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To the knowledge of liverwort flora of Balagan Mountain and Vengeri River Valley (Sakhalin Island, North-West Pacific)

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The liverwort flora of Balagan Mt. and Vengeri River Valley is investigated and 86 species are revealed and annotated in the checklist. The most prominent environmental feature of the studied area is wide distribution of limestone outcrops that identified the high proportion of basiphilous taxa in the flora. The distinctly acidic rocks are absent in the area that resulted in rather low rate of acidophilic taxa in the flora. The distribution of some arctic-alpine taxa (including that of predominantly Mega-Beringian distribution) possesses the relict character in studied area.

Keywords: liverworts, Hepaticae, East Asia, North-West Pacific, Sakhalin Island, flora, protected area.

Liverwort flora of Sakhalin Province (Sakhalin and Kuril Islands) is more or less well investigated in comparison with many other regions of the Russian Far East (possible exception provided by Primorsky Territory only). However, data on intra-regional distribution of liverworts are still scanty that makes difficult any synthesizing and speculations on the flora origin, development and sustainability. Moreover, the 'beliefs' on the rarity of some taxa may be too premature if only a few localities in the macro-region are visited and studied. Balagan Mountain belongs to the Nabilsky Range that is the oldest land-formed bedrocks in Sakhalin Island and is the link on the migration way between Japanese Archipelago and North-East Asia. Indeed, Nabilsky Range houses many rare (in boreal zone) arctic-alpine, including Mega-Beringian in longitudinal respect, taxa (Bakalin et al., 2012). Besides, Nabilsky Range is widely known as an area of common occurrence of extensive limestone outcrops – a relatively rare case in the Russian Far East. Vyshin and Barkalov (1990) reported the effect of limestone occurrence for the vascular plants flora in Nabilsky Range. The same should be likely expected for liverworts. Only a few were known before on limestone bryophyte flora in Sakhalin, where all available data were limited to Vaida Nature Monument (Bakalin et al., 2009). The limestone openings area in Balagan Mt. is much larger than in Vaida Mt. Even this circumstance made the study of limestone areas in Balagan Mt. potentially promising.

Sakhalin Environmental Watch kindly invited authors to visit and explore Vostochnyi Nature Reserve (a protected area of provincial level covering Balagan Mt. and Vengeri River) and offered to our disposal field station in the mouth of Vengeri River as well as the transfer to this hardly accessible area. To avail oneself of the offer we visited the latter reserve with the purpose liverwort and vegetation survey in the summer of 2017. One of us specialized in liverwort taxonomy (Bakalin) was able to visit the reserve for the two weeks in July of 2017 when the most of liverwort specimens were collected. Vegetation studies (by Korznikov) took much longer time and are subject for another research (Korznikov, Popova, 2018). Therefore, the main goals of the present account were to provide new data on liverwort taxonomic diversity and to discuss the peculiar traits of the flora based on the newly obtained materials.

Material and methods

The explorations took two weeks in July of 2017 and were housed in Vengeri River valley from its mouth to uppermost reaches and Balagan Mt. with its some nearest spurs. The main purpose of our work was to compile the list of taxa occurring in the reserve in general, but not to reveal the 'infra-reserve' distribution for each taxon. As a result, we tried to study all communities we met in the course of our exploration, although only limited number of repeats was collected for each revealed taxon. The latter circumstance some-

