

A CONTRIBUTION TO THE LIVERWORT FLORA OF TIMPTON RIVER BASIN (ALDAN UPLAND, SOUTHERN YAKUTIA)

МАТЕРИАЛЫ К ФЛОРЕ ПЕЧЕНОЧНИКОВ БАССЕЙНА Р. ТИМПТОН
(АЛДАНСКОЕ НАГОРЬЕ, ЮЖНАЯ ЯКУТИЯ)

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Abstract

An annotated list of liverworts collected in the forest belt and in the floodplain of the Timpton River in the Aldan Upland includes 80 species. The data on structures associated with reproduction, localities, substrates, habitats, and growth pattern are provided and associated species are listed. Most liverwort species in the study area grow on rocky substrates and decaying wood. Two mainly southern species are new for Yakutia: *Harpanthus scutatus* and *Targionia hypophylla*. *Diplophyllum obtusatum*, *Frullania davurica*, *F. koponenii*, *Porella platyphylla* and *Scapania apiculata* also occur here on their northern limit of distribution in Siberia: .

Резюме

Впервые приводится аннотированный список печеночников для Алданского нагорья, включающий 80 видов. Для каждого вида указано наличие структур, связанных с размножением, выявленные местонахождения, субстрат, местообитания, характер произрастания и сопутствующие виды. Печеночники здесь произрастают в основном на скалистых местообитаниях и гниющей древесине. Два в целом более южных вида приводятся для Якутии впервые: *Harpanthus scutatus* и *Targionia hypophylla*. Кроме того, наиболее северные находки в данном районе имеют *Diplophyllum obtusatum*, *Frullania davurica*, *F. koponenii*, *Porella platyphylla* и *Scapania apiculata*.

KEYWORDS: flora, liverworts, ecology, Yakutia.

INTRODUCTION

The Aldan Upland is located in Southern Yakutia between Olyokma and Uchur Rivers, stretching northward of Stanovoy Range to the Aldan River. The area remained not explored for liverworts until out field studies in 2007 and 2010, but complete list of the collections was not published, though new and rare liverworts for the Southern Yakutia were reported earlier (Sofronova, 2008, 2010, 2013a, 2015; Sofronova, Potemkin, 2008). The present paper summarizes all the data from those expeditions.

STUDY AREA

The Timpton River flows in the central part of the Aldan Upland from south to the north. The area is located within the Aldan Shield, which is an ancient peneplanized surface. The Upland represents a region of intense new uplifts on the ancient crystalline base. The relief has massive ridges with convex peaks, sometimes taking the form of crests, crowned with rocky denudation remains of various shapes. Altitudes of the peaks in the area vary from 1350 to 1933 m, however, the exploration was conducted at 700 m and below, along the Timpton River. In the upper course, river valley is shal-

low, with a relative height of slopes 150–300 m. With the increase of erosion cut, height of slopes increases at places to 600–800 m or more, the slopes becoming more steep, to 35–40°, or at places to 45–50°, making the valley V-shaped. The relative height in the middle reaches of the Timpton River is up to 400–600 m or more. Towards the lower reaches, the relative height of slopes along the river decreases, up to 300 m, surrounding areas being 600 to 980 m a.s.l.

The valley of the Timpton River is strongly meandering, the levels of river terraces are fragmented. Sometimes the terraces are swamped, and small oxbow lakes are occasionally developed. The banks are often composed of boulders and blocks, with a mixture of pebbles and sand. Rock walls are observed on the steep sides of river valleys and on bank slopes eroded by the river. The Aldan Upland is mainly composed of crystalline and metamorphic rocks of the Archaean and Proterozoic age of the Aldan Shield. In many places of the Upland the rocks of this bed-rock come to the surface. They are represented by the most ancient quartzites, granites, gneisses and marbles. In the lower reaches of the Chulman and Timpton Rivers, the carbonate sediments of the Ediacar-

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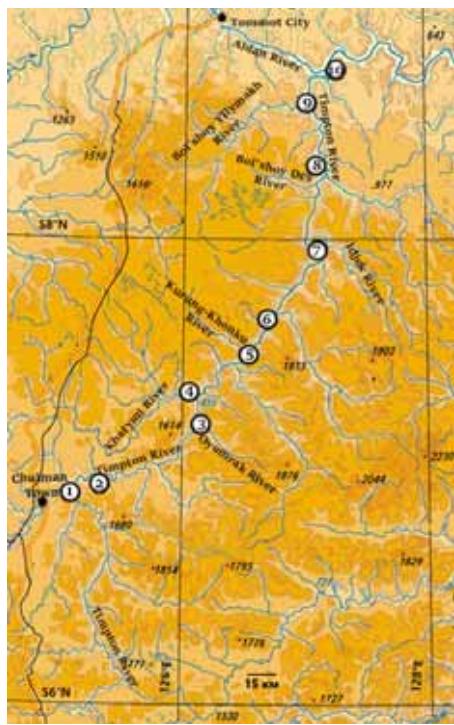


Fig. 1. Collecting localities

1 The lower reaches of the Chulman River and Chulman River Mouth

	630–700	56°52'–55'	124°54'–125°08'
2 Barylas River Mouth	560	56°58'	125°17'–21'
3 Oyumrak River Mouth	480–700	57°04'–14'	125°58'–126°08'
4 Khatymi River Mouth	460–670	57°19'–25'	125°53'–126°17'
5 Kurung-Khonku River Mouth	400–600	57°30'–33'	126°32'–37'
6 Egete River Mouth	380	57°38'	126°41'
7 Idzhek River Mouth	325–400	57°54'–58'	127°03'–09'
8 Bol'shoy Des River Mouth	310	58°08'–58°14'	127°02'–05'
9 Bol'shoy Yllymakh River Mouth	270–300	58°33'–58°41'	127°02'–05'
10 Timpton River Mouth	260–400	58°44'	127°13'

ium (Vendian) and the Lower Cambrian, mainly dolomites and limestones, come to the surface (Rusanov *et al.*, 1967; Desyatkin, 2007; Maigur, 2011; Belyaev, 2015; Mitrofanov, 2015).

