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THE FAMILY PELLIACEAE (MARCHANTIOPHYTA) IN YAKUTIA AND AN APPROACH TO ITS DIFFERENTIATION IN RUSSIA

СЕМЕЙСТВО PELLIACEAE (MARCHANTIOPHYTA) В ЯКУТИИ И ПОДХОД К ДИФФЕРЕНЦИАЦИИ ВИДОВ, ИЗВЕСТНЫХ ИЗ РОССИИ

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Abstract

A revision of Yakutian specimens of the family Pelliaceae was carried out, with the focus to specimens previously attributed to *Pellia endiviifolia*. In addition to studying morphological traits, a molecular phylogenetic study was conducted for the first time, based on samples from different regions of Yakutia. It was established that three species of the Pelliaceae are common in Yakutia: *Apopellia alpicola, A. megaspora*, and *Pellia neesiana*. *Apopellia alpicola* occurs sporadically, both in the mountains and in lowland areas; no localities have been recorded in the Arctic Yakutia. *Apopellia megaspora* is widespread in Yakutia and represented by two haplotypes. The first haplotype is found in five localities in Yakutia, and was previously reported in Russia only on the Taimyr Peninsula. Worldwide, this haplotype is highly disjunctive, being also known from Northwestern North America (Alberta, Canada). The second haplotype has wider range in Russia and was previously known from North European Russia and South Siberia. It is first registered in Yakutia and found from single locality in the western part of the republic. The study does not confirm previous reports of *A. endiviifolia* from Yakutia. Its previous available collections from Yakutia in SASY were re-identified in *A. megaspora* and *A. alpicola*. *Apopellia alpicola* and *A. megaspora* might be confused in Yakutia with *A. endiviifolia, Pellia neesiana*, *P. epiphylla, Calycularia laxa* and *Aneura pinguis* (*A. maxima* phenotype). Key to them is prepared. The key characters are disposition of apical slime hairs, their shape and number of cells, length of cilia of pseudoperichaetium and its shape at the base, presence vs. absence of pluridichotomous thin apical proliferations or their vestiges, and costa/thallus width ratio. Descriptions and illustrations of Yakutian species of Pelliaceae are provided. Their differentiation, ecology and distribution are discussed.

Резюме

Проведена ревизия якутских образцов семейства Pelliaceae, с особым вниманием к образцам, ранее относимым к *Pellia endiviifolia*. В дополнение к изучению морфологических признаков, впервые проведено их молекулярно-филогенетическое исследование, основанное на образцах из разных районов Якутии. Установлено, что в Якутии распространены три вида семейства Pelliaceae: *Apopellia alpicola, A. megaspora* и *Pellia neesiana*. *Apopellia alpicola* встречается спорадически, как в горах, так и в равнинных районах. В арктической Якутии ее местонахождения не отмечены. *Apopellia megaspora* широко распространена в Якутии и представлена двумя генетически различными гаплотипами. Первый гаплотип распространен в мире крайне дизъюнктивно (Сибирь – Северо-Запад Северной Америки (Альберта, Канада)). Он обнаружен в Якутии в пяти местонахождениях, ранее в России он был известен только с Таймыра. Второй гаплотип имеет более широкий ареал в России и известен с Севера Европейской части и из Южной Сибири. В Якутии известен из одного местонахождения в западной части республики. Исследование не подтверждает предыдущие указания *A. endiviifolia* для Якутии. Все имеющиеся коллекции из Якутии в SASY переопределены как *A. megaspora* и *A. alpicola*. В Якутии *Apopellia alpicola* и *A. megaspora* можно спутать с *A. endiviifolia, Pellia neesiana, P. epiphylla, Calycularia laxa* и *Aneura pinguis* (*A. maxima* фенотип). Приводится ключ для дифференциации этих видов. Ключевыми признаками являются распределение, форма и количество клеток апикальных слизевых волосков, длина ресничек псевдоперихеция и его форма у основания, наличие или отсутствие многократно дихотомически ветвящихся тонких веточек либо их зачатков, отношение ширины ребра к ширине слоевища. Приведены описания и иллюстрации якутских видов Pelliaceae. Обсуждаются их отличия, экология и распространение.

KEYWORDS: *Apopellia, Calycularia, Pellia, Aneura*, key, liverworts, molecular phylogeny, morphology, ecology, new records, distribution, ITS1-2 nrDNA and *trn*L-F cpDNA.

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INTRODUCTION

The genus *Pellia* Raddi was described by Raddi (1818) and for a long time was considered as an integral group, with three species known for the flora of Russia: *Pellia epiphylla* (L.) Corda, *P. endiviifolia* (Dicks.) Dumort. and *P. neesiana* (Gottsche) Limpr. In 1974, Bauduin (1974) and then R. N. Shljakov (1976), drew attention to the peculiarity of the location and size of slime hairs at the growth point of these species: in *Pellia endiviifolia* they are located only on the ventral side of the thallus and are formed by several elongated cells, while in *P. epiphylla* and *P. neesiana* they develop on the dorsal and ventral side of the thallus and are very short, 2-celled. This character seemed convenient for distinguishing *P. endiviifolia* from *P. epiphylla* and *P. neesiana*. Taking this into account, Grolle (1983) distinguished *P. endiviifolia* as a separate subgenus *Apopellia* Grolle based on the following characters: 1) location of the slime hairs only on the ventral surface of the thallus *vs.* on both sides; 2) structure of the slime hairs, formed by 3–8 cylindrical cells, rather than 2 cells – short basal and club-shaped distal slime cell; 3) mature perichaetial pseudoperianth is tubular, longer than the calyptra, and not scale-like or ring-shaped, much shorter than the calyptra; 4) semiannular thickenings of the tangential walls of the inner layer of the capsule are absent (underdeveloped) *vs.* not complete or incomplete semiannular; 5) elaterophore with attached elaters, numerous, 80–100[150] and thin, 5–8 μm in diameter *vs.* with few, [(15)20 30(50)] and relatively thick, 15–25 μm in diameter.

In the molecular era, the reclassification of *Apopellia* as a separate genus opposite to former treatment as a section (Schuster, 1992) or as a subgenus (Grolle, 1983) of the genus *Pellia* was implemented by Schütz *et al.* (2016) based on molecular, morphological and biogeographical data, as well as on the ecology of the species. It revealed the separation of *Pellia* into two main clades, each of which corresponds to a morphologically clearly demarcated group. In this regard, two separate genera were recognized within Pelliaceae: the genus *Apopellia* (Grolle) Nebel & D. Quandt that includes, in addition to *A. endiviifolia* (Dicks.) Nebel & D. Quandt, two species known at that time only from North America as *A. alpicola* (L. Söderstr. *et al*.) Nebel & D. Quandt and *A. megaspora* (R.M. Schust.) Nebel & D. Quandt, and the genus *Pellia* with *P. appalachiana* R.M. Schust., *P. columbiana* Krajina & Brayshaw, *P. epiphylla* and *P. neesiana*. In addition to the above-described, according to Grolle (1983), distinctive features 1–5, Schütz *et al*. (2016) note the differences of *Apopellia* and *Pellia* in (6) the type of bordering cells of the antheridial chamber openings (inconspicuous in *Apopellia* and papilloid in *Pellia*), (7) the number of archegonia (up to 10 in *Apopellia* and from 10 to 30 in *Pellia*) and (8) their position (erect and horizontal or ascending), (9) structure of calyptra (smooth or with 2-celled hairs), and (10) structure of apical cell (wedge-shaped in *Apopellia* and semi-disciform in *Pellia*). The distribution of each species of *Apopellia* in the cold and temperate regions of the Holarctic was accurately studied from molecular and morphological evidence by Konstantinova *et al.* (2023). All species are presented by genetically different populations restricted to geographical localities (Schütz *et al.*, 2016; Sawicki *et al*., 2021; Konstantinova *et al*., 2023), who provide a number of molecularly tested localities of all *Apopellia* species in European and Asian Russia. In Russia, all three species occur: *A. alpicola* is presented by single haplotype, *A. megaspora* by two genetically distinct haplotypes, and *A. endiviifolia* by three haplotypes (Konstantinova *et al*., 2023), two of them accepted as cryptic species.

