

LIVERWORTS OF STONE BIRCH FORESTS OF YAKUTIA ПЕЧЕНОЧНИКИ КАМЕННОБЕРЕЗНЯКОВ ЯКУТИИ

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Abstract

Deciduous forests occupy only 1-2% of forested area of Yakutia and do not play a significant role in the forest cover of the republic. However, the species composition of these communities is quite diverse and peculiar. Data on liverwort species composition of birch forests (*Betula lanata* (= *B. ermanii* var. *lanata*) in South Yakutia are given for the first time. In total, 37 species and two varieties of 26 genera of liverworts were recorded there. Two species, *Bazzania tricrenata* and *Diplophyllum obtusatum*, were found in Yakutia only in this type of forest. Although stone birch forests occupy small areas in the territory of the republic, rare species *Anastrophyllum michauxii*, *Frullania koponenii*, *Orthocaulis attenuatus*, *Tritomaria exsecta* are found there. Stone birch forests play a significant role in liverworts diversity conservation. A comparison of stone-birch forests in different parts of Yakutia is given, along with the similar comparison for spruce and larch forests, showing more stable hepatic diversity in stone-birch forest in areas with contrasting climate in comparison with other types of forests.

Резюме

Лиственные леса в Якутии занимают менее 1-2% лесопокрытой площади и не играют существенной роли в лесном покрове республики, однако они вносят разнообразие в растительный мир региона. Данные по видовому составу печеночников березняков Южной Якутии приводятся впервые. Всего в камменноберезовых лесах выявлено 37 видов и 2 разновидности печеночников из 26 родов. Два вида, *Bazzania tricrenata* и *Diplophyllum obtusatum*, ограничены в своем распространении в республике только камменноберезняками. В целом, леса из березы каменной в республике, хотя и занимают крайне небольшие площади, содержат в своем составе ряд редко встречающихся на ее территории видов (*Anastrophyllum michauxii*, *Frullania koponenii*, *Orthocaulis attenuatus*, *Tritomaria exsecta*) и играют важную роль в сохранении разнообразия печеночников Якутии. Видовое разнообразие печеночников в камменноберезняках не сильно изменяется в зависимости от внешних факторов, на него значительнее влияет доступность экотопов, как правило, связанная с конкуренцией со стороны сосудистых растений и мхов. Сравнение флоры печеночников лесов различных типов показывает, что в лиственных и еловых лесах видовое разнообразие сильно зависит от макроклиматических условий, тогда как в камменноберезовых лесах создается среда, позволяющая существовать сходной флоре печеночников в районах с сильно различающимся климатом.

KEYWORDS: flora, liverworts, ecology, deciduous forests, *Betula lanata* (= *B. ermanii* subsp. *lanata*) forests, *Chosenia*, *Populus*, *Larix*, *Picea* forests, Yakutia.

INTRODUCTION

Deciduous forests occupy 1-2% of the total forested area of Yakutia and do not play a significant role in the forest cover of the republic. However they contribute to the plant diversity of the region creating favorable conditions for many plant species which are not typical for larch taiga zone. In the mountain areas of Yakutia deciduous forests are formed mainly by *Chosenia arbutifolia* (Pall.) Skvorts. and *Betula lanata* (Regel) V. Vassil. *Betula pendula* Roth, *Populus suaveolens* Fisch. and *Populus tremula* L. forests are very rare and cover insignificant areas (Timofeev, 2003). The taxa volume and authorship for vascular plants here and below are given in

accordance with the monograph "The conspectus of flora of Yakutia" (Kuznetsova & Zakharova, 2012).

The most common of deciduous forests are *Chosenia* forests growing in mountain river valleys. *Chosenia* is a fast-growing pioneer tree occupying young and loose alluvial deposits. The author has studied dozens of different sites of *Chosenia* forests but only eight species were collected there: *Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Cephaloziella varians*, *Lophozia excisa*, *Plagiochila porelloides*, *Ptilidium ciliare*, *P. pulcherrimum*, and *Tritomaria quinquentata*. In *Betula pendula* forests three species were found: *Cephaloziella* cf. *vari-*

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ans, *Lophozia excisa* and *Ptilidium ciliare*. In *Populus suaveolens* forests only 2 species were recorded: *Plagiochila porelloides* and *Ptilidium pulcherrimum*. In the surveyed *Populus tremula* forests liverworts were not found.

Stone birch (*Betula lanata* (Regel) V. Vassil., or *B. ermanii* Cham. subsp. *lanata* (Regel) A. Skvorts.) is one of the few birch species which forms native forest stands. Its distribution area extends from the Okhotsk Sea in the east to Baikal Lake in the west and from Kolyma River and Verkhoyansk Range in the north to the Korean Peninsula in the south. Stone birch grows in the mountains with cold wet climate (Shemberg, 1986; Volotovskiy & Chevychelov, 1991).

Stone birch is a strong edifier. It often forms single-species stands or can be part of multi-storeyed stands where the stone birch (1) dominates while the percent share of other species does not exceed 30% of the total stand composition, (2) or it is represented by few trees and its share does not exceed 30%. Mixed stone birch forests with coniferous and deciduous species do not occur or are very rare (Shemberg, 1986).

Stone birch is a light-demanding, wind resistant, soil and air humidity demanding plant but at the same time quite cold-resistant. The northern boundary of distribution coincides with January isotherms -25 – -35°C and July ones 12 – 20°C . Normal growing conditions of the stone birch at the northern border of distribution area are limited by accumulated positive temperatures above 5°C exceeding 1000° and by those above 10°C more than 700° . In such cases the number of days with temperatures above 5° and 10° is greater than 100 and 50 days accordingly (Vasiliev, 1941; Kabanov, 1972; Shemberg, 1986). An impact of phytoclimate is also high in the stone birch forests. The temperature close to zero mark (1.3°C) was observed in the morning on 23.VII.1987 at the weather station Toko (849.7 m a.s.l.) located in the lake depression on the Tokinsky Stanovik Range (Volotovskiy & Chevychelov, 1991). At the same time, the temperature 8.5°C was registered on the western slope with *Pinus pumila* shrubs and green moss cover (1285 m a.s.l.), while in the grassy stone birch forest on the eastern slope (1301.3 m above sea level) it was higher, 12.4°C . Stone birch forests usually develop in areas with deep snow cover which prevents strong freezing of soil. The steepness of slopes with stone birch can reach 35° . Soils usually have an acidic to neutral reaction; typical rich brown soils are common, whilerich brown loams are rarer. Permafrost is absent throughout the profile at least since the end of June (Rabotnov, 1936; Shemberg, 1986; Volotovskiy & Chevychelov, 1991; Isaev & Kuznetsova, 2010). Stone birch forests are usually confined to the timberline which extends to altitudes of 1100–1200 m a.s.l. on the Udokan Range, 1300–1400 m on Tokinsky Stanovik Range, and 1000 m on Yudoma-Maya Upland. On the Aldan Upland in the Timpton River Basin stone birch forests grow on

