Ann. Bot. Fennici 47: 81–105 ISSN 0003-3847 (print) ISSN 1797-2442 (online)
Helsinki 30 April 2010

Hepaticae of the Kuril Islands (northwestern Pacific): a transoceanic route from circumboreal to East Asian flora

Vadim A. Bakalin

Institute of Biology and Soil Sci., Stoletiya Vladivostoka Str., 159, Vladivostok 690022, Russian Federation (e-mail: v_bak@list.ru)

Received 22 May 2008, revised version received 27 Nov. 2009, accepted 21 Nov. 2008

Bakalin, V. A. 2010: Hepaticae of the Kuril Islands (northwestern Pacific): a transoceanic route from Circumboreal to East Asian flora. — *Ann. Bot. Fennici* 47: 81–105.

The Kuril Island Chain, which extends 1200 km in a northeast direction from Hokkaido (Japan) towards the shores of the Kamchatka Peninsula (Russian Federation), unites the boreal flora of the southern Kamchatka with the temperate flora enriched with subtropical elements from the lower elevation belts of Hokkaido. The gradual shift in the liverwort flora from the north to the south is analysed and described. It is shown that the border between East Asian and Circumboreal floristic regions (based on an analysis of liverworts) should run either along the Izmena Straight between Hokkaido and Kunashir Islands, or along the Ekaterina Straight between Kunashir and Iturup Islands, the former being a better-justified position.

Key words: Hepaticae, Kuril Islands, liverwort phytogeography, North Pacific, Russian Far East

Introduction

The Kuril Island Chain, which extends 1200 km in a northeast direction from the shores of Hokkaido Island towards the southern tip of the Kamchatka Peninsula, is a transoceanic route linking the distinctive floras of these areas. Available evidence demonstrates an enormous difference between the northern boreal flora of the lower elevation belts of southern Kamchatka and the flora of the temperate area, with its large number of subtropical elements, and its valley and coastline floras of Hokkaido Island. A comprehensive floristic-phytogeographic study of the Kuril Islands as a bridge that occupies an intermediary position between these two floristic regions is thus a promising undertaking.

The gradual north to south change of the Kuril Island flora and *vice versa* has been described for vascular plants (e.g. Barkalov 2002). Now it is possible to evaluate this change using research data on liverworts (Hepaticae). I will not describe a static system but my aim is to study the process of latitudinal change in the Kuril Island flora. I believe that the Kuril Islands represent an instance of gradual change; this is not an instance of just certain species found on specific islands. The goal of my study is to analyze the liverworts of the Kuril Islands and to find the border between the Circumboreal and East-Asian floristic regions.

Study area

The Kuril Islands resulted from modern volcanic processes and are relatively recent geological formations. The exceptions are the Lesser Kuril Ridge and Shumshu Island at the very north of the Greater Kuril Ridge.

The Greater Kuril Ridge represents Cenozoic volcanism with accumulative formations (Bezverkhnii *et al*. 2002). As a large, underwater complex, the ridge formation began in the Paleogene and by the Oligocene several groups of volcanoes had already emerged from the sea to form large islands that were periodically connected to Hokkaido and to the paleo-Kamchatka mainland. Later, in the Miocene and Pliocene, the surface area of the islands decreased. Shoreline contours at the beginning of the Quaternary resembled modern shorelines, their configuration responding primarily to glacio-eustatic ocean regressions (Bezverkhnii *et al*. 2002). Even so, strong volcanic activity took place in the late Pleistocene when a large number of andesite and basaltic stratovolcanoes formed. At the end of the Pleistocene the role of explosive volcanism increased, calderas were formed, and a large ejecta of pyroclastic material occurred, although the caldera sizes and ejecta volumes along the Kuril Ridge were significantly smaller than in Kamchatka. Volcanism, although reduced in strength, continued throughout the Holocene.

The Lesser Kuril Ridge formed much later than the Greater Kuril Ridge. It apparently existed as a chain of large islands in the mid-Oligocene and over time steadily declined in area. The freshest lava eruptions and tufa deposits are dated to the mid-Miocene (Shantser 1974). Today, all that remains of a once large ridge is Shikotan Island with its almost completely eroded ancient mountains and a series of small islands barely breaking the surface and composed of aqueous materials. The largest of these are Zelenyi and Polonskii Islands.

The Kuril Islands have a moderately cold monsoon climate. February is the coldest month, with the average temperatures across the entire archipelago ranging from –6 °C to –7 °C; the temperatures of the warmest months range from +10 °C in the north to +17 °C in the south. The annual precipitation ranges from 1200 mm in the north to 1500 mm in the south. Snow cover is thick and reaches 2.5 meters at the north end of the archipelago. Fog and low cloud cover are frequent summer events, with winter experiencing heavy snowstorms (Anonymous 1994). The data on the islands whose flora is used in this analysis are provided in Table 1.

Although this article does not examine the florogenesis on the modern Kuril Islands, I will note that the latitudinal difference in East-Asian floristic complexes is apparently a consequence of late Tertiary cooling, when the early Tertiary, somewhat uniform, warm and mild climate "boreo-tropical flora" of Wolfe (1975), corresponding to the Arcto-Tertiary flora (Gardner & Ettingshausen 1879, Krischtofovich 1934, Gradstein & Vana 1987) or to the "Gingko-flora" of Popov (1983), began to differentiate along a latitudinal gradient into cold-resistant species with attendant specification (cf. Tiffney 1985). This has been confirmed, at least in part, by an analysis of the East-Asian floristic vascular plant diversity at the genus level and thus explains, for example, why 75% of the genera represented in northeast Asia (farther north than 60° latitude) are found at the southern extreme of the region (farther south than 30° latitude) (Qian *et al*. 2003).

Modern volcanism and modern migrations have influenced the formation of diverse floristic complexes (cf. Bakalin 2006). They consist of varied taxa that appeared at different times and

Table 1. Size and dimensions of four islands in the Kuril chain.

	Shumshu Island	Paramushir Island	Iturup Island	Kunashir Island
Direction	northeast	northeast	northeast	northeast
Length (km)	30	103	200	123
Width (km)	20	28	27	30
Area (km^2)	231	2479	3139	1490

in diverse ecological conditions. These complexes have superimposed themselves on the latitudinal differentiation that has taken place as a result of climate change in the Pliocene and Pleistocene.

Floristic complexes in the Kuril Island were recently described by Barkalov (2002). It is obvious that the taxonomic composition of broad-leaved forests containing many orotemperate species, like *Magnolia hypoleuca*, in the lower elevation belts of Kunashir Island differs significantly from a complex of subarctic thickets of *Pinus pumila* and *Alnus fruticosa*, and low elevation tundras on Paramushir Island. As Barkalov (2002) notes, especially significant differences in floristic composition are found at the edge areas of the archipelago. This distinction is expressed, in one way or another, in almost all known floristic classifications describing the flora of the Kuril Island Chain. However, depending on the instruments used in the analysis (a researcher's intuition, taxonomic analysis at various levels, from the species to the family, habitat analysis) and the research agenda, results can vary. I will briefly characterize the best known systems.

Earlier studies (e.g. Miyabe 1890, Tatewaki 1933) noted differences in the vegetation cover and floristic composition on the Kuril Islands. Kudo (1922 as citated in Barkalov 2002), based on the heterogeneity of the vegetation cover of the Kuril Islands, divided the islands into two areas, with the border betwen them located at the Friz Strait (between Urup and Iturup Islands). The northern half of Kurils belongs to the Subarctic (or northern boreal) region, and the southern to the Temperate East Asian region. Tatewaki (1933) proposed calling this border the Miyabe line. Tatewaki (1957) later divided the Kurils flora into three rather than two districts: northern, central and southern. Hulten (1933) set the border between the Kamchatka and Japanese floristic provinces in the region of Ketoi and Ushushir Islands. However, he noted a gradual shift between two distinct floras in the central part.

Hämet-Ahti *et al*. (1974) classified the bioclimatic vegetation zones in Japan and adjacent regions. As interpreted in this paper, the northern Kurils belong to the middle-boreal zone, the central Kurils, including Urup Island, to the southern boreal zone, and the southern extremity of the archipelago to the hemiboreal zone. One should also note the principal distinction between the latitudinal zoning of the territory and the identification of floristic areas or provinces. The latitudinal zones are comparatively narrow across a considerable length, and often run around the globe. Simultaneously, the regions are identified (Takhtajan 1986) based on the endemism of varied ranking and are more or less clearly defined both in latitudinal and longitudinal extent.

Takhtajan (1986) drew the boundary for the East-Asian and Circumboreal regions along the central Kurils. In his system, the Northern Kurils belong to the Okhotsk-Kamchatka Province and the southern (the largest islands Urup, Iturup, Kunashir and Shikotan) are combined into the Sakhalin–Hokkaido Province that encompass, aside from these islands, the southern portion of Sakhalin Island and Hokkaido. In examining the phytogeography of northeast Asia (northwards of 38° latitude), Qian *et al*. (2003) combined the Northern Kurils, the southern part of the Kamchatka Peninsula, and Commander Islands into a single region. The authors consider the southern Kurils a part of a single region that is combined with the southern portion of Sakhalin Island. Barkalov (2002), based on an analysis of the latest data on the distribution of vascular plant species, set the border between East-Asian and Circumboreal floristic regions between Urup and Simushir Islands, identifying five floristic districts in the Kuril Islands. Krestov (2006) divided the East-Asian and Circumboreal floristic regions along central Sakhalin and the Ekaterina Strait, the latter located between Iturup and Kunashir Islands. Despite the varied placements of the border between the two areas, there is no doubt that it runs somewhere along the Kurils. This means that the Circumboreal floristic system is large in size but has few endemic taxa borders and a comparatively small-sized territory in the East-Asian Region where, according to Takhtajan (1986), there are endemic families and more than 300 endemic genera.

Although all the aforementioned systems claim to be general phytogeographic systems, in fact they are based on vascular plant distributions only. It should be noted that the number of vascular plant species on Kamchatka is 150%

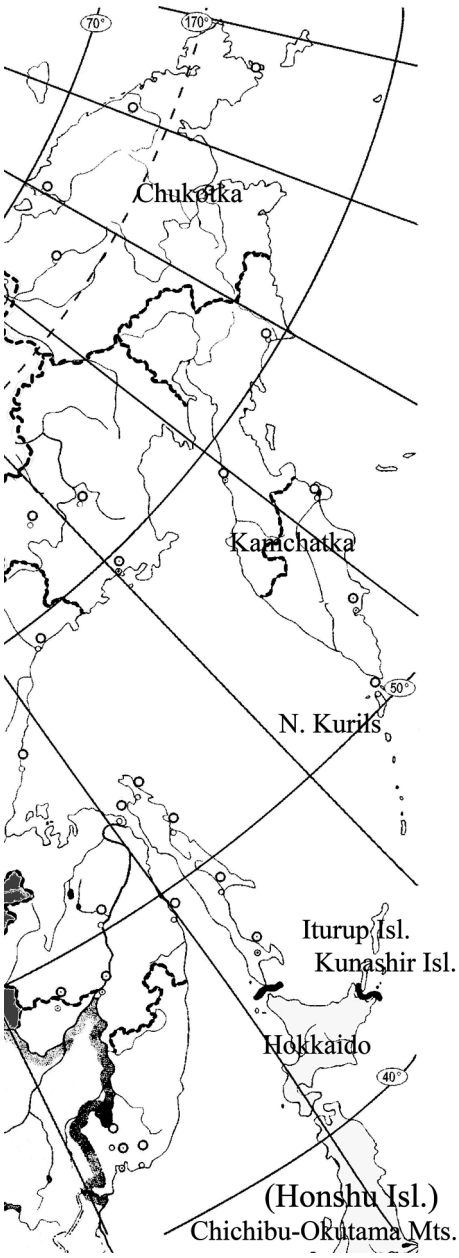

Fig. 1. Map of the regions uder study.

higher than the number of bryophyte species, while the number of lichen species exceeds that of the vascular plans by at least 250%. The only known map of the Kuril Islands that is based on a distribution of bryophytes (Schofield 1992) is a modification of the world system of the floristic kingdoms and regions proposed by Takhtajan (1986). Schofield (1992) combined, without any further detail, all the islands of the Japanese archipelago, southern Sakhalin, northeast China and the Kuril Islands into a single Southeast Asian region.