Despite the significant differences between the species of *Apopellia* and *Pellia*, the identification in a sterile state of species of this group known from Russia and Yakutia, particularly, was based on the presence of pluridichotomous narrow and rhizoid-free apical proliferations, characteristic of *Apopellia endiviifolia, vs.* their absence in *Pellia* species, on the position and structure of the slime hairs near the growth points, and on the ecological preferences. At the same time, the distribution of North American species passed the attention, since the plants in Yakutia were found without sporophytes and we relied upon distribution of slime hairs first of all.

Schütz *et al*. (2016), describing the distribution of the genus *Apopellia*, cite one locality of *Apopellia megaspora* for Russia from the vicinity of the village of Turukhansk on Yenisei River in the Krasnoyarsk Territory (the Lena River was erroneously indicated during the discussion). This location was assigned to *A. alpicola* by Konstantinova *et al*. (2023: 9). In addition, Schütz *et al*. (2016), based on the available literature data, show the distribution of *A. endiviifolia*, covering the entire territory of Russia and the entire territory of the Republic of Sakha (Yakutia).

The work of Konstantinova *et al*. (2023) makes a serious contribution to the understanding of the distribution of the genus and raises a number of questions. Demonstrating distribution of *A. megaspora* in Asian Russia just in southern Siberia and Taimyr, and *A. endiviifolia* in mountains of South Siberia (Altai) only, the authors remained open the question of the distribution of these species in Yakutia and the north of the Far East.

Taking abovementioned facts on differentiation and distribution of *Apopellia* into account, the goal of this study is to characterize morphology, ecology, and distribution of the genus *Apopellia* in Yakutia, paying special attention to their differentiation from each other, species of *Pellia* and *Apopellia endiviifolia*.

MATERIAL AND METHODS

Collections and specimens studied

All specimens stored in the herbarium SASY as *Pellia endiviifolia* were studied in detail with special attention to pluridichotomous apical proliferations or their vestiges. In addition, for the same purpose, specimens of *Apopellia endiviifolia* from LE collected during the sum-

mer months were examined. To understand the distribution of species of the family Pelliaceae and their association with the composition of rocks, all specimens of *P. neesiana* from SASY were also studied.

Morphological study

The study was focused on identifying the key differential characteristics of the species and included the study of thalli and pseudoperichaetia. Morphological description was based on the study of molecularly confirmed and morphologically similar specimens from Yakutia. To avoid misinterpretation, only specimens with pseudoperichaetia were involved in the study. Noteworthy, that work with dried specimens of Pelliaceae demands their slow and gradual wetering to restore structure of thalli and shape of pseudoperichaetia. The pseudoperichaetia of *Apopellia alpicola* and *A. megaspora* might be easily overlooked in dried or strongly wetered specimens.

Molecular study

Sampling for molecular analyses

Eight Yakutian specimens morphologically corresponded with the descriptions of some *Apopellia* species were tested with molecular genetic approach. Two molecular markers (ITS1-2 nrDNA and *trn*L-F cpDNA) were selected as appropriate barcodes follow to results of earlier studies (Schütz *et al*., 2016; Konstantinova *et al*., 2023), which demonstrated their ability to distinguish three known *Apopellia* species and even cryptic taxa in *A. endiviifolia*. Additionally, to produce the dataset for phylogenetic estimation and genetic variability we included GenBank accessions for 13 specimens of *A. megaspora*, six specimens of *A. endiviifolia* (presented by two cryptic species and a form) and five specimens of *A. alpicola* with nuclear and chloroplast data. *Pellia neesiana* from phylogenetically allied genus was selected as an outgroup. The list of specimens included into molecular estimation is shown in Appendix 1.

DNA extraction, amplification and sequencing

The DNA were extracted from dry parts of thalli with the HiPure SF Plant DNA Kit (Magen, China) according the manufacturer's protocol. Polymerase chain reaction 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. The pairs of primers for PCR were followed by White *et al*. (1990) for ITS1-2 and Taberlet *et al*. (1991) for *trn*L-F. The PCR-products were visualized on 1% agarose TAE gels by EthBr staining, cleaned with the Cleanup Mini Kit (Evrogen, Russia), and sequenced in 3730 Avant Genetic Analyzer (Applied Biosystems, USA) with the ABI Prism BigDye Terminator v. 3.1 Kit (Applied Biosystems, USA) following the standard protocol.

Phylogenetic analysis

The nucleotide sequence data for both DNA loci were assembled and alignments were produced in BioEdit 7.0.1 (Hall, 1999). Preliminary phylogenetic test of each ITS1-2 and *trn*L-F datasets did not reveal incongruence, thus phylogeny was reconstructed based on combined ITS1-2+*trn*L-F dataset. The length of total alignment consists of 1488 nucleotide positions: 881 positions belong to the ITS1-2, 607 to the *trn*L-F.

The ITS1-2+*trn*L-F dataset was analysed by the maximum likelihood (ML) method in the program IQ-TREE (Trifinopoulos *et al*., 2016) and the Bayesian approach (BA) in MrBayes v. 3.2.1 (Ronquist *et al*., 2012). The best fit evolutionary model of nucleotide substitutions for combined dataset was TIM2e+G4 that have been determined in program ModelFinder (Kalyaanamoorthy *et al*., 2017). The ultrafast bootstrapping procedure (Hoang *et al*., 2018) with 170 iterations was used for ML estimations. For the Bayesian analysis the GTR+I+G model was implemented; gamma distributions were approximated with four rate categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated chain, and the two starting trees were chosen randomly. The number of generations was one million. Trees were saved every 100th generation. The average standard deviation of split frequencies between two runs was 0.008825. The first 2500 (25%) trees were discarded in each run and 15000 trees from both runs were sampled after burn-in. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

The average pairwise *p*-distances for ITS1-2 and *trn*L-F of tested specimens and related accessions were estimated in Mega 11 (Tamura *et al*., 2021) using the pairwise deletion option for counting gaps.

Results

Molecular phylogenetic study

For eight *Apopellia* specimens from Yakutia were obtained ITS1-2 and *trn*L-F, as well for outgroup a specimen *Pellia neesiana*. Eighteen accessions newly generated in this study were deposited into GenBank (Appendix 1). The ML calculation resulted in a single tree with the arithmetic mean of Log likelihood -5152.723, the BA analysis means of Log likelihood for both sampled runs were -5036.61 and -5036.03, respectively. Obtained in both analytical procedures tree topologies became similar. The BA tree with indication of Bayesian posterior probabilities (PP) and bootstrap support (BS) values from ML analyses is shown in Fig.2. Eight tested specimens from Yakutia were found in two main clades: six specimens put with previously studied specimens of *A. megaspora* and two specimens with accessions of *A. alpicola*. As it was shown earlier, *A. megaspora* is characterized by clear intraspecific divergence with separation of "Alberta-Taimyr"-, "Russia"- and "U.S.A."-subclades (Konstantinova *et al*., 2023, Fig. 1). Only specimen B-02-01 was found here with accessions from "Russia"-subclade, whereas other five specimens (LC-25-01, TA 184, M-03-01, CD 37, V-TC-00-133) were placed with accessions from Taimyr attended to "Alberta-Taimyr"-

subclade (Fig. 1). The specimen B-02-01 provided variability 0.0-0.2% in ITS1-2 and identity of *trn*L-F to other specimens in corresponded subclade (Supplementary Materials, Table SM1). Other five tested Yakutian specimens of *A. megaspora* achieved variability 0-0.3% in ITS1-2 and 0-0.2% in *trn*L-F and provide similar divergence with two specimens from Taimyr. The divergence between specimen B-02-01 and other five Yakutian accessions counts 0.5-0.7% in ITS1-2 and 0.2-0.4% in *trn*L-F that fits well in level of divergences among both subclades nested two different haplotypes.

