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LIVERWORTS OF THE MOUNTAIN TUNDRA BELT OF THE NORTH-EAST YAKUTIA

ПЕЧЕНОЧНИКИ ГОРНОТУНДРОВОГО ПОЯСА СЕВЕРО-ВОСТОКА ЯКУТИИ

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Abstract

The materials collected during several expeditions in the mountains of NE Yakutia are summarized; they include the data on species composition, distribution of liverworts in mountain tundra belt in North-Eastern Yakutia and their ecology. In total, 111 liverwort species were revealed; 15 of them are known within Yakutia only here. *Apotreubia hortoniae, Diplophyllum albicans, Frullania ignatovii, Gymnomitrion brevissimum, G. commutatum, Herbertus aduncus, Isopaches alboviridis, Marsupella arctica, M. boeckii,* and *Pleurocladula albescens* are found in Yakutia in 1–3 localities. Presence in mountain ranges, habitats and substrates (most frequent ones are highlighted), presence of gametangia, sporophytes and brood bodies, and most frequent associated species are given for each species. Liverwort species with sound role in vegetation of mountain tundra are revealed. Liverworts preferably inhabit places where competition with mosses and vascular plants is low; however, they avoid unstable substrates. The highest liverwort diversity was observed along mountain brooks with slow current, while the lowest number of species was revealed on rock-fields, solifluction slopes, and near late snowfields. The high species number was found on frost medallions and in pools in bogs.

Резюме

Впервые обобщены многолетние данные по видовому составу, распространению и экологии печеночников, выявленных в горнотундровом поясе в горных массивах Северо-Востока Якутии. В целом выявлено 111 видов печеночников, из них 15 видов в республике отмечено только здесь. *Apotreubia hortoniae, Diplophyllum albicans, Frullania ignatovii, Gymnomitrion brevissimum, G. commutatum, Herbertus aduncus, Isopaches alboviridis, Marsupella arctica, M. boeckii, Pleurocladula albescens* известны в Якутии из 1–3 местонахождений. В списке для каждого вида указаны встречаемость по отдельным горным хребтам, выявленные местообитания и субстрат (с выделением, где этот вид встречается чаще всего), характер произрастания, наличие структур связанных с размножением и наиболее часто встречающиеся сопутствующие виды. Выявлены виды, участвующие в сложении растительного покрова горных тундр в неблагоприятных условиях местного климата. Печеночники предпочитают здесь заселять местообитания, свободные от конкуренции мхов и сосудистых растений, однако избегают мест с подвижным субстратом. Наибольшее видовое разнообразие отмечено по берегам вялотекущих горных ручьев, наименьшее на каменистых осыпях, солифлюкционных склонах, вокруг снежников. Значительное число видов отмечено на морозных медальонах и в мочажинах болот.

KEYWORDS: flora, liverworts, ecology, glacial and cryogenic shapes of relief, mountain systems of Verkhoyansk and Chersky, Yakutia

Introduction

The territory of Yakutia consists of two large geomorphologic areas: the plateau and folded areas. The latter, represented by mountains and high tablelands, covers two thirds of the territory and is largely centered in the northeast of the republic. This is an expanded mountain area east of the Lena River, consisting of the mountain systems of Verkhoyansk and Chersky, nearly inaccessible due to absence of roads. Recently, however, mining has been expanding in the region. In the ecosystems of the tundra belt, plant communities are depleted. Vegetation cover develops under conditions of low summer temperatures, permafrost, cold and long winters. The mountain tundra is a type of vegetation characterized by treelessness, the development of a cover of mosses and lichens, sometimes perennial herbs and dwarf shrubs. Ecosystems dominated by mosses and lichens are most sensitive to various kinds of pollution. Many liverworts are very sensitive to the anthropogenic impact. The most vulnerable are the species with narrow ecological specialization, disjunctive distribution, and low potential for self-sustaining populations (Gushchina, 1989; Troeva *et al*., 2010).

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Study area

Area under consideration includes mountains of North-East of Yakutiya particularly the Kharaulakhsky, Orulgan, Suntar-Khayata, Sette-Daban, and Ulakhan-Chistay Ranges, Yudomo-Maya Highland, and a number of smaller ranges in the vicinity of the Ust-Nera Settlement (Inyalinsky, Tas-Kystabyt, Olchansky) (Fig. 1).

