



New data on the Porellaceae (Marchantiophyta) in Russia

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ABSTRACT

In the course of preparing the monograph on the liverwort flora of the Russian Far East, two species of the Porellaceae were newly found in this area. *Porella japonica* is first reported for the Russian Federation; the species has the northernmost location worldwide there. *Porella cordaeana* is recorded for the Russian Far East for the first time. The molecular genetic analysis indicates that the studied specimens are genetically closer to the North American accessions of the latter species, rather than the European ones. To date, the known diversity of Porellaceae in the Russian Far East counts 13 species that significantly exceeds its diversity in the rest of Russia. The paper provides morphological descriptions of both species based on the Far Eastern materials, line drawings, and photographs, including those made on living plants.

Keywords: Hepaticae, liverworts, new records, Commander Islands, East Asia, southern Sikhote-Alin, the Russian Far East

РЕЗЮМЕ

Климова К.Г., Бакалин В.А., Мальцева Ю.Д. Дополнения к Porellaceae (Marchantiophyta) в России. В рамках продолжающейся работы по подготовке флоры печеночников российского Дальнего Востока были впервые обнаружены два вида семейства Porellaceae. *Porella japonica* – новый вид для флоры печеночников России, его новое местонахождение – самое северное в мире. *Porella cordaeana* – впервые выявлен для Дальнего Востока России. Результаты молекулярно-генетического анализа свидетельствуют, что собранные нами образцы *P. cordaeana* генетически более близки к североамериканским популяциям этого вида, но не европейским. В настоящее время известное разнообразие Porellaceae на российском Дальнем Востоке составляет 13 видов, что значительно превышает разнообразие семейства на остальной территории России. В статье приводятся морфологические описания двух видов, сделанные на основе дальневосточного материала, штриховые рисунки и фотографии прижизненного облика растений и их частей.

Ключевые слова: Hepaticae, печеночники, новые находки, Командорские острова, восточная Азия, южный Сихотэ-Алинь, Дальний Восток

Porellaceae Cavers is a quite speciose, morphologically and genetically well-defined family of Porellales. It has the greatest diversity in the subtropical mountains in both hemispheres and corresponding belts in the mountains. According to the modern taxonomic concept, it includes two genera – monotypic *Asciodiota* C. Massal. (not known in the Russian Far East, although presented in East Siberia westward) and rather speciose *Porella* L. The latter is characterized by *Frullania*-type branching, bilobed leaves with incubously inserted dorsal lobe that is much larger than ventral lobule, well-developed, comparatively large underleaves, absence of prominent ‘sacs’ in the leaf and underleaf bases, and relatively smooth leaf cuticle. A brief description of the Porellaceae family and its distribution in Pacific Asia was provided in the recently published study by Bum et al. (2025).

According to a previously published revision of Porellaceae for the Russian Far East (Bakalin & Klimova 2019), 11 species of *Porella* were known for this area to date. The ongoing studies during the past few years not only revealed new localities for already known species, but also new taxa for the liverwort flora of the Russian Far East and Russia. The latter is especially remarkable since representatives of the family are quite large and can be easily recognized in the field.

During the study of liverwort floras in two regions of the Russian Far East, very distant from each other, we found two species new to this area, one of which is new to the Russian flora. The goal of the present account is to describe and discuss these records to attract further attention to these taxa in future studies of the liverwort flora of the Far East and adjacent areas.

MATERIAL AND METHODS

Specimen collection and study area

Porella japonica (Sande Lac.) Mitt. was first found by the first author during a liverwort flora investigation in Makarovsky Range (the Southern Sikhote-Alin Mts., Primorye Territory). The species was collected in 2023 in two localities of Makarov Stream valley at the northernmost flank of the Range. In 2024, the studies were continued in the central part of the Range (Pravyy Sobolyatnik Stream basin), where *P. japonica* was also revealed.

The Makarovsky Range is situated in a cool temperate Manchurian Broadleaved-Conifer forest area (Nakamura & Krestov 2005). All specimens were collected in the *Pinus koraiensis*-broadleaved deciduous forest vegetation belt. The climate of the area has a pronounced monsoon character

and, according to the Köppen–Geiger classification, it belongs to Monsoon-influenced warm-summer humid continental climate (Dwb) (Beck et al. 2023, GloH₂O 2024). For the altitude range of 340–600 m a.s.l., where specimens were collected, average annual temperature varies between 1.6 and 3.5°C, annual precipitation is about 752–808 mm, mean temperatures of wettest and warmest quarters (are the same) – 15.6–17.1°C (according to climate data of WorldClim ver. 2.1, Worldclim. 2020–2025). According to Takhtajan (1986), Chen et al. (2018), Wu & Wu (1996), this area belongs to the East Asian floristic region or kingdom for two latter sources.

Porella cordaeana was collected in the course of liverwort flora exploration in 2021 in the northern part of Bering Island (Commander Islands, Kamchatka Territory). The Commanders are located in the northern part of the Pacific Ocean, ca.180 km from the Kamchatka Peninsula. The lack of forests and vast areas covered with meadows and tundra; streams, bogs, and ponds are common for them. Almost the entire Commanders are influenced by the subarctic climate with no dry season and cold summer (Dfc); small areas are under polar (tundra) climate (ET) (Beck et al. 2023, GloH₂O 2024). Collecting locality on Bering Island is characterized by an average annual temperature of 1.1°C, annual precipitation of about 740 mm, a mean temperature of the wettest quarter of 3.8°C, and a mean temperature of the warmest quarter of 9.4°C (WorldClim ver. 2.1, Worldclim 2020–2025).

We expected the species to occur in the Russian Far East (Bakalin & Klimova 2019). Taking into account the possible morphological intergrading of *Porella cordeana* to *P. platyphylla*, an integrative approach was used to exclude the possibility of further speculation regarding the species identity. Thus, the specimens tentatively named as *P. cordaeana* were examined not only by morphological, but also by molecular-genetic methods. A subsequent revision of the herbarium materials has revealed *P. cordaeana* in collections from Mednyi Island (Commander Islands), gathered by Bakalin in 2004. But these specimens were erroneously referred to *P. platyphylla* and published under this name in the revision of Porellaceae for the Russian Far East (Bakalin & Klimova 2019).

During field collecting, the altitude above sea level, vegetation community, substrate, light, and humidity of the liverwort mats were recorded for all specimens discussed in the present study. An expert assessment was used to evaluate light and humidity without the use of any specialized measuring equipment. Each specimen was assigned a unique field number. In both cases (Makarovsky Range and Commanders), collected specimens were delivered to the Laboratory of Cryptogamic Biota of the Botanical Garden-Institute FEB RAS (Vladivostok) in a living state, excluding

the collection from Mednyi Island made in 2004. This made it possible to photograph the general appearance of living plants and oil bodies in leaf cells. The collections were identified using the facilities of the latter laboratory (upright microscope Olympus CX–31, stereo microscopes Zeiss Stemi 2000 and Olympus CZX–16).

During the identification process, associated taxa were also recorded. Immediately after identification, several plants were extracted from the specimen and put into the silica gel for subsequent DNA analysis. The comparative study was carried out using the anatomical and morphological method for all available specimens (including those collected outside of the Russian Far East and kept in VBG), and the obtained morphometric parameters were compared with those available in the literature sources. All collected specimens were deposited in the VBG Herbarium cryptogamic section.

Molecular-genetic analysis

Two specimens of *Porella cordaeana* from the Bering Island were selected for molecular estimation to prove their identification and evaluate the existing divergence. Previously published 75 accessions of 15 *Porella* species (Heinrichs et al. 2011, Hentschel et al. 2007) were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/nucleotide/> accessed on 04.04.2025), based on the principles of relationship and distribution, to complete the dataset. Since the initial BLAST search (<https://blast.ncbi.nlm.nih.gov/Blast.cgi> accessed on 24.02.2025) has revealed the close relationships of our sequenced materials to the *P. cordeana*, we used taxa that were found as closely related to the clade *P. platyphylla* – *P. cordeana* in Heinrichs et al. (2011). Also, according to Heinrichs et al. (2011), *P. arboris-vitae* and *P. obtusata* were selected as an outgroup for tree rooting for ITS1–2 and *P. japonica* for *rbcl*. Specimen voucher details, including GenBank accession numbers, are listed in Appendix 1.

Following Heinrichs et al. (2011), who tested the phylogeny of *Porella* based on ITS1–2 nrDNA, *trnL*–F, and *atpB*–*rbcl* cpDNA, we selected the ITS1–2 as a more suitable marker to check the identity of our specimens. Additionally, *rbcl* was sequenced.

DNA was extracted from dried liverwort tissues using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). Amplification of ITS1–2 and *rbcl* was performed using an Encyclo Plus PCR Kit (Evrogen, Moscow, Russia) with the primers listed in Table 1.

The polymerase chain reaction was performed in a total volume of 20 µL, including 1 µL of template DNA, 0.4 µL of Encyclo polymerase, 5 µL of Encyclo buffer, 0.4 µL of dNTP-mixture (included in Encyclo Plus PCR Kit), 13.4 µL

Table 1. Primers used in polymerase chain reaction (PCR) and cycle sequencing.

Locus	Sequence (5'–3')	Direction	Annealing temperature (°C)	Reference
ITS 1–2 nrDNA	CGTTGTGAGAAGTTCATTTAAACC	forward	64	Feldberg et al. 2016
ITS 1–2 nrDNA	ACCTGCGGAAGGATCATTTG	forward	58	Friedl 1996
ITS 1–2 nrDNA	GATATGCTTAAACTCAGCGG	reverse	58	Milyutina et al. 2010
<i>rbcl</i> cpDNA	ATGTCACCACAAACGGA	forward	50	Fedosov et al. 2016
<i>rbcl</i> cpDNA	TCAAATTCAAACTTGATTTCTTTCCA	reverse	66	Fedosov et al. 2016

(for *rbcl*)/12.4 µL (for ITS1–2) of double-distilled water (Evrogen, Moscow, Russia), 1 µL of dimethylsulfoxide/DMSO (for ITS1–2), and 0.4 µL of each primer (forward and reverse, at a concentration of 5 pmol/µL). Polymerase chain reactions were carried out using the following program:

initial denaturation for 180 sec. at 95°C;
denaturation for 90 sec. at 94°C;
annealing for 30 sec. at 58°C (ITS1–2), 120 sec. at 50°C (*rbcl*);
elongation for 90 sec. at 72°C;
final elongation for 5 min. at 72°C.

Initial denaturation, denaturation, annealing and elongation steps were repeated for 35 cycles.

Amplified fragments were visualized on 1 % agarose TAE gels by EthBr staining and purified using the HiPure Gel DNA Micro Kit (Guangzhou Magen Biotechnology Co., Ltd, China). The DNA was sequenced using the ABI PRISM® BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (Applied Bio-systems, Waltham, MA, USA) with further analysis of the reaction products following the standard protocol on an automatic sequencer 3730 DNA Analyzer (Applied Bio-systems, Waltham, MA, USA) in the Genome Center (Engelhardt Institute of Molecular Biology, Russian Academy of Sciences, Moscow).

