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CAUCASIAN-MANCHURIAN RELATIONSHIPS IN THE HEPATIC FLORA

КАВКАЗСКО-МАНЬЧЖУРСКИЕ СВЯЗИ ВО ФЛОРЕ ПЕЧЕНОЧНИКОВ

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Abstract

The Caucasian-Manchurian relationships in the hepatic floras are analyzed with the purpose to test for similarities and differences between both floras. Similarities proved to be quite few. The Manchurian hepatic flora includes relatively more southern elements in comparison with the Caucasian one. A higher proportion of subtropical elements in Manchuria is explained tentatively by continuous floristic contacts of Manchuria with southwardly adjacent subtropical and tropical mesophytic complexes which are absent southward of the Caucasus. For few pairs of vicarious temperate taxa, distribution gaps are revealed between the Caucasus and Manchuria. This fact may be explained by the evolution of ancestor taxa in the course of geographic isolation of Manchurian and Caucasian populations since Pleistocene.

Резюме

Взаимосвязи во флорах печеночников Кавказа и Маньчжурии проанализированы с целью выявления признаков, их объединяющих и отличающих. Сходство двух флор довольно низко. Флора печеночников Маньчжурии включает большее количество южных элементов, чем кавказская, что, предположительно, может быть объяснено постоянными контактами флоры Маньчжурии с тропическими и субтропическими мезофитными комплексами, распространенными южнее, в отличие от Кавказа, окруженного с юга ксерофитными комплексами Передней Азии. Имеется небольшое количество пар викарных неморальных таксонов, неизвестных в промежутке между Кавказом и Маньчжурией. Вероятно, эти пары являются результатом эволюции от общих предков, распространенных ранее по всему северу Евразии, вследствие географической изоляции, наблюдавшейся между кавказскими и маньчжурскими популяциями с начала плейстоцена.

KEYWORDS: liverworts, Hepaticae, Arcto-Tertiary flora, Caucasus, Manchuria, florogenesis.

INTRODUCTION

Geographically, the Caucasus and Manchuria are very distant from each another, and an attempt to compare their flora may be regarded no more than eccentric at first sight. However, genesis of the flora makes close relationships of these two large lands quite possible. These relationships follow from the gradual global movement of so-called Arcto-Tertiary biome (Gardner & Ettingshausen, 1879; Krischtofovich, 1934; Gradstein & Váňa, 1987) from northern Eurasia southward since the end of Miocene. This migration process of Arcto-Tertiary flora stopped almost to the whole extent in Asia approximately at 50-55° north by xeric landscapes in the Aral-Caspian region, as well as in Mongolia and northern China. Being mesophytic in general features (with a very few exceptions), this flora could not transform into xerophytic one, especially under condition when xeric landscapes were already occupied by floristic complexes adapted to those habitats. Only two southward routes for this mesophytic flora were made possible: to the Caucasus and to Manchuria. Mild temperate and more or less wet climate in these areas conceivably supported conservation (although in a transformed form) of Arcto-Tertiary floristic complexes or their remnants.

The present paper focuses on hepatics, the group of plants characterized by small size that permits them to grow in micro-niches in specific environments sometimes quite contrasting with the general climate of the area. Thus, hepatics are able to survive for a long time as relics when general vegetation undergoes considerable changes. This evidence was exhaustively discussed by Schuster, who states (1983: 465) that "the diminutive bryophytes, therefore, potentially offer a better clue to the solution of phytogeographical problems than do many vascular plants". The main goal of the present study was to analyze distribution patterns and relationships between Caucasian and Manchurian hepatic floras; and, as a result: 1) to reveal differencies and similarities in these floras, 2) to substantiate them, and 3) to find and describe possible remnants of Arcto-Tertiary flora.

For vascular plants, the phenomenon of floristic Caucasian-Manchurian relationships was discussed in detail by the erudite Russian botanist M.G. Popov (1983), although relationships of the Caucasus and East Asia were

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discussed many times earlier both on bryophytes and vascular plants (Abramov & Abramova, 1969, with cited publication within). Popov's main estimations could be summarized as follow. The Arcto-Tertiary flora covered a large area in northern Eurasia and was more or less uniform in taxonomical composition even at the northernmost limits in Spitsbergen, Novaya Zemlya, the Novosibirskiye Islands (Tolmachyov & Yurtzev, 1970) at least since the time on the Oligocene and Miocene boundary, when the integrated uniform Arcto-Teritary type was formed (Budantsev & Golovneva, 2009). Later, as early as in the end of Miocene, the general steady trend of cooling became obvious (cf. Tiffney, 1985), which entailed a grandiose shift of ancient communities southward, accompanied with flora modifications and regional diversifications. The large area northward, where the thermophilous vegetation could not exist anymore, was occupied by rather cold-resistant communities of taiga and tundra at the end of Pliocene and Pleistocene, evolving partly from the Arcto-Tertiary floristic complexes (Popov, 1957). The thermophilic flora shift was described by Popov (1983) who named mesophytic extra-tropical floristic complexes (formed far before global cooling) as *'Ginkgo* flora', contrary to xerophilous *'Welwitschia* flora'. As the result of the aforementioned floristic contact, three hypothetically possible ways southward of Arcto-Tertiary flora were available: to Manchuria, to the Caucasus and to Southern Europe. The third route was strongly reduced due to Pleistocene glaciations (it reached Alps) that mixed up mesophytic '*Ginkgo* flora' with "Old Mediterranean" one. Aside of modern Manchuria and the Caucasus, the '*Ginkgo* flora' remnants probably may occur in the mountainous eastern China (up to 20°N), but it is almost impossible to check this hypothesis currently due to insufficient data for the latter territory and its strong disturbance in the course of human activity.

MATERIAL AND METHODS

Areas compared. The Caucasus, including Small Caucasus Range (within Armenia, Georgia, Azerbaijan and the Russian North Caucasus), covers the territory of 542000 km^2, thus approximately equal to Manchuria, 591000 km^2. The latter is the sum of the eastern Heilongjiang (ca. 200 000 km^2), Jilin (191 000), North Korea (120 000) and the southern half of Primorsky Territory (80000). Both Caucasus and Manchuria are also similar in latitude, ranging from 38° to 45°N. North-eastern Turkey which is referred sometimes to the Caucasus is not considered in the present analysis.

Both Caucasus and Manchuria are mountainous areas, although the Caucasus is much higher (up to 5642 m alt. in Elbrus Peak) than the Manchuria (up to 2744 m alt. in Pektusan Mt., Chanbaishan Range). The differences in climate and vegetation are even greater. Temperate rainforests, a type of vegetation sometimes similar to subtropical ones are developed in the lowlands at the south-eastern coast of the Black Sea and south-western coast of the Caspian Sea (Colchic and Hyrcanic rainforests correspondingly). Altogether they cover an area of ca. 40 000 km^2, or 8% of the Caucasus territory. The mean annual precipitation here reaches 4500 mm per year in some areas. More wet are Colchic forests situated at low elevation, and dominated by *Castanea*, with evergreen *Rhododendron*, *Lauroceras officinalis*, *Ilex colchica*, etc. (Nakhutsrishvili et al., 2011); such vegetation type is totally absent in Manchuria.

Contrary to this, in Manchuria, temperate broadleaved and coniferous-broadleaved forests dominate (lacking subtropical forests at all), and annual precipitation never exceeds 1000 mm per year. However, while precipitation throughout Manchuria is mostly uniform, most part of the Caucasus is relatively dry, having some much wetter oases like Mtirala National Park in Georgian Adjara. Another difference in precipitation is that the Caucasus has a Mediterranean type of precipitation distribution with winter maximum, whereas Manchuria has the monsoon climate type with maximum in summer.

Database. The comparison is based on the literature data and available herbarium collections (the latter from Russian Manchuria and Georgia only). The main literature sources were as following: Konstantinova et al. (1992), Konstantinova et al. (2009) for the Caucasus; Aur & Zhang (1985), Söderström (2000) for Heilongjiang; Piippo (1990) for Jilin; Yamada & Choe (1997) for North Korea; Konstantinova et al. (2009) for southern Primorsky Territory. Many additions published within recent years have been taken into consideration as well (Bakalin & Tigishvili, 2013; Bakalin et al., 2013; Konstantinova, 2011; Konstantinova et al., 2009; Konstantinova & Savchenko, 2009, 2010, 2011, 2012, 2013; Potemkin & Doroshina, 2009). When compiling, I omitted any dubious records from these publications in obvious cases. The finally compiled list includes 369 species, 204 of those indicated for the Caucasus and 290 for Manchuria (Appendix). Data on general geographic distribution of species were also included basing on various sources. The taxonomy and nomenclature of species follow Konstantinova et al. (2009), although some genera were treated in a broader sense than in the latter work.

Classification of distribution patterns. The distribution patterns are classified following Bakalin (2009), where they were discussed in details, with subsequent brief overview in Bakalin (2010). The system uses three-dimensional grid for the classification, including 1) latitudinal distribution, 2) longitudinal distribution and 3) montanity, the latter indicating association with mountain systems, irrespectively of the altitude at which the species grows.

