

Some aspects of the moss population development on the Svalbard glaciers

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Abstract

Glaciers are rather unusual habitat for mosses, but sometimes they can be suitable for some species due to presence of sufficient moisture and cryoconite substrate in the ablation zone. To date, moss populations were found only on a few glaciers in Alaska, Iceland and Svalbard. An origin and development of moss cushions on ice (so called "glacier mice") are still unclear. In this study, some aspects of the moss population development were explored on ice of the Svalbard glaciers – Bertilbreen (Billefjorden) and Austre Grønfjordbreen (Grønfjorden) in 2012 and 2013. On Bertilbreen, populations of *Hygrohypnella polaris* (Lindb.) Ignatov & Ignatova and *Schistidium abrupticostatum* (Bryhn) Ignatova & H.H. Blom were found for the first time. Due to putative morphological features, identification of *S. abrupticostatum* was confirmed by comparing ITS1-2 nrDNA sequence data to BLAST searches (megablast). The results indicated a genetic heterogeneity of the population. Although visually moss-free, examination of cryoconite sediments revealed development of new individuals of *S. abrupticostatum* from filamentous structures consisting of caulonema and rhizoids. The developmental stages of young plants were revealed. Therefore, besides fragmentation of existing cushions, cryoconite sediments provided a source of new moss cushions in glacier populations. Additionally a few plants of *Pohlia* cf. *wahlenbergii* (F. Weber & D. Mohr) Andrews and a gametophyte fragment of *Philonotis* sp. were found in aggregation of cryoconite. Presence of *Paludella squarrosa* (Hedw.) Brid. reported for Bertilbreen has not been confirmed. On Austre Grønfjordbreen *Bryum cryophilum* Mårtensson, *Sanionia uncinata* (Hedw.) Loeske were found invading into some *Hygrohypnella polaris* cushions. Each moss polster on ice represents a separate mini-ecosystem that includes successive colonization events.

Key words: mosses, glaciers, cryoconite, protonema, *Schistidium abrupticostatum*, succession, Svalbard

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Introduction

Rapid melting and retreat of glaciers are widespread phenomena in the Arctic. Sustainable long-term ablation zones on glaciers can provide a suitable habitat for some mosses due to presence of sufficient moisture and cryoconite substrate. Fourteen species have been recorded from this unusual habitat in Alaska and Iceland: *Andreaea rupestris* Hedw., *Ceratodon purpureus* (Hedw.) Brid., *Ditrichum flexicaule* (Schwaegr.) Hampe, *Pohlia nutans* (Hedw.) Lindb., *Polytrichum juniperinum* Hedw. (Benninghoff 1955); *Racomitrium fasciculare* (Hedw.) Brid. (Shacklette, 1966); *Drepanocladus berggrenii* (C. Jens.) Broth. (Heusser, 1972), *Racomitrium crispulum* var. *rupestre* (Hook. f. & Wils.) Dix., *Holodontium pumilum* (Mitt.) Broth., *Dicranoweisia brevistea* Card. (Seki 1974); *Grimmia* sp., *Racomitrium fasciculare* (Hedw.) Brid., *R. ericoides* (Brid.) Brid. (Porter et al. 2008), *Pohlia filum* (Schimp.) Mertensson, *Sanionia uncinata* (Hedw.) Loeske, *Racomitrium fasciculare* (Dickson et Johnson 2014). Due to spheroidal or cylindrical shape of moss cushions, they were named “jökla mýs” in Icelandic (Eythórsson 1951), *i.e.* “glacier mice”. They also were called “unattached mosses” (Martin 1952), “moss balls” (Iwatsuki 1956) and «globular mosses» (Mägdefrau 1987). Many polsters, however, do not have spheroidal but rather flattened shape. Cushions could be lying on pedestals (Porter et al. 2008) or in shallow wells thawed by their insolation (Benninghoff 1955) and slightly sunken into surface of the glacier (N. G. Miller *in* Shacklette 1966). Bibliography on “glacier mice” can be found in *e.g.* Glime 2007, Porter et al. 2008, Belkina et Mavlyudov 2011, Dickson et Johnson 2014.

The moss populations on nine Svalbard glaciers were found by glaciologist B. R. Mavlyudov since 2002. In 2007 he and A. Kudikov collected several specimens on glaciers Bertilbreen and Austre Grønfjord-

breen (Fig. 1). O. A. Belkina identified them as *Paludella squarrosa* (Hedw.) Brid. (from Bertilbreen) and *Ceratodon purpureus* (Hedw.) Brid., *Warnstorfia sarmentosa* (Wahlenb.) Hedenäs, *Sanionia uncinata* (Hedw.) Loeske, *Hygrohypnella polaris* (Lindb.) Ignatov & Ignatova (from Austre Grønfjordbreen). In 2009 the populations of *S. uncinata* and *H. polaris* were studied in more detail, focusing on the distribution of moss polsters on ice, cushion structure, anatomical leaf features, some ecological and biological characteristics facilitating for adaptation to unfavorable conditions on glaciers (Belkina et Mavlyudov 2011).