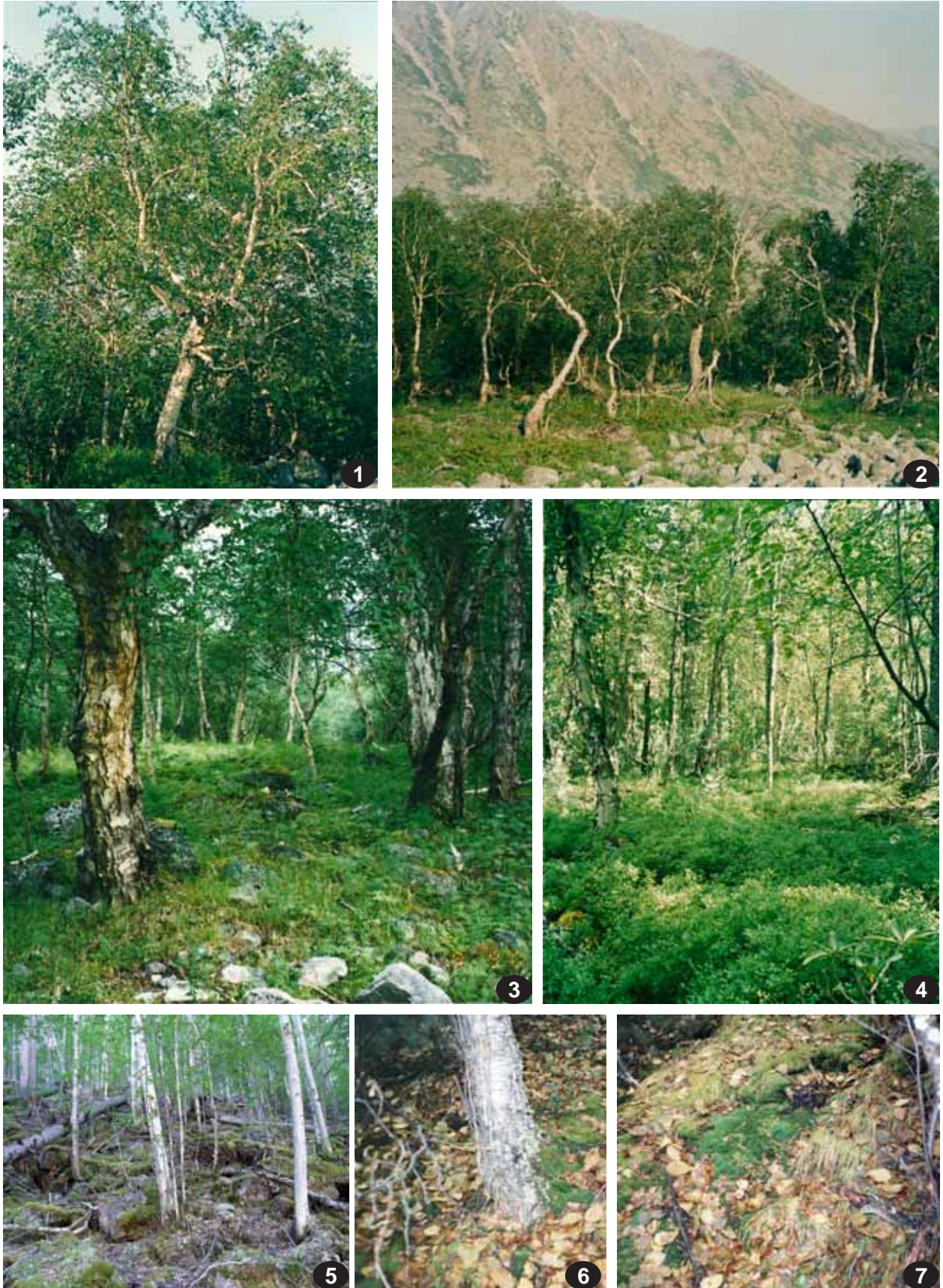
steep slopes of ridges and often extend downwards to the bottom of river valley.

Stone birch forests belong to the Pacific dark coniferous vegetation complex, in particular, they are closely related to forests of *Picea ajanensis* (Lindl. et Gord.) Fisch. ex Carr. They possess a considerable overlap of distribution ranges, similar requirements of growing conditions, often directly contact topographically and form transitional communities with frequent presence of stone birch in *Picea ajanensis* forests. This ancient complex originated in the Tertiary period; in Yakutia, it passed through alternating periods of heavy degradation during glaciations and recovering during interglacial epoch. *Betula lanata* forests in Yakutia can be considered as relic implying to their partial compliance with the terms of general climatic conditions of the region. So it has a restricted ecotopological confinedness (Vasiliev, 1941; Shemberg, 1986; Volotovskiy & Chevychelov, 1991).

In Yakutia stone birch (Figs. 1–7) was recorded for the first time by Birkengof (1932 a, b) in the Tompo River valley and in the upper reaches of Indigirka River. Further information about stone birch forests was provided only for the South Yakutia (Rabotnov, 1936; Tyulina, 1956, 1959, 1962; Volotovskiy & Chevychelov, 1991; Desyatkin, 2007; Isaev & Kuznetsova, 2010). The first typology of stone birch forests in Yakutia was given by Volotovskiy and Chevychelov (1991). They summarized data on forests of the Tokinsky Stanovik, Aldan-Uchur and Stanovoy Ranges. They identified three groups of associations named *Calamagrostis*-forb-, dwarf *Pinus pumila*- and *Hylocomium*-group.