1) Latitudinal distribution types are recognized as follow: **arctic**, species occurring primarily in tundra zone and arctic deserts and further south, in the tundra belt and arctic barrens in the mountains; **boreal,** species distributed in boreal dark coniferous and light coniferous

Table 1. Latitudinal distribution types in Manchurian and Caucasian hepatic floras (taxa with multizonal and indefinite distribution or unclear distribution are omitted): number of species//percentage

	Caucasus	Manchuria
Arctic	52/26	45/16
Boreal	87/44	111/39
Temperate	59/30	92/32
Subtropical	1/<1	36/13

Table 2. Area types of Manchurian and Caucasian hepatics (taxa with indefinite distribution are omitted): number of species/ /percentage

	Caucasus	Manchuria
Circumpolar	133/69	129/47
East-Asian	1/1	88/32
European	15/8	0/0
Asian	2/1	15/5
Eurasian	5/3	6/2
Asian-American	1/1	10/4
Amphi-Oceanic	24/12	21/8
Amphi-Pacific	0/0	6/2
Amphi-Atlantic	2/1	0/0
Mediterranean	8/4	1/<1
European-American	4/2	1/<1

forests, and further south, in corresponding altitudinal belts in the mountains; **temperate,** species whose primary area is in broad-leaved deciduous forests; **subtropical**, species growing primarily in evergreen forests located north of the northern tropics (or south of the southern ones) and in mountain evergreen forests of near-equatorial portion, above 1500-2000 m a.s.l. Subtropical element, as understood here, corresponds to that of Rivas-Martínez et al. (2011), who treated it as "multi-purpose term, which we use to classify the climate, vegetation and territories of the latitudinal belt between parallels 23° and 35°N…" The term "subtropical" in the current use corresponds to the "south temperate" or "meridional" in terminology of Hämet-Ahti et al. (1974). Identification of latitudinal distribution type for each species was based on two evidences: 1) distribution of species (geographic evidence), 2) distribution of closely related species (genetic evidence). The current system of latitudinal distribution types is derived from that of Konstantinova (2000), with additions mainly for temperate and subtropical species categories.

2) Longitudinal diapason (area types) is deliniated as follow: (1) circumpolar type, species distributed throughout one or more rarely several latitudinal zone(s) and in a corresponding mountain belt for the entire or almost entire northern hemisphere; (2) amphioceanic, species distributed usually within a 200 km zone from the sea/ocean coasts (excluding the coast of the Arctic Ocean, where the climate does not fit the 'oceanic'type of other parts of the world), although sometimes penetrating into continental regions; (3) amphipacific which relates to the Pacific region only; (4) amphiatlantic, relating to the Atlantic Ocean; by the main distribution species are subdivided into the (5) Asiatic, (6) Eurasian, (7) Asiatic-American, and (8) East Asian area types, which do not include species referred to types 2-4. The East Asian area type includes species occurring in Eastern China, Indo-China, occasionally penetrating into Malaysia, the Philippines and those confined in Russia to Primorsky and Khabarovsk Territories, to Kamchatskaya and Sakhalinskaya Provincies and Chukotskii Autonomous Okrug. Other accepted area types include (9) European, (10) European-American, for species occurring in Europe and North America, mainly in eastern part of the latter, but excluding the amphiatlantic zone; (11) Mediterranean, species occurring mostly in contemporary vicinities of the Mediterranean Sea and adjacent areas, such as the Black Sea Basin (thus excluding areas with Mediterranean types of climate in Asia, South California, *etc*.); some of species referred to this area type are sparsely spread in Asia around the area covered by the paleogeographical Tethys Sea or other areas, but nevertheless with the area 'core' in the modern Mediterranean region.

The species without clear distribution pattern and distributed in the variety of latitudinal and longitudinal sectors as well as in various vegetation types were called 'indefinite' and were not included into subsequent analysis.

Results

The combined list of Manchurian-Caucasian hepatics includes 369 species, 204 being recorded for the Caucasus and 290 for Manchuria, 125 species occurring in both areas (Appendix 1). Table 1 provides distribution of Manchurian and Caucasian species by latitudinal distribution types and Table 2 shows their longitudinal area types.

Discussion

Chorological comparison

Despite conditions for hepatics in the Caucasus look more favorable (greater altitudinal range and overall vegetation diversity, extensive nival areas, higher precipitation in some local areas resulting in very humid climate), total diversity is much higher in Manchuria than in the Caucasus. This conclusion rests on our feeling that the current state of knowledge is about the same in both areas.

The difference in species diversity can be explained partly by precipitation distribution, *i.e.* the summer precipitation maximum in Manchuria (see above). However, more important seems the fact of co-existence of different zonal elements in the flora of Manchuria, already outlined by Popov (1983) for vascular plants.

The phenomenon is explained by the flora development during the Pleistocene, including: (1) the absence of extensive glaciation in East Asia, (2) a continuous gradient of mesophytic communities "connecting" boreal forests with tropical ones at all stages of biota development. Contrary to the latter, the Caucasus had a limited ability to be enriched by "southern" mesophytes being separated by a xerophytic belt of the Middle East. At the same time, the Caucasus is enriched by xerophytic ancient Mediterranean species, which however are few, as hepatics mostly grow in wet habitats.

The proportions of major zonal elements of each flora are rather similar in both the Caucasus and Manchuria. In both floras, the boreal species dominate (44 and 39% correspondingly), followed by temperate element comprising 30 and 32%. The third in species number is the arctic element represented almost exclusively by arctic-montane taxa. The proportion of such species in the Caucasus is noticeably higher (26%) than in Manchuria (16%); it may be easily explained by a wider distribution of the alpine belt in the higher Caucasian mountains. Even stronger difference takes place in the percentage of subtropical taxa. Only one species, *Cololejeunea rossetiana* can be referred to this element in the Caucasian flora, while 36 species, or 13% of all hepatic flora of Manchuria, are referred here to subtropical element. Thus, in spite of the absence of subtropical vegetation in Manchuria where broadleaved temperate forests are southernmost (contrary to subtropical forests in the South-West Caucasus), the proportion of subtropical species in Manchuria is higher (mainly due to the diversity of the Lejeuneaceae) than in the Caucasus. This fact may be explained by aforementioned continuous contacts of Manchuria with southwardly distributed mesic communities, as well as relatively limited area covered by forests closely related to the subtropical Caucasus, and also strong human impact for the last two or three thousand years in the Caucasus. It is difficult to evaluate which of these factors are most valuable.

The species distribution in each flora among longitudinal area types differs noticeably. Circumpolar species comprise in the Caucasian and Manchurian floras 69 and 47% correspondingly. This distinction may be compared with the trend in the area type formation in Pacific extra-Tropical Asia analyzed by Bakalin (2010). As it was shown (l.c.), circumpolar species comprise in Chukotka 79% and in Kamchatka Peninsula 76%, whereas in the East-Asian floristic region they take 49% in Kunashir Island (south of the Kurils Chain), 36% in Hokkaido and 25% in Central Honshu. A high proportion of East-Asian taxa in Manchuria (32%) and the absence of this group in the Caucasus could be expected. Only one species of this element (*Nardia assamica*) is recorded for the Caucasus, but it is obviously an alien taxon there, introduced with vascular plants during transportation from East Asia to the Batumi Botanical Garden. In the Caucasian hepatic flora, European species take 8% and Mediterranean ones – 4%. Both groups are absent in Manchuria (I consider a record of *Phaeoceros bulbiculosus* in Jilin Province being likely a misidentification). The proportion of amphioceanic species (including both amphiatlantic and amphipacific ones) is not strongly different: 13% in the Caucasus and 10% in Manchuria.

Among 369 taxa recorded in the aggregate Caucasian-Manchurian flora, 125 species are common in both areas. That group includes 25 arctic (mostly arctic-montane) species, such as common throughout Holarctic *Anthelia juratzkana*, *Cephalozia bicuspidata*, *Cephaloziella divaricata*, *Gymnocolea inflata*, *etc*. Boreal fraction is comprised by 70 species that takes more than half of taxa common in both areas. This group includes those almost invariably present throughout taiga zone or corresponding altitudinal belt of southwardly situated mountains (*Barbilophozia lycopodioides*, *Blasia pusilla*, *Calypogeia muelleriana*, *Chiloscyphus polyanthos*, *Jungermannia eucordifolia*, *etc*.). Most of arctic and boreal taxa common for both floras have the circumpolar area type. The temperate group is represented by 27 species; most of them are characterized by amphioceanic distribution (contrary to boreal taxa), *e.g.*, *Anthoceros punctatus*, *Bazzania trilobata*, *Calypogeia arguta*, *Cephalozia catenulata*, *etc*. There are no species of subtropical element occurring in both areas. Species belonging to other area types, aside aforementioned circumpolar and amphioceanic ones, are noticeably scarce, and represent only one species from East-Asian (*Nardia assamica*), Asian (*Lophozia lantratoviae*), Asian-American (*Frullania inflata*) and Mediterranean (aforementioned doubtful record of *Phaeoceros bulbiculosus* in Jilin) groups, as well as 3 Eurasian taxa (*Frullania dilatata*, *Frullania parvistipula* and *Mannia androgyna*).