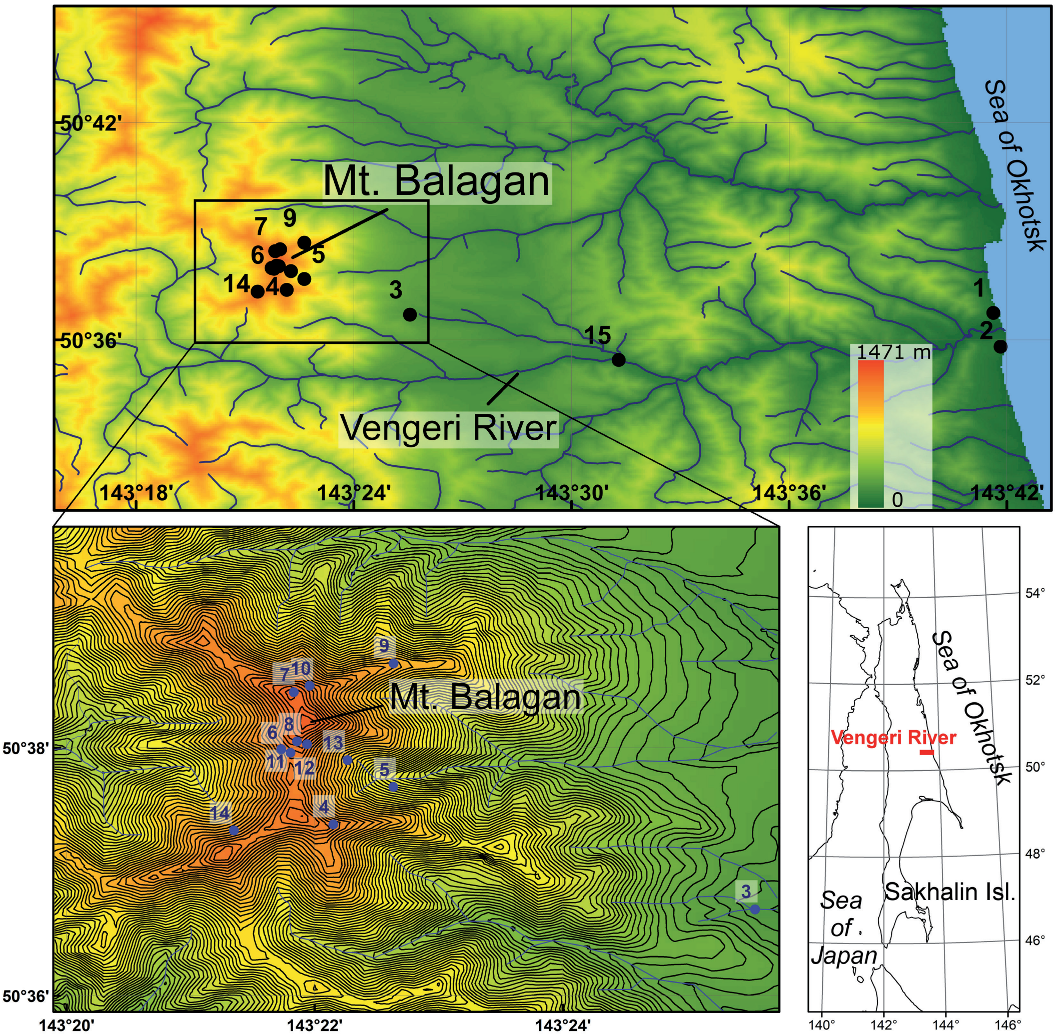

Figure 1. Study area in Vostochnyi Nature Reserve with collection localities of liverworts.

Рисунок 1. Карта района исследований на территории заказника «Восточный» с указанием точек сбора печеночников.

what limited our abilities to speculate on relative frequency of taxa in the area treated.

Each taxon was supplied with information on the substrate, community where it was collected, moisture conditions, geographic coordinates and shadiness. All specimens were transferred alive to the cryptogamic laboratory of the Botanical Garden-Institute (VBGI) where they were keeping in the refrigerator in the temperature close to 0°C and were identified when the most of them remained alive. All identifications, along with 'label data' were input to the specially organized online available herbarium database (http://botsad.ru/herbarium/).

All visited localities are placed in the Figure 1 and described in the Table 1. The localities 1 and 2 are in lower course of Vengeri River, 3 and 15 in the middle course of the river and others are in Balagan Mt. summit area.

Study area

Relief, geology and climate

The study area is located in the basin of Vengeri River situated in the central part of Sakhalin Island, on its eastern coast (the Sea of Okhotsk). Upper reach-

Table 1. The list of collection localities in Vostochnyi Nature Reserve (in accordance with Figure 1).

Таблица 1. Список точек сбора на территории заказника «Восточный» (в соответствии с Рисунком 1).

Locality (точка сбора)	Coordinates (координаты)	Elevation, m a.s.l. (approximated) (высота, м над ур. м. (приблизительная))
1	50°36'45"N 143°41'38"E	90
2	50°35'49"N 143°41'50"E	80
3	50°36'42"N 143°25'33"E	260
4	50°37'23"N 143°22'09"E	1260
5	50°37'41"N 143°22'38"E	850
6	50°37'59"N 143°21'44"E	1330
7	50°38'27"N 143°21'50"E	1430
8	50°38'03"N 143°21'52"E	1370
9	50°38'41"N 143°22'38"E	1140
10	50°38'30"N 143°21'58"E	1330
11	50°37'58"N 143°21'48"E	1290
12	50°38'02"N 143°21'56"E	1390
13	50°37'54"N 143°22'16"E	970
14	50°37'20"N 143°21'21"E	1190
15	50°35'27"N 143°31'18"E	130

es of Vengeri River are near the ridgeline of Nabilsky Range, and its mouth is situated ca. 30 km to the east (Fig. 1). Whereas the lower course of Vengeri River lies in smoothened hilly landscape, its upper reaches near Nabilsky Range ridgeline are in highly dissected, with steep sloped spurs area. Watershed of Nabilsky Range, including Balagan Mt., provides both narrow-peaked ridges and gentle sloped surfaces (Fig. 2). The highest point of Balagan Mt. is 1471 m a.s.l. At its most extent, the valleys of Vengeri River and its small tributaries are narrow and V-shaped in the transverse section. The well-developed floodplains occur in the lower course of the river. The seashore represents abrasion-accumulative terrace with cliffy wall in abrupt coast.

The Nabilsky Range, in general, is composed by Cretaceous and Jurassic-Cretaceous sedimentary rocks where clay-siliceous schistose siltstones and siltstones with lenticular interbeds and boudins of sandstones dominate, whereas lenses of radiolarites and limestones are less often (Evseev, 2009). However, in the vicinity of Balagan Mt. limestone outcrops (Fig. 3) cover the total area of ca. 14 km^2.

The annual temperature of study area is –1.6°C and annual precipitation is 772.4 mm according to the data for the nearest weather station (Pogranichnoe Settl., coast of the Sea of Okhotsk, 30 km to the south from the mouth of Vengeri River). A strong cooling effect observed in the area (in comparison with island inlands) is due to cold East Sakhalin Current that pronouncedly evidenced in the melting of sea ice shield in June. However, narrow valleys have milder microclimates and are protected from the direct influence of cold air from the Sea of Okhotsk.

Figure 2. The landscape overview in Balagan Mt., in the foreground are communities of *Pinus pumila* (Pall.) Regel intermingled with different types of tundroids in upper parts of slopes (photo by K. Korznikov).

Рисунок 2. Ландшафты горы Балаган, на переднем плане заросли кедрового стланика, в верхней части склона перемежающиеся с тудроподобными сообществами разных типов (фото К. Корзникова).

Figure 3. Limestone outcrops in the vicinity of Balagan Mt., in the foreground are *Betula ermanii* Cham. krummholz intermingled with *Pinus pumila* (Pall.) Regel and *Alnus fruticosa* Rupr. thickets (photo by K. Korznikov).

Рисунок 3. Известняковые скалы в окрестностях горы Балаган, на переднем плане каменноберезовое криволесье с вклинивающими «языками» зарослей кедрового и ольхового стлаников (фото К. Корзникова).

