diversity

MDPI

Article

Liverworts of the South Kamchatka Nature Park: Survival in Active Volcanism Land

Vadim A. Bakalin [1,*], Ksenia G. Klimova [1], Eugeniy A. Karpov [2], Daniil A. Bakalin [3] and Seung Se Choi [4,*]

1 Laboratory of Cryptogamic Biota, Botanical Garden-Institute FEB RAS, Makovskogo Street 142, Vladivostok 690024, Russia
2 Volcanoes of Kamchatka, Zavoiko Street 33, Elizovo 684000, Russia
3 AXiiO Oy Company, 135A, Helsinki XR Center, Hämeentie, 00560 Helsinki, Finland
4 Team of National Ecosystem Survey, National Institute of Ecology, Seocheon 33657, Korea
* Correspondence: vabakalin@gmail.com (V.A.B.); hepaticae@jbnu.ac.kr (S.S.C.)

Abstract: Kamchatka, due to its position in hemiarctic northeast Asia on the migration pathways of taxa from Asia to America and vice versa, which has an insular geographical position and provides numerous pieces of evidence regarding current active volcanism, has a peculiar flora. The study of the liverwort flora of the southeastern part of the Kamchatka Peninsula (South Kamchatka Nature Park), which, until now, has been very poorly explored, showed high taxonomic richness and some specificity due to volcanic evidence. In total, 132 species have been recorded in this sector of the "Pacific Ring of Fire". This number is quite high compared to other floras of hemiarctic Asia. The influence of volcanism on flora formation is prominent due to the regular renewal of substrates, the appearance of specific habitats (for example, thermal water outlets), the displacement of vegetation belts, and ashfalls leading to the presence of extended spaces free of vegetation cover and is an area that is open for invaders. The altitudinal zonality, despite the difference of 2000 m in elevation, is not clearly expressed in the flora of the liverworts: arctomontane species descend far down the altitudinal profile, reaching the *Betula ermanii* forests. The "plantless" uppermost belt in the mountains, commonly described in floristic studies of vascular plants, is not actually free of plants if liverwort occurrences are considered. A number of species normally occupy unusual habitats in the studied flora due to contemporary volcanism evidence, e.g., sulfur-rich substrates.

Keywords: liverworts; Kamchatka Peninsula; Northeast Asia; Pacific Ring of Fire; distribution patterns; nonvascular plants

check for updates

Citation: Bakalin, V.A.; Klimova, K.G.; Karpov, E.A.; Bakalin, D.A.; Choi, S.S. Liverworts of the South Kamchatka Nature Park: Survival in Active Volcanism Land. *Diversity* **2022**, *14*, 722. https://doi.org/10.3390/d14090722

Academic Editors: Jakub Sawicki and Grzegorz J. Wolski

Received: 15 August 2022
Accepted: 30 August 2022
Published: 1 September 2022

1. Introduction

Kamchatka is a vast mountainous region on a peninsula located in the northeastern corner of the Eurasian continent and in the northwestern part of the "Pacific Ring of Fire". The country occupies an almost insular position (connected to the Asian continent by a narrow and flat isthmus); the close ties of its flora and fauna with those in North America determine the uniqueness of the biological diversity of Kamchatka. South Kamchatka Nature Park is located in the most humid and volcanically active part of the peninsula, where the "main task" of plants is to survive under regular volcanic eruptions accompanied by catastrophic ashfalls. Scattered and fragmentary data on the liverworts of South Kamchatka Nature Park were the only available data prior to our study. Professional bryologists did not visit the park, excluding the Mutnovskaya Sopka Volcano vicinity, where a large number of liverwort specimens were collected during the beginning of the millennium as part of a comprehensive study of mosses in the area. As part of a multitask field expedition to study the biodiversity of South Kamchatka Nature Park, organized by the Park Directorate of "Volcanoes of Kamchatka", we visited five areas within the park for one month (from 15 July to 15 August 2021) using a helicopter. The vast majority of these areas are close to the epicenters of modern volcanic activity. Four of these five areas (excluding the Mutnovskaya Sopka Volcano area) were difficult to access and were visited by professional hepaticologists for the first time. These areas are rarely visited on a regular basis and are unlikely to be explored again in the near future. Therefore, although collected materials are incomplete, considering the large size of the park, the materials available could be regarded as valuable enough to be considered for publication.

As Eric Hulten wrote in 1974 [1], based on his own field research conducted in southern Kamchatka in 1920–1922 [1] (p. 182), "the country was mostly uninhabited, and very inaccessible, on account of nearly impassable alder thickets on steep mountain slopes". Currently, the territory of the park is still uninhabited and is rarely visited by both tourists and scientists (with the exception of the Mutnovskaya Sopka Volcano area, which is quite popular for sightseeing). In addition to the Mutnovskaya Sopka Volcano, there are two additional tourist attractions for those traveling by helicopter: the Ksudach Caldera and the Khodutkinskie Hot Springs. However, the anthropogenic impact on these areas is minimized due to the very limited area that short-term tourists can access, which is limited to 1–2 h and tourists must remain near the helicopter. Everything else is in a natural and pristine state, as it was long before the arrival of Hulten 100 years ago, with only valuable reservation when the frequent renewal of landscapes and vegetation by volcanic eruptions is considered as pristine.

The aim of the study was to discover the liverwort taxonomic diversity of the South Kamchatka Nature Park (as part of the Parks of "Volcanoes of Kamchatka" Nature Park consortium), to analyze the liverwort distribution patterns within the park, and determine whether the liverwort flora of the park has peculiar traits. This account describes the obtained results.

Historical Background

The data on liverwort diversity within South Kamchatka Nature Park were scattered prior to the present research. The Swedish eminent botanist Eric Hulten was the first botanist to work in the current borders of the park (far before the park was even thought to be organized); he collected liverworts during his visit to Russkaya Bay (Akhomten Bay, as it was referred to in the literature and maps before the middle of the 20th century) in September 1920. Hulten [2] (p. 330) wrote about this event: "In the autumn of the same year I traveled by motor boat to Akhomten Bay on the east coast in order to make a preliminary survey of that part, and stayed there one month". Hulten traveled frequently around South Kamchatka. Although aside Russkaya Bay, he collected only one liverwort species in 1922 in the valley of the Khodutka River basin (Shadutka in [2]). Nevertheless, the specimens collected by Hulten in 1920 and 1922 are interesting as they were collected 13–15 years after the catastrophic eruption of Ksudach Volcano, which took place on 30 March 1907 and is considered one of the most powerful volcanic events to have occurred on Earth during the last 500 years. As Hulten observed [2], even in Russkaya Bay (90 km to southeast), the layer of fresh volcanic ashes reached 5 cm, while the forest in the Khodutka River Valley (likely referring to Pravaya Khodutka, which is in the upper part of the Khodutka River Basin, 36 km nearly northward of Ksudach) was almost completely destroyed (Figure 6 in [2]) and thick ash deposits covered the slopes of Khodutka Volcano. Although Hulten also visited Asacha (Assatcha in [2]), Khodutka and Ksudach Volcanoes, as well as the valleys between them, there are no data on liverwort specimens that he might have collected there.

The first liverwort occurrence data (based on Hulten's collections) were published by Arnell [3], who mentions in his article "Lebermoose aus Kamtschatka" one species from the Khodutka River valley (Shadutka-Fluss in [3])—*Conocephalum japonicum* (as *C. supradecompositum* (Lindb.) Steph.), and eight species from Russkaya Bay (Akhomten in [3]): *Nardia compressa*, *Diplophyllum taxifolium*, *Neoorthocaulis binsteadii* (as *Jungermannia binsteadii* Kaalaas), *Schistochilopsis incisa* (as *Jungermannia incisa* Schrad.), *Scapania undulata* (as *Martinella dentata* (Dumort.) Arnell), *Scapania subalpina* (as *Martinella subalpina* (Nees) Lindb.), *Anthelia julacea* (there widely treated, probably referable to *A. juratzkana*, common species in the park) and *Pleurocladula albescens* (as *Pleuroclada albescens* (Hook.) Spruce).

The next advancement in related studies was completed by Persson [4] based on the same collection by Hulten. He provided data on the distribution of six species in Akhomten Bay: *Lophozia murmanica* (as *L. groenlandica* (Nees) Macoun), *Lophoziopsis longidens* (as *Lophozia longidens* (Lindb.) Macoun), unnamed *Macrodiplophyllum* (which may belong to *Douinia plicata* or *Scapania microdonta* in the current taxonomy), *Gymnomitrion brevissimum* (as *Marsupella varians* (Lindb.) Mull. Frib.), *Neoorthocaulis attenuatus* (as *Orthocaulis attenuatus* (Maert.) Evans) and *Scapania cuspiduligera*.

The next liverwort collections were gathered 80 years after Hulten. One was made by Bakalin in July 2004 during a one-hour stay in Russkaya Bay. The results were included in the account by Bakalin [5] and provide data on the distribution of six species: *Calypogeia muelleriana*, *Cephalozia bicuspidata*, *Jungermannia atrovirens*, *Pseudolophozia sudetica* (as *Lophozia sudetica* (Huebener) Grolle), *Pellia neesiana*, and *Scapania paludosa*. At the same time, advancements in the understanding of liverwort flora in South Kamchatka Nature Park were made by Czernyadjeva et al. [6]. Authors of this cited paper provided 39 liverwort species for the "Mutnovskie Hot Springs"—a highly undefined term since there are many thermal springs and fumaroles (the latter might also be conditionally treated as "hot springs") on the slopes of Mutnovskaya Sopka Volcano). From the manuscript, it could be suggested that authors of the cited work are referring to the area near Dachnye and Medvezhie hot and cold springs, including the surrounding environments that are quite distant from the thermal pools and are not affected by thermal water or steam. The list includes *Anthelia julacea*, *A. juratzkana* (as *A. julacea* subsp. *juratzkana* (Limpr.) Meyl.), *Cephalozia ambigua*, *C. bicuspidata*, *Cephaloziella* cf. *varians*, *C. divaricata*, *Diplophyllum taxifolium*, *Endogemma caespiticia* (as *Jungermannia caespiticia* Lindenb.), *Gymnomitrion adustum* (as *Marsupella adusta* (Nees) Spruce), *G. brevissimum* (as *Marsupella brevissima*), *Isopaches bicrenatus* (as *Lophozia bicrenata* (Schmid.) Dumort.), *Jungermannia exsertifolia*, *Lophozia savicziae*, *Lophoziopsis excisa* (as *Lophozia excisa* (Dicks.) Dumort.), *Marchantia alpestris* (as *M. polymorpha* ssp. *montivagans* Bischl et Boisselier), *Marsupella apiculata* (as *Gymnomitrion apiculatum* (Schiffn.) Mull.), *M. condensata*, *M. emarginata*, *M. sphacelata*, *Nardia assamica*, *N. geoscyphus*, *N. harae* (as *N. scalaris*), *N. insecta*, *N. japonica*, *N. unispiralis*, *Pellia epiphylla*, *P. neesiana*, *Pleurocladula albescens*, *Pseudolophozia debiliformis* (as *Lophozia debiliformis* R.M. Schust et Damsh.), *P. sudetica* (twice, as *Lophozia sudetica* (Huebener) Grolle and then also as *Lophozia rufescens* Schljak.), *Scapania irrigua*, *S. praetervisa* (as *S. mucronata* subsp. *praetervisa* (Meyl.) R.M. Schust.), *S. obscura*, *S. scandica*, *S. subalpina*, *S. uliginosa*, *Solenostoma* cf. *obscurum* (as *Jungermania* cf. *evansii* Vana), *S. hyalinum* (as *Jungermannia hyalina* Lyell), *S. sphaerocarpum* (as *Jungermannia sphaerocarpa* Hook.).

Therefore, prior to the present research, 51 species were recorded for South Kamchatka Nature Park, with almost all data restricted to the unclear definition of "Mutnovskie Hot Springs" at the northern edge of the park, which is within the area that has a specified human impact.

2. Materials and Methods

In total, 76 localities were visited where bryophytes were collected (Figure 1 (a detailed interactive map is also provided at https://hepaticae.ru/south-kamchatka-nature-park/, accessed on 25 May 2022), Table 1). Although the majority of attention was given to the collection of liverworts, mosses were also gathered periodically. The collection sites differed significantly in the length of time spent on their study, in the variety of substrates and communities, and in their size. The collection site selection was predetermined following two parameters. The first consideration was where the helicopter landing site was selected (site selection took into account the multidisciplinary interests of the research team, which included geologists, zoologists and botanists); the second consideration was the accessibility of the landscape elements, while the true conditions and passability of the communities were also considered. After these predeterminations, during only the third stage, we selected collection areas while considering the potential diversity of the community (or landscape element) for sampling during the allotted timeframe. The specimens were collected at the selected point until the "knowledge curve" reached a "plateau", i.e., the number of newly found species at the site ceased to increase. Each new locality that was chosen, which were typically farther than at a distance 200–300 m away, received a new number (and a new geographical coordinate). The distance between collection localities varied and could not be used for statistical purposes. For each specimen collected, their habitat and a very general description of the community were provided.

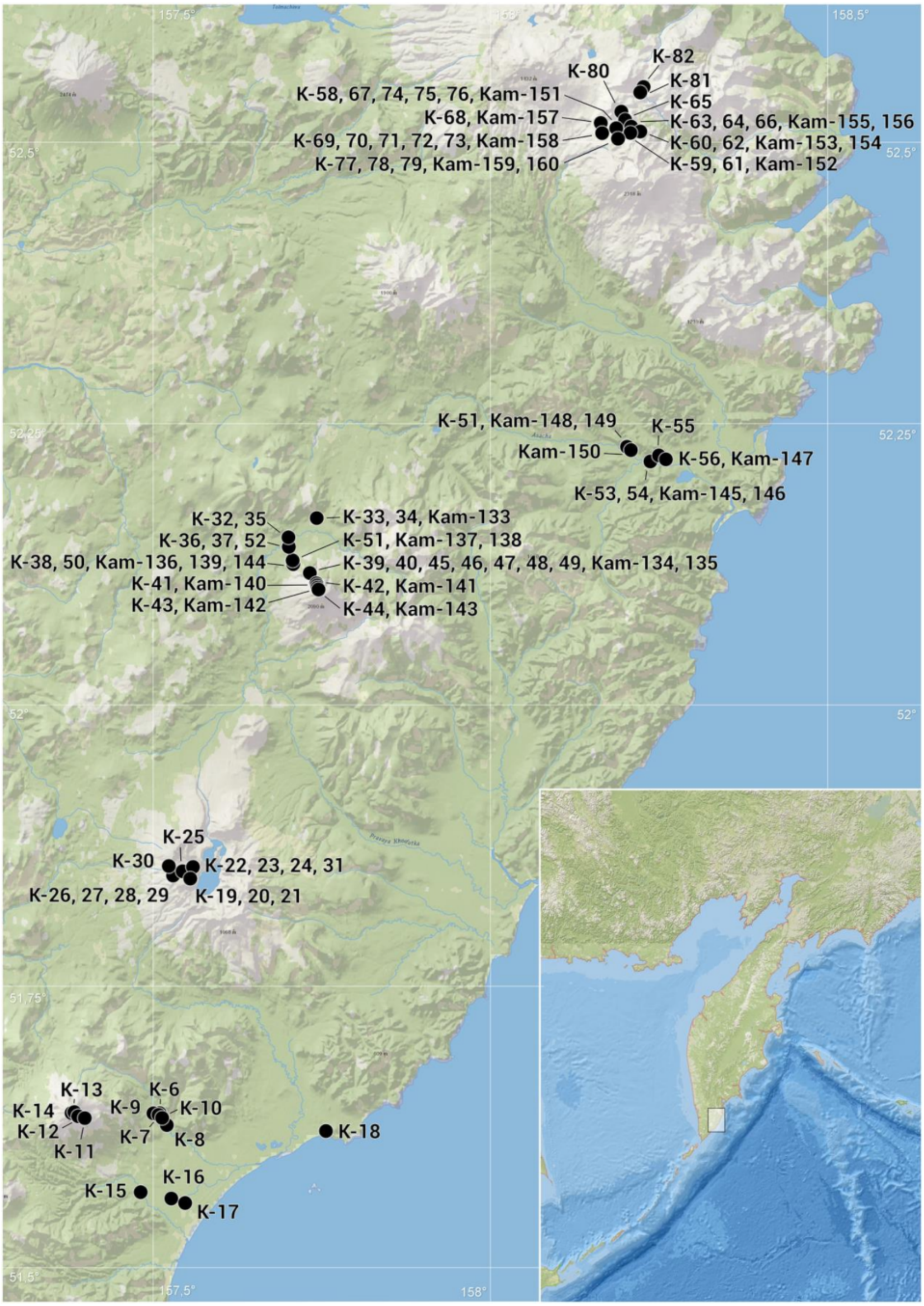

Figure 1. Collection localities corresponding to Table 1. Interactive detailed map can be found in https://hepaticae.ru/south-kamchatka-nature-park/.

Table 1. The collecting localities.