The rest two Yakutian specimens (UB-06-01 and I-L-02-01) were found in a clade of *A. alpicola* with relation to Russian accessions (Fig. 1). Previously the intraspecific divergence in *A. alpicola* was registered only between the Russian and U.S.A. populations (Konstantinova *et al.*, 2023, Fig. 1). Both Yakutian specimens are slightly varied only in ITS1-2 (0.1%) and in 0.0-0.2% differed from other Russian accessions in ITS1-2 with stability in *trn*L-F sequences (Supplementary Materials, Table SM2).

Morphological study

The results of the molecular study showed that two species of the genus *Apopellia*, i.e., *A. alpicola* and *A. megaspora*, occur on the territory of the republic. No pluridichotomous apical narrow and rhizoid-free apical proliferations or their vestiges characteristic of *A. endiviifolia* were found in the course of revision of extensive liverwort collections from Yakutia and regular field observations for over two decades. These facts together with the presence of pluridichotomous apical proliferations or their vestiges in summer rather than only in the autumn collections of *Apopellia endiviifoia* support its absence in Yakutia. According to our data, two species of *Apopellia* and one species of *Pellia* occur in Yakutia (Fig. 2).

Obtained data persuade us to provide amended descriptions of known from Yakutia species of *Apopellia* to facilitate further studies on their distribution in Russia. To keep data together we accomplished descriptions of Yakutian plants below by pertinent, from our point of view, previously published by Schuster (1981, 1992) and Konstantinova *et al*. (2023) data, presented in square brackets. We do not provide variable sizes of thallus cells described in the abovementioned papers because they can't be used as reliable distinctive characters.

TAXONOMY

Apopellia alpicola (R.M. Schust. ex L. Söderstr. *et al*.) Nebel & D. Quandt, 2016, Taxon 65(2): 230. — *Pellia alpicola* R.M. Schust. ex L. Söderstr. *et al*., 2013, Phytotaxa 76(3): 39. — *Pellia endiviifolia* subsp. *alpicola* R.M. Schust., 1991, J. Hattori Bot. Lab. 70: 145, nom. invalid (Art. 40.5; herbarium not specified).

Thallus [3]4–7[9] mm wide and 2–2.5 cm long, thin, sometimes translucent, from greenish, greenish-brown to dark brown or almost black. Thallus wings usually dark green to dark brown, sometimes furcate branched. Costa, as a rule, clearly demarcated from the wings, ca. 1/3 the thallus width (from 1/5 to 2/5, rarely up to 1/2). Slime hairs develop at the growth points only on the ventral side of the thallus, of 3–5 cells apart from the terminal slime papilla, shorter, when near the growth point, longer, when remote. Cells of the slime hairs ca. (20–) 24–32 × 45–95(–105) μm, length:width ratio ca. 2–3:1. Vegetative reproduction unknown.

Dioecious. Male plants unknown. Pseudoperichaetia cylindrical or very slightly oval, 0.9–1 mm in anterior part and extremely variable in posterior part, (0.2)1.8–2 mm that probably depends on their age and/or shade and moisture conditions (Fig. 3A). Pseudoperichaetium mouth ± lobulate-ciliate; the degree of lobation and development of cilia is extremely variable, but the length of uniseriate cilia does not exceed 5(8) cells (Figs. 3C–E). Outer surface of posterior part of the pseudoperichetium sometimes with cilia up to 5 cells long. Sporophytes unknown. The shape of pseudoperichaetia and the degree of development of their anterior part in *Apopellia alpicola* may vary. Sometimes, the anterior part is lacking or incomplete. In this case, it may be similar to the pseudoperichaetium of *A. megaspora* (Fig. 3B and Fig. 4C–D, respectively). However, if *A. alpicola* has an undeveloped anterior part, in *A. megaspora* the posterior part is often reduced. When *A. alpicola* was first found, Schuster (1991) described it as *Pellia endiviifolia* subsp. *alpicola* and distinguished it as a stabilized hybrid of *P. epiphylla* and *P. megaspora* due to often incomplete or lacking anterior part of pseudoperichaetium. So, the species might be confused with both known from Russia species of *Pellia*.

Distribution. Eastern North America from Alaska to California, and New Mexico, in high moutains southwards. In Russia, it was known from the Murmansk Region in NW European part and from Trans-Baikal Territory and republics of Buraytia and Tyva in South Siberia (Konstantinova *et al.*, 2023). In Yakutia, *Apopellia alpicola* occurs in altitudinal diapason from 20 m a.s.l., in the plains of Western Yakutia, to 1231 m a.s.l. in mountains of Eastern Yakutia.

Ecology. In previous reports, the species was described as nearly consistently growing in acidic areas and once found in basic site (Schuster, 1992) or found on neutral or slightly acidic sites (Konstantionova *et al*., 2023).The ecological preferences and distribution of the species in Yakutia complement the previously obtained data. In Yakutia, the species was recorded both on soil over acidic underlying rocks and over a mosaic cover, including outcrops of limestone, dolomite, and igneous rocks of basic composition, which expands the understanding of the ecological amplitude of the species. Recorded on the sand of the bank of a dry stream, on the soil in a forb-sedge meadow, on the soil on stone outcrops. It grows in pure turf or mixed with *Preissia quadrata* (Scop.) Nees and *Mesoptychia* spp.

