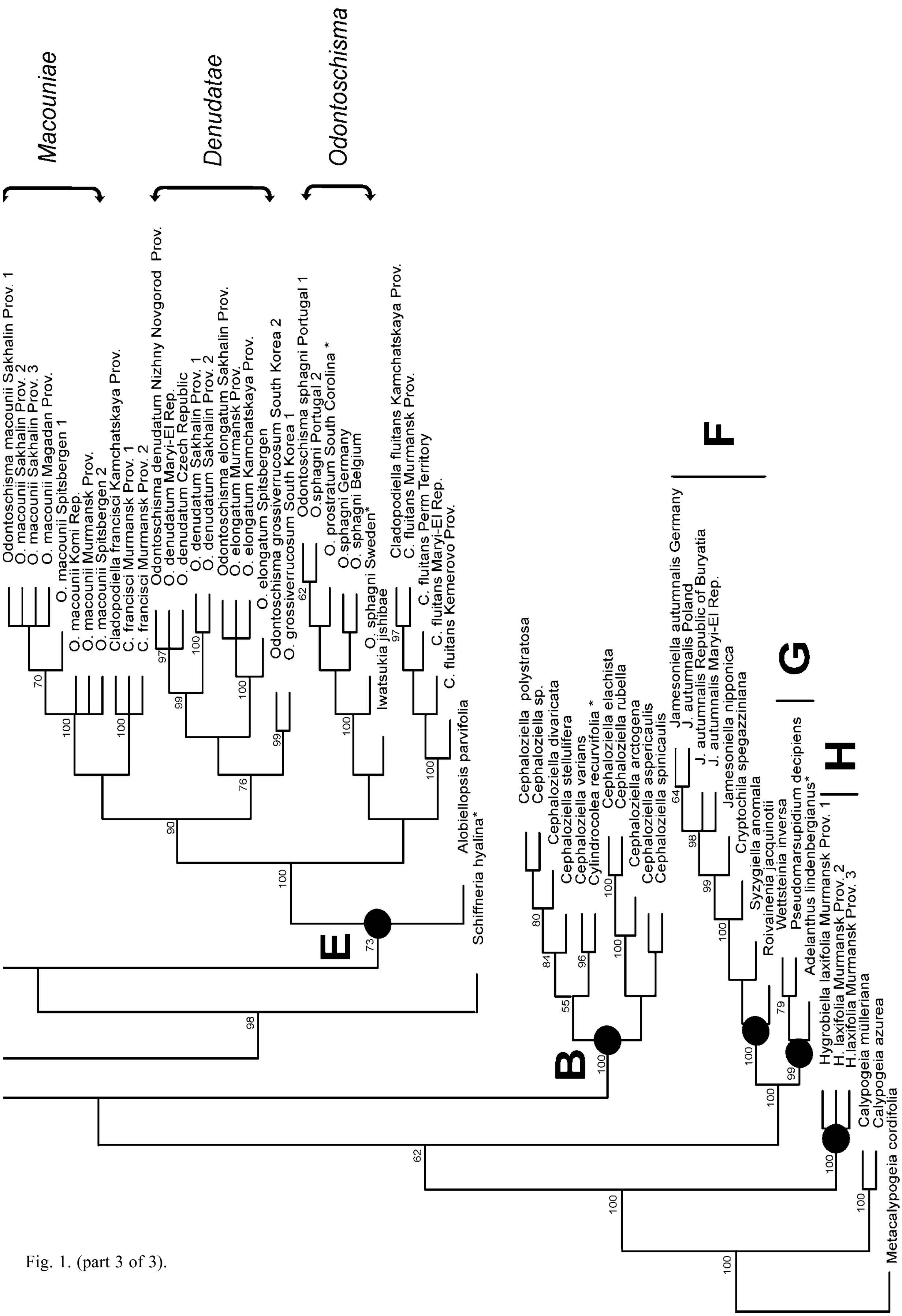


Fig. 1. (part 3 of 3).

maximum likelihood method (ML) using RAxML-VI-HPC v. 7.2.6 (Stamatakis, 2006).

The MP analysis involved a New Technology Search with a search for the minimum-length tree by five reiteration and 1000 bootstrap resamplings; the default settings were used for other parameters. Gaps were treated as missing data, indels were taken into account by a modified complex coding algorithm in SeqState v. 1.4.1 (Müller, 2006).

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 combined alignment.

In the ML analysis two partitions (ITS1-2 and *trn*L-F), GTRGAMMA model, and 500 bootstrap resamplings were used. According to stopping frequency criterion for bootstrapping procedure (Pattengale *et al.*, 2010), even 200 replicates were enough for our dataset for reaching convergence with Pearson average p100 =0.9937.

In the Bayesian analysis, each of partitions (ITS1-2 and *trn*L-F) was separately assigned the GTR+I+G model, and 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 included three heated and one unheated chains, and the two starting trees were chosen randomly. The number of generations was 5 000 000, and trees were saved once every 10 generations. The first 125 000 trees were discarded in each run, and 750 000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated as branch support values. In the BA analysis, trees were sampled after reaching stationarity; average standard deviation of split frequencies between two runs was 0.007938 and the potential scale reduction factor PSRF approached 1 for all parameters.

The infrageneric and infraspecific variability of each DNA loci as the values of the *p*-distances (pd) between samples and species were evaluated in Mega 3.0 (Kumar *et al.*, 2004), using the pairwise deletion option for counting gaps.

RESULTS

ITS1-2 and *trn*L-F sequences from 126 samples were obtained in this study. Additionally, 69 ITS1-2 and 70 *trn*L-F sequences were taken from our previous studies, mainly for species from the Scapaniaceae and Anastrophyllaceae (Yatsentyuk *et al.*, 2004; Vilnet *et al.*, 2008, 2010). Nine sequences of ITS1-2 and 10 sequences of *trn*L-F of hard-to-get South Hemispheric species from the Jamesoniellaceae, Adelanthaceae, and Cephaloziaceae s.l. were taken from GenBank. *Schiffneria hyalina*, *Cylindrocolea recurvifolia* and *Cephaloziella polystratosa* were presented only by *trn*L-F sequences, *Cephalozia macounii* – by ITS1-2. The ITS1-2 and *trn*L-F sequences for *Obtusifolium obtusum* and *Douinia ovata* were produced from different samples.

After exclusion of ambiguously aligned position at the 3'-end of ITS2, the ITS1-2 alignment consisted of 1064 positions. Among them, 739 (69.45%) were variable and 579 (54.42%) were parsimony informative. The *trn*L-F alignment with deletion of ambiguously aligned P8 stem-loop region in *trn*L-intron consisted of 437 sites, the 226 (51.72%) positions were variable and 181 (41.42%) were parsimony informative. The combined alignment of ITS1-2+*trn*L-F used for analyses consisted of 1501 sites, including 965 (64.29%) variable and 760 (50.63%) parsimony informative positions. For MP analysis the dataset with 93 indel coded positions were added to the nucleotide dataset.

The MP analysis with TNT yielded 26 equally parsimonious trees at different runs with a length of 7943 steps (Fig. 1).

In BA analysis arithmetic means of log likelihoods for runs sampled were -28592.21 and -28588.11. The BA tree with means of posterior probabilities (PP) is presented in Fig. 2. ML calculation produced a tree with arithmetic means of log likelihoods -28655.83, the BS values are also indicated in Fig. 2.

All studied samples were found to be combined in eight main clades (A-H) that demonstrated stable group relationships in the obtained trees, with the exception of Cephaloziellaceae position, part of clade B, and also clade C that appeared as a grade in MP tree (Fig. 1, 2).

