Fig. 1. *Arctophila fulva* (Trin.) Anders. in a shallow pond.

Photo: A. I. Zubkov

Fig. 2. A fragment of *Dryas octopetala* tundra.

SOME REGULARITIES IN THE DISTRIBUTION OF THE VEGETATION IN THE ARCTIC TUNDRA*

V. D. Aleksandrova†

THE necessity for dividing the tundra area into subzones had been recognized in the nineteenth century, and during that century and at the beginning of the twentieth it was frequently mentioned by Baer, Ruprecht, Schrenk, Tanfiliev, and Pohle. Trautfetter (1851) showed on the map of European Russia a "tundra region" and subdivided it into two districts: that of "alpine willow", which approximately corresponds to the present "arctic tundra" subzone, and that of "dwarf birch", which approximately corresponds to the present "typical (or moss and lichen) tundra" and "dwarf shrub tundra" subzones (*see* Phytogeographical Map of the U.S.S.R., Scale 1:4,000,000, Acad. of Science of the USSR Press, Leningrad, 1956). It was not until 1916 that Gorodkov in his classic "An attempt to divide the west Siberian lowland into phytogeographical districts" (Gorodkov 1916) provided the first division of the large northern area between the Urals and the Yenisey River into well-defined phytogeographical districts. Among them he recognized and described the "arctic tundra" subzone, which there includes the northern parts of the Yamal and Gydan peninsulas and borders in the south on the "typical tundra" subzone. The term "arctic tundra subzone" was applied to the northernmost floristic subzones in the USSR also by Berg (1930), but he did not show their boundaries on account of lack of data.

In the early 1930's many workers tackled the problem (Andreev 1932, Gorodkov 1933, Reverdatto 1931, Sambuk and Dedov 1934, Sochava 1933a, 1933b, 1934, and Tsinzerling 1932). The majority of these writers used the terms "arctic" or "polygon" tundra. The vegetation zones for the whole "Far North" of the U.S.S.R. were first delimited by Gorodkov (1935). He recognized at the same time that the northernmost part of the continent and the islands in the Arctic Ocean constitute a disinct geographic and vegetation zone, the so-called snow zone, which he divided into the two subzones: "desert-glacial" and "arctic desert". Consequently, a part of the region included in the arctic tundra subzone was now considered to belong into the arctic desert subzone. This was a further step toward a detailed classification of the vegetation of the "Far North".

* Authorized revision by the editor of the author's translation of her article "Nekotorye zakonomernosti razmeshchenya rastitel'nogo porkrova v arkticheskoy tundre" in Problemi severa, Ak. Nauk SSSR. 1:173-87, 1959.

† Present address: Komarov Botanical Institute, Ul. Popova 2, Leningrad 22, U.S.S.R.

According to Gorodkov the arctic tundra subzone is characterized by the following features: (1) absence of shrub communities due to the severity of the climate, the short growing period, and the extreme variation in the depth of the snow cover; (2) occurrence of dry Dryas-moss communities on the sufficiently drained clayey soils, which are however replaced over large areas by barren polygon tundra, especially in situations exposed to intense wind action and with consequently very thin snow cover; (3) the occupation of a large part of the area by arctic bogs, chiefly sedge-moss marshes; (4) the small differences between the vegetation of the uplands and that of river valleys, due to the short periods of inundation in the latter and the shallowness of the active layer.

This characterization by Gorodkov is excellent. It clearly recognizes the fundamental peculiarities of the vegetation, which apply to the subzone as a whole despite the wide regional variations and it points out the differences between this subzone and the typical tundra subzone to the south and the arctic desert subzone to the north.

Important contributions to the division of the tundra into subzones and to the definition of the boundaries of the subzones were made by others, for instance, by the investigations by Andreev in the Yamal Peninsula and in the northern parts of the European tundra (Andreev 1935, 1938, 1947, and (1950), by Zubkov in Novaya Zemlya (Aleksandrova and Zubkov 1937), Govorukhin in the northern parts of the European tundra and the arctic Urals (Govorukhin 1954, 1957), Leskov in the northern part of the European continent and other areas (Leskov 1947), Igoshina in the arctic Urals (Igoshina 1933; Andreev, Igoshina, and Leskov 1935), Tikhomirov (1948a, b) in the Taimyr Peninsula, Sheludyakova (1938) in the north of the Yakut Republic, and others.

The arctic tundra subzone has characteristic zonal features, which were described by Gorodkov. Nevertheless, this subzone is by no means homogeneous over its vast extent. Variations are caused by differences in the history of its geomorphology, climatic conditions, relief, and soil substratum. One finds such contrasts as those between Wrangel Island, which was never glaciated and has a rich and ancient flora, the Taimyr Peninsula with a decidedly continental climate, and Novaya Zemlya, which was several times overrun by ice and has a pronounced maritime climate and a very youthful flora, etc. Gorodkov was able to distinguish five provinces within the arctic tundra subzone of the U.S.S.R. in 1935. Leskov, in co-operation with Gorodkov, drew up a division of the tundra zone of the U.S.S.R. into phytogeographical districts and was able to distinguish eleven different provinces in the arctic tundra "belt" (Leskov 1947).

The vegetation of the arctic tundra subzone has by no means been adequately investigated. Besides comparatively well-studied areas such as Wrangel Island (Gorodkov 1943, 1946, 1958a, b) and the northern part of the Yamal Peninsula (Gorodkov 1916; Andreev 1935, 1938) we have others, e.g., the region between the Yana and Indigyrka rivers, where no botanical investigations have been made. In contrast the South Island of Novaya

Zemlya, considered below, is one of the most intensively studied areas (Baer 1838; Zubkov 1932, 1935; Regel 1932, 1935; Aleksandrova 1937a, b, 1945, 1956; etc.).

The peculiar character of the flora of Novaya Zemlya can be explained by the interaction of three factors: (1) the strictly maritime climate, (2) the youthfulness of the flora and geomorphology, (3) the ruggedness of the landforms and the prevalence of stony ground.

