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Floristic division of the Arctic

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Abstract: The progress in the floristic study of the circumpolar Arctic since the 1940s is summarized and a new floristic division of this region is presented. The treeless areas of the North Atlantic and North Pacific with an oceanic climate, absence of permafrost and a very high proportion of boreal taxa are excluded from the Arctic proper. It is argued that the Arctic deserves the status of a floristic region. The tundra zone and some oceanic areas are divided into subzones according to their flora and vegetation. Two groups of subzones are recognized: the Arctic group (including the Arctic tundras proper and the High Arctic) and the Hypoarctic group.

The Arctic phytochorion is floristically divided into sectors: 6 provinces and 20 subprovinces reflecting the regional features of each sector in connection with flora history, physiography and continentality-oceanity of the climate. Each sector is described and differentiated by a set of differential and co-differential species. The peculiarities of the Arctic flora are manifest in different ways in the various sectors, and endemism is not the universal criterion for subdivision.

Keywords: Chorology; Classification; Flora element; Floristic province; Phytogeography; Polar desert; Syntaxonomy; Tundra vegetation.

Nomenclature: Anon. (1960-1987). Important Russian topographic names are given at least once in the transliteration of the Russian spelling as found in the Times Atlas of the World.

Introduction

Ever since the 1940s, monographs on the Arctic have been published, notably on Alaska and Yukon (Hultén 1941-1950, 1968, 1973), the Canadian Arctic Archipelago (Porsild 1964), Greenland (Böcher et al. 1968), Bear Island (Rønning 1959), Jan Mayen (Lid 1964), Iceland (Löve 1983) and Svalbard (Rønning 1963, 1979). With the appearance of the last issue of the Arctic Flora of the USSR (Anon. 1960-1987) the largest remaining gap in the floristic knowledge of the circumpolar Arctic was filled. The chorological atlases of Hultén (Hultén 1958, 1962-1971; Hultén & Fries 1986) also contributed to our present knowledge.

A detailed floristic division of the Arctic was proposed by Yurtsev et al. 1978 (see also Yurtsev 1978a). Since that time the last four issues of the Arctic Flora of the USSR have been published. Moreover, new floristic monographs in many volumes have been started in the Russian Far East and Siberia, while significant progress has been made in the study of the flora of the Russian Arctic as well as of Alaska and Canada (e.g. Porsild & Cody 1980) and Greenland (Bay 1992).

The present paper is a revision of the publication of 1978 and is based on extensive new data. It is based on two complementary schemes of phytogeographic division of the Arctic, or the tundra zone in its broader sense (Figs. 1 and 2). Fig. 1 deals with the latitudinal phytogeographic zonation of the Arctic and with subzones of the tundra zone, which are essentially circumpolar, except for subzones V and VI. Fig. 2 deals with the floristic division of the Arctic into longitudinal sectors.

A special aim of this paper is to stress the floristic-phytogeographic boundaries in the Arctic for geobotanists concerned with floristical classification of Arctic vegetation and vegetation mapping. The knowledge of such boundaries is a prerequisite for an effective classification of circumpolar arctic vegetation according to the Braun-Blanquet approach (Westhoff & van der Maarel 1973), especially for the syntaxonomical evaluation of geographical variation in plant communities.

Recognition of the Arctic floristic region

The concept of the floristic delimitation of the Arctic is shown by the outer solid line (Fig. 2). In the continental sectors, the southern boundary of the Arctic coincides with the northern limit of the taiga. However, in the oceanic sectors, it crosses treeless areas. In the North-Pacific region the Aleutian and Commander Islands, Pribyloff Islands, Alaska Peninsula and also the Anadyr-Koryak province, characterized by the occurrence of '*stlanik*' vegetation (a formation of creeping shrubs and small trees) are left outside the Arctic proper, just as in the North Atlantic region the Faeroes, Iceland, S, SW and SE Greenland (Böcher 1978), as well as

northernmost Scandinavia. These areas are excluded because of the boreal-oceanic aspect of their floras, which is expressed by a high proportion of boreal, particularly boreal-oceanic, species and other oceanic hypoarctic and low-arctic species alien to the circumpolar arctic areas. In a broader, phytogeographic interpretation of the Arctic as the 'northern polar cold treeless region'- indicated with the solid line in Fig. 1 - the above-mentioned treeless oceanic areas are included in the Arctic phytogeographic region, as the North Atlantic and North Pacific subregions. The Arctic floristic region s.s.- as outlined in Fig. 2 - constitutes the Arctic (phytogeographic) subregion proper.

The floristic integrity of the Arctic is very high, even at the species level. The circumpolar species account for 35 % to over 80 % of the local Arctic floras, apart from other species with wide distribution in the circumpolar Arctic. Takhtajan (1970,1986) considered the Arctic phytochorion as a single province of the (circum-) Boreal region. However, in accordance with the more general trend represented in both classical and modern textbooks such as those of L. Diels, A. Engler and A. Hayek (see i.a. Good 1964; Meusel et al. 1965), as well as in Russian papers (Kuznetsov 1912; see also Tolmachev 1956, 1974) the Arctic phytochorion is ranked here as a separate floristic region.

This opinion is based on the following arguments:
1. No less than 10 % of the species characteristic of the Arctic are endemic. There are even a few widespread endemic and subendemic genera (*Arctophila*, *Dupontia*, *Parrya* s.s., *Phippsia*, *Pleuropogon* s.s.), as well as several endemic or subendemic sections in genera such as *Cerastium*, *Draba*, *Gastrolychnis*, *Oxytropis*, *Papaver*, *Poa*, *Potentilla*, *Puccinellia* and *Taraxacum*, e.g. the *Taraxacum* section *Arctica*.
2. The Arctic flora has a peculiar taxonomic structure, with (1) relatively few species per genus and family; (2) a lack of phyletic lineages (typical of the Boreal region), even at higher taxonomic levels, e.g. the lack of Gymnosperms; (3) a high number of lichens and bryophytes relative to the vascular plants.
3. There is a clear distinction between the Arctic and Boreal floras, regarding ecophysiological and morphological (growth forms) features, different vectors of evolution, different modes of speciation and flora genesis.