Material and methods

My study is based on the data of the liverwort flora from separate areas of the northeast Pacific Asia, on literature (Inoue 1976, Afonina & Duda 1993, Nyushko & Potemkin 2005, Bakalin 2005a, 2005b, Bakalin & Cherdantseva 2006, Yamada & Iwatsuki 2006), and on my own unpublished material (primarily from Kamchatka and the Kurils). Included in the analysis are the floras of Kunashir, Iturup and the Northern Kurils — Paramushir and Shumshu Islands that are divided by a pass less than 3 km wide, moreover, Shumshu Island has a flat relief and, as consequence, low taxonomical diversity. Its flora is almost identical to that of Paramushir, hence does not need to be examined separately. Adjacent territories of variable sizes but similar orography and research history having similar indicators for known taxonomic diversity were for comparison included in the analysis. These territories include the Chukotskii Autonomous Region (hereafter: Chukotka), the Kamchatka Peninsula, Hokkaido and the mountains of the Chichibu-Okutama in the central portion of Honshu (Fig. 1). The liverwort flora on the islands has been included in the analysis along with that of larger areas. I believe this approach is justified since the islands, having very diverse landscapes and being floristically clearly separated from adjacent regions by water barriers, can be examined as analogues to this significantly extended area. This is demonstrated by the fairly similar species diversity in liverworts as well as in other plant groups of large and small islands and the peninsula. The following data for vascular plants are available: Kamchatka 976 species (Yakubov & Chernyagina 2004), Paramushir Island 542 species, Iturup 843 species, and Kunashir 1067 species (Barkalov 2002).

My study is based on the work of Yamada and Iwatsuki (2006) on distribution, but an exception is made for the genus *Leiocolea s. lato*

that is placed in Jungermanniaceae. My interpretation of species boundaries is largely based on their work, but again with several exceptions. I adhere to the so-called "narrow genus concept" adopted in the Bakalin (2005a) list in the treatment of genera and relating to the division of *Jungermannia s. lato* and *Lophozia s. lato*.

My analysis is based on the study of more than 450 species. A compilation of the liverwort data reveals the following: Chukotka has 177 species, Kamchatka Peninsula 218, Northern Kurils (Paramushir and Shumshu Islands) 99, Iturup Island 107, Kunashir Island 149, Hokkaido Island 182, and Chichibu-Okutama Mts. have 230 species (*see* Appendix).

For each included species, the distribution is determined in using a three-dimensional grid, from the arctic to tropical, from East Asian to Circumboreal, and its tendency to be distributed in mountainous areas (montane index). Nine latitudinal types of elements and ten longitudinal types of habitat were identified to classify distributions of the species. The montane index is explained as follows: Depending on the approach, the terms montane or alpine (arcto-alpine, boreo-montane, etc.) are traditionally applied to represent mountain distributions, or to name the types of distribution. Alpine, especially in the western European tradition, frequently designates a belt above the tree line (especially in the Alps). Several authors identify so-called mountain species as latitudinal elements of a flora (cf. Konstantinova 1998). This usually means species that grow in mountains but not in the Arctic. This approach has been repeatedly criticized in the Soviet literature (Bardunov 1974: 81) based on montane species being more likely an ecological group than a zonal-geographic group. It seems to me, however, that even if the term "montane geographic element" is rejected outright, the issue will only be partially resolved: what remains are terminological combinations of words whose meanings are alien to one another. For example, Bardunov (1974), in his analysis of the flora of leafy mosses of the Altai and Sayan Mts., identified arctic–alpine and hypo-arctic montane elements. It is obvious that the term "montane or alpine" classifies species into orographic systems and it does not have a latitudinal meaning. I see the solution in using the term "montane" as the third parameter in describing an area.

This position may require explanation. The term "montane" in the description applies to species associated, by distribution, with mountain systems, this irrespective of the altitude at which they grow. Thus, montane species can be subtropical or boreal and not just arctic. In the latter (arctic) I include taxa encountered in the tundra belt of mountains and/or in tundra planes in the north of the Holarctic. Identifying floristic elements based on the latitude, applying longitudinal distribution (habitat type) and using a "montane index" undoubtedly are not ideal criteria, but are fully adequate to address the issues raised in this work. Tolmachyov (1962: 94) was essentially correct when he wrote that "the attempt to classify the totality of habitats across the planet raises, by necessity, the question of what shared features and which differences in species distribution take preference over other features. Successfully resolving this question in a 'general theoretic sense' is highly unlikely. It can, however, be solved in various ways through an analysis of the flora of specific regions, where the specific goals vary depending on the flora studied and what specific questions of its composition and history are being studied." The same can be said for locating controversial species whose distribution is shifting from one or another group. Of course, a different researcher might place the species differently than I have, and be fully justified in doing so! The system used here, however, has one incontestable advantage: a single measure, a consistent subjective view is used to classify the species.

Floristic elements (latitudinal types) are defined as follows:

Arctic: includes species distributed primarily in a tundra zone and arctic deserts and further south, in a tundra belt and arctic barrens;

Boreal: includes species distributed in boreal coniferous forests, and further south, in corresponding altitudinal belts;

Arctic–boreal: includes species typical for arctic and taiga zones, and further south, in corresponding altitudinal belts;

Southern temperate: includes species whose primary habitat is broad-leaved forests;

Boreal–southern temperate: is a transitional type between boreal and southern temperate elements that includes species distributed in broad-leaved forests but that are broadly penetrating to taiga zone (or belt) and *vice versa*;
Subtropical: includes species distributed primarily in evergreen forests located north of the northern tropics (or south of the southern) and in montane evergreen forests of near-equatorial areas, on mountains above 1000 m a.s.l.;
Southern temperate–subtropical: includes species broadly distributed in both deciduous broad-leaved forests and evergreen subtropical forests;
Tropical–subtropical: includes species whose habitat is primarily in paleo- and/or neotropical areas (representatives of this element known is comparative floras usually have an even broader distribution and at times even penetrate into the zone of broad-leaved forests);
Multi zone: includes species distributed in various zones and mountain belts (for example, species falling into this group are distributed from the Arctic to the tropics but only in one hemisphere or even on the fringe of one continent).

Area types (longitudinal types) are defined as follows:

Circumpolar: includes species distributed in one latitudinal zone or a corresponding mountain belt in the entire or almost entire northern hemisphere;
Amphioceanic: includes species distributed primarily close to oceans, within 200 km, but that often penetrate inland into continental regions influenced by oceanic precipitation systems;
Amphipacific: is the same as above but relating to the Pacific Ocean;
Asian: includes species whose primary distribution is in Asia;
Eurasian: includes species whose distribution is in Eurasia;
Asian–American: includes species whose habitat encompasses Asia and America;
Eastern Asian: includes species whose distribution is in the east of Asia, that is, in eastern China and "Indo-China", but which occasionally penetrate into Malaysia and the Philippines and in Russia are encountered in Primorskii and Khabarovskii Krais, Chukotskii Autonomous Okrug, Kamchatskaya Oblast and Sakhalinskaya Oblast;
Eastern Asian–American: includes species found in eastern Asia and America;
Disjunctive: contains species having significant gaps in distribution;
Multi-areal: means species whose distribution encompasses different continents located in different longitudinal sectors (usually they are nearly cosmopolitan species).

A comparison of taxonomic spectra was carried out based on families, a method broadly applied in Russia to analyze local bryofloras, but seldom applied elsewhere. Basic to that method are assumptions that the character of the flora is determined primarily by representatives of the principal families (ones having the largest number of representatives), as well as by the fact that a similarity in the relative significance of the families in the comparable floras demonstrates the existence of genetic connections among them, which reflect a common origin. Each method clearly has its limitations in practice. The key limitation is that a species within a family can differ from the general pattern in its distribution and ecology. For example, *Radula prolifera* belongs predominately to the south-temperate–subtropical family Radulaceae, but is strictly an arctic species.

Results and discussion

According to Konstantinova (1998: 12) "the position of principal families and their portion in the flora of liverworts in the Arctic and Hypoarctic shows an amazing uniformity. The family Lophoziaceae invariably holds first place and Scapaniaceae the second, these accounting for more than 40% of the species composition of the floras. The family Jungermanniaceae holds the third place. These three principal families contain more than 50% of the species of each flora." I showed (Bakalin 2005b) that the signifi-

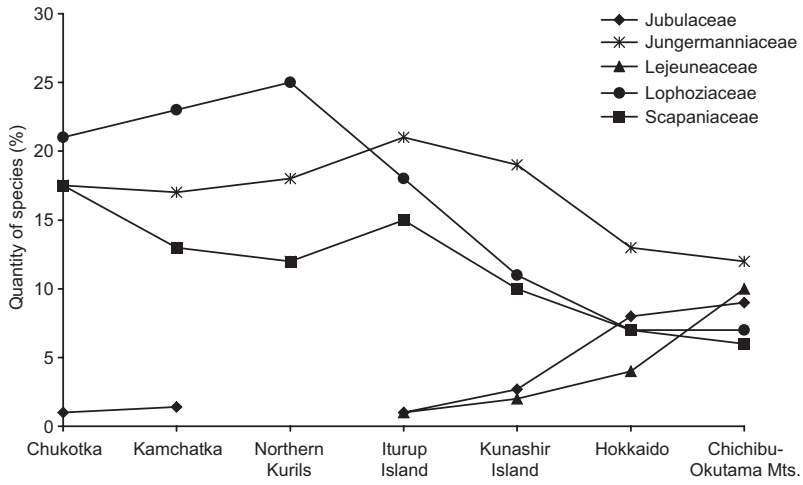

Fig. 2. Changes of contribution of principal families in the structure of regional floras in the north-east Pacific.

cance of the family Jungermanniaceae increased, although Lophoziaceae and Scapaniaceae remain among the principals when Commander Islands are included in Konstantinova's concept of northern Holarctic. This anomaly possibly demonstrates a specific feature of oceanic floras in the northwestern Pacific.