It is worth to note that in *Pinus pumila*-group *Pinus pumila* has 40% coverage, while the cover value of dwarf shrub layer of *Vaccinium vitis-idaea* L. or *Rhododendron aureum* Georgi ranges from so 50 to 80%. On the Aldan Upland in the Timpton River Basin only green moss and *Sphagnum* types of stone birch forests were recorded (Desyatkin, 2007). Forests with grass (*Calamagrostis*-forb and forb-*Calamagrostis*) and dwarf shrub (*Rhododendron aureum*, *Vaccinium myrtillus* L., *V. vitis-idaea*, etc.) layer are common at the Udokan Range. Forests with moss layer (green moss and *Sphagnum*) are rare (pers. comm. of L.V. Kuznetsova). In Eastern Verkhoyansk Range (Suntar-Khayata, Sette-Daban Ranges and Yudoma-Maya Upland) where stone birch grows on the border of its range, stone birch forests with dwarf shrub (*Ledum palustre* L., *Vaccinium vitis-idaea*) and moss layer were studied. Stone birch forests with grass layer were not observed there.

Ground layers in studied stone birch forests may be divided into grass, dwarf shrub and moss types. Forests with grass layer are formed in the best growing conditions. Grass layer is usually continuous (covering up to 100%). *Calamagrostis purpurea* (Trin.) Trin. subsp. *langsдорffii* (Link) Tzvel. (= *Calamagrostis langsдорffii* (Link) Trin.), *Carex pallida* C.A. Mey., *Cystopteris* sp., *Diplazium sibiricum*



Figs. 1-7. Stone birch forests in Yakutia: 1-4: Udokan Range, including general view (1-2), grass type forest (3), and *Vaccinium myrtillus* type (4); Fig. 5. stone birch in Aldan Upland, Timpton River Basin; 6-7: mosses and liverworts on soil in moss stone birch forest in Yudoma-Maya Upland (photos made by L.V. Kuznetsova, 1-4, R.R. Sofronov, 5, author, 6-7).

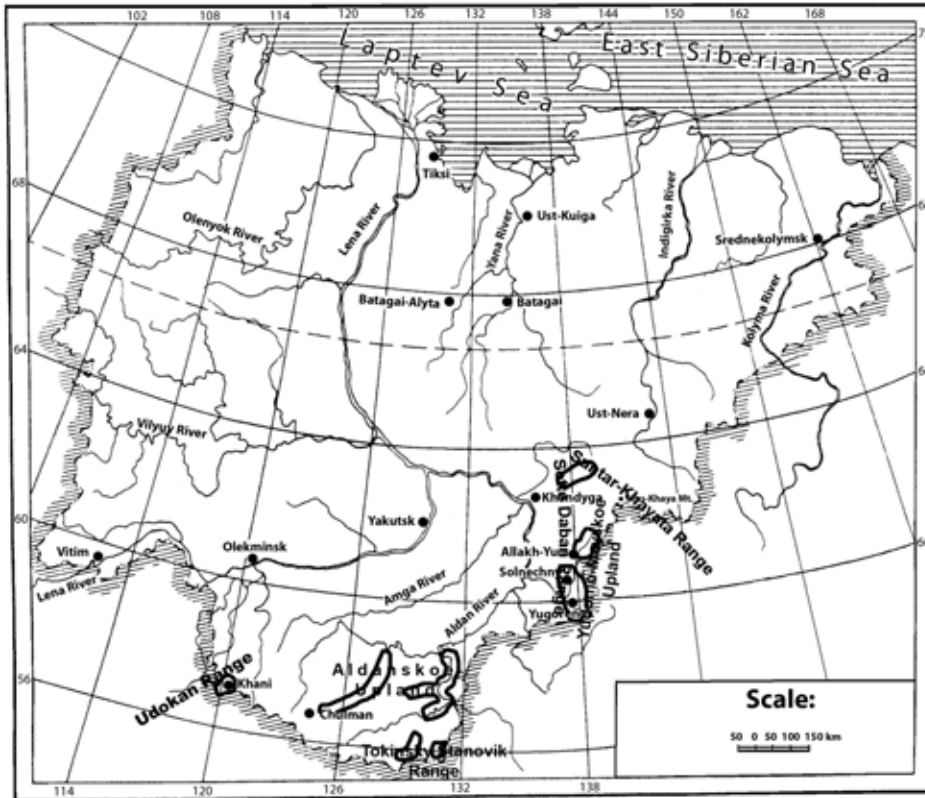


Fig. 8. Map of the study areas.

(Turcz. ex G. Kunze) Kurata, *Viola biflora* L., etc. dominate there. When snow-cover is not deep, soil is freezing and soil moisture is decreased. It leads to a decreasing of humus content and of soil depth. In such conditions stone birch forests with dwarf shrub layer are formed with dominance of *Linnaea borealis* L., *Pyrola asarifolia* Michaux, *Rhododendron aureum*, *Vaccinium myrtillus*, and *V. vitis-idaea* (up to 80%). Stone birch forests of the moss group are formed under conditions of excess flowing moistening and on relatively cold soils with short profile (Volotovskiy & Chevychelov, 1991; Desyatkin, 1994; Desyatkin, 2007; pers. comm. of Kuznetsova). *Hylocomium splendens* (Hedw.) Bruch et al., or, rarer, *Sphagnum girgensohnii* Russow, *Rhytidium rugosum* (Hedw.) Kindb. and *Calycularia laxa* Lindb. et Arnell dominate there.

The climate parameters of studied forests are shown in Table 1.

SPECIES LIST

The list of liverworts from stone birch forests is given in Table 2. It is based primarily on materials collected by the author during field trips. Stone birch forests were studied in the following sites: one forest site in Suntar-Khayata, Sette-Daban and Tokinsky Stanovik Ranges respectively, 3 sites in Yudoma-Maya Upland, 8 sites in Aldan Upland, and 4 sites in Udokan Range (Fig. 8). The herbarium collections are deposited in SASY. Materials of other collectors of this herbarium are also taken into account: from one stone birch forest site in Tokinsky Stanovik and one in Aldan-Uchur Range (Aldan-Uchur Range is a part of the Aldan Upland). Five birch forests were studied on the Udokan Range. Although Volotovskiy and Kuznetsova have made a significant number of descriptions of grass stone birch forests in South

Table 1. Meteorological data of meteorological stations in the study area with their geographic coordinates and altitude.