Each studied flora is characterized by a number of specific taxa, not known in another one. 79 species are particular for the Caucasus; among them 27 belong to the arctic element (*Athalamia hyalina*, *Cephaloziella varians*, *Gymnomitrion corallioides*, *etc*.). Some of these peculiar taxa will be probably found in Manchuria in the course of future investigations, but for most of them a chance to be found is quite low due to the absence of appropriate habitats (no high mountains, with one probable exception of isolated Pektusan Mt.). It is noticeable that most of arctic-montane species found in the Caucasus and unknown in Manchuria are known at the same latitude or even southward in Japan, where a larger spectrum of alpine habitats exist.

The boreal group specific for the Caucasus is fewer in number and counts 17 species. This group includes: 1) amphioceanic *Cephaloziella stellulifera*, *Gymnomitrion obtusum*, *Radula lindenbergiana* (vicarious to very closely morphologically related East-Asian *R. constricta*); 2) circumpolar *Leiocolea badensis*, *Lophozia silvicola*, *Marchantia aquatica*, *Moerckia hibernica*, *Porella cordeana*, *Scapania cuspiduligera*, *S. gymnostomophila*, *S. lingulata*, *S. umbrosa* (some of them can likely be found in Manchuria); Mediterranean *Solenostoma caucasicum*; European *Scapania aequiloba* and *S. helvetica*: European-American *Scapania calcicola*; Caucasian endemics *Lophozia wenzelii* var. *massularioides* and *Plectocolea infusca* var. *memiadzei*.

The temperate element specific to the Caucasus includes a mixture of Mediterranean taxa (*Athalamia spathysii*, *Riccia crinita*, *Southbya tophacea*, *etc*.), vicarious to East-Asian ones (*Calypogeia fissa* is vicarious for *C. tosana*, *Cololejeunea calcarea* for *C. ornata*, *Frullania jackii* for *F. davurica*), species of arid habitats (both European, Eurasian and Mediterranean), such as *Riccia* spp. (*R. ciliifera*, *R. crinita*, *R. gougetiana*, *R. michelii*) and European (*Scapania aspera*, *S. compacta*).

The specific component of Manchurian flora composes 164 species. Twenty of them belong to the arctic element. That group includes 1) amphioceanic taxa, such as *Anastrophyllum assimile*, *Apomarsupella revoluta* as well as amphipacific *Marsupella commutata*; 2) almost circumpolar, such as disjunctively distributed *Crossogyna undulifolia* or rather common *Gymnomitrion apiculatum*, *Marsupella tubulosa* and *Scapania crassiretis*; 3) Asian-American, such as *Fossombronia alaskana* and *Macrodiplophyllum microdontum*; 4) Asian *Scapania rufidula*; 5) Euroasian *Scapania sphaerifera*.

The boreal fraction of specific Manchurian flora totals 41 species, among them East-Asian ones (*Blepharostoma minus*, *Frullania koponenii*, *Lophocolea itoana*, *Nipponolejeunea subalpina*, *Radula constricta*, *etc*.) and circumpolar species which may be later found in the Caucasus, *e.g., Calypogeia neesiana*, *Cephalozia lunulifolia*, *Chiloscyphus fragilis*, *Diplophyllum obtusifolium*, *Lophozia ventricosa* var. *ventricosa*, *Mylia taylorii*, *etc*. ther area types are not extensive and compose a few species, such as amphipacific *Acrobolbus ciliatus*, *Macrodiplophyllum plicatum*, *Plectocolea obscura*, *etc*., amphioceanic *Harpanthus flotovianus* (highly expectable in the Caucasus), Asian-American *Calycularia laxa*, *Jungermannia exsertifolia* and Asian *Frullania davurica*, vicarious to European *F. jackii*. Most of specificity is concentrated within temperate and subtropical element groups. Noticeable examples include temperate East Asian *Athalamia nana*, *Bazzania japonica*, *Cephaloziella microphylla*, *Frullania diversitexta*, *Metacalypogeia cordifolia*, as well as subtropical East Asian *Asterella leptophylla*, *Bazzania tridens*, *Cololejeunea denticulata*, *Frullania osumiensis*, and *Heteroscyphus coalitus* Some of temperate and subtropical species have the amphioceanic (*Metzgeria leptoneura*, *Notothylas orbicularis*) or amphipacific area type (*Cololejeunea macounii*, *Radula auriculata*).

Montane index was originally regarded as the reflection of flora genesis at highly mountainous areas (Bakalin, 2009), although some northerly situated regional floras without high mountain systems (such as Republic of Karelia and Finland) are also characterized by a high proportion of montane species. Such lowland landscape as Yamal Peninsula with nearly absent rock outcrops makes up 121 species (Potemkin, 1993), 75 of them are referred to montane group (62.5%). This fact was explained by a dualistic nature of montane index. High proportion of montane species occurs both in areas with well-developed mountainous relief, and in northern boreal and arctic landscapes. The latter fact may be explained by: 1) noncompensible impoverishment and disappearance of boreal communities northward within boreal zone and 2) larger distribution of tundras and therefore wider distribution of taxa growing in alpine belt in most area ranges (so being primarily montane). Montane species total 118 taxa in Manchuria (40% of the total quantity) and 96 (47%) in the Caucasus. These proportions are quite similar to those in temperate floras, such as in Hokkaido, Chichibu-Okutama massif (Japan), Ontario (Canada) and Auvergne (France) and are noticeably lower than in boreal and subarctic mountainous areas in Kamchatka Peninsula, the Altai Mts., Sayan Mts. (in Russia), Alaska, Finland, or northern Sweden (cf. Bakalin, 2009).

Taxonomical comparison

A comparison of latitudinal distribution types by families may highlight the differences in elements, contrasted by general distributional pattern of each family.

The Porellaceae, a thermophilic family, is represented in both floras by one genus only (if *Macvicaria* is included in *Porella*). Caucasian flora represents 5 species of the genus, while in Manchuria 14 species are known. Common for both areas is boreal circumpolar *P. platyphylla* only. Most species of *Porella* (11) specific for Manchuria, have the East-Asian area type and belong to the subtropical (*P. caespitans*, *P. japonica*, *P. spinulosa*, *P. tosana*) or temperate element (*P. gracillima*, *P. grandiloba*, *P. ulophylla*, *etc*.). Contrary, four of specific Caucasian *Porella* belong to the temperate montane European group (*P. arboris-vitae*, *P. baueri*), temperate montane European-American group (*P. platyphylloidea*, the species closely related to *P. platyphylla*) or are characterized by boreal-montane circumpolar distribution (*P. cordeana*).

The Radulaceae is a monotypic family with mostly tropical-subtropical distribution (Yamada, 1977), with a few species spreading northward (although with one noticeable exception of *Radula prolifera*, which is almost restricted to the Arctic). The family numbers 10 species in compared floras. Only *Radula complanata* with boreal circumpolar distribution occurs in both floras. One species is peculiar for the Caucasus (*Radula lindenbergiana*, vicariously replaced in Manchuria by closely related *Radula constricta*). Other 8 species are specific for Manchuria.

The Lepidoziaceae, a 'southern' family, totals 3 species in the Caucasus and 10 in Manchuria. The largest genus of the family, *Bazzania,* is represented by 2 species in the Caucasus (one of them is not recorded in Manchuria) contrary to 6 species in Manchuria (5 of them are not recorded in the Caucasus). *Lepidozia* makes one species with almost circumholarctic distribution (*L. reptans*) found in the Caucasus only. Two other species of the genus mainly with East Asian distribution, *L. fauriana* and *L. subtransversa,* grow in Manchuria. The third genus of the family is represented by *Kurzia makinoana*, known from Manchuria only.

The Lejeuneaceae is very diverse in the tropics and provides the following material for comparisons: principally subtropical *Cheilolejeunea* is represented by one species (*C. obtusifolia*) known in Manchuria; *Cololejeunea* numbers two species in the Caucasus (both are not known in Manchuria) contrary to 6 species recorded in Manchuria (the taxa recorded from the Caucasus, *Cololejeunea calcarea* and *C. rossetiana*, are replaced in East Asia by morphologically very closely related vicarious *Cololejeunea ornata* and *C. subkodamae*, with the latter not known in Manchuria, but recorded in the Kurils and Japan); *Lejeunea* is represented by two species in the Caucasus (one of them is not known in Manchuria), contrary to 4 in Manchuria (3 absent in the Caucasus); circumtropical *Trocholejeunea* and East-Asian *Nipponolejeunea* occur in Manchuria being absent in the Caucasus (each genus is represented by one species: *Trocholejeunea sandvicensis* and *Nipponolejeunea subalpina*).

Another thermophilous family is the Frullaniaceae, represented in the compared floras by one genus, *Frullania,* and counting 19 and 8 species in Manchuria and the Caucasus respectively. Only 4 species are common in both areas (*F. bolanderi*, *F. dilatata*, *F. inflata*, *F. parvistipula*), although some taxa are represented in both floras by morphological variants (*F. jackii* – *F. davurica*, *F. tamarisci* – *F. appendiculata*, *etc*.). Four taxa specific for the Caucasus are characterized by the European area type (*F. fragillifolia*, *F. riparia*, *etc*.). Twelve of 15 species specific to Manchuria have East-Asian distribution (*F. crispiplicata*, *F. diversitexta*, *F. koponenii*, *F. osumiensis*, *etc*.), two have the Asian area type (*F. davurica*, *F. polyptera*) and one (*F. ericoides*) is characterized by temperate subcircumpolar distribution.

