Phytotaxa 255 (3): 227–239
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.255.3.4

A new species of the genus *Jungermannia* (Jungermanniales, Marchantiophyta) from the Caucasus with notes on taxa delimitation and taxonomy of *Jungermannia* s. str.

NADEZDA A. KONSTANTINOVA[1] & ANNA A. VILNET[1]
[1] *Polar-Alpine Botanical Garden–Institute RAS, 184256, Kirovsk, Russia, email: nadya50@list.ru, anya_v@list.ru*

Abstract

The new species *Jungermannia calcicola* Konstant. et Vilnet, is described based on a critical reinvestigation of morphological features and molecular analyses of *trn*L–*trn*F and *trn*G intron cpDNA sequences of forty samples of *Jungermannia* s. str. The new species is described and illustrated as well as noting its differentiation from allied species and distribution patterns. New data on some taxonomical ambiguities and on the taxa delimitation in the *Jungermannia* s. str. are discussed.

Key words*:* *Jungermannia calcicola* sp. nov., liverworts, taxonomy, molecular systematics, distribution

Introduction

Jungermannia Linnaeus (1753: 1131) is one of the oldest described genera of leafy liverworts. Since its description the treatment of this genus has been drastically changed. At the end of the 20th to the beginning of the 21st centuries most bryologists accepted *Jungermannia* in the wide sense including *Solenostoma* Mitten (1865a: 51)*, Plectocolea* (Mitten 1865b: 156) Mitten (1873: 405), *Liochlaena* Nees in Gottsche *et al.* (1845: 150). But in recent molecular phylogenetic studies *Jungermannia* s. lat. has been proved to be a mixture of phylogenetically unrelated taxa, some of which have been elevated to distinct families, e.g., Solenostomataceae Stotler et Crand.-Stotl. in Crandall-Stotler *et al.* (2009: 190) and Endogemmataceae Konstant., Vilnet et A.V.Troitsky in Vilnet *et al.* (2011: 132). At present *Jungermannia* s. str. includes 8–9 species with a predominantly north holarctic distribution with the exception of *Jungermannia ovatotrigona* (Stephani 1916: 184) Grolle (1971: 90) and probably *J. gollanii* Stephani (1917: 86). The last taxon was recently referred to *Plectocolea* (Bakalin, 2014) but this concept should be tested using molecular data. Although no previous molecular studies have focused specifically on *Jungermannia* s. str., some species of the genus were included in several phylogenetic estimates of Jungermanniales (e.g. Hentschel *et al.* 2007, De Roo *et al.* 2007, Vilnet *et al*. 2010, etc.). Schuster's (1988: 114) statement that the taxonomy of this genus "remains controversial" remains valid. Investigating the numerous collections from different regions of Russia we were faced with the problem of identification of a great amount of specimens some of which did not fit well with described species. Particularly, in the Russian part of the Caucasus we collected a small *Jungermannia* that has a quite specific appearance. It was first collected on limestone along the Kurdzhips River in the Republic of Adygeia, we later gathered it in the Republic of Karachaevo-Cherkessia and then in the Dagestan Republic (Fig. 1). The species is restricted to limestone and it would appear that it is not rare in appropriate habitats. Study of *trn*L–*trn*F and *trn*G intron cpDNA sequences of the majority of *Jungermannia* species clearly separated this taxon from *Jungermannia atrovirens* Dumortier (1831: 5), which is somewhat similar in appearance. The main goal of this paper is the description of the new species, and we simultaneously elucidate some taxonomical problems in the genus.

Materials and methods

Morphology

The morphological investigation is based on specimens from the herbarium of Polar-Alpine Botanical Garden of

Accepted by Matt von Konrat: 14 Nov. 2015; published: 11 Apr. 2016

Kola Science Center of Russia (KPABG). As far as possible we studied specimens from different geographically distant regions. The majority of the specimens were recently collected by N. Konstantinova and A. Savchenko during expeditions to Caucasus, the Murmansk Province, Svalbard and South Siberia. Several specimens from the Far East of Russia and South Korea and some specimens from South Siberia collected mainly by V. Bakalin were also included. All specimens were examined and photographed by light microscopy using Axioplan2 imaging. Identifications of all specimens were verified and revised several times by the senior author.

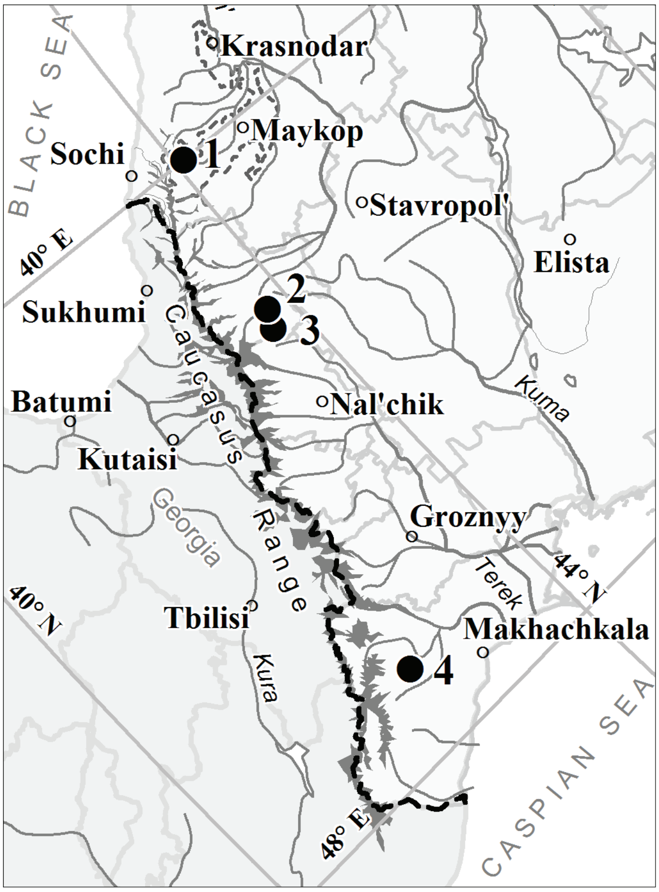

FIGURE 1. The map of distribution of *Jungermannia calcicola* Konstant. et Vilnet. 1—Kurdzhips River (Republic of Adygeia, type locality); 2—Scalistyi Ridge, Gumbashi Mount (Republic of Karachaevo-Cherkessia); 3—Scalistyi Ridge, Bermamyt Mountain (Republic of Karachaevo-Cherkessia) and 4—Gunib Plateau Dagestan Republic).

