

***CEPHALOZIELLA KONSTANTINOVAE***  
**(CEPHALOZIELLACEAE, MARCHANTIOPHYTA),**  
**A NEW LEAFY LIVERWORT SPECIES FROM RUSSIA AND**  
**MONGOLIA IDENTIFIED BY INTEGRATIVE TAXONOMY**

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**Abstract.** In the course of a taxonomic study of the genus *Cephaloziella* (Spruce) Schiffn. (Cephaloziellaceae, Marchantiophyta) in Asia, the new species *Cephaloziella konstantinovae* Mamontov & Vilnet, *sp. nov.*, from the eastern regions of Russia and from the Republic of Mongolia was discovered. The new species is formally described and illustrated here. Morphologically it is similar to *C. divaricata* var. *asperifolia* (Taylor) Damsh., but differs in its leaf shape and thin-walled, inflated stem and leaf cells. The new species can be distinguished from other *Cephaloziella* taxa by the following characters: (i) female bracts entirely free from each other and from bracteole, (ii) perianth campanulate, (iii) cells of perianth mouth subquadrate, (iv) capsule spherical, (v) seta with 8–10 + 4–6-seriate morphology, and (vi) elaters with 1–2 spiral bands. Molecular phylogenetic analyses of nrITS1-5.8S-ITS2 and chloroplast *trnL*-F sequences from 63 samples (34 species, 23 genera) confirm the taxonomical status of the new species. Five specimens of *C. konstantinovae* form a clade placed sister to a clade of *C. elachista* (J. B. Jack) Schiffn. and *C. rubella* (Nees) Warnst.

**Key words:** *Cephaloziella konstantinovae*, distribution, ecology, new species, Hepaticae, taxonomy, ITS1-2 nrDNA, *trnL*-F cpDNA

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## INTRODUCTION

Schiffner (1893) established the leafy liverwort genus *Cephaloziella* (Spruce) Schiffn. to accommodate species of minute size having ventral and lateral branches, small leaf and stem cells, and occasionally underleaves. Schiffner included 20 species in the genus. *Cephaloziella* is virtually cosmopolitan; its species occur on rotten wood, peat bogs, soil and rocks, but a few taxa in tropical forests are corticolous (Schuster 2002).

The genus is the largest in the family Cephaloziellaceae, with 80–90 species and infraspecific taxa (Söderström *et al.* 2016). Its taxonomy is considered notoriously difficult due to the small size of the species and their reduced morphology, as well as high ecological plasticity and morphological

variation. The taxonomy of Cephaloziellaceae has been studied mainly for regional treatments, and authors disagree on circumscription of taxa and evaluation of diagnostic characters (e.g., Arnell 1963; Damsholt 2002; Fulford 1976; Jones 1960; Kitagawa 1965, 1969; Paton 1999; Schumacker & Vána 2005; Schuster 1969, 1971, 1980, 1988, 1995, 1996, 2002; Schuster & Damsholt 1974; Udar & Nath 1976; Schljakov 1979; Udar & Kumar 1980, 1982). The most recently described species of the genus is *Cephaloziella biokoensis* Vána & F. Muell. from Equatorial Guinea (Vána & Müller 2003).

Recently intensified floristic studies in remote regions of Russia – the Arctic, Caucasus, Siberia and the Far East – produced new records for a number of *Cephaloziella* species (Konstantinova *et al.* 2009), allowed revision of numerous

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specimens, and confirmed some opinions of hepatologists on the circumscription of several taxa. Here we apply an integrative approach, considering evidence from DNA sequence variation as well as morphology, ecology and phyto geography, with a special focus on some morphologically unique specimens collected by the senior author in the Trans-Baikal Region of Siberia. These specimens resembled *Cephaloziella* but showed some morphological overlap with Scapaniaceae+Anastrophyllaceae in branching mode and generative features. Phylogenetic analyses of nuclear ribosomal ITS and chloroplast DNA *trnL*-F sequences support the suggestion that these Trans-Baikal plants belong to *Cephaloziella* and are distinct from all putative relatives; hence they are described as a new species, *Cephaloziella konstantinovae*.

## MATERIALS AND METHODS

### TAXON SAMPLING

Species representing the families and genera of Jungermanniales suborder Cephaloziineae (Crandall-Stotler *et al.* 2009) were chosen to test the morphology-based attribution of the new species to *Cephaloziella*. A total of 63 accessions representing 34 species were used for this study (Table 1). We analyzed 12 species (41 samples) from the family Cephaloziellaceae, 10 species (10 samples) from Scapaniaceae, 8 species (8 samples) from Anastrophyllaceae, 2 species (2 samples) from Cephaloziaceae, and 2 species (2 samples) from Odonotoschismataceae. We chose *Cephalozia affinis* Lindb. ex Steph. as outgroup taxon based on the phylogenetic hypotheses presented by Feldberg *et al.* (2013).

The ingroup includes 11 taxa from the genus *Cephaloziella* and one species of the genus *Cylindrocolea* R. M. Schust (Cephaloziellaceae). Ingroup taxa are represented by multiple accessions from different regions. The nucleotide data for 9 specimens were taken from earlier studies and downloaded from GenBank (Vilnet *et al.* 2012; Bakalin & Vilnet 2014). DNA vouchers are listed in Table 1, including GenBank accession numbers and voucher details.

### DNA ISOLATION, PCR AMPLIFICATION AND DNA SEQUENCING

DNA was extracted from dried liverwort tissue using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). Amplification and sequencing were performed using

primers suggested by White *et al.* (1990) for nrITS1-2 and Taberlet *et al.* (1991) for *trnL*-F. PCRs were carried out in 20  $\mu$ l volumes according to the following procedure: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C, 60 s 72°C) and 2 min extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the GFX<sup>TM</sup> PCR DNA and Gel Band Purification Kit (Amersham Biosciences, USA), 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 for the 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

### PHYLOGENETIC ANALYSIS

Two datasets (ITS1-2, *trnL*-F) were automatically aligned in BioEdit 7.0.1 (Hall 1999) using the ClustalW option and then manually corrected. The preliminary phylogenetic analyses revealed no incongruence between the nuclear and the chloroplast DNA datasets; hence they were combined. Lacking sequences were coded as missing.

The ITS1-2+*trnL*-F dataset was analyzed using Bayesian inference (BA) implemented in MrBayes 3.2.1 (Ronquist *et al.* 2012), and by the maximum parsimony method (MP) with NONA under the WinClada shell (Goloboff 1994; Nixon 2002).

The ModelGenerator program (Keane *et al.* 2006) determined the GTR+I+ $\Gamma$  model as the best-fit evolutionary model of nucleotide substitutions for the combined alignment. In the BA, four partitions of the combined alignment (ITS1-2, *trnL*-F) were separately assigned the GTR+I+ $\Gamma$  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 chains and one unheated chain, and the two starting trees were chosen randomly. The number of generations was 10,000,000, and trees were saved once every 10,000<sup>th</sup> generation. Average standard deviation of split frequencies between two runs was 0.009191. Bayesian posterior probabilities were calculated from trees sampled after burn-in (Fig. 1).

Jackknife support was calculated in NONA for 1000 replications (number of search reps 10, hold 10, max tree 100, do max) and shown in Figure 2.

Due to the unusual morphology of the studied Trans-Baikal plants here assigned to *Cephaloziella konstantinovae*, Bayes factor comparison was additionally used to test whether the new species could be related to Anastrophyllaceae or Scapaniaceae rather

**Table 1.** List of taxa, voucher specimens and GenBank accession numbers. The sequences from our previous study are in italics. Initial species identifications from herbarium vouchers are indicated for specimens reclassified in this study based on results of DNA analyses.