Due to the fact of comparatively recent development of cold-resistant lowland communities (like current taiga and tundra) in Northern Hemisphere, approximately at the end of Pliocene, there are no large families of hepatics (and likely mosses, too) having the main taxonomic diversity within boreal and arctic zones. Even diversity of the mostly ‘psychrophilic’ Gymnomitriaceae provides in the Arctic lower (or nearly comparable) number of species than in isolated small areas within the Alps or in Japan. At the same time, there are groups with comparatively high diversity in alpine and boreal belts of mountains; they are discussed below.

The Scapaniaceae (in the narrow sense, including *Scapania*, *Diplophyllum* and *Macrodiplophyllum* only) composes 41 species in the overall Manchurian-Caucasian flora. The largest genus is *Scapania*, totaling 35 species, with 8 species common in both floras. The latter bulk includes circumboreal taiga’ epixylous *S. apiculata* and *S. carinthiaca*, 5 boreal-montane and arctic-montane circumpolar taxa (*S. irrigua*, *S. subalpina*, *S. undulata*, *etc.*), as well as boreal sub-circumpolar *S. verrucosa*. Twelve species are specific for Manchuria, with four East-Asian ones (*S. ampliata*, *S. ciliata*, *S. parvidens*, *S. parvitexta*). The majority of other species has boreal circumpolar distribution, and there are no reasons (outside florogenetics) for their absence in the Caucasus (*S. curta*, *S. paludicola*, *etc*.). One species has arctic-montane Eurasian distribution (*S. sphaerifera*), and probably represents the relict of periglacial communities of the places where no continuous ice-shield was developed during Pleistocene. This species is more or less common in mountain ranges of North-East Asia, becoming noticeably rarer westward and southward, although occurring in South Korea (Chiri-san massif, Choi S.S., pers. comm.). Fifteen species are limited in the distribution by the Caucasus, including 3 European (*S. aequiloba*, *S. aspera*, and *S. helvetica*, a probable vicaropus species for East Asiatic *S. diplophylloides*). Ten species have circumpolar distribution (varying from arctic to temperate); most of them occur in East Asia, but are unknown in Manchuria. Some of these species may be found in the latter (*S. cuspiduligera*, *S. gymnostomophila*, *S. lingulata*, *etc*.), but the records of others (*S. brevicaulis*, *S. kaurinii*, *S. obcordata*) are hardly possible due to their generally arctic and arctic-montane distribution and almost total absence (or high discontinuity) of appropriate habitats in Manchuria. *Diplophyllum* totals 4 species in combined flora. Two species are common in both floras, and two more (closely related, even probably conspecific *D. obtusatum* and *D. obtusifolium*) are limited in distribution by Manchuria. *Macrodiplophyllum* comprises 2 species, both of them are limited to Manchuria only.

The Cephaloziaceae numbers 3 genera in the Caucasian-Manchurian combined flora. The largest one is *Cephalozia*, with 11 species. Four species are common in both floras. *C. ambigua* is recorded for the Caucasus only. Six species are known from Manchuria only, including two (*C. otaruensis*, *C. zoopsioides*) with boreal amphipacific and subtropical East-Asian distribution correspondingly, whose presence is the special trait of Manchurian flora. Two rare circumpolar or ampioceanic epixylous species (*C. lacinulata*, *C. macounii*) and two boreal circumpolar species (*C. leucantha* and *C. lunulifolia*) may be found in the Caucasus. The monotypic arctic montane circumpolar *Pleurocladula* (with *P. albescens* only) is present in the Caucasus only due to the lack of suitable habitats in Manchuria. The third genus (*Nowellia*) known in both floras is represented by temperate amphioceanic *N. curvifolia*, the species disjunctively distributed in Asia, but locally abundant in south boreal and north temperate forests of the Caucasus and Manchuria.

The Gymnomitriaceae has 2 genera (*Gymnomitrion* and *Marsupella*) in the compared floras. *Marsupella* includes 11 species, with only *M. sphacelata* common in both floras. Five taxa are specific for the Caucasus: four arctic-montane ones (*M. brevissima*, *M. condensata*, *M. emarginata*, *M. sparsifolia*) and temperate amphioceanic *M. funckii*. *M. emarginata* is replaced in Manchuria by closely related *M. tubulosa*, other listed species can hardly be found in Manchuria due to the absence of proper habitats. Manchuria is characterized by 5 specific species, including two boreal-temperate montane East Asian endemics (*M. pseudofunckii*, *M. yakushimensis*), arctic-montane amphipacific *M. commutata*, as well as two arctic-montane circumpolar taxa (*M. alpina*, *M. tubulosa*). *Gymnomitrion* numbers 5 taxa in compared floras, with no taxa common for both. Two species are specific for Manchuria: poorly known East Asian *G. uncrenulatum* and arctic-montane circumpolar *G. apiculatum,* which are inexplicably absent in the Caucasus. Contrary, there are 3 specific species for the Caucasus flora, including arctic-montane circumpolar *G. corallioides* and *G. concinnatum* (the latter is expected to be found in Manchuria with high probability since it occurs just southward as near as in northern extremes of South Korea), as well as boreal-montane amphioceanic *G. obtusum*.

Along with aforementioned families showing dissimilarity in taxonomical spectra in the compared floras, the following examples are also noticeable. Five families of the combined Caucasian-Manchurian flora are specific to Manchuria: the Acrobolbaceae (*Acrobolbus ciliatus*), Herbartaceae (*Herbertus dicranus*), Notothyladaceae (*Notothylas orbicularis*), Targioniaceae (*Targionia hypophylla*, *T. indica*), and Lepidoleanaceae (*Trichocoleopsis sacculata*). At a generic level, 18 genera occur in Manchuria only (over half of them are confined in world distribution to the East-Asian floristic region): *Apomarsupella* (*A. revoluta*), *Calycularia* (*C. laxa*), *Cheilolejeunea* (*C. obtusifolia*), *Biantheridion* (*B. undulifolium*), *Cylindrocolea* (*C. recurvifolia*), *Dumortiera* (*D. hirsuta*), *Hattorianthus* (*H. erimonus*), *Heteroscyphus* (*H. coalitus*, *H. planus*), *Kurzia* (*K. makinoana*), *Macrodiplophyllum* (*M. microdontum*, *M. plicatum*), *Metacalypogeia* (*M. cordifolia*), *Mylia* (*M. nuda*, *M. taylorii*, *M. verrucosa*), *Nipponolejeunea* (*N. subalpina*), *Plagiochasma* (*P. japonicum*, *P. pterospermum*, *P. rupestre*), *Tetralophozia* (*T. setiformis*), *Trocholejeunea* (*T. sandvicensis*), *Tuzibeanthus* (*T. chinensis*), *Xenochila* (*X. integrifolia*).

The specificity of the Caucasus in much lower. It numbers three families: Lunulariaceae (*Lunularia cruciata*), Riellaceae (*Riella paulsenii*), Arnelliaceae (*Southbya tophacea*) and four genera with mostly northern distribution: *Moerckia* (*M. blyttii*, *M. hibernica*), *Pleurocladula* (*P. albescens*), *Protolophozia* (*P. debiliformis*), and *Sauteria* (*S. alpina*).

CONCLUSIONS

The comparative analysis of hepatic floras of Manchuria and the Caucasus has revealed a lower specificity of Caucasian hepatic flora in comparison with Manchurian one. The specificity of Caucasian hepatic flora focuses mainly on the taxa of European and 'northern' distribution contrary to Manchurian specificity which is characterized by the presence of East-Asian endemics and, to some degree, of taxa with subtropical distribution.

Richness of the flora of the Southern Russian Far East caused by great diversity of East-Asian species was discussed many times (although without comparison with the Caucasus) both for vascular plants and mosses (*e.g.*, Bardunov & Cherdantseva, 1982, *etc*.). Later Ignatov et al. (2009) emphasized that the outstanding (in comparison with other regions of Russia) diversity of the moss flora of Southern Russian Far East (partly belonging to Manchuria) may be explained by its proximity to moss diversity center in Japan and North-East China. The only comparison of Manchurian and Caucasian flora (based on selected examples, without counting real percentages) was published by Popov (1983). The present conclusion about comparatively more southern character of Manchurian flora versus Caucasian one is coinciding with the result of his analysis of vascular plants (l.c.).

Common for both areas are 125 species. Most of them (70) are boreal and arctic (25) taxa, and all of them occur 'between' Manchuria and Caucasus, *i.e*., in southern and eastern Siberia. Only few (13) amphioceanic taxa (such as *Bazzania trilobata*, *Calypogeia arguta*, *Calypogeia azurea*, *etc*.) have a 'gap' in distribution between Caucasus and Pacific Asia. There is no exact evidence that this common group is really reflecting some similarity in origin (in a sense of florogenetics), but not climatic conditions of lands under influence of oceans.

In general structure Manchurian hepatic flora is more southern than Caucasian one. It contradicts more "northern" character of dominating vegetation in Manchuria. It may be explained partly by old and continuous contacts of the Manchurian flora with South-East Asia via continuous gradient of mesic forests, whereas the Caucasus is surrounded by considerably drier areas from both south and north.