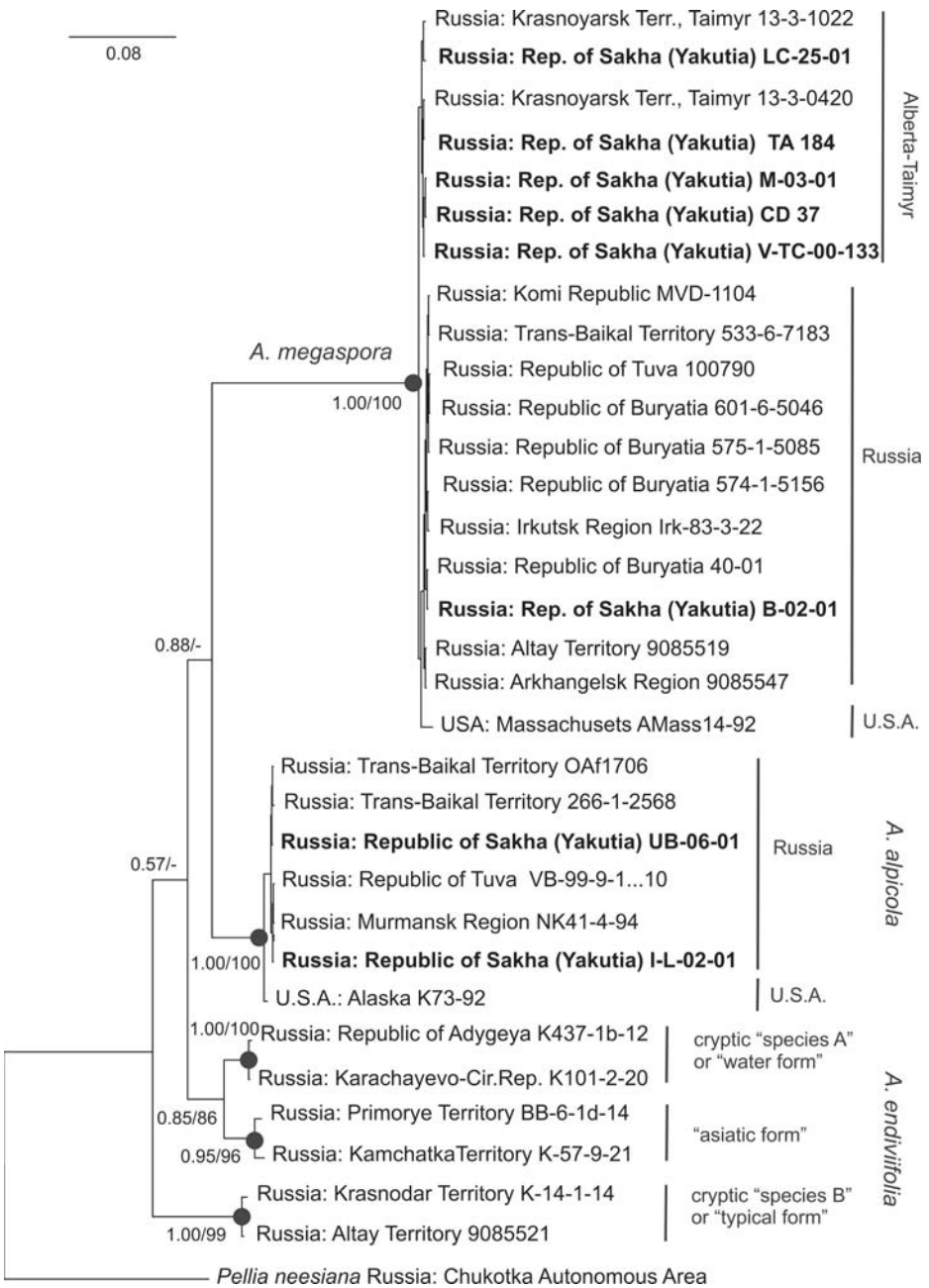

Fig. 1. The BA topology for the genus *Apopellia* reconstructed from combined ITS1-2+*trn*L-F dataset. Bayesian posterior probabilities and bootstrap supports from maximum likelihood more than 0.50 (50%) are indicated. The tested Yakutian specimens are in bold. The clade/subclades names follow to those in Konstantinova *et al*. (2023).

Specimens examined. Western Yakutia: Mirnyi District, Ulakhan-Botuobuya River middle reaches, vicinity of the Arbangda-Siene River Mouth, 62°08'N – 112°35'E, 296 m a.s.l., forb-sedge meadow along the river bank, on soil, with female plants, 14.VIII.2006, E.V. Sofronova (SASY UB-06-01, LE B-0029298), GenBank accession numbers: PZ379504 (ITS1-2 nrDNA), PZ377356 (*trn*L-F cpDNA). Eastern Yakutia: Kobyai District, Kuturginsky Range, Lena River middle reaches, Lyapiske River lower reaches, 64°42'N – 126°42'E, 295 m a.s.l., rocky outcrops along the bank of a dry stream, on fine earth, with female plants, 15.VII.2002, E.I. Ivanova (SASY I-L-02-01), GenBank accession numbers: PZ379503 (ITS1-2 nrDNA), PZ377355 (*trn*L-F cpDNA); Tompo District, Sette-Daban Range, Vostochnaya Khandyga River middle reaches, Siegennekh River lower reaches, 63.067973°N – 137.912667°E, 1070 m a.s.l., near a stream under melted snow, on soil, with female plants, 2.VIII.2017, M.S. Ignatov (SASY SD61).

Apopellia megaspora (R.M.Schust.) Nebel & D. Quandt, 2016, Taxon 65(2): 231. — *Pellia megaspora* R.M. Schust. 1981, J. Bryol. 11: 419, fig. 1–2.

Alive thalli quite tender, translucent, thin, dark green, sometimes with extensive reddish or reddish-violet pigmentation in the area of costa (Fig. 4A). Pigmentation is apparently initiated by harsh growth conditions in Yakutia. The thalli of dried specimens reddish-greenish to brown or black in the costa area, reddish-brown to dark brown in the wings. Costa massive, 2/5 to 1/2 of the thallus width, gradually transforms into the wings. Wings often fragile and only the axial part of the thallus, i.e., the costa area, often preserved. Thalli 5–9 mm wide and 2–2.5 [4–5] cm long, sometimes pseudodichotomously branched. Slime hairs only on the ventral side of the thallus at the growth

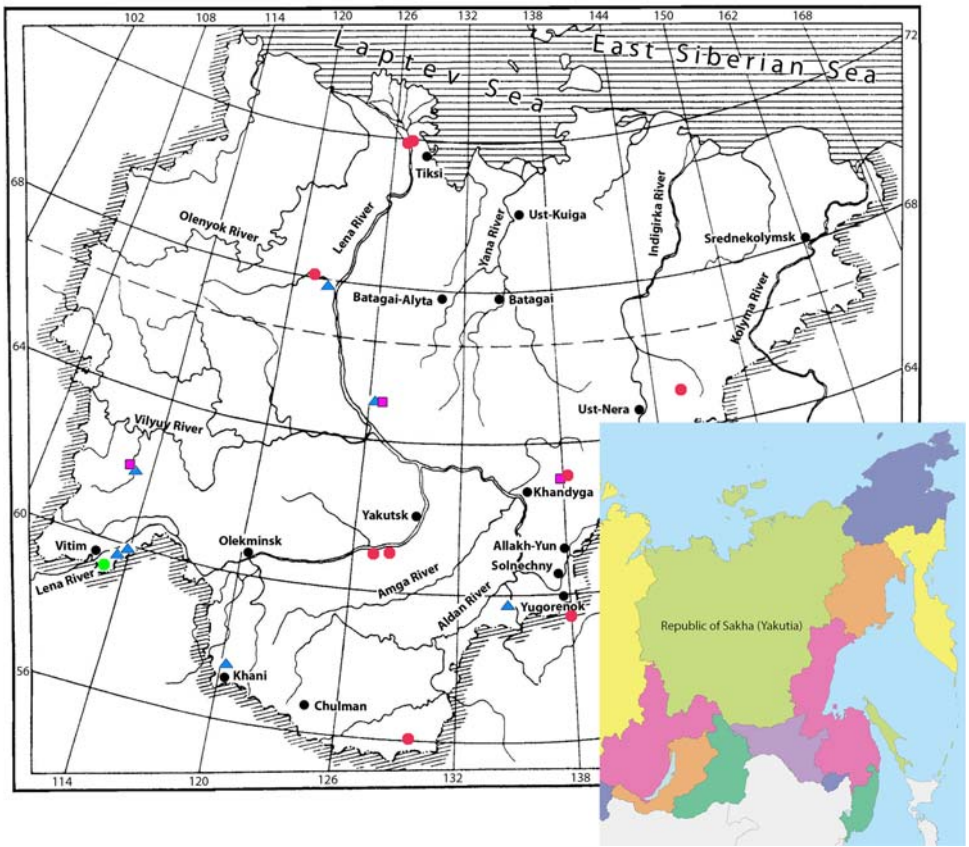

Fig. 2. Distribution of the Pelliaceae species in the Republic of Sakha (Yakutia), based on the Yakutian herbarium (SASY) specimens. *Apopellia alpicola* (pink squares), *A. megaspora* (red circles first haplotype, green circle second haplotype) and *Pellia neesiana* (blue triangles).

points, multicellular, of 2–5(6) elongated cells, apart from the terminal slime papilla; shorter and partly elongated when near the growth point, longer when remote from the growth point. Cells of the slime hairs ca. (22–)30–45×50–220[400–800] µm. Length:width ratio of cells of shorter slime hairs ca. 2.5–3:1, of long slime hairs 3–6[9]:1. Asexual reproduction unknown.

