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REAPPRAISAL OF *GYMNOCOLEA* AND DESCRIPTION OF A NEW GENUS *RUDOLGAEA* (ANASTROPHYLLACEAE, MARCHANTIOPHYTA)

ПЕРЕСМОТР РОДА *GYMNOCOLEA* И ОПИСАНИЕ НОВОГО РОДА *RUDOLGAEA* (ANASTROPHYLLACEAE, MARCHANTIOPHYTA)

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Abstract

A review of the taxonomic composition of the genus *Gymnocolea* is provided. Among 15 species attributed to *Gymnocolea,* only 3 species are recognized within the genus. Their morphological and molecular analyses by *rbc*L, *trn*L-F cpDNA and ITS1-2 nrDNA sequences resulted in the transfer of *G. borealis* and *G. fascinifera* in a new genus *Rudolgaea* named after Rudolf M. Schuster and Olga M. Schuster. Thus, *Gymnocolea* appears to be the monospecific genus with only *G. inflata*.

Резюме

В результате обзора таксономического состава рода *Gymnocolea* показано,что из 15 относимых к этому роду видов в настоящее время признаются только 3 вида: *G. borealis, G. fascinifera* и *G. inflata*. Их морфологический и молекулярный анализ по последовательностям *rbc*L, *trn*L-F хпДНК и ITS1-2 ядДНК привел к выделению *G. borealis* и *G. fascinifera* в новый род *Rudolgaea*, названный в честь Rudolf M. Schuster и Olga M. Schuster. Таким образом, *Gymnocolea* становится одновидовым родом с единственным видом *G. inflata*.

KEYWORDS: *Gymnocolea,* hepatics, liverworts, DNA barcoding, systematics

INTRODUCTION

The genus *Gymnocolea* (Dumort.) Dumort. based on the section *Gymnocolea* Dumort. of the genus *Jungermannia* L. was established by Dumortier with brief diagnosis in French "Péricheze nul. Colésule dressée stepetée, retrécie and dentée au sommet" and three species *Gymnocolea fluitans* (Nees) Dumort*., G. inflata* (Huds.) Dumort., and *G. laxifolia* (Hook.) Dumort.

Later Spruce (1882) established the genus *Hygrobiella* (Hook.) Spruce, based on *Jungermannia laxifolia* Hook. [≡ *Gymnocolea laxifolia* (Hook.) Dumort.] and the section *Cladopus* Spruce of the genus *Cephalozia* (Dumort.) Dumort. for *Jungermannia fluitans* Nees [≡ *Gymnocolea fluitans* (Nees) Dumort.] and *J. francisci* Hook. Afterward, Buch (1927: 89) established the genus *Cladopodiella* instead of the section *Cladopus*, which is presently treated as the section *Cladopodiella* (H. Buch) Gradst. et al. of the genus *Odontoschisma* (Dumort.) Dumort. (Aranda *et al*., 2014).

Since the description of *Gymnocolea*, 15 species were attributed to this genus (https://tropicos.org, accessed 11 Oct 2021). Besides the three species mentioned above, *Gymnocolea affinis* Dumort*., G. arenaria* (Nees) Dumort., and *G. huebeneriana* (Nees) Dumort. proved to be synonyms of *Mesoptychia turbinata* (Raddi) L. Söderstr. & Váňa*, Lophoziopsis excisa* (Dicks.) Konstant. & Vilnet*,* and *Hygrobiella laxifolia*, respectively (Müller, 1954a,b); *Gymnocolea acutiloba* (Schiffn.) Müll. Frib., *G. marginata* (Steph.) S. Hatt., *G. montana* (Horik.) S. Hatt., *G. soerensenii* Kaal. ex Jørg. are morphologically similar to *G. inflata* and presently treated as its synonyms; *G. andina* Buchloh, *G. cylindriformis* (Mitt.) Steere, and *G. multiflora* (Steph.) R.M. Schust. belong to the genus *Gymnocoleopsis* (R.M. Schust.) R.M. Schust. Thus, for now only three species of the genus were accepted, that is *G. borealis* (Frisvoll & Moen) R.M. Schust., *G. fascinifera* Potemkin and *G. inflata* (Bánki *et al.*, 2021b). The relation of *G. borealis* and *G. inflata* was firstly supported from molecular evidence by Cailliau *et al.* (2013).

In 1994, the first author discussed with R.M. Schuster the taxonomic position of *G. fascinifera* which is characterized by unique origin of rhizoids from the ventral leaf base compared with other Lophoziaceae Cavers. R.M. Schuster supposed that *G. fascinifera* could represent a separate genus from *Gymnocolea*. The question remained open because no data on perianth and sporophytes of this species were available.

Potemkin (2003), following Kitagawa (1965), suggested the origin of the family Jungermanniaceae from the Lophozioid ancestor and the position of *Gymnocolea*

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in the Jungermaniaceae. The origin of rhizoids from the ventral leaf base in separate species of Jungermanniaceae supposed their relationship with *Gymnocolea fascinifera*. Subsequent molecular studies have shown a remote position of the genus *Gymnocolea* from the Jungermanniaceae s.l. (Vilnet *et al*., 2010). However, no molecular study of *G. fascinifera* has been made, and Schuster's question about the taxonomic position of *G. fascinifera* was unanswered.

The recent find of *G. borealis* in Russia (Potemkin *et al*., 2021) initiated us to make a joint morphological and molecular study of available materials of *G. fascinifera* to compare these two species and clarify their phylogenetic affinity.

Material and Methods

Sampling for morphological studies

The morphological study was based on the light microscopic investigation of extensive collections of *G. fascinifera* cited by Potemkin (1993), and other collections, the selected representative being as follow: *Gymnocolea borealis*. Norway: 1.X.1968 *Moen* (H); *Moen 79510* (H); Russia: Gydansky Peninsula, *Troeva G1-138* (LE). *Gymnocolea fascinifera*. Russia: Republic of Komi, 24.VII.1963 A. Katenin (LE); Bely Island, 27.VII.1984, *O.V. Rebristaya 21* (LE); Yamal Peninsula, 19.VII.1978, *O.V. Rebristaya 7A* (LE); USA: Alaska, 28.VII.1992, *Potemkin 92-9701* (LE, holotype).

DNA extraction, PCR, sequencing

To test the phylogenetic affinity of *G. fascinifera* we selected ITS1-2 nrDNA, *trn*L-F, and *rbc*L cpDNA sequence data for 46 specimens of liverworts from the suborder Cephaloziineae available in GenBank. The ITS1-2, *trn*L-F and *rbc*L loci for specimen of *G. fascinifera* from Alaska, ITS1-2 and *trn*L-F loci for specimen of *G. borealis* from the Gydansky Peninsula were sequenced here. Our attempts to obtain nucleotide sequence data for two specimens of *G. fascinifera* gathered from the Yamal Peninsula in 1978 and 1984 had no success. The list of specimens with voucher details and GenBank accession numbers are shown in Table 1.