Taxon sampling

Forty specimens corresponded to six *Jungermannia* species based on morphological concepts (Konstantinova *et al.* 2009) as well as three specimens from Caucasus, provisionally assigned to the new species, were included in the molecular phylogenetic estimation. According to the phylogenetic relation of *Jungermannia* (Vilnet *et al*. 2010) the closely allied *Mesoptychia heterocolpos* (Thed. in Hartman 1838: 328) L.Söderstr. & Váňa in Váňa *et al.* (2012: 53) was chosen as an outgroup. Two plastid DNA loci—*trn*L–*trn*F and *trn*G intron—were sequenced for each accession. Sequences for two accessions from the United Kingdom were downloaded from GenBank, sequences for twelve specimens were taken from our previous studies (Yatsentyuk *et al.* 2004, Vilnet *et al.* 2010, Bakalin & Vilnet 2009, Bakalin *et al.* 2015). All studied specimens are listed in Table 1 with notes on preliminary morphological identification and re-identification after molecular analyses, as well as voucher details and GenBank accession numbers.

DNA isolation, amplification and sequencing

DNA was extracted from dried liverwort tissue using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). The amplification and sequencing were performed using primers suggested by Taberlet *et al*. (1991) and Shaw *et al.* (2005) for *trn*L–*trn*F and *trn*G intron, respectively.

PCR were carried out in 20 µl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 58°C for (*trn*L–*trn*F) or 64 °C (for *trn*G intron), 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 GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, U.S.A.), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

TABLE 1. The list of taxa, specimens vouchers and GenBank accession numbers. The accessions of *Jungermannia eucordifolia* downloaded from GenBank are in bold.

Taxon	Preliminary identification	Specimen voucher (Herbarium)	GenBank accession numbers *trn*L-F	*trn*G-intron
Jungermannia atrovirens	*Jungermannia* sp. indet.	Russia: Adygeia Rep., N. Konstantinova, A. Savchenko, K407-6 -07 (KPABG)	KR063604	KR063640
Jungermannia atrovirens f. *tristis*	*J. pumila*	Belgium, N. Konstantinova, 2-20-10-99, 102132 (KPABG)	KR063599	KR063635
J. atrovirens f. *tristis*	*J. atrovirens* f. *tristis*	Russia: Dagestan Rep., N. Konstantinova, K61-1-11 (KPABG)	KR063600	KR063636
J. atrovirens f. *tristis*	*J. atrovirens*	Russia: Krasnodar Territory, **1**, N. Konstantinova, A. Savchenko, K 188-09 (KPABG)	KR063602	KR063638
J. atrovirens f. *tristis*	*J. atrovirens*	Russia: Krasnodar Territory, **2,** N. Konstantinova, A. Savchenko, K 198-1-09, 113060 (KPABG)	KR063603	KR063639
J. atrovirens f. *tristis*	*J. atrovirens*	Russia: Republic of Karachaevo-Cherkessia, **1**, M. Ignatov, E. Ignatova, 4.8.02 (MHA)	GQ220766	no data
J. atrovirens f. *tristis*	*J. atrovirens* f. *tristis*	Russia: Republic of Karachaevo-Cherkessia, **2,** N. Konstantinova, A. Savchenko, K602-3-05 (KPABG)	KR063601	KR063637
Jungermannia borealis	*J. pumila*	Russia: Altay Rep., M. Ignatov, 0/1981 (MHA)	KR063605	KR063641
J. borealis	*J. atrovirens*	Russia: Buryatiya Rep., N. Konstantinova, A. Savchenko, 21-4-02, 104405 (KPABG)	GQ220765	no data
J. borealis	*J. borealis*	Russia: Commander Islands, Bering Isl., **1**, V. Bakalin, K-18-6-02-VB, 103291 (KPABG)	KR063586	KR063618
J. borealis	*J. borealis*	Russia: Commander Islands, Bering Isl., **2**, V. Bakalin, K-21-1-02-VB, 103306 (KPABG)	KR063587	KR063619
J. borealis	*J. borealis*	Russia: Murmansk Prov., N. Konstantinova, A. Savchenko, 131-13-91 (KPABG)	KR063585	KR063617
J. borealis	*J. borealis*	Russia: Sakhalin Prov., V. Bakalin, S-34-2-06 (KPABG)	KR063584	KR063616
Jungermannia calcicola sp. nov.	*Jungermannia* sp. nova	Russia: Adygeia Rep., N. Konstantinova, A. Savchenko, K429-1-07, 112604 (KPABG)	JF421608	KR063630
J. calcicola	*Jungermannia* sp. nova	Russia: Dagestan Rep., N. Konstantinova, K60-9-11 (KPABG)	KR063596	KR063632
J. calcicola	*Jungermannia* sp. nova	Russia: Republic of Karachaevo-Cherkessia, N. Konstantinova, A. Savchenko, K402-8-10 (KPABG)	KR063595	KR063631
Jungermannia eucordifolia	*J. eucordifolia*	Russia: Adygeia Rep., **1**, N. Konstantinova, A. Savchenko, K133-1-09 (KPABG)	KR063591	KR063623
J. eucordifolia	*J. atrovirens*	Russia: Adygeia Rep., **2**, N. Konstantinova, A. Savchenko, K484-5-07, 111759 (KPABG)	KR063594	KR063627

...*Continued on next page*

TABLE 1. (Continued)