Dioicious. Antheridia in unclearly defined, rather small to broad and extensive groups (Fig. 4C). Pseudoperichaetia usually oval, extremely variable that may result from the growth conditions. Upon maturity and growth of thallus, pseudoperichaetia become more and more oval at the base (Fig. 4B; Schuster, 1981, Fig. 1: 6 or the same in Schuster, 1992, Fig. 850: 6). Its anterior part 1–2.5 mm high, while the posterior part usually about 2 mm high, subject to significant reduction over time, up to complete disappearance, leaving sometimes only single or two basal cilia attached directly to the thallus (Fig. 4E). Then only the anterior part of the pseudoperichaetium with 2–3 lobes and without cilia may remain on the thallus (Fig. 4D–F). In the case of a well-developed pseudoperichaetia, their mouth can be strongly incised-lobed and fringed and variably ciliate, with uniseriate from the base cilia 8–20 cells long, often with biseriate insertion above the base (Fig. 4G–H). On the outer surface of the posterior wall of pseudoperichaetium cilia sometimes up to 10 cells long. [Capsule spherical on very long, colorless stalk, 4-valved, 3–4 stratose. Spores almost smooth, exceedingly faintly granulate, their rather thin exine light brown, but spores green in aspect because of the chlorophyllose nature of the several (4–9) cells contained; spores large, ca. 64–77 × 100–115 up to 80 × 110–120 µm. Elaters variable, mostly contorted, (180)240–400(450) µm long × 9–14 µm in diam., 3–4-spiral; elater band 1.5–2 µm wide. Elater-bearers mostly 500–750 µm long × 9–16 µm in diam.; numerous (over 150 per caps.), (2)3–4-spiral]. The structure of the capsule is described by Schuster (1981, 1992) and Konstantinova *et al*. (2023).

Ecology. The ecological behavior of the species in Yakutia generally corresponds to that previously described. The species always occurs in associations with calciphilous liverworts and should be considered as calciphilous. Despite it, *Apopellia megaspora* was found in Yakutia not only in areas of distribution of calcium-containing rocks but also in locality where only acid soils were revealed, namely in Tit-Ary Island in the Lena River (Isaev, 2009). In Tit-Ary Island, *A. megaspora* is associated with *Aneura pinguis* (L.) Dumort., *Arnellia fennica* (Gottsche) Lindb., *Cryptocolea imbricata* R.M. Schust., *Jungermannia polaris* Lindb., *Mannia pilosa* (Hornem.) Frye et L. Clark, *Mesoptychia collaris* (Nees) L. Söderstr. et Váňa, *M. gillmanii* (Austin) L. Söderstr. et Váňa, *M. sahlbergii* (Lindb. et Arnell) A. Evans, *Peltolepis quadrata* (Saut.) Müll. Frib., *Preissia quadrata* (Scop.) Nees, etc. (Sofronova & Potemkin, 2016).

Apopellia megaspora usually occurs along water courses in a flood zone on soil, on soil over rocks. It

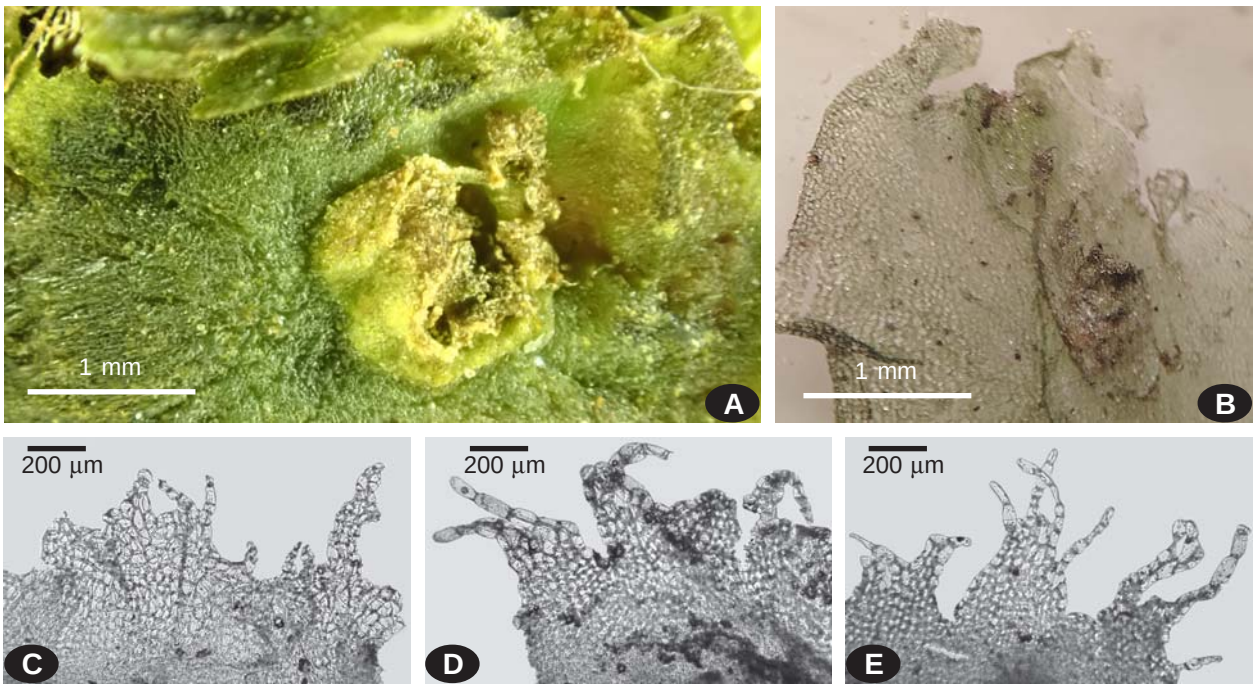

Fig. 3. *Apopellia alpicola*: (A: from Mirnyy District, Ulakhan-Botuobuya River, *Sofronova s.n.*, SASY UB-06-01, LE B-0029298; B–C: from Kobyai District, Lyapiske River, *Ivanova s.n.*, SASYI-L-02-01; D–E: from Tompo District, Siegennekh River, *Ignatov s.n.*, SASYSD61). A: pseudoperichaetium; B: pseudoperichaetium with incomplete anterior part of the mouth; C–D: pseudoperichaetium mouth, anterior parts; E: pseudoperichaetium mouth, posterior part.

often grows in pure mats or associated with *Conocephalum conicum* (L.) Dumort., *Marchantia latifolia* Gray, *Preissia quadrata, Mesoptychia* spp.

Distribution. **North America:** Western North America from Oregon to New Mexico; Eastern North America from Labrador to New York and westwards to Michigan and Minnesota. **Russia**: North European part from the Arkhangelsk Province and Republic of Komi; Siberia: Taymyr Peninsula (North of Krasnoyarsk Territory), North, Western and Eastern Yakutia, South Siberia (Trans-Baikal Territory and republics of Buraytia and Tyva) (Schütz *et al*., 2016; Konstantinova *et al*., 2023; this treatment). In Yakutia, *Apopellia megaspora* also occurs both in mountainous conditions and in the plains, having broader altitudinal range than *A. alpicola*, from 20 to 1231 m a.s.l.