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-6	Middle course of Zhyoltaya River, Zheltovskie Hot Springs area (with outgoing water 55 °C)	51°34′34.09″ N 157°27′44.01″ E	112	*Betula ermanii* forest with forb cover	V.A. Bakalin, 17 July 2021
K-7	Middle course of Zhyoltaya River	51°34′28.84″ N 157°27′38.98″ E	109	Swampy community with *Fe*-rich springs and *Trichophorum*-*Carex*-moss community with scattered low *Salix* shrubs in the river floodplain	V.A. Bakalin, 17 July 2021
K-8	Middle course of Zhyoltaya River	51°33′54.00″ N 157°28′23.10″ E	183	*Salix schwerinii* forest with tall grasses	V.A. Bakalin, 18 July 2021
K-9	Middle course of Zhyoltaya River, small right tributary of the river	51°34′33.39″ N 157°27′10.57″ E	219	*Alnus fruticosa* crooked forest with scattered *Betula ermanii* trees and fern-forb-grass cover	V.A. Bakalin, 19 July 2021
K-10	Middle course of Zhyoltaya River	51°34′18.40″ N 157°27′58.49″ E	107	*Betula ermanii* forest in the floodplain	V.A. Bakalin, 20 July 2021
K-11	Eastern slope of Zheltovskaya Sopka Volcano	51°34′17.14″ N 157°20′56.63″ E	1243	Scoria field with scattered patches of dwarf shrub vegetation and streams flowing from snowfields	V.A. Bakalin, 22 July 2021
K-12	Eastern slope of Zheltovskaya Sopka Volcano	51°34′24.31″ N 157°20′18.29″ E	1610	Scoria field with scattered patches of dwarf shrub vegetation and streams flowing from snowfields	V.A. Bakalin, 22 July 2021
K-13	West peak of Zheltovskaya Sopka Volcano	51°34′36.39″ N 157°19′58.56″ E	1885	N-facing cliffs near snowbed	V.A. Bakalin, 22 July 2021
K-14	South peak of Zheltovskaya Sopka Volcano	51°34′34.77″ N 157°19′42.34″ E	1963	Rock field	V.A. Bakalin, 22 July 2021
K-15	Il′inskaya River middle course	51°30′05.57″ N 157°26′01.77″ E	35	Floodplain forest near river	V.A. Bakalin, 23 July 2021
K-16	Il′inskaya River middle course	51°29′42.60″ N 157°28′50.85″ E	70	*Betula ermanii* forest with tall grass cover	V.A. Bakalin, 23 July 2021
K-17	Il′inskaya River middle course	51°29′27.04″ N 157°30′06.14″ E	30	Swampy *Carex*-dwarf shrub community	V.A. Bakalin, 23 July 2021
K-18	Zhyoltyi Cape near Zhyoltaya River mouth	51°33.551′N 157°42.659′E	12	Wet meadow with shrubby *Salix*	V.A. Bakalin, 25 July 2021
K-19	Ksudach Mts. (Ksudach Volcano Caldera), Klyuchevoye Lake area, its western shore environs	51°47′50.77″ N, 157°30′37.70″ E	588	Small stream middle course, in *Alnus fruticosa* thickets	V.A. Bakalin, 27 July 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-20	Klyuchevoye Lake area, its western shore environs	51°47′51.82″ N 157°30′20.01″ E	633	Small (ca. 8 m height) waterfall surroundings with *Alnus fruticosa* thickets	V.A. Bakalin, 27 July 2021
K-21	Klyuchevoye Lake area, its western shore environs	51°48′06.39″ N 157°29′59.06″ E	759	Dry scoria field with sparse dwarf shrub vegetation	V.A. Bakalin, 27 July 2021
K-22	Klyuchevoye Lake area, its western shore environs	51°48′22.07″ N 157°30′38.41″ E	877	Small narrow range with large block stony field on slopes	V.A. Bakalin, 27 July 2021
K-23	Klyuchevoye Lake area, its western shore environs, "Paryashchy Greben" Ridge	51°48′30.65″ N 157°30′52.27″ E	830	The area with many solfatara at ridgeline surrounded by fine soil and cliffs	V.A. Bakalin, 27 July 2021
K-24	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′33.62″ N 157°30′35.58″ E	778	Dwarf shrub-low grass tundra with many snowbed habitats	V.A. Bakalin, 29 July 2021
K-25	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′07.26″ N 157°29′39.32″ E	782	Dwarf shrub-low grass tundra with many snowbed habitats	V.A. Bakalin, 29 July 2021
K-26	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′00.62″ N 157°28′57.51″ E	825	Cliffs in the caldera bank on its western slope, N-facing cliffs with stream and snowbeds	V.A. Bakalin, 29 July 2021
K-27	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′00.62″ N 157°28′57.51″ E	825	Cliffs in the caldera bank on its eastern slope, N-facing cliffs	V.A. Bakalin, 29 July 2021
K-28	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′00.16″ N 157°28′28.37″ E	928	Scattered tundroid vegetation with scoria fields	V.A. Bakalin, 29 July 2021
K-29	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′07.15″ N 157°28′48.62″ E	904	Vertical N-facing cliffs	V.A. Bakalin, 29 July 2021
K-30	Ksudach Mts. (Ksudach Volcano Caldera), its western fringe	51°48′20.41″ N 157°28′33.39″ E	963	Hummocky tundra	V.A. Bakalin, 29 July 2021
K-31	Ksudach Mts. (Ksudach Volcano Caldera), "Paryashchy Greben" Ridge	51°48′30.65″ N 157°30′52.27″ E	830	Alpine heathland with many solfatara	V.A. Bakalin, 30 July 2021
K-32	Pravaya Khodutka River upper course	52°07′02.8″ N 157°39′26.7″ E	249	Floodplain *Salix* forest with tall grass cover	V.A. Bakalin & K.G. Klimova, 2 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-33	Pravaya Khodutka River upper course	52°08′10.9″ N 157°42′03.7″ E	252	Floodplain *Salix* forest with tall grass cover	V.A. Bakalin & K.G. Klimova, 2 August 2021
K-34, Kam-133	Pravaya Khodutka River upper course	52°08′03.1″ N 157°42′01.0″ E	253	Sedge-grass mire in the river floodplain	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 2 August 2021
K-35	Pravaya Khodutka River upper course	52°07′04.3″ N 157°39′28.9″ E	244	*Salix* floodplain forest	V.A. Bakalin & K.G. Klimova, 2 August 2021
K-36	Pravaya Khodutka River upper course	52°06′27.3″ N 157°39′20.5″ E	246	*Betula ermanii* forest in the river valley	V.A. Bakalin & K.G. Klimova, 2 August 2021
K-37	Pravaya Khodutka River upper course	52°06′27.3″ N 157°39′31.5″ E	242	Thermal pools near hot springs	V.A. Bakalin & K.G. Klimova, 2 August 2021
K-38	Foot of Priyomysh Volcano	52°05′35.0″ N 157°39′46.8″ E	340	*Betula ermanii* crooked forest	V.A. Bakalin & K.G. Klimova, 3 August 2021
K-39, Kam-134	Saddle between Priyomysh and Khodutka Volcanoes	52°04′51.3″ N 157°41′23.5″ E	1001	Dwarf shrub-low grass tundra on flat surface with many boulders and open cliffs	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 3 August 2021
K-40	Gentle N-facing slope of Khodutka Volcano	52°04′49.8″ N 157°41′35.9″ E	996	Low dwarf shrub-moss tundra	V.A. Bakalin & K.G. Klimova, 4 August 2021
K-41, Kam-140	N-facing slope of Khodutka Volcano	52°04′25.0″ N 157°42′01.9″ E	1383	Scattered vegetation surrounded by scoria fields and rocky outcrops	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 4 August 2021
K-42, Kam-141	N-facing slope of Khodutka Volcano	52°04′20.9″ N 157°42′06.4″ E	1484	Scoria fields with clinker boulders and cliffs	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 4 August 2021
K-43, Kam-142	N-facing slope of Khodutka Volcano	52°04′12.1″ N 157°42′11.5″ E	1665	Scoria fields with clinker boulders and cliffs	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 4 August 2021
K-44, Kam-143	Khodutka Volcano crater crown	52°04′04.6″ N 157°42′14.9″ E	1813	Cliffs along crater rim	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 4 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-45	Saddle between Priyomysh and Khodutka Volcanoes	52°04′51.3″ N 157°41′23.5″ E	1001	Dwarf shrub-low grass tundra on gentle slope with many boulders and open cliffs	V.A. Bakalin & K.G. Klimova, 4 August 2021
K-46	S-facing slope of Priyomysh Volcano	52°05′00.2″ N 157°41′21.0″ E	1129	Dwarf shrub tundra on steep slope with many boulders and cliffs	V.A. Bakalin & K.G. Klimova, 5 August 2021
K-47	S-facing slope of Priyomysh Volcano	52°05′02.6″ N 157°41′20.4″ E	1176	Dwarf shrub tundra on steep slope with many boulders and cliffs	V.A. Bakalin & K.G. Klimova, 5 August 2021
K-48	Subapical part of Priyomysh Volcano	52°05′06.5″ N 157°41′17.2″ E	1213	Large block stony field	V.A. Bakalin & K.G. Klimova, 5 August 2021
K-49, Kam-135	Steep N-facing rocky slope of Priyomysh Volcano	52°05′03.8″ N 157°41′00.4″ E	1130	Large cliffs	V.A. Bakalin & K.G. Klimova;K.G. Klimova & V.A. Bakalin, 5 August 2021
K-50, Kam-136	Lower part of N-facing slope of Priyomysh Volcano	52°05′33.6″ N 157°39′58.2″ E	404	*Betula ermanii-Alnus fruticosa* crooked forest with tufa cliffs near temporary stream	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 5 August 2021
Kam-144	Lower part of N-facing slope of Priyomysh Volcano	52°05′33.6″ N 157°39′58.2″ E	404	*Betula ermanii-Alnus fruticosa* crooked forest with N- and W-facing rocks near temporary stream	K.G. Klimova & V.A. Bakalin, 5, 6 August 2021
K-51	Lower part of N-facing slope of Priyomysh Volcano	52°06′07.3″ N 157°39′41.0″ E	262	*Betula ermanii-Alnus fruticosa* crooked forest with tufa cliffs near temporary stream	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin5 August 2021
Kam-137	Lower part of NW-facing slope of Priyomysh Volcano	52°05′55.1″ N 157°39′39.7″ E	264	Deep hole in *Betula ermanii* forest	K.G. Klimova & V.A. Bakalin, 6 August 2021
Kam-138	Nameless lake at the bottom of NW-facing slope of Priyomysh Volcano	52°05′55.2″ N 157°39′35.7″ E	273	*Salix* forest at the lake bank	K.G. Klimova & V.A. Bakalin, 6 August 2021
Kam-139	Lower part of NW-facing slope of Priyomysh Volcano	52°05′35.0″ N 157°39′46.8″ E	340	*Betula ermanii-Alnus fruticosa* crooked forest, narrow rocky valley of temporary stream	K.G. Klimova & V.A. Bakalin, 3 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
Kam-139	Lower part of NW-facing slope of Priyomysh Volcano	52°05′35.0″ N 157°39′46.8″ E	340	Narrow rocky valley of temporary stream surrounded by *Betula ermanii-Alnus fruticosa* crooked forest	K.G. Klimova & V.A. Bakalin, 6 August 2021
K-52	Pravaya Khodutka River upper course	52°06′27.3″ N 157°39′31.5″ E	242	Area near Khodutkinskie Hot Springs, thermal grass-moss community	V.A. Bakalin & K.G. Klimova, 7 August 2021
K-53. Kam-145	Asacha River lower course, the left side of the valley	52°11′11.6″ N 158°12′24.8″ E	15	*Pinus pumila* thickets under scattered *Betula ermanii* canopy	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 8 August 2021
K-54, Kam-146	Asacha River lower course, the left side of the valley	52°11′23.3″ N 158°12′33.6″ E	17	Complex swampy massif with many small lakes (large ponds), its western end	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 8 August 2021
K-55	Asacha River lower course, the left side of the valley	52°11′36.0″ N 158°13′15.2″ E	13	Complex swampy massif with many small lakes (large ponds), its middle part	V.A. Bakalin & K.G. Klimova, 8 August 2021
K-56, Kam-147	Asacha River lower course, the left side of the valley	52°11′24.6″ N 158°13′52.2″ E	14	Complex swampy massif with many small lakes (large ponds), its eastern end	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 8 August 2021
Kam-148	Asacha River lower course, Asacha River flood plain	52°12′03.3″ N 158°10′26.1″ E	18	Small stream in thickets of *Filipendula camtschatica, Heracleum lanatum, Cirsium kamtschaticum*	K.G. Klimova & V.A. Bakalin, 10 August 2021
K-57, Kam-149	Asacha River lower course, area near Asacha Hot Springs	52°12′05.1″ N 158°10′20.6″ E	19	*Betula ermanii-Alnus hirsuta* forest in river valley around hot springs openings	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 10 August 2021
Kam-150	Asacha River lower course	52°11′54.2″ N 158°10′44.1″ E	21	*Betula ermanii* forest with tall grass cover	K.G. Klimova & V.A. Bakalin, 10 August 2021
K-58, Kam-151	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, watershed between Osvistannaya River and Falshivaya River	52°29′47.2″ N 158°09′39.0″ E	1182	The source of small stream on NE-facing slope to Falshivaya River in scoria field	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 12 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-59, Kam-152	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, watershed between Osvistannaya River and Falshivaya River	52°29′37.2″ N 158°10′16.1″ E	1185	The source of small stream on NE-facing slope to Falshivaya River in scoria field	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 12 August 2021
K-60, Kam-153	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, watershed between Osvistannaya River and Falshivaya River	52°29′32.9″ N 158°11′27.9″ E	1153	The source of small stream on NE-facing slope to Falshivaya River in scoria field	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 12 August 2021
K-61	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, watershed between Neozhidannyi Stream and Falshivaya River	52°29′29.05″ N 158°10′55.22″ E	1181	The source of small stream on NE-facing slope to Falshivaya River in scoria field.	V.A. Bakalin & K.G. Klimova, 12 August 2021
K-62, Kam-154	Mutnovskaya Sopka Volcano environs, the foot of NE-facing slope of the volcano, Falshivaya River upper reaches	52°29′41.7″ N 158°11′32.9″ E	1098	Hydrothermal field with streams and fumaroles	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 12 August 2021
K-63, Kam-155	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, Falshivaya River upper reaches	52°29′52.8″ N 158°10′49.3″ E	1072	Small stream upper source	V.A. Bakalin & K.G. Klimova, 12 August 2021
K-64	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, Falshivaya River upper reaches	52°29′52.8″ N 158°10′49.3″ E	1072	Large hydrothermal field with fumaroles	V.A. Bakalin & K.G. Klimova, 12 August 2021
K-65	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, Falshivaya River upper reaches	52°30′18.06″ N 158°10′10.32″ E	1056	Old road on gentle E-facing slope	V.A. Bakalin & K.G. Klimova, 12 August 2021
K-66, Kam-156	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, Falshivaya River upper reaches	52°29′58.1″ N 158°10′22.8″ E	1113	Large fumarole field	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 12 August 2021
K-67	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, the watershed between Falshivaya River and Osvistannaya River	52°30′00.84″ N 158°09′15.83″ E	1178	Hummocky tundra with solifluction spots	V.A. Bakalin & K.G. Klimova, 12 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-68, Kam-157	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River	52°30′05.7″ N 158°07′56.8″ E	994	Tundra in small stream upper reaches near snowbed	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 14 August 2021
K-69	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River, N-facing slope of Pemzovaya Mt.	52°29′43.09″ N 158°07′44.96″ E	1018	Small range composed by white pumice deposits	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-70	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River, N-facing slope of Pemzovaya Mt.	52°29′37.90″ N 158°07′45.12″ E	1043	Small range composed by white pumice deposits	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-71, Kam-158	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River, top of Pemzovaya Mt.	52°29′32.4″ N 158°07′41.5″ E	1061	Small range composed by white pumice deposits	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin, 14 August 2021
K-72	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River, Pemzovaya Mt. area	52°29′35.27″ N 158°08′06.72″ E	1096	Small range composed by white pumice deposits. Metamorphic conglomerate.	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-73	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River, Pemzovaya Mt. area	52°29′43.95″ N 158°08′22.23″ E	1116	Small range composed by white pumice deposits	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-74	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, upper reaches of Osvistannaya River	52°30′00.09″ N 158°09′00.46″ E	1130	Small stream in hummocky tundra	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-75	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, the pass from Osvistannaya River to Falshivaya River	52°30′00.84″ N 158°09′15.83″ E	1178	Hummocky tundra with solifluction spots	V.A. Bakalin & K.G. Klimova, 14 August 2021
K-76	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, the watershed between Osvistannaya River and Falshivaya River	52°29′44.43″ N 158°09′20.98″ E	1229	Hummocky tundra on gentle slope	V.A. Bakalin & K.G. Klimova, 15 August 2021

Table 1. *Cont.*

Locality Number	Geographic Description	Coordinates	Elevation above Sea Level, m	Community	Collectors, Collection Data
K-77, Kam-159	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, the watershed between Osvistannaya River and Falshivaya River, ridge of Otkhodyashchy Range	52°29′22.91″ N 158°09′31.69″ E	1357	Hummocky tundra on steep slope N-facing rocky outcrops surrounded by dwarf shrub-forb tundra on steep slope	V.A. Bakalin & K.G. Klimova, 15 August 2021 K.G. Klimova & V.A. Bakalin, 15 August 2021
K-78, Kam-160	Mutnovskaya Sopka Volcano environs, the foot of N-facing slope of the volcano, the watershed between Osvistannyi Stream and Falshivaya River, ridge of Otkhodyashchy Range	52°29′12.5″ N 158°09′31.9″ E	1516	NW-facing cliffs	V.A. Bakalin & K.G. Klimova; K.G. Klimova & V.A. Bakalin 15 August 2021
K-79	Mutnovskaya Sopka Volcano environs, the watershed between Osvistannyi Stream and Falshivaya River, ridge of Otkhodyashchy Range, "Zhandarm" outlier	52°29′07.08″ N 158°09′35.24″ E	1595	W-facing cliffs in old clinker	V.A. Bakalin & K.G. Klimova 15 August 2021
K-80	Mutnovskaya Sopka Volcano environs, upper course of Falshivaya River	52°30′45.59″ N 158°09′50.67″ E	1045	Hummocky tundra on gentle slope	V.A. Bakalin & K.G. Klimova, 15 August 2021
K-81	Mutnovskaya Sopka Volcano environs, upper course of Falshivaya River	52°31′50.03″ N 158°11′33.90″ E	795	Dachnye Hot Springs environs	V.A. Bakalin & K.G. Klimova 15 August 2021
K-82	Mutnovskaya Sopka Volcano environs, upper course of Falshivaya River	52°32′07.51″ N 158°11′52.54″ E	784	Medvezhie Hot Springs environs	V.A. Bakalin & K.G. Klimova 15 August 2021

All liverwort specimens were delivered alive to the park office; these specimens were then frozen and subsequently transported to Vladivostok to VBGI, where the material was analyzed by V.A.B. and K.G.K. The "shock" nature of freezing led to the death of approximately half of the material, and oil bodies were not preserved in that part of the material. Thus, oil body data are available for only half of the material collected. However, the general appearance of plants (although in some cases they were dead but remained well hydrated) was photographed for approximately 80% of the collected taxa.

Territorially, all visited sites (Table 1) could be subdivided into five clusters selected before the start of this study, considering the interests of all expedition participants and, therefore, being a kind of quintessence of the multidirectional vectors of interests of different specialists. These clusters (Figure 1, interactive version at https://hepaticae.ru/south-kamchatka-nature-park/) are as follows:

1. The middle course of the Zhyoltaya River (K-6 ... K-10); Zheltovskaya Sopka Volcano and one point on the coast at the mouth of the Zhyoltaya River (K-11 ... K-18);
2. Ksudach Mts. (Ksudach Volcano caldera) (K-19 ... K-31);
3. Volcanoes Khodutka, Priyomysh and Khodutkinskie Hot Springs (K-32 ... K-52, Kam-133 ... Kam-144);
4. Lower reaches of the Asacha River (K-53 ... K-57, Kam-145 ... Kam-150);
5. Surroundings of the Mutnovskaya Sopka Volcano (K-58 ... K-82, Kam-151 ... Kam-160).

The diversity of natural communities varied from cluster to cluster, as discussed below.

2.1. Study Area

2.1.1. Landscapes

Shield glaciations in the second half of the Pleistocene were absent in South Kamchatka Nature Park [1], although a number of volcanoes (Zheltovskaya Sopka, Khodutka, Mutnovskaya Sopka) had extensive mountain-valley glaciations with clearly defined terminal moraine complexes (especially in the area of Khodutka Volcano). Some valleys on the east coast were filled with glaciers during the Sartan glaciation (contemporary to the Würm 2 stage in West Europe). Hulten [1] specifically underlines Russkaya Bay glaciation, stating the presence of large glaciers in that bay during the last glaciation.

There are no granite outcrops in the park; the lithology is neutral andesites and basalts [1]. The soil in all cases is represented by volcanic ash overlying partially formed and buried soils in layers of varying thicknesses (depending on the proximity to the volcano eruption center). The size of the particles and chemical composition are also identified by their proximity to the eruption center.

The studied volcanoes (Zheltovskaya Sopka, Mutnovskaya Sopka, Khodutka) are stratovolcanoes and predominantly Quaternary structures. Priyomysh Volcano is considered an older volcano than the other volcanoes visited in the current research.

Khodutka Volcano was active in the Holocene. Approximately 2900 years ago, at the foot of the volcano, there was a powerful eruption with a product volume of 1–1.5 km^3, during which the Khodutkinsky maar crater was formed. The last large eruption of the volcano itself took place 2000–2500 years ago, when a lava flow erupted from its central crater [7].

