Arctoa (2026) **35**: *73–83*
doi: 10.15298/arctoa.35.07

BRYOPHYTE FLORA OF URUP ISLAND (THE KURIL ISLANDS, EAST ASIA)

ФЛОРА МОХООБРАЗНЫХ ОСТРОВА УРУП (КУРИЛЬСКИЕ ОСТРОВА, ВОСТОЧНАЯ АЗИЯ)

ANNA K. KARTASHEVA[1], YURIY S. MAMONTOV[2], ANNA V. SHKURKO[2], ELENA A. GLAZKOVA[3], EKATERINA YU. KUZMINA[3], NADEZHDA S. LIKSAKOVA[3] & TATIANA I. KOROTEEVA[4]

АННА К. КАРТАШЕВА[1], ЮРИЙ С. МАМОНТОВ[2], АННА В. ШКУРКО[2], ЕЛЕНА А. ГЛАЗКОВА[3], ЕКАТЕРИНА Ю. КУЗЬМИНА[3], НАДЕЖДА С. ЛИКСАКОВА[3], ТАТЬЯНА И. КОРОТЕЕВА[4]

Abstract

Urup Island is located in the central Kuril Archipelago, representing an important climatic and vegetational transition zone. Historically, its bryoflora has been poorly investigated. Based on field collections made in 2021 and a revision of published records and herbarium specimens, we present the first annotated checklist of the island's bryophytes. The flora comprises 180 species (133 mosses and 47 liverworts). The checklist documents the southern and northern distribution limits within the archipelago for several temperate East Asian taxa, including *Pallavicinia subciliata* and *Limnohypnum mizushimae* respectively, and provides new locality data for recently described North Pacific endemics, such as *Arvernella pisarenkoi* and *Marsupella subemarginata*. The phytogeographical distribution of areal types across the island is driven by its unique climate variability across a latitudinal gradient and habitat availability like sheltered river gorges and tall-herb meadows as refugia for East Asian elements.

Резюме

Остров Уруп расположен в центральной части Курильского архипелага и представляет собой важную климатическую и флористическую переходную зону. До настоящего времени его бриофлора оставалась слабо изученной. На основе полевых сборов 2021 г., а также ревизии литературных данных и гербарных материалов, представлен первый аннотированный список мохообразных острова. Выявленная флора включает 180 видов (133 вида мхов и 47 видов печеночников). В аннотированном списке задокументированы южные и северные пределы распространения для ряда умеренных восточноазиатских таксонов, включая *Pallavicinia subciliata* и *Limnohypnum mizushimae* соответственно. Приведены новые данные о местонахождениях недавно описанных северотихоокеанских эндемиков, таких как *Arvernella pisarenkoi* и *Marsupella subemarginata*. Пространственное распределение фитогеографических элементов (ареалогических типов) на острове обусловлено особенно выраженной климатической изменчивостью вдоль широтного градиента, а также наличием специфических местообитаний – таких как защищенные речные распадки и высокотравные луга, которые выступают в качестве рефугиумов для восточноазиатских элементов.

KEYWORDS: mosses, liverworts, Kuril Islands, flora, phytogeography, new records

INTRODUCTION

The bryoflora of the Kuril Islands remains unevenly studied. While the most comprehensive data are available for the southern (Kunashir, Iturup) and some northern islands (Paramushir), the moss flora of Urup, one of the largest islands of the archipelago, is still poorly investigated. While numerous species have been reported for the island in scattered records (e.g., Bakalin *et al.*, 2009; Ignatova *et al.*, 2023; Ellis *et al.*, 2022; Sofronova *et al*., 2020; Nyushko & Potemkin, 2007), these data remain unconsolidated and lack the critical reassessment. This gap is significant given that Urup is recognized as the archipelago's phytogeographical boundary between the Circumboreal and East Asiatic floristic regions, where the number of East Asiatic taxa northward of Urup is drastically reduced (Barkalov, 2000).

Urup Island is characterised by a complex topography featuring a central chain of volcanic ridges and a

[1*] – State Museum of Natural History, Stuttgart, Botany department, Rosenstein 1, Kreuzung Ehmann-, Nordbahnhofstrasse, 70191 Stuttgart, Germany. E-mail: kartasheva-2000@mail.ru. ORCID: 0000-0002-9676-0279
[2] – Tsitsin Main Botanical Garden of the Russian Academy of Sciences, Moscow, Russia, 127276. E-mails: yur-mamontov@yandex.ru, shen-ku@bk.ru. ORCIDs: 0000-0003-3851-0738 (Mamontov); 0000-0001-7682-9323 (Shkurko)
[3] – Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia, 197022. E-mails: elena.glazkova@binran.ru, ekuzmina@yandex.ru, nliks@mail.ru. ORCIDs: 0000-0003-4833-5953 (Glazkova); 0000-0002-8871-9604 (Kuzmina); 0000-0002-1940-4078 (Liksakova)
[4] – Institute of Marine Geology and Geophysics, Far Eastern Branch of the Russian Academy of Sciences, Nauki str. 1B, Yuzhno-Sakhalinsk, Russia, 693022. ORCID: 0000-0003-4097-6801

pronounced climatic gradient between its northern and southern parts (Barkalov, 2009). The island's climate is generally cool and hyperoceanic with frequent fogs, conditions that are highly favorable to bryophyte diversity. However, the strong influence of the cold Oyashio Current in the north and the warm Soya Current in the south fosters a contrast in vegetation communities—ranging from ericad-rich tundra in the north to *Betula ermanii* forests with nemoral elements in the south (Pietsch et al., 2003; Vorobiev, 1963; Barkalov, 2002, 2009). This habitat heterogeneity, further amplified by altitudinal zonation and recent volcanic activity, suggests a high potential for a diverse and ecologically stratified bryoflora.

The aim of this paper is to present the first annotated checklist of the bryophytes of Urup Island, based on original field research and revision of published data. The objectives of this study are to document the taxonomic composition of the island's bryoflora and discuss the position of Urup's bryoflora as a boundary island in the archipelago. The current list is likely not exhaustive, since the field routes covered only a limited and accessible part of the island.

History of exploration

Historically, the bryoflora of Urup Island has been critically underexplored compared to other major Kuril Islands. The earliest data on the island's bryophytes were provided by Abramova (1960), who included several moss species from Urup in a regional list without precise locality or habitat data. Later, Nyushko et al. (2008) revised historical herbarium collections (LE) from the central Kurils, reporting 26 species for Urup. While comprehensive bryophyte studies were subsequently published for the adjacent northern and southern islands (Bakalin et al., 2009), data for Urup remained limited to scattered records. Additional records have recently been published in regional updates, including liverwort taxa (e.g., Bakalin et al., 2020) and mosses collected during recent expeditions by Liksakova and Glazkova and identified by Kuzmina (Sofronova et al., 2020; Ellis et al., 2022). However, prior to the present study, no targeted, island-wide bryological inventory had been published.

Vegetation

The vascular vegetation of Urup Island features a mosaic structure dictated by its complex topography, strong oceanic winds, and transitional biogeographical

Fig. 1. Bryophyte habitats on Urup Island. A: Rocky riverbed bordered by rock outcrops and dense tall-herb vegetation with Petasites japonicus. Such stream corridors with exposed boulders and shaded cliff crevices provide habitats for saxicolous bryophytes like *Claopodium pellucinerve*, *Codriophorus carinatus*, *Rhizomnium tuomikoski*, etc. B: A shallow river winding through overgrown banks with dense thickets of *Salix udensis* and *Sasa kurilensis* and tall-herb riparian communities with *Phragmites australis*. Here bryophytes are restricted only to the water margins.C: Wind-exposed coastal terrace featuring dwarf-shrub tundroid communities (with *Empetrum sibiricum*) with Arctic-Alpine pioneer mosses like *Pogonatum urnigerum* on bare soil patches. Fens with *Rhodobryum roseum* and *Scapania paludosa* occur here sporadically.

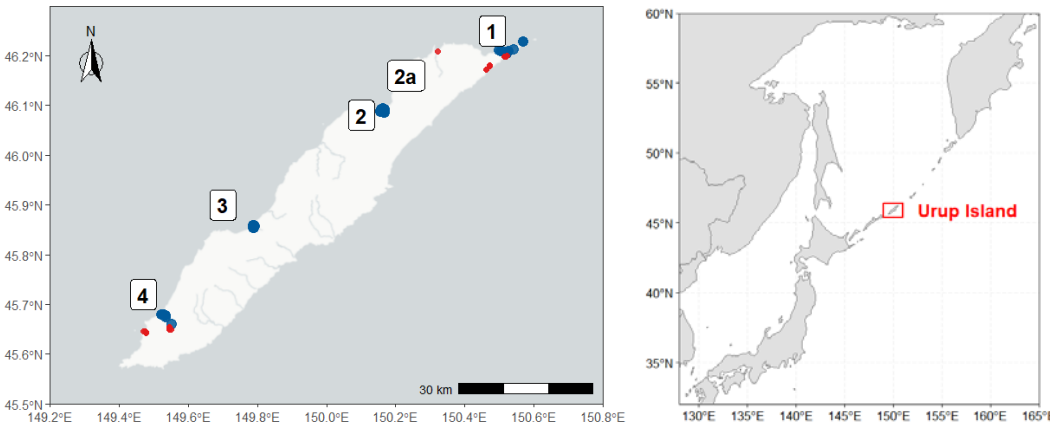

Fig. 2. Collecting localities in Urup: Blue circles: studied areas; red dots: literature records.

position. The island's central mountain ridges act as a physical barrier that blocks cold Pacific winds, creating a highly asymmetrical climate where sheltered inland valleys and the Okhotsk Sea coast remain noticeably milder (Liksakova *et al.*, 2021). Consequently, Urup acts as a major phytogeographical filter, serving as the absolute northern limit for 102 species of East Asiatic vascular plants (Barkalov, 2000). A detailed eco-phytocenotic classification of the island's vegetation was recently provided by Liksakova *et al*. (2021, 2023); the primary vegetation types relevant to bryophyte habitats can be summarized as follows.