Taxon	Preliminary identification	Specimen voucher (Herbarium)	GenBank accession numbers *trn*L-F	*trn*G-intron
J. eucordifolia	*J. eucordifolia*	Russia: Republic of Karachaevo-Cherkessia, **1**, N. Konstantinova, A. Savchenko, K322-1-08, 112468 (KPABG)	KR063588	KR063620
J. eucordifolia	*J. eucordifolia*	Russia: Republic of Karachaevo-Cherkessia, **2**, N. Konstantinova, A. Savchenko, K 488-10-05, 109761 (KPABG)	KR063590	KR063622
J. eucordifolia	*J. eucordifolia*	Russia: Kuril Islands, **1**, Paramushir Isl., V. Bakalin, K-78-1a-04, 107379 (KPABG)	KR063593	KR063626
J. eucordifolia	*J. exsertifolia*	Russia: Kuril Islands, **2**, V. Bakalin, K-84-7-04, 107432 (KPABG)	KR063592	KR063625
J. eucordifolia	*J. eucordifolia*	Russia: Murmansk Prov., N. Konstantinova, A. Savchenko, 225-4-02, 9596 (KPABG)	KR063589	KR063621
J. eucordifolia	*J. cordifolia*	United Kingdom, **1**, Hedderson 8819 (BOL)	no data	**AM397802**
J. eucordifolia	*J. exsertifolia*	United Kingdom, **2**, Long 29178	**AY453774**	no data
J. eucordifolia	*J. exsertifolia*	USA: Wyoming, N. Konstantinova, A69-5-95 (KPABG)	AY327775	KR063624
Jungermannia exsertifolia	*J. atrovirens* f. *tristis*	Russia: Kamchatka Territory, V. Bakalin, K-74-13a-04, 106804 (KPABG)	GQ220764	no data
J. exsertifolia	*J. atrovirens* f. *tristis*	Russia: Republic of Karachaevo-Cherkessia, N. Konstantinova, A. Savchenko, K 421-6-05, 109568 (KPABG)	GQ220763	no data
Jungermannia konstantinovae	*J. konstantinovae*	Russia: Primorsky Territory, V. Bakalin, P-69-16-08, 112870 (KPABG)	GU220586	KR063629
Jungermannia pumila	*J. pumila*	Russia: Kuril Islands, Paramushir Isl., V. Bakalin, K-104-10-04, 107552 (KPABG)	KR063583	KR063614
J. pumila	*J. pumila*	Russia: Tuva Rep., V. Bakalin, 10 July 1999 (KPABG)	AY327771	no data
J. pumila	*J. pumila*	Russia: Trans-Baikal Territory, O. Afonina, 11606 (KPABG)	GU220588	KR063615
Jungermannia pumila subsp. *polaris*	*J. polaris*	Norway: Svalbard, **1**, A. Savchenko, K8B-08, (KPABG)	KR063577	KR063607
J. pumila subsp. *polaris*	*J. polaris*	Norway: Svalbard, **2**, N. Konstantinova, A. Savchenko, K65-05 (KPABG)	KR063580	KR063610
J. pumila subsp. *polaris*	*J. polaris*	Norway: Svalbard, **3**, N. Konstantinova, A. Savchenko, K84-1-10 (KPABG)	KR063579	KR063609
J. pumila subsp. *polaris*	*J. borealis*	Russia: Krasnoyarsk Territory, **1**, T. Otnyukova, 102238 (KPABG)	KR063582	KR063612
J. pumila subsp. *polaris*	*J. borealis*	Russia: Krasnoyarsk Territory, **2**, T. Otnyukova, 102242 (KPABG)	KR063576	KR063606
J. pumila subsp. *polaris*	*J. pumila*	Russia: Magadan Prov., O. Mochalova, 106930 (KPABG)	KR063578	KR063608
J. pumila subsp. *polaris*	*J. borealis*	Russia: Murmansk Prov., **1**, N. Konstantinova, A. Savchenko, 315-3-00, 8170 (KPABG)	GU220589	KR063613
J. pumila subsp. *polaris*	*J. pumila*	Russia: Murmansk Prov., **2**, N. Konstantinova, A. Savchenko, 39-5-98, 6939 (KPABG)	KR063581	KR063611

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TABLE 1. (Continued)

Taxon	Preliminary identification	Specimen voucher (Herbarium)	GenBank accession numbers *trn*L-F	*trn*G-intron
Jungermannia sp. indet.1	*J. exsertifolia*	South Korea: KyongNam Prov., V. Bakalin, Kor-14-36-09, 112882 (KPABG)	GU220587	KR063628
Jungermannia sp. indet. 2	*J. pumila*	Norway: Svalbard, N. Konstantinova, A. Savchenko, K117-1-10 (KPABG)	KR063597	KR063633
Jungermannia sp. indet. 2	*J. pumila*	Russia: Komi Rep., M. Dulin, 23 August 2006 126B=639 MVD (KPABG)	KR063598	KR063634
Mesoptychia heterocolpos	*Mesoptychia heterocolpos*	Russia: Buryatiya Rep., Konstantinova N.A., A. Savchenko, 50-3-01 (KPABG)	KM501494	KM501476

Phylogenetic analyses

The *trn*L–*trn*F and *trn*G intron nucleotide datasets were automatically aligned in BioEdit 7.0.1 (Hall 1999) with ClustalW option and then manually corrected. The preliminary phylogenetic analyses revealed topology congruence between both datasets and they were then combined. All positions of the final alignment were included in the phylogenetic analysis, absent data was coded as missing.

The combined alignment was analyzed by three analytical procedures: the maximum parsimony method (MP) with TNT v. 1.1 (Goloboff *et al*. 2003), the maximum likelihood method (ML) with PhyML v. 3.0 (Guindon *et al.* 2010) and the Bayesian method with MrBayes v. 3.2.1 (Ronquist *et al.* 2012). The parsimony analysis with TNT involved a New Technology Search with search minimal length tree by one iteration and 1000 bootstrap replicates, the default settings were used for other parameters, indels were taken into account by a modified complex coding algorithm in SeqState (Müller 2005). The GTR+I+G model was selected as the best-fit evolutionary model of nucleotide substitutions for alignment using the ModelGenerator software (Keane *et al.*, 2004). In ML analysis this model was used and the rate heterogeneity among sites was modelled using a gamma distribution with four rate categories. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 500 replicates. According to the stopping frequency criterion (FC) for the bootstrapping procedure (Pattengale *et al*. 2010) for our dataset only 200 replicates were enough for reaching BS convergence with Pearson average ρ100 = 0.994521 as estimated by RAxML v. 7.2.6 **(**Stamatakis 2006).

For the Bayesian analysis each of the partitions of combined alignment (*trn*L–*trn*F and *trn*G intron) was separately assigned the GTR+I+G model, and gamma distributions were approximated using four categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated, and two starting trees were chosen randomly. The number of generations was one million, and trees were saved once every 10th generation. The software tool Tracer (Rambaut & Drummond 2007) revealed effective sample size (ESS) as 3136,4299 and auto-correlation time (ACT) as 573,9073 for our data. The first 10,000 trees as determined by Tracer were discarded in each run, and 180,000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated as branch support values from trees sampled after burn-in.

