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Emil Hadač:

The History of the Flora of Spitsbergen and Bear Island and the Age of some Arctic Plant Species

Preface

Since DARWIN's eminent work, the problem of the Origin of Species has not lost its attraction and interest. In the last years the discussion on this problem has revived very vigorously.

As we are not able to give a definition of the Species acceptable for the majority of scientists, as well as an universal method for distinguishing a species from a variety or a genus, it is difficult to find a solid platform for the solution of this question. In this situation we must try to find at least some material to elucidate some ways which led to the origin of one or another wellknown species and hope, that our little contribution will throw some light on the general problem.

There are several methods, which can help us: the physiology, the ecology, the cytotaxonomy, etc. One of them, used already by Darwin him self, is the plant geography.

During the last twenty years, the present author has studied the flora and vegetation of the European Arctic and Subarctic regions, and the mountain flora of Central Europe. Some of his studies have been already published; in this treatise he will try to summarize some results of his work.

The first explorers of the Arctic thought that its flora came to this territory from the south in the postglacial. Another explanation of its occurrence was in this time unthinkable.

The facts, accumulated by several authors, e. g. by BLYTT, A. HANSEN, NORDHAGEN, LYNGE, TH. SÖRENSEN, EILIF DAHL, A. and D. LÖVE, FERNALD, HULTÉN, TOLMAČEV, TICHOMIROV etc., have shown, that at least some of the artic species survived the glaciation or glaciations on spot.

If we now compare the recent distribution of arctic species with the extent of the ice and icefree land and with probable land connections during the Ice Age, we shall be able to find out their ways of migration and in some cases, may be, their approximate age.

The Origin of the Flora of Bear Island

We shall begin with the Bear Island, because it is very small and relatively isolated, and therefore it will be ralatively easy to say something on the origin and age of its flora.

Some years ago (cf. HADAČ 1941b), I published a study on the origin of the flora of this island, but it was written in the Norwegian language in a journal for the popularisation of science, and therefore little known outside of Scandinavia. I shall therefore recapitulate here the results of my study.

Bear Island (Björnöya) is situated at 74°20′—31′ N. Lat. and 18°46′—19°17′ E. Long., about 400 km to the North of Scandinavia, 230 km to the South of Spitsbergen, and still longer from Novaya Zemlya and Greenland. Its rocks are of dolomite, limestone and sandstone. The climate of Bear Island is relatively rough and windy. The year's mean temperature is —3,8° C (+4,2° C in July, —11,2° C in February).

Let us see the relations of the Flora of Bear Island to the neighbouring lands.

In a list of vascular plants, published by O. HANSSEN and JENS HOLMBOE, are 53 of 55 species in common with Spitsbergen, but several species are wanting in Scandinavia, i. e. *Alopecurus alpinus*, *Cerastium Regelii*, *Dupontia Fisheri*, *Draba oblongata* and *Cochlearia groenlandica*. The only two species of Bear Island, common with Scandinavia and lacking in Spitsbergen, are *Hippuris vulgaris* and *Rhododendron lapponicum*.

Hippuris vulgaris has its northern limit in Greenland at 76°30′—76°46′ N. Lat. Its absence from Spitsbergen may be caused by climatic conditions. It spreads mostly by means of birds and may be a relatively recent immigrant to the island.

Rhododendron lapponicum has in Scandinavia a bicentric, continental distribution and has, as supposed by NORDHAGEN (1933), survived the last glaciation in Scandinavia. Its total distribution is shown on map 1. *Rhododendron lapponicum* belongs to the "amphiatlantic" element. Its presence on Bear Island, with oceanic actual climate, suggests its relic character.

The list of mosses of Bear Island was published more than 80 years ago by BERGGREN. Most of them have a wide distribution and were found in Spitsbergen and in Scandinavia as well. But two of them are wanting in Scandinavia. It is *Orthotrichum Breutelii (O. Pylaisei)*, living in Spitsbergen and Greenland, and *Hypnum (Drepanocladus) brevifolium* LINDB., known i Spitsbergen, Greenland and Alaska.

The lichens were studied by the best student of arctic lichens, Bernt LYNGE. From 185 species of lichens 6 are endemic and some have a very interesting distribution: *Lecanora heteroplaca* ZAHLBR. was found outside of Bear Island in Novaya Zemlya only, *Lecanora Nordenskjöldii* VAIN. was found on the East Siberian coast at Pitlekai only, and the same known distribution has *Lecanora torrida* VAIN.

All these facts indicate that the flora of Bear Island has a relatively high age. It is not probable that it came to the island after the last Ice age, except some few recent immigrants. The migration of plants in the Arctic is relatively slow and the migration to such long distances is very rare. Plants in the Arctic migrate, as it seems, not as single individuals, but with their plant communities, step by step.

The migration of such plants, as *Cardamine pratensis* ssp. *angustifolia*, *Deschampsia alpina* and *Saxifraga cernua* on long distances is improbable. They produce no seeds and their bulbils or leaflets are not likely to be transported more than some few kilometers.

The geologists deny the possibility of a land connection of Bear Island with Spitsbergen, Scandinavia or Novaya Zemlya after the last Ice age. But if such plants came during or before the last glaciation to the island, we must find out some possibility of their persistance in some refuges.

The study of HORN and ORVIN (1928) shows that during the last glaciation Bear Island was glaciated partially only. There were several places in the southern as well as in the northern part of the island, which were icefree at least during the last glaciation (see fig. 1.).

If the flora of this island has persisted on spot through the last Ice age, we should find the majority of species, and first of all the rare and endemic species in these refuges.

Let us see, if this supposition is right: the most rare species of vascular flora is *Rhododendron lapponicum:* it grows in a refuge, not outside it. On the other side, *Hippuris*, supposed to be a recent immigrant, was found on the place, which was covered by ice during the Ice age. *Orthotrichum Breutelii* as well as *Hypnum brevifolium* were found in refuges. In all 92% of all lichen species were found in refuges and more than 50% only there. All five endemic lichen species were found in refuges and not outside.

It is evident, that the theory of the survival of the flora of Bear Island during the last Ice age is well founded.

There are geological indices of a land connection between Spitsbergen and Bear Island during the last interglacial. We can thus suppose that the present flora of Bear Island came from Spitsbergen during the last interglacial or before and has endured on the island till now.

As there are not known any endemic species of vascular plants from Bear Island, we can suppose that during the last glaciation the vascular species of Bear Island have not specifically changed. It is of course not impossible that an accurate study will show some differences, but they need not be great, because prof. HOLMBOE was a keen observer and it is not probable that he had overlooked greater differences.

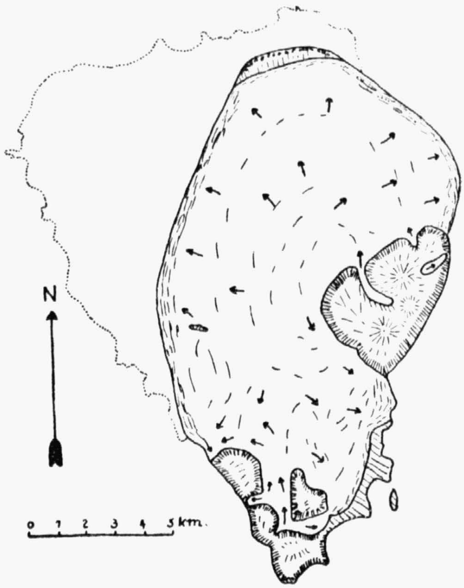


Fig. 1. Bear Island during the last Ice age (After HORN and ORVIN).

The History of the Flora of Spitsbergen

If the persistance of the flora on the small Bear Island is probable, more probable it is in Spitsbergen itself.

Spitsbergen is a large archipelago, where several refuges, not glaciated during at least the last Ice age, are probable. Prof. LYNGE had e.g. suggested several refuges on the northern coast of Vestspitsbergen, but I think there were more of them in the interior of Vestspitsbergen, e. g. in Icefjord.

It is not necessary to discuss further this aspect of the problem. In short we can state that the flora of Spitsbergen as well as the flora of the whole Arctic is very old and has persisted on spot over several Ice ages.

Now, let us analyse the composition of the vascular flora of Spitsbergen, to see if this supposition is right.

Spitsbergian vascular plants can be arranged in several groups with similar total distribution; we can presume that plants with similar distribution had similar history.

1. Circumpolar alpine -arctic group
(23 species, i. e. 15, 9% of the total flora)

Lycopodium selago L. var. *appressum* (DESV.) SIMMONS
Equisetum variegatum ALL. ex SCHLEICH.
Cystopteris Dickieana SIM.
Woodsia glabella R. BR.
Trisetum spicatum (L.) RICHT. (see map 2.)
Eriophorum Scheuchzeri HOPPE
Carex bipartita ALL. (*C. Lachenalii* SCHKUHR)
Carex rupestris BELL.
Carex Bigelowii TORR.
Kobresia caricina WILLD.
Juncus triglumis L.
Juncus castaneus SMITH
Juncus arcticus WILLD.
Oxyria digyna (L.) HILL.
Bistorta vivipara (L). S. F. GRAY
Cerastium alpinum L. s. l.
Minuartia biflora (L.) SCH. et THELL.
Minuartia stricta (SW.) HIERN.
Silene acaulis L.
Saxifraga hieraciifolia WALDST.—KIT.
Saxifraga cernua L.
Saxifraga oppositifolia L.

Empetrum hermaphroditium HAGERUP

Species of this group are distributed throughout the whole Arctic and in very distant mountain ridges of adjacent continents, e. g. in the Caucasus, Himalaya, etc. Some of them were found even in mountains of the southern hemisphere.

The only explanation of such distribution is their tertiary age.

It is difficult to find their place of origin. It was in most cases probably some mountain ridge in Eurasia or America, but even Arctic regions are not excluded. They had good occasion of spreading during the whole Pleistocene period and reached thus such distant localities like the Himalaya or mountains of the southern hemisphere. Following the retreat of ice sheets of the first or second glacial age, they reached the Arctic and then they could penetrate to the whole arctic territory bare of ice and persist there in refuges over the whole period of the Pleistocene.

