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AREA-LIMITS AND ISOLATIONS OF PLANTS IN RELATION TO THE PHYSIOGRAPHY OF THE SOUTHERN PARTS OF GREENLAND

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WITH 10 FIGURES IN THE TEXT

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I. INTRODUCTION

In a previous paper (B. 1951)[1] the view was advanced that there might be a connection between some area-limits of plants and the boundaries between areas with and without alpine physiography. This accordance might be due to historical factors, more particularly that alpine areas during the last ice age had not been covered by a continuous ice-sheet, but appeared as "nunataks", and that some plants had been able to persist on the uncovered mountain sides of the nunatak-areas, but later were unable to spread or had not yet had a possibility of spreading from these refugia to the landscapes which were rounded-off through the action of a large ice-sheet. With reference to a number of Greenland plant distributions which in the previous paper were thought to substantiate this theory, the author would in the present paper like to penetrate more deeply into the problems and to consider some new viewpoints of importance for the discussion of perglacial survival. This discussion will center round two main subjects: (1) the coincidence of some non-ecological area-limits of plants and physiographical boundaries, (2) the location of stations with many isolated occurrences and a particularly rich flora to areas which owing to physiographical conditions have a great possibility of escaping an advance of the ice cap. Before any discussion, however, two requirements have to be fulfilled, viz. the topography must be well-known through accurate maps and aerial photographs and the floristic investigations must be so thorough that the limits and isolations in question can be regarded as established. Today both requirements can even in Greenland be fulfilled to such an extent that some conclusions of general importance may be drawn.

[1] Works by the present writer are quoted as B. followed by a year.

II. PHYSIOGRAPHY AND GLACIATION

According to L. Wager (1933) the Greenland ice cap may have been formed already in the Pliocene Age. The highly elevated Greenland peneplane was then covered by a large ice-sheet which later during interglacial epochs retired from the coasts, but which probably persisted in the central parts. Rests of the old peneplane were demonstrated by L. Wager on the westernmost nunataks around Mt. Forel (Schweitzerland) in the Angmagssalik District, whereas the eastern mountains in this district had an alpine structure. The keeping of the peneplane must be due to the existence of a long lasting continuous immobile ice cover and the alpine structure presupposes a protracted heavy glacial erosion during which the valley systems between the rests of the peneplane were enlarged until local glaciers finally formed the rests as peaks and jaggy ridges. This involves that areas with a marked alpine structure cannot for a considerable time have been covered by a continuous ice-sheet and may thus, if the climatological conditions were not inhibitory, have harboured a number of plants.

Of great importance is the fact that a glacial erosion along the margin of a peneplane will, as time proceeds, make a total covering by ice more and more difficult. The large valleys and fjords which cut into the margin form important drainage systems and the cross valleys which in many cases connect the main valleys or even the fjords form very efficient obstacles to an advancing ice-sheet as they may turn its direction and force the ice down into the main valleys.

A continued heavy glacial activity will of course sooner or later break down even spiky mountains which finally are submerged in an extended ice cap. In southeast Greenland there are many areas which evidently have been entirely covered during maximum extensions of the inland ice. Other areas, however, show no evidence of having been covered. This may primarily be due to different heights of the fringing mountain walls which formed obstacles to extensions of the ice cap, secondarily be a result of drainage of the ice cap. Wide coastal areas which are completely submerged and along which numerous icebergs split off will probably be able to drain the ice cap to such an extent that intermediate areas with spiky mountains will only be subjected to local glaciation.

From the entrance of Scoresby Sund southwards to Kap Farvel there are three major gaps which during periods with higher glacial activity must be used as primary drainage areas, viz. the area south of Kangerdlugssuaq (about 67°—68° lat. N., cf. Map 67 ö1), the area west and south of Angmagssalik (about 63°30′—65°30′ lat. N., Maps 63 ö1, 64 ö1) and the area between about 61°00′ and 62°30′ lat. N.). These areas separate the large alpine landscapes in the former Knud Rasmussens Land, Angmagssalik, Skjoldungen, and the Kap Farvel area. West of Kap Farvel a large roche moutonné landscape is found between the high mountains around and north of Tasermiut (45° long. W.) and Kap Thorvaldsen (48° long. W.). Near Qagssimiut (47° long. W.) the inland ice is separated from the sea only by a narrow coastland of rounded and very low mountains. This part undoubtedly has served as an important drainage area and was completely submerged whereas the high peaks to the west between Kap Thorvaldsen and Sermersût may have formed a chain of semi-nunataks (cf. WEGMANN 1938).

The large coastland of West Greenland south of Disko Bugt forms a contrast to Southeast Greenland by being chiefly a roche moutonné landscape. Apart from scattered high mountains with spiky peaks suggesting former nunataks (e. g. the Norssaerserfik in Frederikshaab district) this part of Greenland has only one large area with an alpine topography, viz. the coastal mountains north of Sukkertoppen (Hamborgerland and the mountains around the outer part of Søndre Strømfjord, cf. NORDENSKJÖLD 1914, BELKNAP 1941, and fig. 5 in B. 1951).

III. TYPES OF PLANT REFUGIA

Dahl (1946) has described different types of unglaciated areas during the Ice Ages and their significance to plant geography. He distinguishes between maritime mountain refugia and continental tundra refugia. No doubt both types occur in Greenland and can in certain regions be studied today. In Southeast Greenland large coastal stretches appear as chains of semi-nunataks, mountains, or capes surrounded by ice on three sides but facing the sea on one side. They correspond to the mountain refugia and they owe their existence mainly to topographical conditions. On the other hand, the tundra refugia, which may be paralleled with some of the large desert-like areas in northernmost Greenland, are conditioned mainly by the climate or by a combination of climate and topography. Whereas climate (high summer temperature, low precipitation) in presentday Greenland without doubt plays an important role for the occurrence of large unglaciated areas in West, North, and Northeast Greenland, it is clearly of secondary importance in the oceanically influenced Southeast Greenland. Unglaciated areas here owe their existence mainly to such physiographic features as the occurrence of very high mountains which cannot be submerged in our day, the occurrence of fringing mountains within which the ice cap is held, and differences as to drainage possibilities of the ice cap. This part of Greenland, thus, lends itself to a closer study of maritime refugia, which by many authors are supposed to have been of great importance in West Scandinavia during the last Ice Age.

If the topographical data which appear from aerial photographs and the modern maps of East Greenland are compared with the botanical observations, it seems possible to separate four types of maritime refugia, which are connected through intermediate types.

(1) *Nunatak refugia.* High mountains projecting above the ice cap and surrounded by ice in all directions. No lowland areas uncovered.

(2) *Semi-nunatak refugia.* Mountains facing the sea on one side, otherwise surrounded by ice. Uncovered lowland areas on the seaward side.

(3) *Cross-valley refugia.* Refugia (as a rule large semi-nunataks) containing cross-valleys cut out during earlier glaciations but later more

or less unglaciated owing to local changes in the drainage of the ice cap (retrogression or removal of the areas with heavy erosion in the main valleys). Uncovered lowlands may occur in the cross-valleys.

(4) *Parallel valley refugia.* Valleys or depressions with the same direction as the main valleys (or fjords) and situated between two parallel long valleys which drain the neighbouring part of the ice cap and which further receive most of the local glaciers formed on the mountains between the three valleys. Unglaciated lowlands may be found in the middle valley, especially if it is situated near the sea in a mountain area appearing as a large semi-nunatak. Evidence of the existence of unglaciated valleys of this type is found today even as part of a nunatak (the unglaciated valley at a height of 500—1000 m above the sea situated between the two huge glaciers, the Sorgenfri Gletscher and the Christian den IV's Gletscher east of Kangerdlugssuaq in East Greenland, cp. Map 68 ö3).

In Southwest Greenland the same four types may have occurred, but there very large land masses undoubtedly must have been covered by an extended ice cap. Of particular interest there, however, is the possibility of the occurrence of refugia of the tundra type. The existence during the last glacial epoch of such a refugium at the head of Søndre Strømfjord was briefly discussed in B. 1949. The area lies in a pronounced roche moutonné landscape which in earlier glacial epochs must have been heavily glaciated. It is furthermore situated between the inland ice and the area of alpine physiography north of Sukkertoppen and has an extremely low precipitation (B. 1954a). This climatic dryness which is a pronounced rain-shadow effect may here even during a period of higher glacial activity have conditioned the occurrence of one or some limited unglaciated areas of a continental climatic character. Today we find several "nunataks" of the roche moutonné type which may give us some idea of how such continental tundra refugia appeared. They evidently owe their existence to climatic as well as physiographic features, more particularly the scarcity in precipitation and the drainage conditions of the ice cap in their surroundings.

IV. SOUTHEAST GREENLAND AND KAP FARVEL

A. The Blosseville Kyst and the Nunataks Behind It.

In this part of East Greenland botanical investigations are not very copious, mainly consisting of the collections and observations made in 1932 by the present writer (B. 1933 a-b) and the unpublished material collected by H. G. WAGER during the British expedition in 1935—36 (cf. H. G. WAGER Appendix Botany in L. WAGER 1937 p. 417). While the material collected by WAGER undoubtedly will bring important new information as regards the flora and the ecological conditions on nunataks (he found flowering plants to an altitude of about 7000 feet and a flora comprising about 40 flowering plants on the nunataks) the material collected by me may be of importance for the discussion of the other types of refugia mentioned above.

Capes which formerly were semi-nunataks are numerous along the inclement Blosseville Kyst of the former Knud Rasmussens Land. Kap Daussy (68°43′) is a very good example. On the steep slope of this cape we have one of the four Greenland stations of the *Ranunculus auricomus* complex and an isolated station for *Carex norvegica* (see B. 1933 b, p. 9, 1938 figs. 40, 42, and 119). At present the cape is not surrounded by ice on its three sides, but this was clearly the case earlier. A little farther south another cape, Kap Ravn (68°30′), is more like a recent semi-nunatak. As may be seen on fig. 1 large glaciers discharge into the fjords on both sides. 18 species were recorded on Kap Ravn among which a few typical low arctic ones, e. g. *Arabis alpina* and *Agrostis borealis*.