Meteorological stations	mean t°C,ann	mean t°C,Jan	min t°C,Jan	mean t°C,July	max t°C,July	annual precipitation, mm
Eastern Verkhoyansk Range						
Vostochnaya (63°14'N – 139°37'E, 1286 m alt.)	-13.7	-35.8	-58	11.3	29	292
Allah-Yun (60°53'N – 137°51'E, 550 m alt.)	-13.9	-44.9	-64	14.6	36	312
Yugorenok (59°46'N – 137°31'E, 380 m alt.)	-10.0	-38.8	-58	16.2	38	374
Aldan Upland + Tokinsky Stanovik Range						
Chulman (56°49'N – 124°52'E, 855 m alt.)	-9.4	-36.6	-61	15.9	35	545
Kanku (57°39'N – 125°58'E, 1204 m alt.)	-10.2	-31.9	-56	13.3	29	538
Toko (56°16'N – 131°07'E, 849 m alt.)	-11.2	-39.8	-65	14.9	34	486
Udokan Range						
Tyanya (59°02'N – 119°46'E, 240 m alt.)	-7.4	-33.6	-60	17.6	38	378
Naminga (56°35'N – 118°30'E, 1440 m alt.)	-11.3	-37.3	-	14.7	-	594

Yakutia, liverworts are almost absent in their scrutinous collections of bryophytes.

The data on liverworts include collections from pure stands of stone birch or from those forest types where stone birch dominates and the share of other species does not exceed 30% of the total composition of stand. Collections from rock outcrops and stone fields as well as from creek banks in these forests were not taken into account.

The nomenclature of liverworts follows Potemkin & Sofronova (2009) and Cailliau *et al.* (2013).

RESULTS

In total, 37 species and 2 varieties of liverworts of 26 genera were recorded in stone birch forests. In forests with moss layer 35 species and 2 varieties were identified, while 13 species were found in stone birch forests with dwarf shrub and grass layer, respectively. Two species, *Bazzania tricrenata* and *Diplophyllum obtusatum*, were found in Yakutia only in stone birch forests.

In stone birch forests of Yakutia, like in *Picea* and *Larix* forests, liverworts are displaced from the ground cover by vascular plants or mosses because of their poor competitiveness (Sofronova, 2012, 2013). In the studied birch forests liverworts grow mainly on rotten wood (25 species and one variety) and on tree butt-ends (21 species and one variety). Much less liverworts were recorded on soil (13 species) and on tree trunks (12 species).

As a rule, liverworts grow on rotten wood as scattered shoots or form small covering (up to 100 sq. cm). They are often mixed, for example *Lepidozia reptans* is intermingled with *Blepharostoma trichophyllum* and few plants of *Sphenolobus minutus*. In a small mat of *Cephalozia bicuspidata* the admixture of minute mats (1 sq. cm) of *Anastrophyllum michauxii* and of few scattered plants of *Ptilidium pulcherrimum* were observed. *Ptilidium pulcherrimum*, *Blepharostoma trichophyllum*, *Tritomaria exsecta*, *Orthocaulis attenuatus*, *Lepidozia reptans*, *Tritomaria quinquedentata*, *Cephalozia bicuspidata*, *Lophozia ventricosa* s. str., and *Ptilidium ciliare* form small mats on rotten wood, while *Anastrophyllum michauxii*, *Crossocalyx hellerianus*, *Schistochilopsis incisa*, *Tritomaria exsectiformis*, *Barbilophozia hatcheri*, *Chiloscyphus profundus*, and *Diplophyllum obtusatum* occur in a minute patches. Only once *Metzgeria pubescens* was found covering a large area (up to 1 sq. m) on wet rotting log. All other species grew on rotten wood as single plants.

Six species and one variety were collected only on rotting wood, *i.e.*, *Anastrophyllum michauxii*, *Crossocalyx hellerianus*, *Diplophyllum obtusatum*, *Lophozia ventricosa* var. *guttulata*, *Metzgeria pubescens*, *Scapania mucronata*, and *S. scandica*. In addition, some typically ground species were also recorded in this type of habitat (*Barbilophozia barbata*, *Plagiochila porelloides*, *Ptilidium ciliare*, *Sphenolobus minutus*, *Tritomaria quinquedentata*, *etc.*), as well as species that usually grow on

rocky substrates (*Diplophyllum obtusatum* and *Metzgeria pubescens*).

Tree butts are favorable places for bryophytes. They differ from ecotops of ground cover and tree trunks. A lot of organic substances and moisture are accumulated there. Liverworts growing on tree bases avoid competition from grasses and dwarf shrubs (Neshataeva *et al.*, 2003). Tree butt liverworts usually do not form a multi-species mixture. In this type of habitats we observed *Ptilidium pulcherrimum* covering a small area, *Orthocaulis attenuatus*, *Cephalozia bicuspidata*, *Ptilidium ciliare*, and *Tritomaria quinquedentata* grew as scattered plants. *Blepharostoma trichophyllum*, *Sphenolobus minutus*, *Tritomaria exsecta*, *Barbilophozia barbata*, *Calypogeia integristipula*, and *Bazzania tricrenata* formed a minute patches. Other species grew by single shoots. Five species and one variety were recorded only on the trunk bases: *Bazzania tricrenata*, *Calypogeia integristipula*, *Lophozia ventricosa* var. *longiflora*, *Mesoptychia gillmanii*, *Orthocaulis kunzeanus*, and *Sphenolobus saxicola*. In general, the same ground species were found on rotten wood and in this ecotope as well. *Sphenolobus saxicola* is one of the common species recorded on rocky substrates. It was also found on tree bases.

According to Neshataeva *et al.* (2003), in Kamchatka old birches have bark with lots of cracks, fractures and thick horizontal branches where organic substrate and moisture favourable for bryophytes growth accumulate. However, in the studied stone birch forests this pattern was not observed. *Frullania bolanderi* and *Ptilidium pulcherrimum* occur frequently on old bark up to 2 meters high on the trunk. Liverworts were often found as single-species extensive continuous covering on the bark of living trees, and rarely forming a mixture. *Ptilidium pulcherrimum*, *Tritomaria exsectiformis*, *Barbilophozia hatcheri* and *B. barbata* form small covers and *Lophozia longidens* grows in a minute patches. There is a record of *Frullania koponenii* covering an area of about 1 sq. m on *Picea ajanensis* bark. Though this species often grows on stone birch bark in *Picea ajanensis* forests (Sofronova, 2013), it was not found on birch trunks in pure stone birch forests. Occasionally *Sphenolobus minutus* also covers large areas. Other species grow as single shoots. *Frullania koponenii* was found only on bark.

Liverworts growing on soil were found mostly in moss type of birch forests and rarely in dwarf shrub one. In grass stone birch forests thick grass layer (100% cover) prevents moss growth (Neshataeva *et al.*, 2003). Small continuous covers were recorded for *Blepharostoma trichophyllum*, *Cephalozia bicuspidata*, *Lophozia ventricosa* s. str., and *Tritomaria quinquedentata*, and up to 1 sq. cm for *Plagiochila porelloides*. *Schistochilopsis incisa* forms large cover and *Calycularia laxa* may form extensive continuous cover (more than 1 sq. m).