True forest communities are limited, represented primarily by low-canopy Erman's birch *(Betula ermanii*) woodlands. Riparian zones and moist river gorges are overgrown with thickets of *Alnus maximowiczii* and *Salix udensis* changing to dense tall-herb riparian vegetation with *Petasites japonicus* near the water streams. There are several types of meadows, e. g., the rich ones with *Sanguisorba tenuifolia* and tall-herb meadows dominated by *Filipendula kamtschatica*. Shielded from the harsh oceanic climate by the central ridges, these valleys harbor East Asian nemoral elements (e.g., *Taxus cuspidata, Toxicodendron orientale*) and provide shaded, humid microhabitats.

Inland slopes and plateaus lacking forest cover are dominated by dwarf stone pine thickets with *Pinus pumila* and continuous thickets of *Sasa kurilensis*. Urup Island represents the absolute northern limit of dominance for this bamboo; it forms impenetrable stands up to 2.5 meters tall with nearly 100% canopy closure (Vorobiev, 1963; Barkalov, 2002). This dense shading severely restricts ground-layer bryophyte growth, forcing moss and liverwort diversity out of the slopes.

The northern part of the island changes dramatically into exposed, wind-swept coastal terraces and ridges occupied by dwarf-shrub tundra communities (with *Empetrum, Vaccinium, Loiseleuria,* etc.).

Finally, the southern marine terraces feature extensive meso-oligotrophic ridge-lake bog complexes. As noted by Liksakova *et al.* (2021), this sloping wetland possesses a highly unusual typological structure; while it resembles so called blanket bogs, its distinct ridge-and-lake morphology differs from any previously described bog types in the region. The ecology of this area is further shaped by historical catastrophic disturbances; approximately 2100 years ago, heavy tephra fallout from neighboring Iturup Island buried southern Urup, causing massive degradation of the peatlands (Razjigaeva *et al*., 2019). Today, this highly stratified, recovering peatland, is characterised by the vast ridge-lake complexes, with *Carex middendorffii* and *Sphagnum papillosum* ridges.

Materials and methods

Collecting localities

Field collections were carried out in August 2021 by A.S. Kartasheva across four main areas representing the principal ecological and elevational zones of Urup Island. In the species checklist, these localities are indicated by numbers 1 to 4 with 2a added for Novokurilskaya Bay from the previous records. Novokurilskaya Bay deserves a distinct locality as it is far enough from the locality 1 and locality 2, although it still resembles Irina Bay by general conditions (Fig. 2).

Locality 1: Kastrikum Cape area, 46°12'–46°13' N, 150°30'–150°34' E, 5–20 m a.s.l.

Located at the wind-exposed northernmost area of the island. Collections were made across a variety of coastal and anthropogenic habitats, including dwarf-shrub tundra communities dominated by *Empetrum*, and lowland bogs. Anthropogenic substrates were also surveyed, including dry rocky soil and concrete crevices on an abandoned airstrip, old wooden planks, and the wet walls of abandoned buildings (Fig. 1c).

Locality 2: Irina Bay and 2a: Novokurilskaya bay, 46°05'N, 150°09'–150°10' E, 0–50 m a.s.l.

This is a topographically complex area characterised by rocky riverbeds, steep clayish and sandy banks, and moist gorges. Because the area is notoriously overgrown with dense, impenetrable vegetation that prevents free walking, bryophyte collection was somewhat biased towards accessible riverbeds and stream margins (Fig. 1ab). Specimens were collected from vertical soil banks, shaded cliff crevices, small rock caves near the water, and in-

stream boulders and meadows. The surrounding vegetation includes tall-herb and rich meadows on the slopes and mixed riparian woodlands, where epiphytic and epixylic collections were made from *Betula* and *Salix* trunks and fallen logs. Locality 2a designates historical literature records.

Locality 3: Lake Tokotan vicinity, 45°51’ N, 149°47’ E, 0–20 m a.s.l.

This locality encompasses the coastal and wetland mosaic surrounding Lake Tokotan. Terrestrial habitats include dry sandy dunes by the sea shore, dense *Carex cryptocarpa* riparian meadows at the water’s edge, and rich tall-herb grasslands dominated by *Filipendula kamtschatica* and *Cacalia robusta.* Forest bryophytes were collected from the soil and roots within alder (*Alnus*) and willow (*Salix*) groves.

Locality 4: Southern Urup (Van-der-Lind Cape / Peschanaya Bay), 45°39’–45°40’ N, 149°31’–149°32’ E, 15–150 m a.s.l.

The southern part of the island features high habitat diversity ranging from moist gorges, meadows, anthropogenic vegetation to extensive peatlands. On the way up to the bog complex the collections were made in moist streams, on shaded cliffs, boulders and soil banks. Then going down from the bog complex, we explored the banks along the streams bordered by tall-herb communities in the vicinity of the goldmines. The area is particularly notable for its extensive ridge-lake bog complexes, where most collections were made.

Phytogeographical element assignment

To analyze the phytogeographical composition of the bryoflora, species were categorized into areal types based on their global distribution. The global ranges for mosses were determined using the Moss Flora of Russia (Ignatov *et al.*, 2017, 2018, 2020, 2022). For liverworts, global distribution data were obtained from the Liverworts and Hornworts of Russia (Potemkin & Sofronova, 2009) and GBIF records. Based on these ranges, each species was assigned to one of five primary phytogeographical elements: Cosmopolitan, Circumboreal, Arctic-Alpine, East Asian, or North Pacific Endemic.

CHECKLIST OF BRYOPHYTES

The species name is followed by the altitudinal range, the locality numbers (1, 2, 2a, 3, 4: Fig. 1), the voucher specimen number in parentheses for less frequently collected species, and a brief habitat description. For common and partly sporadic species the frequency is provided based also on observations in the field. Voucher numbers starting with “u-” and “Yu-” represent collections made by A.S. Kartasheva (in MHA). Literature records are coded as follows: A (Abramova, 1960); N (historical LE collections published in Nyushko *et al*., 2008); B (Bakalin *et al.,* 2009); KL2020 (Kuzmina & Liksakova, 2020 in New bryophyte records. 15); KL2020a (Kuzmina & Liksakova, 2020 in Novosti Sist. Nizsh. Rast. 54); KL2021 (Kuzmina & Liksakova, 2021 in New bryophyte records. 18); KL2023 (Ignatova *et al.*, 2023); L2021 (Liksakova *et al.*, 2021); L2023 (Liksakova *et al*., 2023); and E (Kuzmina *et al*. in Ellis *et al*., 2022). Because Abramova (1960) did not provide specific localities, her records are indicated without assigned locality numbers.

Mosses

Amblystegium serpens (Hedw.) Bruch et al. – 5–50 m – **1 (**u-69**), 2** (u-35). Steep river banks, clayish ground, bare ground in tundra.

Amphidium lapponicum (Hedw.) Schimp. – 30–50 m – **2** (u-54, u-57). Cliff crevices and rock outcrops, by river banks, sporadic.

Andreaea rupestris Hedw. – 10 m – 4 (Yu-1-1). On a rock by a river.

Aquilonium adscendens (Lindb.) Hedenäs, Schlesak & D.Quandt – 5–50 m – **1, 2, 3, 4.** On rocks by creeks, on sandy dunes, common.

A. plicatulus (Lindb.) Hedenäs, Schlesak & D.Quandt – 5–25 m – A, **2a** (B, N).

Arvernella pisarenkoi Ignatov & Ignatova – 15 m – **3** (u-22). Alder grove, on ground, rare.

Aulacomnium palustre (Hedw.) Schwägr. – 150 m – KL2020, B (Brotherus, 1899), **4** (Yu-2-6). Ridge-lake bog, common.

Bartramia ithyphylla Brid. – 20 m – 2 (u-35). Steep river bank on a clay-sand substrate.

B. pomiformis Hedw. – 15 m – **2** (u-31). Rocky riverbed, on rock outcrops with *Distichium capillaceum, Pohlia cruda.*

Brachythecium auriculatum A. Jaeger. – 20 m – **2** (KL2023, u-28). In forests and tall-herb communities on ground.

B. hultenii (E.B.Bartram) Min Li & Y.F.Wang – 10–50 m – **2, 3.** In forests and tall-herb communities on ground, on rocky river banks, common.

B. rivulare Bruch et al. – 5–50 m – **2, 3.** In moist streamside sites and wet forests on soil, rocks, cliffs, tree bases, and logs; also in open or disturbed areas, common.

