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HIDDEN DIVERSITY AND THE TREATMENT OF *JUNGERMANNIA PUMILA* S.L. WITH DESCRIPTION OF A NEW SUBSPECIES FROM THE RUSSIAN FAR EAST

СИСТЕМАТИКА КОМПЛЕКСА *JUNGERMANNIA PUMILA* S.L. С ОПИСАНИЕМ НОВОГО ПОДВИДА С ДАЛЬНЕГО ВОСТОКА РОССИИ

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Abstract

An integrative study of the *Jungermannia pumila* complex in the Northern Palearctic – from Svalbard to the Caucasus and from the British Isles to Kamchatka and Kuril Islands, including specimens collected near the type localities of the taxa showed molecular genetic divergence into three closely related subclades of the same major clade. The major clade is treated here as *J. pumila* s.l. and the obtained subclades are considered as subspecies. One subclade is formed by specimens from the British Isles and Central Europe; these specimens morphologically are in good agreement with *J. pumila* subsp. *pumila*. The second subclade consists of specimens from the northern regions and upper belts of the mountains of Europe and Asia. Some of these specimens morphologically correspond to *J. pumila* subsp. *polaris.* The third subclade includes specimens from the southern regions of the Russian Far East and the mountains of South Siberia. We describe them as a new subspecies *J. pumila* subsp. *orientalis*. Morphological variability of the specimens is significant and overlaps between the subclades. Taking into account comparatively low molecular genetic divergence between the subclades, it may be considered that the discussed three taxa are in the process of diversification and their morphological differentiation is not complete. Therefore, we treat them as subspecies. The variability of individual morphological features and the ecology and distribution of the discussed subspecies were examined.

Резюме

Интегративное исследование комплекса *Jungermannia pumila* в Северной Палеарктике – от Шпицбергена до Кавказа и от Британских островов до Камчатки и Курил, в том числе образцов, собранных вблизи типовых местонахождений, показало молекулярно-генетическую дифференциацию этого комплекса на три близкродственные субклады в пределах основной клады. Последняя трактуется здесь как *J. pumila* s.l., тогда как полученные субклады рассматриваются как подвиды этого вида. Одна субклада образована образцами с Британских островов и из Центральной Европы, которые морфологически хорошо согласуются с трактовкой *J. pumila* subsp. *pumila.* Вторая субклада составлена образцами из северных регионов и верхних горных поясов Европы и Азии; большинство из которых морфологически соответствуют *J. pumila* subsp. *polaris.* Третья включает образцы из южных регионов Дальнего Востока России и гор Южной Сибири, которые описываются здесь как новый подвид *J. pumila* subsp. *orientalis*. Морфологическая вариабельность образцов в пределах субклад значительна и между образцами из разных субклад отмечено перекрывание по морфологическим признакам. Учитывая сравнительно низкую молекулярно-генетическую дивергенцию между субкладами, можно предположить, что три таксона представленные этими субкладами находятся в стадии становления и их морфологическое обособление не завершено. Исходя из этого, данные таксоны трактуются здесь как подвиды. Рассмотрена вариабельность отдельных морфологических признаков этих подвидов, а также их экология и распространение.

KEYWORDS: liverworts, molecular analyses, morphology, phylogeny, systematics, distribution, *trn*L-F, *trn*G-intron

Introduction

Jungermannia L. in its modern narrow sense is a relatively small genus of leafy liverworts (Jungermanniidae, Jungermanniopsida, Marchantiophyta). Eleven species were referred to this genus in the recent world checklist (Söderström *et al*., 2016), and two new species, namely *J. calcicola* Konstant. & Vilnet (Konstantinova & Vilnet, 2016) and *J. afoninae* Mamontov, Konstant. & Vilnet (Mamontov *et al*., 2018), were described subsequently. The only bipolar species of the genus is *J. pumila* With.

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s.l., which, moreover, is one of only two bisexual species in the genus (the second is *J. konstantinovae* Bakalin & Vilnet). As is often (but not always) observed, species with relatively wide geographical and ecological range are morphologically and, in particular, genetically quite heterogeneous. *J. pumila* s.l. seems to be the most polymorphous taxon of *Jungermannia* s.str. both in its molecular characteristics and morphology. This is reflected in its synonymy, which includes about 30 names (see Váňa, 1973).

The problem of interpreting the *J. pumila* complex dates back to the time of Lindberg's description of *J. polaris* Lindb. from Svalbard (Lindberg, 1867). The species was described as dioicous, and Berggren (1875) accepted this characteristic in his treatment of *J. pumila* subsp. *polaris*. However, the type specimen of *J. polaris* preserved in H contains paroicous plants and the reason for such interpretation of this taxon as dioicous by Lindberg (l.c.) is explained by J.Váňa (1973:283) who characterized it as "Parözisch, durch Proterandrie auch scheinbar autözische und diözische Pflanzen vorkommend" (l.c. 281). Later, Schuster (1969) described this taxon as paroicous or sporadically autoicous and Damsholt (2002) characterized it as sporadically heteroicous. Schuster (1969, 1988) considered *J. polaris* as *Solenostoma pumilum* subsp. *polare* (Lindb.) R.M.Schust. and Damsholt (2002) as *J. pumila* subsp. *polaris* (Lindb.) Berggr. However Váňa (1973), Schljakov (1981), Paton (1999), Bakalin (2014), Söderström *et al.* (2016), and Hodgetts *et al*. (2020) have accepted the subdivision of this taxon into two species: *J. pumila* and *J. polaris*. According these authors (l.c.) two taxa are distinguished mainly in the shape of the leaves (mostly wider than long or about as wide as long to almost suborbicular in *J. polaris* vs. noticeably longer than wide, rather ovate to semi-ovate in *J. pumila*), in the shape of the perianth, and, in smaller size of shoots and cells (both in leaves and capsules) in *J. polaris* vs. *J. pumila.* 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 grösstenteils konvergente Modifikationen von *J. polaris* darstellen)". Schuster (1969, 1988) discussed the separation of these taxa in detail and came to conclusion that "Hence the presumption is that there has been, to some extent, genetic segregation into partially isolated populations" (Schuster, 1969: 909), and "no criterion is reliable for separation of two species" (Schuster 1988: 120). Molecular genetic methods that have become widespread in the practice of taxonomic research in the 21st century have made it possible now to test this presumption. The main purpose of our study is to check to what extent such a morphological interpretation of the taxa of this group is supported genetically and to try to find morphological features that make it possible to distinguish the species (subspecies) of the group. We also attempt to find out if there are significant morphological and genetic differences between populations from different geographically remote regions.

MATERIAL AND METHODS

Collections and specimens studied

Specimens of *Jungermannia* spp. stored in the herbarium of the Polar-Alpine Botanical Garden-Institute of Kola Science Center, Apatity, Russia (KPABG) and the herbarium of the Main Botanical Garden, Moscow (MHA) were revised. In addition, we studied five specimens collected in the British Isles specifically for this work by one of the authors (D.G. Long) as well as specimens kindly sent by N.G. Hodgetts.

Váňa (1973: 287) in part of his treatment of the genus wrote that he failed to study the original type material used by Withering in 1796 in the first description of *J. pumila* because he could not find it in the herbaria and concluded that it was most probably lost. He therefore designated a neotype specimen (Váňa, 1975: 365) collected in North Wales (Great Britain) by Carrington & Pearson from Tyn-y-groes, Merioneth in 1879 and distributed in their *Hepaticae Britannicae Exsiccatae* under no. 172 (MANCH, neotype, with isoneotypes in BM and FH). Thus, we studied specimens recently collected by D.G. Long in the area close to the neotype locality of *J. pumila* in North Wales

Long before this study one of the authors (N.A. Konstantinova) studied type specimens of *J. polaris* stored in H-SOL. Unfortunately, we were unable to collect *J. pumila* subsp. *polaris* in its type locality designated by Malmgren, who collected the type specimen "ad Treurenbergbay", the modern name Velcomstvarden (The Placenames of Svalbard: https://web.archive.org/web/20070623065603/http://miljo.npolar.no/Placenames/pages/searchE.asp 2001). However, during several expeditions to Svalbard, the first author had the opportunity to collect and study *J. pumila* subsp. *polaris* from different regions of the archipelago, where the subspecies is not uncommon. That is why many specimens from remote areas in Svalbard were included in the study. Data on selected specimens studied are presented in Appendix 1. Thus we studied specimens of *J. pumila* subsp. *polaris* collected by Konstantinova & Savchenko in Svalbard from where *J. polaris* was described.

Sampling for molecular analyses

Forty-seven specimens attributed to the *J. pumila* complex were included in the molecular phylogenetic study based on two plastid loci – *trn*L-F and *trn*G-intron. Amongst them, accessions for three specimens were taken from the study of Shaw *et al.* (2015), and for eleven from the study of Konstantinova & Vilnet (2016). Thirty-two specimens were involved in the current study for the first time. Six of them are from the British Isles: one specimen was collected in North Wales near the neotype locality of *J. pumila*, three specimens are from Ireland, and two from Scotland. Twenty-six accessions were selected from Norway (Svalbard) and different regions of Russia (Kuril Islands, South and North Siberia, Caucasus, Kola Peninsula). In general, eight accepted and one unidentified species of the genus *Jungermannia* as well as representatives of the genera *Liochlaena* Nees*, Delavayella* Steph. and *Mesoptychia* (Lindb.) A.Evans from Jungermanniaceae were included in the ingroup. *Solenostoma rossicum* Bakalin & Vilnet from the phylogenetically allied family Solenostomataceae was selected as an outgroup taxon. The list of specimens included in the phylogenetic estimation is provided in Appendix 2.

Morphological study

Morphology of the studied taxa is discussed mainly on the basis of the sequenced specimens. The specimens were studied and photographed using light microscopes equipped with digital cameras. In order to better illustrate the three-dimensional objects, photomicrographs were combined using the stacking software HeliconFocus and then reconstructed into line drawings (Fig. 3–4, 6–8).

DNA isolation, PCR amplification and DNA sequencing

The commercial DNeasy Plant Mini Kit (Qiagen, Germany) was used for DNA extraction from dried shoots of *Jungermannia* specimens according with the manufacturer's protocol. The regions of *trn*L-F and *trn*G-intron were amplified and sequenced with pairs of primers provided by Taberlet *et al*. (1991) and Shaw *et al*. (2005). PCR was carried out in 20 mkl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C (*trn*L-F) or 64°C (*trn*G-intron), 60 s 72°C) and 2 min of final extension time at 72°C. The amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the Cleanup Mini Kit (Evrogen, Russia), and 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 Applied Biosystems 3730 DNA Analyzer.

Phylogenetic analysis

The newly obtained sequences were assembled and datasets for *trn*L-F and *trn*G-intron were produced using the program BioEdit 7.0.1 (Hall, 1999) with ClustalW option and manual correction. Preliminary phylogenetic estimation of both datasets suggested congruence of tree topologies. Both datasets were combined into a single *trn*L-F+*trn*G-intron dataset for subsequent analyses with inclusion of all positions.

