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HOW MANY TAXA ARE IN THE GENUS *SACCOBASIS* H. BUCH? EVIDENCE FROM INTEGRATIVE TAXONOMY

РОД *SACCOBASIS* H. BUCH, НЕОЖИДАННЫЙ РЕЗУЛЬТАТ ИНТЕГРАТИВНОГО ИЗУЧЕНИЯ

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Abstract

The genus *Saccobasis* is revised based on an integrative approach. The name *S. polymorpha* is synonymized with *S. polita* because neither molecular nor significant morphological differences were found between these taxa. At the same time, a group of *Saccobasis* specimens is proposed to be considered a new variety *S. polita* var. *arctica* as it forms a separate clade in constructed trees and differs morphologically from previously recognized taxa. Detailed descriptions of the species *S. polita* and its new variety are provided. The differences between *Saccobasis* and morphologically similar taxa, as well as the variability of the main features of the genus are considered. The characteristic features of *S. polita* var. *polita* and *S. polita* var. *arctica* are illustrated with photomicrographs, and the distribution of both taxa is pointed on a map.

Резюме

Проведена ревизия рода *Saccobasis* на основе интегративного подхода. Название *S. polymorpha* синонимизировано с *S. polita* поскольку не обнаружено ни молекулярных, ни существенных морфологических отличий между этими таксонами. При этом группу образцов, образующих отдельную кладу на построенных филогенетических древах и отличающихся рядом морфологических признаков, экологией и распространением, предложено рассматривать как отдельную разновидность *S. polita* var. *arctica*. Приводится подробное описание вида и новой разновидности, рассматриваются их отличия от морфологически сходных видов. Работа иллюстрирована фотографиями признаков *S. polita* var. *polita* и *S. polita* var. *arctica,* а также картой их точечного распространения.

KEYWORDS: Scapaniaceae, *Saccobasis*, molecular phylogeny, morphological variability, new variety *S. polita* var. *arctica*, distribution, ecology

INTRODUCTION

Saccobasis H. Buch is a small genus, including, depending on the interpretation, one or two species. The type species of the genus is *Saccobasis polita* (Nees) H. Buch, which was described as *Jungermannia polita* Nees from a specimen collected by Funk in Austria (Nees, 1836). The species was later attributed to the genus *Tritomaria* Schiffn. ex Loeske and until the beginning of the 21st century was considered by most authors to be a subgenus of the genus *Tritomaria* (Müller, 1906-16; Schuster, 1969; Paton, 1999; Damsholt, 2002). The concept of Buch (1933), who proposed to separate this species into a distinct genus *Saccobasis*, was shared by some Scandinavian (Arnell, 1956) and Russian (Schljakov, 1981; Konstantinova *et al.*, 1992, 2009) bryologists. In the era of molecular genetic research, it was shown that *Saccobasis* is not a representative of the genus *Tritomaria* and even belongs to a different family (Scapaniaceae), while most *Tritomaria* species are attributed to the Lophoziaceae (Vilnet *et al*., 2010).

The second taxon *Tritomaria polita* subsp. *polymorpha* R.M. Schust. was described by Schuster (1969) from Greenland, and was later elevated by Schljakov (1979) and Grolle (1983) to the species rank as *Saccobasis polymorpha* (R.M.Schust.) Schljakov and *Tritomaria polymorpha* (R.M.Schust.) Grolle, respectively. The first interpretation has recently been generally accepted (Söderström *et al*., 2016, Hodgetts *et al*., 2020). However, as Schuster (1988: 110) correctly pointed out, both Schljakov (1979) and Grolle (1983) who accepted this treatment "neither has seen any of the original material". Moreover, as Schuster (1988) emphasized both Schljakov (1979) and Grolle (1983), elevated ssp. *polymorpha* on the basis of a supposed gemmae difference, but the

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idea of differences in the shape of gemmae in these taxa was erroneous (see discussion). The purpose of our study is to revise the genus based on an integrative approach. Within this framework, along with morphological description and illustration of taxa, clarification of ecology and distribution we tried to reveal the genus' heterogeneity and find out whether there are differences in the haplotypes of specimens from different regions and how they correlate with morphologically accepted taxa.

MATERIAL AND METHODS

Taxa sampling

The morphological study is based on a revision of ca. 330 specimens of the genus preserved in KPABG. It is the largest collection of *Saccobasis* in Russia and probably in the world with specimens of the genus from almost all parts of its range apart western Europe and Greenland. For molecular phylogenetic analysis we selected specimens from different regions of Russia and Svalbard (Table 1). These specimens we studied more thoroughly, with a description of the main morphological features. We photographed some of the specimens by light microscopy using an Olympus BX-53 microscope and an Olympus MVX10 microscope equipped with Nikon D700 and Nikon D90 digital cameras, respectively. Data on oil-bodies is based on a study by the first author of a number of fresh specimens during a study of the hepatic flora of the Khibiny Mountains in the late 1970s.

The molecular phylogenetic study is based on twenty specimens from Svalbard, Murmansk and Kemerovo Provinces, Khanty-Mansi and Chukotka Autonomous Areas and Trans-Baikal and Kamchatka Territories. The ITS1-2 nrDNA and *trn*L-F cpDNA sequence data for sixteen specimens were obtained in this study, and four in our previous work (Yatsentyuk *et al*., 2004, Vilnet *et al*., 2010). Additionally, seventeen specimens were newly sequenced to complete the dataset for phylogenetic reconstructions. The voucher details and GenBank accession numbers for specimens tested here are listed in Table 1. The nucleotide sequence data for 34 accessions were downloaded from GenBank, their voucher details and accession numbers are marked in Fig.1.

DNA isolation, amplification and sequencing

DNA was extracted from herbarium specimens with the DNeasy Plant Mini Kit (Qiagen) according with manufacture's protocol. The primers suggested by White *et al*. (1990) were used to amplify the ITS1-2 loci, and primers from Taberlet *et al*. (1991) were used for *trn*L-F.

PCR was carried out in 20 µl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C, 60 s 72°C) and 2 min final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, then purified with Cleanup Mini Kit (Evrogen, Russia) and used as a template in sequencing reactions with the ABI PRISM® BigDye™ Terminator v. 3.1 Sequencing Ready Reaction Kit following the standard protocol provided for Applied Biosystems 3730 DNA Analyzer (Applied Biosystems, USA).

Phylogenetic analysis. Newly obtained nucleotide sequence data were assembled in the program BioEdit 7.0.1 (Hall, 1999) and after that were included in ITS1-2 and *trn*L-F datasets that were automatically aligned with the ClustalW tool and then manually corrected. Both dataset were tested separately for absence of incongruence and then were combined in a single ITS1-2+*trn*L-F dataset for subsequent analyses. All positions of the final dataset were taken into account, absent data were coded as missing.

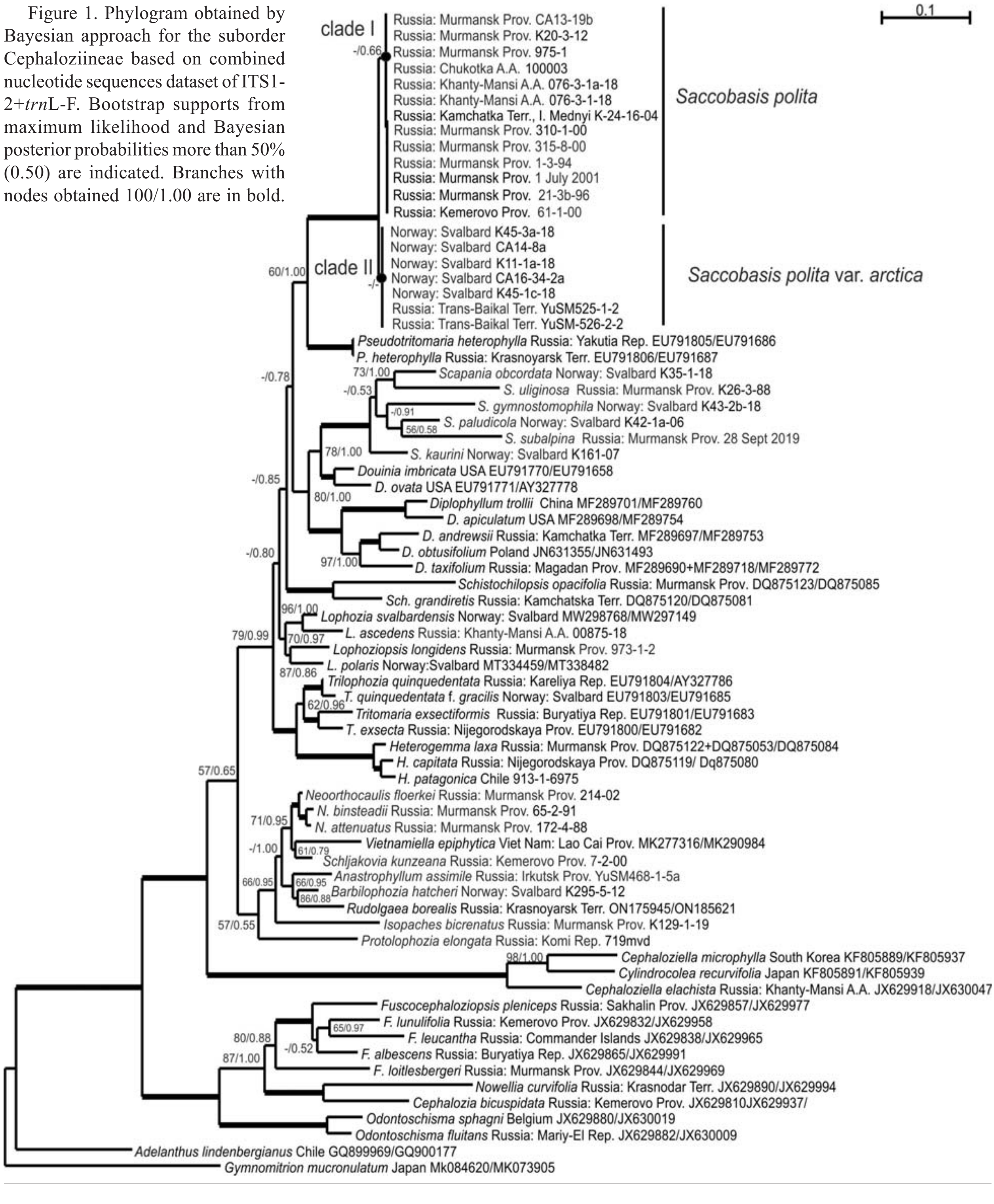
Two analytical procedures were used to estimate phylogeny: the maximum likelihood method (ML) with RaxML (Kozlov *et al.*, 2019) and the Bayesian approach (BA) with MrBayes v. 3.2.1 (Ronquist *et al*., 2012).The program ModelGenerator (Keane *et al*., 2006) determined the GTR+I+G model as the best-fit evolutionary model of nucleotide substitutions. This model was used in ML analysis together with four rate categories of gamma distribution to evaluate the rate of heterogeneity among sites and resampling procedure with 200 replicates and automatic bootstopping (cutoff: 0.030000) to obtain a bootstrap support for individual nodes. For the Bayesian analysis ITS1-2 and *trn*L-F partitions were separately assigned the GTR+I+G model as recommended by program's creators; gamma distributions were approximated with four rate categories. Two independent runs of the Metropolis-coupled ĔCMC 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, and trees were saved every 100 generation. Average standard deviation of split frequencies between two runs was 0.009672. The software tool Tracer 1.7 (Rambaut *et al*., 2018) revealed that the effective sample size is 1076.382 and auto-correlation time is 1672.4546 for our data. 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. A majority rule (MJ) consensus tree was calculated after combining the runs minus burn-in of 25% and the topology was illustrated with FigTree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