B. rotaeanum de Not. – 10–30 m – **3 (**u-23, u-8). On ground in between roots in Alder grove, on moist ground among *Carex cryptocarpa*.

Bryoerythrophyllum recurvirostrum (Hedw.) P.C.Chen. – 20 m – **2** (u-37). On a large boulder in a river, sporadic.

Bryoxiphium japonicum (Berggr.) E. Britton – 10–30 m – **2** (KL2023, u-56, u-59). Cliff crack seepage, sporadic.

Bryum altaicum Broth. – 15 m – **2** (u-35). On clayish ground of a steep river bank.

B. amblyodon Müll.Hal. – 150 m – **1, 3** (u-71n, u-8). On moist ground among *Carex cryptocarpa*, on bare ground of the tundra-like northern part of the island.

B. cyclophyllum (Schwägr.) Bruch & Schimp. – 15 m – **2** (u-55). On a boulder by a creek, sporadic.

B. pseudotriquetrum (Hedw.) P.Gaertn. & al. – 10–20 m – **1 (**u-69n**), 3 (**u-14, u-4), **4** (KL2020**).** On clayish ground in willow thickets, on bare ground in the tundra of the northern part of the island.

Calliergon cordifolium (Hedw.) Kindb. – 5–25 m – A, **2a** (B, N).

Calliergonella lindbergii (Mitt.) Hedenäs – 10–50 m – **2, 3, 4.** On damp ground beside streams, common.

Calliergonellopsis dieckii (Renauld & Cardot) Jan Kučera & Ignatov – 5–50 m – **2** (KL2023, u-52), **4 (**Yu-1-11). On shaded rock outcrops with *Amphidium lapponicum, Dichodontium palustre, Dilutineuron fasciculare*.

Campyliadelphus chrysophyllus (Brid.) Kanda – 20 m – **1, 2.** Rocky ground with *Bryum amblyodon*, sporadic.

Ceratodon purpureus (Hedw.) Brid. – 30–50 m – **3** (u-1, u-6). On dunes by the lake, on the ground of slopes in grasslands.

Chionoloma tenuirostre (Hook. & Taylor) M. Alonso, M.J. Cano & J.A. Jiménez – 15–30 m – **2** (u-54, u-47). On roots of a fallen tree by a stream, in cliff crevices.

Claopodium pellucinerve (Mitt.) Best – 15 m – **2** (u-54). In cliff crevices with *Pterigynandrum filiforme*, rare.

Climacium dendroides (Hedw.) F. Weber & D.Mohr – 5–50 m – **2** (u-59), **4 (**Yu-1-9). On boulders and on ground by streams or in grasslands.

Codriophorus brevisetus (Lindb.) Bednarek-Ochyra &Ochyra – 5–25 m – A, **2a** (B, N).

C. carinatus (Cardot) Bedn.-Ochyra & Ochyra – 20 m – **2.** On boulders by river streams in cliff cracks.

C. mollis (Cardot) Bedn.-Ochyra & Ochyra – 30 m – **4** (Yu-1-17). On a wet boulder with *Grimmia incurva*.

Cratoneuron filicinum (Hedw.) Spruce – 5–25 m – A, **2a** (B, N).

Dichodontium palustre (Dicks.) M. Stech – 15 m – **2 (**u-52)**, 4** (Yu-1-2). On boulders by river streams. Cliff crevices, wet rocky habitats with *Amphidium lapponicum*, sporadic.

D. pellucidum (Hedw.) Schimp. – 20 m – **1, 2.** In between concrete slabs of an abandoned runway, in moist cliff crevices, on vertical rock outcrops in creek beds, sporadic.

Dicranella cerviculata (Hedw.) Schimp. – 5–50 m – **4** (Yu-2-13). Ridge-lake bog.

Dicranellopsis subulata (Hedw.) Bonfim Santos, Siebel & Fedosov. – 10–50 m – **2.** Boulders in riverbeds, rocks, common.

Dicranum baicalense Tubanova – 15 m – **3** (u-12). Tall-herb grassland with *Filipendula kamtschatica* and *Cacalia robusta* together with *Plagiomnium curvatulum, Philonotis capillaris.*

D. fuscescens Turner – 5–25 m – A, **2a** (B, N).

D. laevidens R.S. Williams – 15 m – **1** (u-74n). On ground near an abandoned runway.

D. majus Turner – 10–50 m – A, KL2020, **2a** (B), **1, 2.** Wide range of habitats, on ground in forests, by rivers, on logs, common.

D. pacificum Ignatova & Fedosov – 5–50 m – **2, 4.** On vertical bare ground, with *Douinia plicata.*

D. scoparium Hedw. – A.

D. undulatum Schrad. ex Brid. – A.

Dilutineuron corrugatum (Bedn.-Ochyra) Bedn.-Ochyra, Sawicki, Ochyra, Szczecińska & Plášek – 10 m – **2, 4 (**Yu-1-2, u-64). On rocks by creeks, on old wooden planks.

D. fasciculare (Schrad. ex Hedw.) Bedn. – 30 m – A, KL2020, **2a** (B, N), **2** (u-52, u-53). Cliff crevices.

Distichium capillaceum (Hedw.) Bruch & Schimp. – 5 m – **2** (u-31). Rocky riverbed, on rocks.

Ditrichum zonatum (Brid.) Kindb. – 15 m – **2.** Rocky soil, little niches in rocks.

Dolichomitriadelphus hakkodensis (Besch.) Ignatova, Fedosov & Ignatov – 40 m – **2** (KL2023).

Drepanocladus aduncus (Hedw.) Warnstorf – 5 m – **2** (u-2). Wet sandy river bank.

Fontinalis antipyretica Hedw. – 5 m – 3 (u-17). Willow thicket, next to the water line.

Funaria hygrometrica Hedw. – 15 m – **1** (u-71n). On damp ground by the lighthouse.

Grimmia incurva Schwägr. – 20 m – **4** (Yu-1-17). On a wet rock with *Codriophorus mollis*.

Hygroamblystegium humile (P. Beauv.) Vanderp., Goffinet & Hedenäs – 10–50 m – **3 (**u-8). Among *Carex cryptocarpa*, by the lake.

Hygrohypnella ochracea (Turner ex Wilson) Ignatov & Ignatova – 5–50 m – **2 (**u-35). On clayish ground of a steep river bank.

Hylocomiastrum pyrenaicum (Spruce) M. Fleisch. – A.

Hylocomium splendens (Hedw.) Schimp.– 10–30 m – **A, 3 (**u-21). Meadow fringe by *Alder* grove, on ground.

Jochenia pallescens (Hedw.) Hedenäs, Schlesak & D. Quandt – 20 m – **2** (u-42). On vertical bare ground.

Leskea polycarpa Hedw. – 10 m – **3** (u-11). Tall-herb vegetation with *Filipendula kamtschatica* and *Cacalia robusta.*

Leptodictyum riparium (Hedw.) Warnst. – 5 m – **3** (u-2, u-4). Damp, sandy bank of the river.

Leptobryum pyriforme (Hedw.) Wilson – 15–25 m – **A, 2a** (B, N), **1** (u-69n). On the ground next to the lighthouse.

Limnohypnum mizushimae (Sakurai) Ignatov & Czernjad. – 15 m – **3 (**u-8). On moist ground among *Carex cryptocarpa*.

Mnium heterophyllum (Hook.) Schwägr. – 15 m – **2** (u-59). Rocky creek, on boulders.

M. orientale R.E.Wyatt, Odrzyk. & T.J.Kop – N.

Myuroclada longiramea (Müll. Hal.) M. Li, Y.-F. Wang, Ignatov & Huttunen – 15–70 m – **2, 3, 4.** Common species in various habitats including grasslands and forests, on rocks, ground, tree bases.

Oligotrichum parallelum (Mitt.) Kindb. – 20 m – **4** (Yu-1-22). On clayish ground at the stream's edge.

Philonotis capillaris Lindb. – 15 m – **3** (u-12). Tall-herb grassland with *Filipendula kamtschatica* and *Cacalia robusta* together with *Plagiomnium curvatulum* and *Dicranum baicalense*.

P. fontana (Hedw.) Brid. – N.

P. yezoana Bescherelle & Cardot – 5 m – **2, 3** (u-17, u-34). Willow grove by a river, on *Calamagrostis* sp. tussock in a stream.

Plagiomnium acutum (Lindb.) T.J. Kop. – 30–50 m – **3.** Common in Tokotan lake vicinity. On ground in rich meadows, in Alder groves, in tall-herb meadows.

P. curvatulum (Lindb.) Schljakov – 15 m – **3 (**u-10, u-12). Sand spit, in the thickets on the sand at the water's edge, tall-herb grassland with *Filipendula kamtschatica* and *Cacalia robusta* together with *Philonotis capillaris* and *Dicranum baicalense*.

P. ellipticum (Brid.) T.J. Kop.– 15–25 m – **2a** (B, N), **4** (Yu-1-6). In between rocks along a stream.

P. medium (Bruch & Schimp.) T.J. Kop. – 5–60 m – **1, 2, 3, 4.** Common in various wet habitats like by streams, on rocks and on ground in willows.