To check the veracity of my assumption and to measure the change in taxonomic composition along a latitudinal gradient, I identified the following principal families in the floras (listed in descending order of significance) that were used in the analysis (Table 2): Chukotka: Lophoziaceae, Scapaniaceae, Jungermanniaceae; Kamchatka and Northern Kurils: Lophoziaceae, Jungermanniaceae, Scapaniaceae; Iturup and Kunashir: Jungermanniaceae, Lophoziaceae, Scapaniaceae; Hokkaido: Jungermanniaceae, Jubulaceae, Lophoziaceae; Chichibu-Okutama: Jungermanniaceae, Lejeuneaceae, Jubulaceae. For comparison, in Korea, which occupies an intermediary position between island and continental floras of eastern Asia, the principal families were Lejeuneaceae, Jungermanniaceae and Jubulaceae (Yamada & Choe 1997).

The change in the contribution of principal families along the latitudinal gradient (Fig. 2) shows shifts at Kunashir and Hokkaido Islands. There is a steep increase in the significance of Jubulaceae and Lejeuneaceae, as well as a decrease in the significance of Lophoziaceae and Scapaniaceae. At the same time, within a certain variation, Jungermanniaceae remains a uniformly significant family.

The degree of similarity in the northwest Pacific flora can be measured by the number of common taxa, and the geographic distributions of the species makes it possible to identify the character or nature of the associations. Seventeen species are common to all the areas employed in the analysis i.e., Chukotka, Kamchatka Peninsula, Northern Kurils, Iturup, Kunashir, Hokkaido Islands, and the Chichibu-Okutama mountain range. Predominant among them are arctic and arctic–boreal taxa (14). Two multizonal species are also present. Floristic

Table 2. Contribution of principal liverwort families in the structure of regional floras in north-east Pacific.

	Chukotka	Kamchatka	Northern Kurils	Iturup Island	Kunashir Island	Hokkaido	Chichibu-Okutama Mts.
Jubulaceae	2	3		1	4	14	20
Jungermanniaceae	31	38	18	23	29	24	27
Lejeuneaceae				1	3	7	23
Lophoziaceae	37	51	25	19	16	13	16
Scapaniaceae	31	29	12	15	15	13	14
Total in flora	177	218	99	107	149	182	230

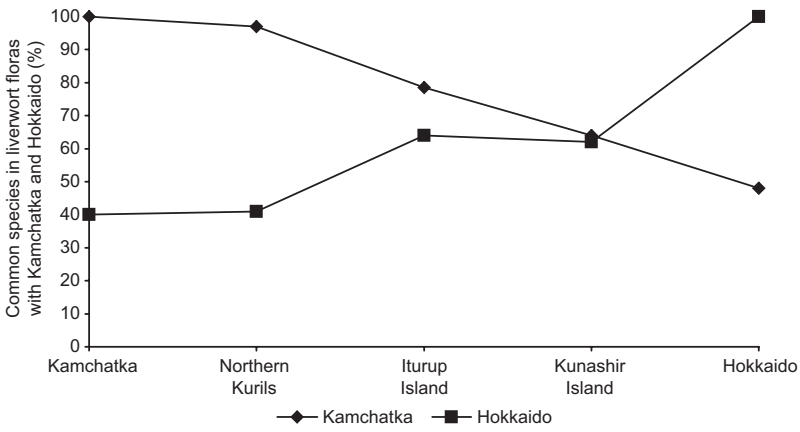

Fig. 3. Changes in shared species in the liverwort floras as compared with those of Kamchatka and Hokkaido.

connections primarily occur via a group of species found on plains in the north, and in mountain tundra and in high mountains in the south.

When limiting the number of flora elements in the analysis (the aforementioned but without Chukotka), three boreal species are added to the group of common species, these being *Conocephalum conicum*, *Pellia endiviifolia*, and *Ptilidium pulcherrimum*, as well as the multizonal East-Asian species *Conocephalum japonicum*. Forty-six species are common to all the areas of the Kurils.

Thirty-one taxa known only from the Northern Kurils were employed in the analysis. The majority of these have arctic, and less often, boreal distributions: *Anthelia julacea*, *Gymnomitrion pacificum*, *Lophozia pellucida* var. *rubrigemma*, *Marsupella brevissima*, *Prasanthus suecicus*, and *Tetralophozia setiformis*. Fifty-four taxa are specific to Kunashir Island, the majority of which have south-temperate or subtropical distribution: *Alobiellopsis parvifolia*, *Bazzania japonica*, *Blepharostoma minus*, *Calypogeia arguta*, *Frullania appendiculata*, *Geocalyx lancistipulus*, *Metzgeria fruticulosa*, *Trichocolea tomentella*, etc.

The south-temperate floristic element in the common species makes its appearance on Iturup Island and becomes prominent on Kunashir Island and further south. Kunashir shares 93 taxa with Hokkaido (more than half of the total flora). Alongside a number of arctic, arctic-boreal and boreal taxa (total 57), the greater portion of which are distributed in the mountains, a significant portion is formed of south-temperate, boreal–south-temperate, subtropical and south-temperate–subtropical species (total 31). As regards their longitudinal distribution, the number of species with the East-Asian range increases sharply (27, plus 2 East Asian–American).

As for the species encountered in more than one region, changes can be observed in quantitative floristic composition from north to south and *vice versa*, with Kamchatka as the starting point in the north and Hokkaido as the end point in the south (Table 3 and Fig. 3). It is obvious that, when moving from north to south, numbers of south-temperate and subtropical taxa increase at the expense of arctic taxa. I am, however, interested in how and where this change occurs. Because of the unwieldiness of analyzing all lati-

Table 3. Quantitative changes in shared species in liverwort floras with Kamchatka and Hokkaido.

	Kamchatka	Northern Kurils	Iturup Island	Kunashir Island	Hokkaido
Kamchatka	218	97	84	95	87
Hokkaido	87	41	69	93	182
Total in flora	218	99	107	149	182

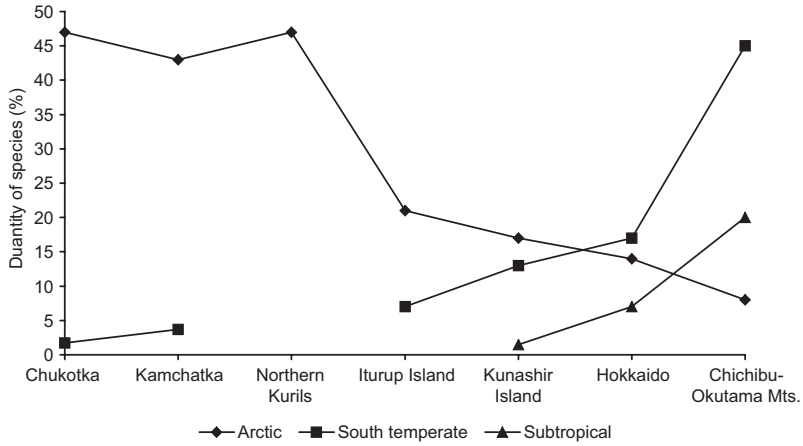

Fig. 4. Changes in the latitude fractional composition of selected floras.

tudinal and longitudinal groups, I identified three reference groups for latitudinal elements and three for longitudinal elements. I selected arctic, south-temperate and subtropical fractions for the latitudinal groups (Table 4 and Fig. 4). The quantitative floristic changes in the fractional composition shift to qualitative ones when moving to the south towards Kunashir and Hokkaido.

I selected three groups of species to present the results of the longitudinal analysis: circumpolar, whose numbers decline towards the south; East Asian that increase in the same direction; and amphioceanic fraction as a neutral group (Table 5 and Fig. 5). The point of intersection of the East Asian and circumpolar species is Hokkaido.

The analysis of latitudinal and longitudinal groups reveals that the flora of the most southern Kuril and Kunashir Islands barely belongs to the East-Asian floristic region and it cannot be assigned to the island floras farther north. At the same time, analyses of vascular plant distributions (Barkalov 2002, Krestov 2006) show that the boundary between the two regions should be set along the Ekaterina Strait or even along the Northern Kurils. I have not encountered a specific case but just a general holarctic pattern. Conclusions of Preston and Hill (1999), who con-

Table 4. Quantitative changes in the latitude fractional composition of selected floras.

Flora elements	Chukotka	Kamchatka	Northern Kurils	Iturup Island	Kunashir Island	Hokkaido	Chichibu Okutama Mts.
Arctic	84	93	47	22	26	26	18
South temperate	3	8		7	20	31	45
Subtropical					2	13	39
Total in flora	177	218	99	107	149	182	230

Table 5. Quantitative changes in the longitude fractional composition of selected floras.

Area type	Chukotka	Kamchatka	Northern Kurils	Iturup Island	Kunashir Island	Hokkaido	Chichibu-Okutama Mts.
Circumpolar	140	166	81	60	73	65	58
Amphioceanic	12	19	8	10	18	16	21
East Asian	2	13	7	25	38	70	113
Total in flora	177	218	99	107	149	182	230

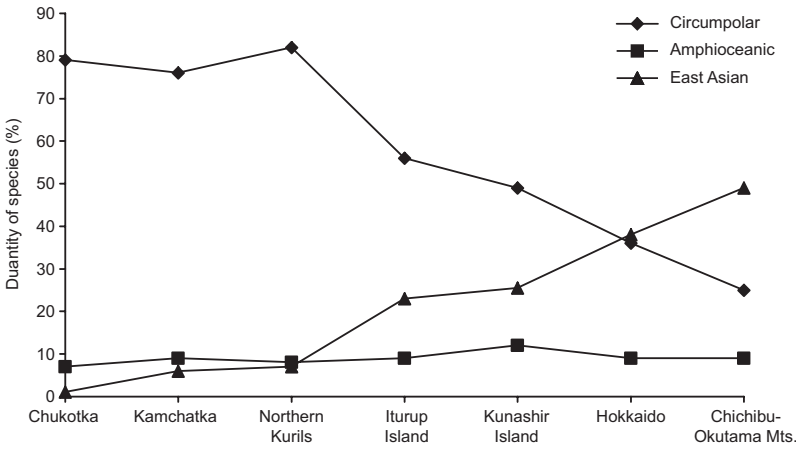

Fig. 5. Quantitative changes in the longitude fractional composition of selected floras.

ducted an analysis of the higher plant distribution in Britain and Ireland, are similar: the mosses and liverworts tend to have more northerly distributions than the vascular plants.

Conclusion

This liverwort research shows a progressive decline of primarily northern holarctic families in the island floras from north to south and an increase in the same direction of primarily subtropical taxa. However, the qualitative shift, when the number of species from the families Lejeuneaceae and Jubulaceae begin to exceed the quantity of species of Lophoziaceae and Scapaniaceae occurs only on Hokkaido and Honshu. The universally high significance of Jungermanniaceae means that it is a specific feature of the liverwort flora of the northwestern Pacific (to the north of subtropics).

An analysis of selected latitudinal floristic elements shows a sharp increase in the number of south-temperate and subtropical species, with a southern shift beginning on Hokkaido. An analysis of longitudinal distributions shows a similar tendency.

