

A NEW SPECIES OF THE GENUS *LOPHOZIA* (LOPHOZIACEAE)  
FROM THE SVALBARD ARCHIPELAGO

НОВЫЙ ВИД ИЗ РОДА *LOPHOZIA* (LOPHOZIACEAE)  
С АРХИПЕЛАГА ШПИЦБЕРГЕН

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Abstract

A new species of liverwort *Lophozia svalbardensis* (Marchantiophyta, Jungermanniopsida) collected in the Nordaustlandet (Svalbard Archipelago) is described. It is characterized by heteroicous inflorescence, presence of low perigynium, crenulate-ciliate perianth mouth, thick walled cells near perianth mouth; colourless to slightly pinkish red tinged gemmae contrasting in color with red-brown marginal cells of the uppermost leaves, two-layer thick base of leaves. A detailed description including illustrations of the species is given. The phylogenetic position of the species is considered, and morphological differences from similar species are discussed.

Резюме

Новый для науки вид *Lophozia svalbardensis* (Marchantiophyta, Jungermanniopsida) описан с Северо-Восточной Земли (архипелаг Шпицберген). Вид характеризуется гетероцией, наличием низкого перигиния, городчато-реснитчатым устьем периантия, толстостенными бесцветными клетками устья периантия, бесцветными до слегка розоватыми выводковыми почками резко контрастирующими с клетками края почко-образующих листьев, двуслойными в основании листьями. Приводится детальное описание и иллюстрации вида, обсуждается его филогенетическое положение, даются отличия от похожих видов.

KEYWORDS: molecular markers, ITS1-2, *trnL*-F, liverworts, taxonomy

INTRODUCTION

In the course of the study of the liverwort flora of Nordaustlandet (Svalbard Archipelago) we collected a species of *Lophozia* with a very peculiar appearance. This bright green and purple red *Lophozia* with numerous large perianth and sporophytes grows abundantly on nonsorted circles among crushed rocks in the arctic desert in Gustav V Land (Figs. 1-2). Based on heteroicous (partly just paroicous) inflorescences we provisionally assigned it to *Lophozia excisa* (Dicks.) Konstant. & Vilnet. Subsequent thorough examination of the samples under a microscope showed that the species differs from *L. excisa* both in the color and shape of gemmae, as well as in the characters of the cell network and a number of other features. Molecular study has shown that the species clearly diverged from phylogenetically allied species. Together with the significant morphological differences identified after a thorough study of the sample, this allowed us to describe the new species – *Lophozia svalbardensis* sp. nov.

MATERIAL AND METHODS

The species was collected on the north-west coast of Nordvika Bay (Murchisonfjorden, Gustav V Land, Nordaustlandet, Svalbard). It covered up to 20-25% of non sorted circles (Fig. 2) and was collected in a large number of mats since it was intended to be published in a set of *Hepaticae Svalbardensia Exsiccatae*. The coordinates of locality were measured using GPS.

The samples were re-examined several times in order to clarify and identify the variability of different characters. Some of them were difficult to describe e.g. it was very hard to find and take a picture of the mouth of the perianth, since they were destroyed at most of them. Only after a thorough study of most of the collected samples was it possible to find gemmae on smaller shoots hidden among perianth bearing shoots. To illustrate the quite characteristic appearance and the most important morphological features we took pictures using Nikon SMZ 800 or they were depicted in drawings. The specimens are deposited in Herbarium of Polar-Alpine Botanical

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Garden-Institute of the Kola Scientific Center, Russian Academy of Science, duplicates will be sent to LE, MW, MHA, VBGI.

#### MOLECULAR DATA

To reveal the affinity of collected species we implemented phylogenetic analyses based on ITS1-2 nrDNA and *trnL-F* cpDNA. Newly sequenced data were obtained for nine specimens, sequences were taken from our previous studies for 30 specimens (Vilnet *et al.*, 2008, 2010; Bakalin & Vilnet, 2019). The newly produced dataset contains the majority of molecularly studied specimens of the genera *Lophozia* and *Lophozioopsis*, a number of other key genera from family Lophoziaceae and Scapaniaceae; the outgroup was represented by *Anastrepta orcadensis* (Hook.) Schiffn. from Anastrophyllaceae. All specimens included in the current study are listed in Appendix 1 with GenBank accession numbers and voucher details.

#### DNA isolation, amplification and sequencing

DNA was extracted from dried liverwort tissue using the DNeasy Plant Mini Kit (Qiagen, Germany). The primers given by White *et al.* (1990) for ITS1-2 and Taberlet *et al.* (1991) for *trnL-F* were used for amplification and sequencing reactions.

PCR was carried out in 20 µl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C, 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 QIAquick Gel Extraction Kit (Qiagen, Germany), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, U.S.A.) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

#### Phylogenetic analyses

The newly obtained ITS1-2 and *trnL-F* nucleotide sequences were assembled and then included in the newly produced dataset in BioEdit 7.0.1 (Hall, 1999). The automatic alignment procedure was done with option of full multiple alignment with default settings for gaps and extension weights in the ClustalW tool. The obtained dataset was manually corrected. The absence of incongruence between two studied loci was shown in preliminary phylogenetic estimation. The combined ITS1-2+*trnL-F* was used in subsequent analyses with inclusion of all positions, absent data at the ends of regions were coded as missing.

Three criteria were implemented to the reconstruction of phylogeny: maximum parsimony (MP) with TNT v. 1.5 (Goloboff & Catalano, 2016), maximum likelihood (ML) with PhyML v. 3.0 (Guindon *et al.*, 2010) and Bayesian reconstruction with MrBayes v. 3.2.1 (Ronquist *et al.*, 2012). The parsimony analysis with TNT involved a New Technology Search for the minimal length tree by five iteration and 1000 bootstrap replicates, default set-

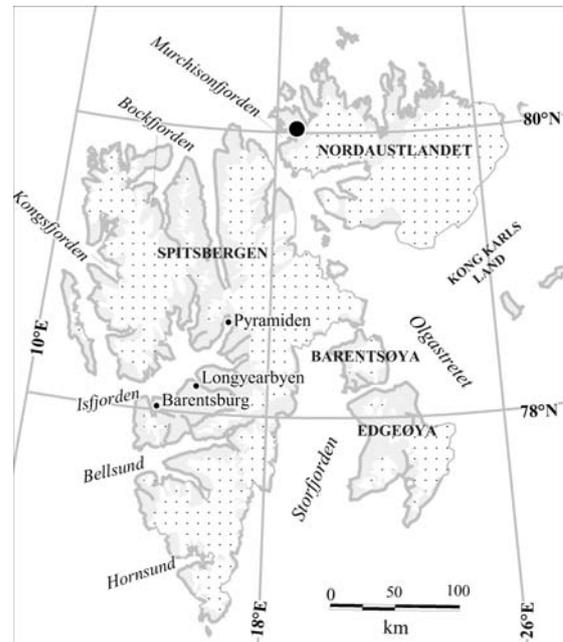


Fig. 1. Map of Svalbard, collecting locality is indicated.

tings were used for other parameters, gaps were treated as missing. The program ModelGenerator (Keane *et al.*, 2006) identified TN+I+Γ as the best-fitting evolutionary model for the ITS1-2+*trnL-F* dataset. This model, gamma distribution with four rate categories to estimate among-site rate heterogeneity were used in the maximum likelihood estimation. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 500 replicates. According to the stopping frequency criterion (FC) for the bootstrap (Pattengale *et al.*, 2010) our dataset should require only 250 replicates to reach convergence with Pearson average  $c100 = 0.994960$  as estimated by RAxML v. 7.2.6 (Stamatakis, 2006).