Табл. 2. Печеночники каменноберезняков Якутии. — Table 2. Liverworts of *Betula lanata* forests in Yakutia.

Species	Community of Stone–Birch			Geomorphic units					
	moss	shrub	grassy	S–KH	S–D	Yu–M	TS	Ald	Ud
<i>Anastrophyllum michauxii</i>	<u>W</u>	–	–	–	–	–	–	+	–
<i>Barbilophozia barbata</i>	<u>TBWS</u>	<u>B</u>	–	+	+	–	–	+	+
<i>B. hatcheri</i>	<u>W</u>	–	<u>TB</u>	–	–	–	–	–	+
<i>Bazzania tricrenata</i>	<u>B</u>	–	–	–	–	–	–	–	+
<i>Blasia pusilla</i>	<u>S</u>	–	–	–	+	–	–	–	–
<i>Blepharostoma trichophyllum</i>	<u>BWS</u>	<u>BWDS</u>	<u>T</u>	–	+	+	–	+	+
<i>Calycularia laxa</i>	<u>S</u>	–	–	–	–	+	–	–	–
<i>Calypogeia integristipula</i>	–	–	<u>B</u>	–	–	–	–	–	+
<i>Cephalozia bicuspidata</i>	<u>WS</u>	–	<u>B</u>	–	–	+	–	+	+
<i>Cephaloziella varians</i>	<u>S</u>	<u>S</u>	<u>W</u>	+	–	+	–	–	+
<i>Chiloscyphus profundus</i>	<u>W</u>	<u>TD</u>	–	–	–	+	–	+	–
<i>Crossocalyx hellerianus</i>	<u>W</u>	–	–	–	–	–	–	+	+
<i>Diplophyllum obtusatum</i>	<u>W</u>	–	–	–	–	–	–	+	–
<i>Frullania bolanderi</i>	<u>TB</u>	<u>T</u>	–	–	–	–	+	+	+
<i>F. koponenii</i>	<u>T</u>	–	–	–	–	–	–	+	–
<i>Isopaches bicrenatus</i>	–	<u>S</u>	–	–	–	+	–	–	–
<i>Lepidozia reptans</i>	<u>BW</u>	<u>WD</u>	–	–	–	+	–	+	+
<i>Lophozia longidens</i>	<u>TB</u>	<u>BW</u>	<u>TW</u>	–	–	–	–	+	+
<i>L. ventricosa</i> var. <i>guttulata</i>	<u>W</u>	–	–	–	–	–	–	+	–
<i>L. ventricosa</i> var. <i>longiflora</i>	<u>B</u>	–	–	–	–	–	–	–	+
<i>L. ventricosa</i> var. <i>ventricosa</i>	<u>BWS</u>	<u>D</u>	<u>W</u>	–	–	+	–	+	+
<i>Mesoptychia gillmanii</i>	<u>B</u>	–	–	–	–	–	–	–	+
<i>Metzgeria pubescens</i>	<u>W</u>	–	–	–	–	–	–	+	–
<i>Orthocaulis attenuatus</i>	<u>BW</u>	<u>BW</u>	–	–	–	–	–	+	+
<i>O. kunzeanus</i>	<u>B</u>	–	–	–	–	–	–	–	+
<i>Plagiochila porelloides</i>	<u>BWS</u>	–	–	–	+	+	+	+	+
<i>Preissia quadrata</i>	<u>S</u>	–	–	–	+	–	–	–	–
<i>Ptilidium ciliare</i>	<u>BW</u>	<u>TW</u>	<u>B</u>	–	–	+	–	–	+
<i>P. pulcherrimum</i>	<u>TBW</u>	<u>BW</u>	<u>TB</u>	–	–	+	–	+	+
<i>Scapania crassiretis</i>	<u>WS</u>	–	–	–	–	+	–	+	–
<i>S. gymnostomophila</i>	<u>S</u>	–	–	–	+	–	–	–	–
<i>S. mucronata</i>	<u>W</u>	–	<u>W</u>	–	–	–	–	+	+
<i>S. scandica</i>	<u>W</u>	–	–	–	–	–	–	+	–
<i>Schistochilopsis incisa</i>	<u>BWS</u>	<u>D</u>	–	–	–	+	–	+	+
<i>Sphenobolus minutus</i>	<u>BW</u>	–	<u>BW</u>	–	–	–	+	+	+
<i>S. saxicola</i>	<u>B</u>	–	–	–	–	–	–	–	+
<i>Tritomaria exsecta</i>	<u>BW</u>	–	–	–	–	–	–	+	+
<i>T. exsectiformis</i>	<u>W</u>	–	<u>BW</u>	–	–	+	–	–	+
<i>T. quinquedentata</i>	<u>TWS</u>	–	<u>B</u>	–	+	+	+	–	+

Abbreviations. Substrate: T – trunk; B – tree base; W – rotten wood; D – decaying plant debris; S – soil. Occurrence exclusively of trunks and tree bases of *Betula lanata* are in boldface and underlined; *Betula lanata* and other trees in boldface, not underlined, on different trees but not on *Betula* underlined in normal font. Regional units: S-KH – Suntar-Khayata Range, S-D – Sette-Daban Range, Yu-M – Yudomo-Maya Upland, TS – Tokinsky Stanovik Range, Ald – Aldan Upland, Ud – Udokan Range. Records of Bakalin (2004) marked with asterisk*. *Lophozia ventricosa* var. *longiflora* is given according to Schuster (1969) circumscription, and var. *guttulata* – according to Bakalin (2005).

Barbilophozia barbata, *Blepharostoma trichophyllum*, *Plagiochila porelloides*, *Schistochilopsis incisa*, *Sphenobolus minutus*, and *Tritomaria quinquedentata* were found on soil in South Yakutian stone birch forests. *Blasia pusilla*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Cephaloziella varians*, *Isopaches bicrenatus*, *Lophozia ventricosa*, *Preissia quadrata*, *Scapania crassiretis*, and *S. gymnostomophila* complemented the list of liverworts growing on soil in south-eastern birch forests (Verkhoyansk Range: Suntar-Khayata and Sette-Daban Ranges, Yudoma-Maya Upland), but *Sphenobolus minutus* didn't occur there. *Bla-*

sia pusilla, *Calycularia laxa*, *Preissia quadrata* and *Scapania gymnostomophila* were found only on soil in stone birch forests. All these species were recorded in Verkhoyansk Range.