Phylogenetic estimations of the genus *Jungermannia* were provided using two approaches: the maximum likelihood (ML) analysis with program IQ-TREE (Nguyen *et al*., 2015) and the Bayesian analysis (BA) with MrBayes v. 3.2.1 (Ronquist *et al.*, 2012). The K3Pu+F+G4 model was selected as the best fit evolutionary model of nucleotide substitutions for combined datasets with the ModelFinder (Kalyaanamoorthy *et al.*, 2017). The ultrafast bootstrapping procedure (Hoang *et al*., 2018) with 1000 replicates was done. The obtained ML tree topologies were redrawn in NJplot (Perričre & Gouy, 1996). For the Bayesian analysis the GTR+I+G model was used as recommended by the program's creators; gamma distributions were approximated with 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 chain, and the two starting trees were chosen randomly. The number of generations was five million. Trees were saved every 100th generation. The average standard deviation of split frequencies between two runs was 0.004291. The first 12500 (25%) trees were discarded in each run, and 75000 trees from both runs were sampled after burn-in. Bayesian posterior probabilities were calculated from trees sampled after burn-in. The FigTree v.1.3.1 was used to visualize Bayesian phylogenetic tree (https://tree.bio.ed.ac.uk/software/figtree/).

The sequence variability for *trn*L-F and *trn*G-intron of the genus *Jungermannia* was estimated as the average pairwise *p*-distances in Mega 11 (Tamura *et al*., 2021) using the pairwise deletion option for counting gaps. Genealogical relationships between haplotypes of the *J. pumila* complex were evaluated in TCS (Clement *et al*., 2000) based on analysis of the combined dataset *trn*L-F+*trn*G-intron, gaps were treated as missing data.

Results

Molecular phylogenetic study

For 32 specimens the nucleotide sequence data of *trn*L-F and *trn*G-intron were newly generated and published in GenBank. The combined *trn*L-F and *trn*G-intron alignment counts 1277 positions, among them *trn*L-F has 534 positions and *trn*G-intron – 743. As a result of ML calculation the single tree with arithmetic mean of Log likelihood -5337.59 was obtained. The arithmetic means of Log likelihood in both runs in the BA analysis were -5500.57 and -5502.00, respectively. The topologies restored from both analytical procedures became highly similar, thus Fig. 1 illustrated an ML tree with indication of bootstrap support (BS) values from ML calculation and Bayesian posterior probabilities (PP) from BA. The increasing of sampling does not influence the phylogenetic affinities among known species of the genus *Jungermannia* and topology of the newly generated tree is congruent with previously published ones (Konstantinova & Vilnet, 2016; Mamontov *et al*., 2018). The multiple sampled specimens of the *J. pumila* complex composed a highly supported terminal clade with BS=97 in ML and PP=1.00 in BA (or 97/1.00) in sister relation (94/1.00) to the *J. borealis* clade (100/1.00). Within the clade of the *J. pumila* complex three subclades (A–C) could be distinguished (Fig. 1). The subclade A contains 24 specimens predominantly from Svalbard and the Russian subarctic or southern mountainous territories – Murmansk and Magadan Regions, Krasnoyarsk Territory, the Republic of Buryatia, Khanty-Mansi Autonomous

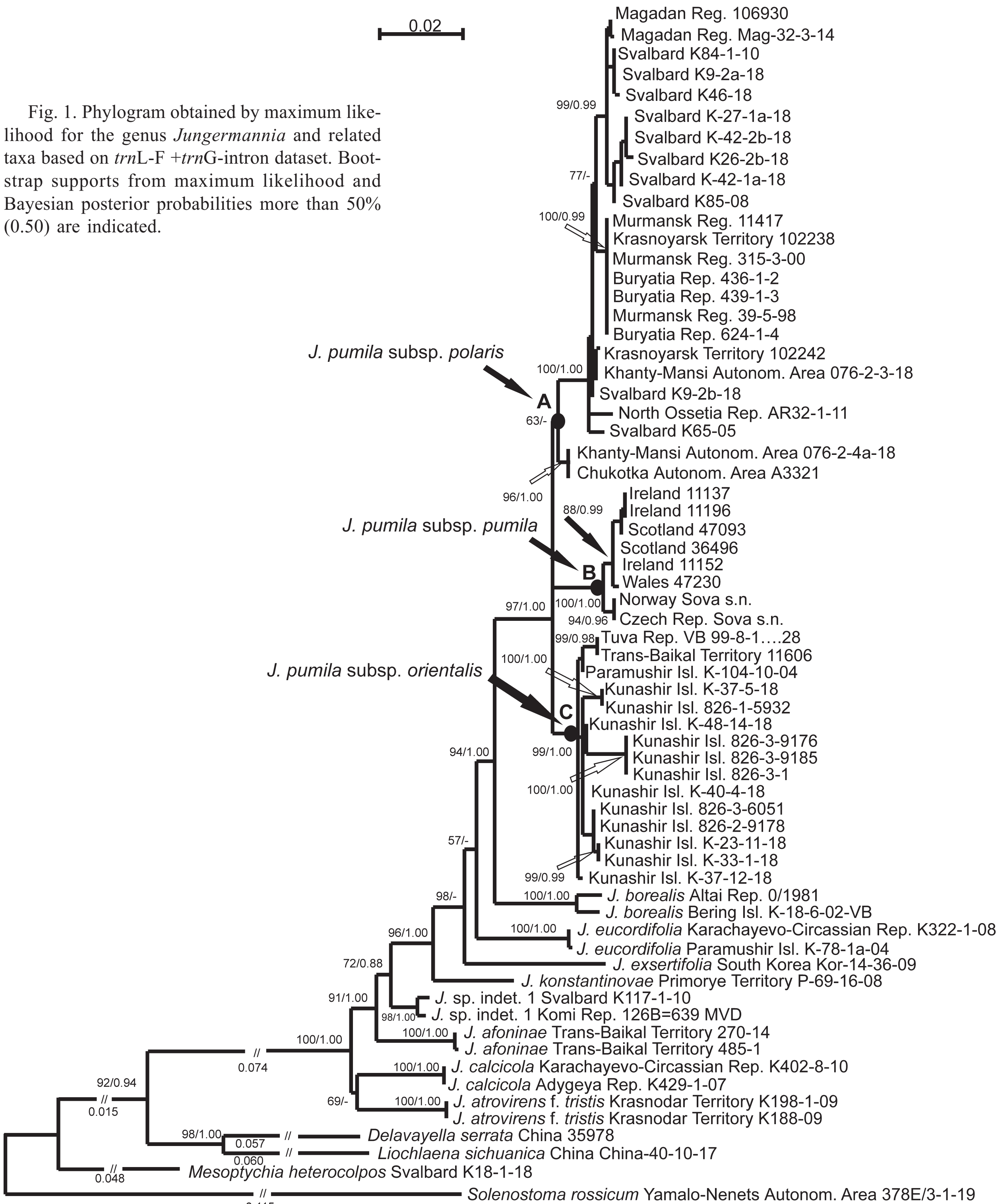

Fig. 1. Phylogram obtained by maximum likelihood for the genus *Jungermannia* and related taxa based on *trn*L-F +*trn*G-intron dataset. Bootstrap supports from maximum likelihood and Bayesian posterior probabilities more than 50% (0.50) are indicated.

Area – Yugra, and the Republic of North Ossetia-Alania (Caucasus). The subclade B supported by 100/1.00 consists of eight European specimens from the United Kingdom (UK), Ireland, Czech Republic and Norway. The specimen *Martin & Long 47230* from a locality nearest to the neotype locality of *J. pumila* in Wales (UK) is also placed in this subclade. The subclade C supported by 99/1.00 unites 13 specimens from Kuril Islands (Kunashir and Paramushir) and two specimens from South Siberia (Trans-Baikal Territory and the Republic of Tuva). The order of subclade divergence is not clear from current estimations, so the subclades perhaps radiated more or less simultaneously.

The nucleotide sequence variability within three subclades of the *J. pumila* complex and other *Jungermannia* species is presented in Table 1.

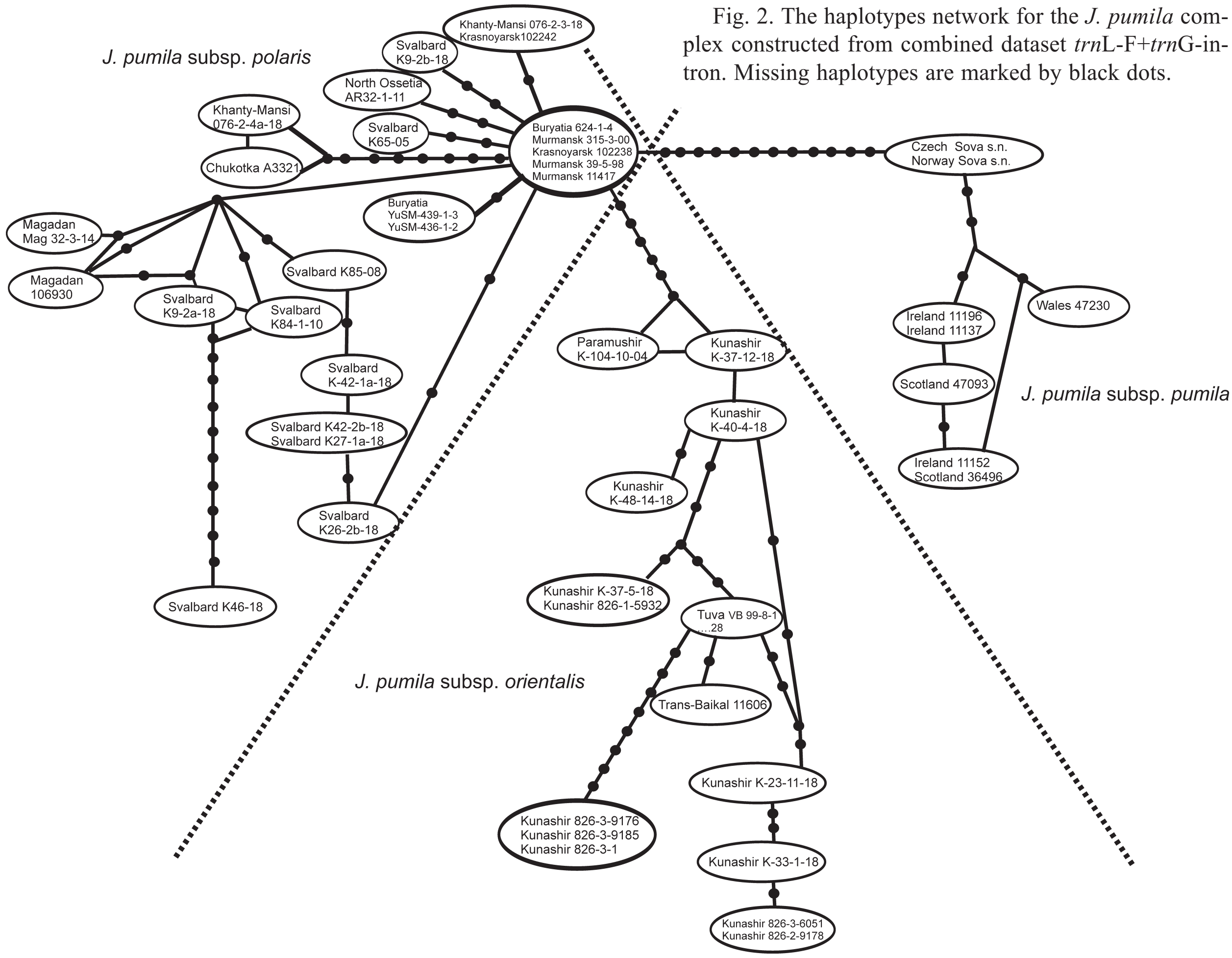

Fig. 2. The haplotypes network for the *J. pumila* complex constructed from combined dataset *trn*L-F+*trn*G-intron. Missing haplotypes are marked by black dots.