The climate of Southern Yakutia is moderately continental, with the mean annual temperature -10.2°C and mean temperature of the warmest month (July) +13.3°C. The coldest month is January with mean temperature of -31.9°C, the absolute minimum reaches -56°C. The annual precipitation reaches 400–800 mm per year. Five months a year the temperature has positive values, the average duration of the frost-free period is 57 days (Izyumenko, 1966, 1968; Desyatkin, 2007; Maigur, 2011).

VEGETATION

The studied area is situated within the Aldan and Uchur mountain middle taiga districts of the South Yakutian province of pine-larch taiga with the participation of dark coniferous species. The dominant type of vegetation is larch forests, the portion of *Larix cajanderi* in the forest cover is about 70%, *Pinus sylvestris* makes up from 7 to 11% and *Pinus pumila* is about 10% of the forest area. Significant areas are occupied by *Betula lanata*, less often by *Betula pendula*, and occasionally by *Populus suaveolens*, *P. tremula*, *Alnus hirsuta*, *Salix* spp. The species composition is greatly influenced by the parent rocks. On acidic metamorphic or igneous rocks larch forests are formed, sometimes with *Picea ajanensis*, *P. obovata*, *Pinus sylvestris*, *Betula ermannii*, and *B. platyphylla*. Larch forests are mostly wet or moist. Ground cover is represented by *Ledum palustre*, *Vaccinium vitis-idaea*, *Hylocomium splendens*, *Aulacomnium turgidum*, and *Sphagnum* spp. (Desyatkin, 2007; Maigur, 2011) (nomen-

ture of vascular plants, mosses and liverworts mainly follows Kuznetsova & Zakharova, 2012, Ignatov *et al.*, 2006 and Söderström *et al.*, 2016, correspondingly).

On crystalline parent rocks along the banks of the Timpton River, in intermountain depressions, as well as at the upper boundary of the forest, *Picea ajanensis* occurs. This Far Eastern boreal-montane species prefers steep slopes covered with plenty of snow. Usually *Picea ajanensis* forms almost pure stands, sometimes with an admixture of *Betula lanata*. These forests are characterized by well-developed shrub and herb ground cover (*Alnus crispa* subsp. *fruticosa*, *Pinus pumila*, *Rhododendron aureum*, *Vaccinium vitis-idaea*, *Ledum palustre*, *Polyodium sibiricum*, *Pyrola asarifolia*, *Calamagrostis purpurea* subsp. *langschorffii*, *Phegopteris connectilis*, *Hylocomium splendens*, *Sphagnum* sp., *Peltigera aphthosa*). Stone birch-dominated (*Betula lanata*) open forests are common on crystalline rocks on steep slopes of ridges and descend to the banks of the river. In the ground layer they include *Calamagrostis langschorffii*, *Carex pallida*, *Viola biflora*, *Vaccinium vitis-idaea*, *V. myrtillus*, *Viola biflora*, *Linnaea borealis*, *Aquilegia sibirica*, *Polyodium sibiricum*, *Streptopus streptopoides*, *Atragene speciosa*, *Hylocomium splendens*, *Ptilium crista-castrensis*, and *Sphagnum girgensohnii*.

The areas where larch forests previously grew were disturbed by fire and now they are occupied by open birch (*Betula pendula*) communities with scattered larch. They are characterized by well-developed shrub and herb ground cover (*Rosa acicularis*, *Pinus pumila*, *Alnus crispa* subsp. *fruticosa*, *Sorbus sibirica*, *Vaccinium vitis-idaea*, *Pyrola* spp., *Calamagrostis purpurea* subsp. *langschorffii*, *Rubus humulifolius*, *Orthilia secunda*, *Carex* spp., *Sorbaria sorbifolia*, *Rhododendron dauricum*, *Maianthemum bifolium*, *Gymnocarpium jessoense*, *Equisetum pratense*, *Lilium pensylvanicum*, and *Hylocomium splendens*). Sparse communities of *Salix viminalis*, *S. schwerinii*, *Populus suaveolens*, and *Chosenia arbutifolia* occur along the banks of rivers and on islands.

On carbonate rocks (lower reaches of the Chulman and Timpton Rivers) pine (*Pinus sylvestris*) forests grow. They include *Rhododendron dauricum*, *Cotoneaster melanocarpus*, *Spiraea media*, *Rosa acicularis*, *Juniperus communis*



Fig. 2. Study area environment and some hepaticas: A: Timpton River Valley; B: 16 rock field in forest belt; C: lichen larch forest; D: stone birch forest; E: *Eriophorum*–*Carex*–*Sphagnum* swamp; F: rocky river bank; G: vertical cliffs with *Sphenolobus saxicola* and other bryophytes and lichens; H: *Frullania davurica* on cliffs face.

nis, Arctous alpina subsp. *erythrocarpa*, *Limnas stellari*, *Arctostaphylos uva-ursi*, *Dryas viscosa*, *D. punctata*, *Empetrum nigrum*, *Lycopodioides sanguinolenta*, *Thymus*, *Cladonia stellaris*, *C. arbuscula*, *C. rangiferina*, *C. amaurocraea*, *Cetraria laevigata*, *C. cucullata*, *Peltigera canina*, and *P. aphtosa*. Moss cover is represented by *Rhytidium rugosum*, *Polytrichum* sp. and *Ptilidium ciliare*. *Picea obovata* grows here on well-moistened soils on carbonate rocks. Spruce forests occupy river terraces and mostly have *Rosa acicularis*, *Ribes glabellum*, *Vaccinium vitis-idaea*, *Pyrola asarifolia*, *Calamagrostis purpurea* subsp. *langsdoerffii*, *Linnaea borealis*, and *Hylocomium splendens* in the ground layer.