Vegetation

The Basin of Vengeri River is situated near the northern boundary of south taiga and belongs to East Sakhalin Mts. vegetation district of dark-conifer forests zone with dominance by *Picea jezoensis* (Siebold & Zucc.) Carrière (Tolmachev, 1955; Krestov et al., 2004). The detailed description of zonal forests of Nabilsky Range was published by N.E. Kabanov (1940), whereas 'alpine' vegetation was only described by Vyshin and Barkalov (1990). Below we provide a brief summary. The names of vascular plants are given according to World Flora Online (http://www.worldfloraonline.org/), with some exceptions: *Alnus fruticosa* Rupr. = *Alnus alnobetula* subsp. *fruticosa* (Rupr.) Raus, *Chosenia arbutifolia* (Pall.) A.K. Skvortsov = *Salix arbutifolia* Pall., *Petasites amplus* Kitam. = *Petasites japonicus* subsp. *giganteus* F. Schmidt ex Kitam., *Senecio cannabifolius* Less. = *Jacobaea cannabifolia* (Less.) E. Wiebe and *Weigela middendorffiana* (Carrière) K. Koch = *Macrodiervilla middendorffiana* (Trautvetter & Meyer) Nakai.

The lowest vegetation belt consists of various types of dark-conifer forests (dominants are *Abies sachalinensis* (F. Schmidt) Mast. and *Picea jezoensis*): 1 – moss-type (with cover of *Dicranum* spp., *Hylocomium splendens* (Hedw.) Bruch et al., *Pleurozium schreberi* (Brid.) Mitt., *Rhytidiadelphus triquetrus* (Hedw.) Warnst.), 2 – shrub-type (*Sorbus sambucifolia* (Cham. & Schltdl.) M. Roem., *Vaccinium ovalifolium* Sm., *Weigela middendorffiana* (Carrière) K. Koch), 3 – fern-type (*Gym-*

Figure 4. *Abies sachalinensis* (F. Schmidt) Mast. and *Picea jezoensis* (Siebold & Zucc.) Carrière forest with *Gymnocarpium dryopteris* (L.) Newman cover in lower course of Vengeri River (photo by K. Korznikov).

Рисунок 4. Пихтово-еловый папоротниковый лес в нижнем течении реки Венгери (фото К. Корзникова).

Figure 5. Dry *Larix cajanderi* Mayr forest with lichen cover and scattered *Pinus pumila* (Pall.) Regel clumps in the middle course of Vengeri River (photo by K. Korznikov).

Рисунок 5. Сухой лишайниковый лиственничник в среднем течении реки Венгери (фото К. Корзникова).

nocarpium dryopteris (L.) Newman, *Leptorumohra amurensis* (Milde) Tzvelev, *Phegopteris connectilis* (Michx.) Watt), 4 – forb and dwarf-shrub type (*Cornus canadensis* L., *Maianthemum dilatatum* (Wood) A. Nelson & J.F. Macbr., *Oxalis acetosella* L.) (Fig. 4). All these types belong to two vegetation associations ***Weigelo middendorffianae–Piceetum jezoensis*** Krestov et Nakamura 2002 and ***Vaccinio vitis-idaeae–Piceetum jezoensis*** Krestov et Nakamura 2002 (union ***Piceion jesoensis*** Suz.-Tok. ex Jinno et Suzuki 1973, order ***Abieti–Piceetalia*** Miyawaki et al. 1968, class ***Vaccinio–Piceetea*** Br.-Bl. in Br.-Bl. et al. 1939) (Krestov, Nakamura, 2002).

The middle and upper parts of mountain slopes are occupied by stone birch forests (*Betula ermanii* Cham.) those are subdivided into following types: 1 – shrub-type (cover of *Acer ukurunduense* Trautv. & C.A. Mey. *Sorbus sambucifolia, Weigela middendorffiana, Vaccinium ovalifolium*), 2 – tall herb-type (*Cirsium kamtschaticum* Ledeb. ex DC., *Filipendula camtschatica* (Pall.) Maxim., *Senecio cannabifolius* Less.); 3 – forb-type. All these types belongs to the association ***Weigelo–Betuletum ermanii*** Nakamura in Miyawaki 1988 (union ***Athyrio brevifrondis–Weigelion middendorffianae*** Ohba 1973, order ***Streptopo–Alnetalia maximowiczii*** Ohba 1973, class ***Betulo ermanii–Ranunculetea acris*** Ohba 1968) (Miyawaki, 1988). Secondary stone-birch forests also often occur on the sites of previously disturbed primary dark-coniferous communities at low altitude. Near the upper limit of timber zone *Betula ermanii* krummholz (Fig. 3) are associated with wind-protected sites like spring valleys or thalwegs opposite to Siberian dwarf pine (*Pinus pumila* (Pall.) Regel) thickets covering more windy places.

Communities of dwarf pine (*Pinus pumila*) and dwarf alder (*Alnus fruticosa* Rupr.) occupy upper parts of slopes and gentle watersheds (Fig. 2). Under the canopy formed by both shrubs a few species of vascular plants and mosses may be observed (*Cornus canadense, Ledum palustre* L., *Maianthemum dilatatum, Rubus pedatus* Sm., *Vaccinium vitis-idaea* L., *Hylocomium splendens, Pleurozium schreberi*). These communities belong to associations ***Vaccinio–Pinetum pumilae*** Maeda et Shimazaki 1951 and ***Ledo–Pinetum pumilae*** Kobayashi 1967, union ***Vaccinio–Pinion pumilae*** Suz.-Tok. 1964, order ***Vaccinio–Pinetalia pumilae*** Suz.-Tok. 1964, class ***Vaccinio–Piceetea.***

Larch forests (*Larix cajanderi* Mayr) are developed after natural fires and widely distributed in low altitudes on smooth, but well drained surfaces. The floristic composition of these communities depends on succession stages. There are the monodominant poor-in-species forests at the initial stages (*Ledum palustre, Vaccinium vitis-idaeae, Polytrichum* spp., and lichens, association ***Ledo palustris–Laricetum cajanderi*** Ermakov et al. 2002) (Fig. 5). Contrary, the late stages of succession show similar floristic composition of understory to dark-conifer forests (association ***Vaccinio ovalifolii–Laricetum cajanderi*** Krestov et al. 2009). Primary larch forests may be rarely observed in swampy habitats

Figure 6. Tundroid community over limestone gravel with *Dryas octopetala* ssp. *ajanensis* (Juz.) Hultén, *Phyllodoce caerulea* (L.) Bab., and *Rhododendron aureum* Georgi near ridgeline (photo by K. Korznikov).