The infrageneric and infraspecific variability of ITS1-2 and *trn*L-F were calculated as the average pairwise *p*-distances in Mega 11 (Tamura *et al*., 2021) using the pairwise deletion option for counting gaps.

Ecology and distribution

Ecology and distribution were evaluated mostly on the basis of data from labels of specimens deposited in KPABG and available in L. (former CRIS, http://isling.org/hepatics). Coordinates of localities in many labels were provided based on GPS measurements as it is indicated on the labels, otherwise they were assigned

Figure 1. Phylogram obtained by Bayesian approach for the suborder Cephaloziineae based on combined nucleotide sequences dataset of ITS1-2+*trn*L-F. Bootstrap supports from maximum likelihood and Bayesian posterior probabilities more than 50% (0.50) are indicated. Branches with nodes obtained 100/1.00 are in bold.



using maps and the descriptions of localities. Distribution data outside Russia and Svalbard were taken from the literature (Schuster, 1969, 1988; Paton, 1999; Damsholt, 2002, 2013) and data from the Global Biodiversity Information Facility (GBIF). On the constructed distribution map various symbols indicate the locations based on herbarium material, as well as the locations from trustworthy publication and locations from GBIF.

RESULTS

Molecular study

ITS1-2 nucleotide sequence data were obtained for 32 specimens and *trn*L-F – for 33 specimens, totally 65 newly generated accessions were deposited in GenBank.

The combined ITS1-2+*trn*L-F alignment for 71 specimens consists of 1555 sites, 1026 of them belong to ITS1-2, 529 to *trn*L-F.

Table 1. Specimens studied in molecular-phylogenetic analyses with GenBank accession numbers.

Taxa	Specimen voucher	nrITS1-2	*trn*L-F
Anastrophyllum assimile (Mitt.) Steph.	Russia: Irkutsk Prov., Yu. Mamontov, YuSM468-1-5a, 120896 (KPABG)	OP584689	OP573528
Barbilophozia hatcheri (A. Evans) Loeske	Norway: Svalbard, N. Konstantinova, K295-5-12 (KPABG)	OP584690	OP573529
Heterogemma patagonica (Herzog & Grolle) L. Söderstr. & Váňa	Chile, Yu. Mamontov, 913-1-6975 (MHA)	OP584684	OP573523
Isopaches bicrenatus (Schmidel ex Hoffm.) H. Buch	Russia: Murmansk Prov., N. Konstantinova, K129-1-19 (KPABG)	OP584691	OP573530
Lophozia ascendens (Warnst.) R.M. Schust.	Russia: Khanty-Mansi A.A., E. Lapshina, 00875-18, 122294 (KPABG)	OP584682	OP573521
Lophoziopsis longidens (Lindb.) Konstant. & Vilnet	Russia: Murmansk Prov., A. Vilnet, 973-1-2, 125223 (KPABG)	OP584683	OP573522
Neoorthocaulis attenuatus (Mart.) L. Söderstr., De Roo & Hedd.	Russia: Murmansk Prov., N. Konstantinova, 172-4-88 (KPABG)	OP584687	OP573526
N. binsteadii (Kaal.) L. Söderstr., De Roo & Hedd.	Russia: Murmansk Prov., N. Konstantinova, 65-2-91 (KPABG)	OP584686	OP573525
N. floerkei (F. Weber & D. Mohr) L. Söderstr., De Roo & Hedd.	Russia: Murmansk Prov., N. Konstantinova, 214-02, 9566 (KPABG)	OP584685	OP573524
Protolophozia elongata (Steph.) Schljakov	Russia: Komi Rep., M. Dulin, 719mvd (KPABG)	OP584692	OP573531
Saccobasis polita (Nees) H. Buch (det. as *polymorpha*)	Russia: Chukotka A.A., E. Kuzmina, 100003 (KPABG)	OP584664	OP573502
S. polita	Kamchatka Terr. I. Mednyi, V. Bakalin, K-24-16-04, 106564 (KPABG)	OP584669	OP573507
S. polita	Russia: Kemerovo Prov., N. Konstantinova, 61-1-00, 101870 (KPABG)	EU791809	EU791690
S. polita (det. as *polymorpha*)	Russia: Khanty-Mansi A.A., E. Lapshina, 076-3-1a-18, 122280 (KPABG)	OP584665	OP573503
S. polita (det. as *polymorpha*)	Russia: Khanty-Mansi A.A., E. Lapshina, 076-3-1-18 (KPABG)	OP584666	OP573504
S. polita	Russia: Murmansk Prov., N. Konstantinova, K20-3-12 (KPABG)	OP584662	OP573500
S. polita (det. as *polymorpha*)	Russia: Murmansk Prov., A. Vilnet, 975-4, 125237 (KPABG)	OP584663	OP573501
S. polita	Russia: Murmansk Prov., N. Konstantinova, 310-1-00, 8167 (KPABG)	OP584667	OP573505
S. polita (det. as *polymorpha*)	Russia: Murmansk Prov., N. Konstantinova, 1-3-94, 8211 (KPABG)	OP584668	OP573506
S. polita (det. as *polymorpha*)	Russia: Murmansk Prov., A. Savchenko, CA13-19b (KPABG)	OP584661	OP573499
S. polita (det. as *polymorpha*)	Russia: Murmansk Prov., N. Konstantinova, 315-8-00, 8247 (KPABG)	EU791808	EU791689
S. polita (det. as *polymorpha*)	Russia: Murmansk Prov., N. Konstantinova, 21-3b-96, 6189 (KPABG)	EU791807	EU791688
S. polita	Russia: Murmansk Prov., V. Bakalin, 1 July 2001 (KPABG)	No data	AF519194
Saccobasis polita (Nees) H.Buch var. *arctica* Konstant., Vilnet, Mamontov	Norway: Svalbard, N. Konstantinova, K11-1a-18, 123564 (KPABG)	OP584672	OP573510
S. polita var. *arctica*	Norway: Svalbard, N. Konstantinova, K45-1c-18, 123658 (KPABG)	No data	OP573511
S. polita var. *arctica*	Norway: Svalbard, N. Konstantinova, K45-3a-18, 123662 (KPABG)	OP584670	OP573508
S. polita var. *arctica*	Norway: Svalbard, A. Savchenko, CA16-34-2a (KPABG)	OP584673	OP573512
S. polita var. *arctica*	Norway: Svalbard, A. Savchenko, CA14-8a (KPABG)	OP584671	OP573509
S. polita var. *arctica*	Russia: Trans-Baikal Terr., Yu. Mamontov, YuSM525-1-2, 119591 (KPABG)	OP584674	OP573513
Saccobasis polita var. *arctica*	Russia: Trans-Baikal Terr., Yu. Mamontov, YuSM-526-2-2 (KPABG)	OP584675	OP573514
Scapania gymnostomophila Kaal.	Norway: Svalbard, N. Konstantinova, K43-2b-18 (KPABG)	OP584678	OP573517
Scapania kaurini Ryan	Norway: Svalbard, N. Konstantinova, K161-07 (KPABG)	OP584681	OP573520
Scapania obcordata (Berggr.) S.W.Arnell	Norway: Svalbard, N. Konstantinova, K35-1-18 (KPABG)	OP584676	OP573515
Scapania paludicola Loeske & Müll. Frib.	Norway: Svalbard, N. Konstantinova, K42-1a-06 (KPABG)	OP584679	OP573518
Scapania subalpina (Nees ex Lindenb.) Dumort.	Russia: Murmansk Prov., N. Konstantinova, 28.09.2019 (KPABG)	OP584680	OP573519
Scapania uliginosa (Lindenb.) Dumort.	Russia: Murmansk Prov., N. Konstantinova, K26-3-88 (KPABG)	OP584677	OP573516
Schljakovia kunzeana (Huebener) Konstant. & Vilnet	Russia: Kemerovo Prov., N. Konstantinova, 7-2-00, 101767 (KPABG)	OP584688	OP573527