In winter the weather of Novaya Zemlya is under the influence of the Icelandic cyclone from which a trough of low pressure extends eastward across the islands. The arctic front, which separates the cold arctic air masses from the warmer maritime air, tends to lie along this trough. These features explain why Novaya Zemlya has comparatively high winter temperatures (the average temperature for March, the coldest month, at Malye Karmakuly is only –15.5°C.) and frequent long periods of high winds. The circulation, which in itself is strong and vigorous, becomes modified and intensified by the mountain chains across its path and thus gives rise to the well-known "bora" of Novaya Zemlya (a katabatic wind, similar to the cold wind of the same name of the northern Adriatic). In spite of the relatively high temperatures, the winter climate of the islands is extremely severe. In order of climatic rigour Malye Karmakuly stands first in the Soviet Arctic: the severity of the climate, calculated according to Bodman's formula (Vize 1940) is 6.1 for the winter and 4.0 for the whole year.

In summer the position of the cyclone shifts to the continent. This shift causes the air over the Arctic Ocean to move toward the mainland, and Novaya Zemlya comes under the influence of cold arctic air masses, which explains why the summers are cold (the average temperature for the warmest month at Malye Karmakuly is 7.0°C.), windy, with sudden changes of the weather, frequent drizzle and fog, and high relative humidity. The absolute minima for every month lie below the freezing point and thus frost is liable to occur in any month. In winter the absolute maxima lie above the freezing point and there is the possibility of a thaw in any month. The cold summers, the strong winds, the great variations in the depth of the often inadequate snow cover, all these peculiarities of the climate exert a profound influence on the vegetation of the area.

Some features of the vegetation of Novaya Zemlya are in large measure due to the youthfulness of the flora. There were no refugia for the preglacial plant species on the islands since during the maximum glaciation their whole area was covered with ice and there was also a maritime transgression of considerable magnitude. The youthfulness of the flora has been demonstrated convincingly by many investigators (Tolmachev 1922, 1930, 1931, 1936; Lynge 1923, 1928; Steffen 1928; and others). Tolmachev asserted that the main body of the flora is of interglacial origin (Tolmachev 1936).

The opinion held by Krechetovich (1946) and Oksner (1946) that Tertiary relicts exist in Novaya Zemlya is undoubtedly wrong since it is incompatible with glacial history and contradicted by the present flora. Recently the age of high coastal marine terraces has been determined more accurately

(Zagorskaya 1959) and it has been proved that they were formed during the inter-glacial marine transgression. This has led to the realization that the flora of Novaya Zemlya is much younger than Tolmachev thought and that plants did not recolonize the area until late-glacial or post-glacial times.

The youthfulness of the flora explains the almost complete lack of endemics; the islands have only three endemic species that all belong in *Taraxacum,* a genus well known for its polymorphism and capability of producing new forms rapidly. The youthfulness of the flora may also account for peculiarities in the distribution of some plants. The differences between the floras of the east and west coasts are well known (Kjellman 1882, Steffen 1928, Tolmachev 1936). On the east coast several East-Siberian species are found, as for instance *Lagotis stelleri, Minuartia macrocarpa, Erysimum pallasii,* which are absent from the west coast. At the mouth of the Savina River, which runs into the Kara Sea, *Sieversia glacialis* was found (Aleksandrova 1935), which does not occur on the west coast. Such an excellent observer as Tolmachev did not find this species around the east end of Matochkin Shar and its absence from there is unquestionable. It is thus confined to a small part of the Kara Sea shore of the South Island. We can assume that *Sieversia glacialis* reached Novaya Zemlya only recently. It is possible that its seeds were transported by wind during the winter across the ice-covered Karskye Vorota (Kara Strait) and Kara Sea (on the distribution of arctic plants by wind see Tikhomirov 1951).

The youthfulness of the flora also explains the absence of *Lloydia serotina* and the nearly complete lack of ericaceous shrubs, which are so common in Greenland, for instance. This lack had already been pointed out by Baer (1838). That the flora of the islands is very young is obvious, since it came into existence only recently (on a geological time scale), and its development is still going on.

Lynge (1928) wrote: "On the whole it is impossible to avoid the impression of a young flora in Novaya Zemlya. It is very probable that the flora would have been richer if it had been older."

It is an important fact that during the post-glacial thermal maximum, when a considerable northward shift of the tree line took place (Tikhomirov 1941, Zubkov 1948), no trees reached Novaya Zemlya. This is proved by the complete lack, at least north of the 71st parallel, of any remains of quaternary tree wood (except drift wood). Apparently shrub tundra with stands of willows and hummocky peat bogs prevailed in Novaya Zemlya during the post-glacial thermal maximum. The remains of quaternary peat bogs have been observed by several investigators (Zubkov 1932, Kudryashev 1925). The author saw them not only on the western, but also on the eastern side of the South Island. Such species as *Vaccinium uliginosum, V. vitis-idaea, Pyrola grandiflora, Betula nana,* and *Comarum palustre,* which are rare, always sterile and occur only in isolated localities, and perhaps also *Rubus chamaemorus,* seem to be relicts from the post-glacial thermal maximum in Novaya Zemlya.

The most conspicuous features of the Novaya Zemlya landscape are the prevalence of strong relief and the wide distribution of stony ground. The whole aspect of the vegetation is strongly influenced by them and this explains why many authors (the first was Baer) raised the question whether tundra exists at all in Novaya Zemlya. The cause for differences in opinion is mainly the lack of sufficiently drained (within the limits of climatic possibilities) upland areas of clayey soils. Many explorers who happened to land in a region where, as at the Kostin Shar, diabase and limestone predominate, did not see a sufficiently developed zonal vegetation (the "climatic climax"), which is, however, well represented in the regions of the strand flats. In many instances the investigators did find the vegetation types of stony ground (various types of lithosere), alpine tundra or polar desert as precursors of the next vegetation zone ("preclimax") or vegetation affected by high altitude.

Another reason for the differences in interpretation was the vagueness of the term "tundra". Only during the nineteen-thirties did the study of the tundra in Russia become established as a special branch of geobotany. Since then there has been so much progress in the theory of classification, the terminology of vegetation units (Sukachev, Shennikov, Lavrenko, Sochava, Ilynsky, and others), and the taxonomy of the arctic vegetation constituting them that the question as to what types of vegetation occur in Novaya Zemlya is much more amenable to correct solution.

There are three types of vegetation units in the South Island of Novaya Zemlya: tundra, bog, and polar desert. There is also some feebly developed aquatic shore vegetation consisting of stands of *Arctophila fulva* and *Hippuris vulgaris*. The submersed vegetation consists almost exclusively of algae (Flerov 1925) and mosses *(Drepanocladus exannulatus, Calliergon sarmentosum,* and *Sphagnum squarrosum)* occur only rarely (Fig. 1).