Riparian meadows are predominantly represented by narrow strips of meadow-like communities with domination of *Heracleum dissectum*, *Sanguisorba officinalis*, *Tanacetum vulgare*, and *Cacalia hastata*.

Swamps occupy small areas and are confined to upper floodplains, often bordering small oxbow lakes with domination of *Carex juncella*, *Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Smilacina trifolia*, *Rubus chamaemorus*, *Oxycoccus microcarpus*, *Iris setosa*, *Chamaedaphne calyculata*, *Comarum palustre*, *Menyanthes trifoliata*, and *Sphagnum* sp.

Peculiar petrophyte plant complexes are formed on stony screes and rockfields, on wide ledges, on steep slopes and steep walls. They include *Scorzonera radiata*, *Aster alpinus*, *Saxifraga bronchialis*, *Allium strictum*, *Campanula rotundifolia* subsp. *langsdoerffiana*, *Chrysanthemum zawadskii*, *Eritrichium jacuticum*, *Artemisia leucophylla*, *A. tanacetifolia*, *Woodsia ilvensis*, *Lycopodioides sanguinolenta*, *L. sibirica*, *Orostachys spinosa*, *Cladonia rangiferina*, and *Peltigera aphtosa*.

Above the forest belt, *Pinus pumila* communities and rockfields predominate; in wetter areas there are thickets of *Rhododendron aureum* and communities of *Salix krylovii* and *S. saxatilis*. The tundra belt is very poorly represented in the study area (Desyatkin, 2007; Maigur, 2011).

SPECIES LIST

In the present list of hepatic taxa are arranged alphabetically. The nomenclature follows Söderström *et al.* (2016) with a few changes. The list is annotated in the following order: species name, abbreviations of structures connected with reproduction, if present, in parentheses: m. pl. – male plant, f. pl. – female plant, andr. – androecea, per. – perianthia, arch. – archegonia, spor. – sporophytes, gem. – gemmae; collecting sites (Table 1 and Fig. 1); substrate, habitats, list of accompanying liverwort species, if available, and growth pattern. The following scale was used for determination of growth pattern: few plants (FP), minute continuous cover (M) – up to 1 sq. cm, small continuous cover (S) – up to 100 sq. cm and large (L) – up to 1 sq. m and extensive continuous cover (E) – more than 1 sq. m. Asterisk before species name means a new record for Yakutia. All speci-

mens are deposited in the Herbarium of Institute for Biological Problems of Cryolithozone SB RAS, Yakutsk (SASY).

Anastrophylleum michauxii (F. Weber) H. Buch (per., fr.) – 1-3, 6, 7 – on decaying wood in larch, stone birch and *Picea ajanensis* forests. In pure mats or mixed with *Cephalozia bicuspidata*, *Blepharostoma trichophyllum*, *Lepidozia reptans*, *Crossocalyx hellerianus*, *Plagiochila poreloides*, *Ptilidium pulcherrimum*, *Trilophozia quinquentata*, *Tritomaria exsecta* et al., FP, M, S.

Barbilophozia barbata (Schmidel ex Schreb.) Loeske – 1-3, 5 – on soil, soil covering rocks and decaying wood in stone birch forests; on *Picea ajanensis* trunk bases and soil covering rocks in *Picea ajanensis* forests; on fine soil in cliff cracks in forest belt. Mixed with *Plagiochila poreloides*, *Tritomaria exsecta*, *Trilophozia quinquentata*, *Lophozia ventricosa*, *Scapania mucronata*, FP, S.

Blasia pusilla L. – 3, 6, 8, 9 – on decaying wood in *Picea ajanensis* forest; on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river; on soil covering rocks in stone birch forest; on sandy soil between boulders or stones near river and on moist sand of steep slope N-facing river bank. In pure mats and mixed with *Anastrophylleum michauxii*, *Cephalozia bicuspidata*, *Plagiochila poreloides*, *Scapania mucronata*, *Solenostoma hyalinum* et al., FP, M, S.

Blepharostoma trichophyllum (L.) Dumort. (per., fr.) – 1-5, 7 – on soil, decaying wood near stream and on stone to boulder base in larch forests; on soil covering rocks, *Picea ajanensis* trunk bases and decaying wood in stone birch forests; on decaying wood in *Picea ajanensis* forests. Mixed with *Lepidozia reptans*, *Tritomaria exsecta*, *Sphenolobus minutus*, *Plagiochila poreloides*, *Ptilidium pulcherrimum*, *Anastrophylleum michauxii*, *Schistochilopsis incisa*, *Tritomaria exsectiformis* et al., FP, M, S.

Calycularia laxa Lindb. et Arnell (m. pl.) – 1 – on soil on SW-facing vertical cliffs along river bank. Mixed with *Sphenolobus minutus*, FP.

Calypogeia integriflora Steph. – 1, 3, 9, 10 – on soil covering rocks in larch and stone birch forests; on soil covering rocks of stone fields in forest belt. In pure mats or mixed with *Sphenolobus minutus*, *Lophozia cf. savicziae*, *Trilophozia quinquentata*, FP, M.

C. muelleriana (Schiffn.) Müll. Frib. – 3, 4, 9 – on soil and *Sphagnum* in larch forests. Mixed with *Mylia anomala*, *Schljakovia kunzeana*, FP.

C. neesiana (C. Massal. et Carestia) Müll. Frib. – 3, 5 – on decaying wood near stream and in niche on soil covering rocks in larch forests. Mixed with *Cephalozia bicuspidata*, *Lepidozia reptans*, *Lophozia ventricosa*, *Sphenolobus minutus*, *Tritomaria exsectiformis*, FP, S.

C. sphagnicola (Arnell et J. Perss.) Warnst. et Loeske – 3 – on *Sphagnum* in *Ledum-Sphagnum* swamp. Mixed with *Mylia anomala*, FP.