In summary, the Arctic flora is a taxonomically, ecologically, biologically, and genetically distinctive complex of young and dynamics species, that occupies a vast natural area. Indeed, the Arctic is a phytogeographic unit of global dimension deserving the rank of a floristic region.

On the phytogeographic zonation of the Arctic

The distinction and characterization of zones and subzones in terms of the floristic composition and structure (physiognomy) as well as the whole set of plant communities largely follows the Russian tradition represented by i.a. V.D. Aleksandrova, V.N. Andreyev, B.N. Gorodkov and V.B. Soczava. The main difference is that 'active' species are also taken into account, i.e. locally frequent, dynamic species with a wide ecological amplitude and a high abundance in at least part of their typical habitat (Yurtsev 1968). The demarcation of zonal units is based on the latitudinal shift of taxonomical, geographical and morphological groups of 'active' species. This criterion may prove to be the most general one, since the composition and structure of plant communities depend on major climatic factors, e.g. summer warmth, but also on edaphic factors.

The scheme presented here (Fig. 1) is partly based on the many new data from the Arctic tundra subzone in Asia, collected and published by research workers of the Komarov Botanical Institute, as well as on data from Edlund & Alt (1989) and Edlund (1990) on the Canadian Arctic, and own observations on Wrangel Island (Ostrov Vrangelya) and in the Canadian Arctic Archipelago. The main difference from older schemes is the demarcation of the subzones of Arctic tundra and High Arctic tundra (or polar desert). The scheme matches the famous circumpolar scheme of Aleksandrova (1980), but differs in some basic criteria and nomenclature. The term 'Subarctic' as used by Aleksandrova is replaced by 'Hypoarctic', because in the Anglo-American and Russian biogeographical literature the term is used in a different meaning. Here, species from both the northern taiga and the southern tundra are called Hypoarctic (*sensu* Tolmachev 1932), and so are some subzones of the tundra zone.

Groups of subzones

Two groups of subzones are distinguished, the Hypoarctic group of subzones (corresponding in general to the Subarctic region of the tundra zone *sensu* Aleksandrova) and an Arctic group, which includes the polar desert region *sensu* Aleksandrova. In the tundra zone, frequently occurring tree species are missing.

Hypoarctic subzones

The Hypoarctic subzones are characterized by hypoarctic species, including oligotrophic low shrubs and dwarf shrubs, forming a closed vegetation cover. Three subzones might be distinguished.
1. *Stlanik subzone*, restricted to northeasternmost Asia (Fig. 1, V) .

2. *Southern Hypoarctic tundra* (Fig. 1, IV).
3. *Northern Hypoarctic tundra* (Fig. 1, III), which probably could be divided further (see Aleksandrova 1980) into middle and northern Hypoarctic tundra.

In the North Atlantic and North Pacific regions with an oceanic climate, and with almost no permafrost and woodlands, the subzones IV and V are replaced by their oceanic counterpart (Fig. 1, VI), where tundra-like heath vegetation, mesic meadows and shrublands alternate; on some islands (e.g. Iceland), and also in S Greenland, birchwood may occur.

In the two southernmost subzones, IV and V, oligotrophic species strongly dominate over the arctic-alpine dwarf shrubs and herbs, at least on acidic bedrock. Boreal species contribute to the flora, and shrubs occupy a significant, locally even sometimes the largest, part of the landscape. Their distribution is controlled by the distribution pattern of snow in the winter. In the stlanik subzone, where the summers are as warm as in the northernmost taiga and forest-tundra, and where the winters are windy with periodical thaws, large areas are covered by *Pinus pumila* thickets. In flood-plains free of permafrost, groves of arboreal *Salicaceae* (*Chosenia, Populus* and some *Salix* spp.) occur regularly. *Populus* and *Salix* groves rarely occur in unit IV as well.

In the middle Hypoarctic tundra subzone, hypoarctic and arctic-alpine complexes are represented equally. Low *Salix* shrubland and thickets leave 'plakors' (flat, mesic, silty, zonal habitats), whereas dwarf *Betula* dwarf-shrub tundra turns into associations of 5 to 20 cm high hemiprostrate shrubs. Windswept sites and snowbeds and snowbanks are occupied by associations of arctic-alpine plants.

The northernmost strip of the hypoarctic tundra represents an ecotone to the arctic tundra. In the Chukotka Peninsula (Chukotskiy poluostrov), shrub vegetation is almost absent in the northern Hypoarctic tundra.

Arctic subzones (Fig. 1, I-II)

In the Arctic subzones the Hypoarctic oligotrophic species are lacking or extremely rare. Dwarf birches and boreal species do not occur here. The vegetation consists mainly of arctic and arctic-alpine species with an mixture of eutrophic Hypoarctic and Arctic-boreal species. There is only a small contrast between the vegetation of flood-plains and interfluvial areas here.

1. Arctic tundra subzone (Fig. 1, II). Here, frequent and dominant species include prostrate, summer-green shrubs (*Dryas, Salix*), and in some southern variants also the hemiprostrate evergreen *Cassiope tetragona*. Its presence, along with the wide distribution of closed vegetation and tundra sedges and cotton-grasses on plakors, justifies the recognition of the southern part of this subzone as a separate phytogeographic unit (Fig. 1, IIs, 'zone of prostrate and dwarf shrubs' of Edlund 1990). In the northern variant of the subzone (Fig. 1, IIn), the flora is further impoverished, the discontinuity of the vegetation cover increases, whereas the role of *Dryas* and *Cyperaceae* is less here; some High Arctic species which occur frequently here are shared with the next subzone.
2. *High Arctic tundra subzone* (Fig. 1, I). Here, the mean July temperature is maximally 2 °C, prostrate shrubs are rare ('herb zone' of Edlund 1990). Even many Arctic and Arctic-alpine species and many genera and families (especially in the *Sympetala*, also *Cyperaceae*) are missing here. The plant cover is discontinuous. However, on moist and better developed soil (in particular on the northern coast of Ellesmere Island), High Arctic tundras (semi-deserts *sensu* Bliss 1981) are common. They are characterized by a rather high cover of bryophytes, crustaceous lichens or blue-green algae, with a mixture of scattered cushion-forming flowering plants.

