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Phytogeography of the Kurile Islands

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Abstract The vascular flora of the Kurile Islands consists of 1367 species, 550 genera and 135 families (582 spp. from the North Kuriles, 334 spp. from the Middle Kuriles, and 1215 spp. from the South Kuriles). The flora of the Kurile Islands is derived from two florogenetic centers, the Beringian and the Japanese. The influence of the Kamchatkan and Japanese floras, which belong to different floristic regions, is clearly seen here. The main change in the composition of the Kuriles flora is observed north of Urup Island, indicating that the floristic boundary separating the Circumboreal and East Asiatic Regions passes through the Bussol Strait (between Simushir and Chirpoi Islands). The northern limits for 102 species of 48 genera and 13 families, which compose the East Asiatic elements in the Kuriles flora, were found on Urup Island.

Key words: Kurile Islands, phytogeography, flora, vascular plants, floristic regionalization.

The Kurile Islands extend from northern Japan (Hokkaido Island) to the southern extremity of the Kamchatka Peninsula (Cape Lopatka), between 43°26′ and 50°55′N and 145°24′ and 156°30′E, separating the Sea of Okhotsk from the North Pacific Ocean (Fig. 1). The Kuriles are divided into two ridges, the Bolshaya Kurilskaya (inner) and Malaya Kurilskaya (external) Ridges, by the shallow Yuzhno-Kurilsky Strait. The Kuriles extend for about 1250 km and have a total area of about 10,200 km^2. The Bolshaya Kurilskaya Ridge is divided by the Krusenshtern and Bussol Straits of approximately 2000 m depth into three groups of islands, the northern (North Kuriles), middle (Middle Kuriles) and southern (South Kuriles). The last group includes the islands of the Malaya Kurilskaya Ridge (Shikotan and Habomai Islands).

There are three major publications on the flora of the Kuriles: Miyabe (1890), Vorobiev (1956) and Tatewaki (1957), in which information on their floristic composition is given. The modern and the most complete information is given in "Vascular Plants of the Soviet Far East" (Kharkevich, 1985–1996).

Materials and Methods

Extensive research on the flora of the Kuriles was carried out by the author in 1978–1997. In addition to the author's collections from Atlasov, Shumshu, Paramushir, Onekotan, Iturup, Kunashir, Kurile plants preserved in the herbaria of St. Petersburg (LE), Moscow (MHA, MW) and Vladivostok (VLA) were checked. Previous literature (Yabe and Yendo, 1904; Kudo, 1922; Tatewaki, 1927; 1934; 1957; Vorobiev, 1956; 1960; Egorova, 1964; 1972; 1981; Chernyaeva, 1973; 1977; Barkalov, 1980; 1981; 1984; 1987; 1988; Alekseyeva, 1983; Voroshilov, 1985; Barkalov and Vyshin, 1989; Takahashi et al., 1997) on the local flora has been reviewed.

The information about the floras of Kamchatka, Sakhalin, Sikhote-Alin Range and the Commander Islands has been taken from the "Vascular Plants of the Soviet Far East" (Kharkevich, 1985–1996), together with some new data. When drawing up the check lists of plants of the Aleutian Islands and Hokkaido, the works of several researchers were used (Miyabe and Kudo, 1930–1934; Hultén, 1960, 1968; Ohwi, 1965; Shimizu, 1982, 1983; Kadota, 1987 etc.).

The ratio of the number of species/number of genera is determined by curvilinear dependence (Malyshev, 1969, 1976). A parameter estimating auto- and allochthonous tendencies in florogenetic processes in a territory is calculated through the formula:

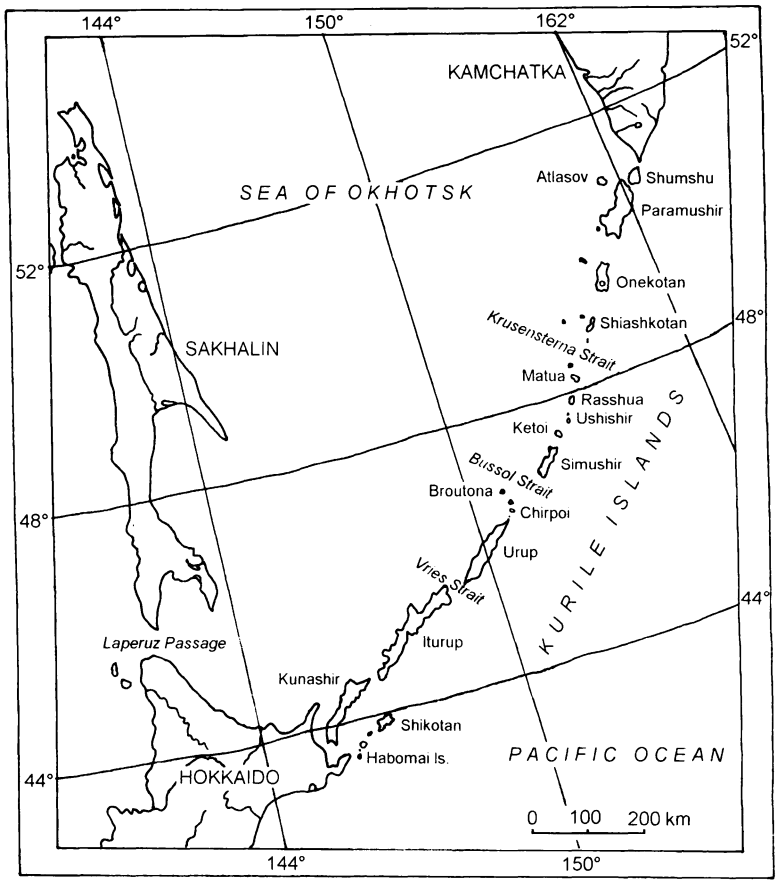

Fig. 1. Map-scheme of the Kurile Islands.