The origin of the Ksudach Volcano took place at the boundary of the early and middle Pleistocene and continued in four stages. Each stage was accompanied by powerful explosive activity that resulted in the formation of calderas. The most active explosive event, which resulted in the formation of calderas and the release of a large amount of pumice material, was observed during the third stage. There were 6–7 large eruptions that released a large amount of pyroclastics at intervals between 8800 and 1700 years ago. A powerful pyroclastic cover was formed and approximately four calderas that overlapped each other were formed. During the final stages, areal volcanism manifested itself in the form of scoria cones with lava flows and extrusions of a different nature. The beginning of the fourth stage was characterized by the deposition of a significant amount of pumice on the bottom of the calderas and in the river valleys on the slopes of the volcano. The last large eruption noted by Hulten [1], taking place in 1907, originated from the Stübel cone. The cone began to form 1400 years ago in the southwestern part of the caldera. To date, its height was determined to reach 77 m above the caldera bottom. Dacitic extrusion is observed at the northeastern foot. The powerful eruption from the Stübel crater was as follows: at its bottom, an explosion funnel 1 × 1.7 km in size was formed. Then, in the north, outside the volcano, a thick cover of pumice deposits (4–5 m) was formed. The crater depression turned into the Stübel Bay of Klyuchevoe Lake. The eruption ended in a powerful phreatic explosion, with the ejection of pumice stones with numerous inclusions of fragments such as olivalites and eucarites (olivine-pyroxene-plagioclase formations). Ashes from this eruption can be traced more than 200 km to the north. Therefore, before the 1907 eruption, there was no crater here. At the beginning of the eruption, its dome was blown off, crushed, and ejected at an angle of 30–40° to the horizon directly to the north. Its volume was 0.5–1.0 km^3 [8,9]. The ejection of the large masses of the material directly to the north has essential value for the presumable survival of the communities in the "Paryashchy Greben" Ridge fumaroles, one of the taxonomic diversity hot spots in South Kamchatka Nature Park. The same could be said as the reason for the well condition and pronounced diversity of the mountain tundra in the western end of Ksudach Caldera: they were also not (or only slightly) damaged by the last catastrophic eruption.

Zheltovskaya Sopka is a rather poorly studied volcano. It is a composite edifice and consists of a large volcano-pedestal crowned with Late Pleistocene caldera, which encloses Late Pleistocene stratovolcano topped with several Holocene extrusive domes. Pumice tufa is presumably related to the Late Pleistocene caldera that is exposed east of the volcano. White pumice from the Holocene Kurile Lake caldera eruption covers the slopes of the volcano; ignimbrite from this eruption fills the valley between the Zheltovskaya Sopka and Ilyinskaya Sopka volcanoes.

During the Holocene, several extrusive domes formed in the summit part of the volcano, each sending a mantle of debris downslope. In addition, several explosive eruptions of Zheltovskaya Sopka are known to have occurred: one of them occurred between 3 and 4 thousand years BP and produced black cinders of basaltic andesite composition; another produced a large andesitic block-and-ash flow and minor fallout ca. 500 years BP and, finally, one of the most recent large eruptions presumably occurred in the 19th century and produced a fallout consisting of heavy subrounded basaltic lapilli rich in allivalite and eucrite inclusions. Both latest eruptions caused large lahars, which moved toward the Pacific coast. The Holocene products of the Zheltovskaya Sopka are low-potassium basalts-andesites. Within the 20th century, a rather small volcanic eruption was observed in 1923, when a small lava flow poured into the crater and onto the southwestern slope. In 1972–1973, fumaroles activity was observed in the crater at the western foot of the extrusive dome. Now, this volcano does not show evident activity [8,10,11].

2.1.2. Climate

In general, the climate of South Kamchatka Park is suboceanic, with mild winters and cool summers. The growing season is very short. Heavy snowmelt at lower elevations usually occurs in early June, although large areas are covered with snow in the mountains above 700–900 m above sea level in July. For example, at 800 m a.s.l., in open areas on the slope of Gorely Volcano (neighboring to Mutnovskaya Sopka Volcano), the first flowers of early flowering *Campanula lasiocarpa* Cham. and *Artemisia arctica* Less. were observed [1] on July 2. The level of snowfall reaches the maximum values for Pacific Asia in the coastal areas of South-East Kamchatka [12]. The small latitudinal extent of the study area (between the extreme points from south to north slightly more than 120 km) does not imply significant climate change of latitudinal origin. However, local fluctuations in climatic indicators, depending on the relief elements, are very prominent. We have determined a number of bioclimates as key points of the study area using the WorldClim database (https://www.worldclim.org/data/bioclim.html). The obtained data are in Table S1, with the abbreviations placed at the end of the paper:

As seen from Table S1, the variation in all bioclimates is associated not with the latitudinal position of the study area but with the height above sea level and remoteness from the seacoast. The average annual temperature is the highest in the middle course of the Ilyinskaya River (+2.11 °C). When moving up the mountains, the average annual temperature becomes negative (approximately from heights exceeding 300 m above sea level, although in the valley of the Asacha River, it is already negative almost at sea level, at 17 m a.s.l.), reaching −4.8 °C on the southern peak of the Zheltovskaya Sopka Volcano (1963 m above sea level). The average temperature of the warmest quarter can be +9 . . . +11 °C in the floodplains, while on the peaks and in the subapical areas in the mountains, it is only +3 . . . +7 °C. The average temperatures of the coldest quarter show a similar trend: from −6 °C in the floodplains to −10 . . . −12 °C in the upper belts. The average annual precipitation increases markedly with height, from 900 mm in the floodplains to 1100 mm near the peaks. The same pattern is observed in the total precipitation of both the warmest and coldest quarters. In fact, the plants are physiologically active within the three warmest months, which deal with 250 to 335 mm of precipitation (the rainfall amount gradually increases toward the summits). These precipitation general indicators are locally superimposed by the redistribution of snow due to elements of micro- and meso-relief, as well as varying degrees of availability (due to the drainage abilities of the substrates) of winter snow precipitation, which are converted into liquid water throughout the summer growing season.

2.1.3. Vegetation

The first valuable review of the landscapes in South Kamchatka, with a mention of the main vegetation communities, was provided by Hulten [2]. He [2] (l.c.: 331) distinguished four main landscape types, of which two belong to South Kamchatka Nature Park: "the eastern dissected coastland" and "the central tableland with volcanoes". Noticeably, most of the length of the Hulten routes in 1920–1922 (the basis for cited work) are precisely in the territory of the current South Kamchatka Nature Park.

More than fifty years later, Hulten [1] published a special paper regarding the vegetation features in South Kamchatka (southward of 53-th latitude). Approximately one-third of the eastern part of South Kamchatka (as it was treated by Hulten) belongs to the current South Kamchatka Nature Park. Moreover, this is an area that Hulten personally studied the most. He treated the vegetation as possessing a hemiarctic appearance ("subarctic" in Hulten [1] (p. 188). Hulten [1] (p. 185) also stressed that "the uniform soil is one of the reasons for the unusually constant and stabilized composition of the plant communities". There is an agreement that certain deviations from the general appearance and composition of communities that we observe are due to small local fluctuations and local causes (e.g., springs of thermal waters).

Subsequently, the general data on the vegetation of South Kamchatka Nature Park are provided in a number of monographs and journal articles devoted to the vegetation of Kamchatka [13,14], although the most striking and useful for visitors of South Kamchatka Nature Park is still the paper by Hulten [1].

Apparently, the first study using mathematical methods to generalize data and calculate the potential nature characteristics and composition of vegetation using bioclimatic indices was conducted by Krestov et al. [12]. The main vegetation types, following the map (based mostly on [15]) provided in the paper, are as follows: *Pinus pumila* (Pall.) Regel thickets, *Betula ermanii* Cham. forests, *Alnus fruticosa* Rupr. thickets and alpine tundra. Floodplain forests are not expressed on the scale of the presented map. The altitudinal belts of South Kamchatka, in its most general form from top to bottom, are as follows [12] (p. 202): 1—plantless belt, 2—alpine tundra, 3—*Pinus pumila*, 4—*Betula ermanii*. It is worth mentioning that the "plantless belt", stretching 1000–1300 m above sea level, can be characterized by the almost complete absence of vascular plants (although Hulten, 1974 notes several species reaching 1600 m above sea level); however, they possess peculiar and species-rich liverwort flora, where liverworts are abundant in microniches. The "plantless belt" was also mentioned before by Krestov et al. [12]. Hulten [1] (p. 182) in his summary, noted that "the volcanic cones along the eastern coast are completely barren of vegetation". Hulten [12] (p. 189) subdivided altitudinal zonality into three widely treated belts: "the lowland zone, alder belt and the alpine, treeless zone". The general features of the vegetation cover of the South Kamchatka Nature Park are also described in the "Flora" section in the site devoted to the South Kamchatka Nature Park of the park's consortium "Volcanoes of Kamchatka" [16].

Generally, the vegetation of South Kamchatka Nature Park develops under a significant variation in altitude (from sea level to 2000 m above sea level), winter reallocation of snow, mountain peak interception of humidity from the Pacific Ocean and the significant influence of volcanic processes (taking place in the present and in prehistorical retrospective). The latter factor is especially obvious above 1000–1200 m above sea level (although often even at lower altitudes), where fresh deposits of pyroclastics, often with extremely high drainage abilities as a substrate, make it extremely difficult for plants to survive. All four listed factors impacted the bryophyte formation. The large snowfields and even permanent glaciers do not lead to the formation (at least in the places we visited) of extended nival (snowbed) communities above the mountain tundra belt, since all the liquid water provided from melting snow is often instantly absorbed by the substrate and does not lead to the formation waterlogged places for a sufficiently long period (necessary for the passage of the growing season).

Of course, for such a group as the liverworts, whose representatives are confined to various kinds of microniches, the distribution of the main vegetation formations says little about the potential species composition. The contradiction between the "external appearance" of communities and the species composition of bryophytes was recently illustrated by the example of the bryoflora of Northern Iturup [17], where the "northern", almost hemiarctic appearance of communities possess hemiboreal, with the large presence of temperate, taxa and bryophyte flora. The main types of vegetation visited by us and from which the liverworts were collected are described below in the order of top to bottom. The descriptions of intrazonal communities are added afterward. The typical landscapes and communities are provided in Figures 2–5.

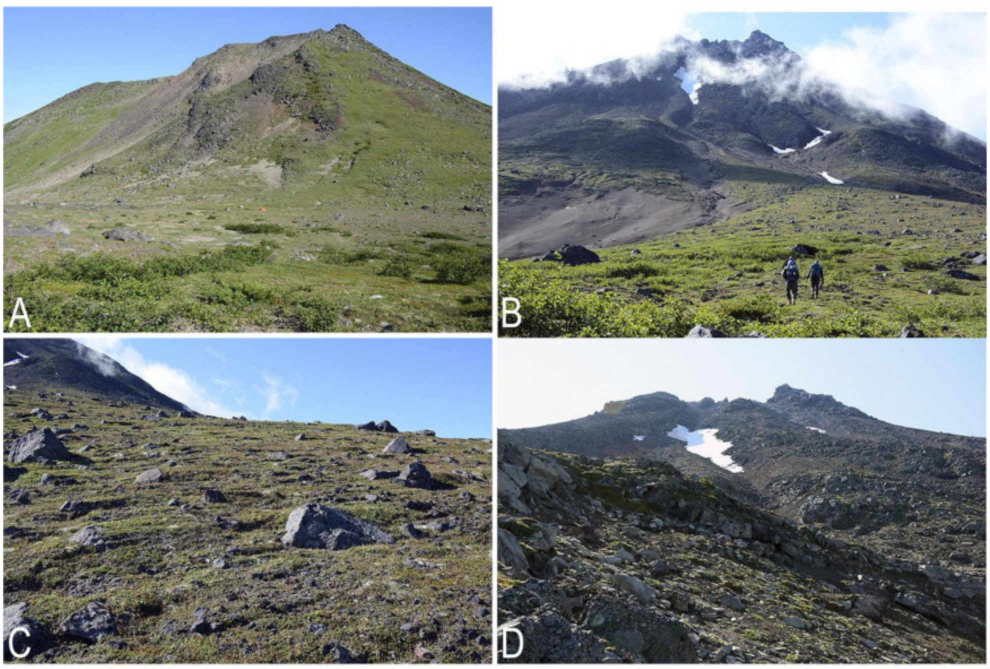

Figure 2. *Cont.*

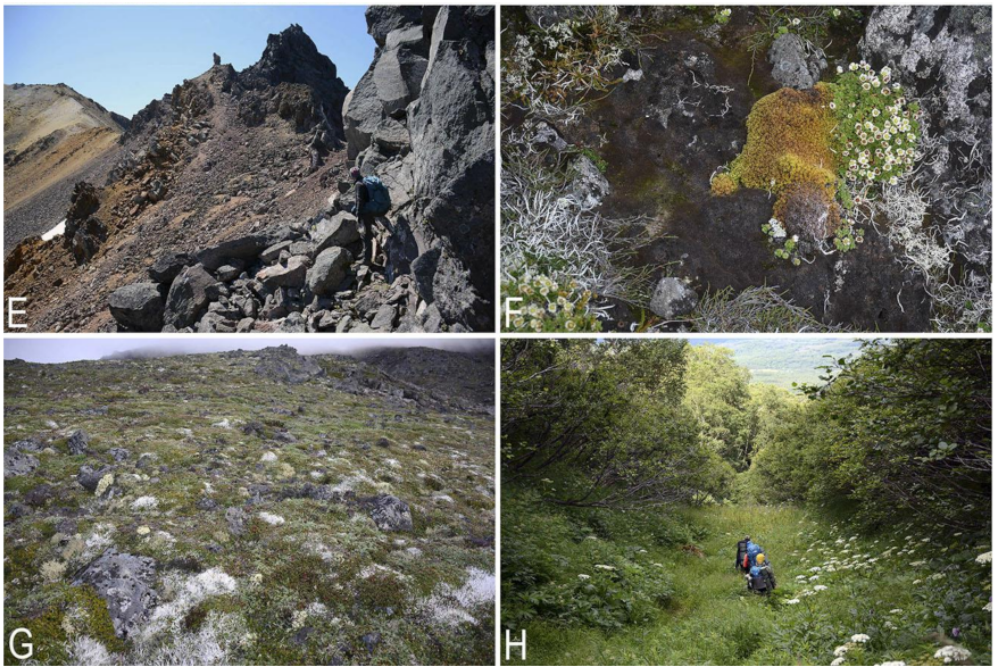

Figure 2. (**A**) S-facing slope of Priyomysh Volcano, dwarf shrub-moss-lichen tundra dominating, *Alnus fruticosa* clumps are in the foreground, 1048 m a.s.l. (**B**) the foot of NW-facing slope of Khodutka Volcano, dwarf *Alnus fruticosa* clumps are in the foreground, that changed by dwarf shrub-lichen-moss tundra and pyroclastic deserts above, 1048 m a.s.l. NW-facing slope of Khodutka Volcano: (**C**) dwarf shrub-lichen tundra with rocky outcrops, 1085 m a.s.l.; (**D**) scattered vegetation on pyroclastic deposits, 1256 m a.s.l.; (**E**) north edge of Khodutka Volcano crater crown, 1813 m a.s.l.; (**F**) *Gymnomitrion kamchaticum* dominating patch, 1654 m a.s.l.; (**G**) dwarf shrub-lichen tundra with rocky outcrops, 1225 m a.s.l. (**H**) *Alnus fruticosa* vegetation belt near the border of *Betula ermanii* forest belt on NW-facing slope of Priyomysh Volcano, 430 m a.s.l. (Photo by K.G. Klimova, 2021).

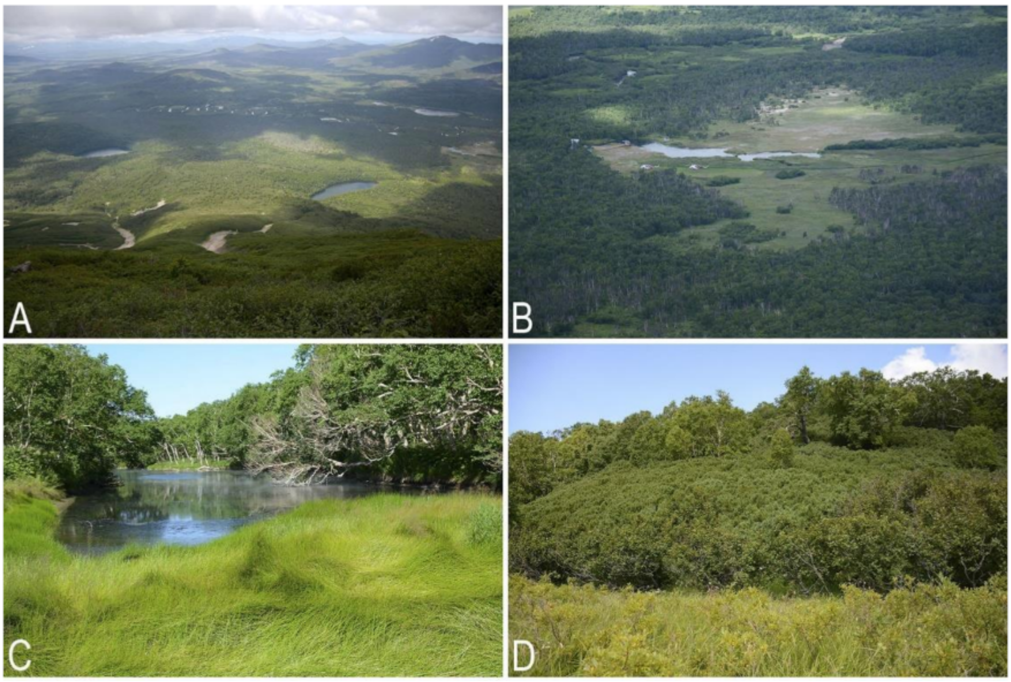

Figure 3. *Cont.*

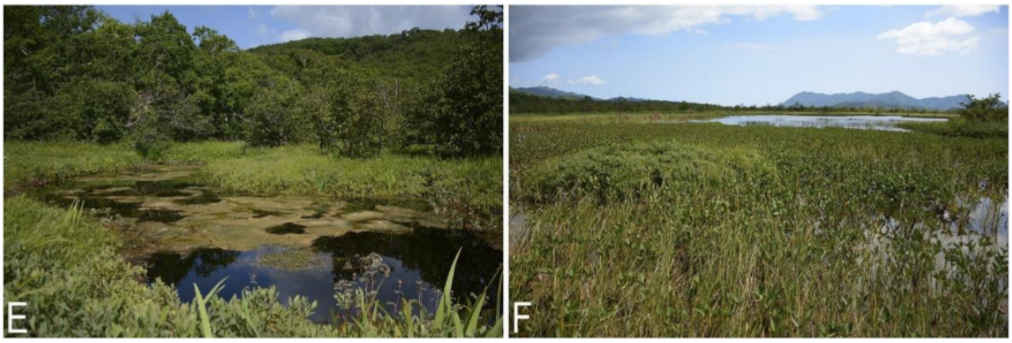

Figure 3. (**A**) view of the Pravaya Khodutka River valley from Priyomysh Volcano (975 m a.s.l.), *Alnus fruticosa* thickets belt with rare *Pinus pumila* clumps are in the foreground, *Betula ermanii* forest is dominating in river valley in the background, grass land in the bottom; (**B**) view of the Khodutkinskie Hot Springs from Priyomysh Volcano (975 m a.s.l.), thermal fields near the river surrounded by *Betula ermanii* forest, open places are occupied by tall herbs (*Filipendula camtschatica*, *Senecio cannabifolius*, *Heracleum lanatum*); (**C**) Khodutkinskie Hot Springs area, *Equisetum fluviatile* community is in the foreground; (**D**) swampy *Salix* thickets in foreground, changed for *Alnus fruticosa* and then for *Betula ermanii*, lower course of Asacha River, 13 m a.s.l.; (**E**) the pond in swampy massif, surrounded by *Betula platyphylla*, *Myrica tomentosa* is in the foreground, lower course of Asacha River, 13 m a.s.l.; (**F**) rich fen with *Menyanthes trifoliata* dominating, lower course of Asacha River (Photo by K.G. Klimova, 2021).