Phylogenetic analyses

The alignments were compiled for the ITS1–2 and *rbcl* loci and aligned using MAFFT (Katoh & Standley 2013) with standard settings and then edited manually in BioEdit ver. 7.2.5 (Hall 1999). All positions of the final alignments were included in the phylogenetic analyses. Absent data at the ends of regions and missing loci were coded as missing data.

Phylogenetic trees were reconstructed using two approaches: maximum likelihood (ML) with IQ-tree ver. 1.6.12 (Nguyen et al. 2015) and Bayesian inference (BA) with MrBayes ver. 3.2.7 (Ronquist et al. 2012).

For the ML analysis, the best-fitting evolutionary model of nucleotide substitutions according to the Bayesian Information Criterion (BIC) value was TN+F+G4 for ITS1–2 dataset and HKY+F+I for *rbcl*, which were determined by ModelFinder (a model selection method implemented in IQ-tree) (Kalyaanamoorthy et al. 2017). Consensus trees were constructed with 1000 bootstrap replicates.

Bayesian analyses were performed by running two parallel analyses using the GTR+I+G model. The analysis consisted of four Markov chains. Chains were run for five million generations, and trees were sampled every 500th generation. The first 2 500 trees in each run were discarded as burn-in; thereafter, 15 000 trees were sampled from both runs to produce a resulting tree. Bayesian posterior probabilities were calculated from the trees sampled after burn-in. The average standard deviation of split frequencies between two runs reached 0.002 in ITS1–2 and 0.004 in *rbcl* before the analysis was stopped.

As phylogenetic trees suggest classic cladistics approach to complete it, with the purpose to visualize molecular affinities hardly suitable for the latter between closely related species, we used Splits tree and Neighbor Net (NN) methods implemented in SplitsTree v. 4.14.2 (Huson & Bryant 2006) and the method of Templeton, Crandall and Sing (TCS), 1992, to visualize molecular relationships. Besides, we

removed sample Com-189-4-21 from the split network because its sequence is significantly shorter than Com-189-5-21, and it assumes an unnatural position on the split network, while the same is not very critical for the phylogenetic tree and the TCS network.

A haplotype network was constructed by the TCS network inference method (Clement et al. 2002) using the PopART package (<http://popart.otago.ac.nz/>, accessed on 08.11.2019) (Leigh 2015). The PopART program automatically removes positions having at least one N or a gap value from consideration. The infraspecific and interspecific variabilities were quantified as the average pairwise *p*-distances calculated in Mega XII (Kumar et al. 2024) using the pairwise deletion option for counting gaps, the proportion of nucleotide sites that are different (d: Transitions + Transversions), and 1000 bootstrap replicates.

RESULTS

Molecular-genetic estimations for *Porella cordaeana*

Three sequences of the newly studied specimens of *P. cordaeana* (2 – ITS1–2 and 1 – *rbcl*) were deposited in GenBank under the accession numbers indicated in Appendix 1.

The ML criterion recovered a bootstrap consensus tree with a log-likelihood = -2663.286 for ITS1–2 (-2186.639 for *rbcl*). The arithmetic means of the log-likelihoods in Bayesian analysis for each sampling run were -2695.42 and -2695.69 for ITS1–2 (-2209.71 and -2208.81 for *rbcl*).

We decided to use the ITS1–2 based tree (Fig. 1) as the main one, and *rbcl* (as supplementary material in Appendix 2). The only thing that is clear from the latter tree is that we have sequenced true *P. cordaeana*. On the ITS1–2 and *rbcl* trees, the specimens we sequenced belong to the *P. cordaeana* clade with the same value of supports: ML – 98 % and BI – 1.00.

The ITS1–2 infraspecific *p*-distance of the tested *P. cordaeana* specimens is 0.52 %, which approximately coincides with the infraspecific *p*-distances of *P. platyphylla* (0.49 %) and *P. navicularis* (0.68 %), and is more than 2 times lower than in *P. platyphylloidea* (1.2 %), and *P. arboris-vitae* (1.36 %). The sequences of *P. obtusata* taken in the dataset turned out to be identical, so the *p*-distance within this clade was 0 %.

The *p*-distances between *P. cordaeana* and *P. platyphylla* is 2.56 %, *P. cordaeana* and *P. platyphylloidea* – 4.93 %, *P. cordaeana* and *P. navicularis* – 2.94 %, which also corresponds to the value of the difference between major clades (from 3.4 % to 5.26 %) (Table 2).

There is no clear differentiation between the American and European subclades on the phylogenetic trees (Fig. 1, Appendix 2); therefore, in addition, we applied the following methods of analysis: the TCS (Fig. 2) and NN (Fig. 3), which helped to reveal affinities and similarities within the clade *P. cordaeana*. Specimens from the Bering Island have synapomorphies that combine them with specimens from America, but not European accessions.

Taking into account the position of the vouchers named as *P. platyphylla* (EF545296, EF547189, EF545295, EF545297) in *rbcl* based tree (Appendix 2), they rather belong to *P. platyphylloidea*.

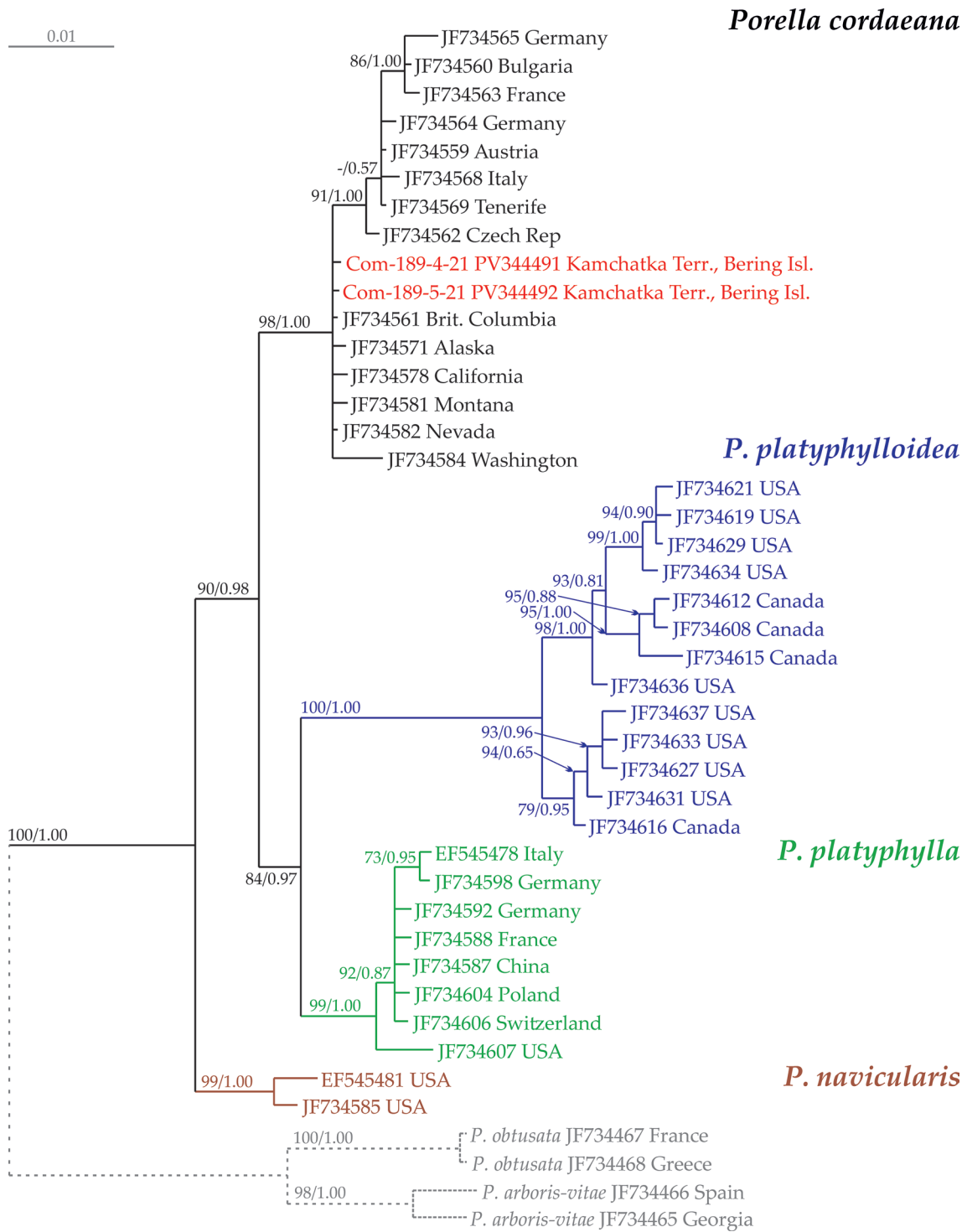


Figure 1 Phylogram obtained in a Maximum Likelihood (ML) analysis for the selected *Porella* taxa based on the ITS1–2 nrDNA dataset. The values of bootstrap support from the ML analysis and Bayesian posterior probabilities greater than 0.50 (50 %) are indicated. Taxon names, GenBank accession numbers and vouchers are provided. Newly studied specimens are marked in red

Table 2. Intraspecific and interspecific *p*-distances, calculation based on ITS1–2 nucleotide sequence data. The numbers of base differences per site from averaging over all sequence pairs within and between each group are shown; “n/c” – non calculated due to presence of single specimen.

N Taxa	Intraspecific <i>p</i> -distances, ITS1–2, %	Interspecific <i>p</i> -distances, ITS1–2, %				
		1	2	3	4	5
1 <i>P. cordaeana</i>	0.52					
2 <i>P. platyphylla</i>	0.49	2.56				
3 <i>P. platyphylloidea</i>	1.20	4.93	4.67			
4 <i>P. navicularis</i>	0.68	2.94	3.40	5.26		
5 <i>P. obtusata</i>	0	8.21	8.34	9.78	7.71	
6 <i>P. arboris-vitae</i>	1.36	7.31	7.74	9.32	7.44	3.65