Totally, 19 species were found in stone birch forests of Verkhoyansk Range, 24 species in Aldan Upland (hereinafter including Tokinsky Stanovik Range), and 26 species in Udokan Range. Species composition of liverworts in Verkhoyansk Range birch forests is significantly depleted in comparison with the Aldan Upland and Udokan Range and includes mainly species widespread in

Verkhoyansk Range: *Cephaloziella varians*, *Ptilidium ciliare*, *Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Cephalozia bicuspidata*, *Plagiochila porelloides*, *Schistochilopsis incisa*, and *Tritomaria quinque-dentata*. The last six species and *Lepidozia reptans*, *Lophozia ventricosa* and *Ptilidium pulcherrimum* are common for liverwort flora of all studied stone birch forests of the republic. Only in birch forests of Verkhoyansk Range 5 species were found (*Blasia pusilla*, *Calycularia laxa*, *Isopachetes bicrenatus*, *Preissia quadrata*, *Scapania gymnostomophila*), all of them were recorded on soil. All these species are frequent in the studied region, usually on soil on creek banks or on rocks covered with soil and rock outcrops. There are many species (16) in South-Yakutian stone birch forests common for the Udokan Range and Aldan Upland. Besides the above mentioned species common for all the studied stone birch forests, seven additional species were found in South Yakutia growing on rotten wood or bark: *Crossocalyx hellerianus*, *Frullania bolanderi*, *Lophozia longidens*, *Orthocaulis attenuatus*, *Scapania mucronata*, *Sphenolobus minutus*, and *Tritomaria exsecta*. Following species were found only in stone birch forests of Aldan Upland: *Anastrophyllum michauxii*, *Diplophyllum obtusatum*, *Frullania koponenii*, *Lophozia ventricosa* var. *guttulata*, *Metzgeria pubescens*, and *Scapania scandica*. The first four taxa are quite rare in the territory of the republic, and *Diplophyllum obtusatum* was found only in this formation. All these species grow on rotten wood, only *Frullania koponenii* was found on the bark. *Metzgeria pubescens* and *Scapania scandica* are common species in the study area, usually growing on soil or on rocks covered with soil. Both species are common in rocky habitats or along streams. *Scapania scandica* is frequently found also in larch forests and rarely in other communities. Only in birch forests of Udokan Range seven liverwort taxa were seen growing mostly on tree trunks bases and rarely on rotting wood: *Barbilophozia hatcheri*, *Bazzania tricrenata*, *Calypogeia integristipula*, *Lophozia ventricosa* var. *longiflora*, *Mesoptychia gillmanii*, *Orthocaulis kunzeanus*, and *Sphenolobus saxicola*.

Bazzania tricrenata was found in the territory of the republic only in stone birch forests. *Barbilophozia hatcheri* was not recorded in the central part of South Yakutia (Aldan Upland, Tokinsky Stanovik Range) and only once found on Yudoma-Maya Upland on soil within *Pinus pumila* community. However, this species is not rare in southwestern Yakutia in the basin of the Vitim River (Sofronova 2006: as *B. lycopodioides*) and in the northern part of the Verkhoyansk Mountain system in Orulgan Range (Sofronova & Sofronov 2012: as *B. lycopodioides*; Sofronova, 2015). It grows mainly in rocky habitats, sometimes in damp tundra. Other species are common in the study area and grow in different plant communities or rocky habitats on various substrates.

Thus, liverworts of stone birch forests common for Verkhoyansk Range, Aldan Upland and Udokan Range

are represented by species widespread in Yakutia (Sofronova, 2005). The only exceptions are two species classified by Konstantinova (2000) as boreal species: *Lepidozia reptans* and *Ptilidium pulcherrimum*; they are quite rare in the Verkhoyansk Range (Sofronova, 2003; Sofronova & Sofronov 2012; Sofronova, 2015).

Most species which are common for stone birch forests of Aldan Upland and Udokan Range are boreal ones occurring mainly in the south of the republic or just in these two regions. In Yakutia, they grow mainly on rotten wood or tree trunks (Troeva *et al.*, 2010). It is interesting to compare the species found only in one of the studied geomorphological units. Thus, the species recorded only to stone birch forests of Verkhoyansk Range belong mainly to arctic-mountain and arctic-boreal-mountain elements and grow on soil. Liverworts restricted to such forests in Udokan Range belong mainly to arctic-boreal-mountain element and were found mainly on tree trunks. At the same time, most liverwort species found only in stone birch forests of Aldan Upland grow on rotten wood. They belong to mountain and boreal elements.

COMPARISON OF LIVERWORTS IN DIFFERENT FOREST TYPES

In the area where stone birch grows, *Larix* and *Picea* also form native forests. Spruce, likewise birch, is very selective to growth conditions (Shcherbakov, 1975; Desyatkin, 1994; Timofeev, 2003), while larch may grow in wider range of habitats. Extreme environmental conditions cause a limited and poor liverwort species composition in larch forests, and these species are mostly resistant to harsh environments (Kolesnikov, 1938).

Larix cajanderi Mayr. dominates in the study area and only once forest of *L. dahurica* Turcz. ex Trautv. was found on the Udokan Range. The range of growing conditions valuable for larch is great. It has an extensive distribution area in Verkhoyansk Range and occupies habitats varying from boggy and water-logged ones of river valleys to the relatively dry areas on the extremely poor rocky soils at the timberline. It is practically a single forest-forming tree occupying 90% of the forested area.

Table 3 shows a comparison of liverwort species composition in larch, spruce and stone birch forests in three districts of Yakutia where stone birch forests occur. Similarly to Table 2, it does not include species that grow in larch and spruce forests on rock outcrops and stone fields, and also along the banks of forest creeks.

Liverwort species composition of Verkhoyansk Range larch forests (47 species and one variety) is more diverse than those of South Yakutia including Aldan Upland and Udokan Range (29 species and one variety). Table 3 illustrates that the majority of liverworts found on Verkhoyansk Range are the species widespread in the region: arctic-boreal-montane (*Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Calypogeia* ssp., *Lophozia* ssp., *Ptilidium ciliare*, *Tritomaria quinque-dentata*, etc.) and arc-

tic-montane (*Mesoptychia sahlbergii*, *Odontochisma macounii*, *Orthocaulis binsteadii*, *Scapania crassiretis*, *S. scandica*, *Schistochilopsis grandiretis*, etc.). Most species found there are boreal (*Chiloscyphus profundus*, *Crossocalyx hellerianus*, *Lepidozia reptans*, *Radula complanata*, etc.) and are not common in the territory of the study area in Verkhoyansk Range.