In 2012, the populations on Austre Grønfjordbreen (*i.e.* Austre Grønfjord Glacier) were re-examined.

In August 2013, we visited Bertilbreen (*i.e.* Bertile Glacier) (Fig. 2) during floristic field study of Pyramidens surroundings and found moss populations on the glacier tongue. Large cushions of mosses (~ 5-10 cm in diameter) were lying on a flat surface and towered above the ice. Smaller tufts (< 5 cm) developed inside cryoconite holes in the ice surface and they almost completely were “immersed” in cryoconite substratum. A significant area of the ice was covered by mineral particles or rounded lumps (0.5-2 cm in diameter) of cryoconite (Fig. 3).

Cryoconite is windblown dust that is deposited on glaciers. It consists of mineral fines enriched with organic material. The mechanism of cryoconite formation consists of inorganic material moved by surface melt water, re-deposition and accumulation on a glacier surface (Belkina et Mavlyudov 2011). Then, dark clusters mineral particles allocated in a cryoconite spot absorb solar radiation more than particle-free neighborhood causing accelerated surface melt that create cryoconite holes. Over time, cryoconite deposits become compact and form rounded lumps.

This survey was aimed to study the development of moss populations on ice: the possible ways of moss origin on glaciers, the importance of cryoconite and cryoconite holes for the retention and develop-

ment of moss diaspores, the growth of the young mosses inside cryoconite clumps, as well as further course of events in the moss cushions in the long-term glacial populations.



Fig. 1. Map of Svalbard. Glaciers: 1 – Austre Grøn fjordbreen, 2 – Bertilbreen.

Study area

Svalbard archipelago (74° - 81° latitude North and 10°-35° longitude East) includes many islands. The largest of them is Vestspitsbergen. The island coastline forms numerous bays. The largest one is the Isfjorden, located in the middle part of the Vestspitsbergen. Isfjorden has some small bays, including Grøn fjorden in the southwest and Billefjorden in northeast. The islands have mountainous relief with highest altitudes ranging 1200-1700 m, but the most mountains are 400-700 m above sea level. The climate is variable within the archipelago. The Barentsburg Meteorological Observatory on Grøn fjorden coast has conducted climate observations for over

60 years. The average annual temperature in Barentsburg is -6.1°C , the average temperature of the warmest month (July) is $+5.5^{\circ}\text{C}$, of the coldest one (February) is -14.7°C . The average date of stable transition temperatures through zero occurs in spring in 4th of June, in autumn - in 21st of September. Average annual precipitation is 570 mm. From 1976 to 2013, there was an increase in mean annual temperature of 0.86°C per 10 years (Antsiferova et al. 2014). The island vegetation includes zones classified as Arctic polar desert, Northern or Middle Arctic tundra, and the Inner fjord zone (Elvebakk 1989, Möller 2000).

There are more than 100 glaciers on Svalbard (Vinogradov *et al.* 2014), with almost 60% of Svalbard covered by ice (Troitsky *et al.* 1975). The coastal areas of Grønfjorden and Billefjorden have less ice cover than many other areas of Svalbard. Mountain-valley glaciers of the regions are melting rapidly. From 1936 to 2002-2003, the tongue of Austre Grønfjordbreen had retreated 1.2 km and its thick-

ness decreased by 130 m on the lower end of tongue and by 20-30 m in upper part of glacier (Mavlyudov 2004). According with our data, Bertilbreen had receded by 1 km and the level of its ice surface fell by 100 m on the end of tongue and by 77 m just above the ice slope. Cryoconite accumulates in the lower part of the glaciers in large quantities.



Fig. 2. The tongue of Bertilbreen (Bertil Glacier), Svalbard.

Material and Methods

In July 2012, during re-examination of moss cushions on Austre Grønfjordbreen (Grønfjorden, Vestspitsbergen Island), tufts with new species were found. Given the small population size, only a few thalli (leafy plants) from each of the three cushions were sampled for determination. The colonizing mosses were identified. Coordinates of localities were measured with GPS 72 "Garmin".