Taxon name	Voucher specimens	GenBank accession number	
		ITS1-2	<i>trnL-F</i>
<i>Alobiellopsis parvifolia</i> (Steph.) R. M. Schust.	Japan, <i>Bryophytes of Asia Fasc. 8, No. 191</i> (KPABG)	JX629894	JX630020
<i>Barbilophozia barbata</i> (Schmidel ex Schreb.) Loeske	Netherlands, <i>Konstantinova 3b-5-99</i> (KPABG)	EU791779	EU791676
<i>Cephalozia affinis</i> Lindb. ex Steph.	Russia, Republic of Adygeya, <i>Konstantinova K473-2-07</i> (KPABG)	JX629827	JX629952
<i>Cephaloziella divaricata</i> (Sm.) Schiffn.	Russia, Sakhalin Province, Sakhalin I., <i>Bakalin S-24-21-09</i> (KPABG)	KF805881	KF805923
<i>C. elachista</i> (J. B. Jack) Schiffn.	Russia, Khanty-Mansi Autonomous Area 1, <i>Kukurichkin OPIVN607/1</i> (KPABG), published as <i>C. rubella</i> in Vilnet <i>et al.</i> (2012)	JX629919	JX630048
<i>C. elachista</i>	Russia, Khanty-Mansi Autonomous Area 2, <i>Kukurichkin OPIVN607/7</i> (KPABG), published in Vilnet <i>et al.</i> (2012)	JX629918	JX630047
<i>C. hampeana</i> (Nees) Schiffn. ex Loeske	Russia, Kamchatka Territory 1, <i>Bakalin 77-14-01-VB</i> (as <i>C. uncinata</i> , KPABG)	KF805866	KF805899
<i>C. hampeana</i>	Russia, Kamchatka Territory 2, <i>Bakalin 98-4-01-VB</i> (as <i>C. subdentata</i> , KPABG)	KF805865	KF805897
<i>C. hampeana</i>	Russia, Murmansk Province, <i>Konstantinova 182-3</i> (as <i>C. subdentata</i> , KPABG)	KF805864	KF805898
<i>C. kiaeri</i> (Austin) Douin	Borneo, Kinabalu, <i>Konstantinova K-8-4</i> (KPABG)	KF805888	KF805935
<i>C. kiaeri</i>	Japan, <i>Bryophyte Selecta Exsiccatae, No. 1218</i> (KPABG)	KF805886	KF805934
<i>C. kiaeri</i>	Republic of Korea, <i>Bakalin Kor-2-14-09</i> (KPABG)	KF805887	KF805933
<i>C. konstantinovae</i> Mamontov & Vilnet, <i>sp. nov.</i>	Russia, Trans-Baikal Territory 1, <i>Afonina 4006-5</i> (KPABG)	KF805882	KF805924
<i>C. konstantinovae</i>	Russia, Trans-Baikal Territory 2, <i>Afonina 4006-6</i> (KPABG), published as <i>C. aspericaulis</i> in Bakalin & Vilnet (2014)	KF471666	KF471664
<i>C. konstantinovae</i>	Russia, Trans-Baikal Territory 3, <i>Afonina 6010-1</i> (KPABG)	KF805883	KF805925
<i>C. konstantinovae</i>	Russia, Trans-Baikal Territory 4, <i>Afonina 05307-7</i> (KPABG), (published as <i>C. aspericaulis</i> in Vilnet <i>et al.</i> 2012)	JX629917	JX630044
<i>C. konstantinovae</i>	Russia, Trans-Baikal Territory 5, <i>Mamontov 169-5</i> (KPABG)	KF805884	KF805926
<i>C. microphylla</i> (Steph.) Douin	Republic of Korea 1, <i>Hepaticae Korea Exsiccatae Fasc. II, No. 23</i> (KPABG)	KF805889	KF805937
<i>C. microphylla</i>	Republic of Korea 2, <i>Hepaticae Korea Exsiccatae Fasc. I, No. 29</i> (KPABG)	KF805890	KF805938
<i>C. rubella</i> (Nees) Warnst.	Russia, Altai Territory, <i>Mamontov 214-14</i> (KPABG)	KF805885	KF805927
<i>C. rubella</i>	Russia, Republic of Altai, <i>Mamontov 330-5-1</i> (as <i>C. elegans</i> , KPABG)	KF853559	KF853560
<i>C. rubella</i>	Russia, Trans-Baikal Territory, <i>Afonina 45907</i> (as <i>C. arctogena</i> , KPABG), published in Vilnet <i>et al.</i> (2012)	JX629916	JX630045
<i>C. spinicaulis</i> Douin	Russia, Primorsky Territory, <i>Bakalin P-63-3-08</i> (KPABG)	KF805896	KF805947
<i>C. spinicaulis</i>	Japan, <i>Deguchi, Exsiccatae Fasc. 5, No. 119</i> (published in Vilnet <i>et al.</i> 2012)	JX629922	JX630043
<i>C. stellulifera</i> (Taylor) Schiffn.	Netherlands, <i>Konstantinova 1e-2-99</i> (KPABG), published in Vilnet <i>et al.</i> (2012)	JX629923	JX630042
<i>C. turneri</i> (Hook.) Müll. Frib.	Russia, Krasnodar Territory, <i>Ignatov &amp; Ignatova 02-24a</i> (KPABG)	KF805892	KF805944

Table 1. Continued.

Taxon name	Voucher specimens	GenBank accession number	
		ITS1-2	trnL-F
<i>C. varians</i> (Gottsche) Steph.	Norway, Svalbard 1, <i>Konstantinova K78-1-06</i> (KPABG)	KF805877 (ITS1) KF805863 (ITS2)	KF805914
<i>C. varians</i>	Norway, Svalbard 2, <i>Konstantinova K115-02</i> (as <i>C. grimsulana</i> , KPABG)	KF805878	KF805915
<i>C. varians</i>	Norway, Svalbard 3, <i>Konstantinova K130-2-04</i> (as <i>C. uncinata</i> , KPABG)	KF805880	KF805920
<i>C. varians</i>	Russia, Altai Territory, <i>Mamontov 219-5</i> (as <i>C. divaricata</i> , KPABG)	KF805876 (ITS1) KF805862 (ITS2)	KF805912
<i>C. varians</i>	Russia, Republic of Karachaevo-Cherkessia 1, <i>Konstantinova K515-1-05</i> (as <i>C. divaricata</i> , KPABG)	KF805874	KF805908
<i>C. varians</i>	Russia, Republic of Karachaevo-Cherkessia 2, <i>Konstantinova K517-2-05</i> (as <i>C. divaricata</i> , KPABG)	KF805873	KF805907
<i>C. varians</i>	Russia, Kamchatka Territory, <i>Bakalin K-105-5-03</i> (KPABG) (published in Vilnet <i>et al.</i> 2012)	JX629924	JX630051
<i>C. varians</i>	Russia, Murmansk Province, <i>Konstantinova K 8-2-12</i> (KPABG)	KF805871 (ITS1) KF805861 (ITS2)	KF805904
<i>C. varians</i>	Russia, Magadan Province, <i>Bakalin Mag-7-40-10</i> (as <i>C. spinigera</i> , KPABG)	KF805872	KF805905
<i>C. varians</i>	Russia, Sakhalin Province, Sakhalin I., <i>Bakalin S-58-3-09</i> (as <i>C. divaricata</i> var. <i>asperifolia</i> , KPABG)	KF805879	KF805917
<i>C. varians</i>	Russia, Trans-Baikal Territory 2, <i>Afonina 07408</i> (as <i>C. divaricata</i> , published in Vilnet <i>et al.</i> 2012, KPABG)	JX629921	JX630050
<i>C. varians</i>	Russia, Trans-Baikal Territory 3, <i>Afonina A1810</i> (KPABG), published as <i>C. polystratosa</i> in Bakalin & Vilnet (2014)	KF471665	JX630046
<i>C. varians</i>	Russia, Trans-Baikal Territory 4, <i>Afonina A2410</i> (KPABG)	KF805867	KF805900
<i>C. varians</i>	Russia, Trans-Baikal Territory 5, <i>Afonina A3010</i> (as <i>C. divaricata</i> , KPABG)	KF805870	KF805903
<i>C. varians</i>	Russia, Trans-Baikal Territory 6, <i>Afonina A4805</i> (as <i>C. polystratosa</i> , KPABG, published in Vilnet <i>et al.</i> 2012)	JX629920	JX630049
<i>C. varians</i>	Russia, Trans-Baikal Territory 7, <i>Afonina, A5610/4</i> , (as <i>C. polystratosa</i> , KPABG)	KF805869	KF805902
<i>C. varians</i>	Russia, Trans-Baikal Territory 8, <i>Afonina, A6010b</i> , (as <i>C. polystratosa</i> , KPABG)	KF805868	KF805901
<i>Cylindrocolea recurvifolia</i> (Steph.) Inoue	Japan, Kiushu, <i>Exsiccatae Bryophytes of Asia Fasc.14 # 344</i> (KPABG)	KF805891	KF805939
<i>Diplophyllum albicans</i> (L.) Dumort.	Russia, Republic of Karachaevo-Cherkesia, <i>Konstantinova &amp; Savchenko, K446-7-05</i> (KPABG)	EU791773	EU791659
<i>Douinia imbricata</i> (M. Howe) Konstant. & Vilnet	USA, Alaska, <i>Konstantinova, 110-2-92a</i> (KPABG)	EU791770	EU791658
<i>Gymnocolea inflata</i> (Huds.) Dumort.	Norway, Spitsbergen, <i>Konstantinova, 118-1-04</i> (KPABG)	EU791787	EU791661
<i>Heterogemma capitata</i> (Hook.) Konstant. & Vilnet	Russia, Nizhny Novgorod Province, <i>Konstantinova, 132-03</i> (KPABG)	DQ875119	DQ875080
<i>Isopaches decolorans</i> (Limpr.) H. Buch	Russia, Republic of Karachaevo-Cherkesia, <i>Konstantinova &amp; Savchenko, K464-3-05</i> (KPABG)	EU791798	EU791680
<i>Lophozia ascendens</i> (Warnst.) R. M. Schust.	Russia, Republic of Buryatia, <i>Konstantinova &amp; Savchenko, 109-3-01</i> (KPABG)	DQ875089	DQ875054
<i>Lophozopsis excisa</i> (Dicks.) Konstant. & Vilnet	Norway, Spitsbergen, <i>Konstantinova, K-21-2-05</i> (KPABG)	DQ875093	DQ875058

Table 1. Continued.

Taxon name	Voucher specimens	GenBank accession number	
		ITS1-2	<i>trnL</i> -F
<i>Neoorthocaulis attenuatus</i> (Mart.) L. Söderstr., De Roo & Hedd.	Russia, Sakhalin Province, <i>Harpel &amp; Cherdantseva, 105728</i> (KPABG)	EU722343	EU727538
<i>Odontoschisma denudatum</i> (Nees) Dumort.	Czech Republic, <i>Konstantinova, 103546</i> (KPABG)	JX629877	JX630008
<i>O. fluitans</i> (Nees) L. Söderstr. & Váňa	Russia, Kamchatskaya Province, <i>Bakalin, K-13-7-03</i> (KPABG)	JX629885	JX630012
<i>Protolophozia elongata</i> (Steph.) Schljakov	Russia, Murmansk Province, <i>Bakalin, 3-1-02</i> (KPABG)	DQ875116	DQ875078
<i>Pseudolophozia debiliformis</i> (R. M. Schust. & Damsh.) Konstant. & Vilnet	Russia, Republic of Karachaevo-Cherkessia, <i>Konstantinova &amp; Savchenko K510-1-05</i> (KPABG)	EF065692	EF065685
<i>Pseudotritomaria heterophylla</i> (R. M. Schust.) Konstant. & Vilnet	Russia, Krasnoyarskiy Territory, <i>Fedosov, 107960</i> (KPABG)	EU791806	EU791687
<i>Saccobasis polymorpha</i> (R. M. Schust.) Schljakov	Russia, Murmansk Province, <i>Konstantinova, 21-3b-96</i> (KPABG)	EU791807	EU791688
<i>Scapania apiculata</i> Spruce	Russia, Republic of Buryatia, <i>Konstantinova, Hepaticae Rossica Exsiccatae № 49</i> (KPABG)	EU791741	EU791633
<i>Schljakovia kunzeana</i> (Huebener) Konstant. & Vilnet	Russia, Murmansk Province, <i>Konstantinova, 181-02</i> (KPABG)	EU722349	EU727544
<i>Sphenolobus minutus</i> (Schreb.) Berggr.	Norway, Spitsbergen, <i>Konstantinova, 68-1-06</i> (KPABG)	EU791789	EU791667
<i>Tetralophozia filiformis</i> (Steph.) Urmi	Russia, Republic of Buryatia, <i>Konstantinova &amp; Savchenko, 13-24-01</i> (KPABG)	EU791792	EU791669
<i>Tritomaria exsectiformis</i> (Breidl.) Loeske	Russia, Republic of Buryatia, <i>Konstantinova, 83-4-01</i> (KPABG)	EU791801	EU791683

than to *Cephaloziella*. Specifically, we contrasted the hypothesis that the new species and Anastrophyllaceae + Scapaniaceae form a monophyletic group (M1) with the hypothesis that they do not form a monophyletic group (M2). In order to do this, the ratio of the marginal likelihoods of the models M1 and M2, the Bayes factor, was computed.