Geologically, the study area is quite diverse the ranges are characterized by the dominance of non-carbonate. Underlying rocks comprise shales, argillites, siltstones, sandstones, as well as rarely arenaceous limestones, calcareous siltstones, limestones, dolomites, marbles. Wide distribution of igneous rocks and intrusions (granites, andesite, basalt, diorites, rhyolites, etc.) is typical for the study area. Sometimes antimony, mercury, arsenic, lead, zinc, nickel, cobalt and other heavy metals are found in rock outcrops (Baranova & Biske, 1964; Korzhuev, 1974; Rusanov *et al*.,1967).

The climate is strongly continental with very low winter and very high summer temperatures. The study area has no analogues both in minimal temperature values and the duration of the period with extremely low temperatures in the Northern Hemisphere and is characterized by significant annual amplitudes. Extremely low temperatures have been recorded in the Oymyakon depression and the Yana intermountain trough: -71°C in Oymyakon and -68°C in Verkhoyansk. Significant annual amplitudes are characteristic for the thermal conditions of Yakutia. The amplitude of absolute minimum and maximum temperatures reaches 104°C in Oymyakon. Although a relatively stable temperature regime at the beginning of winter, that accompanied by increasing of heat irradiation, is gradually broken by mountain temperature inversions. During the anticyclone type of weather, the winter temperatures on the convex relief areas are always higher than in adjacent valleys. However, the absolute minimum temperature in the highlands still reaches levels below 50°C. The average January temperature is -29°C in high mountains to -50°C in spurs. The stable transition of the average daily air temperature above +5°C (beginning of the vegetation period) coincides with June. A distinct feature of the warm period is a quick rise of the average daily temperatures in spring and their quick drop in autumn. July is the warmest month. The average frost-free period lasts 40-90 days. Sometimes frost may occur all summer long. The average July temperature is +6 in high mountains (over 1000 m) to +16°C in spurs and the maximal temperature of July is +21°C to 36°C. The annual precipitation amount for most of the territory is to 150–340 mm, and to 700 mm in the Mus-Khaya Mt. (Izyumenko, 1966, 1968; Mozolevskaya, 1973; Troeva *et al*., 2010).

The whole territory lies in the zone of perennially frozen soils, the thickness of which exceeds 700 m. The average annual temperature of perennial frozen grounds at a depth of 15–20 m reaches -10° to -12°C at high

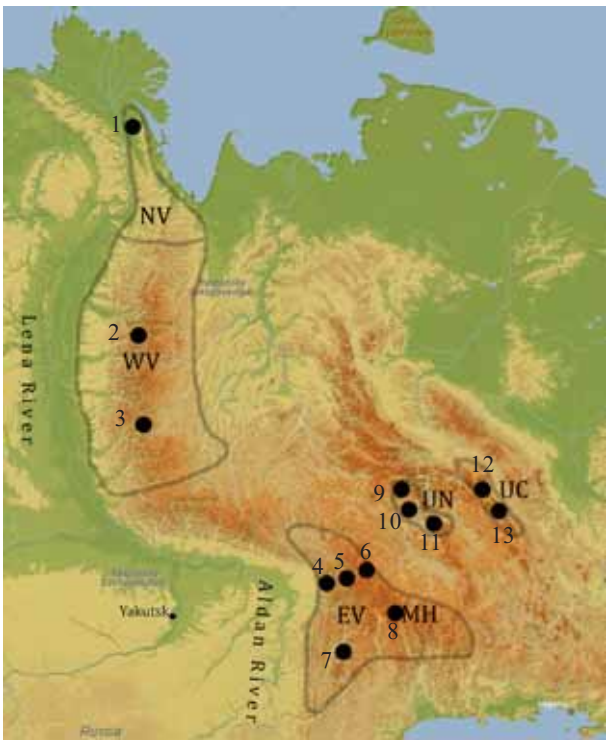

Fig. 1. Map of North-East Yakutia, outlining high-mountain areas, indicating the areas of exploration.

Verkhoyansk mountain systems. Northern Verkhoyansk Range (NV): 1 – Kharaulakh Range; Western Verkhoyansk Range (WV): 2 – Orulgan Range, Tumara River area, 3 – Orulgan Range, Khobol River area; Eastern Verkhoyansk Range (EV): 4 – Sette-Daban Range, Segennyakh River area, 5 – Suntar-Khayata Range, Kyurbelyakh River area, 6 – Suntar-Khayata Range, Kyubyume River area; 7 – Yudomo-Maya Upland, Tarbagannakh Massif area; 8 – Mus-Khaya Mt. (Suntar-Khayata Range).