$$A = \frac{S - å}{S},$$

where A = parameter of the flora autonomy; S = actual number of species; å = number of species by calculation. The calculated number of species is defined on the empirical square-law equation: $å = 314.1 + 0.0045383\,G^2$, where G shows the number of genera in the flora.

Results and Discussion

Floristic Diversity

The vascular flora of the Kurile Islands consists of 1367 species of 550 genera and 135 families. Introduced species form 12.7% of the total species recorded from the Kuriles. These species show synanthropic changes in the flora, and thus represent the alien element. Only a few of them occur on every island or penetrate into natural plant communities. These include: *Phleum pratense, Agrostis gigantea, Trifolium repens, T. pratense, Leucanthemum vulgare* and *Taraxacum officinale.* Other invasive plants are known mostly only from one site on one or two islands, often in ports, along roadsides, near to garbage dumps, and less often as weeds in fields and kitchen gardens. These are: *Alopecurus arundinaceus, Avena fatua, Elymus novae-angliae, Puccinellia distans, Spergula arvensis, Stellaria graminea, Aconogonon divaricatum, Euclidium syriacum* and *Potentilla intermedia.* Invasive plants have penetrated into the Kurile Islands in different times, probably by three routes, from Kamchatka, Sakhalin and Japan.

The quantitative characteristics of the Kuriles flora show a great variety of natural conditions. Each group of the Kurile Islands differs in species richness (Table 1). The flora of the southern Kuriles is about twice as rich as that of the northern Kuriles and three

Table 1. Indices of floristic richness and taxonomic diversity of the Kurile Islands.

Islands		Number of			
		families	genera	species	introduced species
Kurile Islands in the whole		135	549	1367	173
North Kuriles	in the whole	71	248	582	56
	Atlasov	48	123	178	3
	Shumshu	66	210	430	19
	Paramushir	69	236	536	52
	Makanrushi	10	12	12	0
	Onekotan	63	170	303	2
	Shiashkotan	46	114	142	1
	Kharimkotan	7	10	11	0
	Ekarma	27	54	64	0
	Raikoke	3	3	3	0
Middle Kuriles	in the whole	66	186	334	7
	Matua	44	117	160	2
	Rasshua	58	154	236	2
	Ushishir	56	147	209	2
	Ketoi	59	160	240	2
	Simushir	64	172	271	5
South Kuriles	in the whole	128	535	1215	166
	Chirpoi	33	89	105	0
	Brat Chirpoev	1	1	1	0
	Urup	86	267	443	6
	Iturup	113	404	840	96
	Kunashir	129	490	1045	138
	Shikotan	110	349	668	48
	Polonsky	23	41	45	4
	Zeliony	43	108	144	15
	Tanfiliev	28	51	64	6
	Yuri	39	73	85	1
	Diomin	11	18	18	1
	Anuchin	16	29	34	3

times as rich as that of the middle Kuriles. The islands richest in flora are Paramushir, Iturup, Kunashir and Shikotan, and those poorest in flora are the middle Kuriles, Matua, Rasshua, Ketoi and other islands. This may be explained by the more severe (in comparison with the North Kuriles) modern climatic conditions of the area as well as the fact that these islands are small and situated far from the continent, and also include active volcanos.

The richness of the flora of the South Kuriles may be explained by the influence of the warm Soya current, creating favorable climatic conditions for distribution and development of thermophilous plants. The protective role of the longitudinal mountain ranges is significant (from the fogs on the Okhotsk coasts of the islands). On Kunashir Island there are some representatives of East Asian flora, such as *Quercus dentata, Boehmeria tricuspis, Magnolia hypoleuca, Tilia maximowicziana, Acer japonicum, Juglans ailanthifolia, Thymus semiglaber, Nepeta subsessilis* and *Dioscorea batatas*, which also occur in Hokkaido. According to Popov (1965), the preservation of *Quercus crispula* in the central part of Iturup Island could be explained by the influence of the warm current along the Okhotsk coast of the island, and the shelter of this area from penetration by cold and damp Pacific winds by the Grozny mountain range (1200 m alt.).

In order to evaluate the quantitative floris-

Table 2. The quantitative data on floras.