The principal zonal type (the "climatic climax") of vegetation is the tundra that has developed in upland areas. The author considers as tundra those communities on mineral substrata that are composed predominantly of mosses, fruticose and foliaceous lichens, arcto-alpine dwarf shrubs, and herbaceous perennial xero- and meso-microthermophytes (it can be said that all plants of the South Island of Novaya Zemlya are microthermophytes on account of its cold soils. They can be subdivided according to their moisture requirements into xero-, meso-, and hydro-microthermophytes. In addition there is a group of halophytic microthermophytes).

The areas of tundra are accompanied by bogs that develop in the wettest sites (azonal type of vegetation, the "subclimax"). To the bogs belong those plant communities that develop on a peat substratum. Their chief constituents are mosses and perennial herbaceous hydro-microthermophytes, and more rarely (on low peat mounds) also lichens and dwarf shrubs (Fig. 2).

The third type of community is that of the polar desert. It is extrazonal ("preclimax") in the South Island of Novaya Zemlya. It never occurs under normal (average) conditions in the upland areas, only either in wind-swept areas that have a very thin snow cover or at high altitudes in the mountains.

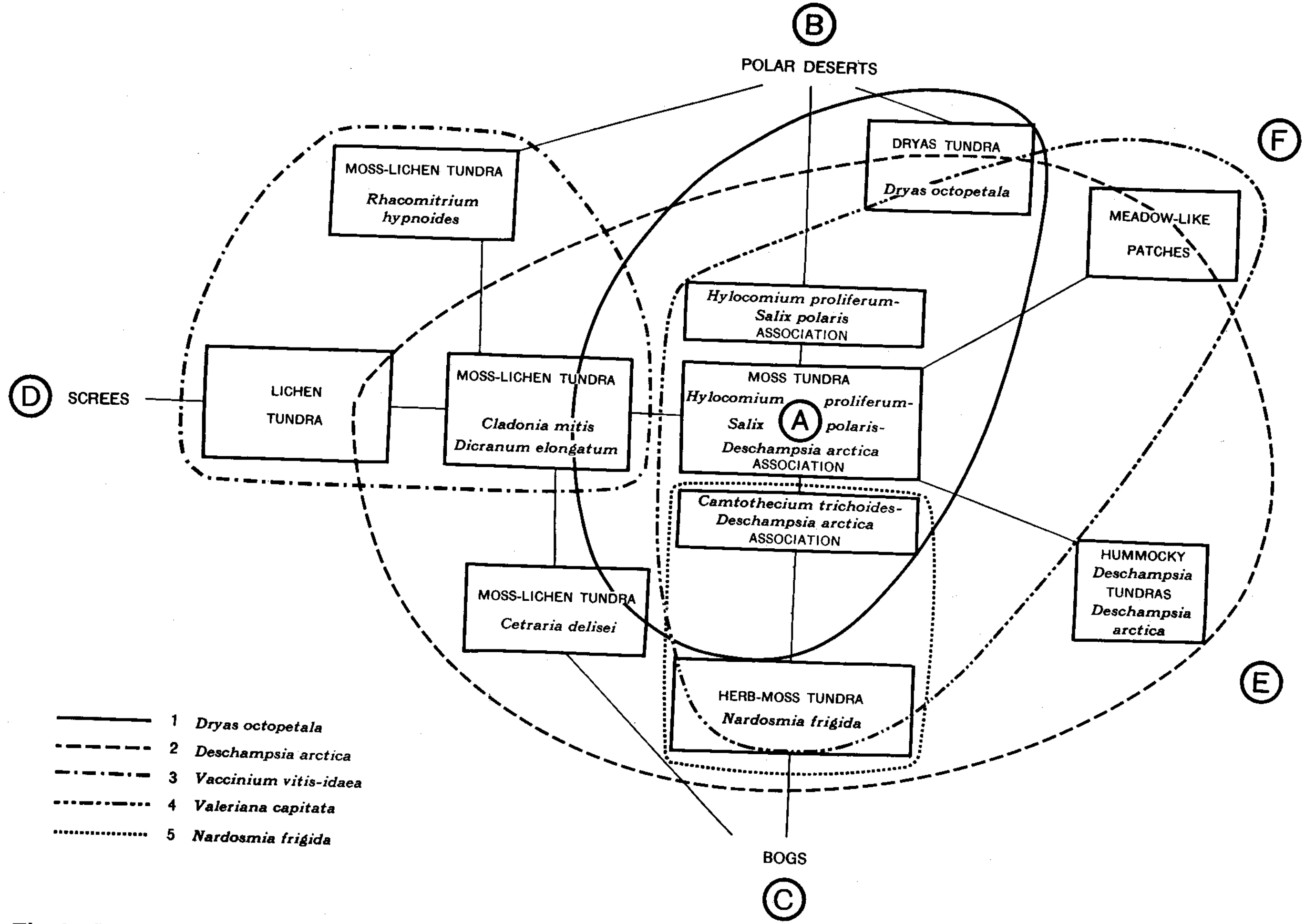

Fig. 3. Diagram showing the ecological ranges of the tundra plant associations and the ecological areas occupied by some plants. *Note:* for *Camtothecium* read *Camptothecium*.

To the polar desert communities belong (Aleksandrova 1956) the micro-communities composed of crustaceous lichens, patches of mosses (*Rhacomitrium hypnoides, Dicranoweisia crispula, Grimmia apocarpa, Andreaea petrophila,* etc.), the representatives of some other tundra species that grow as widely scattered individuals, and the fragments of tundra communities that are confined to the depressions of the microrelief.

The plant communities of the arctic tundra subzone are here near the ecological limit of their distribution. Only in the bogs is the plant cover closed. In the upland areas it is interspersed with patches or polygons of bare ground that occupy from 10 to 65 per cent of the surface. The moss or moss-lichen patches appear as bands that surround the polygons in the form of nets. Wherever even a slight deterioration occurs (through stronger denudation, increasing stone content of the soil, shortening of the growing period in snow patches, etc.) the continuity of the plant cover is destroyed and it finally disintegrates into separate patches.