Chersky mountain systems: Ranges in the vicinity of Ust-Nera (UN): 9 – Inyali Range area, 10 – Olchansky Range area, 11 – Tas-Kystabyt Range area; Ulakhan-Chistay Range (UC): 12 – Tirekhtyakh River area; 13 – Artyk River area.

watersheds in the mountains. Permafrost is a basic factor greatly influencing the distribution and functioning of ecosystems, and vegetation in particular. Soils start thawing right after the snow cover has melted, and they freeze in autumn as soon as the average daily air temperature comes below 0°C. The freezing process proceeds simultaneously in a top-down and a bottom-top direction, and in January both frozen layers meet. Thawing depth values are not constant and depend on the meteorological features of a year. Firmly frozen, ice-bound strata represent waterproof horizons for precipitation and facilitate to some extent soil wetting by oozing out ground moisture during seasonal periods of thawing. Glacial and cryogenic relief is common in the study area. The glacial macro- and microrelief (cirques, trogas, moraines, frost soil heaving, frost cracking, formation of vein ice and polygonal surfaces) and cryogenic processes (solifluction and thermokarst) are quite common (Nekrasov, 1984; Troeva *et al*., 2010).

Fig. 2. Habitats of hepatics: A: dwarf shrubs tundra; B: lichen tundra; C: *Eriophorum+Carex stans* mire; D: mountain tundra belt; E: the snowfields areas; F: stone fields and moving screes; G: sluggish mountain streams; H: banks of fast-flowing stream.

Liverworts in plant communities and landscape

The tundra belt is located above the forest belt and represents a significant proportion of the study area. There are common lichen, mosses, shrub and grass tundra types, cotton grass, sedge and sphagnum bogs. Liverworts on bare stones along the banks of powerful watercourses are absent. Rock outcrops are usually common here. Sluggish mountain streams form banks of soil, which are always covered with mosses. Mountain slopes are covered with stone fields and moving screes.

In mountain tundra liverworts, generally, grow as single-species coverings over 1 sq. cm, or, more often, forming a mixture of 3 to 15 species. In various small cavity the liverworts often form mats up to 10 sq. cm. Mats as large as 10 sq. cm and more are formed on soil surface. Here liverworts occur in small cavity on soil or under stones, between small gravel, under dwarf shrubs or lichens, rarely on soil in multispecies mats. Wet tundra with dominance of *Sanionia uncinata, Aulacomnium turgidum, Hylocomium splendens* var. *obtusifolium, Tomentypnum nitens, Brachythecium* spp., *Bryum* spp., *Dicranum elongatum, Ptilidium ciliare* is developed under conditions of excessive moistening. In these tundras, the following liverworts form large or extensive mats (for growth pattern see below in Species list): *Odontoschisma macounii, Radula prolifera, Sauteria alpina, Scapania simmonsii* on calcium containing substrate and *Schistochilopsis opacifolia*, *Marsupella apiculata* on acid substrate. Slopes of mountains are covered by dwarf shrub and lichens tundras. Here the liverworts are less common. *Cassiope tetragona, C. ericoides, Dryas punctata, D. viscosa, D. octopetala, Salix sphenophylla, Ledum palustre* subsp. *decumbens, Rhododendron lapponicum* subsp. *parvifolium, R. redowskianum*, and *Rhododendron adamsii* dominate in the dwarf shrub tundra. Large mats are characteristic for *Gymnomitrion corallioides, Tetralophozia setiformis, Barbilophozia barbata*. *Gymnocolea inflata* once under a dense canopy of dwarf shrubs on very moist soil formed a large mat. In lichen tundra, the liverworts form small mats only: *Tetralophozia setiformis, Gymnomitrion corallioides, Scapania crassiretis, Ptilidium ciliare, Radula prolifera, Diplophyllum obtusifolium, Sphenolobus minutus, Prasanthus suecicus, Schistochilopsis grandiretis*, etc. In tundra with sparse cover of grasses and sedges, five species form only small mats: *Barbilophozia barbata, Lophoziopsis excisa, Pseudotritomaria heterophylla, Scapania parvifolia*, and *Schljakovia kunzeana*. In depressions with hampered groundwater run-off bogs with *Sphagnum* ssp., *Eriophorum* ssp., *Carex* ssp. are developed. In the bogs, liverworts grow on *Sphagnum* hummocks or in swampy hollows on soil. *Ptilidium ciliare* and *Gymnocolea inflata* form large and extensive cover on soils. *Neoorthocaulis binsteadii, Calypogeia muelleriana, Pseudolepicolea fryei* form small cover on *Sphagnum*. Liverworts on stream banks and rocky substrates reach particular abundance and diversity. On stream soils of the tundra belt *Mesoptychia sahlbergii, Frullania subarctica* form an extensive, while *Gymnocolea inflata, Gymnomitrion concinnatum, Marchantia romanica, Neoorthocaulis hyperboreus, Scapania crassiretis*, and *Pellia endiviifolia* form a large cover. On the rock-fields in niches between the stones *Tetralophozia setiformis, Marsupella emarginata* and *Ptilidium ciliare* develop a large cover. On scree, among small stones, minute and small cover is characteristic for *Trilophozia quinquedentata, Barbilophozia barbata, Blepharostoma trichophyllum, Lophoziopsis excisa, Ptilidium ciliare* and *Scapania parvifolia*. High species diversity is noted on wet cliff. *Tetralophozia setiformis, Frullania subarctica, Gymnomitrion corallioides, Marsupella emarginata, Scapania microdonta* and *Scapania spitsbergensis* form extensive carpets or large patches. In dry rock fissures, the liverworts may form only small cover. They are *Barbilophozia barbata, Gymnomitrion corallioides, Plagiochila porelloides, Radula complanata, Scapania degenii*, and *Tetralophozia setiformis*. Gold mining areas, which are still not extensive in the studied territory, were also examined. Only *Blasia pusilla* were identified here.