Each of the obtained *J. pumila* s.l. subclades is characterized by the nucleotide sequence variability in both genetic loci that is lower or equal to 1 %. The subclade A provides higher variability (0.5% in *trn*L-F and 1.0% in *trn*G-intron) due to specimens from remote localities. The divergence among the three subclades varies from 1.7% to 2.3% in *trn*L-F and from 2.3% to 2.6% in *trn*G-intron. This level of divergence is 1.5–2 times lower than molecular differentiation among other tested *Jungermannia* species. An exception could be a pair comprising the recently described *J. afoninae* and *Jungermannia* sp. indet. 1, which diverged by 2.6% in *trn*L-F and 2.7% in *trn*G-intron, but placed in subsequently diverged clades on the tree.

TCS analysis of the combined dataset produced a network with separation into three haplotype groups (Fig. 2) with specimen distribution corresponding to their positions in the subclades on the phylogenetic tree. The network demonstrates phylogenetic isolation between obtained haplotype groups by a number of missing haplotypes. The greatest diversity with 17 haplotypes (9 of which are from Svalbard) was found in the group that correspond to the subclade A on the tree. The subclade B is presented by five minimally diverged haplotypes from the UK and Ireland. In the subclade C there are 11 haplotypes, 8 of which are from Kunashir.

Phylogeny and morphology

The subclade B containing the Central European and British Isles specimens, including a topotype of *J. pumila* (Fig. 1), is the most homogeneous both genetically and morphologically. Plants in the specimens from this subclade are mostly green or olive green, leaves are distinctly longer than wide and more or less ovate to oblong-ovate, the perianths are fusiform, and the capsules are ellipsoidal. Morphologically (Fig. 3A–I), these specimens are in good agreement with the descriptions of *J. pumila* provided in relevant modern publications (Schuster, 1969; Váňa, 1973; Schljakov, 1981; Paton, 1999; Damsholt, 2002; Bakalin, 2014). The subclade A that we referred to *J. polaris* is morphologically and genetically much more diverse. It includes three groups. Specimens from Magadan Region and different regions of Svalbard are located in the first of these groups and morphologically differ slightly (Fig. 3J–T, 4A–J), mainly in size and color. Some of the specimens composed the subclade A are sterile and previously were referred to other species, in particular, *J. borealis* (Table 1, Fig. 5). The central position is occupied by a genetically homogeneous group of specimens from mountains of the Arctic (Taimyr Peninsula, Krasnoyarsk Territory), subarctic (Kola Peninsula, Murmansk Region) and South Siberia

Table 1. Infra- and interspecific *p*-distances for the genus *Jungermannia*, *trn*L-F/*trn*G-intron, %.

Taxon	Infraspecific *p*-distances, *trn*L-F/*trn*G-intron, %	Interspecific *p*-distances, *trn*L-F/*trn*G-intron, %											
		J. pumila subsp. *polaris*	*J. pumila* subsp. *pumila*	*J. pumila* subsp. *orientalis*	*J. borealis*	*J. eucordifolia*	*J. exsertifolia*	*J. konstantinovae*	*J.* indet. 1	*J. afoninae*	*J. atrovirens*	*J. calcicola*	
J. pumila subsp. *polaris*	0.5/1.0												
J. pumila subsp. *pumila*	0.3/0.3	2.3/2.6											
J. pumila subsp. *orientalis*	0.4/0.5	1.7/2.5	2.2/2.3										
J. borealis	0.8/1.2	3.5/4.4	4.4/4.7	3.7/4.5									
J. eucordifolia	0.2/0.0	5.5/4.8	5.6/5.2	5.1/4.5	4.6/4.8								
J. exsertifolia	n/c/n/c	4.6/6.9	5.0/6.8	4.1/6.3	4.0/5.5	5.6/4.7							
J. konstantinovae	n/c/n/c	3.4/5.1	4.1/5.2	3.6/4.4	2.9/5.9	4.6/5.8	3.8/6.5						
J. indet. 1	0.2/0.6	4.2/5.8	4.4/5.9	3.8/4.9	3.9/5.4	5.1/5.3	4.4/5.8	1.8/4.3					
J. afoninae	0.2/0.0	5.4/6.4	5.6/6.6	4.9/5.7	4.9/6.2	5.9/6.0	5.1/6.8	3.4/5.1	2.6/2.7				
J. atrovirens	0.0/0.0	5.3/6.9	5.2/6.9	5.6/6.4	4.7/6.3	6.1/6.1	5.3/7.0	3.0/5.5	3.3/3.9	4.0/4.5			
J. calcicola	0.0/0.0	5.9/6.2	6.6/6.5	6.1/5.6	5.2/6.2	6.3/5.9	5.8/6.2	3.1/5.6	3.9/3.3	4.4/4.1	4.2/3.6		

(Republic of Buryatia). Plants in this group vary in color: from dull dirty dark green to blackish green, often with light to dark brown upper parts of leaves and more darkly colored margins. The plants are relatively large, varying from 0.7 to 1.2 mm wide; leaves on sterile shoots are slightly longer than wide or as wide as long, ca. (250–) 350–500 × (350–)400–550 µm (Republic of Buryatia, *Mamontov 624-1-4*). In some specimens (e.g. *Otnyukova s.n.*, KPABG 102238) leaves are distinctly elongated, up to 650–680 ěm wide and to 780 µm long. The ratio of shoot width to stem width varies from 4/1 to 6–9/1. Some of these specimens, especially those without perianth were identified as *J. borealis, J. exsertifolia*, or *J. pumila* (Fig.5, Table 1). Spores have been found in the only specimen of this group from the Republic of Buryatia (*Mamontov 436-1-2*); the spores are relatively large, 18–22(–25) µm. The spore size was previously characterized for *J. polaris* as 15–18(–20) µm (Váňa, 1973) or 15–18 µm (Schuster, 1969; Bakalin, 2014).

Closely related to the described group are specimens from remote regions: from Svalbard to the Urals (Khanty-Mansi Autonomous Area) and Taimyr Peninsula (Krasnoyrask Territory) in the north, and the Caucasus (North Ossetia) in the south. Morphologically, they are quite heterogeneous and contain different phases, including (1) olive green, relatively large (1–2 mm wide) plants from the Urals (*Lapshina 076-2-3-18*), (2) middle sized plants with distinctly longer than wide leaves from Taimyr (*Otnyukova s.n.*, KPABG 102242), and (3) very small plants from Svalbard with strongly concave leaves just up to 175 µm long and uaually wider than long (*Konstantinova K9-2-18*, Fig. 4A–J). Interestingly, shoots from different parts of the latter specimen (*Konstantinova K9-2a-18* and *K9-2b-18*), differing mainly in color, are located in different branches of the discussed subclade A. Of particular interest in this subclade is the specimen *Lapshina 076-2-3-18* from the Urals. Plants in this specimen have a cylindrical perianth to 0.8–1 mm wide × 2 mm long, plicate in the upper quarter (ca. 400 µm long) where it narrows to 250–270 µm wide, forming a specific beak-like mouth; the beak is grooved with small ribs sometimes with one-celled teeth along ribs. At the same time, another specimen collected side-by-side on the slope to the stream (*Lapshina 076-2-4-18*, Fig. 3L, M, N, Q–T) is located in a separate branch along with the specimen *Afonina 3321* from Chukotka (Fig. 3J, K, O, P; Fig. 6A–M). The latter is very peculiar and is distinguished by its (1) rather large size of shoots – up to 1.8 mm in the androecial region, (2) large elongated leaves and bracts with the length (1–1.8 mm) significantly exceeding the width (0.7–0.8 mm), (3) irregularly polygonal cells in the upper part of the leaf, 17–19(–22) µm, with minute thickenings and brown-colored walls, (4) large number of pairs (8–12) of androecial bracts, (5) relatively large spores (20–23 µm), (6) many terminal branches (Fig. 3, 6).

The subclade C includes specimens from Kunashir (Fig. 7A–T, 8A–F) and Paramushir islands (Russian Far East) along with two specimens from the Republic of Tuva and Trans-Baikal Territory (South Siberia). Plants in this subclade are rather variable, too. The plants are relatively large in the specimens from the Republic of Tuva (KPABG 101097) and Trans Baikal Territory (*Afonona 11606a*), up to 1.5 mm wide, olive to dirty green, with ovate and distinctly longer than wide leaves (0.6–0.7 wide × 0.75–0.9 mm long). At that in some specimens from Kunashir (e.g. *Mamontov 826-3-9185*) plants are small (up to 0.7 mm wide), brownish, with almost orbicular and suborbicular leaves ca. 0.32–0.35 mm in diameter; gynoecial bracts are wide cordate, often with truncate or elongated apex sometimes ending in several teeth in some specimens and cells of the perianth sometimes with bulging trigones (Fig. 7);

As can be seen from the above, the variability of almost all features both within the entire clade and in the subclades is high. Below we summarized the variability

Fig. 3. *Jungermannia pumila* subsp. *pumila* (A–I from *Long 47230* KPABG, MHA): A, H, – gynoecial bracts. B, F, G, I – leaves. C, D, E – fertile shoots. *Jungermannia pumila* subsp. *polaris* (J, K, O, P from *Afonina 3321*, KPABG, MHA; L, M, N, Q–T from *Lapshina 076-2-4a-18*, KPABG, MHA): N, R, S – gynoecial bracts. Q, T – leaves. K, L, O, P – fertile shoots. Scale bars: 1 mm for A, B, F–I, N, Q–T. 2 mm for C–E, J–M,