DNA was extracted from dried liverwort tissue with DNeasy Plant Mini Kit (Qiagen, Germany). For amplification and sequencing of ITS1-2, *trn*L-F, and *rbc*L the primers suggested by White *et al.* (1990), Taberlet *et al.* (1991), and Kress & Erickson (2007), respectively, were used. PCR was carried out in 20 μl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C (ITS1-2, *trn*L-F), 52°C (*rbc*L), 60 s 72°C), and 2 min of final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the Cleanup Mini (Evrogen, Russia), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, U.S.A.) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analyses

The newly obtained nucleotide sequences for *G. fascinifera* and *G. borealis* were assembled and then included in the produced datasets in BioEdit 7.0.1 (Hall, 1999). The automatical alignment procedure was done with the option of full multiple alignment with default settings for gaps and extension weights in the ClustalW tool. Then obtained dataset was manually corrected, the part of ITS1-2 at the 5'-end and P8 stem-loop region of *trn*L-intron were excluded from alignment due to ambiguously aligned positions, absent data at the ends of regions, and absent loci were coded as missing. The preliminary phylogenetic estimation revealed congruence between three studied loci. The ITS1-2 and *trn*L-F sequence data were cited from single specimen of each species, whereas *rbc*L from other specimens, thus combination of all three loci in single dataset would be incorrect. Thus, two datasets were produced, ITS1-2+*trn*L-F and *rbc*L.

Phylogeny was estimated by three procedures for each dataset: maximum parsimony (MP) with TNT v. 1.5 (Goloboff & Catalano, 2016), maximum likelihood (ML) with PhyML v. 3.0 (Guindon *et al*., 2010), and Bayesian reconstruction with MrBayes v. 3.2.1 (Ronquist *et al.*, 2012). The parsimony analysis with TNT involved a New Technology Search for the minimal length tree by five iterations and 1000 bootstrap replicates, default settings were used for other parameters, gaps were treated as missing. The program ModelGenerator (Keane *et al*., 2006) identified GTR+I+Γ as the best-fitting evolutionary model for ITS1-2+*trn*L-F dataset and TN+I+Γ for the *rbc*L dataset. According to the stopping frequency criterion for the bootstrap (Pattengale *et al*., 2010), the ITS1-2 dataset requires 550 replicates to reach convergence with Pearson average n100 = 0.993802 as estimated by RAxML v. 7.2.6 (Stamatakis, 2006), the *rbc*L dataset – 500 replicates with n100 = 0.992292. The recommended models, number of bootstrap replicates, gamma distribution with four rate categories to estimate among-site rate heterogeneity were used in the maximum likelihood estimation for both datasets.

For the Bayesian analysis, each partition of the combined dataset (ITS1-2, *trn*L-F) and *rbc*L dataset was separately assigned the GTR+I+Γ model that was recommended by the authors of the program; gamma distributions were approximated using four rate 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, and two starting trees were chosen randomly. Chains were run for five million generations and trees were sampled every 1000th generation. The software tool Tracer (Rambaut & Drummond, 2007) revealed effective sample size (ESS) for ITS1-2+*trn*L–F as 15323.9952 and auto-correlation time (ACT) as 1174.7589, ESS for *rbc*L was 14663.5558 and ACT – 1227.6695. As determined by Tracer, the first 500 trees

Table 1. The list of species, included in phylogenetic estimation with GenBank accession number; accessions in bold were sequenced newly for this study

Taxon	Specimen voucher	nr ITS1-2	cp *trn*L-F	cp *rbc*L
Adelanthus lindenbergianus (Lehm.) Mitt.	Chile, Holz, 25 (GOET)	GQ899969	GQ900177	–
	Argentina, Drehwald, 970083 (NY)	–	–	KF852342
Anastrepta orcadensis (Hook.) Schiffn.	Russia, Buryatiya Rep., N. Konstantinova, 59-1-01 (KPABG)	DQ875126	DQ875088	–
	China, Yunnan, D. Long, 34711 (E)	–	–	KF852268
Anastrophyllum assimile (Mitt.) Steph.	USA, N. Konstantinova, A 137-18-95 (KPABG)	EU791776	EU791664	–
Barbilophozia barbata (Schmidel ex Schreb.) Loeske	Netherlands, N. Konstantinova, 3b-5-99 (KPABG)	EU791779	EU791676	–
	Bulgaria, Hentschel Bryo 0753 (GOET)	–	–	DQ312477
Chandonanthus sp.	China, He-Nygren, 492	–	AY463554	–
Crossocalyx hellerianus (Nees ex Lindenb.) Meyl.	Russia, Kareliya Rep., V. Bakalin, 06.08.1997 (KPABG)	EU791788	AY327780	–
Cylindrocolea recurvifolia (Steph.) Inoue	Japan, Bryophytes of Asia, #344 (KPABG)	–	JX630061	–
	Japan, T. Yamaguchi (F)	–	–	KF852297
Gymnocolea inflata (Huds.) Dumort.	Norway, Svalbard, N. Konstantinova, 118-1-04 (KPABG), 1	EU791787	EU791661	KF852306
	Russia: Nizhegorodskaya Prov., Konstantinova, 129-2a-03 (KPABG), 2	GQ220783	GQ220785	–
	United Kingdom, A. Cailliau et al., 3	–	–	JX305549
Gymnomitrion commutatum (Limpr.) Schiffn.	Russia, Sakhalin Prov., Kuril Isl., Iturup I., V. Bakalin, K-58-30-05, 110149 (VBGI)	EU791827	EU791706	–
	China, Yunnan, D. Long, 34684 (DUKE)	–	–	KF943624
Hamatostrepta concinna Váňa & D.G.Long.	Myanmar, D. Long, 34854 (DUKE)	–	–	KF852407
Hattoria yakushimensis (Horik.) R.M.Schust.	Japan, T. Katagiri, 4281 (NICH)	–	LC376049	LC376047
Isopaches bicrenatus (Schmidel ex Hoffm.) H.Buch	Russia, Yakutiya Rep., V. Bakalin, 18.VII.2000 (KPABG)	EU791797	AY327788	–
	USA, Vermont, B. Shaw, 6970 (DUKE)	–	–	KF852384
Lophoziopsis excisa (Dicks.) Konstant. & Vilnet	Norway, Svalbard, N.A. Konstantinova, K-21-2-05 (KPABG)	DQ875093	DQ875058	–
	United Kingdom, Scotland, D. Long, 35611 (E)	–	–	KF852273
Neoorthocaulis attenuatus (Mart.) L.Söderstr., De Roo & Hedd.	Russia, Sakhalinskaya Prov., Harpel, Cherdantseva, 105728 (KPABG)	EU727538	EU722343	–
	Poland, Strebel, 226 (GOET)	–	–	KC184733
Neoorthocaulis floerkei (F.Weber & D.Mohr) L.Söderstr., De Roo & Hedd.	Canada, British Columbia, B. Shaw, F699 (DUKE)	–	–	KF851621
Nowellia curvifolia (Dicks.) Mitt.	Russia, Caucasus, N. Konstantinova, K 123-2-09 (KPABG)	JX629890	JX629994	–
	Dominican Republic, San Jose de Ocoa Prov., Schaefer-Verwimp & Verwimp, 26885 (M)	–	–	KX098918
Odontoschisma fluitans (Nees) L.Söderstr. & Váňa	Russia, Murmansk Prov.,Yu. Mamontov, YuSM-36-2011/1 (KPABG)	JX629915	JX630041	–
	Germany, Bayern, Schaefer-Verwimp & Verwimp, 16482 (M)	–	–	KX098927
Plicanthus birmensis (Steph.) R.M. Schust.	Russia, Primorskiy Kray, V. Bakalin, P-76-5-05 (KPABG)	EU791791	EU791668	–
Plicanthus hirtellus (F.Weber) R.M.Schust.	China, Yunnan, D. Long, 34407 (E)	–	–	KF851524
Pseudolophozia sudetica (Nees ex Huebener) Konstant. & Vilnet	Czech Republic, B. Shaw, 12991 (DUKE)	–	–	KF851655
Rudolgaea borealis (Frisvoll & Moen) Potemkin & Vilnet	Russia, Gydansky Peninsula, E.I. Troeva, G1-138 (LE), 1	**MZ343174**	**MZ353627**	MZ032229
	Sweden, A. Cailliau, T. Hallingbaeck, 2	–	–	JX305563
Rudolgaea fascinifera (Potemkin) Potemkin & Vilnet	USA: Alaska, A. Potemkin, 92-9701 (LE)	**MZ297375**	**MZ298895**	**MZ298896**
Scapania undulata (L.) Dumort.	Russia, Murmanskaya Prov., N. Konstantinova, 208-2-02 (KPABG)	EU791751	EU791642	–
	Italy, Schaefer-Verwimp and Verwimp, 27551(GOET)	–	–	KC184758
Schizophyllopsis sphenoloboides (R.M.Schust.) Váňa & L.Söderstr.	Norway, Svalbard, N. Konstantinova, K 50-3-06 (KPABG)	EU791777	EU791662	–
Schljakovia kunzeana (Huebener) Konstant. & Vilnet	Russia, Murmanskaya Prov., N. Konstantinova, 181-02 (KPABG)	EU727544	EU722349	–
Schljakovianthus quadrilobus (Lindb.) Konstant. & Vilnet	Russia, Tuva Rep., T. Otnyukova, V. Bakalin, 100805 (KPABG)	EU791786	EU791666	–
	USA: Alyaska, B. Shaw, F982b/8 (DUKE)	–	–	KF852393
Sphenolobus minutus (Schreb. ex D.Crantz) Berggr.	Norway, Svalbard, N. Konstantinova, K 68-1-06 (KPABG)	EU791789	EU791667	–
Sphenolobus saxicola (Schrad.) Steph.	Czech Republic, N. Bohemia, B. Buryova, 26.9.1995 (DUKE)	–	–	KF851620
Syzygiella autumnalis (DC.) K.Feldberg, Váňa, Hentschel & Heinrichs	Russia, Buryatiya Rep., N. Konstantinova, 103-1-01 (KPABG)	EU791845	EU791721	–
	USA, Vermont, B. Shaw, 6969 (SIU)	–	–	KF852382
Tetralophozia filiformis (Steph.) Urmi	Russia, Buryatiya Rep., N. Konstantinova, 13-24-01 (KPABG)	EU791792	EU791669	–
	China, Yunnan, B. Shaw, 5790 (DUKE)	–	–	KF852352
Vietnamiella epiphytica Bakalin & Vilnet	Vietnam, Lao Cai Prov., V. Bakalin, V-9-7-17 (VBGI, KPABG), 1	MK277316	MK290984	MK290986