Two floras provide some examples of morphologically very similar, vicariously distributed taxa (sometimes of unclear taxonomic rank) with temperate or even subtropical distribution. This fact may support an assumption about the common origin of some local floras in Manchuria and the Caucasus from one ancestral flora and their subsequent divergence due to geographic isolation. If the latter view is accepted, and if we take into account almost complete absence of subtropical species (even as relicts) in the Caucasus, contrary to great variety of such examples in Manchuria, the following ways of Arcto-Tertiary flora transformation may be suggested: 1) the primary hepatic '*Ginkgo* flora' had features similar to the current mesophytic temperate communities; 2) as the result of progressive cooling, this flora moved southward and transformed during the retreating. The processes during the retreatment were probably similar in the Caucasus and Manchuria, but in the latter an original flora was enriched by elements of tropical and subtropical genesis, the source absent for liverwort flora of the Caucasus. Contrary, Caucasian flora should be treated as (or very related to) Mediterranean one in the broad sense of this name by its geographic position and general floristic characteristics. Thus, the origin of Caucasian flora differs considerably from '*Ginkgo'* flora. Only few lands (e.g., Colchic forests) are favorable for survival of some old mesophytic elements that might be brought there in the course of Arcto-Tertiary forest retreatment. Now such lands may be regarded as possible refugia of '*Ginkgo'* flora interposed within alien (Mediterranean) floristic complexes.

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LITERATURE CITED

ABRAMOVA, A. L. & I. I. ABRAMOV 1969. Eastern-asiatic affinities the Caucasian bryoflora. – *J. Hattori Bot. Lab.* **32**: *151-154.*

AUR, C.-W. & G.-C. ZHANG 1985. Flora heilongjiangensis. Bryophyta: Hepaticae, Anthocerotae. – *North-Eastern Forestry University Press*, *232. (in Chinese)*

[BAKALIN, V.A.] БАКАЛИН В.А. 2009. Флора и фитогеография печеночников (Marchantiophyta, Anthocerotophyta) Камчатки и прилегающих островов – [Flora and phytogeography of hepatics (Marchantiophyta, Anthocerotophyta) in Kamchatka and adjacent lislands] *M., Наука [Moscow, Nauka], 375 pp.*

BAKALIN, V.A. 2010. Hepaticae of the Kuril Islands (northwestern Pacific): a transoceanic route from circumboreal to East Asian flora. – *Ann. Bot. Fennici* **47**(2): *81-105.*

BAKALIN, V.A. & K. TIGISHVILI 2013. Notes of Lophozia. VII. On the distribution of some species of Lophozia in Georgia (Caucasus). – *Arctoa* **22**: *121-123.*

BAKALIN V.A., Z. MANVELIDZE, D. KHARAZISHVILI & N. MEMIADZE 2013. A small collection of hepatics from Adjara, Georgia. – *Arctoa* **22**: *125-130.*

[BARDUNOV, L.V. & V.YA. CHERDANTSEVA] БАРДУНОВ, Л.В., В.Я.ЧЕРДАНЦЕВА 1982. Листостебельные мхи Южного Приморья. – [Mosses of the South of Primorskij Province] *Новосибирск*, *Наука* [*Novosibirsk*, *Nauka*], *206.*

[BUDANTSEV L.YU. & L.B. GOLOVNEVA] БУДАНЦЕВ Л.Ю., Л.Б. ГОЛОВНЕВА 2009. Ископаемые флоры Арктики II. Палеогеновая флора Шпицбергена. – [Fossil flora of Arctic II. Paleogene flora of Spitzbergen] *Марафон*, *Ютас* [*Marafon*, *Yutas*], *380.*

GARDNER, J.S. & C. ETTINGSHAUSEN 1879. A monograph of the British Eocene flora. Filice I. – *London, Paleontogr. Society, 159.*

GRADSTEIN, S.R. & J. VÁŇA 1987. On the Occurrence of Laurasian Liverworts in the Tropics. – *Mem. New York Bot. Gard.* **45**: *388-425.*

HÄMET-AHTI, L., T. AHTI & T. KOPONEN 1974. A scheme of vegetation zones for Japan and adjacent regions. – *Ann. Bot. Fenn.* **11**: *59-88.*

IGNATOV, M.S., E.A. IGNATOVA, O.M. AFONINA & V.V. TELEGANOVA 2009. Moss diversity in Russia: general overview and analysis of the distribution of dioicous species. – *Species and Communities in Extreme Environments* (*Festschrift towards the 75th Anniversary and a Laudatio in Honour of Academician Yuri Ivanovich Chernov*). *Sofia–Moscow*: *303-318.*

[KONSTANTINOVA, N.A.] КОНСТАНТИНОВА Н.А. 2000. Анализ ареалов печеночников Севера Голарктики. – [Distribution patterns of the North Holarctic hepatics] *Arctoa* **9**: *29-94.*

KONSTANTINOVA, N.A. 2011. Contribution to the hepatic flora of the Republic of Dagestan (Eastern Caucasus, Russia). – *Arctoa* **20**: *175-182.*

KONSTANTINOVA, N.A., POTEMKIN A.D. & R.N. SCHLJAKOV 1992. Checklist of the Hepaticae and Anthocerotae of the former USSR. – *Arctoa* **1**: *87-127.*

KONSTANTINOVA, N. A, V. A. BAKALIN et al. 2009. Checklist of liverworts (Marchantiophyta) of Russia. – *Arctoa* **18**: *1-64.*

KONSTANTINOVA, N.A., T.V. AKATOVA & A.N. SAVCHENKO 2009. Hepatics of the Caucasian State Nature Reserve (Western Caucasus, Russia). – *Arctoa* **18**: *121-134.*

KONSTANTINOVA, N.A. & A.N. SAVCHENKO 2009. New liverwort records from Krasnodar Territory. 1. – *Arctoa* **18**: *261-262.*

KONSTANTINOVA, N.A. & A.N. SAVCHENKO 2010. New liverwort records from Republic of Adygeya. 1. *Arctoa* **19**: *270.*

[KONSTANTINOVA, N.A. & A. N. SAVCHENKO] КОНСТАНТИНОВА Н.А., А.Н. САВЧЕНКО 2011. К флоре печеночников сочинского национального парка. – [On the hepatic flora of the Sochi National Park (Western Caucasus)] *Новости Сист. Низш. Раст.* [*Novosti Sist. Nizsh. Rast.*] **45**: *301-317.*

[KONSTANTINOVA, N.A. & A.N. SAVCHENKO] КОНСТАНТИНОВА Н.А., А.Н. САВЧЕНКО 2012. Печеночники окрестностей поселка Лазаревское (Западный Кавказ, Россия). – [Hepatics in surroundings of Lazarevskoe (Western Caucasus, Russia)] *Черноморский бот. журн.* [*Chernomors'kij Bot. Zhurn.*] **8**(1): *56-66.*

KONSTANTINOVA, N.A. & A.N. SAVCHENKO 2013. Russian Caucasus distribution of fourteen hepatics rare and threatened in Europe. – *Polish Bot. J.* **58**(2): *573–584.*

[KRISHTOFOVICH, A.N.] КРИШТОФОВИЧ А.Н. 1934. Курс палеоботаники. – [Paleobotany Manual] *Л.-М.-Грозный-Новосибирск, Горгеонефтеиздат* [*Leningrad-Moskva-Groznyj-Novosibirsk, Gorgeonefteizdat*], *414.*

NAKHUTSRISHVILI, G., N. ZAZANASHVILI & K. BATSATSASHVILI 2011. Regional Profile: Colchic and Hyrcanic Temperate Rainforests of the Western Eurasian Caucasus. – Temperate and Boreal rainforests of the world *Washington-Covelo-London*, *Islandpress*, *214-221.*

PIIPPO, S. 1990. Annotated catalogue of Chinese Hepaticae and Anthocerotae. – *J. Hattori Bot. Lab.* **68**: *1-192.*

[POPOV, M.G.] ПОПОВ М.Г. 1957. К вопросу о происхождении тайги. – [On the origin of taiga]. Сборник статей по результатам исследований в области лесного хозяйства и лесной промышленности в таежной зоне СССР [Sbornik statej po reszultatam issledovanij v oblasti lesnogo khozyajstva i lesnoj promyshlennosti v taezhnoj zone SSSR] *М.-Л., Изд-во Академии наук* [*Moskva – Leningrad, Izd-vo Akademii nauk*], *19-28.*

[POPOV, M.G.] ПОПОВ М.Г. 1983. Филогения, флорогенетика, систематика. Избранные труды. Том 1. – [Phylogeny, florogenetics, systematic. Selected works. Vol. 1.] *Киев, Наукова Думка* [*Kiyev, Naukova Dumka*], *280.*

POTEMKIN, A.D. 1993. The Hepaticae of the Yamal Peninsula, West Siberian Arctic. – *Arctoa* **2**: *57-101.*

[POTEMKIN, A.D. & G. YA. DOROSHINA] ПОТЕМКИН А.Д., Г.Я. ДОРОШИНА 2009. К флоре печеночников российской части Кавказа. – [On the liverwort flora of the Russian part of Caucasus] *Новости Сист. Низш. Раст.* [*Novosti Sist. Nizsh. Rast.*] **43**: *377-391.*

RIVAS-MARTÍNEZ, S., S. RIVAS SÁENZ & A. PENAS 2011. Worldwide bioclimatic classification system. – *Global Geobotany* **1**: *1-634.*

SÖDERSTRÖM, L. 2000. Hepatics from Changbai Mountain, Jilin Province, China. – *Lindbergia* **25**: *41-47.*

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. & B.A. YURTZEV] ТОЛМАЧЕВ А.И., Б.А. ЮРЦЕВ 1970. История арктической флоры в связи с историей Северного Ледовитого океана. [The history of Arctic flora in its relationship with the history of Arctic Ocean] *Северный ледовитый океан и его побережье в кайнозое* [*Severnyj Ledovityj okean i ego poberezh'ye v kainozoye*] *Л., Гидрометеоиздат* [*Leningrad, Gidrometeoizdat*], *87-100.*

YAMADA, K. 1979. A revision of Asian taxa of Radula, Hepaticae. – *J. Hattori Bot. Lab.* **45**: *201–322.*

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

Appendix. The distribution of species within areas compared, montane index, flora element, and area type.