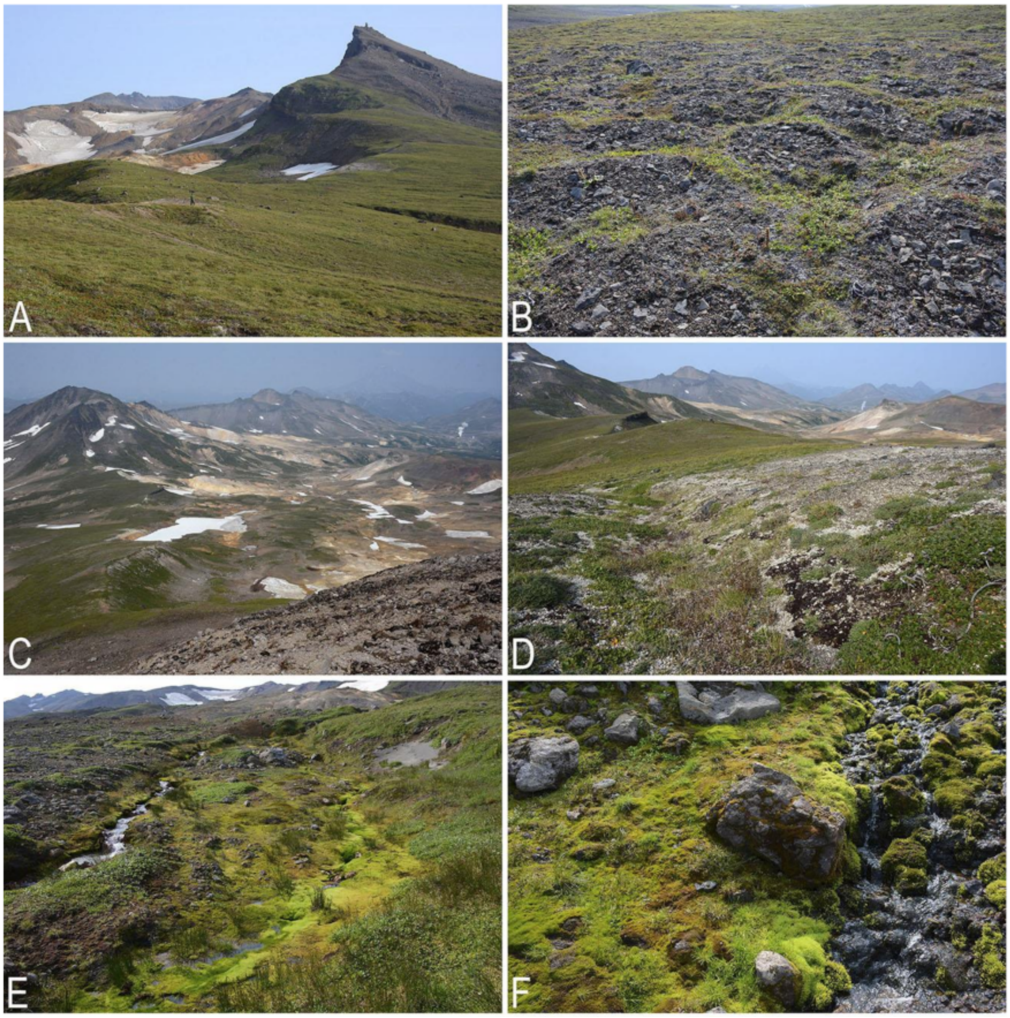

Figure 4. *Cont.*

Figure 4. The foot of N-facing slope of Mutnovskaya Sopka Volcano, watershed between Osvistannaya River and Falshivaya River, 1173 m a.s.l.: (**A**) dwarf shrub-lichen-moss tundra, view of the Otkhodyaschy Range; (**B**) solifluction spots with scattered patches of dwarf shrub-lichen tundra. (**C**) view of the Sopka Dvugorbaya Mt. and sulfurous thermal fields from the Otkhodyaschy Range, 1559 m a.s.l.; (**D**) dwarf shrub-lichen tundra and solifluction spots, dark patches are formed by *Nardia braidlerii*, 1209 m a.s.l. The foot of N-facing slope of Mutnovskaya Sopka Volcano, Falshivaya River basin: (**E**) upper reaches of small stream, a habitat for *Lophozia*, *Scapania* and *Marsupella*, 1185 m a.s.l.; (**F**) stream bank, *Schistochilopsis* and *Pseudolophozia* are occurring here, 1173 m a.s.l.; (**G**) sulfurous thermal field, 1095 m a.s.l.; (**H**) dark patch is formed by *Plectocolea vulcanicola* framing the sulfurous thermal field, 1095 m a.s.l. (Photo by K.G. Klimova, 2021).

Figure 5. *Cont*.

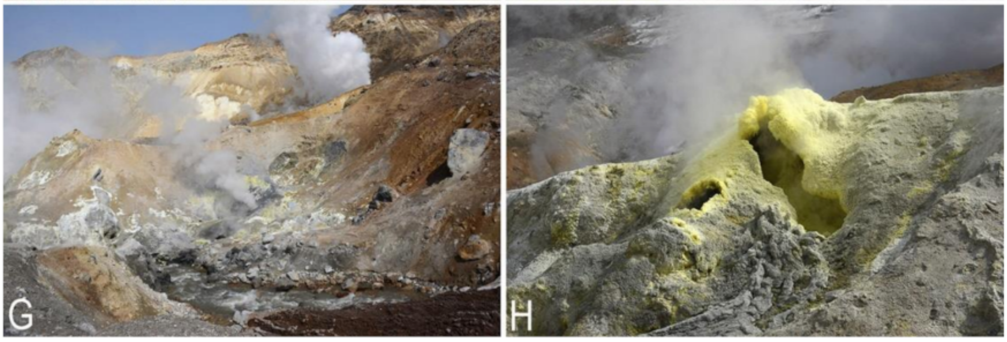

Figure 5. The foot of N-facing slope of Mutnovskaya Sopka Volcano, Falshivaya River basin: (**A**) *Marsupella sphacelata* is dominating here, 1110 m a.s.l.; (**B**) *Plectocolea vulcanicola* on sulfurous strata, 1110 m a.s.l., (**C**) sulfurous thermal field, 1054 m a.s.l.; (**D**) sulfurous stream on thermal field, *Plectocolea vulcanicola* and *Cladopodiella francisci* on sulphur-rich soil, 1054 m a.s.l.; (**E**) sulfurous thermal field, *Plectocolea vulcanicola*, *Marsupella sphacelata* on the border of the field, 1054 m a.s.l. (**F**) Dachnye Hot Springs, steam is going from fumaroles, 790 m a.s.l.; (**G**,**H**) the crater of Mutnovskaya Sopka Volcano, fumaroles and thermal fields on the border of Mutnovsky Glacier, no liverworts or other plants were found here, 1480 m a.s.l. (Photo by K.G. Klimova, 2021).

(1) Pyroclastic "deserts" of the upper belt. The substrate base is represented by scoria fields, ash deposits in horizontal and flat areas, tufa "rocks" and lava clinkers of a short length. There is no closed vegetation cover and only scattered vascular plants (*Oxytropis*, *Astragalus*, *Artemisia*) occur from site to site. Bryophytes are confined to crevices of tufa rocks and lava clinker, as well as to the banks of occasional small (including temporary) streams. *Cryptocoleopsis imbricata* is recorded here in the crevices (in general, it is confined to volcanically transformed habitats throughout the Kamchatka-Kuril-Japan region). The most frequent here are arctomontane *Anthelia juratzkana*, *Cephaloziella varians*, *Gymnomtrion concinnatum*, *G. corallioides*, *G. pacificum*, *Lophozia savicziae*, *Maruspella apiculata* (the last, along with *Gymnomitrion pacificum*, reach the Khodutka volcano crater crown, 1813 m a.s.l., where other plants are absent), *Marsupella boeckii*, *M. condensata*, *M. sphacelata*, *M. sprucei*, *Nardia breidlerii*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *Scapania hyperborea*, *Tetralophozia setiformis*, and *Gymnomitrion adustum* (the last is very rare in Pacific Asia). This zone is also occasionally inhabited by species with a wider belt distribution: *Barbilophozia hatcherii*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnocolea inflata* (it is noteworthy that this species is not found in the swamps of South Kamchatka Nature Park), *G. marginata*, *Hygrobiella squamosa*, *Jungermannia pumila*, *Lophozia longiflora*, *L. murmanica*, *Nardia geoscyphus*, *N. harae*, *N. japonica*, *N. pacifica*, *Pellia neesiana*, *S. irrigua*, *S. paludosa*, *S. parvifolia*, *Schistochilopsis incisa*, *Solenostoma rossicum*, and *Sphenolobus minutus*. It is difficult to trace the differences in floristic composition between these pyroclastic "deserts" and the mountain tundra belt located below. Undoubtedly, the only rarity of the habitats themselves are that they are suitable for the growth of liverworts. It should be noted that although in a typical case pyroclastic deserts should meet tundra, in reality, this is far from consistently observed, and pyroclastic fields descend lower, in direct contact with crooked forests and even stone birch communities. However, in contact with the latter, these pyroclastic deserts are composed only of scoria and ash and do not contain the species mentioned above. Of course, if volcanic activity is hypothetically removed, this could be considered a temporary phenomenon; however, due to the regularity of volcanic eruptions and the influx of ever-new portions of pyroclastics, such a situation can be indefinitely maintained. The average boundary, above which pyroclastic "deserts" are developed, is at the level of 1100–1200 m above sea level, including the reservations mentioned above.

(2) Mountain tundra of various compositions, commonly with dwarf shrubs and lichen-dwarf shrub types that dominate, are sparse and gradually transition into pyroclastic deserts at the upper boundary, merging into a mosaic of rocky outcrops, tundra and crooked forest communities below. Typical dwarf shrubs common in the cover belong to Ericaceae (*Arctous alpina* (L.) Nied., *Phyllodoce caerulea* (L.) Bab., *Vaccinium vulcanorum* Kom., *Bryanthus gmelinii* D. Don, *Loiseleuria procumbens* (L.) Desv.). *Empetrum nigrum* L. is common in the lower part of this belt but almost completely absent toward its upper limit (coenotically replaced by *Phyllodoce* and *Loiseleuria*); infrequent are *Salix arctica* Pall., *S. reticulata* L. and *Spiraea beauverdiana* C.K. Schneid. Locally, *Rhododendron aureum* Georgi forms tufts with green moss cover underneath. In some places, fruticose lichens (*Cetraria*, *Cladonia* s.l.) dominate, while in more humid places, mosses (*Pleurozium*, *Hylocomium*, *Aulacomnium turgidum* (Wahlenb.) Schwägr., *Rhytidium*, *Dicranum*, etc.) occur. The slopes to the streams, where snow accumulates for an extended period of time, are commonly covered by extended communities of *Rhododendron camtschaticum* Pall. Dwarf shrub-forb communities are frequent, with common *Carex koraginensis* Meinsh., *Saussurea* spp., *Anemone*, *Agrostis borealis* Hartm., and *Viola langsdorfii* Fisch. ex Ging., *Trollius*, *Artemisia arctica* Less., *Deschampsia* spp., *Pedicularis* spp. In the same belt, the snowbed habitats (a rarity in pyroclastic "deserts") and other waterlogged areas are common; sometimes they look like patches of moss tundra (they do not form large extended communities). The largest number of liverwort species is found along the edges of bare ground spots (including those of solifluction origin), stream banks, and wet rock crevices. The taxonomic diversity of the liverworts of this belt is the greatest in comparison with the rest: arctomontane *Anthelia juratzkana*, *Cryptocoleopsis imbricata*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. corallioides*, *G. kamchaticum*, *G. pacificum*, *Lophozia heteromorpha*, *L. murmanica*, *L. savicziae*, *L. schusteriana*, *Marsupella apiculata*, *M. boeckii*, *M. condensata*, *M. spruce*, *Pleurocladula albescens*, *Pseudolophozia debiliformis* and *Pseudolophozia sudetica* are common, while *Scapania obcordata* is a rarity. Altitudinally more widespread taxa also occur here: *Barbilophozia hatcherii*, *Blepharostoma neglectum*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Cephaloziella divaricata*, *Diplophyllum albicans*, *D. sibiricum*, *D. taxifolium*, *Douinia plicata* (one of the few participants in the formation of the mats with large green mosses), *Fuscocephaloziopsis pleniceps*, *Gymnocolea inflata*, *G. marginata* (both of which are confined to the rock crevices), *Isopaches bicrenatus*, *Lophozia longiflora*, *Marsupella apertifolia*, *M. subemarginata*, *Nardia breidlerii*, *N. geoscyphus*, *N. harae*, *N. insecta*, *N. japonica*, *N. pacifica*, *Ptilidium ciliare*, *Scapania mucronata*, *S. praetervisa*, *Schistochilopsis incisa*, *Solenostoma hyalinum*, *S. rossicum*, *S. subellipticum*, *Sphenolobus minutus*, *Trilophozia quinquedentate* and *Jungermannia eucordifolia*. Other taxa, such as *Pellia neesiana*, *Scapania irrigua*, *S. subalpine* and *Schistochilopsis pacifica,* are limited by stream banks and are rare. *Calypogeia sphagnicola* was found on *Sphagnum* tuft. The average altitudinal limits of this belt extend from 800 to 1100 m a.s.l. (data on both limits are very approximate).

(3) Crooked forest belt. The leading position here is occupied by *Alnus fruticosa*, while another dominant of hemiarctic Pacific Asia, *Pinus pumila*, does not form communities for extended areas. The cover is dominated by forbs (especially the grass *Calamagrostis langsdorffii* (Link) Trin.) and less often by mosses (*Pleurozium*, *Hylocomium*) and ferns. With the exception of two (out of three generally known in the park) epiphytes, *Ptilidium pulcherrimum* and *P. californicum*, all other species are confined to places where the influence of the *Alnus fruticosa* shrubs is less pronounced: namely, slopes and banks of streams and rocks (mainly composed of pyroclastic products). In this belt, *Barbilophozia hatcherii*, *Calypogeia integristipula*, *Cephalozia bicuspidata*, *Chiloscyphus polyanthos*, *Conocephalum salebrosum*, *Diplophyllum taxifolium*, and *Pellia neesiana* are found on various substrates. On tufa rocks, and starting from a height of 300–400 m above sea level, arctomontane taxa sometimes occur: *Anthelia juratzkana*, *Gymnomitrion kamchaticum* (from 750 m a.s.l.), *Eremonothus myriocarpus*, *Fuscocephaloziopsis pachy-*

caulis, *Peltolepis quadrata* (remarkably, the last three species are found in the South Kamchatka Nature Park only in the crooked forest belt, although in general they are more characteristic for the mountain tundras), *Hygrobiella squamosa*, *Lophozia savicziae*, *Marsupella apiculata*, *M. boeckii*, *M. condensata*, *Nardia breidlerii*, *Pleurocladula albescens*, *Pseudolophozia debiliformis* and *Pseudolophozia sudetica*. The boreal and arctic-boreal *Jungermannia eucordifolia*, *J. pumila*, *Marsupella apertifolia*, *Nardia geoscyphus*, *N. harae*, and *N. pacifica* grow on moist tufa, while along the stream banks, *Scapania paludicola*, *S. subalpina*, and *Trilophozia quinquedentata* can be easily found. The lower altitude of this belt often extends from the side of the first terrace of the valley, or somewhat higher from the base of the slopes of mountains, commonly from 300 to 400 m a.s.l. At the upper limit, this belt sometimes "cuts through" mountain tundra and comes into direct contact with pyroclastic deserts at altitudes of approximately 1000–1200 m above sea level. This altitude level is explained by the fact that during the periodic fallout of ashes, tundras (especially moss and lichen types) suffer more than crooked forests.

(4) Taller elfin forests dominated by *Betula ermanii* (stone birch). They are not widely distributed in the places we studied. In fact, within South Kamchatka, the stone birch forests are an analog of coniferous taiga (coniferous species, except for shrubby *Pinus pumila*, are absent here). In this regard, Hulten's assumption adheres to and is partly confirmed by the distribution of a number of taiga species here [1] (p. 185): "The *Betula* forests of Southern Kamchatka can be regarded as remnants of the Miocene mixed forests, stretching from Oregon River over Alaska to Japan. Their tall, lush undergrowth of *Filipendula camtschatica* and other tall herbs is an indication in the same direction. They can be expected to be surviving traces from a warmer, more genial period". The ground cover is mainly forb (in the study area, the tall grass cover in birch forests is far from being as common as Hulten [1] writes about). Often, there are areas covered almost entirely with *Calamagrostis langsdorffii* mixed with *Thalictrum*, *Veratrum* and other grasses. The absence of shrubs in the undergrowth gives forests a "park landscape" character, as noted 150 years ago by the geologist Woldemar Friedrich Carl von Ditmar (1822–1892; cited here after Hulten [1] (p. 207), original not seen). In some other places, the understory is quite dense and includes *Sorbus sambucifolia* (Cham. et Schltdl.) M. Roem., *Pimus pumila* (in the form of large old clumps up to 3 m high), *Rosa amblyotis* C.A. Mey., *Lonicera chamissoi* Bunge ex P. Kir., etc. Usually, on steep slopes, there are moss-dominating areas with mosses common in the taiga biome: *Pleurozium*, *Hylocomium*, *Polytrichum*, *Rhytidium*, etc. In the valleys of small streams (near watercourses), *Equisetum hyemale* L. can occupy large areas. As expected, there are a number of thermophilic liverwort species that are not found above. The only find of *Barbilophozia barbata* is located here, although the species in general in Kamchatka is not limited to this belt. *Barbilophozia hatcherii* and *B. lycopodioides* occur sporadically. *Cephalozia bicuspidata*, *Chiloscyphus polyanthos*, *Conocephalum salebrosum*, *Nardia insecta*, *Pellia neesiana*, *Pleurocladula albescens*, *Scapania subalpina*, *S. undulata*, and *Trilophozia quinquedentata* are common and abundant along stream banks. *Diplophyllum taxifolium* (generally a common species throughout the whole altitudinal profile), *Douinia plicata*, *Pseudolophozia sudetica*, *Ptilidium ciliare*, and *Solenostoma obscurum* grow on rocks (the last is an oro-boreal species in Pacific Asia). Among the epiphytes, in addition to the *Ptilidium pulcherrimum* and *P. californicum* mentioned above, *Frullania austinii* also occurs here. These three species exhaust the diversity of epiphytes in the park (and in the Kamchatka Peninsula in general). Decaying wood adds several species: *Calypogeia integristipula*, *Fuscocephaloziopsis leucantha*, *F. lunulifolia*, *Lophocolea heterophylla*, *Lophozia guttulata*, *L. longiflora*, *L. silvicola*, *L. silvicoloides*, *L. ventricosa*, *Lophoziopsis longidens* (also found on the bases of tree trunks), *Neoorthocaulis attenuatus*, and *Schistochilopsis incisa*. The boundaries of the distribution of this belt extend from the gentle slopes of the river valleys (in the places we studied, it starts from 15 m a.s.l.) and reach up to 300–500 m a.s.l. According to Hulten [1], *Betula ermanii* forests are never found on alluvial soil,

and their boundary clearly runs along the transition from the slope of the terrace to the bottom of the valley. This conclusion is also confirmed by our observations. On very steep slopes (more than 40°), birch forests do not occur and are replaced by *Alnus fruticosa*. Hulten [1] (p. 212) suggests that "birch forests are suppressed by the dominant alder thickets and have not reached their altitudinal limit".