Cephalozia bicuspidata (L.) Dumort. (fr.) – 3-7 – on soil, decaying wood near stream and in niche on soil cov-

ering rocks in larch forests; on decaying wood and soil covering rocks in stone birch forests; on decaying wood and soil covering rock outcrops in *Picea ajanensis* forests; on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river; on soil covering stone and decaying wood along stream bank. In pure mats or mixed with *Blepharostoma trichophyllum*, *Scapania scandica*, *Sphenolobus minutus*, *Ptilidium pulcherrimum*, *Anastrophyllum michauxii*, *Nardia insecta*, *Pellia neesiana*, *Plagiochila poreloides* et al., FP, M, S, L.

C. lunulifolia (Dumort.) Dumort. – 2 – on decaying wood in larch forest. Mixed with *Tritomaria exsectiformis*, FP.

C. pleniceps (Austin) Lindb. (per., spor.) – 1, 2 – on decaying wood in *Picea ajanensis* forests. In pure mats or mixed with *Lepidozia reptans*, *Blepharostoma trichophyllum*, *Schistochilopsis incisa*, *Tritomaria exsectiformis*, FP, M.

Cephaloziella elachista (J.B. Jack ex Gottsche et Rabenh.) Schiffn. (per.: autoicous) – 7, 9 – on *Sphagnum* in larch forests. In pure mats or mixed with *Mylia anomala*, M.

C. varians (Gottsche) Steph. (fr.) – 1, 3 – on soil on moist S-facing cliffs along river bank; on fine soil in cliff cracks in forest belt. Mixed with *Lophoziaopsis excisa*, *Scapania praetervisa*, FP, S.

Chiloscyphus polyanthus (L.) Corda – 6 – on decaying wood in *Picea ajanensis* forest. Mixed with *Cephalozia bicuspidata*, *Riccardia chamedryfolia*, FP.

Conocephalum salebrosum Szweyk., Buczk. et Odrzyk. – on moist sand of steep slope N-facing river bank. Mixed with *Marchantia latifolia*, FP.

Crossocalyx hellerianus (Nees ex Lindemb.) Meyl. (gem.) – 1, 2, 7 – on decaying wood in larch, stone birch, *Picea ajanensis* forests and on stream bank. Mixed with *Tritomaria* ssp., *Anastrophyllum michauxii*, *Lepidozia reptans*, *Ptilidium pulcherrimum*, *Blepharostoma trichophyllum*, *Lophozia guttulata*, FP, M, S.

Diplophyllum obtusatum (R.M. Schust.) R.M. Schust. (per.: autoicous, fr.) – 3, 7, 8 – on soil and decaying wood in stone birch forests; on soil covering rocks in *Picea ajanensis* forests. In pure mats or mixed with *Cephalozia bicuspidata*, *Gymnocolea inflata*, *Marsupella emarginata*, *Scapania crassiretis*, *S. scandica*, *Sphenolobus minutus*, FP, M, S, L.

D. obtusifolium (Hook.) Dumort. (per., fr.: paroicous) – 1, 9 – on soil covering rocks in niche between stones in larch forest; on soil on SW-facing vertical cliffs along river bank. In pure mats or mixed with *Sphenolobus minutus*, *Tritomaria exsecta*, FP, M.

Frullania bolanderi Austin (gem.) – 1-4, 9 – on *Betula lanata*, *B. pendula*, *Sorbus sibirica* trunks in birch forests; on *Picea ajanensis*, *Betula lanata* and *Alnus crispa* subsp. *fruticosa* trunks in *Picea ajanensis* forests. In pure mats or mixed with *Ptilidium pulcherrimum*, *Plagiochila poreloides*, S, L.

F. davurica Hampe ex Gottsche – 5 – on stone under ledge of W-facing cliff (shaded place) in forest belt. In pure mats, L.

F. koponenii S.Hatt. (gem., f. pl.) – 1, 3, 9 – on *Picea ajanensis* trunk in *Picea ajanensis* forests; in caves of S-facing cliff along river bank. In pure mats, M, S.

Gymnocolea inflata (Huds.) Dumort. – 1, 7 – on soil in *Eriophorum-Carex-Sphagnum* swamp by the lake; on soil covering rocks outcrops in *Picea ajanensis* forest. Mixed with *Cephalozia bicuspidata*, *Diplophyllum obtusatum*, *Marsupella emarginata*, *Odontoschisma fluitans*, *Scapania crassiretis*, *S. scandica*, FP, M.

Haplomitrium hookeri (Lyell ex Sm.) Nees – 2 – on sandy soil in cracks of N-facing rock outcrops along river bank. Mixed with *Jungermannia polaris*, FP.

**Harpanthus scutatus* (F. Weber et D. Mohr) Spruce – 9 – on decaying wood in stone birch-*Hylocomium* forest with *Picea ajanensis* on S-facing slope. Mixed with *Scapania mucronata*, *Tritomaria exsecta*, FP.

Isopaches bicrenatus (Schmidel ex Hoffm.) H. Buch (gem., per.; paroicous) – 5, 9 – on sandy soil of path in pine forest; on fine soil in niches between stones of stone field in forest belt. In pure mats or mixed with *Sphenolobus saxicola*, FP, S.

Jungermannia borealis Damsh. et Váňa (per.) – 9 – on soil and poured stones along river bank; on soil on S-facing cliffs cracks in birch forest. In pure mats, S, L.

J. polaris Lindb. (per.: paroicous) – 2, 7, 8 – on sandy soil on S, N-facing cliffs and between stones along river banks. In pure mats or mixed with *Haplomitrium hookeri*, *Plagiochila poreloides*, *Scapania praetervisa*, FP, M, S.

Lepidozia reptans (L.) Dumort. (fr.) – 1-3, 5, 7 – on decaying wood, on *Betula* trunk bases and stone in niche at the base of boulder in larch forests; on *Picea ajanensis* trunk bases and decaying wood in stone birch forests; on decaying wood in *Picea ajanensis* forests. In pure mats or mixed with *Sphenolobus minutus*, *Blepharostoma trichophyllum*, *Trilophozia quinquedentata*, *Anastrophyllum michauxii*, *Cephalozia pleniceps*, *Plagiochila poreloides*, *Tritomaria* ssp., *Lophozia ventricosa* et al., FP, M, S.