	Caucasus	Manchuria	Montane	Arctic	Boreal	Temperate	Subtropical	Circumpolar	East Asian	European	Asian	Euroasian	Asian-American	Amphioceanic	Amphipacific	Amphiatlantic	Mediterranean	European-American	Indefinite
Acrobolbus ciliatus (Lindb.) Schiffn.		+	+		+										+				
Anastrophyllum assimile (Mitt.) Steph.		+	+	+										+					
A. michauxii (F. Weber) H. Buch	+	+			+			+											
Aneura pinguis (L.) Dumort.	+	+			+														+
Anthelia julacea (L.) Dumort.	+	+	+	+				+											
A. juratzkana (Limpr.) Trev.	+	+	+	+				+											
Anthoceros agrestis Paton	+	+				+		+											
A. punctatus L.	+	+				+		+											
Apomarsupella revoluta (Nees) R.M. Schust.		+	+	+										+					
Apometzgeria pubescens (Schrank) Kuwah.	+	+	+		+			+											
Asterella gracilis (F. Weber) Underw.	+	+	+	+				+											
A. leptophylla (Mont.) Grolle		+	+				+		+										
A. lindenbergiana (Corda) Lindenb.	+	+	+	+				+											
Athalamia nana (Shim. et S. Hatt.) S. Hatt.		+	+			+			+										
A. hyalina (Sommerf.) Hatt.	+		+	+				+											
A. spathysii (Lindenb.) S. Hatt.	+					+											+		
Barbilophozia barbata (Schmid. ex Schreb.) Loeske	+	+	+		+			+											
Barbilophozia hatcheri (Evans) Loeske	+	+	+	+				+											
B. lycopodioides (Wallr.) Loeske	+	+	+		+			+											
Bazzania bidentula (Steph.) Steph.		+				+			+										
B. flaccida (Dumort.) Grolle	+					+				+									
B. japonica (Sande Lac.) Lindb.		+				+			+										
B. ovifolia (Steph.) Hatt.		+				+			+										
B. tricrenata (Wahlenb.) Lindb.	+	+	+		+			+											
B. tridens (Reinw., Blume et Nees) Trevis		+					+		+										
B. trilobata (L.) S. Gray	+	+				+								+					
Blasia pusilla L.	+	+			+														+
Blepharostoma minus Horikawa		+			+				+										
B. trichophyllum (L.) Dumort.	+	+			+			+											
Calycularia laxa Lindb. et Arnell		+	+		+								+						
Calypogeia arguta Nees et Mont.	+	+				+								+					
C. azurea Stotler et Crotz	+	+				+								+					
C. fissa (L.) Raddi	+					+								+					
C. integristipula Steph.	+	+	+		+			+											
C. muelleriana (Schiffn.) Müll.Frib.	+	+	+		+			+											
C. neesiana (C. Massal. et Carest) Müll.Frib.		+	+		+			+											
C. sphagnicola (H.Arnell & J.Perss.) Warnst. et Loeske	+	+	+		+			+											
C. suecica (Arnell et J. Perss.) Mull. Frib.	+	+			+									+					
Cephalozia ambigua C.Mass.	+		+	+				+											
C. bicuspidata (L.) Dumort.	+	+		+				+											
C. catenulata (Huebener) Lindb.	+	+				+								+					
C. connivens (Dicks.) Lindb.	+	+			+			+											
C. lacinulata Jack ex Spruce		+				+								+					
C. leucantha Spruce		+	+		+			+											
C. lunulifolia (Dumort.) Dumort.		+	+		+			+											
C. macounii (Austin) Austin		+			+			+											
C. otaruensis Steph.		+			+										+				
C. pleniceps (Aust.) Lindb.	+	+	+		+			+											
C. zoopsioides Horikawa		+					+		+										
Cephaloziella aspericaulis Joerg.	+			+										+					
C. divaricata (Sm.) Schiffn.	+	+	+	+				+											
C. grimsulana (Jack ex Gott. & Rabenh.) Lacout	+	+	+	+				+											
C. microphylla (Steph.) Douin		+				+			+										
C. rubella (Nees) Warnst.	+	+			+			+											
C. spinicaulis Douin		+				+							+						
C. stellulifera (Spruce) Schiffn.	+				+									+					
C. turneri (Hook.) Müll.Frib.	+					+										+			
C. varians (Gottsche) Steph.	+		+	+				+											
Cheilolejeunea obtusifolia (Steph.) S. Hatt.		+				+			+										
Chiloscyphus fragilis (A.Roth) Schiffn.		+			+			+											
C. pallescens (Ehrh. ex Hoffm.) Dumort.	+	+			+			+											
Chiloscyphus polyanthos (L.) Corda	+	+			+			+											

	Caucasus	Manchuria	Montane	Arctic	Boreal	Temperate	Subtropical	Circumpolar	East Asian	European	Asian	Euroasian	Asian-American	Amphioceanic	Amphipacific	Amphiatlantic	Mediterranean	European-American	Indefinite
C. rivularis (Schrad.) Hazsl.		+			+			+											
Cladopodiella fluitans (Nees) Buch	+	+			+			+											
Cololejeunea calcarea (Libert.) Schiffn.	+		+			+				+									
C. denticulata (Horikawa) S. Hatt.		+					+		+										
C. japonica (Schiffn) S. Hatt. in Mizut.		+					+		+										
C. longifolia (Mitt.) Benedix in Mizut.		+	+				+		+										
C. macounii (Spruce in Underw.) A. Evans		+	+			+									+				
C. ornata A.W. Evans		+	+			+			+										
C. rossetiana (C. Mass.) Schiffn.	+						+										+		
C. spinosa (Horikawa) Pande et Misra		+					+				+								
Conocephalum conicum (L.) Und.	+	+			+			+											
C. japonicum (Thunb.) Grolle		+				+			+										
C. salebrosum Szweik., Buczk., Odrzyk.	+	+			+			+											
Crossocalyx hellerianus (Nees) Meyl.	+	+			+			+											
Crossogyna autumnalis (DC.) Schljakov	+	+				+		+											
C. undulifolia (Nees.) Müll.Frib.		+		+				+											
Cylindrocolea recurvifolia (Steph.) H. Inoue		+	+			+			+										
Diplophyllum albicans (L.) Dumort.	+	+	+	+										+					
D. obtusatum (R.M. Schust.) R.M. Schust.		+	+		+								+						
D. obtusifolium (Hook.) Dumort.		+	+		+			+											
D. taxifolium (Wahlenb.) Dumort.	+	+	+		+			+											
Dumortiera hirsuta (Sw.) Nees		+					+							+					
Eremonotus myriocarpus (Carr.) Lindb. & Kaal.	+	+	+	+										+					
Fossombronia alaskana Steere et Inoue		+		+									+						
F. angulosa (Dicks.) Raddi	+					+										+			
F. foveolata Lindb.	+					+		+											
F. pusilla (L.) Nees	+	+			+									+					
Frullania appendiculata Steph.		+				+			+										
F. bolanderi Aust.	+	+			+			+											
F. crispiplicata Yuzawa et S. Hatt.		+				+			+										
F. davurica Hampe		+			+						+								
F. dilatata (L.) Dumort.	+	+				+						+							
F. diversitexta Steph.		+				+			+										
F. ericoides (Nees) Mont.		+				+		+											
F. fragillifolia (Tayl.) Gottsche	+					+				+									
F. fuscovirens Steph.		+					+		+										
F. hamatiloba Steph.		+	+			+			+										
F. inflata Gottsche	+	+				+							+						
F. jackii Gotsche	+		+			+				+									
F. kagoshimensis Steph.		+					+		+										
F. koponenii S. Hatt.		+			+				+										
F. muscicola Steph.		+				+			+										
F. osumiensis (S. Hatt.) S. Hatt.		+					+		+										
F. parvistipula Steph.	+	+				+						+							
F. pedicellata Steph.		+					+		+										
F. polyptera Tayl.		+				+					+								
F. riparia Hampe ex Lehm.	+					+				+									
F. schensiana C. Massal.		+	+			+			+										
F. tamarisci (L.) Dumort.	+					+				+									
F. taradakensis Steph.		+				+					+								
Geocalyx graveolens (Schrad.) Nees	+	+			+			+											
G. lancistipulus (Steph.) S. Hatt.		+				+			+										
Gymnocolea inflata (Huds.) Dumort.	+	+	+	+				+											
Gymnomitrion apiculatum (Schiffn.) Müll.Frib.		+	+	+				+											
G. concinnatum (Lightf.) Corda	+		+	+				+											
G. corallioides Nees	+		+	+				+											
G. obtusum Lindb.	+		+		+									+					
G. uncrenulatum Gao et Chang		+			+				+										
Harpanthus flotovianus (Nees) Nees		+	+		+									+					
H. scutatus (F. Weber et D. Mohr) Spruce	+	+				+		+											
Hattorianthus erimonus (Steph.) R.M. Schust. et Inoue		+					+		+										
Herbertus dicranus (Taylor ex Gottsche et al.) Trevis		+	+	+				+											