In August 2013, 30 moss polsters and

visually moss-free globular lumps of cryoconite were collected randomly from ice of Bertilbreen (Billefjorden, Vestspitsbergen) (Fig. 4). Sample size varied 0.5-5 cm. Occasionally, several subsamples were taken from larger polsters. Few moss specimens were identified in the field. Other moss samples were studied in the laboratory where they were washed from cryoconite particles and examined under a microscope (Fig. 5).

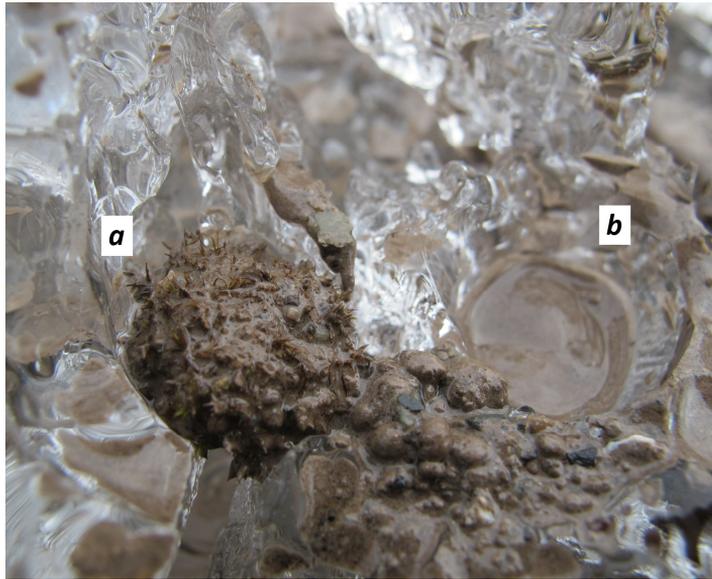


Fig. 3. Moss cushion (a) and cryoconite hole (b) on surface of Bertilbreen.



Fig. 4. Moss cushions of *Schistidium abrupticostatum* (a, b, c) and visually moss-free globular lumps (d) of cryoconite gathered from ice of Bertilbreen.

In laboratory, 10 lumps of cryoconite samples lacking any leaves or stems on their surface were mechanically crushed and studied under microscopes Mikmed-6 var. 7SD (LOMO, Russia) and Axioplan 2 imaging Universal (Carl Zeiss, Germany). Then, moss taxa were separated for determination.

For the three *Schistidium* specimens with ambiguous morphological features from Bertilbreen, we used DNA sequence data to confirm identifications. For DNA isolation, PCR amplification and DNA sequencing we followed protocols described in Konstantinova *et al.* (2011).

Nuclear ribosomal ITS region (ITS1-2) was chosen as an informative locus to species determination based on earlier study of the genus *Schistidium* in Russia (Ignatova *et al.* 2009). GenBank accession numbers and voucher details for Svalbard's specimens are listed in Table 1. BLAST

searches with megablast algorithm (*see link in Other Sources*) were used to distinguish the group of closely related species to three sequenced specimens of *Schistidium*. To test phylogenetic affinity of the Svalbard specimens, we used ITS1-2 sequences of 11 specimens from GenBank (accession numbers and geographical localities are shown in Fig. 6) and performed a maximum parsimony (MP) analysis with TNT v. 1.1 (Goloboff *et al.* 2000). The MP analysis involved a New Technology Search with a search for the minimum-length tree by one reiteration and 1000 bootstrap resamplings; the default settings were used for other parameters, indels were taken into account by a modified complex coding algorithm in SeqState (Müller 2005). The calculation of genetic distances (*p*-distances) was provided with Mega 5.1 (Tamura *et al.* 2011) to characterize infra-specific sequence variability.

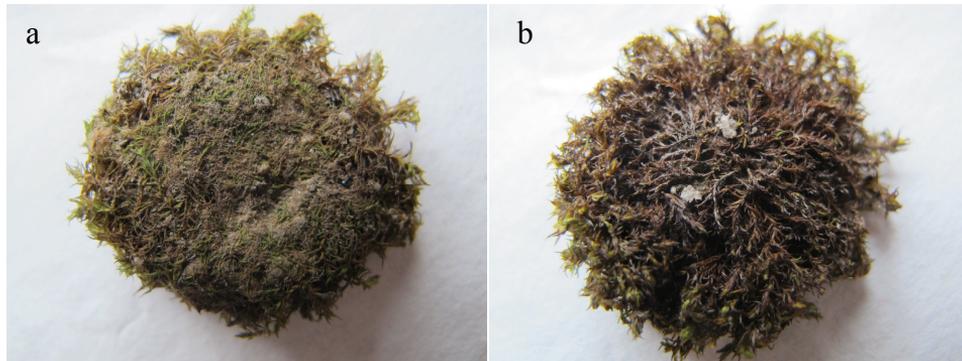


Fig. 5. *Schistidium abrupticostatum*: upper (a) and lower (b) sides of cushion after washing.