Lophocolea heterophylla (Schrad.) Dumort. (per., fr.) – 2, 3, 7 – on decaying wood in stone birch and *Picea ajanensis* forests. In pure mats or mixed with *Blepharostoma trichophyllum*, *Ptilidium pulcherrimum*, *Tritomaria exsecta*, *Anastrophyllum michauxii*, *Lepidozia reptans*, *Lophozia guttulata*, *Scapania scandica* et al., FP, M, S.

L. minor Nees – 9 – on moist sand of steep slope N-facing river bank. Mixed with *Plagiochila poreloides*, *Preissia quadrata*, *Scapania praetervisa*, FP.

Lophozia cf. guttulata (Lindb. et Arnell) A. Evans (gem.) – 2, 3 – on decaying wood in stone birch and *Picea ajanensis* forests. Mixed with *Ptilidium pulcherrimum*, *Blepharostoma trichophyllum*, *Crossocalyx hellerianus*, *Lepidozia reptans*, *Lophocolea heterophylla*, *Tritomaria exsectiformis*, *Schistochilopsis incisa* et al., FP.

L. cf. savicziae Schljakov (gem.) – 9 – on soil covering rocks in niche between stones in larch forest. Mixed with *Sphenolobus minutus*, *Calypogeia integristipula*, *Tritomaria exsecta*, FP, M.

L. ventricosa (Dicks.) Dumort. (gem.) – 1-3, 5, 6 – on soil, decaying wood and in niche on soil covering rocks in larch forests; on decaying wood in birch forest; on decaying wood and on soil covering rocks in *Picea ajanensis* forests. Mixed with *Barbilophozia barbata*, *Lepidozia reptans*, *Lophozia longidens*, *Plagiochila poreloides*, *Scapania mucronata*, *Sphenolobus minutus*, *Tritomaria exsecta*, *T. exsectiformis* et al., FP, M, S.

L. cf. wenzelii (Nees) Steph. (gem.) – 7 – on soil between hillocks of *Sphagnum* in larch forests. Mixed with *Ptilidium ciliare*, *Sphenolobus minutus*, FP.

Lophoziospis excisa (Dicks.) Konstant. et Vilnet (gem., andr., arch.: paroicous, fr.) – 1, 3 – on *Peltigera* in larch forest; on soil in niches between stones of stone field on S-facing slopes and fine soil in cliff cracks in forest belt. In pure mats or mixed with *Cephaloziella varians*, *Ptilidium ciliare*, FP, S.

L. longidens (Lindb.) Konstant. et Vilnet (gem.) – 3, 5, 10 – on stone in niche at the base of boulder in larch forest; on decaying wood in *Picea ajanensis* forest; on fine soil in niches between stones of stone field in forest belt. In pure mats or mixed with *Lepidozia reptans*, *Lophozia ventricosa*, *Ptilidium ciliare*, *Sphenolobus minutus*, *S. saxicola*, *Tritomaria exsecta*, FP, M, S.

Mannia fragrans (Balb.) Frye et L. Clark s. str. (fr.) – 7 – on sandy soil on S-facing cliffs along river bank. In pure mats, S.

Marchantia latifolia Gray (= *Marchantia polymorpha* subsp. *ruderale* Bischl. et Boissel.-Dub.) (gem., f. pl.) – 1, 9 – on moist soil in a ravine in larch forest; on moist sand of steep slope N-facing river bank. Mixed with *Conocephalum salebrosum*, FP, S.

M. polymorpha L. s. str. – 8 – on wet soil of stream bank. In pure mats, S.

Marsupella emarginata (Ehrh.) Dumort. (per., andr.) – 1, 2, 7 – on soil covering rocks near small waterfall on W-facing slope in stone birch forest; on soil covering rocks outcrops in *Picea ajanensis* forest; on soil covering stone along stream bank; on sandy soil in cracks of N-facing rock outcrops along river bank. Mixed with *Scapania crassiretis*, *Cephalozia bicuspidata*, *Diplophyllum obtusatum*, *Gymnocolea inflata*, *Pseudotritomaria heterophylla*, *Scapania scandica*, FP, M, S.

Mesoptychia gillmanii (Austin) L. Söderstr. et Výta – 1 – on soil on SW-facing vertical cliffs along river bank. In pure mats, S.

Metzgeria pubescens (Schrank) Raddi – 1, 3, 4, 7 – on decaying wood and soil covering rocks in stone birch forests; on *Picea ajanensis* trunk bases and soil covering rocks in *Picea ajanensis* forests; in moist niche at the base of boulder in *Picea ajanensis* forest. In pure mats or mixed with *Blepharostoma trichophyllum*, *Lepidozia*

reptans, *Plagiochila poreloides*, *Sphenolobus minutus*, *Trilophozia quinquedentata*, *Tritomaria exsecta*, FP, M, S, L.

Mylia anomala (Hook.) Gray (gem., per.) – 1, 3, 7, 9 – on *Sphagnum* in *Ledum-Sphagnum* swamp and larch forests. In pure mats or mixed with *Calypogeia muelleriana*, *C. sphagnicola*, *Cephaloziella elachista*, FP, M, S.

Nardia insecta Lindb. (immature spor.) – 3 – on moist soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river. Mixed with *Cephalozia bicuspidata*, *Pellia neesiana*, *Scapania scandica*, FP, M.

Odontoschisma fluitans (Nees) L. Söderstr. et Váňa – 1, 3 – on soil in *Eriophorum-Carex-Sphagnum* swamp by the lake; on sandy soil between boulders near river. Mixed with *Gymnocolea inflata*, *Scapania undulata*, FP, E.

