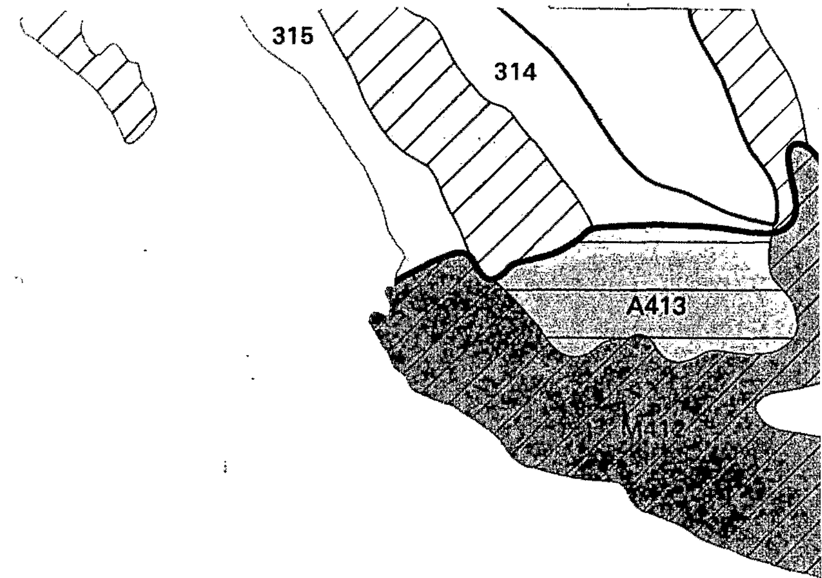

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ECOREGIONS OF NORTH AMERICA

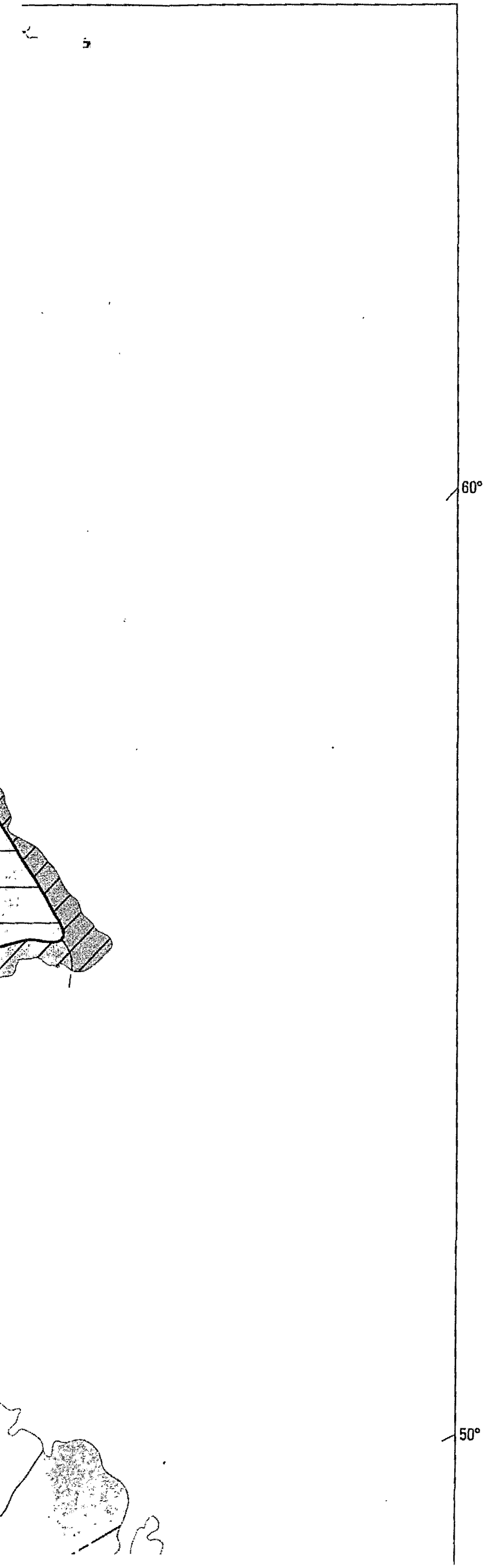
AFTER THE CLASSIFICATION OF J. M. CROWLEY

By

Robert G. Bailey, U.S. Forest Service

Assisted by Charles T. Cushwa, U.S. Fish and Wildlife Service

1981



ECOREGIONS

The ecoregions outlined on this map represent ecosystems of regional extent. Regions are distinguished according to the Crowley classification, based on their distinctive climates, vegetation, and soils. The boundaries and numeric codes are modified and refined from ecoregion maps of North America (Crowley, unpublished), Canada (Crowley 1967), and the United States (Bailey 1976).

The complete ecoregion code is a three-digit number that identifies the three ecologic levels—domain, division, and province—into which the continent has been divided for the purpose of fish and wildlife analysis and data management. This scheme is one of many that geographers have proposed to break down the complex ecological mosaic into simple patterns. Note that it is highly generalized; sharp local differences occur, notably in highland areas. These areas are shown on the map by letter codes and overprint symbols.

The domains are subcontinental areas of broad climatic similarity, such as lands having the dry climates of Köppen (Trewartha 1943).

The divisions, which are subdivisions of the domains, are determined by isolating areas of differing vegetation and regional climates, generally at the level of the basic climatic types of Köppen. Usually the zonal soils are related.

The provinces correspond to broad vegetation regions having a uniform regional climate and the same type or types of zonal soils. For example, the Boreal Forest Province (133) is the ecoregion characterized by the subarctic continental—boreal coniferous forest—podzol ecosystem. Generally, each province is characterized by a single climax plant formation, but two or more climaxes may be represented within a single province. This often happens on mountains where each altitudinal zone may have a different climax. Highlands where, due to the influence of altitude, the climatic regime differs substantially from adjacent lowlands to cause complex vertical climate-vegetation zonation are distinguished. More details are presented in Bailey (1976).

Additional copies of this map are available from the Eastern Energy and Land Use Team, Route 3, Box 44, Kearneysville, West Virginia 25430.

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100 POLAR DOMAIN

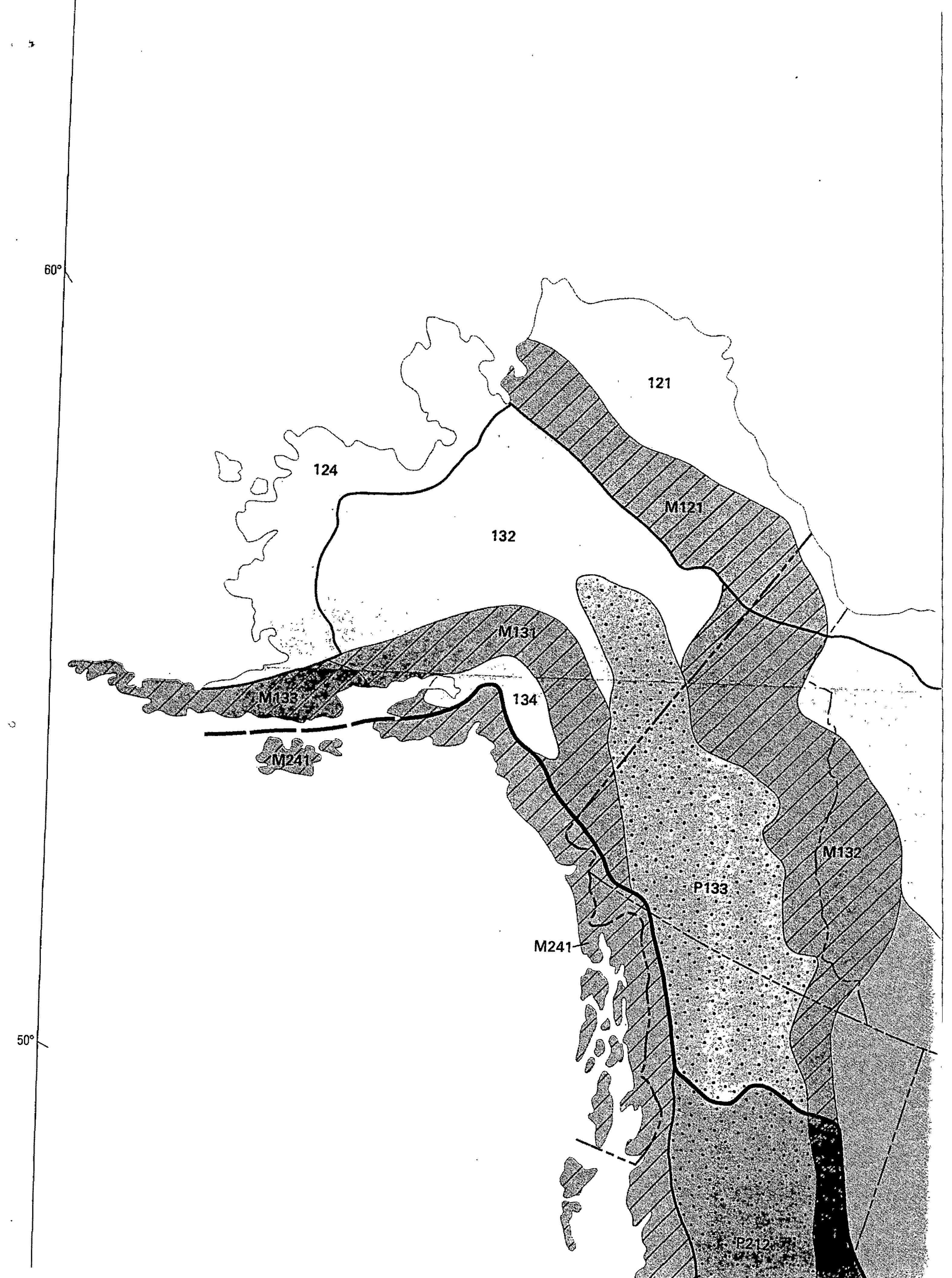
H110 ICECAP REGIME HIGHLANDS*
- A111 Greenland Icecap Province

120 TUNDRA DIVISION
- 121 Low Arctic Tundra Province
- 122 High Arctic Tundra Province
- 123 Polar Desert Province
- 124 Bering Tundra Province

H120 TUNDRA REGIME HIGHLANDS*
- M121 Brooks Range Province
- M122 Northeast Seaboard Mountains Province
- M123 Southeast Greenland Mts. Province

130 SUBARCTIC DIVISION
- 131 Subarctic Parkland Province
- 132 Yukon Forest Province
- 133 Boreal Forest Province
- 134 Coastal Trough Forest Province

H130 SUBARCTIC REGIME HIGHLANDS*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ALEKSANDROVA

The Arctic and Antarctic: their division into geobotanical areas

The Arctic and Antarctic: their division into geobotanical areas

XXIX KOMAROV LECTURE PRESENTED 14 OCTOBER 1974

The Arctic and Antarctic: their division into geobotanical areas

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1

Division of the Arctic into geobotanical areas

Since so much will be said about division into geobotanical areas, it is first and foremost necessary to define my concept in this respect. By division into geobotanical areas I intend to divide the vegetation cover so that the characteristics of the vegetation, that is, the totality of the plant communities distributed over a given territory, can be considered as diagnostic. Other traits should be considered as characterizing.