Results

On Bertilbreen, two population-forming species were identified: *Hygrohypnella polaris* and *Schistidium abrupticostatum*. The latter did not have sporophytes and putative features of leaves were insufficient to species identification. Gametophytes in few cushions had wide lower leaves similar to *S. rivulare* (Brid.) Podp.,

but in some other cushions – similar to *S. sordidum* I. Hagen. Leafy plants in most cushions have narrow leaves like *S. abrupticostatum*, but without clear transition between lower and upper parts of leaf lamina.

The ITS1-2 sequences were obtained for three doubtful *Schistidium abrupticostatum* specimens from Svalbard, 11 base

pairs (bp) of 3'-end ITS1 and 67 bp of 5'-end 5.8S rDNA for all specimens and 66 bp in ITS1 of specimen #B 9/5-13 were not sequenced and coded as missing data in the alignment. The total length of *S. abrupticostatum* ITS1-2 varied from 846 till 851 bp due to several 2bp indels. BLAST search (magablast) by ITS1-2 revealed that all three molecularly studied specimens of *Schistidium* with atypical features were highly similar to specimens of *S. abrupticostatum* gathered in Kola Peninsula, Severnaya Zemlya and Taimyr in Russia and Canada. (see link in Other Sources). The ITS1-2 nucleotide alignment of three tested specimens and 11 specimens of *S. abrupticostatum* and closely allied *S. rivulare*, *S. sordidum* and *S. platyphyllum* downloaded from GenBank consisted of 983 character sites, among them 742 (75.48%) were constant, 218 (22.17%) were variable and 153 (15.56%) were parsimony informative positions.

The MP analysis with TNT yielded two equally parsimonious trees at different runs

with a length of 759 steps, with CI = 0.904762 and RI = 0.930851 calculated in Mega 5.1. The resulted MP topology is shown in Fig. 6. In the MP analysis the Svalbard specimens were resolved in one clade with other specimens of *S. abrupticostatum*, phylogenetically remotest from *S. rivulare* and *S. sordidum* as previously was shown by Ignatova et al. (2009). It should be mentioned that Bertilbreen specimens did not form a distinct subclade within *Schistidium abrupticostatum*-clade. The infraspecific sequence variability within known *S. abrupticostatum* specimens achieved 1.6% by ITS1-2 that doubled the values of *p*-distances in *S. rivulare*, *S. sordidum* or *S. platyphyllum* (see Table 2). Taking into account the broad circumpolar Arctic and subarctic distribution of *S. abrupticostatum*, subspecies differentiation or cryptic speciation could be assumed. Future taxonomical studies should pay special attention to such enigmatic species as *S. abrupticostatum*.

Specimen vouchers	GeneBank accession number	
	ITS1	ITS2
Norway: Svalbard, Bertilbreen, Billefjord, Bertil Glacier, O. Belkina, B 9/3-13 (KPABG)	KP277106	KP277109
Norway: Svalbard, Bertilbreen, Billefjord, Bertil Glacier, O. Belkina, B 9/5-13 (KPABG)	KP277107	KP277110
Norway: Svalbard, Bertilbreen, Billefjord, Bertil Glacier, O. Belkina, B 9/2a-13 (KPABG)	KP277108	KP277111

Table 1. The list of taxa, specimens vouchers and GenBank accession numbers for studied samples of *Schistidium abrupticostatum* (Bryhn) Ignatova & H.H. Blom.

Species	Value of within species <i>p</i> -distances, %	Value of between species <i>p</i> -distances, %			
		<i>Sa</i>	<i>Sr</i>	<i>Ss</i>	<i>Sp</i>
<i>S. abrupticostatum</i>	1.6				
<i>S. rivulare</i>	0.8	9.5			
<i>S. sordidum</i>	0.8	7.2	13.5		
<i>S. platyphyllum</i>	0.8	8.4	12.3	10.2	

Table 2. The values of *p*-distances for selected *Schistidium* species, calculated from ITS1-2. *Sa* - *S. abrupticostatum*, *Sr* - *S. rivulare*, *Ss* - *S. sordidum*, *Sp* - *S. platyphyllum*.



Fig. 6. Maximum parsimony (MP) phylogenetic tree for the selected *Schistidium* species based on ITS1-2 sequence data. Bootstrap support values more than 50% are indicated. The geographical locality and GenBank accession number are shown for each specimen. The specimens sequenced in this study are underlined.