Areas	Number* of			Autonomy parameter
	families	genera	species	
Kurile Islands	130	487	1194	−0.165
Sakhalin	122	462	1196	−0.073
Kamchatka	90	342	963	+0.123
Sikhote-Alinj	138	603	1558	−0.261
Hokkaido	162	666	1638	−0.421
Aleutian Islands	67	201	431	−0.154

* introduced spp. are excluded.

tic richness of the Kuriles, a comparison with the adjacent areas, i.e. Kamchatka, Sakhalin, Sikhote-Alin Range, Commander Islands, Aleutian and Hokkaido, has been made (Table 2). The vascular flora of the Kurile Islands in terms of the total number of species is close to that of the flora of Sakhalin, which is on the same latitude, but the territory of Sakhalin is much larger than that of the Kuriles. In the case of taxonomic diversity (total number of genera and families), however, the Kurile flora is richer than that of Sakhalin. The floras of Kamchatka and the islands of the Commander-Aleutian chain are less diverse than that of the Kuriles. Only Sikhote-Alin Range and Hokkaido are floristically richer than the Kuriles.

The value for the parameter of autonomy is positive, thus indicating the prevalence of an autochthonous tendency in the development of the flora, only in the case of Kamchatka (Table 2). Negative values for this parameter indicate the prevalence of allochthony in florogenesis in all the other territories, including the Kuriles. The proximity of the Kuriles to Kamchatka (in the north) and Hokkaido (in the south), the changes in paleogeographical conditions in this area during the Quartenary as a result of fluctuations in the level of the global ocean, development of tectonic processes, volcanic activities and the changes of climatic conditions increased the allochthonous origins of the flora in this territory.

Chorological Analysis of the Flora

In the flora of the Kurile Islands I distinguish six chorological elements: (1) Circumpolar, (2) Asiatic-American, (3) Euro-Asiatic, (4) Asiatic, (5) East Asiatic and (6) Endemic. Some of them are further subdivided into groups. In establishing the groups, the specific features of areas of distribution as well as floristic relations of the Kurile Islands with the adjacent territories were considered. The East Asiatic element includes species distributed in the East Asiatic floristic region (Takhtajan, 1978).

In the flora of the Kuriles, species of the East Asiatic group prevail (518 spp.), being about 2–2.5 times the number of species in the Circumpolar (268 spp.), Asiatic-American (176 spp.) or Asiatic (158 spp.) groups (Table 3). There are fewer species with Euro-Asiatic areas of distribution (51 spp.). These include: *Botrychium lunaria, Ceratophyllum demersum, Ranunculus monophyllus*, and *Epilobium montanum*. The number of species with Asiatic-American distribution increases from south to north. In contrast, the East Asiatic species decrease in number from south to north, and only a few of them penetrate further north along the Bolshaya Kurilskaya Ridge, which is the northern limit of their distribution. These are: *Padus ssiori* (known up to Simushir), *Sasa kurilensis* (up to Ketoi), *Taxus cuspidata* (up to Matua), *Fragaria yezoensis* and *Aconogonon savatieri* (up to Shiashkotan), *Weigela middendorffiana* (up to Onekotan), *Ilex rugosa* and *Petasites amplus* (up to Paramushir), and *Rubia jesoensis* (up to Shumshu). The role of the species with Circumpolar, Asiatic-American and Asiatic areas of distribution in the composition of the Kuriles flora

Table 3. Ratios of chorological elements in the flora of the Kuriles. A, total number of species; B, percentage of total number of species in the flora of the Kurile Islands (first column of the table); percentage of total the number of species in the floras of the groups of islands (second to fourth columns).

1	Chorological element (group)	Kurile Islands		North Kuriles		Middle Kuriles		South Kuriles	
		A	B	A	B	A	B	A	B
1.	Circumpolar	268	22.4	199	37.8	107	32.7	210	20.0
2.	Asiatic-American	176	14.6	152	28.7	97	29.4	129	12.2
2a.	Asiatic-American proper	73	6.1	59	11.2	32	9.8	54	5.1
2b.	Amphi-Pacific	51	4.2	44	8.2	25	7.3	36	3.3
2c.	North Pacific	52	4.3	49	9.3	40	12.2	39	3.7
3.	Euro-Asiatic	51	4.2	17	3.2	9	2.8	47	4.5
4.	Asiatic	158	13.3	113	21.5	74	22.6	128	12.3
4a.	Asiatic proper	11	0.9	4	0.8	4	1.2	11	1.0
4b.	North Asiatic	12	1.0	6	1.1	5	1.5	10	1.0
4c.	North-East Asiatic	24	2.0	21	4.0	5	1.5	11	1.0
4d.	Okhotian	99	8.3	70	13.3	59	18.0	95	9.2
4e.	Kamchatkan	12	1.0	12	2.3	1	0.3	1	0.1
5.	East Asiatic	518	43.3	35	6.9	33	10.4	516	49.2
5a.	East Asiatic proper	187	15.6	14	2.9	6	2.1	184	17.5
5b.	Japanese-Mandshurian	90	7.5	3	0.6	3	0.9	90	8.6
5c.	Japanese-Korean	46	3.8	4	0.8	4	1.2	46	4.4
5d.	Japanese	196	16.3	15	2.9	20	6.1	196	18.7
6.	Endemic	25	2.2	9	1.9	7	2.1	18	1.8

increases from south to north.