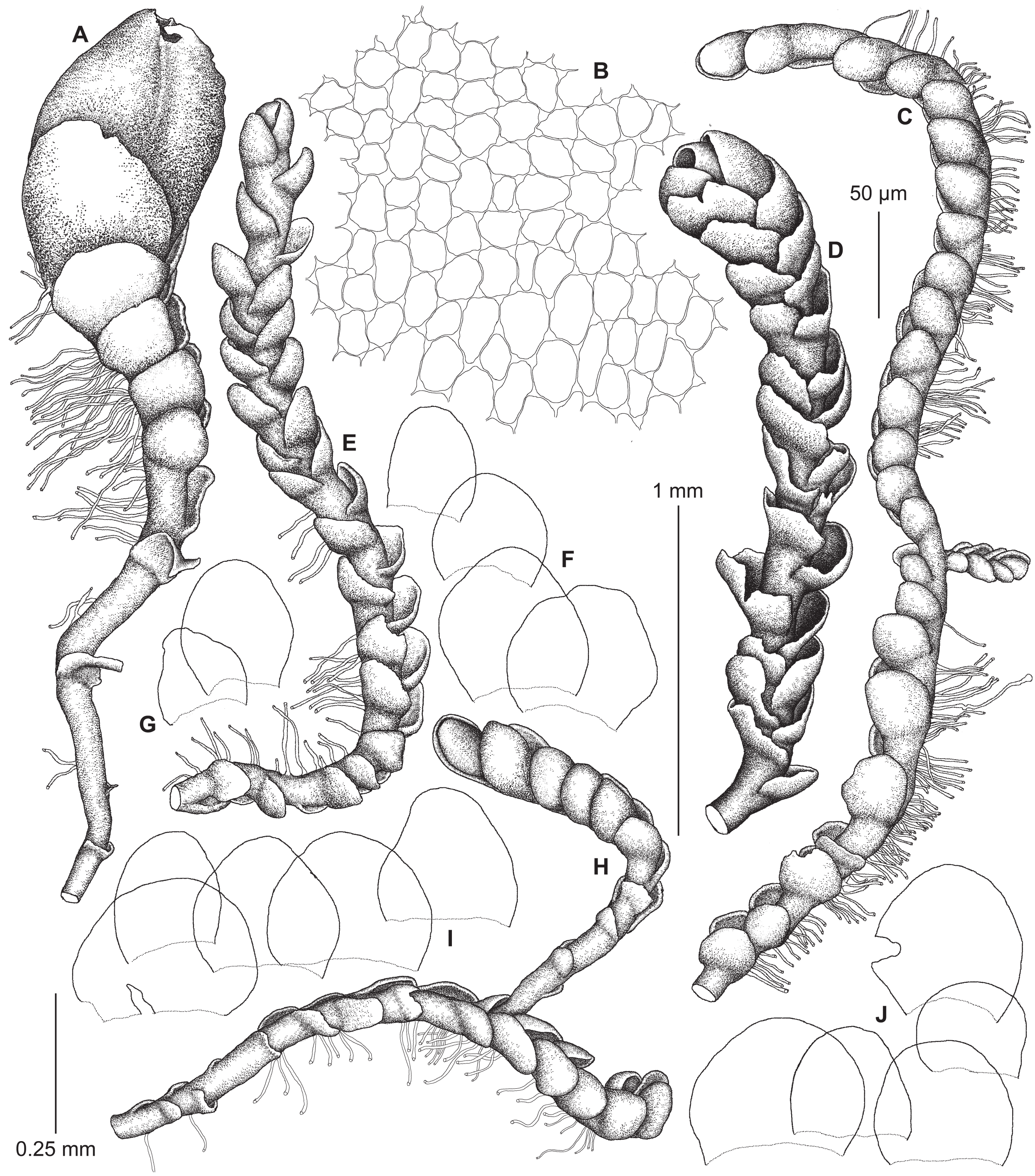

Fig. 4. *Jungermannia pumila* subsp. *polaris* (from *Konstantinova & Savchenko K9-2-18*, KPABG, MHA): A – fertile shoot. B – midleaf cells. C–E, H – sterile shoots. F, G, I, J – leaves. Scale bars: 50 µm for B. 0.25 mm for E. 1 mm for A, C–E, H.

of all the main features of *J. pumila* s.l.

Color of plants varies from yellow-brown to dark brown or almost black, sometimes glossy black, often with more deeply colored margins of leaves.

Size of plants varies in subclade A from very small, 0.2–0.3 mm wide and 4–8 mm long in some specimens from Svalbard (e.g. *Konstantinova & Savchenko K9-2a-18*) to 0.6–0.7 mm wide (near perianth 0.9 mm wide) in the specimen *Mochalova s.n*. (KPABG 106930) from Magadan Region, to 1.3 mm wide (the specimens *Konstantinova & Savchenko 39-5-98* and *315-3-00* from Murmansk Region), and to 2 mm wide in the specimen *Lapshina 076-2-4a-18* from the Polar Urals. The plant sizes in the specimens from subclades C range even further from 0.5 to 2.5 mm wide. In specimens from the British Isles (subclade B), the plants are up to 1.5 mm wide on sterile shoot sectors, and to 2–2.5 mm wide in the gynoecial region.

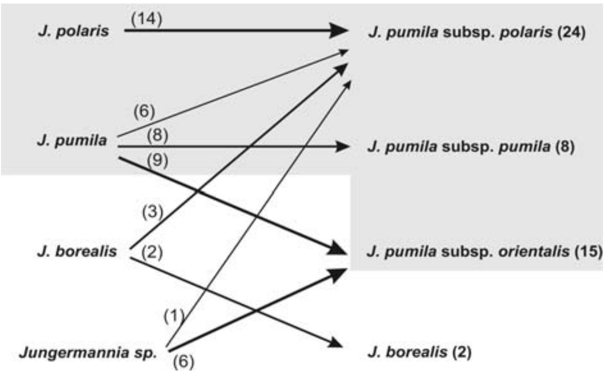

Fig. 5. Revised species identifications in the *J. pumila* complex based on *trn*L-F and *trn*G-intron sequence data. Changes in species identification of 49 specimens are indicated by arrows. Arrow thickness is equivalent to the number of specimens renamed during the study. The number of specimens is marked in brackets.

Leaves are wide semi-ovate to oblong and mostly longer than wide with length/width ratio 1–1.4/1 in most Western European specimens (subclade B), in some South Siberian (*Bakalin VB 99-8-1….28*) and Kuril Islands (e.g. *Bakalin K-104-10-04*) specimens in the subclade C and in the single specimens in subclade A (e.g. Krasnoyarsk Territory, *Otnyukova s.n.*, KPABG 102242). In some specimens in the subclade A, leaves are semi-ovate with cordate base, as long as wide or slightly wider than long, with length/width ratio ca. 0.8/1. In mostly northern and high mountains specimens (e.g. Svalbard, *Savchenko K85-08*; North Ossetia (Caucasus), *Rumyantseva AR32-1-11*) leaves are slightly to distinctly concave, that corresponds tothe arctic *J. polaris* fo. *cavifolia* (R.M.Schust.) Konstant. & Potemkin (Svalbard, *Konstantinova & Savchenko K9-2a-18*).

Cells of leaves are thin-walled, with almost colorless to deep brown or red-brown walls. In the upper part of leaves, cells are rather irregular, polygonal, almost isodiametric and small, (17–)19–22(–25) µm. Cells at the leaf bases are usually distinctly elongate, up to (15–)17–25 × (25–) 30–50(–75) µm. However, in some specimens from Kuril Islands, cells at the leaf bases are sometimes not elongated and just slightly larger than midleaf cells.

Trigones in leaf cells vary from mostly minute to small, rarely large. In the upper part of the perianth in some specimens from the Russian Far East (subclade C) trigones are always distinct, rather large and even bulging.

Cuticle is mostly distinctly striolate-papillose, rarely almost smooth.

Oil-bodies are from 2–6 to 7–8 per cell, spheroidal and 4–5 µm in diameter (Schuster, 1969) to ellipsoidal (Fig. 9M, N). In one of specimens from Kunashir (*Bakalin & Klimova K-37-12-18*), oil-bodies are biconcentric according to personal communication of V.A. Bakalin, and photo he kindly provided (Fig. 9M, N, 10J).

Sexuality is paroicous to heteroicous but paroicous inflorescence is not always easy to discover. At the time when androecia are clearly developed, a rudimentary perianth may be unnoticeable. On the other hand, when the perianth is well-developed with the sporophyte maturing inside it, the antheridia already have died off and only the ventricose androecial bracts can indicate the paroicous inflorescence. In such cases the false impression of a dioicous inflorescence can be created. Schuster (1969: 911) noted that *Solenostoma pumilum* subsp. *polaris* (? *Jungermannia pumila* subsp. *polaris*) can be “heteroecious with long androecial branches”. We have also seen it in the specimen *Afonina 3321* from Chukotka (Fig. 6D).

Androecial bracts are from 2 pairs in small northern and high-mountain plants to 5–6 pairs in Western European plants. In the Chukotka specimen (subclade A), shoots bear up to 12 pairs of the bracts.

Gynoecial bracts are in one to two pairs, larger than leaves, ovate to cordate, from (350–)400–650 µm wide × 500–700 µm long to 1.2 mm wide × 1.1–1.3 mm long in the specimens from Wales (Fig. 3A, H). In specimen from Paramushir (*Bakalin K104-10-04*), the bracts are 1.1–1.2 wide × 1.3–1.45 mm long. The apex rounded to bluntly pointed, sometimes ending in small one or two or several 1-celled teeth (some specimens from Kunashir, e.g. *Mamontov 826-3-9176*, Fig. 7B, C, E, J, L, P–T), or emarginate.

Perianths are up to 2.3 mm long and 0.7–0.9 mm wide, distinctly fusiform (in some specimens from the British Isles), with maximum width near the middle. More often the periants are widest around 1/3 of its length from the apex; in specimens from Svalbard the perianths are often widest near 1/4 of the length. In most of the studied plants, the upper part of the perianths is plicate with several distinct ribs and large ventral grooves. In some specimens, ribs near the perianth mouth are toothed, and sometimes the perianth may become beaked (e.g. Urals, *Lapshina 076-2-3-18*). Cells below of the perianth mouth are mostly isodiametric or just slightly elongated but always distinctly elongated towards base of the perianth, up to 70–80 (–100) µm (Fig. 9 A, B, C, E, F).

Capsule is described by Váňa (1973) as “fast kugelig” but in all sporophyte-bearing plants studied by us capsules were oblong, clearly longer than wide.

Spores are brown, (15–)18–23(–25) µm in diameter, varying often in size in the same capsule (Fig. 9 K). In the specimen from Paranushir with numerous sporophytes (*Bakalin K104-10-04*), spores are (20–)22–25(–28) µm. In literature, spores are described as slightly smaller: (16–) 17–20(–22) µm and 15–18 µm for *Solenostoma pumilum* subsp. *pumilum* and *S. pumilum* subsp. *polaris*, respectively, in Schuster (1969); 16–24 µm for *Jungermannia pumila* in Paton (1999); 17–24 µm and 15–18(–20) µm for *J. pumila* subsp. *pumila* and *J. pumila* subsp. *polaris*, respectively, in Damsholt (2002).

Elaters are up to 9 µm across (but 6–7 µm in Schuster, 1969) with two spirals 4 µm wide (Fig. 9 K, L).

Seta is rather massive, hyaline, up to 420 µm wide in some young sporophytes.