Immediately north of Kap Ravn the south-facing mountains may be instanced as showing the cross-valley effect. These mountains which slope down towards Wiedemanns Fjord and the main valley continuing this fjord towards the west appear to be protected from being submerged by ice. They constitute the southernmost part of a large spiky mountain area which is situated between two very large ice tongues (Borggraven and Kronborg Gletscher). The valley which continues Wiedemanns Fjord towards the west is a transverse valley and although glaciated it will never receive any considerable amount of ice because the main drainage areas of the big Kronborg Gletscher is to the west between

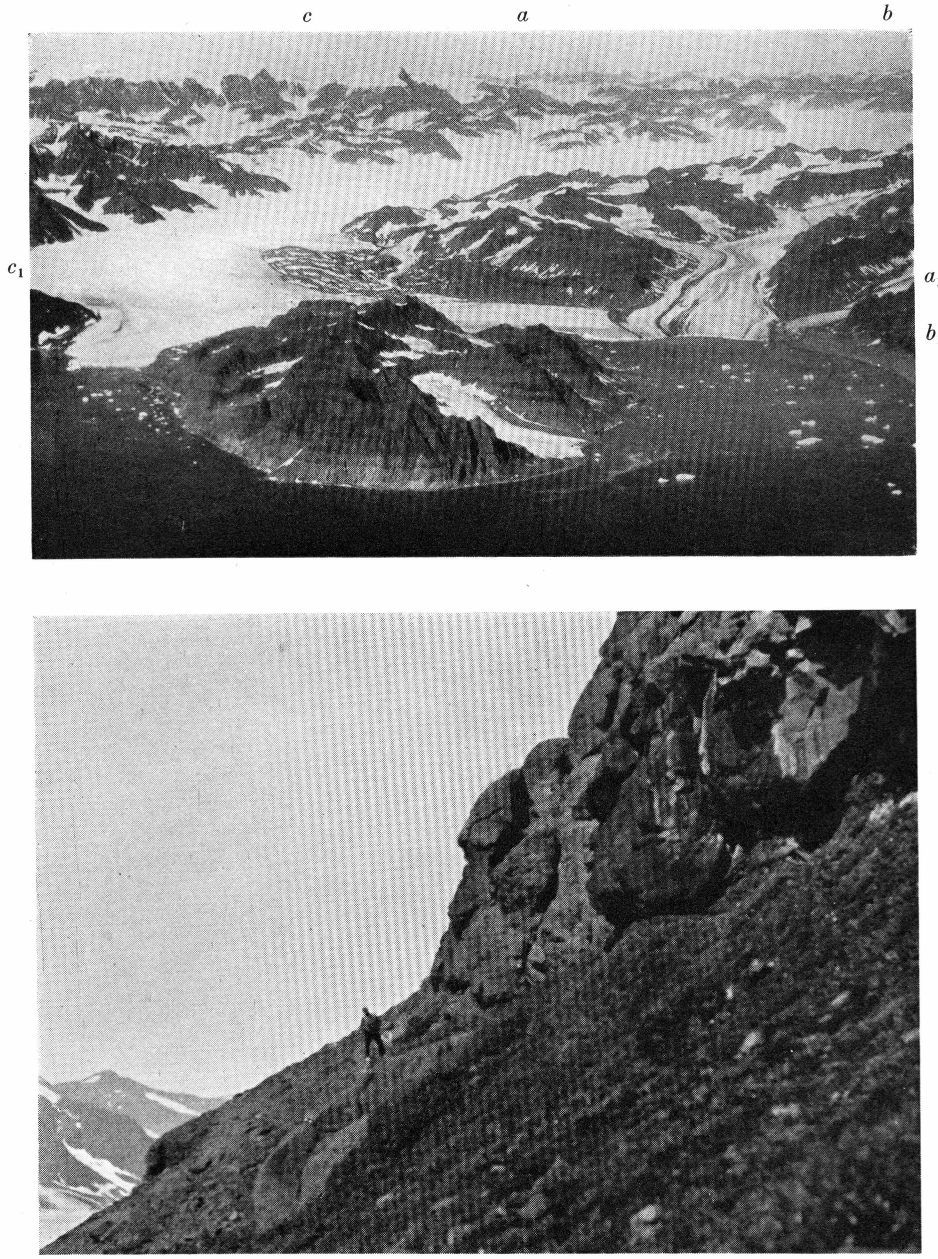

Fig. 1. Kap Ravn and Wiedemanns Fjord in East Greenland. Above: Aerial view with the cape in the middle, separated from the rest of the country by a transverse valley. The south-facing steep side in the transverse valley (a—a_1) harbours a very rich flora. On the extreme right there is another south-facing slope with an equally rich vegetation in Wiedemanns Fjord (b—b_1). A picture from the latter place is seen below. The vegetation is a herb-field rich in species, with a considerable contingent of southern species. — Above: Aerial view 21212 (1933), Geodetic Institute copyright; below: TWB phot. 1932.

Kap Ravn, Kap Stephensen, and Kap Rink. It is also protected from being submerged from the Borggraven glacier, which discharges into Vedels Fjord towards the east. The sunny south- and southwest-exposed slopes at the head of Wiedemanns Fjord and the transverse valley have a very rich flora comprising 91 vascular plants (Fig. 1; B. 1933 a-b Loc H) among which many are southern or even boreal elements. Some of these occurrences are greatly isolated outpost stations of southern species (e. g. *Botrychium lanceolatum*, *Polystichum lonchitis*, *Carex macloviana*). On fig. 1 it is evident that the two places with the very rich flora (a-a_1, b-b_1) are situated above the screes of basalt boulders which might have been formed as lateral moraines during the last Ice-age at the same time as the smoothed part of the mountain at c-c_1 was submerged.

The cross-valley effect may be much more pronounced in Mikis Fjord. The inner part of this fjord is a cross-valley and it is protected by the more northerly Watkins Fjord which is another cross-valley. The large ice masses north of Mikis Fjord are now partly forced down towards Watkins Fjord, partly turned eastwards through a transverse valley which debouches into I. C. Jacobsens Fjord. In Mikis Fjord only local glaciation takes place and the spiky mountains surrounding it makes it probable that the same may have been the case at least during the last glaciation. Its flora is of the same character as that at the head of Wiedemanns Fjord and also contains a number of much isolated stations (*Equisetum variegatum*, *Leucorchis albida*, *Carex bicolor*, the two last-mentioned southern species having been found there by H. WAGER).

B. Angmagssalik District.

The flora of this important area has especially become known through C. KRUUSE's collections in the beginning of this century (KRUUSE 1912) and through the supplementary collections made especially by R. BÖGVAD on the Seventh Thule Expedition in 1933 (B. 1938).

The large Sermilik fjord forms a main drainage system of the inland ice. As it is on both sides surrounded by rounded-off mountains it seems during a great glaciation to have been filled by a considerable glacier tongue. East of the fjord the broad, not glaciated alpine country is intersected by narrow fjords and many transverse valleys and close to the sea split up into numerous larger and smaller islands. The innermost part of the alpine country is continued towards the north as a very large number of nunataks, of the flora of which we are unfortunately ignorant. A more intensive glacial activity than that of the present time will no doubt result in most valleys and fjords being glaciated so that the landscape is to some degree changed into nunataks. The transverse-valley effect, however, will very easily be able to cause that fairly large ice tongues are deflected so that fairly large ice-free areas arise. An advance of ice from the north will, e. g., be intercepted and turned towards the southeast by Ikerasagssuaq, so that the Angmagssalik island is only exposed to local glacial activity.

(a) Recent plant distributions and topographical main features.

Fig. 2 shows partly the boundary between the roche moutonné landscape and the alpine landscape in the district and partly the distribution of *Ranunculus glacialis* and *Pedicularis hirsuta.* It cannot be denied that the agreement between the plant distributions and the alpine topography here is so complete as might be desired. Both species are widely distributed arctic species and furthermore the *Ranunculus* is a species with an oceanic-alpine distribution. As *R. glacialis* today is thriving on the mountains of the Faroes, it also ought to be able to grow on northern exposures and mountain peaks in the area south of Angmagssalik. The power of spreading of the species is perhaps not very great. Perhaps the spreading especially takes place by means of reindeer (cf. Norman 1895). Still, it has a wide Atlantic distribution to where it may have migrated across wide sea areas. *Pedicularis hirsuta* is found in the Godthåb region (fig. 98 in B. 1938) and therefore also ought to be able to grow more southerly than at Angmagssalik. Its power of spreading at long distances perhaps is fairly small (seeds not very small).

Three species, which all are eastern or of European origin, are in the whole of Greenland known only from the Angmagssalik district, viz. *Alchemilla wichurae*, *Sedum acre* (B. 1938, fig. 52), and *Hieracium angmagssalikense* which is related to *H. sundbergii* in Scandinavia.

An isolated area of occurrences in the Angmagssalik region has such northern species as *Potentilla hyparctica* (fig. 58 in Seidenfaden & Sørensen 1937), *Pirola grandiflora*, *Antennaria porsildii*, *Juncus castaneus* (figs. 82, 105, and 130 in B. 1938), *Draba crassifolia*, and *Juncus arcticus* (figs. 35 and 44 in Gelting 1934). All these species are found east of the physiographical boundary-line in fig. 2. On the other hand, *Dryas integrifolia* and *Betula nana*, which both occur in an isolated area at Angmagssalik (figs. 32, 66, and 67 in B. 1938), are found at the head of the Sermilik fjord in areas with smoothed mountains.

The following southern species are of isolated occurrence in the Angmagssalik district: *Ranunculus reptans*, *R. acer*, *Subularia aquatica*, *Callitriche anceps*, *Mertensia maritima*, *Juncus subtilis*, *Sparganium angustifolium* (maps figs. 46, 47, 51, 94, 133 in B. 1938), *Gentiana aurea* (fig. 14 in B. 1950), *Galium brandegei*, and *Alopecurus aequalis* (figs. 28 and 25 in B. 1952a). All these species as well are only found east of the physiographical boundary-line in fig. 2.