Specimens examined. Northern Yakutia: Bulun District, Lena River Delta, Kharaulakhsky Range, 72°00.216'N – 127°07.977'E, 27 m a.s.l., cut bank of a stream, on the soil, with female plants, 24.VII.2009, E.V. Sofronova (SASY XY 174); Bulun District, Lena River Delta, Tit-Ary Island, 71°59'N – 127°02'E, 20 m a.s.l., cotton grass-moss tundra, on sand, with female plants, 29.VII.2009, E.V. Sofronova (SASY TA 184), GenBank accession numbers: PZ379508 (ITS1-2 nrDNA), PZ377360 (*trn*L-F cpDNA); Zhigansk District, Lena River lower reaches, Muna River middle reaches, 68°03'N – 121°27'E, 57 m a.s.l., bank of the Ese-Tirekhteekh stream, on the soil, 20.VIII.2003, with female plants, E.V. Sofronova (SASY M-03-01, LE B-0029299), GenBank accession numbers: PZ379507 (ITS1-2 nrDNA), PZ377359 (*trn*L-F cpDNA). Western Yakutia: Lensk District, Vitim River lower reaches, left bank of the Bystraya River near its mouth, 59°20.826'N – 112°52.843'E, 194 m a.s.l., cut bank of a stream, on soil, with female plants, 16.VIII.2002, E.V. Sofronova (SASY B-02-01), GenBank accession numbers: PZ379506 (ITS1-2 nrDNA), PZ377358 (*trn*L-F cpDNA). Central Yakutia: Khangalass District, Lena River middle reaches, Yuettiakh River Mouth, 61°04.773'N – 127°14.247'E, 110 m a.s.l., cut bank of a stream, on the soil, with female plants, 9.VII.2001, E.V. Sofronova (SASY); Khangalass District, Lena River middle reaches, right bank of the Oddokun River near the mouth, 61°13.042'N – 128°14.963'E, 129 m a.s.l., cut bank of a stream, on soil, 4.IX.2025, E.V. Sofronova (SASY LS-25-01), GenBank accession numbers: PZ379510 (ITS1-2 nrDNA), PZ377362 (*trn*L-F cpDNA). Eastern Yakutia: Tompo District, Sette-Daban Range, Vostochnaya Khandyga River middle reaches, Neprokhodimy Stream, 63°09'N – 138°06'E, 900 m a.s.l., stream bank, on the soil, with female plants, 8.VIII.2001, E.V. Sofronova (SASY); Tompo District, Sette-Daban Range, Vostochnaya Khandyga River middle reaches, Siegennekh River lower reaches, 63°03.410'N – 137°57.480'E, 513 m a.s.l., rocky outcrops along the river bank, on soil covered stones, with female and male plants, 19.VII.2015, E.V. Sofronova (SASY SD37, LE B-0029300), GenBank accession numbers: PZ379509 (ITS1-2 nrDNA), PZ377361 (*trn*L-F cpDNA); Tompo District, Sette-Daban Range, Vostochnaya Khandyga River middle reaches, Siegennekh River lower reaches, 63°03.736'N – 137°57.201'E, 555 m a.s.l., rocky outcrops along the stream bank, on soil, with female plants, 29.VII.2016, E.V. Sofronova (SASY SD54); Moma District, Ulakhan-Chistay Range, Moma River upper reaches, Tirekhtyakh River middle reaches, 64°52'46.8"N – 146°31'24.2"E, 1231 m a.s.l., bank of a stream flowing out of the mountain lake, on soil, with female plants, 14.VII.2018, E.V. Sofronova (SASY). Southern Yakutia: Ust-Maya District, Yudoma River middle reaches, Medvezhiy Creek near its mouth, 59°49'N – 138°01'E, 370 m a.s.l., bank of the stream, on soil, with female plants, 9.IX.2000, E.V. Sofronova (SASY); Neryungri District, Tokin-

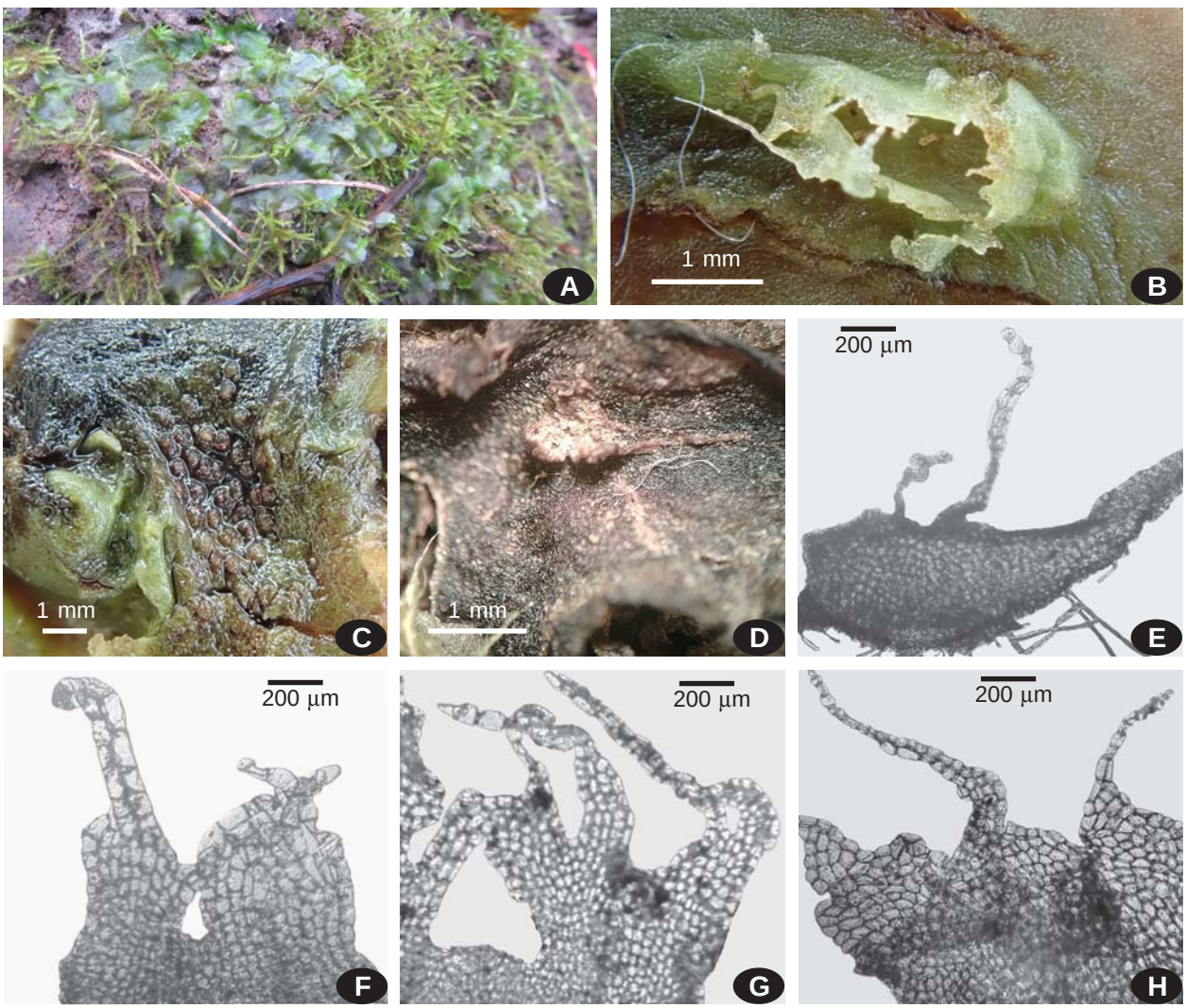

Fig. 4. *Apopellia megaspora*: (A: from Khangalass District, Oddokun River, *Sofronova s.n.*, SASY LS-25-01; B, D, H: from Zhigansk District, Muna River, *Sofronova s.n.*, SASY M-03-01, LE B-0029299; C: from Tompo District, Siegennekh River, *Sofronova s.n.*, SASY SD37, LE B-0029300; E: from Lensk District, Vitim River, *Sofronova s.n.*, SASY B-02-01; F–G: Bulun District, Lena River Delta, Kharaulakhsky Range, *Sofronova s.n.*, SASY XY 174). A: alive thalli on the soil of cut bank of a stream; B, D: pseudoperichaetia; C: androecium; E: two basal cilia attached directly to the thallus; F: anterior part of the pseudoperichaetiu mouth of *A. megaspora*, without posterior part; G–H: mouth of a well-developed pseudoperichaetium.

sky Stanovik Range, Tuksani River middle reaches, 56°03'N – 129°57'E, 750 m a.s.l., rocky outcrops along the stream bank, on soil in cracks, 4.VIII.2000, K.A. Volotovsky (SASY V-TS-00-133), GenBank accession numbers: PZ379505 (ITS1-2 nrDNA), PZ377357 (*trn*L-F cpDNA).