The floristic sectors of the Arctic

The delimitation of floristic provinces and subprovinces is mainly based on the distribution boundaries of vascular plant species, as derived from modern floristic and chorological works. The peculiarity of any sector can be estimated in terms of numbers and proportions of the following categories of species (cf. Yurtsev 1983) and will be considered below with regard to the situation in the Arctic region.
1. Differential species: either confined to a sector (endemics) or to only one sector within the Arctic, or at least not present in any neighbouring sector.
2. Co-differential species: species whose ranges overlap only within a particular sector. With respect to the circumpolar Arctic, we are mainly dealing with the western and eastern elements.
3. Negative differential species: species lacking in a particular sector while present in any of the neighbouring ones.
4. Negative co-differential species: species whose absence is restricted to a particular sector, while reaching their western or eastern boundary.

The present scheme is qualitative, based on the complex weighing of similarities and dissimilarities between the phytochoria according to different criteria. Six provinces and 22 subprovinces are distinguished. The provinces are natural groups of subprovinces based on the above criteria. Moreover, three lower units are distinguished, i.e. areas which cannot be assigned to a neighbouring subprovince and are not sufficiently differentiated floristically to become a subdivision of their own. The various sectors will be described briefly.

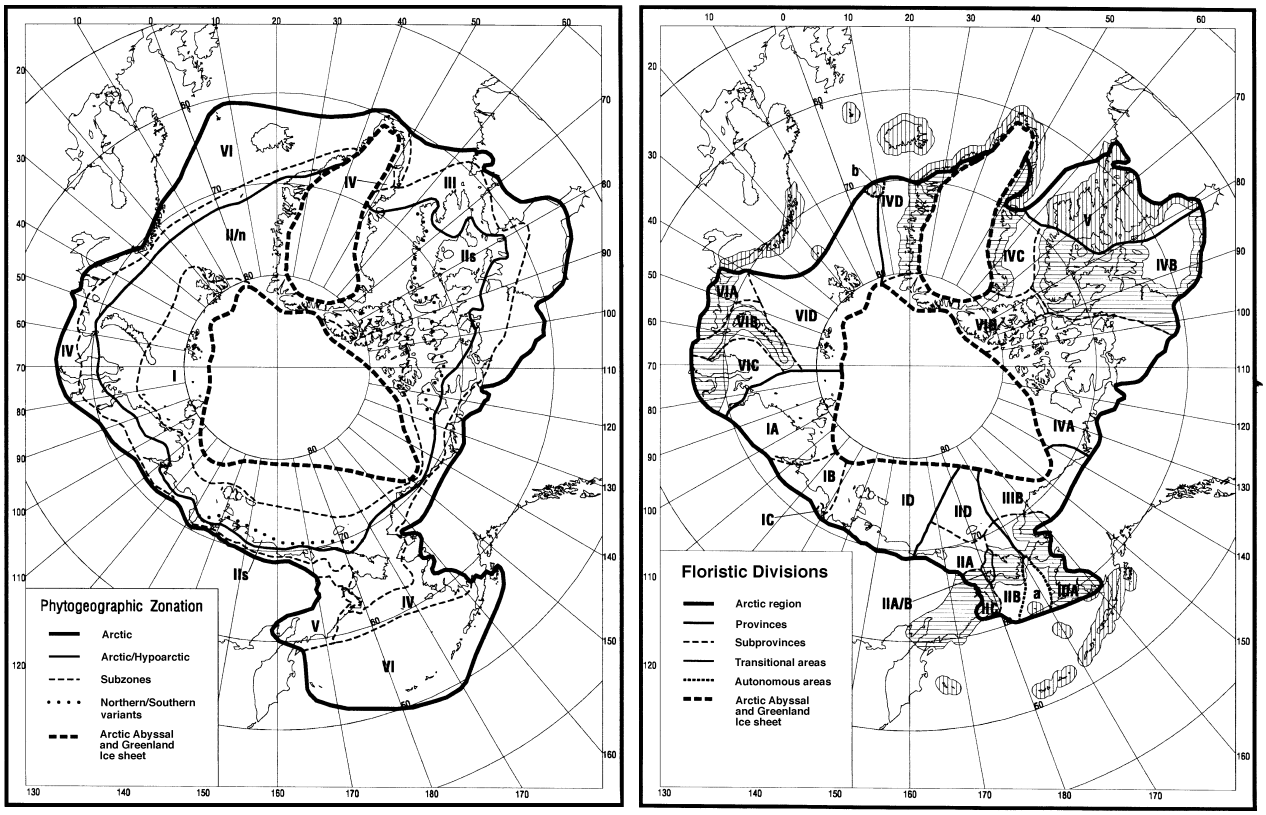

Fig. 1. (left) Phytogeographic zonation of the Arctic. I = High Arctic tundra subzone; II = Arctic tundra subzone; IIn = Northern variant; IIb = Southern variant; III = Northern Hypoarctic tundra subzone; IV = Southern Hypoarctic tundra subzone; V = *Stlanik* subzone; VI = Zonal equivalents of IV and V outside the tundra zone.

Fig. 2. (right) Floristic division of the Arctic. I = East Siberian province; subprovinces IA: Taymyr, IB: Anabar-Olenek; IC: Kharaulakh, ID: Yana-Kolyma; II = Chukotka province, subprovinces IIA: Continental Chukotka; IIB: Beringian Chukotka; IIC: South Chukotka; IID: Wrangel Island; IIA/B: Amguema transitional area; III = Alaska province; subprovinces IIIA: Beringian Alaska and IIIB: Northern Alaska; IV = Canada-Greenland province; subprovinces IVA: Central Canada; IVB: West Hudsonian, IVC: West Greenland; IVD: East Greenland; IVE: Ellesmere-North Greenland; V = Baffin-Labrador province; VI = European-West Siberian province; subprovinces VIA: Kanin-Pechora; VIB: Ural-Novaya Zemlya; VIC: Yamal-Gyda; VID Svalbard; a. North Beringian insular autonomous area; b. Jan Mayen insular autonomous area. Vertically shaded: treeless areas mainly outside the Arctic region, dominated by oceanic complexes; horizontally shaded: areas with oceanic and continental complexes mainly within the Arctic region; not shaded: with continental complexes within the Arctic.