Pellia neesiana (Gottsche) Limpr. (f. pl.) – 3 – on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river. Mixed with *Cephalozia bicuspidata*, *Nardia insecta*, FP.

Plagiochila poreloides (Torr. ex Nees) Lindenb. (andr.) – 1-3, 5, 7, 9 – on soil covering rocks in larch forest; on soil and soil covering rocks in stone birch forests; on *Picea ajanensis* trunk bases, decaying wood and soil covering rocks in *Picea ajanensis* forests; on moist sand of steep slope N-facing river bank; on soil on S, W-facing cliffs and sandy soil in cracks of N, S-facing rock outcrops along river banks. Mixed with *Barbilophozia barbata*, *Tritomaria exsecta*, *Trilophozia quinquedentata*, *Lepidozia reptans*, *Scapania crassiretis*, *Anastrophyllum michauxii*, *Frullania bolanderi*, *Lophozia ventricosa*, *Scapania mucronata* et al., FP, M, S.

Porella platyphylla (L.) Pfeiff. – 9 – on soil covering rocks in cracks between stones in larch forest; in caves of S-facing cliff along river bank. In pure mats or mixed with *Neckera pennata*, S, L.

Preissia quadrata (Scop.) Nees (m. pl., f. pl., fr.) – 1, 9 – on soil on stones and cliffs in birch forests; on soil on SE-facing rock outcrops along river bank; on moist sand of steep slopes N-facing river bank. Mixed with *Scapania praetervisa*, *Lophocolea minor*, *Plagiochila poreloides*, *Trilophozia quinquedentata*, FP, S.

Pseudotritomaria heterophylla (R.M. Schust.) Konstant. et Vilnet (gem.) – 2 – on sandy soil in cracks of N-facing rock outcrops along river bank. Mixed with *Marsupella emarginata*, *Scapania crassiretis*, M. Almost all gemmae are colorless, few slightly colored only.

Ptilidium ciliare (L.) Hampe (andr.) – 1, 3, 5, 7 – on soil, on *Betula* trunk bases, stone in niche at the base of boulder and *Peltigera* in larch forests. In pure mats or mixed with *Lepidozia reptans*, *Sphenolobus minutus*, *S. saxicola*, *Blepharostoma trichophyllum*, *Lophozia* spp., *Trilophozia quinquedentata* et al., FP, S.

P. pulcherrimum (Weber) Vain. (per.) – 1-5, 7, 9 – on *Picea obovata* trunk bases and decaying wood in larch forests; on *Betula pendula*, *Picea ajanensis* trunks, decaying wood and soil in birch forests; on *Picea ajanen-*

sis, Larix, Alnus crispa subsp. *fruticosa* trunks and decaying wood in *Picea ajanensis* forests; on decaying wood on stream bank. In pure mats or mixed with *Tritomaria* ssp., *Blepharostoma trichophyllum*, *Frullania bolanderi*, *Cephalozia bicuspidata*, *Crossocalyx hellerianus*, *Lophozia guttulata*, *Schistochilopsis incisa*, *Trilophozia quinquentata* et al., FP, M, S.

Radula complanata (L.) Dumort. (gem., per.: paroicos) – 9 – on soil covering rocks in cracks between rocks in larch forest. Mixed with *Plagiochila poreloides*, S.

Reboulia hemisphaerica (L.) Raddi s. str. (fr.) – 1, 5, 8, 9 – on soil of cliffs in birch forest; soil covering rocks in *Picea ajanensis* forest; on soil on S,W-facing cliffs cracks in forest belt; on sandy soil between stones near river and moist sand of steep slope N-facing river bank. Mixed with *Scapania gymnostomophila*, *Plagiochila poreloides*, *Tritomaria exsecta*, *T. scitula*, FP, S.

Riccardia chamedryfolia (With.) Grolle – 6 – on decaying wood in *Picea ajanensis* forest. Mixed with *Cephalozia bicuspidata*, *Chiloscyphus polyanthus*, FP.

Scapania apiculata Spruce (gem.) – 6 – on decaying wood in *Picea ajanensis* forest. Mixed with *Anastrophyllum michauxii*, *Blasia pusilla*, *Cephalozia bicuspidata*, *Scapania crassiretis*, *S. mucronata*, FP, M.

S. brevicaulis Taylor (gem., per.) – 8 – on sandy soil between stones near river. In pure mats, S.

S. crassiretis Bryhn (gem., per., andr.) – 1-7 – on soil and decaying wood near stream in larch forests; on soil, decaying wood and soil covering rocks in stone birch forests; on decaying wood, soil covering rocks and soil near stream in *Picea ajanensis* forests; on soil on SW-facing vertical cliffs in forest belt; on sandy soil in cracks of N-facing rock outcrops along river banks and soil covering stone along stream bank. In pure mats or mixed with *Blepharostoma trichophyllum*, *Cephalozia bicuspidata*, *Plagiochila poreloides*, *Trilophozia quinquentata*, *Blasia pusilla*, *Marsupella emarginata*, *Scapania scandica*, *Pseudotritomaria heterophylla* et al., FP, S.

S. curta (Mart.) Dumort. – 2, 6 – on decaying wood in *Picea ajanensis* forest; on sandy soil in cracks of N-facing rock outcrops along river bank. In pure mats or mixed with *Lophozia ventricosa*, *Tritomaria exsecta*, FP, M.

S. gymnostomophila Kaal. (gem.) – 9 – on soil of cliffs cracks in birch forests. In pure mats or mixed with *Reboulia hemisphaerica*, *Tritomaria scitula*, FP, M.

S. irrigua (Nees) Nees (gem., andr.) – 3 – on sandy soil between boulders near river. In pure mats or mixed with *Scapania paludicola*, FP, S.

S. microdonta (Mitt.) Müll. Frib. (gem.) – 5 – on fine soil in niches between stones of stone field in forest belt. Mixed with *Sphenolobus saxicola*, FP.