Where conditions become most unfavourable a further change may be observed; the tundra communities disappear completely and are replaced by the scattered plants of areas of shattered rocks and of polar desert, plants that belong mostly to the crustaceous lichens. The loss of continuity of the plant cover is accompanied by a change in its structure, layers are no longer recognizable and the individual plants form a horizontal (one-layered) mosaic.

In the tundra communities of the upland regions two or three layers can usually be distinguished, a layer of moss, one of fruticose lichens, and one of herbaceous plants, or of a combination of these and dwarf shrubs. The layers are poorly developed and dwarfed, since the total height of the vegetation is not more than 10 to 20 cm. The upper herbaceous layer is very sparse and the horizontal mosaic is well developed. It is closely dependent on the distribution of the main constituents of the patterned ground (stone rings, stone stripes, etc.), and on the microrelief. The severer the environment the closer is the response of the vegetation to the slightest change in the microrelief. Because the high permafrost table impedes drainage, every slight depression leads to the formation of bog; on the elevated portions of the relief denudation factors find their fullest expression. The plant mosaic is best developed on stone polygons ("stone nets").

Correlating the various tundra formations of the South Island of Novaya Zemlya with environment factors and arranging them in a diagram (Fig. 3) it will be found that the centre should be allotted to the moss-tundra, which is best adapted to the climatic conditions and most typical of the upland areas with clayey soils (the "climatic climax" of the area). Its most characteristic association consists of the moss *Hylocomium proliferum,* the shrub *Salix polaris,* and the grass *Deschampsia arctica.*

Along the line A — B are shown the changes that occur when one moves to more open sites, where the denudation forces are stronger; these sites are drier and have a thinner snow cover. The trend is here to another type of vegetation, that of the polar desert.

The line A — C leads to wet, poorly drained sites with heavier snow cover. Along it the succession tends toward the development of bog.

The line A — D shows the effect of the increase of the rock content of the soil. With an increasing number of stones the vegetation type changes from moss tundra on clayey soil to the moss-lichen tundra on stony-clayey and patterned ground and finally to the vegetation on scree and rockslopes with a predominance of crustaceous lichens. When weathering of the screes and rocks takes place the succession is reversed (from D to A).

Along the line A — E the amount of solifluction increases and one finds a succession from moss tundra to hummocky *Deschampsia* tundra. This transition occurs when the water-logged clayey soil slides downhill and the continuity of the plant cover is destroyed. Under these conditions a more stable community is formed, consisting of tufts of *Deschampsia arctica* and mosses, which together cover about 50 per cent of the ground, with the grass accounting for two-fifths of the cover.

Along the line A — F are indicated the changes that are caused by lemming burrows and fox mounds (the "disclimax") leading eventually to the formation of meadow-like patches. The enriching of the soil with nitrogen stimulates the development of a dense cover of grasses and herbs at such spots (the "nival" meadow-like patches that develop in more southerly tundras on the sites of snow patches are absent from the South Island of Novaya Zemlya, where no closed plant cover can develop on snow patches on account of the drastically shortened growing period).

It is of interest to compare the author's scheme with those devised for other tundra areas. For the tundras of the Kolsky Peninsula, which are according to their origin closely related to forests, a scheme was proposed by Tsinzerling (1932). Sochava (1934) devised one for the Anabar tundras, which belong to the "typical" tundra subzone. In the author's scheme, which applies to the arctic tundra subzone, the differences between the chief environmental factors that are apparent in tundra and forest zones are still more clearly expressed than in that of Sochava.

Of the five principal factors mentioned above, which determine the ecological and lifezone range and the trend of succession in the arctic subzone, those of (1) denudation, (2) solifluction, and (3) manuring are the most localized. Those of bog formation and of stone content are more general. The first is common in all zones that have a humid climate, the second depends on the composition of the soil in the area. Comparing this scheme with those evolved for other tundra subzones or for the northern forests shows that crossing the boundary between the forest and tundra zones involves a change of the whole system of principal environmental factors governing the succession trends in the plant cover.

Because of the absence of heaths and the wide distribution of moss-spotted tundra and sedge-grass marshes on the plains of the South Island of Novaya Zemlya, the island belongs to the arctic tundra subzone. The northern boundary of this subzone may be drawn a little to the north of Matochkin Shar (Fig. 4).

Between the arctic tundra subzone and the arctic deserts proper lies a transitional subzone. It may be called the southern variant of the polar deserts and stretches as far as the Admiralteistva Peninsula. It contains glaciers but no ice-cap. Vegetation is colonizing the areas that have recently become ice-free or emerged from the sea. On the mountain slopes polygonal polar deserts predominate on ground covered with stone nets. Under more favourable local conditions patches of tundra communities occur as well as small areas of arctic mineral bogs (without a peat substratum) and remains of relict peat bogs.

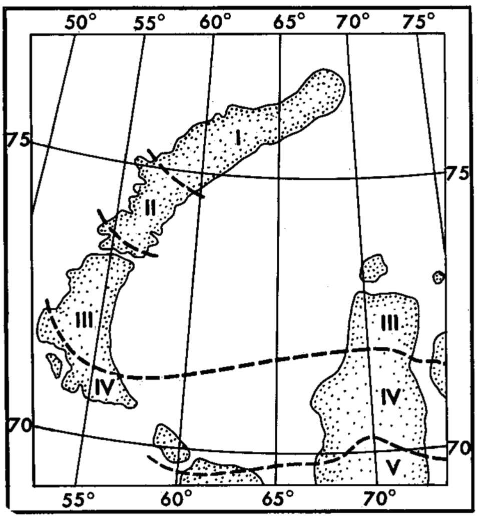

Fig. 4. Diagram showing the altitudinal zonation in the Novaya Zemlya area. I — the polar desert zone; II — the southern variant of the polar desert zone; III — the northern variant of the arctic tundra subzone; IV — the southern variant of the arctic tundra subzone; V — the subzone of the typical tundra.

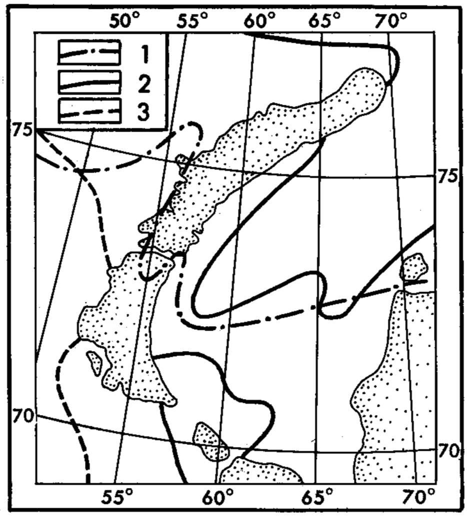

Fig. 5. The July isotherm of 5°C. and the limits of ice in the Novaya Zemlya area in July. (from Marine Atlas of the U.S.S.R., 1951). 1 — July isotherm of 5°C.; 2 — average limit of drift ice; 3 — extreme southern limit of drift ice.