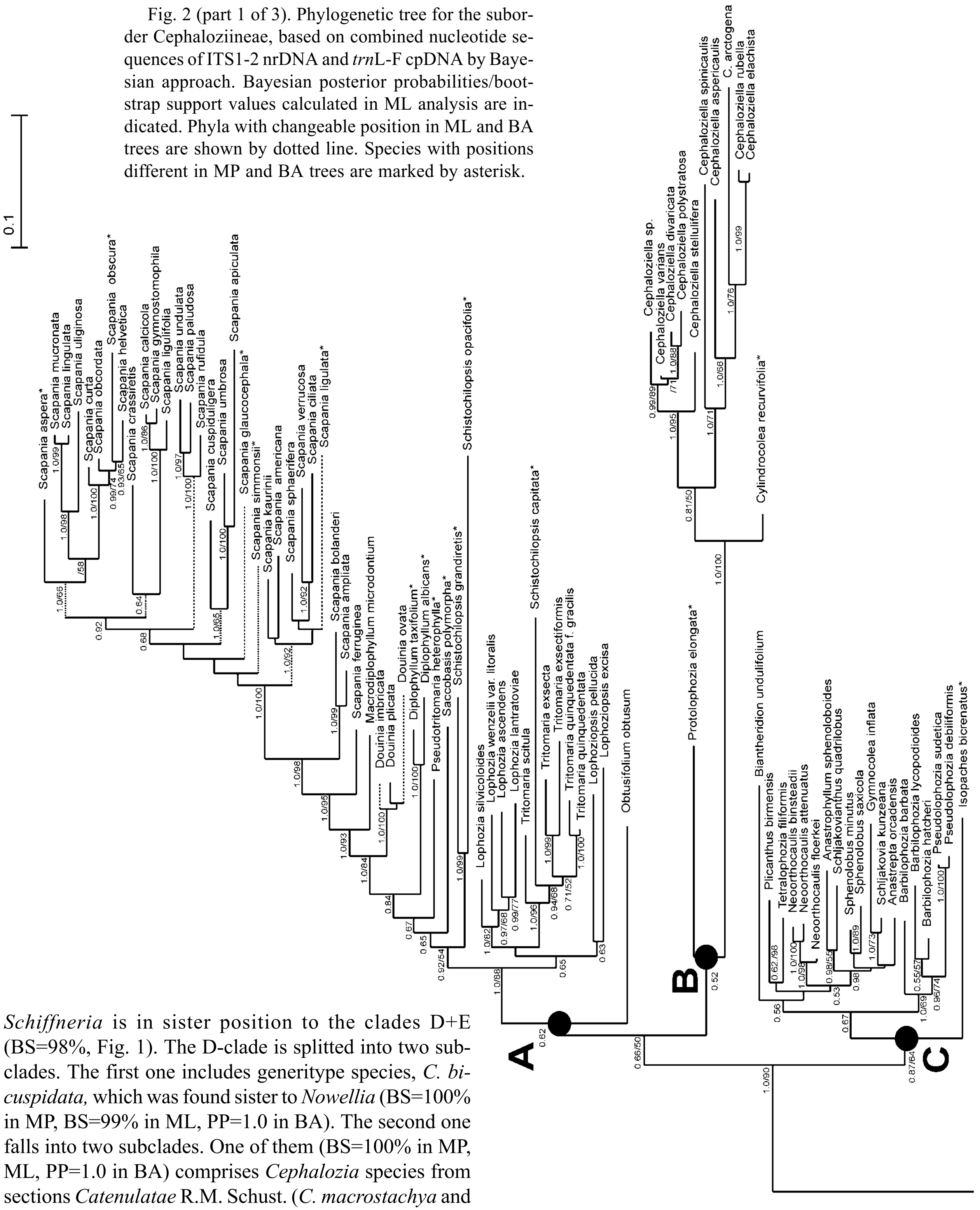
The clade A is composed of representatives of the Scapaniaceae, the weakly supported basal position in this clade belongs to *Obtusifolium obtusum* and *Protolophozia elongata* in MP tree (BS<50%, Fig.1) or only to *Obtusifolium obtusum* in BA/ML tree (PP=0.62 in BA, Fig. 2). *Protolophozia elongata* was found within the clade B in a sister position to the Cephaloziellaceae (Fig. 2) with PP=0.52.

The Anastrophyllaceae (C clade in BA/grade in MP) is found in a sister position to the Scapaniaceae in the MP tree (BS<50%) (Fig. 1). We obtained the genus *Isopaches* H. Buch at the base of the Anastrophyllaceae with insufficient support in two calculations (BS=64% in ML, PP=0.87 in BA) (Fig. 2) or in a sister lineage to the A+C (BS=98% in MP) (Fig. 1). Previously *Isopachaes* was found only in sister position to the Anastrophyllaceae +Scapaniaceae-clade (Vilnet *et al.*, 2010: Figs. 1, 2; BS=100%, PP=1.0).

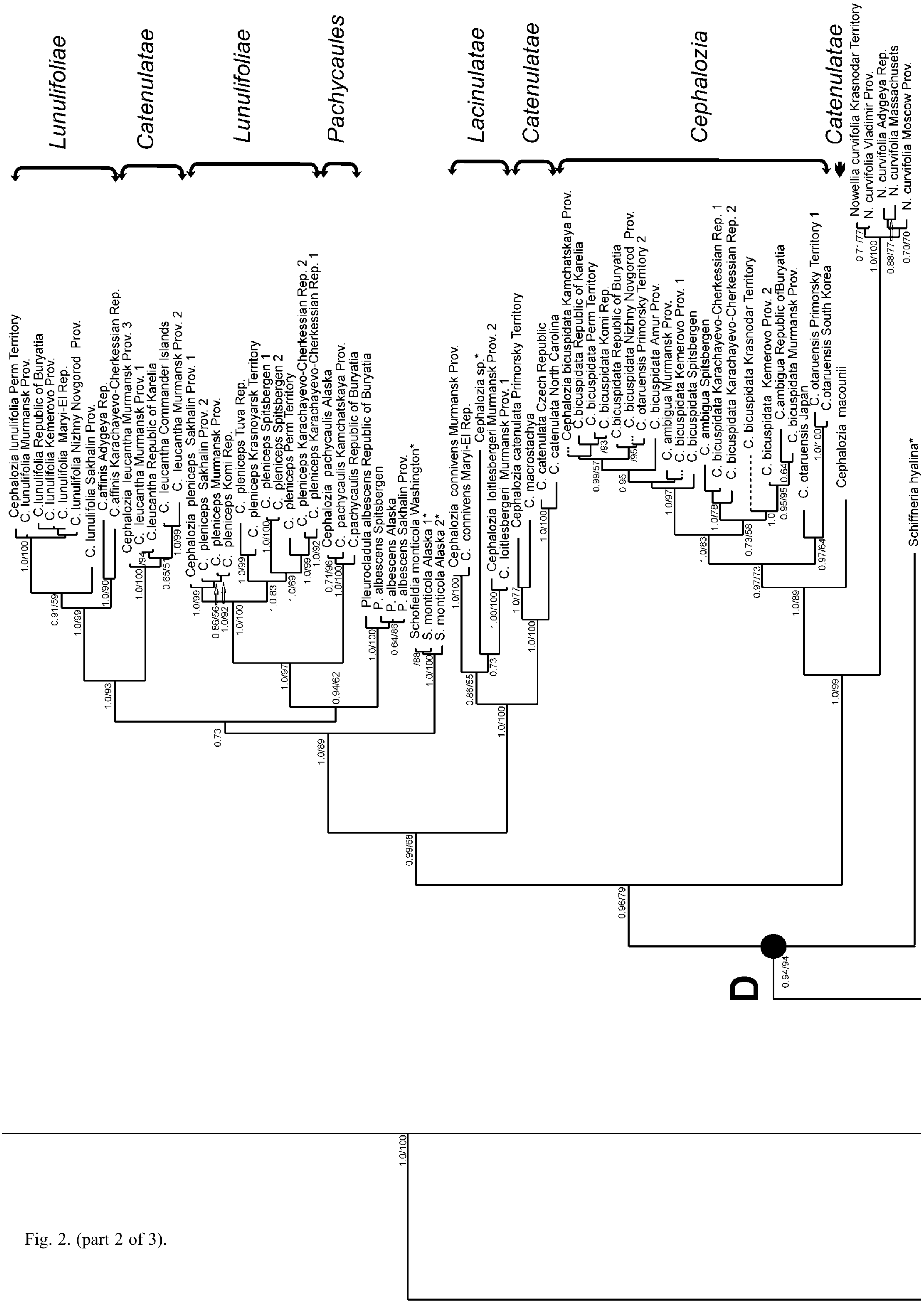
The Cephaloziellaceae (clade B) resolved in the unsupported relationship to the A+C+D+E clades in MP tree (Fig. 1), or sister to the A-clade in ML (BS=50%) and BA (PP=0.66) (Fig. 2).

The clades D and E were found to be sisters (BS<50% in MP, BS=99% in ML, PP=1.0 in BA) and consist of species from the Cephaloziaceae s.l. The genera *Cephalozia*, *Pleurocladula* Grolle, *Schofieldia* J.D. Godfrey, *Nowellia* and *Schiffneria* are resolved in clade D (BS=78% in MP with the exception of *Schiffneria*, BS=94% in ML, PP=0.94 in BA). On MP topology

Fig. 2 (part 1 of 3). Phylogenetic tree for the suborder Cephaloziineae, based on combined nucleotide sequences of ITS1-2 nrDNA and *trn*L-F cpDNA by Bayesian approach. Bayesian posterior probabilities/bootstrap support values calculated in ML analysis are indicated. Phyla with changeable position in ML and BA trees are shown by dotted line. Species with positions different in MP and BA trees are marked by asterisk.