(5) Floodplain forests are composed of *Salix schwerinii* E.L. Wolf, less often in edge areas, supplemented with *Alnus hirsuta* (Spach) Turcz. ex Rupr. *Populus suaveolens* Fisch. is rare and is found as only single trees. *Chosenia arbutifolia* (Pall.) A.K. Skvortsov, which is quite common in the river floodplains north of South Kamchatka, has never been observed by us. Hulten [1] also writes about the rarity of this species in South Kamchatka. Tall grasses up to 2–2.5 m tall dominate in the cover: *Cacalia hastata* L., *Senecio cannabifolius* Less. and *Filipendula camtschatica* (Pall.) Maxim. There are no epiphytes or epixylous taxa. All liverworts known here are found along the banks of watercourses (rivers, including flooded formed riverbeds, and large streams): *Blasia pusilla*, *Cephalozia bicuspidata*, *Marchantia latifolia*, *Pellia neesiana*, *Scapania paludosa*, and *S. pseudouliginosa* were collected here. *Diplophyllum taxifolium* was collected in rock niches. In places where old willow trees fall out, the cover of tall grass often does not allow new willows to settle under it, and the tall grass cover remains dominant without an upper tree layer for a long time. Hulten [1] explained this phenomenon by the extreme shading of substrates, especially under *Filipendula camtschatica*. According to his measurements, the illumination at the soil surface under the *F. camtschatica* is 140 times lower compared to open space, and in the middle part of this plant cover (at a height of approximately 1 m above ground), 90 times. This illumination is much lower than the illumination at a height of half a meter in *Alnus fruticosa* crooked forests, which is reduced by 15–40 times compared to open spaces [1]. In wide river valleys on alluvial soil in the park, *Betula platyphylla* Sukaczev occasionally occurs with forb cover and shrubs in the undergrowth, but there are no liverworts in its communities.

(6) Swamps, although belonging to intrazonal communities, occur in the park only in the lower altitudinal belt: in almost flat river valleys (but not in floodplains, where the only large areas covered by monodominant *Equisetum fluviatile* L. eutrophic fens were seen). The largest studied massif is located in the valley of the lower course of the Asacha River. Other rather extended studied massifs are located in the vicinity of the Zheltovskie thermal Springs and in the upper reaches of the Pravaya Khodutka River. The swamps are represented both by oligotrophic communities ('hochmoore') with *Sphagnum magellanicum* Brid., *S. papillosum* Lindb. and *Oxycoccus palustris* Pers., to lowland eutrophic areas with hollows occupied by *Scorpidium scorpioides* (Hedw.) Limpr. and *Warnstorfia*. The various transitions between these extremes are also present. Dwarf shrub-moss communities occur on hummocks and often contain *Myrica tomentosa* (DC.) Asch. et Graebn., *Vaccinium uliginosum* L., *V. vitis-idaea* L., *Empetrum nigrum* and *Andromeda polifolia* L., as well as herbaceous plants, most often *Sanguisorba tenuifolia* Fisch. ex Link. Among bryophytes (usually over *Sphagnum* spp.) *Calypogeia kamchatica*, *C. sphagnicola*, *Cephalozia bicuspidata*, *Cephaloziella elachista*, *Fuscocephaloziopsis loitlesbergerii*, *F. pleniceps*, *Mylia anomala*, *Riccardia chamedryfolia*, *R. decrescens*, *Scapania paludicola*, and *S. pseudouliginosa* occur. The taxonomic diversity of liverworts here is not as high as might be expected, given the external diversity and extent of the swamps. The probable reason for this lower number of liverworts is a strong depletion of the cover due to rather regular ash falls (especially after the catastrophic eruption as that of Ksudach Volcano in 1907). Meanwhile, keeping this as a working hypothesis, it is necessary to note one contradiction associated with the presence of *Heterogemma laxa* here, which rarely forms vegetative propagules and sporangia (in Pacific Asia, nothing is known). In addition, in Pacific Asia, it is a very rare species: only three are reported in the region: one more in central Kamchatka [18] and one more on Kunashir Island (unpublished), and the third is in the present paper.

Therefore, it is not clear what allowed such rare and difficult-to-spread species as *H. laxa* to survive in a swamp in the lower course of the Asacha River.

(7) A special discussion is necessary regarding the habitats associated with the outcrops of mineralized thermal waters and hot-to-warm steam openings that are of volcanic origin. The flora of the surroundings of thermal streams in the lower altitudinal belt (the Zheltovsky, Asachinsky, Khodutkinsky thermal pools were studied here) is composed entirely of the taxa from adjacent communities. All species can also be found along cool stream banks and in adjacent forest communities: *Chiloscyphus polyanthos*, *Conocephalum salebrosum*, and *Pellia endiviifolia*. Two groups of "hot springs" (Dachnye and Medvezhie) are situated within the crooked forest belt. Due to the sulfurous composition of the water, *Plectocolea vulcanicola* is found here, one of the few obligate thermophilic sulfurophilic taxa. Another taxon growing here, *Cephalozia bicuspidate*, is also found in cold streams with water not rich in sulfur. However, in the area of thermal mineral springs, taking advantage of reduced competition (and possibly increased temperature), it develops especially large patches composed of unusually robust plants. Above the crooked forests, there are no typical thermomineral water springs in the park. Instead, solfataras and fumaroles are presented here. The main emission of water occurs in the form of steam, which then partially condenses into water. The soil in the vicinity of such solfataras is usually highly enriched in sulfur, which decreases the list of potentially occurring species. Such "springs" are very abundant on the slope of the Mutnovskaya Sopka Volcano and include several groups. The main dominant species, as shown below (in Dachnye and Medvezhie hot springs), is *Plectocolea vulcanicola*. In addition, *Cladopodiella francisci* (in the South Kamchatka Nature Park, this species was found only in thermal habitats in soil enriched with sulfur, which was quite unexpected), *Lophozia schusteriana*, *Marsupella sphacelata*, and *Nardia assamica* were found here. The greatest floristic interest provides the vicinity of fumaroles located on the so-called "Paryashchy Greben" (Steaming) ridge in the Ksudach caldera. Here, in the immediate vicinity of the steam jets (the temperature of soil and steam varies greatly, from +20 to +60 °C), a number of species were found: *Blasia pusilla*, *Cephaloziella divaricata*, *Cladopodiella francisci*, *Conocephalum japonicum* (one of the northernmost occurrences in the world), *Cryptocolea imbricata*, *Endogemma caespiticium*, *Fossombronia alaskana*, *Gymnomitrion commutatum*, *G. concinnatum*, *Marsupella sprucei*, *M. subemarginata*, *Nardia assamica*, *Riccia bifurca*, *Scapania paritexta*, and *Solenostoma rossicum*. All of the above are not obligate sulfurophilic taxa, and the finding of *Scapania parvitexta* generally was completely unexpected from a phytogeographical point of view: this hemiboreal species is distributed from the southern tip of the Kuril Islands and extends to Japan, the Korean Peninsula, the southern and middle parts of the Sikhote-Alin and eastern China.

Significant areas in the lower altitudinal belt are occupied by meadows on the seacoasts and on the alluvium above (up to heights of approximately 300 m a.s.l., cf. [1]), but liverworts are absent in them.

In general, there are no clear regularities in the distribution of species along the altitudinal profile, except for the presence of a small number of species in the stone birch belt, which are not found above. The arctomontane taxa, on the contrary, descend widely into the crooked forests and, possibly, would also extend into the stone birch forests if there were extended rock massifs there. Periodically (on a geological scale) significant to near complete destruction of the vegetation cover leads to the constant "displacement" of species, as well as the depletion of the composition and targeted selection toward generative-active taxa. The species composition of swampy communities is quite poor, and the area of thermal springs is nonspecific, with the exception of only sulfurophilic *Plectocolea vulcanicola*.

3. Results

During the field work, 667 specimens of liverworts were collected and identified. A total of 1184 identifications were completed (since the vast majority of specimens contained more than one species in the mat). The compiled list of taxa, including literature data, includes 132 species and 3 varieties of liverworts. A total of 11 identified species are included in the Red Data Book of Kamchatka, and 6 more are listed for the flora of the Kamchatka Territory for the first time. The list of species, with appropriate explanations, is provided below.

List of Taxa

The taxa are arranged alphabetically, and the nomenclature mostly follows Söderström et al. [19] with some updates from recent literature. Each species is annotated by (1) altitudinal range, where the species was collected (in the case of a limited number of collection localities, which were far from each other, altitudes are given separated by commas), (2) selected specimens examined field numbers according to locality numbers in Table 1 (only one per locality is indicated), (3) accompanying taxa (if there were any), (4) literature reference, if there was a previous record on the area treated and the notes on some taxa (if any).

There are 132 species and 3 varieties of liverworts, of which 117 species were found by us. Species new to the Kamchatka Peninsula are marked with asterisks (*), species included in the last edition of the Red Data Book of Kamchatka [20] are marked by # symbol, and the taxa reported in the literature but absent in our collections are marked by ° symbol.

°***Anthelia julacea*** (L.) Dumort.—reported for Akhomten (Russkaya) Bay by Arnell [3], where they may be widely treated and corresponds to *A. juratzkana* (very common species in the park) and later was reported in a narrow sense (so definitely *A. julacea* s. str.) by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Anthelia juratzkana (Limpr.) Trevis.—404–1885 m a.s.l.—Selected specimens examined: K-13-2-21, K-23-14-21, K-24-2-21, K-25-1-21, K-26-11-21, K-28-1-21, K-29-12-21, K-39-1-21, K-41-5-21, K-42-1-21, K-43-3-21, K-45-7-21, K-58-6-21, K-59-3-21, K-60-1-21, K-65-2-21, K-67-3-21, K-70-1-21, K-75-1-21, K-76-3-21, Kam-134-2-21, Kam-140-2-21, Kam-144-6-21, Kam-151-1-21, Kam-157-2-21—Accompanying species: *Cephalozia bicuspidata*, *Cephaloziella varians*, *Cladopodiella francisci*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. corallioides*, *Lophozia murmanica*, *L. savicziae*, *L. ventricosa*, *Marsupella apertifolia*, *M. apiculata*, *M. condensata*, *M. sphacelata*, *M. sprucei*, *Nardia breidleri*, *N. harae*, *N. japonica*, *N. pacifica*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania* cf. *parvitexta*, *Schistochilopsis pacifica*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Barbilophozia barbata (Schreb.) Loeske—107 m a.s.l.—Selected specimens examined: K-10-7-21—Accompanying species: *Barbilophozia lycopodioides*, *Ptilidium ciliare*.

Barbilophozia hatcheri (A. Evans) Loeske—107, 588, 963, 994, 1129, 1243 m a.s.l.—Selected specimens examined: K-10-1-21, K-11-4-21, K-19-2-21, K-30-3-21, K-46-4-21, K-68-5-21—Accompanying species: *Lophozia longiflora*, *Lophoziopsis longidens*, *Pleurocladula albescens*, *Ptilidium californicum*, *Sphenolobus minutus*.

Barbilophozia lycopodioides (Wallr.) Loeske—107 m a.s.l.—Selected specimens examined: K-10-5-21—Accompanying species: *Lophoziopsis longidens*, *Ptilidium ciliare*.

Blasia pusilla L.—249, 830 m a.s.l.—Selected specimens examined: K-23-16-21, K-32-2-21—Accompanying species: *Conocephalum japonicum*, *Nardia assamica*.

****Blepharostoma neglectum*** Vilnet et Bakalin—340–1357 m a.s.l.—Selected specimens examined: K-49-7-21, K-77-1-21, Kam-135-2-21, Kam-139-3-21, Kam-144-7-21—Accompanying species: *Calycularia laxa*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Lophozia savicziae*, *Schistochilopsis incisa*, *Trilophozia quinquedentata*.

****Blepharostoma primum*** Vilnet et Bakalin—404 m a.s.l.—Selected specimens examined: Kam-144-8-21—Accompanying species: *Diplophyllum taxifolium*, *Solenostoma obscurum*.

Calycularia laxa Lindb. et Arnell—340, 1130, 1383 m a.s.l.—Selected specimens examined: K-41-1-21, K-49-4-21, Kam-139-11-21—Accompanying species: *Blepharostoma neglectum*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Lophozia savicziae*, *Pleurocladula albescens*, *Schistochilopsis incisa*, *Sphenolobus minutus*, *Trilophozia quinquedentata*.

Calypogeia integristipula Steph.—340 m a.s.l.—Selected specimens examined: Kam-139-20-21—Accompanying species: *Fuscocephaloziopsis leucantha*, *F. lunulifolia*, *Lophozia silvicola*, *Schistochilopsis incisa*.

°***Calypogeia muelleriana*** (Schiffn.) Müll. Frib.—reported for Russakaya Bay by Bakalin (2005).

Calypogeia kamchatica Bakalin, Troizk., Maltseva—19–253 m a.s.l.—Selected specimens examined: K-34-10-21, K-7-12-21, Kam-133-5-21, Kam-149-15-21—Accompanying species: *Aneura pinguis*, *Cephalozia bicuspidata*, *Fuscocephaloziopsis pleniceps*, *Pellia neesiana*, *Riccardia decrescens*.

Calypogeia sphagnicola (Arnell et J. Perss.) Warnst. et Loeske—13, 14, 1130 m a.s.l.—Selected specimens examined: K-49-5-21, K-55-4-21, K-56-4-21, Kam-147-2-21, Kam-147-3-21—Accompanying species: *Cephalozia bicuspidata*, *Cephaloziella elachista*, *Fuscocephaloziopsis* cf. *loitlesbergeri*, *Heterogemma laxa*, *Lophozia savicziae*, *Mylia anomala*.

°***Cephalozia ambigua*** C. Massal.—reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Cephalozia bicuspidata (L.) Dumort.—17–1516 m a.s.l.—Selected specimens examined: K-25-1-21, K-26-11-21, K-39-11-21, K-41-11-21, K-42-3-21, K-45-7-21, K-49-1-21, K-57-14-21, K-58-12-21, K-59-2-21, K-61-1-21, K-62-11-21, K-66-1-21, K-67-2-21, K-76-1-21, K-78-2-21, K-81-3-21, K-82-2-21, K-9-1-21, Kam-134-2-21, Kam-139-1-21, Kam-146-1-21, Kam-149-1-21, Kam-151-4-21, Kam-152-1-21, Kam-153-1-21, Kam-154-1-21, Kam-159-3-21, Kam-160-2-21—Accompanying species: *Aneura pinguis*, *Anthelia juratzkana*, *Calycularia laxa*, *Calypogeia kamchatica*, *C. sphagnicola*, *Cephaloziella varians*, *Cladopodiella francisci*, *Diplophyllum albicans*, *D. sibiricum*, *Fuscocephaloziopsis pleniceps*, *Gymnocolea inflata*, *G. marginata*, *Gymnomitrion commutatum*, *Lophocolea heterophylla*, *Lophozia longiflora*, *L. savicziae*, *L. schusteriana*, *L. ventricosa*, *Marsupella apiculata*, *M. boeckii*, *M. condensata*, *M. sphacelata*, *Nardia breidleri*, *N.* cf. *hiroshii*, *N. harae*, *N. japonica*, *N. pacifica*, *Pellia neesiana*, *Plectocolea vulcanicola*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania* cf. *mucronata*, *S. paludicola*, *S. paludosa*, *S. parvifolia*, *Schistochilopsis incisa*, *S. pacifica*, *Solenostoma obscurum*, *S. rossicum*, *Sphenolobus minutus*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs" and Bakalin [5] from Russakaya Bay.

Cephaloziella divaricata (Sm.) Schiffn.—830, 1357 m a.s.l.—Selected specimens examined: K-31-5-21, K-77-2-21—Accompanying species: *Endogemma caespiticia*, *Nardia assamica*, *Scapania obcordata*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs"

Cephaloziella elachista (J.B. Jack) Schiffn.—13 m a.s.l.—Selected specimens examined: K-55-5-21—Accompanying species: *Calypogeia sphagnicola*, *Cephalozia sp.*, *Heterogemma laxa*.

Cephaloziella varians (Gottsche) Steph.—340, 1484 m a.s.l.—Selected specimens examined: K-42-3-21, Kam-139-18-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Marsupella apiculata*, *Solenostoma obscurum*. Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs" as *C.* cf. *varians*.

Chiloscyphus polyanthos (L.) Corda—19–219 m a.s.l.—Selected specimens examined: K-10-14-21, K-6-7-21, K-9-12-21, Kam-149-9-21—Accompanying species: *Scapania undulata*.

#***Cladopodiella francisci*** (Hook.) Jørg.—830–1178 m a.s.l.—Selected specimens examined: K-23-9-21, K-64-1-21, K-67-3-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Fossombronia* cf. *alaskana*, *Gymnocolea inflata*, *G. marginata*.

Conocephalum japonicum (Thunb.) Grolle—830 m a.s.l.—Selected specimens examined: K-23-13-21, K-31-21-21—Accompanying species: *Blasia pusilla*, *Endogemma caespiticia*, *Nardia assamica*, *Riccia bifurca*. Previously reported by Arnell [3] from "Shadutka-Fluss".

Conocephalum salebrosum Szweyk., Buczk. et Odrzyk.—18–588 m a.s.l.—Selected specimens examined: K-19-5-21, K-6-8-21, K-9-19-21, Kam-148-2-21.

#Cordaea flotoviana Nees—109 m a.s.l.—Selected specimens examined: K-7-1-21—Accompanying species: *Riccardia chamedryfolia*.

#Cryptocolea imbricata R.M. Schust.—830 m a.s.l.—Selected specimens examined: K-23-1-21—Accompanying species: *Marsupella boeckii*.

#Cryptocoleopsis imbricata Amak.—404–1665 m a.s.l.—Selected specimens examined: K-26-6-21, K-29-10-21, K-41-8-21, K-43-4-21, Kam-140-2-21, Kam-144-4-21—Accompanying species: *Anthelia juratzkana*, *Blepharostoma neglectum*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion concinnatum*, *Lophozia* cf. *schusteriana*, *L. savicziae*, *Marsupella apertifolia*, *M. apiculata*, *Nardia geoscyphus*, *N. harae*, *N. pacifica*, *Pleurocladula albescens*, *Trilophozia quinquedentata*.

Diplophyllum albicans (L.) Dumort.—904–1885 m a.s.l.—Selected specimens examined: K-11-11-21, K-13-9-21, K-29-3-21, K-39-10-21, K-42-1-21, K-43-2-21, K-45-9-21, K-48-1-21, K-49-4-21, Kam-134-2-21, Kam-135-1-21, Kam-141-1-21, Kam-142-1-21—Accompanying species: *Anthelia juratzkana*, *Blepharostoma neglectum*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Cryptocoleopsis imbricata*, *Diplophyllum taxifolium*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. corallioides*, *Lophozia savicziae*, *Marsupella apiculata*, *M. condensata*, *M. sprucei*, *Nardia harae*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Schistochilopsis incisa*, *Solenostoma rossicum*, *S. subellipticum*, *Sphenolobus minutus*, *Trilophozia quinquedentata*.

Diplophyllum sibiricum Bakalin et Vilnet—1130 m a.s.l.—Selected specimens examined: K-49-1-21, Kam-135-1a-21—Accompanying species: *Cephalozia bicuspidata*, *Diplophyllum taxifolium*, *Fuscocephaloziopsis pleniceps*, *Scapania parvifolia*, *Solenostoma subellipticum*, *Sphenolobus minutus*.

Diplophyllum taxifolium (Wahlenb.) Dumort.—219–1885 m a.s.l.—Selected specimens examined: K-13-9-21, K-22-1a-21, K-26-4-21, K-27-12-21, K-29-10-21, K-38-2-21, K-39-6-21, K-41-6-21, K-46-1-21, K-48-1-21, K-49-6-21, K-79-1-21, K-9-5-21, Kam-135-1-21, Kam-139-10-21, Kam-144-8a-21, Kam-158-2-21—Accompanying species: *Anthelia juratzkana*, *Blepharostoma neglectum*, *B. primum*, *Calycularia laxa*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. sibiricum*, *Fuscocephaloziopsis leucantha*, *F. lunulifolia*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. corallioides*, *Lophozia savicziae*, *L. schusteriana*, *L. silvicola*, *Marsupella apertifolia*, *M. boeckii*, *Nardia geoscyphus*, *N. harae*, *Pellia neesiana*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Schistochilopsis incisa*, *Solenostoma obscurum*, *S. subellipticum*, *Sphenolobus minutus*, *Trilophozia quinquedentata*. Previously reported by Arnell [3] from Akhomten Bay and by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Douinia plicata (Lindb.) Konstant. et Vilnet—262, 1130, 1176 m a.s.l.—Selected specimens examined: K-47-1-21, K-49-2-21, K-51-5-21—Accompanying species: *Lophozia savicziae*, *Scapania parvifolia*, *Sphenolobus minutus*.