Species list

The list of liverworts is given in Table 1. It is based on materials collected by the author. Lists of species for separate mountain ranges have been published previously (Sofronova, 2000, 2003, 2011, 2015, 2018, 2019; Sofronova & Potemkin, 2016 a,b; Sofronova & Sofronov, 2010, 2012; Sofronova *et al*., 2015). In total, 67 specimens from tundra belt were collected in the Kharaulakh Range, 155 – in western Verkhoyansk Range, over 200 – in eastern Verkhoyansk Range, 173 – in vicinity of the Mus-Khaya Mt., 56 – in vicinity of the Ust-Nera Settlement, 83 – in the Ulakhan-Chistay Range. All specimens are stored at the Herbarium of Institute for Biological Problems of Cryolithozone SB RAS, Yakutsk (SASY). Accepted abbreviations in Table 1 (See Fig. 1):

Discussion

For the first time, a list of liverworts of the tundra belt of the North-East of Yakutia has been compiled. In total, 111 species of liverworts were recorded in all habitats of the mountain tundra belt of the North East of Yakutia, 15 species are limited in its distribution only to tundra belt (*Apotreubia nana, Diplophyllum albicans, Frullania ignatovii, Gymnomitrion brevissimum, G. commutatum, Herbertus aduncus, Isopaches alboviridis, Marsupella arctica, M. boeckii, Pleurocladula albescens, Marsupella apiculata, Neoorthocaulis hyperboreus, Prasanthus suecicus, Radula prolifera, Scapania kaurinii*). First ten species were recorded only 1–3 times in the republic. *Gymnomitrion concinnatum, Marsupella apiculata, Scapania kaurinii, Radula prolifera*, and *Prasanthus suecicus* are fairly common in the tundra belt. In tundra communities, 87 species were identified, 61 spe-

Table 1. List of hepatics of high-mountains of Yakutia. Abbreviations are as follow:

Areas (cf also map in Fig. 1): NV – northern Verkhoyansk Range (Kharaulakh Range, in its boreal part), WV – western Verkhoyansk Range (Orulgan Range), EV – eastern Verkhoyansk Range (SH – Suntar-Khayata Range, SD – Sette-Daban Range, Yudomo-Maya Upland), MH – Mus-Khaya Mt. as a part of the Suntar-Khayata Range, UN – vicinity of the Ust-Nera Settlement (including Inyali Range, Tas-Kystabyt Range, Olchansky Range), UC – Ulakhan-Chistay Range.

Substrate: S – soil (S – soil, PS – peaty soil and decaying plantresidues), R – rocky substrates (S – stones with soil, F – fine earth, R – bare stone), M – mosses (Sph – on and/or among *Sphagnum*, D – on and/or among *Dicranum*).

Habitats: T – tundra (S – dwarf shrubs (mainly *Dryas* ssp., *Cassiope* ssp., dwarf willows *Salix reticulata, S. sphenophylla*, etc., *Rhododendron redowskianum*, etc.), M – mosses, L – lichens); M – mires (C – *Carex* ssp., E – *Eriophorum* ssp., S – *Sphagnum* ssp.). B – banks of mountain streams; R – SF (stone fields), R (rocky outcrops), S (screes).

GP – growth pattern (FP – few plants, M – minute cover, up to 1 sq. cm; S – small, up to 100 sq. cm; L – large, up to 1 sq. m; E – extensive cover, more than 1 sq. m).