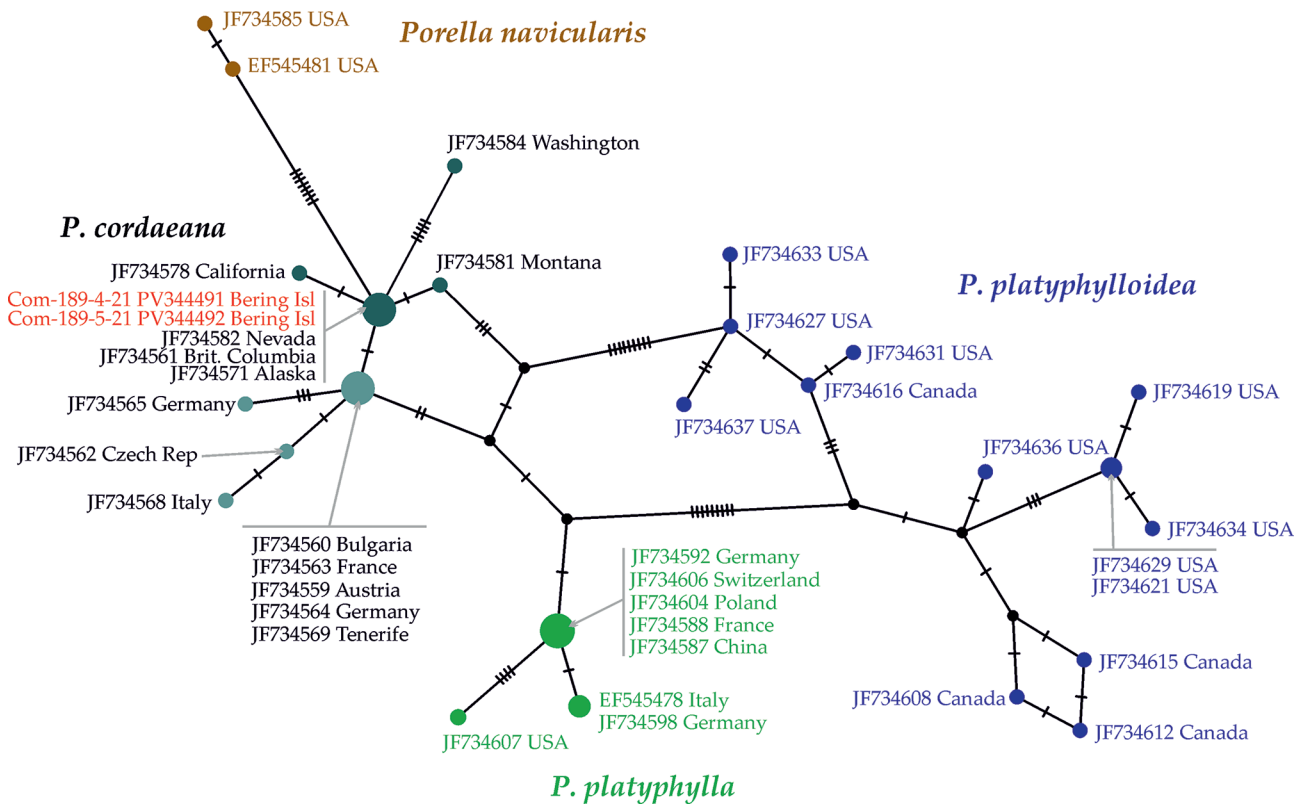


Figure 2 TCS haplotype network of ITS1–2 nrDNA. Dashes indicate the number of nucleotide substitutions. Newly studied specimens are marked in red

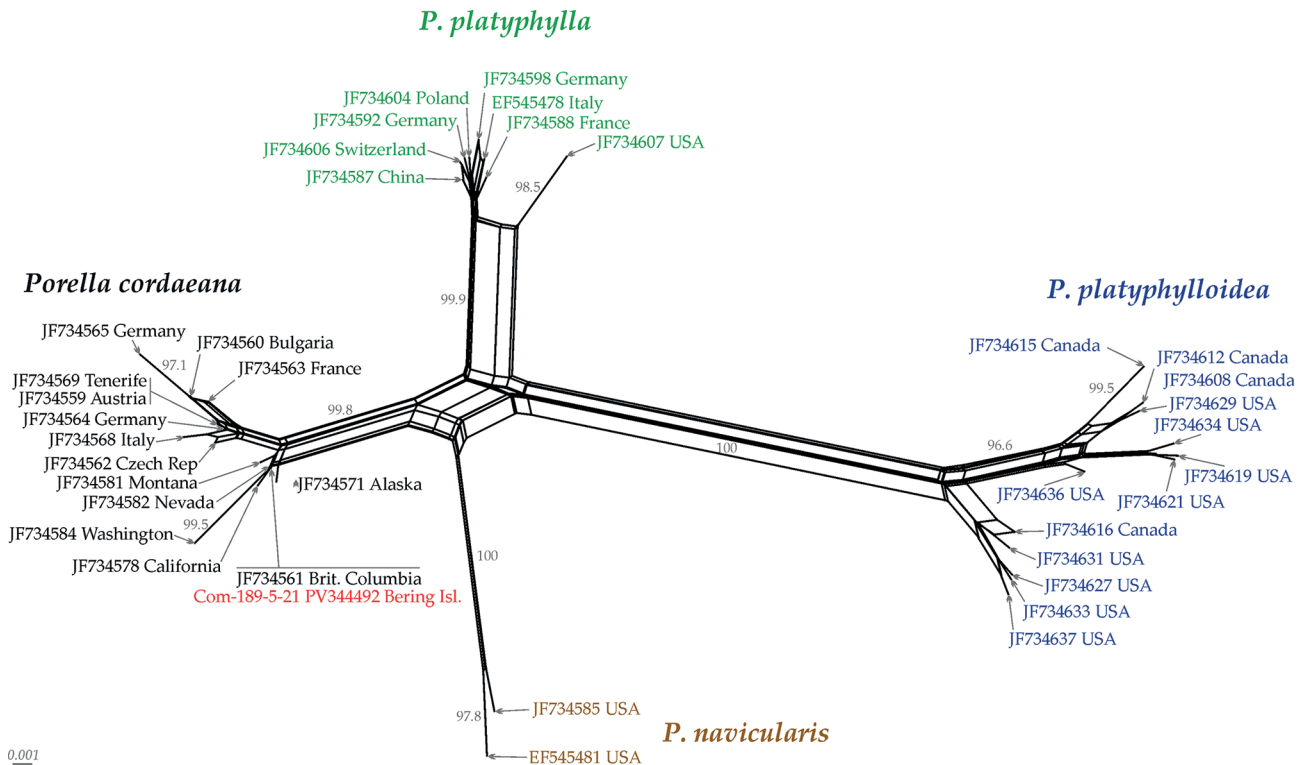


Figure 3 NeighborNet split network for *Porella* species, based on ITS1–2 nrDNA dataset. Support values of 75 or higher are indicated. Newly studied specimen is marked in red

Identity of *Porella japonica* materials

Comparison of the collected materials from Primorye Territory with descriptions published in Horikawa (1930), Hattori (1978), Schuster (1980), Bakalin (2018), Bum et

al. (2025) and morphometric study of available herbarium materials from VBGI (four specimens from Japan, two from the Republic of Korea, and one from Vietnam) confirmed their belonging to the typical modification of *Porella japonica*.

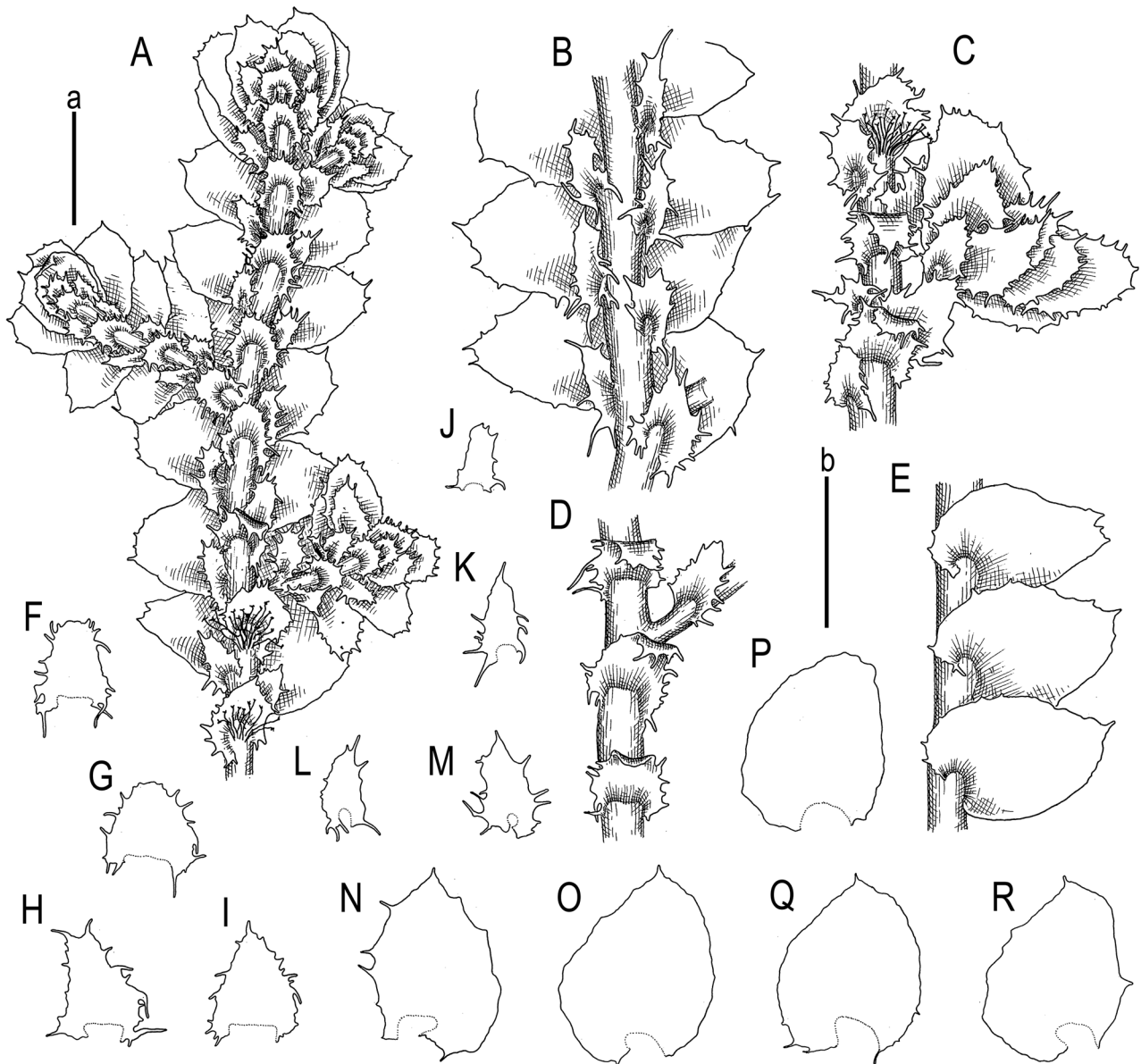


Figure 4 *Porella japonica* (Sande Lac.) Mitt.: A – plant habit, ventral view; B – shoot, fragment, ventral view, underleaves detached; C – shoot with gynoecium, fragment, ventral view, dorsal lobes detached; D – shoot, fragment, ventral view, dorsal and ventral lobes detached; E – shoot, fragment, dorsal view, one row of dorsal lobes, ventral lobes, and underleaves detached; F–I – underleaves; J–M – ventral lobes; N–R – dorsal lobes. Scales: a – 1 mm, for A; b – 1 mm, for B–R (all from Prim-36-8-24, VBG1)

Due to the available data, the species is known from four specimens, all collected in the hemiboreal forest belt of the Makarovsky Range.