Table 2. The value of *p*-distances, ITS1-2/*trn*L-F, % for the genera *Saccobasis* and *Pseudotritomaria heterophylla.*

Taxon	Variability within taxa	Variability between taxa		
		S. polita var. polita	*S. polita var. arctica*	*P. heterophylla*
Saccobasis polita	0.2/0.0			
S. polita var. arctica	0.3/0.0	1.0/0.6		
P. heterophylla	0.1/0.0	8.0/9.7	8.9/9.1	

The ML calculation resulted in a single tree with the arithmetic means of Log likelihood –19549.34, in the BA analysis for both sampled runs were –19313.96 and –19309.51, respectively.

In both calculations trees with common topology were obtained, thus the BA topology was selected to illustrate phylogenetic affinities and presented in Fig. 1 with indication of bootstrap support (BS) values from ML analyses and Bayesian posterior probabilities (PP) from BA. The topology for suborder Cephaloziineae obtained here is in agreement with previous publications (Vilnet *et al.*, 2010; Feldberg *et al.*, 2013), but the family Lophoziaceae appears to be polyphyletic.

Twenty accessions from the genus *Saccobasis* have a highly supported terminal position (BS=100%, PP=1.00) in the family Scapaniaceae with a sister relation to the genus *Pseudotritomaria* Konstant. & Vilnet (BS=60%, PP=1.00). Two clades could be recognized within *Saccobasis*: the first one included thirteen specimens from Murmansk and Kemerovo Provinces, Khanty-Mansi and Chukotka Autonomous Areas and Kamchatka Territory (PP=0.66), the second five specimens from Svalbard and

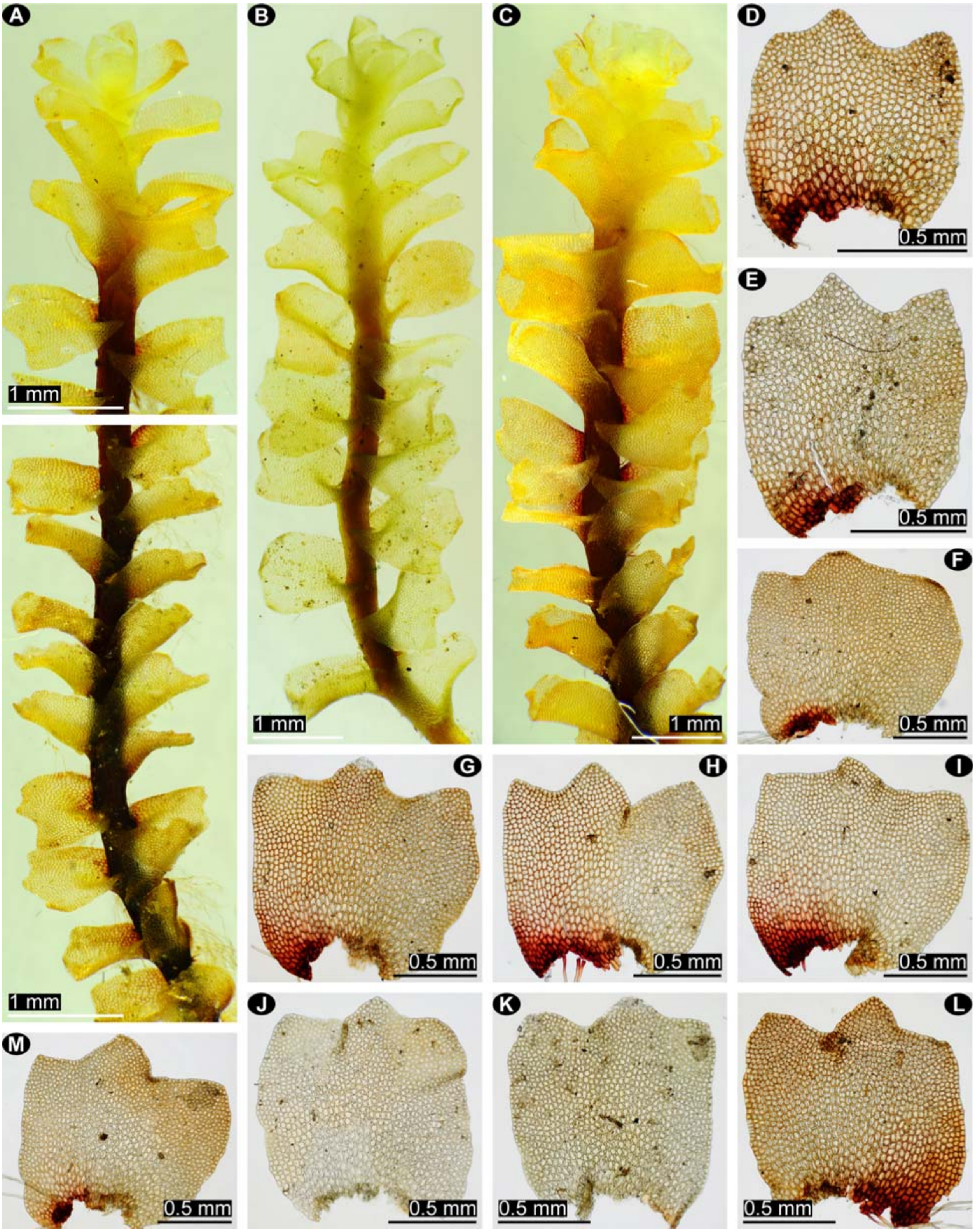


Fig. 2. *Saccobasis polita*: A-C – habit. D-M – leaves. All from *Bakalin 01.VII.2001*, Hep. Ross. Exs., No. 19 (MHA).

two from Trans-Baikal Territory (that clade did not achieve support).

The *p*-distance variability (Table 2) within the first *Saccobasis* clade is 0.2% in ITS1-2 and absent in *trn*L-F, in the second clade is 0.3% in ITS1-2 and absent in *trn*L-F. The clades diverge from each other in 1.0% in ITS1-2 and 0.6% in *trn*L-F. The sister related *Pseudotritomaria heterophylla* (R.M. Schust.) Konstant. & Vilnet from the monotypic genus highly diverges from both clades of *Saccobasis* (8.0–8.9% in ITS1-2 and 9.1–9.7% in *trn*L-F).