Pure cushions of *Hygrohypnella polaris* were arranged alternately with pure cushions of *Schistidium abrupticostatum* on ice surface, at a distance 0.1-3 m from each other (78° 40' 50" N, 16° 17' 5" E). Tufts of *H. polaris* (Fig. 7) were larger and located mostly upslope, on flat horizontal ice surface. Cushions of *S. abrupticostatum* (Fig. 8) grew mostly down the slope of the glacier tongue, within the cryoconite holes. They were more numerous, smaller and almost completely enveloped with the cryoconite, than turfs of *H. polaris*. One cushion of *S. abrupticostatum* was found lying (not growing!) on rock in medial moraine (Fig. 9). Concentric layers inside the polsters and "balls" were not found contrary to Benninghoff (1955) who described many layers for cushions in Alaska. Three layers – cryoconite core, discolored (brownish) parts of mosses and their short green tips were observed in the samples from Austre Grønfjordbreen (Belkina et Mavlyudov 2011).

Many plants of *S. abrupticostatum* had gametangia – archegonia and antheridia in a synoicous inflorescence.

Microscopic examination of "bare" cryoconite deposits (0.5 cm diameter) showed that 3 of 10 lacked any mosses or frag-

ments. Other cryoconite samples (0.5-2 cm) had few or many thread-like structures – protonema. It is known that filamentose protonema of Musci develops three kinds of filaments: chloronema, caulonema and rhizoids (Nehira 1983). The filaments can change morphotype from one into another. In cryoconite material, the protonema was presented by rhizoids and caulonema. Rhizoids were brownish with oblique cross walls and permeate the entire cryoconite globules (Fig. 10a). Green caulonema formed short branches, consisting of 1-several widened cells with chloroplasts (Fig. 10b-d). In its other parts the caulonema produced a few buds with developing gametophytes of *Schistidium abrupticostatum* (Fig. 11). Different stages of buds were observed (Fig. 12). The cryoconite deposits sometimes contained both a few fragments of adult plants and numerous protonemata. In some cases, we observed protonema (brown rhizoids) originated from vegetative parts of plants – leaf costa or stem (Fig. 13).

In some specimens, the long unbranched protonema (or rhizoids) was found near mature plants in well-developed cushions of *S. abrupticostatum*: the filamentous structures stretched along the stems or whole leafy plants.

Two additional species were identified in the cryoconite lumps. Inside the one lump, a single occurrence of *Philonotis* sp. was found in good condition. Another cryoconite globule contained small tuft of *Pohlia* cf. *wahlenbergii* (F. Weber & D. Mohr) Andrews.

After 2013 field study, we could not confirm the presence of *Paludella squarrosa* (Hedw.) Brid. on Bertilbreen. The specimen of this species was collected first by B. R. Mavlyudov and A. Kudikov in 2007 (Belkina et Mavlyudov 2011). In the same time, they gathered also specimen of *Schistidium abrupticostatum* in "near the glacier" location and, perhaps, could confuse the labels.

In 2012, the moss populations on Austre

Grønfyordbreen were located on the previous place (77° 55' 54" N, 14° 18' 50" E in 2012 vs. 77° 56' 02" N, 14° 18' 47" E in 2009) while glacier tongue retreated. So the locality was almost on the edge of the tongue. In 2009, polsters of *Hygrohypnella polaris* were pure tufts. Three years later, a few individuals of *Bryum cryophilum* Mårtensson and *Sanionia uncinata* were found among *H. polaris* in three large cushions. *Bryum cryophilum* is hydro-hygrophytic species widespread on adjacent slopes as well as common moss *S. uncinata*. The population of the latter species also occurs on the same tongue of glacier. Therefore we registered the next stage of cushion development – emergence of a di- and multi-species community.



Fig. 7. Cushion of *Hygrohypnella polaris* on Bertilbreen ice.

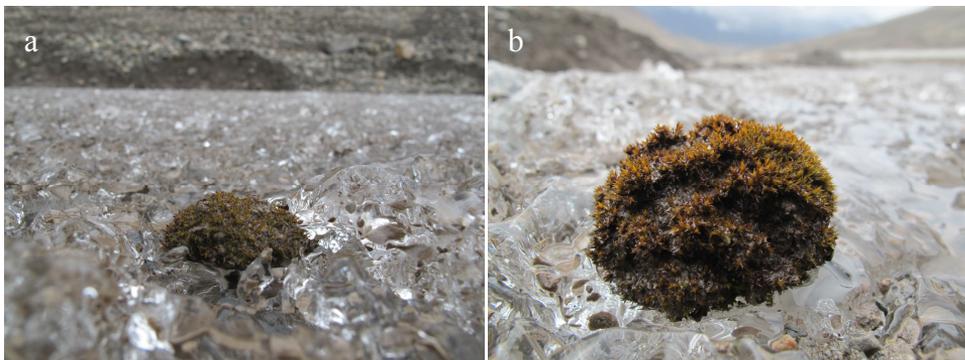


Fig. 8. Cushions of *Schistidium abrupticostatum*: *a* – in small cavity, *b* – on flat surface.