The infrageneric and infraspecific variability of *trn*L–*trn*F and *trn*G intron for the genus *Jungermannia* species was estimated as the value of the *p*-distances between specimens and species, as calculated in Mega 5.1 (Tamura *et al.* 2011) using the pairwise deletion option for counting gaps.

Results

In total, *trn*L–*trn*F sequences were obtained for 30 specimens, *trn*G intron for 36 specimens and these were then used to produce a combined alignment with previously published data. The combined alignment for 43 specimens of *Jungermannia* and the outgroup taxon consists of 1,237 character sites, among them 504 sites belong to *trn*L–*trn*F, 733 sites to the *trn*G intron. The number of invariable sites in the *trn*L–*trn*F region and *trn*G intron are 401 (79.56 %) and 445 (60.71%) respectively, variable positions are 102 (20.24%) and 169 (23.10%), parsimony informative positions 75 (14.88%) and 105 (14.32%). In the combined alignment there are 946 (76.48%) constant positions, 271 (21.91%) variable and 180 (14.55%) parsimony informative positions. Thus, the both tested cpDNA loci reveal similar level of variability.

The MP analysis with TNT yielded five equally parsimonious trees at different runs with a length of 662 steps, with CI = 0.789731 and RI = 0.926180 calculated in Mega 5.1. The ML calculation resulted in a tree, the arithmetic means of Log likelihood was –3,920.50474. Arithmetic means of Log likelihoods in BA analysis for both runs sampled were –3,966.87 and –3,972.66.

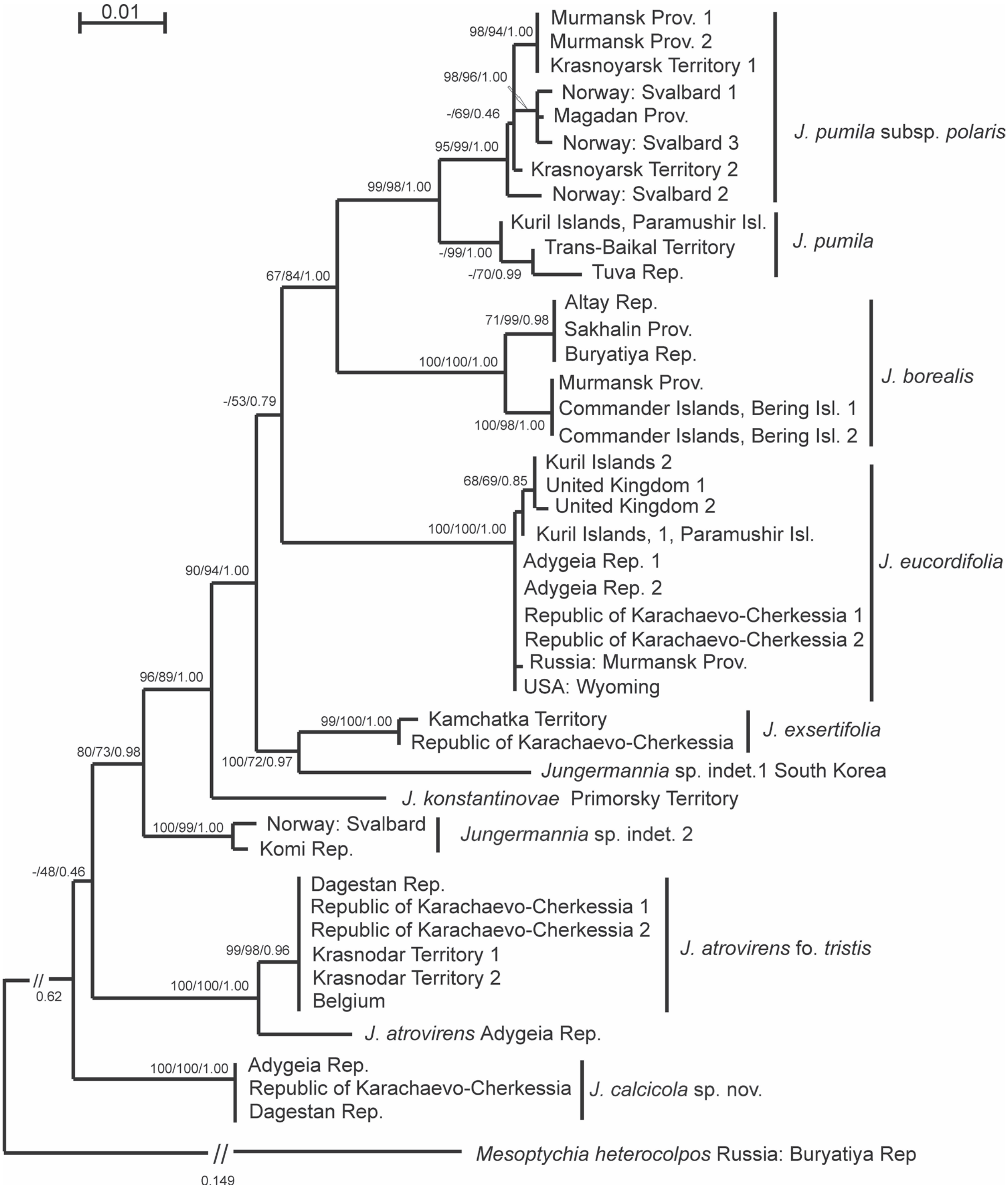

FIGURE 2. Phylogram obtained in a maximum likelihood calculation for the genus *Jungermannia* based on combined nucleotide sequences dataset of *trn*L–*trn*F and *trn*G-intron cpDNA. Bootstrap support values of maximum parsimony, maximum likelihood analyses and Bayesian posterior probabilities more than 50% (0.50) are indicated. The values of length for cut branches are shown.