Рисунок 6. Каменистое тудроподобное сообщество на водоразделе с доминированием *Dryas octopetala* ssp. *ajanensis* (Juz.) Hultén*, Phyllodoce caerulea* (L.) Bab. и *Rhododendron aureum* Georgi (фото К. Корзникова).

Figure 7. Late snow melt habitat surrounded by *Pinus pumila* (Pall.) Regel thickets and spots of tundroids on a watershed (photo by R. Shatrov).

Рисунок 7. Местообитания с поздно истаивающим снегом в окружении зарослей кедрового стланика и тундроподобных сообществ на водоразделе (фото Р. Шатрова).

(association ***Chamaedaphno calyculatae–Laricetum cajanderi*** Krestov et al., 2009, class ***Vaccinio–Piceetea***) (Krestov et al., 2009).

Riverside vegetation consists of softwood tall-herbs forests. *Alnus hirsuta* (Spach) Turcz. ex Rupr., *Chosenia arbutifolia* (Pall.) A.K. Skvortsov, *Populus suaveolens* Fisch., and *Salix udensis* Trautv. & C.A. Mey are the main dominants. Floodplain communities belong to association ***Filipendulo palmatae–Salicetum udensis*** Korznikov et Popova 2018 (class ***Salicetea sachalinensis*** Ohba 1973) (Korznikov, Popova, 2018).

The highest altitude mountain vegetation may be called "tundroids" (alpine tundra-like communities). The dominants of these communities are ericoid dwarf-shrubs (*Arctous alpina* (L.) Nied., *Ledum decumbens* (Aiton) Lodd. ex Steud., *Loiseleuria procumbens* (L.) Desv., *Phyllodoce caerulea* (L.) Bab., *Rhododendron aureum* Georgi, *Vaccinium vitis-idaeae*), *Carex rupestris* All., *Pedicularis koidzumiana* Tatew. & Ohwi, *Salix berberifolia* Pall., *Sieversia pentapetala* (L.) Greene, and lichens (class ***Carici rupestris–Kobresietea bellardii*** Ohba 1974) (Ohba, 1974) (Fig. 6, 7). The limestone outcrops (distributed near ridgeline only) provide quite peculiar habitat that results in the development of sparse vegetation by *Dendranthema mongolicum* (Ling) Tzvelev, *Dryas octopetala* ssp. *ajanensis* (Juz.) Hultén, *Leontopodium discolor* Beauverd, *Oxytropis calcareorum* N.S. Pavlova, *Rhododendron adamsii* Rehder, *Thymus japonicus* (Hara) Kitag. The forb subalpine vegetation is developed in the relatively wet sites with nutrient-rich soil (dominants are *Anemonastrum sachalinense* (Miyabe & T. Miyake) Starod, *Geranium erianthum* DC., *Trollius miyabei* Sipliv.; union ***Trollio–Ranunculion acris japonica*** Ohba 1969, order ***Trollio–Ranunculetalia acris japonica*** Ohba 1973, class ***Betulo ermanii–Ranunculetea acris***) (Miyawaki, 1988). These communities are gradually replaced by tall-herb vegetation in lower altitudes (association ***Cirsio kamtschaticae–Polygonetum sachalinensis*** (Ohba 1973) Ohba et Sugawara 1982, class ***Filipendulo–Artemisietea montanae*** Ohba 1973) (Ohba, Sugawara, 1982; Miyawaki, 1988) with cover of *Aconogonon weyrichii* (F. Schmidt) H. Hara, *Filipendula camtschatica, Macropodium pterospermum* F. Schmidt, *Petasites amplus* Kitam., *Senecio cannabifolius.*

Results

As a result of collection identification 86 species and one variety of liverworts were revealed. They are distributed across three main vegetation belts that deeply interpenetrating one to another: forests (mostly *Picea-Abies,* rarely *Larix*), krummholz and tundroids. Below all revealed taxa are listed in alphabetical order, with nomenclature mostly following to the World liverwort and hornwort checklist (Söderström et al., 2016). The species name is followed by number of locality, elevation range in the area treated and the brief note on habitat. Other comments are occasionally added.

List of species

Anthelia juratzkana (Limpr.) Trevis. – 4, 7, 14; 1190–1435; krummholz and tundroid belts, on open moist argillaceous slate rocky outcrops, also those on a slope to stream.

Arnellia fennica (Gottsche) Lindb. – 9; 1140; several collections from one locality in krummholz belt, in open mesic crevices of limestone rocky outcrops.

Barbilophozia barbata (Schreb.) Loeske – 12; 1385; one collection from tundroid belt, on open mesic humus covering limestone outcrops.

Barbilophozia lycopodioides (Wallr.) Loeske – 6; 1335; one collection from tundroid belt, on open mesic humus covering limestone outcrops.

Bazzania trilobata (L.) Gray – 3; 260; one collection from dark coniferous forest, on a slope to stream.

Blepharostoma trichophyllum (L.) Dumort. subsp. *trichophyllum*. – 1, 5, 9, 15; 90–1140; *Picea-Abies* forest on the first coastal terrace, also *Larix* forest and krummholz belt, over partly shaded humus on slopes to streams and in open mesic crevices in limestone rocky outcrops.*

Blepharostoma trichophyllum (L.) Dumort. subsp. *brevirete* (Bryhn et Kaal.) R.N. Schust. – 5, 12; 850–1385; krummholz and tundroid belts, on open moist limestone rocky outcrops.

Calypogeia integristipula Steph. – 1, 2, 7, 14, 15; 90–1435; common from low elevation dark coniferous forests to tundroid belt, it occurs on moist fallen decaying tree trunks, moist humus between boulders (including those of limestone) and soil on slopes to streams.