P. vesicatum (Besch.) T.J. Kop. – 15 m – **2 (**u-14)**, 4** (Yu-1-8, Yu-1-13). Willow groves, by streams on rocks and on the ground.

Plagiothecium cavifolium (Brid.) Z.Iwats. – 20 m – **2, 3.** On ground in meadows, tall-herb meadows.

P. denticulatum (Hedw.) Schimp. – 15 m – **2, 3.** In forests and tall-herb communities on ground, on rocky river banks.

P. japonicum Sakurai – 10 m – **3** (u-20). On the ground in Alder grove.

P. nemorale (Mitt.) A.Jaeger – 10–30 m – **3(**u-22)**, 4** (Yu-1-11). On rocks in alder groves, on shaded cliffs.

P. obtusissimum Broth. – 20 m – **2.** On vertical bare ground.

Platyhypnum duriusculum (De Not.) Ochyra – 10–30 m – **4.** On wet boulders and rocks by streams.

Pleuroziopsis ruthenica (Weinmann) Kindberg ex E. Britton –

5–30 m – **A, 2a (B, N), 4** (Yu-1-7). In tall herbs by a stream on the ground.

Pleurozium schreberi (Brid.) Mitt. – 5–40 m – A, KL2020, **2a** (B, N), **4** (Yu-2-16). On Ridge-lake bog.

Pogonatum contortum (Menzies ex Brid.) Lesq. – 15 m – **2** (u-41). Wet riverbed, on the ground, sporadic.

P. inflexum (Lindb.) Sande Lac. – 10–20 m – **4** (Yu-1-21). On rocky ground, sporadic.

P. japonicum Sull. & Lesq. – 15 m – A, **2, 4.** In different habitats, on slope ground, in rocky riverbeds.

P. urnigerum (Hedw.) P. Beauv. – 20 m – **1** (u-62). On a path on the ground.

Pohlia cruda (Hedw.) Lindb.– 10–50 m – **1, 2, 3.** Rather common, on the ground under overhanging rocks in cavities.

P. nutans (Hedw.) Lindb.– 5–150 m – **1, 2, 3, 4.** Common on bare ground across the island, abundant on the ridge-lake bog.

P. wahlenbergii (F.Weber & D.Mohr) A.L.Andrews – 10–30 m – **2** (u-35), **3** (u-14). Perhaps more common, in the current collection was found in willow grove by a stream.

Polytrichastrum alpinum (Hedw.) G.L.Sm. – 5–50 m – A, **1, 2, 3, 4.** Rather common in various habitats on ground among *Carex cryptocarpa*, in between roots in Alder grove.

Polytrichum commune Hedw. – 150 m – **4.** Common on the big ridge-lake bog, southern part of the island.

P. densifolium Wilson ex Mitt. – 15 m – **4** (Yu-2-7). Common on the big ridge-lake bog, southern part of the island.

P. juniperinum Hedw. – 250 m – 4 (L2021).

P. pallidisetum (Funck) G.L. Sm. – 40 m – **2** (u-42). On a vertical soil outcrop.

P. strictum Menzies ex Brid.– 5–25 m – A, KL2020, **2a** (B, N).

Pseudobryum cinclidioides (Huebener) T.J.Kop. – 5–25 m – **2a** (B, N).

Pseudohygrohypnum subeugyrium (Renauld & Cardot) Jan Kučera & Ignatov – 5–25 m – **2a** (B).

Pterigynandrum filiforme Hedw. – 15 m – **1**, **2** (u-54). On a boulder by a creek with *Claopodium pellucinerve*, sporadic.

Racomitrium lanuginosum (Hedw.) Brid. – 10–20 m – **4** (u-64, KL2020). On old planks.

Rhizomnium magnifolium (Horik.) T.J. Kop. – 5–50 m – **2a** (B, N), **1** (u-60). Bare ground in tundra-like community with *Empetrum*, northern.

R. nudum (E.Britton & R.S.Williams) T.J. Kop. – 30 m – **2** (KL 2023 u-31)**, 4** (Yu-1-18). Cliff crevices, wet rocky habitats, rather common, admixed in many specimens.

R. striatulum (Mitt.) T.J. Kop. – 5–50 m – **2** (u-31, u-59). On rocks by creeks, on sandy dunes, common.

R. tuomikoskii T.J. Kop. – 30–50 m – **2** (u-20), **3** (u-31, u-48). Cliff crevices and rock outcrops, by river banks, sporadic.

Rhodobryum roseum (Hedw.) Limpr. – 15 m – **1** (u-72n). Alder grove, on ground, rare.

Rhynchostegium aquaticum A. Jaeger – 10 m – **3** (u-14). Willow grove by a stream, on ground.

Rhytidiadelphus japonicus (Reimers) T.J. Kop. – 10–150 m – **1, 2, 3, 4 (KL2023)**. In various habitats across the island, on ground, rocks, tree bases, on a ridge-lake bog, very common.

R. squarrosus (Hedw.) Warnst. – 32–250 m – **1** (L2023).

R. subpinnatus (Lindb.) T.J. Kop. – 47 m – **2a** (KL2020), **1.** Tall-grass alder forest dominated by *Filipendula kamtschatica* on the gentle lower part of the slope.

R. triquetrus (Hedw.) Warnst. – 5–25 m – A, **2a** (B, N).

Sanionia uncinata (Hedw.) Loeske – 30 m – **A, KL2020, 1, 2, 2a (B), 3, 4.** A common species in various habitats and on substrates. Occurs on ground in forests, grasslands, riverbanks and seashores on ground, rocks, trees and logs.

Schistidium konoi (Broth.) Ignatova & H.H. Blom. – 30 m – **2** (u-45). On a boulder by a stream.

S. lancifolium (Kindberg) H.H. Blom. – 5–60 m – **1, 2, 3, 4.** On rocks, boulders, tree bases in grasslands, forests by rivers, common.

S. papillosum Culm. – 30 m – **2** (u-52). Cliff crevices by a stream, sporadic with *Amphidium lapponicum.*

S. rivulare (Brid.) Podp. – 150 m – **4** (Yu-1-16). Cliff crevices by a stream, sporadic.

Sciuro-hypnum brotheri (Peris) Ignatov et Huttunen – 40 m – **2** (KL2023).

S. curtum (Lindb.) Ignatov– 5–50 m – **2** (u-41). Wet riverbed, on the ground.

S. plumosum (Hedw.) Ignatov & Huttunen – 30 m – **1, 2, 3, 4.** Tree bases, rock outcrops, bare ground in various habitats.

S. populeum (Hedw.) Ignatov & Huttunen. – 30–50 m – **3** (u-20). Alder grove, on a tree base.

S. reflexum (Starke) Ignatov & Huttunen – 5–50 m – **1, 2, 3, 4.** Occurs in different habitats across the island as an epiphyte, on rocks and on ground, tree bases, common.

Sphagnum alaskense R.E. Andrus & Janssens – 15 m – **1** (E), **4 (**Yu-2-5). Ridge-lake bog, small mires on sea terrace.

S. capillifolium (Ehrh.) Hedw. – 150 m – **4** (KL2020).

S. compactum Lam. & DC. – 250 m – **4** (L2021).

S. divinum Flatberg & K. Hassel – 150 m – **4** (KL2020).

S. fallax (H. Klinggr.) H. Klinggr. – 150 m – **4** (KL2020).

S. fuscum (Schimp.) H.Klinggr. – 150 m – **4** (KL2020).

*S. girgensohni*i Russow – 253 m – **1** (E).

S. jensenii H. Lindb. – 150 m – **4** (KL2020a).

S. majus (Russow) C. E. O. Jensen – 150 m – **4** (KL2020a).

S. mirum Flatberg et Thingsgaard – 150 m – **4** (KL2020a).

S. papillosum Lindb. – 20 m – **4** (KL2020).

S. rubiginosum Flatberg – 10–50 m – **4.** Ridge-lake bog, common.

S. russowii Warnst. – 5–50 m – **4 (**Yu-2-5, KL2020). Ridge-lake bog in the southern part of the island.

S. warnstorfii Russow – 30 m – **1** (E).

Thamnobryum subserratum (Hook. ex Harv.) Nog. & Z.Iwats. – 10–30 m – **3 (**u-23, u-8). On ground in between roots in Alder grove, on moist ground among *Carex cryptocarpa*.

*T. neckeroide*s (Hook.) E. Lawton – 2–25 m – **2a** (KL2020).

Tortula edentula Ignatova & Ignatov – 20 m – **1** (u-70n). On a wall of an abandoned building.

Trachycystis flagellaris (Sull. & Lesq.) Lindb. – 10–30 m – **1, 2, 3, 4.** Very common across the island, on ground by streams in wet places, tree bases, boulders.

Trematodon ambiguus (Hedw.) Hornsch. – 15–100 m – **4.** On a bog, in between *Sphagnum*, on bare ground of the southern part of the island.

Ulota drummondii (Hook. & Grev.) Brid. – 30 m – **2** (u-39). On the fallen willow logs, on wet bark by a river.

Warnstorfia fluitans (Hedw.) Loeske – 5–25 m – A, **2a** (B, N).

Liverworts

Aneura pinguis (L.) Dumort. – 5–25 m – **2a** (B).