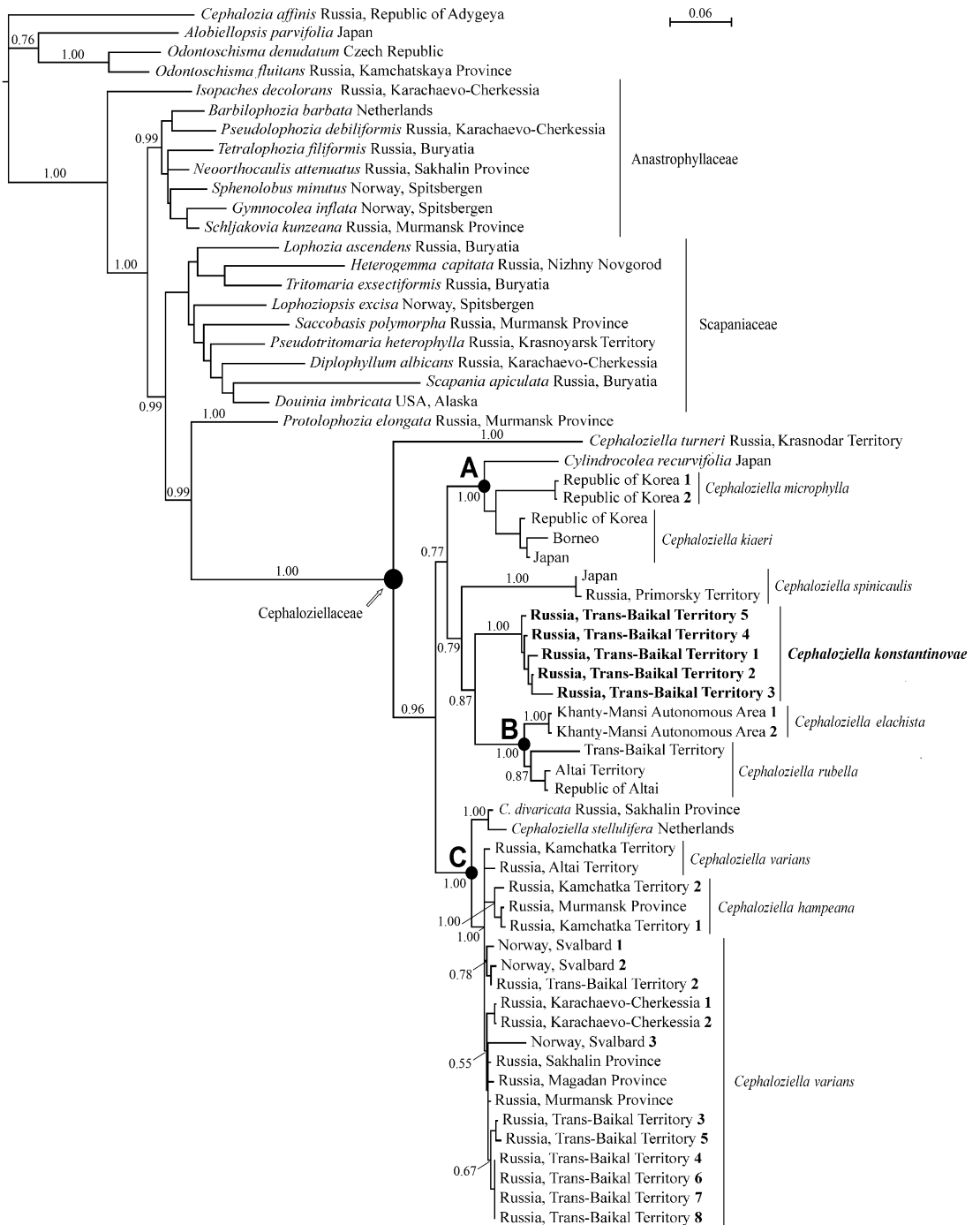
The logarithm of the Bayes factor is the difference in the logarithms of the marginal model likelihoods (Kass & Raftery 1995). A rough estimate of the marginal model likelihoods can be obtained as a harmonic mean of the likelihood values of the MCMC samples (Newton & Raftery 1994). MrBayes 3.2.1 provides that method for estimating the logarithm of the marginal model likelihoods (Ronquist *et al.* 2011). The harmonic mean of the likelihood values of the MCMC samples is the logarithm of the marginal model likelihood (Ronquist *et al.* 2011).

To test the hypotheses, a hard constraint (M1) and a negative constraint (M2) were specified. In the step of the hard constraint, the constrained tree was defined wherein *Cephaloziella konstantinovae* was forced to belong to clade Anastrophyllaceae + Scapaniaceae.

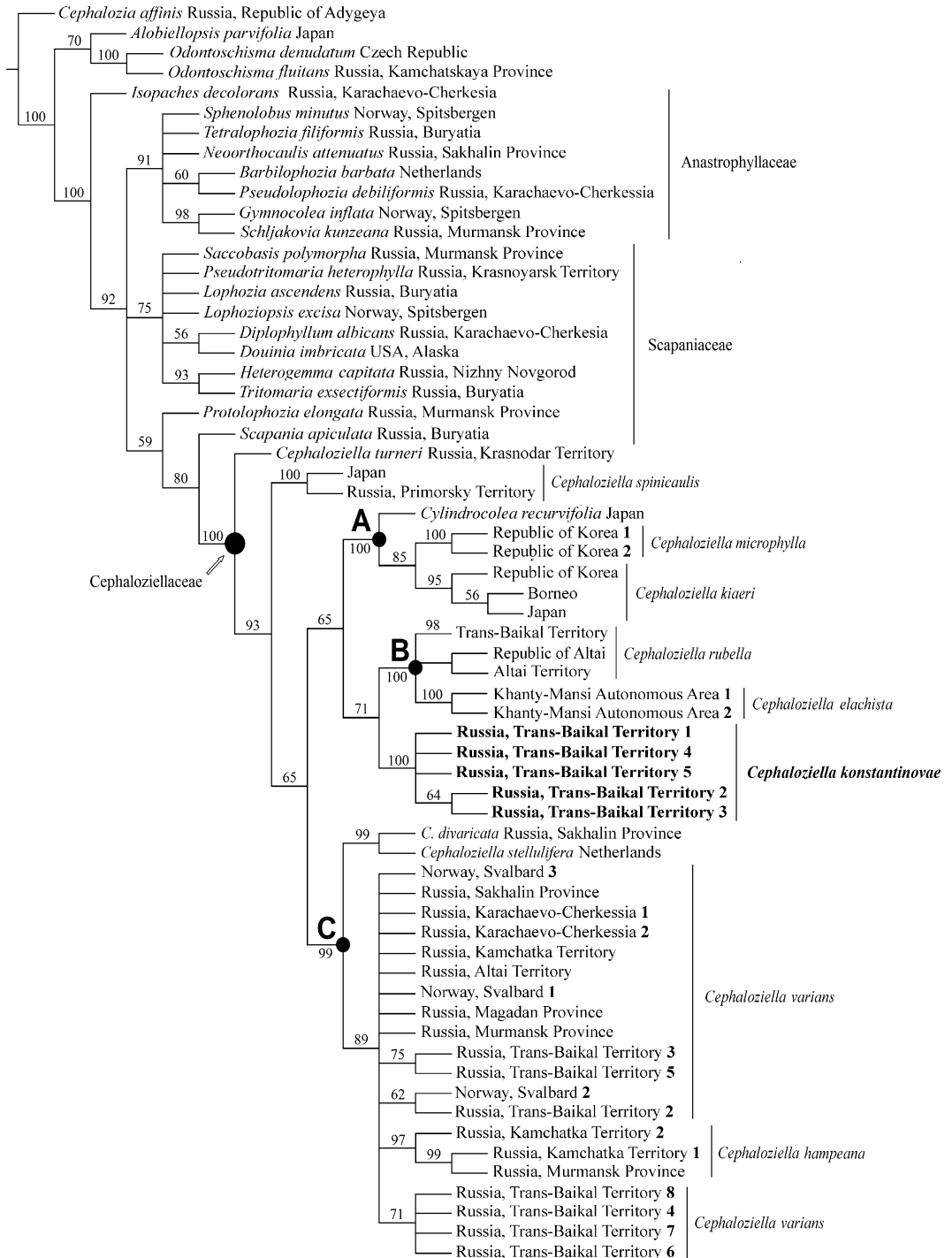
It allowed us to force a partition to always be present in the sampled trees. The harmonic mean from the MCMC-based search was recorded under M1. In the step of the negative constraint, the constrained tree was defined wherein *Cephaloziella konstantinovae* was forced not to belong to Anastrophyllaceae + Scapaniaceae. It allowed sampling across all trees that do not contain the specified partition. The harmonic mean from the MCMC-based search was recorded under M2. The difference between harmonic means from both runs, the logarithm of the Bayes factor, was calculated. The corresponding interpretation was found in the table of Kass and Raftery (1995). To use this table, twice the difference in the harmonic means was calculated (Ronquist *et al.* 2011).