East Siberian Province (Fig. 2, I)

Distinctive features of the continental Siberian floras are particularly pronounced. The typical representatives of the floras of the Atlantic and Beringian sectors are almost totally lacking; negative differential taxa, i.e. species in common with the remainder of the American Arctic, which are missing, include *Campanula uniflora, Festuca baffinensis, Loiseleuria procumbens, Phyllodoce coerulea, Silene acaulis* and many others.

From the Yenisey River eastward we find more and more East Siberian species, while fewer rare western species (present only in W Taymyr) disappear. Towards the eastern boundary few East Siberian species disappear, whereas many species from the east side of the Kolyma River, i.e. Chukotkan, amphi-Beringian and American-Chukotkan species appear.

The East Siberian province is not homogeneous; there is a clear longitudinal floristical gradient. The subprovinces constitute a natural swarm with its centre in the Kharaulakh subprovince. The High Arctic floras of the Severnaya Zemlya and the New Siberian Islands (Novosibirskiye ostrova) are more related to each other than to those of other neighbouring High Arctic areas: Novaya Zemlya, Franz Josef Land (Zemlya Frantsa Iosifa) and Wrangel Island. Four subprovinces are distinguished in the East Siberian province.

Taymyr subprovince (Fig. 2, IA)

The western element is represented by some plants of the Atlantic sector, e.g. *Festuca viviparoidea, Poa alpina*, along with West Eurasian species: *Betula nana* s.s., *Oxytropis sordida* ssp. *sordida, Pedicularis dasyantha*, and a few boreal plants in common with northern West Siberia (e.g. *Cardamine macrophylla, Trollius asiaticus*). West Taymyr, as compared with East Taymyr, is richer in 'western' (zonally more southern) and poorer in 'eastern' (mainly Arctic and Arctic-alpine) species. Characteristic of Taymyr are disjunctions in the distribution areas of many Arctic halophytes (e.g. *Arctanthemum hultenii, Calamagrostis deschampsioides, Carex glareosa, C. subspathacea, Honkenya peploides* s.l.) as well as the full representation of the High Arctic element (Matveyeva & Chernov 1976). There are few endemics, e.g. *Puccinellia byrrangensis, P. jenisseensis, P. gorodkovii*. A similar situation is found in the Subarctic mountains of the sector, e.g. the Putorana Plateau (Gory Putorana), which are isolated from the South Siberian mountain floras. A few species are co-endemic for Taymyr and Putorana (e.g. *Oxytropis putoranica* and *O. tichomirovii*).

Anabar-Olenëk subprovince (Fig. 2, IB)

In this subprovince very few endemic taxa, i.a. *Artemisia lagopus* ssp. *triniana*, occur. Other differential taxa are lacking. Eastern species clearly prevail over western species and the saturation with eastern elements in the direction of the Kharaulakh Mts (Kharaulakhskiy khrebet). As in the next subprovince, the High Arctic element is poorly represented, whereas the coastal halophyte complex is more important.

Kharaulakh subprovince (Fig. 2, IC)

Despite its small area, the Kharaulakh subprovince is a 'structural axis' of the Province: to the west the flora becomes impoverished step by step, first regarding East Siberian and East Siberian-American species. East of the Kharaulakh Mts., there is an abrupt disappearance of mountain taxa from the northern plains of East Yakutia. The Kharaulakh area combines floristic features of montane Northeastern Asia and montane northern central Siberia. Characteristic of the whole province is the striking prevalence of eastern over western co-differential taxa, which points to a closer relationship with the Beringian sector and Arctic Canada than with the Atlantic sector.

Endemism on the race level is insignificant, e.g. *Artemisia lagopus* ssp. *abbreviata, Oxytropis inopinata, O. sordida* ssp. *arctolenensis*, but many Northeast Asian mountain plants appear, including the subendemics of the Verkhoyansk Range, such as *Androsace gorodkovii, Gorodkovia jacutica* and *Hyalopoa lanatiflora*, and some representatives of more distant Asian areas, i.a. *Caragana jubata*. East of the Kharaulakh Mts. some central Siberian species and races disappear, e.g. *Oxytropis arctica* ssp. *taimyrensis* and *Silene paucifolia*, and some races are replaced, i.a. in *Saxifraga oppositifolia* s.l. and *S. serpyllifolia* s.l.

Yana-Kolyma subprovince (Fig. 2, ID)

This sector has been little explored. Endemics are not known. Differential taxa are mainly restricted to large river valleys, e.g. *Artemisia dracunculus* and *Thellungiella salsuginea*. Western co-differential taxa are few and usually do not reach the Kolyma River, e.g. *Carex ensifolia* ssp. *arctisibirica* and *Oxytropis nigrescens* s.s. Eastern co-differential species appear in the Indigirka drainage area, and even more species in the Kolyma River drainage, e.g. *Carex lugens*.

The lowland character of this sector determines the absence of over 60 species known from both the Kharaulakh Mts. and Chukotka, 36 species lacking in the Arctic east of the Kharaulakh Mts., and over 80 species appearing to the east of the Kolyma River. The flora of the New Siberian Islands is particularly poor in Arctic-alpine species; it lacks, for example, all Arctic-alpine *Pedicularis* species, all legumes and *Hierochloë alpina*. On the other hand, the High Arctic complex is almost completely represented (except *Poa abbreviata*).

Chukotka province (Fig. 2, II)

This province includes the predominantly mountainous area on the Chukotka Peninsula from the right bank of the Kolyma River up to Bering Strait. It includes i.a. the northern parts of the Anyuy and Anadyr Mts., the Chukotka Mts., as well as the lowlands of the Chaun and Lower Anadyr Rivers. The partly mountainous Wrangel Island and the flat Ayon Island are remnants of the flooded shelf area. Chukotka and Alaska constitute the Beringian sector of the Arctic. The vast shelf in this sector emerged more than once in Quaternary time.