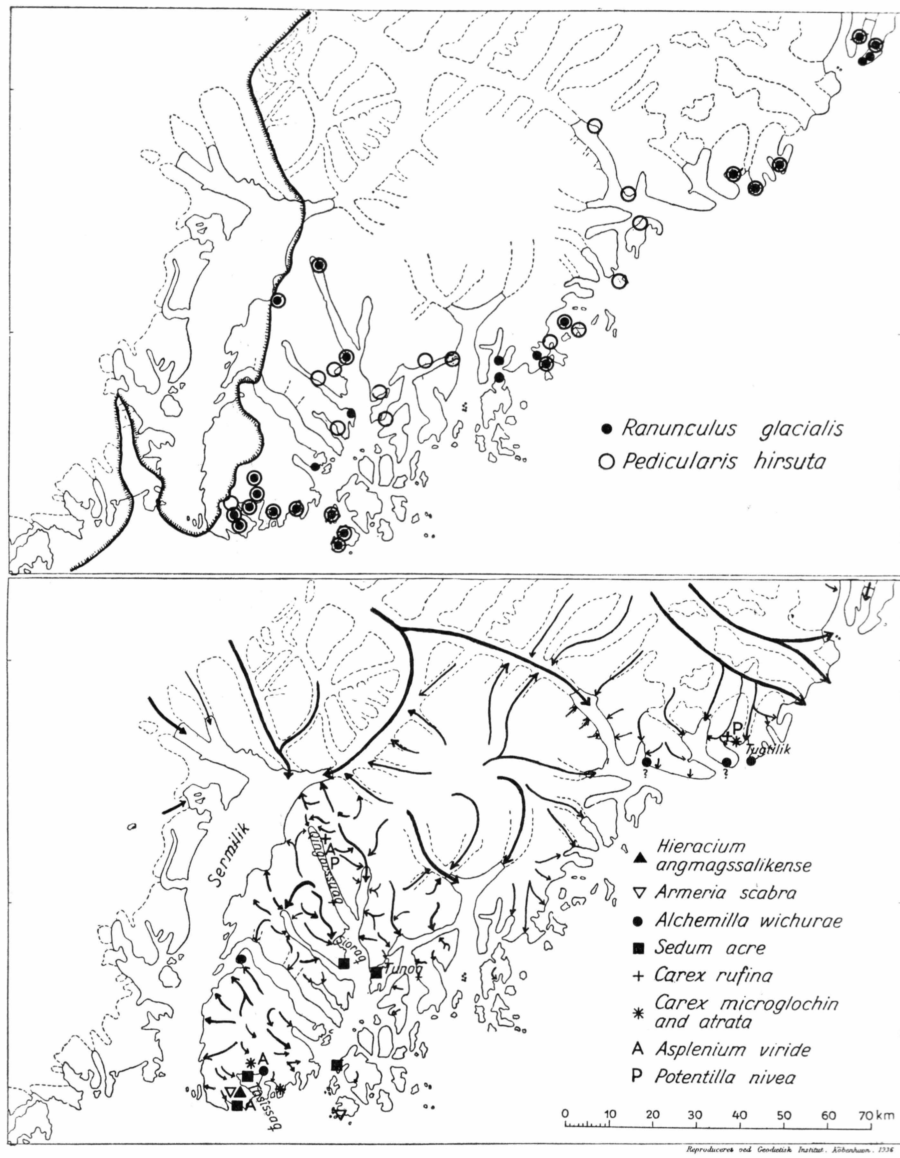

Fig. 2. Two maps of the Angmagssalik district. On the map above are indicated the limit of the smoothed mountain form and the distribution of *Ranunculus glacialis* and *Pedicularis hirsuta*. The map below shows the direction of the local glaciers according to the topographical conditions. Furthermore a number of important isolations in the Angmagssalik district (*Alchemilla wichurae*, *Sedum acre*, *Hieracium angmagssalikense*) and some very rare species such as *Armeria scabra*, *Carex microglochin*, *C. atrata*, *C. rufina*, *Asplenium viride*, and *Potentilla nivea*.

The agreement found between topography and isolated occurrences of plants thus is great, but we cannot make too sure conclusions from it.

In the first place, the western side of the Sermilik fjord has not been thoroughly investigated, and in the second place, the Angmagssalik country projects as a bulge into Danmarksstrædet, and thus perhaps becomes especially exposed to recent immigration of eastern species from Iceland. However, such species as *Callitriche anceps* and *Juncus subtilis* have not been recorded from Iceland, and *Ranunculus acer* has another racial composition there than at Angmagssalik.

The question therefore arises whether the considerable roche-moutonné area southwest of Angmagssalik mentioned on p. 5 was not during the last Glacial Age completely glaciated and served as a gigantic drainage area of the inland ice, so that great parts of the alpine landscape in the Angmagssalik region was so little glaciated that even lowland areas there were ice-free and might harbour a relatively southern flora.

The species termed northern above are with the exception of *Dryas* and *Betula* concentrated at the head of the fjord Qíngorssuaq (cf. Kruuse 1912 pp. 73—83 and 125—37). Kruuse there also mentions *Cassiope tetragona*, which he thinks occurs isolated there. However, this has proved to be less correct as Bögvad later found it in a number of stations in the district (see B. 1938); on the other hand there is reason to discuss Kruuse's theory that *Cassiope* in Qíngorssuaq should be a relict which survived during the Glacial Age on the high, pointed and jagged peaks there. Kruuse probably was of opinion that *Cassiope* grew together with other species in an alpine nunatak area, but the question is whether parts of the lowlands were not ice-free as well.

(b) Recent plant distributions and local physiographical conditions.

In direct continuation of the discussion above it will in what follows be discussed how the local conditions during a greater glaciation than the present one may have been and whether it is possible to see any connexion between a characteristic local flora and special physiographical conditions. Especially in three places in the Angmagssalik region there is a particularly rich flora, amongst other things including isolated occurrences of some species.

1. Qíngorssuaq (Angmagssalik Fjord) (fig. 3). As appears from Kruuse's investigations, the richest flora is concentrated to the mountains around the head of the fjord, viz. Cassiopefjeld, Kilikisâq, Qáqarssuaq, and Falkefjeld. In fig. 2 below, conditions of drainage during a greater glaciation are indicated by arrows placed in the valleys. It can be established there that the locality is protected from a greater glaciation through the transverse-valley as well as the parallel-valley effect. Ice advances from the north will be forced into the Sermilik fjord through

the transverse valley, which is filled by the Midgårdgletscher. Ice advances from the east from the firn around Rytterknægten will be intercepted by the parallel valley in continuation of Tasîssârssik, and besides, this firn will mainly be drained off through the chief glacier towards the southeast to Sermiligâq, where the mountains on both sides of the fjord show clear signs of wearing-down as a consequence of glacial erosion. The possibility is then left of a glaciation of Qíngorssuaq as a consequence of increased accumulation of ice in the area; but it will be seen that the chief drainage will occur in the parallel valleys, viz. Ikerasaussaq and Sioraq towards the west and Tasîssârssik towards the east and the Sermilik fjord towards northwest.

Most species of rare or isolated occurrence around the Qíngorssuaq fjord are northern (*Cassiope tetragona*, *Arnica*, *Potentilla nivea*, *P. hyparctica*, *Pirola grandiflora*, *Campanula uniflora*, *Draba crassiflora*, *Erigeron unalaschensis*, *Antennaria porsildii*, and *Woodsia glabella*) and might be supposed to have managed in a nunatak area. *Juncus castaneus* and *Carex rufina* might also have grown there, while it is more difficult to imagine that *Juncus arcticus* occurred there. Finally there are such southern species as *Asplenium viride*, *Gentiana aurea*, and *Bartsia alpina* var. *jensenii*. They might best have occurred on an ice-free south-facing slope not too high above sea level. Especially the mountain Qáqarssuaq seems to me to possess all conditions of having harboured lowland plants (cp. fig. 3 and +, A, P in the Qínqorssuaq area, fig. 2 below).

There are also several other floristically rich stations in the interior part of the Angmagssalik Fjord (Tasîssârssik, Sioraq, Tunoq; see KRUUSE *loc. cit.*), where the possibility of lowland refuges is great. The mountains east of Tasîssârssik are mainly drained southwards to Sioralik; at Sioraq the Qingâq mountain must be assumed to have had ice-free slopes with southern exposures towards the fjord, and at Tunoq the south-facing slopes cannot possibly have been covered by the small glacier which will develop in the valley going in a northwest direction across the creek.

2. Tasîssaq near the town of Angmagssalik. Around this creek and east and west of it there is a very rich and interesting flora. As appears from fig. 2 below, the draining of local firn areas on the Angmagssalik island will especially take place westwards to Sermilik and southeastwards through the valley which continues the creek Sangmileq. Under more intensive glacial activity the greater part may be submerged, but hardly the mountains of the south coast, which form a range with altitudes between 700 and 1000 metres above sea level. This range is protected from submerging from the north by the transverse valleys at the mountain Præstefjeldet and the Sermilik road, which will deflect possible glaciers and force them down to Tasîssaq. Qordlortoq Sø,

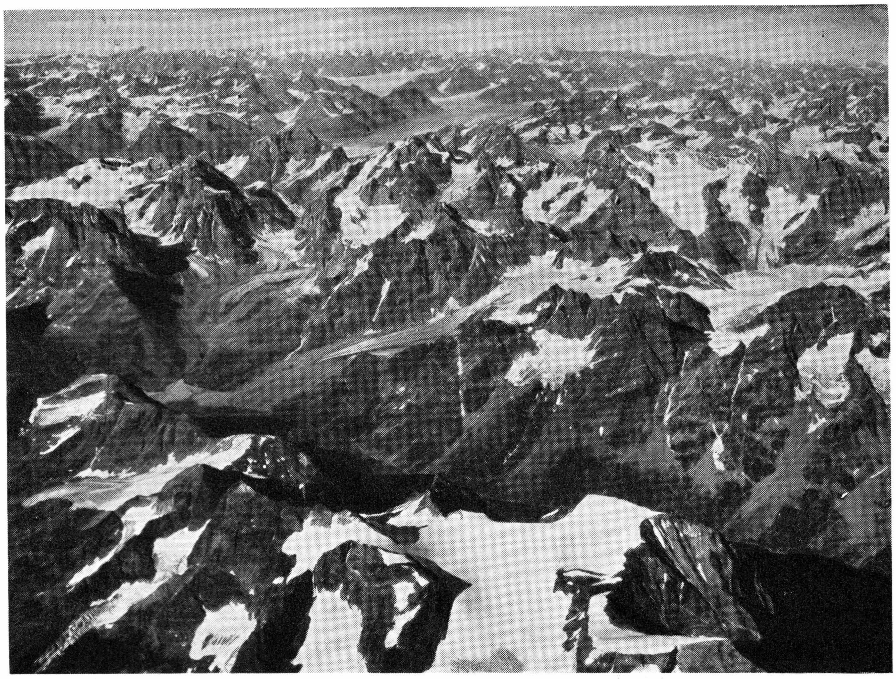

Fig. 3. View of Qíngorssuaq in the interior of Angmagssalik Fjord. The locality harbours a very interesting flora explored by C. Kruuse. In the background in the middle the large glacier is seen which goes down to the head of Sermilik; in the foreground Cassiopefjeld. — GJ/20919 Geodetic Institute copyright.

which is situated north of Tasîssaq, may also during a glacial period have been protected from the considerable, steep mountains in the east and west, but then has no doubt absorbed a small glacier coming from the north.