Calypogeia muelleriana (Schiffn.) Müll. Frib. – 10, 14; 1190–1330; krummholz and tundroid belts, over *Sphagnum* on mossy slopes.

Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske – 4; 1260; one collection in tundroid belt, over *Sphagnum* mat on steep slope.

Cephalozia bicuspidata (L.) Dumort. – 1; 90; surprisingly rare species in the area treated; only one collection in *Picea-Abies* forest on the first coastal terrace was revealed, on moist fallen decaying tree trunk.

Chiloscyphus polyanthos (L.) Corda – 1, 3; 90–260; in various types of forests at low elevation, on moist decaying wood and humus near streams.

Clevea hyalina (Sommerf.) Lindb. – 13; 974; one collection from krummholz belt, in crevices filled with fine soil in limestone rocky outcrops. Another specimen of "*Clevea*?" was collected at the elevation of 1335 m a.s.l., but it is very scanty and free of any generative structures thus the clear identification seems hardly possible.

Clevea nana (Shimizu & S. Hatt.) Borovich. & Bakalin – 5; 850; several collections in the same site in krummholz belt, in mesic open crevice in limestone rocky outcrops.

Conocephalum salebrosum Szweyk., Buczk. & Odrzyk. – 1, 5, 13; 90–974; from low elevation forests to krummholz belt, on moist to wet limestone outcrops and humus along streams.

Diplophyllum albicans (L.) Dumort. – 10; 1330; one collection from tundroid belt, on open moist argillaceous slate cliff.

Diplophyllum taxifolium (Wahlenb.) Dumort. – 2, 4, 14, 15; 80–1260; from low elevation *Picea-Abies* forests to krummholz belt; moist humus on slopes and hummock sides, open cliffs and soil on a slope to stream.

Douinia plicata (Lindb.) Konstant. et Vilnet – 1, 2, 7, 8; 80–1435; from low elevation *Picea-Abies* forests to tundroid belt, on moist to mesic decaying fallen wood, open wide crevices filled with humificated soil, also ground cover in tundra-like mesic communities.

Eocalypogeia schusteriana (S. Hatt. & Mizut.) R.M. Schust. – 9, 12; 1140–1371; krummholz and tundroid belts, in open moist crevices in limestone outcrops.

Frullania bolanderi Austin – 3; 260; one collection in floodplain forest from *Salix* tree bark.

Frullania koponenii S. Hatt. – 2; 80; one collection in *Picea-Abies* forest in the first coastal terrace from *Abies* tree bark.

Frullania subarctica Vilnet, Borovich. et Bakalin – 5, 8, 12; 850–1385; krummholz and tundroid belts, in open mesic crevices in limestone outcrops, also over mosses in mesic tundra-like community on steep slope.

Fuscocephaloziopsis leucantha (Spruce) Váňa et L.Söderstr. – 2, 14; 80–1190; widely distributed from *Picea-Abies* forests in low elevation to krummholz belt, on moist decaying wood and open moist soil on a slope to stream.

Fuscocephaloziopsis lunulifolia (Dumort.) Váňa et L.Söderstr. – 80–1190; from *Picea-Abies* forests in low elevation to krummholz belt, on moist decaying wood (including those of *Pinus pumila*) and open moist soil on a slope to stream.

Fuscocephaloziopsis pachycaulis (R.M.Schust.) Váňa et L.Söderstr. – 4, 14; 1190–1260; krummholz and tundroid belts, on moist open cliffs on a slope to stream.

Fuscocephaloziopsis pleniceps (Austin) Váňa et L.Söderstr. – 4; 1260; one collection in krummholz belt, where over *Sphagnum* mat on steep slope.

* Our very preliminary genetic studies in *Blepharostoma* show the high heterogeneity of the material referable to *B. trichophyllum* s.l. across North Asia. Some new taxa may be probably described in the future; therefore, our indication of two subspecies should be regarded as very preliminary and based on the morphological concept.

Gymnomitrion corallioides Nees – 10; 1330; one collection in tundroid belt from open mesic cliff of argillaceous slate.

Harpanthus flotovianus (Nees) Nees – 2; 80; one collection in *Picea-Abies* forest on the first coastal terrace, wet hollow.

Jungermannia atrovirens Dumort. – 4, 5; 850–1260; krummholz belt, on moist open limestone cliffs on a slope to stream.

Jungermannia exsertifolia Steph. – 14; 1190; several collections from one locality in krummholz belt, on moist open argillaceous slate cliffs on a slope to stream.

Jungermannia pumila With. – 4, 5, 6, 7, 13; 850–1435; krummholz and tundroid belts, on moist open limestone cliffs and in their crevices filled with fine soil on slopes to streams, rarely in edges of solifluction spots.

Lejeunea alaskana (R.M. Schust. & Steere) Inoue & Steere – 5, 8, 9, 12; 850–1385; krummholz and tundroid belts, on moist, open to partly shaded limestone outcrops and in their crevices, on mesic moss mats in tundra-like communities on steep slopes.

Lepidozia reptans (L.) Dumort. – 15; 130; one collection from *Larix* forest, on moist cliff in part shade.

Lophozia ascendens (Warnst.) R.M. Schust. – 3; 260; several collections from one locality in *Picea-Abies* forest, on decaying wood.

Lophozia guttulata (Lindb. & Arnell) A. Evans – 9; 1140; one collection from krummholz belt, on decaying *Pinus pumila* branch.

Lophozia longiflora (Nees) Schiffn. – 4; 1260; one collection from krummholz belt, on open moist cliff on steep slope to stream.

Lophozia savicziae Schljakov – 14; 1190; one collection in tundroid belt from the community developed over argillaceous slates, over moist *Sphagnum* mat on steep slope.

Lophozia silvicola H. Buch – 1, 9; 90–1140; from low elevation *Picea-Abies* forests to krummholz belt, on moist fallen decaying wood in part shade.

Lophozia silvicoloides N. Kitag. – 9, 11; 1140–1284; krummholz and tundroid belts, on moist *Sphagnum* mats on steep slopes and decaying branches of died *Pinus pumila*.