A conclusion can be drawn as to where the boundary of the East Asian floristic region in the Pacific Ocean is located. The northerly break-point is in the region of the Ekaterina Pass between Kunashir and Iturup Islands, although irrefutable qualitative changes in the floristic complexes only begin to occur on Hokkaido. This conclusion concurs, in several aspects, with the latest research on the geography of vascular plants (Krestov 2006), which draws the floristic boundary between Kunashir and Iturup Islands.

Acknowledgments

This manuscript was translated into English by Misha Jones, to whom I am sincerely grateful. I am also grateful to Dr. Valentina Ya. Cherdantseva for a thorough reading of the manuscript and for her comments. I am indebted to three anonymous readers who provided constructive comments on this article. This research was partially supported by the Russian Foundation for Basic Research (No. 06-05-64137), FEB RAS (Nos. 06-III-A-06-153, 06-III-B-06-190) and the Russian Science Support Foundation.

References

Afonina, O. M. & Duda, J. 1993: Liverworts of Chukotka. — *Bot. Zh.* 78: 77–93. [In Russian with English summary].

Anonymous 1994: *Atlas of Sakhalin Region. Part II. Kuril Islands*. — VKF, Yuzhno-Sakhalinsk.

Bakalin, V. A. 2005a: New data on distribution of liverworts on Kamchatka Peninsula (North-West Pacific, Russia). — *Arctoa* 14: 155–162.

Bakalin, V. A. 2005b: The liverwort flora of Bering Island (North-West Pacific, Russia). — *Lindbergia* 30: 79–92.

Bakalin, V. A. 2006: Ecological features and trends in the formation of the flora of liverworts under the impact of current volcanic and glacial activities: the example of Ushkovskii Volcano, Kamchatka. — *Russian Journal of Ecology* 37: 13–18.

Bakalin, V. A. & Cherdantseva, V. Ya. 2006: Bryophytes of northern Kuril Islands (North-West Pacific). — *Arctoa* 15: 131–153.

Bardunov, L. V. [Бардунов, Л. В.] 1974: [*The mosses of Altai and Sayan*]. — Nauka, Novosibirsk. [In Russian].

Barkalov, V. Yu. [Баркалов, В. Ю.] 2002: [Outline of vegeta-

tion]. — In: Storozhenko, S. Y., Bogatov, V. V. & Leley, A. S. [Стороженко, С. Ю., Богатов, В. В. & Лелей, А. С.] (eds.), [*Flora and fauna of Kuril Islands*]: 35–66. Dalnauka, Vladivostok. [In Russian].

Bezverkhniy, V. L., Pletnev, V. L. & Nabiullin, A. A. [Безверхний, В. Л., Плетнев, С. П. & Набиуллин, А. А.] 2002: [Outline of geological structure and development of the Kuril Islands System and adjacent regions]. — In: Storozhenko, S. Yu., Bogatov, V. V. & Leley, A. S. [Стороженко, С. Ю., Богатов, В. В. & Лелей, А. С.] (eds.), [*Flora and fauna of Kuril Islands*]: 23–34. Dalnauka, Vladivostok. [In Russian].

Gardner, J. S. & Ettingshausen, C. 1879: *A monograph of the British Eocene flora. Filice I.* — Paleontogr. Soc., London.

Gradstein, S. R. & Vana, J. 1987: On the occurrence of Laurasian liverworts in the tropics. — *Mem. New York Bot. Garden* 45: 388–425.

Hulten, E. 1933: Studies on the origin and distribution of the flora in Kurile Islands. — *Bot. Not., Lund* 1–3: 325–243.

Inoue, H. 1976: Hepaticae and Anthocerotae of the Chichibu-Okutama Mountains, Central Japan. — *J. Hattori Bot. Lab.* 37: 186–216.

Konstantinova, N. A. [Константинова, Н. А.] 1998: [*The main patterns of liverwort floras northern Holarctic*]. — Moskva. [In Russian].

Krestov, P. V. [Крестов, П. В.] 2006: [*Vegetation cover and phytogeographic lines of northern Pacific*]. — TINRO-tsentr, Vladivostok. [In Russian].

Krischtofovich, A. N. [Криштофович, А. Н.] 1934: [*Course of paleobotany*]. — Gorgeonefteizdat, Leningrad-Moskva-Groznyy-Novosibirsk. [In Russian].

Kudo, Y. 1922: Flora of the island Paramushir. — *J. Coll. Agricultural Hokkaido Imp. Univ. Sapporo* 11: 23–283.

Miyabe, K. 1890: The flora of the Kurile Islands. — *Mem. Boston Soc. Nat. Hist.* 4: 203–275.

Nyushko, T. I. & Potemkin, A. D. 2005: Liverworts of Sakhalin and Kuril Islands: a statement of study. — In: Afonina, O. M. (ed.), *Actual problems of bryology*: 135–142. Saint-Petersburg. [In Russian with English summary].

Popov, M. G. [Попов, М. Г.] 1983: [*Phylogeny, florogenetic, florography, systematic. Part I*]. — Naukova Dumka, Kiev. [In Russian].

Preston, C. D. & Hill, M. O. 1999: The geographical relationships of the British and Irish flora: a comparison of pteridophytes, flowering plants, liverworts and mosses. — *J. Biogeography* 26: 629–642.

Qian, H., Krestov, P., Fu, P.-Y., Wang, Q.-L., Song, J.-S. & Chourmouzis, C. 2003: Phytogeography of Northeast Asia. — In: Kolbek, J. (ed.), *Forest vegetation of Northeast Asia*: 51–91. Kluwer Acad. Publishers, Dordrecht, Boston, London.

Schofield, W. B. 1992: Bryophyte distribution patterns — In: Bates, J. W. & Farmer, A. M. (eds.), *Bryophytes and lichens in a changing environment*: 103–130. Clarendon Press, Oxford.

Shantser, A. E. [Шанцер, А. Е.] 1974: Stages of paleorelief development. — In: Luchinsky, I. A. [Лучински, И. А.] (ed.), [*Kamchatka, Kuril and Commander Islands*]: 58–82. Nauka, Moskva. [In Russian].

Takhtajan, A. L. 1986: *Floristic regions of the world*. — Univ. California Press, Berkeley.

Tatewaki, M. 1933: The phytogeography of the Middle Kurils. — *J. Fac. Agr. Hokkaido Univ.* 29: 191–363.

Tatewaki, M. 1957: Geobotanical study on the Kurile Islands. — *Acta Horti Gotoburgensis* 21: 43–123.

Tiffney, B. H. 1985: Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. — *J. Arnold Arboretum* 66: 73–94.

Tolmachyov, A. I. [Толмачев А. И.] 1962: [*Principles of Areology*]. — Izdatel'stvo Leningradskogo Universiteta, Leningrad. [In Russian].

Wolfe, J. A. 1975: Some aspects of plant geography of the northern hemisphere during the Late Cretaceous and Tertiary. — *Ann. Missouri Bot. Garden* 62: 264–279.

Yakubov, V. V. & Chernyagina, O. A. 2004: *Catalogue of flora of Kamchatka* (*vascular plants*). — Kamchatpress, Petropavlovsk-Kamchatski. [In Russian with English summary].

Yamada, K. & Choe, D.-M. 1997: A checklist of Hepaticae and Anthocerotae in the Korean Peninsula — *J. Hattori Bot. Lab.* 81: 281–306.

Yamada, K. & Iwatsuki, Z. 2006: Catalog of the hepatics of Japan — *J. Hattori Bot. Lab.* 99: 1–106.

Appendix. Taxa, their localities in the study area and their general distributions. Abbreviations: Ch = Chukotka, K = Kamchatka Peninsula, NK = Northern Kurils, It = Iturup Island, Kun = Kunashir Island, H = Hokkaido, CO = Chichibu-Okutama Mts. Taxonomy is based on Bakalin (2005a) and Yamada and Iwatsuki (2006). Families are arranged alphabetically.

Taxa	Locality	General distribution
Acrobolbaceae		
Acrobolbus ciliatus (Lindb.) Schiffn.	CO	montane, boreal-temperate, amphipacific
Allisoniaceae		
Calycularia crispula Mitt.	K, Kun, H, CO	temperate–subtropical, circumpolar
C. laxa Lindb. & Arnell	Ch, K, Kun	montane-arctic, Asian–American
Aneuraceae		
Aneura maxima (Schiffn.) Steph.	CO	temperate–subtropical, East Asian
A. pinguis (L.) Dumort.	Ch, K, NK, It, Kun, H, CO	multizonal, multiareal
Riccardia aeruginosa Furuki	NK, Kun	multizonal, East Asian
R. palmata (Hedw.) Carruth.	K, Kun, H, CO	boreal, circumpolar
R. chamaedryfolia (With.) Grolle	K, Kun, H	boreal, circumpolar
R. latifrons (Lindb.) Lindb.	K, Kun, H, CO	arctic–boreal, circumpolar
R. multifida (L.) Gray ssp. *decrescens* (Steph.) Furuki	It, Kun, H, CO	temperate, East Asian
R. nagasakiensis (Sreph.) S. Hatt.	CO	temperate-subtropical, East Asian (only Japan)
R. planiflora (Steph.) S. Hatt.	H, CO	temperate, East Asian (only Japan)
R. subalpina Furuki	Kun, H	montane, arctic–boreal, East Asian (only Japan)
R. vitrea Furuki	It	temperate, East Asian
Antheliaceae		
Anthelia julacea (L.) Dumort.	Ch, K, NK	montane, arctic, circumpolar
A. juratzkana (Limpr.) Trev.	Ch, K, NK, It, Kun, H	montane, arctic, circumpolar
Anthocerotaceae		
Anthoceros agrestis Paton	K	temperate, circumpolar
A. fusiformis Austin	H	temperate, American
A. punctatus L.	CO	temperate, circumpolar
Phaeoceros carolinianus (Michx.) Prosk.	H	temperate–subtropical, circumpolar
P. gemmifer (Horikawa) J. Haseg.	CO	temperate–subtropical, East Asian
P. laevis Prosk.	CO	temperate, amphioceanic
Arnelliaceae		
Arnellia fennica (Gottsche) Lindb.	Ch	montane, arctic–boreal, circumpolar
Aytoniaceae		
Asterella crassa Shimizu & S. Hatt.	CO	montane, temperate, East Asian (only Japan)
A. cruciata (Steph.) Horikawa	CO	temperate, East Asian (only Japan)
A. gracilis (F. Weber) Underw.	K, Ch	montane, arctic, circumpolar
A. saccata (Wahlenb.) A. Evans	K, Ch	montane, arctic–boreal, circumpolar
A. yoshinagana (Horikawa) Horikawa	CO	montane, temperate, East Asian