The floras of Chukotka and Alaska are linked in several ways. One group of taxa is differential for the Beringian sector as a whole ('Yukon-Kolyma element') and another group of strictly-Beringian species is common to the maritime parts of Chukotka and Alaska (Hultén 1937, 1963; Yurtsev 1972, 1974). The floras of those parts of Chukotka and Alaska that are remote from Bering Strait, are also linked by the presence of many continental species absent in the vicinity of Bering Strait. Therefore, phytogeographers such as Hultén (1973) and Meusel et al. (1965) unite Chukotka and the Arctic parts of Alaska and Yukon into a single amphi-Beringian province. However, in view of the present state of knowledge, the author prefers to regard Chukotka

and the Arctic Alaska-Yukon area as twin provinces making up the Beringian sector of the Arctic, each of them subdivided into continental and suboceanic subprovinces.

The Chukotka flora shows distinctive Asian features, in particular of mountainous Northeastern Asia, whereas the Alaskan flora shows some characteristic features of a North American (in particular North Rocky Mountains) flora, this even on the generic level. In comparison with other Arctic provinces, both Chukotka and Arctic Alaska have a more pronounced endemism, which is comparable to that of many non-Arctic territories. Some endemic species are characteristic of one of the two provinces, while being widely distributed within the province. The province also has many differential taxa, including subendemics, in common with more southern mountainous areas (e.g. the monotypic genus *Ermania* in Chukotka).

As a floristic boundary, the Bering Strait is much more important than any other boundary in the Beringian sector, although climate and landscape at either side are rather similar. Even in periods when the strait floor was dry, it partly functioned as an edaphic barrier (Johnson & Parker 1967; Yurtsev 1973, 1974). The islands in the central part of the Bering Sea form an independent, 'neutral' floristic sector, an 'oceanic wedge', which naturally subdivides the Beringian sector (see below).

The number of species disappearing towards the western limit of the province is close to 150; 60 of them are disjunct over the level areas of the East Yakutian Arctic and 70 - 80 disappear at its eastern limit. West of the former boundary, few species appear, east of Bering Strait just about 100.

The continental and Beringian (suboceanic) parts of both the Chukotka (the greatest part of it) and Alaska provinces are separated as subprovinces. Their floristic differences are certainly related to the present differences in climate, which were no doubt lesser in former times of shelf exposure.

The largest numbers of 'western' and 'eastern' elements of the Chukotka flora (more than 70 - 80 in each group) are concentrated on the one hand in the Anyuy Mts. and the vicinities of Chaun Bay (Chaunskaya Guba), and on the other hand in the easternmost Chukotka Peninsula, most of them occurring only sporadically there.

Continental Chukotka subprovince (Fig. 2, IIA)

Because of the many continental western species or even genera, e.g. *Chosenia*, *Dracocephalum*, *Leontopodium*, *Thymus*, this subprovince seems to form a continuation of East Siberia. However, it differs from the latter by the presence of many amphi-Beringian and Chukotka species such as *Hedinia czukotica*. The frequency of occurrence of steppe species and communities reaches here its maximum for the entire Arctic.

Beringian Chukotka subprovince (Fig. 2, IIB)

At the western boundary of this subprovince continental western species disappear abruptly. Further eastward this trend continues, while there is a gradual increase in the number of oceanic eastern species, both Beringian and American, culminating in the easternmost part of the Chukotka Peninsula, where local endemics in the genera *Arabidopsis*, *Oxytropis*, *Potentilla*, *Pucciphippsia* and *Taraxacum* occur as well.

Amguema transitional area (Fig. 2, IIA/B)

The largest number of overlapping 'western' and 'eastern' distribution areas is found in the area of the middle and lower reaches of the Amguema River and the Iskamen' Range in the westernmost Chukotka Peninsula. We regard this as a distinct, transitional area separating, but also linking the Continental Chukotka subprovince (Fig. 2, IIA) and the Beringian Chukotka subprovince (Fig. 2, IIB) (Yurtsev 1972, 1973, 1974).

South Chukotka subprovince (Fig. 2, II C).

The area of the common overlapping of ranges of oceanic and continental species extends from the Amguema transitional area southward to the eastern part of the Anadyr lowlands (Anadyrskaya Nizmennost') - with some adjacent mountains and the easternmost Koryak Mts. included, i.e. beyond the range of *Pinus pumila* (Yurtsev 1978b). Here an assemblage of 'southern' species appears : alpine, hypoarctic or boreal, alien to the rest of Chukotka, such as *Aruncus kamschaticus*, *Cassiope anadyrensis*, *C. ericoides*, *Mertensia pubescens*, *Rhododendron aureum*, *Saxifraga merckii* and many others. Endemics are practically lacking, but a few interesting subendemics, in common with the neighbouring Anadyr-Koryak province of the Boreal region, do occur, e.g. *Oxytropis sublongipes* and *Potentilla anadyrensis*.

Wrangel Island subprovince (Fig. 2, IID)

Finally, the area including Wrangel Island and its small associate, Herald Island (Ostrov Geral'd), is considered nowadays as the fourth subprovince of the Chukotka province (Petrovsky 1988a,b; Yurtsev 1987). Compared with the other three subprovinces this subprovince shows many characteristic features, including a relatively large number (22) of endemic species and subspecies (apart from six subendemics), some of them being very distinctive, e.g. *Hierochloë wrangelica*, *Oxytropis uniflora* of the *Baicalia*-section (vicarious to *O. putoranica*) and *Potentilla wrangelii*. The most abundant local endemics are found in the genera *Papaver* and

Taraxacum. About 400 species of vascular plants are known from the island. As a comparison, this is many more than in the whole Canadian Arctic Archipelago! The island's flora reveals interesting connections with floras of distant continental areas of both East Siberia and North America, leaving aside the mainland of Chukotka, and it has an enriched High Arctic element, including *Braya thorild-wulffii, Gastrolychnis triflora* and *Poa hartzii*, all Canadian-Greenland High Arctic halophytes.

Alaska Province (Fig. 2, III)

The Alaskan coast of the Bering Strait and neighbouring seas is more extensive as compared to the Chukotkan; it is warmed up by a warm sea current. The overwhelming majority of the western co-differential and differential taxa of the province have their distribution limit on, or not far from the mountainous left bank of the Mackenzie River in its lowest reaches, and only a few in the easternmost Brooks Range; the same is true of the differential taxa of the North Alaska subprovince. Moreover, many species extend to somewhat east of the Mackenzie River, show a large disjunction further eastward, e.g. *Cardamine bellidifolia, Draba fladnizensis, Saxifraga hieracifolia* and *Thalictrum alpinum*, or do not occur further in the Arctic from there on, e.g. *Boschnjakia rossica* and *Viola epipsiloides*. Hardly any boundary of this importance is found within the Arctic region, except for the even more important inter-regional floristic boundary occurs south of the Arctic, along the eastern foot of the northern Rocky Mountains.