Anthelia juratzkana (Limpr.) Trevis. – 30 m – **1** (u-69n), **2a** (B), **4** (B). On bare ground in the tundra of the northern part of the island.

Blasia pusilla L. – **2a** (B).

Blepharostoma trichophyllum (L.) Dumort. – 10–100 m – **1, 2,**

3, 4. Very common across the island growing among various mosses.

Calypogeia muelleriana (Schiffn.) Müll.Frib. – 10–500 m – B (from LE collections on Kojosan Mt.).

C. cf. *azurea* Stotler & Crotz. – 15 m – **4** (Yu-1-14). On clayey bank of the creek.

C. pseudointegristipula Bakalin, A.V.Troitsky & Maltseva – 25 m – **4** (Yu-1-4, Yu-2-13). On a cliff. On a ridge-lake bog.

Cephalozia bicuspidata (L.) Dumort. – 30 m – **1** (u-71n), **2** (u-56), **4** (B). On a cliff, in a damp crack. On soil.

Cephaloziella divaricata (Sm.) Schiffn. – 5–150 m – **2a** (B), **4** (B).

Chiloscyphus polyanthos (L.) Corda – 30 m – **2** (u-34) – On *Calamagrostis* turf, in water.

Conocephalum conicum (L.) Dumort. – 30 m – 2 (u-41). Wet gorge.

C. japonicum (Thunb.) Grolle – 30 m – **2a** (B), 3 (u-31). Stony bed of the creek, on stone.

C. salebrosum Szweyk., Buczk. & Odrzyk. – 30 m – **3 (**u-26). Tall-herb meadow on a small slope. On soil.

Diplophyllum albicans (L.) Dumort. – 30–100 m – **3 (**u-57)**, 4** (Yu-1-14). On cliffs near rivers.

D. taxifolium (Wahlenb.) Dumort. – 15–60 m – **2a** (B), **2, 4** (B). Very common around Irina bay, on trees with *Lophocolea heterophylla*, on damp cliffs, near creeks with *Conocephalum japonicum*.

Douinia plicata (Lindb.) Konstant. & Vilnet – 40 m – **2 (**u-32). Vertical soil exposure in Obzhitaya Creek valley.

Gymnocolea inflata (Huds.) Dumort. – 150 m – **4** (Yu-2-13). On a ridge-lake bog.

Gymnomitrion faurieanum (Steph.) Horik. – 30 m – **3** (u-57). Bezdol'nyi River valley. On a cliff on the river side.

Isopaches bicrenatus (Schmid. ex Hoffm.) H. Buch – 100–150 m – **4** (B).

Jungermannia pumila subsp. *orientalis* Konstant., Vilnet & Mamontov.– 30 m – **2** (u-48). Wet gorge, on an overhanging boulder.

Lophocolea heterophylla (Schrad.) Dumort. – 20–40 m – **2, 3**. On logs in Alder forests, high grass meadows on soil.

Marsupella apertifolia Steph. – 10–40 m – **2**. On cliffs by rivers with *Diplophyllum albicans*.

M. subemarginata Bakalin & Fedosov – 30 m – **2** (u-57). On rocky riverbanks with *Pseudolophozia sudetica, Radula japonica, Diplophyllum taxifolium, Gymnomitrion faurieanum.*

Microlejeunea punctiformis (Taylor) Steph. – 30 m – **2** (u-57-2). On a cliff on a riverside with *Diplophyllum albicans.*

Mylia anomala (Hook.) S.Gray – A.

Nardia geoscyphus (De Not.) Lindb. – 40 m **– 1** (u-69n), **4** (B). On soil near the lighthouse.

N. scalaris S.Gray subsp. *scalaris* – 100–150 m – **4** (B).

Nipponolejeunea subalpina (Horik.) S.Hatt. – 20 m – **2a** (B), **4** (Yu-1-3). On stone on the river bank.

Pallavicinia subciliata (Austin) Steph. – 40 m – **4** (Yu-1-4). Rybnyi Creek valley, on a cliff with *Calypogeia pseudointegristipula.*

Pellia endiviifolia (Dicks.) Dumort. – 5–25 m – **2a** (B).

P. neesiana (Gottsche) Limpr. – 30 m – **1** (u-60), **2** (u-31)**, 4** (B)**.** Obzhitaya Creek valley, stony bed of the creek with *Conocephalum japonicum.*

Plagiochila porelloides (Torrey ex Nees) Lindenb. – 5–25 m – **2a** (B).

*Plectocolea hyalina (*Lyell) Mitt. – 100–150 m – **4** (B).

P. infusca Mitt. – 30 m – **2** (u-32). Obzhitaya Creek valley, on a cliff with *Blepharostoma trichophyllum.*

P. obovata (Nees) Lindb. – 15 m – **1**. On bare soil around Kastrikum cape with *Cephalozia bicuspidata.*

P. obscura A. Evans – 30 m – **2**. Obzhitaya Creek valley. Stony bed of the creek with *Diplophyllum taxifolium.*

Preissia quadrata (Scop.) Nees – 30 m – **2** (u-51) – On a cliff near a river.

Pseudolophozia sudetica (Nees ex Huebener) Konstant. & Vilnet – 30–50 m – **2.** On rocky river banks, common.

Radula complanata (L.) Dumort. – A.

R. japonica Gottsche ex Steph. – 30 m **– 2** (u-51). On rocky river banks with *Marsupella subemarginata.*

R. obtusiloba Steph. – 60 m – **2, 3**. Tall-herb sloping meadow, in Alder thickets, on soil between roots.

Riccardia chamedryfolia (With.) Grolle – 10–40 m **– 1** (u-60), **2 (**u-25, u-41), **4** (B). On bare soil, wet gorges, in moss turfs. Also reported by Nyushko & Potemkin, 2007.

Scapania curta (Mart.) Dum. – 5–150 m – **2a** (B), **4** (B).

S. paludosa (Müll.Frib.) Müll.Frib. – 15 m – **1 (**u-72n). Fen, on ground with *Dicranum majus*.

S. scandica (Arnell & H. Buch) Macvicar – 5–150 m – **2a** (B), **4** (B).

S. subalpina (Nees ex Lindenb.) Dumort. – 30 m – **2** (u-46). Wet cliff on river bank.

S. undulata (L.) Dumort. – 40 m – **2, 4**. On clayey banks of the creeks, on rocks by streams, common.

Excluded or doubtful records

Dicranum hakkodense Cardot – A. The collection in LE made by Abramova was revised by Nyushko and assigned to *D. hakkodense* before its split into *D. hakkodens*e and *D. pacificum.* Further clarification is required.

Rhytidiadelphus squarrosus (Hedw.) Warnst. – 32–250 m – **1** (L2023). Doubtful. The species was not confirmed by molecular studies in the Russian Far East, while some phenotypes of *R. subpinnatum* are hardly distinguishable from it.

Sphagnum pulchrum (Lindb. ex Braithw.) Warnst. – 250 m – **1**, **4** (L2021, L2023). The species belong to taxonomically difficult complex. Re-examination of one specimen originally identified as *S. pulchrum* in L2021 revealed it to be S. cf. *fallax*.

S. subfulvum Sjörs – 250 m – **4** (L2021). Re-examination of the specimen revealed it to be *S. fuscum*.

Discussion

Phytogeographic distribution

The current checklist highlights Urup Island as an important biogeographical crossroad within the Kuril Archipelago, supporting a diverse bryophyte flora. It is predominantly composed of Circumboreal taxa, however, the island's strong floristic connection to the warmer southern Kurils and mainland Asia is evidenced by East Asian elements forming the second largest chorological group. North Pacific endemic and arctic-alpine taxa comprise a smaller but ecologically significant portion of the flora, reflecting the island's specialized northern coastal tundra habitats.

Consequently, phytogeographical elements are not evenly distributed; rather, their distribution is structured by the island's complex topography and microclimates (Fig. 3a).

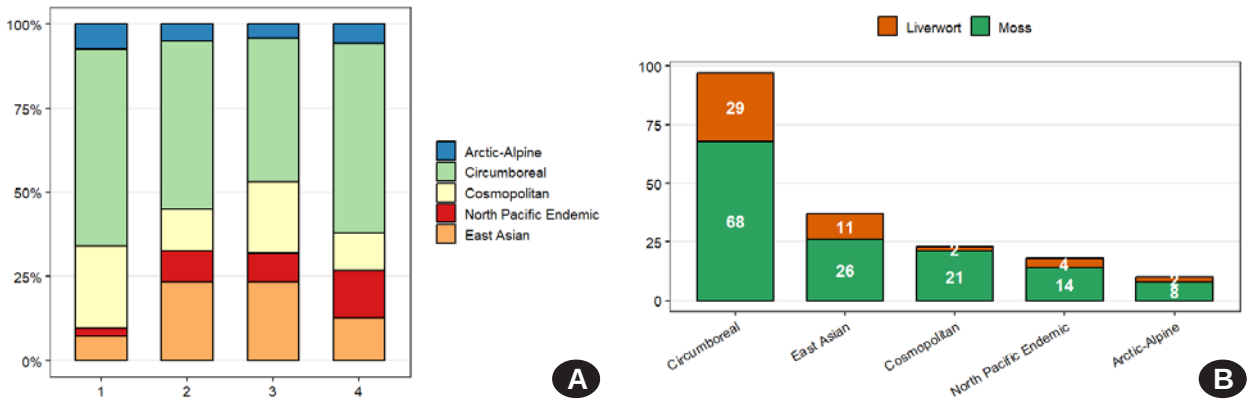

Figure 3. Phytogeographical element distribution across A: island localities; B: mosses and liverworts.