Having no fossil remains, it is difficult to tell when they did come to Spitsbergen, but it is probable that they belong to the eldest element of its flora.

Several species of this group belonged to the central European tundra formation ("Dryas flora") during the Pleistocene. Thus ŚRODOŃ found in a locality near Lublin in Polen in Rissian deposits i. a.: *Oxyria digyna*, *Bistorta vivipara*, *Cerastium alpinum*, *Silene acaulis*, *Saxifraga cernua*, *Saxifraga oppositifolia*.

2. Circumpolar arctic — subarctic group
(37 species, i. e. 25,5% of the flora)

Equisetum boreale BONG.
Calamagrostis neglecta (EHRH.) GAERTN. v. *borealis* KEARN.

Poa glauca M. VAHL ssp. *conferta* (BL.) HOLMB.
Poa alpigena (E. FR.) LINDM. ssp. *iantha* (LAEST.) HADAČ 1942
Phippsia algida (SOLAND) R. BR.
Festuca Richardsonii HOOK. ssp. *cryophila* (KRECZ.) LOEVE 1956
Carex marina DEW.
Carex subspathacea WORMSKJ.
Carex saxatilis L.
Juncus biglumis L.
Tofieldia borealis WAHLENB.
Koenigia islandica L. (v. *artica* HADAČ)
Stellaria humifusa ROTTB. (see map 3.)
Sagina intermedia FENZL
Minuartia rubella (WAHLENB.) GRAEBN.
Ranunculus hyperboreus ROTTB.
Ranunculus pygmaeus ROTTB.
Cardamine pratensis L. ssp. *angustifolia* (HOOK.) SCHULZ
Cardamine bellidifolia L. (see map 4.)
Draba nivalis LILJEBL.
Draba cinerea ADAMS.
Draba alpina L.
Cochlearia groenlandica L.
Saxifraga tenuis (WAHLENB.) SMITH
Saxifraga nivalis L.
Saxifraga foliolosa R. BR.
Saxifraga rivularis L.
Saxifraga hirculus L.
Saxifraga cespitosa L.
Rhodiola rosea L.
Potentilla nivea L.
Vaccinium microphyllum (LGE.) HAGERUP
Cassiope tetragona (L.) G. DON
Mertensia maritima (L.) S. F. GRAY (v. *tenella* TH. FR.)
Campanula arctica (LGE) HRUBY
Erigeron unalaschkense (DC.) VIERH.
Erigeron eriocephalum J. VAHL

This group seems to be somewhat younger than the previous one. The origin of the species of this group must be somewhere in the Arctic in the early Pleistocene. They spread during the Ice ages and formed their broad circumpolar distribution. Some of them reached even the mountains in the south of continents adjacent to the Arctic, i. e. *Ranunculus pygmaeus*, *Saxifraga nivalis* etc., where they have a pronounced relic character.

All of them occur in Scandinavia and in Iceland.

3. Circumpolar arctic group

(18 species, i. e. 12,4% of the flora)

Equisetum scirpoides (L.) RICH.
Hierochloe alpina (LILJEBL.) ROEM et SCHULT. (see map 5.)
Arctagrostis latifolia (R. BR.) GRISEB.
Poa arctica R. BR.
Carex maritima GUNN. v. *setina* (CHRIST.) FERN.
Carex misandra R. BR.
Luzula nivalis LAEST.
Luzula confusa LINDB.
Stellaria longipes GOLDIE v. *humilis* FENZL
Melandrium apetalum (L.) FENZL
Ranunculus nivalis L.
Ranunculus sulphureus SOLAND.
Braya purpurascens (R. BR.) BGE.
Draba daurica DC.

Draba lactea Adams
Cochlearia arctica Schlecht.
Pedicularis hirsuta L.
Potentilla pulchella R. Br.

(*Potentilla pulchella* belongs probably to this group, although its known area is not fully circumpolar. It is not known between Wrangel Island and Waygats and therefore it is included by most authors in the amphi-atlantic element. But I think that the gap in its distribution is due to the imperfect exploration of the Arctic Siberian coast.)

The species of this group are old arctic species (eoarctic), fitted to the arctic conditions and not occurring in subarctic regions. They are e. g. lacking in Iceland except *Poa arctica*, which formed in Iceland and in southern Scandinavia the ssp. *herjedalica*. All were found in Scandinavia, but several of them have there bicentric distribution (*Luzula nivalis, Stellaria longipes, Melandrium apetalum, Draba lactea*). This centric distribution may be caused in some cases by climatic conditions, but in some cases it can be explained by historical causes only, by survival in refuges.

The age of species of this group is about the same as in group 2., i. e. early Pleistocene.

4. Circumpolar high arctic group
(21 species, i. e. 14,5% of the flora.)

Alopecurus alpinus Sm. (see map 6.)
Deschampsia brevifolia R. Br. (map 7)
Poa abbreviata R. Br. (map 8.)
Dupontia Fisheri R. Br. (inclus. ssp. *psilosantha*, map. 9.)
Puccinellia angustata (R. Br.) Rand. et Redf.
Colpodium Vahlianum (Liebm.) Nevski
Festuca brachyphylla Schult.
Pleuropogon Sabinei R. Br. (map 10.)
Cerastium Regelii Ostf.
Honckenya diffusa (Hornem.) Loeve 1950
Melandryum furcatum (Raf.) Hadač 1942 (map 11.)
Ranunculus affinis R. Br.
Eutrema Edwardsii R. Br. (map 12.)
Draba subcapitata Simmons (map 13.)
Draba macrocarpa Adams
Draba oblongata R. Br.
Draba micropetala Hook.
Saxifraga setigera Pursh
Potentilla emarginata Pursh
Dryas octopetala L. var. *minor* Hook.
Arnica angustifolia Vahl (map 11.)

This group is formed by very old, eoarctic species of early Pleistocene origin; some of them are perhaps still older. *Dupontia Fisheri* and *Pleuropogon Sabinei* belong to the monotypic genera, endemic in the Arctic.

R. Ju. Roshevic (1952) came to the conclusion that *Dupontia Fisheri* is of preglacial origin. Its absence in Scandinavia is caused, after this author, by the circumstance that the main distribution of this species was made in postglacial epoch.

I cannot agree with this conclusion. If *Dupontia* could reach Spitsbergen, separated at least since the last interglacial from Novaya Zemlya and the mainland by the sea, why should it not attain Scandinavia by land? Why should

Dupontia wait somewhere the whole Pleistocene, for half a million years, and then suddenly first begin to migrate (see map 9.).

Pleuropogon Sabinei originated, as assumed by Roshevic (1952) in early Pleistocene on dry land north of Beringia, now submerged, but its spreading was very slow. Therefore it did not reach Scandinavia nor Spitsbergen. "Na Špicbergene i na materike Evropy on, očevidno, nikogda ne vstrečalsja.", writes Roshevic, l. c. This assumption does not fit Spitsbergen, where *Pleuropogon* was found in Icefjord and Wijdefjord and published by several authors. I have seen its material in the Botanisk Museum at Oslo; there cannot be doubt about its occurrence in Spitsbergen. Its absence from Scandinavia must be caused by another factor than the slowness of its spreading. (See map 10.)

Another species of this group, *Puccinellia angustata*, was studied thoroughly by Th. Sörensen (1953). He came to the conclusion that this very old arctic species reached Spitsbergen prior to the last interglacial, before the land connection of N. E. Greenland and Spitsbergen was broken.

Festuca brachyphylla originated probably in the high mountains of North America, but it came very soon to the Arctic and now it has circumpolar distribution.

Eutrema Edwardsii has its original home in the Altai or Sayan mountains, where live its related species, but came probably very early to the Arctic (see map 12.).

Saxifraga setigera has its next related species in Central Asia.

The mother-species of *Honckenya diffusa* is *Honckenya peploides*, which has a more southern distribution. *Honckenya diffusa*, a sea shore plant, is known also on the northern shore of Iceland.

Dryas octopetala v. *minor* is segregated from the main species and has decidedly high arctic distribution. *Dryas octopetala typica* does not grow either in Spitsbergen or in Novaya Zemlya. During the Pleistocene, *Dryas octopetala* was a leading species in the tundra formation of Central Europe.

Alopecurus alpinus is likewise a very old species. It has an enclave in the mountains of Scotland, but is lacking in Scandinavia (see map 6.). It was found in the stomach of the siberian mammoth (Tichomirov and Kuprijanova, 1954).

Arnica angustifolia has in Arctic Scandinavia a very related endemic species, *Arnica alpina*. It is probable that before the last or penultimate glaciation *Arnica angustifolia* penetrated to Scandinavia, then the ice sheat segregated the scandinavian population and during the isolation this population in somewhat changed conditions was transformed in a new species, *Arnica alpina* (see map 11.).

The same fits also for *Melandrium furcatum* (circumpolar) and M. *angustiflorum* (artic Scandinavia, western Siberia, see map 11.).

The species of this group do not occur in Scandinavia. The cause of it can be different. Some of them, as shown on *Arnica* and *Melandrium*, reached Scandinavia before the last or penultimate glaciation, but there they changed in to new, endemic species. Others were probably exterminated there during the last Ice age or even by the interglacial conditions and being now "rigid", they are not able to regain the lost area. But the absence from Scandinavia of some species may be ruled by present climatic conditions. Let us confront their actual distribution with some isotherms (see map 14.). They follow the

—15° isotherm for mean temperature for January, not only in the siberian section, but also in Greenland. I will not say that the isotherm —15° in January rules their distribution, but it may be an indicator for other, more important climatic factors. Anyway, the conform area of so many species could not be accidental.

All facts indicate that the species of this group must be very old, at least from early Pleistocene and that their area of distribution was formed mainly before the last or even the penultimate glaciation.