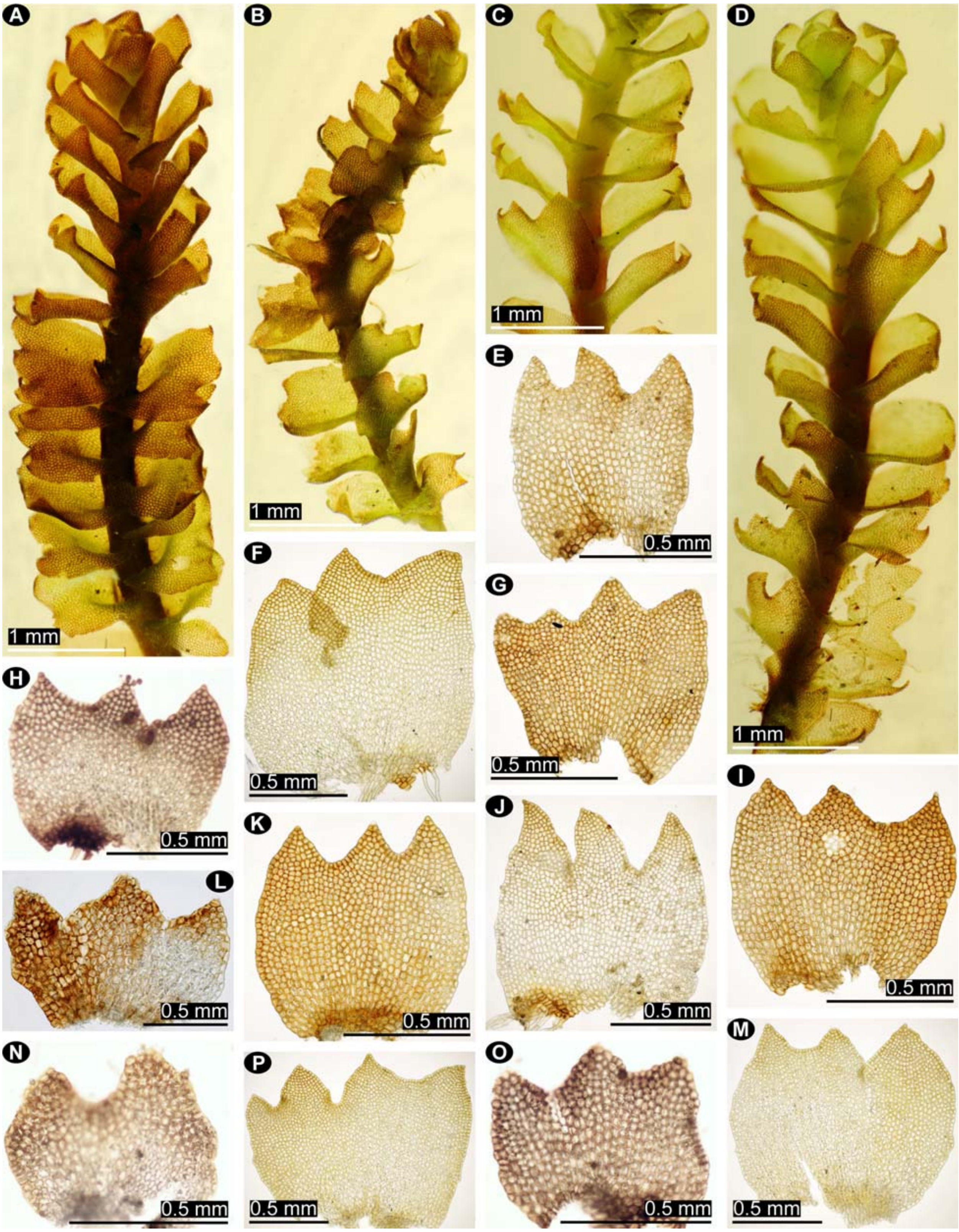


Fig. 3. *Saccobasis polita* var. *arctica*: A-D – habit. E-P – leaves. A-G, I-K, M, P from *Mamontov 526-2-2* (KPABG, MHA). H from *Savchenko CA-14-8a* (KPABG, MHA). L, N, O from *Savchenko CA-16-34-2a* (KPABG, MHA).

Morphology

Below we summarize variability of the main diagnostic features based on the sequenced specimens from the first clade with an emphasis on morphological differences, if any, of specimens from the second clade.

The plants size from the first clade varies from 1.2 mm wide and 10 mm long (specimen from Chukotka Autonomous Area) to 2–2.5(–3) mm wide (Murmansk

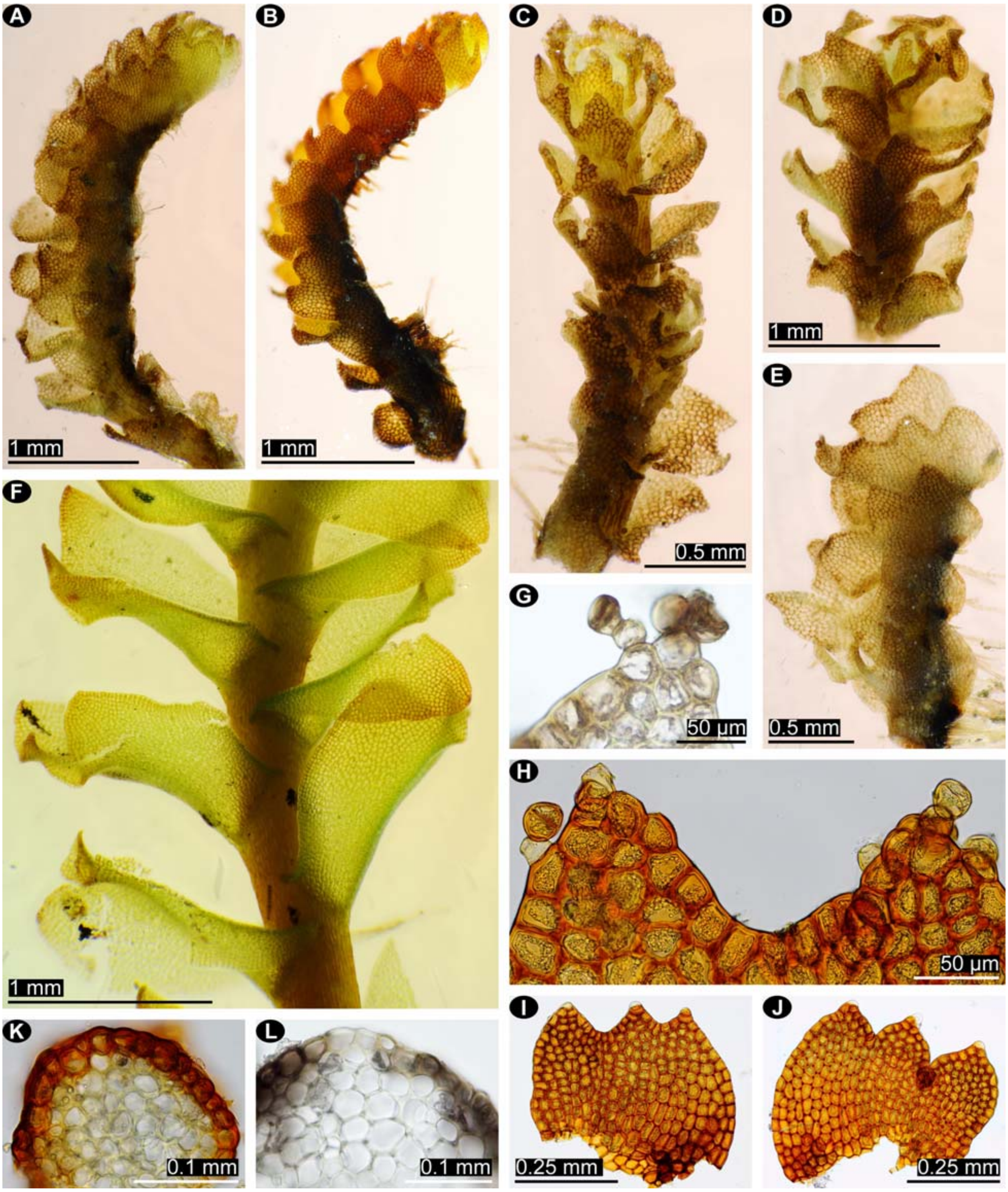


Fig. 4. *Saccobasis polita* var. *arctica*: A-E – habit. F – part of shoot showing leaf insertion, dorsal view. G, H – leaf lobe apices showing gemma formation and mature gemmae. I, J – leaves. K, L – stem cross sections. A, C-E, L from *Savchenko CA-16-34-2a* (KPABG, MHA). B, H-K from *Konstantinova K45-3a-18* (KPABG, MHA). F from *Mamontov 526-2-2* (KPABG, MHA). G from *Savchenko CA-14-8a* (KPABG, MHA).

Province, Fig. 2A–C) while plants in the second clade are much smaller: from (0.4–) 0.6 to 1.1 mm wide in plants from Svalbard (Fig. 4: A-D), but up to 1.8(–2) mm wide in plants from Trans-Baikal Territory (Fig. 3A-D, 4F).

Color of plants. In the first clade the color of plants varies from green with purplish red secondary pigmentation of uper part of leaves and more deeply brown or purplish red brown basal part of leaves to warm brown color of the whole plant with the same or red brown col-

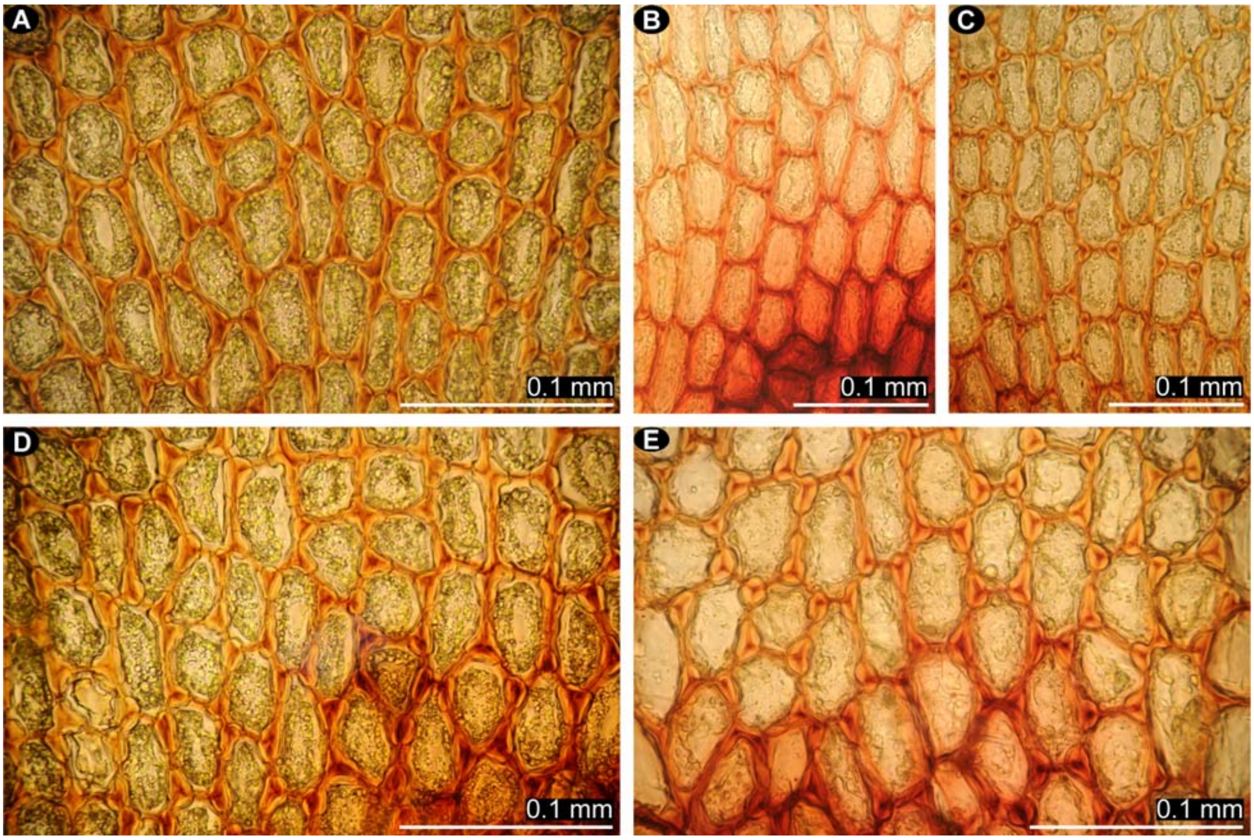


Fig. 5. *Saccobasis polita* var. *arctica*: A, D – basal leaf cells. *Saccobasis polita*: B, C, E – basal leaf cells. A, D from *Mamontov 526-2-2* (KPABG, MHA). B, C, E from *Bakalin 01.VII.2001*, Hep. Ross. Exs., No. 19 (MHA).