Schiffneria is in sister position to the clades D+E (BS=98%, Fig. 1). The D-clade is splitted into two subclades. The first one includes generitype species, *C. bicuspidata,* which was found sister to *Nowellia* (BS=100% in MP, BS=99% in ML, PP=1.0 in BA). The second one falls into two subclades. One of them (BS=100% in MP, ML, PP=1.0 in BA) comprises *Cephalozia* species from sections *Catenulatae* R.M. Schust. (*C. macrostachya* and *C. catenulata)* and *Lacinulatae* R.M. Schust. (*C. connivens* and *C. loitlesbergeri*). The second subclade (BS=91% in MP, BS=89% in ML, PP=1.0 in BA) includes species previously assigned to 3 sections of *Cephalozia* (*Catenulatae* (*C. leucantha*), *Lunulifoliae* R.M. Schust. (*C. lunulifolia, C. affinis* and *C. pleniceps*)*,* and *Pachycaules* R.M. Schust. (*C. pachycaulis*)), and two monotypic genera, *Pleurocladula* and *Schofieldia*. *Cephalozia leucantha* was found to be nested together with specimens of *C. lunulifolia* and *C. affinis* (section *Lunulifoliae*) (BS=85% in MP, BS=93% in ML, PP=1.0 in BA). *C. pachycaulis* is clustered with *C. pleniceps* (BS=96% in MP, BS=97% in ML, PP=1.0 in BA). *Pleurocladula albescens* is sister to the clade of *C. pachycaulis* + *C. pleniceps* in all topologies (BS<50% in MP, BS=62% in ML, PP=0.94 in BA). *Schofieldia monticola*



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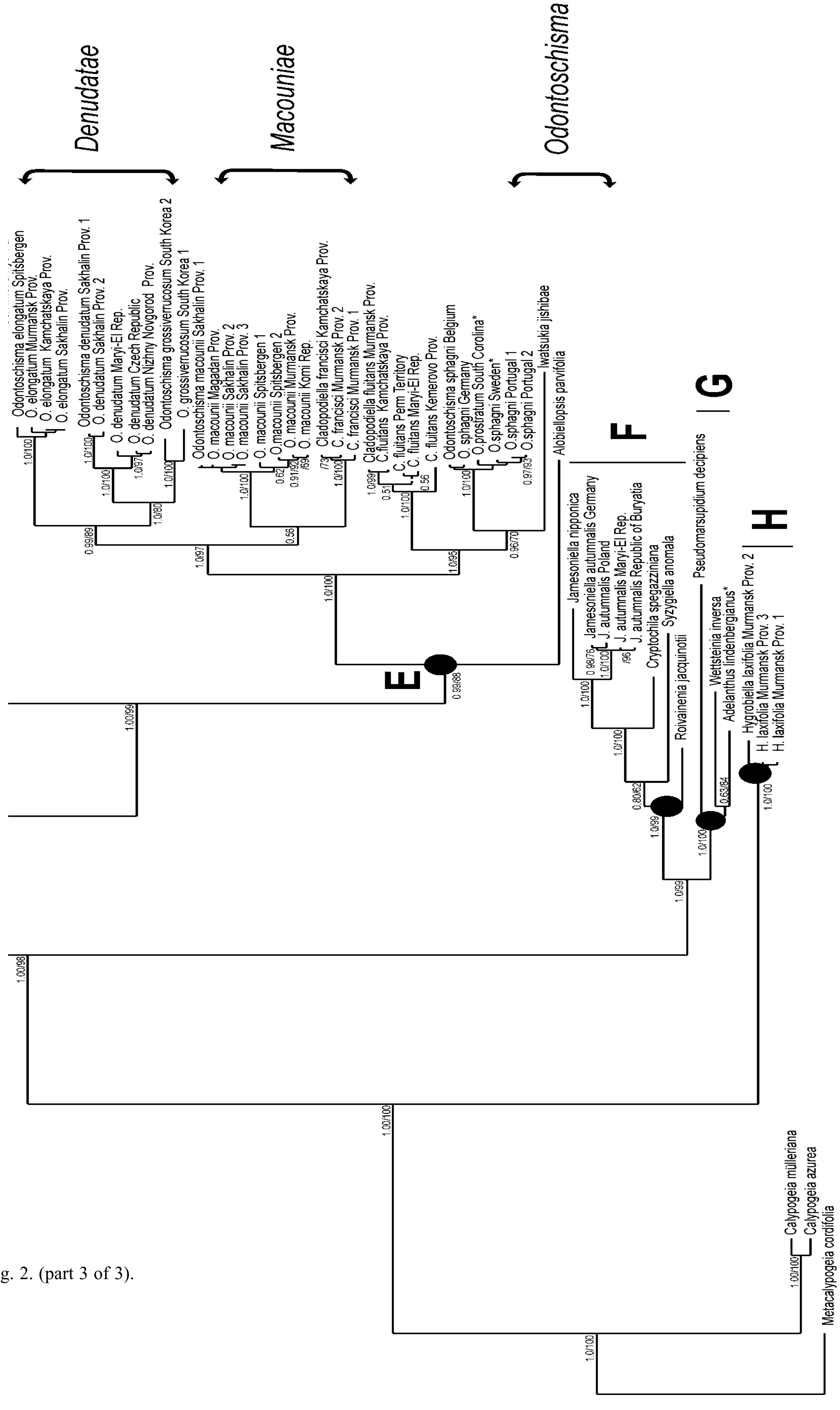

Fig. 2. (part 3 of 3).

is related to *C. pachycaulis* + *C. pleniceps* + *P. albescens* (BS=52% in MP) (Fig.1) or placed at the base of subclade composed of *C. leucantha, C. lunulifolia, C. affinis, C. pachycaulis, C. pleniceps,* and *P. albescens* (BS=89% in ML, PP=1.00 in BA) (Fig. 2).

The genera *Odontoschisma*, *Cladopodiella*, *Iwatsukia* N. Kitag. and *Alobiellopsis* R.M. Schust. are located in clade E (BS=73% in MP, BS=88% in ML, PP=0.99 in BA). Two species from the oligotypic genus *Cladopodiella* are intermingled in a clade with six species from the genus *Odontoschisma* and *Iwatsukia jishibae* (BS=100% in MP and ML, PP=1.0 in BA). *Cladopodiella francisci* turned out be sister to *O. macounii* (BS<50% in MP and ML, PP=0.56 in BA). *Cladopodiella fluitans* composed a clade with *O. prostartum, O. sphagni* and *Iwatsukia* (BS<50% in MP, BS=95% in ML, PP=1.0 in BA). The genus *Iwatsukia* was found in a sister relation to *O. prostartum* + *O. sphagni*-clade (BS=70% in ML, PP=0.96 in BA). *Alobiellopsis parvifolia* took up a basal position in clade E (BS=73% in MP, BS=88% in ML, PP=0.99 in BA).

The sister relationship of clade F (BS=100% in MP, BS=99% in ML, PP=1.0 in BA) (Jamessoniellaceae) and clade G (BS=99% in MP, BS=99% in ML, PP=1.0 in BA) (Adelanthaceae) got the highest supports (BS=100% in MP, BS=99% in ML, PP=1.0 in BA). The basal position on obtained trees belongs to clade H (BS=100% in both MP and ML, PP=1.0 in BA) containing samples from the monotypic genus *Hygrobiella* Spruce.

For species from genera *Cephalozia, Pleurocladula, Schofieldia, Nowellia, Odontoschisma* and *Cladopodiella, p*-distances for ITS1-2 and *trn*L-F loci between samples and species were calculated, and results alongside with their discussion would be presented in the following section.

DISCUSSION

1. **Family subdivision and relationships**

Analysis of the newly produced enlarged dataset for the suborder Cephaloziineae supported our previous conclusion (Vilnet *et al.*, 2010) concerning molecular phylogeny of the Scapaniaceae (clade A, Figs. 1, 2) and Anastrophyllaceae (clade C). The family Anastrophyllaceae proved to be separated from the Scapaniaceae after inclusion of clade B with representatives of the Cephaloziellaceae and *Protolophozia elongata* in ML and BA analyses (Fig. 2). *Protolophozia* and *Obtusifolium* were classified into the Scapaniaceae (Heinrichs *et al.*, 2005; Crandall-Stotler *et al.*, 2009), but their relation to this family still could not be supported robustly from molecular data (cf. Fig. 1 and Fig. 2). The implemented approach resolved the genus *Isophaches* which is placed now in the Anastrophyllaceae in basal position of this family or sister to clades A+C (Figs. 1, 2). Apparently, unstable position of these genera in different phylogenetic reconstructions could be explained by the absence of their extant relatives.