In larch forests of Verkhoyansk Range only 27 species were recorded. Most of them are common species in Verkhoyansk Range: *Isopaches bicrenatus*, *Mesoptychia heterocolpos*, *M. sahlbergii*, *Orthocaulis* ssp., *Scapania* ssp., *Schistochilopsis grandiretis*, etc. They belong to arctic-boreal-montane and arctic-montane elements and grow mainly on the soil. Among liverworts found only in larch forests in Verkhoyansk Range there is a significant number of boreal species: *Chiloschyphus profundus*, *Crossocalyx hellerianus*, *Radula complanata*, and *Riccardia* spp.). Perhaps their absence in larch forests in other regions is caused by unfavorable growing conditions. At the Udokan Range and Aldan Upland *Larix* is often displaced by *Picea*, *Betula* and *Duschekia fruticosa* from snowy and moist habitats, and *Larix* forests occupy the largest areas on dry slopes where liverworts usually do not grow. Therefore liverworts in South Yakutian *Larix* forests are very scarce and mainly represented by widespread aforementioned arctic-boreal-montane species. Arctic-boreal-montane *Cephalozia lunulifolia* and boreal *Cephalozia loitlesbergeri* are rare species in Yakutia. They were found on the Udokan Range. The latter species was found in the republic only here (Sofronova, 2012).

Spruce forests in Yakutia, similarly with stone birch forests, occupy 1-2% of the forested area. *Picea obovata* Ledeb. is the only spruce species growing in Verkhoyansk and Udokan Ranges. Forests of *Picea ajanensis* are not rare for the Aldan Upland (Sofronova 2013). Although *Picea obovata* in Yakutia behaves as a facultative calciphilous species, while *Picea ajanensis* is confined to acidic soils (Desyatkin, 1994; Timofeev, 2003), they have a significant number of common species and the number of calciphilous liverworts in *Picea obovata* forests does not exceed those growing in *Picea ajanensis* forests (Sofronova, 2013). Apparently, liverworts prefer microclimate of spruce forests which is different from that in larch or birch forests, and moss and vascular plants species composition in these forests have a significant influence on species diversity of liverworts. Totally, 15 species were recorded in *Picea* forests of Verkhoyansk Range, 45 species and one variety on Aldan Upland, and 17 species on Udokan Range. Most liverworts found in *Picea* forests of Verkhoyansk Range are widespread species belonging to arctic-boreal-montane or cosmopolite geographic element: *Aneura pinguis*, *Blasia pusilla*, *Blepharostoma trichophyllum*, *Lophozia excisa*, and *Ptilidium ciliare*. Two species found on rotten wood, *Lophozia excisa* and *Scapania glauco-*

cephala, are restricted to this area; the last species is quite rare in the territory of the republic and usually grows in dark coniferous forests (Sofronova, 2005). Liverworts diversity is also rather low in spruce forests of Udokan Range. Widespread, mainly arctic-boreal-montane species prevail here: *Blepharostoma trichophyllum*, *Cephalozia bicuspidata*, *Sphenolobus minutus*, and *Tritomaria quinqueidentata*. They grow on various substrates. Some other liverworts apparently belong to this element, too, but likely prefer areas with humid climate, e.g., *Gymnocolea inflata*, *Lophozia longidens*, *Scapania irrigua*, and *S. subalpina*; they were found on rotten wood in the study area. These species are rare in Verkhoyansk Range which is different from South Yakutia not only by extreme continental climate but also by very low annual precipitation.

Compared with Verkhoyansk Range, the number of boreal species found on rotting wood or tree trunks is greater: *Chiloscyphus profundus*, *C. polyanthos*, and *Scapania mucronata* were found in Verkhoyansk Range *Picea* forests but *Lophozia ascendens*, *Ptilidium pulcherrimum* and *Radula complanata* didn't occur there. Only in *Picea* forests of Udokan Range five species were found which are rare or sporadic in Yakutia: arctic-montane *Lophozia* cf. *savicziae*, *Solenostoma confertissimum* grew on rotten wood; arctic-boreal-montane *Scapania irrigua* and *S. subalpina* and boreal *Radula complanata* were found on trunk of poplar tree. In the territory of the republic *Radula complanata* usually grows on stone fields, in rock crevices, in mountain tundra or on bark of deciduous trees. *Picea* occupies the most moistened habitats on the slopes of Aldan Upland. The largest number of liverworts was recorded there in spruce forests: 45 species and one variety. Mainly arctic-boreal-montane and boreal species grow under their canopy. Among arctic-boreal-montane liverworts widespread species growing on different substrates prevail: *Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Ptilidium ciliare*, *Sphenolobus minutus*, *Tritomaria quinqueidentata*, etc. Such species as *Gymnocolea inflata*, *Lophozia longidens*, *L. ventricosa* var. *longiflora*, and *Scapania curta* prefer humid areas and grow mostly on rotten wood. Some boreal liverworts rare in the republic were also found; they grow on rotten wood or on trunks of various trees: *Frullania bolanderi*, *F. kopenhagenii*, *F. parvistipula*, *Lophozia ascendens*, and *Orthocaulis attenuatus*. All these species were found only in South Yakutia. 29 species were recorded only in spruce forests of the Aldan Upland. Most of them are boreal species and grow mostly on rotten wood or tree trunks. Some of them are common in the region: *Chiloscyphus profundus*, *Crossocalyx hellerianus*, *Lepidozia reptans*, *Tritomaria exsectiformis*, etc. However, most of them are rare in Yakutia, e.g., *Frullania* ssp., *Orthocaulis attenuatus*, *Scapania apiculata*, and *Tritomaria exsecta*. The

Табл. 3. Печеночники лиственничных, еловых и каменноберезовых лесов. — Liverworts in *Larix*, *Picea* and *Betula lanata* forests in Yakutia.