or at the base as in specimens from Chukotka Autonomous Area and Kamchatka Territory (Mednyi Island). In the second clade the color of the base of leaves usually does not differ from the color of the leaves which often are brown, bright bronze-brown and only at the tops of shoots red brown or as in plants from Trans-Baikal Territory which are green with light brown in the upper part of the leaves (Fig. 3: E–P). Greasy lustre which is one of the characteristic of *Saccobasis polita* is present in some specimens from both clades. Damsholt (2002, 2013) characterized *Tritomaria* (*Saccobasis*) *polita* as having "purplish-red secondary pigmentation of ventral leaf base", whereas *T. polita* subsp. *polymorpha* on exposed sites as having brown to reddish-brown pigmentation of ventral leaf bases.

Stem. The dorsal and ventral sides of stem are mostly differently colored. Particularly, the ventral side of shoots is always brown or red brown in plants from both clades. But in plants from the first clade the dorsal side may even be green contrasting with dark red or purple brown or almost purple black ventral side, while in plants from the second clade both sides are more often brown with the dorsal side more light brown than the ventral especially in upper part of shoots. Differences in the color of dorsal and ventral sides of stem seem to be much more obvious in plants from the first clade.

Cells of dorsal side of stem. Schuster (1969: 699) considered "extremely elongated narrow cortical cells of the stem" as one of the important features distinguishing *Saccobasis* from *Tritomaria.* We found, however, that this feature also varies greatly. Schuster (1969: 693) described dorsal cortical cells in *Saccobasis* as "4–8 × as long as wide". In dwarf forms from Svalbard cells on dorsal side of stem are just slightly thick walled, almost without trigones, and are only twice as long as wide, (18–)20–25(–27) × 38–50 µm, while in plants from the first clade cells of dorsal side are (2–)4–6(–8) times as long as wide, (18–)20–25 × 60–100(–125) µm.

Leaves. One of the unexpected results was that in the first clade, along with plants with almost square three-lobed leaves typical for *S. polita* (Fig. 2: D-M), we found plants with leaves that are up to 1.5 as wide as long e. g. specimens from Chukotka (KPABG-100003) and Khanty-Mansi Autonomous Areas (076-3-1a-18, KPABG-122280). That corresponds to the description of *S. polymorpha* as these specimens were identified. On the other hand, both the sequenced specimens from Trans-Baikal Territory that are located in the second clade, were dominated by plants with almost square leaves (Fig. 3: F, E, J, K). In British Isles leaves in *Saccobasis* (as *Tritomaria*) *polita* may be both "slightly narrower than to slightly wider than long" according to Paton (1999).

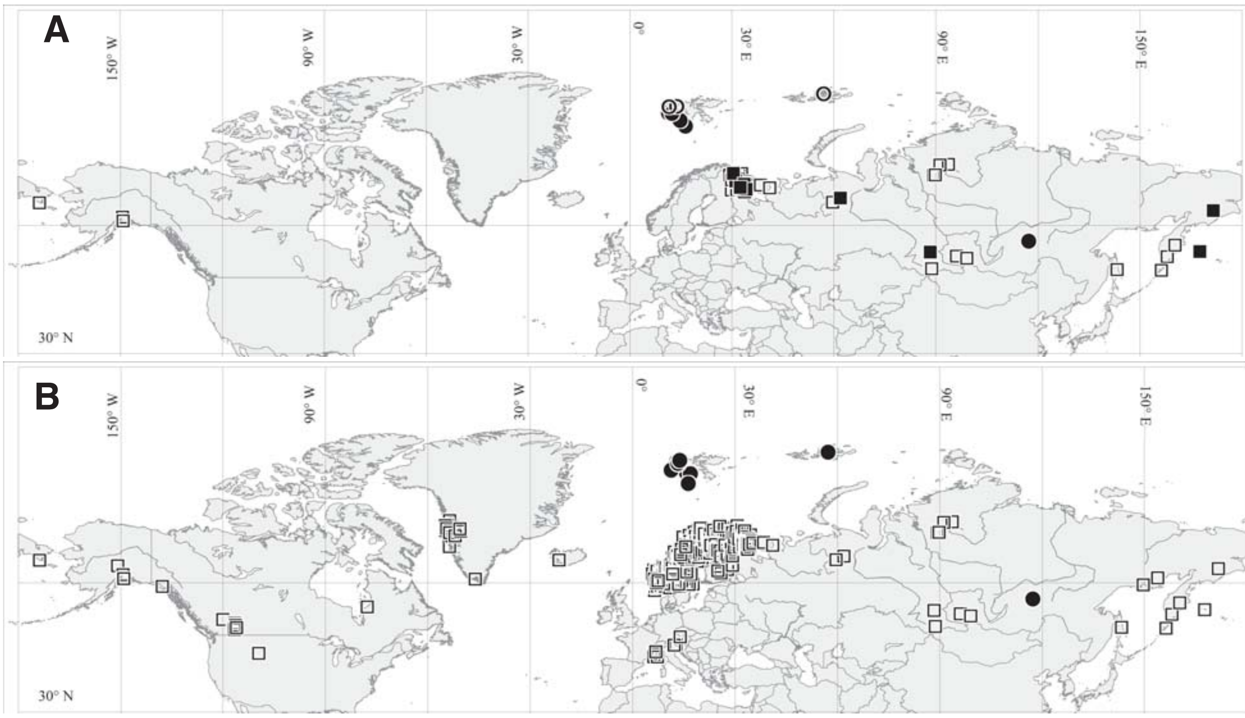


Fig. 6. Distribution map of *Saccobasis* taxa. A: *S. polita* s.l. based on sequenced and studied specimens. Black circles – sequenced specimens of *Saccobasis polita* var. *arctica*, unpainted circles – studied specimens of *S. polita* var. *arctica*, black squares – sequenced specimens of *S. polita var. polita,* unpainted squares – studied specimens of *Saccobasis polita* var. *polita.* B: distribution map of *Saccobasis polita* s.l. based on all available data. Black circles: *S. polita* var. *arctica*; squares *S. polita* var. *polita.*

Lobes variability. One of the important characteristics of the genus is relatively short-lobed leaves with three more or less equal obtuse lobes. We found that the admixture of two- and four-lobed leaves is obviously not a rare phenomenon in the Arctic and subarctic regions. However, in the specimens from the first clade, the admixture of two- and four-lobed leaves is insignificant, and in some specimens such leaves are found rather as an exception. Two- and four-lobed leaves are also found in plants from the British Isles (Paton, 1999: 254). In specimens from the second clade, all plants from Svalbard have a noticeable admixture of two- or four-lobed leaves and in the dwarf forms two-lobed leaves can dominate, whereas in larger forms from Trans-Baikal Territory four- or two-lobed leaves are extremely rare. In general, the small Arctic forms from the second clade (the majority of specimens from Svalbard) have most or at least some of the lobes pointed (Fig. 3: E–P), unlike the specimens from the first clade where the leaf lobes are blunt or rounded at apex (cf. Figs. 2: D–M).

Thus, the admixture of two- and four-lobed leaves can hardly serve as a good diagnostic feature. The small size and significant admixture of two-lobed leaves often caused such plants to be referred subsp. *polymorpha*, e.g. plants from Chukotka Autonomous Area (first clade).

Sinuses are very variable in specimens from both clades. In plants of the first clade, one leaf sinus may be semicrescentic or even shallow crescentic just 0.1–0.15 leaf length, while others are angulate sometimes sharp at base and to 0.25(–0.3) leaf length. In plants from the second clade sinuses are more often angulate or broadly angulate and 0.15–0.25 leaf length (cf. Fig. 2: D–M and Fig. 3: E-P).

Gemmae. Of the several specimens containing gemmae, four are specimens from the second clade and only one is from the first clade. In the single specimen from the first clade, gemmae were green, whereas in specimens from the second clade gemmae were both green and brown (Fig. 4: H, G). Moreover, in some specimens, plants with both green and brown gemmae were present. It seems that on young leaves hidden in older leaves gemmae always are green, while on older open leaves they tend to be brown.