To the north of the Admiralteistva Peninsula lies the polar desert zone proper. There vegetation is only found on the open ground outside the edge of the ice-cap. Plant associations of the tundra type hardly ever occur and there are only tiny fragments of moss and moss-lichen communities in little depressions of the microrelief and microcommunities of crustaceous lichens. Flowering plants are very rare and grow as single individuals. There are no accumulations of peat. The transition to the true polar desert is accompanied by an abrupt impoverishment of the flora. North of the 75th parallel only 79 species of vascular plants are found, whereas the southern part of the North Island has 148 species in the west and 141 species in the east, and the South Island 202 species (Tolmachev 1936). Thus the well-defined boundaries between phytogeographical, floristic, and physiographical zones coincide north of the Admiralteistva Peninsula.

In the arctic tundra subzone of Novaya Zemlya two distinct zonal variants can be clearly discerned, that is, a southern and a northern variant of the arctic tundra subzone. The boundary between the two can be drawn from Cape Severny Gussiny Noss (Northern Goose Nose Cape) southeast to the mouth of the Kumzha River.

The vegetation of the southern variant is distinguished from that of the northern by the predominance of moss-spotted tundras, great development of low-mound bogs, and the noticeable frequency of taller dwarf shrubs (*Salix reptans* and *S. lanata*) in the plant cover. This type of vegetation is to be found in the southwestern part of Gussinaya Zemlya (Goose Land) and on Mezhdusharsky Island.

To the northern variant of the arctic tundra subzone belongs the vegetation of the northeastern part of Gussinaya Zemlya and of the Kara Sea side of the island north of the Kumzha River. It is characterized by greater abundance of lichens, almost complete lack of low-mound bogs and great rarity of willows as tall as *Salix reptans;* only fully prostrate willows *(Salix polaris, S. arctica, S. reticulata,* etc.) grow there.

It is of interest to compare these subzone divisions with those that Andreev (1938) has distinguished in the northern part of the Yamal Peninsula. He called his two subzones of the arctic tundra (1) the "southern arctic tundra" subzone and (2) the "arctic tundra" subzone. Both differ from the more southern tundras in that they have been without trees for all post-glacial time, lack the shrub tundras, and show a preponderance of moss and lichen tundras and of arctic marshes. The transition from the "southern arctic tundra" subzone to the "arctic tundra" is indicated by the disappearance of even the oligotrophic and mesotrophic bogs and the increasing prevalence of tundras with very scant plant cover and an abundance of barren polygons. Andreev (1938) remarks that for his "arctic tundra" subzone "polygon moss and lichen tundras and polygon marshes are characteristic".

The changes in plant cover from north to south in Yamal Peninsula are the same as in Novaya Zemlya. Differences in the vegetation of the two areas depend chiefly on the amount of frost action. On the Yamal Peninsula frost cracks are well developed, but in Novaya Zemlya they occur only sporadically. High winter temperatures and deep snow cover inhibit formation of polygon marshes as well as of frost cracks in the moss-spotted tundras. Only in mountainous areas in the South Island of Novaya Zemlya can polygons be found in clayey soil and then only in places where no snow accumulates in winter owing to the winds. But in such places stony soils and not clay are more frequent and there not only the fine material but also small stones are blown away by the wind (Zubkov 1934). Therefore, frost cracks are rare even in the mountains. The origin of the bare spots in most parts of the tundras on the South Island, particularly in Gussinaya Zemlya and Mezhdusharsky Island is not connected with ice-wedge polygons and wind and snow erosion because the tundras are covered with deep snow all winter (Aleksandrova 1937a, 1937b). The bare spots are caused by solifluction and by frost heaving, i.e., vertical movement of soil material due to the alternation of freezing and thawing. On the bogs the snow cover is very deep, in 1933 it was from 20 cm. to 130 cm., on an average 56 cm. deep (Aleksandrova 1937b). This, and the relatively high winter temperatures, explains why there are no frost cracks in the bogs and why marshes with polygons are absent. That the snow cover in spite of being compacted provides effective insulation is shown by the author's observations that in the middle of February the temperature under 80 cm. of snow was not lower than -3°C and later not lower than -9°C. (under 50 cm. to 80 cm. of snow it was -7°C. and -12°C. respectively).

Besides the climatic differences there are essential differences in geology, relief, and soil substratum between the South Island of Novaya Zemlya and the Yamal Peninsula. Consequently, Novaya Zemlya and Yamal Peninsula have been assigned to different phytogeographical provinces (Gorodkov 1935, Leskov 1947).

Furthermore, it should be pointed out that in Novaya Zemlya the boundaries between the vegetation subzones do not follow the parallels of latitude: in the west to east direction they are sharply deflected southward. This is a natural effect of the climatic differences between the Kara Sea side and the western side of the islands (Fig. 5).

During a floristic reconnaissance of the basins of the Rogatsheva, Savina, and Abrosimova rivers (Aleksandrova 1945) three altitudinal belts of vegetation were found. In the first belt (from sea-level to an altitude of 200 m.) chiefly alpine arctic tundras were found in areas where the ground contains sufficient clayey material and where the rocks weather into small particles; only under very unfavourable conditions is the vegetation of the open polar desert type. Bogs are here well developed.

In the second belt, the lower belt of alpine polar deserts (between 200 m. and 300 m. above sea-level), the rock and scree slopes either do not possess any vegetation at all or at most an extremely poor one. The surfaces of the rocks are covered with crustaceous lichens. Between the stones tiny cushions of mosses and single groups of lichens find shelter and there are scattered individuals of flowering plants. Alpine arctic tundras and small arctic bogs are to be found only under especially favourable conditions in well-sheltered situations. As a rule, the open vegetation of the alpine polar desert but not that of the tundra communities develops on ground that contains a sufficient amount of small particles of weathered rock.