For the Bayesian analysis each partition of the combined alignment (ITS1-2, *trnL-F*) was separately assigned the GTR+I+Γ model that recommended by authors of the program; gamma distributions were approximated using four rate categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated, and two starting trees were chosen randomly. Chains were run for ten million generations and trees were sampled every 100<sup>th</sup> generation. The software tool Tracer (Rambaut & Drummond, 2007) revealed effective sample size (ESS) as 29112.5555 and auto-correlation time (ACT) as 618.2968 for our data. As determined by Tracer, the first 10 000 trees in each run were discarded as burn-in, thereafter 180 000 trees were sampled from both runs. The average standard deviation of split frequencies between two runs was 0.001357. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

The infrageneric and infraspecific variability of ITS1-2 and *trnL-F* for the genus *Lophozia* was calculated as

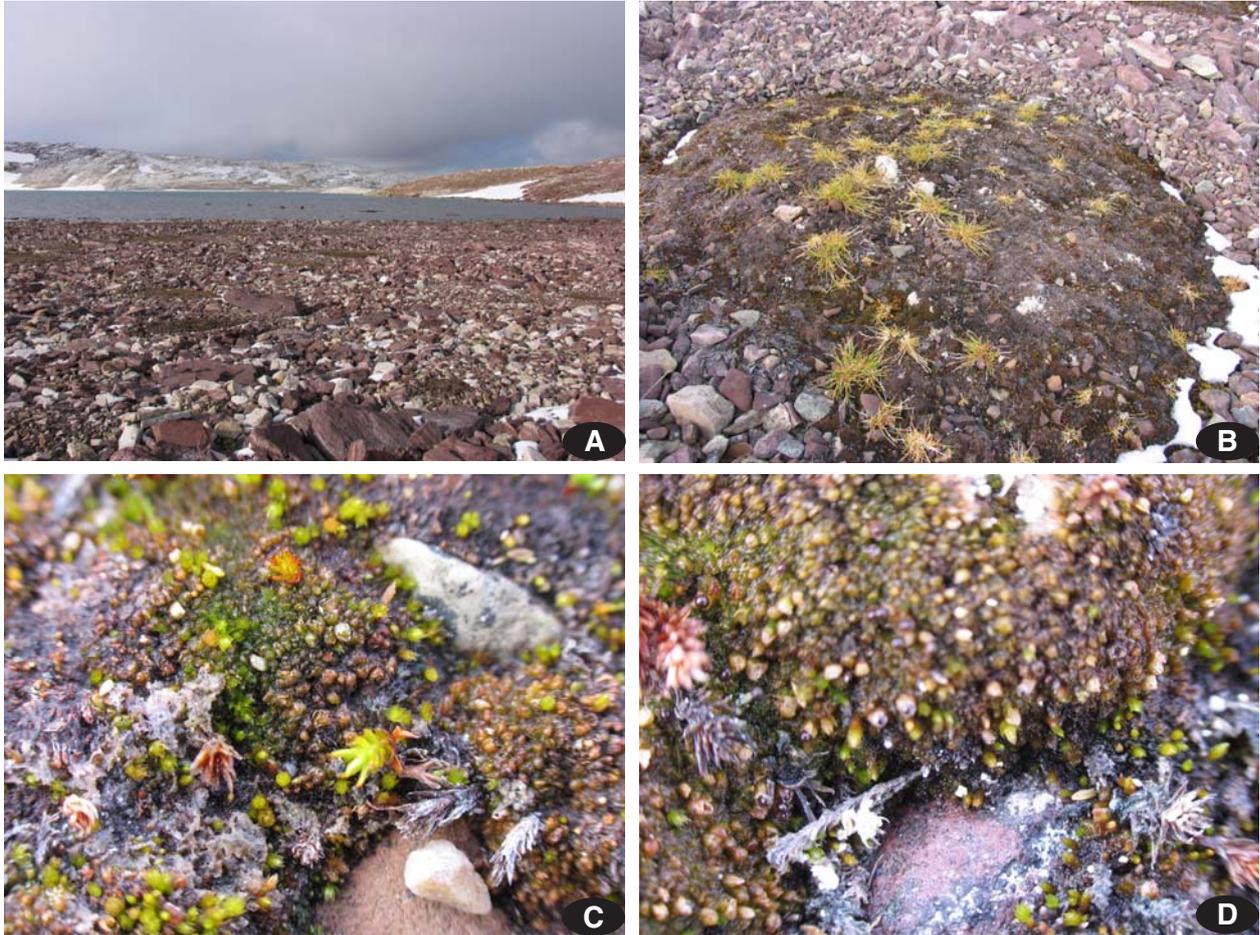


Fig. 2. A: The plain with a glacial lake surrounded by a the rocky polar desert on coast of Nordvika Bay (Murchisonfjorden); B: Non sorted circle covered bryophytes, dark red-brown spots are cushions of *Lophozia svalbardensis*; C: Mats of *Lophozia svalbardensis*; D: Mats of *Lophozia svalbardensis* with numerous perianth with destroyed colourless perianth mouth.

the average pairwise  $p$ -distances in Mega 5.1 (Tamura *et al.*, 2011) using the pairwise deletion option for counting gaps.

#### RESULTS

In total, ITS1-2 and *trnL*-F nucleotide sequences were newly obtained for nine specimens and deposited into GenBank. The combined ITS1-2+*trnL*-F alignment for 39 specimens consists of 1409 sites, among them 894 sites belong to ITS1-2 and 515 sites to *trnL*-F. The number of conservative positions in ITS1-2 and *trnL*-F is 497 (55.59%) and 360 (69.90%), respectively, the number of variable positions is 360 (40.27%) and 145 (28.16%), and the number of parsimony-informative positions is 226 (25.28%) and 86 (16.70%). In the combined alignment there are 857 (60.82%) conservative sites, 505 (35.84%) variable sites and 312 (22.14%) parsimony informative positions.