The first person to suggest a distinction between diagnostic characteristics, according to which groups of objects may be separated, and characterizing ones, according to which the units are further differentiated, was Tuomikoski (1942). In respect to their nature, the diagnostic characteristics are analogous to the indicator characteristics of a correlation swarm (Terent'yev, 1931, 1959). Takhtadzhyan (1966: 41–2) points to their significance for plant taxonomy and Vasilyevich (1964, 1966) as well as Nitsenko (1966) have shown their importance for the classification of vegetation. The application of diagnostic and characterizing traits is expedient also for the botanical–geographical division into areas (Aleksandrova, 1974). (Note: It is suggested that the division of an area based on any botanical characteristics be called botanical – geographical). The first group of characteristics, the diagnostic ones, defines the limits and establishes the rank and configuration of distinct areas. The second group, the characterizing traits, describes the distinguished areas, emphasizes their particularity and confirms the significance and rank of the boundaries between them.

The choice of various diagnostic traits separates the different systems for dividing vegetation cover into areas. According to this criterion, the distinction is first and foremost floristic, when the character of the flora serves as the diagnostic characteristic, or geobotanical, when the character of the vegetation plays this role. Although the flora and vegetation form a single unit, the flora exists in the form of definite plant associations, and the taxa of the flora in a given region appear as the components of the plant communities. There is, however, a distinct difference between divisions into floristic and into geobotanical areas. In the first case, the taxa of the plant systematists are the focus of attention. If, thereby, the very varied characteristics of the plants are considered, including their role in the composition of the plant communities, all these traits can be used as characters, describing given species. In the second case, the central problem for the division of the vegetation into areas is its classification (Shennikov, 1940: 25–30; Sochava, 1948*a*, *b*, 1952: 530; Braun-Blanquet, 1964: 720–56; Schmithüsen, 1968; Karamysheva & Rachkovskaya, 1973: 171–2; etc.). It is fundamentally possible to set up specific, phytocoenological characteristics here which are outside the concepts of the floristics, such as, e.g., the structure of the plant communities.

In addition, supplementary characteristics are added to define a distinct area which, together with the diagnostic traits, plays a role in its description. If a wide variety of traits, both of the flora and of the vegetation, are used as characterizing, we obtain as a result a synthetic (Lavrenko, 1968; and others) or a complex (Yurtsev, 1966; and others) botanical–geographical division into areas. It should be noted that according to the nature of the diagnostic characteristics, this division becomes, when applied by E. M. Lavrenko, a geobotanical one, and when applied by B. A. Yurtsev, a floristic one.

In the Arctic, the principles of the classification of the vegetation and its division into areas have been differently developed within the USSR and abroad. In part, it is explained by the fact that there are different geobotanical provinces in the different parts of the circumpolar Arctic.

Classification and division into areas of the arctic vegetation outside the USSR

In the western hemisphere, the application of basic, diagnostic characteristics for the division of the Arctic into areas in respect to the degree of closedness of the vegetation is very widespread. This goes back to

the principles of classification formulated by Warming (1888) who, when describing the vegetation of Greenland, distinguished two vegetation 'formations': the 'Field-Flur' or fell-field (literally: desert-like ground) and 'Heide' or 'heath' (literally: wasteland, in a sense close to what is understood by that term in Shennikov, 1938: 487). According to Warming (1928: 299) the fell-field is the formation where 'plants grow singly often with great intervals, though here and there denser spots of vegetation occur, consisting of one or more species, and it is the substratum (loose soil, rock) which lends its generally grey or greyish black tinge to the surface'. 'Heath' differs from 'fell-field' in that here the vegetation cover is closed. By heath, Warming implied not only the kind of heath where the ericaceous dwarfshrubs form a closed cover with interlacing branchlets and the space between them is filled by mosses, lichens, and grasses (Warming, 1928: 302), but also lichen-heaths and moss-heaths. By the latter, Warming meant mainly forms of *Rhacomitrieta*. In addition, Warming distinguished copses (thickets of shrubs), as well as 'herb-field and grass-field in well-ventilated soil', 'freshwaters vegetation', 'moors and meadows' and 'shore vegetation'. The terms 'heath' and 'fell-field' introduced by Warming as well as some additional ones, e.g., the term 'barrens' for areas with a very disrupt vegetation, are widely used in foreign literature, both for the purpose of vegetation classification (cf. Beschel, 1963*b*; and others) and also as additional concepts to characterize vegetation (Böcher, 1954, 1963*b*; and others). It should be noted here that although some authors imply by the term 'heath' only associations dominated by ericaceous shrubs, this term is, as a rule, applied solely for the purpose of emphasizing the predominance of a closed cover, some small part of which also may be bare ground. Thus, Porsild (1951: 12) calls the dwarfshrub tundra 'dwarfshrub heath' and the lichens and moss tundras 'lichen and moss heaths'. Churchill (1955: 609) uses the term 'heath' for the tussocky tundras of Alaska. Beschel (1963*b*: 102–3) described from Axel Heiberg Island beside 'mesic heath (*Cassiope tetragona, Trisetum spicatum, Potentilla hyparctica*)' also 'dry mesic heath (*Dryas integrifolia, Poa arctica, Thamnolia vermicularis*)', and so on. Often, expressions such as 'Dryas-heaths' and even 'Festuca-heaths', and so on are met with. The vagueness in the use of the term 'heath' can be explained by the fact that, in the English language, this word has two meanings: first wasteland, i.e., useless, 'wasted' land, and second dwarfshrub thickets of the heather family (Ericaceae).

The criterion of a closed vegetation cover, widely applied outside the USSR, forms the basis for the division of the Arctic into three major regions: the low-arctic, the middle-arctic, and the high-arctic. According to Polunin (1960: 382; cf. also Knapp, 1965: 92), a closed cover predominates in the low-arctic. In the middle-arctic, the vegetation cover is closed only over large parts of the lowlands; in the high-arctic, there is a patchy cover only under the most favorable conditions, usually with wide spaces between. More essential characteristics have been added by Rønning, who states that the low-arctic is where the vegetation is closed over large distances and is especially rich in grasses, sedges and shrubs; the middle-arctic is where the vegetation is closed only in lowlands and differs by the absence of such dwarfshrubs as *Betula nana* and species of *Vaccinium, Phyllodoce coerulea*, and others; the high-arctic, finally, is where the vegetation is met with only in patches or as widely separated, single individuals (Rønning, 1969: 29).

It should be noted that the degree of closedness of the cover is, to a considerable extent, related to the local and not to the circumpolar character of the vegetation. Thus, in the basin of the Khatanga and Anabar rivers in eastern Siberia 'spotty' tundras with barren nonsorted circles are distributed along the actual forest limit, and even within the northern edge of the open woodland there are spots of barren ground. Sochava (1933*c*: 361) wrote in a paper on the tundra of the Anabar basin: 'in the dwarfbirch-willow subzone, just as to the north of it, the spotty tundras are widely distributed. There is nothing in this subzone that can be considered less fundamentally distinctive than spotty tundras in the subzone of the arctic tundras'. At the same time, hummocky tundras with a closed vegetation cover have developed at the northern edge of the Yamal Peninsula, and so on. Also within the areas of the polar deserts, it is possible to find extensive patches with a closed cover of crustose, fruticose and foliose lichens, mosses and liverworts, in rare cases associated with flowering plants. Therefore, the extent of barren ground cannot be considered everywhere in the Arctic as a diagnostic characteristic for the distinction of major, zonal subdivisions.

The classificatory units of the Scandinavian school have also been utilized for the study of the vegetation within the limits of the Arctic.

Böcher (1954, 1963*b*; and others), studying mainly the sociations, used two parallel systems for their further unification. As the primary distinction of the higher units, he used principally a physiognomical classification: shrub communities, dwarfshrub communities, and so on (Böcher, 1963*b*: 268–72: etc.). Secondarily, he used groups of indicator species for the unification of sociations: Ar – arealogeographical, Cl – climatic, Hb – ecological, EG – ecological-geographical ones. By means of the indicator species he recognized 'groups of sociations' and 'vegetation types'. On the basis of these, he identified 'vegetation complexes' and 'vegetation areas', appearing similar to regional subdivisions (Böcher, 1954; 11–12). Proceeding from these units Böcher accomplished a profound, basic areal division of the vegetation of southwestern Greenland (Böcher, 1954).

Areal divisions based on physiognomic and floristic – physiognomic indicators have also been published: Porsild (1951: 11) divided the American Arctic into four provinces, Polunin (1951: 310) divided all of the circumpolar Arctic into ten sectors, and so on.

There exist also works on the classification of the arctic vegetation based on the methods of the Braun-Blanquet school. Thus, Hadač (1946) has described a number of associations from Spitsbergen and decided on their position in a system of units of higher rank; he included, for instance, the associations *Carisetum subspathaceae* Hč. and *Puccinellietum phryganodis* Hč. in the alliance *Puccinellion phryganodis* Hč., the order *Puccinellietalia phryganodis* Hč, and the class *Puccinellio–Salicornieta* Topa 1939, and so on. Rønning, when describing the *Dryas* tundras of Spitsbergen, placed them within the alliance *Dryadion* Du Rietz 1942 and the order *Seslerietalia* Br. -Bl. 1951 (Rønning, 1965: 11). Hofmann (1968) studied the vegetation of Spitsbergen with these methods; they have also been applied in Greenland (Molenaar, 1974) and arctic Canada (Thannheiser, 1975) and so on. However, the results of the classification according to the Braun-Blanquet school have not been used for the purpose of division into geobotanical areas.

Classification and division into areas of the arctic vegetation inside the USSR

Within the Soviet Union, the development of principles for the classification of vegetation aiming at a division into areas, has followed along physiognomic (in combination with this or that life form) and floristic-physiognomic lines from the very beginning. Thus, Trautvetter (1851) divided the East European tundras into two 'districts': 'the district of the alpine willows' (the arctic tundras) and 'the district of the low-grown birches' (the subarctic tundras). The southern boundary of the polar (according to Schrenk, 1854), the northern (according to Zhitkov, 1913), or the arctic (according to Pohle, 1910, and Gorodkov, 1916) tundras has been drawn along the northern limit of distribution of shrub thickets. Pohle (1910) distinguished also within the limits he had outlined for the 'subarctic zones' of the tundras in the European North, regions of the type of provinces: 'the western region' (from Norway to the Timan) and 'the eastern region' (from Timan to the Urals).

During the nineteen thirties, more serious contributions to the problems of classification and differentiation of the vegetation were put forward by Sochava (1933*c*, 1934*b*, for the Anabar Basin), Andreyev (1935 and others, for the East-European tundras), and Gorodkov (1935*c*). The latter accomplished a geobotanical areal division of the entire USSR tundra zone. As the highest classificatory unit, Gorodkov used the vegetation type, established on the basis of physiognomic, ecological, and partly also phylocoenogenetic criteria: the vegetation on snow (algae on the melting snow cover), on skeletal soils of the arctic deserts, on boulder fields, tundra-type vegetation, tundra meadows, subalpine shrub thickets, hydrophytic and mesophytic flood-plain meadows and shrublands, shrub thickets, forests, and bogs. His highest unit for the geobotanical division was the zone, and the second rank was the subzone. In addition, he distinguished twelve provinces, dividing all the subzones in a longitudinal direction. This remarkable work by Gorodkov has received wide acclaim and has been used as a basis for the illustration of the arctic territories on small-scale vegetation maps of the USSR (Lavrenko, 1939; Sochava, 1949, 1964*a*; etc.).