Taxonomic treatment

Porella japonica (Sande Lac.) Mitt., 1891, Trans. Linn. Soc. London, Bot. 3(3): 202. \equiv *Madotheca japonica* Sande Lac., 1856 [1857], Syn. Hepat. Jav. 105: pl. 21. (Figs 4, 5)

Description. Plants prostrate to loosely ascending near apices, green to deep green and brownish green, 40–50 mm long and 1.5–2.0 mm wide. Stem green to deep brownish green, regularly pinnately to sparsely bipinnately branched, 290–370 μ m wide. Rhizoids virtually absent, except the terminal areas of branches where those touch the substrate, brown, densely branched at the distal parts, in spreading fascicles originating from ventral side of stem in areas adjacent to underleaf bases, 0.4–1.0 mm long. Leaf dorsal lobe imbricate (then covering 1/3–1/10 of the leaf situated above), obliquely ovate with obtuse apex, nearly plane to slightly undulate, 0.95–1.10 \times 0.75–1.00 mm, at dorsal side

arcuately inserted and barely decurrent, margin loosely ciliate, often very irregularly toothed or even ciliate with cilia on wide base with uniseriate ends of 4–5 cells long, with at least 1–2 larger teeth at lobe apices and sometimes with short obtuse or long, variously incurved teeth near dorsal base, if present then commonly ending by cilia up to 5 cells long. Leaf ventral lobes distant, loosely appressed to the stem, nearly plane, arcuately inserted, not or barely decurrent ventrally, 0.45–0.80 mm long and 0.25–0.40 mm wide (if without teeth taking into account), 0.30–0.65 mm wide (if measured including teeth), oblong triangular to irregularly oblong, with acuminate to obtuse apex, sparsely toothed, but always with teeth of various shape at lobe bases, sometimes with large appendage-like structure with several teeth. Underleaves distant, nearly plane to slightly convex (if to view from ventral side of the shoot), sometimes with reflexed apex, triangular with mostly truncate, or sometimes acuminate apex, barely to shortly decurrent in the both sides (to 1/5–1/4 of stem width), sparsely irregularly toothed throughout, always with teeth of various shape and length in decurrencies, 0.40–0.70 \times 0.45–0.60 mm. Cells in dorsal

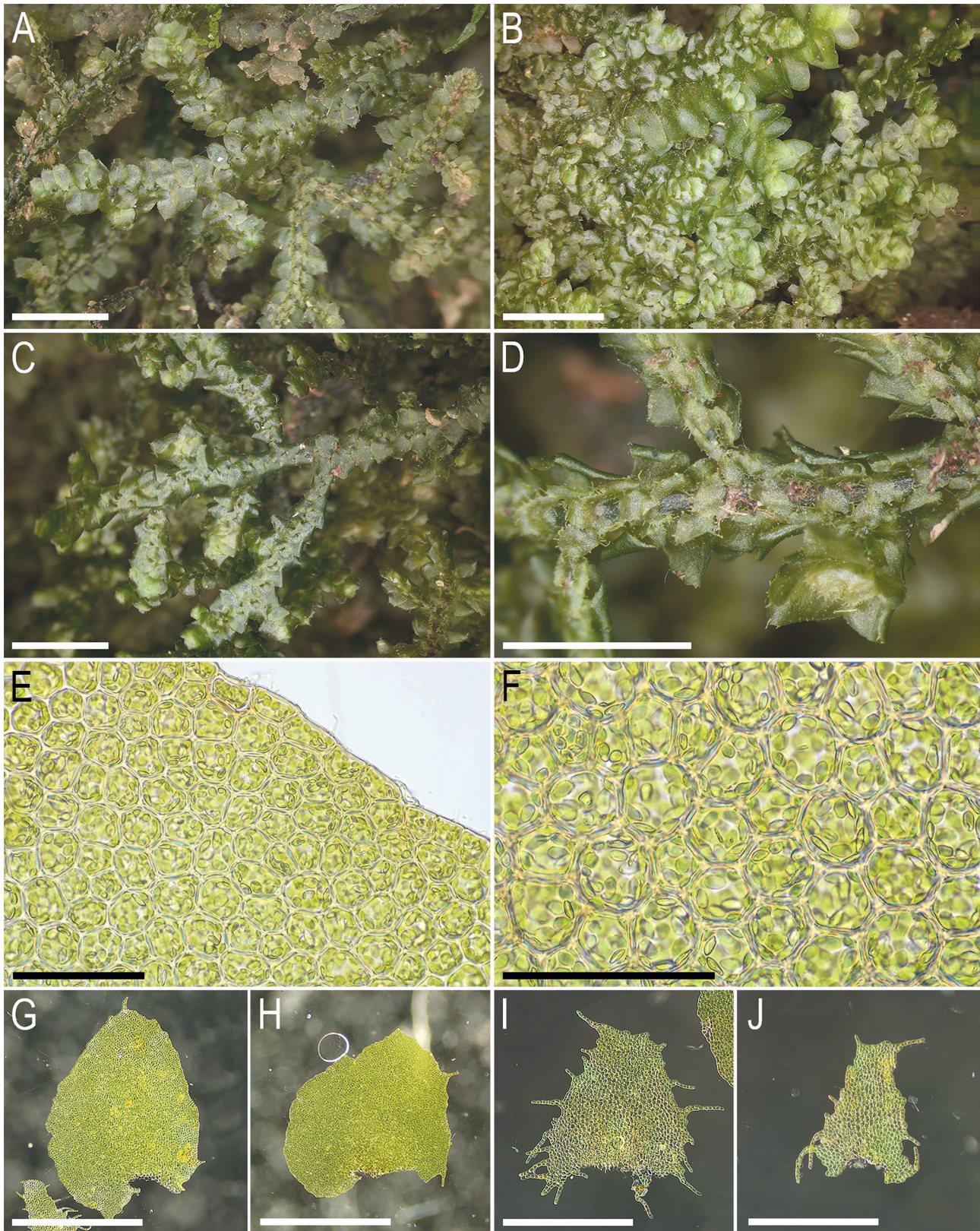


Figure 5 *Porella japonica* (Sande Lac.) Mitt.: A – shoots in a mat in dorsal and ventral view; B – part of a mat, over *Porella grandiloba* Lindb. shoot; C – shoot in mesic conditions, dorsal view; D – shoot in mesic conditions, fragment, ventral view; E – oil bodies in dorsal lobe margin cells; F – oil bodies in midleaf cells; G, H – dorsal lobes; I – underleaf; J – ventral lobe. Scales: 3 mm for A, C, D; 5 mm for B, 1 mm for C; 50 μm for E, F; 1 mm for G, H; 500 μm for I, J (A, F from Prim-17-26-23, B, E, G, I, J from Prim-36-8-24, C, D, H from Prim-18-1-23, VBG1)

lobe middle subsodiametric to shortly oblong, $15.0\text{--}22.5 \times 10.0\text{--}22.5 \mu\text{m}$, walls somewhat thickened, trigones moderate in size, concave; cuticle virtually smooth; oil bodies in the dorsal lobe middle (6–)7–11(–12) per cell, homogenous,

spherical to elliptical and shortly oblong, $3.75\text{--}6.25 \times 2.5\text{--}3.75 \mu\text{m}$. Dioicous. [Androecia not seen, the description is extracted from Horikawa (1930: 643): “Androecia in short lateral branches, oblong-oval, bracts in 2–4 pairs, closely

imbricate, ventricose”]. Gynoecia on short lateral branches, with no or 1–2 pairs of sterile leaves below bracts; 6–8 archegonia per gynoecium; bracts conduplicate, unequally lobed, bract lobes ovate, with obtuse or acuminate apices, crispate to dentate and ciliate along margin, bract dorsal lobe $1.15 \times 0.7\text{--}0.8$ mm, bract ventral lobe $0.75\text{--}0.9 \times 0.4\text{--}0.5$ mm; bracteole obovate to ovate, margin dentate to dentate-ciliate mostly in the upper half of the bracteole, with slime papillae at the base, bracteole apex commonly with two prominent teeth and short sinus between (therefore obscurely emarginate). IKI reaction negative.

Differentiation. Among East Asian taxa, two species may be mistaken for *Porella japonica*. The first, *P. densifolia* (not known in the Russian Far East, but may be expected there) differs in leaf dorsal lobe upper halves narrowed that are triangular with truncate apex (versus generally obtuse to rounded apex in *P. japonica*), slightly larger leaf dorsal lobe cells (although measurements are greatly overlapping) with thin walls (versus walls obscurely thickened in *P. japonica*) and especially in the shape of leaf ventral lobes and underleaves those are greatly overlapping (covering up to the half of above) and rounded in the apices, versus variously toothed not or shortly overlapping, rarely entire-margined ventral lobes and underleaves, but then distant and obtuse in apices in *P. japonica*.

The second candidate for the misidentification is *Porella oblongifolia* that is characterized by considerable large leaf dorsal lobe cells (22–32 μm wide, versus 10–25 μm in *P. japonica*), linguulate to slightly falcate leaf dorsal lobes (versus ovate leaf dorsal lobes in *P. japonica*), yellowish green plant color (versus more deeply green colored plants in *P. japonica*) and considerable larger plants (2.3–4.8 mm wide versus 1.5–2.0 mm wide in *P. japonica*). Besides, the ventral leaf lobe is commonly longer decurrent, sometimes reaching 0.5 stem width in *P. oblongifolia*, versus decurrent less than 0.2 of stem width in *P. japonica*. The leaf dorsal lobes of *P. oblongifolia* are also commonly comparatively longer, with length exceeding the width by 1.4–1.9 times, while in *P. japonica*, the leaf lobes are only 1.1–1.2 times longer than wide or even as long as wide.

The study of available herbarium material (VBGI) collected in Japan, Republic of Korea and Vietnam identified by various bryologists reveals that along with the typical form to which the Far Eastern plants of *P. japonica* belong and which is described in many published studies (Hattori 1944, Inoue 1976, Bum et al. 2025), the plants with entire or almost entire ventral lobes and mostly entire and bilobed underleaves are also occurring across the species area (but were not found in the Far East). Such modifications Horikawa depicted for his illustration of *P. japonica* (Horikawa 1930). This modification (the status was not tested genetically) occurs in different sites of the species range and was observed by several authors (Kamimura 1952, Pócs 1968, Bum et al. 2025), but was differently treated. Kamimura (1952) treated it as a variety – *P. japonica* var. *pusilla* (Steph.) Kamim.; Pócs (1968) regarded as a form – *P. japonica* fo. *pusilla* (Steph.) Pócs. In any case, both authors agreed that *P. pusilla* (Steph.) S. Hatt. is not a species, but only a morphological variant within the variability of *P. japonica*. Hattori (1978) in his synopsis of Asiatic Porellaceae did not mention these combinations at all, and subsequently Yamada & Iwatsuki (2006) followed his conception. Later, the listed names were not maintained in the world checklist of liverworts (Söderström et al. 2016). *Porella japonica* is a morphologically malleable species, as was considered previously (Inoue 1955, Hattori 1967, Pócs 1968, Schuster 1980, etc.), and plants that differ from the typical form can be the result of adverse environmental conditions or may also reflect genetic differentiation. The latter was not resolved within the framework of the present account and requires further study.

Ecology. In the Russian Far East, the species occurs at 341–601 m a.s.l. in *Pinus koraiensis*-broadleaved forests in stream

valleys of northern stretching, where it covers the vertical surface of rocks and rocky blocks. In other parts of the species range, the ecology of the species is similar to that of the Far Eastern in the general traits, although with some additions. In Japan, the species also prefers various rocks (Horikawa 1930), often limestone rocks (Hara 1956) and tree trunks in evergreen and deciduous broadleaved forests (Inoue 1976). In the Republic of Korea, the species grows on shady surfaces of rocks and tree bases in mountains and valleys (Bum et al. 2025). Besides, as it is evident from our studied specimens and literature sources, in Japan, Korea, and Vietnam, sometimes species grows on trunks of living trees.