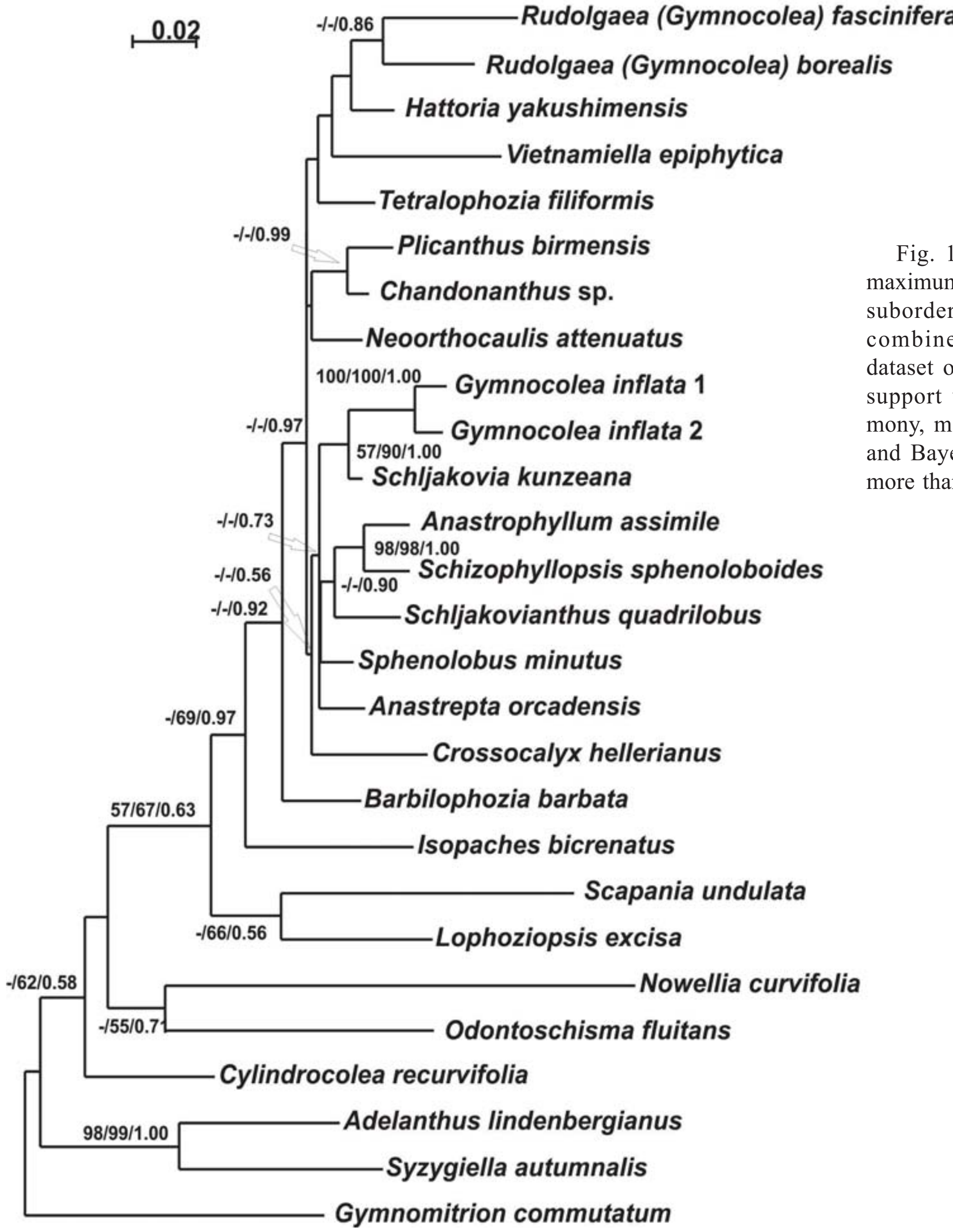

Fig. 1. Phylogram obtained in a maximum likelihood analysis for the suborder Cephaloziineae based on combined nucleotide sequences dataset of ITS1-2+*trn*L-F. Bootstrap support values of maximum parsimony, maximum likelihood analyses and Bayesian posterior probabilities more than 50% (0.50) are indicated.

in each run were discarded as burnin, thereafter 9000 trees were sampled from both runs for each dataset. The average standard deviation of split frequencies between two runs for ITS1-2+*trn*L–F was 0.004813, for *rbc*L 0.003465. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

The infrageneric variability of ITS1-2, *trn*L-F, and *rbc*L for the family Anastrophyllaceae were calculated as the average pairwise *p*-distances in Mega 5.1 (Tamura *et al.*, 2011) using the pairwise deletion option for counting gaps.

Results

Molecular results

For *Gymnomitrion fascinifera* ITS1-2, *trn*L-F, and *rbc*L nucleotide sequences were newly obtained, for *G. borealis* ITS1-2 and *trn*L-F (Table 1). The combined ITS1-2+*trn*L-F alignment for 27 specimens consists of 1373 sites, among them, 977 sites belong to ITS1-2 and 396 sites to *trn*L-F. The number of conservative positions in ITS1-2 and *trn*L-F is 461 (47.18%) and 235 (59.34%), respectively, the number of variable positions is 352 (36.03%) and 132 (33.33%), and the number of parsimony-informative positions is 192 (19.65%) and 67 (16.91%). In the *rbc*L alignment of 26 specimens with 1120 positions, there are 828 (73.93%) conservative sites, 262 (23.39%) variable sites, and 142 (12.67%) parsimony informative positions.