The tree topologies achieved by the three methods are highly congruent. Thus, on Fig. 2 we provide the ML tree with indication of bootstrap support values (BS) calculated by MP and ML analyses and posterior probabilities (PP) calculated by Bayesian analyses. All studied *Jungermannia* specimens located in seven clades and two phyla that mainly corresponds with current taxa delimitation. The multiple sampled *Jungermannia pumila* Withering (1796: 883) s. lat. (99/98/1.00) and *J. borealis* Damsh. & Váňa (1977: 5) (100/100/1.00) located in a sister relation (BS = 67% in MP, BS = 84% in ML, PP = 1.00 in BA or 67/84/1.00). The clade of *Jungermannia pumila* is subdivided into two robustly supported subclades, one of them grouping specimens from subarctic regions of Russia and Svalbard (95/99/1.00), the other from mountains of South Siberia and Paramushir Island (–/99/1.00). The next slightly supported divergence (-/53/0.79) is composed by a clade of *Jungermannia eucordifolia* Schljakov (1981: 37) specimens (100/100/1.00). The clade of two specimens provisionally referred by us to *J. exsertifolia* Steph. (1917: 86) s. str. (99/100/1.00) is related to a specimen from South Korea (100/72/0.97) that also was provisionally identified as *J. exsertifolia,* but clearly molecularly distinct from the Russian specimens and here named *Jungermannia* sp. indet. 1. *Jungermannia konstantinovae* Bakalin & Vilnet (2009: 161) from Primorsky Territory was located in a separate clade. Two specimens previously identified as *Jungermannia pumila* from Svalbard and Komi Republic were placed together (100/99/1.00) in a position remote from the terminal *J. pumila*-clade and cited here as *Jungermannia* sp. indet. 2. The specimens of *Jungermannia atrovirens* are in a single but subdivided clade (100/100/1.00) with separation from specimen from the Adygeia Republic. The clade (100/100/1.00) composed by three Caucasian specimens referred to a previously unknown species by morphology was found in sister relation to other studied Jungermannia on a constructed topology that could be explained by taxa sampling insufficient for the current phylogenetic estimate of the genus. The relation of this clade could be clarified in a subsequent study with extended taxa and DNA markers sampling.

TABLE 2. The value of infrageneric and infraspecific *p*-distances for the genus *Jungermannia,* n/c—non calculated value due to single specimen only or unsequenced DNA locus.

	Infraspecific p-distances, %	Infrageneric *p*-distances, % (*trn*L-F/*trn*G-intron)										
Taxon	*trn*L-F/*trn*G-intron	*pumila* var. *polaris*	*pumila* var. *pumila*	*borealis*	*eucordifolia*	sp. indet.1	*exsertifolia*	*konstantinovae*	sp. indet. 2	*calcicola*	*atrovirens* f. *tristis*	*atrovirens*
pumila var. *polaris*	0.2/0.7											
pumila var. *pumila*	0.5/0.4	1.7/2.2										
borealis	0.5/0.7	3.4/4.1	3.6/4.1									
eucordifolia	0.3/0.1	5.2/4.7	4.8/4.1	5.1/4.7								
sp. indet.1	n/c/ n/c	5.2/6.6	4.9/5.9	4.5/5.6	5.7/4.6							
exsertifolia	0.2/-	4.3/-	4.3/-	3.0/-	4.9/-	3.6/-						
konstantinovae	n/c/ n/c	3.7/5.0	4.0/4.1	3.3/5.9	4.6/5.9	3.8/6.4	2.7/-					
sp. indet. 2	0.2/0.6	4.5/5.7	4.1/4.7	4.3/5.4	5.1/5.2	4.4/5.7	3.7/-	1.8/4.3				
calcicola	0.0/0.0	5.9/6.2	6.2/5.6	5.7/6.3	6.4/6.0	5.9/6.2	4.7/-	3.2/5.8	4.0/3.4			
atrovirens f. *tristis*	0.0/0.0	5.5/6.8	5.8/6.2	5.2/6.4	6.3/6.2	5.5/7.0	4.8/-	3.1/5.6	3.3/4.0	4.3/4.0		
atrovirens	n/c/n/c	5.6/7.1	5.6/6.6	5.3/6.3	5.9/6.9	5.37.5	4.7/-	3.0/6.1	3.3/4.4	4.8/4.6	0.9/1.9	

The estimate of infraspecific *p*-distances reveal the greatest diversity between specimens located in *Jungermannia pumila*-clade (*trn*L–*trn*F = 0.9%, *trn*G intron = 1.3%, data not shown). The separate calculation in subclade with eight specimens of *J. pumila* from Arctic and Subarctic achieves diversity in the *trn*L–*trn*F = 0.2%, in the *trn*G intron = 0.7%, for the subclade with three specimens from southern mountains—*trn*L–*trn*F = 0.5%, *trn*G intron = 0.4% that corresponds with infraspecific diversity in other widely distributed species (for example, *J. borealis*: *trn*L–*trn*F = 0.5%, *trn*G intron = 0.7%; *J. eucordifolia* *trn*L–*trn*F = 0.3%, *trn*G-intron = 0.1%) (Table 2). The values of *p*-distances between both subclades of *J. pumila* are *trn*L–*trn*F = 1.7% and *trn*G intron = 2.2% which is almost two times lower than the divergence between other *Jungermannia* species. The subsequent revision of morphological features of molecularly tested specimens allowed us to detect some diagnostic characters of *J. polaris* in a number of Arctic and Subarctic accessions whereas three other were classified as *J. pumila*. Taking low level of genetic diversity and insufficient morphological differentiation into account the treatment of *Jungermannia polaris* Lindberg (1866: 560) as a subspecies of *J. pumila* seems more natural. The specimen of *Jungermannia atrovirens* from the Adygeia Republic is differentiated from invariable in DNA sequences six specimens of *J. atrovirens* from Russian part of Caucasus and Belgium both in *trn*L–*trn*F and *trn*G intron (0.9%, 1.9% consequently). It supports the subdivision of the recently broadly treated *J. atrovirens* into two taxa and recognition of large forms of this species as *J. atrovirens* f. *tristis* (Nees) Schljakov (1975: 316). The specimen of *Jungermannia* sp. indet.1 from South Korea differs from Russian accessions of *J. exsertifolia* in 3.6% by *trn*L–*trn*F, as well as the clade of *Jungermannia* sp. indet. 2 (Komi Rep. and Svalbard) is clearly separated from other known *Jungermannia* species. Further study is required to elucidate the taxonomy of these genetic units. Three specimens of the provisionally new taxon from distant regions of Caucasus do not reveal variability in studied DNA loci and their molecular divergence from other *Jungermannia* species varied from 3.2% to 6.4% in *trn*L–*trn*F and from 3.4% to 6.3% in *trn*G intron, clearly supporting it as a distinct species described here as *Jungermannia calcicola* sp. nov.