The MP analysis with TNT yielded 19 equally parsimonious trees with a length of 1636 steps, with CI = 0.619224 and RI = 0.709245. The ML criterion recovered a tree with a Log likelihood of -7703.55. Arithmetic means of Log likelihoods in Bayesian analysis for each sampling run were -7505.17 and -7505.48.

The tree topologies achieved in all estimations became highly congruent. On the Fig. 3 the tree topology from ML analysis is presented with ML and MP bootstrap support values (BS) and Bayesian posterior probabilities (PP) for each node. In common, tree topology is congruent with those published in our previous studies (Vilnet *et al.*, 2008, 2010; Bakalin & Vilnet, 2019). The tested specimen from Svalbard was found in sister relation to specimen of *Lophozia ascendens* (Warnst.) R.M.Schust. from Buryatiya Republic without support in MP, BS = 61% in ML, PP = 0.7 in BA or -/61/0.70. This clade is related to *Lophozia lantratovae* Bakalin (-/84/1.00) and then to a clade with specimens related to *L. wenzelii* (Nees) Steph. – *L. ventricosa* (Dicks.) Dumort. – *L. austrosibirica* Bakalin (-/70/0.99). The last relation in the genus *Lophozia* (-/81/1.00) belongs to clade of *L. silvicoloides* N. Kitag. and recently described *L. fuscovirens* Bakalin & Vilnet (-/89/1.00).

To support taxonomic treatment of tested specimen, the infraspecific and infrageneric  $p$ -distances for ITS1-2/*trnL*-F loci were calculated for species of the genus *Lophozia* (Table 1). The level of infraspecific distances among majority of species did not exceed 1%, with ex-

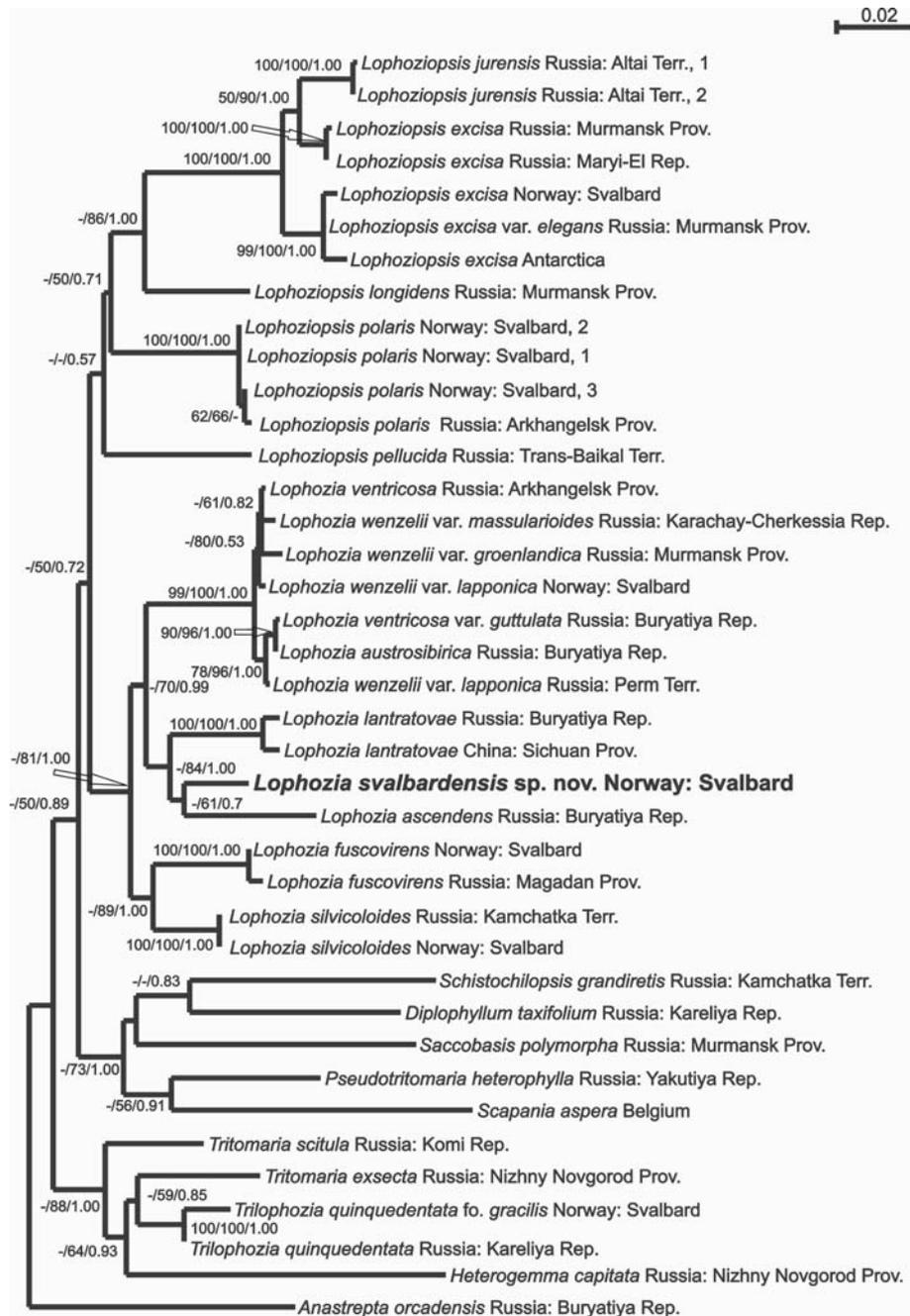


Fig. 3. Phylogram obtained in a maximum likelihood analysis for the families Lophoziaceae and Scapaniaceae based on combined nucleotide sequences dataset of ITS1-2+trnL-F. Bootstrap support values of maximum parsimony, maximum likelihood analyses and Bayesian posterior probabilities more than 50% (0.50) are indicated.

ception of *L. lantratovae* (1.1/0.2%). The variability in the complex of allied taxa from the clade of *L. wenzelii-ventricosa-austrosibirica* was agreed with infraspecific, which again sharply raises the question of revision of this complex. The tested sample from Svalbard differed from the all species of *Lophozia* in 4.4 – 5.9/1.9 – 4.0%, which corresponded to the level of differentiation of species in this group being evaluated 4.9-7.5/1.7–5.1%. (Table 1). The phylogenetic affinity and level of sequence divergence allow us to attend Svalbard's specimen to a species new to science – *Lophozia svalbardensis* sp. nov.