The MP analysis with TNT yielded 5 equally parsimonious trees with a length of 1715 steps, with CI = 0.617857 and RI = 0.436842 for the ITS1-2+*trn*L-F

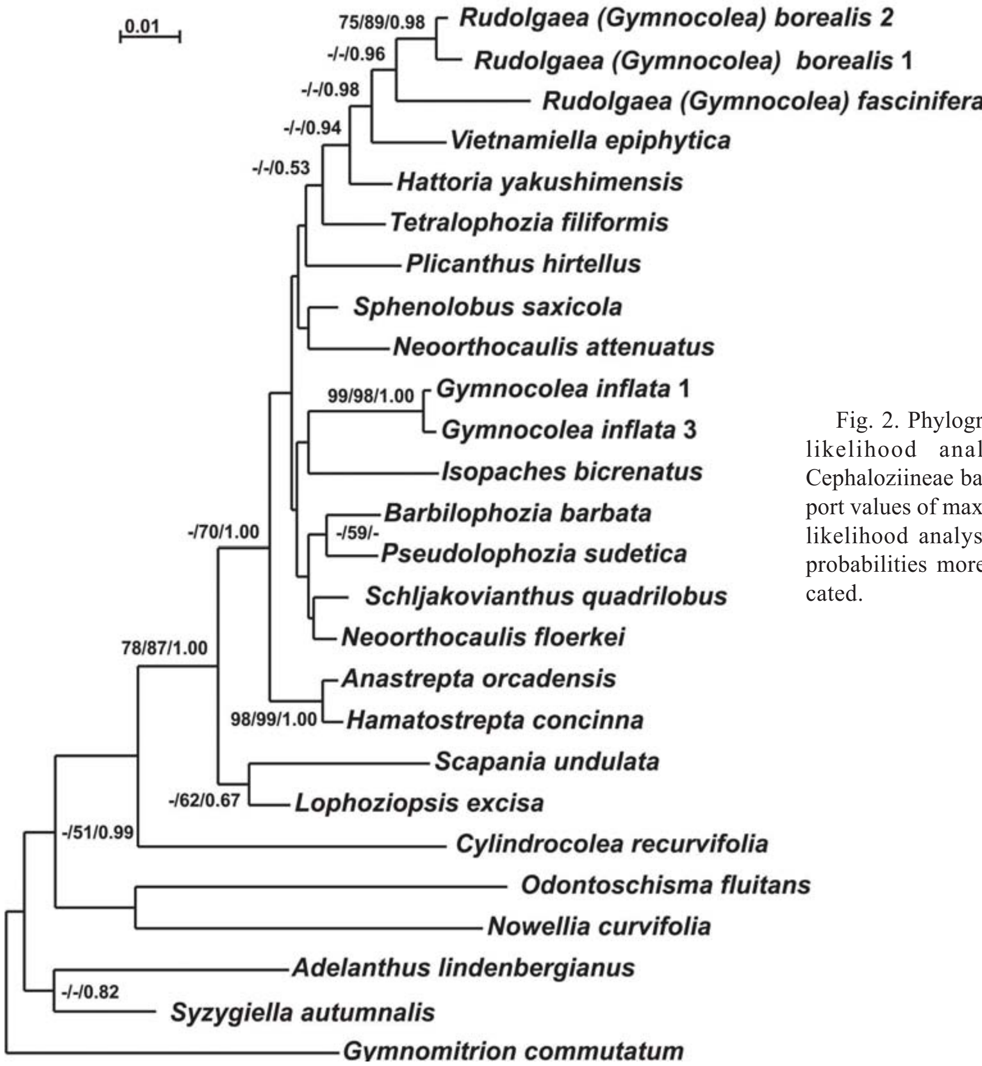

Fig. 2. Phylogram obtained in a maximum likelihood analysis for the suborder Cephaloziineae based on *rbc*L. Bootstrap support values of maximum parsimony, maximum likelihood analyses and Bayesian posterior probabilities more than 50% (0.50) are indicated.

dataset. The MP calculations for *rbc*L resulted in 7 equally parsimonious trees with a length of 567 steps, with CI = 0.557407 and RI = 0.449309. The ML criterion recovered a tree with a Log likelihood -7221.21 for ITS1-2+*trn*L-F and -4422.13 for *rbc*L. Arithmetic means of Log likelihoods in Bayesian analysis for each sampling run were -6968.49 and -6969.90 for ITS1-2+*trn*L-F and -4181.88 and -4182.04 for the *rbc*L dataset.

The tree topologies achieved in all estimations from both datasets became highly congruent with each other. In Fig. 1 the tree topology from ML analysis of ITS1-2+*trn*L-F is presented with ML and MP bootstrap support values (BS) and Bayesian posterior probabilities (PP) for each node. In Fig. 2 the ML tree for the *rbc*L dataset with BS from MP and ML calculations and PP from BA was provided. The backbone affinity within family Anastrophyllaceae is poorly supported in both calculations but similar with relations published in Bakalin *et al.* (2020). *Gymnocolea fascinifera* and *G. borealis* composed a clade in both trees: with 0.86 PP in ITS1-2+*trn*L and 0.96 PP in *rbc*L. In other estimation relation of both species has not got bootstrap support. The closest relatives to them appear to be recently described *Vietnamiella epiphytica* from Sino-Himalaya and *Hattoria yakushimensis* from Japan. The two specimens from remote localities of the type species of the genus *Gymnocolea* – *G. inflata* – are placed in a clade separated from *G. fascinifera* + *G. borealis* by several phyla with other genera.

The infraspecific *p*-distances calculation was provided for species *G. borealis* based on *rbc*L and *G. inflata* for ITS1-2, *trn*L-F and *rbc*L. The variability of *rbc*L between two samples of *G. borealis* from Sweden and the Gydansky Peninsula is 0.6%, the variability among specimens of *G. inflata* from Svalbard and the Nizhny Novgorod Region is 2.1% in ITS1-2 and 0.9% in *trn*L-F, between specimens from Svalbard and the United Kingdom is 0.4% by *rbc*L (data not shown). The multiplied samples of *G. borealis* and *G. inflata* were grouped and *p*-distances were calculated for the family Anasrophyllaceae (Tables 2a, b). The specimens of *G. fascinifera* and *G. borealis* are distinct from each other in the same range (5.3% in ITS1-2, 5.5% in *trn*L-F, 3.1% in *rbc*L or 5.3/5.5/3.1) as they both differ from *G. inflata* (4.4-5.2/6.6-7.8/3.5-4.4%). Taking into account position on phy-

Table 2. The value of *p*-distances between genera of family Anastrophyllaceae: a) based on ITS1-2 and *trn*L-F, b) based on *rbc*L.

a)