S. mucronata H. Buch (gem., andr.) – 1, 3, 6, 9, 10 – on decaying wood in birch forests; on *Picea ajanensis* trunk bases, decaying wood and soil covering rocks in *Picea ajanensis* forests; on soil on moist S-facing cliffs

cracks along river bank and fine soil in niches between stones of stone field in forest belt. In pure mats or mixed with *Tritomaria exsecta*, *Anastrophyllum michauxii*, *Blasia pusilla*, *Cephalozia bicuspidata*, *Barbilophozia barbata*, *Lophozia ventricosa*, *Plagiochila poreloides*, *Scapania rufidula* et al., FP, M, S.

S. paludicola Loeske et Müll. Frib. – 1, 3 – on sandy soil between boulders and on rock outcrops near river. Mixed with *Scapania irrigua*, *S. rufidula*, S.

S. praetervisa Meyl. (gem., per., andr.) – 1, 7, 9 – on soil on stone in birch forest; on moist sand of steep slope N-facing river bank; on soil and sand on S-facing cliffs along river banks. Mixed with *Plagiochila poreloides*, *Preissia quadrata*, *Cephaloziella varians*, *Jungermannia polaris*, *Lophocolea minor*, *Trilophozia quinquentata*, FP, M.

S. rufidula Warnst. (andr.) – 1, 3, 7 – on sandy soil on rock outcrops near river; on soil in moist S-facing cliffs cracks along river bank; on soil covering stone along stream bank. Mixed with *Scapania crassiretis*, *S. mucronata*, *S. paludicola*, FP, M.

S. scandica (Arnell et H. Buch) Macvicar (incl. *Scapania parvifolia* Warnst.) (gem., per.) – 1-5, 7 – on soil and decaying wood near stream in larch forests; on decaying wood in birch forest; on soil covering rocks outcrops in *Picea ajanensis* forest; on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river; on decaying wood and soil on SW-facing vertical cliffs in forest belt, on sandy soil in cracks of N-facing rock outcrops along river banks. In pure mats or mixed with *Blepharostoma trichophyllum*, *Scapania crassiretis*, *Schistochilopsis incisa*, *Sphenolobus minutus*, *Cephalozia bicuspidata*, *Plagiochila poreloides*, *Ptilidium pulcherrimum*, *Tritomaria exsecta* et al., FP, M.

S. undulata (L.) Dumort. (gem., andr.) – 3, 7 – on sandy soil between boulders near river and soil covering stone along stream bank. Mixed with *Marsupella emarginata*, *Odontoschisma fluitans*, FP, S.

Schistochilopsis incisa (Schrad.) Konstant. (gem., andr.) – 1-5, 7, 9 – on soil, decaying wood near stream and soil covering rocks in larch forests; on decaying wood in stone birch and *Picea ajanensis* forests; on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river; on soil on SW-facing vertical cliffs along river bank and soil covering stone along stream bank. Mixed with *Sphenolobus minutus*, *Blepharostoma trichophyllum*, *Tritomaria exsectiformis*, *Scapania scandica*, *Lepidozia reptans*, *Cephalozia* ssp., *Lophozia guttulata*, *Ptilidium pulcherrimum* et al., FP, M, S.

Schljakovia kunzeana (Huebener) Konstant. et Vilnet – 4 – on soil in *Ledum-Sphagnum* larch forest. Mixed with *Calypogeia muelleriana*, FP.

Solenostoma confertissimum (Nees) Schljakov (andr., arch. not marked) – 3 – on soil under *Alnus crispa* subsp. *fruticosa* stand on E-facing slope to the river. Mixed with *Schistochilopsis incisa*, S.

S. hyalinum (Lyell) Mitt. – 3, 8 – on sandy soil between boulders and rocks near river. In pure mats and mixed with *Blasia pusilla*, FP, S.

Sphenolobus minutus (Schreb. ex D. Crantz) Berggr. (per., andr., fr.) – 1-5, 7, 9, 10 – on soil, *Betula* trunk bases, in niche on soil covering rocks and decaying wood in larch forests; on decaying wood and soil on cliffs in birch forests; on soil covering rocks in *Picea ajanensis* forests; on soil on S, W-facing cliffs cracks and fine soil in niches between stones of stone field in forest belt. In pure mats or mixed with *Schistochilopsis incisa*, *Lepidozia reptans*, *Ptilidium ciliare*, *Blepharostoma trichophyllum*, *Scapania scandica*, *Tritomaria* ssp., *Calycularia laxa*, *Lophozia ventricosa* et al., FP, M, S, L.

S. saxicola (Schrad.) Steph. (fr.) – 1, 3-5, 9, 10 – on soil and in niche on soil covering rocks in larch forests; on soil in niches between stones of stone fields in forest belt. In pure mats or mixed with *Sphenolobus minutus*, *Lophozia ventricosa*, *Ptilidium ciliare*, *Lophozia longidens*, *Scapania microdonta*, *S. mucronata*, *Trilophozia quinquedentata*, FP, M, S, L.

**Targionia hypophylla* L. (fr.) – 1 – on soil on moist shaded W-facing cliffs cracks along river bank. In pure mats, S.

Trilophozia quinquedentata (Huds.) Bakalin (per., andr.) – 1-5, 10 – on stone in niche at the base of boulder in larch forest; on soil and soil covering rocks in stone birch forests; on soil, decaying wood and *Picea ajanensis* trunk bases in *Picea ajanensis* forest; on soil on S, W-facing cliffs cracks and fine soil in niches between stones of stone field in forest belt. Mixed with *Sphenolobus minutus*, *Lepidozia reptans*, *Plagiochila poreloides*, *Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Scapania crassiretis*, *S. praetervisa*, *Plagiochila poreloides* et al., FP, S.