The Cephaloziellaceae (clade B) presented by the genera *Cephaloziella* (Spruce) Schiffn. (10 species) and *Cylindrocolea* (1 species), is found to be sister to the Scapaniaceae-clade (clade A) in BA and ML analyses with weak supports (Fig. 2). A similar relationship of the clade *Cephaloziella*+*Gymnocoleopsis multiflora* (Steph.) R.M. Schust. to the Scapaniaceae-clade without sufficient support was obtained by De Roo *et al.* (2007) in the analysis of *trn*G and *rps*4. The Cephaloziellaceae was resolved as a sister group to the Scapaniaceae+Anastrophyllaceae-clade in the analysis of five DNA loci of two *Cephaloziella* species and *Stenorrhipis madagascariensis* (Steph.) Grolle (Forrest *et al.*, 2006; with BS=70% in MP, PP=1.00 in BA) as well as on *rbc*L sequences of *Cylindrocolea recurvifolia* and three *Cephaloziella* species (Hentschel *et al.*, 2007; with BS=52% in MP and BS=80% in ML). In the current MP analysis the Cephaloziellaceae-clade appears near the tree base (Fig. 1), that has never been achieved before. Schuster (1980) accepted the Cephaloziellaceae in the closest affinity to the Cephaloziaceae s.l. even as a “merely a reduced extreme or subfamily”, but extended taxon sampling in molecular analysis suggests the Cephaloziellaceae as a lineage remote from the Cephaloziaceae s.l. and with unclear affinity.

Among ten studied by us genera of the Cephaloziaceae s.l., nine were combined in two sister clades D and E, whereas the genus *Hygrobiella* was separated and placed in the basal clade H (Figs. 1, 2). Basing on trigonous perianth, 2-stratose capsule wall, reduced seta, presence of hyalodermis, *etc.*, most authors placed this monotypic genus in the Cephaloziaceae s.l. (Schuster, 1974; Schljakov, 1979; Grolle, 1983, *etc.*). On the other hand, *Hygrobiella* differs significantly from the rest of the Cephaloziaceae s.l. in broad ventral merophytes with large bifid (leaf-like) underleaves, gynoecia and androecia on leading branches, capsule with all epidermal cell walls having similar thickenings, variable (1 or 2- seriate) antheridial stalk. Some of these features (*e.g.* broad ventral merophytes with large bifid, leaf-like underleaves) favored the segregation of *Hygrobiella* in a separate family Hygrobiellaceae (Jørg.) Konstant. & Vilnet. Müller (1954) was probably the first who published this family name, but without Latin diagnosis, thus making it illegetimate. Müller’s conception of Hygrobiellaceae, which included in addition to *Hygrobiella* also *Pleurocladula* and even *Anthelia,* met no wide acceptance by hepaticologists. Schuster (1974) noted quite isolated position of *Hygrobiella* and considered it in the monotypic subfamily Hygrobielloideae. Our data show that *Hygrobiella* does not relate to the Cephaloziaceae s.l., and be better classified as a separate family (Konstantinova & Vilnet, 2009).

Apart of *Hygrobiella,* the tree topologies support in general the monophyly of Cephaloziaceae s.l. (Schuster, 1974, 2002), with allocation of several subfamilies, particularly the Cephalozioideae, Schiffnerioideae, Odontoschismatoideae and Allobielloideae in two main subclades. But position of some genera, *e.g. Cladopodiella,* and species disagree with existing treatments.

Our results admit treating the Odontoschismataceae both as a subfamily of Cephaloziaceae s.l. or as a separate although closely related family. The latter seems to correspond better with morphological distinctions of the Odontoschismataceae including presence of oil-bodies, underleaves with numerous slime papillae, stem without hyalodermis, 2-3-stratose capsule wall, *etc.* The treatment of the Odontoschismatoideae as a distinct family with genera *Cladopodiella* and *Odontoschisma* has been proposed by Müller (1940) and then supported by Schljakov (1975).

Of three genera assigned by Schuster (2002) to the subfamily Alobielloideae, two were involved in this study (*Iwatsukia* and *Alobiellopsis*). The relation of the highly isolated disjunctively distributed genus *Iwatsukia* to the *Odontoschisma sphagni* + *O. prostartum*-clade got different supports, as well as the placement of the only studied species of the oligotypic genus *Alobiellopsis* in the basal phylum of clade E (Fig. 1, 2). Remote positions on the trees demonstrate isolation between *Alobiellopsis* and *Iwatsukia.* The taxonomy and phylogeny of poorly known subfamily Alobielloideae could be solved only with additional sampling of Southern Hemispheric species. Before that we include the Alobielloideae in the Odontoschismataceae with some doubt.

The position of the isolated genus *Schiffneria* in close relationshop to Cephaloziaceae s. str. is highly supported in ML/BA trees (Fig. 2) and agrees with the previous results (He-Nygren *et al.*, 2006; Forrest *et al.*, 2006). However MP tree indicates *Schiffneria* reliable relationship to both Cephaloziaceae s.str. and Odontoschismataceae (Fig. 1). Earlier the genus has been classified in the monotypic subfamily Schiffnerioideae R.M. Schust. (Schuster, 1972). As only the *trn*L-F sequence for *Schiffneria* has been studied, we hesitate to provide any definite conclusion.

Thus, at present we accept the Cephaloziaceae in a narrow circumscription, as well as the Odontoschismataceae and Hygrobiellaceae.

2. **Genera subdivision and relationships**

Almost half of the worldwide species diversity of the genera *Cephalozia* and *Odontoschisma* were included in the present study. On the trees both genera were found as non-monophyletic, and the obtained species relationships partially agree with the existing infrageneric systems.

All studied here *Cephalozia* species belong only to one of four recognized by Schuster (1974) subgenera of the *Cephalozia*, particularly to the largest and more widespread subgenus *Cephalozia*. It was found to be not monophyletic, due to *Pleurocladula, Schofieldia* and *Nowellia* nested within it.

One most striking result is that *C. bicuspidata*-complex (including *C. ambigua* and *C. otaruensis*) and *C. macounii* is placed in the clade related to *Nowellia,* not to other species of the subgenus *Cephalozia.* Schuster (1974) considered the "*Bicuspidata*-complex" as the most primitive in the subgenus *Cephalozia,* which differs from the rest of *Cephalozia* species by ability to develop secondary pigmentation, the simply bifid bracts and bracteole without marginal dentation; subtransverse non-decurrent leaves with leaf insertion dorsally approaching stem midline with no more than one cell row free of leaf bases. The genus *Nowellia* shares all above mentioned features with this complex. This fact evidently allowed Spruce (1882) to treat *Nowellia* as a synonym of *Cephalozia,* because *Nowellia* "has no true character which is not shared by other true Cephalozias". Nevertheless, basing on its striking appearance, *Nowellia* has been always treated as a distinct genus (Schuster, 1974; Schljakov, 1979; Grolle, 1983, *etc.*). The branch length of the *Nowellia*-clade suggests its rather distant affinity to the *Cephalozia bicuspidata*-clade and, together with distinct morphology, allows to keep *Nowellia* as a separate genus.

The rest of studied *Cephalozia* species are intermingled in one clade with *Pleurocladula* and *Schofieldia.* The two latter genera were considered by Schuster (1974, 1995) as taxa characterized by many generalized features. Schuster (1993, 1995) discussed in detail these taxa and suggested that *Schofieldia, Pleurocladula* and *Cephalozia pachycaulis* "seem to occupy a special evolutionary niche in the Cephalozioideae". These taxa share a number of plesiomorphic features (Schuster, 1995): thin-walled, not pigmented polygonal or rectangular cells without oil-bodies, fleshy stem without hyalodermis, *Frullania*-type or lateral-intercalary branching, *etc.* The most striking is *Schofieldia*. It has *Schistochilopsis*-like or scapanioid aspect, disticous-leaved shoots with dense loosely conduplicate-canaliculate leaves, small lamellate underleaves, characteristic gemmae formation on specialized, cylindrical stalks, formed of 3-4 superposed cells. It is "the most interesting endemic hepatic discovered in North America this century" (Schuster, 1995: 40), and at the same time "it remains somewhat uncertain" whether *Schofieldia* should be retained in Cephalozioideae or "placed in its own family" (l.c.). In spite of dubious position of *Schofieldia* on trees, in our result it is always nested within *Cephalozia* (Figs. 1, 2). Schuster (1974) supposed relationship of *Pleurocladula* to *C. bicuspidata* or *C. pleniceps*. Schljakov (1979) considered *Pleurocladula* in affinity to *Hygrobiella* and classified both genera in the subfamily Hygrobielloideae. Our analysis supports affinity of circumpolar arctic-montane *Pleurocladula* to *C. pachycaulis* and *C. pleniceps*.