	Species	*p*-distances ITS1-2/*trn*L-F, %																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*Rudolgaea (Gymnocolea) fascinifera*																	
2	*Rudolgaea (Gymnocolea) borealis*	5.3/5.5																
3	*Hattoria yakushimensis*	-/5.8	-/3.6															
4	*Vietnamiella epiphytica*	7.7/5.8	10.1/3.3	-/2.8														
5	*Tetralophozia filiformis*	5.3/5.6	6.6/3.6	-/2.2	7.7/1.9													
6	*Plicanthus birmensis*	6.2/5.3	6.5/4.7	-/4.2	8.6/3.0	4.3/2.8												
7	*Chandonanthus* sp.	-/5.0	-/3.8	-/3.2	-/2.6	-/2.9	-/1.8											
8	*Neoorthocaulis attenuatus*	5.0/6.7	6.4/5.0	-/4.4	8.2/3.3	3.6/3.0	3.9/3.6	-/3.2										
9	*Gymnocolea inflata*	4.4/7.8	6.2/6.6	-/6.9	7.6/6.5	4.3/6.4	4.6/7.4	-/7.7	3.5/7.4									
10	*Schljakovia kunzeana*	4.1/6.4	5.8/4.7	-/3.6	7.9/3.0	4.0/2.2	4.4/3.3	-/2.9	3.3/3.0	1.5/6.5								
11	*Anastrophyllum assimile*	6.2/6.7	6.7/5.8	-/5.0	8.2/4.4	4.9/3.6	4.6/5.0	-/4.7	4.3/4.7	4.0/7.9	4.0/2.8							
12	*Schizophyllopsis sphenoloboides*	5.0/7.5	7.0/6.1	-/5.3	8.1/4.7	4.4/3.9	4.9/5.3	-/5.0	3.7/5.0	4.0/8.2	3.9/3.0	3.2/1.4						
13	*Schljakovianthus quadrilobus*	5.9/7.5	6.4/5.5	-/4.4	8.4/4.4	4.3/2.8	4.6/5.0	-/4.4	3.2/4.7	3.9/8.1	3.9/2.8	4.2/3.6	3.6/3.9					
14	*Sphenolobus minutus*	5.0/6.1	5.5/4.5	-/3.2	7.5/3.5	3.6/2.2	4.1/3.5	-/2.9	2.9/2.9	3.1/7.7	2.8/1.3	3.8/3.2	3.5/3.5	3.2/2.6				
15	*Anastrepta orcadensis*	4.1/6.9	5.7/5.3	-/5.3	7.3/4.2	3.3/3.3	3.9/4.4	-/4.1	2.7/4.2	2.7/7.5	2.5/2.8	3.5/3.3	3.5/3.6	3.2/4.2	2.1/3.2			
16	*Crossocalyx hellerianus*	6.4/9.6	7.0/8.6	-/7.5	9.1/8.2	4.8/7.1	5.2/7.9	-/7.5	4.0/7.5	4.7/10.6	4.4/5.7	5.4/7.5	5.1/7.5	4.2/6.4	3.8/5.7	3.3/7.9		
17	*Barbilophozia barbata*	6.5/5.3	7.3/3.9	-/3.9	8.2/3.3	5.0/2.8	4.7/3.3	-/3.8	4.4/4.2	4.6/5.7	4.5/3.3	4.5/.9	4.4/4.7	4.4/5.0	4.4/3.8	4.1/4.4	5.7/6.8	
18	*Isopaches bicrenatus*	5.8/5.6	10.8/3.9	-/3.9	11.8/3.9	8.3/3.6	9.1/4.6	-/3.9	8.2/4.9	8.9/7.7	8.7/3.6	9.2/4.9	9.0/5.6	8.7/4.3	8.4/3.7	8.1/4.9	8.8/6.0	9.2/3.3

b)

	Species	*p*-distances *rbc*L, %												
		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Rudolgaea (Gymnocolea) fascinifera*													
2	*Rudolgaea (Gymnocolea) borealis*	3.1												
3	*Hattoria yakushimensis*	3.4	2.1											
4	*Vietnamiella epiphytica*	3.6	2.6	1.9										
5	*Tetralophozia filiformis*	3.6	2.1	2.1	2.6									
6	*Plicanthus hirtellus*	4.1	2.5	2.8	2.9	2.3								
7	*Neoorthocaulis attenuatus*	3.8	2.4	2.9	2.9	2.7	2.6							
8	*Gymnocolea inflata*	4.4	3.5	3.0	4.1	3.1	3.4	3.4						
9	*Schljakovianthus quadrilobus*	3.1	1.6	2.3	2.9	2.2	2.5	1.9	2.9					
10	*Sphenolobus saxicola*	3.4	1.8	2.1	2.6	2.0	2.1	1.8	3.1	1.3				
11	*Anastrepta orcadensis*	3.8	2.4	2.5	2.8	2.4	2.6	2.7	3.6	1.8	1.7			
12	*Hamatostrepta concinna*	4.1	2.7	2.7	3.1	2.6	2.8	3.0	3.8	1.9	2.0	0.6		
13	*Barbilophozia barbata*	4.3	2.9	2.2	3.1	2.4	3.2	2.4	3.1	1.8	2.2	2.2	2.4	
14	*Isopaches bicrenatus*	4.1	2.9	3.7	2.9	3.6	3.6	3.1	3.4	3.0	3.1	3.4	3.6	3.1

Fig. 3. *Rudolgaea fascinifera* (*Potemkin 92-9701*, LE, holotype). A, B: habit of plants. Scales:1 mm.

logenetic trees with supported relation to *Hattoria* and *Vietnamiella* only in BA estimation of *rbc*L data, level of molecular differentiation from *Gymnocolea*, *Hattoria* and *Vietnamiella* and morphological features clearly distingushed them from three cited genera, we suggested *G. fascinifera* and *G. borealis* as well-defined species that should be transferred from the genus *Gymnocolea* to a new genus described here.

Rudolgaea Potemkin & Vilnet, gen. nov. Figs. 3–6

Diagnosis: Being morpholgically distinct in habit, leaf shape and areolation from the related *Hattoria* and *Vietnamiella* it resembles *Gymnocolea inflata* and *Odontoschisma fluitans*. It differs from *Gymnocolea inflata* in the occurrence of some rhizoids or their fascicles from ventral leaf bases, lack of caducous perianths, outer cortical cells of larger shoots mostly ± smaller than inner stem cells, often tangentially orientated and occasionally thick-walled. It is distinct from *Odontoschisma fluitans* in the origin of some rhizoids or their fascicles from ventral leaf bases, distinctly striolate-papillose leaf and stem surface, and terminal furcate branching.

Type: *Rudolgaea fascinifera* (Potemkin) Potemkin & Vilnet (≡ *Gymnocolea fascinifera* Potemkin).

Etymology. The genus bears the name of Prof. Rudolf Mathias Schuster (Rudy) and his wife, Olga Marguerite Schuster, his permanent companion and assistant for over 60 years, from their marriage in 1943 to her death in 2005.

Rudolgaea fascinifera (Potemkin) Potemkin & Vilnet, comb. nov. Figs. 3–5

Basionym: *Gymnocolea fascinifera* Potemkin, 1993, Arctoa 2: 76.

Description: Potemkin, 1993.

Illustrations: Potemkin, 1993: Figs 5, 6; this article: Figs. 3–5.

Distribution. Indefinite yet, probably undercollected and overlooked; recorded from the Yamal Peninsula, West Siberian Arctic and the Seward Peninsula, Alaska (Potemkin, 1993), Komi Republic (Potemkin, 2008), Chelyabinsk Region (Ivchenko & Potemkin, 2015), and probably from subarctic Yakutia (Sofronova *et al.*, 2015).