Reproduction: G – gemmae, P – perianthia, pseudoperianthia or other protective structures of gynoecia/sporophytes (+p – paroicous), A – androecia, fr – sporophytes); number of crosses means frequency: + less than 50%, ++ at least 50%, +++ always.

Those habitats and substrates where the species most frequent and its more often abundance (GP) are in boldface.

Species	Area						Substrate			Habitats				GP	Reproduction		
	NV	WV	EV	MH	UN	UC	S	R	M	T	M	B	R		G	P	A	Fr
Aneura pinguis	+	+	+	+	+	+	**S**	S	Sph	**S**,M,L	S	**B**		**FP**,M,S		+		+
Anthelia juratzkana	+	+	+	+	+	+	**S**	S,F	Sph	**M**,L,S	C,E	B	R,**SF**	**FP**,M,S		+p		+
Apotreubia cf. hortoniae			SH				S					B		FP				
Arnellia fennica	+					+	S			S			R	FP,S				
Asterella saccata		+					S			M			R	FP		+		
Barbilophozia barbata	+	+	+	+		+	**S**	**F**,S		M,G,S		B	**SF**,R,S	**FP,S**,M,L				
Barbilophozia hatcheri	+	+	SH				S	**S**,F		M			**R**,SF	**FP,S**	+			
Barbilophozia sudetica				+	+	+	**S**	S,F		M,S		B	**SF**,R	**FP,S**,M	++	+	+	+
Blasia pusilla	+					+	S					B	R	FP,S				
Blepharostoma trichophyllum	+	+	+	+		+	**S**,PS	S,F,R	Sph	**M,S**,L	S,C	B	**R**,SF,S	**M,S**,FP		+		+
Calycularia laxa			SH	+	+	+	**S**	F		M,S		**B**	SF	**FP**,S		+	+	+
Calypogeia muelleriana						+			Sph		E			S				
Cephalozia bicuspidata	+		+	+	+	+	**S**,PS	S,F,R	Sph	**S,M**,L,G	C,S,E	**B**	SF,R	**M**,FP,S		++		+
Cephaloziella divaricata		+				+	S						R	FP,M		+	+	+
Cephaloziella rubella				+			S			S				M		+p		+
Cephaloziella varians		+	+	+	+	+	**S**	F,S		**S,G**,L	E	**B**	R,SF	**FP,M**,S	++	+		+
Clevea hyalina		+				+	**S**	S		M		B	R	FP		+		+
Cryptocolea imbricata	+		SH		+	+	**S**			S,M,L	S	**B**		**FP**,S		+	+	
Diplophyllum albicans						+	S					B		S	+			
Diplophyllum obtusifolium			SH	+		+	**S**	F		**S,L**		B	**R**,SF	**M**,FP,S	+	++p		+
Diplophyllum taxifolium				+	+		**S**	S		M,L		**B**	**R**,SF	**M**,FP,S	+			
Endogemma caespiticia						+	S					B		FP				
Eocalypogeia schusterana		+				+	S	S		S			R	FP,M				
Frullania ignatovii			SH	+				F,S		L			R	M,S				
Frullania subarctica	+		+	+		+	S	**S**				B	**R**	**S**,L,E				
Fuscocephaloziopsis pleniceps		+	+	+			**S**	S		**S**,M,L		B		**S**,M,FP		+	+	+
Gymnocolea inflata				+		+	**S**	F		S,M	**C**	**B**	R	**L,S**,M,FP,E		++		+
Gymnomitrion brevissimum						+	S			L				M		+		+
Gymnomitrion commutatum				+			S			S			R	FP,M				
Gymnomitrion concinnatum		+	+	+	+	+	**S**	**S**,F		M,S,L		B	**R,**SF	**S,FP**,M,L		+	+	+
Gymnomitrion corallioides	+	+	+	+	+	+	**S**	F,S		L,S,M		B	**R**,SF	**S,M**,L,FP		+	+	+
Herbertus aduncus				+		+	S	S				B	R	FP,S				
Isopaches alboviridis				+		+	S			S				**FP**,M	++		+	
Isopaches bicrenatus		+	+	+	+	+	**S**	F		**L,S**,M,G		B	R,SF	M,FP	++	+p		+
Jungermannia borealis		+	+			+	**S**	R,S				**B**	R	**S**,M,FP		+	+	
Jungermannia polaris	+	+		+		+	**S**	**F**,S		S		**B**	**R**	**M,FP**,S		++p		++
Lejeunea alaskana			+			+	S	S				B		M,S				
Lophozia savicziae		+	+	+	+	+	**S**	S	Sph	S	E	**B**	R	FP,M,S	++			
Lophozia ventricosa				+		+	S,PS				C			FP,S	+			
Lophozia wenzelii				+	+	+	S	S	Sph		E		SF,R	FP	+++			
Lophoziopsis excisa		+	+	+	+	+	**S**	**F**,S		**S**,G,L,M			**SF,R**,S	**FP,M**,S	++	+p		+
Lophoziopsis pellucida		+		+		+	S			M		B		FP,M	+++		+	
Lophoziopsis polaris	+	+	+	+	+	+	**S**	S,F	D	**M**,S,L,G		**B**	R	**FP,M**,S	++		+	
Lophoziopsis propagulifera		+	+	+			**S**	S		**L**,M			R	FP,M	+	+		+
Mannia pilosa	+	+					S						R	FP		+		+
Marchantia polymorpha subsp. polymorpha						+	PS				S			FP				
Marchantia romanica	+	+	+	+	+	+	**S**	S		S		**B**	**R**	**FP**,S,L		+	+	+