## RESULTS

Nuclear ribosomal ITS sequences and chloroplast DNA *trnL*-F sequences were newly generated for 31 specimens. The ITS1-2+*trnL*-F alignment



**Fig. 1.** Phylogenetic tree for suborder Cephaloziineae based on combined ITS1-2+trnL-F nucleotide sequence data from 63 specimens constructed by Bayesian methodology. Bayesian posterior probabilities greater than 0.50 are indicated.



**Fig. 2.** Phylogenetic tree for suborder Cephaloziineae based on combined ITS1-2+trnL-F nucleotide sequence data from 63 specimens constructed by maximum parsimony method. Jackknife support values greater than 50% are indicated.

(63 specimens) included 1822 character sites, among them 852 constant positions; 296 were variable and 674 parsimony-informative.

Arithmetic means of log likelihoods in the BA analysis in both runs sampled were  $-15,143.52$  and  $-15,145.63$ . The Bayes factor calculation revealed the harmonic mean estimate for model M2 as  $-15,205.20$  in log units. For model M1 it is  $-15,383.98$  in log units, which is *ca* 179 log units worse than the previous model. Twice the difference between the harmonic means is 358 log units. A log difference above 5 is considered to be very strong evidence in favor of the better model (Kass & Raftery 1995). Thus, the harmonic mean estimator gives very strong evidence in favor of *Cephaloziella konstantinovae* being distant from both Anastrophyllaceae and Scapaniaceae.

The Bayesian and the parsimony topologies were largely similar (Figs 1 & 2). The majority of *Cephaloziella* accessions are found in three clades – A, B and C – which are stable in both BA and MP trees but differently supported in the calculations. Clade A (JS = 100%, PP = 1.00) includes *Cephaloziella kiaeri* (Austin) Douin, *C. microphylla* (Steph.) Douin and *Cylindrocolea recurvifolia* (Steph.) Inoue.

Clade B (JS = 100% in MP, PP = 1.00 in BA) of BA and MP topologies contains *C. elachista* (J. B. Jack) Schiffn. and *C. rubella* (Nees) Warnst. The specimen ‘Trans-Baikal Territory’ of *C. rubella* forms a long branch in the Bayesian tree and a separate subclade in the MP tree. The well-supported (JS = 100%, PP = 1.00) subclade including two specimens of *Cephaloziella spinicaulis* Douin is placed differently in BA and MP topologies.

Five specimens of the new species *C. konstantinovae* from Trans-Baikal Territory form a distinct subclade (JS = 100%, PP = 1.00) resolved as sister to clade B in BA and MP. Clade C (JS = 99%, PP = 1.00) includes specimens of *C. divaricata* (Sm.) Schiffn., *C. hampeana* (Nees) Schiffn. ex Loeske, *C. stellulifera* (Taylor) Schiffn. and *C. varians* (Gottsche) Steph. The species *C. turneri* (Hook.) Müll. Frib. forms a sister relationship with all other Cephaloziellaceae elements in the BA and MP trees.

## DISCUSSION

### MORPHOLOGICAL SIMILARITY OF *CEPHALOZIELLA KONSTANTINOVAE* WITH THE TAXA OF CEPHALOZIINEAE

In the present study the narrow concept of Cephaloziellaceae of Schuster (2002) rather than the wide concept of Söderström *et al.* (2016) is accepted; however, we take the proposals of Crandall-Stotler *et al.* (2009), Gradstein *et al.* (2014) and Patzak *et al.* (2016) into account. We consider the genera *Allisoniella* E. A. Hodgs. (incl. *Protomarsupella* R. M. Schust.), *Amphicephalozia* R. M. Schust., *Cephalojonesia* Grolle, *Cephalomitron* R. M. Schust., *Cephaloziella*, *Cephaloziopsis* (Spruce) Schiffn., *Chonecolea* Grolle, *Cylindrocolea* R. M. Schust., *Gymnocoleopsis* (R. M. Schust.) R. M. Schust., *Kymatocalyx* Herzog (incl. *Stenorrhypis* Herzog) and *Phycolepidozia* R. M. Schust. as elements of Cephaloziellaceae *s.str.*

Although the present analyses did not resolve deeper nodes of *Cephaloziella*, it is clear that our new species is nested within this genus.

Being first recognized from the Trans-Baikal Territory in 2009, the new species was found subsequently in the Republic of Buryatia, southern Siberia, in Primorsky Territory, the Russian Far East, and the Republic of Mongolia. Due to the presence of well-developed underleaves and multicellular outgrowths on the abaxial leaf face, the sterile specimens of this species were initially identified as *Cephaloziella divaricata* var. *asperifolia* (Taylor) Damsh. or *C. byssacea* var. *asperifolia* Macvicar (in herb. VBG) and published as *C. aspericaulis* Jørg. or *C. divaricata* var. *asperifolia* (Taylor) Damsh. for the Trans-Baikal Territory, Russia (Konstantinova & Afonina 2009; Afonina *et al.* 2012; Czernyadjeva *et al.* 2013) or *C. microphylla* (Steph.) Douin for Tuv Aimag of Mongolia (Tsegmed & Bai 2013). The senior author’s collections contain fertile plants with mature androecia, perianthia and sporophytes. These plants’ characteristics are as follows: (i) female bracts entirely free from each other and from bracteole, (ii) perianth campanulate, (iii) cells of perianth mouth rounded-rectangular to subquadrate, (iv) capsule spherical, (v) seta with 8–10



+ 4–6-seriate morphology, and (vi) elaters with 1–2 spiral bands. According to Schuster (2002), none of the genera of Cephaloziellaceae have this combination of character states of the reproductive structures. In *Chonecolea*, which is considered an element of Cephaloziellaceae by Patzak *et al.* (2016), all of those characteristics are present, but the spore surface in *Chonecolea* is reticulate, whereas in *Cephaloziella konstantinovae* as well as other Cephaloziellaceae (except *Cylindrocolea reticulata*) the spore surface is finely granulate, papillose or verruculose.

In seta morphology, *Cephaloziella konstantinovae* resembles the genera *Allisoniella*, *Amphicephalozia*, *Cephalomitron* and *Chonecolea* of Cephaloziellaceae *s.str.* In *Cephaloziella konstantinovae* the seta is 8–10 + 4–6-seriate, whereas in the monospecific genus *Cephalomitron* the seta is 8 + 4-seriate (Schuster 2002), in *Chonecolea* it varies from 4 + 5-seriate to 8 + 4-seriate (Schuster 1980; Jones 1985), and in *Amphicephalozia amplexicaulis* R. M. Schust. the seta has 8–9 outer + 4–6 smaller internal cells (Schuster 2002). The genus *Allisoniella* has a seta with 8 outer + (3)4 to 12–14 smaller inner cells (Schuster 2002); however, *Allisoniella subbipartita* (C. Massal.) R. M. Schust. & J. J. Engel is illustrated to have a seta with 9 outer + 8–13 inner cells (Schuster 2002: Fig. 247: 7 & 8). In contrast, the genera *Cylindrocolea*, *Kymatocalyx*, *Cephaloziopsis* and *Phycolepidozia* of Cephaloziellaceae *s.str.* have 4 + 4-seriate setae; *Cephalojonesia* and *Cephaloziella* have 4(5) + 4(5)-seriate and 4(5–6) + 4(5)-seriate setae, respectively (Grolle & Vanden Bergen 1970; Schuster 2002).

It should be noted that the 8–10 outer seta cells of *Cephaloziella konstantinovae* do not occur in other members of Cephaloziellaceae *s.str.* In this character the new species is similar to some elements of Lophoziaceae *sensu* Schuster (1969), where the seta consists of numerous cell rows or is reduced to (2–3)4 inner and (6–7)8 outer rows in some taxa (Schuster 1969: 219). According to Schuster (2002) this seta anatomy occurs in *Lophozia badensis* (Gottsche) Schiffn. (nowadays considered as *Mesoptychia badensis* (Gottsche) L. Söderstr. & Váňa of Jungermanni-

aceae) and *Anastrophyllum hellerianum* (Nees *ex* Lindenb.) R. M. Schust. [syn. *Crossocalyx hellerianus* (Nees *ex* Lindenb.) Meyl.], but it is never fixed at the 8+4 state in these taxa (Schuster 2002).

On the other hand, in Lophozioideae *sensu* Schuster (1969) the area of one inner cell of the seta (in cross section) approximates that of one outer cell of the seta (Schuster 1969: Fig. 163: 2, Fig. 235: 7–10, Fig. 242: 2, Fig. 244: 4). In all species of Cephaloziellaceae *s.str.*, especially in *Cephalojonesia*, *Cephaloziella*, *Cephaloziopsis*, *Cylindrocolea*, *Kymatocalyx* and *Phycolepidozia*, the inner cells of the seta are reduced in size, so that the area of inner cells (in cross section) does at best reach the size of one outer cell (Douin 1908, 1920; Grolle & Vanden Bergen 1970; Schuster 2002). This character is also observed in *Cephaloziella konstantinovae* where the collective area of inner seta cells (in cross section) is almost equal to that of one outer seta cell (Figs 25 & 27).

Within Lophozioideae, *Gymnocoleopsis capensis* (S. W. Arnell) R. M. Schust. has a seta morphology of the 8 + 4-type, but the inner cells (in cross section) are reduced in size (Arnell 1963; Schuster 2002). On the other hand, a close affinity between *Gymnocoleopsis* and *Cephaloziella* was shown in a molecular phylogenetic study of Lophoziaceae (De Roo *et al.* 2007), and the genus *Gymnocoleopsis* is now placed within Cephaloziellaceae *s.str.* (Crandall-Stotler *et al.* 2009; Váňa *et al.* 2013).