Distribution. Species has a pronounced, broadly East Asian distribution widely spreading to SE Asia, reaching the southernmost flank of insular Pacific Asia: Japan, Korea, China (Anhui, Sichuan, Taiwan), Vietnam, India (Panjab), Sumatra, Borneo, Philippines (Pócs 1968, Hattori 1978, Bum et al. 2025). According to the Global Biodiversity Information Facility (GBIF), there are several additional Chinese occurrences in Chongqing, Shaanxi, and Tibet (Yang & Zheping 2023, Teisher & Stimmel 2025), but they can be based on preliminary identifications and are not officially published. In Russia, the species was found only in the southernmost part of the Southern Sikhote-Alin Mts. (southern part of Primorye Territory) – Makarovsky Range.

Specimens examined: RUSSIA, PRIMORYE TERRITORY, Partizansky District, Sikhote-Alin Mts. (southern part), Makarovsky Range, upper course of Makarov Stream, *Pinus koraiensis*-broadleaved forest in stream valley (with dry stream bed), $43^{\circ}10'34.0''\text{N } 133^{\circ}27'13.5''\text{E}$, 585 m a.s.l., covering vertical surface of rocky block, mesic, in part shade, 24.09.2023, Klimova Prim-17-26-23 (VBGI); *ibid.* *Pinus koraiensis*-broadleaved forest in stream valley (with dry stream bed) with rocks and rocky outcrops along stream bed, $43^{\circ}10'28.9''\text{N } 133^{\circ}27'17.3''\text{E}$, 601 m a.s.l., covering vertical surface of rocky block, moist, in part shade, 24.09.2023, Klimova Prim-18-1-23 (VBGI); *ibid.* confluence of Pravyy Sobolyatnik and Levyy Sobolyatnik streams, $43^{\circ}10'25.6''\text{N } 133^{\circ}22'22.3''\text{E}$, 341 m a. s. l., 27.09.2024, Klimova Prim-33-21-24 (VBGI), coniferous (*Pinus koraiensis*, *Abies nephrolepis*)-broadleaved (*Acer*, *Ulmus*, *Juglans*, *Tilia*, etc.) forest in stream valley, covering vertical surface of rocks, mesic, in part shade; *ibid.* confluence of Pravyy Sobolyatnik Stream and its first left tributary, $43^{\circ}09'39.5''\text{N } 133^{\circ}23'43.3''\text{E}$, 486 m a.s.l., coniferous (*Abies nephrolepis*, *Picea ajanensis*, *Pinus koraiensis*)-broadleaved forest in stream valley, soil covering vertical surface of rocks, moist, in part shade, 27.09.2024, Klimova Prim-36-8-24 (VBGI); JAPAN, SHIKOKU, KOCHI PREF., between Maji and Yanase, Maji-mura, Aki-gun, 500 m a.s.l., on moist rocks along small stream, 20.11.1983 Inoue H. (VBGI, published in H. Inoue in Bryophyta Selecta Exsiccatae, under No. 770); HONSHU, SHIZUOKA PREF., Oi-gawa River, Oma dam, 16.07.1951, Takaki N. 10608 (VBGI); *ibid.*, KYOTO PREF., Kibune, $35^{\circ}07'18''\text{N } 135^{\circ}45'46''\text{E}$, 300–400 m a.s.l., broadleaved (evergreen and deciduous)-coniferous (*Cryptomeria*) mixed forest in the valley, moist cliffs in part shade, 02.2014, Bakalin J-3-27-14; TOTTORI PREF., Kouchi, Kouchi Shrine, Nosaka River valley, $35^{\circ}25'17''\text{N } 134^{\circ}05'28''\text{E}$, 171 m a.s.l., broadleaved (evergreen and deciduous) –coniferous (*Cryptomeria* and *Chamaecyparis*) mixed forest in the valley, tree trunk on slope to valley in part shade, 12.03.2013, Bakalin J-6-2-13 (VBGI); REPUBLIC OF KOREA, CHUNGCHŒONGNAM-DO, Nonsan-si, Beolgok-myeon, Surak-ri, Mt. Daedun, Surak valley, $36^{\circ}08'08.7''\text{N } 127^{\circ}18'21''\text{E}$, 319 m a.s.l., shaded rocks in *Zelkova-Betula* forest, 31.03.2009, Choi S.S. 3383 (VBGI, published in Hepaticae Korea Exsiccatae Fasc. 1, No. 27); JEOLLANAM-DO, Suin Forest Reservation, lower course of Suin Stream, $34^{\circ}43'17.1''\text{N } 126^{\circ}51'44.1''\text{E}$, 153 m a.s.l., broadleaved forest with some evergreen shrubs on northern

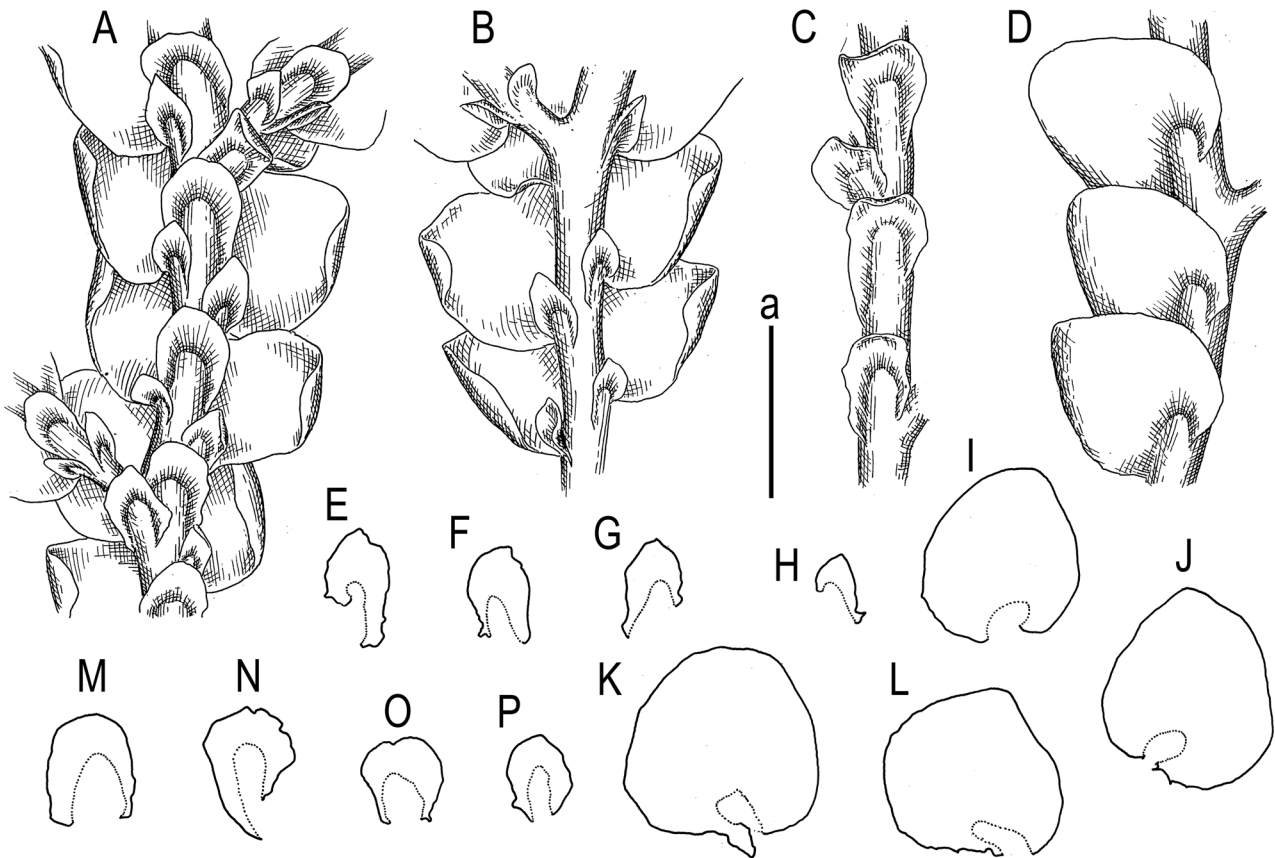


Figure 6 *Porella cordaeana* (Huebener) Moore: A – plant habit, fragment, ventral view; B – shoot, fragment, ventral view, underleaves detached; C – shoot, fragment, ventral view, dorsal ventral lobes detached; D – shoot, fragment, dorsal view, one row of dorsal lobes, ventral lobes, and underleaves detached; E–H – ventral lobes; I–L – dorsal lobes; M–P – underleaves. Scales: a – 2 mm, for all (A–C from Com-189-5-21, D–P from Com-189-6-21, VBGI)

slope of mountain, wetted stone near stream, 20.06.2009, Bakalin Kor-22-8-09 (VBGI); VIETNAM, LÀO CAI PROV., Sa Pa District, Hoàng Liên Sơn Range, Hoàng Liên National Park, one of the ways to the Phan Xi Păng Peak, 21°19'08.4"N 103°47'16.8"E, 2003 m a.s.l., evergreen south subtropical mountain forest in deep valley, mesic trunk of living tree, in part shade, 18.04.2017, Bakalin & Klimova V-4-72-17 (VBGI).

Porella cordaeana (Huebener) Moore, 1876, Rep. Irish Hepat.: 618. ≡ *Jungermannia cordaeana* Huebener, 1834, Hepaticol. Germ.: 291. (Figs. 6, 7)

Description. Plants prostrate to loosely ascending near apices, green to yellowish green, old material yellowish brownish in the herbarium, 40–60 mm long and 3.0–3.5 mm wide. Stem green to brownish-green and deep brown, regularly pinnately to bipinnately branched (branching of *Frullania*-type), 540–550 μm wide. Rhizoids virtually absent. Leaf dorsal lobe loosely imbricate (often covering not more than 1/4 of the leaf situated above), nearly plane or slightly convex with incurved apical part, orbicular ovate to broadly ovate, with obtuse, sometimes slightly narrowed apex, (1.1)1.25–1.3 × 1.7–2.1(2.2) mm, at dorsal side arcuately inserted and not or barely decurrent, margin entire to loosely crispate, sometimes with irregular 1–2 small teeth on wide base near dorsal lobe base, along dorsal leaf side with 3–4 slime papillae. Leaf ventral lobes distant, sometimes slightly undulate and/or revolute along margin (if to look from ventral side of the shoot), subparallel to the stem, 0.5–0.6 mm long and 0.65–0.8 mm wide, arcuately inserted, decurrent for 1–2 of stem widths ventrally, triangular ovate to obliquely ovate and obliquely triangular, with obtuse apex, commonly with wide irregular teeth at lobe bases (more often in decurrencies). Underleaves

distant, sinuately inserted, decurrent for 0.7–2.0(–3.0) of stem widths in the both sides, sometimes with very slightly recurved apex and/or margins, suborbicular, ellipsoidal, widely ovate to irregular in shape with obtuse to rounded apex, with entire to loosely crispate margins, 0.4–0.5 × 0.65–0.8(–1.0) mm. Cells in dorsal lobe middle shortly oblong to subsodiametric, 22.5–32.5(37.5) × 17.5–22.5 μm, with somewhat thickened walls, trigones convex; oil bodies 11–20 per cell, shortly oblong, homogenous. Dioicous. [Androecia not seen, the description is extracted from Damsholt (2002:593): “Male plants with terminal androecia at short lateral branches, androecia oblong-ovoid, spicate, composed by 2–9 pairs of strongly imbricate bracts, each bract is subequally bilobed, smaller than the leaves, long-keeled, saccate at base; subtending 1 antheridium; bracteole free”]. Gynoecia on short lateral branches, without pairs of sterile leaves below bracts; 3–7 archegonia per gynoecium; bracts conduplicate, unequally lobed, with dorsal one twice larger than ventral, with crispate margin, bract lobes ovate, with obtuse or acuminate apices, dorsal lobe 1.15 × 0.7–0.8 mm, ventral lobe 0.75–0.9 × 0.4–0.5 mm; bracteole obovate to ovate, dentate to dentate-ciliate mostly in the upper half of the bracteole, with slime papillae at the base; perianth 2.8–3.0 × 1.6–2.0 mm, with two lateral and one ventral keels, dorsiventrally compressed. IKI reaction positive.