Taxonomy

Jungermannia calcicola **Konstant. et Vilnet, sp. nova.** Fig.3.

The species is characterized by a combination of wide leaves and relatively collenchymatosus cells that are characteristic for *Solenostoma* s. str. with absence of perigynium and non beaked perianth that are diagnostic for *Jungermannia.* Other differentiating features are imbricate, distinctly concave to cap-shaped leaves and 3-spiral elaters.

Type:—Russia, Caucasus: Republic of Adygeia, left bank of Kurdzhips River, 44°04’59” N–39°59’59” E, 1495 m elev., in crevices on wet cliff, on limestone rock with admixture of single plants of *Mesoptychia badensis* (Gottsche ex Rabenh.) L.Söderstr. et Váňa, (2012: 52), *Mesoptychia collaris* (Nees) L.Söderstr. et Váňa, 2012: 53, 11 October 2007, *N.A. Konstantinova & A.N. Savchenko #K429-1-07* (holotype KPABG). GenBank # JF421608 (*trn*L–*trn*F cpDNA), KR063630 (*trn*G intron cpDNA).

Plants 0.3–1 (1.2 just below perianth) mm wide and 4–8 (–10) mm long, grass-green—to fuscous green, not branched or sparsely branched, often with single subfloral innovation, branches both terminal and intercalary. Stolons rare in nearest part of shoot. Rhizoids numerous up to the apex of shoot, light brown, (7–)8–10 µm wide, very long, many times longer than wide of shoot up to 1.3 mm. Stem in cross section rounded, 140–170 µm, cells in the middle isodiametric, thin walled with minute trigones, (15–)17–19 µm. Cells of dorsal side of stem distinctly elongated, 22–25 × 31–40(–48) µm. Leaves very obliquely inserted, imbricate, distinctly concave to cap shaped**,** suborbicular, on sterile shoots mostly wider than long (350)380–450(500–530) µm wide and (270–)300–360(–460) µm long, near gametangia slightly larger 500–530 wide × 370–450 µm long. Cells thin walled with distinct trigones, marginal cells 15–17 µm, in the middle (15–)17–20 × 19–25(–28) µm, cuticle coarsely striate-papillose. Oil bodies 2–3(–4) per cell, dark grey, large, from almost spherical 6–8(–10) µm to widely elliptical 8–9 × 10–12(–14) µm. Dioicous. Bracts lager than leaves 690–740 µm wide and 550 µm long. Perianth terminal, distinctly pluriplicate exerted from bracts for 0.5 of its length, obovoid, not beaked, with more or less rounded apex, mouth with one-celled cilia-like teeth that are (11–)12–15(–16) × (26–)45–54 µm, cells below mouth more or less isodiametric, 15–18(–21) × 19–20(–23) µm, perigynium absent. Perianth and immature sporophytes were present in most collected specimens, but mature sporophytes were only found in a specimen collected by G. Doroshina on Scalistyi Ridge (G114388), so the description of capsules, spore and elaters is based on this specimen. Capsules dark brown, spherical, epidermal cells with nodular thickenings. Elaters (7–) 8–9 µm wide, 3-spiral with band to 2 µm wide; spores 12–16 µm, reddish-brown (Fig. 3).

Ecology:—The species is restricted to strictly calcareous (limestone) substrates. It occurs at relatively high elevation (1450–2090 m) mostly in crevices of rocks, between and under rocks or in grottos where air humidity is relatively high. The species usually grows creeping on rock in thin mats. Associated species are *Mesoptychia* spp. and *Conocephalum* spp.

Distribution:—So far the species is known from the Caucasus, particularly from the republics of Adygeia, Karachaevo-Cherkessia and Dagestan (Fig. 1).

Additional specimens (paratypes) studied:—Republic of Karachaevo-Cherkessia: Scalistyi Ridge, Gumbashi Mount, 43°46’18” N–42°13’15” E, alt. 2065 m, *N.A. Konstantinova & A.N. Savchenko #K-402-8-10* (KPABG; GenBank accessions ##KR063595, KR063631); Bermamyt Mountain, 43°41’21” N–42°27’47” E, alt. 2443 m, 13 July 2010, *G. Doroshina*, *#G114388* (KPABG); eastern Caucasus, Republic of Dagestan, Gunib Plateau northwest-facing rock outcrops, 42°24’01” N–46°54’ 09” E, alt. 2090 m, *N.A. Konstantinova*, *#K60-9-11* (KPABG; GenBank accessions ##KR063596, KR063632).