The genera *Protolophozia* (R. M. Schust.) Schljakov and *Pseudocephaloziella* R. M. Schust. of the former Lophoziaceae resemble *Cephaloziella konstantinovae* in the absence of nodular thickenings on the cell walls and the presence of well-developed underleaves. However, the phylogenetic relationships of *Pseudocephaloziella* remain unclear because the sporophyte characters are unknown and nucleotide sequence data are not available. The genus *Protolophozia* differs from *Cephaloziella konstantinovae* in seta morphology. According to Schuster (1988: 63, Fig. 5: 10), the seta in *Protolophozia elongata* (Steph.) Schljakov consists of 17 outer and 20 inner cells that do not differ in size. Moreover, the phylogenetic position of *Protolophozia* is not yet established. Schuster

(2002) considers *Protolophozia* (incl. *P. elongata*) to be a subgenus within the genus *Lophozia*. Heinrichs *et al.* (2005) proposed to merge Lophoziaceae into Scapaniaceae; in Konstantinova *et al.* (2009), *Protolophozia* was placed within Scapaniaceae *s.str.* (excl. genera later assigned to Anastrophyllaceae). Vilnet *et al.* (2012) found inconsistent positions of *Protolophozia elongata* in a series of phylogenetic analyses; however, Váňa *et al.* (2013) proposed to include *Protolophozia* in Cephaloziellaceae. In the obtained phylogenetic trees (Figs 1 & 2), *Protolophozia elongata* is related to the clade of Anastrophyllaceae + Scapaniaceae rather than to Cephaloziellaceae.

The bracts and bracteoles are entirely free in *Cephaloziella konstantinovae*, *Amphicephalozia*, *Cephalojonesia*, *Cephaloziopsis* and *Chonecolea*, but more or less connate at the base in *Allisoniella*, *Cephaloziella*, *Cephalomitron*, *Cylindrocolea*, *Kymatocalyx* and *Phycolepidozia*.

For the abovementioned reasons, the seta structure as well as the shape of bracts and bracteole and the degree of their connection probably are not sufficient to delimitate genera of Cephaloziellaceae *s.str.* It may be that vegetative characters, particularly the branching mode and the presence/absence of underleaves, are of greater taxonomic importance.

The campanulate perianth and the subisodiametric cells of the perianth mouth of *Cephaloziella konstantinovae* resemble the character state of *Cephalojonesia incuba* Grolle & Vanden Bergen, *Cephaloziopsis exigua* (Inoue) Inoue & R. M. Schust. (syn. *Metacephalozia exigua* Inoue; Inoue 1973), and the species of *Chonecolea* and *Cylindrocolea* subg. *Cylindrosocyphus* (Douin) R. M. Schust., namely *Cylindrocolea atroviridis* (Sim) Váňa, *C. reticulata* Udar & Ad. Kumar and *C. rhizantha* (Mont.) R. M. Schust. However, the spherical capsule and 1–2-spiralled elaters of *Cephaloziella konstantinovae* otherwise occur only in *Chonecolea* species and *Cylindrocolea reticulata*.

The combination of characters of *Cephaloziella konstantinovae* is unusual for the family Cephaloziellaceae *s.str.* Some of these characters are presented in isolated species of oligospecific genera

and subgenera – *Allisoniella*, *Amphicephalozia*, *Cephalojonesia*, *Cephaloziopsis*, *Cylindrocolea* subg. *Cylindrosocyphus* – but have been found collectively (excl. spore surface) only in *Chonecolea*. Furthermore, the type of reproductive structures found in *Cephaloziella konstantinovae* is unknown in other species of the genus *Cephaloziella*.

*Cephaloziella konstantinovae* lacks ventral branching but has *Frullania*-type terminal branches. This branching mode is untypical for Cephaloziellaceae *s.str.* but occurs in Lophoziaceae sensu Schuster (1969). However, Schuster (1988: 189) points to the presence of *Frullania*-type branches in *Cephaloziella byssacea* (Roth) Warnst. and other members of *Cephaloziella* (Schuster 2002: 107). Fulford (1976) describes *Frullania*-type branches in *Cylindrocolea* and *Cephaloziella subtilis* (Lindenb. & Gottsche) Steph. The shoots of *Cephaloziella crispata* N. Kitag., *C. indica* Udar & Ad. Kumar and *C. stellulifera* (Taylor) Schiffn. were described as simple or having only a few lateral branches (Kitagawa 1969; Udar & Kumar 1980; Schuster 1980); also in *Cylindrocolea*, ventral-intercalary branching may be absent (Schuster 2002: 91).

In stem anatomy *Cephaloziella konstantinovae* resembles some other members of Cephaloziellaceae *s.str.*, namely all species of *Cephaloziopsis*, *Chonecolea*, *Cylindrocolea* subg. *Cylindrosocyphus*, *Cephalojonesia incuba*, *Cephaloziella crispata* and *C. stephanii* Schiffn. ex Douin.

*Cephaloziella konstantinovae* differs in some significant characters from species of Lophoziaceae sensu Schuster (1969). Members of the former Lophoziaceae are currently considered to belong to three families: Anastrophyllaceae (Söderström *et al.* 2010), Scapaniaceae, and Jungermanniaceae *s.str.* (Hentschel *et al.* 2007; Crandall-Stotler *et al.* 2009; Konstantinova *et al.* 2009; Vilnet *et al.* 2010). *Cephaloziella konstantinovae* differs from Anastrophyllaceae by the absence of any thickenings in cell walls, and from Scapaniaceae by the presence of regular well-developed (0.5–0.7 of leaf length) underleaves. The family Jungermanniaceae nowadays includes only the genera *Delavayella* Steph., *Jungermannia* L., *Eremonotus* Pearson, *Liochlaena* Nees and *Mesoptychia*

(Lindb.) A. Evans (Crandall-Stotler *et al.* 2009; Vána *et al.* 2012; Shaw *et al.* 2015). Members of these genera have large oil-bodies (Damsholt 2002), and fusiform to obovoid perianths with the mouth contracted to a narrow beak. In contrast, *Cephaloziella konstantinovae* has much smaller oil-bodies and a campanulate perianth with an uncontracted mouth; in other *Cephaloziella* species the oil-bodies are small as well, and the perianths are somewhat but not strongly contracted to the truncate mouth (Damsholt 2002; Schuster 2002).

PHYLOGENETIC RELATIONSHIPS  
AND MORPHOLOGICAL FEATURES WITHIN  
HOLARCTIC *CEPHALOZIELLA*

Our molecular phylogenies compelled us to reexamine the morphology of the included *Cephaloziella* accessions and to revise species identifications. Plants initially identified as *Cephaloziella arctogena* (R. M. Schust.) Konstant. ('Trans-Baikal Territory') with large underleaves on sterile shoots and without gemmae were found in one clade in the Bayesian tree together with plants determined as *C. elegans* (Heeg) Schiffn. ('Republic of Altai') characterized by purplish and violet pigmentation, broad leaf lobes (up to 9 cells wide), distinct underleaves, the presence of gemmae, and *C. rubella* ('Altai Territory') with narrow leaf lobes (5–7 cells wide), claret red to violet pigmentation, and small indistinct underleaves on both fertile and gemmiferous shoots. We consider our molecular data to be supportive of a treatment of *C. arctogena* and *C. elegans* as varieties of *C. rubella*: *C. rubella* var. *arctogena* R. M. Schust. and *C. rubella* var. *elegans* (Heeg) R. M. Schust. respectively. It should be noted that the specimen 'Trans-Baikal Territory' of *C. rubella* forms a long branch in the Bayesian tree and a separate subclade in the MP tree.

The *C. rubella* clade is resolved as sister to *C. elachista* in both BA and MP topologies. *Cephaloziella elachista* is the type of section *Schizophyllum* (Müll. Frib.) Jørg., and *C. rubella* is the type of section *Rubellae* R. M. Schust. Hence, section *Rubellae* probably should be reduced to a synonym of section *Schizophyllum*.

The close affinity between *Cylindrocolea recurvifolia* and other species of *Cephaloziella*

is evident from the presented phylogenetic trees. This species is nested within clade A together with *C. kiaeri* and *C. microphylla*, being related to them in several identical nucleotide substitutions as well as unique insertions and deletions in both ITS1-2 and *trnL-F*. Accordingly, *Cylindrocolea recurvifolia* should be treated as *Cephaloziella recurvifolia* (Steph.) S. Hatt. Members of clade A share autoicy and an East Asian origin.

*Cephaloziella spinicaulis* is resolved within the group of clades A, B, and *C. konstantinovae* in the Bayesian tree, or a well-supported subclade distant to clades A, B, and C in the MP topology. It resembles species of clade A in its tendency to form flagelliform shoot apices and frequent axillary postical intercalary branches. However, it is a dioecious species with (i) a disjunctive, probably relictual distribution in East Asia and eastern North America, and (ii) a conspicuously roughened stem with numerous spine-like, simple or bifurcate projections of 1–4 cells arranged in longitudinal lines.

*Cephaloziella turneri* is separated from all other Cephaloziellaceae elements in the BA and MP topologies. The remote affinity of *C. turneri* to other congeneric species was also shown in Feldberg *et al.* (2013). This species produces angulate gemmae, whereas other analyzed species of *Cephaloziella* have smooth elliptical gemmae.

*Cephaloziella varians* appears to be a highly variable species that is widely distributed in Russia, especially in the mountains of southern Siberia and the Russian Far East. All studied specimens are identical in *trnL-F* and have minor differences in ITS sequences. All specimens have irregular and entire (not bifid) underleaves of different sizes. The majority of these specimens consist of sterile plants only, and were thus initially assigned to *C. divaricata* or *C. polystratosa* (R. M. Schust. & Damsh.) Konstant. Some autoecious specimens were initially determined as *C. grimsulana* due to having obtuse or rounded leaves and large leaf cells, or as *C. uncinata* and *C. spinigera* due to the presence of elongated, somewhat hooked leaves and small leaf cells.

The 'true' *Cephaloziella divaricata* seems to be rare in Russia. Only a single specimen from Sakhalin (*Bakalin S-24-21-09*) is found

in one clade with the specimen identified earlier as *C. stellulifera* (Taylor) Schiffn. from the Netherlands (*Konstantinova 1e-2-99*). The plants of *C. divaricata* from Sakhalin are sterile and have regular well-developed (ca 0.5 of leaf length) bifid underleaves, whereas the specimen of *C. stellulifera* contains plants bearing only paroecious inflorescences, well-developed bifid underleaves up to 0.7 of leaf length, and large cells at the base of leaf lobes, 17–19  $\mu\text{m}$ .