Fig. 9. *Schistidium abrupticostatum* lying (not growing) on rock in medial moraine of Bertilbreen.

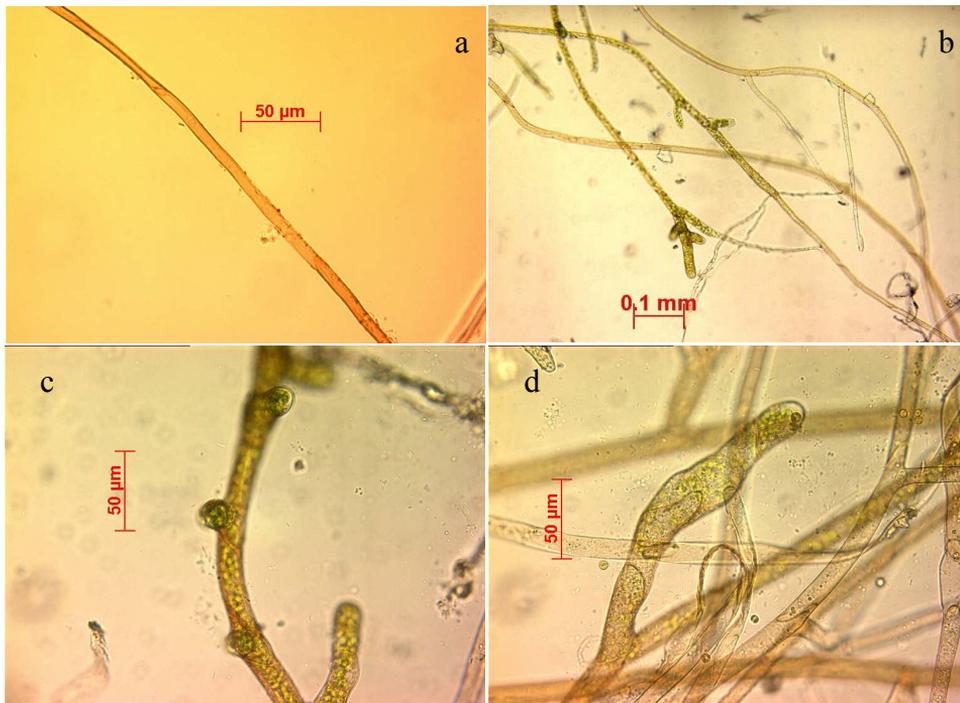


Fig. 10. Protonema of *S. abrupticostatum*: a – rhizoid with slanting cross walls, b – caulonema with widened green cells at the initial stage of buds development (b-d).



Fig. 11. Buds of *S. abrupticostatum* on caulonema (*a, b*).

