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) Warmst.

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

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 & Váňa 2005; Schuster 1969, 1971, 1980, 1988, 1995, 1996, 2002; Schuster & Damsholt 1974; Udar & Nath 1976; Shljakov 1979; Udar & Kumar 1980, 1982). The most recently described species of the genus is Cephaloziella biokoensis Váňa & F. Müll. from Equatorial Guinea (Váňa & 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...
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 phytogeography, 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-Baikalian 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 Odontoschismataceae. 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 µl 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™ 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+Γ 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+Γ 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 10,000th 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-Baikalian 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                  |
|            |                   | trnL-F                  |
| *Alobiellopsis parvifolia* (Steph.) R. M. Schust. | Japan, *Bryophytes of Asia* Fasc. 8, No. 191 (KPABG) | JX629894 | JX630020 |
| *Barbilophozia barbata* (Schmidel ex Schreb.) Loeske | Netherlands, *Konstantinova* 3b-5-99 (KPABG) | EU791779 | EU791676 |
| *Cephaloziella affinis* Lindb. ex Steph. | Russia, Republic of Adygeya, *Konstantinova* 473-2-07 (KPABG) | JX629827 | JX629952 |
| *Cephaloziella divaricata* (Sm.) Schiffn. | Russia, Sakhalin Province, Sakhalin I., *Bakalin* S-24-21-09 (KPABG) | KF805881 | KF805923 |
| *C. elachista* (J. B. Jack) Schiffn. | Russia, Khanty-Mansi Autonomous Area 1, *Kukurichkin* OP1VN607/1 (KPABG), published as *C. rubella* in Vilnet *et al.* (2012) | JX629919 | JX630048 |
| *C. elachista* | Russia, Khanty-Mansi Autonomous Area 2, *Kukurichkin* OP1VN607/7 (KPABG), published in Vilnet *et al.* (2012) | JX629918 | JX630047 |
| *C. hampeana* (Nees) Schiffn. ex Loske | Russia, Kamchatka Territory 1, *Bakalin* 77-14-01-04 (as *C. uncinata*, KPABG) | KF805866 | KF805899 |
| *C. hampeana* | Russia, Kamchatka Territory 2, *Bakalin* 98-4-01-01-04 (as *C. subdentata*, KPABG) | KF805865 | KF805897 |
| *C. hampeana* | Russia, Murmansk Province, *Konstantinova* 182-3 (as *C. subdentata*, KPABG) | KF805864 | KF805898 |
| *C. kiaeri* (Austin) Douin | Borneo, Kinabalu, *Konstantinova* K-9-4 (KPABG) | KF805888 | KF805935 |
| *C. kiaeri* | Japan, *Bryophyte Selecta* Exsiccatae, No. 1218 (KPABG) | KF805886 | KF805934 |