Endogemma caespiticia (Lindenb.) Konstant., Vilnet et A.V. Troitsky—830 m a.s.l.—Selected specimens examined: K-23-18a-21, K-31-22-21—Accompanying species: *Cephaloziella divaricata*, *Conocephalum japonicum*, *Fossombronia sp.*, *Nardia assamica*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] as *Jungermannia caespiticia* Lindenb. from "Mutnovsky Hot Springs".

Eremonotus myriocarpus (Carrington) Pearson—633 m a.s.l.—Selected specimens examined: K-20-9-21.

****Fossombronia alaskana*** Steere et Inoue—830 m a.s.l.—Selected specimens examined: K-31-12-21—Accompanying species: *Riccia bifurca*.

Frullania austinii J.J. Atwood, Vilnet, Mamontov et Konstant.—19 m a.s.l.—Selected specimens examined: K-57-1-21.

Fuscocephaloziopsis cf. ***loitlesbergeri*** (Schiffn.) Váňa et L. Söderstr.—13 m a.s.l.—Selected specimens examined: K-55-4-21—Accompanying species: *Calypogeia sphagnicola*, *Mylia anomala*.

Fuscocephaloziopsis leucantha (Spruce) Váňa et L. Söderstr.—340 m a.s.l.—Selected specimens examined: Kam-139-19-21—Accompanying species: *Calypogeia integristipula*, *Diplophyllum taxifolium*, *Fuscocephaloziopsis lunulifolia*, *Lophozia silvicola*, *Schistochilopsis incisa*.

Fuscocephaloziopsis lunulifolia (Dumort.) Váňa et L. Söderstr.—340 m a.s.l.—Selected specimens examined: Kam-139-12-21—Accompanying species: *Calypogeia integristipula*, *Diplophyllum taxifolium*, *Fuscocephaloziopsis leucantha*, *Lophozia silvicola*, *Schistochilopsis incisa*, *Trilophozia quinquedentata*.

Fuscocephaloziopsis pachycaulis (R.M. Schust.) Váňa et L. Söderstr.—340–588 m a.s.l.—Selected specimens examined: K-19-1-21, Kam-139-14-21, Kam-144-5-21.

Fuscocephaloziopsis pleniceps (Austin) Váňa et L. Söderstr.—253, 1130 m a.s.l.—Selected specimens examined: K-34-10-21, K-49-1-21, Kam-133-4-21—Accompanying species: *Calypogeia kamchatica*, *Cephalozia bicuspidata*, *Diplophyllum sibiricum*, *Scapania parvifolia*, *Sphenolobus minutus*.

Gymnocolea inflata (Huds.) Dumort.—1098–1516 m a.s.l.—Selected specimens examined: K-59-3-21, K-62-12-21, K-67-3-21, K-78-3-21, Kam-154-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Cladopodiella francisci*, *Marsupella* cf. *condensata*, *Pleurocladula albescens*, *Pseudolophozia sudetica*.

***Gymnocolea marginata** (Steph.) S. Hatt.—1001–1516 m a.s.l.—Selected specimens examined: K-39-9-21, K-62-11-21, K-71-1-21, Kam-160-1-21—Accompanying species: *Cephalozia bicuspidata*, *Cladopodiella francisci*, *Lophozia murmanica*, *Marsupella sphacelata*, *Pleurocladula albescens*, *Pseudolophozia sudetica*.

#Gymnomitrion adustum Nees—1243 m a.s.l.—Selected specimens examined: K-11-2-21—Accompanying species: *Nardia breidleri*, *Pseudolophozia sudetica*. Previously reported by Czernyadjeva et al. [6] as *Marsupella adusta* (Nees) Spruce from "Mutnovsky Hot Springs".

°***Gymnomitrion brevissimum*** (Dumort.) Warnst.—Reported by Arnell [3] as *Marsupella varians* (Lindb.) Mull. Frib. from Akhomten Bay and by Czernyadjeva et al. [6] as *Marsupella brevissima* (Dumort.) Grolle from "Mutnovsky Hot Springs". Taking into account the recent segregation of *Gymnomitrion kamchaticum* [21] to which many previous reports of *G. brevissimum* could be referred, the distribution of the latter in South Kamchatka remains questionable.

Gymnomitrion commutatum (Limpr.) Schiffn.—830–1383 m a.s.l.—Selected specimens examined: K-23-12-21, K-28-1-21, K-29-2-21, K-31-20-21, K-39-1-21, K-41-10-21, K-45-9-21, K-46-1-21, K-48-1-21, Kam-134-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion concinnatum*, *G. corallioides*, *Lophozia savicziae*, *Marsupella apiculata*, *M.* cf. *apertifolia*, *M. condensata*, *M. subemarginata*, *Nardia harae*, *N. japonica*, *Pseudolophozia debiliformis*, *P. sudetica*, *Solenostoma rossicum*.

Gymnomitrion concinnatum (Lightf.) Corda—825–1885 m a.s.l.—Selected specimens examined: K-11-11-21, K-13-1-21, K-26-1-21, K-29-1-21, K-31-1-21, K-39-12-21, K-41-10-21, K-43-3-21, K-44-1-21, Kam-141-1-21—Accompanying species: *Anthelia juratzkana*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion commutatum*, *G. corallioides*, *G. pacificum*, *Marsupella aleutica*, *M. apiculata*, *M. condensata*, *M. sprucei*, *Nardia harae*, *Pleurocladula albescens*, *Pseudolophozia sudetica*.

Gymnomitrion corallioides Nees—830–1885 m a.s.l.—Selected specimens examined: K-13-1-21, K-23-4-21, K-29-4-21, K-31-1-21, K-43-7-21, K-44-2-21, K-79-1-21, Kam-159-5-21—Accompanying species: *Anthelia juratzkana*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. pacificum*, *Marsupella apiculata*, *M. sprucei*, *Pseudolophozia sudetica*.

Gymnomitrion kamchaticum Mamontov, Vilnet et Konstant.—759–1045 m a.s.l.—Selected specimens examined: K-21-1-21, K-26-2-21, K-28-2-21, K-80-1-21.

#Gymnomitrion pacificum Grolle—1001–1813 m a.s.l.—Selected specimens examined: K-39-7-21, K-41-7-21, K-43-7-21, K-44-2-21, Kam-143-1-21—Accompanying species: *Gymnomitrion concinnatum*, *G. corallioides*, *Marsupella apiculata*.

Heterogemma laxa (Lindb.) Konstant. et Vilnet—13, 14 m a.s.l.—Selected specimens examined: K-55-5-21, K-56-7-21, Kam-147-1-21—Accompanying species: *Calypogeia sphagnicola*, *Cephaloziella elachista*, *Mylia anomala*.

Hygrobiella squamosa Bakalin et Vilnet—588, 1182 m a.s.l.—Selected specimens examined: K-19-8-21, K-58-13-21—Accompanying species: *Jungermannia* cf. *pumila*, *Scapania hyperborea*.

Isopaches bicrenatus (Schmidel) H. Buch—1001 m a.s.l.—Selected specimens examined: K-45-8a-21—Accompanying species: *Solenostoma hyalinum*. Previously reported by Czernyadjeva et al. [6] as *Lophozia bicrenata* (Schmid.) Dumort. from "Mutnovsky Hot Springs".

Jungermannia atrovirens Dumort.—Reported by Bakalin [5] from Russkaya Bay.

Jungermannia cf. ***exsertifolia*** Steph.—1182 m a.s.l.—Selected specimens examined: K-58-11-21. Previously reported by Czernyadjeva et al. [6] as *Jungermannia exsertifolia* from "Mutnovsky Hot Springs".

Jungermannia eucordifolia Schljakov—219, 1072 m a.s.l.—Selected specimens examined: K-9-11-21, Kam-155-1-21.

Jungermannia pumila With.—219, 1182 m a.s.l.—Selected specimens examined: K-58-13a-21, K-9-7-21—Accompanying species: *Hygrobiella squamosa*, *Scapania hyperborea*, *Scapania paludosa*.

Lophocolea heterophylla (Schrad.) Dumort.—19 m a.s.l.—Selected specimens examined: K-57-17-21, Kam-149-12-21—Accompanying species: *Cephalozia bicuspidata*.

Lophozia guttulata (Lindb. et Arnell) A. Evans—70 m a.s.l.—Selected specimens examined: K-16-1-21.

Lophozia heteromorpha R.M. Schust. et Damsh.—782 m a.s.l.—Selected specimens examined: K-25-3b-21.

Lophozia longiflora (Nees) Schiffn.—107, 1043, 1181 m a.s.l.—Selected specimens examined: K-10-1-21, K-61-1-21, K-70-4-21—Accompanying species: *Barbilophozia hatcheri*, *Cephalozia bicuspidata*, *Marsupella sphacelata*, *Nardia harae*, *N. insecta*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Scapania paludosa*, *Schistochilopsis incisa*, *Solenostoma rossicum*.

Lophozia murmanica Kaal.—994–1357 m a.s.l.—Selected specimens examined: K-11-12-21, K-62-15-21, K-68-2-21, K-74-3-21, K-75-2-21, K-77-4-21, Kam-159-1-21—Accompanying species: *Anthelia juratzkana*, *Gymnocolea marginata*, *Lophozia savicziae*, *Marsupella apiculata*, *M. condensata*, *M. sphacelata*, *Nardia pacifica*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Scapania praetervisa*, *S. subalpina*, *Sphenolobus minutus*. Previously reported by Persson [4] as *L. groenlandica* (Nees) Macoun from Akhomten Bay.

Lophozia savicziae Schljakov—778–1665 m a.s.l.—Selected specimens examined: K-24-3a-21, K-25-1-21, K-29-3-21, K-43-2-21, K-48-1-21, K-49-2-21, K-70-1-21, K-77-3-21, K-78-2-21, Kam-142-1-21, Kam-158-1-21, Kam-159-2-21—Accompanying species: *Anthelia juratzkana*, *Blepharostoma neglectum*, *Calycularia laxa*, *Calypogeia sphagnicola*, *Cephalozia bicuspidata*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Douinia plicata*, *Gymnomitrion commutatum*, *Lophozia murmanica*, *Marsupella apiculata*, *Nardia insecta*, *N. japonica*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania parvifolia*, *Schistochilopsis incisa*, *Solenostoma rossicum*, *Sphenolobus minutus*, *Trilophozia quinquedentata*. Previously reported by Czernyadjeva et al. from "Mutnovsky Hot Springs".

Lophozia schusteriana Schljakov—825, 1098, 1182 m a.s.l.—Selected specimens examined: K-26-7-21, K-58-2-21, K-62-17-21—Accompanying species: *Cephalozia bicuspidata*, *Diplophyllum taxifolium*, *Marsupella sphacelata*, *Nardia harae*, *N. japonica*, *Pleurocladula albescens*.

Lophozia silvicola H. Buch—15, 340 m a.s.l.—Selected specimens examined: Kam-139-19-21, Kam-145-2-21—Accompanying species: *Calypogeia integristipula*, *Diplophyllum taxifolium*, *Fuscocephaloziopsis leucantha*, *F. lunulifolia*, *Neoorthocaulis attenuatus*, *Ptilidium californicum*, *Schistochilopsis incisa*.

Lophozia silvicoloides N. Kitag.—340 m a.s.l.—Selected specimens examined: Kam-139-17-21.

Lophozia ventricosa var. ***rigida*** R.M. Schust.—1182 m a.s.l.—Selected specimens examined: Kam-151-4-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Marsupella sphacelata*, *Pseudolophozia sudetica*.

Lophozia ventricosa (Dicks.) Dumort.—404–1357 m a.s.l.—Selected specimens examined: K-25-2-21, K-50-1-21, K-58-12-21, Kam-159-6-21—Accompanying species: *Cephalozia bicuspidata*, *Nardia pacifica*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *Scapania* cf. *mucronata*.

°***Lophoziopsis excisa*** (Dicks.) Konstant. et Vilnet—Reported by Czernyadjeva et al. [6] as *Lophozia excisa* (Dicks.) Dumort. from "Mutnovsky Hot Springs".

Lophoziopsis longidens (Lindb.) Konstant. et Vilnet—15–107 m a.s.l.—Selected specimens examined: K-10-3-21, K-16-2-21, K-53-1-21—Accompanying species: *Barbilophozia hatcheri*, *B. lycopodioides*, *Neoorthocaulis attenuatus*, *Ptilidium californicum*. Previously reported by Persson [4] as *Lophozia longidens* (Lindb.) Macoun from Akhomten Bay.

Marchantia alpestris (Nees) Burgeff—183–404 m a.s.l.—Selected specimens examined: K-33-1-21, K-8-4-21, Kam-144-1-21. Previously reported by Czernyadjeva et al. [6] as *M. polymorpha* ssp. *montivagans* Bischl. et Boisselier from "Mutnovsky Hot Springs".

Marchantia latifolia Gray—1516 m a.s.l.—Selected specimens examined: Kam-160-3-21.

****Marsupella aleutica*** Mamontov, Vilnet, Konstant. et Bakalin—830 m a.s.l.—Selected specimens examined: K-31-7a-21—Accompanying species: *Gymnomitrion concinnatum*.

Marsupella apertifolia Steph.—633–1130 m a.s.l.—Selected specimens examined: K-20-1-21, K-26-15-21, K-27-12-21, K-29-7-21, K-74-4-21—Accompanying species: *Anthelia juratzkana*, *Cryptocoleopsis imbricata*, *Diplophyllum taxifolium*, *Nardia pacifica*, *Pellia neesiana*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania subalpina*.

Marsupella apiculata Schiffn.—782–1885 m a.s.l.—Selected specimens examined: K-13-1-21, K-25-3a-21, K-29-3-21, K-41-10-21, K-42-3-21, K-43-1-21, K-44-1-21, K-63-2-21, K-75-2-21, K-78-1-21, Kam-134-2-21, Kam-142-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Cephaloziella varians*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *Gymnomitrion commutatum*, *G. concinnatum*, *G. corallioides*, *G. pacificum*, *Lophozia murmanica*, *L. savicziae*, *Marsupella condensata*, *M. sprucei*, *Nardia breidleri*, *N. harae*, *Pseudolophozia sudetica*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] as *Gymnomitrion apiculatum* (Schiffn.) Müll.Frib. from "Mutnovsky Hot Springs".

Marsupella boeckii (Austin) Lindb. ex Kaal.—340–1357 m a.s.l.—Selected specimens examined: K-23-1-21, K-26-5-21, K-31-3-21, K-38-2-21, Kam-139-1-21, Kam-139-15-21, Kam-159-4-21—Accompanying species: *Cephalozia bicuspidata*, *Cryptocolea imbricata*, *Diplophyllum taxifolium*, *Marsupella* cf. *subemarginata*, *M. sprucei*, *Nardia assamica*, *N. breidleri*, *N. geoscyphus*, *N. insecta*, *N. pacifica*, *Pleurocladula albescens*, *Pseudolophozia* cf. *debiliformis*, *P. sudetica*, *Scapania irrigua*, *S. parvifolia*, *Solenostoma obscurum*.

Marsupella condensata (Ångstr. ex C. Hartm.) Lindb. ex Kaal.—778–1383 m a.s.l.—Selected specimens examined: K-24-3-21, K-25-3a-21, K-28-1-21, K-29-12-21, K-41-10-21, K-75-2-21, Kam-134-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Gymnomitrion commutatum*, *G. concinnatum*, *Lophozia murmanica*, *Marsupella apiculata*, *Nardia harae*, *N. japonica*, *Pleurocladula albescens*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Marsupella emarginata (Ehrh.) Dumort.—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs". Taking into account the recent advances in taxonomy of this species-complex [22], the distribution of this species in its "narrow sense" in South Kamchatka looks hardly possible.

Marsupella sphacelata (Giesecke ex Lindenb.) Dumort.—1056–1182 m a.s.l.—Selected specimens examined: K-58-10-21, K-61-1-21, K-62-11-21, K-65-1-21, K-66-2-21, Kam-151-4-21—Accompanying species: *Aneura pinguis*, *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Gymnocolea marginata*, *Lophozia longiflora*, *L. murmanica*, *L. schusteriana*, *L. ventricosa*, *Nardia harae*, *N. pacifica*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Scapania paludosa*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Marsupella sprucei (Limpr.) Bernet—830–1885 m a.s.l.—Selected specimens examined: K-11-11-21, K-13-1-21, K-23-7-21, K-31-6-21, K-41-5-21—Accompanying species: *Anthelia juratzkana*, *Diplophyllum albicans*, *Gymnomitrion concinnatum*, *G. corallioides*, *Marsupella apiculata*, *M. boeckii*, *M.* cf. *subemarginata*, *Nardia assamica*, *Pseudolophozia sudetica*, *Scapania parvitexta*.

Marsupella subemarginata Bakalin et Fedosov—830, 904 m a.s.l.—Selected specimens examined: K-23-12-21, K-29-9-21—Accompanying species: *Gymnomitrion commutatum*, *Nardia harae*.

Marsupella cf. ***tubulosa*** Steph.—830 m a.s.l.—Selected specimens examined: K-23-17-21—Accompanying species: *Marsupella* cf. *boeckii*, *Nardia assamica*, *Scapania* cf. *parvitexta*.

Mylia anomala (Hook.) Gray—13, 14 m a.s.l.—Selected specimens examined: K-55-4-21, K-56-3-21, Kam-147-1-21—Accompanying species: *Calypogeia sphagnicola*, *Heterogemma laxa*.

Nardia assamica (Mitt.) Amak.—784, 830 m a.s.l.—Selected specimens examined: K-23-11-21, K-31-10-21, K-82-6-21—Accompanying species: *Blasia pusilla*, *Conocephalum japonicum*, *Endogemma caespiticia*, *Marsupella boeckii*, *M.* cf. *tubulosa*, *M. sprucei*, *Nardia harae*, *Scapania* cf. *parvitexta*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Nardia breidleri (Limpr.) Lindb.—340–1243 m a.s.l.—Selected specimens examined: K-11-3-21, K-20-4-21, K-21-3-21, K-24-1-21, K-38-1-21, K-39-11-21, K-45-7-21, K-58-5-21, K-59-1-21, K-60-1-21, K-62-3-21, K-63-2-21, K-65-2-21, K-68-7-21, K-69-1-21, K-75-1-21, K-76-1-21, Kam-139-23-21, Kam-151-1-21, Kam-157-1-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Gymnomitrion adustum*, *Lophozia* cf. *ventricosa*, *Marsupella apiculata*, *M. boeckii*, *Nardia harae*, *N. pacifica*, *Pleurocladula albescens*, *Pseudolophozia sudetica*.

Nardia compressa (Hook.) Gray—Reported by Arnell [3] from Akhomten Bay and also collected by Bakalin in 2004 in the same place.

Nardia geoscyphus (De Not.) Lindb.—340–1384 m a.s.l.—Selected specimens examined: K-20-11-21, K-26-6-21, K-29-10-21, K-38-2-21, Kam-140-1-21—Accompanying species: *Cryptocoleopsis imbricata*, *Diplophyllum taxifolium*, *Lophozia* cf. *silvicoloides*, *Marsupella boeckii*, *Nardia harae*, *Nardia pacifica*, *Pleurocladula albescens*, *Pseudolophozia sudetica*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Nardia harae Amakawa—759–1484 m a.s.l.—Selected specimens examined: K-21-3-21, K-23-10-21, K-26-11-21, K-31-13-21, K-39-11a-21, K-42-1-21, K-45-7-21, K-46-1-21, K-61-1-21, K-62-17-21, K-76-1-21, Kam-134-2-21, Kam-159-7-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion commutatum*, *G. concinnatum*, *Lophozia longiflora*, *L. schusteriana*, *Marsupella apiculata*, *M. condensata*, *M. sphacelata*, *M. subemarginata*, *Nardia assamica*, *N. breidleri*, *N. geoscyphus*, *N. pacifica*, *Pellia neesiana*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Scapania parvitexta*, *S. paludosa*, *Schistochilopsis pacifica*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] as *N. scalaris* Gray from "Mutnovsky Hot Springs".