#### TAXONOMY

***Lophozia svalbardensis*** Konstant., Vilnet & Mamontov sp. nov.

Type: Norway, Svalbard, Nordaustlandet, Gustav V Land, Murchisonfjorden, south-east slope on north-west coast of Nordvika Bay, 80°3'13"N – 18°48'26"E (80.053638 N – 18.807244E), 196 m alt. bank of lake, rock field, on covered by bryophytes nonsorted circles among crushed rocks, 17 August 2007, coll. Konstantinova N.A. & A.N.Savchenko K135-3-07 (Holotype KPABG; Isotypes MHA, MW, LE, VBGI SYKO). Figs. 4-7

**Etymology:** The name refers to the area where the species was collected

**Diagnosis.** The species is characterized by 1) heteroicous inflorescence; 2) presence of small perigynium; 3) crenulate-ciliate with teeth up to 4 cells long perianth mouth; 4) slightly to distinctly thick walled cells of perianth mouth; 5) colorless to slightly pinkish red tinged gemmae contrasting in color with red-brown marginal cells of uppermost leaves; 6) leaves two layer thick near the base.

**Description**

Plants in dense low mats, with abundant perianth and sporophytes, purple to brick-red-brown in upper parts and green below, sterile shoots just 0.5–0.7 mm, near perianth to 1.2 (1.3) mm wide and just 3–4 mm long, with several subfloral innovations that easily became fertile again, branching lateral-terminal or lateral intercalary, stem fleshy, soft textured, dark brown on ventral side and light brown to dark green on dorsal side especially in upper part, cross-section 15–20 cells high, almost round to subelliptical, 300–400 × 400–450 μm with fungi infections up to 0.5–0.75 high, cells in ventral side of cross section ca. (12)15–20(25) μm in upper part 25–35(40) μm. Rhizoids numerous in very dense mats, colorless to slightly brownish, very long. Leaves purple or red-brown to almost black distally and light-green or colorless proximally, on sterile shoots imbricate distinctly concave, subquadrate 480 × 480 μm as wide as long or slightly wider than long, 450–480 × 400–430 μm with broadly obtuse-triangular to shallow lunate sinus ca. 0.15–0.3 of leaf length, lobes with dorsal lobes slightly smaller, obtuse to subacute, rarely acute. Cells of leaves with distinct rather large trigones and slightly thick-walled, in upper part of leaves with red-brown colored walls, along the margin approximately the same size as in the middle 20–25 μm, at base slightly larger, elongated to 22 × 32–37 (42) μm, at leaf base and sometimes up to 0.3 leaf length two layers thick. Cuticle smooth. Gemmae on juvenile small leaves hidden in uppermost leaves on small sometimes androecious branches or sporadic on plants with young perianth, gemmae mostly colorless with admixture of slightly pinkish contrasting with intensely rich red-brown color of the upper parts of the surrounding leaves, very variable in shape and size, ellipsoidal to rounded triangular and rare rectangular with rounded and more or less

thickened angles 1–2 (3) celled, 22 × 22 μm, 18–20 × 30 μm, 25 × 25 μm, 25 × 30 μm, 27 × 33 μm, 22 × 37–40 (42) μm. Leaves on small leaved gemmiparous shoots wider than long, ca. 450 × 350 μm, 550 × 350 μm.

Heteroicous. Antheridia just below perianth in female bracts or in 2–3 pairs below gynoecia or on rather small leaved gemmiparous branches, male bracts are slightly larger than leaves, slightly ventricose at the base on dorsal side, 1.1–1.3 mm wide and 0.7–1.1 mm long divided in 2–3 uneven lobes, two-lobed leaves often with large lobe-like teeth at base ca. 5 cells wide and up to half of leaf length, on dorsal side with scattered small teeth on margins, leaf lobe ending by uniseriate 1–3 (5) cells long apices of almost isodiametric and slightly reduced in size to upper cell, sometimes two cell wide in the middle. Antheridia with uniseriate stalk up to 7 cells long.

Young inflorescences look like dense crispate heads. Female bracts larger than leaves, wavy and crispate on margins, much wider than long, to 1700 μm wide and 900 μm long, divided up to 0.4 their length in 3–5 lobes with curved margins of sinuses, lobes end up in to 4-celled teeth, cells of teeth are thick walled, 25 × 25–30 μm, on both sides of bracts there are scattered one-two celled teeth, bracteole small, connate on one side with bract. Perianths large, ca. 1.3 mm wide and 2 mm long, cylindrical, plicate in upper part, almost fully free, slightly contracted to mouth, distinct but short perigynium present in some plants, ca 0.2–0.25 of perianth length. Mouth destroyed very soon after fertilization, colorless, crenulate-ciliate with scattered teeth 1–4 cells long, cells of teeth slightly elongated 20 × 25 μm apart of distinctly elongated upper cell that to 14 × 35 μm. Cells just below mouth thick-walled, dark red-brown apart uppermost that are hyaline and very soon destroyed after fertilization. Cells in upper part of perianth very variable in shape and size, from 12–14 × 25 μm and 14 × 14 μm to 20 × 32 μm, 25–30 × 30–35 (38) μm in the middle, gradually became much longer below to 25–37 × 45–75 (100) μm. Spores dark red-brown, fine granulate. ca. 13–15 μm in diameter. Elaters 2–spiral, 8–13 μm wide, with band ca. 1.5–2 μm wide.

**Differentiation**

*Lophozia svalbardensis* differ from the somewhat similar paroicous *Lophozia excisa* in shape and color of

Table 1. The value of infrageneric *p*-distances for the genus *Lophozia*, n/c – non calculated value due to single specimen only.

| Taxon  | Within species/<br>clade, ITS1-2/<br><i>trnL</i> -F, % | Between species/clade, ITS1-2/ <i>trnL</i> -F, % |         |         |         |         |   |
|--|--|--|---------|---------|---------|---------|---|
|  |  | 1  | 2       | 3       | 4       | 5       | 6 |
| 1 <i>wenzelii-ventricosa-austrosibirica</i><br>clade | 0.9/0.3  |  |         |         |         |         |   |
| 2 <i>lantratovae</i>                                 | 1.1/0.2  | 6.1/4.6  |         |         |         |         |   |
| 3 <i>svalbardensis</i>                               | n/c/n/c  | 5.3/3.2  | 4.3/4.0 |         |         |         |   |
| 4 <i>ascendens</i>                                   | n/c/n/c  | 7.2/3.2  | 6.2/3.5 | 5.4/1.9 |         |         |   |
| 5 <i>fuscovirens</i>                                 | 0.6/0.0  | 6.9/2.7  | 6.4/4.2 | 5.9/3.9 | 7.5/3.8 |         |   |
| 6 <i>silvicoloides</i>                               | 0.0/0.0  | 5.8/2.8  | 5.1/5.1 | 4.2/3.5 | 5.4/3.6 | 4.9/1.7 |   |