| *C. kiaeri* | Republic of Korea, *Bakalin* Kor-2-14-09 (KPABG) | KF805887 | KF805933 |
| *C. konstantinovae* Mamontov & Vilnet, sp. nov. | Russia, Trans-Baikal Territory 1, *Afonia* 4006-5 (KPABG) | KF805882 | KF805924 |
| *C. konstantinovae* | Russia, Trans-Baikal Territory 2, *Afonia* 4006-6 (KPABG), published as *C. aspericaulis* in Bakalin & Vilnet (2014) | KF471666 | KF471664 |
| *C. konstantinovae* | Russia, Trans-Baikal Territory 3, *Afonia* 6010-1 (KPABG) | KF805883 | KF805925 |
| *C. konstantinovae* | Russia, Trans-Baikal Territory 4, *Afonia* 05307-7 (KPABG), published as *C. aspericaulis* in Vilnet *et al.* (2012) | JX629917 | JX630044 |
| *C. konstantinovae* | Russia, Trans-Baikal Territory 5, *Mamontov* 169-5 (KPABG) | KF805884 | KF805926 |
| *C. microphylla* (Steph.) Douin | Republic of Korea 1, *Hepaticae Korea* Exsiccatae Fasc. II, No. 23 (KPABG) | KF805889 | KF805937 |
| *C. microphylla* | Republic of Korea 2, *Hepaticae Korea* Exsiccatae Fasc. I, No. 29 (KPABG) | KF805890 | KF805938 |
| *C. rubella* (Nees) Warnst. | Russia, Altai Territory, *Mamontov* 214-14 (KPABG) | KF805885 | KF805927 |
| *C. rubella* | Russia, Republic of Altai, *Mamontov* 330-5-1 (as *C. elegans*, KPABG) | KF853559 | KF853560 |
| *C. rubella* | Russia, Trans-Baikal Territory, *Afonia* 45907 (as *C. arctogenas*, KPABG), published in Vilnet *et al.* (2012) | JX629916 | JX630045 |
| *C. spinicaulis* Douin | Russia, Primorsky Territory, *Bakalin* P-63-3-98 (KPABG) | KF805896 | KF805947 |
| *C. spinicaulis* | Japan, *Deguchi*, *Exsiccatae* Fasc. 5, No. 119 (published in Vilnet *et al.* 2012) | JX629922 | JX630043 |
| *C. stellulifera* (Taylor) Schiffn. | Netherlands, *Konstantinova* 1e-2-99 (KPABG), published in Vilnet *et al.* (2012) | JX629923 | JX630042 |
| *C. turneri* (Hook.) Müll. Frib. | Russia, Krasnodar Territory, *Ignatov & Ignatova* 02-24a (KPABG) | KF805892 | KF805944 |
| Taxon name | Voucher specimens | GenBank accession number |
|------------|-------------------|-------------------------|
| *C. varians* (Gottsche) Steph. | Norway, Svalbard 1, Konstantinova K78-1-06 (KPABG) | KF805877 (ITS1) KF805863 (ITS2) KF805914 |
| *C. varians* | Norway, Svalbard 2, Konstantinova K115-02 (as *C. grimsulous*, KPABG) | KF805878 KF805915 |
| *C. varians* | Norway, Svalbard 3, Konstantinova K130-2-04 (as *C. uncinata*, KPABG) | KF805880 KF805920 |
| *C. varians* | Russia, Altai Territory, Manontov 219-5 (as *C. divaricata*, KPABG) | KF805876 (ITS1) KF805862 (ITS2) KF805912 |
| *C. varians* | Russia, Republic of Karachaevo-Cherkessia 1, Konstantinova K515-1-05 (as *C. divaricata*, KPABG) | KF805874 KF805908 |