5. The arctic — subarctic amphiatlantic group
(3 species, i. e. 2,1% of the flora)

The group of plants with amphiatlantic distribution is not homogeneous. I think it is better to exclude first of all such species, which have their main distribution in the mountains of Europe: this is the European alpine-atlantic group.

Even the rest of amphiatlantic species is not homogeneous. There are species with more oceanic character, which evidently made their way across the Atlantic via Iceland, and others more continental, which crossed the Atlantic via N. E. Greenland — Spitsbergen. Some of them grow on Iceland, too, but there they are concentrated in the northern and northwestern parts. They might have been dispersed along the northern coasts of the land connection between Greenland, Iceland and Scandinavia. These two groups must have "wintered" in refuges of different character, the first in coastal, the other in tundra refuges (cf. EILIF DAHL 1946).

The arctic-subarctic amphiatlantic group contains in Spitsbergen three species only:

Cassiope hypnoides (L.) DON. (*Harrimanella hypn.* (L.) COVILLE) (see map 15.)
Deschampsia alpina (L.) R. et SCH.
Draba rupestris R. BR.

Cassiope hypnoides must be a very old species, having no near relatives. It extends from Ural to Arctic Eastern America. I think that *Cassiope* was amphiatlantic already in late Tertiary times, but this is only an impression; we have no proof of it.

Deschampsia alpina and *Draba rupestris* have a very similar area, extending from Novaya Zemlya to Labrador. The spreading of the viviparous *Deschampsia alpina* across the sea is hardly thinkable; the land connection between Scandinavia, Iceland and Greenland was realised, as shown by LÖVE & LÖVE (1956) (see also HADAČ 1948), before the last Ice age, may be during the penultimate glaciation.

6. The arctic amphiatlantic group
(6 species, i. e. 4,2% of the flora)

Carex ursina DEW. (see map 16.)
Carex nardina E. FRIES
Eriophorum triste (TH. FR.) HADAČ et LOEVE 1950 (map 17.)
Minuartia Rossii (R. BR.) GRAEBN. (map 18.)
Papaver Dahlianum NORDH. ssp. *Dahlianum* m. var *spitsbergense* LOEVE 55 (see map 18.)
Campanula uniflora L. (map 19.)

Carex ursina extends from the American Arctic to Taymyr and is lacking in Scandinavia and Iceland. The occurrence of this sea shore plant in the interior of Spitsbergen on early postglacial or even late-glacial terraces, now distant from the sea-shore, indicates that it came to Spitsbergen earlier than in postglacial.

Carex nardina grows in Alaska, Arctic Eastern America, Greenland, N. Iceland, Spitsbergen and in Arctic Scandinavia.

Eriophorum triste is hitherto known in the Arctic American archipelago, northern half of Greenland, N. W. Iceland, Spitsbergen and Novaya Zemlya.

The distribution of *Minuartia Rosii* is little known. It was found in Alaska, N.E. Arctic America, N. and N. E. Greenland and Spitsbergen. Its main area lies thus in Arctic America.

Papaver Dahlianum was described by NORDHAGEN from Norway. Later, it was found in Spitsbergen in somewhat different population (cf. HADAČ 1944). This form was recognized by LÖVE as a separate variety, var. *spitsbergense*. But besides this variety, distributed from the lowlands to 915 m in Sassenquarter, there is another well distinct *Paper* with sulphureous and not white-yellowish flowers and ellipsoid capsule, with different form of the stigma and darker hairiness. Its main distribution is in the mountains, not in the lowland of Icefjord. This plant was published in my study on the Flora of Sassen Quarter (1944) as "*Papaver sp.*", i. e. as specifically different from *P. Dahlianum*. Later, it was described by LÖVE (1955) as *P. Dahlianum* var. *hadacianum* LÖVE. I think, it deserves at least a rank of subspecies, i. e. *Papaver Dahlianum* NORDH. ssp. *hadacianum* (LOEVE) m., comb. nova, based on *P. Dahlianum* v. *hadacianum* LOEVE 1955.

The other taxon (v. *spitsbergense*) must be thus with the var. *Dahlianum* LOEVE grouped under *P. Dahlianum* ssp. *Dahlianum* m.

The ssp. *Dahlianum* is known, as shown by LÖVE, in N. E. America and the northern half of Greenland, Spitsbergen and arctic Scandinavia, but it is probably growing in Novaya Zemlya, too.

Campanula uniflora extends from the most eastern part of Siberia over Arctic America, Greenland, Iceland, Scandinavia and Spitsbergen to Novaya Zemlya. It has centric distribution in Scandinavia.

It is probable, that this group went by the northern way, i. e. N. E. Grrenland — Spitsbergen (or reverse). This land connection is supposed by Th. SÖRENSEN to exist latest in the Mindel-Rissian interglacial. The species in question must thus be of early Pleistocene age.

7. The European alpine-atlantic group

(8—9 species, i. e. 5,6—6,2% of the flora)

Salix reticulata L.
Salix herbacea L. (map 20)
Betula nana L. (map 20.)
Ranunculus glacialis L. (*Backwithia glacialis* LOEVE et LOEVE) (map 20. and 21.)
Arabis alpina L. (map 20.)
Saxifraga aizoides L. (map 20.)
Potentilla Crantzii (CR.) BECK
Poa alpina L. var. *vivipara* L.
?*Festuca vivipara* (L.) SM.

Species of this group originated doubtless in European mountains, as the Pyrenées, Alpes, Carpathians, etc., in early Pleistocene. During the Ice age they descended from the mountains and made a basis of the widespread tundra vegetation of this time. It is the well known "Dryas flora". They were found e.g. in Rissian deposites in Polen (cf. ŚRODOŃ, l. c.) simultaneously with the still older element of alpine-arctic circumpolar species, cited above. It was: *Arabis alpina, Betula nana, Salix herbacea, S. reticulata.* After the retreat of the ice sheet they came to Scandinavia and England, from there to Iceland, Greenland and the Arctic America, and of the N. E. to Western Siberia, Novaya Zemlya and Spitsbergen (see map 20, 21.).

The areas of *Saxifraga aizoides, Arabis alpina, Betula nana, Salix herbacea* and *Potentilla Crantzii* are very similar. *Ranunculus glacialis* and *Poa alpina vivipara* were found in European mountains, in Scandinavia, Novaya Zemlya, Spitsbergen, Faeroe Islands, Iceland, Jan Mayen and N. E. Greenland, *Poa alpina vivipara* also in Scotland and Bear Island.

Salix reticulata did not reach Iceland and Greenland, and in Arctic America it is replaced by the ssp. *orbicularis* FLOD.

To this group belongs perhaps the alps „*Festuca vivipara*" complex, but the taxonomy of this complex needs to be more elucidated.

8. The Eurasiatic group

(2 species, i. e. 1,4% of the flora)

Potentilla multifida L.
Gentiana tenella ROTTB, (*Lomatogonium tenellum* (ROTTB.) LOEVE)

Potentilla multifida is known from the Alpes as well as from Himalaya, Altay and Kamtschatka, it was found also in N. E. Scandinavia. In Spitsbergen it is very rare.

Gentiana tenella grows in the European as well as in the central asiatic mountains, in the whole arctic Euroasia, Scandinavia, Iceland and Greenland.

Such enormous distribution shows that both species were formed already in tertiary times.

9. The Beringian group

(5 species, i. e. 3,5% of the flora)

Arctophila fulva (TRIN.) ANDERS. (see map 22.)
Ranunculus lapponicus L.
Chrysosplenium tetrandrum (LUND.) TH. FRIES
Rubus chmaemorus L.
Puccinellia phryganodes (TRIN.) SCR. et MERR.

Species of this group were formed in preglacial or early Pleistocene in Beringia and spread to East and West.

Arctophila fulva, like *Puccinellia phryganodes,* attained Scandinavia first in late glacial time, when the Bothnian Bay communicated with the Barents Sea; it has several localities in the Bothnian Bay, but none on the Norwegian coast.

The taxonomy and distribution of *Puccinellia phryganodes* were studied recently by SÖRENSEN (1953). Its original home was Beringia, where occurs SÖRENSENS "Beringian type", which should be perhaps better called ssp. *phryganodes* (TRIN.) m., based on *Poa phryganodes* TRIN. In Arctic America grows the "Greenland type" of SORENSEN, with chromosome number 2n = 21, on the Siberian coast and in Scandinavia lives the "Fennoscandian type" (perhaps better called ssp. *sibirica*), with chromosome number 2n = 28, and in Novaya Zemlya and Spitsbergen the "Spitsbergen type", or better ssp. *vilfoidea* (ANDS.) m., based on *Catabrosa vilfoidea* ANDS., with the chromosome number 2n = 28.

Thus, the *Puccinellia phryganodes* s. l. never crossed the Atlantic (Greenland Sea). "It did not occur in the Atlantic sector of the Arctic prior to the breaking of the Greenland Sea... That is to say that it did not reach Spitsbergen till late Quaternary times" (SÖRENSEN, l. c.).

10. The East-Siberian group

(8 species, i. e. 5,5% of the flora)

Phippsia concinna (TH. FR.) LIND
Luzula Wahlenbergii RUPR. (map 23.)
Salix polaris WAHLENB. (map 23.)
Ranunculus Pallasii SCHLECHT. (map 23.)
Polemonium boreale ADAMS
Petasites frigidus (L.) FR.
Parrya nudicaulis (L.) REGEL
Taraxacum arcticum (TRAUTV.) DAHLST.

The centrum of origin of this group is probably in the non-glaciated part of Eastern Siberia, where they were formed in the early Pleistocene. *Salix polaris* was common in the tundra vegetation of Central Europe already during the Rissian glaciation (cf. ŚRODOŃ, l. c.).

Most of this group have not reached Greenland. If we accept SORENSEŃS hypothesis of land connection between Spitsbergen and Greenland until the penultimate interglacial (M—R), we can thus date their arrival to Spitsbergen to the second half of the Pleistocene.