The sections subdivision of *Cephalozia* proposed by Schuster (1974) partly corresponds with the obtained trees topologies (Figs. 1, 2). Clustered together, *C. macrostachya* and *C. catenulata* from section *Catenulatae* were found in a sister position to closely allied and morphologically quite similar species *C. connivens* and *C. loitles-*

bergeri from the section *Lacinulatae*. Previously classified in section *Catenulatae* (Schuster, 1974), *C. leucantha* was found in a clade with *C. lunulifolia* from the *Lunulifoliae. Cephalozia leucantha* differs from the species of section *Catenulatae* in non dentate lobes of female bracts and bracteoles and pale green or whitish color, sharing these features with species from section *Lunulifoliae.* Schuster (1974) noted that it was "more distantly allied" to another species of section *Catenulatae*, but supposed that *C. leucantha* "to some extend… bridges the gap" between sections *Cephalozia* and *Catenulatae*, which was not supported by our results as well. Two species assigned by Schuster (1974) to the section *Lunulifoliae* (*C. lunulifolia* and *C. pleniceps*) were found in distinct clades. Close relationships of *P. pachycaulis* from the monotypic section *Pachycaules* to *C. pleniceps* noted by Schuster (1993) is well supported by their sister position in our analysis.

According to obtained trees, the perimeter of the former *Cephalozia* should be reevaluated. We propose to keep the name *Cephalozia* for *C. bicuspidata*-complex and *C. macounii*, because *C. bicuspidata* is a generitype of *Cephalozia*. We segregate the rest of *Cephalozia, Schofieldia* and *Pleurocladula* in a separate genus to avoid the establishing of several mono- and oligotypic genera. According to priority, this genus has to be named *Pleurocladula.*

As discussed above, the obtained trees support the treatment of *Cladopodiella* in the Odontoschismataceae. The type species of *Cladopodiella* (*Cladopodiella fluitans*) is placed with the type species of *Odontoschisma* (*Odontoschisma sphagni*), whereas *Cladopodiella francisci* was found in a weakly supported sister relationship to *Odontoschisma macounii* (monotypic section *Macouniae* R.M. Schust.). Majority of researches noted the phylogenetic affinity of *Cladopodiella* to *Cephalozia* and treated it in the subfamily Cephalozioideae (Arnell, 1956; Schuster, 1974; Grolle, 1983). Schljakov (1979) placed *Cladopodiella* in the Odontoschismataceae basing on features common with *Odontoschisma*: absence of hyalodermis, presence of oil-bodies in leaves cells, similarity in sporophyte anatomy, *etc.* Later Schuster (2002: 80) assumed that *Cladopodiella* "is probably best assigned to the Odontoschismatoideae" as well. The obtained here location of *Cladopodiella* within the *Odontoschisma*-clade support their presumable relationships, but clusterization of species from both genera in intermingled subclades is hard to be explained.

In general, section subdivision of *Odontoschisma* suggested by Schuster (1974) is well supported here. Morphologically similar species *Odontoschisma denudatum* and *O. elongatum* that sometimes were treated as subspecies (Potemkin, 1998) compose sister clades, which agrees with their segregation in the section *Denudatae* R.M. Schust. East Asiatic species *O. grossiverrucosum* fits well in this section as well. *Odontoschisma maconii* from *Macouniae* is placed a separate lineage, *O. prostartum* and *O. sphagni* from section *Odontoschisma* compose a clade.

3. **Infraspecific variation**

Infraspecific variation of ITS1-2 and *trn*L-F sequences in the genus *Cephalozia* is higher than in the *Odontoschisma*. The highest level of DNA variability was found for multiply sampled *C. pleniceps* (pd=0-3.9 % for ITS1-2, and 0-3% for *trn*L-F) and *C. lunulifolia* (pd=0-3.2% for ITS1-2, and 0-2.5% for *trn*L-F). Two samples of *C. affinis* from Caucasus are located in the separate clade sister to *C. lunulifolia* (pd=3.1-4% for ITS1-2, and 3.2-4.8% for *trn*L-F). This taxon was synonymized with *C. lunulifolia* by Grolle (1955) and some authors followed this treatment (Schljakov, 1979). According to Schuster (1974: 795), "the inflorescence seems to be the sole reliable difference for separating the two taxa". Our data rather supported the treatment of *C. affinis* as a separate species. But it is also possible to explain the difference of the Caucasian plants by long isolation of populations, similar to that shown for *Jubula hutchinsiae* subsp. *caucasica* (Konstantinova & Vilnet, 2011).

Three taxa from the *C. bicuspidata*-complex (*C. bicuspidata, C. ambigua, C. otaruensis*) are intermingled in one clade. The value of *p*-distances between the representatives of this clade varies from 0.1 to 5.2% for ITS, and from 1-2.0 to 3.3% for *trn*L-F. Separate analyses of ITS1-2 and *trn*L-F dataset (not shown) for this group revealed the incongruence between single locus based trees, moreover, most specimens apparently possess several copies of ITS1-2. We failed to find any morphological justification for smaller clades found in the *C. bicuspidata*-clade. To clarify relation in the *C. bicuspidata*-complex more careful study should be implemented.

Other studied *Cephalozia* species are characterized by low level of nucleotide sequence variation, as in the case for *Odontoschisma* species. The populations of *O. elongatum* from remote localities possessed an identical *trn*L-F sequences, and only a sample from Svalbard differed in ITS1-2 (pd=0-0.5%) from Murmansk and Kamchatka populations. One specimen of *O. denudatum* from the Kuril Islands was separated from European populations (pd=1.2% for ITS1-2, and 0.1% for *trn*L-F). The Far Eastern *O. macounii* ITS1-2 sequences differed by 0.5% and *trn*L-F – by 0.6 % from those of European populations. Thus, processes of diversification are presented in remote populations of *Odontoschisma,* but their level is quite low compared with *Cephalozia*. For American sample of *O. prostratum* and European samples of *O. sphagni,* full identity of *trn*L-F loci was achieved. Several substitutions in ITS1-2 (pd=0-0.5%) could be assigned rather to infraspecific variability than to interspecific one. These taxa are quite similar morphologically and differ "in only minor and inconstant features" (Schuster, 1974: 860), particularly leaves in *O. sphagni* are rotundate, more or less concave and antically secund, whereas in *O. prostartum,* leaves are usually distinctly longer than broad, hardly concave as well as more distinctly bordered. But all these features are very malleable and occur in different combinations. Obtained molecular data rather support the conspecificity *O. prostartum* and *O. sphagni*.

TAXONOMICAL REARRANGEMENTS

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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. Sequences from our previous studies are underlined, sequences downloaded from GenBank are in bold.

Taxon	Herbarium voucher	Accession no.	
		*trn*L-F	ITS1-2
Adelanthus lindenbergianus (Lehm.) Mitt.	Chile, Holz, 25 (GOET)	GQ900177	GQ899969
Alobiellopsis parvifolia (Steph.) R.M. Schust.	Japan, Bryophytes of Asia Fasc. 8 #191 (KPABG)	JX630020	JX629894
Anastrepta orcadensis (Hook.) Schiffn.	Russia, Republic of Buryatia, Konstantinova, 59-1-01 (KPABG)	DQ875088	DQ875126
Anastrophyllum sphenoloboides R.M. Schust.	Norway, Spitsbergen, Konstantinova & A. Savchenko, K 50-3-06 (KPABG)	EU791662	EU791777
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	Netherlands, Konstantinova, 3b-5-99 (KPABG)	EU791676	EU791779
B. hatcheri (A. Evans) Loeske	Norway, Spitsbergen, Konstantinova & A. Savchenko, K 60-4-06 (KPABG)	EU791674	EU791781
B. lycopodioides (Wallr.) Loeske	Russia, Murmansk Prov., Konstantinova,16-4-00 (KPABG)	EF090627	EF090632
Biantheridion undulifolium (Nees) Konstant. & Vilnet	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 85-1-02 (KPABG)	EU791672	EU791795
Calypogeia azurea Stotler & Crotz	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 20-01 (KPABG)	JX630063	JX629936
C. muelleriana (Schiffn.) Müll.Frib.	Russia, Perm Territory, Konstantinova, K 367-1-04 (KPABG)	JX630062	JX629935
Cephalozia sp.	Russia, Primorsky Territory, V. Bakalin P-61-7-08 (KPABG)	JX630029	JX629903
Cephalozia affinis Lindb. ex Steph.	Russia: Adygeya Rep., Konstantinova, K473-2-07 (KPABG)	JX629952	JX629827
C. affinis	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 400-8-05 (KPABG)	JX629951	JX629825
C. ambigua C. Massal.	Norway, Spitsbergen, Konstantinova, K109-1-04 (KPABG)	JX630026	JX629900
C. ambigua	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 76-1-02 (KPABG)	JX630023	JX629897
C. ambigua	Russia, Murmansk Prov., O. Belkina, B 72/6-10 (KPABG)	JX630022	JX629896