| *C. varians* | Russia, Republic of Karachaevo-Cherkessia 2, Konstantinova K517-2-05 (as *C. divaricata*, KPABG) | KF805873 KF805907 |
| *C. varians* | Russia, Kamchatka Territory, Bakalin K-105-5-03 (KPABG) (published in Vilnet et al. 2012) | JX629924 JX630051 |
| *C. varians* | Russia, Murmansk Province, Konstantinova K 8-2-12 (KPABG) | KF805871 (ITS1) KF805861 (ITS2) KF805904 |
| *C. varians* | Russia, Magadan Province, Bakalin Mag-7-40-10 (as *C. spinigera*, KPABG) | KF805872 KF805905 |
| *C. varians* | Russia, Sakhalin Province, Sakhalin 1., Bakalin S-58-3-09 (as *C. divaricata var. asperifolia*, KPABG) | KF805879 KF805917 |
| *C. varians* | Russia, Trans-Baikal Territory 2, Afonina 07408 (as *C. divaricata*, published in Vilnet et al. 2012, KPABG) | JX629921 JX630050 |
| *C. varians* | Russia, Trans-Baikal Territory 3, Afonina A1810 (KPABG), published as *C. polystratosa* in Bakalin & Vilnet (2014) | KF471665 JX630046 |
| *C. varians* | Russia, Trans-Baikal Territory 4, Afonina A2410 (KPABG) | KF805867 KF805900 |
| *C. varians* | Russia, Trans-Baikal Territory 5, Afonina A3010 (as *C. divaricata*, KPABG) | KF805870 KF805903 |
| *C. varians* | Russia, Trans-Baikal Territory 6, Afonina A4805 (as *C. polystratosa*, KPABG, published in Vilnet et al. 2012) | JX629920 JX630049 |
| *C. varians* | Russia, Trans-Baikal Territory 7, Afonina, A5610/4, (as *C. polystratosa*, KPABG) | KF805869 KF805902 |
| *C. varians* | Russia, Trans-Baikal Territory 8, Afonina, A6010b, (as *C. polystratosa*, KPABG) | KF805868 KF805901 |
| *Cylindrocolea recurvifolia* (Steph.) Inoue | Japan, Kiushu, Exsiccatae Bryophytes of Asia Fasc.14 # 344 (KPABG) | KF805891 KF805939 |
| *Diplophyllum albicans* (L.) Dumort. | Russia, Republic of Karachaevo-Cherkessia, Konstantinova & Savchenko, K446-7-05 (KPABG) | EU791773 EU791659 |
| *Douinia imbricata* (M. Howe) Konstant. & Vilnet | USA, Alaska, Konstantinova, 110-2-92a (KPABG) | EU791770 EU791658 |
| *Gymnocolea inflata* (Huds.) Dumort. | Norway, Spitsbergen, Konstantinova, 118-1-04 (KPABG) | EU791787 EU791661 |
| *Heterogemma capitata* (Hook.) Konstant. & Vilnet | Russia, Nizhny Novgorod Province, Konstantinova, 132-03 (KPABG) | DQ875119 DQ875080 |
| *Isopaches decolorans* (Limpr.) H. Buch | Russia, Republic of Karachaevo-Cherkessia, Konstantinova & Savchenko, K464-3-05 (KPABG) | EU791798 EU791680 |
| *Lophozia ascendens* (Warnst.) R. M. Schust. | Russia, Republic of Buryatia, Konstantinova & Savchenko, 109-3-01 (KPABG) | DQ875089 DQ875054 |
| *Lophozia excisa* (Dicks.) Konstant. & Vilnet | Norway, Spitsbergen, Konstantinova, K-21-2-05 (KPABG) | DQ875093 DQ875058 |
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 allow 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