Nardia cf. ***hiroshii*** Amakawa—1185 m a.s.l.—Selected specimens examined: K-59-2-21—Accompanying species: *Cephalozia bicuspidata*, *Pleurocladula albescens*, *Pseudolophozia sudetica*.

Nardia insecta Lindb.—340, 404, 1043 m a.s.l.—Selected specimens examined: K-38-3-21, K-70-2-21, Kam-144-1a-21—Accompanying species: *Lophozia longiflora*, *L. savicziae*, *Marsupella boeckii*, *Nardia japonica*, *Pleurocladula albescens*, *Solenostoma obscurum*, *S. rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Nardia japonica Steph.—928–1182 m a.s.l.—Selected specimens examined: K-28-1-21, K-58-3-21, K-70-2-21, Kam-153-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Gymnomitrion commutatum*, *Lophozia savicziae*, *L. schusteriana*, *Marsupella condensata*, *Nardia insecta*, *Pleurocladula albescens*, *Solenostoma rossicum*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs". The segregation of *N. pacifica* from *N. japonica* [23] make possible the report by Czernyadjeva et al. [6] belong to *N. pacifica*.

#*Nardia pacifica* Bakalin—340–1130 m a.s.l.—Selected specimens examined: K-20-6-21, K-25-2-21, K-26-11-21, K-27-11-21, K-29-7-21, K-39-11a-21, K-65-1-21, K-68-3-21, K-74-2-21, Kam-139-1-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Cryptocoleopsis imbricata*, *Lophozia murmanica*, *L. ventricosa*, *Marsupella apertifolia*, *M. boeckii*, *M. sphacelata*, *Nardia breidleri*, *N. geoscyphus*, *N. harae*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania subalpina*, *Schistochilopsis pacifica*.

Nardia unispiralis Amakawa—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Neoorthocaulis attenuatus (Mart.) L. Söderstr., De Roo et Hedd.—15 m a.s.l.—Selected specimens examined: K-53-1-21, Kam-145-1-21—Accompanying species: *Lophozia silvi-*

cola, *Lophoziopsis longidens*, *Ptilidium californicum*, *P. pulcherrimum*. Previously reported by Persson [4] from Akhomten Bay.

Neoorthocaulis binsteadii (Kaal.) L.Söderstr., De Roo et Hedd.—Reported by Arnell [3] as *Jungermannia binsteadii* Kaal. from Akhomten Bay.

Pellia endiviifolia (Dicks.) Dumort.—19 m a.s.l.—Selected specimens examined: K-57-9-21, Kam-149-2-21.

Pellia epiphylla (L.) Corda—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Pellia neesiana (Gottsche) Limpr.—109–1153 m a.s.l.—Selected specimens examined: K-19-4-21, K-20-7-21, K-26-16-21, K-27-4-21, K-29-11-21, K-31-17a-21, K-34-11-21, K-51-1-21, K-6-15-21, K-7-2-21, K-8-5-21, K-9-1-21, Kam-139-10-21, Kam-153-1-21, Kam-157-3-21—Accompanying species: *Aneura pinguis*, *Calypogeia kamchatica*, *Cephalozia bicuspidata*, *Diplophyllum taxifolium*, *Marsupella apertifolia*, *Nardia harae*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania pseudouliginosa*, *S. subalpina*, *Trilophozia quinquedentata*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs" and Bakalin [5] from Russkaya Bay.

Peltolepis quadrata (Saut.) Müll. Frib.—588, 633 m a.s.l.—Selected specimens examined: K-19-7-21, K-20-10-21.

Plectocolea vulcanicola (Schiffn.) Bakalin—784–1113 m a.s.l.—Selected specimens examined: K-64-2-21, K-66-10-21, K-81-1-21, K-82-1-21, Kam-156-1-21—Accompanying species: *Cephalozia bicuspidata*.

Pleurocladula albescens (Hook.) Grolle—340–1516 m a.s.l.—Selected specimens examined: K-20-3-21, K-24-3a-21, K-25-1-21, K-26-11-21, K-27-11-21, K-29-10-21, K-38-2-21, K-39-11-21, K-41-1-21, K-45-7-21, K-58-1-21, K-59-2-21, K-61-3-21, K-62-11-21, K-68-3-21, K-69-2-21, K-70-1-21, K-74-2-21, K-78-2-21, Kam-139-7-21, Kam-144-6-21, Kam-152-1-21, Kam-157-2-21, Kam-158-2-21, Kam-160-4-21—Accompanying species: *Anthelia juratzkana*, *Barbilophozia hatcheri*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnocolea marginata*, *Gymnomitrion concinnatum*, *Lophozia longiflora*, *L. murmanica*, *L. savicziae*, *L. schusteriana*, *L. ventricosa*, *Marsupella apertifolia*, *M. boeckii*, *M. condensata*, *M. sphacelata*, *Nardia breidleri*, *N.* cf. *hiroshii*, *N. geoscyphus*, *N. harae*, *N. insecta*, *N. japonica*, *N. pacifica*, *Pellia neesiana*, *Pseudolophozia debiliformis*, *P. sudetica*, *Scapania subalpina*, *Schistochilopsis incisa*, *S. pacifica*, *Solenostoma rossicum*, *Trilophozia quinquedentata*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs" and Arnell [3] as *Pleuroclada albescens* (Hook.) Spruce from Akhomten Bay.

Preissia quadrata (Scop.) Nees subsp. ***hyperborea*** R.M. Schust.—404 m a.s.l.—Selected specimens examined: Kam-144-3-21.

Pseudolophozia debiliformis (R.M. Schust. et Damsh.) Konstant. et Vilnet—633–1610 m a.s.l.—Selected specimens examined: K-11-6-21, K-12-2-21, K-20-3-21, K-21-2a-21, K-25-1-21, K-26-5a-21, K-27-4-21, K-39-8-21, K-48-1-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnomitrion commutatum*, *Lophozia savicziae*, *L. ventricosa*, *Marsupella apertifolia*, *Nardia pacifica*, *Pellia neesiana*, *Pleurocladula albescens*, *Scapania subalpina*. Previously reported by Czernyadjeva et al. [6] as *Lophozia debiliformis* R.M. Schust et Damsh. from "Mutnovsky Hot Springs".

Pseudolophozia sudetica (Nees ex Huebener) Konstant. et Vilnet—340–1885 m a.s.l.—Selected specimens examined: K-11-1-21, K-13-4-21, K-21-3-21, K-24-3a-21, K-26-10-21, K-29-4-21, K-31-6-21, K-38-2-21, K-39-11-21, K-41-5-21, K-59-2-21, K-61-1-21, K-68-6-21, K-74-5-21, K-78-3-21, Kam-139-5-21, Kam-144-6-21, Kam-151-4-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Gymnocolea marginata*, *Gymnomitrion adustum*, *G. commutatum*, *G. concinnatum*, *G. corallioides*, *Lophozia longiflora*, *Lophozia murmanica*, *L. savicziae*, *L. ventricosa*, *Marsupella apertifolia*, *M. apiculata*, *M. boeckii*, *M.* cf. *condensata*, *M.* cf. *subemarginata*, *M. sphacelata*, *M. sprucei*, *Nardia breidleri*, *N.* cf. *hiroshii*, *N. geoscyphus*, *N. harae*, *N. pacifica*, *Pleurocladula albescens*, *Scapania irrigua*, *S. paludosa*, *S. parvitexta*, *S. subalpina*, *Solenostoma rossicum*, *Trilophozia quinquedentata*. Previously reported by Czernyadjeva et al. [6] (once as *Lophozia sudetica* and next time as *L. rufescens* Schljak.)

from "Mutnovsky Hot Springs" and Bakalin [5] as *Lophozia sudetica* (Huebener) Grolle from Russkaya Bay.

Pseudolophozia sudetica var. ***anomala*** (Schljakov) Konstant. et Vilnet—1153, 1516 m a.s.l.—Selected specimens examined: Kam-153-1-21, Kam-160-4-21—Accompanying species: *Cephalozia bicuspidata*, *Pellia neesiana*, *Pleurocladula albescens*.

Ptilidium californicum (Aust.) Pears—15–633 m a.s.l.—Selected specimens examined: K-10-10-21, K-20-2-21, K-51-2-21, K-6-1-21, Kam-145-1-21—Accompanying species: *Barbilophozia hatcheri*, *Lophozia silvicola*, *Lophoziopsis longidens*, *Neoorthocaulis attenuatus*, *Ptilidium pulcherrimum*.

Ptilidium ciliare (L.) Hampe—107, 963 m a.s.l.—Selected specimens examined: K-10-7-21, K-30-1-21—Accompanying species: *Barbilophozia barbata*, *B. lycopodioides*.

Ptilidium pulcherrimum (Weber) Vain.—15–404 m a.s.l.—Selected specimens examined: K-10-12-21, K-36-1-21, K-51-2-21, K-53-3-21, K-6-1-21, Kam-136-1-21, Kam-150-1-21—Accompanying species: *Neoorthocaulis attenuatus*, *Ptilidium californicum*.

Riccardia chamedryfolia (With.) Grolle—109, 112 m a.s.l.—Selected specimens examined: K-6-11-21, K-7-10-21—Accompanying species: *Cordaea flotoviana*.

#Riccardia decrescens (Steph.) S. Hatt.—109 m a.s.l.—Selected specimens examined: K-7-12-21—Accompanying species: *Calypogeia kamchatica*.

#Riccia bifurca Hoffm.—830 m a.s.l.—Selected specimens examined: K-31-21-21—Accompanying species: *Conocephalum japonicum*, *Fossombronia alaskana*.

°***Scapania cuspiduligera*** (Nees) Müll.Frib.—Reported by Persson [4] from Akhomten Bay.

Scapania hyperborea Jørg.—1182 m a.s.l.—Selected specimens examined: K-58-13-21—Accompanying species: *Hygrobiella squamosa*, *Jungermannia pumila*.

Scapania irrigua (Nees) Nees—825, 1243 m a.s.l.—Selected specimens examined: K-11-1-21, K-26-5-21—Accompanying species: *Marsupella boeckii*, *M.* cf. *subemarginata*, *Pseudolophozia* cf. *debiliformis*, *P. sudetica*. Previously reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Scapania mucronata H. Buch—1129 m a.s.l.—Selected specimens examined: K-46-5-21.

Scapania obcordata (Berggr.) S.W. Arnell—1357 m a.s.l.—Selected specimens examined: K-77-2-21—Accompanying species: *Cephaloziella divaricata*.

Scapania obscura (Arnell et C.E.O. Jensen) Schiffn.—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Scapania paludicola Loeske et Müll. Frib.—17–273 m a.s.l.—Selected specimens examined: K-34-1-21, K-51-6-21, Kam-138-1-21, Kam-146-1-21—Accompanying species: *Aneura pinguis*, *Cephalozia bicuspidata*.

Scapania paludosa (Müll. Frib.) Müll. Frib.—252–1182 m a.s.l.—Selected specimens examined: K-33-2-21, K-58-14-21, K-61-1-21, K-62-10-21, K-66-8-21, K-68-1-21, Kam-151-3-21—Accompanying species: *Cephalozia bicuspidata*, *Jungermannia* cf. *pumila*, *Lophozia longiflora*, *Marsupella sphacelata*, *Nardia harae*, *Pseudolophozia sudetica*. Previously reported by Bakalin [5] from Russkaya Bay.

Scapania parvifolia Warnst.—1130, 1357 m a.s.l.—Selected specimens examined: K-49-1-21, Kam-159-4-21—Accompanying species: *Cephalozia bicuspidata*, *Diplophyllum sibiricum*, *Douinia plicata*, *Fuscocephaloziopsis pleniceps*, *Lophozia saviczіae*, *Marsupella boeckii*, *Sphenolobus minutus*.

****Scapania parvitexta*** Steph.—830 m a.s.l.—Selected specimens examined: K-31-6-21—Accompanying species: *Marsupella* cf. *subemarginata*, *M. sprucei*, *Pseudolophozia sudetica*.

Scapania praetervisa Meyl.—1357 m a.s.l.—Selected specimens examined: K-77-5-21—Accompanying species: *Lophozia murmanica*. Previously reported by Czernyadjeva et al. [6] as *S. mucronata* subsp. *praetervisa* (Meyl.) R.M. Schust. from "Mutnovsky Hot Springs".

Scapania pseudouliginosa Potemkin, Bakalin, Vilnet et Klimova—109, 249 m a.s.l.—Selected specimens examined: K-32-1-21, K-7-2-21—Accompanying species: *Pellia neesiana*.

Scapania scandica (Arnell et H.Buch) Macvicar—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Scapania subalpina (Nees ex Lindenb.) Dumort.—244–1130 m a.s.l.—Selected specimens examined: K-19-6-21, K-27-4-21, K-35-1-21, K-74-1-21—Accompanying species: *Lophozia murmanica*, *Marsupella apertifolia*, *Nardia pacifica*, *Pellia neesiana*, *Pleurocladula albescens*, *Pseudolophozia debiliformis*, *P. sudetica*. Previously reported by Arnell [3] as *Martinella subalpina* (Nees) Lindb. from Akhomten Bay and by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Scapania uliginosa (Lindenb.) Dumort.—Reported by Czernyadjeva et al. [6] from "Mutnovsky Hot Springs".

Scapania undulata (L.) Dumort.—107 m a.s.l.—Selected specimens examined: K-10-13-21—Accompanying species: *Chiloscyphus polyanthos*. Previously reported by Arnell [3] as *Martinella dentata* (Dumort.) from Akhomten Bay.

Schistochilopsis incisa (Schrad.) Konstant.—340–1383 m a.s.l.—Selected specimens examined: K-41-1-21, K-49-4-21, K-70-4-21, K-77-3-21, Kam-139-20-21, Kam-159-3-21—Accompanying species: *Blepharostoma neglectum*, *Calycularia laxa*, *Calypogeia integristipula*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. taxifolium*, *Fuscocephaloziopsis leucantha*, *F. lunulifolia*, *Lophozia longiflora*, *L. savicziae*, *L. silvicola*, *Pleurocladula albescens*, *Scapania* cf. *praetervisa*, *Sphenolobus minutus*, *Trilophozia quinquedentata*. Previously reported by Arnell [3] as *Jungermannia incisa* Schrad. from Akhomten Bay.

#Schistochilopsis pacifica Bakalin—340, 825 m a.s.l.—Selected specimens examined: K-26-11-21, K-27-10-21, Kam-139-13-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Nardia harae*, *N. pacifica*, *Pleurocladula albescens*, *Pseudolophozia* cf. *debiliformis*, *P.* cf. *sudetica*.

Solenostoma hyalinum (Lyell) Mitt.—1001 m a.s.l.—Selected specimens examined: K-45-8-21—Accompanying species: *Isopaches bicrenatus*. Previously reported by Czernyadjeva et al. [6] as *Jungermannia hyalina* Lyell from "Mutnovsky Hot Springs".

Solenostoma obscurum (A. Evans) R.M. Schust.—340, 404 m a.s.l.—Selected specimens examined: K-38-3-21, Kam-139-15-21, Kam-144-8a-21—Accompanying species: *Blepharostoma primum*, *Cephalozia bicuspidata*, *Cephaloziella varians*, *Diplophyllum taxifolium*, *Lophozia sp.*, *Marsupella boeckii*, *Nardia insecta*. Previously reported by Czernyadjeva et al. [6] as *Jungermannia* cf. *evansii* Vana from "Mutnovsky Hot Springs".

#Solenostoma rossicum Bakalin et Vilnet—778–1043 m a.s.l.—Selected specimens examined: K-23-14-21, K-24-3a-21, K-28-1-21, K-31-5-21, K-70-1-21, Kam-134-2-21—Accompanying species: *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *Endogemma caespiticia*, *Gymnomitrion commutatum*, *Lophozia longiflora*, *L. savicziae*, *Marsupella apiculata*, *M. condensata*, *Nardia assamica*, *N. harae*, *N. insecta*, *N. japonica*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Scapania* cf. *parvitexta*.

Solenostoma sphaerocarpum (Hook.) Steph.—Previously reported by Czernyadjeva et al. (2005) as *Jungermannia sphaerocarpa* Hook. from "Mutnovsky Hot Springs". This report may belong to *S. rossicum* described after Czernyadjeva et al. [6] and to which at least the vast majority of *S. sphaerocarpum* records in Kamchatka are belonged.

Solenostoma subellipticum (Lindb. ex Heeg) R.M. Schust.—1130 m a.s.l.—Selected specimens examined: Kam-135-1-21—Accompanying species: *Diplophyllum albicans*, *D. sibiricum*, *D. taxifolium*.

Sphenolobus minutus (Schreb.) Berggr.—963–1357 m a.s.l.—Selected specimens examined: K-30-3-21, K-39-6-21, K-46-2-21, K-49-1-21, Kam-159-1-21—Accompanying species: *Barbilophozia hatcheri*, *Calycularia laxa*, *Cephalozia bicuspidata*, *Diplophyllum albicans*, *D. sibiricum*, *D. taxifolium*, *Douinia plicata*, *Fuscocephaloziopsis pleniceps*, *Lophozia murmanica*, *L. savicziae*, *Scapania parvifolia*, *Schistochilopsis incisa*.

Tetralophozia setiformis (Ehrh.) Schljakov—1213, 1484 m a.s.l.—Selected specimens examined: K-42-4-21, K-48-2-21.

Trilophozia quinquedentata (Huds.) Bakalin—262–1130 m a.s.l.—Selected specimens examined: K-29-5-21, K-49-6-21, K-51-3-21, Kam-135-2-21, Kam-139-10-21, Kam-144-2-21—Accompanying species: *Blepharostoma neglectum*, *Calycularia laxa*, *Cryptocoleopsis imbricata*, *Diplophyllum albicans*, *D. taxifolium*, *Fuscocephaloziopsis lunulifolia*, *Lophozia savicziae*, *Pellia neesiana*, *Pleurocladula albescens*, *Pseudolophozia sudetica*, *Schistochilopsis incisa*.

4. Discussion

Volcanism is perhaps the most important factor that makes the floristic composition of the liverwort flora of South Kamchatka Nature Park peculiar in comparison with other regions of northeast Asia (excluding, of course, certain areas within the Kamchatka Peninsula and northern Kurils). This influence is expressed in the destruction of floristic complexes by ash falls and the creation of specific habitats (including travertine cones, tufa "cliffs" and sulfur-rich substrates). At the same time, the influence of volcanic evidence on the floristic composition, taken together, is rather negative and results in powerful selection toward the predominance of actively reproducing species (both generatively and by vegetative propagules). However, it is worth mentioning that a number of generatively nonactive species avoided this filtering. For example, *Heterogemma laxa* was found in a swamp, which undoubtedly is covered sometimes with layers of volcanic ash. A similar example might be provided by *Nardia compressa*, although it was collected on the coast with damp sheer cliffs, where the influence of ash falls is strongly decreased due to the steepness of the slope.