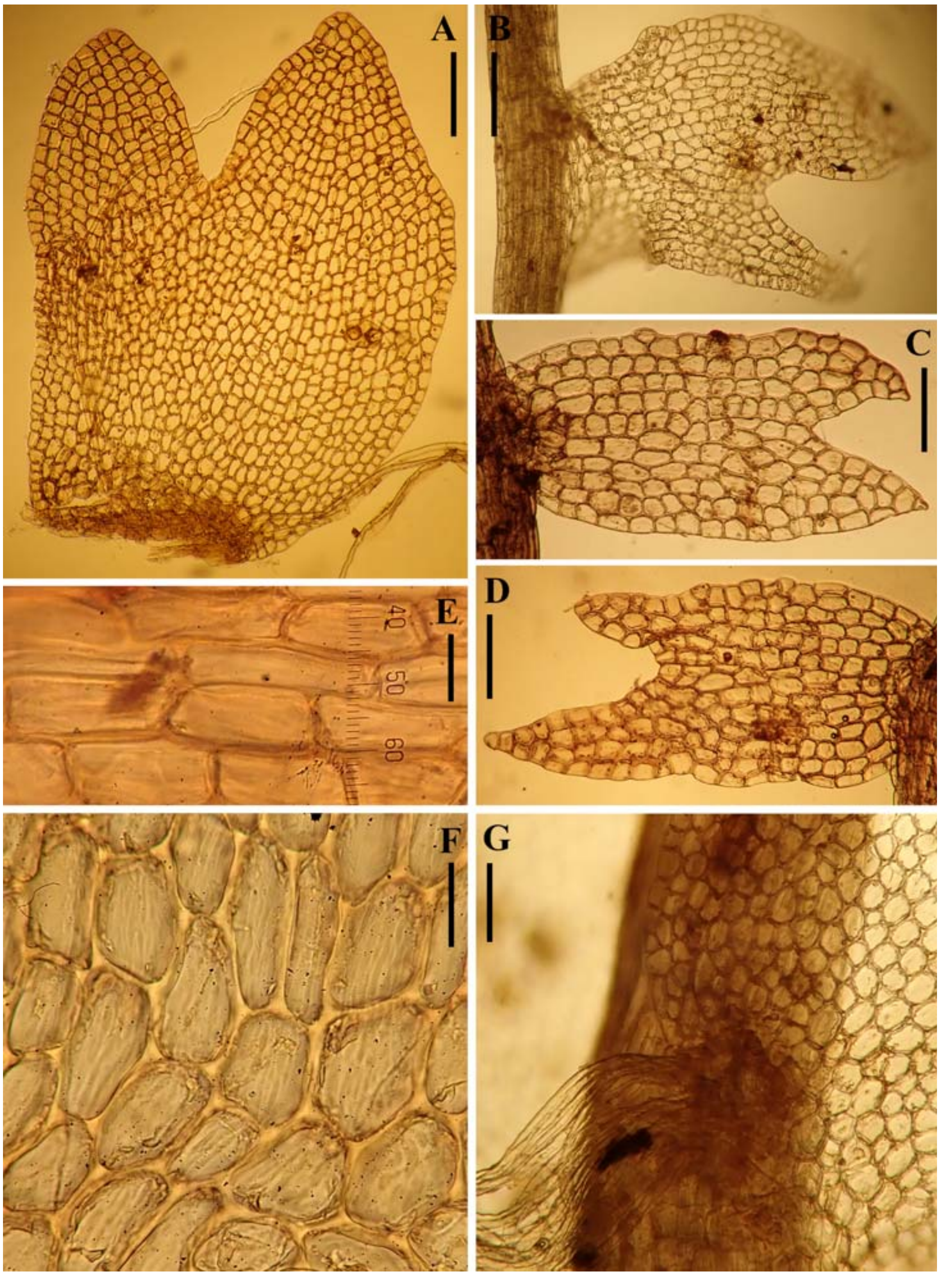

Fig. 4. *Rudolgaea fascinifera* (*Potemkin 92-9701*, LE, holotype).
A–D: leaves; E: dorsal cortical cells; F: basal leaf cells with striolate papillose surface; G: ventral leaf base with rhizoids. Scales: A, B: 160 µm, C, D: 125 µm, E, F: 25 µm, G: 100 µm.

Rudolgaea borealis (Frisvoll & Moen) Potemkin & Vilnet, comb. nov. Fig. 6

Basionym: *Lophozia borealis* Frisvoll & Moen, 1980, Lindbergia 6: 138. f. 1–3.

Descriptions: Frisvoll & Moen, 1980; Damsholt, 2002, 2013.

Illustrations: Schuster, 1969: Fig. 251: 14–18 as *Gymnocolea inflata* (illustrated specimen *RMS 45791* attributed to *G. borealis* by Schuster, 1986: 6); Frisvoll & Moen, 1980: Figs. 1–4; Damsholt, 2002: Plate 53, reprinted in Damsholt, 2013: Plate 46; Potemkin *et al.* (2021): Fig. 1.

Distribution. Arctic and subarctic, probably circumpolar, indefinite yet because of specific habitats.

KEY TO SPECIES OF *RUDOLGAEA* AND *GYMNOCOLEA*

1. Pigmented plants blackish brown, sometimes with traces of purple, not lustrous when wet; rhizoids never originate from leaf bases; cortical cells of larger shoots subequal to inner stem cells and orientated largely radially; perianths common, frequently caducous; on acid soil, rocks, in oligotrophic mires, and wet habitats .... *Gymnocolea inflata* s.l.

— Pigmented plants yellow and golden brown, when wet lustrous, or scorched brown and not lustrous; some rhizoids or their fascicles, when present, originate from ventral leaf bases; cortical cells of larger shoots mostly ± smaller than inner stem cells and