Specimens initially identified as *C. uncinata* R. M. Schust. ('Kamchatka Territory 1'), *C. subdentata* Warnst. ('Murmansk Province') and *C. hampeana* (Nees) Schiffn. ex Loeske ('Kamchatka Territory 2') share largely similar DNA sequences. They were all placed in *C. hampeana* due to these features: (i) leaf cells 14–16  $\mu\text{m}$  wide, (ii) leaf lobes up to 7–8 cells wide at base, (iii) the absence of underleaves, and (iv) strongly connate (up to 2/3 their height) female bracts and bracteoles. The taxonomy of the morphologically similar species *C. uncinata* and *C. hampeana* needs additional study.

Members of clade C are morphologically heterogeneous yet show only low levels of ITS and *trnL-F* sequence variation. Follow-up studies need to include more variable marker systems and more extensive sampling.

#### DESCRIPTION OF THE NEW SPECIES

***Cephaloziella konstantinovae*** Mamontov & Vilnet, *sp. nov.* Figs 3–29

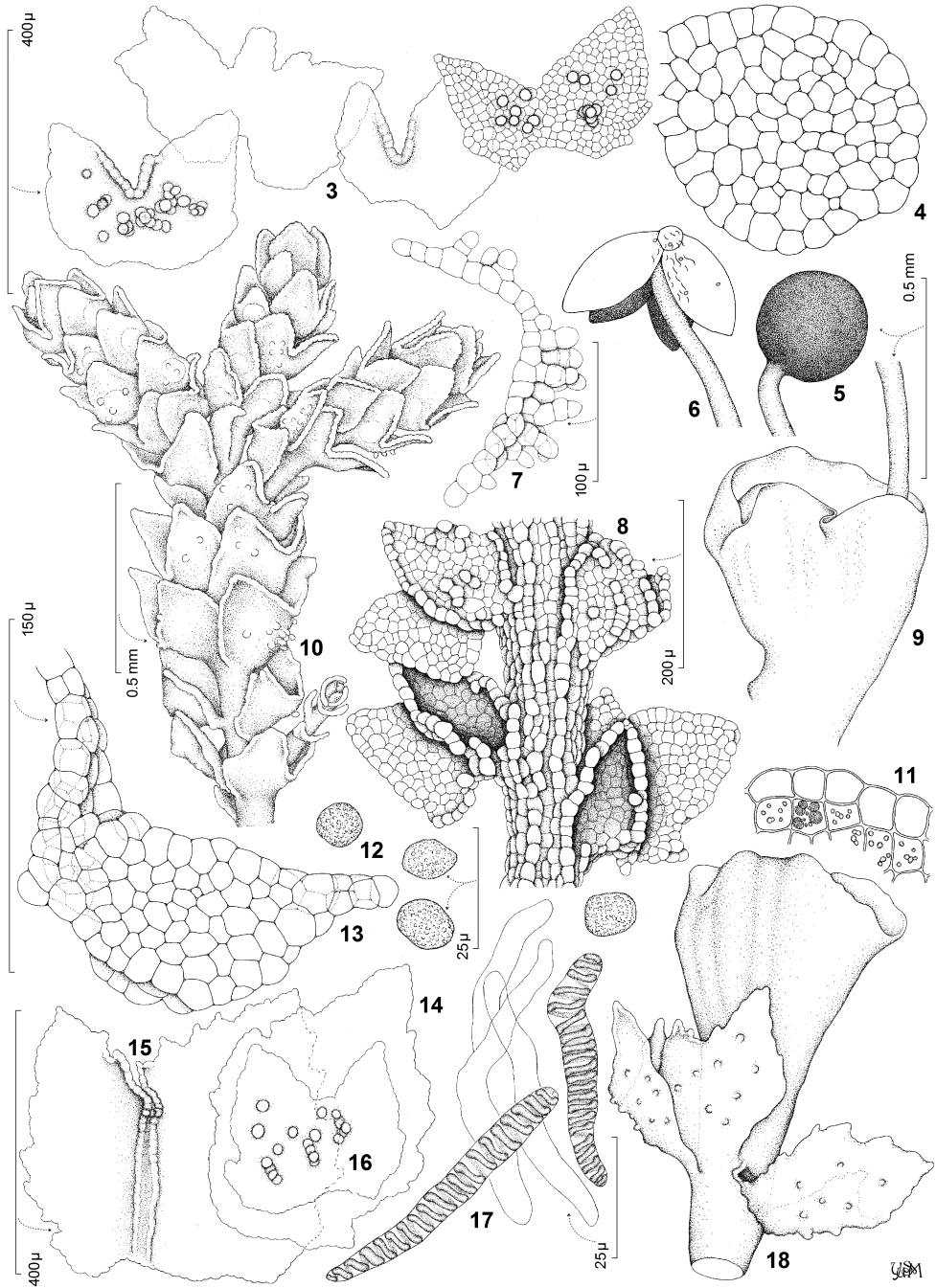
**DIAGNOSIS.** The new taxon resembles many other species of *Cephaloziella* by its large underleaves and multicellular outgrowths on the dorsal leaf face, but differs by unusual characters of the reproductive structures: (i) female bracts and bracteole not connate, (ii) campanulate perianth, (iii) rectangular to subquadrate cells of perianth mouth, (iv) spherical capsule, (v) seta composed of 8–10 outer and 4–6 inner cell rows, and (vi) elaters with 1–2 spiral bands.

**TYPE:** RUSSIA, TRANS-BAIKAL TERRITORY, Kheny-Chikoyskoye Nagor'e Uplands, Sokhondinskiy State Biosphere Reserve, valley of Sokhondo River, 49°30'N,

111°04'E, 1205 m a.s.l., 23 Aug. 2011, *Mamontov 166-7* (HOLOTYPE: KPABG; ISOTYPES: G, LE, MHA, NICH).

**DESCRIPTION.** Plants delicate, dull green, with red-brown secondary pigmentation mostly on leaf margins, shining in dry condition, ascending to erect (Figs 20 & 24). Shoots up to 0.6 mm wide and 5 mm long. Stems 70–160  $\mu\text{m}$  in diameter, 9–12 cells across. Cortical and medullary region indistinct in cross section, cells thin-walled throughout (Figs 4 & 13), peripheral cells somewhat larger, 10–16(–19)  $\mu\text{m}$ , central cells 10–13(–17)  $\mu\text{m}$ . Cortical cells of the stem thin-walled, inflated, mostly rounded-rectangular in view from above, 18–35  $\mu\text{m}$  long, 11–19  $\mu\text{m}$  wide. Branching abundant, terminal and lateral-intercalary (Figs 10, 20, 21, 24), without ventral-intercalary branches and subfloral innovations. Rhizoids small, hyaline, indistinct. Leaves succubous, distant, almost transversely inserted, concave-conduplicate, with reflexed margins, subquadrate to oblate, or obtrapezoidal, 200–260  $\mu\text{m}$  long, 280–410  $\mu\text{m}$  wide, asymmetrical, divided 0.4–0.8 of the length into two divergent lobes 5–20 cells wide at base, sometimes trilobed (Fig. 3), armed on abaxial face with outgrowths similar to marginal teeth, 1–4 cells long and 1–3 cells wide at base, (Figs 3, 7, 8, 10, 16, 18, 19–22, 24). Leaf lobes unequal or rarely nearly equal-sized, dorsal lobe usually smaller (shorter and more narrow) than ventral one, apex acute to obtuse, or rounded, sinus acute to obtuse. Leaf margins mostly irregularly crenulate by convex and projected cells, usually with 1–3 irregular, obtuse or rounded teeth 1–4 cells long and 1–7 cells wide at base, unistratose throughout (Figs 3, 8, 22, 23). Leaf cells rectangular to rounded, uniformly thin-walled, inflated, 11.5–16(–20)  $\mu\text{m}$  wide at base of lobes. Oilbodies 3–7 per cell, 1–3  $\times$  1–2.3  $\mu\text{m}$ , spheroidal to ellipsoid, smooth (Fig. 11). Underleaves mostly 0.5–0.7 of leaf length, 130–180(–250)  $\mu\text{m}$  long and 65–130(–180)  $\mu\text{m}$  wide, 4–6(–12) cells wide, entire or with lateral teeth or lobes (Figs 20, 22, 26), margins crenulate by convex, projecting cells. Gemmae not observed.