Species	Area						Substrate			Habitats				GP	Reproduction		
	NV	WV	EV	MH	UN	UC	S	R	M	T	M	B	R		G	P	A	Fr
Marsupella apiculata				+		+	**S**	F		**M**	E		**R**,SF	**FP,S**,L		+		+
Marsupella arctica						+	S			L				FP				
Marsupella boeckii					+	+	S	S					R	M		+	+	
Marsupella emarginata			+	+	+	+	S	S,F				B	**R**,SF	**S**,FP,M,L,E		++		+
Marsupella sprucei				+	+	+	**S**	S		**M**,L		B		FP,M		+++p		++
Mesoptychia badensis		+	SD				**S**	S		**S**,M			R	**M**,FP,S		++		
Mesoptychia gillmanii	+	+		+		+	S			**M**,S		**B**	R	**S,FP**,M		+p		+
Mesoptychia heterocolpos	+	+	+	+		+	**S**		Sph	**M**,S		**B**		**FP**,M,S	+			
Mesoptychia sahlbergii	+	+	+			+	**S**	S,F		S,M		**B**	**R**,SF	FP,M,S,E				
Moerckia flotoviana						+	S					B		FP		+		+
Mylia anomala				+				S					R	M				
Nardia geoscyphus	+	+	+			+	**S**	F		**M**,S		B	R	**FP**,S		+p		+
Neoorthocaulis binsteadii			+	+		+	S		Sph	M,L	**S**,E			**FP,S**,M	+	+	+	
Neoorthocaulis hyperboreus		+					S			M		B		FP, L				
Odontoschisma macounii	+	+	+	+		+	**S**	S		**M,S**		B	R	**M,FP**,S,L	+			
Oleolophozia perssonii		+	SD			+	**S**	S		S		B	R	FP,M,S	+++		+	
Pellia endiviifolia						+	S					B		FP,L		+		
Peltolepis quadrata						+	S					B		S		+	+	+
Plagiochila arctica	+	+		+		+	**S**	S		S,G		**B**	**R**,SF	**FP**,M				
Plagiochila porelloides	+	+	+	+		+	**S**	F,S		S,L,M,G		**B**	**R**,SF	FP,M,S				
Pleurocladula albescens				+			S			M				FP				
Prasanthus suecicus				+		+	S			**S,L**,M	E		R	**S,FP**,M		+p		+
Preissia quadrata		+	+			+	S			**S**,M		**B**	R	**FP,S**,M		+	+	+
Pseudolepicolea fryei						+			Sph	M	**C**			FP,M,S		+		
Pseudotritomaria heterophylla	+	+	+	+	+	+	**S**	S,F		**M**,S,L,G		**B**	**R**,SF	**M,FP**,S	++	+	+	
Ptilidium ciliare	+	+	+	+		+	**S**	**F**,S	Sph	**M,S**,L	**E**,S	B	**SF**,RS	**FP,S**,M,L,E				
Radula complanata		+	+				S	F		**M**		B	**R**	FP,S	+	+p	+	
Radula prolifera		+	+	+		+	**S**	S		**S,M**,L	S	B	R	**S**,M,FP,L		+		
Riccardia chamaedrifolia			+	+	+		S			S	C	**B**		FP				
Riccardia palmata						+	PS		**Sph**		C			**FP**,M				
Sauteria alpina		+					S			M				L		+		+
Scapania brevicaulis		+					S			M				S	+			
Scapania crassiretis	+	+	+	+	+	+	**S**	S,F		**M**,L,S	S	**B**	**SF**,R	**FP,S**,L	++			