The most morphologically similar and genetically related to *Porella cordaeana* taxon is *P. platyphylla*, also possessing an IKI positive reaction. The latter was the reason the specimens from Mednyi Island were originally mistakenly treated as a depauperate modification of *P. platyphylla*, erroneously regarding that the occurrence of *P. cordaeana* is hardly possible in the Far East. The main difference occurs in the ventral side of the shoots. The leaf ventral lobes of *P. cordaeana* are

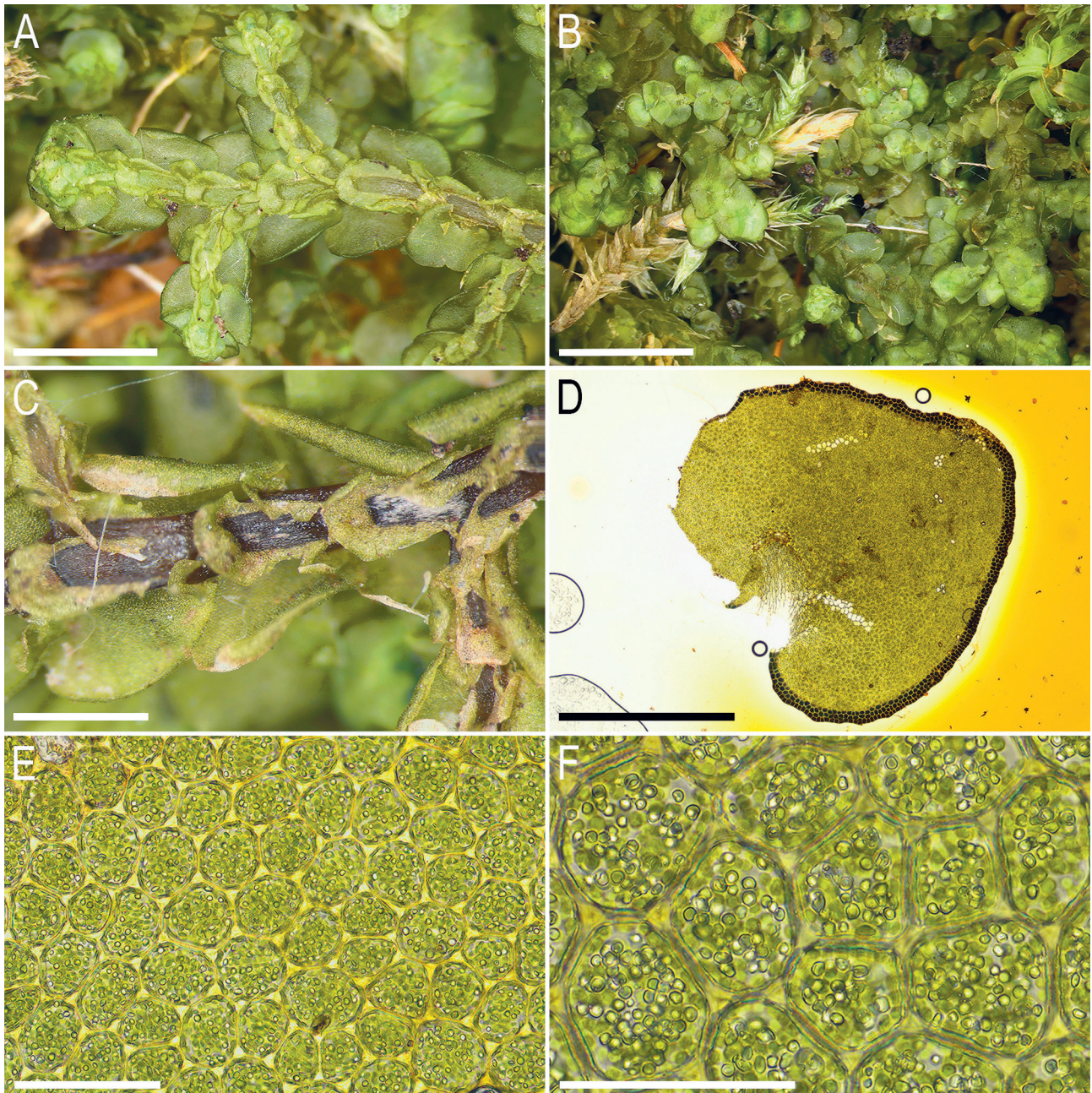


Figure 7 *Porella cordaeana* (Huebener) Moore: A – shoot, fragment, ventral view; B – part of a mat, dorsal view; C – fragment of shoot in mesic conditions, ventral view; D – dorsal lobe during positive IKI reaction process; E, F – oil bodies in midleaf cells. Scales: 3 mm for A; 5 mm for B, 1 mm for C; 1 mm for D; 50 μ m for E, F (A, B, D, E from Com-189-6-21, C, F from Com-189-5-21, VBGI)

triangular in the general outline (with some deviations), narrower than the stem and never overlapping above situated, while *P. platyphylla* is characterized by oblong to ellipsoidal ventral lobes, which are commonly overlapping. The same to a lesser extent concerns also the underleaf shape that is commonly narrower than the stem and not or hardly overlapping above situated in *P. cordaeana*, but wider than the stem and commonly overlapping in *P. platyphylla*.

Ecology. Outside of the Russian Far East, the species usually prefers various rocky substrates (including rocks and stones adjacent to rivers and streams), also tree trunks, tree trunk bases, open roots (Schljakov 1982, Paton 1993, Damsholt 2002, Bakalin 2018), rarely soil in humid places in broadleaved to coniferous communities. The habitat in Bering Island is somewhat outside of the ecological scope of the species described above. *Porella cordaeana* was collected on a steep south-facing forb meadow-covered slope on

humus with plant debris under the shade of forbs. The latter seems not to be the usual habitat for *Porella* species, but likely common for them in the Aleutian Arch. For instance, *P. cordaeana* and *P. fauriei* were also found in herb gully and on herb slope, correspondingly, in addition to cliff shelves on Attu Island (Falbot et al. 2018).

Distribution. The species is the most abundant in Europe and the west coast of North America, although several scattered localities are known in the rest of North America and Eurasia. In Europe, the species is widely distributed from north to south, reaching northern Africa, from the western extremes to the east, where it touches West Asia in Turkey and the Caucasus; also known in Central Asia (Hindu Kush Range) (Paton 1999, Damsholt 2002).

In North America, it occurs on the West Coast from the Aleutians to California and New Mexico (Alaska, Washington,

Oregon, California, Colorado, Nevada, Montana, Idaho, New Mexico) (Bakalin 2018, Talbot et al. 2018). In Russia, it is known from the North-West of the European part, the Caucasus, and the Khamar-Daban Range in southern Siberia (Konstantinova et al. 2009).

According to the data in GBIF, there is a specimen of *Porella cordaeana* collected in Chongqing Province of China by Gao Qian (高谦) in 1958 (Yang & Zheping 2023, <https://www.gbif.org/occurrence/4043569700>). The specimen is officially not published, was unavailable for our study, and it is difficult to guess whether it really belongs to *Porella cordaeana* or to another taxon.

Specimens examined: RUSSIA, KAMCHATKA TERRITORY, Commander Islands, northern part of Bering Island, vicinity of Nikolskoe Settlement, Nakovalnya Mt., forb vegetation on steep south-facing slope, 43°58'36"N 145°39'56"E, 10 m a.s.l., humus and plant debris shaded by forbs, mesic, 13.09.2021, Klimova & Bakalin, Com-189-4-21, Com-189-5-21, Com-189-6-21 (VBGI); *ibid.*, northern part of Mednyi Island, valley of temporary stream in 1.5 km of Preobrazhenka River mouth, 54°46'45"N 167°35'00"E, 50 m a.s.l., on wet stone in streambed of temporary stream, 02.07.2004, Bakalin K-53-16-04 (KPABG 106965, duplicate in VBGI).

DISCUSSION

Both studied species possess strikingly different distribution types from one another. Both findings show the liverwort flora of the Russian Far East is still imperfectly known; however, the further estimations are different.

The occurrence of tropical-subtropical broadly East Asian *Porella japonica* in the Southern Sikhote-Alin Mts. was quite unexpected. Especially, taking into account the practical reason that *Porella* taxa are quite large and are hardly overlooked in the collecting in the southern part of the Sikhote-Alin, which is the most studied part of these mountains that attracted bryologists for about the last 100 years (Gambaryan 1990). The Makarovsky Range, where the species was collected, is easy to access for botanical researchers, and maybe some studies of liverworts were conducted there. However, collected specimens were either not properly processed and/or were not published. At the plain view, it is difficult to estimate the qualitative landscape or geological differences between the Makarovsky Range and other ranges in the adjacent areas. In this respect, it is worth mentioning that during the preparation of the revision of Porellaceae in the Russian Far East (Bakalin & Klimova 2019), 412 specimens of *Porella* were studied; nevertheless, *P. japonica* was not found. This may suggest scattered distribution of *Porella japonica* within the southern flank of Primorye Territory, as with a number of other rare taxa in the Far East, such as *Chandonanthus birmensis* Steph. ex Schiffn. and *Xenochila integrifolia* (Mitt.) Inoue (Geltman 2024). *Porella japonica*, therefore, can be distributed very locally, in some small refugia within valleys of small streams, small river basins, or small mountain ranges. Before (Klimova & Bakalin 2024), we considered the Makarovsky Range as a home for the southernmost taxa of liverworts known in Russia, and called it the most 'southern' local liverwort flora in Russia. The finding of *P. japonica* confirms the Makarovsky Range as a 'hot spot' of taxonomic diversity for most of the southernmost liverwort taxa in Russia at the northern limit of their range as well.