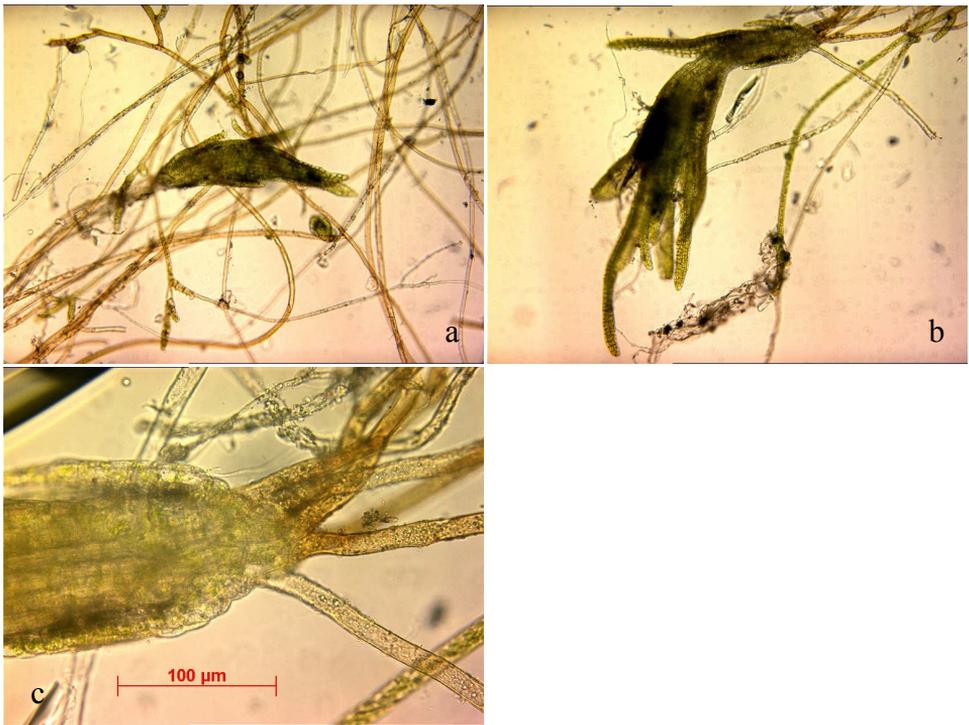


Fig. 12. Young plants of *S. abrupticostatum* developing on caulonema (*a, b*) and the base of them (*c*).

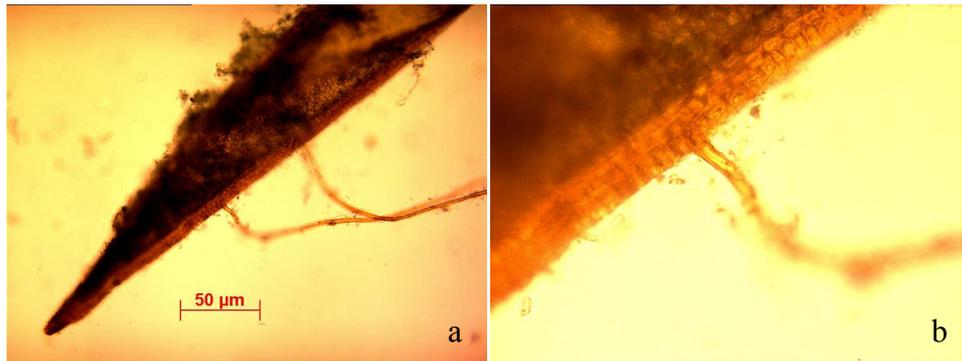


Fig. 13. Filamentous structure (rhizoids) originated from leaf costa (a, b).

Discussion

On Bertilbreen, the population of *Hygrohypnella polaris* is smaller than of *Schistidium abrupticostatum*. It is interesting, that *H. polaris* is not so frequent in surroundings of the glaciers, but this species grows also on Austre Grønfyordbreen. A way of *H. polaris* occurrence on the ice is unclear now and theoretically could be various. This hygro-hydrophytic species was able to survive and create long living populations on ice. Outside the glaciers, this species grows on stony sites flooded temporarily with water, and is, therefore, widely distributes in Svalbard. Sporophytes of *H. polaris* have not been found on archipelago as well as gametangia or sporophytes on glaciers.

Schistidium abrupticostatum produces gametangia, but does not develop sporophytes. In 2009 on Austre Grønfyordbreen, some gametophytes of *Sanionia uncinata* had antheridia and didn't form sporophytes too, although this species can produce mature capsules beyond the glaciers. In different moss populations from Alaskan and Iceland glaciers, no sporophytes were recorded too (Shacklette 1966, Heusser 1972, Seki 1974, Porter et al. 2008, Dickson et Johnson 2014). However, in 2003, *S. uncinata* was able to develop mature cap-

sules on Walker Glacier in Southeastern Alaska (Dickson et Johnson 2014). Perhaps, some species growing on glaciers can develop sporophytes occasionally in most favorable years. But it is not typical way of "glacial mice" reproduction. Failure of sex reproduction of many mosses is widespread in the high polar regions. Moreover, "majority of bryophytes produce neither spores nor specialized asexual propagules and are dependent on gametophyte branching, fragmentation and regeneration for colony establishment, development and maintenance, and for local dispersal" (Longton 1988).

Biological and ecological properties, which ensure the successful colonization of glaciers by mosses were discussed in detail previously (Belkina et Mavludov 2011). Most important features are tolerance to low temperature (including low temperature limits of photosynthesis), the ability to grow on a limited and moving substratum, e.g. on cryoconite sliding down on the ice surface, reproduction and dispersal by vegetative diaspores, a patient (=stress-tolerant) life strategy, and hygro- and hydrophytic ecological preferences.

Benninghoff (1955) assumed that polsters can develop from a young plant in the

vegetative phase or from a fragment of an older plant. They branch, grow and form flat and then round polsters, which is what we observed on Austre Grønfjordbreen.

Our data indicated that new cushions of *Schistidium abrupticostatum* developed young plants from protonema inside globules of cryoconite. The lumps were rich in developing filamentous structures, which originated from either small plant fragments trapped in substratum or can be a result of spore germination. Development of moss protonema on glacial surface was described by e.g. Uetake et al. (2014). They studied novel biogenic aggregation containing protonemal gemmae and protonema of *Ceratodon purpureus* that were collected on a glacier in the Rwenzori Mountains, Uganda.