As appears from the figure, a great many species have been concentrated at Tasîssaq. Sceptics will of course immediately remark that this place is the one best known in the district. However, the accumulation of rarities is so great that it is very tempting to imagine that many of the mountains along the south coast and at Qordlortoq had ice-free south-facing slopes where the plants could pull through. Besides the species indicated on the map there are at Tasîssaq isolated occurrences of *Montia lamprosperma* (figs. 34—35 in B. 1938), *Ranunculus acer*, *R. reptans*, *Subularia aquatica* (fig. 51 in B. 1938), *Alchemilla filicaulis* var. *denudata*, *Viola palustris* (pp. 127—128 and fig. 73 in B. 1938), *Mertensia maritima*, *Galium brandegei*, *Sparganium angustifolium*, *Deschampsia flexuosa* (fig. 115 in B. 1938), *Juncus subtilis*. At any rate it is a question of southern species and to no small extent of aquatic plants, for which reason it might be supposed that the refuge included the small ponds west of Tasîssaq. This is not inconceivable, either, considering the above reflections on conditions of draining of possible large firns formed on the Angmagssalik island.

The outer islands at Angmagssalik are of course of great interest in this connexion, not the smallest, flat skerries, but the larger ones, which have high mountains and which only show signs of local glaciation. Unfortunately KRUUSE recorded a limited number of stations, only, thus he recorded none from the large island south of Ikerasak and Tunoq with its 600 to 900 m high peaks. At Kap Dan on the southernmost island Kulusuk he found an isolated occurrence of *Armeria scabra* ssp. *sibirica*, a plant also found by several collectors at Tasîssaq, but otherwise not between Scoresbysund and Kap Farvel. Kap Dan is an about 300 m high, steep mountain, situated far out, and Kulusuk is situated about 10 km from the large Angmagssalik island and twice as far from the mainland. The island presumably had its own firn, but its glaciers have flowed round the cape and other high points on the coasts. On the island farther north BØGVAD at Umîvik found one of the *Sedum acre* stations in the district. Umîvik is situated on the lowermost part of the south slope of an 855 m high mountain clearly modelled by local glaciers but protected from glacial covering through extension of the local central firn of the island by the fjord Torssukátak and the mountain on the south side of this fjord.

3. Tugtilik and Kap Wandel. As appears from fig. 2 below, two of the largest and most productive glaciers, K. I. V. Steenstrups Nordre and Søndre Bræ, are situated immediately north of the small fjord Tugtilik. Farther south Kangerdlugssuatsiaq cuts in and ends in the Glacier de France, which drains a large area. Kap Wandel and the mountains near Vahls Fjord do not bear the impress of erosion of an extended ice-cap and must have been seminunataks. The Tugtilik fjord itself continues in a main valley running in the same direction as the ice fjords, thus a longitudinal valley. This valley is, however, quite small as compared with the valley in the Nigertussoq fjord southwest of Tugtilik, which by erosion of two tributary glaciers from K. I. V. Steenstrups Søndre Bræ has made a bend and formed a transverse valley which protects Tugtilik from advances of the ice in the direction of the longitudinal valley. A small transverse valley leads from the main valley northeast towards another offshoot from K. I. V. Steenstrups Søndre Bræ, and this valley in the case of greater glacial activity will be filled by a glacier which moves in two directions in the main valley, fills its bottom and advances to Tugtilik in the east and Nigertussoq in the west. Such an advance will not, however, be able to cover the south slopes of the 800 m high mountain on the north coast of the fjord. This mountain

must have stood as a seminunatak in the range of seminunataks from Kap Wandel to Nasigfik.

The flora of Tugtilik is very rich, especially on the south slope mentioned (B. 1933b, p. 18—19). I found 82 species there myself on one day, among them isolated occurrences of *Carex rufina*, *C. atrata*, *C. microglochin*, and *Saxifraga aizoides*. Later Bøgvad and the Wager brothers, amongst others, have visited the area and supplemented my finds by the northern *Potentilla nivea* and other species.

When studying Kruuse 1912, pp. 172—182, it is interesting to see how a rich a flora is found on such mountains in the Tugtilik region which according to their alpine structure and extreme situation must have been seminunataks. The stations of the species *Alchemilla wichurae*, which is characteristic of the Angmagssalik region, are of special interest. In the description of the station at Nordfjord (pp. 172—173) Kruuse first describes the flora on the terraces at the eastern cape of the fjord. There were no floral sights there, but when he turned the corner of the cape to the "almost vertical south side, which was the lee-side when the glacier once passed over the point" (the cape), he found *Alchemilla wichurae* together with several other southern species (among them *Juniperus* and *Coptis*). On Kap Wandel Kruuse (*loc. cit.* p. 175) found a herb field rich in species on the south slope, comprising 58 species, among them *A. wichurae* and the rare *Stereodon rufescens*. Kap Wandel must undoubtedly have been a seminunatak. From this station the herbarium of the Botanical Museum in Copenhagen contains good and typical material of *A. wichurae*. On the other hand the material from Nordfjord and Nigertussoq mentioned by Kruuse may have been sent out from the museum as exchange-sheets, and, therefore, these stations are not quite reliable until new material has been brought back and verified.

In this connection it is worth pointing out that typical material of *A. wichurae* is available in the museum from two stations on the Angmagssalik Ø (cp. map fig. 2) one near Tasîssaq (see the discussion above on p. 15) and one at Kûgarmiut in the western end of the strait Ikerasagssuaq. Kruuse's description of that place (l. c. p. 113) is very interesting. He says that the mountains surrounding this valley form parallel ranges with very jaggy and sharp ridges, which hardly have been scoured by the ice; only the extreme (western) mountains are rounded and eroded down to an altitude of 700 m. Evidently they have had the same altitude (1000 m) and shape as the mountains behind them, which they have protected from the push of the ice. The place, which Kruuse here describes, is at the boundary between alpine physiography and roche moutonné indicated on fig. 2.

C. Akorninarmiut-Tingmiarmiut in Southeast Greenland.

This area both in the south and the north borders on large previous outlets from the inland ice characterized by low smoothed mountains. In return the area itself, with the island of Skjoldungen as a natural centre, is a rugged alpine country. Map 63 Ø1 and the aerial views (fig. 4) show a very interesting glacier deflection round the botanical oasis Dronning Maries Dal (valley) west of Skjoldungen. Two considerable and active glaciers drain off the inland ice west of the valley. One of these, Thryms Gletscher, flows into a transverse valley and turns into the small creek Nørrevig north of Dronning Maries Dal, while the other, Skinfaxe, curves towards the southeast to the Kagssortôq fjord. The forms of the mountains on Langenæs peninsula southeast of the outlet of Thryms Gletscher suggest that in former times a very large ice stream passed towards the sea there. Similar conditions seem to have prevailed at Kagssortôq on Kong Skjolds Halvö. On the other hand Skjoldungen has been shaped by local glaciers and the mountains on Mørkesund and Sønder Skjoldungesund as well as the more northerly peninsulas Mjølner and Rolf Krages Halvö and a number of areas on Sehesteds Fjord and at Tingmiarmiut.

Through the Norwegian and Danish botanical investigations in this area (DEVOLD & SCHOLANDER 1933, SEIDENFADEN 1933) it has been established that a very rich flora is connected with the alpine mountain forms. The particularly interesting finds in Dronning Maries Dal (*Potentilla ranunculus* (p. 37), *Rubus saxatilis*, *Arabis holboellii*, *Polygala serpyllifolia*) would seem to indicate that thanks to the glacier deflection there has been a small lowland refuge there. The main valley and its transverse valley have of course been filled with glaciers, but above these small local glaciers the peaks Tvillingetoppe (1541 m) and Drøneren (1980 m) have risen and probably had partially ice-free south and east slopes with vegetation.

Besides the above-mentioned species of a highly isolated occurrence the alpine area mentioned has isolated occurrences of the following species: *Selaginella selaginoides*, *Equisetum variegatum*, *Botrychium boreale* and *lanceolatum*, *Asplenium viride*, *Betula nana*, *Stellaria monantha*, *Limosella aquatica*, *Gentiana aurea*, *Linnaea borealis*, *Erigeron compositus*, *Hieracium stelechodes*, *Taraxacum purpuridens*, *T. rhodolepis*, *Roegneria doniana* var. *virescens*, *Calamagrostis poluninii*, *Anthoxanthum odoratum* ssp. *alpinum*, *Juncus arcticus*, and *Kobresia myosuroides*.

Several of these species have their northern limit in East Greenland where the alpine structure ceases, and they are joined by *Athyrium alpestre* and *Nardus stricta*, the distribution of which also includes the alpine area at Kap Farvel and, in the case of *Athyrium*, the mountains at Ivigtut, but which otherwise are absent from West Greenland.