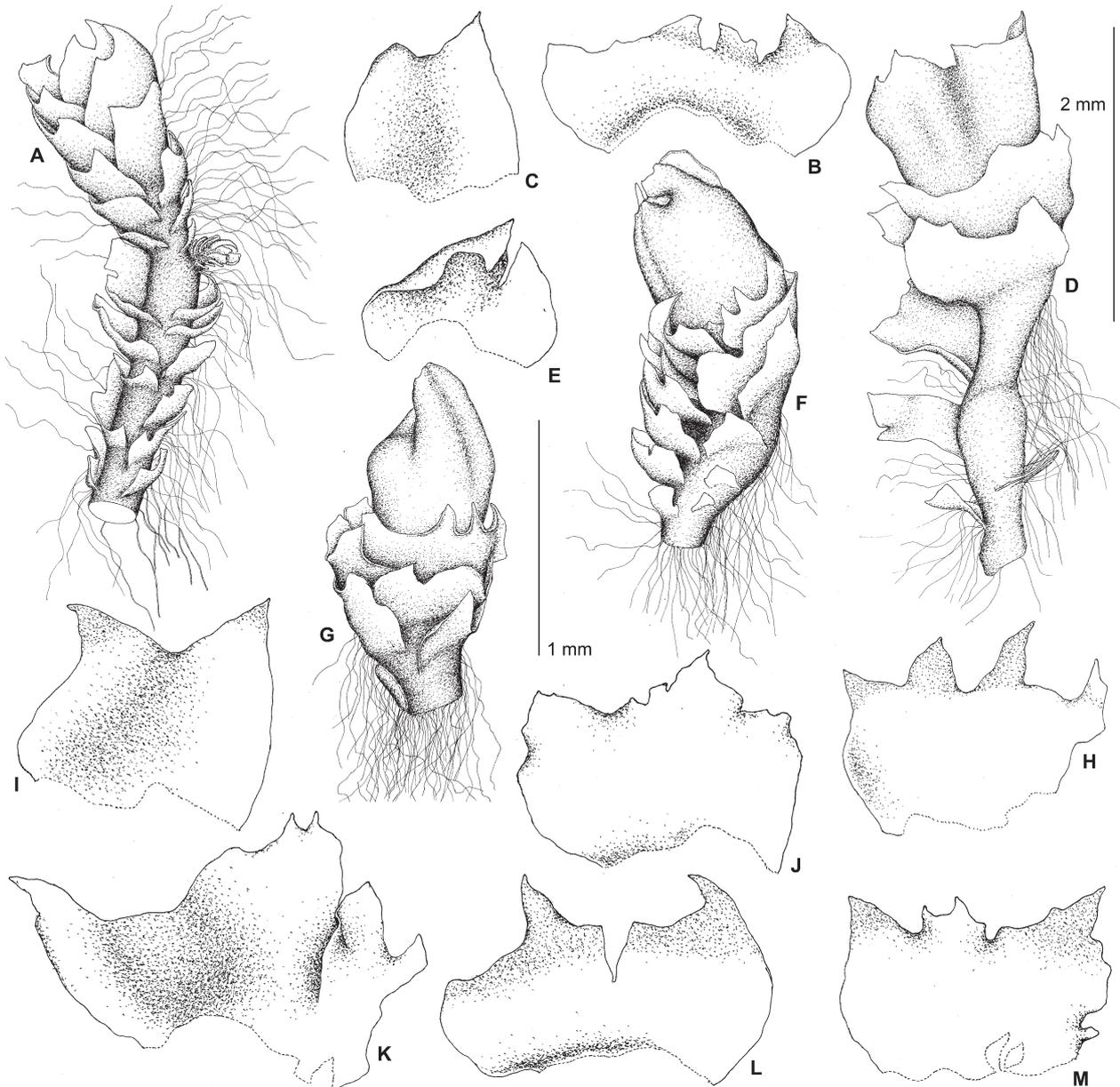


Fig. 4. A, D, F, G – fertile (paroicous) shoots. B, H, J-M – female bracts. C, E, I – male bracts. K – female bract with bracteole. Scale bars: 1 mm to B, C, E, I-M. 2 mm to A, D, F, G. All from *Konstantinova & Savchenko K135-3-07* (KPABG).

gemmae, shape and size of midleaf cells, crenulate-ciliate mouth of perianth, heteroicous inflorescences (Table 2). Based on heteroicous inflorescence, crenulate-ciliate female bracts, decolorate crenulate-ciliate mouth of perianth, thick walled cells of perianth mouth the species may be confused with *Isopaches bicrenatus* (Schmidel ex Hoffm.) H. Buch. From the latter species *Lophozia svalbardensis* differs in the shape and color of gemmae, lack of specific smell that is very characteristic for *I. bicrenatus*, stem cross section which is up to 20 cells high vs. 8–9 cells high in *I. bicrenatus*. From phylogenetically closely related *Lophozia ascendens* and *L. lantratorvae*, the species strongly differs in heteroicous inflorescence, shape of female bracts, the color of gemmae, color of leaves (Table 2).

#### *Ecology and distribution*

The species is known from the type locality where it is abundant on nonsorted circles in the rocky polar desert, covering up to 25% of the surface of nonsorted circles on which it forms a red-brown crust (Fig. 2). The species grows in almost pure mats with admixture of single shoots of *Anthelia juratzkana* (Limpr.) Trevis., *Cephalozia bicuspidata* (L.) Dumort. and *Prasanthus suecicus* (Gottsche) Lindb. Given that the species produces a lot of spores, it is most likely widespread in the Arctic and adjacent mountains.

#### DISCUSSION

*Lophozia* is a small genus of liverworts, with an incredibly confusing interpretation of the most of its species. According to the World checklist of liverworts (Söderström *et al.*, 2016), it includes 18 species, of which