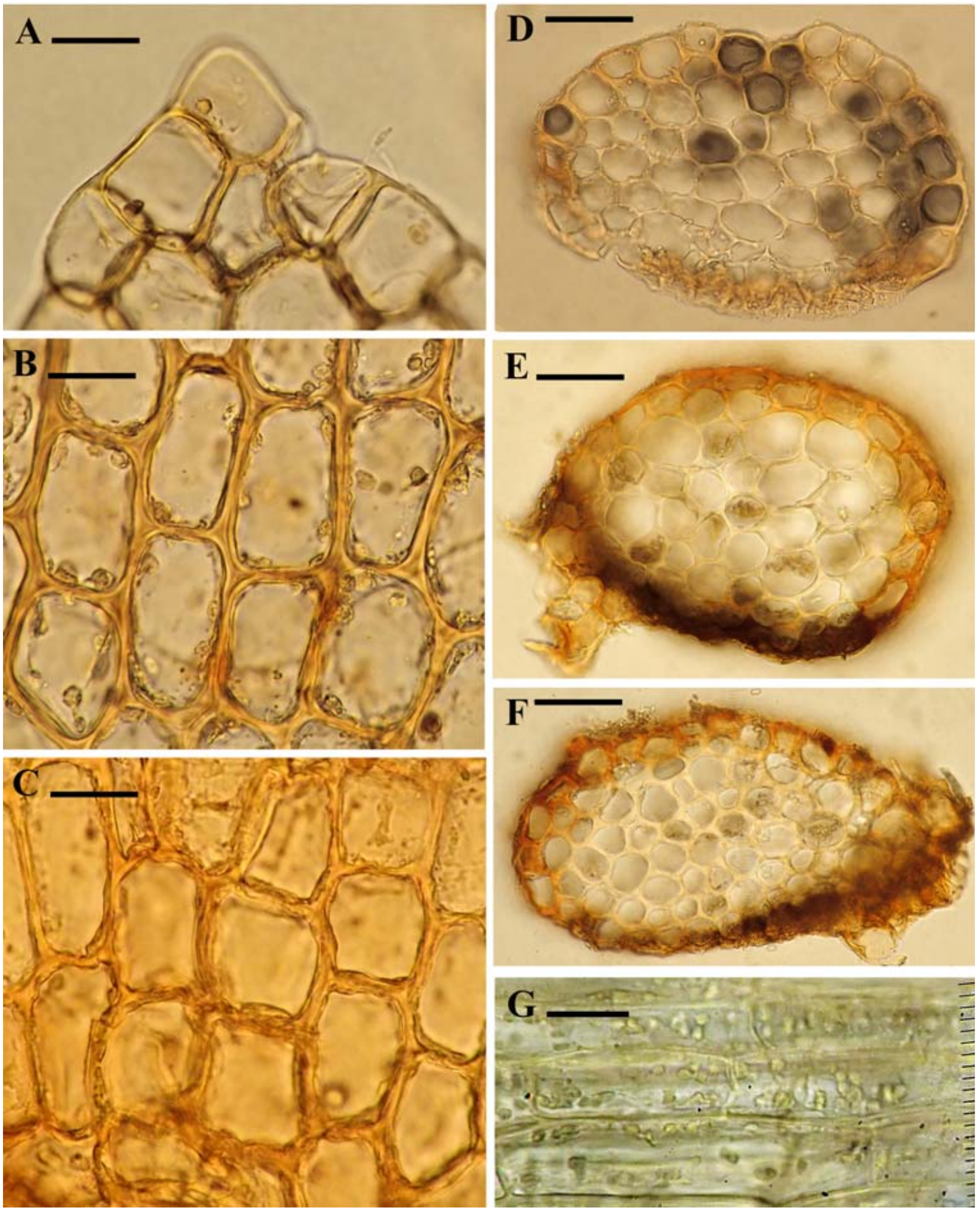

Fig. 5. *Rydolgaea fascinifera* (*Potemkin 92-9701*, LE, holotype). A–C: cells of leaf lobe apex, leaf middle and base, respectively; D–F: stem transverse sections; G: ventral cortical cells of stem. Scales: A–C: 25 µm, D–F: 80 µm, G: 18 µm.

often orientated tangentially in larger stem cross-sections; perianth rare, not caducous; in acid to subneutral wet habitats 2

2. Pigmented plants yellow and golden brown, when wet lustrous; rhizoids absent, few or ± abundant in some shoot sectors, single rhizoids sometimes originate from leaf bases; leaf and stem surfaces remarkably striolate papillose; leaf cells with 1–6(–8) oil bodies; cortical cells 12–20(–25) µm wide; stem (7–)9–11 cells high; in subneutral wet habitats with dense vegetation, in moderately to extremely rich fen vegetation, in carpets to lawns, where the groundwater level in summer lies well below the surface, never in intermediate fens and on hummocks in Scandinavia; in wet hollows of cotton-grass-sedge bog between flat mounds in the Gydansky Peninsula .... *Rudolgaea borealis*

— Pigmented plants scorched brown, never lustrous; rhizoids very few or sparse, in more or less distinct fascicles from the ventral leaf base and adjacent part of the stem (leaves detach with rhizoids); leaf and stem surface faintly striolate papillose or smooth; leaf cells with (2–)5–12(–16) oil bodies; cortical cells broader, (20–)23–28(–30) µm wide or when subisodiametric (28–)30–34(–38) µm wide; stem (5–)6–8(–11) cells high; in acid wet habitats, including troughs of polygonal tundras, in *Sphagnum* tussock bog and bogs with flowing water, in herb-willow, grass-cotton grass and sedge-lichen-moss tundras, often among *Drepanocladus* s.l. and *Sphagnum*, with *Scapania paludicola* var. *rotundiloba*, *Ptilidium ciliare*, *Pseudolepicolea fryei*, *Barbilophozia kunzeana*, *B. binsteadii*, *Gymnocolea inflata*, *Odontoschisma elongatum*, *Blepharostoma*, etc. (Potemkin, 1993) .... *Rudolgaea fascinifera*

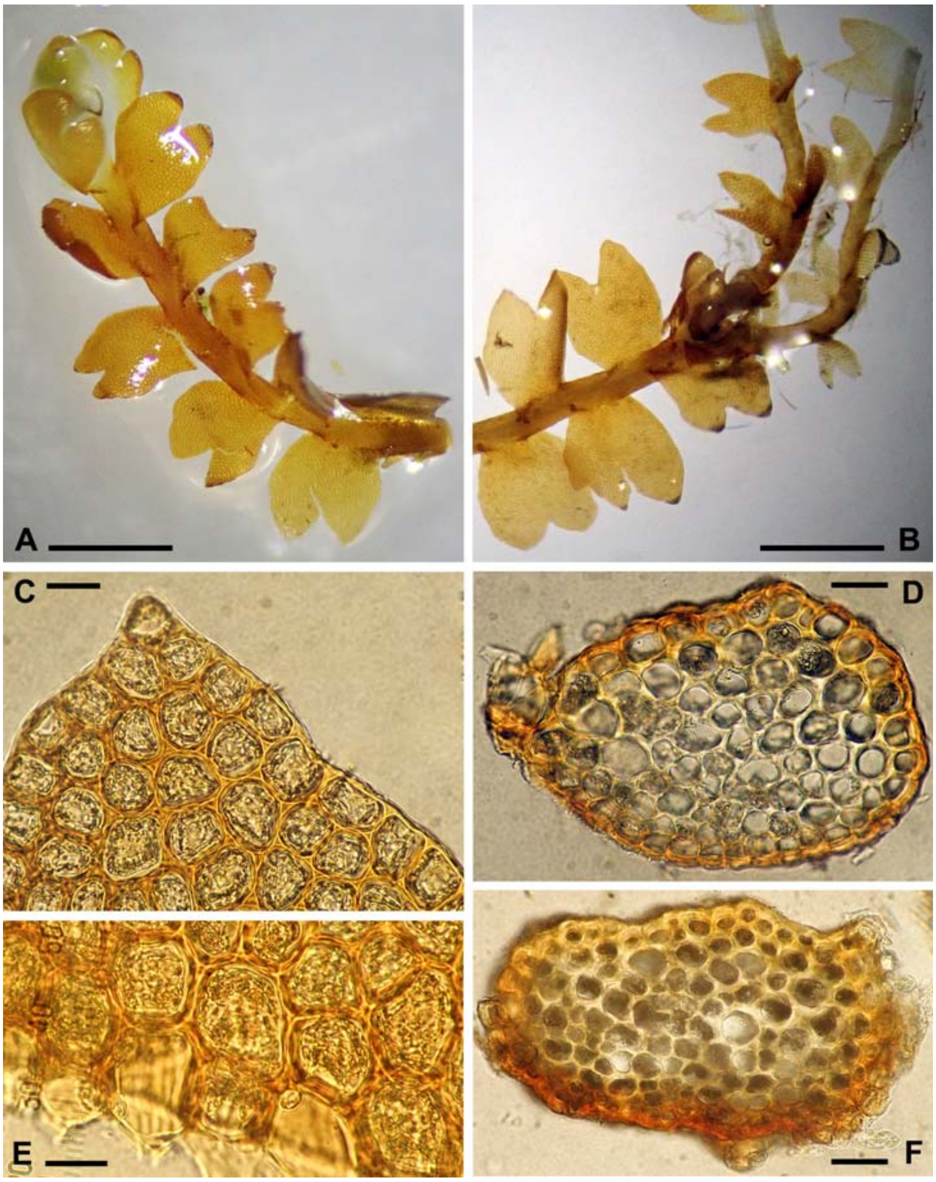

Fig. 6. *Rudolgaea borealis* (*Troeva G1-138*, LE). A, B: shoot sectors; C: lobe; D, F: stem transverse sections; E: basal leaf cells. Scale bars: for A, B: 750 µm; C: 18 µm; D, E: 30 µm; F: 19 µm. From Potemkin *et al.* (2021).