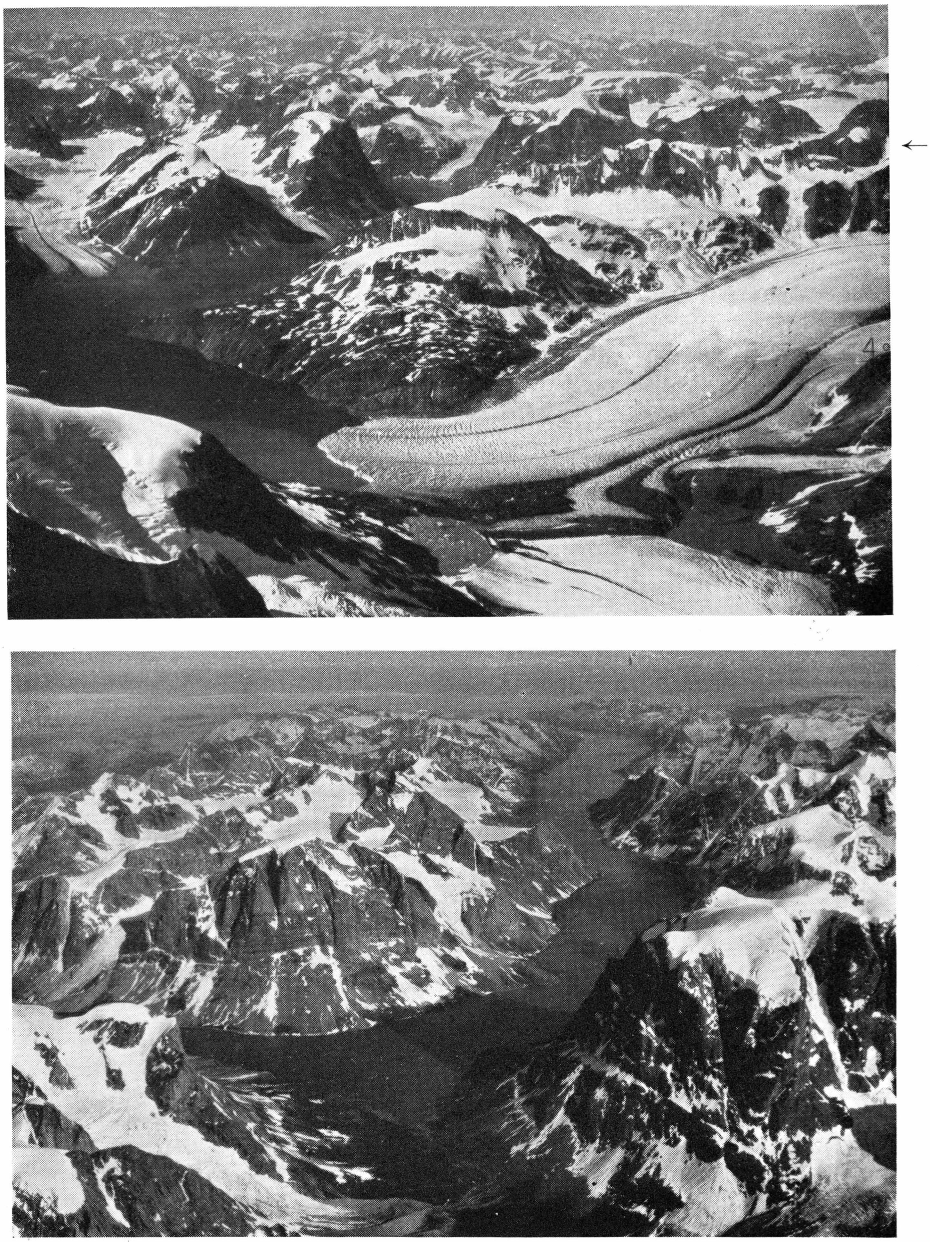

Fig. 4. From the floristically very interesting inland at Skjoldungen in Southeast Greenland. In the picture above: Thryms Gletscher, which is deflected towards the north and drains off the inland ice, the valley, Dronning Marie's Dal (above, at the arrow) thus receiving no more than local glaciers. The picture below shows this valley in the foreground and one of the local glaciers on the left mountain side. In the background from the west: Skjoldungen and Sønder Skjoldungesund completely surrounded by alpine mountain forms. — Above: I T/27752, below: IV/27686, both Geodetic Institute copyright.

D. The Kap Farvel Region.

At a certain time, but not during the last Glacial Age, the inland ice covered the country and shaped the large valleys, which probably already came into existence as river valleys before the Glacial Age. The later activity of local glaciers and glacial streams has transformed the country to a rugged alpine region. From firns between the large valleys (fjords) the glaciers advanced towards these, transverse valleys (often called Itivdlerssuaq) frequently being formed in this way.

The transverse-valley effect is extremely prominent on the peninsula between the Sermilik and the Tasermiut fjords (fig. 5). Farthest north the two fjords are connected by a deeply cut Itivdlerssuaq. This valley at an advance of the inland ice will deflect the stream of ice towards the east and west and prevent submerging of the region farther south. The dimensions of the valley suggest that it must have functioned already during the last Glacial Age. In the area south of Itivdlerssuaq local firns have been drained off by several longitudinal valleys, but they have not been able to influence the area at the 4000 feet high Ivnarssuaq mountain, which towards the north is protected by another transverse valley. At Ivnarssuaq a possible glacier in Tasermiut cannot have done more than covering the foot of the mountain. Thus there are great chances that its southern slope was partially ice-free. Just from the slope towards Tasermiut an isolated finding of *Linnaea borealis* has been recorded. The nearest stations are at Ivigtut and Neria and in Dronning Maries Dal (p. 18).

Of particular interest, however, is the Kap Farvel region itself, which is cut off by Tasermiut in the west and Lindenows Fjord in the north. These two fjords are now cutting into the land so deeply that their heads are only about 10 miles from one another. Within this area the inland ice has a narrow connexion with the firn which covers the country between Prins Christian Sund and Lindenows Fjord. If we imagine an extension of the ice cap towards the region between Tasermiut and Ilua, it will be drained off by larger glaciers to the heads of these fjords. The region farther south will only get local firns and glaciers. It is evident that the very large valley in continuation of Kangikitsoq has harboured a huge glacier, which drained off most of the northern part of the area. Farther south the draining-off was towards Kangerdluk, Taserssuaq, and Tasermiut through local glaciers.

Botanically the Qingua valley at Taserssuaq (fig. 6) is a famous locality because of its rich and varied vegetation and wood-like birch copses (see HARTZ 1894, OLDENDOW 1935). A closer examination of the surroundings of this valley by means of the photos taken by the Geodetic Institute makes it evident that this valley, the direction of which is the

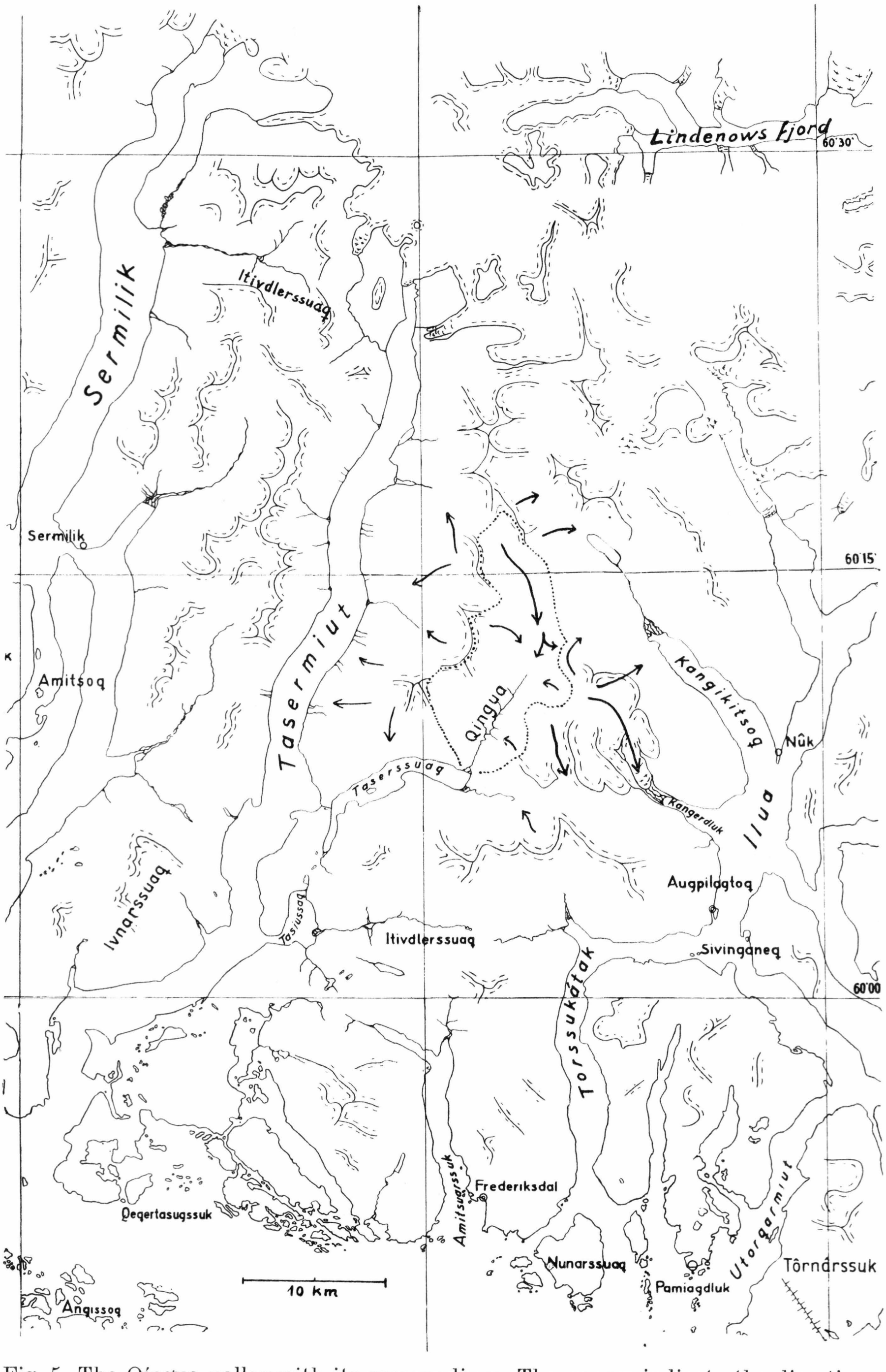

Fig. 5. The Qíngua valley with its surroundings. The arrows indicate the directions of the glacial streams, the dotted line surrounds the area drained off through the valley.

same as that of the main longitudinal valleys (the fjords) and which therefore has been formed very early and not during the last Glacial Age, has a very small area to drain off. Most of the ice which is accumulated in this region is drained off to Kangerdluk and Kangikitsoq in the east and Tasermiut in the west, in other words a pronounced parallel-valley effect. In fig. 5 the area which is drained off by the Qíngua valley, is framed by a dotted line. Especially in the northernmost part some ice will be able to accumulate, and if the firn is extended there, a glacier will flow into the bottom of the valley; however, the threshold to the valley towards Kangikitsoq is so low that some of the ice will be able to move this way. If, as there is much to indicate, this took place as early as during the last Glacial Age, it may have caused that ice enough to cover the whole valley could not form, at any rate not enough to cover the valley slopes closest to the Taserssuaq lake.

The particular topographical conditions around the Qíngua valley thus make it probable that this valley during the last Glacial Age was a lowland refuge of the parallel-valley type. Isolated occurrences of two species are recorded from the valley, viz. of *Rubus saxatilis*, which is otherwise known from Dronning Maries Dal only (p. 18) and *Subularia aquatica*, which is only known from Tasîssaq (p. 15) and the head of Tunugdliarfik, thus from other localities where the topographical conditions suggest that there have been ice-free areas. In our day birch copses of an appreciable height according to Hartz, *loc. cit.*, grow to an altitude of 100 m above sea level, and the species will grow to an altitude of about 250 m. Up there the trees are procumbent and thus are protected by the snow in winter. Is it a too daring assumption that the birch held its own in this way in the lowlands on sunny sides of the mountains during the last Glacial Age? If the Greenland birch (*Betula pubescens* coll.) demonstrably constitutes a special form cycle which is not identical with Icelandic or American races, this will highly strengthen such a survival hypothesis.