Mannia fragrans (Balb.) Frye & Clark	Ch, CO	montane, arctic–boreal, circumpolar
M. laevigata Shimizu & S. Hatt.	CO	montane, temperate, East Asian (only Japan)
M. pilosa (Horn) Frey & Clark	Ch, K	montane, arctic, circumpolar
M. sibirica (Mull.Frib.) Frey & Clark	Ch	boreal–temperate–subtropical, circumpolar
M. triandra (Scop.) Grolle	Ch, H	montane, arctic–boreal, circumpolar
Plagiochasma japonicum (Steph.) Hass.	CO	montane, tropical-subtropical, circumpolar
P. pterospermum C. Massal.	H	montane, temperate, Asian
Reboulia hemisphaerica (L.) Raddi	Kun, H, CO	montane, multizonal, multiareal
Blasiaceae		
Blasia pusilla L.	Ch, K, NK, It, Kun, H, CO	multizonal, multiareal
Cavicularia densa Steph.	H	temperate, East Asian
Calypogeiaceae		
Calypogeia angusta Steph.	H, CO	temperate, East Asian
C. arguta Nees & Mont.	Kun, H, CO	temperate, amphioceanic
C. azurea Stotler & Crotz	K, H, CO	temperate, amphioceanic
C. integristipula Steph.	Ch, K, It, Kun, H	montane, arctic–boreal, circumpolar
C. japonica Steph.	H	subtropical, East Asian
C. muelleriana (Schiffn.) Mull. Frib.	Ch, K, NK, It, Kun, CO	montane, arctic–boreal, circumpolar
C. neesiana (C. Massal. & Carest) Mull. Frib.	Ch, K, Kun, H, CO	montane, arctic–boreal, circumpolar
C. neogaea (R.M. Schust.) Bakalin	K, NK, It, Kun	boreal–temperate, East Asian–American
C. sphagnicola (Arnell & J.Perss.) Warnst. & Loeske	Ch, K, It, H	montane, arctic–boreal, circumpolar
C. suecica (Arnell & J. Perss.) Mull. Frib.	Kun	boreal, amphioceanic
C. tosana (Steph.) Steph.	H, CO	temperate, East Asian
Eocalypogeia schusteriana (S. Hatt. & Mizut.) R.M. Schust.	Ch	montane, arctic–boreal, Asian–American
Metacalypogeia alternifolia (Gottsche, Lindenb. & Nees) Grolle	H	temperate–subtropical, East Asian
M. cordifolia (Steph.) H. Inoue	Kun, H, CO	temperate, East Asian (also disjunction in Attu, Aleutians)
Cephaloziaceae		
Alobiellopsis parvifolia (Steph.) R.M. Schust.	Kun	boreal, East Asian
Cephalozia ambigua C. Massal.	Ch, K	montane, arctic, circumpolar
C. bicuspidata (L.) Dumort.	Ch, K, NK, It, Kun, H	arctic–boreal, multiareal
C. catenulata (Huebener) Lindb.	H, CO	temperate–subtropical, amphioceanic
C. connivens (Dicks.) Lindb.	K, Kun, H	boreal, circumpolar
C. leucantha Spruce	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, circumpolar
C. loitlesbergeri Schiffn.	K	boreal, circumpolar
C. lunulifolia (Dumort.) Dumort.	Ch, K, NK, It, Kun, CO	montane, arctic–boreal, circumpolar
C. otaruensis Steph.	K, It, H, CO	boreal, amphipacific
C. pachycaulis R.M. Schust.	K, NK, Kun	montane, arctic–boreal, Asian–American
C. pleniceps (Aust.) Lindb.	Ch, K, NK, It, Kun	montane, arctic–boreal, circumpolar
C. zoopsioides Horikawa	CO	subtropical, East Asian
Cladopodiella fluitans (Nees) H. Buch	Ch, K, NK, It, Kun, H	boreal, circumpolar

continued

Appendix. Continued.

Taxa	Locality	General distribution
C. francisci (Hook.) H. Buch *ex* Joerg.	K, It, Kun, H	montane, arctic–boreal, amphioceanic
Hygrobiella laxifolia (Hook.) Spruce	K, NK, It, Kun, H	montane, arctic–boreal, amphioceanic
Iwatsukia jishibae (Steph.) N. Kitag.	Kun, CO	montane, tropical–subtropical, circumpolar
Nowellia curvifolia (Dicks.) Mitt.	Kun, H, CO	temperate, amphioceanic
Odontoschisma denudatum (Mart.) Dumort.	Ch, Kun, H, CO	temperate, circumpolar
O. elongatum (Lindb.) A. Evans	Ch, K, NK	montane, arctic, circumpolar
O. grossiverrucosum Steph.	CO	temperate–subtropical, East Asian
O. macounii (Aust.) Underw.	Ch, K	montane, arctic, circumpolar
Pleurocladula albescens (Hook.) Grolle	Ch, K, NK, It, Kun, H	montane, arctic, circumpolar
Schiffneria hyalina Steph.	CO	tropical–subtropical, presumably East Asian
Schofieldia monticola Godfrey	K	montane, arctic, amphipacific
Cephaloziellaceae		
Cephaloziella arctogena (Schust.) Konstant.	Ch, K, NK, Kun	montane, arctic, circumpolar
C. aspericaulis Joerg.	Ch	arctic, amphioceanic
C. hampeana (Nees) Schiffn.	K	boreal, circumpolar
C. divaricata (Sm.) Schiffn.	Ch, K, NK, It, H	montane, arctic, circumpolar
C. elachista (Jack *ex* Gottsche & Rabenh.) Schiffn.	It, Kun	boreal–temperate, amphioceanic
C. elegans (Heeg.) Schiffn.	Ch, K	boreal, disjunctive
C. grimsulana (Jack *ex* Gottsche & Rabenh.) Lacout	Ch, K	montane, arctic, circumpolar
C. microphylla (Steph.) Douin	H, CO	temperate–subtropical, East Asian
C. rubella (Nees) Warnst.	Ch, K	boreal, circumpolar
C. spinicaulis Douin	H, CO	temperate, Asian–American
C. spinigera (Lindb.) Joerg.	Ch, K	montane, arctic, circumpolar
C. uncinata R.M. Schust.	K	arctic, circumpolar
C. varians (Gottsche) Steph. (= *C. arctica* Bryhn & Douin)	Ch, K, NK	montane, arctic, circumpolar
Cylindrocolea recurvifolia (Steph.) H. Inoue	H	temperate–subtropical, East Asian
Cleveaceae		
Athalamia nana (Shim. & S. Hatt.) S. Hatt.	H, CO	montane, temperate, East Asian
A. hyalina (Sommerf.) S. Hatt.	Ch, K, NK	montane, arctic, circumpolar
Peltolepis quadrata (Saut.) Mull. Frib.	K, H	montane, arctic, circumpolar
Sauteria alpina (Nees) Nees	Ch, K, NK, H	montane, arctic, circumpolar
Codoniaceae		
Fossombronia alaskana Steere & Inoue	Ch, Kun	arctic–boreal, East Asian–American
F. foveolata Lindb. var. *cristula* (Austin) R.M. Schust.	H	temperate, East Asian–American
Conocephalaceae		
Conocephalum conicum (L.) Underw.	K, NK, It, Kun, H, CO	boreal, circumpolar
C. japonicum (Thunb.) Grolle	Ch, K, NK, It, Kun, H, CO	multizonal, East Asian

Geocalycaceae		
Geocalyx graveolens (Schrad.) Nees	Ch, K, Kun	boreal, circumpolar
G. lancistipulus (Steph.) S. Hatt.	Kun, H, CO	temperate, East Asian
Harpanthus flotovianus (Nees) Nees	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, amphioceanic
H. scutatus (F. Weber & D. Mohr) Spruce	H, CO	temperate, circumpolar
Gymnomitriaceae		
Eremonotus myriocarpus (Carr.) Lindb. & Kaal.	Ch, K, NK, Kun, CO	montane, arctic–boreal, circumpolar
Gymnomitrion apiculatum (Schiffn.) Mull. Frib.	Ch, K, NK, Kun	montane, arctic, circumpolar
G. concinnatum (Lightf.) Corda	Ch, K, NK, It, Kun, H, CO	montane, arctic, circumpolar
G. corallioides Nees	Ch, K, Kun, H, CO	montane, arctic, circumpolar
G. pacificum Grolle	Ch, K, NK	montane, arctic, amphipacific
Marsupella adusta (Nees) Spruce	K, Kun	montane, arctic, amphioceanic
M. alata S. Hatt.	H	montane, arctic, East Asian
M. alpina (Gottsche *ex* Limpr.) H. Bern.	K, NK, Kun	montane, arctic, circumpolar
M. arctica (Berggr.) Bryhn & Kaal.	Ch	arctic, circumpolar
M. boeckii (Aust.) Lindb. *ex* Kaal.	Ch, K, NK, Kun, H	montane, arctic, circumpolar
M. brevissima (Dumort.) Grolle	K, NK	montane, arctic, circumpolar
M. funckii (F.Web. & Mohr) Dumort.	K, Kun	montane, temperate, amphioceanic
M. disticha Steph.	CO	montane, arctic, East Asian (only Japan)
M. sparsifolia (Lindb.) Dumort.	K	montane, arctic, circumpolar
M. commutata (Limpr.) H. Bern.	Ch, K, It, Kun, H, CO	montane, arctic, disjunctive
M. condensata (Aongstr. *ex* C.Hartm.) Lindb. *ex* Kaal.	Ch, K	montane, arctic, circumpolar
M. emarginata (Ehrh.) Dumort.	Ch, K, NK, Kun	montane, arctic–boreal, circumpolar
M. sphacelata (Gieseke *ex* Lindenb.) Dumort.	K, NK, It, Kun	montane, arctic–boreal, circumpolar
M. sprucei (Limpr.) H. Bern.	Ch, K, NK, It	montane, arctic, circumpolar
M. tubulosa Steph.	K, Kun, H, CO	montane, arctic–boreal, circumpolar
Prasanthus suecicus (Gottsche) Lindb.	Ch, K, NK	montane, arctic, circumpolar
Herbertaceae		
Herbertus aduncus (Dicks.) Gray	Ch, K, H, CO	montane, arctic–boreal, Asian–American
H. sakuraii (Warnst.) S. Hatt.	H, CO	montane, arctic–boreal, circumpolar
Jubulaceae		
Frullania appendiculata Steph.	Kun, H, CO	subtropical, East Asian
F. bolanderi Aust.	K, H	boreal–temperate, circumpolar
F. davurica Hampe	K, H, CO	boreal–temperate, Asian
F. densiloba Steph. in A. Evans	H, CO	subtropical, East Asian–American
F. dilatata (L.) Dumort.	K	temperate, Euro–Asian
F. diversitexta Steph.	CO	subtropical, East Asian
F. fauriana Steph.	CO	montane, temperate, East Asian (only Japan)
F. hamatiloba Steph.	H, CO	montane, temperate, East Asian
F. inflata Gottsche	It, H, CO	temperate–subtropical, Asian–American

continued

Appendix. Continued.