The East Asiatic element is subdivided into the following four groups: East Asiatic proper; Japanese-Mandshurian; Japanese-Korean; and Japanese. The Japanese group indicates a floristic relation of the Kurile Islands to Japan and includes species with mostly insular areas of distribution, i.e. Kuriles, Sakhalin and Japanese Islands. The group includes: *Abies sachalinensis, Picea glehnii, P. jezoensis, Phellodendron sachalinense, Lonicera glehnii, Padus ssiori, Skimmia repens, Viola kitamiana, Rhodiola ishidae, Aster glehnii, Clinopodium sachalinense, Petasites amplus, Cardiocrinum glehnii, Hosta rectifolia, Carex blepharicarpa, C. jacens, C. koidzumii, Brylkinia caudata* and *Sasa* spp. Some of them, *Selaginella shakotanensis, Salix reinii, Ilex rugosa, Ephippianthus sachalinensis* and *Solanum megacarpum*, are also distributed in continental parts of the Russian Far East (eastern part of Sikhote-Alin and coast along the Tatarsky Strait).

There are a small number of species distributed on the southern Kuriles and Sakhalin, but not known from Japan: *Larix kurilensis, Minuartia barkalovii, Myosotis sachalinensis, Veronica schmidtiana* and *Taraxacum miyakei*. These are only provisionally referred to the Japanese element.

Some species are common to the south of the Far East (Ussuri, North-East China and the north Korean Peninsula): *Cerasus maximowiczii, Euonymus macroptera, Lonicera chrysantha, Actinidia arguta, Schisandra chinensis, Chloranthus japonicus, Adonis amurensis, Schizopepon bryoniifolius, Waldsteinia ternata* and *Carex dispalata*. These plants belong to the Japanese-Mandshurian, Japanese-Korean and also partly East Asiatic proper groups. They are typical representatives of the East-Asiatic floristic region and characteristic for the South Kuriles.

Floristic relations of the Kurile Islands with the American continent are shown by the presence of Asiatic-American element, which can be subdivided into three groups. The more widely distributed species, which

penetrate into the Asian continent, are referred to as the Asiatic-American (proper) chorological group. The Amphi-Pacific group is represented by species distributed in the coastal zone of the Pacific Ocean. The third, the North Pacific group, includes species known from the Alaska Peninsula to the Japanese Islands. The species of this group may be found on Sakhalin, but not in the Arctic Region. The majority of the Amphi-Pacific and North Pacific species are widely distributed in the Kurile Islands and are abundant in their habitats. These include: *Aconitum maximum, Harrimanella stelleriana, Cassiope lycopodioides, Phyllodoce aleutica, Rhododendron kamtschaticum, Parageum calthifolium, Geranium erianthum, Lagotis glauca, Pennellianthus frutescens, Arnica unalaschcensis, Cirsium kamtschaticum* and *Platanthera chorisiana.*

It should be noted that the North Pacific species are distributed mainly in the islands, as well as along sea coasts in the continental areas. For this territory taken as a biogeographical and paleogeographical unit, Yurtsev (1974) adopted the term "Hultenia", proposed by Tatewaki (1963a; 1963b) primarily for the Commander-Aleutian chain. Yurtsev also includes in Hultenia the east coast of the Kamchatka Peninsula and the Kurile Islands northwards from Urup. Yurtsevs concluded that Hultenia is extremely rich in Pacific boreal, subalpine and alpine species, but poor in arctic, arctic-alpine and continental boreal, subalpine and alpine species. Only in the south of Hultenia (the northern and middle Kuriles, as well as south of the Kamchatka Peninsula) do some of the American species occur in Asia; these are *Allocarya orientalis, Erigeron peregrinus, Agrostis alaskana, A. exarata, Carex kelloggii, Luzula piperi* and *L. kobayasii.*

Some genera show a disjunct Amphi-Pacific distribution. They occur in the Kurile Islands, Japan, some continental areas of Asia and the American coast of the Pacific Ocean, but are absent in Kamchatka or in the area of the Bering Strait. These include: *Diphylleia, Caulophyllum, Magnolia, Fauria, Mitchella, Trillium, Disporum* and *Pogonia.* The presence of these genera indicates ancient relations with East Asian and North American floras. A good example of such a disjunctive distribution is the genus *Fauria* (Menyanthaceae), with the unique species, *F. crista-galli.* This is known from the Pacific states of North America and also the mountains of Iturup Island, as well as in Hokkaido and Honshu Islands. The Asiatic populations of *F. crista-galli* are considered as subspecies *F. crista-galli japonica* (Franch.) Gillet, with the chromosome number 2=68, while the American nominotypical subspecies has 2n=102 (Shimizu, 1982). The disjunction of geographical distribution of *F. crista-galli*, and the difference between Asian and American populations testify to the ancient age of the species. One more example is *Rubus pedatus*, which is distributed similarly to the previous species, but a little wider, including Sakhalin and Kunashir Islands. It is known in Asia mainly in subalpine vegetation with *Pinus pumila* and *Rhododendron aureum*, but also occurs in mountain spruce forests. In the case of *Osmunda japonica, Lysichiton camtschatcense, Symplocarpus renifolius, Diphylleia grayi* and *Carex tsuishikarensis*, which are distributed in East Asia (including southern Kuriles), they are replaced on the American continent by closely related species (*O. cinnamomea, L. americanum, S. foetidus, D. cymosa*, and *C. oligosperma*) which also supports the ancient isolation of these taxa before speciation.