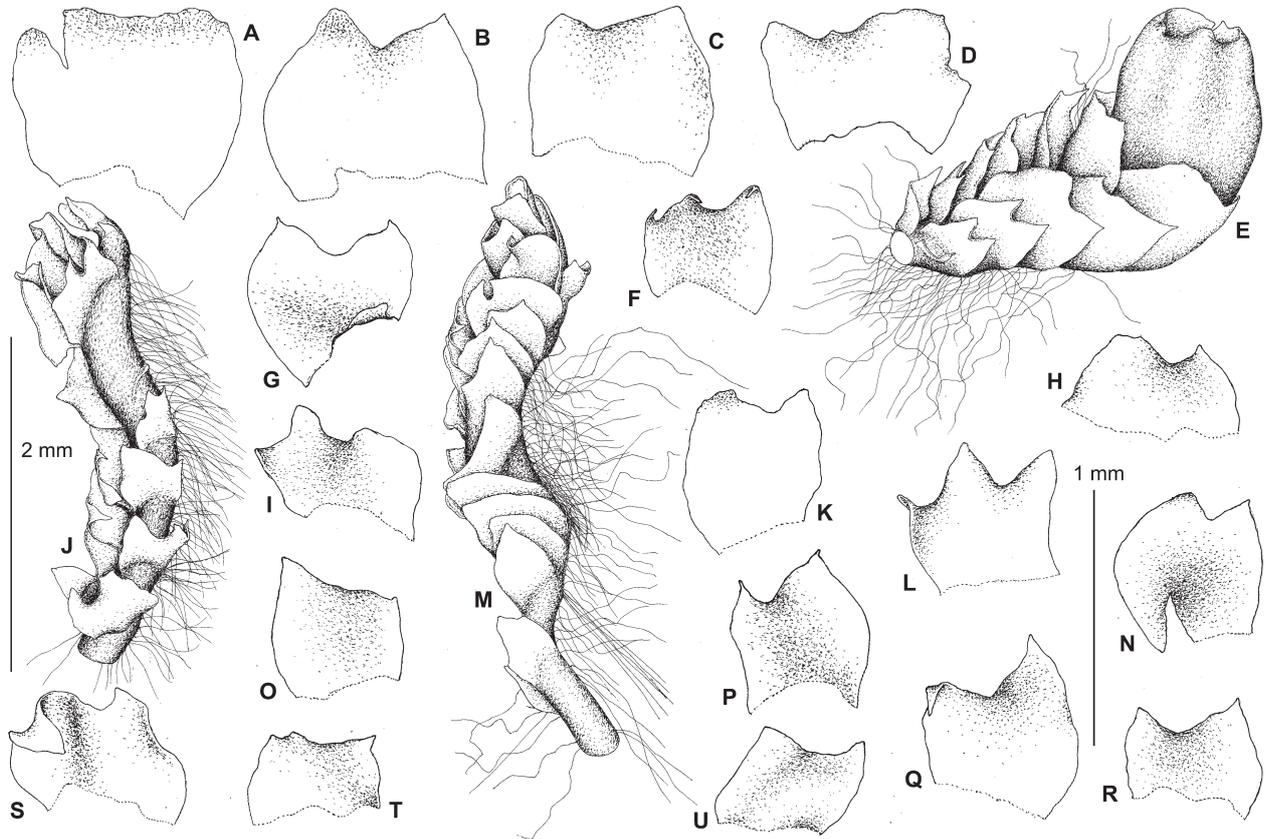


Fig. 5. A-D, F-I, K, L, N-U – sterile leaves. E – fertile (paroicous) shoot. J, M – sterile shoots. Scale bars: 1 mm to A-D, F-I, K, L, N-U. 2 mm to E, J, M. All from *Konstantinova & Savchenko K135-3-07* (KPABG).

only five are marked as fully accepted, seven species are marked as knowledge problem and six are referred to category “serious doubts”. Some of the described entities were tested molecularly, however, the problem is that the interpretations of the species included in different molecular studies differ. Critical revision of the entire genus on an integrative basis has never been done. Moreover, such a study will unavoidably face the need to first understand and relate dozens of described names as well as to check involved in molecular study specimens. Given the very poor preservation of the most type specimens and the fact that they often contain just several individuals, and sometimes only sterile plants, this is a possibly unsolvable problem. A more or less appropriate approach is to gradually unravel the tangle of accumulated problems based on study type specimens and choosing neotypes from the molecularly studied samples. The described new species is, in our opinion, an example of a description of a species that meets these requirements. As shown above, *L. svalbardensis* differs well both morphologically and molecularly. *Lophozia svalbardensis* is the only heteroicous species of *Lophozia* sensu Konstantinova *et al.* (2009), all species of which with the exception of *L. austrosibirica* are dioicous. The latter species was described as paroicous (Bakalin, 2003) but the species level of this taxon is not supported by our molecular study (Fig.3)

*Lophozia svalbardensis* is the fifth species of liverworts described from the Svalbard Archipelago along with *Marsupella arctica* (Berggr.) Bryhn et Kaal. (described as *Sarcoscyphus emarginatus* var. *arcticus* Berggr.), *Scapania spitsbergensis* (Lindb.) Müll.Frib. (as *Martiniellius spitsbergensis* Lindb.), *Jungermannia polaris* Lindb., *Scapania obcordata* (Berggr.) S.W.Arnell (as *Sarcoscyphus obcordatus* Berggr.). All of these species were described from Svalbard in the last third of the 19th century and it took ca. 150 years for it to become clear that they are not rare in most sectors of the arctic and adjacent areas. Most likely, the species described by us is not uncommon in the Arctic, which is still very poorly studied in relation to liverworts.

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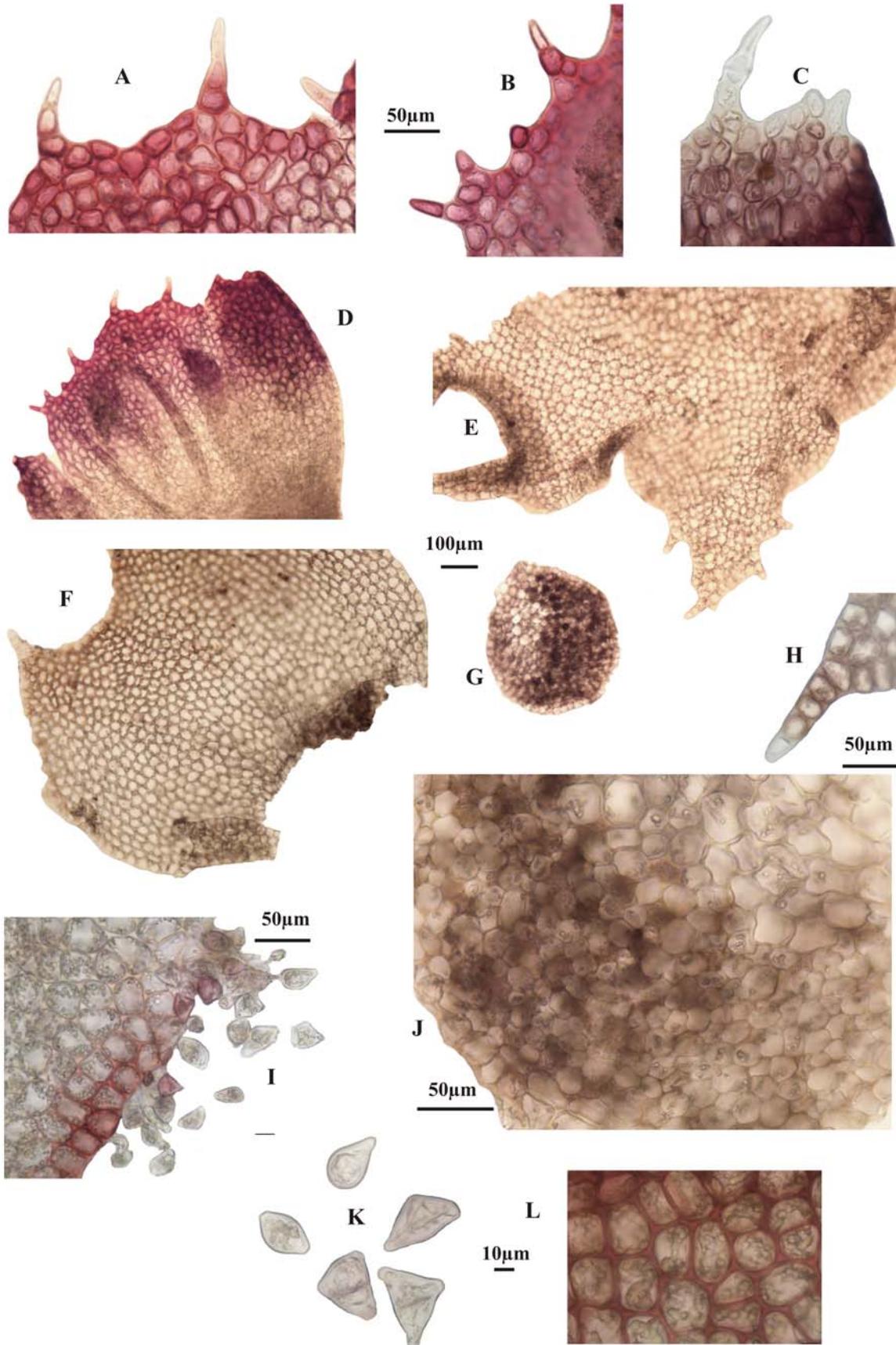