The third zone is the upper belt of the alpine polar deserts (at altitudes greater than 300 m. above sea-level). On the central watershed of the mountain range there are no plant communities in the narrow sense of the term, except the microcommunities of crustaceous lichens. At the head of the Savina River there is hardly any vegetation on the rocky mountain tops or upper slopes. Crustaceous lichens grow on the surfaces of the rocks, and between the stones can be found scattered tiny depressed cushions of

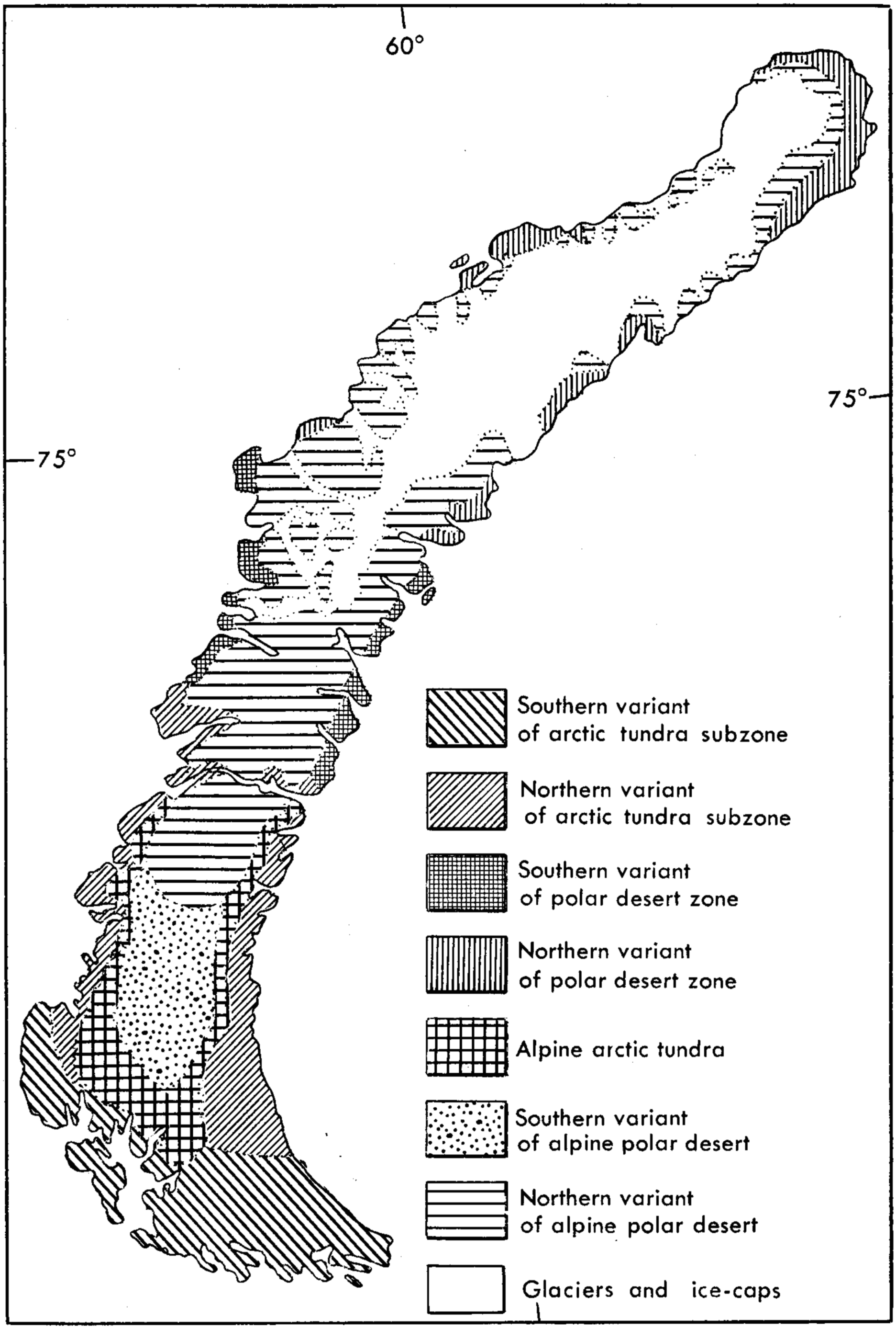

Fig. 6. Map showing the latitudinal and vertical zonation on Novaya Zemlya.

the mosses *Rhacomitrium hypnoides* and *Schistidium apocarpum* var. *glacialis* and single small individuals of *Stereocaulon* sp. On the lower parts of the slopes *Dicranoweisia crispula, Andreaea petrophila,* and single plants of *Cardamine bellidifolia* appear in addition to the above. Here and there on the bare scree slopes fragments of moss-lichen and herb-moss associations occur. On the gentle damp slopes of the wet clayey alluviums single small cushions of *Cetraria delisei,* isolated individuals of *Saxifraga rivularis,* dwarf tufts of *Phippsia algida* or *Deschampsia arctica* grow and all are very depauperate. The flowering plants, accompanied by few stems of a moss find shelter behind the features of the microrelief and have a miserable aspect. *Cerastium regelii,* for instance, has only two or four leaves and *Saxifraga cernua* is a dwarf not more than 3 to 4 cm. high.

The scheme of vertical zonation for the whole of Novaya Zemlya is presented in Fig. 6. The boundaries in the areas beyond that in which the author worked are based on Zubkov's data (Alexandrova and Zubkov 1937). The northern part of the North Island belongs into the northern variant of the polar deserts. It is still more impoverished than the southern one described above.

The investigations in the South Island of Novaya Zemlya have led to the recognition of the following regularities in the plant cover.

(1) In the arctic tundra subzone there are these types of vegetation: tundras, bogs, and polar deserts. In addition there is a feebly developed aquatic vegetation. Tundras occupy the upland sites and represent the vegetation characteristic of the zone (the "climatic climax"), bogs occur in wet situations (the "subclimax"); polar deserts are extrazonal (the "preclimax") and are either to be found in the mountains at high elevations or on the plains in certain localities, that is, in exposed sites where high winds prevent the formation of a snow cover (the "precursor" of the next, more northern vegetation zone of the polar deserts).