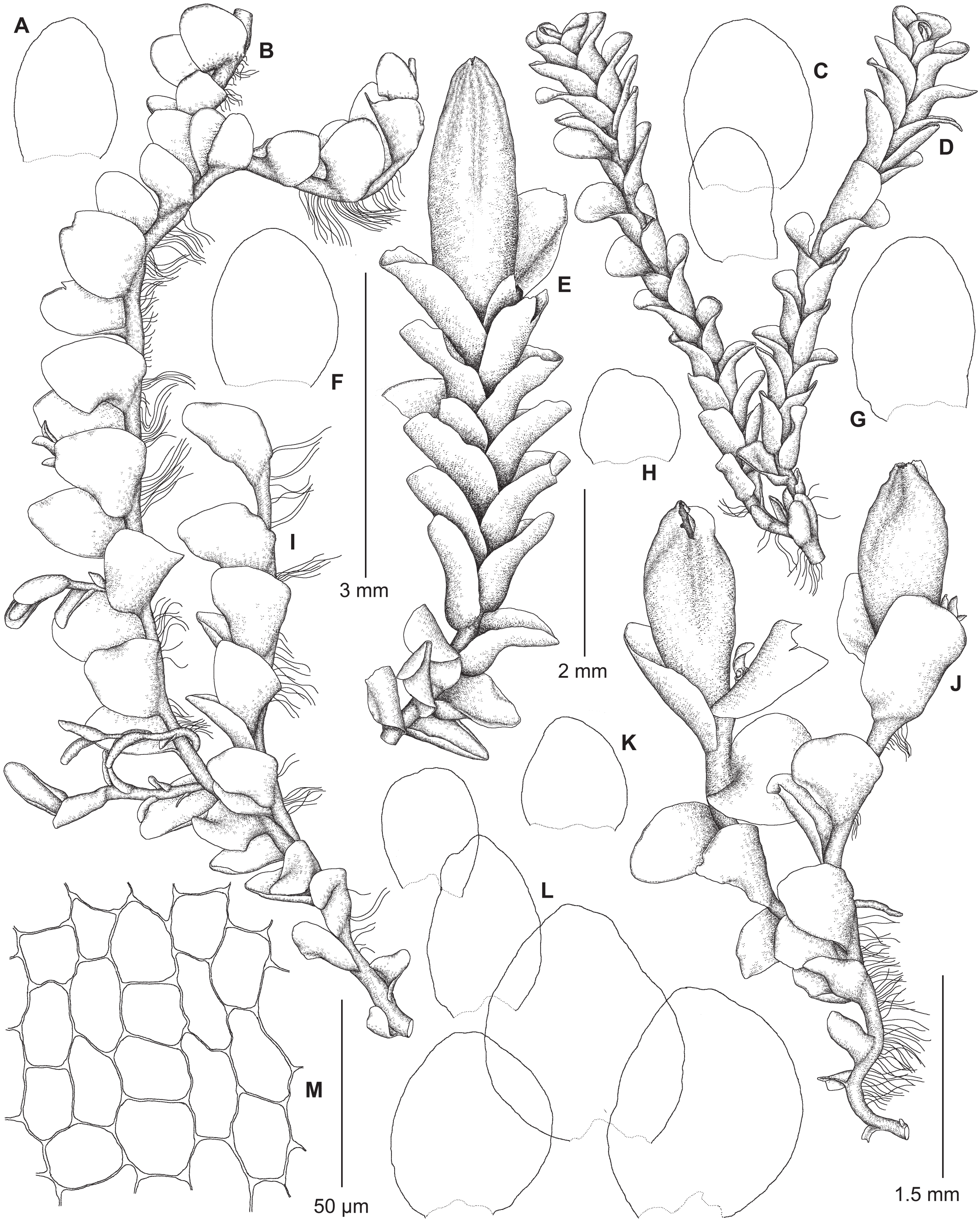

Fig. 6. *Jungermannia pumila* subsp. *polaris* (from *Afonina 3321*, KPABG, MHA): A, C, F–H, K – leaves. B – sterile shoot. D – androecial shoot. E, J – paroicous shoots. L – five gynoecial bracts. M – midleaf cells. Scale bars: 50 µm for M. 1.5 mm for A, C, F–H, K, L. 2 mm for B, D, J. 3 mm for E.

DISCUSSION

According to the data obtained in this study, *J. pumila* s.l. is characterized with a significant molecular-genetic heterogeneity and high haplotype diversity within the subclades (Fig. 2) which reflects, in turn, morphological diversity. Both morphological and molecular genetic diversifications within the *J. pumila* complex, in our opinion, are not sufficient for interpreting the obtained subclades and mor-

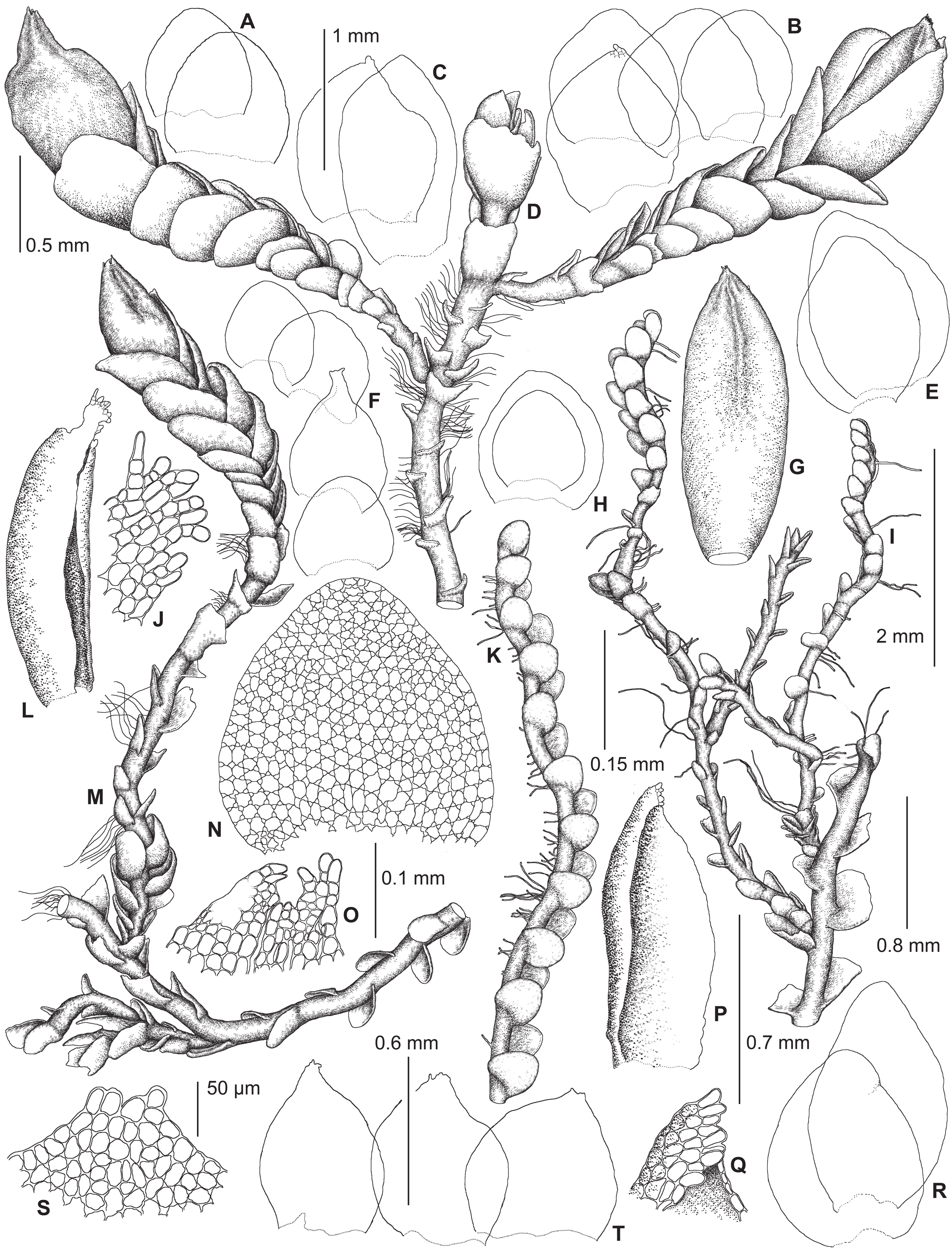

Fig. 7. *Jungermannia pumila* subsp. *orientalis* (A, C from *Mamontov 826-3-9176*, KPABG, MHA; B, D, F, H–Q from *Mamontov 826-3-9185*, KPABG, MHA; E, G, R from *Bakalin & Klimova K-23-11-18*, KPABG; S, T from *Mamontov 826-3-1*, KPABG): A, F, H, N – leaves. B, C, E, L, P, R, T – gynoecial bracts. D, M – fertile shoots. G – perianth. I, K – sterile shoots. J, Q, S – apices of qynoecial bracts with cells indicated. O – cells of perianth mouth. Scale bars: 50 µm for S. 0.1 mm for J, O, Q. 0.15 mm for N. 0.5 mm for B, D, F, H, I, M. 0.6 mm for T. 0.7 mm for L, P. 0.8 mm for K. 1 mm for A, C. 2 mm for E, G, R.

Fig. 8. *Jungermannia pumila* subsp. *orientalis* (from *Mamontov 826-1-5932*, KPABG, MHA): A, C – fertile shoots. B – gynoecial bracts. D, E – leaves. F – midleaf cells. Scale bars: 50 µm for M. 1.5 mm for A, C, F–H, K, L. 2 mm for B, D, J. 3 mm for A, C.

photypes as separate species. Thus, we consider *J. pumila* as a complex taxon, which is currently in the process of diversification, a single species comprising several subspecies. Taking into account the level of divergence between the molecular subclades of the *J. pumila* complex, and the geographical (and thus ecological) separation between the groups of haplotypes composing the subclades, we propose the specimens from subclade C to be described as a new subspecies *J. pumila* subsp. *orientalis*.

Jungermannia pumila With**.** subsp**. orientalis** Konstant., Vilnet & Mamontov, subsp. nova (Fig. 7, 8)

TYPE: RUSSIA: Trans-Baikal Territory, Kyra District, 49°52'60.00'' N, 112°03'00.00'' E, 1310 m a.s.l., stony course of brook, 16.VIII.2006, *Afonina 11606a* [Holotype: KPABG(H)112675!]. Isotypes MHA!, LE!.

Diagnosis. The subspecies differs from *J. pumila* subsp. *pumila* and subsp. *polaris* in: (1) the abundant intercalary branching with numerous small-leaved shoots; (2) the often obtusely pointed gynoecial bracts with a lateral notch, sometimes with a serrated apex, (3) the tendency to form large bulging trigones in the leaf cells; (4) the biconcentric oil-bodies (seen in only one specimen): (5) the generally larger spores and epidermal cells of the capsule wall; (6) the *trn*L-F and *trn*G-intron sequences. Since sporophytes are present in only few specimens, and oil-bodies have been studied in only one specimen, the last two features require verification to clarify possible variability.

Etymology. The name refers to the main area of distribution of the subspecies.

Description. **Plants** variable in size from rather small, just 0.5 mm wide to 1mm wide of sterile shoots to 1–1.5 (2–2.5) mm wide in gametangia zone and to 8–9 mm long, olive to dirty green, warm-brown green and dirty blackish green. **Branches** ventral-intercalary in the middle or at base of shoot, soetimes with abundant numerous small-leaved shoots. **Stem** in cross section ellipsoidal, 11 cells thick, one lay of outer cells is slightly lager then inner ca. (20)25–30 µm, with underlying cells slightly smaller, ca. 18–20 µm in the midlle – mixture of relatively small 17–18 µm and large to 25 µm cells with distinct trigones. **Rhizoids** scattered or rather numerous, colorless or brown. **Leaves** slightly to distinctly concave, from slightly wider than long ca. 300–550 µm wide and (270)450–500 µm long, to distinctly longer then wide, 400 µm wide × 550 µm long, or wide ovate, ca. 600–650 µm wide × 650–800 µm long. **Cells** along along margin (12)14 × 18(20) µm, in the middle isodiametric very variable irregularly pentagonal and quadrangular 15–18 (20) µm × 17–22 µm, at base usually elongated, 17–23(25) µm wide and (20) 25–45 (60) µm long, cell walls thin, hyaline to reddish brown, with small to distinct in some specimens large trigones. Cuticle from almost glad striolate papilose. Paroicous. **Female bracts** in one-two pairs larger than leaves, ovate to cordate from (0.35)0.4–0.65mm wide × 0.5–0.7 mm long to 1.1–1.3 mm wide × 1.2–1.4 (1.6) mm long, with apex rounded to bluntly pointed sometimes ending in small one or two one cells theeth or several theeth or emarginate. **Androecia** in three-four pairs below perianth, male bracts are slightly lager than leaves, slightly ventricose at the base. Perianth long exserted to 0.7 of its length, fusiform towards apex and base gradually narrowed, plicate in upper part, ending in several one-celled fingerlike teeth; 0.6–0.9 mm wide × 2.3 mm long, 3-stratose in the middle. **Capsule** ellipsoidal, red- to black-brown, capsule wall 2- layered. **Spores** 20-24(27) µm, brown, finely verruculose, elaters are up to 9 µm across with two spirals 4 µm wide.