Damsholt (2002) described gemmae of *Tritomaria polita* as “ovoid-ellipsoidal, 2-celled, (17–)20–22 × (22–)26–31 µm, yellowish brown” for subsp. *polymorpha* and “ovoid-ellipsoidal, 2-celled, 16–17 × 25–28 µm, greenish” for subsp. *polita.* In Murmansk Province, plants with gemmae have been collected repeatedly. Everywhere they have ellipsoidal light brown gemmae, which, along with the presence of single two- or four-lobed leaves, led to identification of such specimens as *Saccobasis polymorpha*. On the constructed trees, all studied specimens from Murmansk Province both with and without gemmae are placed in the first clade which we refer to *S. polita.* Thus, the gemmae from specimens of the two obtained clades do not differ either in shape or color.

Oil-bodies. We found that the number of oil-bodies is quite variable and varies in different plants in the same mat in specimens from Khibiny Mountains (Murmansk Province) where they were described almost immediately after collection. In many studied specimens the number of oil-bodies varies from 2 to 10 per cell, but in most cells there were 5–7 oil-bodies – both in wide or relatively narrow leaves, in which wide/length ratio varies from 0.9 to 1.1 and in plants with brown gemmae. Thus, the number of oil-bodies does not correlate with the width of leaves, the color of gemmae and the other characteristics, so it cannot be a reliable diagnostic feature. Both Schuster (1969, 1988) and Damsholt (2002, 2013) stressed that the number of oil-bodies in *Tritomaria polita* is slightly less than in *T. polita* subsp. *polymorpha*, 2–7 versus 4–11. However, Patton (1999: 254) described *T. polita* in the British Isles as having 3–10 oil-bodies per cell.

Female bracts and perianth. Plants with perianth were found in several specimens from Murmansk Province including one that was sequenced (315-8-00, KPABG-8247). In this specimen the female bracts are at least partly shallowly 3–5-lobed and mostly much wider than long (1.2–1.4 as wide as long) and the perianths are partly 2–3-stratose. However, even in this specimen, as in other studied specimens, there were plants with relatively narrow female bracts.

Both Schuster (1969) and Damsholt (2002) stressed the differences in the shape of female bracts between the two subspecies. However, there are certain discrepancies in their descriptions. In particular, Damsholt (2002: 190) in differentiation wrote that female bracts "usually twice as wide as long", while Schuster (1988: 112) described female bracts in this subspecies as "to 3075 µm wide × 1845 µm long; 2-lobed merely 1525 µm wide × 1435 µm long", so just from 1.7:1 to 1.1:1".

Thus, all the features considered by Schuster (1969, 1988) and Damsholt (2002, 2013) as diagnostic for *Saccobasis polymorpha* were found in plants from both clades.

Differentiation. *Saccobasis* is a well-distinguished and easily identifiable genus throughout its range, with the exception of the high Arctic, where it is sometimes represented by very small dwarf forms that may be difficult to identify. The genus is distinguished by quite specific leaf insertions that are attached on characteristic sinuous and clearly interlocking by 2-3 cells on the dorsal side V-shaped line, forming the pocketlike leaf base. Such insertion of leaves is not found in other genera of leafy liverworts of the Holarctic and in combination with shallowly divided mainly obtuse three-lobed leaves, narrow mostly strongly elongated mostly thick walled cells of the stem surface, large isodiametric in the middle and distinctly elongated at base cells of leaves with very characteristic bulging trigones and with more or less distinct middle lamella makes it easy to distinguish it from species of the genus *Tritomaria* s.l. (including *Trilophozia* (R.M.Schust.) Bakalin), in which it was previously placed. Additionally, *Saccobasis* differs from *Trilophozia* by: (1) relatively symmetrical leaves with more or less even lobes vs. strongly asymmetric with distinctly uneven lobes in *Trilophozia*; (2) rounded to obtuse, never cuspidate lobes, vs. distinctly cuspidate lobes in *Trilophozia*; (3) ellipsoidal gemmae vs. polygonal in *Trilophozia*; (4) much larger and distinctly elongated basal leaf cells (up to 25–27 × 75–125 µm). With symmetrical more or less evenly lobed leaves, large cells and bulging trigones *Saccobasis* is similar to *Pseudotritomaria* Konstant. & Vilnet, which differs from *Saccobasis* in: (1) cuspidate lobes of leaves and especially sharply cuspidate and dentate female bracts; (2) constant presence of gemmae that are angular to stellate; (3) crenulate dentate perianth mouth vs. not dentate perianth mouth in *Saccobasis*; (4) more pellucid shoots.

At the same time, the appearance of *Saccobasis* can vary greatly depending on the habitat in which it occurs. In particular, at the first glance, large swamp forms are very different from small forms of the High Arctic and tundra forms found along the banks of streams in the highlands. The latter may cause the greatest difficulties in identification because in small Arctic forms the main distinguishing features of the genus (peculiar insertion of leaves, three-lobed leaves with shallow sinuses and obtuse lobes and even trigones) are very weakly expressed. In particular, in cracks on spots in the spotted tundra in Svalbard we collected very small dark brown plants with dominance of two-lobed leaves that are slightly obliquely inserted just inconspicuously decurrent ventral sides and with lobes rather pointed, and dorsal stem cells of which are just slightly elongated and with relatively small trigones of the leaf cells. It can be difficult for an inexperienced researcher to attribute such forms to *Saccobasis*. Nevertheless, the combination of rather large leaf cells with distinct trigones and distinct middle lamella even in very small forms, interlocked on dorsal side of stem attachment of leaves that are slightly, but characteristically decurrent on dorsal and ventral sides, elongated at least partially at base of leaf cells (even in very small forms), as well as single more or less characteristic three-lobed leaves and the ellipsoidal gemmae allow to attribute them to *Saccobasis*. Moreover, the combination of these features gives plants an extremely peculiar appearance, allowing them to be immediately attributed to this genus even when viewed under lens.

Discussion

Our study presents a large range of specimens from different regions of Eurasia from the Murmansk Province and Svalbard in the west to Chukotka Autonomous Area and Kamchatka Territory in the East and Trans-Baikal Territory in the south, but it does not include specimens from central Europe, from where *S. polita* was described. It was also not possible to study specimens from Greenland, from where *Tritomaria polita* subsp. *polymorpha* was described. All this makes the interpretation of the results very difficult. We nevertheless reveal a problem with the interpretation of *T. polita* subsp. *polymorpha* and we consider it necessary to "put the problem on the table" using Schuster's figurative expression.

As shown above, almost all the features previously considered diagnostic for the separation of *Saccobasis polita* and *S. polymorpha* do not work as such. One of the serious misconceptions Schuster (1969) had when he described *Tritomaria polita* subsp. *polymorpha* was the idea that the gemmae of *T. polita* are angulate, whereas those of *T. polita* subsp. *polymorpha* are ellipsoidal. It was based on Müller's (1906-16:614) description the gemmae of *Saccobasis polita* (*Sphenolobus politus* (Nees) Steph.) as "triangular or polygonal, often stellate" (trans. from German "drei- oder mehreckig, oft sternförmig"). At the same time, ellipsoidal gemmae were described for subsp. *polymorpha* by Schuster (1969) and he considered supposed differences in shape of gemmae between subsp. *polita*, and subsp. *polymorpha* (*Saccobasis polymorpha*) as "perhaps most important of all". However, as Schuster stressed later (Schuster, 1988: 110) Müller's indication of polygonal gemmae was based on the incorrect attribution of *Jungermannia polita* var. *acuta* Kaal. ex Schiffn. to *Saccobasis polita*, whereas *Jungermannia polita* var. *acuta* represents *Tritomaria scitula* (Taylor) Jørg. Thus, it turns out that the difference between the two taxa considered most significant was erroneous.

These misconceptions about the shape of the gemmae have dominated in Russia until recently, since it was given in the description of *Saccobasis* in Schljakov (1980), which is widely used in Russia. Damsholt (2013) revealed a difference in the color of the gemmae that he described as green in subsp. *polita* and brown in subsp. *polymorpha*, however, as shown in the results above, the color of gemmae can vary on the same plant and in plants in the same mats.

Morphologically, most specimens from the first clade correspond to the description of *S. polita* or the taxon characterized by Schuster (1988: 111) as intermediate. But in the same clade there is also a specimen from Chukotka Autonomous Area containing rather small plants about 1.2 mm wide, brown in color, with leaf width/length ratio around 1.1–1.3 and with an admixture of two-lobed leaves that suggests *S. polymorpha*. Damsholt (2013) states that "overlapping distribution in Greenland of ssp. *polita* and *polymorpha* indicates the close relationship between the two and the difficulties in realizing, what taxon is at hand". Obviously this is true for all subarctic regions like Murmansk Province, Subpolar Ural (Khanty-Mansi Autonomous Area), Chukotka Autonomous Area and Kamchatka Territory (see above) where specimens identified both as *polita* and *polymorpha* are mixed in the first clade (Fig. 1; Table 1). In addition, plants from the British Isles, judging by the description of Paton (1999) and referred by her to *Tritomaria polita*, are in most respects similar to plants from the Murmansk region and the Scandinavian countries. Thus, analysis of specimens from the first clade identified both as *Saccobasis polita* and *S. polymorpha*, shows that the shape and color of gemmae, the ratio of leaf length and width, the variability of the number of lobes, color of leaf base and number of oil-bodies are not reliable features for distinguishing the two described taxa. So none of the features, which were cited by Schuster (1969, 1988), Schuster & Damsholt (1974), Damsholt (2002, 2013) and Schljakov (1979) as distinguishing the two subspecies/species, are supported from molecular evidence. Based on the obtained data, it is most likely that *S. polymorpha* is a synonym of *S. polita*. However, this assumption is preliminary and requires confirmation, in particular by sequencing both Central European and West Greenland specimens.