The Okhotian group of species is closely related to the Japanese group, and, at the same time, to Amphi-Pacific and North Pacific groups. In the flora of the Kurile Islands 99 species of the Okhotian type of distribution were found. These include *Betula ermanii, Polystichum microchlamys, Trollius riederianus, Urtica platyphylla, Stellaria fenzlii, Rosa rugosa, Thermopsis lupinoides, Artemisia stelleriana, Carex hakkodensis, Agrostis flaccida* and *etc.* The ancient Okhotia probably had an important role in the origin of insular and coastal floras of the Sea of Okhotsk basin.

The endemic element in the flora of the Kurile Islands is poorly represented. Endemic families and genera are absent, but there are 25 endemic species, forming about 2% of the total number of indigenous species in the Kuriles flora. These include: *Astragalus kawa-*

kamii, Hedysarum confertum, Oxytropis itoana, O. kunashiriense, O. retusa, Minuartia kurilensis, Ixeridium kurilense, Leontopodium kurilense, Saussurea kurilensis, Taraxacum ketoense, T. kojimae, T. shumushuense, T. vulcanorum, T. yetrofuense, Carex chishimana and *C. ushishirensis*. Some of them are not clearly distinguished from related widely distributed species.

As was pointed out by Tolmachev (1959) for the flora of Sakhalin, the originality of the flora in some areas cannot always be expressed by endemic elements. Especially, where the land-sea interactions are active, the floristic limits do not always coincide with the actual topographical boundaries. This is especially true for the Kurile Islands, where different groups of islands belong to different global floristic subdivisions. A large group of East Asiatic species distributed on the southern Kuriles, as well as on the south (sometimes the centre) of Sakhalin, on Hokkaido Island, and rarely on mountains of northern and central Honshu, forms about 10% of the total specific structure of the Kuriles flora. This group can be considered as endemic to the southern Kuriles, southern Sakhalin and northern Japan, and in the Kuriles it represents a hemi-endemic element.

The hemi-endemic element can be subdivided into a number of groups. One of them (nearly 80 species) consists of species distributed on the South Kuriles, southern Sakhalin and in the north of Japan, sometimes penetrating to the North Kuriles and occurring on mountains of northern or central Honshu. These include *Picea glehnii, P. jezoensis, Abies sachalinensis*, some representatives of the genus *Sasa* and *Petasites amplus*. To the next group (about 50 species), we refer species distributed on the South Kuriles and the northern Japan (*Cerasus nipponica, Acer tschonoskii, Ilex sugerokii, Skimmia repens, Aster glehnii* and *Saussurea fauriei*). Some of the Kurile-Japanese species (*Salix hidaka-montana, Gentiana nipponica, Mertensia pterocarpa, Carex albata* and *Calamagrostis urelytra*) penetrate to the middle or northern Kuriles, but are absent in Kamchatka. Only four species (*Larix kurilensis, Rhodiola sachalinensis, Veronica schmidtiana* and *Taraxacum miyakei*) occur in the South Kuriles and Sakhalin and are unknown in Hokkaido. These groups are important for reconstruction of the florogenetic relations in the Kuriles; they have much in common, and historically are connected with an ancient South Okhotian land, now split up, but more or less entire in the past. They have probably originated in this area. Many of these species are common on the southern Kuriles and, as a rule, are abundant in their habitats. As examples of rare species we can cite *Betula maximowicziana, Tilia maximowicziana, Acer japonicum, Rubus pseudojaponicus, Myrmechis japonica, Viola kitamiana, Tofieldia okuboi* and *Dactylostalyx ringens*.

Endemics of the Kuriles and Kamchatka (sometimes also the Commander Islands) are few (11). All of them represent geographical races of some widely distributed species, and quite often they are considered by taxonomists as intraspecific taxa (*Carex krascheninnikowii, Calamagrostis litwinowii, Salix parallelinervis* and *Carex pyrophila*). It is necessary to notice that their southern limit of distribution is in Paramushir. The flora of the northern and middle Kuriles is poor in endemics, as well as in hemi-endemic species.

From the lower number of endemics in the flora of the Kuriles and the unclear morphological distinctions from closely related species of Kamchatka, Sakhalin and Hokkaido we conclude that Kurilean endemism is relatively "young". This probably indicates the recent (in geological terms) insular isolation, and also explains the allochthonous processes, which took place in this area in the past. Most of the endemics on the Kuriles are probably of Pleistocene age. Neo-endemism is one of the characteristic features of the Kuriles flora.

The Quartenary played an important role in formation of the Kuriles flora. A significant fall in temperature promoted formation of glacial cover upon part of Northeast and East Asia, including the Kuriles. On Paramushir traces of at least two Quartenary glaciations have been found (Vlassov, 1958; Chemekov, 1972). Some authors (Kanayev, 1960; Zhelubovsky and Pryalukhina, 1964) found them on the other islands of the Bolshaya Kurilskaya Ridge. The formation of glacial cover and subsequent general downturn of

the Global Oceanic level promoted formation of a bridge of land between the Kamchatka Peninsula and Hokkaido. The temporary southward advance of the upper limit of the forest belt facilitated migrations of alpine species by this bridge both northwards and southwards. Deforestation of the northern Kuriles is a consequence of glacial periods. The preserves of taiga and nemorose elements have a relic character and suggest that coniferous broadleaved forests s had a wider distribution in the Kuriles in the geological past.