| Taxon name | Voucher specimens | GenBank accession number |
|------------|-------------------|--------------------------|
| **Neoorthocaulis attenuatus** (Mart.) L. Söderstr., De Roo & Hedd. | Russia, Sakhalin Province, Harpel & Cherdantseva, 105728 (KPABG) | EU722343 EU727538 |
| **Odontoschisma demudatum** (Nees) Dumort. | Czech Republic, Konstantinova, 103546 (KPABG) | JX629877 JX630008 |
| **O. fluitans** (Nees) L. Söderstr. & Váňa | Russia, Kamchatskaya Province, Bakalin, K-13-7-03 (KPABG) | JX629885 JX630012 |
| **Protolophozia elongata** (Steph.) Schljakov | Russia, Murmansk Province, Bakalin, 3-1-02 (KPABG) | DQ875116 DQ875078 |
| **Pseudolophozia debiliformis** (R. M. Schust. & Damsh.) Konstant. & Vilnet | Russia, Republic of Karachaevo-Cherkessia, Konstantinova & Savchenko K510-1-05 (KPABG) | EF065692 EF065685 |
| **Pseudotritomaria heterophylla** (R. M. Schust.) Konstant. & Vilnet | Russia, Krasnoyarskiy Territory, Fedosov, 107960 (KPABG) | EU791806 EU791687 |
| **Saccobasis polymorpha** (R. M. Schust.) Schljakov | Russia, Murmansk Province, Konstantinova, 21-3b-96 (KPABG) | EU791807 EU791688 |
| **Scapania apiculata** Spruce | Russia, Republic of Buryatia, Konstantinova, Hepaticae Rossica Exsiccatae № 49 (KPABG) | EU791741 EU791633 |
| **Schljakovia kunzeana** (Huebner) Konstant. & Vilnet | Russia, Murmansk Province, Konstantinova, 181-02 (KPABG) | EU722349 EU727544 |
| **Sphenolobus minutus** (Schreb.) Berggr. | Norway, Spitsbergen, Konstantinova, 68-1-06 (KPABG) | EU791789 EU791667 |
| **Tetralophozia filiformis** (Steph.) Urmi | Russia, Republic of Buryatia, Konstantinova & Savchenko, 13-24-01 (KPABG) | EU791792 EU791669 |
| **Tritomaria exsectiformis** (Breidl.) Loeske | Russia, Republic of Buryatia, Konstantinova, 83-4-01 (KPABG) | EU791801 EU791683 |
Fig. 1. Phylogenetic tree for suborder Cephaliziineae 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.
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 spini-caulis 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. Protomar-supella R. M. Schust.), Amphicephalozia R. M. Schust., Cephalojonesia Grolle, Cephalomitrion R. M. Schust., Cephaloziella, Cephaloziopsis (Spruce) Schiffn., Chonecolea Grolle, Cylindrocolea R. M. Schust., Gymnocoleopsis (R. M. Schust.) R. M. Schust., Kymatocalyx Herzog (incl. Stenorrhipsis 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. VBGI) and published as C. aspericaulis Jörg. 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 siliques. 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 sub-truncate, (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, Cephalomitrion and Chonecolea of Cephaloziellaceae s.str. In Cephaloziella konstantinovae the seta is 8–10 + 4–6-seriate, whereas in the monospecific genus Cephalomitrion 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 Protolophozia elongata (Steph.) 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 Lophoziaeae 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 Anastrophylaceae + 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, Cephalomitrion, Cylindrocolea, Ky-matocalyx 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. Cylindroscyphus (Douin) R. M. Schust., namely Cylindrocolea atroviridis (Sim) Vána, 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. Cylindroscyphus – 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 atypical for Cephaloziellaceae s.str. but occurs in Lophoziaeae 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. Cylindroscyphus, Cephaloziella incuba, Cephaloziella crispata and C. stephanii Schiffn. ex Douin.