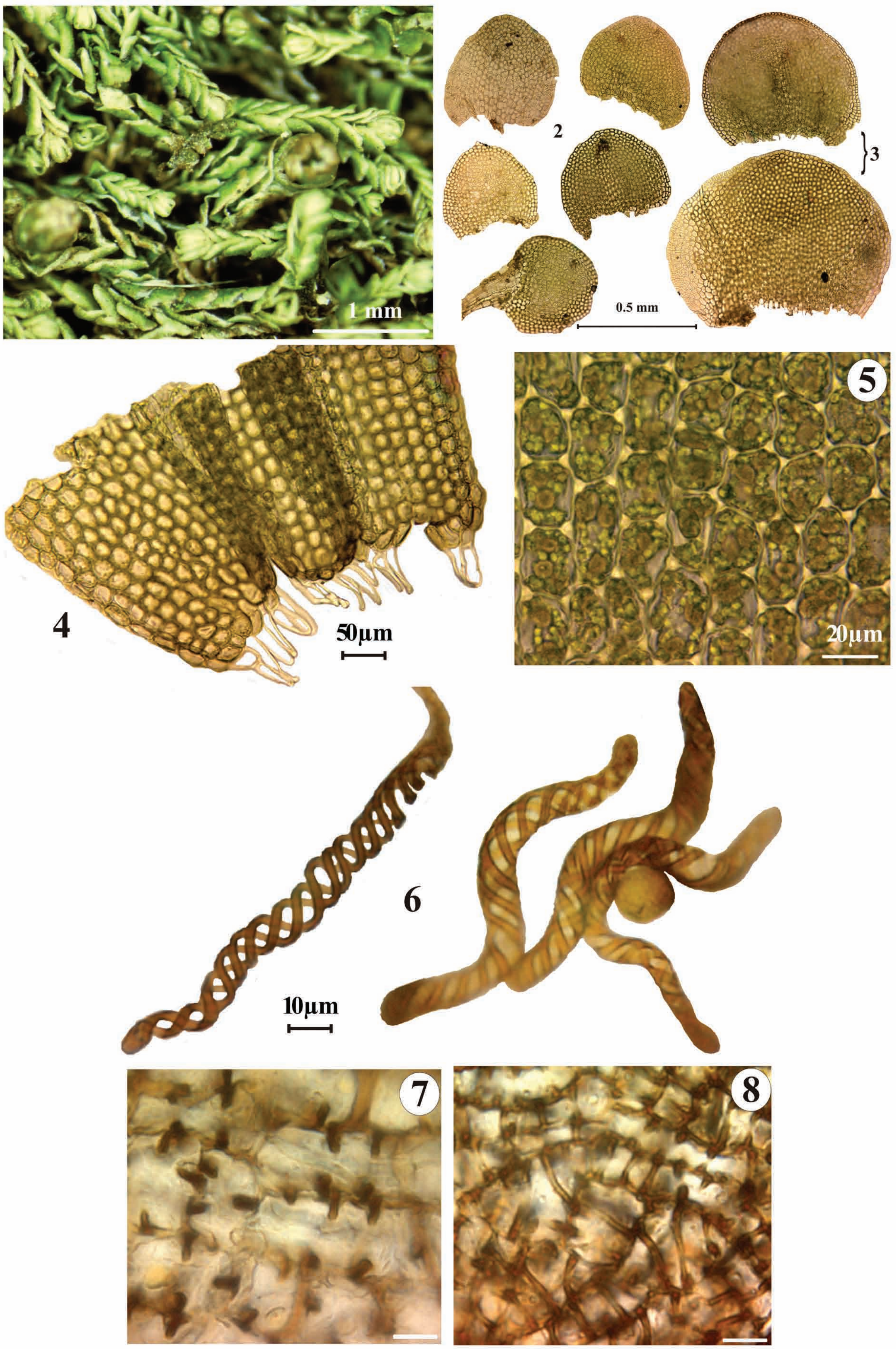

FIGURE 3. *Jungermannia calcicola* Konstant. et Vilnet. 1—Plants of *Jungermannia calcicola*; 2—leaves on sterile shoot; 3—bracts; 4—perianth mouth; 5—cells of the middle of leaf with oil-bodies; 6—cells of perianth; 6—elaters; 7–8—cells of capsule wall.

Differentiation:—The species can be confused with *Jungermannia atrovirens* from which it differs in 1) the generally smaller size, the width of plants without perianth usually not exceeding 0.3–0.5 mm; 2) the shape of the leaves that are wider than long with wide/length ratio (1.2–)1.3–1.5, with the most wider part near the middle whereas in *J. atrovirens* the leaves are usually longer than wide or slightly wider and more or less cordate; 3) the bracts appressed not spreading vs. spreading or erect-spreading in *J. atrovirens*; 4) distinct and usually relatively large trigones especially in perianth cells; and 5) 3-spiral elaters whereas in *J. atrovirens* they are 1–2 spiral.

Etymology:—The epithet indicates that this species is found on calcareous substrates.

KEY FOR THE SPECIES OF *JUNGERMANNIA* S.STR. OCCURING IN RUSSIA

1. Paroicous (rare heteroicous), mostly fertile, usually small, not exceed 1.2 mm (1.5) wide 2
- Dioicous 4
2. Plants prostrate, creeping, leaves distant, flattened, rarely slightly concave, broadly ovoid, very obliquly inserted, plants occurring on Ca-rich substrates, known only from the type locality in the Far East of Russia .... *J. konstantinovae*
- Leaves usually approximate to imbricate, more rarely distant, but then leaves are concave, scale like and wide of stem is 0.25–0.4 wide of shoot, plants apart some arctic forms semi-erect 3
3. Leaves longer than wide, width of stem do not exceed 0.2–0.25 wide of shoot .... *J. pumila* subsp. pumila
- Leaves as wide as long, usually concave or caniculate, wide of stem is 0.25–0.4 wide of shoot .... *J. pumila* subsp. *polaris*
4. Plants large, (1.5) 2–4 (6) mm wide, usually dark green, leaves narrow inserted, broadly triangular and cordate at base, sheathing the stem, often with dark red or reddish brown cell walls, perianth mouth crenulate, cells below mouth generally elongate .... *J. eucordifolia*
- Plants usually less than 2 mm wide, leaves not or slightly sheathing the stem and not or slightly cordate at base 5
5. Plants very small, width of shoot without perianth not exceed 0.5–1 mm, leaves imbricate, distinctly concave to cap shaped, suborbicular, on sterile shoots mostly wider than long, widest in lower third of leaf , wide/length ratio (1.2–)1.3–1.5, cells with distinct and relatively large trigones, elaters 3-spiral .... *J. calcicola*
- Plants usually more than 0.7 mm wide, leaves flattened, slightly concave or cucullate near apex but never cap shaped, as wide as long or longer than wide, elaters 2 spiral 6
6. Plants dull green to yellowish-brown and brown, leaves flat or concave, androecia consist of 6–10 pairs of bracts, species restricted to Ca-rich substrates .... *J. atrovirens*
- Plants dark green to blackish and black-brown, leaves slightly concave, androecia consist of 3–4 pair of bracts, species restricted to acidic or neutral substrates 7
7. Plants small with shoots 0.7–1.2 (1.3) mm wide, leaves distinctly cucullate at apex, laterally appressed to the stem ...... J. *borealis*
- Plants (1)1.2–2.5 mm wide, leaves usually flat or slightly concave, spreading, cells of leave walls often rusty-red or brown .... *J. exsertifolia*