The Alaska province is notable not so much for the Rocky Mountains flora element (although it is fairly well expressed too), but rather for the prevalence of floristic connections with Arctic Siberia over those with the Rocky Mountains (cf. Porsild & Cody 1980). The impoverishment of the flora eastward from the Mackenzie River is only partly compensated by the appearance of species which are absent in Alaska (see below). At the western boundary of the province, in the Bering Strait area, the flora loses about 100 species. The floristic asymmetry of the coasts of the strait is strengthened on the American side by the much more massive northward expansion of boreal and 'southern' maritime species, alien to the Arctic.

Two subprovinces are recognized. The boundary between the two subprovinces is drawn via the belt of the highest concentration of the distribution limits of 'western' and 'eastern' taxa (this according to the material from Hultén 1968, 1973 and Young 1974): (a) Point Lay; (b) the upper reaches of the Colville River, (c) the headwater of the Noatak River and then (d) westward along the timberline.

Beringian Alaska subprovince (Fig. 2, IIIA)

This sector has a vast latitudinal extension and is divided by two large bays, the Kotzebue and Norton Bays, cutting deep inland. It borders a *Picea* forest area along almost its whole length. In contrast to the Beringian Chukotka subprovince the Beringian Alaska subprovince is situated almost entirely in the southern hypoarctic tundra subzone and characterized by a still greater importance of boreal (including woodland) species as well as an increasing role of continental species. A few endemics in the genera *Beckwithia, Douglasia* s.s., *Papaver* and *Smelowskia* are found here.

Among the western co-differential taxa of the Beringian Alaska subprovince, in common with the Chukotka peninsula, there also prevail plants characteristic of more southern coasts of the Bering Sea and North Pacific, but there is a sufficient number of co-endemics (i.e. endemics shared by neighbouring phytochoria) and subendemics of the maritime parts of Chukotka and Alaska (e.g. *Artemisia globularia, Papaver walpolei, Rumex krausii,* and *Stellaria dicranoides = Arenaria chamissonis,*) as well as predominantly Asian taxa (e.g. *Oxygraphis glacialis, Rhododendron camtschaticum* ssp. *glandulosum* and *Saxifraga nudicaulis* ssp. *nudicaulis*). The distribution pattern of many species is asymmetrical on the Asian and American side. Thus in Alaska, unlike Chukotka, *Carex krausei, C. marina, Luzula rufescens* avoid the coasts of the strait, while *Rosa acicularis*, and, to some extent, *Dianthus repens* and *Silene repens*, do not.

North Alaska subprovince (Fig. 2, IIIB)

This sector comprises the more continental (central and eastern) parts of the Brook Range along with its northern foothills, and the Richardson Mts., as well as the Arctic slope of Alaska with its cold, true Arctic climate. The flora of the whole western part of the Brooks Range with its spurs and foothills is a transitional entity analogous, to some extent, to that of the Amguema area in Chukotka, with characteristic overlapping distribution areas of oceanic and continental (and other true Arctic) species. But the southwest-northeast gradient in both climate and floristic composition is well expressed even within the Seward Peninsula, i.e. in unit IIIA.

Among the differential and eastern co-differential taxa of the North Alaska subprovince those with a disjunction over the central parts of the Beringian sector (including steppe plants) predominate over the purely American taxa. The secondary gaps in the distribution areas of continental species can be attributed to the influence of the Holocenic sea transgression on the climate.

North Beringian autonomous area (Fig. 2, II/IIIa)

This area includes the Diomede Islands in the central part of Bering Strait along with St. Lawrence Island and St. Matthew Island in the northern, shallow part of the Bering Sea. Unlike the offshore islands, these four islands lack the majority of species characteristic of either coast of the strait, with the exception of a few Asian and American taxa. True oceanic species are more important here, mostly also found on the Aleutian and Commander islands, for instance *Nesodraba grandis* on Big Diomede (Ramanov) Island and *Conioselinium chinense* on the St. Lawrence Islands (Young 1971).

Canada-Greenland and Baffin-Labrador provinces (Fig. 2 , IV and V)

The Canada-Greenland province (Fig. 2, IV) comprises a vast Arctic area, extending from 60 ° - 83 °06' N. Moreover its land/sea ratio is high, even outside the mainland (except 'barren edge', sensu Beschel 1969). The northern (tundra) part of the Labrador Peninsula, and the southern and southeastern parts of Baffin Island, are influenced by oceanic boreal air masses, and they have many floristic characters in common with S Greenland, though the number of true Arctic (including some continental) species is larger than in S Greenland. For this reason, these areas are kept in the Arctic flora region as a separate Baffin-Labrador province (Fig. 2, V). However, its floristic similarities with the neighbouring subprovinces of the Canada-Greenland province are obvious, thus the rank of the Baffin-Labrador province needs further research.

The Canada-Greenland province lacks many species (including amphi-Beringian and amphi-Atlantic) which are characteristic of the two other American provinces. This, together with the presence of certain differential and co-differential taxa (e.g. the endemic diploid *Taraxacum holmenianum*, cryohalophytes such as *Gastrolychnis triflora* s.s., *Braya thorild-wulfii, Poa hartzii*) account for the mutual floristic resemblance of the five subprovinces.

Central Canada subprovince (Fig. 2, IVA)

The flora is markedly continental, with a clear influence from the adjacent 'Cordilleran-Beringian-Siberian' flora of the Alaskan province. There are also some floristic connections with the Siberian Arctic, e.g. *Astralagus tolmaczevii, Draba subcapitata, Oxytropis arctica* s.s., as well as an interesting set of endemic species, including *Parrya arctica*, which forms a monotypic genus according to some Russian taxonomists. The northernmost part of the subprovince - belonging to the herb zone of Edlund (1990) or the High Arctic tundra subzone - is much impoverished.