Leskov (1947) has suggested another system for geobotanical division. Basically, it differs from the Gorodkov system by the rejection of the concept of zone as a taxonomic category in the system of differentiating units. Guided by the principles advanced by Lavrenko (1946: 63–4; 1947) and differing from Gorodkov in his approach to the classification of the vegetation, Leskov distinguished four regions

within the limits of the Soviet Arctic: (1) the high-arctic nival, (2) the arctic tundra, (3) the Euro-Siberian shrub region (including the European-West Siberian and Central Siberian provinces), and (4) the Beringian shrub region. The forest-tundras were included in the latter two. Subsequently, Norin (1957, 1961, etc.) formulated the concept 'forest-tundra type of vegetation' and raised the forest-tundra to the rank of a zone. Included in it was also the southern part of the subzone of the shrub-tundras, *sensu* Gorodkov.

An outline for a division, according to which the boundary between the arctic and subarctic tundras appears as the basic limit of first rank, was developed by V. B. Sochava. While using traits connecting the vegetation with important factors in the environment as well as with phylocoenogenetic criteria as diagnostic characteristics, he distinguished the 'arctic belt', including in it the arctic tundras and the polar deserts, and the 'humid' (Sochava, 1948*a*) or the 'temperate' belt (Sochava, 1952), uniting the subarctic tundras with the adjoining, more southerly areas. In the Soviet Far North three 'geobotanical fields' (subdivisions at the rank of province) were recognized within the limits of the arctic belt. The tundra areas of the temperate belt were divided into seven 'geobotanical fields'. This outline was later used with some alterations by Sochava for making a physical–geographical division of Asia into areas (Sochava & Timofeyev, 1968) and for drawing the northern boundary of the Subarctic (Sochava *et al.*, 1972: 3).

The contribution made by B. A. Yurtsev to the differentiation of the arctic vegetation cover should also be mentioned. Although the complex botanical–geographical differentiation by Yurtsev can be considered as floristic, since the characters of the flora appear as diagnostic traits, his results are of great importance for understanding the geobotanical differentiation, thanks to the fact that they take into account a wide array of descriptive characteristics: ecological, biological, coenological, and phylocoenogenetic ones (Yurtsev, 1968*b*) as well as the characteristics of the landscape related to the vegetation cover (Yurtsev, 1966: 17–19, etc.). Yurtsev distinguishes the botanical–geographical 'hyparctic belt' and the adjacent 'arctic' and 'boreal' belts. In spite of using different arguments, he draws the boundary between the arctic and the hyparctic belts just like Sochava along the southern limit of the arctic tundras, which confirms the great importance of this line as a boundary of highest rank. Yurtsev divides the hyparctic circumpolar belt into five provinces.

The system of regional units, as applied by Lavrenko (1947, 1968), was useful to me (Aleksandrova, 1964, 1971*b*). However I suggest separating vegetation types not according to Lavrenko's ideas but to a complex of characteristics, including the specificity of the structure, the character of the typical synusia, and so on. A reconsideration of the principles for the delimitation of the vegetation types of the tundras and of the polar deserts has resulted in a division of the Arctic into geobotanical regions: the polar deserts and the tundras. The latter region is divided into two subregions: the arctic and the subarctic tundras. My own points of view are expressed in detail below.

The higher taxonomic units for the classification of the arctic vegetation

The difficulty, when classifying the vegetation of the Arctic, is primarily connected with the clearly expressed co-dominance of the majority of the plant associations developed there: very often mosses, lichens, herbs, dwarfshrubs and semiprostrate shrubs co-dominate in the same phytocoenosis. Because of this, the application of the principles widely used in the USSR for differentiating higher units of the vegetation on the basis of the dominating biomorph, meets with considerable obstacles.

Supporters of the distinction of the vegetation types according to the dominating lifeform consider that in the tundra zone there is no single, zonal type of vegetation. They try to distinguish the tundra associations into a few types: the lichen-, the moss-, the dwarfshrub- and the shrub-types (Leskov, 1947, and others). However, as a rule, as was mentioned above, there appear in the tundra associations as co-dominants some life forms among which it is difficult to distinguish the main dominant for which this characteristic is the single one of the essential zonal characteristics for the zonal, mesic associations of the tundra zone.*

* Translator's note. The expression 'zonal, mesic association, habitat, etc.' is here used for the Russian term 'plakor', derived from a Greek word for 'surface, flatland', and is used to describe the zonal type of growth on mesic habitats, neither too wet, nor too dry, neither too sheltered nor too exposed, and covered by neither too little nor too much snow.

The tundra type of vegetation was identified by Gorodkov (1935*c*, 1946*b*; etc.), but Sochava had already expressed himself categorically on the identification of the tundra type of vegetation. He wrote that 'the tundra is a type of vegetation, – a plant community in the wide sense of that word, characterized by the following properties: it is from time immemorial without trees; it is dominated by arctic–alpine plants (by these are understood also the hyparctic forms; that term was introduced later by Tolmachev, V.A.), or by mosses and lichens; it has a special type of soil formation ... and some other features' (Sochava, 1931: 127). Concepts of 'tundra types of vegetation' have been formed by many Soviet tundra geobotanists (Andreyev, 1954: 8, 12; Norin, 1966; etc.).

Katenin (1972*a*, *b*) distinguished the tundra associations of the East European forest–tundra into three vegetation types: the shrub-tundra type, the dwarfshrub tundra type, and the herbaceous tundra type according to the lifeforms of the plants which compose the upper tier of the community. The classification by Katenin appears logically well composed and better than many present ones, because of its factual basis. He has many comprehensive tables with complete species lists and each association is based on descriptions of two to sixty stands. However, the classification was worked out for the local conditions in the area which the author studied, and when proceeding northward and into areas with a distinctly continental climate, where the layers degrade and a horizontal mosaic develops, it becomes less applicable.

For the differentiation of vegetation types, I myself take into consideration a complex of diagnostic characteristics, including the combination of definite ecobiomorphs and geographical groups of species, the composition of the characteristic synusia, not necessarily the dominating one, but one closely connected with the type of community under consideration, and the characteristics of the structure. The types and subtypes described below can then be distinguished as somewhat deviating from those in my previous publications (Aleksandrova, 1971*b*). (An *ecobiomorph* is a life-form adapted to certain environmental (ecological) conditions; e.g. hekistothermal mesophilous

Karamysheva & Rachkovskaya (1973: 180), 'most frequently, these are species indicating a connection between this territory and the surrounding ones and appearing as evidence of paleogeographical events'.

I consider the terms of the latitude zonation (zone, subzone, belt) as complementary ones, having no taxonomical ranks within the geobotanical division.

When drawing up the boundaries, I happen to clash with the geographical continuum as one of the expressions of the generally particular continuities inherent in the vegetation cover (cf. Aleksandrova, 1969*a*: 12–22, etc.). The problem of geobotanical boundaries in connection with the continua at the regional level has been discussed by Sochava (1965, etc.). The degree of smoothness in transition from one area to another and the shape of the borders may be entirely different (Karamysheva *et al.*, 1969). In the Arctic, the change in vegetation occurs more smoothly latitudinally, while the transition from one province to another is more 'abrupt'. At the same time, it is necessary to take into consideration that using one characteristic may make the progress look gradual, while another character may permit us to decide at what boundary there is a definite limit. Thus, in general, the zonal, mesic associations in the tundras change more smoothly, and the non-zonal, non-mesic ones considerably more abruptly. The progress from the northern belt of the subarctic tundras to the southern belt of the arctic ones, as described below, pp. 88–90) may serve as an example.

2

The geobotanical regions of the Arctic: the tundra region

In the territories spreading northward from the forest limit, we can distinguish two regions (Fig. 1)–the tundra region, and the region of the polar deserts. Diagnostic characteristics for differentiating these areas are: (1) the development on zonal, mesic habitats of different types of vegetation of tundra and of polar desert type, none of which is met with on zonal, mesic habitats in adjacent regions (but which may be found on non-zonal, non-mesic habitats: tundra associations may occur in especially favorable local conditions in the southern belt of the polar deserts, and polar desert associations in the definitely unfavorable conditions in the northern part of the tundra region); (2) the lack in the region of the polar deserts of the majority of the non-zonal, non-mesic types of vegetation, developed in the tundra region (described above under nos. 3–5, 7, 8, 10–12). As an especially conspicuous characteristic appears the lack in the polar deserts of mires with a peat layer so that in connection with it the polar deserts are situated north of the area of *Carex stans*.

The characterizing properties of the flora confirm the essential differences of the vegetation covers in these regions. The hyparctic element of the flora is lacking in the polar deserts, although it still plays a decisive role in the arctic tundras and is predominant in the tundras of the subarctic. In the polar deserts, a number of families are lacking such as Polypodiaceae, Liliaceae, Betulaceae, Empetraceae, Vacciniaceae, and many others. High-arctic species predominate, such as *Phippsia algida*, *Poa abbreviata*, etc. The sharp decrease in the number of species of vascular plants, which apparently do not exceed 50–60 species, is also typical. In spite of the fact that the floristic difference is of a negative nature, it does represent a complex, qualitatively

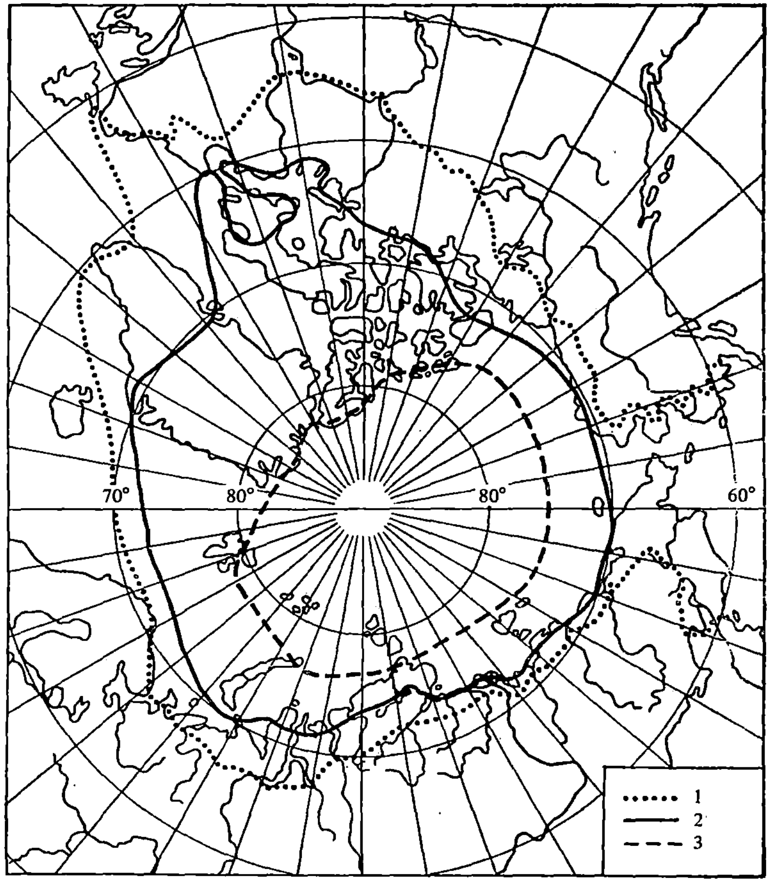

Fig. 1. The geobotanical regions and subregions of the Arctic. The southern boundary of: 1, the tundra region; 2, the subregion of the arctic tundras; 3, the region of the polar deserts.

different from that of the tundra region. The region of the polar deserts agrees most completely with the '1st zone' of the floristic zonation as outlined by Young (1971) and with the 'glacial variant of the subzone of the higharctic tundras' according to the botanical–geographical zonation by Rebristaya & Yurtsev (1973).