Polemonium boreale and *Taraxacum arcticum* differ from the other six species in their occurrence in N. E. Greenland. But *Taraxacum* may be easily spread by the wind to longer distances, and *Polemonium boreale* is a bird cliff plant and could be transported by the sea birds.

11. The Greenland — Spitsbergen group?

(4 species, i. e. 2,8% of the flora)

The distribution and in some cases the taxonomy of these species are not sufficiently known so that the existence of this group is problematical.

Poa Hartzii is a good species, known in several places in W. and E. Greenland, on Spitsbergen and Ellesmereland. It should be perhaps better placed in the arctic amphiatlantic group. As the land connection between Greenland and Spitsbergen was destroyed probably during the penultimate interglacial, its arrival to Spitsbergen must be dated to the early Pleistocene.

Festuca hyperborea was described not many years ago. It is hitherto known in Spitsbergen, E. and N. E. Greenland and N. W. Iceland, but it is probable that it will be found elsewhere.

Carex pseudolagopina is known in E. and W. Greenland and Spitsbergen. But it is possible that it has a wider distribution. V. I. KRECZETOVICZ (1952) has *C. pseudolagopina* as a synonym to *C. amblyorhyncha* KRECZ., but in his map of distribution of this species there are no records of its occurrence in Greenland or Spitsbergen.

Ranunculus Wilanderi NATH. is known in Spitsbergen and E. Greenland.

Poa Hartzii GANDOGER em. SOERENSEN 1933
Festuca hyperborea HOLMEN 1952
Carex pseudolagopina SOERENSEN
Ranunculus Wilanderi NATH.

12. The Novaya Zemlya — Spitsbergen group

(4 species, i. e. 2.8% of the flora)

Carex parallela LAEST. (map 24.)
Arenaria pseudofrigida (OSTF. et DAHL) VAAGE 1932 (map 24.)
Pedicularis dasyantha HADAČ 1942 (map 24.)
? *Taraxacum brachyceras* DAHLST.

Carex parallela and *Arenaria pseudofrigida* belong to the "amphiatlantic" species. Both are known in E. Greenland, Spitsbergen, Novaya Zemlya, W. Siberia and Scandinavia. The main area of their distribution lies in the European Arctic. They came to E. Greenland via Spitsbergen perhaps in early Pleistocene.

Somewhat similar is the distribution of *Taraxacum brachyceras*. It is known in Waygats, in several localities on Spitsbergen and in E. and S. E. Greenland, but it is lacking in Scandinavia.

Pedicularis dasyantha grows in Spitsbergen, Novaya Zemlya and in Arctic Siberia (see also VVEDENSKIJ in KOMAROV, Flora SSSR). It never reached Greenland nor Scandinavia. We can thus date its origin approximately to the penultimate Ice age.

13. The Spitsbergen group (endemics)

(3 taxons, 2,1% of the flora)

Ranunculus spitsbergensis HADAČ 1942
Puccinellia vacillans (TH. FR.) SCHOLANDER
Papaver Dahlianum NORDH. ssp. *hadacianum* (LOEVE) m.

Ranunculus spitsbergensis is, perhaps, of a hybridogenous origin, but certainly not a recent hybrid. It spreads vegetatively only. Its occurrence in several places in Vestspitsbergen, separated by glaciers, and even on Edge Island, could be realised during the last interglacial, not later.

Puccinellia vacillans is known in several localities in the Spitsbergen archipelago and in one locality of Novaya Zemlya. It originated probably in the late Pleistocene in Spitsbergen and reached the coast of Novaya Zemlya.

Papaver Dahlianum ssp. *hadacianum* is hitherto known in Spitsbergen only, but it belongs to a little known group of plants. It is probable that it could be found elsewhere.

14. The recent immigrants

(1 species, 0,7% of the flora)

Cakile maritima SCOP.

If we do not respect the alien plants and apophytes, introduced to Spitsbergen in recent times by men, there is only *Cakile*, found on the sea shore in Isfjorden distant from harbours, which can be pointed out as a recent immigrant in the flora of Spitsbergen. The whole archipelago is nowadays so isolated from the other lands in the neighbourhood that a recent immigration of the indigenous flora (except perhaps some sea shore plants) seems hardly possible.

The Flora of Spitsbergen is thus composed of 14 more or less different elements:

The circumpolar alpine arctic group	15,9%
circumpolar arctic-subarctic group	25,5%
circumpolar arctic group	12,4%
circumpolar high arctic group	14,5%

arctic-subarctic amphiatlantic group	2,1%
arctic amphiatlantic group	4,2%
European alpine atlantic group	6,2%
eurasiatic group	1,4%
beringian group	3,5%
East Siberian group	5,5%
Greenland-Spitsbergen group	2,8%
Novaya Zemlya-Spitsbergen group	2,8%
Spitsbergen group (endemics)	2,1%
recent immigrant:	0,7%

Discussion and summary

If we want to discuss the age of arctic biota, we should know the life conditions in the Arctic during the end of Tertiary and in Pleistocene. Unfortunately, our knowledge of climate of the Miocene and Pliocene in Arctic regions is next to nothing. But some facts, concerning the conditions in Iceland, may perhaps throw some light on our problems.

B. LINDQUIST had recently determined in icelandic Miocene deposits remains of a *Betula*, corresponding very well to the recent Scandinavian and Icelandic *Betula callosa*. If this identification is right, the life conditions in Iceland in Miocene could not be much different from the present conditions. If such conditions were in Iceland, then we may expect at least subarctic conditions in the Arctic north of Iceland during the Miocene.

Under such supposition, the origin of a great part of the Arctic flora could not be dated from Pleistocene, as do most of the biologists, but from the late tertiary epoch. This supposition can thus explain many problems of plant distribution in the Arctic as well as in the high mountains of Eurasia and America, as shown e. g. by LÖVE and LÖVE (1956).

The submarine relief of the Arctic basin and the Northern Atlantic shows us that in Tertiary epoch the dry land had probably greater extent in this region than nowadays (see fig. 2.). Dry land connected probably Spitsbergen and Franz Josefs Land with the Eurasian continent; there was a broad stripe of dry land north of the East Siberian coast and from Beringian region, the Arctic American archipelago was united with Greenland and the North American continent, and there was a land connection between Greenland and Scotland or Scandinavia, and probably also between N. Greenland and Spitsbergen. There was no serious obstacles for the eldest arctic biota in their spreading from America to Eurasia or vice versa.

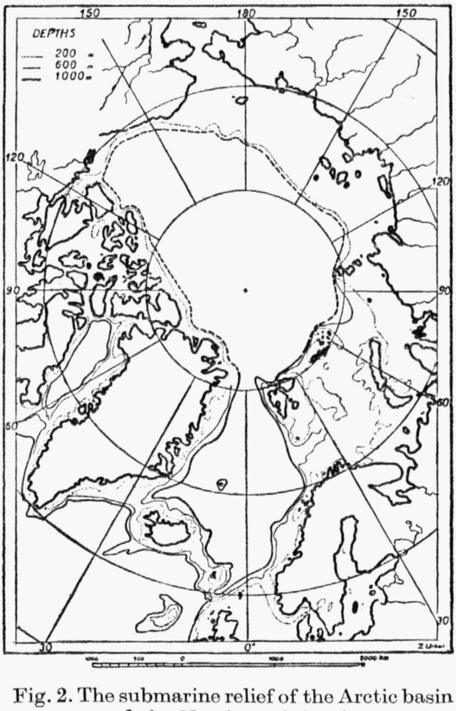


Fig. 2. The submarine relief of the Arctic basin and the Northern Atlantic.

The glaciation has destroyed a great part of land connections. Sea transgressions separated N. America from E. Asia, Greenland from Iceland and Spitsbergen, etc. These connections were perhaps restored for shorter or greater intervals during the Pleistocene, may be in Riss or Mindel-Rissian interglacial but we have hitherto no solid geological proofs for these hypothetical connections, postulated by several biologists.

A great part of Arctic America and Eastern Siberia was never glaciated, and in other parts of the Arctic there were smaller icefree refuges. Arctic biota could thus live in the Arctic region from late Tertiary to recent times (see maps 25. and 26.).

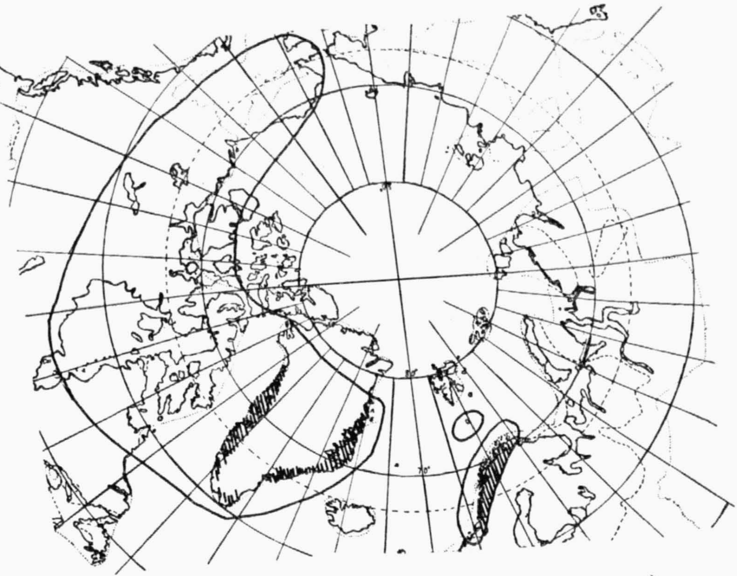
The original stock of late tertiary arctic species was mixed with immigrants from the Eurasian and American mountains, following the retreats of ice shield. Under new conditions of life new species arose and some died out . . .

The Spitsbergen archipelago was a part of the Arctic. Its isolation was realised probably during or after the penultimate glaciation. We can thus expect a prevailing part of species common to the whole Arctic, and only few endemic taxa. This is also the fact: more than 68% of vascular plant species are circumpolar, and the endemic element counts little more than 2% of the whole indigenous flora.