	Caucasus	Manchuria	Montane	Arctic	Boreal	Temperate	Subtropical	Circumpolar	East Asian	European	Asian	Euroasian	Asian-American	Amphioceanic	Amphipacific	Amphiatlantic	Mediterranean	European-American	Indefinite
Heteroscyphus coalitus (Hook.) Schiffn.		+					+		+										
H. planus (Mitt.) Schiffn.		+					+		+										
Isopaches bicrenatus (Schmid. ex Hoffm.) H. Buch	+	+	+		+			+											
I. decolorans (Limpr.) Buch	+		+	+				+											
Jubula hutchinsiae (Hook.) Dumort. ssp. *caucasica* Konstant. et Vilnet.	+		+			+											+		
J. japonica Steph.		+					+		+										
Jungermannia atrovirens Dumort.	+	+	+		+			+											
J. borealis Damsh. & Vana	+		+	+				+											
J. eucordifolia Schljak.	+	+	+		+			+											
J. exsertifolia Steph.		+	+		+								+						
J. pumila With.	+	+	+		+			+											
Kurzia makinoana (Steph.) Grolle		+				+							+						
Leiocolea badensis (Gottsche) Schiffn.	+		+		+			+											
L. bantriensis (Hook.) Joerg.	+	+			+														
L. collaris (Nees) Schljakov	+	+	+		+			+											
L. heterocolpos (Thed. ex Hartm.) Buch	+	+	+		+			+											
L. turbinata (Raddi) H. Buch	+		+			+				+									
L. ussuriensis Bakalin		+	+			+			+										
Lejeunea cavifolia (Ehrh) Lindb.	+	+			+			+											
L. compacta (Steph.) Steph.		+					+		+										
L. japonica Mitt.		+				+			+										
L. patens Lindb.	+					+				+									
L. ulicina (Tayl.) Gottsche et al.		+					+					+							
Lepidozia reptans (L.) Dumort.	+	+			+			+											
L. fauriana Steph.		+	+			+			+										
L. subtransversa Steph.		+	+		+				+										
Liochlaena lanceolata Nees	+	+			+			+											
Liochlaena subulata (Evans) Schljak.	+	+			+			+											
Lophocolea bidentata (L.) Dumort.	+	+				+		+											
Lophocolea compacta Mitt.		+	+			+			+										
Lophocolea cuspidata (Nees) Limpr.	+	+				+								+					
Lophocolea heterophylla (Schrad.) Dumort.	+	+			+			+											
Lophocolea horikowana S. Hatt.		+	+			+			+										
Lophocolea itoana H. Inoue		+	+		+				+										
Lophocolea minor Nees	+	+			+			+											
Lophozia ascendens (Warnst.) R.M. Schust.	+	+			+			+											
L. excisa (Dicks.) Dumort.	+	+			+			+											
L. guttulata (Lindb. et Arnell) A. Evans	+	+			+			+											
L. lantratoviae Bakalin	+	+	+			+					+								
L. longidens (Lindb.) Macoun	+	+			+			+											
L. propagulifera (Gott.) Steph.	+	+	+	+				+											
L. silvicola H. Buch	+				+			+											
L. sudetica (Nees ex Hueb.) Grolle	+	+	+	+				+											
L. ventricosa (Dicks.) Dumort. var. *ventricosa*		+			+			+											
L. ventricosa var. *longiflora* (Nees) Macoun	+	+			+			+											
L. wenzelii (Nees) Steph. var. *wenzelii*	+	+	+	+				+											
L. wenzelii var. *groenlandica* (Nees) Bakalin	+		+	+				+											
L. wenzelii var. *massularioides* Bakalin	+		+		+												+		
Lunularia cruciata (L.) Lindb.	+					+													+
Macrodiplophyllum microdontum (Mitt.) H.Perss.		+	+	+									+						
M. plicatum (Lindb.) H.Perss.		+	+		+										+				
Mannia androgyna (L.) A. Evans	+	+	+			+						+							
M. fragrans (Balb.) Frye et Clark	+	+	+		+			+											
M. pilosa (Horn) Frey et Clark		+	+	+				+											
M. sibirica (Müll.Frib.) Frey et Clark		+	+	+				+											
Marchantia alpestris (Nees) Burgeff		+	+	+				+											
M. aquatica (Nees) Burgeff	+		+		+			+											
M. latifolia Gray	+	+																	+
M. paleacea Bertol.	+	+				+													+
Marsupella alpina (Gott. ex Limpr.) H.Bern		+	+	+				+											
M. brevissima (Dumort.) Grolle	+		+	+				+											

	Caucasus	Manchuria	Montane	Arctic	Boreal	Temperate	Subtropical	Circumpolar	East Asian	European	Asian	Euroasian	Asian-American	Amphioceanic	Amphipacific	Amphiatlantic	Mediterranean	European-American	Indefinite
M. commutata (Limpr.) H.Bern.		+	+	+										+					
M. condensata (Aongstr. ex C. Hartm.) Lindb. ex Kaal.	+		+	+				+											
M. emarginata (Ehrh.) Dumort.	+		+	+				+											
M. funckii (F.Web. et Mohr) Dumort.	+		+			+								+					
M. sparsifolia (Lindb.) Dumort.	+		+	+				+											
M. sphacelata (Gieseke ex Lindenb.) Dumort.	+	+	+	+				+											
M. pseudofunckii S. Hatt.		+	+		+				+										
M. tubulosa Steph.		+	+	+				+											
M. yakushimensis (Horikawa) S. Hatt.		+	+		+				+										
Metacalypogeia cordifolia (Steph.) H. Inoue		+				+			+										
Metzgeria conjugata Lindb.	+	+	+			+													+
M. furcata (L.) Dumort.	+	+	+		+			+											
M. leptoneura Spruce (= *M. hamata*)		+					+							+					
M. lindbergii Schiffn.		+				+			+										
M. violacea (Ach. ex F. Weber et D. Mohr) Dumort.	+					+								+					
Moerckia blyttii (Moerck) Brockm.	+		+	+				+											
M. hibernica (Hook.) Gottsche	+		+		+			+											
Mylia nuda H. Inoue et Yang		+					+		+										
M. taylorii (Hook.) S. Gray		+	+		+			+											
M. verrucosa Lindb.		+				+			+										
Nardia assamica (Mitt.) Amakawa	+	+	+		+				+										
N. compressa (Hook.) S.Gray	+		+	+										+					
N. geoscyphus (De Not.) Lindb.	+		+	+				+											
N. scalaris S.Gray	+		+	+				+											
Nipponolejeunea subalpina (Horikawa) S. Hatt.		+	+		+				+										
Notothylas orbicularis (Schwein) Sull.		+				+								+					
Nowellia curvifolia (Dicks.) Mitt.	+	+				+								+					
Obtusifolium obtusum (Lindb.) S.W. Arnell	+	+	+	+				+											
Odontoschisma denudatum (Mart.) Dumort.	+	+				+		+											
Orthocaulis attenuatus (Mart.) Evans	+	+			+			+											
O. floerkei (F. Weber et D. Mohr) H. Buch	+		+	+				+											
O. kunzeanus (Hueb.) Buch		+		+				+											
O. quadrilobus (Lindb.) Buch	+	+	+		+			+											
Pallavicinia lyelli (Hook.) Carruth.	+	+				+								+					
Pedinophyllum interruptum (Nees) Lindb.	+	+				+		+											
P. truncatum (Steph.) H. Inoue		+				+			+										
Pellia endiviifolia (Dicks.) Dumort.	+	+			+			+											
P. epiphylla (L.) Corda	+	+			+			+											
P. neesiana (Gott.) Limpr.	+	+			+			+											
Peltolepis quadrata (Saut.) Müll.Frib.	+	+	+	+				+											
Phaeoceros bulbiculosus (Brot.) Prosk.	+	+				+											+		
P. carolinianus (Michx.) Prosk.	+					+		+											
P. laevis Prosk.	+	+				+								+					
Plagiochasma japonicum (Steph.) Hass.		+	+				+	+											
P. pterospermum C. Massal.		+	+			+					+								
P. rupestre (Forst.) Steph.		+																	+
Plagiochila asplenioides (L.) Dumort.	+	+			+			+											
P. dendroides (Nees) Lindenb.		+					+		+										
P duthiana Steph.		+	+		+						+								
P. gracilis Lindenb. et Gottsche		+	+		+								+						
P. hakkodensis Steph.		+	+			+			+										
P. japonica Sande Lac.		+				+			+										
P. ovalifolia Mitt.		+	+			+			+										
P. porelloides (Torrey ex Nees) Lindenb.	+	+			+			+											
P. sciophila Nees et Lindenb.		+					+				+								
P. trabeculata Steph.		+	+			+			+										
Plectocolea comata (Nees) S. Hatt.		+					+				+								
P. erecta Amakawa		+	+			+			+										
P. hyalina (Lyell) Mitt.	+	+			+			+											
P. infusca Mitt. var. *infusca*		+				+			+										
P. kurilensis (Bakalin) Bakalin et Vilnet		+				+			+										