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
C. bicuspidata (L.) Dumort.	Norway, Spitsbergen, Konstantinova, K 103-3-04 (KPABG)	JX629939	JX629813
C. bicuspidata	Russia, Amur Prov., V. Bakalin, 37-11-00 (KPABG)	JX629941	JX629817
C. bicuspidata	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 84-2-01 (KPABG)	JX629942	JX629811
C. bicuspidata 1	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K318-3-08 (KPABG)	JX630024	JX629898
C. bicuspidata 2	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 488-2-05 (KPABG)	JX629949	JX629820
C. bicuspidata	Russia, Kamchatskaya Prov., V. Bakalin, K 50-30-02-VB (KPABG)	JX629947	JX629818
C. bicuspidata	Russia, Republic of Karelia, V. Bakalin, 109280 (KPABG)	JX629944	JX629814
C. bicuspidata 1	Russia, Kemerovo Prov., Konstantinova, 60-2-00 (KPABG)	JX629937	JX629810
C. bicuspidata 2	Russia, Kemerovo Prov., Konstantinova, K 61-4-00 (KPABG)	JX629938	JX629821
C. bicuspidata	Russia, Komi Rep., M. Dulin, 234MVD, 103615 (KPABG)	JX629943	JX629812
C. bicuspidata	Russia, Krasnodar Territory, Konstantinova & A. Savchenko, K449-3-08 (KPABG)	JX630025	JX629899
C. bicuspidata	Russia, Murmansk Prov., Konstantinova, 196-3-02 (KPABG)	JX629948	JX629819
C. bicuspidata	Russia, Nizhny Novgorod Prov., Konstantinova, 133-2-03 (KPABG)	JX629946	JX629816
C. bicuspidata	Russia, Perm Territory, Konstantinova, K 324-2-04 (KPABG)	JX629945	JX629815
C. catenulata (Huebener) Lindb.	Czech Republic, Konstantinova, 103548 (KPABG)	JX629961	JX629834
C. catenulata	Russia, Primorsky Territory, V. Bakalin, P-4-2-10 (KPABG)	JX630030	JX629904
C. catenulata	USA, North Carolina, Konstantinova, 07.06.1992 (KPABG)	JX629960	JX629835
C. connivens (Dicks.) Lindb.	Russia, Maryi-El Rep., Konstantinova, K 451-3-04 (KPABG)	JX629962	JX629842
C. connivens	Russia, Murmansk Prov., E. Borovichev, BE 25-12-09 (KPABG)	JX629963	JX629843
C. leucantha Spruce	Russia, Commander Islands, V. Bakalin, K-22-12-02-VB (KPABG)	JX629965	JX629838
C. leucantha	Russia, Republic of Karelia, V. Filin, 100405 (KPABG)	JX629967	JX629840
C. leucantha 1	Russia, Murmansk Prov., Konstantinova, 193-10-02 (KPABG)	JX629968	JX629841
C. leucantha 2	Russia, Murmansk Prov., Konstantinova, K 207-5-07 (KPABG)	JX629964	JX629837
C. leucantha 3	Russia, Murmansk Prov., V. Bakalin, VB 29-7-01 (KPABG)	JX629966	JX629839
C. loitlesbergeri Schiffn. 1	Russia, Murmansk Prov., Konstantinova, 44-10-03 (KPABG)	JX629970	JX629845
C. loitlesbergeri 2	Russia, Murmansk Prov., Konstantinova, 503-8-04 (KPABG)	JX629969	JX629844
C. lunulifolia (Dumort.) Dumort.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 33-1-01 (KPABG)	JX629959	JX629833
C. lunulifolia	Russia, Kemerovo Prov., Konstantinova, 84-2-00 (KPABG)	JX629958	JX629832
C. lunulifolia	Russia, Maryi-El Rep., Konstantinova, 464-2-04 (KPABG)	JX629956	JX629830
C. lunulifolia	Russia, Murmansk Prov., Konstantinova, 193-2-89 (KPABG)	JX629957	JX629831
C. lunulifolia	Russia, Nizhny Novgorod Prov., Konstantinova, 107-1-03 (KPABG)	JX629954	JX629829
C. lunulifolia	Russia, Perm Territory, Konstantinova, K 343-1-04 (KPABG)	JX629953	JX629828
C. lunulifolia	Russia, Sakhalin Prov., J.Harpel & V. Czerdantseva, 26934 (KPABG)	JX629955	JX629826
C. macounii (Austin) Austin	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 48-4-01 (KPABG)	no data	JX629824
C. macrostachya Kaalaas	USA, North Carolina, Konstantinova, 07.06.1992 (KPABG)	JX629971	JX629836
C. otaruensis Steph.	Japan, Bryophytes of Asia #220 (KPABG)	JX629950	JX629823
C. otaruensis 1	Russia, Primorsky Territory, V. Bakalin, P-50-4-08 (KPABG)	JX630028	JX629902
C. otaruensis 2	Russia, Primorsky Territory, V. Bakalin, P-74-68-05 (KPABG)	JX630027	JX629901
C. otaruensis	South Korea, Gangwon-do, S.-S. Choi, Hepaticae Korea Exsiccatae Fasc. I. # 95 (KPABG)	JX630020	JX629895

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
C. pachycaulis R.M. Schust.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko,, 117-01 (KPABG)	JX629972	JX629846
C. pachycaulis	Russia, Kamchatskaya Prov., V. Bakalin, 82-3-01-VB (KPABG)	JX629973	JX629847
C. pachycaulis .	USA, Alaska, Konstantinova, 114-1d (KPABG)	JX629974	JX629848
C. pleniceps (Austin) Lindb. 1	Norway, Spitsbergen, Konstantinova, K 115-1-06 (KPABG)	JX629984	JX629855
C. pleniceps 2	Norway, Spitsbergen, Konstantinova, K 142-2-04 (KPABG)	JX629984	JX629854
C. pleniceps 1	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 314-1-08 (KPABG)	JX629975	JX629849
C. pleniceps 2	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 321-2-08 (KPABG)	JX629981	JX629851
C. pleniceps	Russia, Komi Rep., M. Dulin, 719mvd, 112071 (KPABG)	JX629976	JX629856
C. pleniceps	Russia, Krasnoyarsk Territory, V. Fedosov, 107972 (KPABG)	JX629982	JX629852
C. pleniceps	Russia, Murmansk Prov., Konstantinova, K 200-6-08 (KPABG)	JX629978	JX629858
C. pleniceps	Russia, Perm Territory, Konstantinova, K339-1-04 (KPABG)	JX629980	JX629850
C. pleniceps 1	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, K-82-17-04 (KPABG)	JX629979	JX629859
C. pleniceps 2	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, K 82-18-04 (KPABG)	JX629977	JX629857
C. pleniceps	Russia, Tuva Rep., V. Bakalin, VB-99-6-1…33 (KPABG)	JX629983	JX629853
Cephaloziella sp.	Russia, Republic of Buryatia, O. Afonina, A4805 (KPABG)	JX630049	JX629920
Cephaloziella stellulifera (Taylor ex Spruce) Schiffn.	Netherlands, Konstantinova, 1e-2-99 (KPABG)	JX630042	JX629923
C. arctogena (R.M.Schust.) Konstant.	Russia, Republic of Buryatia, O. Afonina 45907 (KPABG)	JX630045	JX629916
C. aspericaulis Jørg.	Russia, Republic of Buryatia, O. Afonina 5307 (KPABG)	JX630044	JX629917
C. divaricata (Sm.) Schiffn.	Russia, Republic of Buryatia, O. Afonina, A07408 (KPABG)	JX630050	JX629921
C. elachista (J.B.Jack ex Gottsche & Rabenh.) Schiffn.	Russia, Khanty-Mansi Aotonomous Area, G. Kukurichkin, OP1BH607/7 (KPABG)	JX630047	JX629918
C. polystratosa (R.M. Schust. et Damsh.) Konstant.	Russia, Republic of Buryatia, O. Afonina, A1810 (KPABG)	JX630046	no data
C. rubella (Nees) Warnst.	Russia, Khanty-Mansi Aotonomous Area, G. Kukurichkin, OP1BH607/1 (KPABG)	JX630048	JX629919
C. spinicaulis Douin	Japan, Deguchi, Ex 5 (1998) IV 119 (KPABG)	JX630043	JX629922
C. varians (Gottsche) Steph.	Russia, Kamchatskaya Prov., V. Bakalin, K-105-5-03 (KPABG)	JX630051	JX629924
Cladopodiella fluitans (Nees) H. Buch	Russia, Kamchatskaya Prov., V. Bakalin, K-13-7-03 (KPABG)	JX630012	JX629885
C. fluitans	Russia, Kemerovo Prov., Konstantinova, 81-2-00 (KPABG)	JX630011	JX629884
C. fluitans	Russia, Maryi-El Rep., Konstantinova, K 455-5a-04 (KPABG)	JX630009	JX629882
C. fluitans	Russia, Murmansk Prov.,Yu. Mamontov, YuSM-36-2011/1 (KPABG)	JX630041	JX629915
C. fluitans	Russia, Perm Territory, A. Bezgodov, AB 667-94 (KPABG)	JX630010	JX629883
C. francisci (Hook.) Jørg.	Russia, Kamchatskaya Prov., V. Bakalin, K-10-10-03 (KPABG)	JX630015	JX629888
C. francisci 1	Russia, Murmansk Prov., Konstantinova, 67-97 (KPABG)	JX630013	JX629886
C. francisci 2	Russia, Murmansk Prov., Konstantinova, 114-3-87 (KPABG)	JX630014	JX629887
Cryptochila spegazziniana (Spruce) Grolle	Argentina, Drehwald, 910171A (GOET)	**GQ900189**	**GQ899980**
Cylindrocolea recurvifolia (Steph.) Inoue	Japan, Bryophytes of Asia #344 (KPABG)	JX630061	no data
Diplophyllum albicans (L.) Dumort.	Russia, Karachaevo-Cherkesia Rep., Konstantinova & A. Savchenko, K446-7-05 (KPABG)	EU791659	EU791773
D. taxifolium (Wahlenb.) Dumort.	Russia, Republic of Karelia, V. Bakalin, 28.07.1998 (KPABG)	AY327762	EU791772
Douinia imbricata (M. Howe) Konstant. & Vilnet	USA, Alaska, Konstantinova, 110-2-92a (KPABG)	EU791658	EU791770