The wind-exposed northern part (Locality 1) is predictably dominated by Circumboreal, Cosmopolitan, and Arctic-Alpine taxa, mirroring the vascular flora of the coastal tundra-like communities. Additionally, as historically one of the most accessible areas on the island, this cape has been anthropogenically impacted which gave habitats for cosmopolitan pioneer species. The highest proportion of temperate East Asian elements occurs in the central zones (Localities 2 and 3) rather than the southernmost tip. The East-Asian element expansion is driven by the presence of deep, sheltered river gorges and dense tall-herb meadows, which act as thermal and humidity refugia protecting sensitive taxa from harsh oceanic winds. On the contrary, at the southern end of the island (Locality 4), East Asian elements decline while Circumboreal and North Pacific Endemic elements expand. The Locality 4 collection included intensive sampling on the oligotrophic ridge-lake bogs, which naturally inflated the proportion of Circumboreal as well as North Pacific Endemic wetland species. This highly specialized, hyperoceanic wetland habitat is characterised by Amphi-Beringian taxa like *Sphagnum alaskense* and *S. rubiginosum*.

The moss-to-liverwort phytogeographical element distribution is roughly a 2:1 to 3:1 ratio, which reflects the natural taxonomic diversity between them globally (Fig. 3b). However, a distinct deviation occurs within the Cosmopolitan element, which includes 19 mosses but only 2 liverworts (*Aneura pinguis* and *Cephalozia bicuspidata*), explained by very few liverworts being true Cosmopolitan globally.

Notes on rare and interesting bryophyte species

Arvernella pisarenkoi

The genus *Arvernella* has a remarkable discovery history. Originally it was described as a surprising endemic to France (Hugonnot & Hedenäs, 2015), but known distribution was recently expanded by the discovery of *A. sibirica* in South Siberia (Pisarenko *et al.*, 2022) and *A. pisarenkoi* in the Russian Far East. So far this species was only known from its type locality near the Chamginsky Pass, Sakhalin (Ignatov et al., 2021). This is the first record for Kuril Islands, which extends the species' known distribution southwards. On Urup, it was found growing on the ground among roots in an *Alnus fruticosa* grove intermixed with *Myuroclada longiramea* (Fig 4a). The identity of the species is confirmed by molecular analysis (Kartasheva *et al*., in Kuznetsova *et al*., 2025). The discovery of this minute moss highlights the high potential for detecting these overlooked taxa in the Far East.

Bryoxiphium japonicum

This species occurs around southern regions of the Far East of Russia – in Primorie, Sakhalin Island, South and Middle Kuril Islands. However, all records from Kamchatka and the Northern Kurils were revised to *B. norvegicum*, which puts the current finding as a northmost boundary of the species in the Archipelago. It is a picturesque and very characteristic East Asian species that was found in wind-protected boulder niches next to a water stream as an admixture (Fig 4b), not forming continuous mats as it does in more suitable climates.

Calypogeia cf. *azurea*

The reliable identification of *Calypogeia azurea* relies heavily on the presence of deep blue oil bodies in living plants, as these structures are fugacious and degrade rapidly in dried herbarium specimens (Potemkin *et al*., 2017). Due to historical taxonomic confusion with the rejected name *C. trichomanis* (L.) Raddi and morphological overlap with related species such as *C. muelleriana*, verified records of true *C. azurea* in the Russian Far East remain exceedingly rare. Within the Kuril Archipelago, it was previously confirmed only as far north as Iturup Island. The collection from Urup Island (Locality 4) represents a notable potential northward range extension; however, because it was identified from preserved material, it is tentatively assigned as *C.* cf. *azurea*.

Calypogeia pseudointegristipula

This species was recently described as new to science. Prior to its recognition, populations in the Russian Far East were repeatedly misidentified as the widespread *C. integristipula*, obscuring its true distribution (Bakalin *et al.*, 2020). Currently, *C. pseudointegristipula* is noted as a common species in the southernmost Russian Far East (Primorsky Territory, Sakhalin, and Kunashir).

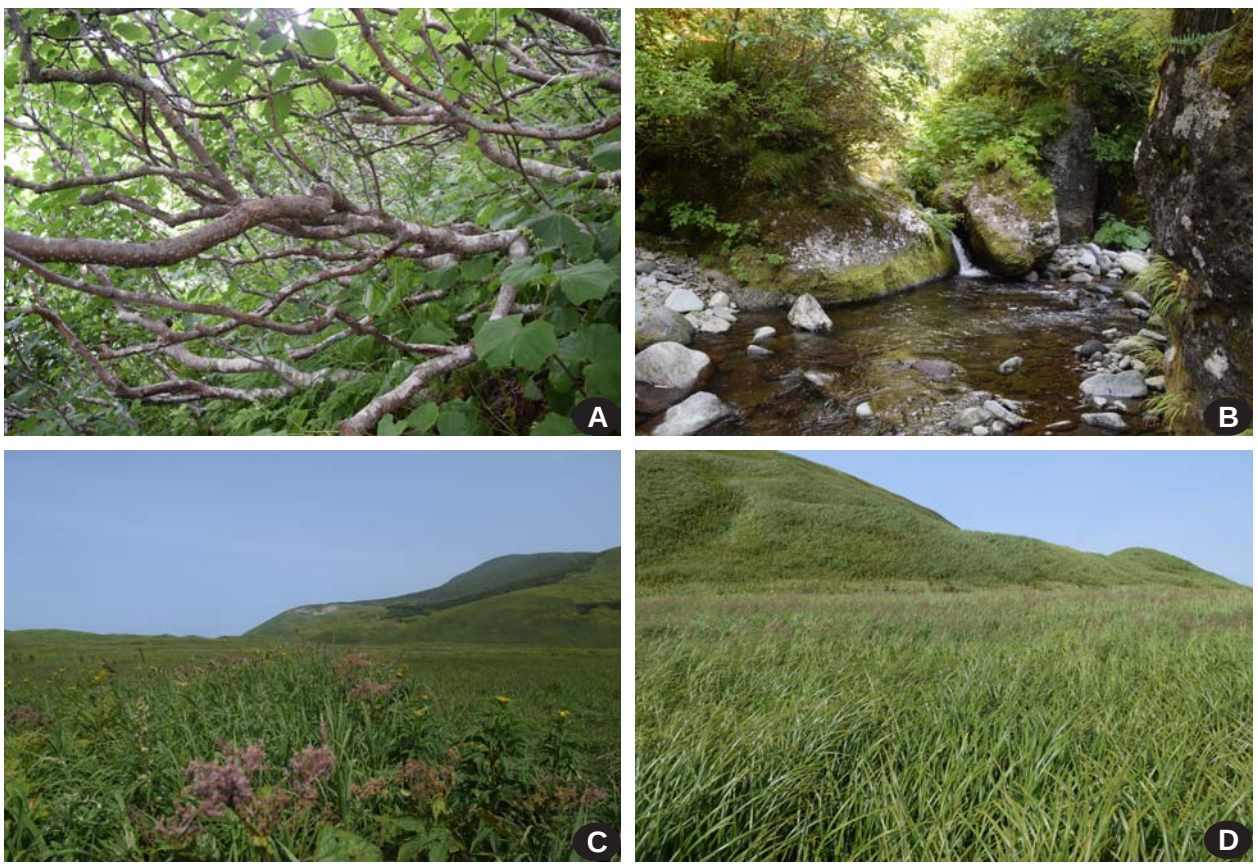

Figure 4. A – Alder forest with *Arvernella pisarenkoi*; B – The stream with boulders and crevices where *Bryoxiphium japonicum* was found; C – tall-herb grassland with *Filipendula kamtschatica* and *Cacalia robusta* where *Dicranum baicalense* was growing on the ground; D – Tokotan lake shore overgrown with *Carex cryptocarpa* with *Limnohypnum mizushimae* on the damp soil.

The Urup specimens were collected on a cliff and within the southern ridge-lake bog complex (Locality 4). While *C. integristipula* is widely known to inhabit bogs, this collection represents the first time *C. pseudointegristipula* has been specifically recorded in this habitat.

Dicranum baicalense

This species was recently described by Tubanova and Dugarova (2022) from southern Siberia (Buryatia and the Transbaikal Territory) and from the southern Russian Far East (Amur Region and Primorsky Territory). The current collection is a new record for Sakhalin Province and the easternmost locality for the species. On Urup Island it was collected in a tall-herb grassland with *Filipendula kamtschatica* and *Cacalia robusta* together with *Plagiomnium curvatulum,* and *Philonotis capillaris* (Fig 4c).

Limnohypnum mizushimae

A very rare species, reported in Japan from several localities on Honshu and Hokkaido (Kanda, 1975); in Russia, the species has been recorded at only two sites: in Kamchatka (Afonina *et al*., 2022) and on Shikotan Island (Bakalin *et al*., 2009). On Urup it was found among *Carex cryptocarpa* on damp soil by the lake Tokotan (Fig 4d) (Kartasheva & Ignatova in Sofronova *et al*., 2022).