(2) The principal environmental factors that lead to trends in spatial changes of the vegetation (ecological ranges, changes along environmental gradients in space) as well as in chronological changes (successions) are (a) denudation, which increases with increasing exposure to wind action and the resulting decrease in snow depth; (b) accumulation of stagnant water in poorly drained situations, often accompanying deep snow cover; (c) the amount of stones in the soil; (d) solifluction; (e) manuring of the soil by animals. A comparison of the ecological ranges of the tundra associations in the arctic tundra subzone with that in the other tundra subzones and in the northern forest zone shows that the complex of principal environmental factors undergoes a complete change when one passes from a tundra to a northern forest zone.

(3) The arctic tundra subzone on the South Island of Novaya Zemlya, as well as on the northern part of the Yamal Peninsula (Andreev 1938) can be divided into two zonal subdivisions. The southern variant of the arctic tundra subzone is characterized by a noticeable element of willows as tall as *Salix reptans* in the plant cover of the moss-spotted tundras and by the

wide distribution of low-mound bogs. The northern variant is characterized by the scarcity of willows as tall as *reptans* (only the entirely prostrate species *Salix polaris, reticulata, arctica,* and others occur there), by the almost complete lack of low-mound bogs and by the prevalence of moss-sedge arctic marshes.

(4) The arctic tundra subzone in Novaya Zemlya can be divided into three belts according to altitude.

(a) The lower alpine belt (that of the alpine arctic tundras); it is characterized by the wide distribution of tundra and bog associations on suitable soils (soils that are sufficiently weathered and have a high content of fine particles).

(b) The intermediate alpine belt (= the lower belt of the alpine polar desert); there is found as a rule the open vegetation of the polar deserts on soils with a sufficiently high content of fine particles, but tundras and bogs occur only under specially favourable conditions.

(c) The upper alpine belt (= the upper belt of the alpine polar desert); there the tundra communities are absent, only fragments of them occur in sheltered depressions of the microrelief; accumulation of peat is completely suppressed, and the dominants of the bog communities disappear; only the open vegetation of the polar desert and the microcommunities of crustaceous lichens persist.

References

Aleksandrova, V. D. 1935. On the finding of *Sieversia glacialis* R. Br. on Novaya Zemlya. Trudy Vses. arktich. inst. 22:51-4. In Russian.

————————1937a. Winter forage of reindeer on Novaya Zemlya. Sov. olenevodstvo 9:127-38. In Russian with English summary.

————————1937b. Reindeer breeding in Novaya Zemlya. Priroda 1937, No. 4, p. 79-90. In Russian.

————————1945. A sketch of the vegetation of Novaya Zemlya along the transect from Rogacheva Bay to Savina Bay. Probl. arkt. Nos. 5-6, p. 89-109. In Russian.

————————1956. The vegetation of the southern island of Novaya Zemlya between 70°56′ and 72°12′N. Rastit. krain. sev. SSSR. i ee osv. 2:187-306. In Russian.

Aleksandrova, V. D., and A. I. Zubkov. 1937. Physico-geographical sketch of Novaya Zemlya. Mezhdun. geol. Kongress. 17 sessia SSSR. Novozemlskaia ekskurs. Leningrad, Chast' 1, p. 29-75. In Russian, also in English as: Zubkov, A. I. and V. D. Aleksandrova: Physico-geographical outline of Novaya Zemlya (*In* Samolovich and Ermolaev: The Novaya Zemlya Excursion, 1937, Pt. 1, p. 28-65. Guide book 21 for the excursions. 17th International Geological Congress, Moskow and Leningrad, 1937).

Andreev, V. N. 1932. Subzones of the tundras of the European Far North. Priroda 1932, No. 10, p. 889-906. In Russian.

————————1935. Vegetation and natural regions of the eastern part of Bolshezemel'skaya Tundra. Trudy Polarn. Kom. Ak. Nauk SSSR. 22, 97 pp. In Russian.

————————1938. Observations of the tundra reindeer pastures by means of the aeroplane. Trudy Leningrad inst. polarn. zemled., ser. Olenevodstvo 1:7-132. In Russian with English summary.

————————1947. Geobotanical exploration of the Pechora River basin in 1940-6. Sov. botanika, No. 4, p. 239-43. In Russian.

——————1950. Arctic and high-mountain deserts. Tundras. Map of the European part of the U.S.S.R., scale 1:2,500,000. Explanatory text, p. 35-58. In Russian.

Andreev, V. N., K. N. Igoshina, and A. I. Leskov. 1935. Reindeer pastures and vegetation cover of the northern cis-Ural region. Sov. olenevodstvo 5:171-406. In Russian.

Baer, K. E. von. 1838. Végétation et climat de Novaia-Zemlie. Bull. Acad. Imp. Sc. St. Petersburg 3:171-92. Text in German.

Berg, L. S., 1930. Geographical zones of the U.S.S.R. Leningrad. 401 pp. In Russian.

Flerov, B. K. 1925. Fresh-water algae of the Belushiy Peninsula, Novaya Zemlya. Trudy Plov. Morsk. nauchn. inst. 12:12-46. In Russian.

Gorodkov, B. N. 1916. An attempt to divide the west-Siberian lowland into botanico-geographical regions. Izd. ezhegodn. Tobolsk gub. museya 27:1-51. In Russian.

——————1933. Natural grazing lands of the tundra part of the far eastern province. Sov. olenevodstov No. 2, p. 119-164. In Russian with English summary.

——————1935. Vegetation of the tundra zozne in the U.S.S.R. Izd. Ak. Nauk SSSR., 141 pp. In Russian.

——————1943. Polar deserts of Wrangel Island. Bot. zhurn. SSSR. 28:127-43. In Russian with French summary.

——————1946. Botanical-geographical sketch of the Far North and Arctic of the U.S.S.R. Leningrad Gerzen ped. inst. Uchenye sapiski. 49:73-125. In Russian.

——————1958a. The vegetation and soils of Wrangel Island. Rast. krain. sev. SSSR. i ee osv. 3:5-58. In Russian.

——————1958b. Analysis of the vegetation of the arctic desert zone on the basis of the investigations on Wrangel Island. Rast. krain. sev. SSSR. i ee osv. 3:59-94. In Russian.

Govorukhin, V. S. 1954. Tundras. *In:* Alekhin, V. V.: Vegetation of the U.S.S.R. in principal zones. Chapt. IV. Moskva: Sov. Nauka, 512 pp. In Russian.