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LITERATURE CITED

ARANDA, S., S. GRADSTEIN, J. PATIÑO, B. LAENEN, A. DÉSAMORÉ & A. VANDERPOORTEN. 2014. Phylogeny, classification and species delimitation in the liverwort genus *Odontoschisma* (Cephaloziaceae). – *Taxon* **63**(5): *1008–1025.*

BAKALIN, V., A. VILNET & V.S. NGUYEN. 2020. *Vietnamiella epiphytica* – a new genus and species of Anastrophyllaceae (Hepaicae). – *The Bryologist* **123** (1): *48–63*.

BÁNKI, O., Y. ROSKOV, L. VANDEPITTE, R.E. DEWALT, D. REMSEN, S P.CHALK, T. ORRELL, M. KEPING, J. MILLER, R. AALBU, R. ADLARD, E. ADRIAENSSENS, C. AEDO, E. AESCHT, N. AKKARI, M.A. ALONSO-ZARAZAGA, B. ALVAREZ, F. ALVAREZ, G. ANDERSON ET AL. 2021. Catalogue of Life Checklist (Version 2021-09-21). – Catalogue of Life. https://doi.org/10.48580/d4sv

BUCH, H.R.V. 1927. *Cladopodiella* statt *Cladopus*. – *Memoranda Societatis pro Fauna et Flora Fennica* **1**: *89–90*.

CAILLIAU, A, D.G. LONG, M.J. PRICE & M. PERRET. 2013. Phylogeny and systematic position of *Mesoptychia* (Lindb.) A. Evans. – *Plant Systematics and Evolution* **299**: *1243–1251*.

DAMSHOLT, K. 2002. Illustrated flora of Nordic Liverworts and Hornworts. – *Lund, Nord. Bryol. Soc., 837 pp.*

DAMSHOLT, K. 2013. The liverworts of Greenland. – *Lund, Nord. Bryol. Soc., 626 pp.*

DUMORTIER, B.-C. 1835. Recueil d'observations sur les Jungermanniacées. Fasc. I – Revision des genres. – *Tournay : J.-A. Blanquart, 27 pp.*

FRISVOLL, A.A. & A. MOEN. 1980. *Lophozia borealis* sp. nov., a rich fen hepatic from Fennoscandia. – *Lindbergia* **6**: *137–146*.

GOLOBOFF, P.A. & S. CATALANO. 2016. T.N.T. version 1.5, including a full implementation of phylogenetic morphometrics. – *Cladistics* **32**: *21–238*.

GUINDON, S., J.F. DUFAYARD, V. LEFORT, M. ANISIMOVA, W. HORDIJK & O. GASCUEL. 2010. New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. – *Systematic Biology* **59**: *307–321*.

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

[IVCHENKO, T.G. & A.D. POTEMKIN] ИВЧЕНКО Т.Г. & А.Д. ПОТЕМКИН. 2015. Печеночники болотных экосистем южноуральского региона (в пределах Челябинской области). – [Liverworts of mire ecosystems of South Urals within Chelyabinsk Province] *Arctoa* **24**: *574–583*.

KEANE, T.M., C.J. CREEVEY, M.M. PENTONY, T.J. NAUGHTON & J.O. McINERNEY. 2006. Assessment of methods for amino acid matrix selection and their use on empirical data shows that ad hoc assumption for choice of matrix are not justified. – *BMC Evolutionary Biology* **6**: *29*.

KITAGAWA, N. 1965. A revision of the family Lophoziaceae of Japan and its adjacent regions. 1. – *Journal of the Hattori Botanical Laboratory* **28**: *239–291*.

KRESS, W.J. & D.L. ERICKSON. 2007. A two-locus global DNA barcode for land plants: the coding *rbc*L gene complements the non-coding *trn*H-*psb*A spacer region. – *PLoS ONE* **2**: *e508*.

MÜLLER, K. 1954a. Die Lebermoose Europas (Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 3 Aufl., 6 Band), 1 Abth., 4 Lieferung. – *Akademische Verlagsgesellschaft: Leipzig, pp. 481–640.*

MÜLLER, K. 1954b. Die Lebermoose Europas (Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, 3 Aufl., 6 Band), 1 Abth., 5 Lieferung. – *Akademische Verlagsgesellschaft: Leipzig, pp. 641–756.*

PATTENGALE, N.D., M. ALIPOUR, O.R.P. BININDA-EMONDS, B.M.E. MORET & A. STAMATAKIS. 2010. How many bootstrap replicates are necessary? – *Journal of Computational Biology* **17**: *337–354*.

POTEMKIN, A.D. 1993. The Hepaticae of the Yamal Peninsula, West Siberian Arctic. – *Arctoa* **2**: *57–101*.

[POTEMKIN, A.D.] ПОТЕМКИН А.Д. 2003. К вопросу о путях эволюции и объеме семейств Jungermanniaceae и Lophoziaceae (Hepaticae). – [On evolutionary trends and circumscription of the families Jungermanniaceae and Lophoziaceae (Hepaticae)]. *Ботанические исследования в азиатской России. Материалы XI съезда Русского ботанического общества (18–22 августа, Новосибирск–Барнаул)*[*Botanical studies in Asian Russia. Proceedings of XI Congress of Russian Botanical Society (18–22 August 2003, Novosibirsk – Barnaul)*] **1**: *214–216*.

[POTEMKIN, A.D.] ПОТЕМКИН А.Д. 2008. Новые находки печеночников в Республике Коми. 1. – [New liverwort records from Republic of Komi. 1] *Arctoa* **17**: *198.*

POTEMKIN, A.D., A.A. VILNET, E.I. TROEVA & K.A. ERMOKHINA. 2021. *Gymnocolea borealis* (Anastrophyllaceae, Marchantiophyta) in Asia and Russia: morphology, ecology, distribution, and differentiation. – *Novosti Sistematiki Nizshikh Rastenii* **55**(2): *487–494*.

RAMBAUT, A. & A.J. DRUMMOND. 2007. Tracer v1.4. – *Available from: http://beast.bio.ed.ac.uk/Tracer.*

RONQUIST, F., M. TESLENKO, P. van der MARK, D.L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J.P. HÜLSENBECK. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systematic Biology* **61**: *539–542*.

SCHUSTER, R.M. 1969. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 2. – *New York; London, Columbia Univ. Press, 1062+xii pp.*

SCHUSTER, R.M. 1986. *Gymnocolea borealis* (Frisvoll & Moen) Schust. [*Lophozia* (*Leiocolea*) *borealis* Frisvoll & Moen] in North America. – *Lindbergia* **12**: *5–8*.

SOFRONOVA, E.V., A.D. POTEMKIN, Yu.S. MAMONTOV & R.R. SOFRONOV. 2015. Liverworts of the Mus-Khaya Mountain (Yakutia, Asiatic Russia). – *Arctoa* **24**: *156–164*.

SPRUCE, R. 1882. On *Cephalozia* (a genus of Hepaticae), its subgenera and some allied genera. – *Malton: Printed for the author, 101 pp.*

STAMATAKIS, A. 2006. RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. – *Bioinformatics* **22**: *2688–2690*.

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

TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI & S. KUMAR. 2011. MEGA 5: Molecular Evolutionary Genetics Analysis Using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Method. – *Molecular Biology and Evolution* **28**: *2731–2739*.

VILNET, A.A., N. A. KONSTANTINOVA & A.V. TROITSKY. 2010. Molecular insight on phylogeny and systematics of the Lophoziaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. – *Arctoa* **19**: *31–50*.

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

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