Lophozia ventricosa (Dicks.) Dumort. – 14; 1190; one collection from dark coniferous forest in its upper limit, on moist boulder near stream.

Lophoziopsis pellucida (R.M. Schust.) Konstant. & Vilnet – 9, 13; 974–1140; krummholz and tundroid belts, over humificated soil developed on limestone outcrops and in their open moist crevices.

Mannia triandra (Scop.) Grolle – 6, 13; 974–1335; tundroid belt, in open crevices and niches of limestone outcrops filled with fine soil.

Marchantia alpestris (Nees) Burgeff – 4, 5, 14; 850–1260; krummholz belt, on open moist cliffs and fine soil on slopes to streams.

Marsupella boeckii (Austin) Lindb. ex Kaal. – 4, 14; 1190–1260; krummholz and tundroid belts, on open moist argillaceous slate cliffs on slopes to streams.

Marsupella tubulosa Steph. – 7; 1435; one collection from tundroid belt, on moist argillaceous slate cliff on steep slope.

Mesoptychia badensis (Gottsche ex Rabenh.) L. Söderstr. & Váňa – 6, 9, 12, 13; 974–1385; krummholz and tundroid belts, in open wet to mesic limestone cliff crevices, on fine limestone deposits (eluvium?) near small streams.

Mesoptychia gillmanii (Austin) L. Söderstr. & Váňa – 4, 5; 850–1335; krummholz and tundroid belts, on moist, open to partly shaded, limestone cliffs on slopes to streams.

Mesoptychia heterocolpos (Thed. ex Hartm.) L. Söderstr. & Váňa – 7, 9; 1140–1435; krummholz and tundroid belts, on humus on open steep slope and in open mesic crevices in limestone cliffs.

Metasolenostoma ochotense (Bakalin & Vilnet) Vilnet & Bakalin – 2; 80; several collections from one locality in *Picea-Abies* forest on the first coastal terrace, on moist clayish soil on steep slope to stream.

Metzgeria pubescens (Schrank) Raddi. – 5, 12; 850–1385; krummholz and tundroid belts, on open mesic limestone cliffs.

Mylia anomala (Hook.) Gray – 10, 14; 1190–1330; tundroid belt, over moist *Sphagnum* mats on steep slopes, only in the areas of argillaceous slates distribution.

Mylia taylorii (Hook.) Gray – 10; 1330; one collection from tundroid belt, over moss patches on steep slope.

Mylia verrucosa Lindb. – 1, 2, 5, 14, 15; 80–1190; from low elevation *Picea-Abies* and *Larix* forests to krummholz belt, on moist, partly shaded fallen decaying wood and lying *Pinus pumila* branches, rarely on humus on steep slopes to streams at low elevation.

Nardia geoscyphus (De Not.) Lindb. – 4; 1260; one collection from krummholz belt, on moist open cliff on a slope to stream.

Nardia japonica Steph. – 7, 14; 1190–1435; tundroid belt, on moist open, fine to clayish soil on steep slopes to streams.

Neoorthocaulis binsteadii (Kaal.) L. Söderstr., De Roo & Hedd. – 4, 10, 14; 1190–1330; tundroid belt, on moist *Sphagnum* mats on steep slopes.

Odontoschisma macounii (Austin) Underw. – 5, 9; 850–1140; krummholz and tundroid belts, in mesic open to partly shaded crevices in limestone outcrops.

Pellia neesiana (Gottsche) Limpr. – 2, 3, 14; 80–1190; from low elevation *Picea-Abies* forests to tundroid belt, in wet hollows in the forest, on moist open clayish soil on slopes to streams and moist humus along watercourses.

Peltolepis quadrata (Saut.) Müll. Frib. – 4, 5, 6, 13; 850–1335; krummholz and tundroid belts, in moist to mesic limestone cliff crevices and large niches, including those filled with humificated fine soil.

Plagiochila ovalifolia Mitt. – 1; 90; one collection from low elevation *Picea-Abies* forest on the first coastal terrace, on moist fallen decaying tree trunk.

Plagiochila porelloides (Torr. ex Nees) Lindenb. – 9; 1140; one collection from krummholz belt, in open mesic crevice in limestone outcrops.

Plectocolea cf. *ovalifolia* (Amakawa) Bakalin & Vilnet – 7; 1435; one collection from tundroid belt, on moist humus on slope.

Pleurocladula albescens (Hook.) Grolle – 4, 14; 1190–1260; tundroid belt, on open moist argillaceous slate cliffs on slopes to streams.

Porella gracillima Mitt. – 5; 850; one collection from krummholz belt, on mesic limestone outcrops on steep slope.

Preissia quadrata (Scop.) Nees – 4, 5, 6, 13; 850–1335; krummholz and tundroid belts, on moist limestone boulders and in crevices in limestone outcrops on slopes to streams.

Pseudolophozia debiliformis (R.M. Schust. & Damsh.) Konstant. & Vilnet – 7, 14; 1190–1435; tundroid belt, on open moist argillaceous slate cliff on a slope to stream and moist humus on steep slopes.

Pseudolophozia sudetica (Nees ex Huebener) Konstant. & Vilnet – 4, 7; 1260–1435; tundroid belt, on the edge of solifluction spot.

Ptilidium ciliare (L.) Hampe – 6; 1335; one collection from tundroid belt, where it grew in mesic dwarf shrub-moss community developed over limestone ledge.

Ptilidium pulcherrimum (Weber) Vain. – 1, 15; 90–130; low elevation *Picea-Abies* and *Larix* forests, on moist fallen decaying wood and *Larix* tree trunks.

Radula complanata (L.) Dumort. – 3; 260; one collection from *Picea-Abies* dominated forest, on *Betula* trunk, in part shade.

Riccardia palmata (Hedw.) Carruth. – 2; 80; one collection from low elevation *Picea-Abies* forest, on moist fallen decaying tree trunk.