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
D. ovata (Dicks.) H. Buch	USA, Washington, A. Potemkin, 95/401 (KPABG)	AY327778	no data
D. ovata	USA, Washington, Konstantinova, A116-95 (KPABG)	no data	EU791771
D. plicata (Lindb.) Konstant. & Vilnet	Russia, Kamchatskaya Prov., V. Bakalin, 22.08.2001	AF519198	EU791768
Gymnocolea inflata (Huds.) Dumort.	Norway, Spitsbergen, Konstantinova, 118-1-04 (KPABG)	EU791661	EU791787
Hygrobiella laxifolia (Hook.) Spruce 1	Russia, Murmansk Prov., Konstantinova, 15-1-98 (KPABG)	JX630052	JX629933
H. laxifolia 2	Russia, Murmansk Prov., Konstantinova, 361-3-00 (KPABG)	JX630053	JX629932
H. laxifolia 3	Russia, Murmansk Prov., Konstantinova, K201-1-04 (KPABG)	JX630054	JX629931
Isopaches bicrenatus (Hoffm.) H. Buch	Russia, Yakutia, V. Bakalin, 18.07.2000 (KPABG)	AY327788	EU791797
Iwatsukia jishibae (Steph.) Kitag.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 48-1-01 (KPABG)	EU791680	EU791798
Jamesoniella autumnalis (DC.) Steph.	Germany, Schroeder, 8327/2 (JE)	**GQ900198**	**GQ899989**
J. autumnalis	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 103-1-01 (KPABG)	EU791721	EU791845
J. autumnalis	Russia, Maryi-El Rep., Konstantinova, K 448-5-04 (KPABG)	EU791720	EU791844
J. autumnalis	Poland, Jedrzeiko & Zarnowiec, 151 (JE)	**GQ900201**	**GQ899991**
Jamesoniella nipponica S. Hatt.	China, Zhu, 20060728-14 (HSNU)	**GQ900208**	**GQ899998**
Lophozia ascendens (Warnst.) R. M. Schust.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 109-3-01 (KPABG)	DQ875054	DQ875089
L. lantratoviae Bakalin	Russia, Republic of Buryatia, V. Bakalin, 76-7-01 (KPABG)	DQ875055	DQ875090
L. silvicoloides N. Kitag.	Russia, Murmansk Prov., Konstantinova, 356-4-00 (KPABG)	DQ875064	DQ875099
L. wenzelii (Nees) Steph. var. *litoralis* (S.W. Arnell) Bakalin	Russia, Murmansk Prov., V. Bakalin,12-3-02 (KPABG)	DQ875074	DQ875110
Lophoziopsis excisa (Dicks.) Konstant. & Vilnet	Norway, Spitsbergen, Konstantinova, K-21-2-05 (KPABG)	DQ875058	DQ875093
L. pellucida (R. M. Schust.) Konstant. & Vilnet	Russia, Murmansk Prov., Konstantinova, 39-2a-03 (KPABG)	EF065687	EF065695
Macrodiplophyllum microdontium (Mitt.) Perss.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 146/12-01 (KPABG)	AF519199	EU791769
Metacalypogeia cordifolia (Steph.) H. Inoue	Russia, Primorsky Territory, V. Bakalin, P-66-18a-06 (KPABG)	JF421597	JX629934
Neoorthocaulis attenuatus (Mart.) L. Söderstr., De Roo, & Hedd.	Russia, Sakhalin Prov., Harpel, Cherdantseva, 105728 (KPABG)	EU722343	EU727538
N. binsteadii (Kaal.) L. Söderstr., De Roo & Hedd.	Russia, Amur Prov, V. Bakalin, 34-3-00VB (KPABG)	EU722345	EU727540
N. floerkei (E. Weber & D. Mohr) L. Söderstr., De Roo & Hedd.	Russia, Perm Territory, Konstantinova, K 322-4-04 (KPABG)	EU722347	EU727542
Nowellia curvifolia (Dicks.) Mitt.	Russia, Adygeya Rep., Konstantinova, K 488-2-07 (KPABG)	JX629993	JX629889
N. curvifolia	Russia, Krasnodar Territory, Konstantinova, K 123-2-09 (KPABG)	JX629994	JX629890
N. curvifolia	Russia, Moscow Prov., A. Obuchova, 112973 (KPABG)	JX629995	JX629891
N. curvifolia	Russia, Vladimir Prov., Yu. Kokoshnikova, 112328 (KPABG)	JX629996	JX629892
N. curvifolia	USA, Massachusets, Konstantinova, ACH-10-92 (KPABG)	JX629997	JX629893
Obtusifolium obtusum (Lindb.) S.W. Arnell	Russia, Murmansk Prov., V.A. Bakalin, 01.07.2001 (KPABG)	AY327769	no data
O. obtusum	Russia, Perm Territory, Konstantinova, K-315-1-04 (KPABG)	no data	DQ875118
Odontoschisma denudatum (Moart.) Dumort.	Czech Republic, Konstantinova, 103546 (KPABG)	JX630008	JX629877
O. denudatum	Russia, Maryi-El Rep., Konstantinova, K 450a-04 (KPABG)	JX630005	JX629874
O. denudatum	Russia, Nizhny Novgorod Prov., Konstantinova 164-1-03 (KPABG)	JX630007	JX629876
O. denudatum 1	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, 110284 (KPABG)	JX630006	JX629875