Autoecious, but pseudodioecious due to the fragility of the plants. Androecia on main shoots



**Figs 3–18.** *Cephalozia konstantinovae* Mamontov & Vilnet, sp. nov. 3 & 16 – leaves, abaxial face, 4 & 13 – stem cross sections, 5 – closed capsule, 6 – opened capsule, 7 – cross section of leaf base, 8 – part of shoot, dorsal aspect, 9 & 18 – perianths, 10 – cluster of male branches, 11 – cells of perianth mouth with oil-bodies (light) and chloroplasts (black) indicated, 12 – spores, 14 – female bracteole, 15 – female bract, 17 – elaters. 3, 4, 7, 8, 10, 11, 13–16 from *Mamontov 166-7* (KPABG); 6, 9, 17 from *Mamontov 169-5* (KPABG); 5, 12, 18 from *Afonina 6010* (KPABG).

and on clusters of short terminal branches (Figs 10 & 21), bracts usually in 3–4 pairs, strongly concave, with reflexed margins, similar in size with leaves. Antheridium single per bract, body globose to subglobose, stalk uniseriate. Gynoecia terminal on main shoot or on short branches. Female bracts (Figs 15 & 28) in one pair, larger than leaves, up to 450  $\mu\text{m}$  long and 500  $\mu\text{m}$  wide, entirely free from each other, not to slightly saccate, margins dentate by large irregular multicellular teeth 1–5 cells high, bilobed to 1/3 of their length. Female bracteole (Fig. 14) 430–470  $\mu\text{m}$  long and 300–350  $\mu\text{m}$  wide, with acute to obtuse apex, bilobed less than 1/3 of length, or unlobed, entirely free from bracts, sometimes absent. Perianth 0.7–1.2 mm long, up to 0.6 mm wide, usually campanulate, slightly plicate near apex, longly exerted beyond bracts, mouth wide and wavy, truncate (Figs 9, 18, 28). Perianth surface usually covered by outgrowths 1–2 cells long, 1–2 cells wide at base, similar to outgrowths originated on dorsal leaf surface (Figs 28 & 29); marginal cells of perianth mouth rounded-rectangular to subquadrate, 11–15  $\times$  11–18  $\mu\text{m}$ , thin-walled throughout, convex (Fig. 11). Seta 0.4–0.8 cm long, with 8–10 outer and 4–6 inner cells in cross section; cross-section area of an outer cell varies in the range of 402–1060  $\mu\text{m}^2$ , and the collective cross-section area of inner cells varies from 405 to 630  $\mu\text{m}^2$  (Figs 25 & 27). Capsule spherical, dark brown, ca 250–300  $\mu\text{m}$  in diameter (Figs 5 & 6). Spores light brown, rounded to elliptical, 8.8–12.5  $\times$  8.2–11.5  $\mu\text{m}$ , verruculose (Fig. 12). Elaters 4.7–7.5  $\mu\text{m}$  in diameter, up to 65  $\mu\text{m}$  long, with 1–2 spiral bands (Fig. 17).

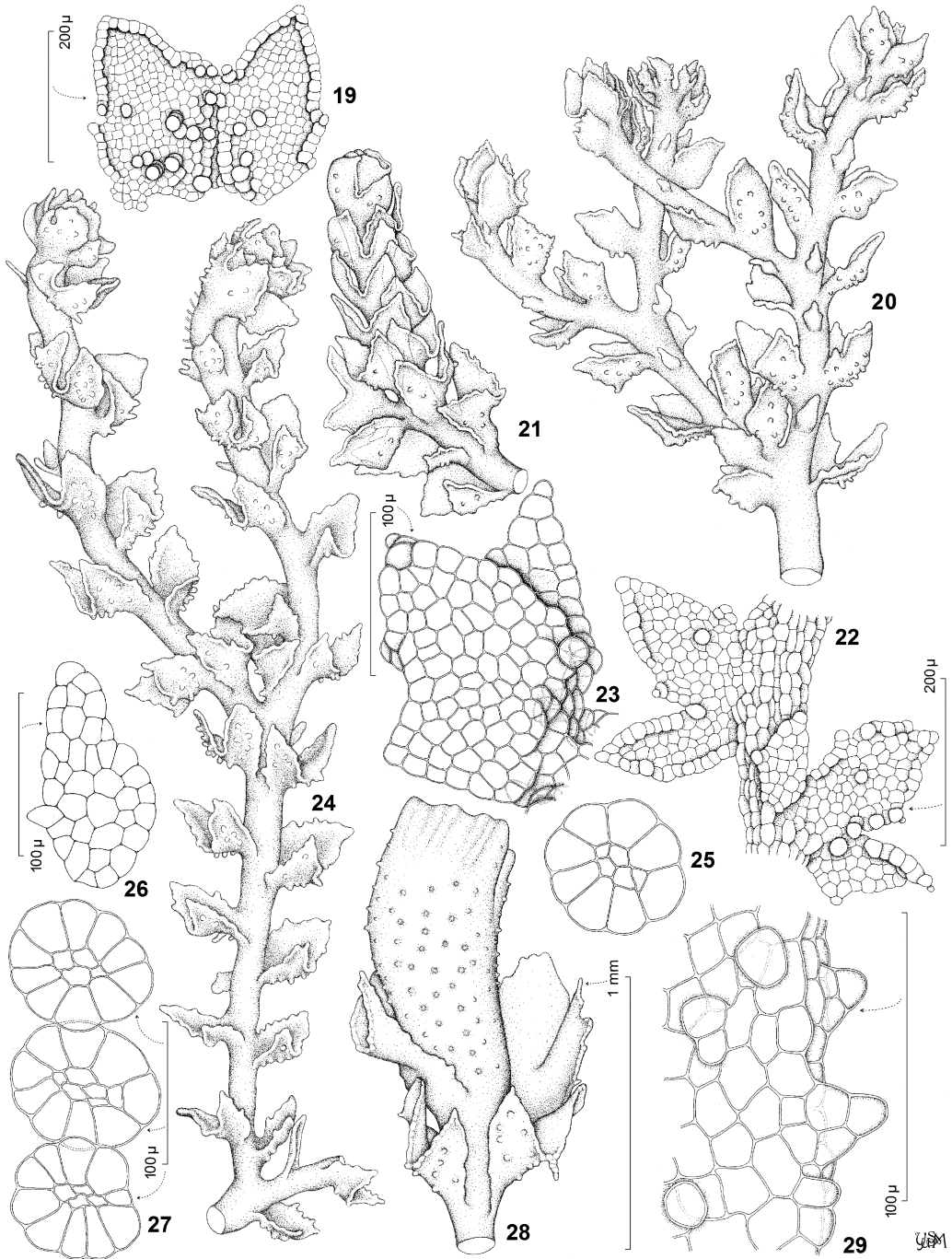
**ETYMOLOGY.** The species is named in honor of Prof. Dr. Nadezhda A. Konstantinova, eminent Russian hepaticologist.

**DISTRIBUTION.** In Siberia, *Cephaloziella konstantinovae* is common in low mountain areas in the south of the Republic of Buryatia and Trans-Baikal Territory, and possibly common in the north of Mongolia (Bulgan and Tuv Provinces), but becomes more rare towards the north. It was collected sporadically on the Barguzin and South Muya ranges in the north of Buryatia, and on Kodar Range in the north of Trans-Baikal

Territory, but was not found north of 57°N. In Primorye Territory, the Russian Far East, *C. konstantinovae* was collected only once.

**ECOLOGY.** In Siberia, *C. konstantinovae* occurs in low mountain steppe communities and forests dominated by *Larix dahurica* Turcz. and *L. sibirica* Ledeb., but was not found in mountain forests where *Pinus pumila* (Pall.) Regel occurs. It grows in pure dense patches on soil in rock niches or on thin soil overlying vertical rock surfaces in partial shade, and also as an admixture to other saxicolous hepatics, especially of the genus *Frullania* Raddi. The elevation range in Trans-Baikal Territory and the Republic of Buryatia (ca 49–56°N) is ca 500–1600 m a.s.l. However, in Tuv Aimag, in northern Mongolia, it was collected at 1840 m a.s.l. (Tsegmed & Bai 2013, as *Cephaloziella microphylla*). The liverworts most commonly associated with *C. konstantinovae* in all types of habitats were *Frullania muscicola* Steph., *F. inflata* Gottsche, *F. bolanderi* Austin and *F. parvistipula* Steph. Also, *Metzgeria pubescens* (Schrank) Raddi, *Barbilophozia barbata* (Schmidel ex Schreb.) Loeske, *Frullania davurica* Hampe, *Lophoziopsis excisa* (Dicks.) Konstant. & Vilnet, *Metzgeria furcata* (L.) Corda and *M. temperata* Kuwah. were collected together with *C. konstantinovae* on rocks in forests, whereas *Clevea nana* (Shimizu & S. Hatt.) Borovich. & Bakalin, *Reboulia hemisphaerica* (L.) Raddi and *Targionia hypophylla* L. were associated with *Cephaloziella konstantinovae* mostly on rocky steppe slopes along trails and water-courses. In Primorye Territory, *C. konstantinovae* was found on cliff outliers in broadleaved forest on a west-facing mountain slope at ca 280 m a.s.l., associated with *Frullania muscicola* and *Acrolejeunea sandvicensis* (Gottsche) J. Wang & Gradst.

**OTHER SPECIMENS EXAMINED (PARATYPES).** RUSSIA: TRANS-BAIKAL TERRITORY: Khentey-Chikoyskoye Nagor'e Uplands, upper of Bukukun River, 1463 m alt., 49°37'N, 111°00'E, 24 July 2007, *Afonina 04808-8* (LE); same uplands, valley of Ende River, 1184 m alt., 49°26'N, 110°51'E, 11 July 2010, *Afonina 1810-1* (MHA); same place, 1161 m alt., 15 July 2010, *Afonina 2910-2* (G), *2910-4* (NICH), *2910-6* (JE), *2910-7* (VBGI), *2910-8* (KPABG); same place, 1161 m alt., 49°27'N, 110°50'E, 15 July 2010, *Afonina 3010-4* (G);



**Figs 19–29.** *Cephaloziella konstantinovae* Mamontov & Vilnet, *sp. nov.* 19 & 23 – leaves, abaxial face, 20 – habit, ventral aspect, 21 – male branch, 22 – part of shoot, ventral aspect, 24 – habit, dorsal aspect, 25 & 27 – cross sections of seta, 26 – enlarged underleaf, 28 – perianth, 29 – perianth surface. 19, 22, 23 from *Mamontov 166-7* (KPABG); 20, 21, 24, 26–29 from *Afonina 6010* (KPABG).