	Caucasus	Manchuria	Montane	Arctic	Boreal	Temperate	Subtropical	Circumpolar	East Asian	European	Asian	Euroasian	Asian-American	Amphioceanic	Amphipacific	Amphiatlantic	Mediterranean	European-American	Indefinite
P. obovata (Nees) Lindb.	+	+	+	+				+											
P. obscura A. Evans		+	+		+										+				
P. subelliptica (Lindb. ex Kaal.) Evans	+	+	+	+				+											
P. truncata (Nees)		+					+		+										
Pleurocladula albescens (Hook.) Grolle	+		+	+				+											
Plicanthus birmensis (Steph.) R.M. Schust.		+					+		+										
Porella arboris-vitae (With.) Grolle	+		+			+				+									
P. baueri (Schiffn.) C.E.O. Jens.	+		+			+				+									
P. caespitans (Steph.) S. Hatt.		+					+		+										
P. chinensis (Steph.) S. Hatt.		+				+					+								
P. cordeana (Huebener) H. Buch	+		+		+			+											
P. densifolia (Steph.) S. Hatt.		+					+		+										
P. fauriei (Steph.) S. Hatt.		+			+				+										
P. gracillima Mitt.		+				+					+								
P. grandiloba Lindb.		+				+			+										
P. japonica (Sande Lac.) Mitt.		+					+		+										
P. nitens (Steph.) S. Hatt. in Hara		+				+			+										
P. oblongifolia S. Hatt.		+					+		+										
P. platyphylla (L.) Pfeiff.	+	+			+			+											
P. platyphylloidea (Schwein.) Lindb.	+		+			+												+	
P. spinulosa (Steph. S. Hatt.		+					+		+										
P. tosana (Steph.) S. Hatt.		+					+		+										
P. ulophylla (Steph.) S. Hatt.		+				+			+										
P. vernicosa Lindb.		+				+			+										
Preissia quadrata (Scop.) Nees	+	+	+		+			+											
Protolophozia debiliformis (Schust.) Konst.	+			+										+					
Ptilidium ciliare (L.) Hampe	+	+		+				+											
P. pulcherrimum (G.Web.) Vain.	+	+			+			+											
Radula aquilegia (Hook. F. et Tayl.) Gott. et al.		+				+						+							
R. auriculata Steph.		+	+			+									+				
R. cavifolia Hampe		+	+			+			+										
R. complanata (L.) Dumort.	+	+			+			+											
R. constricta Steph.		+			+				+										
R. fauriana Steph.		+	+		+				+										
R. japonica Gottsche in Steph.		+				+			+										
R. lindenbergiana Gottsche ex Hartm.	+				+									+					
R. obtusiloba Steph.		+				+			+										
R. tokiensis Steph.		+				+			+										
Reboulia hemisphaerica (L.) Raddi ssp. *hemisphaerica*	+	+	+																+
R. hemisphaerica ssp. *australis* R.M. Schust.	+		+																+
R. hemisphaerica ssp. *orientalis* R.M. Schust.		+	+																+
Riccardia chamaedryfolia (With.) Grolle	+	+				+		+											
R. latifrons (Lindb.) Lindb.	+	+			+			+											
R. multifida (L.) Gray ssp. *decrescens* (Steph.) Furuki		+				+			+										
R. multifida (L.) Gray ssp. *multifda*	+	+			+			+											
R. palmata (Hedw.) Carruth.	+	+			+			+											
Riccia bifurca Hoffm.	+	+				+		+											
R. crinita Tayl.	+					+											+		
R. cavernosa Hoffm.		+			+			+											
R. ciliifera Link ex Lindenb.	+					+						+							
R. crystallina L. emend. Raddi		+				+													+
R. fluitans Lindenb.		+				+													+
R. frostii Austin		+			+			+											
R. glauca L.		+				+		+											
R. gougetiana Dumort. et Mart.	+					+				+									
R. huebeneriana Lindenb.		+				+		+											
R. lamellosa Raddi	+																		+
R. michelii Dumort. et Mart.	+					+				+									
R. sorocarpa Bisch.	+	+				+		+											
Ricciocarpos natans (L.) Corda	+	+																	+
Riella paulsenii Porsild	+					+					+								
Sauteria alpina (Nees) Nees	+		+	+				+											

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Scapania aequiloba (Schwaegr.) Dumort.	+		+		+					+									
S. ampliata Steph.		+	+		+				+										
S. apiculata Spruce	+	+			+			+											
S. aspera M. et H. Bernet	+					+				+									
S. brevicaulis Tayl.	+		+	+				+											
S. calcicola (Arnell et J. Perss.) Ingham	+				+													+	
S. carinthiaca Jack ex. Lindb.	+	+			+			+											
S. ciliata Sande Lac.		+				+			+										
S. compacta (A. Roth) Dumort.	+					+		+											
S. crassiretis Bryhn		+	+	+				+											
S. curta (Mart.) Dumort.		+	+		+			+											
S. cuspiduligera (Nees) Müll.Frib.	+		+		+			+											
S. gymnostomophila Kaal.	+		+		+			+											
S. helvetica Gottsche	+		+		+					+									
S. irrigua (Nees) Nees	+	+	+		+			+											
S. kaurinii Ryan	+		+	+				+											
S. lingulata H. Buch	+		+		+			+											
S. massalongii Müll.Frib.		+	+		+													+	
S. mucronata H. Buch	+	+	+		+			+											
S. nemorea (L.) Grolle	+					+								+					
S. obcordata (Berggr.) S. W. Arnell	+			+				+											
S. paludicola Loeske & Müll.Frib.		+			+			+											
S. paludosa (Müll.Frib.) Müll.Frib.	+		+	+				+											
S. parvidens Steph.		+	+		+				+										
S. parvifolia Warnst. var. *parvifolia*		+			+			+											
S. parvitexta Steph.		+	+		+				+										
S. preatervisa Meylan	+		+	+				+											
S. rufidula Warnst.		+	+	+							+								
S. scandica (H.Arnell & Buch) Macv.	+	+	+	+				+											
S. sphaerifera H. Buch.		+	+	+								+							
S. subalpina (Nees ex Lindenb.) Dumort.	+	+	+	+				+											
S. umbrosa (Schrad.) Dumort.	+				+			+											
S. undulata (L.) Dumort.	+	+	+		+			+											
S. uliginosa (Lindenb.) Dumort.		+	+	+				+											
S. verrucosa Heeg	+	+	+		+			+											
Schistochilopsis cornuta (Steph.) Konstant.		+			+				+										
S. incisa (Schrad.) Konst.	+	+			+			+											
Solenostoma appressifolium (Mitt.) Váňa et D.G. Long		+	+			+					+								
S. caucasica (Vana) Konst.	+		+		+												+		
S. confertissimum (Nees) Schljak.	+		+	+				+											
S. fauriana (Beauverd) Bakalin		+	+			+			+										
S. gracillimum (Sm.) Schust.	+					+								+					
S. handelii Schiffn.	+					+						+							
S. major (S. Hatt.) Bakalin et Vilnet		+	+			+			+										
S. pseudopyriflorum Bakalin et Vilnet		+				+					+								
S. pyriflorum Steph.		+				+							+						
S. sphaerocarpum (Hook.) Steph.	+	+	+	+				+											
Southbya tophacea (Spruce) Spruce	+					+											+		
Sphenolobus minutus (Schreb.) Berggr.	+	+	+	+				+											
S. saxicola (Schrad.) Steph.		+	+	+				+											
Targionia hypophylla L.		+																	+
T. indica Udar et Gupta		+				+					+								
Tetralophozia setiformis (Ehrh.) Schljak.		+	+	+				+											
Trichocolea tomentella (Ehrh.) Dumort.	+	+				+								+					
Trichocoleopsis sacculata (Mitt.) Okam.		+					+		+										
Tritomaria exsecta (Schmid. ex Schrad.) Loeske	+	+			+			+											
T. exsectiformis (Breidl.) Schiffn. ex Loeske	+	+			+			+											
T. quinquedentata (Huds.) H. Buch	+	+	+	+				+											
Trocholejeunea sandvicensis (Gottsche) Mizutani		+					+	+											
Tuzibeanthus chinensis (Steph.) Mizut.		+	+				+		+										
Xenochila integrifolia (Mitt.) H. Inoue		+					+		+										
Total number of species	**204**	**290**	**163**	**72**	**128**	**124**	**37**	**165**	**88**	**15**	**16**	**8**	**10**	**32**	**6**	**2**	**8**	**3**	**15**