Quite different estimations may be expected for *P. cordaeana*. Although we formally expected *Porella cordaeana* in the Russian Far East (Bakalin & Klimova 2019), its discovery on the Commander Islands is currently the northernmost location of *Porella* taxa known in the Far East (55°N). The results of the phylogenetic analysis show that the plants from Bering Island are genetically closer to the North American populations of *Porella cordaeana*. That may suggest the natural introduction of the species from the North American part of the area (e.g., from neighboring Aleutians), which is also confirmed by the robust gap of Commander Island populations from the other Eurasian occurrences. One of the issues for further exploration may be the identification of genetic relationships of South Siberian and Chinese (if the report cited above in Yang & Zheping (2023) is correct) populations that look equally distant both from the nearest occurrences westward and eastward.

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LITERATURE CITED

- Bakalin, V.A. 2018. *Bryophyte Flora of North America, Provisional Publication. Porellaceae* Cavers. Available from: <https://www.mobot.org/plantscience/BFNA/V3/Porellaceae.htm>. Last accessed 10.07.2025.
- Bakalin, V.A. & K.G. Klimova 2019. Porellaceae (Hepaticae) in the Russian Far East. *Botanica Pacifica* 8(1):105–131.
- Beck, H.E., T.R. McVicar, N. Vergopalan, A. Berg, N.J. Lutsko, A. Dufour, Z. Zeng, X. Jiang, A.I.J.M. van Dijk & D.G. Miralles 2023. High-resolution (1 km) Köppen–Geiger maps for 1901–2099 based on constrained CMIP6 projections. *Scientific Data* 10:724.
- Bum, H.M., S.J. Park, N. Yun, V.A. Bakalin & S.S. Choi 2025. Taxonomy of the genus *Porella* (Porellaceae, Marchantiophyta) on the Korean Peninsula. *Plants* 14:1260.
- Chen, Y.-S., T. Deng, Z. Zhou & H. Sun 2018. Is the East Asian flora ancient or not? *National Science Review* 5(6):920–932.
- Clement, M., Q. Snell, P. Walke, D. Posada & K. Crandall 2002. TCS: Estimating Gene Genealogies. In: *Proceedings of the 16th international parallel and distributed processing symposium, Washington, DC, USA, 15–19 April 2002*, p. 33, IEEE, Fort Lauderdale, FL, USA.
- Damsholt, K. 2002. *Illustrated flora of Nordic liverworts and hornworts*. Nordic Bryological Society, Lund: 840 pp.
- Fedosov, V.E., A.V. Fedorova, A.E. Fedosov & M.S. Ignatov 2016. Phylogenetic inference and peristome evolution in haplolepidous mosses, focusing on Pseudoditrichaceae and Ditrichaceae s.l. *Botanical Journal of the Linnean Society* 181:139–155.
- Feldberg, K., J. Váňa, J. Krusche, J. Kretschmann, S.D.F. Patzak, O.A. Pérez-Escobar, N.R. Rudolf, N. Seefelder, A. Schäfer-Verwimp, D.G. Long, ... & J. Heinrichs 2016. A phylogeny of Cephaloziaceae (Jungermanniopsida) based

- on nuclear and chloroplast DNA markers. *Organisms Diversity & Evolution* 16(4):727–742.
- Friedl, T. 1996. Evolution of the polyphyletic genus *Pleurastrum* (Chlorophyta): Inferences from nuclear-encoded ribosomal DNA sequences and motile cell ultrastructure. *Phycologia* 35:456–469.
- Gambaryan, S.K. 1990. History of the study of liverworts of the Far East. In: *Cryptogamic studies in the Far East* (L.N. Vasilieva et al., eds), pp. 141–148, Akademia Nauk SSSR, Dalnevostochnoe Otdelenie, Vladivostok (in Russian). [Гамбарян С.К. 1990. История изучения печеночных мхов Дальнего Востока // Криптогамические исследования на Дальнем Востоке / под ред. Л.Н. Васильевой и др. Владивосток: ДВО АН СССР. С. 141–148].
- Geltman, D.V. (ed.) 2024. *Red data book of the Russian Federation. Plants and fungi*. VNIИ "Экология", Moscow, 944 pp. (in Russian). [Красная книга Российской Федерации. Растения и грибы / отв. ред. Д.В. Гельтман. М.: ВНИИ "Экология". 944 с.].
- GloH2O. 2024. *Köppen-Geiger Global 1-km climate classification maps*. Available from: <https://www.gloh2o.org/koppen/>. Last accessed 26.11.2024.
- Hall, T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41:95–98.
- Hara, H. 1956. A review of *Porella* from Shikoku, southern Japan. *Research reports of Kochi University* 4(12):1–27.
- Hattori, S. 1944. Contributio ad Floram Hepaticaeum Astro-Kiushiensem. *Bulletin of the Tokyo Science Museum* 11:1–203 (in Japanese).
- Hattori, S. 1967. Studies on Asiatic species of the genus *Porella* (Hepaticae). I. Some little known Asiatic species of *Porella*. *Journal of the Hattori Botanical Laboratory* 30:129–151.
- Hattori, S. 1978. Studies on Asiatic species of the genus *Porella* (Hepaticae). VII. A synopsis of Asiatic Porellaceae. *Journal of the Hattori Botanical Laboratory* 44:91–120.
- Heinrichs, J., H.-P. Kreier, K. Feldberg, A.R. Schmidt, R.-L. Zhu, B. Shaw, A.J. Shaw & V. Wissemann 2011. Formalizing morphologically cryptic biological entities: New insights from DNA taxonomy, hybridization, and biogeography in the leafy liverwort *Porella platyphylla* (Jungermanniopsida, Porellales). *American Journal of Botany* 98(8):1252–1262.
- Hentschel, J., R.-L. Zhu, D.G. Long, P.G. Davison, H. Schneider, S.R. Gradstein & J. Heinrichs 2007. A phylogeny of *Porella* (Porellaceae, Jungermanniopsida) based on nuclear and chloroplast DNA sequences. *Molecular Phylogenetics and Evolution* 45(2): 693–705.
- Horikawa, Y. 1930. Studies on the Hepaticae of Japan. III. *Science Reports of the Tôboku Imperial University, Ser. 4, Biology* 5:623–650.
- Huson, D.H. & D. Bryant 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23:254–267.
- Inoue, H. 1955. Studies on the genus *Porella* (Hepaticae) in Chichibu-Okutama Area, Central Japan. *Bulletin of the Chichibu Museum of Natural History* 6:23–37 (in Japanese).
- Inoue, H. 1976. *Illustrations of Japanese Hepaticae*–2. Tsukiji Shokan Publishing Co., Tokyo. 193 pp. (in Japanese with English preface, foreword and figure legends).
- Kalyanamoorthy, S., B.Q. Minh, T.K.F. Wong, A. Von Haeseler & L.S. Jermini 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14:587–589.
- Kamimura, M. 1952. *Contributio ad floram Hepaticarum Shikokuensem*. Kochi, Seikando, 185 pp.
- Katoh, K. & D.M. Standley 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780.
- Klimova, K.G. & V.A. Bakalin 2024. Liverworts of the Makarovsky Range (Primorye Territory): apparently the most «southern» local liverwort flora in Russia. In: *Abstracts of the conference "Plants in Monsoonal Climate – X: East Asian plant gene pool and climate", September 24–28, 2024, Vladivostok, Russia*, p. 42, BGI FEB RAS, Vladivostok (in Russian) [Климова К.Г., Бакалин В.А. 2024. Печеночники Макаровского хребта (Приморский край): по-видимому, самая «южная» локальная гепатикофлора России // Тезисы докладов конференции «Растения в муссонном климате – X: Растительный генофонд востока Азии и климат», 24–28 сентября 2024 г., Владивосток, Россия. Владивосток: БСИ ДВО РАН. С. 33].
- Konstantinova, N.A., V.A. Bakalin, with contributions on regional floras from E.N. Andrejeva, A.G. Bezgodov, E.A. Borovichev, M.V. Dulin, Yu.S. Mamontov 2009. Checklist of liverworts (Marchantiophyta) of Russia. *Arctoa* 18:1–64.
- Kumar, S., G. Stecher, M. Suleski, M. Sanderford, S. Sharma & K. Tamura 2024. MEGA12: Molecular evolutionary genetic analysis version 12 for adaptive and green computing. *Molecular Biology and Evolution* 41:msae263.
- Leigh, J.W. & D. Bryant 2015. Popart: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6:1110–1116.
- Milyutina, I.A., D.V. Goryunov, M.S. Ignatov, E.A. Ignatova & A.V. Troitsky 2010. The phylogeny of *Schistidium* (Bryophyta, Grimmiaceae) based on the primary and secondary structure of nuclear rDNA internal transcribed spacers. *Molecular Biology* 44:883–897.
- Nakamura, Y. & P. Krestov 2005. Coniferous forests of the temperate zone of Asia. In: *Ecosystems of the World 6. Coniferous forests* (F. Andersson, ed.), pp. 163–220, Elsevier B.V., Amsterdam.
- Nguyen, L.-T., H.A. Schmidt, A. von Haeseler & B.Q. Minh 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32:268–274.
- Paton, J.A. 1999. *The liverwort flora of the British Isles*. Harley Books, Colchester, 626 pp.
- Pócs, T. 1968. The genus *Porella* in Vietnam. *Journal of the Hattori Botanical Laboratory* 31:65–93.
- Ronquist, F., M. Teslenko, P. van der Mark, D.L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M.A. Suchard & J.P. Huelsenbeck 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542.
- Schljakov, R.N. 1982. *The liverworts and hornworts of the North of the USSR. 5. Lophocoleaceae–Ricciaceae*. Leningrad, Nauka, 196 pp. (in Russian). [Шляков Р.Н. 1982. Печеночные мхи Севера СССР. 5. Лофоколеевые–Риччиевые. Ленинград: Наука, 196 с.].
- Schuster, R.M. 1980. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian, vol. 4*. Columbia University Press, New York and Guildford, Surrey, 880 pp.
- Söderström, L., A. Hagborg, M. von Konrat, S. Bartholomew-Began, D. Bell, L. Briscoe, E. Brown, D.C. Cargill, D.P. Costa, B.J. Crandall-Stotler, ... & R.L. Zhu 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59:1–828.
- Takhtajan, A.L. 1986. *Floristic regions of the world*. University of California Press, Los Angeles, London, 522 pp.

- Talbot, S.S., W.B. Schofield, J. Váňa & S.L. Talbot 2018. Liverworts from Attu Island, Near Islands, Aleutian Islands, Alaska (USA) with comparison to the Commander Islands (Russia). *Botanica Pacifica* 7(2):127–141.
- Teisher, J. & H. Stimmel 2025. *Tropicos MO specimen data*. Missouri Botanical Garden. Occurrence dataset. <https://www.gbif.org/occurrence/1261619213/>. Last accessed 25.02.2025. <https://doi.org/10.15468/hja69f>
- Templeton, A.R., K.A. Crandall & C.F. Sing 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132:619–633.
- Worldclim 2020–2025. Available from: <https://www.worldclim.org/>. Last accessed 17.07.2023.
- Wu, Z.Y. & S.G. Wu. 1996. A proposal for a new floristic kingdom (realm): the E. Asiatic Kingdom, its delineation and characteristics. In: *Proceedings of the First international symposium on floristic characteristics and diversity of East Asian plants* (Zhang, A.L. & S.G. Wu, eds), pp. 3–24, Chinese Higher Education Press, Beijing.
- Yamada, K. & Z. Iwatsuki 2006. Catalog of the hepatics of Japan. *Journal of the Hattori Botanical Laboratory* 99:1–106.
- Yang L. & X. Zheping 2023 *Contributions of plant specimen data inside China*. Chinese Academy of Sciences (CAS). Occurrence dataset. Available from: <https://www.gbif.org/occurrence/4043819838>, <https://www.gbif.org/occurrence/4044886425>, <https://www.gbif.org/occurrence/4044944906>, <https://www.gbif.org/occurrence/4045039874>, <https://www.gbif.org/occurrence/4044919338>, <https://www.gbif.org/occurrence/4045510460>, <https://www.gbif.org/occurrence/4043569700>. Last accessed 25.02.2025. <https://doi.org/10.15468/9us6fb>.