Sauteria alpina (Nees) Nees – 4,13; 974–1260; tundroid belt, in moist crevices in limestone outcrops.

Scapania cuspiduligera (Nees) Müll. Frib. – 13; 974; one collection from tundroid belt, on thin humus layer over limestone outcrop on steep slope.

Scapania diplophylloides Amakawa & S. Hatt. – 6; 1335; one collection from tundroid belt, in crevice in argillaceous slate cliff on steep slope.

Scapania gymnostomophila Kaal. – 4, 6, 9, 11, 12, 13; 974–1385; tundroid belt, in open moist to mesic limestone cliff crevices.

Scapania paludosa (Müll. Frib.) Müll. Frib. – 14; 1190; several collections from one locality in tundroid belt, on open moist argillaceous slate cliffs near stream.

Scapania parvifolia Warnst. – 4; 1260; one collection from tundroid belt, in moist crevice in argillaceous slate cliff on steep slope.

Schistochilopsis incisa (Schrad.) Konstant. – 1, 2, 3, 10; 80–1330; low elevation *Picea-Abies* forests to tundroid belt, on moist decaying wood, boulders and argillaceous slate cliffs.

Schljakovia kunzeana (Huebener) Konstant. & Vilnet – 6, 12; 1335–1385; tundroid belt, in limestone cliff crevices filled with humus and on thin layer of mesic humus over limestone outcrops.

Schljakovianthus quadrilobus (Jørg.) Konstant. & Vilnet var. *glareosus* (Jørg.) Konstant. & Vilnet – 5, 12; 850–974; krummholz belt, in mesic open crevices in limestone outcrops.

Solenostoma obscurum (A. Evans) R.M. Schust. – 4; 1260; one collection in tundroid belt, in moist argillaceous slate cliff crevice on steep slope to stream.

Solenostoma subellipticum (Lindb. ex Heeg) R.M. Schust. – 14; 1190; one collection from tundroid belt, on open moist soil (argillaceous slate eluvium) on steep slope to stream.

Sphenolobus minutus (Schreb.) Berggr. – 4, 9, 15; 130–1260; from low elevation *Larix* forest to tundroid belt, over *Sphagnum* mats on steep slopes, in mesic crevices in argillaceous slate cliff, on decaying *Pinus pumila* branches.

Sphenolobus saxicola (Schrad.) Steph. – 7, 14; 1190–1435; tundroid belt, ground cover in mesic tundra-like community and *Sphagnum* mats on steep slopes.

Tetralophozia setiformis (Ehrh.) Schljakov – 7; 1435; one collection from tundroid belt, on dry argillaceous slate outcrops on the ridge-line.

Trilophozia quinquedentata (Huds.) Bakalin – 4, 6, 11, 12; 1260–1335; krummholz and tundroid belts, on moist boulders and cliffs (including those of limestone) on steep slopes to streams.

Tritomaria exsecta (Schmidel ex Schrad.) Schiffn. ex Loeske – 4, 8, 12; 1260–1385; krummholz and tundroid belts, in mesic limestone cliff crevices filled with fine soil (eluvium), and on thin layer of humus over limestone outcrops.

Discussion

Two main landscape features determines the character of the studied flora. The **first one** is the dominant coverage of limestone outcrops and limestone based eluvium and deluvium fines in upper elevations starting from 800 m a.s.l. The latter results in abundance of calciphilous taxa (like *Arnellia fennica, Mesoptychia badensis,* etc.), whereas bright acidophilic taxa (*Marsupella, Gymnomitrion, Tetralophozia,* several species of *Scapania, Nardia geoscyphus, Solenostoma obscurum, S. subellipticum,* etc.) are extremely rare or absent. Acidophilous taxa in the area treated are restricted to argillaceous slate deposits those are mechanically quite unstable, possess high drainage abilities (quickly become dry) and commonly crumbling down. Additionally, slates are rather neutral in reaction, but not acidic. Due to the latter circumstances, argillaceous slates cannot "compensate" the absence of acidic rocks like granites.

The following examples are illustrative: *Gymnomitrion* is represented by one species only – *G. corallioides,* – although *G. concinnatum* should be more expectable if only phytogeography would be taken into account. *Cephalozia bicuspidata* is unexpectedly rare (found only once). This fact is very prominent, especially if the absence of *C. otaruensis* Steph. (common vicariant of the latter in East Asia) would be taken into account. *Diplophyllum albicans, Jungermannia exsertifolia, Marsupella tubulosa* and a number of other acidophilous taxa common in Sakhalin Island were collected only once or a few times.

The 'limestone fraction' includes not only strictly calciphilous taxa, but also some neutrophilous or Ca-tolerant species that are able to grow over pure limestone. Among Ca-tolerant taxa are *Metzgeria pubescens, Barbilophozia barbata, B. lycopodioides, Calypogeia integristipula, Conocephalum salebrosum, Schljakovia kunzeana, Trilophozia quinquedentata.* Another phenomenon (somewhat related to the previous) is that some taxa possesses themselves as strictly calciphilous in our area, sometimes are not so strictly calciphilous northward, where observed on other basic or even neutral substrata. Among them are *Athalamia hyalina, Blepharostoma trichophyllum* var. *brevirete, Lejeunea alaskana, Mannia triandra, Mesoptychia gillmanii, Odontoschisma macounii, Peltolepis quadrata, Preissia quadrata, Sauteria alpina.*

Summarizing, the first landscape feature is resulted in the higher frequency of calciphilous taxa, but poor representation of acidophilic ones in comparison with liverwort composition in adjacent areas having no such extensive limestone outcrops, e.g. in Chamga Mt. (Bakalin et al.., 2012).