The origin of the fragments or spores of *S. abrupticostatum* (as well as other mosses) in cryoconite remains unclear. They could roll down from surrounding slopes, be brought by wind or birds and appear from melting glacial ice. An ability of multicellular organisms to survive in permafrost for a long time and regenerate afterwards at above-zero temperature was shown for seeds of vascular plants (Yashina et al. 2012) and for moss spores (Troitsky et al. 2012) as well. La Farge et al. (2013) observed successful regeneration of subglacial bryophyte gametophytes following 400 years of ice entombment and emerging from the ice margin in central Ellesmere Island (Canadian Arctic Archipelago). Although the populations were often discolored (blackened), some plants were able to develop green stem apices or lateral branches suggesting *in vivo* regrowth. *In vitro* growth experiments on the biological viability of moss gametophytes confirmed that four species (*Aulacomnium turgidum* (Wahlenb.) Schwägr., *Distichium capillaceum* (Hedw.) Bruch et al., *Encalypta procera* Bruch and *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr) were regenerated from cultures derived from subglacial specimens. Road et al.

(2014) studied regrowth from shoots and rhizoids of the moss *Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth. obtained from permafrost on Signy Island, maritime Antarctica. Gametophyte material capable to perform some regrowth was collected in a depth of 110 cm and was radiocarbon dated to 1533-1693 cal years. Authors also documented new growth of the liverwort of *Cephaloziella* sp. These findings demonstrate the resilience of bryophytes and their totipotent capacity (the ability of a cell to dedifferentiate into a meristematic state (analogous to stem cells) and develop a new plant). These features allow mosses and liverworts to establish, colonize, and be substantial component of polar terrestrial ecosystems (La Farge et al. 2013).

Majority of studies of glacier-related communities focus rather on microorganisms, such as bacteria, cyanoprokaryotes, algae, fungi, protozoa (e.g. Wharton et al. 1985, Hodson et al. 2008, Mueller et Pollard 2004, Sävström et al. 2002, Edwards et al. 2013) than mosses and their communities. In long-term populations on Austre Grønfjordbreen, every moss cushion was continuing to catch and accumulate cryoconite particles moving down on ice surface inside the cushion. This additional substratum and source of nutrient in moist moss polsters were creating suitable conditions for settlement of other mosses – *Bryum cryophilum* and *Sanionia uncinata*. Earlier, in 2009, a similar process was observed on mammal bone on the same glacier. *Ceratodon purpureus* had colonized the center of a spherical cushion of *Sanionia uncinata* on the both butt-ends of the bone (Belkina et Mavlyudov 2011). Our data are consistent with those of Dickson et Johnson (2014) who studied early plant succession on the Walker Glacier (southeastern Alaska). They described the establishment of *Sanionia uncinata*, *Pohlia filum* (Schimp.) Mårtensson, basidiomycete fungus and seedlings of (c.f.) *Epilobium* on existing cushions of *Racomitrium*

fasciculare (= *Codriophorus fascicularis* (Hedw.) Bendarek-Ochyra & Ochyra). Earlier, Coulson et Midgley (2012) studied invertebrate diversity inside “moss balls” (cushions of *Racomitrium* s. l.) on the Falljökull, Iceland. All studied moss cushions contained invertebrates: species of Collembola (with 0-73 individuals per “glacier mouse”), Tardigrada (about 200 individuals per “mouse”) and Nematoda (1000 per “mouse”). Therefore, mosses play an important role in colonization of glacier surface by higher organisms. The formation of the bi- or multispecies moss polsters can be regarded as the next stage of succession in communities on glaciers.

Conclusion

Moss cushions are established on glaciers not only by falling from surrounding slopes or emerging on surface from melting ice, but also as young, developing plants from filamentous structures (caulonema or rhizoids). In Svalbard, an increasing number of cushions appear to be the result of further growth and development, branching, in particular, of the new mosses inside cryoconite lumps as well as fragmentation of large cushions. DNA analysis revealed that moss cushions constituting an “ice” population of *Schistidium abrupticostatum* are genetically heterogeneous. This indicates an origin of diaspores and

then protonema from different sources but now it is not clear from what. Generally, mosses do not form gametophytes in such harsh conditions even if they produce them in communities surrounding the glaciers. Various mosses could be accidentally brought on the glacier surface and remain in substratum, but only a few species may create long-living populations there. Each moss cushion on the ice presents a small ecosystem with subsequent successional changes. Moss polsters on ice facilitate colonization by many organisms, including other moss species on glacier surface.

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