West Hudsonian subprovince (Fig. 2, IVB)

This sector is mainly characterized by the absence of differential species of the Baffin-Labrador province and differential and western co-differential taxa of the Central Canadian subprovince. Overlapping distribution areas are shown by western (West American and Siberian-West-American) co-differential taxa; e.g. *Cardamine digitata, Salix alaxensis, S. lanata* ssp. *richardsonii* and *Oxytropis arctobia*, and eastern co-differential taxa: the amphi-Atlantic *Cerastium alpinum, Diapensia lapponica, Harrimanella hypnoides* and *Salix herbacea*; the 'amphi-oceanic' *Phyllodoce coerulea*, and the East American *Salix calcicola* and *S. planifolia*. Two subendemics, *Oxytropis bellii* and *O. hudsonica*, occur.

West Greenland subprovince (Fig. 2, IVC)

This subprovince is mainly defined by overlapping distribution areas of amphi-Atlantic and other oceanic Arctic-alpine species from (non-Arctic) South Greenland, and true Arctic, Arctic-alpine and many other continental species (including Hypoarctic and Hypoarctic-montane ones, which usually also occur in the Canadian Arctic Archipelago and frequently also in North and/or East Greenland). A floristic W-E gradient is partly transformed here into a latitudinal gradient. Some species from NE Canada, e.g. *Arabidopsis mollis, Artemisia borealis* and *Pedicularis lanata* are found.

East Greenland subprovince (Fig. 2, IVD)

An analogous situation occurs in the East Greenland subprovince (Fig. 2, IVD), where the transformation of the floristic gradient is still more pronounced. Some continental species from Siberia (e.g. *Draba sibirica, Polemonium boreale, Potentilla lyngei, P. rubella* and *P. stipularis*) penetrate, as well as differential amphi-Atlantic taxa (e.g. *Arenaria pseudofrigida* and *Beckwithia glacialis*). Taxa such as *Arctous alpina, Draba cana* and *Dryopteris fragrans*, which are absent in S and N Greenland, but present in W and E Greenland, are considered as differential taxa of the E Greenland subprovince. *Arnica angustifolia, Carex atrofusca, C. marina* and *Ranunculus nivalis*, common in E and W Greenland, are rare in N Greenland (Bay 1992).

Ellesmere-North Greenland subprovince (Fig. 2, IVE)

This subprovince shows a continental Arctic to High Arctic type of flora. The main diagnostic features of the flora are negative: the absence of (1) amphi-Atlantic and other oceanic Arctic and Arctic-alpine species, (2) western co-differential taxa of the Central Canadian subprovince (e.g. *Caltha arctica, Gentiana arctophila, Salix polaris* and *Senecio frigidus*) and (3) legumes.

Some floristic differences between the Canadian

and Greenland parts of this sector are of minor importance, e.g. the presence of *Carex membranacea, Hultenniella integrifolia* and the endemic *Puccinellia poacea* on the Ellesmere and Axel Hedberg Islands, and *Arenaria pseudofrigida*, *Dryas punctata* and *Juncus castaneus* in North Greenland. The inner parts of the Axel Hedberg and Ellesmere Islands and the '*Dryas* area' in Peary Land are arid and have a warmer summer. They are floristically connected to distant areas in Siberia and North America.

Unlike the Arctic to High Arctic Ellesmere-North Greenland subprovince, all other subprovinces show a zonal range from the Hypoarctic tundras (southern or northern) up to the Arctic ones, whereas the Baffin-Labrador province is situated mostly in the southern subzone with 'islets' of forest-tundra. Most parts of the Canada-Greenland province were subjected to Pleistocene glaciations and subsequent isostatic sea transgressions. The southern islands were covered by the Laurentide Ice Sheet. Parts of the westernmost Canadian Arctic archipelago were not glaciated and remained an area of continuous development of the Arctic flora, resulting in a local Central Canadian endemism.

Other parts of the archipelago north of the Laurentide Ice Sheet, e.g. the Queen Elisabeth Islands, with flat or plateau relief, might have remained unglaciated and above sea level during certain intervals of the Late-Pleistocenic glaciation. This view is supported by the presence of the subendemic *Taraxacum holmenianum*, the only diploid species in the polyploid section *Arctica*, and the isolated occurrence of some Beringian taxa, such as *Acomastylis rossii* and *Saxifraga eschscholtzii*.

Jan-Mayen autonomous area (Fig. 2, IVD/VID,b)

This area (like the North Beringian) is characterized by an impoverished, true oceanic Arctic flora which does not resemble any of the neighbouring American or European provinces in particular. Circumpolar species prevail, but amphi-Atlantic species are present as well. A few endemic microspecies of *Taraxacum* have been described.

European-West-Siberian (Nenetsk) province (Fig. 2, VI)

This province covers the whole West Eurasian sector of the true Arctic (from 67° to 82° N); it is subdivided into four subprovinces, each corresponding to a major geomorphological unit. They form a natural swarm, its 'nucleus' being the mountain axis Ural - Pay Khoy - Novaya Zemlya, which runs through several vegetation zones, from steppe into polar desert.

The obvious negative features of the province are: the absence of (1) East Siberian, East Siberian-North American and North American species; (2) North Atlantic Hypoarctic and boreal species (and Arctic-alpine species such as *Alchemilla alpina*); (3) boreal and even boreal-nemoral taxa, e.g. *Calluna vulgaris* and *Nardus stricta*. There are few endemic and other differential taxa in the province or its subprovinces, i.a. *Gastrolychnis angustiflora* s.s., *Papaver lapponicum* ssp. *jugoricum, Pedicularis dasyantha, P. sudetica* ssp. *arcto-europaea*. The longitudinal floristic gradient is complicated by an 'inversion' in the Ural-Novaya Zemlya subprovince where the East Siberian species (and partly, the amphi-Atlantic) are better represented than in the adjacent lowland areas (Igoshina 1966). The presence of species of the genera *Alchemilla, Euphrasia, Gnaphalium, Hieracium* etc. is a distinctive feature of the Atlantic sector.

The flora of this province was subjected to the destructive action of Quaternary marine transgressions and glaciations (Tolmachev 1970) as well as to the expansion of forest and shrub vegetation. Most favourable for the dispersal of the Siberian and East Siberian continental elements was the cold and dry period of the Late Pleistocene, synchronous with the great sea regression.