At the same time, the specimens in the second clade do not fit well with any of the descriptions. Such plants partially coincide with Schuster's description of dwarf or juvenile forms of *S. polymorpha*. Taking into account some molecular differences revealed between the two clades and obvious morphological differences, we consider it possible to describe such plants as a new variety *S. polita* var. *arctica*.

Taxonomy

Saccobasis H. Buch, Memoranda Soc. Faun. Flor. Fenn. 8: 291. 1933. Type: *Jungermannia polita* Nees (≡*Saccobasis polita* (Nees) H. Buch).

Plants from small 0.5–1 mm wide and 2–3 mm long to medium sized up to 2.5 mm wide and 3–4(–5) cm long, light green, warm brown to deeply red brown and sometimes almost black. Branching *Frullania*-type, rarely ventral-intercalary, cells on dorsal side distinctly elongated. Both cortical cells of stem leaves cells extremely pachydermous. Cortical cells of stem mostly extremely elongated up to 4–8 as long as wide. Leaf insertion is very characteristic with both dorsal and ventral ends of insertion arched upward what gives the plant an unique appearance. Leaves in majority uniformly three-lobed with mix sometimes of single two- or four-lobed leaves. Lobes broad, relatively short and obtuse. Leaf cells large, from isodiametric in the upper part and in the middle to distinctly elongated up to 25–30 × 50–75(–100) μm at base, extremely pachydermous. Gemmae rare and sparse, on young leaves, green to brown. Dioicous. Androecia terminal becoming later intercalar, male bracts slightly smaller than vegetative leaves ventricose and often red-brown at base in 3–4(–5) pairs, antheridian stalk one-celled. Perianth cylindrical, deeply plicate in upper part, locally 2–3-stratose, slightly narrow to the mouth, that is entire. Sporophytes are extremely rare throughout their range. Capsule ovoid, dark brown, 3(–4)-stratose, epidermal cells with nodular trigones, inner cells with semi-annular and annular thickenings, spores reddish brown, verruculose 13–18 µm, elaters bispiral, 7–9 µm wide with band 2–3 µm wide (based on specimen from Murmansk Province, KPABG-4043).

The following is a description of *Saccobasis polita* s.l. based mostly on specimens from the first clade with addition and comments on specimens from the second clade as well as studied specimens from KPABG. The differences between the two varieties are given in the key below.

Saccobasis polita (Nees) H.Buch, Memoranda Soc. Faun. Flor. Fenn. 8: 291, 1933. — *Jungermannia polita* Nees, Naturg. Eur. Leberm. 2:145, 1836; *Diplophyllum politum* Dumort., Hep. Europ., 50, 1874: *Sphenolobus politus* (Nees) Steph. Spec. Hep. 2: 169, 1902; *Tritomaria polita* (Nees) Jørg. Bergens Mus. Ĺrbok 1919–1920 (7): 4. 1922; *Tritomaria polita* subsp. *polymorpha* R.M.Schust., Hepat. Anthocerotae N. Amer. 2: 700-704 f. 234 (1–11), 1969; *Saccobasis polymorpha* (R.M. Schust.) Schljakov Novosti Sist. Nizsh. Rast. 16: 205, 1979, syn. nov.

Plants erect or rarely decumbent, green, light warm brown to deeply red brown and sometimes almost black to the base of plant, from small, just 0.8–1.2 mm wide and 0.5–1 cm long on rocks and spots of bare soil in tundra to medium sized, 1.5–2.5(3) mm wide and 10–15 mm to 30–35 mm long in wetlands and depressions in swampy forest. **Stems** simple or sporadically branched, branches mostly *Frullania*- type, rarely ventral-intercalar, 0.1–0.17 as wide as shoot on dorsal side green or light brown with much darker colored ventral side that vary from brown, red brown to dark brown or almost black. Cells on dorsal side distinctly elongated, 12–20 × (40–)50–100(–125) µm. **Cross section** 300–450 × 400–500 µm, 17–19 cells high, cortical cells in 1–3 rows, thick-walled, 12–17 µm, cells of medula thin-walled, large, 25–30(–37) µm, mixed with more smaller cells (17–20 × 20 µm), in ventral part in several rows just slightly smaller (12–)17–20 µm, sometimes with mycorrhiza. **Rhizoids** numerous and dense in lower part of shoot but becoming sparse up to the apices, red brown especially at base to colorless, relatively long. **Leaves** soft, canaliculate to slightly concave especially in dwarf arctic forms, transversely oriented, in large forms often characteristically deflected approximately from the middle almost perpendicular to the stem or suberect attached on characteristic sinuous and clearly interlocking by 2–3 cells on dorsal side V-shaped line forming pocket-like leaf base**,** with dorsal side almost not decurrent in dwarf forms and slightly decurrent on dorsal and ventral side in large forms, from more or less undulate to not undulate in small arctic forms, mostly three-lobed with single two- or four-lobed leaves, subquadrate to obtrapezoidal from 0.8–0.9 mm wide and 0.8–0.9 long to 1.7 mm wide and 1.6 mm long to wider than long 1- 1.5 mm wide and 0.8- 0.9 mm long, in swamp forms to 2 mm wide and 1.7 mm long, from more or less symmetrical to often with one lobe larger than another. Both leaf lobes and sinuses obtuse to rounded to angular with often one sinus wide obtuse to crescentic and second one more deeper and obtuse to angular up to 0.25(–0.3) leaf length. **Cells** in the middle from isodiametrical to slightly elongated, (20–) 25 × 25–33 µm, clearly larger and elongated at base where 25–30 × 35–45 µm in small plants to 25–37 × 50–85(–100) µm in large lax forms of swampy areas. Trigones distinct, large to bulging and confluent, in some arctic forms rather small, cell walls with more or less distinct middle lamella. Cuticle more or less distinct verrucose striolate. **Oil-bodies** vary even within one leaf from (2–)3–4 to 10(–12) per cell, but more often 4–7 light grey granulate, spherical to ellipsoidal, 6–8 × 6–10 µm.

Gemmae rare, apart of small arctic forms colorless or light green on small juvenile leaves hidden inside often brown-colored apical leaves or more or less light brown on upper leaves, often just single or in very small amount, one or two celled, ovoid and wide ellipsoidal from 17 × 20 to 17–20 × 25–28 µm.

Dioicous. Male and female plants mixed in the same mats. **Androecia** terminal later becoming intercalar, of (3–)4–6 pair of bracts, male bracts slightly smaller than leaves more concave and often red brown at base and often with distinctly uneven lobes of that ventral is wider and longer, imbricate with 2–4 antheridia, antheridian stalk one celled. **Female** bracts slightly larger than leaves, as wide as long or wider than long, 1.4–2.2 mm wide and 1.2–2 mm long, width/length ratio vary from 1.4:1.1 to 1:1.1, often with distinctly lager ventral lobes or symmetrical (2–)3–5-lobed, more wavy and more distinctly plicate than sterile leaves, with turned back crescending or wide obtuse sinuses that varies within one mat or even one plant from 0.11–0.13 to 0.25 of leaf length. **Perianth** to 1–1.2 mm wide and 2–3 mm long, almost fully emerged upon maturation, more or less cylindrical, deeply plicate especially in upper part, locally 2–3 stratose especially in folds, slightly narrow to the mouth, which is almost even or somewhat lobed and entire, cells of mouth almost isodiametric much smaller, often just 15–20 µm in one to several rows and gradually and unevenly turning into elongated lager cells. Sporophytes occur very rarely, known for type subspecies only. **Capsule** ovoid, dark brown, the wall 3(–4)-stratose, epidermal cells with nodular trigones, inner cells with semiannular and annular thickenings, spores reddish brown, verruculose 13–18 µm, elaters bispiral, 7–9 µm wide with bands 2–3 µm wide.

Saccobasis polita (Nees) H. Buch var. **arctica** Konstant., Vilnet & Mamontov*,* **var. nov**. (Figs. 3, 4, 5:A, D)

Diagnosis. Differs from *Saccobasis polita* in smaller size, color of shoots without purple secondary pigmentation, often concave leaves that are not deccurent, noticeable admixture of two- or four-lobed leaves, mostly pointed leaf lobes, and angulate sinuses, shorter cells on dorsal side of shoot and at leaf base.

Type: Norway: Svalbard, Wedel Jarlsberg Land, Recherchefjorden, Lagerneset, 77°31'31.8" N – 14°45'54" E, river terrace, patterned ground tundra on gentle slope, on frost boils, on side of micro-bumps and in crevices, dominate in mats with admixture of *Anthelia juratzkana* (Limpr.) Trevis., *Blepharostoma brevirete* (Bryhn et Kaal.) Vilnet et Bakalin, *Cephaloziella varians* (Gottsche) Steph., *Odontoschisma macounii* (Austin) Underw., 19.VIII.2018, *Konstantinova & Savchenko # K45-3a-18* (KPABG-123662, holotype), paratypes all specimens cited below. GenBank accession numbers are OP584670 for ITS1-2 and OP573508 for *trn*L-F.

Etymology. The name refers to the restriction of the variety to the difficult high arctic and subarctic mountains habitats.