Scapania curta		+		+		+	S,PS	F			S		**R**	**M**,FP	+			
Scapania cuspiduligera	+	+	+	+		+	**S**	F		**M**		**B**	SF,R	**FP, M**,S	++	+	+	
Scapania degenii	+	+				+	**S**	F		**M**		B	**R**	FP,S	+			
Scapania gymnostomophila	+	+	+			+	**S**	**F**,S		**M**,S		B	**R**,SF	**M**,FP,S	+++		+	
Scapania hyperborea		+		+		+	**S**	S,F		M,S		B	R,SF	**FP**,M,S	+	+	+	
Scapania irrigua			SH		+		S			S		B		S	+++			
Scapania kaurinii			+	+	+		**S**	**S**,F				**B**	**R**,SF	**S**,FP,M	+	+p		+
Scapania microdonta			+	+	+	+	S	**F**,S		L			**SF**,R	**FP,S**,L	+			
Scapania mucronata				+			S			S,M				FP,M		+		
Scapania obcordata				+			S	S		M		B		FP,S	+++			
Scapania paludicola					+	+	**S**,PS		**Sph**	G	S,E	**B**		**FP**,S				
Scapania parvifolia	+		+	+	+	+	**S**,PS	S,F	Sph	**S,M**,L,G	C,E	B	R,SF,S	**M,FP**,S	++	+	+	+
Scapania praetervisa		+	+			+	S			S,G		B		**FP**,S	++			
Scapania rufidula			+		+	+	S					**B**	R	FP,S	+		+	
Scapania scandica				+	+		S			S	C	B		**M**,S	+	+	+	
Scapania simmonsii	+	+	+	+		+	**S**	S		**M,S**		B	SF,R	**FP**,M,S,L			+	
Scapania sphaerifera		+	+	+	+	+	S	**F**,S					**SF**,R	**FP**,M	+++			
Scapania spitsbergensis		+	+	+	+		**S**	**S**,F		M			**SF**,R	**S**,M,FP,L	+	+p		
Scapania zemliae		+						S					R	S	+	+		
Schistochilopsis grandiretis	+	+	+	+		+	**S**		Sph	**M,S**,L	C,S	B	**R**	**FP,M**,S	+			
Schistochilopsis incisa	+	+	+	+		+	**S**,PS			**M**	**S**,C	B	SF,R	**FP**,M,S	+	+	+	+
Schistochilopsis opacifolia	+	+	+	+	+	+	**S**	S		**M**,L		**B**		**FP**,M,L	++	+		+
Schljakovia kunzeana		+	+	+		+	**S**,PS	S		**S**,G	S	B	SF	**FP,S**,M				
Schljakovianthus quadrilobus	+	+		+			**S**	F		S		**B**	R	**FP**,M				
Solenostoma confertissimum			SH	+			S			**M**,L,S		B		**FP**,S		+p		+
Solenostoma hyalinum			SH	+			S	S			C	B		FP,S				
Solenostoma obovatum	+		+	+		+	S			M	E	**B**	R	**FP**,M,S		+p	+	+
Sphenolobus minutus	+	+	+	+	+	+	**S**,PS	S,F	**D**,Sph	**S,L**,M	C,E,S	B	**SF**,R	**FP,M**,S	+	+	+	
Sphenolobus saxicola	+	+	+	+	+	+	**S**	**F**,S		**S,L**,M		B	**SF,R**	**FP,S**,M				
Tetralophozia setiformis	+	+	+	+	+	+	S	**F**,S		**L**,S			**SF**,R	**S,L**,FP,M				
Trilophozia quinquedentata	+	+	+	+	+	+	**S**,PS	**F**,S,R	Sph	**M**,S,L,G	**C**,S,E		**SF**,R,S	**S,FP**,M	+	+	+	