The high mountains and some of the coastal areas outside the limits of the modern Arctic Region have some similarities with the Arctic in their floristic structure (Young, 1978). The southern limit of the Arctic was changeable, reflecting the existence of a wide transition zone, including the northern borders of the Boreal Region. In the periods of Pleistocenic glaciation the direct floristic exchange between mountains of the Kurile Islands and the Arctic Region (especially with the Beringian sector) was facilitated by significant changes in the Arctic border to the south. In the maximum of the early Quartenary glaciation the arctic-alpine species in the process of developing their circumpolar areas of distribution probably advanced southwards by the Kurile bridge of land. During the late Qurtenary glaciation the floristic exchange was complicated because of dissociation into some insular areas. In this period (about 20,000 years ago) only Shumshu and Paramushir were incorporated to Kamchatka, while others (with the exception of Kunashir), already formed large islands formed by morphotectonic blocks and divided by straits (Onekotan-Shiashkotan, Urup-Chirpoi and other blocks). This can be shown for the modern high-mountainous flora of Paramushir, where a number of arctic-alpine species are found, while they are absent on the other islands of the Kuriles archipelago and in Japan.

Southwards from the Arctic Region the participation of the arctic-alpine species in the mountains flora is gradually reduced. This is shown, for example, with the Kurile Islands. The greatest number of arctic-alpine species (64) is observed in the flora of the North Kuriles. These include: *Ranunculus sulphureus, Cerastium beeringianum, Koenigia islandica, Salix polaris, Sibbaldia procumbens, Polemonium boreale, Pedicularis capitata, Artemisia furcata, Carex capillaris, Festuca altaica* and *Poa arctica*. In the South Kuriles arctic-alpine species are rare and (or) represented by small populations. At the same time the flora of these islands is rich in alpine, and especially montane species. This can be explained by the climatic conditions in this area from the end of the last glaciation which has resulted in a rise in the upper limit of the forest belt and reduction of the mountain tundra belt to fragmentary sites. On the Bogatyr mountain range (Iturup Island) a number of alpine and montane species occur, which are known in northern Japan (e.g. *Pedicularis apodochila, Viola kitamiana, Tofieldia okuboi, Fauria crista-galli, Bothryostege bracteata* and *Platanthera minor*) and Sakhalin (*Minuartia barkalovii*), as well as some Kurilean endemics (*Pulsatilla taraoi* and *Saussurea kurilensis*), which are absent on Kunashir Island.

Floristic Regionalization of the Kurile Islands

The phytogeography of the Kurile Islands has been discussed by numerous authors (Kudo, 1922; 1925; 1927; Hultén, 1933; Tatewaki, 1933; 1947; 1963b; Vassiliev, 1946; Vorobiev, 1948, 1963; Tolmachev, 1959; Seledets, 1969; Hämet-Ahti et al., 1974; Khokhryakov, 1989; Nedoluzhko, 1990; 1997) since Engler (1899, citation by Tatewaki, 1958) suggested the Kurile archipelago as a route for plant migration in the Cenozoic. Takeda (1914) reached the same conclusion, based on widely distributed arctic-alpine species in the Kurile Islands and the mountains of Japan. Tolmachev (1948) paid attention to the similarity of the high mountain floras of Japan and Beringia, which could be explained by the existence of the Kurile land bridge in the past.

The early researchers (Miyabe, 1890; Kudo, 1922, 1927; Hultén, 1933; Tatewaki, 1933) had already pointed out that the flora of the Kuriles was heterogeneous in structure. The southern islands are closer to Hokkaido, while the northern islands are closer to Kam-

chatka, but these parts of the Kuriles belong to different phytochoria. In the flora of the South Kuriles occur representatives of the Magnoliaceae, Chloranthaceae, Ulmaceae, Paeoniaceae, Rutaceae, Aceraceae, Anacardiaceae, Alismataceae, Dioscoreaceae and Lemnaceae. Of the total of 487 genera in the Kuriles flora 49% are absent in the northern islands. These include: *Adiantum, Phyllitis, Abies, Picea, Magnolia, Juglans, Schisandra, Daphniphyllum, Ulmus, Quercus, Paeonia, Actinidia, Fauria, Gastrodia, Cardiocrinum* and *Brylkinia* (55 genera—22%—are woody). On the other hand, the northern Kuriles possess one family (Zannichelliaceae), as well as 13 genera (e.g. *Delphinium, Armeria, Koenigia, Subularia, Kobresia* and *Vahlodea*), which are lacking in the southern Kuriles.