This chapter gives a more detailed description of the tundra region and Chapter 3 of the polar desert regions.

The tundra region is distinguished by the development on zonal, mesic habitats of a tundra type of vegetation (cf. p. 10) together with

herb-moss, polygonal, and hillocky mires with flat-topped peat mounds, as well as other non-zonal, non-mesic types of vegetation (cf. nos. 3–8, 10–12, pp. 11–14). Open woodlands penetrate as extra-zonal associations from the south, and polar desert-communities from the north.

Two subregions can be distinguished within this region: the subarctic tundras, and the arctic tundras.

It is correct to divide the tundra region into two areas of subregional rank on the basis of a combination of important characteristics, of which the presence on zonal, mesic habitats of particular subtypes of vegetation is decisive. Typical for these subtypes are the different characteristic synusiae, distinguished not only according to species composition, but also in respect to the ecobiomorphs: in the subregion of the subarctic tundras, these synusiae consist of semiprostrate hyparctic shrubs (*Betula nana*, *B. exilis*, *B. glandulosa*, etc.) and dwarfshrubs (*Vaccinium uliginosum* ssp. *microphyllum*, *Empetrum hermaphroditum*, *Ledum decumbens*, etc.), but in the subregion of the arctic tundras, the synusiae are composed of arctic–alpine and arctic dwarfshrubs (*Salix polaris*, *Dryas octopetala*, *D. punctata*, *D. integrifolia*, *Cassiope tetragona*, etc.). The reduction in the number of non-zonal, non-mesic types of vegetation in the subregion of the arctic tundras is another important diagnostic difference: the thickets of shrubs disappear – an especially important character – there are no snow-dependent nival meadow-like communities, and associations of prostrate elfin-wood and open woodland are no longer met with.

A still higher rank is given to the boundary between the arctic and the subarctic tundras by Sochava and Yurtsev, who draw a boundary between different botanical–geographical belts along this line. According to Sochava (1948*a*, *b*, 1952), the arctic tundras belong to the arctic belt, characterized by circumpolar arctic fratria of formations (Buks, 1973; Il'ina, 1975), while the subarctic tundras belong to the temperate, or subarctic belt (Sochava *et al.*, 1972), where different fratriae of formations occur. According to Yurtsev (1966, 1974*a*), the subregion of the arctic tundras belongs to the arctic botanical–geographical belt, while the subarctic (in his terminology: the hyparctic) tundras are part of the hyparctic belt.

To define the transition from one subregion to the other, the principal differences in the history of the formation of the vegetation within the arctic and the subarctic tundras must be considered, as well as the critical decrease in the average amount of heat, which leads to a change in all physico-geographical complexes. As has been pointed out by Tolmachev & Yurtsev (1970), the hyparctic flora, predominating in the subarctic tundras, has developed from components of degenerating forest and non-forest associations from the Pliocene, pre-adapted to the increasingly drier and colder conditions during the late Pliocene and the Pleistocene; these are various communities of shrubs and open woodland, predominantly of deciduous species, such as willows, shrubby birches, and alders, different types of bog-associations, etc. A decisive influence was exerted during the initial formation of the arctic tundras by the alpine tundra (the 'gol'tsy')* of northeastern Asia, particularly in its continental sector. According to Tolmachev & Yurtsev (1970: 90–92) a number of species have penetrated into the Arctic from the 'gol'tsy', such as *Cassiope tetragona*, *Dryas punctata*, *Novosieversia glacialis*, *Erysimum pallasii*, including the definitely arctic species of *Pedicularis*, the precursor of *Braya purpurascens*, and species of *Ranunculus*. Other species originated from close to central Asia. There are also arctic–alpine taxa which now have a circumpolar distribution and some species with an Angaran connection florogenetically, such as *Kobresia bellardii*, *K. simpliciuscula*, *Carex rupestris*, and even circumpolar species of Asiatic origin, such as *Oxyria digyna*, *Alopecurus alpinus*, *Saxifraga cernua*, *Eriophorum scheuchzeri*, *Potentilla hyparctica*, *Eutrema edwardsii* and *Gastrolychnis apetala*; some species represented a special alpine element, derived from the ancient Beringia: *Cardamine bellidifolia*, *Salix arctica*, *Luzula confusa*, and *Poa arctica*. Species can also be traced which have connections with the American mountains (*Poa abbreviata*, *Pleuropogon sabinei*) or xerophytic highlands (*Lesquerella arctica*, etc.) and so on.

The difference between the arctic and the subarctic tundras is enhanced by the fact that the arctic tundras have remained treeless throughout all the periods of the Holocene, a fact confirmed by paleobotanical data (Giterman *et al.*, 1968; etc.). Besides there occurred a repeated expansion of forest into the subarctic tundra territory during periods of warming climate, leading to the enrichment of its flora by boreal species as reflected in the composition and structure of its associations.

* Translator's note: 'gol'tsy' is a Siberian term for the alpine tundra belt above the timberline.

The boundary between the subarctic and the arctic subregions of the tundra region oscillates around the 6 °C isotherm for July.

The subregion of the subarctic tundras

In zonal, mesic habitats of this subregion, plant communities have developed which belong to the subarctic subtype of the tundra type vegetation. As typical synusiae, hyparctic shrubs and dwarfshrubs dominate or participate. The most typical of these, having a primary diagnostic value, are the polar birches, *Betula nana*, *B. exilis*, *B. middendorffii* and *B. glandulosa*. In non-zonal, non-mesic habitats, different vegetation types are found: herb-moss, lowland, oligotrophic mires with a 30–60 cm-thick peat layer and heterogeneous hillocky and polygonal mires, as the typical components of which appear *Betula nana*, *B. exilis* and other hyparctic shrubs and dwarfshrubs, growing on the sloping parts of frost peat mounds and on raised borders of low-center polygons, thickets of shrubs in the watershed areas and in valleys, meadow associations in river valleys, nival and other hekistothermic tundra-like communities, tundra–steppe and steppe associations (in northeastern Asia and in Greenland), and finally open woodland and prostrate krummholz communities.

The important role played in the vegetation cover by the boreal element of the flora together with the predominating hyparctic element is typical for the subregion of the subarctic tundras. To the boreal element belong first and foremost those arboreal species, the areas of which penetrate far into the subregion of the subarctic tundras (*Larix gmelinii* in prostrate form up to 72°55′ N) and a large number of species of herbs and dwarfshrubs (*Deschampsia flexuosa*, *Calamagrostis langsdorffii*, *Comarum palustre*, *Chamaenerium angustifolium*, *Vaccinium myrtillus*, etc.). At the same time, the participation of arctic species is distinctly expressed, especially of such moderately arctic species as *Carex ensifolia* ssp. *arctisibirica*, *C. lugens*, *Arctagrostis latifolia*, *Arctophila fulva*, etc. The enrichment by boreal species and the generally hyparctic character of the flora is connected with the history of its formation, which has been described above.

Within the limits of the subregion of the subarctic tundras, a number

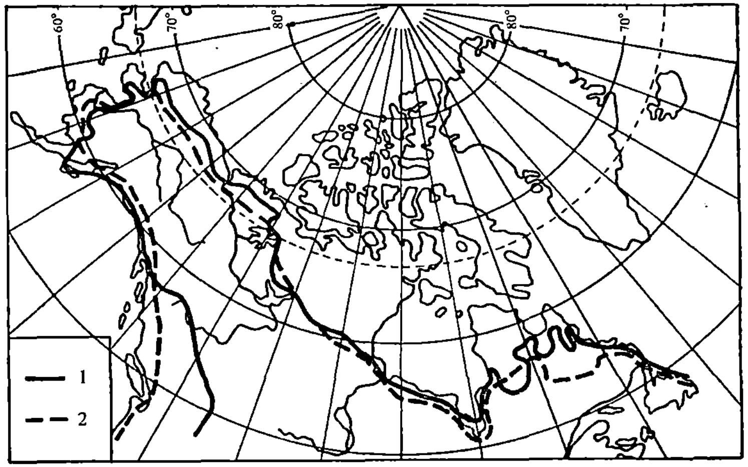

Fig. 10. Northern limit of the distribution of *Populus balsamifera* L. (1) and of *Populus tremuloides* Michx. (2). According to Hustich, 1966.

Populus tremuloides and *Betula papyrifera*. Yurtsev (1974*a*: 106–125) attributes these differences to the peculiarities caused by the Pleistocene history of the Bering landbridge. According to him, the Bering landbridge reached a width of 1500 km when it was broadest during the time of maximum emergence and might therefore have been divided into at least three zones: northern and southern coastal zones, and an interior more continental one. The northern zone could have been characterized by the dry conditions of the arctic tundras. The interior area may have corresponded to the continental variant of the hyparctic tundras. The southern coastal area of the Beringian landbridge, experiencing a softening of the climate due to the air masses from the Pacific Ocean, could as this author suggested have been represented by a zone of non-forested, coastal, hyparctic landscapes and been open to Beringian, north Pacific and other types of species of maritime origin. It is possible that there was a sporadic exchange between the coniferous forest floras of Asia and America (these having already developed independently during the Miocene) during the Pleistocene period, favoring such an exchange. In the opinion of Yurtsev (1974*a*: 121), such an exchange of Asiatic and American species of taiga trees could, however, occur just over the territory limited to the 'neutral' lowland of the Bering landbridge, which separated the mountainous highlands of Asia and America and

was periodically destroyed by the transgression of the sea. Another factor was the deterioration of the climate, which resulted in weather conditions unfavorable for the growth of trees. These peculiarities of the paleogeography account, on the one hand, for the similarities in the tundra vegetation of northeastern Asia and northwestern America, and on the other hand, for the complete change in the composition of the woody species which form the polar forest limits in these territories.

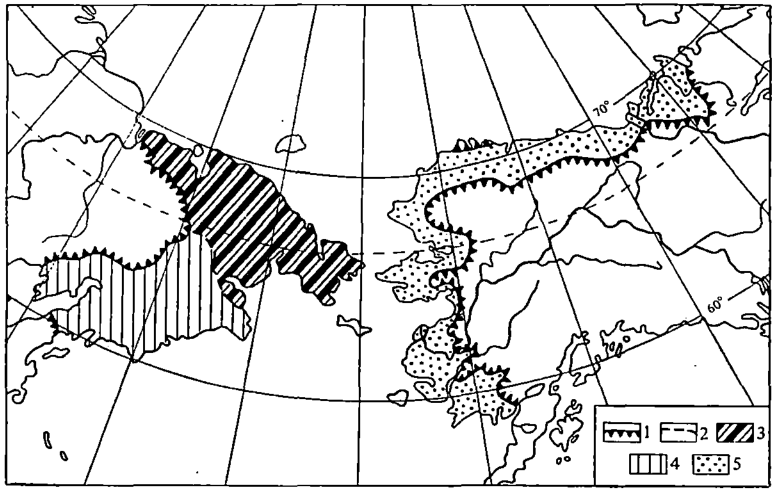

Fig. 11. The Chukotka–Alaska Province of the subarctic tundras. Boundaries: 1, provincial; 2, subprovincial. Subprovinces: 3, the Chukotka; 4, the Anadyr–Penzhina; and 5, the Alaska subprovinces.

Three geobotanical subprovinces can be distinguished within the Chukotka–Alaska province: the Chukotka, the Anadyr–Penzhina, and the Alaska subprovinces (Fig. 11).