The **second feature** is relatively low elevation of the mountains (the highest visited point is 1435 m a.s.l. that is near to the highest point of Balagan Mt. (1471 m alt.) that results in poor development of alpine vegetation called here as tundroids. The tundra-like communities are the result of severe wind regime and dryness of substrates. Tundroids are mostly developed on steep slopes, rarely occupying horizontal surfaces with late snow melt in open areas adjacent to the mountain ridges. Wide distribution of tundroids at the elevations above 900 m a.s.l. is the result of their penetration to the krummholz belt by some relief elements. Moreover, krummholz vegetation does not realize its altitudinal potential in Balagan Mt. Due to drier conditions in tundroids, some typical 'tundra' hygrophytes sometimes do not occur in the highest elevation and observed downward, where moisture conditions are more favorable for them. The bright examples are *Pleurocladula albescens* and *Gymnomitrion corallioides.*

As it was noted before (Bakalin et al., 2012), Nabilsky Range is the 'hot spot' for a number of northern bryophyte flora elements in their southernmost edges of worldwide distribution. This observation was made basing on the study of Chamga Mt. (belongs to the same range). The same pattern is obvious in the flora of Balagan Mt. The next taxa are in the southern limit of distribution in the studied area: *Arnellia fennica, Cephalozia pachycaulis, Eocalypogeia schusteriana, Frullania subarctica* (the latter was known southward in the single locality in Japanese Southern Alps), *Gymnomitrion corallioides* (records from Japan are incorrect, cf. Bakalin, 2016), *Lophozia savicziae, Lophoziopsis pellucida, Mesoptychia badensis* (replaced in East Asia by other small-sized *Mesoptychia,* cf. Bakalin et al., 2015), *Neoorthocaulis binsteadii, Pseudolophozia debiliformis.* Some of these taxa are possible 'remnants' of the late Pleistocene cooling and their distribution in studied area possess relict character.

The occurrence of southern taxa in their northern limits in the studied flora is much rare occasion. This may be due to two reasons: 1) undercollecting in the low elevation and/or 2) unsuitable environments in low elevation that houses typical *Picea-Abies* boreal forest and is quite far from hemiboreal mixed forests of the southern Sakhalin enriched with temperate East Asian elements. These hemiboreal forests occur at least 2ºN southward of the studied area. With some reservations, we refer to the group of 'southern' taxa *Clevea nana* (East Asian temperate mountain caliciphilous taxon) and *Porella gracillima* (mainly hemiboreal-temperate basiphilous East Asian taxon) those are near the northern limits of their distribution in Asia. It worth noting, even such boreo-temperate taxa like *Frullania bolanderi, F. koponenii* are quite rare in the studied flora.

The absence of true mossy swamps in the area is resulted in vanishing of some 'swampy' taxa, although such as *Calypogeia sphagnicola, Mylia anomala, Neoorthocaulis binsteadii,* are growing in tundroid belt over *Sphagnum* mats on steep slopes.

Since calciphilous taxa in the most cases should be more drought tolerant than acidophilous ones, this group in liverworts is less represented in comparison with mosses (those can be prominently rich taxonomically in the studied flora). This 'calciphilous' group, nevertheless, contains such rare in the Russian Far East (mostly sparse worldwide too) taxa like *Eocalypogeia schusteriana, Lejeunea alaskana, Lophoziopsis pellucida.* However, their rarity in North-East Asia (to which Sakhalin Island belong at least northward of Poyasok Isthmus) is mostly determined by rarity of limestone and other basic rock outcrops rather than other (including phytogeographic and life strategy) reasons.

The 'weedy' taxa are rare in the area treated, with *Marchantia alpestris* is probably the only example. *Metasolenostoma ochotense* and *Nardia japonica* inhabit the places with disturbed vegetation cover but hardly could be regarded as weeds.

As commonly, the question on study 'perfectness', or now much of the real taxonomic diversity we have revealed, is the most intricate. The revealed 87 taxa (86 species and one variety) are not a few in comparison with other local floras investigated in the middle of Sakhalin and the southern Far East. Bakalin et al. (2009) enumerated 57 taxa for liverwort flora of Vaida Nature Monument situated relatively near and characterized by similar nature conditions (including large limestone outcrops and tundra-like communities in the upper elevations of the hills). Chamga Mt. and its surroundings (probably 30 km by straight line from our area) houses 107 liverwort taxa (Bakalin et al., 2012). However, the latter mountain provides better representation of meso-hygrophitic habitats than occurs in Balagan Mt. Although pure limestone outcrops are absent in Chamga Mt., the latter has many acidic and basic outcrops. This makes possible the occurrence both basiphilous (including some not strictly calciphilous) taxa along with number of acidophilous species in Chamga Mt. We assume Chamga Mt. liverwort flora is underinvestigated and its real diversity may be estimated as near to 120 taxa, whereas the real taxonomic diversity of Vostochnyi Nature Reserve liverwort flora may reach ca. 100 species in the future purposeful researches.

The peculiarity of Balagan Mt. liverwort flora again confirms the high value of Nabilsky Range for conservation purposes and the actuality of the further explorations of the area, including, for instance, Lopatina Mt. that is the highest peak of the range. The knowledge on liverwort flora of Nabilsky Range is highly valuable due to phytogeographical reasons, also since the range is the most ancient extant land formation in Sakhalin Island.

As the conclusion, we should emphasize that the most interesting trait of the studied flora is the calciphilous fraction, many taxa of which are on the southernmost edge of their distribution worldwide that additionally cast the light for the Sakhalin flora genesis in general.

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К познанию флоры печеночников горы Балаган и долины реки Венгери (о-в Сахалин, северо-западная Пацифика)

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В результате изучения флоры печеночников горы Балаган и долины реки Венгери выявлено 87 видов, аннотированный список которых представлен в настоящей статье. Наиболее яркой экологической особенностью района является обилие обнажений известняков, что обеспечивает высокий процент базифильных таксонов во флоре. Настоящие кислые породы, напротив, не представлены, в результате чего ацидофильные таксоны отсутствуют или редки. Распространение ряда арктоальпийских видов (включая таксоны с преимущественно мега-берингийским распространением) в исследуемом районе, вероятно, носит реликтовый характер.

Ключевые слова: печеночники, Hepaticae, Восточная Азия, северо-западная Пацифика, Сахалин, флора, охраняемая территория.

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