Northwards the gradual loss of thermophilous and mostly woody species is observed. To the north from Iturup such genera as *Abies, Picea, Populus, Ulmus* and *Quercus* are absent, though *Taxus, Acer, Toxicodendron, Kalopanax, Ilex* and *Sasa* do penetrate to the north. Hultén (1933), stating about the origin of the Kuriles flora and the distribution of its component species, showed that there was a gradual transition between the Kamchatkan and Japanese floras, so the boundary between them is not distinct. In his opinion, the most significant changes in floristic structure took place somewhere in the area of Ketoi and Ushishir Islands. Ketoi Island is the northern limit for the distribution of *Sasa kurilensis*. Tolmachev (1959) thought that the floristic boundary on the Kuriles is situated in the area of the Ketoi or Rasshua Islands. Vorobiev (1948) was the first to propose the idea that the boundary in question should pass between Chirpoi and Urup Islands: northwards from Urup Island *Sasa kurilensis* does not form continuous thickets, and Japanese elements become reduced.

Tatewaki (1933) proposed that the boundary between the Boreal and East Asiatic floras should be called the "Miyabe Line". He developed this idea in a series of papers (Tatewaki, 1947; 1958; 1963b). However the boundary dividing these two large floristic regions on the Kurile Islands was put forward by him mainly from geobotanical observations. The boundaries based on geobotanical subdivisions pass slightly further to the south than the floristic subdivisions (Malyshev, 1973).

A floristic line, separating adjacent choria, corresponds to a zone of condensation of the limits of distribution for taxa (Tolmachev, 1974). We have shown that on Iturup the northern limits of distribution have 20 families, 98 genera and 261 species (Table 4). On Urup the northern limits have 13 families, 48

Table 4. Northern and southern limits of distribution for taxa in the flora of the Kuriles.

Islands	Number of					
	families		genera		species	
	Northern limit	Southern limit	Northern limit	Southern limit	Northern limit	Southern limit
Atlasov	47	0	121	0	177	0
Shumshu	19	0	84	2	236	8
Paramushir	2	1	14	10	83	76
Onekotan	1	0	3	1	19	23
Shiashkotan	0	0	2	0	1	9
Matua	0	0	0	0	4	2
Rasshua	1	0	3	0	9	2
Ushishir	0	0	0	0	0	6
Ketoi	1	0	5	1	13	6
Simushir	3	0	3	0	9	5
Urup	14	0	54	3	112	15
Iturup	20	3	98	11	261	81
Kunashir	14	15	90	116	236	332
Shikotan	1	104	6	333	20	620

genera and 102 species (e.g. *Osmundastrum asiaticum, Plagiogyria matsumurana, Botryostege bracteata, Hydrangea paniculata, Cerasus nipponica, Skimmia repens, Toxicodendron orientale, Acer mayrii, Aralia cordata, Kalopanax septemlobus, Euonymus macroptera, Viburnum furcatum, Ligularia hodgsonii, Hemerocallis esculenta, Clintonia udensis, Polygonatum humile* and *Oreorchis patens*). On Simushir the northern limits have only three families, three genera and nine species. The number of East Asiatic taxa northwards of Urup is significantly reduced.

The floras of Urup and Iturup are the most closely related (416 species in common). The number of species in common in Urup with floras of the other islands of the Kurile Archipelago decreases both northwards and southwards (with the exception of Iturup). The percentages of species in common with other islands are: Iturup, 94%; Kunashir, 86%; Shikotan, 75%; Paramushir; 63%, the middle Kurile Islands, not more than 55%. These quantitative characteristics indicate that northwards of Urup there is a significant change in the floristic structure of the Kuriles, so the floristic borders dividing Circumboreal and East Asiatic Regions should pass in this area.

Thus, in the author's opinion, the Kurile Islands must be subdivided into 5 floristic districts: 1) North Kurile District, 2) Middle Kurile District, 3) Urup District, 4) Iturup-Kunashir District, 5) Shikotan-Habomai District (Fig. 2).

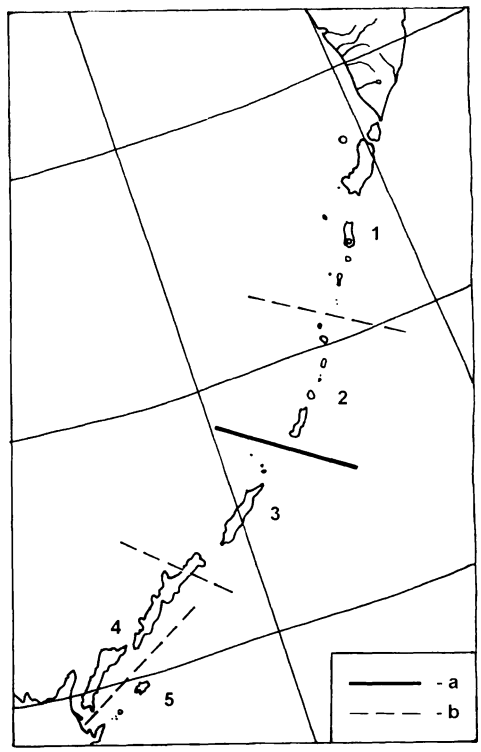

Fig. 2. Scheme of the floristic regionalization of the Kurile Islands (a, boundary between Circumboreal and East Asiatic Regions; b, boundaries of districts). 1, North Kurile District; 2, Middle Kurile District; 3, Urup District; 4, Iturup-Kunashir District; 5, Shikotan-Habomai District.