Pellia neesiana (Gottsche) Limpr., 1876, Krypt.-Fl. Schlesien 1: 329 – *Pellia epiphylla* f. *neesiana* Gottsche, 1867, Hedwigia 6: 69.

Thalli clear to pale or yellowish green, often purplish red along in the costal area, rather thin and translucent (particularly toward thallus margin). The thallus wings usually conspicuously undulate to sinuous. Thalli 6–8(9) to 9–12 mm wide and 1–3 cm long, strap-shaped, sporadically furcately branched. Thallus growth points on dorsal and ventral sides with 2-celled, short, colorless slime hairs, consisting of the basal cell and cell-like slime papilla. Asexual reproduction unknown.

Dioicous. Male thalli with elongated androecia with 2–3 rows of distinctly projecting purplish-red antheridial pouches. Female thalli with anteriory inclined subcylindric pseudopreichaetia about 3 mm long with ± crenulate mouth. [Calyptra more or less exserted beyond the mouth of the pseudoperichaetium at maturity. Capsule subspherical, blackish green, walls 2–3-layered, outer layer with nodular thickenings at the angles and sometimes also with intermediate nodular ones, inner cells with incomplete semiannular bands. Spores yellow-green, chlorophyllose, pluricellular due to endosporic germination, 50–66 × 70–100(116) µm, oval. Elaters 7–8 µm wide, long and slender, mostly bispiral; elaterophores 20–30, at base of the capsule].

Ecology. In Yakutia, the species is recorded both in areas with a variegated composition of underlying rocks, and in areas with widespread occurrence of calcium-containing rocks (Chabda River).

Distribution. Europe, Asia, North America, Greenland, Iceland. Everywhere in Russia. In Yakutia, it is most often recorded in plains. However, once it was found in the Udokan Range (Southern Yakutia) at 1070 m a.s.l. along the bank of a stream flowing from a mountain lake of glacial origin.

Specimens examined. Northern Yakutia: Zhigansk District, Lena River lower reaches, Muna River Mouth, 67°52'N – 123°°02'E, 29 m a.s.l., stream bank, on the soil, with female plants, 15.VIII.2003, E.V. Sofronova (SASY). Western Yakutia: Mirnyi District, Ulakhan-Botuobuya River middle reaches, Dyukku-Uulaakh lower reaches, 62°07'N – 112°40'E, 350 m a.s.l., stream bank, on the soil, with female plants, 16.VIII.2006, E.V. Sofronova (SASY); Lensk District, Pilka River upper reaches, near the mouth of the Ileyka River, 59°37.811'N – 113°23.479'E, 316 m a.s.l., river bank, on soil, with female plants, 21.VIII.2002, E.V. Sofronova (SASY); Lensk District, Pilka River middle reaches, Kudalakh River near the mouth, 59°43.000'N – 113°38.123'E, 309 m a.s.l., bank of a river channel, on soil, with female plants, 25.VIII.2002, E.V. Sofronova (SASY). Eastern Yakutia: Kobyai District, Kuturginsky Range, Lena River middle reaches, Lyapiske River lower reaches, 64°41'N – 126°16'E, 110 m a.s.l., bank of a stream, on soil, with male plants, 15.VII.2002, E.I. Ivanova (SASY). Southern Yakutia: Neryungri District, Udokan Range, Angara River upper reaches its mouth in Angara Lake, 57°18'N – 120°24'E, 1070 m a.s.l., stream bank, on soil, with male plants, 20.VII.2002, E.V. Sofronova (SASY); Ust-Maya District, Maya River lower reaches, Chabda River lower reaches, Chabda Nature Reserve, 59°45.741'N – 134°47.971'E, 177 m a.s.l., cut bank of a stream, on soil, 25.VIII.2001, E.V. Sofronova (SASY).

A KEY TO KNOWN FROM RUSSIA SPECIES OF *APOPELLIA, PELLIA, ANEURA* AND *CALYCULARIA LAXA*

1. Ventral scales present, narrow, 2–3-celled, at the base purplish red [or sometimes colorless], with short lateral outgrowth or slime papilla. Narrow female or broad male dorsal scales present on fertile thalli …….…… *Calycularia laxa*
— Ventral scales absent; instead of them, uniseriate slime hairs present on ventral or both sides of the growth points. Male and female gametangia without covering scales on dorsal surface of fertile thalli 2
2. Gametangia on main thallus. Purple pigmentation often present. Slime hairs on ventral side of the growth points, of several elongated cells, or on the both sides, short, 2-celled 3
— Gametangia on abbreviated lateral branches. Purple pigmentation absent. Slime hairs ventral, 1-celled, long ..... *Aneura pinguis*
3. Slime hairs elongated, on ventral side only 4
— Slime hairs short, on dorsal and ventral sides 6
4. Pluridichotomous apical narrow and rhizoid-free apical proliferations or their vestiges absent. Mature pseudoperichaetium oval to rounded at the base, to 2–2.5 mm high, with long uniseriate cilia of the mouth to 5(6) or 20-cells long 5
— Pluridichotomous apical narrow and rhizoid-free apical proliferations present. Mature pseudoperichatium ± rounded at the base, 3–5 mm high, with short, uniseriate, 1–2-celled teeth of the mouth .... *Apopellia endiviifolia*
5. Bases of mature pseudoperichaetia ± elongated and usually oval (Fig. 4B, D; see also Schuster, 1992: Fig. 850: 6); the posterior wall tends to be reduced; only two cilia may persist instead it. Uniseriate cilia of the mouth variable in length, longest from 8 to 20 cells long with often biseriate insertion above the base; often destroyed with age. Costa broad, 2/5–1/2 thallus width ..... *Apopellia megaspora*
— Bases of mature pseudoperichaetia ± rounded or very rare, when anterior part reduced, oval (Fig. 3A–B). Posterior part of pseudoperichaetium always present. Uniseriate cilia of the mouth shorter, longest to 5(6) cells long. Costa narrower, 1/5–2/5(1/2) thallus width ..... *Apopellia alpicola*
6. Dioicous. Pseudoperichaetium cylindric. Male thalli with strongly projecting and usually purple antheridial cameras along costa ..... *Pellia neesiana*
— Paroicous. Pseudoperichaetium scale-like. Antheridial cameras beyond perichaetium, slightly projecting, often not pigmented ..... *Pellia epiphylla*

DISCUSSION

The use of DNA barcodes allow to robustly determine *Apopellia* specimens and support new records of *A. alpicola* and *A. megaspora* for the Republic of Sakha (Yakutia). *Apopellia megaspora* appears to be more widely distributed species in the region and its specimens presented two genetically distinct haplotypes. The first haplotype is highly disjunctive (Siberia – northwestern part North Amenrica (Alberta, Canada)); it was previously known in Russia only from two localities in Taimyr (Konstantinova *et al*., 2023), but now it is additionally discovered from five localities in Yakutia. The second more widely distributed haplotype was known in the north of European Russia and South Siberia and now it is firstly registered in Yakutia. Both Yakutian specimens attended by integrative approach to *A. alpicola* support a genetic stability in Russian populations of this species, that are clearly diverged from the population from the U.S.A.