Discussion

All known species of the genus *Jungermannia* s. str. with the exception of the south American *J. ovatotrigona,* and the recently described *J. yamatoensis* Bakalin & Furuki (2014: 423) were included in this molecular study. Apart from the recently described and poorly known *J. konstantinovae* and the predominantly Asiatic *J. exsertifolia* s. str. all *Jungermannia* taxa tested here are widespread circumpolar arctic montane (*Jungermannia pumila, J. pumila* subsp. *polaris* (Lindb.) Schuster (1988: 121), *J. borealis*) or montane (*J. eucordifolia, J. atrovirens*) species. The only bipolar species of the genus is *Jungermannia pumila* s. lat. It seems to be the most polymorphous taxon of *Jungermannia* s. str. both in molecular characteristics and morphology. Recently most authors with the exception of Schuster (1969, 1988) have accepted the subdivision of this taxon into two species: *J. pumila* and *J. polaris* (Váňa 1973, Damsholt 2002, Paton 1999, etc.). *Jungermannia pumila* and *J. polaris* are separated by: 1) fusiform gradually narrowed to the mouth perianth in *J. pumila* versus more or less parallel-side or broadened upwards and abruptly narrowed to the mouth in *J. polaris*; 2) oval, usually longer than wide leaves in *J. pumila* whereas in *J. polaris* leaves are much broader and widest below the middle; 3) slightly lager cells of leaves without trigones and colourless walls of cells in *J. pumila*. But in his comprehensive study of *Jungermannia* Váňa (1973: 285) stressed that "arktische Pflanzen von beiden Arten sind sehr schwer zu unterscheiden und durch mehrere scheinbare Übergänge verbunden (die aber grosstenteils konvergente Modifikation von *J. polaris* darstellen)". Schuster (1969, 1988) discussed the separation of these taxa in detail and came to the conclusion that "no criterion is reliable for separation of two species" (Schuster 1988:120). Our data rather support this statement (see Fig. 2 and Table 2). Our sampling is unfortunately too limited to come to a definite conclusion at this point. We found that very small plants from the arctic (Svalbard) and the far north (Murmansk and Magadan Provinces and north of the Krasnoyarsk Territory) with small cells, brown walls and distinct trigones that is characteristic for *J. polaris* often have "*pumila*" type of perianth and ovate, slightly longer than wide leaves etc. We referred such plants to *J. pumila* subsp. *polaris* whereas relatively large plants with distinctly fusiform perianth and much more narrow leaves from South Siberia and Paramushir Island were referred to *J. pumila* subsp. *pumila*. Taking the great variability and wide distribution of these taxa into consideration we believe that more profound study of this complex is needed.

Jungermannia borealis is represented in this study by two different forms. Particularly specimens from northernmost territories—Murmansk Province and Commander Islands (Fig. 2)—fit well in this species being relatively small with leafy shoots that do not exceed one mm wide and characteristic for the species narrowly to broadly ovate leaves that are distinctly concave and cucullate. Specimens from South Siberia (Republic Altay and Buryatiya) and Sakhalin are much larger (1.5–2 wide) and have more larger and narrower leaves (up to 0.6 × 1 mm, wide-length ratio to 1: 1.5) that are flat. As was stated by J. Paton (1999: 272) *J. borealis* is "nearly as variable as *J. pumila* and includes phases that are relatively robust with rather large cells and others in which the perianth resemble those of *J. polaris*". If such forms merit any taxonomical status remains unclear.

The studied specimens of *J. eucordifolia* are quite similar both morphologically and molecularly. Only minute differences were found between specimens of *J. eucordifolia* from very outlying areas including different regions of Europe, Caucasus, Far East and North America (Fig. 2). Following Váňa (1973) most authors recognize this taxon as *Jungermannia exsertifolia* subsp. *cordifolia* (Dumortier 1874: 59) Váňa (1973: 268) (Paton 1999, Damsholt 2002, etc.) and attribute specimens from Japan, Korea and China to *J. exsertifolia* subsp. *exsertifolia*. Bakalin (2014) in his treatment of *Jungermannia* for Russian Far East referred not only Far Eastern specimens but as well as specimens from Caucasus, Murmansk Province and from North America to *J. exsertifolia* subsp. *exsertifolia*. That drastically changed the present ideas about the distribution of this taxon, but Bakalin (l.c.) did not give any comments on his statement. The specimens from Kamchatka and Caucasus we sequenced were placed in a clade separate from *J. eucordifolia* (Fig. 2). These specimens were provisionally attributed by us to *J. exsertifolia* subsp. *exsertifolia* based on a combination of relatively small size, narrow not cordate and slightly sheeting the stem leaves. The position obtained on the phylogenetic trees (Fig. 2) and the level of genetic distances (Table 2) allow to consider *J. eucordifolia* and *J. exsertifolia* as two clearly distinct species with highly overlapping distribution. A subsequent study with extended specimen sampling especially from eastern Asia including the study of the type of *J. exsertifolia* is needed to clarify the species delimitation in this group.

The result of this study additionally supports the recently described *J. konstantinovae* (Bakalin & Vilnet 2009) as a distinct species due to its clearly separated phylogenetic position (Fig. 2).

The sampling of *Jungermannia atrovirens* s. lat. is in this study restricted to specimens from Caucasus and one specimen from Belgium. All but one specimen represent large plants with ovate, longer than wide leaves that agree well with f. *tristis* and only one specimen was referred by us to the typical *Jungermannia atrovirens*. Insufficient sampling did not allow us to determine if *Jungermannia atrovirens* f. *tristis* merits a higher taxonomical status as was indicated by Schuster (1969).

Conclusions

This investigation has led to the recognition of an increased diversity of *Jungermannia* s. str. than prior studies. In addition to the newly described taxon, *J. calcicola,* there maybe other undescribed taxa that require further investigation, e.g., South Korean specimens that are provisionally referred to *J. exsertifolia*. Probably some intraspecific taxa in *J. borealis* should be distinguish based both on morphology and DNA data. A taxon with putative *J. pumila* morphology from Svalbard and Komi Republic that differs distinctly from other specimens of *J. pumila* on the DNA markers can be regarded as a cryptic species.

The taxonomical status of the ambiguously treated *J. eucordifolia* was supported by their phylogenetic affinity and level of genetic diversity from allied taxa. The long forgotten *J. atrovirens* f. *tristis* seems is the distinct taxon but if it merit status of species need to be studied. Our attempt to solve existing taxonomical problems in *Jungermannia* s. str. has elucidated a number of new questions and it is clear that the further investigation is required to have a complete understanding of the *Jungermannia* taxonomy.

Acknowledgments

The map and photos were prepared by Mr. A.N. Savchenko, to whom the authors are sincerely grateful. A. Hagborg is gratefully acknowledged for fruitful consideration and correction of English and taxon citations. We thank Prof. J. Váňa and Dr. Matt von Konrad for valuable comments and some correction on the manuscript. The work was partially supported by the RFBR (15-04-03479)

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