The positive impact of volcanism on taxonomic diversity is difficult to measure. As a matter of fact, from the entire list of found taxa, we can say with certainty that only two of them would not have been found if it were not for active volcanism. The first species is *Plectocolea vulcanicola*, which grows only on substrates rich in sulfur (the species range extends from Central, Eastern and Southern Kamchatka to Java Island, and everywhere, this species is confined to similar habitats in volcanic regions). The second species, *Cryptocoleopsis imbricata*, grows on andesite rocks and andesitic ash and ranges from central Kamchatka to Japan. This plant also does not occur outside areas of active volcanism (although sometimes seen at fairly significant distances from active volcanoes). Two more species were found in South Kamchatka Nature Park on only sulfur-containing substrates: *Cladopodiella francisci* and *Marsupella sphacelata*; however, for both, sulfur-containing substrates are not only the main substrate but rather an exception to the general rules. Several species were found in "Parashchy Greben" Ridge (most interesting is *Scapania parvitexta*) in the thermal steam-affected area. This result may also be due to the positive impact of active volcanism on taxonomic diversity.

Within the flora, there are few truly rare species in Northeast Asia that give a peculiarity to the taxonomic composition. These species are *Gymnomitrion adustum*, *Hetergemma laxa*, *Scapania parvitexta* and *Solenostoma obscurum*. This list can be supplemented with taxa whose taxonomic status is in doubt: *Gymnocolea marginata*, *Lophozia ventricosa* var. *rigida*, *Nardia harae*. "False" specificity is given by recently described (in the last decade) taxa, whose distribution is still poorly known, and they are likely more widespread than it is now assumed. These records include *Blepharostoma* spp., *Calypogeia kamchatica*, *Gymnomitrion kamchaticum*, *Marsupella aleutica*, *Nardia pacifica*, *Scapania pseudouliginosa* and *Schistochilopsis pacifica*.

Due to the short time frame of the research, it was not possible to visit a number of habitats and collect even known species, such as *Nardia compressa* and *Neoorthocaulis binsteadii*. The latter may imply the high possibility that several more taxa were not collected. However, a small number of epixylous taxa is a rather natural feature of the studied flora. It is unlikely that there will be many more of them, even with careful research, since their main refuge is dark coniferous forests on the Kamchatka Peninsula that are absent in the South Kamchatka Nature Park. A common feature for all local floras of Kamchatka is a low number of calciphilous and even basiphilous taxa. At one site (Asachinskie Hot Springs), we examined travertine cones, one of the few alkaline substrates on the peninsula, but no specific basiphilous species were found there. The only basiphylous species in the entire flora of South Kamchatka Nature Park is *Peltolepis quadrata*, which grows on volcanic ash (possibly with an alkaline reaction of water extract) in the crevices of tufa cliffs.

The distribution of species across the park is uneven, and the number of taxa in each locality is usually directly proportional to the diversity of habitats. The richest, in terms of the number of species, are the floras of the vicinity of the Zheltovskaya Sopka Volcano, the caldera of the Ksudach Volcano (Ksudach Mts.) and the vicinity of the Khodutka Volcano plus Khodutkinskie Hot Springs. An intermediate number of species is known from the vicinity of Mutnovskaya Sopka Volcano, and the smallest number is known from the area of the Asacha River.

The uniqueness of sites (meaning here the number of species known only from one site) shows two separate ways: a small number of "unique" species can be accompanied by a large total number of species, and vice versa. As an example, site four (lower course of the Asacha River) is noteworthy: its "uniqueness" is explained by the presence of species of oligotrophic swamps, which are widely distributed there, although the total number of species is quite low. Meanwhile, the swamps in South Kamchatka Nature Park, including those of the oligotrophic type, are quite common, and the species "unique" for this site may be found in other places of the park in future research.

4.1. Taxa Known from Only One Site

Only in the vicinity of the Zheltovskaya Sopka Volcano and the middle course of the Zhyoltaya River were 10 species found. This is a heterogeneous group including (1) distinctly rare in NE Asia amphi-oceanic arctic-montane *Gymnomitrion adustum* and *G. pacificum*, and (2) taxa of wet habitats of the lower vegetation belt: *Chiloscyphus polyanthos*, *Cordaea flotoviana*, *Jungermannia eucordifolia*, *Riccardia chamedryfolia* and *Riccardia decrescens*. Three more taxa are generally widespread in Kamchatka, but for unclear reasons, they were found in South Kamchatka Nature Park only in this area: *Barbilophozia lycopodioides*, *Scapania undulata*, and *Solenostoma subellipticum*. The presence of the last three species only here is most likely an accidental phenomenon.

The second cluster (Ksudach Mts. (Ksudach caldera)) houses 15 species known only at this location. Among them, there are four relatively rare taxa in Asian Russia: *Endogemma caespiticia*, *Fossombronia alaskana*, *Riccia bifurca*, and *Scapania parvitexta*. They were collected only on fine earth near the so-called fumaroles of "Paryashchy Greben" Ridge. One more specific species, *Peltolepis quadrata*, is distinctly basiphylous and probably indicates a local distribution in the area of volcanic ash with an alkaline reaction of water extract. *Cryptocolea imbricata* is a predominantly Beringian species that is rare in the world but common in some places in East Kamchatka (for example, in Ganalsky Range). Other species only known to be found here are more widely distributed, or their distribution is still poorly understood (recently described): *Conocephalum japonicum*, *Eremonotus myriocarpus*, *Fuscocephaloziopsis pachycaulis, Lophozia heteromorpha*, *L.* cf. *silvicoloides*, *Marsupella aleutica*, *M. subemarginata*, *M.* cf. *tubulosa* and *Schistochilopsis pacifica*.

The third cluster (Khodutka Volcano surroundings and the Khodutkinskie Hot Springs) includes 10 species found only here. Among them are quite rare in Northeast Asia *Calycularia laxa*, *Diplophyllum sibiricum*, *Douinia plicata*, and *Solenostoma obscurum*. Some more widespread species are also present: *Cephaloziella varians*, *Isopaches bicrenatus*, *Scapania mucronata*, *S. parvifolia*, *Solenostoma hyalinum*, and *Tetralophozia setiformis*. It is necessary to underline the latter species, which is very widespread in the mountains of the Northern Holarctic. However, this species avoids areas of active volcanism, as it very rarely reproduces vegetatively and generatively; therefore, it has limited opportunities for reappearance in places where it was destroyed as a result of natural disasters. Since the species is easily recognizable, its accidental omission in other studied clusters is unlikely, and its absence in other areas is due to the general pattern of volcanic transformation of the flora. Another explanation may be connected with the strong acidophyly of *T. setiformis*, whereas andesite rocks (the habitat where the species may be observed and that are widely distributed in the park) provide only slightly acidophilic-to-neutral water solution reaction.

The fourth cluster (lower course of the Asacha River) is characterized by the presence of nine "unique" species. The most striking is *Frullania austinii*, occasionally found in Kamchatka in floodplain forests with *Alnus hirsuta* and *Betula* in epiphytic habitats in the southern, western and eastern parts of the peninsula. In addition, eight species are known to be found only here. They are mainly inhabitants of swamps or wet habitats, which are poorly represented in other clusters: *Cephaloziella elachista*, *Fuscocephaloziopsis* cf. *loitlesbergeri*, *Heterogemma laxa*, *Lophocolea heterophylla*, *Mylia anomala*, *Nardia* cf. *hiroshii* and *Pellia endiviifolia*. In addition, there is *Neoorthocaulis attenuates*, a rare species in the "birch taiga" in the Kamchatka Peninsula. Notably, although we call it the *Betula ermanii* forest species, *Neoorthocaulis attenuatus* occurs on old lying trunks of living *Pinus pumila* clumps occurring in the forest understory. In contrast to expectations, this species does not go above *Betula* forests to the crooked forest belt in Kamchatka despite the occurrence of the same host species (*Pinus pumila*).

Surprisingly, in the last cluster (Mutnovskaya Sopka Volcano surroundings), the area where the largest number of liverwort specimens were collected, the number of "unique" species was the smallest. This site houses five specific taxa, and most of them are arcto-montane species of wet habitats: *Jungermannia* cf. *exsertifolia*, *Scapania hyperborea*, *S. obcordata*, *S. praetervisa*, and *Plectocolea vulcanicola* (the latter is a species of sulfur-rich substrates).

4.2. Taxa Included in the Red Data Book of Kamchatka Territory

The latest edition of the Red Data Book of Kamchatka lists 11 species found in South Kamchatka Nature Park (approximately 1/4 of the list of liverworts included in the latter book): *Cordaea flotoviana*, *Cryptocolea imbricata*, *Cryptocoleopsis imbricata*, *Gymnomitrion adustum*, *G. pacificum*, *Nardia pacifica*, *Riccardia decrescens*, *Riccia bifurca*, *Schistochilopsis pacifica*, and *Solenostoma rossicum*. These are, for the most part, relatively rare species in northeast Asia. The most interesting find is *Gymnomitrion adustum*, mentioned above, whose location on the Zheltovskaya Sopka Volcano is the fourth in Russia and one of the northernmost in Asia. The second locality in the Kamchatka Peninsula was found for *Riccia bifurca*, while the first locality in the peninsula is from the thermal pool surrounding the Malkinskie Hot Springs. It is worth mentioning that in South Kamchatka Nature Park, this species was also collected in a thermal habitat (moist, warm fine earth near fumaroles). Therefore, due to currently available data, this species is facultatively "thermophilic" in Kamchatka that was not noted in any other areas of this species distribution. Among the 11 species mentioned above, 5 are also protected in the territory of Nalychevo Nature Park, 6 are protected in the land territory of the Commander Reserve and 2 are protected in Bystrinsky Nature Park. A total of 2 species, *Gymnomitrion adustum* and *Riccia bifurca,* are not known in the nature parks and reserves of the Kamchatka Territory and are therefore under protection in the peninsula in South Kamchatka Nature Park only.

4.3. New Records of the Liverwort Flora of the Kamchatka Peninsula

Six species were collected for the first time in the Kamchatka Peninsula. Three of them are recently described taxa: *Blepharostoma neglectum*, *Blepharostoma primum*, and *Marsupella aleutica*. *Fossombronia alaskana* is reported because this species was collected with sporophytes, which made it possible to determine the species name. Previously, *Fossombronia* sp. was reported for Kamchatka, under which *F. alaskana* was most likely hidden; however, a reliable identification of the species was impossible due to the absence of sporophytes at that time. *Gymnocolea marginata* is formally listed for the first time in Kamchatka, even though this is a critical species, and its taxonomic status needs to be clarified in the course of taxonomic study. Finally, the discovery of *Scapania parvitexta*, an East Asian species distributed in Korea, China, and Japan (described from the latter), South Kurils, and the southern and middle parts of the Sikhote-Alin Mts, was completely unexpected. We can only speculate that the area where the species was discovered ("Parayshchy Greben" Ridge in Ksudach Caldera) is on the bird migration route, and some birds "know" about the warming effect of fumaroles and frequently visit them for warming and rest. This may be the reason for the disjunct occurrence of this species in Kamchatka.

4.4. The Localities Needing Strict Protection

Since the park is a protected area, the especially valuable sites subject to special conservation should be identified and monitored on a regular basis. Considering the obtained results, we selected some localities reliable for special attention:

1. The apical part of Zheltovskaya Sopka Volcano. Its flora includes a complex of mountain species, including the very rare and generally more southern *Gymnomitrion adustum*;
2. "Paryashchy Greben" Ridge in Ksudach Caldera (Ksudach Mts.). Among others, this is a unique locality for *Fossombronia alaskana* and *Scapania parvitexta* in the Kamchatka Peninsula;
3. Rocky complexes in the western part of the Ksudach Mts., which are habitats for a number of species characteristic of relatively undisturbed mountain tundra that are rare (due to volcanic activity) in South Kamchatka Nature Park.

5. Conclusions

The study revealed a rather taxonomically rich and predominantly hemiarctic liverwort flora. The flora composition reflects the impact of present and past volcanic activity, because the volcanic activity may have eliminated several taxa that were not able to provide propagules abundantly. However, the presence of some species with low propagation activity does not support this thesis. Compared to another flora of the eastern volcanic belt of Kamchatka (as a part of the Pacific Ring of Fire), for which we have reliable information, in Nalychevo Nature Park, the flora of South Kamchatka Nature Park is taxonomically richer. A total of 132 species are recorded here versus 84 [24] in Nalychevo Nature Park. This difference in species number may be explained by possible under collection in Nalychevo Nature Park. In addition, we should note that during the field work in South Kamchatka Nature Park, we did not study any mountains located further than 20–30 km from currently active volcanoes. Therefore, we may suspect that if mountains situated far from recent eruption centers are studied, then several additional taxa may be recorded. Little attention was also given to lake-swamp landscape complexes. Considering the circumstances mentioned above, the reported number of liverwort species, although quite high, can still be further increased by at least 10–20% in the course of a targeted study of previously unexplored natural complexes. For now, the liverwort flora of the South Kamchatka Nature Park may be regarded as the "model", and virgin flora developed in the hemiarctic northwest corner of the Pacific Ring of Fire.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14090722/s1, Table S1: Bioclimatic data.

Author Contributions: Conceptualization, V.A.B. and K.G.K.; methodology, V.A.B., S.S.C. and K.G.K.; validation, S.S.C. and K.G.K.; formal analysis, D.A.B.; investigation, V.A.B., K.G.K., D.A.B. and S.S.C.; resources, V.A.B., K.G.K.; data curation, D.A.B., S.S.C. and K.G.K.; writing—original draft preparation, all coauthors; writing—review and editing, K.G.K., E.A.K. and S.S.C.; visualization, K.G.K., D.A.B.; supervision, V.A.B.; project administration, V.A.B.; funding acquisition, V.A.B. and S.S.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Russian Foundation for Basic Research, grant number 20-04-00278; Russian Academy of Sciences: grant number 122040800088-5; Korean National In-stitute of Ecology: grant number NIE-A-2022-01.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: V.A.B. and K.G.K. are sincerely grateful to the directorateof the Volcanoes of Kamchatka consortium for its generous support of our field research. The work of V.A.B. and K.G.K. was partially supported by the Russian Foundation for Basic Research (grant no. 20-04-00278) and is within the frame of the institutional research project "Cryptogamic Biota of Pacific Asia" (no. 122040800088-5). Additionally, the work of SC was partially supported by a grant from the National Ecosystem Survey of the National Institute of Ecology (NIE-A-2022-01).

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp—min temp))
BIO3	Isothermality (BIO2/BIO7) (×100)
BIO4	Temperature Seasonality (standard deviation ×100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

References

1. Hultén, E.G. The plant cover of Southern Kamchatka. *Ark. Bot. Kungl. Sven. Akademien. Ser.* **1974**, *7*, 81–257.
2. Hultén, E.G. Some Geographical Notes on the Map of South Kamtchatka. *Geogr. Ann.* **1923**, *5*, 329–350.
3. Arnell, N.W. Lebermoose aus Kamtschatka. *Hedwigia* **1927**, *67*, 110–112.
4. Persson, H. Contribution to the bryoflora of Kamchatka. *Rev. Bryol. Lichenol.* **1970**, *37*, 209–221.
5. Bakalin, V.A. New data on distribution of liverworts on Kamchatka Peninsula (North-West Pacific, Russia). *Arctoa* **2005**, *14*, 155–162. [CrossRef]
6. Czernyadjeva, I.V.; Potemkin, A.D.; Zolotov, V.I. Bryophytes of vicinity of Mutnovsky Hot Springs (Southern Kamchatka). *Bot. Zhurnal* **2005**, *90*, 23–39.
7. Melekestsev, I.V.; Braitseva, O.A.; Ponomareva, V.V. A.; Ponomareva, V.V. A new approach to definition of the term "active volcano". In *Geodynamics and Volcanism of the Kurile-Kamchatka Island-Arc System*; Ivanov, B.V., Ed.; IVG&G FEB RAS: Petropavlovsk-Kamchatsky, Russia, 2001; pp. 191–203.
8. Kamchatka Volcanoes. Institute of Volcanology and Seismology (Kamchatka, Russia). Available online: http://www.kscnet.ru/ivs/volcanoes/holocene/main/main.htm (accessed on 24 April 2022).
9. Andrews, B.J.; Gardner, J.E.; Tait, S.; Ponomareva, V.V.; Melekestsev, I.V. Dynamics of the 1800 14C yr BP caldera-forming Eruption of Ksudach Volcano, Kamchatka, Russia. In *Volcanism and Subduction: The Kamchatka Region. Geophysical Monograph Series*; Eichelberger, J., Gordeev, E., Izbekov, P., Kasahara, M., Lees, J., Eds.; American Geophysical Union: Washington, DC, USA, 2007; Volume 172, pp. 325–342. [CrossRef]
10. Kamchatka Territory. Regional History Site. Available online: http://www.kamchatsky-krai.ru/geography/volcanoes/zeltovsky.htm (accessed on 24 April 2022).
11. Kirillov, V.I. (Ed.) *Kamchatka: Tourist Guide*; RIO KOT: Petropavlovsk-Kamchatsky, Russia, 1994; pp. 1–228.
12. Krestov, P.V.; Omelko, A.M.; Nakamura, Y. Vegetation and natural habitats of Kamchatka. *Ber. Reinhold-Tuxen-Ges.* **2008**, *20*, 195–218.
13. Neshataeva, V.Y. *Vegetation of the Kamchatka Peninsula*; KMK Scientific Press: Moscow, Russia, 2009; pp. 1–560.
14. Neshataeva, V.Y. The plant cover of the Kamchatka Peninsula and its geobotanical subdivision. *Trans. Karelian Res. Cent. RAS* **2011**, *1*, 3–22.
15. Kruchinin, A.F. (Ed.) *Atlas of Forests of the USSR*; Glavnoe Upravlenie Geodezii i Kartografii SM USSR: Moscow, Russia, 1973; pp. 1–222.

16. Network of Volcanoes of Kamchatka Nature Parks. Available online: https://www.vulcanikamchatki.ru/territoriya/klaster_yuzhnokamchatskij/ (accessed on 15 August 2022).
17. Bakalin, V.; Fedosov, V.; Pisarenko, O.; Borovichev, E. The bryophyte flora of northern Iturup (north-west Pacific): Between the circumboreal and East Asian floristic regions. *J. Bryol.* **2019**, *41*, 249–262. [CrossRef]
18. Bakalin, V.A. *Distribution of Bryophytes in the Russian Far East. Part. I. Hepatics*; Izd-vo DVFU: Vladivostok, Russia, 2010; pp. 1–175.
19. Söderström, L.; Hagborg, A.; von Konrat, M.; Bartholomew-Began, S.; Bell, D.; Briscoe, L.; Brown, E.; Cargill, D.C.; Costa, D.P.; Crandall-Stotler, B.J.; et al. World checklist of hornworts and liverworts. *PhytoKeys* **2016**, *59*, 1–828. [CrossRef] [PubMed]
20. Bakalin, V.A.; Klimova, K.G. Part 5. Liverworts and hornworts. In *Red Data Book of Kamchatskiy Krai. Vol. 2. Plants*; Chernyagina, O.A., Ed.; Kamchatpress: Petropavlovsk-Kamchatsky, Russia, 2018; pp. 171–218.
21. Mamontov, Y.S.; Vilnet, A.A.; Konstantinova, N.A.; Bakalin, V.A. Two new species of Gymnomitriaceae (Marchantiophyta) in the North Pacific. *Bot. Pac.* **2019**, *8*, 67–80. [CrossRef]
22. Bakalin, V.A.; Fedosov, V.E.; Fedorova, A.V.; Nguyen, V.S. Integrative taxonomic revision of *Marsupella* (Gymnomitriaceae, Hepaticae) reveals neglected diversity in Pacific Asia. *Crypto Gamie Bryol.* **2019**, *40*, 59–85. [CrossRef]
23. Bakalin, V.A.; Klimova, K.G. A note on *Nardia japonica* Steph. (Gymnomitriaceae). *Bot. Pac.* **2016**, *5*, 43–50. [CrossRef]
24. Bakalin, V.A.; Klimova, K.G. Liverwort flora of Nature Park "Nalychevo" (Kamchatka Peninsula). *VL Komar. Meml. Lect.* **2018**, *65*, 29–54. [CrossRef]