Kanin-Pechora subprovince (Fig. 2, VIA)

Here we find most northward extensions of boreal species (in particular European), even on the Kolguyev Islands. The Arctic and Arctic-alpine complex is impoverished, endemism is very poor and of a low rank (e.g. *Gentiana arctica, Koeleria pohleana*). Some oceanic species penetrate, e.g. *Calluna vulgaris, Ligusticum scoticum* and *Primula farinosa* into the western parts of the subprovince and of continental species, e.g. *Astragalus umbellatus, Salix nummularia* and *Trifolium lupinaster*, into the eastern parts (of the Ural). Few East Siberian species - absent in the West Siberian lowland and present in the Ural Mts. - occur sporadically, e.g. *Crepis chrysantha* and *Silene paucifolia.*

Ural-Novaya Zemlya subprovince (Fig. 2, VIB)

The mountainous relief and the diversity of rocks and the expansion of forest and shrub vegetation favoured the preservation of various, sometimes contrasting flora elements. The barrier function of this mountain chain between the Siberian and European floras was of less importance. The montane floras of the subprovince typically show the floristic features of the Nenetsk province: European and amphi-Atlantic oceanic on one hand, and Siberian (boreal, continental Arctic, Arctic-alpine and Hypoarctic species) on the other, coexist.

This subprovince includes the western foothills of the Polar Ural Mts. east of the 'Ruprecht line' (Rebristaya 1977) and is characterized by the highest richness within the province. This is due to: (1) overlapping distribution

areas of western and eastern species; (2) far southward extensions of Arctic and even High Arctic species; (3) a distinct longitudinal floristic gradient (differences between the European and Asian slopes of the mountain range) and a more gradual latitudinal gradient. Several endemics arose from hybridization between Siberian and European taxa, e.g. *Trollius* × *apertus* = *T. europaeus* × *T. asiaticus*. The level of endemism is slightly higher here than in the adjacent subprovinces. Endemics of East Siberian affinity are e.g. *Astragalus gorodkovii*, *A. igoshinae* and *Taraxacum platylepium*.

Yamal-Gydan (West Siberian) subprovince (Fig. 2, VIC)

This subprovince contrasts with the previous subprovince in terms of a low floristic richness in association with various negative features of its flora: the gap in the distribution areas of many montane, predominantly East Siberian species; the absence of scores of 'eastern' (trans-Yenisey) species along with western ones (European, amphi-Atlantic, etc.) reaching the Ural Mts. Many 'western' species are confined to the lower Ob drainage up to the Taz Peninsula, and are lacking in the Gydan Peninsula; some of them are also recorded outside the Arctic from the mountains on the right bank of the Yenisey River. Most of the western elements are restricted to the southernmost areas whereas the role of the eastern counterparts increases northwards. Endemism is almost totally lacking here.

Svalbard subprovince (Fig. 2, VID)

This subprovince has a rather poor flora, which corresponds very well to its high latitudinal position and extensive (even at present) glaciation. Endemism is negligible and involves only apomictic or hybrid taxa (*Potentilla* × *insularis*, *Puccinellia svalbardensis*, *Saxifraga* × *svalbardensis*). In the Svalbard archipelago (especially on Spitsbergen Island), the amphi-Atlantic, Arctic and Arctic-alpine species, are associated with American Arctic and High Arctic species such as *Carex hepburnii*, *Minuartia rossii* and *Poa hartzii* and Eurasian Arctic plants, e.g. *Phippsia concinna* and *Salix polaris*, only few of which are present in Franz Josef Land. The flora of the latter lacks the eastern co-differential element, but includes some western (amphi-Atlantic) co-differential taxa. The floristic connections of Spitsbergen and Novaya Zemlya are very remarkable, even involving some taxa endemic or subendemic to the province, notably *Draba gredinii* and *Pedicularis dasyantha*.

Concluding remarks

The floristic peculiarity of the different sectors of the Arctic floristic region is expressed in different ways, by missing species, step-by-step one-sided enrichment of the flora, or overlapping distribution areas of taxa. Endemism is very unevenly represented in the Arctic floras and in itself cannot provide a basis for the division of the whole floristic region. The largest numbers of endemic taxa are recorded in the Chukotka and Alaska provinces forming the Beringian sector. Many subendemic taxa (up to the generic level) are also concentrated here.

The only reliable approach to the delimitation of the different Arctic sectors is to take into account the whole set of distinctive characters. Of special importance are the proportions of continental and oceanic species, and the penetration of boreal and alpine species. On the whole, continental species along with 'neutral' ones, contribute to the unity in the geographic structure of the Arctic flora, whereas the oceanic, as well as many boreal elements contribute to the differentiation. This implies that the integrity of the Arctic flora increased during former periods of global (eustatic) sea regression. After the great regression in the late Pliocene-Early Pleistocene, many present-time Arctic landscapes and floras might have developed for the first time (Yurtsev 1986).

On the other hand, the integrity of the Arctic flora certainly decreased during periods of large sea transgressions, albeit that some of them may have occurred at different times in different sectors (Tolmachev 1970). Before the formation of a permanent ice cover in the Arctic Ocean in the Late Pliocene, oceanic species were probably widespread in the Arctic (Herman & Hopkins 1980). This ice cover was probably more stable in the Siberian-American than in the Atlantic sector of the Arctic Ocean. The extensive, essentially mountainous regions of northern East Siberia and northwestern Canada as well as the continental areas of the Beringian sector supported a continuous development of continental flora complexes in the Arctic.

In the cold periods of the Pleistocene, many mountainous territories of the Atlantic sector and some of the Beringian ones were centres of more or less large glaciations. While becoming free of continental ice, some areas were colonized partly by continental plants from the inland and shelf refuges, partly by oceanic species following the southern - seaward - margins of retreating glaciers. In this way the mixed flora composition of some 'suboceanic' sectors (Fig. 2) might be explained.

Finally, the analysis of the scheme presented permits an explication of the greater richness and peculiarity of the flora of the Beringian sector and their special role in the formation of the whole Arctic floristic region (cf. Young 1974, 1978; Yurtsev 1972, 1974, 1978a,b, 1987).

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