Differentiation of infraspecific taxa. Small plants from the Arctic and subarctic regions, the Urals, the Caucasus, and the alpine and subalpine belts of the high mountains of South Siberia with rather humid climate, characterized by the relatively wide leaves and the perianth widest in the upper 1/4 or 1/3 and tapering relatively slightly to the base, can be more or less confidently referred to *J. pumila* subsp. *polaris.* Plants occurring mostly in the low mountains in the areas with temperate climate of Europe, and characterized by the elongated leaves and the long emergent, fusiform, widest near the middle perianth can be treated as *J. pumila* subsp. *pumila*. Plants occurring in the light coniferous forest belts in the mountains of South Siberia characterized with the sharply continental, rather dry climate (with the annual precipitation of ca. 300–400 mm), as well as the plants from the Southern Kurils, including those characterized by the leaves as long as wide or slightly longer then wide and widest near the base we referred to the new subspecies *J. pumila* subsp. *orientalis*. However, the plants of *J. pumila* s.l. from the other altitudinal belts of mountains in Siberia and the Russian Far East, as well as the mountains in Europe, need separate study to determine the subspecies which they belong to.

Differentiation of species in the genus

In general, *J. pumila* s.l. differs from all other species of the genus, excluding *J. konstantinovae*, in its paroicous or heteroicous inflorescence. Small plants of *J. pumila* s.l. (both of *J. pumila* subsp. *orientalis* and *J. pumila* subsp. *polaris*) differ from the other very small species of the genus, *J. konstantinovae* in the imbricate, more or less concave, not flattened leaves and by the ecology and distribution. *J. konstantinovae* is still known only in the south of Primorye Territory, the Russian Far East where it was collected on calcareous cliffs near sea at low altitude (ca. 300 m alt.), in deep ravine surrounded by scattered oak and *Rhododendron* L. shrubs.

Jungermannia afoninae is similar in size to both *J. konstantinovae* and the small phases of *J. pumila* s.l., and occurs on calcareous cliffs both at high and low altitudes in Transbaikalia and the south of the Russian Far East (Amur Region). However, *J. afoninae* is dioicous, has usually flattened (as in *J. konstantinovae*) leaves and is abundantly fertile, usually with the gynoecial and androecial shoots (often with characteristic intercalary androecia) in the same mat. From the paroicous *Solenostoma subellipticum* (Lindb. ex Heeg) R.M.Schust., which in the Arctic and subarctic may be similar in size and appearance, *J. pumila* subsp. *polaris* differs in: 1) the perianth that is free (but can be hidden in the bracts when young) and lacks a perigonium (in *S. subellipticum* the perianth is as long as bracts when mature and reveals a distinct perigonium); 2) the almost isodiametric or slightly elongated cells below two to several rows of slightly elongated cells of perianth mouth (in *S. subellipticum* these cells are distinctly elongated); 3) smaller leaf cells. However, it is impossible to distinguish the vegetative shoots of these species in any satisfactory way.

KEY TO THE SPECIES OF *JUNGERMANNIA* S.STR. RECORDED IN RUSSIA

1. Paroicous or heteroicous, mostly fertile, usually small, not exceeding 1.2 mm wide (1.5 to 2.3 mm in the gametangial region) 2
— Dioicous or not fertile, never paroicous 5
2. Plants prostrate, creeping, leaves distant, flattened, rarely slightly concave, broadly ovate, very obliquely inserted, plants occurring on *Ca*-rich substrates .... *J. konstantinovae*
— Leaves usually approximate to imbricate, more rarely distant, but then leaves concave, scale-like and stem width 0.25–0.4 width of shoot, plants (apart from some arctic forms) semi-erect .... 3 (*J. pumila* s.l.)
3. Perianth mostly cylindrical, sightly narrowed to the base and tapering to the beak-like or open mouth widest near upper 0.25–0.3 of perianth length, leaves as wide as long or wider than long, rarely longer than wide, broadly ovate, usually concave or canaliculate .... *J. pumila* subsp. *polaris*
— Perianth large, more or less distinctly fusiform, widest at the middle or slightly higher 4

4. Leaves variable, broadly ovate, somewhat cordate at base, female bracts bluntly pointed, with apex sometimes serrated, plants often with numerous intercalary small-leaved branches ...... *J. pumila* subsp. *orientalis*

Leaves mostly longer than wide, not cordate at base, numerous intercalary small-leaved branches absent .... *J. pumila* subsp. *pumila*

5(1). 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 6

6. Plants very small, width of shoot without perianth not exceeding 0.5–1 mm; leaves suborbicular, on sterile shoots mostly wider than long, widest in lower third, calciphiles 7

— Plants usually more than 0.7 mm wide, leaves flattened, slightly concave or cucullate near apex but never cup-shaped, oblong cordate, semi-orbicular to broadly ovate mostly as wide as long or slightly longer than wide 8

7. Plants light grass-green with imbricate, distinctly concave to cap shaped leaves, with the leaf width/length ratio (1.2–)1.3–1.5; elaters 3-spiral .... *J. calcicola*

— Plants green to dark green and blackish green, with mostly flat not imbricate leaves, elaters 2-spiral .... *J. afoninae*

8. Plants dull green to yellowish-brown and brown, leaves flat or concave, androecia consisting of 6–10 pairs of bracts, species restricted to *Ca*-rich substrates .... *J. atrovirens*

— Plants dark green to blackish or black-brown, leaves slightly concave, androecia consisting of 3–4 pairs of bracts, species restricted to acidic or neutral substrates 9

9. 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 not cuculate at apex, spreading, leaf cell walls often rusty-red or brown.... *J. exsertifolia*

Distribution. *J. pumila* s.l. is widely distributed in Eurasia, North America, Africa, as well as in Greenland, Japan, Iceland, Macaronesia and the Azores (Damsholt, 2002). It occurs from near sea level in the British Isles and the north of Eurasia up to 2250 m a.s.l. in central Europe (Váňa, 1973) and subsp. *polaris* to 3500 m a.s.l. in California (Bakalin, 2014). In Kamchatka Peninsula, the species is recorded at 1300 m a.s.l. (Bakalin, 2014). In the Caucasus (Konstantinova *et al.*, 2021), the species (subsp. *polaris*) was collected at an altitude of about 2900 m a.s.l. In the tropics, the species was found near 3000 m a.s.l. in Tanzania (Váňa, 1973). The distribution of each of the subspecies is more or less strictly limited. *J. pumila* subsp. *polaris* is restricted to Arctic and subarctic regions, as well as the mountains further south (from tundra to coniferous forest mountan belts) in Eurasia and North America (Schuster, 1969, Damsholt, 2002). *J. pumila* subsp. *pumila* occurs mostly in temperate areas of Europe and North America (Schuster, 1969, Damsholt, 2002), not higher than 920 m in the British Isles (Paton, 1999). *J. pumila* subsp. *orientalis* is at present known from Kuril Islands and South Siberia. The ranges of *J. pumila* subsp. *polaris* and *J. pumila* subsp. *orientalis* are still known to overlap only in South Siberia, however an occurrence of the latter subspecies in the West of North America may be expected.

Ecology. *J. pumila* s. str. is characterized by Váňa (1973) as occurring on silicate substrates, especially sandstones, less often granite, gneiss, mainly on damp rocks and stones along streams and rivers, often in areas of periodic flooding. In the British Isles, the species apparently has a wider ecological range, occurring both on acidic and mildly basic rocks (Paton, 1999; specimens studied). *J. pumila* subsp. *polaris* occurs mostly in areas with basic rocks on moist humus covered rocks, in crevices between rocks, in moist tundra, often along or in bed of temperate streams and on moist cliffs. *J. pumila* subsp. *orientalis* occurs on moist clay soil near streams and on moist to rather dry cliffs near waterfalls.

Future perspectives

A number of questions remain unclear and require separate study of the *J. pumila* complex in Asia and North America. One of the questions is whether the presence of biconcentric oil-bodies is characteristic of *J. pumila* subsp. *orientalis*. There is almost no data on sporophytes and spore sizes, and it is not clear if an elongated capsule and larger spores are characteristic of the subspecies. Therefore, it is important to study living material and collect specimens with perianths, androecia, and sporophytes in the areas where the presence of *J. pumila* subsp. *orientalis* is confirmed. The distribution of the accepted subspecies in Asia is also interesting, taking into account supposed distinctions between *J. pumila* subsp. *orientalis* and *J. pumila* subsp. *polaris* in the ecology. Indeed, *J. pumila* subsp. *polaris* has been confirmed to occur in different areas (and, therefore, different environments) than *J. pumila* subsp. *orientalis* both in Siberia and the Russian Far East.

This time, the maximal haplotype diversity within the *J. pumila* complex is registered for *J. pumila* subsp. *polaris* in Svalbard, and for *J. pumila* subsp *orientalis* in the Southern Kurils. However, this diversity correlates with the number of specimens studied in the mentioned archipelagos from where *Jungermannia* specimens were