The alpine area of the Kap Farvel region is separated from the Tingmiarmiut-Akorninarmiut area by a fairly large landscape of smoothed rocks about lat. 62° N., where the inland ice will easily be able to cover the greater part of the country. The distribution of *Nardus stricta* (B. 1938 fig. 117) just has a gap there, but the dots gather in the two alpine areas, in order then to disappear in the large landscape of smoothed rocks in the Julianehåb district. A completely corresponding distribution is that of *Athyrium alpestre*, which, however, has a station on an island off the gap mentioned and which reappears at Ivigtut, close to the western alpine area (see B. 1952b). The Atlantic species *Juncus squarrosus* (fig. 130 in B. 1938) like *Isoetes lacustris* is connected with the Kap Farvel region; this also applies to a number of *Hiera-*

Fig. 6. The Qíngua valley near Taserssuaq lake near Tasermiut fjord in South Greenland. The valley is seen from the south and the inland ice is just seen in the upper corner on the left. — 501 C I NØ, Geodetic Institute copyright.

cium species (e. g. *H. scholanderi*) and to *Cornus canadensis* (B. 1952b, p. 197). These species perhaps, because of the climatic requirements, will only thrive in this southern coastal area. *Cornus canadensis*, however, grows in woods in forests across the North American continent, and therefore just ought to be able to grow in the warm inland areas in Greenland. Its occurrence, therefore, may be due to perglacial survival on the mountains at Kap Farvel. This species and *Juncus squarrosus* ought to be searched for in future in the Qíngua valley.

V. SOUTHWEST GREENLAND

West of the Kap Farvel region several considerable changes in the physiographical conditions take place. The most important fact is that a "shore flat", often in the form of an archipelago of low, rounded-off rocks, has developed there in large areas. Furthermore, that areas with a pronounced alpine structure are rarer. There is much to indicate that the development of the physiographic forms has extended through a prolonged period, or rather, that changes in the distribution of the continuous ice-cover have been more frequent and greater than in Southeast Greenland. In the latter region there is today a connexion between the breadth of the coastland and topography. Where the mountains are high and peaked, the icecap is forced back, and where they are low and rounded off, it advances almost to the sea. There are no appreciable ice-free areas due to climatic conditions; everything depends on draining and the height of the mountains. In Southwest Greenland, on the other hand, there are considerable ice-free stretches where the inland ice is not dammed behind high mountains. One might imagine a rather violent advance of the icecap without this causing a submerging of all the roche moutonné landscapes. It is my working hypothesis that the last Glacial Age in Southwest Greenland did not lead to a total cover of the areas polished off by the previous Glacial Ages. As appears from what follows, this hypothesis has arisen as an explanation of a number of enigmatic plant distributions today.

Unfortunately Southwest Greenland in spite of many botanical collections and studies is still very heterogeneously investigated. Therefore the mention of conditions there must be restricted to a few selected regions.

A. The Julianehåb Region.

This region is well-known through investigations made especially by L. K. ROSENVINGE, in recent times especially by EILIF DAHL, JOHS. GRØNTVED, and N. POLUNIN. Particularly at the heads of the large fjords Tunugdliarfik and Igaliko Fjord a considerable number of findings have been made of species which either are only found there (e. g. *Cystopteris*

Fig. 7. The country north of Igaliko in South Greenland as seen from the inland ice. The large massif in the foreground (Akuliaruseq) has deflected the glacial streams so that a refuge perhaps has arisen on the leeside. 501 E-S/859 Geodetic Institute copyright.

montana, *Selaginella rupestris*), or which must be considered to have a more disjointed distribution in Greenland, often connected with localities where the possibility of ice-free refuges is great (e. g. *Potentilla ranunculus*, fig. 10 p. 36, *Antennaria affinis*, fig. 20 in B. 1952, *Roegneria violacea*, fig. 11 a in B. 1950). It is natural to explain the richness in species at the heads of the fjords from the prevailing favourable subarctic climate. Matters are not, however, so simple. The fact that a species like *Potentilla ranunculus* is only found in there, cannot be due to the climate only, as this species can live under low arctic climatic conditions in the Disko region (fig. 10). Therefore, there is is reason to look at the forms of the mountains in the inmost part of the country.

Fig. 7 shows the Akuliaruseq mountains between Iterdlak and the Igaliko creek in Igaliko Fjord. Both at Igaliko and at Qagssiarssuk in Iterdlak there is a very interesting flora rich in species with isolated occurrences of *Primula egaliksensis*, *Drosera rotundifolia*, *Parnassia kotzebuei*, *Orchis rotundifolia*, *Gentiana amarella*, *Carex mackenziei*, and *Anthoxanthum odoratum* ssp. *alpinum*, to mention some of the most important. It is seen that the mountain is high and at the top has a rugged structure. Obviously it has not been submerged, but has functioned as a barrier against the icecap and forced it towards the southeast and southwest to the heads of the two fjords. When the comparatively low, rounded-off country towards the south in the background of the picture was completely ice-covered, of course only the highest peaks projected from the ice as typical nunataks, but the question is whether the glaciers of the last Glacial Age were not situated considerably lower so that on the lee-side of Akuliaruseq, which faces the south and the fjord as a spit of land, a refuge arose. The area is close to the Qagssimiut trough, which has been the main outlet of the ice-cap. Furthermore, the draining of the ice-cap which took place at the two heads just as at the heads of Tunugdliarfik and its Qôroq branch, must have been rather appreciable. On the whole the draining may have been so great that farther south there could be only local firns and glaciers. These may very well, as in parts of Southwest Greenland today, have been widely distributed during the last Glacial Age, but everywhere there has been small recesses which avoided glaciation and could harbour a flora.

B. The Arsuk-Frederikshaab Region.

WEGMAN (1938) mentions a western area with alpine topography in the Arsuk region, viz. the outer coastal mountains from Kap Thorvaldsen to Sermersût near Arsuk. In and near this area, which at a certain time must have formed a range of seminunataks, there are several isolated occurrences, of which B. 1951 mentions *Asplenium viride* and *Viola selkirkii*, but to which we may now add a station for *Athyrium alpestre*. Furthermore there may be reason to mention that *Ranunculus acer* occurs there, but is not known from the coast at the Qagssimiut hollow (see fig. 47 in B. 1938). It is a fact of great interest that *Hieracium alpinum* and *Carex atrata* occur there, too, but not farther north, although in East Greenland they go far north. A similar case is that of *Viola palustris*, which, however, has one station at lat. 63°5′ N. The case of *Hieracium alpinum* is particularly interesting as this species might a priori be considered a species which spreads very quickly. Considering that it has not reached its ecological limit in West Greenland, one must doubt the effectivity of its spreading by the wind or consider it a new immigrant. The latter view might have been the best explanation, if not for the very fact that its northernmost area in West Greenland was the

Arsuk alpine area and its northern limit coincided with the trough near the great offshoot of the inland ice, "Frederikshaabs Isblink".

Conditions of draining of the inland ice in that area are interesting. Between the two large outlets at Qagssimiut in the south and Frederikshaabs Isblink in the north there are especially three broad fjords which end in productive glaciers from the inland ice, viz. Sermiligârssuk, Sermilik, and Kuánersôq. Together with the two large outlets these fjords during the last Glacial Age probably have prevented the inland ice from advancing everywhere where the great glaciation had been.

A favourable position must have been held by the small peninsula between Sermilik and Kuánersôq. The ice cap is at present drained off through valleys which lead to the heads of these fjords. During the last Glacial Age it presumably advanced beyond the peninsula, but struck a broad transverse valley which turned the ice streams northwards and southwards into the two fjords. Farther west the peninsula rises to 818 m above sea level, and it is very doubtful whether it has been possible, considering the forming of the transverse valley east of it, to cross this elevation. Immediately west of the highest part there is a creek, Kangerdluarssuk (about lat. 61°53′ N.), which thus may have been protected from any ice-cover and only been exposed to local glaciation. In this creek Th. Holm 1886 found the European species *Geranium silvaticum*. This is still the only station of this species recorded from Greenland. It was found on rocks in willow copses. The place is situated away from the areas which in early times were colonized by the Norsemen. Porsild (1932 p. 68) regards the plant as a casual immigrant by natural ways or as a relic. The way of spreading of the species and the size of the seeds make recent immigration from Iceland less probable. I find it more likely that the creek on the sunny side had a refuge where this subarctic species could hold its own. In Norway and Sweden *Geranium silvaticum* ascends to the willow scrub limit, but it may go a little further. Thermically this limit corresponds to the limit of the low arctic area, which in West Greenland today is at lat. 72° N., in outer-coast regions, however, at about lat. 69°30′. Thermic conditions at about 62° during the last Glacial Age may perhaps have been as on Disko today.

C. The Godthaab Region.

Botanical investigations made there are rather comprehensive. Plant collections have been made by, amongst others, J. Vahl and later M. P. Porsild (see M. P. Porsild 1935) and A. E. Porsild. Ecological investigations have been made by Trapnell 1933 and Iversen 1954. Finally Iversen has made pollen analytical investigations in the interior of the fjord complex, see Iversen 1934, 1953.

A study of Map 64 V 2 of the Geodetic Institute (published 1954) as well as the Map 64 V 1 (published 1956) shows that the northern and western parts have completely smoothed mountain forms, which is evidence of total submerging. On the other hand, the islands in Godthåbsfjord and the Godthåb peninsula between Ameralik and Godthåbsfjord have mountain forms which must be due to local glacier activity. The alpine structure is not so pronounced as in East Greenland, which would seem to indicate that—apart from the highest peaks—it did not come into existence until during the last Glacial Age. If this point of view proves correct, there has been an ice-front almost as far out as a line through Storø, Qôroq, Itivdleq, Eqaluit in Ameragdla; farther west, on the other hand, there has been local glacier activity and a possibility of ice-free south-facing slopes in the outer part of Ameralik, approximately from the large transverse valleys which lead across the peninsula from Qôroq to Qârusulik and Tuapagssuit. Such a fjord as Kobbefjord has had a similar situation as the above-mentioned Kangerdluarssuk farther south, as in the east it is protected first by transverse valleys and then by mountains more than 1000 m high with many small valleys and in the north and the south has large fjords which give an effective draining to the inland ice. In other words there is also a parallel-valley effect in Kobbefjord. If the theory of a connexion between plant isolations and topography is correct, it ought to be possible to point out isolated occurrences at Ameralik and on the islands in Godthåbsfjord. Indeed, this appears to be the case. The small island Umánaq near Storø has *Arabis holboellii* and *Lycopodium clavatum*, and on Sadlen *Linnaea borealis* has recently been found. The following species have been found in the outer part of Ameralik: *Pedicularis groenlandica*, *Puccinellia laurentiana* (the only known stations for these species in Greenland, see PORSILD 1946, SØRENSEN 1953), *Vahlodea atropurpurea*, *Galium triflorum*, *Listera cordata*, and *Ranunculus acer*, farther inland *Arabis holboellii*, *Ranunculus cymbalaria*, *Orchis rotundifolia*, *Carex praticola*, *Botrychium boreale*, and *Erigeron compositus*. Several of these perhaps on closer exploration of West Greenland will appear to be less isolated at Godthåb, but at present it must be stated that we have fairly many rare plants in the very part of the fjord in which the chance of lowland refuges is greatest.