The Chukotka subprovince of the subarctic tundras

East of the Kolyma River, the tussocky tundras with *Eriophorum vaginatum* associated with *Carex lugens* assume a zonal, mesic position and become generally the dominating type of tundra on the plains and in the low mountains. As reported by Katenin (1974: 1587), who investigated the vegetation along the middle course of the Amguema River, this is the most widely distributed formation, which is associated with the transition to thickets of *Pinus pumila.* The latter, growing prostrate between mountain tundras with lichens dominated by species such as *Cornicularia divergens* and *Cetraria nivalis*, occurs up to the summits of the mountains as odd specimens at an altitude of 500–700 m.

In this subprovince, mires are found in a few localities but they occupy only limited areas. These mires are situated in depressions where sedge associations of *Carex rotundata* or *C. stans* and mosses and mires with flat-topped peat mounds occur. The latter are overgrown with shrubs, mainly *Betula exilis*, and a large quantity of dwarfbushes such as *Vaccinium uliginosum*, *Ledum decumbens*, which grow on tussocks formed by *Eriophorum vaginatum*; *Carex rotundata* occurs in herbaceous tier. Mosses such as *Drepanocladus exannulatus* grow in the watery troughs between the mounds. There are also many peatmosses.

In the western part of the subprovince *Larix cajanderi* forms the forest limit, and in the river valleys stands of *Chosenia arbutifolia* are met with. In addition, there is *Betula cajanderi*, and in the south *Betula ermanii.*

The Alaska subprovince of the subarctic tundras

The associations on zonal, mesic habitats in the subarctic tundras of the Alaska subprovince, including also the part east of Mackenzie River as far as Anderson River, are very similar to those in Chukotka. Here, as there, tussocky tundras with *Eriophorum vaginatum* associated with *Carex lugens* are widely distributed. Hultén (1968) and a number of American ecologists (Churchill, 1955; Britton, 1966, etc.) mention also *E. vaginatum* ssp. *spissum* for Alaska. But I follow Porsild's (1957*a*) and other investigators' (Wiggins & Thomas, 1962; Tolmachev, 1966, etc.) opinion that this eastern American cottongrass does not reach to Alaska.

Carex consimilis is also part of the herbaceous associations, and this variant of the tussocky tundras is endemic to this subprovince. It should be mentioned here that most of the authors dealing with the vegetation of Alaska call this sedge *C. bigelowii* Torr. s.l., while following Hultén (1968) who considered *C. bigelowii* a circumpolar species and *C. ensifolia* Turcz. and *C. consimilis* Holm as its subspecies. However, Porsild (1955, 1957*a*) as well as Wiggins & Thomas (1962: 51) and Hultén in his earlier work (1964: 51) distinguish *C. consimilis* as a species of its own, quite well separated from the amphi-atlantic *C. bigelowii* s.str.

The specificity of this subprovince is also accentuated by the occurrence of the American species *Betula glandulosa* in the shrub thickets and by the participation in a number of associations of American grasses, *Calamagrostis canadensis*, etc., and herbs, *Lupinus arcticus*, etc. There is also, as mentioned above (on p. 59), a complete shift in the woody species forming the forest limit.

The vegetation of the subprovince of Alaska has been described by a number of authors (Palmer & Rouse, 1945; Hanson, 1951, 1953; Churchill, 1955; Bliss, 1956; Bliss & Cantlon, 1957; Britton, 1957, 1966; Viereck & Little, 1972; Corns, 1974, etc.). The most extensive information on the composition of the plant associations is found in the form of comprehensive tables published by Hanson, Churchill and Corns. The tussocky tundras with *Eriophorum vaginatum* and *Carex lugens*, sometimes also with *C. consimilis*, seem to be the most characteristic and the most widely distributed. Occasionally there is an admixture of low-growing shrubs, such as *Betula exilis*, *Salix pulchra*, etc., and, with the exception of the northern variant of the tussocky tundras, also of *Alnus fruticosa.*

(Note: After having studied herbarium material from Alaska, S. K. Cherepanov has suggested that what is found here is not the eastern American *A. crispa* s.str., described from Labrador, but actually *A. fruticosa* (cf. also Yurtsev *et al.*, 1972: 769–70).)

In these tundras there are also hyparctic dwarfshrubs such as *Ledum decumbens*, *Vaccinium vitis-idaea* ssp. *minus*, *V. uliginosum* ssp. *microphyllum*, *Empetrum hermaphroditum*, and others. Between the cottongrass tussocks grow green mosses and peatmosses, and on the edges of the tussocks, lichens.

In the southern belt of the subarctic tundras, beside the omnipresent tussocky tundras on level ground with loamy soils, shrub tundras are met with in areas of low mountains and on stony slopes (Hanson, 1953: 122–3), where low-growing *Betula exilis* with an admixture of *Salix pulchra*, *S. alaxensis*, and *S. lanata* ssp. *richardsonii* predominate and *Spiraea beauverdiana* is occasionally met with. In the ground tier there are many dwarfshrubs, such as *Vaccinium uliginosum* ssp. *microphyllum*, *V. vitis-idaea* ssp. *minus*, *Empetrum hermaphroditum*, *Ledum* *decumbens*, *Loiseleuria procumbens*, *Salix phlebophylla*, *S. reticulata*, etc. Typical among the graminoid species are *Carex podocarpa*, *Calamagrostis canadensis*, etc., among the mosses *Hylocomium splendens*, *Drepanocladus uncinatus*, *Ptilidium ciliare*, and among the lichens *Cladonia rangiferina*, *C. sylvatica*, *C. pleurota*, and *Cetraria cucullata*.

On slopes varying from gentle to steep, dwarfshrub tundras are observed up to 200 m altitude with *Vaccinium uliginosum* ssp. *microphyllum*, *Empetrum hermaphroditum*, *Ledum decumbens*, *Vaccinium vitis-idaea* ssp. *minus*, *Loiseleuria procumbens*, *Arctous alpina*, and an admixture of low-growing *Betula exilis*, and *Salix pulchra*, mosses and lichens. On slopes of increasing steepness at low elevation, dwarfbirches, *Betula exilis* and *B. glandulosa*, as well as their hybrids, are widely distributed, forming associations of various density, from open to closed thickets, and height from 0.7 to 1.3 m, associated with willows such as *Salix lanata* ssp. *richardsonii*, *S. pulchra*, and others, which are usually 30–50 cm taller than the birches. The moss carpet is formed mainly by *Hylocomium splendens*. There are many dwarfshrubs: *Vaccinium uliginosum* ssp. *microphyllum*, etc. In openings between them lichens have often developed, e.g. *Cladonia rangiferina*, *C. sylvatica*, *C. cornuta*, *Cetraria cucullata* and *C. islandica* (Hanson, 1953: 119–23).

In brook and river valleys, thickets of *Salix alaxensis*, *S. glauca*, and *S. fuscescens* grow together with some grasses (*Calamagrostis canadensis*, *Festuca altaica*, etc.), herbs, and dwarfshrubs. On well drained slopes, associations of *Alnus fruticosa* with a considerable abundance of *Calamagrostis canadensis* are found. In the more open associations of alder there is an admixture of birches, willows, *Spiraea beauverdiana*, a number of herbaceous species, dwarfshrubs, mosses and lichens. In the southern part of the subprovince, localities are found with tall thickets of *Betula glandulosa*, associated with small amounts of *B. exilis*, alder, willows, and *Spiraea*. *Dryas* tundras are typical of the upper parts of the slopes and on mountain tops at elevations up to 500 m. Some arctic and hyparctic species are also present here.

The mires along the edges of lakes, rivers and brooks and in moist draws are represented by herb–moss associations with *Carex aquatilis*, *C. stans* and *C. rotundata*. Flat-mounded and polygonal mires with large hummocks, overgrown with *Betula exilis*, *Rubus chamaemorus*, willows, and hyparctic dwarfbushes, peatmosses and other mosses, are widely distributed in depressions.

The major part of the area investigated by Corns (1974) does also belong to the southern belt of subarctic tundras. His area is situated east of the Mackenzie River delta, but does not include the lowland on its northeastern side or the Tuktoyaktuk Peninsula. Beside the tussocky tundras, which here are at the eastern limit of their distribution area and already begin to constitute a lesser part of the vegetation, a major role in the vegetation cover is played by tundras with low-growing birches on the summits and gentle slopes of hills. Here, low-growing *Betula exilis* associated with *Salix glauca* s.l., *S. pulchra*, and occasionally with *Alnus fruticosa* dominate, and there are many hyparctic dwarfshrubs as well as mosses and lichens. Along the rivers there are tall (1.5–2 m) shrubs, such as *Salix lanata* ssp. *richardsonii*, *S. alaxensis*, *S. pulchra*, and *Alnus fruticosa*. The latter reaches up to 3–4 m in height in favorable habitats.

The Umiat region described by Churchill (1955) belongs to the middle belt of the subarctic tundras. It covers a rolling plain, stretching northwards from Brooks Range. Here tussocky tundras predominate, with *Eriophorum vaginatum*, usually associated with *Carex lugens*, but sometimes with *C. consimilis*. Churchill (1955) uses the epithet *E. spissum* Fern. (=*E. vaginatum* ssp. *spissum* (Fern.) Hult.) for the cottongrass; the latter is, however, as mentioned above, not found in Alaska. There are also many dwarfshrubs, as e.g. *Vaccinium vitis-idaea* ssp. *minus* and *Ledum decumbens*, often mixed with *Cassiope tetragona*, and plenty of low-grown willows, *Salix glauca* s.l., *S. pulchra*, etc. Prostrate *Betula exilis* is a constant, and sometimes there are scattered specimens of *Alnus fruticosa*. Besides *Cassiope tetragona* and *Salix phlebophylla*, there are admixtures of such arctic species as *Luzula confusa*, *L. nivalis*, *Hierochloë alpina*, and *Poa arctica*. Along brooks and rivers and in gullies on watersheds, thickets of willows, and rarely of alders, are met with, but together with the latter species much *Arctagrostis latifolia* occurs. On hills and the upper part of the slopes on ridges in localities strongly exposed to winds during the winter spotty tundras with *Dryas integrifolia* have developed, in which there is some admixture of low-grown willows such as *Salix pulchra* and *S. glauca* s.l. Polygonal mires are widely distributed.

The absolute elevation of the landscape lowers towards Point

Barrow, where the relief becomes almost flat and the number of lakes and swampy areas increases. With the exception of the area immediately adjacent to Point Barrow, which is referred to the subregion of the arctic tundras where there are no more tussocky cottongrass tundras and *Betula exilis* is lacking, the coastal lowlands belong to the northern belt of the subarctic tundras. There is no more *Alnus fruticosa*, the role of the low-grown shrub thickets in the tussocky tundras is diminished, and the variability and number of the plant associations are decreased (Britton, 1966: 31), while the role of the arctic species is increased.

The fact that it is correct to distinguish Alaska as an area at the subprovincial level is emphasized by its floristic uniqueness. There are a number of endemics and subendemics (*Artemisia comata*, *Erigeron muirii*, etc.), eastern co-differentiating species (*Lupinus arcticus*, etc.) and a large number of differentiating cordilleran species (cf. Yurtsev, 1974*a*).

The forest limit is formed by *Picea glauca* and *P. mariana*, and there are also found *Larix laricina (L. alaskensis)*, *Betula papyrifera*, *Populus balsamifera* and *P. tremuloides*.