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
O. denudatum 2	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, K-48-26-07 (KPABG)	JX630032	JX629906
O. elongatum (Lindb.) A. Evans	Norway, Spitsbergen, Konstantinova, K 142-1-04 (KPABG)	JX630001	JX629870
O. elongatum	Russia, Kamchatskaya Prov., V. Bakalin, 107-9-03 (KPABG)	JX630003	JX629872
O. elongatum	Russia, Murmansk Prov., Konstantinova, K 202-2-07 (KPABG)	JX630004	JX629873
O. elongatum	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, K 125-39-04 (KPABG)	JX630002	JX629871
O. grossiverrucosum Steph. 1	South Korea, Gangwon-do, S.-S. Choi, Hepaticae Korea Exsiccatae Fasc. I. # 97 (KPABG)	JX630037	JX629911
O. grossiverrucosum 2	South Korea, KyongNam Prov., V. Bakalin, Kor-11-11d-09 (KPABG)	JX630038	JX629912
O. macounii (Austin) Underw. 1	Norway, Spitsbergen, Konstantinova, K 65-3-06 (KPABG)	JX630000	JX629869
O. macounii 2	Norway, Spitsbergen, Konstantinova, K101-2-10 (KPABG)	JX630036	JX629910
O. macounii	Russia, Komi Rep., M. Dulin, 258 MVD, 103620 (KPABG)	JX629998	JX629867
O. macounii	Russia, Magadan Prov., V. Bakalin, Mag-7-1-10 (KPABG)	JX630031	JX629905
O. macounii	Russia, Murmansk Prov., Konstantinova, 45-2-98 (KPABG)	JX629999	JX629868
O. macounii 1	Russia, Sakhalin Prov., V. Bakalin, S-27-22-06 (KPABG)	JX630035	JX629909
O. macounii 2	Russia, Sakhalin Prov., V. Bakalin, S-32-27b-06 (KPABG)	JX630034	JX629908
O. macounii 3	Russia, Sakhalin Prov., V. Bakalin, S-61-31-09 (KPABG)	JX630033	JX629907
O. prostratum (Sw.) Trevis.	USA, South Corolina, Konstantinova, 07.06.1992 (KPABG)	JX630016	JX629881
O. sphagni (Dicks.) Dumort.	Belgium, H. van Melick, 209263 (KPABG)	JX630019	JX629880
O. sphagni	Germany, H. van Melick, 211710 (KPABG)	JX630018	JX629879
O. sphagni 1	Portugal, H. van Melik, 211510 (KPABG)	JX630040	JX629914
O. sphagni 2	Portugal, H. van Melik, 211528 (KPABG)	JX630039	JX629913
O. sphagni	Sweden, H. van Melick, 209256 (KPABG)	JX630017	JX629878
Pleurocladula albescens (Hook.) Grolle	Norway, Spitsbergen, Konstantinova, K 148-1a-04 (KPABG)	JX629989	JX629863
P. albescens	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 133-3-01 (KPABG)	JX629991	JX629865
P. albescens	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin K 100-14-04 (KPABG)	JX629990	JX629864
P. albescens	USA, Alaska, Konstantinova, 90-1-92b (KPABG)	JX629992	JX629866
Plicanthus birmensis (Steph.) R.M. Schust.	Russia, Primorsky Territory, V. Bakalin, P-76-5-05 (KPABG)	EU791668	EU791791
Protolophozia elongata (Steph.) Schljakov	Russia, Murmansk Prov., V. Bakalin, 3-1-02 (KPABG)	DQ875078	DQ875116
Pseudolophozia debiliformis (R.M. Schust. & Damsh.) Konstant. & Vilnet	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 510-1-05 (KPABG)	EF065685	EF065692
P. sudetica (Nees ex Huebener) Konstant. & Vilnet	Russia, Murmansk Prov., V. Bakalin, 4.06.1998 (KPABG)	AF519195	DQ875113
Pseudomarsupidium decipiens (Hook.) Grolle	Mexico, Gradstein & Velasquez s.n. (GOET)	**GQ900218**	**GQ900008**
Pseudotritomaria heterophylla (R.M. Schust.) Konstant. & Vilnet	Russia, Krasnoyarskiy Territory, V. Fedosov, 107960 (KPABG)	EU791687	EU791806
Roivainenia jacquinotii (Mont.) Grolle	Argentina, Milde & Busch Bryo 1880 (GOET)	**GQ900220**	**GQ900010**
Saccobasis polymorpha (R.M. Schust.) Schljakov	Russia, Murmansk Prov., Konstantinova, 21-3b-96 (KPABG)	EU791688	EU791807
Scapania americana Müll. Frib.	USA, Washington, Konstantinova, A 22-6a-95 (KPABG)	EU791655	EU791764
S. ampliata Steph.	South Korea, KyongNam Prov., V. Bakalin, Kor-11-16a-09 (KPABG)	JX630055	JX629929
S. apiculata Spruce	Russia, Republic of Buryatia, Konstantinova, Hepaticae Rossica Exsiccatae № 49 (KPABG)	EU791633	EU791741
S. aspera Bernet & M. Bernet	Belgium, Konstantinova, 2-20-3-99 (KPABG)	EU791627	EU791735

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
S. bolanderi Austin	USA, Washington, Konstantinova, A10-4a-95 (KPABG)	EU791657	EU791767
S. calcicola (H. Arnell & Perss.) Ingham	Germany, Konstantinova, 28.08.86 (KPABG)	EU791648	EU791757
S. ciliata Sande Lac.	Russia, Primorsky Territory, V. Bakalin, P-3-3-07 (KPABG)	JX630056	JX629925
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, Republic of Buryatia, Konstantinova & A. Savchenko, 24-1-02 (KPABG)	EU791643	EU791752
S. ferruginea (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees	India, Sikkim, D. Long, 22492 (KPABG)	AF519193	EU791766
S. glaucocephala (Taylor) Austin	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 64-5-02 (KPABG)	EU791644	EU791753
S. gymnostomophila Kaalaas	Russia, Murmansk Prov., Konstantinova, 13-1-98 (KPABG)	EU791649	EU791758
S. helvetica Gottsche	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K414-1-05 (KPABG)	EU791620	EU791728
S. kaurinii Ryan	Russia, Chita Prov., V. Bakalin, 11-1-00 (KPABG)	EU791650	EU791759
S. ligulata Steph.	Russia, Sakhalin Prov., Kuril Islands, V. Bakalin, K-42-36-07 (KPABG)	JX630057	JX629926
S. ligulifolia (R.M. Schust.) R.M. Schust.	Norway, Spitsbergen, Konstantinova, K49-10 (KPABG)	JX630060	JX629928
S. lingulata H. Buch	Russia, Magadan Prov., V. Bakalin, Mag-22-17-10 (KPABG)	JX630059	JX629930
S. mucronata H. Buch	Russia, Tuva Rep., V. Bakalin, 100854 (KPABG)	EU791629	EU791737
S. obcordata (Berggr.) S.W. Arnell	Norway, Spitsbergen, Konstantinova, 123-1-04 (KPABG)	EU791626	EU791734
S. obscura (Arnell et C.E.O. Jensen) Schiffn.	Russia, Magadan Prov., V. Bakalin, Mag-22-6-10 (KPABG)	JX630058	JX629927
S. paludosa (Müll. Frib.) Müll. Frib.	Russia, Kemerovo Prov., Konstantinova, 4-3-00 (KPABG)	EU791638	EU791747
S. rufidula Warnst.	Russia, Yakutia, V. Bakalin, 35-3-00 (KPABG)	EU791637	EU791746
S. simmonsii Bryhn & Kaalaas	Russia, Murmansk Prov., Konstantinova, 45-9-98 (KPABG)	EU791653	EU791762
S. sphaerifera H. Buch & Tuom.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 92-2-01(KPABG)	EU791656	EU791765
S. uliginosa (Sw. ex Lindenb.) Dumort.	Russia, Murmansk Prov., V. 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, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, 609/6-05 (KPABG)	EU791654	EU791763
Schiffneria hyalina Steph.	Japan, Mizutani, 15961	**AY463585**	no data
Schistochilopsis capitata (Hook.) Macoun	Russia, Nizhny Novgorod Prov., Konstantinova, 132-03 (KPABG)	DQ875080	DQ875119
S. grandiretis (Lindb. & Kaalaas) Schiffn.	Russia, Kamchatskaya Prov., V. Bakalin, 99-5-01-VB (KPABG)	DQ875081	DQ875120
S. opacifolia (Meyl.) Konstant.	Russia, Karachaevo-Cherkessian Rep., Konstantinova & A. Savchenko, K 468-6b-05 (KPABG)	EF065688	GQ220784
Schljakovia kunzeana (Huebener) Konstant. & Vilnet	Russia, Murmansk Prov., Konstantinova, 181-02 (KPABG)	EU722349	EU727544
Schljakovianthus quadrilobus Konstant. & Vilnet	Russia, Tuva Rep., T. Otnyukova & V. Bakalin, 100805 (KPABG)	EU791666	EU791786
Schofieldia monticola J.D. Godfrey 1	USA, Alaska, Konstantinova, 90-1-92b (KPABG)	JX629987	JX629861
S. monticola 2	USA, Alaska, Konstantinova, 90-4-92 (KPABG)	JX629986	JX629860
S. monticola	USA, Washington, Konstantinova, A 19-1b-95 (KPABG)	JX629988	JX629862
Sphenolobus minutus (Schreb.) Berggr.	Norway, Spitsbergen, Konstantinova, K 68-1-06 (KPABG)	EU791667	EU791789
S. saxicola (Schrad.) Steph.	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 123-3-02 (KPABG)	DQ875086	DQ875124

Taxon	Herbarium voucher	*trn*L-F	ITS1-2
Syzygiella anomala (Lindenb. & Gottsche) Steph.	Costa Rica, Lyon, 257 (GOET)	**GQ900225**	**GQ900015**
Tetralophozia filiformis (Steph.) Urmi	Russia, Republic of Buryatia, Konstantinova & A. Savchenko, 13-24-01 (KPABG)	EU791669	EU791792
Tritomaria exsecta (Schmidel) Loeske	Russia, Nizhny Novgorod Prov., Konstantinova, 103-1-03 (KPABG)	EU791682	EU791800
T. exsectiformis (Breidl.) Loeske	Russia, Republic of Buryatia, Konstantinova, 83-4-01 (KPABG)	EU791683	EU791801
T. quinquedentata (Huds.) H. Buch	Russia, Republic of Karelia, V. Bakalin, 2.VII.1997 (KPABG)	AY327786	EU791804
T. quinquedentata f. *gracilis* (Jens.) R.M. Schust.	Norway, Spitsbergen, Konstantinova, K 118-2-06 (KPABG)	EU791684	EU791802
T. scitula (Tayl.) Jørg.	Russia, Komi Rep., M. Dulin, G101301 (KPABG)	EU791681	EU791799
Wettsteinia inversa (Sande Lac.) Schiffn.	Indonesia, Gradstein, 11014 (GOET)	**GQ900275**	**GQ900066**