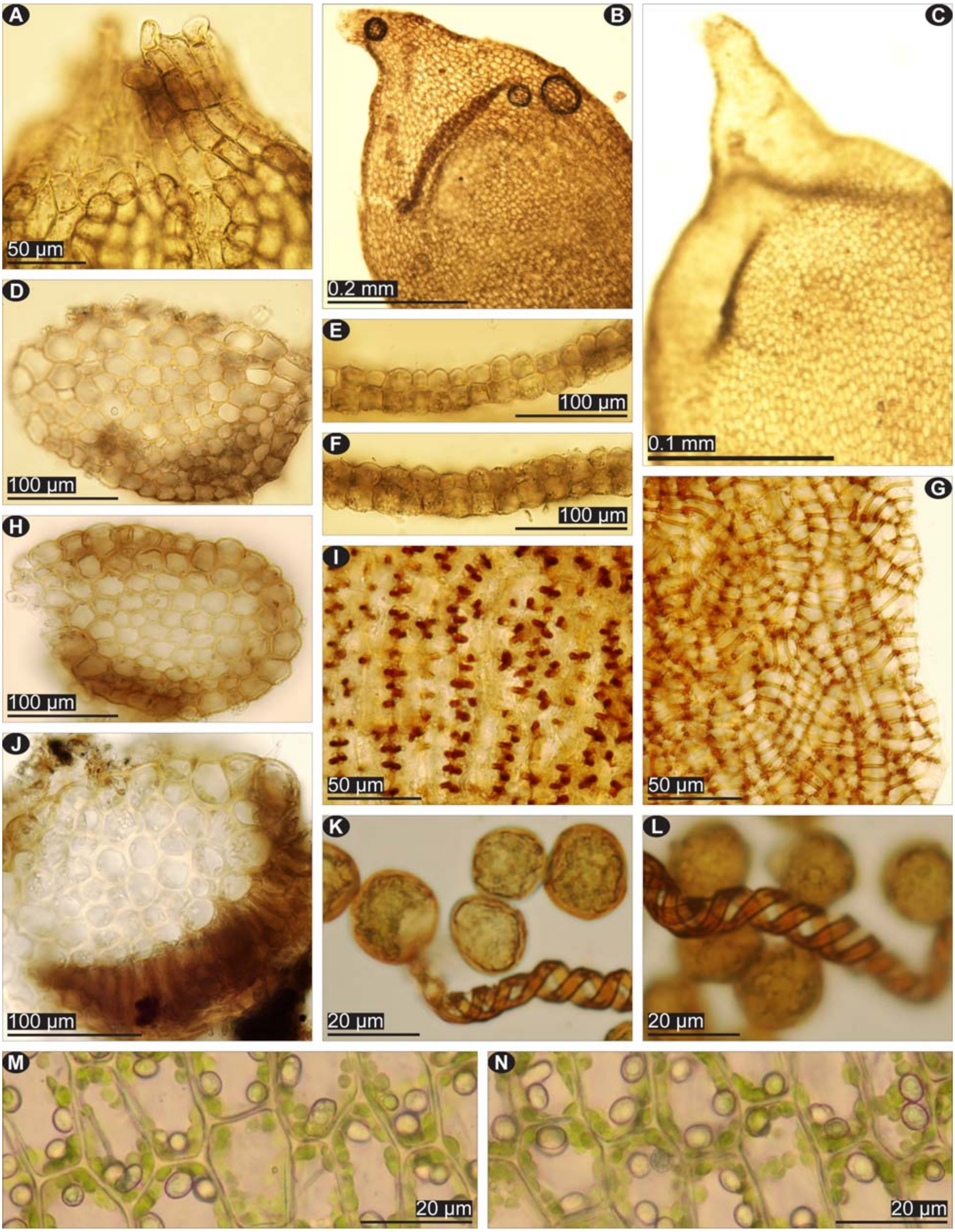

Fig. 9. *Jungermannia pumila* subsp. *polaris* (A, B, C, D, E, F, from *Lapshina 076-2-4a-18*, KPABG, MHA): A – perianth mouth. B, C – upper parts of perianths. D, H – stem cross sections. E, F – perianth cross section. *Jungermannia pumila* subsp. *pumila* (G, I, J, K, L from *Long 47230* KPABG, MHA): G – internal surface of capsule wall. I – external surface of capsule wall. J – stem cross section. K, L – spores and elaters. *Jungermannia pumila* subsp. *orientalis* (H from *Bakalin K-23-11-18*, KPABG; M, N from *Bakalin K-37-12-18*, KPABG): H – stem cross section. M, N – leaf cells with biconcentic oil-bodies indicated.

collected and sequenced, as a number of collections determined as *J. polaris* and *J. pumila* from South Siberia and the whole North America have not been involved in the molecular studies. The involvement of such specimens would further clarify the origin, taxonomy and distribution of the Asian and North American representatives of the *J. pumila* complex.

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Appendix 1. Selected specimens studied

Jungermannia pumila

UNITED KINGDOM: Wales, Merioneth, Afon Wen valley, NE of Tyn-y-Groes, north of Dolgellau. Steep-sided wooded valley; on eroding vertical shaded bank by stream, 15.IX.2021, *Martin & Long 47230* [KPABG(H)124712]. **Scotland,** Peeblesshire, March Sike, Gameshope valley, Tweedsmuir Hills, Grid: NT 1339 1954, v.-c. 78, ca. 470 m a.s.l., steep rocky gully, on damp sloping rocks, 7.V.2021, *Long & Bell 47093* [KPABG(H)124710]; Roxburgh: Tinnis Burn, east bank below Redmoss Bridge, Liddesdale, Grid: NY 4574 8396, v.-c. 80, ca. 118 m a.s.l., calcareous rocky river bank wirh *Alnus* and *Picea*, on shady rock face, 7.II.2007, *Long*, *Kungu & Flagmeier 36496* [KPABG(H)124711].

IRELAND: Co. Mayo, VC H27, Leenaun, N. of, L86906312, ca. 50 m a.s.l., wet shaded rocks in small wooded ravine, 11.IX.2021, *Hodgetts 11137* [KPABG(H)124708]; Co. Mayo, VC H27, Leenaun, N. of, L86946306, ca. 15 m a.s.l., damp rocks in small wooded ravine, 11.IX.2021, *Hodgetts 11135* [KPABG(H)124709]; Co. Kerry, VC H1, Torc Cascade, V96637 84478, ca. 125 m a.s.l., rock crevices by small tributary but below main waterfall, 16.IX.2021, *Hodgetts 11176* [KPABG(H)124707]; Co. Kerry, VC H1, Blackwater Bridge, V79860 68586, ca. 20 m a.s.l., damp rocks by stream, 17.IX.2021, *Hodgetts 11196* [KPABG(H)124706]; Co. Kerry, VC H1, Lough Anascaul, Q583050, ca. 105 m a.s.l., wet rocks on NE-facing hillside, 14.IX.2021, *Hodgetts 11152* [KPABG(H)124705].

Jungermannia pumila subsp. *polaris*

NORWAY: Svalbard: Wedel Jarlsberg Land, Dunderbukta: Dunderdalen, northern part, 77°28'46.77'' N, 14°02'19.55'' E, 25 m alt., on side of moss covered rock, on peat soil, 17.VIII.2018, *Konstantinova & Savchenko K26-2b-18* [KPABG(H)123625] and hollow with stream, 77°28'46.77'' N, 14°02'19.55'' E, 25 m a.s.l., on loamy waterlogged soil covered huge rock, 17.VIII.2018, *Konstantinova & Savchenko K27-1a-18* [KPABG123731]; Recherchefjorden, Lagerneset, 077°31'35.40'' N, 14°45'28.30'' E, 3 m a.s.l., north-west faced rock ourcrop, on edge of moss mats and under mats, on soil, 19.VIII.2018, *Konstantinova & Savchenko K42-1a-18* [KPABG(H)123710], ibid K42-2b-18 [KPABG(H)123714]. **Sarcapp Land**, Stormbukta, 76°43'08.64'' N, 016°18'44.06'' E, 17 m a.s.l., at the base of the slope of the moraine terrace, moss tundra, on humus soil on side a hummock 4-5 cm high, among mosses, 15.VIII.2018, *Konstantinova & Savchenko K9-2-18* [KPABG(H)123553]; **Billefjorden**, Pyramiden, the upper part of Mimerdalen, right bank of Torelva River, 78°37'26.00'' N, 15°58'54.00'' E, 279 m a.s.l., at the bottom of mountain heights 325 m, on spots between rocks, 1.VIII.2008, *Konstantinova & Savchenko K85-08* [KPABG(H)123553], west coast of Petunia-bukta, near east end of Svenbreen, 78°43'38.00'' N, 16°23'16.00'' E, 104 m a.s.l., east facing slope, gneiss cliffs on high bank of nrook, on sand, 29.VII.2008, *Konstantinova & Savchenko K67-1a-08* [KPABG(H)11641].

RUSSIA: Murmansk Region. Khibiny Mountains: left tributary of Mayvaltayouk, at base of slope a wetland area in the floodplain, 9.VIII.1998, *Konstantinova 39-5-98* [KPABG(H)6939] and Takhtarvumchorr Mount, the molybdenum circus, mossy stream crossed the road to the circus, on dying mosses on the soil near the water, 20.VIII.2000, *Konstantinova 315-3-00* [KPABG(H)8170]. **Republic of North Ossetia**, the Alania National Park, North Caucasus, Southern slope at base of Goldor Mount, 3.7 km to the north from from Komy-Art mountaineering base, upper reach of Karonkom River, 42°56'17.00'' N, 43°31'08.00''E, 2960 m a.s.l., bank of brook, on soil, 20.07.2011, *Rumyantseva AR32-1-11* [KPABG(H)123174]. **Khanty-Mansi Autonomous Area**, Beresovskiy District, Subpolar Ural, Upper Khulga River Basin, 5 km to the north-west from Balbanty Lake, upper reaches of the Balbanshor stream, 65°13'22.48'' N, 61°55'21.50'' E, 625 m a.s.l., on banks of brook under snowfields, on water-washed rocks, 14.VII.2018, *Lapshina 076-2-3-18* [KPABG(H)122277], ibid. on a turf-covered slope along the shore, *Lapshina 076-2-4-18* [KPABG(H)122277]. **Krasnoyarsk Territory**: Putorana Plateau, 75 km east of Norilsk, valley of Glubokoye Lake, along the stream, 5.VIII.1990 *Otnyukova s.n.* [KPABG(H)102238, as *J. borealis*]; 100 km south of Norilsk, valley of Toolokand River, Larix-Picea with Betula herb-moss forest, 150 m alt., on rocks at the bottom of the pit, 28.VII.1990, *Otnyukova s.n.* [KPABG(H)102242, as *J. borealis*]; **Buryatiya Republic**, Severo-Baikalsky District, Barguzin State Reserve, Barguzin Range, waterfall in Shumilikha River valley, 54°04'34.87'' N, 109°36'54.33'' E, 1408 m a.s.l., subalpine belt, *Salix* sp.-*Pinus pumila*-grass community, on boulders near the waterfall, in niches, 13.VII.2014, *Mamontov 436-1-2* [KPABG(H)126153, as *J. borealis*]; *ibid*., Shumilikha River valley, near Lake Pervoeje, 54°04'26.31'' N, 109°37'25.71'' E, 1514 m alt., alpine belt, grass community on bank of brook, on soil near the brook water, 14.VII.2014, *Mamontov 439-1-3* [KPABG(H)126152, as *J. borealis*]; Kabansky District, Baikal State Reserve, Khamar-Daban Range, Verkhnyaya Khanadagaita River valley, unnamed lake in the river head, 51°15'07.67'' N, 104°58'24.06'' E, 1783 m a.s.l., *Phyllodoce caerulea*-*Bergenia crassifolia*- herb subalpine meadow near the lake, on soil of the shore wall, near the lake water, 18.VII.2016, *Mamontov 624-1-4* [MHA]. **Magadan Region**, Olskiy District, Yama River, five kilometers below the mouth of the Studenaya River. wet river rocks with alder shrubs, 18.IX.2003, *Mochalova s.n.* [KPABG(H)106930, as *J. pumila*]. **Chucotka Autonomous Area**, Kukun' River Valley, Lorinskie Hot Springs, 65°34'49''.N, 171°29'54.06''E, 82 m a.s.l., community of liverworts on bare soil spots alomg streams with cold water, 23.VII.2021, *Afonina 3321* [KPAB, MHA].

Jungermannia pumila subsp. *orientalis*

RUSSIA: Trans-Baikal Territory, Kyra District, 49°52'60.00'' N, 112°03'00.00'' E, 1310 m a.s.l., stony course of brook, 16.VIII.2006, *Afonina 11606a* [KPABG(H)112675]. **Republic of Tuva**, Nature Reserve "Asas", Todzha valley, SE shore of Azas Lake, 96°35' E, 52°23' N, 950-1200 m a.s.l., the water-washed bank of the stream, 10.VII.1999, *Bakalin VB-99-8-1…28* [KPABG(H)101097, KPABG(H)101181]. **Sakhalin Region**: **Kunashir**, Kuril'skiy State Reserve, Severjanka River valley, Rudnaja Village vicinity, 44.32278 N, 145.99278 E, 20 m a.s.l., narrow gorge with waterfall in stream valley, on soil on rocky slope, near the stream water, 22.IX.2020, *Mamontov 826-1-5932* [KPABG]; *ibid*., on moist stones near the waterfall, *Mamontov 826-2-9178*, *826-3-1*, *826-3-9176*, *826-3-6051*, *826-3-9185* [KPABG]; Lower Severyanka River, small stream near river mouth, 44.32278 N, 145.99278 E, 25 m a.s.l., open moist clayish soil near stream, 25.VIII.2018, *Bakalin & Klimova K-23-11-18* [VBGI 58301]; Dal'niy Stream upper course, 44.45794 N, 146.11731 E, 774 m a.s.l., 06. IX.2018, *Bakalin & Klimova K48-14-18* [KPABG(H)126155]; Gornaya River valley dominated by *Picea-Abies* forest, 44.42972 N, 146.23667 E, 105 m a.s.l., 31. VIII.2018, *Bakalin & Klimova K-37-5-18* [VBGI58305, KPABG(H)126157]; Lower course of Gormaya River, narrow valley dominated by *Picea-Abies* forest, partly shaded moist cliff near stream, 31.VIII.2018, *Bakalin & Klimova K-37-12-18* [KPABG(H)122497]; Confluence of two small rivulets in Gormaya River valley, 44.43778 N, 146.20333 E, 213 m a.s.l., wet white (composition apperently acidic) cliff, *Bakalin & Klimova K-33-1-18* [VBGI57061, KPABG(H)126154]; Lower Ptichiya River, 44.44028 N, 146.27833 E, 327 m a.s.l., area near waterfall, pyroclastic deposits along stream, open, mesic, 30. IX.2018, *Bakalin & Klimova K-40-4-18* [VBGI58305, KPABG(H)126137]. **Paramushir**, right tributary of Kokhmayuri River, 50ş26'55" N, 155 ş52'05" E, 400 m a.s.l., rocky cliffs by the stream, in the shady wet crevices, 28.VII.2004, *Bakalin K-104-10-04* [KPABG(H)107552].