Species	Larch forests			Spruce forests			Stone-birch forests		
	EV	Ald+TS	Ud	EV	Ald+TS	Ud	EV	Ald+TS	Ud
<i>Anastrophyllum michauxii</i>					++			+	
<i>Aneura pinguis</i>	++			+	+				
<i>Arnellia fennica</i>					+				
<i>Barbilophozia barbata</i>	++		+		++		++	+	+
<i>B. hatcheri</i>									+
<i>Bazzania tricrenata</i>									+
<i>Blasia pusilla</i>				+	+		+		
<i>Blepharostoma trichophyllum</i>	+++	+	+	++	++	+	++	+	+
<i>Calycularia laxa</i>							+		
<i>Calypogeia integristipula</i>	+	+	+		++				+
<i>C. muelleriana</i>	+++	+	+						
<i>Cephalozia bicuspidata</i>	++	+	+		++	+	+	+	+
<i>C. connivens</i>	++								
<i>C. loitlesbergeri</i>			+						
<i>C. lunulifolia</i>			+*						
<i>C. pleniceps</i>	+++	+	+		++				
<i>Cephaloziella divaricata</i>	+								
<i>C. elachista</i>			+*						
<i>C. rubella</i>		+	+						
<i>C. spinigera</i>	+								
<i>C. varians</i>							++		+
<i>Chiloscyphus minor</i>				+		+			
<i>C. polyanthos</i>				+	+	+			
<i>Chiloscyphus profundus</i>	+				+		+	+	
<i>Crossocalyx hellerianus</i>	+				++			+	+
<i>Cryptocolea imbricata</i>	+								
<i>Diplophyllum obtusatum</i>								+	
<i>D. obtusifolium</i>					+				
<i>D. taxifolium</i>					++				
<i>Frullania bolanderi</i>					++			++	+
<i>F. koponenii</i>					++			+	
<i>F. parvistipula</i>					++				
<i>Gymnocolea inflata</i>					+	+			
<i>Isopaches bicrenatus</i>	+						+		
<i>Jamesoniella undulifolia</i>			+*						
<i>Lepidozia reptans</i>	+	+	+		++		+	+	+
<i>Lophozia ascendens</i>					+	+			
<i>L. excisa</i>	++		+	+					
<i>L. longidens</i>	++	+			++	+		+	+
<i>L. cf. savicziae</i>						+			
<i>L. ventricosa</i> var. <i>guttulata</i>								+	
<i>L. ventricosa</i> var. <i>longiflora</i>	++		+		++				+
<i>L. ventricosa</i> var. <i>ventricosa</i>	++	+	+		++		+	+	+
<i>Marchantia latifolia</i>		+							
<i>Marsupella emarginata</i>					+				
<i>Mesoptychia gillmanii</i>	+								+
<i>M. heterocolpos</i>	+++			+	+	+			
<i>M. sahlbergii</i>	++			+					
<i>Metzgeria pubescens</i>					+			+	
<i>Mylia anomala</i>	++		+						
<i>M. taylorii</i>					+				
<i>Odontoschisma macounii</i>	+++				+				
<i>Orthocaulis attenuatus</i>					+			+	+
<i>O. binsteadii</i>	++								
<i>O. hyperboreus</i>			+*						
<i>O. kunzeanus</i>	+								+
<i>Plagiochila porelloides</i>	++			+	++		++	++	+
<i>Preissia quadrata</i>				+	+		+		
<i>Ptilidium pulcherrimum</i>		+			++	+	+	+	+
<i>P. ciliare</i>	+++	+	+	+	+		+		+
<i>Radula complanata</i>	+					+			
<i>Reboulia hemisphaerica</i>					+				

Табл. 3. продолжение. — Table 3. continued.

Species	Larch forests			Spruce forests			Stone-birch forests		
	EV	Ald+TS	Ud	EV	Ald+TS	Ud	EV	Ald+TS	Ud
<i>Riccardia cf. chamedryfolia</i>	+				+				
<i>R. cf. latifrons</i>	+								
<i>R. cf. multifida</i>	+								
<i>R. cf. palmata</i>	+								
<i>Scapania apiculata</i>					+				
<i>S. brevicaulis</i>	+		+						
<i>S. crassiretis</i>	+	+		+	++		+	+	
<i>S. curta</i>					+				
<i>S. glaucocephala</i>				+					
<i>S. gymnostomophila</i>	++						+		
<i>S. irrigua</i>	+					+			
<i>S. mucronata</i>	++	+		+	++	+		+	+
<i>S. paludicola</i>	++								
<i>S. plicata</i>	+								
<i>S. scandica</i>	++				++			+	
<i>S. subalpina</i>						+			
<i>Schistochilopsis grandiretis</i>	++								
<i>S. incisa</i>	+		+		++		+	+	+
<i>Solenostoma confertissimum</i>						+			
<i>Sphenolobus minutus</i>	+++	+	+		++	+		++	+
<i>S. saxicola</i>	++	+			+				+
<i>Tritomaria exsecta</i>					++			+	+
<i>Tritomaria exsectiformis</i>	+++		+		++		+		+
<i>T. quinquedentata</i>	+++	+			++	+	++	+	+
<i>T. scitula</i>	+			+					

Abbreviations of regions: EV – eastern Verkhoyansk Range (includes Suntar-Khayata Range, Sette-Daban Range, Yudomo-Maya Upland), TS – Tokinsky Stanovik Range, Ald – Aldan Upland, Ud – Udokan Range. In the case of EV and Ald+TS. Number of crosses (+) means the number of regional subdivisions (out of mentioned above for regions) where the species was found.

number of arctic-boreal-montane species is comparatively high. Species common species in region, e.g., *Barbilophozia barbata*, *Calypogeia integristipula*, *Cephalozia pleniceps*, etc., grow there on different substrates. However, some arctic-boreal-montane species were also found, growing on rotten wood, rocks covered with soil, in niches between roots of spruce or on roots: *Diplophyllum obtusifolium* and *D. taxifolium*. Another species belonging to arctic-montane and montane elements were found only in spruce forests of Aldan Upland; they grew on soil or rocks covered with soil: *Arnellia fennica*, *Marsupella emarginata*, *Scapania scandica*, and *Sphenolobus saxicola*. Among species rare in the territory of Yakutia, in addition to above mentioned ones, montane *Anastrophyllum michauxii* and *Mylia taylorii* can be mentioned. *Mylia taylorii* is found in the republic only there.

A general comparison of forests (Table. 3) shows that liverwort flora of larch and spruce forests is the richest in only one of the three regions compared. A number of species is lowering in accordance with deteriorating of growing conditions of these trees. It is the most contrasting in larch forests where liverwort species diversity may significantly reduce. At the same time, this pattern is not observed in stone birch forests (Table. 3). This fact confirms an assumption of high capacity of stone birch as an edifier, creating an environment that allows existing of similar liverwort flora in areas with very different climate.

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