The Canadian province of the subarctic tundras

The Canadian province of the subarctic tundras begins east of Anderson River, at the easternmost limit for the distribution of the tussocky cottongrass tundras with *Carex lugens*. The tundras with low-growing *Betula glandulosa* and the hyparctic dwarfshrub tundras with an admixture of this species may be considered endemic for this province. Although *B. glandulosa* is found also in Greenland, it occurs only in the small, southwestern part of the subarctic tundras there, adjoining the southern tip of Greenland, which is situated outside the tundra region. In the dwarfshrub tundras it is, as a rule, substituted by *B. nana*.

The western boundary of this province coincides almost completely with the eastern limit of 'Greater Beringia' in Yurtsev's sense (1974*a*: 49). It is also an important boundary from the point of view of orography and climate as well as paleogeography in connection with the major differences in the Quaternary history of the landscape. The complicated relief of Alaska – the result of mesozoic orogenesis and subsequent processes of uplift, erosion, and partial denudation, glacial excavation, and accumulation – changes east of the Mackenzie River into the region of the Canadian Shield. Along its western edge the mesozoic folds of the Alaskan area turn southeastwards. On the surface of the Shield appear Precambrian, crystalline bedrocks. In its form the Shield reminds one of a gigantic bowl, the rims of which are raised, particularly at the eastern edge, forming the northern part of Labrador, Baffin Island, and the southern part of Greenland, while the central part is depressed, forming the Hudson's Bay synclinal. The western part of the Shield consists of the Laurentian Upland with elevations from 150 to 500 m and a strongly levelled surface as a result of protracted denudation and scouring by glaciers, which has left here not so much accumulated debris as eroded forms of relief. Along the northern coast and around Hudson's Bay there are marine, postglacial sediments. Except for the northern tip of Labrador the climate is strongly continental, although somewhat milder than in eastern Siberia.

While neither Chukotka nor Alaska were completely covered by glaciers during the maximal phase of the Glacial Age, the territories of the Canadian Shield were fully enveloped by an icesheet. According to Ignat'yev (1963: 241), who has reviewed data from foreign literature, the Cordilleras in the west and Baffin Island and Labrador in the east served as centers for the formation of the glacial icesheets. The Cordilleran Icesheet, about 3 km thick, did not spread very far east of the mountain ranges and was built up mainly by the transfer of moisture from the Pacific Ocean. In contrast, the eastern Laurentian Icesheet received much moisture from the atmospheric airmasses originating over the Atlantic Ocean. It therefore spread out extensively. At the period of maximum extension, the two icesheets coalesced, forming a glacial sheet reaching from the Cordilleras to the eastern coast of the continent. The total glaciated areas exceeded by 2.5 times the areas under glacial cover in Europe. The last of the icesheets, the Wisconsin, reached its maximum 20 000–40 000 years B.P.; it disappeared from the continent about 6500 years B.P. The Greenland Icesheet and other major glaciers of the Arctic islands remain as relicts of it. During its retreat the icesheet split into two parts, the Labrador and the Keewatin Icesheets, separated by Hudson's Bay; along the edges enormous ice-dammed lakes were formed, as relics of which the large Canadian lakes still exist. At the same time the streams of meltwater raised the surface of the oceans, which in many places submerged the continent.

fewer than on the west coast. In the less dense willowbrush there is much *Empetrum hermaphroditum* and other hyparctic dwarf-shrubs. On slopes in areas with a 'suboceanic' régime, meadow-like communities are often observed, which have an extremely variable composition (*Alchemilla glomerulans, A. filicaulis, A. alpina, Taraxacum croceum, Polygonum viviparum,* and many others). *Salix herbacea* is common there. Nival meadow-like communities are represented by associations with *Sibbaldia procumbens, Cerastium cerastoides, Gnaphalium supinum,* and others associated with *Salix herbacea,* which dominates in habitats with late-melting snow. *Cassiope tetragona* does not occur in such localities, but *Harrimanella hypnoides* is often found there.

As a consequence of the strongly dissected relief, mires are not often found and occupy only small areas. In the herb–moss associations *Eriophorum scheuchzeri* is usually the dominant herb, sometimes associated with *E. angustifolium. Calliergon stramineum* is the most common moss. The mires consist mostly of flat-topped peat mounds, where the moss–turf of *Sphagnum subnitens, Aulacomnium* ssp., etc. is covered by thickets of *Salix glauca* ssp. *callicarpaea,* or has a cover of hyparctic dwarfshrubs, such as *Vaccinium uliginosum* ssp. *microphyllum, Empetrum hermaphroditum, Phyllodoce coerulea,* etc., with an admixture of *Salix glauca* ssp. *callicarpaea, Carex bigelowii* and other herbaceous species as well as lichens, *Cetraria nivalis, Cladonia mitis,* etc. The cover is not infrequently formed of *Salix herbacea* with which usually *Carex bigelowii* and *Polygonum viviparum* are associated.

Characteristically, *Salix herbacea,* which as already mentioned is more aggressive here, is present in almost all the mire associations. I also refer to the wetlands the halophytic associations at the seashore composed of *Puccinellia phryganodes, Carex glareosa, Stellaria humifusa* or *Carex subspathacea* (Böcher, 1933*b*; Molenaar, 1974, etc.).

Cryophytic associations in the inland areas exposed to föhn winds are formed by *Carex rupestris, Kobresia bellardii,* etc., as described by Schwarzenbach (1960).

The subregion of the arctic tundras

The subregion of the arctic tundras has been distinguished as a special botanical–geographical region by all the investigators of the Arctic. In his zonation of European Russia Trautvetter (1851) named this subregion 'the area of the alpine willows' (he called the subarctic tundras 'the area of the lowgrown birches'). Pohle (1910) used the epithet 'the arctic zone of the tundra region'. Sochava (1933*c*) called it 'the subzone of the arctic non-fruiting dwarfshrub tundras' and Leskov (1947) used the name 'the belt of arctic tundras'. Sochava included this territory in a region of higher rank, 'the arctic belt'. In a physicogeographical zonation he later used the term 'the Arctic' (Sochava & Timofeyev, 1968) for the land area situated north of 'the Subarctic' (Sochava *et al.,* 1972). 'The Arctic' is, according to Sochava, characterized mainly by special circumpolar fratriae of formations (Buks, 1973, 1974; Il'ina, 1975), while the territories of the subarctic tundras are included in different areas characterized by different fratriae. Yurtsev (1966, etc.) has also separated the arctic and the subarctic tundras by a boundary of higher rank, dividing the 'arctic belt' and the 'hyparctic' one. As a basis for this, he used the different origins of the floras in the arctic belt and the hyparctic one (cf. above, p. 22). The boundary between the arctic and the subarctic tundras has been designated by Böcher (Böcher *et al.,* 1968: 11) as the southern limit of the 'high-arctic belt'. He stressed the lack of shrub thickets in the latter belt. Rønning (1969: 29) called it the border between the 'low arctic' and the 'middle arctic', and Young (1971) the border between floristic zones '3' and '4' (with some exceptions).

The border between the arctic and the subarctic tundras oscillates around the 6° C July isotherm. Grigor'yev (1946:6, 70–3) considered that along this border there occurs an essential change in the character of the atmospheric circulation and the radiation balance, which affects all components in the physico-geographical complex. It is also important that when the polar forest border oscillated in postglacial time, it never crossed this border. Paleobotanical data confirm this (cf. Giterman *et al.,* 1968: 235, etc.) and accordingly, the territories of the arctic tundras have remained treeless throughout the Holocene.

The vegetation cover at the transition from the subregion of the subarctic tundras to the subregion of the arctic tundras is subject to essential changes, namely, the type of arctic associations on zonal, mesic habitats differs sharply from the subarctic one, thickets of hyparctic shrubs disappear in the arctic subregion as do nival, meadow-like communities, floodplain meadows, birchbrush on the peat mounds and raised borders of the low centre polygons in polygonal mires. No more open woodland or prostrate krummholz associations are met with. The most important character is the disappearance of the shrub thickets. This trait is well correlated with all the rest and may be considered as the fundamental diagnostic character for drawing the line between the arctic and the subarctic subregions within the tundra region.

Although a number of scientists have drawn boundaries of higher rank between the Arctic and the Subarctic – Pohle and Young between zones, Sochava and Yurtsev between botanical-geographical belts – I shall distinguish the arctic tundras at the level of a subregion of the geobotanical tundra region, where on zonal, mesic habitats the tundra type of vegetation is represented by its arctic subtype as described above (on p. 21). The complete disappearance from the composition of the zonal arctic associations of any admixture of birches is considered as the basic, diagnostic difference from the Subarctic. *Betula nana* (*B. tundrarum* according to the treatment by Perfil'yev and Cherepanov) does occur in some non-zonal, non-mesic habitats within the area of the arctic tundras, but only as a rare, relict plant of no importance for the composition of the vegetation cover. Thus, during my three years of work on the South Island of Novaya Zemlya, I came upon *Betula nana* (*B. tundrarum*) only once on a gentle, southeast exposed slope on the mainland shore of the Rogachev River delta. It grew in the form of a compact, flat cushion on the ground, measuring 20–25 cm in diameter and 5–6 cm in height, and was densely leafy and sterile.

In spite of the fact that the bareness of the ground is always more intense in the subregion of the arctic tundras than in that of the subarctic tundras (cf. the widely developed 'spotty tundras' and – in habitats with a scanty snow cover – the strongly developed polygonal tundras), there are also in this subregion in certain areas tundra associations with a continuous vegetation cover, as for instance in northern Yamal (Mikhailichenko, 1936) and in northwestern Taimyr (Tikhomirov, 1948*b*), etc. In the zonal, mesic phytocoenoses of the arctic, spotty tundras (as also in those tundras in the Subarctic), the root systems of the plants under the bare spots are close under the ground surface (Aleksandrova, 1962, cf. Fig. 19). This appears to be one of the important, diagnostic characters, distinguishing these phytocoenoses

from those in the polar deserts. The first one to point out this character was Perfil'yev (1928).

In the subregion of the arctic tundras the occurrence of the boreal element of the flora is strongly reduced, and so is that of the hyparctic element, at least to a certain degree, although hyparctic species do occur (*Eriophorum angustifolium, Valeriana capitata, Nardosmia frigida,* and others), which penetrate into this zone and are participants in the composition of the plant associations. A number of high-arctic species, which are lacking farther south, appear here, such as *Poa abbreviata, Puccinellia angustata, Ranunculus sabinei, Draba subcapitata, D. oblongata, Saxifraga platysepala,* etc.

Within the limits of the subregion of the arctic tundras, it is possible to distinguish two latitudinal belts, the southern, and the northern belts (cf. Fig. 2).

The southern belt of the arctic tundras

Except where there is a spatial separation in the form of an island (e.g. Novaya Zemlya, etc.), the southern belt of the arctic tundras makes direct contact with the northern subarctic tundras. In the transition zone their associations on zonal, mesic habitats are often similar in composition and structure, although birch species are essentially lacking in the arctic zonal, mesic communities. To a certain extent low growing willow brush is still present, mainly consisting of arctic species such as *Salix reptans, S. arctica,* and Siberian arctic–alpine ones such as *S. sphenophylla,* but also a few hyparctic ones, usually in the form of prostrate, single individuals of, e.g. *Salix pulchra.* Although shrub thickets are completely lacking, it is possible to come across some single low shrubs of species such as *Salix lanata, S. lanata* ssp. *richardsonii,* and *S. arctophila* in swampy localities. Some of the hyparctic dwarfshrubs continue to play an episodic role in the vegetation cover. Thus, e.g., *Vaccinium vitis-idaea* ssp. *minus* is found on Novaya Zemlya as single, sterile individuals in some lichen tundras, and in the Alazeya–Kolyma district it is part of the associations in an arctic variant of the tussocky tundras. *Vaccinium uliginosum* ssp. *microphyllum* penetrates far into the arctic tundras of the eastern Canadian Arctic Archipelago and is also found in arctic Greenland. The peatmosses are well developed in the mires of the southern belt of the arctic tundras; *Sphagnum fimbriatum* is capable of developing big, flat hummocks, *S. squarrosum* of forming carpets, 3–4 m in diameter. In the Kolyma River district of this belt, the peatmosses dominate on the raised borders of the low center polygons in tetragonal bogs (Perfil'yeva & Rykova, 1975). In the Atlantic areas, e.g. on the southern part of Novaya Zemlya, the arctic variant of mires with flat-topped peat mounds is well developed, where on top of the mounds cloudberry brush (*Rubus chamaemorus*) may be found, but most years in a sterile condition (Aleksandrova, 1956).