Jungermannia exertifolia

RUSSIA: Sakhalin Region: **Kunashir**, Kuril'skiy State Reserve, Severjanka River valley, Rudnaja Village vicinity, 44.32278 N, 145.99278 E, 20 m a.s.l., narrow gorge with waterfall in stream valley, on moist stones near the waterfall, 22.09.2020, *Mamontov 826-2-9180* [KPABG].

Appendix 2. Taxa used in molecular phylogenetic analysis

Taxon	Specimen voucher	GenBank accessions *trn*L-F	*trn*G-intron
Delavayella serrata Steph.	China, Aug-2006, *Long 35978*	MW429508	MW429508
Jungermannia afoninae Mamontov, Konstant. & Vilnet	Russia: Trans-Baikal Territory, *Mamontov 270-14-2*, KPABG 123571	MH133199	MH133193
	Russia: Trans-Baikal Territory, *Mamontov 485-1*, KPABG	MH133204	MH133198
J. atrovirens fo. *tristis* (Nees) Schljakov	Russia: Krasnodar Territory, *Konstantinova & Savchenko K188-09*, KPABG 113046	KR063602	KR063638
J. atrovirens fo. *tristis*	Russia: Krasnodar Territory, *Konstantinova & Savchenko* K198-1-09, KPABG 113060	KR063603	KR063639
J. borealis Damsh. & Váňa	Russia: Republic of Altai, *Ignatov 0/1981* (MHA)	KR063605	KR063641
J. borealis Damsh. & Váňa	Russia: Kamchatka Territory, Commander Islands, Bering Isl., *Bakalin K-18-6-02-VB*, KPABG 103291	KR063586	KR063618
J. calcicola Konstant. & Vilnet	Russia: Republic of Adygeya, *Konstantinova & Savchenko K429-1-07*, KPABG 112604	JF421608	KR063630
J. calcicola Konstant. & Vilnet	Russia: Karachayevo-Circassian Republic, *Konstantinova & Savchenko K402-8-10*, KPABG 114200	KR063595	KR063631
J. eucordifolia Schljakov	Russia: Karachayevo-Circassian Republic, *Konstantinova & Savchenko K322-1- 08*, KPABG 112468	KR063588	KR063620
J. eucordifolia Schljakov	Russia: Sakhalin Region, Kuril Islands, Paramushir Isl., *Bakalin K-78-1a-04*, KPABG 107379	KR063593	KR063626
J. exsertifolia Steph.	South Korea: KyongNam Province, *Bakalin Kor-14-36-09*, KPABG 112882	GU220587	KR063628
J. konstantinovae Bakalin & Vilnet	Russia: Primorye Territory, *Bakalin P-69- 16-08*, KPABG 112870	GU220586	KR063629
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K46-18*, KPABG 123664 (as *J. polaris*)	PP567044	PP567070
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K9-2a-18*, KPABG 123553 (as *J. polaris*)	PP567045	PP567071
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K84-1-10,* KPABG (as *J. polaris*)	KR063579	KR063609
J. pumila subsp. *polaris*	Norway: Svalbard, *Savchenko K85-08*, KPABG (as *J. polaris*)	KR063577	KR063607
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K-42-1a-18*, KPABG 123710 (as *J. polaris*)	PP567046	PP567072
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K26-2b-18*, KPABG 123625 (as *J. pumila*)	PP567047	PP567073
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K42-2b-18*, KPABG 123714 (as *J. polaris*)	PP567048	PP567074
J. pumila subsp. *polaris*	Norway: Svalbard, Konstantinova & Savchenko *K27-1a-18*, KPABG 123731 (as *J. polaris*)	PP567049	PP567075
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K65-05*, KPABG (as *J. polaris*)	KR063580	KR063610
J. pumila subsp. *polaris*	Norway: Svalbard, *Konstantinova & Savchenko K9-2b-18*, KPABG 123553 (as *J. polaris*)	PP567053	PP567079
J. pumila subsp. *polaris*	Russia: Republic of Buryatia, *Mamontov 436-1-2*, KPABG 126153 (as *J. polaris*)	PP567052	PP567078
J. pumila subsp. *polaris*	Russia: Republic of Buryatia, *Mamontov 439-1-3*, KPABG 126152 (as *J. polaris*)	PP567051	PP567077
J. pumila subsp. *polaris*	Russia: Republic of Buryatia, *Mamontov 624-1-4*, KPABG 126151 (as *J. polaris*)	PP567050	PP567076
J. pumila subsp. *polaris*	Russia: Khanty-Mansi Autonomous Area, *Lapshina 076-2-3-18*, KPABG 122277 (as *J. pumila*)	PP567054	PP567080
J. pumila subsp. *polaris*	Russia: Krasnoyarsk Territory, *Otnyukova s.n*, KPABG 102238 (as *J. borealis*)	KR063582	KR063612
J. pumila subsp. *polaris*	Russia: Krasnoyarsk Territory, *Otnyukova s.n.*, KPABG 102242 (as *J. borealis*)	KR063576	KR063606
J. pumila subsp. *polaris*	Russia: Magadan Region, *Bakalin Mag 32-3-14*, KPABG 126159 (as *J. pumila*)	PP567043	PP567069
J. pumila subsp. *polaris*	Russia: Magadan Region, *Mochalova s.n.*, KPABG 106930 (as *J.* cf. *pumila*)	KR063578	KR063608
J. pumila subsp. *polaris*	Russia: Murmansk Region, *Konstantinova & Savchenko 39-5-98*, KPABG 6939 (as *J. pumila*)	KR063581	KR063611
J. pumila subsp. *polaris*	Russia: Murmansk Region, *Konstantinova & Savchenko 315-3-00*, KPABG 8170 (as *J. borealis*)	GU220589	KR063613

Taxon	Specimen voucher	GenBank accessions *trn*L-F	*trn*G-intron
J. pumila subsp. *polaris*	Russia: Murmansk Region, *Kucera*, CBFS 11417 (as *J. polaris*)	KF943040	no data
J. pumila subsp. *polaris*	Russia: Republic of North Ossetia, *Rumyantseva AR32-1-11*, KPABG 123174 (as *J. polaris*)	MW887529	MW887538
J. pumila subsp. *polaris*	Russia: Chukotka Autonomous Area, *Afonina 3321*, MHA (as *Jungermannia* sp.)	PP567055	PP567081
J. pumila subsp. *polaris*	Russia: Khanty-Mansi Autonomous Area, *Lapshina 076-2-4a-18*, KPABG 122279 (as *J. pumila*)	PP567056	PP567082
J. pumila subsp. *pumila*	Czech Republic, *Sova s.n.*, DUKE (as *J. pumila*)	KF943071	KF942908
J. pumila subsp. *pumila*	Wales, *Martin & Long 47230*, KPABG 124712 (as *J. pumila*)	PP567059	PP567085
	Ireland, *Hodgetts Flora Ireland 11137*, KPABG 124708 (as *J. pumila*)	PP567062	PP567088
J. pumila subsp. *pumila*	Ireland, *Hodgetts Flora Ireland 11152*, KPABG 124705 (as *J. pumila*)	PP567057	PP567083
J. pumila subsp. *pumila*	Ireland, *Hodgetts Flora Ireland 11196*, KPABG 124706 (as *J. pumila*)	PP567061	PP567087
J. pumila subsp. *pumila*	Norway, *Sova s.n.*, DUKE (as *J. pumila*)	KF943070	KF942907
J. pumila subsp. *pumila*	Scotland, *Long, Kungu & Flagmeier 36496*, KPABG 124711 (as *J. pumila*)	PP567058	PP567084
J. pumila subsp. *pumila*	Scotland, *Long & Bell 47093*, KPABG 124710 (as *J. pumila*)	PP567060	PP567086
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-23-11-18*, KPABG 126156 (as *J. pumila*)	PP567065	PP567091
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-33-1-18*, KPABG 126154 (as *J. pumila*)	PP567064	PP567090
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-37-5-18*, KPABG 126157 (as *J. pumila*)	PP567066	PP567092
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-37-12-18*, KPABG 122497 (as *J. pumila* cf.)	PP567063	PP567089
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-40-4-18*, KPABG 126158 (as *J. pumila*)	PP567068	PP567094
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Bakalin & Klimova K-48-14-18*, KPABG 126155 (as *J. pumila*)	PP567067	PP567093
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-1-5932*, KPABG 126786 (as *Jungermannia* sp.)	PP801044	PP801038
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-2-9178*, KPABG 126787 (as *Jungermannia* sp.)	PP801045	PP801039
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-3-1*, KPABG 126788 (as *Jungermannia* sp.)	PP801046	PP801040
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-3-6051*, KPABG 126789 (as *Jungermannia* sp.)	PP801047	PP801041
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-3-9176*, KPABG 126790 (as *Jungermannia* sp.)	PP801048	PP801042
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Kunashir, *Mamontov 826-3-9185*, KPABG 126791 (as *Jungermannia* sp.)	PP801049	PP801043
J. pumila subsp. *orientalis*	Russia: Sakhalin Region, Kuril Islands, Paramushir Isl., *Bakalin K-104-10-04*, KPABG 107552 (as *J. pumila*)	KR063583	KR063614
J. pumila subsp. *orientalis*	Russia: Trans-Baikal Territory, *Afonina 11606a*, KPABG 112675 (as *J. pumila*)	GU220588	KR063615
J. pumila subsp. *orientalis*	Russia: Republic of Tuva, *Bakalin VB 99-8-1….28*, KPABG 101097 (as *J. pumila*)	AY327771	no data
Jungermannia sp. indet. 1	Norway: Svalbard, *Konstantinova & Savchenko K117-1-10* KPABG	KR063597	KR063633
	Russia: Komi Republic, *Dulin 23.08.2006 126B=639 MVD*, KPABG	KR063598	KR063634
Liochlaena sichuanica Bakalin & Vilnet	China: Sichuan Province, *Bakalin China-40-10-17*, KPABG 122540	MH686187	MK073909
Mesoptychia heterocolpos (Thed. ex Hartm.) L. Söderstr. & Váňa	Norway: Svalbard, *Konstantinova & Savchenko K18-1-18*, KPABG 123478	MT338487	MT338480
Solenostoma rossicum Bakalin & Vilnet	Russia: Yamalo-Nenets Autonomous Area, *Lapshina 378E/3-1-19*, KPABG 124440	ON185619	ON185620