Taxa	Locality	General distribution
F. inflexa Mitt.	CO	subtropical East Asian
F. koponenii S. Hatt.	Kun, H	temperate Asian
F. motoyana Steph.	CO	subtropical East Asian (only Japan)
F. muscicola Steph.	Kun, H, CO	temperate-subtropical East Asian
F. nepalensis (Spreng) Lehm. & Lindenb.	CO	montane, temperate–subtropical, East Asian
F. nisqualensis Sull.	Ch	montane, arctic, Asian–American
F. oakesiana Austin ssp. *takayuensis* (Steph.) R.M. Schust.	H	montane, boreal–temperate, East Asian
F. osumiensis (S. Hatt.) S. Hatt.	CO	subtropical, East Asian
F. parvistipula Steph.	H	temperate–subtropical, Euro-Asian
F. pedicellata Steph.	H, CO	subtropical, East Asian (only Japan)
F. sackawana Steph.	CO	subtropical, East Asian (only Japan)
F. schensiana C. Massal.	CO	montane, temperate–subtropical, East Asian
F. tamarisci (L.) Dumort.	Ch	montane, boreal–temperate, circumpolar
F. taradakensis Steph.	H, CO	subtropical, East Asian
F. usamiensis Steph.	CO	montane, temperate, East Asian
F. valida Steph.	CO	subtropical, East Asian (only Japan)
Jubula japonica Steph.	H, CO	subtropical, East Asian
Neohattoria herzogii (Hatt.) Kamim.	Kun, H, CO	montane, boreal–temperate, East Asian
Jungermanniaceae		
Crossogyna autumnalis (DC) Schljakov	Ch, K, Kun, H, CO	temperate, circumpolar
C. undulifolia (Nees.) Mull. Frib.	Ch	arctic–boreal, circumpolar
Cryptocolea imbricata R.M. Schust.	Ch, K	arctic, circumpolar
Cryptocoleopsis imbricata Amak.	K, NK, Kun, H	montane, arctic, East Asian
Hattoriella morrisoncola (Horikawa) Bakalin	CO	montane, boreal, East Asian
Jungermannia atrovirens Dumort.	K, NK, H, CO	montane, arctic, circumpolar
J. borealis Damsh. & Vana	K, Ch	montane, arctic, circumpolar
J. eucordifolia Schljakov	Ch, K, NK, lt, Kun	montane, arctic–boreal, circumpolar
J. exsertifolia Steph.	Ch, K, NK, lt, Kun, H, CO	montane, arctic, East Asian
J. polaris Lindb.	Ch, K, NK	montane, arctic, circumpolar
J. pumila With.	Ch, K, NK, lt, Kun, H	montane, arctic, circumpolar
Leiocolea collaris (Nees) Schljakov	Ch	montane, arctic–boreal, circumpolar
L. badensis (Gottsche) Schiffn.	Ch	montane, arctic–boreal, circumpolar
L. bantriensis (Hook.) Joerg.	Ch, K	montane, arctic–boreal, circumpolar
L. chichibuensis (H. Inoue) H. Inoue	CO	montane, arctic–boreal, East Asian (only Japan)
L. gillmanii (Aust.) A. Evans	Ch, K	montane, arctic–boreal, circumpolar
L. heterocolpos (Thed. *ex* Hartm.) H. Buch var. *heterocolpos*	Ch, K, NK	montane, arctic–boreal, circumpolar
L. heterocolpos (Thed. *ex* Hartm.) H. Buch var. *harpanthoides* (Bryhn & Kaal.) S.W. Arnell	Ch	montane, arctic, circumpolar

Leiocolea igiana (S. Hatt.) H. Inoue	CO	montane, arctic–boreal, East Asian (only Japan)
L. mayebarae (S. Hatt.) Furuki & Mizut.	CO	montane, arctic–boreal, East Asian (only Japan)
L. rutheana (Limpr.) Mull. Frib.	Ch, K	montane, arctic–boreal, circumpolar
L. lanceolata Nees	CO	boreal, circumpolar
Liochlaena subulata (A. Evans) Schljakov	Kun, H	boreal–temperate, circumpolar
Mesoptychia sahlbergii (Lindb.) A. Evans	Ch	montane, arctic, Asian–American
Mylia anomala (Hook.) S. Gray	Ch, K, NK, It, Kun, H	montane, arctic–boreal, circumpolar
M. taylorii (Hook.) S. Gray	Ch, It, Kun, CO	montane, arctic–boreal, circumpolar
M. verrucosa Lindb.	It, Kun, H, CO	temperate, East Asian
Nardia assamica (Mitt.) Amak.	K, It, Kun, H, CO	montane, arctic–boreal, East Asian
N. breidleri (Limpr.) Lindb.	K, NK, It, Kun	montane, arctic, circumpolar
N. compressa (Hook.) S. Gray	K, NK	montane, arctic, amphioceanic
N. geoscyphus (De Not.) Lindb.	Ch, K, NK, H	montane, arctic, circumpolar
N. insecta Lindb.	Ch, K	montane, arctic, circumpolar
N. japonica Steph.	Ch, K, NK, It, Kun, H, CO	montane, arctic, circumpolar
N. scalaris S. Gray	Ch, K, NK, It, Kun, H, CO	montane, arctic, circumpolar
N. subclavata (Steph.) Amak.	It, Kun, H, CO	montane, arctic–boreal, East Asian
N. unispiralis Amak.	K, It, Kun, H	montane, arctic, East Asian
Plectocolea biloba Amak. *(= J. cephalozioides* Amak.)	H	montane, arctic–boreal, East Asian
P. erecta Amak.	CO	montane, temperate, East Asian (only Japan)
P. hattoriana Amak.	H	montane, arctic–boreal, East Asian (only Japan)
P. hyalina (Lyell) Mitt.	Ch, K, It, Kun, H	arctic–boreal, circumpolar
P. infusca Mitt. var. *ovicalyx* (Steph.) Bakalin	H, CO, It, Kun	montane, boreal, East Asian
P. infusca Mitt. var. *ovalifolia* Amak.	K, NK, Kun, H, CO	boreal–temperate, East Asian
P. obovata (Nees) Lindb.	K, NK	montane, arctic, circumpolar
P. obscura A. Evans	K	montane, arctic–boreal, amphioceanic
P. rigidula S. Hatt.	Kun	montane, temperate, East Asian (only Japan)
P. rosulans (Steph.) S. Hatt.	It, Kun, CO	temperate-subtropical East Asian
P. subelliptica (Lindb. *ex* Kaal.) A. Evans	Ch, K, NK	montane, arctic–boreal circumpolar
P. torticalyx (Steph.) S. Hatt.	CO	temperate–subtropical, East Asian (only Japan)
Plectocolea truncata* (Nees) Bakalin, *comb. nov.		
Basionym: *Jungermannia truncata* Nees, Enum. Pl. Crypt. Jav.: 29. 1830.	CO	tropical–subtropical, East Asian
P. virgata Mitt.	It, H, CO	montane, boreal–temperate, East Asian
P. vulcanicola Schiffn.	K, It, Kun, H	montane, arctic–boreal, East Asian
Solenostoma caespiticium (Lindenb.) Steph.	Ch, K, It, Kun	montane, arctic–boreal, amphioceanic
S. confertissimum (Nees) Schljakov	Ch, K	montane, arctic, circumpolar
Solenostoma fauriana* (Beauverd) Bakalin, *comb. nov.		
Basionym: *Jungermannia fauriana* Beauverd in Steph. Spec. Hep. 6: 571. 1924.	Kun	montane, temperate, East Asian

continued

Appendix. Continued.

Taxa	Locality	General distribution
S. fusiforme (Steph.) R.M. Schust.	K, It, Kun, H, CO	montane, arctic, East Asian
S. gracillimum (Sm.) R.M. Schust.	K	boreal–temperate, circumpolar
S. handelii Schiffn.	Kun	montane, boreal–temperate, Asian
S. jenseniana (Grolle) Bakalin	K, It, CO	montane, arctic, circumpolar
S. koreanum Steph.	K, NK, It, Kun, CO	montane, arctic, East Asian
S. pyriflorum Steph. var. *pyriflorum*	It, H, CO	montane, arctic–boreal, Asian (disjunction in Appalachians)
Solenostoma pyriflorum* Steph. var. *minutissima* (Amak.) Bakalin, *comb. nov. Basionym: *Jungermannia pyriflora* Steph. var. *minutissima* Amak., J. Hattori Bot. Lab. 22: 61. 1960.	It, Kun	montane, boreal, East Asian
S. rubrum (Gottsche *ex* Underw.) R.M. Schust.	Ch	arctic–boreal, amphipacific
S. sphaerocarpum (Hook.) Steph. var. *nana* (Nees) R.M. Schust.	K	arctic–boreal, circumpolar
S. sphaerocarpum (Hook.) Steph. var. *sphaerocarpum*	Ch, K, Kun, CO	montane, arctic–boreal, circumpolar
Lejeuneaceae		
Acrolejeunea pusilla (Steph.) Grolle & Grandst.	CO	subtropical, East Asian (only Japan)
Cheilolejeunea khasiana (Mitt.) N. Kitag.	H, CO	montane, temperate, East Asian
C. obtusifolia (Steph.) S. Hatt.	CO	montane, temperate, East Asian
Cololejeunea japonica (Schiffn) S. Hatt.	CO	subtropical, East Asian
C. longifolia (Mitt.) Benedix	CO	subtropical, East Asian
C. macounii (Spruce in Underw.) A. Evans	Kun, H, CO	montane, temperate–subtropical, amphipacific
C. spinosa (Horikawa) Pande & Misra	CO	subtropical, Asian
Dicranolejeunea yoshinagana (S. Hatt.) Mizut.	CO	montane, temperate–subtropical, East Asian
Drepanolejeunea angustifolia (Mitt.) Grolle	CO	montane, subtropical, East Asian
Lejeunea aquatica Horikawa	CO	subtropical, East Asian
L. compacta (Steph.) Steph.	H, CO	subtropical, East Asian
L. discreta Gottsche	CO	subtropical, East Asian (only Japan).
L. flava (Sw.) Nees	CO	subtropical, Asian–American
L. japonica Mitt.	Kun, H, CO	subtropical, East Asian
L. kodamae Ikegami & H. Inoue	CO	montane, temperate, East Asian (only Japan)
Lejeunea parva (S. Hatt.) Mizut	H, CO	temperate–subtropical, East Asian
Lejeunea ulicina (Tayl.) Gottsche & al.	CO	montane, subtropical, Euro-Asian
Leucolejeunea subalpina (S. Hatt.) S. Hatt.	CO	montane, boreal–temperate, East Asian (only Japan)
Nipponolejeunea pilifera (Steph.) S. Hatt.	H, CO	montane, boreal–temperate, East Asian
N. subalpina (Horikawa) S. Hatt.	It, Kun, H, CO	montane, boreal–temperate, East Asian
Ptychanthus striatus (Lehm. & Lindenb.) Nees	CO	tropical–subtropical, Asian (with disjunction in Africa)
Trocholejeunea sandvicensis (Gottsche) Mizut.	CO	temperate–subtropical, circumpolar
Tuzibeanthus chinensis (Steph.) Mizut.	CO	montane, subtropical, East Asian