Figure 6. A - C – perianth mouth; D – young perianth; E – lobes of female bract; F – male bract with the multicellular tooth on dorsal side; G – stem cross-section; H – apex of male bract; I – leaf margin with gemmae; J – sector of stem cross-section; K – gemmae; L – cells in midleaf. All from *Konstantinova & Savchenko K135-3-07* (KPABG).

Table 2. Comparison of several morphological characters of *Lophozia svalbardensis* with some species.

| Criterion                     | <i>Lophozia svalbardensis</i>  | <i>Lophozopsis excisa</i>   | <i>Lophozia ascendens</i>   | <i>Lophozia lantratovae</i>   |
|-------------------------------|--|---|---|---|
| Stem                          | Dark brown on ventral side   | Dark brown  | Pale yellowish green, do not differ on ventral side   | Pale brown on ventral side  |
| Sexuality                     | Heteroicous, copiously fertile   | Paroicous, copiously fertile  | Dioicous, rarely with perianths   | Dioicous, rarely with perianths   |
| Female bract                  | Crispate, 3-5 lobed, edentate or with scattered one-celled teeth   | Crispate, irregularly 3-5 lobed, with edentate or finely dentate margins  | With 2-3(4) triangular, entire-margined lobes   | Without teeth, 2-3 lobed  |
| Perianth mouth                | Crenulate-ciliate, with scattered teeth 1-4 cells long, the teeth with elongated upper cell 20 × 35 μm   | Lobed, with crenulate lobes, with rather elongate thin-walled, finger-shaped marginal cells whose distal ends only are free | Lobulate-laciniate, with laciniae 6-10 cells long, 3-5 cells wide with 1-2 short teeth at base and uniseriate apices 2-5 cells long | With scattered 1(2) celled blunt teeth  |
| Leaves                        | 450-480 × 400-430 μm   | 950 × 1100 μm in smaller phases   | Narrow to ovate rectangular, longer than wide, 560-770 × 750-860 μm   | Ovate to rectangular, as wide as long or longer than wide                                 |
| Color of leaves               | Purple or red-brown to almost black distally and light-green or colourless proximally  | Pure green or in upper parts red to carmine or brownish-red   | Pale to yellowish green   | Light to bright green   |
| Cells in the middle of leaves | 23-25 × 25-27 μm   | (27)28-30(32) × 30-35(40) μm  | (20)24-27 × 27-30(35) μm  | (18)20-27(30) × (25)27-40(45) μm  |
| Cell walls                    | Slightly thick walled especially at perianth mouth   | Always thin walled  | Thin walled   | Thin walled   |
| Trigones                      | Distinct, rather large, bulging  | Very small  | Distinct, usually bulging trigones  | Distinct  |
| Gemmae                        | In amorphous masses on juvenile leaves, hidden in uppermost leaves, never form a globules  | Sparse on uppermost leaves  | Abundant, in globules like masses at apices of uppermost leaves   | Abundant, in globules like masses at apices of uppermost leaves                           |
| Shape and color of gemmae     | Mostly colourless to slightly pinkish 1-2 celled, ellipsoidal to rounded triangular and rectangular with rounded and more or less thickened angles | Vinaceous to purplish or purplish brownish, pyramidal to polyhedral-polyangulate  | Yellowish green, angular to stellate  | Pale brown to brown with admixture of colour less, 3-4, rare 5 angulate, 10-16 × 13-18 μm |

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Appendix 1. The list of tested specimens with voucher details and GenBank accession numbers, accessions start with MW obtained in this study.