APPENDIX 1. The list of voucher details and GenBank accession numbers for the specimens used in the phylogenetic analysis in the present paper. The newly obtained sequences are marked in bold.

GenBank name	Accepted name	Specimen Voucher	GenBank Accession Number	
			ITS1–2 nrDNA	<i>rbcl</i> cpDNA
<i>Porella acutifolia</i> (Lehm. et Lindenb.) Trevis.	<i>Porella acutifolia</i> (Lehm. et Lindenb.) Trevis.	Indonesia, Gradstein 10311 (GOET)	-	EF545309
<i>Porella acutifolia</i> (Lehm. et Lindenb.) Trevis.	<i>Porella acutifolia</i> (Lehm. et Lindenb.) Trevis.	Papua New Guinea, Toia 212 (JE)	-	EF545310
<i>Porella arboris-vitae</i> (With.) Grolle	<i>Porella arboris-vitae</i> (With.) Grolle	Georgia, Zuendorf, 24757 (JE)	JF734465	-
<i>Porella arboris-vitae</i> (With.) Grolle	<i>Porella arboris-vitae</i> (With.) Grolle	Spain, Tenerife, Eckstein, 7110 (JE)	JF734466	-
<i>Porella caespitans</i> var. <i>cordifolia</i> (Steph.) S. Hatt. ex T. Katag. et T. Yamag.	<i>Porella caespitans</i> var. <i>cordifolia</i> (Steph.) S. Hatt. ex T. Katag. et T. Yamag.	China, Li et Wang 1301 (GOET)	-	EF545318
<i>Porella caespitans</i> var. <i>cordifolia</i> (Steph.) S. Hatt. ex T. Katag. et T. Yamag.	<i>Porella caespitans</i> var. <i>cordifolia</i> (Steph.) S. Hatt. ex T. Katag. et T. Yamag.	North Korea, Huneck K 86-12 (JE)	-	EF545317
<i>Porella caespitans</i> var. <i>nipponica</i> S. Hatt.	<i>Porella caespitans</i> var. <i>nipponica</i> S. Hatt.	China, Koponen 46872 (JE)	-	EF545314
<i>Porella campylophylla</i> (Lehm. et Lindenb.) Trevis.	<i>Porella campylophylla</i> (Lehm. et Lindenb.) Trevis.	Bhutan, Bhutan 10649 (JE)	-	EF545311
<i>Porella</i> cf. <i>campylophylla</i> (Lehm. et Lindenb.) Trevis.	<i>Porella</i> cf. <i>campylophylla</i> (Lehm. et Lindenb.) Trevis.	China, Long 34391 (E)	-	EF545308
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Germany, Heinrichs et al., 3767	JF734565	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Ahonen et Engblom 27 (H)	-	AY302457
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Austria, Heinrichs, 1437	JF734559	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Bulgaria, Huneck BG-H-85-4 (JE)	JF734560	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Canada, Brit. Columbia, Schofield et al., 100739 (F)	JF734561	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Czech Rep, Buryova, 4390 (DUKE)	JF734562	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	DL Erickson, Long, 35602 (DUKE)	-	EF590566
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	France, Frahm Bry. Vog. Exs. 97	JF734563	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Germany, Hentschel Bryo 01730 (GOET)	-	EF545287
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Germany, Hentschel, 2460	JF734564	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Italy, Raimondo, 117L (JE)	JF734568	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Poland, Bieszczady National Park, J. Szweykowski, 10311 (POZW)	-	KR014931
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Poland, Bieszczady National Park, K. Buczkowska, 42068 (POZW)	-	KR014932
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Russia, Russian Far East, Kamchatka Territory, Aleutsky District, Commander Islands, Bering Isl., K.G. Klimova & V.A. Bakalin, Com-189-4-21	PV344491	PV358606
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Russia, Russian Far East, Kamchatka Territory, Aleutsky District, Commander Islands, Bering Isl., K.G. Klimova & V.A. Bakalin, Com-189-5-21	PV344492	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	Tenerife, Eckstein, 2322 (JE)	JF734569	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	United Kingdom, British Isles, Long 34092 (E)	-	EF545286
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	USA, Alaska, F Schofield et Talbot, 98861	JF734571	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	USA, California, Norris, 72907	JF734578	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	USA, Montana, Vitt, 35492 (F)	JF734581	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	USA, Nevada, Shevock, 27633	JF734582	-
<i>Porella cordaeana</i> (Huebener) Moore	<i>Porella cordaeana</i> (Huebener) Moore	USA, Washington, Schofield et Harpel, 120651, (DUKE)	JF734584	-
<i>Porella grandiloba</i> Lindb.	<i>Porella grandiloba</i> Lindb.	Japan, Ohnishi 4741 (HIRO)	-	EF545299
<i>Porella grandiloba</i> Lindb.	<i>Porella grandiloba</i> Lindb.	North Korea, Huneck K 86-30 (JE)	-	EF545301
<i>Porella japonica</i> (Sande Lac.) Mitt.	<i>Porella japonica</i> (Sande Lac.) Mitt.	Japan, Deguchi 36624 (HIRO)	-	EF545300
<i>Porella japonica</i> (Sande Lac.) Mitt.	<i>Porella japonica</i> (Sande Lac.) Mitt.	Piippo 60751 (H)	-	AY302459
<i>Porella madagascariensis</i> (Nees et Mont.) Trevis.	<i>Porella madagascariensis</i> (Nees et Mont.) Trevis.	Sri Lanka, Eggers SL 7,05 (JE)	-	EF545315
<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	USA, Shevock, 31794 (GOET)	JF734585	-
<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	USA, Whittemore et Noyes 4393 (GOET)	-	EF545293

APPENDIX 1. Continued.

GenBank name	Accepted name	Specimen Voucher	GenBank Accession Number	
			ITS1-2 nrDNA	<i>rbcL</i> cpDNA
<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	<i>Porella navicularis</i> (Lehm. et Lindenb.) Pfeiff.	USA, Whittemore 4405 (GOET)	EF545481	EF545294
<i>Porella obtusata</i> (Taylor) Trevis.	<i>Porella obtusata</i> (Taylor) Trevis.	France, Asakawa, H-0001F (GOET)	JF734467	-
<i>Porella obtusata</i> (Taylor) Trevis.	<i>Porella obtusata</i> (Taylor) Trevis.	Greece, Samos, Düll, 24 (JE)	JF734468	-
<i>Porella perrottetiana</i> (Mont.) Trevis.	<i>Porella perrottetiana</i> (Mont.) Trevis.	Bhutan, Long 10727 (JE)	-	EF545306
<i>Porella perrottetiana</i> (Mont.) Trevis.	<i>Porella perrottetiana</i> (Mont.) Trevis.	Japan, Deguchi Bryophytes of Asia 4/96 (GOET)	-	EF545307
<i>Porella perrottetiana</i> (Mont.) Trevis.	<i>Porella perrottetiana</i> (Mont.) Trevis.	Japan, Yamaguchi 12583 (HIRO)	-	EF545305
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Bulgaria, Hentschel Bryo 0763 (GOET)	-	EF545290
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Canada, Schofield 106589 (UBC)	-	EF545297
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Canada, Williams et Cain s.n. (GOET)	-	EF545296
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	China, Gao et Fu, 399 (HSNU)	JF734587	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	France, Frahm, Bry. Vog. Exs. 120	JF734588	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Germany, Bavaria, Truderinger Wald, A. Sousa et J. Bechteler 14 M-0291459 (M)		MK478429
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Germany, Heinrichs, 840	JF734592	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Germany, Hentschel et Heinrichs, 3138	JF734598	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Germany, Hentschel Bryo 01567 (GOET)	-	AM392296, EF545289
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Italy, Eckstein 4632 (GOET)	EF545478	EF545291
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Poland, Stebel Hep. Polon. Exs. 317	JF734604	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	Switzerland, Huneck sn (JE)	JF734606	-
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	USA, Holmberg et Darigo 22 (GOET)	-	EF545295
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	USA, Schofield et al. 114561 (UBC)	-	EF547189
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	USA, Worthington 32690 (GOET)	-	EF545292
<i>Porella platyphylla</i> (L.) Pfeiff.	<i>Porella platyphylla</i> (L.) Pfeiff.	USA, Worthington, 32690a (GOET)	JF734607	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	Canada, Belland et al. 17828 (DUKE)	JF734608	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	Canada, Ireland, 23230 (F)	JF734616	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	Canada, Ley, 379 (GOET)	JF734615	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	Canada, Schofield, 89524 (F)	JF734612	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Bachmann, 416 (DUKE)	JF734636	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Breil, 6028 (DUKE)	JF734634	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Brown s.n. (GOET)	JF734637	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Churchill, 9221 (GOET)	JF734633	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Holmberg s.n. (GOET)	JF734627	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Majestyk, 5125 (DUKE)	JF734619	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Raabe, 2707 (GOET)	JF734631	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Risk, 1460 (DUKE)	JF734621	-
<i>Porella platyphylloidea</i> (Schwein.) Lindb.	<i>Porella platyphylloidea</i> (Schwein.) Lindb.	USA, Shaw, 4915 (DUKE)	JF734629	-
<i>Porella subobtusa</i> (Steph.) S. Hatt.	<i>Porella subobtusa</i> (Steph.) S. Hatt.	Japan, Deguchi et Yamaguchi Bryophytes of Asia 4/97 (HIRO)	-	EF545316
<i>Porella ulophylla</i> (Steph.) S. Hatt.	<i>Porella ulophylla</i> (Steph.) S. Hatt.	China, Zhu 20060122-1 (GOET)	-	EF545313
<i>Porella ulophylla</i> (Steph.) S. Hatt.	<i>Porella ulophylla</i> (Steph.) S. Hatt.	Japan, Honshu, Hiroshima, Shiwa, H. Tsubota 6020 (HIRO)	-	AB476577
<i>Porella ulophylla</i> (Steph.) S. Hatt.	<i>Porella ulophylla</i> (Steph.) S. Hatt.	Japan, Ibaraki, Tsukuba, Y. Inoue 8267 (TNS)	-	LC791194

APPENDIX 2. Phylogram obtained in a Maximum Likelihood (ML) analysis for the selected *Porella* taxa based on the *rbcL* cpDNA dataset. The values of bootstrap support from the ML analysis and Bayesian posterior probabilities greater than 0.50 (50 %) are indicated. Taxon names, GenBank accession numbers and vouchers are provided. Newly studied specimen is marked in red.