1. The North Kurile District includes the southern extremity of the Kamchatka Peninsula (Cape Lopatka) and the adjacent Kurile Islands, southwards from the First Kurile Strait to the Kruzenshtern Strait: Atlasov, Shumshu, Paramushir, Onekotan, Shiashkotan and others islands. Dwarf shrubs (*Pinus pumila* and *Duschekia fruticosa*) dominate the vegetation. The flora is considerably enriched by arctic-alpine species such as *Primula tschuktschorum, Salix polaris, Ranunculus sulphureus, Chamaenerion latifolium, Carex capillaris, Kobresia myosuroides, Festuca altaica* and *Hierochloe pauciflora*. Some representatives of the American flora are characteristic of this area. These are *Allocarya orientalis, Erigeron peregrinus, Carex kelloggii, C. pluriflora*, and *Agrostis alaskana*.

2. The Middle Kurile District includes islands from the Kruzenshtern Strait up to Boussol Strait (Raikoke, Matua, Rasshua, Ushishir, Ketoi, Simushir and some small islands). In floristic structure and plant communities this district is the closest to the first. Floristic peculiarities of this part of the Kuriles are represented by East Asiatic elements (*Sasa* and *Taxus*), as well as by *Betula ermanii*. Matua Island is peculiar by its extremely poor flora: here not only Ermans birch, but also dwarf pine are absent. This is probably due the activity of the Sarychev Volcano on this island.

3. The Urup District includes not only Urup, but also some small islands: Brouton, Chirpoi, Brat Chirpoev as well as the northern part of Iturup (northwards from Vetrovoi Isthmus). The floristic structure and spec-

trum of families in this area is closer to that of the Iturup-Kunashir and Shikotan-Habomai Districts. There are some East Asiatic elements on Urup, *e.g. Plagiogyria matsumurana, Botryostege bracteata, Hydrangea paniculata, Skimmia repens, Toxicodendron orientale, Acer mayrii, Aralia cordata, Kalopanax septemlobus* and *Viburnum furcatum*, which are not represented in the northern districts mentioned above. In the north of Iturup (Medvezhiy Peninsula) there are solitary trees or small groves of *Quercus crispula*. According to Takahashi et al. (1997) the flora of Chirpoi is more similar to that of Urup than that of Simushir. This may be due in part to the possible temporary connection between Chirpoi and Urup during the greatest Pleistocene sea regression. Urup and Chiornye Bratiya (including Chirpoi and Brat Chirpoyev Islands) are connected in one, Urup morphotectonic block (these islands stand on the same shallow seabed). Therefore, the floristic boundary cannot pass between these islands, but slightly northwards of Chirpoi (between Simushir and Chirpoi Islands).

4. The Iturup-Kunashir District includes Iturup (southwards from Vetrovoi Isthmus) and Kunashir Islands. It is much richer than the others, with more thermophilous elements, which are representatives of the East Asiatic flora: e.g. *Magnolia hypoleuca, Quercus crispula, Q. dentata, Acer tschonoskii, A. japonicum, Betula maximowicziana, Daphniphyllum humile, Bothrocaryum controversum, Schizophragma hydrangeoides* and *Boehmeria tricuspis*.

5. The Shikotan-Habomai District: Shikotan, Zeliony Islands and a number of small islands of Malaya Kurilskaya Ridge are very peculiar. Here *Pinus pumila* is absent, being replaced ecologically by *Juniperus sargentii*. None of the species of *Quercus*, *Kalopanax*, *Actinidia arguta*, or many of the high-mountain species occur on these islands. The small islands (Zeliony, Yuri, Polonsky, Tanfiliev and others) form a flat surface about 20 m above s.l. blown by strong winds. Here herbaceous-shrubby vegetation exists, but trees are almost absent. The majority of the small islands are swampy.

Two of these districts, the North Kurile and the Middle Kurile, can be considered as the South Kamchatka-North Kurile area within the Okhotian-Kamchatkan Province of the Circumboreal Region. The other three districts, together with Hokkaido (except its most southern part), can be considered the South Kurile-Hokkaido area (=*Botryostege bracteata* area, according to Khokhryakov, 1989) within the Sakhalin-Hokkaido Province of the East Asiatic Region.

Thus, the vascular flora of the Kurile Islands is derivative of two florogenetic centers, Beringian and Japanese. Here the influence of the floras of Kamchatka and Japan, impoverishment of species composition caused by insular isolation and the influence of volcanic activity can be clearly observed. The main floristic boundary on the Kuriles should be drawn not between Urup and Chirpoi Islands or between Urup and Iturup Islands, but slightly further north, between Simushir and Chirpoi Islands (the Boussol Strait).

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千島列島の植物地理学

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千島列島の維管束植物相は，135科550属1367種から構成され（北千島から582種，中千島から334種，および南千島から1215種が知られている），カムチャッカと日本の植物相の影響が強い．千島列島における維管束植物相の構成要素の大きな変化は，中千島のウルップ島北部において認められるが，このことは，環亜寒帯域と東アジアの植物相を区分する境界線をシムシル島とチルポイ島の間のブッソル海峡に設定しうることを示している．実際に，ウルップ島が，東アジア要素を構成する13科48属102種の分布北限となっている．