| Taxon  | Specimen voucher   | GenBank accession number |                     |
|--|--|--------------------------|---------------------|
|  |  | ITS1-2 nrDNA             | <i>trnL-F</i> cpDNA |
| <i>Anastrepta orcadensis</i> (Hook.) Schiffn.                        | Russia: Buryatiya Rep., N. Konstantinova, 59-1-01, 102486 (KPABG)                                | DQ875126                 | DQ875088            |
| <i>Diplophyllum taxifolium</i> (Wahlenb.) Dumort.                    | Russia: Kareliya Rep., V. Bakalin, 28-Jul-1998 (KPABG)   | EU791772                 | AY327762            |
| <i>Heterogemma capitata</i> (Hook.) Konstant. & Vilnet               | Russia: Nizhny Novgorod Prov., N. Konstantinova, 132-03, 106019 (KPABG)                          | DQ875119                 | DQ875080            |
| <i>Lophozia ascendens</i> (Warnst.) R.M. Schust.                     | Russia: Buryatiya Rep., N. Konstantinova, 1 09-3-01, 104300 (KPABG)                              | DQ875089                 | DQ875054            |
| <i>L. austrosibirica</i> Bakalin                                     | Russia: Buryatiya Rep., V. Bakalin, 15-9-99, 109664 (KPABG)                                      | DQ875105                 | DQ875069            |
| <i>L. fuscovirens</i> Bakalin & Vilnet                               | Norway: Svalbard, A. Savchenko, CA16-12-1c, 121433 (KPABG)                                       | MK774737                 | MK779914            |
| <i>L. fuscovirens</i> Bakalin & Vilnet                               | Russia: Magadan Prov., V. Bakalin, Mag-50-16-11, 122642 (KPABG)                                  | MK007092                 | MK012212            |
| <i>L. lantratovae</i> Bakalin  | China: Sichuan Prov., V. Bakalin, China-35-9-17, 122581 (KPABG), 37536 (VBGI)                    | MK007086                 | MK012206            |
| <i>L. lantratovae</i> Bakalin  | Russia: Buryatiya Rep., V. Bakalin, 76-7-01, 102544 (KPABG)                                      | DQ875090                 | DQ875055            |
| <i>L. silvicoloides</i> N. Kitag.                                    | Norway: Svalbard, N. Konstantinova, K241-1b-12 (KPABG)   | MW298767                 | MW297148            |
| <i>L. silvicoloides</i> N. Kitag.                                    | Russia: Kamchatka Terr., V. Bakalin, K-57-23-02-VB, 104240 (KPABG)                               | DQ875098                 | DQ875063            |
| <i>L. spitsbergensis</i> Konstant. & Vilnet                          | Norway: Svalbard, N. Konstantinova, K-135-3a-07 (KPABG)  | MW298768                 | MW297149            |
| <i>L. ventricosa</i> (Dicks.) Dumort.                                | Russia: Arkhangelsk Prov., Franz Josef Land, Ziegler Island, A. Savchenko, CA19-29-10a-1 (KPABG) | MT422262                 | MT431406            |
| <i>L. ventricosa</i> var. <i>guttulata</i> (Lindb. & Arnell) Bakalin | Russia: Buryatiya Rep., N. Konstantinova, 81-1-01, 104253 (KPABG)                                | DQ875108                 | DQ875072            |
| <i>L. wenzelii</i> var. <i>groenlandica</i> (Nees) Bakalin           | Russia: Murmansk Prov., N. Konstantinova, G9329 (KPABG)  | DQ875109                 | DQ875073            |
| <i>L. wenzelii</i> var. <i>lapponica</i> H. Buch & S.W. Arnell       | Norway: Svalbard, N. Konstantinova, 124-2-04 (KPABG)   | DQ875112                 | DQ875076            |
| <i>L. wenzelii</i> var. <i>lapponica</i> H. Buch & S.W. Arnell       | Russia: Perm Terr., A. Bezgodov, MW298769 AB 206-09 (KPABG)                                      | MW297150                 |                     |
| <i>L. wenzelii</i> var. <i>massularioides</i> Bakalin                | Russia: Karachay-Cherkessia Rep., V. Onipchenko, 31-Aug-1983, 102608 (MHA)                       | DQ875111                 | DQ875075            |
| <i>Lophozopsis excisa</i> (Dicks.) Konstant. & Vilnet                | Norway: Svalbard, A. Savchenko, CA 364-2a-11 (KPABG)   | MW298770                 | MW297151            |
| <i>L. excisa</i> (R.M. Schust.) Konstant. & Vilnet                   | Russia: Murmansk Prov., N. Konstantinova, 41-2-97, 6146 (KPABG)                                  | DQ875092                 | DQ875057            |

|  |  |          |          |
|--|--|----------|----------|
| <i>L. excisa</i> (Dicks.) Konstant.& Vilnet                            | Russia: Maryi-El Rep., N. Konstantinova, K437-2-04, 108028 (KPABG)                             | EF065691 | EF065684 |
| <i>L. excisa</i> (Dicks.) Konstant.& Vilnet                            | Antarctica, L. Kurbatova, L125 (KPABG)   | MW298771 | MW297152 |
| <i>L. excisa</i> var. <i>elegans</i> (R.M. Schust.) Konstant.& Vilnet  | Russia: Murmansk Prov., N. Konstantinova, K129-7-19 (KPABG)                                    | MW298772 | MW297153 |
| <i>L. jurensis</i> (Meyl. ex Muell. Frib.) Mamontov & Vilnet           | Russia: Altai Terr., 1, Yu. Mamontov, YuSM-214-7 (KPABG)                                       | MF803151 | MF803153 |
| <i>L. jurensis</i> (Meyl. ex Müll. Frib.) Mamontov & Vilnet            | Russia: Altai Terr., 2, Yu. Mamontov, YuSM-214-8 (KPABG)                                       | MF803150 | MF803152 |
| <i>L. longidens</i> (Lindb.) Konstant.& Vilnet                         | Russia: Murmansk Prov., N. Konstantinova, 360-2-00, 8110 (KPABG)                               | DQ875094 | DQ875059 |
| <i>L. pellucida</i> (R.M. Schust.) Konstant. & Vilnet                  | Russia: Trans-Baikal Terr., Yu. Mamontov, 356-3-6 (KPABG)                                      | MW298773 | MW297154 |
| <i>L. polaris</i> (R.M. Schust.) Konstant.& Vilnet                     | Norway: Svalbard, 1, A. Savchenko, CA 19-29-3 (KPABG)  | MW298774 | MW297155 |
| <i>L. polaris</i> (R.M. Schust.) Konstant.& Vilnet                     | Norway: Svalbard, 2, A. Savchenko, CA 367-2b-11 (KPABG)  | MW298775 | MW297156 |
| <i>L. polaris</i> (R.M. Schust.) Konstant.& Vilnet                     | Norway: Svalbard, 3, N. Konstantinova, K129-1-07 (KPABG)                                       | MT334459 | MT338482 |
| <i>L. polaris</i> (R.M. Schust.) Konstant.& Vilnet                     | Russia: Arkhangelsk Prov., Franz Josef Land, Ziegler Island, A. Savchenko, CA 19-29-12 (KPABG) | MT422257 | MT431401 |
| <i>Pseudotritomaria heterophylla</i> (R.M. Schust.) Konstant. & Vilnet | Russia: Yakutiya Rep., V. Zolotov, E. Sofronova, 13-Jul-2003 (KPABG)                           | EU791805 | EU791686 |
| <i>Saccobasis polymorpha</i> (R.M. Schust.) Schljakov                  | Russia: Murmansk Prov., N. Konstantinova, 21-3b-96, 6189 (KPABG)                               | EU791807 | EU791688 |
| <i>Scapania aspera</i> M. Bernet & Bernet                              | Belgium, N. Konstantinova, 2-20-3-99, 102125 (KPABG)   | EU791735 | EU791627 |
| <i>Schistochilopsis grandiretis</i> (Lindb. ex Kaal.) Konstant.        | Russia: Kamchatka Terr., V. Bakalin, 99-5-01-VB, 104017 (KPABG)                                | DQ875120 | DQ875081 |
| <i>Trilophozia quinquentata</i> (Huds.) Bakalin                        | Russia: Kareliya Rep., V. Bakalin, 02-Jul-1997 (KPABG)   | EU791804 | AY327786 |
| <i>T. quinquentata</i> fo. <i>gracilis</i> (R.M.Schust.) Konstant.     | Norway: Svalbard, N. Konstantinova, K 118-2-06 (KPABG)   | EU791802 | EU791684 |
| <i>Tritomaria exsecta</i> (Schmidel) Schiffn. ex Loeske                | Russia: Nizhny Novgorod Prov., N. Konstantinova, 103-1-03, 105966 (KPABG)                      | EU791800 | EU791682 |
| <i>T. scitula</i> (Taylor) Joerg.                                      | Russia: Komi Rep., M. Dulin, 101301 (KPABG)  | EU791799 | EU791681 |