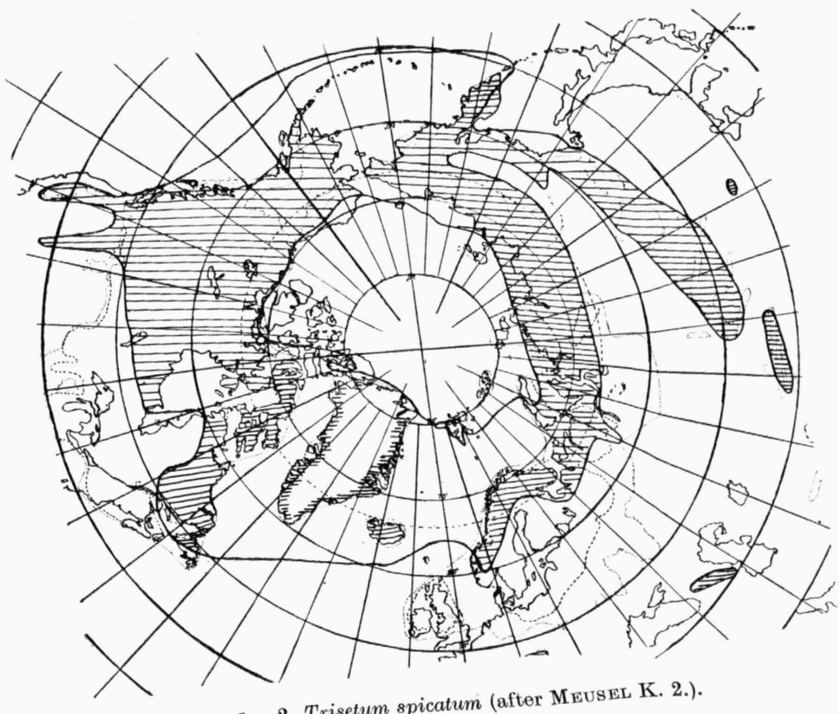
Through the analysis of the geographic areas of all indigenous vascular plants known in Spitsbergen, the present author came to the conclusion, that about 18% of the species originate from the Tertiary epoch, more than 72% are of early Pleistocene age, and 8—9% arose during the late Pleistocene, i. e. after the penultimate interglacial.

The eldest species of the Arctic region are thus — if we accept the dating of Milankovič — more than one million years old, the greatest part is about 400—600.000 years old, and the youngest species, forming only about 8% of the total flora, are approximately 50—250.000 years old.

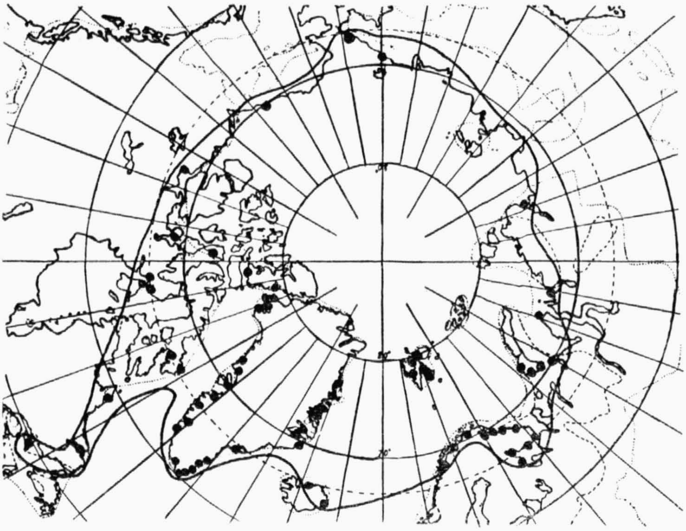
Thus, the formation of a new species in the Arctic is a very slow process. New species arise under topographical or ecological isolation of a limited population under somewhat changed life conditions, lasting for several ten thousands of years.



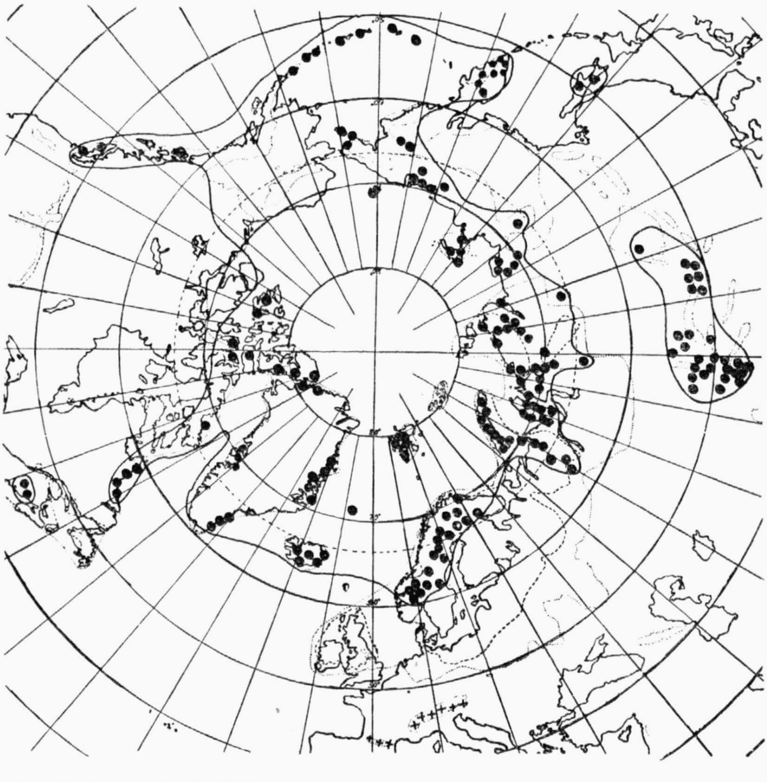
Map 1. *Rhododendron lapponicum* (after NORDHAGEN).



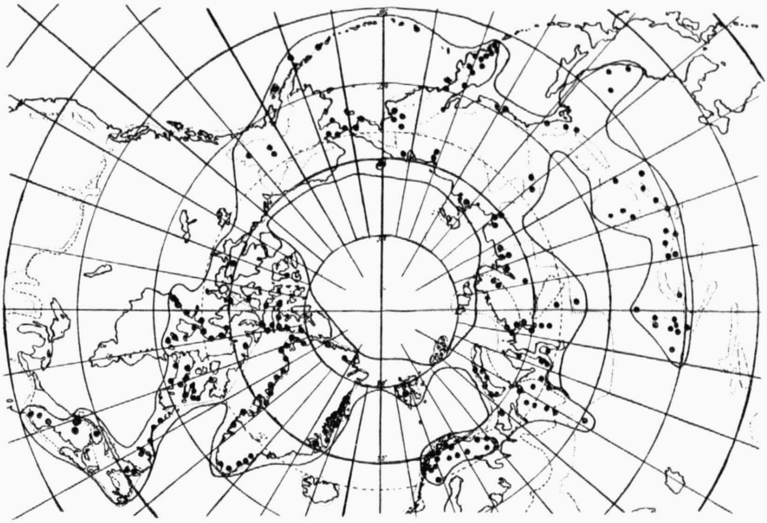
Map 2. *Trisetum spicatum* (after MEUSEL K. 2.).



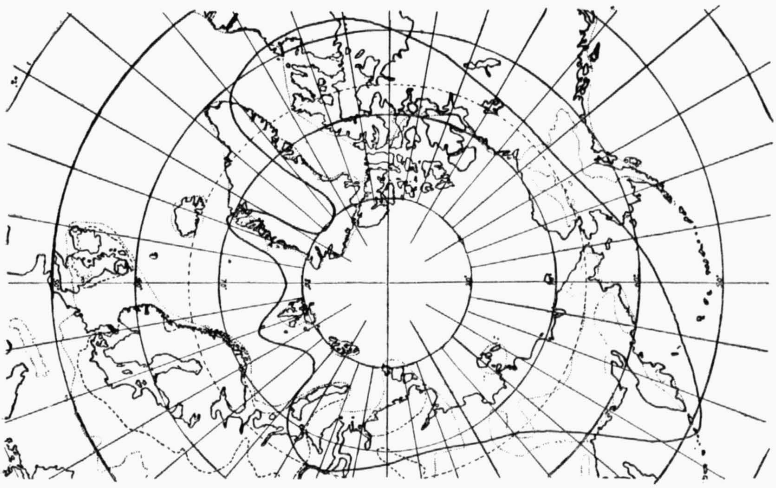
Map 3. *Stellaria humifusa.*



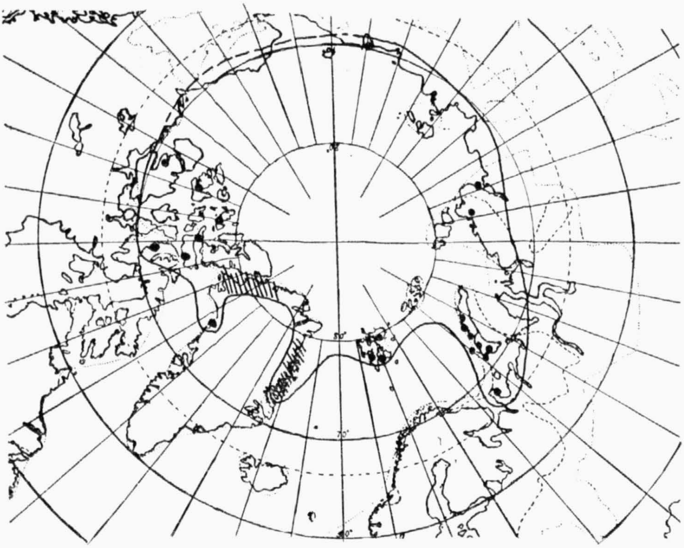
Map 4. *Cardamine bellidifolia* ● and *C. alpina* + (chiefly after Buš 1952).