The two varieties can be distinguished as follows:

l. Plants brown to dark and even black-brown, the color of the base of leaves usually does not differ from color leaves, small, (0.4–)0.6–1.2(–2) mm wide, cells on dorsal side of stem 2, rarely 3 times as long as wide, leaf lobes mostly pointed ending by one or sometimes two superposed cells, both sinuses mostly angulate, sometimes sharp at base and to 0.25(–0.3), leaf length, shoots often with noticeable admixture of two- or four-lobed leaves. Occurs on bare soil in crevices on frost boils in patterned ground tundras or on rocks in brook beds — *S. polita* var. *arctica*

1. Plants green to warm brown with purplish red secondary pigmentation and more deeply brown or purplish red brown basal part of leaves, mostly medium sized, (1.2–)1.5–3 mm wide, cells of dorsal side are (2–)4–6 (–8) times as long as wide, leave lobes obtuse or rounded, one sinuses often semi crescentic or even shallow crescentic just 0.1–0.15 leaf length, while the second can be angulate sometimes sharp at base and to 0.25(–0.3) leaf length, leaves mostly 3-lobed but single 4- or 2-lobed leaves occur. Occurs in moist humus-rich habitats — *S. polita* var. *polita*

Ecology. The type variety is a hydrophilic basiphile occurring in moist habitats as a pioneer directly on damp, mainly basic, sediments and rocks or on humus-rich soil and peat covered basic rocks, e.g. on banks of rivulets or in beds of streams drying up, in *Alnus fruticosa* Rupr. tickets, in swampy and peaty areas with basic seepages both in ravines and on rock outcrops, at base of cliffs, in swampy depression with *Ledum palustre* L. and *Alnus fruticosa* Rupr. in forests near sea-side, in sedge-moss and sedge subshrubs tundra on edges of pools, in pools in hummocky boggy tundra. The species often occur in pure turfs or mats or mixed with other bryophytes. Most often its associates are bryophytes of rich or eutrophic mires or stream sides *Aneura pinguis* (L.) Dumort., *Blepharostoma trichophyllum* (L.) Dumort., *Harpanthus flotovianus* (Nees) Nees, *Odontoschisma elongatum* (Lindb.) A.Evans, *Scapania uliginosa* (Lindenb.) Dumort., *Trilophozia quinquedentata* (Huds.) Bakalin, *Campylium stellatum* (Hedw.) C.E.O. Jensen, *Loeskypnum badium* (Hartm.) H.K.G. Paul, *Meesia uliginosa* Hedw., *Scorpidium revolvens* (Sw. ex anon.) Rubers,, *Warnstorfia sarmentosa* (Wahlenb.) Hedenäs, and weak calciphytes like *Mesoptychia gillmanii* (Austin) L. Söderstr. & Váňa, *M. heterocolpos* (Thed. ex Hartm.) L. Söderstr. & Váňa. *Saccobasis polita* var. *arctica* is found in more xeric habitats. All specimens from Svalbard and Franz Josef Land were collected in crevices in patterned ground tundra on frost boils. Specimens from Trans-Baikal Territory were found on rocks in river valley in forest zone near timberline. Associates of *Saccobasis polita* var. *arctica* are arctic and montane species like *Anthelia juratzkana* (Limpr.) Trevis., *Blepharostoma brevirete* (Bryhn & Kaal.) Vilnet & Bakalin, *Jungermannia polaris* Lindb., *Cephaloziella varians* (Gottsche) Steph., *Odontoschisma macounii* (Austin) Underw., *Marsupella arctica* (Berggr.) Bryhn & Kaal. and *Schljakovianthus quadrilobus* (Lindb.) Konstant. & Vilnet.

Distribution. *Saccobasis polita* is an arctic-montane species (Fig. 6, 7). It is most widespread in the oceanic and suboceanic areas with predominance of basic rocks. In Europe it occurs scattered in mountains of central and western including north-western Europe and Iceland and the British Islands (Paton, 1999; Damsholt, 2002) in the west to Svalbard in the north where the species is present as var. *arctica*. In the European part of Russia the species is not rare in the Murmansk Province, but much rarer both to the south where it is recorded only in the north of Republic of Karelia (Bakalin, 1999) and to the east where it occurs in Nenets Autonomous District (Potemkin, 2008) and Urals (Zinovjeva, 1973). In Asia the species is not rare in mountains in oceanic and suboceanic areas of Far East of Russia, particularly in Chukotka Autonomous Areas and Kamchatka Territory (Konstantinova *et al*., 2009; Bakalin, 2010) and occurs scattered in humid areas of mountains of South (Váňa & Ignatov 1995; Konstantinova *et al*., 2003) and Baikal Siberia (authors' unpublished data, see specimens examined), where it probably is not rare in appropriate localities. In the north of Asia the species is found in single localities on eastern slopes of Urals (Storozheva, 1986, Konstantinova & Lapshina, 2017), on Putorana Plateau (Bakalin *et al*., 2016) and several localities in the Taimyr Peninsula (KPABG, isling.org/hepatics). The species is probably more widespread in poorly studied northern and mountain regions of Asia and will be found more to be common in future studies.

In the western hemisphere the species is rather common in West and South Greenland (Damsholt, 2013), not rare in western and northern part of North America from Alaska and Yukon to British Columbia but rather rare in east America from Ellesmere I. to Newfoundland and Quebec (Schuster, 1969).

Selected specimens examined: *Saccobasis polita*. RUSSIA, Republic of Karelia, 17.VIII.1989, *Konstantinova #215-2-89* (KPABG-2911). Rybachiy Peninsula, 19.VII.1978, *Konstantinova # 83-2-78* (KPABG-6138); Monche tundra, 28.VI.2009 *Borovichev # BE37-21-09* (KPABG-19158); Paz River Valley, 02.VIII.1994, *Kostina* s.n. (KPABG-8622); Khibiny Mountains,09.VIII.1998, *Konstantinova #39-1-98* (KPABG-6937), ibid. 10.VIII.1996, *# 21-3b-96* (KPABG-6189), ibid. 20.VIII.2000, *#310-1-00* (KPABG-8167); Iokan'ga River Valley, 18.IX.1997, *Konstantinova # 60-2-97* (KPABG-6203). Khanty-Mansi Autonomous Area, 14.VII.2018, *Lapshina* s.n. (KPABG-122280), ibid. 10.VIII.2015, *Lapshina #1771* (KPABG-121323). Kemerovo Province, 28.VI.2000, *Konstantinova #61-1-00* (KPABG-101870). Krasnoyarsk Territory, Taimyr Peninsula 23.VII.2021 *Lapshina* # YSU-MH-04421 (YSU, KPABG); Eastern Sayan, 5.VIII.1993, *Vasiljev* (KPABG 103028) Eastern Sakhalin Province, 11.IX.2009, *Bakalin #S-61-37-09*, Hep. Ross. Exs., Fasc. VI, No. 143 (KPABG-116071); Chukotka Autonomous Okrug (Area), 15.VII.1988, *Kuzmina #D1(20)* (KPABG-100003). Kamchatka Territory, 01.VII.2004, *Bakalin # K-24-16-04* (KPABG-106564). AUSTRIA, as *Tritomaria polita* (Nees) Jørg., 23.VIII.1882, *Breidler*, Hep. exic. S.O. Lindberg, Fasc. II, No. 462 (KPABG-s.n.). USA, Alaska, Matanuska-Susitna Borough, all as *Saccobasis polymorpha*: 04.VII.1992, *Konstantinova #88-2-92* (KPABG-123744), ibid. 04.VII.1992, *Konstantinova # 94-1-92* [KPABG-123771], ibid. 07.VII.1992, *Konstantinova, # 120-9-92* [KPABG-123867].

Saccobasis polita (Nees) H.Buch var. *arctica* Konstant., Vilnet, Mamontov (paratypes): RUSSIA, Franz Josef Land, Ziegler (Tsigler) Island, 25.VII.2019, *Savchenko # CA19-30-5b* (KPABG-122768). Trans Baikal Territory, *Mamontov # 525-1-2* (KPABG-119591), ibid. *# 526-2-2* (KPABG, MHA). NORWAY: Svalbard, Sørkapp Land, Stormbukta, 15.VIII.2018, *Konstantinova & Savchenko # K11-1a-18* (KPABG-123564); Prins Karls Forland, 06.VIII.2016, *Savchenko #CA16-34-2a* (KPABG-121469); Wedel Jarlsberg Land, Recherchefjorden, 19.VIII.2018, *Konstantinova & Savchenko #K45-2b-18* (KPABG-123661), ibid. 19.VIII.2018, *# K45-1c-18* (KPABG-123658); Haakon VII Land, 07.VIII.1974, *Frisvoll # TRH74005* (KPABG-122658, dupla).

CONCLUSION

Studying a large number of *Saccobasis* specimens from different regions using an integrative approach led us to the unexpected conclusion that the morphological differences between the plants from the two subclades obtained in our molecular study, do not correspond to the morphological differences of the two species/subspecies described in the genus as they are recently treated (Schuster, 1969, 1988; Damsholt, 2002, 2013, Schljakov, 1980). We found a large variability in almost all morphological features by which these species differ, while no more or less persistent distinguishing features were found neither in morphology nor molecularly. As a result the previously recognized *S. polymorpha* is proposed to be synonymized with the type species of the genus. At the same time, specimens from Svalbard and Trans-Baikal Territory differ from the rest of the specimens both morphologically and genetically and we propose to consider them an Arctic variety of the species which is restricted to the most severe habitats. It should be emphasized, however, that this conclusion is preliminary, since we were unable to conduct molecular genetic studies of specimens from the type localities.

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