The northern belt of the arctic tundras

The transition to the northern belt is recognized by the following, basic characteristics: (1) in the zonal, mesic habitats with moderate snow cover associations with semi-prostrate willows (*Salix reptans,* etc.) have disappeared and only dwarfwillows remain, such as *Salix polaris* the stems of which are buried in the moss carpet, as well as a few prostrate types like *Salix nummularia, S. reticulata,* etc. In the northern Canadian Arctic Archipelago and Greenland there is also some creeping *S. arctica;* (2) In non-mesic habitats with scanty snow cover polygonal tundras are widely distributed, where the bare surface (spots, polygons) occupies a considerably larger area than that covered by vegetation, which is confined to net-like strips along the cracks between the polygons. (3) The mires with flat-topped peat mounds have disappeared on Novaya Zemlya, and throughout this circumpolar belt homogeneous herb–moss mires and/or tetragonal mires are absolutely predominant. Besides, a special type of soil ('arctic tundra, slightly gleyified soils'; cf. Karavayeva, 1962: 112, 126–7) has developed under the associations on zonal, mesic habitats. It is different from the more southern types of lightly developed gleyification. Here it is slightly acid (close to neutral) in reaction and has a number of other characteristic traits (Aleksandrova, 1963: 22).

The provinces of the subregion of the arctic tundras

When delimiting the geobotanical provinces in the subregion of the subarctic tundras, a leading role is played by the distribution of associations dominated or characterized by hyparctic or hyparctic–alpine species such as *Betula nana, B. exilis, B. middendorfiii, B. glandulosa, Salix phylicifolia, S. planifolia, S. pulchra, S. alaxensis, S. glauca,*

S. glauca ssp. *callicarpaea, Alnus fruticosa, A. crispa, Eriophorum vaginatum, E. spissum, Carex soczavaeana,* and others. In the subregion of the arctic tundras, however, the decisive role is played by the distribution of associations with dominating or characterizing arctic or arctic–alpine species, such as *Salix polaris, S. arctica, Dryas octopetala, D. punctata, D. integrifolia, Alopecurus alpinus, Deschampsia brevifolia, Cassiope tetragona,* and so on. Although a part of these species have a circumpolar distribution area, their role in the composition of the vegetation cover differs considerably in certain parts of this subregion.

The differences between the provinces in the subregion of the arctic tundras are less well expressed than in the subregion of the subarctic tundras. While in the latter it is possible to distinguish five geobotanical provinces and 15 subprovinces, in the arctic tundras we can only distinguish four provinces and six subprovinces. This major similarity in the vegetation is also reflected in the geobotanical division made by Sochava, who characterized the arctic belt as a single arctic 'fratria of formations' (Il'ina, 1975, etc.), while the subarctic tundras were separated into different regions characterized by different 'fratriae'. The decrease in provincial distinctiveness is, to a considerable extent, related to the fact that the higher the latitude the more uniform is the circumpolar flora (Young, 1971).

In this subregion four geobotanical provinces can be distinguished: the Novaya Zemlya–West Siberian–Central Siberian, East Siberian, the Wrangel Island–West American, and the East American–Greenland provinces (Fig. 17).

Because the vegetation cover at the northern rim of the continents has been studied only to a limited degree and is still insufficiently known, my division into provinces should be considered as preliminary in character.

The Novaya Zemlya–West Siberian–Central Siberian province of the arctic tundras

This province reaches from Novaya Zemlya to the western side of the Olenek Bay. In spite of the differences in the vegetation cover, which increase from west to east, it is united by the wide distribution, especially on zonal, mesic habitats in the southern belt of the subregion, of the arctic variant of the tundras, endemic to this province with its

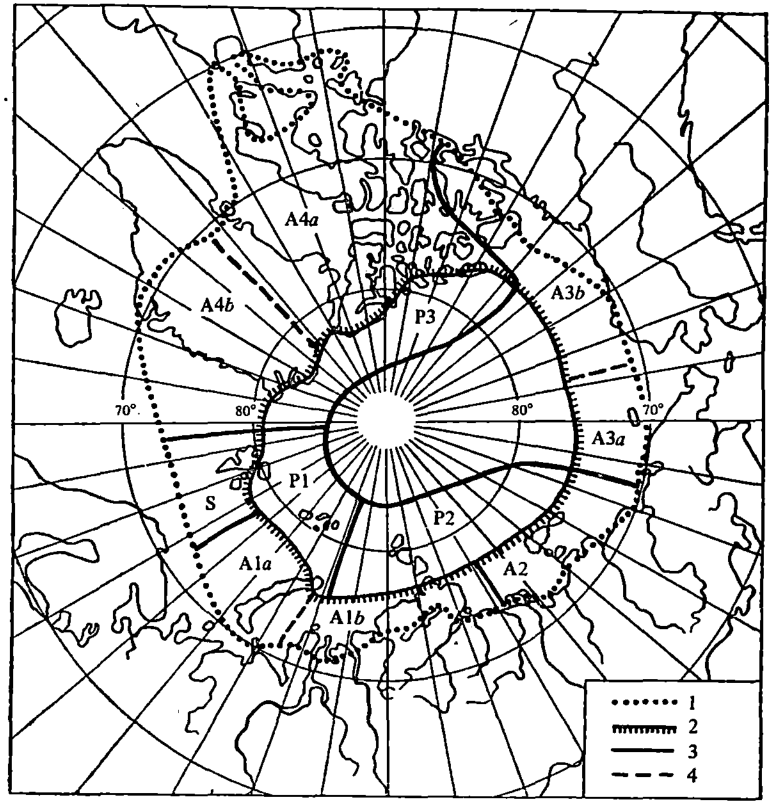

Fig. 17. The geobotanical provinces and subprovinces of the subregion of the arctic tundras and the region of the polar deserts. Southern boundaries of: 1, the subregion of the arctic tundras, and 2, the region of the polar deserts. 3,–, provincial boundaries, 4,–––, subprovincial boundaries. Provinces of the Arctic tundras: A1, the Novaya Zemlya–West Siberian–Central Siberian province with: A1*a*, the Novaya Zemlya–Vaigach, A1*b*, the Yamal–Gydan–Taimyr–Anabar subprovinces. A2, the East Siberian province; A3, the Wrangel Island–West American province with: A3*a*, the Wrangel Island, A3*b*, the Cape Barrow and the southwestern Canadian Arctic Archipelago subprovinces; A4, the northeastern Canadian–North Greenland province with: A4*a*, the northeastern Canadian-northwestern Greenland, A4*b*, the northeast Greenland subprovinces. S, the Spitsbergen autonomous district. Provinces of the Polar Deserts: P1, the Barents; P2, the Siberian; P3, the Canadian.

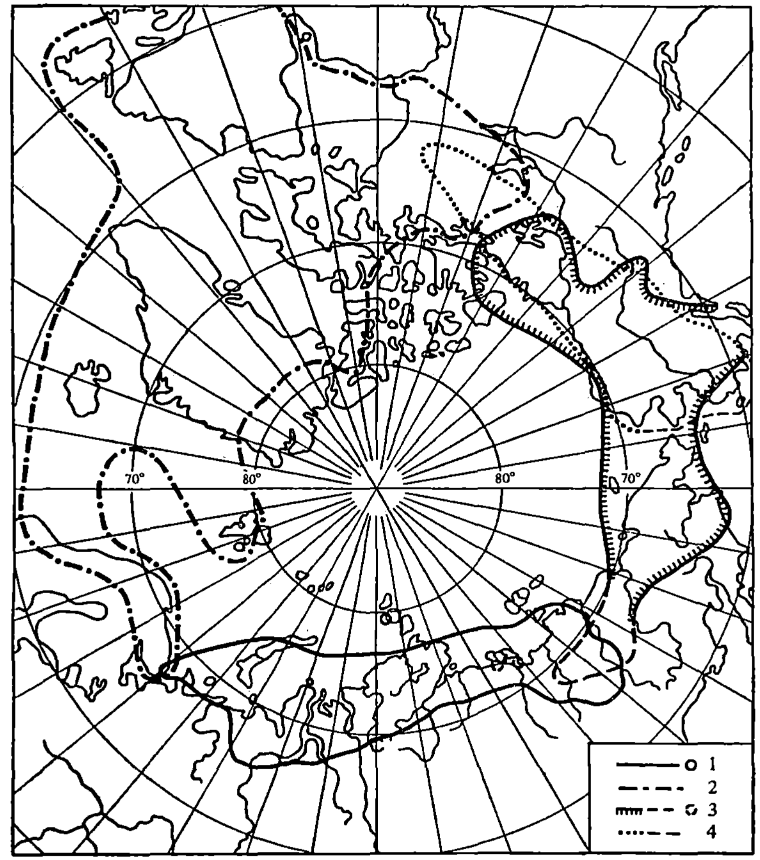

Fig. 18. The distribution areas of 1, *Carex ensifolia* ssp. *arctisibirica* Jurtz., 2, *C. bigelowii* Torr. s.str., 3, *C. lugens* Holm, and 4, *C. consimilis* Holm. According to Porsild, 1957*a*, Hultén, 1964:51, Yegorova, 1966.

abundance of *Carex ensifolia* ssp. *arctisibirica.* It differs from the subarctic form of the tundras in the absence of *B. nana,* or *B. exilis.* Towards the west, starting in Spitsbergen, associations with *Carex ensifolia* ssp. *arctisibirica* disappear as this species drops out of the flora (Fig. 18). In the East Siberian province of the arctic tundras *Carex ensifolia* ssp. *arctisibirica* continues to occur as far east as the Indigirka River, but its activity at that latitude decreases sharply, although farther south it continues to be abundant as far as the Lena River and, locally, in the mountain areas of northern Verkhoyansk Mountains.

Description of the

Ecoregions of the United States

Compiled by Robert G. Bailey

Prepared in cooperation with the U.S. Fish and Wildlife Service for use with the map Ecoregions of the United States

FOREST SERVICE • U.S. DEPARTMENT OF AGRICULTURE
Ogden, Utah May 1978

Bailey, Robert G.
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This manual briefly describes and illustrates the nation's ecosystem regions as shown on the 1976 map, "Ecoregions of the United States." The description of each region includes a discussion of land-surface form, climate, vegetation, soils and fauna.

Contents

Introduction

Public land management agencies are increasingly involved in regional and national long-range planning and in efforts to classify all lands according to their capabilities and availability to produce goods and services in a balanced national program. During the past few years, these agencies have generally recognized the need for a comprehensive system for classifying ecosystems as an aid to achieving quality land management.