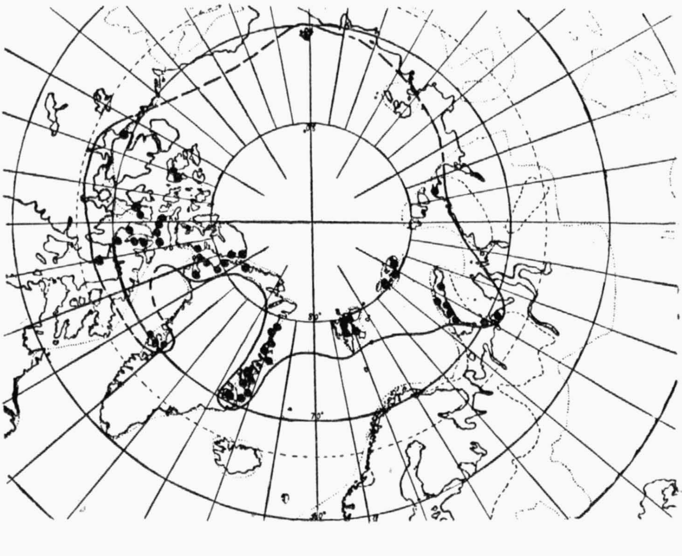
Map 5. *Hierochloe alpina* (chiefly after Areal I., k. 7.).



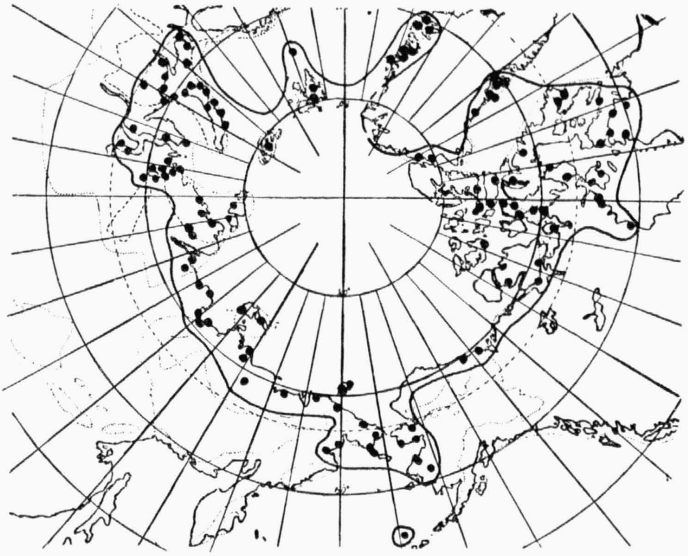
Map 6. *Alopecurus alpinus.*



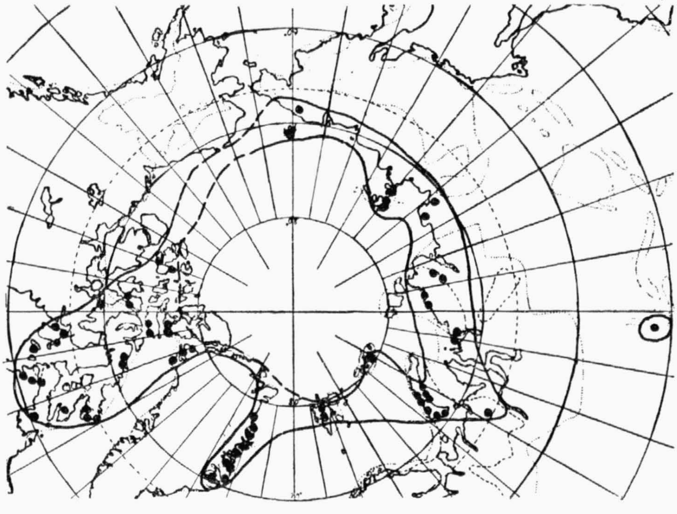
Map 7. *Deschampsia brevifolia*



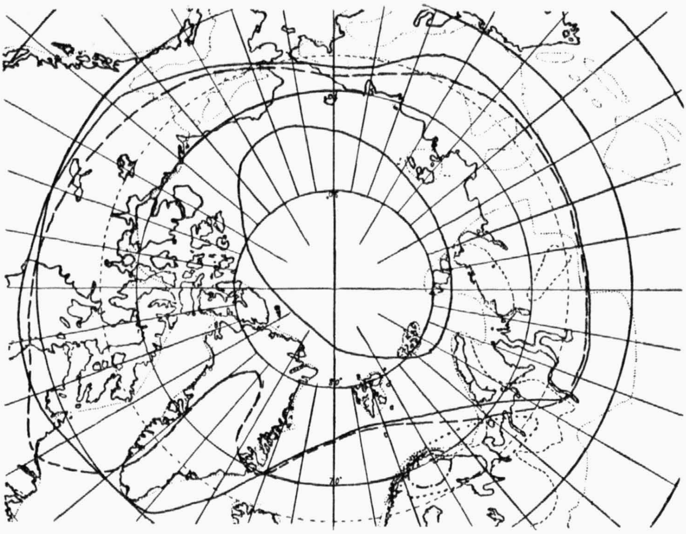
Map 8. *Poa abbreviata* (chiefly after Areal I., k. 2.).



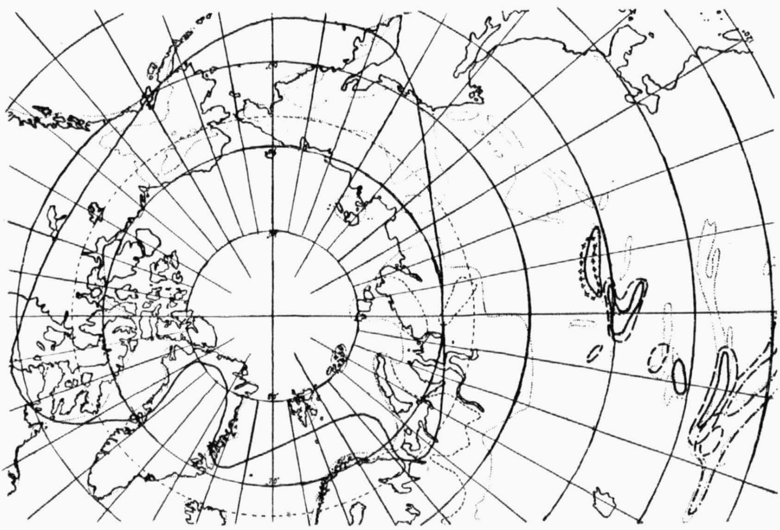
Map. 9. *Dupontia Fisheri* (chiefly after Areal I.).



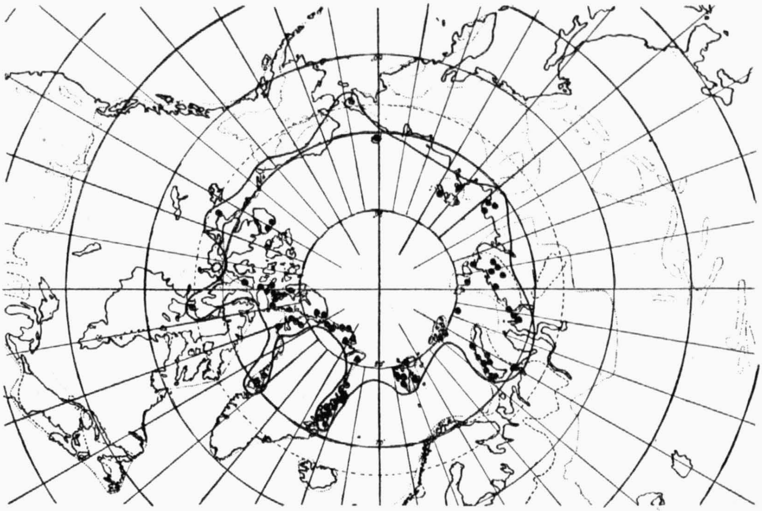
Map 10. *Pleuropogon Sabinei* (partly after Roshevic 1952).



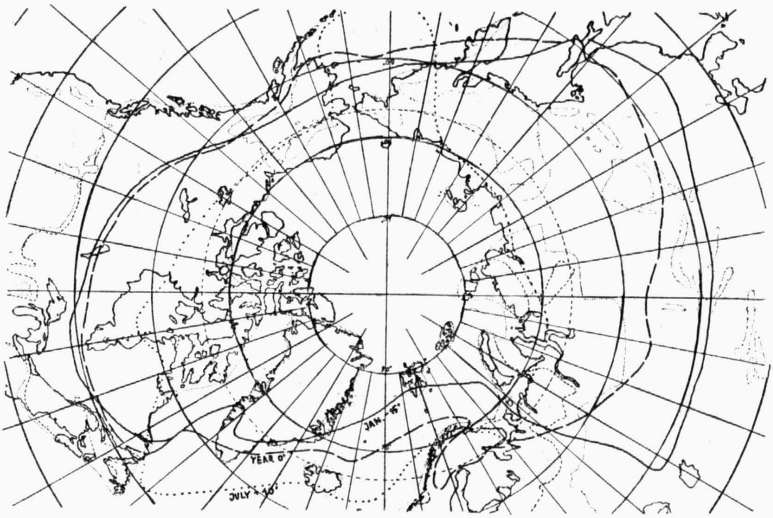
Map 11. *Arnica angustifolia* ———, *Arnica alpina* —.—.—. *Melandrium furcatum* – – –, and *M. angustiflorum* ·······.