IVERSEN (1953) is very pessimistic as regards the idea of the survival of southern species during the last Glacial Age. His diagrams originate from the area which has been totally submerged. He builds his criticism of my views on the fairly sudden frequency of *Betula nana* from Atlantic time inclusive in the interior of the fjord. As the species does not become of importance until the Postglacial Age, it cannot, according to his views, have lived in Greenland during the last Glacial Age, but must have immigrated postglacially. And all species with similar or greater thermic requirements have therefore been unable to hold their own as well. IVERSEN's argumentation is interesting, but little convincing. He omits making the present distribution completely clear. In Northeast America it has been found in very few stations; thus it is of European origin and should have immigrated postglacially from Iceland. But there is nothing to indicate that it should have reached the Angmagssalik district and from there have migrated round Greenland in the south or the north to Godthåb (see maps fig. 31—32 in B. 1938). It is even in Southeast Greenland clearly connected with the two areas with an alpine structure at Angmagssalik and Skjoldungen, and both in East and West Greenland it grows as far north as about lat. 75° N. Even in Northeast Greenland at lat. 73° N. it ascends to 600 m above sea level (SØRENSEN 1933) and in Scoresbysund to about 900 m above sea level (HARTZ 1895 p. 341). There is much to indicate that the Greenland population of *Betula nana* just constitutes a particular arctic continental race, which may have persisted in a number of different places (e. g. at Qíngorssuaq in East Greenland) and which in the Postglacial Age has not spread to all the places where it may grow. Near Godthåbsfjord it may very well have grown in the outer part of Ameralik on a south-facing slope between local glaciers, and with the prevailing easterly winds in the fjord in the autumn and winter it may have had difficulties in spreading into the area inland which is optimal to it. It may also have been driven away from the area (cf. many species with a distribution north and south of the fjord system; see B. 1952 pp. 75—76) and then again have spread southwards from its northern refuges. The late arrival at the totally glaciated Tungmeragdlip taserssua in Godthåbsfjord thus is no counter-evidence of the assumption of the survival of southern species during the last Glacial Age.

In the inmost part of Godthåbsfjord IVERSEN found a *Sisyrinchium* (cfr. S. *montanum*), which, in spite of its occurrence in Søndre Strømfjord, he still believes to be an adventive species introduced by the Norsemen from America. With reference to the remarks below, it cannot, however, be precluded that the species has been growing in continental tundra refuges, and that it spread from these in the Postglacial Age. According to BÖCHER & LARSEN (1950) the Greenland plant has the chromosome number 2n = 32. This number differs very much from that found in plants from the regions around the Gulf of St. Lawrence where the number is 2n = 96. (Material from nature received through the Botanical Garden in Montreal). The North American plants are much higher and with darker blue flowers than those from Greenland which probably ought to be referred to a seperate species. These facts clearly make an immigration by man from the St. Lawrence region very improbable. On the other hand the Greenland *Sisyrinchium* with 2n = 32 may possibly also occur in Central Canada and, if so, its small area in Greenland today may be a remnant of a connected area from immediately after the Glacial age. In this case the plant is a late-glacial relict. A description of the Greenland plant is found in Böcher, Holmen & Jakobsen (1957).

D. The Region between Sukkertoppen and Holsteinsborg.

The glaciated firn area around Evighedsfjord is in direct connexion with the inland ice eastwards and cuts West Greenland in two. B. (1952a pp. 72—77) mentions numerous examples of species with their limit north or south of this firn and is of opinion that it is a question partly of climatically conditioned limits, partly of historically conditioned ones.

During the last Glacial Age this firn area evidently had a greater distribution or rather, similar large firn areas seem to have existed north of the outer part of Søndre Strømfjord (lat. 66°—66°30′ N.) and at Nordre Isortoq (about lat. 67°15′ N.), from which glaciers have advanced partly towards the sea, partly towards the large fjord valleys. As mentioned above, it is not, however, certain that the inland ice has everywhere advanced so far as to be united with these firns on the high coastal mountains. Climatic conditions of the same type as in the present time may have caused (1) that the coastal firns received the precipitation and ice accumulation due to low pressure which advanced northwards along West Greenland, (2) that the hinterland became extremely dry as a consequence of rain-shadow effect. The drought would partly prevent the ice-cap from getting local supplies of any importance, partly give rise to great melting in summer, and thus the ice-cap would be unable to cover the whole country. A great importance for the appearance of tundra refuges of this type must of course be attached to the conditions of draining. If we look at the most interesting area at the head of Søndre Strømfjord, it must be recognized that the draining of an advancing ice-cap there must have been very effective. North of lat. 67° N. the main advances will be caught in two valley systems, Isortoq and an extensive valley which through the lakes Langsøerne and Taserssuaq extends to the northern branches of the Ikertôq fjord. Ice advances south of lat. 67° N. will be caught by the valleys which end in Umîvit, the southern creek of Søndre Strømfjord, and in Angujârtorfik and Sarfartôq farther out on the south side of the fjord. This means that the part of the ice-cap which directly threatened the inner northern creek of the Strømfjord was small. An ice tongue in the Sandflugtdalen valley might be stopped near Keglen, which must have been formed by two ice tongues (fig. 8), and the large glacier which has been filling the valley Ørkendalen, according to glacial striae east of the lake Store Saltsø seems to have forked in such a way that one tongue advanced to Taserssuatsiaq, another to

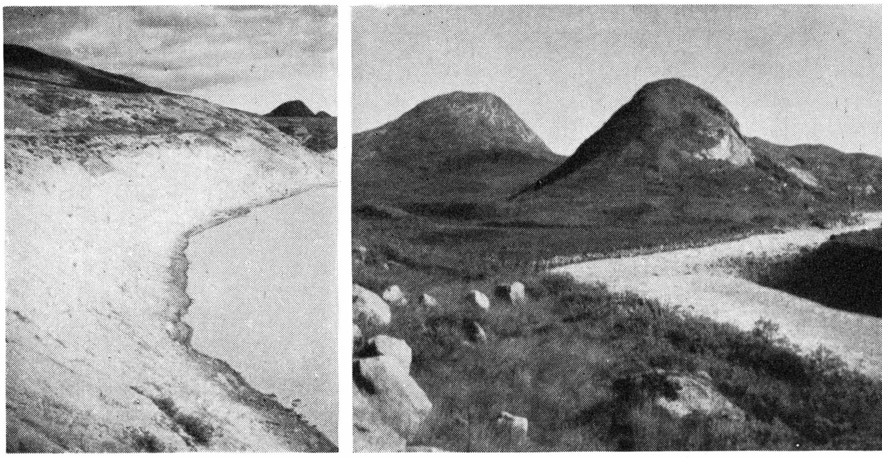

Fig. 8. From Sandflugtdalen east of the head of Søndre Strømfjord. On the right: The two mountains ("Keglen" in the background) which stand up in the valley bear evidence of glacier erosion on both sides. Only west of these mountains, at which the ice had a stagnation line, large loess deposits are found. On the left: Large terraces in deposits of gravel, sand and loess west of Keglen. No terraces are found east of that mountain. — TWB phot. 1946.

the narrow outlet of the valley (B. 1954a, fig. 2). In the Umîvît branch glacier deposits parallel to the valley (fig. 9) suggest that the ice only advanced to the inner corner of the creck about a mile from the station Vandfaldskløften. A support of the hypothesis about an ice-cap margin as the one sketched out here is the fact that the large loess deposits and terraces in the region are found only west of it and that Store Saltsø with its large and strange moss loess deposits (see B. 1949) comes to be situated between the two branches of the Ørkendal glacier. Besides the two above-mentioned ice tongues from the ice-cap, the region has no doubt had several local firns on the plateaux and local glaciers as well (e. g. in Ringsødal), but the latter have not necessarily covered the south-facing slopes or prominent parts of the north-facing slopes. All this is, of course, speculation, as such a possible ice-front line may only have been a stagnation line and need not at all have corresponded to the limitation in the last Glacial Age. The reason why it is still discussed is that the occurrences of rare or isolated plants in the region are highly accumulated in the ice-free area suggested. As appears from the list below, it is a question of a very considerable number of species, and species which in many cases cannot possibly have lived in coastal mountain refuges, as they are obviously attached to a highly continental climate and conditions of the soil connected with this. It should not, however, be forgotten that if the theory of inland refuges at the head of the fjord should prove to be wrong, there is also a possibility of such refuges

Fig. 9. The previously glaciated country around Søndre Strømfjord. On the left the large river to the Umîvît branch; along the river marginal morainal ridges are seen (b). At a certain time a large glacier filled the valley up to the uppermost moraine and sent a tongue to the highland lakes on the right in the figure. The uppermost top of the loess-covered south slope of Nákajanga on Umîvît (near Vandfaldskløften) is seen at a—a_1. In the background: the middle of the fjord. — 505 Hv/g. III Geodetic Institute copyright.

nearer to the outer coast. We have many of these species at Itivdlínguaq, and farther north in the region towards Ikertôq there are isolated occurrences of *Roegneria violacea* and *Primula egaliksensis*. These localities are situated on the inner side of the supposed coastal mountain firns.

On the outer side, towards the sea, there is alpine structure in a large area from Hamborgerland near Sukkertoppen to Itivdleq in lat. 66°32′ N. (see fig. 5 in B. 1951). There has evidently been a possibility of seminunataks and lowland refuges there as a consequence of transverse-valley and parallel-valley effects and even though the mountain forms on the Holsteinsborg peninsula are not exactly clearly alpine, the same effects will easily have been able to cause that this peninsula was only locally glaciated during the last Glacial Age, so that Kællingehætten and Præstefjeldet had ice-free southern slopes. The very rich flora on the

Isolated or rare plants in the Søndre Strømfjord area found immediately west of the suggested margin of the ice-cap. Details in B. 1952.