Lepidoleanaceae		
Trichocoleopsis sacculata (Mitt.) Okam.	H, CO	subtropical, East Asian
Neotrichocolea bissetii (Mitt.) S. Hatt.	CO	subtropical, East Asian
Lepidoziaceae		
Bazzania japonica (Sande Lac.) Lindb.	Kun	temperate–subtropical, East Asian
B. bidentula (Steph.) Steph.	K, It, H, CO	temperate, Asian
B. pompeana (Sande Lac.) Mitt.	CO	subtropical, East Asian (only Japan)
B. ovifolia (Steph.) S. Hatt.	K, It, Kun, H, CO	temperate, East Asian
B. tricrenata (Wahlenb.) Lindb.	K, It, Kun, H, CO	montane, arctic–boreal, circumpolar
B. trilobata (L.) S. Gray	It, Kun, H, CO	temperate, amphioceanic
B. tridens (Reinw., Blume & Nees) Trevis	CO	subtropical, East Asian
B. yoshinagana (Steph.) Steph. in S. Hatt.	H, CO	montane, boreal–temperate, East Asian (only Japan)
Kurzia makinoana (Steph.) Grolle	K, It, Kun, H, CO	boreal–temperate, Asian–American
Lepidozia filamentosa (Lehm. & Lindenb.) Gottsche	CO	montane, arctic–boreal, amphipacific
L. reptans (L.) Dumort.	Ch, K, It, Kun, H, CO	boreal, circumpolar
L. subtransversa Steph.	H	montane, boreal, East Asian
L. vitrea Steph.	Kun	temperate–subtropical, East Asian
Lophocoleaceae		
Chiloscyphus fragilis (A. Roth) Schiffn.	Ch, K, NK, It, Kun	boreal, circumpolar
C.pallescens (Ehrh. *ex* Hoffm.) Dumort.	Ch, K, H	boreal, circumpolar
C. polyanthos (L.) Corda	Ch, K, It, Kun, H, CO	boreal, circumpolar
C. rivularis (Schrad.) Hazsl.	K, NK	boreal, circumpolar
Heteroscyphus coalitus (Hook.) Schiffn.	H, CO	subtropical, East Asian
H. planus (Mitt.) Schiffn.	CO	subtropical, East Asian
H. tener (Steph.) Schiffn.	H, CO	subtropical, East Asian
Lophocolea compacta Mitt.	H, CO	montane, boreal–temperate, East Asian
Lophocolea cuspidata (Nees) Limpr.	Kun, CO	temperate, amphioceanic
L. heterophylla (Schrad.) Dumort.	K, NK, It, Kun, H, CO	boreal, circumpolar
L. horikowana S. Hatt.	CO	montane, temperate–subtropical, East Asian (only Japan)
L. itoana H. Inoue	K, It, CO	montane, boreal–temperate, East Asian
L. minor Nees	Ch, K, It, Kun, H, CO	arctic–boreal, circumpolar
Lophoziaceae		
Anastrepta orcadensis (Hook.) Schiffn.	CO	montane, temperate, amphioceanic
Anastrophyllum assimile (Mitt.) Steph.	H, CO	montane, arctic, amphioceanic
A. michauxii (F. Weber) H. Buch	K, Kun, H, CO	boreal, circumpolar
A. sphenoloboides R.M. Schust.	K, Ch	montane, arctic, circumpolar
Barbilophozia barbata (Schmid. *ex* Schreb.) Loeske	Ch, K, H, CO	montane, arctic–boreal, circumpolar
B. hatcheri (A. Evans) Loeske	Ch, K, NK, It	montane, arctic–boreal, circumpolar
B. lycopodioides (Wallr.) Loeske	Ch, K, NK	montane, arctic–boreal, circumpolar
B. rubescens (R.M. Schust. & Damsh.) Karttunen & Söderström	K	arctic, circumpolar

continued

Appendix. Continued.

Taxa	Locality	General distribution
Crossocalyx hellerianus (Nees) Meyl.	Kun	boreal, circumpolar
Gymnocolea inflata (Huds.) Dumort.	Ch, K, NK, It, Kun	montane, arctic–boreal, circumpolar
Isopaches alboviridis (R.M. Schust.) Schljakov	Ch	arctic, Asian–American
I. bicrenatus (Schmid. *ex* Hoffm.) H. Buch	K, NK, It, Kun	montane, arctic–boreal, circumpolar
I. decolorans (Limpr.) H. Buch	K	montane, arctic, disjunctive
Lophozia ascendens (Warnst.) R.M. Schust.	K, H	boreal, circumpolar
L. excisa (Dicks.) Dumort.	Ch, K, NK	arctic–boreal, circumpolar
L. heteromorpha R.M. Schust. & Damsh.	K	arctic, area unclear
L. lacerata N. Kitag.	K, It	montane, arctic–boreal, East Asian
L. lantratoviae Bakalin	K	montane, boreal, Asian
L. longidens (Lindb.) Macoun	Ch, K	montane, arctic–boreal, circumpolar
L. pellucida R.M. Schust.	Ch	montane, arctic, circumpolar
L. pellucida R.M. Schust. var. *rubrigemma* (R.M. Schust.) Bakalin	K, NK	montane, arctic, area unclear
L. polaris (R.M. Schust.) R.M. Schust. & Damsh.	K, Ch	montane, arctic, circumpolar
L. propagulifera (Gottsche) Steph.	K, Ch	montane, arctic, circumpolar
L. savicziae Schljakov	Ch, K, NK, It	montane, arctic, circumpolar
L. schusteriana Schljak.	Ch, K	arctic, Asian–American
L. silvicola H. Buch	K, NK, It, Kun	arctic–boreal, circumpolar
L. silvicoloides N. Kitag.	K, It, Kun, H	montane, arctic–boreal, East Asian
L. sudetica (Nees *ex* Huebener) Grolle var. *sudetica*	K, NK, It, Kun, CO	montane, arctic, circumpolar
L. sudetica (Nees *ex* Huebener) Grolle var. *anomala* (Schljakov) Schljakov	Ch, NK, It	montane, arctic, circumpolar
L. ventricosa (Dicks.) Dumort. var. *guttulata* (Lindb. & Arnell) Bakalin	K, NK, It, Kun, CO	arctic–boreal, circumpolar
L. ventricosa (Dicks.) Dumort. var. *longiflora* (Nees) Macoun	Ch, K, NK, It, H	arctic–boreal, circumpolar
L. ventricosa (Dicks.) Dumort. var. *ventricosa*	Ch, K, NK, It, Kun	arctic–boreal, circumpolar
L. wenzelii (Nees) Steph. var. *groenlandica* (Nees) Bakalin	K	montane, arctic, circumpolar
L. wenzelii (Nees) Steph. var. *lapponica* H. Buch & S.W. Arnell	K	montane, arctic, circumpolar
L. wenzelii (Nees) Steph. var. *wenzelii*	Ch, K, NK, Kun, H	montane, arctic, circumpolar
Obtusifolium obtusum (Lindb.) S.W. Arnell	K	montane, arctic–boreal, circumpolar
Orthocaulis attenuatus (Mart.) A. Evans	K, It, H, CO	boreal, circumpolar
O. binsteadii (Kaal.) H. Buch	K, Ch, NK	montane, arctic, circumpolar
O. floerkei (F. Weber & D. Mohr) H. Buch	Ch, K, NK	montane, arctic, circumpolar
O. hyperboreus (Schust.) Konstant.	Ch, K, NK	montane, arctic, circumpolar
O. kunzeanus (Hueb.) H. Buch	Ch, K, NK	arctic–boreal, circumpolar
O. quadrilobus (Lindb.) H. Buch	Ch, K, NK	montane, arctic–boreal, circumpolar
Plicanthus birmensis (Steph.) R.M. Schust.	CO	tropical–subtropical, East Asian

P. hirtellus (F. Weber) R.M. Schust.	CO	tropical–subtropical, multiareal
Protolophozia debiliformis (Schust.) Konstant. var. *concolor* R.M. Schust.	K, It	arctic–boreal, circumpolar
P. debiliformis (R.M. Schust.) Konstant. var. *debiliformis*	K	arctic, amphioceanic
P. elongata (Steph.) Schljakov	Ch	arctic–boreal, amphioceanic
Saccobasis polita (Nees) H. Buch	Ch, K, NK	montane, arctic, amphioceanic
S. polymorpha (R.M. Schust.) Schljakov	Ch	montane, arctic, amphioceanic
Schistochilopsis cornuta (Steph.) Konstant.	Kun, H, CO	temperate, East Asian
S. grandiretis (Lindb. *ex* Kaal.) Konstant.	Ch, K	montane, arctic, circumpolar
S. hyperarctica (Schust.) Konstant.	Ch, K	arctic, circumpolar
S. incisa (Schrad.) Konstant.	Ch, K, NK, It, Kun, H, CO	arctic–boreal, circumpolar
S.laxa (Lindb.) Konstant.	K	boreal, amphioceanic
Schistochilopsis opacifolia (Culm. *ex* Meyl.) Konstant.	Ch, K, NK, It	montane, arctic, circumpolar
S. cavifolius (H. Buch & S.W. Arnell) Mull. Frib.	Ch, K	montane, arctic, circumpolar
Sphenolobus minutus (Schreb.) Berggr.	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, circumpolar
S. saxicola (Schrad.) Steph.	Ch, K, CO	montane, arctic, circumpolar
Tetralophozia setiformis (Ehrh.) Schljakov.	Ch, K, NK, CO	montane, arctic, circumpolar
Tritomaria exsecta (Schmid. *ex* Schrad.) Loeske	K, Kun, H, CO	boreal, circumpolar
T. exsectiformis (Breidl.) Schiffn. *ex* Loeske	Ch, K	boreal, circumpolar
T. heterophylla R.M. Schust.	Ch	arctic, circumpolar
T. quinquedentata (Huds.) H. Buch	Ch, K, NK, It, Kun, H	montane, arctic–boreal, circumpolar
T. scitula (Tayl.) Joerg.	Ch	montane, arctic–boreal, circumpolar
Makinoaceae		
Makinoa crispata (Steph.) Miyake	H, CO	montane, boreal–temperate, East Asian
Marchantiaceae		
Bucegia romanica Radian	Ch	montane, arctic, disjunctive
Marchantia alpestris (Nees) Burgeff	Ch, K, NK	montane, arctic, circumpolar
M. aquatica (Nees) Burgeff	K, Kun	montane, arctic–boreal, circumpolar
M. paleacea Bertol.	Kun, H, CO	multizonal, multiareal
M. polymorpha L.	Ch, K, NK, It, H, CO	multizonal, multiareal
Preissia quadrata (Scop.) Nees	Ch, K, NK, Kun, H, CO	montane, arctic, circumpolar
Metzgeriaceae		
Apometzgeria pubescens (Schrank) Kuwah.	Ch, K, Kun, H, CO	montane, boreal–temperate, circumpolar
Metzgeria conjugata Lindb.	It, Kun	montane, temperate–subtropical, multiareal
M. fruticulosa (Dicks.) A. Evans	CO, Kun	temperate–subtropical, amphioceanic
M. furcata (L.) Dumort.	CO	montane, boreal–temperate, circumpolar
M. leptoneura Spruce	CO	subtropical, amphioceanic
M.a lindbergii Schiffn.	H	subtropical, East Asian
Notothyladaceae		
Notothylas orbicularis (Schwein) Sull.	H, CO	temperate, amphioceanic

continued

Appendix. Continued.