cies in moss tundra, 58 species in shrub tundra, and 38 species in lichen tundra were found. Much less liverworts (14 species) were recorded in grass tundra. Totally, 35 species were recorded in bogs, 16 species in *Sphagnum* bogs, and 15 species in *Carex* and *Eriophorum* bogs respectively. Totally, 79 species were found on rocky habitats, 75 species on rocky outcrops, 38 in stone fields, and 6 species on screes. Eighty species grew along the banks of mountain streams.

The liverworts take part in overgrowing of glacial and cryogenic shapes of relief along with vascular plants, mosses and lichens. In the study area, they were found on frost medallions, frost heave (frost mound), in flark (swampy hollow), frost cracks, solifluction flows, surroundings of snowfields.

A number of liverworts in the study area was often associated with frost medallions. When the amount of soil water is considerable, increasing of its amount resulted in rupture of ground surface, extrusion of unfrozen ground through it and formation of such cryogenic clayey spots that often are overgrown by liverworts. Liverworts growing on frost medallions avoid competition with mosses and lichens. The most common on frost medallions in Verkhoyansk and Chersky mountain systems are *Anthelia juratzkana, Cephalozia bicuspidata, Cephaloziella varians, Gymnomitrion corallioides, Isopaches bicrenatus, Lophoziopsis polaris, Odontoschisma macounii, Prasanthus suecicus, Pseudotritomaria heterophylla, Scapania parvifolia, Schistochilopsis* ssp., *Sphenolobus minutus*, etc., whereas *Gymnomitrion brevissimum, Isopaches alboviridis, Marsupella sprucei*, and *Nardia geoscyphus* are rare here.

In regions with permafrost, the formation of frost heave (frost mound) is a common occurrence. Soil swelling occurs with an uneven increase in their volume during freezing, which occurs both due to an increase in the volume of water available in the soil and the influx of moisture that migrates from the outside to the freezing front. Lichens and mosses abundantly grow on the hillocks; liverworts are rare here (*Gymnomitrion corallioides, Ptilidium ciliare, Sphenolobus minutus*, and *Trilophozia quinquedentata*).

Common species often grow in bog flarks (swampy hollow) – *Aneura pinguis, Blepharostoma trichophyllum, Calypogeia muelleriana, Cephalozia bicuspidata, Cephaloziella varians, Neoorthocaulis binsteadii, Ptilidium ciliare, Radula prolifera, Scapania crassiretis, Scapania paludicola, Scapania parvifolia, Schistochilopsis grandiretis, Schistochilopsis incisa, Sphenolobus minutus, Trilophozia quinquedenta*, etc. and less often *Cryptocolea imbricata, Lophozia savicziae*.

Frost cracks are quite significant in the study area. In frost cracks the following common for Verkhoyansk and Chersky mountain systems species were mentioned: *Blepharostoma trichophyllum, Fuscocephaloziopsis pleniceps, Lophoziopsis excisa, L. polaris, Mesoptychia badensis, M. heterocolpos, Plagiochila porelloides, Scapania simmonsii, Tritomaria quinquedentata*, etc. In deep frost cracks with water the following species that are common for Verkhoyansk and Chersky mountain systems were mentioned: *Calycularia laxa, Cephalozia bicuspidata, Lophoziopsis excisa, Scapania scandica, Sphenolobus minutus*.

Cryogenic solifluction develops on grounds subjected to shallow fire-setting and over wetted by water from melted snow and rain, that can not percolate through frozen ground. As a result, the over wetted melted ground masses flow along the frozen and fixed by ice slope surfaces. The terrace gentle slopes (5°–20°) in the surroundings of Mus-Khaya Mt., a weakly fixed layer of broken stones due to solifluction were covered with the lichen-dwarf shrub tundra with *Ledum palustre* subsp. *decumbens, Vaccinium vitis-idaea*, and *Cassiope ericoides*. There on wet soil, under the dense cover of dwarf shrubs *Gymnocolea inflata* covered up to 15 % of depressions surface. It was associated with *Isopaches alboviridis* and *Cephalozia bicuspidata*.

The snowfields areas in the study area are poorly developed. They are confined to the North-faced slopes and most of them melt away at the end of summer. Near investigated snowfields areas the liverworts were mostly absent. It may be explained by the exceeding mobility of soil around the snowfields areas. Only several hepatics were collected in the niches under stones. They are *Blepharostoma trichophyllum, Barbilophozia barbata, Lophoziopsis excisa, Mesoptychia badensis, Preissia quadrata, Ptilidium ciliare, Scapania parvifolia, Solenostoma obovatum*, and *Trilophozia quinquedentata*.

In the study area, the valleys of lateral trough streams are usually less deep as compared to the main trough. This results in formation of waterfalls in such places up to 30-50 m high. Several species that are rarely on territory of Yakutia were collected there. In such places, *Frullania ignatovii, F. subarctica, Herbertus aduncus, Lejeunea alaskana, Marchantia romanica, Marsupella apiculata* and *M. boeckii* were collected.

Thereby, liverworts most frequently inhabit places where the competition with mosses and vascular plants is low; however, they avoid moving, unstable substrates. The highest liverwort diversity was observed along mountain brooks with slow current, while the lowest number of species was revealed on rock-fields, solifluction slopes, and near late snowfields. The high species number was found on frost medallions and in pools in bogs. In areas of gold mining only one liverwort species, *Blasia pusilla*, was revealed.

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Supplementary material

Table 2 with most common associated species for each species.