Regional variations in climate, vegetation, and landform are important in the development of ecosystems; and, often, different regions have very different management problems. For this reason, it is important to recognize regional differences at the highest level in the classification. This regionalization facilitates (1) planning at the national level, where it is necessary to study management problems and potential solutions on a regional basis; (2) organization and retrieval of data gathered in a resource inventory; and (3) interpretation of inventory data, including differences in indicator plants and animals among regions.

A map titled "Ecoregions of the United States," published in 1976, shows an initial attempt to systematically divide the country into ecosystem regions. This map, along with a brief narrative that described the approach and development of the system, was prepared by the Forest Service for the Interior Department's Fish and Wildlife Service as an aid in its National Wetlands Inventory. This map is now being used in making assessments required by the 1980 Resources Planning Act and in the Roadless Area Review and Evaluation (RARE II) program.

The supporting descriptions of the areas shown on the map are first published here. They make the meaning of the map clearer and further explain the principles of the classification system. The objective has been to provide a broad synthesis of our current knowledge about the ecosystem geography of the country that may be a useful reference for persons who desire an overview on a comparable basis.

This publication gives, for each province, a brief description of the dominant physical and biological characteristics, under five headings: land-surface form, climate, vegetation, soils, and fauna. The descriptions are based on information compiled from many sources. The principal ones are listed in Selected References. Land-surface form is described using the terminology and classification of E. H. Hammond (1964). Climate descriptions are based largely on Köppen's classification, summarized in Appendix 1. Soil information is given by naming the principal soil orders of the Soil Taxonomy (Soil Survey Staff 1975).

The approximate area of each province and section, and the proportionate extent of each in the United States are listed in Appendix 2. The Yukon Parkland Province (1310) has been deleted because it was felt to be an unrealistic and arbitrary division of interior Alaska. All land formerly shown on the map as being in the Yukon Parkland is now shown in the Yukon Forest Province.

Dr. Charles B. Hunt reviewed the descriptions and made many helpful suggestions. Further revision of both map and descriptions will be required as new information becomes available and as improved methods for organizing and presenting information are devised.

1000 Polar Domain

Climates of the polar group, located at high latitude, are controlled chiefly by polar and arctic air masses. As a group, these climates have low temperatures, a severe winter season, and only small amounts of precipitation. Maximum precipitation in all the polar climates comes in summer. In areas where summers are short and temperatures are generally low throughout the year, temperature efficiency rather than effectiveness of precipitation becomes critical in influencing plant distribution and soil development. Two major divisions have been recognized and delimited in terms of temperature efficiency — the tundra and the subarctic (taiga).

1200 Tundra Division

The northern continental fringes of North America from the Arctic Circle northward to about the 75th parallel lie within the outer zone of control of arctic-type air masses. These conditions produce the tundra climate, that Köppen designated by symbol *ET*. Average temperature of the warmest month is colder than 50°F. (10°C.) but warmer than 32°F. (0°C.).

The tundra climate has a very short, cool summer and a long, severe winter. At most only 188 days in the year have a mean temperature warmer than 0°C., and sometimes these are as few as 55. Precipitation is light, often less than 8 in. (200 mm.), but since the potential evaporation is also very low, the climate is humid.

Vegetation on the tundra consists of grasses, sedges, and lichens, with willow shrubs. Traced southward the vegetation changes into birch-lichen woodland, then into the needleleaf forest. In some places, a distinct tree line separates the forest from tundra. Köppen used this line, which coincides approximately with the 50°F. (10°C.) isotherm of the warmest month, as a boundary between subarctic and tundra climates.

The soil particles of tundra are produced almost entirely by mechanical breakup of the parent rock and have suffered little or no chemical alteration. Inceptisols with weakly differentiated horizons are dominant. Continual freezing and thawing of soil moisture has disintegrated the soil particles. Like the soils of the northern continental interior, soils of the tundra are affected by the permanently frozen condition called permafrost. The permafrost layer is more than 1,000 ft. (300 m.) thick over most of this region; seasonal thaw reaches only 4 to 24 in. (10-60 cm.) below the surface.

Geomorphic processes have a distinctive pattern in the tundra regions, and a variety of curious landforms results. Under a protective sod of small plants, the soil water melts in summer producing a thick mud which may flow downslope to create bulges and terraces and lobes on slopes. The freeze and thaw of water in the soil sorts the coarse particles and gives rise to patterned ground with such features as stone rings, stone polygons and stone stripes. The coastal plains have numerous lakes of thermokarst origin, formed by melting of ground ice.

1210 Arctic Tundra Province

Northern Arctic coastal plain, 68,900 sq. mi. (178,500 sq. km.)

Land-surface form. — The north coast of Alaska is a broad, level plain, generally less than 1,000 ft. (300 m.) in elevation. Rolling foothills rise near the Colville River and gain altitude southward into the Brooks Range. The entire province is under continuous permafrost to depths of 2,000 ft. (600 m.) in some areas. In summer, thousands of lakes and marshes dot the plain.

Climate. — The severe Arctic climate reaches temperatures of -60°F. (-51°C.) in winter. Average annual temperature is only 10°F. (-12°C.) to 20°F. (-6°C.). Precipitation is very low throughout the year; average annual precipitation is only 7 in. (180 mm.). The extremely northern location of this province subjects it to great differences in amount of sunlight received at various times of the year. In summer the sun remains above the horizon from only 2 to as many as 85 days depending on the latitude; in winter it can remain below the horizon for as long as 67 consecutive days. All sunlight is received at oblique angles that average 41°. The growing season averages only 2 weeks per year.

Vegetation. — Permafrost limits the rooting depth of plants and forces surface water drainage; this creates extensive marshes and lakes. Cottongrass-tussock, the most widespread vegetation system in the Arctic, is associated with sedges, dwarf shrubs, lichens, mosses, dwarf

Watersedge tundra of the Arctic Tundra Province on the Arctic coastal plain of Alaska. (U.S. Fish and Wildlife Service.)

birch, Labrador-tea, and cinquefoil. These highly productive systems produce 500-1,000 (227-454 kg.) pounds/acre, and are important sources of food for caribou and waterfowl. Several forbs flower brightly in the short summer.

Soils. — The soils are wet, cold Inceptisols that have weakly differentiated horizons. Soils occupying south slopes and low moraines are well drained and loamy with permafrost and ice features. They are underlain by coarse outwash and till. Localized areas of poorly drained clayey soils occupy uplands. Soils of the lowlands are deep, wet, and silty. There is no surface water in winter and only moderate flows in the summer. Supplies of ground water are very limited.

Fauna. — Mammals of the Arctic include brown bear, wolf, wolverine, caribou, Arctic hare, mink, weasel, and lemming. Ptarmigans, ravens, hawks, and open country owls are common. Shore and lake areas are rich habitat for millions of migrating waterfowl and shorebirds during the summer months. Polar bear, walrus, and Arctic fox are common on the ice pack and coastal areas during the winter. Gyrfalcon have also been seen on sea ice.

1220 Bering Tundra Province

Seward Peninsula, Bering Sea and Bristol Bay coastal plains, 86,700 sq. mi. (224,600 sq. km.)

Land-surface form. — The Bering Tundra is a western extension of the Arctic coastal plain, a broad lowland area rising gradually to the eastward. General topography is less than 1,000 ft. (300 m.) in elevation, broken in places by small mountain groups that rise 2,500-3,500 ft. (800-1,100 m.). Standing water is present in thousands of shallow lakes and marshes along the coast. Two large braided rivers, the lower Yukon and Kuskokwim, flow out of the province to the southwest.

Climate. — The Bering Tundra climate is less severe than that on the Arctic slope but it also has cold winters and warm summers. Annual precipitation averages 17 in. (430 mm.). Temperatures range from 90°F. (32°C.) to -70°F. (-57°C.). Permafrost is continuous under most of the area.

Vegetation. — Vegetation along the wet coastal areas is chiefly sedge and cottongrass; woody plants grow on higher sites. Birch-willow-alder thickets interspersed with alpine tundra vegetation are extensive on the Seward Peninsula and in transition zones between the beach and forest. The lower Yukon and Kuskokwim valleys are dominated by white spruce, mixed with cottonwood and balsam poplar. It is a tall, relatively dense growth, with dense undergrowth of thinleaf alder, willow, rose, dogwood, and various species of berry bushes.

Soils. — Coastal soils are wet, cool, Inceptisols over silt, sand, and marine sediments. The lower Yukon and Kuskokwim valley bottoms have pockets of Entisols with no soil horizons. Ground water throughout the area is limited, but some is available in the major river valleys. Surface water ceases to flow in winter on the Seward Peninsula, but flows continuously further south.

Fauna. — River bottom lands provide excellent habitat for furbearers, game birds, and moose. Upland and coastal areas support brown and black bear, wolf, wolverine, coyote, caribou, reindeer, snowshoe hare, red fox, lynx, beaver, moose, squirrels, mice, weasel, mink, and marten. Along the northern Bering Sea coast, polar bear, walrus, and Arctic fox are occasionally found. The coastal areas provide extensive and excellent habitat for migrating waterfowl and shorebirds. Other bird species in the area include ospreys, falcons, grouse, ravens, golden eagles, and various hawks and owls.

Highland Provinces

M1210 Brooks Range Province

Northern Alaska, 53,300 sq. mi. (138,000 sq. km.)

Land-surface form. — The Brooks Range is a northern extension of the Rocky Mountain system and extends 600 mi. (970 km.) westward from Canada to the Chukchi Sea. Its rugged mountains reach elevations of 9,000 ft. (2,700 m.) in the east and decrease to 3,000 ft. (900 m.) in the west. Broad U-shaped valleys and morainal topography show evidence of glaciation. A series of rolling plateaus and low mountains, the Arctic foothills, borders the coastal plain to the north.

Climate. — The climate of the Brooks Range is similar to that of the Arctic coastal plain, but precipitation increases at the higher altitudes and at the east end of the range. Precipitation averages 7 to 15 in. (180-390 mm.), but drainage is rapid because soils have low holding capacity and steep slopes. Summer temperatures reach 90° to 100°F. (32° to 38°C.), but winter temperatures drop as low as -75°F. (-60°C.). Since the province lies above the Arctic Circle, it experiences several days of 24-hr. sunlight in June, and several sunless days in December.

Vegetation. — In the higher alpine areas, plant cover is discontinuous over barren rock. It consists chiefly of low mats of such herbaceous and shrubby species as dwarf arctic birch, crowberry, Labrador-tea, arctic willow, resin birch, and dwarf blueberry. Lower elevations may be covered by a very productive mat of sedge and shrub that is valuable as forage for caribou. Cottongrass, bluejoint, mosses, dwarf willow, dwarf birch, Labrador-tea, and bistort are common. Regeneration of most species is extremely slow; some mosses require more than 60 years to recover from disturbance.

Soils. — The mountains are underlain by folded and faulted limestone, the foothills by various sediments. Soils are rocky and poorly developed. Inceptisols cover the lower slopes. Glacial and alluvial deposits occur in the valleys and at the base of the mountain slopes. Permafrost is continuous under the entire area.

Fauna. — The Brooks Range is an important big game area in Alaska and supports brown and black bear, wolf, wolverine, caribou, and Dall sheep. Smaller mammals include marmot, red and Arctic fox, ground squirrel, lemming, and pika. Raptors prominent in many areas include golden eagles, marsh hawks, gyrfalcons, snowy and other open country owls. Brooks Range is an important resting area for migrating waterfowl and songbirds during the summer.