Taxa	Locality	General distribution
Pallaviciniaceae		
Hattorianthus erimonus (Steph.) R.M. Schust. & H. Inoue	H, CO	temperate–subtropical, East Asian
Moerckia blyttii (Moerck) Brockm.	K, NK	montane, arctic, circumpolar
M. hibernica (Hook.) Gottsche	Ch	montane, boreal, circumpolar
Pallavicinia lyelli (Hook.) Carruth.	Kun	multizonal, amphioceanic
P. longispina Steph.	CO	temperate, East Asian (only Japan)
Pelliaceae		
Pellia endiviifolia (Dicks.) Dumort.	Ch, K, NK, It, Kun, H, CO	boreal, circumpolar
P. epiphylla (L.) Corda	Ch, K, H	boreal, circumpolar
P. neesiana (Gottsche) Limpr.	Ch, K, H, CO, NK, It, Kun	arctic–boreal, circumpolar
Plagiochilaceae		
Pedinophyllum truncatum (Steph.) H. Inoue	Kun, H, CO	temperate East Asian
Plagiochila arctica Bryhn & Kaal.	Ch	arctic Asian–American
P. hakkodensis Steph.	H, CO	montane, boreal–temperate, East Asian
P. dendroides (Nees) Lindenb.	CO	subtropical, East Asian
P. elagans Mitt.	H	montane, boreal–temperate, Asian
P. flexuosa Mitt.	CO	montane, temperate–subtropical, East Asian
P. gracilis Lindenb. & Gottsche	CO	montane, temperate–subtropical, East Asian
P. fruticosa Mitt.	CO	montane, boreal, East Asian–American
P. nepalensis Lindenb.	CO	montane, boreal–temperate, Asian
P. orbicularis (S. Hatt.) S. Hatt.	H	montane, temperate–subtropical, East Asian
P. ovalifolia Mitt.	H, CO	montane, temperate–subtropical, East Asian
P. parvifolia Lindenb.	CO	subtropical, East Asian
P. porelloides (Torrey *ex* Nees) Lindenb.	Ch, K, It, Kun, H	arctic–boreal, circumpolar
P. satoi S. Hatt.	H, CO	montane, boreal, East Asian
P. sciophila Nees & Lindenb.	CO	montane, subtropical, Asian
P. semidecurrens Lehm. & Lindenb. var. *semidecurrens*	CO	montane, temperate, East Asian
Plagiochilion mayebarae S. Hatt.	CO	temperate, East Asian
Porellaceae		
Macvicaria ulophylla (Steph.) S. Hatt.	H, CO	temperate–subtropical, East Asian
Porella caespitans (Steph.) S. Hatt.	H	subtropical, East Asian
P. densifolia (Steph.) S. Hatt.	CO	temperate–subtropical, East Asian
P. fauriei (Steph.) S. Hatt.	It, Kun, H	montane, boreal-temperate
P. gracillima Mitt. var. *gracillima*	H	boreal–temperate, Asian
P. grandiloba Lindb.	H, CO	temperate–subtropical, East Asian
P. japonica (Sande Lac.) Mitt.	CO	subtropical, East Asian
P. oblongifolia S. Hatt.	CO	temperate–subtropical, East Asian

P. perrottetiana (Mont.) Trev.	CO	subtropical, Asian
P. setigera (Steph.) S. Hatt.	CO	montane, temperate–subtropical, Asian
P. stephaniana (C. Massal.) S. Hatt.	CO	subtropical, East Asian
P. vernicosa Lindb.	H, CO	temperate–subtropical, East Asian
Pseudolepicoleaceae		
Pseudolepicolea fryei (Perss.) Grolle & Ando	Ch	arctic, Asian–American
Ptilidiaceae		
Ptilidium californicum (Aust.) Pears.	K, NK, It	boreal–temperate, amphipacific
P. ciliare (L.) Hampe	Ch, K, NK, It, H, CO	montane, arctic–boreal, circumpolar
P. pulcherrimum (G. Web.) Vain.	K, NK, It, Kun, H, CO	boreal, circumpolar
Radulaceae		
Radula auriculata Steph.	H	montane, boreal–temperate, amphipacific
R. brunnea Steph.	H, CO	montane, boreal, East Asian
R. chinensis Steph.	CO	montane, temperate–subtropical, East Asian
R. complanata (L.) Dumort.	Ch, K, NK, It, H	boreal, circumpolar
R. constricta Steph.	K, H, CO	boreal–temperate, East Asian
R. fauriana Steph.	H, CO	montane, arctic–boreal, East Asian
R. japonica Gottsche	It, Kun, H	temperate–subtropical, East Asian
R. kojana Steph.	CO	montane, subtropical, East Asian
R. obtusiloba Steph.	Kun, H, CO	temperate, East Asian
R. perrottetii Gottsche	CO	subtropical, East Asian
R. prolifera Arnell	Ch, K	arctic, Asian–American
R. tokiensis Steph.	CO	boreal–temperate, East Asian
Ricciaceae		
Riccia bifurca Hoffm.	Ch	temperate, circumpolar
R. cavernosa Hoffm.	Ch, K	boreal–temperate, circumpolar
R. glauca L.	Ch, K, CO	boreal–temperate, circumpolar
R. fluitans Lindenb.	H	multizonal, multiareal
R. huebeneriana Lindenb.	K, CO	temperate, circumpolar
R. lamellosa Raddi	K	multizonal, multiareal
R. miyakeana Schiffn.	CO	unclear, distribution
R. sorocarpa Bisch.	CO	temperate, circumpolar
Ricciocarpos natans (L.) Corda	K, H, CO	multizonal, multiareal
Scapaniaceae		
Diplophyllum albicans (L.) Dumort.	K, NK, It, Kun, H, CO, Ch	montane, arctic, amphioceanic
D. andrewsii A. Evans	H, CO, It, Kun	montane, arctic–boreal
D. obtusatum (R.M. Schust.) R.M. Schust.	K	boreal, Asian–American
D. obtusifolium (Hook.) Dumort.	Ch, K	montane, arctic–boreal, circumpolar
D. serrulatum (Mull. Frib.) Steph.	H, CO	temperate, East Asian
D. taxifolium (Wahlenb.) Dumort.	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, circumpolar

continued

Appendix. Continued.

Taxa	Locality	General distribution
Macrodiplophyllum microdontum (Mitt.) H. Perss.	Ch, K, H	montane, arctic, Asian–American (in North America only in Alaska)
M. plicatum (Lindb.) H. Perss.	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, amphipacific
Scapania ampliata Steph.	H, CO, It, Kun	montane, arctic–boreal, East Asian
S. bolanderi Austin	Kun, H, CO	montane boreal–temperate ,Asian–American
S. brevicaulis Tayl.	Ch, K	montane, arctic, circumpolar
S. kaurinii Ryan	Ch, K	montane, arctic, circumpolar, Asian–American
S. ciliata Sande Lac.	H, CO	montane, boreal, East Asian
S. crassiretis Bryhn	Ch, It, H	montane, arctic, circumpolar
S. curta (Mart.) Dumort.	Ch, K, It, CO	montane, arctic–boreal, circumpolar
S. cuspiduligera (Nees) Mull. Frib.	Ch, K, CO	montane, arctic, circumpolar
S. degenii (Schiffn) Mull. Frib.	Ch, K	montane, boreal, circumpolar
S. diplophylloides Amak. & S. Hatt.	NK, It, Kun	montane, arctic–boreal, East Asian (only Japan and Kurils)
S. glaucocephala (Tayl.) Aust.	K	boreal, circumpolar
S. gymnostomophila Kaal.	Ch, K	montane, arctic circumpolar
S. hyperborea Joerg.	Ch, K, NK	arctic–boreal, circumpolar
S. integerrima Steph.	It	montane, temperate, East Asian
S. irrigua (Nees) Nees	Ch, K, NK, It	arctic–boreal, circumpolar
S. ligulata Steph.	CO	montane, boreal, East Asian
S. ligulifolia (R.M. Schust.) R.M. Schust.	Ch	arctic, Asian–American
S. lingulata H. Buch	K, NK, It, Kun	arctic–boreal, circumpolar
S. mucronata H. Buch	Ch, K, NK	arctic–boreal, circumpolar
S. nemorea (L.) Grolle	Ch	boreal–temperate, amphioceanic
S. obcordata (Berggr.) S.W. Arnell	Ch, K	arctic, circumpolar
S. obscura (Arnell & C.E.O. Jensen) Schiffn.	K	montane, arctic, amphioceanic
S. ornithopodioides (With.) Waddel.	CO	montane, temperate, Euro–Asian
S. paludicola Loeske & Mull. Frib.	Ch, K, NK, It, Kun	arctic–boreal, circumpolar
S. paludosa (Mull. Frib.) Mull. Frib.	Ch, K, NK, It, Kun	montane, arctic, circumpolar
S. parvifolia Warnst.	Ch, K, Kun	arctic–boreal, circumpolar
S. parvitexta Steph.	It, Kun, H, CO	montane, boreal–temperate, East Asian
S. preatervisa Meylan	Ch, K	montane, arctic, circumpolar
S. rufidula Warnst.	Ch	montane, arctic, Asian
S. scandica (Arnell & H. Buch) Macv. var. *argudentata* H. Buch	K	distribution, unclear
S. scandica (Arnell & H. Buch) Macv. var. *scandica*	Ch, K, H	montane, arctic, circumpolar
S. simmonsii Bryhn & Kaal.	Ch	arctic–boreal, circumpolar
S. spitsbergensis (Lindb.) Tuomik.	Ch	montane, arctic, circumpolar
S. subalpina (Nees *ex* Lindenb.) Dumort.	Ch, K, NK, Kun	montane, arctic, circumpolar

S. tundrae (Arnell) H. Buch	Ch	arctic, circumpolar
S. uliginosa (Lindenb.) Dumort.	Ch, K	montane, arctic, circumpolar
S. umbrosa (Schrad.) Dumort.	K, Kun	boreal, circumpolar
S. undulata (L.) Dumort.	Ch, K, NK, It, Kun, H, CO	montane, arctic–boreal, circumpolar
S. zemliae S.W. Arnell	Ch	arctic, amphioceanic
Targioniaceae		
Targionia hypophylla L.	K, CO	multizonal, multiareal
Treubiaceae		
Apotreubia nana (S. Hatt. & H. Inoue) S. Hatt. & Mizut.	CO	temperate, East Asian–American (in America only British Columbia)
Trichocoleaceae		
Blepharostoma minus Horikawa	Kun, H, CO	temperate, East Asian
B. trichophyllum (L.) Dumort. var. *brevirete* Bryhn & Kaal.	Ch, K, NK	montane, arctic, circumpolar
B. trichophyllum (L.) Dumort. var. *trichophyllum*	Ch, K, It, Kun, H, CO	montane, arctic–boreal, circumpolar
Trichocolea tomentella (Ehrh.) Dumort.	Kun, CO	temperate, amphioceanic
Wiesnerellaceae		
Dumortiera hirsuta (Sw.) Nees	H, CO	multizonal, amphioceanic
Wiesnerella denudata (Mitt.) Steph.	CO	tropical–subtropical, East Asian