Marsupella apertifolia

Long treated as a variety of *M. emarginata* or *M. tubulosa*, recent molecular evidence has confirmed *M. apertifolia* as a distinct, independent species (Bakalin *et al*., 2019). It is a montane, temperate endemic of the Japan-Korea-Kuril region. Within Russia, it was previously confirmed only from Iturup Island (Bakalin *et al*., 2021). On Urup it was collected on riverside cliffs alongside *Diplophyllum albicans* (Locality 2), which is an example of northward range extension. This finding helps clarify the geographical range of this North Pacific endemic, which was recently reinstated to the species level.

Marsupella subemarginata

This semi-cryptic, suboceanic species was only recently described to science, having been segregated from the widespread *M. emarginata* complex based primarily on molecular phylogenetic data (Bakalin *et al*., 2019). The true distribution of *M. subemarginata* is still being mapped, but it appears restricted to oro-boreal areas with strong oceanic influences and consistent precipitation (e.g., Kamchatka, Japan, Wrangel Island, and the Swiss Alps). The collection of this species on Urup Island provides a new important geographical data point in the North Pacific. On Urup, it was found growing on a rocky riverbank alongside *Pseudolophozia sudetica* and *Diplophyllum taxifolium* (Locality 2).

Microlejeunea punctiformis

The discovery of this species on Urup Island represents its global northernmost locality. This taxon has a

predominantly warm-temperate to subtropical East Asian distribution; it is absent from Hokkaido in Japan and was previously known in Russia only from the southernmost Kurils (Kunashir and Shikotan). Asian populations, formerly assigned to the European-American *M. ulicina* (Taylor) A. Evans, are now recognized as the distinct species *M. punctiformis* (Zhu & So, 2001; Söderström *et al*., 2016). In addition, the Urup collection is ecologically notable: while previous records within the Russian Far East have been strictly restricted to epiphytic habitats, the Urup population was discovered growing epilithically on a riverside cliff alongside *Diplophyllum albicans* (Locality 2). This documents a rare substrate shift for the species in this region, likely driven by the need for microclimatic stability at the northern edge of its global range.

Pallavicinia subciliata

The discovery of this oceanic, temperate-to-tropical Asian species on Urup Island is a new global northernmost limit for the taxon. Previously, its known northern range in Russia was restricted to the Primorsky Territory and the southernmost Kuril Island of Kunashir (Mamontov *et al*., 2015); in Japan, it does not extend north of Honshu. While typically recorded on humus in shaded, mixed coniferous-broadleaved or boggy forests in the Russian Far East, the Urup population was collected epilithically from a cliff in the Rybnyi Creek valley (Locality 4) alongside the recently described endemic *Calypogeia pseudointegristipula*. This demonstrates how sheltered riparian microhabitats allow southern temperate lineages to persist at harsher northern conditions.

Thamnobryum subserratum

Although this species has a broad distribution across Southeast Asia and has recently been recognized in Europe, it remains exceptionally rare in Russia. Previously, it was known in the country from only two collections: on rocks near hot springs on Kunashir Island and on cliffs in the Primorsky Territory. Its discovery on Urup Island represents only the third known Russian locality and a significant northward range extension within the Kuril Archipelago. Interestingly, while *T. subserratum* is typically a saxicolous species associated with forest cliffs and rocks, the Urup populations were found growing on the ground among roots in an alder grove and on moist soil among *Carex cryptocarpa* (Locality 3), expanding the known ecological amplitude of this rare taxon in the Russian Far East (Ignatova & Ignatov, 2011).

Tortula edentula

This North Pacific endemic was only recently described, originally known from Shikotan Island and subsequently found on Bering Island in the Commander Archipelago. Because its taxonomic status was clarified only recently, its distribution is likely wider than currently documented, allowing for relatively straightforward new discoveries in the region. During the present study on Urup Island, it was found growing on the wet concrete wall of an abandoned building near Kastrikum Cape (Locality 1) (Kartasheva & Fedorova in Kuznetsova *et al*., 2025). This finding not only confirms its presence on Urup but also demonstrates the ability of this rare regional endemic to pioneer anthropogenic substrates.

ACKNOWLEDGEMENTS

The authors are grateful to the Russian Geographical Society for organizing the expedition during which the material was collected. We extend our sincere thanks to the Expeditionary Activity Support Center (ЦСЭД) for their crucial assistance with logistics, organization, and ensuring safety under the severe conditions of an uninhabited island. We are deeply indebted to M.S. Ignatov and E.A. Ignatova for their invaluable help with species identification and their continuous guidance and support throughout this study. Finally, we thank all members of the expedition team for their support in the field. The study by A.V. Shkurko and Yu.S. Mamontov was performed within the State assignment (Nos. 122042500074-5 and 122042700002-6).

LITERATURE CITED

[ABRAMOVA, A.L.] АБРАМОВА А.Л. 1960. О мхах Курильских островов. – [On mosses of Kuril Islands] *В кн.: Материалы по природным ресурсам Камчатки и Курильских островов* [*In: Materialy po prirodnym resursam Kamchatki i Kurilskikh ostrovov*]. *Магадан* [*Magadan*], 87–97.

AFONINA, O.M., I.V. CZERNYADJEVA, O.YU. PISARENKO & V.E. FEDOSOV. 2022. Mosses of the northern Russian Far East, an annotated check-list. – *Botanica Pacifica* **11**(2): *103–130*. https://doi.org/10.17581/bp.2022.11206

ANDRUS, R.E. & J.A. JANSSENS. 2003. *Sphagnum alaskense*, a new species from western North America. – *The Bryologist* **106**(3): *435–438*. https://doi.org/10.1639/08

BAKALIN, V.A., V.YA. CHERDANTSEVA, M.S. IGNATOV, E.A. IGNATOVA & T.I. NYUSHKO. 2009. Bryophyte flora of the South Kuril Islands (East Asia). – *Arctoa* **18**: *69–114*.

BAKALIN, V.A., S.S. CHOI & S.J. PARK. 2021. Revision of Gymnomitriaceae (Marchantiophyta) in the Korean Peninsula. – *PhytoKeys* **176**: *77–110*. https://doi.org/10.3897/phytokeys.176.62552

BAKALIN, V.A., K.G. KLIMOVA, V.S. NGUYEN, A.V. TROITSKY, Y.D. MALTSEVA & S.S. CHOI. 2020. A review of *Calypogeia* (Marchantiophyta) in the eastern Sino-Himalaya and Meta-Himalaya based mostly on molecular data. – *PhytoKeys* **153**: *111–154*. https://doi.org/10.3897/phytokeys.153.52920

BAKALIN, V. A., V. E. FEDOSOV, A.V. FEDOROVA & V.S. NGUEN. 2019. Integrative taxonomic revision of *Marsupella* (Gymnomitriaceae, Hepaticae) reveals neglected diversity in Pacific Asia – *Cryptogamie, Bryologie* **40**(7): *59–85*. https://doi.org/10.5252/cryptogamie-bryologie2019v40a7

BARKALOV, V.YU. 2000. Phytogeography of the Kurile Islands. – *Natural History Research, Special Issue* **7**: *1–14*.

[BARKALOV, V.YU.] БАРКАЛОВ В.Ю. 2002. Очерк растительности. – [Outline of the vegetation] *В кн.: Растительный и животный мир Курильских островов* [*In: Flora and fauna of the Kuril Islands*]. *Владивосток* [*Vladivostok*], *35–66*.

[BARKALOV, V.YU.] БАРКАЛОВ В.Ю. 2009. Флора Курильских островов. – [Flora of the Kuril Islands]. *Владивосток, Дальнаука* [*Vladivostok, Dalnauka*], *468 pp.*

BROTHERUS, V.F. 1899. Neue Beiträge zur Mossflora Japans. – *Hedwigia* **38**: *204–247*.

ELLIS, L.T., O.M. AFONINA, M.H.B. ALIA, M. BURGHARDT, B.

CABEZUDO, M.J. CANO, A.C. COTTET, J. CSIKY, J. DEME, P. ERZBERGER, M. EVANGELISTA, E.A. GLAZKOVA, ... E.YU. KUZMINA, N.S. LIKSAKOVA et al. 2022. New national and regional bryophyte records, 70. – *Journal of Bryology* **44**(2): *1–9*. https://doi.org/10.1080/03736687.2022.2095145

HUGONNOT, V. & L. HEDENÄS. 2015. *Arvernella microclada* Hugonnot & Hedenäs (Amblystegiaceae), a new minute species from France, requiring a separate genus. – *Journal of Bryology* **37**(3): 214–222. https://doi.org/10.1179/1743282015Y.0000000005

IGNATOV, M.S., O.M. AFONINA, E.A. IGNATOVA et al. 2006. Checklist of mosses of East Europe and North Asia. – *Arctoa* **15**: *1–130*. https://doi.org/10.15298/arctoa.15.01

IGNATOV, M.S., E.A. IGNATOVA & O.I. KUZNETSOVA. 2021. A rare European endemic moss genus *Arvernella* is discovered in Sakhalin, Russian Far East, where it is also rare. – *Arctoa* **30**: *168–174*. https://doi.org/10.15298/arctoa.30.01

[IGNATOV, M.S., E.A. IGNATOVA, V.E. FEDOSOV, V.I. ZOLOTOV, T. KOPONEN, I.V. CZERNYADJEVA, G.YA. DOROSHINA, D.YA. TUBANOVA & N.E. BELL] ИГНАТОВ М.С., Е.А. ИГНАТОВА, В.Э ФЕДОСОВ, В.И. ЗОЛОТОВ, Т. КОПОНЕН, И.В. ЧЕРНЯДЬЕВА, Г.Я. ДОРОШИНА, Д.Я. ТУБАНОВА, Н.Е. БЕЛЛ. 2017. Флора мхов России. Т. 2. – [Moss flora of Russia. Vol. 2]. *М., КМК* [*Moscow, KMK Scientific Press*], *560 pp*.