——————1957. Tundra. Bolshaya Sov. Enzikl. Vol. 43:396-7. In Russian.

Igoshina, K. N. 1933. Botanical and economical characteristics of reindeer pastures in the district of the Obdorsk zonal station. Sov. olenevodstvo 1:165-205. In Russian.

Kjellman, F. R. 1882. Die Phanerogamenflora von Nowaja Semlja und Waigatsch. Wiss. Ergebn. der Vega Exped. Vol. 1, p. 319-52.

Krechetovich, V. I. 1946. The importance and role of the phytogeographical method for palaeographical reconstructions. Trudy Inst. geogr. Ak. Nauk SSSR. 37:326-7. In Russian.

Kudryashev V. V. 1925. Peat bogs of Belushiy Peninsula (Novaya Zemlya). Trudy Plov. mor. inst. 12:107-19. In Russian with German summary.

Leskov, A. I. 1947. The arctic tundra region. *In:* Lavrenko, *Edit.*, Division of the U.S.S.R. into geobotanical districts. Izv. Ak. Nauk SSSR., p. 14-17. In Russian.

Lynge, B. 1923. Vascular plants from Novaya Zemlya. Norske Novaja Semlja eksped., 1921. Rept. sci. res. No. 13, 151 pp. Oslo: Norske videnskaps-akademi.

——————1928. Lichens from Novaya Zemlya. Norske Novaja Semlja eksped. Rept. sci. res. No. 43, 299 pp. Oslo: Norske videnskaps-akademi.

Oksner, A. M. 1946. Discussion on the report of V. I. Krechetovich: The importance and role of the phytogeographical method for palaeographic reconstructions. Trudy inst. geogr. Ak. Nauk SSSR. 37:349. In Russian.

Perfil'ev, A. I. 1928. Materials on the flora of Novaya Zemlya and Kolguev islands. Arkhangel'sk, Severn. pechatnik, 73 pp. In Russian.

Regel, K. V. 1932. Pflanzensoziologische Studien aus dem nördlichen Russland. I. Die Fleckentundra von Nowaja Zemlja. Beitr. zur Biologie der Pflanzen, Bd. 20:7-24.

——————1935. III. Die Reliktenvereine in der Arktis. Die Moore von Nowaja Semlja. Beitr. zur Biol. der Pflanzen, Bd. 23:105-21.

Reverdatto, V. V. 1931. Vegetation of Siberia; an attempt to define its natural divisions. Izv. vses. geogr. obshch. 63:43-70. In Russian.

Sambuk, F. V., and A. A. Dedov. 1934. Subzone of the cis-Pechora tundras. Trudy Plov. mor. Inst. Ak. Nauk SSSR. Geobotanika 1:29-52. In Russian with German summary.

Sheludyakova, V. A. 1938. Vegetation of the Indigirka River basin. Sov. botanika Nos. 4-5, p. 43-79. In Russian.
Sochava, V. B. 1933a. Tundras of the Anabar River basin. Izv. Gos. geogr. ob-va. 65:341-64. In Russian with German summary.
——————1933b. Natural grazing lands of the tundra zone of Yakutia. Sov. olenevodstvo No. 2, p. 47-110. In Russian with English summary.
——————1934. Plant associations of the Anabar tundra. Bot. zhurn. SSSR. 19:264-304. In Russian with German summary.
Steffen, H. 1928. Beiträge zur Flora und Pflanzengeographie von Nowaja Semlja, Waigatsch und Koljugov. Bot. Zentralbl., Beihefte 44:282-361.
Tikhomirov, B. A. 1941. On the forest phase in the post-glacial history of the north Siberian vegetation and its relicts in the recent tundra. Ak. Nauk SSSR. Bot. inst. Materiali po ist. flory i rast. SSSR. 1:315-74. In Russian with English summary.
——————1948a. A contribution to the knowledge of the extreme polar limits of the flora of Eurasia. Mosk. obshch-vo. ispytat. prirody. Byull. 53:91-102. In Russian.
——————1948b. On the characteristics of the flora of the western coast of the Taymyr Peninsula. Petrozavodsk, 85 pp. In Russian.
——————1951. On the role of the wind in the plant distribution in the Far North. Priroda 1951, No. 8, p. 23-5. In Russian.
Tolmachev, A. L. 1922. A contribution to the history of the flora of Novaya Zemlya and Vaygach. Priroda 1922, Nos. 3-5, p. 107-14. In Russian.
——————1930. On the origin of the flora of Vaygach and Novaya Zemlya. Trudy Bot. museya Ak. Nauk SSSR. 22:181-205. In Russian.
——————1931. Materials on the flora of European arctic islands. Zhurn. bot. ob-va. 16:459-72. In Russian with German summary.
——————1936. A review of the flora of Novaya Zemlya. Arctica No. 4, p. 143-78. In Russian with German summary.
——————1939. Some principles of the distribution of arctic plant communities. Bot. zhurn. SSSR. No. 5, p. 504-17. In Russian.
Trautfetter, R. 1851. On vegetative-geographical districts of European Russia. Estestven. ist. gub. Kievsk. ucheb. okruga. Botanika, ch. geogr. Kiev. 20 pp. In Russian.
Tsinzerling, Yu. D. 1932. Geography of the vegetative cover of the northwestern section of the U.S.S.R. Trudy Geomorf. inst. Ak. Nauk SSSR. 4, 377 pp. In Russian with German summary.
Vize, V. Yu. 1940. Climate of the seas of the Soviet Arctic. Leningrad, 124 pp. In Russian.
Zagorskaya, N. G. 1959. Novaya Zemlya. *In:* Quaternary deposits of the Soviet Arctic. Trudy n.-i. inst. geol. Minist. Geol. i okhr. nedr SSSR. 91:20-36. In Russian.
Zubkov, A. I. 1932. Tundra of Gusinaya Zemlya. Trudy bot. museya Ak. Nauk. SSSR. 25:57-99. In Russian.
——————1934. On the intensity of the deflation process in the Arctic. Byull. Arkt. inst. 4:311-12, 341-2. In Russian and English.
——————1935. Reindeer husbandry and reindeer pastures on Novaya Zemlya. Trudy arkt. inst. 22:7-34. In Russian with English summary.
——————1948. New data on the distribution of forest vegetation on the Taymyr Peninsula in post-glacial time. Doklady Ak. Nauk. SSSR. 61:721-3. In Russian.