same place, 1162 m alt., 49°26'N, 110°51'E, 24 Aug. 2011, *Mamontov 169-5* (KPABG), *169-11* (MO), *173-5-2* (G), *178-13-1* (E), *178-8-1* (NICH); Khentey-Chikoyskoye Nagor'c Uplands, valley of Ende River, lower reaches of Khukhje-Bajtsa Brook, 1214 m alt., 49°27'N, 110°52'E, 27 Aug. 2011, *Mamontov 182-4-2* (KPABG); same uplands, valley of Agutsa River, 1164 m alt., 49°38'N, 111°27'E, 17 July 2010, *Afonina 3410-1* (LE), *3410-2* (KPABG); same uplands, valley of Agutsa River, 1399 m alt., 49°40'N, 111°26'E, 22 July 2010, *Afonina 5510-3* (NICH), *5510-4* (LE); same place, 1300 m alt., 49°40'N, 111°26'E, 23 July 2010, *Afonina 6010-1* (G, KPABG, MHA), *Afonina 6010-5* (LE); same uplands, valley of Ingoda River, 1332 m alt., 49°56'N., 111°10'E., 17 July 2013, *Mamontov 372-1-1* (NICH); same uplands, Khapcheranginskiy Range, valley of Tyrin River, 1078 m alt., 49°05'N, 112°20'E, 29 July 2005, *Afonina 6805-1* (KPABG); same uplands, near Kyra settlement, valley of Kyra River, 890 m alt., 49°33'N, 112°00'E, 17 Aug. 2011, *Mamontov 112-2* (MHA); same uplands, valley of Sokhondo River, 1205 m alt., 49°30'N, 111°04'E, 23 Aug. 2011, *Mamontov 166-6* (VBGI), *166-8-1* (MHA), *166-8-2* (NICH), *166-8-3* (KPABG); same uplands, Atsinskiy Range, upper reaches of Vankina Brook, 1466 m alt., 50°09'N, 109°09'E, 11 Aug. 2011, *Mamontov 94-1* (LE), *94-2* (MO) *94-10-3* (KPABG), *94-11-1* (G), *94-8-1* (JE); Malkhanskiy Range, Cheremkhovo Pass, valley of Vyezdzhaya Brook, 1181 m alt., 50°44'N, 110°22'E, 13 Aug. 2011, *Mamontov 104-2-1* (G), *104-2-2* (GOET), *104-3-2* (VBGI), *104-3-3* (KPABG); same place, 1360 m alt., 50°44'N, 110°22'E, 14 Aug. 2011, *Mamontov 105-2-6* (UBC); Dauriski Range, 7 km NNE of Kaidalovo railway station, 755 m alt., 51°41'N, 114°00'E, 15 July 2007, *Afonina 05307-4* (SASY), *05307-6* (LE), *05307-7* (KPABG); same range, Aratsagon Mt., 956 m alt., 51°54'N, 114°25'E, 13 July 2012, *Mamontov 264-6-6* (MO), *264-11-1* (NY), *264-11-2* (HSNU), *264-11-3* (MHA), *264-13-1* (KPABG), *264-18-2* (KPABG), *264-7-1* (NY), *264-8-2* (MHA), *264-8-3* (NICH), *264-8-4* (LE), *264-8-5* (MW), *264-9-1* (LE), *264-9-2* (NICH), *264-9-3* (MHA), *264-9-4* (MW); same place, 813 m alt., 13 July 2012, *Mamontov 265-3-12* (MHA), *265-5-2* (KPABG), *265-5-3* (KPABG), same place, 892 m alt., 13 July 2012, *Mamontov 262-1-6* (NICH); same place, *Czernyadjeva 2-12* (MHA); same range, 5 km to the east of Duldurga Settlement, Elo-Rahanai Mt., 772 m alt., 50°50'N, 113°24'E, 13 July 2006, *Afonina 4006-2* (GOET), *4006-3* (MHA), *4006-4* (KPABG), *4006-5* (KPABG), *4006-6* (KPABG), *4006-7* (LE), *4006-8* (G); Kiya River near Schilka Town, 509 m alt., 51°53'N, 115°58'E., 17 July 2007, *Afonina 06107*

(LE); Cherskiy Range, road to Usugly settlement, 683 m alt., 52°33'N, 115°27'E, 15 July 2012, *Mamontov 268-6-1* (MO), *268-6-2* (HSNU), *268-6-3* (TNS); Stanovoye Nagor'c Uplands, Kodar Range, valley of Srednij Sakukan River, 1300 m alt., 56°54'N, 117°51'E, 3 July 2013, *Mamontov 352-1-1* (KPABG), *352-1-2* (G), *352-3-1* (JE), *352-3-2* (NICH). – REPUBLIC OF BURYATIA: East Sayan Mts., Okinskoe Plateau, valley of Oka River, 1599 m alt., 52°08'N, 100°20'E, 11 July 2015, *Mamontov 553-1-1* (KPABG), *553-1-2* (LE), *553-1-2* (MHA); Selenga River valley, 564 m alt., 51°32'N, 107°20'E, 25 July 2013, *Mamontov 374-1-1* (KPABG); Naushki town surroundings, 721 m alt., 50°23'N, 106°07'E, 23 July 2013, *Tubanova 01-13* (UUH). – PRIMORYE TERRITORY: Mikhajlovskij Range, 280 m alt., 43°51'N, 132°55'E, 3 June 2010, *Bakalin P-3-6a-10* (VBGI). MONGOLIA: BULGAN PROVINCE: Gurvanbulag District, Hogno-Hanuul, 1396 m alt., 47°26'N, 103°44'E, 18 June 2010, *Choi M5046* (VBGI). – TUV AIMAG: Erdene sum, valley of Terelj River, 15 June 1974, *Golubkova & Tsogt 29* (MHA); same district (aimag) Altanbulag sum, Khustai range, Khoshoot Mt., 23 July 2002, *Tsegmed 13276* (MHA).

NOTE. Most of the collections of *Cephaloziella konstantinovae* are sterile; therefore, an identification key for sterile plants of *Cephaloziella* from the Holarctic characterized by outgrowths on the abaxial leaf face is provided. The key is based on the studied type specimens of *Cephaloziella hunanensis* W. E. Nicholson and *Prionolobus matsuurai* S. Hatt. – the synonyms of *Cephaloziella microphylla* – and also the type specimen of *C. acantophora* (S. Hatt.) S. Hatt., the specimens of *C. massalongii*, *C. phyllacantha* and *C. spinicaulis* housed in KPABG, VBGI and LE, as well as the descriptions of the three latter species in Schuster (1980, 1988) and Damsholt (2002). The key distinctions of *C. divaricata* var. *asperifolia*, *C. uncinata* var. *mamillosa* R. M. Schust. & Damsh. and *C. mamillifera* R. M. Schust. & Damsh. are provided according to the descriptions in Schuster (1988); the key distinctions of *C. subtilis* (Lindenb. & Gottsche) Steph. follow its description in Fulford (1976). It should be noted that some of morphological distinctions of *C. mamillifera* are questionable. Schuster (1988: 214) notes that *C. mamillifera* has 'Leaves ... entire-margined ...', but this statement contradicts illustrations presented in the same publication,



particularly Figure 19: 2, 7–11, Figure 25: 3, 7 and Figure 26: 1, 2, 4, 16, where the leaves are toothed at the base or along the whole leaf margin.

KEY TO MORPHOLOGICALLY SIMILAR SPECIES  
OF *CEPHALOZIELLA* FROM THE HOLARCTIC

1. Stem armed throughout with numerous spine-like, simple or bifurcate, outgrowths 1–4 cells in height, arranged in longitudinal lines . . . . . *C. spinicaulis*
- 1\* Stem without such spine-like outgrowths . . . . . 2
  2. Stem armed with few and low, unicellular rounded outgrowths or short ridges . . . . . 3
  - 2\* Stem smooth . . . . . 4
3. Terminal branches, when present, *Acromastigum*-type, rarely *Frullania*-type. Dioecious . . . . . *C. aspecaulis*
- 3\* Terminal branches, when present, *Frullania*-type. Autoecious, but often sterile or pseudo-dioecious . . . . . *C. mamillifera*
4. Apices of leaves and underleaves (at least in some) consisting of a long 1-celled, acute and hyaline, thorn-like and somewhat curved or hooked tooth . . . . . *C. phyllacanta*
- 4\* Apices of leaves and underleaves not consisting of such thorn-like teeth . . . . . 5
5. Abaxial leaf surface and leaf margins ciliate, with numerous spine-like, 1–3-cells-long cilia. Underleaves absent or obsolete . . . . . *C. acantophora*
- 5\* Leaves not copiously ciliate. Underleaves present or absent . . . . . 6
  6. Almost all leaf cells dorsally projecting by high, acute or conical mamillae. Dorsal leaf surface with acute, 1(–2)-celled teeth. Underleaves vestigial to rather well developed, rarely absent. Autoecious. . . . . *C. microphylla*
  - 6\* Cells of leaf base dorsally smooth or mamilliose, or with outgrowths, remaining leaf cells smooth (not projecting) . . . . . 7
7. Leaf lobe apex acuminate, formed of (1–)2 superimposed cells. Outgrowths on dorsal leaf surface acute, conical to spiniform, of 1–2 superimposed cells, originated at base or near leaf sinus. Leaf margins at base usually with a few acute, 1–2 cells long teeth, rarely entire. Underleaves present, frequently bilobed, lobes with one to several marginal teeth . . . . . *C. massalongii*
- 7\* Leaf lobe usually ending in one cell. Outgrowths on dorsal leaf surface uni- to multicellular, obtuse to rounded, but not spiniform. Leaf margins with acute to obtuse unicellular teeth, or with obtuse to rounded teeth with multiple-row bases, or entire. Underleaves present or absent . . . . . 8
8. Cells of stem and leaves thin-walled, convex throughout. Leaves mostly unequally bilobed, margins crenulate or with remote, broadly obtuse teeth . . . . . 9
- 8\* Cells of stem and leaves more or less thick-walled. Leaves subequally bilobed, margins toothed with acute to obtuse cells . . . . . 10
9. Outgrowths on abaxial leaf surface usually unicellular. Underleaves absent on sterile shoots. Female bracts and bracteole strongly connate, forming a cup (North America: Mexico) . . . . . *C. subtilis*
- 9\* Outgrowths on abaxial leaf surface usually multicellular. Underleaves present on sterile shoots, well-developed, up to 0.7 of leaf length. Female bracts and bracteoles entirely free from each other (North Asia: Russia, Mongolia) . . . . . *C. konstantinovae*
10. Leaf margins dentate in lower half. Dioecious . . . . . *C. divaricata* var. *asperifolia*
- 10\* Leaf margins entire. Autoecious . . . . . *C. uncinata* var. *mamillosa*

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