Cephaloziella konstantinovae differs in some significant characters from species of Lophoziaeae sensu Schuster (1969). Members of the former Lophoziaeae are currently considered to belong to three families: Anastrophylaceae (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 Anastrophylaceae 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
contracted mouth; in other oil-bodies and a campanulate perianth with an uncontracted mouth. 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 autoecy 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 relicual 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 obtruse 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 µm.

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 µm 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.

**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, Khen-tey-Chikoyskoye Nagor’e Uplands, Sokhonodinsky 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 µm 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) µm, central cells 10–13(–17) µm. Cortical cells of the stem thin-walled, inflated, mostly rounded-rectangular in view from above, 18–35 µm long, 11–19 µm 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 oblanceolate, 200–260 µm long, 280–410 µm 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, 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, sometimes trilobed (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) µm wide at base of lobes. Oil-bodies 3–7 per cell, 1–3 × 1–2.3 µm, spheroidal to ellipsoidal, smooth (Fig. 11). Underleaves mostly 0.5–0.7 of leaf length, 130–180(–250) µm long and 65–130(–180) µm 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. Cephaloziella 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 µm long and 500 µm 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. 16) 430–470 µm long and 300–350 µm 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 exserted 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 × 11–18 µm, 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 µm², and the collective cross-section area of inner cells varies from 405 to 630 µm² (Figs 25 & 27). Capsule spherical, dark brown, ca 250–300 µm in diameter (Figs 5 & 6). Spores light brown, rounded to elliptical, 8.8–12.5 × 8.2–11.5 µm, verruculose (Fig. 12). Elaters 4.7–7.5 µm in diameter, up to 65 µm 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 north 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* Turecz. 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, *Lophoziosis 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 watercourses. 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**: Khtenty-Chikoyskoye Nagor’e Uplands, upper of Bukukun River, 1463 m alt., 49°37´N, 111°00´E, 24 July 2007, *Afonina* 40880-8 (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. Cephalozia 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°56´N., 110°51´E, 24 Aug. 2011, Mamontov 553-2-1 (MHA); same uplands, valley of Ingoda River, 1332 m alt., 49°33´N., 112°00´E, 17 July 2010, Afonina 3410-2 (KPABG); same uplands, valley of Agutsa River, 1214 m alt., 49°27´N., 110°52´E, 27 Aug. 2011, Afonina 264-8-5 (KPABG); same uplands, valley of Sokhondo River, 1300 m alt., 49°40´N, 111°26´E, 23 July 2010, Afonina 6010-1 (G, KPABG, MHA), Afonina 6010-5 (LE); same place, valley of Ingoda River, 1332 m alt., 49°56´N., 110°10´E, 17 July 2013, Mamontov 372-1-I (NICH); same uplands, Khapcheranginskiy Range, valley of Tyrin River, 1078 m alt., 49°05´N, 112°20´E, 17 Aug. 2013, 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 (KPABG), 166-8-1 (MHA), 166-8-2 (NICH), 166-8-3 (KPABG); same uplands, Atsin斯基 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); Malkhansky Range, Cheremkhovo Pass, valley of Vyetzhayha River, 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); Daursky 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, Czernyadyjeva 2-12 (MHA); same range, 5 km to the east of Duldurga Settlement, Elogo-Rahanaiy 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 Usugy 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); Stanoyvoye Nagore’ Uplands, Kodar Range, valley of Srednij Sukakan 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 (UHU). – PRIMORYE TERRITORY: Mikhailovskij Range, 280 m alt., 43°51´N, 132°55´E, 3 June 2010, Bakalin P-3-6a-10 (VBGI), MONGOLIA: BULGAN PROVINCE: Gurvanbulag District, Hogo-Hanuul, 1396 m alt., 47°26´N, 103°44´E, 18 June 2010, Choi M5046 (VBGI). – TUY AIMAG: Erdene sum, valley of Terelj River, 15 June 1974, Golubkova & Tsogt 29 (MHA); same district (aimag) Altanbualg 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 Priono bobus 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. mammillifera 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. mammillifera are questionable. Schuster (1988: 214) notes that C. mammillifera 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, *Aceromastigum*-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. phyllocanta*

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 mamilllose, 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. massalognii*

7. Leaf lobe usually ending in one cell. Outgrowths on dorsal leaf surface unicollearular, 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 .......................... *C. konstantinovae*

8. Cells of stem and leaves more or less thick-walled. Leaves subequally bilobed, margins toothed with acute to obtuse cells ......................... 9

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*

**ACKNOWLEDGEMENTS.** We cordially thank Dr. Vadim A. Bakalin and Dr. Tsogin Tsogmed for lending their collections of *Cephaloziella* from the Russian Far East and Mongolia. We are grateful to Dr. Masami Mizutani (NICH) for sending us the type specimens of *Cephaloziella acantophora*, *C. hunanensis* and *Prionolobus matsuurai*. We are greatly indebted to Dr. Jochen Heinrichs, Dr. Michael Ignatov, Dr. Yelena Kossovich-Anderson, Dr. Matt Renner, Dr. Alexey Troitsky, and the reviewers of *Polish Botanical Journal* for helpful suggestions and language improvement. This study was supported in part by the Russian Foundation for Basic Research (research project nos. 15-04-03479, 16-04-01156, 16-34-50278) and the Russian Federation President’s Program for support of PhD researches (MK-3328.2011.4).

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