[IGNATOVA, E.A., T.I. KOROTEEVA, V.E. FEDOSOV, M.S. IGNATOV, E.YU. KUZMINA, N.S. LIKSAKOVA, A.V. SHKURKO, A.K. EZHKIN & V.V. KAGANOV] ИГНАТОВА Е.А., Т.И. КОРОТЕЕВА, В.Э. ФЕДОСОВ, М.С. ИГНАТОВ, Е.Ю. КУЗЬМИНА, Н.С. ЛИКСАКОВА, А.В. ШКУРКО, А.К. ЕЖКИН, В.В. КАГАНОВ. 2023. Дополнение к флоре мхов Южных Курил (Российский Дальний Восток). – [Supplement to the moss flora of the South Kuril Islands (Russian Far East)] *Ботанический журнал* [*Botanicheskii Zhurnal*] **108**(5): *473–483*. http://dx.doi.org/10.31857/S0006813623050046

IGNATOVA, E.A. & V.E. FEDOSOV. 2008. Species of *Dicranum* (Dicranaceae, Bryophyta) with fragile leaves in Russia. – *Arctoa* **17**: *37–57*. https://doi.org/10.15298/arctoa.17.05

IGNATOVA, E.A. & M.S. IGNATOV. 2011. The genus *Thamnobryum* (Neckeraceae, Bryophyta) in Russia. – *Arctoa* **20**: *137–152*. https://doi.org/10.15298/arctoa.20.10

KANDA, H. 1975. A revision of the family Amblystegiaceae of Japan I. – *Journal of Science of the Hiroshima University, Series B, Division. 2, Botany* **15**: *201–276*.

KUZNETSOVA, O.I., O.M. AFONINA, A.N. BERSANOVA, A.V. FEDOROVA, V.E. FEDOSOV, M.S. IGNATOV, E.A. IGNATOVA, E.I. IVANOVA, A.S. KARTASHEVA & A.P. SEREGIN. 2025a. Bryophyte molecular barcoding records. 12. – *Arctoa* **34**: *69–72*. https://doi.org/10.15298/arctoa.34.07

KUZNETSOVA, O.I., O.A. BELKINA, E.A. BOROVICHEV, E.A. CHUBAR, A.V. FEDOROVA, V.E. FEDOSOV, M.S. GOLSTEIN, M.S. IGNATOV, E.A. IGNATOVA, A.S. KARTASHEVA et al. 2025b. [Bryophyte molecular barcoding records. 13] – *Arctoa* **34**(2): *209–216*. https://doi.org/10.15298/arctoa.34.18

[LIKSAKOVA, N.S., E.A. GLAZKOVA & E.YU. KUZMINA] ЛИКСАКОВА Н.С., Е.А. ГЛАЗКОВА, Е.Ю. КУЗЬМИНА. 2021. К растительности острова Уруп (Курильские острова). – [To the vegetation of Urup Island (the Kuriles)] *Ботанический журнал* [*Botanicheskii Zhurnal*] **106**(8): 731–755. (In Russian). https://doi.org/10.31857/S0006813621080068

[LIKSAKOVA, N.S., E.A. GLAZKOVA, E.YU. KUZMINA & S.F. KHOKHLOV] ЛИКСАКОВА Н.С., Е.А. ГЛАЗКОВА, Е.Ю. КУЗЬМИНА, С.Ф. ХОХЛОВ. 2023. Новые данные о растительности и почвах о. Уруп (Курильские острова). – [New data on vegetation and soils of Urup Island (Kuril Islands)] *Ботанический журнал* [*Botanicheskii Zhurnal*] **108**(3): *228–247*. https://doi.org/10.31857/S0006813623030079

MAMONTOV, YU.S., N.A. KONSTANTINOVA, A.A. VILNET & V.A. BAKALIN. 2015. On the phylogeny and taxonomy of Pallaviciniales (Marchantiophyta). – *Arctoa* **24**(1): *108–110*. https://doi.org/10.15298/arctoa.24.12

[NYUSHKO, T.I. & A.D. POTEMKIN] НЮШКО Т.И., А.Д. ПОТЕМКИН. 2007. Новые находки печеночников в Сахалинской области. 1. Курильские острова. – [New liverwort records from Sakhalin Province. 1. Kuril Islands]. *Arctoa* **16**: *181–213*.

NYUSHKO, T.I., E.A. IGNATOVA & M.S. IGNATOV. 2008. Contribution to moss flora of the Kuril Islands (Russian Far East). – *Arctoa* **17**: *165–168*.

PIETSCH, T.W., V.V. BOGATOV, K. AMAOKA, Y.N. ZHURAVLEV, V.Y. BARANOV, S.H. GAGE et al. 2003. Biodiversity and biogeography of the islands of the Kuril Archipelago. – *Journal of Biogeography* **30**(9): *1297–1310*. https://doi.org/10.1046/j.1365-2699.2003.00956.x

PISARENKO, O.YU., O.I. KUZNETSOVA, E.A. IGNATOVA & M.S. IGNATOV. 2022. A further range extension of the genus *Arvernella* (Bryophyta) – *Arctoa* **31**: *1–6*. https://doi.org/10.15298/arctoa.31.01

[POTEMKIN, A.D. & E.V. SOFRONOVA] ПОТЕМКИН А.Д., Е.В. СОФРОНОВА. 2009. Печеночники и антоцеротовые России. Т. 1. – [Liverworts and hornworts of Russia. Vol. 1]. *СПб., Якутск* [*St. Petersburg, Yakutsk*], *368 pp*.

POTEMKIN, A.D., E.A. BOROVICHEV & E.G. GINZBURG. 2017. *Calypogeia azurea* (Calypogeiaceae, Marchantiophyta) in the Northwestern European Russia. – *Novosti Sistematiki Nizshikh Rastenii* **51**: *263–273*. https://doi.org/10.31111/nsnr/2017.51.263

RAZJIGAEVA, N.G., L.A. GANZEY, T.A. GREBENNIKOVA, N.I. BELYANINA, K.S. GANZEI, V.M. KAISTRENKO, KH.A. ARSLANOV, F.E. MAKSIMOV & A.V. RYBIN. 2019. Multiproxy record of late Holocene climatic changes and natural hazards from paleolake deposits of Urup Island (Kuril Islands, North-Western Pacific). – *Journal of Asian Earth Sciences* **181**: *1–12*. https://doi.org/10.1016/j.jseaes.2019.103916

SOFRONOVA, E.V., O.M. AFONINA, M.A. BOYCHUK, G.YA. DOROSHINA, V.E. FEDOSOV, G.N. GANASEVICH, M.V. KAZAKOVA, E.YU. KUZMINA, E.D. LAPSHINA, N.S. LIKSAKOVA et al. 2020. New bryophyte records. 15. – *Arctoa* **29**: *75–97*. https://doi.org/10.15298/arctoa.29.16

SOFRONOVA, E.V., O.M. AFONINA, O.A. BELKINA, M.A. BOYCHUK, V.V. CHAKOV, I.V. CZERNYADJEVA, G.YA. DOROSHINA, M.V. DULIN, A.P. DYACHENKO, V.E. FEDOSOV et al. 2022. New bryophyte records. 19. – *Arctoa* **31**(2): *227–246*. https://doi.org/10.15298/arctoa.31.24

SÖDERSTRÖM, L., A. HAGBORG, M. VON KONRAT, S. BARTHOLOMEW-BEGAN, D. BELL, L. BRISCOE et al. 2016. World checklist of hornworts and liverworts. – *PhytoKeys* **59**: *1–828*. https://doi.org/10.3897/phytokeys.59.6261

TATEWAKI, M. 1957. Geobotanical studies on the Kuril Islands. – *Acta Horti Gotoburgensis* **21**: *43–123*.

TUBANOVA, D.YA. & O.D. DUGAROVA. 2022. *Dicranum baicalense* (Dicranaceae, Bryophyta), a new species from Russia. – *Arctoa* **31**(2): *145–154*. https://doi.org/10.15298/arctoa.31.16

[VOROBIEV, D.P.] ВОРОБЬЕВ Д.П. 1963. Растительность Курильских островов. – [Vegetation of the Kuril Islands]. *Москва, Ленинград* [*Moscow, Leningrad*], *92 pp*.

ZHU, R.-L. & M.L. SO. 2001. Epiphyllous liverworts of China. – *Nova Hedwigia, Beiheft* **121**: *1–418*.

Receved 15 April 2026 *Accepted 18 June 2026*