*Ranunculus cymbalaria.**
Arabis arenicola, B. 1952, fig. 9.
— *holboellii.**
Braya linearis, fig. 10 p. 36.*
— *novae-angliae*, B. 1950 fig. 10 (under the name *Torularia humilis*).*
Arctostaphylos uva-ursi, B. 1951 fig. 5 b, 1954 fig. 58.*
Gentiana detonsa, B. 1950, fig. 12.
— *aurea*, B. 1950, fig. 14.*
— *tenella.*
Galium brandegei, B. 1952a, fig. 28.*
Antennaria affinis, B. 1952a, fig. 20.*
Potamogeton alpinus ssp. *tenuifolius*, B. 1952a, fig. 22.
— *gramineus*, B. 1952a, fig. 22.*
Scirpus pauciflorus, B. 1950, fig. 11, 1951, fig. 7.*
Carex capitata (excl. ssp. *arctogena*), B. 1950, fig. 1.*
— *amblyorhyncha*, B. 1952a, p. 49.
Roegneria violacea, B. 1950, fig. 11.*
Juncus alpinus ssp. *nodulosus*, B. 1952a, fig. 28.*
— *ranarius*, B. 1950, fig. 13.*
Sisyrinchium sp., B. 1948.
*Orchis rotundifolia.**

* Not found east of the suggested ice-cap margin and presumably rare or absent there.

latter mountain may be due to local richness in lime in the soil (Note. Isolated southern station for the calciphilous *Potentilla vahliana*, occurrence of *Draba crassifolia*), but other isolated occurrences at Holsteinsborg (*Ranunculus acer*, *Anemone richardsonii*, *Linnaea borealis*, *Pirola secunda*, *Hieracium ivigtutense*) and S. Kangerdluarssuk (67° 5′, only Greenland station for *Cerastium arvense*) might suggest that there were some coastal mountain refuges there. Whereas such a species as *Arctostaphylos uva ursi* has been found immediately behind the rugged mountains, the species mentioned, and in the south *Arctostaphylos alpina* (fig. 34 in Gelting 1934), are connected with the area with an alpine structure mentioned here. Some of these species may of course have been carried to the region postglacially by birds (*Arctostaphylos*, *Anemone richardsonii*), but this is not very probable as regards e. g. *Ranunculus acer*. The recent finding of a special variety of *Hieracium acranthophorum* on a station in the alpine area at the entrance to Nordre Isortoq (B. 1957) is a further support of the theory of maritime plant refugia in the Holsteinsborg region.

VI. FINAL REMARKS

The facts communicated above include a number of details and furthermore some more general considerations have been advanced which without proving the hypothesis about the survival in Greenland of relatively southern species during the last Glacial Age, contribute to making it probable. If we take stock of this hypothesis it must, however, be admitted that it is still shaky, but the same applies to the counter-hypothesis that only fairly few of the most hardy arctic species could survive the last Glacial Age (OSTENFELD 1926, IVERSEN 1953). The reason is the simple one that both hypotheses are weakened to almost an equally high degree by a number of conditions unknown at present, the clarification of which is of very great importance for our getting any farther. We may summarize our missing knowledge as follows:

(1) We lack ecological-physiological experiments in the form of cultivation experiments which can decisively demonstrate the climatic requirements of the species, especially their thermic requirements. Many species, also southern ones, no doubt have a great temperature tolerance, and their limits in Greenland are not conditioned by temperature, but by the length of the day, humidity or other factors.

(2) We lack investigations of the racial contents of the Greenland plant species. If the Greenland biotypes have other climatic requirements than biotypes from other places, this is of great interest to the discussion about survival.

(3) We lack sufficient measurements which may substantiate how great a climatic deviation a special microclimate means in relation to the macroclimate prevailing in the same place. A distinct deterioration of the macroclimate is, of course, accompanied by a corresponding deterioration in the various microclimates, but the difference between macro- and microclimate in a given place, as far as our experiences go, can be so great that it is easily imagined that a species could exist in a pocket with a very favourable microclimate, whereas the surrounding macroclimate was completely uninhabitable to it.

(4) Thermic conditions during the last Glacial Age in Greenland are not known any more than other climatic conditions. We can only surmise as to the degree of climatic deterioration. During the glacial maxima the mean annual temperature may only have been 4—7° C. lower than at present (see FLINT 1948). Accordiog to LIVINGSTONE (1955) it is very likely that climate changes during the late Pleistocene have been much smaller, at least in terms of vegetational consequences, in unglaciated Arctic Alaska than in the temperate zone, and this result is not contradicted by the evidence found by IVERSEN in Godthåbsfjord where even the lowest levels contained the pollen of various thermophilous species indicating that the temperatures at the time of ice retreat were not markedly different from present ones.

(5) The position of the margin of the ice-cap in Greenland during the last Glacial Age is unknown.

(6) The attempts made from glaciological quarters at calculating the economy of the ice-cap involve considerable uncertainty (see LOEWE 1930, FLINT 1943, DEMOREST 1943, MILTHERS 1950). It will be of fundamental importance for the questions of the refuges to try to investigate to how high a degree the previous main outlets of the ice-cap (roche moutonné landscapes, etc.; see the text above) through the draining-off created by them (especially by the breaking-off of icebergs) can have been able to protect interjacent areas from being submerged.

(7) The available pollen analytical material from Greenland is too slender as basis of a rejection of the hypothesis of the survival of southern species. We lack palynological data from places where the flora and topographical conditions suggest that there has been a refuge. The existence of small refuges on the parts of seminunataks facing the sea can only with difficulty be disproved through palynological investigations.

The seven points clearly show how far we shall have to go before a real judgment can be made. In order to get any farther both geologists and biologists must continue their investigations and tackle the matter from many angles. As to purely botanical investigations, we probably hardly get much farther through the floristic investigations of Greenland; for even if still more isolated occurrences and highly disjointed areas should be found, it cannot be denied that a large number of such occurrences can also be explained as the results of an unfavourable development during the Postglacial Age. In the late Glacial Age the species, as e. g. pointed out by Dr. JOHS. IVERSEN, may have had connected areas, but the development of the soil, at any rate as regards the calciphilous species, was unfavourable, for which reason such species

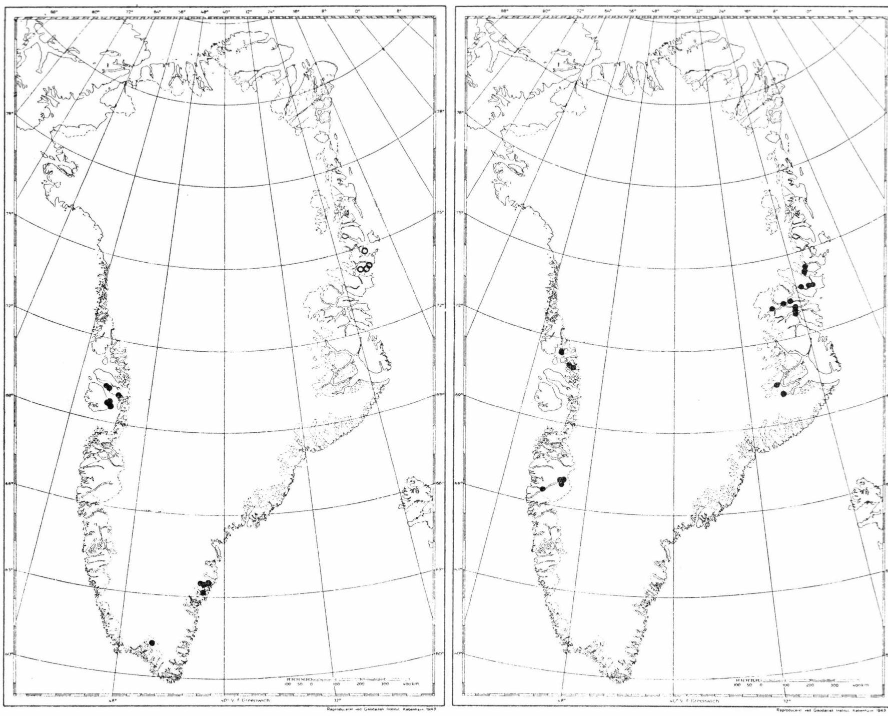

Fig. 10. The distribution within Greenland of *Braya linearis* (dots on map on the right), *Potentilla ranunculus* (dots on map on the left), and *Potentilla rubella* (open rings on the map on the left). The species of *Potentilla* are probably endemic and *Braya linearis* has its nearest stations outside Greenland in Norway.

now occur isolated in certain localities rich in lime. In the case of other species conditions of competition perhaps were changed in an unfavourable direction so that they are now found at scattered stations only, where there is no connected vegetational cover.

The type of purely botanical investigations which in the best way will be able to contribute to our understanding of the survival problems is cultivation experiments under controlled circumstances in a greenhouse arranged especially for this purpose. Furthermore, comparative cultivation experiments which may show how the biotypes of a species occurring in Greenland behave as compared with others from other countries (cf. Points 1—2 above). In this connexion I may remind of the experiments with *Arabis holboellii* (B. 1954b), which suggest that the Greenland strains of this species differ from the American ones. This species belongs to the southern floral element of Greenland, but it is extremely tolerant as regards summer heat. The triploid Greenland strains grow almost as excellently so northerly as in Scoresbysund as on an experimental field or in pots in Denmark, and they will also stand cultivation in hothouses under thermic conditions reminding of those in the Mediterranean countries.

It is probable that the Greenland races of *A. holboellii* constitute a separate endemic unit. The same may be the case with *Potentilla ranunculus* Lge., which hardly occurs outside Greenland[1] but seems to be related to the Canadian *P. diversifolia* Lehm. and to the endemic North-east Greenland species *P. rubella* Th. Sør. (cp. A. E. Porsild 1951 pp. 222—223). *P. ranunculus* has a very disrupted range in Greenland (fig. 10) and according to its ecological behaviour it is not arctic but rather a low-subarctic plant. If this plant is a post-glacial immigrant we are forced to suppose that it was extinct (or almost so) in North America, from where it must have come, and further that it immigrated to three separate areas in Greenland.

This species as well as other endemics among the apomictic complexes *Antennaria* and *Hieracium* which ecologically are southern types may at present give the best support for the hypothesis of survival in Greenland of relatively southern species during the last Glacial Age.

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[1] According to Fernald (1899 in A. E. Porsild 1951) known from Ramah in northern Labrador.

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