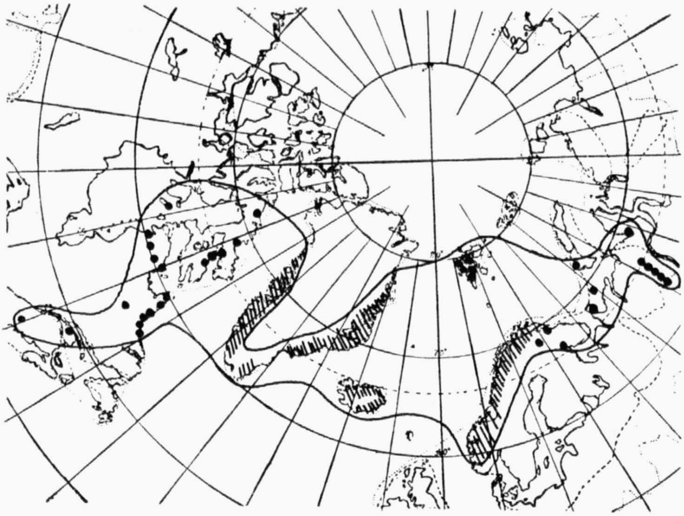
Map 12. *Eutrema Edwardsii* ———, *E. cordifolium* + + +, *E. integrifolium* – – –, *E. Przewalskii* —.—.—.



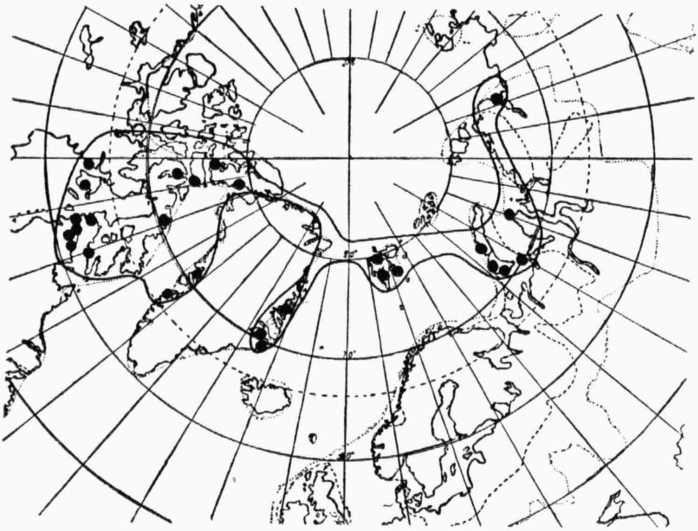
Map 13. *Draba subcapitata* (chiefly after Areal I. k. 14.).



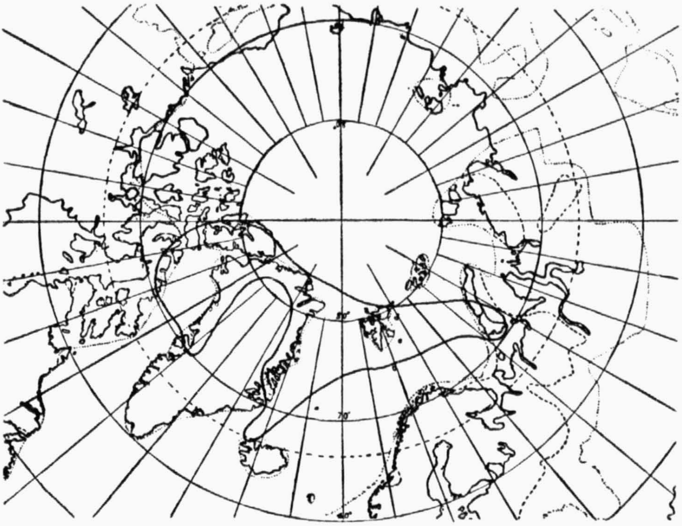
Map 14. Isotherms: ······ July ∅ 10° C, ——— January ∅—15° C, – – – year ∅ 0° C.



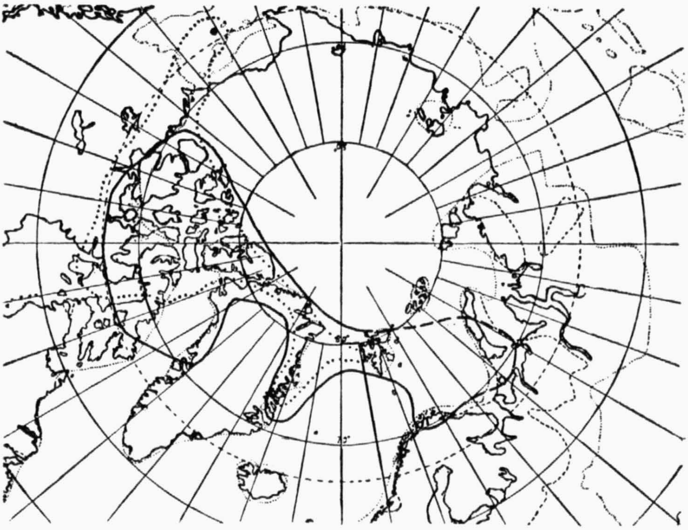
Map 15. *Cassiope hypnoides* (after LÖVE et LÖVE 1956).



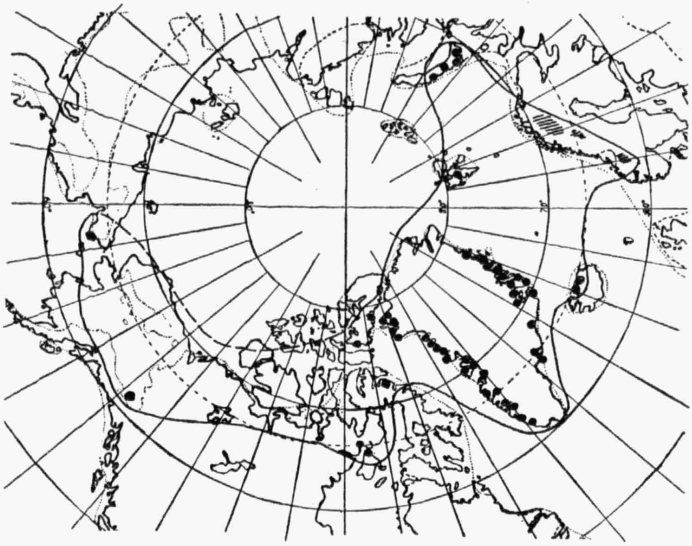
Map 16. *Carex ursina.*



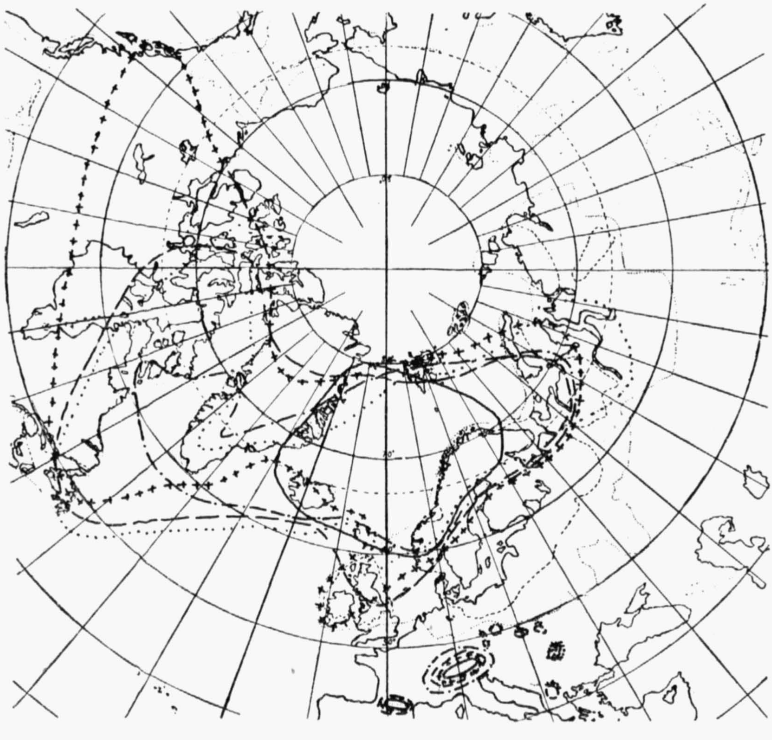
Map 17. *Eriophorum triste* (after LÖVE).



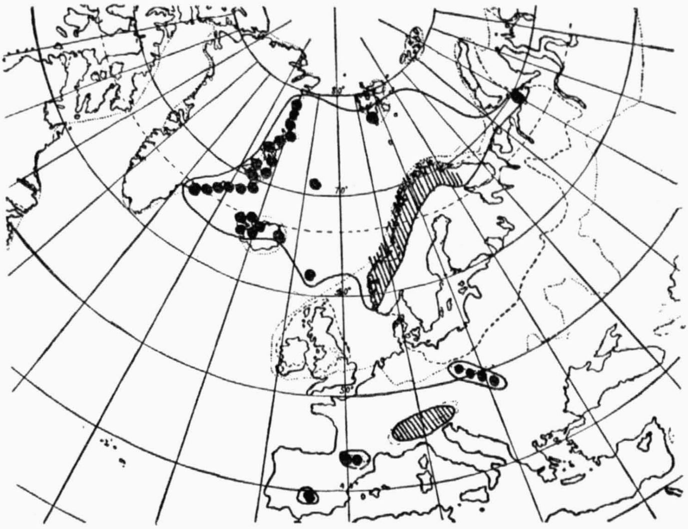
Map 18. *Minuartia Rossii* ······, and *Papaver Dahlianum* ———.