The present study revealed that the overlap of characters in sterile thalli is greater than previously shown (Schütz *et al*., 2016; Konstantinova *et al*., 2023). The Yakutian specimens have a stronger developed costa in *A. megaspora* that is getting most remarkable in thalli with fragile and destroyed wings. The anthocyanin pigmentation was equally recorded in both species. The shape of pseudoperichaetia depends much on many factors, for example, substrate moisture, shading, etc. In both species, the pseudoperichaetim may become much inclined, getting nearly horizontal (Figs. 3B; 4D).

No association with latitudinal and altitudinal gradients was noted. Both species can grow both on plains and in mountainous areas, and *Apopellia alpicola* has not yet been found in the Arctic territories, while *A. megaspora* grew in abundance on the island of Tit-Ary in the Lena River delta and the Kharaulakhsky Range. Numerous measurements of thalli and pseudoperichaetia persuade us to rely on shape of pseudoperichaetium and the length of its cilia as the only trustworthy characters. To grasp their variability see the descriptions and the key above.

Taking into account the broad range of *Apopellia alpicola* and *A. megaspora* together with their possible confusion with *A. endiviifolia*, *Pellia neesiana*, *P. epiphylla*, *Calycularia laxa* Lindb., and even *Aneura pinguis* (L.) Dumort. (*A. maxima* (Schiffn.) Steph. phenotype), which occur or may occur at least in southern or western Yakutia, approaches to their differentiation are important. The species of *Apopellia* and *Pellia* differ from *Aneura* Dumort. in the position of gametangia on main thallus (vs. on abbreviated lateral branches), slime hairs of several cells (vs. elongated 1-celled), at least partial presence of secondary, mainly purple, pigmentation of alive thalli (vs. lack of any pigmentation of alive thalli). The species of *Apopellia*, when sterile, may resemble *Calycularia laxa* that is distinguished from *Apopellia* in having purplish red ventral scales, 2–3-celled at the base, rather than colorless slime hairs. Differentiation of *Calycularia* from *Pellia* s.l. was discussed by Potemkin (1990, 1993) and Konstantinova & Mamontov (2010). *Apopellia endiviifolia* is easily distinguished from *A. alpicola* and *A. megaspora* when pluridichotomous, narrow and rhizoid-free, apical proliferations or their vestiges are present. Differentiation of the other species of *Apopellia,* as well as *Pellia* without pseudoperichaetia, is unreliable and not recommended because of considerable variation of characters of sterile thalli, ecological requirements and altitudinal distribution through the range. This fact persuades us to pay special attention to collecting time of *Apopellia* favorable for find of thalli with pseudoperichaetia. According to the collected specimens examined, the best time for *Apopellia* collecting in Yakutia is the second half of summer, since mid of July to the very beginning of September. This period and autumn are also favorable for collecting Pelliaceae with pseudoperichaetia in the European part of Russia, where the gynoecia and pseudoperichaetia begin to form in summer and mature capsules may be seen only in spring after snow melting. This might be easily observed in the European part of Russia but still impossible in Yakutia, where collecting places of *Apopellia* are remote and difficult to access in early spring.

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Appendix 1. The list of specimens included in molecular phylogenetic estimation with voucher details and GenBank accession numbers. Accessions obtained in this study are in bold.

Taxon	Specimen voucher	GenBank accession number	
		ITS1-2 nrDNA	*trn*L-F cpDNA
A. alpicola	Trans-Baikal Terr., *Afonina OAf1706* (KPABG-113953)	OQ832111	OQ817875
	Trans-Baikal Terr., *Mamontov 266-1-2568* (MHA)	OQ968335	OQ957420
	Tuva, *Bakalin VB-99-9-1...10* (KPABG-100916)	OQ832110	OQ817874
	Yakutia, *Ivanova s.n. 15.07.2002* (SASY I-L-02-01)	**PZ379503**	**PZ377355**
	Yakutia, *Sofronova s.n. 14.08.2006* (SASY UB-06-01)	**PZ379504**	**PZ377356**
	Murmansk, *Konstantinova NK41-4-94* (KPABG-1010)	OQ832113	OQ817877
	Alaska, *Konstantinova K73-92* (KPABG-124324)	OQ832112	OQ817876
A. endiviifolia			
	Adygeya, *Konstantinova K437-1b-12* (KPABG-115935)	OQ832118	OQ817882
	Karachayevo-Circassian, *Konstantinova K101-2-20*	OQ832116	OQ817880
	Primorye, *Borovichev BB-6-1d-14* (KPABG-119443)	OQ832114	OQ817878
	Kamchatka, *Bakalin K-57-9-21* (MHA-9085523)	OQ968339	OQ957424
	Krasnodar, *Konstantinova K-14-1-14* (KPABG-126669)	OQ832121	OQ817885
	Altay (MHA-9085521)	OQ968340	OQ957425
A. megaspora	Taimyr, *Fedosov 13-3-1022* (KPABG-116853)	OQ832100	OQ817864
	Komi, *Dulin MVD-1104* (KPABG-116783)	OQ832109	OQ817873
	Buryatia, *Konstantinova 40-01* (KPABG-102436)	OQ832102	OQ817866
	Tuva, *Otnyukova s.n.* (KPABG-100790)	OQ832101	OQ817865
	Buryatia, *Mamontov 574-1-5156* (KPABG-125753)	OQ832106	OQ817870
	Buryatia, *Mamontov 575-1-5085* (KPABG-125754)	OQ832107	OQ817871
	Buryatia, *Mamontov 601-6-5046* (KPABG-125755)	OQ832108	OQ817872
	Trans-Baikal, *Mamontov 533-6-7183* (KPABG-125752)	OQ832105	OQ817869
	Irkutsk, *Bakalin Irk-83-3-22* (VBGI)	OQ832104	OQ817868
	Yakutia, *Sofronova s.n. 04.09.2025* (SASY LC-25-01)	**PZ379510**	**PZ377362**
	Taimyr, *Fedosov 13-3-0420* (KPABG-116907)	OQ968336	OQ957421
	Massachusets, *AMass14-92* (KPABG-123492) topotype	OQ832103	OQ817867
	Altay (MHA-9085519)	OQ968337	OQ957422
	Arkhangelsk (MHA-9085547)	OQ968338	OQ957423
	Yakutia, *Sofronova s.n. 16.08.2002* (SASY B-02-01)	**PZ379506**	**PZ377358**
	Yakutia, *Sofronova s.n. 20.08.2003* (SASY M-03-01*)*	**PZ379507**	**PZ377359**
	Yakutia, *Sofronova s.n. 29.07.2009* (SASY TA 184)	**PZ379508**	**PZ377360**
	Yakutia, *Sofronova s.n. 19.07.2015* (SASY CD 37)	**PZ379509**	**PZ377361**
	Yakutia, *Volotovsky 04.08.2000* (SASY V-TC-00-133)	**PZ379505**	**PZ377357**
P. neesiana	Chukotka Autonomous Area, *15.08.1982* (LE)	**PZ406317**	**PZ410456**

Supplementary materials: Tables of p-distance values.
https://kmkjournals.com/upload/PDF/Arctoa/35/Arctoa_35_97_107_Tables_SM1_SM2.pdf