Tritomaria exsecta (Schmidel) Schiffn. ex Loeske (gem., per., andr.) – 1-3, 5-9 – on decaying wood and soil covering rocks in larch forests; on soil, soil covering rocks and decaying wood in stone birch forests; on *Picea ajanensis* trunk bases, decaying wood and soil covering rocks in *Picea ajanensis* forests; on decaying wood on stream bank. In pure mats or mixed with *Blepharostoma trichophyllum*, *Sphenolobus minutus*, *Plagiochila poreloides*, *Lepidozia reptans*, *Ptilidium pulcherrimum*, *Crossocalyx hellerianus*, *Anastrophyllum michauxii*, *Lophozia* ssp. et al., FP, M, S.

T. exsectiformis (Breibl.) Schiffn. ex Loeske (gem., fr.) – 2, 5 – on decaying wood in larch and *Picea ajanensis* forests. In pure mats or mixed with *Lepidozia reptans*, *Schistochilopsis incisa*, *Blepharostoma trichophyllum*, *Cephalozia* ssp., *Lophozia ventricosa*, *Ptilidium pulcherrimum*, *Sphenolobus minutus* et al., FP, M.

T. scitula (Taylor) Juurg. (gem., andr.) – 9 – on soil in S-facing cliffs cracks in stone birch forest. Mixed with *Reboulia hemisphaerica*, *Scapania gymnostomophila*, M.

DISCUSSION

There are rather few species in the study area which grow in a wide range of habitats, including soil, fine earth on rocks and in rock crevices, decaying wood and trunk bases; these are *Barbilophozia barbata*, *Blepharostoma trichophyllum*, *Lepidozia reptans*, *Metzgeria pubescens*, *Scapania mucronata*, *Sphenolobus minutus*, *Trilophozia quinquedentata*, and *Tritomaria exsecta*.

Unlike in more northern parts of Yakutia, most liverwort species do not grow in a ground cover in the study area, being likely displaced from soil by dense vegetation formed by vascular plants. They occupy rocky substrates and decaying wood, and may grow on soil only occasionally in boggy areas or in moist to wet places, on ravine slopes and river banks. In rocky habitats, liverworts are usually found in moist, shaded cracks, niches between stones, on shaded by trees cliff walls with water seepage from melting permafrost at the base of slope or in the forested flood-valleys and on river banks.

Only few species were found in dry rocky habitats: *Frullania davurica*, *F. koponenii*, *Porella platyphylla*, *Sphenolobus saxicola*, and occasionally *Sphenolobus minutus* and *Scapania microdonta*.

Boulders along river and stream banks with occasional floods are inhabited by *Blasia pusilla*, *Jungermannia borealis*, *J. polaris*, *Marsupella emarginata*, *Scapania brevicaulis*, *S. crassiretis*, *S. rufidula*, and *S. undulata*.

Decaying wood was found to be the only substrate for *Anastrophyllum michauxii*, *Cephalozia lunulifolia*, *C. pleniceps*, *Chiloscyphus polyanthus*, *Crossocalyx hellerianus*, *Harpanthus scutatus*, *Lophocolea heterophylla*, *Lophozia guttulata*, *Riccardia chamedryfolia*, *Scapania apiculata*, and *Tritomaria exsectiformis*.

Calypogeia sphagnicola, *Cephaloziella elachista* and *Mylia anomala* grow only on *Sphagnum* and *Calypogeia muelleriana* – on soil and on *Sphagnum*.

Frullania bolanderi was found only on trunks, while *F. koponenii* grew on trunks and in caves of cliff; *Ptilidium pulcherrimum* inhabited tree trunks, decaying wood and soil.

Two main types of habitats, decaying wood and rocks, are characteristic for *Blasia pusilla*, *Calypogeia neesiiana*, *Cephalozia bicuspidata*, *Diplophyllum obtusatum*, *Lophozia ventricosa*, *Lophozia longidens*, *Plagiochila poreloides*, *Scapania crassiretis*, *S. curta*, *S. scandica*, and *Schistochilopsis incisa*.

Among the most interesting records in the Aldan Upland, some southern species should be listed; they are found here at the northern limit of their distribution in Yakutia: *Diplophyllum obtusatum*, *Frullania davurica*, *F. koponenii*, *Harpanthus scutatus*, *Porella platyphylla*, *Scapania apiculata*, and *Targionia hypophylla*.

Targionia hypophylla is found for the first time in Yakutia. This is the northernmost locality of this species in Russia. Its nearest localities are in the Trans-Baikal Territory – in the Alkhanay National Park (Potemkin & Afon-

ina, 2007) and on Kodar Range (Mamontov, personal communication).

Harpanthus scutatus is also recorded for the first time in the republic. There is only one more northern known locality of this species in Asia, in Verkhne-Tazovsky Nature State Reserve in Yamal-Nenets Autonomous District (Czernyadjeva & Potemkin, 2002). Otherwise it was found in a few places in West Siberia (Czernyadjeva & Potemkin, 2002; Lapshina, 2003) and South Siberia (Kazanovsky & Potemkin, 1995; Váňa & Ignatov, 1995; Bakalin, 2001).

The localities on the Aldan Upland of three other species, *Diplophyllum obtusatum*, *Frullania davurica*, *F. koponenii*, are the northernmost for Russia. It seems that the narrow valley and high rocky banks of the river provide a suitable microclimate for these more southern species. *Picea ajanensis*, the host plant of the latter species, also grows at the northwestern boundary of its overall distribution in the study area. *Diplophyllum obtusatum* was known earlier in the territory of the Republic from the Udokan Range (Bakalin, 2004), *Frullania davurica* and *F. koponenii* – from Tokinsky Stanovik Range (Sofronova, 2013b).

Scapania apiculata is a rare species in Yakutia, earlier known from few localities in its southern part, in Udokan Range (Bakalin, 2004) and in the upper course of Lena River near the mouth of the Pilka River (Sofronova, 2006). *Porella platyphylla* is also a rare species in Yakutia, previously known from the National Natural Park “Lena Pillars” in Central Yakutia (Sofronova, 2007). Altogether, many of these species occur there on the northern limit of distribution.

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