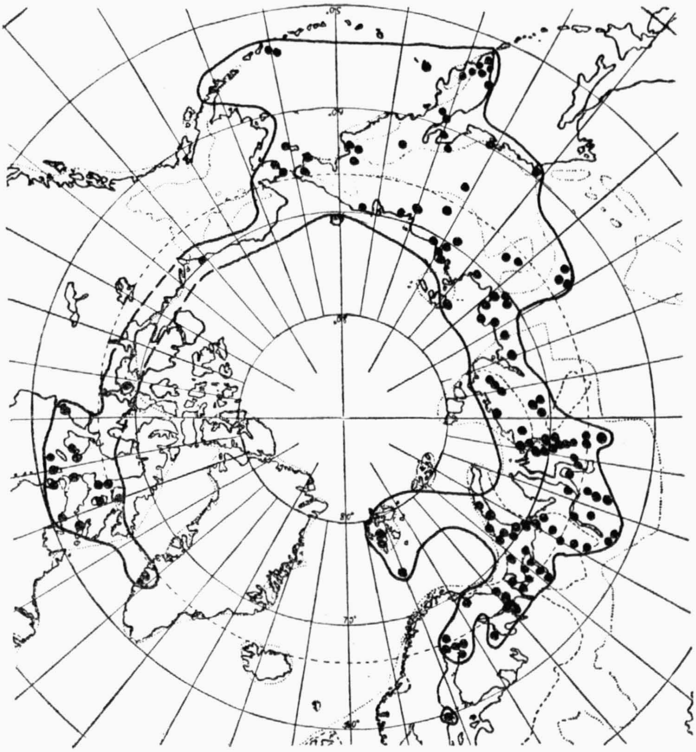
Map 19. *Campanula uniflora.*



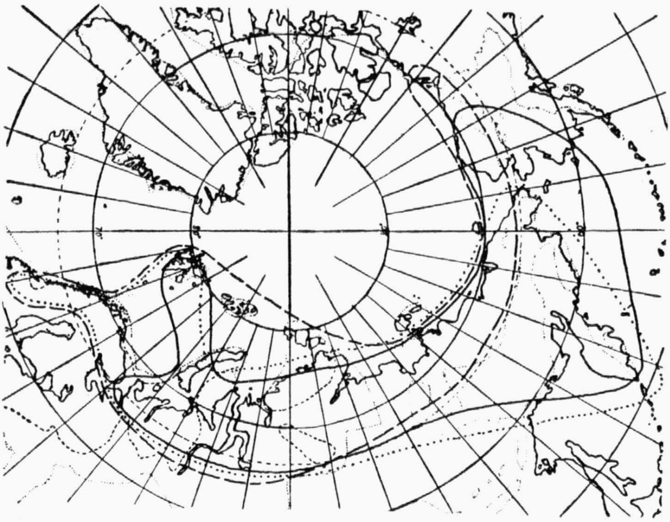
Map 20. *Arabis alpina* ·······, *Saxifraga aizoides* + + +, *Salix herbacea* — — —, *Ranunculus glacialis* ———, *Betula nana* —·—·—.



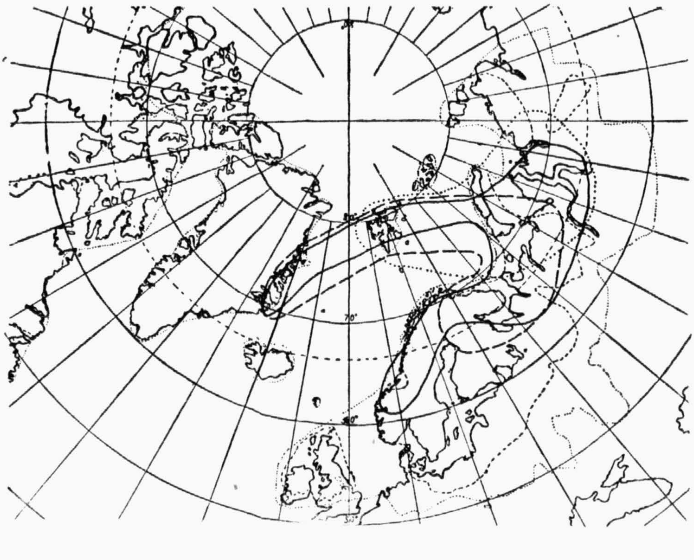
Map 21. *Ranunculus glacialis* (after Löve et Löve 1956).



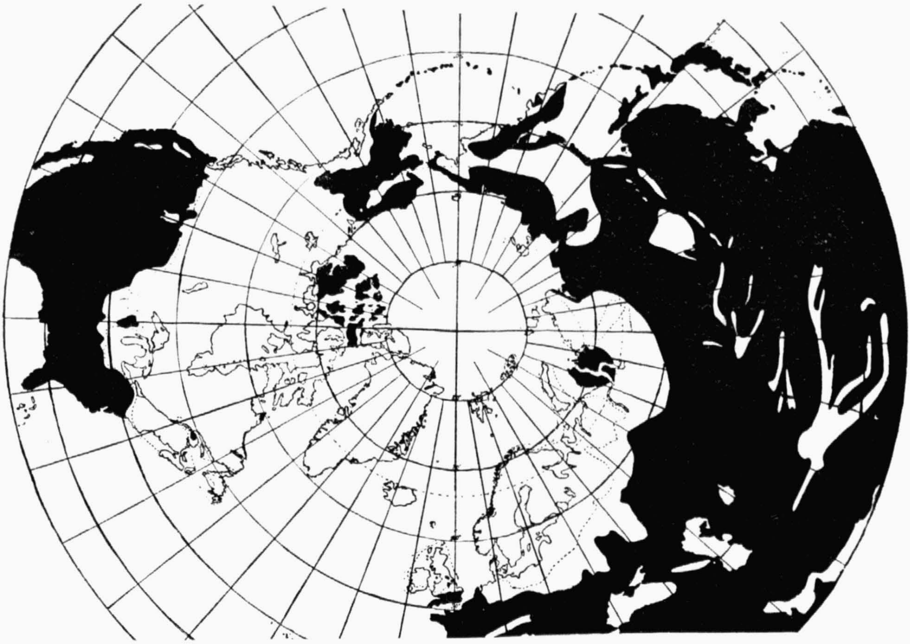
Map 22. *Arctophila fulva* (chiefly after Areal I. k. 9.).



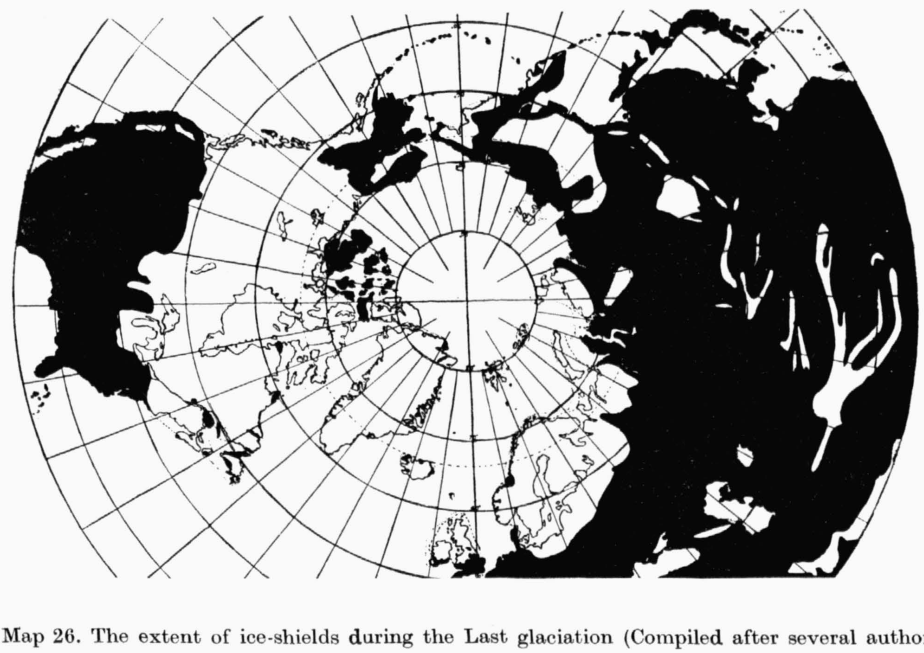
Map 23. *Ranunculus Pallasii* ———, *Luzula Wahlenbergii* ······, *Salix polaris* — —



Map 24. *Pedicularis dasyantha* ······, *Arenaria pseudofrigida* — — —, *Carex parallela* -



Map 25. The extent of ice-shields during the Great glaciation. (Compiled after several authors.)



Map 26. The extent of ice-shields during the Last glaciation (Compiled after several authors.)

Emil H a d a č :

Historie květeny Špicberk a Medvědího ostrova a stáří některých arktických druhů rostlin

V posledních dvaceti letech jsem studoval květenu a rostlinstvo evropské Arktidy, Subarktidy a středoevropských pohoří. V této studii jsem se pokusil shrnout výsledky svých studií, týkající se stáří některých druhů cévnatých rostlin Arktidy.

Prvá kapitola ukazuje, že květena Medvědího ostrova přetrvala alespoň poslední ledovou dobu na místě. Jsou pro to důkazy jak biogeografické, tak i — a to je důležité — doklady geologické. Za tu dobu, kdy květena ostrova byla isolována, tj. od posledního interglaciálu, nedošlo na tomto ostrově ke vzniku nějakých nových druhů — pokud můžeme aspoň soudit podle dosavadních výzkumů. Ukazuje to, že druhy cévnatých rostlin v Arktidě jsou velmi stálé.

Rozborem areálů všech druhů cévnatých rostlin, známých ze Špicberk, došel jsem k závěru, že nemalý počet, asi 18 %, druhů je stáří tercierního, jsou tedy stálé po dobu snad více než jednoho milionu let; převážná většina druhů, 72 %, pochází z první poloviny Pleistocénu (stáří 400—600 000 let), a nejmladší druhy, tvořící jen asi 8 % špicberské květeny, pocházejí z mladšího Pleistocénu a jsou tedy asi 50 000—250 000 let staré.

Je tedy vznik druhů v Arktidě pochodem velmi pomalým. Ke vzniku druhů přispívá isolace omezené populace, která za poněkud změněných podmínek, působících po několik desítek tisíciletí, vytvoří nový, odchylný taxon.

Za provedení mapek děkuji as. M. Barešovi z VPŠ v Plzni, za jazykovou kontrolu anglického textu vděčím své manželce, Aleně Hadačové a odb. as. Zd. Růžkovi z VPŠ v Plzni.

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